THE TAXONOMY AND FUNCTIONAL ANATOMY OF SOUTHERN AFRICAN ECHIURANS

by

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PREFACE

For the sake of convenience, this thesis is presented in two parts : the first part dealing with taxonomy and distribution and the second with functional anatomy. The thesis consists of published papers, manuscript papers and papers that have already been submitted for publication. In addition, interlinking sections have also been included, especially in the taxonomic part of the thesis,in order to bring together all the information into a single comprehensive account.

The following three papers have already been published:

1. Some aspects of the anatomy of *Ochetostoma caudex* (Echiura) from the east coast of southern Africa with remarks on its taxonomic status. *S. Afr. J. Zool*. 1983, 18: 47-55.

2. A key to the species of *Anelassorhynchus* (Echiura) with a description of a new species from the east coast of southern Africa. *S. Afr. J. Zool*. 1984, 19: 16-21.

3. The geographic distribution of Echiura from southern Africa. *S. Afr. J. mar. Sci*. 3: 11-21.

The manuscript entitled: "Ochetostoma (Echiura) from southern Africa with the description of a new species" has been submitted for publication in the Annals of the South African Museum.

The following three manuscripts are in the process of being submitted for publication:

1. *Thalassema* (Echiura) from southern Africa with the description of a new species.
   South African Journal of Zoology.

2. Burrowing, locomotion and other movements of the echiuran *Ochetostoma caudex*.
   Journal of Zoology, London.

3. The reproductive system, gametogenesis and annual reproductive cycle of *Ochetostoma caudex* (Phylum Echiura).
   Acta Embryologiae et Morphologiae Experimentalis.

A glossary of anatomical terms which are important in the classification and descriptions of echiurans is included at the beginning of the section on taxonomy. Keys for the identification of families and subfamilies of the class Echiurida are provided, followed by a key to the genera of the Echiuridae and Thalassematidae. Although the family Echiuridae is represented in southern Africa by a single species (*Echiurus antarcticus*), it is also diagnosed and discussed in order to complete the taxonomic account. Species already well known as well as those not available in the present collection have been rediagnosed.

The comprehensive reference list at the end of the thesis includes the references given at the end of each manuscript as well as those appearing elsewhere in the thesis. It was felt that a single and complete reference list would be more convenient for future researchers interested in this group of animals.

THE TAXONOMY AND FUNCTIONAL ANATOMY OF SOUTHERN AFRICAN ECHIURANS

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ABSTRACT

The southern African echiuran fauna currently comprises two families, four genera and eighteen species. The taxonomic positions of three other species, one of *Ochetostoma* and two of *Thalassema*, remain to be resolved. Of the recorded species, three are new to science and a further five are new records for the southern African region. This survey reveals that there are ten species of *Ochetostoma*, four of *Thalassema* and three of *Anelassorhynchus*. The family Echiuridae contains a single genus, *Echiurus* and in southern Africa, *E. antarcticus* is the only species recorded to date. Full descriptions of the new species and those formerly inadequately described are given. The diagnoses of some others are modified and, where necessary, additional notes added. Keys for the identification of families, genera and species are provided and the taxonomic characters are evaluated and discussed. The zoogeographic distribution of the southern African species is mapped and an attempt has been made to analyse the recorded species on the basis of faunistic provinces.

The phylogenetic position of the Echiura in the system of the animal kingdom is discussed. The lack of any form of segmentation of the mesodermal bands during embryonic development seems to justify their status as a separate phylum.

The biomechanics of burrowing, locomotion and trunk irrigatory movements of *Ochetostoma caudex* are described and compared with the activities of some other animals with unsegmented coelomic cavities. Pressure changes within the coelom have been measured with the use of electronic recording techniques and the results interpreted in relation to direct visual observation.

The anatomy of the reproductive system and the process of gametogenesis in *O. caudex* have been investigated with light and electron microscopes. Some observations on aspects of breeding behaviour and spawning are also included.

PART 1

TAXONOMY and DISTRIBUTION

INTRODUCTION

Echiurans are soft-bodied, burrowing animals with a spatulate proboscis at the anterior end as a result of which they are commonly referred to as spoon or tongue worms. They are common inhabitants of the rocky shores of the intertidal zone, although some deep water forms have been reported. A few species have also extended into estuaries. They are widely distributed and have been reported from all seas and all latitudes.

At present, very little is known about the echiuran fauna of southern Africa. No scientist from southern Africa has taken any interest in this group of animals. There is no single comprehensive report on the recorded species or on their range of distribution. The whole of the existing information on the phylum is confined to a very small number of publications. The only notable works on this group in southern Africa are those of Wesenberg-Lund (1959, 1963) and Stephen and Cutler (1969). A few publications, however, have referred to new species and new records (Jones & Stephen 1955, Biseswar 1983, 1984, 1985).

The descriptions of a number of species are extremely brief and lack critical information which can be used to distinguish them. It is thus apparent that many species need re-examination and redescription. In addition, some of the species are based on single individuals which means that nothing is known about the variations that occur within the species.

Only ten species have previously been recorded from the southern African region. A further three new species are described here and several new records added bringing the total number of named species for southern Africa to eighteen. The discovery of additional localities of some of the species previously recorded in the region sheds further light on their range of distribution. There are three further specimens in the present collection, one belonging to the genus *Ochetostoma* and two to *Thalassema*, that are probably new to science. Unfortunately two of them, belonging to the genus *Thalassema*, are too badly damaged to allow adequate descriptions. Any further decisions regarding their taxonomic positions will have to await the collection of additional material.

In the present investigation, many species are redescribed and/or re-diagnosed and some of the taxonomic problems are highlighted. The composition and zoogeographical implications of the fauna are discussed partly from the published works and partly from surveys made along our coastline. Keys to the families, genera and species have been constructed for the identification of species occurring in southern Africa.

It is anticipated that such an investigation should be of help to current and future workers and could lead to a better understanding of the phylum as a whole.

MATERIALS AND METHODS

This investigation is based largely on specimens that were collected over a period extending from March 1981 to October 1985. During this period numerous trips were undertaken, specifically in search of these animals, to several localities along the eastern and southern coasts. The recent records of a number of species from Isipingo and Park Rynie Beaches on the

Natal coast are mainly the result of more intensive investigations in these areas than elsewhere. During 1984-85, some of the localities in the vicinity of Durban were visited approximately once every month due to their accessibility. Along the Zululand coast collecting was confined mainly to three areas, namely, Mission Rock, Cape Vidal and Mapalane. A few species of Ochetostoma were also obtained from Embotyi on the Transkei coast, approximately 40km north of Port St Johns. During 1984 collecting trips were also undertaken to several rocky shores in the vicinity of East London and Cape Town.

As some species of echiurans have also been reported to occur in brackish water and in debris amongst the roots of marine angiosperms, some of these habitats were also explored.

In addition, the entire Reference Collection of the University of Cape Town was examined. Several species were also obtained as a result of requests made to other universities and institutions in southern Africa.

Precise information about the location and the nature of the sediment from which specimens were obtained was noted and in most cases, live animals were photographed. Specimens brought to the laboratories were either narcotized or maintained in well aerated aquaria in sediment obtained from their original habitats.

Narcotization of specimens was achieved by the addition of small quantities of magnesium sulphate to sea water over a period of three to four hours. This method proved to be very successful and the animals usually died with their proboscides and trunks fully extended. Injection of specimens with 10% formalin after narcotization is strongly recommended as preserving fluids do not pass easily through the body wall.

Measurements of the proboscides and trunks were usually made prior to fixation and preservation in 5% formalin. All the specimens were subsequently dissected and where possible variations were noted. Descriptions and drawings of the external and internal anatomy were made under a dissecting microscope with a drawing tube attachment. The setae were carefully removed, mounted in glycerine and drawn with the aid of a camera lucida. For studies of histological details, organs were embedded in paraffin wax and sectioned with a rotary microtome. The transverse sections, ranging from 7 to 10 µm, were stained either with Mallory's triple stain or haematoxylin and eosin. In a few cases, detailed investigations of certain organs such as the ciliated funnels of the anal vesicles and the gonostomal lips were made with the scanning electron microscope.

TAXONOMY

Explanation of terms as used for echiurans

The anatomical terminology used in the classification and descriptions of echiurans are given below. Some of the anatomical features have also been described in an earlier paper (Biseswar, 1983).

anal vesicles - A pair of elongate, blind-ending, often tubular or sac-like excretory structures lying in the coelomic cavity and discharging their products into the rectum.

ciliated funnels - Minute, ciliated funnel- or cup-shaped structures borne on the outer surface of the anal vesicles.

ciliated groove - A ciliated channel that runs along the ventral surface of the mid-intestine as far as the precloacal caecum.

collateral intestine or siphon - A narrow tube associated with the mid-gut for a considerable part of its length. Its function is not clearly understood.

circular muscle - The outermost muscle layer of the body wall.

dorsal blood vessel - A prominent blood vessel which lies in the anterior part of the body cavity, dorsal to the foregut. It passes anteriorly and enters the proboscis.

genital groove - A depression or furrow that extends from the genital pores to the mouth on the ventral surface of some genera of the Bonellidae.

genital pore - The external opening of the gonoduct through which eggs or sperm are discharged to the exterior.

gonoducts (nephridia) - Elongate or sac-like organs attached to the anterior and ventral surface of the body wall that serve for the temporary storage of eggs and sperm. They usually occur in pairs. Their number is constant within a species gonostomal lips - Lip-like extensions of the gonostome. They may be inconspicuous, expanded or leaf-like or extended into long threads which may or may not be spirally coiled.

gonostome - The opening of the gonoduct into the coelom through which gametes pass from the coelomic fluid into the gonoduct.

heart - A term used to describe the pulsating dorsal vessel.

interbasal muscle - A narrow, cylindrical muscle that connects the cone-shaped setal sacs of the two ventral setae.

longitudinal muscle bands - The longitudinal muscle layer of the body wall that is aggregated into bands which are visible externally.

neuro-intestinal blood vessel - A blood vessel that arises from the ventral vessel just posterior to the setae and joins the dorsal blood vessel.

oblique muscles - The innermost muscle layer of the body wall which may be either in the form of a continuous sheet or arranged in fascicles between the longitudinal muscle bands.

papillae - Wart-like or rounded, glandular structures that are found on the surface of most echiurans.

posterior (anal) setae - One or two rings of hook-like structures that encircle the posterior extremity of the trunk.

post-pharyngeal diaphragm - A thin-walled septum that incompletely separates the anterior part of the coelom from the general body cavity.

presiphonal intestine - Part of the intestine that lies anterior to the siphonal region.

rectal caecum (rectal diverticulum) - A blind, pouch-like structure of unknown function which arises from the rectum.

replacement setae - Reserve setae which do not project from the ventral surface of the body wall until they replace the functional ones.

ring vessel - A ring of vascular tissue which surrounds the posterior section of the foregut. Also referred to as intestinal ring sinus by some authors.

setal sac - A conical sheath that encloses the proximal end of each of the ventral setae.

ventral blood vessel - A prominent vessel that runs alongside the ventral nerve cord and terminates at the rectal caecum.

ventral groove - A ciliated groove on the ventral surface of the proboscis along which food particles and mucus are directed to the mouth.

ventral setae - Bristle - or hook-like structures that pierce the ventral body wall just posterior to the mouth. They are usually present as a pair.

DIAGNOSIS OF PHYLUM, CLASSIFICATION AND KEYS

Diagnosis

Bilaterally symmetrical, unsegmented, coelomate animals with subcylindrical or sac-like trunk. Proboscis muscular, extensible, attached to anterior end of trunk, cannot be retracted within body. Mouth anterior, at base of proboscis; anus posterior, at extremity of trunk. Alimentary canal long, highly coiled. Collateral intestine or siphon associated with considerable part of alimentary canal! Ventral setae one pair, situated on ventral surface of body just posterior to mouth. Anal setae in one or two rings, encircling posterior region of trunk, present in only two genera. Gonoducts one to numerous, usually arranged in pairs in body cavity. Eggs and sperm stored in gonoducts and discharged to exterior through genital pores. Anal vesicles excretory, one pair, usually bearing ciliated funnels or tubules, opening into rectum. Vascular system closed, consisting of dorsal, ventral and neuro-intestinal blood vessels except in one genus. Nerve cord ventral, unsegmented. Gonads diffuse, lying in mesentery above nerve cord, in mesenteries near rectum or located within body wall. Sexes separate; no external signs of sexual dimorphism except in the Bonellidae. Fertilization external; larva trochophore.

Classification

The most recent systems of classification of the phylum Echiura are those of Stephen and Edmonds (1972) and Datta Gupta (1976). A comparison of the two schemes is given in Table A. The system of classification proposed by Datta Gupta (1976) has been adopted by the present author

Table A. A comparison of two most recent systems of classification of the phylum Echiura.

Author	Phylum	Class	Order	Family	Subfamily
Stephen &			Echiuroinea	Bonellidae	Echiurinae
Edmonds	Echiura	Echiurida		Echiuridae	Thalassematinae
(1972)					
			Xenopneusta	Urechidae	
			Heteromyota	Ikedaidae	
			Xenopneusta	Urechidae	
		Echiurida			
Datta Gupta	Echiura				
(1976)					
					Ochetostomatinae
			Echiuroinea	Thalassematidae	
					Thalassematinae
				Ikedaidae	
		Sactosomatida		Echiuridae	
				Bonellidae	Acanthohaminginae
					Archibonellinae
					Acanthobonellinae
					Bonellinae

except that the class Sactosomatida has been omitted. In agreement with Stephen and Edmonds (1972), the creation of a separate class Sactosomatida seems to be unwarranted as the class is based on a single species, inadequately described from one damaged specimen. Stephen and Edmonds appear to be justified in placing Sactosoma vitreum amongst the species inquirendae and species incertae sedis.

According to the scheme proposed by Datta Gupta (1976), the families included in the order Echiuroinea are the Echiuridae, Thalassematidae, Bonellidae and Ikedaidae while the order Xenopneusta contains a single family, the Urechidae. The order Xenopneusta differs in lacking a closed blood vascular system and includes forms where the posterior region of the intestine is enlarged and modified for anal respiration. Stephen and Edmonds (1972) recognize a separate order Heteromyota to include the family Ikedaidae.

Only two families, namely the Echiuridae and the Thalassematidae have been recorded in southern Africa to date.

Other important differences between the two systems of classification are also present in the arrangement of the families and subfamilies (see Table A). Stephen and Edmonds (1972) have created two subfamilies within the family Echiuridae, namely the Echiurinae and Thalassematinae. An important deviation from this system of classification is the recognition of the Thalassematidae as a separate family by Datta Gupta (1976) and its subdivision into two subfamilies, the Ochetostomatinae and the Thalassematinae. This system of classification is preferred by the present author because the absence of anal setae in the family Thalassematidae is an important feature which clearly separates it from the Echiuridae and hence deserves to be raised to the rank of family. Furthermore, the subdivision of the family Thalassematidae into two subfamilies Ochetostomatinae and Thalassematinae seems to be very appropriate, the basis of the distinction being the disposition of the dermal longitudinal muscles, which in the Ochetostomatinae are aggregated into distinct bands whereas in the Thalassematinae form a continuous sheet.

Keys to the families and subfamilies of the class Echiurida.
[Adapted from Stephen & Edmonds (1972) and Datta Gupta (1976)].

1 Species with marked sexual dimorphism. Proboscis either simple or bifid; gonoducts one or two; anal vesicles usually branched and bearing stalked funnels. Male small, degenerate and parasitic in or on the female; posterior or anal setae absent.
Bonellidae 6

- Species without sexual dimorphism. Proboscis not bifid; gonoducts paired; anal vesicles usually sac-like and not branched; male not parasitic; anal setae either present or absent 2

2 Anal setae present 3
Anal setae absent 4

3 Two rows of anal setae. Gonostomes without spirally coiled lips ....Echiuridae

- One row of anal setae. Gonostomes with elongate spirally coiled lips ....Urechidae

4 Gonoducts unpaired and numerous (200 - 400); gonostome terminal
..............................Ikedaidae

- Gonoducts from one to seven pairs; gonostome lateral.
Thalassematidae 5

5 Longitudinal muscles of body wall gathered into a varying number of well defined bands ....Ochetostomatinae

- Longitudinal muscles of body wall continuous, not aggregating into bands ....Thalassematinae

6 A genital groove generally bearing setae extending from the genital pore to the mouth ....Acanthohaminginae

- Genital groove absent 7

7 Gonoducts two, a median pouch present, with or without an internal opening ....Archibonellinae

- Gonoduct one, median pouch absent 8

8 Male sac distinctly marked off by a constriction in the gonoduct ....Acanthobonellinae

- Male sac not distinctly marked off in the gonoduct...Bonellinae

Key to the genera of Echiuridae and Thalassematidae

The present key has been adapted from those provided by Stephen & Edmonds (1972) and Datta Gupta & Menon (1976). Only four genera, Echiurus, Ochetostoma, Anelassorhynchus and Thalassema, have been recorded from southern Africa to date.

1 Two rings of anal setae. A post pharyngeal diaphragm incompletely separates the body into two parts..........................Echiurus.

- Anal setae absent. No post-pharyngeal diaphragm..................2

2 Longitudinal muscles of body wall gathered into a varying number of longitudinal bands..3

- Longitudinal muscles of body wall continuous without aggregating into bands 6

3 Gonoducts numerous, in three to fourteen groups of one to four gonoducts per group, the groups being arranged in pairs. .... Ikedosoma.

- Gonoducts not numerous and not arranged in groups.................4

4 Oblique muscles distinctly fasciculated. Gonoducts one to seven pairs with spirally coiled gonostomal lips.........Ochetostoma.

- Inner layer of oblique muscles not separated into transverse fascicles. Gonoducts one to three pairs..........................5

5 Gonostomal lips spirally coiled. A strong interbasal muscle always present..Listriolobus.

- Gonostomal lips not spirally coiled. Interbasal muscle either present or absent...................................Lissomyema.

6 Gonostomal lips elongate and usually spirally coiled ....Anelassorhynchus.

- Gonostomal lips not elongate and not spirally coiled..............7

7 Gonostomal lips expanded into a leaf-like structure with irregularly sculptured margins. Anterior extremity of proboscis expanded or fan-like.................................Arhynchite.

- Gonostomal lips not leaf-like but inconspicuous or semi-circular. Anterior extremity of proboscis not expanded or fan-like ....Thalassema.

Family Thalassematidae
Genus Ochetostoma

OCHETOSTOMA (ECHIURA) FROM SOUTHERN AFRICA WITH THE DESCRIPTION OF A NEW SPECIES

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(With 35 figures and 1 table)

(Manuscript submitted for publication in the Annals of the South African Museum but not yet accepted).

ABSTRACT

In southern Africa, the genus *Ochetostoma* is currently represented by ten species. *O. natalense* is here described as new to science. *O. baronii*, *O. kempi*, *O. palense*, *O. decameron* and *O. formosulum* are redescribed and figured; the first four are new records for the region. The status of one species from Park Rynie Beach, on the Natal coast, remains to be resolved. *O. capense* and *O. arkati* are briefly diagnosed. *O. caudex* and *O. erythrogrammon*, recorded from several localities, are fairly well known and their taxonomic positions have been discussed in an earlier paper. A key for the identification of all the species in the genus is provided and the distribution of the southern African forms is briefly discussed.

CONTENTS

INTRODUCTION

At present, our knowledge of the southern African echiuran fauna is rather scanty. This is the fourth in a series of papers on the systematics and distribution of the echiurans of Africa south of 20°S. The third paper (Biseswar 1985) dealt with the genera and species of echiurans from southern Africa and mapped their distribution, partly from the published works and partly from surveys made along our coast.

The present paper is a comprehensive report on the species of Ochetostoma from these waters. In their monograph, Stephen & Edmonds (1972) have outlined some of the taxonomic problems encountered in the group. It is evident from the literature that many of the species listed in this genus need re-examination and redescription.

MATERIALS AND METHODS

Collecting trips, specifically in search of these animals, were undertaken to several localities along the Natal and Cape coasts. Most of the shallow water material used in this study was, however, obtained from the rocky shores of the Natal coast. Some species were also obtained as a result of requests made to several universities and institutions in South Africa.

Living specimens were photographed and then narcotized by adding small quantities of magnesium sulphate to sea water. Measurements of the proboscis and trunk were taken after preser=vation in 10% formalin. All the specimens were subsequently dissected and, where possible, variations were noted. Gross morphology was studied with the aid of a camera lucida.

KEY TO THE SPECIES OF THE GENUS OCHETOSTOMA

The keys for the species Ochetostoma, provided by Datta Gupta & Menon (1971) and Stephen & Edmonds (1972) have been modified to accommodate O. natalense. An attempt has also been made to update the existing keys in the light of additional information obtained from the re=descriptions of some of the species. In the present key, other less rigorous characters have also been included to assist in the identifi=cation of single individuals. A discussion of the structure and terminology of the group is included in a previous paper (Biseswar 1983).

1 Gonoducts 7 pairs 2

- Gonoducts 5 pairs or less 3

2 First pair of gonoducts presetal. Twelve longitudinal muscle bands..

O. zanzibarense Stephen & Robertson, 1952.

- All gonoducts postsetal; 7 longitudinal muscle bands

O. senegalense Stephen, 1960.

3 Five pairs of gonoducts 4

- Four or fewer pairs of gonoducts 5

4 First three pairs of gonoducts presetal; 19 longitudinal muscle bands ....O. hornelli (Prashad, 1921).

- First two pairs of gonoducts presetal; 10-11 longitudinal muscle bands ....O. bombayense (Prashad & Awati, 1929)

5 Gonoducts four pairs with first pair presetal 6

- Gonoducts three or fewer pairs 7

6 Ten longitudinal muscle bands .....O. decameron (Lanchester, 1905).

- 17-20 longitudinal muscle bands....O. kempi (Prashad, 1919).

7 Gonoducts three pairs; only 1st pair presetal 8

- Gonoducts 2 pairs 12

8 Proboscis slightly bifurcated with ventral and terminal rims crenated. 18 longitudinal muscle bands. Colour of trunk pink

O. indosinense Wesenberg-Lund, 1939.

- Proboscis not bifurcated, margins smooth 9

9 Small flat papillae confined to anterior and posterior surfaces of trunk.

Living specimens red in colour.

Usually 12-13 longitudinal muscle bands, occasionally 11-14..

.................................*O. australiense* Edmonds, 1960.

- Papillae distributed over entire surface of trunk, much larger posteriorly 10

10 Alimentary canal short, about three times trunk length. 15 longitudinal muscle bands. Bright green in life ....

O. palense Ikeda, 1924.

- Alimentary canal long, about five times trunk length 11

11 Integument thin and transparent in middle region of trunk.

12-18 longitudinal muscle bands ....

O. erythrogrammon Leuckart & Rüppel, 1828

- Integument thick and opaque throughout.

Usually 16-22 longitudinal muscle bands, very occasionally 14-16..

O. caudex (Lampert, 1883)

12 Interbasal muscle absent 13

Interbasal muscle present 20

13 Lateral edges of proboscis modified 14

Lateral edges of proboscis not modified 17

14 Gill-like processes along basal edges of proboscis. Eight longitudinal muscle bands ....O. arkati (Prashad, 1935).

- Proboscis without gill-like structures 15

15 Proboscis with dendritic outgrowths

Seven longitudinal muscle bands ....

.... O. septemyotum Datta Gupta, Menon & Johnson, 1963

- Proboscis without dendrite outgrowths but proximal border with processes with scalloped edges 16

16 Oesophageal diverticulum present

13 longitudinal muscle bands

Trunk with 30-35 rings of large oblong papillae ....

.... O. mercator Wesenberg-Lund, 1954

- Oesophageal diverticulum absent. 12-13 longitudinal muscle bands. Skin smooth with only a few rings of papillae at posterior end of trunk .... O. glaucum (Wesenberg-Lund, 1957).

17 Eight longitudinal muscle bands. Proboscis one-third trunk length. Integument translucent ....O. octomyotum Fisher, 1946.

- Muscle bands 10 or more 18

18 Trunk yellow in colour, covered with small uniformly distributed papillae. 10-11 muscle bands......... O. hupferi (Fischer, 1895).

- Trunk not yellow, papillae more densely packed at posterior end..... 19

19 Trunk light green to bluish in colour, up to 25mm long and transparent in middle region. 13 longitudinal muscle bands .... *O. pellucidum* (Fischer, 1895).

- Trunk reddish-purple, up to 94mm in length. Integument thick and opaque. 17-20 longitudinal muscle bands .... *O. natalense* sp. nov.

20 Muscle bands less than 10 21

- Muscle bands more than 10 22

21 Posterior end of trunk with a ring of elongate papillae. Trunk up to 35mm in length. 7-8 muscle bands .... *O. formosulum* (Lampert, 1883)

- Posterior end of trunk without elongate papillae. Trunk up to 120mm in length. 7-8 muscle bands .... *O. capense* Jones & Stephen, 1955.

22 Interbasal muscle extends over pharynx. Trunk greyish-green. 14 longitudinal muscle bands ....*O. manjuyodense* (Ikeda, 1905).

- Interbasal muscle passes below pharynx 23

23 Proboscis readily deciduous. Oblique muscles between longitudinal bands well developed. 17-19 muscle bands .... *O. baronii* (Greeff, 1879)

- Proboscis not readily deciduous. Oblique muscles between longitudinal bands weakly developed. 18-21 muscle bands .... *O. myersae* Edmonds, 1963.

Ochetostoma Leuckart & Rüppel, 1828

Generic diagnosis

Longitudinal muscle layer of body gathered into distinct bundles. Inner oblique muscles between the longitudinal bands form fascicles. No anal or posterior setae. Gonoducts are paired, ranging from 1-7 pairs. Gonostomal lips elongate and usually coiled.

Type species: *Ochetostoma erythrogrammon* Leuckart & Rüppel, 1828

Remarks

The genus is the largest of all the echiurans and comprises 24 species. It was only after Spengel's paper in 1912 and Wharton's in 1913 that the taxonomic importance of the condition of the oblique muscles was realized (Stephen & Edmonds 1972). Unfortunately, some of the earlier descriptions contain no information about the oblique muscles and hence the generic position of a number of species that have been assigned to the genus *Ochetostoma* is doubtful. They may belong to the genus *Listriolobus*. More detailed redescriptions of some of the species, based on additional material, are required before their taxonomic positions can be satisfactorily resolved.

Distribution of *Ochetostoma*

The genus is very widely distributed in tropical and subtropical waters of the Indian, Atlantic and Pacific Oceans. The majority of the species is confined to shallow waters of the inter=tidal zone but a few have been reported from considerable depths. In their monograph, Stephen and Edmonds (1972) give the range of distribution of each species.

Ochetostoma natalense sp. nov.

Figs. 1-6, Table 1.

Records

Park Rynie Beach (31°19'S/30° 44'E) and Isipingo Beach (29°05'S/30° 56'E), Natal coast.

Holotype

SAM-A21924 in the South African Museum, Cape Town. Adult male, Park Rynie Beach, collected by K.S. Ganga, 18 October 1982. The specimens from Park Rynie Beach occurred in coarse sand under a projecting ledge of rock facing the shore, while those from Isipingo were found under loose rocks in a rock tunnel. At both localities, the specimens were found in the intertidal area, close to the high water mark.

Paratypes

SAM- A21925 in the South African Museum. Seven specimens from Park Rynie and Isipingo Beaches, collected by author, 1983 and 1984.

Description

Trunk length of holotype 80mm and proboscis length 58mm. Of the paratypes, 5 sexually mature since gametes present in gonoducts. Trunk length of sexually mature specimens ranges from 54 to 94mm and of proboscis from 30mm to 58mm (Table 1). Hence proboscis ranges from about one-third to three-quarters the trunk length.

Table 1. Measurements in millimetres after narcotization and preservation in 10% formalin.

Length of trunk and proboscis	Trunk length	Ratio of proboscis to trunk length	
* 138	80	0,73	holotype
* 120	85	0,41	paratypes
* 111	71	0,56	
* 110	69	0,59	
* 69	54	0,56	
* 126	94	0,34	
86	50	0,72	
82	47	0,74	

* denotes specimens with gametes in their gonoducts

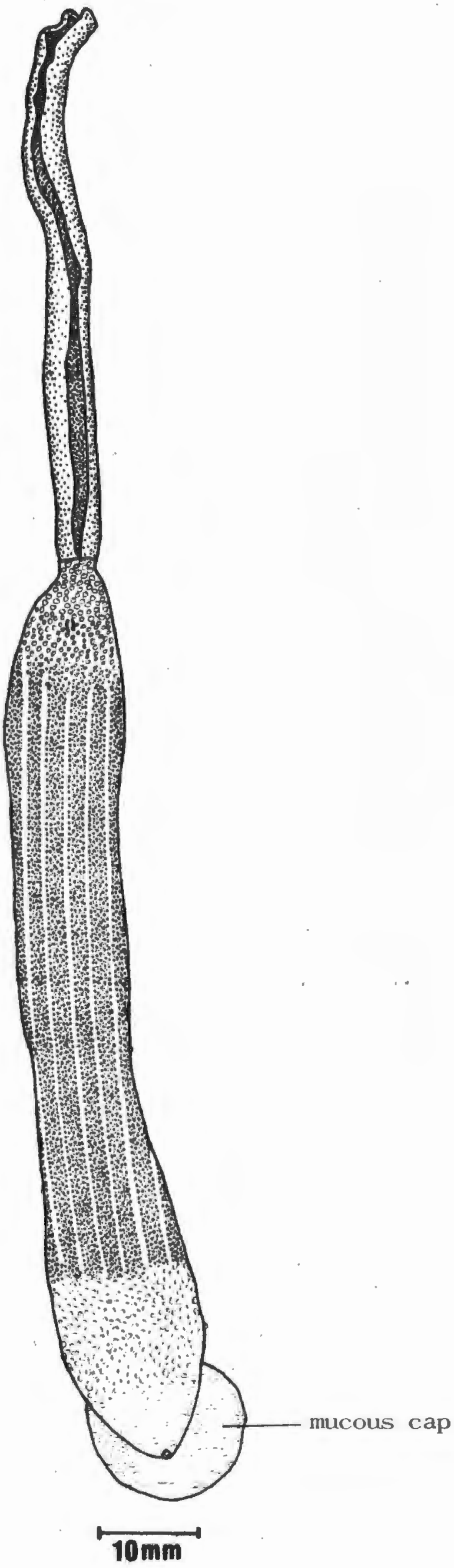

Fig. 1. Ventral aspect of Ochetostoma natalense sp. nov.

Colour

In living specimens, proboscis is pale-yellow. Trunk with reddish-purple longitudinal stripes marking longitudinal muscle bands, interspaces bluish-grey. Posterior extremity of trunk white, tinged with green in a few specimens. In preserved specimens, colour changes to pale-pink.

External features

Proboscis

Proboscis fleshy, non deciduous and of unform diameter through= out (Fig.1). Spatula-shaped in live animals but in preserved specimens, lateral edges curl inwards to form a tubular structure. Lateral margins of proboscis smooth and free at base.

Trunk

Trunk sausage-shaped, more or less of uniform diameter (Fig.1). Papillae minute, densely arranged over most of trunk except at posterior end where they are very prominent, round to ovoid in shape. Size and distribution of papillae uniform in all specimens. A white mucous cap encases posterior extremity of trunk in formalin preserved specimens.

Entire integument thick and opaque.

Longitudinal muscle bands range from 17 to 20, inner oblique muscle layer between longitudinal bands forming distinct fascicles.

Ventral setae one pair, located at anterior end of trunk, close behind mouth.

Genital pores two pairs, opening posterior to setae.

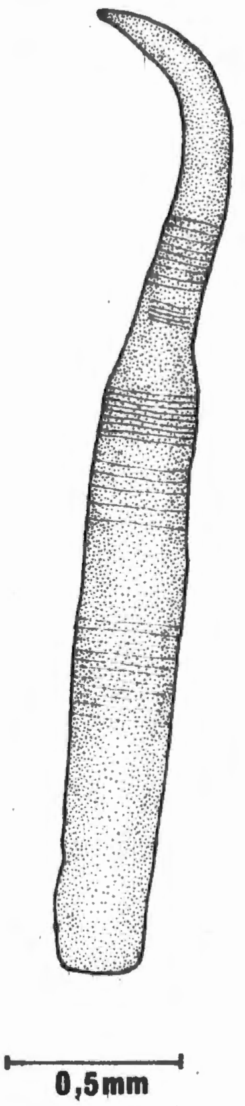

Fig. 2. Right functional seta of *O. natalense*.

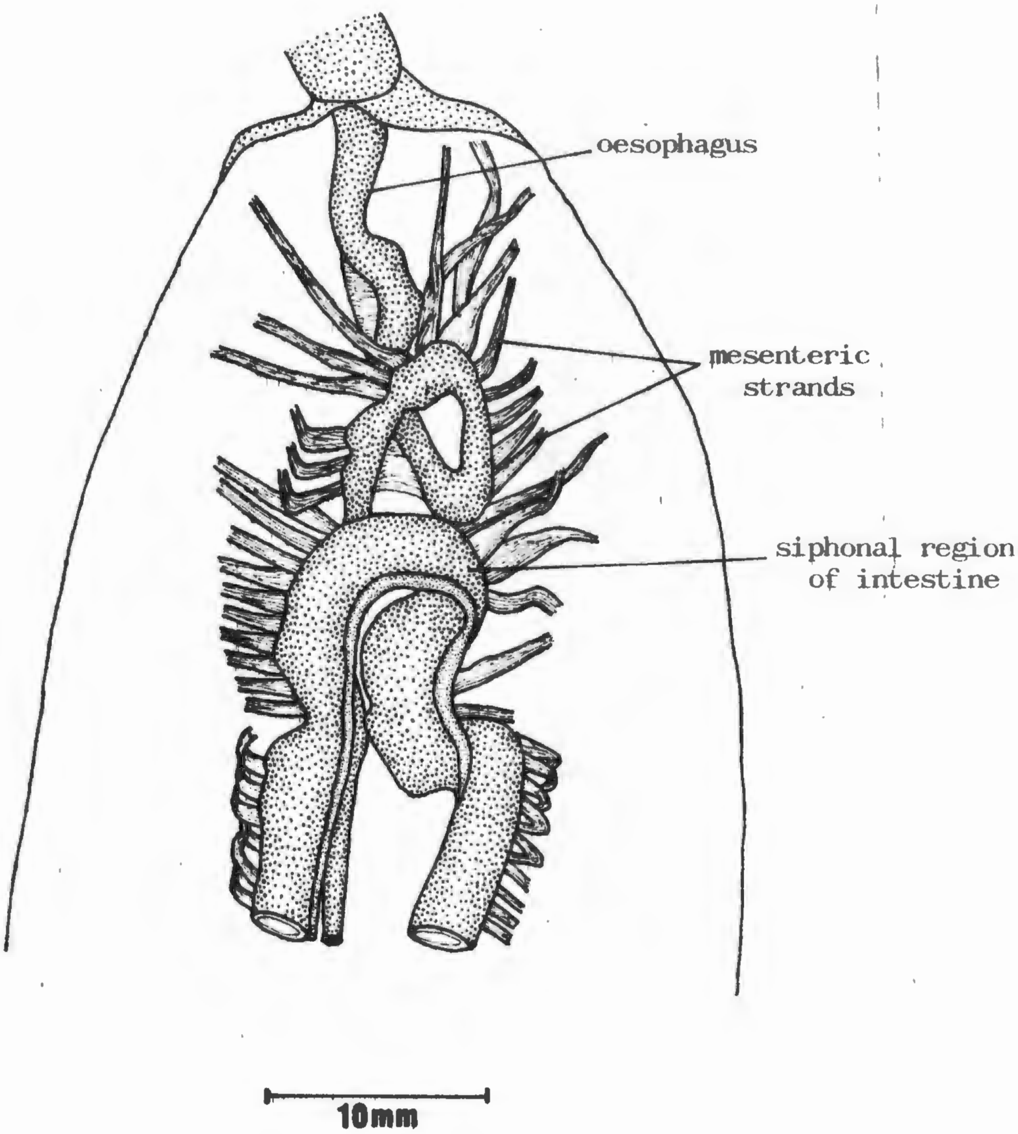

Fig. 3. Anterior part of the alimentary canal of *O. natalense* showing the mesenteric strands.

Setae

Each seta consists of a cylindrical shaft with curved terminal end tapering towards tip (Fig. 2). Much narrower distal third of seta golden-yellow in colour while proximal two-thirds dark brown. Concentric markings present mainly on middle two-thirds of shaft. Each seta is invested in connective tissue and supported by radiating muscle strands as in other related species. There is no interbasal muscle between setae.

Internal anatomy

Alimentary canal

Alimentary canal is considerably longer than trunk and intricately coiled (Fig.3). In holotype, numerous, closely arranged mesenteric strands fasten gut to body wall (Fig.3). Mesenteric strands fewer in paratypes and more sparsely arranged. Foregut comparatively small, terminating at ring vessel. After ring vessel, intestine pursues complicated course through body cavity forming several ascending and descending limbs. A double sheet of mesentery fastens oesophagus to anterior part of body wall.

Intestine proper commences soon after ring vessel and is differentiated into presiphonal, siphonal and postsiphonal regions. Presiphonal region marked by presence of a ciliated groove which in holotype is about 36mm long. Intestine considerably dilated and extremely thin-walled in region of siphon whereas in postsiphonal region it is narrow with fairly thick walls. Last part of intestine of uniform diameter, leading into more or less straight rectum. Small, spherical rectal caecum present in all specimens.

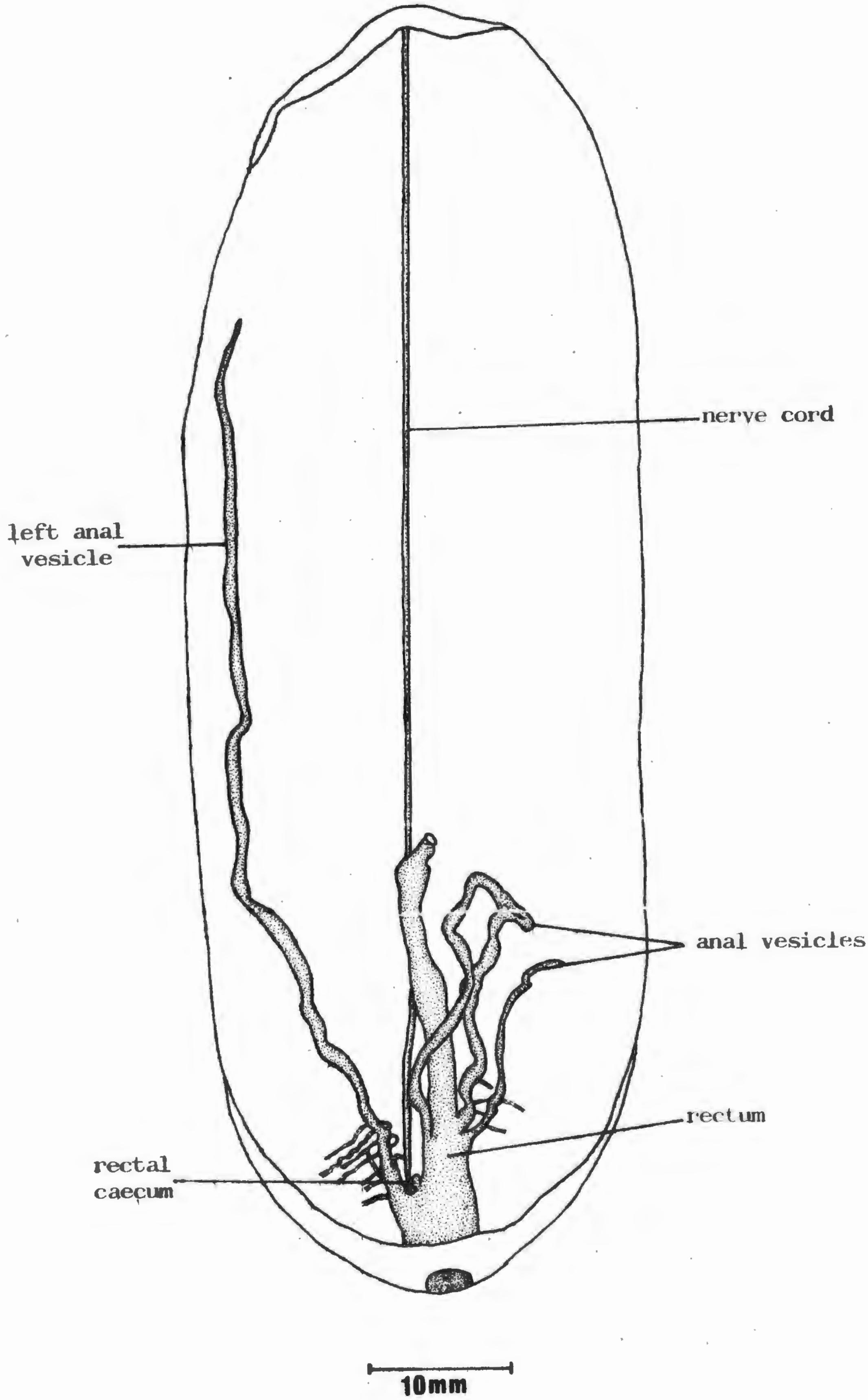

Fig. 4. Dorsal dissection of the trunk of O. natalense showing the abnormal anal vesicles of the holotype.

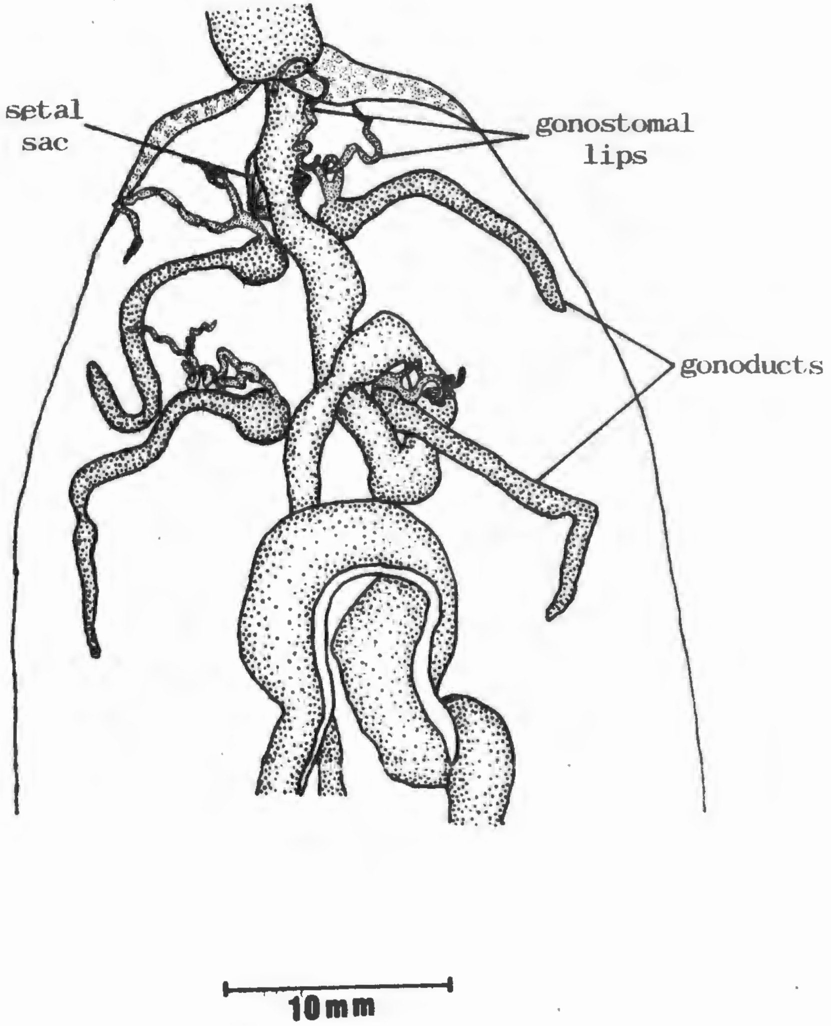

Fig. 5. Anterior end of the trunk cavity of O. natalense illustrating the gonoducts.

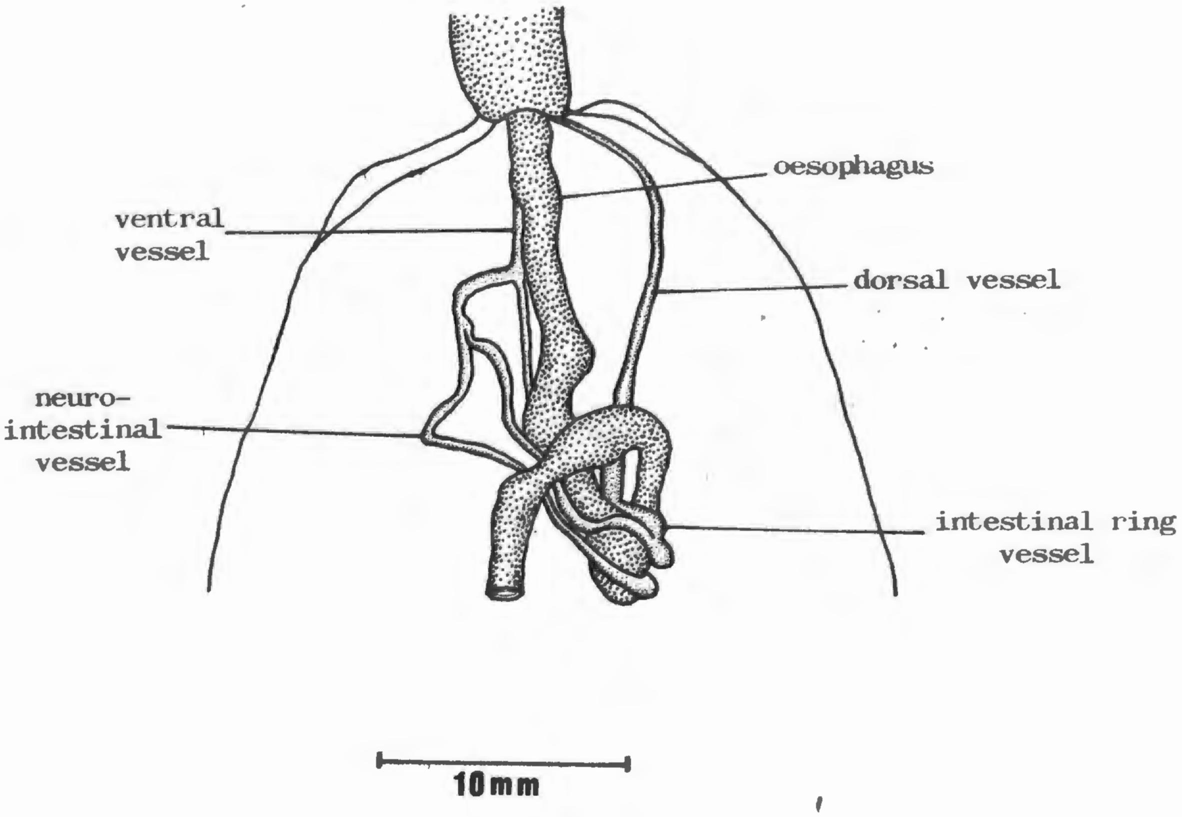

Fig. 6. Anterior end of the trunk cavity of O. natalense showing blood vessels.

Anal vesicles

Anal vesicles elongate, distensible tubes lying in coelom and opening into rectum.

In holotype, anal vesicles are abnormal. Left anal vesicle about three-quarters length of trunk while right one about one-fifth as long. In addition to these, a third anal vesicle present, which, instead of terminating blindly, forms a loop and reopens into rectum (Fig.4). All three vesicles covered with numerous, tiny ciliated funnels.

In paratypes, as in other related species, anal vesicles are normal and are almost equal to or longer than trunk. Numerous thin, mesenteric strands fasten proximal end of vesicle to body wall while distally they loosely interweave through coils of intestine.

Gonoducts

Two pairs of elongate, tubular gonoducts are located behind setae; posterior pair much larger (Fig.5). In holotype gonoducts swollen at base. Gonostomal lips elongate and spirally coiled. Opening of gonostome basal in position. Gonoducts considerably distended due to presence of gametes in sexually mature individuals.

Blood system

Intestinal ring sinus is an incomplete vascular ring located at end of foregut (Fig.6). Neuro-intestinal vessel elongate, double for most of its length. Dorsal vessel, after arising from ring sinus, continues anteriorly, dorsal to oesophagus and pharynx and enters proboscis.

Remarks

Distinctive features of the present species from southern Africa include the number and location of the gonoducts in relation to the setae, the presence of 17 to 20 longitudinal muscle bands, the nature of the integument, the characteristic shape and distribution of the dermal papillae and the absence of an interbasal muscle. The interbasal muscle is a useful taxonomic character in echiurans. Other features of lesser significance are the colour and size of the animals and the ratio of the proboscis to the trunk lengths.

In the genus Ochetostoma, there are 13 species that possess two pairs of gonoducts (See Key).

The species O. arkati, described originally from Calcutta, India, differs from O. natalense in several respects. In the former species, the longitudinal muscles are gathered into 7 to 8 bands and the proboscis is short, about a third to a quarter of the trunk length. However, the most important distinguishing feature of O. arkati is the presence of short, branched, gill-like processes along the edges of the posterior half of the proboscis.

The species, O. septemyotum differs from other known echiurans in the genus in possessing a proboscis where the lateral margins are produced into a series of folds with dendritic outgrowths that are bent inwards into the proboscis groove.

The following species: O. baronii, O. capense, O. myersae and O. formosulum are distinct from O. natalense in possessing an interbasal muscle which passes through a loop of the neuro-intestinal vessel. In addition, there are several other differences in the proboscis, integument and dermal papillae that separate the above species from O. natalense.

O. hupferi from Nyango, West Africa is based on a single damaged specimen recorded from a depth of 11m. In the latter species, the trunk is small, light yellow in colour and covered with small uniformly distributed papillae. The proboscis is 5mm in length and the ventral setae are large, golden-yellow in colour. Fischer's description (1895) mentions that the longitudinal muscle layer is gathered into 10 to 11 bands. The most important differences between O. hupferi and O. natalense lie in the number of longitudinal muscle bands, in the size of the ventral setae and in the distribution of the dermal papillae. Differences are also present in size as well as in the colour of live animals.

The original description of O. manjuyodense is based on a single specimen from Manjuyodi, Philippines in which the proboscis was missing. Fisher (1948) merely recorded this species from Hawaii. The trunk is 18mm in length and has a greyish-green tint. The dermal papillae are minute, almost invisible to the naked eye, except at the posterior end where they are somewhat larger and arranged almost in circular rows. A very distinctive feature in this species is the interbasal muscle which extends over the pharynx. The longitudinal muscles are gathered into 14 broad bands. The anal vesicles are covered with numerous short-stalked funnels which are visible to the naked eye. In addition to the interbasal muscle, important differences also occur in the size and distribution of the dermal papillae, in the number of muscle bands and in colour of the animals.

O. mercator, described by Wesenberg-Lund (1954) is known only from the holotype. In this species, the trunk is 25mm long and the proboscis which is broad, fleshy and non-deciduous, is one-fifth its length. An important feature that distinguishes this species from *O. natalense* is the presence of 30-35 rings of large, oblong papillae on the trunk. Another difference lies in the longitudinal muscle layer, which in *O. mercator* is gathered into 13 bands. The proboscis of *O. mercator* is also much smaller in comparison with the length of the trunk.

Fisher (1946) erected the species, *O. octomyotum* from several specimens collected from the Californian coast. His description mentions that the trunk of full grown specimens is 110mm long and the proboscis ranges from one-third to the full length of the body. The longitudinal muscle layer is gathered into 8 bands but in the posterior third of the trunk it forms a continuous sheet. The integument of *O. octomyotum* is translucent. Thus important differences between the two species lie mainly in the number of longitudinal muscle bands and in the nature of the integument. As in *O. natalense*, the ventral setae have no interbasal muscle.

O. pellucidum has been described originally from several specimens from the West African coast at depths of 10m. In this species, the trunk which is light green to bluish in colour is 25mm long and the proboscis is about one-quarter its length. The longitudinal muscles are gathered into 13 bands. Fischer's description (1895) mentions that the integument is opaque anteriorly and posteriorly but transparent in the middle region. Hence differences exist in the number of longitudinal muscle bands and in the nature of the integument. Other differences are present in the colour and size of the specimens. Furthermore, the anal vesicles of *O. pellucidum* are only about one-quarter as long as the trunk and the ventral setae are large.

The species O. glaucum is known from two rather badly preserved specimens. According to the description provided by Wesenberg-Lund (1957), the trunk is about 22mm in length and the proboscis is 6mm long. An interesting feature in this species is the presence of two rows of processes on the proximal part of the proboscis. The outer row consists of rather long lobes with slightly scalloped edges. The integument is smooth with only a few rings of papillae on the posterior part of the trunk. There are 12 to 13 longitudinal muscle bands. This species differs significantly from O. natalense in the structure of the proboscis, in the distribution of the papillae and in the number of longitudinal muscle bands.

Thus it is evident that O. natalense differs significantly from the other known species of Ochetostoma that possess two pairs of gonoducts to justify the establishment of a new species.

Ochetostoma baronii (Greeff, 1879)

Figs 7-10

Thalassema baronii Greeff, 1879: 151, pl.6, figs 62-67. Selenka, 1885: 8. Shipley, 1899a: 55-56; 1899b: 336, 345-346, pl. 33, figs 1, 7. Sluiter, 1902: 47. Augener, 1903: 348. Verrill, 1904: 40-41. Lanchester, 1905:34. Fischer, 1922: 15. Hérubel, 1924: 108-109.

Thalassema kefersteini A ten Broeke, 1925: 94.

Ochetostoma baronii: Fisher, 1946: 241.

Stephen, 1960: 513. Mackie, 1961: 247-249.

Stephen & Edmonds, 1972: 429. Amor, 1976: 123-125.

Ochetostoma edax Fisher, 1946: 245-247, fig. 14.

Present records

One sexually mature female, Pontá Torres, west coast of Inhaca Island, collected by Zoology Department, Witwatersrand University during 1956-63. Two juvenile specimens, Park Rynie, Natal, collected by the author on 28 May and 8 September 1983.

Previous records

Numerous localities in tropical and sub-tropical waters of the Indian, Atlantic and Pacific Oceans.

Type locality

Arrecife, Canary Islands (Atlantic Ocean).

Habitat

At both localities, the specimens were found under rocks in the intertidal zone. While the specimen from Inhaca Island occurred in mud in a permanent pool, those from Park Rynie were discovered in relatively coarse sand.

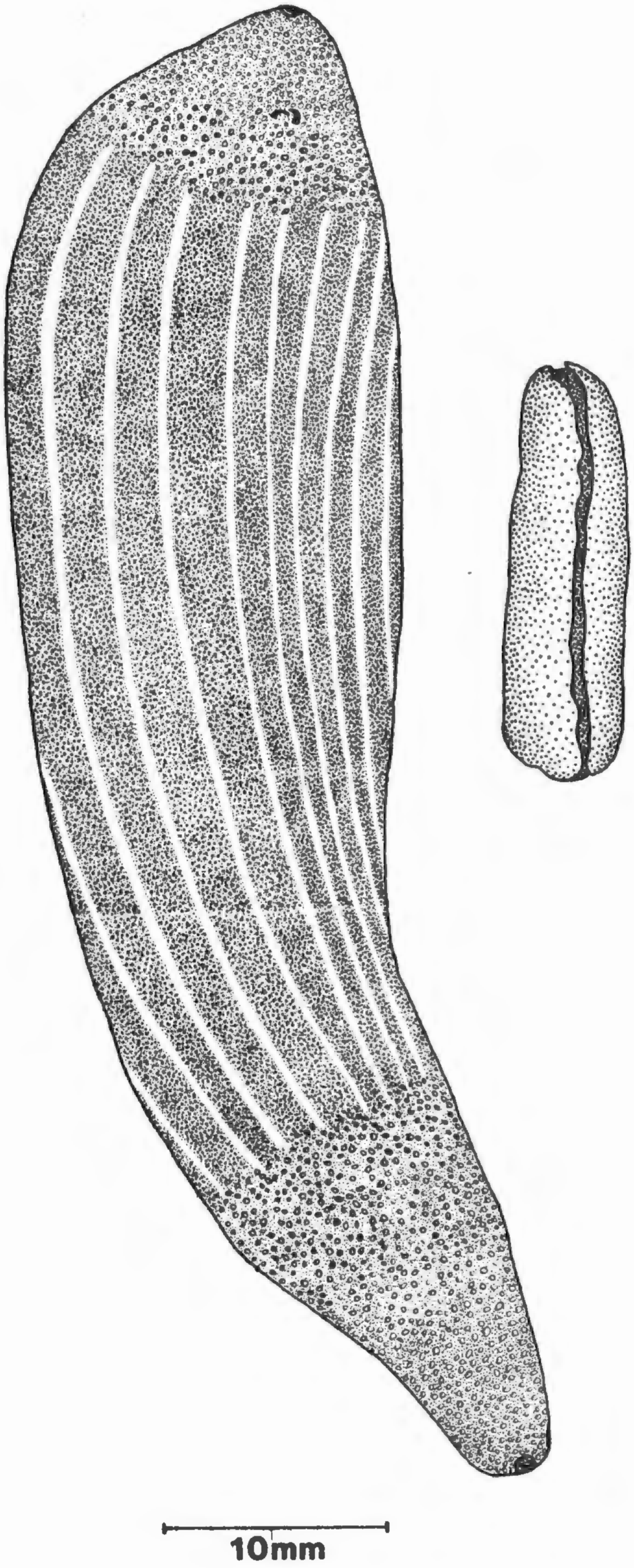

Fig. 7. Ventral view of trunk and detached proboscis of <u>O. baronii</u>.

Description

Size of specimens

Trunk of preserved specimen from Inhaca Island 66mm long, greatest diameter 17mm. Proboscis 18mm long, detached from specimen.

Measurements of specimens from Park Rynie Beach made after narcotization with magnesium sulphate and preservation in formalin. Trunk length of Park Rynie specimens 21mm and 30mm and proboscis length 6mm and 8mm respectively. Hence proboscis from about a quarter to one-third trunk length.

Colour

Colour of trunk purple in live specimen from Inhaca Island, proboscis pale yellow with fine green stripes. Colour of trunk and proboscis of both specimens from Park Rynie rich dark green. Green coloration due to symbiotic algae. In preserved specimens, colour ranges from pale pink to dull greyish-brown.

External features

Proboscis

Proboscis markedly deciduate. In living specimens may exceed half length of trunk. Proboscis spatula-shaped in living specimens but tubular when preserved (Fig. 7). Anterior and lateral margins smooth and free at base of proboscis. In smaller specimen from Park Rynie, proboscis detached during narcotization.

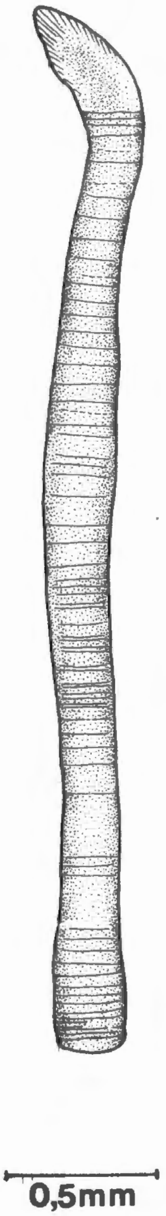

Fig. 8. Left functional seta of O. baronii.

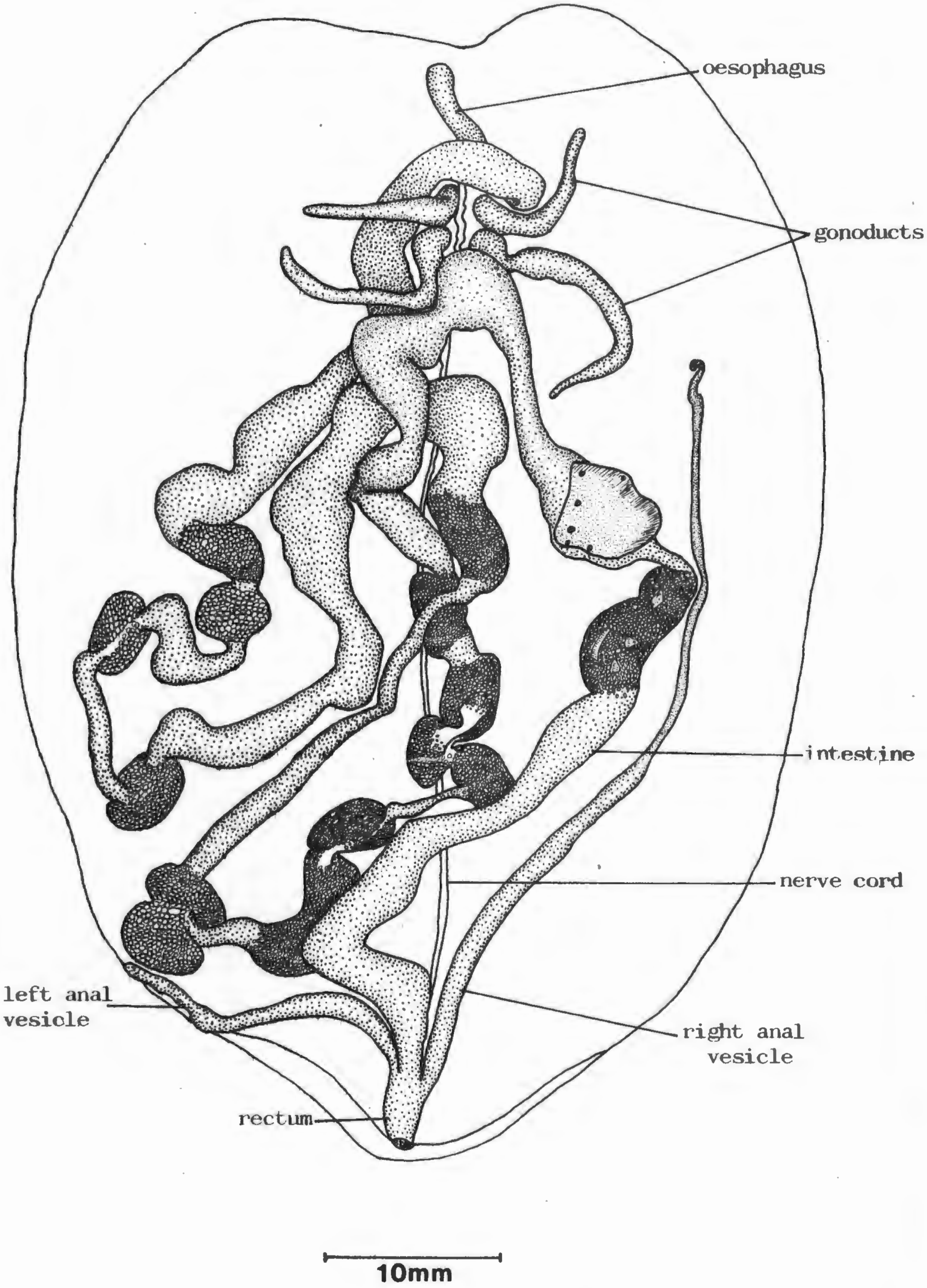

Fig. 9. Dorsal dissection of the trunk of O. baronii illustrating the alimentary canal and anal vesicles.

Trunk

Trunk sausage-shaped, more or less of uniform diameter in both specimens from Park Rynie. Trunk of Inhaca specimen broad anteriorly but tapering at posterior end (Fig.7).

Entire integument of trunk densely covered with minute, rounded papillae. Papillae irregularly distributed, more closely arranged at extremities of trunk and larger posteriorly. Much smaller papillae interspersed among larger ones.

Integument translucent, parts of alimentary canal and nerve cord visible. Longitudinal muscles gathered into 18-20 bands. Inner oblique muscles between longitudinal bands distinctly fasciculated.

Setae

Setae one pair, located on antero-ventral surface of trunk, just posterior to mouth (Fig.7). Genital pores 2 pairs, opening behind setae. Each seta consisting of a cylindrical shaft with curved terminal end (Fig.8). Distal bent end slightly flattened. Cylindrical part of shaft with faint concentric markings. Setae invested in connective tissue and located in cone-shaped setal sacs as in other species. Cylindrical interbasal muscle present.

