DEVELOPMENTAL AND TAXONOMIC STUDIES OF SYDNEY HARBOUR KINORHYNCHA

by

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DECLARATION

I hereby declare that none of the work presented in this thesis has been submitted to any other university or institution for a higher degree. The information contained in this thesis is the result of my own original investigations, except where appropriate acknowledgements have been made.

Rosemary Brown.....

Rosemary Brown

DEDICATION

This thesis is dedicated to the man who said "Throw in the drag again, I really do enjoy rowing", and to some little boys who carried buckets of mud up cliffs without spilling any.

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This study of Australian Kinorhynchs could not have been carried out without the generosity of two American taxonomists. Dr. Woody Horning of the Macleay Museum, University of Sydney, has spent uncounted hours instructing me in scientific writing and illustration. To him I owe the better aspects of the style of this thesis and of the four publications included in it. Dr. Robert Higgins of the Smithsonian Institution, who has pioneered so much meiobenthic study, enthusiastically shared his knowledge, his expertise, and his comprehensive collection of Kinorhynch literature.

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CONTENTS

FIGURES

PLATES

54. Cuticular canal from membrane cell.
55. Hypodermal membrane system cell.
56. Membranes in cuticular pit.
57. Cuticular pit with trichoscalid-type membrane system.
58. Longitudinal section of sensory spot cilium.
59. Transverse section through sensory spot cilia.
60. Cilium in the mucous cell of seta.
61. Cilia in scalid.
62. J-1 posterior margin.
63. J-2 posterior margin.
64. J-3 posterior margin.
65. J-4 posterior margin.
66. J-5 posterior margin.
67. J-6 posterior margin.
68. J-1 sensory spot morphology.
69. Adult sensory spot morphology.
70. J-4 lateroterminal spinelet arrangement.
71. J-5 lateroterminal spinelet arrangement.
72. J-6 mid-dorsal spinose ridge.
73. Male posterior margin.
74. Pycnophyes faveolus cuticular sculpturing.
75. Pycnophyes faveolus cuticular sculpturing in detail.
76. Echinoderes teretis sieve plate.
77. Echinoderes teretis sieve plate detail.

INTRODUCTION

"Come....
Where the spent lights quiver and gleam;
Where the salt weed sways in the stream;
Where the sea beasts ranged all round
Feed in the ooze of their pasture ground;"

Matthew Arnold
The Forsaken Merman
37-40 (1869).

INTRODUCTION

The principal aim of the research project reported in this thesis is the description of kinorhynch head processes to provide data for taxonomic and systematic use. Observations are recorded of the morphology and ultrastructural histology of the scalids (head processes) of Kinorhynchus phyllotropis Brown and Higgins, 1983 - the first kinorhynch from Australia to be described.

Since the discovery of kinorhynchs in 1841 more than one hundred adult species have been recorded. These descriptions have been based on characters seen on trunk cuticle - sensory spots, muscle scars, hair perforation patterns, positions of setae, spines and adhesive tubes, morphology of the exoskeleton, and divisions and arrangements of the segmental plates. There is a significant disadvantage in using these classical characteristics. "Hoyer's medium is necessary to soften the specimen so that, by judicious manipulation of the coverslip, the specimen will assume a dorsoventral position...A disadvantage of normal Hoyer's medium is its tendency to clear the specimen too much" (Higgins 1983). This disadvantage may be partially overcome by modifying the composition of Hoyer's medium. However, with the passing of time, features such as sensory spots and muscle scars invariably fade.

This clearing process would not affect scalid number or scalid arrangement, but these kinorhynch head characters have not yet been used to distinguish between species, nor to distinguish between the juveniles and adults of any single species. No comparative study of head characters has been published.

It might be thought that a thorough description of a kinorhynch head would be sufficient to reveal useful taxonomic characters. This is not so. The adult head is a small spheroid, crowded with scalids, and investigative techniques distort it. It is not possible to confidently assign scalids to precise locations by observation alone. If an interpretation of the adult head is to be trusted by taxonomists, it needs to be supported by evidence, such as data on scalid ontogeny.

Few observations of scalid ontogeny have been published, and these are summarised later in this thesis, at the beginning of appropriate chapters. Some of these observations have been confirmed by study of K. phyllotropis. Zelinka's observation (1928, Plate 11, Fig. 3) has been confirmed that scalids are not crowded on the heads of young homalorhagid kinorhynchs, whereas scalids are crowded on the heads of later stages (Zelinka 1928, Plate 17, Fig. 5). A scalid point of origin is easily discerned in the head of a young juvenile. Different types of scalids can be seen to occupy the same locations in successive instars of the six juvenile stages. The same types of scalids occupy the same

sites on the adult head. The location of adult scalids can be confidently described when these scalids are traced from the early juvenile head where they are easily seen. Once the locations of scalids are known, scalid characteristics can be confidently investigated.

To describe scalid ontogeny it is necessary to ensure that all juvenile stages are examined by the study, and again this is not as simple as might be hoped. Descriptions of juvenile forms given in the accounts of Nyholm (1947 a, b) and Higgins (1961a) are contradictory and incompatible. So it is necessary to collect all organisms that might possibly be juvenile kinorhynchs and to sort them into a continuous series with kinorhynch characteristics. The ideal way of doing this would be to cultivate a kinorhynch population in the laboratory for several seasons and to remove juveniles from this population at frequent intervals. Unfortunately, several studies have shown that, while kinorhynchs can survive in laboratory conditions, these kinorhynchs have not been known to complete a life cycle in the laboratory (Boykin 1965, Kozloff 1972, Merriman and Corwin 1973). The alternative to a culture study should be the study of a field population from which a sufficient quantity of juveniles is sampled frequently enough to show a continuum of characters from the smallest juvenile to the adult.

Which character should form the criterion for establishing such a continuous series of juveniles? When I began the project reported in this thesis, I believed that trunk length would be an adequate index of whether a juvenile series was complete. Then in 1980 Higgins and Fleeger published their study showing that seasonal factors can influence size parameters much more than had been appreciated. Summer and winter populations of Echinoderes coulli Higgins, 1977b showed no overlap at all in the ranges of trunk lengths measured. I abandoned the idea of establishing a complete juvenile series based on trunk length. Instead characters of trunk cuticle were examined.

This line of investigation entailed a limited investigation of the sub-cuticular histology of ciliated or cuticular structures in both head and trunk. Ciliated head structures include the external scalids, the oral styles (scalids) and the internal scalids between the oral scalids and buccal aperture. These are described in the first chapters of this thesis. The alimentary canal and the excretory system have cuticular components and these are described in chapters following those describing head cuticular processes. The latter part of the thesis contains a chapter describing the histology of cells penetrating the cuticle of trunk plates - cuticular pore cells, ciliated hollow setae, membrane cells with cuticular ducts and ciliated cells below sensory spots.

To ensure that a complete and homogeneous juvenile series had been examined, posterior segment characters were selected and used to correlate a developmental series based on trunk characters with a developmental series based on head characters. These posterior segment characters include the relationship of the posterior mid-dorsal spine to the terminal margin, the morphology of the terminal margin and the morphology of the posterior mid-dorsal spine. These characters have the advantage that they can be seen with light microscopy in the same specimens that show the scalid characters. However the morphology of the terminal margin is probably a species specific character and only useful for distinguishing between developmental stages of K. phyllotropis.

The final chapter of the thesis examines patterns of cuticular variation between kinorhynch species, discussed in two conventional taxonomic descriptions of Sydney Harbour kinorhynchs, a homalorhagid and a cyclorhagid. Both of these demonstrate a radical degree of variation - the homalorhagid in cuticular embossing and the cyclorhagid in mid-dorsal spination. However, neither species could be considered to be aberrant. Their novel traits give insight into the variation permitted by the organisation of kinorhynch trunk cuticle. Other studies of interstitial fauna from the Sydney region have shown the presence of representative, non-aberrant forms. Comparison studies between these species and species from other continents has given

systematic perspectives that could not be obtained without the contribution of the Australian material (Brown 1981, Sasaki 1981, Sasaki and Brown 1983).

Sydney Harbour has provided particularly favourable conditions for kinorhynch research. Dense populations of the subject species are found in the northern arm. The scalid ontogeny study has required an abundant supply of kinorhynch specimens, for only a small proportion of a sample contains animals with extruded heads unless techniques are practised to promote head extrusion. Kinorhynchus phyllotropis is a large kinorhynch, and so it has been possible to perfect manipulations that squeeze out the retracted head without damaging the body. Another favourable factor is that the only sympatric species is a Pycnophyes that can be separated from the Kinorhynchus without elaborate magnification.

The first Australian to collect and describe a kinorhynch was Professor T. Harvey Johnston of Adelaide University, who was the Zoologist on Mawson's Antarctic Expedition of 1911-1914. Johnston, it was, who provided the pair of tweed trousers which flew from the masthead of the Aurora approaching Hobart. In 1938 Johnston described the Mawson material as Campyloderes macquariae. In this description he acknowledged his assistant, Mr. H. Hamilton, who at Macquarie Island scraped from the under surfaces of stones the material from which Johnston

obtained his kinorhynchs. Johnston's description was most generously detailed for its time yet none of his observations have been challenged in subsequent distribution records of this species (Higgins 1965, Moore 1973). Moreover, Johnston was the first taxonomist to recognise that a kinorhynch species which appears to have fourteen body segments has in fact only thirteen. He pointed out a common error in the interpretation of the posterior segments. Adult kinorhynchs are now recognised as having only thirteen segments (Higgins 1983).

The present thesis, the second Australian kinorhynch study, has benefited directly from Johnston's contribution. The taxonomic descriptions given here utilise his observations of posterior segment structure. I am proud to record this sequel to Harvey Johnston's work.

MATERIALS AND METHODS

"There is a path on the sea's azure floor
No keel has ever ploughed that path before."

Shelley
Epipsychidion
408-9 (1821).

"So follow me, follow, down to the hollow,
And there let us wallow
In glorious, glorious mud."

Flanders and Swan
The Hippopotamus Song
Chorus (1957).

MATERIALS AND METHODS

Collection of specimens

Field stations were selected by studying the Royal Australian Navy's Hydrographic Survey Maps (AUS 200 and AUS 204) and selecting likely areas of fine silt deposition. Kinorhynchs usually inhabit soft sediment with a high organic content (Higgins 1969).

Field stations were selected in 12 localities (Fig. 1).

Field Station 1. Hunter Bay (Balmoral) Sydney Harbour. 33o49'30"S, 151o15'24"E. Visual bearings: intersection of line connecting Grotto Point beacon with Waltons' wharf and line connecting Balmoral Naval Station Headquarters and Balmoral "Island". Collections made of sandy mud at 4-6 m depth in 1977 on 14 Aug; in 1978 on 19 Feb; in 1979 on 17 Mar and 10 Sep; in 1980 on 20 Apr, 5 May, 22 Jun, 14 Dec, and 28 Dec; and in 1981 on 22 Mar and 15 Dec. Kinorhynchus phyllotropis and Pycnophyes sp. Polychaetes in same sediments include many Prionospio sp., Aricidea sp., Micronephtys sp., Exogone spp., and Pionosyllis sp., identified by H. Paxton.

Field Station 2. Spring Cove (Manly) Sydney Harbour. 33o49'S, 151o17'6"E. Visual bearings: transects approaching buildings on Store Beach. Collection made of sandy mud at 4-10 m depth on 10 Sep 1979. Pycnophyes sp. and K. phyllotropis.

Field Station 3. Wellington Reserve marina (Fairlight) Sydney Harbour. 33o48'3"S, 151o15'6"E. Visual bearings: transect parallel with shoreline of Wellington reserve between outer moorings. Collection made of sandy mud at 2-6 m depth on 10 Sep 1979. Pycnophyes sp. and K. phyllotropis.

Field Station 4. Watson's Bay. 33o51'18"S, 151o16'48"E. Visual bearings: transect parallel with Marine Parade from Watson's Bay wharf to Gibson's Beach. Collection made of sand at 4-8 m depth on 10 Sep 1979. No kinorhynchs.

Field Station 5. Rose Bay. 33o52'12"S, 151o16'0"-30"E. Visual bearings: interrupted transect along line connecting Lynne Park shoreline with Rose Bay Park shoreline. Collection made of fine sand at 2-4 m depth on 10 Sep 1979. No kinorhynchs.

Field Station 6. Taylor's Bay (Mosman) Sydney Harbour. 33o50'36"S, 151o14'48"E. Visual bearings: transect along line between Ashton Park and Chowder Head cliffs. Collection made of sandy mud at 6 m depth on 10 Sep 1979. No kinorhynchs.

Field Station 7. McCarr's Creek (Church Point) Pittwater, Broken Bay. 33o39'18"S, 151o16'30"E. Collection made of sandy mud at 2-4 m depth on 12 Jul 1979. Echinoderes sp. not found in Sydney Harbour.

Field Station 8. Careel Bay (Stokes Point) Pittwater, Broken Bay. 33o36'42"S, 151o19'24"E. Collection made of sandy mud at 2 m depth on 12 Jul 1979. Echinoderes spp. not found in Sydney Harbour.

Field Station 9. Erina Creek (Gosford) Brisbane Water, Broken Bay. 33o26'18"S, 151o21'33"E. Visual bearings: transects taken directly across path of power lines strung from concrete boat ramp. Collection made of coarse mud at 3-5 m depth on 12 Jul 1979. Echinoderes sp. found in Sydney Harbour.

Field Station 10. Pelican Island Channel, Brisbane Water, Broken Bay. 33o28'12"S, 151o20'E. Collection made of mud at 1 m depth on 12 Jul 1979. Echinoderes sp. not found in Sydney Harbour.

Field Station 11. Hardys Bay (Kilcare) Brisbane Water, Broken Bay. 33o31'12"S, 151o21728"E. Collection made of mixed sediments (recently dredged) on 12 Jul 1979. No kinorhynchs.

Field Station 12. Cunningham's Reach (Hunter's Hill) Lane Cover River, Sydney Harbour. 33o49'30"S, 151o08'45"E. Visual bearings: sandbanks along shoreline between Boronia Park and Field of Mars Wildlife Refuge. Collection made of coarse mud in lower intertidal region on 5 Nov 1979. Echinoderes sp.

Samples of subtidal muddy silt from these field stations were collected with a Higgins epibenthic dredge (Higgins 1961a) towed by a boat travelling at slow speed, or pulled by hand from a sandbank in shallow reaches (Cunningham's Reach). On submerged muds this dredge travels smoothly on its two broad runners which support a transverse steel bar angled to plane off the top centimetres of sediment which then collect in a canvas bag trailed behind. If the dredge encounters sand or weed it travels jerkily and becomes much harder to pull. This signal, conveyed up the hand-held tow line, indicates that the site will not produce kinorhynchs.

Sediment from the dredge was emptied into a plastic garbage can. Kinorhynchs were later extracted from the sediment by covering

the sediment with two to three times its volume of sea water, stirring the sediment to suspension, and pumping a fine stream of air bubbles through the suspension by means of a bicycle pump to which an aquarium aerator stone had been attached. Kinorhynchs became attached to the bubbles by their hydrophobic cuticular plates and travelled to the surface film where they were trapped. To assist this process it was necessary to remove mucilaginous algae or gastropods from the sample. After aeration the sample was left for a few minutes to clear the surface of sediment and then the surface was blotted with a sheet of paper, the organisms were lifted off, and washed into a net.

Samples designated for head study were then subjected to the osmotic shock of being rinsed in fresh water to promote head eversion before further processing.

Processing for Light Microscopy

Whole mounted specimens were arranged on microscope slides so that they could be used to obtain measurements and indices for taxonomic descriptions.

These specimens were fixed in Bouin's fixative, then mounted in Hoyer's medium onto a Cobb aluminium frame with the aid of an Irwin Loop. The Irwin Loop could be used to produce head eversion in adults and large juveniles by a garotting technique. The bottom of the loop was placed transversely across the neck of the specimen and pressure was applied until the head began to

protrude. Then the loop was placed at right angles to the long axis of the specimen and pressure was exerted along the midline by kneading the trunk until the head was completely everted. This technique succeeded with most large specimens, but only damaged young juveniles and specimens of small genera.

Each microscope slide was covered with a small cover slip which was manipulated to orient the specimen in a dorsoventral position. The cover slip was ringed with lacquer. It has been noted that after a few months of storage gas bubbles appear around specimens in some microscope slides. Another artifact that occurs in a proportion of stored slides is the appearance of oily droplets around some of the specimens. The causes of these aberrations are unknown. Some of the kinorhynchs stored in national museums overseas have suffered the same deterioration.

Specimens of K. phyllotropis were sectioned for light microscope examination. The purposes of these observations were firstly, to gain information on kinorhynch anatomy which has not been illustrated in the literature, secondly, to see whether there were marked changes of body organisation during juvenile development which could be investigated in detail with electron microscopy, and thirdly to provide an anatomical context for the small fields of view provided by the transmission electron microscope (TEM).

The following specimens were sectioned for examination by light microscopy:

Specimen no.

J-1/1 Trunk length 230 um. Incomplete series of transverse sections (specimen torn)

J-1/2 Trunk length 250 um. Serial transverse sections

J-1/3 Trunk length 250 um. Serial sagittal sections

J-1/4 Trunk length 240 um. Serial frontal sections

J-2/1 Trunk length 370 um. Serial transverse sections

J-2/2 Trunk length 340 um. Serial frontal sections

J-2/3 Trunk length 330 um Serial frontal sections

J-3/1 Trunk length 410 um. Serial transverse sections

J-3/2 Trunk length 410 um. Serial transverse sections

J-3/3 Trunk length 440 um. Serial frontal sections

J-4/1 Trunk length 450 um. Incomplete series of transverse sections (poorly stained)

J-4/2 Trunk length 530 um. Serial transverse sections

J-4/3 Trunk length 470 um. Serial transverse sections

J-4/4 Trunk length 450 um. Serial frontal sections

J-5/1 Trunk length 550 um. Serial transverse sections

J-5/2 Trunk length 540 um. Serial frontal sections

J-6/1 Trunk length 620 um. Serial transverse sections

J-6/2 Trunk length 570 um. Serial frontal sections

Male 1 Trunk length 790 um. Serial transverse sections (young)

Male 2 Trunk length 850 um. Serial transverse sections (old)

Male 3 Trunk length 690 um. Serial frontal sections

Female 1 Trunk length 620 um. Incomplete series of transverse sections (block broke)

Female 2 Trunk length ? Incomplete series of sagittal sections of posterior segments with spermatophore

Female 3 Trunk length 630 um. Serial frontal sections.

All juvenile stages as well as male and female adults were sectioned completely in both frontal sections and transverse sections. Representative frontal sections were photographed and drawn as Fig. 23. Kinorhynchs for light microscope sectioning were embedded in Spurr's embedding medium by the procedure outlined below, sectioned in one micrometre "thick" sections, placed in sequence on eight drops of water arranged on a microscope slide, stained with methylene blue, washed by dipping into a Coplin jar, dried, covered with Spurr's embedding medium and then with a long coverslip pressed down with a lead weight. Initially these sections were mounted in D.P.X., but this was found to wrinkle the embedding medium.

Processing for Transmission Electron Microscopy (TEM)

Specimens of K. phyllotropis (and one Pycnophyes sp. specimen) were sectioned for TEM examination. The purpose of this examination was to provide detailed information on head and trunk cuticular structures, as well as cuticularised systems such as the alimentary canal and the excretory system.

Samples were fixed in 2% glutaraldehyde with 0.1M sodium cacodylate and 1.5% sucrose in sea water, post-fixed in cold 1% osmium tetroxide in sodium cacodylate buffer, and stored in a buffer of 0.1M sodium cacodylate, 1.5% sucrose and sea water (Anderson and Personne 1970). Specimens were dehydrated in alcohol and transferred in graduated steps to Spurr's embedding medium and then polymerised. In almost one half of all juvenile kinorhynch samples prepared this way, the embedding medium penetrated the tissues but not the body cavities. Cells were embedded in polymerised plastic, but the areas between the cells held crumbling unpolymerised plastic. The method was constantly modified in an attempt to prevent this result - dehydration, embedding and polymerisation techniques were changed - but the success of this processing remained idiosyncratic. For some unknown reason adult kinorhynchs embedded without problems.

Specimens were sectioned and stained by placing the grid downwards on

one drop of 50% ethyl alcohol,

one drop of uranyl acetate in 50% ethyl alcohol, 20-30 min.,

three drops of 50% ethyl alcohol in succession,

three drops of distilled water in succession,

one drop of lead citrate (Reynold's solution), 5-10 min.,

three drops of distilled water in succession,

then lowered sideways into a specimen tube of distilled water 2-3 times.

Grids were then photographed with the camera of a JEOL JEM 100 CX transmission electron microscope.

The following specimens were sectioned and examined by TEM:

Specimen no.		
J-1:1	Trunk length 230 um.	Representative transverse sections
J-1:2	Trunk length 240 um.	Representative transverse sections
J-1:3	Trunk length 230 um.	Representative sagittal sections
J-2:1	Trunk length 320 um.	Representative transverse sections
J-3:1	Trunk length 410 um.	Representative transverse sections
J-4:1	Trunk length 490 um.	Representative transverse sections
J-5:1	Trunk length 580 um.	Representative transverse sections
J-6:1	Trunk length 610 um.	Representative transverse sections

Male 1 Trunk length 710 um. Transverse sections anterior to pharynx

Male 2 Trunk length 780 um. Representative sagittal sections

Male 3 Trunk length 680 um. Representative transverse sections

Female 1 Trunk length 730 um. Representative transverse sections

Female 2 Trunk length ? Sagittal sections of posterior segments and attached spermatophore.

Processing for Scanning Electron Microscopy (SEM)

Specimens of K. phyllotropis and Pycnophyes sp. were processed for scanning electron microscopy. The purpose of SEM examination was to provide information on surface cuticular features of all juvenile stages, as well as males and females. Samples were fixed as for TEM study, then transferred to distilled water in small aluminium foil cups (moulded on an SEM stub), which were lowered in a metal basket into liquid nitrogen for rapid freezing, and then dried under vacuum. Some specimens were then subjected to dissection with double-sided adhesive tape. The purpose of this procedure was to give information on cuticular structures viewed from the inside of the cuticle, but the technique also gave information on the SEM appearance of spermatozoa (Brown 1983).

Specimens to be dissected were first mounted dorsally or ventrally on SEM stubs covered with double-sided tape.

Kinorhynchs could be transferred and carefully positioned on SEM stubs by rubbing them with an eye-lash attached to an orange stick, so that they were electrostatically attracted to the eye-lash. Then a second strip of tape was placed over these kinorhynchs and pressed against them with finger pressure. The second strip was torn away and placed over a second stub. The strips were trimmed.

Fractured and whole-mounted specimens were coated with a layer of gold and photographed using a JEOL T20 SEM.

Illustrations

Specimens and micrographs were illustrated in the form of habit studies, semi-schematic illustrations, micrograph montage illustrations, schematic diagrams and symbolic representations.

Habit studies of the external scalids of juvenile and adult heads were drawn from light microscope preparations in both dorsal and ventral views (Figs. in Appendices 1-3). This was judged to be the best form of presenting evidence because the depth of field of scanning electron micrographs was not sufficient to be considered convincing. Habit studies were similarly drawn to illustrate the taxonomic descriptions.

Semi-schematic illustrations were produced to show the relationships of cuticular structures to other organs. Such

illustrations are more suitable than habit studies for formal publication where it might be assumed that a reader has a degree of acquaintance with kinorhynch literature. Examples of these illustrations are Fig. 3, a longitudinal section through the head, and Fig. 13A, a longitudinal section through the oral cone.

Micrograph montage illustrations were drawn from groups of transmission electron micrographs. This was done where the field was too big to be photographed in one low power micrograph, as in Fig. 5 of a transverse section through the top of the introvert, which was drawn from three micrographs which overlapped in their fields of view. This technique was also used to illustrate relationships of TEM sections to the whole structure as in the illustrations of internal scalids (Figs. 14-17).

Schematic representations have been devised to show the relationships of cuticular structures such as external and internal scalids to the axis of symmetry of the kinorhynch body plan. The kinorhynch head is decaradial. The kinorhynch trunk is bilaterally symmetrical down the midline and it is dorsoventrally flattened. To show the relationship of internal scalids to external scalids, a diagram with ten radii was produced (Fig. 19A). The development of different types of external scalids was illustrated with diagrams of juvenile and adult heads drawn around the long axis of the body, and simplified to the point of geometric abstraction (Fig. 8).

(Readers not familiar with kinorhynchs have commented that these diagrams are helpful.)

Symbolic representations have been produced for kinorhynch specialists, to facilitate comparison between species, and between developmental stages. Two symbolic systems have been employed in this study.

One system (Figs. 4, 6 and 8) is a set of seven geometric shapes used to symbolise each of the seven rings of external scalids. Ring one scalids are represented by a triangle, ring two scalids by a circle, ring three scalids by a square, ring four by an oval, ring five by a rayed hexagon, ring six by a rayed diamond and ring seven by a finned circle. This system has been carefully chosen by Robert P. Higgins and me to facilitate a coordinated approach to the taxonomic use of head characters. The symbols have been selected for their accessibility and for their visual proximity to the subjects they represent.

The other symbolic representation, the "Chinese fan" diagram, (Figs. 7, 20, 2.5, 2.10, 2.15, 3.5) has been devised in this study to show the positions of the external scalids during developmental stages of K. phyllotropis. Previous workers have illustrated the positions of external scalids with concentric circle diagrams. Concentric diagrams involve a distortion which frustrates their usefulness. The trichoscalids of ring seven are spaced widely around the circumference of a circle, whereas on

the head they are crowded together. The ten large scalids of ring one are massed around the centre of the concentric system, whereas in the head they are less crowded than the fourteen trichoscalids. Another difficulty is provided by the phenomenon that everted heads of kinorhynchs are rarely seen in a perfect dorsoventral relationship with the first and tenth sectors lying directly apposed. The kinorhynch head is spheroid and it accommodates to being flattened in a microscope slide by folding, wrinkling or tearing. However it is important to understand which head sector is being observed, for there are differences between the sectors especially in the asymmetrical seventh ring. The "Chinese fan" representation shows a head that has been sliced between the sixth and seventh sectors and spread flat. With this representation it is possible to take a specimen with an extruded head and to identify the sectors being observed. To do this with a concentric circle diagram involves turning the diagram round and round until the appropriate orientation is recognised, and this is rendered extremely difficult by the distortion. It is possible that the concentric circle diagram will be used to compare patterns of external scalid insertion among different taxa. But for the purpose of comparing the scalid arrangement at any stage of development with a specimen on a microscope slide, the "Chinese fan" diagram is a decided improvement.

Figures have been numbered with two numbering systems. Text figures have been numbered consecutively. Appendix figures have

been numbered in two parts. The first part refers to a particular appendix, and the second part is the number of the figure among the sequence in that appendix. Figure 3.12 is the twelfth figure in Appendix 3.

Taxonomic Data

The data resulting from microscopic analyses are expressed in a standard format of abbreviations and terminology (Higgins 1967, 1969). Measurements are given in micrometres (um). Ratios (e.g. SW/TL) are expressed as a percentage of total length (TL) measured at the mid-line, from the anterior margin of segment 3 (first trunk segment) to the posterior margin of segment 13 (last trunk segment), exclusive of spines. Maximum sternal width (MSW) is measured at the antero-ventral margin of the widest pair of sternal plates as first encountered in measuring each segment from anterior to posterior. Sternal width at segment 12, or standard width (SW), is measured at the anterior margins of the twelfth sternal plates. Segment length (SL) is a measurement of the chord formed by the optical section view of the left (or right) margin of each segment from the anterior edge of the pachycyclus (thickened anterior portion of each segment) to the posterior margin of the segment.

RESULTS

"O what an endlesse worke
I have in hand,
To count the seas
abundant progeny
Whose fruitful seede farre
Passeth those in land"

Spenser
The Fairie Queen.
iv, 12 (1609).

RESULTS

Chapter 1.

External scalids of the head of adult Kinorhynchus phyllotropis

Previous work

Significance of the kinorhynch head

Kinorhynchs are among the smallest metazoa. Understanding of their complex histology is still elementary, and electron microscope investigations have already upset some long standing tenets. Conventional wisdom accepted Zelinka's observation that the kinorhynch epidermis was syncytial until transmission electron microscope study showed that epidermal intercellular spaces are extremely small, smaller than RER cisternae (Moritz and Storch 1972a). A statement that kinorhynchs lack cilia has been included in definitions of the phylum (Chitwood 1958, Higgins 1981, Hyman 1951). However, while kinorhynchs may lack motile cilia, they do not lack modified cilia. Moritz and Storch (1972 a, b) showed that in the kinorhynch external scalid "an apically open spine is invaded by two receptor cells distally bearing cilia" (Welsch and Storch 1976). Each scalid has a proximal section or socket containing a striated rootlet, and a distal section or endpiece packed with bundles of tubules which project from the scalid tip into the ambient water.

The kinorhynch head is an introvert. Incessant head eversion practised by living kinorhynchs has given the group its name (Gk. "kineo" = movement; "rhynchos" = snout). The significance attached to the kinorhynch head is likely to increase if the current themes of kinorhynch systematics continue to be heard. Current publications suggest, on the bases of similarities of scalid arrangement (e.g. pentaradial symmetry), presence of an eversible proboscis protected by neck plates, and similarities of the muscular pharyngeal bulb (triradiate lumen with radially oriented contractile elements), that kinorhynchs be united with priapulids (van der land 1968, Lang 1953) as well as nematomorphs (Malakhov 1980, Morris 1977) and possibly with the recently described Loricifera (Kristensen 1983). "The sister group of the Loricifera is probably the Kinorhyncha, with which, in general organisation, they share several unique characters such as the type of mouth cone with oral stylets; the first row of blunt scalids or clavoscalids; and the presence of a ventral closing apparatus. However, TEM investigations of both Kinorhyncha and Loricifera are necessary to support this hypothesis." (Kristensen 1983).

The following chapters describe the head of K. phyllotropis in detail, and so the anatomy of the head is schematised in Fig. 3. This figure differs from textbook illustrations of the kinorhynch head (de Beauchamp in Grasse 1965, Fig. 1131; Hyman 1951, Fig. 84C), and the following pages explain why this is so.

Arrangement of External Scalids in Homalorhagid Kinorhynchs

Zelinka (1928) observed that there are seven rings of recurved spines or scalids around the outside of the head of adult homalorhagid Pycnophyes communis Zelinka, 1928, and of the last juvenile stage as well. Zelinka counted 88-90 scalids arranged as follows:

Ring 1 - 10 scalids
2 - 10
3 - 20
4 - 10
5 - 10
6 - 14-15
7 - 14-15 (sometimes 12 or 13)

Zelinka observed that the kinorhynch head is divided into 10 sectors or antimeres, and he numbered these antimeres clockwise, with antimeres 1 on the right side of the mid-dorsal axis. Zelinka drew the mid-dorsal axis passing through the ring one scalid on the boundary between antimere 10 and antimere 1. Zelinka's midventral axis runs through the ring one scalid on the boundary between antimere 5 and antimere 6. Zelinka schematised the arrangement of the scalids around the ten antimeres with a concentric circle diagram (1928, Fig. 3) and a "Mercator's projection" (1928, Fig. 4). Both diagrams are reproduced here

(Fig. 2) so that Zelinka's findings can be compared with those of the present study.

Remane (1936) published a modified ("abgeändert") version of Zelinka's diagram without indicating the nature of the modification, and Remane's diagram was reproduced by Lang (1949). Lang's copy is also reproduced in Fig. 2.

Boykin (1965) counted the scalids of the homalorhagid Kinorhynchus ilyocryptus Higgins, 1961b and found that the total number and the scalid arrangement agreed with Zelinka's account. Boykin made the first attempt at detailed measurement of scalids, giving one figure, presumably an average, for the scalid length in each scalid ring. These measurements are included in Appendix 1, Table A.

Types of scalids

Zelinka (1928) described three types of homalorhagid scalids, the large spined scalids or spinoscalids of the first ring, the similar but smaller scalids of rings 2-6, and the trichoscalids or thread-covered scalids of the seventh ring. (When Zelinka described these adult scalids in pages 22-23 of his Monograph he referred his descriptions to figures depicting the last juvenile stage of P. communis).

The scalids of rings 1-6 are composed of a basal socket connected to a curved endpiece by a hinge of flexible cuticle. Zelinka (1928, Plate 17, Fig. 5) illustrated the ring 1 spinoscalid with a medial spine arising near the origin of the socket and projecting over the hinge joint at the distal end of the socket.

Optical sections or cut sections through the socket cuticle hanging over the hinge joint of scalids 2-6 were illustrated by Zelinka (1928, Plate 17, Fig. 6), Remane (1936, Fig. 236), Hyman (1951, Fig. 82e) and Moritz and Storch (1972b, Figs. 1, 5c). Some authors have interpreted these sections as showing a spine on ring 2-6 scalids. Merriman and Corwin (1973) interpreted the Moritz and Storch figures of Kinorhynchus giganteus Zelinka, 1928 as showing two spines per scalid. Remane (1936) noted that in some living specimens the spine appeared to be somewhat folded back. ("An dieser Grenzfalte kann der Stachel passiv nach hinten abgeknickt werden, eine Erscheinung, die sofort am lebenden Tier auffällt.") Such an appearance would be compatible with that of a flap of flexible cuticle overhanging the hinge. Boykin (1965) described the spine of the ring 1 spinoscalid, but made no mention of spines on other scalids.

Zelinka (1928) described trichoscalids as having a round section in contrast with the triangular section of previous rings. He noted that trichoscalids are covered with fine hairs and are borne on a scale in homalorhagid kinorhynchs. Boykin (1965)

observed that the sinuous trichoscalid walls are constructed of rings of cuticle connected by flexible membranes.

Scalid structure and cellular contents

As mentioned above, Moritz and Storch (1972 a, b) examined the ultrastructure of scalids of K. giganteus and found the elements of bipolar receptor cells bearing cilia in both spinoscalids and trichoscalids. These elements are found in basal cells occupying the socket of a spinoscalid or the proximal end of a trichoscalid. Bipolar receptor cell features include a striated rootlet (foot) of a cilium, a basal body, membrane systems arranged in characteristic piles, secretion granules and Golgi fields. Some basal cells are associated with bundles of tubules passing along the endpiece of the scalid to a terminal pore. These cilia are also found in the sense organs of nemerteans, turbellarians, molluscs, polychaetes and oligochaetes (Welsch and Storch 1976).

Moritz and Storch (1972b) observed two different types of spinoscalids. Type 1 spinoscalids have a robust joint between the socket and endpiece, and cuticle composed of parallel, electron-dense units which are arranged in layers each with a different grain orientation, as in plywood. A basal cell found in the socket of the type 1 spinoscalid (Moritz and Storch 1972b, Fig. 1) sends cytoplasmic processes through the constriction of

the scalid joint, and into the endpiece where they penetrate the cuticle distal to the flexible joint. This cell contains characteristic membrane systems. Two receptor cells containing cilia are also found in the scalid socket and they both send bundles of tubules to the tip of the scalid. The striated rootlets of these cilia are found in the socket. Thus the scalid has two sensory "windows" - a terminal pore, and a region of cuticle distal to the hinge joint.

Type II spinoscalids have electron-dense strips running the length of the scalid endpiece which stand out on the surface relief of the cuticle. The cuticle itself is composed of electron-dense U-shaped units forming scalloped striations near the cuticle surface. The hinge joints of these scalids are indistinct. Moritz and Storch did not attempt to correlate these types of spinoscalids with scalids of specific rings on the kinorhynch head.

Observations of present study

Scalid arrangement

Sections of the introverted head show that the adult *K. phyllotropis* has 89 scalids (Figs. 4 and 6). The arrangement of these scalids can be schematised in a plane diagram (Fig. 7). To utilise this plane diagram, especially for comparison with

juvenile stages, it is necessary to define two new terms.

"Odd sectors: those sectors of the head determined by the mid-dorsal line; from the mid-dorsal sector, every alternate sector is also an odd sector.
Even sectors: those sectors of the head determined by the midventral line; from the midventral sector every alternate sector is also an even sector."
Sectors are numbered clockwise.

Whole mounts of the everted head (Figs. 1.1-1.4) show that these scalids are arranged in seven rings as follows:

Table 1. Number of external scalids in each ring in adult Kinorhynchus phyllotropis.

Ring	No. of Scalids	Nos. allocated to scalids in Fig. 4
1	10	1-10
2	5 + 5	11-20
3	10	21-30
4	15	31-45
5	15	46-60
6	15	61-75
7	6 + 8	76-89
TOTAL	89	

Comparison of Fig. 7 with Zelinka's "Mercator's projection" diagram (Fig. 2B) shows that his observation of scalid arrangement in Pycnophyes communis is identical with observations of scalid arrangement in K. phyllotropis.

Zelinka's scalid count, however, assigned the scalids as follows:

Ring 1 - 10 scalids
2 - 10
3 - 20
4 - 10
5 - 10
6 - 14-15
7 - 14 or 15 (sometimes 12 or 13).

The apparent differences between scalid counts occur because ten of the twenty scalids which Zelinka assigned ring 3 may have been on a different level, viz. ring 4. Zelinka put these ten scalids on a different level when he drew them in his concentric circle diagram (see Fig. 2A) and his Mercator's projection diagram (see Fig. 2B). Remane's (1936, Fig. 217; also Fig. 2C) redrawing of Zelinka's concentric circle diagram changed the placement of ring 3 scalids in even-numbered antimeres without recording that this change had been made. The Remane version was adopted by Lang (1949, Fig. 2). See also Fig. 2C. At this point it might be asked why fastidious observers such as Zelinka, Remane, Lang and

Boykin accepted a homalorhagid scalid arrangement assigning 20 scalids to ring 3, when only 10 are assigned to ring 3 in the present homalorhagid study. The accuracy of the K. phyllotropis assignment, at least in the first four rings, is demonstrated by the habit studies in Appendix 1 and by the developmental history of the scalids. The answer to this question may lie in one of Boykin's careful statements. "Whereas the number of scalids may be accurately counted in sections, it is virtually impossible to assign a given scalid to a given row in whole mounts, hence the measurements given below may not be entirely correct." As Appendix 1, Table A indicates, the scalid length in K. ilyocryptus is much smaller than the scalid length in K. phyllotropis, although this varies from sector to sector, and from specimen to specimen, as is shown by comparison of Tables 1B and 1C of Appendix 1. In K. ilyocryptus scalid measurement is further complicated by the flexible papillae on which the scalids originate, which are not seen in K. phyllotropis. Kinorhynchus phyllotropis is a large species in which scalid arrangement could be expected to be clearer than in small species.

Comparison of Figs. 6 and 7 with Zelinka's diagrams will show that there is another significant deviation in the K. phyllotropis scheme. Zelinka drew the mid-dorsal axis passing through the ring one scalid between sectors 10 and 1 (Figs. 2A and 2B). In Figs. 6 and 7 of K. phyllotropis the mid-dorsal axis passes through the ring 2 scalid of sector 10, it has been

shifted eighteen degrees anticlockwise. There are concomitant shifts in the mid-ventral and lateral axes. The need to make this untidy adjustment is dictated by two separate sets of observations.

The first set of observations concerns the location of the midventral axis. The evidence is derived from data on the trichoscalids (scalids covered with threads) of ring 7. As indicated by Figs. 5, 1.3, 1.4 and by Table 1B, the midventral trichoscalid is smaller than all other trichoscalids. This trichoscalid is not located between sectors 5 and 6 as Zelinka's schemes would indicate, but is found in the centre of sector 5, the true midventral axis.

The second set of observations concerns the location of the lateral axes, for which the evidence comes principally from juvenile scalid development data. Study of trichoscalid ontogeny shows that, while the adult has fourteen trichoscalids in the last scalid ring (Figs. 5, 6, 7), the first four juvenile stages have only six (Figs. 2.5, 2.10, 2.15, 3.5). Eight trichoscalids develop from a form of scalid found only in the first four juvenile stages, called, in this study, a "protrichoscalid". Mid-dorsal and midventral protrichoscalids alternate with the six trichoscalids, but two protrichoscalids occur together on each of the two lateral axes (cf. Figs. 2.3-2.4, and especially Figs. 2.8-2.9 and 3.3-3.4 where sequential protrichoscalids are shown

on both sides of the body). Data on the first four juvenile stages show that these lateral axes occur in the centre of sectors 3 and 7, in line with the ring two scalids of those sectors. Zelinka's scheme would place them in line with the ring one scalids between sectors 7 and 8, and between sectors 3 and 4. The location of the true lateral axis is not only indicated by projecting the lateral suture line anteriorly into the scalids. The sectors in which the true lateral axes are located are shown by the number of trichoscalids between the paired protrichoscalids. This is explained in the following paragraph.

The six trichoscalids of the early juvenile stages are arranged so that there are two trichoscalids on each side of the body. The body shape of homalorhagid kinorhynchs is a triangular prism. Two trichoscalids occur on each of the three sides of this triangular prism. Thus the early juvenile stages of this homalorhagid have a bilaterally symmetrical trichoscalid arrangement. Four trichoscalids are found dorsal to the lateral axes and two trichoscalids are ventral. These trichoscalids form, in the adult, trichoscalids that are slightly longer than the eight trichoscalids which are derived from protrichoscalids. This is shown in Appendix 1, Table 1A and Table 1B. Table 1A shows that the four dorsal trichoscalids which have been present in all juvenile stages have lengths of 82, 81, 83 and 79 um. Four of the alternating scalids which have developed from protrichoscalids have lengths of 72, 79, 75 and 77 um. Table 1B

shows that the two ventral scalids which have been present in all juvenile stages measure 73 and 78 um. Three of the alternating scalids which have developed from protrichoscalids have lengths of 69, 61 (the midventral scalid), and 69 um.

Adult external scalid morphology (Fig. 4; Plates 2-10)

If K. phyllotropis external scalids are grouped according to morphology there are four kinds of external scalids. These four groups are

:ring 1 spinoscalids which have type II characteristics (Moritz and Storch 1972 a, b)

:ring 2-4 scalids which have type I characteristics and an endpiece devoid of hairs except for a V-shaped chevron of long hairs near the scalid hinge, these scalids are now designated by the term "smooth scalids"

:ring 5-6 scalids which have type I characteristics and an endpiece thickly fringed with cuticular hairs, these scalids are now designated by the term "fringed scalids"

:ring 7 trichoscalids which are covered with fine threads, and differ from other scalids in having a round section, not a triangular section.

Ring 2-6 scalids will not be referred to as spinoscalids because they do not have spines. The allocation of these four types of scalids to the different scalid rings is shown in Figs. 5, 6, 8 and 9.

Morphology of the adult ring 1 spinoscalid (Figs. 4A, 1.1, 1.3; Plate 7)

The ring 1 spinoscalid is the widest and longest scalid of the head. On each side of the origin of this scalid there is a flap formed of three or more hollow fused cuticular hairs, each 15 um long. The origin itself is marked by two parallel cuticular ridges which pass along the socket to the scalid joint. Between the cuticular ridges there is a groove lined with hollow cuticular hairs. This groove houses the hirsute hollow spine which arises from the scalid origin. This spine has an oval lumen which 0.6 um at its widest diameter, and is covered with hollow, fine cuticular hairs 6-8 um long. The joint of the ring 1 scalid is a fine constriction of cuticle at the end of the socket. Endpiece cuticle carries fine longitudinal grooves along the surfaces which rest against the head cuticle. The tip of the endpiece is bluntly rounded.

Morphology of the adult ring 2-4 scalid (Figs. 4B, 1.1, 1.3; Plate 8)

The head cuticle near the origins of scalids of rings 2-4 bears 8 um long cuticular hairs, arranged in tufts, flaps or lines of 7-25 hairs (Figs. 1.1, 1.3). The apex of the socket often carries a line of solid single hairs which are wider than other

cuticular hairs. The distal end of the socket carries a fringe of 6-8 hairs, each 4-5 um long. Scanning electron microscopy reveals that there is no spine at the distal end of the socket, although the cuticle does project over the robust knuckle of the hinge joint (Plate 8). Should a longitudinal section of the scalid be cut through this overhanging cuticle and its terminal fringe, the appearance would be identical with Fig. 5c Moritz and Storch (1972b), an appearance which may have been interpreted as showing two spines in K. giganteus (Merriman and Corwin 1973). Light microscopy of K. phyllotropis (Figs. 1.1, 1.3) shows that the spine-like appearance is always seen at one or both sides of the scalid, never in the centre. In K. phyllotropis the appearance of a spine on ring 2-4 scalids is given by an optical section of overhanging cuticle. The joint forms a distinct knuckle. The endpiece of the ring 2-4 socket is devoid of hairs except for a V-shaped chevron of about 22 solid hairs pointing down the endpiece, located on the proximal part of the endpiece along the sides of the triangular section. The tip of the endpiece is pointed.

Morphology of the adult ring 5-6 scalid (Figs. 4C, 1.1, 1.3; Plate 9)

In the head cuticle the origin of the socket is marked by a line of 10-15 cuticular hairs of uniform length. The length in different specimens varies from 4 um to 9 um. The external morphology and the cytoplasmic contents of the ring 5-6 scalids

are similar to ring 2-4 scalids. The fringe terminating the socket contains up to 25 stiff, hollow hairs, usually 2-3 um long, with one or two hairs, 8 um long, on each side. These cover a robustly articulated joint. The endpiece of these scalids is thickly covered with cuticular hairs. The endpiece has a characteristic flatiron section, with hairs projecting from the triangle apex. These solid hairs are 2 um long, and number eight to ten in a transverse count. There are 23 rows of hairs in the first 10 um interval of the proximal endpiece.

Morphology of the adult ring 7 trichoscalid (Figs. 4D, 1.1, 1.3; Plate 10)

Healthy kinorhynchs evert and retract their heads every few seconds. The first scalids to emerge upon eversion are the oral styles and the trichoscalids. When the head is fully everted the trichoscalids hang around it like tassels around a 10 ribbed umbrella. When the head is retracted, an action which Boykin (1965) compared to an umbrella being collapsed incorrectly, the trichoscalids are the last scalids to be pulled under the sheltering neck plates or placids. It is not surprising that the trichoscalids are contructed for maximal flexibility.

The adult trichoscalid is set on a scale which is attached to the head cuticle on its lower margin. A scale measures 20 um long and 12 um wide, and has recurved lateral margins. The trichoscalid socket is 6 um long with a cuticle devoid of hairs.

The hairs borne on proximal rings of cuticle are 3-5 um long, and they become shorter on distal rings.

Adult external scalid ultrastructure

Ultrastructure of the adult ring 1 spinoscalid (Plates 2-5, 13, 16, 18)

In early and late juvenile stages the origin of this scalid has been seen to contain a complex of submicrovillar cisternae (Plate 5) associated with a central vacuole or phaosome (Whittle 1976, Whittle and Golding 1974). This light sensitive organelle has not been seen in the adult. The ring one spinoscalid has a triangular section (Fig. 4, Plate 4) in which the apex of the triangle lies against the head cuticle and the base of the triangle forms the outer aspect of the scalid. By contrast, in other scalids the base of the triangular section rests against the head cuticle, and the apex points outwards (Plate 3). The socket, which tapers from a width of 15 um to 8 um, is covered with 0.5-0.8 um thick cuticle, the thickest cuticle of all scalids except trichoscalids in ring seven. This cuticle is composed of a fibrous inner layer, 0.3-0.5 um thick, and a densely-staining outer layer 0.2-0.3 um thick. Neither layer has electron-dense striations. On each side of the outer surface of the socket there is a ridge of darkly-staining cuticle, oval in section, which curves away from the central axis of the scalid near the scalid origin. In the cytoplasm below this ridge the

striated rootlet of the receptor cell cilium is found (Plate 16). In transverse section this striated rootlet is seen as a 0.4 um round body containing either a dark core with a non-staining cortex, or a non-staining core with 7-9 dark spots around the circumference. The socket origin contains a large nucleus intruding from the anterior region of the circum-oral nerve ring. Three, sometimes two, tracts of nerve cell processes from the mid-region of the circum-oral nerve ring also pass through the socket (Plate 13). These tracts usually contain about seven processes, but some have twenty. An average nerve cell process has a diameter of 0.5 um. Most processes appear to contain a microfilament. Microfilaments can be seen in both dendrites and axons of invertebrates (Welsch and Storch 1976). These cells are identified as nerve cell processes because of their similarity to tracts in the midventral nerve cord. The cuticle of the scalid joint is not thickened to form supporting spurs, and does not form a distinct swelling on the ring 1 scalid. The endpiece of the ring one scalid is covered by two types of cuticle. The outer surface, which forms the base of the triangular section, is composed of uniform, unstriated cuticle 0.5 um thick (Plates 3, 4). The 0.25 um thick cuticle of the sides is composed of Moritz and Storch (1972 a, b) type II cuticle with alternating thick and thin striations (Plate 18). This type II cuticle can be seen invading the unstriated cuticle in striped elaborations within the angles at the base of the triangular section. When the endpiece cuticle is viewed in longitudinal section the

electron-dense striations are seen to form structures near the cuticle surface, each shaped like an inverted U. The U-shaped striations, 0.1 um high and 0.12 um wide, are separated from the dark cuticle of the surface by a non-staining region 0.06 um thick. The cuticle surface is contoured by longitudinal, electron-dense strips 0.2-0.4 um high, which give the cuticle a ribbed profile when it is viewed in section. In transverse sections each longitudinal strip is seen to subtend two dark lines (0.25-0.3 um high) passing down towards the cytoplasm. There is a thinner line between each pair of lines. The endpiece of the ring one scalid is packed with cilia. Near the hinge there are only 20-40 bundles each containing a ring of 10-12 tubules. These are mostly located in the centre of the spinoscalid, but a few large bundles are also seen near the cuticle of the outer surface. A more distal section of the endpiece shows the same distribution of large bundles of tubules passing through the centre and many more small cells around the sides of the scalid. The tip of the adult ring 1 spinoscalid has not been sectioned.

Ultrastructure of the adult ring 2-4 scalid (Figs. 4, 10, 11A; Plates 2-4, 14, 61)

These scalids have a triangular section in which the apex of the triangle forms the outer aspect, and the base of the triangle rests against the head cuticle. The base of the triangular section is composed of dark cuticle, 0.5 um thick. This

sometimes appears to be formed of two layers separated by non-staining points. The sides of the triangular section are formed of fibrous cuticle 0.1-0.3 um thick, with a dark outer layer 0.04 um thick (Plate 4). As in the ring 1 socket, a nucleus and tracts of nerve fibres are found in the origin of the socket, surrounded by undifferentiated hypodermal cells with dark secretion granules and Golgi apparatus. A cell fills the distal half of the socket under the apex of the socket triangle (Fig. 10). This cell contains the type I characteristic piles of membranes described by Moritz and Storch (1972a, plate 2a; 1972b, plate 4d) but in this scalid membranes have uniform thickness and resemble mitochondria (Plate 14). Only trichoscalids show piles of thin membranes separated by a thick membrane (Plate 53) as reported by Moritz and Storch. In K. phyllotropis a thick membrane passes to the cuticular pore in the endpiece cuticle near the hinge. Three, occasionally four, axons pass around the membrane cell into the endpiece. In the ring two scalid socket the striated rootlets of two bipolar receptor cells have been observed near the distal end of the socket (Plate 61, labels C). These striated rootlets, 6 um long, with a striation periodicity of 75 nm, are separated from the cilia tubules by a double granule and a dark band. The rootlets are rod-shaped. The origin of the ring two scalid is flanked by the 1.5 um diameter blocks of the outer head retractor muscles, which insert into the cuticle under the ring one socket origin (cf. Figs. 3.6, 3.8). The hinge of the scalid of rings 2-4 is thickened by spurs of

dark cuticle to which the joint cuticle is attached, as shown in Fig. 1, Moritz and Storch, 1972b.

Distal to the hinge there is a shield-shaped differentiation of the endpiece cuticle, only seen by light microscopy (Figs. 1.1, 1.3). This can not be correlated with any surface feature when the scalids are viewed by electron microscopy. It seems possible that this represents an area with different refraction characteristics from the other cuticle. It is also the area of the sensory window depicted in Fig. 1, Moritz and Storch, 1972b.

The endpiece of the ring 2-4 scalid has the characteristic flatiron shape in transverse section (Figs. 4B, 5A; Plates 2-4). This shape is maintained to the tip of the scalid where the terminal pore is located (Fig. 11A; Plate 15). Just proximal to this pore the cuticle is reinforced by a V-shaped brace under the apex of the triangular section and a ridge in the middle of the base, which, unlike that of K. giganteus (Moritz and Storch 1972b, Figs. 6a, 7a) does not project beyond the lateral fins. The endpiece of the ring 2-4 socket is devoid of hairs except for a V-shaped chevron of about 22 solid hairs pointing down the endpiece, located on the proximal part of the endpiece along the sides of the triangular section. The endpiece of these scalids is covered with Moritz and Storch type I cuticle (Plates 17, 18). In longitudinal sections this is seen as a dark outer layer, 0.04 um thick over a striated layer, 1.5-1.6 um thick, in which the

striations form an angle of around 30 degrees with the surface layer. Below this, a darker striated layer, 3.5-4.0 um thick, has striations which are almost perpendicular to the surface. In transverse sections the layer below the surface is seen as being perpendicular to the surface and the layer between this and the lumen appears to be obliquely striated. In tangential sections (Plate 17) the striations form layers as in plywood. The endpiece contains 2-4 bundles of tubules near the apex of the triangular section. Some of these bundles have a regular arrangement of 9 + 2 singlets or doublets without projecting arms, but other bundles are composed of concentric circles of many tubules. These tubules have been sectioned projecting from the tips of these scalids as shown in Figs. 6-7, Moritz and Storch 1972a.

Ultrastructure of the adult ring 5-6 scalid (Plates 2, 3)

No striated rootlet has been observed in these scalids in the present study. The lumen of the socket contains two large nuclei, intruding into the socket origin, and the characteristic apical cell with piles of membranes and loops of rough endoplasmic reticulum. At one side of the socket this cell is indented by a tract of three or four nerve cell processes passing from the lower part of the socket origin towards the endpiece. These scalids have the most robust hinge of all scalids, with marked thickening of the cuticle around the hinge. The endpiece of these scalids is composed of type I cuticle covered with a

fringe of cuticular hairs. The endpiece has the characteristic flatiron section, with hairs projecting from the triangle apex. These solid hairs are 2 um long, and number eight to ten in a transverse count. There are 23 rows of hairs in the first 10 um interval of the proximal endpiece. The cytoplasm of the endpiece of these scalids is sometimes seen to contain up to three bundles of tubules. In the proximal endpiece these bundles are seen in the centre of the lumen, and may consist of an outer ring of 14 tubules and an inner ring of 5 tubules. In the distal endpiece bundles of 10-12 tubules are occasionally seen in the apex of the triangular section. They project from a terminal pore.

Sphincter (Fig. 3, label CM)

Previous scalid rings have overlain the 10 densely nucleated lobes of the anterior region of the circum-oral nerve ring, and nuclei in these lobes have intruded into the scalid origins. These nerve cells have been identified by their close resemblance to the cells of the midventral nerve cord. The seventh ring overlies the fibrous mid-region of the circum-oral nerve ring, and a tract of neuronal processes without associated nuclei passes into the scalid origin. The hypodermis between the nerve ring and the cuticle is interrupted by the musculature controlling head eversion. A circular muscle is found between scalid rings five and six, in same position as shown by Zelinka in Pycnophyes communis (1928, Plate 19, Fig. 2). Near this circular muscle the large inner head retractor muscles insert

onto the cuticle of the scales which carry ring 7 trichoscalids. The fibrous region of the circum-oral nerve ring lies between this musculature the cuticle lining the recess around the oral cone. Nerve cells from this fibrous region pass up around the circular muscle and into the apertures of anterior scalids. In many specimens cuticle covering the sphincter shows a wrinkle passing between scalid rings six and seven (Fig. 1.3).

Ultrastructure of the adult ring 7 trichoscalid (Fig. 5; Plates 25-26, 53)

The cuticle consist of a dark outer layer and a fibrous inner layer. The dark outer layer is elaborated into the fibrous inner layer as a punctate lobe (Fig. 5; Plates 26, 53). An endocuticular elaboration is found on each side of the trichoscalid scale which typically measures 3 um long and 1 um wide, and contains about 180 non-staining spots. It is flexible enough to be thrown into folds in the retracted head.

Socket cuticle consists of a darkly staining outer layer 0.75 - 0.80 um thick and a fibrous inner layer, 1.3-1.5 um thick, with the fibres running parallel to the circumference of the socket and continuing to the fibrous layer of the head cuticle in which fibres run parallel to the circumference of the head. This fibrous inner layer is 3 um thick on the floor of the socket, thins out along the sides of the socket, and is not seen under the dark roofing cuticle. A thick tract of neuronal processes

passes into the trichoscalid socket and passes along under the roofing cuticle. The central region of the socket is occupied by the characteristic membrane cell, and the membranes connect with single and double canals in the roofing cuticle of the socket near the first flexible joint (Plate 26). A connection between membrane cell and roofing cuticle of the endpiece has been seen in previous scalid rings, as well as in K. giganteus (Moritz and Storch 1972b, Fig. 1).

Transverse sectioning shows that the trichoscalid contains six cells, some containing cilia tubules which have also been seen in the trichoscalids of juveniles (cf. Plate 26). The terminal groove from which tubules project (Plate 6) is large enough to be resolved by 10 000 magnification with scanning electron microscopy in both adults and juveniles. No other scalids had a terminal pore large enough to be seen by SEM, although they were looked for.

Summary

1. Observations of adult K. phyllotropis (and studies of juvenile development) show that the numbers of scalids in rings 1-7 are 10, 10, 10, 15, 15, 15, 14, forming a total of 89.

2. The ring 1 spinoscalid has a spine on the socket and type II striations in the cuticle of the endpiece. The spine, set on the outer surface of the socket, is flanked by two ridges of solid cuticle underneath which lie receptor cells containing the striated rootlets of cilia. The endpiece is packed with 20-40 bundles of cilia tubules.

3. Ring 2-6 scalids have no spines on the socket and have type I joints and cuticular striations. The rootlet of a cilium may be seen in the socket of the ring 2 scalid. Ring 2-6 scalids have 3-4 nerve cell processes in the socket, and 2-4 bundles of cilia tubules in the endpiece.

4. Ring 2-4 scalids have a single band of hairs across the endpiece; ring 5-6 scalids are fringed down both sides of the endpiece.

5. There is a sphincter between ring 6 and ring 7 which marks the division between the anterior nucleated lobes and the neuronal process region of the circum-oral nerve ring.

6. Trichoscalid cuticle contains punctate endocuticular elaborations in the trichoscalid scale and sensory canals in the socket cuticle.

7. The mid-dorsal trichoscalid and all alternating trichoscalids are longer than the others, except for those originating in the lateral angles of the body. This irregularity is the consequence of trichoscalid ontogeny.

8. Each pair of trichoscalids originating in the lateral angles of the body is shorter than the neighbouring trichoscalids, and the midventral trichoscalid is shorter than all other trichoscalids. This arrangement, the result of trichoscalid ontogeny, has necessitated redefining the head mid-dorsal axis as a line passing between the ring 1 scalids of the first head sector. It is not a line passing through a ring 1 scalid as it was defined by Zelinka (1928).

RESULTS

Chapter 2.

External scalids of early juvenile stages of *Kinorhynchus phyllotropis*

Previous work

No observations have been published on the structure of the head in early juvenile stages of kinorhynchs. Zelinka's homalorhagid observations began with later juvenile stages. However Kozloff (1972) gave some details of early juvenile heads when he described the hatching process of a cyclorhagid kinorhynch subsequently described as *Echinoderes kozloffi* Higgins, 1977a. In this kinorhynch the head is not extruded prior to hatching. In the egg the scalids are directed anteriorly, and resemble a bunch of fibres. Hatching occurs when the egg membrane is ruptured by the first head extrusion. The reddish eye spots of *E. kozloffi* are not visible until after the first moult.

1. FIRST JUVENILE STAGE OR J-1

Scalid arrangement and number

The first juvenile stage has the smallest number of scalids of any stage. The J-1 external scalid arrangement consists of four

rows, not seven as in the adult (Fig. 8). The smooth scalids of rows 2-4 are not seen. The J-1 scalid count is 44 scalids and 10 proscalids (Fig. 2.5). The morphology and arrangement of these scalids are illustrated in Figs. 2.1-2.4 and the measurements of the scalids illustrated in these figures are summarised in Tables 2A and 2B. Five specimens of K. phyllotropis, with everted heads showing this scalid arrangement, had trunk lengths of 190, 195, 210, 220 (moulting) and 240 um.

Distinguishing characteristics of J-1 scalid arrangement

1. Four rings of external scalids are found on the head.
2. A pair of proscalids (described on page 55) is present in the second ring (ring 5) of odd sectors (defined on page 34).
3. As in the J-2, every scalid has a fringed endpiece except the ring 1 scalid.

J-1 external scalid morphology

Morphology of the J-1 ring 1 spinoscalid

The ring 1 spinoscalid socket has a short spine arising from the origin of the socket, seen as a hollow hair, 0.6 um wide, three times the maximum width of other lateral hairs. The cuticle of the base of the triangular section is just perceptibly thickened to form a slight ridge on each side of the socket. The joint can be seen with the light microscope as a thin line in the cuticle (Figs. 2.1-2.4). The endpiece, like the socket, has a triangular

section with the apex of the triangle resting against the head cuticle. The tip of the endpiece is bluntly rounded.

Morphology of the J-1 ring 5 proscalid

The proscalid has not been previously described. It is found where a new scalid will appear in the rings of following stages (cf. Plate 22 label P). The proscalid is a beak-like process arising from the head cuticle. Its free-standing apex is seen to project well out from the head cuticle when the proscalid is viewed in profile (e.g. Figs. 2.3 and 2.4, sector 3 proscalid). Proscalid dimensions vary from sector to sector, and from specimen to specimen (Tables 2A, 2B).

Morphology of the J-1 ring 5-6 scalid

The ring 5-6 scalid has a socket devoid of hairs and devoid of a spine. The joint is an exposed knuckle of thick cuticle. The fringe at the distal end of the socket is only represented by five short hairs on each side of this knuckle.

The endpiece distal to the joint appears, on light microscopy, to have the "window-like" appearance seen in the adult. This is a feature of all scalids of the rings between the first and last rings in all stages of development. Cuticular "windows" are shown in the figures of dorsal and ventral aspects of the everted head, and will not be commented on in other sections describing

juvenile scalids.

The endpiece has a fringe of about 18 short hairs, each about 1 um long running down each side of the longitudinal ridge which faces away from the head cuticle. The presence of this double fringe indicates that these scalids are fringed scalids, and that they belong to ring 5.

Morphology of the J-1 ring 7 protrichoscalid

This type of scalid is only found in the last ring of the first four juvenile stages of this species. It has a socket 8-14 um long, which is nearly as long as the endpiece. This socket is much wider than the endpiece. It tapers from 5 um to 3 um, while the endpiece is 2-2.5 um wide. The sides of the endpiece do not taper uniformly, and the endpiece may appear to be hook-shaped. There are no hairs or cuticular rings on this scalid.

Morphology of the J-1 ring 7 trichoscalid

The six trichoscalids have a socket that is devoid of hairs. TEM shows that the J-1 socket is not mounted on a scale as in the adult, but on a narrow stem, 3.5 um long. The rings of thick cuticle which reinforce the trichoscalid wall bear solid cuticular hairs each 3 um long. At the tip of the trichoscalid a groove, 3 um long, can be seen with SEM examination.

J-1 external scalid ultrastructure

Ultrastructure of the J-1 ring 1 spinoscalid

In the hypodermal layer near the ring 1 socket is located a complex of submicrovillar cisternae associated with a central vacuole or phaosome (see Whittle 1976, Whittle and Golding 1974). In later juvenile stages submicrovillar cisternae are seen in the ring 1 scalid socket (Plate 5) where cyclorhagid eye spots are located (cf. Zelinka 1928, Plate 2, Fig. 12). This observation conforms with Kozloff's observation, recorded in the first paragraph of this chapter, that the cyclorhagid eye spot appears after the J-1 stage. The socket is 2.5-3 um wide and has the same triangular section as in the adult. It is encased in darkly staining cuticle which is 0.4 um thick on the outer surface, or base of the triangular section, and 0.1 um thick on the sides. There is no fibrous cuticular layer. Underneath the ridges surmounting the socket, one or two striated rootlets are seen in transverse section, of similar appearance and dimension to cilia rootlets seen in the adult. In cytoplasm near these rootlets there are 3-4 nerve cell processes, which pass down the socket near the thick cuticle of the triangle base, towards the joint, where there is a large, vacuolated cell. The centre of the socket is occupied by 2-3 large bundles of tubules, some in the form of a ring of nine doublets. The apex of the triangular section, which lies against the head cuticle, contains 15-20 small bundles of tubules. No nucleus has been observed in this

socket.

The endpiece of the J-1 ring 1 spinoscalid would have the same triangular section as the socket, but the 0.16 um thick cuticle (cf. 0.25-0.5 um thick in the adult) is so thin that the triangle sides usually bulge. Unlike the adult cuticle there are no striations, but there are longitudinal electron-dense strips on the outer cuticle as in the adult. These cuticular ridges are characteristic of type II scalids. Transverse sections of the endpiece show diffuse cytoplasm containing membranes and 15-40 bundles of tubules, diminishing to three near the tip.

Ultrastructure of the J-1 ring 5-6 scalid

The 2-3 um wide socket of the ring 5-6 scalid is encased in dark cuticle without fibrous cuticle lining. The socket has an apical cell and a central tract of 3-4 nerve cells containing processes with the characteristic appearance of a microfilament. No nucleus intrudes into this socket, but transverse sections of the head show that the nucleated lobes of the anterior region of the circum-oral nerve ring are located inside the hypodermis lining the head cuticle. The joint of the ring 5-6 scalid is a thick knuckle of cuticle, as is characteristic of type I scalids (Plate 11). The sides of the spinoscalid endpiece are composed of type I cuticle as in the adult, with oblique striations seen in transverse section. This is the only cuticle striation pattern to be seen in the early juvenile stages. The cytoplasm of the

endpiece contains groups of granules under the apical cuticle.

Ultrastructure of the J-1 ring 5 proscalid

Sections of the J-1 proscalid show that it has walls of dense cuticle 0.3-0.5 um thick, and that it contains diffuse cytoplasm.

Sphincter

In the head tissue behind ring 5-6 scalids lies the circular muscle, or sphincter, that was seen in the adult between scalid rings 5 and 6 (see page 49). This muscle is therefore present throughout postembryonic development.

Ultrastructure of the J-1 ring 7 protrichoscalid

The socket holds a core of cytoplasm containing membranes, but, in the three specimens sectioned during this study, the endpiece cytoplasm showed no organised structure.

Ultrastructure of the J-1 ring 7 trichoscalid

The socket aperture in the head cuticle is clearly seen by light microscopy (Figs. 2A-2B). Cytoplasm in the socket contains canals which connect with canals in the roofing cuticle as in the adult. Trichoscalid hairs are composed of solid cuticle.

2. SECOND JUVENILE STAGE OR J-2

Scalid arrangement and number

The J-2 scalid arrangement consists of five rows, containing a total of 54 scalids and 5 proscalids (Fig. 2.10). The proscalids occur in all odd sectors (defined page 34). The morphology and arrangement of these scalids are illustrated in Figs. 2.6-2.9. (Figs. 2.8-2.9 depict a J-2 specimen with torn head cuticle which was selected because it shows the two protrichoscalids in sectors 2 and 3, as well as 6 and 7, which mark both of the lateral axes.) The measurements of the scalids are summarised in Tables 2C-2D. Thirteen specimens of K. phyllotropis, with everted heads showing this scalid arrangement, had trunk lengths of 230, 230, 240, 250, 250, 250, 260, 280, 300, 310 (moulting), 320, 330 and 330 um.

Distinguishing characteristics of J-2 scalid arrangement

1. Five rings of scalids are present.
2. A proscalid is seen in the second ring (ring 4) of every odd sector.
3. As in the J-1 the endpiece of every scalid is fringed with hairs, except in the ring one scalids.

J-2 External scalid morphology

Morphology of the J-2 ring 1 spinoscalid

The socket bears a hirsute hollow spine, 16 um long, with an oval lumen, reaching 0.4 um in diameter. The spine lies in a cuticular groove covered with short hairs, bordered on each side by a ridge of thick cuticle, which curves away from the top of the spine as in the adult. Dimensions of the socket and cuticle are similar to those of the J-1. The cuticle of the ring 1 endpiece is thick enough to give rigidity to the spinoscalid sides. They do not bulge as much as in the J-1.

Morphology of the J-2 ring 4 proscalid

SEM examination shows that J-2 proscalids may be smooth, or may have a central rib, 0.25 um high, running from the origin to the tip of the scale. In some proscalids the origin is marked by a pair of cuticular ridges, up to 10 um long, running up the head cuticle like the ridges at the origin of ring one socket. A typical proscalid measures 32 um from the beginning of the these parallel ridges to the tip, and 12 um long in the free-standing interval. Maximum width is 4 um.

Morphology of the J-2 ring 5-6 fringed scalid

Light microscopy suggests that the socket is covered by a layer of cuticle which is separated from the other head cuticle. Socket cuticle often looks as if it stands free from the head cuticle. This appearance is seen in most scalids between the first and last rings in all juvenile stages, including the J-1.

It can be clearly seen in the detailed diagrams of juvenile heads included in Appendices 2-3. However, neither scanning nor transmission electron microscopy shows any free-standing sheaths of cuticle on the scalid sockets. A possible explanation for this appearance being seen only by light microscopy is that the socket cuticle has different rigidity from the remaining head cuticle, and forms these characteristic folds in light microscope preparations, which, unlike electron microscope preparations, are flattened and distorted.

The ring 5-6 scalid socket, which is 8 um wide, originates with a line of 2-8 hairs, each 4 um long. A line of up to 12 hairs, each 4 um long, may be seen passing down the socket ridge of ring 4 scalids to the distal end of the socket. Ring 3-4 sockets terminate in a fringe of 10-12 hairs, each 1-2 um long.

The ring 5-6 scalid endpiece has an apical ridge carrying, down each side, a one layer thick fringe of about 30 robust hairs, each 4 um long.

Morphology of the J-2 ring 7 protrichoscalid

Plate 24 shows the J-2 protrichoscalid with a fringe at the distal end of the socket projecting over the curved, or hook-shaped, endpiece. From the perspective of this micrograph it can be seen that this endpiece could be described as being centred on "the posteriomedial border of a plate of minute

denticles" (see Discussion pp. 180-181).

Morphology of the J-2 ring 7 trichoscalid

The J-2 trichoscalid is not borne on a short stem as in the J-1, but on a constricted ring of cuticle.

J-2 External scalid ultrastructure

Ultrastructure of the J-2 ring 1 spinoscalid

The cuticle lacks a fibrous inner layer. A tract of 6-8 nerve cell processes passes into the origin of the socket. No nucleus is associated with this tract. In the single specimen sectioned for TEM, the lumen of the socket was occupied by 1-4 vacuolated cells, with up to 12 bundles of tubules surrounding these cells. Some tubules are in doublet form. The cuticle of the spinoscalid sides is reinforced by scalid type II longitudinal strips, but the cuticle lacks type II striation. Near the tip of the spinoscalid the cuticle of the apex is reinforced by a V-shaped strut of cuticle, and the cytoplasm within this V of cuticle contains a circle of six tubules. Two to twelve bundles of tubules are seen in sections along the endpiece.

Ultrastructure of the J-2 ring 4 proscalid

The proscalid is composed of uniform, dark cuticle, which attains 1 um thickness in the centre of the proscalid. At the proscalid

origin, the cytoplasm within the proscalid contains three simple cells, but the scale tip appears to contain no organised cytoplasm. Cuticle at the tip is seen as a layer of fused hairs.

The anlagen of the numerous proscalids of the subsequent J-3 stage have been observed in the hypodermis under scalid origins. These anlagen are seen as one to two semicircles of rounded, hollow bodies, 0.2 um in diameter, with electron-dense cores. There are 10-15 bodies in each semi-circle. These bodies are identified as scale anlagen by their resemblance to sections of scale tips.

Ultrastructure of the J-2 ring 5-6 fringed scalid

The origin of the socket is filled with a large cell containing an irregularly shaped nucleus surrounded by extensive Golgi fields. Lobes of this cell pass back through the hypodermis below the head cuticle to the nucleated region of the circum-oral nerve ring. Beside this cell there are seen Y-shaped hypodermal cells at the sides of the scalids, with one arm of the Y passing into each of two adjacent sockets. Inside the socket there are four large cells, one of which fills the apex of the triangular section. In the centre of the socket there is a tract of three nerve cell processes, each containing a central granule. In one section the sockets of ring 5 and ring 6 scalids were sectioned in one plane, and sockets with Golgi fields and sockets with

nerve tracts were seen in alternate sectors. Transverse sections show that the endpiece contains two to three circles of granules similar to tubule bundles under the apex of the triangular section. The cuticle shows type I striations.

Ultrastructure of the J-2 ring 7 protrichoscalid

Dark granules may be seen in the cytoplasm inside the proscalid.

Ultrastructure of the J-2 ring 7 trichoscalid

Sections show that two cells, with diffuse cytoplasm, fill the trichoscalid lumen.

3. THIRD JUVENILE STAGE OR J-3

Scalid arrangement and number

The J-3 scalid arrangement consists of six rows, containing a total of 59 scalids and 15 proscalids (Fig. 2.15). The proscalids are found in all even sectors. The morphology and arrangement of these scalids are illustrated in Figs. 2.11-2.14 and the measurements of these scalids are summarised in Tables 2E-2F. Thirteen specimens of K. phyllotropis, with everted heads showing this scalid arrangement, had trunk lengths of 320, 320, 330, 360, 370, 380 (moult), 380, 380, 380, 380, 390 (moult), 390 and 400 um.

Distinguishing characteristics of the J-3 scalid arrangement

1. Six rings of external scalids are present.
2. Three scales are seen in ring 2 of every alternate segement.
3. The third scalid ring contains scalids in even sectors only. These are smooth scalids with the endpiece devoid of fringing.

J-3 External scalid morphology

Morphology of the J-3 ring 1 spinoscalid

The socket bears a hirsute hollow spine, 15-17 um long, with an oval section of diameters 2 um by 1 um, and a lumen 0.5 um wide. The cuticular ridges that pass up the socket beside this spine are filled with thickened cuticle measuring 2 um by 0.7 um.

