MORPHOLOGY AND TAXONOMY OF SOME NEMATODES OF THE ORDERS TERATOCEPHALIDA, ENOPLIDA, DORYLAIMIDA, CHROMADORIDA AND ISOLAIMIDA

by

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"life lays on us a duty:

to doubt and to ask questions"

W.K. Clifford

To my parents

PREFACE

"We are born to search after the truth;

to possess it belongs to a greater power."

Montaigne

The science of taxonomy or the organisation and labelling of organisms may strike many as dull and stuffy but everyone working in this fascinating field finds that it leads to some of the most searching and interesting questions. Taxonomists are confronted by a well organised world of nature, exactly that what prompted the great taxonomist Linnaeus to develop his clear, hierarchical method of classification. But at the same time they are faced with a bewildering diversity and variation within this organised whole. Seeking to order the stable units in the midst of this diversity is the descriptive task of taxonomy. But many taxonomists go further than that, they seek a theory and ask: what causes life to be ordered? Here they land in the middle of philosophical debate and controversy. The field of taxonomy has, unfortunately, been divided by arguments about what a species is, how to demarcate a species, and even whether they are real or not. Today this "species question" is phrased in broader terms. The real question is not whether species are fixed but whether there is any stable, objective unit in nature. What do the patterns of similarity and difference mean - creation according to a common plan with the potential of variation, or descent from a common ancestor with modifications? Charles Darwin believed that change is unlimited, that species are infinitely variable. He thought that species could vary indefinitely and in any direction. Creationists on the other hand, believe that change is limited by a basic organic "unit", the "created kind" and within the boundary of that fundamental unit, variation can be profuse, but it can never lead to the creation of a new basic type. This is near the essentialism as taught by Aristotle nearly 2000 years ago. Aristotle thought that each species embodies an eternal, unchanging ideal or archetype. The problem with this view is that it assumed a single form or pattern. Most biologists until the time of Darwin held to the typological view, a view considered by many scientists today as very plausible. This theory holds that the organic world is discontinuous, that all major groups of organisms are separate and breed true to type. A species is also defined by a cluster of characteristics - each member of the species may have some but not all of the diagnostic features. Another view is cladism, founded by the entomologist, Willy Hennig. It is concerned with the patterns found in nature and involves the finding of the positive and verifiable characters of the various species and determining how all species fit into the animal kingdom.

This preface is essentially intended to emphasise the following admonition of Thomas Huxley: " My business is to teach my aspirations to conform themselves to fact, not to try and make facts harmonise with my aspirations......Sit down before fact as a little child, be prepared to give up every preconceived notion, follow humbly wherever and to whatever abysses nature leads, or you shall learn nothing ". I also tried to emphasise that every scientist must, from time to time, stop and think for himself and not just accept the most widely - quoted viewpoint. I sincerely hope that this moral does not end here but instead runs through the rest of this book as well.

This work has already been published or submitted for publishing in various zoological or nematological journals and is presented in this book in the same format as required by the editors concerned. Abstracts will therefore be followed by either a " resumé " (in French) or an "uittreksel" (in

Afrikaans), depending on the magazine in which it was published.

It is a pleasure to acknowledge the kind help and assistance of various colleagues during the writing of this work. They offered advice on various points and I have always profited greatly from their counsel. In particular I want to express my sincere gratitude to my promoter, Prof. J. Heyns, who untiringly helped me to complete this study and whom I know enjoys these beautiful animals as I do. Also to my parents and Steve, for their unceasing motivation, my deepest gratitude.

CHAPTER 1

INTRODUCTION

INTRODUCTION

Nematodes were described by Aristotle as early as 300 BC but, as in almost all branches of science, advancement in nematology has been greatest within the last century, especially with the discovery of the light microscope and later, the scanning electron microscope. Since the late eighteenth century men began to realise that nematodes were probably the most abundant and widely dispersed group of metazoans which makes nematology an excellent discipline for the study of analogy, convergence, homology and divergence. More recently these simple metazoans also proved to be first - class models for behavioural, genetic, ontogenetic, nutritional, cryptobiotic and biochemical studies.

The present study is a contribution to the knowledge of the morphology and taxonomy of rare and little - known nematode genera, mostly from South Africa. Like a good taxonomical classification this chapter will start with a brief historical review of nematode classification, a short summary of their general and unique features and end with a brief presentation of the different nematode genera and species studied during this project.

Nematode taxonomy seems to have started when Linnaeus, in the twelfth edition of his "Systema Naturae" (1767) was the first to give a scientific name to a free - living nematode : *Chaos redivivus*. Lamarck, at the beginning of the nineteenth century, was the first to classify these animals in the class Vermes. Later Oken included nematodes in the group Nematoda. To me, the major turning points of nematode systematics were the works of Bastian, de Man, Cobb, Chitwood and Andrássy. H.C. Bastian (1837 - 1915), the first outstanding authority in the classification of nematodes, described 100 new species, and 22 new genera. J.G. de Man (1851 - 1930) was the second major taxonomist. He divided the class Nematoda into seven orders, the majority of which are still valid today. N.A. Cobb (1859 - 1932), a contemporary of de Man and seen by many as the greatest nematologist of all times, gave nematology its name and constructed the first and only key including fresh water, marine and soil nematodes. He was also the first to classify nematodes as an independent phylum under the name Nemata (Cobb, 1920). Associated with Cobb during those early years was W.E. Chambers, artist and microscopist. From his gifted hands nematology received the finest illustrations of nematodes that have ever been made, and it is doubtful that they will ever be equalled. One of the most outstanding workers in the systematics of nematodes was unquestionably B.G. Chitwood (1907 - 1972). His monograph (1950) is a complete study of the morphology, as well as the classification of nematodes. He divided the phylum into two classes, the Phasmidia and Aphasmidia on the basis of the presence or absence of phasmids. In 1958 he rejected these two names and replaced it with Secernentea and Adenophorea, referring back to von Linstow's (1905) categories. Andrássy (1976) divided the class Nematoda (he regards the Nematoda as a class of the phylum Nemathelminthes) into three subclasses : the Secernentia (Orders : Tylenchida, Ascarida, Strongylida and Spirurida) ; the Torquentia (Orders : Chromadorida, Desmosclecida, Monhysterida and Araeolaimida); and the Penetrantia (Orders : Enoplida, Trichocephalida, Dorylaimida and Dioctophymatida). According to this system thirteen orders are recognised, eight of which represent freeliving forms and five, animal parasites.

Before attempting to relate nematodes to other groups, a summary of their features is necessary : According to Andrássy (1976) nematodes are unsegmented, strongly elongated, cylindrical, unciliated Protostomia. At least some of their organs display cell constancy which make the organs strictly determined in structure. The cuticle is strongly resistant to undesirable elements and functions as a flexible skeleton. The peripheral musculature comprises longitudinal smooth muscle elements. This was taken from Andrássy (1976), but according to Maggenti(1981) each contractile element contains five bands in longitudinal section, comparable to the H, A and I-bands in vertebrate and invertebrate striated muscle. The muscles are situated between hypodermal chords and directly connected to longitudinal nerves. The digestive system is simple in morphology and course, its anterior part triradiate. The excretory system is basically one-celled, to which occasionally one or two accessory cells adhere. Separate respiratory and circulatory organs are absent. Cleavage of the egg is equatorial and growth is accompanied by moulting. Development is direct. Nematodes are bisexual. This was taken from Andrássy (1976), but according to Maggenti (1981) this statement is only in principle true. In some species only the female is known and then reproduction is generally accomplished by parthenogenesis, which may be either meiotic or mitotic. Hermaphroditism is rare in nematodes but there are many reports of individuals with both male and female characteristics. These are not hermaphrodites, but intersexes, and generally abnormal females. Normal females have a separate genital pore and males, a cloaca and cuticularized spicules. The genital primordium is clearly separate in the young gastrula. Nematodes are extraordinary versatile in habitat and are represented by both freeliving and parasitic forms. Freeliving nematodes may inhabit the sea, fresh water or land. In specimen number nematodes are first, and in species number, third among the Metazoa.

The relationship of nematodes to other organisms remains unclear and they have been assigned to no less than four phyla. Nematodes are often grouped with one or more of the following : the Rotifera, Gastrotricha, Kinorhyncha, Priapulida and Nematomorpha, all members of the Pseudocoelomata. Remane (1963) stated that the relationship of the so -

called Pseudocoelomata is one of the most difficult problems in systematic zoology and argued that the "pseudocoelom" may have developed independently in each group. Today many nematologists hold the concept that nematodes belong to the phylum Nemata or Nematoda (whichever name is preferred) and that the other related groups are each to be placed within its own separate phylum (Maggenti, 1981). In this study the opinion that the Nematoda represents a phylum is followed.

The classification of nematodes within the phylum Nematoda can be very confusing, even to nematologists and to the general biologist all nematodes may look alike, except for size. Many of the higher groups within the phylum have been established by earlier workers on a very limited knowledge of the great number of genera and species actually existing. For this reason extensive revisions have been made as information increased. A good example of the confusion that may result when inadequate information is used when classifying nematodes is the following: Bastian's original description of _Tylenchus_ (1865) was meagre and his figures left much to be desired. He stated that members of this genus possess only one ovary. However, Bütschli (1873) and de Man (1880, 1884) placed species with two ovaries in this genus and for about 60 years it has been a "dumping ground" of tylenchids of various forms. Filipjev (1934, 1936) was the first to finally bring order into the taxonomy of Tylenchs when establishing the genera _Rotylenchus_, _Pratylenchus_, _Tetylenchus_ and _Ditylenchus_ to receive certain groups of related species. Another example is the classification of the root - knot nematodes (_Meloidogyne_ spp.) : The first root - knot nematode was described by Cornu (1879) ; a swollen form, inducing nodules in sainfoin roots. From published abstracts Cornu knew that four plant parasitic nematodes had been described : _Anguillula tritici_ Steinbuch, 1799; _A. dipsaci_ Kuhn, 1857; _Heterodera schachtii_ Schmidt, 1871 and _A. radicicola_ Greeff, 1872, and the last of these induced swellings in the host roots. He had no access to the original descriptions of the four species and could not be sure that his species was identical to A. radicicola. He therefore regarded it as new, naming it Anguillula marioni. Muller (1884) studied the host range of root - knot nematodes and concluded that there was only one species, A. radicicola. Because he observed eggs in the swollen females, he transferred it to the genus Heterodera Schmidt, 1871. For the next 50 years the accepted name for the root-knot nematode was Heterodera radicicola (Cornu, 1849) Muller, 1884. In 1938 Goodey, studying Greeff's original paper, noted that the description of Anguillula radicicola was in fact of a slender species belonging to the genus presently known as Ditylenchus Filipjev, 1936. Consequently Goodey recognised Cornu's A. marioni as the first and only described root - knot nematode species, and transferred it to the genus Heterodera as H. marioni, which was the accepted name for the root-knot nematode until 1949. Goeldi (1892) was the first to recognise root-knot nematodes as a genus. He introduced it as Meloidogyne for the type species M. exigua. Unaware of Goeldi's work, Cobb (1924) introduced the name Caconema for the same taxon with C. radicicola as type species. Neither proposal was well founded and it was only in 1949 that Chitwood, on the basis of cuticular patterns of the perineum, definitely identified five different root-knot nematode species and convincingly established the root-knot nematodes as a genus for which he re-introduced Goeldi's name, Meloidogyne.

The classification of nematodes into species and genera is based on visible differences in structures as seen with the light microscope. Surface markings, as well as internal structures form the basis for separation of species. Recent technical advances such as scanning electron microscopy (SEM) are increasing the possibility of identification beyond that of the light microscope. The SEM has been useful as a taxonomic tool particularly in genera such as Meloidogyne where it was found that all stages of the life cycle possess characters with taxonomic value (Eisenback, 1980; 1982). Features clarified by SEM help to support and complement our present classification of lower, as well as higher categories and are especially useful in supplementing species descriptions. The basic idea of taxonomy today is to use all tools available to clarify the morphology, biochemistry and genetics of nematodes to establish a sound classification. Croll & Matthews (1977) rightfully stated: "Classification is never final: it is a continuing and dynamic synthesis of all biological information".

The present project started with a study of the genera Teratocephalus, Metateratocephalus and Euteratocephalus, all members of the order Teratocephalida. These animals presented a challenge as they are all extremely small which limit the possibilities to clarify their features. In this study the scanning electron microscope proved to be invaluable and previously unknown features could be observed clearly, contributing greatly to the knowledge of the morphology and taxonomy of this little -known group.

The taxonomic position of the genus Tobriloides represented in this study by T. loofi n.sp., is problematic as it has features of both the families Tobrilidae and Onchulidae. With the present study males are described for the first time within this genus and this, together with the morphological study of all the specimens, enabled the author to classify the genus within the Onchulidae. The paper on Tobriloides loofi n.sp. is also the first report of the genus from South Africa and only the second in the world.

Specimens of Lenonchium fimbricaudatum n.sp. were collected from wet sand in the Kruger National Park, South Africa, and represent the fifth report of this genus in the world. Increased knowledge of features such as the four mucro's on the tail, remnants of caudal glands and the peculiar structure of the supplements of the males are presented in this study.

A lack of knowledge on the morphology of the genus Isolaimium lead to an uncertainty about its phylogeny and consequently, its systematic position. Staining and sectioning of a few specimens of I. africanum, together with a thorough examination of all the specimens from Southern Africa, clarified the relationship of the genus, as well as many morphological features of the species.

Small nematodes with some very peculiar features were flushed from the hollow trunk of a liquid amber tree in Florida, U.S.A.. These specimens were made available to me and on examining them they proved to be a new genus of the family Aulolaimoididae.

The last specimens to be examined within this study were members of the genus Desmodora, collected from Lake Sibayi, Natal. This lake represents an unique habitat as it became land locked about 5000 years ago, giving its then marine species only five millennia to slowly adapt to a life in fresh water. These specimens possess so many unique characters that they are described herein as belonging to a new subgenus within the Desmodora.

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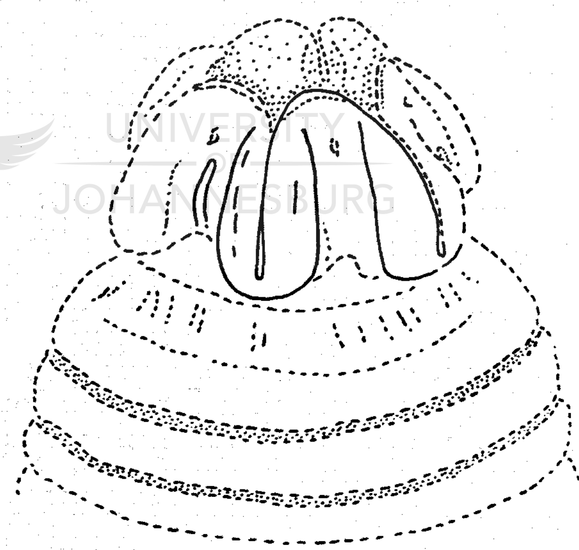
CHAPTER 2



DESCRIPTIONS OF ONE NEW AND TWO KNOWN SPECIES OF TERATOCEPHALIDAE (NEMATODA) FROM SOUTH AFRICA

(Published in Phytophylactica 21: 367 - 377)

ABSTRACT

Keywords: Teratocephalus, Metateratocephalus, taxonomy, SEM

The history of Teratocephalus and Metateratocephalus are briefly given and the diagnosis of Metateratocephalus is emended to include features discovered by scanning electron microscopy (SEM). One new species, Teratocephalus diversiannulatus, is described; Teracephalus lirellus Anderson, 1969 and Metateratocephalus crassidens (de Man, 1880) Eroshenko, 1973 are recorded for the first time from South Africa and described. Scanning electron micrographs on the morphology of these three species are included.

Uittreksel

'n Geskiedkundige oorsig van die twee genera Teratocephalus en Metateratocephalus word kortliks gegee, asook 'n gewysigde diagnose van Metateratocephalus om sekere nuwe kenmerke, soos gesien met die skandeerelektronmikroskoop (SEM), in te sluit. 'n Nuwe spesie, Teratocephalus diversiannulatus word beskryf en twee bestaande spesies, T. lirellus Anderson, 1969 en Metateratocephalus crassidens (de Man, 1880) Eroshenko, 1973 word vir die eerste keer uit Suid-Afrika aangemeld en beskryf. Skandeerelektronmikroskoopfoto's van die bogenoemde drie spesies is ook in hierdie artikel ingesluit.

INTRODUCTION

Specimens of Metateratocephalus crassidens (de Man, 1880) Eroshenko, 1973; Teratocephalus lirellus Anderson, 1969 and T. diversiannulatus n.sp. were collected in April 1987 from moist soil in the Landdroskloof, Hottentots-Holland Nature Reserve, Cape Province, South Africa. The soil samples were taken from the summit of a narrow ravine, situated at an altitude of 1350 m with an annual mean rainfall of ±3500 mm. The vegetation consists mainly of Cape Fynbos and various mosses. This is the first report of Metateratocephalus and Teratocephalus species from South Africa, although two Euteratocephalus species have already been described from various localities in this country by Heyns (1977).

MATERIALS AND METHODS

Specimens were extracted with the sugar flotation technique, killed by gentle heat, fixed in FAA, processed to glycerine by Thorne's slow method and mounted on permanent slides. Slide numbers refer to the collection of the Department of Zoology, Rand Afrikaans University, where the material is housed. Specimens were also fixed (Swart & Heyns, 1987) and examined with the scanning electron microscope (SEM). Measurements and drawings were made with the aid of a Zeiss Standard 18 research microscope equipped with a camera lucida. The body and curved structures of all specimens were measured along the median line. Light microscope photographs were taken with a MC63 photomicrographic camera and differential interference contrast.

DESCRIPTIONS

Genus: *Teratocephalus* de Man, 1876

syn: *Mitrephorus* Linstow, 1877

Andràssy (1958) proposed the family Teratocephalidae to accommodate the two genera *Teratocephalus* and *Euteratocephalus*. In a revision of this group in 1984 he placed the genera *Teratocephalus* and *Steratocephalus* Andràssy, 1984 in the subfamily Teratocephalinae, and the genera *Euteratocephalus* Andràssy, 1958 and *Metateratocephalus* Eroshenko, 1973 in the subfamily Metateratocephalinae Eroshenko, 1973. Andràssy proposed the genus *Steratocephalus* for those species of *Teratocephalus* with a prominently punctated cuticle and a vulva situated in an anterior position (±40%). In *Teratocephalus* the cuticle is without punctations, except in the lateral field of a few species. The vulva of this group is also in a more posterior position (±65%). No head bristles were reported in either *Teratocephalus* or *Steratocephalus*. During the abovementioned sampling in the Cape Fynbos of the Landdroskloof, two species of *Teratocephalus* were found, one of which is regarded as new and the other conspecific with *T. lirellus* Anderson, 1969.

Teratocephalus diversiannulatus sp.n. (Fig. 1A-J; 2A-F)

Females (n=4): L = 569 (542-598) µm; L' = 438 (402-465) µm; a = 28,3 (26,0-30,2); a' = 21,8 (19,2-22,3); b = 3,9 (3,7-4,3); b' = 3,2 (3,0-3,7); c = 4,4 (3,8-5,0); c' = 13,2 (11,2-15,7); V = 50,8 (46,6-54,7)%; V' = 65,9 (63,0-68,5)%; G_1 = 59,5 (41,5-82,5) µm; G_2 = 18,3 (11,5-30,0) µm; Tail = ±129 µm

Males (n = 2): L = 524 (423-626) µm; L' = 388 (327-450) µm; a = 36,8 (30,1-43,5); a' = 27,1 (23,2-31,0); b = 4,2 (3,9-4,6); b' = 3,2 (3,0-3,3); c = 4,0 (3,6-4,4); c' = 11,0 (8,0-14,1); T = 44,2 (38,9-49,5)%;

T' = 47,3 (43,4-51,2)%; Tail = ±131 µm

Holotype female: L = 583 µm; L' = 466 µm; a = 30,1; a' = 22,3; b = 3,7; b' = 3,0; c = 4,9; c' = 11,2; V = 54,0%; V' = 67,5%; G_1 = 63,3 µm; G_2 = 13,3 µm; Tail = 117,5 µm

Small, ventrally curved when heat-relaxed. Longitudinal ridges: 8 in neck region; 12 in mid-body, 8 in anal region. Body coarsely annulated, annules 1,4 - 2,0 µm wide.

First 8 neck annules prominent, 1,9 - 2,3 µm wide, well-separated from each other and very conspicuous (Fig. 2A). Striae in neck region deep and widened at their bases. Striae in rest of body deep and tapered. Lateral field protuberant, incisures two, crenate. Amphid aperture small, pore-like, within first striation posterior of head (Fig. 2D and F). First three annules always compressed at base of head, compared to next five (Fig. 2B). Excretory pore 1-2 annules anterior to nerve ring. Duct not observed in fixed specimens. Nerve ring at 60% - 66% of oesophagus length, 82,4 - 87,3 µm from anterior end. Oesophagus 123 - 144 µm long, narrowing slightly just anterior to basal bulb. Basal bulb oval in shape, valves moderately developed. Intestine expanded posterior of basal bulb and narrowing again in the region of the gonads. Rectum conspicuous, slightly sclerotized, about 24 µm long. Anus covered by cuticular fold (Fig. 2E). Head width 7,7 - 8,5 µm, wider than neck at base of stoma. Cephalic plicae 5,3 - 5,5 µm long, contours straight. Lips six, each with a small, longitudinal slit-like aperture situated centrally on the anterior half (Fig. 2 B, D & F). Each subventral and subdorsal lip has a short setum in a central, but posterior position (Fig. 2B and D). Stoma, excluding telostom, 4,5 - 6,4 µm long, cheilo-, pro- and mesostom wide. Metastom narrowing, telostom tapered. Metarhabdions not well-sclerotized, oval in shape. Oesophageal collar enclosing telostom. Female monodelphic, prodelphic. Ovary directed posteriorly, ending about 12 annules anterior of vulva. Uterus double (Fig. 1C, D and E). Post-uterine sac 11,5 - 30,0 µm long. In Fig. 1E sperm cells can be seen in the post-uterine sac.

Male monorchic, testis long, well-developed with terminal germinal part reflexed for less than one body width. Spicules cephalated, ventrally curved, 18(15-21) um in length. Gubernaculum absent. One pre-anal supplementary organ on 11th annule, 18 µm from anus, 1 pair of caudal papillae on either side of anus and 1 pair postanal, located 13 annules (19 µ) posterior of anus (Fig. 1I). Apparently the vas deferens joins the intestinum almost at the point where it leaves the body. The course of the vas deferens in this area is obscured by the spicules and muscles associated with the spicules.

Body narrowing behind anus. Tail similar in both sexes, tapering gradually to a delicately bifurcated terminus, annulated throughout. Posterior part of tail always coiled.

Holotype: Female on slide RAU 2919. Paratypes: Three females on slides RAU 2915, RAU 2918 and RAU 4099; and two males on slides RAU 2915 and RAU 2921.

Type locality and habitat: Landdroskloof, Hottentots-Holland Nature Reserve, Cape Province, South Africa. Found in moist soil with much organic material. Vegetation: Cape Fynbos and mosses.

DIAGNOSIS

Teratocephalus diversiannulatus n.sp. can be distinguished from all known species of Teratocephalus by the prominence of the first eight neck annules. It comes close to T. bisexualis Meyer & Coomans, 1977 by having males and a large post-uterine sac in some specimens. Teratocephalus diversiannulatus differs from T. bisexualis in the position of the vulva which is almost equatorial in T. diversiannulatus (47%-55%) and post-equatorial (56%-59%) in T. bisexualis. There are 16 to 18 longitudinal cuticular ridges in T. bisexualis compared to 8 to 12 in I. diversiannulatus.

Teracephalus diversiannulatus also resembles T. costatus Andrássy, 1958 in its coarsely annulated body with annules 1,8 - 2,4 µm wide in T. costatus and 1,4 - 2,0 µm in T. diversiannulatus. Furthermore, there are 8 longitudinal ridges in T. costatus and 8 - 12 in T. diversiannulatus and and the posterior part of the tail in both species is always coiled. However, T. diversiannulatus differs from T. costatus in the position of the vulva (T. costatus: V = 54% - 60%; T. diversiannulatus: V = 47% - 55%) and the modification of the first 8 neck annules, which are undifferentiated in T. costatus. Moreover, a double uterus is present in all females of T. diversiannulatus n.sp., whereas such a structure is apparently absent in T. bisexualis and T. costatus.

Andrássy (1984) synonymised T. decarinus Anderson, 1969 with T. costatus, even though Anderson described a double uterus in T. decarinus and Andrássy (1958, 1984) did not mention it in T. costatus. In a recent publication by Hernandes & Jordana (1988), a male of T. costatus is described for the first time. The males of the South African population are longer than the Hernandes & Jordana male (423 - 626 µm compared with 413 µm) and have longer tails (131 µm compared with 78 µm). The single preanal supplementary papilla of the South African males is in a slightly more posterior position than the pair described by Hernandes & Jordana (1988) of T. costatus (10 annules anterior of anus compared with 11 annules). The females of Hernandes & Jordana population of T.costatus are also shorter (430 - 477 µm) than the South African females (542 - 598 µm) and have fewer longitudinal ridges in midbody (8 compared with 12).

Teratocephalus diversiannulatus is also near T. tilbrooki Maslen, 1979, especially as both species have males and double uteri in the females. Teratocephalus tilbrooki differs, however, from T. diversiannulatus in the following aspects: the absence of longitudinal body ridges in T. tilbrooki conpared with 8 - 10 ridges in T. diversiannulatus; a longer male and female body length (T. tilbrooki female:535 - 650 µm and male:530 - 730 µm compared with T. diversiannulatus female:542 - 598 µm and male:423 - 626 µm) and the prominence of the first 8 neck annules in T. diversiannulatus. The males of T. tilbrooki also differs from those of T. diversiannulatus by the more anterior position of the preanal supplementary papillae (18 - 23 annules anterior of anus compared with 10 in T. diversiannulatus. Maslen (1979) described 2 preanal papillae in T. tilbrooki whereas only one was found in T. diversiannulatus. The position of the postanal papillae also differs (20 - 26 annules posterior of anus in T. tilbrooki compared with 13 annules in T. diversiannulatus.

REMARKS

During the present study, the SEM was used to clarify some of the peculiar morphological structures of Teratocephalus. The head is dominated by six lips formed by six deep incisures bordered, on either side by thickened cuticle (Fig. 2B) which form six ridges (plicae?). A very interesting observation is the presence of four head setae on the subventral and subdorsal lips (Fig. 2B). Six small, slit-like structures (apertures) can also be seen on the anterior half of each lip (Fig. 2F). This arrangement is similar to the normal 6+4- arrangement of outer labial and cephalic papillae in most other nematodes. No inner labial papillae were observed exteriorly on the heads of the specimens so it is assumed that the papillae terminate in the head cuticle as in the Cephalobidae. According to all descriptions, one of the distinguishing features of Teratocephalus, is the absence of "head bristles" or head setae. When Andrássy (1958) described T. costatus, he showed two setum-like structures near the lips. Unfortunately, he did not mention this in his description and since these structures are in a different position to the setae seen in the present SEM-micrographs, one cannot be sure of their nature or value.

Another interesting feature is the female reproductive system in T. diversiannulatus. The females are monodelphic prodelphic and have a small to large post-uterine sac. The uterus proper consists of two parts: one sac-like and the other more slender (Fig. 1D). These two parts join each other near the oviduct. The structure of the sac-like part suggests the function of a spermatheca although sperm was found in the post-uterine sac and not in the sac-like part of the uterus (Fig. 1E).

A double uterus was also described by Maslen (1979) in T. tilbrooki and T. rugosus and by Anderson (1969) in some Canadian species of Teratocephalus. This structure is especially clearly defined in T. decarinus. In cross-sections Anderson (1969) found that the uterus is double from the diverticulum to the uterus proper. The two uteri joined at the proximal end of the diverticulum near the oviduct. Posteriorly they joined again at the crusta formeria. No function other than egg transport could be found to explain the presence of these double uteri (Anderson, 1969).

Unfortunately, no cross-sections could be made of the present species, due to scarcity of material.

<u>Teratocephalus</u> <u>lirellus</u> Anderson, 1969 (Fig. 3A-H; 4A-I).

Females (n = 2): L = 417 (411-420) µm; L' = 306 (293-331) µm; a = 29,5 (23,9-32,9); a' = 21,3 (18,9-23,6); b = 4,0 (3,8-4,2); b' = 2,9 (2,8-3,1); c = 3,9 (3,3-4,8); c' = 13,7 (8,5-17,1); Tail = 110 (86-128) µm; V = 49,9 (47,9-52,8)%; G_1 = 55,0 (46,8-68,0) µm; G_2 = 11,2 (4,3-20,8) µm

Male (n = 1): L = 533 µm; L' = 387 µm; a = 41,0; a' = 29,8; b = 4,8; b' = 3,6; c = 3,7; c' = 13,0; T = 32,7%; Tail = 140 µm

Small, arcuate when heat-relaxed. Eight longitudinal cuticular ridges visible in neck-region, becoming more numerous posteriorly. Approximately sixteen body ridges discernable in mid-body, giving the cuticle a block-like appearance (Fig. 4D). Cuticle thick, coarsely annulated, annules 1,3 - 1,7 µm wide. Margins of annules somewhat angular. Lateral field protuberant, incisures two, crenate (Fig. 4F). Amphid aperture small, circular, on first annule posterior of head. Nerve ring at 60-63% of oesophagus length, 65 - 67 µm posterior of head. Excretory pore (Fig. 4E) just posterior of nerve ring. Excretory duct not seen in fixed specimens but can be observed in live ones (Fig. 4C). Hemizonid clearly visible: 67,5 - 70,0 µm from anterior end in female, 76,0 µm in male. Head width 7 - 8 µm, about equal to neck width at base of stoma. Cephalic plicae about 5 µm long, contours straight. Lips six, separated from each other (Fig. 4B). Each subventral and subdorsal lip with a prominent cephalic (?) setum (Fig. 4B). Each lip with a slit-like aperture (outer labial papillae?). No external evidence of inner labial papillae. Stoma 4 - 4,5 µm long, excluding telostom. Cheilo-, pro- and mesostom wide, metastom narrowing, telostom narrow. Metarhabdions small, oval, sclerotized. Oesophagus approximately 104 µm long, narrowing slightly just anterior of basal bulb. Basal bulb of female rounded to ovoid, that of male, elongate to ovoid. Dense tissue surrounding oesophagus just anterior of basal bulb. Cardia small. Intestine expanded behind basal bulb, markedly narrower in region of gonads. Rectum approximately 17 µm long. Anus covered by fold in cuticle (Fig. 4G).

Female monodelphic, prodelphic. Ovary directed posteriorly to 14 - 16 µm anterior of vulva. Genital track poorly differentiated. Post-uterine sac 11,2 (4,3-20,8) µm long. Oviduct seems to enter ovary near its middle.

Male monorchic, testis 212 µm long, well-developed. Germinal part of testis reflexed for about one body width. Vas deferens seems to join intestinum at about the posterior portion of the rectum. Course of the vas deferens obscured in this region by the spicules. Spicules cephalated and strongly curved ventrally, almost semi-circular, 15 µm long, measured along the median line. No gubernaculum present. A single, protuberant preanal supplementary papilla observed on 13th annule, 17 µm anterior of cloaca. Caudal papillae in two pairs: one pair postanal, located 14 annules posterior of cloacal opening and one pair adanal.

Body narrowing behind anus, tapering gradually, annulated to the tip. Terminal part of tail bifurcated (Fig. 4H).

DISCUSSION

The South African specimens agree with the original description of T. lirellus Anderson, 1969 in almost every detail except for the number of cuticular ridges and the absence of males in T. lirellus. Teratocephalus lirellus has 18-24 longitudinal cuticular ridges, whereas the present specimens have only 16-18. However, because of the extremely small size of the nematodes and the relatively large number of ridges, it is difficult to count the number of ridges accurately. and a small error should be allowed for.

The South African specimens also resemble the population of T. terrestris (Butchli, 1873) de Man, 1876, described by Meyer and Coomans (1977) from Kenya, especially as males were found in both populations. These authors, however, recorded that T. terrestris has no longitudinal body ridges, the vulva is post-equatorial (52% - 56%) and the male tail is short (c = 5-6) compared to that of the present population (c = 3,3-4,8). The vulva is almost equatorial (47% - 52%) in the South African specimens.

Teratocephalus rugosus Maslen, 1979 is also close to the population from South Africa, especially as males are also described in this species but the males of T. rugosus and the South African population differ from each other in the position of the preanal supplementary papillae which are 13 - 17 annules anterior of the anus in T. rugosus compared to 13 annules in the South African specimens. Maslen also described a pair of preanal papillae whereas only one was observed in the males of the South African population. The spicules are also longer in T. rugosus (17-23 µm) compared with that of the South African population (15µm).

The females of T. rugosus are longer (555-735 µm) than those of the present population (411 - 420 µm), with a longer tail (104 - 200 µm compared with 86 - 128 µm)

REMARKS

As four head setae were found in both Teratocephalus diversiannulatus n.sp. and the South African population of T. lirellus, it is assumed that a SEM-study of the Teratocephalinae will, in all probability, reveal the presence of head setae in all species of this group, since these setae are very difficult to descern with the light microscope, even when one is aware of their presence.

Genus: Metateratocephalus (de Man, 1880) Eroshenko, 1973.

Eroshenko (1973) proposed the genus Metateratocephalus for those species of Euteratocephalus with no cephalic setae, and no papilloid supplementary organs in males. He placed the new genus, which contained only the two species: M. typicus Eroshenko, 1973 and M. crassidens (de Man, 1880), Eroshenko, 1973 in the subfamily Metateratocephalinae. M. crassidens was originally described by de Man as Teratocephalus crassidens, then it was transferred to Euteratocephalus by Andràssy (1958), and again transferred by Eroshenko (1973) to the present genus. In 1984 Andràssy synonymised M. typicus with M. crassidens and since he considered T. crassidens of De Coninck (1935) as different from de Man's crassidens, he proposed the name M. deconincki for De Coninck's species. Andràssy (1985) also described a further species, M. gracilicaudatus from Hungary which brought the species belonging to Metateratocephalus to the following: M. gracilicaudatus Andràssy, 1985; M. deconincki Andràssy, 1984 and M. crassidens (de Man, 1880) Eroshenko, 1973.

According to Andràssy (1984), Metateratocephalus lacks true head bristles, in contrast to Euteratocephalus with four true bristles, but he described the labial region as divided into six lobes, each terminating in a bristle-like tip. Meyer & Coomans (1977), also mention the lack of cephalic bristles in M. crassidens, the well-offset head, and the poorly developed, irregular lateral field.

During the 1987-survey of the Landdroskloof, a species of Metateratocephalus was collected which agrees with both Andràssy's (1984 & 1985) and Meyer & Coomans (1977) descriptions of Metateratocephalus crassidens, except that the collected specimens have ten prominent setae on the head region (discernable with both the light microscope and the SEM). These ten setae are arranged in the normal 6+4-configuration and seem to represent 6 outer labial and 4 cephalic setae. Fortunately, the senior author examined specimens of M. crassidens from Kenya (the same ones described by Meyer & Coomans) and was able to find head setae in these specimens too. Interestingly, Eroshenko (1973) showed these setae in their proper places when describing M. typicus (See his Fig. 1, page 4770) but failed to mention them in his description apparently considering them part of the tip of each lip. Consequently, the diagnosis of the genus is emended to include this characteristic. It is possible that further SEM-studies will reveal head setae in all other species of Metateratocephalus.

Another interesting observation was the amphid morphology of the South African Metateratocephalus population. The amphids seem to have large, spiral apertures when seen with a light microscope but under the SEM have a small, tube-like aperture which overlies the subcuticular spiral structure underneath (Fig. 6A & B). The cuticle, when seen with the light microscope has fine annulations and coincident rows of fine punctations. These punctations could not be observed with the SEM and are thus assumed to be subcuticular. Fine annulations could, however, be observed with the SEM.

Metateratocephalus Eroshenko, 1973

Generic diagnosis (emended): Metateratocephalinae. Body small, 300 - 500 µm in length. Head well-offset with 10 setae arranged in the normal 6+4-configuration around the head. Cuticle thin with fine annulations, rows of fine punctations (probably subcuticular) coinciding with annulations. Punctations more prominent in lateral field. Stoma short, with wide prostom and sclerotized rhabdions. Amphids large spiral organs; aperture small, tube-like. Anterior part of oesophagus cylindrical, bulbus well-developed. Gonads of female, double, short and reflexed. Gonad of male single, long, well-developed, anteriorly reflexed. Tail conoid to filiform, dorsally curved. Males rare, with caudal papillae. Tail dorsally curved.