Internal anatomy

Alimentary canal

Alimentary canal long, coiled, about five times trunk length (Fig.9). Foregut extremely small, ending at intestinal ring vessel. Gizzard and crop not distinguishable as no distinct boundaries present externally. Fine mesenteric strands fasten alimentary canal to body wall at several points. Numerous dilatations present in intestine due to

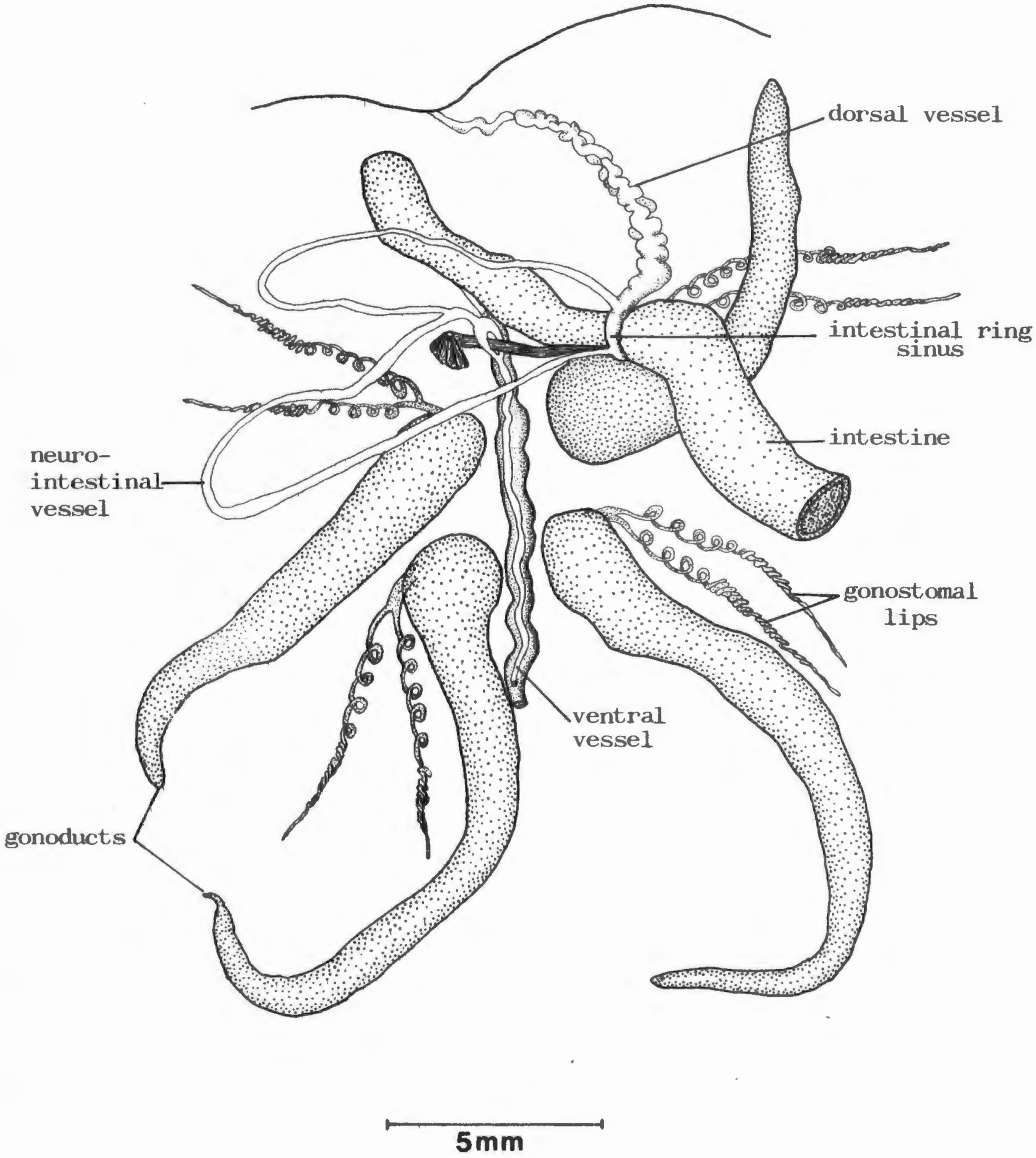

Fig. 10. Anterior end of the trunk cavity of O. baronii showing the blood system and gonoducts.

presence of sand grains and shell fragments. Contents of intestine not in the form of pellets. Small precloacal caecum opening into rectum ventrally.

Anal vesicles

Anal vesicles thin-walled, unbranched, blind-ending tubes opening into rectum (Fig.9). Right anal vesicle of Inhaca specimen two-thirds length of trunk, without ciliated funnels. Left vesicle approximately one-quarter length of trunk with tiny unstalked funnels on distal third.

Right anal vesicle of smaller specimen from Park Rynie almost as long as trunk; left one less than one-third trunk length. Both vesicles in larger specimen almost equal to trunk length. Ciliated funnels present on vesicles of both specimens.

Gonoducts

Gonoducts 2 pairs, located posterior to ventral setae (Fig.10). Gonoducts of Inhaca specimen considerably distended due to presence of numerous ova. Gonostomal lips long, spirally coiled (Fig.10). Openings of gonostomes basal in position.

Both specimens from Park Rynie Beach still immature. Gonoducts oval in smaller specimen, somewhat elongate in larger one.

Blood system

Neuro-intestinal vessels paired, elongate, connecting dorsal and ventral vessels by means of intestinal ring sinus (Fig.10). Ring sinus located at end of foregut. Interbasal muscle passes through loop of neuro-intestinal vessel. Dorsal vessel weakly-coiled with numerous small dilatations, passes anteriorly and enters proboscis. Ventral vessel continues posteriorly, alongside nerve cord, terminating in region of rectal caecum.

Remarks

The discovery of O. baronii from Inhaca Island and Park Rynie are new records for the southern African region. This marks an extension in the range of distribution southwards from the Zanzibar coast.

Although this species is fairly well known, there are a few taxonomic problems that need clarification.

O. baronii, described originally as Thalassema baronii by Greeff (1879), is based on specimens collected from the Canary Islands. Accor= ding to Greeff, the trunk is up to 80mm in length, dark green in colour with violet longitudinal muscle bands and white papillae scattered over the surface. The longitudinal muscle layer is gathered into 17-19 bands. Selenka's description (1885), however, mentions the presence of 20-23 muscle bands. An interesting feature mentioned by Greeff (1879), Selenka (1885) and Shipley (1899 a) is the presence of short branching outgrowths on the anal vesicles.

The present specimens of O. baronii from the east coast of southern Africa closely approach the description given by Greeff (1879), except for differences in the structure of the anal vesicles. All the specimens lack the branched outgrowths and conform with the descriptions provided by Fisher (1946), Lanchester (1905) and Amor (1976).

Furthermore, the specimens from southern Africa as well as those examined by Amor (1976), have a markedly deciduous proboscis, a feature that seems to have gone unnoticed by the previous authors.

Amor (1976) examined the type specimens of *O. kefersteini* and *O. edax* and compared them with numerous specimens of *O. baronii* collected from the Canary Islands. From this investigation she concluded that both *O. edax* and *O. kefersteini* were synonymous with the species of Greeff. The present study supports Amor's conclusion.

The species *O. kefersteini*, erected by A. ten Broeke (1925), is based on several specimens from the West Indies. In the latter species, as in *O. baronii*, the integument is transparent and the longitudinal muscles are arranged into 18 bands. In the original description, A. ten Broeke mentions the presence of a single pair of gonoducts. Bock (1942) and Amor (1976) re-examined some of A. ten Broeke's specimens and observed that there were two pairs of gonoducts with spirally coiled gonostomal lips. Furthermore, Amor established that the inner oblique muscle layer was fasciculated, a fact not mentioned by A. ten Broeke. This confirms that the species is an *Ochetostoma* and is identical to *O. baronii*.

The species, *O. edax* is based on several specimens collected from California by Fisher (1946). In this species, also, the two pairs of gonoducts are situated posterior to the setae and the gonostomal lips are spirally coiled. Fisher reports the presence of an interbasal muscle which passes through a small loop of the neuro-intestinal vessel. The longitudinal muscles are gathered into 16 or 17 bands. His description also mentions that the body wall is translucent in the middle region and the papillae are numerous and usually larger on the posterior third or fourth of the trunk. The length of the trunk ranges from 25 to 50mm and the deciduate proboscis is about one-quarter as long.

Fisher (1946) considered *O. edax* as a species distinct from *O. baronii* because of differences in the number of longitudinal muscle bands. It is now known, however, that this number is not a very reliable taxonomic character because of the variation that occurs within a species and the considerable overlap among several closely related forms.

The species, *O. myersae* appears to be closely related to *O. baronii*. This species, described by Edmonds (1963), is based on four specimens from Long Reef, New South Wales. According to Edmonds, the colour of living specimens is chlorophyll green. The length of the trunk ranges from 20 to 35mm and the proboscis, which is not readily deciduate, is about a quarter to half the length of the trunk. The longitudinal muscles are gathered into 18 to 21 bands. An important difference between *O. myersae* and *O. baronii* lies in the oblique muscles which in the former species are weakly developed. The integument is covered with soft, white, wart-like papillae which are large and most conspicuous on the posterior third of the trunk. Edmonds (1963) reports the presence of two pairs of postsetal gonoducts in three of his specimens and only one pair in his largest specimen. As in *O. baronii*, an interbasal muscle is present which passes through a loop of the neuro-intestinal vessel. The anal vesicles are thin, elongate and lack branched outgrowths. The ciliated funnels are borne on very short stalks.

Edmonds (1963) compared the Australian specimens with a specimen of *O. edax* described by Fisher (1946) from Puerto Refugio (U.S.N.M. Cat. No. 20623). He observed that the body wall of *O. edax* was much thinner and the papillae were more prominent in the middle region of the trunk. Consequently, he regarded *O. myersae* as a distinct species from *O. edax*.

Differences between O. baronii and O. myersae lie mainly in the integument, the proboscis and in the size and arrangement of the dermal papillae. The differences appear to be sufficiently distinctive to warrant the separation of these two species.

Ochetostoma formosulum (Lampert, 1883)

Figs 11-15

Thalassema formosulum Lampert, 1883: 339-340. Shipley, 1899b: 348. Sluiter, 1902: 48, fig. 13. Wharton, 1913: 248-249. Prashad, 1921: 35-37.

Ochetostoma formosulum: Fisher, 1946: 241. Wesenberg-Lund, 1963: 140-141. Datta Gupta et al, 1963: 57, figs 1a-1c. Stephen & Edmonds, 1972: 433.

Present records

Two specimens, one sexually mature, collected from Durban Bay by the UCT ecological survey of 1963. One of these specimens (dissected) was redescribed by Wesenberg-Lund (1963).

Previous records

Manila, Shanghai, Indonesia, India.

Type locality

Manila.

Distribution

Indo-West-Pacific, from Japan through the Philippines and Indonesia to the east coast of southern Africa.

Habitat:

Both specimens occurred in sand at a depth of 8-9 metres.

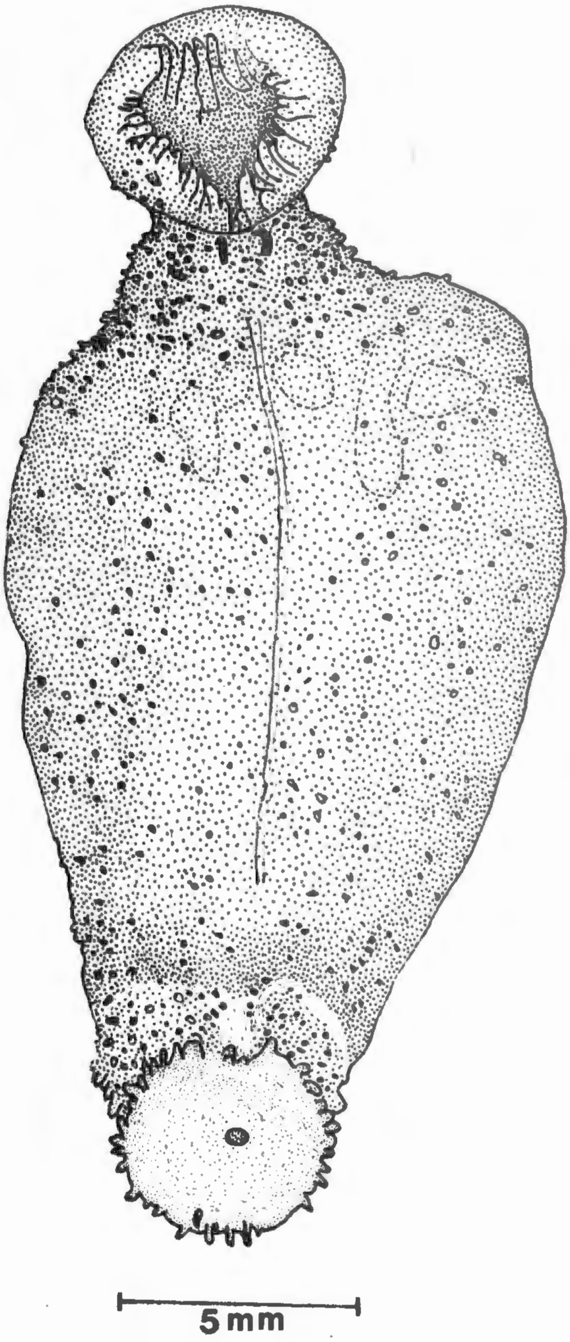

Fig. 11. Ventral aspect of O. formosulum.

Description

Size

Trunk of intact sexually mature specimen 22mm long, greatest diameter 11mm. Proboscis 5mm long, less than one-quarter trunk length.

Colour

Dissected specimen cream, intact specimen pinkish-brown.

External features

Proboscis

Proboscis fleshy, highly contracted, nondeciduous and more or less spherical in outline (Fig.11). A series of tight ridges on lateral edges, margins frilled. Dorsal surface with small, scattered papillae. Proboscis with broad incision at anterior end. Lateral margins fuse posteriorly, forming a narrow lower lip.

Trunk

Trunk broad at anterior end, tapering posteriorly (Fig.11). White papillae sparsely distributed over middle two-thirds or more of trunk, more closely arranged at extremities. Papillae arranged in rings at posterior end (Fig.11). Anus at tip of small, smooth conical projection. A ring of large, elongate papillae around base of conical projection about 3mm away from posterior tip of trunk.

Integument very thin and transparent, somewhat thicker and opaque posteriorly. Nerve cord, gonoducts and parts of alimentary canal visible through transparent body wall.

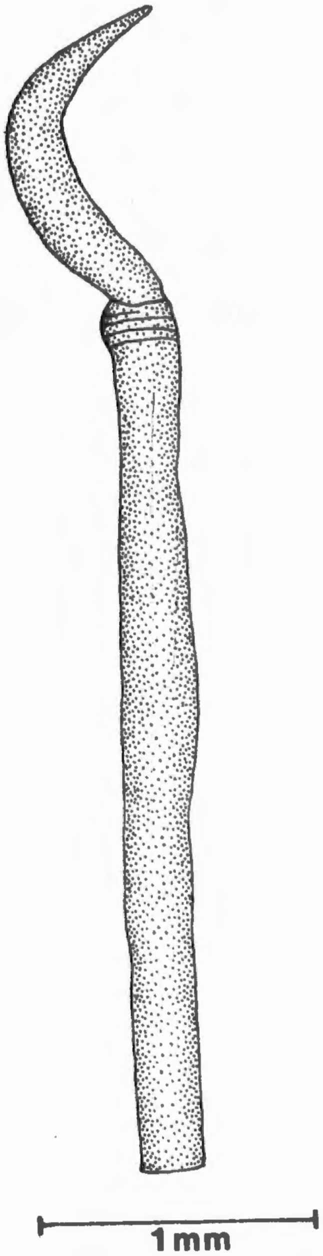

Fig. 12. Left functional seta of O. formosulum.

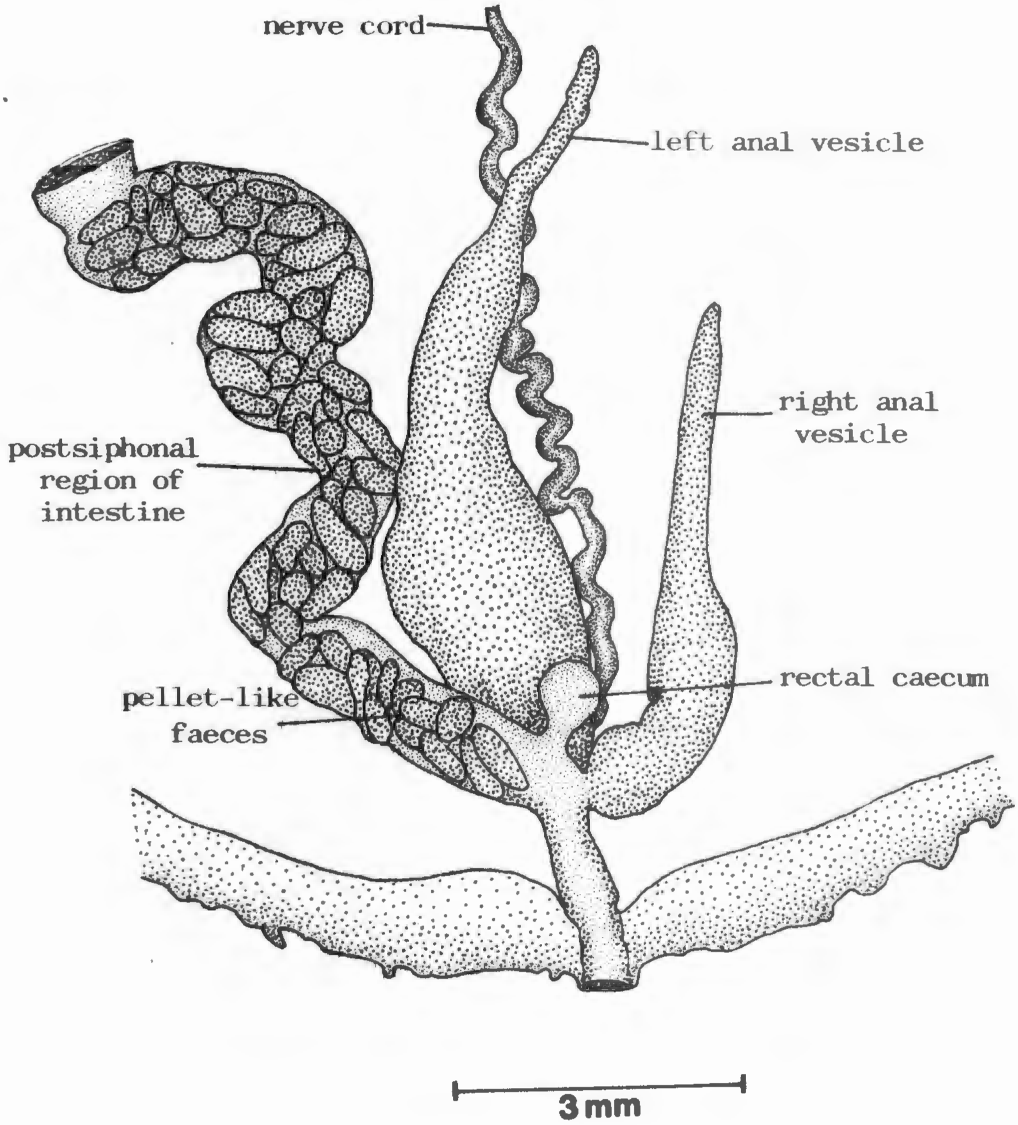

Fig. 13. Posterior end of trunk cavity of O. formosulum showing the anal vesicles and posterior part of alimentary canal.

Ventral setae large, situated a few millimetres posterior to junction of proboscis and trunk (Fig.11).

Genital pores 2 pairs, postsetal.

Muscle layers continuous over most of trunk. Longitudinal muscle bands indistinct except in posterior third of trunk where narrow bands faintly discernible. Inner oblique muscle layer fascicu= lated, visible only in posterior end of trunk.

Setae

Setae golden-brown in colour, hook-like, about 4mm long (Fig.12). Terminal bent end flattened and clearly demarcated from straight, cylin= drical part of shaft by a conspicuous ridge. Both setae located in special sacs, supported by numerous radiating muscle strands. Interbasal muscle cylindrical, passing through small loop of neuro-intestinal vessel (Fig.12).

Internal anatomy

Alimentary system

Alimentary canal long, highly coiled tube, fastened to body wall at several points by thin mesenteric strands. Pharynx club-shaped with thick muscular walls. Oesophagus narrow, more or less of uniform diameter. Foregut long, terminating at intestinal ring sinus. Pre= siphonal region of intestine with a ciliated groove. Intestine considerably dilated, extremely thin-walled and transparent in region of siphon. Entire intestine compactly filled with small, sausage-shaped faecal pellets consisting of fine sand particles (Fig.13).

Rectal caecum small, spherical.

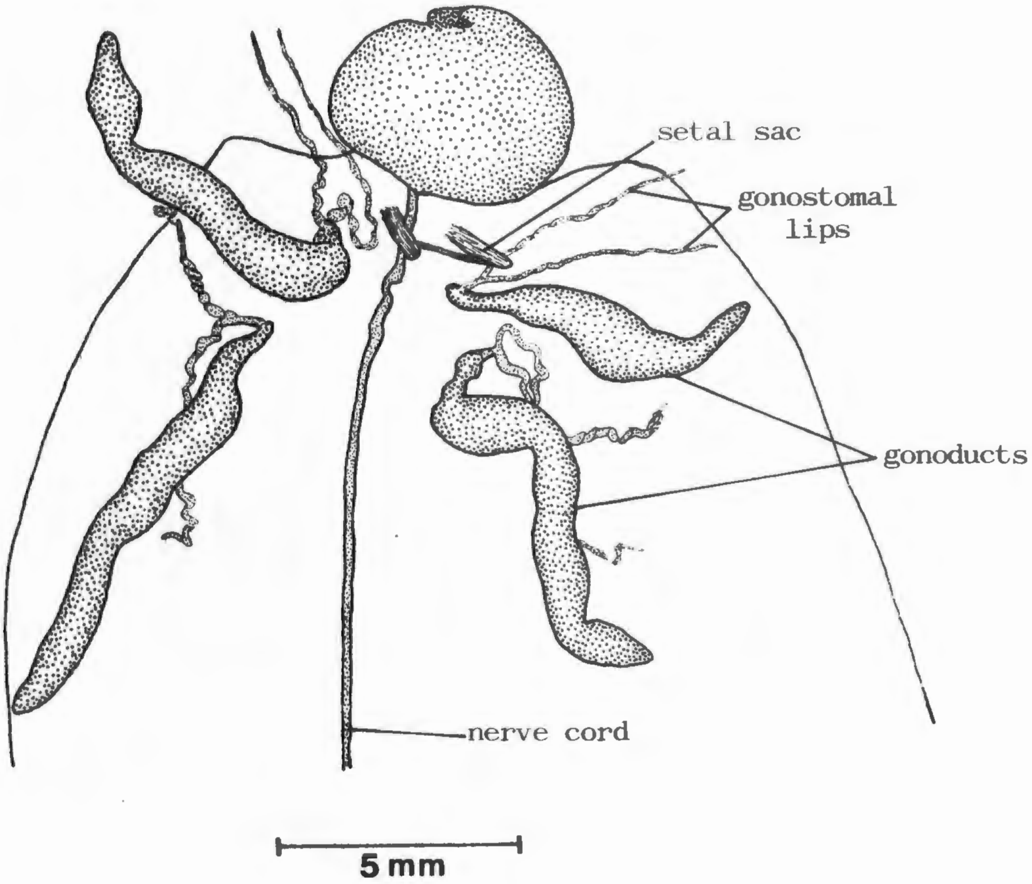

Fig. 14. Anterior part of the trunk cavity of O. formosulum showing the gonoducts.

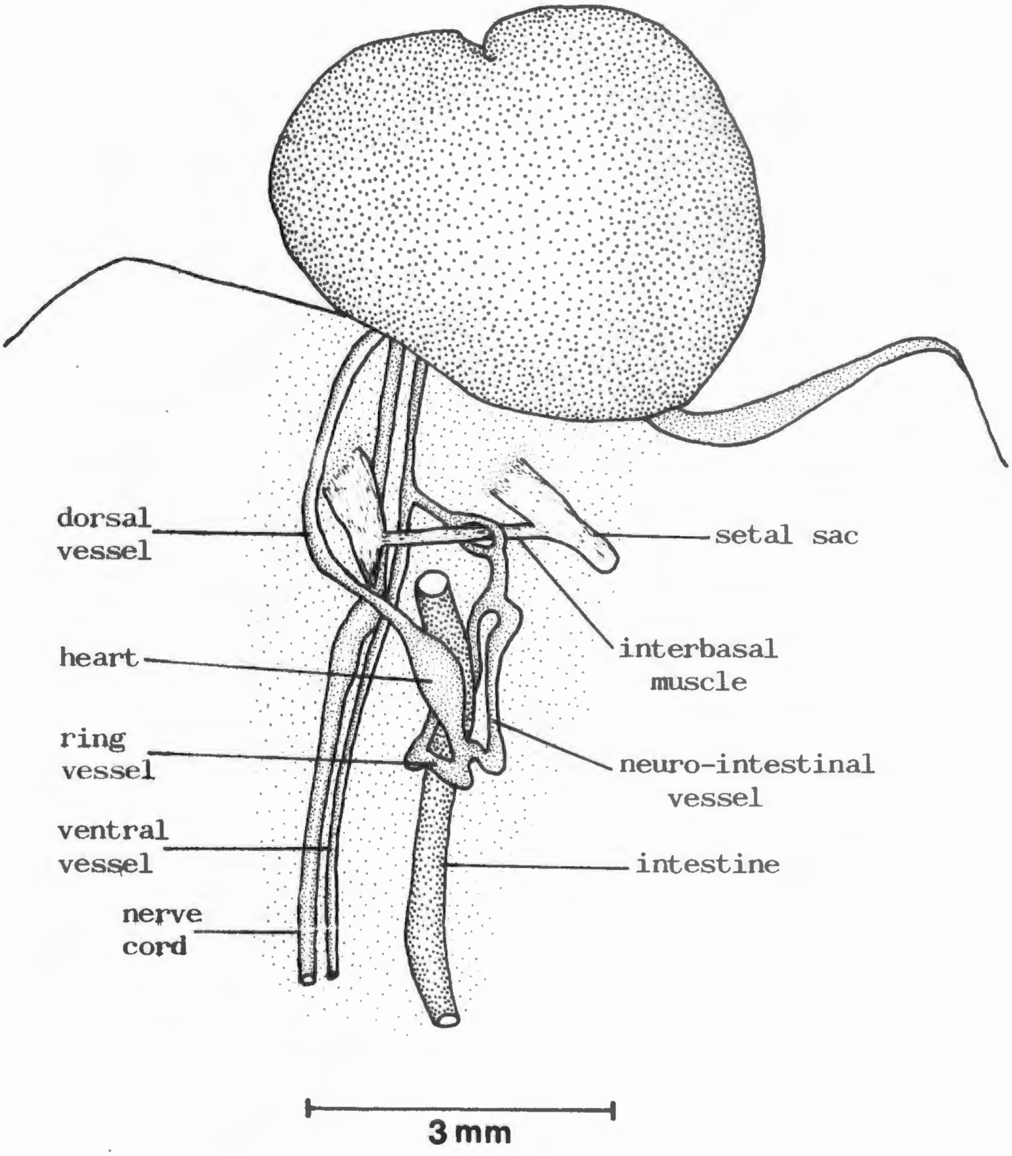

Fig. 15. Anterior part of the trunk cavity of O. formosulum showing the blood vessels.

Anal vesicles

Anal vesicles small, about one-third trunk length, unbranched and transparent (Fig.13). Anal vesicles narrow anteriorly but consider= ably dilated and sac-like posteriorly. Ciliated funnels minute, stalked, sparsely distributed over surface of both vesicles.

Gonoducts

Gonoducts 2 pairs, posterior to ventral setae (Fig.14) oval in juvenile specimen but elongate, tubular and considerably distended in sexually mature individual due to presence of numerous ova. Gonostomal lips thin, spirally coiled; gonostomal openings basal in position.

Blood system

Intestinal ring sinus is an incomplete vascular ring at posterior end of foregut (Fig.15). Dorsal vessel prominent, continuing anteriorly and entering proboscis. Paired neuro-intestinal vessels short, stout, forming small loop around interbasal muscle (Fig.15). Heart conspicuous at posterior end of dorsal vessel. Ventral vessel terminating posteriorly in rectal caecum.

Remarks

Ochetostoma formosulum is described originally from a single specimen from Manila by Lampert (1883). This species was later recorded and described from several other localities in the Indo-West-Pacific Ocean. Wesenberg-Lund (1963) recorded and described a single specimen collected from a central sand bank in Durban Bay. Although this species is fairly well known, a few taxonomic problems still require to be resolved.

The most important distinguishing features of O. formosulum are: the presence of two pairs of postsetal gonoducts with spirally coiled gonostomal lips, a very thin and transparent integument, 6-8 longitudinal muscle bands and an interbasal muscle which passes through a loop of the neuro-intestinal vessel. Other taxonomic features include: the size of the proboscis to the trunk length, the frilled lateral margins of the proboscis and the characteristic shape and distribution of the dermal papillae.

It is rather surprising to note that with the exception of Wharton (1913), none of the other authors have mentioned the presence of an interbasal muscle in this species. In their Key to the species of Ochetostoma, Datta Gupta & Menon (1971) are incorrect in including O. formosulum with those species that lack an interbasal muscle.

The description provided by Lampert (1883) mentions 30mm for the length of the trunk and 8mm for the proboscis. With the exception of the dermal papillae, the present specimens from Durban Bay closely correspond with Lampert's description. According to Lampert (1883) and Wharton (1913), the papillae are not arranged in transverse or longitudinal rows on any part of the trunk.

Sluiter's description (1902) is based on 21 specimens from Siboga that were well preserved. The trunk ranges from 15 to 23mm in length and the proboscis from 4 to 6mm. Sluiter also mentions the presence of a conical projection and a ring of large papillae at the posterior extremity of the trunk.

Wharton's description (1913) is based on a single individual from Samar. The trunk is 35mm long and the proboscis is less than one-third its length.

The trunk of the single specimen described by Wesenberg-Lund (1963) is 17mm long and the proboscis is 6mm. Hence from the description provided by the above authors, it is apparent that the proboscis ranges from a quarter to one-third the trunk length. Regarding the dermal papillae, Wesenberg-Lund (1963 : 140) states:"The dermal organs show a slight tendency to an annular arrangement; they are nowhere especially crowded, and a small area round the posterior end seems almost smooth".

The anal vesicles are broad and sac-like in the intact specimen from Durban Bay and hence similar to those described by Lampert (1883), Wharton (1913) and Datta Gupta et al (1963). Wesenberg-Lund (1963), however, describes these organs as white, transparent tubes.

Ochetostoma formosulum appears to be related to O. septemyotum and O. arkati in possessing two pairs of gonoducts and 7-8 longitudinal muscle bands. The latter two species, however, besides lacking an interbasal muscle, also differ significantly in the structure of their proboscides. In O. septemyotum, the lateral margins of the proboscis are produced into a series of folds with dendritic outgrowths, while in O. arkati, gill-like structures are present along the basal edge of the proboscis.

Ochetostoma decameron (Lanchester, 1905)

Figs 16-20

Thalassema decameron Lanchester, 1905:35, pl.1, fig.5.

Ochetostoma decameron Fisher, 1946: 241. Stephen & Edmonds, 1972: 432.

Present records

One sexually mature specimen, Park Rynie Beach (31° 19'S/30° 44'E), Natal coast, collected by the author, 8 September 1983.

Previous records

Ohwaka Bay, Zanzibar (Type locality).

Holotype

Deposited by Lanchester in the British Museum (Natural History).

Habitat

The specimen occurred in sand, under rocks in the intertidal area, close to the high water mark.

Description

Size

Trunk of preserved specimen 18mm long, greatest diameter 6mm. Proboscis half trunk length.

Colour

In living specimen, proboscis pale yellow; trunk reddish-purple. Colour of preserved specimen pale pink.

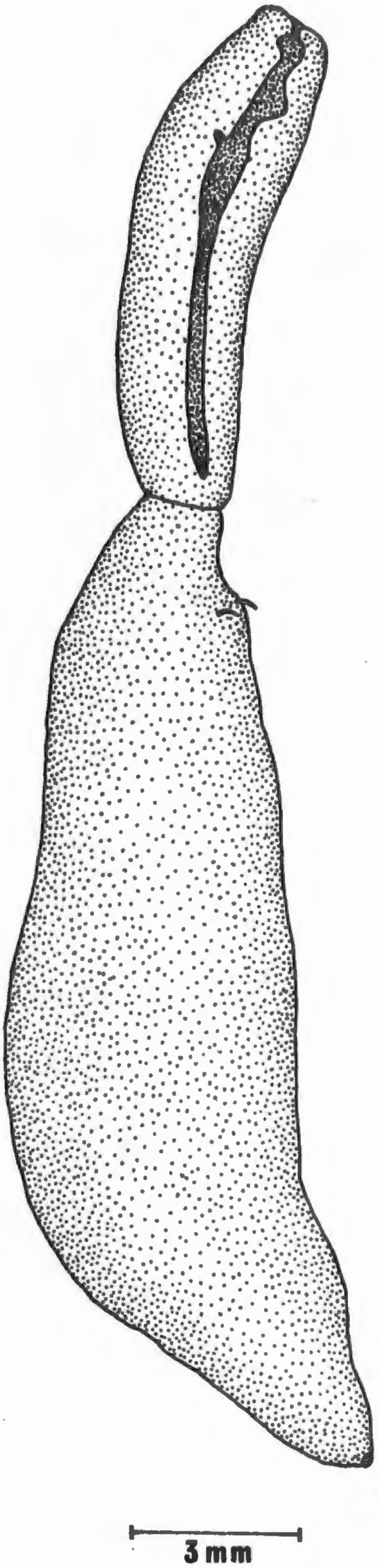

Fig. 16. Ventral aspect of <u>O</u>. <u>decameron</u>.

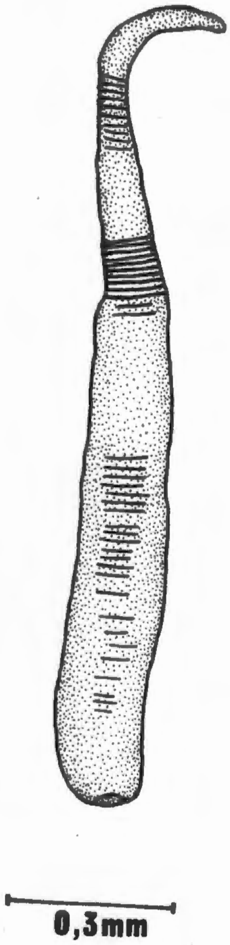

Fig. 17. Left functional seta of O. decameron.

External features

Proboscis

Proboscis fleshy, nondeciduous, spatula-shaped in living specimen but in preserved condition lateral margins roll inwards forming a tube (Fig.16). Anterior and lateral margins smooth. Small, rounded papillae visible on dorsal surface under dissecting microscope. Lateral margins of proboscis unite at base forming a narrow lower lip ventral to mouth.

Trunk

Trunk broad in middle region, tapering more towards posterior end (Fig.16). Integument thin and transparent. Small, rounded papillae irregularly distributed over entire surface of trunk, more closely arranged at extremities. Trunk papillae larger than those on proboscis and not of uniform size. Much smaller papillae interspersed among larger ones.

Longitudinal muscle bands not visible from external surface but under dissecting microscope, 10 inconspicuous bands apparent only in middle region of trunk. Longitudinal and inner oblique muscles form a continuous sheet in mid-dorsal region of trunk. Oblique muscles weakly developed, arranged in fascicles between longitudinal bands.

Setae

Setae one pair, golden-yellow, located about 3mm away from anterior end of trunk (Fig.16). Each seta consisting of a cylindrical shaft with a curved terminal end tapering in a sharp point (Fig.17). Distal third of seta much narrower. Interbasal muscle absent.

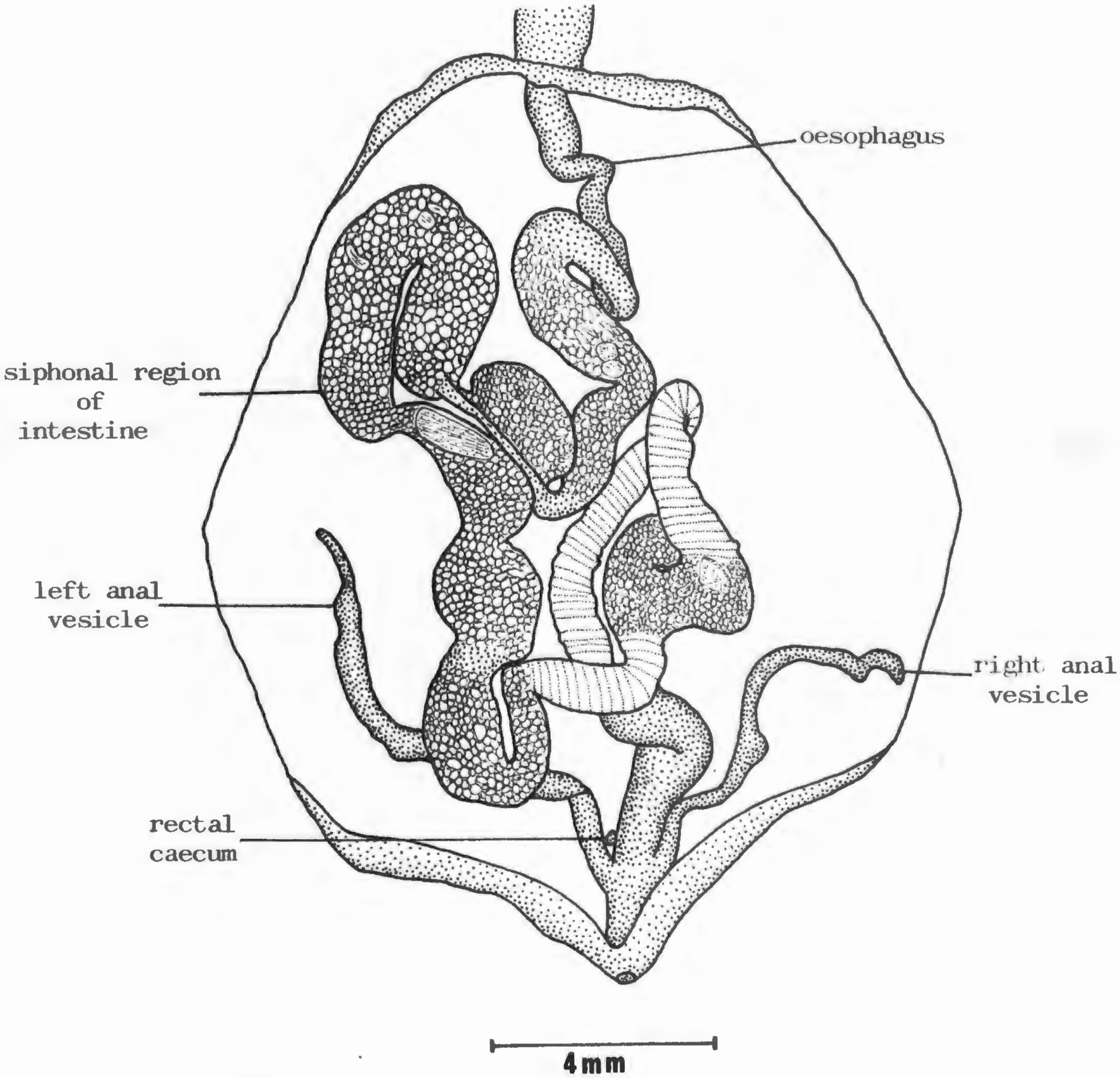

Fig. 18. Dorsal dissection of the trunk showing the alimentary system and anal vesicles of O. decameron.

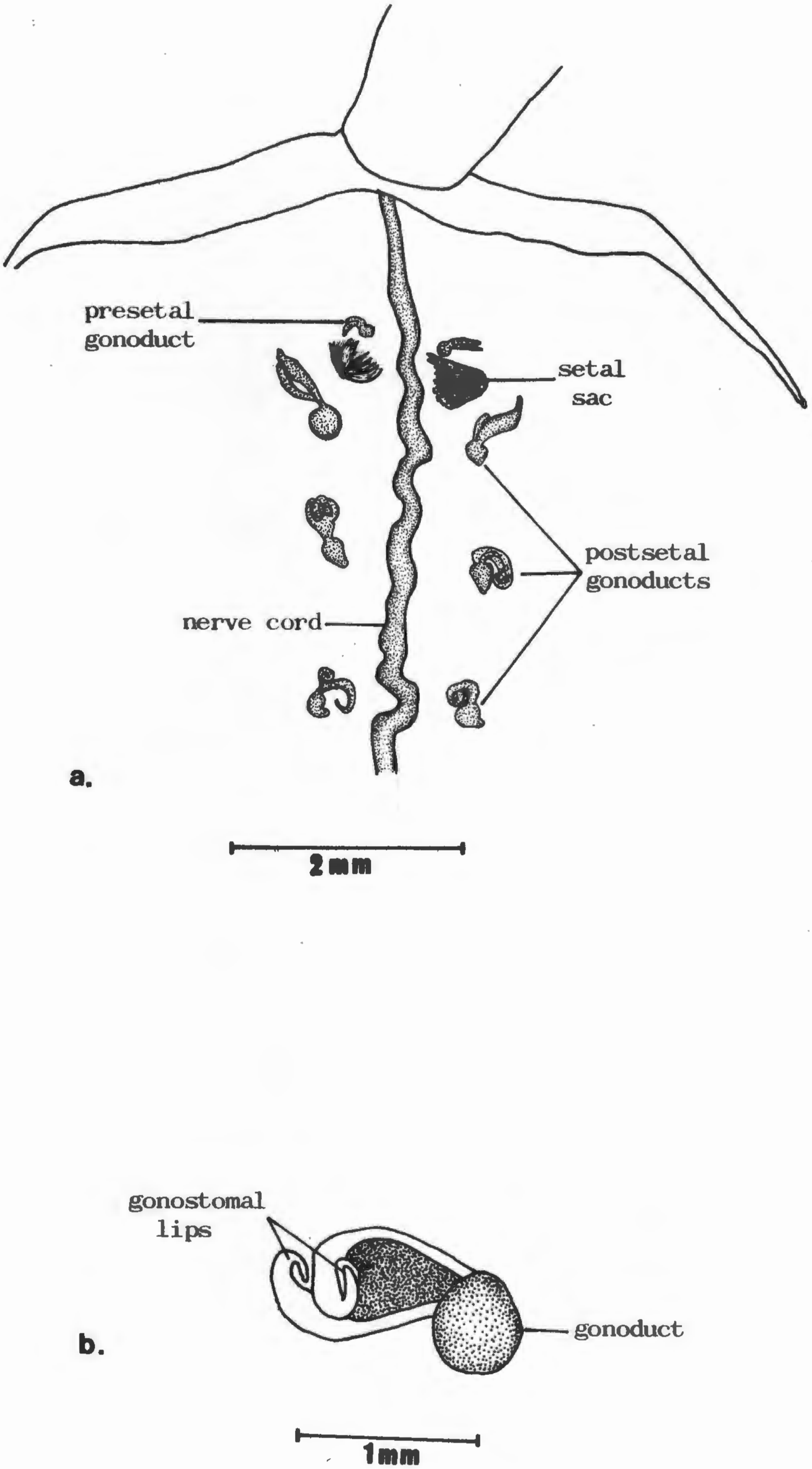

Fig. 19a. Anterior part of the trunk cavity of *O. decameron* showing the gonoducts.
b. First postsetal gonoduct from left.

Internal anatomy

Alimentary canal

Alimentary canal comparatively short, consisting of a few irregular coils (Fig.18). Foregut short, narrow tube of uniform diameter, terminating at ring sinus. Thin-walled presiphonal and siphonal regions of intestine compactly filled with coarse sand grains and shell fragments. Intestinal contents not in the form of pellets. Few thin mesenteric strands fastening alimentary canal to body wall. A small spherical rectal caecum present.

Anal vesicles

Anal vesicles thin-walled, transparent tubes, about half length of trunk (Fig.18). Ciliated funnels few, unstalked over surface of both vesicles.

Gonoducts

Gonoducts 4 pairs, white in colour; first pair anterior to ventral setae while remaining 3 pairs postsetal in position (Fig.19a). Presetal gonoducts smallest of all, situated just anterior to cone-shaped setal sacs and partially obscured by muscle strands radiating from base of setae. Gonoducts spherical to oval and equidistant from each other. Postsetal gonoducts distended due to presence of gametes. Gonostomal lips broad, weakly coiled and large in comparison to size of gonoducts (Fig.19b). Gonostomal openings basal in position.

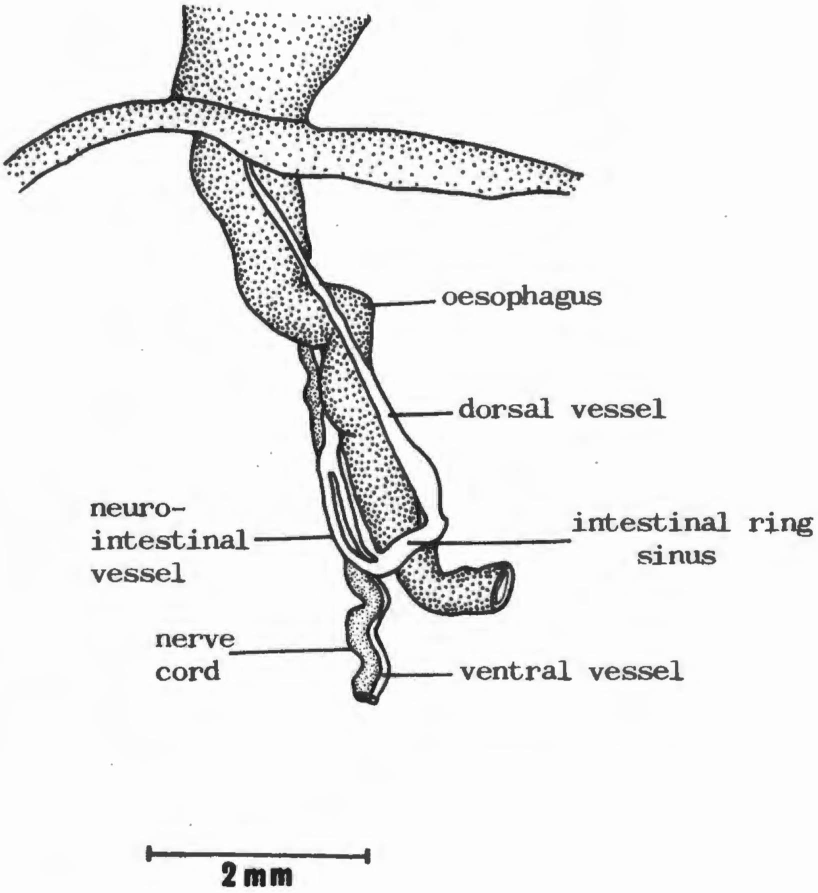

Fig. 20. Anterior part of the trunk cavity of O. decameron showing blood vessels.

Blood system

Neuro-intestinal vessels short, connecting dorsal and ventral vessels by means of intestinal ring sinus. Paired neuro-intestinals unite anteriorly before opening into ventral vessel (Fig.20). Dorsal vessel prominent, passing anteriorly and entering proboscis. Ventral vessel continuing posteriorly, alongside nerve cord and terminating in rectal caecum.

Remarks

Ochetostoma decameron is based on a single specimen from Zanzibar in which the proboscis was missing. Its discovery from Park Rynie is a new record for southern Africa. The description provided by Lanchester (1905) is extremely brief and according to Stephen & Edmonds (1972), the taxonomic position of this species is still un=certain. Nothing is known about the size of the specimen, the structure of the proboscis, the disposition of the oblique muscles and the distribution of the dermal papillae. Lanchester mentions the presence of four pairs of gonoducts, with the first two pairs presetal in position. The body wall is extremely thin and the longitudinal muscles are aggre=gated into 10 fairly broad but inconspicuous bands. According to Stephen & Edmonds (1972), the holotype in the British Museum (Natural History) is damaged and the muscle systems are not clearly evident.

Important distinguishing features of the present specimen from Park Rynie include: four pairs of gonoducts, 10 longitudinal muscle bands, a thin and transparent integument, the narrow lower lip of the proboscis and the characteristic shape and arrangement of the dermal papillae. Other features of lesser taxonomic importance are the colour and size of the specimen.

The present specimen closely approaches Lanchester's description in the number of gonoducts and longitudinal muscle bands as well as in the nature of the integument. An important difference, however, lies in the location of the gonoducts in relation to the ventral setae.

The localities of the specimens also indicate that they probably belong to the same species. Several species of echiurans that have been reported from the coasts of Zanzibar are currently being discovered further south, at least as far as the Natal coast.

O. decameron appears to be related to *O. kempi* in possessing four pairs of gonoducts. According to Prashad (1919), the trunk of *O. kempi* is 77mm long and the longitudinal muscles are gathered into 20 bands. The integument of the latter species is thick and opaque. Hence, significant differences are present in the size of the animals, in the number of longitudinal muscle bands and in the nature of the integument. Another distinguishing feature lies in the oblique muscles, which in *O. decameron* are weakly developed.

Additional material in the future will give a better understanding of the variations within *O. decameron* and its taxonomic position.

Ochetostoma kempi (Prashad, 1919)

Figs 21 - 25

Thalassema kempi Prashad, 1919: 336-337, fig.2; 1935:41.

Ochetostoma kempi: Fisher, 1946: 241. Datta Gupta & Menon, 1971: 176-177, fig.2. Stephen & Edmonds, 1972: 437.

Present records

One specimen, Isipingo Beach (29°05'S/30°56'E), Natal coast, collected by author, 12 May 1983.

Previous records

Andaman Islands (Type locality).

Holotype

Deposited by Prashad in the Indian Museum.

Habitat

The specimen occurred in sand, under rocks in a rock tunnel, in the intertidal zone close to the high water mark.

Description

Size

Trunk of preserved specimen 69mm in length, greatest diameter 16mm. Proboscis 39mm long, slightly exceeding half length of trunk.

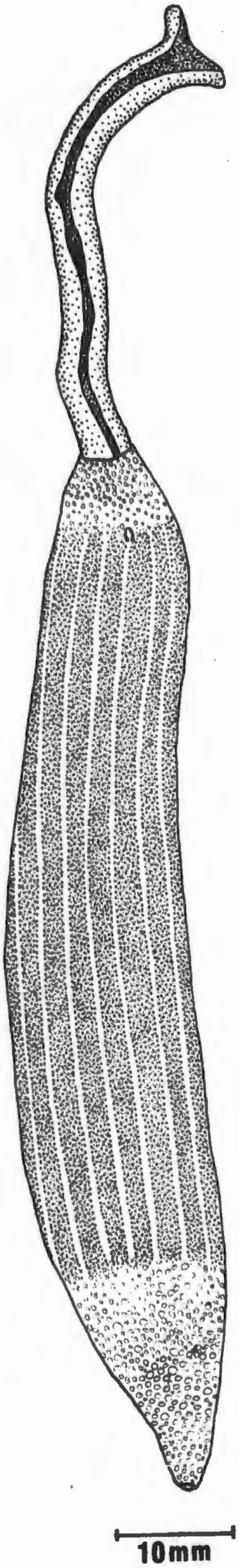

Fig. 21. Ventral aspect of O. kempi.

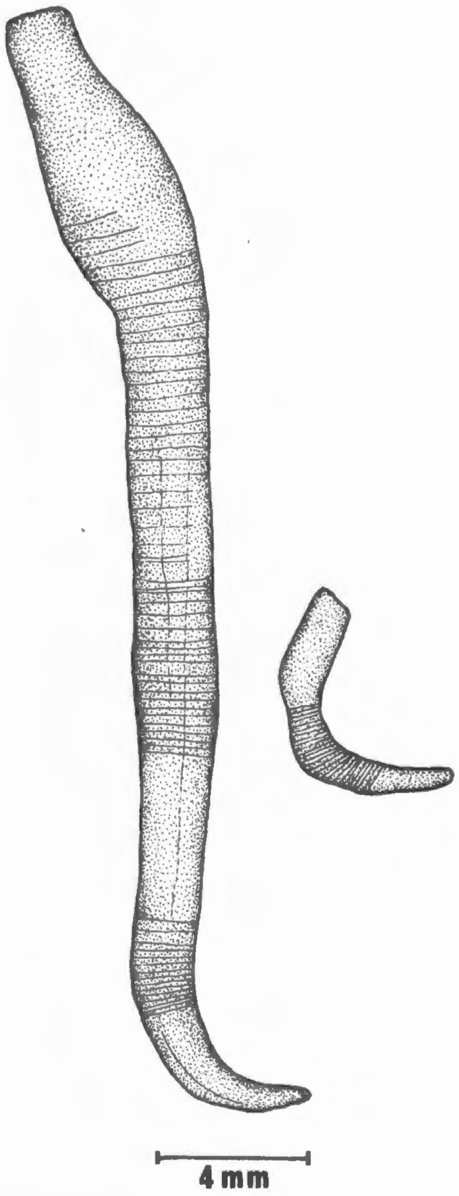

Fig. 22. The right functional and the much smaller non-functional setae of O. kempi.

Colour

In live animal, proboscis pale yellow, trunk with reddish-purple stripes marking longitudinal muscle bands. Interspaces narrow, bluish-grey in colour. In preserved condition, colour of specimen changes to light brown.

External features

Proboscis

Proboscis fleshy, non-deciduous, slightly truncated at anterior end. Spatula-shaped in live specimen but in preserved state, lateral margins curl inwards forming a narrow tube (Fig.21). Lateral margins of proboscis smooth and free at base.

Trunk

Trunk sausage-shaped, tapering posteriorly (Fig.21). Small, rounded papillae irregularly distributed over entire surface of integument. Papillae minute on anterior two-thirds or more of trunk but larger posteriorly. Entire integument thick and opaque. Longitudinal muscle layer gathered into 17-19 bands; inner oblique muscles between longitudinal bands distinctly fasciculated. A pair of golden-yellow setae located about 8mm away from anterior end of trunk.

Setae

Each seta consisting of a cylindrical shaft with curved terminal end, tapering in a pointed tip (Fig. 22a). Proximal end of shaft slightly bent. Non-functional or replacement seta small, in close association with right functional one (Fig. 22b). Fine concentric ridges on surface of both setae. Interbasal muscle absent.

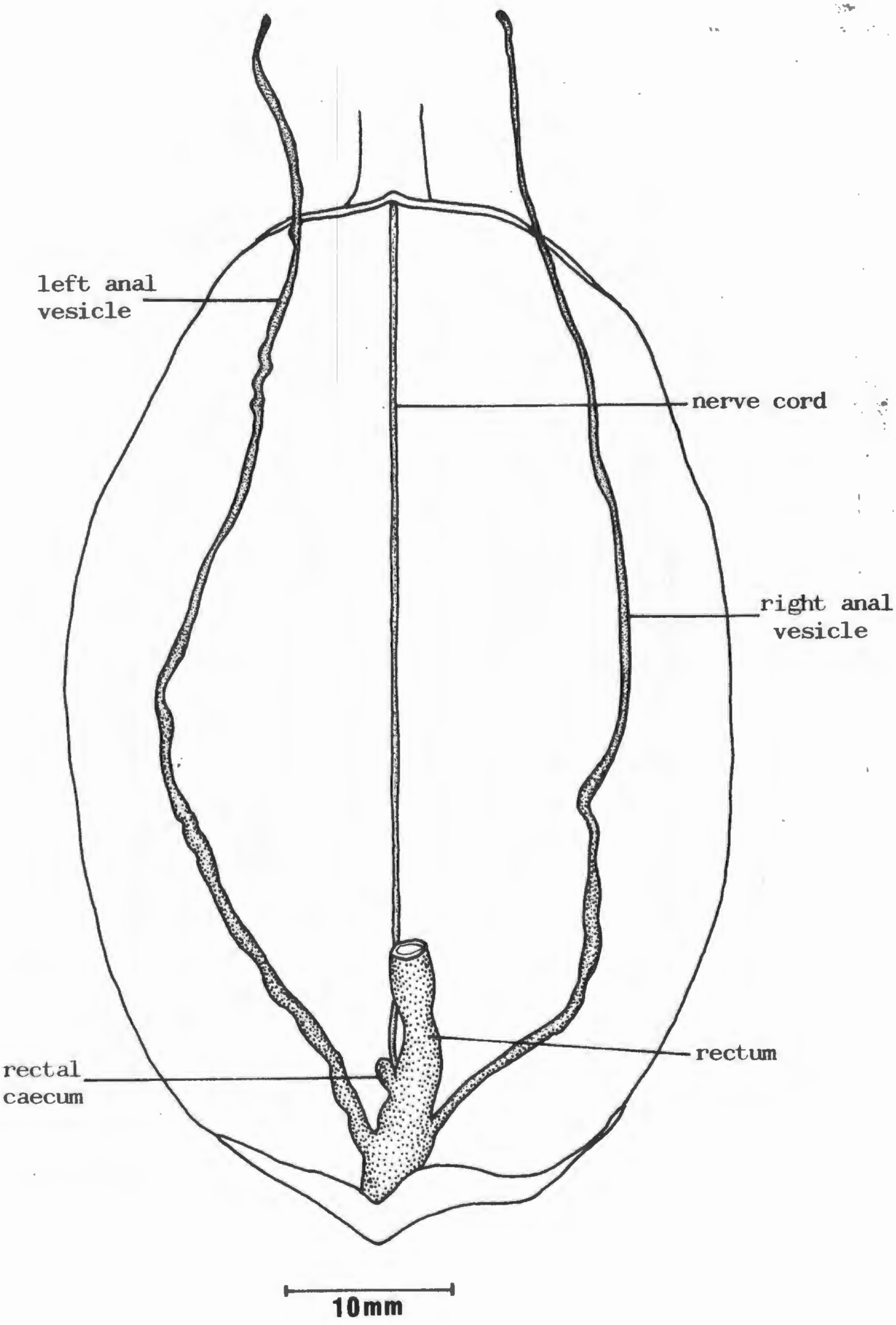

Fig. 23. Dorsal dissection of the trunk of O. kempi showing the anal vesicles.

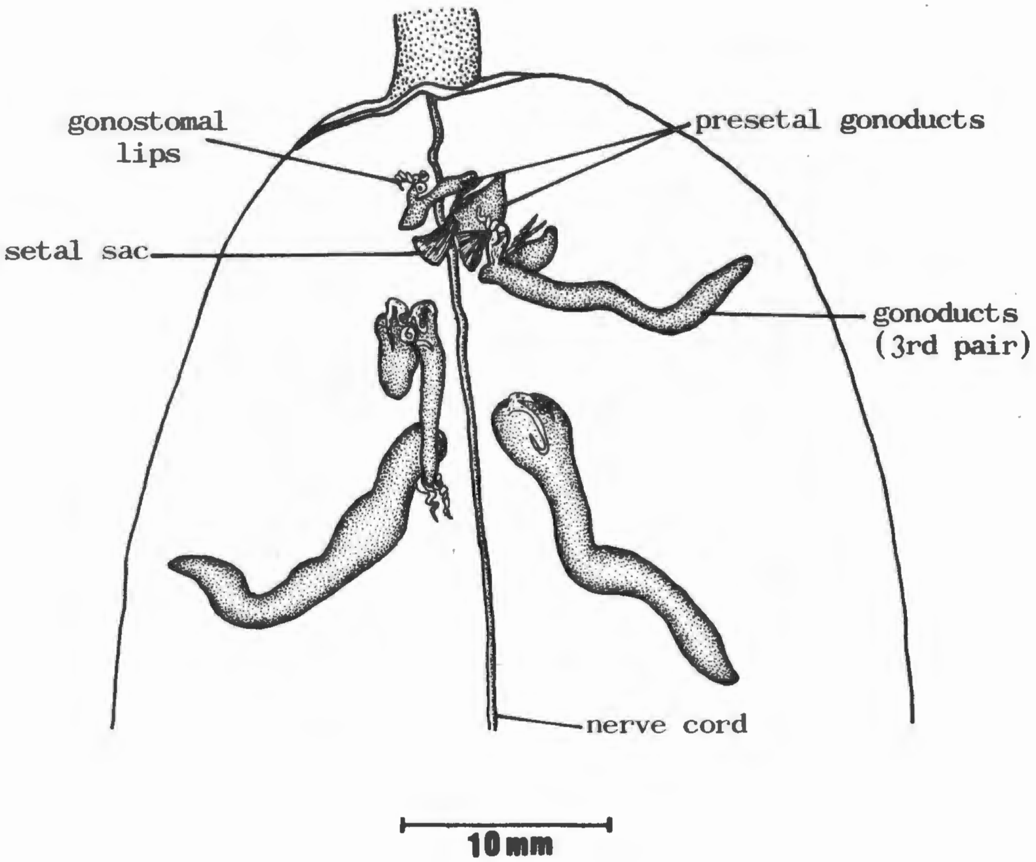

Fig. 24. Anterior part of the trunk cavity of O. kempi showing the gonoducts.

Internal anatomy

Alimentary canal

Alimentary canal slightly coiled, several times length of trunk. Intestine attached to body wall at several points by very thin and elongate mesenteric strands. Ventral sheet of mesentery attaching oesophagus to body wall. Foregut small, ending at ring sinus. Intestine subdivided into presiphonal, siphonal and postsiphonal regions as in other related species. Presiphonal region with ciliated groove. Intestine considerably dilated and extremely thin-walled in region of siphon. Gut compactly filled with fine sand grains and shell fragments, not moulded into pellets.

Rectal caecum large and spherical (Fig. 23).

Anal vesicles

Paired anal vesicles long, slender tubes exceeding length of trunk (Fig. 23). Numerous, tiny, unstalked ciliated funnels on surface of both vesicles.

Gonoducts

Gonoducts 4 pairs, first pair presetal (Fig. 24). Arrangement of gonoducts asymmetrical; right presetal gonoduct slightly anterior to corresponding one on left. Second and third pairs on both sides located very close to each other, with second pair anterolateral in position to third pair. First and second pairs of gonoducts small, more or less oval while fourth pair elongate, tubular and largest of all (Fig. 24).

Gonostomal lips small, spirally coiled, opening into base of gonoduct.

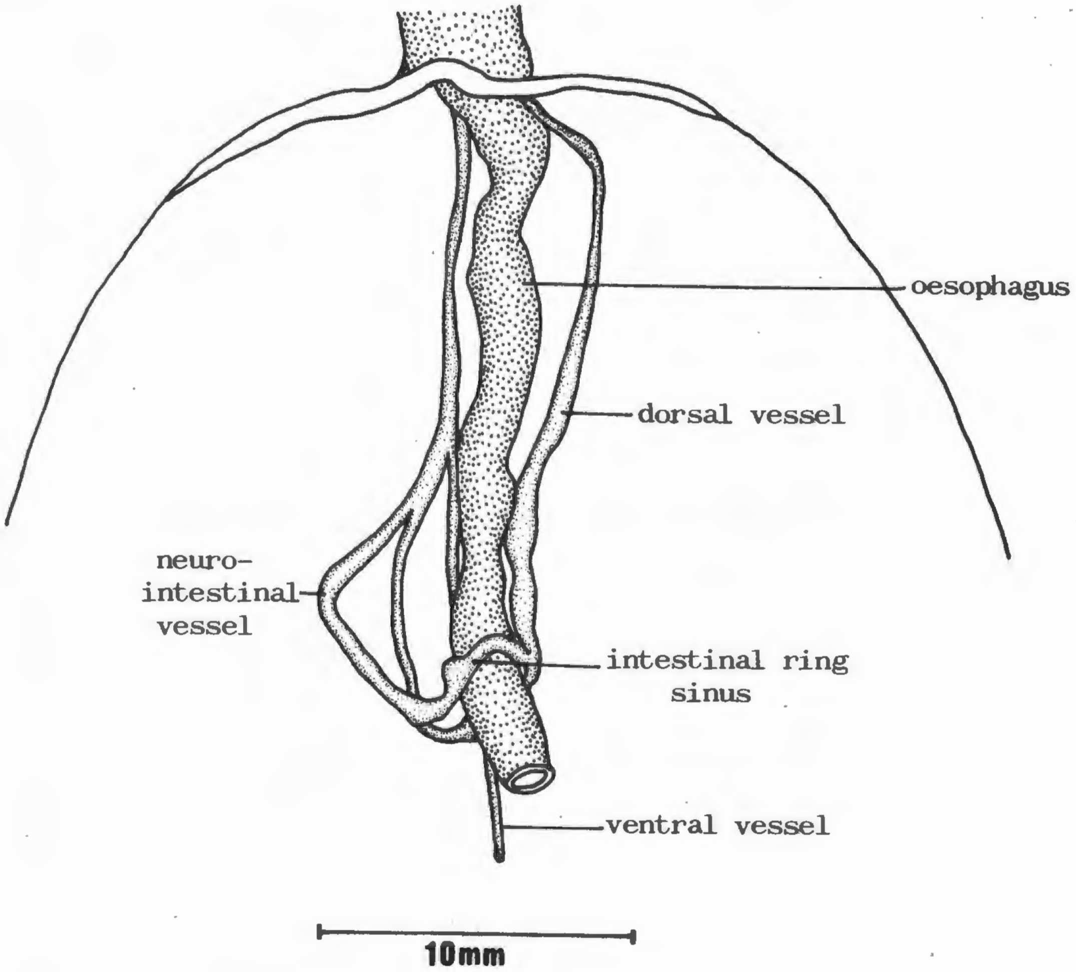

Fig. 25. Anterior part of the trunk cavity of O. *kempi* showing blood vessels.

Blood system

Ring sinus at end of foregut is an incomplete vascular ring (Fig. 25). Paired neuro-intestinal vessels unite prior to opening into ventral vessel. Dorsal vessel prominent, arising from ring sinus and passing anteriorly into proboscis. Ventral vessel terminating in rectal caecum.

Remarks

The discovery of O. kempi from Isipingo is a new record for southern Africa. However, it is not unusual for this typically Indian Ocean species to be distributed as far west as the east coast of southern Africa.

This species, originally described as Thalassema kempi by Prashad (1919), is based on a single specimen from the Andaman Islands. According to the description provided by Prashad, the trunk, which is 77mm in length, is wider in the middle region but gradually tapers at both ends. The proboscis is short and stumpy and slightly truncated at the anterior end. It is 17mm long and hence less than a quarter the trunk length. Prashad's description states that both the proboscis and trunk are covered with papillae. On the proboscis, the papillae are minute and just visible, while on the trunk they are small anteriorly but gradually increase in size at the posterior end. A few large papillae are also scattered among the smaller ones over the whole surface. The longitudinal muscle layer is gathered into 20 bands. According to Prashad (1919) there are four pairs of gonoducts located posterior to the ventral setae. The first two pairs are poorly developed but the fourth pair is the best developed of all. The anal vesicles are very much contracted and about one-third the length of the trunk.

Prashad (1935), however, re-examined his type specimen of O. kempi in the Indian Museum and found that the first two pairs of gonoducts were presetal in position. Consequently, he amended his original description.

The present specimen from Isipingo differs from the type specimen in several respects. The most important differences lie in the position of the gonoducts in relation to the ventral setae, the size and arrangement of the dermal papillae and the length of the anal vesicles. In the Isipingo specimen, the papillae on the anterior two-thirds of the trunk are small and evenly distributed and are not interrupted by larger papillae. The differences in the size of the proboscis and anal vesicles could be due to the different degrees of contraction of these organs during narcotization and fixation. It is very likely that Prashad's description is based on a specimen that was highly contracted.

Datta Gupta & Menon (1971) identified a specimen, also collected from the Andaman Islands, as O. kempi. According to these authors, the proboscis is nearly tubular with the lateral margins slightly indented. The body is covered with rounded papillae which are prominent towards the posterior end. An interesting feature about their specimen is that the extreme posterior end of the trunk is devoid of papillae and is made up of concentric fleshy rings. The longitudinal muscle layer is gathered into 20 bands. These authors also mention the presence of four pairs of gonoducts, with the first pair presetal in position. Hence the arrangement of the gonoducts in relation to the ventral setae conforms with the specimen from Isipingo. The size and distribution of the dermal papillae and the anatomy of the blood system are also very similar. The specimen described by Datta Gupta & Menon (1971), however, differs in lacking a rectal caecum. The posterior end of the trunk of their specimen also appears to be rather unusual.

