THE ANATOMY AND TAXONOMY OF *AMORPHONEMERTES KUBERGENSIS* GEN. ET SP. NOV. (NEMERTINI) FROM THE TROMSØ AREA (NORWAY)

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The anatomy and taxonomy of a new heteronemertine, *Amorphonemertes kubergensis,* are described and illustrated. The species is characterized by, *inter alia,* a thick paleonemertine-like basement membrane, a proboscis with four nerves and three muscle layers with single and groups of longitudinal muscle fibres in the outer longitudinal muscle layer, well developed subepidermal circular muscle fibres in the posterior brain and mouth regions and well-developed longitudinal muscle fibres (horizontal muscle plate) dorsal to the foregut. The material was collected in the Tromsø area (Norway).

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KEYWORDS: Nemertini; Amorphonemertes kubergensis gen. et sp. nov.; anatomy; taxonomy.

INTRODUCTION

The heteronemertine fauna of the west coast of Sweden has been investigated by among others BERGENDAL (1900, 1903), GERING (1912) and CANTELL (1972, 1975, 1976, 1982). Norwegian heteronemertines have been studied by among others PUNNET (1903), CANTELL (1975, 1982) and SENZ (1993).

In this paper a new species belonging to a new genus *Amorphonemertes* from the Tromsø area (northern Norway) is described. In order that the intraspecific variation exhibited by this species could be investigated several individuals (of different size) were collected in 1975 and 1994. From the literature it is evident that species belonging to different genera need careful descriptions of their anatomy if better generic diagnosis are to be formulated (CANTELL 1982; GIBSON 1985). It is often a problem of nemertine research that incomplete specimens have been described i.e., specimens lacking their proboscis or posterior parts or without descriptions of their outer pigmentation. New characters have also been used since the original descriptions were made, especially the morphology of the proboscis, which seems to be an important character.

MATERAL AND METHODS

The nemertines upon which the following description is based were collected from the Tromsø area, Norway, in 1975 and 1994. The sampled material was placed in tubs and covered with stagnant water. The body length was measured with a drawing compass during normal extension. Living worms were observed and then anaesthetized with MS 222 or 7.5 % $MgCl_2$ before fixation. Bouin's fluid was the normal fixative and Heidenhains's iron-haematoxylin-eosin or Azan the normal stains. Descriptions were made from serial sections of four different specimens cut transversely.

TAXONOMY

Genus *Amorphonemertes* gen. nov.

Diagnosis. Basement membrane with amorphous intercellular substance containing few cells and a lot of fibres. Proboscis containing three layers (outer longitudinal, middle circular, inner longitudinal) and four proboscis nerves. The outer longitudinal muscle layer with both single and groups of longitudinal muscle fibres.

Type species. *Amorphonemertes kubergensis* sp. nov.

Etymology. The generic name *amorphous* refers to the amorphous intercellular substance in the basement membrane.

Amorphonemertes kubergensis sp. nov.

Diagnosis. Head triangular, margins with a pair of horizontal cephalic furrows. Caudal cirrus present. No eyes. Well-developed subepidermal circular muscles especially laterally in the posterior brain and the mouth regions. Dermal glands in the outer one-fourth to one sixth of the zone between the epidermal basement membrane and the outer circular muscle layer. Dermis not separated from the outer longitudinal muscles by a connective tissue layer. A lot of longitudinal muscle fibres between the dermal glands in the anterior region of the foregut. Numerous horizontal, dorsoventral and oblique

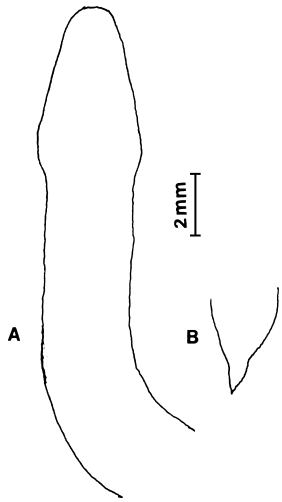


Fig. 1. Drawings of the anterior (A) and posterior (B) regions of *Amorphonemertes kubergensis* gen. et sp. nov.

muscle fibres in the region of the cerebral organs. Dorsoventral muscle fibres present between the lateral intestinal diverticula. Foregut provided with a distinct dorsal longitudinal muscle layer (horizontal muscle plate). Proboscis with two muscle crosses. A ventral vessel at about the level of the brain commissures. One pair of efferent ducts posteriorly in the excretory system. Where the dorsal ganglia separate from the ventral they are 2.5-3 times larger than the latter. Neurochord-like cells present. Apical sensory organs comprise three ciliated pits. Sexes are separate.