Metateratocephalus crassidens (de Man, 1880) Eroshenko, 1973 (5A-G & 6A-I). Females (n = 10): L = 428 (387-458) µm; a = 22,5 (17,8-26,3); b= 4,0(3,8-4,6); c = 7,5(6,4-8,2); V = 52 (51-53)%; G_1 = 40,4 (30,0-64,0) µm; G_2 = 31,6 (25,0-64,3) µm; c' = 5,7 (4,5-6,5); Tail = 58,0 (49,0-71,5) µm

Male (n = 1) : L = 509 µm; a = 30,86; b = 4,2; c = 8,0; c' = 5,0; Tail 64,0 µm

Small, moderately ventrally curved when heat-relaxed. Lip region offset, much wider than neck at base of lips, 6 µm high and 11 µm wide. Six conspicuous lips each with a long setum (5 µm long) situated in a central position (Fig. 6B). A shorter setum, situated just posterior of the longer one, on each subdorsal and subventral lip (Fig. 6B).
Cuticle thin with fine annulations, about 0,6 µm apart and rows of fine punctuations coinciding with annulation (Fig 6C). Punctations becoming more prominent in posterior regions and forming two distinct, but irregular rows in the lateral field . These punctations seem to be subcuticular as it cannot be observed with the SEM (Fig. 6A & B). The specimens on Fig. 6E & G shows an annulated, punctated cuticle but as it was left in ethanol for about a week, due to circumstances, and as considerable shrinkage was visible on it's body, it's features cannot be accepted as valid. The laterally situated setum however, as well as the caudal pores (Fig 6G) was

also observed with the light microscope and can be accepted as a normal feature.

A peculiar feature is the large, oval body pores occurring on the neck- and tail regions of the larvae (Fig. 8C). The pores in the neck region are arranged in no particular pattern (Fig 6A) but on the tail they are arranged in a spiral. These pores start a few microns anterior of the anus and continue in a spiral along the tail where it stops at about 1/4 of the tail length. Morphologically they seem to consist of a pore within a pore. Body pores (on neck and tail) do not occur in adults.

Stoma 4,5 - 5,0 µm in length, with a wide prostom (3,7 - 5,0 µm). Stoma consisting of well-sclerotized cheilorhabdions, fused pro- and mesorhabdions, small, oval metarhabdions and thin, tapering telorhabdions. Oesophagus length 93 - 117µm in female, 120µm in male, somewhat constricted near the basal bulb. Basal bulb rounded to ovate with prominent valves. Nerve ring distinct, at ±52% of oesophagus length and 56 to 61µm from anterior end. Spiral organ, part of excretory system, situated within the body cavity, on lateral side of body, 8-10 µm anterior of basal bulb. Excretory pore (Fig. 6H), 60 - 78µm from anterior, end, just posterior of nerve ring, on same level as hemizonid. Dense tissue obscure part of oesophagus just anterior to basal bulb. Cardia indistinct. Intestine posterior of basal bulb expanded and thick-walled.

Amphid apertures (under light microscope) big, spiral, diameter about 4um (Fig. 6C). Distance from middle of amphids to tips of lips 15 - 18µm, about 1,2 - 1,5 times head width from anterior. Amphids as seen with SEM, quite different (Fig. 6A&B). Spiral amphid aperture is covered by cuticle with a prominent tube-like outgrowth situated in approximately the middle of the spiral structure underneath. With a few setae scattered over entire body, one of which can be seen in the vicinity of the excretory pore (Fig.

6I).

Females didelphic, amphidelphic. Ovaries reflexed, both on same side of intestine. Vagina short, rest of genital tract difficult to discern. One egg observed: 27,7 x 9,0um. Tail of female elongate, conoid, dorsally curved in posterior 1/3 and 49 - 72um long. Tail tip not bifurcated, but tapered to a fine point. One caudal setum observed on either side of anus (Fig. 6G). No phasmids recognised by either SEM or light microscope (Fig. 6G). Rectum 7 - 8um long or 1,4 times anal body diameter.

Male monorchic, testis long, well-developed, anteriorly reflexed for about 4 body widths. Spicules cephalated, delicately sclerotized and ventrally arcuate. Gubernaculum present but difficult to observe, about 7um long. Length of spicules 21um. A single hair-like supplementary organ, 24um from cloaca, can be observed. Two pairs of caudal papillae, 2 adanal (slightly posterior of cloacal opening), and 2 postanal, approximately 18 um posterior of cloacal opening. The male tail also curves into a slow spiral and is therefore difficult to measure and to draw.

DISCUSSION

The females of the present population closely resemble those of M. crassidens, except for the position of the vulva which is almost equatorial 52(51-53)% in the South African population and post-equatorial (53% - 60%) in M. crassidens according to Andrassy (1984). The M. crassidens-population from Kenya, described by Meyer & Coomans (1977) has a vulva position of 50% - 53% which agrees well with that of the South African population. However, the male found in our population is longer (509um) than the male described by Eroshenko 1973 (330um). The a-, b- and c-values also differ in the two males: a = 31 in South African population compared with 23 in Eroshenko's description; b = 4,2 in population from

South Africa compared with 3,9 in description of Eroshenko; c = 8,0 in South African population compared with 9,3 in Eroshenko's population. Males are very scarce in this genus and only two have been found in this species. The fact that the two males differ so markedly can be anticipated as they come from two different continents (Africa and Asia) and from different habitats (South African population from Cape Fynbos and mosses, Eroshenko's population from mosses in a spruce-fir forest). The position of the amphid (1,2 - 1,5 head widths from anterior end in South African population and 1,5 head widths in M. crassidens) and the tail (c = 4,5 - 6,5 in South African specimens and 4,5 - 6,0 in M. crassidens) place the South African population firmly in M. crassidens. It differs from M. gracilicaudatus Andrássy, 1985 mainly in the longer, filiform tail of the latter species (c = 6,3 - 7,2) and from M. deconincki Andràssy, 1984 in the position of the amphids which are 3 headwidths from the anterior end in M. deconincki and 1,2-1,5 headwidths in the present species.

REMARKS

In the present population a laterally situated spiral organ can be observed within the body cavity, just anterior to the basal bulb (Fig. 5A & B). This organ is connected to the excretory pore by a tubule which indicates that it is part of the excretory system. It bears some resemblance to the odd loop of the excretory tube in some Plectidae (Chitwood & Chitwood, 1974). Cobb (1914) saw an "organ of unknown significance" just anterior to the basal bulb in Teratocephalus cornutus and Loof (1971) found a similar organ in M. crassidens. De Man (1880) also mentions a peculiar structure in the same species.

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NOTE

After this manuscript was submitted for publication, a paper by S.V. Boström on teratocephalids appeared in Revue de Nématologie 12(2): 181-190 (1989). He found scattered body pores in all adults of *M. crassidens* whereas it was only found in juveniles in the present study. It may be concluded that these pores occur in all stages (adults and juveniles) of this species.

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FIG. 1A-J Teratocephalus diversiannulatus n. sp. A: Anterior part of holotype female; B: Anterior region of male; C: Reproductive system of female, showing large post-uterine sac; D: Reproductive system of female, showing double uteri (arrows); E: Reproductive system of female, showing sperm in post-uterine sac (arrow); F: Reproductive system of male; G: Head of female, external view; H: Female tail; I: Anal region of male, showing genital papillae (one pair post-anal, one pair adanal and a single preanal papilla; J: Heat-relaxed body posture of male & female.

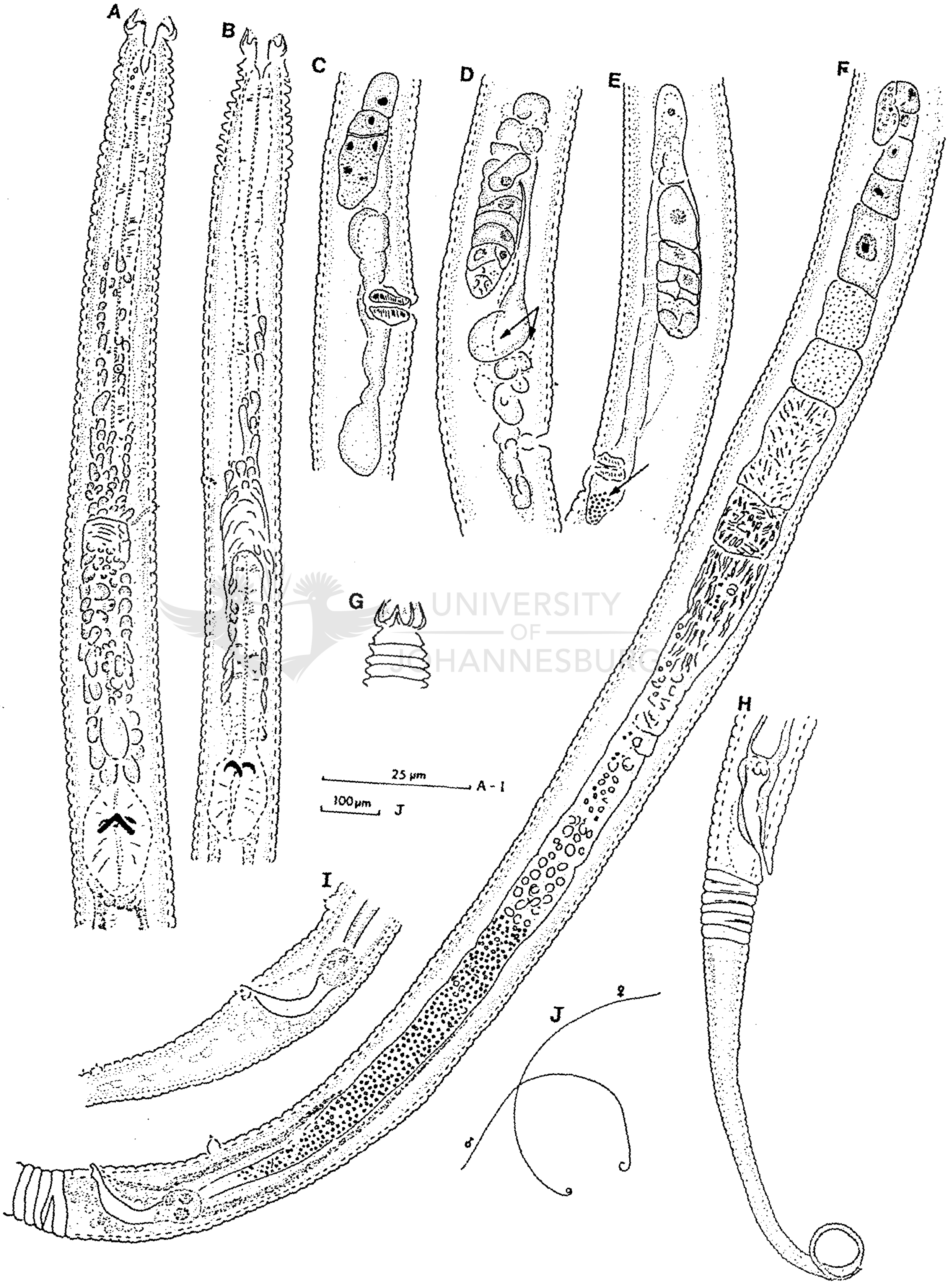
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FIG. 2A-F Teratocephalus diversiannulatus n. sp. A: Anterior region of female, showing prominent neck-annules (1400X); B: Female lip region. Arrow indicates head setum (6500X); C: Vulval area (3100X); D:Female lip region. Arrow a indicates head setum, arrow b indicates amphid aperture situated between first two neck annules. (sd.l = subdorsal lip; l.l. = lateral lip; sv.l = subventral lip) (8900X); E: Anal area of female, showing slight cuticular fold over anus (3500X); F: Female lip region. Arrow a indicates aperture on lateral lip; arrow b indicates head setum on subventral lip; arrow c indicates amphid aperture (8000X)

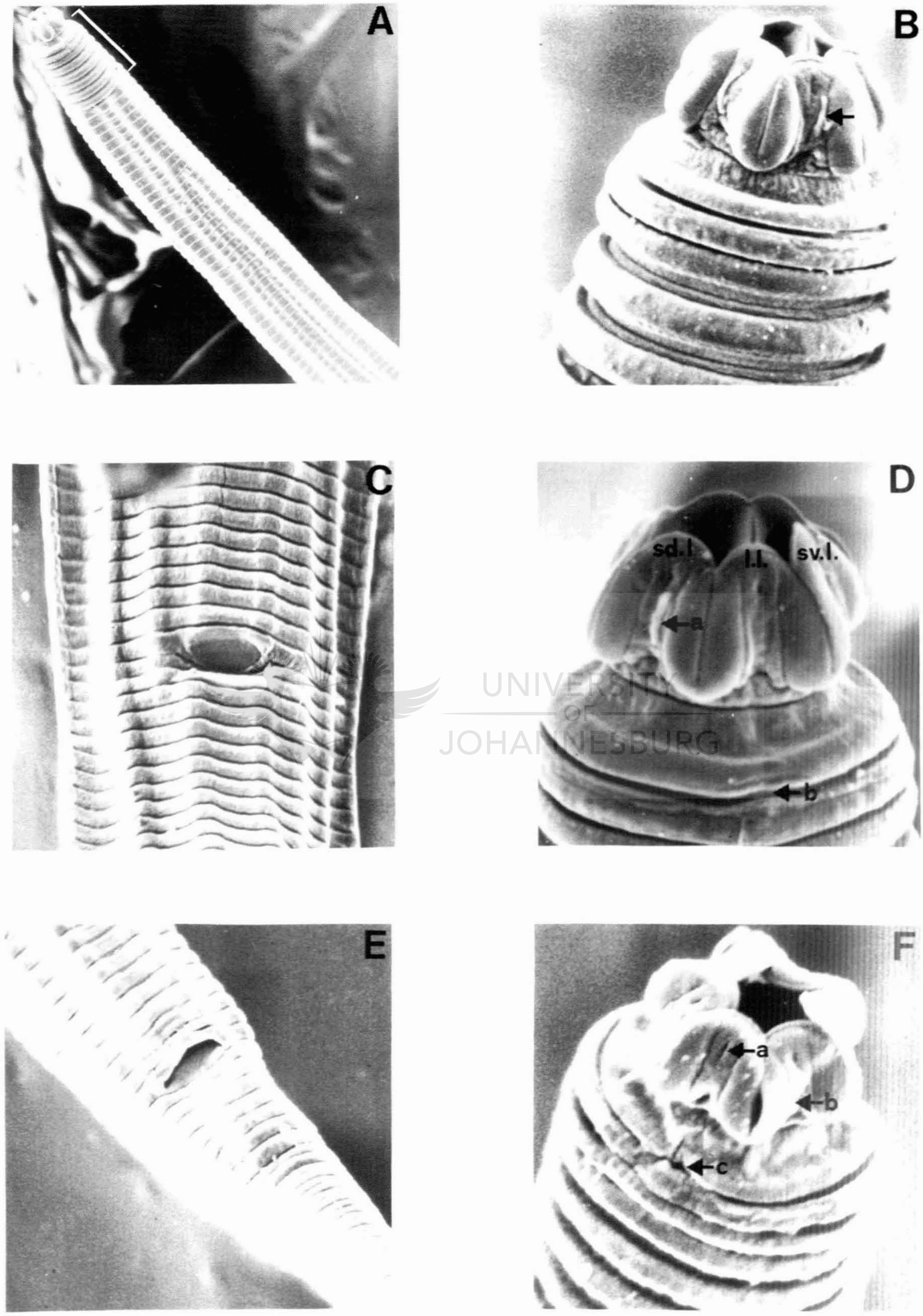
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FIG. 3A-H *Teratocephalus lirellus* Anderson, 1969. A: Male reproductive system; B: Anterior region of male; C: Anterior region of female; D: Female reproductive system; E: Head of female, external view; F: Head of male, external view; G: Anal region of male, showing genital papillae; H: Female tail

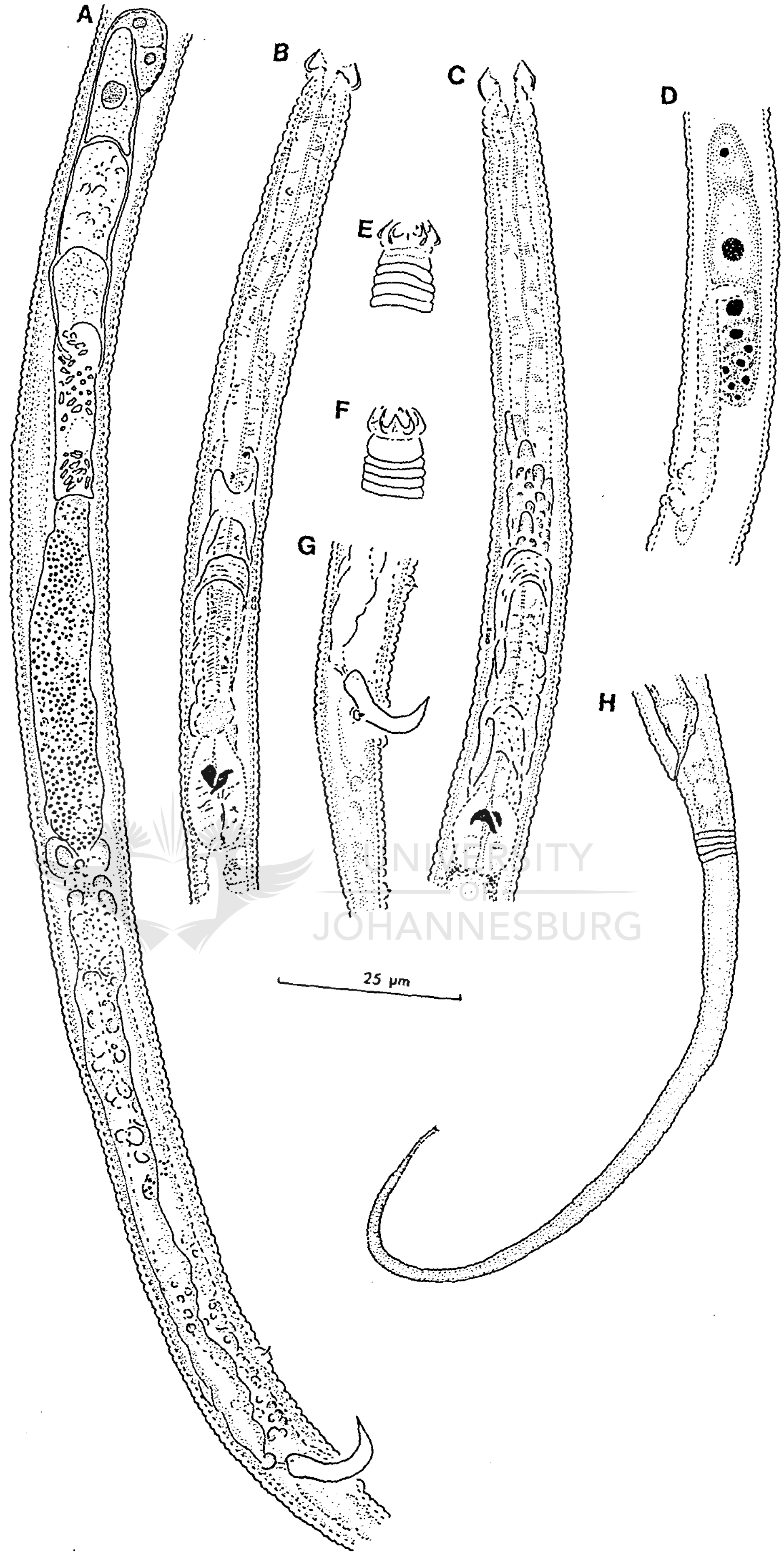
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FIG. 4A-I Teratocephalus lirellus Anderson, 1969. A: Anterior region of female (2300X); B: Female head region. Arrow a indicates aperture on lip, arrow b indicates head setae (8000X); C: Excretory duct of live female under light microscope. Arrow indicates duct leading to excretory pore (2000X); D: Block-like appearance of cuticle in mid-body of female. Arrow indicates lateral field (4000X); E: Excretory pore (arrow) of female (4000X); F: Lateral field of female under light microscope (2000X); G: Anal region of female, lateral view (6200); H: Female tail showing forked terminus (12200X); I: Posterior region of female, showing longitudinal ridges in this area (1350X)

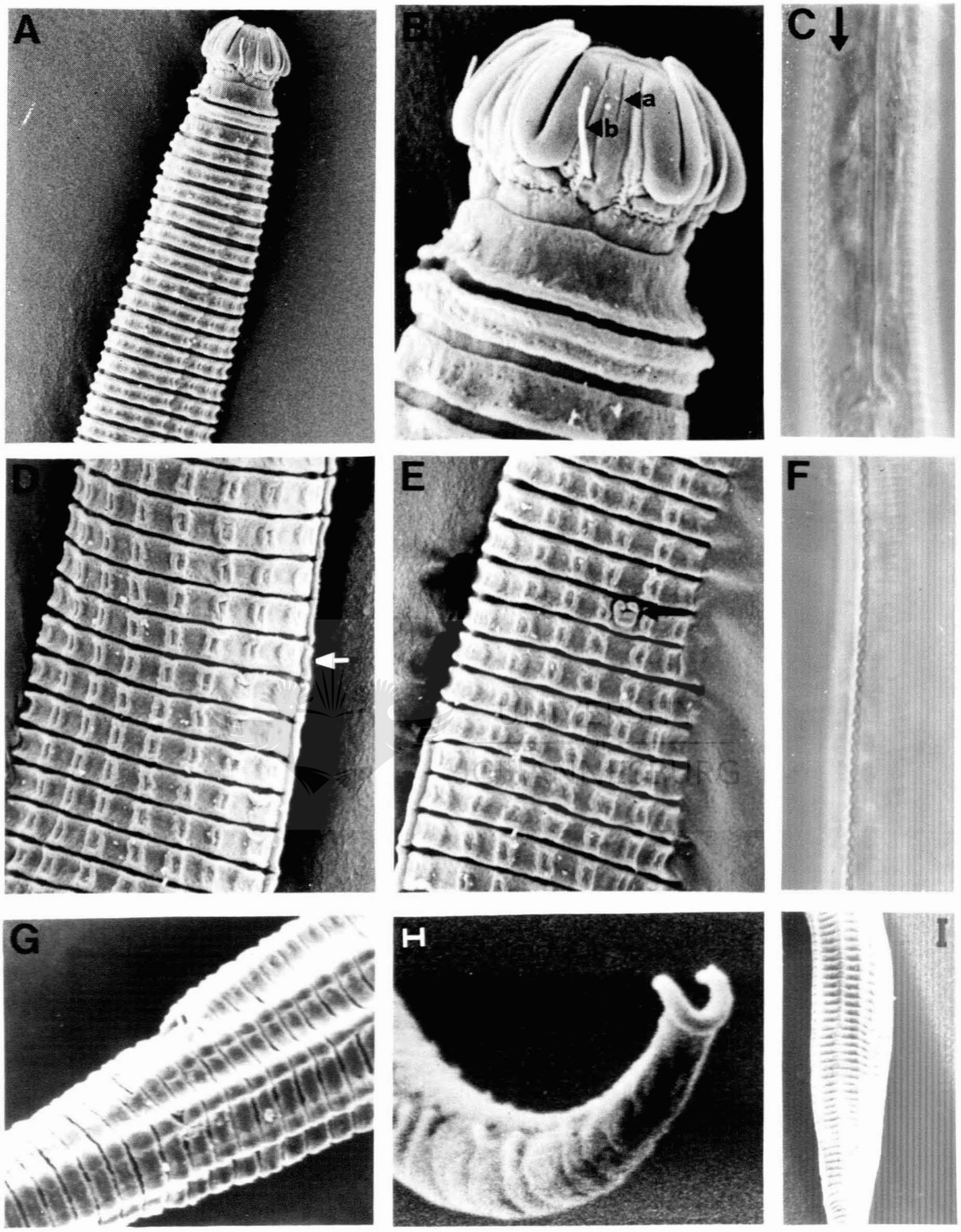
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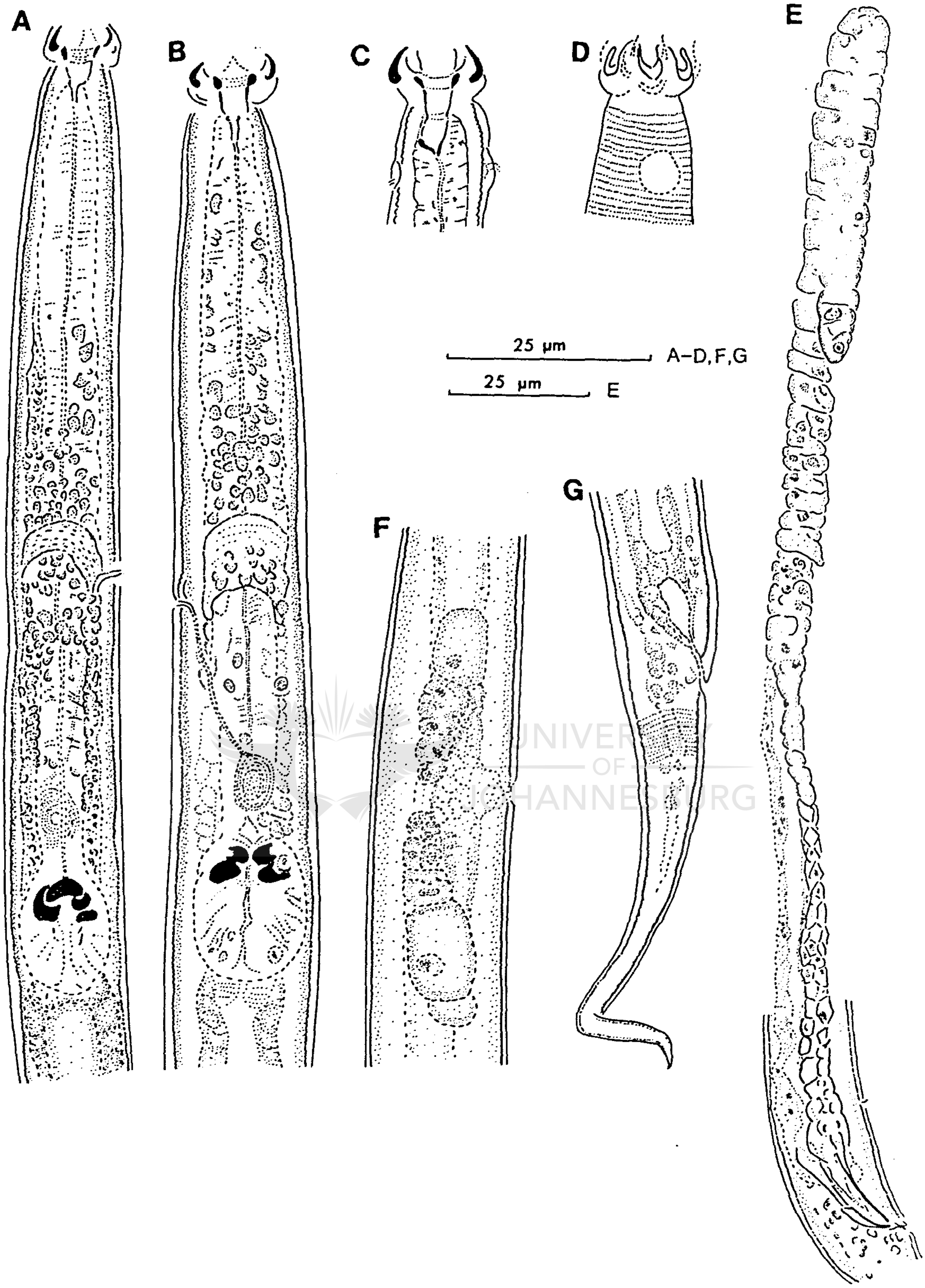
FIG. 5A-G Metateratocephalus crassidens (De Man, 1880) Eroshenko, 1973. A: Anterior region of female; B: Anterior region of male; C: Head region of female; D: Head region of female, external view; E: Reproductive system of male; F: Reproductive system of female; G: Female tail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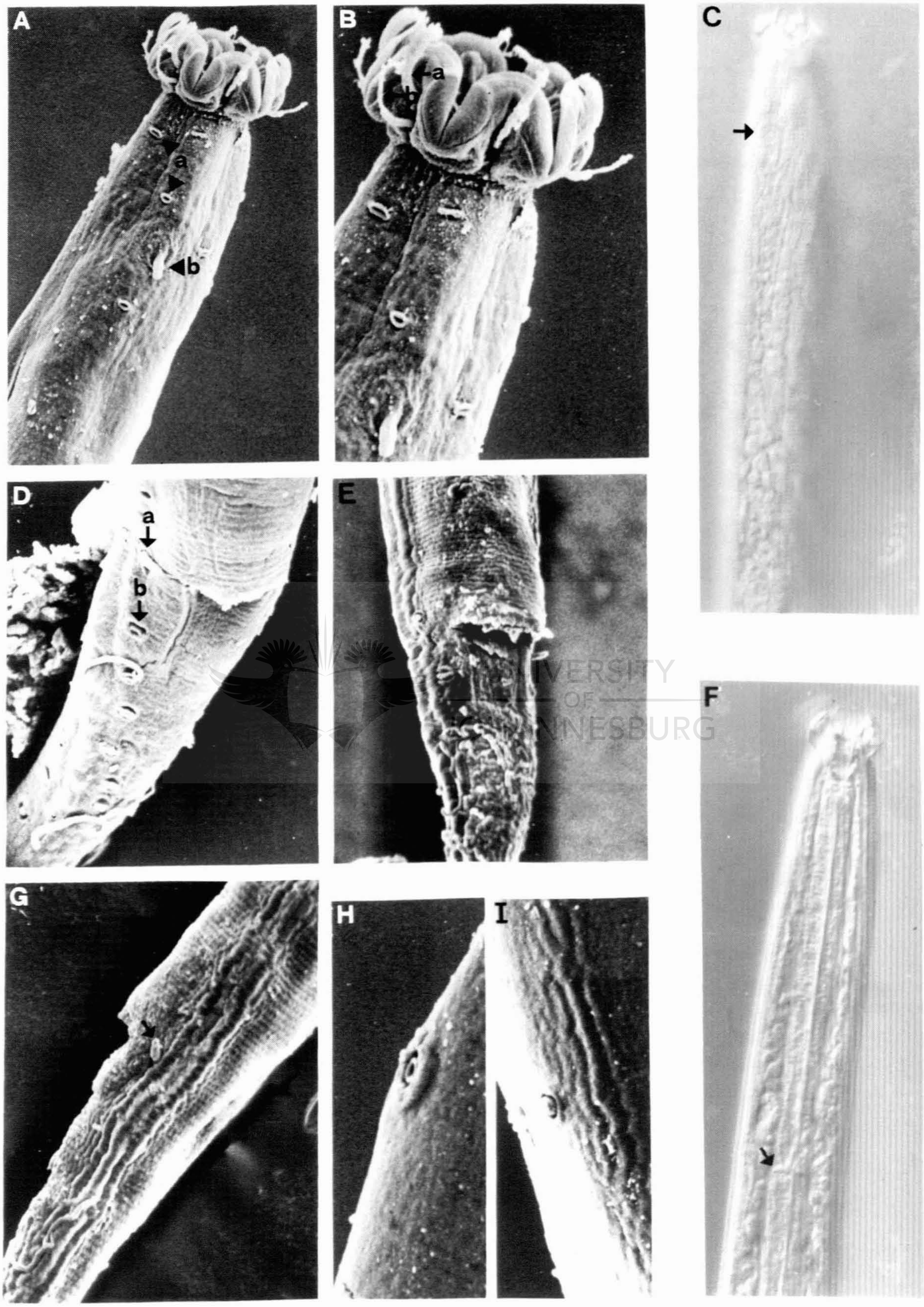
E
F
G
25 µm A–D, F, G
25 µm E

FIG. 6A-I Metateratocephalus crassidens (De Man, 1880) Eroshenko, 1973. A: Anterior region of larva, showing body pores (arrow a) and amphid aperture (arrow b) (3000X); B: Head region of female, showing outer labial setae (arrow a) and cephalic setae (arrow b) (5000X); C: Anterior region of live female under light microscope. Arrow indicates spiral amphid. Note subcuticular punctations on body (1000X); D: Anal region of larva, showing anal setum (arrow a) and caudal body pores (arrow b) (4000X); E: Anal region of larva, ventro-lateral view, showing anal setae and caudal body pores (3200X); F: Anterior region of female. Arrow indicates excretory duct in live female under light microscope (1000X); G: Anal region of female, showing anal setum (arrow) and lateral field (4300X); H: Excretory duct on ventral side of larval body (8100X); I: Body setum on dorsal side of larval body (5600X)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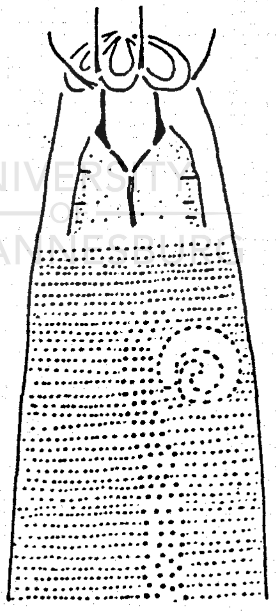
CHAPTER 3



A REVIEW OF THE GENUS EUTERATOCEPHALUS ANDRÀSSY, 1958, WITH A DESCRIPTION OF E. PUNCTATUS N.SP.

(Accepted by Revue de Nématologie)

SUMMARY

Specimens of Euteratocephalus Andràssy, 1958 from localities in Africa (Kenya and South Africa), South America (Bolivia and Brazil), Australia and Europe (Belgium, The Netherlands, Germany) were studied. The ornamentation on the subcuticle overlying the lateral field was used as the main character to distinguish the three species of the genus. Euteratocephalus spiraloides (Micoletzky, 1913)Andràssy 1958 is re-instated as a valid species. Euteratocephalus capensis Heyns, 1977 and E. hirschmannae Heyns, 1977 are synonymized with E. palustris (de Man, 1880) Andràssy, 1958 and E. spiraloides, respectively. Euteratocephalus punctatus n.sp. is described from Kenya, Bolivia and Brazil. This new species is characterized by the subcuticular ornamentation overlying the lateral field: a smooth area, 2.5-4 um wide, comprising 60-95% of the total body length and bordered by large punctations.

RÉSUMÉ

Révision du genre Euteratocephalus Andràssy, 1958 et description d' Euteratocephalus punctatus n.sp.

Des spécimens de Euteratocephalus Andràssy, 1958, provenant d'Afrique (Kenya, 'Afrique du Sud), d'Amérique du Sud (Bolivie, Brésil), d'Australie et d'Europe (Belgique, Pays-Bas, Allemagne) ont été étudiés. Les trois espèces du genre Euteratocephalus peuvent être différenciées par le type de l'ornementation sous-cuticulaire au niveau du champ latéral. Euteratocephalus spiraloides (Micoletzky, 1913) Heyns, 1977 est revalide. Euteratocephalus capensis Heyns, 1977 et E. hirschmannae Heyns, 1977 sont considérés comme des synonymes mineuis de E. palustris (de Man, 1880) Andràssy, 1958 et E. spiraloides, respectivement. Euteratocephalus punctatus n.sp. provenant du Kenya, de Bolivie et du Brésil est décrit; cette nouvelle espèce est caractérisée par le type de l'ornementation sous-cuticulaire au nivecu des champ latéral: partie centrale sans ornementation large de 2.5a4 um et s'etendant sur 60-95% de la longueur du corps; bordée de larges points.

In 1958, Andràssy erected the genus Euteratocephalus to accommodate two species of the genus Teratocephalus de Man, 1876 with finely annulated cuticles, large spiral amphids and paired ovaries: E. palustris (de Man, 1880) Andràssy, 1958 (the generotype) and E. crassidens (de Man, 1880) Andràssy, 1958. He also synonymized Teratocephalus cornutus Cobb, 1914 and T. spiraloides Micoletzky, 1913 with E. palustris and erected the family Teratocephalidae to accommodate Euteratocephalus and Teratocephalus Eroshenko (1973) transferred E. crassidens to the genus Metateratocephalus Eroshenko, 1973 and placed this genus, together with Euteratocephalus in the subfamily Metateratocephalinae Eroshenko, 1973. As a result Euteratocephalus contained only one species: E. palustris. Heyns (1977) re-instated T. spiraloides as a valid species of Euteratocephalus. He also regarded the specimens from Germany which Hirschmann (1952) had identified as E. palustris, as different from de Man's E. palustris but conspecific with a new species from South Africa which he named E. hirschmannae. Heyns (1977) further described a new species from South Africa, E. capensis, so that the genus then contained four species.

Anderson (1969) placed Teratocephalus demani Stefanski, 1924 in Euteratocephalus, but Andrássy (1984) transferred it to the genus Steratocephalus. Mukhina (1981) described a new species, Euteratocephalus minor, Andrássy (1984) however, synonymized it with Metateratocephalus crassidens, de Man, 1880.

In the present paper, the results are presented of a study of about 90 specimens of Euteratocephalus from eight countries on four continents and the re-examination of the type material of E. hirschmannae and E. capensis. It is concluded that today the genus Euteratocephalus consists of three species: E. palustris, E. spiraloides and E. punctatus n.sp. Euteratocephalus capensis and E. hirschmannae are synonymized with E. palustris and E. spiraloides, respectively.

Materials and methods

Specimens were killed and fixed in hot 4% formalin and transferred to anhydrous glycerin (De Grisse, 1969). For SEM studies, specimens mounted in glycerin were hydrated to distilled water, post-fixed in 1% OsO_4, dehydrated in a graded ethanol-series, critical point dried, sputter-coated with gold and viewed with an ISI SS 60 SEM at 6kV. Measurements of body length and all curved structures were made along the curved median line.