Unfortunately, these authors do not give any details regarding the size of their specimen. However, from their illustration it is apparent that the proboscis is about half the length of the trunk.

The specimen from Isipingo is ascribed to O. kempi on the basis of the number of gonoducts and longitudinal muscle bands. According to Datta Gupta (1976) and Saxena (1983), the number of gonoducts is constant within a species and is an important taxonomic character in echiurans.

O. kempi appears to be related to O. decameron in possessing four pairs of gonoducts. Significant differences, however, occur in the size of the animals, in the number of longitudinal muscle bands and in the nature of their integuments.

Additional material in the future should give a better understanding of the variations within O. kempi.

Ochetostoma palense (Ikeda, 1924)

Figs 26 - 30

Thalassema palense Ikeda, 1924: 39-41, figs 13-15.

Ochetostoma palense: Stephen & Edmonds, 1972: 440.

Present records

One specimen, Isipingo Beach (29° 05'S/30° 56'E), Natal coast, collected by author, 13 June 1983.

Previous records

Holotype only.

Habitat

The specimen occurred in coarse sand under rocks in a rock tunnel, in the intertidal area, close to the high water mark.

Description

Size

Trunk of preserved specimen 22mm long, greatest diameter of trunk 7mm. Proboscis 7mm long, about one-third trunk length.

Colour

In living specimen, proboscis pale yellow, trunk reddish-purple. Preserved specimen white.

External features

Proboscis

Proboscis spatulate, non-deciduous; lateral margins smooth and free at base. In preserved specimen, lateral edges of proboscis curl inwards forming a tube (Fig. 26).

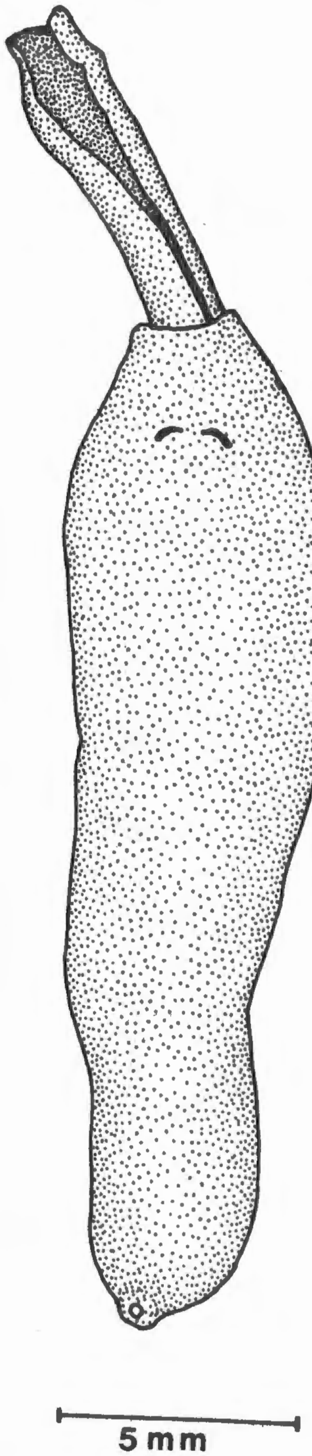

Fig. 26. Ventral aspect of *O. palense*.

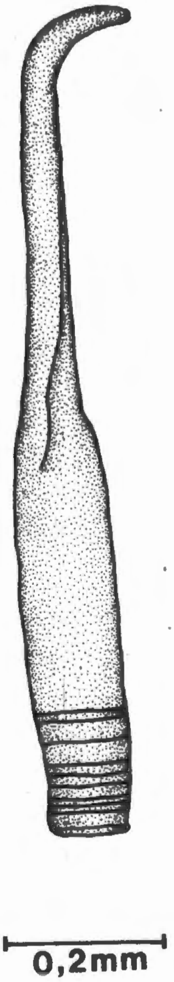

Fig. 27. Right functional seta of O. palense.

Trunk

Trunk cylindrical, tapering gradually towards posterior end (Fig. 26). Anus at tip of small conical projection.

Papillae small, rounded, irregularly distributed over entire surface of trunk, more closely arranged at posterior end. Integument extremely thin and transparent. Nerve cord and other internal organs visible through transparent body wall. Longitudinal muscle bands not visible externally. In dissected specimen, 15 inconspicuous muscle bands apparent only in posterior half of trunk. Interspaces narrow. In anterior half of trunk longitudinal and oblique muscles forming a continuous sheet. Oblique muscles between longitudinal bands weakly fasciculated.

Setae

Setae minute, golden-yellow, about 3mm away from anterior end of trunk. When dissected out and viewed under compound microscope, each seta consists of a straight shaft with a curved terminal end (Fig.27). Proximal half of shaft broader with a few concentric markings at base.

Interbasal muscle absent.

Alimentary canal

Alimentary canal comparatively short, about three times trunk length and with relatively few coils (Fig. 28). Intestine attached to body wall by a few, thin mesenteric strands. Foregut is a narrow tube, about 4mm long, ending at ring sinus. Presiphonal region of intestine 6mm in length, marked by presence of a ciliated groove.

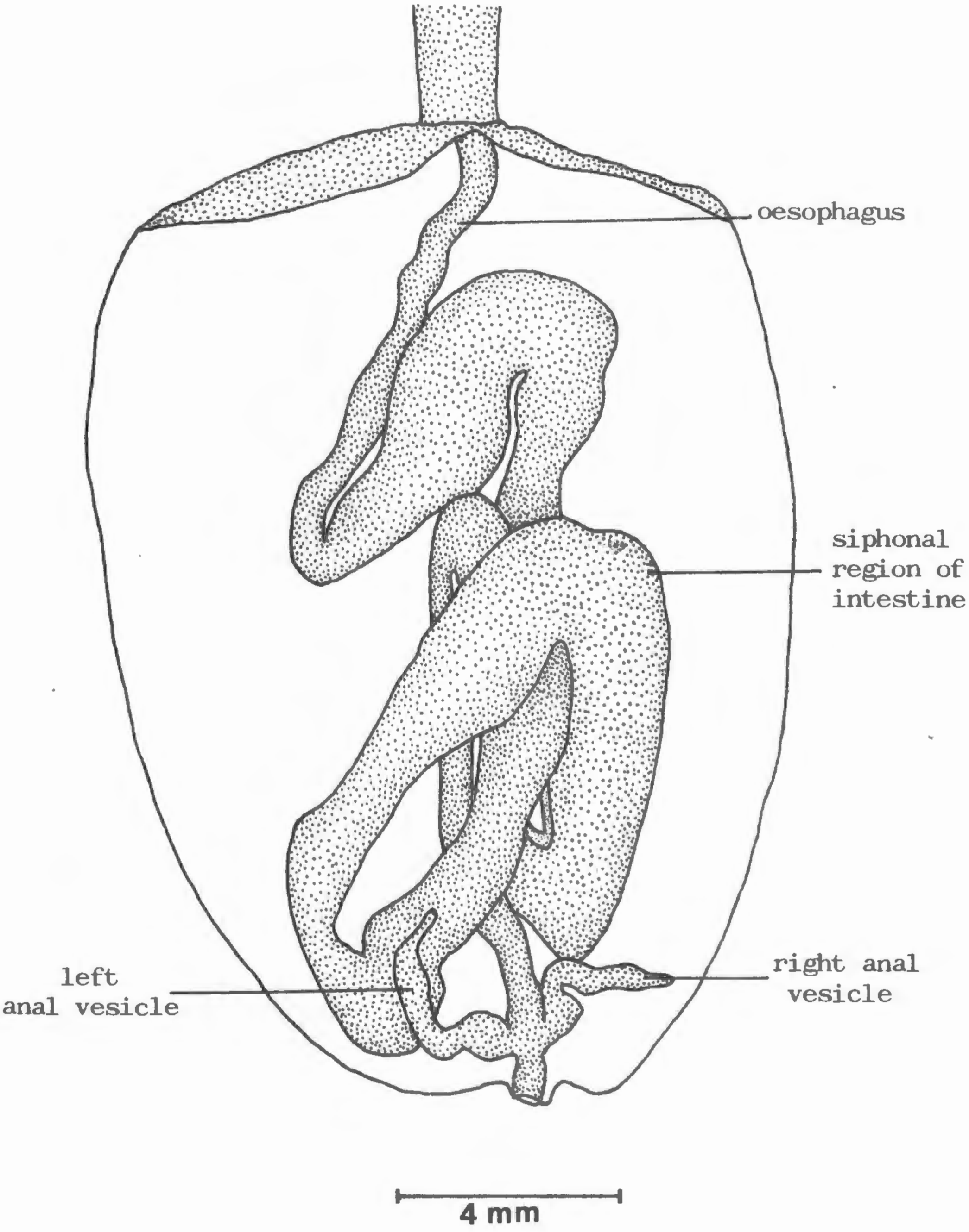

Fig. 28. Dorsal dissection of the trunk of O. palense showing the alimentary canal.

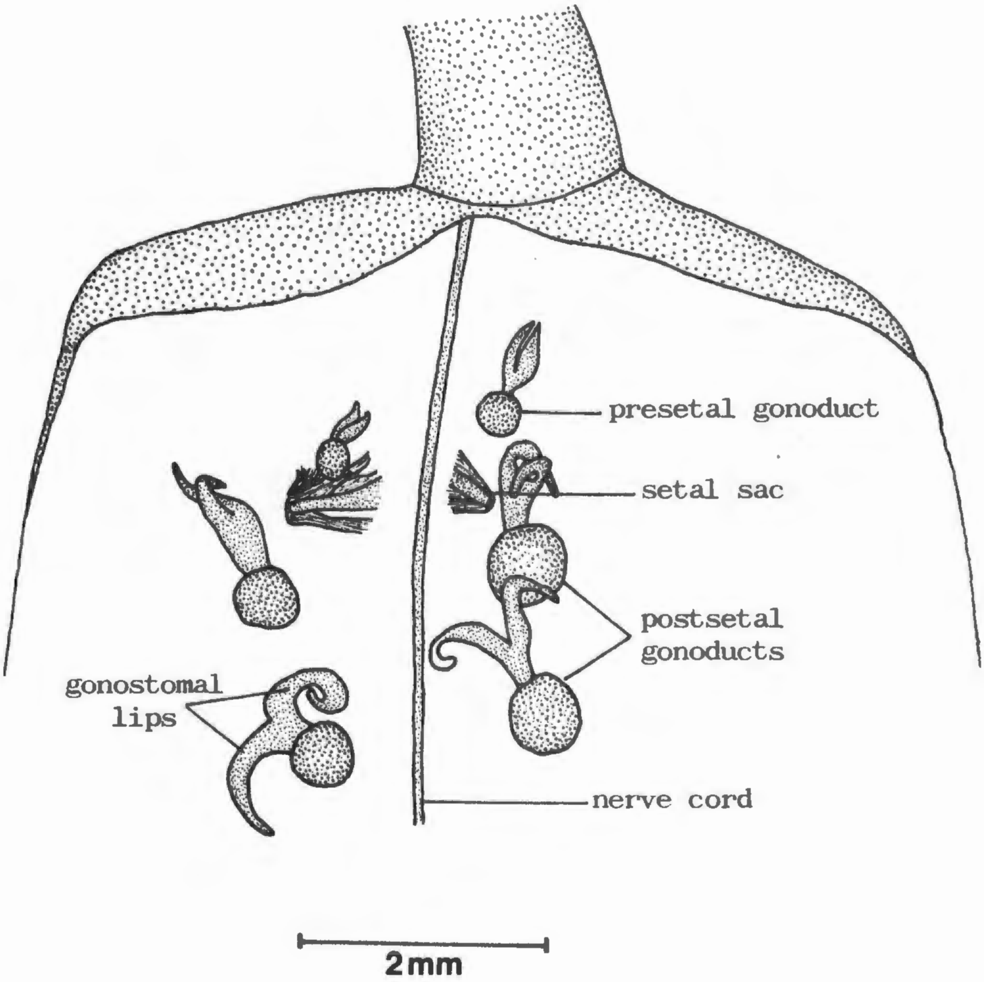

Fig. 29. Anterior part of the trunk cavity of O. palense showing the gonoducts.

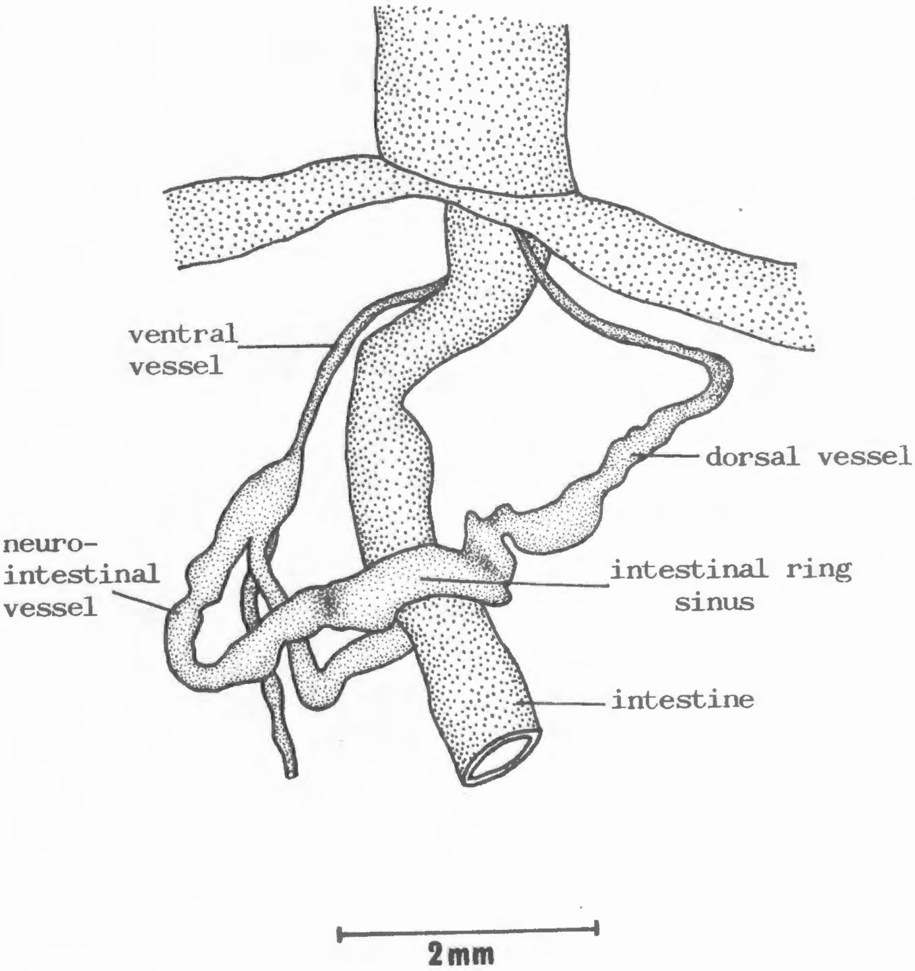

Fig. 30. Anterior part of the trunk cavity of O. palense showing blood vessels.

Ciliated groove commences soon after ring sinus and leads into intestinal siphon. Siphonal region of intestine considerably dilated and extremely thin-walled. Intestine narrows in postsiphonal region and leads into more or less straight rectum.

A small, spherical rectal caecum present.

Anal vesicles

Anal vesicles (Fig. 28) small, blind-ending tubes, less than one-quarter trunk length. Ciliated funnels minute, unstalked, on surface of both vesicles.

Gonoducts

Gonoducts three pairs, spherical to somewhat oval in shape with weakly coiled gonostomal lips (Fig. 29). First pair of gonoducts pre=setal. Gonostomal lips broad, unlike condition in several other species of Ochetostoma. Second and third pairs of gonoducts much larger than first pair.

Blood system

Intestinal ring sinus is an incomplete vascular ring at end of foregut (Fig. 30). Paired neuro-intestinal vessels unite before opening into ventral vessel. Dorsal vessel prominent, arising from ring sinus and entering proboscis.

Remarks

Ochetostoma palense, originally described as Thalassema palense by Ikeda (1924), is based on a single specimen from Palau Islands, Japan. The holotype is small, about 22mm in its entire length, of which about one-quarter belongs to the proboscis. The pear-shaped trunk is 8mm at its widest part. Ikeda's description mentions that the animal is uniformly bright green in life. The thin and transparent integument is covered with minute papillae which are larger and more closely arranged at the extremities of the trunk. The longitudinal muscles are gathered into 15 bands that are apparent only on a small portion of the anterior part of the trunk. An interbasal muscle is absent. There are three pairs of spherical gonoducts with slightly coiled gonostomal lips. The first pair of gonoducts are presetal. The anal vesicles are thinwalled tubes, over half the length of the trunk, with few unstalked funnels. A rectal caecum is absent. According to Ikeda (1924), the alimentary canal is short as compared with the size of the animal, with a few irregular coils.

The present specimen from Isipingo is similar to the Japanese specimen in the size of the animals, in the distribution of the dermal papillae, the nature of the integument as well as in the number of gonoducts and longitudinal muscle bands. In both specimens the gonostomal lips are weakly coiled and the interbasal muscle is absent. The specimen from Isipingo, however, differs in possessing a rectal caecum. Differences are also present in the colour of the animals as well as in the lengths of the anal vesicles.

O. palense appears to be closely related to O. erythrogrammon and Wesenberg-Lund (1939) is of the contention that both the species are synonymous. However, there are several features which tend to separate the two species. An interesting feature of the specimen from Isipingo is that the alimentary canal is comparatively short, about three times the trunk length. In *O. erythrogrammon* it is long and highly coiled and measurements made in a few specimens have shown that it is five times as long as the trunk. The gonostomal lips of *O. palense*, unlike those of *O. erythrogrammon*, are not thread-like and are only weakly coiled. Another distinguishing feature is that the longitudinal muscle bands of *O. palense* are not conspicuous throughout the trunk. Furthermore, the oblique muscles between the longitudinal bands are very weakly developed.

Stephen & Edmonds (1972) have refrained from placing *O. palense* in the synonymy of *O. erythrogrammon* mainly because of the differences in the dimensions of the alimentary canal and in the disposition of the gonostomal lips. In view of the above differences, it has been decided to retain *O. palense* as a species distinct from *O. erythrogrammon*. Any further decisions will have to await the collection of more, preferably adult, material.

Ochetostoma sp. indet.

Figs 31-35

Present records

One sexually mature female, Park Rynie Beach, Natal, collected by author, 7 June 1982.

Habitat

The specimen occurred in the intertidal zone in relatively coarse sand under a projecting ledge of rock facing the shore.

Description

Size

Trunk of preserved specimen 40mm in length, greatest diameter 8mm. Proboscis 11mm, about one-quarter as long as trunk.

Colour

Proboscis pale yellow in living specimen. Longitudinal stripes marking longitudinal muscle bands dark red, interspaces bluish-grey. Colour of preserved specimen pale pink.

External features

Proboscis

Proboscis non-deciduous, shovel-shaped with smooth lateral and terminal margins (Fig. 31). Lateral margins of proboscis fuse at base forming a narrow lower lip ventral to mouth. Ventral groove

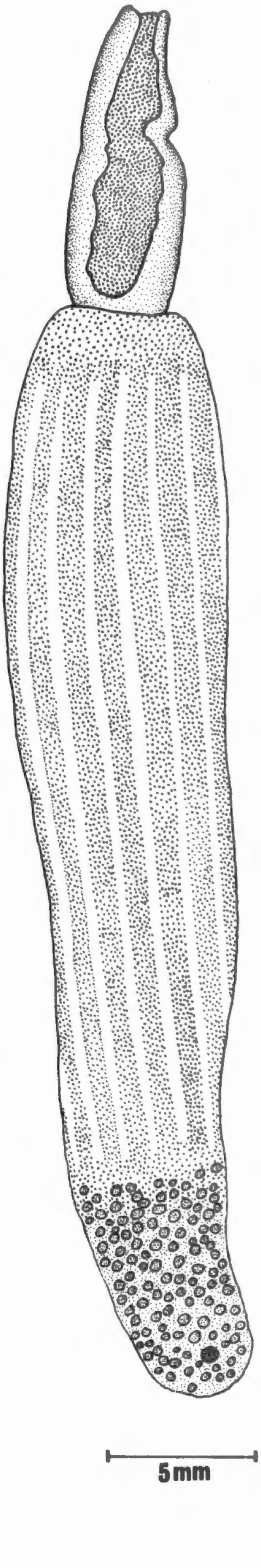

Fig. 31. Ventral aspect of Ochetostoma sp. indet.

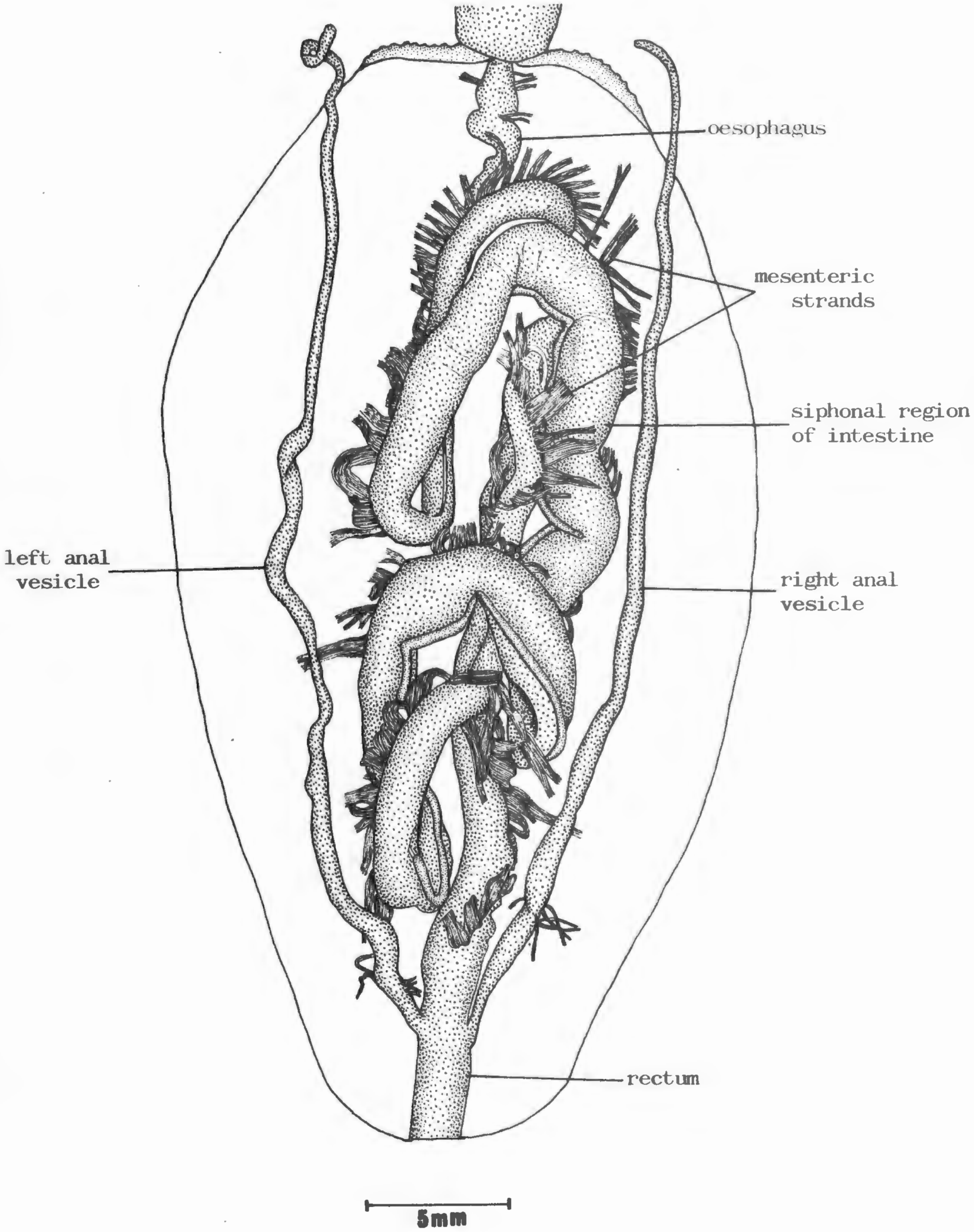

Fig. 32. Dorsal dissection of the trunk of Ochetostoma sp. indet. showing the alimentary system and anal vesicles.

of proboscis smooth but dorsal surface covered with minute, densely arranged, rounded papillae.

Trunk

Trunk sausage-shaped, tapering more towards posterior end (Fig. 31). Entire integument densely covered with small, rounded papillae. Papillae much larger and white in colour at posterior end of trunk. Longitudinal muscles aggregated into 20 bands; inner oblique muscles between longitudinal bands distinctly fasciculated. Entire integument thick and opaque.

Ventral setae missing. Two tiny scars on integument indicate that setae have fallen off.

Interbasal muscle absent.

Internal anatomy

Alimentary canal

Alimentary canal long, consisting of several ascending and descending limbs. An interesting feature is the presence of numerous, closely arranged, white mesenteric strands along entire length of gut (Fig. 32).

Oesophagus comparatively short, terminating at ring vessel. A ventral sheet of mesentery fastens oesophagus to body wall. Inte=stine shows usual divisions into presiphonal, siphonal and post=siphonal regions. Presiphonal region of intestine with a ciliated groove commencing soon after ring vessel. In region of siphon, intestine considerably dilated and thin-walled.

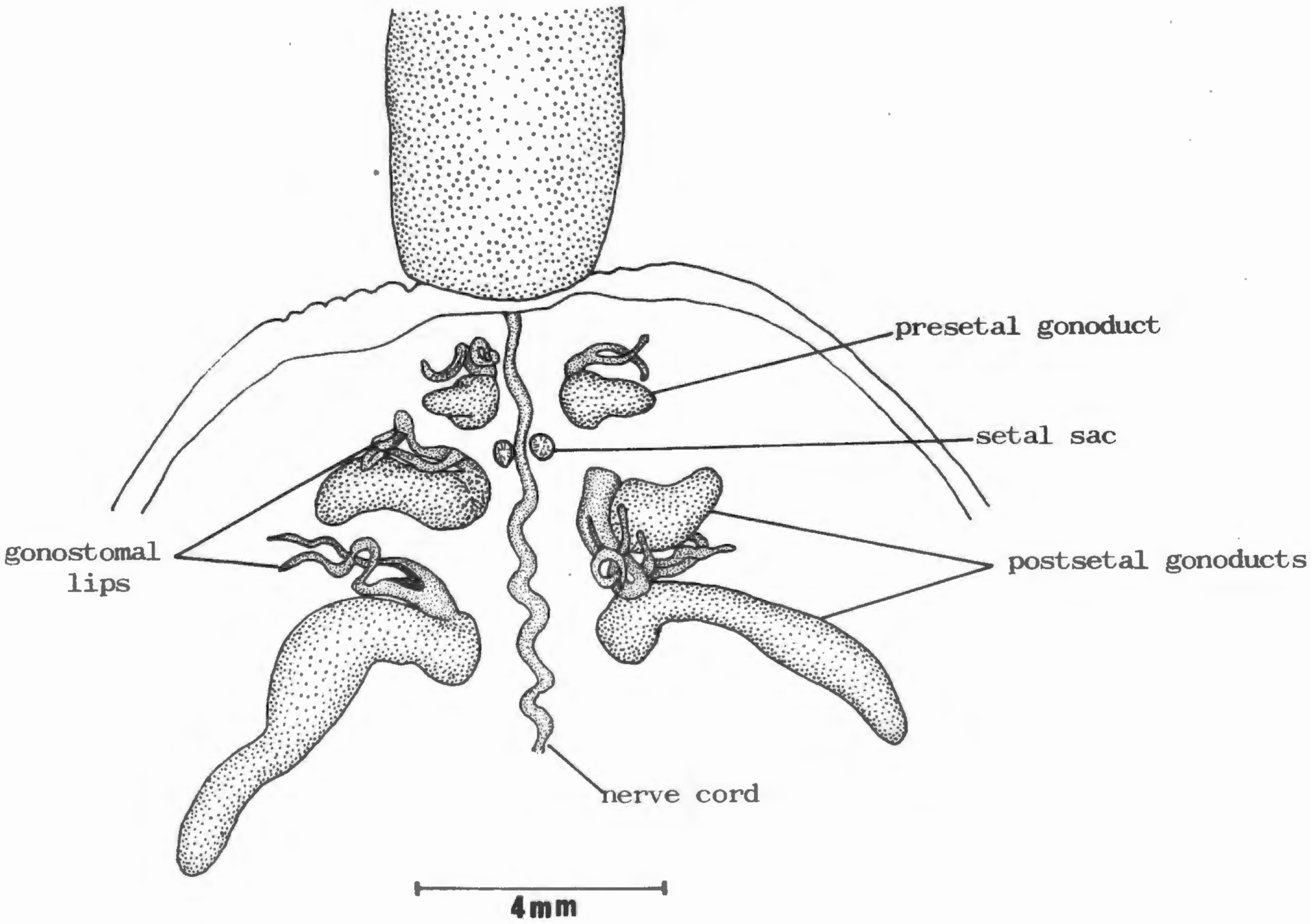

Fig. 33. Anterior part of the trunk cavity of Ochetostoma sp. indet. showing the gonoducts.

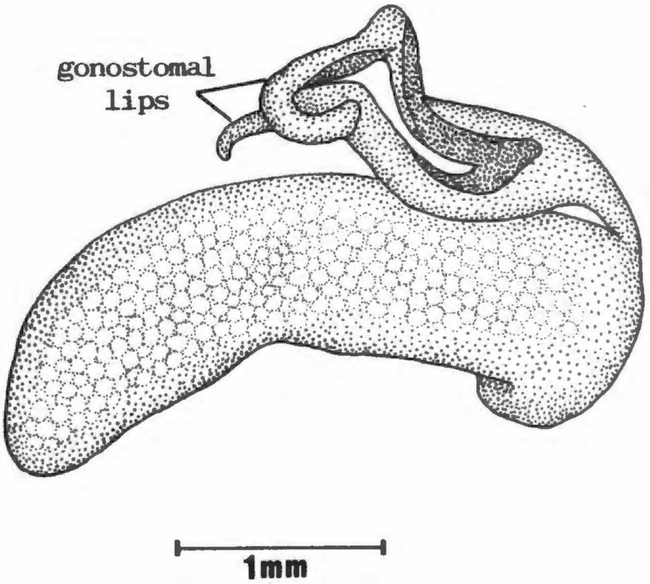

Fig. 34. First postsetal gonoduct of Ochetostoma sp. indet.

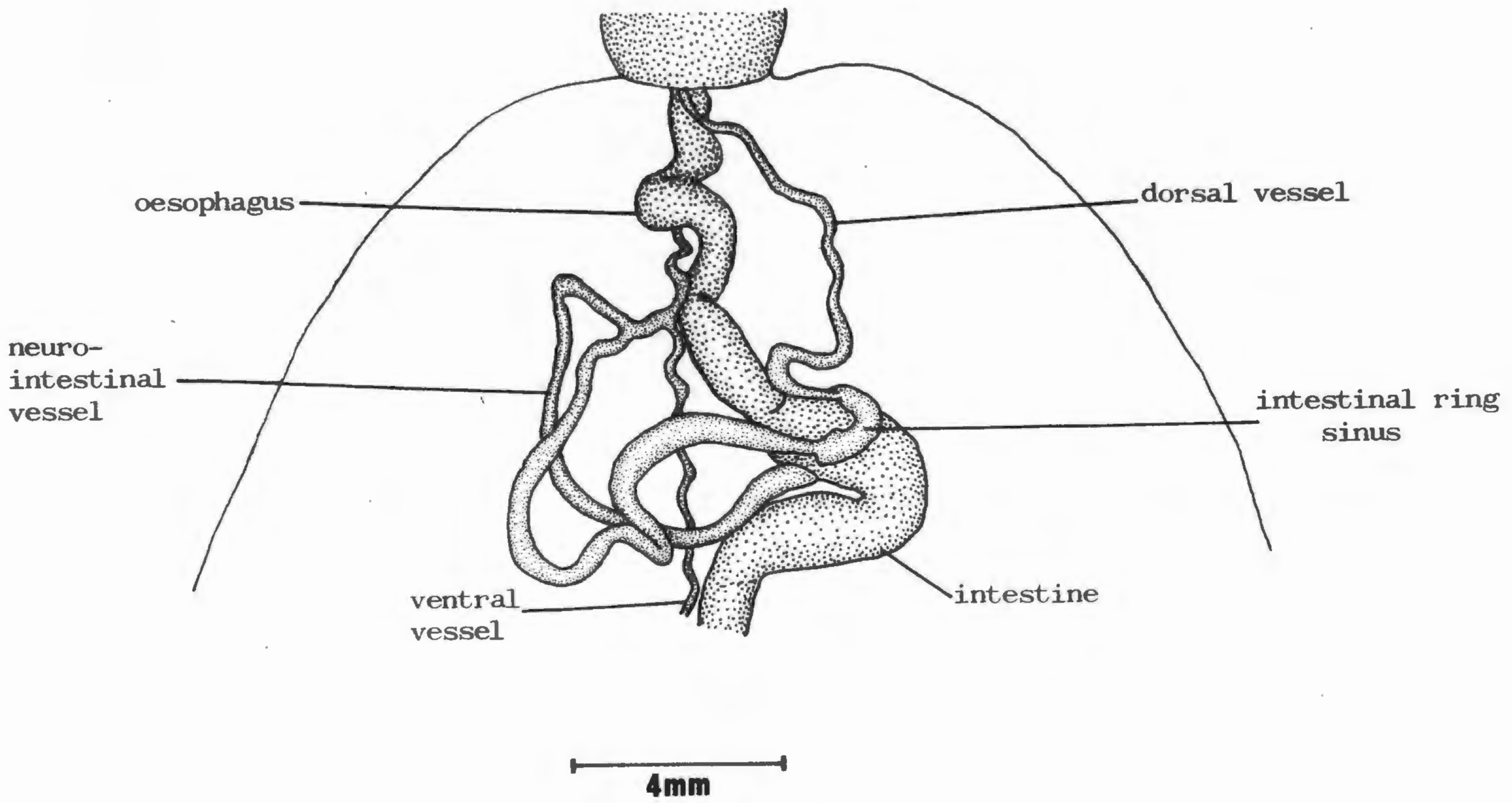

Fig. 35. Anterior part of the trunk cavity of Ochetostoma sp. indet. showing the blood vessels.

A small, spherical rectal caecum present.

Anal vesicles

Anal vesicles paired distensible tubes exceeding length of trunk (Fig. 32). Both vesicles covered with tiny, unstalked ciliated funnels. Funnels more numerous at distal ends of vesicles.

Gonoducts

Gonoducts three pairs, tubular, light brown in colour. First pair smallest, located anterior to ventral setae (Fig. 33). Gonostomal lips small, weakly coiled (Fig. 34), unlike condition in several other species of *Ochetostoma*. Gonostomes robust, and not thread-like in appearance. Proximal end of gonostome broad and sac-like.

All gonoducts compactly filled with eggs, visible through transparent wall.

Blood system

Ring sinus is an incomplete vascular ring located at end of foregut (Fig. 35). Paired neuro-intestinal vessels unite before opening into ventral vessel. As in other species, dorsal vessel passes anteriorly and enters proboscis.

Remarks

Important features of the present specimen include: the presence of unusually large number of mesenteric strands attaching the gut to the body wall, the narrow lower lip of the proboscis, the structure of the gonostomes and the ratio of the proboscis to the trunk length. Another distinguishing feature seems to be the small size of the sexually mature specimen.

O. erythrogrammon, O. caudex, O. palense, O. australiense and O. indosinense possess three pairs of gonoducts and 12 to 22 longitudinal muscle bands and hence appear to be related to the specimen from Park Rynie Beach.

The trunk length of sexually mature specimens of O. caudex ranges from 72mm to 105mm (Biseswar 1983) and in O. erythrogrammon from 80-160mm (Stephen & Edmonds 1972). In both these species, the proboscis is one-third to three-quarters as long as the trunk. The sexually mature specimen from Park Rynie, however, is small, with a trunk length of only 40mm and the proboscis is about one-quarter as long.

In addition to the marked differences in size, the specimen from Park Rynie has a proboscis in which the lateral margins unite posteriorly to form a narrow lower lip.

Another distinguishing feature of the present specimen lies in the structure of the gonostomes. The gonostomal lips, unlike those of O. caudex and O. erythrogrammon, are comparatively small and are not spirally coiled. Furthermore, in the latter two species, the mesenteric strands that fasten the gut to the body wall are relatively few.

In the sexually immature specimen of O. palense, the trunk is about 22mm long and somewhat transparent. The trunk is bright green in life and the longitudinal muscle layer is gathered into 15 bands which are apparent only on a small portion of the anterior part of the trunk. Hence O. palense differs from the present specimen in the colour of the trunk as well as in the nature of the integument. Another important feature that distinguishes O. palense is the presence of a comparatively short alimentary canal with a few irregular coils. Ikeda's description (1924) also mentions the absence of a rectal caecum.

In O. australiense the proboscis is up to 41mm long and the trunk is up to 102mm in length. The Australian specimens usually have 12-13 longitudinal muscle bands, very occasionally 11-14. The gonostomal lips are long and spirally coiled. According to Edmonds (1960), the anterior and posterior surfaces of the trunk bear small flat papillae. Differences between O. australiense and the present specimen are evident in the size of the animals, the number of longitudinal muscle bands, the structure of the gonostomal lips and in the nature and distribution of the dermal papillae.

O. indosinense, described from South Annam by Wesenberg-Lund (1939), is known only from the holotype. In this species, the proboscis is 9mm long and the trunk length is 50mm. According to the description provided by Wesenberg-Lund, the proboscis is slightly bifurcated with the ventral and terminal rims crenated. The proboscis is light green in life and the trunk is pink. There are 18 longitudinal muscle bands with narrow interspaces. The gonostomal lips are long but not coiled.

O. indosinense differs from the present specimen in several respects. The proboscis of O. indosinense is not like that of a typical Ochetostoma. Furthermore, the inner oblique muscle layer is very thin and continuous. O. indosinense also differs in lacking a rectal caecum. Differences are also present in the colour of live animals.

There seems little doubt, therefore, that the specimen from Park Rynie differs in several respects from other known species of Ochetostoma that possess three pairs of gonoducts. A closer study of additional specimens in the future may well indicate that the present specimen belongs to a species new to science.

Ochetostoma arkati (Prashad, 1935)

Thalassema arkati Prashad, 1935: 41-42, figs 1-4.

Ochestoma arkati: Wesenberg-Lund 1959: 203-204, figs 13-14; 1963: 141.

Diagnosis

Proboscis short and stumpy, a third to a quarter of total length of animal; edges of posterior half form short, branched, gill-like processes. Ventral margins of proboscis free at base. Dorsal surface of proboscis smooth; ventral side trough-shaped, deepest at proximal end. Trunk oval, up to 38mm in length, covered with minute, round to oval papillae which are very sparse or absent in middle region. Borders of anus deeply crenulated and scalloped. Area around anus smooth, thin-skinned and devoid of papillae. Longitudinal muscle layer gathered into 7-8 bands, separated by broad interspaces. Two pairs of post-setal, tubular gonoducts almost as long as trunk; gonostomal lips elongate and spirally coiled. Anal vesicles yellowish, very thin and about one-third length of animal.

Distribution: Sandheads off the mouth of the River Hooghly (Ganges Delta); Nigeria and the southern African coast, Port Elizabeth and Cape Town. It is very likely that this species has a wide distri= bution through the western part of the Indo Pacific, and the southern part of the eastern Atlantic.

Remarks

Prashad's description (1935) is based on three specimens from the Ganges Delta. Wesenberg-Lund (1959, 1963) reported 14 more specimens from Nigeria, Cape Town and Port Elizabeth that agreed with Prashad's description except that the number of longitudinal muscle bands was 7-8 instead of eight. *O. arkati* differs from all other species in the genus in possessing branched, gill-like processes along the edges of the posterior half of the proboscis. Unfortunately it was not possible to obtain any material of *O. arkati*.

Ochetostoma capense Jones & Stephen, 1955

Ochetostoma capensis Jones & Stephen, 1955: 273-278, figs 1-3. Wesenberg-Lund, 1963: 142.

Diagnosis

Proboscis small, in preserved specimens about one-eighth of trunk length and in living specimens one-twelfth to one-third; ventral edges crenate when proboscis is extended, but thrown into a series of tight ridges when contracted. Colour varies from cream, through different shades of cream-yellow, to light orange. Trunk up to 120mm when fully extended, thickly covered with papillae on anterior ventral surface but fewer at posterior end. Papillae dispersed in rows in middle region of trunk. Colour of trunk variable, ranging from dark grey-brown to purple brown. Trunk cylindrical or sausage-shaped and typically widest at posterior end. Longitudinal muscles gathered into seven main bands, most conspicuous at ends of trunk. A few weakly developed bands occur inbetween the main bands. Two pairs of tubular, postsetal gonoducts, usually half to three-quarters as long as trunk, but sometimes quite short. Gonostomal lips extended into long spiral filaments. Interbasal muscle present, passes through a loop of neuro-intestinal vessel. Anal vesicles long, thin, brown tubes of variable length, from one- to three-quarters of trunk length and bearing minute, ciliated funnels which are most numerous towards their free ends. Rectal caecum present.

Distribution: Zwartkops River, Langebaan Lagoon and Durban Bay.

Remarks

O. capense is based on a large number of specimens. It is the only estuarine species so far recorded from southern Africa and is probably endemic. This species appears to be related to O. septemyotum Datta Gupta, Menon & Johnson, 1963 but differs significantly in the structure of the proboscis. This species has already been illustrated and fully described.

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Some aspects of the anatomy of *Ochetostoma caudex* (Echiura) from the east coast of southern Africa with remarks on its taxonomic status

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The degree of variation within the species *Ochetostoma caudex* was determined from 32 specimens collected from the east coast of southern Africa. The shape and distribution of the dermal papillae were uniform in all the specimens. The number of longitudinal muscle bands ranged from 14 to 21 with 16 to 19 being the most common. In most specimens the anal vesicles were almost equal to or slightly longer than the trunk and were covered with numerous, unstalked ciliated funnels. A comparison of *O. caudex* with related species (*O. australiense, O. palense, O. indosinense* and *O. erythrogrammon*) revealed differences which justify the retention of *O. caudex* as a distinct species. Hence the contention by some authors that *O. caudex* and *O. erythrogrammon* are synonymous, appears unjustified. *O. griffini* and *O. multilineatum* may prove to be conspecific with *O. caudex*. *O. kokotoniense* and *O. stuhlmanni* are too poorly known for a detailed comparison.

S. Afr. J. Zool. 1983, 18: 47 – 55

Die omvang van variasie binne die spesie *Ochetostoma caudex* is met behulp van 32 voorbeelde wat langs die ooskus van suidelike Afrika versamel is, bepaal. Die vorm en verspreiding van die huidpapille was uniform by al die voorbeelde. Die aantal lengtespierstroke het gevarieer van 14 tot 21 met 16 tot 19 die algemeenste aantal. By die meeste voorbeelde was die anaalbuise net so lank of selfs ietwat langer as die romp en hulle word bedek deur 'n groot aantal ongesteelde gesilieerde tregters. 'n Vergelyking van *O. caudex* met verwante spesies (*O. australiense, O. palense, O. indosinense* en *O. erythrogrammon*) openbaar verskille wat die behoud van *O. caudex* as 'n afsonderlike spesie regverdig. Gevolglik is die standpunt van sommige outeurs dat *O. caudex* en *O. erythrogrammon* sinoniem is, ongegrond. *O. griffini* en *O. multilineatum* mag blyk gelyksoortig te wees met *O. caudex*. *O. kokotoniense* en *O. stuhlmanni* is te swak bekend vir 'n gedetailleerde vergelyking.

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Three echiuran genera are known from South African waters, namely, *Echiurus* Guérin-Méneville 1831, *Ochetostoma* Leuckart and Rüppell 1828, and *Thalassema* Lamarck 1801.

Twenty-eight species have been assigned to the genus *Ochetostoma* but the generic position of at least eight of these is in doubt (Stephen & Edmonds 1972). The following five species have been recorded from South African waters: *O. arkati* (Prashad 1935); *O. capensis* Jones & Stephen 1955; *O. erythrogrammon* Leuckart & Rüppell 1828; *O. mercator* Wesenberg-Lund 1954 and *O. formosulum* (Lampert 1883).

Both Satô (1939) and Wesenberg-Lund (1939, 1963) consider *O. caudex* (Lampert 1883) and several other closely related species in this genus to be synonymous with *O. erythrogrammon*. Although *O. erythrogrammon* is fairly well known, *O. caudex* was based on a single specimen described as *Thalassema caudex* from the Red Sea by Lampert (1883). *O. caudex* was rediscovered (Shipley 1898 and Prashad 1935), but the descriptions are very brief and based on few individuals. Furthermore, the internal anatomy of *O. caudex* has not been thoroughly investigated and practically nothing is known of the variations that occur within the species. Stephen & Edmonds (1972) are also of the opinion that there is insufficient knowledge of the range of variation within this species and several others. Hence they have ' . . . refrained from considering them as synonymous until a closer study can be made of additional specimens' (p 427). A number of species in the genus *Ochetostoma* cannot be recognized positively on the basis of the existing literature.

The aim of this investigation was to determine whether knowledge of the anatomy of more individuals of the species *O. caudex*, will be of help in its taxonomic evaluation.

Materials and Methods

This investigation is based on 32 specimens of *O. caudex* collected at three localities along the east coast of southern Africa. Eight specimens were collected on 27 May 1977 at Embotyi (30°31′S/29°41′E) on the Transkei coast. These specimens were found under small, flat stones overlying coarse, clean sand in the intertidal zone.

The remaining 24 specimens were collected on the Natal coast over a period extending from March 1981 to October

1982 from Isipingo Beach (29°05′S/20°56′E) and Park Rynie Beach (31°19′S/30°44′E). These echiurans were also found in the intertidal zone close to the high water mark. Practically all those from Isipingo were found in a rocky cave facing the sea. Most of the specimens from Park Rynie Beach were found in sand under a projecting ledge of rock facing the shore. Sometimes as many as 15 specimens were collected in the same habitat suggesting that this species is gregarious. Occasionally isolated specimens were also found under loose rocks in the littoral zone.

Living specimens were photographed both in the fully extended and contracted states. Measurements were taken after the specimens were narcotized and preserved in formalin. All the specimens were subsequently dissected to determine the range of variation of various structures and organs. Gross morphology was studied with the aid of a camera lucida while detailed investigations of certain structures, such as the anal vesicles and nephrostomal lips were made with the scanning electron microscope. Furthermore, the anal vesicles and nephrostomal lips were serially sectioned for histological details.

Results

Size of specimens

Of the 32 specimens, 11 were sexually mature since gametes were present in the nephridia. The trunk length of sexually mature specimens ranges from 72 to 105 mm and the proboscis length from 20 to 49 mm (Table 1). The size of these animals, however, varies considerably depending on their state of contraction at fixation.

Table 1 Measurements in millimetres of sexually mature specimens

Length of trunk & proboscis	Trunk length	Proboscis length	Greatest diameter of trunk
130	93	37	15
123	97	27	12
112	80	32	12
105	74	31	11
149	105	44	16
96	72	24	12
115	79	36	10
123	74	49	13
102	75	27	12
124	86	38	12
95	75	20	14
Average			
115,9	82,7	33,2	12,6

External features

The following description of the external features is based on all 32 specimens.

Proboscis

The fleshy, pale-yellow proboscis (Figure 1) is non-deciduous. It has a shallow ventral groove along its entire length. In living specimens the proboscis is spatulate whereas in preserved specimens the lateral edges tend to curl inwards forming a tubular structure. In most of the specimens the lateral edgs of the proboscis are tinged with green. When fully extended, the proboscis is almost as long as the trunk.

Figure 1 Lateral view of living specimen illustrating the general body form and the shape of the proboscis.

Trunk

The body is cylindrical, tapering more towards the posterior end (Figure 1). Living specimens have reddish-purple longitudinal stripes marking the longitudinal muscle bands while the interspaces are bluish-grey. However, there is variation in the colouration of the trunk; in some specimens the longitudinal bands are dark brown. The posterior end of the trunk is white and here the brightly coloured longitudinal bands become inconspicuous. In some, the extreme posterior end of the trunk is tinged with bright green. Specimens preserved in formalin become brown in colour. The body wall is relatively thick, tough and opaque except in the antero-ventral region of the trunk where it is somewhat translucent.

The entire integument of the trunk is densely covered with papillae. These papillae are minute, transversely elongated and arranged regularly in circular rows over most of the trunk except posteriorly where they are more prominent, and round to ovoid in shape. The posterior papillae appear as white spots and do not have any definite pattern or arrangement. The shape and distribution of the papillae are uniform in all the specimens. Under certain states of contraction of the trunk, rings of rounded prominences appear on the longitudinal muscle bands.

In formalin-preserved specimens, a white mucous cap encases the extreme posterior end of the trunk but this is not apparent in living specimens.

A pair of small pointed yellowish-brown setae is located antero-ventrally about 5 to 7 mm posterior to the proboscis-trunk junction. Just anterior to the setae is the first pair of nephropores while the remaining two pairs are post-setal in position. Both the setae and nephropores are visible to the unaided eye.

Setae

The setae (Figure 2) are elongate, cylindrical, hook-like structures, tapering towards the tip. The terminal end is

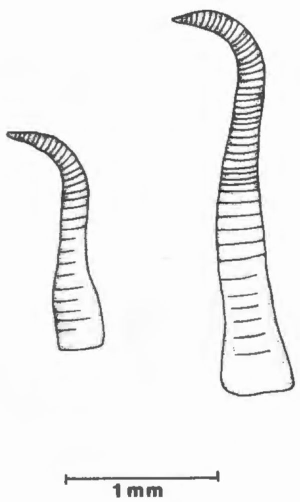


Figure 2 The left non-functional (replacement) and the functional setae.

curved at right angles to the main axis of the shaft and directed posteriorly. The distal third of the seta which protrudes from the ventral body wall has numerous closely arranged concentric markings. These markings, however, are less pronounced and sparsely arranged in the proximal two-thirds of the shaft.

As in other species belonging to the genus *Ochetostoma*, the setae are located in special sacs and are supported by numerous radiating muscle bands. These muscles have a cone-like arrangement and radiate from the base of the setal sac to the body wall. The largest muscle bands insert on the medial aspect of the shaft. Among the thicker muscle bands a number of finer strands are present. There is no interbasal muscle present in *O. caudex*.

In some specimens replacement setae are present and are about half the size of the functional ones. They are enclosed in their own sheaths and do not appear to protrude from the ventral body wall. No variations in the structure of the setae were observed.

Internal anatomy

Alimentary canal

The alimentary canal (Figure 3) of *O. caudex* is of considerable length and highly convoluted, forming several loops. It is attached to the body wall at several points by thin mesenteric strands. The mouth is situated more or less on the ventral side of the extreme anterior end of the trunk at the base of the proboscis. It leads into a somewhat dilated muscular pharynx which is attached to the body wall by numerous radiating muscle strands. The oesophagus is a straight tube of uniform diameter attached to the body wall anteriorly by a ventral mesentery. At the posterior end of the oesophagus is a dorsal constriction which probably demarcates it from the remainder of the alimentary canal. Just posterior to the constriction, the intestine forms a loop and then pursues a complex course through the body cavity.

The gizzard and crop cannot be distinguished as there are no distinct boundaries externally.

By far the greater part of the alimentary canal is formed by the intestine proper. As in other members of this genus, the middle portion of the alimentary canal is subdivided into the pre-siphonal, siphonal and post-siphonal regions. The intestine, especially in the region of the siphon, is extremely thin-walled and translucent. In a number of specimens the gut was compactly filled with coarse sand grains and shell fragments.

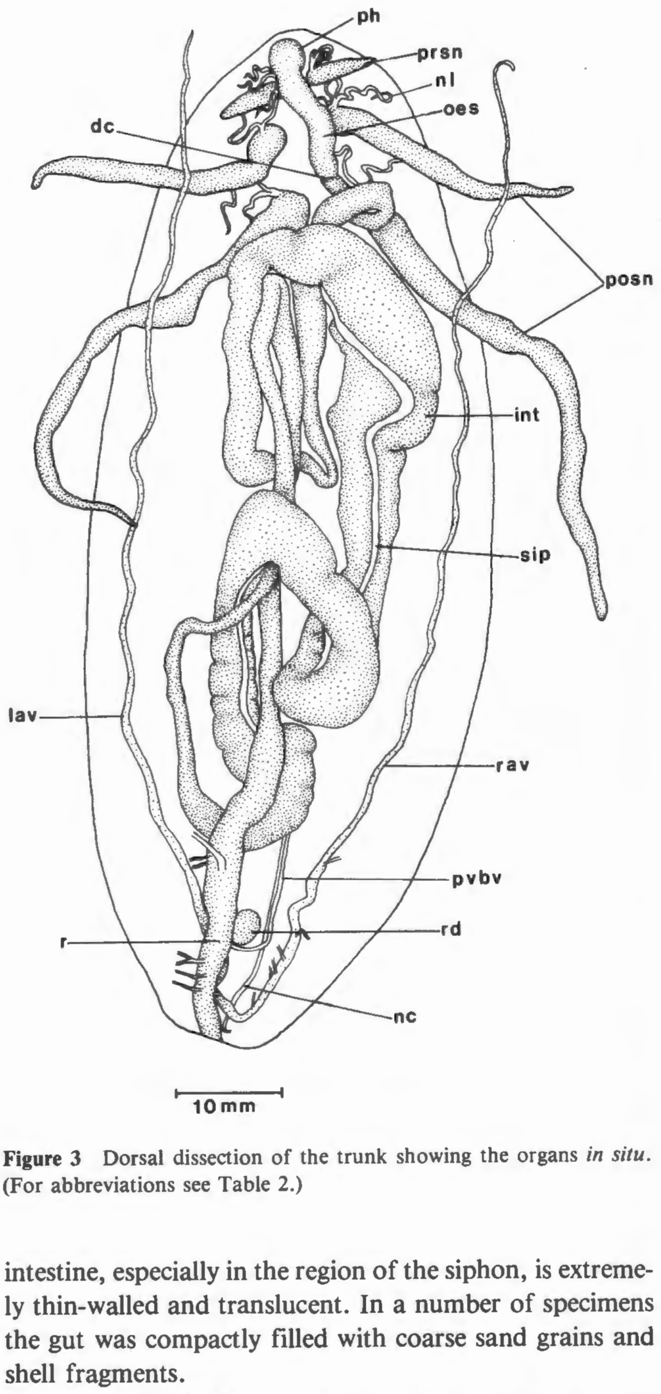


Figure 3 Dorsal dissection of the trunk showing the organs *in situ*. (For abbreviations see Table 2.)

The intestine leads into a more or less straight tube, the rectum, which opens to the exterior by way of the terminal anus. The rectal diverticulum, a small spherical sac opening ventrally into the rectum, was found in all the specimens.

Anal vesicles

The anal vesicles or anal sacs are paired, elongate, blind-ending tubes which lie in the coelom and open into the rectum just posterior to the rectal diverticulum (Figure 3). Proximally, they are fastened to the body wall by a number of connective tissue strands but distally they weave loosely through the coils of the alimentary canal. In most of the specimens the anal vesicles were found to be almost equal to or slightly longer than the trunk. They were shorter and extended up to about the middle of the trunk in a few specimens. In one specimen the right anal vesicle was as long as the trunk but the left one was only about one-third its length. The length of these vesicles appears to depend also on the degree to which they are contracted.

The outer surface of these vesicles, facing the coelom, is covered with numerous minute, unstalked, ciliated funnels (Figure 4). These funnels are more or less cone-shaped and scanning electron micrographs show numerous projections around the rim or lip from which groups of long cilia arise (Figure 5). Light microscopic studies of longitudinal sections of the funnels, however, reveal that the inside of the cup is also heavily ciliated. Cross-sections of the anal sacs show that the wall consists of three layers (Figure 6).

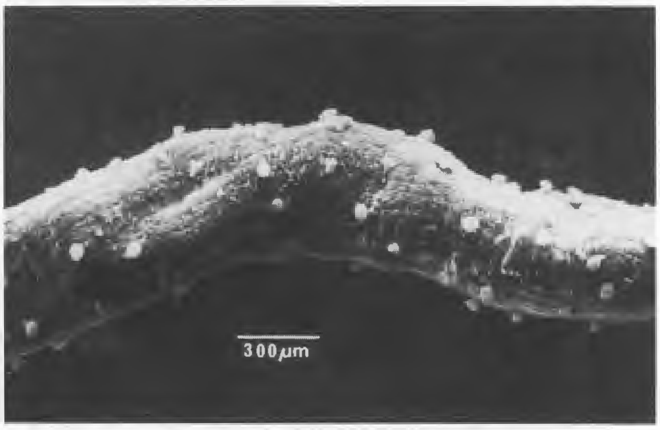


Figure 4 Scanning electron micrograph of part of anal vesicle showing the distribution of the funnels.

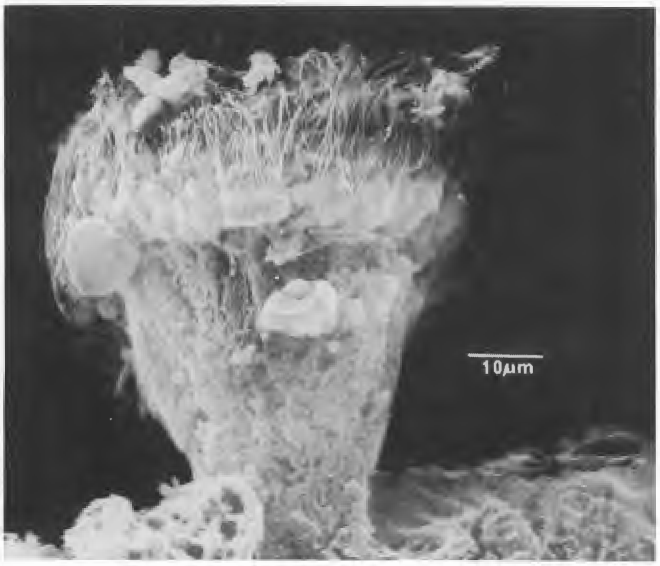


Figure 5 Scanning electron micrograph of a single funnel.

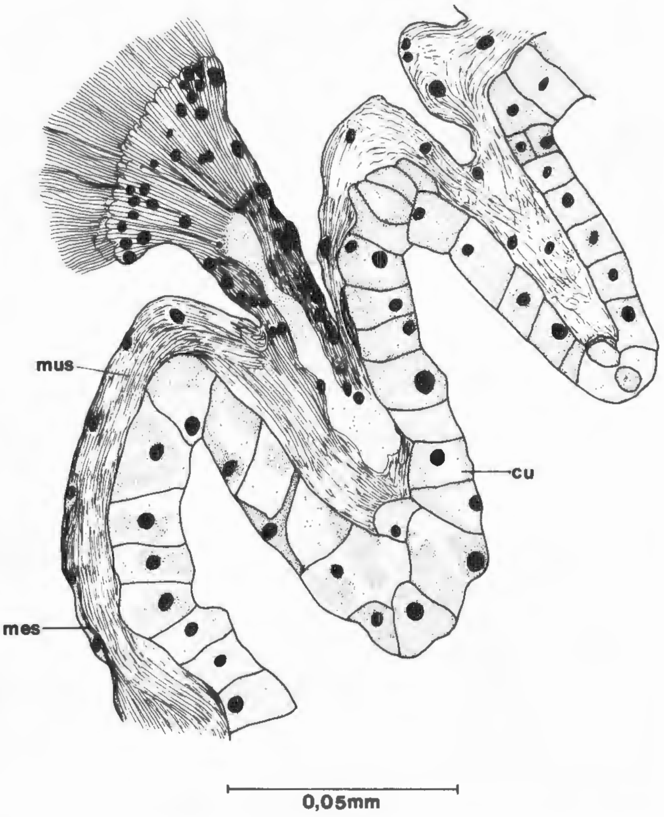


Figure 6 Cross-section illustrating the histological structure of the anal vesicle. (For abbreviations see Table 2.)

The outer surface is lined by a mesothelial layer of squamous cells which is continuous with the walls of the funnel. Immediately beneath the squamous cells is the muscle layer which in turn is followed by a layer of cuboidal epithelial cells with granular cytoplasm around the lumen of the sac. The role of the anal sacs in producing a filtrate of coelomic fluid through the ciliary activity of the funnels has been clearly demonstrated in *Bonellia viridis* by Harris & Jaccarini (1981).

Nephridia

The three pairs of nephridia (Figures 3, 7) or segmental organs are located in the anterior part of the body cavity on either side of the nerve cord. One pair lies anterior to the ventral setae, while the other two pairs are post-setal in position. The nephridia have the same basic structure but increase in size posteriorly, the third pair being the largest.

Each nephridium consists of an elongate vesicle with a pair of deeply grooved nephrostomal lips that extend into

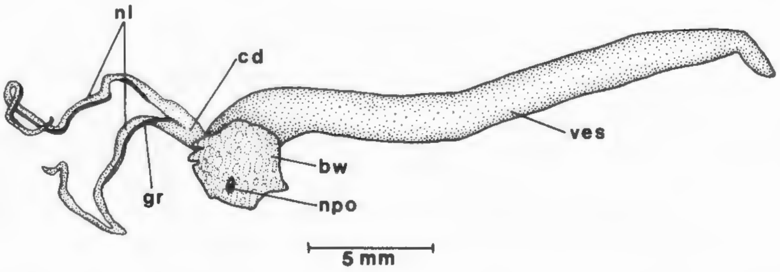
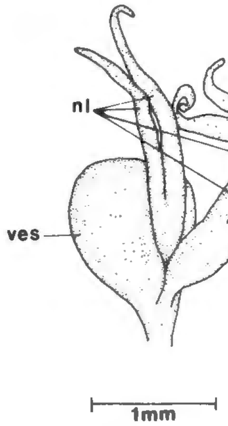


Figure 7a A single nephridium of a sexually mature female (the right one of the first post-setal pair). (For abbreviations see Table 2.)

7b



7c

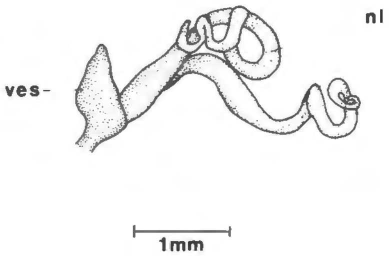


Figure 7b & c Variation in the structure of the nephridia. (b) First pre-setal nephridium from the left. (c) Left nephridium (first of the post-setal pair). (For abbreviations see Table 2.)

long, coiled whip-like structures or flagella. Histological study of the structure of the flagellum shows that it is composed of muscle fibres and loose connective tissue with a groove on one side that is lined with ciliated cuboidal cells (Figure 8). The two flagella unite proximally to form a short and narrow duct which opens into the base of the nephridial vesicle. The ciliated nephrostomal lips serve to convey the reproductive cells from the body cavity into the vesicle. In some cases, coelomocytes were observed in the grooves.

The size of the nephridial vesicles varies according to the state of maturity of the animal. In sexually mature specimens the second and third pairs of vesicles are enormously developed and distended owing to the presence of gametes.

The nephridia of *O. caudex* sometimes show variations from the normal condition. In one individual, the vesicle of one of the nephridia was small and globular in shape with two pairs of nephrostomal lips, while in another specimen, although the vesicle was small, the nephrostomal lips were rather elongate. Occasionally, variations were also observed in the number and position of the nephridia. In one specimen the nephridia on the right were in the normal position but on the left, four were present; one pre-setal and the remaining three post-setal. The third and fourth nephridia were situated very close to each other. In yet another individual, only two post-setal nephridia were present on the left although those on the right were normal.

Blood vascular system (Figure 9)

With some minor variations, the blood system does not show any marked deviation from the general pattern described in other closely related species. The dorsal blood vessel is a very prominent vessel which lies dorsal to the foregut. Posteriorly this vessel joins the intestinal ring vessel. There is a conspicuous dilation present at the posterior end of the dorsal vessel. Anteriorly this vessel continues into the proboscis, dorsal to the pharynx.

From the ring vessel arise two neuro-intestinal vessels which pass anteroventrally. A small dilation is also present on the left lateral vessel at its point of origin. The mid-ventral vessel gives off smaller vessels to the oesophagus. The two neuro-intestinal vessels unite ventrally to form a single vessel which then splits into the anterior and posterior ventral vessels. The former passes forward ventral to the oesophagus and pharynx and enters the proboscis, while the latter continues alongside the ventral nerve cord and then passes dorsally to supply the rectum just posterior to the rectal diverticulum. Both the dorsal and neuro-intestinal vessels lie loosely in the coelom unattached by mesenteries either to the gut or the body wall.

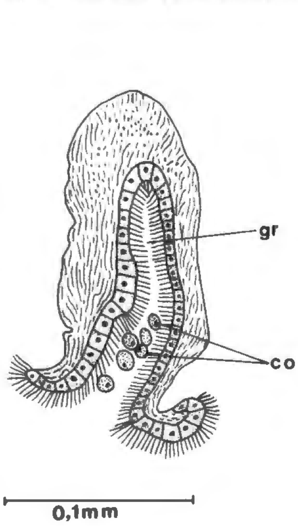


Figure 8 Cross-section of the nephrostomal lip illustrating the ciliated groove. (For abbreviations see Table 2.)