Morphology of the J-3 ring 2-4 proscalid

The three proscalids which occur in rings 2-4 of all even sectors are similar to those described in the J-2. SEM examination shows that each of these proscalids has a central rib, as described in some J-2 proscalids. The J-3 proscalids mark a region of longitudinal growth in the kinorhynch head. The central proscalid occurs where a new scalid with a smooth endpiece will be found in the J-4. The lateral proscalids are replaced by two rings of smooth scalids in the J-4.

Morphology of the J-3 ring 4 smooth scalid

The first smooth scalid is a narrow scalid without any hairs on the socket or the endpiece.

Morphology of the J-3 ring 5-6 fringed scalid

The ring 5-6 scalid has a socket carrying a line of hairs, each hair 4 um long. The endpiece has a fringe of hairs one layer thick attached to each side of the apical ridge. There are about eight hairs in a count from side to side, and each hair is about 1 um long. Shorter hairs are seen near the tip of the endpiece.

Morphology of the J-3 ring 7 protrichoscalid

This scalid is similar to that of the J-2 in appearance, but is larger. Measurements in J-2 specimens (Tables 2C-2D) show a protrichoscalid length range of 19-31 um and in the J-3 of 26-37 um (Tables 2E-2F).

Morphology of the J-3 ring 7 trichoscalid

The origin of the trichoscalid is marked by a vertical line of hairs in the head cuticle. Such a line has 10-12 hairs, each about 6 um long. These hairs are seen in subsequent stages and in the adult. The trichoscalid is mounted on a cuticular constriction as in the J-2, but in the J-3 this constriction bears a lobe of cuticle which is 1 um long (measured from TEM micrographs). It marks the site of the trichoscalid scale.

J-3 external scalid ultrastructure

Ultrastructure of the J-3 ring 1 spinoscalid

There are two layers of cuticle in J-3 ring 1 spinoscalid, an outer darkly-staining layer, 0.2 um thick, and in inner fibrous layer 0.2-0.3 um thick. There are no striations in the cuticle. Sectioned ring 1 spinoscalids have a regular triangular outline not seen in previous stages. Twenty five to thirty nerve cell processes, forming several tracts, pass through the socket, but no cell nucleus is seen. Proximal sections of the endpiece show that 25-30 bundles of tubules occupy the central region, and that these pass between two cells, one occupying the apex of the triangular section and the other lying along the base. Distal sections show vacuolated cytoplasm in the endpiece with bundles of tubules between the vacuoles.

Ultrastructure of the J-3 ring 4 smooth scalid

Socket cuticle has an outer darkly-staining layer and an inner fibrous layer. One to three nuclei intrude into the socket origin from the circum-oral nerve ring. Endpiece cuticle has type I striation. Cytoplasm in the endpiece is vacuolated, with 2-3 bundles of tubules passing between vacuoles.

Ultrastructure of the J-3 ring 5-6 fringed scalid

Unlike previous stages, the socket cuticle has an outer layer and

an inner fibrous layer. One or two nuclei intrude in the socket origin, and distal to these there is a cell containing piles of membranes surrounded by cytoplasm. Some sections show a cell with two membrane systems, each measuring 0.4-0.8 um. A membrane pile consists of 10-12 parallel double membranes, and the pile is surrounded by a double membrane connecting with these parallel membranes (cf. Plate 14). As in the adult these membrane systems resemble mitochondria because the membranes are of equal thickness. Between the membrane cells a tract of three nerve cell processes passes. The endpiece cuticle has type I striations. The vacuolated cytoplasm in the endpiece does not contain bundles of tubules.

Ultrastructure of the J-3 ring 7 protrichoscalid

This is similar to that described for the J-2.

Ultrastructure of the J-3 ring 7 trichoscalid

Some sections of trichoscalid show a central cell, sometimes containing a vacuole.

Summary

1. Observations made on the first three juvenile stages of K. phyllotropis show that the scalid number of the J-1 is 54, of the J-2 is 59 and of the J-3 is 74.

2. All three early juvenile stages have shield-shaped proscalids in rings below ring 1, in positions which will be occupied by smooth scalids in the following stage.

3. All three early juvenile stages have six trichoscalids and eight protrichoscalids. There are two trichoscalids on each of the three sides of the body.

4. In all three early stages the ring 1 spinoscalid lacks cuticular striation but has other type II characteristics. Cuticle consists of fibrous endocuticle and unstriated epicuticle which bears longitudinal strips along the endpiece. A spine, set into outer surface of the socket, is flanked by two ridges of solid cuticle under which lie the striated rootlets of cilia. The endpiece is packed with 15-20 bundles of cilia tubules.

5. The anterior ring smooth scalid, which has an endpiece devoid of fringing, is first seen in the J-3 stage. Endpiece cuticle shows type I striation, and the endpiece contains 2-3 bundles of cilia tubules.

6. The ring 5-6 fringed scalid is seen in all three early juvenile stages. The socket cuticle consists of a dark outer layer and fibrous endocuticle is not seen until the J-3 stage.

Endpiece cuticle shows type I striations in all three stages, and is fringed with short stout hairs. The socket contains 3-4 nerve cell processes. The endpiece contains cells with granules, but no bundles of tubules were observed.

7. The protrichoscalid has a plate-like socket that is bigger than the curved endpiece, and has not been seen to contain cellular structures. There are no cuticular rings or well developed hairs.

8. The trichoscalid is connected to the head cuticle by a thin stem, which develops a lobe by the third juvenile stage. There is no trichoscalid scale and no punctate endocuticular elaboration. Canals perforate the socket cuticle. The unstriated cuticle is thickened into rings which carry solid hairs. Trichoscalids contain cell membranes, but have not been seen to contain cilia tubules.

RESULTS

Chapter 3.

External scalids of late juvenile stages of *Kinorhynchus phyllotropis*

Previous work

Zelinka (1928) illustrated the heads of unspecified late juvenile stages of *Pycnophyes* species. These illustrations show that juvenile heads are not crowded with scalids (Plate 11, Fig. 3), that there are seven rings of scalids (Plate 17, Figs. 3-6), that ring 1 scalids have spines (Plate 11, Fig. 6; Plate 17, Figs. 5-6), that all rings of scalids except trichoscalids may appear to have spines (Plate 17, Fig. 6) or that rings 2-6 may not appear to have spines (Plate 17, Fig. 5).

1. FOURTH JUVENILE STAGE OR J-4

Scalid arrangement and number

The J-4 is the last stage in which the scalid number is incomplete, the last stage in which the ring 1 spinoscalids have unstriated cuticle, the last stage in which protrichoscalids appear, and the last stage in which the trichoscalids lack bundles of tubules. There are 84 scalids in the J-4 (Fig. 3.5).

These have developed from the 59 J-3 scalids and from the 15 J-3 proscalids. Ten of the J-3 proscalids have produced 20 new scalids and two new scalid rings, rings 3 and 4. Proscalids are absent, but this growth region below the first scalid ring is still active in the J-4. Localised cuticular bulges are seen in the odd sectors of the J-4 head (Figs. 3.1, 3.3) between scalid rings 1 and 3 (Figs. 3.2, 3.4). (Note that odd sectors bear odd numbers - sectors 1, 3, 5 are odd sectors). These sectors will carry five new scalids in the J-5. These are the last scalids to form.

The morphology and arrangement of J-4 scalids are illustrated in Figs. 3.1-3.4, and the measurements of these scalids are summarised in Tables 3A-3B. Sixteen specimens of K. phyllotropis, with everted heads showing this scalid arrangement, had trunk lengths of 370, 370, 380, 380, 400, 400, 410, 410, 450 (moulting), 450 (moulting), 460, 470, 470, 470, 470 and 510 um.

Distinguishing characteristics of the J-4 scalid arrangement

1. There are two scalids in the scalid series in the centre of each sector, never three as in later stages.
2. A scalid with a smooth endpiece devoid of fringing is found in every even sector of ring 2.
3. There are no proscalids, but eight protrichoscalids are present.

J-4 external scalid morphology

Morphology of the J-4 ring 1 spinoscalid

The socket is similar to the socket of the J-3, except that the distal end bears a small flap on each side formed of two fused hairs (shown by sectioning as in Plate 16). The spine of the J-4 spinoscalid is 25-30 um long. The endpiece is similar to that in the J-3, and 15-20 bundles of tubules can be counted in transverse sections.

Morphology of the J-4 ring 2-4 smooth scalid

In odd sectors, the origin of the ring 2 scalid may be marked by a cuticular bulge which marks the site where the last scalid will appear in the J-5. This bulge is seen most clearly in scanning electron micrographs of the emerging head. The socket bears a line of short hairs on the apical ridge, and terminates in a fringe of hairs, which are 4 um long in the centre, and up to 8 um long on each side. The ring 2-4 scalid endpiece is similar to that seen in the J-3 ring 3.

Morphology of the J-4 ring 5-6 fringed scalid

The ring 5-6 scalid socket is similar to that seen in the J-3 rings 4-5, except that the origin of the socket is marked by a line of 4-8 hairs, each 6 um long, which passes across the head cuticle. The endpiece of this scalid has a double fringe of 1 um

long hairs, and a second layer of hairs, each 0.5 um long, which stand up along the ridge of the endpiece. One 5 um interval of the endpiece carries a line of 16 hairs.

Morphology of the J-4 ring 7 protrichoscalid

Protrichoscalids are similar to J-3 protrichoscalids, both in size and configuration.

Morphology of the J-4 ring 7 trichoscalid

The trichoscalid resembles that of the previous stage, except that the lobe of the developing scale is 3 um long. A 5 um long interval of trichoscalid bears seven hairs. This appears to be half the hair density of fringed scalids, and half the hair density of the trichoscalid anlagen reported below. However trichoscalid hair spacing is increased by rings of bare, flexible cuticle which separate the hair-bearing rings.

J-4 external scalid ultrastructure

Ultrastructure of the J-4 ring 1 spinoscalid

Ring 1 ultrastructure is similar to that of the J-3, and 20-30 bundles of cilia tubules are seen per transverse section. In the single J-4 specimen sectioned for TEM, no vacuoles were seen, and there were no small cells between the cilia tubules and the cuticle.

Ultrastructure of the J-4 ring 2-4 smooth scalid

The cytoplasmic contents of these scalids show no clear picture of cell differentiation.

Ultrastructure of the J-4 ring 5-6 fringed scalid

The endpiece of this scalid contains three bundles of cilia tubules under the apex of the triangular section.

Ultrastructure of the J-4 ring 7 protrichoscalid

The J-4 protrichoscalid contains the anlagen of the trichoscalid which will appear in the J-5 (Plates 27-28). The following description is based entirely on observations made on the single specimen sectioned for TEM examination.

A developing trichoscalid is seen as a membrane-bound tract of dense cytoplasm, 1 um in diameter, which gives off a fringe of cytoplasmic processes, each 0.4-0.7 um long with a dense core. The core of a thread is seen as one dark line in longitudinal section, but a transverse section shows that it is composed of two bodies (Plate 27 arrow). The fringing processes all slant towards the tip of the developing trichoscalid, like the hairs covering the fully developed trichoscalid. Over a distance of 2.5 um there are seven of these processes, a density comparable to that the fringing hairs of the ring 5-6 scalid.

Ultrastructure of the J-4 ring 7 trichoscalid

The J-4 trichoscalids were sectioned longitudinally because they were flexed. This trichoscalid contains cilia tubules, but the number of bundles has not been established.

2. FIFTH JUVENILE STAGE OR J-5

Scalid arrangement and number

The J-5 is the first juvenile stage with a full adult complement of scalids (Plate 19), the first stage to show striation in the cuticle of ring 1 spinoscalid, and to show punctate endocuticular elaborations in the trichoscalid scales. There are 89 scalids (Fig. 7). The morphology and arrangement of these scalids are illustrated in Figs. 3.8-3.9, and the measurements of these scalids are summarised in Tables 3C-3D. Twenty specimens of K. phyllotropis showing J-5 characteristics, with everted heads showing this scalid arrangement, had trunk lengths of 400, 470, 480, 480, 490, 500, 510, 520, 520, 530, 540, 540, 550 (moulting), 550, 550, 570, 590 (moulting), 590 (moulting), 590 and 600 um.

J-5 Characteristics

The J-5 does not appear to have any unique scalid characteristics. Posterior dorsal spination of the J-5 trunk is the definitive characteristic. The J-5 differs from all other stages in having the following combination of characters - a

small lateral spine adjacent to the unarticulated spinose protuberance on the lateroterminal margin of the posterior segment (Plate 71), and a posterior mid-dorsal spine inserted into a flexible mid-dorsal fold of thin cuticle which is wider than the spine (Fig. 24; Plate 66). (These characteristics are described in Chapter 8 of this section of the thesis, which deals with the life cycle of K. phyllotropis). The J-5 is also the only stage in which a full adult complement of scalids is associated with a trunk covered with juvenile, hyaline cuticle.

J-5 external scalid morphology

Morphology of the J-5 Ring 1 spinoscalid

The origin of the socket is marked, on each side of the scalid, by a wing of three hairs, fused at their proximal ends (cf. Plate 7). This wing is 18 um long. The J-5 ring 1 spinoscalid resembles that of earlier stages; it is the largest spinoscalid with hyaline cuticle and therefore shows the subcuticular ridges most clearly (Plates 19 and 21).

Morphology of the J-5 ring 2-4 smooth scalid

Ring 2 scalids in odd sectors are thinner than other scalids (cf. OS 2 with ES 2 in Plate 19 and Figs. 3.6-3.9). The socket ridge bears a line of flat hairs, each about 6 um long. Endpiece cuticle carries a chevron (V-shaped line) of 6-14 flat hairs, each 4-6 um long.

Hairs on the head cuticle

Lines of very long cuticular hairs mark the origins of scalids from ring 4 to ring 7. These hairs measure up to 20 um long. In specimens fixed during head eversion they are seen to fan out in an erect position. It is possible that these stiff fans of hairs might increase sensory stimulation of the scalids by creating eddies in water flowing around the extruding head.

Morphology of the J-5 ring 5-6 fringed scalid

This resembles the J-4 fringed scalid except that a thick crest of hairs is seen on the apex of the socket.

Morphology of the J-5 ring 7 trichoscalid

The J-5 has 14 trichoscalids and no protrichoscalids. The midventral trichoscalid is smaller than all the others. A possible explanation for this is that the midventral nerve cord would interrupt the circum-oral nerve ring at this point. This interruption could reduce the exposure of this area to neurosecretory factors promoting growth. The trichoscalids which replace the protrichoscalids of previous stages are smaller than the trichoscalids in positions always occupied by trichoscalids. As Table 3C shows, the dorsal trichoscalids which developed from protrichoscalids had lengths, in the specimen in which they were measured, of 69, 70, 66, 66 and 59 um. The trichoscalids in positions always occupied by trichoscalids measured 75, 72, 76

and 70 um. Ventral trichoscalids (Table 3D) which had developed from protrichoscalids measured 57, 49 (the midventral trichoscalid) and 61 um in the specimen in which they were measured. The ventral trichoscalids in positions always occupied by trichoscalids measured 64 and 75 um. This difference persists into the adult stage. The J-5 trichoscalid is carried on a simple scale without recurved margins.

J-5 external scalid ultrastructure

Ultrastructure of the J-5 ring 1 spinoscalid

Submicrovillar cisternae (SMC), which are photoreceptor organelles (Whittle 1976, Whittle and Golding 1974), are located in the origin of the ring 1 spinoscalid, which is 8.75 um wide. (An SMC complex has also been sectioned near the ring 1 spinoscalid of the J-1, and is illustrated in the J-5, Plate 5). There is no nerve ring nucleus in the J-5 ring one socket, but nucleated epidermal cells are found on each side of the socket origin. Two tracts of nerve cells pass into the apex of the socket and pass down the sides. A kinocilium is seen under the cuticular ridge on the right side of the socket. The sides of the J-5 ring one scalid endpiece show type II striation and longitudinal cuticular strips characteristic of type II scalids. Transverse sections of the endpiece show that each dark longitudinal strip (standing 0.4 um above the surrounding cuticle) subtends one or two dark lines (0.9 um long), which pass

through the cuticle to the cytoplasm. The cytoplasm has a central cell containing 15-25 large bundles of tubules, and an equal number of small cells.

Head cuticle surrounding scalids

As in the J-3 and J-4, the head cuticle is composed of two layers - a thin, darkly-staining outer layer, and an inner fibrous layer. In the J-5 the inner fibrous layer is thicker on each side of the ring one socket origin, and forms a plaque 0.6 um thick, twice as thick as the fibrous cuticle around it. This plaque would occupy a position below the tuft of hairs marking the origin of the ring two scalid. The plaque is similar in configuration to the punctate endocuticular elaboration of a trichoscalid, and although it does not contain spots, it does not stain evenly like the surrounding cuticle.

Outer head retractor muscles associated with scalids

The outer head retractor muscles insert onto the cuticle below the ring one scalids in all stages (see Figs. 3.6 and 3.8). The bulge of the muscle insertion is seen most clearly by SEM in the J-5, probably because greater muscle bulk is being combined with thin cuticle.

Ultrastructure of the J-5 ring 2-4 smooth scalid

The contents of the socket include a nerve ring nucleus protruding into the socket origin, an apical cell with membrane

systems resembling mitochondria, 3-4 nerve cell processes in the centre of the socket, and a flat, thin hypodermal cell on either side. The endpiece contains a central cell and three bundles of microtubules around the base of the triangular section.

Ultrastructure of the J-5 ring 5-6 fringed scalid

The socket contains a nucleated cell at its origin, and in the ring 5 socket, this cell contains a pile of rough endoplasmic reticulum. In the ring 5 socket a cell with a membrane system is located near the hinge joining the socket to the endpiece. Three nerve cell processes pass through the socket. The endpiece of this scalid is similar to that of the J-4, and contains two cells with membrane piles and two cells containing bundles of cilia tubules.

Ultrastructure of the J-5 ring 7 trichoscalid

Lobes on either side of the trichoscalid origin contain punctate endocuticular elaborations as in the adult (cf. Fig. 5a). Three counts of the non-staining spots show 61, 78 and 93 spots per lobe. Between these lobes there are cells with the type I membrane system. These membranes do not resemble mitochondria; they have thick and thin membranes as described in K. giganteus (Moritz and Storch 1972 a, b). A cell in the socket origin contains granular cytoplasm with strands of rough endoplasmic reticulum. A cell passing down the centre of the trichoscalid contains a bundle of cilia tubules (Plate 25).

3. SIXTH JUVENILE STAGE OR J-6

Scalid arrangement and number.

The last juvenile stage has a full complement of 89 scalids (Fig. 7).

The morphology and arrangement of J-6 scalids are illustrated in Figs. 3.10-3.13 and the measurements of these scalids are summarised in Tables 3E-3F. Twelve specimens of *K. phyllotropis* showing J-6 characteristics, which had everted heads with this scalid arrangement, had trunk lengths of 590, 610, 620 (moulting), 620, 620, 630 (moulting), 630, 630, 630, 630, 650 and 650 um.

J-6 Characteristics

J-6 scalids can be distinguished from J-5 and adult scalids by their ultrastructural features. J-6 scalids show adult features such as nuclei in the socket origin of the ring 1 spinoscalids, and scales with recurved margins which connecting trichoscalids to the head cuticle. These features are not seen in earlier juvenile stages. Unlike the adult, the J-6 does not have nerve ring nuclei intruding into the fringed scalid socket. J-6 head cuticle, typically 0.4 um thick, is half the thickness of adult cuticle, but nearly twice as thick as J-5 cuticle.

Posterior dorsal spination of the J-6 trunk is the definitive characteristic. The mid-dorsal spines are inserted into an inflexible mid-dorsal ridge of thick cuticle which is narrower than the spine (Fig. 24, Plates 67 and 72). (This characteristic is described in Chapter 8 of this section of the thesis, which deals with the life cycle of K. phyllotropis). The J-6 cuticle is browner than previous juvenile stages, and appears to be more rigid (see Plate 67).

J-6 external scalid morphology

Morphology of the J-6 ring 1 spinoscalid

The origin of the socket is marked by a wing of three hairs which are fused along their entire length (Plates 7 and 16).

Morphology of the J-6 ring 2-4 smooth scalid

Head cuticle beside the origin of the J-6 ring 2-4 scalid carries a horizontal line of 3-12 thick hairs, each 10 um long. This line may be straight or curved. As in the J-5 this scalid is thinner than other scalids (Figs. 3.10 - 3.13). The socket ridge carries a vertical line of 8-12 flat hairs, 0.5 um wide and 3 um long. The terminal fringe of this socket has 16-20 hairs which are 3-5 um long in the centre with 2-4 hairs on each side which are twice as long. The ring 2-4 scalid endpiece has a chevron of 8-14 hairs, each 4 um long located 10-20 um distal to the scalid

joint. SEM examination shows that some scalids of some specimens also have a few weak hairs down the apical ridge of the scalid.

Morphology of the J-6 ring 5-6 fringed scalid

The origin of the ring 5-6 scalid is marked by a line of 4-12 hairs which may be of uniform length (6 um) or may increase in length closer to the socket (2 um to 8 um). The socket ridge bears 2-8 weak hairs, 2 um long. The terminal fringe is a double layer of stumpy hairs, 0.5-1.0 um long. The socket does not contain nuclei, but does contain an apical membrane cell with a tract of three nerve cell processes underneath it. Nuclei in the lobes of the circum-oral nerve ring are located behind the socket origin. The endpiece of the ring 5-6 scalid is covered with fringing hairs, each 2 um long. In transverse section it is seen to contain 2-3 bundles of tubules in the apical angle of the lumen.

Morphology of the J-6 ring 7 trichoscalid

The trichoscalid projects from the centre of a scale which is attached to the head cuticle on the scale posterior margin. SEM examination shows that the scale has a recurved margin as in the adult.

Tables 3E and 3F show that, as in the J-5, trichoscalids of sectors previously occupied by protrichoscalids are slightly shorter than the trichoscalids of sectors that always carried

trichoscalids. The former are 56, 59 and 63 um long; the latter are 61, 65 and 66 um long. Table 3F shows that the midventral trichoscalid is the shortest of all (49 um long). Trichoscalids in trichoscalid sectors are 61 and 64 um long, trichoscalids in protrichoscalid sectors are 49 and 57 um long.

J-6 external scalid ultrastructure

Ultrastructure of the J-6 ring 1 spinoscalid

The origin of the spinoscalid, which is 11.6-12.0 um wide, holds a complex of submicrovillar cisternae. In the apex of the triangular spinoscalid section two nuclei associated with the circum-oral nerve ring intrude into the socket. The sides of the triangle are occupied by hypodermal cells and tracts of 3-4 nerve cell processes. Further along the socket, in sections taken at the level of the kinocilium under the cuticular ridge, there is a tract of 6-8 nerve cell processes in the centre of the socket. The sides of the J-6 ring one endpiece show type II cuticle striation and electron-dense longitudinal strips which project like cooling fins, and are 0.25 um high as in the adult. Each fin-like strip subtends two dark strips which are seen, in transverse section, to pass down through the cuticle for 0.2 um as in the adult and to have an additional dark line beside each pair. The endpiece is filled with bundles of tubules. About fifteen large bundles occupy the centre of the scalid. These are surrounded by 100-130 small cells.

The only ring 1 scalid which was sectioned at the tip was in the J-6 specimen. Sections behind the tip showed that the scalid is an oval, 2.2 um by 1.4 um. The roofing cuticle is unstriated, but the sides, or acute end of the oval tip, show type II striation. Under the dark roofing cuticle there is the characteristic bracket-shaped organelle in the cytoplasm, and this encloses seven bundles of tubules. The remaining cytoplasm has granules and vacuoles. Closer to the tip the scalid has an oval section measuring 2.75 um by 1.75 um, and all the cuticle is striated. Cytoplasm is packed with granular bodies, and is penetrated by a groove, 1 um long, which contains seven ciliary bundles of tubules. The tips of ring 1 scalids have not been previously described.

Ultrastructure of the J-6 ring 2-4 smooth scalid

One or two nuclei from the circum-oral nerve ring intrude into the socket origin, surrounded by flat hypodermal cells. Between the large nucleated cells and the hypodermal cells a tract of nerve cell processes enters the socket on each side. These tracts unite in the centre of the socket to form a tract of 3-4 processes passing towards the endpiece. The distal end of the socket apex is filled with a characteristic membrane cell. In the cuticle of the ring 2 scalid there is a cell containing thick walled tubules which penetrate the cuticle distal to the fringe over the joint - a "sensory window"? The smooth scalid endpiece

contains one cell with 2-3 bundles of tubules, some with distinct doublet form. The tip of this scalid has been sectioned, showing that dark unstriated cuticle, with an irregular outline, encloses granular cytoplasm around a groove containing two cilia. The scalid tip at this level measures 0.6 um by 0.7 um. The groove in the side of the scalid is 0.8 um deep, and the sides of the groove project beyond the scalid for 0.4 um.

Ultrastructure of the J-6 ring 5-6 fringed scalid

The socket of this scalid does not contain nuclei, but does contain an apical membrane cell with a tract of three nerve cell processes passing underneath it. Nuclei from the lobes of the circum-oral nerve ring are seen in the hypodermis behind the socket origin.

Ultrastructure of the J-6 ring 7 trichoscalid

Fibrous cuticle around the scalid has a maximum thickness of 3 um, as in the adult. Another adult feature is the punctate endocuticular elaboration along the cuticle seen in the trichoscalid scale. In the J-6 this measures 1 um wide and 2 um long. The number of non-staining spots in sections of this spotty lobe have been counted as 48, 66, 101 and 102. The inner head retractor muscles, which measure 9 um by 3 um in transverse section, insert onto the cuticle below the trichoscalid scale. The origin and the socket of the J-6 trichoscalid are filled with a membrane cell with piles of thin membranes interleaved with

occasional thick membranes. The lumen of the distal end of the trichoscalid contains cells with three bundles of tubules. The tip of the trichoscalid has been sectioned to show that the trichoscalid ends in oval sections of thick cuticle tapering from 0.8 um by 0.6 um to 0.6 um by 0.4 um, pierced by a central canal 0.15 um in diameter.

Summary

1. Observations made on the last three juvenile stages of Kinorhynchus phyllotropis show that the scalid number of the J-4 is 84, while the J-5 and J-6 have the full adult complement of 89. J-5 specimens are distinguished from J-6 juveniles by posterior mid-dorsal spination characteristics.

2. None of the last three juvenile stages have shield-shaped proscalids.

3. The J-4 is the only juvenile stage in this species possessing protrichoscalids but lacking proscalids. The J-4 is the last stage to retain such early juvenile features as unstriated cuticle in the ring 1 spinoscalid, and absence in the trichoscalids of punctate endocuticular elaborations and bundles of cilia tubules.

4. In all late juvenile stages the ring 1 spinoscalid resembles that seen in the early stages, except that there is a flap of

fused hairs at the origin of the socket, and the endpiece of the J-5 and J-6 has type II striation in the side cuticle. Photoreceptor submicrovillar cisternae are seen in the origin of this scalid.

5. In all late juvenile stages the ring 2-4 smooth scalid has a crest of hairs along the socket ridge, and a V-shaped band of hairs across the proximal region of the endpiece. The socket contains a cell with piles of membranes resembling mitochondria under the socket ridge and a tract of 3-4 nerve cell processes. In the last two stages the socket also contains a nucleated cell from the circum-oral nerve ring. The endpiece contains 2-3 bundles of cilia tubules.

6. In the J-5 and J-6, lines of long hairs arise from the head cuticle near the origins of scalids in rings 4-7. These hairs fan into an erect position during head eversion.

7. In all late juvenile stages the ring 5-6 fringed scalid has few hairs on the socket while the endpiece is thickly fringed. The socket contains a cell with membrane piles under the apical ridge, and a tract of three nerve cell processes in the centre. The endpiece contains 2-3 bundles of cilia tubules.

8. The ring 7 protrichoscalid contains trichoscalid anlagen in the J-4. The 14 trichoscalids of later stages are carried on scales with posterior margins attached to the head cuticle.

Chapter 4.

Oral cone, internal scalids and oral styles

Previous work

1. Oral cone

Delage and Herouard (1897) stated that the kinorhynch head had three segments, the pharynx crown, the oral cone and the external scalid region. However, Zelinka (1907) said "Vom Kopfe, dem 1. Segment, ist der Hals ganz gesondert." This has usually been interpreted to mean that the head with its scalids represents the first segment, and the neck with the closing flaps or placids represents the second segment. "The approximately spherical head constitutes the first zonite, it bears a central mouth and five to seven circlets of posteriorly directed spines, the scalids of Zelinka....The second zonite or neck is covered with large plates or placids" (Hyman 1951). However, Southern (1914) interpreted Zelinka's words as meaning that the oral cone is the first segment, and the scalid rings the second segment. Although Zelinka corrected Southern (1928, p. 336) the present study presents some evidence that Southern's version is closer to the truth.

2. Oral styles

The literature reports that adult kinorhynchs have seven rings of external scalids (Hyman 1951, Kristensen 1983, Zelinka 1928). However Dr. Robert Higgins (1979, pers. comm.) noted that some oral styles are spined, that the oral styles of early juvenile stages are adnate to the oral cone, and suggested that the oral styles constitute a ring of scalids.

3. Internal scalids

In cyclorhagid kinorhynchs rings of accessory styles or teeth have been observed inside the oral cone. They are seen in the deep groove between the oral styles and the pharynx crown at the beginning of the alimentary canal. They were first described by Reinhard in 1883. "The snout forms several turns: the first is covered with needles and passes into the second, carrying nine bristles, this last into the third, attached to the upper part of the oesophagus; it has bristles of a smaller size" (translated from Russian). Delage and Herouard (1897) described them as the spines of the first proboscis segment. Zelinka (1928, p. 123) described these in Echinoderes dujardinii (Claparède, 1863) as follows: "Forceful squeezing of the oral cone brings into view the covering apparatus of the Cyclorhagids which would function to prevent sucking in of foreign bodies into the circular inner recess between the oral cone and the head. There are three rows of tufts, of which the first consists of the shortest styli (Plate 1, Fig. 6, "ch 2"). The middle ring consists of

separately beating tufts which are set on rounded prominences (b, Fig. 6, Plate 1), the lowest is seen as a simple ring row ("p2"). Besides these, there is one single preparation showing a structural arrangement consisting of two rows of accessory styli ("ch" and "pl")." ("Durch gewaltsames Vorpressen des Mundkegels werden die Schutzeinrichtungen be den Cyclorhagen offenbar, die ein Eindringen von Fremdkörpern in den Ringgraben zwischen Mundkegel und Kopf verhindern sollen. Es sind dies drei Kreise von Borsten, von denen der oberste aus kurzen Stäbchen besteht (ch2 Fig. 6, Taf. 1), der mittlere die Borsten zu auseinander strebenden Bundeln gesammelt enthält, die auf gerundeten Hügeln sitzen (b Fig. 6, Taf. 1), der unterste eine einfache Borstenreihe zeigt (p2). Ausserdem gewährt ein solches Präparat Einblick in die Gebilde, die als akzessorische Styli dienen und aus zwei Reihen bestehen (chl und pl).") Zelinka's label "ch 2" translates as "chitinous rod" and "b" as "tuft-forming organised hairs", "pl" as "accessory styli of the Cyclorhagids", and "p2" as "hair striations in the oral tube." The E. dujardinii spines were illustrated (Zelinka 1928, Plate 1, Fig. 6).

Similar spines were illustrated in Fig. 2 of the description of the cyclorhagid Condyloderes multispinosus (McIntyre, 1962) (= Centroderes multispinosus), but there is no mention of these spines in the description.

There are at least three instances in literature on homalorhagid kinorhynchs where the presence of head processes inside the oral cone has been mentioned or illustrated. Southern (1914) in his description of Pycnophyes zelinkaei, the first recorded Irish kinorhynch, wrote "The fully expanded proboscis has eight short spines guarding the mouth. Just behind the tip there are two rings of slender spines, eight in each ring. The spines in the anterior row point backwards, those in the posterior row forwards. This part of the proboscis constitutes the first segment of the body, according to the nomenclature used by Zelinka. The second segment is much stouter, conical in shape, and bears four rings of spines, the anterior spines being the longest and the posterior the shortest....The third segment...consists of a curved dorsal plate and three ventral plates." As mentioned Southern believed that the oral cone and its lining constitute the first body segment, and the rings of external scalids constitute the second body segment.

Southern's illustration (1914, Plate 12, Fig. 33E) depicts a kinorhynch head which can be interpreted as showing a muscular pharynx which has eviscerated through the mouth opening, pulling out the lining of the oral cone. Two rings of spines are inserted onto the lining of the oral cone. The posterior ring of spines points upwards. These appear to be the oral styles, of which Southern counted eight. Anterior to this ring there is another ring of spines pointing downwards, and at the top of the

eviscerated oral cone there are nine spines pointing upwards.

When Mr. Simon Cohen drew the homalorhagid Pycnophyes frequens, the first kinorhynch to be reported from the United States (Blake 1930, Fig.1), he showed a complete specimen with similar features. The eviscerated oral cone bears two rings of processes. The posterior ring points upwards and the anterior ring points downwards. Neither ring is mentioned in the description.

Malakhov and Spidonov (1980) in their SEM study of Pycnophyes kielensis Zelinka, 1928, noted that "In a number of instances there are from the mouth opening five styles of the inner circle" (translated from Russian).

Present study

1. Oral cone (Fig. 12; Plates 1, 23)

The oral style arises from an oral scalid base, an elongated cuticular prominence showing V-shaped markings that are characteristic of homalorhagid trunk cuticle (Plates 42-44, 49). This superficial cuticular embossing gives the oral scalid base the appearance of a wood rasp. The protractor muscles of the pharynx (Boykin 1965, Figs. 63 and 64) insert into cuticle at the

bottom of the oral scalid base. Tissue inside the oral scalid base contains large nuclei, seen from the first juvenile stage onwards. In later developmental stages tracts of nerve fibres can be seen passing into the oral scalid. The oral scalid bases are separated by Y-shaped inter-basal strips. In transverse sections of the head a strip looks like a pair of ram's horns because both edges of the strip are rolled into a scroll (Plate 13, label IB). These scrolls are distinctive landmarks. The inter-basal strip is a cuticular elaboration without any remarkable histology. Its function is probably to impart flexible mechanical support to the distensible oral cone.

A pectinate fringe of cuticle encircles the oral cone below the oral scalid bases. The trunk segments of many kinorhynchs especially cyclorhagids (Plates 67, 76, 77) usually end in such a pectinate fringe. Another feature of a kinorhynch segment boundary is the attachment point of a longitudinal muscle. In K. phyllotropis this is seen at the insertion of the protractor muscles of the pharynx into the cuticle above the pectinate fringe. These features suggest that the first segment comprises only the oral cone, excluding the external scalids. Segment two of this kinorhynch would be the region between the bottom of the oral cone and the first trunk segment. Thus it is argued that Southern's disposition of the head segments is preferable to Zelinka's disposition. Zelinka's illustrations do not show a pectinate fringe around the oral cone, but they are mentioned and

illustrated on trunk segment boundaries. It is likely that future studies of head innervation and embryological development will show that the head consists of more than one segment, and that the neck, now designated as a full segment, will be found to be no more than an intersegmental ligament or arthrocorium.

The term "segment" is here used because it is widely accepted in kinorhynch literature. No attempt is being made here to relate the concept of pseudometameric segmentation to the kinorhynch body plan. "Es ist unmöglich, eine scharfe Unterscheidung zwischen unsegmentierten, pseudometameren und metameren segmentierten Typen von Körperarchitekturen durchzuführen, obwohl es praktisch sein kann, diese Begriffe beizubehalten (jedoch definiert) als rein anatomische Bezeichnungen ohne grosse Präzision." (Clarke 1980). ("It is not possible to make definite distinction between unsegmented, pseudosegmented and metamerically segmented types of body plan, and of little practical use as the concepts as presently defined can not be applied with any precision.")

Around the summit of an everted oral cone there is a pleated outer rim formed of finely folded cuticle, and a fimbriated inner rim formed of cuticle bearing ridges with short cuticular threads or fimbriae. These combs of cuticle may, like the combs of hairs found between the external scalids, serve to create eddies in the ambient water thereby increasing the stimulation of the nearby

sensory scalids. The fimbriated inner rim can be seen to its fullest extent in a kinorhynch specimen that has suffered pharyngeal prolapse so that the the pharynx crown topping the muscular pharyngeal bulb emerges through the mouth opening, pulling out the lining of the oral cone. In adult K. phyllotropis the inner rim is composed of thin cuticular ridges 18 um long, separated by 2-4 um intervals of cuticle. The fimbriae are mostly located on the centres of these ridges, and a cluster of small threads is located at the top of each ridge. The pleats of the outer rim form a band 25 um long, there is a 1 um gap between each pleat except behind the oral scalids where the cuticle is not pleated.

2. Oral styles (Plates 13, 23, 30)

Sections of the oral styles (Fig. 11b; Plate 30) show that these processes are scalids, and so oral styles will hereafter be called oral scalids in this thesis. Oral scalids are identified as scalids by the similarity between their ultrastructural organisation and that of the external scalids. The striated rootlet of a cilium is found under the apical cuticle near the oral scalid origin, and bundles of tubules are surrounded by a bracket-like organelle at the oral scalid tip. In K. phyllotropis it would appear that every alternate oral scalid has a short spine (Figs. 12a, 18a; Plate 23), but the presence of a spine on every second scalid has not been proved in this study. This spine suggests a relationship between the oral style and the

ring 1 spinoscalid. The profiles of these scalids are similar, especially in transverse sections taken near their origins. It has been known that the kinorhynch head is divided into ten sectors (Zelinka 1928) and that there are nine oral scalids, but the literature does not report which antimere lacks an oral scalid. Head sections examined during this study show that there is no oral scalid in the centre of the mid-dorsal antimere (Figs. 18-20).

3. Internal scalids (Figs. 12-20; Plates 29, 31-36)

Inside the head there are three rings of scalids which have not been described. These rings are located around the inner wall of the oral cone (Fig. 3). Each ring carries a different type of scalid. In this thesis the form of scalid inserted on the anterior ring will be termed a scleroscalid 1, the form of scalid inserted on the middle ring will be termed a scleroscalid 2 and the form of scalid inserted on the posterior ring will be termed a helioscalid. These processes are identified as scalids because, like the external scalids (Plate 15), they contain bundles of tubules surrounded by a bracket-like organelle (Fig. 11; Plate 32). Like the external scalids some are organised into a socket and an endpiece with cuticular spurs at the intervening joint, and they terminate in a groove from which projects the tubular bundle of a modified sensory cilium.

In specimens with everted heads, the internal scalids can be seen as a bundles of rods over the pharyngeal crown (Figs. 3.6-3.10). Specimens which have suffered the common form of collection injury that has been termed pharyngeal prolapse are the best material in which to study the internal scalids. In prolapsed specimens the anterior structures of the alimentary canal emerge through the mouth opening, presumably because the pharyngeal protractor muscles have ruptured. This brings structures normally on the inside of the head to the exterior, and at the same time reverses their direction. Normally the internal scalids point in the same direction as the oral scalids. For this reason the partially eviscerated head of a K. phyllotropis specimen has been illustrated semischematically to show the location of the internal scalids in such a specimen (Fig. 13a).

The first ring of internal scalids - scleroscalids 1. (Figs. 13-15; Plates 29, 31, 35, 36)

The scleroscalid 1 is 15-20 um long and 1-2 um wide (Figs. 14, 15b, 15c). The tip emerges from the inner rim of the oral cone at the same level as the tip of the scleroscalid 2, but the shorter scleroscalid 1 is inserted onto a higher level of the cuticle lining the oral cone than the scleroscalid 2. Sections show that one bundle of tubules, containing 7 or 7 + 2 tubules in singlet form, runs the length of the scalid (Figs. 15 b-g). This modified cilium projects through a sub-terminal slit (Fig. 15d) which is clearly visible with SEM examination (Figs. 15a; Plates

35-36). TEM examination shows that the walls of the scleroscalid 1 are 0.25 um thick and are composed of diffusely striated dense cuticle (Figs. 15f, 15g; Plates 29, 31). The lumen of the scleroscalid 1 is often narrower than the walls (Figs. 15b, 15g), and the only structure identified in this lumen has been one bundle of tubules. Near the tip of both types of scleroscalid the tubules travel through a passage in the cuticle that is separate from the main lumen filled with cytoplasm (Plate 31). The scleroscalid 1 is attached to the inner wall of the oral cone by a sheet of cuticle along most of the length of the scleroscalid (Fig. 15c).

The ten scleroscalids 1 are inserted only the walls of the oral cone opposite the external scalids of the first ring (Figs. 18, 19).

<u>The second ring of internal scalids - scleroscalids 2</u> (Figs. 13, 14 and 16; Plate 1)

The scleroscalid 2 is 40 um long from the point of origin to the tip. The sclerotised endpiece is 25 um long and 2-4 um wide. Sections of this endpiece (Figs. 16 b-d) show that it contains 4-5 bundles of tubules running the length of the endpiece. These emerge through a sub-terminal slit which is just more than 0.5 um long when measured by TEM (Figs. 16a; Plates 30, 31). The curved endpiece of a scleroscalid 2 is attached to the inner wall of the oral cone by a sheet of cuticle which is of variable thickness

(Fig. 16d). This suspensory sheet is so long that the scleroscalids 2 hang well out from the lining of the oral cone. The arrangement of the internal scalids resembles that of the vanes of a turbine, and this means that the tips of the scalids are seen to be displaced clockwise in relation to the scalid origin. Because the scleroscalid 2 hangs well away from the oral cone lining, it can appear to be located at the same level as the lowest ring of internal scalids, the helioscalids, especially in sections taken near the level of the scalid tip.

The thickness of the dense unstriated cuticle investing this scleroscalid is the same as the cuticle of the scleroscalid 1, but the scleroscalid 2 has the additional support of a ridge running along the outer edge of the scalid endpiece (Figs. 16 a-c). The endpiece connects to a triangular socket, which does not have sclerotised cuticle (Figs. 14, 16a), by a flexible membrane supported by spurs of thickened cuticle (Fig. 16d, label j). This hinge joint is less developed than the joints of external scalids. Sections taken at the level of the joint show bundles of tubules passing up the endpiece of the scleroscalid 2, but no striated ciliary rootlets have been shown to be associated with these tubules as they are in external scalids. TEM examination shows that the origin of the scleroscalid 2 is marked by a tuft of minute hairs, up to 1 um long (Fig. 14a). This feature is also seen at origins of external scalids.

The third ring of internal scalids - helioscalids (Figs. 11c, 14 and 17; Plates 32-34)

The innermost ring of scalids have a semicircular section in which the circumference bears ridges comparable to the ridges which run the length of ring one external scalids. This profile resembling a rising sun is responsible for the designation "helioscalids." The helioscalids form the innermost ring of the entire scalid array. The helioscalid, unlike the scleroscalid, is free-standing along its entire length (Plate 34, label HS). It is 38 um long, with a triangular socket 15 um long separated from the endpiece by a flexible joint that can be distinguished with the light microscope. Sections of the endpiece show three bundles of tubules which usually consist of tail-less singlet tubules (Fig. 11c; Plate 32). These bundles are surrounded by the bracket-like organelle seen in external scalids.

The helioscalid is longer than any other internal scalid, and sections cut through the helioscalid tip are further displaced from the scalid origin than equivalent sections of other scalids. For this reason, sections taken through the helioscalid may suggest that it is located between a scleroscalid 1 and a scleroscalid 2 (Figs. 1, 18a) or between the oral scalid axes. The interbasal strips between the oral scalids are marked by ram's horn scrolls of cuticle (Fig. 18a; Plate 13). However, examination of the whole scalid array with light microscopy shows

that the helioscalid originates on the axis between each pair of scleroscalids 1 and the scalid insertion onto the cuticle is in the same axis as an oral scalid (Fig. 13). The inclination of a long curved helioscalid appears to displace distal sections in a clockwise direction (Fig. 18). The real relationship of the helioscalid origin to origins of other scalids is shown diagramatically in Fig. 19a.

The helioscalid endpiece is supported by ridges of cuticle running the length of the endpiece as in the ring one external scalid (Figs. 17c, 17d; Plates 1, 35). The socket is free of these ridges as in the ring one external scalid (Fig. 17e). The origins of the pharyngeal protractor muscles insert onto the cuticle around these scalids.

Pharynx crown (Plate 1; Figs. 3, 12a, 13a, 18a and 19a)

The pharynx crown encircling the opening of the alimentary canal is a striking circular structure in the centre of the head. Moritz and Storch, who first described the hollow, electron-dense units comprising the pharynx crown, likened it to an eel basket (1972a). An electron micrograph showing the pharyngeal crown in the centre of the oral cone is the first plate of this thesis. It shows how the radiating electron-dense units are surrounded by ten lobes which contain granules resembling zymogen granules in their appearance. It also shows a tongue of tissue passing from these lobes through the dense units into the lumen of the pharynx

crown. Moritz and Storch identified such tissue in K. giganteus as a regularly arranged system of microvilli, which are perpendicular to the longitudinal axis of the pharynx crown, and which contain high-contrast inclusions close to the pharynx lumen. The regularly arranged cuticle around these microvilli appears to be built of such inclusions. TEM examination of the pharynx crown lumen of K. phyllotropis has shown that it may contain emulsion-like material, suggesting that active secretion occurs through the microvilli.

The crown itself forms ten points around the mouth opening - it is shaped like a crown (Figs. 12a). The sides of the crown are covered by ten lobes or fluted ridges packed with zymogen-like granules. At the top of each lobe there is a single small dense body, of unknown structure and function (Fig. 19a).

The oral scalids and internal scalids during juvenile development of K. phyllotropis

Internal scalids have been sectioned in each of the six juvenile stages, and nine oral scalids have been counted in each stage.

In the first and second juvenile stages the internal scalids are seen in transverse section as dense cuticular structures forming circles (0.75 um diameter) or triangles (up to 1.5 um long and 0.5 um wide) in which the thickness of the walls is the same at

the width of the lumen. These internal scalids contain cytoplasm or tubules.

In the third juvenile stage all scleroscalids have a tear-drop shape in transverse section. Scleroscalids 2 are 2.5 um long and 1 um wide, and are connected to the oral cone by a sheet of cuticle 1.5 um long. Scleroscalids 1 are 1.75 um long, 0.75 um wide, and have a stalk 1 um long. Helioscalids, 2 um wide, have walls that are smooth at the proximal end, but which bear 2-3 longitudinal ridges near the distal end.

By the fourth juvenile stage, the scleroscalids 2 bear a ridge along their length as in the adult, and they are 2.75 um long and 1 um wide, and are connected to the walls of the oral cone by an undulating sheet of cuticle 3 um long. Helioscalids are 1.5 um long and 1 um thick, and have a sun-ray profile.

In the fifth juvenile stage scleroscalids 1 are 2.5 um long and 0.5 um wide. Helioscalids, fully rayed with clearly defined bundles of tubules, are the same size as in the fourth stage. Scleroscalids 2 have not been photographed.

In the sixth and final juvenile stage the scleroscalids 2 are nearly 3 um long and 1 um wide, with a sheet of anchoring cuticle 7 um long. Scleroscalids 1 are 2 um long, 1.5 um wide, and have a stalk 2 um long. Helioscalids are 2 um wide and 1.5 um thick.

Positions of the oral scalids and internal scalids in relation to external scalids

Fig. 20 schematises the relative positions of all head scalids, both internal and external. It can be seen that the scalids of this kinorhynch are usually arranged in groups of five. The significance of this arrangement is discussed in the Discussion section of this thesis (pp. 175-6).

Function of the internal scalids

Delage and Herouard (1897) stated that the internal scalids only appeared outside the body when the head was fully extruded, a condition rarely observed. The present study has not shown this degree of head eversion in any specimen, but head evisceration has revealed these concealed organs. The internal scalids are not the sensilla of a snout or proboscis that probes around the kinorhynch head, although eviscerated specimens might suggest this (Plate 33).

Zelinka (1928) and Remane (1936) believed that the internal scalids constituted a sorting mechanism. "Die Borsten sind nach vorn gerichtet und haben nach Zelinka die Aufgabe, das Eindringen von Fremdkörpern in die Ringfurche zu verhindern." (Remane 1936, p. 291). "The bristles point foward and have, as Zelinka said, the function of keeping particles out of the ring furrow (between the pharynx crown and the oral scalids)." The only feature of

the internal scalids which supports this hypothesis is the thickness of the scleroscalid wall which would protect cilia tubules from particle damage. The internal scalids are not arranged to form a barrier. If grit should intrude into the circum-oral furrow it would be just as detrimental to scleroscalid suspensory cuticle and nerve tracts as to any other cuticle in the region.

The tips of the scleroscalids have sub-terminal slits that are large enough to be seen by SEM examination (Plates 35, 36). The only other scalids which have such large terminal slits are the trichoscalids. The trichoscalids are the first external scalids to emerge when the head everts. As shown by Fig. 12a and Plate 35 the scleroscalids also project when the pharynx crown moves up during head eversion. So it is likely that the sensory input from trichoscalids and scleroscalids has special significance. This does not explain the particular role of sensory processes inside the head. Such an explanation can be given if the hypothesis is accepted that the muscular pharynx (Fig. 3; Plates 37-38), an efficient sucking organ (Boykin 1965), coordinates with the head to form a pump. Withdrawal of the head would create a current of water up the streamlined trunk of the kinorhynch. If the muscular pharynx sucks in this water as the head everts then more water and nutrient material would be drawn into the space left when the head retracts into the trunk. Ingestion of inappropriate material would be prevented if the

pharyngeal bulb did not open. Instead, this material would be dispersed when the head pushed out again. If the ambient water is rich in nutrient material it would be to the kinorhynch's advantage to accelerate the pumping process. The internal scalids provide a sensory window between the muscles of the pharyngeal bulb and the introvert retractors. In this location the internal scalids could taste the solution reaching the oral aperture and function to coordinate the sucking action of the pharyngeal bulb with the water moving action of the piston-like introvert. In the Discussion section of this thesis there is further elaboration of this hypothesis, especially in relation to other cuticular structures (pp. 170-4).

Summary

1. The top of the oral cone has a pleated outer rim and a fimbriated inner rim. Nine processes are set into the outer rim and these insert onto oral scalid bases, with scrolled edged interbasal strips between them. Below these the head is encircled by a pectinate fringe, which, like the pectinate fringe marking trunk segment boundaries, is associated with the insertion of a longitudinal muscle. Thus the oral cone may represent the first body segment.

2. The processes which have been called oral styles are oral scalids because they have the scalid ultrastructure of a ciliated receptor cell. The oral scalid contains a striated rootlet, bundles of tubules and a bracket-like organelle. Every alternate oral scalid apparently carries a basal spine.

3. The oral cone lining carries three rings of processes which have been mentioned in the literature but which have not been recognised as scalids. These processes have the scalid ultrastructure of a ciliated receptor cell. They contain bundles of tubules. Scalids of the innermost rings have simple joints, and tubules are surrounded by bracket-like organelles. These processes are termed internal scalids.

4. The internal scalid of the anterior ring is termed a scleroscalid 1. This scalid has a wall as thick as the scalid lumen, and near the tip of the scalid the tubules pass through a channel in this wall which branches off the lumen. Tubules emerge through a sub-terminal slit. The scalid is attached to the oral cone lining by a sheet of cuticle.

5. The internal scalid of the middle ring is termed a scleroscalid 2. This scalid has similar features to the scleroscalid 1 but it is bigger and there is a longitudinal ridge of cuticle projecting from the outer edge of the scalid. Tufts of small hairs are located at the origin of this scalid.

6. The internal scalid of the posterior ring is termed a helioscalid because the cuticle projects in rays. This scalid is curved and completely free-standing. Otherwise it is similar to the previous scalids.

7. The pharynx crown surrounding the opening of the alimentary canal has ten points, which subtend ten small bodies of unknown function. The sides of the pharynx crown are covered by ten lobes containing zymogen-like granules.

8. Schemata are presented to illustrate the arrangement of the oral scalids and the internal scalids in relation to the external scalids and the ten head sectors.

Chapter 5.

Cuticular structures of the alimentary canal

Previous work

The oral aperture of kinorhynchs is formed by the rigid cylinder of the pharynx crown, discussed at the end of the previous chapter. The pharynx crown is set at the anterior end of a muscular pharyngeal bulb, and the intestine passes from this to the cuticle-lined endgut (Zelinka 1928). There has been inventive discussion on the subject of secretory activity around the kinorhynch mouth. Reinhard (1881) wrote that he saw the ducts of canals opening into the bottom of the proboscis. Delage and Herouard (1897) dismissed this idea "si vraiment ce sont des glandes et surtout si elles s'ouvrent hors de la bouche, elles doivent plutôt être venimeuses." Subsequent investigation has indicated the existence of glandular tissue within the introvert, both in the pharyngeal crown (Moritz and Storch 1972 a, b) and the pharyngeal bulb (present study). There is no evidence as yet that these glands produce venom.

In homalorhagid kinorhynchs the pharyngeal bulb has a cuticle-lined epithelium surrounded by three lobes of radially-oriented muscle fibres attached to stout inner and outer basement membranes (Dujardin 1851, Pagenstecher 1875, Zelinka

1928). Zelinka illustrated salivary glands around the outside of the pharyngeal muscle lobes of Pycnophyes communis (1928, Plate 26, Fig. 4). Remane described and illustrated two pairs of salivary glands located posterior to the pharynx (1936, Fig. 239).

The presence of a basement membrane between the muscle fibres and the epithelium distinguishes kinorhynchs from other aschelminthes with a myoepithelial foregut such as gastrotrichs and nematodes (Marcus 1958, Ruppert 1982).

The posterior end of the kinorhynch alimentary canal is lined with cuticle, and a microvillous intestine connects this with the cuticle-lined pharynx. In Pycnophyes Zelinka (1928, p.127, Plate 12, Fig. 7) and Remane (1936, p.299) described a sphincter separating the midgut from the endgut. Remane described the endgut as pear shaped, lacking cilia ("wimperlos" = ? lacking microvilli) and lined with cuticle. Boykin (1965) measured 20-30 um length of cuticle lining the endgut of K. ilyocryptus.

Present study (Plates 37-41)

Salivary glands have not been seen in K. phyllotropis, neither around the pharyngeal lobes, nor around the intestine. However, cells packed with round, electron-opaque vesicles are seen in the pharynx epithelium, and secrete material through the cuticle lining the pharynx (Plate 38). Two such cells are seen in the

epithelium of each of the three lobes. Transverse sections of the pharyngeal bulb show six secretory cells, each with an associated nucleus. Micrographs of the secretion process show a vesicle discharging a droplet through the cell membrane which is interrupted at the point of secretion (Plate 41). The secretion ballooning into the pharynx is covered with dark material. Placoids of cuticle line the pharynx lumen.

Three J-1 specimens were sectioned in this study (two were sectioned transversely, and one was sectioned longitudinally). All showed a developmental separation between the radial muscle fibres and the epithelium (Plate 37). The space between the inner basement membrane of the radial muscle fibres and the cells of the epithelium averages 1.5 um in width. This separation is not seen in the J-2 stage or any later stage. Separation of epithelium from a bell of muscle is reminiscent of the arrangement found in setcoronarian priapulids (Por 1983, Por and Bromley 1974). However the priapulid muscular bell has an inner and outer layer of circular muscle separated by longitudinal muscle. Kinorhynch pharyngeal fascia are arranged radially.

The cuticularised sections of the gut are separated by an intestine lined with a microvillous brush border. Bacteria have been seen in the gut contents (Plate 39). These bacteria resemble ectocommensal bacteria growing on the cuticle (Plate 40) which appear to comprise part of the diet of this kinorhynch.

No sphincter has been observed at the beginning of the cuticularised endgut in K. phyllotropis, but the microvillous section of the midgut does end with a slight constriction of the lumen. Cuticle of the endgut is seen as a single sheet and does not have the placoid-like appearance of cuticle lining the pharyngeal bulb.

Summary

1. Cuticle lining the muscular pharyngeal bulb forms placoids covering secretory cells inside the pharyngeal epithelium. There are two secretory cells in each of the three sides of the triangular pharynx.

2. The first juvenile stage shows separation of the epithelium from the pharyngeal musculature as in some priapulids. This separation is not seen after the first juvenile stage.

3. Bacteria have been photographed in the otherwise unidentifiable gut contents of this kinorhynch.

4. The endgut has no sphincter and is lined with uninterrupted cuticle.

RESULTS

Chapter 6.

Cuticular structures of the excretory system

Previous work

Reinhard (1887) described ciliated sacs ("Wimperepithelium bedeckt") in the eighth segment of Echinoderes. Schepotieff (1907) described three pairs of such sacs with "Flimmerhaaren" (1908), possibly translating as "flame cells". Zelinka (1894, 1908, 1928) described the protonephridia of both cyclorhagid and homalorhagid kinorhynchs as single pairs of tubes containing flagella. These tubes pass through the hypodermis of segment 10 and open at the lateral margins of the dorsal plate of segment 11. In the homalorhagid Pycnophyes communis the excretory tubes open by sieve plates ("Porenfeld" Zelinka 1928, Pl. 13, Fig. 10). In Kinorhynchus ilyocryptus, Boykin (1965) found an excretory tube opening through a circular field of pores on the ventral aspect of the tergite of segment 11 and observed flagella beating.

Present study (Plates 42-46)

In K. phyllotropis the excretory apertures are in very small tubules of cuticle which open on the dorsal plate of segment 11, close to the lateral margin. These tubules are set into the

cuticle in a circular depression surrounded by a cuticular fringe. Six to twelve tubules have been counted in this cluster. Two longer tubules or setae emerge from the nearby cuticle, one located 20 um anterior to the cluster and the other 15 um mesial to the cluster. In the J-1 three tubules are fused to form a perforated cuticular prominence, not a depression as seen in later stages.

TEM examination of the tubules shows that they extend below the cuticle to penetrate the hypodermis. In adults the tubules have a diameter of 0.5 um which decreases to 0.3 um in the J-2. In the J-1 the tubules have much thinner walls than later stages. In the hypodermis tubule structure becomes complex. Tubules may branch or they may have alveolar expansions. They do not form a single excretory tube as reported in other kinorhynchs. The short setae inserted away from the tubule cluster have not been sectioned below the cuticle. During early juvenile stages these setae have six to nine projecting rays of cuticle on the outside of each setal tube.

This study has not shown whether the above features are associated with any other body system or whether there is any sexual dimorphism.

Significance of cuticular excretory tubules

The cuticular aperture of this kinorhynch is not just another form of sieve plate. For comparison a cyclorhagid sieve plate is shown in Plates 76 and 77. Excretory tubules, or cuticular conduits, are fewer in number than sieve plate pores and are more complex in structure, extending above and below the cuticle. Furthermore, it is possible that the excretory cells associated with cuticular conduits differ from the nephridia that have been described in association with sieve plates. Such nephridia were not observed in any stage of development in this species, although cuticular conduits were sectioned in every specimen.

Goodrich (1945) summarised previous knowledge of kinorhynch body-cavities. "The extensive body-cavity has no regular epithelial lining and appears to be of pseudocoelic nature..the gonadial sacs and genital ducts no doubt represent the coelomic sacs and their coelomoducts." However K. phyllotropis does not appear to have any body-cavity at all. Even the pharyngeal muscles do not lie freely, but are surrounded by ladder-like arrangements of membranes. It is likely that these membranes were observed in this study because they were better conserved by a polymerised mounting medium than by agents used for light microscopy. However it is also possible that other homalorhagid species do have the spacious body cavities of classical descriptions. If so, these species need to osmoregulate both intracellular contents and the body fluids filling large body

cavities. These species could be expected to differ from K. phyllotropis and any similarly constructed homalorhagids where the osmoregulatory load is only derived from cellular contents and small extracellular spaces.

It is also possible that homalorhagids with sieve plates have different osmoregulatory requirements from homalorhagids with cuticular conduits. Ecological data does not support this hypothesis. Kinorhynchus phyllotropis is stenohaline, its distribution being restricted to open waters within the headlands of Sydney Harbour. The sieve plated species K. ilyocryptus is distributed in open sea water in the San Juan Archipelago, while another homalorhagid with a sieve plate, P. communis, was collected by Zelinka from field stations located in open waters of the Bay of Naples and Gulf of Trieste, more than 1 km from the coast (Higgins 1983).

Differences between the excretory systems of species with sieve plates and species with cuticular conduits should be better understood when the histology of the excretory tubes has been described.

Summary

1. In K. phyllotropis the excretory tube does not open onto the cuticle by a sieve plate as has been reported in other kinorhynchs, but in a cluster of cuticular tubules located in slight cuticular depresssion in the same area as sieve plates are located.

2. In the first juvenile stage, excretory tubules are fused together to form a small perforated cuticular prominence.

3. The tubule cluster is associated with two short hollow setae which are ribbed in early juvenile stages.

4. In the hypodermis the tubules ramify and appear to have alveolar expansions. There is no clearly defined excretory tube.

Chapter 7.

Subcuticular histology of unciliated and ciliated apertures onto trunk plates

Previous work

1. Cuticular pores

Reinhard (1887) first described fine pores in the cuticular plates which formed rows near posterior margins of most trunk plates. Zelinka (1928) expanded the subject with details of pore or canal distribution in several kinorhynch families. He used the term "Knöpfchenreihen" (rows of knobs) for lines of punctations at the posterior margins of the plates and this term has been employed in taxonomic papers written in the English language (Higgins 1961b, 1966a; Lang 1949). Boykin (1965) described the cuticular pits in K. ilyocryptus: "They are circular or elliptical in cross section, often dichotomously branched, and 0.7-1.0 u in diameter. As they are fairly evenly distributed over the surface of all the plates, about 1.3-1.7 u between centers, 1200-1400 may adorn a single sternite. Although they are hollow, sometimes showing cytoplasmic strands within, they probably do not open to the outside." Merriman (1972) noted that in the cyclorhagid Echinoderes dujardinii (= dujardini), (Claparède, 1863) the apparently perforate character of the cuticle is not confirmed by scanning electron micrographs of the

surface or by transmission electron micrographs of sectioned material.

No function has been suggested for these cuticular pores, nor has it has not been noted that they are capable of secreting material through the cuticle. It has been known that kinorhynch cuticle carries plant and animal ectocommensals (Higgins 1961a; Zelinka 1914, 1928). The possibility of a symbiotic relationship between kinorhynchs and ectocommensals has not been explored, and knowledge of kinorhynch diet is limited to the observation of diatom tests seen in kinorhynch gut contents (Zelinka 1928). Higgins (1961) reported that attempts to culture kinorhynchs with various combinations of diatoms, unicellular green algae, and sediment from the collection sites succeeded in maintaining kinorhynchs for as long as six months, but that no feeding was apparent and that the internal organs atrophied after a few months. This experience was repeated by Boykin (1965). Weiser (1960) stated intuitively that kinorhynchs are pure deposit feeders, and this idea has been taken up in general text books "Mud dominates their lives. They feed on organic detritus in mud." (Meglitsch 1972).

2. Membrane cells

Moritz and Storch (1972b) observed in K. giganteus type 1 scalids and trichoscalids cells with characteristic piles of membranes. In type 1 scalids these cells sent processes through the cuticle.

An apical section of the socket of this scalid contained a membrane system with thickenings between particular lamellae (Moritz and Storch 1972a, Plate 4d; Moritz and Storch 1972b, Plate 2a), while other sections showed membrane systems without these characteristic thickenings (Moritz and Storch 1972b, Plate 4b). The authors noted that many arthropod mechanoreceptors bear distal cilia and parallel systems of modified microvilli (tubular bodies) whose function is apparently to coordinate stimulus transmission. They suggested that membrane cells in scalids have a parallel function. Noting that membrane cells pass through the scalid joint, the authors suggest that membrane cells function to carry stimuli through a region subject to mechanical stress.

3. Ciliated sensory spots

Zelinka (1928) described sensory cells which formed longitudinal series running down the trunk, two dorsal series, two dorsolateral series, two ventrolateral series and two ventral series. Boykin (1965) noted that sensory cells occurred in funnel shaped endocuticular pits. In 1973 SEM pictures of cyclorhagid cuticle pits were published by Merriman and Corwin (Echinoderes dujardini sic.) and Moore (Campyloderes macquariae). The pits of both species showed a central aperture surrounded by cuticular papillae. Similar structures were described in the homalorhagid Pycnophyes kielensis (Zelinka, 1928) by Malakhov and Spidonov (1980) and in priapulids (Kirsteuer and Rutzler 1973; van der Land 1968, 1970).

4. Ciliated seta cells

Zelinka (1928) and Boykin (1965) noted that lateral seta cells are associated with mucous cells; Moritz and Storch (1972a) noted that there is the striated rootlet of a cilium between the mucoid droplets; Brown and Higgins (1983) noted that setae are hollow.

Present study

1. Cuticular pores (Fig. 21; Plates 47-51)

The juvenile and adult cuticle of K. phyllotropis is porous. Fine canals pass through the cuticle of dorsal and ventral trunk plates. The inner opening of such a canal is a round aperture 0.2-0.4 um in diameter. This aperture forms the opening of a straight tube containing extensions from nearby hypodermal cells. The cells contain mitochondria and their cytoplasmic extensions contain vesicles and material extruded from round inclusion bodies in the hypodermal cells. The straight section of the cuticular canal passes through the fibrous endocuticle and branches before passing through the dense epicuticle where the ends of the canal dilate to form small pits in the outer layer of cuticle. The surface openings are sheltered by V-shaped prominences of the external cuticle. These prominences have been mentioned (p.95) as imparting a surface relief similar to that of a wood rasp. SEM examination shows that there are two openings on each side of each prominence (Plate 49 arrows).

The density of these canals increases throughout juvenile development. There are approximately 6 canals per 25 square micrometres in the J-1, 10 canals per 25 square micrometres in the J-6 and 15 canals per 25 square micrometres in the adult. The adult density averages 1.5 um between centres, as Boykin reported in K. ilyocryptus.

The large punctations at the top of "Knöpfchenreihen" are formed by invaginations of the inner cuticle. These have not been seen to have pores opening onto the surface cuticle. Unperforated cuticle extends from these invaginations of inner cuticle to the accessory pachycycli. The "Knöpfchenreihen" are not formed by rows of pores on the inner cuticle and no rows of pores are seen on the outer cuticle either. It seems likely that this punctation seen with the light microscope but not with SEM is caused by intracuticular material with different light refractive properties from the surrounding cuticle.

Cuticular glands secrete fluid droplets through the kinorhynch cuticle (Plate 51). This secretion could function to protect the animal from abrasion by sedimentary particles, or it could serve to provide a substrate for the rich garden of diatoms, algae and other ectocommensals that grow on kinorhynch cuticle (Plate 52). These include unicellular bacteria (Plate 40). Unicellular bacteria have been photographed in the kinorhynch gut contents (Plate 39). It cannot be said whether the kinorhynchs eat these

bacteria, or whether they benefit from substances produced by the bacteria.

2. Membrane cells (Plates 53-57)

Membrane systems which resemble mitochondria have been observed in type 1 scalids (Plate 14). Membrane cells with thick and thin membranes as described in K. giganteus (Moritz and Storch 1972b) have been photographed in trichoscalids (Plates 26, 53) of K. phyllotropis. These cells open to the exterior through canals in the cuticle. Cells containing membrane systems fill pits in dorsolateral and ventrolateral cuticle of the trunk plates (Plates 54-56). Some of these cells contain thickenings between individual lamellae (Plate 57) and closely resemble cells in trichoscalids (Plate 53). Other cells contain piles of membranes without characteristic thickenings (Plates 55 and 56). These resemble similar cells in K. giganteus. A fine canal, 0.04 in diameter, passes through the cuticle from a membrane cell (Plate 54). The presence of the same cell type in the scalid sense organs and in the trunk plates suggests that sensory information is imparted through the trunk plates. It seems possible, since no tangoreceptive organelle is known, that membrane systems have a chemosensory function, receiving stimuli from the immediate environment of epicuticular flora and fauna.

3. Ciliated sensory spots (Plates 58, 59, 68, 69)

The sensory spots of K. phyllotropis contain a central aperture

and a lateral aperture in all stages from the J-1 to the adult (Plates 68-99). In this they resemble priapulid sensory spots (Kirsteuer and Rützler 1973, van der Land 1968, 1970). Kinorhynchus phyllotropis sensory spots contain modified cilia. This is typical of the majority of animal sense organs, the main exceptions being many invertebrate eyes and vertebrate taste receptors (Barber 1974). In K. phyllotropis the striated rootlet of a cilium is found in the hypodermal cell beneath the cuticular pore of a sensory spot (Plate 58). This is surrounded by a collar which produces a circle of nine microvilli (Plate 59). The number of microvilli is invariably nine. This ultrastructure is similar to that of the mechanoreceptor of the priapulid Priapulus caudatus (Lamarck, 1816) described by Moritz and Storch (1971), but it differs from the elongated striated rootlets of scalid cilia (Plate 61; Fig. 10).

4. Ciliated seta cells (Fig. 22; Plate 60)

The hollow seta cells of K. phyllotropis emerge from large mucous cells. There are no tracts of free cilia near these setae so it is unlikely that the secreted mucous serves to transport food, waste, or the kinorhynch itself. It is possible that the mucous secreting setae cement together the mud grains around a kinorhynch, effectively providing a tube around the kinorhynch trunk, which lacks locomotory organs. This tube could have the effect of providing a microclimate which would enhance ectocommensal activity.

Summary

1. Fine branching canals pass through trunk plate cuticle which contain extensions from hypodermal cells. Cuticular canals are present at all stages of development, but their density increases in successive stages. The surface openings of the canals are located at the sides of the V-shaped prominences characteristic of homalorhagid cuticle.

2. Cuticular canals may secrete material to protect cuticle from abrasion. Cuticular secretion may also provide a substrate for the ectocommensal bacteria and diatoms which grow on kinorhynch cuticle, and which are seen in gut contents.

3. Membrane cells of the type seen in the sensory external scalids (trichoscalids) have been observed in the large cuticular pits of trunk plates, opening to the exterior by fine canals.

4. Trunk membrane cells may be chemoreceptors, functioning to coordinate stimuli from the epicuticular community of ectocommensals.

5. The hollow lateral seta of this species passes through the cuticle from a mucous cell containing a striated rootlet.

6. The production of mucous from these processes could serve to cement together mud grains, thus promoting a stable environment around the ectocommensal community on the trunk cuticle, stability further enhanced by the lack of kinorhynch locomotory appendages.

7. The hypodermal cell below a sensory spot contains the striated rootlet of a cilium which is surrounded by a collar from which emerge nine microvilli.

8. Ciliated sensory spot cells have a similar ultrastructure to the mechanoreceptors of some priapulids.

Chapter 8

Life history of *K. phyllotropis*

Previous work

Kinorhynchs from Normandy, France, were the first kinorhynchs to be described (by Dujardin in 1851) and to be classified (by Claparède in 1863). Claparède believed these kinorhynchs to be planktonic stages of a form that metamorphosed elsewhere. This view contrasted with that of Leuckart (1854) who believed them to be dipteran larvae. Claparède conferred the name *Echinoderes dujardinii* upon the kinorhynch that Dujardin had discovered, and gave the name *E. monocercus* to a sympatric kinorhynch with a long mid-terminal spine. Metschnikoff (1865) recognised that the latter was a juvenile form of *E. dujardinii* and stated that colourless opaque kinorhynchs were juvenile stages. Greeff (1869) illustrated kinorhynch "embryos" which were later recognised as large sperm. Panceri (1876) and Reinhard (1887) recognised juveniles or "larvae" with small size and immature gonads.

Zelinka (1894) mentioned that moulting specimens were found in his collections, and (1896) that the smallest forms had 11 segments and longer, more numerous spines. Schepotieff (1907) suggested that metamorphosis occurred when small forms with

indistinct cuticular divisions changed to forms with distinct segmentation and golden-brown colouration. He also reported that newer segments were budded off anamorphically i.e. from the tail end. Zelinka (1907) disagreed, saying that newer segments were formed within the tail region, and that juveniles did not have indistinct segmentation except, in some forms, in the terminal region. Zelinka (1908) further disagreed with Schepotieff (1907) that moulting did not involve the head or snout. Zelinka (1928) accepted and erected larval genera. These are discussed at the end of this section. Although Zelinka agreed that metamorphosis occurred, he deduced that in Pycnophyes there were five or more moults following the six (or more) juvenile stages.

Remane (1936) stated that kinorhynch juvenile development was direct and without a metamorphosis in which juvenile organs were replaced by adult organs. He summarised the special features of juvenile kinorhynchs as follows:

1. Cuticle is thin and pliable without pachycycli or armour joints, the intersegmental division being represented by a contriction around the body which is absent in the posterior segments where the number of segments can only be discerned by the lateral or dorsal spines.
2. The minimal number of segments is 11, which would appear to be the situation when the kinorhynch hatches, other juvenile stages have 12 and 13 segments, and adults have 13 segments.

3. Even in juveniles with visible gonads there are no penile spines, no genital openings, and in male homalorhagids, no adhesive tubes.
4. Spines tend to be longer and more numerous in juveniles.

Nyholm (1947 a, b) wrote the first account of a kinorhynch life history. This was obtained by culturing Echinoderes (= Echinoderella) elongata (Nyholm, 1947b) through several stages of development. In a text describing nine of the ten illustrated stages (1947b, Figs. 12-13), Nyholm outlined a developmental series progressing from an ovoid non-segmented form, to a cardioid non-segmented form, then through 4-segmented, 6-segmented, 8-segmented and 9-segmented stages that were non-motile, apparently non-moulting, and lacked heads. (Kozloff, in 1972, speculated that these observations were made on dead and decaying specimens). Nyholm's next stage had 11 segments and resembled that drawn by Zelinka. This was followed by a 12 and a 13 segmented stage, and then by the adult. Nyholm employed the names of Zelinka's larval genera for his developmental stages and these are discussed at the end of this section.

Higgins (1961) observed development in E. bookhouti Higgins, 1964 and P. beaufortensis Higgins, 1964. He separated the juveniles from his samples into size groups and observed them for moulting and subsequent change of length. He found six capitate, motile, preadult size groups, the smallest having 11 segments. However

he cautioned that the apparent number of segments was only a matter of personal judgement because the 11th segment contained the potential 12th and 13th segments and deciding the segment number rested on whether one line or two were discernible.

Kozloff (1972) observed and photographed juvenile E. kozloffi hatching from the egg. These juveniles had 11 segments and a head. They were motile, and ingested diatoms a few minutes after hatching.