Type locality. The Tromsø area (Norway), shell gravel, including *Chlamys* shells, 30-50 m depth.

Type material. *Holotype*. A 135 mm long specimen from outside Kuberget, the Tromsø area (Norway), 30-50 m, shell gravel, deposited as a series of cross-sections at the Zoological Institute, Uppsala (Z.I.U.), Cat. No. Nemertini 9. Paratypes. Three specimens (sectioned material) from the same locality. Z.I.U. Cat. Nos. Nemertini 10-12.

Etymology. The specific name *kubergensis* comes from the name of the locality (Kuberget), where it was found.

Description

External characters. The worms are 10-135 mm long. The biggest specimen (135 mm long) is 5 mm wide and the length of the head 6 mm. The margins of the body are somewhat sharpened in the cephalic furrow and midintestinal regions.

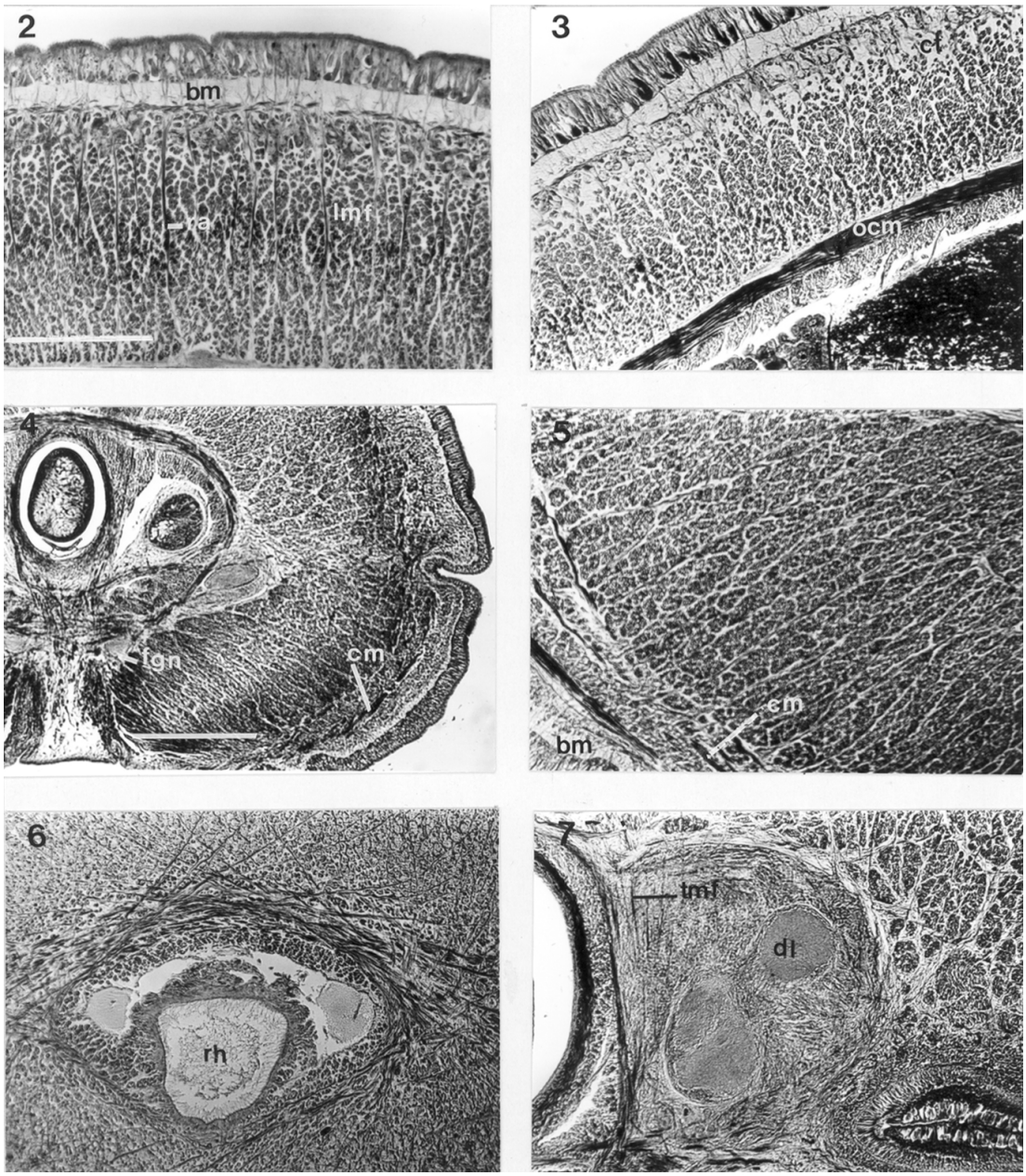
The triangular shape of the head is shown in Fig. 1A. The colour of the full-grown specimens is grey-green, somewhat brighter ventrally. Smaller specimens (10-35 mm long) are more yellow-white. A caudal cirrus is present (Fig. 1B). Anteriorly the cerebral ganglia are tinged a roseate colour and visible through the body wall. The extreme tip and margins of the head are paler.