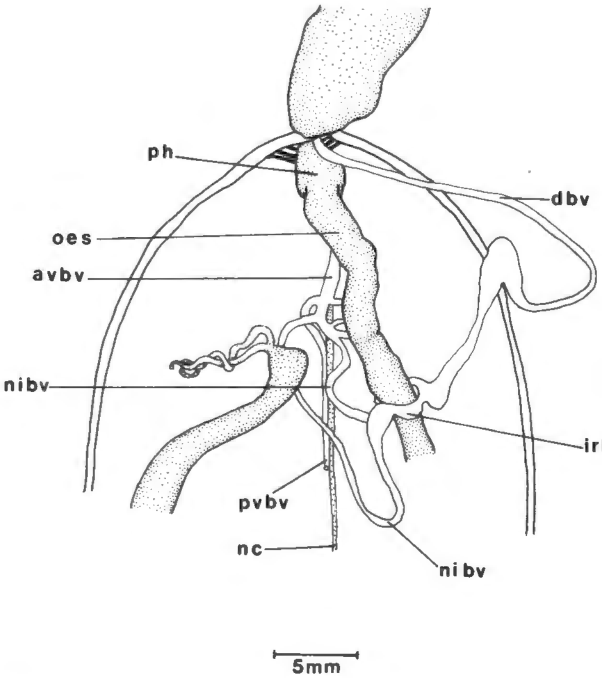


Figure 9 Anterior part of the alimentary canal illustrating the blood vessels. (For abbreviations see Table 2.)

Table 2 Key to abbreviations

avbv	anterior ventral blood vessel
bw	body wall
cd	common duct
co	coelomocytes
cu	cuboidal epithelium
dbv	dorsal blood vessel
dc	dorsal constriction
gr	groove
int	intestine
irbv	intestinal ring blood vessel
lav	left anal vesicle
mes	mesothelial layer
mus	muscle layer
nc	nerve cord
nibv	neuro-intestinal blood vessel
nl	nephrostomal lips
npo	nephropore
oes	oesophagus
ph	pharynx
posn	post-setal nephridia
prsn	pre-setal nephridium
pvbv	posterior ventral blood vessel
r	rectum
rav	right anal vesicle
rd	rectal diverticulum
ves	vesicle
sip	siphon

Trunk musculature

In the 32 dissected specimens, the number of longitudinal muscle bands ranged from 14 – 21. In the majority of the specimens (24) this number varied from 16 – 19. In seven specimens, however, the number was found to be between 19 – 21, while in only a single individual the muscle bands ranged from 14 – 16. Variations in the number may occur in different regions of the trunk of the same individual owing to the splitting of the longitudinal muscle bands. There seems to be no correlation between the number of longitudinal muscle bands and the size of specimens. In one specimen, for instance, where the proboscis was only 13 mm in length and the trunk 24 mm, there were 20 – 21 muscle bands present. The oblique muscles between the longitudinal muscle bundles are fasciculated.

Discussion

According to Stephen & Edmonds (1972) the distribution of this species is as follows: Red Sea and Indian Ocean (Lampert 1883); Rotuma (Shipley 1898); Andaman and Nicobar Islands (Prashad 1935). Its discovery on the east coast of southern Africa has considerably extended its range of distribution. However, it is not surprising for this typically Indian Ocean species to be distributed as far west as the east coast of South Africa.

Lampert (1883) gives no details regarding the size of his specimens of *O. caudex*. The description provided by Shipley (1898) of his specimens from Rotuma, however, mentions 18 to 25 mm for the length of the proboscis and 50 to 70 mm for the length of the trunk. Prashad's description (1935) of *O. caudex* is based on three specimens that were well preserved and his largest specimen had a total length of 73 mm (54,5 mm for the length of the trunk and 18,5 mm for the length of the proboscis). Measurements of sexually mature specimens from South Africa reveal large sizes for the species.

The South African specimens of *O. caudex* differ in certain respects from the description provided by Lampert (1883). According to the above author the papillae on the body wall lie on raised ridges which correspond to the longitudinal muscle bands. Careful observation of living specimens, however, has shown that the longitudinal ridges are not permanent structures but become evident only under certain states of contraction. When the animal is completely relaxed these longitudinal ridges become less pronounced and in well-narcotized specimens, the body appears relatively smooth. The South African specimens also differ in that the papillae are distributed over the entire surface of the trunk and are not confined to the longitudinal muscle bands as stated by Lampert (1883). Unfortunately Shipley (1898), gives no details regarding the nature and distribution of the dermal papillae for his Rotuma specimens. The distribution of the dermal papillae of the South African specimens, however, is very similar to the description provided by Prashad (1935). A noticeable feature of *O. caudex* is that the shape and distribution of the papillae are uniform in all the specimens. This seems to be an important characteristic of this species and may be diagnostic. This is further substantiated by the fact that authors who have described species of *Ochetostoma* have not reported variations within the species as far as the shape and arrangement of the papillae are concerned.

Lampert (1883) and Shipley (1898) report the presence of 16 to 18 muscle bands in *O. caudex* while Prashad (1935) mentions 18 to 19. In the South African specimens, however, the number ranges from 14 to 21. Since the description of *O. caudex* by the early authors was based on few specimens, very little was known of the variation in the number of longitudinal muscle bands within this species.

From the descriptions of *O. erythrogrammon* by several authors (Shipley 1899; Satô 1935, 1939; Stephen & Robertson 1952; Wesenberg-Lund 1954, 1957, 1959a, 1959b; Webb 1972) it is evident that there is a considerable variation in the number of longitudinal muscle bands in this species also. According to Stephen & Edmonds (1972) the number in *O. erythrogrammon* usually ranges from 13 to 18. Stephen & Robertson (1952) and Webb (1972), however, report the presence of only 12 longitudinal muscle bands. Therefore it is apparent that the number of longitudinal muscle bands cannot be used as a reliable taxonomic criterion because of the considerable overlap that occurs among several closely related species.

The most recent systems of classification of the phylum Echiura are these of Stephen & Edmonds (1972) which have been modified from those of Bock (1942) and Fisher (1946, 1949). Stephen & Edmonds (1972) state that they have been unable to construct a complete key to the genus *Ochetostoma* and have encountered problems especially in the classification of those species that possess three pairs of nephridia and 12 to 18 longitudinal muscle bands. The species falling into this group include: *O. caudex; O.*

kokotoniense and *O. stuhlmanni* (Fischer 1892); *O. australiense* Edmonds 1960; *O. palense* (Ikeda 1924); *O. griffini* (Wharton 1913); *O. indosinense* Wesenberg-Lund 1939 and *O. erythrogrammon.*

Satô (1939), mainly because of the considerable overlap in the number of longitudinal muscle bands, considers *O. caudex, O. kokotoniense* and *O. stuhlmanni* to be synonymous with *O. erythrogrammon* while Wesenberg-Lund (1939, 1963), in addition to these, also includes *O. palense* and *O. multilineatum* (Fischer 1914) in the synonymy.

O. kokotoniense and *O. stuhlmanni* have been very briefly diagnosed and described and on the basis of the existing literature it is extremely difficult to make satisfactory comparisons with other closely related species. The former species, from Zanzibar, is known from a single specimen in which the proboscis was missing while the latter has been described from three mutilated specimens from the same locality (Stephen & Edmonds 1972). *O. kokotoniense* possesses 17 to 18 longitudinal muscle bands and therefore cannot be separated from *O. caudex* on the basis of this feature. However, it differs from *O. caudex* in the nature and arrangement of the dermal papillae. According to Stephen & Edmonds (1972) smaller papillae are distributed over the whole surface in definite transverse rows, interrupted by rings of larger papillae.

The length of the trunk of *O. stuhlmanni* averages 20 mm and the proboscis 5 mm (Shipley 1899). Stephen & Edmonds (1972) have incorrectly given the length of the proboscis as 0,5 mm. The specimens comprising this species appear to be much smaller when compared to *O. caudex*. However, this size difference cannot be used as a reliable distinguishing feature since Shipley's description does not mention whether the specimens studied were juvenilies or sexually mature individuals. Another difference of lesser significance appears to be in the length of the anal vesicles which in *O. stuhlmanni* are only half as long as the trunk (Shipley 1899). Stephen & Edmonds (1972) have refrained from placing *O. stuhlmanni* in the synonymy of *O. kokotoniense* mainly because of the difference in the number of longitudinal muscle bands. More detailed redescriptions based on additional specimens from or near the type locality are required before the taxonomic position of these two species can be satisfactorily determined.

O. australiense is known from numerous specimens from the eastern coast of Australia and closely resembles *O. erythrogrammon* (Stephen & Edmonds 1972). The description of this species by Edmonds (1960) is based on 21 specimens, 12 of which were dissected. It differs from *O. caudex* in the number of longitudinal muscle bands. According to Edmonds (1960), the number is usually 12 to 13, occasionally 11 to 14. Another distinguishing feature lies in the dermal papillae, which in *O. australiense* are small and flat and confined to the anterior and posterior surfaces of the trunk. Differences are also apparent in the colour; living specimens are red but preserved specimens are pale pink or straw coloured. The proboscis also is unlike that of *O. caudex*. In living specimens the proboscis is white and when fully extended appears to be quite flat, more or less ribbon-like in appearance (Edmonds 1960).

In their monograph, Stephen & Edmonds (1972) state that an interbasal muscle is present in *O. australiense*. However, this does not correspond to Edmonds' original description (1960) of the species.

O. palense, described as *Thalassema palense* by Ikeda (1924) from the Palau Islands, Japan, differs from *O. caudex* in several respects. The animals are uniformly bright green in life. The trunk is pear-shaped and the integument is very thin and somewhat transparent except in the anterior and posterior regions where it is a little thicker and opaque. Ikeda's description (1924) mentions 15 longitudinal muscle bands that are confined only to a small anterior portion of the trunk. Another distinguishing feature is that the alimentary canal is rather short in relation to the size of the animal. Furthermore, there are comparatively few unstalked funnels present on the anal vesicles and there is no rectal diverticulum.

O. griffini, originally described as *Thalassema griffini* by Wharton (1913), is known from numerous specimens from the Philippines. According to the above author, the length of the trunk of the largest specimens ranges from 120 to 140 mm when fully extended and the proboscis from 50 to 80 mm. Stephen & Edmonds (1972) have incorrectly given the length of the trunk as 12 to 14 mm in their monograph. This gives an erroneous impression of the relative proportions of the proboscis and trunk. The anal vesicles appear to differ slightly from those of *O. caudex*. Wharton's description (1913) mentions that the anal vesicles are clear and transparent sacs about one-half the length of the body. Another difference is that the papillae in the posterior end of the trunk are arranged in more or less definite rings (Wharton 1913). Besides these two relatively minor differences, it is difficult to find any other feature that will distinguish *O. griffini* from *O. caudex* and it seems very likely that the two species are identical. Furthermore, the habitats of both appear to be very similar.

The description of *O. indosinense* by Wesenberg-Lund (1939) is based on a single specimen from Nhatrang, South Annam. The most important differences between *O. indosinense* and *O. caudex* lie in the nature of the proboscis, the body wall and the nephrostomal lips. According to Wesenberg-Lund (1939), the proboscis is slightly bifurcated, the ventral rims crenated and its dorsal surface is covered with ovoid or cylindrical papillae. In addition the trunk, unlike that of *O. caudex*, is pointed at each end and the body wall is very much thinner and transparent in the middle. An important distinguishing feature is that the oblique muscle layer is very thin and continuous. The nephrostomal lips, although elongate, are not coiled. Furthermore, a rectal diverticulum is absent. Differences are also apparent in the colour of the animals. In the live specimen, the proboscis is light green and the body is pink (Wesenberg-Lund 1939).

O. multilineatum, described originally as *Thalassema multilineatum* by Fischer (1914), is based on a single specimen from the West African coast. It differs from *O. caudex* in possessing anal vesicles which are only one-quarter the length of the body. Since the proboscis was lacking in the type specimen, it is very likely that this structure is deciduous in *O. multilineatum*. The maximum number of longitudinal muscle bands in *O. caudex* is not known to exceed 21 whereas in *O. multilineatum* these muscles are gathered into 21 to 22 longitudinal bands (Fischer 1914). Apart from these minor differences it is difficult to find any other feature that will clearly distinguish *O. multilineatum* from *O. caudex* and these two species may well be synonymous.

O. erythrogrammon, originally described from the Red Sea, has been reported from numerous localities from both the Indian and Pacific Oceans. From the description of this species by Stephen & Edmonds (1972) it is evident that the colour of the proboscis differs from that of *O. caudex*. The dorsal surface of the proboscis is bright green and the ventral side is yellow with a violet line on each side.

Satô (1935, 1939) states that the dermal papillae in *O. erythrogrammon* are distributed quite irregularly being more closely crowded and larger at the two ends of the trunk. According to Stephen & Robertson (1952) the papillae occur all over the body, being small and scattered in the middle, but more crowded and larger at the ends. Wesenberg-Lund (1957, 1959a) states that the papillae are densely crowded at the ends of the trunk and are arranged in rings at the posterior end. In the central part the skin is distended and transparent. Webb (1972) in his description of a single specimen of *O. erythrogrammon* from Isipingo Beach, mentions that the middle third of the trunk is covered with very small, indistinct and scattered papillae, while in the posterior third the papillae are larger and more numerous. Hence the shape and distribution of the papillae in *O. erythrogrammon* differ from those of *O. caudex*.

From the literature on *O. erythrogrammon* it is evident that the integument of these two species is also different. Both Satô (1939) and Webb (1972) state that the integument of *O. erythrogrammon* is generally thin and translucent except in the region of both extremities of the trunk. In contrast to this, practically the entire integument of *O. caudex* is relatively thick and opaque.

According to Satô (1939) the colour of the trunk of *O. erythrogrammon* is bluish-green in the fresh state and hence unlike that of *O. caudex*.

In contrast to the numerous unstalked funnels present on the anal vesicles of *O. caudex*, Wesenberg-Lund (1954, 1959a) reports the presence of a few unstalked funnels in *O. erythrogrammon*. However, Webb (1972) states that the funnels have long stalks, the greater part of which lie against the vesicle. Very little is known of the structure of these funnels in *O. erythrogrammon* and more detailed investigations are required before further comparisons can be made. Detailed scanning electron microscopic studies may reveal new features of taxonomic value.

Despite the overlap in the number of longitudinal muscle bands in *O. erythrogrammon* and *O. caudex*, it is interesting to note that the maximum number of muscle bands in the former is not known to exceed 18.

Wesenberg-Lund (1959a, 1959b) also reports the presence of a rectal diverticulum in all the specimens of *O. erythrogrammon* investigated by her. Satô's contention that the rectal diverticulum is present in some specimens of *O. erythrogrammon* but apparently absent in others requires verification.

In conclusion, although *O. caudex* and *O. erythrogrammon* appear to be closely related there are certain differences, especially in the nature of the integument and in the shape and distribution of the dermal papillae, which are sufficiently distinctive to warrant separation at species level. Other differences of lesser importance, such as the range in variation of the longitudinal muscle bands and the distribution of the funnels on the anal vesicles, also tend to set the species apart. In the light of the available information, Satô (1939) and Wesenberg-Lund (1939, 1963) are unjustified in assuming that these two species are conspecific. More detailed investigations on both the species would probably shed more light on the position.

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Family Thalassematidae

Genus <u>Thalassema</u>

THALASSEMA (ECHIURA) FROM SOUTHERN AFRICA WITH THE DESCRIPTION OF A NEW SPECIES

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(Intended for publication in the South African Journal of Zoology).

ABSTRACT

Four species of *Thalassema* are currently known from southern Africa of which *T. jenniferae* is here described as new to science. *T. diaphanes* and *T. philostracum* are redescribed and figured. The discovery of *T. diaphanes* from the Natal coast marks an extension of its range of distribution. *T. thalassemum* is briefly diagnosed but material of this species was not available. The taxonomic positions of two species of *Thalassema*, examined from the UCT collection, remain to be resolved. Adequate descriptions of both these specimens were not possible as the internal organs were badly damaged. A key for the identification of all the species in the genus is provided and the distribution of the southern African forms is discussed.

CONTENTS

INTRODUCTION

The present paper gives a detailed account of the species of *Thalassema* recorded from southern Africa south of 20°S. In an earlier paper, the distribution of the genera and species of echiurans from this region was mapped and discussed (Biseswar, 1985). In view of the taxonomic problems encountered in this genus, it was deemed advisable to re-examine and redescribe some of the species with the intention of including a wider range of taxonomic characters. It was also felt that a single comprehensive report with a key to all the species would be useful to future workers in this field.

MATERIALS AND METHODS

Numerous collecting trips were undertaken, during spring low tide, to several rocky shores along the Natal and Cape coasts over a period extending from March 1981 to October 1985. Some material was also obtained from the Reference Collection of the University of Cape Town.

Information about the location and the nature of the sediment was noted and living animals were photographed. Narcotization of specimens was achieved by the addition of small quantities of magnesium sulphate to sea water over a period of three to four hours. Measurements were taken after the specimens were injected and preserved in 10% formalin. Descriptions and drawings of the external and internal anatomy were made under a dissecting microscope with a drawing tube attachment.

Key to the species of the genus *Thalassema*

It is difficult to construct a satisfactory key as some of the species are very briefly described and lack useful taxonomic data which can be used to distinguish them. The taxonomic position of *T. marshalli*, described by Prashad (1935), is uncertain as no mention is made of the nature of the gonostomal lips. *T. marshalli* might well belong to the genus *Anelassorhynchus*. A description of the anatomical terminology is given in an earlier paper (Biseswar, 1983).

Stephen & Edmonds (1972) have done little more than arrange the species on the basis of the number of gonoducts that they possess. The present key will need updating in the future as additional information becomes available from redescriptions of some of the species. Therefore, in the present key, other less rigorous characters have also been included to assist in the identification of single individuals.

Thalassema jenniferae sp. nov. can be easily distinguished from the others in the genus in possessing three pairs of gonoducts.

Key to the species of <u>Thalassema</u>:

1 Gonoducts one or two pairs 2

- Gonoducts three pairs, first pair presetal ....<u>T. jenniferae</u> sp. nov.

2 Gonoducts one pair 3

- Gonoducts two pairs 10

3 Anal vesicles lacking 4

- Anal vesicles present 5

4 Body smooth, microscopic papillae only in middle of body. Proboscis ribbon-like, longer than trunk ....<u>T. antarcticum</u> Stephen, 1941.

- Body not smooth; papillae over entire body surface. Proboscis small,about one-third trunk length ....<u>T. ovatum</u> Sluiter, 1902.

5 Gonostomal lips folded or crumpled.......<u>T. elapsum</u> Sluiter, 1912.

- Gonostomal lips not folded or crumpled...........................6

6 Interbasal muscle present.......................................7

- Interbasal muscle absent..9

7 Papillae swollen, scale-like and bent forwards; gonostomes located on stalks....................<u>T. hartmani</u> Fisher, 1947.

- Papillae not swollen and scale-like; gonostomes not stalked......8

8 Skin thin and transparent; papillae of uniform size distributed over entire body surface but more concentrated at anterior and posterior ends..................<u>T. diaphanes</u> Sluiter, 1888.

- Skin thick and opaque; body smooth except at extremities where papillae are prominent ....<u>T. owstoni</u> Ikeda, 1904.

9 Papillae overlapping, arranged in regular rows. ....T. mortenseni Fischer, 1923.

- Papillae not overlapping, irregularly distributed, more closely packed at anterior and posterior ends; anal vesicles long...... ....T. arcassonense Cuénot, 1902.

10 Proboscis with branching gill-like structures ....T. marshalli Prashad, 1935.

- Proboscis without gill-like structures 11

11 Opening of gonostome on a peduncle; no rectal caecum.......... ....T. sydniense Edmonds, 1960.

- Opening of gonostome not on a peduncle; rectal caecum present...12

12 Gonostome fan-shaped. Papillae arranged in transverse series ....T. philostracum Fisher, 1947.

- Gonostome not fan-shaped; papillae irregularly distributed......13

13 Gonostomal lips semicircular and frilled; papillae largest and most densely packed in posterior region of trunk................ ....T. thalassemum (Pallas, 1766).

- Gonostomal lips smooth, forming an incomplete circle; papillae largest just behind proboscis.......T. steinbecki Fisher, 1946.

Genus *Thalassema* Lamarck

Generic diagnosis

Longitudinal and inner oblique layers of muscle continuous and not grouped into bands or fascicles. Proboscis well-developed but anal setae absent. Gonoducts from one to three pairs; gonostomal lips not elongate and not spirally coiled. No sexual dimorphism.

Type species (From Stephen & Edmonds, 1972).

Lumbricus thalassema Pallas, 1766:8

(= *Thalassema neptuni* Gaertner of Pallas,

1774, and other authors).

Remarks

The genus *Thalassema* comprises about 14 species although some of the species may be synonymous. The descriptions of some of the species by the earlier authors are very brief and lack information on several characters which can be used to distinguish them. Stephen & Edmonds (1972) have separated the species into two groups, one possessing one pair of gonoducts and the other two pairs. An interbasal muscle and a rectal caecum are present in many species.

Two other genera, namely, *Anelassorhynchus* and *Arhynchite* are close to *Thalassema* in having longitudinal and oblique muscle layers that are continuous and not aggregated into bands or fascicles. The distinction between *Anelassorhynchus* and *Thalassema* is based on the shape of the gonostomes which in the former are elongate and spirally coiled. *Arhynchite*, on the other hand, is distinguished by the presence of a slender, ribbon-like proboscis with a small expanded or fan-like extremity. The latter genus possesses a single pair of gonoducts with gonostomes having a single lip produced into a leaf-like organ, the margins of which are irregularly sculptured.

Distribution of Thalassema

Although many species have been recorded from warmer tropical and subtropical waters of the Indian, Atlantic and Pacific Oceans, a few are either restricted to or have extended into temperate or cold waters. The recorded localities of the species in the latter category include the Falkland Islands in the south and the coasts of England, Ireland, France and the Mediterranean in the northern hemisphere. Most of the species appear to be inhabitants of shallow waters of the intertidal zone with only a few having been reported from considerable depths. In their monograph, Stephen & Edmonds (1972) give the range of distribution of each species.

Thalassema jenniferae sp. nov.

Figs. 1-6

Records

Four specimens collected from Park Rynie Beach (31°19'S/30° 44'E), Natal coast (Type locality).

Holotype

One sexually mature specimen, in the Natal Museum, Pietermaritzburg, Republic of South Africa No 3330, collected by author from the inter= tidal area close to the high water mark, 7 June 1982. The specimen occurred in fairly coarse sand, under small stones beneath a projecting ledge of rock facing the shore.

Paratype

One sexually mature specimen, in the Natal Museum, collected from the same locality. Museum number same as for holotype.

Etymology

The species is named after Dr Jennifer A. Day of the Department of Zoology, University of Cape Town in appreciation of the assistance given during the course of this research.

Description

Size

Measurements were made after narcotization with magnesium sulphate and preservation in 10% formalin. Length of proboscis of holotype 19mm, trunk 33mm long, greatest diameter of trunk about 8mm. Length of proboscis of paratype 16mm, trunk 31mm long. Hence length of proboscis ranges from one-half to two thirds trunk length.

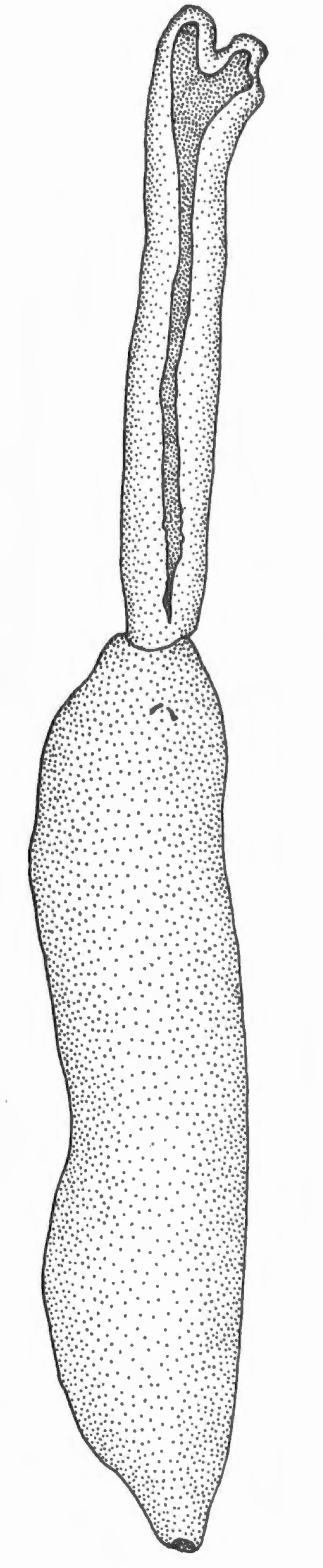

Fig. 1. Ventral aspect of Thalassema jenniferae.

Colour in life

Trunk reddish-pink, proboscis pale yellow. Colour of specimens preserved in formalin, off-white.

External features

Proboscis

Proboscis elongate, non-deciduous, slightly expanded at distal end, anterior and lateral margins smooth (Fig. 1). In preserved condition, lateral edges curl inwards forming a tube. Lateral margins of proboscis unite at base forming a narrow lower lip.

Trunk

Trunk cylindrical or sausage-shaped, tapering towards posterior end (Fig. 1). Longitudinal and inner oblique muscle layers continuous without any tendency of aggregating into bands or fascicles. Body wall extremely thin and transparent throughout, with the result that internal organs and contents of gut visible. Papillae minute, round, irregularly distributed over entire surface of trunk. Papillae slightly larger and more closely arranged at extremities of trunk. In living specimen, papillae appear as white spots.

Ventral setae small, located a few millimetres posterior to junction of proboscis and trunk.

Genital pores 3 pairs, first pair located anterior to setae while remaining two pairs postsetal in position.

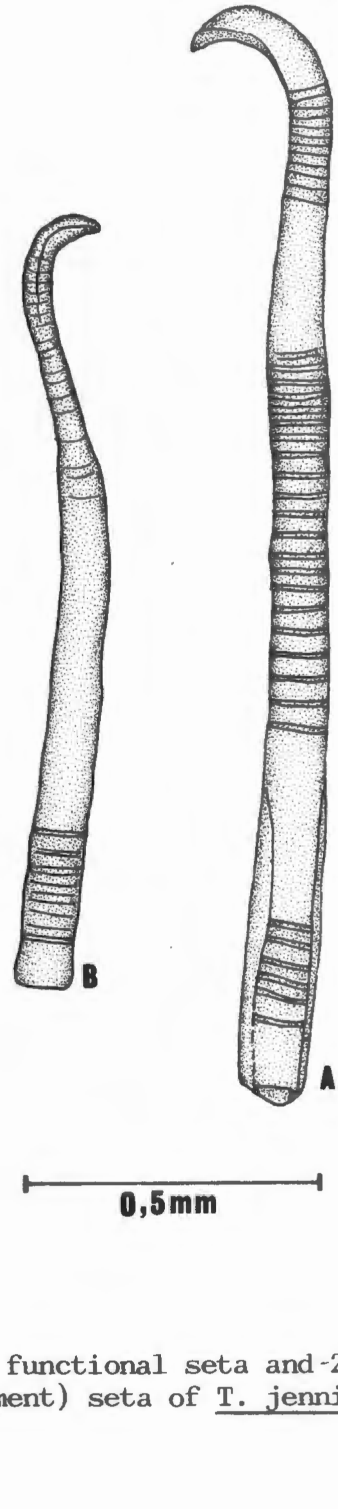

Fig. 2A. The left functional seta and 2B the left non-functional (replacement) seta of T. jenniferae.

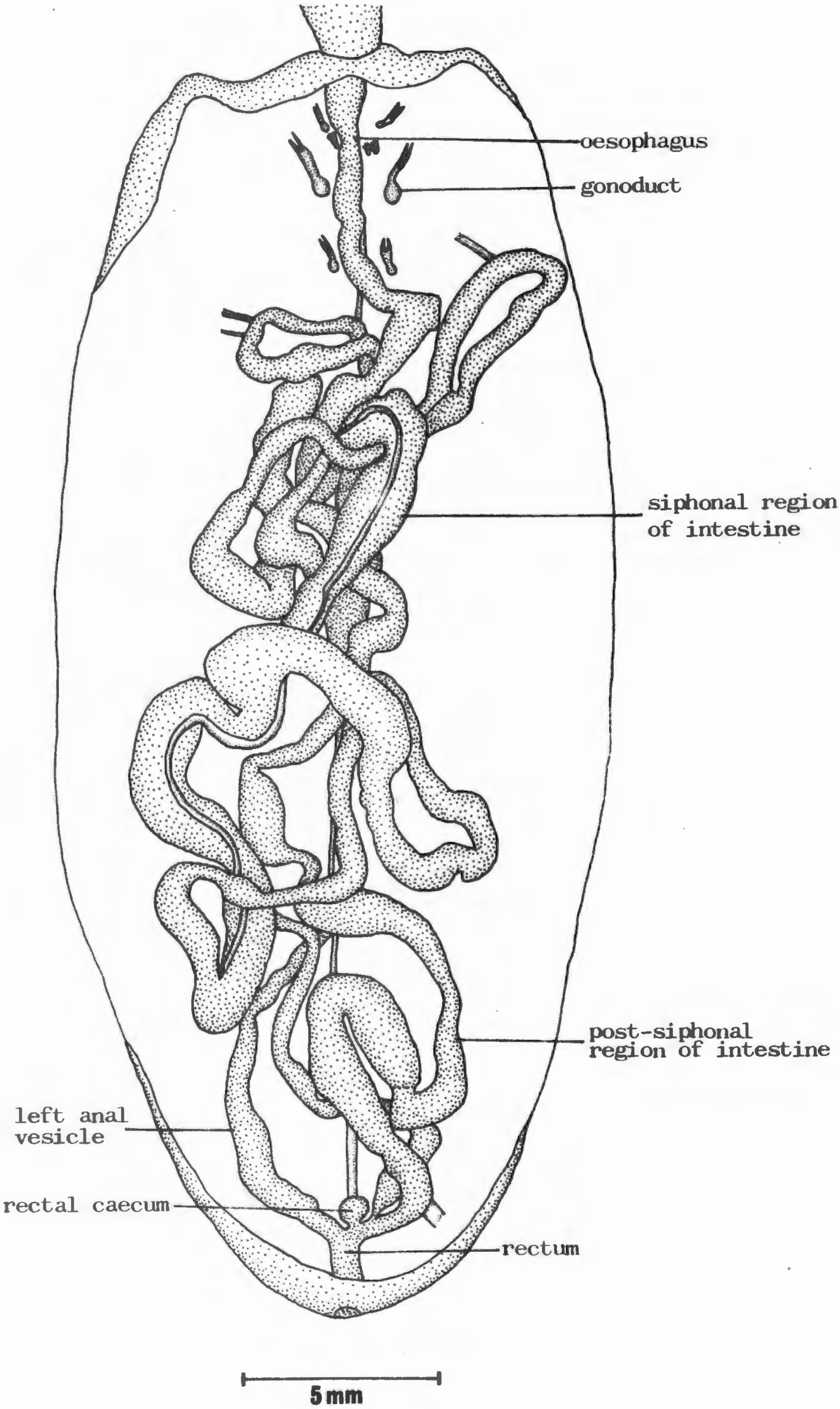

Fig. 3. Dorsal dissection of the trunk of T. jenniferae showing the alimentary system, gonoducts and anal vesicles.

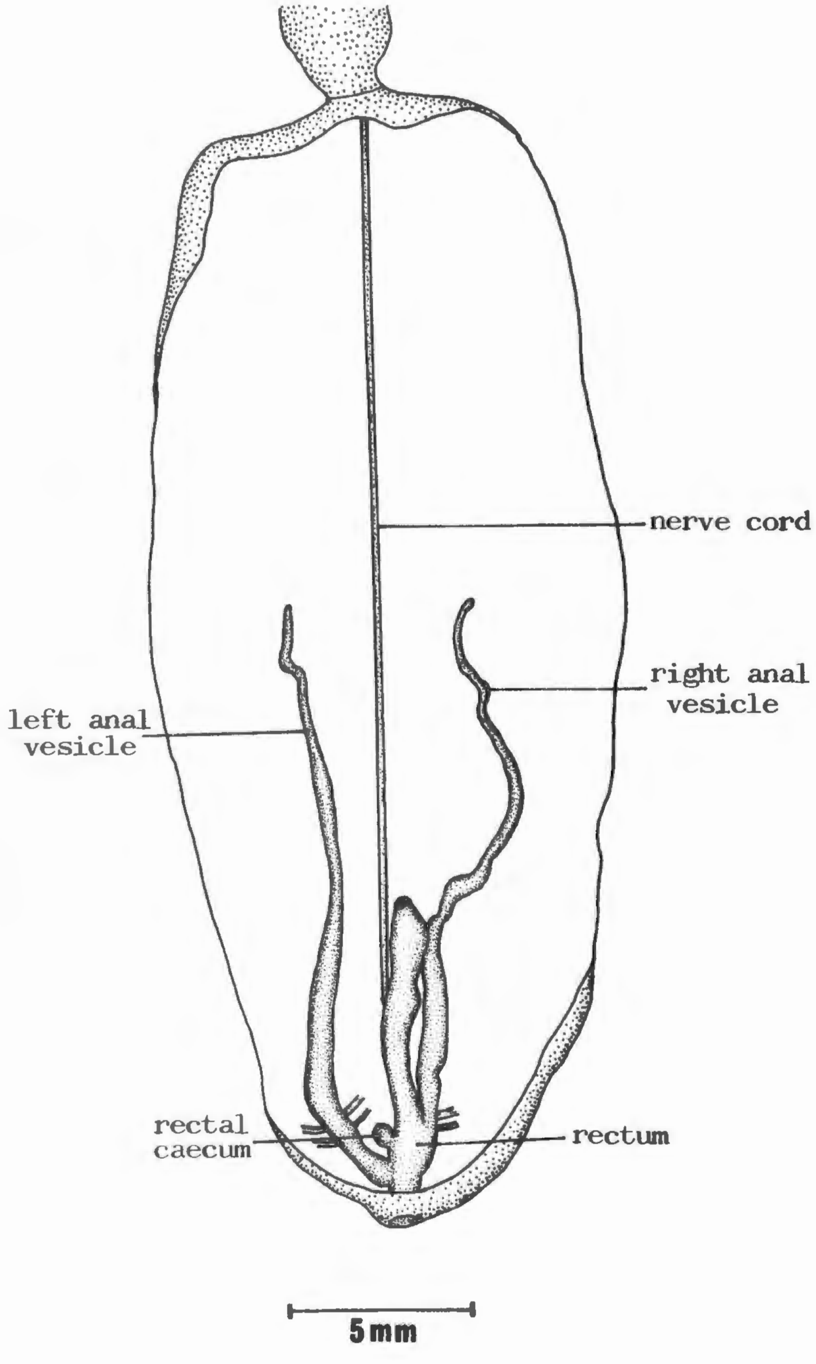

Fig. 4. Dorsal dissection of the trunk of T. jenniferae showing the anal vesicles.

Setae

Setae hook-like, golden yellow in colour. Each consisting of a cylindrical shaft with a curved terminal end (Fig. 2A). Terminal bent end slightly flattened. Fine concentric markings present mainly on cylindrical part of shaft. Replacement setae (Fig. 2B) also found in close association with functional ones. Internally, bases of setae located in cone-shaped setal sacs supported by a number of thin muscle strands. Interbasal muscle absent.

Internal anatomy

Alimentary canal

Alimentary canal extremely long and coiled, about nine times the trunk length, attached to body wall by few, thin and delicate mesenteric strands (Fig. 3). Foregut small, terminating at ring sinus. Presiphonal region of intestine with a ciliated groove. Intestine thin-walled, transparent, containing shell fragments and coarse sand particles, not moulded into pellets.

Rectal caecum small, spherical.

Anal vesicles

Anal vesicles thin-walled, about one-half length of trunk, narrow distally but becoming slightly distended towards proximal end (Fig. 4). Ciliated funnels minute, unstalked, sparsely distributed over surface of both vesicles.

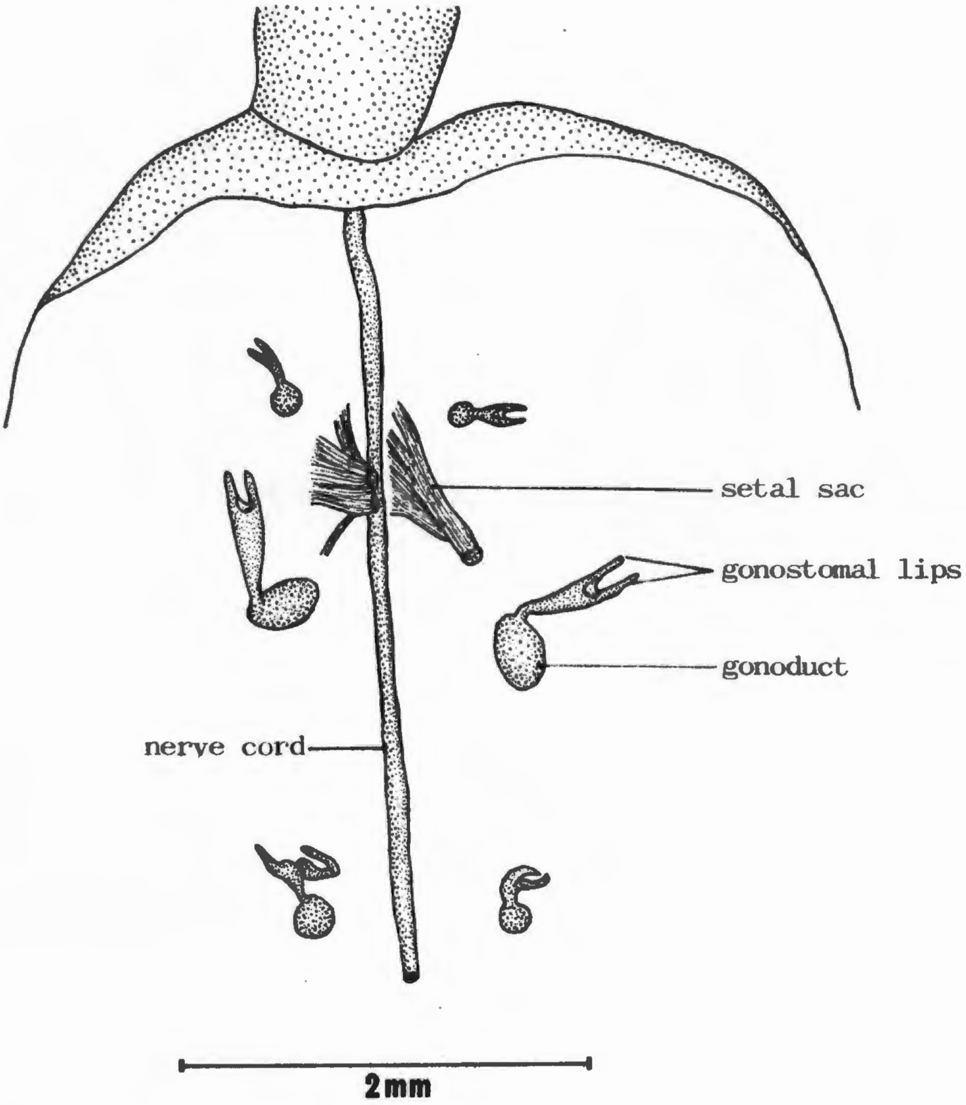

Fig. 5. Anterior end of trunk cavity of T. jenniferae illustrating the gonoducts.

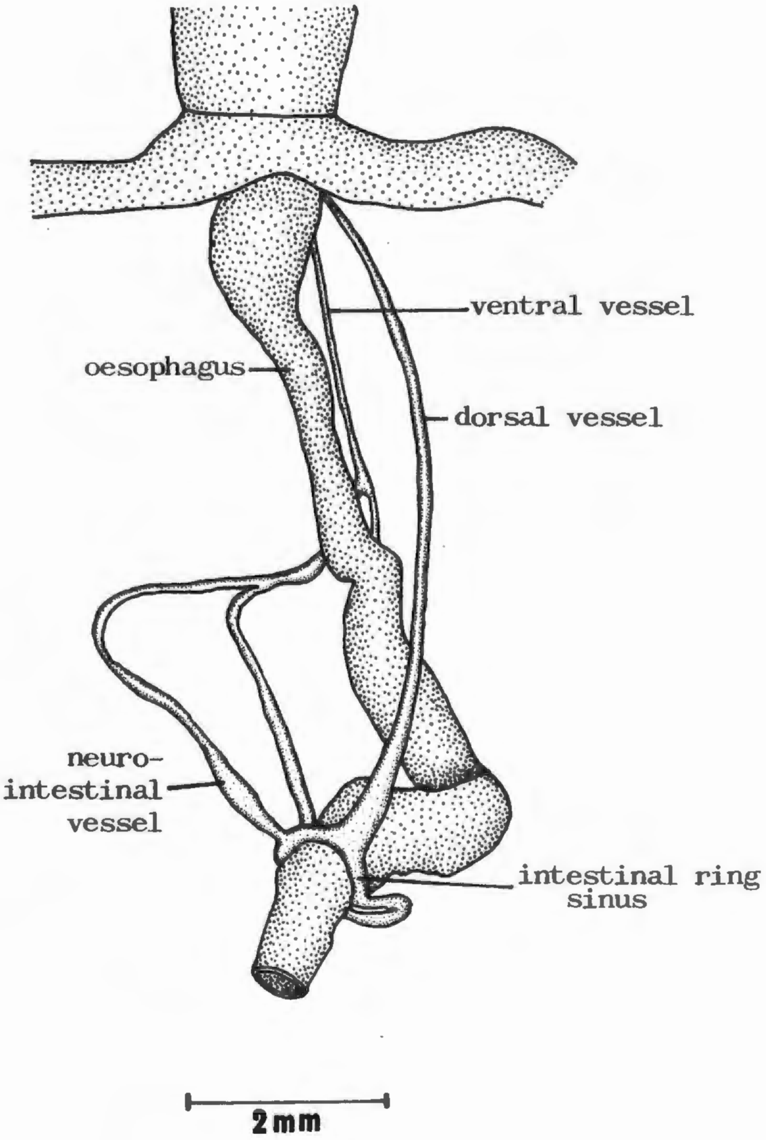

Fig. 6. Anterior end of trunk cavity of T. jenniferae illustrating the blood vessels.

Gonoducts

Gonoducts three pairs, small, spherical to somewhat oval in shape (Fig. 5). First pair located anterior to ventral setae, second pair largest of all. Gonostomes sac-like, larger than gonoducts, directed anteriorly (Fig. 5). Gonostomal lips not spirally coiled. In holotype, gonostomal lips are small while in paratype they are somewhat elongate. Gonoducts of both specimens distended, white in colour due to presence of sexual cells.

Blood system

Intestinal ring sinus in the form of an incomplete vascular ring around posterior end of foregut (Fig. 6). Neuro-intestinal vessel paired but uniting before opening into ventral vessel. Dorsal vessel short, passing forwards into proboscis.

Remarks

Some of the important characters used for the identification of species in the genus Thalassema are the number as well as the location of the gonoducts in relation to the ventral setae, the shape of the gonostomes, the structure of the proboscis and the presence or absence of the inter=basal muscle, anal vesicles and rectal caecum.

Important distinguishing features of the new species from Park Rynie Beach are the presence of three pairs of gonoducts, the sac-like gonostomes with gonostomal lips that are not spirally coiled and the extremely thin and glass-like integument. Other distinguishing characters include the presence of a narrow lower lip to the proboscis, the characteristic shape and distribution of the dermal papillae, the small, spherical to somewhat oval gonoducts and the small size of the sexually mature specimens.

The gonostomal lips in the new species are unlike the spirally coiled and thread-like structures characteristic of the genus *Anelassorhynchus*.

Stephen & Edmonds (1972), in their monograph on the phyla Sipuncula and Echiura, ascribe one or two pairs of gonoducts to the genus *Thalassema*. However, in view of the number present in the new species, their diagnosis of the genus requires emendation.

According to Datta Gupta (1976) the number of gonoducts is fairly constant within a species. Saxena (1983) also, assessed the reliability of this organ as a taxonomic character in echiurans and concluded that the number as well as their location in relation to the ventral setae are useful characters for separating species. The presence of three pairs of gonoducts in the new species thus separates it from all the other species of *Thalassema* that have been described to date.

The gonostomes of the new species are almost identical to those of *T. philostracum*, described by Wesenberg-Lund (1959a, 1963) from material collected from Tropical West Africa and the Natal coast. The latter species, however, differs markedly in possessing two pairs of postsetal gonoducts and an interbasal muscle. Other differences between the two species lie in the distribution of the papillae, in the nature of the body wall and in the structure of the proboscides.

Thalassema diaphanes Sluiter, 1888

Figs. 7-10

Thalassema diaphanes Sluiter, 1888:244-248, pl.3, figs.1-7; 1891:111; 1902:49. Shipley, 1899:336-337, pl.33, fig.2; 1902:128, pl.6, fig.2. Wharton, 1913:261. Prashad, 1935:41. Wesenberg-Lund, 1959a:199; 1959b:214-216. Stephen & Edmonds, 1972:455.

Present records

Two specimens, Natal dredgings, collected by UCT ecological survey, 9 September 1964. Exact locality not given. Determined as *Thalassema neptuni* in UCT collection (NAD 47 U/C).

Previous records

West coast of Africa; Ivory coast; Cape Town; Andaman Islands; Maldive and Laccadive Islands; Bay of Batavia, Indonesia.

Type locality

Bay of Batavia, at depth of 17-19m.

Distribution

Circumtropical, ranges from Indonesia through the Andaman, Maldive and Laccadive Islands south-westwards to the Natal coast. From the Natal coast it extends southwards into temperate waters in the vicinity of Cape Town and then reappears along the west African coast. No records are as yet available from the coast of South West Africa.

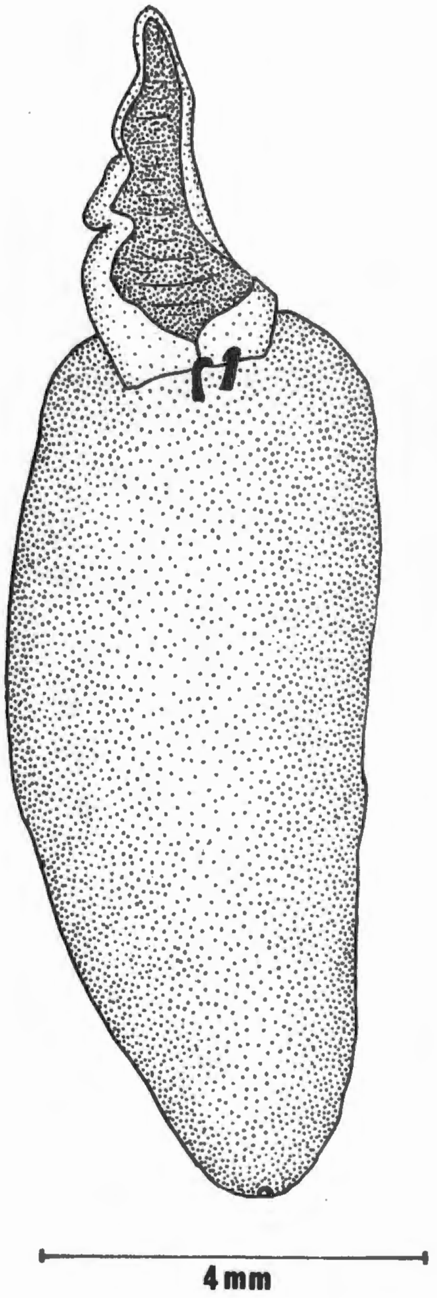

Fig. 7. Ventral aspect of T. diaphanes.

Description

The larger specimen with a trunk length of about 36mm was dissected and the proboscis was missing. Trunk length of small intact specimen 9mm; proboscis 4mm long, about half the trunk length.

Colour

Colour of specimens preserved in alcohol, uniform light brown.

External features

Proboscis

Proboscis contracted, tapering towards tip (Fig.7). Lateral edges wrinkled but without modifications, ventral surface with a series of ridges, dorsal surface smooth. Proboscis more or less flat distally but at proximal end lateral edges curl inwards to form a funnel around mouth. Lateral edges free at base of proboscis.

Trunk

Trunk cylindrical, tapering slightly towards posterior end (Fig.7). Papillae small, elongate, irregularly distributed over most of trunk, visible with unaided eye. Papillae larger at posterior end of trunk and somewhat rounded.

Body wall thin and transparent.

Ventral setae large, situated close to junction of proboscis and trunk.

Genital pores one pair, postsetal.

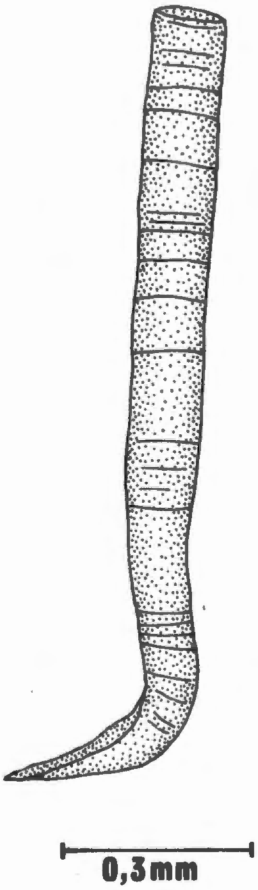

Fig. 8. Right functional seta of T. diaphanes.

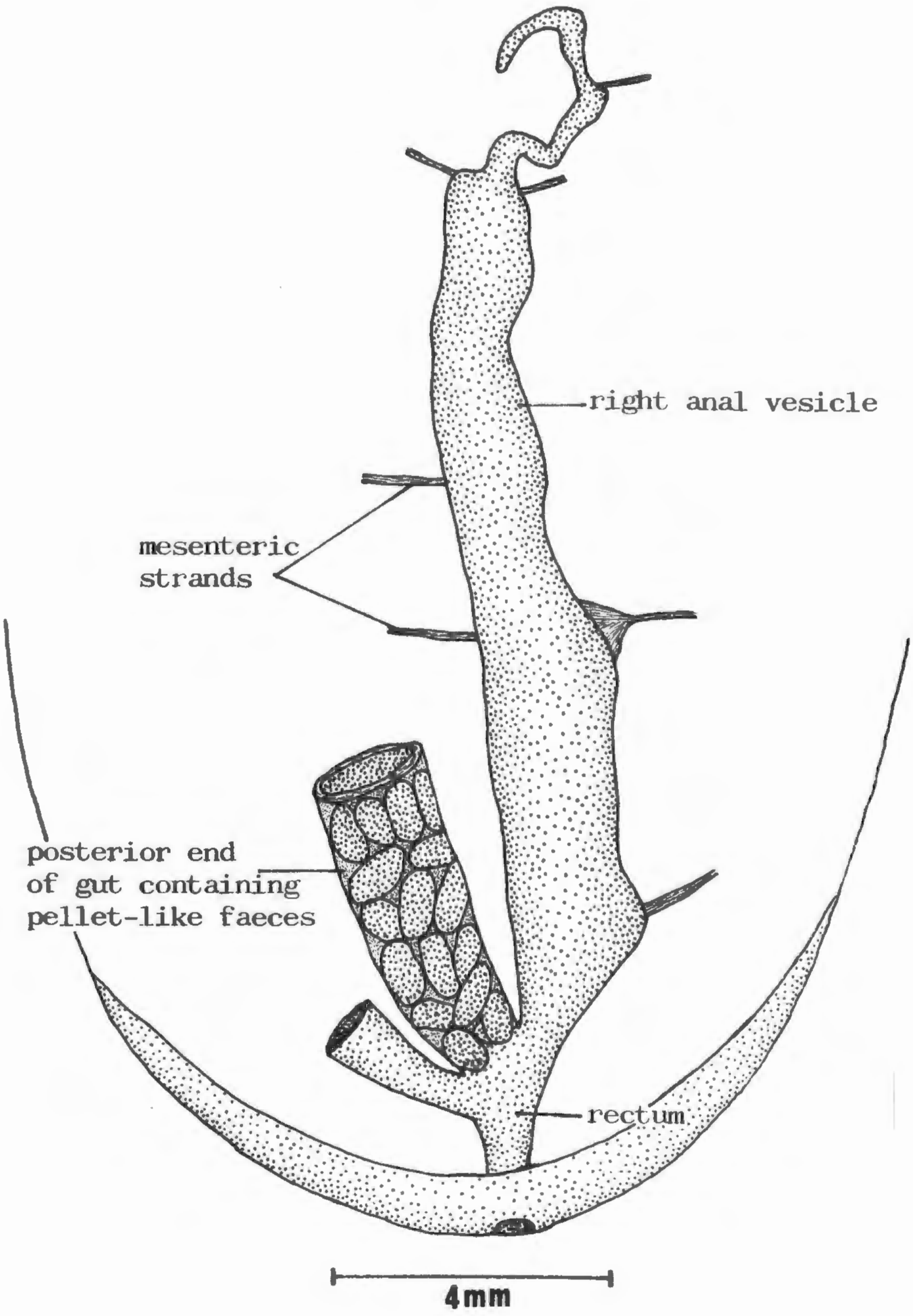

Fig. 9. Right anal vesicle of <u>T. diaphanes</u>.

Setae

Setae one pair, golden yellow in colour. Each consisting of a cylindrical shaft with curved distal end terminating in a sharp point (Fig.8). Distal curved end slightly flattened. Faint concentric markings present mainly on cylindrical part of shaft. Replacement setae also present in close association with functional ones. Internally, setae invested in connestive tissue with numerous muscle strands arising from base. Cylindrical interbasal muscle passes through loop of neuro-intestinal vessel.

Internal anatomy

Alimentary canal

Alimentary canal long, highly coiled, attached to body wall at several points by thin mesenteric strands. Oesophagus narrow, more or less of uniform diameter with thick muscular walls. Foregut small, terminates where neuro-intestinal vessel joins dorsal vessel. Presiphonal region of intestine with ciliated groove. Intestine delicate, extremely thin-walled and transparent. Entire intestine compactly filled with small, sausage-shaped faecal pellets consisting of very fine sand particles. Intestinal siphon extremely narrow and indistinct.

Rectal caecum absent.

Anal vesicles

Anal vesicles thin-walled and transparent, narrow anteriorly but considerably dilated and sac-like posteriorly (Fig.9). Ciliated funnels minute, stalked and sparsely distributed over surface of both vesicles.

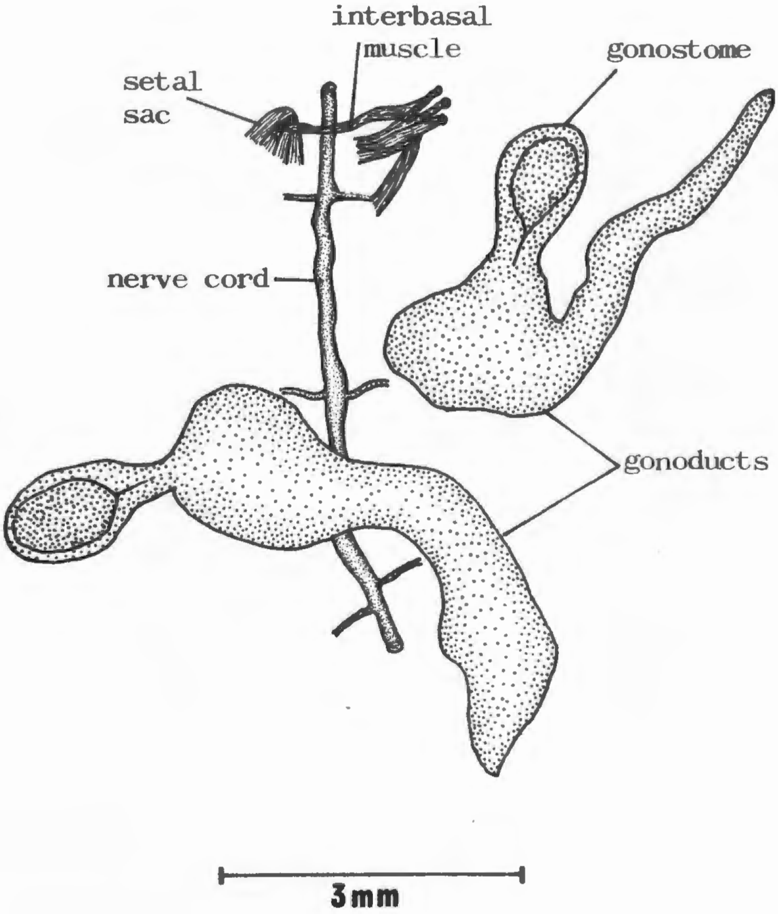

Fig. 10. Diagram illustrating the gonoducts and setal sacs of <u>T. diaphanes</u>.

Gonoducts

Gonoducts one pair, elongate, tubular and swollen at base. Gonoducts located posterior to ventral setae (Fig.10). Gonostomes oval with smooth margins. Margins unite to form a funnel-shaped structure before opening into base of gonoduct.

Blood system

Only ventral blood vessel and parts of neuro-intestinal vessels visible, the remainder damaged in both specimens. Neuro-intestinal vessel forms a small loop around interbasal muscle.

Remarks

Thalassema diaphanes, described originally from a single specimen from the Bay of Batavia, in Indonesia by Sluiter (1888), was later recorded and redescribed from several other localities in the Indo-West-Pacific and east Atlantic Oceans. In southern Africa this species was last recorded by Wesenberg-Lund (1959a) from the vicinity of Cape Town. The single specimen was obtained from a depth of 28m. Its discovery from the Natal coast now extends the range of distribution along the southern African coastline. Although this species is fairly well known, a few taxonomic problems still require elucidation.

The most important distinguishing features of T. diaphanes are: the presence of one pair of postsetal gonoducts with flat, oval gonostomes; a thin and transparent integument covered with minute papillae; a cylindrical interbasal muscle which passes through a small loop of the neuro-intestinal vessel; the distended sac-like anal vesicles and the absence of a rectal caecum.

It is rather surprising to note that with the exception of Wesenberg-Lund (1959a), none of the other authors have mentioned the presence of an interbasal muscle in this species.

According to Sluiter's description (1888), the proboscis is 30mm long and equals the length of the trunk. The integument is thin and transparent and the papillae are small white specks scattered over the body, more concentrated at the anterior and posterior ends. A rectal caecum is lacking. The anal vesicles are small and transparent, about 5mm long. The descriptions provided by Shipley (1899) and Prashad (1935) mention that the proboscis forms a tube before joining the trunk, although otherwise they do not add much to Sluiter's original description of the species.

The single specimen described by Wesenberg-Lund (1959a) from the Cape Town area was badly preserved and the proboscis was missing. According to the latter author, the papillae are densely crowded at both ends of the trunk, especially posteriorly, where they are annularly arranged.

Wesenberg-Lund (1959b) examined three further specimens of T. diaphanes from Tropical West Africa. The trunk length of the largest specimen was 34mm but the proboscides were missing in all three specimens. According to the latter author, the integument is thin, tough but not transparent. The gonostomes are large, stalked with ovoid apertures and the anal vesicles are slightly more than half the length of the trunk with extremely thin walls. With the exception of Wesenberg-Lund (1959b), none of the other authors give any details regarding the shape of the gonostomes.

The present specimens from Natal conform closely with Sluiter's description except that the lateral margins of the proboscis do not unite posteriorly to form a tube before joining the trunk. The present investi= gation sheds more light on the shape and structure of the gonostomes and confirms the presence of an interbasal muscle in this species.

The species most nearly related to T. diaphanes seems to be T. owstoni, described from the Uraga Channel, Japan, by Ikeda (1904). Ikeda had doubts in erecting this species because of its close resemblance to T. diaphanes. However, he distinguished the Japanese specimen from T. diaphanes because of the thicker body wall and on differences in the distribution of the dermal papillae. From his illustration of the segmental organs it is also apparent that the gonostomes differ in the two species. The gonostomes of T. owstoni are ciliated, funnel-shaped structures located on small stalks. In view of the above differences, it is probably best to consider the two species distinct, at least until more material becomes available.

Thalassema philostracum Fisher, 1947

Figs. 11-13

Thalassema philostracum Fisher, 1947: 351-353, pl.8. Wesenberg-Lund, 1959a:199-201, Fig.12; 1963:139. Stephen & Edmonds, 1972:458.

Present records

One specimen, Kosi Bay estuary, collected by UCT ecological survey. Specimen dissected and identified by Wesenberg-Lund (1963).

Previous records

Gulf of Florida, and Beaufort, North Carolina; Tropical West Africa.

Type Locality

Lemon Flats, Florida. Holotype. U.S.N.M. No. 20802.

Distribution

T. philostracum seems to have a predominantly north Atlantic distribution having been recorded from the coasts of Florida, the Caribbean and Tropical West Africa north of the equator. However, like many Atlantic polychaetes, this species also occurs on the east coast of southern Africa as far north as Kosi Bay on the Natal coast.

Description

Size

Trunk 12mm in length; proboscis 6mm, one-half as long as trunk.

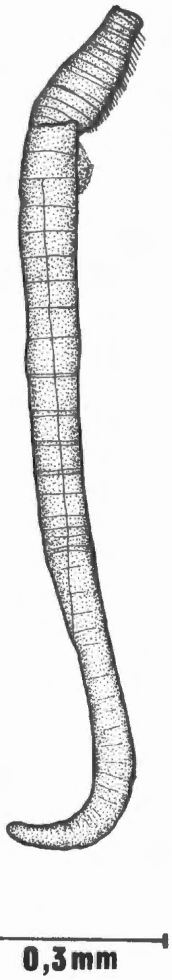

Fig. 11. Right functional seta of T. philostracum.

Colour

Colour of specimen preserved in alcohol, beige.

External features

Proboscis

Proboscis fleshy, contracted, lateral edges curled inwards with a series of tight ridges. Distal end damaged, ventral groove with transverse wrinkles due to contraction, dorsal surface with microscopic papillae arranged in transverse rows. Lateral margins of proboscis free at base.

Trunk

Body wall moderately transparent. Trunk uniformly covered with elliptical papillae, arranged in transverse rows, slightly larger at posterior end.

Ventral setae situated close to junction of proboscis and trunk.

Genital pores 2 pairs, postsetal.

Setae

Setae golden-yellow in colour, hook-like, about 1,5mm long (Fig.11). Proximal end of cylindrical shaft slightly bent, curved distal end terminating in a pointed tip. Fine concentric ridges on surface of both setae, more closely arranged on proximal bent part of shaft. Setae located in cone-shaped setal sacs supported by numerous muscle strands. Interbasal muscle not observed, probably dissected out or damaged.

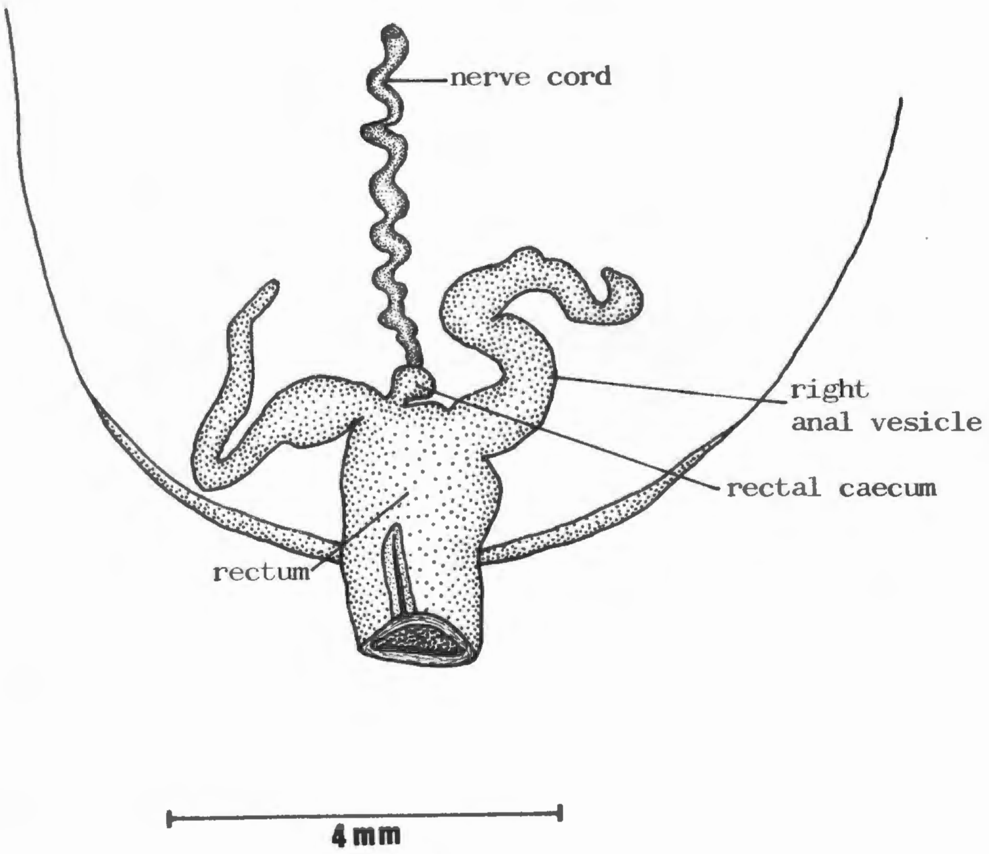

Fig. 12. Posterior end of trunk cavity of T. philostracum showing the anal vesicles.

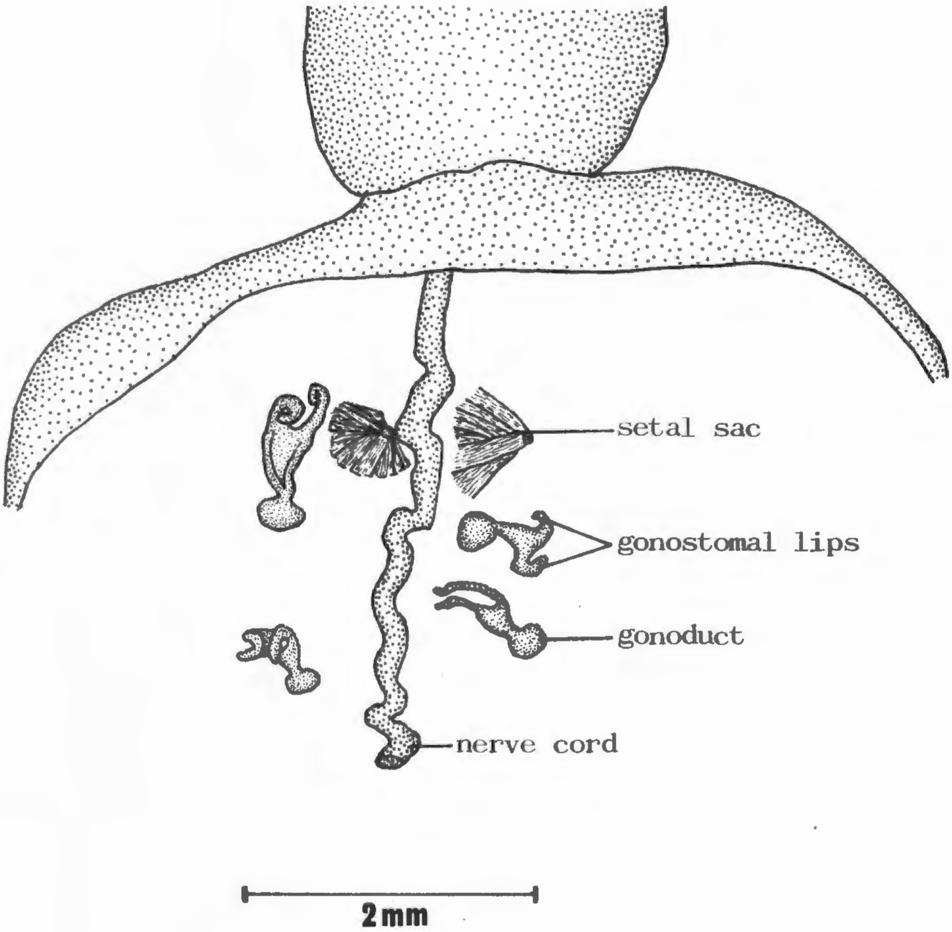

Fig. 13. Anterior part of the trunk cavity of T. philostracum showing the gonoducts.