Zelinka's juvenile genera were as follows. Echinoderid larval genera consisted of Hapaloderes (the smallest juvenile stage of Echinoderes species, a stage characterised by a long mid-terminal spine), Habroderes (older juvenile echinoderids with pigmented eye spots) and Habroderella (older juvenile echinoderids without pigmented eye spots). Habroderella was regarded as a juvenile form of the adult genus Echinoderella which did not have pigmented eye spots, as opposed to Echinoderes which did have pigmented eye spots. As eye spot pigment disappears in preserved specimens this is not a reliable character. Echinoderella was synonomized with Echinoderes by Karling (1954). Zelinka's pycnophyid larval genera consisted of Centrophyes (early stages with a mid-terminal spine) and Hyalophyes (older juveniles with lateral terminal spines but no mid-terminal spine). Leptodemus was erected for juvenile stages of Kinorhynchus which were all characterised by absence of distinct terminal spination.

Nyholm (1947b) used Zelinka's terms for both Pycnophyes and Kinorhynchus to name the developmental stages of P. flaveolatus and P. communis Zelinka, 1928. Nyholm said that an embryonic stage was followed by two stages of immobile larvae, followed by a motile, non-feeding "leptodemus" stage with 6-7 segments and a non-differentiated head, followed by a 8-9 segmented stage with a differentiated head. This was followed by a "centrophyes" stage and a "hyalophyes" stage and then the adult.

Present study

1. Direct development (Fig. 23)

The findings of the present study show that the life history of this species is direct, and that differentiation of gut structures and of terminal segments proceeds throughout juvenile life. The six juvenile stages possess heads and internal organs (Fig. 23). These internal organs include excretory organs (which are not illustrated in Fig. 23, but which are described in chapter 6).

2. Numbers of segments (Fig. 24; Plates 62-67, 70-73)

The present study confirms Higgins (1961a) observation that all juvenile segments are potentially present in the first juvenile stage. However, the first 7 trunk segments (segments 3-9) are always more clearly demarcated than the last 4 trunk segments (segments 10-13). The intersegmental divisions of anterior

segments 3-9 are deep intersegmental grooves. The intersegmental divisions of posterior segments 10-13 are no more than lines of pronounced cuticular sculpturing. In fact, segment 13 can only be readily discerned in favourable orientations by SEM. It is seen as the area posterior to a line of cuticular markings connecting the mid-dorsal spine of segment 12 to the lateral spine of segment 12. From the J-4 stage onwards the lateral spine of segment 13 can also be seen (Plates 65-67, 70, 71). The laterotерminal spinose process characteristic of this species (Brown 1983, Figs. 2 and 5) is visible from the J-5 stage onwards (Plate 71).

3. Mid-dorsal spines (Fig. 24)

All trunk segments except the first and last carry a mid-dorsal spine in these juveniles (but not in the adult, cf. Plate 73). The mid-dorsal spines of trunk segments 4-9 are more acutely pointed than the spines of the posterior segments, although in the J-1 all spines are acutely pointed.

4. Posterior margin of the terminal segment (Fig. 24; Plates 62-67, 70-73)

The posterior margin of the terminal segment shows characters distinguishing each juvenile stage from other juvenile stages. These characters are as follows:

J-1 The terminal mid-dorsal spine, which projects beyond the posterior margin of the terminal segment, is acutely pointed. Lateral spines on all segments are also acutely pointed. There is no unarticulated spinose protuberance at the lateroterminal margin of the tergal plate.

J-2 The terminal mid-dorsal spine, which projects beyond the posterior margin of the terminal segment, is blunt, as is the case with posterior spination of all following juvenile stages. There is no unarticulated spinose protuberance at the lateroterminal margin of the tergal plate.

J-3 The terminal mid-dorsal spine reaches the posterior margin of the terminal segment. There is no unarticulated spinose protuberance at the lateroterminal margin of the tergal plate.

J-4 The terminal mid-dorsal spine does not reach the posterior margin of the terminal segment. There is an unarticulated spinose protuberance at the lateroterminal margin of the tergal plate with no interruption of the posterior margin between the protuberance and the lateral spine of the 12th segment. This spinose protuberance is characteristic of this species, and a similar protuberance was described in Kinorhynchus anomalus (Lang, 1953), (cf.Brown and Higgins 1983).

J-5 The terminal mid-dorsal spine does not reach the posterior margin of the terminal segment. There is an unarticulated spinose protuberance at the lateroterminal margin of the tergal plate with a small spine adjacent and lateral to the protuberance. The small spine represents the lateral spine of the presumptive 13th segment. As in all previous juvenile stages the posterior mid-dorsal spines are set into a mid-dorsal fold of thin cuticle which is much wider than the spines. This cuticular fold is usually flexed so that the spines lie against the laterodorsal cuticle.

J-6 The terminal mid-dorsal spine does not reach the posterior margin of the terminal segment. There is an unarticulated spinose protuberance at the lateroterminal margin of the tergal plate with a small spine adjacent and lateral to the protuberance. In the last juvenile stage the posterior mid-dorsal spines are set into a mid-dorsal ridge of thick cuticle which is narrower than the spines. This ridge of cuticle is inflexible.

The posterior margins of the adult terminal segments in this species have been described in Brown, 1983. Light microscope examination shows genitalia in J-6 specimens which the SEM reveals to be forming below the cuticle. There are no gonopores in juveniles.

Summary

1. There are six juvenile stages in K. phyllotropis each possessing a head, alimentary canal and excretory tubules.

2. In all juvenile stages the posterior margins of the first seven trunk segments are clearly delineated by a cuticular constriction, while the posterior segments are indicated by lateral and mid-dorsal spines and by lines of cuticular markings. The formation of segment 13 in the J-5 and J-6 stages is indicated by the growth of very small lateral spines and by the appearance of a line of cuticular markings connected to these lateral spines.

3. The first juvenile stage differs from all others in having an acutely pointed mid-dorsal spine projecting over the posterior margin of the terminal segment as well as acutely pointed lateral spines.

4. The second juvenile stage differs from all others in having a blunt mid-dorsal spine projecting over the posterior margin of the terminal segment, lateral spines are also blunt as in subsequent juvenile stages.

5. The third juvenile stage differs from all others in having the blunt posterior mid-dorsal spine extending to the posterior margin of the terminal segment, but not projecting beyond it.

6. The fourth juvenile stage differs from all others in having an unarticulated spinose protuberance on the laterоterminal margin of the posterior segment with no interruption of this margin between the protuberance and the lateral spine of the twelfth segment.

7. The fifth juvenile stage differs from all others in having the following combination of characters - a small lateral spine adjacent to the unarticulated spinose protuberance on the laterоterminal margin of the posterior segment and a posterior mid-dorsal spine inserted into a flexible mid-dorsal fold of thin cuticle which is wider than the spine.

8. The sixth juvenile stage differs from all others in having the following combination of characters - a small lateral spine adjacent to the unarticulated spinose protuberance on the laterоterminal margin of the posterior segment and a posterior mid-dorsal spine inserted into an inflexible mid-dorsal ridge of thick cuticle which is narrower than the spine.

Chapter 9.

Pycnophyes faveolus sp. n.

Figures 25-34; Plates 74-75

Material. Fifty adults from Hunter Bay, Middle Harbour, Sydney Harbour (Port Jackson), 33o 49'30"S., 151o15'24"E. Collected from sandy mud at 4-6 m depth, in 1980 on 20 Apr, 22 Jun, 14 Sep, and 14 Dec, in 1981 on 22 Mar and 15 Nov by R.Brown.

Diagnosis.- Trunk segments 3-12 tapering slightly beginning with segment 8; lateral terminal spines long, robust, straight, 144-173 um, 20-27 percent of trunk length; cuticle with band of rugate sculpturing parallel to slightly denticulate dorsoanterior margin of first trunk segment; areas of distinctive faveolate cuticle lateral on segments 4-12, and parallel to dorsal and ventral anterior margins of segments 10-12.

Description.- Adults (Figs. 25-43), trunk length 618-712 um; trunk segments nearly uniform in width, tapering in segments posterior to segment 7; MSW-7 133-160 um, 19-24 percent of trunk length. Second segment consisting of 4 slightly incised dorsal placids and 4 even-margined ventral placids (Figs. 25, 27, 31).

Trunk segments (Figs. 25-26) without mid-dorsal spinous processes. Single seta, 12 um long, situated mid-dorsally on segments 3, 4 and 8, pairs of setae situated mid-dorsally on segments 5, 7, 9, 10 and 11; dorsolateral setae, 10-12 um long, located on segments 4-11; lateral setae, 12-14 um long, located on segments 3-4, 6-12, 2 located laterally on segment 12, lateral seta of segment 5 located ventral to lateral line; ventrolateral setae, 18-20 um long, on segments 3, 5-11 in males and 3-11 in females (Figs. 25, 27, 31). Sensory spots situated dorsolaterally on segments 3-12, lateral to line of dorsolateral setae on segments 3-12 and ventrolaterally on segments 3-12, mesial to ventrolateral seta in segment 3, lateral to line of ventrolateral setae on segments 6-11, and in line with preceding seta in 4 (male), 5, and 12. Pachycycli well developed on all trunk segments, midventral thickenings ("Mittelwülste") near anteromesial margins of ventral plates 10-12. Armour joints overlaid dorsally and ventrally by patches of rugate cuticle bounded mesially by prominent ridges of cuticle, not bounded posterodorsally by ridges of cuticle but bound posteroventrally by prominent ridges of cuticle aligned anterolaterally, and associated with areas of punctate cuticular sculpturing (Figs. 25, 27 and 31); bands of rugate cuticle forming irregular cells dorsally and regular cells ventrally around anterior margins of segments 10-12 containing dorsolateral ridge of cuticle aligned anteroposteriorly; anterior margins of segments 4-12 usually overlaid by band of cemented detritus. Large muscle scars

dorsolateral on tergal plate of first trunk segments, similar muscle scars on on episternal plates; paired dorsolateral cuticular scars with long axis oriented towards posteromedial margin on segments 4-12; small round ventrolateral cuticular scars on segments 4-12, mesial to setae; elongate areas of thin cuticle containing 4-6 pores anterior to dorsolateral muscle scars.

First trunk segment (segment 3) with only slight extensions of anterolateral margins of tergal plate (Figs. 27, 28, 31, 32); anterior tergal margin denticulate, border sculptured by rugate cuticle (Figs. 28, 32). Large round muscle scars on each side of tergal plate with anterior cuticle puckered into 4 (rarely 6) longitudinal folds. Thin area of cuticle at anteromesial margin of episternal plates deeply divided vertically and horizontally into four equal patches, anterolateral patch of thin cuticle vertically divided by indistinct groove. Midsternal plate with single area of thin cuticle along anterior border. Lateral margin of this plate showing slight lateral divergence about one third of the way posteriorly.

Segment 4 of male with prominent adhesive tubes 32-35 um long (Figs. 25, 27). Segments 5-11 similar, differences between segments already noted in distribution of setae, sensory spots and muscle scars.

Sternal plates of segment 12 almost extending to terminal margin of segment 13 except when segment 13 protruded; tergal plate evenly rounded.

Tergal plate of segment 13 with fine posterior serrations covering posterior, rim with slight protuberance mesial to laterоterminal spines; posterior tergal margin parallel with evenly-rounded margins of sternal plates (Figs. 29-30, 33-34). Posterior margins of terminal segments usually obscured by nidus of cemented detritus (Plate 74). Males with two pairs of penile spines (30-35 um long) between anterolateral margins of terminal sternal plates, separated by single gonopore bearing 10 um long hairs (Fig. 29). Females with single gonopore between two horizontal lips between anterolateral margins of terminal sternal plates anterior to laterоterminal spine (Fig. 33).

Morphometric data for adult specimens from Middle Harbour are given in Table 9.1.

Holotype - Adult male, TL 683 um (Figs. 25-30).
Museum Accession Data.
Allotype - Adult female TL 682 um (Figs. 31-34).
Museum Accession Data.
Paratypes -
Museum Accession Data.

Variations within the Middle Harbour Population. The characters given in the description varied among the fifty specimens of the material examined as follows. Four specimens showed variation in the arrangement of the "Mittelwülste" midventral thickenings, in one specimen the outer margin was not defined, in a second specimen the posterior margin was extended into a point, a third specimen contained this cuticular thickening only in segment 12, and in the fourth specimen, which had the widest recorded sternal width, there were double "Mittelwülsten" on the left side of segment 11. Two other specimens has malformed ventral plate boundaries. The first showed asymmetry of the sutures between the episternal and midsternal plates. The second showed an even separation of the anterior half of the midventral suture of segment 4. One specimen had two mid-dorsal setae on segment 3 (while all others had one). Mid-dorsal setae were most commonly broken off on segments 4-7 leaving a stub or an open pore. In both males and females 16 of the 50 laterotерminal spines were broken. Two males carried spermatophore-like bodies on the terminal segments.

Table 9.1.- Measurements (um) and indices (%) for Pycnophyes faveolus adults from Middle Harbour (see Methods section, p. 25, for character abbreviations.)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	MM	25	618-712	657.1	23.5	4.7	3.6
	FF	25	629-695	667.8	18.3	3.7	2.8
	MF	50	618-712	662.4	21.5	3.0	3.2
SW	MM	25	112-136	120.6	7.8	1.6	6.4
	FF	23*	118-136	127.3	5.0	1.0	3.9
	MF	48	112-136	123.8	7.3	1.1	5.9
SW/TL	MM	25	16.5-19.7	18.4	1.0	0.2	5.4
	FF	23*	18.4-20.2	19.0	0.5	0.1	3.0
	MF	48	16.5-20.2	18.7	0.9	0.1	4.7
MSW-7	MM	25	133-160	142.8	8.4	1.7	5.9
	FF	23*	137-156	146.3	5.6	1.2	3.8
	MF	48	133-160	144.5	7.3	1.1	5.1
MSW/TL	MM	25	19.7-24.0	21.7	1.2	0.2	5.4
	FF	23*	19.4-24.0	21.7	1.1	0.2	5.1
	MF	48	19.4-24.0	21.7	1.1	0.2	5.2
LTS	MM	24#	148-173	159.0	5.4	1.1	3.4
	FF	22#	144-160	151.5	4.1	0.9	2.7
	MF	46	144-173	155.4	6.1	0.9	3.9

LTS/TL	MM	24#	20.3-26.7	24.3	0.8	0.2	3.3
	FF	22#	20.6-24.1	22.5	1.0	0.2	4.5
	MF	46	20.3-26.7	23.4	1.3	0.2	5.5

* Two specimens appear to be narrow because they are tilted to the side by epiphytes. These specimens show lateral sensory spots most clearly
# Specimens have the tips broken off both laterolateral spines.

Variation between populations.

Pycnophyes faveolus was collected 10 Sept 1979 in the North Harbour, both at Spring Cove, near the Quarantine Station Beach off North Head, and near the Wellington Reserve north of Forty Baskets Beach. In both of these sites it is the dominant kinorhynch species, although Kinorhynchus phyllotropis is also present. At Hunter Bay, Middle Harbour, collections typically include one P. faveolus for every 40-60 K. phyllotropis. North Harbour specimens of P. faveolus differ from the Middle Harbour specimens in their morphometric measurements (Tables 9.1 and 9.2) and in the absence of balls of detritus cemented to posterior segments. Their laterolateral spines are usually carried at right angles to the body, and not obliquely as in the Middle Harbour species. The tips of their straight laterolateral spines have a curved outer contour, whereas spines of Middle Harbour specimens taper evenly. The cuticle texture is coarser in the North Harbour populations. None of these characters are valid taxonomic characters, they are likely to be due to habitat differences. In recognised characters such as patterns of

cuticular sculpturing and distribution of sensory spots, muscle scars and setae, the North Harbour specimens are the same as those from Middle Harbour.

Etymology. This species name is from the Latin favus (honeycomb) referring to the bands of sculptured cuticle forming small cells encircling the posterior segments, and the areas of similar sculpturing over the armour joints (Plate 75).

Morphometric data for adult specimens of P. faveolus from Spring Cove, North Harbour are given in Table 9.2.

Table 9.2.- Measurements (um) and indices (%) for Pycnophyes faveolus from North Harbour (see Methods section, p. 25, for character abbreviations).

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	MM	8	528-605	562.7	25.9	9.1	4.6
	FF	7	523-592	556.7	25.8	9.7	4.6
	MF	15	524-605	560	25.1	6.5	4.5
SW	MM	8	115-128	121.6	5.6	2.0	4.6
	FF	7	118-131	126.0	4.0	1.5	3.2
	MF	15	115-131	123.6	5.3	1.4	4.3
SW/TL	MM	8	19.3-24.2	21.7	1.7	0.6	8.0
	FF	7	21.4-24.2	22.8	1.0	0.4	4.6
	MF	15	19.3-24.2	22.2	1.5	0.4	6.9
MSW-7	MM	8	130-141	133.4	5.8	2.1	4.4
	FF	7	130-144	137.1	4.9	1.9	3.6
	MF	15	123-144	135.1	5.6	1.4	1.4
MSW/TL	MM	8	22.0-25.9	23.7	1.6	0.6	6.7
	FF	7	23.2-25.9	24.7	1.0	0.4	4.0
	MF	15	22.0-26.3	24.2	1.4	0.4	5.7
LTS	MM	8	132-169	147.8	10.6	3.8	7.2
	FF	7	131-158	146.8	9.2	3.5	6.3

	MF	15	131-169	147.3	6.7	2.5	6.6
LTS/TL	MM	8	23.2-28.0	26.3	1.4	0.5	5.5
	FF	7	24.7-27.7	26.4	1.3	0.5	4.8
	MF	15	23.2-28.0	26.3	1.3	0.3	5.0

Discussion.

Pycnophyes faveolus is distinguished from all other species by the bands of rugate cuticle encircling the anterior margins of the penultimate posterior segments, the presence of two mid-dorsal setae on some segments and the distribution of patches of punctate cuticle. These last two characters have been omitted from early descriptions of Pycnophyes species which must be separated from elongate P. faveolus on morphometric differences.

Of the 23 presently identifiable species of Pycnophyes only two have been collected from the Pacific region (Higgins 1983). They are P. sanjuanensis Higgins, 1960, from the San Juan Archipelago between Vancouver Island and the United States mainland, and P. chilensis Lang, 1953, from the Gulf of Ancud, Chile.

Pycnophyes faveolus most closely resembles P. sanjuanensis. In both species the lateral margins of segment three project laterally and anteriorly to form hornlike processes, the cuticle along the tergal anterior border of segment three is sculptured into ridges (which are "shingled" or "reticulate" in P. sanjuanensis, and irregular in P. faveolus), the margins of the midsternal plates of segment three show lateral divergence, thin areas of cuticle are present along the anterior margin of segment three sternal plates, and the setal formula is identical. Pycnophyes faveolus differs from P. sanjuanensis in possessing four, not two, ventral placids, in the absence of midtergal

processes, in the distribution of sensory spots, in the configuration of the posterior segment margins and in trunk length. Pycnophyes faveolus is usually less than 700 um long and P. sanjuanensis is more than 800 um long.

The other Pacific species, P. chilensis, like P. faveolus has four ventral placids, and has pores in the ventral plates (mentioned in the description of P. chilensis without information on their location or arrangement). The two species differ in the possession of long midtergal processes and laterotermínal spines by P. chilensis (ratio of laterotermínal spine to trunk length 35%) not seen in P. faveolus (laterotermínal spines 25% of trunk length).

Double mid-dorsal setae have not been described in other species, but P. zelinkaei Southern, 1914 has a row of fine hairs anterior to the serrated posterior margin of the trunk segments.

Bands of faveolate cuticle encircling posterior segments have not been described in other species of Pycnophyes. These are the segments which do not develop deep intersegmental grooves during juvenile development. In many Pycnophyes species these segments have striking midventral thickenings of the pachycycli, the bean-shaped "Mittelwülste" of Zelinka, which are not seen in anterior segments. Segments 3-9 differ from segments 10-12 in juvenile morphology and in adaptation of the cuticle for muscle

attachment. In P. faveolus there is also a difference in the cuticular embossing of these two regions of the trunk.

There is some evidence that cuticular sculpturing in these kinorhynchs is only coming to notice with modern microscope methods. When the Falklands species P. odhneri Lang, 1949, was redrawn in 1953 with better optics, additional cuticular sculpturing was illustrated. The Belize species P. iniorhaptus Higgins, 1983, one of the first kinorhynchs to be described with the aid of scanning electron microscopy, showed the previously unknown character of patches of punctate cuticle located laterally on each sternal plate of segments 4-12. These patches have been recognised in P. faveolus, with a slightly more ventral location. The faveolate cuticle of P. faveolus would be difficult to miss with any microscope, especially where the encrusting mud has fallen off the cuticle, but it is possible that more subtle sculpturing of posterior segments may not have been discernible with early microscopes.

Chapter 10.

Echinoderes teretis sp. n.

Figures 35-41; Plates 76, 77.

Material. Twenty five adults (13 males, 12 females) from Erina Creek, Brisbane Water (Broken Bay), 33o 26' 18"S., 151o 21' 33"E., collected in 1979 on 12 Jul by R.B., and 25 adults (14 males and 11 females) from Hunters Hill - Cunninghams Reach, Lane Cove River, (Port Jackson), 33o 49' 30"S., 151o 08' 45"E., collected in 1979 on 5 Nov by R.Brown.

Diagnosis.- Mid-dorsal spines absent except for small, poorly cuticularised spinous process on segment 6, lateral spines present on segments 8 and 9, lateral adhesive tubes present on segments 7 and 10, lateral terminal accessory spines absent in both sexes, segment 3 with little punctation, segment 12 tergite with distinctive line of single punctations.

Description.- Adults (Figs. 35-41), trunk length 207-264 um, MSW-7 57-78, 26-33 percent of trunk length; SW 38-48 um, 16-24 percent of trunk length. Second segment with 16 placids, about 15 um long, wide posteriorly, narrow anteriorly, posterior margin of midventral placid wider (12-13 um) than posterior margin of other placids (8 um), anterior margins of alternate placids

rounded, overlapped by large trichoscalid plates, anterior margins of intervening placids truncate with deep sub-terminal groove, except for midventral placid with anterior margin indented by two longitudinal grooves.

Trunk segments with cuticular perforation sites (producing hairs not shown in illustrations) imparting a distinctive pattern on each segment, segment 3 with little punctation, segment 12 tergite with distinctive line of single punctations; pectinate fringe on posterior margins of segments 3-13 particularly fine on segments 11 and 12; extensions of terminal tergal plate distinctive, short (ca. 7 um), interrupted along mesial margin and distinctively contoured by cuticular prominence (? sensory spot) in centre, bearing thin spinose process extending beyond tergal extension in male, but shorter than tergal extension in female; terminal sternal plates evenly rounded; cuticle of both dorsal and ventral terminal plates finely striated. Poorly cuticularised mid-dorsal spinose process, 12-15 um long, on segment 6 (which may be reduced or absent in some specimens); lateral adhesive tubes on segments 7 and 10; lateral spinose processes, 10-15 um long on segments 8 and 9; lateral terminal accessory spines absent in both sexes; lateral terminal spines 106-141 um long, 46-65 percent of trunk length. Males with 3 pairs of penile spines, two inserted laterally usually intertwined and shortest spine inserted dorsally.

Pachycycli well developed with thick dorsolateral and lateral spurs and ridges; midventral thickening especially developed on segments 9-11; elongate single muscle scars on dorsal midline of segments 3-5, paired oval muscle scars near dorsal midline of segments 6-12; muscle scars located near centre of ventral plates of segments 4-12 changing from rectangular to elongate in posterior segments. Paired mid-dorsal sensory spots on segments 4, 7-9 and possibly on 13; lateral sensory spots on dorsal aspect of segments 4-7 (series seen to continue posteriorly to segment 11 only on laterally mounted specimens); pair of lateral sensory spots on ventral aspect of segment 5, paired sensory spots on ventral plates of segments 3, 4, and 9, 10. Muscle from midventral thickening to head of lateral terminal spine crossing over muscle from lateral pachycyclus to head of lateral terminal spine. Sieve plate, 18 um long and 5 um wide, with anterior third covered by pectinate fringe of segment 10, seen laterally on segment 11 in laterally mounted specimens only (Plate 76, 77).

Males differ from females in having terminal tergal spinous processes projecting beyond the tergal extension of segment 13, and in the presence of 3 pairs of penile spines (Figs. 38-41).

Morphometric data for adult specimens are given in Tables 10.1 and 10.2.

Holotype.- Adult male, TL 221 um (Figs. 35-39). Museum Accession Data.

Allotype - Adult female, TL 224 um (Figs. 40-41) Museum Accession Data.

Paratypes - Museum Accession Data.

Table 10.1 - Measurements (um) and indices (%) for Echinoderes teretis adults from Erina Creek, Brisbane Water, Broken Bay (see Methods section, p. 25, for character abbreviations).

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	MM	13	211-264	227.8	15.1	4.2	6.6
	FF	12	213-256	228.5	13.5	3.9	5.9
	MF	25	211-264	228.1	14.1	2.8	6.2
SW	MM	13	38-44	41.3	1.8	0.5	4.5
	FF	12	38-49	44.1	3.2	0.9	7.3
	MF	25	38-49	42.6	2.9	0.6	6.7
SW/TL	MM	13	16.7-19.5	18.2	0.9	0.3	2.5
	FF	12	16.5-21.0	19.3	1.6	0.5	8.3
	MF	25	16.5-21.0	18.7	1.4	0.3	7.5
MSW-7	MM	13	57-69	63.2	3.9	1.1	6.1
	FF	12	62-78	67.3	4.1	1.2	6.1
	MF	25	57-78	65.2	4.4	0.9	6.7
MSW/TL	MM	13	26.0-30.8	27.8	1.5	0.4	5.4
	FF	12	26.3-33.0	29.5	2.0	2.0	6.9
	MF	25	26.0-33.0	28.6	2.0	0.4	6.8
LTS	MM	12*	108-130	119.6	6.3	1.8	5.3
	FF	12	114-141	130.6	7.9	2.3	6.1
	MF	24	108-141	124.3	9.6	1.9	7.7
LTS/TL	MM	12	46.5-57.3	52.3	3.4	1.0	6.5
	FF	12	48.1-65.3	57.6	5.2	1.5	9.1
	MF	24	46.5-65.3	54.4	5.7	1.1	10.5

* Tips broken off both spines in one specimen.

Table 10.2.- Measurements (um) and indices (%) for Echinoderes teretis adults from Hunters Hill (Cunninghams Reach, Lane Cove River, Port Jackson). (See Methods section, p. 25, for character abbreviations).

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	MM	14	207-243	226	11.9	3.2	5.3
	FF	11	207-250	226	13.6	4.1	6.0
	MF	25	207-250	226	12.4	2.5	5.4
SW	MM	14	41-49	45.3	3.2	0.8	7.1
	FF	11	44-49	46.7	1.4	0.3	3.2
	MF	25	41-49	45.9	2.6	0.5	5.7
SW/TL	MM	14	17.3-23.7	20.1	1.9	0.5	9.7
	FF	11	19.0-23.2	20.8	1.4	0.4	6.7
	MF	25	17.3-23.7	20.4	1.7	0.3	8.5
MSW-7	MM	14	57-71	65.6	3.9	0.1	6.0
	FF	11	61-72	66.7	2.7	8.2	4.0
	MF	25	57-72	66.1	3.4	0.7	5.2
MSW/TL	MM	14	26.2-32.4	29.1	1.7	0.5	5.9
	FF	11	26.4-32.6	29.6	1.9	0.6	6.3
	MF	25	26.2-32.6	29.3	1.8	0.4	6.1
LTS	MM	13*	106-131	118.9	7.7	2.1	6.4
	FF	10*	115-132	123.5	5.3	1.7	4.2
	MF	23	106-132	120.9	7.0	1.5	5.8
LTS/TL	MM	13*	47.7-58.9	52.5	3.5	9.6	6.6
	FF	10*	48.0-60.4	55.3	4.0	1.3	7.2
	MF	23	47.7-60.4	53.7	3.9	0.8	7.2

*Tips broken off both spines in one specimen.

Discussion

The taxonomic characters used to identify Echinoderes species are morphometric data and the position and length of spines (and histologically similar adhesive tubes). Since the development of optical contrast microscopes in the 1950's, cuticular markings such as muscle scars, sensory spots and hair perforation patterns have also been incorporated into the description, principally by R. P. Higgins. In E. teretis spination characteristics are not informative, for there are no true mid-dorsal, lateral or laterotерminal accessory spines. This spination deficiency is shared by only five other species of the 33 Echinoderes species currently considered identifiable (Higgins 1983). Each of these five species is easily distinguished from E. teretis, and it seems likely that its affinities lie with more extensively spined species, especially if the small flexible mid-dorsal spinose process on segment 6 is the last vestige of a recently-lost array of spines. This discussion will firstly describe the features which distinguish E. teretis from the five other species which also lack minor spines, and secondly will explore this species' similarity to corpulent spined species.

In E. capitatus Zelinka, 1928 from the Mediterranean, there are distinctive broad anterior segments which are as wide as the widest body segments, broad mid-ventral ridges and segment 12 sensory setae (spines) in the female but not in the male. None

of these characteristics are seen in E. teretis.

In the South African species E. maxwelli (Omer-Cooper, 1957), the described length of 600 um has been remeasured by Higgins (1977b) as 328 um. This is close to the range of 207-264 um measured in E. teretis. Higgins also notes "Some hairs or cuticular processes extend from the ventral surface of the 13th segment in the vicinity of the lateral processes of the tergal and sternal plates." Such cuticular processes are seen on the dorsal tergal plates in E. teretis. Higgins says "The 'lateral sensory setae' reported on segment 8 and 10 of E. maxwelli are on segments 7 and 10; these are short (L-7, 11 um; L-10, 20 um) thin spines which are probably adhesive tubes." Higgins observed that segment 11 was elongated producing the "cuticular anal sheath" exaggerated in the illustration of E. maxwelli. These characteristics appear to distinguish E. maxwelli from E. teretis , which has lateral adhesive tubes on segments 7 and 10, as well as 10-12 um spines on segments 8 and 9, and no cuticular sheath from segment 11. The holotype of E. maxwelli was examined by me in the British museum. I interpreted the "cuticular anal sheath" as being formed by telescoped posterior segments as seen in E. teretis. I also observed hairs or cuticular processes on the dorsal plate of segment 13 overlying the lateroterminal spine, as in E. teretis.

In E. bengalensis Timm, 1958 the stated measurement of 400-438 um is illustrated as 292 um, the lateral spines on segments 7 and

10, stated as 15 um long, are illustrated as 25-47 um long. It is possible that these characters fall within the range for E. teretis. (The stated trunk length makes this species the longest Echinoderes species measured, save for E. canariensis Greeff, 1869 claimed to be 0.3-0.45 mm long). However there are no spines described on segments 8 and 9, and the lateral terminal spines are described and illustrated as being 25-47 um long, which compares with a range of 106-141 um in E. teretis.

Echinoderes caribiensis Kirsteuer, 1964 has lateral terminal accessory spines in the male only, leading Higgins (1977b), and Higgins and Rao (1979) to speculate that these may have been misidentified penile spines. Echinoderes caribiensis has a length of 370 um and lateral spines on segment 11, both of which distinguish it from E. teretis.

In the aberrant intertidal species E. coulli Higgins, 1977b there are two female morphotypes, multiple penile spines, dense cuticular punctation and processes extending from the posterior ventral plates, none of which are seen in E. teretis.

In E. andamanensis Higgins and Rao, 1979 there are no mid-dorsal spines but lateroterminal accessory spines are present in the female and absent in the male. The presence of lateral spines on segment 11 and adhesive tubes on the female fourth segment distinguish this species from E. teretis, as does the 22.6-24.1%

ratio of the maximum sternal width to the trunk length.

In E. teretis this ratio is 29%, which is greater than that of any of the other 17 species for which this index has been established. Some of the unusual characteristics of E. teretis are shared by a plump Red Sea species E. brevicaudatus (= brevispinosus) Higgins, 1966a which has a 26% ratio. Other species usually have an MSW/TL ratio around 20%. Echinoderes brevicaudatus has short mid-dorsal spines on segments 6-10, short lateral spines on segments 7-11, adhesive tubes on segment 4, and different placid arrangement from E. teretis. However other characteristics show surprising similarities. The pachycycli bear ridges and spurs not recorded in the slimmer species, and the arrangement of dorsal muscle scars and sensory spots is similar, especially in anterior segments. The posterior tergal extensions have similar profiles with raised central cuticle. This has not been described in other species. The punctation pattern of these two species is similar, and in both species each segment has a posterior pectinate fringe. The posterior ventral plate of E. brevicaudatus has a spinose projection similar to that of E. teretis.

Echinoderes abbreviatus Higgins, 1983 from Belize has an average trunk length of 227.6 um (cf.227.1 um in E. teretis), and an average maximum sternal width of 57.2 um (cf. 65.6 um in E. teretis) giving a MSW/TL ratio of 25.3% (cf. 29% in E. teretis).

This species has lateral spination comparable to E. brevicaudatus, but has mid-dorsal spines on segments 6, 8 and 10 only. (This dorsal spination formula is shared by the Red Sea species E. riedli Higgins, 1966a, the Arctic species E. arlis Higgins, 1966b and E. newcaledoniensis Higgins, 1967, but these three species have elongated trunks and significantly longer lateral terminal spines). The only significant similarity between the Sydney species and the Belize species is the skin punctation pattern - there are differences in placids, cuticular scars, shape of pachycycli and posterior segments.

Speculation as to whether similarity between E. teretis and E. brevicaudatus suggests affinity between these species will have to await further work. There are no published descriptions of Echinoderes species from Indonesia or Australia. However it is possible that the large ratio of maximum sternal width to trunk length in E. teretis is a character that is influenced by seasonal factors, the water temperature and the availability of food. On morphological characters alone, the closest species to E. teretis appears to be the South African species E. maxwelli.

During the present study, three other Echinoderes species were collected from other central N.S.W. estuaries - Port Hacking, Botany Bay and Pitt Water (Broken Bay). "Echinoderes is probably the common kinorhynch found in estuarine sediments" (Higgins 1983). Echinoderes teretis has been collected in the headwaters

of both Sydney Harbour (Port Jackson) and Brisbane Water (Broken Bay), both collections being made at the entrances of narrow rivers entering these drowned estuaries. Other Echinoderes habitats were located in tidal waters at the estuarine mouths (Fig. 1).

DISCUSSION

"Creatures the most strange and the most incongruous - odd in their shapes, odd in their manners, odd in their movements, swim, or rotate, or creep or wriggle over the field of vision, till the little pellet of brown mud...proves a complete microcosm. Many such pellets will not have passed under the eye of the curious observer before he will pretty certainly have become familiar with a little creature of attractive appearance and lively manners...Its movements are not so rapid as those of many animalcules, and therefore it affords a fair object for the young microscopist, while its form is so peculiar as to be easily recognised."

Philip Henry Gosse (1864) in the first kinorhynch paper written in English,

The Natural History of the Hairy-backed Animalcules (Chaetonotidae). The Intellectual Observer: Review of Natural History, Microscopic Research, and Recreative Science. 5(6): 387-406.

"wir mussen eben zwischen Form und Ansicht, zwischen Sein und Schein unterscheiden."

Carl Zelinka (1908) Zur Anatomie der Echinoderen. Zoologischer Anzeiger, 33 (19-20) 629-647.

DISCUSSION

1. Taxonomic characteristics of the head

Kinorhynch taxonomy is not easy. Higgins (1971) wrote that of the 21 taxonomists who had described kinorhynchs, 17 had written 1 paper each, and 2 had written 2 papers each. The remaining taxonomy had been carried out by Zelinka and Higgins. Twelve years later the figures had scarcely changed. As indicated in Higgins (1983) 6 additional taxonomists had written 1 paper each, and in 1983 2 papers were produced by the present author. This "preponderance of single-attempt publications" (Higgins 1971) does not appear to be the result of difficulty in finding kinorhynchs. Hyman (1951) explained the paucity of kinorhynch literature in the following celebrated words "They simply have not been sought for in an intensive manner. The author...obtained two or three kinds of kinorhynchs at the first attempt in Puget Sound." Following Hyman's example meiobenthologists have looked for and found kinorhynchs on most of the world's coasts, but very few of these kinorhynchs have been described (Higgins 1983).

Higgins (1971) noted "extensive experience is necessary before any taxonomist can be effective in his area of

specialisation." In fact descriptions written in half of the "single-attempt publications" published after 1971 have since been modified. Yet, as Higgins (1971) noted "Unless more researchers can be recruited to the ranks of those willing to accept such challenges, Kinorhyncha literature may continue to be as cryptic as the environment in which these animals dwell."

As mentioned in the Introduction to this thesis, kinorhynch taxonomy has been based on such trunk cuticle characteristics as cuticular contouring, muscle scars, sensory spots, areas of thin cuticle, and shape of the pachycycli. With light microscopy it can be most difficult to distinguish between muscle scars and sensory spots or between external and internal cuticular thickenings. In the days before the advent of the scanning electron microscope the art of interpreting these features must have been inordinately difficult to master, and this probably accounts for the inadequacy of many taxonomic descriptions.

The genitalia have provided useful characters in other taxa with cuticular exoskeletons. Brown (1983) recorded the first description of the morphology of kinorhynch genitalia, noting that kinorhynch genitalia are difficult to observe, and in fact, have not been seen at all in some classes.

By contrast the kinorhynch head is not difficult to observe if it is extruded. Extrusion can be promoted by the known technique of subjecting living animals to osmotic shock. A garotting technique (described in Materials and Methods p.11) is useful for extracting the heads of large preserved kinorhynchs. Retracted heads of kinorhynchs can also be revealed by the technique of tearing specimens into two longitudinal slices with double-sided sticky tape prior to SEM examination (described in Materials and Methods p.19). Specimens are fragmented by this technique, but the resulting fragments may offer useful morphological information (see Brown 1983, Plate 8b).

It is likely that more progress might have been made in eliciting taxonomic characters from homalorhagid heads if the early literature had not been somewhat misleading as to the arrangement of homalorhagid external scalids. Here the scanning electron microscope has provided useful information on the four different types of external scalids, for only two types, spinoscalids and trichoscalids, were recognised prior to the present study. However, allocation of the different scalids to different rings could only be done with certainty after scalid ontogeny had been established. For this, Kinorhynchus phyllotropis, a large and abundant homalorhagid, was a most appropriate species to provide a thorough basic description of both external and internal

scalids. The next step will be a scalid description of another large homalorhagid to ascertain patterns of variation. As these are yet unknown it has been necessary to write a full description of the K. phyllotropis head to provide a basis for comparison. The literature gives at least two clues as to potential variations of scalid characteristics in this genus. In K. ilyocryptus the external scalids are mounted on flexible papillae (Boykin 1965), in K. phyllotropis only the trichoscalids have this type of origin. All other scalids are inserted directly onto the head and often contain large nuclei at the points of origin. In K. giganteus the profiles of type I scalid tips differ from those of K. phyllotropis. In K. giganteus the three projections from the base of the triangular section are rounded, and of about equal length. In K. phyllotropis they are pointed and the central projection is shorter (cf. Moritz and Storch 1972b, Plate 6a with Plate 15 of this thesis). It might be predicted that other distinctive taxonomic characters will include the arrangement of lines of hairs between scalids and between scalid rings (Figs. 1.1, 1.3), the presence or absence of appendages such as the flap of fused hairs on the Ring 1 scalid socket of K. phyllotropis (Plate 7) which has not been mentioned in other kinorhynchs, the shape of the trichoscalid scale, which has recurved margins in K. phyllotropis (Figs. 1.1, 1.3; Plate 10) and the

disposition of any hairs on the smooth scalids of Rings 2-4, which form chevrons in K. phyllotropis (Plate 8). It is also possible that the internal scalids might vary in morphology among different taxa, and to ascertain this it will be necessary to examine specimens with prolapsed heads - specimens which might otherwise be discarded.

The most productive source of taxonomic data is likely to be the development patterns of juvenile scalids. These differ in the two homalorhagid genera Kinorhynchus and Pycnophyes. Differences have been observed in juveniles of P. faveolus and in juveniles of an undescribed Pycnophyes species collected by R. P. Higgins. In Pycnophyes particular juvenile stages can be easily identified by spination characteristics, and it is not difficult to detect differences between stages of scalid development in corresponding Pycnophyes and Kinorhynchus juveniles. Tables such as Fig. 9 of this thesis can be constructed to incorporate data on juvenile scalid patterns, even incomplete data. It is anticipated that such data will become standard in kinorhynch taxonomic descriptions.

2. Kinorhynch feeding and scalid function

The hypothesis is offered that the different types of scalids of K. phyllotropis serve to sense detailed

information on the productivity of trunk plate flora (Plates 40, 52). It is suggested that this flora, diatoms and bacteria, is housed between the cuticle and sediment aggregated by threads of mucus secreted from the ends of hollow setae. An additional hypothesis is offered that kinorhynchs benefit from staying in one place by creating a microclimate inside a mucus cover and feeding on the products of ectocommensal bacteria, diatoms and ciliates.

Kinorhynch scalids all appear to have a sensory function for all contained sensory cilia, and some contain photoreceptor submicrovillar cisternae (Plate 5). No scalids are glandular or raptorial. Such a rich array of anterior sensory processes suggests that kinorhynchs require detailed knowledge of their immediate environment. The most consistent aspect of that environment is the bacteria-covered porous trunk cuticle (Fig. 21; Plates 40, 49-50, 51). Kinorhynchs secrete mucus into their environment through the hollow setae found on every trunk segment (Fig. 22; Plate 60). This mucus does not assist translocation - kinorhynchs do not possess external tracts of cilia. Mucous threads may serve to carry adsorbed bacteria in the food current to the mouth, or to cover the cuticle thereby providing an optimal microclimate for bacterial productivity. In such a microclimate, energy would enter the system by insolation, as is indicated by the

rich diatom flora carried by most kinorhynchs (Higgins 1961; Plate 52). Ciliates also grow on kinorhynchs (Zelinka 1914). If kinorhynchs invest energy in improving their immediate environment with a blanket of mucus, and in sampling it with scalids, it would be expected that they would also have adaptations for staying in that environment. They do have these adapations. Kinorhynchs are not known to construct tubes to control their environment, but they do have appendages which minimise their movement through the surrounding sediment. The only long appendages possessed by kinorhynchs are single or double terminal spines which would function to impede translocation. Higgins (1967) has observed that kinorhynch terminal spines are longer in coarser sediments - their length appears to be related to stabilising the kinorhynch in relation to the sediment grains around it.

Kinorhynchs would be handicapped by the impediment of long terminal spines if they were browsing feeders constantly moving to better pastures. It can be said that this argument is belied by the fact that some kinorhynchs are known to have limited movement between paired terminal processes. However these kinorhynchs pass through several stages of juvenile development in which they have one long single terminal spine and in other genera adults have an single spine notable for its length, which may exceed that

of the rest of the animal. Such a spine would anchor the kinorhynch as a tap root anchors a tree.

The external scalids contain extensions of the circum-oral nerve ring, and they are closely associated with head retractor muscles (Fig. 3). The internal scalids are closely associated with the pharyngeal sucking muscles. Thus the scalids are in a position to mediate the production of a food-bearing current up the streamlined trunk plates by stimulating the action of a pumping introvert. During head retraction the introvert would draw a food-current up along the trunk plates, and this current would be scavenged by pharyngeal suction as the head emerged again. The internal scalids are situated where they would sample the current entering the oral cone, and where they could reduce pharyngeal suction if the food current did not provide appropriate stimuli.

The structures revealed as scalids by this study, oral styles and internal scalids, have features which support the above hypotheses. Some scalids are adnate to the oral cone. These scalids are the oral scalids of early juvenile stages and the scleroscalids of all stages (Figs. 2.1, 13-18). They are also the scalids which would be most affected by a current of water being sucked into the pharynx, and their tethers may serve to prevent them from being sucked in too.

Scleroscalids differ from other scalids in their thickly sclerotised walls which presumably protect them from abrasion by the feeding current. Helioscalids do not have thick walls, they have longitudinal strips like the Ring 1 spinoscalids. Unlike the scleroscalids, the helioscalids appear to be protected by the pharynx crown when the head is withdrawn because they lie at the lowest level of the introvert.

3. Phylogenetic implications of kinorhynch head structure

i. Radial symmetry

The present study has shown that the kinorhynch head processes are arranged in a radial plan with 5 scalids in the unit of repeat. It is seen (Fig. 20) that 9 of the 11 scalid rings are arranged in fives or multiples of 5. In the oral scalid ring the mid-dorsal scalid is absent, so there are only 9 scalids of which 5 lack spines (Fig. 18a). There are 14 trichoscalids, 8 of these being derived from juvenile protrichoscalids (Figs. 2.5, 2.10, 2.15). Loricifera likewise have scalid rings in multiples of 5 in the 20 clavoscalids of the anterior ring. These are derived from 8 juvenile clavoscalids (Kristensen 1983).

Radial head symmetry may be a secondary condition; the general body plan of kinorhynchs is bilateral. Jägersten

(1972) stated that a burrowing mode of life tends to encourage the development of radial symmetry as the result of uniform contact with the surrounding medium. A converse opinion was expressed by Lang (1963) and echoed by Morris (1977) that the bilateral kinorhynch character of dorsoventral musculature is derived or 'converted' from circular musculature. Lang's argument was partly based on Nyholm's (1947b) report that in kinorhynchs the division of the trunk plates into segments takes place successively during ontogeny. The present study suggests that the trunk plates are divided into segments from the first juvenile stage (Fig. 24, Plate 62) and that bilateral features such as sensory spots are present from the first juvenile stage onwards (Plate 68). Radial symmetry has not been seen in trunk structures at any stage of development, but has been seen in the head, with the exception of the development of the posterior scalid ring. Protrichoscalid arrangement is bilaterally symmetrical.

Kinorhynch scalid disposition is quincunxial (Merriman 1972). A quincunx is an arrangement of five objects in a square or rectangle with one at each corner and one in the middle. In kinorhynchs this is seen when a pair of scalids in one circle is followed by a single intermediate scalid in the following circle, which is followed by a pair of scalids underlying the first pair (Figs. 7, 20). This arrangement

is seen in some priapulids, and in all priapulids the basic number of scalids in a circle is 25 (Calloway 1975). Calloway explained that a quincunxial disposition prevented scalids from meshing with nearby scalids during head invagination. A most economic arrangement for achieving a quincunx is the kinorhynch arrangement of radial symmetry with a repeat unit of 5 scalids. Economy is required around the equator of the spheroid kinorhynch head because this is the region with most cuticle to compress when the head is withdrawn. It is also the region where scalids of circles 4-6 are located (Fig. 8), and these are the quincunxial rows. A pair of scalids alternates with a single scalid in each circle, and this arrangement is staggered in successive circles (Figs. 7, 20).

In summation it can be said that small invertebrates probing sediment with a proboscis are likely to fare better with a quincunxial disposition of proboscis processes, and that radial symmetry in groups of fives is an economical means of achieving this disposition. Such an arrangement is seen in priapulids and kinorhynchs. However Jägersten's argument, cited above, suggests that the presence of such an arrangement in interstitial fauna is as likely to result from convergent evolution as from possession of common ancestry. In K. phyllotropis the anterior probing scalids have a radially symmetrical arrangement, while posterior

scalids have a bilaterally symmetrical arrangement in early juvenile stages. If it is accepted that ontogeny repeats phylogeny, it seems likely that radial symmetry is a secondary development promoted by kinorhynch association with a uniform surrounding sediment.

ii. Proscalids

The present study has shown that type I scalids are preceded by beak-like or tooth-like proscalids, with a morphology previously undescribed in kinorhynchs (Figs. 8, 21-15). Such a scalid is illustrated in the loriciferan Higgins larva (Kristensen 1983, Fig. 12) and described as the dorsal teeth of the sixth scalid row. The scalids of the priapulomorph priapulid Tubiluchus corallicola van der Land, 1968 are conical and slightly curved with one or two small cuticular tubes at the tip (Kirsteuer and van der Land 1970). The scalids of another priapulomorph Halicryptus spinulosus (von Siebold, 1849) are described as being "triangularly flattened" (Merriman 1981) and these scalids have some resemblance to kinorhynch proscalids. There is great diversity in the scalid morphology of priapulids, loriciferans and kinorhynchs, and any degree of similarity is noteworthy.

iii. Type I scalids

The present study has shown that K. phyllotropis has fringed type I scalids, a type that has not been described before. In this species all type I scalids lack spines. Hirsute "spinoscalids" have been illustrated and described in female Loricifera (Kristensen 1983, Figs. 2, 9), and they, too, appear to lack spines. As in kinorhynchs, loriciferan scalids contain modified ciliary structures.

Loriciferan scalids differ from the fringed kinorhynch scalids in that they appear to have three divisions while the kinorhynch scalids have only two. Loriciferan scalids are fringed on the socket or base; kinorhynch scalids are fringed on the endpiece. In K. phyllotropis the fringed scalid, complete with type I cuticle, is the first scalid with striated cuticle to appear in a completely filled scalid ring (Figs. 9 and 10). This scalid is seen in the J-1. Smooth scalids with type II cuticle are not seen until the J-3. Spinoscalids with striated type II cuticle appear as late as the J-5, as do trichoscalids borne on scales with endocuticular punctation. It could thus be argued that a fringed spineless scalid with type I cuticle is a conservative kinorhynch scalid, so it will be significant if the similar loriciferan scalids also show cuticular striation.

In K. phyllotropis spines are only found on some oral scalids and in all Ring 1 type II scalids. The term "spinoscalid" can be misleading when no spine is present. It is likely that further SEM studies will differentiate between spined and spinelss scalids in other genera, and the term will be used more sparingly.

iv. Future investigation

It is not known which kinorhynch genera are most conservative. It is known that some kinorhynch genera show neotenic features of cuticle and genitalia (Higgins 1968, 1969, 1983). This is true neoteny, not merely secondary simplification, for the juveniles of one such genus, Paracentrophyes, are the only kinorhynchs known in which juveniles have penile spines (Higgins 1983). It can be anticipated that the scalid development of this group will provide new information on conservative patterns of scalid arrangement and structure.

The three species of neotenic Cateriidae (Higgins 1968) are kinorhynchs which mostly live in intertidal beach sands. They have been found in America (Brown and Higgins 1983, Gerlach 1956), Africa (Delamare Deboutteville 1957), India (Higgins and Rao 1979; Rao and Ganapati 1966) and Europe (Gerlach 1969). They have not yet been found in Australia.

The Cateriidae are diagnosed (Higgins 1968) as possessing a posterior row of "undifferentiated scalids, homologous to trichoscalids of other taxa but without cuticular ringing or hairs, each centered on the posteriomedial border of a plate of minute denticles." This description could easily be applied to the protrichoscalids seen in the posterior row of the first three juvenile stages of K. phyllotropis (cf. Gerlach 1969, Fig. 7 with Plate 24). This scalid is also devoid of hairs except for the socket fringe which certainly projects like a plate of minute denticles. Cuticular ringing is absent. Therefore it is possible that the same scalid type exists in the neotenic Cateriidae and in early juvenile Kinorhynchus. If so, it is likely that this scalid type is conservative, and its presence in juveniles of scalid bearing outgroups such as seticoronarian priapulids and loriciferans would suggest apomorphy.

Such a scalid has been photographed and illustrated in the Higgins larva of the loriciferan Nanaloricus mysticus Kristensen, 1983 (ibid. Figs. 12 and 16). Spineless scalids with large triangular sockets fringed with "denticles" have small endpieces and have been termed "hook scalids". These scalids have two divisions, not three. There is remarkable resemblance between two unlabelled hook scalids shown in Kristensen's Fig. 16 and the protrichoscalids illustrated in

Figs. 1.1-14 and 2.1-4. The curved shape of the kinorhynch protrichoscalid endpiece appears to resemble the hooked endpiece of the loriciferan scalid. The terminal divisions of other scalids in both animals are straight-sided.

The contribution of the present study to knowledge of scalid morphology can be summarised as follows. Previously, kinorhynch scalids were recognised as being spinoscalids or trichoscalids. Homalorhagid kinorhynchs were known to have type I, type II or trichoscalid cuticle. Adult homalorhagids are now known to have three types of internal scalids (helioscalids, large scleroscalids 1 and small scleroscalids 2), oral scalids (with and without spines), and external scalids classified as type II spinoscalids, type I smooth scalids, type I fringed scalids and trichoscalids - making 8 (or 9) adult scalid types. Two additional scalid types have been observed in juveniles, tooth-like proscalids and protrichoscalids which have a large socket (or plate) with a terminal border of hairs (or denticles) and a smooth unringed endpiece.

The first juvenile stage of K. phyllotropis has only 3 of these scalid types present in a fully developed form - the type I fringed scalid, the tooth-like proscalid and the protrichoscalid. Two of these scalid forms have been described or illustrated in juvenile Loricifera, the tooth

scalid and the protrichoscalid or hook scalid. Neither of these scalid types has been reported among the widely diverse scalid types of "aschelminth" outgroups, and their presence in these two phyla increases the likelihood of a common ancestry.

Sharing these two scalid types may not seem to be much to go on, but then the chances of finding any apomorphic characters at all are extremely low. "Many of the links between the various invertebrate taxa are (and may always remain) a puzzle to us, being hidden behind two thousand million years of evolution" (Platt 1981). Given this, it is startling to find any closely homologous structures on the heads of these two miniscule invertebrates, one retrieved from the shelly gravels of Britanny and the other from the sandy muds of Sydney Harbour. The possibility of finding other homologies in the cateriid kinorhynchs merits the search.

SUMMARY

Observations of adults and juveniles of the homalorhagid kinorhynch Kinorhynchus phyllotropis Brown and Higgins, 1983 show that the numbers of scalids conform with counts made on other species, but the disposition of scalids into rings differs from that previously described. Two types of spineless type I scalids have been shown to occupy specific rings. These spineless scalids, smooth scalids and fringed scalids, have not been distinguished in other species.

In this species the ring one scalid is the only scalid with a spine. This spine, which projects from the socket, is seen in adults and in all six juvenile stages. In the first four juvenile stages, during which new scalids appear, the ring one spinoscalid lacks cuticular striation but possesses other type II characteristics. In the last two juvenile stages, which have a complete complement of scalids, ring one spinoscalids have type II cuticular striation.

All spineless scalids, except the trichoscalids, have type I cuticular striation during each stage of development.

Only the spinoscalid ring, or first ring, and the last ring of fringed scalids have the full scalid complement throughout

development. New scalids appear after the moult completing each of the first four stages. During the first three stages a proscalid or a protrichoscalid occupies the site where a scalid will appear in the following stage. The previously undescribed proscalid is a shield-shaped beak of cuticle. The previously undescribed protrichoscalid has a plate-like socket bearing stout fringing hairs and a small curved endpiece. In the fourth juvenile stage the protrichoscalid contains trichoscalid anlagen.

As a result of scalid ontogeny trichoscalids do not conform to the symmetric decaradial arrangement of all other scalids. In the first juvenile stage there are two trichoscalids on each of the three sides of the body. The other eight trichoscalids appear in the fifth juvenile stage when other adult features also appear such as trichoscalid scales with endocuticular punctation.

The nine oral styles around the oral aperture contain modified cilia. These scalids are here termed oral scalids. There is no oral scalid in the mid-dorsal sector. Alternate oral scalids bear spines.

Within the oral cone there are three additional rings of scalids, here called scleroscalids 1, scleroscalids 2 and helioscalids, and they number ten, five and five respectively.

The arrangement of all scalids can be schematised to facilitate comparison studies of different species.

In this species the cuticle of trunk plates is perforated by densely scattered pores, and by canals passing from cells containing cilia, and by canals from cells containing membrane systems similar to those seen in trichoscalids. Material is secreted through this perforated cuticle. The outer cuticle carries ectocommensal diatoms, algae and bacteria. Bacteria are seen in the gut contents.

The setae of this species are specialised cuticular apertures. They are hollow tubes, located above mucous cells containing cilia.

There is another specialised cuticular aperture on segment 11, where cuticular excretory tubules occupy the site of the sieve plates described in other species.

Two undescribed Sydney Harbour species, the homalorhagid Pycnophyes faveolatus and the cyclorhagid Echinoderes teretis, have characteristic cuticular features.

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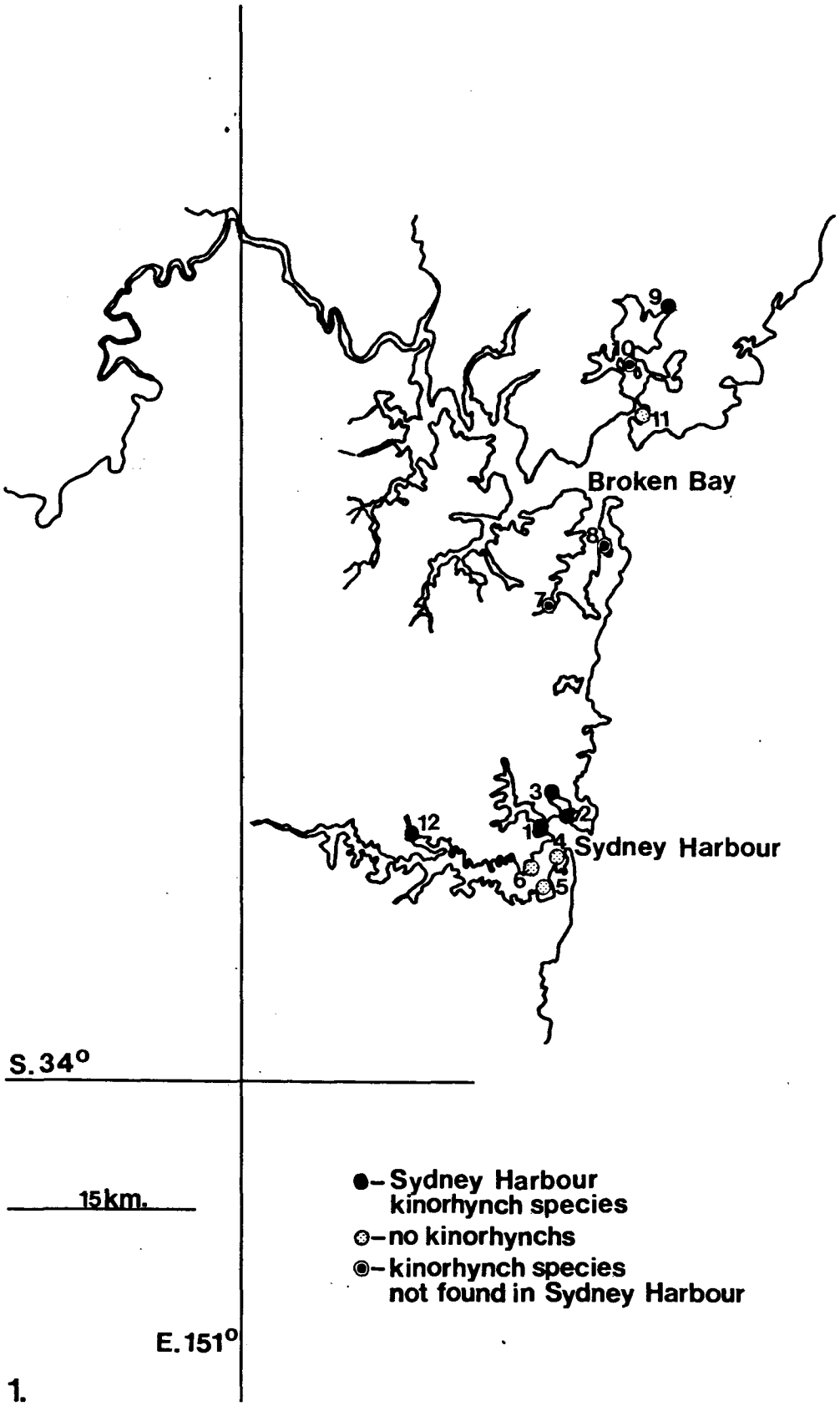
Figure 1. Map of Sydney Harbour and Broken Bay field stations.


Broken Bay
Sydney Harbour
S.34°
15km.
E.151°
●– Sydney Harbour kinorhynch species
⊗– no kinorhynchs
◉– kinorhynch species not found in Sydney Harbour

1.

Figure 2. The arrangement of scalids around the heads of homalorhagid kinorhynchs - diagrams illustrating the observations of previous workers. These diagrams are reproduced from original publications so that the observations of previous studies can be visually compared with observations of the present study.

A. The concentric circle diagram of Zelinka (1928, Fig. 3).

B. Zelinka's 'Mercator's projection' diagram (1928, Fig. 4)

C. Lang's (1949, Fig. 2) reproduction of Remane's (1936, Fig. 217, 1) modified version of the Zelinka diagram illustrated in A.

NOTE. Zelinka, Remane and Lang concluded that the numbers of scalids in successive rings is usually 10, 10, 20, 10, 10, 15, 14.

The present study concludes that the numbers of scalids in successive rings is 10, 10, 10, 15, 15, 15, 14.

In his Mercator's projection, Zelinka himself showed the same scalid disposition in the middle rings as revealed by the present study. The numbers of scalids along the horizontal lines are 15, not 10. In his concentric circle diagram Zelinka drew the middle ring scalids 15 to a circle, but he actually numbered them 10 to a circle. Remane produced an altered version of the diagram which agreed with the scalid numbering, but not, perhaps, with the observation.

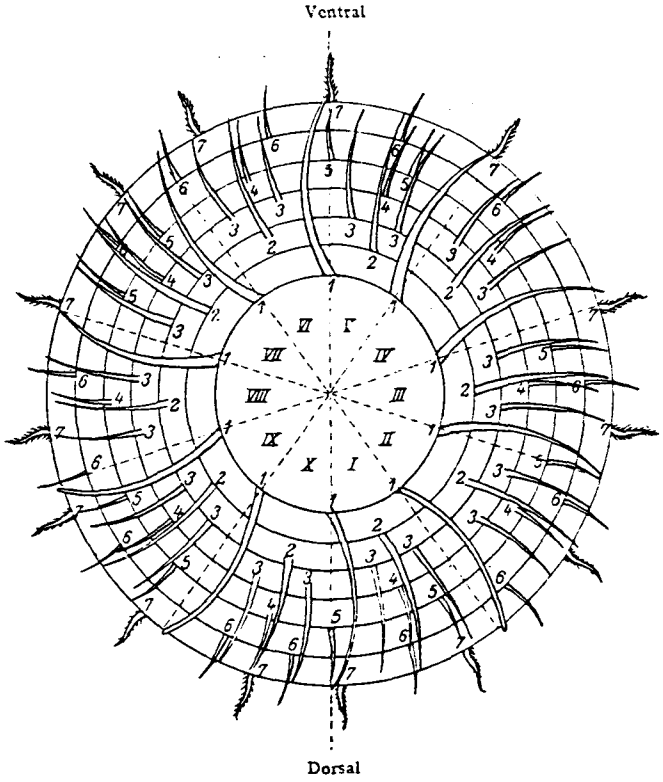


Fig. 3. Schema der Skalidenverteilung in der Ansicht von oben auf die Längsachse des Tieres. *Pycnophyes communis* n. sp. I—X die zehn Sektoren; 1—7 die sieben Skalidenkreise.

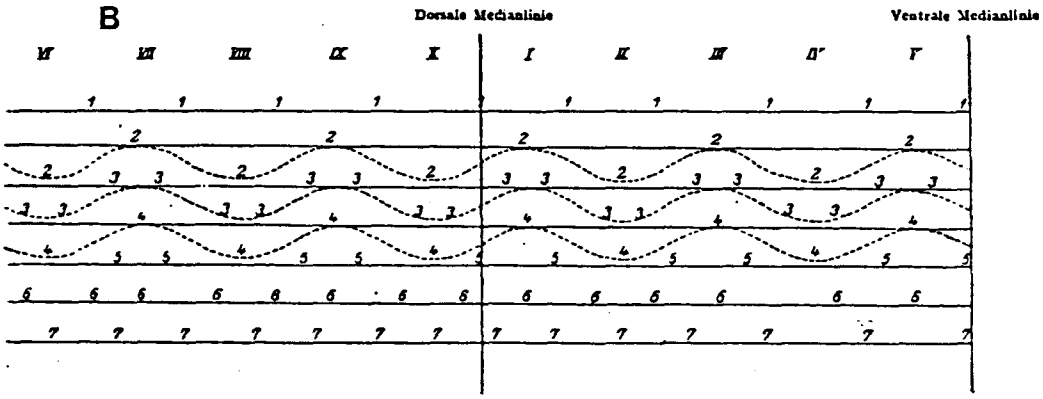


Fig. 4. Schema der Skalidenverteilung in Mercators Projektion bei *Pycnophyes communis* n. sp. I—X die zehn Sektoren, zu beiden Seiten der dorsalen Medianlinie angeordnet. 1—7 die sieben Skalidenkreise.

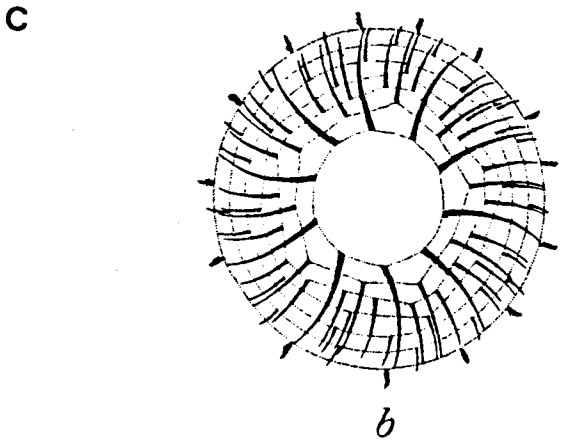


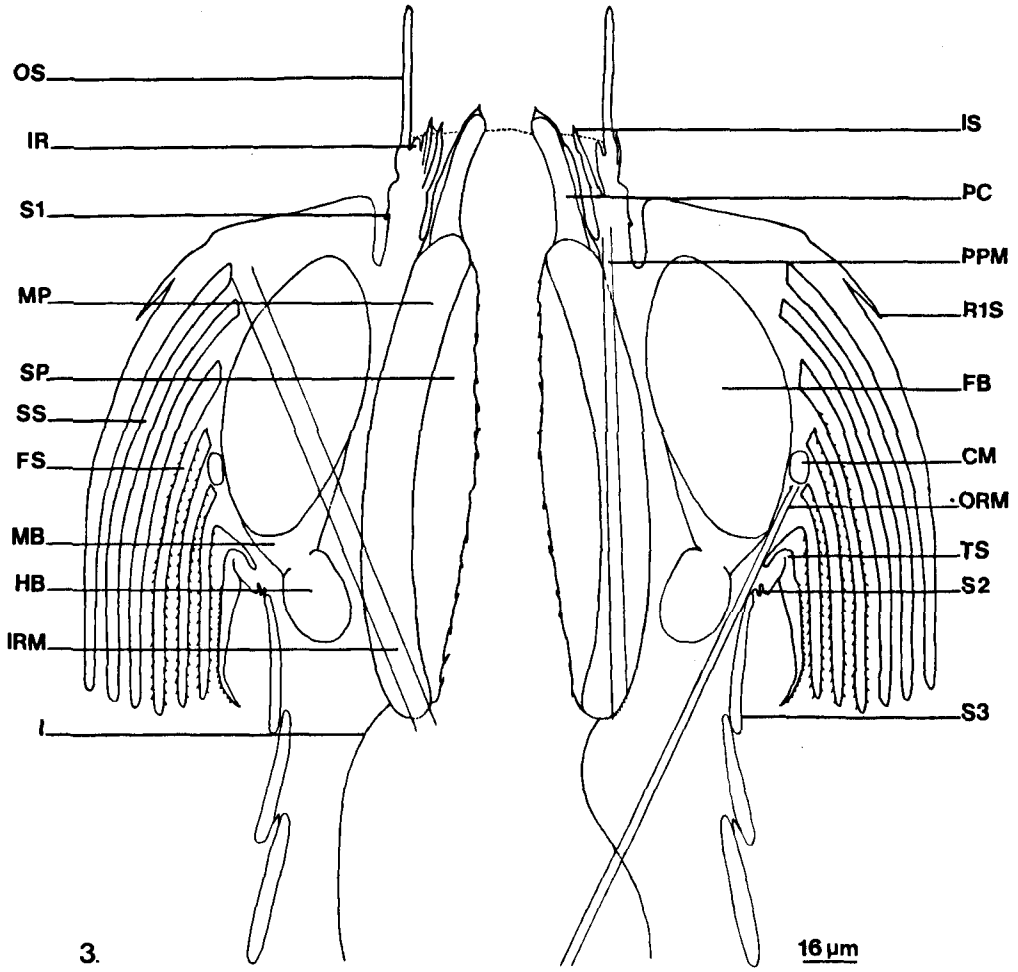
Fig. 2. The arrangement of the scalids in a) *Echinoderes dujardinii* (from ZELINKA), b) *Pycnophyes communis* and c) *Campyloderes vanhöffeni* (from REMANE).

2.

Figure 3. Schematic diagram of the everted head of an adult *Kinorhynchus phyllotropis*.

Key.
Symbols on left side of diagram
FS - fringed external scalid
HB - posterior section of the circum-pharyngeal nerve ring, or hind-brain which is composed of lobes of nuclei
I - intestine
IR - inner fimbriated rim of the oral cone
IRM - inner retractor muscle of the head which inserts onto the cuticle below the ring one spinoscalid
MB - mid-section of the circum-pharyngeal nerve ring, or mid-brain, which is composed of nerve cell processes
MP - muscular lobe of trilobed pharyngeal bulb, with radially arranged contractile elements
OS - oral style
S1 - circle of fringed cuticle probably indicating the posterior boundary of the first segment of the kinorhynch head
SP - secretory tissue inside the pharyngeal bulb which is lined with rough cuticle
SS - smooth external scalid

Symbols on right side of diagram
CM - circular muscle of the head
FB - anterior section of the circum-pharyngeal nerve ring, or fore-brain, which is composed of ten nucleated lobes which intrude into the sockets of the first six rings of external scalids
IS - internal scalid, scleroscalids are drawn on the left side of the diagram and a helioscalid on the right side
ORM - outer retractor muscle of the head which inserts onto the cuticle between the external scalids of rings five and six
PC - pharyngeal crown
PPM - protractor muscle of the pharynx which inserts onto the cuticle below the oral style bases
R1S - ring one spinoscalid showing the spine on the socket
S2 - the trichoscalid ring marking the posterior boundary of segment 2 of the kinorhynch head.
S3 - posterior margin of the first plate of the trunk marking the posterior boundary of segment 3.
TS - trichoscalid inserted onto scale with punctate endocuticular elaboration.



3.

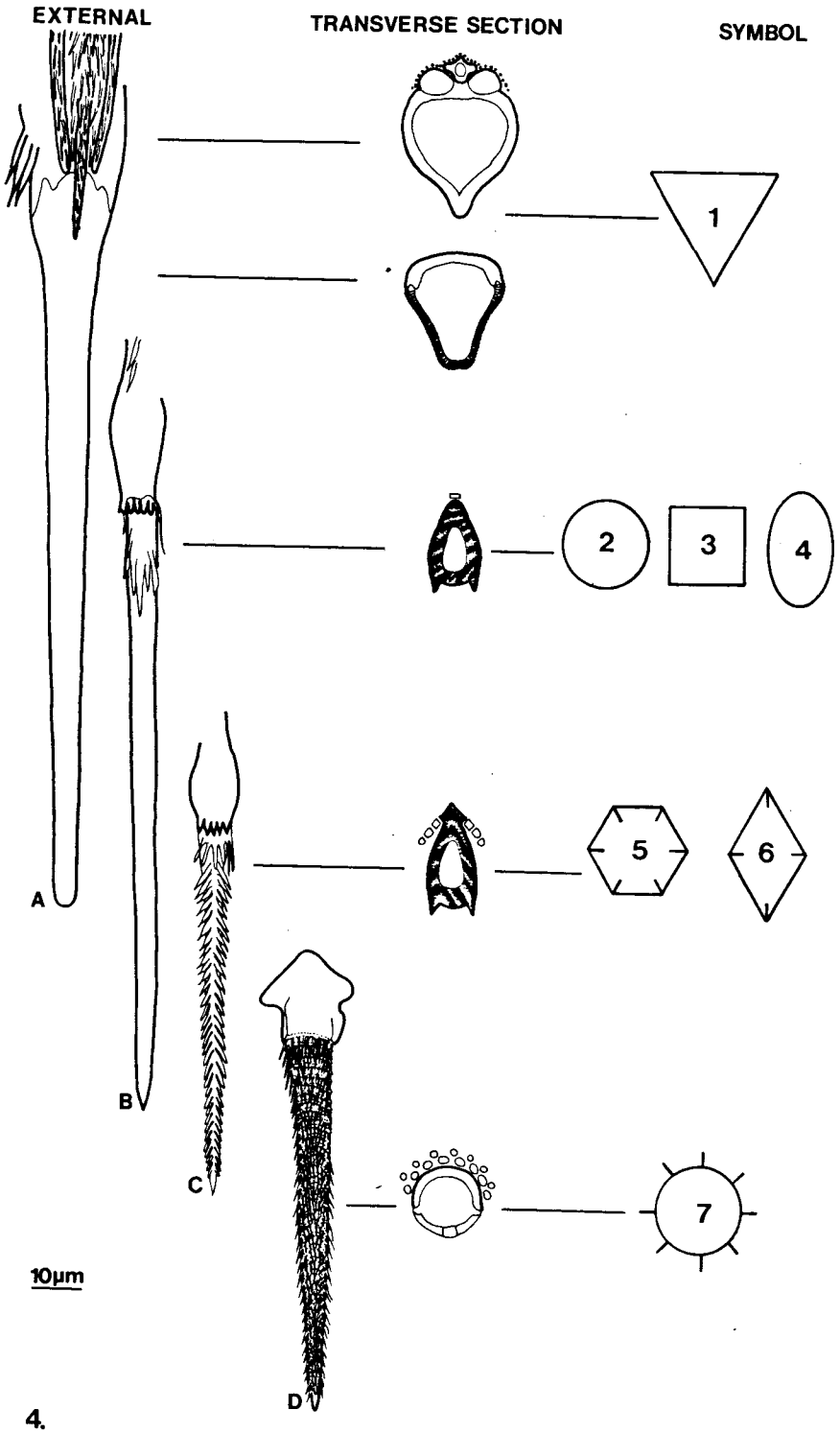
Figure 4. The four different kinds of scalids found in adult Kinorhynchus phyllotropis - external view, transverse section, symbols and numbers of the rings in which this type of scalid is found.