Body wall (Figs 2-3). The epidermis, up to about 54 μm tall in the region of the cephalic lacuna, is thicker in the intestinal region (up to 84 μm). It is composed of numerous oval gland cells, which stain red or blue with Azan, the red being predominant. Below the epidermis a thick connective tissue layer, 24-48 μm thick, overlies outer circular and inner longitudinal subepidermal muscle layers. The true membrane is distinct, immediately beneath the epidermal cells as a typical thin fibrous entity. Below this there is an amorphous intercellular substance containing few cells and a lot of fibres. The subepidermal dispersed circular muscle layer (nearest to the basement membrane) is thicker in the foregut region (21 μm) than in the midintestinal region (6 μm).

Dermis (Figs 2-3). The dermis occupies about one-fourth to one-sixth of the zone between the epidermal basement membrane and the outer circular muscle layer. Towards the posterior region its development is gradually reduced. Internal to both subepidermal muscle layers there are groups (of different sizes) of gland cells. Between the groups of dermal gland cells around the mouth and anterior foregut region there are groups of longitudinal muscle fibres surrounded by connective tissue (Fig. 2). The numbers of longitudinal muscle fibres become fewer in the intestinal region (Fig. 3). The dermis is penetrated by radial muscle fibres surrounded by connective tissue (Fig. 2). Single dermal gland cells are internal to others along the radial muscle fibres in the foregut region. There is no clear boundary of connective tissue between the muscular and dermal zones.

Abbreviations in the figures.

bm	basement membrane	dl	dorsal lobe	pr	proboscis
cf	cephalic furrow	dvm	dorsoventral muscle fibres	prba	proboscis barb
cm	circular musculature	fgn	foregut nerve	prn	proboscis nerve
cc	cerebral organ	ilm	inner longitudinal muscle layer	ra	radial muscle fibres
ct	connective tissue	lmf	longitudinal muscle fibres	rh	rhynchodaeum
dc	dorsal commissure	ocm	outer circular muscle layer	tmf	tangential muscle fibres
dg	dorsal ganglion	olmpr	outer longitudinal muscle layer of proboscis	vec	ventral commissure



Figs 2-7. *Amorphonemertes kubergensis* gen. et sp. nov. Figs 2-3, 5-7: The same scale bar 0.2 mm (see fig. 2); Fig. 4: Scale bar 0.5 mm. 2. Cross-section through dermis in the region of the foregut. 3. Cross-section through dermis in the region of the midintestine. 4. Cross-section through the region of the anterior mouth. 5. Cross-section in the region of the mouth showing the subepidermal circular muscle fibres. 6. Cross-section through the region of the cephalic lacuna. 7. Cross-section through the region of the dorsal lobes of the brain.

Typically there are also thin dispersed circular muscle fibres (derived from the subepidermal circular muscle layer) in the cephalic lacunar and mouth regions. They are especially distinct laterally in the posterior brain and the mouth regions (Figs 4-5). In the posterior mouth region the subepidermal muscle fibres are concentrated below the basement membrane.