Internal anatomy

Alimentary canal long and coiled, ruptured in several places, attached to body wall by numerous, closely arranged mesenteric strands especially in presiphonal and siphonal regions of intestine. Foregut short, terminating at ring sinus. Presiphonal region with a ciliated groove. Walls of intestine in region of siphon extremely thin and delicate. Posterior part of intestine compactly filled with shell fragments and coarse sand grains.

Rectal caecum small, spherical, opening into rectum ventrally (Fig.12).

Anal vesicles

Paired anal vesicles thin-walled tubes, about one-third trunk length (Fig.12). Microscopic, unstalked, ciliated funnels sparsely distributed over surface of both vesicles.

Gonoducts

Gonoducts 2 pairs, small, spherical, located posterior to ventral setae (Fig.13). Anterior pair slightly larger than posterior pair. Gonostomes sac-like, much larger than gonoducts, with short gonostomal lips. Gonostomal lips directed forward and not spirally coiled.

Blood system

Only dorsal blood vessel, ring sinus and parts of neuro-intestinal vessels visible, the remainder damaged. Dorsal vessel short and prominent. Ring sinus located at posterior end of short foregut. Neuro-intestinal vessels paired.

Remarks

Thalassema philostracum, described by Fisher (1947), is known originally from numerous specimens. The descriptions provided by Fisher (1947) and Wesenberg-Lund (1959a, 1963) mention the presence of an interbasal muscle in this species but, unfortunately, the relationship of this muscle to the neuro-intestinal vessel is not known.

Important distinguishing features of this species include : two pairs of sac-like, postsetal gonoducts with short, anteriorly directed gonostomal lips, the characteristic distribution of the papillae and the presence of an interbasal muscle. Other features of lesser taxonomic value are the comparatively short anal vesicles and the presence of microscopic papillae arranged in transverse rows on the dorsal surface of the proboscis. The proximal bent end of the cylindrical shaft of the setae may also be a useful feature in distinguishing T. philostracum from the other related species in the genus. Another interesting feature is the presence of numerous, closely arranged mesenteric strands attaching the gut to the body wall.

The specimen from Kosi Bay conforms in many respects with Fisher's description but an important difference lies in the shape of the gonostomes, which according to Fisher are fan-shaped.

Several species of Thalassema are known with two pairs of gonoducts and the species that seems to be most nearly related to T. philostracum is T. steinbecki, also described by Fisher (1946). The latter species is known from a number of localities from Baja California to Ecuador. According to Fisher's description of T. steinbecki the proboscis, which is as long as the trunk, is broad proximally but ribbon-like distally. The papillae are scattered over the trunk and are largest just behind the proboscis and on the posterior third of the trunk. There is a well-developed interbasal muscle which passes through a loop of the neuro-intestinal vessel. The anal vesicles are almost as long as the trunk with numerous ciliated funnels. Fisher's description also mentions that the gonostomes are simple ciliated funnels with smooth lips forming an incomplete circle.

Hence *T. philostracum* differs significantly from *T. steinbecki* in the shape of the gonostomes, in the size and distribution of the papillae on the trunk and in the structure of the proboscides. Differences are also present in the relative proportions of the proboscis and trunk lengths and in the lengths of the anal vesicles. Furthermore, the setae of *T. steinbecki* consists of a straight shaft with the curved terminal end set at right angles to the shaft.

From the descriptions of *T. philostracum* by the above authors, it is evident that some aspects of its internal anatomy require further investigation. Unfortunately the material examined by Wesenberg-Lund (1959a, 1963) was not in a satisfactory condition as the alimentary and blood vascular systems were damaged. Detailed redescriptions based on additional material in the future will probably shed more light on some other taxonomic characters.

Thalassema sp. A.

Figs. 14-17

Present records

One juvenile specimen, Natal dredgings, collected by UCT ecological survey on 9 September 1964. Exact locality and depth not known.

Material examined

The specimen was already dissected and with the exception of the foregut and rectum the rest of the alimentary canal had been removed. However, the gonoducts, setae, anal vesicles, ventral nerve cord and parts of the blood system were still intact. The external features were in a satis=factory condition.

Identified as T. indivisum in the UCT collection (NAD 70u/c).

Description

Size

Length of trunk 13mm; proboscis 8mm long, more than half the trunk length.

Colour

Colour of specimen preserved in 70% alcohol, beige.

Proboscis

Proboscis thin and delicate, somewhat contracted and possibly capable of considerable extension in the living animal. Distal end of proboscis bilobed, towards proximal end, lateral edges rolled inwards to form a cylinder (Fig.14). Lateral edges of proboscis smooth and free at base.

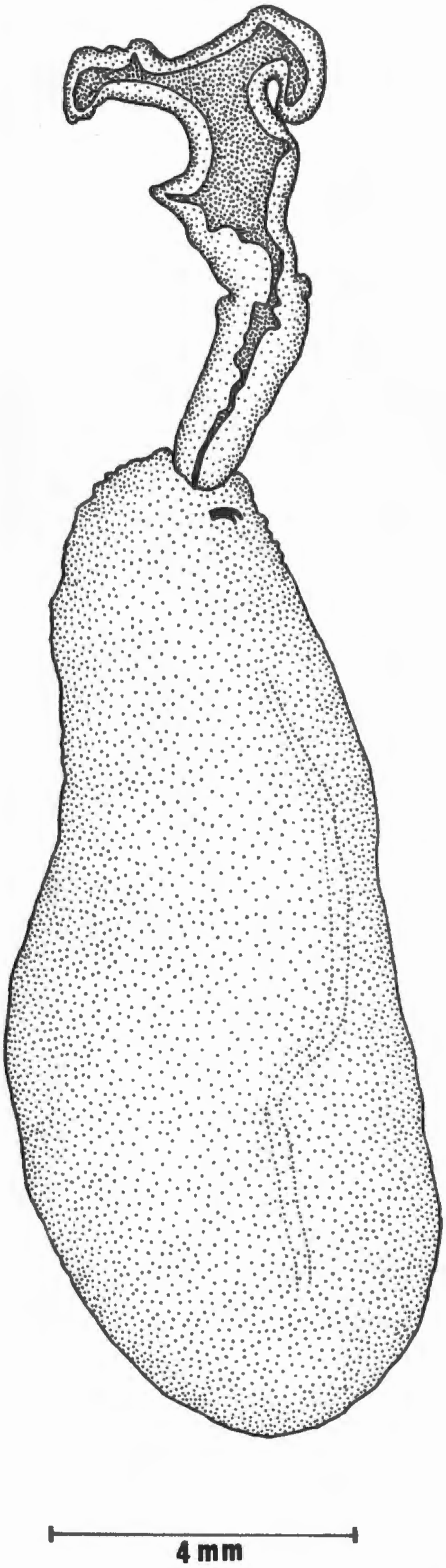

Fig. 14. Ventral aspect of Thalassema sp. A.

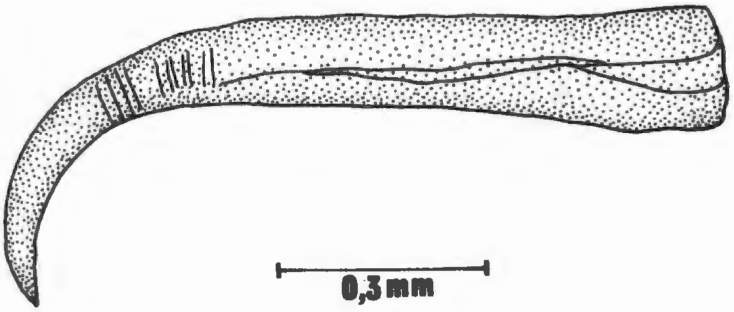

Fig. 15. Right functional seta of Thalassema sp. A.

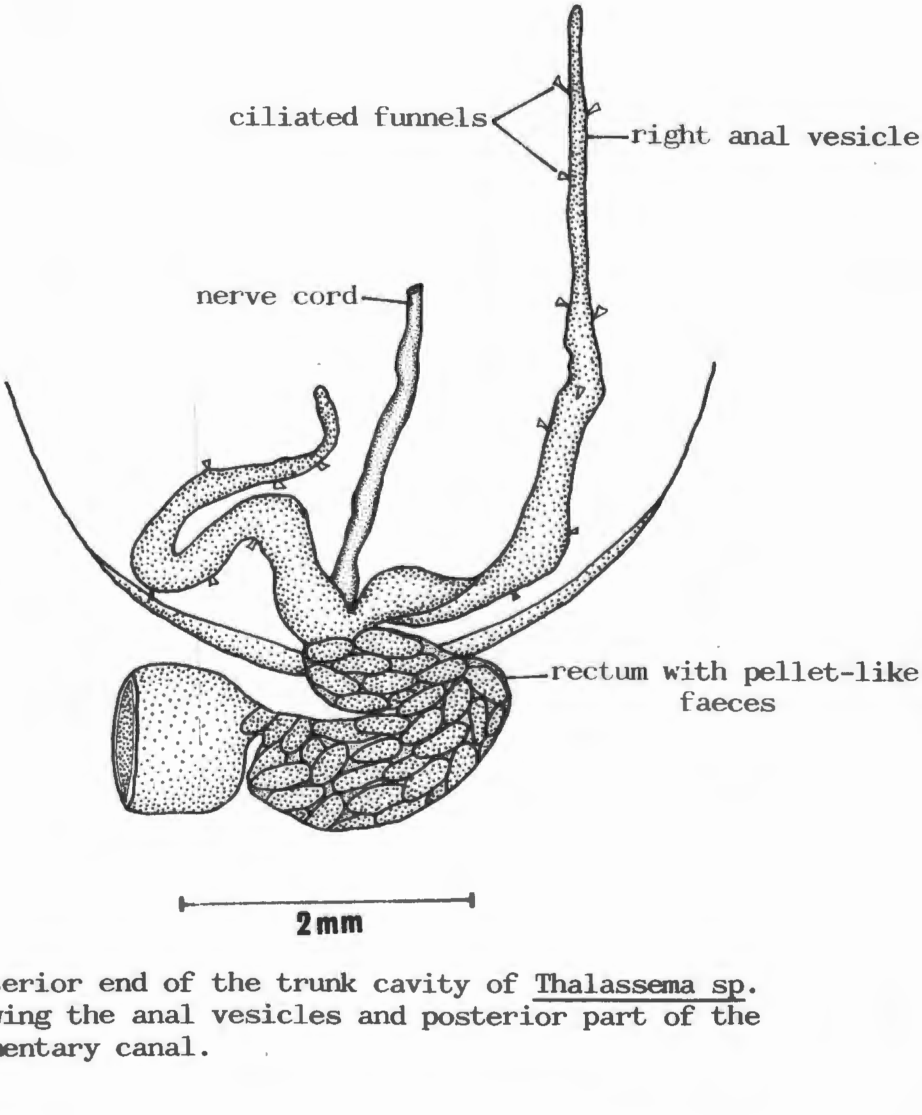

Fig. 16. Posterior end of the trunk cavity of Thalassema sp. showing the anal vesicles and posterior part of the alimentary canal.

Trunk

Trunk sac-like, distended posteriorly (Fig.14). Skin thin and transparent, covered with minute, elongate papillae projecting from surface. Papillae round to somewhat oval in shape and more closely arranged at anterior and posterior ends of trunk.

Ventral setae one pair, minute, situated a few millimetres posterior to mouth.

Genital pores one pair, postsetal.

Setae

Setae hook-like, short and robust (Fig.15), golden-yellow in colour. Diameter of cylindrical shaft broader towards proximal end, distal curved end not flattened. Setae located in large, cone-shaped setal sacs with well developed muscle strands radiating from base. Interbasal muscle absent.

Internal anatomy

Alimentary canal

Foregut short, terminating at ring sinus. Contents of gut in the form of sausage-shaped faecal pellets. Rectal caecum not observed.

Anal vesicles

Anal vesicles small, less than one-quarter the trunk length, narrow anteriorly but distended and sac-like posteriorly (Fig.16). Ciliated funnels minute, stalked, sparsely distributed over surface of both vesicles.

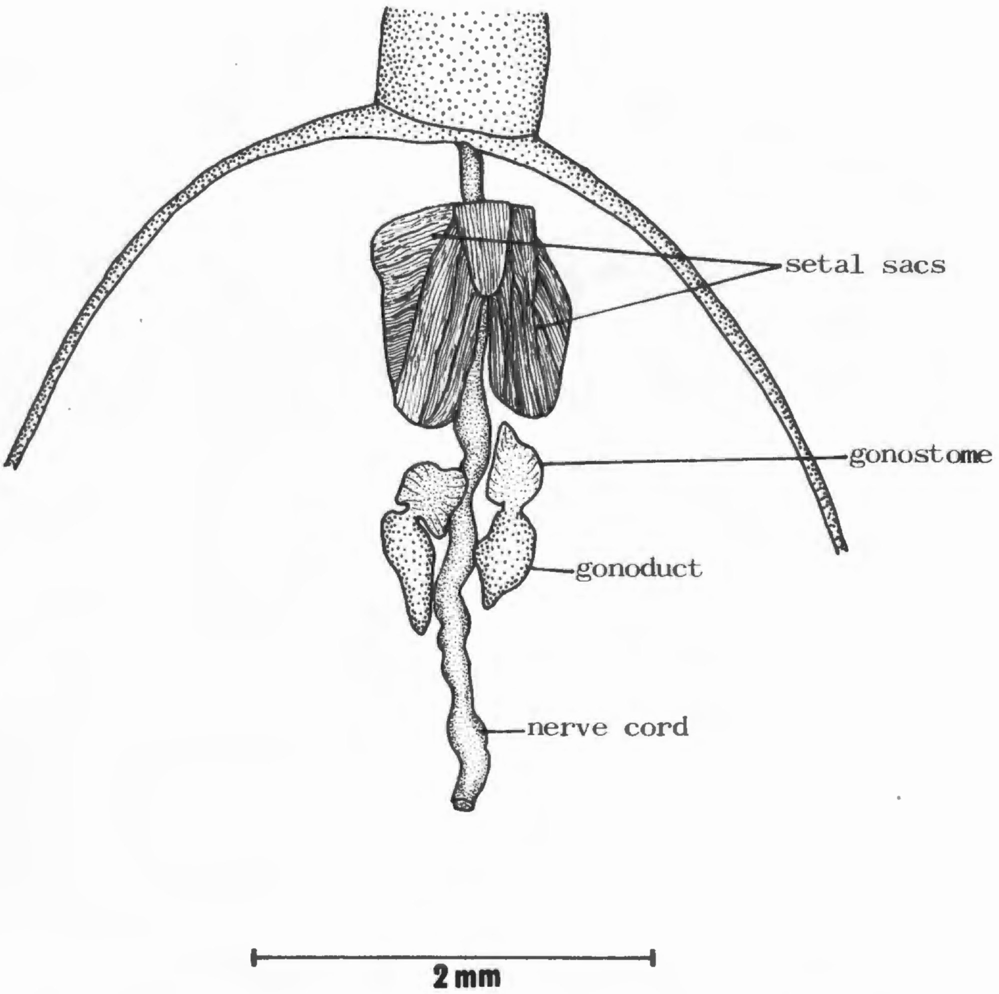

Fig. 17. Anterior part of trunk of Thalassema sp. showing the gonoducts and setal sacs.

Gonoducts

Gonoducts one pair, small, oval to somewhat elongate, posterior to cone-shape setal sacs (Fig. 17). Gonoducts located close to each other on either side of ventral nerve cord. Gonostomes broad, leaf-shaped, almost equal in size to gonoducts, margins smooth. Openings of gonostomes basal in position.

Remarks

Due to the poor state of the internal organs, it is not possible to give a detailed account of the digestive and blood vascular systems. The specimen definitely belongs to the genus Thalassema as the longitudinal and oblique muscle layers are continuous and the gonostomes are not elongate and spirally coiled.

Important distinguishing features of the specimen include the bilobed proboscis, a single pair of postsetal gonoducts with expanded, leaf-like gonostomes, a thin and transparent integument and the characteristic shape and distribution of the dermal papillae.

It has been found that the interbasal muscle is an important taxonomic character in echiurans. Of the species of Thalassema having one pair of gonoducts, the descriptions of T. antarcticum, T. elapsum and T. ovatum contain no information on the interbasal muscle. The latter muscle, however, is absent in T. arcassonense, T. fuscum and T. mortenseni.

T. antarcticum, described by Stephen (1941), is based on two specimens from the Falkland Islands. The proboscis of the holotype is 52mm long and the trunk is short, measuring only 27mm in length. In their monograph, Stephen and Edmonds (1972) have incorrectly given the length of the proboscis as 5,2mm. The tip of the ribbon-like proboscis is not bifurcate but the edges are indented. According to Stephen's description, the setae are rectangular in shape and are only slightly bent at the tip. The trunk of T. antarcticum is cylindrical and smooth in appearance and hence significantly different from the specimen on hand and the other species in the genus. Other important differences between the two species lie in the structure of the proboscides and ventral setae as well as in the relative proportions of the proboscis and trunk lengths.

The description of T. elapsum by Sluiter (1912) is based on 10 specimens, in all of which the proboscis was missing. According to the latter author, the gonostomes are merely folded or crumpled. The trunk is up to 35mm in length and covered with papillae which are arranged in circles. Sluiter's description is brief and lacks critical information which can be used to distinguish this species from the others in the genus. The circular arrangement of the papillae on the trunk of T. elapsum, however, distinguishes it from the specimen from Natal. Another distinguishing feature lies in the structure of the gonostomes. It also seems very likely that T. elapsum has a deciduous proboscis since this organ was missing in all ten specimens.

T. ovatum is described by Sluiter (1902) from numerous specimens from Indonesia. The proboscis is 3mm long, but considerably longer in life and the trunk measures 10mm in length. Microscopic papillae are regularly distributed over the surface of the trunk. The terminal ends of the ventral setae are sickle-shaped. The gonostomes are large flaps and not spirally coiled. According to Sluiter (1902), anal vesicles were not found in any of the specimens. The specimen on hand differs significantly from T. ovatum in a number of characters. Differences are apparent in the ventral setae and in the arrangement of the dermal papillae. T. ovatum also differs in lacking anal vesicles. Furthermore, according to the figure provided by Sluiter, the proboscis is not bilobed terminally.

T. arcassonense, described from France by Cuénot (1902), is known only from the holotype. The proboscis of this species is 20mm long and almost square at the tip. The trunk, which is 110mm in length, is covered with papillae more closely arranged at the extremities. A rectal caecum is present. The specimen on hand differs from T. arcassonense in the structure of the proboscis and in the relative proportions of the proboscis and trunk lengths.

The description of T. fuscum by Ikeda (1904) is based on a single specimen from Japan. The proboscis is 20mm long and truncated at the apex while the cylindrical trunk is 75mm in length. Large papillae are irregularly distributed over the entire body surface and more closely arranged at both ends. According to the description provided by Ikeda, the anal vesicles are almost as long as the trunk with sparsely distributed ciliated funnels arranged on short stalks. The gonostomes are large and funnel-shaped. Ikeda's description does not contain any information on the interbasal muscle but from his figure it is clearly evident that this muscle is absent. In their monograph, Stephen and Edmonds (1972) are in error in ascribing a well-developed interbasal muscle to this species. Thus important differences between the two species lie mainly in the shape of the proboscis, the relative proportions of the proboscis and trunk lengths and in the size of the trunk papillae. Another difference, though of lesser importance, lies in the size of the anal vesicles. These differences indicate that T. fuscum is a species distinct from the specimen on hand.

The description of T. mortenseni by Fischer (1923) is based on two specimens from Hong Kong,in both of which the proboscis was missing. This species is characterised in having exceedingly large overlapping papillae arranged in regular rows. The gonoducts are fairly elongate and the anal vesicles are short and bear ciliated funnels. The size and the characteristic distribution of the papillae distinguish T. mortenseni from the present specimen as well as the other species in the genus. It also seems probable that T. mortenseni possesses a deciduous proboscis. Fisher's description, however, is rather brief and contains little or no information on several important taxonomic characters.

There seems little doubt, therefore, that the specimen from Natal differs in several respects from the other species of Thalassema possessing a single pair of gonoducts. The bilobed proboscis seems to be a distinctive feature. A more detailed study of additional material in the future will shed more light on its taxonomic position and may well indicate that the specimen is new to science.

Thalassema sp. B.

Figs. 18-19

Present records

One specimen, UCT records: Cape Peninsula (Ref. No. CP 207), collected 1 November 1932. Exact locality, depth and nature of sediment unknown. Trunk damaged in middle region; anterior end of trunk cavity already opened by a mid-dorsal incision.

Size

Length of trunk 23mm; proboscis 12mm long, about one-half trunk length.

Colour

Colour of living specimen unknown. In alcohol, colour beige, posterior end of trunk light brown.

External features

Proboscis

Proboscis flat, ribbon-like and of uniform width throughout (Fig.18). Lateral margins straight, smooth and free at base. Dorsal and ventral surfaces with a series of transverse creases probably due to contraction. Proboscis possibly capable of considerable extension in the living animal.

Trunk

Trunk cylindrical, narrow anteriorly but somewhat distended in the posterior third (Fig.18). Body wall moderately transparent in middle region of trunk but thick and opaque at extremities. Anterior and posterior ends of trunk covered with small elliptical papillae arranged roughly in transverse rows at posterior end. A ring of larger papillae around anus. Body smooth in middle region. Longitudinal and oblique muscle layers continuous.

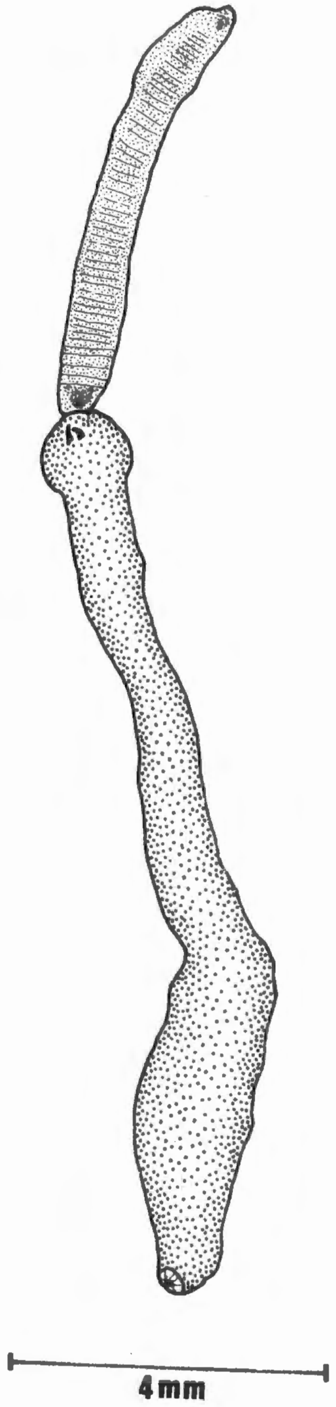

Fig. 18. Ventral aspect of Thalassema sp.B.

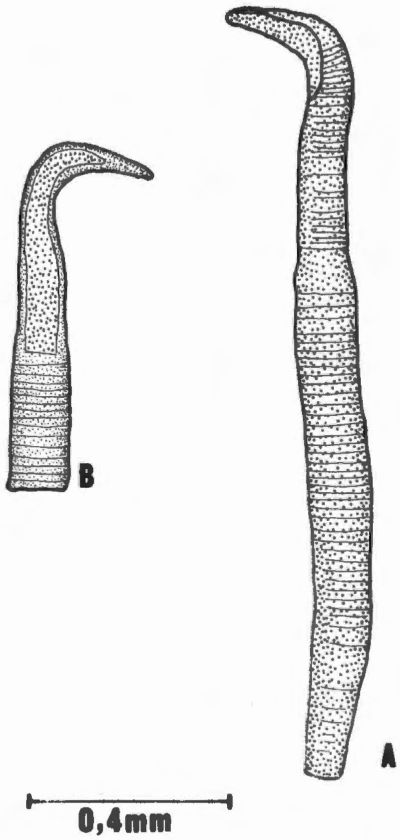

Fig. 19A. The right functional seta. B. The right non-functional (replacement) seta.

Setae

Setae one pair, located on ventral surface of trunk just posterior to mouth. Distal bent end flattened (Fig.19A) and golden-yellow in colour. Cylindrical part of shaft reddish-brown with concentric markings. Proximal end of setae invested in connective tissue and located in large cone-shaped setal sacs. Setal sacs situated close to each other, supported by numerous radiating muscle strands inserting on body wall. A small non-functional or replacement seta also present in close association with right functional one (Fig.19B). Tip of replacement seta golden-yellow, cylindrical shaft dark brown. Interbasal muscle absent.

Internal anatomy

Except for the setal sacs, ventral nerve cord and remains of blood vessels and gonoducts, the rest of the internal organs are macerated and in a very poor condition. A small vessel passing ventrally in between the setal sacs probably represents the remains of the neuro-intestinal vessel. Coarse sand grains and shell fragments occur loosely in the body cavity.

A single, tubular gonoduct on the right, just posterior to the ventral seta,is in a fairly satisfactory condition. A small, inconspicuous, crumpled gonostome opens into the base of the gonoduct. The gonoduct is white in colour and distended,probably due to the presence of gametes. Remains of some whitish tissues attached to the body wall to the left of the nerve cord and in a position corresponding to the right gonoduct probably indicates the position of the left one.

Remarks

Important distinguishing features of the specimen include the flat, ribbon-like proboscis, a single pair of post-setal gonoducts with small crumpled gonostomes, the elongate pencil-shaped trunk and the arrangement of small, elliptical papillae more or less in transverse rows on the posterior part of the trunk.

Because of the poor state of the internal organs it is not possible to make detailed comparisons with the other species. The flat proboscis seems to be an important feature of the specimen. Unfortunately several species of *Thalassema* have been described in which the proboscides were missing. Of the species of *Thalassema* possessing one pair of gonoducts, *T. antarcticum* and *T. elapsum* appear to be related to the present specimen. According to Stephen (1941), the proboscis of *T. antarcticum* is ribbon-like and much longer than the trunk when fully extended. *T. antarcticum*, however, differs significantly in lacking papillae on the body. Furthermore, from Stephen's figure it is evident that the lateral margins of the proboscis are curled inwards forming a ventral groove.

T. elapsum is described originally from 10 specimens, in all of which the proboscis was missing. According to the description provided by Sluiter (1912) the trunk is covered with papillae which are arranged in circles and more closely arranged anteriorly and posteriorly. The shape of the gonostomal lips of *T. elapsum* conforms closely with those of the present specimen. Unfortunately, further comparisons are virtually impossible.

The proboscis of the specimen from Cape Peninsula seems to be rather characteristic in the genus, so that it should not prove difficult to identify further specimens as belonging to the same species.

Thalassema thalassemum (Pallas, 1766)

Lumbricus thalassema Pallas, 1766: 8-9, pl.1, fig.6.

Thalassema neptuni Gaertner of Pallas, 1774: 1-15. Greeff, 1879:145. Reitsch, 1886:313. Lankester, 1881:350. Jameson, 1899:535, 2 pls. and 1 text-fig. Shipley, 1899:351, pl. 33, figs.5 and 6. Stewart, 1900:218. Southern, 1913:39. Fischer, 1914:20; 1922:14. Leigh-Sharpe, 1928:499-504, pls. 14-15. Cuénot, 1922:22-23, figs.12(a-b). Wesenberg-Lund, 1959a:199. Stephen & Cutler, 1969:114.

Thalassema thalassemum: Fisher, 1946:230. Stephen & Edmonds, 1972:459-460.

Diagnosis

Proboscis about three times trunk length when fully extended. Trunk brightly coloured, up to 70mm in length, covered with papillae which are largest and most densely aggregated at posterior end. Integument trans=parent. Ventral setae one pair, connected by interbasal muscle. Gonoducts two pairs, postsetal in position. Gonostomes semicircular and frilled. Anal vesicles tubular, about two-thirds trunk length with unstalked ciliated funnels. Dorsal and neuro-intestinal vessels connected through well developed ring sinus at end of foregut. Interbasal muscle passing through loop of neuro-intestinal vessel. Foregut with a ciliated groove. Rectal caecum present.

Distribution: This species has a wide distribution, having been recorded from West Africa, British Isles, coasts of Ireland, France and the Mediterranean. It has been recorded previously from southern Africa at Port Elizabeth and Durban.

Remarks

Unfortunately it was not possible to obtain any specimens of T. thalassemum. This species, however, is well known, having been described from numerous localities. Shipley (1899) incorrectly states that the gonostomal lips are elongate and spirally coiled. The specimens described by Stephen and Cutler (1969) were obtained at depths of up to 138m. Stewart (1900) mentions some variations in the number of gonoducts of T. thalassemum.

This species seems to be very closely allied to T. steinbecki, described from the North Pacific Ocean by Fisher (1946). T. steinbecki, however, differs in having gonostomes with smooth margins. Furthermore, the papillae of T. steinbecki are roughly aligned in transverse rows and the proboscis is about as long as the trunk, ribbon-like and expanded distally. Differences between the two species are also evident in the size of sexually mature specimens.

Acknowledgements

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Family Thalassematidae
Genus *Anelassorhynchus*

A key to the species of *Anelassorhynchus* (Echiura) with a description of a new species from the east coast of southern Africa

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A new echiurid species of the genus *Anelassorhynchus* Annandale 1922, collected from Isipingo Beach along the Natal coast (Republic of South Africa) is described. Although the genus is widely distributed and numerous species have been recorded from the Indian and Pacific Oceans, only two species, *A. indivisus* (Sluiter 1900) and *A. moebii* (Greeff 1879), are currently known from the southern African region. The new species, *A. gangae* **sp. nov.**, appears to be related to *A. porcellus* Fisher 1948 and to *A. adelaidensis* Edmonds 1960. It differs from these two species mainly in the nature of the integument and in the arrangement of the dermal papillae. A key for the identification of all the species in the genus is provided.

S. Afr. J. Zool. 1984, 19: 16 – 21

'n Nuwe spesie van die Echiura-genus, *Anelassorhynchus* Annandale 1922, wat by Isipingostrand langs die Natalse kus versamel is, word beskryf. Hoewel die genus wydverspreid voorkom en baie Indiese- sowel as Stille Oseaan-spesies opgeteken is, is tans net twee spesies, *A. indivisus* (Sluiter 1900) en *A. moebii* (Greeff 1879), in die Suider-Afrikaanse gebied bekend. Dit lyk of die nuwe spesie, *A. gangae*, verwant is aan *A. porcellus* Fisher 1948 en *A. adelaidensis* Edmonds 1960. Dit verskil van hierdie twee spesies hoofsaaklik t.o.v. die aard van die huid en die rangskikking van die huidpapille. 'n Sleutel vir die identifisering van al die spesies in die genus word voorsien.

S.-Afr. Tydskr. Dierk. 1984, 19: 16 – 21

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The echiurid fauna of southern Africa is at present confined to four genera: *Thalassema, Ochetostoma, Echiurus* and *Anelassorhynchus*. Three species of *Thalassema*, six of *Ochetostoma* and only one of *Echiurus* have been recorded from southern African waters while the genus *Anelassorhynchus* is represented by two species, *A. indivisus* and *A. moebii*. *A. indivisus*, originally described as *T. indivisum* by Sluiter (1900), from off the coast of Spain was also recorded by Stephen & Cutler (1969) from off the Natal coast in waters 47 to 57 m deep. *A. moebii* (Greeff 1879), originally known from Mauritius, has been recorded from three other localities in the Indian Ocean. The latter species was also collected by von Weber in the vicinity of Durban (Sluiter 1898).

Sixteen species have so far been assigned to the genus *Anelassorhynchus*, but the specimens on hand are not referable to any of the known species. In the present paper, *A. gangae* is described and compared with other related species in the genus.

Anelassorhynchus Annandale 1922

Generic diagnosis

Longitudinal and inner oblique layers of muscle not grouped into bands or fascicles. Posterior setae absent. Gonostomal lips elongate and spirally coiled.

Type species: *Thalassema branchiorhynchus* Annandale & Kemp 1915

Remarks

Prior to 1922, the genus *Thalassema* comprised echiurans where the longitudinal and inner oblique layers of muscle were continuous and not grouped into bands or fascicles. The genus *Anelassorhynchus* was erected by Annandale (1922) to contain two estuarine species which possessed gill-like outgrowths on the proboscis (Stephen & Edmonds 1972). Fisher (1946) considered these gill-like processes to be adaptations to an unusual environment and therefore an unsatisfactory character on which to base the genus. He proposed that the condition of the gonostomal lips should be the main distinguishing character. This is a reliable taxonomic character in differentiating these two closely related genera.

Distribution of *Anelassorynchus*

The genus is widely distributed and numerous species have been recorded from several localities in the Indian and Pacific Oceans. The majority of the species are confined to shallow waters of the intertidal zone but a few have been reported from the abyssal regions of the ocean. In their monograph, Stephen & Edmonds (1972) give the range of distribution of each species.

Key to the species of the genus *Anelassorhynchus*

The key for the species *Anelassorhynchus*, provided by Stephen & Edmonds (1972) and Datta Gupta (1974) has been modified in order to accommodate *A. gangae*. No attempt has been made to synonymize any of the species. In this key other, less rigorous characters have also been included to assist in the identification of single individuals.

1	Gonoducts one pair	2
–	Gonoducts more than one pair	3
2	Trunk up to 230 mm in length, body wall slightly translucent. Interbasal muscle present	*A. abyssalis* Fisher, 1949
–	Trunk up to 14 mm in length, body wall thin and transparent. Interbasal muscle absent	*A. indivisus* (Sluiter, 1900)
3	Gonoducts two pairs	4
–	Gonoducts three pairs or more	12
4	Numerous minute spinelets in place of each seta	*A. chaetiferus* Datta Gupta, Menon & Johnson, 1963
–	Two ventral setae	5
5	Proboscis reduced to a small collar about one-nineteenth the body length	*A. microrhynchus* (Prashad, 1919)
–	Proboscis well developed, at least one-fifth body length	6
6	Margin of proboscis with outgrowths	7
–	Margin of proboscis without outgrowths	8
7	Proximal margin of proboscis with dendritic outgrowths and distal margin serrated	*A. dendrorhynchus* (Annandale & Kemp, 1915)
–	Proximal margin of proboscis with two rows of gill-like outgrowths, distal margin of proboscis smooth	*A. branchiorhynchus* (Annandale & Kemp, 1915)
8	Proboscis from one-quarter to one-fifth the length of the trunk. Anal vesicles short	*A. sabinus* (Lanchester, 1905)
–	Proboscis half or more than half the trunk length. Anal vesicles long	9
9	Trunk papillae arranged in groups. Anal vesicles with few scattered funnels. Proboscis non-deciduous	***A. gangae* sp. nov.**
–	Trunk papillae not arranged in groups. Anal vesicles with numerous funnels. Proboscis deciduous	10
10	Integument thin and transparent	*A. semoni* (Fischer, 1896)
–	Integument thick and opaque	11
11	Trunk rich dark green	*A. adelaidensis* Edmonds, 1960
–	Trunk sandy grey	*A. porcellus* Fisher, 1948
12	Proboscis anteriorly bilobed	13
–	Proboscis not bilobed	14
13	Gonoducts located posterior to the ventral setae without any tendency to cluster	*A. loborhynchus* Datta Gupta & Menon, 1965
–	Gonoducts located anterior as well as posterior to ventral setae with a tendency to cluster	*A. fisheri* Datta Gupta, 1974
14	Three pairs of gonoducts, first pair anterior to the ventral setae	15
–	Three pairs of gonoducts located posterior to the ventral setae	16
15	Anterior extremity of anal vesicles attached to body wall by slender muscle. Body uniformly covered with small, closely arranged papillae	*A. inanensis* (Ikeda, 1904)
–	Anterior extremity of anal vesicles not attached to body wall. Papillae irregularly scattered over body and often arranged in clumps	*A. moebii* (Greeff, 1879)
16	Anal vesicles with ciliated funnels set on small stalks. Trunk covered with dark green papillae closely crowded at the extremities. No ring vessel	*A. mucosus* (Ikeda, 1904)
–	Anal vesicles without ciliated funnels. Papillae scattered over whole surface of trunk but posteriorly larger and more numerous and arranged in regular rows. Ring vessel unknown	*A. vegrandis* (Lampert, 1883).

Anelassorhynchus gangae sp. nov.

Present record. Isipingo Beach (29°05'S/30°56'E), Natal coast, approximately 15 km south of Durban (Type locality).

Holotype. Sexualy mature female, in the Natal Museum, Pietermaritzburg, Republic of South Africa No 2670, collected by Mr K.S. Ganga, 26 March 1982.

Paratype. One sexually mature male, in the Natal Museum, collected by the author, 27 April 1983. Museum number same as for holotype.

Habitat. Both specimens were found in a rocky tunnel in the intertidal zone, close to the high water mark. Numerous specimens of *O. caudex* were also found in the same habitat. The holotype occurred between two slabs of sandstone in the wall of the tunnel while the paratype was discovered under a slab of rock in relatively muddy sand.

Description

Size

Measurements were taken after the specimens were narcotized with magnesium sulphate and preserved in formalin. In the holotype, the proboscis which is 53 mm long slightly exceeds half the length of the trunk. The trunk length is 90 mm and its greatest diameter is 23 mm. In the paratype the trunk is 100 mm in length and its greatest diameter is 21 mm. The proboscis, which was detached during narcotization, measures less than half the length of the trunk. The size of these animals, however, varies depending on their state of contraction at fixation.

Colour in life

The trunk is uniformly grey in both specimens but the colour of the proboscis differs slightly. In the holotype the proboscis is white in colour but in the paratype it is pale yellow. The proboscis of both specimens is edged with light brown. A dark red line, probably the ventral blood vessel, is visible along the mid-ventral surface of the trunk. In formalin preserved specimens, the colour of the trunk changes to brown.

External features

Proboscis. The proboscis (Figure 1), which is fleshy and non-deciduous, is of uniform width throughout its length with a shallow ventral depression or groove leading to the mouth. In preserved specimens, the lateral edges tend to curl inwards to form a tubular structure. The lateral margins fuse at the base to form a narrow lower lip. The two lateral nerves of the proboscis are visible from the ventral surface.

Trunk. The trunk is cylindrical or sausage-shaped and more or less of uniform diameter throughout its length (Figure 1). The papillae are minute and barely visible to the unaided eye.

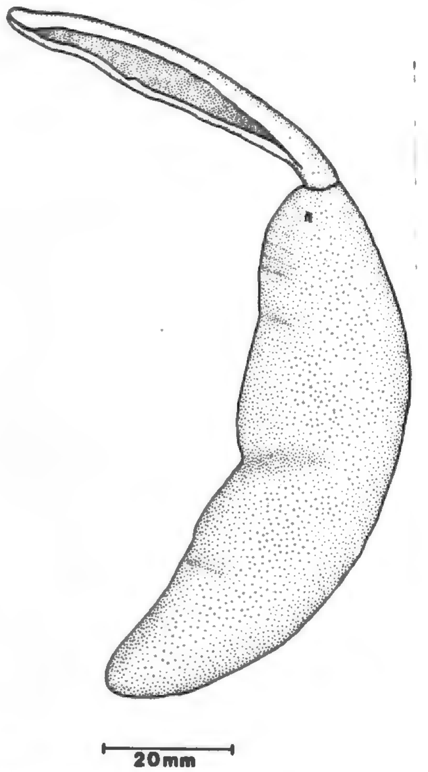

Figure 1 Ventral aspect of *A. gangae*.

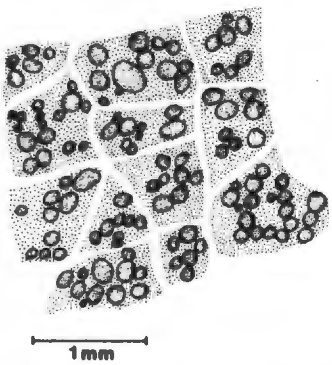

Figure 2 A part of the integument from the midventral surface of the trunk showing the arrangement of the papillae.

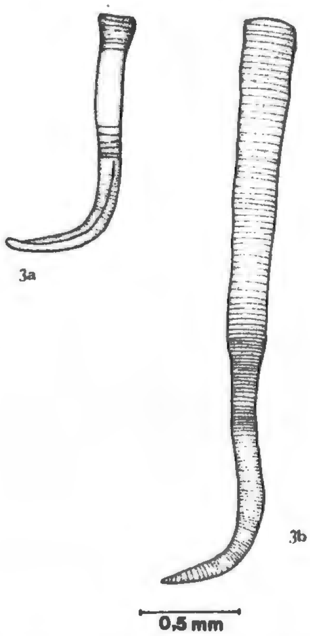

Figure 3 (a) The right non-functional (replacement) seta. (b) The right functional seta.

Under the dissecting microscope, however, these papillae are densely arranged over the entire surface of the integument. A noticeable feature is that the rounded papillae are arranged in groups of various shapes and sizes, separated by narrow interspaces (Figure 2). The size of the papillae, however, varies within a group. Under certain states of contraction, the narrow, irregularly arranged interspaces separating groups of papillae are visible to the unaided eye. A white mucous cap encased the posterior extremity of the trunk after preservation in formalin.

Setae (Figures 3a & b). The two yellowish-brown ventral setae are situated about 5 mm posterior to the junction of the proboscis and trunk. Two pairs of genital pores are located behind the setae. The setae are cylindrical hook-like structures about 3 mm in length. When dissected out, each seta consists of a long straight shaft with a curved terminal end. The much narrower distal third of the shaft is yellowish-brown in colour while the proximal two-thirds is dark brown. More or less equidistant concentric rings are present over the entire surface of the shaft. As in other related species, the setae are invested in connective tissue and located in cone-shaped setal sacs, supported by a number of radiating muscle strands. There is no interbasal muscle.

In the holotype, a second, much smaller, replacement seta is present in close association with the right functional one. The curved distal end of the non-functional seta is slightly flattened and the concentric markings are not very pronounced. In the paratype, however, the non-functional seta is on the left.

Internal anatomy

Alimentary canal. The alimentary canal is extremely long and is attached to the body wall at several points along its length by numerous thin mesenteric strands.

The mouth is situated at the extreme anterior end of the trunk at the base of the proboscis, which surrounds the aperture to form a funnel. The mouth leads into a spacious muscular pharynx which is attached anteriorly by a number of radiating strands of mesentery (Figure 4).

The oesophagus is of uniform diameter and opens into a somewhat dilated, oval crop (Figure 4) which appears white in colour. A thin sheet of transparent ventral mesentery attaches the oesophagus to the body wall. Externally, the crop can be clearly distinguished from the adjoining oesophagus and intestine by its shiny appearance. The characteristic ring vessel is located at the posterior end of the crop.

A noticeable feature is the presence of extremely long and thin mesenteric strands which extend anteriorly to fasten the crop and adjoining intestine to the body wall (Figure 4).

After the ring vessel, the intestine forms a loop and then pursues a complicated course through the body cavity, forming several ascending and descending limbs. The intestine can be divided into the presiphonal, siphonal and postsiphonal regions. The presiphonal region of the intestine is long and is marked by the presence of a ciliated groove. This groove commences soon after the first loop of the intestine and then merges with the intestinal siphon. In the region of the intestinal siphon, the intestine is of much bigger diameter with extremely thin walls. The postsiphonal intestine is a long and narrow tube

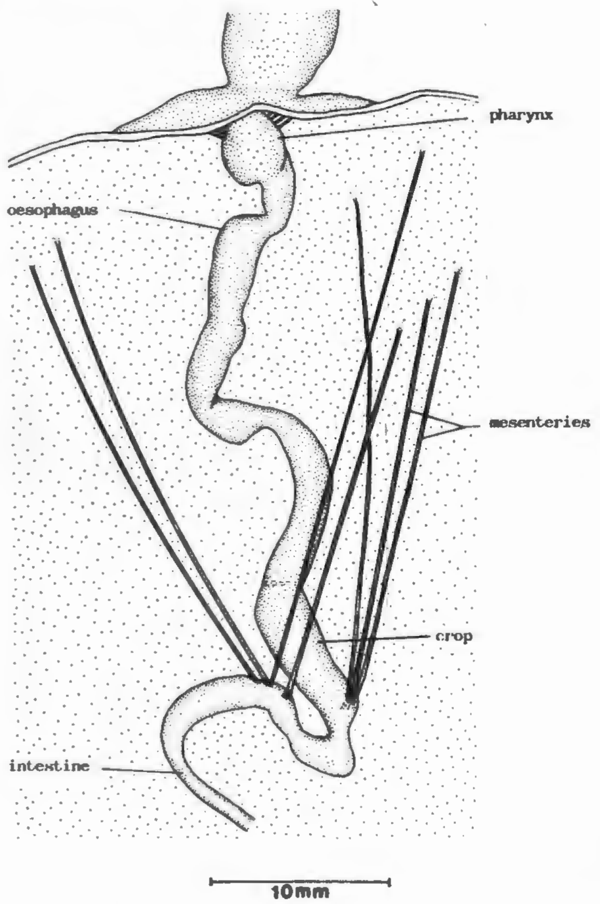

Figure 4 Anterior end of the alimentary canal illustrating the elongate mesenteric strands.

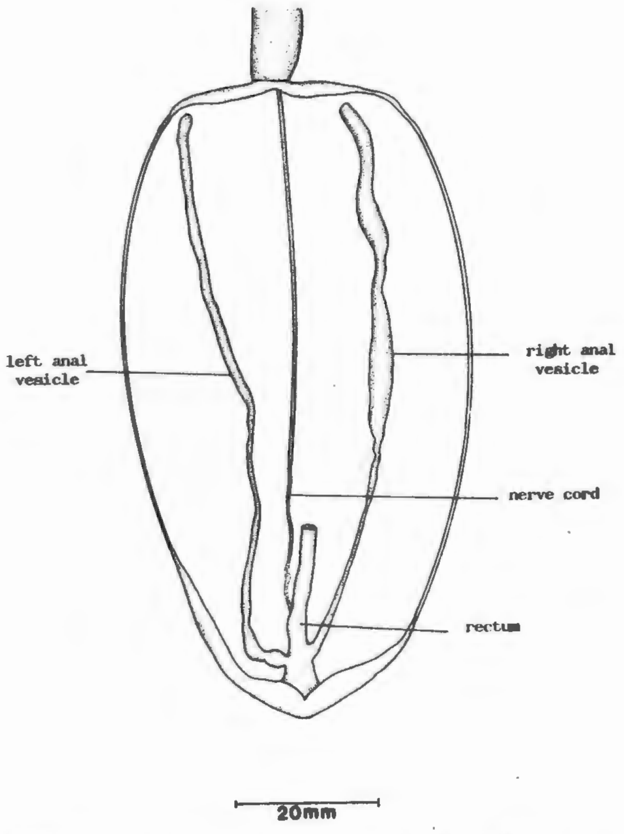

Figure 5 Dorsal dissection of the trunk showing the anal vesicles.

which is compactly filled with fine sand grains, small shell fragments and other miscellaneous hard debris. The intestinal contents are not in the form of pellets. Posteriorly, the intestine leads into the rectum, which is a straight tube of much bigger diameter. A rectal caecum is absent in this species.

Anal vesicles (Figure 5). The paired, blind-ending anal vesicles open posteriorly into the rectum. They are highly distensible tubes with extremely thin walls. Proximally, these vesicles are fastened to the body wall by numerous fine strands of mesentery but distally they are free and loosely interweave through the coils of the alimentary canal. In the holotype, the vesicles are almost as long as the trunk. They are somewhat distended in the anterior two-thirds, thereafter they narrow considerably but dilate once again before opening into the rectum. In the paratype, however, they are much longer, about one and a half times the trunk length. They are narrow distally but also become dilated before opening into the rectum. Minute, unstalked ciliated funnels are very sparsely distributed over the surface of the vesicles.

Gonoducts (Figure 6). Two pairs of elongate, tubular gonoducts are located in the anterior part of the body cavity on either side of the ventral nerve cord; the posterior pair being much the larger. Both the pairs are located posterior to the ventral setae. The gonoducts of both specimens are considerably distended due to the presence of gametes. In the holotype, the terminal ends of the gonoducts are pointed and strongly curved but in the paratype they are rounded and smooth. The second pair of gonoducts in the paratype has a few constricted and dilated portions. These different shapes of the gonoducts are probably due to the different degrees of inflation caused by the storing of sexual cells within them. The paired gonostomal lips are elongate and spirally coiled. These longitudinally grooved gonostomal lips unite proximally to form a short, common duct which opens into the base of the gonoduct. In the holotype, the right anterior gonoduct possesses a single gonostomal lip.

Blood system (Figure 7). The characteristic ring vessel surrounds the posterior end of the crop. The conspicuous dorsal vessel, which arises from the ring vessel, continues anteriorly, dorsal to the foregut. In the region of the pharynx it gives off a branch to the body wall before entering the proboscis. Two elongate neuro-intestinal vessels also arise from the ring vessel and pass anteroventrally. Both these vessels remain separate from each other for a considerable part of their length but unite to form a single vessel before opening into the ventral vessel.

Remarks

The separation of species in this genus is based mainly on the following features: the number as well as the position of the gonoducts in relation to the ventral setae, the nature of the body wall, the shape and arrangement of the dermal papillae, the structure of the proboscis, the presence or absence of ciliated funnels on the anal vesicles, an interbasal muscle, the neuro-intestinal vessel and the rectal diverticulum.

Distinctive features of the present species include the characteristic shape and arrangement of the dermal papillae, the nature of the integument and the presence of unusually long mesenteric strands which attach the crop and adjoining intestine to the anterior part of the body wall.

Of the 16 described species, the following eight possess two pairs of gonoducts: *A. adelaidensis* Edmonds 1960, *A. bran-*

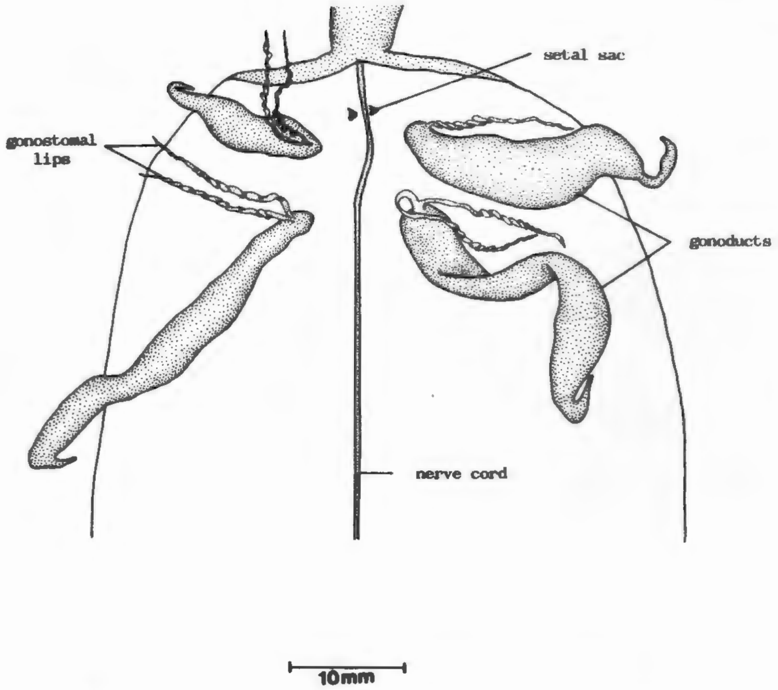

Figure 6 Anterior end of the trunk cavity illustrating the gonoducts.

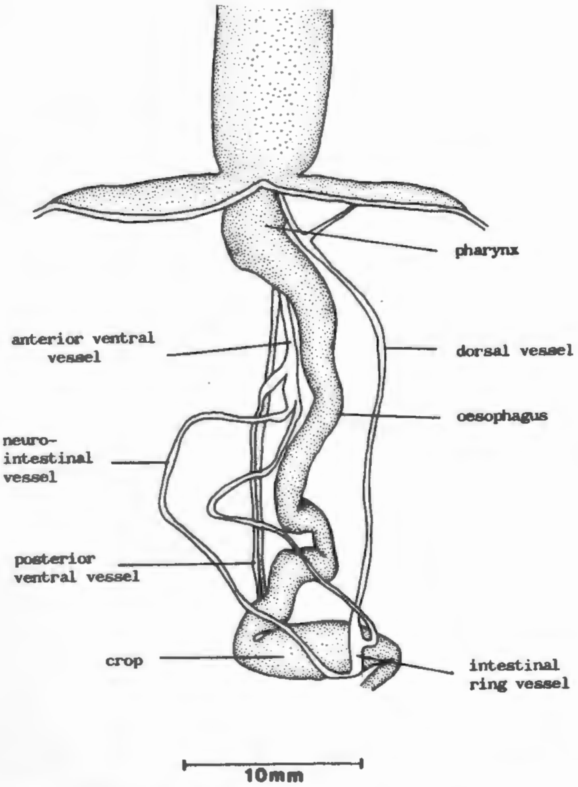

Figure 7 Anterior end of alimentary canal showing blood vessels.

chiorhynchus (Annandale & Kemp 1915), *A. chaetiferus* Datta Gupta, Menon & Johnson 1963, *A. dendrorhynchus* (Annandale & Kemp 1915), *A. microrhynchus* (Prashad 1919), *A porcellus* Fisher 1948, *A. sabinus* (Lanchester 1905) and *A. semoni* (Fischer 1896).

Both *A. branchiorhynchus* and *A. dendrorhynchus* possess dendritic outgrowths on the proboscis (Stephen & Edmonds 1972) and hence are distinct from *A. gangae* and the other species in the genus.

The species *A. chaetiferus* differs from all other known echiurids by possessing muscle pads in which eight spinelets are embedded (Datta Gupta *et al.* 1963). Another unusual feature in this species is that there is no typical demarcation between the proboscis and the trunk.

A. microrhynchus is based on a single specimen from India described as *Thalassema microrhynchus* by Prashad (1919a). An important feature that distinguishes it from *A. gangae* is that the proboscis is reduced to a small collar about one-nineteenth of the body length (Prashad 1919a). Furthermore, the presence of two rows of ciliated funnels on the surface of the anterior half of the anal vesicles in *A. microrhynchus* also tends to separate these two species.

The species *A. sabinus* has been described rather briefly by Lanchester (1905) from five specimens. He mentions that the animals are small with a total length of 10 mm and the proboscis is one-fifth the body length. In addition to the marked difference in size, *A. sabinus* also differs from *A. gangae* in possessing an integument that is rather thin and transparent. Both Prashad (1919b) and Sato (1939) state that the anal vesicles are short in *A. sabinus*; Prashad's figure also shows a well-developed caecum.

In the species *A. semoni* the integument is thin and transparent (Fischer 1896). The papillae are of uniform size and are very closely arranged at the posterior end of the body. The anal vesicles are more than half the length of the trunk. According to Fischer (1896) the right gonoduct opens in front of the setae, the rest behind. Wharton (1913) reports two specimens with a trunk length of 70 mm and a proboscis about three-quarters as long as the trunk. Both his specimens possessed two pairs of gonoducts, one pair in front of and the other behind the setae. Wesenberg-Lund (1959) also mentions that the papillae are more densely crowded round the posterior end of the trunk. In two of the specimens that were dissected, both the pairs of gonoducts were post-setal in position. Hence there is considerable variation in the position of the gonoducts in this species. The most important differences between *A.*

Table 1 Comparison of *A. gangae, A. porcellus* and *A. adelaidensis*

	A. gangae	*A. porcellus*	*A. adelaidensis*
Size	length of trunk up to 100 mm; proboscis : trunk is 1:2	length of trunk up to 70 mm; proboscis : trunk is 1:2	length of trunk up to 100 mm; proboscis : trunk is 1:2,5
Colour (living specimen)	proboscis white to pale yellow with light brown margins; trunk uniform grey	trunk sandy-grey	groove or trough of proboscis light green; trunk rich dark green
Proboscis	non-deciduous	deciduous	deciduous
Shape	trunk sausage-shaped; proboscis of uniform diameter	trunk plump and sac-like; proboscis tapers slightly anteriorly	trunk cylindrical; proboscis tapers anteriorly, margin not frilled
Papillae	minute, arranged in groups of various shapes and sizes distributed uniformly over entire surface of trunk; groups of papillae separated by narrow interspaces	numerous, flat, largest on anterior and posterior surfaces of trunk, transversely aligned	numerous, small, flat; not arranged in groups
Body wall	thick and opaque	thick in large specimens; slightly translucent in smaller ones; skin closely wrinkled transversely	skin wrinkled
Anal vesicles	almost as long as or longer than trunk with few scattered funnels.	long, slender; brown in colour with numerous small unstalked funnels	long, slender; brown in colour with numerous minute brown funnels

semoni and *A. gangae* lie in the nature of the integument and in the arrangement of the dermal papillae.

The two species most nearly related to *A. gangae* seem to be *A. porcellus* and *A. adelaidensis*. The characteristic features of these three species are summarized in Table 1. Fisher's original description of *A. porcellus* (1948) is based on a number of specimens collected from several localities in Hawaii. This species was redescribed by Edmonds (1960) from 12 specimens collected from the Heron Islands, Queensland. The description of *A. adelaidensis* by Edmonds (1960) is based on eight specimens from South Australia. The differences which distinguish *A. gangae* from *A. porcellus* and *A. adelaidensis* mainly concern the nature of the body walls, the shape and distribution of the dermal papillae and the arrangement of the funnels on the anal vesicles. Other differences of lesser significance are the relative sizes of the specimens, the nature of the proboscides and the form and colouration of the trunk of living specimens.

Further material should give a better understanding of the variation within *A. gangae* as well as determining whether the shape and distribution of the dermal papillae are of a distinctly different type from those reported for *A. porcellus* and *A. adelaidensis*.

Acknowledgements

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Anelassorhynchus indivisus (Sluiter, 1900)

Thalassema indivisum Sluiter, 1900:18. Stephen, 1965:80-82, figs. 1 and 2. Stephen & Cutler, 1969: 113-114.

Anelassorhynchus indivisus: Stephen & Edmonds, 1972:448.

Type locality: Off the coast of Spain (56°43'40"N, 8° 28' 30" W); at 90m.

Diagnosis

Proboscis up to 60mm in length, broadening anteriorly, white overall with some light-yellow at distal end, lateral margins fuse at base forming a tube about 1,5 to 2mm long. Trunk almost as long as proboscis, yellowish-grey in alcohol and ridged by contraction. Body wall thin and transparent. Papillae of various sizes and shapes, scattered over entire surface of trunk, concentrated mainly on ridges and larger posteriorly. Gonoducts one pair; gonostomal lips drawn out into long coiled filaments. Alimentary canal fastened to body wall by numerous mesenteries. Anal vesicles small, less than one-quarter trunk length with numerous ciliated funnels.

Distribution: This species, described originally from the coast of Spain was later recorded from the Red Sea. Its discovery from off the Natal coast is an interesting extension of its range of distribution.

Remarks

Anelassorhynchus indivisus, described originally as Thalassema indivisum by Sluiter (1900), is based on 6 specimens. It is very likely that all his specimens were juveniles as the proboscides were up to 4mm long and the trunks measured up to 9mm in length. Sluiter's description, however, makes no mention of the blood systen, setae, interbasal muscle and rectal caecum.

Stephen and Cutler (1969) described two specimens collected from off the Natal coast in the vicinity of Durban. The specimens were obtained at depths of 47 and 57m in sediment that consisted of muddy sand and shells. The larger specimen had a trunk length of 14mm and the proboscis was 11 mm long.

A single large specimen with a trunk length of 60mm was taken by the Israel South Red Sea Expedition (Stephen, 1965). The proboscis of this specimen was as long as the trunk with the distal end expanded into a fan-like structure. Stephen's description mentions the presence of a single pair of gonoducts with extremely long and coiled gonostomal lips. The entire surface of the trunk is closely covered with circular rows of papillae. According to Stephen, the papillae are more or less of uniform size and hence unlike those of Sluiter's specimens. In all other respects, Stephen (1965) found his specimen to be identical with Sluiter's des=cription.

The description provided by Stephen and Cutler (1969) is brief and does not give any details regarding the shape of the gonostomes.

Unfortunately it was not possible to obtain any material of _A_. _indivisus_.

Anelassorhynchus moebii (Greeff, 1879)

Thalassema moebii Greeff, 1879:152, pl.6, figs. 68-69. von Drasche, 1881:621. Fischer, 1895:20; 1896:336. Shipley, 1899:350; 1902:129, pl.6, figs. 3(a-b). Sluiter, 1898:444-445; 1902:49. Augener, 1903:348. Lanchester, 1905:34. Wesenberg-Lund, 1959:71-72.
Anelassorhynchus moebii: Fisher, 1946:222. Stephen & Edmonds 1972:449.

Type locality: Mauritius.

Diagnosis

Proboscis of preserved specimens from 30 to 42mm in length, ribbon-like, broadened distally and slightly indented, light green with bright yellow edges. Lateral edges of proboscis fuse proximally forming a short tube or funnel around mouth. Trunk from 48 to 80mm in length, greyish-yellow, passing in places into violet, with violet stripes running diagnonally round body. Papillae irregularly distributed over entire surface of trunk, often arranged in clumps. Gonoducts three pairs, tubular, first pair opening in front of setae. Gonostomal lips elongate, spirally coiled. Ventral setae short, delicate, located a considerable distance posterior to mouth. Anal vesicles long tubes with ciliated funnels. Neuro-intestinal vessel paired. Rectal caecum absent.

Distribution: This species has a Tropical Indo-West-Pacific distribution having been recorded from Mauritius, Zanzibar, Maldive Islands, Indonesia and the Natal coast in the vicinity of Durban.

Remarks

Anelassorhynchus moebii was the first echiuran to be recorded from southern Africa, collected from the Natal coast in the vicinity of Durban (Sluiter, 1898). Unfortunately it was not possible to obtain any material of this species. The description provided by Wesenberg-Lund (1959) is based on 28 specimens from Mauritius. According to this author, a rectal caecum is absent. Her largest specimen had a trunk length of 80mm and the contracted proboscis was 30mm long. This species appears to be very closely related to A. inanensis (Ikeda, 1904) and Wesenberg-Lund may be justified in regarding them to be synonymous.

Family Echiuridae

Genus _Echiurus_

FAMILY ECHIURIDAE DE BLAINVILLE, 1827

DIAGNOSIS

Proboscis well-developed, often easily detached from trunk. Trunk with rows of papillae most prominent on posterior surface. Gonoducts from one to three pairs, without spirally coiled gonostomal lips. Two rings of anal setae at posterior end of trunk. A pair of ventral setae present in all genera. Post-pharyngeal diaphragm almost separates coelom into two parts. Neuro-intestinal vessel in direct connection with dorsal vessel through a ring vessel as in _Thalassema_. Anal vesicles not branched, usually elongate with small ciliated funnels.

Type Genus

Echiurus Guérin-Méneville, 1831

REMARKS

The presence of two rings of anal setae and a post-pharyngeal diaphragm is characteristic of the family. The family contains one genus and four species, one consisting of two subspecies. The geographic distribution of the species of _Echiurus_, however, shows that it is essentially a cold-water genus confined to high latitudes of the Northern and Southern Hemispheres. Only _E. antarcticus_ is known from southern Africa, having been recorded from off the Natal coast in the vicinity of Durban.

Echiurus Guérin-Méneville, 1831

Generic diagnosis

Two rings of anal setae at posterior end of trunk. A post-pharyngeal diaphragm is present which almost separates the coelom into two parts. Gonostomes without spirally coiled lips.

Type species

Lumbricus echiurus Pallas 1766

Distribution of Echiurus

Confined mainly to cold waters of the Arctic and Antarctic. Recorded localities include Coast of Chile, South Georgia, west coast of Ireland, Alaska, Greenland, North Sea and the Scandinavians coasts. Some species, however, have been recorded from the Mediterranean. The recorded localities for each species are given by Stephen & Edmonds (1972).

Key to the species of Echiurus (Adapted from Stephen & Edmonds (1972))

1. Gonoducts one pair ....*E. sitchaensis*
   Gonoducts two to three pairs 2

2. Gonoducts two pairs 3
- Gonoducts three pairs; proboscis T-shaped.........*E. antarcticus*

3. Gonostome attached through body wall to tube of gonoduct .... *E. abyssalis*
- Gonostome attached to tube of gonoduct in body cavity 4

4. Proboscis deciduous. Ventral setae straight ......

   E. echiurus echiurus.

\- Proboscis adherent. Ventral setae curved ......

   E. echiurus alaskanus.

Echiurus antarcticus Spengel, 1912

Echiurus antarcticus Spengel, 1912 : 200-208.

Stephen 1941 : 245-246, pl. 7, fig. 1.

Wesenberg-Lund, 1955 : 17-18.

Stephen & Cutler, 1969 : 112-113.

Type locality

Cumberland Bay, South Georgia.

Holotype : Reichsmuseum, Stockholm.