A. Ring 1 spinoscalid. External view, transverse section of socket and of endpiece, found in Ring 1 symbolised by a triangle.

B. Ring 2-4 smooth scalid. External view, transverse section of smooth endpiece, found in Ring 2 symbolised by a circle, Ring 3 symbolised by a square, and Ring 4 symbolised by an oval.

C. Ring 5-6 fringed scalid. External view, transverse section of fringed endpiece, found in Ring 5 symbolised by a rayed hexagon, and Ring 6 symbolised by a rayed diamond.

D. Ring 7 trichoscalid. External view, transverse section of thread-covered endpiece, found in Ring 7 symbolised by a finned circle.



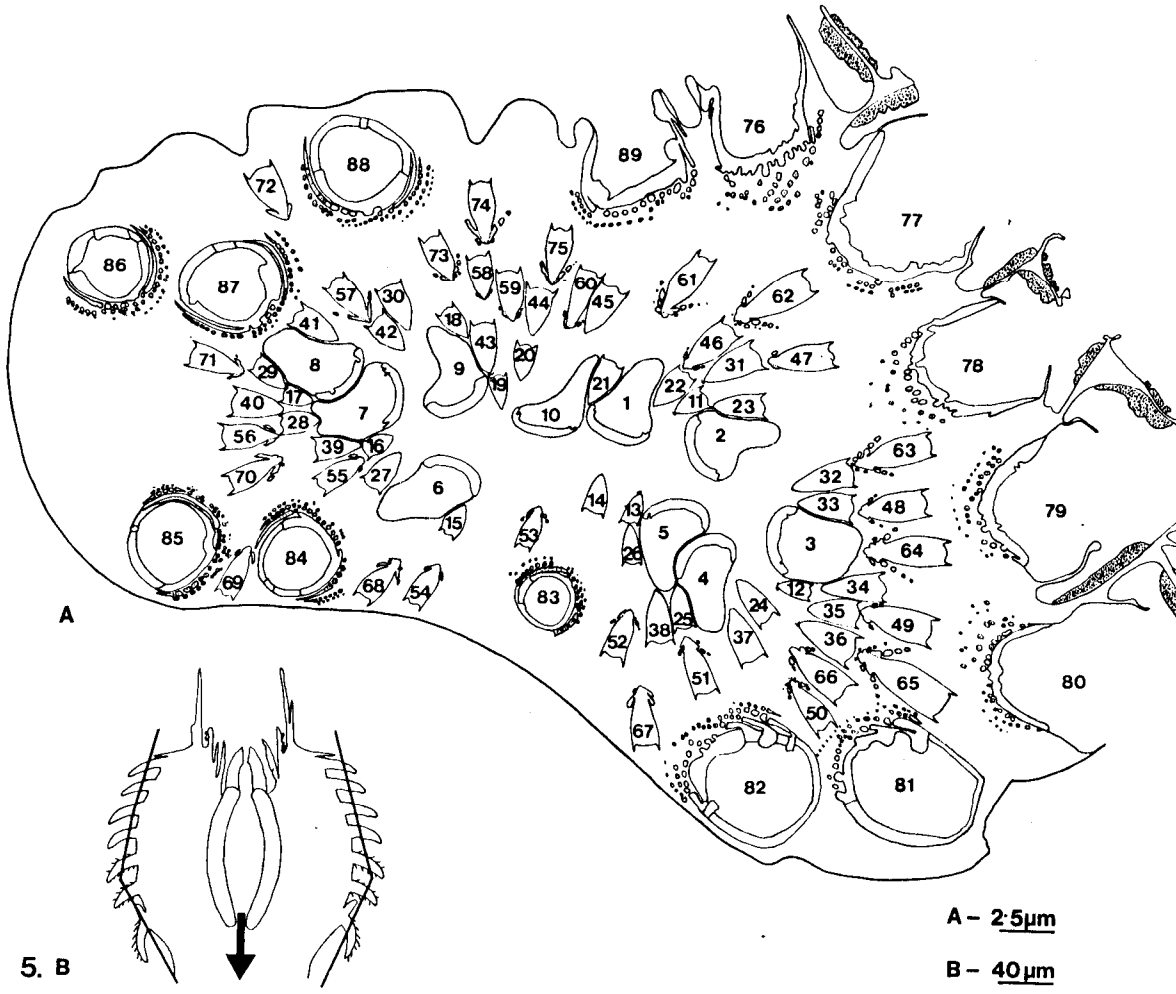
4.

Figure 5 A.
Transverse section of the introverted head of an adult Kinorhynchus phyllotropis sectioned slightly obliquely near origins of the trichoscalids. This diagram shows that this kinorhynch has 89 scalids, that the midventral trichoscalid is smaller than the other thirteen trichoscalids, and that transverse section profiles show that there are four different kinds of external scalids (as compared with two or three kinds recognised previously).

Scalids are numbered as follows:

Ring	Total number of scalids in scalid ring	Nos. allocated to scalids in Fig. 4.
1	10	1-10
2	10	11-20
3	10	21-30
4	15	31-45
5	15	46-60
6	15	61-75
7	14	76-89

Figure 5 B. Schematic diagram of everted head with dark lines showing planes of section of individual scalids seen in Fig. 5A. Fig. 5A shows a head that has been withdrawn into the trunk, a head that has been pulled down in the direction shown by the dark arrow.



5. B

Figure 6. Symbolic representation of scalid arrangement in the introverted head of Kinorhynchus phyllotropis.

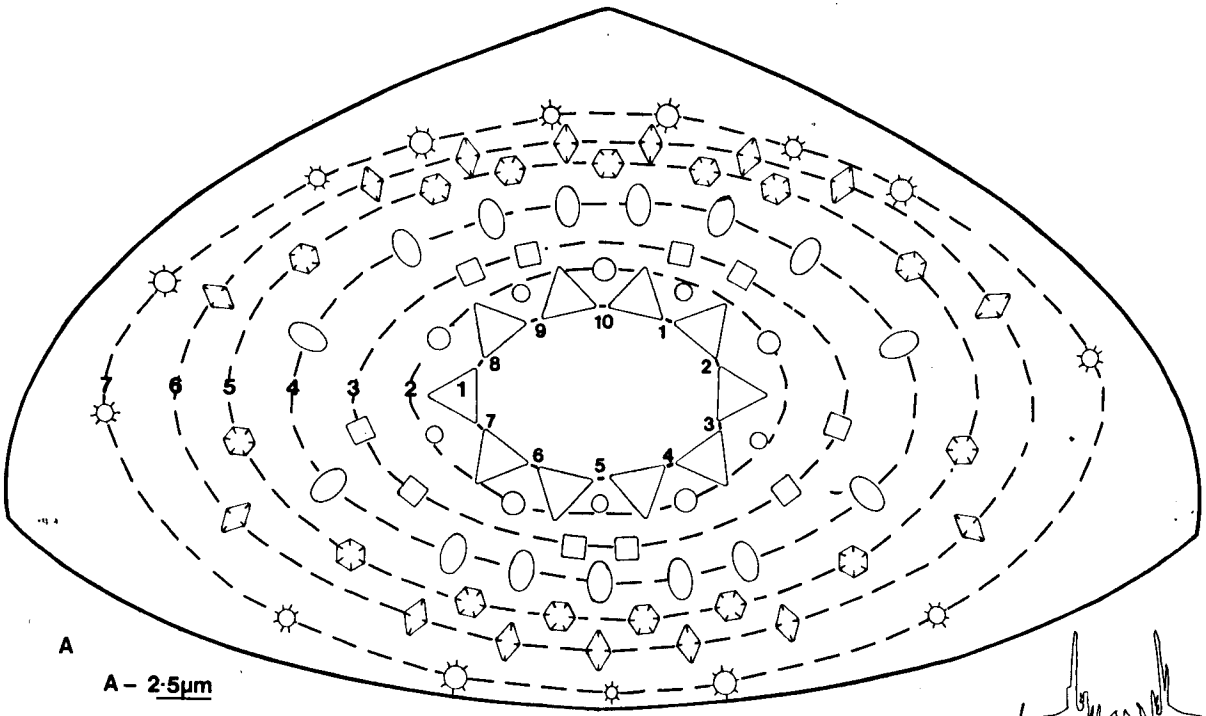
Inner ring of numbers are head sector numbers
Left line of numbers are scalid ring numbers.

Note
In Ring 7, the trichoscalid ring, the midventral trichoscalid is smaller than all other trichoscalids. This trichoscalid signals the midventral axis. The dorsoventral axis is located so that it passes through the scalids of Ring 2. It does not pass through the scalids of Ring 1, as it was illustrated by Zelinka (refer Fig. 2).

The midventral trichoscalid has a large trichoscalid on each side of it. There are two smaller trichoscalids lateral to each of these large trichoscalids. These smaller trichoscalids mark the lateral angles of the kinorhynch body. They show that the lateral angles occur in head sectors 7 and 3 (as defined by Zelinka). This disposition of smaller trichoscalids is dictated by the presence of two large trichoscalids on each of the three sides of the body. These six large trichoscalids are the only trichoscalids that have been present on the head since the first juvenile stage.

Zelinka's definition of the dorsoventral axis would necessitate that a large trichoscalid be found in the mid-dorsal angle. Large trichoscalids are not found here in adults. No trichoscalids are found in the mid-dorsal angle of early juveniles.

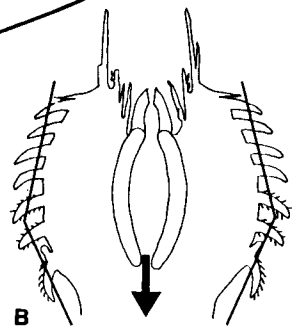
Figure 6 B. Schematic diagram of everted head with dark lines showing planes of section of individual scalids seen in Fig. 6A. Fig. 6A shows a head that has been withdrawn into the trunk, a head that has been pulled down in the direction shown by the dark arrow.



A

A – 2·5µm

6. B – 40µm



B

Figure 7. Schematic representation of scalid arrangement ("Chinese fan diagram") in *Kinorhynchus phyllotropis* adults, and in fifth and sixth juvenile stages.

White circles - scalid series running down centre of each head sector.
Odd sectors have three scalids
Even sectors have two scalids

Black rings - scalid series found on sides of each sector.

Black lines - trichoscalids of ring 7.

This diagram schematises the insertion of the external scalids as they would appear if an everted head were split open longitudinally between sectors six and seven, and spread flat. This diagram enables identification of the external scalids on a flattened head seen in a light microscope slide.

7.

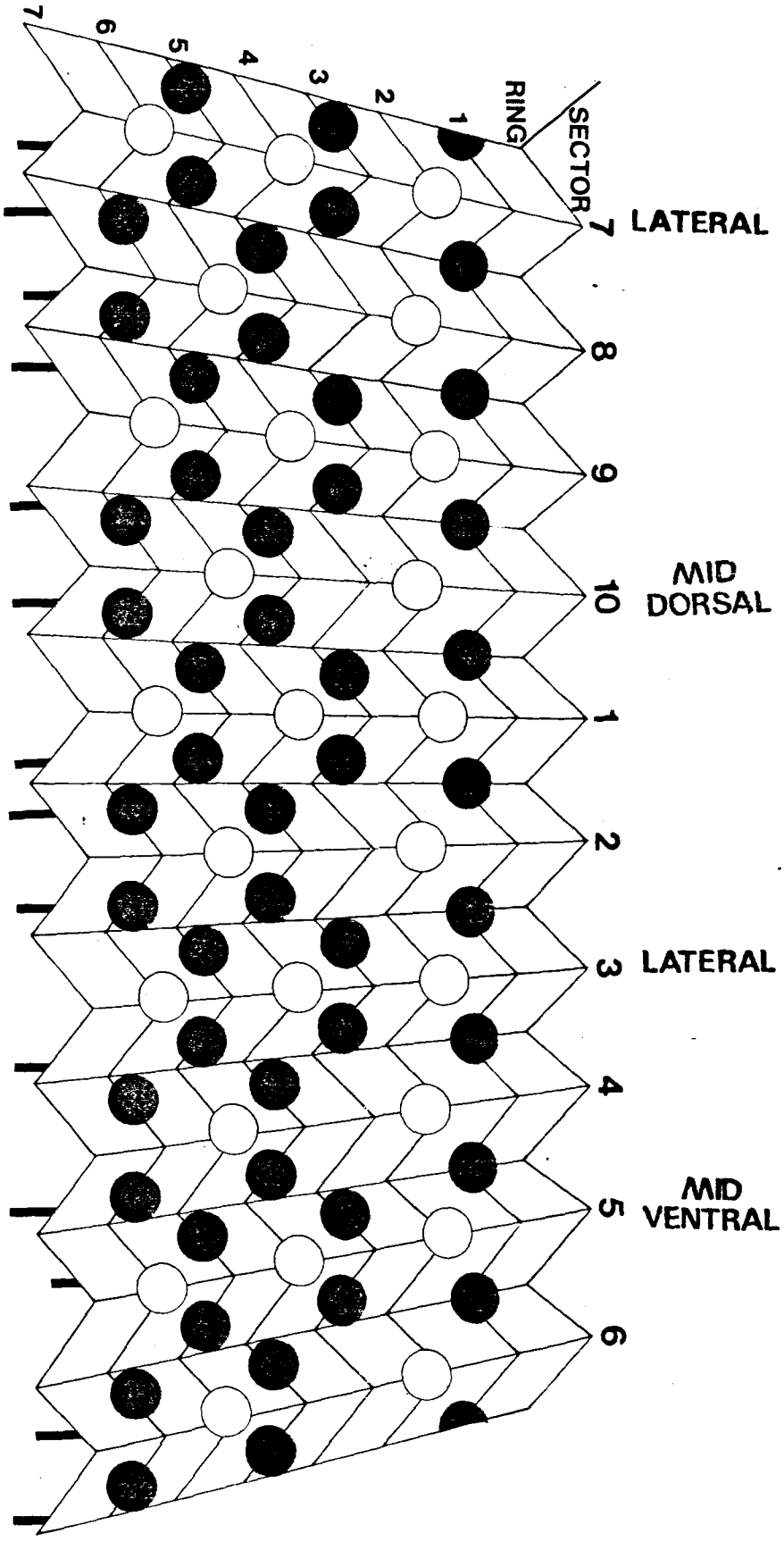

RING
SECTOR
7
6
5
4
3
2
1
LATERAL
8
9
MID
DORSAL
10
1
2
3
LATERAL
4
5
MID
VENTRAL
6

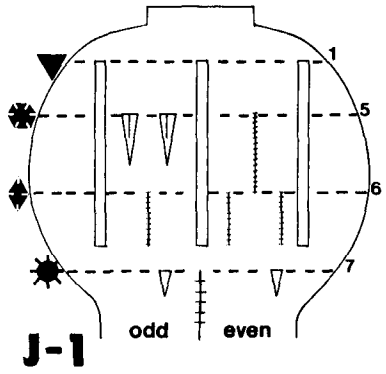
Figure 8. Semischematic diagram of the arrangement of external scalids in all stages of the life cycle of Kinorhynchus phyllotropis.

Symbols on the left side of the head correspond to the ring numbers on the right side of the head.

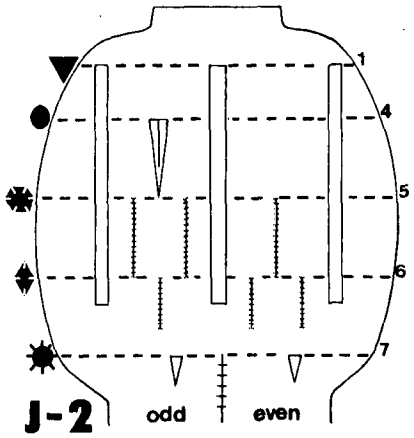
Ring 1 spinoscalid - triangle
Ring 2 smooth scalid - circle
Ring 3 smooth scalid - square
Ring 4 smooth scalid - oval
Ring 5 fringed scalid - rayed hexagon
Ring 6 fringed scalid - rayed diamond
Ring 7 trichoscalid - finned circle

This diagram is a visual representation of the data given in the following table diagram (Fig. 9). It contains the same information. The scalids are depicted as lines on the head and the proscalids and protrichoscalids as triangles. Ring 1 spinoscalids are shown as white strips; fringed scalids and trichoscalids have small cross lines.

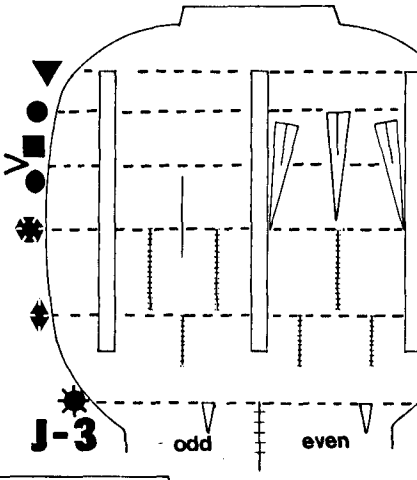
Odd sectors are indicated by the word "odd"; even sectors are indicated by the word "even". (Odd sectors include the mid-dorsal sector and every alternate sector, are numbered with odd numbers, and have three scalids down the centre of the sector in the complete scalid array. Even sectors include the midventral sector and every alternate sector, are numbered with even numbers, and have two scalids down the centre of the sector in the complete scalid array).



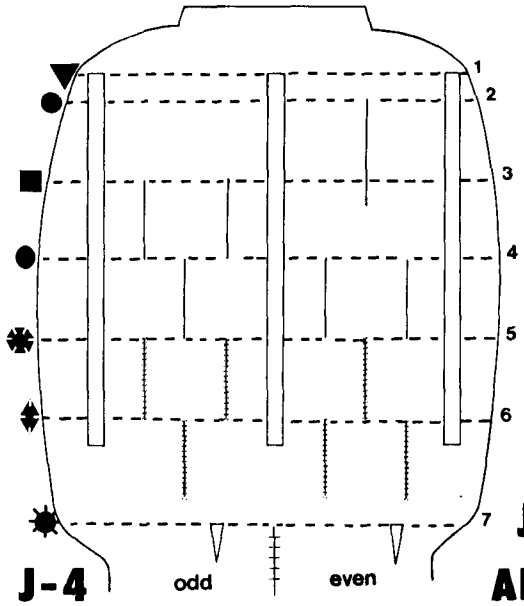
J-1



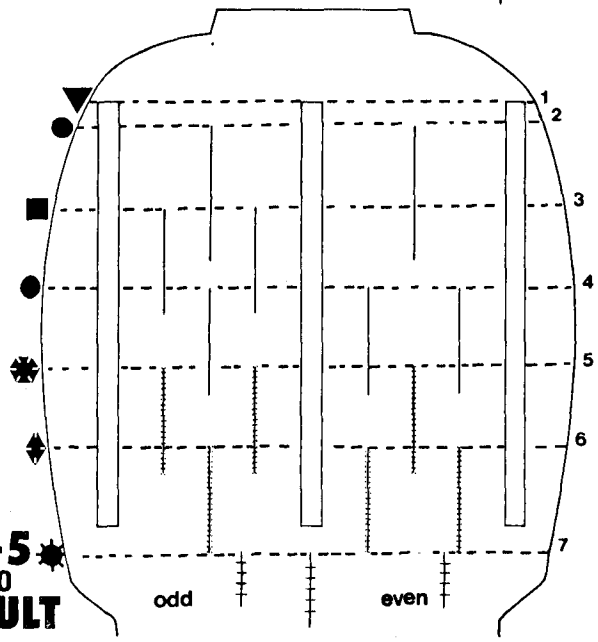
J-2



J-3



J-4



J-5 TO ADULT

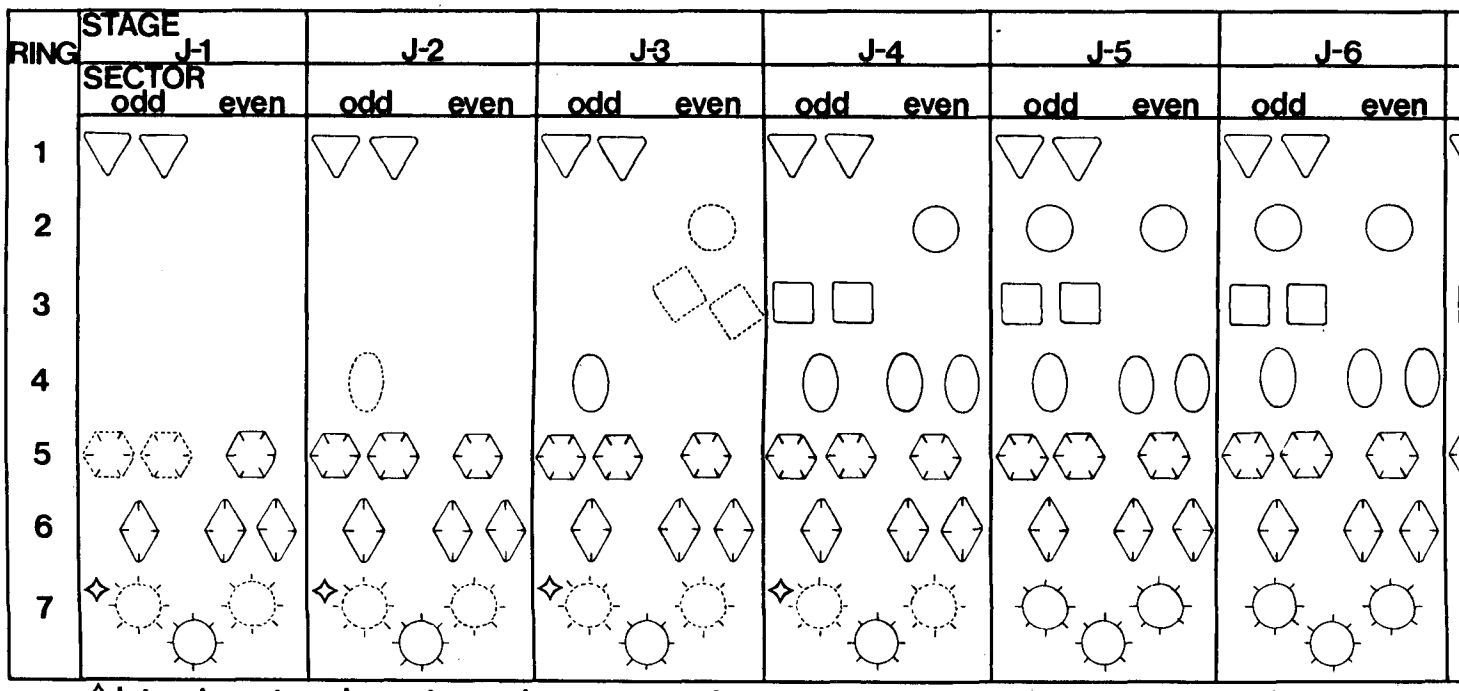
Figure 9. Schematic diagram of the arrangement of external scalids in all stages of the life cycle of Kinorhynchus phyllotropis.

This diagram is a tabloid representation of the data given in the previous pictorial diagram (Fig. 8). It contains the same information, and is designed to present that information for incorporation into taxonomic descriptions, so that one species can be compared with another.

Key

Ring 1 spinoscalid - triangle
Ring 2 smooth scalid - circle
Ring 3 smooth scalid - square
Ring 4 smooth scalid - oval
Ring 5 fringed scalid - rayed hexagon
Ring 6 fringed scalid - rayed diamond
Ring 7 trichoscalid - finned circle
Proscalids and protrichoscalids - dotted symbols

Odd sectors are indicated by the word "odd"; even sectors are indicated by the word "even". (Odd sectors include the mid-dorsal sector and every alternate sector, are numbered with odd numbers, and have three scalids down the centre of the sector in the complete scalid array. Even sectors include the midventral sector and every alternate sector, are numbered with even numbers, and have two scalids down the centre of the sector in the complete scalid array).



✧lateral sectors have two adjacent protrichoscalids

9.

Figure 10 A. Longitudinal section through the joint of a Ring 2, type I smooth scalid.

Figure 10 B. Transverse section through the socket near the joint of a Ring 2, type I smooth scalid.

Figure 10 C. Schematic diagram of everted head showing planes of section in Figs. 10A and 10B.

Key.

CC - ciliated cell containing striated rootlet and tubular bundles

EC - epidermal cell

FC - fibrous cuticle

J - joint of scalid

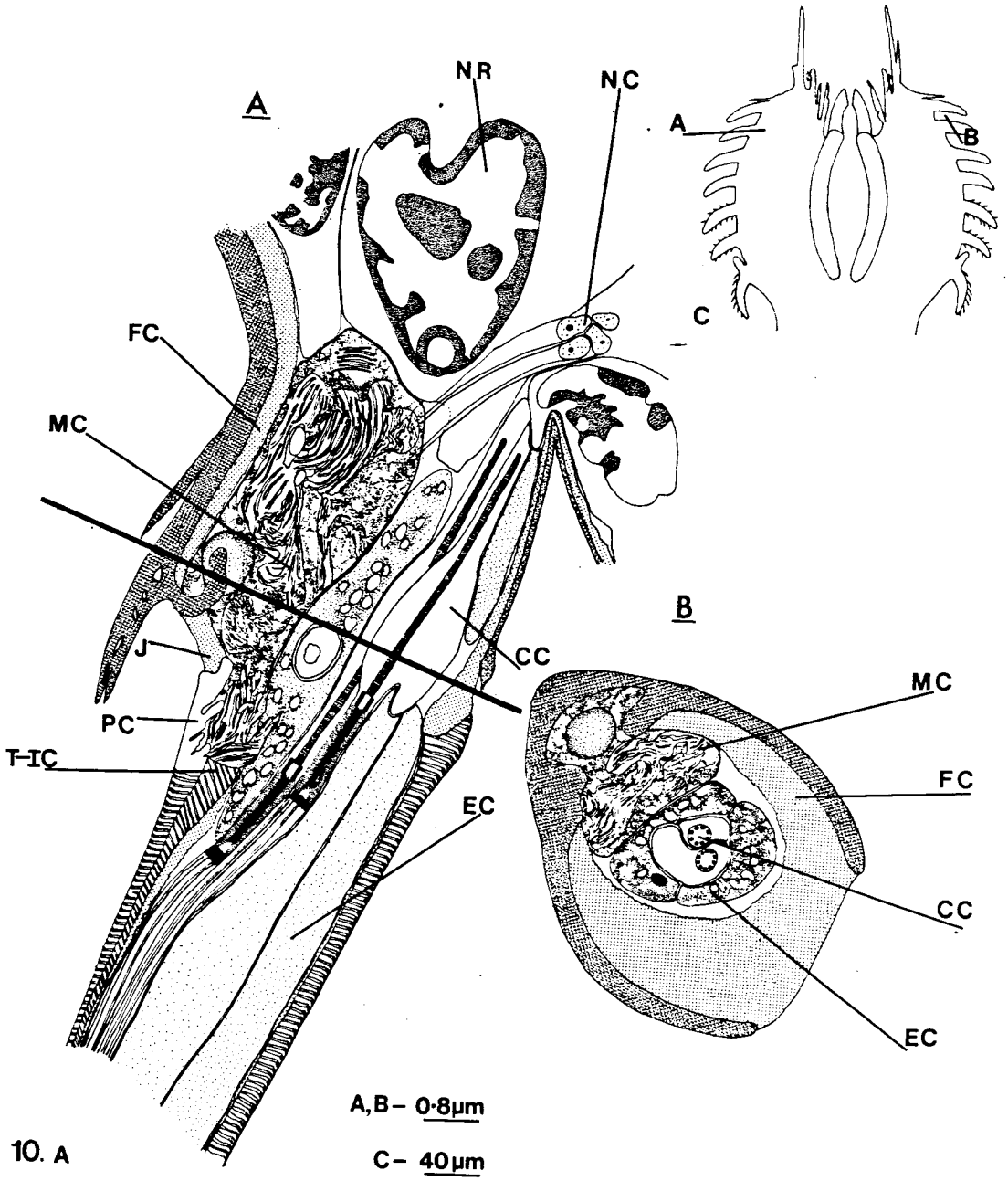
MC - membrane cell containing characteristic piles of membranes

NC - nerve cell process, containing microfilament

NR - nerve ring nucleus from the ten-lobed circum-oral nerve ring

PC - perforated cuticle below the joint, a possible sensory window

T-I C - type I cuticle with two layers of striation



10. A

Figure 11. Scalid tips transversely sectioned to show ultrastructural similarity of bundles of tubules in these modified cilia.

Drawings made from transmission electron micrographs.

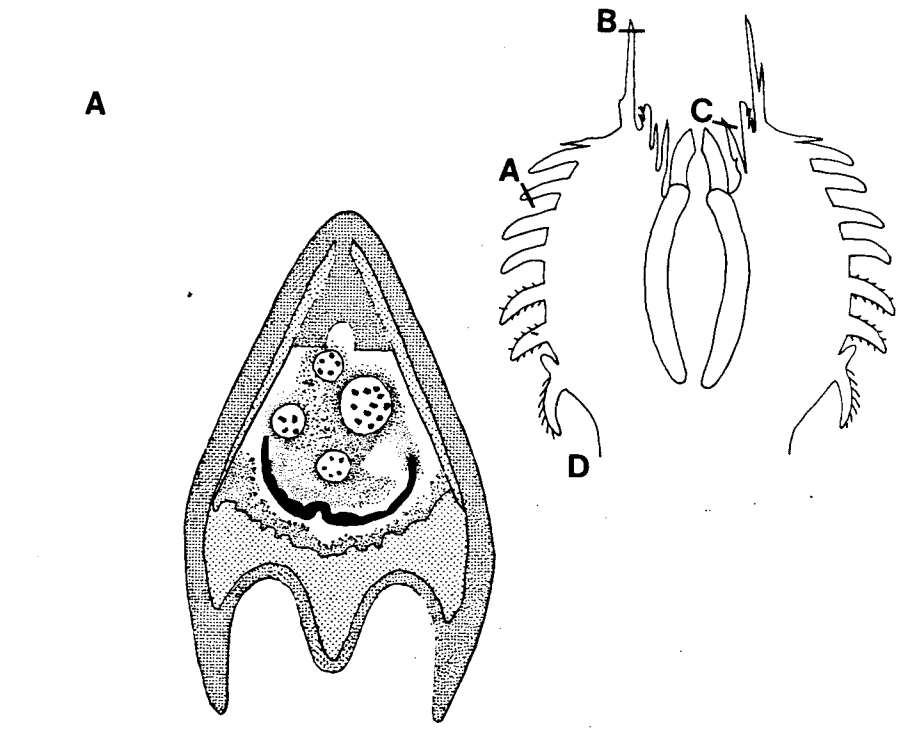
A. External scalid.
This is a type I scalid as previously described in K. giganteus (Moritz and Storch 1972b, Fig. 7a).

B. Oral scalid (= oral style).
The oral scalid has a thick layer of fibrous cuticle which surrounds the cytoplasm completely. The layer of dense outer cuticle is also thick, especially on the aspect which faces away from the oral aperture. As in the external scalid the oral scalid contains bundles of tubules and a bracket-shaped organelle of unknown structure and function.

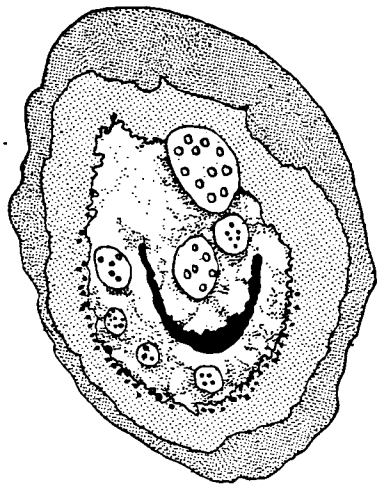
C. Inner scalid.
This is a helioscalid. The rays of dense outer cuticle normally face the inner wall of the oral cone. In this section the fibrous cuticle is only seen along the base of the inner scalid which faces away from the walls of the oral cone. In the cytoplasm there are three bundles of tubules and a bracket-like organelle. These structures identify this appendage as a scalid.

DENSE STIPPLE - Outer layer of dense cuticle.
LIGHT STIPPLE - Inner layer of fibrous cuticle.

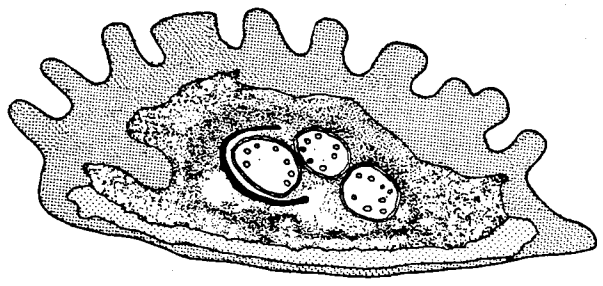
D. Schematic diagram of everted head showing planes of section of previous diagrams.



B



C



A, B – 0·17µm

C – 0·25µm

D – 40 µm

11.

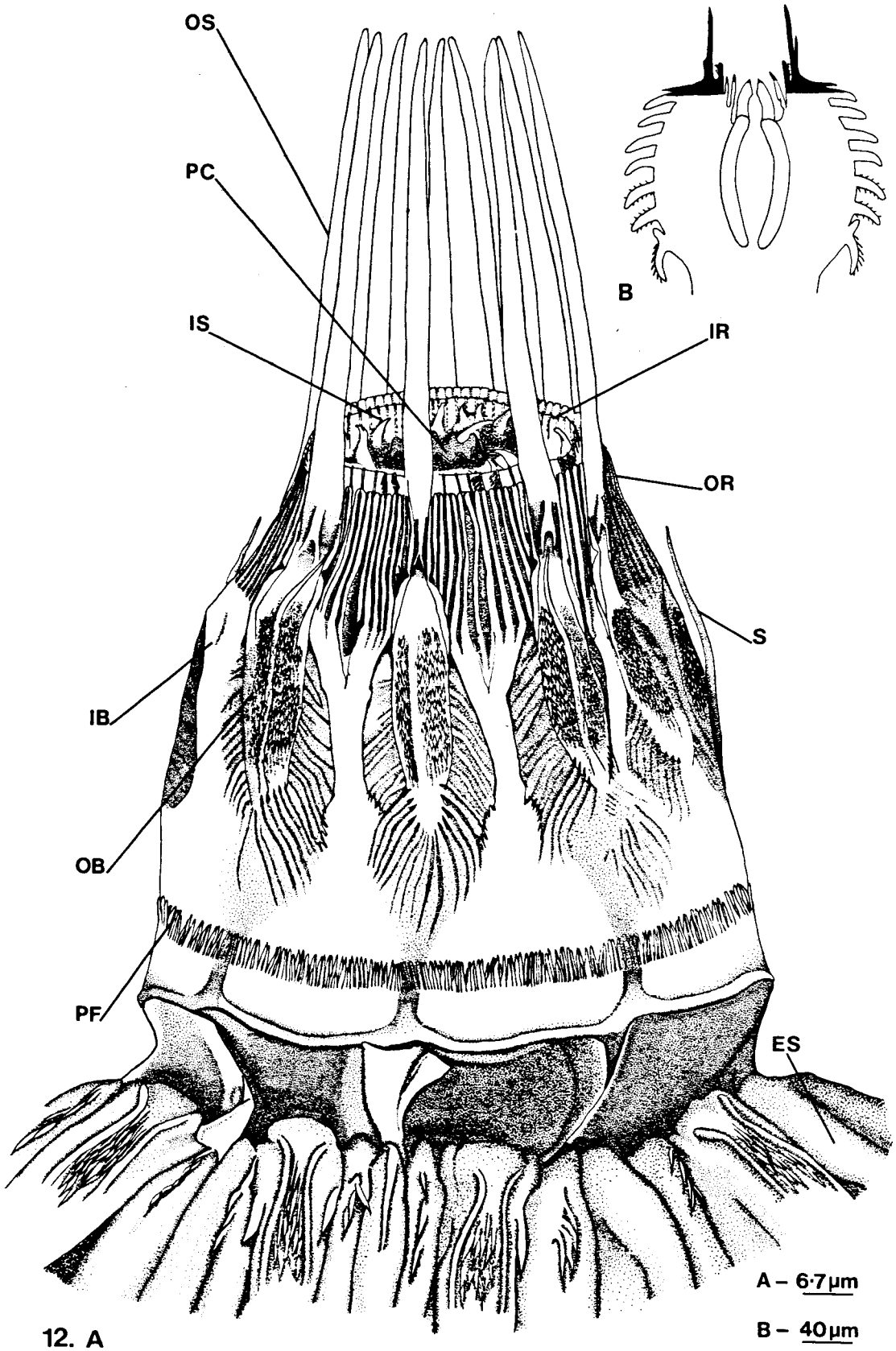
Figure 12 A. The oral cone of an adult Kinorhynchus phyllotropis.

This diagram has been drawn from several scanning electron micrographs.

Key.

- ES - proximal ends of external scalids
- IB - interbasal strip of cuticle with edges scrolled underneath
- IR - inner rim of oral aperture formed of cuticle folded into ridges bearing short threads or fimbriae
- IS - internal scalid attached to inner wall of oral cone
- OB - oral scalid base, a ridge of cuticle containing nuclei and nerve fibres. The protractor muscles of the pharynx insert onto cuticle below the oral style bases
- OR - outer rim of oral aperture formed of finely pleated cuticle
- OS - oral scalid
- PC - pharyngeal crown of dense cuticle located on the top of the muscular pharyngeal bulb
- PF - pectinate fringe marking the posterior boundary of the first segment. The protractor muscles of the pharynx insert onto cuticle just above this fringe
- S - spine seen on alternate oral scalids.

Figure 12 B. Schematic diagram of everted head showing region illustrated by Figure 12 A shaded in black.



12. A

Figure 13 A.
Schematic diagram of the partially eviscerated head of an adult Kinorhynchus phyllotropis specimen with a trunk length of 800 um.

This schematic diagram shows a kinorhynch head in which the pharyngeal bulb has prolapsed through the oral aperture, dragging the inner scalids out through the oral aperture. Specimens with this common form of collection injury are the best material to show the inner scalids.

The structures on the left side of the diagram are surface features. The structures on the right side of the diagram are internal structures viewed in a lower plane of focus. These features are also illustrated in Fig.12A (surface features) and Fig. 3 (internal structures). The internal scalids are shown forming a band across the pharynx crown to demonstrate their anatomic relationships. The cause of the prolapse is the ruptured pharyngeal protractor muscle illustrated on the upper right hand section of the picture.

ARROWS - Arrows show the normal orientation of the structures beside them. In a head which has not undergone prolapse those structures would be arranged so that the heads of the arrows would all point to the top of the diagram.

DOTTED LINES - Dotted lines indicate where the epidermis is folded back upon itself in the normal head.

Figure 13 B. Schematic diagram of everted head showing area illustrated in Figure 13 A shaded in black.

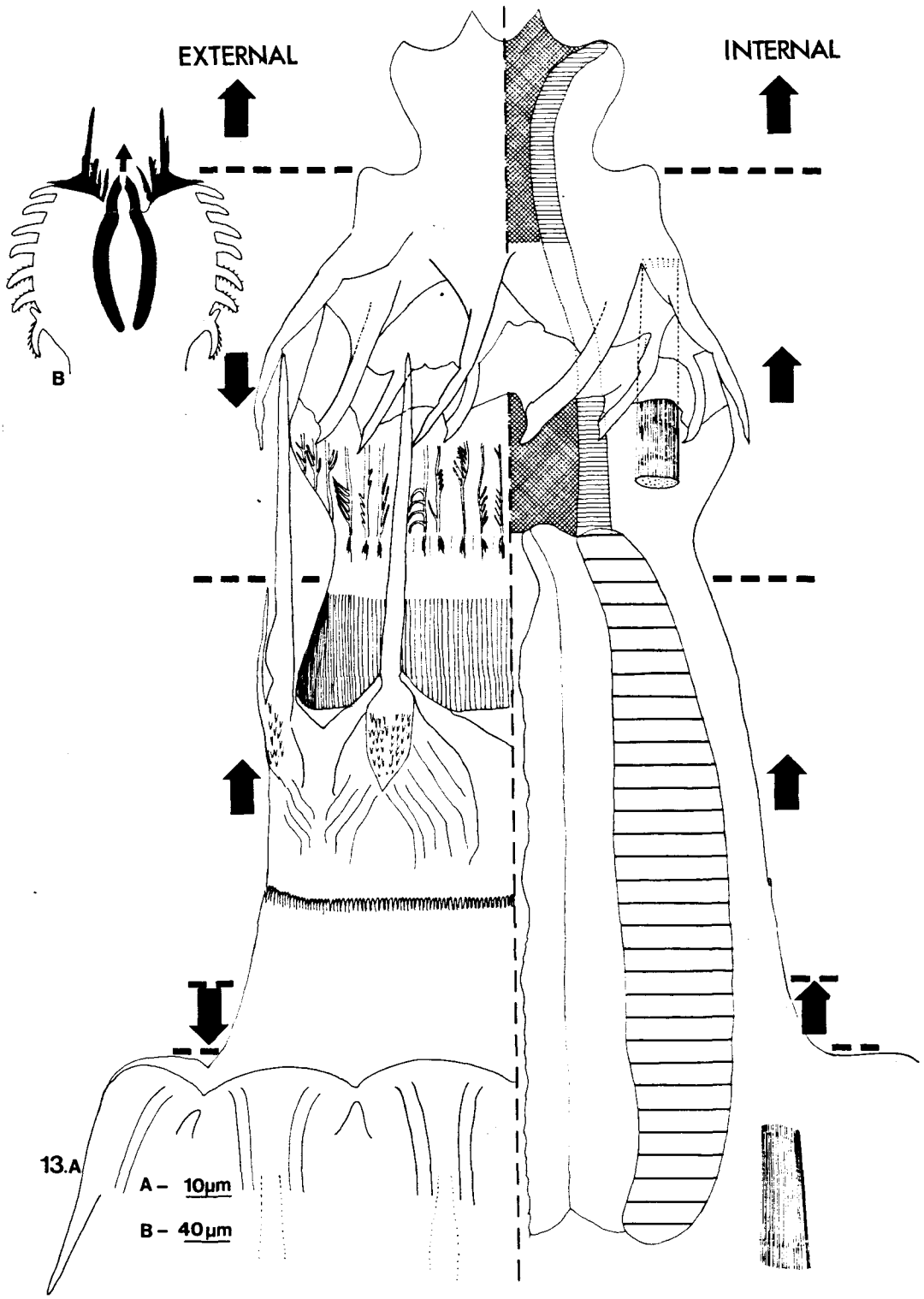

EXTERNAL
INTERNAL
B
13.A
A – 10µm
B – 40µm

Figure 14 A. The internal scalids.

This diagram was drawn from the specimen illustrated in Fig. 13A, with some details added from scanning electron micrographs of the inner scalids.

1 - scleroscalid 1
2 - scleroscalid 2
3 - helioscalid

Figure 14 B. Schematic diagram of everted head showing area illustrated in Figure 14 A shaded in black.

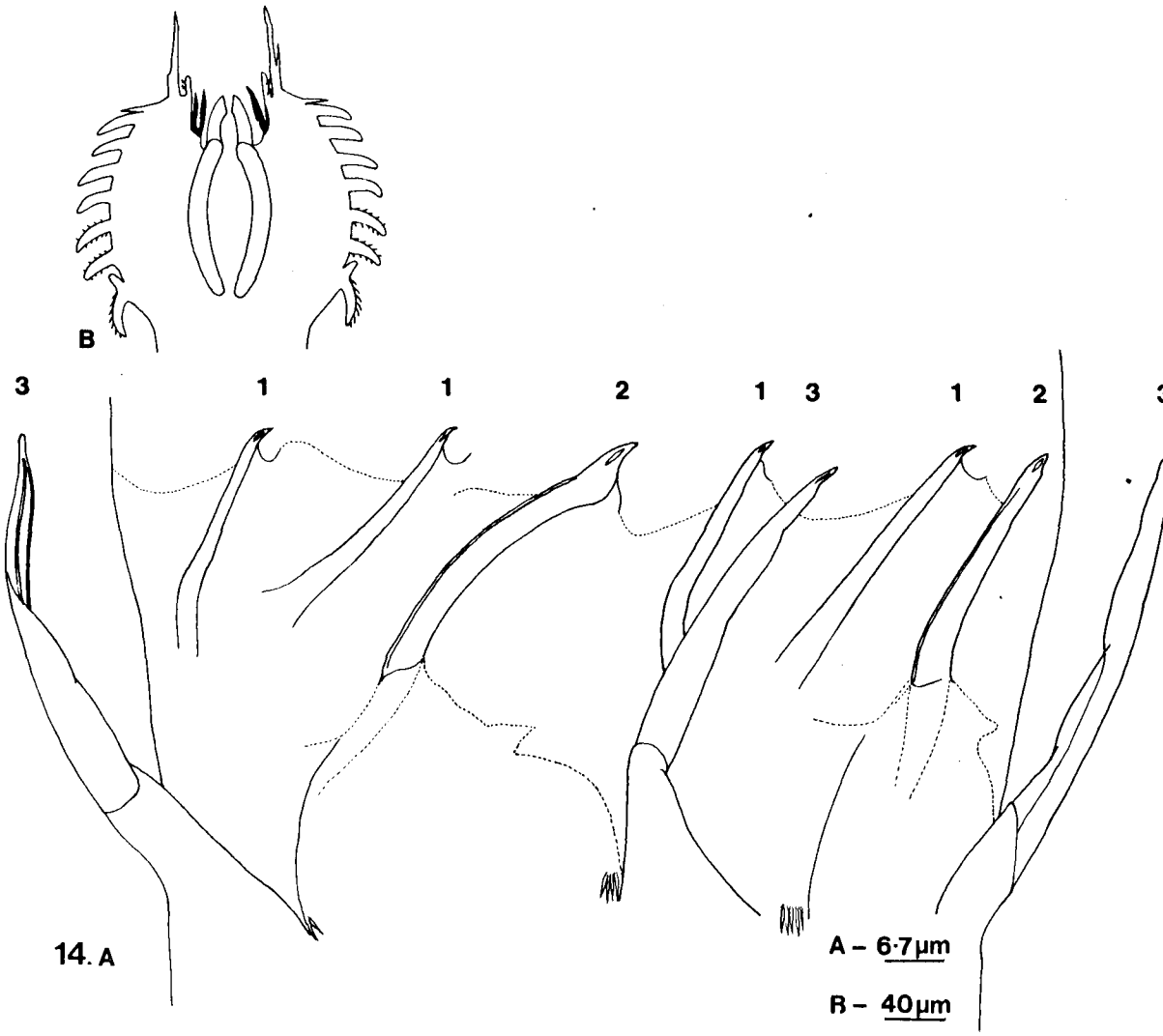

B
3
1
1
2
1
3
1
2
14. A
A – 6·7µm
B – 40µm

Figure 15 A. Scleroscalids 1.

A. Scleroscalid 1 drawn from a scanning electron micrograph.

SINGLE LINES indicate the plane of section through this scalid that are illustrated in the associated figures, drawn from transmission electron micrographs.

B. Longitudinal section through the edge of a scleroscalid 1 showing ciliary tubules projecting through the slit in the scalid tip.

C. Longitudinal section through the central plane of a scleroscalid 1 showing one bundle of tubules travelling through a passage in the cuticle that is separate from the lumen filled with cytoplasm.

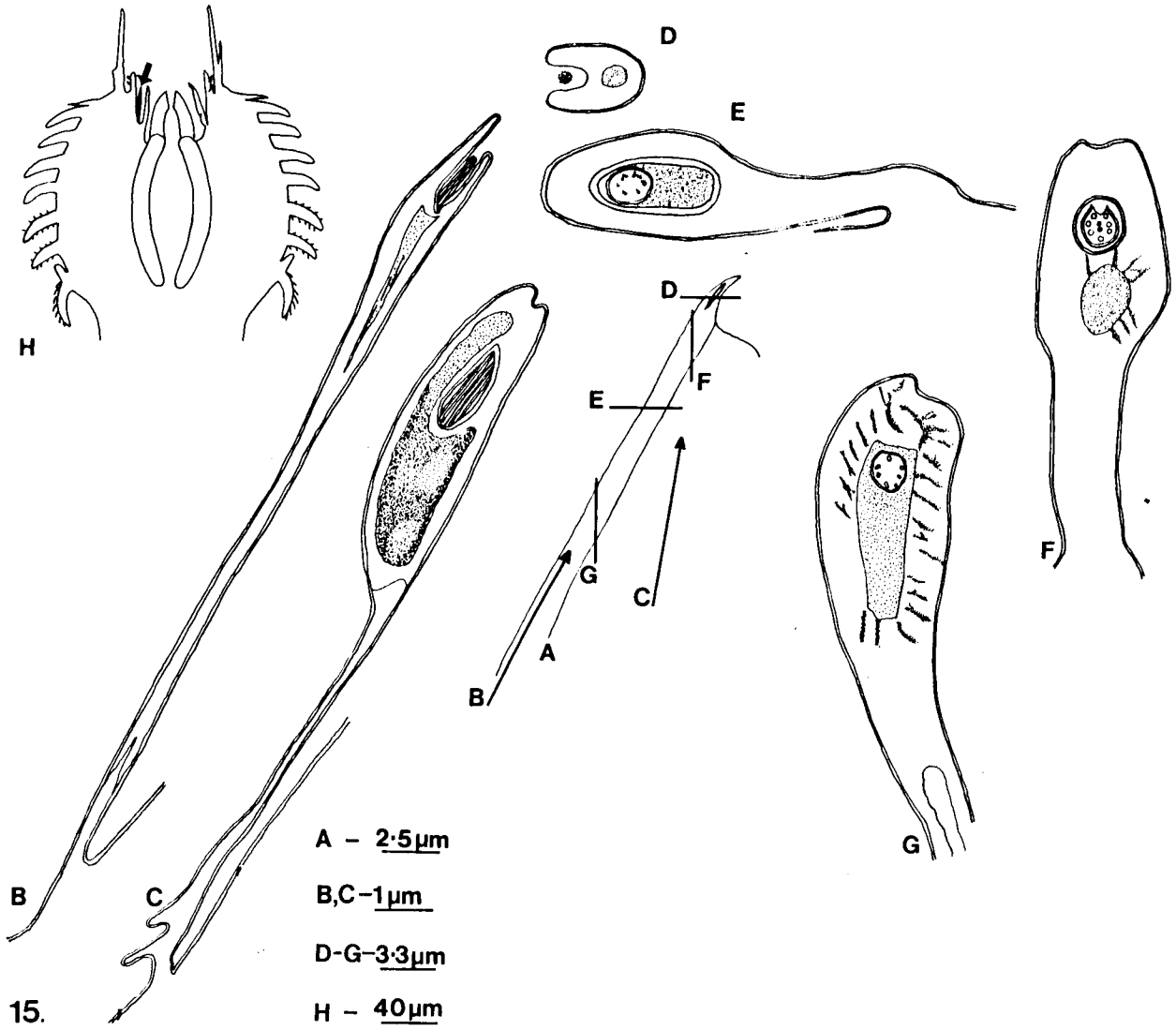
D. Transverse section through the tip of a scleroscalid 1 showing tubules projecting from the apical slit into the ambient water, and a scalid lumen surrounded by thick cuticle.

E. Transverse section cut just behind the tip of a scleroscalid 1 showing a bundle of tubules passing through the cytoplasm of the scalid lumen. The scalid is anchored to the inner wall of the oral cone by a buttress of cuticle.

F. Oblique section cut near the tip of a scleroscalid 1 showing one bundle of tubules passing through the thick cuticular walls of the scalid separate from the cytoplasm of the scalid lumen. The thick walls of the scleroscalid are diffusely striated.

G. Oblique section cut through the shaft of a scleroscalid 1 showing one bundle of tubules passing through the lumen of the scalid, and thick walls of diffusely striated cuticle.

H. Schematic diagram of everted head showing location of scleroscalid 1 (arrow).



15.

Figure 16. Scleroscalids 2.

A. Scleroscalid 2 drawn from a scanning electron micrograph.

SINGLE LINES indicate the planes of section through this scalid that are illustrated in the associated figures, drawn from transmission electron micrographs.

B. Oblique section taken near the tip of a scleroscalid 2 showing one bundle of tubules passing through the thick walls of the scleroscalid separate from the thick walls of the scalid lumen. The thick walls of the scalid are reinforced by a small ridge of cuticle running the length of the shaft.

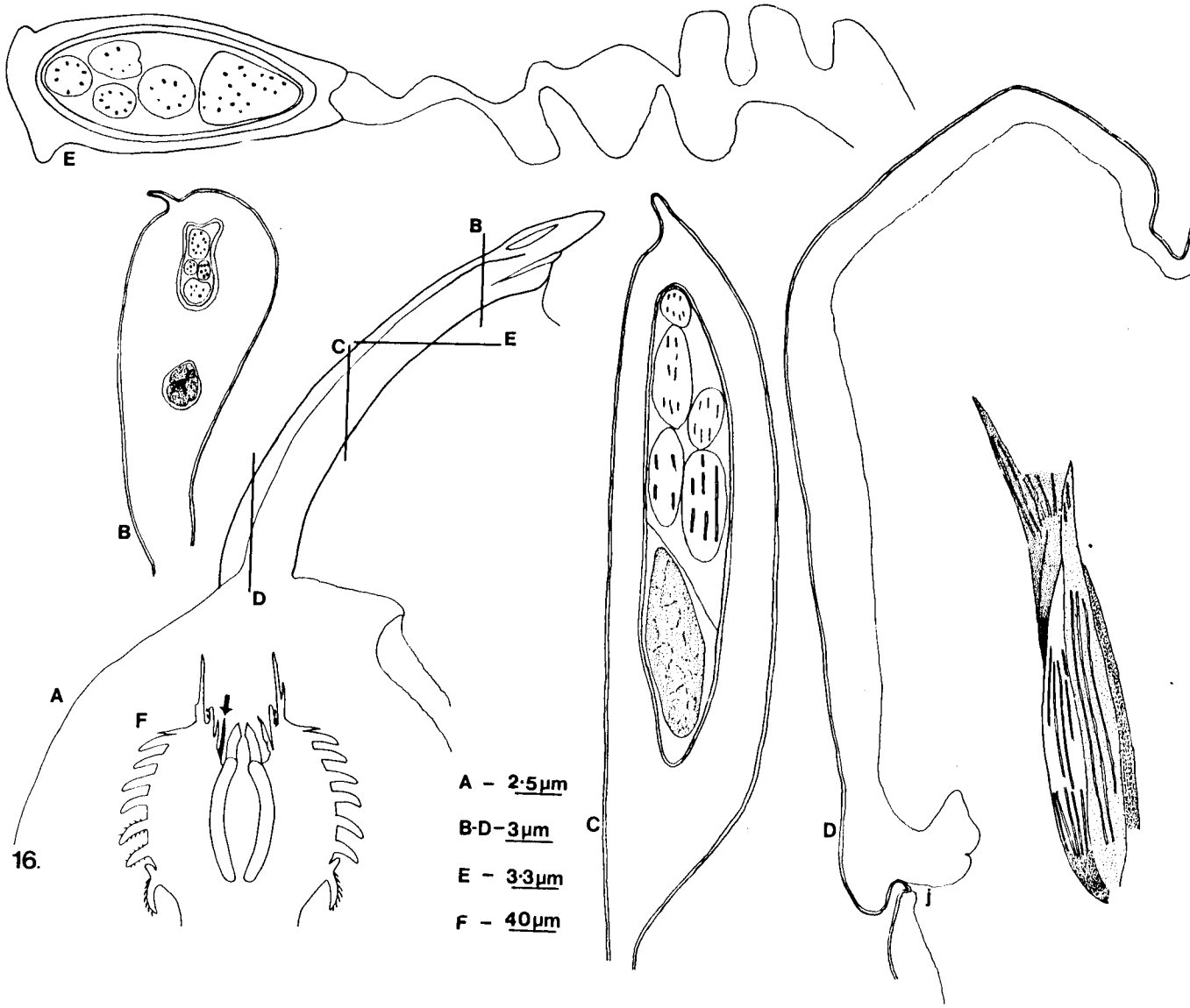
C. Oblique section cut through the shaft of a scleroscalid 2 showing five bundles of tubules passing through the lumen of the scalid. The thick walls of the scalid are reinforced by a small ridge of cuticle running the length of the shaft.

D. Oblique section cut through the base of a scleroscalid 2 showing a number of bundles of tubules passing into the scleroscalid.

J - flexible cuticle and cuticular spur of scalid joint.

E. Transverse section taken through the shaft of a scleroscalid 2 showing five bundles of tubules passing through the scalid lumen. The cuticular buttress of varying thickness which attaches the scalid to the inner walls of the oral cone is shown on the right side of the scleroscalid shaft. This can also be seen in Plate 1.

F. Schematic diagram of everted head showing location of scleroscalid 2 (arrow).



16.

Figure 17. Helioscalids.

A. Helioscalid drawn from a scanning electron micrograph. The swelling at the scalid base covers the pharyngeal protractor muscle.

SINGLE LINES indicate the planes of section through this scalid that are illustrated in the associated figures, drawn from transmission electron micrographs.

B. Longitudinal section through part of the curved shaft of the helioscalid.

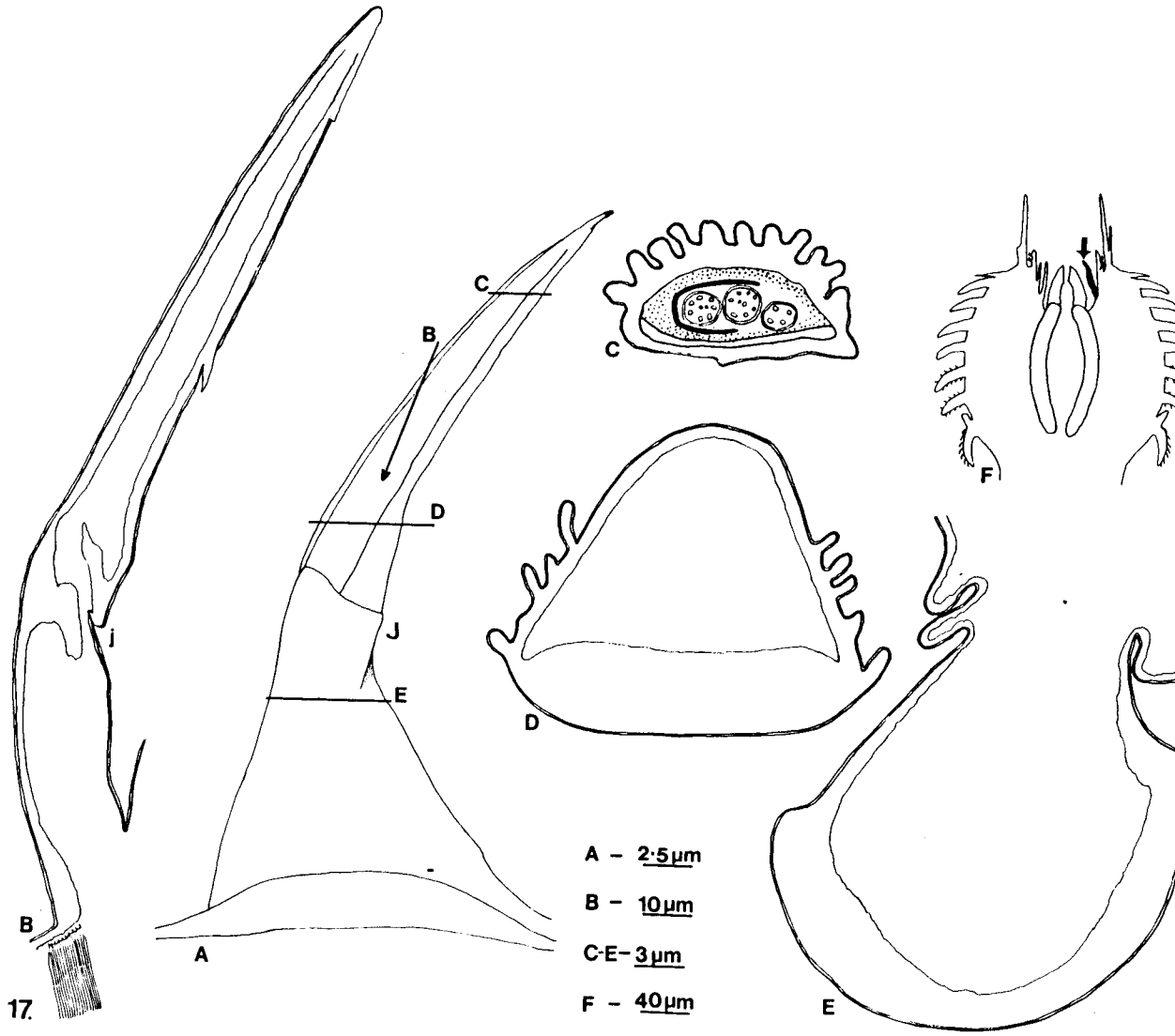
J - flexible cuticle and cuticular spurs of scalid joint.

C. Transverse section cut near the tip of a helioscalid showing three bundles of tubules surrounded by a bracket-like organelle passing through the scalid lumen. The helioscalid endpiece is supported by ridges of cuticle running the length of the endpiece which lie against the head cuticle. Such ridges are seen in the ring 1 spinoscalids.
Note: This section is smaller than the section illustrated in Fig. 11 because it was cut closer to the scalid tip of the same specimen.

D. Transverse section cut near the socket of a helioscalid showing that the ridged cuticle is found only on the sides of the triangular section, not the apex. The base of the triangle, facing away from the walls of the oral cone, is composed of thick cuticle, as in the ring 1 spinoscalid.

E. Transverse section cut through the socket of a helioscalid showing that this socket has no supporting ridges or rays. In this it resembles the socket of the ring 1 spinoscalid.

F. Schematic diagram of everted head showing location of a helioscalid (arrow).

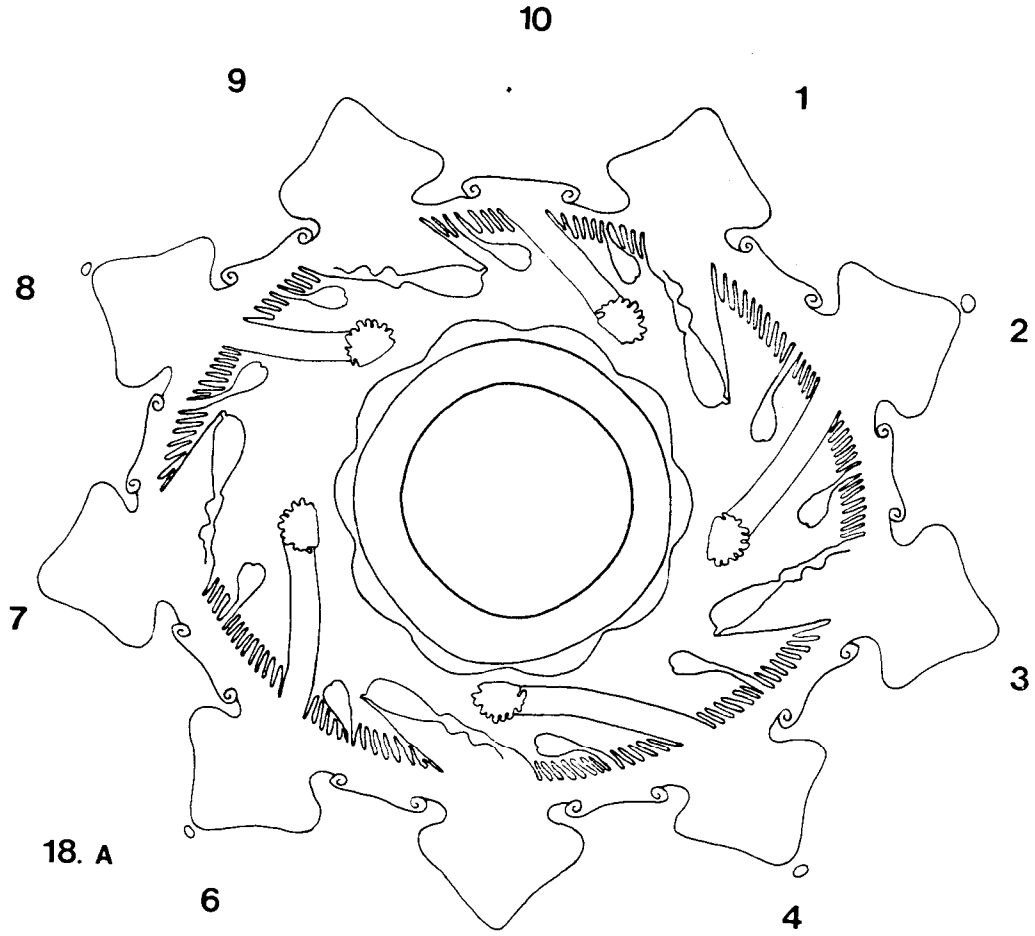


17.

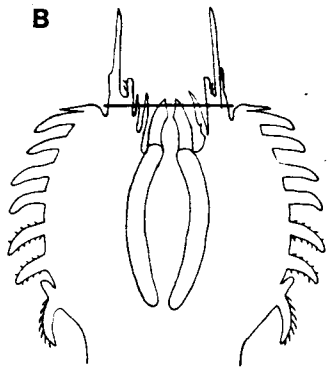
Figure 18 A.
Semischematic section of the oral cone showing the relationships of the oral scalids and the internal scalids as they appear in sections such as the frontispiece of this thesis. Distal sections of the helioscalids appear to be displaced in a clockwise direction because the free-standing helioscalids hang out from the oral cone walls, and because the shaft of the helioscalid is curved.

Numbers indicate the head sectors.

Figure 18 B. Schematic diagram of an everted head showing the plane of section of Figure 18 A.



18. A



A – 2µm

B – 40µm

Figure 19 A. Schematic transverse section of the introvert showing the distribution of anterior scalids in the head sectors.

Large numbers indicate the head sectors.

Small numbers indicate different anterior scalid rings. This numbering system is used only in this diagram.

The head rings shown in this diagram are:

Centre - pharynx crown surrounded by ten ribs of tissue. (The pharynx crown is surmounted by ten points anteriorly.)

Ring one - helioscalids

Ring two - scleroscalids 2

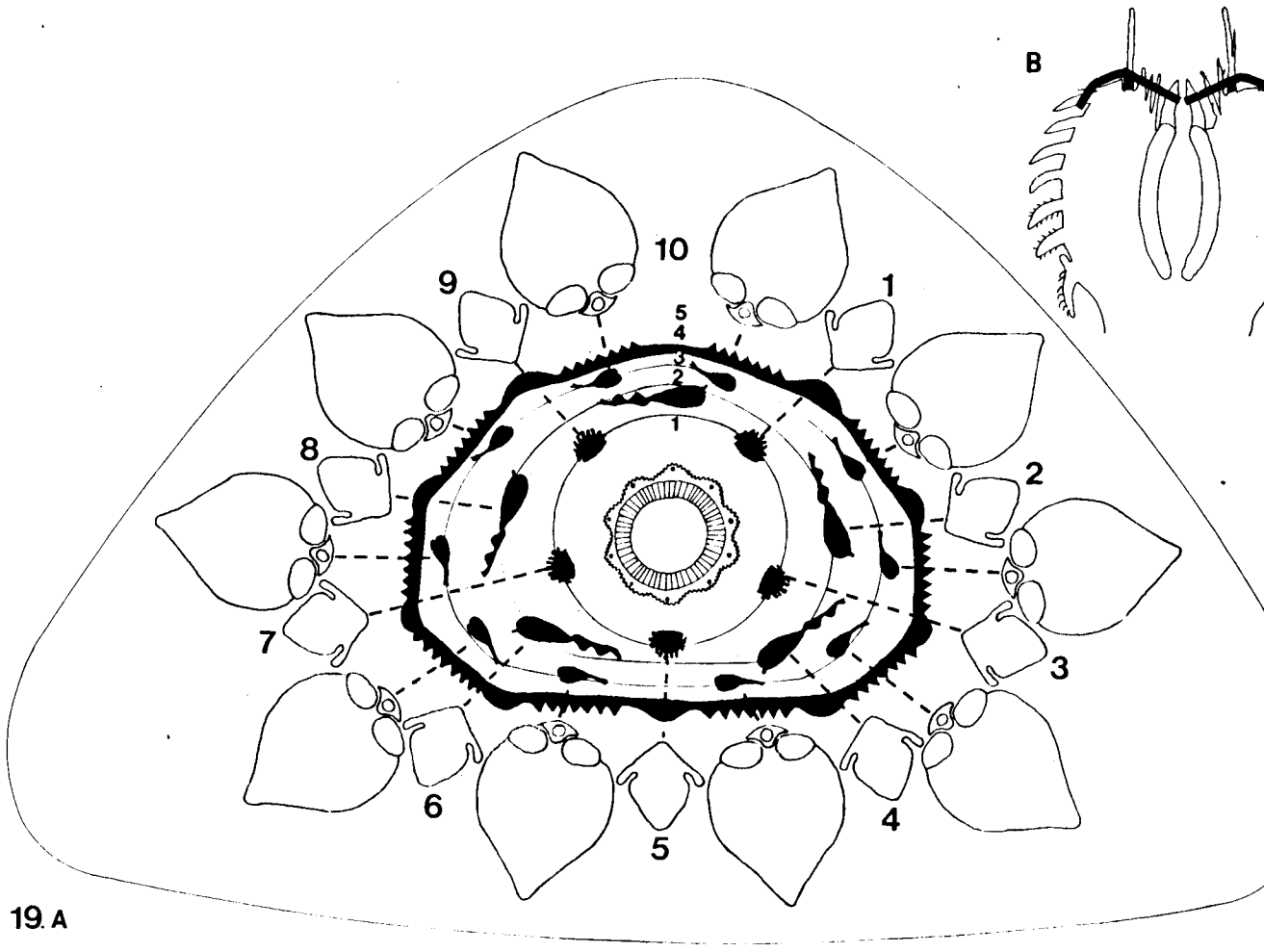
Ring three - scleroscalids 1

Rim of the oral cone

Ring four - oral scalids

Ring five - ring 1 spinoscalids

Figure 19 B. Schematic diagram of everted head showing position of scalids in Figure 19 A.



19. A

Figure 20. Schematic representation of internal and external scalid arrangement ("Chinese fan diagram") in Kinorhynchus phyllotropis adults.