Body musculature (Figs 6-9). The arrangement of the main body wall muscle layers is typically heteronemertine and consist of outer longitudinal, circular and inner longitudinal layers, and in addition a variety of muscle fibres, single or in bundles, cross the body in various directions.

The outer longitudinal muscle layer is best developed and is mingled with the dermis; together the two regions are up to 770 µm deep. The radial muscle fibres are rather thin.

The outer circular muscle layer forms a partially tangential ring around the cephalic lacunae (Fig. 6). The tangential fibres are distinct. Some of the muscle fibres can be followed laterally above the cephalic furrows. In the brain region a number of muscle fibres lead from the outer circular muscle layer and pass outwards through the ganglion layer (Fig. 7) and also through the fibrous core. Posteriorly occasional tangential muscle fibres emerge from outer circular muscle.

In the cephalic lacunar and brain regions the inner longitudinal muscle layer is well developed (Fig. 6). In the brain region the inner longitudinal muscle layer is widest ventrally (up to 90 µm) (Fig. 8). The inner longitudinal muscle layers continue into the caudal cirrus, but the outer longitudinal muscle layer cannot be discerned.

Close to the cerebral organs the circular muscle layer of the proboscis sheath ventrally forms distinct horizontal, dorsoventral and oblique muscle fibres (Fig. 9). The dorsoventral muscle fibres comprise parallel bunches of fibres (Fig. 9).

In the somewhat sharpened body margins near the cephalic furrows there are thin dorsoventral muscle fibres both dorsal and ventral of the cephalic furrows.

Rhynchodaeum (Fig. 6). The rhynchodaeum opens from the subterminal proboscis pore and forms a tubular chamber. The epithelium of the rhynchodaeum has long cilia anteriorly (Fig. 6) but shorter posteriorly. Anteriorly it has a few empty gland cells. The rhynchodaeum is enclosed by abundant longitudinal muscle fibres, which in turn are surrounded by circular muscle fibres. The circular muscle fibres are laterally intermingled with the longitudinal muscle fibres. Just anterior to the brain these muscle fibres form a muscle sphincter (60 µm) around the posterior part of the rhynchodaeum.

Rhynchocoel (Fig. 10). The diameter of the rhynchocoel diminishes posteriorly. The rhynchocoel reaches to the end of the worm.

Below the epithelium there is a distinct connective tissue layer. The rhynchocoel is surrounded by two muscle layers comprising an inner longitudinal (9 µm) and thicker outer, circular muscle layer (42 µm). Posteriorly both are thinner.

In the regions of the cerebral organs and the mouth isolated fibres of the circular muscle layer in the rhynchocoel wall are ventrally somewhat interwoven with bundles of longitudinal muscle fibres in the horizontal muscle plate.

There are cross-overs between the rhynchocoel circular musculature and the outer circular musculature.

There are also dorsolateral tangential muscle fibres from the rhynchocoel circular musculature in the intestinal region.

Proboscis (Figs 10-13). The proboscis is divisible into three main regions. The first region adjoins the insertion and is characterized by an outer epithelium and a thick longitudinal muscle layer with two proboscis nerves which subsequently form a nerve plexus (a neural sheath with about four proboscis nerves) and a flat epithelium.

The second region which is very short, shows a thicker outer epithelium, an outer longitudinal muscle layer with single and groups of longitudinal muscle fibres (there are posteriorly only single longitudinal muscle fibres), a circular muscle layer, an inner longitudinal muscle layer and a flat endothelium (Figs 10-11).

The third region is characterized by the lack of outer longitudinal muscles.

Below the flat endothelium there is a thin inner circular muscle layer.

Two muscle crosses extend from the circular muscle layer through the longitudinal muscle fibres to the flat endothelium.