Euteratocephalus palustris (de Man, 1880) Andrássy, 1958

(Figs 1-3)

MEASUREMENTS

See Table 1

DESCRIPTION (based on the specimens from Belgium; n = 15; Fig. 1D, E, H)

Female: Body moderately curved when heat-relaxed, curvature slightly more pronounced in tail region. Body tapering from vulva towards both extremities. Lip region confluent with body. Six well developed lips with six outer labial setae (5 µm long) and four slightly shorter cephalic setae. No inner labial setae observed. Amphideal aperture a small, oval opening. Anterior part of stoma 3-4 µm wide with sclerotized walls, tapering posteriorly. Cuticle overlying lateral field in anterior region demarcated by a narrow (1 µm wide) smooth area bordered on either side by two rows of slightly larger dots. This smooth area stretches from about 12 µm posterior of head and ends about 170 µm posterior to head. From this point onwards to 60-80 µm anterior to the anus, the four rows of dots remain close together, increasing to 6 rows at mid-body. A narrow smooth area (about 2 µm wide) appears again between the two innermost rows of dots just anterior to the anus (Fig. 1 H). This smooth area ends about 50 µm from the tail tip. Along the lateral field this smooth area constitutes 24-26% of the total body length. Oesophagus cylindrical, narrowing anteriorly of basal bulb. Nerve ring well developed. Excretory pore almost on same level as nerve ring. Dense gland-like tissue surrounds oesophagus just anterior to basal bulb. A laterally situated organ resembling a spiral situated 10-15 µm anterior to the basal bulb. The small tubule seen in some specimens running from this organ towards the excretory pore suggests an excretory function for this organ. Basal bulb well-developed, with strong valves. Intestine expanded in its anteriormost part where it joins the basal bulb. Lumen of intestine thin-walled. Reproductive system didelphic, amphidelphic. Ovaries reflexed, their tips usually not touching each other. G_1 = 49-116 µm; G_2 = 41-139 µm. Vagina short. Other parts of reproductive system difficult to discern. Both gonads on left side of intestine, except in one female where both are on right side. Rectum 15-20 µm long. Tail elongate-conoid, ventrally curved. Caudal ventro sublateral setae situated 7-10 µm posterior to anus.

Male: not found.

COMPARISON WITH OTHER POPULATIONS

Population from South Africa, originally described as *E. capensis* (n = 20; Table 1, Fig. 3 E,G).

Female: Body shorter and tail slightly shorter in relation to body length resulting in a higher c-ratio. Almost no cuticular ornamentation over lateral field in anterior part and at mid-body. Smooth area occupies 18-23% of body length, starting about 100 µm anterior to anus and ending 50 µm from tail tip (see Fig. 2 B in Heyns, 1977).

Population from The Netherlands (n = 14; Table 1; Fig. 1 A,B,C,F,G):

Female: Smooth area overlying the lateral field occupies only 10-12% of the total body length in anterior 50-60 µm of body. Lateral field elsewhere demarcated by four rows of prominent punctations. In the midbody region of some specimens no cuticular ornamentation could be observed on lateral field. Tips of reflexed ovaries usually touching each other.

Population from Kenya (n = 3; Table 1; Fig. 2 A,B,C,E,F,G):

Female: Body shorter and broader, tail slightly shorter, and smooth area overlying the lateral field occupying about 33% of total body length. Smooth area (1-2 µm wide) starts 12-15 µm from head and extends posteriorly to 50-53 µm from anterior end. It starts again at 140 µm from anus and ends 50 µm from tail tip. Caudal laterosubventral setae situated 5-13 µm posterior to anus.

Population from Australia (n = 2; Table 1; Fig. 2 D,H,I):

Female: Body shorter and broader. Smooth area overlying the lateral field occupies 30-35% of total body length. This smooth area (1-2 µm wide) starts from 10 µm to about 100 µm posterior to head, and again from 100 µm anterior to anus to 25-30 µm from tail tip. Caudal laterosubventral setae at 6-10 µm posterior to anus.

Population from Bolivia (n = 3; Table 1; Fig. 3 A,B,F):

Female: The smooth area overlying the lateral field extending over 25-30% of the total body length, occupying about 100 µm of the lateral field anteriorly and about 200 µm posteriorly. Caudal latero-subventral setae situated 7-9 µm posterior to anus.

Population from Germany (n = 10; Table 1; Fig. 3 C,D,H):

Female: Body more slender. The smooth area overlying the lateral field occupies only about 18% of the total body length. The smooth area itself is also narrower (1-1.5 µm wide) and starts posteriorly only 10 µm from anus.

Remark:

It is interesting to note (Table 1) that nearly all specimens from the southern hemisphere are on average shorter and broader than the specimens from the northern hemisphere.

HABITATS AND LOCALITIES

Belgium: Wet soil, brooklet, 12 m altitude, Morkhoven (Antwerpen province), collected by D. De Waele on 5.6.1978; wet soil around roots of grasses, brooklet, 420 m altitude, Amberloup (Luxemburg province), collected by D. De Waele on 24.4.1980; Wet soil around roots of reed (Phragmites sp.), brooklet, 280 m altitude, Bertrix (Luxemburg province), collected by D. De Waele on 22.5.80.

South Africa: White sand among the roots of bulrush (Prionium sp.) in the Palmiet River, near Hermanus; soil on the bottom of a small stream near Kleinmond; soil, small river in the Elgin district; soil, mountain stream in the Cederberg mountains. All localities are situated in the southwestern Cape Province.

The Netherlands: Soil from pastures near Biesbosch, Snijdersveerbeek (Aalten); rhizosphere grasses in moist soil near Bennekom; moist soil among cranberry roots near Terschelling.

Kenya: Mosses (Aulacomnium turgidum (Wahl) Schwgz. along the border of Thompson Tarn , Mount Kenya, altitude 4310 m, collected by A. Coomans on 31.7.1975.

Australia: Soil rhizosphere among ferns growing around a small pool in a mangrove swamp, near Algen, eastern Australia.

Bolivia: Benthic sample from the littoral zone of Lago Khara Khota, Cordillera Real, altitude 3992 m, collected by D. De Waele on 11.7.1979; benthic sample from the littoral zone of Lago Khota (near to the Rio Pauchintani), Cordillera Real, altitude 4450 m, collected by D. De Waele on 7.8.1979.

Germany: In moist soil at Waltersberg, Murnau.

Euteratocephalus spiraloides (Micoletzky, 1913) Andrássy, 1958

syn *Euteratocephalus hirschmannae* Heyns, 1977

(Fig. 4 D,E,G,H)

MEASUREMENTS

See Table 2

DESCRIPTION (based on the female from Bolivia)

Female: Body slightly ventrally curved with curvature more pronounced in posterior third. Body tapering towards both extremities. Lip region confluent but narrower than body, 4 µm high and 8 µm wide. Six outer labial setae (5 µm long), as well as four slightly shorter cephalic setae present in lip region. No inner labial setae observed. Amphideal aperture an oval-shaped pore, located 14 µm from anterior end. Subcuticle overlying lateral field with four to six irregular rows of prominent punctations, diminishing in size away from lateral field. Lateral subcuticular ornamentation extends from 10 µm posterior to head to 50 µm from tail tip. Anterior part of stoma wide, well-sclerotized, 5 µm wide and about as long. Posterior part of stoma tapering, thin-walled. Oesophagus cylindrical, narrowing slightly anterior to basal bulb. Nerve ring conspicuous, about 100 µm from anterior end. Excretory pore at about same level as nerve ring. A peculiar spiral organ, situated laterally in body cavity just anterior to basal bulb, 157 µm from anterior end. A broad band of tissue surrounds the oesophagus in this area, obscuring the tubule from the spiral organ. Basal bulb well developed with strongly-developed valves. Intestine widens slightly just after junction with oesophagus. Lumen of intestine thin-walled. Reproductive system amphidelphic, didelphic.

Vagina short, ovaries reflexed, tips almost touching. Gonads on left side of intestine. Tail elongate-conoid, ventrally curved, tapered to fine point. Caudal laterosubventral setae 8-11 µm behind anus.

Male: Not found.

COMPARISON WITH OTHER POPULATION

Population from South Africa, originally described as *E. hirschmannae* (n = 6; Table 2):

Female: Distance from anterior end to excretory pore 96-102.5 µm; distance from anterior end to nerve ring 93-97,5 µm and distance from anterior end to spiral organ (situated before basal bulb) 150-154 µm. Lateral subcuticular ornamentation extends from 10 µm posterior to head and consists of about 4 irregular rows of prominent punctations. These prominent punctations become obscure towards the vulval region but can again be distinguished as 4-6 irregular rows of prominent punctations in the anal region. The punctations extends till 50 µm from the tail tip.

HABITATS AND LOCALITIES

Bolivia: Wet soil, aquaduct of the Cerro Mario Lloco, Cordillera Real, altitude 4800 m, collected by D. De Waele on 22.7.1979.

South Africa: Wemmer Pan, Johannesburg, South Africa; water among roots of a willow tree in a stream running into Wemmer Pan from the southern suburbs of Johannesburg.

Euteratocephalus punctatus n.sp.
(Figs. 4 A,B,C,F; 5,6)

MEASUREMENTS

See Table 3

DESCRIPTION (based on the specimens from Kenya; n = 7; Figs 4 A-C & F, 5):

Female: Body moderately ventrally curved, tail in some specimens excessively ventrally curved. Lip region confluent with, but narrower than body. Six conspicuous lips, each with a long outer labial setum (3-4 µm long) situated in a posterior and central position. Four cephalic setae (4 µm long), each situated on a subdorsal or subventral lip, just posterior to the outer labial setae (Fig. 5 D). No inner labial setae observed. Amphideal apertures small, oval (Fig. 5 A). Cuticle thin with fine annulations, about 0.5 µm apart. Rows of fine punctations on the subcuticle coinciding with annulations. Subcuticle overlying the lateral field with a large, smooth area (3.5-4 µm wide; stretching over 67-92% of the body length) between innermost rows of large punctations except in vulval area where ornamentation consists of only four irregular rows of large punctations. These punctations and the smooth area can be seen clearly on the subcuticle in the oesophageal region of a damaged specimen. Several small setae present on the body: one in a lateral position in the region of the excretory pore, one in the vulval region, usually two laterally between vulva and anus, and two caudal latero-subventral, 7-9 µm posterior to anus. Large, oval body pores randomly spaced in anterior region (Fig. 5 A). More posteriorly pores are arranged in one row on each side of the lateral field (Fig. 5 A). Pores end about 50-60 µm from tail tip. Stoma 3.5 µm wide and 3.5-4 µm long. Stoma walls well sclerotized. Oesophagus slightly constricted in region of nerve ring. Dense tissue obscures oesophagus 20-30 µm anterior to basal bulb. Laterally situated spiral organ situated 15-20 µm anterior to basal bulb (Fig. 4 B). Excretory pore well-defined with well-defined valves. Intestine expanded where junction occurs with oesophagus. Lumen of intestine thick-walled. Reproductive system didelphic, amphidelphic. Vagina 4-6 µm long, ovaries reflexed, tips almost touching. Both gonads on left side of intestine. One egg observed, 25 µm x 86 µm. Tail elongate-conoid, tapering to a sharply pointed terminus, the annulations apparently extending to the tail tip. Rectum 13-18 µm or 1-1.4 anal body diameters long.

Male: Not found.

COMPARISON WITH OTHER POPULATIONS

Population from Sergine, Brazil (n = 5; Table 3; Figs 6 A, B, E):

Female: Smooth area overlying lateral field 1.5-3 µm wide, stretching over only 67% of total body length. Subcuticle overlying lateral field in mid-body demarcated by 4 rows of large punctations.

Population from Iguassu River, Brazil (n = 1; Table 3):

Female: Body longer and the amphid situated slightly more anteriorly. The smooth area overlying the lateral field extends uninterruptedly over 78% of the total body length. Smooth area is 3 µm wide, starts 13.5 µm posterior to head and ends 33.5 µm from tail tip.

Population from Bolivia (n = 5; Table 3; Fig. 6 C,D,F):

Female: Body on average longer and broader. The smooth area overlying the lateral field extends uninterruptedly over 92% of the total body length. Smooth area is 2.8-3.5 µm wide, starts 15 µm posterior to head and ends about 32 um from tail tip.

TYPE SPECIMENS

Holotype female (slide RAU 5548) and three paratype females (slides RAU 5549-5551) deposited in the nematode collection of the Instituut voor Dierkunde, Rijksuniversiteit Gent, Ghent, Belgium. Three paratypes (slides RAU 5552-5554) are deposited in the nematode collection of the Rand Afrikaans University, Johannesburg, Republic of South Africa.

TYPE HABITAT AND LOCALITY

Benthic sample from the littoral zone of Hut Tarn, Mount Kenya, altitude 4488 m, collected by D. De Waele on 27.7.1975.

OTHER HABITATS AND LOCALITIES

Brazil: Soil around the roots of coconut palms; sand around the roots of reeds on the bank of the Iguassu river, collected by J. Heyns.

Bolivia: Benthic sample from the littoral zone of the lake at the base of the Cerro Mullu Apacheta, Cordillera Real, altitude 4820 m, collected by D. De Waele on 12.7.1979.

Kenya: Benthic sample from the littoral zone of Hall Tarn, Mount Kenya, altitude 4293 m, collected by D. De Waele on 5.8.1975; benthic sample from the littoral zone of "Greatest" Hall Tarn, Mount Kenya, altitude 4293 m, collected by D. De Waele on 5.8.1975; benthic sample from the littoral zone of Naro Moru Tarn, Mount Kenya, altitude 4190, collected by A. Coomans on 3.8.1975.

DIAGNOSIS

Euteratocephalus punctatus n.sp. is characterized by the ornamentation on the subcuticle overlying the lateral field. This area is demarcated by a broad 2.5-4 µm wide, smooth area stretching over about 67-92% of the total body length. The smooth area is bordered by two rows of large punctations on each side. The head is dominated by six well-developed lips with six outer labial setae and four slightly shorter cephalic setae. Amphideal aperture is a small, oval opening.

RELATIONSHIPS

Euteratocephalus spiraloides does not have a smooth area overlying the lateral field. In E. palustris the smooth area is much narrower (1-2,5 µm wide) and stretches over only 10% to about 40% of the total body length. The lateral field in E. spiraloides is also demarcated by up to six rows of large dots or sometimes not demarcated at all. The body of E. punctatus is, on average, shorter than that of E. spiraloides (570-888 µm in E. punctatus n.sp. vs 820-965 µm in E. spiraloides).

DISCUSSION

The main character used in the present study for separation of the species is the ornamentation at the level of the lateral field. Features such as head width and height tend to vary even within populations depending also on whether the lips are in an "open" or "closed" position (Figs 5 A & B). A protruding vulva, observed in many specimens of E. hirschmannae, also occurs in some specimens of E. palustris (Fig. 3 D). Furthermore, the morphometrical data are of limited value since much overlapping occurs between species (compare Tables 1, 2 & 3).

In the body length and subcuticular ornamentation overlying the lateral field, the population of The Netherlands was intermediate between E. palustris and E. spiraloides (Table 1; Figs 2 A-C). The population from Brazil was also intermediate between E. palustris and E. punctatus n.sp., especially in the width of the subcuticular ornamentation overlying the lateral field (Figs 6 A, B & E).

In describing E. capensis, Heyns (1977) probably overlooked the fact that the smooth area overlying the lateral field stretches over only a relatively short distance in the anterior and posterior regions [Fig. 2 (p. 116) of Heyns, 1977]. The same pattern of lateral ornamentation was also found in E. palustris populations from Belgium, The Netherlands, Germany, Australia and some specimens from Bolivia and Kenya (Figs 1-3). Therefore E. capensis is synonymized with E. palustris.

In his description of T. spiraloides, Micoletzky (1914) depicted the punctations constituting the transverse striae in the anterior region, as unbroken over the lateral field with no smooth area overlying the lateral field. We observed a similar pattern in the type specimens of E. hirschmannae and one specimen from Bolivia although the punctations overlying the lateral field tend to be slightly more pronounced in especially the anterior and posterior regions of some specimens. Therefore we synonymize E. hirshmannae with E. spiraloides and amend the description of E. spiraloides to include the specimens of Euteratocephalus with no smooth area demarcating the lateral field.

Key for the species of Euteratocephalus based on the few relatively stable features found during the present study:

1. Lateral field demarcated by a few rows of large, modified punctations or not demarcated at all .... *E. spiraloides*

Lateral field demarcated by a smooth area, bordered by large, modified punctations 2

2. Smooth area comprising about 60-95% of total body length. Width of smooth area 2.5-4 µm............ ....*E. punctatus* n.sp.

Smooth area comprising about 10-40% of total body length. Width of smooth area 1-2.5 µm.................................. *E. palustris*

The taxonomic position of the teratocephalids has always been problematic since these nematodes possess a mixture of characters from different orders (Goodey, 1963; Andrássy, 1958, 1976, 1984). Andrássy (1958) considered the teratocephalids intermediate between the cephalobids and plectids (that is between the Phasmidia/Secernentea and Aphasmidia/Adenophorea). Goodey (1963) on the other hand, placed the teratocephalids between the Rhabditida and Araeolaimida, and stressed their affinities to both orders. Inglis (1983) splitted the Teratocephalidae (Andrássy,1958) into two families, the Teratocephalidae and Metateratocephalidae (Eroshenko, 1973) Inglis, 1983, and suggested their assignment to different orders. Boström (1989) also suggested a further separation of the genera *Metateratocephalus* and *Teratocephalus*. During the present study we found *Euteratocephalus* closer to *Metateratocephalus* than to *Teratocephalus* (This is in accordance with Eroshenko, 1973 and Andrássy, 1976 and 1984). The former two genera both have distinct body pores, no prominent body annules and a peculiar spiral-shaped organ with a possible excretory function [compare Figs 1 A & D and 5 A of the present paper with Figs 5 B and 6 A - I in Swart, Meyer & Heyns (1989)]. In contrast, *Teratocephalus* has no distinct body pores nor a spiral-shaped excretory organ but has prominent body annules [see Figs 1 A and 4 A-I in Swart, Meyer & Heyns (1989)].

The spiral-shaped, laterally situated organ, mentioned above, was observed within the body cavity of all species of Euteratocephalus just anterior to the basal bulb (Figs 1 A & D; 2 D; 3 B & C; 4 B & D; 6 A & C). The small tubule seen in some specimens, extending from this organ towards the excretory pore suggests a probable excretory function. Two caudal latero-subventral setae were observed in all species about 5-13 µm posterior to the anus. The setae bear no resemblance to phasmids, but a transmission electron microscope study would probably resolve their true nature, as was also suggested by Boström (1989) for Metateratocephalus crassidens.

SEM revealed the following additional information on Euteratocephalus (Fig. 5): The cephalic sense organs are arranged in the normal configuration of six outer labial setae, four cephalic setae and two amphids (Figs 5 B & D). No inner labial setae were observed. The amphids have small, oval apertures (Fig. 5 A), whilst the spiral aperture observed with the light microscope is situated subcuticularly. The punctations observed with the light microscope on the subcuticle overlying the lateral field could be seen with SEM on the subcuticle of a damaged specimen (Fig. 5 C). Another interesting observation is the presence of large oval body pores occurring along the lateral sides of the body (Fig. 5 A). These pores are irregularly arranged anteriorly, but form one row on each side of the lateral fields posteriorly.

Euteratocephalus palustris seems to be the most widespread species occurring in Europe, Asia, Africa, Australia, U.S.A. and South America. Euteratocephalus spiraloides, also widespread, has been found in Europe, Africa and South America, while E. punctatus n.sp. is known from Africa and

South America only. Interestingly, all three species were found in Bolivia.

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TABLE 1 Morphometrical data of Euteratocephalus palustris (de Man, 1880) Andrássy, 1958

Locality	The Netherlands E. palustris (de Man, 1880)	Belgium	The Netherlands	Germany	Australia	Bolivia	Kenya	South Africa Types of E. capensis
n		15	14	10	2	3	3	20
L (μm)	800-1000	738.7(685.0-967.5)	882 (720-950)	888 (830-920)	555 (550-560)	788 (683-875)	681 (650-740)	680 (640-740)
a	35-52	27.5(23.5-29.8)	42.1 (25-52)	33.9 (29.8-36.8)	19.6 (18.9-20.3)	31.4(24.4-35.1)	22.5(20.0-24.6)	27 (24-34)
b	4.0-4.5	4.5(4.3-4.9)	4.5 (4.0-4.5)	4.7 (4.7-4.9)	4.6 (4.5-4.6)	4.4(4.3-4.5)	4.2(4.16-4.26)	4.4 (3.9-4.8)
c	6-10	8.0(7.6-8.9)	9.6 (7.3-10.0)	8.9 (8.2-9.6)	8.0 (7.9-8.1)	8.8(8.5-9.5)	8.0(7.0-8.8)	9.9 (8.3-11.3)
c'		7.7(6.2-9.6)	7.2 (6-9)	6.0 (5.5-6.7)	5.2 (4.8-5.5)	6.3(5.1-7.2)	5.6(4.5-6.0)	5.8 (4.8-6.8)
Tail length (μm)		92.9(82.5-108.8)	91.9 (82-101)	99.8 (96-108)	68.5 (68-69)	89.5 (81-94)	80.1(74-84)	67 (58-82)
Oesophagus length (μm)		164 (159-194)	196.9(179-208)	187.7(177-195)	120.5(120-121)	180(159-195)	163(157-173)	154.5(150-160)
Lip height (μm)		3.9 (3.5-4.5)	3.3(2.9-3.5)	4.5(4.4-4.8)	4.4	3.0	3.8(3 - 4)	3.8 (3 - 4)
Lip width (μm)	8	7.8 (7.0-8.5)	7.3 (7 - 8)	9.0(7.0-8.5)	9.1 (8.5-9.6)	7.5 (7.5-8.0)	7.2(7.0-7.5)	8.4 (8-9)
V (%)	50-52	51.2(49.0-54.4)	52.5(50.0-55.5)	49.3(47.8-51.3)	50.3(49.5-51.5)	53.1(50-55)	51.3(49.6-52.0)	52.5 (50-55)
Amphid to anterior end (μm)	14.3 (12.5-17.5)	14.3 (12.5-17.5)	14.3 (13.5-16.0)	16.7(15.5-17.5)	10.9(10.3-11.5)	13.7(12.5-14.5)	15.1(14.0-16.5)	13.9 (13-15)
Excretory pore to anterior end (μm)		90.4(80.0-107.5)	103.4(92-109)	123.2(117.5-131.5)	73.8(71.5-76.0)	90.6 (81-100)	76(71-80)	77.3(72-85)

TABLE 2 Morphometrical data of *Euteratocephalus spiraloides* (Micoletzky, 1914) Andrássy, 1958

Locality	East Alps *E. spiraloides* (Micoletzky, 1914)	South Africa Paratypes: *E. hirschmannae*	Bolivia
n	4	6	1
L (µm)	890 (855-965)	860 (820-910)	920
a	29.7(27.8-31.5)	35 (33-39)	31.3
b	4.6 (4.4-4.8)	4.5 (4.2-4.9)	4.9
c	10.7(9.3-11.7)	10.3(9.6-11.0)	9.2
c'		6.0 (5.3-6.4)	6.2
Tail length (µm)		84 (80-95)	100.1
Oesophagus length (µm)		191.3(185-195)	187.5
Lip height (µm)		3 - 4	4
Lip width (µm)		8 - 9	8
V (%)	52.8(51.5-54.2)	51 (48-53)	52
G_1 (µm)		5.7-7.2	14.3
G_2 (µm)		5.5-8.5	12.8
Amphid to anterior end (µm)		16 - 19	13
Excretory pore to anterior end (µm)		96 - 102.5	99
Nerve ring to anterior end (µm)		93 - 97.5	100

TABLE 3 Morphometrical data of <u>Euteratocephalus</u> <u>punctatus</u> n.sp.

Locality	Kenya Holotype	Paratypes	Bolivia	Brazil	Brazil Iguassu River
n	1	6	5	5	1
L (µm)	765	667 (570-800)	832 (790-888)	650 (635-657)	816
a	33.3	31.2(27.5-35.0)	28.9(28.7-29.6)	37.5(33.5-44.0)	31.4
b	4.5	4.4 (4.0-4.5)	4.6(4.4-4.6)	4	4.5
c	8.0	8.0 (7.5-9.0)	10.0(9.0-11.2)	8 (8.0-8.5)	8.9
c'	6.0	6.5 (5.5-8.0)	5.6 (4.5-6.7)	7 (6.5-8.0)	6.1
Tail length (µm)	93	84.4(69-102)	83.3(79-88)	79 (77-82)	91.5
Oesophagus length (µm)	180	154.7(138-182)	179.6(167.5-192.8)	160 (158-163)	179.5
Lip height (µm)	3.0	3.2 (3.0-3.5)	3.8 (3.0-4.5)	3.4 (3.3-3.8)	4.0
Lip width (µm)	8.0	7.8 (7.5-8.0)	8.6 (8-9)	7.1 (7.0-7.5)	8.0
V (%)	53	51.7 (48-53)	50.6 (49.6-52.2)	50.0(48.5-51.0)	48.7
Amphid to anterior end (µm)	18.5	18.1 (15.5-20.5)	13.8 (13-15)	11 (10-12)	14.5
Excretory pore to anterior end (µm)	98	82 (66-101)	93.5 (87-102)	85 (82-89)	93
Nerve ring to anterior end (µm)	93	75.8 (63-94.5)	87.7 (84-92)	80 (75-83)	91

Fig. 1. Euteratocephalus palustris (de Man, 1880) Andrássy, 1958 - A, B, C, F, G: Population form The Netherlands. - A: Anterior region showing spiral organ (arrow); B: Head region showing amphid, cuticular punctations (forming striations) and punctations overlying the lateral field; C: Tail showing cuticular punctations and punctations overlying the lateral field; F: Mid-body region; G: Tail of another female showing smaller punctations on lateral field. - D, E, H: Population from Belgium. - D: Anterior region showing spiral organ (arrow); E: Mid-body region; H: Tail showing cuticular striations and punctations overlying the lateral field.

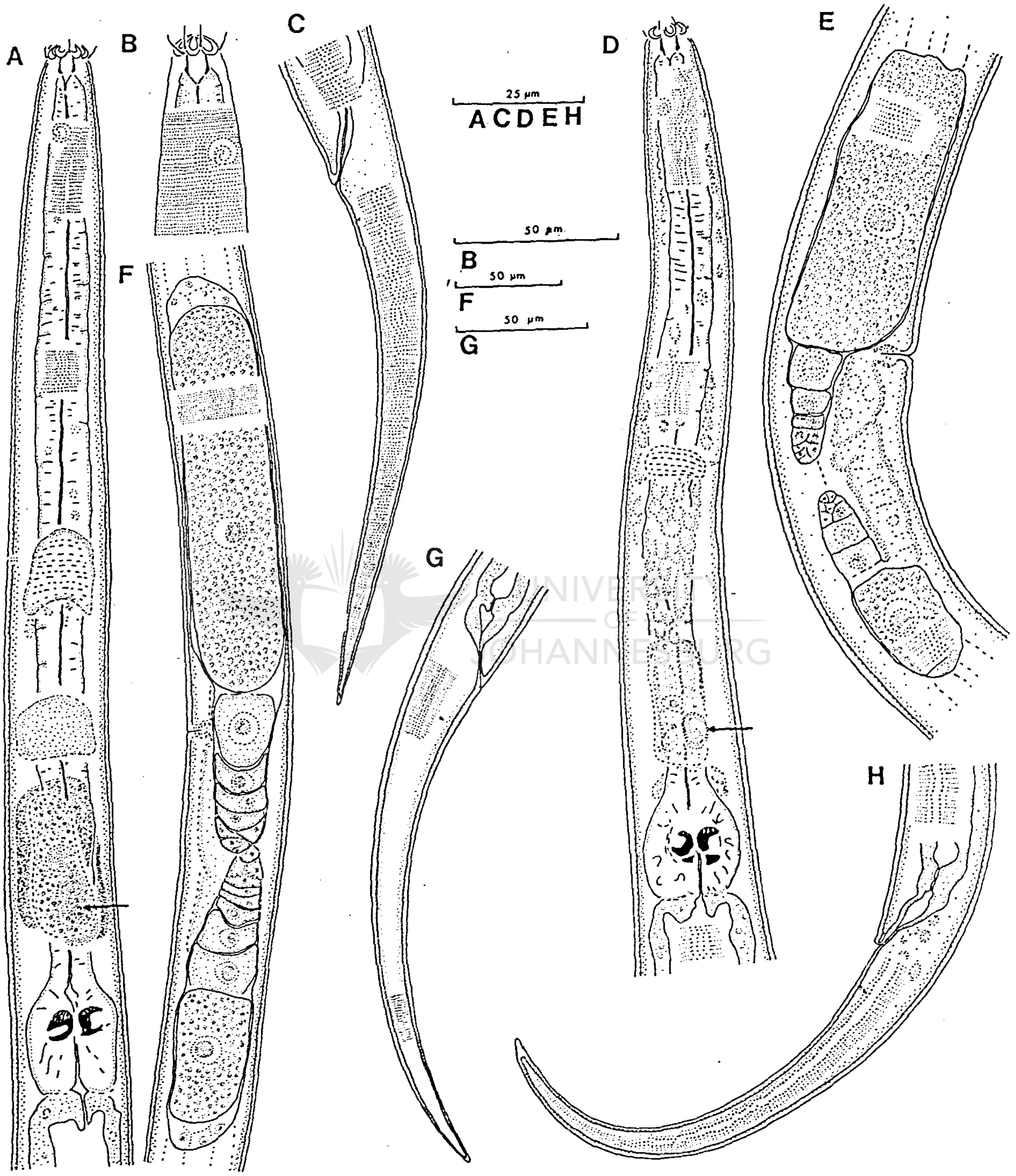

A
B
C
D
E
F
G
H
25 µm
ACDEH
50 µm
B
50 µm
F
50 µm
G

Fig. 2. Euteratocephalus palustris (de Man, 1880) Andrássy, 1958. A,B,C,E,F,G: Population from Kenya. A: Anterior region; B: Anterior region (external view); C: Mid-body region (external view) showing the absence of prominent punctations overlying the lateral field in this region; E: Detail of valves within basal bulb; F: Tail region, internal and external view; G: Mid-body region showing didelphic reproductive system; D,H,I: Population from Australia. D: Anterior region showing spiral organ (arrow); H: Tail; I: Mid-body region.

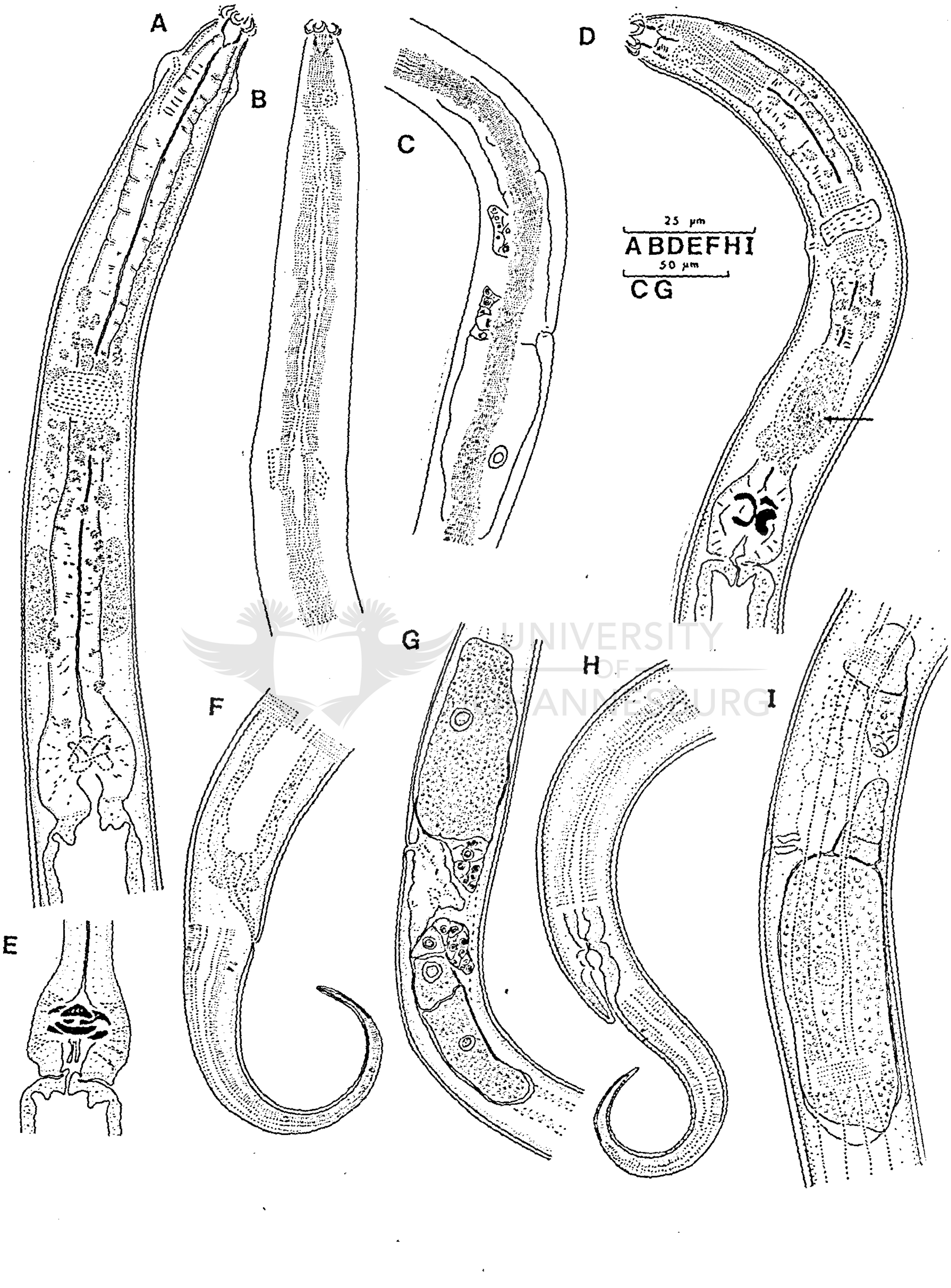

A
B
C
D
25 µm
ABDEFHI
50 µm
CG
E
F
G
H
I

Fig. 3. Euteratocephalus palustris (de Man, 1880) Andrássy, 1958. A,B,F: Population from Bolivia. A: Head; B: Anterior region showing excretory pore, spiral organ (arrow) and basal bulb with prominent valves; F: Tail. C,D,H: Population from Germany. C: Anterior region showing spiral organ (arrow); D: Mid-body region; H: Tail. E,G: Population from South Africa (originally described as E. capensis Heyns, 1977). E: Head; G: Mid-body region.

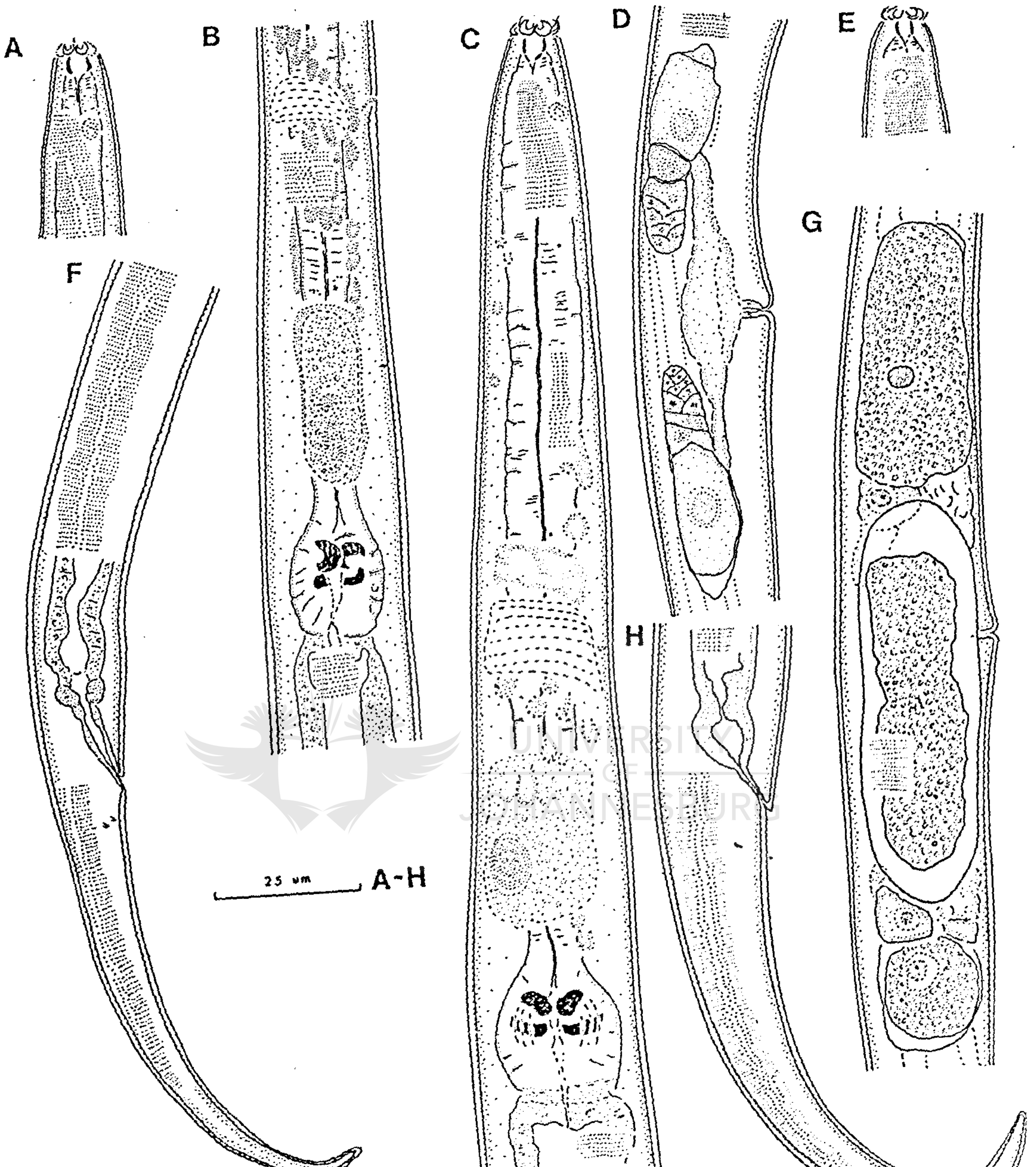

A
B
C
D
E
F
G
H
25 um
A-H

Fig. 4 A,B,F Euteratocephalus punctatus n.sp.; (population from Kenya): A: External view of body showing smooth area overlying lateral field; B: Anterior region showing spiral organ (arrow); C: Tail; F: Mid-body region. D,E,G,H Euteratocephalus spiraloides (Micoletxky, 1913) Heyns, 1977 (population from Bolivia): D: Region of nerve ring and basal bulb showing spiral organ (arrow); E: Mid-body region; G: Head; H: Anal region showing punctations overlying the lateral field.