Horizontal numbers - numbers of head sectors

Vertical numbers - numbers of external scalid rings

HS - helioscalids

SS 2 - scleroscalids 2

SS 1 - scleroscalids 1

OS - oral scalids

White circles - external scalid series found in the centre of each head sector

Black circles - external scalid series found on the sides of each sector

Black lines - trichoscalids of ring 7

LATERAL - lateral axis of the body

MID
DORSAL - mid-dorsal axis of the body

MID
VENTRAL - midventral axis of the body

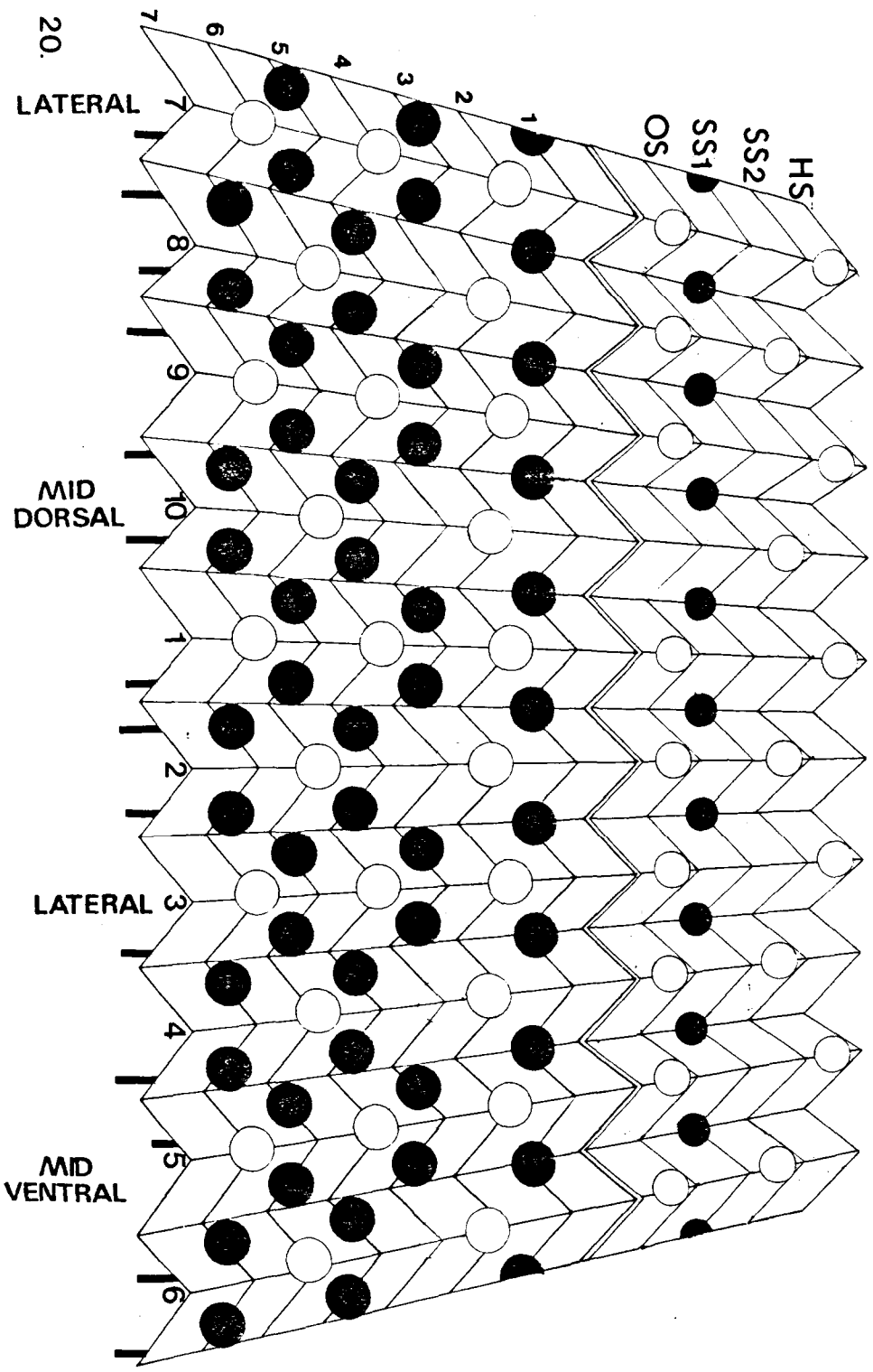
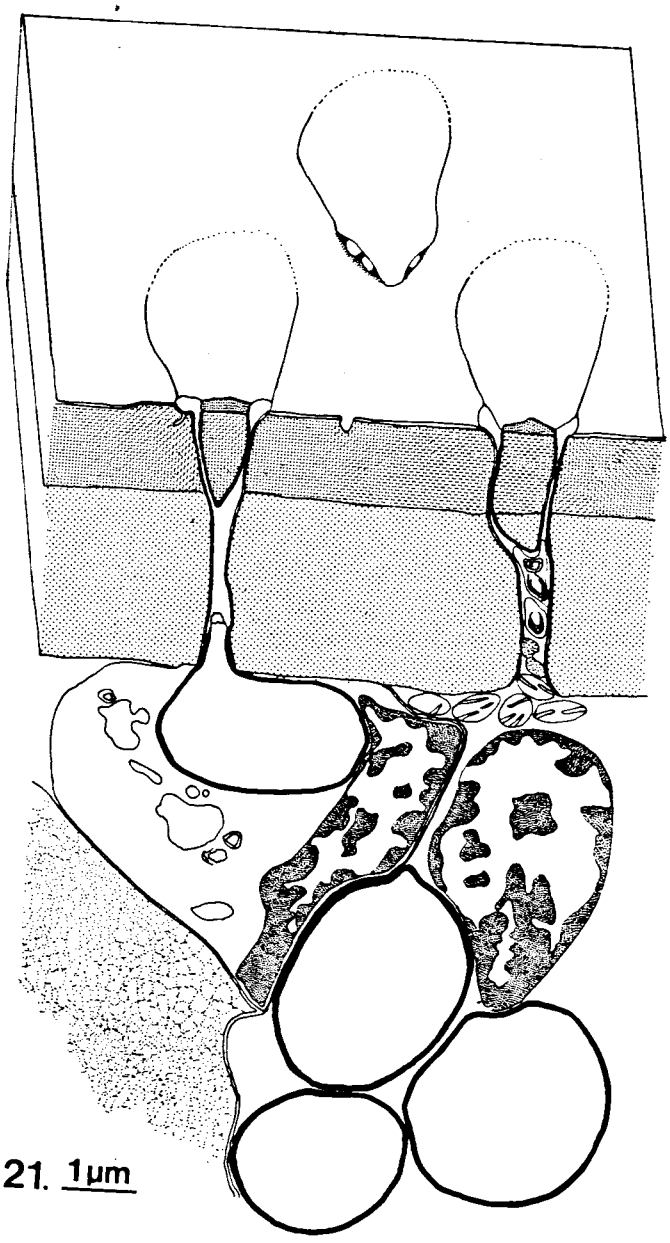

20.
LATERAL
MID
DORSAL
LATERAL
MID
VENTRAL
1
2
3
4
5
6
7
OS
SS1
SS2
HS

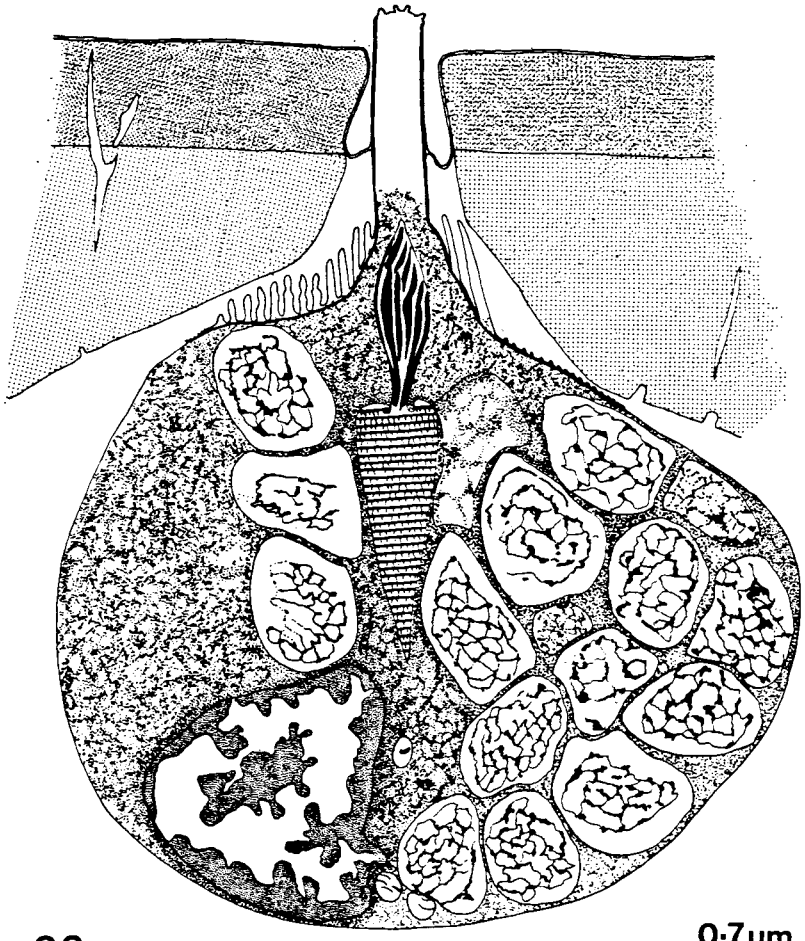
Figure 21. Section through trunk cuticle showing branching canals passing right through cuticle and opening onto surface through pores located beside epicuticular elevations. These elevations give homalorhagid cuticle a characteristic texture resembling that of a wood rasp.

This figure illustrates structures shown in Plates 47-49.



21. 1µm

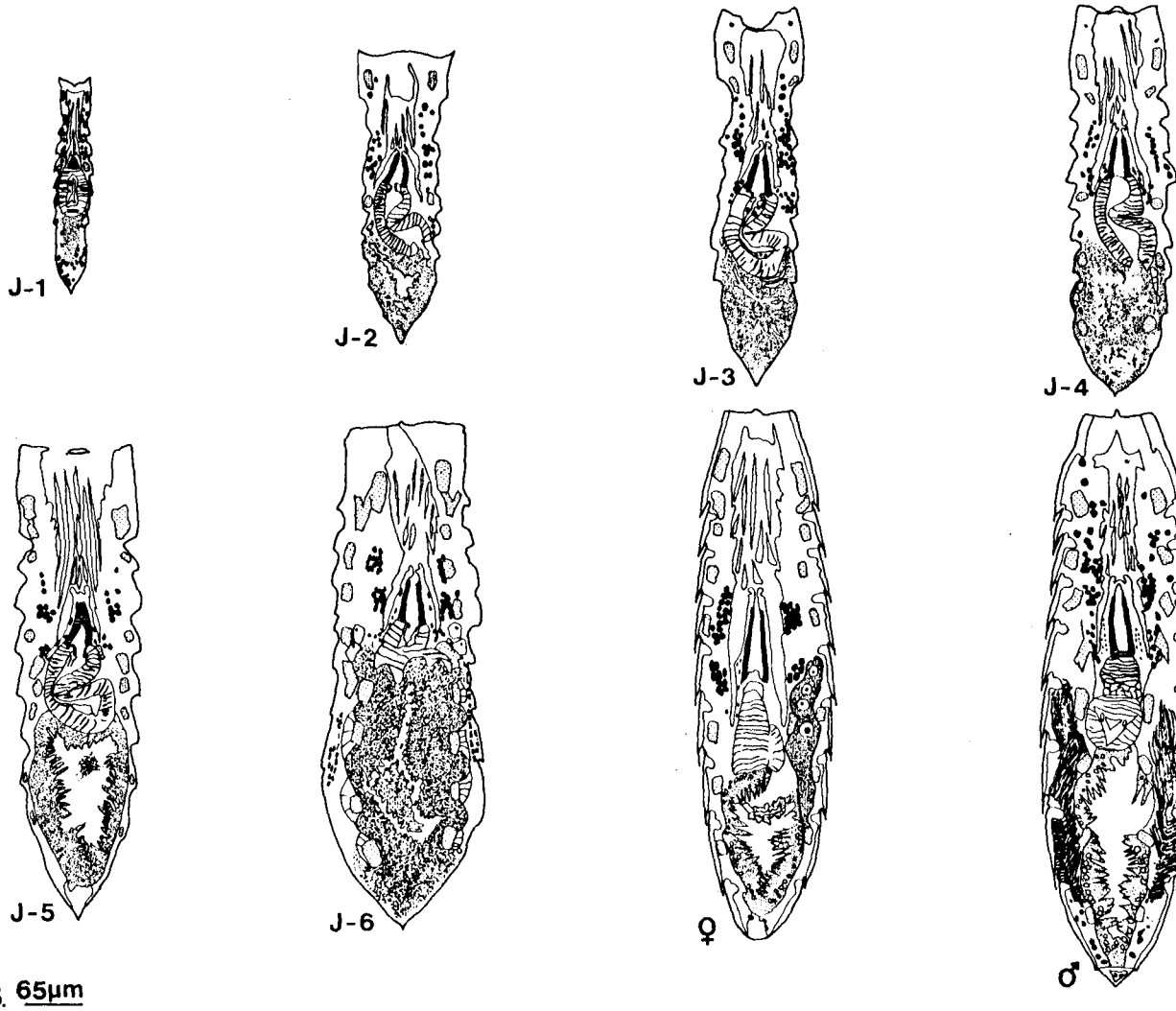
Figure 22. Section through seta pore in trunk cuticle showing striated rootlet and shaft of a cilium embedded in a mucous cell (cf. Plate 60).



22.

0·7µm

Figure 23. Specimens of each juvenile stage, plus a male and a female Kinorhynchus phyllotropis sectioned through the frontal plane. These sections show that every juvenile stage of this species has a head and viscera. These sections also show that development is direct. Differentiation of internal structures procedes throughout juvenile life.



23. 65µm

Figure 24. Specimens of each juvenile stage of Kinorhynchus phyllotropis showing changes in the relationship of the posterior mid-dorsal spine to the terminal margin during growth.

J-1 acutely pointed mid-dorsal spine projects over posterior margin of terminal segment

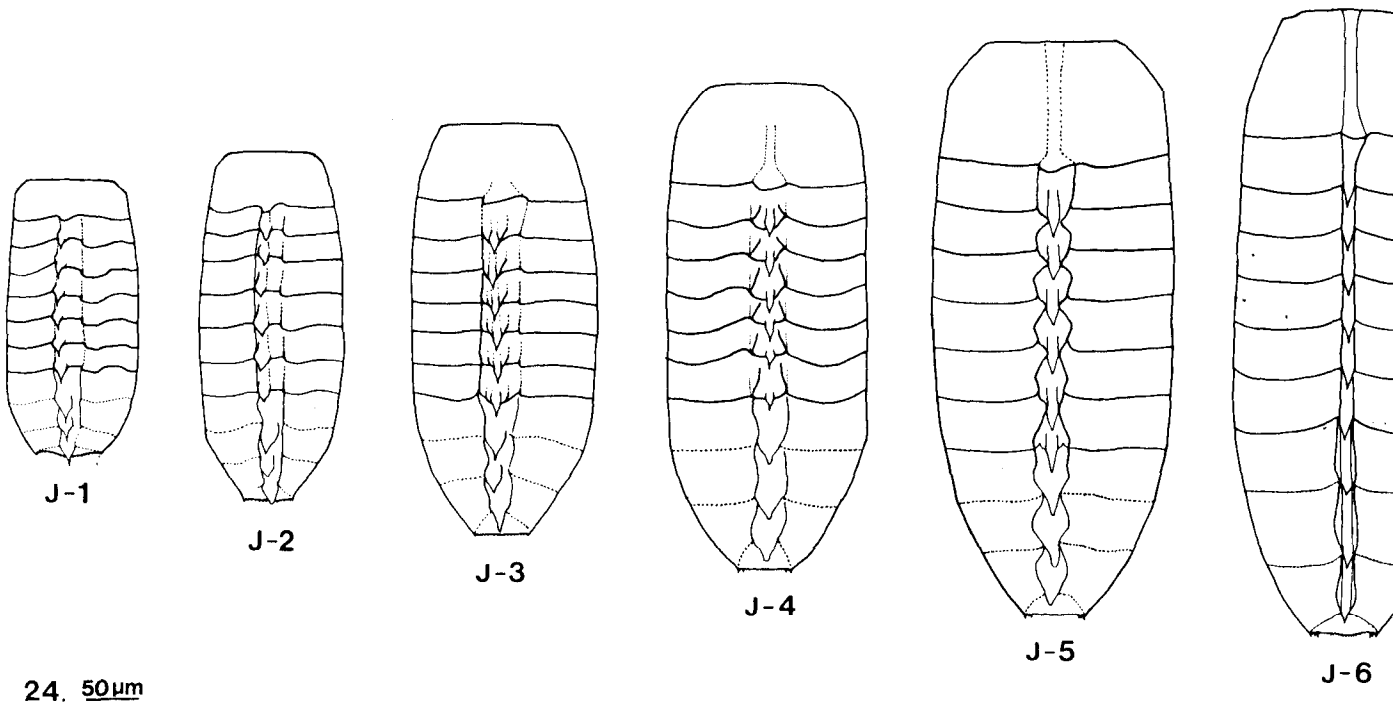
J-2 blunt mid-dorsal spine projects over posterior margin of terminal segment

J-3 blunt mid-dorsal spine projects as far as posterior margin of terminal segment

J-4 one very small spinose process medial to the lateral spine of the twelfth segment (cf. Plate 70)

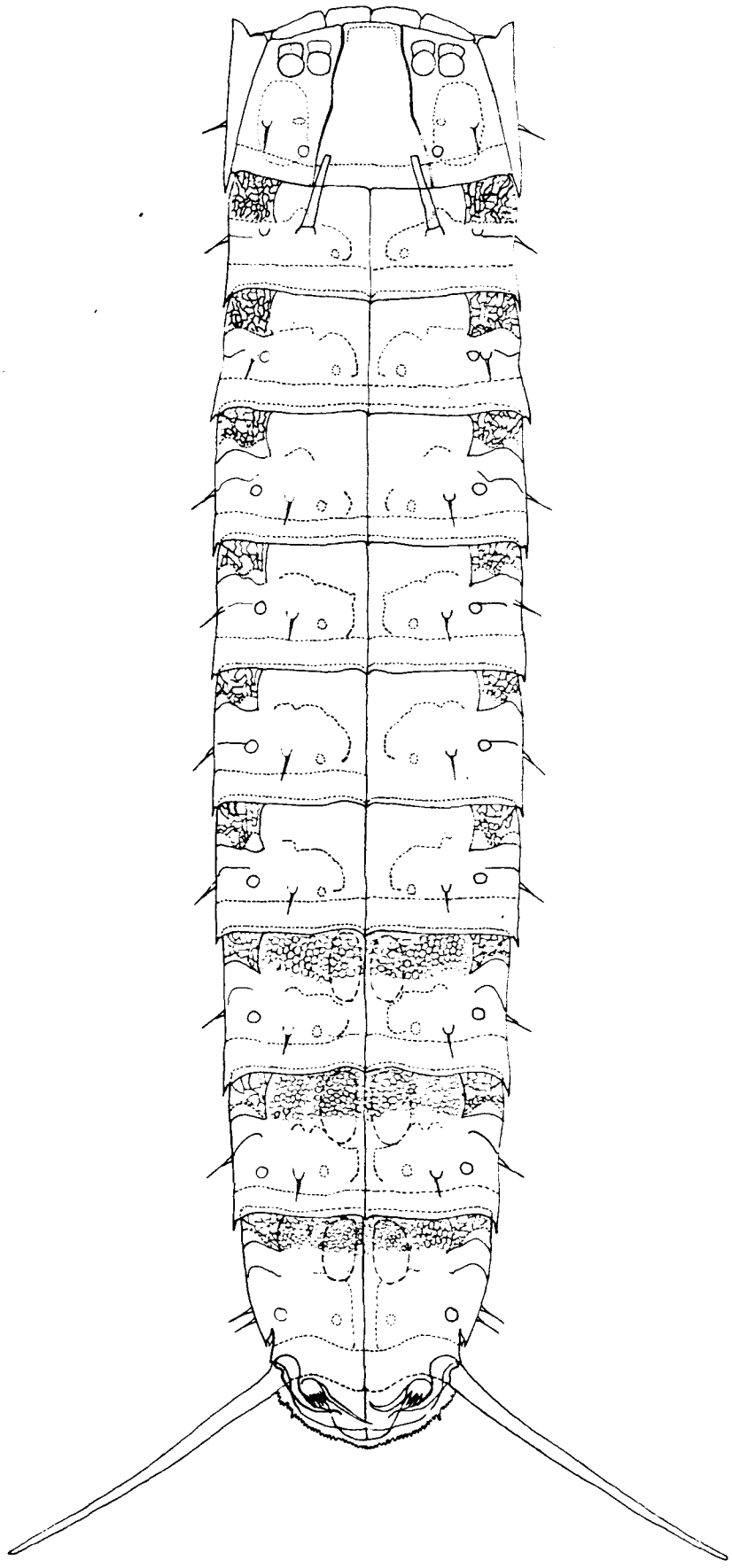
J-5 two very small spines medial to the lateral spine of the twelfth segment (cf. Plates 66, 71) and posterior mid-dorsal spine inserted into a flexible mid-dorsal fold of thin cuticle which is wider than the spine (cf. Plate 66)

J-6 two very small spines medial to the lateral spine of the twelfth segment (cf. Plates 67, 71) and posterior mid-dorsal spine inserted into an inflexible mid-dorsal ridge or thick cuticle which is narrower than the spine (cf. Plate 72).



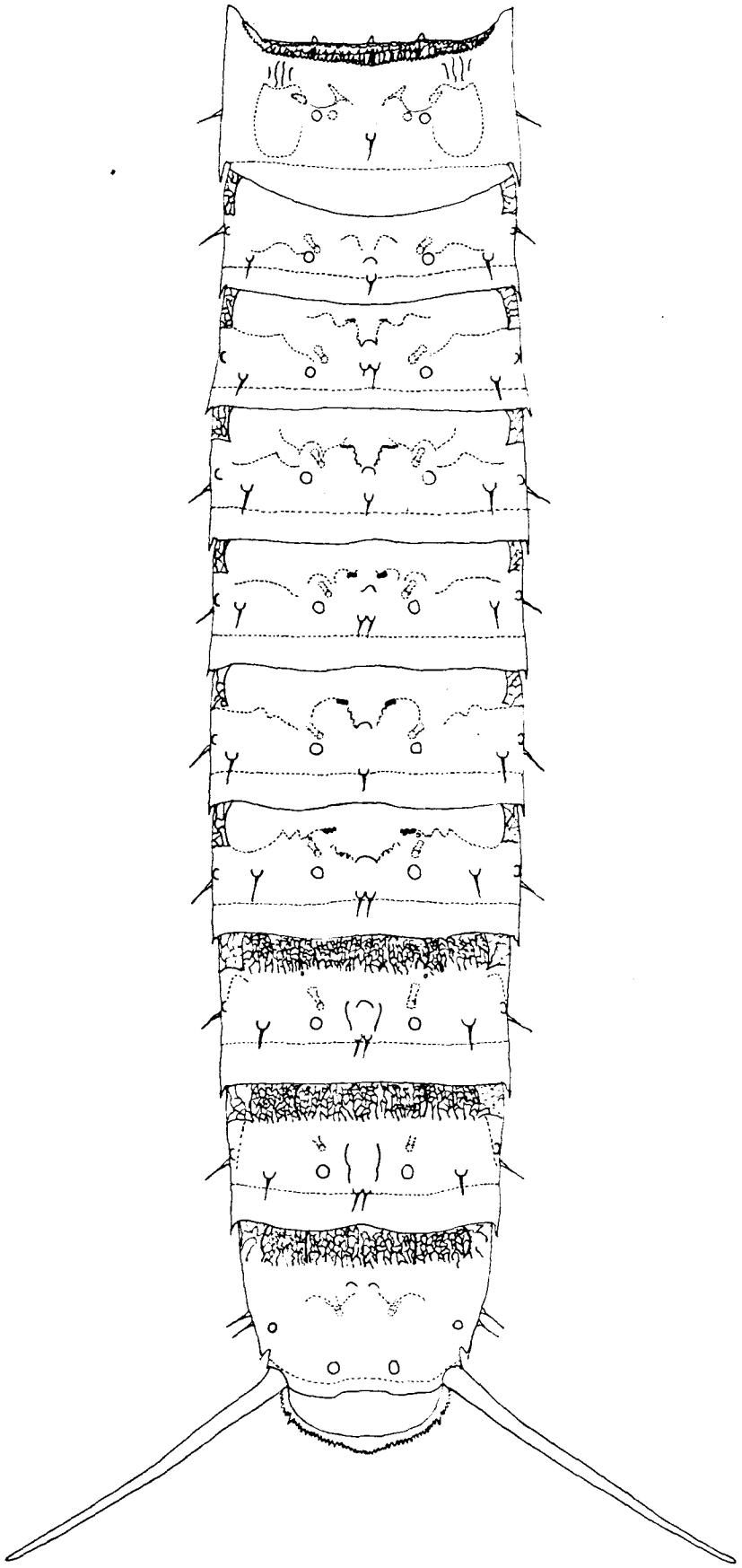
24. 50μm

Figure 25.
Pycnophyes faveolus sp.n., male - neck and trunk segments, ventral view.



25. 40µm

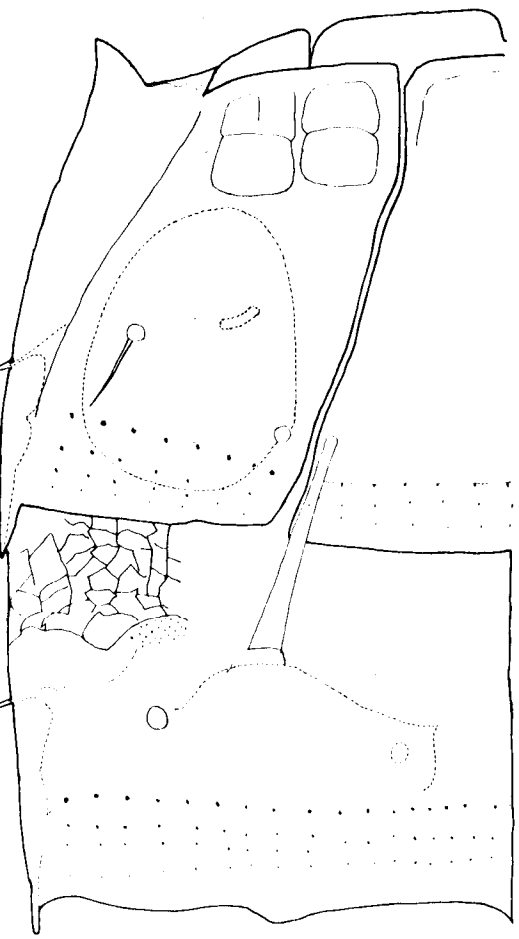
Figure 26.
Pycnophyes faveolus sp.n., male - neck and trunk segments, dorsal view.



26. 40 µm

Figure 27.
Pycnophyes faveolus sp.n., segments 3-4, ventral view, lateral half, male.

Figure 28. Same, dorsal view.



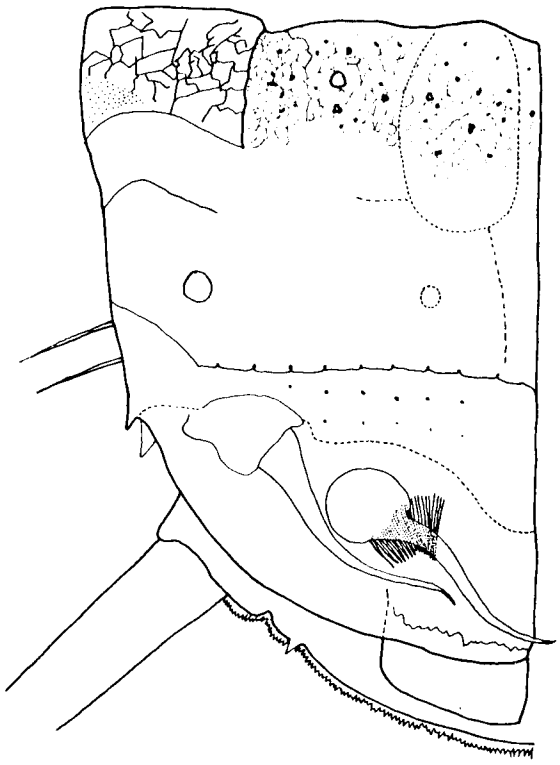
27.

28.

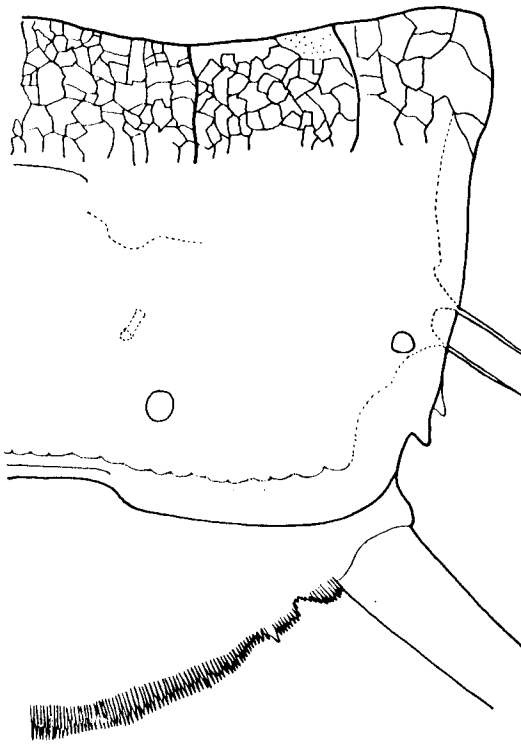
10 µm

Figure 29.
Pycnophyes faveolus sp.n., segments 12-13, ventral view, lateral half, male.

Figure 30. Same, dorsal view.



29.

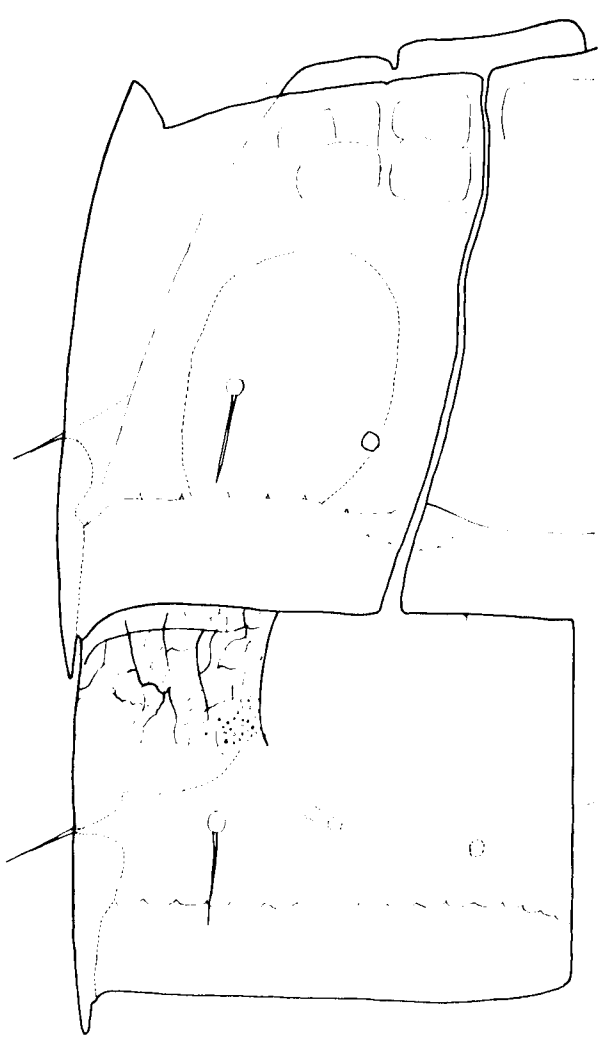


30.

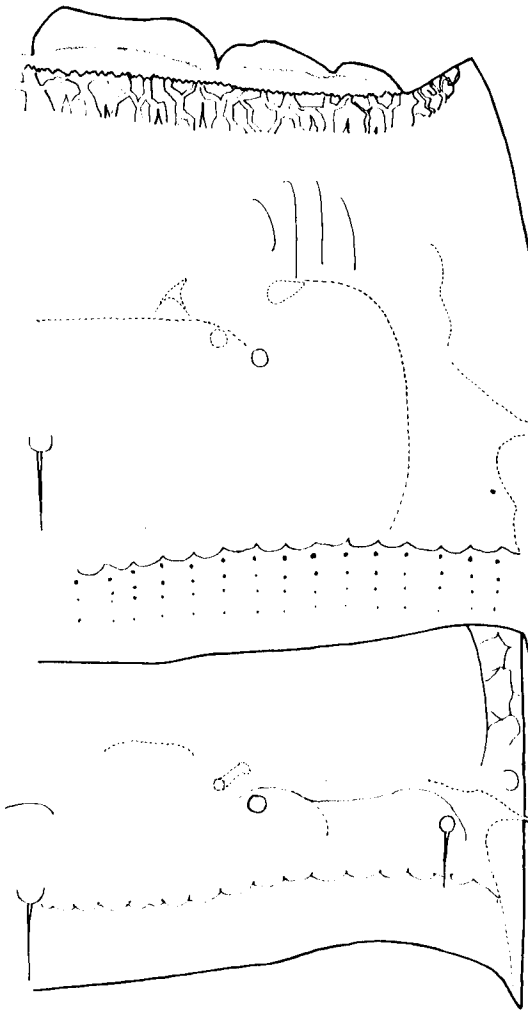
10 µm

Figure 31.
Pycnophyes faveolus sp.n., segments 3-4, ventral view, lateral half, female.

Figure 32. Same, dorsal view.



31.

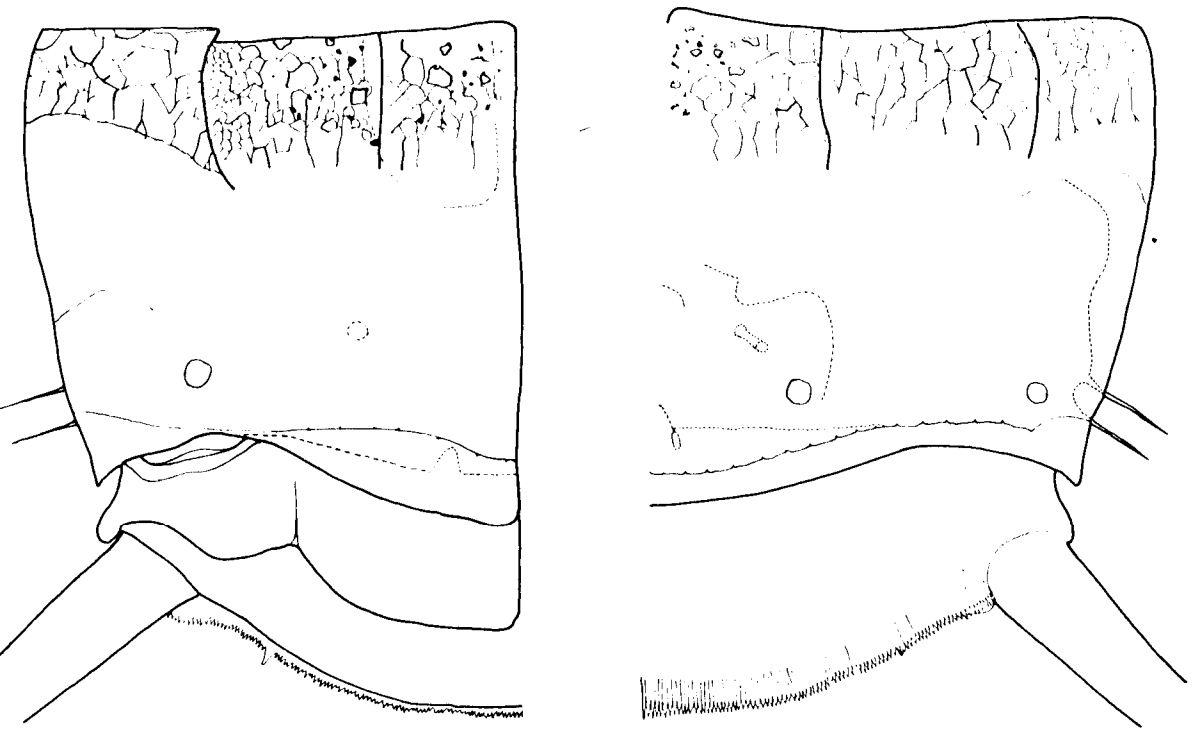


32.

10 µm

Figure 33.
Pycnophyes faveolus sp.n., segments 12-13, ventral view, lateral half, female.

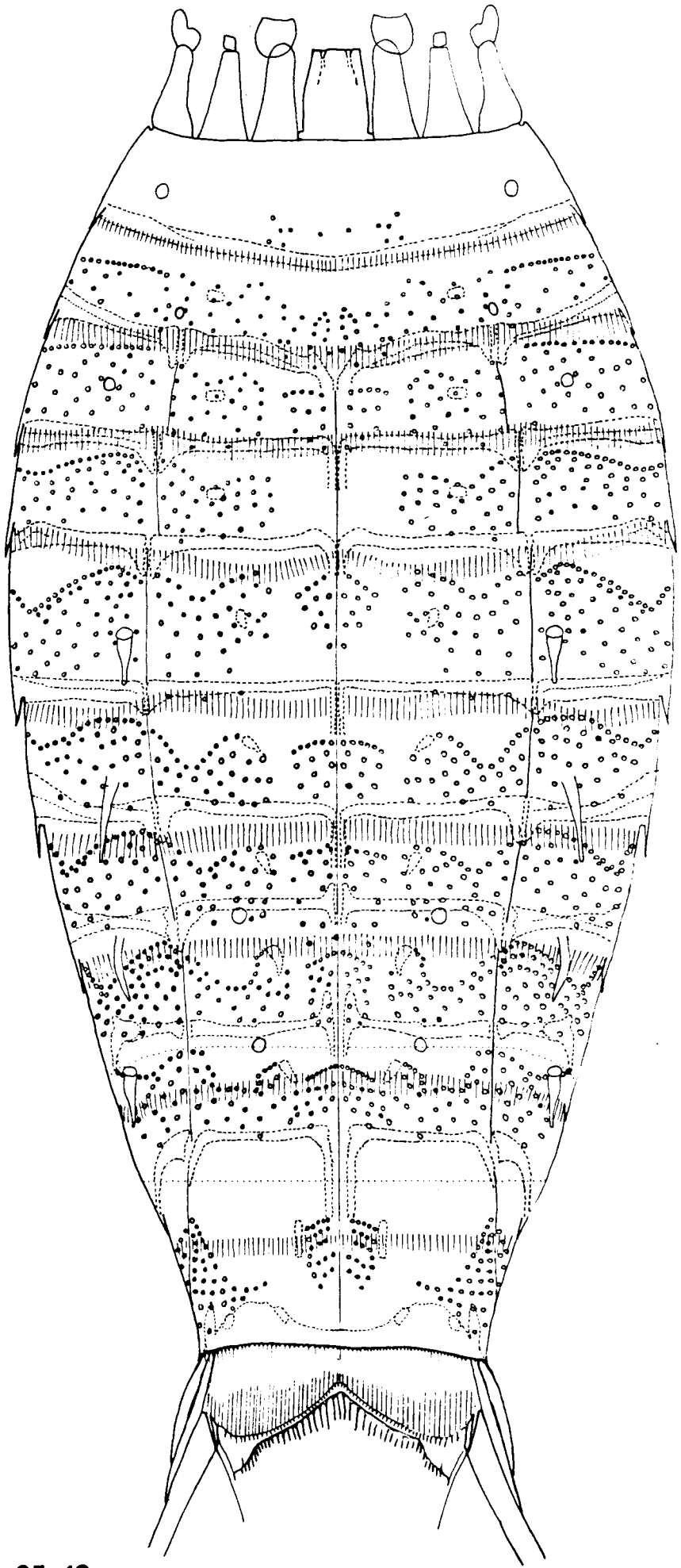
Figure 34. Same, dorsal view.



34.

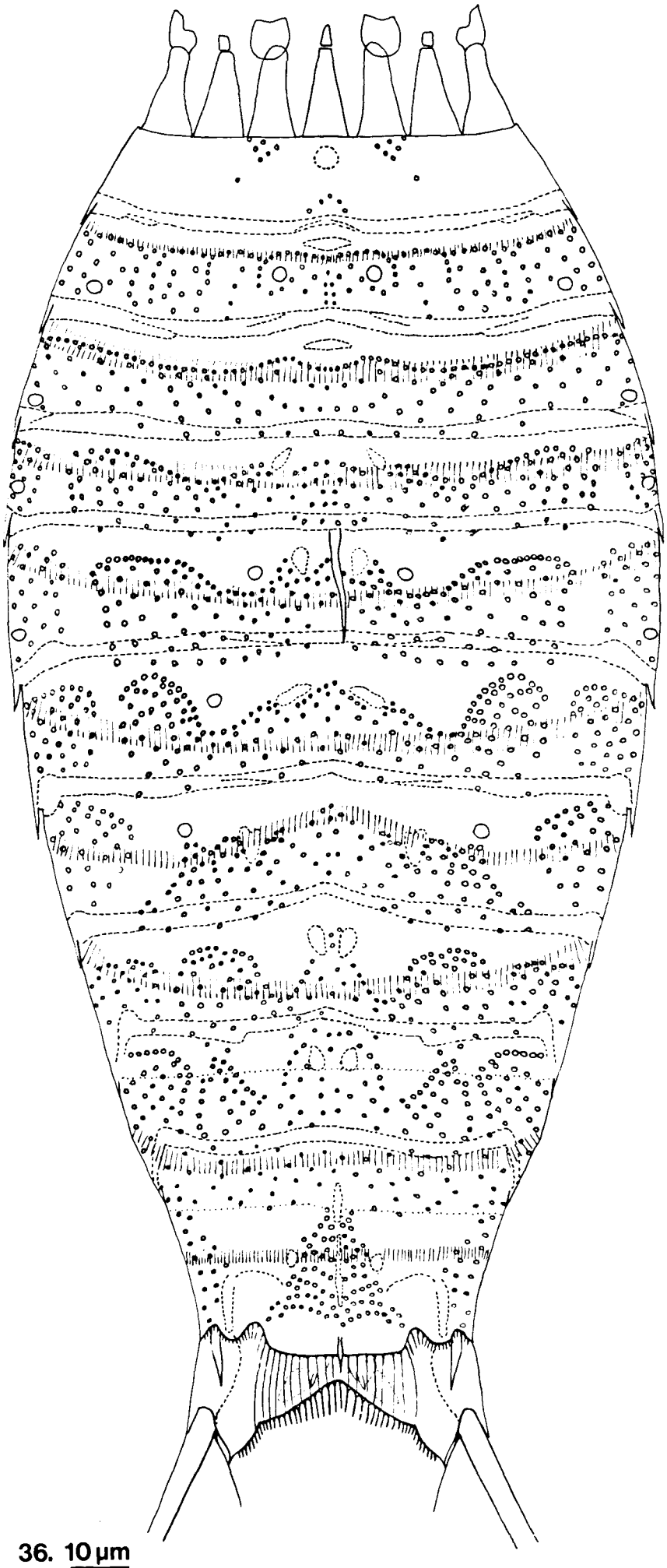
10 µm

Figure 35.
Echinoderes teretis sp.n., male - neck and trunk segments, ventral view.



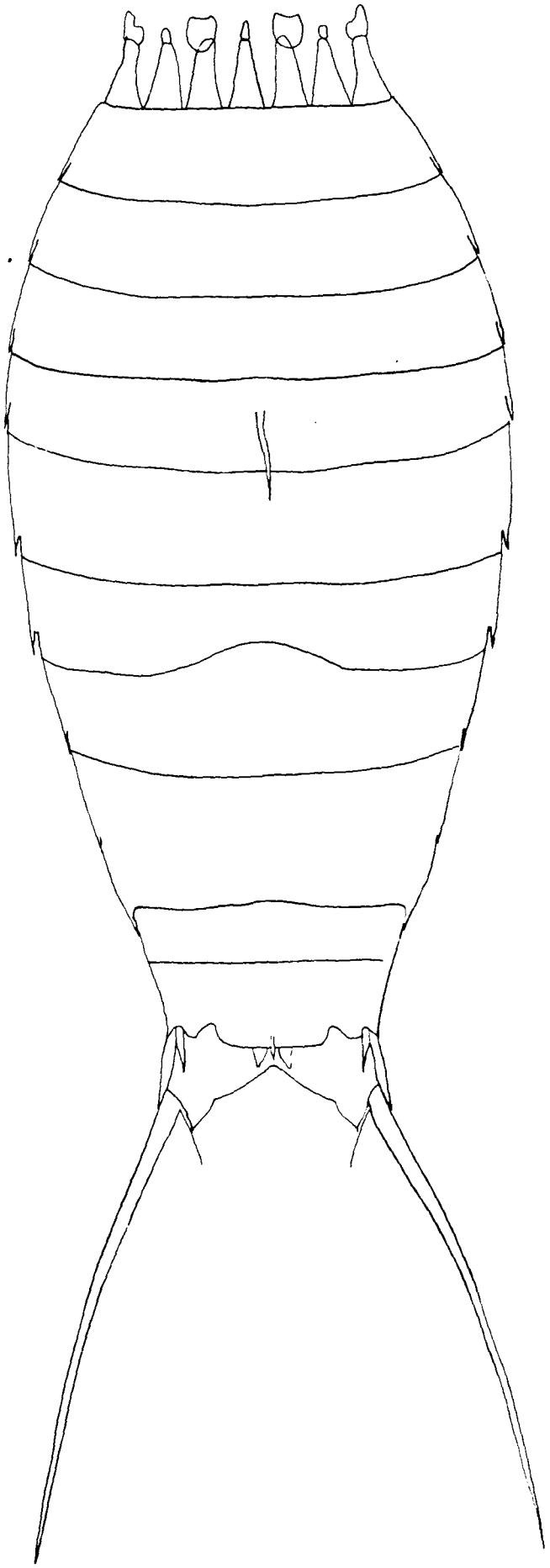
35. 10 µm

Figure 36.
Echinoderes teretis sp.n., male - neck and trunk segments, dorsal view.



36. 10 µm

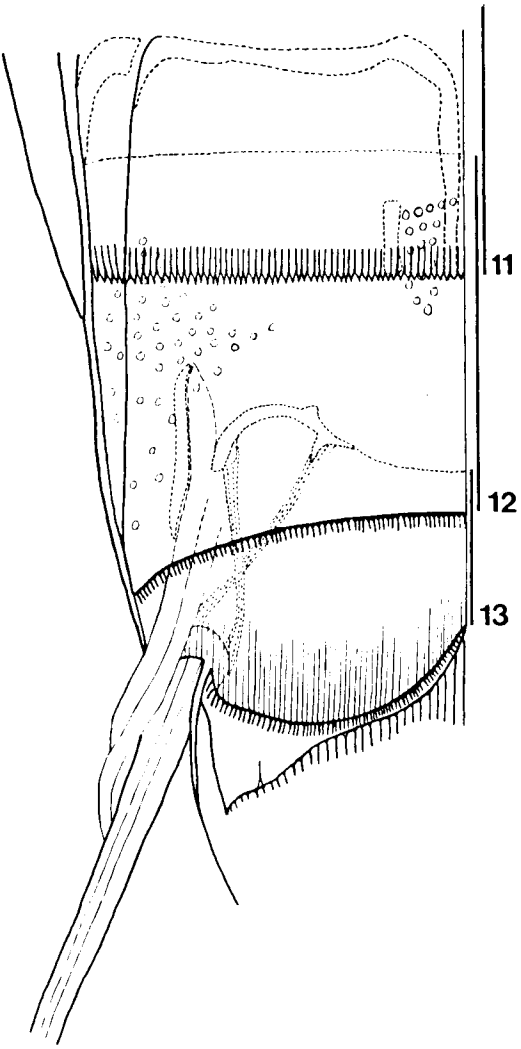
Figure 37.
Echinoderes teretis sp.n., male - neck and trunk segments, dorsal and terminal spines.



37. 14 µm

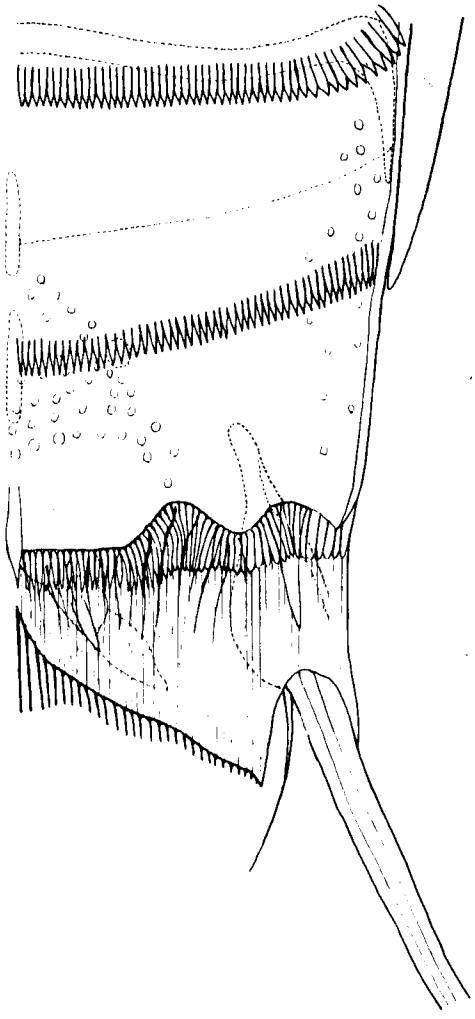
Figure 38.
Echinoderes teretis sp.n., segments 12-13,
ventral view, lateral half, male.

Figure 39. Same, dorsal view.



38.

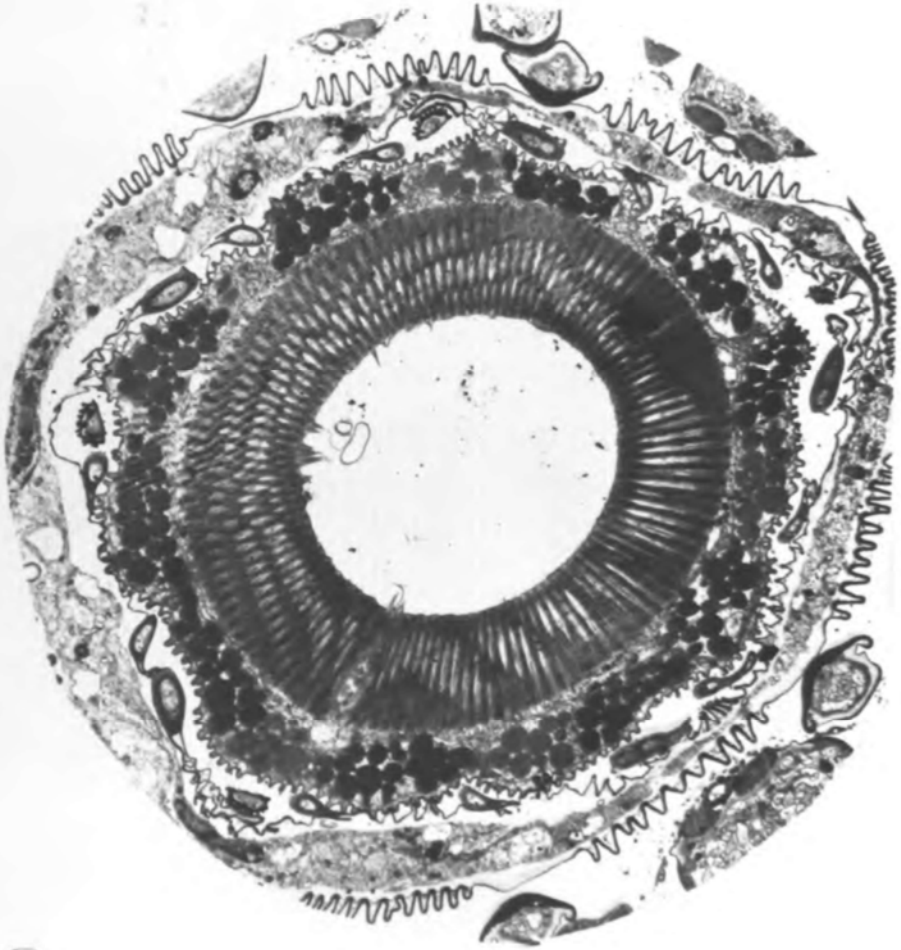
5µm



39.

PLATE 1. ORAL CONE

Transverse section of the oral cone of Kinorhynchus phyllotropis showing the lumen of the pharynx (centre) surrounded by radially arranged units of the pharynx crown and granules of pharynx crown tissue. The oral cone encircles pharynx crown tissue. Outside the oral cone there are oral scalids and ring 1 spinoscalids. Inside the oral cone are seen sections of the internal scalids described in this study. Transmission electron microscope study of specimen Male 1.



1

5μm

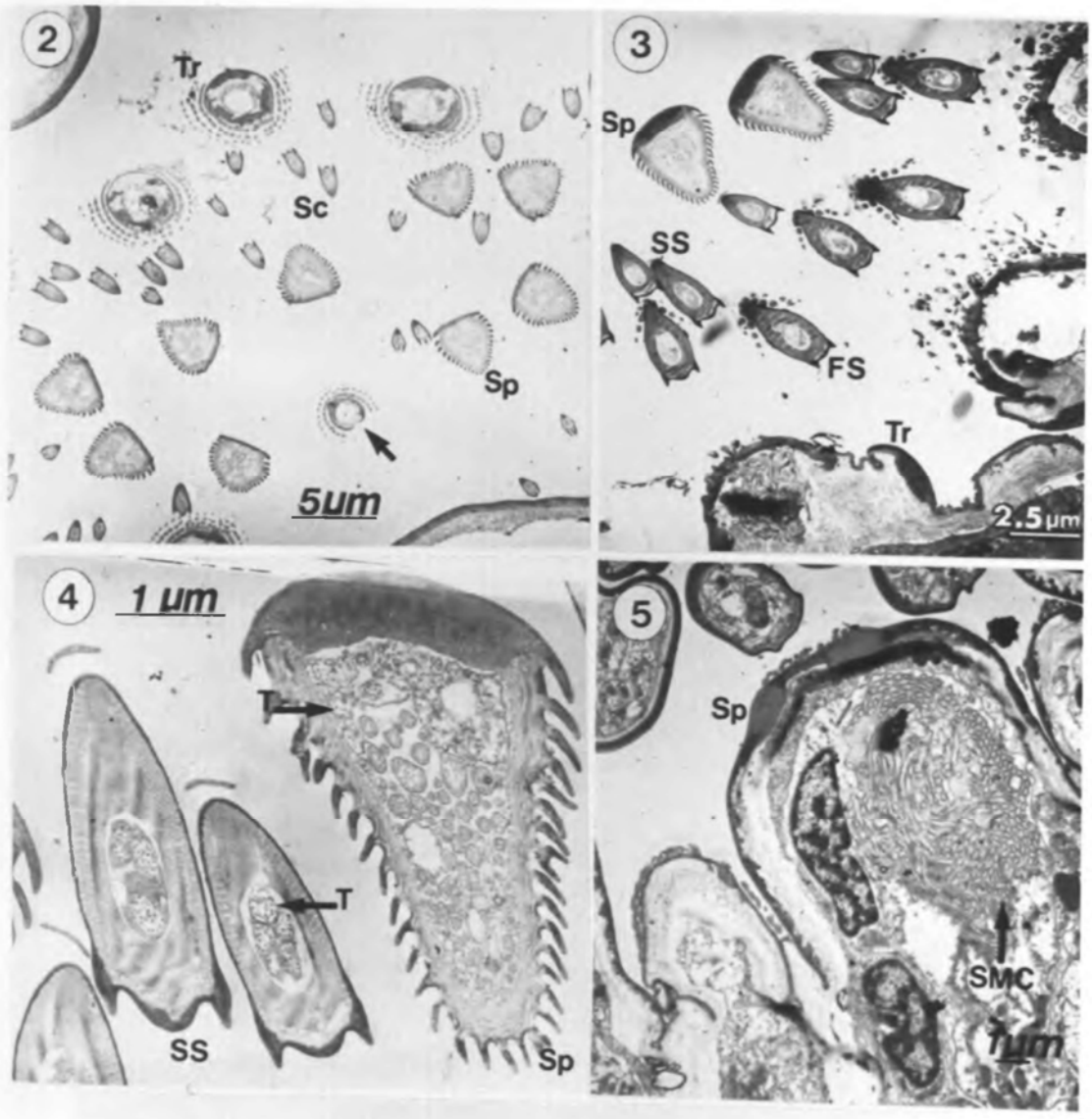
PLATE 2. SPINOSCALIDS, SCALIDS AND TRICHOSCALIDS
Transverse section of the retracted introvert cut at the level of scalid tips. Transmission electron microscope study of specimen J-5:1.
KEY
Sp - Ring 1 spinoscalid sectioned through endpiece
Sc - Scalids of rings 2-6
Tr - Trichoscalids covered with cuticular hairs
arrow - Small midventral trichoscalid

PLATE 3. SPINOSCALIDS, SMOOTH SCALIDS, FRINGED SCALIDS AND TRICHOSCALIDS
Transverse section of the retracted introvert cut at the level of trichoscalid insertion onto head cuticle. Transmission electron microscope study of specimen J-6:1.
KEY
Sp - Ring 1 spinoscalid
SS - Ring 2-4 smooth scalid
FS - Ring 5-6 fringed scalid
Tr - Ring 7 trichoscalid

PLATE 4. CILIA TUBULES IN SCALIDS AND SPINOSCALIDS
Transverse section of the endpieces of ring 2-4 smooth scalids and a ring 1 spinoscalid showing bundles of tubules in ciliated receptor cells. The spinosocalid (right) shows type II striations in the cuticle and electron-dense strips running the length of the endpiece, both characteristics of a type II scalid. Two smooth scalids (centre and left) show type I striations in the cuticle. The flat hair sectioned at the apex of the triangular scalid section is one of the V-shaped band of hairs seen on the otherwise hairless endpiece of the smooth scalid. Transmission electron micrograph of specimen Male 3.
KEY
Sp - Ring 1 spinoscalid endpiece
SS - Ring 2-4 smooth scalid endpiece
T - Tubules of ciliated receptor cell

PLATE 5. SUBMICROVILLAR CISTERNAE IN THE INSERTION OF A RING 1 SPINOSCALID
Transverse section of submicrovillar cisternae, light sensitive organelles, in the socket insertion of a ring 1 spinoscalid. The central vacuole or phaosome is not seen in this plate. Transmission electron micrograph of specimen J-5:1.
KEY
Sp - Ring 1 spinoscalid socket insertion
SMC - Submicrovillar cisternae

PLATE 6. OPENING IN THE TIP OF A TRICHOSCALID
Longitudinal section through the tip of a trichoscalid showing the opening of the groove from which sensory cilia project. Transmission electron micrograph of specimen Male 2.
KEY
G - Open-ended groove containing sensory cilia


2
Tr
Sc
Sp
5um
3
Sp
SS
FS
Tr
2.5 µm
4
1 µm
T
T
SS
Sp
5
Sp
SMC
1µm

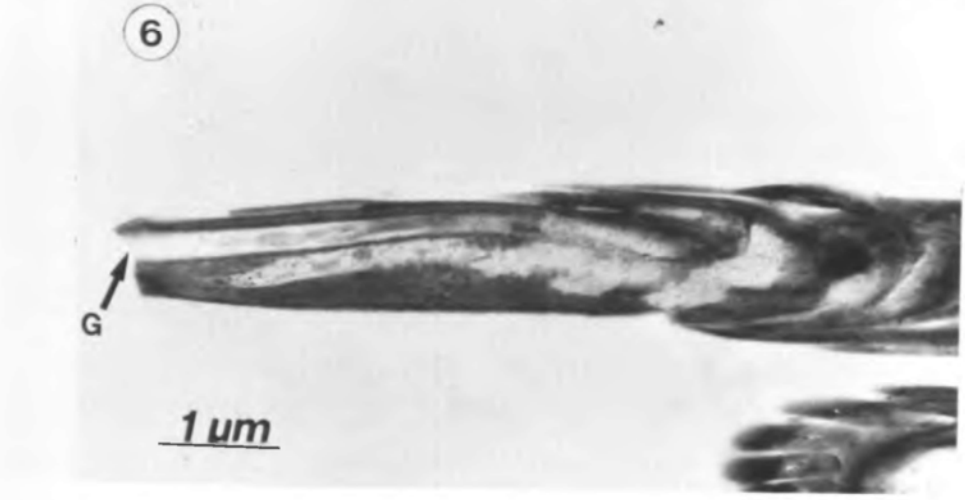
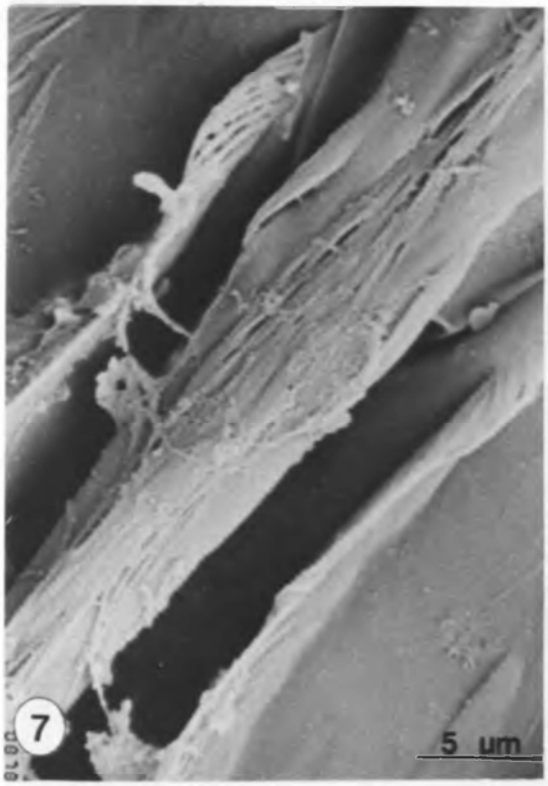

6
G
1 µm

PLATE 7. RING 1 SPINOSCALID SOCKET AND ENDPIECE
Socket (top right) and endpiece (bottom left) of a ring 1 spinoscalid. Two flaps formed of fused hairs mark the indistinct joint of the spinoscalid. A hair-covered spine is recessed into the outer surface of the spinoscalid. Scanning electron micrograph of adult.

PLATE 8. SMOOTH SCALIDS
Three smooth scalids of the type found in rings 2-4. The socket of each scalid bears a line of hairs, the characteristically distinct joint is covered by a fringe of hairs and a V-shaped chevron of hairs is seen on the smooth endpiece. Scanning electron micrograph of adult.

PLATE 9. FRINGED SCALIDS (AND OTHERS)
Two fringed scalids of the type found in rings 5-6, (diagonal centre and bottom left), covered by the endpieces of two ring 1 spinoscalids and a smooth scalid. Scanning electron micrograph of J-4 specimen.

PLATE 10. TRICHOSCALIDS
Two ring 7 trichoscalids borne on scales with recurved margins. Scale cuticle has punctate endocuticular elaborations (spotty lobes) seen in sections of trichoscalids. Scanning electron micrograph of adult.


7
5 um

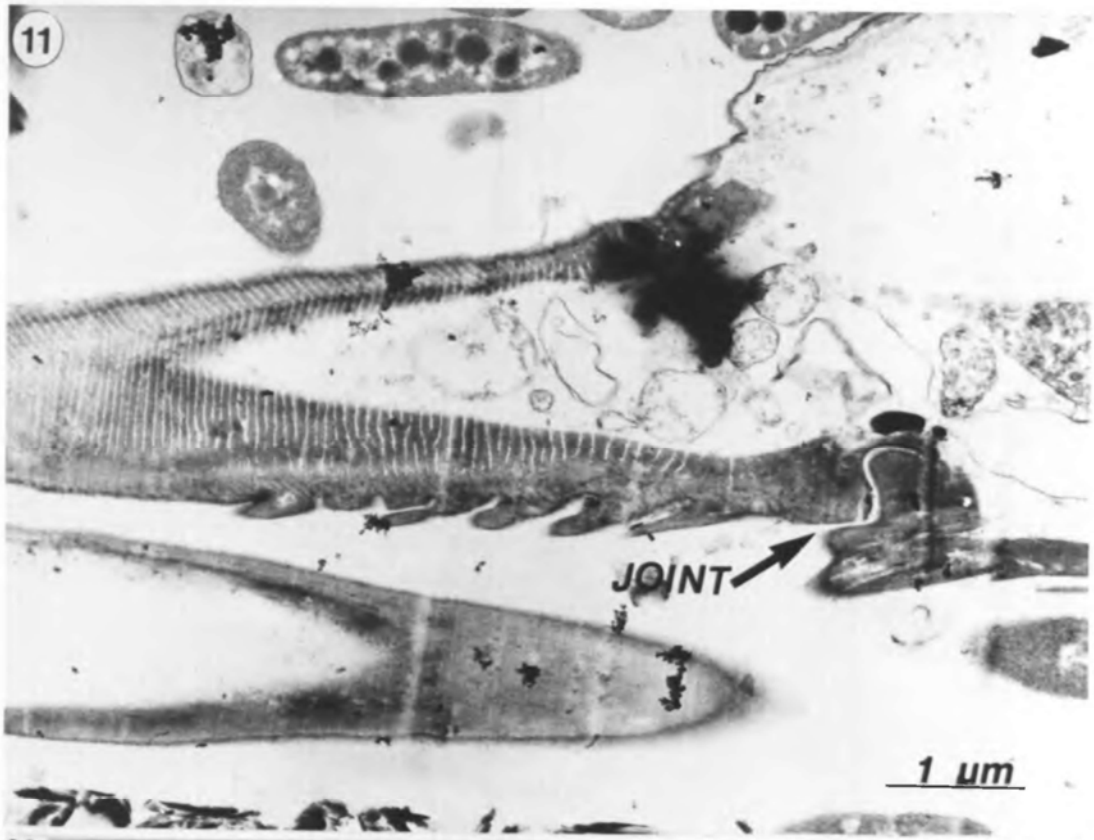

8
5 µm


9
5 um


10
5 µm

PLATE 11. JUVENILE SCALID CUTICLE
Longitudinal section of unstriated cuticle of J-1 spinoscalid and striated cuticle of J-1 scalid. The robust joint is characteristic of the type I scalid. Transmission electron micrograph of a J-1 specimen.

PLATE 12. JUVENILE SCALID MORPHOLOGY
A J-3 fringed scalid showing the robust joint clearly. Below the fringed scalid there is a smooth scalid showing a V-shaped chevron of flat hairs on the endpiece. At the bottom of the plate there is the warped endpiece of a ring 1 spinoscalid with thin cuticle which would lack striations. Scanning electron micrograph of a J-3 specimen.


11
JOINT
1 µm

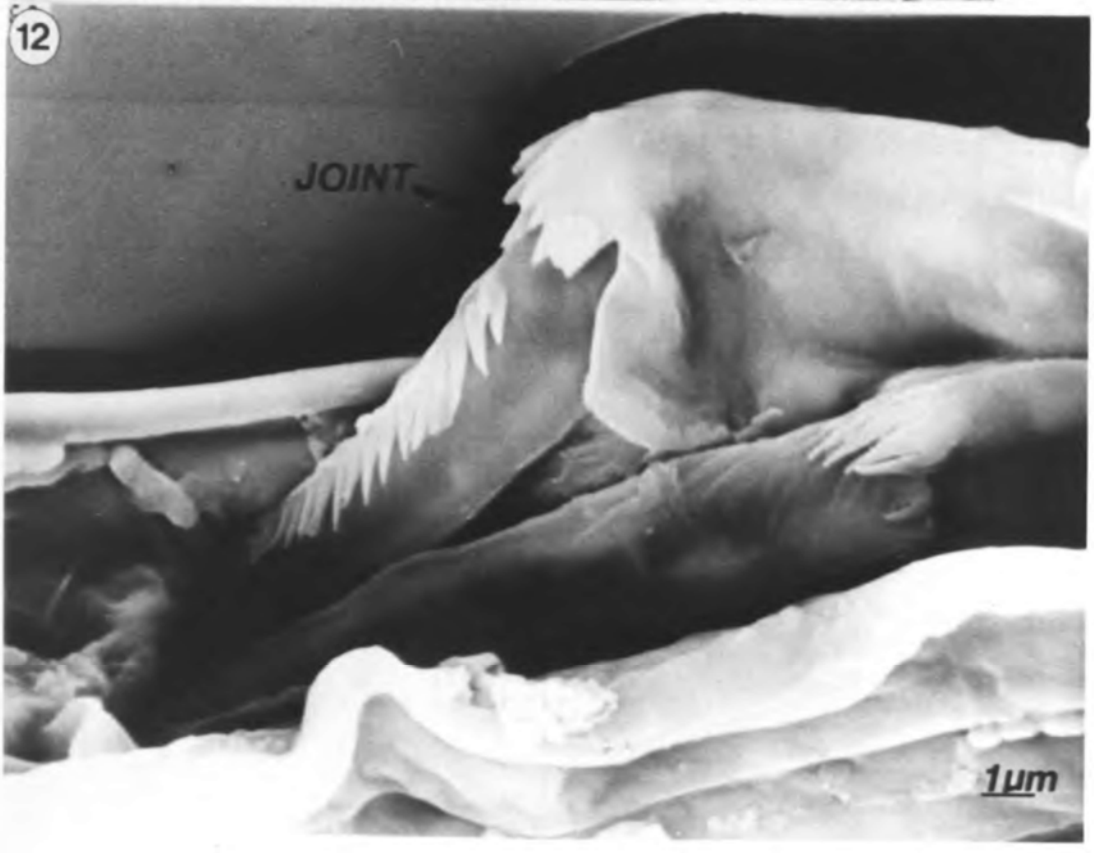

12
JOINT
1µm

PLATE 13. NERVE CELLS IN A SPINOSCALID AND AN ORAL SCALID

Transverse section of the retracted oral cone (left) and external scalids (right) showing a spinoscalid sectioned near its insertion onto the head cuticle. Oral scalids have been sectioned at the level of insertion onto the oral cone. Between the oral scalids are scrolled edges ("ram's horns") of interbasal strips (cf. Plate 23). Each nerve cell contains a microfilament. (Nerve cells have been identified by their close resemblance to cells of the midventral nerve cord.) Transmission electron micrograph of specimen Male 2.

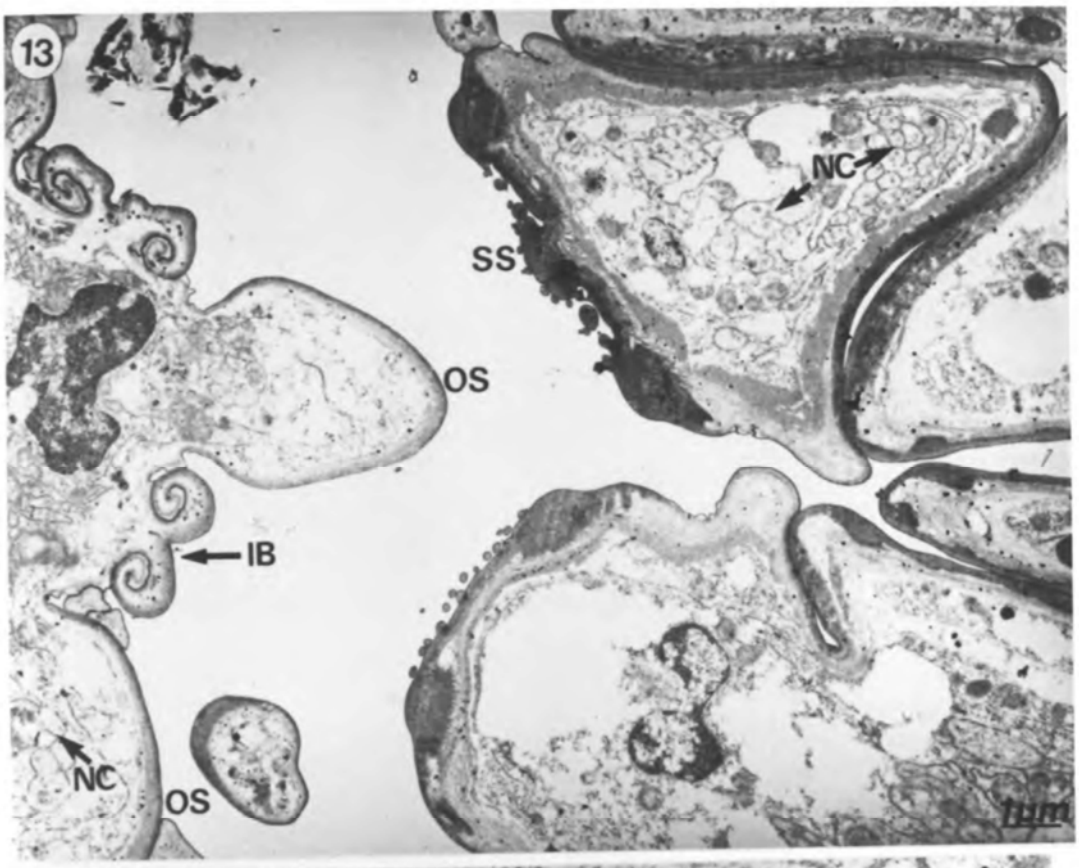
KEY

IB - Interbasal strip with scrolled edges between oral scalid bases
NC - Nerve cells inside scalid, each containing microfilament
OS - Oral scalid inserted onto oral cone
SS - Spinoscalid socket cut anterior to insertion of spine

PLATE 14. MEMBRANE CELLS IN A SCALID SOCKET

Transverse section of a scalid socket showing membrane cells originally described in the type I scalid of K. giganteus. These do not have piles of thick and thin membranes as seen in the scalids of K. giganteus and the trichoscalids of K. phyllotropis (Plates 26, 53). The membrane systems of K. phyllotropis ring 2-6 scalids can not be distinguished from mitochondria. Transmission electron micrograph of Female 1.

MC - Membrane or mitochondrial cell.


13
NC
SS
OS
IB
NC
OS
1um

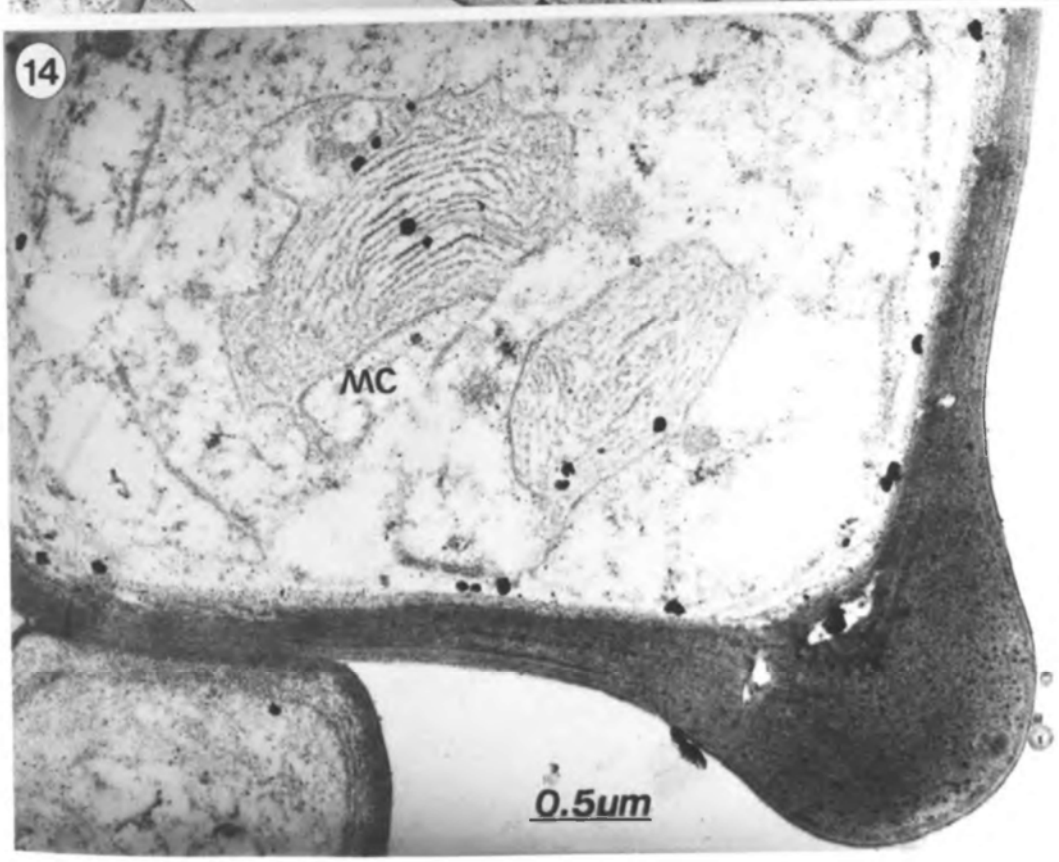

14
MC
0.5um

PLATE 15. CILIA TUBULES IN SCALID TIPS
Transverse sections of three scalid tips showing bundles of tubules from sensory cilia, surrounded by a bracket-like organelle. In this scalid the apex of the triangular section points away from the head cuticle. Transmission electron micrograph of J-6 specimen.

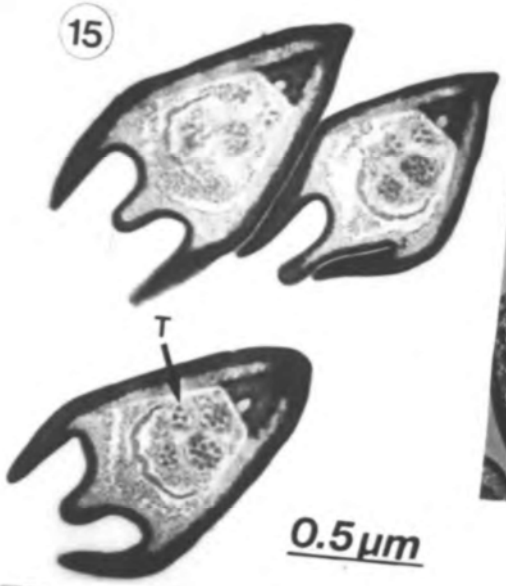
KEY
T- Tubules of sensory cilia embedded in cells running along the scalid endpiece. The tubules project from the open extremity of the scalid.