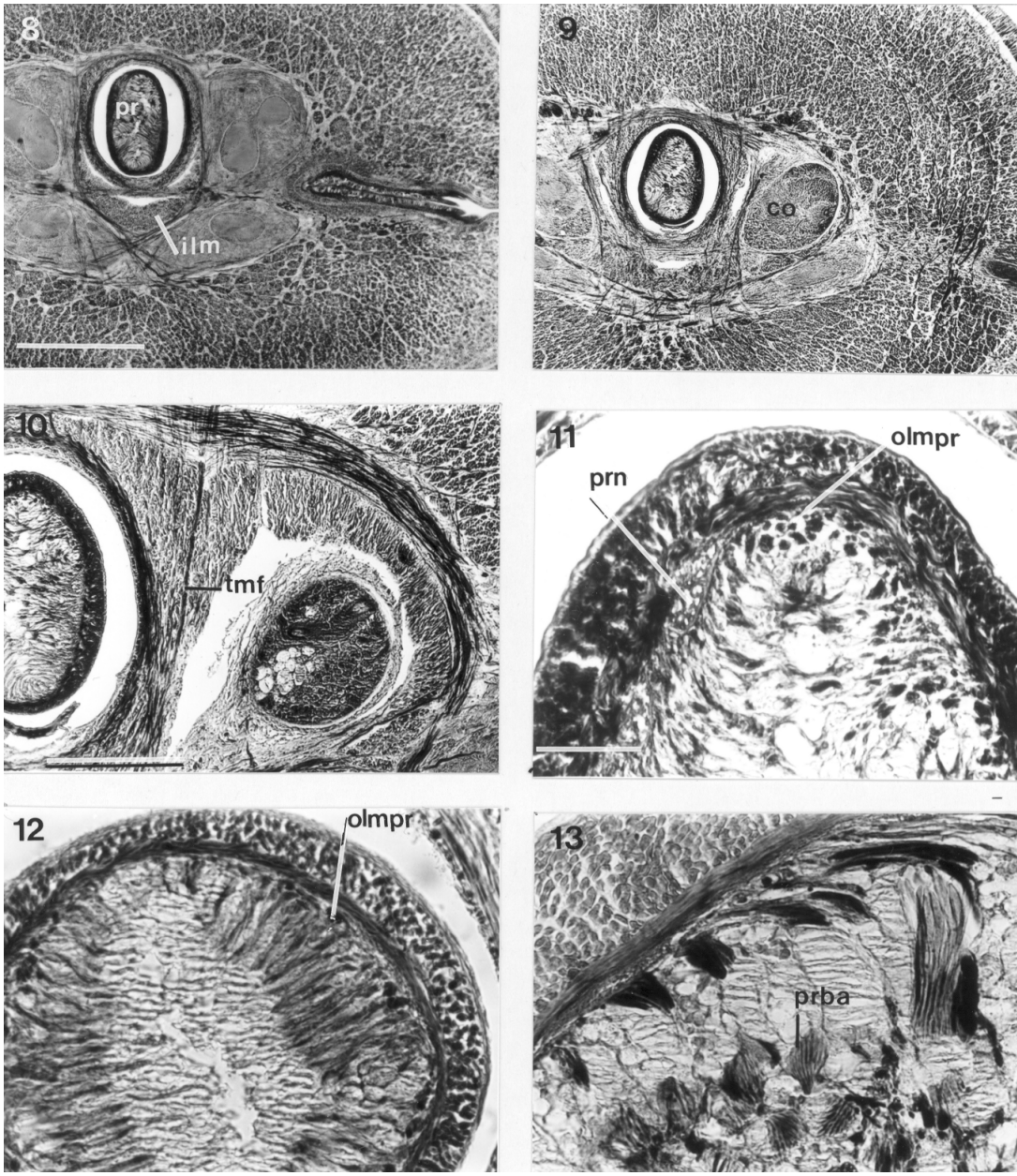
Short proboscis barbs or rhabdites are present, arranged into batteries (Fig. 13).

Digestive apparatus (Fig. 14). For most of its length the foregut is provided with a somatic musculature in the form of a few circular muscle fibres laterally and ventrally. Dorsal to the anterior mouth region the transverse (120 µm) and longitudinal muscle fibres (90 µm) are more abundant (Fig. 14). Lateral to the epithelium of the mouth there are dorsoventral muscle fibres (split off from the dorsal transverse muscle layer) which dorsally turn laterally into the outer longitudinal muscle layer. There are also radial muscle fibres lateral to the epithelium of the mouth (Fig. 14).

Dorsal to the foregut there is laterally up to 39 µm thick longitudinal muscle layer (horizontal muscle plate) (medially 9 µm thick). In the midintestinal region it comprises only a single row of fibres, the same occurring posteriorly.