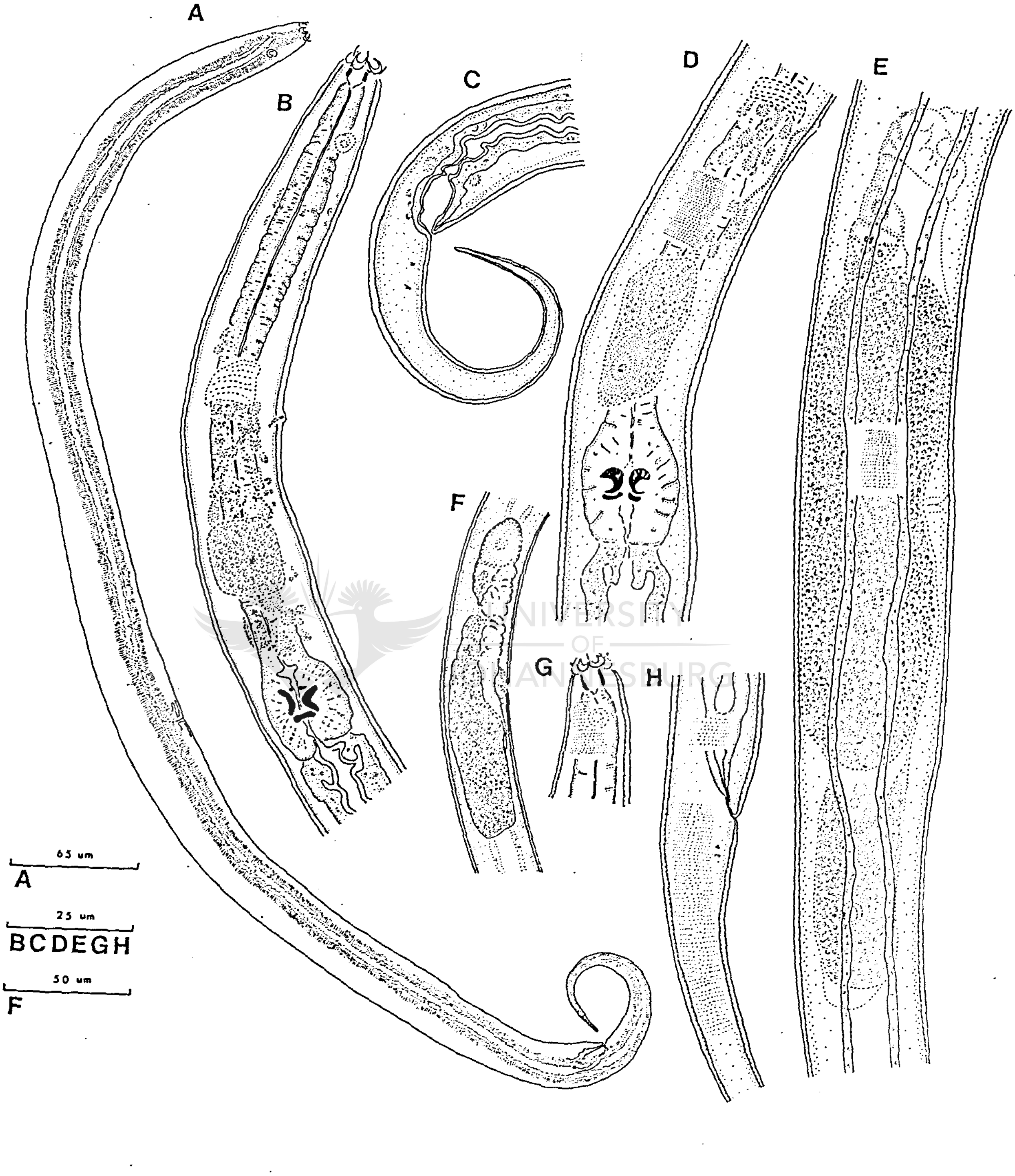

A
B
C
D
E
F
G
H
65 um
A
25 um
BCDEGH
50 um
F

Fig. 5 A,B,C,D Euteratocephalus punctatus n.sp (Kenyan population). A: Anterior region. Arrow indicates amphideal aperture (a.a.). Bar equals 8 um; B: External morphology of the head. Bar equals 1.3 um; C: Punctations (arrow) on subcuticle overlying the lateral field. Bar equals 5 um; D: External morphology of the head (o.l.s. - outer labial setum; c.s. = cephalic setum). Bar equals 1.3 um.

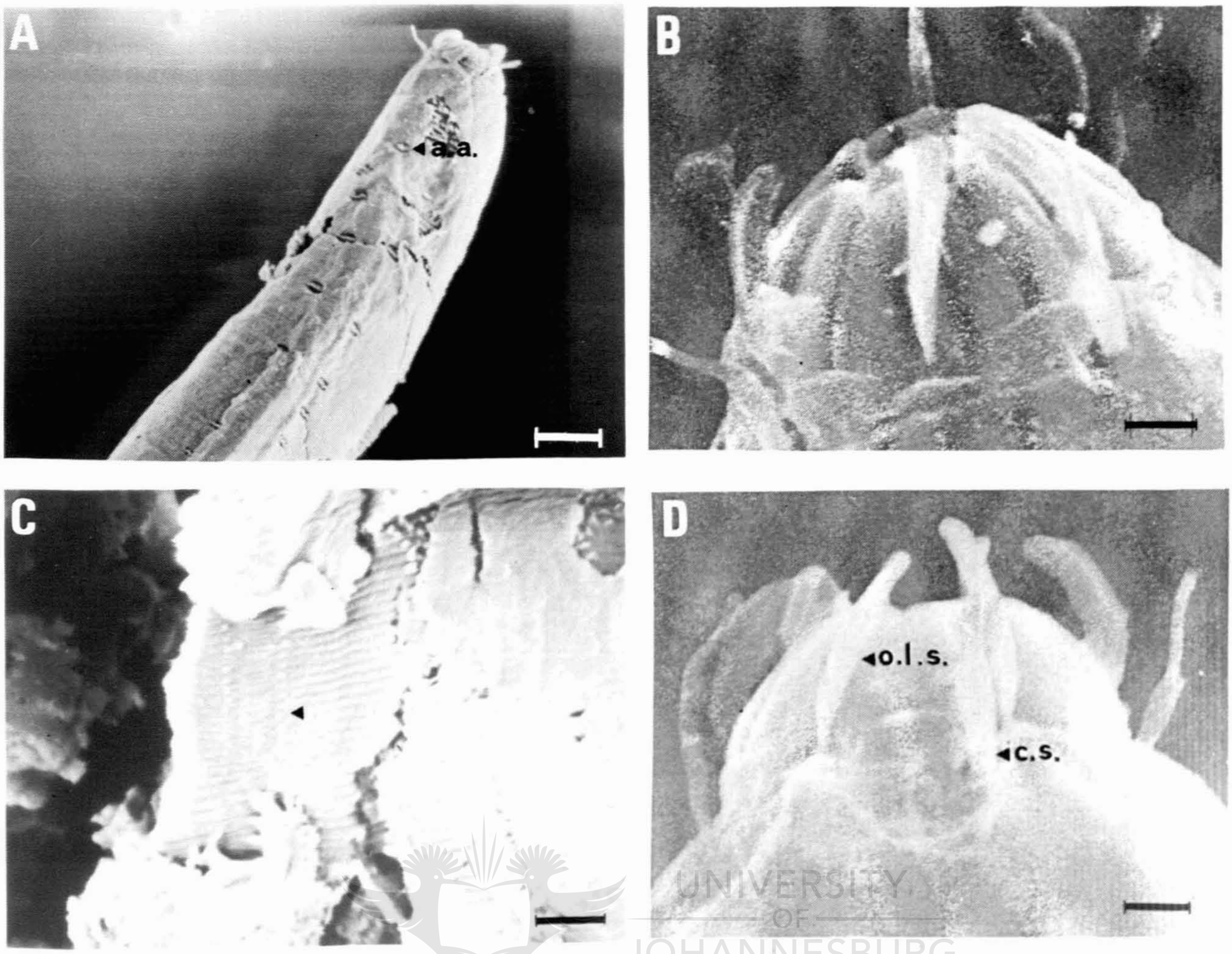
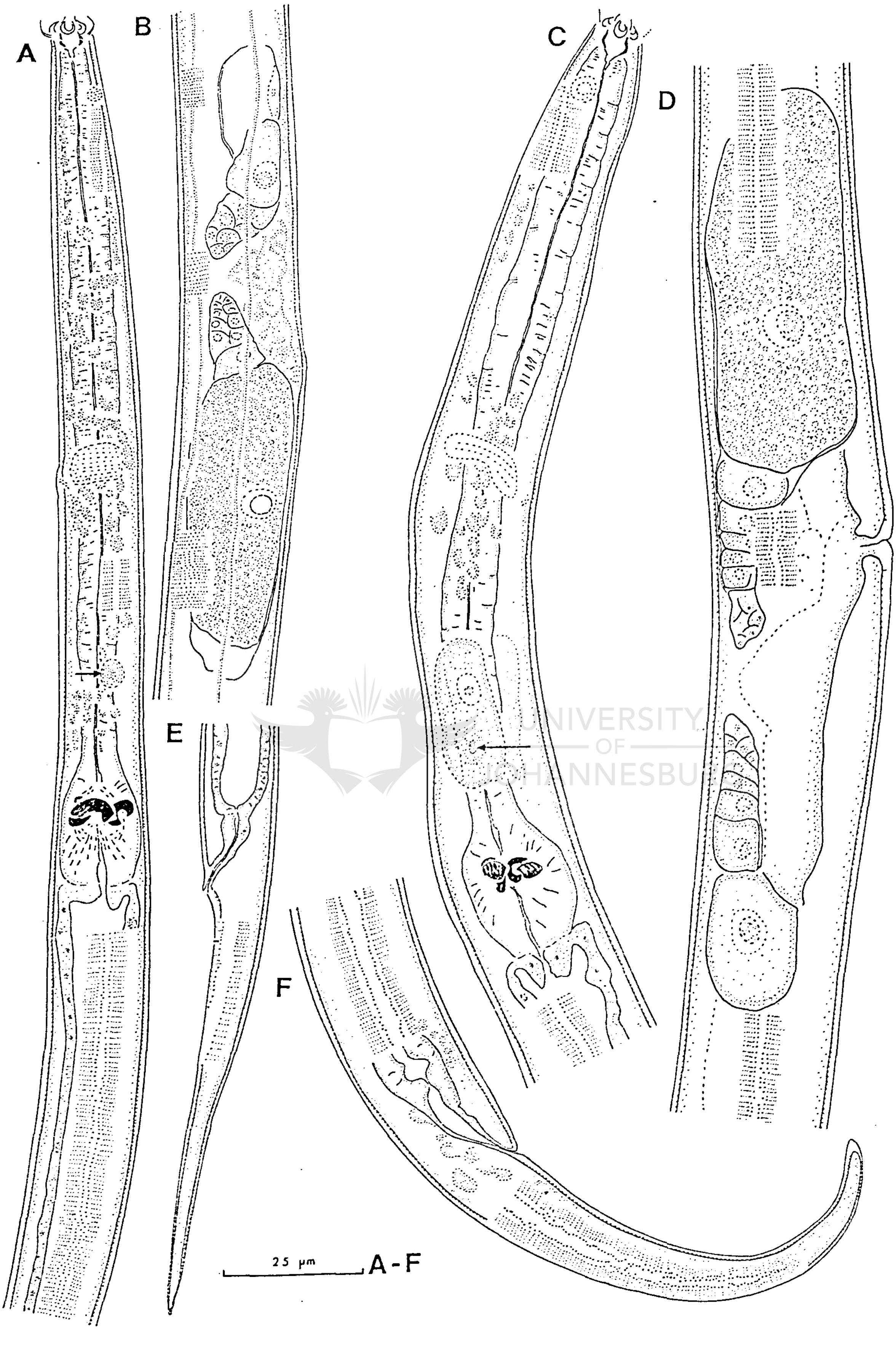
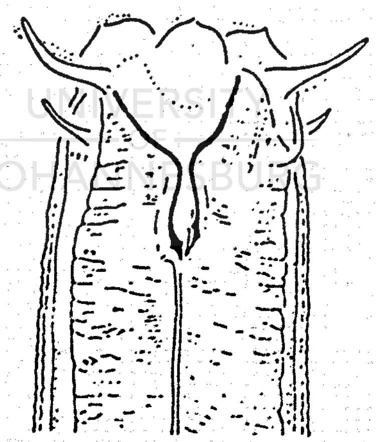

A
a.a.
B
C
D
o.l.s.
c.s.

Fig. 6. Euteratocephalus punctatus n.sp. A,B,E: Population from Brazil. A: Anterior region showing spiral organ (arrow); B: Mid-body region; E: Tail; C,D,F: Population from Bolivia. C: Anterior region showing spiral organ (arrow); D: Mid-body; F: Tail.


A
B
C
D
E
F
25 µm
A - F

CHAPTER 4



DESCRIPTION OF *TOBRILOIDES LOOFI* N.SP. FROM NATAL, SOUTH AFRICA (NEMATODA: ONCHULIDAE)

(Published in South African Journal of Zoology 25: 138 - 143)

ABSTRACT

Tobriloides loofi n.sp. has a huge cardia, 3 whorls of cephalic setae and an onchulid structure of the posterior oesophagus, which place it in the rare genus *Tobriloides* Loof, 1973. It differs mainly from the only other species in this genus, *Tobriloides choii* Loof, 1973, in its large size, the presence of males in *T. loofi* and the position of the vulva (midbody in *T. loofi* and more posterior in *T. choii*). This is the first description of a member of the genus *Tobriloides* from South Africa, as well as the first record of a new species within this genus in 16 years. Line drawings, light- and scanning electron micrographs are included in the text, as well as a short discussion of intergenus relationships of *Tobriloides*.

Uittreksel

Tobriloides loofi n.sp. word gekenmerk deur die groot kardia, drie kringe sefaliese setae en die onchuliede (gestratifiseerde) struktuur van die posterior gedeelte van die oesofagus. Hierdie kenmerke plaas *Tobriloides loofi* n.sp., tesame met die enigste ander spesie, *Tobriloides choii* Loof, 1973, in die seldsame genus *Tobriloides* Loof, 1973. Hierdie twee spesies verskil hoofsaaklik van mekaar op grond van die langer liggaam, teenwoordigheid van mannetjies en ekwatoriale ligging van die vulva in *T. loofi*, teenoor die kort liggaam, afwesigheid van mannetjies en die posterior ligging van die vulva in *T. choii*. Hierdie artikel verteenwoordig die eerste beskrywing van 'n spesie van *Tobriloides* uit Suid-Afrika, asook die eerste aanmelding in 16 jaar van 'n nuwe spesie in hierdie genus. Lyntekeninge, lig- en skandeerelektronmikrograwe is

ingesluit in die teks, asook 'n kort beskrywing van intergenusverwantskappe van Tobriloides.

INTRODUCTION

Several samples taken from moist soil under indigenous grasses and shrubs at Leisure Bay, Natal South Coast, South Africa, yielded specimens which seemed to represent a new species of *Tobrilus*. On closer examination the huge cardia, onchulid structure of the posterior part of the oesophagus and arrangement of cephalic setae, pointed to the little-known genus *Tobriloides* Loof, 1973, known only from a single species from Korea. This paper is only the second report of the genus *Tobriloides* and presents the first description of males in the genus.

MATERIALS AND METHODS

Specimens were killed by gentle heat, fixed in FAA, processed to glycerine by Thorne's slow method and mounted on permanent slides. Two paratypes, one female and one male, are deposited in the National Collection of Nematodes, Plant Protection Research Institute, Pretoria. All other mounts are deposited in the collection of the Department of Zoology of the Rand Afrikaans University. Specimens were prepared for scanning electron microscopy (SEM) (Swart & Heyns, 1987) and viewed with an ISI SS60 scanning electron microscope. Light microscope photographs were taken with a MC63 photomicrographic camera and differential interference contrast. Measurements and drawings were made with the aid of a Zeiss Standard 18 research microscope equipped with a drawing tube. The body and all curved structures were measured along the median line.

DESCRIPTION

Tobriloides loofi n.sp. (Figures 1A-Q, 2A-F, 3A-D; Table 1).

Female: Body cylindrical, tapering more posteriorly than anteriorly. Body width at mid-body about 1,6 times that of head width. Body curved ventrally when heat-relaxed but some specimens more irregular in posture. Body annules prominent, 1,5 - 2,5 µm wide. No lateral fields. A lateroventral and laterodorsal row of body setae on either side of body. Setae in each row about 35 µm apart, beginning about 88 µm from anterior end and ending in anal region. No setae observed on tail. One row of ventral setae present, about 7 in oesophageal region and again 7 to 9 in an area from 450 µm anterior of anus to anal region. A few dorsal setae also present, restricted to oesophageal region. Due to swelling of the cuticle during fixation, the body setae seem to be virtually inside the cuticle (Fig. 2F). They are however, clearly visible in SEM-micrographs.

Head truncate, continuous with body contour. Six large, well-developed lips surrounding the hexagonal oral opening. The incisures around the oral opening are not of equal depth - the ventral and subdorsal incisures being deeper than the dorsal and subventral ones (Fig. 1C, 2C). Each lip bears a single short labial setae (Fig. 2A). The second circlet of six long (15 µm) cephalic setae are situated posterior to the lips. The third whorl of four cephalic seta (about 6 µm long) occurs more posteriorly, 13 - 18 µm from anterior, almost at the level of the amphids.

The stoma consists of an anterior, funnel-shaped chamber, about 13,7 µm wide, and a narrower posterior part with two small teeth situated in the subventral walls about 30 µm from the anterior end (Fig. 1B & F). These teeth are both forwardly directed. The base of the posterior chamber of the stoma seem to have a tooth-like projection in its dorsal wall (Fig. 1B, D & G) which we interpret as a thickening of the metarhabdions before it fuses with the telorhabdions.

Amphid aperture crescent-shaped (Fig. 2D), situated about 17,5 - 20,0 μm from anterior end. Fovea not clearly seen but apparently funnel-shaped.

Oesophagus cylindroid, 504-555 μm long, enveloping the stoma. Posterior 1/3 with prominent onchulid structure (transverse muscle bands).

Nerve ring around anterior 23-32% of oesophagus, sometimes difficult to discern. Oesophagus well-developed but becoming narrower posteriorly where it fuses with the huge cardia (Fig. 1H& I). Cardia about 55-60 μm long, slightly overlapping the intestine (Fig. 1H) and containing up to 30 nuclei. Cardia lumen triradiate (Fig. 1L), less conspicuous than lumen of oesophagus. The walls of the cardia lumen thicken at the point where it joins the intestine (Fig. 1H&M). Some sort of valve may be present at this point as muscles seem to be attached onto the thickened walls of the lumen (Fig. 1M).

At the junction between the cardia and the oesophagus, two cell-bodies or glands can be seen in more or less lateral positions, 463-517 μm from anterior (Fig. 1H& I). These cells have a granular cytoplasm with what seem to be vacuoles. One, and in some individuals, two nuclei can be discerned within the cytoplasm (Fig. 1H & I). Up to five vague cells with a much more homogenous cytoplasm were also found surrounding the cardia (Fig. 1I). Oesophageal glands could not be seen.

Excretory duct and pore very difficult to see under light microscope (visible in only one individual) but seems to be slightly anterior to nerve ring. Excretory pore seen with SEM, small but well-defined (Fig. 2B).

Female reproductive system didelphic, amphidelphic. Vulva transverse, oval-shaped, with grooved sides (Fig. 2E). Vagina short, uterus well-developed, usually filled with sperm cells (Fig. 1K). Sperm cells large, about 13 µm x 10 µm, their surface covered by minute punctations (Fig. 1K & 2F). Oviduct short, consisting of a single row of 6-7 disc-shaped cells (Fig. 1K). The oviduct enters the ovary close to the germinal zone (Fig. 1K). Growth zone of ovary contains many well-demarcated oocytes in different stages of ripening. No eggs were present in female reproductive system.

Tail of female 176-208 µm long, tapering gradually towards the tip, ending in a spinneret (Fig. 1O). Tail contains three well-developed caudal glands, as well as about 8 coelomocytes.

The cuticle 3 - 3,5 µm thick, appearing in some sections to have a striated subcuticle (Fig. 1B & D, 2F, 3C) of which the striations coincide with the annulations on the outer surface.

Male: Description as for female, with the following differences: Body always curved ventrally when heat-relaxed. Posterior 1/3 of body curled into a loose or tight spiral (Fig. 1Q). Amphid apertures 16 - 21,5 µm from anterior end. Oesophagus length 487 - 553 µm. The two large glandular bodies on either side of junction between cardia and oesophagus 418- 506 µm from anterior. Tail length 153 - 175 µm, slightly shorter than that of female. About 5 coelomocytes observed in tail region.

Reproductive system diorchic, outstretched (Fig. 1A), consisting of two well-developed testes containing numerous spermatozoa (Fig. 1A & 3D) and a common spermioduct. Spermatozoa large with a club-like anterior part of 15 µm x 10-15 µm and a tapering posterior part, the length of which is uncertain.

Spermioduct wide and lateral to intestine. No muscular ejaculatory duct present. Spermioduct seems to merge with intestine about 20 µm anterior to anus (Fig. 1N).

About 6 ejaculatory glands can be recognised laterally on either side of the intestine (Fig. 1N). The ducts of these glands first run parallel to the intestine, then curve downwards to a more ventral position. and open into the spermioduct somewhere before the junction between rectum and spermioduct. The exact point of merging is obscured by the spicules and muscles in this area.

Eight, and in one male seven, supplements can be seen which are located midventrally at 31; 60; 95; 131; 163; 196; 229 and 251 µm anterior to the anus (Fig. 1N). Each supplement consists of a rounded section about 20µm long and 15 µm wide with deep transverse grooves (Fig. 3A & B). In the centre of this area there is a papillae-like structure surrounded by an elevated ring. In 3 of the 7 males the first supplement (S_1) was only 4 µm in length, whereas S_2 - S_8 were each 20 µm long. In the other 3 males, all supplements, (S_1 - S_8) were 20 µm in length (1 male had only 7 supplements all 20 µm long). The length of the supplements were taken across the rounded section of the supplement along the median line. Under the light microscope a small duct could be seen running inwards from the papilla to a small chamber (Fig. 1N & 3C).

Spicules well-developed, moderately ventrally curved, 45 - 54 µm long; lateral alae present; gubernaculum distinct, about 30 µm long. A weak muscular sheath, appearing as a faint ellipsoid ring, surrounds the proximal part of each spicule (Fig. 1N). The proximal part of each spicule also surrounded by a cell body which is probably part of the spicule-capsule (A. Coomans, personal communication 1989).

Holotype: Female on slide RAU 4139. Paratypes: 4 females on slides RAU 4134 and RAU 4139 (collection of RAU) and No 24730 (National Collection at N.I.P.B.) and 8 males on slides RAU 4135, RAU 4137, RAU 4139, RAU 4140 and RAU 4141) (Collection at RAU) and No 24730 (National Collection at P.P.R.I.).

Type locality and habitat: Next to Dolphin Street, Leisure Bay, Natal South Coast, South Africa. Found in moist soil under indigenous grasses, trees and shrubs. Collected by J. Heyns and M. Hutsebaut, September 1988.

Diagnosis

Tobriloides loofi n.sp. can be distinguished from Tobriloides choii Loof, 1973 by the following: The presence of quite a few males in T. loofi compared to the absence of males in T. choii; the longer female body length (T. loofi female: 2,91 - 3,24 mm compared to T. choii female 1,41 - 1,77 mm) and the midbody position of the vulva in T. loofi (V = 49,5 - 52,9%) compared to the more posterior position in T. choii (V = 56 - 62%). The tail length also differs: Tobriloides loofi has a shorter tail compared to body length (c= 14,26 - 17,44) against T. choii with a c-value of 7,6 - 9,1. The distal part of the tail in Tobriloides loofi is curved in one plain whereas that of T. choii is always bent sideways. When studying specimens of Tobriloides loofi n.sp., the authors were surprised to find only one gland cell on either side of the oesophago-cardiac junction, as Loof (1973) observed two pairs (four cells) in the same vicinity in T. choii. (Fortunately, the authors could examine specimens of T. choii and confirmed Loof's observation (Fig. 1E). In some individuals of T. loofi however, the two cells each have 2 nuclei in their cytoplasm (Fig. 1H & I) which may suggest a transitional stage between a 2-cell state and a 4-cell state.

Discussion:

The taxonomic position of Tobriloides is uncertain because of its similarities to the families Tobrilidae, Onchulidae and Prismatolaimidae (Tsalolikhin, 1983). Loof (1973) placed Tobriloides in the family Tripylidae Oerley, 1880, subfamily Tobrilinae De Coninck, 1965 because of its cylindrical oesophagus enveloping the stomatal cavity, presence of "cardiac glands", caudal glands and a spinneret and the shape and anterior location of the amphids. Tsalolikhin (1981) raised the subfamily Tobrilinae to family level. In a revision of this group Tsalolikhin

(1983) pointed out that Tobriloides has more characters in common with the Onchulidae Andrássy, 1963 than with Tobrilidae and transferred the genus to that family.

The new representative, Tobriloides loofi n.sp., adds to the knowledge about the genus, especially since it is the first time males have been found. Some features of the males are close to that of Kinonchulus sattleri Riemann, 1972, a member of the Onchulidae. They both possess a non-muscular seminal duct, common to all primitive nematodes (Riemann, 1972) and a muscular envelope around the proximal part of each spicule. The club-like spermatozoa with filamentous tails also link the two genera. All these characters place Tobriloides firmly in the Onchulidae but its resemblance to Tobrilidae (especially the presence of a spinneret and caudal glands) suggests its descent from an aquatic ancestor.

Acknowledgements.

Thanks are due to Prof. P.A.A. Loof (Landbouwhogeschool, Wageningen, Netherlands) for supplying slides of Tobriloides choii from Korea. Also to Prof. J.H. Swanepoel (Departement of Zoology, RAU) for kindly translating some of the Russian papers.

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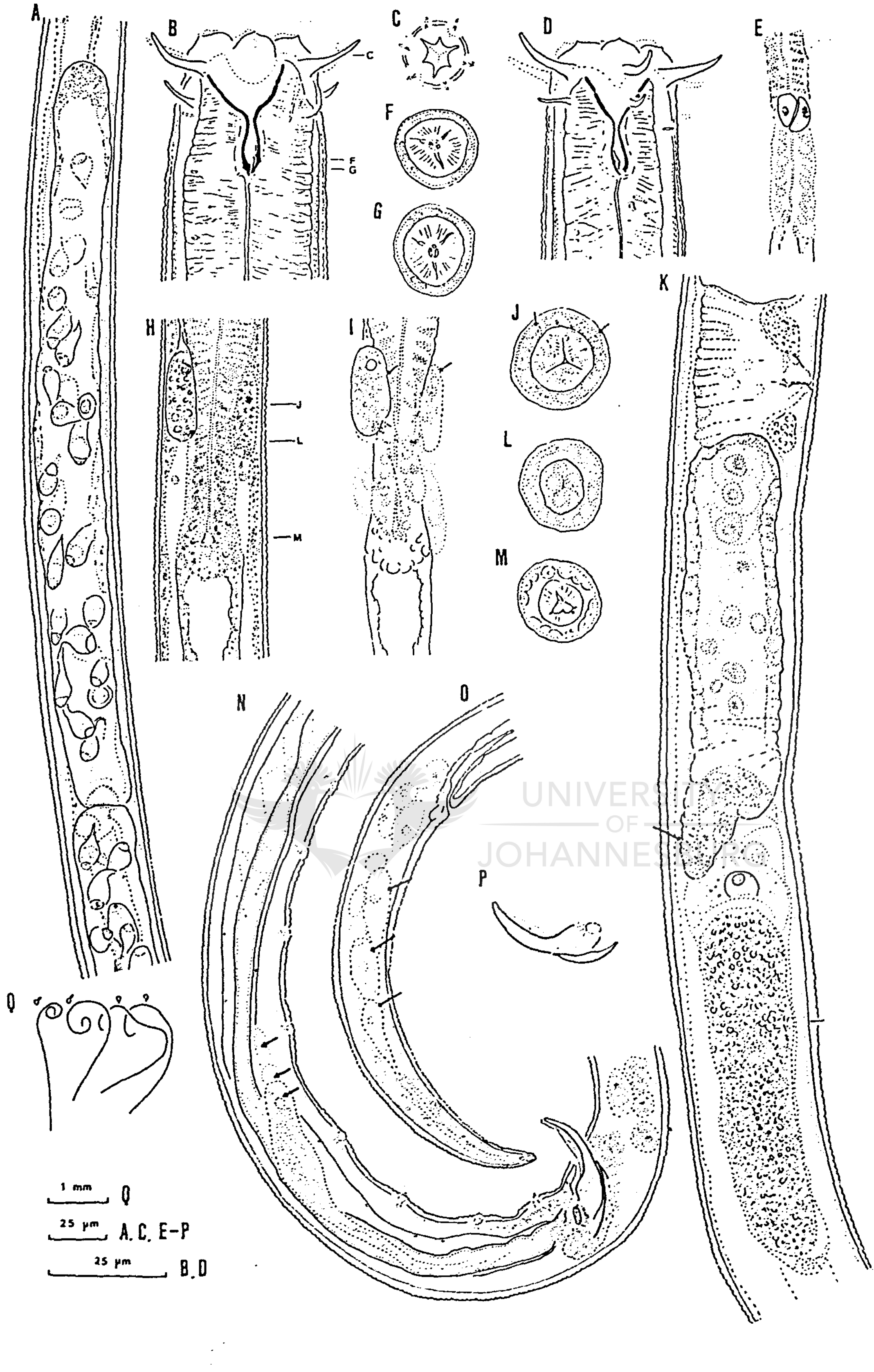
TABLE 1: MORPHOMETRICAL DATA OF TOBRILOIDES LOOFI N.SP.

	Holotype	Paratypes ♀ (n=3)	Standard deviation	Paratypes ♂ (n=8)	Standard deviation
L	3,0	3,0(2,9-3,2)	0,11	2,9(2,7-3,2)	0,19
a	50,9	57,5(50,9-72,1)	4,57	70,5(66,8-79,1)	4,19
b	5,5	5,8(5,5-6,1)	0,22	5,6(5,2-5,9)	0,23
c	16,2	15,0(14,3-17,4)	1,14	17,4(15,8-19,6)	1,34
c'	5,2	5,7(4,7-6,5)	0,73	4,3(2,9-4,8)	0,67
Tail length (µm)	187,5	192,5(176,3-207,5)	11,71	168,8(153,8-175,0)	8,38
Oesophagus length (µm)	555,5	529,6(503,9-555,5)	20,19	524,9(486,5-552,5)	28,62
Anterior-nerve ring (µm)	130,0	134,8(120,0-166,3)	16,10	130,0(123,8-150,0)	8,31
% Nerve ring	23,4	25,6(23,4-32,2)	3,75	25,6(23,0-30,8)	3,29
Head width (µm)	31,0	31,3(30,0-33,0)	1,03	31,5(30,0-34,0)	1,60
Stoma length (ant. & post. chambers) (µm)	11,0	11,8(8,0-13,0)	2,32	10,8(8,0-12,0)	1,41
Stoma width (µm)	15,0	13,7(7,5-17,0)	3,53	13,5(12,0-17,0)	1,69
Anterior - amphid aperture (µm)	18,5	19,0(17,5-20,0)	0,95	19,4(16,0-21,5)	2,01
Annule width (µm)	2,0	1,9(1,5-2,0)	0,20	2,0(1,5-2,5)	0,34
Cuticle width (µm)	3,1	3,4(3,0-3,5)	0,21	3,0(2,8-3,5)	0,21
T (%)				42,9(39,9-53,7)	4,64
Spiculum length (µm)				54,1(45,0-63,0)	6,09
Gubernaculum length (µm)				30,3(23,0-36,0)	4,29
V%	52,3	51,2(49,5-52,9)	1,35		
OV_1%	41,0	39,8(37,4-41,9)	1,77		
OV_2%	64,1	64,5(61,4-67,4)	2,57		

Figure 1 A-D: Tobriloides loofi n.sp. A: Anterior testes with spermatozoa, B: Lateral view of female head, C: Face view, showing hexagonal oral opening with longer ventral and subdorsal incisures, D: Lateral view of male head, E: Junction between oesophagus and cardia showing two of the four cardiac glands in Tobriloides choii Loof, 1973 F-Q: Tobriloides loofi n.sp., F: Cross section at level of two subventral teeth, G: Cross section at level of base of second stomatal chamber, H: Junction between oesophagus and cardia showing glandular cells on each side of junction, I: Junction between oesophagus and cardia of the same individual, showing the glands and cells in this region. Arrows indicate glandular bodies on each side of junction, J: Cross section through body just anterior to junction between oesophagus and cardia. Arrows indicate glandular bodies, K: Posterior branch of female genital track. Arrow indicates oviduct, L: Cross section through cardia showing triradial lumen, M: Cross section through base of cardia showing thickened walls of lumen which is triradiate at this point, N: Male tail region. Arrows indicate ejaculatory glands, O: Female tail. Arrow indicate caudal glands (O), P: Spicules and gubernaculum, Q: Relaxed body posture.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25 µm B, D

Figure 2 A-F: SEM- and light micrographs of Tobriloides loofi n.sp. A: Lateral view of male head, B: Male cuticle in oesophageal region showing the excretory pore (arrow), a ventral papilla and a lateroventral one, C: Face view of female head, showing anterior chamber of stoma, D: Close-up of female head with amphid aperture, long cephalic seta and more posteriorly situated short cephalic seta, E: Vulva, F: Sperm cells (arrows a & b) in female genital tract and retracted body setae (arrows c & d) Bar equals 10 μm.