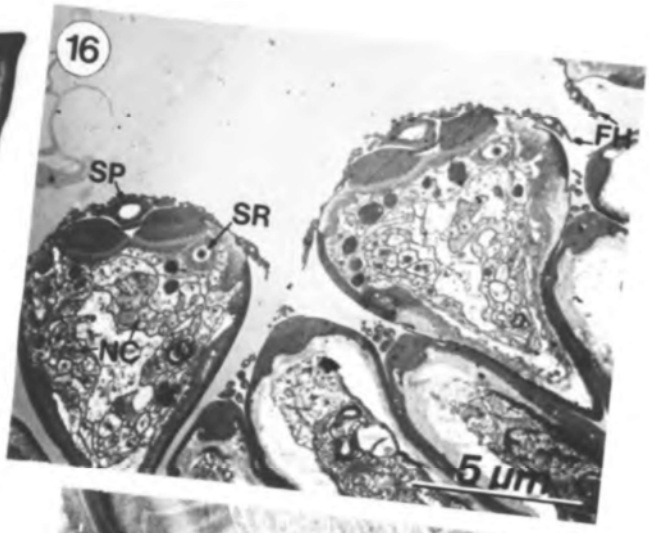
PLATE 16. STRIATED ROOTLETS OF CILIA IN SPINOSCALID SOCKETS
Transverse section of the sockets of two ring 1 spinoscalids cut near spinoscalid origins. Sections show how the apex of the triangular section lies against the head cuticle. The base of the triangular section shows the oval sections of ridges of thick cuticle with a hollow, hair-covered spine recessed between them. Outside each ridge there is a flap of 3-4 fused hairs. Underneath one ridge of each scalid there is the striated rootlet of a cilium, sectioned transversely. The socket contains nerve cells, each containing a microfilament. Transmission electron micrograph of specimen J-6:1.

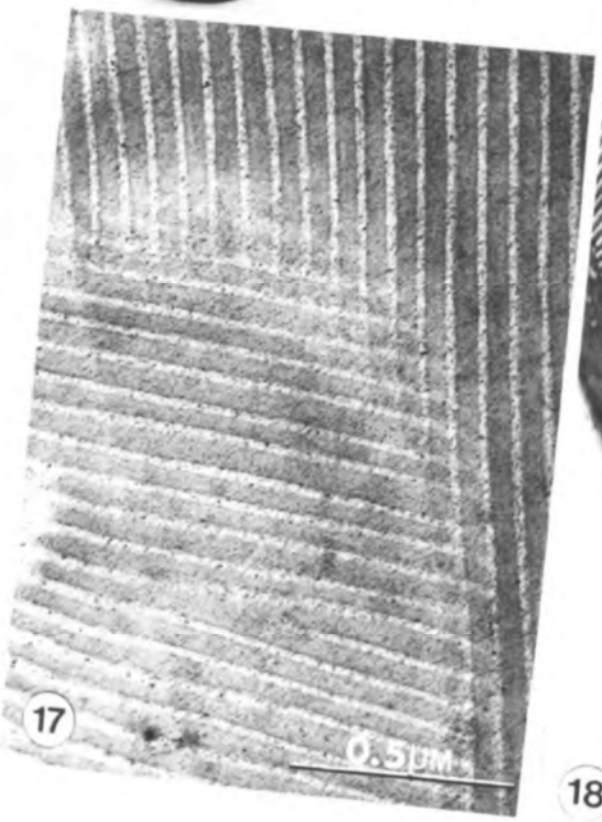
KEY
FH - Fused hairs forming flap at side of socket
NC - Nerve cells each containing microfilament
SP - Hollow recessed spine of spinoscalid
SR - Striated rootlet of cilium

PLATE 17. TYPE I CUTICLE FOUND IN SCALID ENDPIECES
Tangential section of scalid endpiece cuticle showing two layers of striations set at 75o angles to each other. Transmission electron micrograph of specimen Female 1.

PLATE 18. TYPE II AND TYPE I CUTICLE
Longitudinal section of ring 1 spinoscalid endpiece cuticle - type II cuticle.
Longitudinal section ring 2-6 scalid endpiece cuticle - type I cuticle. U-shaped units as described in K. giganteus are seen in the type II cuticle on the right side. Transmission electron micrograph of specimen Female 1.


15
T
0.5µm


16
SP
SR
Ne
FH
5 µm


17
0.5µm

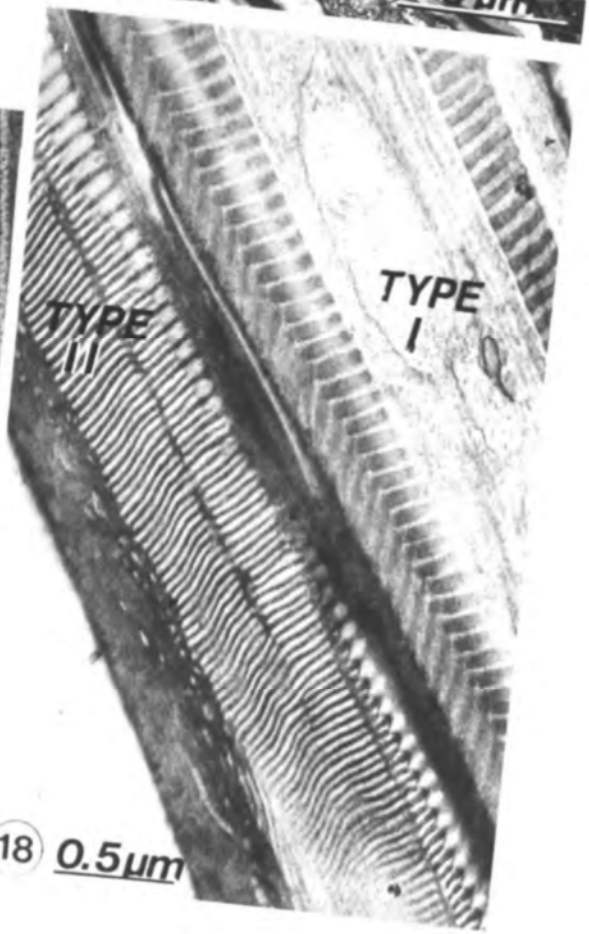

TYPE II
TYPE I
18 0.5µm

PLATE 19. ADULT EXTERNAL SCALID ARRANGEMENT
An everted adult head showing scalid arrangement (cf. Figs. 6-9, 1.1-4).
Scanning electron micrograph of adult.

KEY
OS - Odd sector, contains three scalids in series down centre of sector
ES - Even sector, contains two scalids in series down centre of sector
1-7 - Numbers of scalid rings

PLATE 20. J-2 EXTERNAL SCALID ARRANGEMENT
An everted J-2 head showing scalid arrangement (cf. Figs. 8-9, 2.6-10).
Scanning electron micrograph of J-2 specimen.

KEY
P - Proscalid
1-7 Numbers of scalid rings

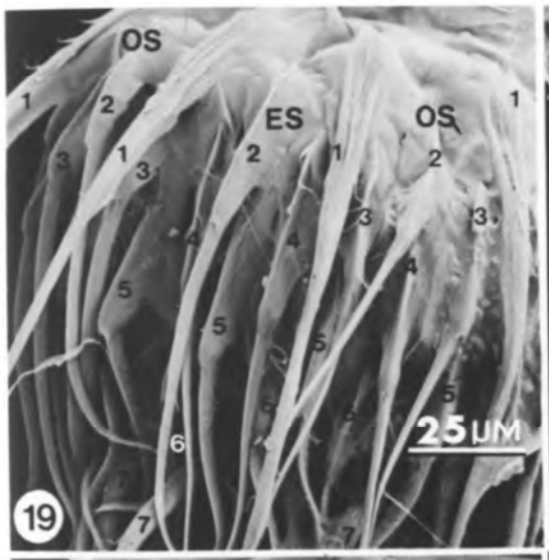
PLATE 21. SOCKET MORPHOLOGY OF ADULT RING 1 SPINOSCALID
Enlarged view of plate 20 specimen showing features of socket (cf. Plates 7, 16).

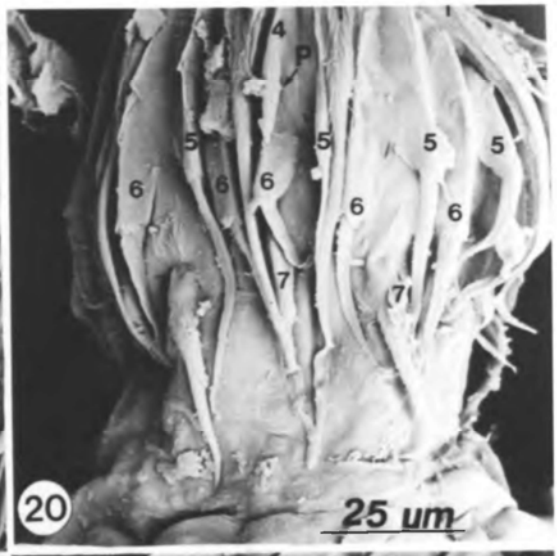
PLATE 22. J-3 EXTERNAL SCALID ARRANGEMENT
An everted J-3 head showing scalid arrangement (cf. Figs. 8-9, 2.11-15).
Scanning electron micrograph of J-3 specimen.

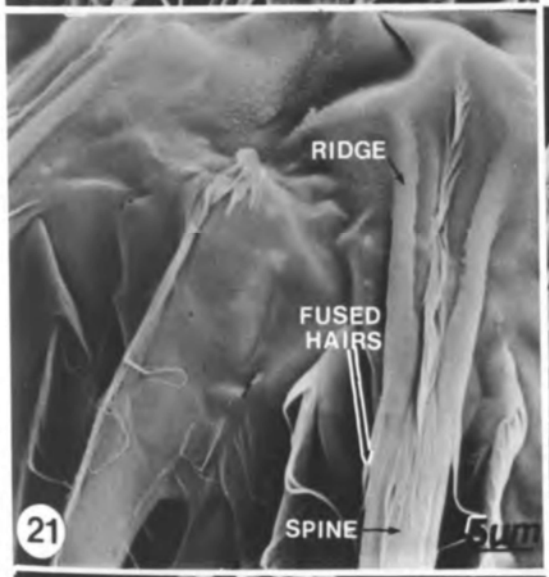
KEY
P - Proscalid found in even sectors.

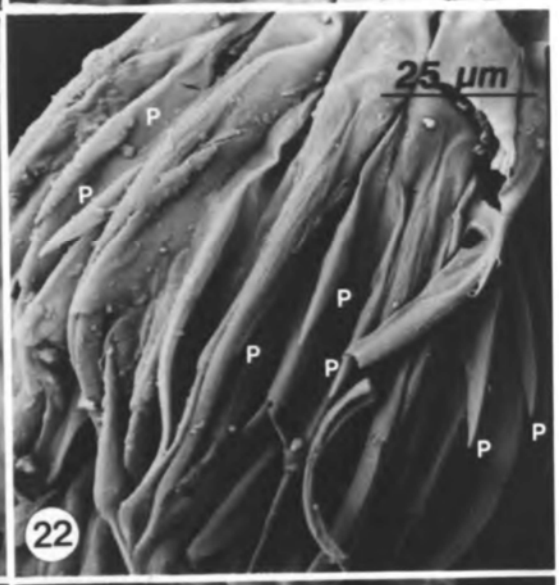
PLATE 23. EXTERNAL FEATURES OF ADULT ORAL CONE
Extruded oral cone (cf. Plate 13, Fig. 12) showing oral scalids (top of micrograph), spine on socket of each alternate oral scalid, interbasal strip with scrolled edges between oral scalid bases, and a pectinate fringe. Fringe and associated longitudinal muscle attachment probably mark the posterior margin of the first body segment.

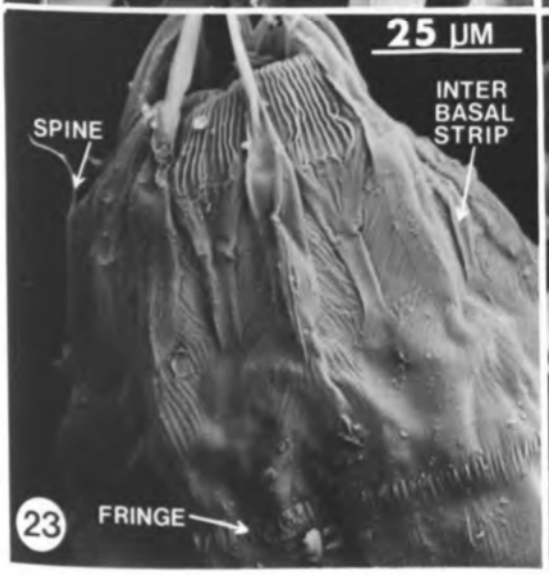
PLATE 24. PROTRICHOSCALID MORPHOLOGY
Two protrichoscalids, each showing a large socket, small curved endpiece, and socket fringe resembling a "plate of minute denticles" as in the neotenic genus Cateria. These scalids appear to resemble the hook scalids of Loricifera. Scanning electron micrograph of J-2 specimen.


OS
ES
OS
25 µM
19


25 um
20


RIDGE
FUSED HAIRS
SPINE
5µm
21


25 µm
22


25 µM
SPINE
INTER BASAL STRIP
FRINGE
23


1µm
24

PLATE 25. CILIA TUBULES IN TRICHOSCALID TIP
Transverse section of trichoscalid cut near trichoscalid tip showing cilia tubules (cf. Plate 6 of trichoscalid longitudinal section). Transmission electron micrograph of specimen J-5:1.

KEY
T - tubules of cilia

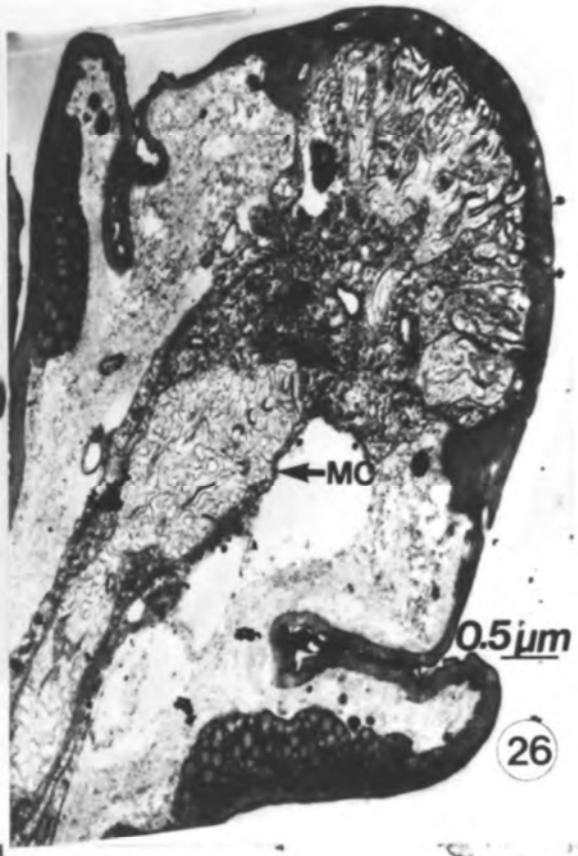
PLATE 26. TRICHOSCALID ORIGIN
Transverse section of trichoscalid origin showing punctate endocuticular elborations ("spotty lobes") within the cuticle of the trichoscalid scale (top left and bottom centre). The membrane cell in the centre of the trichoscalid communicates with the exterior through pits in the cuticle of the trichoscalid origin. This membrane cell has thick and thin membranes as described in K. giganteus (cf. Plate 55 which shows this feature more clearly). Transmission electron micrograph of specimen J-5:1.

KEY
MC - Membrane cell

PLATE 27. PROTRICHOSCALID
Transverse section of the large socket of a J-4 protrichoscalid showing a trichoscalid developing in the the centre. The trichoscalid is a membrane-bound area of dense cytoplasm which gives off a fringe of processes. Transverse sections of these processes show that they contain two bodies (arrow). Transmission electron micrograph of specimen J-4:1.

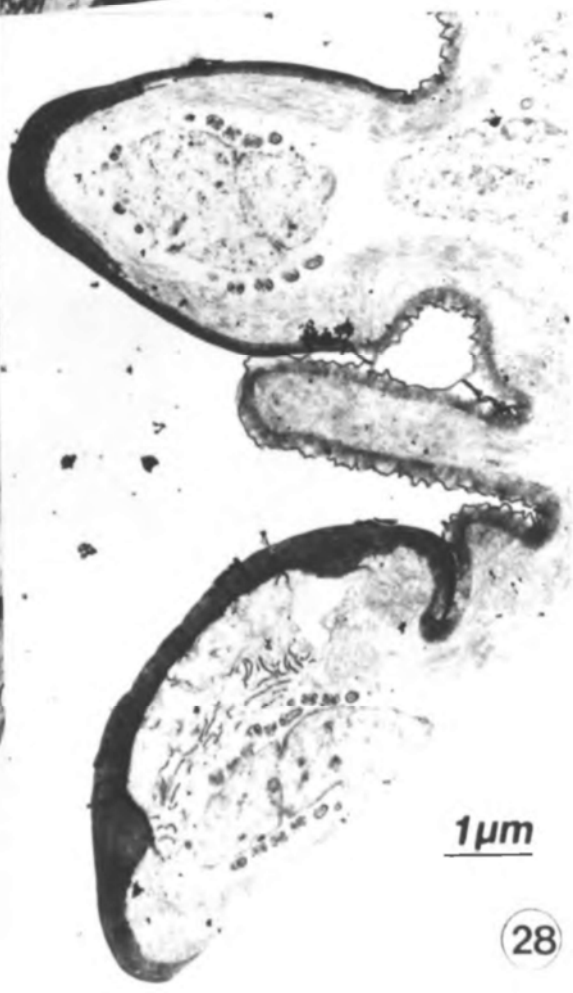
PLATE 28. TWO PROTRICHOSCALIDS
Transverse sections through two J-4 protrichoscalids showing the trichoscalids developing inside them. The lower protrichoscalid is seen enlarged in Plate 27. Transmission electron micrograph of specimen J-4:1.

25



26

27



28

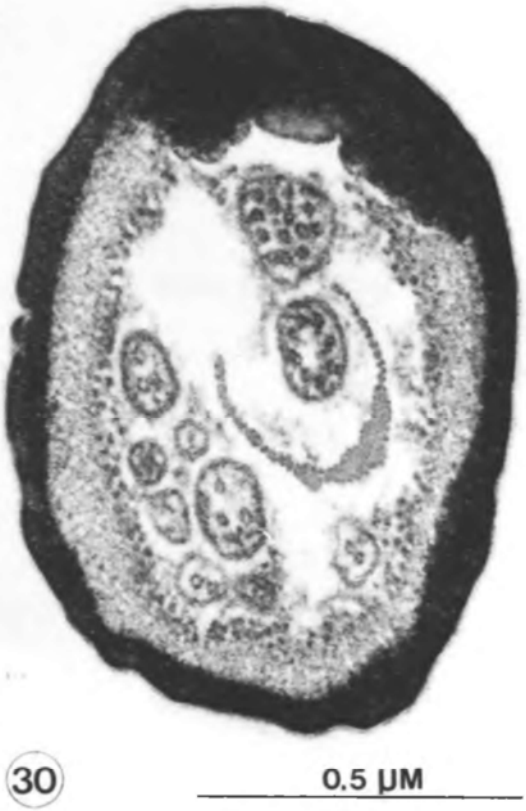
PLATE 29. SCLEROSCALID 1- INTERNAL SCALID
Transverse section through the mid-region of an internal scalid of the first ring - a scleroscalid 1. A bundle of cilia tubules is seen in the scleroscalid cell, and the thick walls show diffuse striations. Transmission electron micrograph of specimen Female 1.

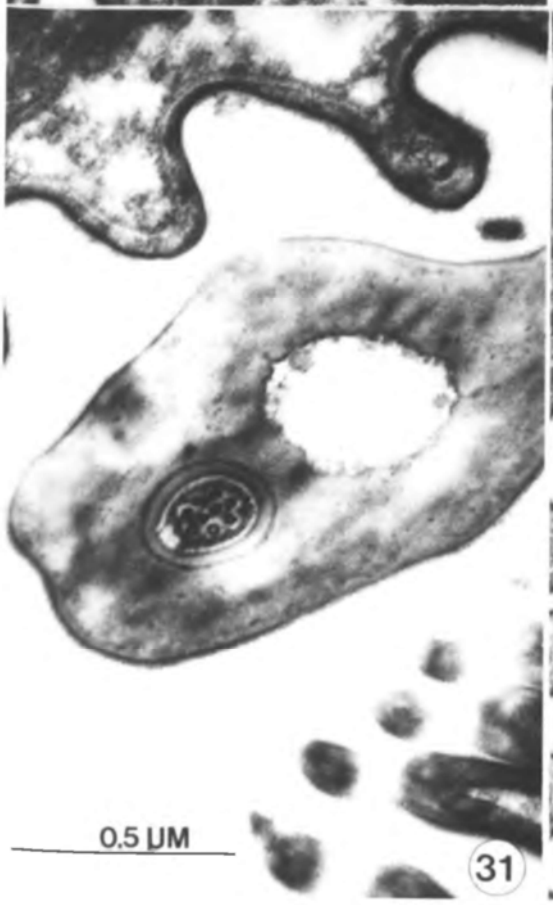
PLATE 30. ORAL SCALID
Transverse section through an oral scalid showing ten bundles of cilia tubules and a bracket-like organelle. Transmission electron micrograph of specimen J-5:1.

PLATE 31. SCLEROSCALID 1 - INTERNAL SCALID
Transverse section cut near the tip of a scleroscalid 1 showing a bundle of cilia tubules passing through a passage in the thick scleroscalid wall. Transmission electron micrograph of specimen Female 1.

PLATE 32. HELIOSCALID - INTERNAL SCALID
Transverse section of helioscalid showing three bundles of cilia tubules and a bracket-like organelle.


0.5 µM
29


30
0.5 µM


0.5 µM
31

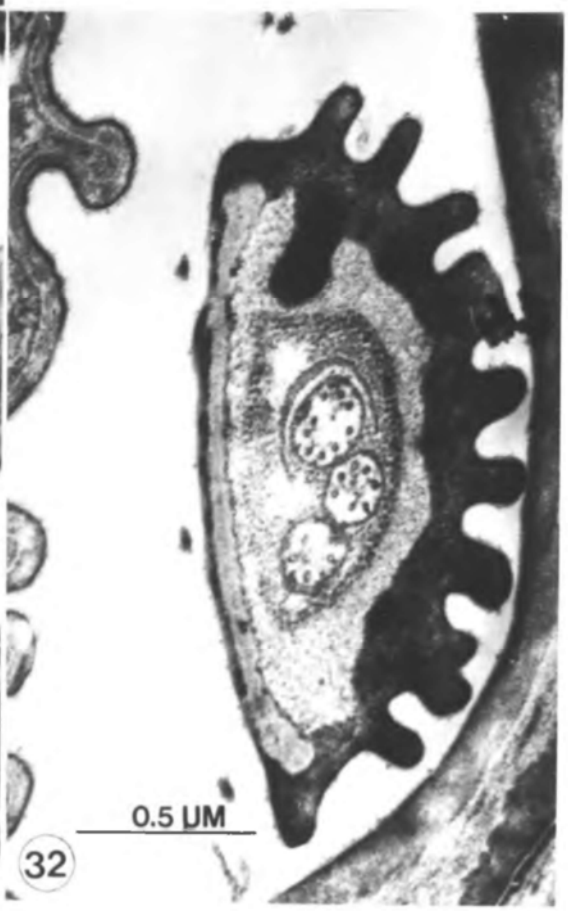

0.5 µM
32

PLATE 33. INTERNAL SCALIDS ON A PROLAPSED HEAD
A prolapsed head in which the pharyngeal crown (top left) has extruded through the oral cone (centre) pulling out the lining of the oral cone. The external scalids are seen at the bottom of the micrograph (cf. Fig. 13). Scanning electron micrograph of adult specimen.

PLATE 34. DETAIL OF INTERNAL SCALIDS
Detail of previous plate showing helioscalids standing free from wall of oral cone with adnate scleroscalids between them (cf. Fig. 14). Scanning electron micrograph of adult specimen.

KEY
HS - Helioscalid

PLATE 35. INTERNAL SCALIDS SEEN IN A PARTIALLY PROLAPSED HEAD
A partially prolapsed head in which the pharyngeal crown has moved up but not extruded through the oral cone. The tips of scleroscalid protrude from the inside walls of the oral cone. Bent oral scalids can be seen (lower right). Scanning electron micrograph of adult specimen.

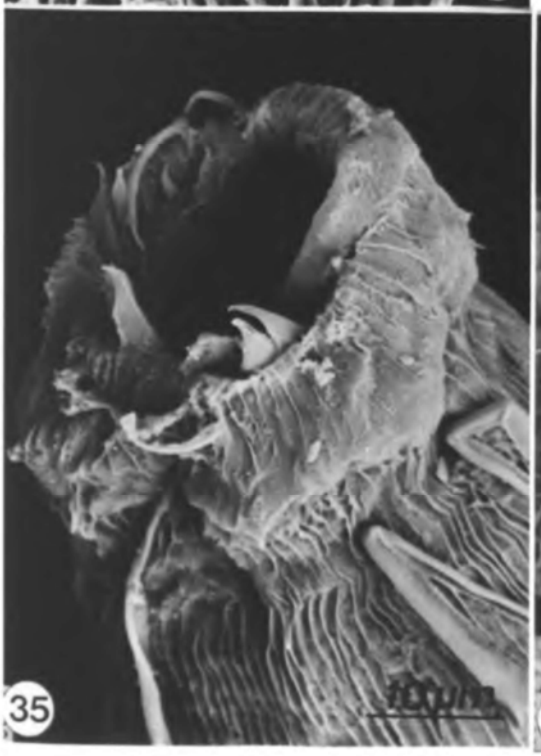
PLATE 36. DETAIL OF SCLEROSCALIDS
Detail of previous plate showing slits in tips of scleroscalids. Figs. 15B and 15D show cilia tubules projecting from these slits. Scanning electron micrograph of adult specimen.

KEY

SS - Scleroscalid


25 µm
33


HS
25 µm
34


35


SS
1µm
36

PLATE 37. CUTICULAR LINING OF J-1 PHARYNGEAL BULB
Transverse section of a J-1 pharyngeal bulb showing triradiate lumen of the gut (centre) surrounded by the anlagen of a secretory epithelium. The epithelium is surrounded by a basement membrane and by a developmental space, as it was in all three J-1 specimens sectioned. Around the developmental space developing pharyngeal pump muscles are located. Transmission electron micrograph of specimen J-1:2.

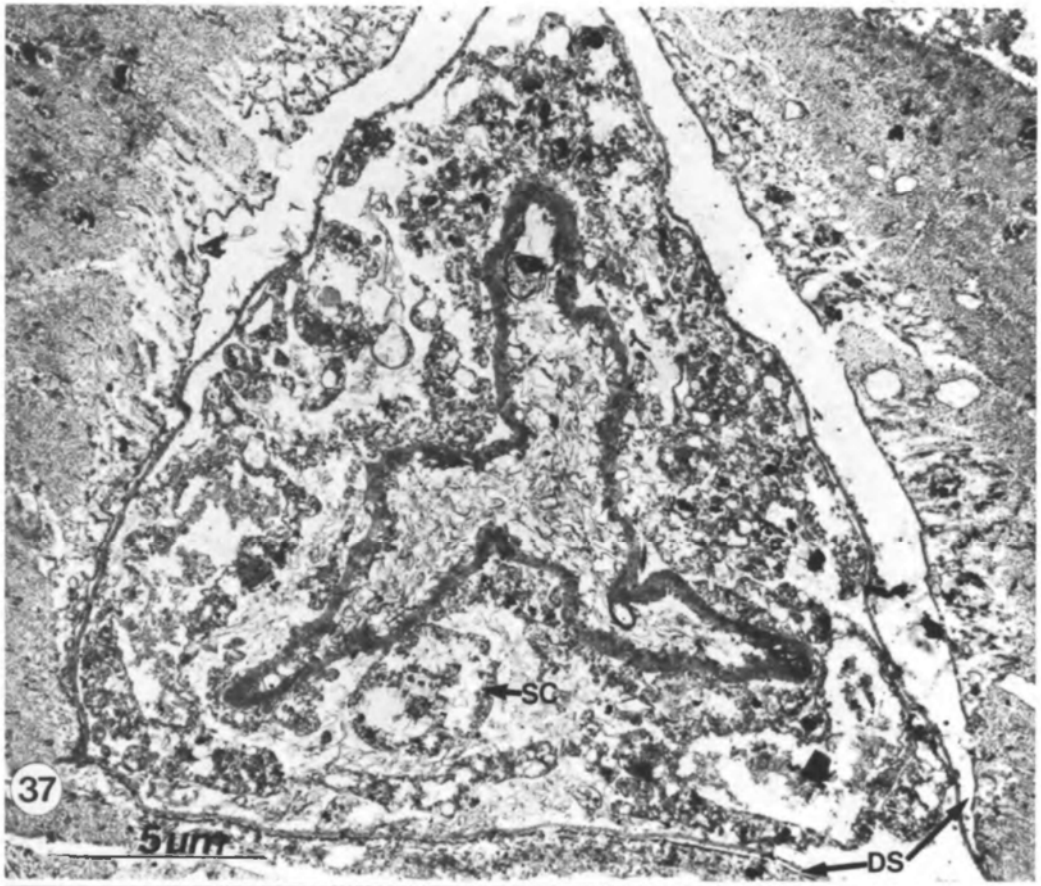
KEY

DS - Developmental space
SC - Secretory cell associated with cuticular lining of foregut.

PLATE 38. CUTICULAR LINING OF J-6 PHARYNGEAL BULB
Transverse section of a J-6 pharyngeal bulb showing triradiate lumen of the gut (centre) surrounded by a secretory epithelium. The epithelium is surrounded by a thick basement membrane, in turn surrounded by radiating myofibrils of the three lobes of the pharyngeal pump. The secretory epithelium is covered by cuticular placoids lining the pharynx (cf. Plate 41). Transmission electron micrograph of specimen J-6:1.

KEY

SC - Secretory cell.


SC
37
5um
DS

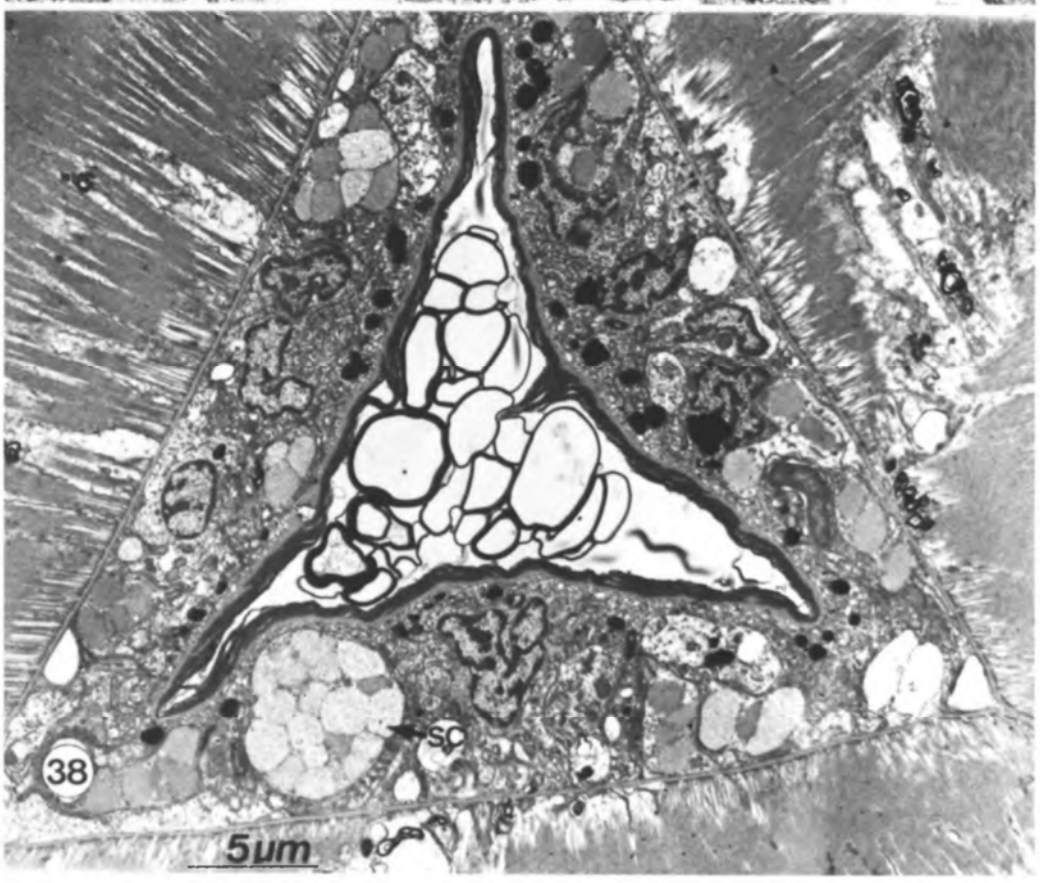

SC
38
5µm

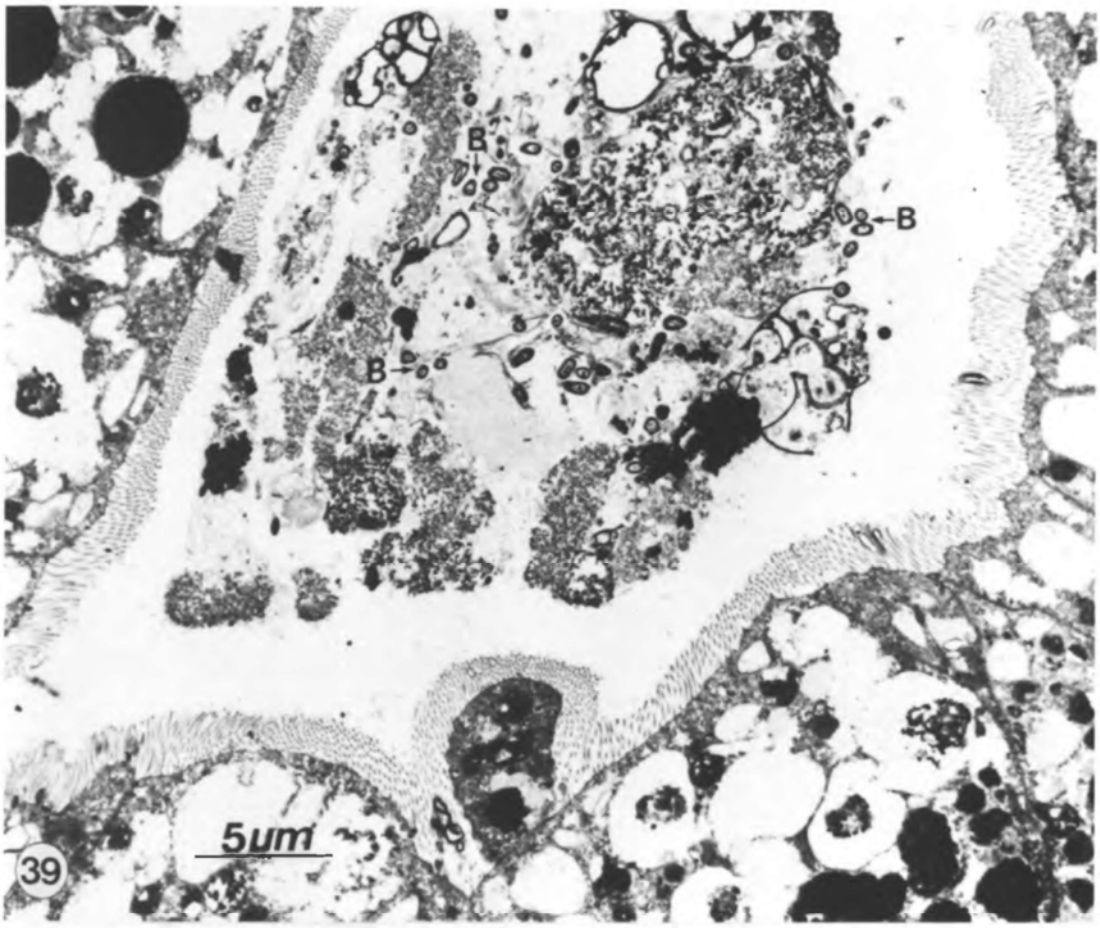
PLATE 39. BACTERIA IN THE GUT CONTENTS
Transverse section of the anterior midgut. The lumen of the midgut (centre) is surrounded by cells each with a microvillous brush border. Plant cell walls and bacteria can be seen in the gut contents. Transmission electron micrograph of specimen J-6:1.

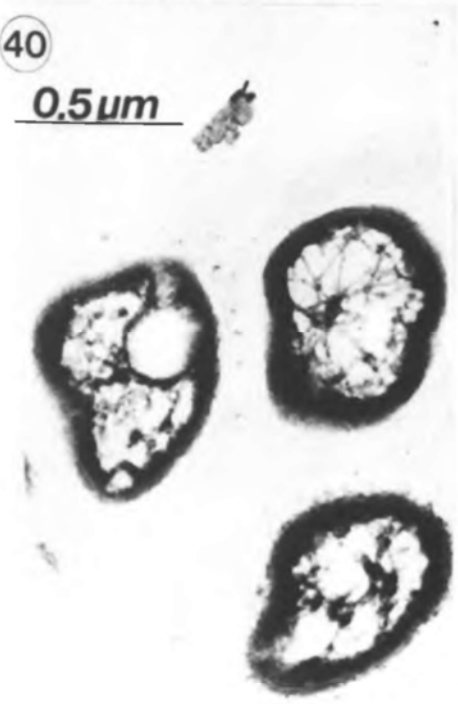
KEY

B - Bacteria

PLATE 40. ECTOCOMMENSAL BACTERIA GROWING ON THE CUTICLE OF TRUNK PLATES
Bacteria from the trunk plate flora of specimen Male 1 (cf. Plate 52).

PLATE 41. SECRETION INTO THE PHARYNGEAL BULB
Section cut near section shown in Plate 38. This section shows secretion through placoids of cuticle lining the foregut by epithelial secretory cells. Transmission electron micrograph of specimen J-6:1.


B
B
B
5µm
39


40
0.5µm

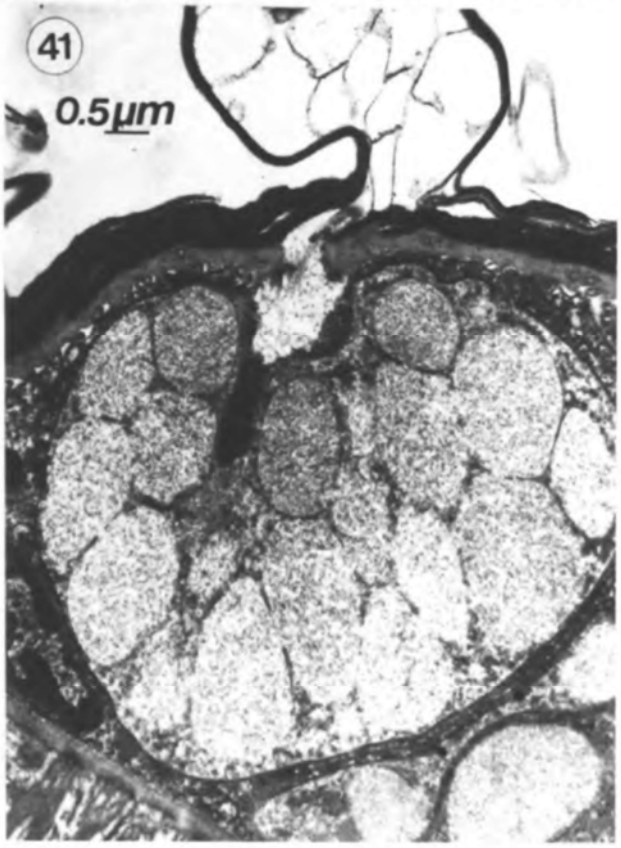
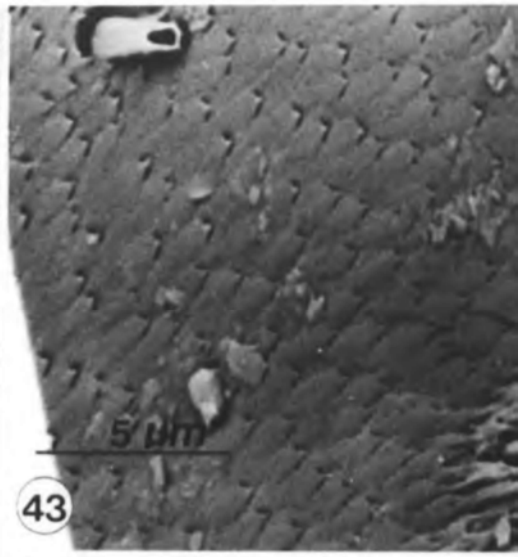

41
0.5µm

PLATE 42. CUTICULAR EXCRETORY STRUCTURES
Lateral margin of a segment 11 tergite showing cuticular hairs along the dorsoventral margin (left) a long, hollow lateral seta (lower left), six cuticular tubules set into a depression surrounded by a cuticular fringe (lower left), and two nearby longer tubules or setae. A sensory spot can be seen to the right of the upper tubule in the top centre of the micrograph (cf. Plate 69). Scanning electron micrograph of adult specimen.

PLATE 43. CUTICULAR EXCRETORY TUBULES
Lateral margin of a segment 11 tergite showing a cluster of cuticular tubules and a longer tubule (top left). The "wood rasp" texture imparted to cuticular plates by triangular cuticular sculpturing can be seen in this micrograph (cf. Plate 49 and Fig. 21). Scanning electron micrograph of adult specimen.

PLATE 44. MORPHOLOGY OF CUTICULAR EXCRETORY TUBULES
Twelve cuticular tubules. Cuticular pores can be discerned in the cuticle to the right of these tubules (cf. Plates 47 and 48). This scanning electron micrograph of an adult specimen is taken at approximately one tenth of the magnification of the transmission electron micrograph shown in Plate 45.


5 µm
42


5 µm
43

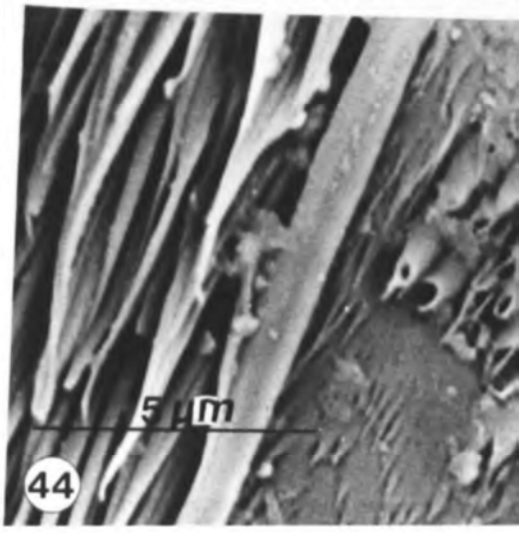

5 µm
44

PLATE 45. STRUCTURE OF CUTICULAR EXCRETORY TUBULES
Section cut through twelve cuticular excretory tubules passing through the cuticle and into the hypodermis showing that these excretory cuticular tubules are not a form of sieve plate for they ramify above and below the cuticle. Transmission electron micrograph of specimen J-6:1.

PLATE 46. DETAILED STRUCTURE OF CUTICULAR EXCRETORY TUBULES
Section cut through the ends of six cuticular excretory tubules showing that in the hypodermis they may branch, or they may have alveolar expansions. Transmission electron micrograph of specimen J-5:1.

PLATE 47. CUTICULAR CANALS CONTAINING CYTOPLASMIC EXTENSIONS FROM THE HYPODERMIS
Section of adult cuticle showing cytoplasmic extensions from hypodermal cells in Y-shaped cuticular canals. The cytoplasm contains vesicles - evidence of active secretion. Transmission electron micrograph of specimen Female 1.

PLATE 48. CUTICULAR CANALS CONTAINING EXTRUSIONS FROM HYPODERMAL INCLUSION BODIES
Section of adult cuticle showing extrusions from hypodermal inclusion bodies in Y-shaped cuticular canals. Material in the canals is evidence of a process of active secretion onto the epicuticle. Transmission electron micrograph of specimen Female 1.


0.5μm
45


0.5μm
46


0.5μm
47

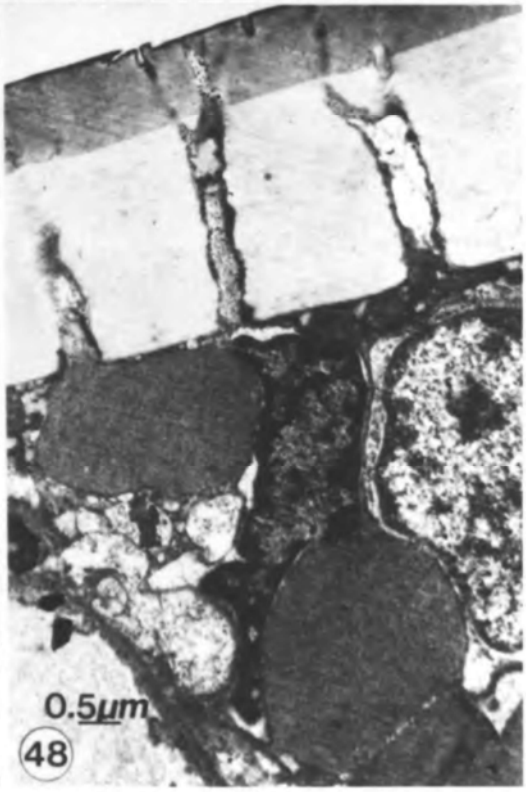

0.5μm
48

PLATE 49. PORES IN THE EPICUTICLE
Juvenile dorsal cuticle showing pairs of cuticular pores (three arrows) in the shadows of cuticular prominences (cf. Fig. 21). Scanning electron micrograph of J-5 specimen.

PLATE 50. PORES IN THE ENDOCUTICLE
Internal view of adult ventral cuticle showing single pores - the lower opening of Y-shaped canals (cf. Plates 47, 48 and Fig. 21). The cuticular window of the midsternal seta of segment 7 is seen lower left (cf. Fig. 22). Scanning electron micrograph of adult specimen.

PLATE 51. SECRETION ONTO THE EPICUTICLE THROUGH CUTICULAR PORES
Adult dorsal plate cuticle showing many droplets of secretion - evidence that the droplets have been secreted through cuticular pores. Scanning electron micrograph of adult specimen.

PLATE 52. THE "GARDEN" THAT GROWS AROUND UNDISTURBED KINORHYNCH CUTICLE
Cuticular plates (plate margin lower left, cf. previous plate) showing diatoms and algal fragments that typically grow around the cuticle of live K. phyllotropis. Preparation for microscopic examination usually removes this garden, except in the large spaces below overlapping segmental plates where bacteria have also been photographed (Plate 40). Scanning electron micrograph of adult specimen.

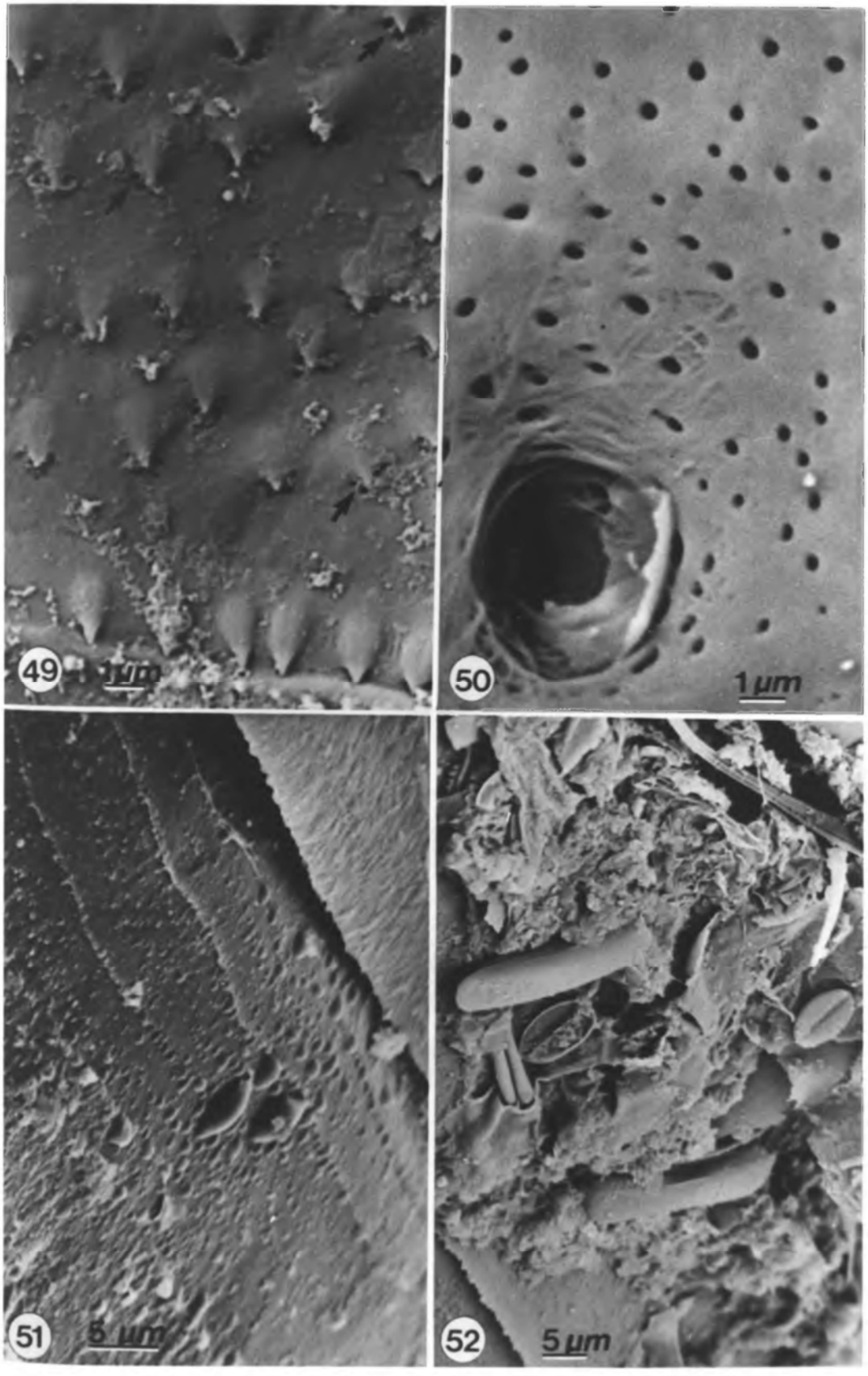

49
1 µm
50
1 µm
51
5 µm
52
5 µm

PLATE 53. TRICHOSCALID CELL WITH MEMBRANE SYSTEM
Origin of a trichoscalid showing punctate endocuticular elaboration in trichoscalid scale (top right) and cell with membrane system (centre) as described in spinoscalids of K. giganteus. Thick membranes are seen between layers of thin membranes. The layer of fibrous cuticle is thickest in trichoscalids. Transmission electron micrograph of specimen J-6:1.

PLATE 54. CANAL PASSING THROUGH CUTICLE FROM HYPODERMAL MEMBRANE SYSTEM CELL
Section through juvenile cuticle showing a subcuticular pit containing the membrane system of a subcuticular cell and a fine canal connecting this pit to the surface of the cuticle. Similar canals are found in the socket cuticle of trichoscalids. Transmission electron micrograph of specimen J-5:1.

PLATE 55. HYPODERMAL MEMBRANE SYSTEM CELL
Membrane lamellae (bottom right) of a hypodermal cell entering a subcuticular pit (top left). This pit is located on the dorsolateral aspect of the first trunk segment. Transmission electron micrograph of specimen J-6:1.

PLATE 56. MEMBRANES IN A CUTICULAR PIT
Details of thick and thin membranes in the cuticular pit shown in Plate 55. Transmission electron micrograph of a serial section of specimen J-6:1.

PLATE 57. CUTICULAR PIT WITH A TRICHOSCALID-TYPE MEMBRANE SYSTEM
Thick and thin membranes, as reported in the spinoscalids of K. giganteus and the trichoscalids of K. phyllotropis (Plate 53), are also seen in cuticular pits. This cuticular pit was located near the mid-dorsal axis of segment 5 anterior to the pachycyclus of specimen Female 1. Transmission electron micrograph.

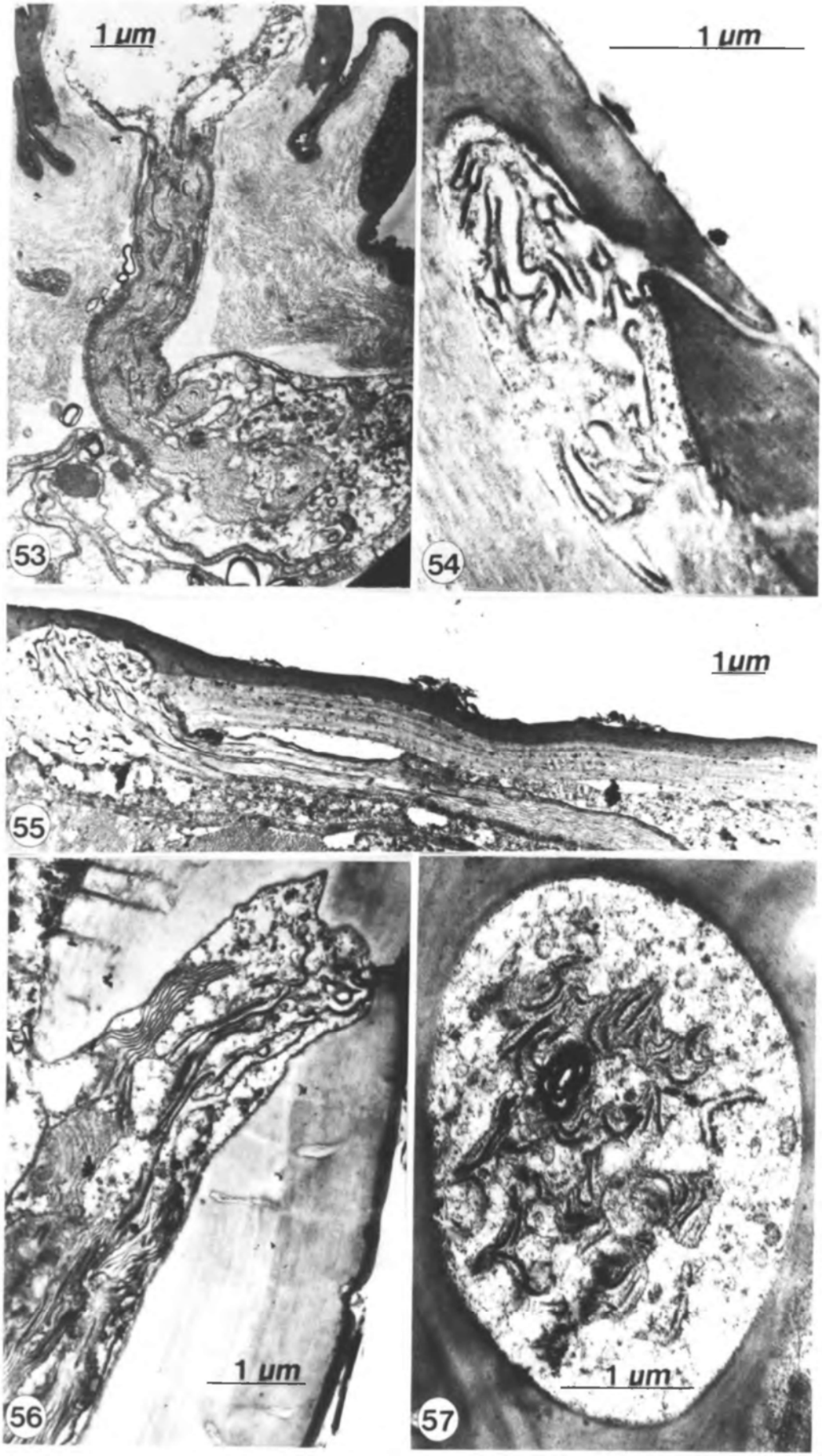

1 µm
53
1 µm
54
1µm
55
1 µm
56
1 µm
57

PLATE 58. LONGITUDINAL SECTION OF A SENSORY SPOT SHOWING THE STRIATED ROOTLET OF A CILIUM

Longitudinal section of the aperture of a sensory spot of the dorsal series showing the structures of a cilium in the subcuticular cell, including a striated rootlet (bottom right). Cuticular prominences characteristic of a sensory spot are seen on the epicuticle (cf. Plates 68 and 69). Transmission electron micrograph of specimen Female 1.

PLATE 59. TRANSVERSE SECTION OF A SENSORY SPOT SHOWING CILIARY STRUCTURES

Section through a large and a small cilia cell each containing a striated rootlet. The striated rootlet of the larger cell is surrounded by nine modified microvilli, resembling a priapulid mechanoreceptor. The epicuticle shows the cuticular elaboration of a sensory spot (top right). Transmission electron micrograph of specimen J-6:1.

PLATE 60. CILIUM IN THE MUCOUS CELL OF A SETA

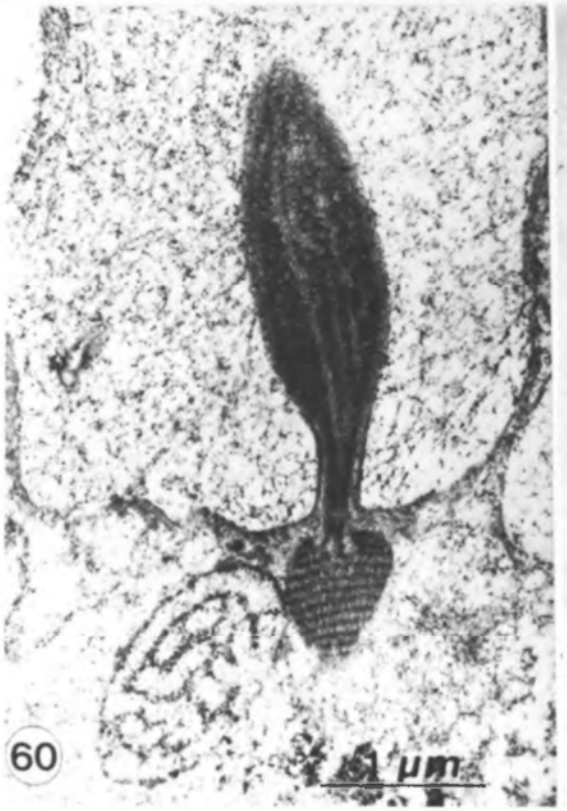
Striated rootlet and shaft of a cilium in the mucous cell of a seta (cf. Fig. 22). Transmission electron micrograph of specimen Female 1.

PLATE 61. CILIA IN A SCALID

Two striated rootlets (arrows) in two cilia cells of a scalid. This micrograph is one of the serial sections from which Fig. 10 was drawn. Transmission electron micrograph of specimen Female 1.


58
1 µm


C
C
59
1 µm


60
1 µm


C
C
61
1 µm

PLATE 62. J-1 POSTERIOR MARGIN
Posterior margin of J-1 showing that the acutely pointed mid-dorsal spine projects beyond the terminal segment and that there is no unarticulated spinose protuberance at the laterotерminal margin of the tergal plate. Lateral spines on all segments are also acutely pointed in the J-1. Scanning electron micrograph of J-1 specimen.

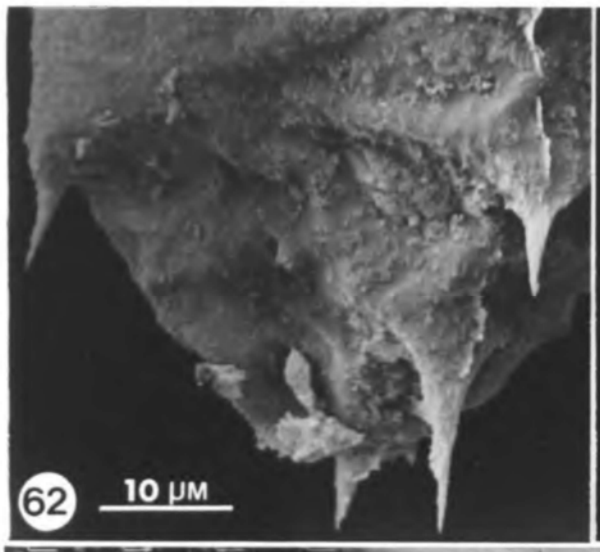
PLATE 63. J-2 POSTERIOR MARGIN
Posterior margin of J-2 showing that the bluntly pointed mid-dorsal spine projects beyond the terminal segment and that there is no unarticulated spinose protuberance at the laterotерminal margin of the tergal plate. Lateral spines on all segments are bluntly pointed in the J-2 and subsequent juvenile stages. Scanning electron micrograph of J-2 specimen.

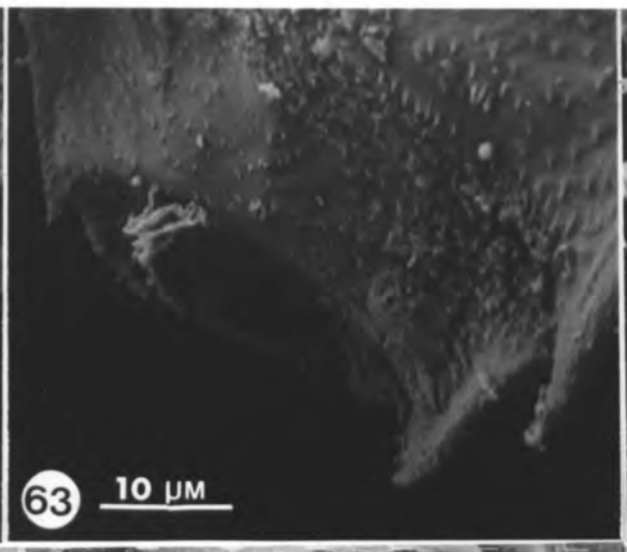
PLATE 64. J-3 POSTERIOR MARGIN
Posterior margin of J-3 showing that the mid-dorsal spine of the terminal segment reaches the posterior margin, and that there is no unarticulated spinose protuberance at the laterotерminal margin of the tergal plate. Scanning electron micrograph of J-3 specimen.

PLATE 65. J-4 POSTERIOR MARGIN
Posterior margin of J-4 showing that the mid-dorsal spine of the terminal segment does not reach the posterior margin of the terminal segment as in all subsequent juvenile stages, and that there is <u>one</u> spinose process at the laterotерminal margin of the tergal plate (cf. Plate 70). Scanning electron micrograph of J-4 specimen.

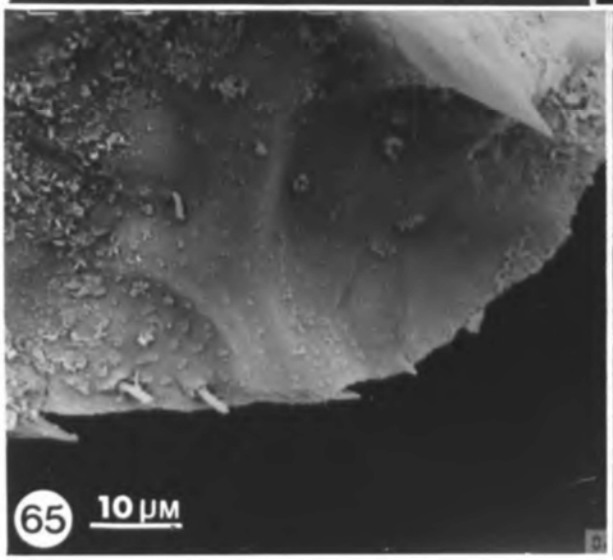
PLATE 66. J-5 POSTERIOR MARGIN
Posterior margin of J-5 showing that there are <u>two</u> spinose processes at the laterotерminal margin of the tergal plate (cf. Plate 71). Two such spinous processes are found in the subsequent juvenile and adult stages. As in all previous juvenile stages the posterior mid-dorsal spine is set into wide folds of thin cuticle in which the spine lies on its side against the dorsal cuticle (cf. Fig. 24). Scanning electron micrograph of J-5 specimen.

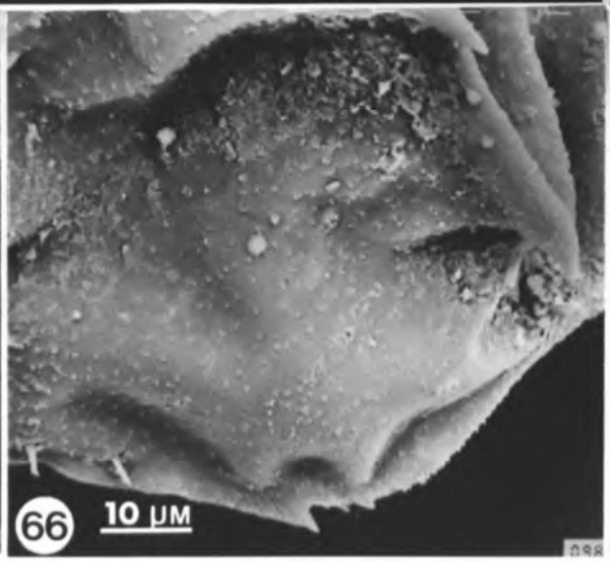
PLATE 67. J-6 POSTERIOR MARGIN
Posterior margin of J-6 showing that the posterior mid-dorsal spine is set into a narrow ridge of thick cuticle which does not flex. Scanning electron micrograph of J-6 specimen.


62
10 µm


63
10 µm


64
10 µm


65
10 µm


66
10 µm

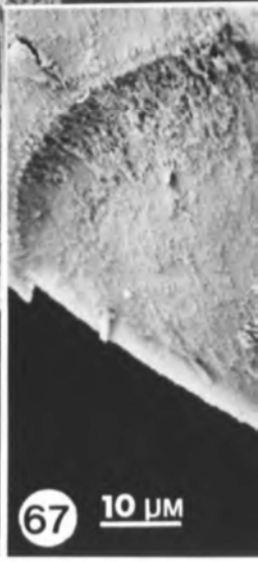

67
10 µm

PLATE 68. J-1 SENSORY SPOT
J-1 dorsolateral sensory spot on first trunk segment showing a central and a lateral cuticular aperture. The lateral aperture is associated with a tube. Scanning electron micrograph of J-1 specimen.

PLATE 69. ADULT SENSORY SPOT
Adult ventrolateral sensory spot on first trunk segment showing a central and a lateral cuticular aperture. The lateral aperture is associated with a tube. Scanning electron micrograph of adult specimen.

PLATE 70. THE SINGLE LATEROTERMINAL SPINOSE PROCESS OF THE J-4
The lateroterminal margin of a J-4 juvenile showing the single lateroterminal spinelet which characterises this stage. This spine is the lateral spine of segment 13. The lateral spine of segment 12 is clearly visible in all stages. Scanning electron micrograph of J-4 specimen.
KEY
L12 - Lateral spine of segment 12
L13 - Lateral spine of segment 13

PLATE 71. THE TWO LATEROTERMINAL SPINOSE PROCESSES OF LATE JUVENILE AND ADULT STAGES
The lateroterminal margin of a J-5 juvenile showing the two lateroterminal spinelets which characterise this and subsequent stages. The second spine is the unarticulated spinose process of segment 13 which characterises this species and K. anomalus. Scanning electron micrograph of J-5 specimen.
KEY
L12 - Lateral spine of segment 12
L13 - Lateral spine of segment 13
SP - Unarticulated spinose process of segment 13 found in this species

PLATE 72. MID-DORSAL SPINOSE RIDGE OF THE J-6
The narrow ridge which bears spines in the J-6 does not fold over sideways as do the wide folds seen in younger stages (cf. Fig. 24). Scanning electron micrograph of J-6 secimen.
KEY
12 - Segment 12
13 - Developing segment 13

PLATE 73. MALE POSTERIOR MARGIN
Dorsal view of posterior margin of adult male showing development of segment 13 and of the unarticulated spinose process of this species. Two pairs of penile spines are also visible. Scanning electron micrograph of male specimen.
KEY
12 - Segment 12
13 - Segment 13
PS - Penile spine
SP - Unarticulated spinose process of segment 13

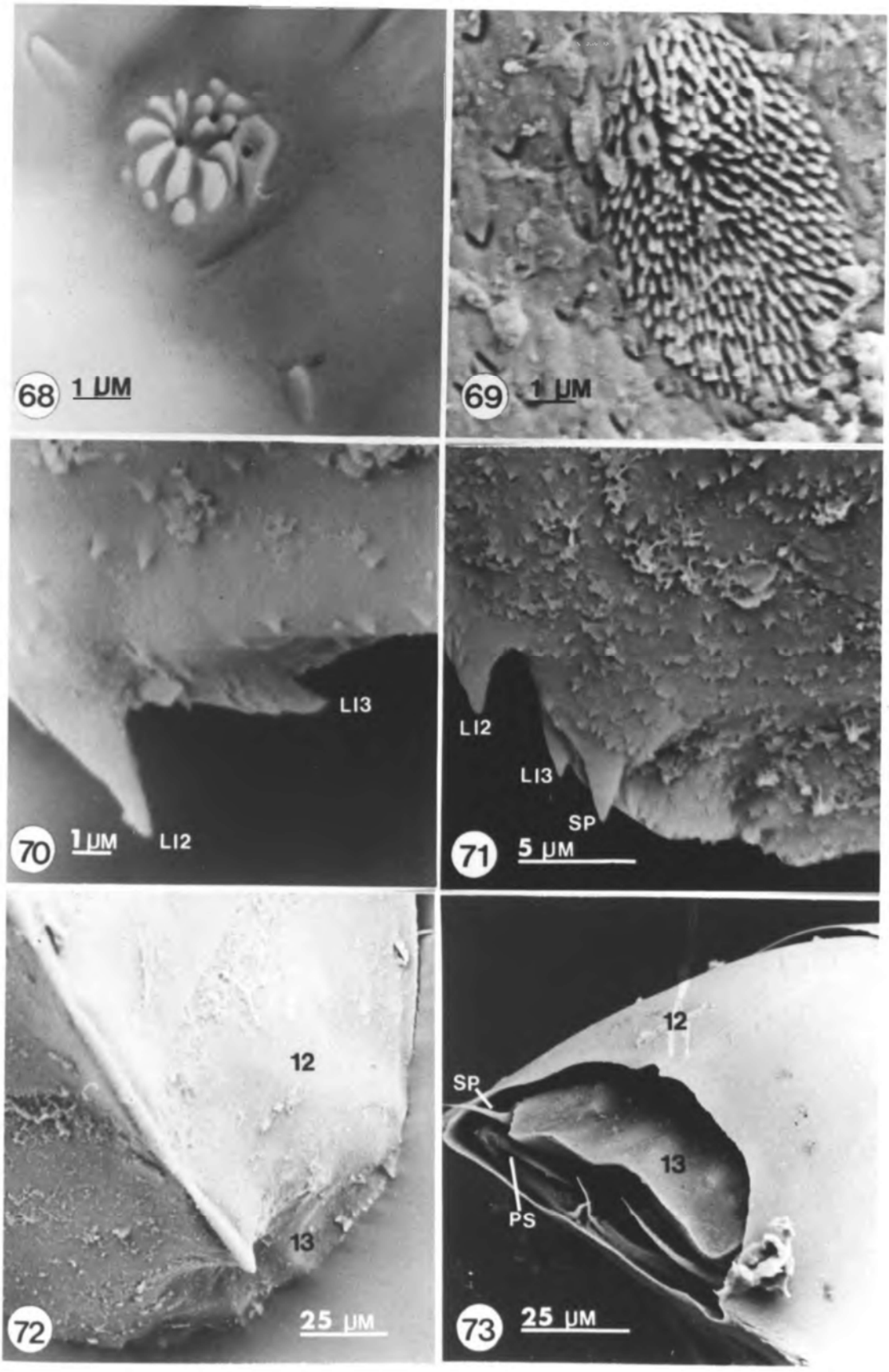
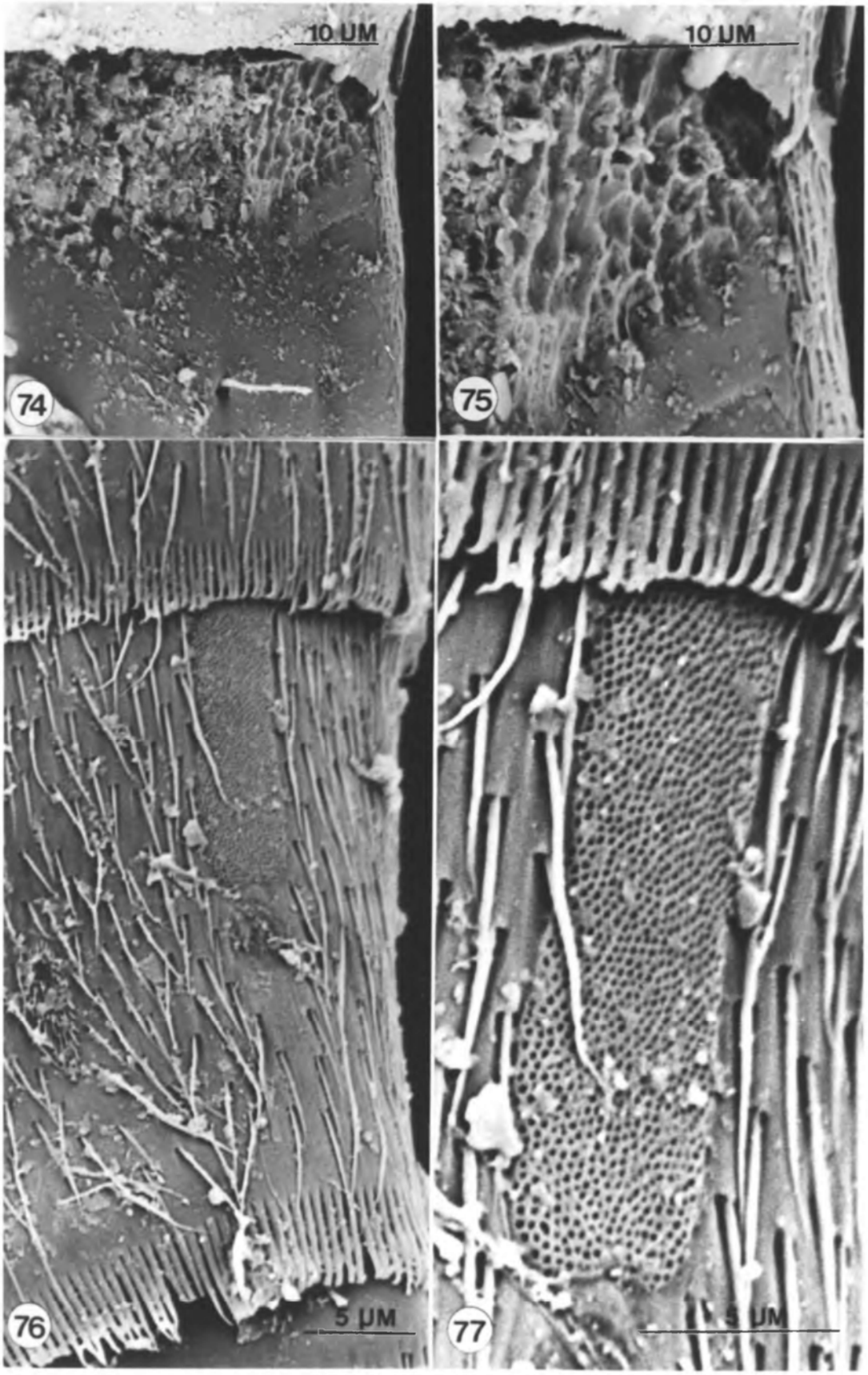

68 1 µM
69 1 µM
LI3
LI2
70 1µM
LI2
LI3
SP
71 5 µM
12
13
72 25 µM
12
SP
13
PS
73 25 µM

PLATE 74. PYCNOPHYES FAVEOLUS - CUTICULAR SCULPTURING
Right sternite of segment 6 of P. faveolus showing the faveolate cuticular sculpturing characteristic of this species. Scanning electron micrograph of male specimen.