Diagnosis

Proboscis T-shaped, 50-65mm in length and 11-15mm at its broadest part. Colour of proboscis milky-white to cream, edges light brown. Anterior end expanded into two flaps, posterior part rolled into a short tube 2-4mm in length. Differentiated ridge of tissue in midline along ventral side of proboscis. Trunk with transverse striations and longitudinal rows of large papillae. Small papillae between well-marked rows of large papillae also in rows but indistinct. Anterior setae strongly curved, situated about 1 cm behind mouth. Number of anal setae very variable, from 8-10 in anterior row and 5-6 in posterior row. Gonoducts three pairs.

Distribution

Echiurus antarcticus is a cold-water species having been recorded from several localities in South Georgia and the coast of Chile. It has been found at depths ranging from 10 to 344 m. The two specimens recorded by Stephen & Cutler (1969), from off the Natal coast near Durban, came from a depth of 86 m.

Remarks

Echiurus antarcticus has been described in considerable detail by Spengel (1912). According to Spengel, this species has three pairs of gonoducts, but possibly only two in one specimen. Stephen (1941) was unable to come to a definite decision on the number of gonoducts from his Discovery specimens but was able to ascertain the presence of only two pairs in three of his specimens that were in a satisfactory condition. Unfortunately, the specimens examined by Wesenberg-Lund (1955) were also poorly preserved and the internal organs, including the gonoducts, were badly damaged. Stephen & Cutler (1969) report the presence of only two gonoducts, both on the right side of one specimen and two pairs on each side of the nerve cord in the other. Hence there appears to be considerable intraspecific variation in the number of gonoducts.

Another discrepancy lies in the distribution of the dermal papillae. Spengel's description (1912) mentions that small papillae are irregularly scattered between the rows of large papillae. Stephen (1941) and Wesenberg-Lund (1955), on the other hand, state that the small papillae, although indistinct in places, are also arranged in rows.

This species is closely related to E. echiurus (Pallas, 1766) and according to Stephen (1941), they cannot be separated on the basis of the number of gonoducts. The appearance of the trunk and the distribution of the papillae are similar in both. Significant differences, however, exist in the shape and structure of their proboscides. The proboscis of E. echiurus is in the form of a short truncated cylinder and hence markedly different from the T-shaped proboscis of E. antarcticus. This feature seems to be sufficiently distinctive to warrant a separation of the two species.

The description of E. antarcticus, provided by Stephen & Cutler (1969), is based on two specimens collected from off the Natal coast in the vicinity of Durban. The trunk measured 15 mm in length in both specimens and the probodcides were missing. One of these specimens (NAD 53 E) was obtained by the present author from the UCT collection but in the internal organs were too badly damaged to allow a thorough re-examination. As this species is confined to cold waters of the Antarctic region, its occurrence in warm subtropical waters of the Natal coast is rather unusual and marks an interesting extension of its range of distribution.

Although this species is sufficiently well known, some uncertainty still exists with regard to the number of gonoducts. Additional material in the future will probably shed more light on the position.

DISTRIBUTION

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THE GEOGRAPHIC DISTRIBUTION OF ECHIURA FROM SOUTHERN AFRICA

*R. BISESWAR**

The echiuran fauna of southern Africa currently comprises two families, four genera and 16 species of which one has recently been described as new to science and four are new records for the region. The taxonomic characters distinguishing the genera are given. The zoogeographic distribution of the southern African species is outlined and discussed. Knowledge of the echiuran fauna is too scanty to throw any light on the division of the coastline into faunistic provinces.

Die echiura-fauna van suider-Afrika bestaan, volgens huidige inligting, uit twee families, vier genera en 16 spesies waarvan een onlangs as nuut vir die wetenskap beskryf en vier as nuut vir die gebied aangegee is. Die taksonomiese kenmerke vir uitkenning van die genera word verskaf. Die soögeografiese verspreiding van die suider-Afrikaanse spesies word gekarteer en bespreek. Kennis van die echiura-fauna is te skraps om enige lig op die indeling van die kuslyn in faunistiese provinsies te werp.

Echiurans are sausage-shaped animals with a spatulate proboscis at the anterior end, as a result of which they are commonly referred to as spoon or tongue worms. The trunk, which is brightly coloured in a number of species, is covered with round or oval papillae. Echiurans are generally burrowers and common inhabitants of the intertidal zone, although some deep-water forms have been reported. A few species have also extended into brackish waters. They are widely distributed and have been reported from all seas and all latitudes.

At present, little is known about the echiuran fauna of southern Africa. There is no single comprehensive report on the recorded species or on their range of distribution. The whole of the existing information on the phylum is confined to a very small number of publications. Significant works on this group in southern Africa are those of Wesenberg-Lund (1959, 1963) and Stephen and Cutler (1969). Also, a few publications have referred to new species and new records (Jones and Stephen 1955, Webb 1972, Biseswar 1983, 1984). None of these papers deals with the zoogeography of the southern African forms.

The present paper lists the genera and species of echiurans from southern Africa and maps their distribution, partly from published works and partly from recent surveys made along the coast. Such an investigation should be of help to current and future workers and could lead to a better understanding of the phylum as a whole.

MATERIALS AND METHODS

Distribution charts were reconstructed from the literature and from field notes on specimens collected mainly along the Natal coast. Living specimens were photographed and narcotized with magnesium sulphate. Measurements of the proboscis and the trunk were made prior to fixation and preservation in 10-per-cent formalin. Specimens were later dissected and, where possible, morphological variations were noted. Some species of echiurans were also obtained as a result of requests made to universities and institutions in South Africa.

TAXONOMY

The phylum Echiura at present comprises five families, 34 genera and approximately 140 species. A complete key to the families and subfamilies in the class Echiurida has been given by Datta Gupta (1976). According to the system of classification adopted by him, the families included in the order Echiuroinea are the Echiuridae, Thalassematidae, Bonellidae and Ikedaidae. The order Xenopneusta contains a single family, the Urechidae. Only two families, the Echiuridae and the Thalassematidae, have to date been recorded in southern Africa.

The family Echiuridae includes forms that possess

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two rows of posterior (anal) setae and anal vesicles with sessile funnels. It is represented by a single genus, *Echiurus*, which contains four species, one consisting of two subspecies. In southern Africa, *E. antarcticus* is the only representative of the family.

The family Thalassematidae includes forms where the gonoducts have lateral gonostomes and 1–7 pairs or paired groups of gonoducts. It is subdivided into two subfamilies, the Ochetostomatinae and Thalassematinae, distinguished on the disposition of the longitudinal muscles of the body wall. In the Ochetostomatinae, the longitudinal muscles are aggregated into distinct bands, whereas in the Thalassematinae they form a continuous sheet.

The subfamily Ochetostomatinae contains five genera, *Ochetostoma*, *Listriolobus*, *Ikedosoma*, *Platylobostoma* and *Lissomyema*, but, to date, only *Ochetostoma* has been recorded from southern Africa. The genus *Ochetostoma* has the most species of any of the Echiura, although some may be synonymous. In southern Africa, it is represented by nine species (see Fig. 1).

The subfamily Thalassematinae comprises three genera, *Thalassema*, *Anelassorhynchus* and *Arhynchite*. *Arhynchite* is not known from southern Africa, but *Thalassema* and *Anelassorhynchus* are represented by three species each.

Generic characters of the southern African forms

Echiurus

(i) two rows of posterior (anal) and one pair of anterior setae,
(ii) 1–3 pairs of gonoducts,
(iii) no coiled gonostomal lips,
(iv) post-pharyngeal diaphragm present and almost separating the coelom into two parts.

Ochetostoma

(i) longitudinal muscle layer of body wall gathered into distinct bundles,
(ii) inner oblique muscles between the longitudinal muscle bands fasciculated,
(iii) no posterior setae,
(iv) 1–7 pairs of gonoducts,
(v) gonostomal lips elongate and usually coiled.

Thalassema

(i) longitudinal and inner oblique layers of muscle continuous and not grouped into bands or fascicles,
(ii) no posterior setae,
(iii) 1–2 pairs of gonoducts,
(iv) gonostomal lips inconspicuous.

Anelassorhynchus

(i) longitudinal and inner oblique layers of muscle continuous and not grouped into bands or fascicles,
(ii) no posterior setae,
(iii) gonostomal lips elongate and spirally coiled.

ECHIURAN FAUNA OF SOUTHERN AFRICA

The first echiuran to be recorded from southern Africa was *Anelassorhynchus moebii* (Greeff, 1879), which was collected by von Weber from the Natal coast in the vicinity of Durban (Sluiter 1898). The species, originally described as *Thalassema moebii* from Mauritius, has been recorded from several other localities in the Indo-West-Pacific region, a zoogeographical region used by Day (1967) for benthic polychaetes.

Jones and Stephen (1955) described, from numerous specimens, a new species, *Ochetostoma capense*, from the estuary of the Zwartkops River near Port Elizabeth. The same species was later reported from Durban Bay and Langebaan Lagoon.

Four years later, Wesenberg-Lund (1959) recorded three species, *Thalassema diaphanes* Sluiter, 1889, *Ochetostoma erythrogrammon* Leuckart & Rüppell, 1828 and *O. arkati* (Prashad, 1935), from the vicinity of Cape Town. The single specimen of *T. diaphanes* was obtained from a depth of 28 m. Twelve specimens of *O. arkati* were collected by the "Atlantide" Expedition of 1945/46. Wesenberg-Lund (1963) also reported two specimens of *O. arkati* from Port Elizabeth.

A single specimen collected from Isipingo Beach, Natal, was ascribed to *Ochetostoma erythrogrammon* by Webb (1972).

In 1963, Wesenberg-Lund gave a taxonomic account of the sipunculans and echiurans in the collection of the University of Cape Town. Although there were no new species, two, *Ochetostoma formosulum* (Lampert, 1883) and *Thalassema philostracum* Fisher, 1947, were new records for the area. *O. formosulum* had been collected at a depth of 8–9 m from a central sand bank in Durban Bay and *T. philostracum* from Kosi Bay.

Stephen and Cutler (1969) recorded a further three species, *Analassorhynchus indivisus* (Sluiter, 1900), *Thalassema neptuni* Gaertner, 1774, and *Echiurus antarcticus* Spengel, 1912, from off the Natal coast in the vicinity of Durban. According to these authors,

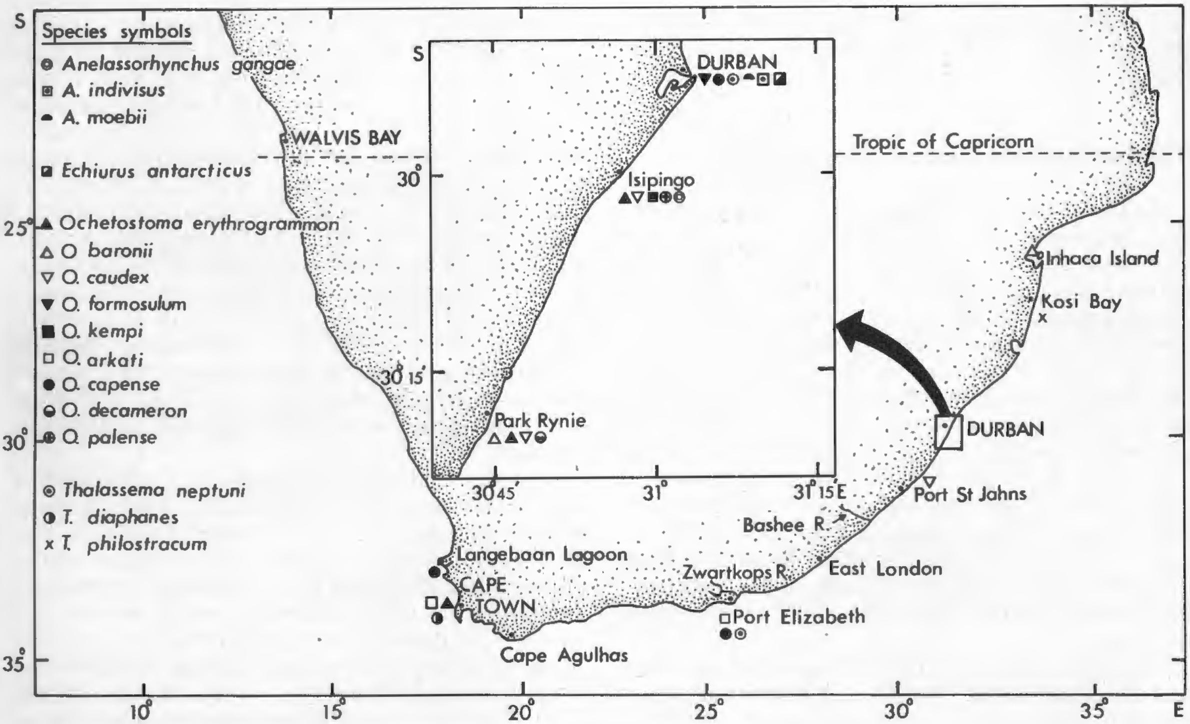

Fig. 1: Map of southern Africa showing localities where Echiura have been collected

T. neptuni had previously been recorded from Port Elizabeth. All three are sublittoral species and Stephen and Cutler (op. cit.) give an account of their latitudinal and bathymetric distribution. The discovery of *E. antarcticus* in subtropical waters off the Natal coast was of particular note because the species had previously been known only from the Antarctic region.

From 1969 until 1982, there were no reports on new species or new records from southern Africa. However, over a period extending from May 1977 to October 1982, numerous specimens ascribed to *Ochetostoma caudex* were collected from three East Coast localities: Embotyi, in the vicinity of Port St Johns on the Transkei coast, and Isipingo and Park Rynie beaches on the Natal coast. Both Satô (1939) and Wesenberg-Lund (1939, 1963) contend that *O. caudex* and *O. erythrogrammon* are synonymous. However, as a result of a detailed investigation of the degree of variation within these *O. caudex*, Biseswar (1983) recommended that the species be retained distinct from *O. erythrogrammon*.

A single specimen in the collection of the Department of Zoology, University of the Witwatersrand, has now been identified as *O. baronii* (Greeff, 1879). It was collected some time between 1956 and 1963 from Ponta Torres on the west coast of Inhaca Island. In 1983, two more specimens of the species were found at Park Rynie. Both localities are new records for this species.

A new species of *Anelassorhynchus*, *A. gangae*, was described from two specimens taken on Isipingo beach by Biseswar (1984). Both specimens were found in a rocky tunnel in the intertidal area, close to the high-water mark. Also in 1983, a further three species, *Ochetostoma kempi* (Prashad, 1919), *O. decameron* (Lanchester, 1905) and *O. palense* (Ikeda, 1924), were collected from Isipingo and Park Rynie for the first time.

Figure 1 shows the localities where these different species have been collected.

GEOGRAPHIC DISTRIBUTION OF SOUTHERN AFRICAN ECHIURANS

Echiurans are widely distributed and have been reported from all the oceans, from the Arctic to the Antarctic. The vast majority of the species appears to be tropical-subtropical in distribution, and the greatest variety is found in the Indo-West-Pacific region.

Distribution off the southern African coast

Although most of the species are common inhabitants of the intertidal zone, a few have been reported from considerable depths. Of the species currently known from southern Africa, *Echiurus antarcticus*, *Anelassorhynchus indivisus* and *Thalassema neptuni* have been collected at depths ranging from 45 to 138 m, and *T. diaphanes* has been reported from a depth of 28 m. A few species have also extended into estuaries. To date, *Ochetostoma capense* is the only estuarine species known from southern Africa. At Zwartkops River, where they have been collected in large numbers, the animals burrow in the mud to a depth of 15–20 cm (Jones and Stephen 1955). *O. capense* has been reported to occur as far as 3,5 km upstream from the estuary mouth, and it can therefore survive in areas where the salinity is comparatively low.

The differences in the distribution of the intertidal marine biota along southern African shores are primarily caused by various ocean currents. From the work of Stephenson (1939, 1944, 1948) and Stephenson and Stephenson (1972) on the intertidal fauna and flora of southern Africa, it is generally accepted that three faunistic provinces are present.

(i) The subtropical fauna is found along the East Coast, extending from 20°S to the vicinity of East London. This region is greatly influenced by the Agulhas Current. According to Day (1967) the transitional zone lies in the vicinity of Port St Johns or the mouth of the Bashee River (see Fig. 1).

(ii) The warm temperate fauna along the South Coast from East London to Cape Agulhas is influenced by the cooler inshore counter-current.

(iii) The cold temperate fauna occurs along the West Coast from Cape Agulhas to the vicinity of Walvis Bay and is influenced by the Benguela Current.

Between Cape Point and Cape Agulhas there is an overlap region with a mixture of West Coast and South Coast biotas.

According to Day (1974), the East Coast fauna is particularly diverse, with many tropical species, but relatively few endemic or cosmopolitan ones, and the warm temperate fauna of the South Coast contains a few tropical species but many warm-water endemics and some cosmopolitan forms. The cold temperate fauna of the West Coast contains many cold-water endemics and some cosmopolitan species.

According to Ekman (1967), a distinct drop in temperature occurs immediately north of Cape Town, so that this point constitutes the boundary between two temperate regions. Griffiths (1974), as cited by Brown and Jarman (1978), states that there is a real break in the intertidal fauna near Cape Point, but that this break is masked when records from deeper water are included. Briggs (1974) includes the east coast of southern Africa in his Western Indian Ocean Province, the south coast in his Agulhas Province, and the west coast as a separate South West Africa Province of the warm temperate region. Millard (1978), who analysed the distribution of the southern African hydroids, considers the South and West Coast sublittoral areas to represent a single temperate province.

It is thus evident that differences of opinion have been expressed regarding the biogeographical boundaries of the southern African marine provinces. It is also becoming apparent that the distribution of the organisms of the intertidal, rocky areas is somewhat different from those inhabiting deeper waters. According to Brown and Jarman (1978) "... our concepts of marine biogeographical divisions are largely dependent on the modes of life of the particular species considered and especially as far as benthic forms are concerned, on the depths from which organisms are sampled for analysis" (p. 1245).

The species of echiurans currently known from southern Africa have been reported from the eastern and southern coasts and a very small part of the west coast extending northwards from Cape Town to Langebaan Lagoon. No records are as yet available from the coast of South West Africa. Some species reported from the vicinity of Cape Town, however, reappear in the tropical Atlantic Ocean. This may be because of the strong influence of the Benguela Current which sweeps up the West Coast and facilitates northward transport of the planktonic larvae.

Of the 16 species currently known from southern Africa, 10 have been recorded from single localities and at this stage do not lend themselves to distributional analysis within the region. Of the same 16 species, 14 are known from the subtropical waters of the Natal coast (Fig. 1). This is not surprising because Natal, besides being a part of the southern African region, also forms the south-western boundary of the Indo-West-Pacific region. Of the species recorded from the Natal coast, four, *Ochetostoma erythrogrammon*, *O. capense*, *O. caudex* and *Thalassema neptuni* have extended southwards into warm temperate waters.

O. erythrogrammon has been recorded from the

Table I: Zoogeographical composition of the southern African echiurans

Species	Zoogeographical classification							
	Indo-West-Pacific			East Pacific	East Atlantic	West Atlantic	Southern	Components according to Day (1967)
	East Indian	West Indian	West Pacific					
Ochetostoma erythrogrammon	○	○	○	○	○	○		Cosmopolitan ○
O. baronii	○	○	○	○	○	○		
Thalassema neptuni		○	○		○	○		
T. philostracum			□		□	□		Atlantic □
T. diaphanes	▲		▲		▲			Circumtropical ▲
O. arkati	▲	▲			▲			
O. caudex	■	■	■					Indo-West-Pacific ■
O. formosulum	■	■	■					
O. kempi	■	■						
O. decameron		■						
O. palense		■	■					
Anelassorhynchus moebii	■	■	■					
Echiurus antarcticus		•		•			•	Southern •
O. capense		△			△			Endemic △
A. gangae		△						
A. indivisus		⊙			⊙			Foreign ⊙

East and South-West Coasts but has yet to be reported from the South Coast, whereas *O. caudex* and *T. neptuni* appear to be restricted to the eastern and southern coasts. *O. capense* is known from all three faunistic provinces of southern Africa. The Zwartkops River estuary, where this species has been recorded in large numbers, may be the centre of distribution.

The discovery of *O. baronii* from Inhaca Island and Park Rynie beach on the Natal south coast marks an extension in the known range of this species southwards from Zanzibar. It is very likely that *O. baronii* will be found to occur in all three faunistic provinces, because it is known to be a shallow-water species of widespread distribution.

O. arkati appears to be restricted to the south and south-west coasts of southern Africa.

The strong influence of the Mozambique and Agulhas Currents in the dispersion of some of the tropical and subtropical species of the East Coast into temperate waters of southern latitudes is clearly evident.

Zoogeographical components of the fauna

Because the southern African echiurans are poorly known, a better picture is obtained when the world distribution is considered. For this discussion, the faunistic components outlined by Day (1967) for the distribution of the benthic polychaetes is used. According to Day's scheme, the fauna is divided into the following components: cosmopolitan, circumtropical, Atlantic, tropical Indo-West-Pacific, endemic, southern, and foreign. The distribution of the echiurans recorded in South Africa from two or more localities is analysed on the basis of these faunistic components in Table I.

Cosmopolitan component — The cosmopolitan component includes those species found in the tropical and cold temperate zones of all the oceans. Three of the southern African species, *Ochetostoma erythrogrammon, O. baronii* and *Thalassema neptuni* are cosmopolitan in distribution, although no records are yet available from the Southern Ocean. These

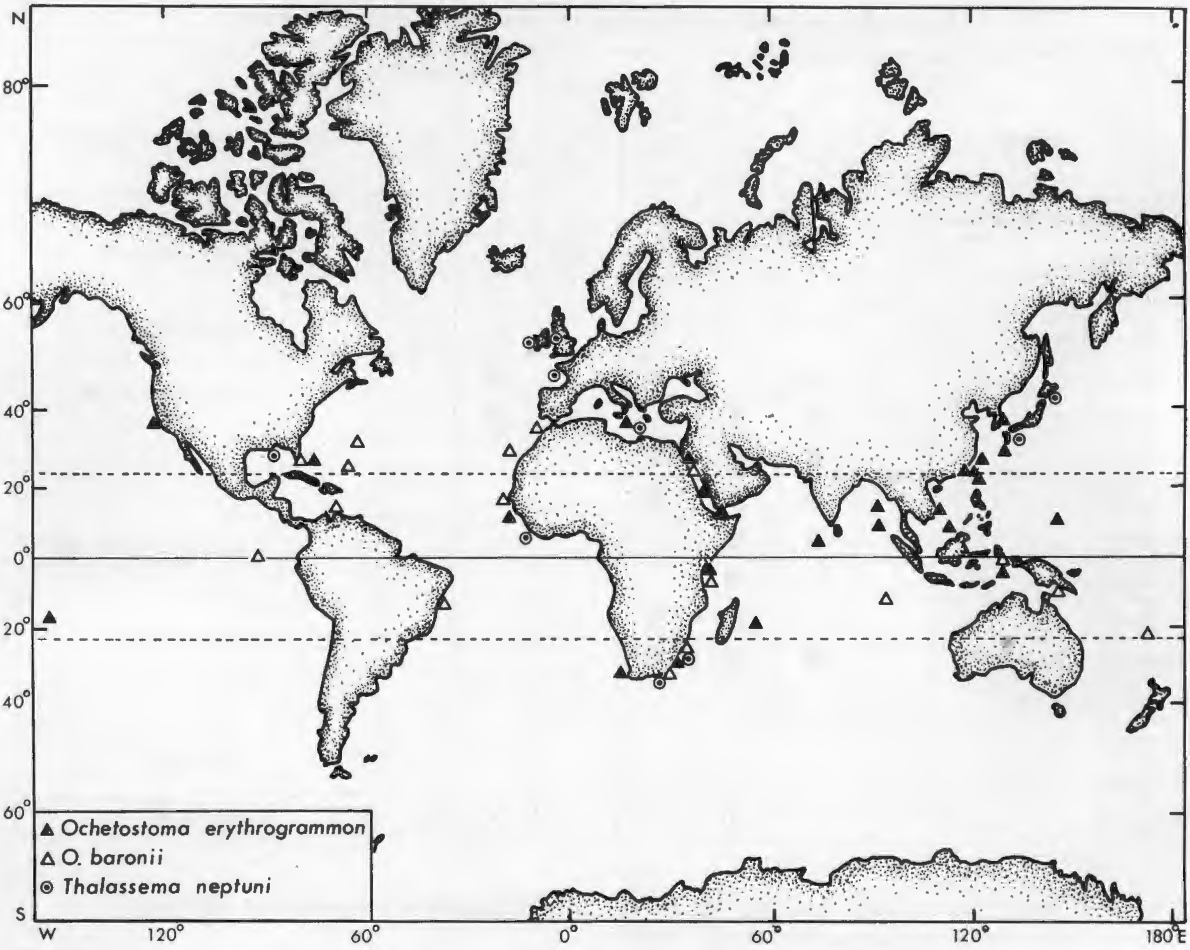

Fig. 2: Geographical distribution of cosmopolitan species of Echiura

species are found mainly between latitudes 40°N and 40°S (Fig. 2).

O. erythrogrammon has been recorded from numerous localities in the Indo-West-Pacific region, ranging from the Caroline Islands and several other localities in the western Pacific to the coast of East Africa. Along the coast of eastern Africa, it ranges southwards from the Red Sea into the subtropical waters of the Natal coast. In the South-East Atlantic, it has penetrated cold temperate waters in the vicinity of Cape Town. In the North Atlantic, *O. erythrogrammon* is known from three widely separated localities (Fig. 2), ranging from the Bahamas across the Atlantic Ocean to the West African coast and the coasts bordering the Mediterranean Sea. Studies on some of the major groups of West African invertebrates also show that an appreciable number of the species are transatlantic (Briggs 1974). The northern limit of *O. erythrogrammon* in the eastern Pacific is Monterey Bay on the coast of California.

In the Indo-West-Pacific, *O. baronii* ranges from the Loyalty Islands westwards through the East Indies to the Red Sea. It extends southwards through Zanzibar and Inhaca Islands to Park Rynie on the Natal south coast (Fig. 2). In the western Indian Ocean, *O. baronii* has been recorded from Zanzibar by Lanchester (1905). In the North Atlantic it is found on the coasts of Florida, the West Indies and Bermuda and, in the east, in the Azores and Canary Islands. In the eastern Pacific it has been recorded at the Galapagos Islands.

T. neptuni has been taken at depths of up to 138 m

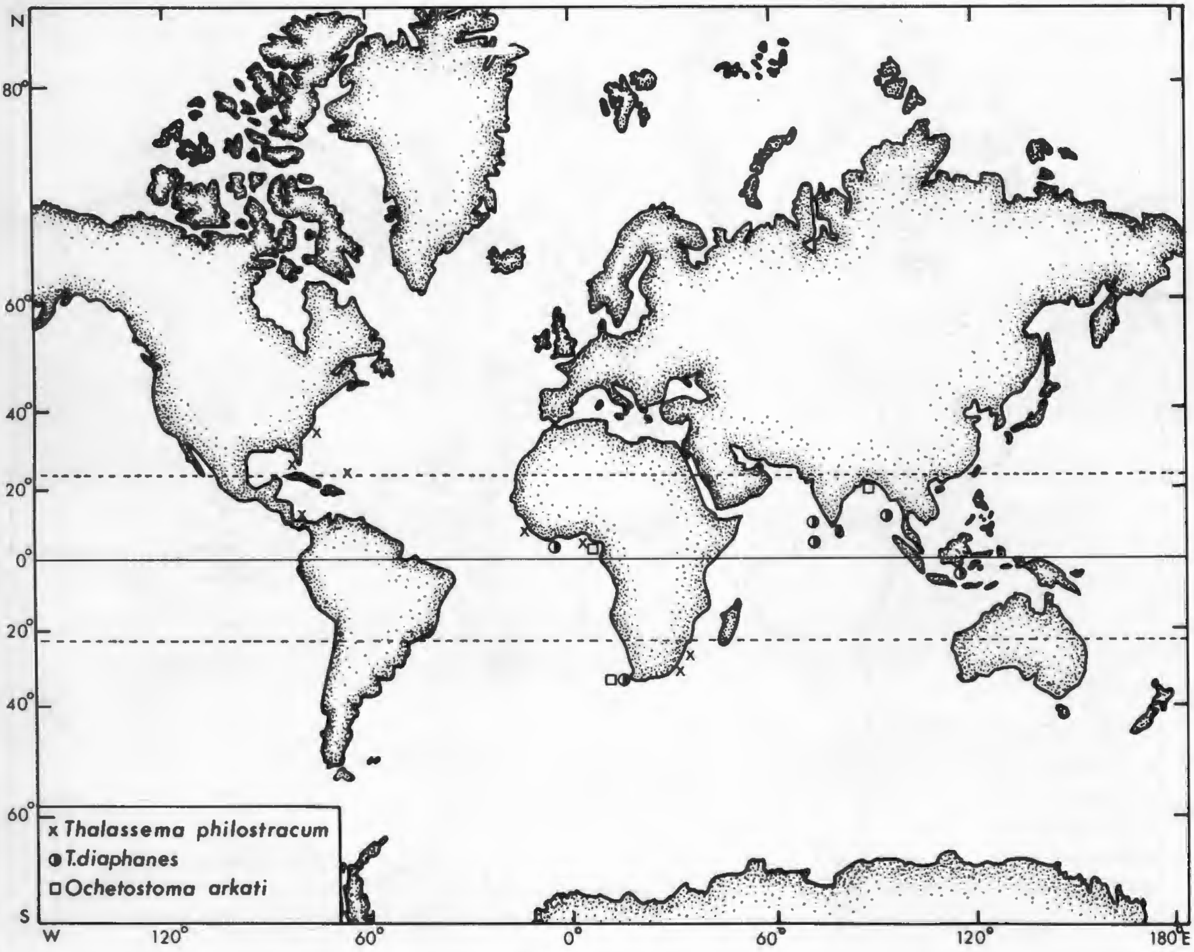

Fig. 3: Geographical distribution of circumtropical and Atlantic species of Echiura

(Stephen and Cutler 1969). The reasons for the few recorded localities for *T. neptuni* in the Indo-West-Pacific region and its apparent absence in the eastern Pacific is probably the fact that very little is known about the sublittoral and bathyal forms. In the south-western Indian Ocean, this species extends as far as Port Elizabeth, and in the North Atlantic it has penetrated cold temperate waters of the west coasts of France, Ireland and the United Kingdom (Fig. 2).

Circumtropical component — The circumtropical component includes those species distributed in tropical and subtropical waters of both the Indo-Pacific and Atlantic. Two species that may be included in this category are *Thalassema diaphanes* and *Ochetostoma arkati*. Although both species have been reported from the Indian and eastern Atlantic Oceans, no records, as yet, are available from the eastern Pacific (Fig. 3). *T. diaphanes* ranges from Indonesia through the Andaman, Maldive and Laccadive islands south-westwards into the temperate waters in the vicinity of Cape Town. It reappears on the tropical West African coast. *O. arkati*, originally recorded from the Ganges Delta, has a similar pattern of distribution (Fig. 3).

Atlantic component — The Atlantic component includes those species which are common in the tropical and temperate waters of the North Atlantic. *Thalassema philostracum* is the only species which seems to have a North Atlantic distribution, having been recorded from the coasts of Florida, the

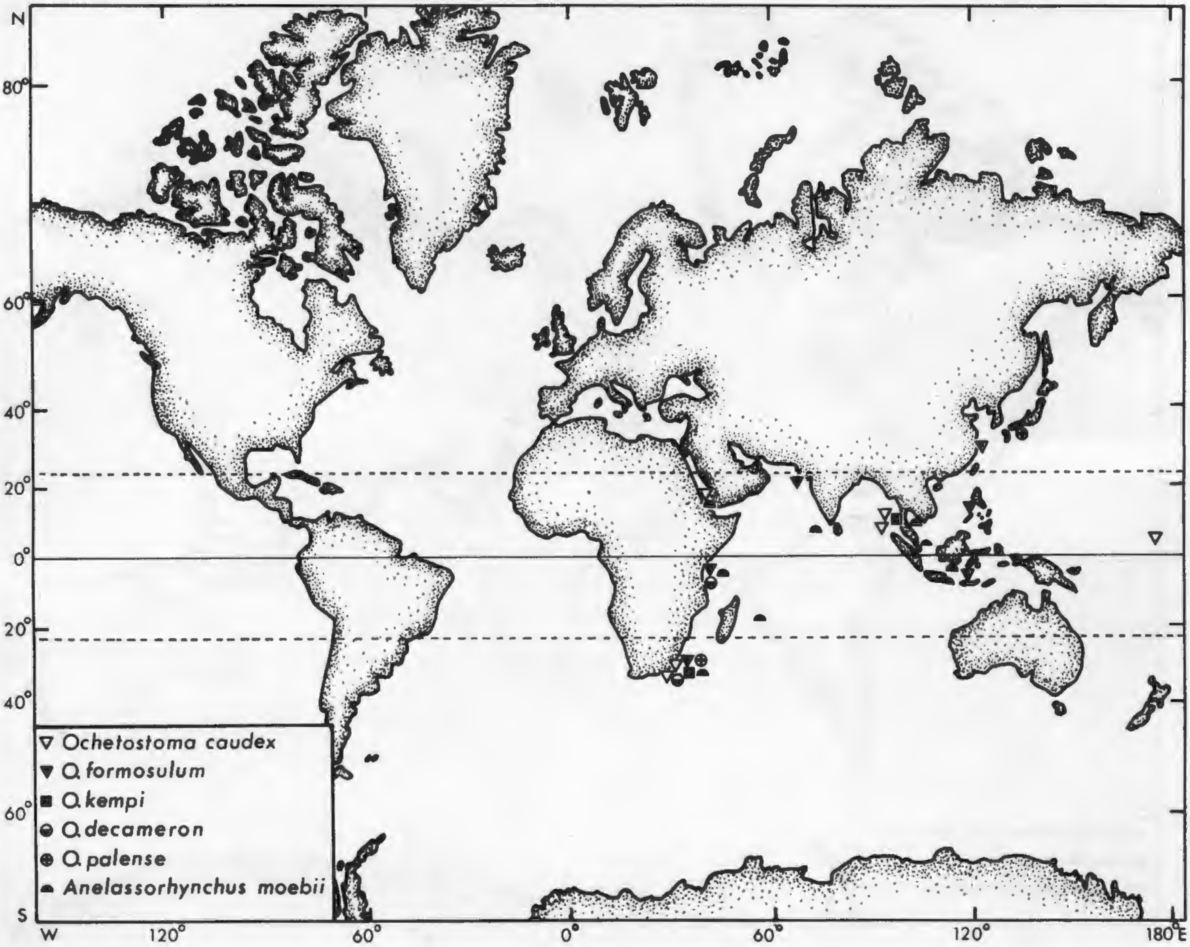

Fig. 4: Geographical distribution of Indo-West-Pacific species of Echiura

Caribbean and tropical West Africa north of the Equator (Fig. 3). However, like many Atlantic polychaetes, this species also occurs on the east coast of southern Africa, as far north as Kosi Bay on the Natal coast.

Tropical Indo-West-Pacific component — Six species, *Ochetostoma caudex*, *O. formosulum*, *O. kempi*, *O. decameron*, *O. palense* and *Anelassorhynchus moebii*, are restricted to the tropical Indian Ocean or the western Pacific, though they may also extend into warm temperate waters (Fig. 4). The western limit is the east coast of Africa and the eastern limit is Rotuma Island in the western Pacific. In southern Africa, all these species are restricted predominantly to the subtropical waters of the East Coast.

Endemic component — Those species not recorded from beyond the limits of southern Africa, here defined as south of 20°S, have been classified as endemic. *Ochetostoma capense*, known originally from the Zwartkops River estuary and later reported from Durban Bay and Langebaan Lagoon, is such a species. Since the description of this species in 1955, it has not been recorded from beyond the southern African region. Another species which may also be included in this component is *Anelassorhynchus gangae*. The endemic component of southern African Echiura is extremely small in comparison with other groups of marine organisms. Further research may well result in an increase in the number of endemics.

Southern component — This component includes

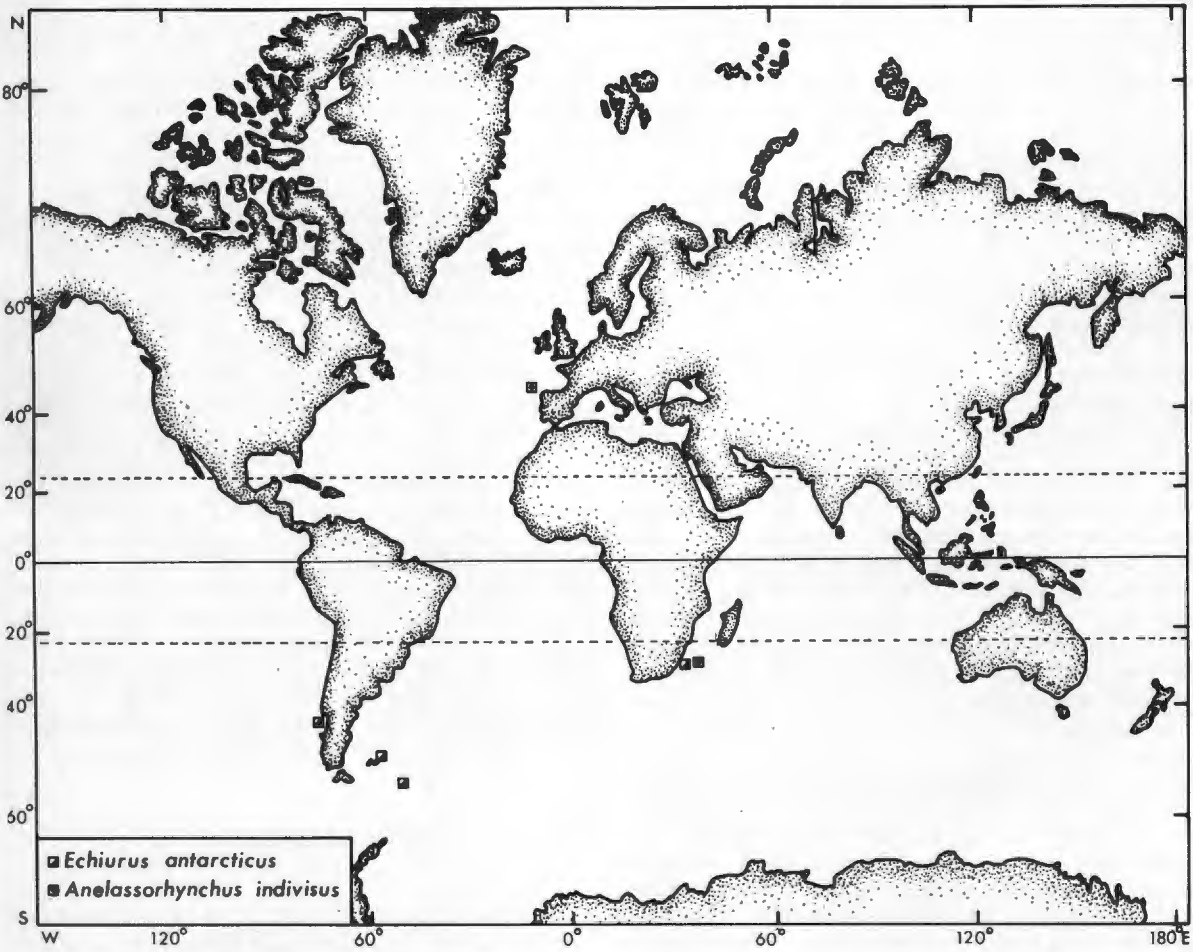

Fig. 5: Geographical distribution of *Echiurus antarcticus* and *Anelassorhynchus indivisus*

those species that are distributed in temperate or cold waters of the Southern Hemisphere only. The southern component is represented by a single species, *Echiurus antarcticus*, and its range includes South Georgia, the Falkland Islands and the coast of Chile (Fig. 5). The occurrence of *E. antarcticus* in warm subtropical waters of the Natal coast may therefore be construed as rather unusual.

Other foreign species — This group includes species for which the distribution is not sufficiently well known for them to be placed in any of the above categories. *Anelassorhynchus indivisus*, originally recorded from off the coast of Spain at a depth of 90 m, seems to be foreign to southern Africa (Fig. 5). Its distribution, however, is still imperfectly known and it may be more common on the Atlantic coast than elsewhere.

DISCUSSION

Current knowledge of the southern African echiuran fauna is rather scanty, especially concerning the West Coast. Briggs (1974) also states that the fauna of his South West Africa Province is very poorly known, compared to that of the neighbouring Agulhas Province.

There is evidently a need for a critical appraisal of the validity of several species of echiurans. It will remain difficult to draw a clear picture of geographic distribution until such time as some of the taxonomic problems have been resolved and all species precisely defined. A number of species are based on single or very few individuals, recorded from one or two localities only, and hence do not add much to a zoogeographical discussion.

Most of the species from southern Africa have been recorded from shallow waters of the intertidal zone, and virtually nothing is known about sublittoral or bathyal forms. Exploratory expeditions in the future may well advance our knowledge of an almost unknown fauna.

In southern Africa, because of the few recorded localities for each species, it is difficult to make an analysis of the distribution on the basis of faunistic provinces. Unlike the polychaetes and other benthic fauna, the present investigation seems to indicate that echiurans are not strictly confined to certain marine provinces. Several tropical and subtropical species have penetrated warm temperate and even cold temperate waters. From a study of the geographic distribution of echiurans in the world's oceans, Mathew (1976) has concluded that the adaptability of these animals to various salinities and depths is the main reason for their wide distribution.

From the present study, it appears that the east coast of southern Africa has a relatively rich fauna of echiurans, especially of the genus *Ochetostoma.* All three cosmopolitan species are known to occur along the Natal coast. The recent records of a number of species from Isipingo and Park Rynie beaches are mainly the result of more intensive investigations in these areas than elsewhere. Further investigation will, no doubt, extend the distribution of the already known Natal forms southwards into the temperate waters of the higher latitudes.

The greatest abundance of species is found in the tropical and subtropical waters of the Indo-West-Pacific region. A large number of species have been recorded from the coasts of Japan and the western Pacific, and this region may be the centre of the origin and distribution of the Echiura. It is not considered unusual for the ranges of some of these species to extend south-westwards into the subtropical and warm temperate waters of the east coast of southern Africa. Several species have been reported from the coast of Zanzibar, and further investigation may well extend their distribution further south. According to Briggs (1974), the richest and most diverse faunal area in the world is the triangle formed by the Philippines, the Malay Peninsula and New Guinea. Briggs, however, does not regard this triangle as a separate faunal area, but considers the whole of the Indo-West-Pacific region as constituting one huge province.

Echiurans always live in protected places and are well adapted for a burrowing mode of life. In southern Africa most of the species have been collected from rocky shores in the intertidal zone. In most cases, specimens were under rocks on the surface of the sand, but occasionally they were found buried in gravel to a depth of 25 cm. As detritus feeders, they usually occur in sediment rich in organic matter. In a few instances, individuals were lodged in rock crevices and could be removed only with the aid of special tools. It may well be, therefore, that their apparent scarcity in southern Africa and elsewhere is a direct result of the difficult habitat for collection.

Further, echiurans, together with sipunculans and polychaetes, enjoy an efficient stage of larval distribution. Significant contributions have been made by Scheltema (1968) and Scheltema and Hall (1965, 1975) on the distribution of sipunculan species by means of pelagosphaera larvae. The dispersal of pelagic larvae by ocean currents has also enabled echiuran species to colonize new or remote geographic regions. According to Newby (1940), changes which transform the trochophore of the echiuran *Urechis caupo* into a young worm occur some time between the 25th and 60th days. Additional information on the duration of pelagic larval life and dispersal by ocean currents will certainly advance our understanding of the distribution of species.

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DISCUSSION

From the present investigation it is evident that our current knowledge of the echiuran fauna of southern Africa is rather scanty. Although several new localities have been added and a few new species described, there is scope for further taxonomic research. The absence of any recorded localities along the coast of South West Africa is not surprising as most of the shore remains inaccessable.

As the echiurans are benthic animals occurring in cryptic habitats such as burrows within sand, under rocks and in rock crevices, they are not readily available. This probably has deterred biologists in southern Africa from undertaking systematic studies on this group. Some of these habitats do not seem to have been sufficiently explored in the past.

It is not always easy to obtain all the relevant information on echiurans as descriptions are scattered in a wide range of journals, some of which are obscure. The monograph by Stephen and Edmonds (1972) is a significant contribution on the phyla Sipuncula and Echiura as it has helped in bringing most of the literature together. The above authors have correctly pointed out that the identification of sipunculans and echiurans is not always an easy matter. As soft-bodied animals they are often much contracted and distorted unless they have been carefully narcotized and preserved. In the contracted state they are difficult to dissect and describe. It has been found that preserving fluids do not easily penetrate the body wall. Hence the alimentary canal and other internal organs are usually damaged unless specimens are injected immediately after narcotization.

Several problems have been encountered in the taxonomy of the echiurans as many species are described from single and/or incomplete specimens. Unless additional specimens are available from or near the type localities in the future, it will be difficult to have a clear picture of the range of variations within species. Furthermore, some of the species described by the earlier authors are extremely brief and lack important details which can be used to distinguish them. Sometimes it is difficult to differentiate between species of *Ochetostoma* and *Listriolobus* because some of the earlier descriptions make no mention of the nature of the oblique muscles between the longitudinal muscle bands. The disposition of this muscle layer is an important taxonomic character for distinguishing the two genera. In *Ochetostoma* this muscle is arranged in fascicles while in *Listriolobus* it forms a continuous sheet.

In view of the difficulties usually encountered in naming and describing preserved and contracted soft-bodied animals, the investigation of additional morphological characters has been advocated by some authors. It is rather unfortunate that many descriptions, especially by the earlier authors, contain very little or no information on the digestive and blood vascular systems. Both these systems display some interesting variations that are useful in distinguishing species.

Although in their descriptions authors have mentioned the number of gonoducts present, some provide no information as to whether these organs are presetal or postsetal in position. In some cases, the descriptions of the gonoducts and gonostomes are very brief with the result that it becomes difficult to have an accurate picture of their shape and structure unless they are well illustrated.

Another problem commonly encountered is that, although many authors give details regarding the size of specimens, they provide no information as to whether the animals are sexually mature or juveniles.

It is regrettable that several species of *Ochetostoma*, *Thalassema* and *Anelassorhynchus* are based on specimens in which the proboscides were missing. The validity of some of these species, based on single and incomplete specimens, is questionable. In the present study it has been found that echiurans, even those with detached proboscides, survive well under laboratory conditions if kept in sediment obtained from their original habitats. Several animals were able to regenerate their proboscides over a period of 6 to 8 months. In view of this finding, it seems advisable to maintain incomplete specimens in well aerated aquaria before describing them.

More detailed investigations of certain structures are also required. Scanning electron microscope studies of the anal vesicles and especially of the ciliated funnels of two species of *Ochetostoma* revealed certain significant differences (Biseswar, 1982). Such studies in the future might be useful in diagnosing closely related species.

A wide range of taxonomic characters has been used for the separation of species in the phylum Echiura. Some of these characters, however, appear to be highly variable. A number of important modifications occur with respect to the longitudinal and inner oblique muscles. In those genera where the longitudinal muscle layer is aggregated into bands, numerical differences in the muscle bands are used for the identification of species.

It has been found that the number of longitudinal muscle bands is not a reliable taxonomic character because of variations within a species and the considerable overlap that occurs among several closely related forms. This problem is especially noticeable in the genus Ochetostoma where several species have been erected on the basis of minor differences in the number. Hence it is not possible to determine whether some of these species are valid or whether they are conspecifics. From an examination of 32 specimens of O. caudex, the number of muscle bands was found to range from 14 to 21 (Biseswar, 1983).

The size of certain organs such as the anal vesicles seems to vary within a species and hence is not a reliable taxonomic character. Sometimes measurements of the proboscides and trunks could also be misleading as specimens are often much contracted and distorted unless they have been satisfactorily preserved.

In the family Echiuridae there is considerable intraspecific variation in the number of setae in the anterior and posterior rows and hence this feature is of no taxonomic value.

The number and the position of the gonoducts in relation to the ventral setae are very useful taxonomic characters for separating species. According to Datta Gupta (1976) and Saxena (1983), the number is fairly constant within a species although some intraspecific variations have been reported. Whether the gonoducts are presetal or postsetal in position is also an important feature. The shape and position of the gonostomes are also useful characters at both the generic and specific levels. A variety of shapes has been reported in the gonostomes. In Ochetostoma and Anelassorhynchus these structures are elongated and spirally coiled, while in Thalassema they are small and usually inconspicuous.

Several features of the proboscis have been found to be useful in distinguishing species. In the families Thalassematidae and Echiuridae the proboscis is usually a simple spatula-shaped structure with a ventral groove leading to the mouth. Deviations from this basis pattern may be useful in distinguishing some of the species. The lateral margins of the proboscis may be smooth, frilled or may possess dendritic or gill-like outgrowths. In *O. arkati*, for instance, the presence of branched gill-like processes along the edges of the posterior half of the organ (Prashad, 1935) clearly sets this species apart from the others in the genus. Another interesting feature is that the proboscis may be markedly deciduous in some, for example *O. baronii*. In *O. formosulum*, *T. diaphanes* and a few others, the lateral margins of the proboscis fuse at the base to form a tube around the mouth while in others, the lateral margins are free at the base.

Regarding the blood system, interspecific variations with respect to the intestinal sinus and neuro-intestinal vessel are usually present. An association of the neuro-intestinal vessel with the interbasal muscle is typical of a large number of species. This important feature seems to have been overlooked by many investigators. The interbasal muscle is a narrow muscular band of tissue that connects the sheaths of the two ventral setae. A common trend in the Echiuridae and Thalassematidae appears to be for this muscle to pass through a loop of the neuro-intestinal vessel. The interbasal muscle is a distinctive character in echiurans and the present study reveals no intraspecific variations. Although *O. formosulum* has been recorded and described from several localities in the Indo-West-Pacific Ocean, it is rather surprising that with the exception of Wharton (1913), none of the other authors have mentioned the presence of an interbasal muscle in this species. *T. diaphanes* is another example in which this muscle has been overlooked. It is thus apparent that several species need reexamination and redescription.

The size, shape and the specific arrangement of the papillae are also important distinguishing characters in echiurans. In some species the papillae may be irregularly distributed over the entire surface of the trunk while in others they may be aggregated into groups or aligned in transverse rows.

In view of the difficulties usually encountered in this group, the use of biochemical techniques in systematic studies could provide useful information in the future. Studies based on karyotypes may also prove to be taxonomically useful.

Cutler (1975) has emphasized the importance of including precise or adequate information about the location or the nature of the environment from which specimens are collected. He has voiced a plea for the inclusion, in systematic papers, of precise information with regard to position, depth, sediment type and temperature. This information will... "enable us to describe species on the basis of their niche as well as their morphology" (Cutler 1975, p. 31).

The geographical distribution of the southern African echiuran fauna has already been discussed and an attempt made to analyse the recorded species on the basis of faunistic provinces (Biseswar, 1985). Many genera and species of Echiura have been found in the tropical and subtropical waters of the Indo-West-Pacific region. It is not considered unusual for some of these to extend south-westwards into the subtropical waters of the Natal coast. More detailed studies of the duration of pelagic larval life and their transport by ocean currents should give us a better understanding of their patterns of distribution.

The endemic component of the echiurans from southern Africa is extremely meagre in comparison with other groups of marine organisms. There are at present, four species, O. capense, O. natalense, A. gangae and T. jenniferae that appear to lie in this category. Further research may well result in an increase in the number of endemic forms.

Many of the species recorded and described in this investigation have been obtained mainly from shallow waters of the intertidal zone. More systematic dredgings are bound to yield many more species and increase our knowledge of the horizontal and vertical distributions of the already known forms.

Phylogenetic relationships

The phyla Sipuncula and Echiura have been arbitrarily combined in the past under the phylum Gephyrea and were usually regarded as constituting a class of the Annelida. The phylum Echiura was established largely as a result of the studies of Newby (1940) on the embryology and development of Urechis caupo. According to this author the echiurans, though related to the annelids, differ considerably in their mode of development and show no trace of segmentation in the mesodermal bands. Although the Echiura is a much smaller phylum, the members comprising this group far exceed the Sipuncula in morphological diversity. Many authors, however, still find it convenient to study both the groups together because of their traditional association.

Hadźi (1976) defends the standpoint of an evolutionary line from the freely moving Annelida passing by way of the tubicolous and burrowing Annelida to the Echiura and finally to the Sipuncula. However, the definition of a primitive annelid still remains controversial and no clear picture of such an ancestral form has yet emerged. Although certain morphological and biochemical characters tend to support the origin of the echiurans and sipunculans from a common ancestral stock, the two groups appear to be too diverse to lie on a common line of descent. Two independent evolutionary lines of origin rather than a single one appears to be more convincing.

On the basis of biochemical evidence for determining phylogenetic relationships, Florkin (1976) derives both the sipunculans and echiurans from a preannelid stock and suggests that the sipunculans represent a collateral evolutionary line retaining more primitive features than the annelids. The echiurans, rather than the sipunculans, appear to be more closely related to the annelids. Besides similarities in certain morphological features, such as the ventral nerve cord and segmental organs (metanephridia), some biochemical characters also tend to support a closer kinship. Florkin (1976) has pointed out that chitin biosynthesis appears as a primitive characteristic of the animal cell and is present in the protostomes including the Echiura. The absence of chitin in the sipunculans reinforces the idea that they represent a separate group, distinct from the Echiura. Furthermore, the introvert of the Sipuncula is not homologous to the proboscis of the Echiura.

Although there seems to be general agreement among authors that lack of segmentation is a primitive character, no compelling arguments have been put forward for the derivation of echiurans from segmented ancestors. Clark (1962) put forward the view that a primitive annelid exhibited complete segmentation of the body-wall musculature, septa and internal organs. The gradual reduction or loss of septa in many groups of annelids is the reason advanced in support of this view. This reduction or loss presumably occurred, during the course of evolution, due to a change from a free-moving to a burrowing mode of life.

Mettam (1967), also, is of the view that metamerism and parapodia are primitive annelid features and that the primary function of the septum is to form a barrier to hydrostatic pressure during peristaltic locomotion. It has been shown that an undivided coelomic cavity is well suited to mostly sedentary tube dwellers. The loss of septa often provides a means of pumping water through the burrow by peristalsis. According to Trueman (1976), a continuous coelomic cavity enables the force generated by all body muscles to be applied whenever maximal locomotory forces are needed as in movement through a sandy substratum. The main disadvantage of a single coelomic compartment, on the other hand, is that muscular activity in any part of the body affects the whole fluid muscle system (Trueman, 1975). According to Mettam (1969), "a continuous coelomic cavity is an adaptive feature not necessarily a primitive one". (p. 354).

Although there is no trace of septa in echiurans, the paired gonoducts are probably the only organs that give some indication of their origin from segmented ancestors. The gonoducts occur from one to seven pairs in some species and are confined to the anterior part of the body cavity. It seems probably that during evolution, the loss of septa in these animals occurred with the concomittant reduction or loss of gonoducts in a postero-anterior direction due to a change from an actively moving to a burrowing mode of life.

The annelids and echiurans have a number of features in common and it is very likely that both groups evolved from a common ancestor. The trochophore larva is common to both groups and similarities also exist in the structure of the ventral nerve cord. Although the setae of echiurans are never segmentally arranged, the development of these structures is almost identical in both groups (Newby, 1940). The prostomium of annelids is variously modified in the different groups and this organ is homologous to the proboscis of the Echiura. In view of the similarities, then, the separation of the echiurans to an independent higher systematic category of phylum, seems to be an overvaluation. A similar view has also been expressed by Hadźi (1976) with regard to the sipunculans, which are even more distantly related to the annelids than are the echiurans. The lack of any form of segmentation of the mesodermal bands during development, however, is the main reason advanced for establishing a separate phylum for the echiurans.

It is thus evident that the phylogenetic position of the Echiura remains enigmatic. More detailed studies of the developmental stages of other species of echiurans should shed more light on their phylogeny.

PART II

FUNCTIONAL ANATOMY

Introduction

Reports on various aspects of the functional anatomy of echiurans are currently available in the literature. In spite of the recent interest on this group, a great deal of work still remains to be done. It is rather surprising that the echiurans have not been fully exploited for they survive quite well under laboratory conditions, and are generally amenable to experimental procedures.

In comparison with some other species, the sexually dimorphic form, Bonellia viridis, appears to have attracted the most attention. Significant works on this species include those of Jaccarini & Schembri (1977), who described in detail the specific role of the cilia in the capture, transfer and selection of food. The locomotory and other movements of the proboscis and trunk have also been investigated in con=siderable detail (Schembri & Jaccarini, 1977). Bosch & Michel (1979) studied the ultrastructural and histochemical characteristics of the various glands of the proboscis. From these studies, they have speculated on the physiological functions of the various types of secretions. The paper by Harris and Jaccarini (1981) is a significant contribution to an understanding of the structure and function of the anal sacs of this species. According to these authors, a unidirectional flow of the filtrate into the sacs is maintained by the ciliary activity of the funnels.

Several papers have also appeared on some other species. Bornö (1971) investigated the proteolytic enzymes of Echiurus echiurus. The carbohydrate and lipid levels in the blood of Urechis caupo were analysed by Lawrence et al (1971). Menon & Datta Gupta (1976) made a comparative study of the circulatory system and blood flow in Rubricellatus pirotansis, Listriolobus brevirostris and Ochetostoma septemyotum. The presence of DNA in the nuclei of the haemocytes in the coelomic fluid of Lissomyema exilii was demonstrated by Ditadi (1976). Ochi (1976) determined the various cytoplasmic inclusions in the erythrocytes of *Urechis unicinctus* and *Ikedosoma gogoshimense* and also reported on the characteristics of haemoglobin. Datta Gupta & Singh (1976) made a detailed histochemical study of the gonoducts and anal vesicles and provided evidence to show that in dimorphic species, the female gonoducts function in the nutrition of the modified male. On the basis of the presence of urates, they also demonstrated that the anal vesicles have an excretory function.

Current literature, however, contains very few detailed reports on locomotion, burrowing and other movements in echiurans. Investigations are of a general nature, based largely on visual observations. The hydraulic mechanism of echiurans has not been investigated with the use of electronic recording techniques. It appeared worthwhile, therefore, to undertake such a study on *Ochetostoma caudex* and compare the findings with some other animals that have unsegmented coelomic cavities.

Although the mature and nearly mature eggs of *Urechis* have been studied intensively by cytologists and biochemists, the process of gametogenesis in echiurans has not received a corresponding amount of attention. There is very little information also, on the structure and location of the gonads and on breeding behaviour and spawning. Owing to a paucity of information in these areas, it was felt necessary to investigate some aspects of reproductive biology.

BURROWING, LOCOMOTION AND OTHER MOVEMENTS OF THE ECHIURAN, *OCHETOSTOMA CAUDEX*

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Burrowing, locomotion and other movements of the echiuran, *Ochetostoma caudex*.

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(With 11 figures in the text)

ABSTRACT

Burrowing, locomotory and other movements of the echiuran, *Ochetostoma caudex*, have been examined and discussed. A continuous body cavity enables the worm to undergo peristaltic waves to pump water through the burrow without causing locomotion. The animal is capable of both forward and backward locomotion in its burrow. During forward locomotion, retrograde peristaltic waves are utilized which advance the animal in a step-wise fashion. Pressure changes within the coelom during burrowing, locomotion and during irrigation movements have been measured with the use of electronic recording techniques and the results interpreted in relation to direct visual observation. The structural and functional specializations for burrowing are discussed and compared with the activities of *Priapulus caudatus*, *Sipunculus nudus* and *Bonellia viridis*.

Contents

Results

Introduction

A great deal of work has been done on the mechanics of locomotion and burrowing into soft substrata on a wide variety of soft-bodied animals.

The use of electronic techniques for recording internal and external pressure changes, together with cine film analyses, have considerably enhanced our understanding of burrowing and other activities in a variety of marine invertebrates (Hoggarth & Trueman, 1967; Trueman 1966a, b; Seymour, 1971). According to Trueman and Ansell (1969), there are certain limitations on studies based entirely on visual observations because the animal is soon lost from view beneath the substratum. With the use of electronic recording techniques these limitations are largely avoided.

Despite the increased interest, no detailed analysis of locomotory and burrowing activities have appeared on the phylum Echiura, other than the cine film analysis of locomotory and other movements of *Bonellia viridis* by Jaccarini & Schembri (1977) and Schembri and Jaccarini (1977). The lack of knowledge on locomotion and burrowing activities on echiurans is probably because these animals are not widely available.

Ochetostoma caudex is an excellent example of a burrowing animal with a single unsegmented coelomic cavity. The animals are of comparatively large size (trunk lengths of up to 105mm) and are easy to maintain under laboratory conditions. Two other examples of animals with continuous body cavities are *Priapulus caudatus* and *Sipunculus nudus*. It has been shown that a continuous fluid-filled body cavity provides a means of pumping water through the burrow by peristalsis (Mettam, 1969). Another advantage of an unsegmented coelomic cavity is to enable the animal to produce high pressures whenever maximal locomotory forces are required as in movement through a sandy substratum (Trueman & Foster-Smith, 1976).

The hydraulic mechanism of Priapulus caudatus has received considerable interest in recent years. The original account of the mechanism of locomotion and burrowing in this animal by Hammond (1970) has been re-examined and extended by Hammond (1980) and several others (Elder & Hunter 1980; Hunter et al 1983). The only reference on the sipunculans is the detailed analysis of the mechanism of burrowing of Sipunculus nudus by Trueman & Foster-Smith (1976).

The aim of the present investigation is to analyse the mechanics of locomotion, burrowing and other activities of Ochetostoma caudex with the use of pressure recording techniques. A comparison is also made with the activities of Priapulus caudatus, Sipunculus nudus and Bonellia viridis. It is anticipated that the present study will serve as a stimulus for further research on this group of animals.

Material and methods

Specimens of Ochetostoma caudex were collected from the rocky shores of Isipingo and Park Rynie Beaches on the Natal coast. The specimens occurred in the intertidal area, close to the high water mark. In the laboratory they were kept in sediment maintained in well aerated aquaria. Observations were made on animals burrowing into the surface of sand, burrowing alongside the walls of an experimental aquarium or performing movements in shallow water on the surface of sand in an open enamel tray. All the animals used were between 7.5 and 9.3cm in the length of the trunk.

Detailed analyses of the movements of the animals were made by visual and cinematographic techniques. Body fluid pressure recordings were completed within five days of collection although animals that were kept in sediment taken from their natural habitats remained active and healthy for almost a year.

Body fluid pressure was measured by means of a Gould Statham (P23) transducer, the output being recorded on a Siemens Minograf 62 multichannel recorder. The transducer was connected by flexible nylon tubing to a hypodermic needle of 1mm bore, inserted into the body cavity in the posterior-trunk region. The hypodermic needle was curved back upon itself so as not to be forced out of the body during burrowing. There was negligible loss of body fluid when the cannula was inserted.

For histological studies, the proboscis and parts of the body wall were fixed in Bouin's fluid and embedded in paraffin wax. Transverse sections were cut at 7 µm and stained with Mallory's triple stain or haematoxylin and eosin.

Anatomy of Ochetostoma caudex

The anatomy of the animal, as well as the dimensions of the proboscis and trunk, have been given in an earlier paper (Biseswar, 1983). Ochetostoma caudex is essentially a sac-like animal with a cylindrical trunk and a spatula-shaped proboscis arising from the anterior end, dorsal to the mouth. The entire body surface is covered with papillae of varying size and shape. At the anterior and posterior ends of the trunk, the papillae are larger and more closely arranged. Numerous mucous-secreting glands, which serve a useful function in these burrowing forms, are located in the papillae.

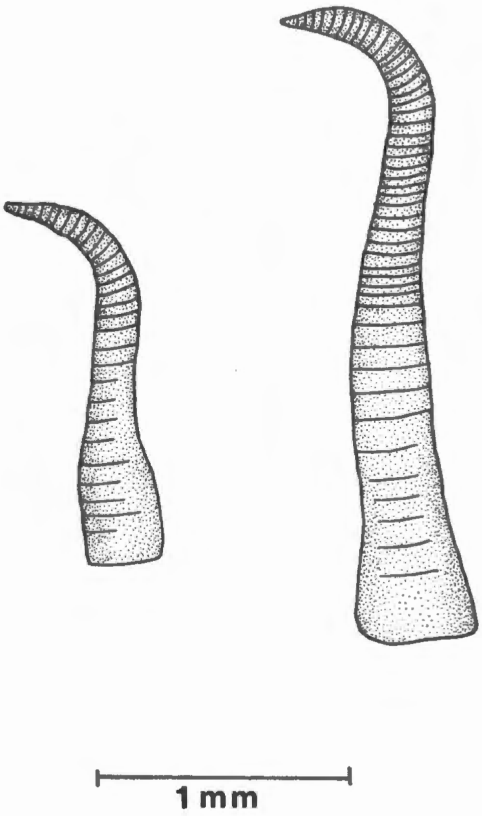

FIG. 1. The left non-functional (replacement) and the functional setae of Ochetostoma caudex (From Biseswar, 1983).

There are no internal septa dividing the coelomic cavity so that the coelom functions as a single hydraulic unit.

The proboscis is capable of considerable extension and in the live animal may equal or slightly exceed the length of the trunk. The lateral edges of this organ are curled upwards so that the ventral groove leading to the mouth is dorsal in position. In the fully extended state the leading end is somewhat expanded while the stem is tubular. In *Ochetostoma*, as in some other echiuran genera (*Echiurus*, *Listriolobus*, *Urechis*), the proboscis is a simple structure and more or less of uniform width while in *Bonellia* the terminal end is bifurcated.

At the anterior and ventral surface of the trunk, just posterior to the mouth, is a pair of setae. The setae are cylindrical, hook-like structures tapering to a sharp point (Fig. 1). The tip is curved at right angles to the main axis of the shaft and directed posteriorly. As in other species belonging to the genus *Ochetostoma*, the setae are located in special sacs supported by numerous radiating muscle strands. In some specimens replacement setae were also observed in close association with the functional ones (Fig. 1).