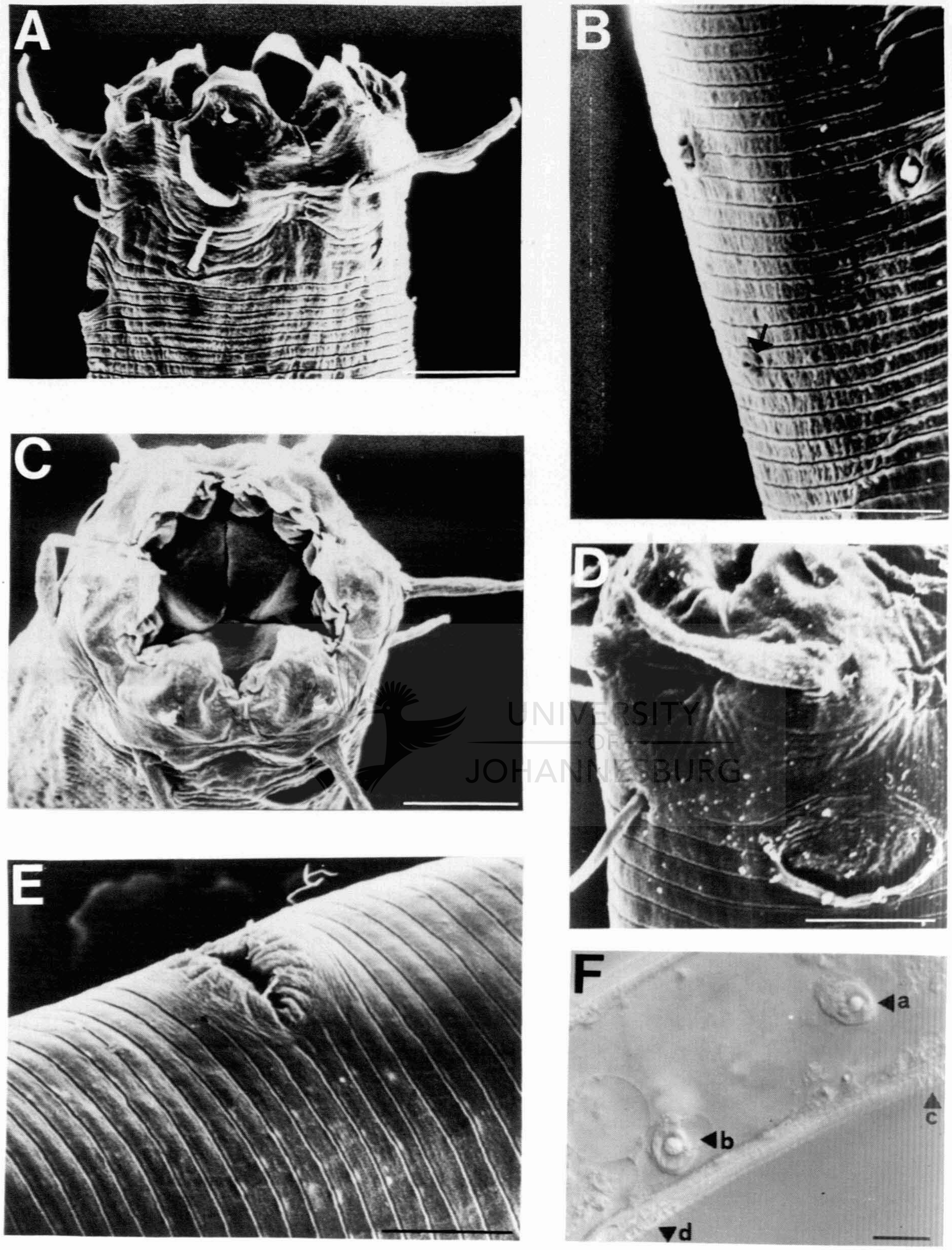
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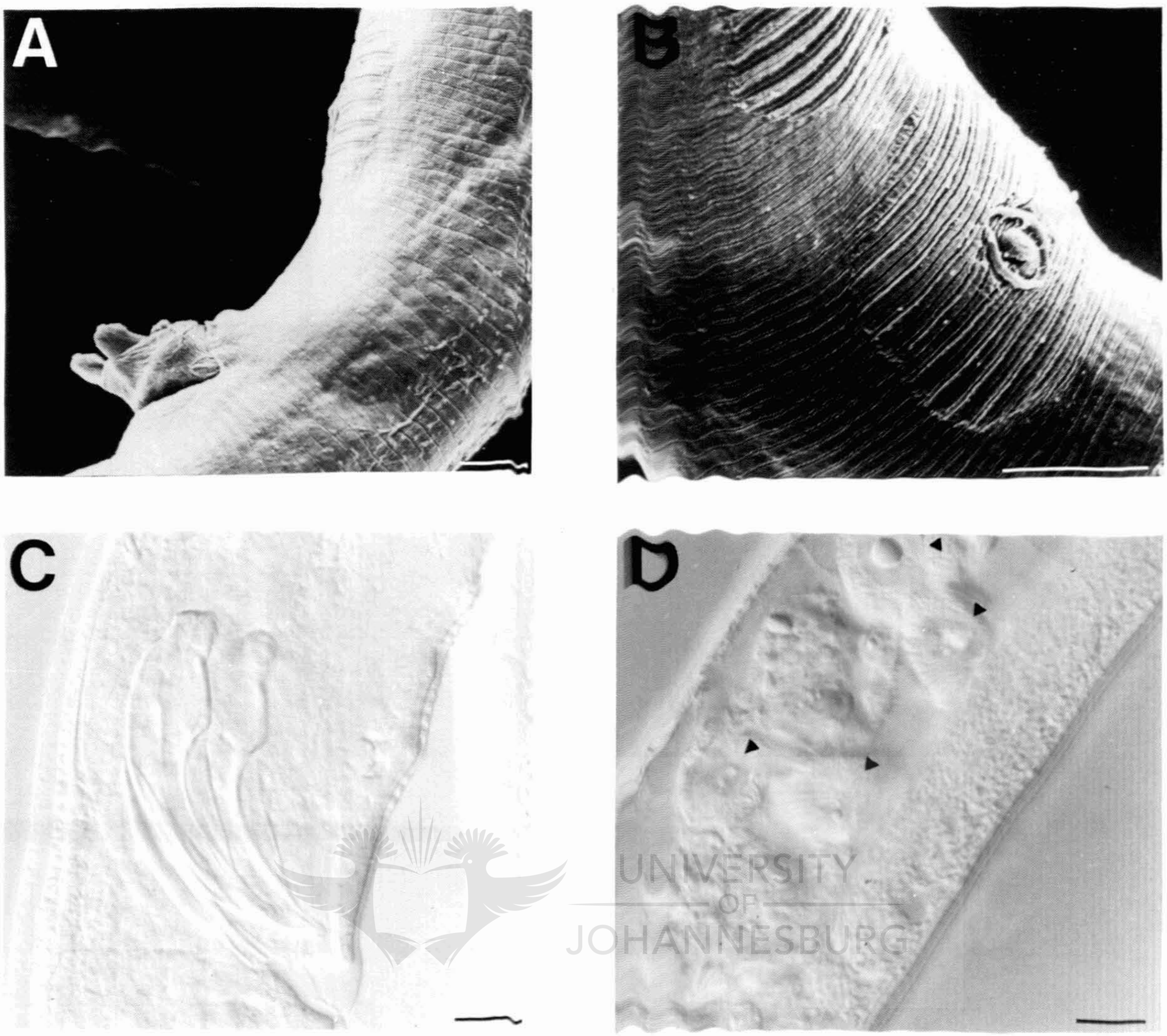
Figure 3 A-D: SEM- and light micrographs of Tobriloides loofi n.sp. A: Male tail showing partly protruding spicules and the eighth supplement (S_8), B: Subventral view of supplement, C: Spicules, gubernaculum and alae, D: Spermatozoa in testes (arrows). Bar equals 10 µm.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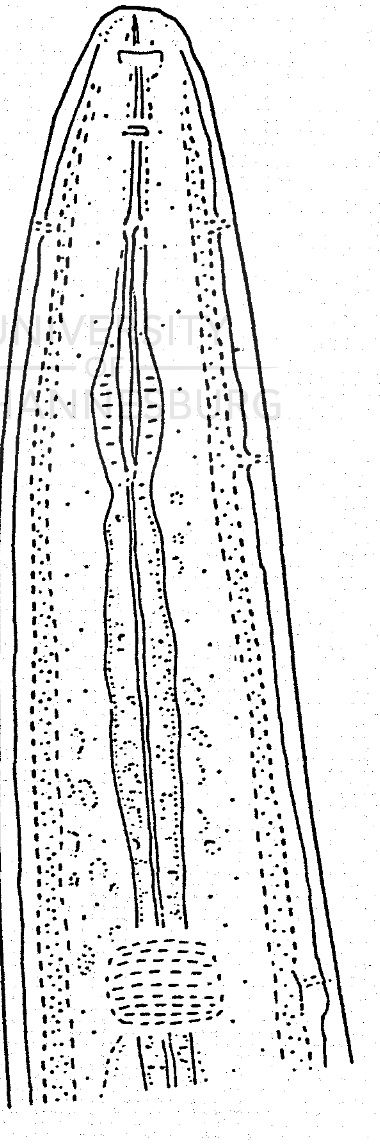
CHAPTER 5



LENONCHIUM FIMBRICAUDATUM N.SP. FROM SOUTH AFRICA, WITH A KEY TO THE SPECIES OF LENONCHIUM (NEMATODA: NORDIIDAE)

(Accepted by Revue de Nematologie)

SUMMARY

Lenonchium fimbricaudatum n.sp. was collected from wet sand on the banks of the Sabie River in the Kruger National Park, South Africa. It resembles L. longidens (Furstenberg & Heyns, 1966) Jairajpuri, 1967 but differs from that species mainly in the possession of a hyaline tail tip, occupying 18-30% of the tail length. Furthermore, the tail and spicules are shorter in L. fimbricaudatum than in L. longidens and the nerve ring is more anteriorly situated. Some interesting morphological features of L. fimbricaudatum, i.e. the structure of the supplements and the tail tip with four mucro's are presented on scanning electron micrographs. As a result of the present study, we regard L. denticaudatum (Imamura, 1931) Siddiqi, 1969 as a valid species. A dichotomous key is given for the five recognised species of Lenonchium.

The genus Lenonchium was proposed by Siddiqi (1965) to receive a new species of Dorylaimidae, Lenonchium oryzae, which has a linear odontostyle with small aperture, a rod-like odontophore with slightly swollen base, filiform tails in both sexes, a transverse vulva and an amphidelphic reproductive system. Jairajpuri (1967) gave additional data on L. oryzae, and transferred Dorylaimoides longidens Furstenberg & Heyns, 1966 to Lenonchium. Dorylaimus denticaudatus Imamura, 1931 was later also transferred to this genus by Siddiqi (1969). Ahmad and Jairajpuri (1988) emended the diagnosis of the genus Lenonchium and added a new species, L. macrodorum. They regarded L. denticaudatum as a species inquirenda and considered its position in Lenonchium as doubtful. We tend to disagree with this viewpoint as some unusual features described by Imamura (1931) - i.a. caudal glands and "sharp points" on the tail terminus - agree well with features found in the new species herein described as Lenonchium fimbricaudatum n.sp. The genus Lenonchium is therefore represented at the moment by five species: L. oryzae, L. longidens, L. macrodorum, L. denticaudatum and L. fimbricaudatum.

MATERIALS AND METHODS

Specimens were extracted by a modified sieving-sedimentation method (Loubser, 1985), killed by gentle heat, fixed in FAA, processed into glycerine by Thorne's slow method and mounted on Cobb double coverslip slides. All descriptions, measurements and drawings were made with the aid of a Zeiss Standard 18 research microscope equipped with a drawing tube. The body and all curved structures were measured along the median line.

For SEM study mounted nematodes were slowly hydrated to distilled water and post-fixed in 1% osmium tetroxide. They were critical point dried, sputter-coated with gold (30 nm) and viewed with an ISI SS 60 scanning electronmicroscope at 6 kV.

Lenonchium fimbricaudatum n.sp.

(Figs 1&2)

Measurements: See Table 1

Description

Female: Body moderately curved ventrad when heat-relaxed. Cuticle finely striated, subcuticle slightly loose. Cuticle with minute radial striae, becoming more prominent towards tail region. Radial dots prominent, arranged in fine rows in anterior region, becoming randomly spaced posteriorly. Lip region slightly offset unevenly striated. Cephalic papillae morphologically different from labial papillae. Lip region about 6.6 μm high and 14.4 μm wide. Amphid aperture a wide slit (Fig. 2A), amphid stirrup-shaped, no supportive structures evident. Odontostyle 29-33.5 μm long, slightly curved with small aperture. Odontophore equal to or slightly less than odontostyle in length (28-33 μm). Guiding ring single appears double when stylet is extended, about 17.6 μm from anterior end. Oesophagus with swelling around posterior half of odontophore, followed by a constriction, then widening again. Basal expansion occupying about 60% of total oesophagus length. The approximate positions of the oesophageal gland nuclei as percentage of oesophagus length, are the following: DN=43%; S_1N_1=58%; S_1N_2=64%; S_2N_1 & S_2N_2=82%. Gland orifices obscure. Nerve ring about 134 μm or 3 body widths from anterior end. Hemizonid-like structure opposite nerve ring on ventral side of body. Small tube in same vicinity (vestigial excretory pore or extremely prominent ventral pore?). Cardia about 21 μm long and 15 μm wide. Prerectum about 115 μm or three anal body widths long. Rectum about one anal body width long, obscured by five to six rectal glands. Tail approximately 200 μm or five anal body widths long, filiform, striated to very tip. Tail tip appearing jagged under light microscope, but in SEM micrograph seen to have four fingerlike projections or mucro's. Glandular cells, resembling caudal glands, present in tail. Ducts of these glands terminating halfway down tail length. Hyaline portion in tail tip occupying about 18-30% of tail length. Reproductive system didelphic, amphidelphic. Uterus well-developed, usually packed with spermatozoa, especially in proximal half. Sphincter six to eight body widths from vulva. Ovaries well-developed, reflexed for about nine body widths. From one to four eggs in each uterus, eggs 104-142 μm in length with shell 4-7 μm thick. Vulva seems to be a short, longitudinal oval aperture with heavily sclerotized lips and with small punctations covering the sclerotized region.

Male. Description as for female with the following differences. Ventral curvature of body more pronounced in posterior half, especially in tail region. Tail 147,5-198 µm long, shorter than that of female. Hyaline tip of tail occupying 25-30% of tail length. Three to five coelomocytes observed in tail region. Prerectum about 124 µm or three anal body widths long.

Reproductive system diorchic, one testis anteriorly directed, the other reflexed backwards with common spermoduct. Spermoduct lateral to intestine, no muscular ejaculatory duct present. Spermoduct seems to merge with the intestine about 46 µm anterior to cloacal opening. Three to four rectal glands can be observed in the region of the spicules The course of their ducts could not be followed in any of the specimens. The body musculature in the anal region is very pronounced in all males and many organs are obscured by them. Three pairs of prominent caudal papillae observed on either side of tail posterior of anus. The three pairs of papillae are respectively at the following approximate distances posterior of cloacal opening: first subventral pair at 6-15 µm; second subventral pair at 25-34 µm and subdorsal pair at 31-54 µm. One subventral papilla present on either side just anterior of cloacal opening. Supplements consisting of an adanal pair, 4-10 µm anterior of cloacal opening, and 21-26 ventromedian ones in a contiguous series ending 45-55 µm from the adanal pair. Adanal pair consisting of simple, elevated papillae while the ventromedian supplements each consists of an elevated papilla surrounded by longitudinal ridges. The supplements are situated in a differentiated area with prominent striae extending from the anteriormost supplement, beyond the cloacal opening for 20% of the tail length. This area may be the same as that mentioned by Imamura (1931) in L. denticaudatus as "a peculiar postanal ventromedian cuticular rib, which is about as long as the central thickening of the spicules." Spicules 69-76 µm long, well developed. Lateral guiding pieces also well-developed, 11-20 µm long.

Type habitat and locality:

Wet sand on banks of Sabie River, about 10 km from Skukuza Rest Camp, under Phragmites species. Collected on 3 September 1989 by J. Heyns in the Kruger National Park, Transvaal, South Africa.

Type specimens:

Holotype: Female on slide RAU 5101

Paratypes: 18 females on slides RAU 5101 - RAU 5106, RAU 5109, RAU 5110 and RAU 5112 and three males on slides RAU 5110 and RAU 5111. In addition specimens are deposited in the nematode collections of the following institutions: two females, one male and one juvenile on slide no. 24769 in the National Collection of the Plant Protection Research Institute (P.P.R.I.), Pretoria; one female, two males and two juveniles in the Instituut voor Dierkunde, Rijksuniversiteit Gent, Ghent, Belgium; two females, one male and one juvenile in the Muséum National d'Histoire Naturelle, Paris, France and two females and two males in the USDA, Beltsville, Md, U.S.A.

Diagnosis

Lenonchium fimbricaudatum has a linear odontostyle, a rod-like odontophore with a slightly swollen base and a long, filiform tail with hyaline portion and four fingerlike projections or mucro's on the tail tip. The vulva is a longitudinal opening with sclerotized lips.

Relationships

L. fimbricaudatum n.sp. is very similar to L. longidens, from which it differs in the following:

Female. Presence of a hyaline tail tip in L. fimbricaudatum against the absence of a hyaline tail tip in L. longidens, the shorter tail length (L. fimbricaudatum: 170-237 µm, compared to L. longidens: 230-270 µm and the slightly shorter body length (L. fimbricaudatum: 4,9-6,7 mm, compared to L. longidens: 5,4-7,1 mm) L. fimbricaudatum can be distinguished from L. oryzae, L. macrodorum and L. denticaudatum mainly by its great body length (L. fimbricaudatum: 4,8-6,7 mm against L. oryzae: 2,2-2,9 mm, L. macrodorum: 2,5-3,3 mm and L. denticaudatum: 2,5-3,7 mm) and the presence of a large hyaline area in the tail tip.

Male. Presence of a hyaline tail tip in L. fimbricaudatum against no hyaline tail tip in L. longidens, the shorter tail length (L. fimbricaudatum: 147,5-198 µm compared to L. longidens: about 240 µm); the spiculum length (L. fimbricaudatum: 69-76 µm against L. longidens: 82-97 um) and the slightly shorter body length (L. fimbricaudatum: 4,8-6,5 mm against L. longidens: 5,3-7,1 mm).

Discussion.

Examination of type specimens of L. longidens revealed the presence of four pairs of caudal papillae in the male tail region, situated from 3 µm anterior of cloacal opening to about 54 µm posterior of the opening. It is interesting to note that what Furstenberg and Heyns(1966) interpreted as broken tails, are in fact the four projections of the tail tip, giving the impression under the light microscope, of a jagged broken-off tip. The occurrence of a longitudinal vulva is apparently limited to the South

African species - L. longidens and L. fimbricaudatum, being transverse in the other Lenonchium species.

L. fimbricaudatum is a typical member of the genus Lenonchium, bringing the number of species in this genus to five. The use of the SEM in this study lead to a better understanding of some features of Lenonchium, especially the morphology of the head, the cuticle, the supplements and the tail tip. This is also the first time that rectal and possibly caudal glands are described in this genus.

KEY TO SPECIES OF LENONCHIUM

1. Body length greater than 4 mm, vulva longitudinal 2

   Body length less than 4 mm, vulva transverse 3

2. Tail with hyaline tip .... L. fimbricaudatum n.sp.

   Tail without hyaline tip .... L. longidens

3. Number of ventromedian supplements seventeen or less

   .... L. denticaudatum

   Number of ventromedian supplements more than seventeen

   4

4. Odontostyle length less than 20 µm .... L. oryzae

   Odontostyle length more than 30 µm .... L. macrodorum

Acknowledgements

We thank Dr Esther van den Berg of the P.P.R.I. for kindly supplying slides of L. longidens, and the RAU and FRD for financial support.

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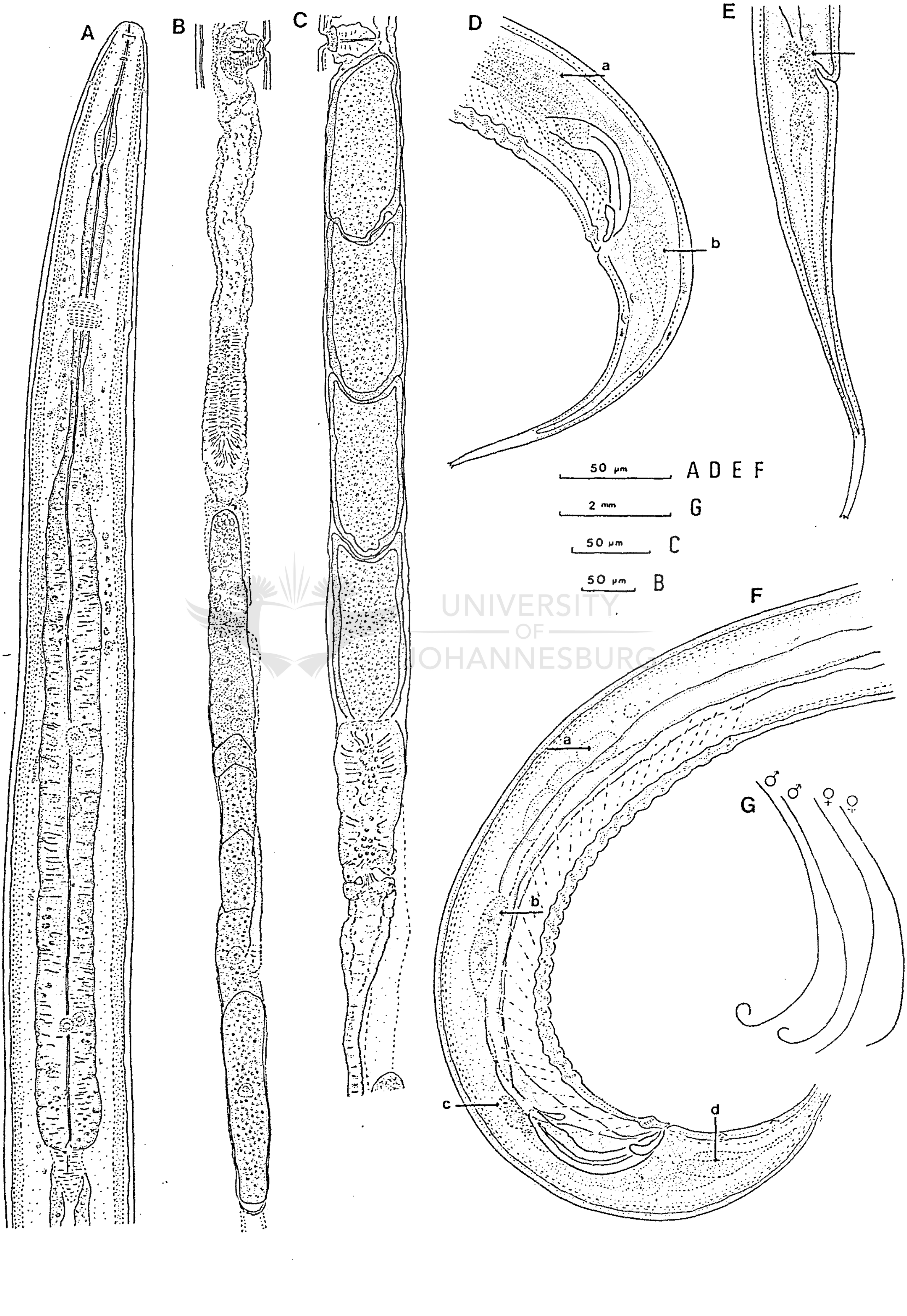
TABLE 1. Morphometrical data of *Lenonchium fimbricaudatum* n.sp.

	Holotype	Paratypes (♀) n = 25	Standard Deviation	Paratypes (♂) n = 8	Standard Deviation
L (mm)	6.2	5.6(4.9-6.7)	0.5	5.7(4.8-6.5)	0.6
a	103.4	91.1(76.5-111.3)	9.1	91.3(79.3-105.9)	10.6
b	11.8	11.1(9.6-12,.)	0.8	11.6(9.5-13)	1.2
c	28	28.4(23.7-36.6)	3.2	34.2(24-38.3)	4.7
c'	5.6	5(3.9-6.1)	0.6	3.8(3.3-4.4)	0.4
Tail length (µm)	220	200(170-237)	20.7	169.6(147.5-198)	20.2
Oesophagus length (µm)	520	502.5(445-555)	26.3	496,(430-555)	49.2
Anterior to nerve ring (µm)	140	134.6(123-141.5)	8.5	140.8(133-147)	5.1
Head height (µm)	6.0	6.6(6-8)	0.7	6.4(5.5-7)	0.6
Head width (µm)	14	14.4(13.1-16)	0.7	14.6(13-16)	1.0
Odontostyle length (µm)	30	30.9(29-33.5)	1.0	31.1(30-34)	1.6
Odontophore length (µm)	30	30.4(28-33)	1.8	29.9(26.5-32)	1.6
Total spear length (µm)	60.5	61.3(54.5-64.5)	2.0	60.5(56.5-64)	2.3
Anterior to guide ring (µm)	19	17.6(15.8-19.5)	1.1	17.6(17-20)	1.1
Thickness of cuticle (µm)	2.4	2.3(2-3)	0.4	2.2(2-2.5)	0.2
V(%)	48.4	45.0(41.8-48.1)	1.9		
OV_1 (%)	28.6	25.2(20.1-32.4)	3.9		
OV_2 (%)	61.7	63.8(56.2-69.3)	4.0		
T (%)				34.4(30.8-37.8)	2.6
Spiculum length (µm)				73.6(69-76)	2.4
Lateral guiding piece length (µm)				16.4(11.5-20.5)	2.6
Number of supplements				24(21-26)	1.7

Fig. 1. Lenonchium fimbricaudatum n.sp. A: Anterior region of female; B Female reproductive system; C. Female reproductive system with four eggs; D: Male tail. (arrow a indicates rectal glands; arrow b indicates cells resembling caudal glands); E: Female tail (arrow indicates rectal glands); F. Male tail (arrow a and b indicate coelomocytes; arrow c, rectal glands; arrow d, cells resembling caudal glands); G: Heat-relaxed body posture.



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50 μm A D E F
2 mm G
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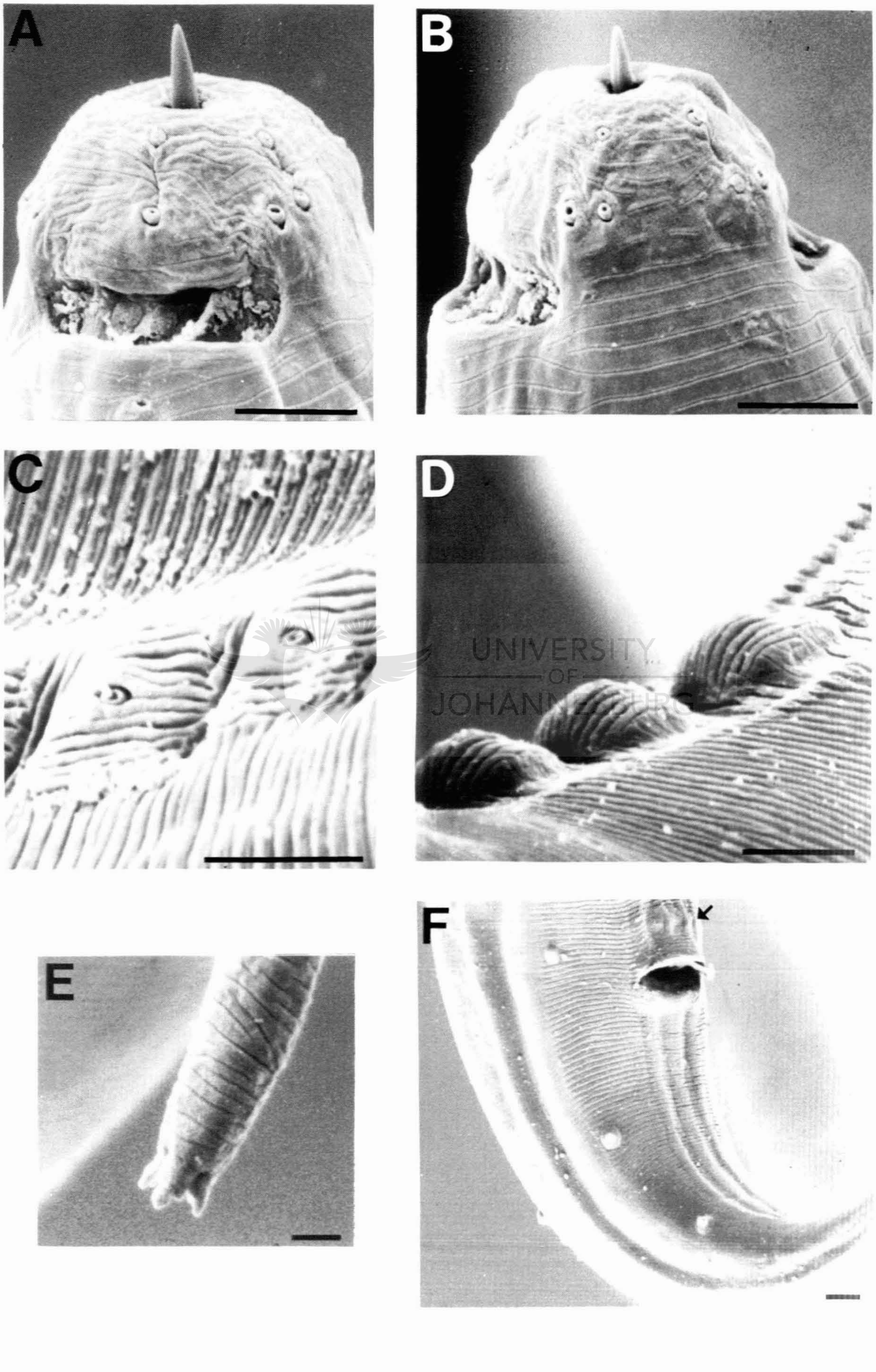
♂ ♂ ♀ ♀

Fig. 2. Lenonchium fimbricaudatum n.sp. A: Head of female (lateral view); B: Head of male (ventral view) C: Supplements; D: Supplements (side view) E: Tail tip of female; F: Male tail - region of cloacal opening (arrow indicates adanal pair of supplements). (Bar equivalents: A,B,F = 5 µm; C,D = 1 µm; E=0.1 µm).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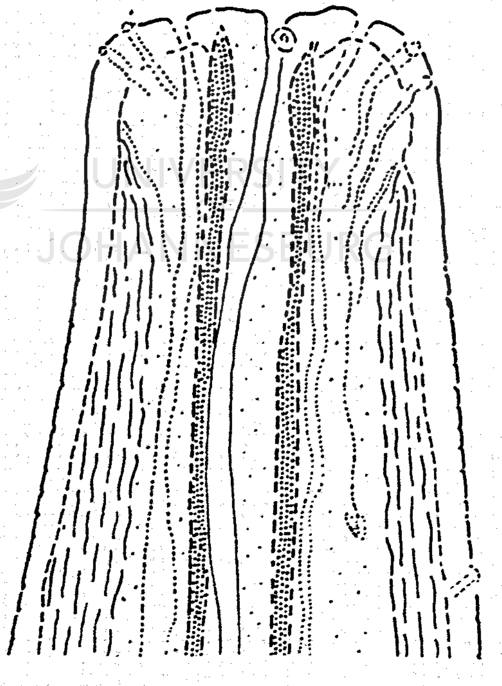
CHAPTER 6



ON THE MORPHOLOGY AND TAXONOMY OF ISOLAIMIUM COBB, 1920 WITH SPECIAL REFERENCE TO I. AFRICANUM HOGEWIND & HEYNS, 1967

(Submitted to Phytophylactica)

ABSTRACT

Key words: Isolaimida, morphology, taxonomy.

The anterior region of specimens of I. africanum was stained and sectioned to examine taxonomically important characters such as the number and position of oesophageal glands and the origin of the six inner labial receptors. In view of the results the authors retained Isolaimida as a separate order, probably most closely related to the order Dorylaimida. Numerous specimens of Isolaimium from several localities throughout southern Africa, as well as the type material of Hogewind & Heyns' three species: I. incus, I. africanum and I. multistriatum, were examined. The results lead the authors to synonymize I. multistriatum with I. africanum but retain I. incus as a valid species.

Uittreksel

DIE MORFOLOGIE EN TAKSONOMIE VAN ISOLAIMIUM COBB, 1920 MET SPESIALE VERWYSING NA I. AFRICANUM HOGEWIND & HEYNS, 1967

Die studie behels die sny en kleuring van die anterior gedeelte van eksemplare van I. africanum, waardeur die aantal en posisie van die esofageale kliere en die oorsprong van die ses binneste labiale sinsorgane bepaal is. Hierdie organe is taksonomies belangrik en die resultate van die studie het die skrywers oortuig dat Isolaimida as 'n aparte orde behou moet word wat morfologies baie met die orde Dorylaimida ooreenstem. Verskeie eksemplare van die genus Isolaimium is vervolgens vanaf elf lokaliteite in suidelike Afrika bestudeer. Die tipe-eksemplare van die

spesies wat deur Hogewind en Heyns (1967) beskryf is (I. africanum, I. multistriatum en I. incus) is ook met mekaar en met die bogenoemde eksemplare vergelyk waarna I. multistriatum met I. africanum gesinonimiseer is. I. incus is egter as aparte spesie behou.

INTRODUCTION

The genus Isolaimium Cobb, 1920 displays some exceptional morphological features which have, over the years, intrigued several nematode taxonomists (Filipjev & Schuurmans Stekhoven, 1941; T. Goodey, 1951; Timm, 1961, 1969; Andrássy, 1962; De Coninck, 1965; Théodorides, 1965; Yeates, 1967; Hogewind & Heyns, 1967 and Bernard, 1984). In spite of the interest shown in this genus, interpretation of some aspects of its morphology, notably the number and position of oesophageal glands, the symmetry of the oesophago-intestinal valve and the nature and origin of the inner labial receptors (represented by tubes), have remained obscure. Largely as a result of this lack of knowledge and the consequent uncertainty about its phylogenetic relationship, the systematic placing of the genus remained uncertain. Consequently, it has been associated with a variety of groups by successive authors (e.g. an aberrant genus of the Mermithidae; the Axonolaimidae; the superfamily Dorylaimoidea; the genus Cryptonchus (Ironidae); and the Bathyodontidae).

Several Isolaimium species have been described from South Africa (Hogewind & Heyns, 1967), but subsequently, more recent collections have casted doubt on the validity of two of these, viz. I. africanum and I. multistriatum, since many intermediate forms were found.

In view of the above, it was decided to (1) make a more detailed study of the morphology of one population of I. africanum, (2) compare this with other available populations of *I. africanum* and *I. multistriatum* and resolve the uncertainty about the identity of these two species, (3) redefine the species and (4) assess the taxonomic position of the genus.

MATERIALS AND METHODS

Specimens were killed by gentle heat, fixed in FAA, processed to glycerine by Thorne's slow method and mounted on permanent slides. Slide numbers refer either to the nematode collection at the Department of Zoology, RAU or the National Collection of Nematodes at the Plant Protection Research Institute, Pretoria. Light microscope photographs were taken with a MC 63 photomicrographic camera and differential interference contrast. Measurements and drawings were made with the aid of a Zeiss Standard 18 research microscope equipped with a drawing tube. The body and all curved structures were measured along the median line. The length of the oesophagus was taken from the anterior end of the body to the base of the oesophagus. The position of the nerve ring was also measured from the anterior end.

Specimens intended for staining and sectioning, were collected at Rustenburg, Transvaal. These were killed by gentle heat, fixed in FAA and dehydrated in the following ethanol series: 70%, 80%, 90%, 96% and 2 x 100%. Two specimens (both males) were embedded in Transmit Resin embedding medium and polymerized at 70 °C for 18 hours. Sections of 3 µm thickness were cut dry with the use of a AS 500 semi-thin microtome and placed on clean glass slides. Prior to staining, the resin was removed by immersing the slides for three minutes in a saturated solution of NaOH in absolute ethanol. Staining was accomplished with the standard azocarmine-azan (Aniline blue-Orange G) method (Romeis, 1968). The rest of the specimens were stained with Light Green S.F. (CI. 42095) colouring agent, counterstained in aqueous eosin, processed to glycerine by Thorne's slow method and mounted on permanent slides.

MORPHOLOGY OF ISOLAIMIUM AFRICANUM

A population of what appeared to be typical *I. africanum* was available at an easily accessible site at Rustenburg, Transvaal, thus it was decided to use this material for the morphological study. Ample material was also available for a study of the different juvenile stages.

Structure of head and anterior part of alimentary canal

The structure of the stoma, oesophagus and cardia is difficult to explain and can be better understood by comparing the *in toto* view with a series of cross sections in Figs. 1 & 2.

The oral opening is rounded (see also Fig. 1A & B of Heyns & Swart, 1988). The cylindrical stoma has a wide, triradiate lumen with strongly sclerotized walls. The lumen of the stoma becomes narrower and the sclerotization thinner where it joins the oesophageal lumen (Fig. 1G). The walls of the oesophageal lumen are thickened in the region of mergence with the stoma (Fig. 3D). The oesophageal lumen is minute in size but the sides of the radii are strongly sclerotized, converging distally. The radial muscles of the oesophagus are concentered, being attached to the thickened lining of the lumen. The oesophago-intestinal valve (cardia) appears to consist of 12-16 cells, is dorso-ventrally symmetrical and the lumen is not sclerotized. In the sectioned specimens seven oesophageal glands could be seen with their openings on the same levels as their nuclei. The position of the gland nuclei and openings are as follows, from anterior to posterior, expressed as a percentage of the oesophageal length: S_1O = 79%; D_1O = 82%; S_2O = 86%; S_3O = 87,5%; D_2O = 92%; S_4O = 94% and D_3O = 97%.

Seven oesophageal gland nuclei were also observed in one fourth stage juvenile (whole mount), but in all other adults only six openings and 3-4 nuclei could be seen (Fig. 3B). A possible explanation for this may be the orientation of a specimen which may obscure some of the openings and render them difficult or impossible to observe. The positions of the oesophageal gland openings and nuclei in stained <u>in toto</u> mounted specimens (male and female; n = 12) are as follows: S_1O = 82-87%; D_1O = 87-89%; S_2O = 89-93%; S_3O = 90-94%; D_2O = 97% and S_4O = 96-98%.