In some parts of the foregut and intestinal regions (laterally and ventrally) there are single circular muscle fibres and inside these in some places single longitudinal muscle fibres. Mostly the inner longitudinal muscle layer borders on the epithelium of the foregut.

The single circular muscle fibres around the foregut



Figs 8-13. *Amorphonemertes kubergensis* gen. et sp. nov. Figs 8-9: The same scale bar 0.5 mm (see fig. 8); Fig. 10: Scale bar 0.2 mm; Figs 11-13: The same scale bar 0.05 mm (see fig. 11). 8. Cross-section through the region where the dorsal brain lobes are separated. 9. Cross-section through the region of the cerebral organs. 10. Cross-section through the region of the posterior cerebral organs. 11. Cross-section through proboscis in region 2. 12. Cross-section through proboscis in a smaller specimen (25 mm long). 13. Cross-section through proboscis showing the proboscis barbs.

are thickened between the foregut and intestine (30 µm).

Dorsoventral muscle fibres extend between the lateral intestinal diverticula.

There are subepithelial glands in the foregut.

Circulatory system (Figs 4, 6, 8-10, 14-16). The cephalic lacuna lies dorsal and lateral to the rhynchodaeum (Fig. 6). It possesses strands of muscle fibres passing across it and longitudinally. Therefore the

anterior part of the cephalic lacuna is divided into three or four chambers. Just anterior to the muscle sphincter around the posterior part of the rhynchodaeum it forms two vessels. At about the level of the brain commissures these anastomose to form a ventral lacuna (Fig. 15), which then splits into two lateral and one ventral (Fig. 8). In the region of the cerebral organs the ventral lacuna is divided into two lacunae (Fig. 4). Behind the mouth the lacunae reach right across the foregut and form a subalimentary plexus.

Posterior to the mouth the lateral lacunae become smaller. In the intestinal region they are situated ventrolaterally.

The dorsal vessel, which appears at about the level of the anterior brain region, anteriorly forms a rhynchocoelic villus (Fig. 10). It emerges from the rhynchocoel wall in the posterior region, and then runs posteriorly just above the gut.

Transverse connectives are present in the intestinal region between the dorsal vessel and the lateral vessels.

Nervous system (Figs 4, 7-8, 14-16). The brain is enclosed by distinct outer and inner neurilemma. It is surrounded by a lot of circular muscle fibres (Fig. 15). Some of the circular fibres can be followed laterally dorsal to the cephalic furrows.

Where the dorsal ganglia separated from the ventral they are 2.5-3 times as large as the latter (Fig. 16). There are distinct dorsal lobes (Fig. 7). A distinct dorsolateral nerve leaves the brain in the region of the brain commissures.

The foregut nerves, which lead from the inner margins of the ventral cerebral ganglia behind the ventral commissure, pass on either side of the mouth (Fig. 4). They are connected by five commissures (the fifth is broadest) anterior to the mouth and one behind it.

Anterior to the brain a dorsal nerve runs above the cephalic lacuna. Posterior to the dorsal brain commissure, a single nerve leads off in the midline to form the unpaired middorsal nerve which extends posteriorly outside the body wall circular muscle layer (Fig. 14). There are distinct dorsolateral nerves coming from the dorsal nerve to the outer longitudinal muscle layer in the regions of the cerebral organs and the mouth. There are also thin radial nerves along the radial muscle fibres coming from the peripheral neural sheath.

There are neurochord-like cells (50-60 µm) medially both dorsally and ventrally behind the commissures of the brain.

Sense organs (Figs 9-10, 17). There are no eyes. Apical sensory organs are present and consist of three ciliated pits situated at the tip of the head. There are frontal glands dorsally and ventrally in the region of the cephalic lacuna and posteriorly to the commissures of the brain. Posterior to the commissures some glands are still evident ventrally.

The cephalic furrows are deep and somewhat dilated posteriorly. The cephalic furrow opens posteriorly into the cerebral canal at a small papilla (Fig. 17). The epithelium of the cerebral canal contains many gland cells (Fig. 17), but there are no glands in the epithelium of the cephalic furrows. Posteriorly the whole of the median cephalic furrow epithelium is closely associated with neuroganglionic tissues.