Histological structure of the proboscis

The proboscis consists of epidermis overlying a areolar connective tissue layer within which occur the muscles, blood vessels and nerves. External to the dorsal epidermal layer, which consists of a columnar epithelium, is a thin layer of cuticle (Fig. 2a). The cells of the ventral epithelium lining the groove and the margins are densely ciliated. Beneath

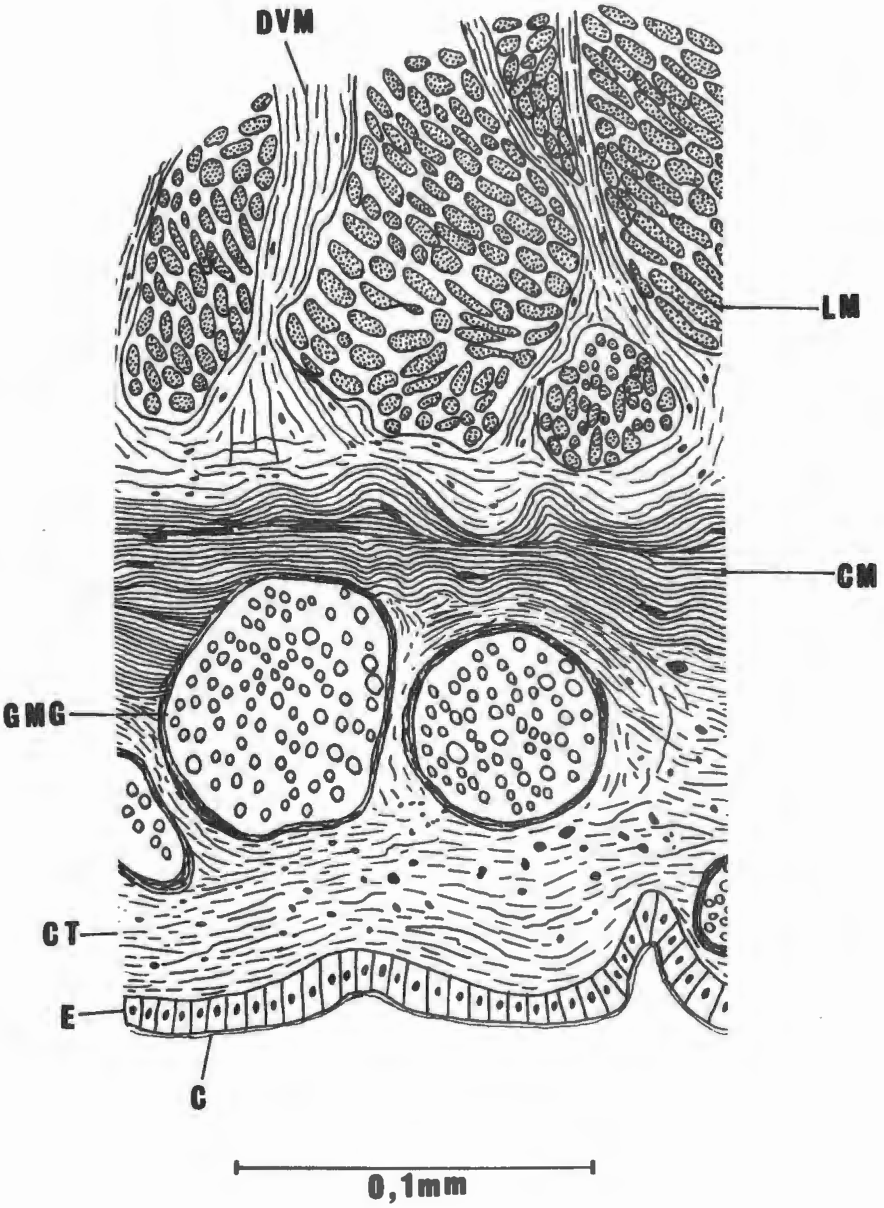

FIG. 2a. Partial transverse section of the proboscis showing the dorsal epithelial layer, granular mucous glands and the muscle layers. C, cuticle; CM, circular muscle; CT, connective tissue; DVM, dorso-ventral muscle; E, epithelium; GMG, granular mucous gland; LM, longitudinal muscle.

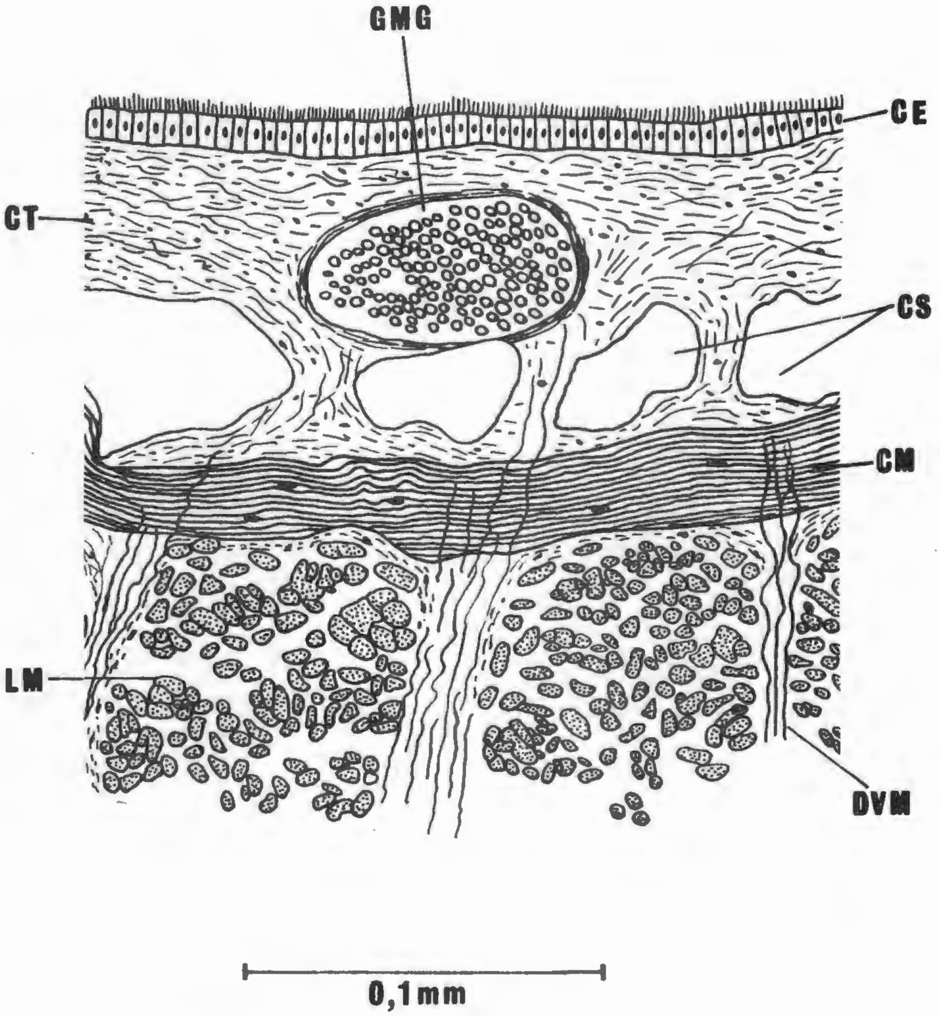

FIG. 2b. Partial transverse section of the proboscis showing the ventral ciliated epithelium, coelomic spaces and the muscle layers. CE, ciliated epithelium; CM, circular muscle; CS, coelomic spaces; CT, connective tissue; DVM, dorso-ventral muscle; GMG, granular mucous gland; LM, longitudinal muscle.

the dorsal epidermal cells are present numerous, large, granular mucous glands (Fig. 2a). Some of the glands even extend into the circular and longitudinal muscle layers. The areolar tissue serves as a packing tissue between the glands and the longitudinal muscle bundles.

There are two thin layers of circular muscles; one lies beneath the dorsal granular mucous glands while the other layer occurs on the ventral side, internal to the chain of coelomic spaces (Figs. 2a & b). The coelomic spaces are found in the connective tissue layer of the ventral side.

The bulk of the proboscis is made up of longitudinal muscle bundles which form the inner core (Figs. 2a & b). The large mucous glands are absent on the ventral surface but a second type of gland is sparsely distributed in the connective tissue. The granules of this gland stain light-green with Mallory's triple staining technique. A few of these glands also occur on the dorsal surface, either below or among the granular mucous glands.

Much finer, dorso-ventral muscle fibres run from the dorsal to the ventral surface of the proboscis. These muscles traverse the connective tissue between the longitudinal muscle bundles (Fig. 2a & b).

Histological structure of the body wall

The body wall is made up of an epidermis consisting of a single layer of cuboidal epithelial cells and three muscle layers (Fig. 3). The epidermis is lined by a thin cuticle on the outside. The subepidermal connective tissue is of variable thickness around the body. The circular muscle,

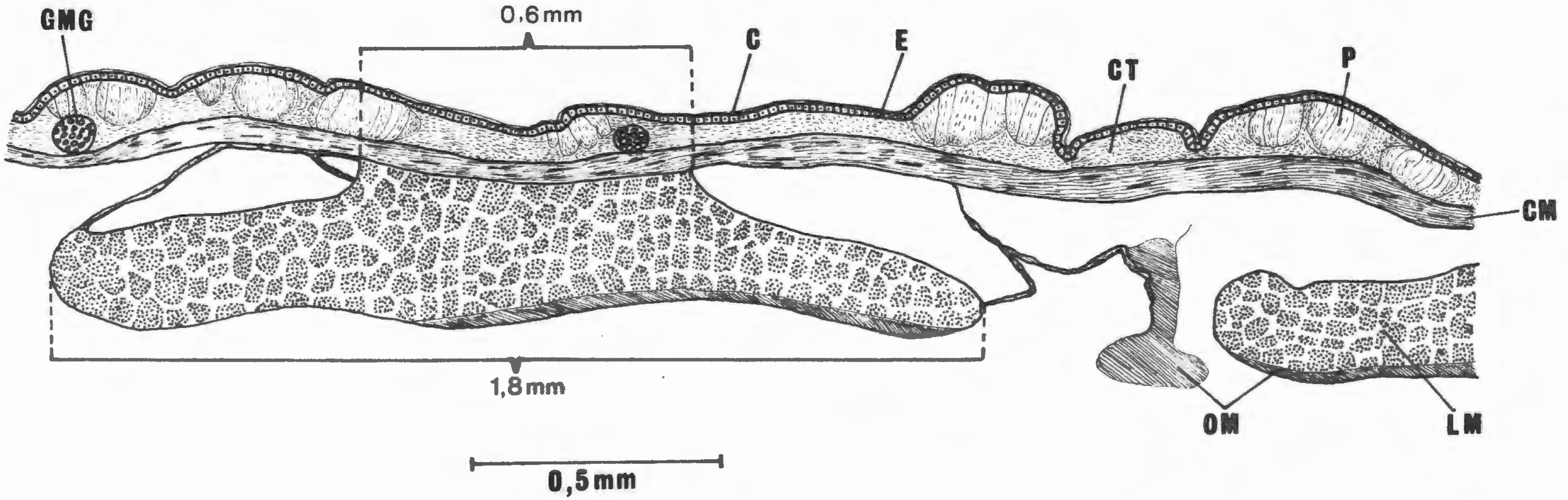

FIG. 3. Transverse section of the body wall showing the arrangement of the muscle layers. C, cuticle; CM, circular muscle; CT, connective tissue; E, epithelium; GMG, granular mucous gland; LM, longitudinal muscle; OM, oblique muscle; P, papillae.

which forms a continuous sheet around the animal, is also of varying thickness (Fig. 3). Measurements on fixed material showed that in a sexually mature animal with a trunk length of 9.3cm, the thickness of the circular muscle ranged from 10-70 µm with a mean thickness of 30 µm.

In echiurans there are two major trends in the arrangement of the longitudinal muscles. These muscles are gathered into discrete bundles of varying number in genera such as Ochetostoma and Listriolobus while in others, like Anelassorhynchus, Thalassema and Ikedosoma, they form a continuous layer. The number of longitudinal muscle bands in O. caudex usually ranges from 16-19 and occasionally from 19-22. In cross-section, the longitudinal bands are sub-triangular with the broadest part of the band lying adjacent to the inner oblique muscles (Fig. 3). The thickness of the bands ranges from 250 to 380 µm (mean 290 µm).

The oblique muscle layer in Ochetostoma is arranged in fascicles while in Anelassorhynchus, Thalassema and Listriolobus it forms a continuous sheet. The thickness of the oblique muscle bundles ranges from 50 to 80 µm (mean 65.5 µm). Hence the combined thickness of the circular and oblique muscles is much smaller than that of the longitudinal muscles.

Results

General observations

Whilst collecting specimens on the rocky shores of the Natal coast, O. caudex was seen to inhabit U-shaped burrows in which the walls were consolidated by mucus. In all cases the animals were found lying horizontally in the sand, at the bottom end of the U. They were also found to occur free under stones in shallow water and in crevices and galleries in rocks. Specimens were collected in fairly large numbers from a sheltered rock tunnel at Isipingo Beach where the sediment was slightly muddy and consisted of a mixture of coarse sand grains, shell fragments and other hard miscellaneous debris. In the laboratory the animals were kept in similar sediment taken from their natural habitats. In well aerated aquaria, they survived for almost a year. If the sediment was hard and repeated attempts at burrowing met with little success then the animals died after a few days. This problem was overcome by artificially constructing burrows for some. This was done by simply excavating longitudinal furrows and burying the animals to a depth of about 6 cm.

<u>Ochetostoma</u> is very sensitive to light and if left on the surface of sand in an aquarium will instantly engage in exploratory movements in search of suitable shelter. Burrows are usually not constructed if natural ones are readily available. The animals usually become concealed within a relatively short period when crevices and stones are present in the immediate vicinity. In the absence of suitable objects on the surface, the animals begin excavating their own burrows.

As detritus feeders, echiurans direct sand grains, coral fragments and finely divided particles into their mouths with the aid of their highly muscular, spatulate proboscis. Organic matter is extracted from the ingested material. The proboscis moves over the substratum with its morphologically ventral surface uppermost. Movement of this organ is due to muscular activity. The anterior end is used to shovel the sand which is then transported along the ventral groove, towards the mouth.

Histological evidence indicates that cilia play a significant role in the movement of fine particles that adhere to the mucous film, while larger ones are propelled by muscular action. Large sand grains, un=suitable for ingestion, are moved along the groove and rejected at the posterior end of the proboscis. This indicates that there is selection of food material.

For their respiratory needs, the animals rely on diffusion of oxygen through the entire body surface. It has been established that the respiratory pigment in the erythrocytes of all echiurans is haemoglobin. Besides oxygenation of the coelomic fluid, the blood circulating in the blood vessels is also oxygenated. Regular peristaltic contractions of the trunk cause the flow of fresh water through the burrow.

Behaviour outside the burrow

Animals removed from their burrows and left in an aquarium will undergo regular repetitive cycles of muscular activity. During sedentary periods, retrograde peristaltic waves usually pass down the body at an average rate of five per minute. Sometimes the peristaltic waves are reversed and move in the opposite direction. Occasionally, two or three contraction waves were observed to pass along the trunk at the same time. These movements correspond with the movements associated in ventilating the burrow which, in nature, is always kept open at both ends. The velocity of the peristaltic waves decreases as the waves approach the posterior end of the trunk.

During sedentary periods on the surface of sand, the proboscis usually engages in various types of exploratory movements and feeding may also occur.

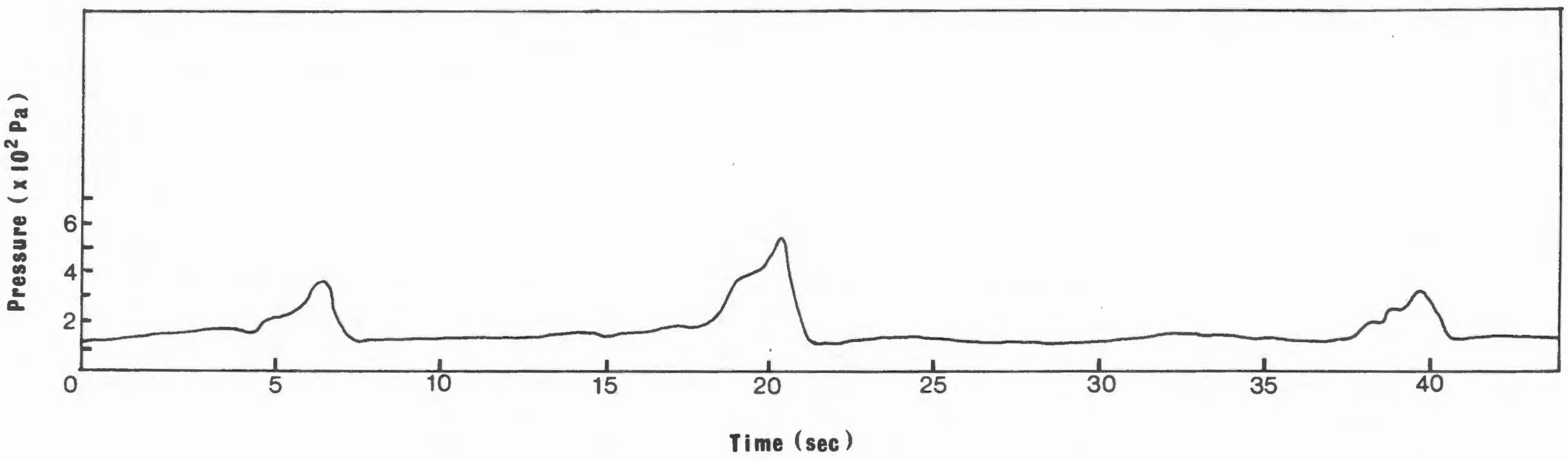

FIG. 4. Recording of coelomic pressure of a quiescent worm on the surface of sand undergoing irrigation waves.

Internal hydrostatic pressure was found to fluctuate in accordance with various states of activity. Very small fluctuations of coelomic pressure were recorded during stationary periods associated with the passage of small peristaltic waves along the trunk. During such periods of very slight activity the coelomic pressure was found to be fairly constant at 1.3×10^2 Pa. The general body turgor is maintained by this resting pressure. During periods of more vigorous irrigation, the internal hydrostatic usually lies between 1.3 and 5.3×10^2 Pa (Fig. 4) with occasional pressure peaks that exceeded this upper limit.

The animal showed violent "escape reactions" immediately after cannulation and pressure peaks of up to 4×10^3 Pa were recorded. This marked increase in coelomic pressure is due to the sudden and very forceful contraction of the longitudinal muscles. In the contracted state the animal becomes oval in shape and remains quiescent for about 5 secs after which relaxation of the longitudinal muscle occurs and the coelomic pressure drops to 1.3×10^2 Pa.

Locomotion

Locomotory waves of muscular contraction in soft-bodied, worm-like animals may travel in the same direction as the movement of the animal (direct wave, synkinetic locomotion) or in the opposite direction (retrograde wave, antikinetic locomotion (Trueman, 1975). The latter author defines these terms in relation to the direction of movement of the animal. According to Mettam (1969), whether locomotion is synkinetic or antikinetic depends on the tonic state of the longitudinal muscle that is in firm contact with the substratum.

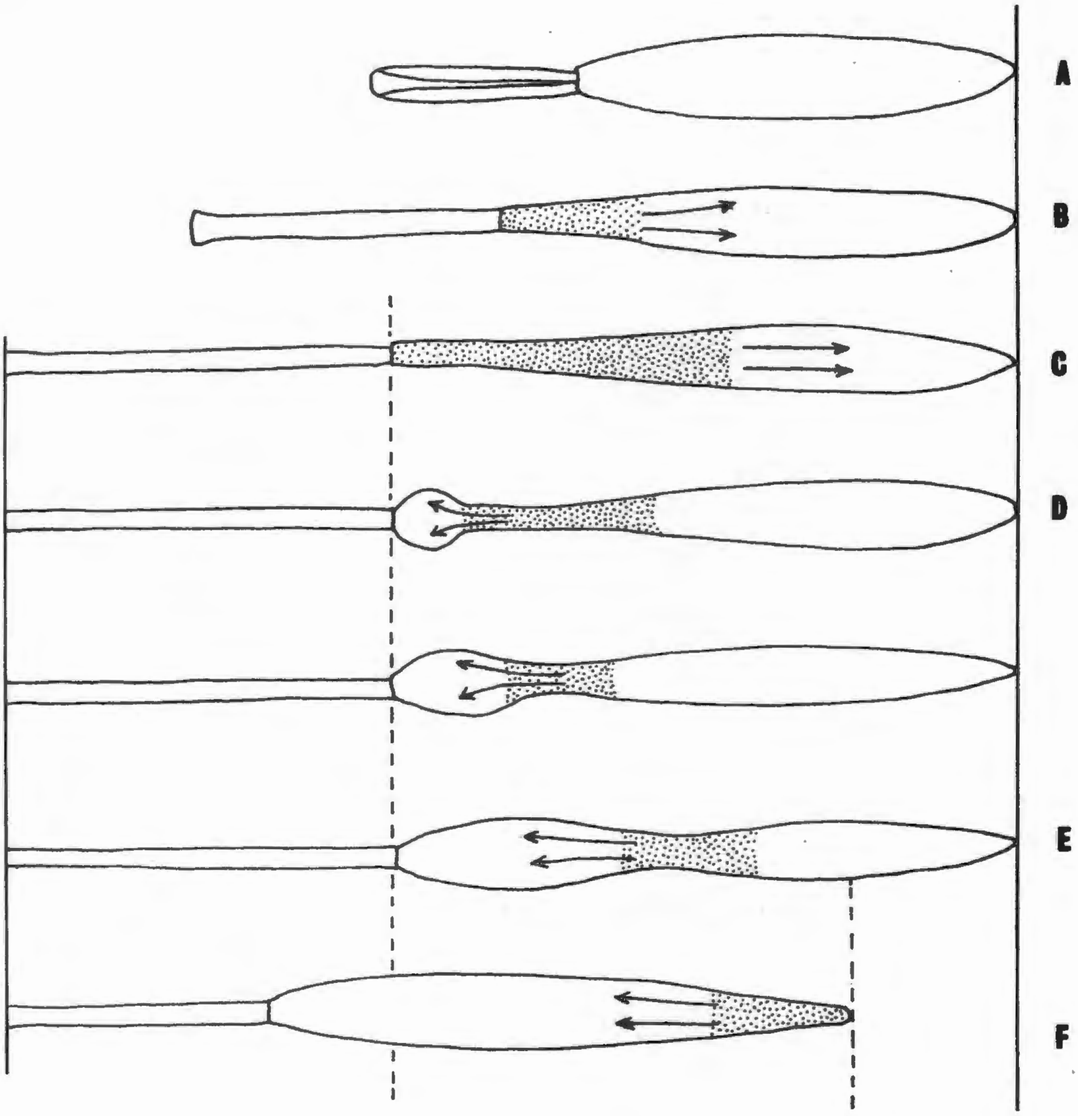

FIG. 5. Schematic representation of the relationship between muscular activity and change of body shape during antikinetic forward locomotion on the surface of sand. The arrows indicate the direction of movement of the coelomic fluid and viscera.

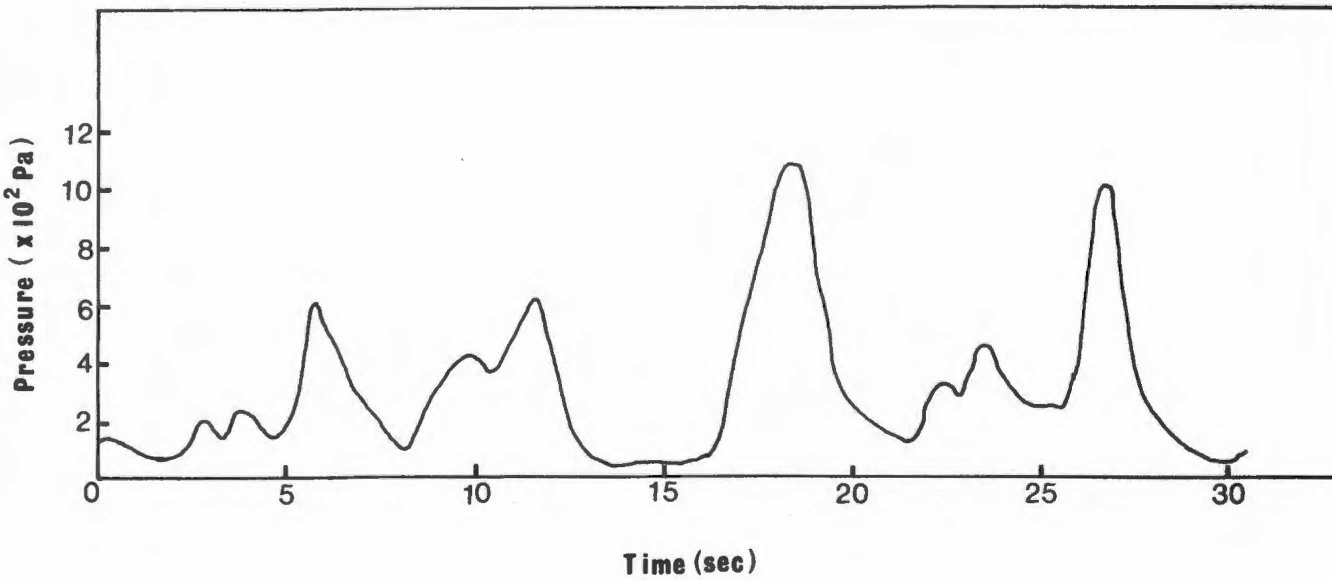

FIG. 6. Recording of the fluctuations of coelomic pressure in Ochetostoma caudex during rapid forward locomotion.

Ochetostoma caudex is capable of both forward and backward locomotion in its burrow. The power for locomotion is provided by the contraction of the longitudinal, circular and oblique muscles acting against a hydrostatic skeleton. The paired ventral setae play no role during locomotion as the animals move and feed with their morphologically ventral surface uppermost. Ochetostoma is also capable of moving quite efficiently on a smooth glass surface or when the proboscis is detached from the trunk.

Antikinetic forward locomotion

The sequence of events that occur during locomotion conforms to the basic mechanism of alternate formation of penetration and terminal anchors common to most soft-bodied animals (Trueman, 1968). The changes in the shape of the proboscis and trunk are illustrated in Fig. 5.

Forward locomotion on the surface of the substrate takes place by the passage of retrograde peristaltic waves that cause thinning and anterior extension of the animal followed by the contraction of the longitudinal muscle which pulls the posterior part of the body forwards. Be repeating this sequence of events, locomotion takes place in a series of steps. During rapid locomotion, vigorous fluctuations of coelomic pressure occur and the animal's internal hydrostatic pressure lies between 0.5 to 10.9 x 10^2 Pa (Fig. 6).

It was convenient to correlate the precise characteristics of the pressure changes with the changes in body shape during slow forward locomotion rather than during faster movements. For this reason, the lettering of the phases in Figs. 5 and 7 is the same. It is also convenient to take as a

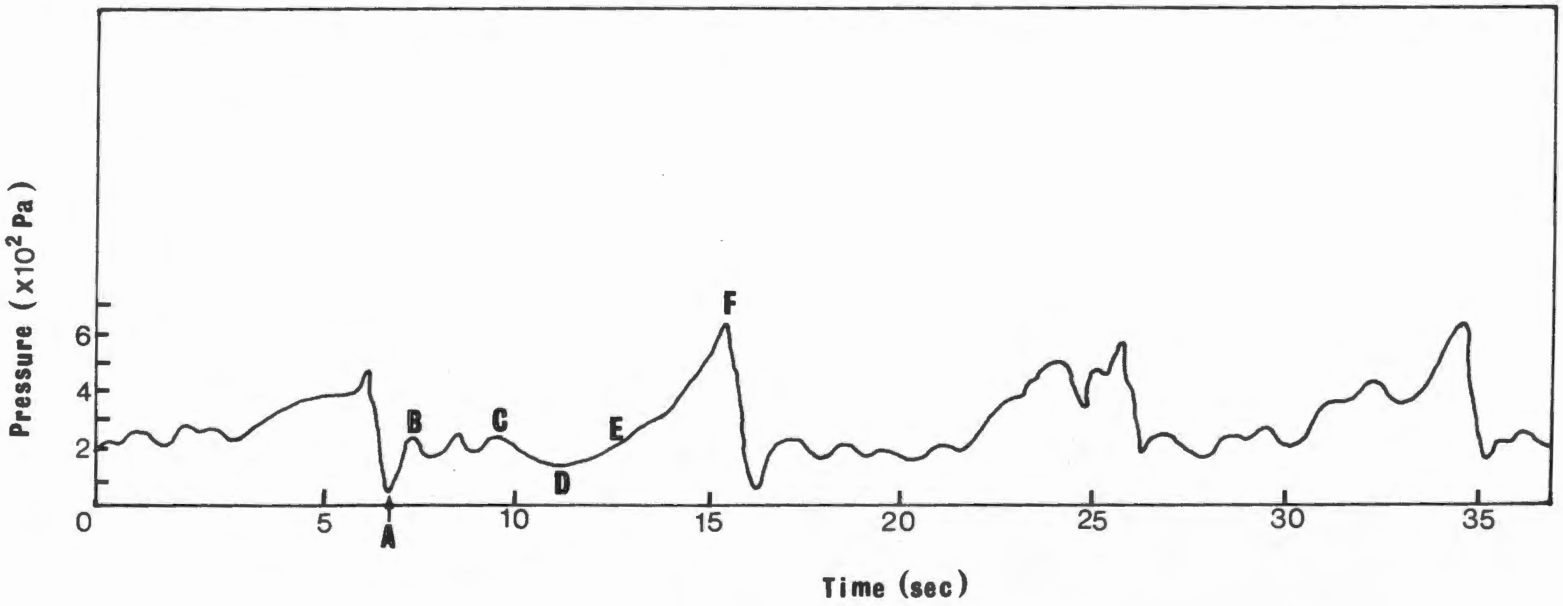

FIG. 7. Recording of the fluctuations of coelomic pressure during slow forward locomotion on the surface of sand. Approximate duration of each cycle 10 sec.

starting point when the animal is inactive with the proboscis and trunk muscles relaxed (A, Fig. 5). In Ochetostoma the resting pressure is in the region of 1.3×10^2 Pa. Forward locomotion is usually preceded by the thinning and anterior extension of the proboscis brought about by the contraction of the circular muscle. Contraction of this muscle layer takes place almost simultaneously throughout the entire length of the proboscis as there is no evidence of the propagation of peristaltic waves. Elongation of the proboscis is followed by waves of circular muscle con= traction that pass backwards along the trunk (B-C, Fig. 5). The internal hydrostatic pressure rises at the onset of the contraction waves (A-B, Fig. 7) and may reach peaks of up to 4.0×10^2 Pa. The marked decrease in the diameter of the trunk indicates that circular muscle contraction is aided by the simultaneous contraction of the oblique muscles.

During forward extension, the accumulation of coelomic fluid in the posterior distended region of the trunk anchors the animal. Vigorous movement of the coelomic fluid also pushes the viscera in a posterior direction. The distension of the posterior part of the trunk is caused by the partial contraction of the longitudinal muscle.

Once maximum forward extension has taken place, contraction of the longitudinal muscle at the extreme anterior end of the trunk occurs. This results in the formation of a dilation which becomes progressively larger (D-E, Fig. 5). The appearance of the anterior dilation is usually accompanied by a slight drop in coelomic pressure (D, Fig. 7).

The coelomic fluid now moves forward and begins to accumulate in the anterior distended region of the trunk which serves as the anterior anchor (D-E, Fig. 5). The forward displacement of the viscera and the weight of the proboscis must also help in anchorage. This is followed by forceful contraction of the longitudinal muscle which shortens the animal and pulls the posterior part of the body forwards (E-F, Fig. 5). Maximum pressure peaks of up to 10.9×10^2 Pa were recorded as a result of longitudinal muscle contraction during rapid locomotion (Fig. 6). The maximum pressure corresponding to longitudinal muscle contraction during slower movements, however, was about 6×10^2 Pa (F, Fig. 7). A marked drop in coelomic pressure, after the contraction of the longitudinal muscle, coincides with short periods in the cycle during which the circular and longitudinal muscles are completely relaxed. This sudden drop in coelomic pressure, as indicated by the troughs following the high pressure peaks, may be as low as 0.5×10^2 Pa (Fig. 7). After the posterior part of the body is pulled forwards, thinning and anterior extension occur again and the whole cycle of activities is repeated. During slow forward locomotion, each cycle lasts for about 10 seconds (Fig. 7).

Antikinetic backward locomotion

Ochetostoma caudex, like *Bonellia viridis* (Schembri & Jaccarini, 1977), is also capable of antikinetic backward locomotion with the contraction waves beginning at the posterior end of the trunk and passing forwards. Fluctuations of internal hydrostatic pressure were similar to those recorded during antikinetic forward locomotion. The changes in body shape during antikinetic backward locomotion are illustrated in Fig. 8. Circular muscle contraction waves cause thinning and elongation of the posterior end of the trunk while the animal remains anchored anteriorly. After the posterior end has been extended maximally, a dilation appears at the posterior end of the trunk which becomes progressively larger. At this stage, the posterior end of the trunk is pulled slightly forwards. The accumulation of coelomic fluid in the dilated region forms an anchor.

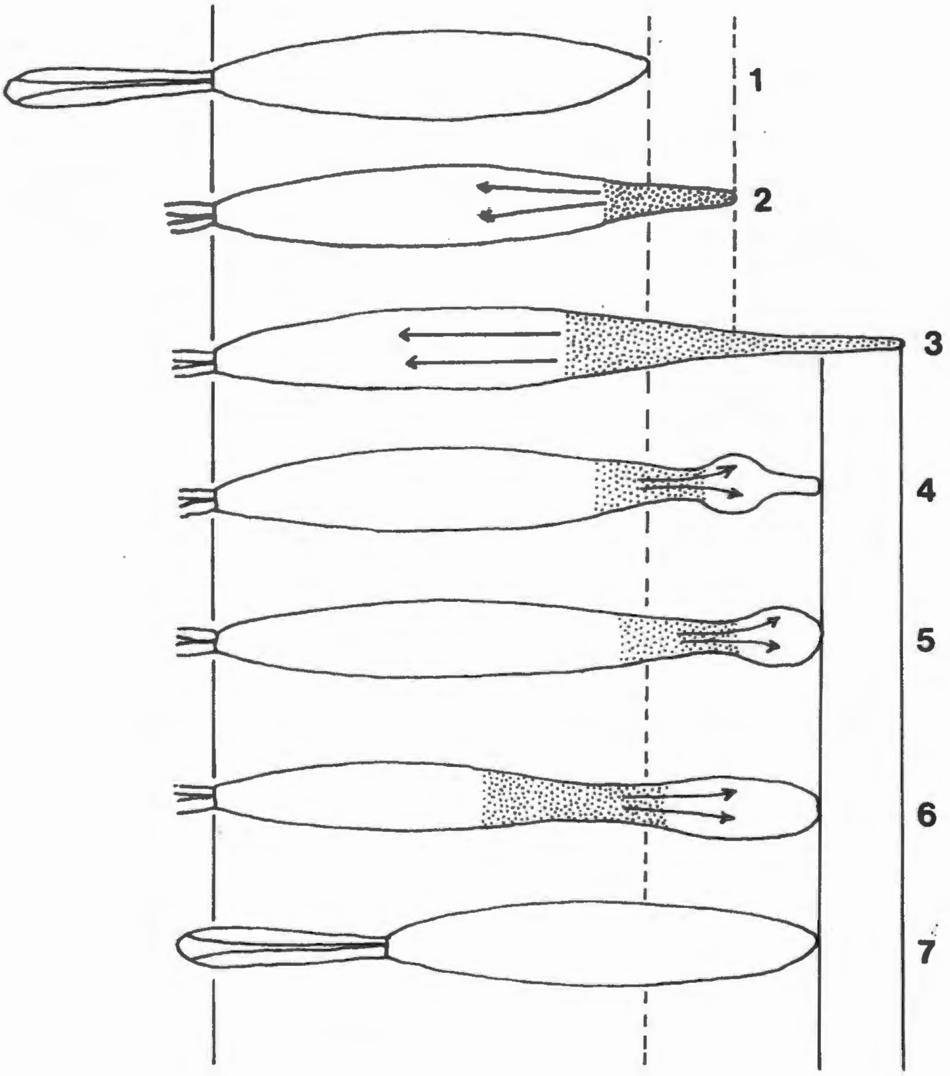

FIG. 8. Schematic representation of the relationship between muscular activity and change of body shape during antikinetic backward locomotion on the surface of sand. The arrows indicate the direction of movement of the coelomic fluid and viscera.

This is followed by the contraction of the longitudinal muscle which pulls the anterior part of the animal backwards (Fig. 8). By repeating this sequence of activities, the animal moves in a step-like manner. Movement in the reverse direction is just as rapid as in forward locomotion.

The animals were observed to undergo both forward and backward locomotion in their natural burrows. This may be useful during feeding on suspended particulate matter in different parts of the burrow with the aid of mucus and ciliary action.

Synkinetic backward locomotion

In addition to forward and backward antikinetic locomotion, synkinetic backward locomotion was also observed in _O. caudex_. In this method of locomotion very slight posterior elongation of the animal occurs. Antero-posterior contraction waves passing along the trunk in rapid succession allow gradual displacement of the posterior region. The dilated region of the trunk between two contraction waves makes new contacts with the substratum as it passes backwards, causing posterior slippage of the animal. The papillae on the longitudinal muscle bands appear as raised ridges and offer additional resistance against the substratum.

Burrowing behaviour

Ochetostoma has developed a mechanism suitable for the penetration of the sand in which it lives. The spacious body cavity and the development of a strong muscular proboscis are undoubtedly associated with a burrowing mode of life. The pressure exerted by the coelom is equal at all points so that the coelom acts as a single hydrodynamic unit.

The mechanism of burrowing is essentially similar to that employed by other soft-bodied animals and takes place in a series of steps or digging cycles. When the anterior end of the trunk is drawn into the burrow, the digging cycles become more regular and are repeated a number of times during the digging period. As defined by Trueman (1975), the term 'digging period' is applied to the duration of burrowing activity from the time of commencement of burrowing until a stable position is attained in the substratum. In Ochetostoma, the digging period was taken to end at the stage when the posterior tip of the trunk was just hidden inside the burrow. The animals, however, did not stop burrowing at this stage but commenced excavating the horizontal tunnel.

In Ochetostoma, the burrowing period varies greatly in duration and is dependent on the physical properties of the sediment. In sediment taken from their natural habitats, the burrowing time was found to range from 20-30 minutes. In loose sand the animals were usually concealed by excavating shallow furrows on the surface. This was achieved by thrusting aside the sand with the aid of the proboscis. By secreting large quantities of mucus, the proboscis and trunk were enveloped by fine sand particles adhering to the mucous film. The animals were completely concealed in this way in oblique furrows in about 10 to 15 minutes. After this, the probing of the sand by the proboscis for the construction of the vertical limb of the burrow commenced.

In Ochetostoma, the digging period may be conveniently divided into separate phases.

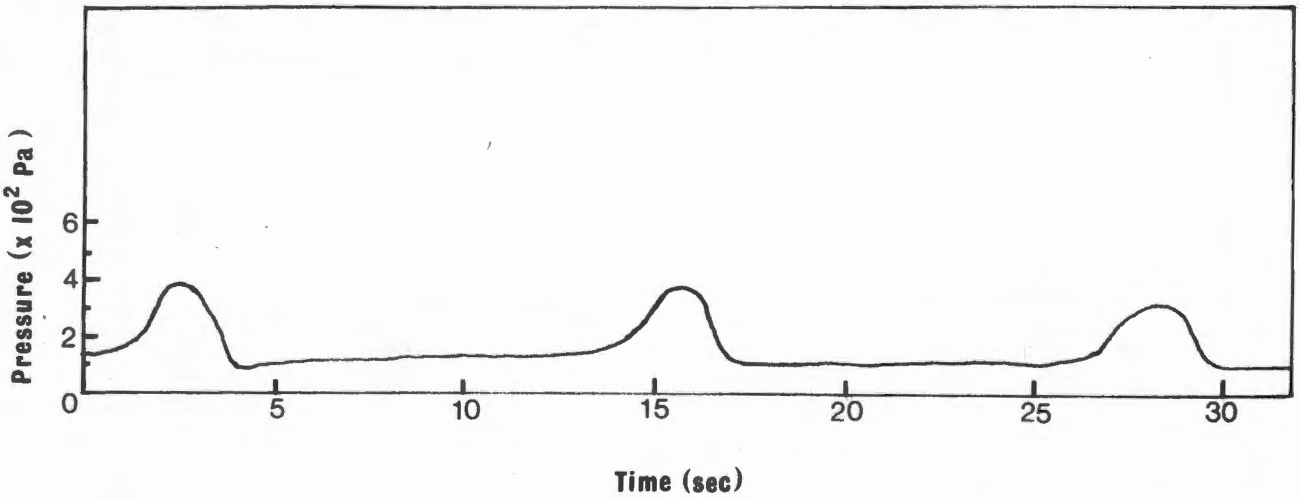

FIG. 9. Recording of coelomic pressure of Ochetostoma caudex during initial penetration of the substrate by the action of the proboscis.

Initial penetration by action of proboscis

The movements of the proboscis are dependent on its own circular and longitudinal muscles. Turgidity of this organ is due to the muscles acting against the internal fluid present in the coelomic spaces.

The first part of the burrow is constructed vertically downwards. The animal lies on the surface of the sand either on its side or with its morphological ventral surface facing upwards. During this first part of the digging period, the terminal end of the proboscis is curved downwards to probe the sediment. Initial penetration is achieved by repeated protrusion and retraction of the proboscis. The force applied to the substrate is small at this stage because the penetration anchor is due to the weight of the body on the sand. According to Trueman (1975), the stronger the penetration anchor the greater the force against the substrate. Pressure fluctuations in the coelom are of low amplitude at this stage and lie between 1 to 4×10^2 Pa (Fig. 9). The peristaltic waves on the trunk are similar to those observed during irrigation of the burrow.

The sand grains loosened from the burrow are transported backwards along the ventral groove of the proboscis and discarded posteriorly. Transport of the particles along the ventral groove is achieved by muscular contractions as well as by ciliary action and mucus. The extension and retraction movements of the proboscis continue until the entire organ is hidden inside the burrow. During withdrawal, the proboscis also drags back some of the sand. Copious amounts of mucus secreted by the proboscis during this stage protect it from mechanical abrasion. The mucus also serves a useful purpose by removing loose sand grains from the burrow. During withdrawal, sand particles adhering to the mucus, especially in the ventral groove, are deposited on the surface.

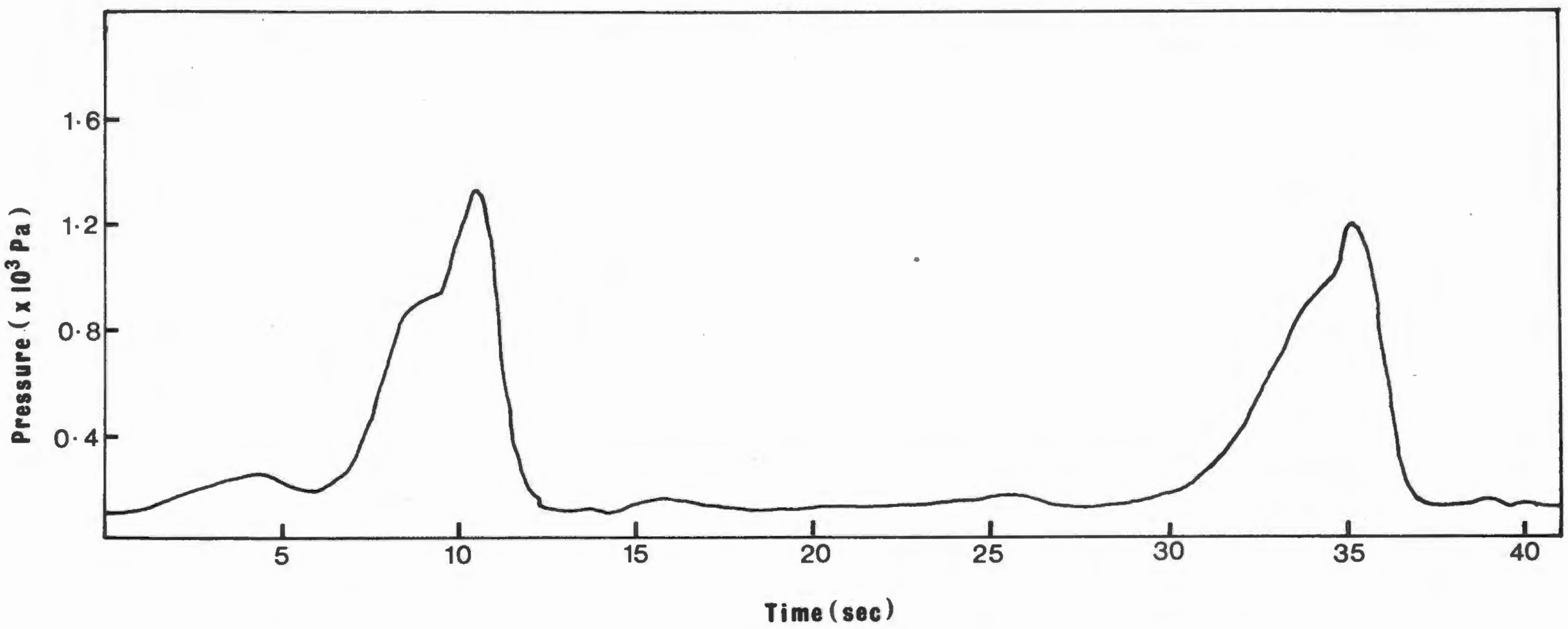

FIG. 10. Recording of coelomic pressure of *Ochetostoma caudex* burrowing actively in sand. During this phase of the digging period the anterior third of the trunk was hidden inside the burrow. The observations in Figs 10 and 11 were made with the worm adjacent to the glass wall of an experimental aquarium.

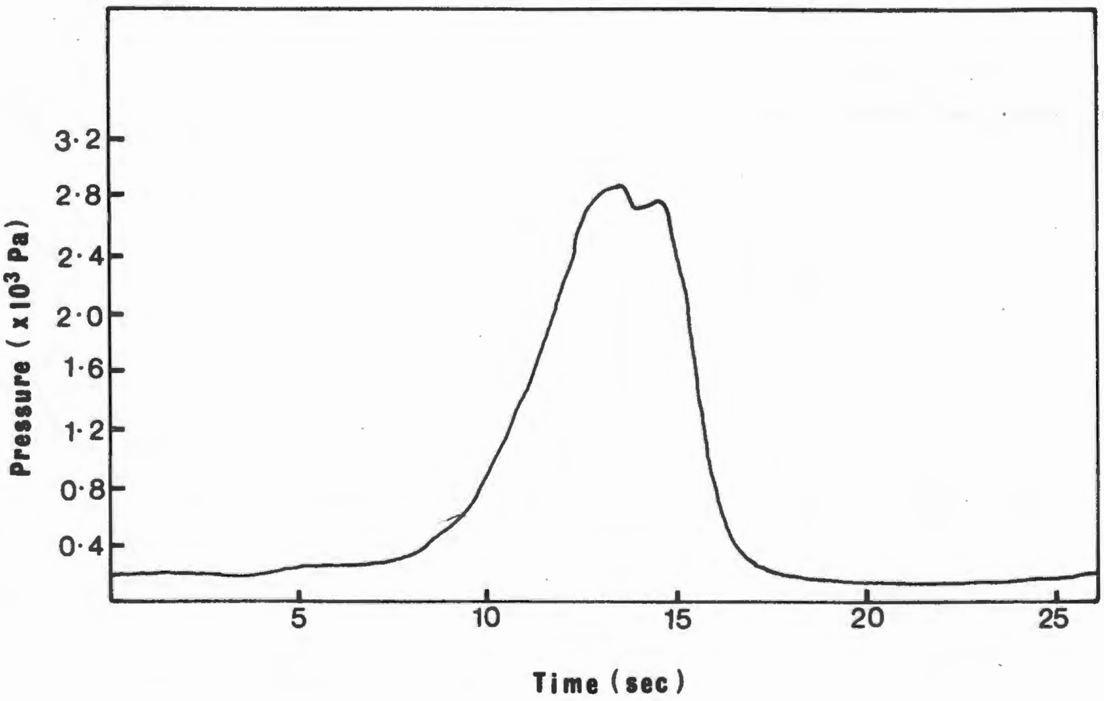

FIG. 11. Recording of coelomic pressure of Ochetostoma caudex burrowing in the vertical position. During this stage; the anterior two-thirds of the trunk was hidden inside the burrow.

Formation of terminal and penetration anchors

During the initial stage of burrowing with the aid of the proboscis, the worm progresses by relatively weak pushing or probing movements and penetration into the substrate is rather slow. When the anterior end of the trunk is drawn into the burrow, the second phase of the digging period begins and movement into the sand becomes fairly rapid. During this stage of the digging period, the posterior dilated region of the trunk on the surface of the sand serves as the penetration anchor while the proboscis is extended to displace more sand.

The events associated with each digging cycle were most clearly observed when the animals were allowed to burrow alongside the wall of a glass aquarium. In this way it was possible to correlate burrowing activity with changes in internal hydrostatic pressure. Each digging cycle commences with forward extension of the proboscis and the anterior end of the trunk followed by forceful contraction of the longitudinal muscle so as to draw more of the body into the burrow. These digging cycles are repeated several times during the burrowing period. After forward extension, the anterior end of the trunk inside the burrow is dilated by the contraction of the longitudinal muscle to form the terminal anchor. The dilated body wall is pressed outwards so as to obtain sufficient grip. The ventral setae, located at the anterior end, must also help in anchorage.

Pressure peaks of 1.3×10^3 Pa were recorded when sufficient anchorage was obtained after the anterior end of the trunk was pulled into the burrow (Fig. 10). These pressure peaks are associated with the contraction of the longitudinal muscle in order to pull the posterior part of the body forwards. As depth of burial increases the internal hydrostatic pressure may reach peaks of up to 3.0×10^3 Pa (Fig. 11). Minor pressure peaks sometimes observed at the peak of the pressure pulse (Fig. 11) indicates that shortening of the trunk as a result of longitudinal muscle con= traction does not occur in one continuous movement.

Both direct and retrograde waves were observed during this stage of the burrowing period. A backward wave in Ochetostoma results in thinning and elongation of the anterior end with consequent extension into the sand while postero-anterior peristaltic waves help to enlarge and consolidate the burrow.

Excavation of the burrow is also aided by the backwardly directed, hook-like setae which scrape the walls and drag back loose sand grains.

When the anterior half or more of the trunk is pulled into the burrow, the posterior part of the body is lifted off the ground and the animal continues burrowing while in the erect position. The contraction waves are easily observed in the posterior part of the trunk still protruding from the sand. At this stage of the burrowing period, the penetration anchor is formed by the dilation of the trunk outside the burrow. While the distended body wall grips the burrow, the anterior end thins and elongates to penetrate further.

During the initial stages of penetration into the substratum, the digging cycles follow each other in fairly rapid succession at intervals of 15 to 20 seconds (Fig. 10). Burrowing activity, however, gradually slows down during later stages as deeper and harder sediment is encountered. Continuous recording of coelomic pressure showed short periods of vigorous burrowing activity followed by long periods where little or no activity was observed. Fluctuations of pressure of low amplitude at this stage are associated with the passage of small peristaltic waves down the body similar to those observed during irrigation of the burrow. A marked slowing down of burrowing activity may also be due to fatigue.

After burial is complete and the posterior tip of the trunk is pulled in, the animal commences excavating the horizontal section of the burrow. Entry is gained by thrusting aside the sand with the aid of the proboscis. The sediment is merely compacted and no more sand is removed from the burrow. This probably explains their preference for particular substrata. During this phase of the burrowing period there is a drop in coelomic pressure.

Dilation and consolidation of the burrow

A natural Ochetostoma burrow does not collapse when the animal is removed after having penetrated several centimetres below the surface of the sand. This shows the extent to which the walls are consolidated during the burrowing process. Animals withdrawn after burrowing are covered in mucus and adhering sand particles. This mucus is obviously important in compacting the walls and thus keeping the burrow open for the constant passage of irrigation currents of water. The anterior dilation anchor, in addition to serving as an anchor against which more posterior parts of the trunk may be pulled into the sand, also exerts pressure laterally and helps to compact the sides of the burrow. The powerful shortening of the trunk resulting from the contraction of the longitudinal muscle also helps to dilate and strengthen the walls. Another advantage of a single large coelom is that it allows for considerable dilation of the trunk.

In some cases, animals were observed to rotate or twist in their burrows in order to consolidate the walls. This usually occurred when the anterior half of the trunk was drawn into the burrow and the animals were in the erect position.

Discussion

Many accounts of burrowing, locomotion and other activities in echiurans by the earlier authors are of a very general nature, based largely on visual observations. The most recent detailed investigations, of locomotory and other movements of the proboscis and trunk of Bonellia viridis, based on cine film analyses, are those of Jaccarini & Schembri (1977) and Schembri & Jaccarini (1977).

Fisher and MacGinitie (1928) studied the locomotory, burrowing and irrigatory movements of the echiuran, Urechis caupo. The latter animal inhabits U-shaped burrows in the mud of shallow estuaries (Hall, 1931). There are distinct similarities between O. caudex and Urechis caupo in the mechanisms of locomotion and burrowing. Both animals are capable of undergoing forward and backward locomotion in their burrows. According to Fisher & MacGinitie (1928), respiratory movements in U. caupo take place by antero-posterior peristaltic contractions of the trunk as well as by periodic inhalations and exhalations of water through the anus. In O. caudex, however, there is no evidence of anal respiration.

Lawry (1966a, b) investigated the anatomy of the neuromuscular system of Urechis caupo and analysed the neuromuscular mechanisms of burrow irrigation. As in O. caudex, the velocity of the peristaltic waves decreases as the waves approach the posterior end of the trunk. According to this author, Urechis is continuously active and undergoes about 1280 peristaltic waves in 24 hours with the removal of 29 litres of water. From his neurophysiological investigations he established a hierarchy of pacemaker regions in the nerve cord. Lawry (1966b) discovered that this hierarchy was normally dominated by the pacemaker in the proboscis. These pacemakers were reported to respond with increased frequency to oxygen, epinephrine and acetylcholine.

Gislén (1940) gave an account of the creeping, burrowing, respiratory and swimming movements of *Echiurus echiurus*. The animal moves forward by means of synkinetic waves but uses antikinetic waves during burrowing. During locomotion, the animal uses its ventral setae and sometimes its anal setae as anchors. According to Gislén, *Echiurus echiurus* excavates U-shaped burrows by alternately scraping the substrate with its ventral setae and then anchoring by dilating the anterior end of the trunk. The burrowing mechanism in *O. caudex*, however, differs in that initial entry into the substrate is gained by the probing action of the proboscis only. The setae are not used during this stage of the burrowing period as the animal lies on the surface with its ventral surface uppermost.

From the observations made of locomotion and burrowing in *Ochetostoma caudex*, it is evident that these activities take place in a series of step-like movements involving alternate formation of penetration and terminal anchors. Each step during burrowing is characterized by the forward extension of the proboscis and anterior trunk region followed by the contraction of the longitudinal muscle so as to pull more of the trunk into the burrow. Internal hydrostatic pressure increases as burrowing proceeds suggesting that anchorage improves with increasing depth. Essentially similar mechanisms are used by many other soft-bodied animals (Trueman & Ansell, 1969; Trueman, 1975).

According to Trueman & Ansell (1969), animals with a continuous body cavity can utilize either synkinetic or antikinetic waves to move along a burrow, whereas all septate animals must use antikinetic waves for this purpose.

The patterns of internal pressure fluctuations in *Ochetostoma caudex*, *Priapulus caudatus* and *Sipunculus nudus* during locomotion and burrowing are basically similar. In the latter two animals, proboscis eversion is associated with a marked increase in coelomic pressure. The maximum pressure recorded in the case of Priapulus was about 1 x 10^4 Pa (Hammond, 1980). According to Elder and Hunter (1980), Priapulus may employ relatively high coelomic pressures of up to 6 x 10^3 Pa during escape reactions but normal burrowing takes place at pressures that are lower than 2 x 10^3 Pa. The maximum pressure generated in the trunk of Sipunculus for eversion of the proboscis is 1.8 x 10^4 Pa (Trueman & Foster-Smith, 1976). In the latter animal, also, much lower pressures are found after burial is complete. In Ochetostoma caudex, high pressure peaks of 4 x 10^3 Pa were recorded during escape reactions but lower pressures of up to 3 x 10^3 Pa were usually employed during normal burrowing.

It is thus apparent that much higher internal pressures are required in S. nudus and P. caudatus for eversion of the proboscis. Ochetostoma differs significantly from the latter two in possessing a proboscis that cannot be retracted into the trunk. Furthermore, the coelomic spaces in the proboscis of Ochetostoma are not continuous with the main trunk coelom. The proboscis, with its own muscle systems, functions as a separate hydraulic unit and its movements are independent of those of the trunk. Hence the extension of the proboscis is not brought about by the movement of fluid from the trunk coelom. Jaccarini & Schembri (1977), also, have been unable to find a connecting channel between the coelomic space of the proboscis and trunk of Bonellia viridis. As detritus feeders, the independent movements of the proboscis in echiurans may be related to their feeding habits and way of life in general.

Ochetostoma, unlike Priapulus, inhabits semi-permanent U-shaped burrows, the walls of which are consolidated with mucus. Digging cycles are frequently interrupted in dilating and compacting the walls of the burrow.

Priapulus, being a predator, is probably highly active, moving about in soft mud in search of polychaetes and other invertebrates. According to Hammond (1980), a powerful and rapid eversion of the proboscis may be useful to Priapulus in capturing slow-moving prey.

The sipunculans dwell in benthic habitats, ranging from intertidal shores to abyssal depths. They usually burrow into sand, mud, or gravel and, in the tropics, they have been reported to occur in burrows within dead coral or other calcareous rock. The trunk is cylindrical and the mouth, completely or partially surrounded by tentacles, is located at the anterior end of the long introvert. Movement through sand is achieved essentially by the forceful thrusting of the introvert. The extensive coelom and the structure of the body wall and introvert are specialisations for a burrowing mode of life.

In both Ochetostoma and Sipunculus the maximum pressure peak is produced by contraction of the longitudinal musculature of the trunk, whereas in Priapulus it is generated by the contraction of the circular muscle. According to Hammond (1980), the main disadvantage of circular muscle contraction prior to proboscis eversion is that it causes a reduction in the diameter of the body and loss of anchorage in the substratum.

In contrast to Ochetostoma and Sipunculus, locomotion in Priapulus is accomplished by direct peristaltic waves. It has been stated that a direct peristaltic wave is well suited to an animal burrowing in soft mud (Elder, 1973). According to Hunter et al (1983), a direct peristaltic wave effects continuous trunk advance as it passes forwards and a small force is directed forward by the anchorage of a large posterior end.

In *Ochetostoma*, the terminal anchor is formed by the dilation of the body at the anterior end. *Priapulus* forms an unusually large terminal anchor by dilating the praesoma (Hammond 1970; Elder & Hunter, 1980 and Hunter et al, 1983). In *Sipunculus*, also,the anterior tip of the proboscis is dilated to form the terminal anchor just prior to the contraction of the longitudinal muscle (Trueman & Foster-Smith, 1976).

There is a marked similarity between *Ochetostoma caudex* and *Bonellia viridis* in the mechanism of locomotion and the rate at which peristaltic waves are propagated along the trunk. However, unidirectional locomotion as a result of both synkinetic and antikinetic waves occurring in strict alternation, as reported by Schembri and Jaccarini (1977) in *B. viridis*, was not observed in *O. caudex*. According to the latter authors, *Bonellia* does not excavate its own burrow but occupies natural ones. The large bilobed proboscis of *Bonellia* is not suited to an actively burrowing mode of life. Furthermore, extension of the proboscis of *Bonellia* is achieved predominantly by ciliary action and muscular contractions play a minor role (Jaccarini & Schembri, 1977).

Summary

Ochetostoma caudex is a soft-bodied marine invertebrate which inhabits semi-permanent U-shaped burrows in the intertidal zone. It is well adapted for burrowing in coarse sand. Pressure changes in the coelomic fluid during locomotion, burrowing and during trunk irrigatory movements have been recorded and related to the various phases of muscular activity by direct visual observation and from cinematographic records. *Ochetostoma caudex* is capable of both forward and backward locomotion in its burrow.

As with many other soft-bodied burrowing animals, penetration into the substrate takes place in a series of steps or digging cycles. Each step is characterized by the forward extension of the proboscis and the anterior region of the trunk followed by the contraction of the longitudinal muscle so as to pull more of the trunk into the burrow. As depth of burial increases, the internal hydrostatic pressure rises and may reach peaks of up to 3.0×10^{3} Pa suggesting that anchorage improves with increasing depth. The structural and functional specializations for burrowing are discussed and compared with the activities of *Priapulus caudatus*, *Sipunculus nudus* and *Bonellia viridis*.

I wish to thank Dr Jennifer A. Day of the Department of Zoology, University of Cape Town, for critically reading the manuscript and making some helpful suggestions. Thanks are also due to Professor E.R. Trueman (lately Beyer Professor of Zoology in the University of Manchester) for stimulating interest in this field of research and for helpful discussions on the mechanics of burrowing. The assistance given by Mr P. Gathiram with the body fluid pressure recordings is gratefully acknowledged. I also owe a great deal of gratitude to my colleagues, Messrs K.S. Ganga and G.K. Moodley, for assistance with the collection of specimens.

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THE REPRODUCTIVE SYSTEM, GAMETOGENESIS AND ANNUAL REPRODUCTIVE CYCLE OF OCHETOSTOMA CAUDEX (PHYLUM ECHIURA).

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THE REPRODUCTIVE SYSTEM, GAMETOGENESIS AND ANNUAL REPRODUCTIVE CYCLE OF OCHETOSTOMA CAUDEX (PHYLUM ECHIURA)

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ABSTRACT

The anatomy of the reproductive system and the process of gametogenesis in Ochetostoma caudex have been studied with light and electron microscopes. Some aspects of the reproductive behaviour and spawning have also been discussed. The gonads develop in the body wall, in the interspaces of the longitudinal muscle bands. Gametes are released into the coelomic fluid at an advanced stage of development. Before spawning, mature gametes are selectively gathered into three pairs of tubular gonoducts. These organs are located in the anterior part of the body cavity on either side of the ventral nerve cord. Each gonoduct opens into the coelom through a pair of grooved, thread-like gonostomes and to the outside via a genital pore.

The developing oocyte, surrounded by numerous accessory cells, remains attached to the ovary until considerable growth has already occurred. During this phase the oocyte becomes enclosed by a thick coat, penetrated by numerous cytoplasmic processes, through which nutrients are channelled into the ooplasm. The nearly mature egg, once released into the coelomic fluid, is devoid of the surrounding coat and cytoplasmic processes. In the gonoduct the mature oocyte has a mean diameter of 460 µm. The cytoplasm contains an enormous number of spherical yolk granules. The surface of the oocyte is smooth and devoid of any indentations.

Spermatogenic cells develop in clusters in the body wall. Many spermatocytes remain connected to one central cytoplasmic mass and sperm differentiation proceeds synchronously within a given cluster. The mature spermatozoon is of the primitive type, consisting of a low acrosomal cap, a midpiece with a single large mitochondrion and a long filamentous tail.

In this species gametogenesis and gamete release occur throughout the year with peak periods reached during the warmer months, probably lasting from the beginning of February to the end of April.

INTRODUCTION

Several investigators have reported on the ultrastructural changes during egg and sperm differentiation in various invertebrates. In the phylum Echiura, notable works include those of Yamamoto *et al* (1973), who studied the whole oogenetic process in the coelomic fluid of *Urechis unicinctus*. Gould-Somero & Holland (1975) describe the fine structure of immature and mature oocytes of *Urechis caupo*. These authors consider *U. caupo* as excellent material for the study of oogenesis since oocytes of all stages are available throughout the year. Sawada *et al* (1975) gave a detailed account on the ultrastructural changes during sperm differentiation in *Ikedosoma gogoshimense*. Using histochemical techniques, Menon & Sareen (1976) investigated the synthesis of nutritive materials in the eggs of *Rubricellatus pirotansis*. Our current knowledge of the annual cycle of oogenesis, spawning and larval settlement of the echiuran, *Listriolobus pelodes* is sufficiently advanced as a result of the studies of Pilger (1980). Literature also contains accounts on various aspects of the reproductive biology of the sexually dimorphic bonellids.

In recent years intensive biochemical and physiological studies have been made on the eggs of *Urechis caupo* (Schwartz, 1970; Gould-Somero & Holland, 1975; Paul, 1975a & b; Paul & Gould-Somero, 1976; Davis & Davis, 1978; Jaffe et al, 1979 and several others). Many of the investigations, however, are confined to the eggs in the mature or nearly mature stages and to their structural changes after fertilization. Early developmental events have not received the same amount of attention.

There are no accounts on egg and sperm differentiation in the genus Ochetostoma. Little is known about the structure and location of gonads and the cytodifferentiation of the male gametes in echiurans. Furthermore, very little information is available on reproductive behaviour and spawning. In this paper, the reproductive system of Ochetostoma caudex is described and the process of gametogenesis investigated with light and electron microscopes. Some information on aspects of the breeding behaviour has also been included for its possible value to future investigators.

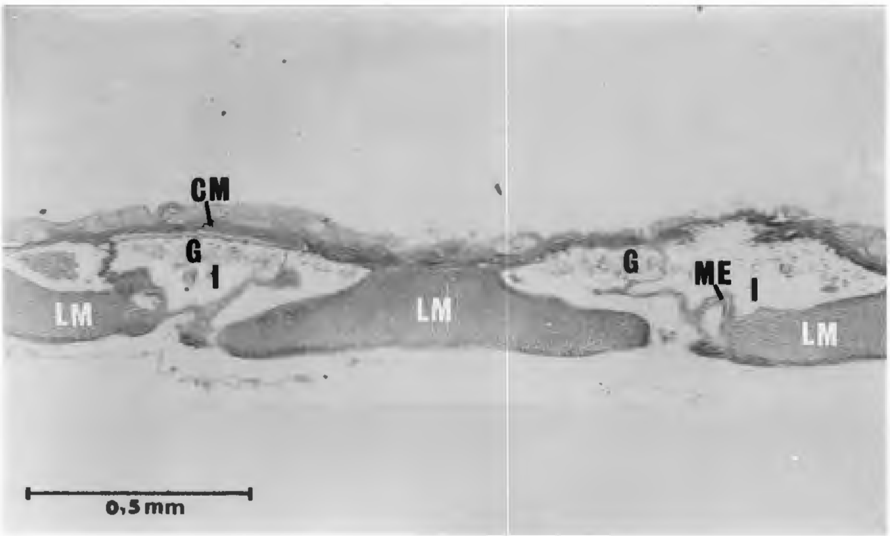
MATERIALS AND METHODS

Adult specimens of Ochetostoma caudex were collected intertidally from Isipingo Beach (29° 05'S/20° 56'E) and Park Rynie Beach (31° 19'S/30° 44'E), on the Natal coast.