The stoma and anterior part of the oesophagus are surrounded by six prominent, cuticularized tubes (Fig. 1 A-J & Fig. 2B-K), which begin as six circular openings around the mouth opening. The six tubes run posteriad, parallel to the stoma and the first part of the oesophagus to join nerve cells (ganglia?) at about 100 µm from the anterior end, confirming their sensory nature. Six outer labial papillae occur in the usual position on the six amalgamated lips, with four cephalic papillae slightly more posterior. A small tubule leads from each papilla to each of the six tubes surrounding the stoma, but whether they actually merge with them, is not certain (Figs 1C & 2C). An amphid aperture and tubule can be seen at 12-15 µm from the anterior end.

<u>Cuticle</u>

The cuticle of <u>I. africanum</u> was reported to be adorned by punctations, transverse striae towards the anterior end and longitudinal lines over most parts of the body (Hogewind & Heyns, 1967 and Heyns & Swart, 1988). The present study revealed that the transverse striae are preceded by punctations starting at about 17 µm from the anterior end and that these become arranged in transverse lines at 20-25 µm from anterior. At about mid-stoma level these punctations become re-aligned in longitudinal rows

(Fig. 3E - specimen from Venda from the 1988-study of Heyns & Swart), with the cuticle separating the rows becoming more and more prominent until only the cuticular ridges are visible at midbody. The visibility of the punctations (which still exist between the ridges) varies from specimen to specimen, apparently depending on whether or not they are gravid. A peculiar feature found in specimens in the present study, is the lateral cuticular thickening overlying the lateral chords (Fig. 1D-L & 2D-T). These longitudinal lateral swellings start at about 20 µm from the anterior end, but their extent is unfortunately not known since sectioning was discontinued at mid-body. It is uncertain whether these paired lateral thickenings of the cuticle are homologous with the lateral alae commonly found in ascarids and chromadorids (Chitwood & Chitwood, 1974).

<u>Somatic musculature</u>

In Fig. 2F it can be seen that the somatic musculature is polymyarian, coelomyarian.

<u>Juvenile stages</u>

Four juvenile stages could be distinguished within this population:

<u>J1</u>: one specimen (Fig. 4A-D).

Measurements: L = 1,72 mm; a = 41; b = 8,2; c = 44,1; c' = 1,3; tail length = 39 µm.

This juvenile presented a peculiar feature. A heart-shaped amphidial chamber was observed, with a pore-like aperture near its middle (Fig. 3A). No similar chamber was seen in any of the other juvenile stages, nor in adults. Laterally, just posterior of the widest contour of the head, a pair of peculiar slit-like cuticular structures can be seen (Fig. 4B). The tail is also interesting since it has a 11 µm long fingerlike terminal projection (Fig. 4C). The transverse striae on the cuticle are very prominent throughout the body except over the lateral chords and the tail, where longitudinal lines are visible. A definite lateral field can be observed in this specimen. Two cells and one in the process of division could be seen within the genital primordium.

J2: two specimens (Fig. 4E).

Measurements: L = 1,9 - 2,3 mm; a = 47,5 - 49,4; b = 9,2 - 10,2; c = 52,3 - 53,1; c' = 1,2 - 1,3; tail length = 35 - 44 µm; number of longitudinal lines on cuticle at mid-body = 88 - 96.

Head and sense organs developed as in adult. Longitudinal lines prominent, stretching from about level of mid-stoma to tail tip. Tail longer than that of average adult, conical. Genital primordium consists of two parts, each with a genital cell. About 7 - 10 somatic cells could be discerned.

J3: seven specimens (3 females, probably 4 males) (Fig. 4F).

Measurements: L = 2,7 - 3,4 mm; a = 51,9 - 69,4; b = 10,7 -14,3; c = 62,9 - 93,9; c' = 1,1 - 1,2; tail length = 35 - 57,5 µm; number of longitudinal cuticular lines at mid-body = 72 - 128.

Head and tail developed as in adults. Tail on average relatively longer than in adults. Cuticular lines and punctations developed as in adults. Number of longitudinal lines very variable. Genital primordium elongated and differentiated into two branches. In two females a few cells could be seen approximately in the position where the future vagina will be formed.

J4: two specimens (females) (Fig. 4G).

Measurements: L = 2,8 - 2,9; a = 53,1 - 57; b = 11,7 - 11,9; c = 72,5 - 79,7; c' = 1 - 1,1; tail length = 36 - 40 µm. Number of longitudinal cuticular lines at mid-body = 80 - 88.

Except for the developmental stage of the reproductive system, morphology is the same as that of adult females.

The two branches of the genital tract well-developed and small ovaria already reflexed. Vagina already developing.

I. africanum and *I. multistriatum*

When Hogewind & Heyns (1967) described *I. africanum* and *I. multistriatum*, they distinguished between the two species on the basis of the number of longitudinal striae ("about 80" in *I. africanum* against "at least 120" in *I. multistriatum*); the differently shaped tail (convex-conoid in *I. africanum* against "more pointed" in *I. multistriatum*) and the shape of the lip region ("slightly offset" in *I. africanum* and "not offset" in *I. multistriatum*). The validity of these two species will be discussed later.

EXAMINATION OF SEVERAL POPULATIONS PROVISIONALLY IDENTIFIED AS *I. AFRICANUM* OR *I. MULTISTRIATUM**:

1. Population from Mont-aux-Sources, Natal, South Africa

   (1 ♀ , Table 1)

   Slide number: RAU 1923. Collected on 15/10/84 by J. Heyns.

   In all its characters this single specimen corresponds well with *I. africanum*.

2. Population from Mbabane, Swaziland (2j)

   Slide number: RAU 1086. Collected in November 1984 by J. Heyns and M. Luc.

   Measurements: L = 3,4 - 3,5 mm; a = 77,5 - 79,5; b = 13,1 - 13,5; c = 87,5 - 88,9; c' = 1,13 - 1,1 ; Number of longitudinal lines at midbody = 88.

   These two juveniles (J4) correspond closely with *I. africanum* in measurements and general morphology.

* Populations are compared with the original descriptions of *I. africanum* and *I. multistriatum*.

3. Population from Pigg's Peak, Swaziland (3 ♀ , 9 ♂; Table 1 & 2)

Slide numbers: RAU 1044-1049; 1055-1057; 1086; 1595 & 1603.

Collected in November 1984 by J. Heyns and M. Luc.

Females: All morphometrical data correspond well with that of I. africanum except the number of longitudinal lines at midbody (100 - 104 against ± 80). The heads of these females varies from offset to barely offset.

Males: The number of longitudinal lines at mid-body differs from that of I. africanum (80 - 100 against ± 80). The spicules of one male are very long (68 µm against 52 - 61 µm in I. africanum). All other data corresponds well with that of I. africanum.

4. Population from Ndumu Game Reserve, Natal, South Africa (1 ♀ ; Table 1).

Slide number: RAU 3781. Collected on 9/12/87 by M. Hutsebaut.

All data correspond well with that of I. africanum except the following: The tail is shorter in relation to body length (c = 121,3 against c = 56 - 106); the number of longitudinal lines at midbody is higher (96 against ± 80) and the head is slightly more affset than that depicted for I. africanum.

5. Population from Underberg, Natal, South Africa (1 ♂; Table 1)

Slide number: RAU 667. Collected in March 1981 by R.H.G. Harris.

This single male specimen agrees quite well with I. africanum except for the smaller body (L = 3,2 mm vs 3,9 - 5,7 mm) and larger number of longitudinal lines at midbody (104 vs about 80).

6. Population from Rustenburg, Transvaal, South Africa

(n = 2 ♀ , 6 ♂ (2 sectioned); 12 j); Table 1 & 2; Figs. 1, 2, 3 and 4. Slide numbers: RAU 2410, RAU 3629 and RAU 6069-6073.

Collections made on 18/5/85 by J. Heyns and again on 18/7/89 by J. Heyns and A. Coomans.

The morphology and morphometrical data of the Rustenburg specimens agree well with that of the original description of I. africanum except for the following: The females are slightly shorter (L = 3,4 - 3,7 mm against L = 3,9 - 5,7 mm) and the number of cuticular longitudinal lines at midbody of both males and females is also higher (72 - 98 lines against ± 80). The transverse striae formed by the cuticular punctations are prominent in the anterior part of the body only, where it sometimes overlaps with the longitudinal lines to form rectangular blocks. Hogewind & Heyns (1967) reported transverse striae to be present over the entire body of I. africanum. The same pattern could be seen in some specimens, expecially adult females. Hogewind & Heyns (1967) also stressed that the transverse striae occur on the outer surface of the cuticle. In the present study we found that the punctations forming the transverse striae often seem to be beneath the outer cuticle due to the prominence of the longitudinal ridges giving a recessed appearance to the punctations and thus also to the transverse striae. Another slight deviation from the description of I. africanum is the lip region which is not always as distinctly offset. This feature varies appreciably within the population. Since it is not regarded as an important diagnostic character, we do not hesitate to identify this population as I. africanum.

7. Population from Sandwich Bay, Namibia (1 ♀ , 1 ♂; Table 1)

Slide numbers: RAU 2409 and RAU 2410. Collected on 26/7/83 by J. Heyns.

Female: All morphometrical data corresponds well with that of I.

africanum except the following: The number of longitudinal striae at midbody is significantly higher viz 112 against ± 80, and the body is slightly shorter (3,8 mm against 3,9 - 5,7 mm). The head is expanded, clearly set off from the rest of the body, in agreement with I. africanum.

Male: The body is shorter than that of I. africanum (3,4 mm against 3,6 - 5,9 mm) and the number of longitudinal lines at midbody is higher (100 against ± 80). Other morphometrical data corresponds very well with that of I. africanum.

8. Population from Stormsrivier, Cape Province

(3 ♀, 3 ♂; Table 1 & 2)

Slide numbers: RAU 3672, 3674, 3675, 3681, 3682 and 3683.

Collected on 24/10/85 by J. Heyns and A. Coomans.

Females: The head width varies between 22 µm - 25 µm with a corresponding neck width of 17,5 - 21,5 µm, resulting in an expanded, clearly offset head in some specimens and a slightly offset head in others. The morphometrical data correspond well to that of I. africanum, but differ in the following: The number of longitudinal lines at mid-body (120 - 136 against ± 80) and a slightly shorter body (L = 3,5 - 3,6 mm against L = 3,9 - 5,7 mm). These specimens differ from I. multistriatum only in the shorter body (L = 3,5 - 3,6 mm against L = 4,1 - 5,2 mm).

Males: These specimens are very near I. africanum, but differ in the following: The number of longitudinal lines at midbody (96 - 128 against ± 80); the short body of one male (L = 3,5 mm against L = 3,6 - 5,9 mm) and the short spicules (47 - 52 µm against 52 - 61 µm). The number of longitudinal lines at midbody of one male is the same as that of the females of I. multistriatum (128 against 120 or more), but the bodies of all males are shorter (3,5 - 3,8 mm) than that given for the females of I. multistriatum (4,1 - 5,2 mm). No males were described for I. multistriatum.

9. Population from Hluhluwe, Natal, South Africa
(1 ♀, 3 ♂; Table 1)

Slide number: RAU 5777. Collected in July 1990 by E. van den Berg.

Female: This specimen is near I. africanum in all morphometrical data but differs from it in the following: The body is very large (L = 6,4 mm against L = 3,9 - 5,7 mm in I. africanum) and the number of longitudinal lines at midbody is much higher (200 against ± 80 in I. africanum. This number is even much higher than in I. multistriatum (more than 120 longitudinal lines at midbody).

Males: The morphometrical data of these specimens are close to that of I. africanum, but differ from it in the following: The body is longer than in I. africanum (L = 6,1 - 7 mm against L = 3,6 - 5,9 mm) and one (the longest) specimen has eight supplements against the 2 - 6 in I. africanum. The number of longitudinal lines at midbody is also higher in these males than in those of I. africanum (152 - 176 against ± 80).

10. Population from Lake St. Lucia, Natal, South Africa
(1 ♀; 1 ♂; Table 1)

Slide number: RAU 5781. Collected on 14/7/90 by A. Botha.

Female: Body length is less than in I. africanum (3,2 mm vs 3,9 - 5,7 mm) and the number of longitudinal lines at midbody is much higher (136 against about 80). As far as the latter feature is concerned, it corresponds well with *I. multistriatum* (120 or more lines), but the body is much shorter than that given for *I. multistriatum* (L = 3,2 mm vs 4,1 - 5,2 mm). The b-value (13,1) for this female does not correspond with that of either *I. africanum* (b = 14 -23) or *I. multistriatum* (b = 14 - 19). In body size this female corresponds with the females of the Underberg- and Mtubatuba populations.

Male: As in the case of the female, the number of longitudinal lines (120) corresponds with *I. multistriatum*, while head shape, body length, etc. agree with *I. africanum*. It should be stressed however, that it was found during this study that in most populations there is a difference in the number of lines between males and females (see Table 1), and that the description of *I. multistriatum* was based on females only.

11. Population from Thabazimbi, Transvaal, South Africa
(2 ♀ , 2 ♂; Table 1 and 2)

Slide numbers: P.P.R.I. 9670 and 9671. Collected on 28/3/69 by E. van den Berg and D. Argo. These specimens differ much among themselves.

Females. One female is relatively more slender than *I. africanum* (a = 97 against a = 49 - 91) and the number of longitudinal lines is higher in both females (96 and 112 against ± 80 in *I. africanum*).

Males: The body of one male is relatively thinner than in *I. africanum* (a = 115,5 against a = 58 - 93). The relative length of the oesophagus of the other male is slightly less than that of *I. africanum* (b = 23,1 against a = 14 - 21). The number of longitudinal lines at midbody of both males is also higher than in *I. africanum* (96 against ± 80).

All other morphological features and data correspond quite well with *I. africanum*.

12. Population from Mtubatuba, Natal, South Africa

(1 ♀ ; Table 1)

Slide number RAU 1908. Collected on 31/5/85 by J. Heyns and P.J.F. Jacobs.

The morphometrical data of this specimen corresponds well with that of I. africanum, but the well offset head and small body corresponds to that of I. incus (L = 3,2mm against L = 3 - 3,7mm in I. incus). The post-equatorial position of the vulva (59%) does not correspond with that of I. africanum (V = 48 - 53%) and for I. incus only males are known. At present we decided to regard this specimen as an undescribed species.

Because of the variation found among specimens within the same population, and the frequent occurrence of populations with specimens with intermediate features or features corresponding to either I. africanum or I. multistriatum, we decided to re-examine the type specimens of both these species.

I. africanum Hogewind & Heyns, 1967 (Table 2):

Females: As in original description, except that there is considerable variarion in head shape (from offset to slightly offset to confluent), tail form (rounded to slightly conoid) and number of longitudinal striae at mid-body (88 - 120).

Males: Morphometrical data correspond well to that of the original description, but as in the female there is variation in head form (from slightly offset to confluent) and number of longitudinal striae at mid-body (76 - 100).

I. multistriatum Hogewind & Heyns, 1967 (Table 2).

The morphometrical data as given in the original description are accurate but variation occurs in head form (slightly offset to not offset), tail form (conical to slightly elongated-rounded) and number of longitudinal striae at mid-body (small variation: 120 - 124).

The type specimens of I. incus were also studied and all morphometrical data were found to correspond well to that of the original description. The extremely offset head, and small number of longitudinal lines set it apart from all other species.

CONCLUSION

Comparing the specimens from the different localities, the following becomes apparent: Males have on average less longitudinal lines at mid-body than females. Some morphological features are also quite variable within populations, for instance the head form (Fig. 5), the number of longitudinal lines on the cuticle at mid-body, arrangement of punctations on the cuticle and tail form (Table 2). The study of the juveniles from Rustenburgkloof also showed great variation in cuticular features within one population.

The re-examination of the type specimens of I. africanum and I. multistriatum showed the same variability as that found in the various populations studied (See also Table 2). The morphometrical data of I. africanum also overlap with those of I. multistriatum to a great extent (see also Hogewind & Heyns, 1967), as do the head form, tail form and, to a lesser extent, the longitudinal lines at midbody. We are therefore of the opinion that it is impossible to distinguish between the two species, and thus propose to synonymize I. multistriatum with I. africanum.

Emended description of I. africanum, syn. I. multistriatum.

Female: L = 4,3 (3,2 - 6,4) mm; a = 70,8 (55,5 - 97); b = 16,8 (13,1 - 22); c = 82,5 (64,6 - 121,3); V = 51,7 (49 - 53,3)% (The one female of the Mtubatuba-population with a V-value of 59% was not brought into consideration when calculating the mean values).

Male: L = 4,3 (3,2 - 7); a = 77,3 (64 - 115,5); b = 16,8 (14,5 - 23,1); c = 76,9 (60,2 - 98,7).

Female: Heat relaxed body posture in form of letter C. Cuticle marked with punctations, forming transverse striae over anterior part of body and longitudinal lines over middle and posterior parts. Visibility of individual punctations varies among specimens. Number of longitudinal lines at midbody varies from 76 to 200 in number. Distance between consecutive lines varies from 0,9 - 1,8 µm. Head barely offset to well-offset. Lips amalgamated. Head contour in face-view hexagonal with slight invaginations in ventral and dorsal sides, giving it an appearance of bilateral symmetry. Lip region 19,5 - 32 µm wide, depending on viewing angle. Cuticular swellings present just posterior of head, visible in most specimens. Oral opening rounded. Stoma cylindrical, 91 - 128 µm long, 4 - 7 µm wide, with strongly sclerotized walls (1 - 2 µm thick). Stoma and anterior part of oesophagus surrounded by six prominent, cuticularized tubes, representing the inner labial papillae, beginning as six roundish openings situated around stoma aperture. These tubes join nerve cells at about 1/3 of oesophagus length. Familiar complement of six outer labial papillae, four cephalic papillae and two amphid apertures present on head. Oesophagus cylindroid, 226 - 326 µm long; walls of lumen thickened where they join the stoma. Oesophageal lumen minute in size but sides of radii strongly sclerotized, converging distally. Radial muscles of oesophagus concentered. Oesophago-intestinal valve elongate-conoid, dorso-ventral in symmetry. Seven oesophageal gland nuclei present, three dorsal and four subventral in position. Orifices at same level as nuclei, all situated in posterior 1/3 of oesophagus. Nerve ring situated at about 60% of oesophagus length. Tail dorsally convex, ventrally concave, bluntly rounded to pointed, 40,5 - 72 µm long (0,9 - 1,6 times body diameter). Subcuticle thickened around tail terminus and longitudinal striae form distinct annules around tail tip. One to two pairs of caudal papillae, observed in subventral to lateral positions on the tail. Rectum slightly longer than anal body diameter, prerectum absent. Lateral field observed in J1, but not in other larval stages or adults. Lateral cord width equal to about one-third of body diameter. Lateral cuticular swellings representing lateral alae observed in anterior part of body. Reproductive system didelphic, amphidelphic. Vulva large, roundish, sunken below body surface, with small, inner lips. Vagina short, not muscular. Uterine egg measures 65 - 76 by 36 - 44 µm. Egg shell about 3,4 µm thick.

Male: Description as for female with the following slight differences: Number of longitudinal lines at midbody varies from 72 - 176 with distances between consecutive lines 0,9 - 2 µm. Lip region 19,5 - 32, 5 µm wide, offset to barely offset from rest of body. Stoma 81 - 141 µm long, 4 - 6 µm wide, walls 1 - 2 µm thick. Gonads diorchic, outstretched. Spicules strongly arcuate, cephalated, with a median division stretching for 3/4 of spiculum length. Spicules 47 - 89 µm long. Gubernaculum parallel to spicules with small side-pieces and posterior apophyses 5 - 8 µm long. Two to eight mid-ventral supplements present. Caudal papillae in subventral positions, one to two pairs. Tail 40,5 - 72 µm or 0,9 - 1,4 anal body diameters long.

Emended description of the genus Isolaimium:

Diagnosis: Isolaimidae. Body elongate, 3 - 7 mm. Cuticle marked with punctations set in longitudinal and transverse rows, forming transverse striae and longitudinal lines over varying parts of the body, depending on the species. Punctations distinctly visible or faint. Head sensilla represented by familiar complement of six inner labial receptors (represented by six tubes), six outer labial papillae, four cephalic papillae and two laterally situated pore-like amphid apertures. Oesophagus cylindrical to clavate, its lumen minute but with well-sclerotized radii. Stoma long, tubular, triradiate with sclerotized walls which are thickened towards the anterior. Cardia long, cylindrical to pyramidal, dorso-ventral in symmetry. Seven oesophageal glands observed in one species, number and position unknown in other species. Vulva transverse, female gonads didelphic, amphidelphic. Male gonads diorchic, outstretched; spicules thick, arcuate to falcate, cephalate or non-cephalate, internally divided or not. Short gubernaculum has two (or four) apophyses. Papilloid supplements in male pre-anal, midventral. Caudal papillae present on tails of both males and females. Tail short, conoid, with bluntly rounded to pointed tip.

TYPE SPECIES: Isolaimium papillatum Cobb, 1920.

The systematic position of Isolaimium:

Cobb (1920) erected the genus Isolaimium and classified it in the order Isolaimia. Cobb failed to observe amphids in the type and only species, I. papillatum Cobb, 1920. Filipjev & Schuurmans Stekhoven (1941) classified the genus in the Mermithidae, while T. Goodey (1951) placed it hesitantly in the subfamily Cylindrolaiminae, family Axonolaimidae. Timm (1961) observed a pore-like amphid aperture in I. stichtochroum Timm, 1961 and regarded *Isolaimium* as an aberrant genus in the superfamily Dorylaimoidea. On account of the long, cylindrical stoma and oesophagus, Timm (1961) also related it to the subfamily Cryptonchinae, family Ironidae. Andrássy (1962) redescribed *I. papillatum*, related it to the genus *Cryptonchus* and for the first time remarked on the peculiar nature of the labial papillae, which he likened to the taste buds on the human tongue. De Coninck (1965) suggested that *Isolaimium* had a strong affinity with the Bathyodontidae, while Théodoridès (1965) regarded the genus as insufficiently known, and tentatively placed it in the Mermithidae. Yeates (1967), in agreement with De Coninck, included the genus in the Bathyodontidae. Hogewind & Heyns (1967) described three new species from South Africa: *I. africanum*, *I. incus* and *I. multistriatum*. They reported six thick-walled tubes leading inwards from what they regarded as the inner circle of labial papillae and mentioned that they could not see amphid apertures in any of the three species. Timm (1969) emended the name of the order from Isolaimia to Isolaimida and considered it to lie between the orders Dorylaimida and Trichosyringa. Bernard (1984) reported the normal complement of six plus six plus four papillae on the head region of *I. hamatispiculatum* Bernard (1984). He also found that all papillae were connected to fine tubes and that two minute pore-like amphid apertures occurred just posterior to the cephalic papillae. Heyns & Swart (1988) conducted a SEM-study on specimens of *I. africanum*, confirmed Bernards' observations and found that the six inner labial sensilla are represented by six tubes with distinct openings around the central mouth opening. In view of the above features found in *I. africanum* and the general features of the genus as described in the emended diagnosis, the following conclusions can be drawn regarding its systematic position: *Isolaimium* has a few outstanding characters such as paired, longitudinal cuticular swellings overlying the lateral chords; a peculiar bilateral symmetrical head shape, a rounded mouth opening (hexaradiate in groups with similar stoma, e.g. *Cryptonchus tristis*); cuticular punctations arranged in transverse and longitudinal lines; six inner labial receptors transformed to six tubes, and finally the peculiar pattern (discussed above) of the oesophageal gland nuclei and their orifices (see also Table 3). This supports the placement of *Isolaimium* in an order of its own. However, the genus has some characters corresponding well with that of certain members of the Dorylaimida (Table 3). The body musculature is polymyarian, coelomyarian as in the majority of the Dorylaimida (Chitwood & Chitwood, 1974), it has a thickened, triradial oesophageal lumen, no caudal glands, a single ventromedian row of supplements in the male, dorso-ventral symmetry of the oesophago-intestinal valve and caudal pores on the tail. A pore-like amphid aperture, as in *Isolaimium*, is not typical for the Dorylaimida but does occur in certain groups, e.g. some Longidoridae. A marked difference from the Dorylaimida is the presence of a tubular triradial stoma with sclerotized walls, and absence of any spear. This type of stoma is characteristic of *Cryptonchus*, family Ironidae (Enoplida) and *Bathyodontus*, family Bathyodontidae (Dorylaimida). The oesophago-intestinal valve of both these genera is however, triradial and not dorso-ventral in symmetry. *Isolaimium* has even more features in common with the genus *Cryptonchus*: Cobb (1913) observed tiny cuticular punctations in *C. tristis* (Ditlevsen, 1911) Filipjev, 1934, and so did Anderson (1968) in some of his Canadian specimens of *C. tristis*. The cuticular punctations in *Isolaimium* are however, more prominent and arranged in lines. The stoma of *Cryptonchus* is described as a long, triquetrous cylinder with sclerotized walls (Anderson, 1968), the anterior extremity of the stoma extending a short distance into the labial region where its walls are thin and often appear crescentic (the same as in *I. africanum*). Below, near the base of the lips the walls of the stoma are thickened in *Cryptonchus*, exactly as in *I. africanum* (see also Hogewind &

Heyns, 1976). The location of oesophageal gland nuclei and their outlets is controversial in Cryptonchus. Chitwood & Chitwood (1937) found five glands in the base of the oesophagus, Anderson (1968) reported three nuclei in the base and two (one dorsal and one subventral), more anteriad. Coomans & Loof (1970) also found five oesophageal glands nuclei (1 dorsal and 2 subventral pairs) in C. tristis and pointed out that the pattern is essentially the same as that of the Bathyodontidae. This is however quite different from the pattern found in I. africanum during the present study. Coomans & Loof (1970) found two pairs of ventrosublateral orifices posteriorly in the oesophagus of Isolaimium (they did not mention which species), but they were not able to find a dorsal orifice though they thought that it might lie close to the nerve ring.

In conclusion, we suggest that Isolaimida be retained as a separate order, probably most closely related to the Dorylaimida with some features remarkably close to that of the genus Cryptonchus. It might be mentioned here that Coomans & Loof (1970) preferred to place Cryptonchus in the Bathyodontidae (order: Dorylaimida) rather than in the Ironidae as suggested by Anderson (1968).

REMARKS

A peculiarity of the bilateral symmetrical head of Isolaimium which may cause difficulty in determining the correct head form (offset or not), is depicted in Fig. 4. Fig. 4 (H - J) represents the head regions of specimens from Thabazimbi showing different head shapes depending on the viewing angle. The peculiar cuticular thickenings just posterior of the head are probably due to the lateral cuticular swellings (alae) discussed earlier. This swelling can also be observed in an I. africanum specimen from Venda (Fig. 3 C). Fig. 4 (K - L) depicts the head regions of specimens from Lake St. Lucia from different viewing angles.

ACKNOWLEDGEMENTS

Thanks are due to Dr. Esther van den Berg (P.P.R.I., Pretoria) for the loan of slides of *Isolaimium* from Thabazimbi, as well as the type specimens of *I. africanum, I. multistriatum* and *I. incus*.

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TABLE 1. Morphometrical data of different populations of _I. africanum_.

Locality	Sandwich Bay		Thabazimbi		Rustenburg.		Pigg's Peak		Ndumu
	♀	♂	♀	♂	♀	♂	♀	♂	♀
Number of individuals	1	1	2	2	2	4	3	9	1
L	3,8	3,4	5 -5,6	4,6 - 5,5	3,4 - 3,7	3,9 (3,7 - 4,1)	4 (3,9 - 4,1)	3,8 (3,6 - 4)	5,7
a	66,7	65,8	88,8-97	88 -115,5	61 - 64	64 (58,7-67,7)	63,5(62,9-64)	72,3 (62 -105)	91,7
b	17	15,7	20,5-21,5	19,3 -23,5	13,4-15,1	15,6(15,1-17,1)	14 (13,1-14,9)	14,5(13-15,8	22
c	74,5	60,2	83,6-91,8	78,6 -95,3	64,6-68,5	76,5(59,4-96	87 (82-93)	72 (63,2-78)	121,3
c'	1,2	1,4	1,6	1,3-1,5	1,3-1,4	1,2(0,9 -1,4)	1,1(1,04-1,2)	1,2(1,05-1,3)	1,04
Tail length (μm)	51	56,4	60 -61	48,5-70	52 -54	53 (40,4-69)	46 (42 -50)	53 (48-59)	47
Head width (μm)	23,5	25	25,5-28	26,5-28	27	26 (24-28)	26 (25-28)	25 (23,5-28)	29
Neck width (μm)	21,5	20	21,5-25	23	26 - 26,5	25 (23-26)	26 (25-26,5)	24,8(23-28)	24
Stoma width (μm)	5	5	5-6	5	4 - 5	5,8(5-6)	5,3 (5-6)	5,2(5-6)	5
Stoma wall width (μm)	1,5	1-1,5	1,5-1,8	2	1,5-2	1,5 (1-2)	2	1,8 (1,5-2)	1,5
Stoma length (μm)	95	97	91-110	86-100	95-96	90 (81-96)	104 (102-106)	96 (87-105)	105
Oesophagus length (μm)	226	215	245-262,5	238-240	248-256	249 (238-258)	283 (275-299)	262 (250-280)	260
Anterior to nerve ring (μm)	144,3	135	163 - 180,5	156 - 160	168 - 176	176(165 -185)	183 (176 -199)	163 (161 - 166)	176
Cardia length (μm)	15	29	32,5-45	-	32	32(29-37)	21(18-22,5)	28(18-47)	25
Number of longitudinal lines at midbody	112	110	96-112	80-96	84	87(72-98)	141(132-148)	114 (104-128)	96
Distance between longitudinal lines	1-1,5	1-1,5	1-1,8	1,5-1,8	1,5-1,8	1,5-2	1	1	1,5-1,8
V (%)	50		52,4-52,8		49-54,6		50,5 (49-52)		51,1
T (%)		44		48-50,6		40,5 (34-45)		42 (39,7-44)	
Spiculum length (μm)		51		58-65		56(51-58)		57 (50-68)	
Number of supplements		6		2-5		2-5		3-4	
Caudal papillae	3-4	4	4	4	2	2	4	4	2

TABLE 1. Morphometrical data of different populations of I. africanum. (continued)

Locality	Ndumu	Hluhluwe		Mtubatuba	Mount aux Sources	Underberg	Stormsrivier		St. Lucia	
	♀	♀	♂	♀	♀	♂	♀	♂	♀	♂
Number of individuals	1	1	3	1	1	1	3	3	1	1
L	5,7	6,4	6,6(5,9-7)	3,2	3,7	3,2	3,6(3,5-3,7)	3,6(3,5-3,8)	3,2	3,7
a	91,7	70,3	81,2(78-83,1)	58,2	63,8	72,8	70(69-70)	68,4(68,2-68,6)	55,5	69,8
b	22	19,6	18,2(16-20)	13,4	15,3	14,8	15(14,7-15,3)	15,3(14,9-15,7)	13,1	14,7
c	121,3	104,1	98,7(84-110,4)	62,1	77,1	71,7	80(68,6-91,4)	75(63-84,4)	76,7	66,1
c'	1,04	1	1,01(0,9-1,1)	1,4	1,1	1,3	1,4(1,3-1,4)	1,3(1,2-1,4)	1,2	1,3
Tail length (μm)	47	61,5	64,5(58-72)	51,5	48	44,5	46(40,5-51)	52(45-55,5)	42	56
Head width (μm)	29	31	30(29-32,5)	26	24	23	24,5(22-26)	24(22-25)	24	19,5
Neck width (μm)	24	31	29(28-31)	20	23	21,5	19(18-20)	19,7(17,5-21,5)	21,5	19
Stoma width (μm)	5	7	5,7(5,5-6)	5-6	5	5	4,8(4,5-5)	4,7(4-5)	6	6
Stoma wall width (μm)	1,5	1,5-2	1,7(1,5-1,8)	1,5	1	2	1,8(1,5-2)	1,8(1,3-2)	1,5-2	1,5-2
Stoma length (μm)	105	128	138(134-141)	101	89	86	104(100-109)	106(105-109)	109	114
Oesophagus length (μm)	260	326	348,7(330-366)	237,5	240	215	239(238-240)	238(228-249)	245	253
Anterior to nerve ring (um)	176	216	230(222,5-241)	157	161	138	164(160-168)	166(160-174)	173	185
Cardia length (μm)	25	33	34(30-37,5)	22	16	16	15,5(14-17)	22,5(19-26)	20	26,3
Number of longitudinal lines at midbody	96	200	157(152-176)	80	76	104	128(120-136)	109(96-128)	136	120
Distance between longitudinal lines(μm)	1,5-1,8	1	1	1-1,5	1,5-1,8	1	1	1	0,9-1	0,9-1
V (%)	51,1	50,4		59	53,1		52,9(51,7-54)		53,3	
T (%)			42,8(39-44)			52,9		45		56,2
Spiculum length (μm)			79(74-89)			47		49(47-52)		57
Number of supplements			6-8			4		4-5		4
Caudal papillae	2	4	4	-	4	4	4	4	6	4

TABLE 2 Comparisons of populations of I. africanum from different localities

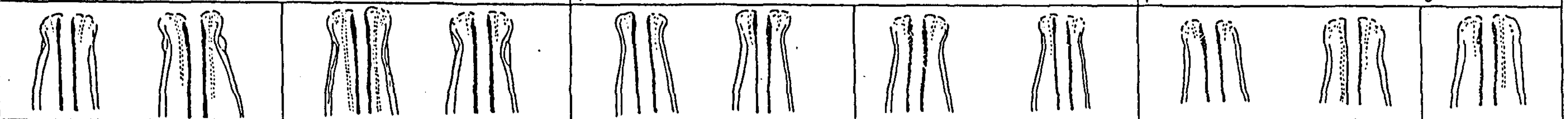
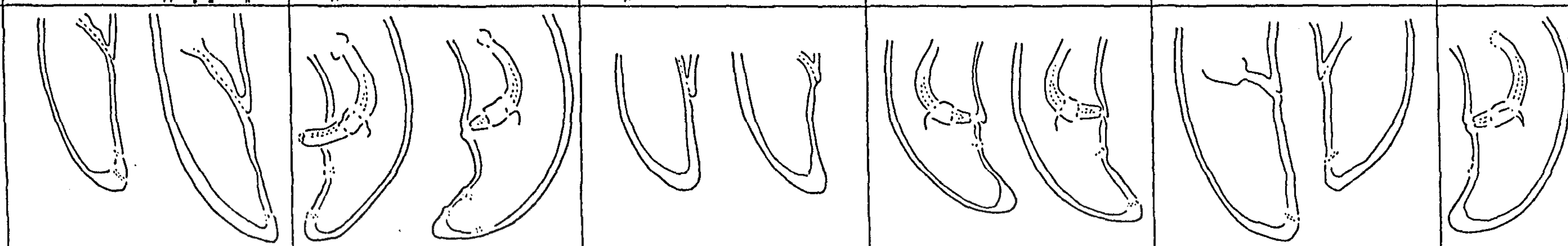
LOCALITY	THABAZIMBI ♀		♂		STORMSRIVIER ♀		♂		PIGG'S PEAK ♀		♂
HEAD FORM											
TAIL FORM											
NUMBER OF LONGITUDINAL LINES AT MIDBODY	112	96	80	96	120	136	96	104	120	128	126

TABLE 2 (continued)

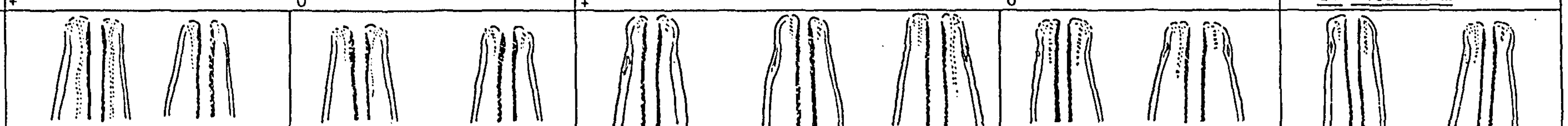
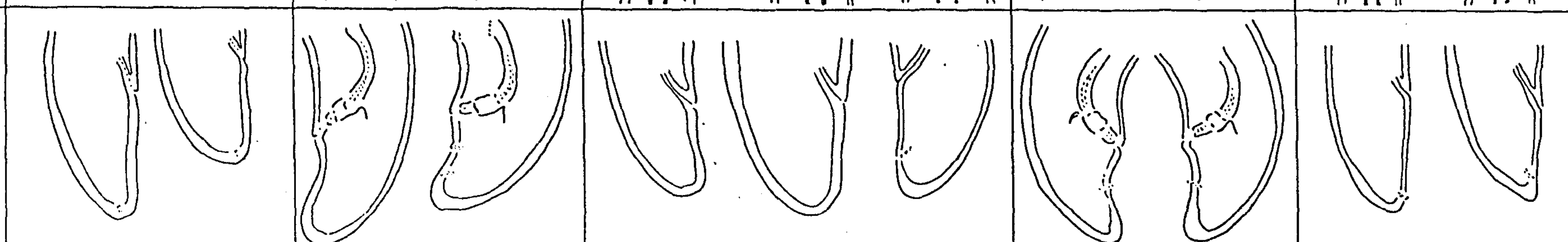
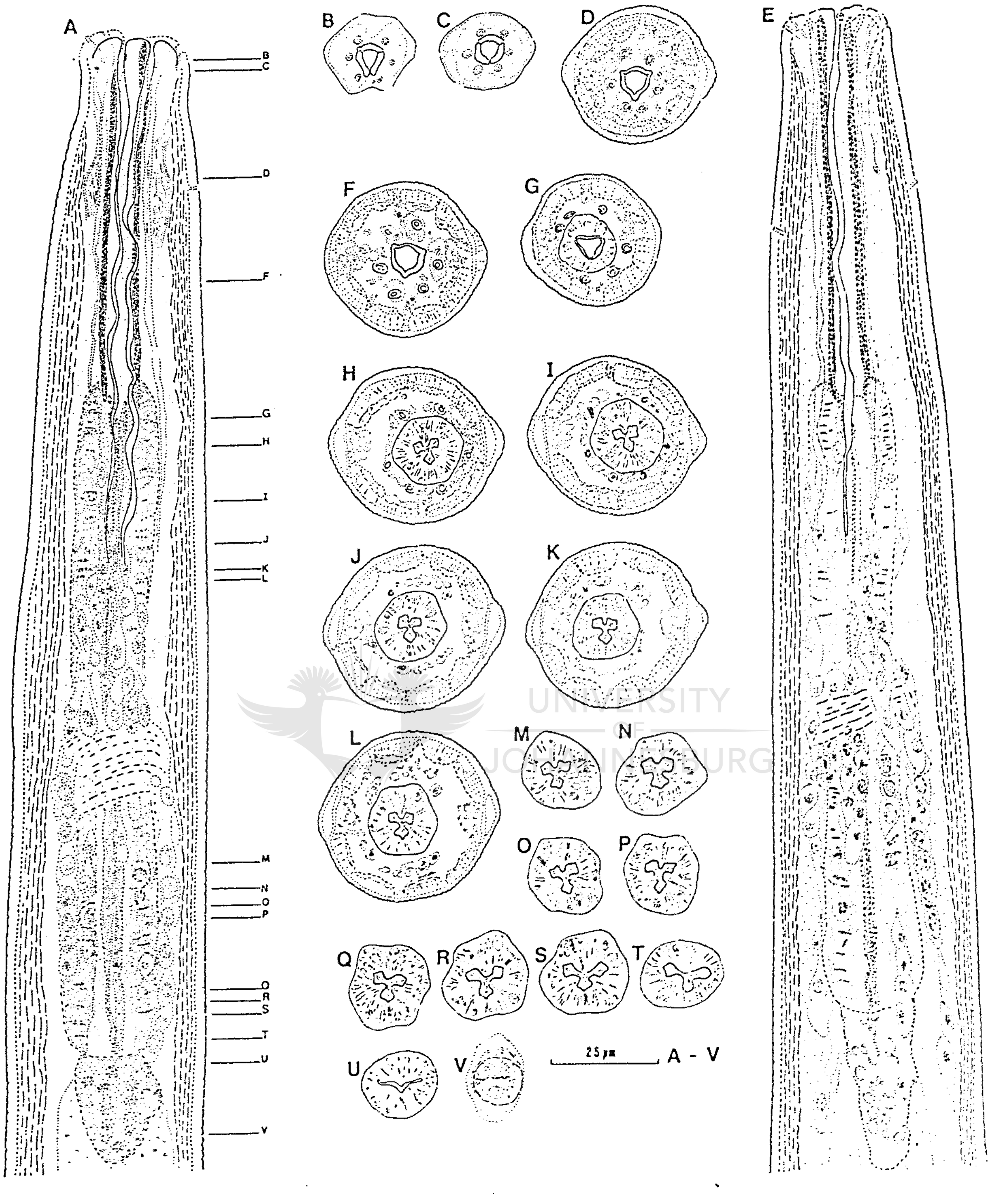
LOCALITY	RUSTENBURG ♀		♂		I. africanum - Holotype & paratypes ♀			♂		Holotype & paratype of I. multistriatum = I. africanum ♀	
HEAD FORM											
TAIL FORM											
NUMBER OF LONGITUDINAL LINES AT MIDBODY	84	84	96	84	88	120	96	100	76	124	120

TABLE 3 Comparison of <u>Isolaimium</u> with three other groups regarding some characters.