The cerebral organs are about 90 µm high and 105 µm broad, and their posterior ends are enclosed by large blood lacunae. The cerebral canals, which are lined by long, densely arranged cilia, turn through up to three 90° bends before terminating near the posterior sides of the organ. After leading inwards the cerebral canals turn posteriorly and run dorsally. Near the posterior margins of the cerebral organ the canals turn through another 90°, run inwards and finally forwards to end in a mass of ganglionic and gland cells.

Each organ possesses upper and lower glandular components flanking a thick neural core.

The cerebral organs, besides being enclosed by a distinct connective tissue membrane, are also surrounded by loose connective tissue and a few circular muscle fibres (Fig. 10).

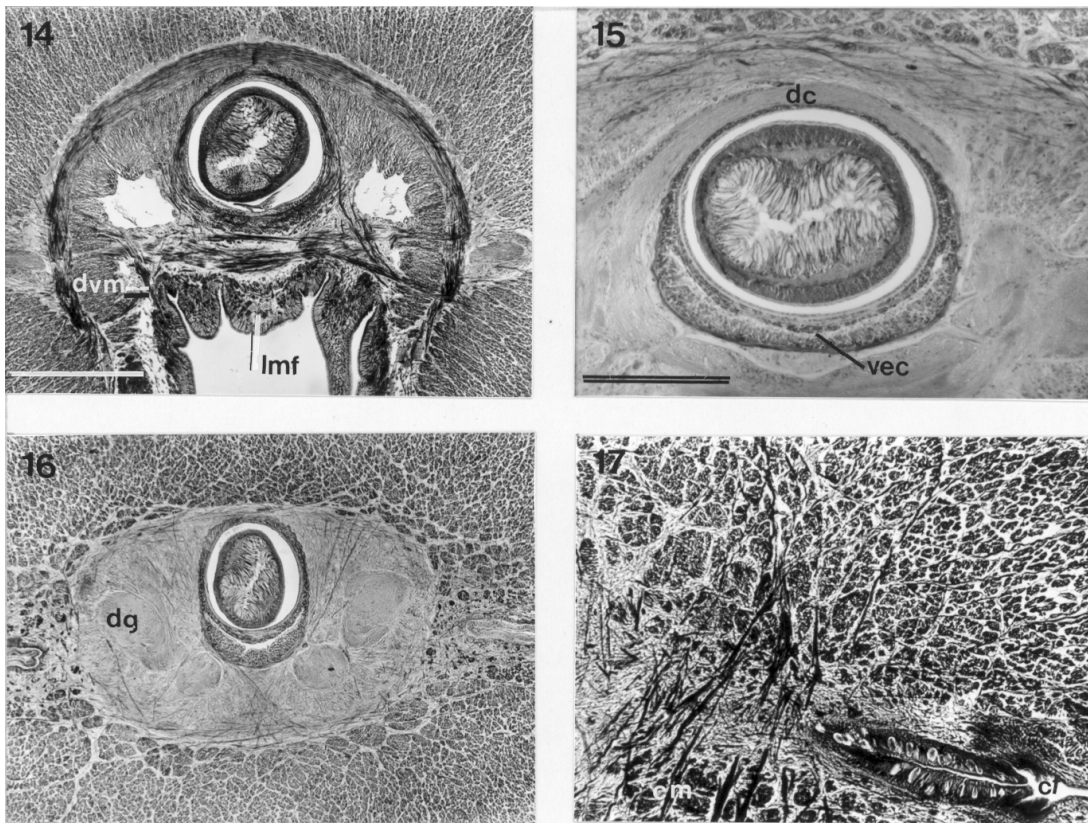
Parenchyma and connective tissue. Parenchymatous connective tissue is plentiful lateral to the rhynchocoel, and around the intestine, gonads and lateral blood vessels. In the intestinal region there is more connective tissue in the outer longitudinal muscle layer than in the foregut.

Excretory organs. Several nephridial canals are distributed around the foregut. They are situated in the lumen of the lateral lacunae and the lacunae around the foregut. One pair of efferent ducts has been observed at the posterior ends of the nephridial region.

Reproductive organs. The sexes are separate. Sexually mature females were observed in June-July. Eggs are about 72 µm in diameter. Gonoducts were present.