For light microscope observations of the gonads, strips of the body wall of sexually mature specimens taken from the middle region of the trunk, were embedded in paraffin wax and sectioned at 5-7 μm. The gonoducts and gonostomal lips were also sectioned for histological details. Sections were stained either with Mallory's triple stain or with haematoxylin and eosin. Photographs were taken with a Carl Zeiss photomicroscope.

For transmission electron microscope investigations, strips of the body wall as well as mature sperm and eggs, removed from the gonoducts of formalin-preserved specimens, were thoroughly washed in distilled water and post-fixed with 2% osmium tetroxide for one hour. After

Fig. 1 Transverse section of body wall of *O. caudex* showing the position of the gonads. CM, circular muscle; G, gonad; I, interspace; LM, longitudinal muscle band; ME mesentery.


CM
G
I
LM
LM
G
ME
I
LM
0,5 mm

dehydration through a series of graded ethanol, the speicmens were embedded in low-viscosity epoxy resin. Ultra-thin sections were stained with 2% aqueous uranyl acetate and lead citrate and viewed in a Philips TEM 301 at 80 Kev with a 30 µm objective aperture.

Sperm removed from the gonoducts were washed and dehydrated in an ethanol series. They were then critical-point dried, mounted on a stub with double-sided scotch tape, coated with gold and viewed in a Hitachi scanning electron microscope.

REPRODUCTIVE SYSTEM

As a rule echiurans are dioecious and, with the exception of the bonellids, show no external signs of sexual dimorphism. Sexual dimorphism of the bonellids distinguishes them from all other members of the phylum. The male is usually small, planarian-like and parasitic in or on the female form.

In some species of Echiura, the gonads are situated on the ventral blood vessel in the posterior part of the body, close to the rectal caecum. In Ochetostoma caudex, on the other hand, they develop in the interspaces between the longitudinal muscle bands of the body wall (Fig. 1). However, they are not visible in dissected specimens and their presence can only be ascertained when the body wall, taken from the middle region of the trunk of sexually mature specimens, is sectioned. In histological preparations it is possible to distinguish the ovary from the testis. The triangular interspaces in which the gonads lie are bordered externally by a circular muscle layer of the body wall, laterally by longitudinal muscle bands and internally by the oblique muscles, which are arranged in fascicles. The germ cells proliferate from peritoneal mesenteries lining and traversing the triangular spaces.

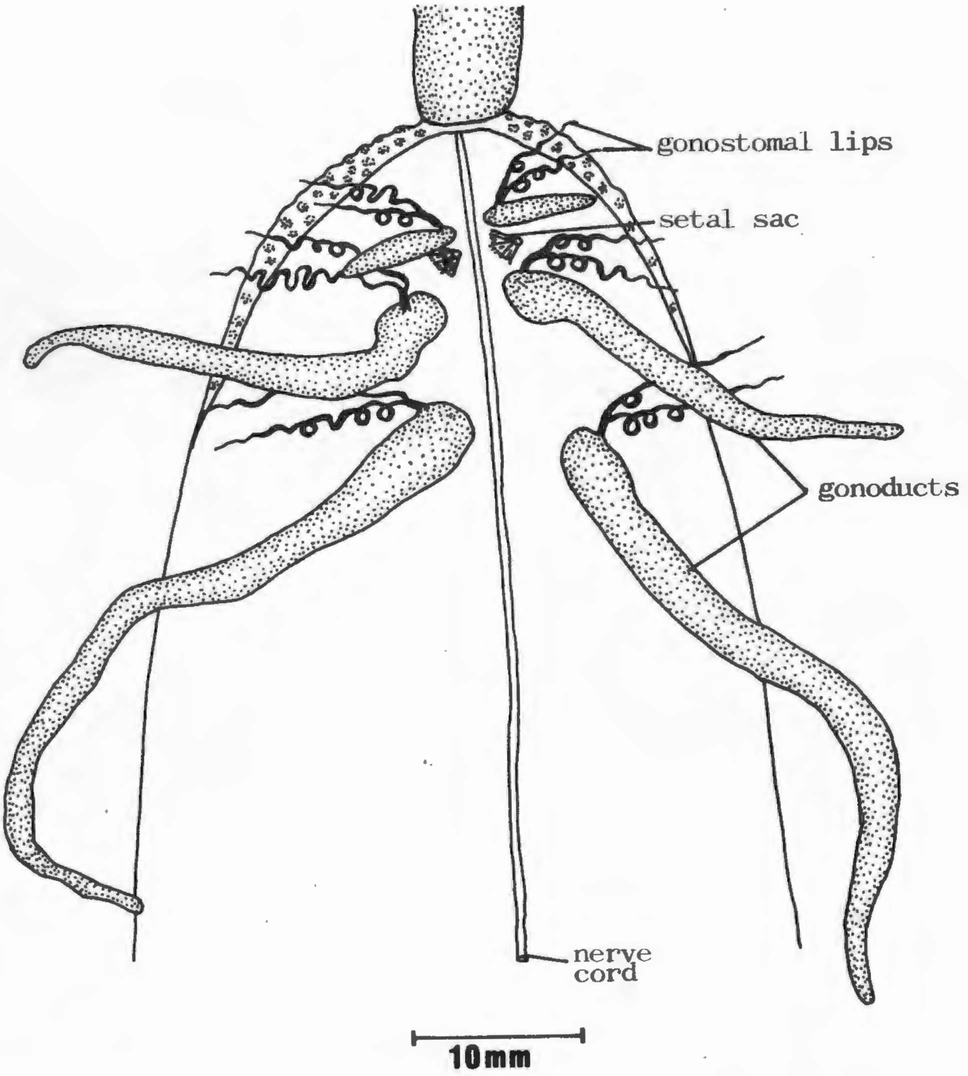


Fig. 2. Dissection of the anterior trunk cavity of Ochetostoma caudex illustrating the gonoducts.

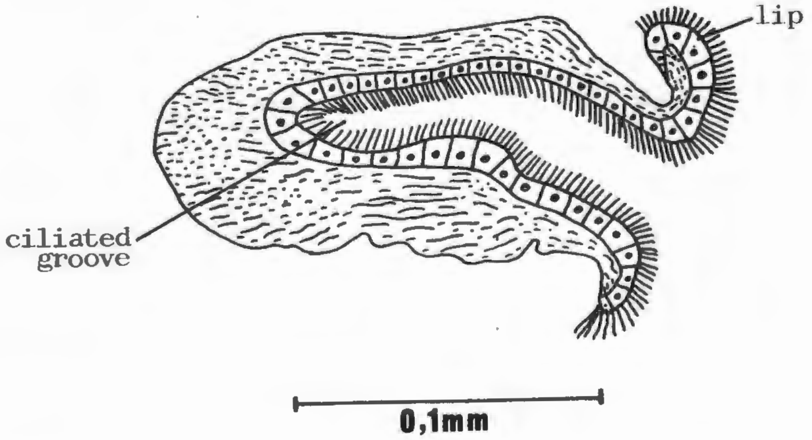


Fig. 3. Cross-section of the gonostomal lip of Ochetostoma caudex illustrating the ciliated groove (From Biseswar, 1983).

Sections of the body wall of sexually mature specimens show germ cells in various stages of development. Gametes are released, at a fairly advanced stage of development, into the coelom where they undergo the remainder of their growth and differentiation. Before spawning, the mature gametes are selectively gathered from the coelomic fluid into the three pairs of gonoducts by the ciliary action of the gonostomes. The collection and storage of gametes is facilitated by regular peri=staltic contractions of the trunk which cause vigorous movements of the coelomic fluid. The length of time the gametes are retained in the gonoducts, prior to spawning, is not known.

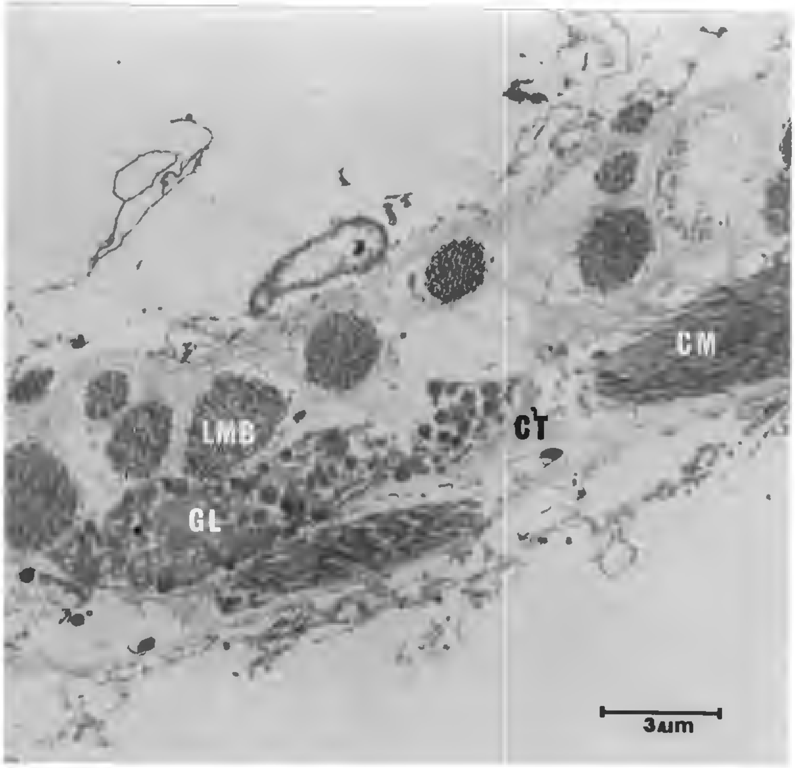
GONODUCTS

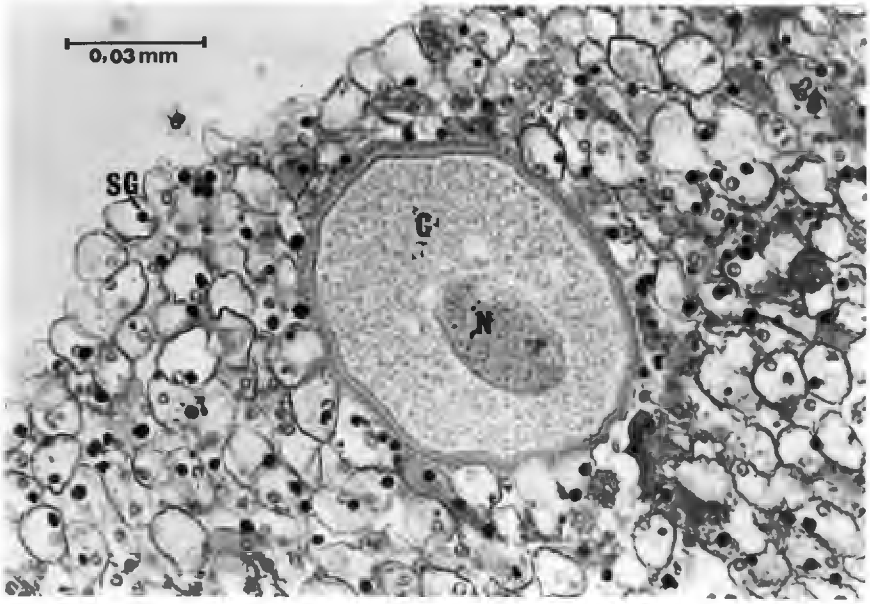
The gonoducts or segmental organs of echiurans are used for gamete storage and discharge. Their number is definite for each species (Saxena, 1983).

The gonoducts of O. caudex have been briefly described in an earlier paper (Biseswar, 1983). These organs are located in the anterior part of the body cavity on either side of the ventral nerve cord (Fig. 2). One pair lies anterior to the ventral setae, while the remaining two pairs are post-setal in position. The gonoducts are tubular, blind-ending organs with the same basic structure but differ in size. In some sexually mature specimens, the third pair may equal or slightly exceed half the length of the trunk. Each gonoduct opens into the coelom through a pair of deeply grooved, thread-like, spirally coiled gonostomes (Fig. 2) and to the outside via a genital pore. The genital pores are situated at the anterior end of the trunk on either side of the nerve cord, close to the ventral setae.

Fig. 4 Transmission electron micrograph of wall of gonoduct. CM, circular muscle; CT, connective tissue; GL, gland; LMB, longitudinal muscle bundles.

Fig. 5 Developing oocyte in the body wall of O. caudex surrounded by oogonia which serve as nurse or accessory cells. C, cytoplasm; N, nucleus; SG spherical granule.


CM
LMB
CT
GL
3µm


0,03 mm
SG
G
N

The two gonostomes are attached to each gonoduct by a short common duct. In living specimens the elongate gonostomes undergo continuous twisting or writhing movements,hence coming into contact with all parts of the coelomic fluid.

Histological studies of a gonostome show that it is composed of muscle fibres interspersed with loose connective tissue (Fig. 3). A single layer of ciliated cuboidal cells lines the groove. The beating of the cilia convey the gametes along the grooves into the gonoducts. The epithelial lining of the common duct is also densely ciliated.

Electron micrographs of the wall of a gonoduct reveal that it is composed of circular and longitudinal muscles, supported by connective tissue. The longitudinal muscles are arranged in bundles and disposed at irregular intervals (Fig. 4). Proximally, the ventral wall of the gonoduct is much thicker and contains a few sparsely distributed mucous-secreting glands. In this region, the internal lining together with the underlying tissue is thrown into minute finger-like projections.

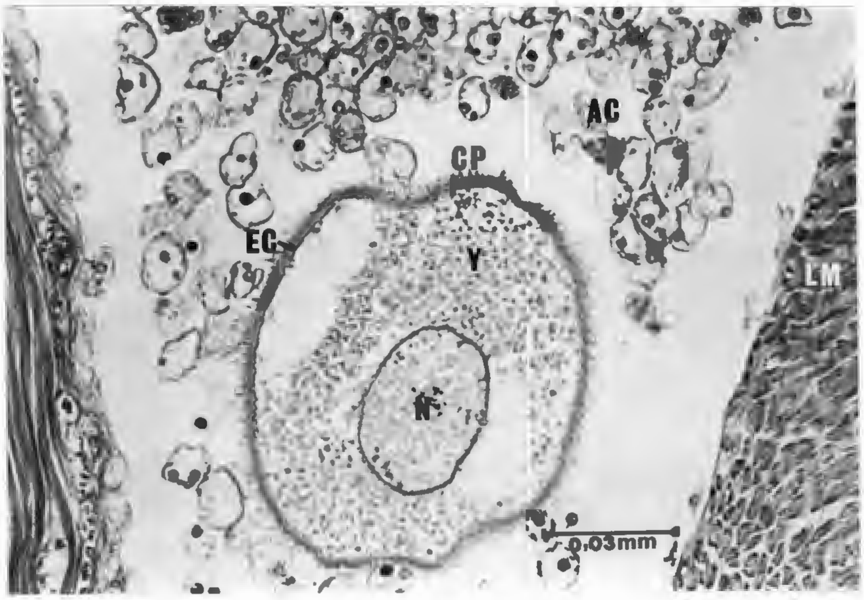
OOGENESIS

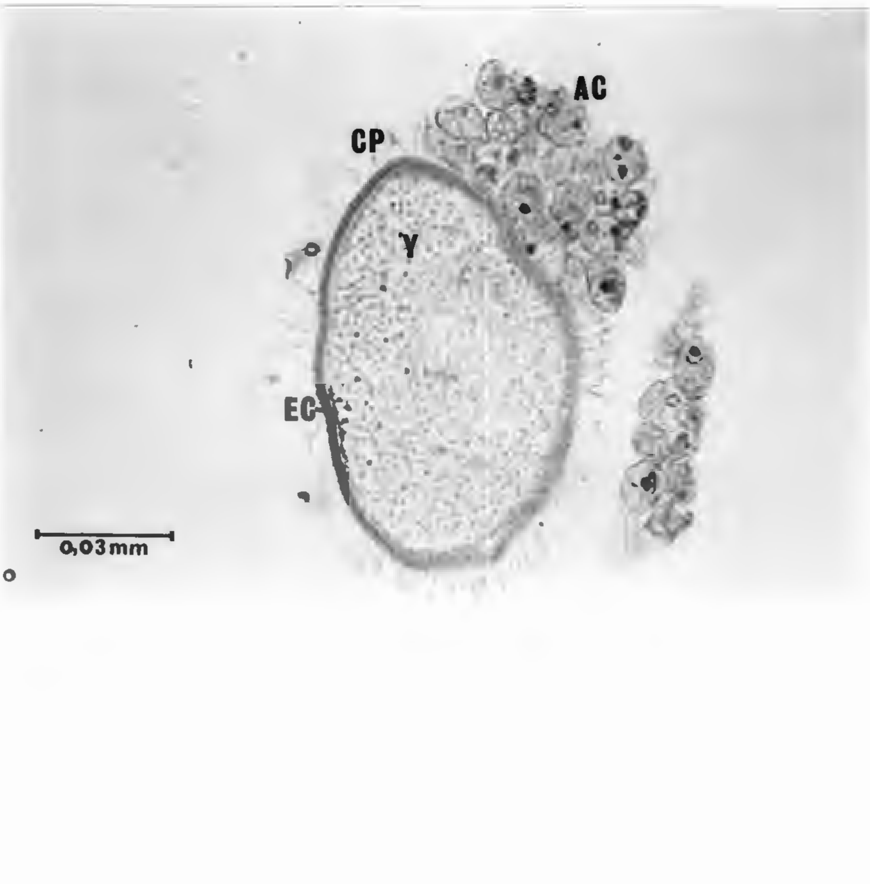
Oocyte growth in _O_. _caudex_ can be divided into three phases, the generative phase in which oogonia are proliferated from the peritoneal mesentery, the vitellogenic phase during which nutrients are channelled into the oocyte from surrounding accessory or nurse cells, and the mature phase or terminal stage in which metabolic activities gradually cease prior to spawning.

In sexually mature females, the triangular interspaces are occupied by developing oocytes as well as primordial germ cells or oogonia

Fig. 6 Oocyte surrounded by a thick coat penetrated by numerous cytoplasmic processes. AC, accessory cells; CP, cytoplasmic processes; EC, enveloping coat; LM, longitudinal muscle band; N, nucleus; Y, yolk granules.

Fig. 7 Oocyte in the latter stages of vitellogenesis with surrounding coat and elongate cytoplasmic processes. AC, accessory cells; CP, cytoplasmic processes; EC, enveloping coat; Y, yolk granules.





7

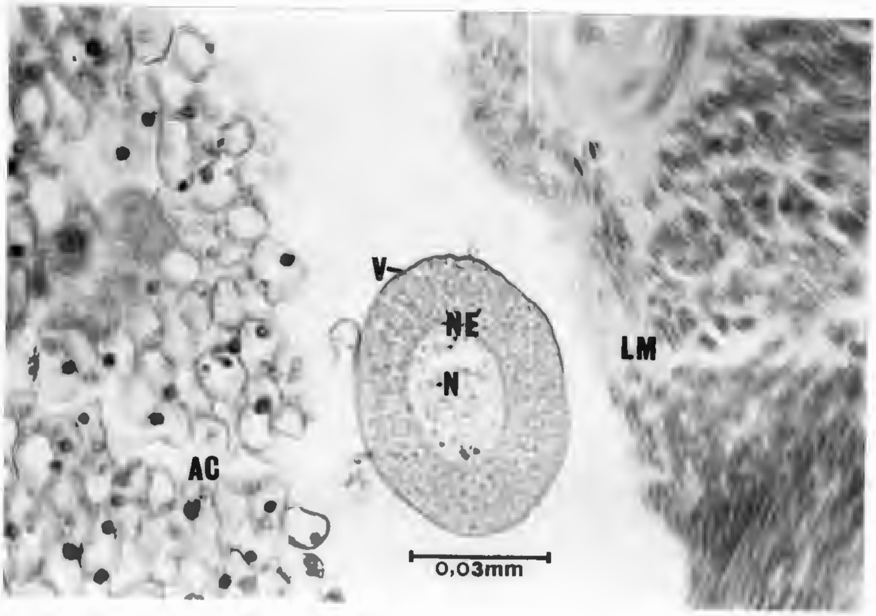
(Fig. 5). The oogonia proliferate from specialized mesenteries that are found associated with small blood vessels. When the oogonia occur singly or in small isolated groups, they appear spherical, each with a diameter of about 12,4 µm. The spherical shape, however, is distorted when the cells are closely aggregated into clusters (Fig. 5). The rounded nucleus is eccentrically located and has a diameter of about 3,9 µm. In the peripheral cytoplasm of each cell is a dense spherical granule which at first sight might be mistaken for a nucleus (Fig. 5). This granule stains yellow to dark-brown with Mallory's triple stain and appears to be associated with the synthesis of yolk material.

Some of the cells within a cluster begin to grow disproportionally to become egg cells or ova. The remainder, however, do not differentiate but remain attached to the developing oocytes as nurse or accessory cells (Fig. 5). Hence the egg grows at the expense of the surrounding cells. Under the light microscope, the early oocyte can be readily distinguished by its larger diameter and darkly-staining cytoplasm. In the early stages, the developing oocytes are somewhat spherical with a wavy or sculptured surface because of their close apposition to the adjacent cells in the cell mass.

As development proceeds, the structure of the oocyte surface changes considerably. An interesting and rather unusual phenomenon observed in O. caudex is the formation of a thick envelope or capsule around the oocyte, external to the vitelline membrane (Fig. 6). This enveloping coat becomes penetrated by numerous cytoplasmic processes, of uncertain origin, which gradually elongate and come into contact with the surrounding accessory cells (Fig. 6 and 7). Through these

Fig. 8 Nearly mature oocyte at the end of the vitellogenic phase without its enveloping coat. AC, accessory cells; LM, longitudinal muscle band; N, nucleus; NE, nuclear envelope; V, vitelline membrane.

Fig. 9 Photomicrograph showing the release of the oocyte as a result of the rupture of the enveloping coat. AC, accessory cells; EC, enveloping coat.


V
NE
N
LM
AC
0,03mm

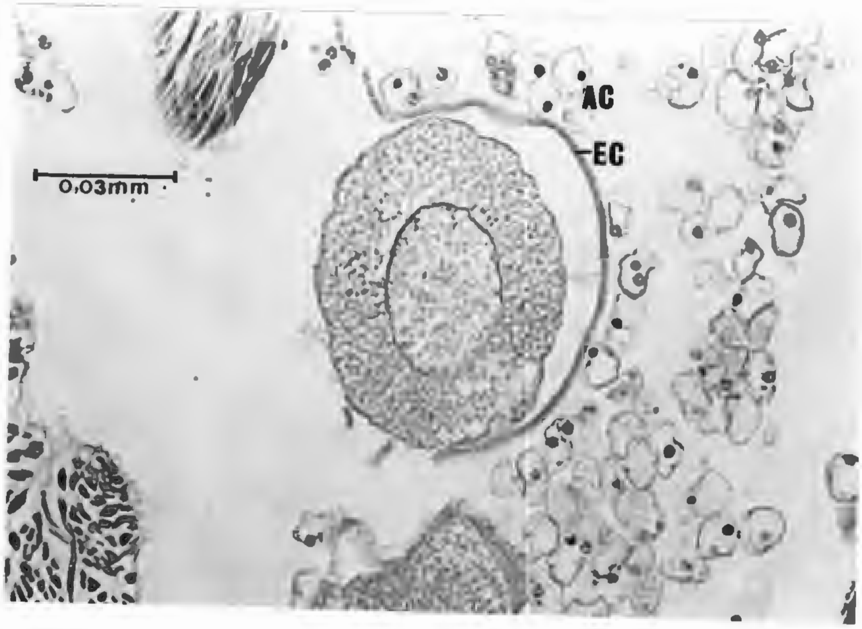

AC
EC
0,03mm

Fig. 10 Photomicrograph showing separation of the oocyte from its surrounding coat.

Fig. 11 Transverse section of gonoduct with mature oocytes.


0,03mm

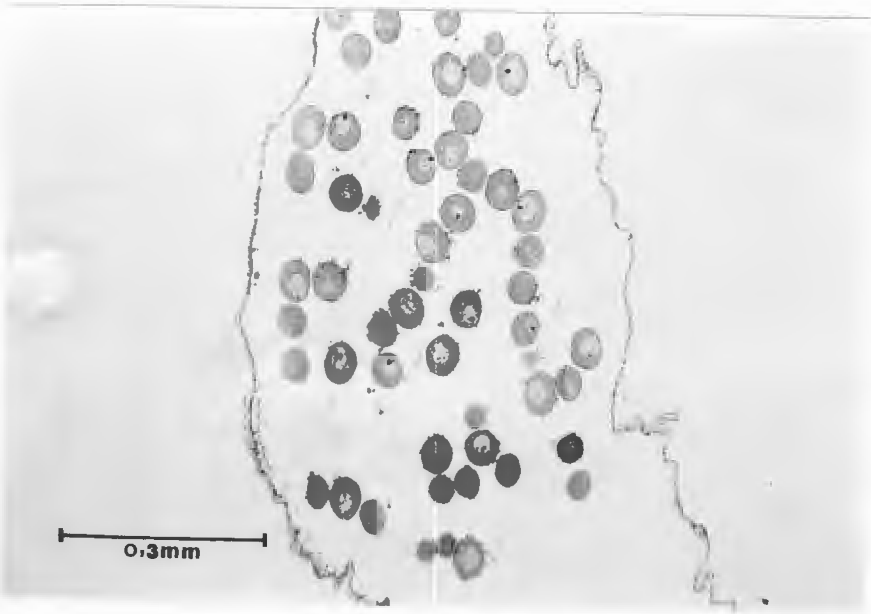
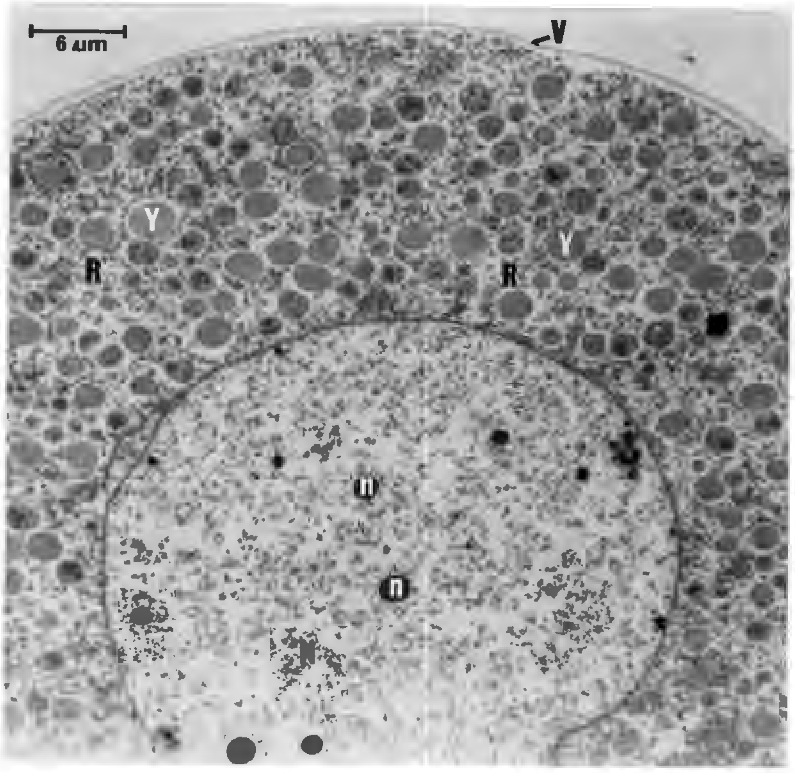

0,3mm

Fig. 12a Transmission electron micrograph of a mature oocyte from the gonoduct. N, nucleus; n, nucleoli; R, ribosomes; V, vitelline membrane; Y, yolk granules.

Fig. 12b Cytoplasmic inclusions in the mature oocyte of O. caudex. CG, cortical granules; N, nucleus; NE, nuclear envelope; R, ribosomes; Y, yolk granules.


6 µm
V
Y
R
R
Y
n
n
N

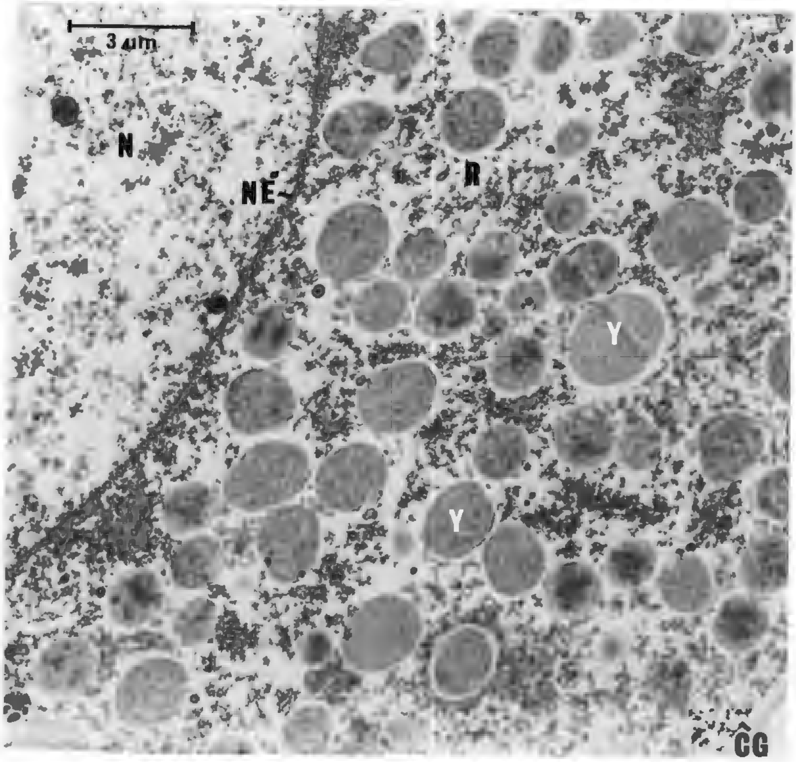
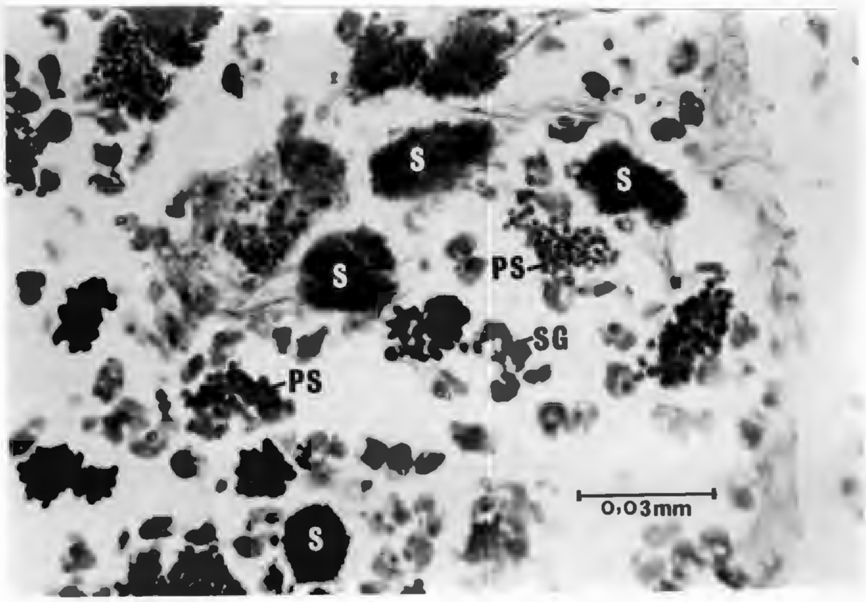
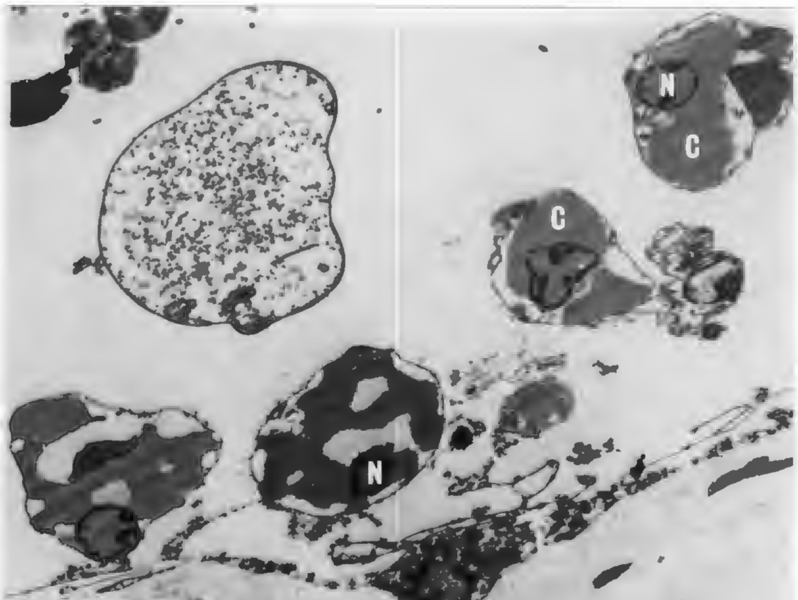

3 µm
N
NE
R
Y
Y
CG

Fig. 13 Photomicrograph of clusters of male sexual cells, in various stages of development, in the body wall of O. caudex. PS, primary spermatocytes; S, spermatids; SG, spermatogonia.

Fig. 14 Spermatogonia with eccentrically located nuclei. C, cytoplasm; N, nucleus.


S
S
S
PS
SG
PS
S
0,03mm


N
C
C
N
3 μm

The eggs within the gonoducts are in the germinal vesicle stage of development. They are all of the same form and size, being spherical with a diameter of about 460 µm and contain an enormous amount of yolk material. The germinal vesicle measures about 236 µm in diameter. The yolk granules vary in size and are evenly distributed throughout the cytoplasm (Fig. 12a). Cortical granules are not distinguishable with any degree of certainty in the electron micrographs but small, spherical structures in the peripheral cytoplasm, just beneath the cell membrane, may represent these structures (Fig. 12b). Ribosomes are abundant throughout the cytoplasm, either free or associated with the nuclear envelope (Figs. 12a & 12b), but the specific stage in oogenesis during which their synthesis takes place is not known. The vitelline membrane is smooth and lacks microvilli. Since it appears as a distinct structure soon after the vitellogenic phase, it is assumed that the accessory cells are also responsible for its secretion. Unlike the condition in some other species of echiurans, the surface of the mature oocyte is devoid of any indentations.

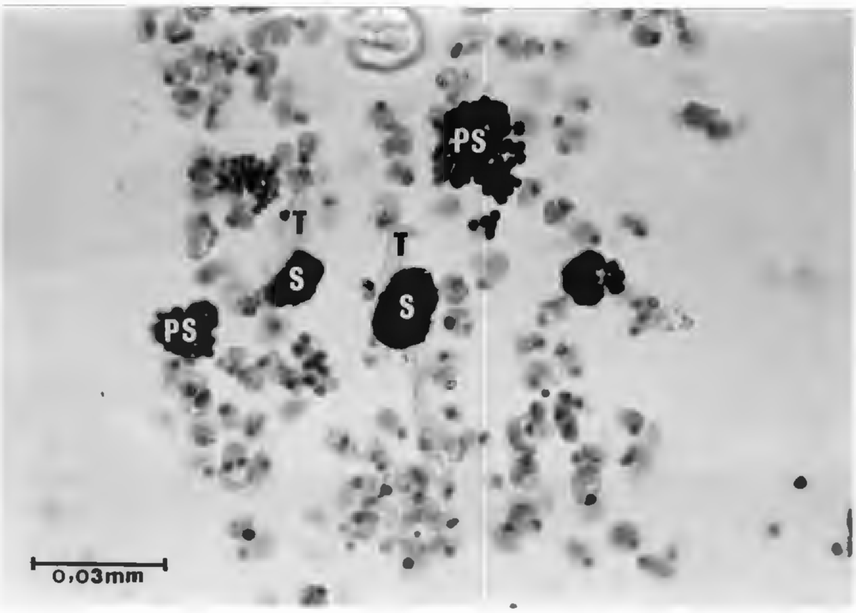
The nuclear envelope consists of two unit membranes. The nucleoplasm is coarsely grandular and the nucleolus, even in the mature egg, occurs in numerous fragments (Fig. 12a).

SPERMATOGENESIS

Light microscope observations of sections of the body wall of a male specimen show clusters of sexual cells in various stages of development (Fig. 13). The spermatogonia are spherical to somewhat oval cells with darkly staining, eccentrically located nuclei (Fig. 14). Electron micrographs reveal irregular, electron-dense areas in the cytoplasm with patches of clear spaces. Some of the spermatogonia divide to form spermatocytes which then differentiate into mature spermatozoa.

Fig. 15 Photomicrograph of differentiating male germ cells in the body wall of O. caudex. PS, primary spermatocytes; S, spermatids; T, tails of spermatids.

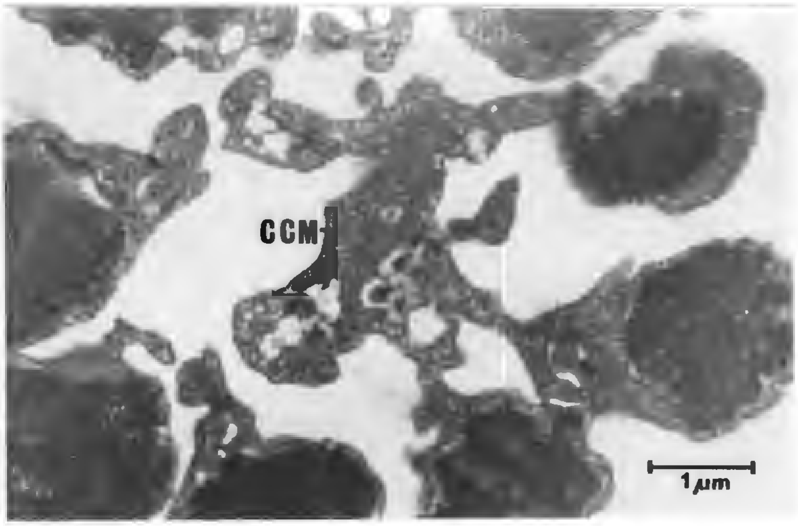
Fig. 16 Transmission electron micrograph of a cluster of secondary spermatocytes. C, cytoplasm; CCM, central cytoplasmic mass; N, nucleus.

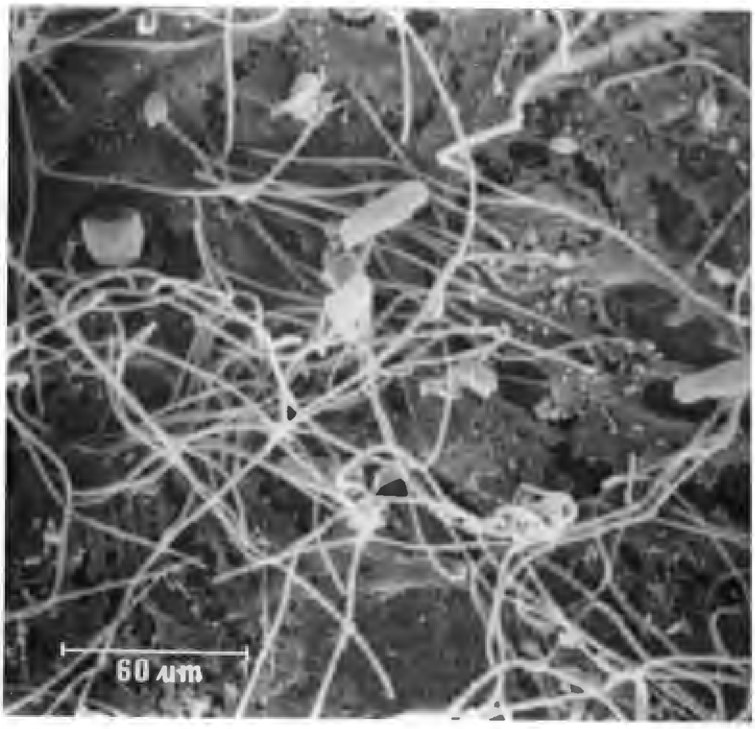

PS
T
T
S
S
PS
0,03mm


CCM
N
C
N
1 μm

Fig. 17 A cluster of spermatocytes connected to the central cytoplasmic mass. CCM, central cytoplasmic mass.

Fig. 18 Scanning electron micrograph of mature spermatozoa in the gonoduct of O. caudex.


CCM
1 µm


60 µm

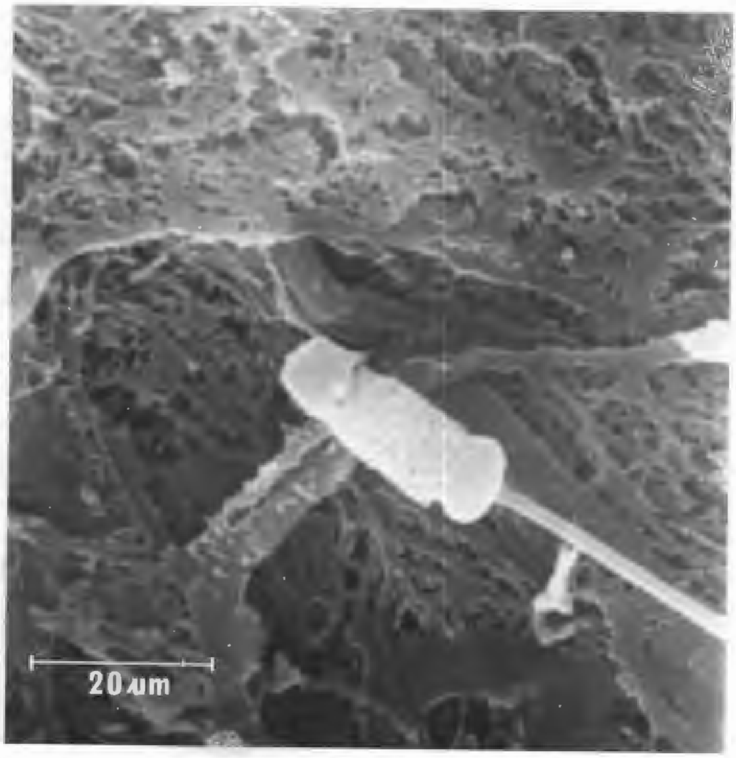
It was not possible to make a clear distinction between the primary and secondary spermatocytes. However, the closely aggregated, rounded cells occurring in clusters in Figure 15 are considered to be primary spermatocytes while the cluster of cells depicted in Figure 16, probably represent secondary spermatocytes as their nucleoli have all disappeared. In the latter case, the cytoplasm forms a thin rim around the large spherical nucleus.

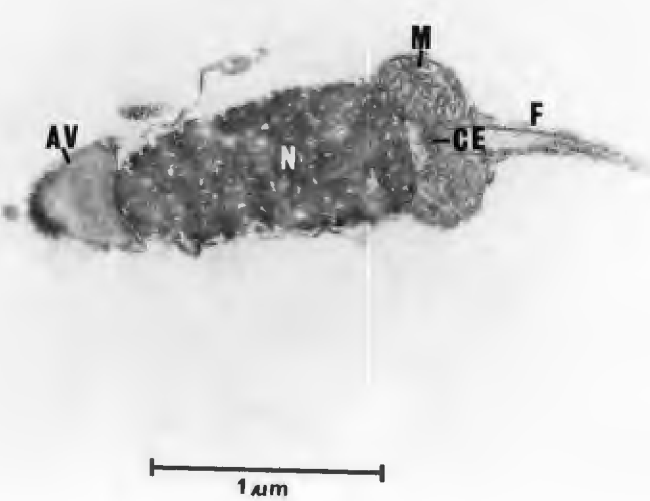
In a cluster, a variable number of differentiating germ cells are connected to a central cytoplasmic mass (Fig. 17). As development proceeds, the cells gradually become orientated all around the central mass. The origin of the central cytoplasmic mass is uncertain, but it is probable that it is produced by the spermatogonia. All the cells in a cluster appear to be in the same stage of development and are connected by means of cytoplasmic bridges (Fig. 17). In a single cluster, the events of differentiation appear to be synchronized and according to Longo & Dornfeld (1967), the protoplasmic continuity is the basis for this synchrony. In the early spermatids the flagella are partially formed.

As spermiogenesis proceeds, the spermatid nuclei become elongated and, in the late spermatid stage, the mitochondrion and flagellum are located on the side of the cell away from the central mass. In the early spermatids several mitochondria are distributed unevenly but they gradually coalesce to form one large mitochondrion around the base of the flagellum.

Fig. 19 Scanning electron micrograph of a mature spermatozoon.

Fig. 20 Transmission electron micrograph of a mature spermatozoon from the gonoduct of O. caudex. AV, acrosomal vesicle; CE centriole; F, flagellum; M, mirochondrion; N, nucleus.


20 µm


M
F
AV
N
CE
1 µm

In the mid-stage of spermiogenesis, the acrosomal vesicle is located near the centrioles. As spermiogenesis proceeds this vesicle moves away from the flagellum to the side of the nucleus facing the central mass. A similar observation was also made by Sawada et al (1975) in the echiuran Ikedosoma gogoshimense.

As the cytoplasmic mass is gradually depleted, the mature spermatozoa separate from the cluster and are released into the coelom. From here they are selectively gathered into the gonoducts prior to spawning. In scanning electron micrographs the spermatozoa, removed from the gonoducts, appear as a tangled mass of threads (Fig. 18). Each spermatozoon is characterised by the presence of a cylindrical head and a long tail (Fig. 19).

The spermatozoa of O. caudex have the typical morphology of the primitive sperm, similar to those of other species with external fertilization. Transmission electron micrographs of mature sperm reveal that each comprises a low acrosomal cap, a midpiece with a single large, horseshoe-shaped mitochondrion and a long filamentous tail (Fig. 20). The head measures about 1,9 µm in length with a diameter of about 0,6 µm in the middle region. The acrosomal vesicle is rounded anteriorly and has a shallow invagination posteriorly. Of the two types of electron-dense materials in the vesicle, the less dense material occurs towards the apex. In O. caudex there is a single large mitochondrion surrounding the base of the flagellum (Fig. 20). The axoneme originates from one of the centrioles, the other being disposed at right angles to it

(Fig. 20). The flagellum is typical, with two central filaments and nine peripheral pairs.

REPRODUCTIVE BEHAVIOUR AND SPAWNING

In sexually mature specimens the gonoducts become greatly distended by the accumulation of gametes. A relative decrease in the volume of these organs indicates that spawning has occurred. Thus in specimens where spawning had already occurred, the gonoducts, although enormously developed, are found to be in a collapsed state. It is possible to determine the sex of an animal by making smear preparations of the reproductive cells after incising the walls of the gonoducts since the gonoducts are not completely evacuated at spawning.

The present observations are based on specimens that were collected intertidally, from two rocky shore localities on the Natal coast, more or less at monthly intervals, over a period extending from February 1982 to August 1985. Although some specimens were obtained from crevices and galleries in rocks, most were collected from sediment under stones, in a sheltered rock tunnel at Isipingo Beach. In the latter habitat, the sediment was slightly muddy and consisted of coarse sand grains, shell fragments and other hard miscellaneous debris.

Since specimens were not readily available in sufficient numbers or with ease, it was not possible to study a single population in any one locality for a period of one year. In this investigation, speculations of the breeding habits are based on the state of the gonoducts of specimens collected at regular intervals throughout the year. Specimens with sexual cells stored in their gonoducts were encountered throughout the year. However, an examination of a fairly large sample collected in May 1983 showed that, in the majority of cases, spawning had already occurred prior to the onset of the winter season. These observations encourage the suggestion that although gametogenesis and gamete release take place throughout the year, peak periods are reached during the warmer months, probably lasting from the beginning of February to the end of April.

The act of spawning, observed on only two occasions, is displayed by the expulsion of gametes in a forceful stream through the genital pores of all the gonoducts. Practically all the eggs or sperm are ejected in a single spawning. In the water the eggs and sperm appear milky white. Specimens were observed to spawn in mid-April after transport to the laboratory where they were maintained in well aerated sea water at a temperature of about 25°C. Since the water in the container, used to transport the specimens, was much warmer it is felt that spawning was triggered in the laboratory by a sudden change in temperature. Unfortunately no temperature readings were taken. Further work on the reproductive behaviour of O. caudex may produce interesting results.

DISCUSSION

GONADS

There is very little current information on the origin of germ cells and gonads in echiurans. In *O. caudex* the gonads are not of definite form. The similarity in cytology of peritoneal cells and oogonia indicates that the germ cells arise from the peritoneum present in the triangular interspaces of the longitudinal muscle bands. In *Ochetostoma bombayense* (Awati & Deshpande, 1933) and in *Listriolobus pelodes* (Pilger, 1980), on the other hand, the gonads are situated on the ventral blood vessel in the posterior region of the body, close to the rectal caecum. Contrary to the condition in *O. caudex*, in the latter two species the oocytes are released from the gonads at an early stage and continue their development in the coelomic fluid before being accumulated in the gonoducts.

Although the mature and immature oocytes of *Urechis* have been intensively studied by various authors (Davis & Wilt, 1972; Yamamoto *et al*, 1973; Gould-Somero & Holland, 1975; Paul, 1975a & b; Paul & Gould-Somero, 1976; Davis & Davis, 1978; Jaffe *et al*, 1979 and others), it is rather surprising that the gonad has never been observed. Hence studies on ultrastructural changes during oocyte differentiation are based on eggs in the coelomic fluid. MacGinitie (1935), however, has reported that in *Urechis caupo*, the oocytes originate in a certain part of the body but provides no details. Since the longitudinal muscles in *Urechis* are aggregated into discrete bundles as in *O. caudex* it is probable that the origin and location of the gonads are similar in both species.

OOGENESIS

Many researchers have reported on ultrastructural changes in the oocytes of various invertebrate species. In O. caudex each stage in oogenesis is defined cytologically by size, appearance of nucleus and the nature of cytoplasmic inclusions. Similar developmental stages have been shown in the coelomic oocytes of other echiurans, although variations do occur in the peristence of accessory cells, size and shape of oocytes and the nature of the egg envelope.

A striking characteristic of the Echiura is the extragonadal development of the germ cells, where the major part of the differentiation occurs in the coelomic fluid. The presence of nurse cells in association with the differentiating oocytes is an essential feature of a number of species. These nurse cells provide nutrients for the developing oocytes and presumably contain precursors for yolk material. In Urechis unicinctus, however, there are no follicle or accessory cells around the oocytes and, according to Yamamoto et al (1973), the vitelline coat is formed by the oocyte itself. In Urechis caupo as well, the oocytes, which occur in abundance in various stages of development throughout the year, develop naked in the body cavity, without surrounding accessory cells. Since changes occurring in the oocytes of Urechis in the gonadal phase have not been investigated, the existence of accessory cells associated with the oocytes in the early developmental stages must not be precluded.

The oocytes of Ikedosoma develop singly, but each has a cap of nurse cells (Sawada & Ochi, 1962). The eggs of Thalassema moebii and Hamingia arctica are also reported to develop with accessory cells (Baltzer, 1931). In Rubricellatus pirotansis, another echiuran, the egg is detached from the mesentery when it is 40 µm in diameter and floats in the coelomic fluid with a ball-like cap of nurse cells at the anterior end (Menon & Sareen, 1976). According to these authors, the developing egg receives its nourishment from the nurse cells through a tubular outgrowth of the egg. Through this tube the nutrients are passed into the oocyte to promote vitellogenesis. A similar cap of nurse cells is also present in *Acanthobonellia vulgaris* and *Ochetostoma septemyotum* while it is absent in *Listriolobus brevirostris* and *Thalassema thalassemum* (Menon & Sareen, 1976).

Oogenesis in *0. caudex* differs in several respects from the pattern described above. The oocyte remains attached to nurse cells until fairly late in oogenesis, that is, after considerable growth has already occurred. Just before the egg enters the coelomic cavity, the surrounding coat and cytoplasmic processes are shed. As far as can be ascertained such a developmental process has not yet been reported in the oogenesis of any other species.

Interspecific variations occur in the size and shape of mature oocytes and in the structure of the egg envelope. The mature eggs of *Urechis unicinctus* measure 120 to 130 µm in diameter (Yamamoto *et al*, 1973) while those of *Urechis caupo* range from 115 to 120 µm (MacGinite, 1935). Hence the eggs of both these species are much smaller than those of *0. caudex*, which measure about 460 µm in diameter. The larger and much yolkier egg of *0. caudex* may be correlated with its prolonged growth phase in the ovary and continued association with a large number of accessory cells.

The unfertilized eggs of Urechis are characterised by the presence of an indentation (MacGinitie, 1935; Gould-Somero & Holland, 1975). It has been suggested that this indentation facilitates selective transport of the mature eggs along the grooved lips of the gonostomes into the gonoducts. The indentation is reported to disappear after fertilization, when the egg assumes a spherical shape.

In striking contrast to the eggs of O. caudex, the surface of the oocyte of Urechis spp. is provided with numerous microvilli (Yamamoto et al, 1973; Gould-Somero & Holland, 1975). The primary function of the microvilli during oogenesis is assumed to be the absorption of nutrients. In the absence of microvilli in O. caudex it seems very likely that diffusion of nutrients into the cytoplasm of the oocyte occurs across the entire vitelline membrane.

RNA synthesis in growing Urechis eggs has been the subject of intensive studies. Gould-Somero & Holland (1975) have shown that RNA synthesis in Urechis is continuous throughout the oocyte growth period, with some synthesis even continuing in the mature oocyte. Similar observations have also been reported during oogenesis of sea urchin eggs (Verhey & Moyer, 1967). The synthesis of RNA in the oocytes of O. caudex needs investigation. This species may prove to be favourable material for such biochemical studies in the future.

SPERMATOGENESIS

The ultrastructure of the mature spermatozoon and the process of spermatogenesis are basically similar in O. caudex and Ikedosoma gogoshimense. In both species, the spermatogenic cells occur in clusters and many spermatids remain connected to one central cytoplasmic mass. Sperm differentiation occurs synchronously within a single sperm-ball. When the sperm reach maturity, they are released from the cluster and collected into the gonoducts. Differentiating germ cells, in the form of clusters, are also characteristic of the sipunculan, Golfingia ikedai (Sawada, 1980), and the polychaete, Travisia japonica (Ochi et al, 1977). It is therefore possible that this mode of sperm differentiation may be a common feature in many or in several groups of invertevrates.

Sections of the body wall of O. caudex, containing the gonads, show germ cells in various stages of development as well as fully-differentiated spermatozoa. It is therefore assumed that the sperm attain a sufficiently advanced stage of development before they are released into the coelomic fluid. Whether differentiating spermatogenic cells, in the form of clusters, are also released into the coelom is uncertain as no investigations of developmental stages in the coelomic fluid were undertaken. The central cytoplasmic mass is probably a characteristic feature in the Echiura. Sawada et al (1975) consider this central mass to be homologous with the cytophor of oligochaete spermatids. It has been suggested that the central mass has an important role in synchronizing the differentiation of the germ cells associated with it (Longo & Dornfeld, 1967). It is probable that the central cytoplasmic mass is the product of the division of a single cell, the spermatogonium.

The Golgi apparatus is an important factor in acrosome formation in many species (Anderson et al, 1967). Sawada et al (1975) and Sawada (1980) have reported that the electron-dense contents of the acrosomal vesicle are derived from the Golgi complex. Ochi et al (1977) also observed proacrosomal vesicles in the vicinity of the Golgi cisternae. According to the latter authors, dense materials are deposited in Golgi vesicles, which coalesce to form the acrosomal vesicle. The present ultrastructural studies on sperm differentiation are in agreement with the findings of the above authors.

The mature spermatozoa of both O. caudex and Ikedosoma gogoshimense are almost identical, characterised by low acrosomal caps and a single middle-piece mitochondrion surrounding the centrioles. A single large mitochondrion is also found in the spermatozoa of echinoderms (Longo & Anderson, 1969a). The spermatozoa of some other invertebrates such as Spisula solidissima (Longo & Anderson, 1969b); Arenicola brasiliensis (Sawada, 1975); Travisia japonica (Ochi et al, 1977) and Golfingia ikedai (Sawada, 1980) are charactersied by the presence of four mitochondria in the mid-piece. There are five mitochondria in Mytilus edulis (Niijima & Dan, 1965; Longo & Dornfeld, 1967) while six have been reported in Lumbricus terrestris (Anderson et al, 1967).

REPRODUCTIVE CYCLE

Our current knowledge about the reproductive behaviour and spawning in echiurans is limited. No observations have been made on the spawning of echiurans under natural conditions in the field. Factors controlling the simultaneous release of gametes by males and females in neighbouring burrows have yet to be analysed. Since these animals shed their gametes into the sea, synchronization of spawning is essential to assure fertilization.

From the observations that have been reported by some of the authors, it is now apparent that gamete production is seasonal in some species while being continuous in others. Ohkawa (1958) mentions that spawning in _Urechis unicinctus_, from Japan, occurs in winter and lasts from the beginning of October to the end of February. Yamamoto _et al_ (1973) report the presence of small oocytes in the coelomic fluid of this species in early October with only a few eggs in the gonoducts. These authors, however, discovered mature eggs in the gonoducts in addition to growing oocytes in various stages of development in the coelomic fluid in early November.

In _Urechis caupo_ from off southern California, on the other hand, eggs and sperm may be obtained from the animals continuously throughout the year (MacGinitie, 1935). Similar observations have also been made by Gould-Somero and Holland (1975), who investigated oocyte differentiation in this species.

From ecological investigations on *Echiurus echiurus*, Gislen (1940) has concluded that spawning in this species occurs in mid-winter.

The breeding season of *Ochetostoma bombayense* lasts from June to November and during this period the gonoducts are filled with eggs (Awati & Deshpande, 1933).

Sawada and Ochi (1962), who investigated fertilization and development in the echiuran *Ikedosoma gogoshimense*, mention that the oogonia first appear in the coelomic fluid in May and June and differentiation continues into winter.

Pilger (1980) studied the annual cycle of oogenesis, spawning and larval settlement of the echiuran *Listriolobus pelodes*, a species particularly amenable to such investigations as it occurs in large aggregations off the coast of southern California. Here, small oocytes are released from the gonad through most of the year but mature oocytes are present from mid-fall through spring (Pilger, 1980). The duration of oogenesis has been estimated to be 5 to 6 months. Spawning is said to take place over an extended period from late winter through spring and individuals are spawned out by summer.

Detailed information is still needed on various aspects of the breeding behaviour of *O. caudex*. Studies of large numbers of individuals in their natural habitats, over a period of one year, will provide us with more reliable seasonal data. From observations on the presence of sexual cells in the gonoducts of specimens collected at fairly regular intervals, it is evident that gametogenesis and gamete release occur throughout the year. A sudden change in temperature may be one of the factors responsible for triggering gamete release in this species. Since oocytes are readily available during all seasons of the year, O. caudex may well prove to be an ideal species for further oogenetic studies.

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Discussion

In recent years, interesting reports have appeared on some aspects of the functional anatomy of echiurans while other aspects are virtually unknown. The sexually dimorphic bonellids appear to have received more attention in comparison with some other species. The paper by Harris & Jaccarini (1981) on the structure and function of the anal sacs of Bonellia viridis is a significant contribution. It has been shown that a unidirectional flow of the filtrate into the sacs is maintained by the ciliary activity of the funnels. A comparative analysis of the anal sac fluid with the coelomic fluid, and surrounding sea water has revealed that the filtrate passes unmodified to the outside. According to these authors, the sacs do not appear to have a clear iono- or osmoregulatory function. Further work of a similar nature on some other species may provide useful information for comparative studies.

Virtually nothing is known about salinity and temperature tolerances of echiurans. Many species are known to inhabit shallow waters of the intertidal zone where salinity and temperature conditions are subject to considerable variations. A study of some of these factors should provide a better understanding of the vertical and horizontal distribution of species. Harris & Jaccarini (1981) obtained interesting results from their experimental work on the osmotic behaviour of Bonellia in various concentrations of sea water. These authors found that Bonellia gained weight after being transferred to a lower salinity but did not regulate its volume after transfer into 75% sea water. Furthermore, it was established that this species did not tolerate 50% sea water. The difficulty in obtaining sufficient material for experimental work of this nature, is probably why such investigations have never been carried out.

Although the anatomy of the vascular system and the circulation through the major vessels of echiurans is fairly well known, the course of the blood flowing back through the ventral vessel is still somewhat obscure. A comparative study of the blood systems of *Rubricellatus pirotansis*, *Listriolobus brevirostris* and *Ochetostoma septemyotum* by Menon & Datta Gupta (1976) has revealed some interesting features both morphologically and physiologically. These authors have suggested that the blood flowing posteriorly through the ventral vessel finds its way back to the ring sinus through the system of sinuses which lie on either side of the intestinal siphon. This explanation seems reasonable as there are no distinct vessels returning the blood from the posterior part of the trunk to the ring sinus. More detailed investigations based on radio-opaque contrast medium will probably shed more light on this problem.

In spite of the extensive studies on the coelomic fluid of echiurans, there are still aspects that need further investigation. As a result of previous studies, it has become apparent that the coelomic elements show interesting variations in different species. Menon (1976) has suggested that a study of the coelomic corpuscles may be useful in understanding the affinities of the different genera of echiurans. This author has reported the presence of three different types of corpuscles in *Rubricellatus pirotansis*. Ditadi (1976) has determined the coelomic volume, haematocrit, and mean corpuscular volume of *Lissomyema exilii* and that of other large cavitated worms. Using histochemical techniques, the latter author has demonstrated the presence of DNA in the nuclei of the haemocytes.

Current knowledge of the mechanism of food capture, transfer and the selection of food in echiurans is rather limited. Proboscis ciliation and the specific role of different types of cilia of Bonellia viridis have been studied in detail by Jaccarini & Schembri (1979). In addition to feeding, the cilia on the terminal lobes of the proboscis of this species aid in attachment and hence have an important role in locomotion.

Although the gross morphology and the histological details of the different parts of the alimentary system are fairly well known, very few accounts are available on the digestive enzymes of echiurans. Chuang (1963) has investigated the digestive enzymes of Ochetostoma erythrogrammon and has established the presence of a strong amylase, a strong protease, a moderately strong esterase and a weak maltase. In starved specimens, the pH value of the midgut fluid was found to vary from 7,0 to 8,2. Bornö (1971) has reported on the proteolytic enzymes of Echiurus echiurus. According to him, the pH value in the gut rises from about 7,5 in the pharynx to about 9,5 in the posterior part of the midgut and then falls to about 8,2 in the hindgut. The proteolytic activity curve showed a broad optimum around pH 10 at casein digestion. Bornö observed a strong tryptic but no chymotryptic activity. Furthermore, he established the presence of dipeptidase activity in this species. It is thus apparent that further biochemical and physiological studies on the digestive enzymes are required on other species.

Although some significant contributions have been made on locomotion, burrowing and on other movements in echiurans, the investigations are based largely on visual observations and lack the advantages of modern electronic recording techniques. In the present thesis, the hydraulic mechanism of O. caudex was investigated in detail and the results compared with those of some other animals with unsegmented coelomic cavities. It is surprising that this exceptionally favourable material for such studies has been so little used. It is hoped that further research in this direction will help supplement the present findings.

The mature and nearly mature eggs of *Urechis* have been studied intensively by cytologists and biochemists. Numerous detailed reports have appeared, in recent years, on the changes occurring in the eggs after fertilization. Our knowledge of the early developmental stages is somewhat limited and fragmentary. It was therefore considered worthwhile to undertake a study of the reproductive organs and the process of oogenesis and spermatogenesis in *O. caudex*. Although not very conclusive, some observations on the breeding behaviour of this species have also been included as a starting point for further research. More reliable data is needed on the spawning of echiurans under natural conditions.

In addition to the possible areas broadly outlined above, there are several other aspects of the functional anatomy of echiurans that require further study.

SUMMARY

The southern African echiuran fauna currently comprises two families, the Echiuridae and Thalassematidae, four genera, *Ochetostoma*, *Thalassema*, *Anelassorhynchus* and *Echiurus* and eighteen species. In accordance with the system of classification adopted by Datta Gupta (1976), the family Thalassematidae is subdivided into two subfamilies, the Ochetostomatinae and Thalassematinae. The family Echiuridae contains a single genus, *Echiurus* and in southern Africa, *E. antarcticus* is the only species recorded to date. This survey reveals that there are ten species of *Ochetostoma*, four of *Thalassema* and three of *Anelassorhynchus* in southern Africa. The taxonomic positions of three other species, one of *Ochetostoma* and two of *Thalassema*, remain to be resolved. Of the recorded species, three are new to science and a further five are new records for the region. Full descriptions of the new species and those formerly inadequately described are given. The diagnoses of some others are modified and, where necessary, additional notes added. Keys for the identification of families, genera and species are provided.

The geographic distribution of the southern African species is mapped and discussed and an attempt has been made to analyse the recorded species on the basis of faunistic provinces.

The phylogenetic position of the Echiura in the system of the animal kingdom is discussed. The lack of any form of segmentation of the mesodermal bands during embryonic development seems to justify their status as a separate phylum.

In the present investigation, some aspects of the functional anatomy have also been included. The biomechanics of burrowing, locomotion and trunk irrigatory movements of *Ochetostoma caudex* are described in detail and the results compared with those of some other animals with unsegmented

coelomic cavities. Pressure fluctuations within the coelom have been measured with the use of electronic recording techniques and the results interpreted in relation to direct visual observation.

The anatomy of the reproductive system and the process of gametogenesis in Ochetostoma caudex have been studied with light and electron micro=scopes. In this species, gametogenesis and gamete release occur throughout the year with peak periods reached during the warmer months, probably lasting from the beginning of February to the end of April. Although not very conclusive, some observations on the breeding behaviour of this species have also been included as a starting point for further research.

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