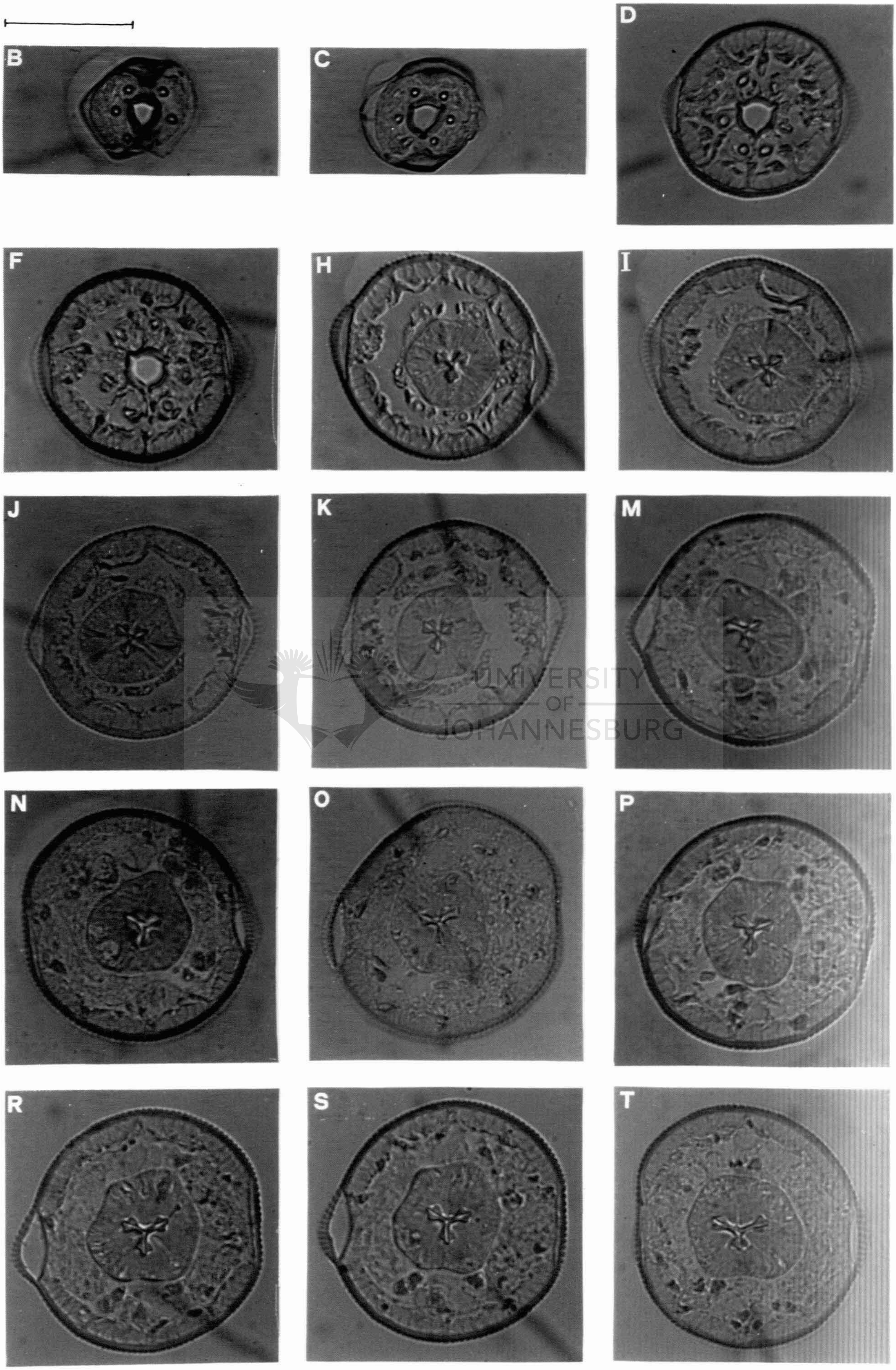
	<u>Isolaimium</u>	Dorylaimida	Enoplida (*Cryptonchus*)	Chromadorida
Cylindrical, sclerotized stoma	★		★	
Thickened triradial oesophageal lumen	★	★	★	
Face view shows bilateral symmetry	★			
Rounded mouth opening	★			
Cuticular punctations arranged in lines and striae	★			
Six inner labial receptors (tubes)	★			
Seven oesophageal glands 3 dorsal; 4 subventral)	★			
Body musculature polymyarian coelomyarian	★	★	★	
Absence of caudal glands	★	★		
Presence of caudal papillae	★	★		
Oesophago-intestinal valve dorso-ventral in symmetry	★	★		
Lateral alae	★			★
Amphid aperture pore-like	★	★ (some)		

FIG. 1. Isolaimium africanum Hogewind & Heyns, 1967. Population from Rustenburg. A: Anterior body region of male; B, C, D & F - V: Cross sections at levels as indicated by corresponding letters in Fig. A; E: Anterior body region of female.



A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
25 µm
A - V

FIG. 2. Isolaimium africanum Hogewind & Heyns, 1967. B - T: Micrographs of cross sections at levels as indicated by corresponding letters in Fig. 1 A. Bar equals 25 µm.


B
C
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S
T

FIG. 3. _Isolaimium_ _africanum_ Hogewind & Heyns, 1967. (A, B & D: Rustenburg population; C & D: Venda population. From Heyns & Swart, 1988). A: Anterior region of J1. Arrow indicates amphidial chamber; B: Basal region of oesophagus in female showing six oesophageal gland orifices; C: Head region of female, lateral view. Rectangle indicates position of amphid aperture; D: Mergence of stoma and oesophageal lumen. Arrow indicates thickened walls of oesophageal lumen; E: Detail of cuticle at mid-stoma leve. Bar equals 10 μm.

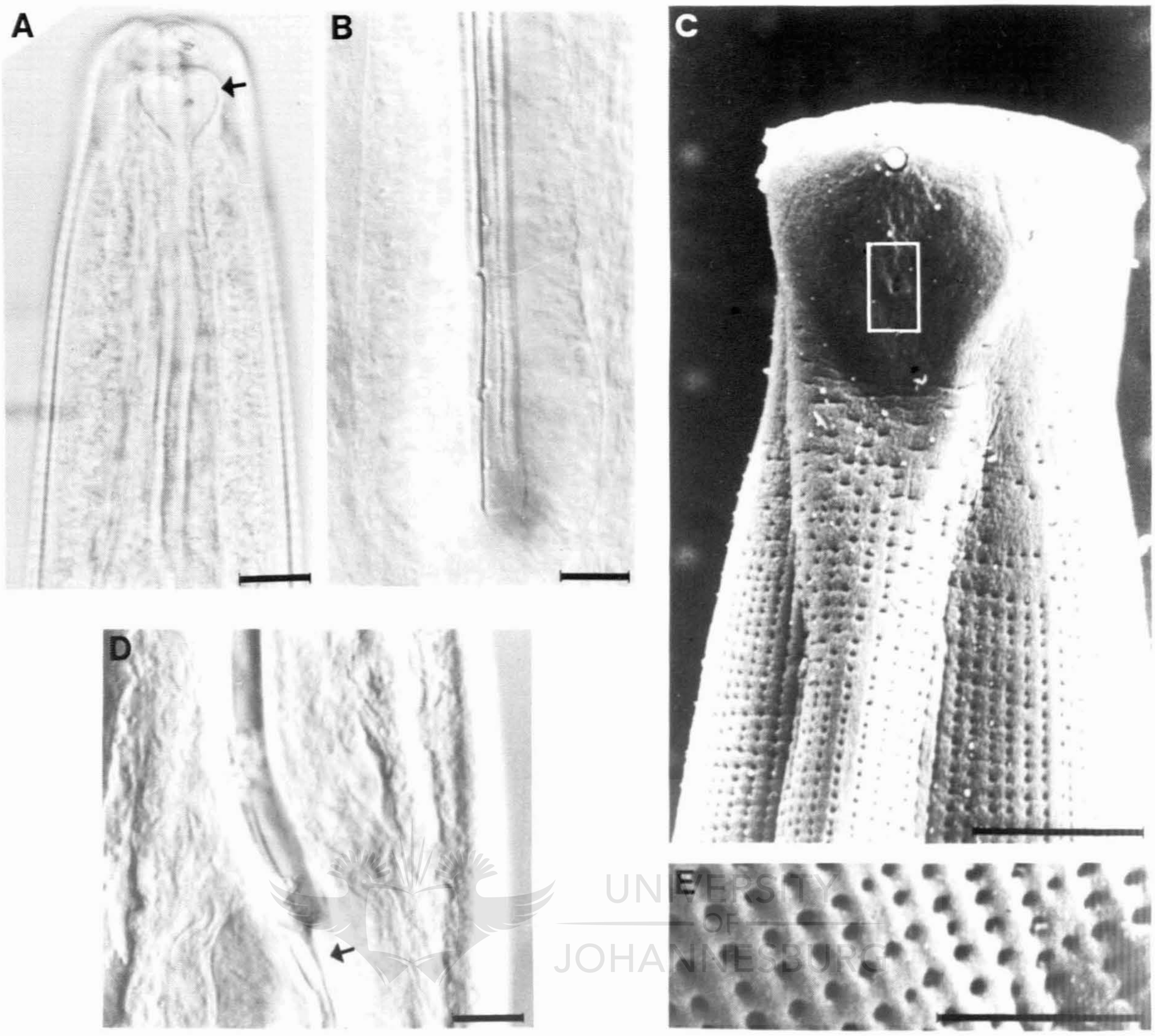

A
B
C
D
E

FIG. 4. <u>Isolaimium africanum</u> Hogewind & Heyns, 1967. (A - G: Rustenburg population; H - J: Thabazimbi population; K & L: St. Lucia population). A: Anterior region of J1; B: Head of J1; C: Tail region of J1; D: Reproductive system of J1; E: Reproductive system of J2; F: Reproductive system of J3; G: Reproductive system of J4; H - J: Head regions of three different females from different viewing angles; K & L: Head regions of two females from different viewing angles.

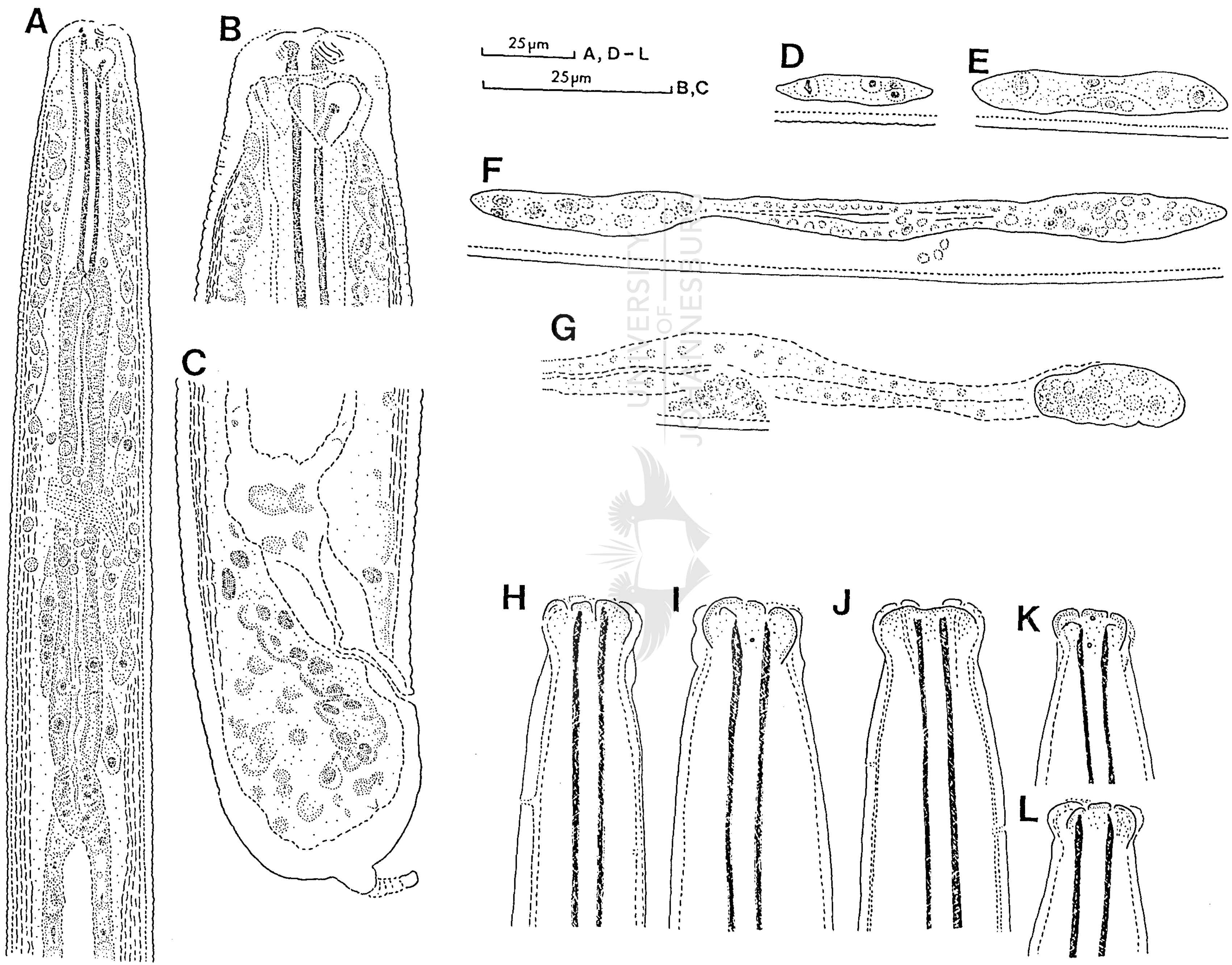
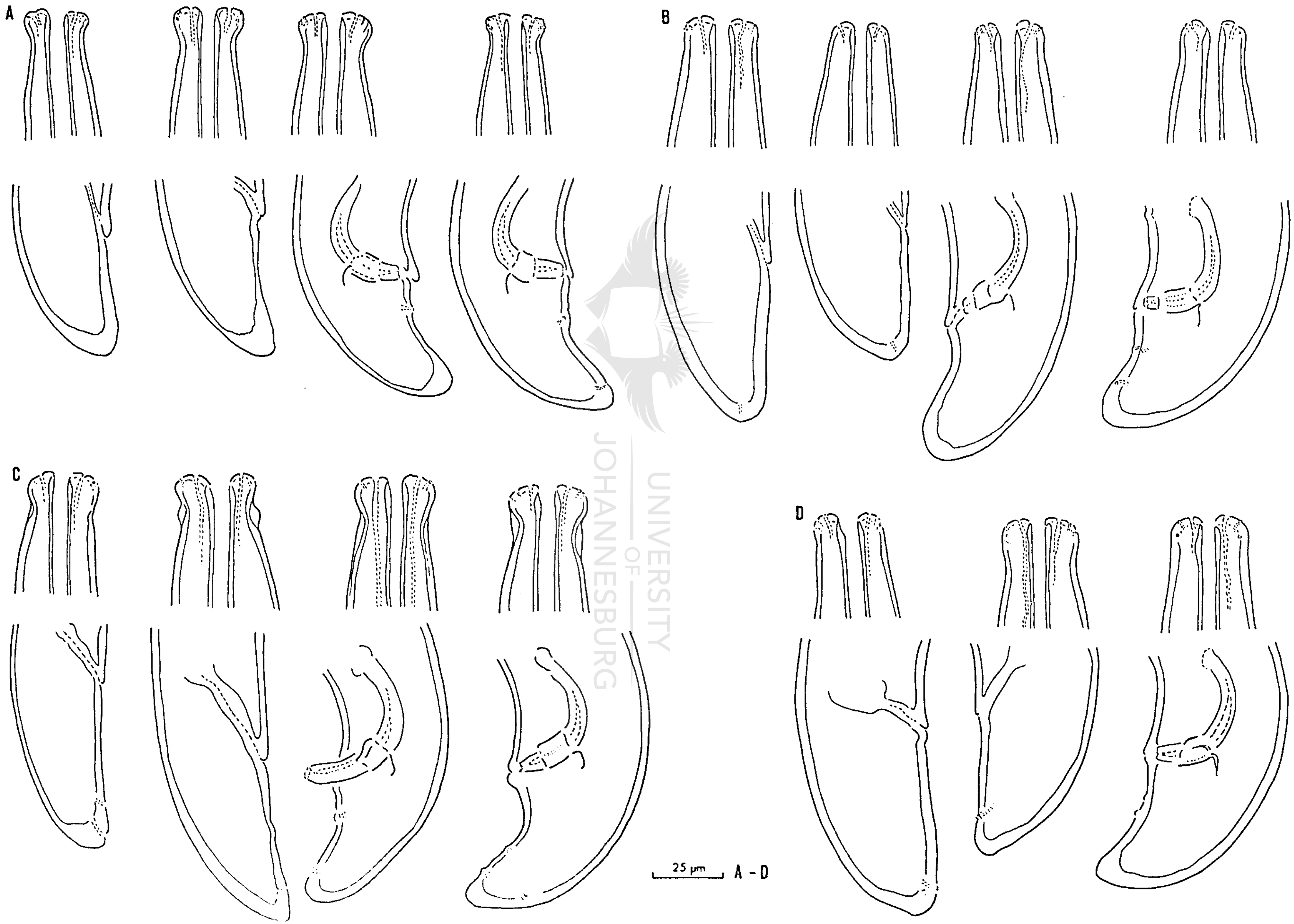
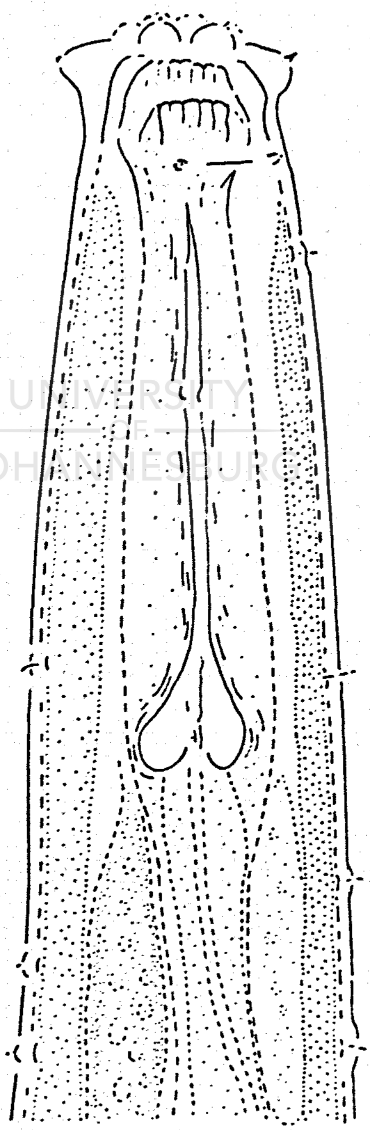

A
B
C
D
E
F
G
H
I
J
K
L
25µm A, D – L
25µm B,C

FIG. 5. Head and tail morphology of specimens of four populations of Isolaimium africanum Hogewind & Heyns, 1967. A: Population from Stormsrivier; B: Population from Rustenburg; C: Population from Thabazimbi; D: Population from Pigg's Peak.


A
B
C
D
25 µm A - D

CHAPTER 7



DESCRIPTION OF *CLADOCEPHALUS ESSERI* N. GEN., N. SP. FROM FLORIDA, U.S.A. (NEMATODA: AULOLAIMOIDIDAE).

(Submitted to the Afro-Asian Journal of Nematology)

ABSTRACT

Numerous specimens of an aulolaimoidid nematode were collected from a hollow sweetgum log (*Liquidambar styraciflua*) near Gainesville, Florida. These specimens are described as a new species, *Cladocephalus esseri*, belonging to a new genus *Cladocephalus*. The history of the family Aulolaimoididae is briefly given as well as a key to the genera within the family. Scanning electron micrographs of the head region of *C. esseri* n. sp. are also included.

Key words: Aulolaimoididae, *Cladocephalus*, SEM, taxonomy.

INTRODUCTION

Dr. R.P. Esser collected numerous specimens of an unknown Aulolaimoididae species by flushing a freshcut, hollow sweetgum log with water. He fixed them in stained lactophenol and kindly made them available to us for study. We found that these specimens represent a new species which belong to the family Aulolaimoididae, but does not fit into any of the existing genera of this family. We are accordingly proposing a new genus, *Cladocephalus*, to receive this species, which we name after its discoverer, as *Cladocephalus esseri* n. gen. n. sp.

MATERIALS AND METHODS

Specimens were permanently fixed in stained lactophenol, following the method described by Esser (1973). For mounting on permanent slides the specimens were rehydrated to water in a graded lactophenol/water series and processed into glycerine according to Thorne's slow method.. After this the rib-like structures in the buccal cavity became more distinct than in the lactophenol infiltrated specimens. Drawings and measurements were made with the aid of a Zeiss Standard 18 research microscope equiped with a drawing tube. Coiled and curved structures were measured along the median line. For scanning electron microscopy (SEM), lactophenol-infiltrated specimens were hydrated in a graded lactophenol/water series and post-fixed in 1% OsO_4. They were dehydrated in a graded ethanol-series, sputter-coated with gold and viewed with an ISI SS 60 scanning electron microscope at 6kV.

Cladocephalus n. gen.

Generic diagnosis: Aulolaimoididae, Aulolaimoidinae.

Body straight in female, ventrally curved in tail region of male. Head with well-developed, prominent labial papillae. Cuticle with fine, transverse striations. Buccal cavity supported by two minute, rib-like structures. Amphid apertures slit-like. Odontophore flanged, stylet dorylaimoid. Oesophagus composed of three sections. Muscular basal bulb with valvular chamber. Vulva transverse, situated slightly before midbody. Female reproductive system variable, most specimens being didelphic, amphidelphic, the rest monodelphic, prodelphic. Male reproductive system diorchic, testes outstretched. Spicules slightly ventrally curved, gubernaculum distinct. Adanal pair and ventromedian supplements present. Tails of both sexes elongate-conoid. Hemizonid distinct. Somatic muscles prominent and well-defined.

Type species: Cladocephalus esseri n. gen., n. sp.

Differential diagnosis: Cladocephalus n. gen. differs from all other genera of the Aulolaimoididae in the very prominent, protruding labial papillae. It further differs from Aulolaimoides Micoletzky, 1915 in the absence of a muscular vagina, the presence of a well-defined hemizonid and the presence of more than two ventromedian supplements in the male. Cladocephalus n. gen. also differs from Adenolaimus Andràssy, 1973 in the elongate conoid tail, the presence of ventromedian supplements in the male and the presence of two ovaries in most specimens, and from Oostenbrinkia Ali, Suryawanshi & Ahmed, 1973 in the elongate-conoid tail, the rib-like structures in the buccal cavity and the presence of a valvular chamber in the basal bulb.

The name Cladocephalus is derived from the Greek clad = branch/sprout, referring to the prominence of the outer labial papillae; and cephal = head.

DESCRIPTION

Cladocephalus esseri n. sp.

(Fig. 1 A-J; 2 A-H; 3 A,B)

Measurements: See Table 1

Female: Body straight when heat-relaxed, tapering towards both extremeties. Cuticle with fine, transverse striations. Head region 8-9 µm wide with one whorl of six prominent inner labial papillae surrounding the stoma, one whorl of six huge protruding outer labial papillae and one whorl of four, less prominent cephalic papillae at the same level as the amphid apertures (about 5 µm from anterior end). Amphid apertures small, slit-like, about 2 µm wide. Buccal cavity supported by two delicate, rib-like structures encircling its lumen at 2,5 µm and 5 µm from the anterior end respectively. Spear 22 - 27 µm long, consisting of a delicate odontostyle (7 - 11 µm long) and a flanged odontophore (13,5 - 18 µm long). Flanged base of odontophore 3 - 4 µm wide, surrounded by muscles. Oesophagus composed of three sections: (1) An anterior, slender part comprising about

60% of oesophagus length, surrounded by glandular tissue which gradually expands posteriorly where it joins the next part; (2) a middle part, occupying 5 - 7% of the oesophagus length, surrounded by granular tissue which in some individuals appears as three, distinct organs or glands surrounding the oesophageal lumen; (3) a well-developed, muscular basal bulb, comprising about 30% of the oesophagus length. A distinct valvular chamber is present within the basal bulb and the orifices of five oesophageal gland cells can be observed opening into the lumen of the bulb. The gland nuclei themselves are however, obscure. Oesophageal lumen well-defined with the muscles surrounding the lumen expecially well-developed in the all three sections of the oesophagus. This prominent lining stretches from the posterior end of the odontophore to the anterior end of the basal bulb. Cardia distinct, 6 - 5 µm long, 7 µm wide. Nerve ring indistinct in most specimens, located at about 60% of oesophagus length, 4,2 - 4,5 body widths from anterior end. Hemizonid 4 - 8 µm posterior to level of nerve ring. Lateral cords 5 µm wide. Somatic muscles well-defined and arranged in a distinct herring-bone pattern. About 16 ventral and 20 dorsal somatic papillae, ranging from about 10 µm behind the head to the level of the anus. A few somatic papillae were also observed laterally on the body with two on each side of the tail. Female reproductive system variable. About 75% of all females have a didelphic, amphidelphic and 25% a monodelphic, prodelphic reproductive system (Fig. 2 B). The monodelphic females usually have a distinct but rudimentary posterior branch. Of interest is the many "abnormal" forms in which the ovaries are flexed (Fig. 2 D, E, F). Ripe oöcytes are about 70 µm long and 15 µm wide. Egg shell on average 2 µm thick. Vagina distinct, about 6 µm long, mostly anteriorly directed, not distinctly muscular. Vulva a transverse slit. Rectum 18 µm long, distinct. Anal body width 9 - 10,8 µm. Tail elongate-conoid.

Male: Body curved ventrad, especially in tail region. Reproductive system diorchic, sperm spindle-shaped, spicules slightly curved ventrad, gubernaculum distinct. One pair of well-defined adanal supplements, and four obscure, widely spaced ventromedian supplements. Five pairs of caudal papillae present on tail, two subventral pairs about 10 µm and 20 µm from cloacal opening, and three subdorsal pairs about 10 µm, 30 µm and 40 µm from cloacal opening. Prominent glandular tissue observed in anal region. Three to four rectal glands and about six ejaculatory glands situated in an area 12 - 40 µm anterior to cloacal opening. Spermoduct not muscular. Rest of general morphology similar to that of female.

Type specimens: Holotype: Female on slide RAU 5555. Paratypes: 61 females on slides RAU 5556 - RAU 5559, RAU 5562; RAU 5566 - RAU 5574 and two males on slide RAU 5566. Specimens are also deposited in the nematode collections of the following institutions: six females and one male in the Instituut voor Dierkunde, Rijksuniversiteit Gent, Ghent, Belgium; eight females in the USDA, Beltsville, Md, U.S.A. and seven females and 1 juvenile at Florida Dept. Agric., Gainesville, Florida, U.S.A.

Type locality and habitat: The specimens were collected from a hollow sweetgum log (*Liquidambar styraciflua*. The tree was located in a live oak, sweetgum, slash pine "mesic hammock", a Florida ecological designation, near Gainesville, Florida.

Diagnosis: Lip region with well-developed, prominent labial papillae. Buccal cavity supported by two delicate, rib-like structures, both forming rings anteriorly. Basal bulb muscular with distinct valvular chamber. Female reproductive system variable, either didelphic, amphidelphic with reflexed ovaries or monodelphic, prodelphic with reflexed ovary and rudimentary posterior uterine branch. Distinct spicules and gubernaculum, two prominent adanal supplements and a series of widely spaced ventromedian supplements.

Differential diagnosis: In its small size Cladocephalus esseri n. sp. resembles Aulolaimoides altherri Andrássy, 1968, but can be distinguished from this species by the prominence of the labial papillae, the position of the vulva (V = 43-47,5% in C. esseri n. sp. against V = 29% in A. altherri) and the female reproductive system being either didelphic, amphidelphic or monodelphic, prodelphic in C. esseri n. sp. and monodelphic, opisthodelphic in A. altherri. The hemizonid is prominent in C. esseri n. sp., lacking in A. altherri.

Discussion: Micoletzky (1915) erected the genus Aulolaimoides for the single species, A. elegans Micoletzky, 1915. Thorne (1939) emended the generic diagnosis but regarded Aulolaimoides as a genus of uncertain position which he tentatively placed in the family Leptonchidae Thorne, 1935. Clarke (1961) placed Aulolaimoides in the Campydoridae Thorne, 1935, together with two other genera: Campydora Cobb, 1920 and Tyleptus Thorne, 1939. However, he described this family as a "taxonomic expediency" with the sole function, the gathering together of three genera with a valve-like chamber in the basal bulb, not fitting into any other family. Andrássy (1964) added Aulolaimoides phoxodorus, emended the generic diagnosis of Aulolaimoides and tentatively placed it in the family Leptonchidae Thorne, 1935. Jairajpuri (1964) established the family Aulolaimoididae for the single genus Aulolaimoides. This new family was characterised by the morphology of the stylet, the three-part oesophagus, the buccal cavity supported by minute ribs, the morphology of the spicules and the presence of a gubernaculum. Adenolaimus was proposed by Andrássy (1973) for Adenolaimus dadayi Andrássy, 1973. It also has a three-part oesophagus, but can be separated from Aulolaimoides by the short, rounded tail. Ali, Suryawanshi & Ahmad (1973) erected the new genus Oostenbrinkia for the single species Oostenbinkia oostenbrinki Ali, Suryawanshi & Ahmad, 1973. It differs from Aulolaimoides and Adenolaimus in having amphidelphic gonads with the vulva situated at mid-body. Cladocephalus n. gen. is placed in the family Aulolaimoididae on account of the three-part oesophagus, flanged odontophore and delicate, rib-like structures in the buccal cavity. Other similarities and differences between the four genera are listed in Table 2. Noteworthy of Cladocephalus esseri n. gen., n. sp. is the morphology of the head with its huge outer labial papillae, prominent inner labial papillae and posterior position of the cephalic papillae (at the level of the amphid apertures). Also remarkable is the variability of the female reproductive system, which may be either didelphic or monodelphic.

ACKNOWLEDGEMENTS

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TABLE 1 MORPHOMETRICAL DATA OF <u>CLADOCEPHALUS</u> <u>ESSERI</u> N. SP.

	Holotype	Paratypes (♀)	Standard deviation (♀)	Paratypes (♂)	Standard deviation (♂)
Number	1	74		3	
L (mm)	0,44	0,44 (0,37-0,48)	0,02	0,44 (0,41-0,46)	0,02
a	24,4	24,7 (21,4-27,7)	1,4	27,5 (26,7-28,7)	0,9
b	4,3	4,2 (3,5-5,1)	0,3	4,1 (3,7 - 4,6)	0,4
c	5,6	5,4 (4,3-7,2)	0,3	5,9 (5,7 - 6,4)	0,3
c′	7,9	8,4 (7,1-10,7)	0,8	6,9 (6,1 - 7,6)	0,7
V(%)	44,9	45 (43-47,5)	1,1		
tail length (μm)	79	80,9 (64-108)	6,6	74,1 (67-80,5)	5,7
oesophagus length (μm)	102	103,5 (89-122)	5,7	107,8 (99-112)	9,3
basal bulb length (μm)	29	29,9 (26-34)	1,3	29 (28-30)	1,0
odontostyle length (μm)	10	8,7 (7 -11)	0,7	8,5 (8-9)	0,6
odontophore length (μm)	15	15,1 (13,5-18)	0,8	14,1 (13-15)	1,0
stylet length (μm)	25	23,8 (22-27)	1,0	22,6 (21-24)	1,1
T (%)				28,7 (24-32,5)	4,3
spiculum length (μm)				13 (13-13)	0
gubernaculum length (μm)				3,7 (3 -5)	1,2

TABLE 2 COMPARISON OF THE GENERA CLADOCEPHALUS N. GEN., AULOLAIMOIDES, ADENOLAIMUS AND OOSTENBRINKIA

	Cladocephalus n. gen.	Aulolaimoides	Adenolaimus	Oostenbrinkia
Tail	Elongate-conoid	Elongate-conoid to filiform	Short, rounded	Cylindrical, rounded
Female genital tract	Didelphic, amphidelphic or monodelphic, prodelphic	Monodelphic, opistho-delphic	Monodelphic, opistho-delphic	Didelphic, amphidelphic
Vulva-position	Slightly pre-equatorial	Anterior 1/3 of body	Anterior 1/3 of body	Mid-body
Vagina	Distinct, musculature weak	Distinct, musculature prominent	Distinct, musculature prominent	Distinct, mus-culature weak
Head region	Head papillae prominent, protruding	Head papillae indistinct	Head papillae indis-tinct	Head papillae indistinct
Buccal cavity	With delicate, rib-like structures	With delicate, rib-like structures	With delicate rib-like structures	No rib-like structures
Valvular chamber in basal bulb	Present	Present	Present	Absent
Supplements	One adanal pair and ventromedian series	Adanal pair and ventro-median series	Absent	No males found
Gubernaculum	Present, well defined	Present, well defined	Present, but indis-tinct	No males found
Hemizonid	Prominent	Not observed	Not observed	Present, but indistinct

FIG. 1. Cladocephalus esseri n. sp. A. Anterior region of holotype female; B. Anterior region of female, showing herring-bone pattern of somatic muscles; C. Anterior region of male; D. Head of holotype female; E. Female reproductive system, showing a ripe oocyte; F. Male reproductive system; G. Ventral view of anal region of female, showing two pairs of lateral somatic papillae on tail; H. Tail region of female; I. Female reproductive system - didelphic amphidelphic, with reflexed ovaries.