Characters during different stages of size. Cantell (1975) studied different sizes of *Micrura fasciolata* and showed that the morphological characters were fully developed when the worms attained a length of 5 mm.

Most of the characters were observed in a 10 mm long specimen of *Amorphonemertes kubergensis* i. e., an outer longitudinal muscle layer in proboscis with a row of lon-



Figs 14-17. *Amorphonemertes kubergensis* gen. et sp. nov. Figs 14, 16: The same scale bar 0.5 mm (see fig. 14); Figs 15, 17: The same scale bar 0.2 mm (see fig. 15). 14. Cross-section through the region of the mouth. 15. Cross-section through the region of the brain commissures. 16. Cross-section through the region of the dorsal and ventral ganglia. 17. Cross-section through the region of the cephalic furrows.

gitudinal muscle fibres, four proboscis nerves, a ventral lacuna in the region of the brain and a lot of longitudinal muscle fibres in the dermis, dorsal to the foregut. The laterally distinct subepidermal circular muscle layer in the posterior brain and the mouth region is not yet developed. There is only one nerve commissure between the foregut nerves in front of the mouth.

A 25 mm long specimen has groups of longitudinal muscle fibres in the outer longitudinal muscle layer (Fig. 12).

It is important that fully-grown specimens are studied when new species are described.

Remarks

This species is described as a new genus and new species, *Amorphonemertes kubergensis*, because of the special paleonemertine-like basement membrane. This character is the major autapomorphy. Below the true membrane there is an amorphous intercellular substance containing few cells and a lot of fibres.

This species has among others a regionally differentiated proboscis that contains an outer longitudinal muscle layer with single and groups of longitudinal muscle fibres, middle circular and inner longitudinal muscle layers, four proboscis nerves, two muscle crosses, a dermis which is not separated from the body wall outer longitudinal muscle layer by a connective tissue layer, a foregut with distinct dorsal longitudinal muscle fibres (horizontal muscle plate), an anterior blood system developed into a foregut plexus, distinct dispersed subepidermal circular muscle fibres laterally in the posterior brain and the mouth regions and neurochord-like cells.

Gibson (1985) suggested that nemertines having a proboscis with outer longitudinal, middle circular and inner longitudinal layers should be included in the family Cerebratulidae. The present species has a proboscis with a third layer containing both single and groups of longitudinal muscle fibres and is included in the family Cerebratulidae.

Besides the thick paleonemertine-like basement mem-

brane, a proboscis with outer longitudinal muscle layer containing both single and groups of longitudinal muscle fibres and distinct dispersed subepidermal circular muscle fibres laterally in the posterior brain and mouth regions are considered to be apomorphies for the species.

Amorphonemertes kubergensis gen. et sp. nov. shares a lot of similarities with the morphology of *Cerebratulus praealbescens* (CANTELL 1982), but differs in having a thick paleonemertine-like basement membrane, in having a triangular head and demarcated from the adjacent body region, a proboscis with an outer longitudinal muscle layer with single and groups of longitudinal muscle fibres, four proboscis nerves, more distinct subepidermal circular muscle fibres laterally in the posterior brain and mouth regions, the subepidermal circular muscle layer nearest to the basement membrane more concentrated, a ventral blood lacuna in the brain and also deeper cephalic furrows. Both species have one pair of efferent ducts in the excretory system.

PUNNET (1903) has described among others two species with grey pigmentation from Norway, *Micrura atra* (colour dark grey above, lighter on the ventral side. Head a very deep grey, almost black) and *Cerebratulus norvegicus* (colour light grey-brown above, much paler below). Because the species have similar pigmentation and the genera at that time were not well defined I compare these species with *Amorphonemertes kubergensis.*

Micrura atra differs from *Amorphonemertes kubergensis* gen. et sp. nov. in among others having two layers in its proboscis, excretory organs with more than one pair of efferent ducts, the dorsal ganglion in the brain not much larger than the ventral ganglion and no frontal glands.

Cerebratulus norvegicus differs from *A. kubergensis* gen. et sp. nov. in among others frontal glands practically being absent and having more than one pair of efferent ducts in the excretory system.

Amorphonemertes kubergensis gen. et sp. nov. has an interesting functional morphology with muscle fibres in diverse directions (as described above) which can change the shape of the worm in different directions.

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