PLATE 75. DETAIL OF PREVIOUS PLATE
Detail of faveolate cuticle seen in previous plate.

PLATE 76. ECHINODERES TERETIS - SIEVE PLATE
Ventral aspect of segment 11 tergite of E. teretis showing sensory spot (central left), sieve plate (cf. excretory tubules in Plates 42-44) and pectinate fringe marking segment boundary (cf. Plate 23). Scanning electron micrograph of female specimen.

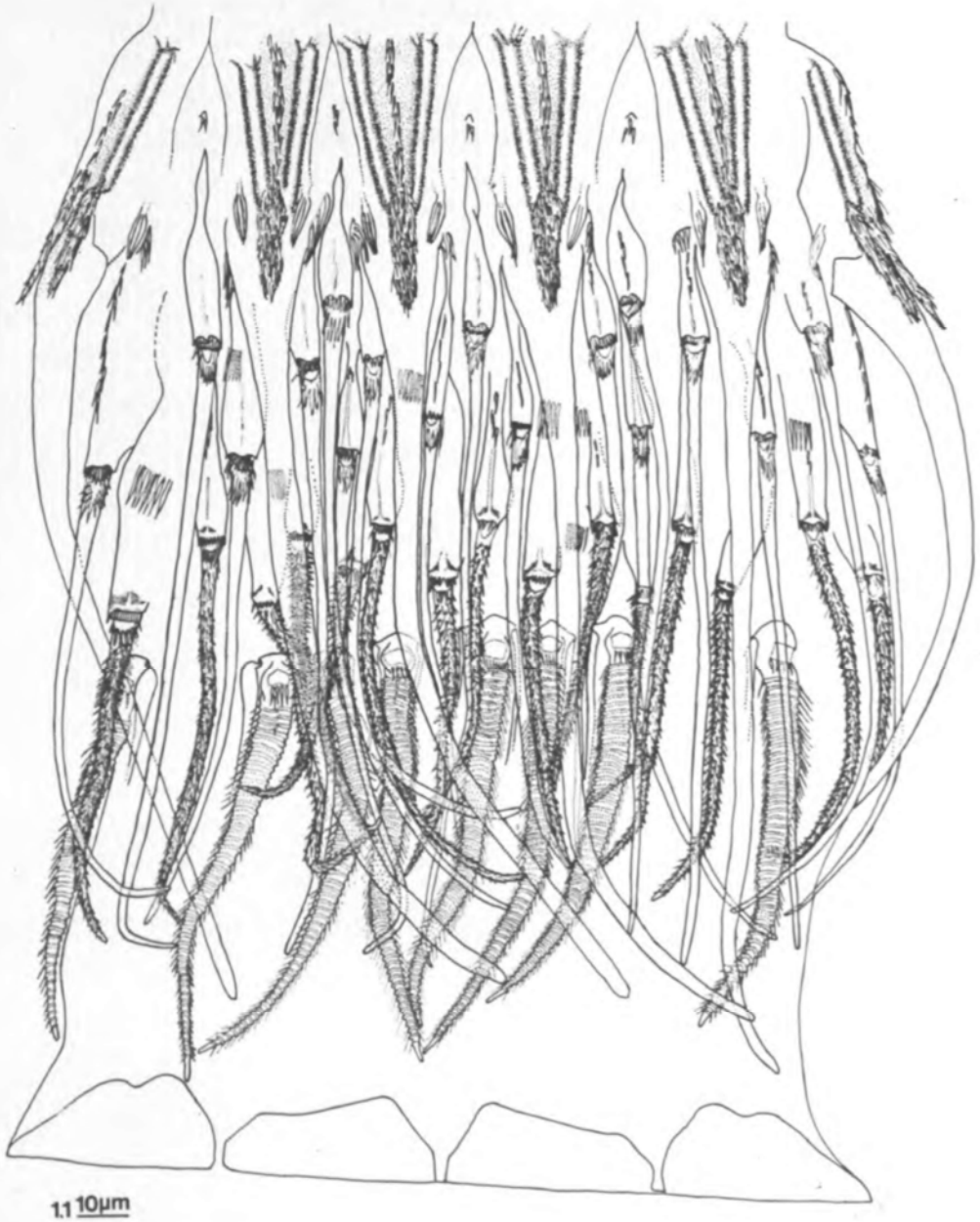
PLATE 77. DETAIL OF PREVIOUS PLATE
Detail of sieve plate seen in previous plate.


10 UM
74
10 UM
75
76
5 UM
77
5 UM

APPENDIX ONE

FIGURE 1.1. Dorsal aspect of the everted adult head of a female Kinorhynchus phyllotropis specimen with a trunk length of 740 um.

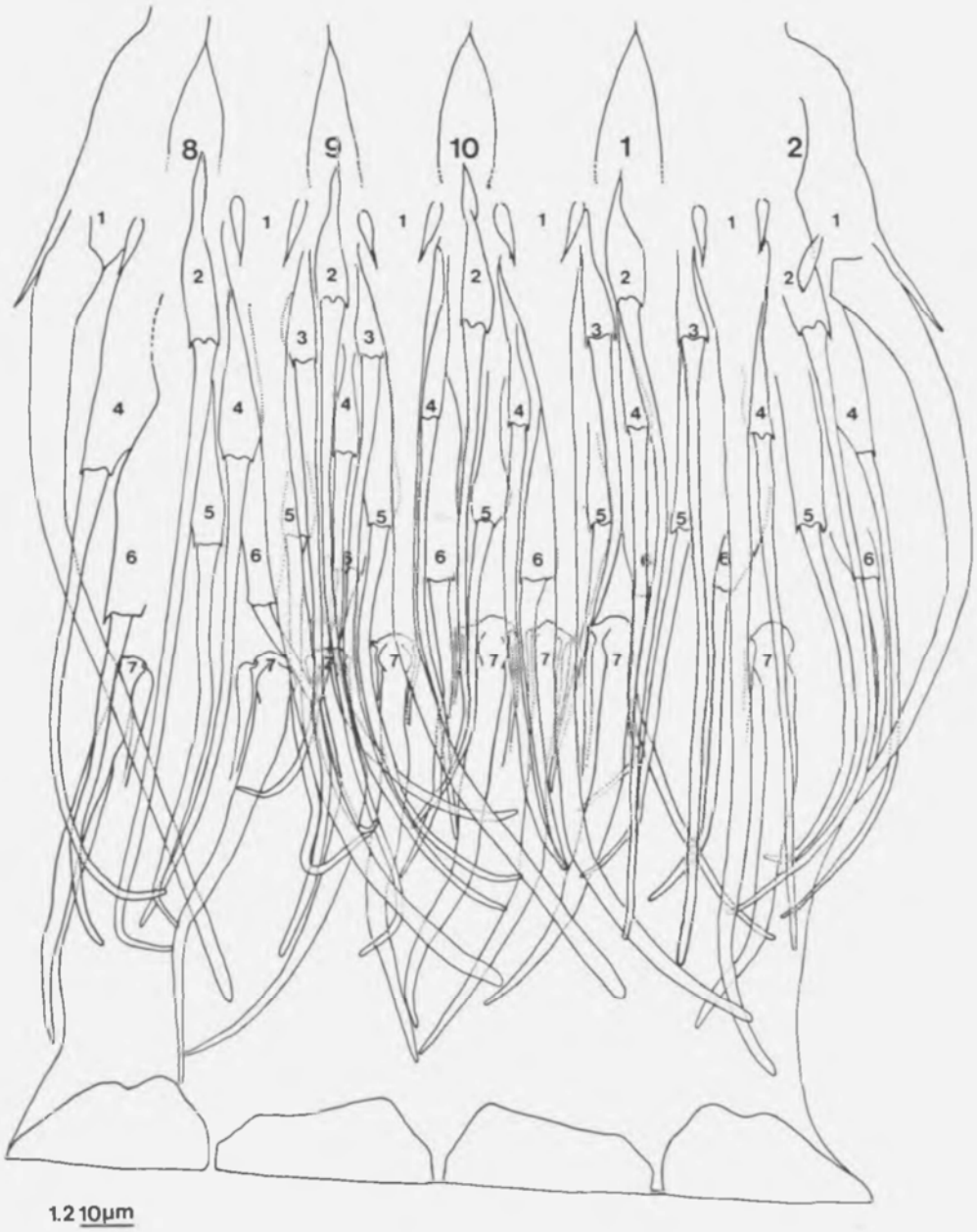
Scalid lengths are given in Table 1A.



1.1 10µm

FIGURE 1.2. Head sector and scalid ring designation of scalids shown in Figure 1.1.

Large numbers show head sector designation.
Small numbers show scalid ring designation.

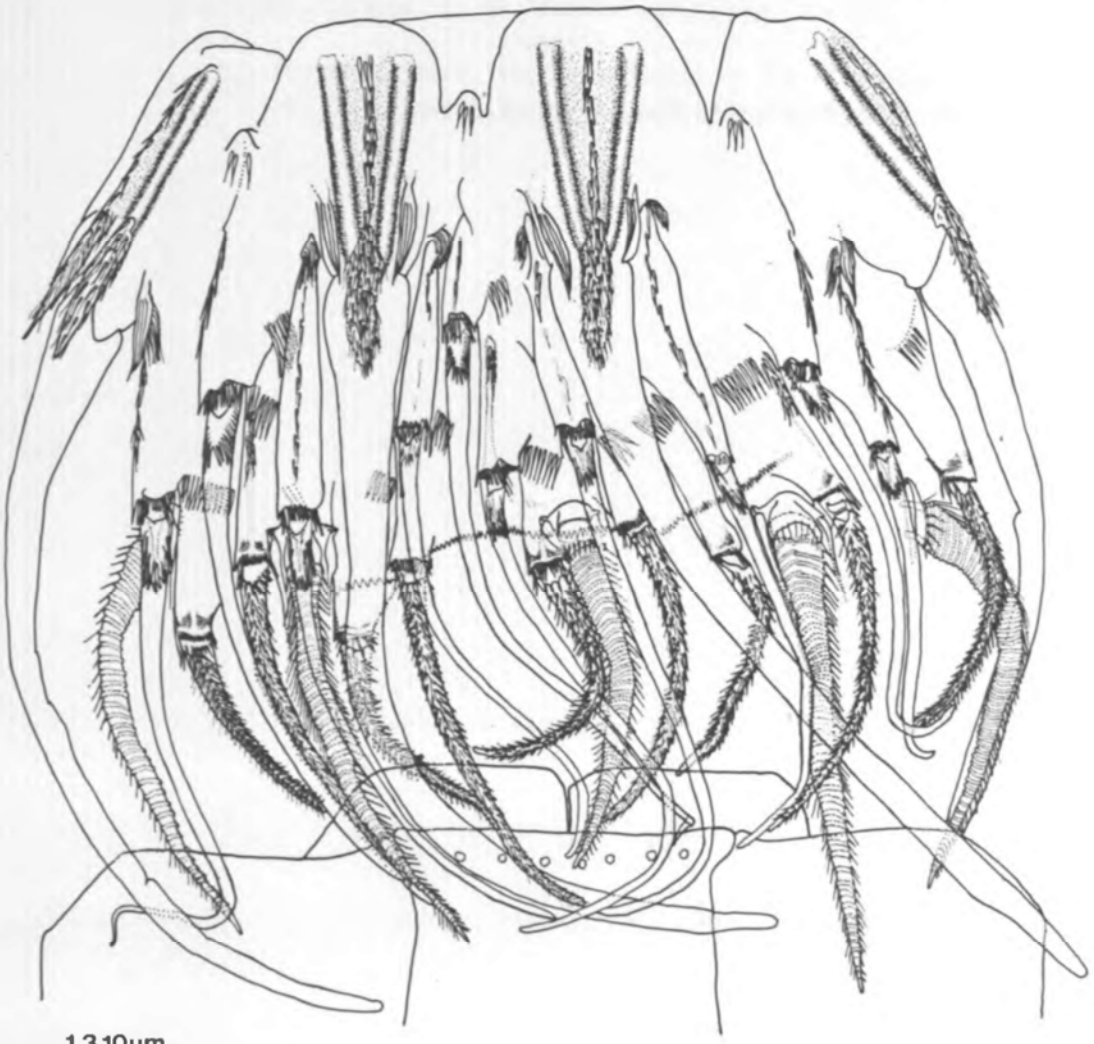


1.2 10µm

FIGURE 1.3. Ventral aspect of the everted adult head of a male Kinorhynchus phyllotropis specimen with a trunk length of 710 um.

Scalid lengths are given in Table 1B.

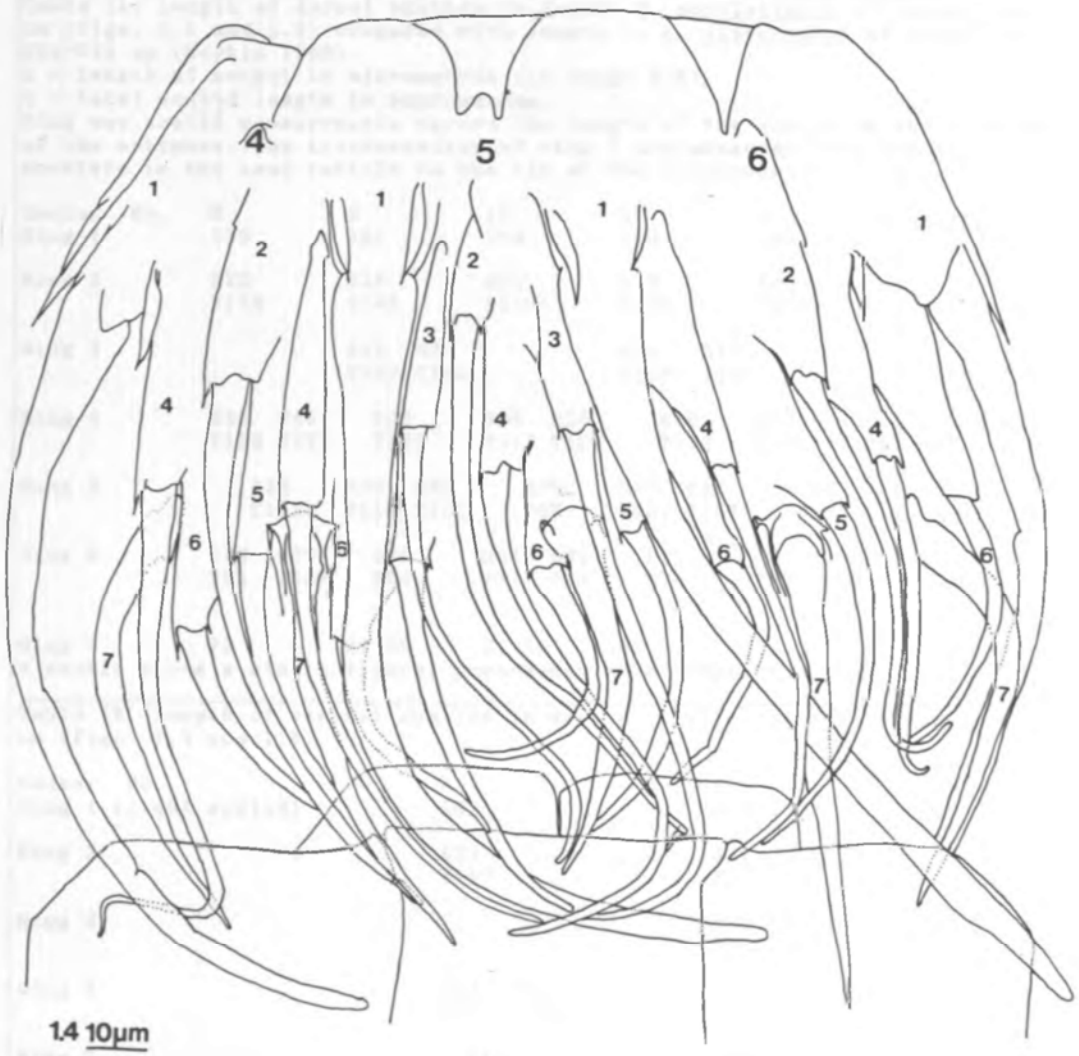
The midventral trichoscalid, shorter than all other trichoscalids, marks the midventral axis.



1.3 10µm

FIGURE 1.4. Head sector and scalid ring designation of scalids shown in Figure 1.3.

Large numbers show head sector designation.
Small numbers show scalid ring designation.



1.4 10µm

Table 1A. Length of dorsal scalids in female K. phyllotropis of trunk length 740 um (Figs. 1.1 and 1.2) compared with length in K. ilyocryptus of trunk length 612-745 um (Boykin 1965).
S = length of socket in micrometres (in rings 2-6).
T = total scalid length in micrometres.
Ring one scalid measurements record the length of the scalid on the right side of the antimere. The trichoscalids of ring 7 are measured from the top of the aperture in the head cuticle to the tip of the trichoscalid.

Sector No.	8	9	10	1	2	K.	ilyocryptus	*
Ring 1	159	161	158	164	166	I	121	I
						I		I
Ring 2	S22	S16	S21	S18	S23	I		I
	T139	T144	T110+	T139	T116+	I	73	I
						I		I
Ring 3		S21 S20		S19 S17		I		I
		T136 T132		T108+ T137		I	58-62	I
						I		I
Ring 4	S39 S40	S35	S34 S35	S30	S32 S32	I	Not stated	I
	T133 T133	T125	T117 T120	T132	T130 T126	I	Not stated	I
						I		I
Ring 5	S28	S32 S32	S26	S35 S35	S28	I		I
	T103	T110 T112	T87	T86+ T107	T101	I	58-62	I
						I		I
Ring 6	S30 S33	S30	S31 S31	S31	S30 S30	I		I
	T91 T58+	T84	T91 T88	T76	T92 T69+	I	58-62	I
						I		I
						I		I
Ring 7	72	82 79	81 75	83 77	79	I	50-52	I

* Boykin gives a single figure, presumably an average, for these scalid lengths

Table 1B. Length of ventral scalids in male K. phyllotropis of trunk length 710 um (Figs. 1.3 and 1.4)

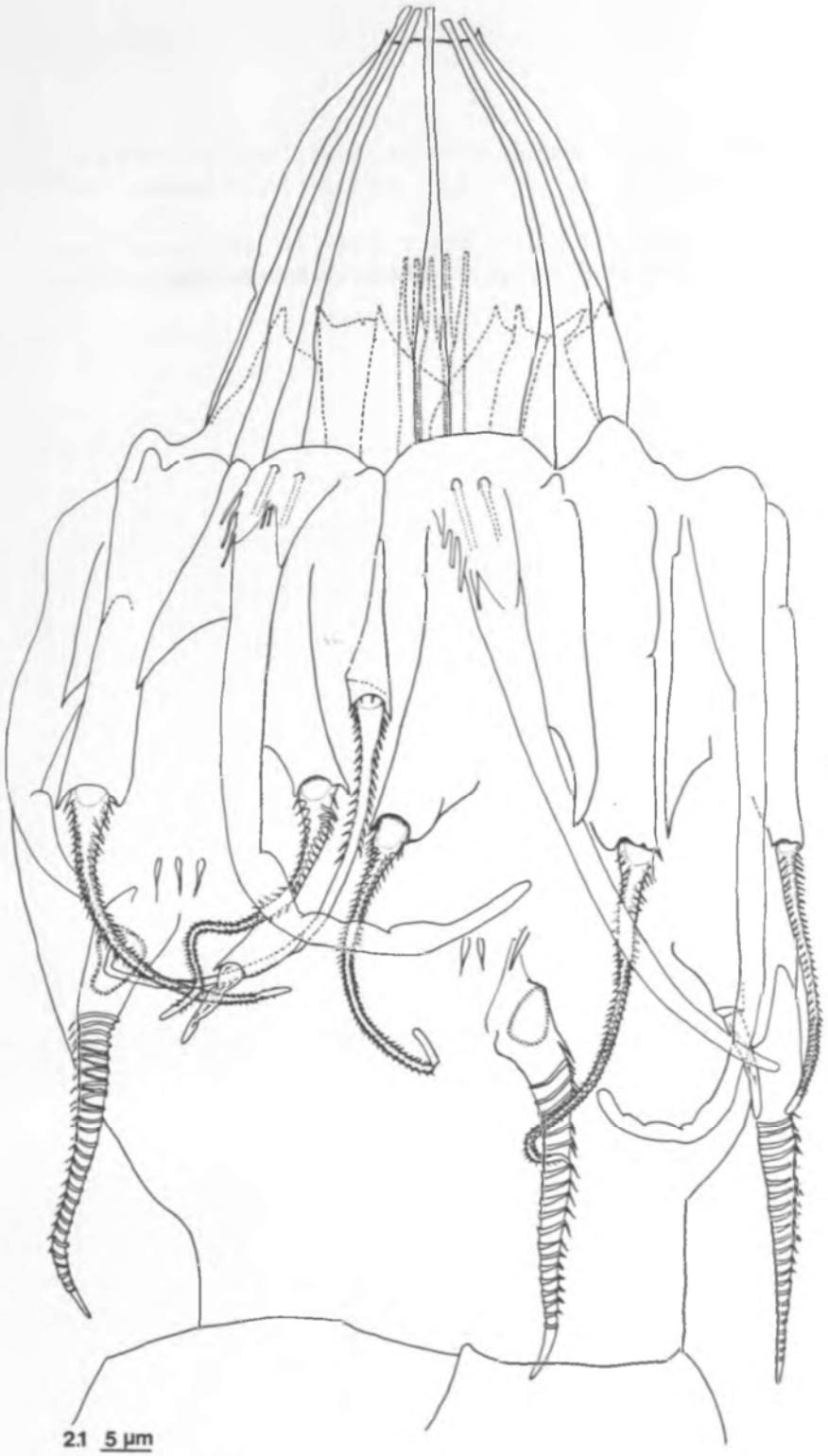
Sector No.	4	5	6
Ring 1 (right scalid)	161	163	153
Ring 2	S23	S16	S21
	T117	T117	T95
Ring 3		S30 S30	
		T111 T114	
Ring 4	S43 S42	S23	S38 S38
	T137 T136	T122	T111 T90
Ring 5	S32	S27 S27	S31
	T86	T92 T81+	T90
Ring 6	S26 S26	S21	S25 S28
	T65+ T68	T68	T69 T72
Ring 7	69 73	61	78 69

APPENDIX TWO

FIGURE 2.1. Dorsal aspect of the everted J-1 head of a Kinorhynchus phyllotropis specimen with a trunk length of 240 um.

Scalid lengths are given in Table 2A.

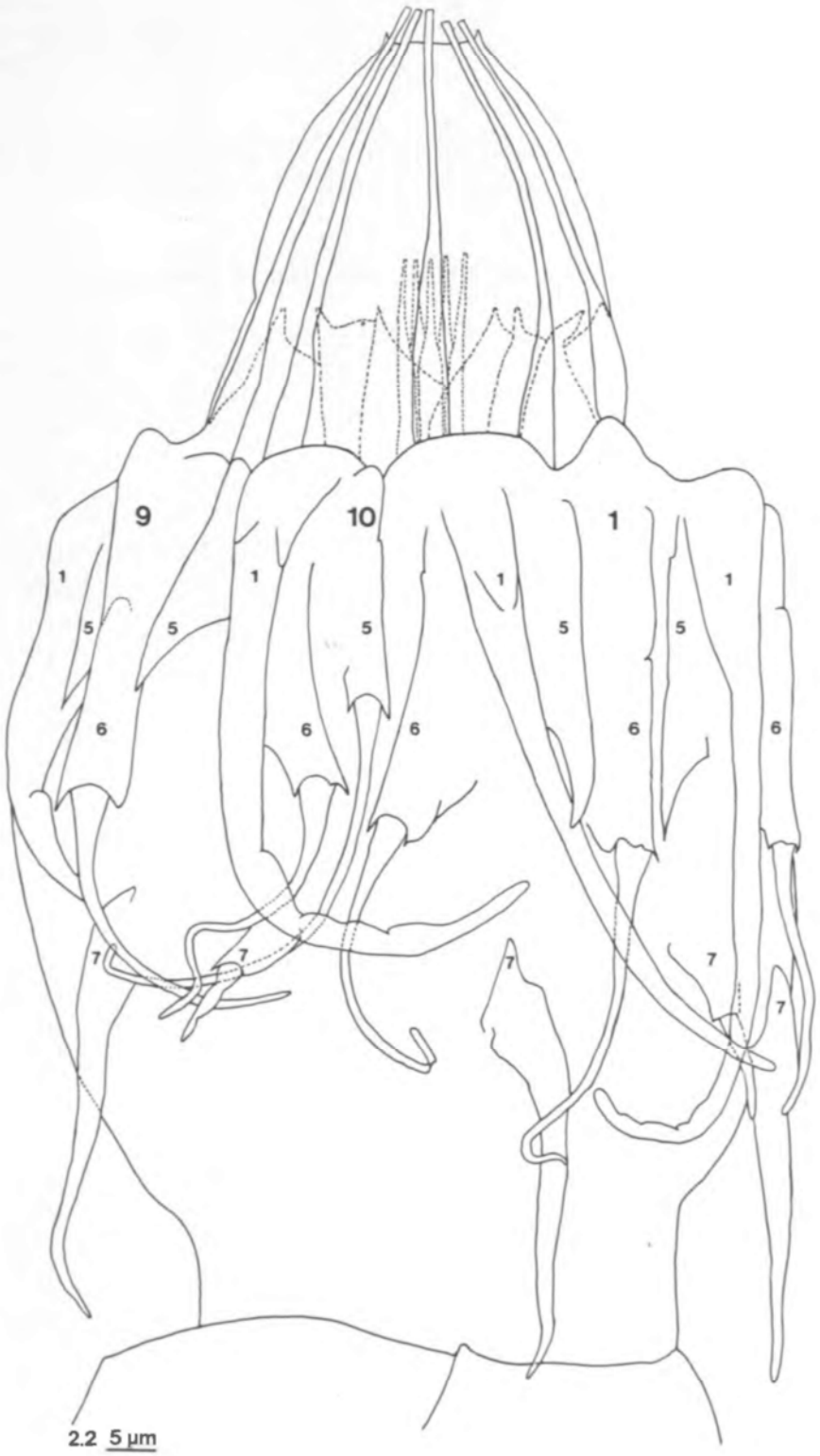
Oral scalids are adnate to the oral cone in early juvenile stages.



2.1 5 µm

FIGURE 2.2. Head sector and scalid ring designation of scalids shown in Figure 2.1.

Large numbers show head sector designation.
Small numbers show scalid ring designation.

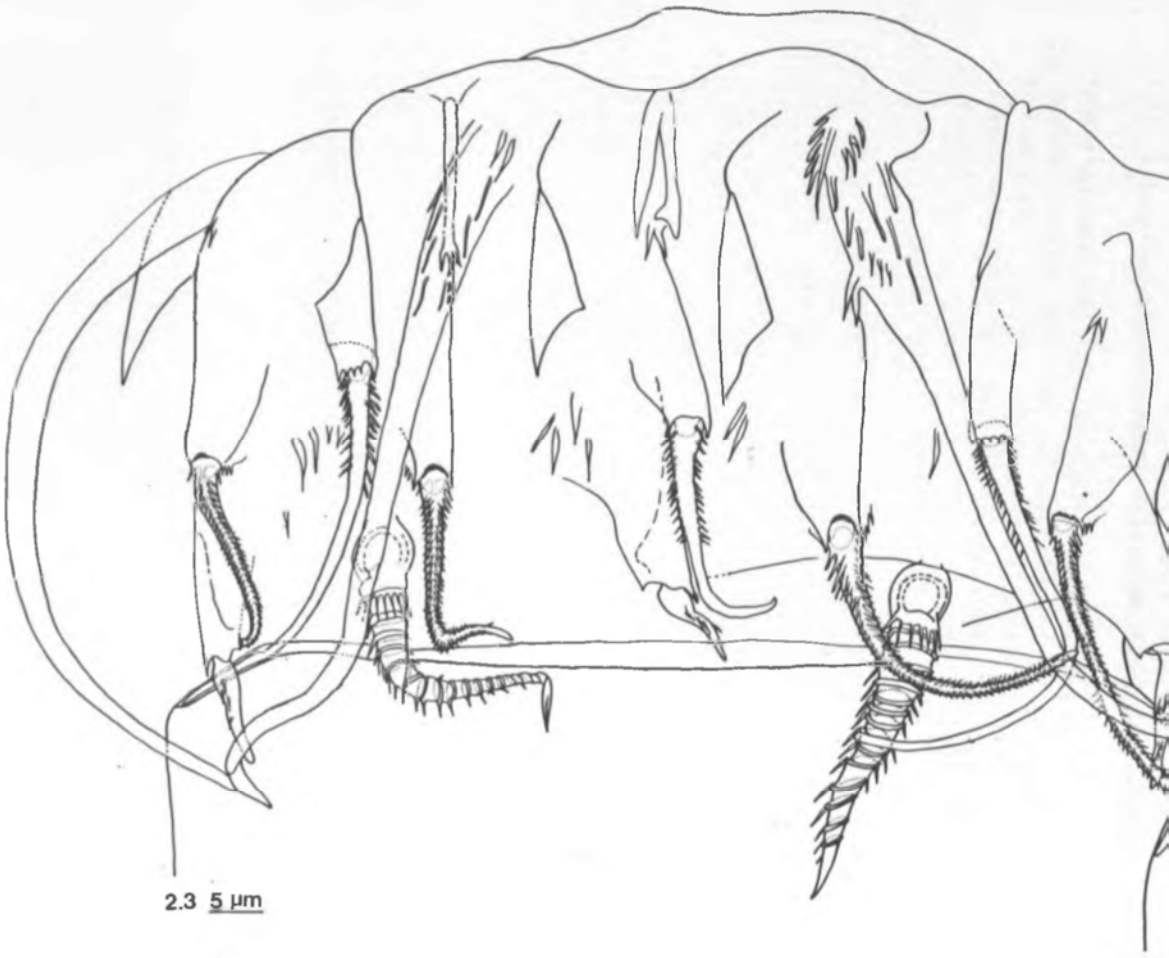


2.2 5 µm

FIGURE 2.3. Ventral aspect of the everted J-1 head of a Kinorhynchus phyllotropis specimen with a trunk length of 210 um.

Scalid lengths are given in Table 2B.

There are two protrichoscalids in sequence (not separated by a trichoscalid) on the right side of the diagram, in head sectors 6 and 7. Pairs of protrichoscalids are only found in the lateral angles of the head.

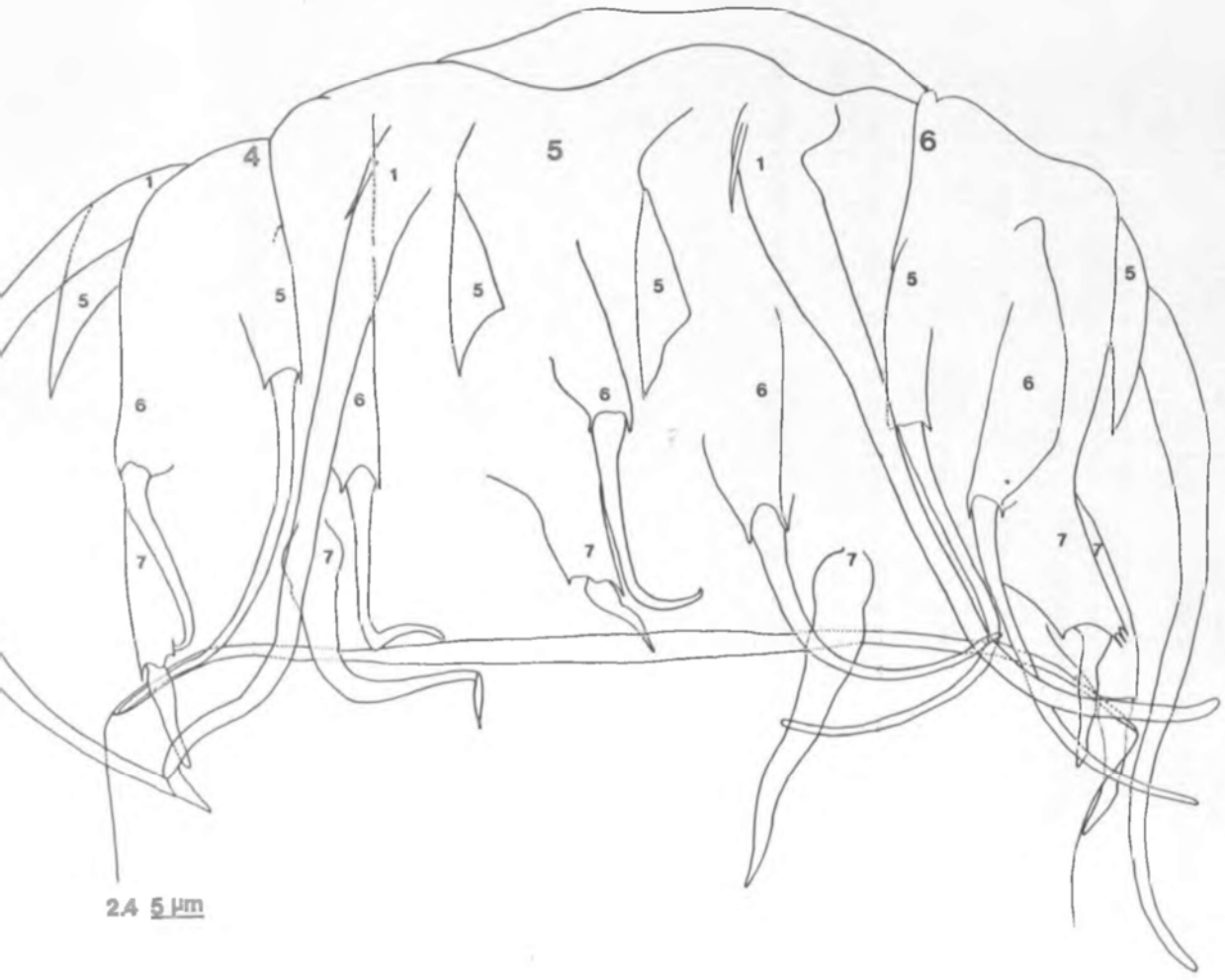


2.3 5 µm

FIGURE 2.4. Head sector and scalid ring designation of scalids in Figure 2.3.

Large numbers show head sector designation.
Small numbers show scalid ring designation.

There are two protrichoscalids in sequence (not separated by a trichoscalid) on the right side of the diagram, in head sectors 6 and 7. Pairs of protrichoscalids are only found in the lateral angles of the head.



2.4 5 µm

FIGURE 2.5. Schematic representation of scalid arrangement in the first juvenile stage, or J-1, of *Kinorhynchus phyllotropis*.

Horizontal numbers are the numbers of the head sectors as designated by Zelinka (1928, Figs. 3-4; Fig. 2 of this thesis).
Vertical numbers are the numbers of the scalid rings.

KEY

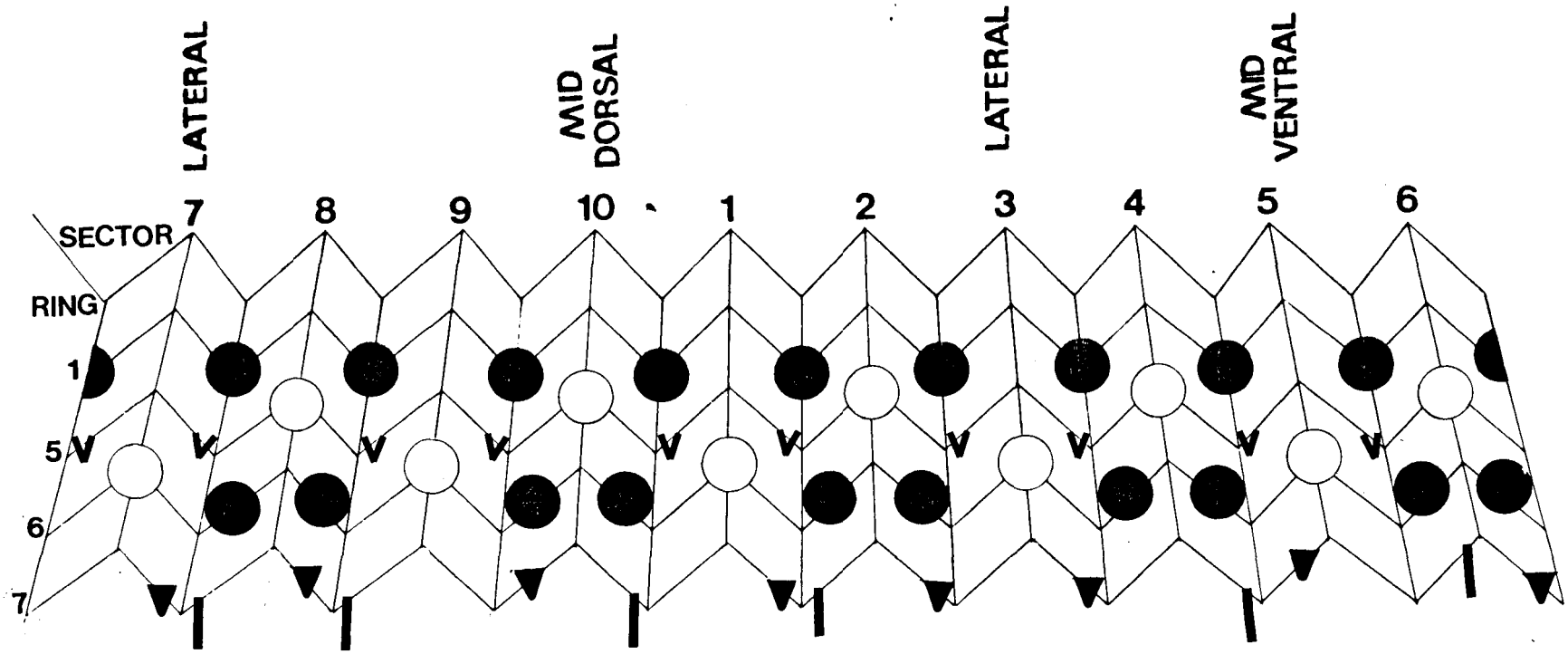
White circle - scalid belonging to the series in the centre of the head sector.

Black circle - scalid belonging to the series at the sides of the head sector.

V - proscalid

Black triangle - protrichoscalid

Black line - trichoscalid.


LATERAL
MID DORSAL
LATERAL
MID VENTRAL
SECTOR
RING
7
8
9
10
1
2
3
4
5
6
1
5
6
7

J-1

2.5

Table 2A. Length of dorsal scalids in J-1 K. phyllotropis of trunk length 240 um (Figs. 2.1 and 2.2.)
S = length of socket in micrometres (in rings 6-7).
T = total scalid length in micrometres.
Trichoscalids are measured from the top of the aperture in the head cuticle to the tip of the trichoscalid.

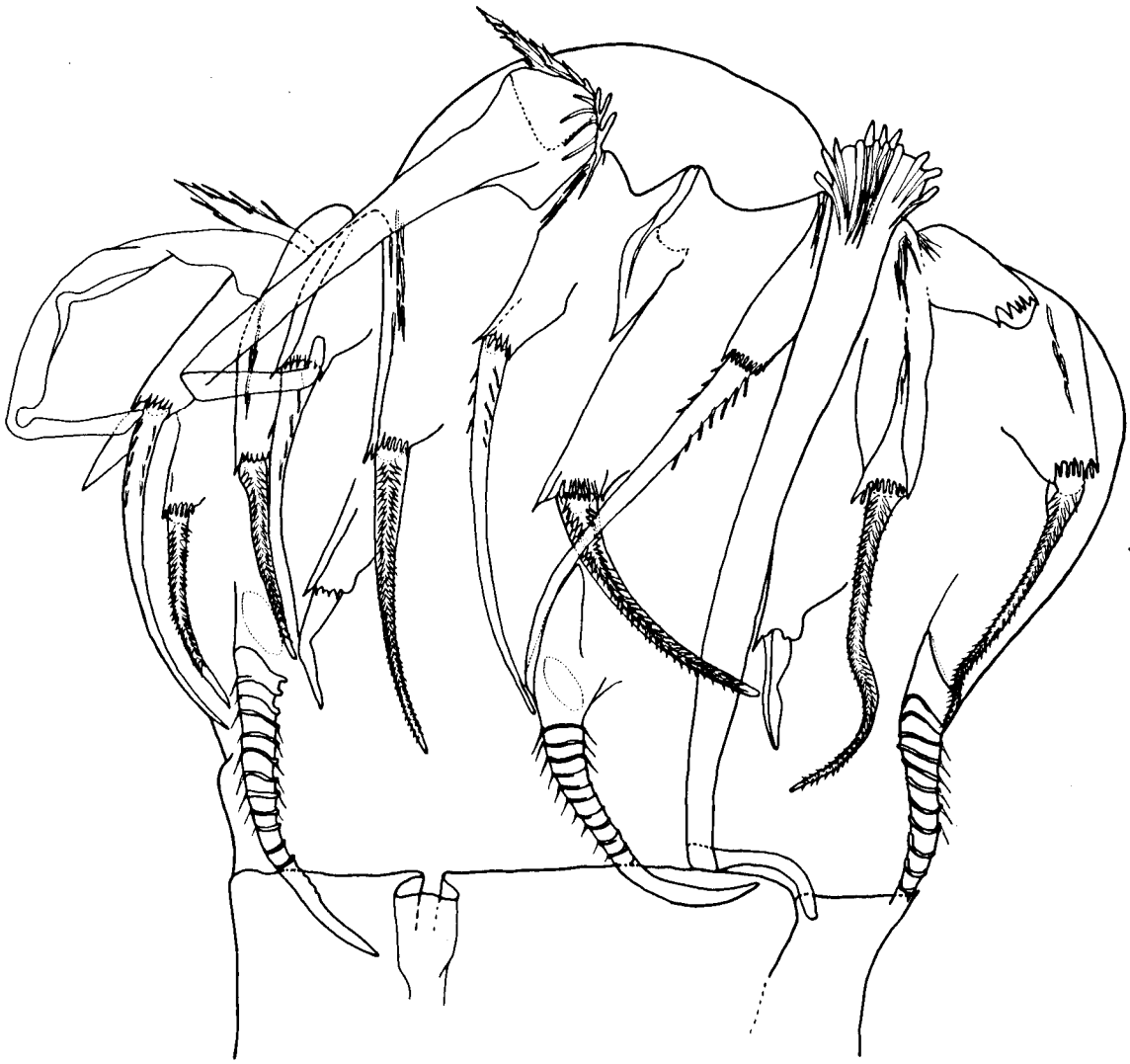
Sector No.	9	10	1	2
Ring 1 (right scalid)	39+	71	70	77
Ring 5 scalid		S16 T65		
Ring 5 proscalid	25 25		28 28	
Ring 6 scalid	S19 T53	S23 S26 T57 T60	S19 T52	S22 T50+
Ring 7 protrichoscalid		S8 T17	S8 T18	
Ring 7 trichoscalid	40	39	39	

Table 2B. Length of ventral scalids in J-1 K. phyllotropis of trunk length 210 um (Figs. 2.3 and 2.4).

Sector No.	4	5	6	7
Ring 1 (right scalid)	69	64	78	68
Ring 5 scalid	S14 T53		S16 T62	
Ring 5 proscalid		17 19		20
Ring 6 scalid	S22 S22 T40+ T43	S22 T53	S20 S21 T60 T58	
Ring 7 protrichoscalid				
S12 T22		S14 T23	S14 T25	S13 T25
Ring 7 trichoscalid	32		32	

FIGURE 2.6. Dorsal aspect of the everted J-2 head of a Kinorhynchus phyllotropis specimen with a trunk length of 280 um.

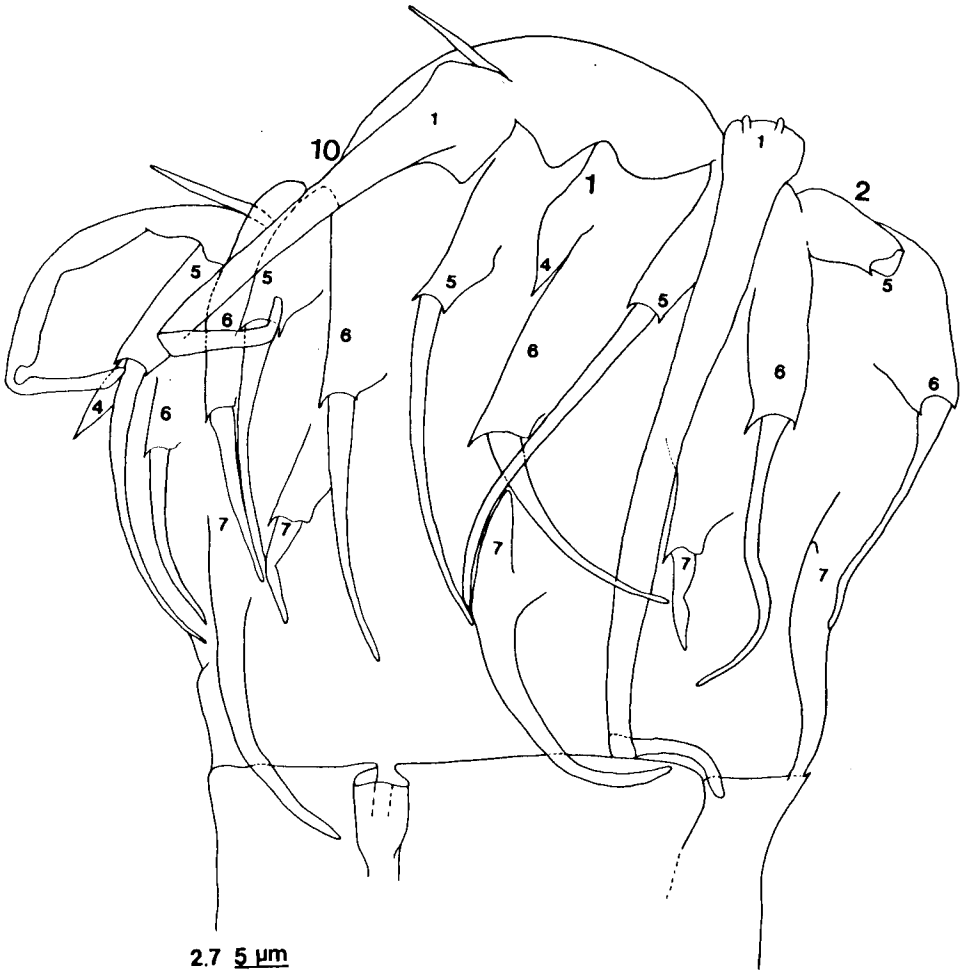
Scalid lengths are given in Table 2C.



2.6 5 µm

FIGURE 2.7. Head sector and scalid ring designation of scalids shown in Figure 2.6.

Large numbers show head sector designation.
Small numbers show scalid ring designation.



2.7 5 µm

FIGURE 2.8. Ventral aspect of the everted J-2 head of a Kinorhynchus phyllotropis specimen with a trunk length of 300 um.

Scalid lengths are given in Table 2D.

Pairs of protrichoscalids are located in head sectors 2 and 3, and 6 and 7. These pairs of protrichoscalids indicate the true lateral axes.

Two ventral trichoscalids are seen between these paired lateral protrichoscalids. In the first three juvenile stages there are two trichoscalids on each of the three sides of the body.

The only other specimen showing both pairs of lateral trichoscalids was the J-4 specimen, drawn in Figs. 3.3 and 3.4.

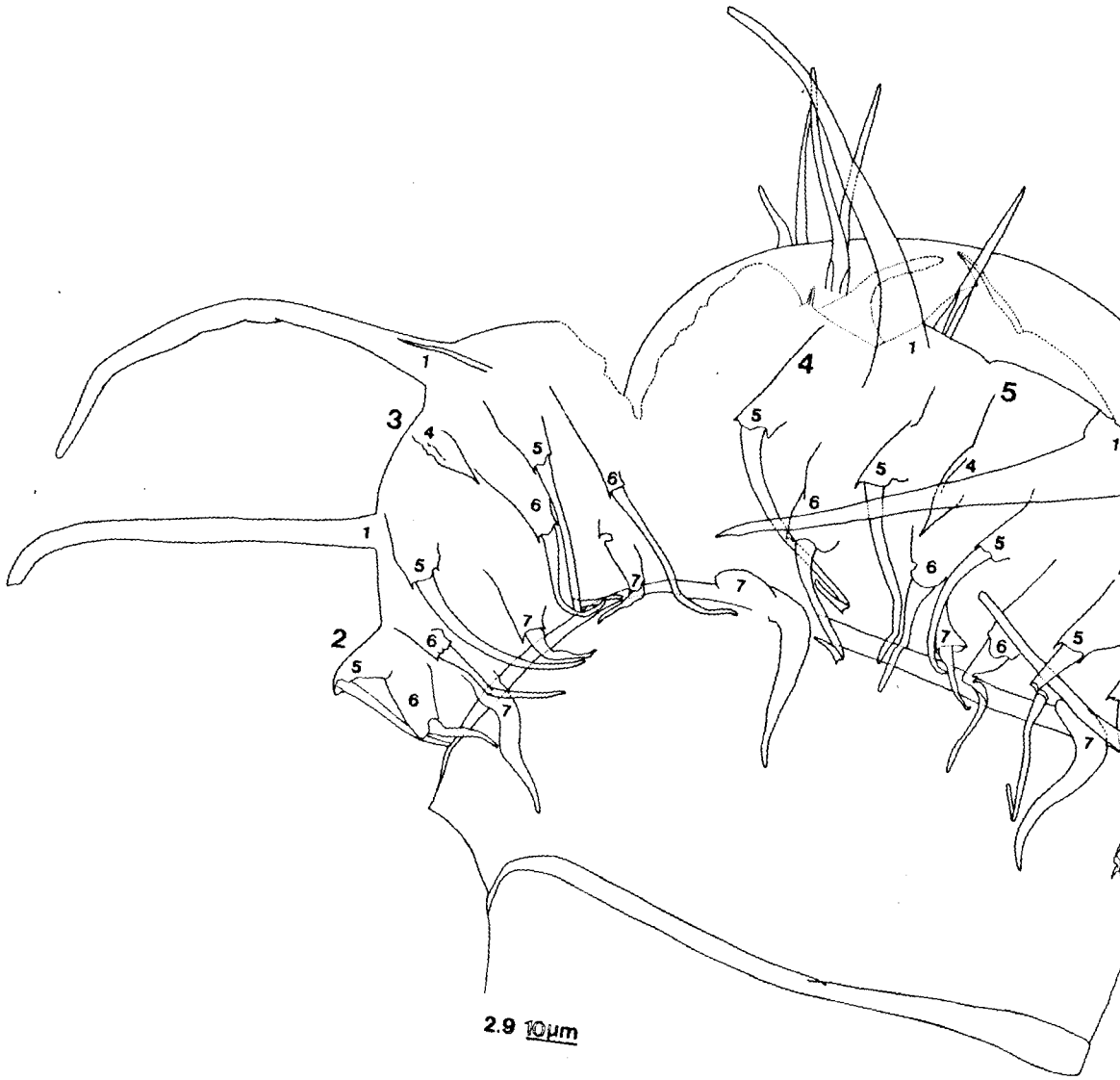
2.8 10µm

FIGURE 2.9. Head sector and scalid ring designation of scalids shown in Figure 2.8.

Large numbers show head sector designation.
Small numbers show scalid ring designation.

Pairs of protrichoscalids are located in head sectors 2 and 3, and 6 and 7. These pairs of protrichoscalids indicate the true lateral axes.

Two ventral trichoscalids are seen between these paired lateral protrichoscalids. In the first three juvenile stages there are two trichoscalids on each of the three sides of the body.



2.9 10µm

FIGURE 2.10. Schematic representation of scalid arrangement in the second juvenile stage, or J-2, of Kinorhynchus phyllotropis.

Horiztonal numbers are the numbers of the head sectors as designated by Zelinka (1928, Figs. 3-4; Fig. 2 of this thesis).
Vertical numbers are the numbers of the scalid rings.

KEY

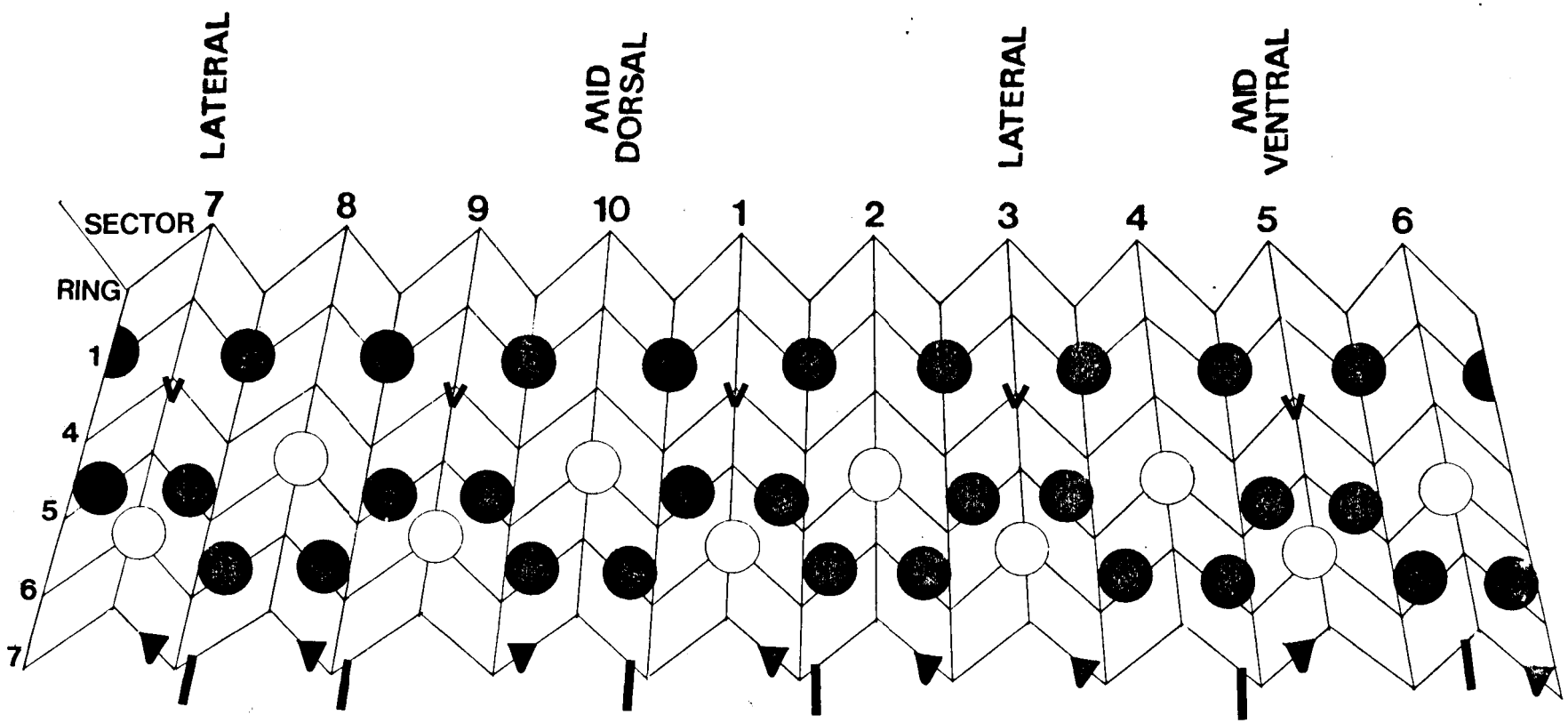
White circle - scalid belonging to the series in the centre of the head sector.

Black circle - scalid belonging to the series at the sides of the head sector.

V - proscalid

Black triangle - protrichoscalid

Black line - trichoscalid.


LATERAL
MID DORSAL
LATERAL
MID VENTRAL
SECTOR
RING
7
8
9
10
1
2
3
4
5
6
1
4
5
6
7

J-2

2.10

Table 2C. Length of dorsal scalids of J-2 K. phyllotropis of trunk length 280 um.(Figs. 2.6 and 2.7).
S = length of socket in micrometres (in rings 5-7).
T = total length of scalid in micrometres.

Sector No.	10	1	2
Ring 1 (right scalid)	54	76	
Ring 4 proscalid		10	
Ring 5 scalid	S21 T39		
Ring 6 scalid	S19 T47	S19 S19 T44 T48	S18 T48
Ring 7 protrichoscalid	S11 T21	S9 T19	
Ring 7 trichoscalid	34	31	22+

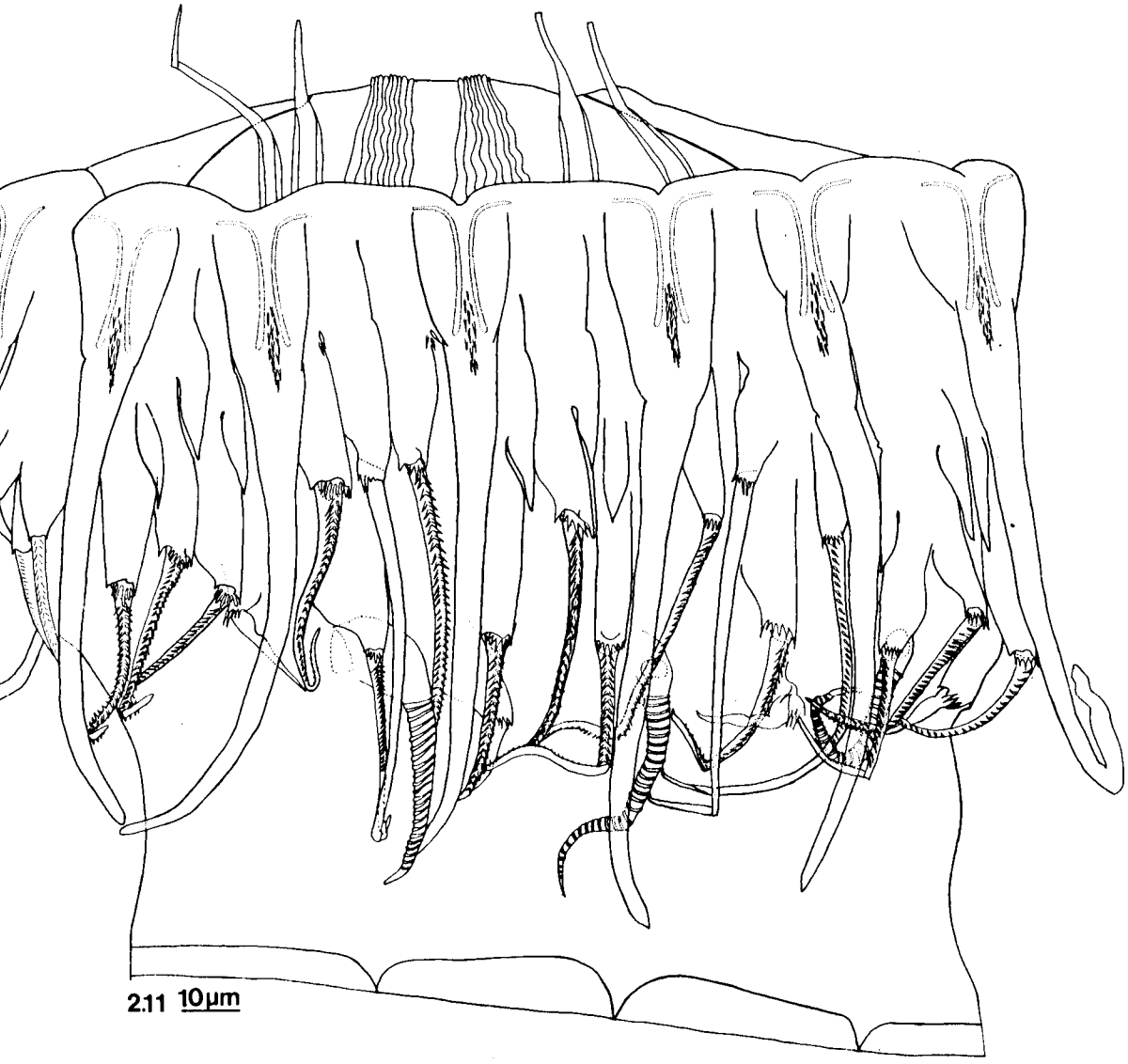
Table 2D. Length of ventral scalids of J-2 K. phyllotropis of trunk length 300 um. (Figs. 2.8 and 2.9)

Sector No.	2	3	4	5	6
Ring 1 (right scalid)	74	90	96	88	97
Ring 4 proscalid		12		10	
Ring 5 scalid	S14 T39+	S16 S12 T55 T50	S11 T61	S16 S13 T54 T42	S14 T62
Ring 6 scalid	S14 S12 T29 T40	S16 T42	S10 S18 T49 T49	S17 T41	S22 S23 T51 T65
Ring 7 protrichoscalid	S15 T31	S11 T21		S10 T23	S15 T25
Ring 7 trichoscalid	33	38		34	

FIGURE 2.11. Dorsal aspect of the everted J-3 head of a Kinorhynchus phyllotropis specimen with a trunk length of 380 um.

Scalid lengths are given in Table 2E.

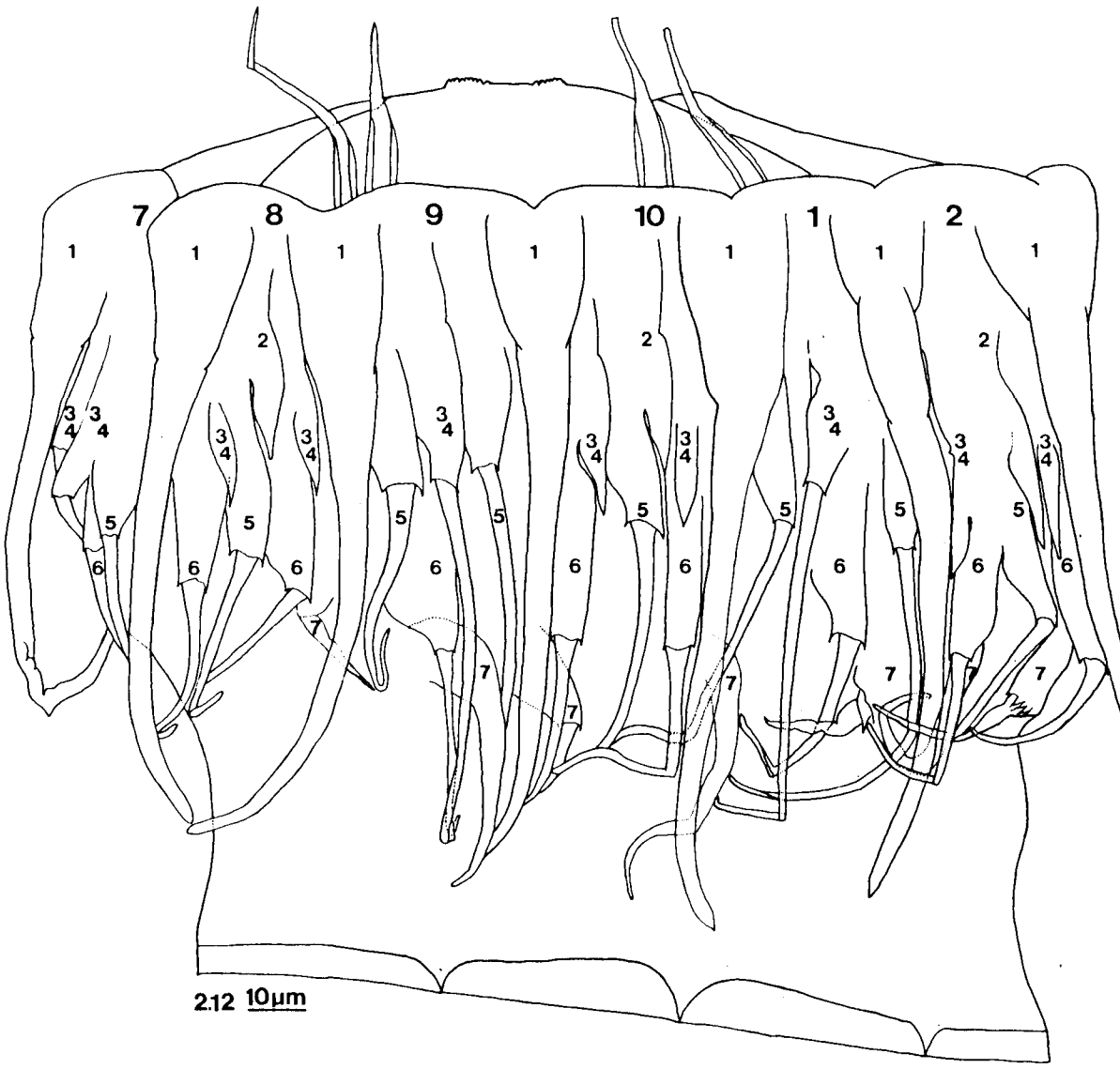
This figure shows the first appearance of smooth scalids.



2.11 10µm

FIGURE 2.12. Head sector and scalid ring designation of scalids shown in Figure 2.11.

Large numbers show head sector designation.
Small numbers show scalid ring designation.


7
8
9
10
1
2
2.12 10µm

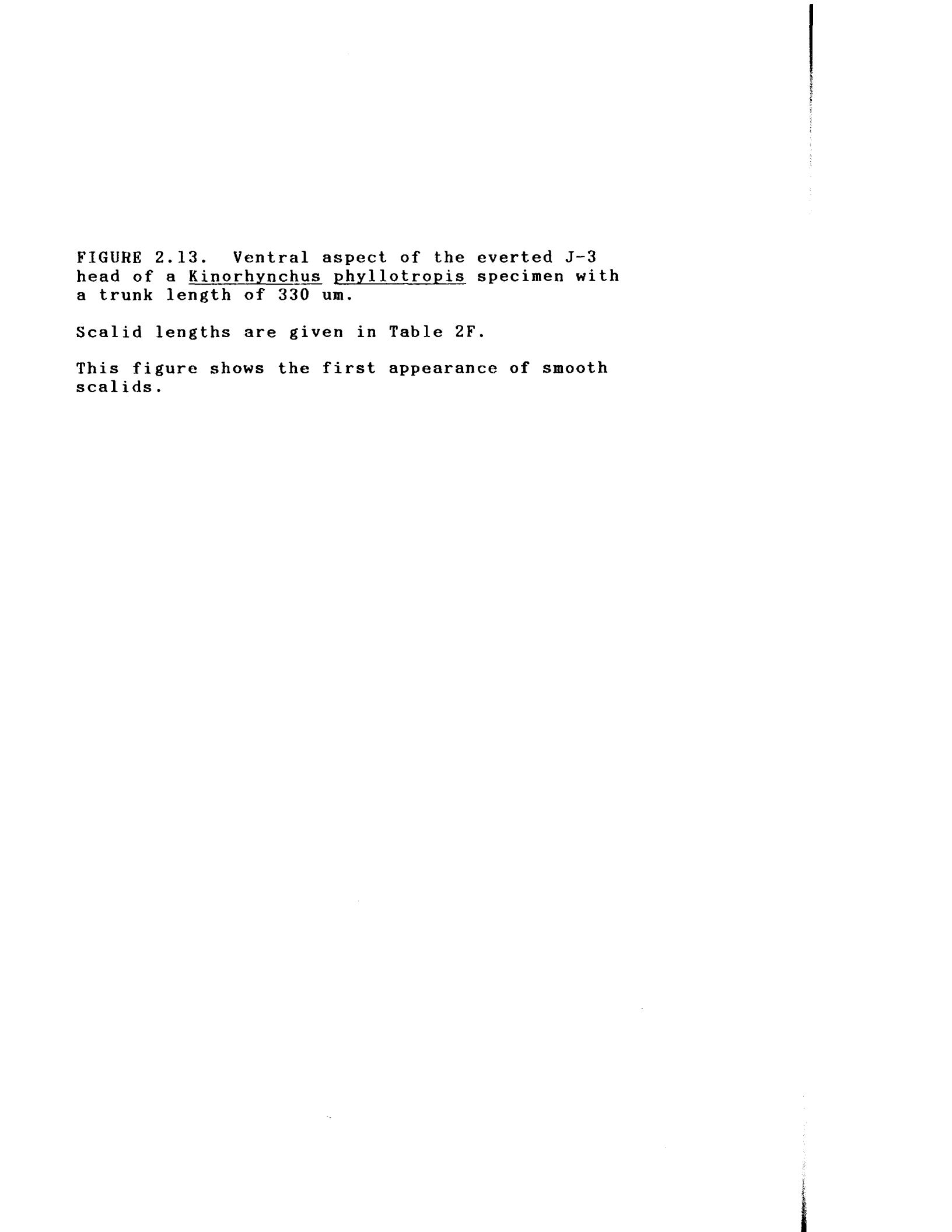
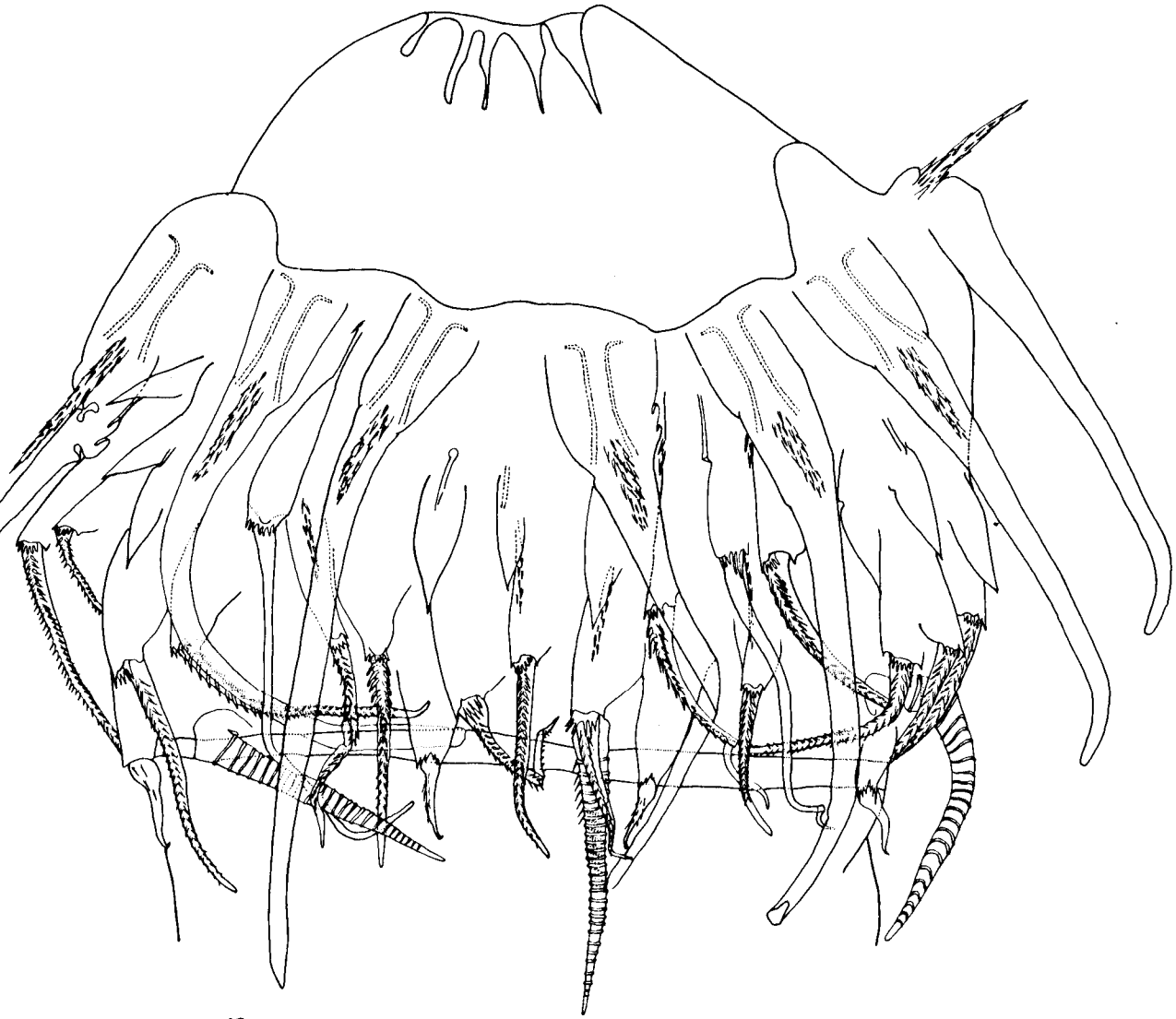


FIGURE 2.13. Ventral aspect of the everted J-3 head of a Kinorhynchus phyllotropis specimen with a trunk length of 330 um.

Scalid lengths are given in Table 2F.