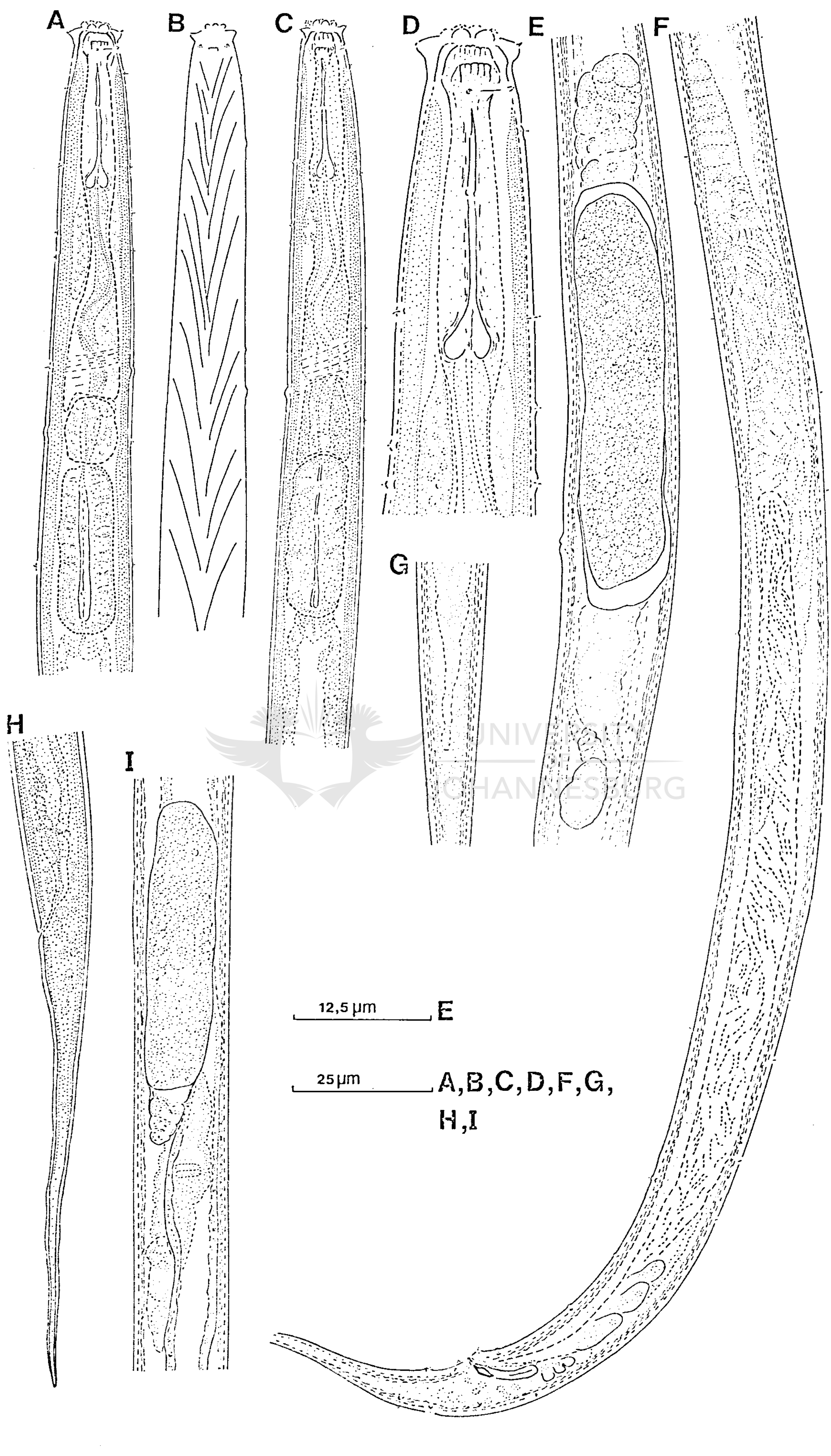

A
B
C
D
E
F
G
H
I
12,5 µm E
25 µm A,B,C,D,F,G,
H,I

FIG. 2. Cladocephalus esseri n. sp. Reproductive systems, representative of the female population (both young and adult). A. Adult female: didelphic, amphidelphic, reflexed ovaries; B. Adult female: monodelphic, prodelphic with ovary apparently reflexed, rudimentary posterior branch. C. Adult female: didelphic, amphidelphic, reflexed ovaries; D. Young female: didelphic, amphidelphic, outstretched ovaries; E. Young female: didelphic, amphidelphic anterior branch with double flexure in ovary; F. Young female: didelphic, amphidelphic; G. Young female: didelphic, amphidelphic; H. Young female: monodelphic, prodelphic with short postuterine sac, ovary reflexed.

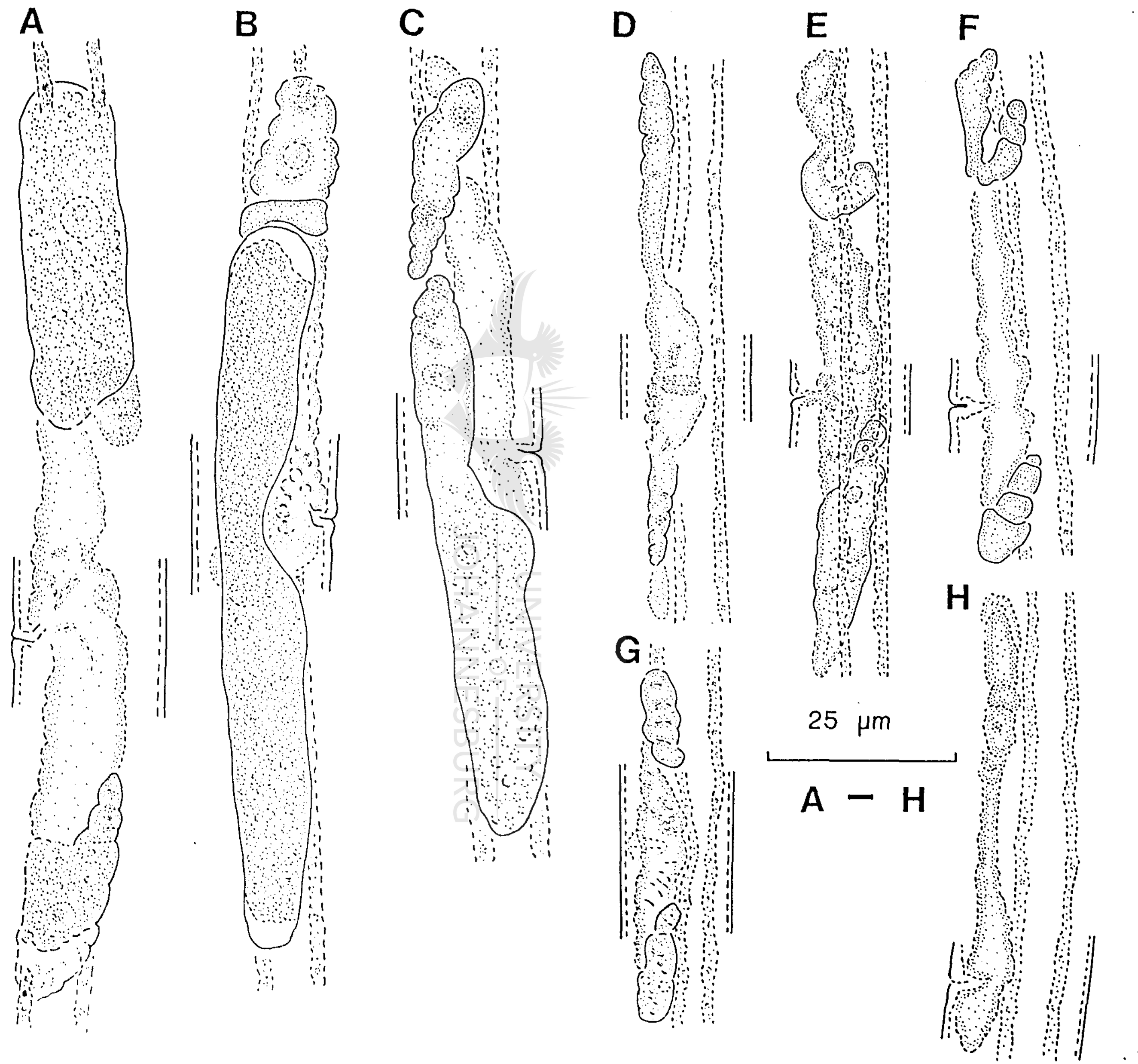
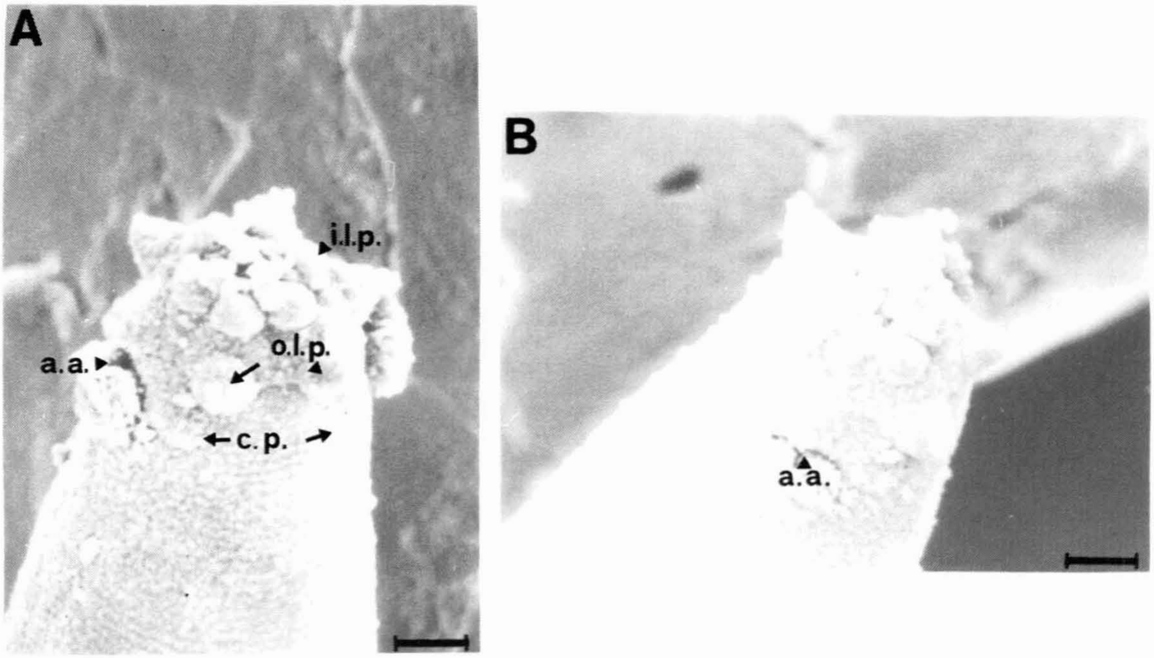
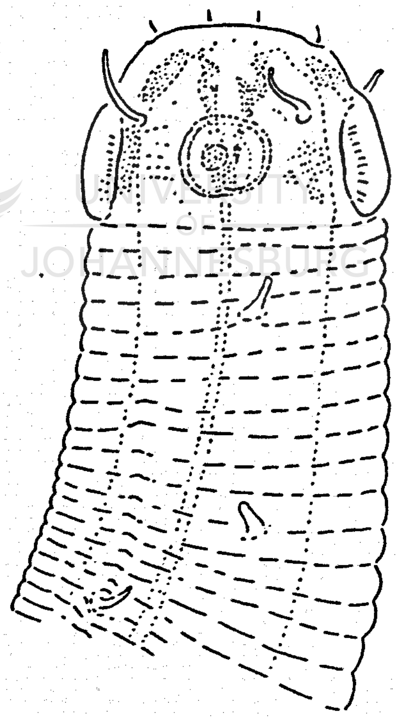

A
B
C
D
E
F
G
H
25 μm
A — H

FIG. 3. Cladocephalus esseri n. sp. A. Head region of female; B. Head of female - frontal view. Bar equals 2 µm (a.a. = amphid aperture; c.p. = cephalic papillae; i.l.p. = inner labial papilla; o.l.p. = outer labial papilla).


A
i.l.p.
a.a.
o.l.p.
c.p.
B
a.a.

CHAPTER 8



DESMODORA (SIBAYINEMA) NATALENSIS SUBG. NOV, SPEC. NOV FROM LAKE SIBAYI, SOUTH AFRICA (NEMATODA: DESMODORIDA)

(Submitted to Phytophylactica)

ABSTRACT

Key words: Desmodorinae, taxonomy, SEM

Specimens of the genus Desmodora were collected from a freshwater lake in Natal, South Africa. They are described as a new species belonging to a new subgenus, Sibayinema, which can be distinguished from two closely-related subgenera Desmodora De Man, 1889 and Zalonema Cobb, 1920 by the coursely annulated cuticle adorned with longitudinal rows of brush-like ornamentations and the peculiar shape of the amphid aperture in males.

Uittreksel

DESMODORA (SIBAYINEMA) NATALENSIS SUBG. NOV., SPEC. NOV. UIT SIBAYI-MEER, SUID-AFRIKA (NEMATODA: DESMODORIDA)

Eksemplare van die genus Desmodora is in 'n varswatermeer versamel in die noorde van Natal, Suid-Afrika. Hierdie eksemplare word as 'n nuwe spesie beskou, behorende tot 'n nuwe subgenus Sibayinema wat van die twee naverwante subgenera, Desmodora De Man, 1889 en Zalonema Cobb, 1920 verskil in die opvallend-geannuleerde kutikula, borselvormige kutikulêre annulasies en ongewone vorm van die mannetjie se amfiedopening.

INTRODUCTION

About 5000 years ago Lake Sibayi, part of the lake system of northern Natal and previously a series of lagoons, became land-locked due to geological movements (Lester, 1972) and today it is about twelve meters above sea level, filled with fresh water and separated from the Indian Ocean by a three kilometre wide strip of forested dunes. Marine fish trapped in its depths have already adapted to fresh water (Lester, 1972). The climate of this region is subtropical with general high temperatures and fairly well-distributed rainfall. Specimens of the new subgenus Sibayinema were collected from the sandy bottom of Lake Sibayi, between reeds and grasses.

MATERIALS AND METHODS

Specimens for permanent mounts and study with LM were killed and fixed in hot FAA (70°C), dehydrated, processed into glycerine according to Thorne's slow method and mounted on permanent slides. Drawings and measurements were made with the aid of a Zeiss Standard 18 research microscope equipped with a drawing tube. All light microscope photographs were taken with the aid of this microscope equipped with a MC63 photomicrographic camera (Ilford Pan F 50 ASA film) and differential interference contrast (Nomarski). Coiled and curved structures were measured along the median line.

For scanning electron microscopy (SEM), specimens were killed with gentle heat, fixed in buffered 2,5% gluteraldehyde, post-fixed in buffered 1% OsO_4 and dehydrated in a graded ethanol series (Swart & Heyns, 1987). They were sputter-coated with gold and viewed with an ISI SS60 scanning electron microscope at 6 kV.

SYSTEMATICS

The genus Desmodora was established by De Man (1889) with D. communis (Bütschli, 1874) De Man, 1889 as type species. Gerlach (1963) proposed a subdivision of Desmodora into the following subgenera: Croconema Cobb, 1920 (syn: Aculeonchus Kreis, 1928); Bolbonema Cobb, 1920; Desmodora De Man, 1889; Desmodorella Cobb, 1933; Pseudochromadora Daday, 1899 (syn: Micromicron Cobb, 1920; syn: Bradylaimoides Timm, 1961); Xenodesmodora

Wieser, 1951 (syn: Bla Inglis, 1963) and Zalonema Cobb, 1920 (syn: Heterodesmodora Micoletzky, 1924). Inglis (1968) pointed out that there is considerable confusion in the systematics of the members of Desmodora with perforated tails, namely Croconema and Xenodesmodora, especially as the type species C. cinctum Cobb, 1920 and X. porifera Wieser, 1951 are not well-described and known from females only. He proposed (1976) that all species of Desmodora with perforated tails be included in Croconema until information on new forms might solve the position of species within this heterogenous group. Inglis (1976) synonymized Xenodesmodora with Croconema since there is no distinct difference between these two subgenera. During the present study the authors were immediately struck by the heavily ornamented cuticle as well as by the peculiar crescent-shaped amphid aperture of the male. The perforated tail tip would place this species in the subgenus Croconema, but since there are so many characters in which it differs from Croconema (as well as from Xenodesmodora) the authors decided to place it in a new subgenus of its own.

Sibayinema subg. nov.

Diagnosis: Desmodora, Desmodoridae

Sibayinema subg. nov. is characterized by a coarsely annulated cuticle with longitudinal rows of brush-like ornamentations (adults). Eight rows of somatic setae are present along the body (two rows subventrally, two rows subdorsally and two rows sublaterally). Cephalic sense organs arranged in three crowns of six inner labial setae, six longer outer labial setae and four cephalic setae. Cephalic setae situated at level of anterior margin of amphid aperture. No subcephalic setae observed on head capsule. Amphid aperture circular in female, larger and crescent-shaped in male. Lumen of basal bulb strongly sclerotized and divided into two parts, coinciding with a division in the musculature of the basal bulb. Head capsule not annulated and without a suture dividing it into anterior and posterior parts. Prominent lateral cuticular differentiation present. Tail tip perforated, not annulated. Pre-anal supplements appear to be represented by a row of ventro-median setae. Well-developed, cephalated spiculums present; gubernaculum plate-like, without apophysis.

Type species: Desmodora (Sibayinema) natalensis spec. nov.

Differential diagnosis: Sibayinema subg. nov. differs from all other subgenera within the genus Desmodora in the longitudinal rows of brush-like ornamentations on the cuticle and the crescent-shaped amphid aperture in the male. It agrees with Croconema and Xenodesmodora in having a perforated tail tip, but differs from both in the presence of one dorsal and two subventral teeth in the buccal cavity, the absence of subcephalic setae on the head capsule, the presence of a row of pre-anal ventromedian setae in the male and the division in the musculature and the lining of the lumen of the basal bulb. Sibayinema subg. nov. differs from Pseudochromadora mainly in the amphid aperture in females (circular in the former; spiral in the latter) and the lateral cuticular differentiation (brush-like in Sibayinema; small in Pseudochromadora). Sibayinema subg. nov. can be separated from Zalonema in the position of the cephalic setae at the anterior margin of the amphid apertures, the absence of subcephalic setae on the head capsule and the presence of lateral cuticular differentiation, teeth in the buccal cavity, pre-anal setae in the male and a punctate tail tip. From Desmodora it differs mainly in the absence of subcephalic setae, absence of a suture dividing the head capsule in anterior and posterior parts and the presence of divisions within the lining of the lumen and musculature of the basal bulb. Sibayinema subg. nov. also differs from Desmodorella in the coarse cuticular annulation, the circular amphid aperture in the female, the absence of a division of the head capsule and the presence of divisions within the basal bulb. It can be differentiated from Bolbonema in the position of the cephalic setae at the anterior margin of the amphid aperture, the presence of a division in the basal bulb and a perforated tail tip.

Desmodora (Sibayinema) natalensis spec. nov.

(Figs. 1 & 2)

MEASUREMENTS: See Table 1

Male: Body posture of heat-relaxed specimens ranging from extended to various curved postures. Body cylindrical, attenuated at tail end. Head appears flattened anteriorly and bulges from just posterior of cephalic setae to the beginning of the first annule. This bulging area is further differentiated by subcuticular punctations forming fine lines traversing the thickened cuticle of this region (Fig. 1H). Cephalic sense organs arranged in three crowns of six inner labial setae surrounding the stoma, six outer labial setae (about 2 µm in length) and four cephalic setae (about 7 µm in length). No subcephalic setae present on head capsule. Cephalic setae situated at 6,5 - 7,5 µm from anterior end. Amphid aperture crescent-shaped (Fig. 2A&B), 11-14 µm long and 13-16,5 µm wide. Buccal cavity funnel-shaped, with well-sclerotized walls. One distinct dorsal tooth and two smaller subventral teeth present in anterior part of stoma. Oesophagus slender with distinct basal bulb. Walls of oesophageal lumen thick, those of basal bulb strongly sclerotized and horizontally divided into two parts. Musculature of basal bulb also horizontally divided into two distinct parts, division coinciding with the two breaks in the lumen walls. Excretory pore not observed. Nerve ring situated at 60% of oesophagus length. Numerous cells observed in oesophageal region. Cardia well-developed, consisting of about 16 to 20 cells, about 16 µm long (more than half body width). Cuticle 1,5-1,8 µm thick, distinctly annulated, annulations 1,5-2 µm wide. Cuticle of head and posterior 15-17 µm of tail not annulated. This most posterior part of tail with distinct punctations (Fig. 2F). Somatic setae arranged in eight rows along body, two rows subdorsally, two rows subventrally and two rows (with very few setae) sublaterally. These eight rows of somatic setae stretches from the 10th - 13th annule posterior of head to about the cloacal region. Eight pairs of somatic setae observed on tail, all in a subventral position. About nine setae can be observed just anterior of the cloacal opening, as well as a ventral row of about 32 long setae stretching from the cloacal opening to the level of the proximal part of testis (about 280-286 µm anterior of cloaca). The somatic setae situated on the first 10-13 annules are arranged randomly (Fig. 2A). Fourteen to eighteen longitudinal rows of brush-like ornamentations are situated along the body, beginning from about the 15th annule posterior of head, to the cloacal area. These longitudinal rows may end abruptly, to be continued again further along the body (Fig. 3D). Each brush-like ornamentation situated on an annule, consists of two or three "sheets" each with a fringed border. No individual "sheets" can be observed in the ornamentation overlying the lateral fields, only long "fringes" are present.

Genital system monorchic, testis outstretched, on left side of intestine. Numerous elongated sperm cells (about 4 µm long) observed in distal part of testis. Vas deferens contains fine, rounded granule-like structures in it's proximal part, followed by a region with elongated sperm cells as well as big rounded structures (appears the same as those found in the distal part of the uterus in some females). Vas deferens not muscular. Spicules equal in length, ventrally curved with well-developed capitulum. Gubernaculum plate-like with no apophysis. Three caudal glands present, spinneret 3,5-4 µm long, numerous small cells present in tail.

Female: Description as for male with the following differences: Amphid aperture circular, corpus gelatum rod-like. Amphid aperture rounded, 10-12 µm wide and 10-12 µm high. Somatic setae on tail situated subdorsally and subventrally, 10-12 in number. Genital system didelphic, amphidelphic with reflexed ovaries, both branches on right side of intestine. Numerous elongated sperm cells present in proximal part of uterus. Ovaries short, occupying about 23% of total body length. Egg 59 µm x 27 µm with egg shell 1,5-3 µm thick. Vagina sclerotized, dilatory muscles not conspicuous. Vulva invaginated; a transverse, slit-like opening. Rectum 40-42 µm long.

Juveniles: On the basis of cuticular structures and morphometrical data, only one juvenile stage could be distinguished.

Juvenile 4: 11 specimens ( )

Measurements: L = 0,8 - 1,1 mm; a = 26,5 - 32,9; b = 7,2 - 8,3; c
c = 8,8 - 11,1; c' = 4,1 - 5,5

Cuticular ornamentation different from that of adult. About 22 longitudinal rows of spine-like ornamentations cover the annules from about the 17th annule posterior of head to anal region (Fig. 3A). Some spines appear to be lying flat against the cuticle while others seem to be in a more erect position (Fig. 3C). In some spines (the erect ones) individual "sheets" can already be seen. The cuticle overlying the lateral field seems to be differentiated in a thickened crest (Fig. 3C). The amphid aperture is rounded and smaller than in the adult, 8-10 µm long and 8,5-11 µm wide. The bulging of the posterior part of the head capsule is also more pronounced in the juvenile than in the adult (Figs. 3B & D).

Type locality and habitat.

Samples were taken about two metres from the western shore in the sandy bottom of Lake Sibayi. The samples were taken by A. Swart on the 18th

April 1990.

Type specimens:

Holotype male on slide RAU 2738. Thirty-eight female, 11 juvenile and 12 male paratypes on slides RAU 2717 to RAU 2739 deposited in the nematode collection of the Department of Zoology, Rand Afrikaans University, Johannesburg.

Differential diagnosis.

Desmodora (Sibayinema natalensis) spec. nov. is close to Desmodora (Desmodora) schultzi Gerlach, 1950 but can be differentiated from the latter by the following: The brush-like cuticular ornamentations in D. natalensis spec. nov. are arranged in 14 to 18 longitudinal rows while the hair-like cuticular ornamentations of D. schultzi are arranged in 12 longitudinal rows. The lumen and musculature of the basal bulb are divided by transverse divisions in D. natalensis while no such divisions were observed in D. schultzi. No subcephalic setae were observed on the head capsule of D. natalensis whereas 16 subcephalic setae occur in D. schultzi. D. natalensis also differs from D. schultzi in the number of subventral teeth in the stoma: two in D. natalensis and only one in D. schultzi. D. natalensis corresponds with the subgenus Zalonema in the horizontal divisions within the muscles and lining of the lumen of the basal bulb. The presence of ornamentations on the cuticle, the shape of the amphid aperture in the male and the punctate tail tip are different from that of any species within the subgenus Zalonema.

REMARK

The invaginated vulva surrounded by a few gland-like cells is similar to that described for Calomicrolaimus compridus (Gerlach, 1956) Gourbault &

Vincx, 1988, but no copulatory plug was observed in any female of Desmodora (Sibayinema) natalensis spec. nov.

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TABLE 1. MORPHOMETRICAL DATA OF DESMODORA (SIBAYINEMA) NATALENSIS SPEC. NOV.

	Holotype (♂)	Mean & range ♂	Standard deviation	Mean & range ♀	Standard deviation
Number of individuals	1	12		39	
L (mm)	0,9	1(0,8-1,1)	0,1	1,1(0,8-1,3)	0,1
a	34,1	39,5(32,6-45,7)	5,0	31,5(24-42,6)	4,2
b	7,1	7,6(6,7-8,8)	0,6	8,1(6,7-9,1)	0,6
c	8,4	9,5(8,4-10,6)	0,8	10,4(8,6-12,3)	0,8
c'	5,2	5(4,2-5,6)	0,4	5,4(4,5-6,5)	0,4
T(%)	51,3	52,7(49,1-57,2)	2,9	-	-
Spiculum length (μm)	35	34,9(29-40)	3,3	-	-
Gubernaculum length (μm)	15	12,5(11-15)	1,5	-	-
Tail length (μm)	102	101,5(79-115)	9,6	101,8(90-115)	6,9
Oesophagus length (μm)	121	125,8(114-148,5)	10,8	131,4(118,5-152)	7,7
Basal bulb width (μm)	19	18,9(17,5-21)	1,3	21,9(20-23,5)	1,5
Basal bulb length (μm)	21	21,2(19,5-22)	1,4	26,3(23-29)	2,5
Stoma length (μm)	10	9,2(8-11)	1,2	8,9(8-11)	1,5
Stoma width (μm)	3,5	3,2(2,5-4)	0,6	3,4(3-5)	0,6
Anterior to 1st tooth (μm)	4,5	4,3(4-6)	1,0	4,5(3-6,5)	1,2
Anterior to 2nd tooth (μm)	5,5	5,2(4,5-7)	1,1	5,6(4,5-8)	1,0
Head width (μm)	19	19,7(18,5-22,5)	1,1	21,2(20-23)	0,9
Anterior to amphid (μm)	10	9,4(9-10)	0,8	9,5(8-10)	0,9
Anterior to nerve ring (μm)	63	73,2(59-91)	9,6	75,5(66,5-91)	6,6
V (%)				62,7(58,7-65,8)	1,5
OV_1 (%)				52,9(47,6-57,9)	2,1
OV_2 (%)				74,9(70,2-80,7)	2,3

FIGURES 1 A-K: Desmodora (Sibayinema) natalensis spec. nov. A. Anterior region of holotype male; B. Cross-section of juvenile head (J4) showing dorsal tooth; C. Female tail; D. Testis, cloacal region and tail of holotype male; E. Cross-section of juvenile head at level of amphid apertures (J4); F. Female head; H. Juvenile (J4) head showing circular amphid and subcuticular punctations of head capsule; G. Male tail; I. Female reproductive system showing ripe oöcyte and posterior ovary; J. Anterior ovary; K. Heat-relaxed body posture of two males and two females.

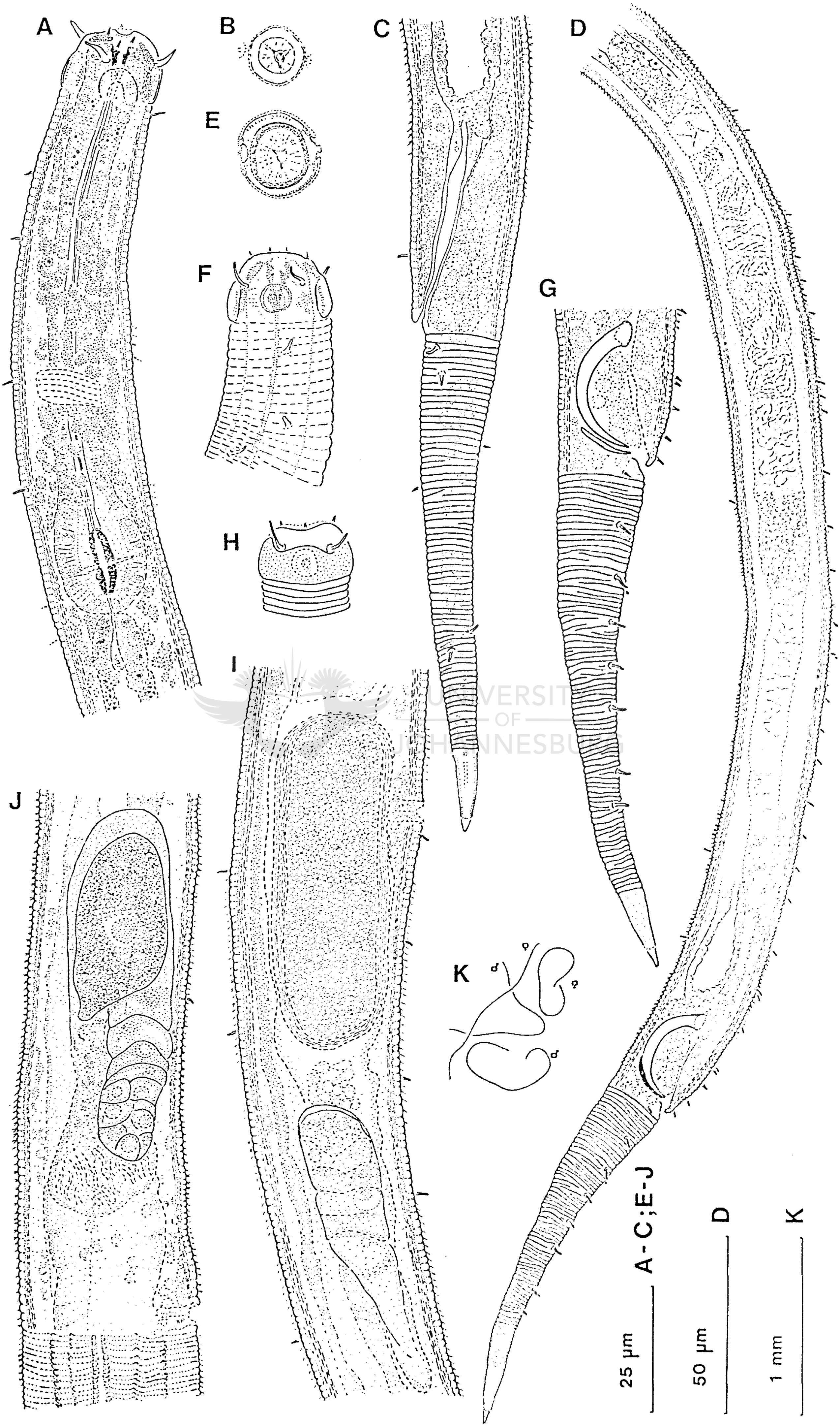
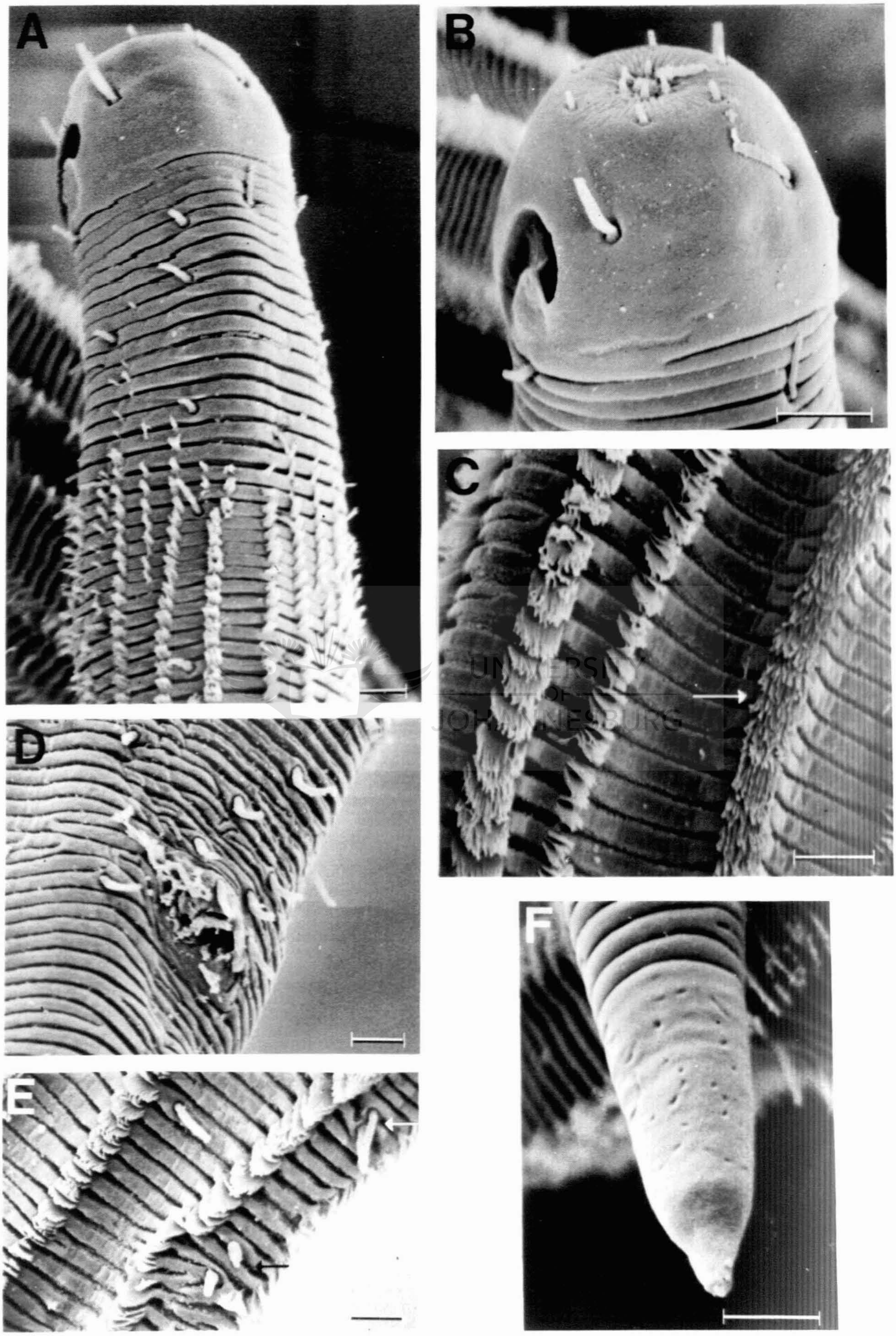

A
B
C
D
E
F
G
H
I
J
K
A-C;E-J
25 µm
D
50 µm
K
1 mm

FIGURE 2 A-F: Desmodora (Sibayinema) natalensis spec. nov. A. Anterior region of male; B. Frontal view of male head showing crescent-shaped amphid aperture; C. Cuticular ornamentations in midbody (male). Arrow indicates lateral cuticular differentiation; D. Cloacal region of male; E. Ventral pre-anal setae in male (arrows); F. Tail tip of male showing punctations. Bar equals 5 μm.


A
B
C
D
E
F