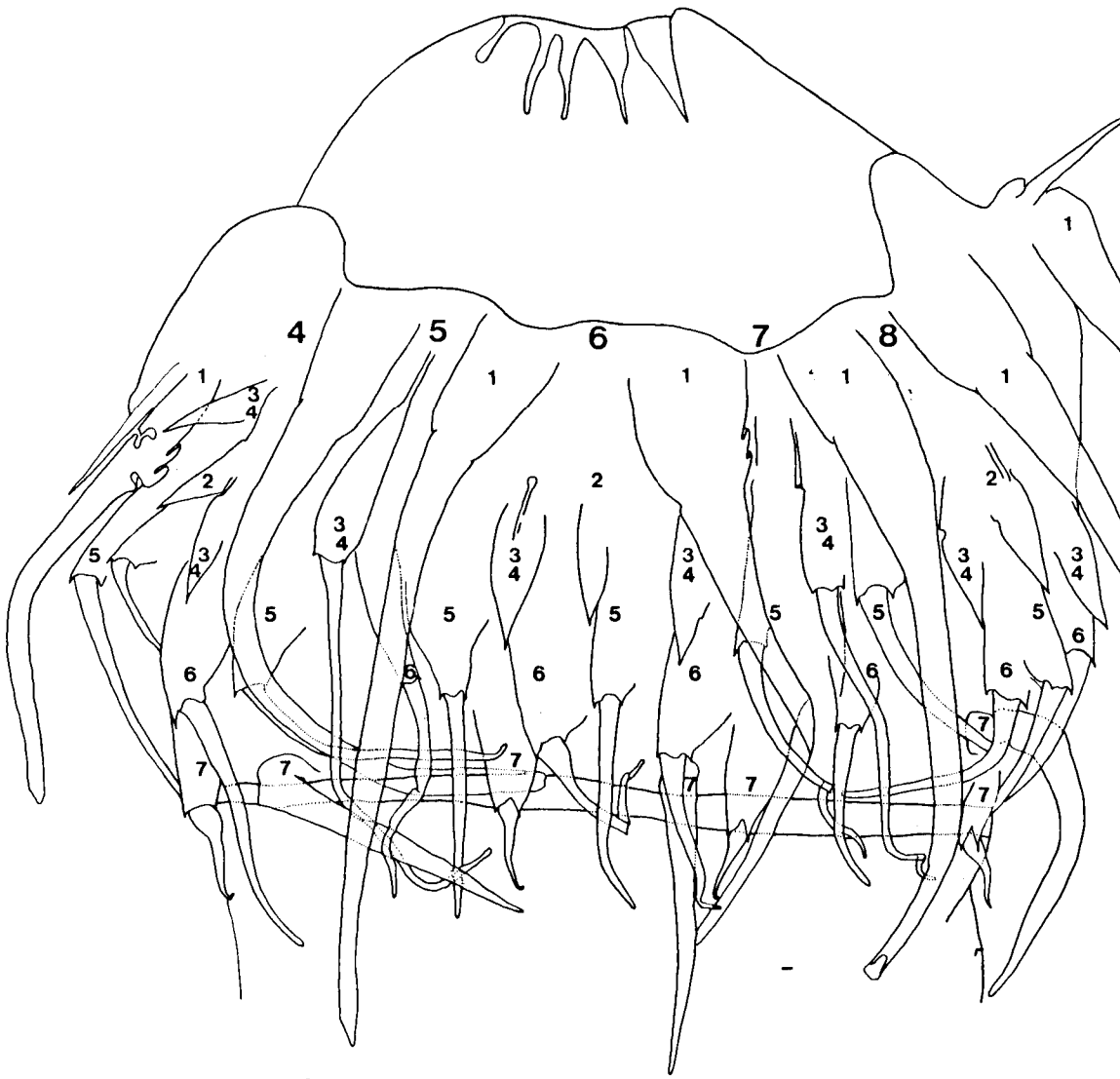
This figure shows the first appearance of smooth scalids.



2,13 10µm

FIGURE 2.14. Head sector and scalid ring designation of scalids shown in Figure 2.13.

Large numbers show head sector designation.
Small numbers show scalid ring designation.



214 10µm

FIGURE 2.15. Schematic representation of scalid arrangement in the third juvenile stage, or J-3, of Kinorhynchus phyllotropis.

Horizontal numbers are the numbers of the head sectors as designated by Zelinka (1928, Figs. 3-4; Fig. 2 of this thesis).
Vertical numbers are the numbers of the scalid rings.

KEY

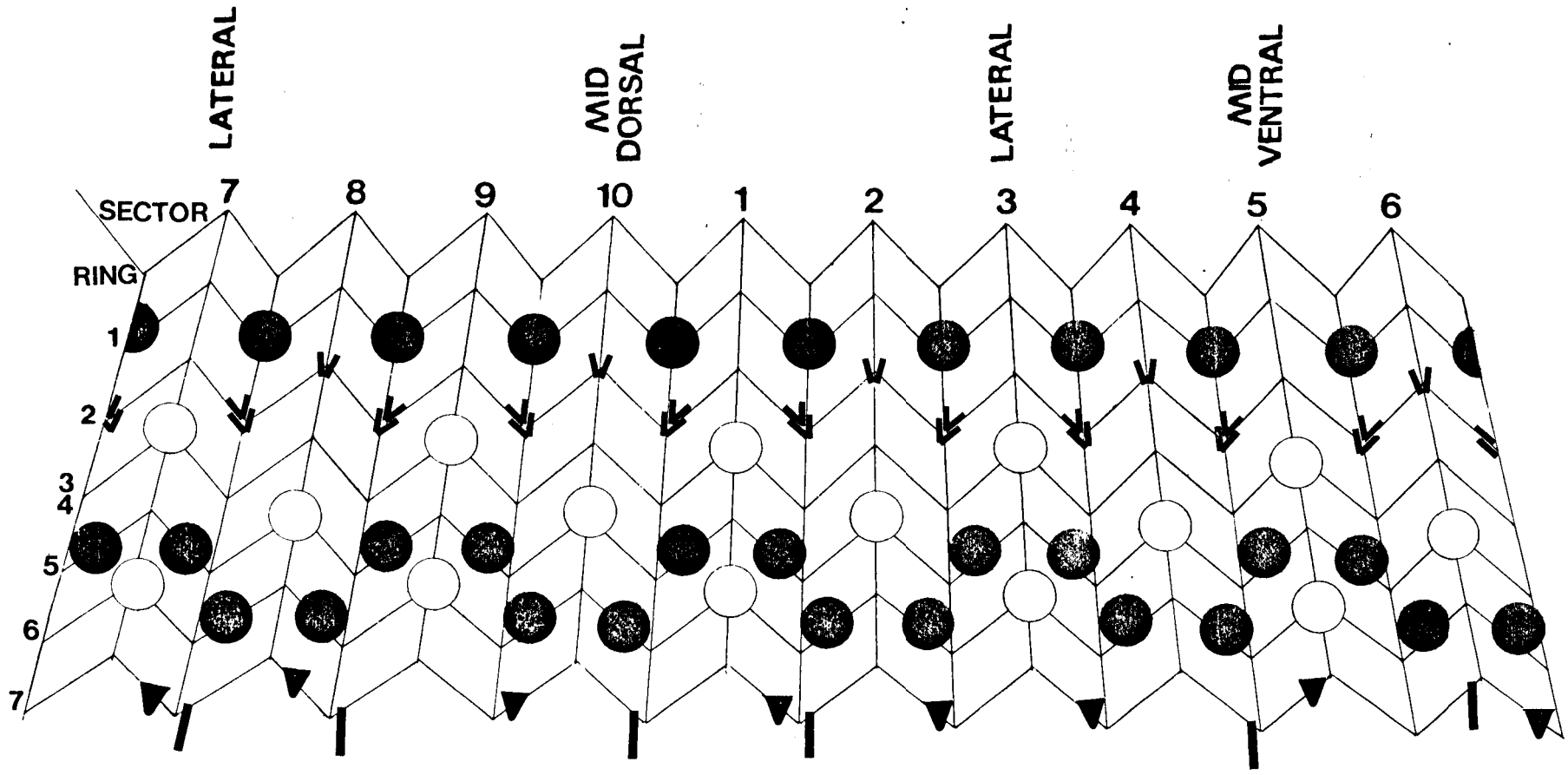
White circle - scalid belonging to the series in the centre of the head sector.

Black circle - scalid belonging to the series at the sides of the head sector.

V - proscalid. (Two fused proscalids are seen in the fused 3/4 scalid rings which separate in the following stage of development).

Black triangle - protrichoscalid.

Black line - trichoscalid.


LATERAL
MID DORSAL
LATERAL
MID VENTRAL
SECTOR
RING
7
8
9
10
1
2
3
4
5
6
1
2
3
4
5
6
7

J-3

Table 2E. Length of dorsal scalids of J-3 K. phyllotropis of trunk length 380 um (Figs. 2.11 and 2.12)
S = total length of socket in micrometres (in rings 3/4-7)
T = total length of scalid in micrometres.

Sector No.	8	9	10	1	2
Ring 1 (right scalid)	116	113	124	121	127
Ring 2 proscalid	24		24		25
Ring 3/4 proscalid and scalid	22 23	S28 T95	28 25	S19 T89	23 24
Ring 5 scalid	S22 T58		S21 T58		S24 T66
Ring 6 scalid	S21 S21 T52 T45+	S29 T66	S28 S27 T59 T68	S28 T59	S21 S24 T61 T56
Ring 7 protrichoscalid	S19 T37		S18 T31	S15 T35	S16 T31
Ring 7 trichoscalid		43	49		48

Table 2F. Length of ventral scalids of J-3 K. phyllotropis of trunk length 330 um (Figs. 2.13 and 2.14).

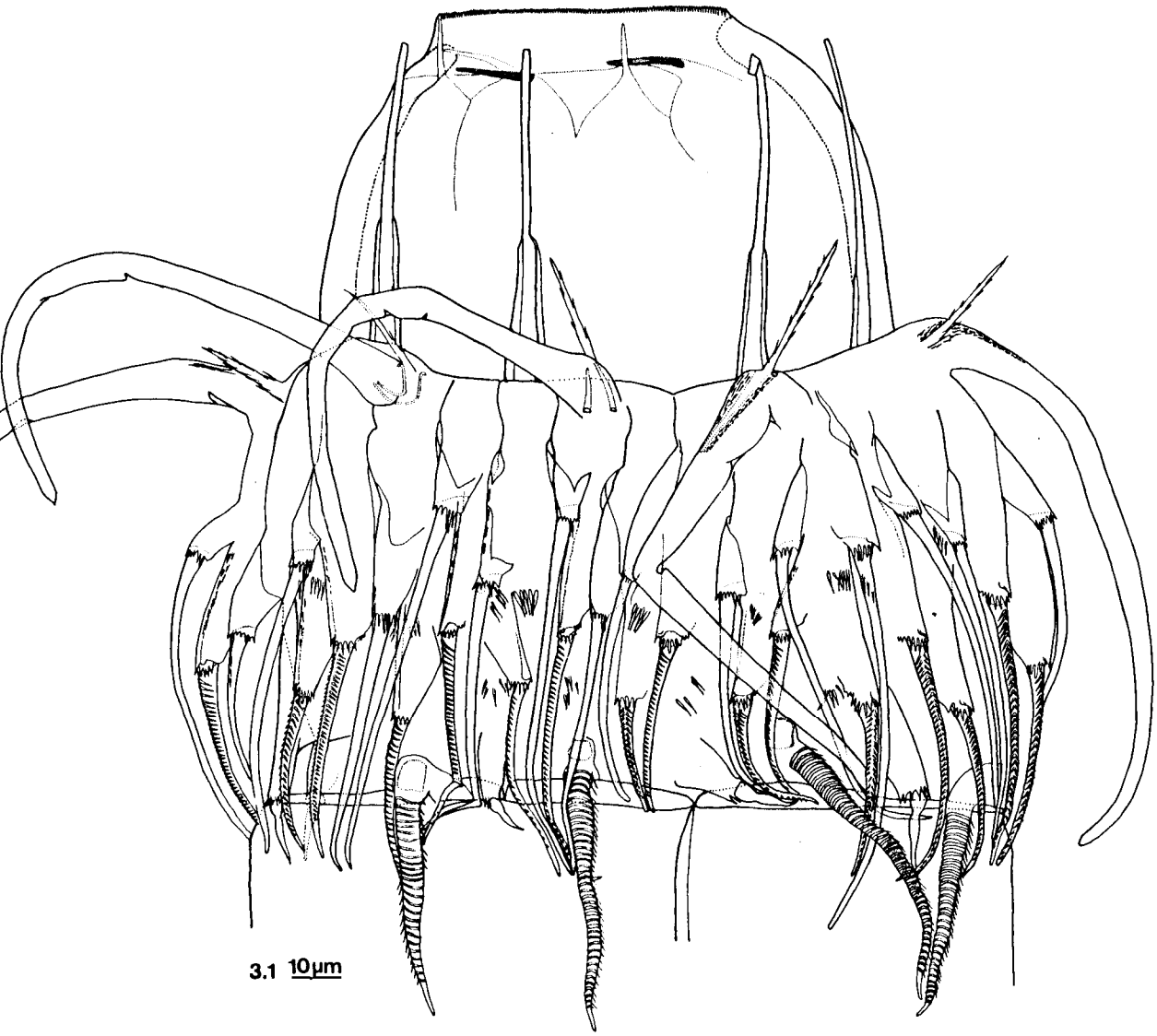
Sector No.	4	5	6	7	8
Ring 1 (right scalid)	118	117	105+	110	103
Ring 2 proscalid	18		19		19
Ring 3/4 proscalid and scalid	19 19	S29 T99	23 24	S28 T87	18 21
Ring 5 scalid			S25 T56		
Ring 6 scalid	S28 S24 T68+ T71	S24 T63	S27 S25 T60 T54	S23 T51	S23 T59
Ring 7 protrichoscalid	S16 T33	S17 T32	S17 T29	S14 T26	
Ring 7 trichoscalid	48		50		58

APPENDIX THREE

FIGURE 3.1. Dorsal aspect of the everted J-4 head of a Kinorhynchus phyllotropis specimen with a trunk length of 370 um.

Scalid lengths are given in Table 3A.

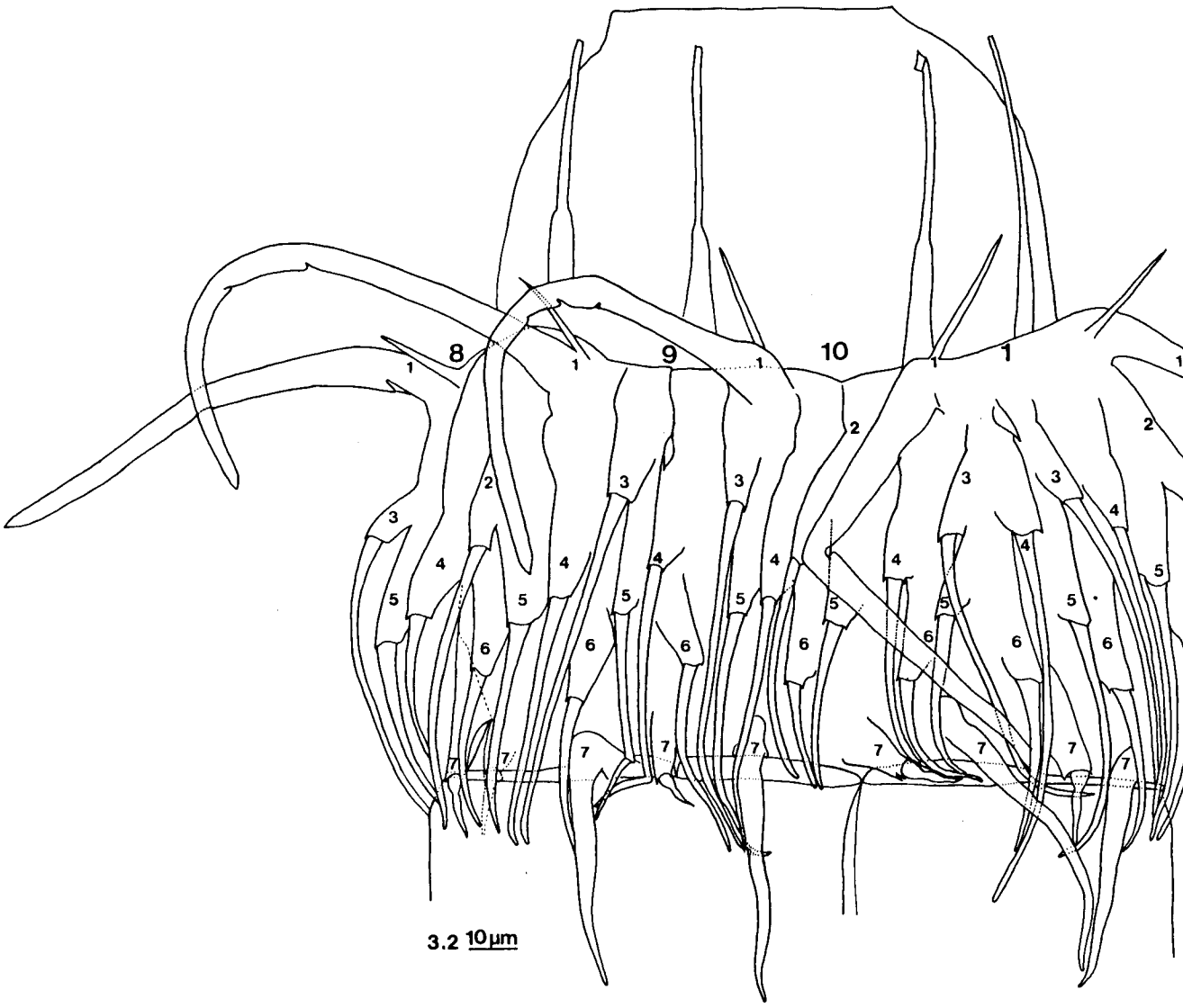
This diagram shows internal scalids inside the oral cone.



3.1 10µm

FIGURE 3.2. Head sector and scalid ring designation of scalids shown in Figure 3.1.

Large numbers show the head sector designation.
Small numbers show the scalid ring designation.

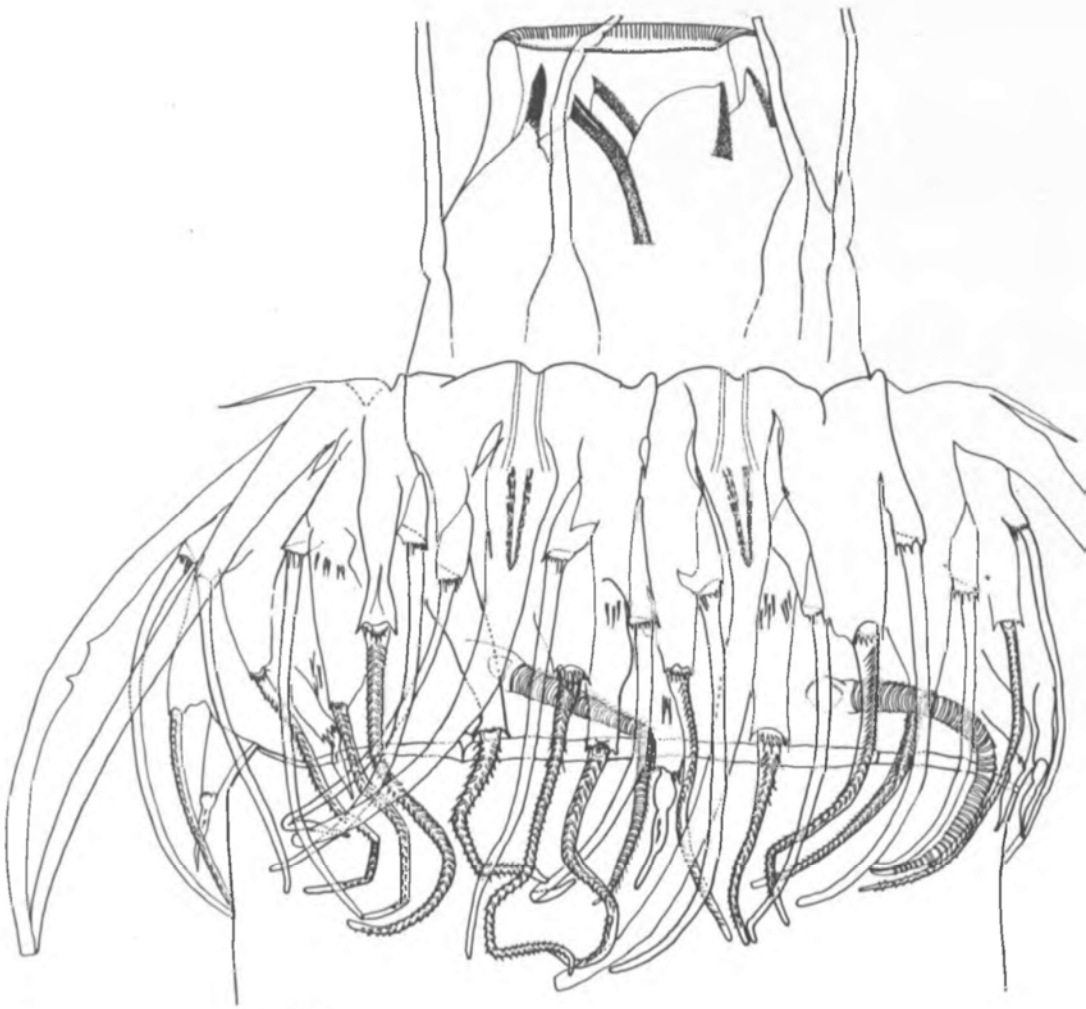


3.2 10µm

FIGURE 3.3. Ventral aspect of the everted J-4 head of a Kinorhynchus phyllotropis specimen with a trunk length of 390 um.

This diagram shows internal scalids inside the oral cone.

Scalid lengths are given in Table 3B. The pair of smaller trichoscalids in head sectors 6 and 7, and head sectors 2 and 3, mark the location of the true lateral axes. In other sectors long and short trichoscalids alternate with each other.

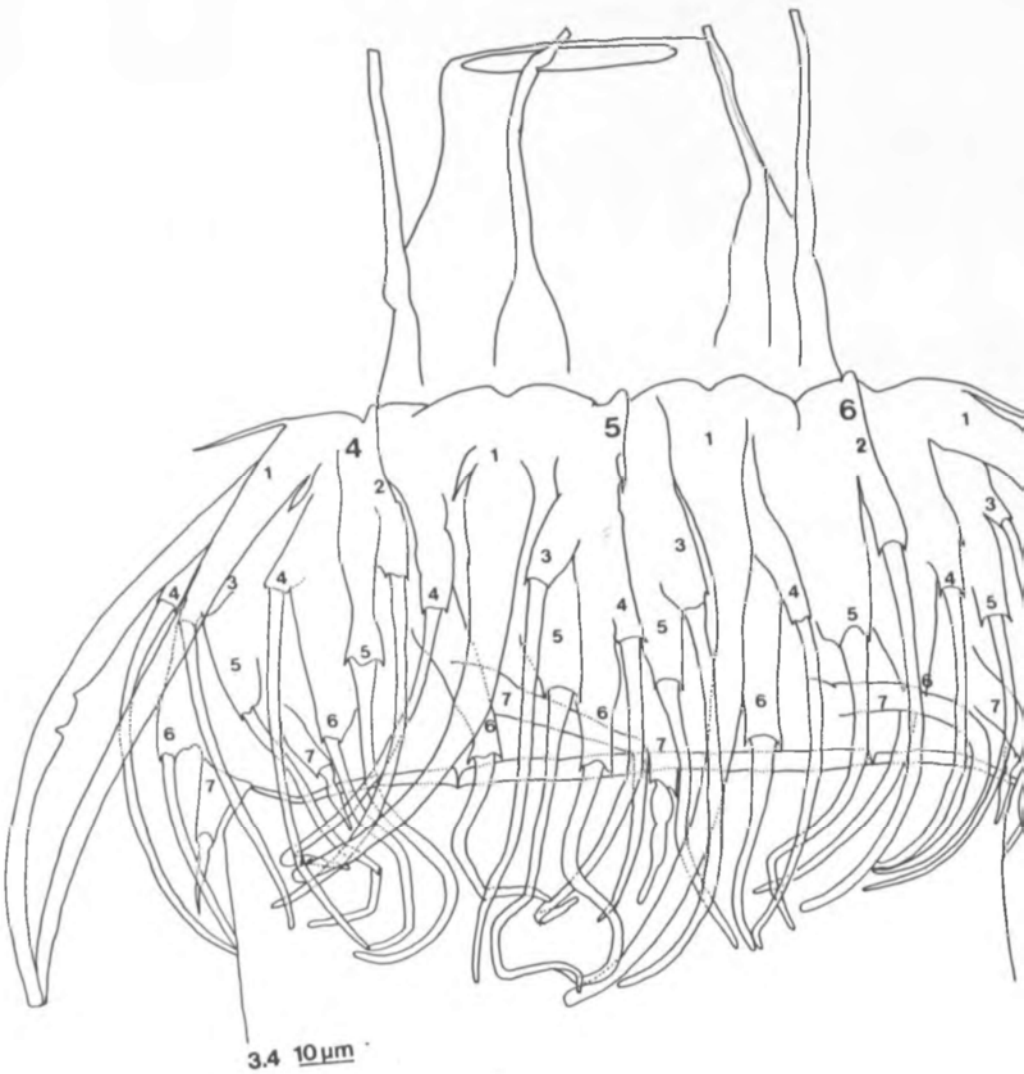


3.3 10 µm

FIGURE 3.4. Head sector and scalid ring designation of scalids shown in Figure 3.3.

Large numbers show the head sector designation. Small numbers show the scalid ring designation.

Scalid lengths are given in Table 3B. The pair of smaller trichoscalids in head sectors 6 and 7, and head sectors 2 and 3, mark the location of the true lateral axes. In other sectors long and short trichoscalids alternate with each other.



3.4 10µm

FIGURE 3.5. Schematic representation of scalid arrangement in the fourth juvenile stage, or J-4, of Kinorhynchus phyllotropis.

Horizontal numbers are the numbers of the head sectors as designated by Zelinka (1928, Figs. 3-4; Fig. 2 of this thesis).
Vertical numbers are the numbers of the scalid rings.

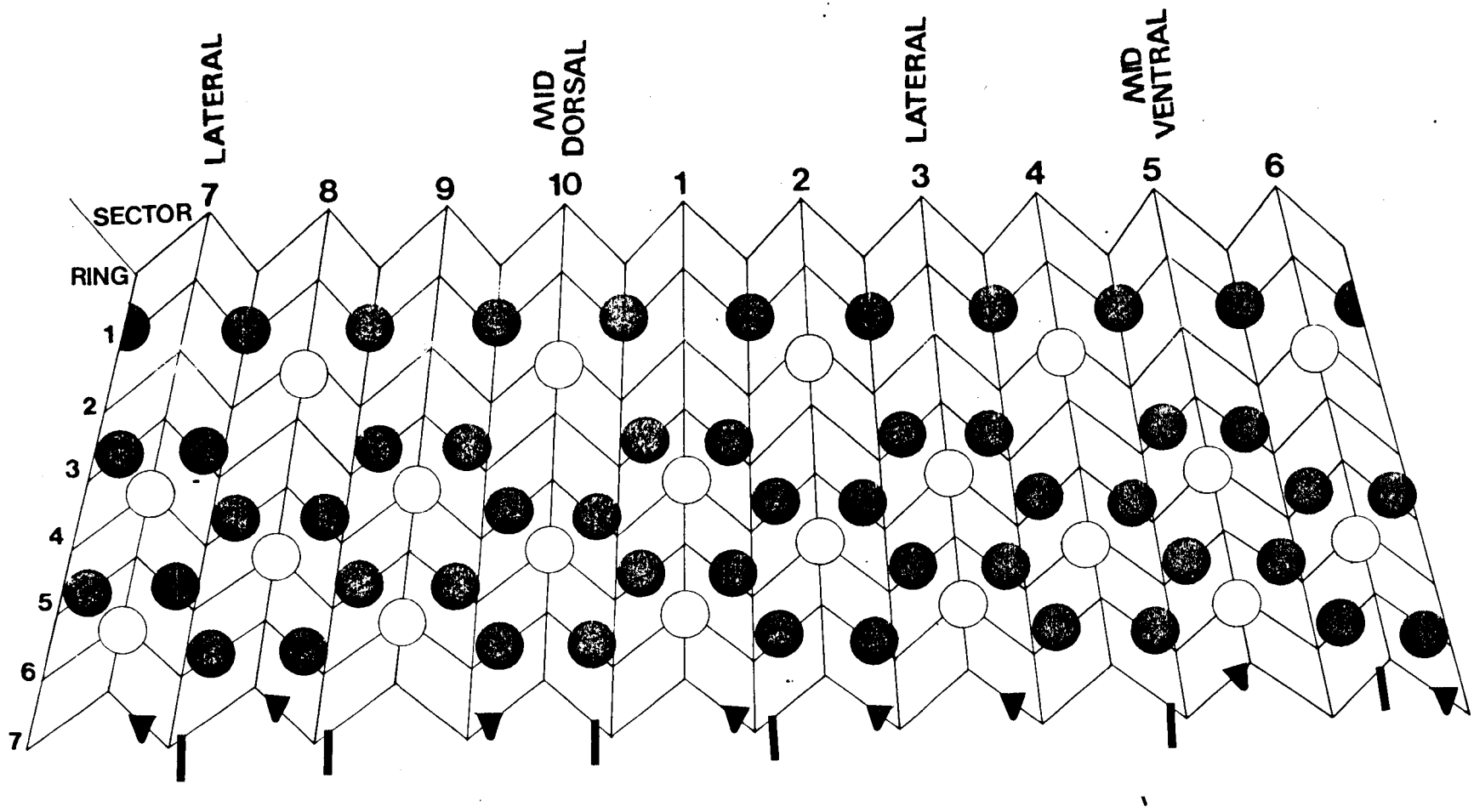
KEY

White circle - scalid belonging to the series in the centre of the head sector.

Black circle - scalid belonging to the series at the sides of the head sector.

Black triangle - protrichoscalid.

Black line - trichoscalid.


LATERAL
MID DORSAL
LATERAL
MID VENTRAL
SECTOR
RING
7
8
9
10
1
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3
4
5
6
1
2
3
4
5
6
7

J-4

Table 3A. Length of dorsal scalids of J-4 K. phyllotropis of trunk length 370 um (Figs. 3.1 and 3.2)
S = length of socket in micrometres (in rings 2-7)
T = total length of scalid in micrometres.

Sector No.	8	9	10	1	2
Ring 1 (right scalid)	125	122	120	126	
Ring 2	S22 T86		S29 T76		
Ring 3		S18 S17 T94 T92		S18 S18 T88 T66+	
Ring 4	S22 S27 T54+ T81	S17 T75	S29 S16 T84 T74	S17 T95	
Ring 5	S22 T77	S26 S25 T74 T77	S24 T52	S21 S28 T57 T79	S21 T71
Ring 6	S23 S23 T58 T57	S18 T62	S18 S18 T42 T49	S26 T61	S28 S28 T62 T68
Ring 7 protrichoscalid	S15 T29		S16 T26	S12 T25	
Ring 7 trichoscalid	53	59	68		53+

Table 3B. Length of ventral scalids of J-4 K. phyllotropis of trunk length 390 um. (Figs. 3.3 and 3.4).

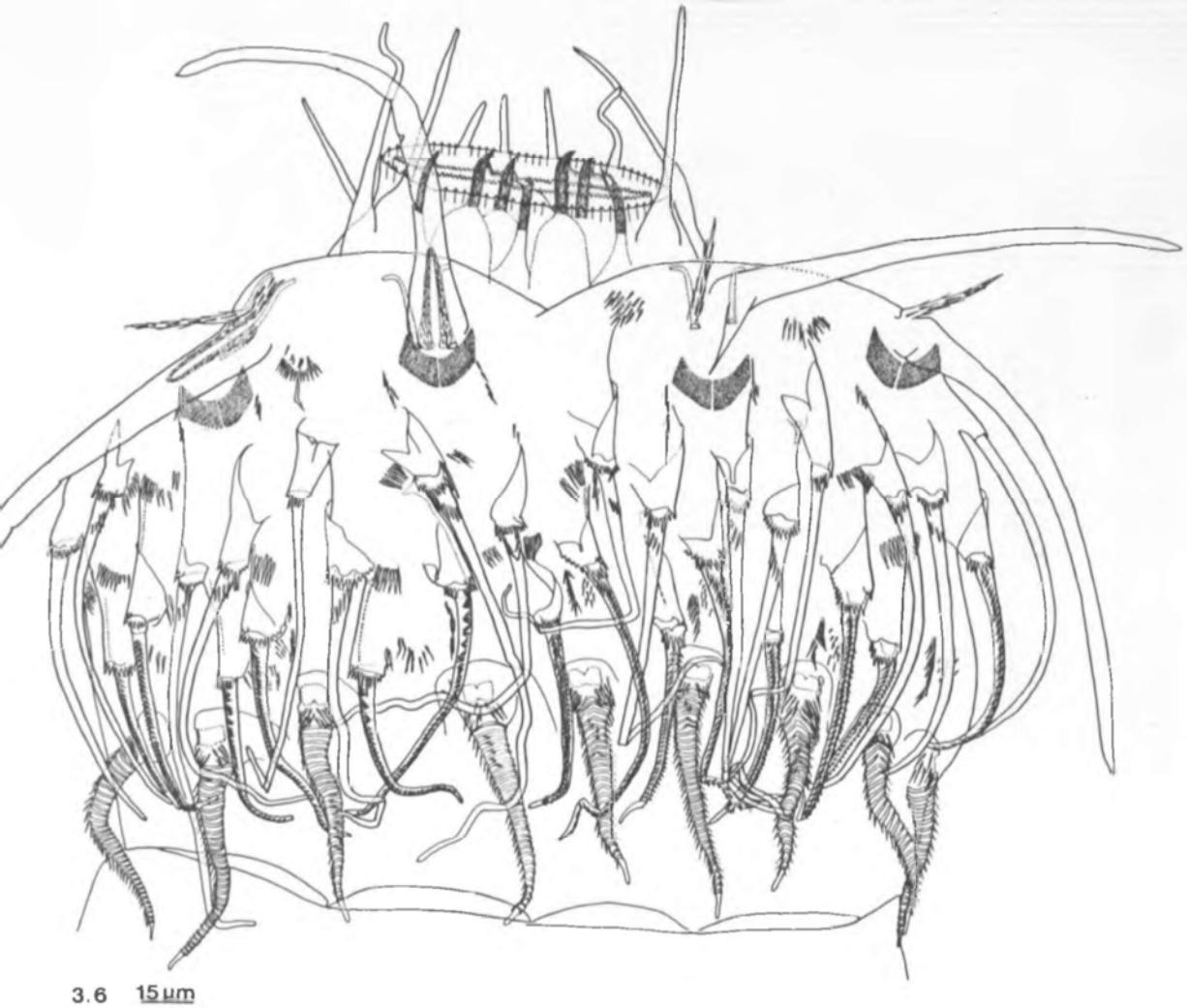
Sector No.	4	5	6
Ring 1 (right scalid)	95	123	123
Ring 2	S14 T86		S15 T91
Ring 3		S28 S20 T91 T100	
Ring 4	S20 S15 T88 T84	S24 T94	S24 S18 T88 T78
Ring 5	S29 T103	S26 S18 T102 T75	S29 T98
Ring 6	S28 S29 T77 T75	S23 T77	S26 S23 T68 T72
Ring 7 protrichoscalid	S14 S14 I T29 T26 I	S17 T40	I S20 S16 I T34 T29
Ring 7 trichoscalid	64		70

FIGURE 3.6. Dorsal aspect of the everted J-5 head of a Kinorhynchus phyllotropis specimen with a trunk length of 510 um.

Scalid lengths are given in Table 3C.

This diagram shows internal scalids inside the oral cone as well as the insertion of the outer head retractor muscles below the origin of the scalid ring one scalids.

J-5 specimens are wider than others. The body is well developed but the cuticle is flexible juvenile cuticle. It has been necessary to use a smaller enlargement factor for J-5 head diagrams than for other juvenile stages.



3.6 15 µm

FIGURE 3.7. Head sector and scalid ring designation of scalids shown in Figure 3.6.

Large numbers show the head sector designation.
Small numbers show the scalid ring designation.

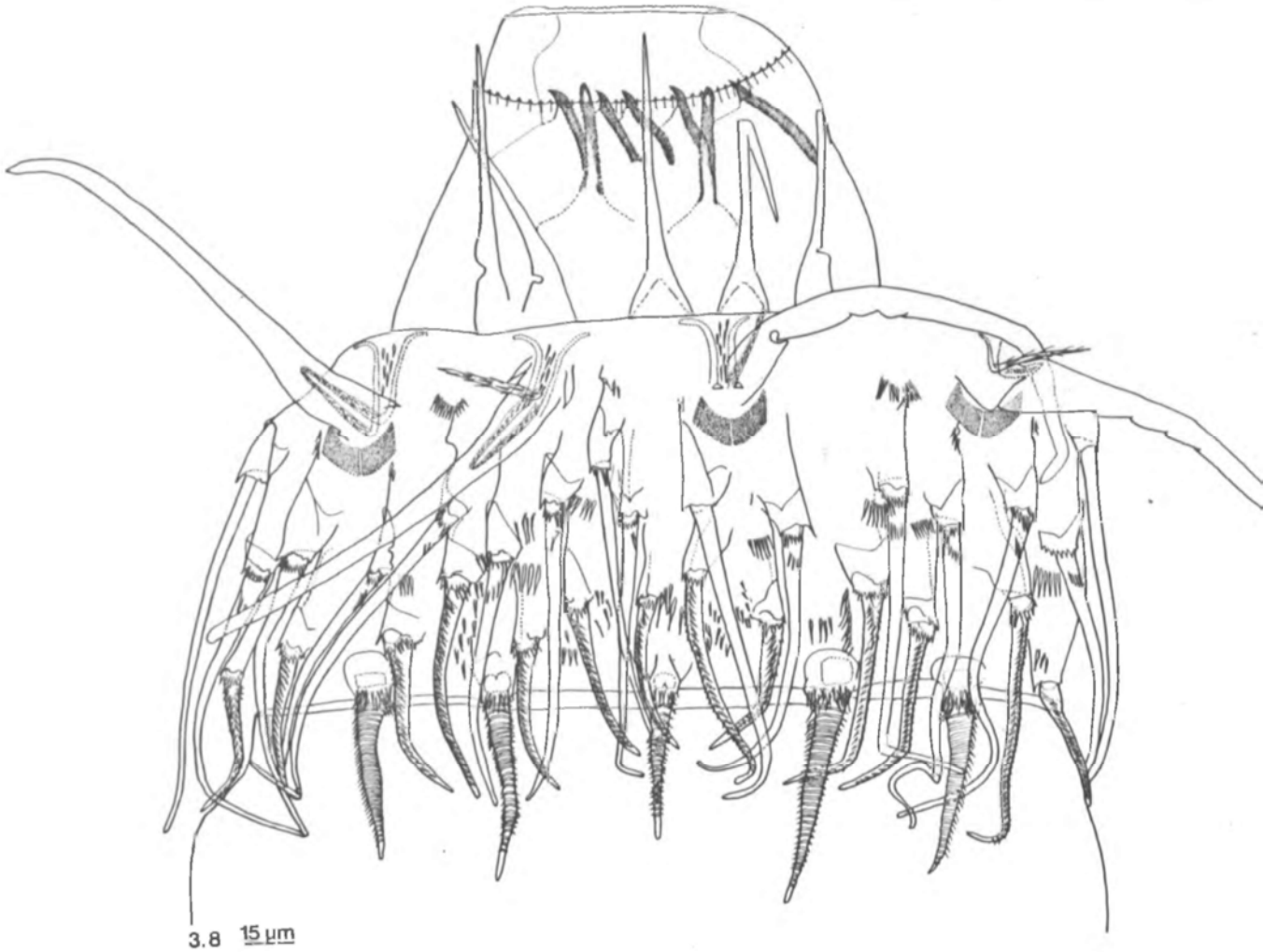
3.7 15 µm

FIGURE 3.8. Ventral aspect of the everted J-5 head of a Kinorhynchus phyllotropis specimen with a trunk length of 500 um.

Scalid lengths are given in Table 3D. The smallest trichoscalid marks the midventral axis.

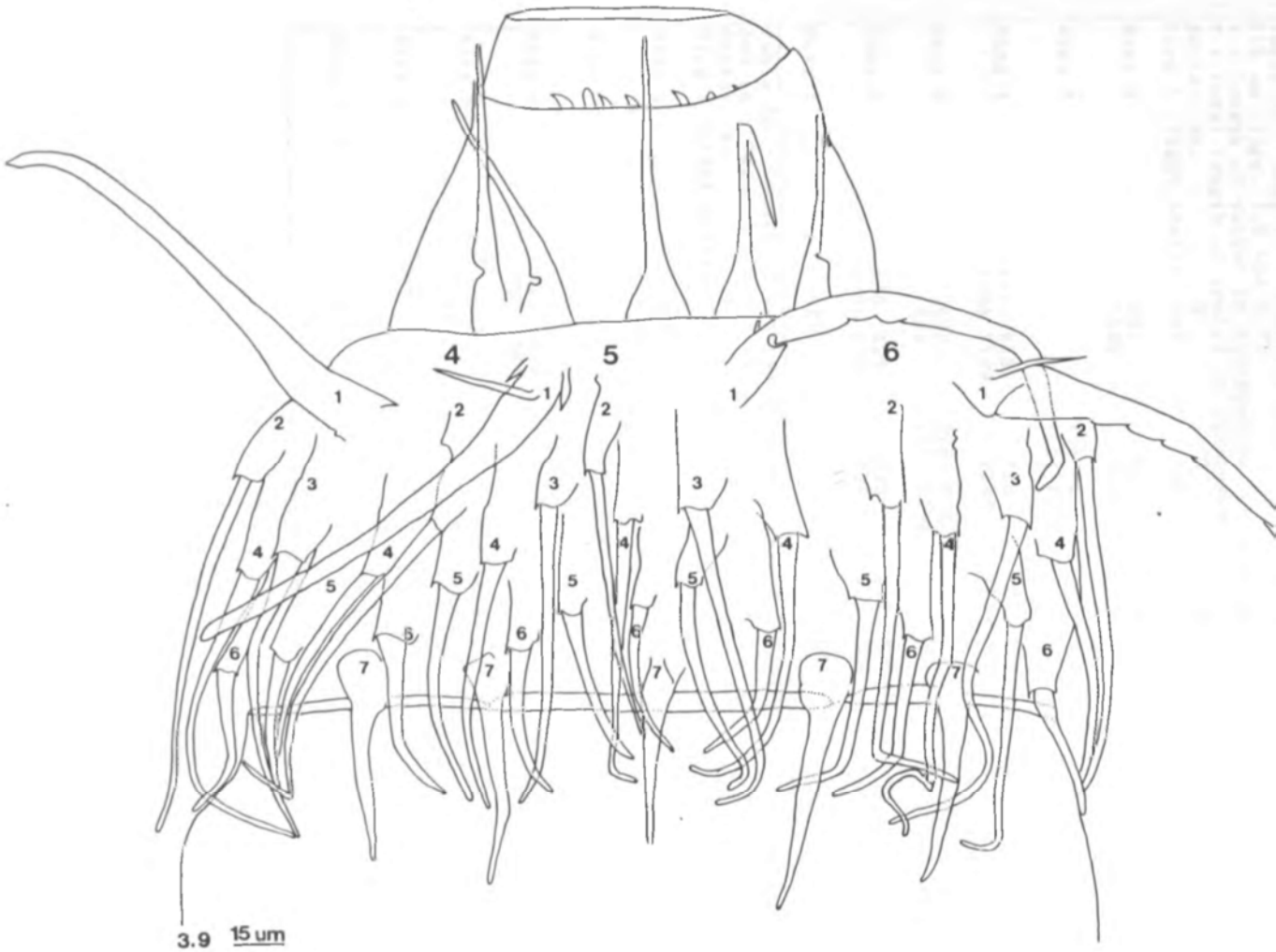
This diagram shows internal scalids inside the oral cone as well as the insertion of the outer head retractor muscle below the origin of the ring one scalids.

J-5 specimens are wider than others. The body is well developed but the cuticle is flexible juvenile cuticle. It has been necessary to use a smaller enlargement factor for J-5 head diagrams than for other juvenile stages.



3.8 15 µm

FIGURE 3.9. Head sector and scalid ring designation of scalids shown in Figure 3.8. Large numbers show the head sector designation. Small numbers show the scalid ring designation.



3.9 15 um

Table 3C. Length of dorsal scalids of J-5 K. phyllotropis of trunk length 510 um (Figs. 3.6 and 3.7).
S = length of socket in micrometres (in rings 2-6)
T = total length of scalid in micrometres.

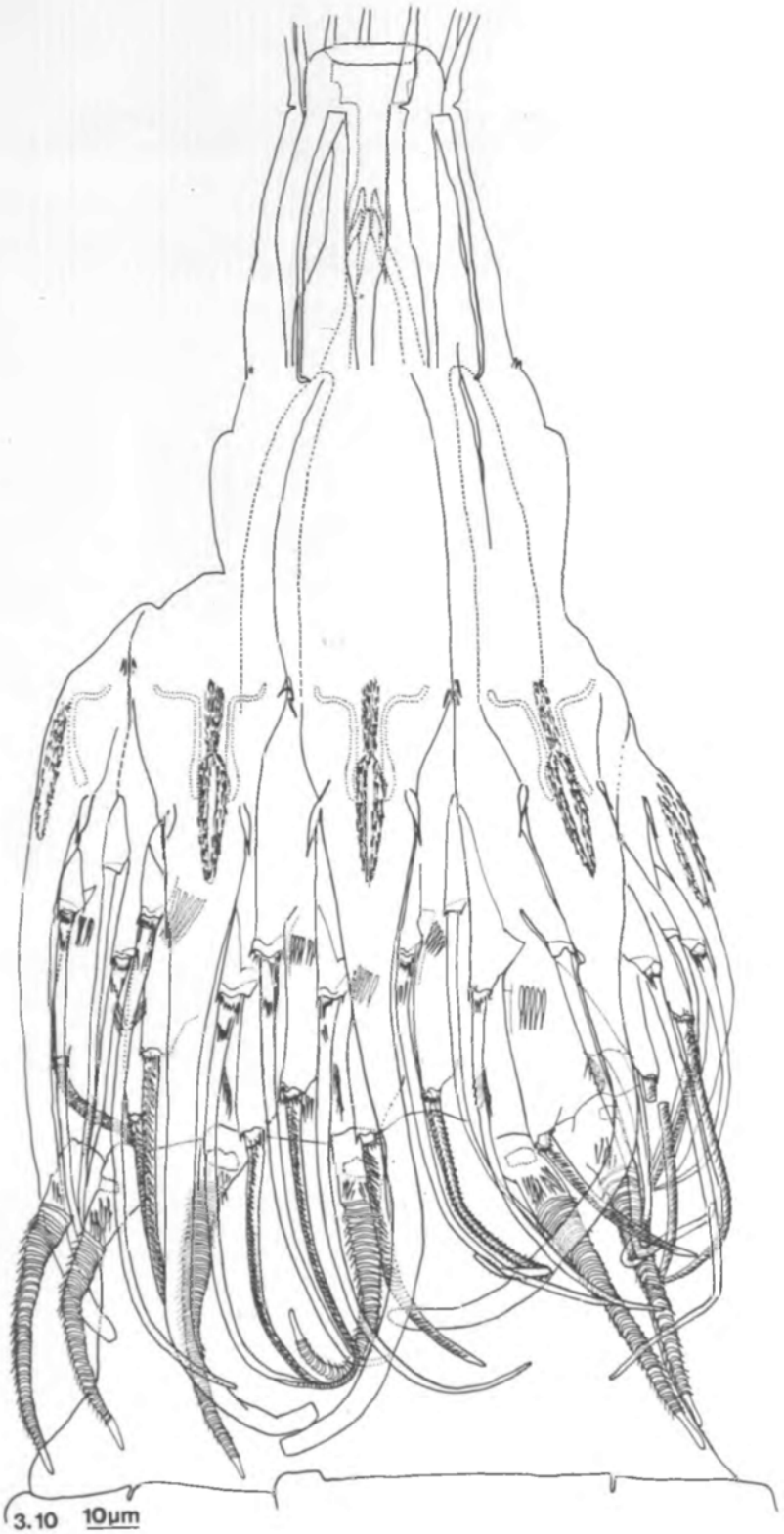
Sector No.	8	9	10	1	2
Ring 1 (right scalid)	142	142	151	156	
Ring 2	S22 T120	S21 T117	S21 T109	S30 T132	
Ring 3		S30 S19 T124 T112		S16 S19 T118 T118	
Ring 4	S21 S12 T105 T120	S22 T109	S24 S27 T124 T132	S15 T111	
Ring 5	S22 T94	S25 S19 T94 T100	S19 T105	S15 S22 T103 T99	
Ring 6	S30 S27 S70+ S76	S33 T88	S18 S22 T79 T84	S22 T81	
Ring 7	69	75 70	72 66	76 66	70 59

Table 3D. Length of ventral scalids of J-5 K. phyllotropis of trunk length 500 um. (Figs. 3.8 and 3.9).

Sector No.	4	5	6
Ring 1 (right scalid)	132	147	141
Ring 2	S16 T133	S22 T114	S24 T127
Ring 3		S15 S25 T108 T121	
Ring 4	S22 S18 T85 T97	S15 T97	S15 S15 T84 T120
Ring 5	S18 T82	S18 S18 T51 T82	S18 T94
Ring 6	S18 S18 T67 T67	S21 T67	S13 S12 T55 T72
Ring 7	57 I I I	64 49	75 61

FIGURE 3.10. Dorsal aspect of the everted J-6 head of a Kinorhynchus phyllotropis specimen with a trunk length of 630 um. Scalid lengths are given in Table 3E.

This diagram shows internal scalids inside the oral cone.



3.10 10µm

FIGURE 3.11. Head sector and scalid ring designation of scalids shown in Figure 3.10.

Large numbers show the head sector designation.
Small numbers show the scalid ring designation.

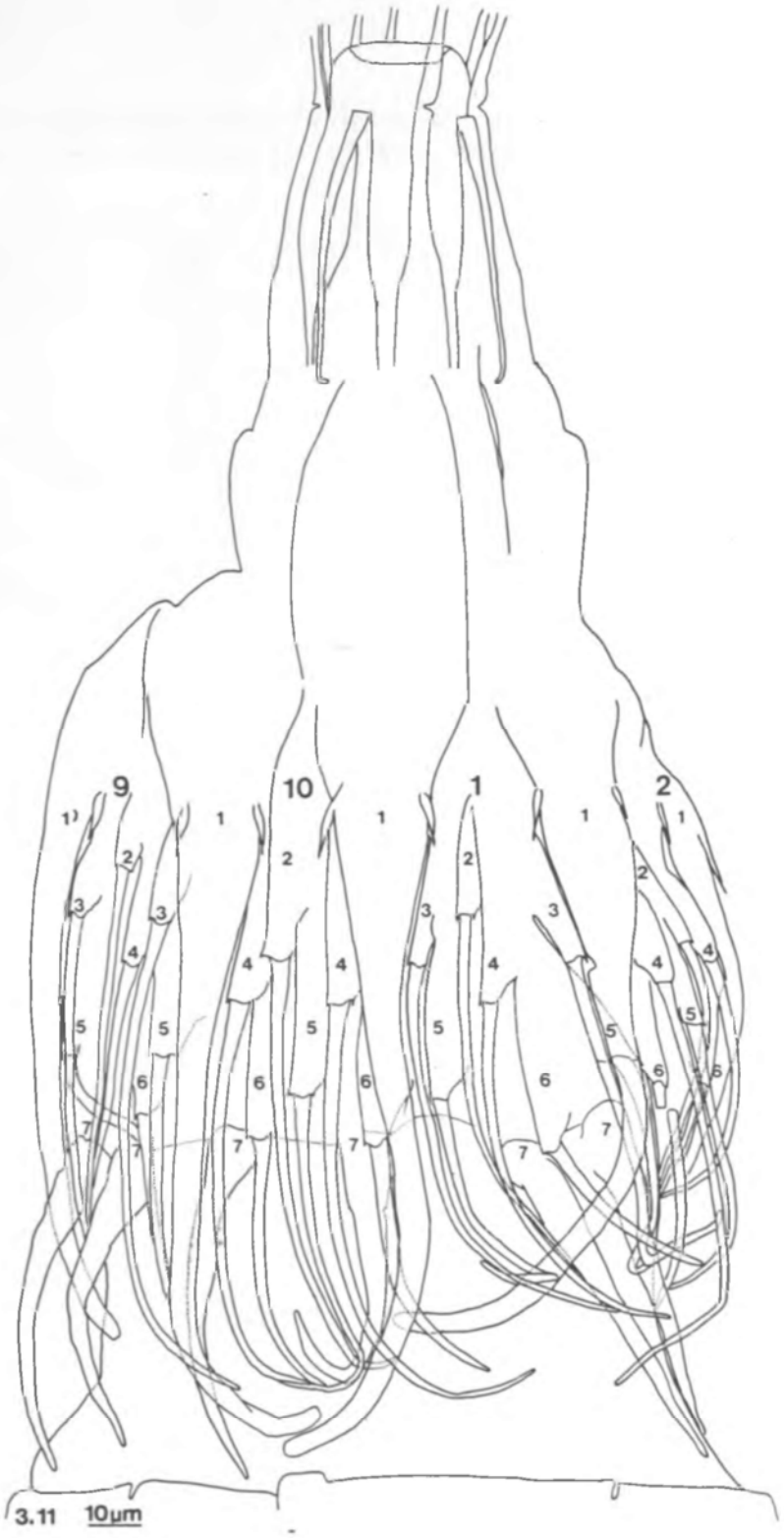
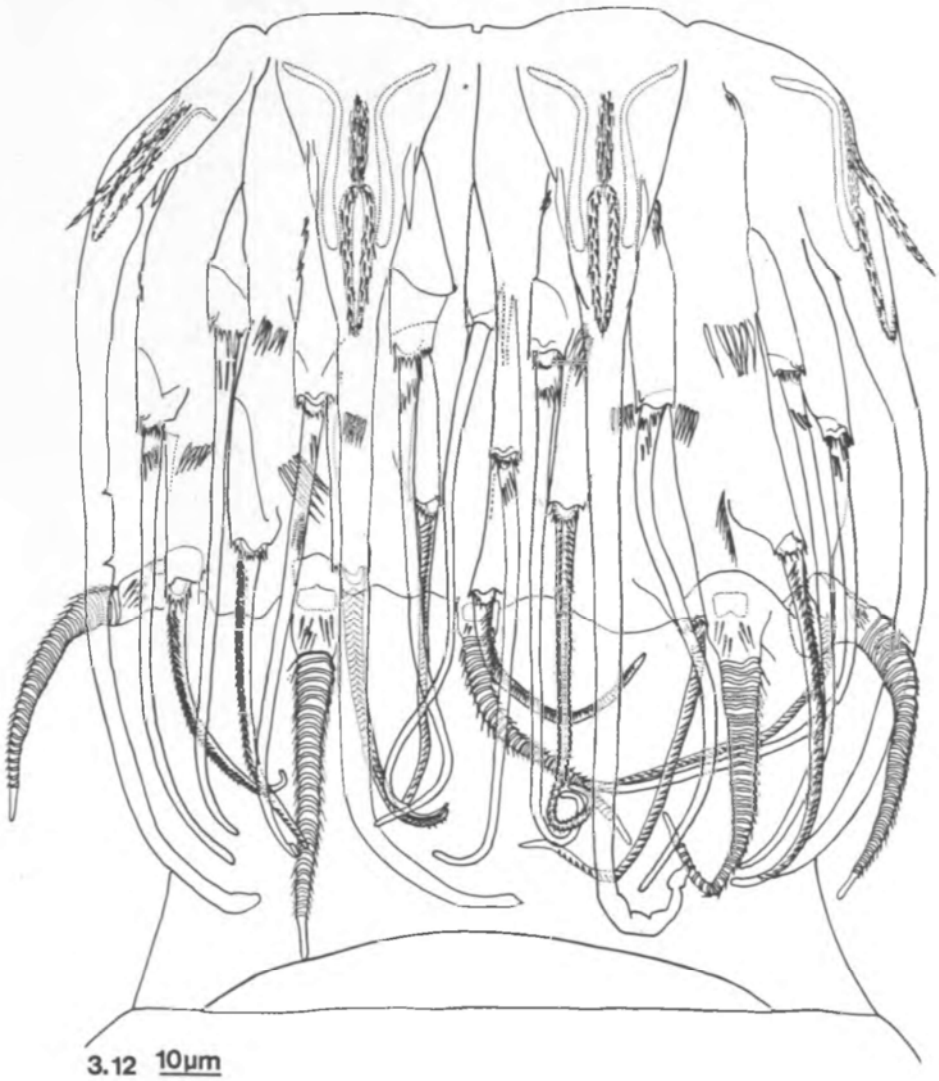

9
10
1
2
3.11 10µm

FIGURE 3.12. Ventral aspect of the everted J-6 head of a Kinorhynchus phyllotropis specimen with a trunk length of 590 um.

Scalid lengths are given in Table 3F.

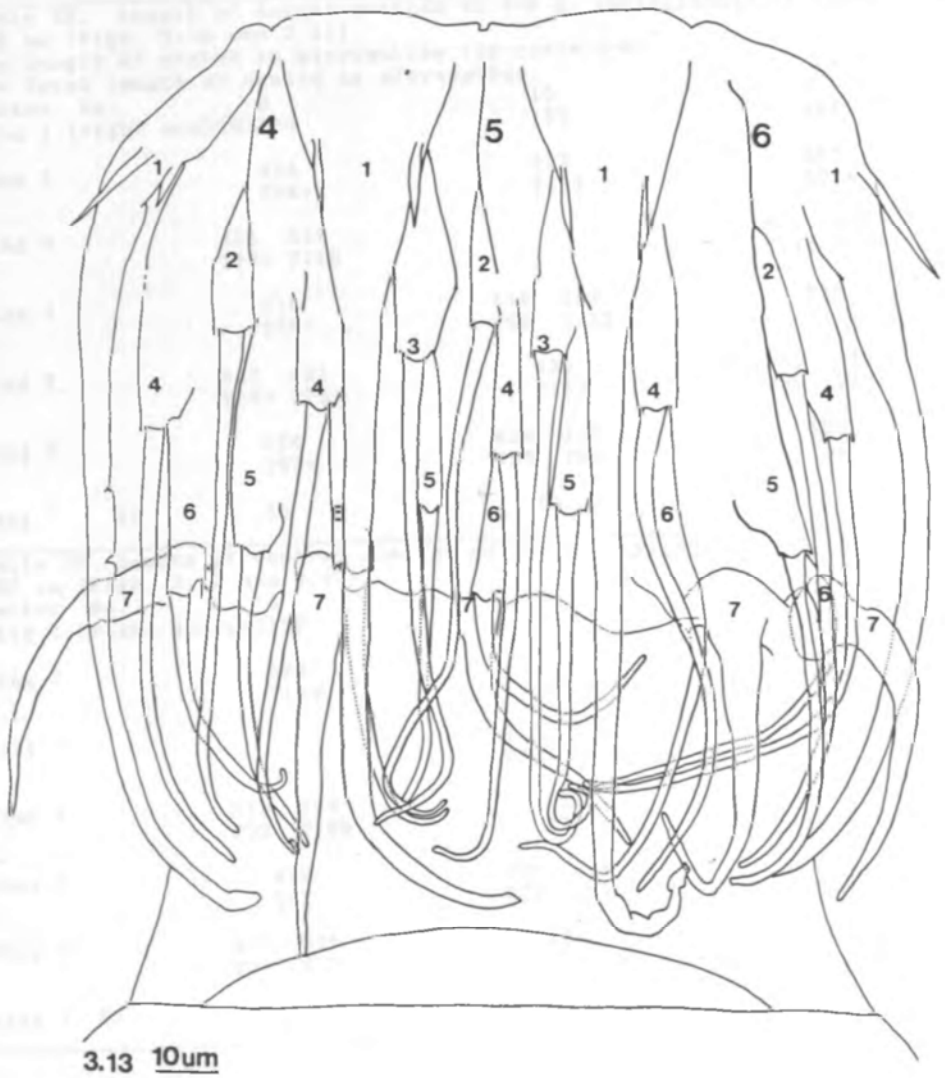
The smallest trichoscalid marks the midventral axis.



3.12 10µm

FIGURE 3.13. Head sector and scalid ring designation of scalids shown in Figure 3.12.

Large numbers show the head sector designation.
Small numbers show the scalid ring designation.



3.13 10um

Table 3E. Length of dorsal scalids of J-6 K. phyllotropis of trunk length 630 um (Figs. 3.10 and 3.11).
S = length of socket in micrometres (in rings 2-6)
T = total length of scalid in micrometres.

Sector No.	9	10	1
Ring 1 (right scalid)	154	155	151
Ring 2	S14 T84+	S22 T109	S21 T97+
Ring 3	S15 S17 T73+ T116		S21 S24 T110 T103
Ring 4	S18 T54+	S18 S29 T99 T132	S35 T112
Ring 5	S28 S31 T50+ T75+	S32 T103	S30 S32 T82 T80+
Ring 6	S24 T47+	S30 S32 T83 T83	S29 T66
Ring 7	61 56	65	59 66 63

Table 3F. Length of ventral scalids of J-6 K. phyllotropis of trunk length 590 um (Figs. 3.12 and 3.13).

Sector No.	4	5	6
Ring 1 (right scalid)	152	148	142
Ring 2	S24 T106	S24 T115	S25 T111
Ring 3		S17 S12 T98 T104	
Ring 4	S19 S24 T93 T100	S25 T99	S29 S32 T112 T120
Ring 5	S28 T82	S25 S28 T78+ T91	S31 T92
Ring 6	S27 S25 T69 T77	S31 T75	S31 S26 T92 T73
Ring 7	55 61	49	64 57

Due to copyright laws, the following articles have been omitted from this thesis. They appear in the page range 386-440. Please refer to the following citations for details.

Brown, Rosemary (1981) Saccocirridae (Annelida: Archiannelida) from the Central Coast of New South Wales, *Australian Journal of Marine and Freshwater Research* Vol. 32(3), P. 439-456

Sasaki, Shun-ichi and Brown, Rosemary (1983) Larval Development of Saccocirrus uchidai from Hokkaido, Japan, and Saccocirrus krusadensis from New South Wales, Australia (Archiannelida, Saccocirridae), *The Zoological Society of Japan*, vol. 56, No. 4. P. 299-314

Brown, Rosemary and Higgins, Robert P. (1983) A new species of kinorhynchus (homalorhagida, pycnophyidae) from australia with a redescription and range extension of other kinorhyncha from the South Pacific, *Zoologica Scripta*, Vol. 12, No. 3, p. 161-169

Brown, Rosemary (1983) Spermatophore Transfer and Subsequent Sperm Development in a Homalorhagid Kinorhynch, *Zoologica Scripta*, Vol. 12, No. 4, p. 257-266.

DISCUSSION ADDENDUM

THE EVOLUTION AND RELATIONSHIP OF THE ASCHELMINTHS.

The opening chapters of invertebrate zoology textbooks traditionally discuss the lower invertebrates such as protozoans, sponges, cnidarians and flatworms, while later chapters deal with simple coelomate phyla such as annelids and molluscs. Between lower invertebrate chapters and coelomate chapters the content is less predictable. This is the space given to minor phyla, small worm-like or sac-like animals with scarcely an appendage for a systematist to grasp. Some of the difficulties involved in contructing a phylogeny for the simpler metazoa have been outlined by Anderson (1982). Firstly, it is very difficult to exclude the possibility of parallel or convergent evolution when comparing simple kinds of animal organisation with few interacting components. Secondly, there is a real possibility that the metazoans had more than one origin from protozoans. Textbook authors have no consensus to guide their treatment of the minor phyla, and many solve the problem by omitting them altogether, thus conveying the erroneous impression that they are rare.

Much of the work on minor phyla was carried out in the late nineteenth century, when phylogeny was regarded as philosophy, and when publications were vehicles of debate as much as disseminators of factual information. To deduce an ordered system from this melange of fact and inference required an exceptional intellect. Such an intellect was Libby Hyman. In 1951 she redefined the phylum Aschelminthes erected by Grobben (1908). Hyman's superphylum comprised classes Rotifera, Gastrotricha, Kinorhyncha, Priapulida, Nematoda and Nematomorpha. Hyman published her work just before electron microscopy began to open up fresh fields of investigation. One of the first contributions of the new tool was to weaken a signifant character in the definition of aschelminths. The pseudocoelomate phyla were shown to have little in common by way of body cavity organisation. Some pseudocoels were even artefacts produced by alcohol shrinkage of tissue. Despite this setback the concept of the aschelminths has been found to be useful for more than thirty years - it conjures up an image of worm-like animals, with

hairs, bristles or hooks on their heads, some surrounded by cases and some by elaborate cuticle. And even with the aid of the electron microscope, progress in elucidating the affinities of these small invertebrates has been painfully slow. Indeed kinorhynch affinities would still be back where they were in 1851, between the crustaceans and the worms, were it not for the description of two new metazoan forms, the seticoronarian priapulids in 1974 and the loriciferans in 1983.

What are the characters defining Phylum Aschelminthes and what is the present status of these characters?

Hyman (1951) defined the Aschelminthes as being pseudocoelomate, unsegmented or superficially segmented, possessing a digestive tube lacking a muscular wall (except in priapulids), with an anus located well posterior to the mouth. Ultrastructural investigations carried out since 1951 have shown that these characters are difficult to apply with precision. There is difficulty in stating whether these characters are present or absent in some organisms.

This difficulty is experienced especially in distinguishing between the coelomate and pseudocoelomate condition. A coelom is a persistent blastocoele (Hyman 1959) or body cavity lined with peritoneal epithelium (Fransen 1980). Hyman's definition depends on embrological studies, yet to be carried out on many metazoan groups. Later authors have found that the perivisceral arrangements of many groups are intermediate between being cell-packed or occupied by chambers lined with epithelium. There is no sharp distinction between coelomate and pseudocoelomate animals regarding body cavity contents, partitioning or cellular lining (Remane 1963). Pseudocoelomate groups may be regarded as having a secondarily reduced coelom (Siewing 1976). There is no satisfactory way of defining a pseudocoel in embryological or anatomical terms, such that it can be distinguished from a coelom, and the phyla described as pseudocoelomate occupy an uncertain phylogenetic position (Clark 1964; 1979a; 1979b). Solid body constructions may be derived from coelomate origins as a result of the expansion of lining cells or the lack of initial cavity formation (Fransen 1980).

The same difficulty has been experienced in deciding whether organisms are segmented, superficially segmented, or unsegmented. It is not possible to make definite distinction between unsegmented, pseudosegmented and metamerically segmented types of body plan (Clark 1980).

Aschelminth digestive tubes lack a muscular wall but this character is not distinctive, and is found in other small metazoans. Absence of splanchnic musculature is found in sipunculids (Hyman 1959) whose developmental features show clear similarities to annelids and molluscs (Rice 1983). Lobatocerebrid annelids also have a mid-gut lacking muscle (Rieger 1980). Large priapulids have muscular intestines (Hyman 1951) but the small seticoronarian priapulid Maccabaeus tentaculatus lacks any intestinal thickening (Por and Bromley 1974).

Location of an anus well posterior to the mouth only serves to distinguish an organism from a member of one of the lophophorate phyla - the Phoronida, Kamptozoa and Ectoprocta (Bryozoa).

What evidence of aschelminth relationships is provided by the fossil record?

Some aschelminths (rotifers and kinorhynchs) are chitin producers (Jeuniaux 1975). The earliest evidence of chitinozoans are Precambrian traces of chitin dated 1 000 million years ago. These microfossils are situated in the fossil record between the 3 500 million year silicified cells of stromatolites and the oldest fossils of multicellular animals, which are found in Precambrian assemblages dated at 640 - 560 million years (Glaessner 1969; Clark and Cook 1983; Conway Morris 1985b). Contemporary aschelminth forms appear much later - nematodes in Scandinavian and American Carboniferous strata (Stϕrmer 1963; Schram 1973), priapulomorph priapulids in American Carboniferous strata (Schram 1973), and rotifers in South Australian Eocene beds (Southcott and Lange 1971). There have been no published finds of kinorhynch fossils.

The intervening fossil record provides few insights into aschelminth evolution. The earliest assemblages of multicellular animals have been found in late Precambrian (Vendian) strata of all continents except Antarctica. These distinctive biota are termed Ediacaran faunas after the type locality. These faunas have been interpreted as the first wave of metazoan diversification in which most if not all metazoan body plans were established (Valentine 1981, cited Conway Morris 1985a). They have also been interpreted as non-metazoans which lacked viscera, in which metabolites diffused through bag-like body compartments arranged in folia or in quilted compartments (Seilacher 1983, cited Conway Morris 1985b). Pledge (1974) states that twenty five percent of the South Australian Ediacaran fossils have been referred to the Polychaeta and that the two species of Spriggina show polychaete cirri and parapodia, while the five species of Dickonsonia resemble the contemporary polychaete Spinther. The fact that coelomates were well established by the late Precambrian provides some argument that primordial pseudocoelomate aschelminths may have appeared before the Ediacaran faunas, but such an argument would carry little conviction to archicoelomate theorists.

The Ediacaran assemblages contained soft bodied animals. Animals with hard parts were preserved in Cambrian assemblages. The Cassiar mountains of British Columbia have yielded cone shaped sclerites in assemblages of small shelly fossils. These sclerites, designated Lapworthiella, have uncertain suprageneric relationships, although they have been interpreted as the disassociated spicule coat of a metazoan (Conway Morris and Fritz 1984). The cones vary around 1 mm in length, with an aperture (measured from a micrograph) of 0.15 mm at the narrow end, while the wider end varies according to the size of the fossil fragment. The fossils are characterised by the possession of denticulate circular ridges and ornamented inter-ridge areas studded with granular protuberances arranged in lines or semicircles. A longitudinal furrow is sometimes present. These microfossils have been recovered from limestone. The shells have presumably been replaced by acid resistant phosphate, and L. filigrana Conway Morris and Fritz, 1984 has concentric internal phosphatic lamellae. These

growth rings indicate that the sclerite grew by accretion mediated by secretion from basal cells. The tapered tubes of Lapworthiella, with their rings of denticles, have superficial resemblance to the appearance of an everted priapulid pharynx, but the comparison does not stand up to analysis. Priapulid denticles are staggered in their arrangement, and these denticles are radially arranged. The pharyngeal teeth (or denticles) of priapulids are consistently multipointed, whether they are from living species such as Tubiluchus corallicola (Kirsteuer and Rützler 1973), or from fossils such as Middle Cambrian Ottoia prolifica (Banta and Rice 1976). Lapworthiella denticles are single pointed. Finally, twenty species of Lapworthiella have been recognised, apparently without any mineralisation of soft parts (Conway Morris and Fritz 1983). In priapulid type metazoans the pharynx is not the largest or toughest part of the body, and would be unlikely to be preserved in twenty different species without any trace of the proboscis armature. Although L. filigrana has the dimensions of a small aschelminth, it resembles, in its habit and in its internal growth rings, the conical shell of an organism such as a scaphopod mollusc. Alternatively the presence of a longitudinal furrow suggests that the shell may have been secreted in sections like the valves of a barnacle.

Lower Cambrian strata from all continents except Antarctica contain deciduous stalked sclerites attributed to species of Halkiera of the order Sachitida of uncertain phylum designation. Halkiera is known from isolated sclerites and sclerite moulds, with one specimen of three overlapping sclerites. A model of Halkiera has been reconstructed by Bengtson and Conway Morris (1983) using as a template the Middle Cambrian sachitid Wiwaxia. Wiwaxia is only known from five locations in the Stephen Formation of British Columbia, including the Burgess Shale and Ogyopsis Shale members. Wiwaxia has been recovered as isolated sclerite compression fossils, both moulds and internal casts and from a few specimens of the whole animal, preserved as thin organic films on a fine-grained slate. One specimen appears to be exuviating, another is articulated. Bengtson and Conway Morris caution that the similarity of sclerite morphology is not a strong indication that these genera are homologous, for similar sclerite

characters are found in aplacophoran molluscs, pangolins and spruce cones. However there is some evidence that this similarity of sclerite structure is not the result of convergence. There is similarity of sclerite structure as shown by internal moulds, and there is evidence that sclerites were moulted. The feeding aparatus of Wiwaxia resembles a molluscan radula in its morphology and location in the foregut. Bengtson and Conway Morris noted that "it seems conceivable that they (sachitids) were derived from a turbellarian-like worm in a manner reminiscent of the now widely accepted hypothesis of mollusc origins (see Stasak 1972)". However, Conway Morris (1985b) argued that characters such as the mollusc radula or the arthropod jointed leg, which are regarded with present-day hindsight as being the hallmark of particular groups, may have been present, in simple form, in many early groups. For reasons unknown, these characters may have been lost in some groups and elaborated in other groups. The sachitid form of feeding apparatus may have been present in Cambrian forms which gave rise to non-radulate phyla. This type of feeding apparatus cannot be easily related to the typical aschelminth arrangement of circumoral processes, and aschelminths do not possess stalked or deciduous dermal spines or plates.

The features shared between sachitids and aschelminths are elongate body shape and moulting habit. These characters are not sufficient to warrant any claim of phylogenetic affinity. However there are some members of the meiofauna which do appear to have significant similarity to the the sachitids. They are the interstitial turbellaria and the acochlid molluscs. The macrostomid turbellarian Acanthomacrostomum spiculiferum has an endoskeleton of calcarious spicules (Swedmark 1964). This species is known only from sub-littoral shell-sand banks, similar to the Burgess Shale facies. The interstitial opisthobranchs Rhodope and Hedylopsis have rod-like spicules in place of a shell. The spicules are mainly oriented in the longitudinal axis of the animal. In H. spiculifera, which is 3-4 mm long, the spicules are thinly distibuted; in H. brambelli, which is 2 mm long, spicules are more densely distributed; and in H. loricata, which is 0.8 mm long, spicules are so densely distributed that the

visceral sac has a constant form (Swedmark 1968). Hedylopsis loricata has the same length as a Burgess Shale specimen of Wiwaxia corrugata preserved in the act of moulting (Fig. 10, Bengtson and Conway Morris 1984). Some interstitial groups have been regarded as being secondarily simplified and having a neotenic character. These groups include polychaetes (Westheide 1984) and kinorhynchs (Higgins 1983). However the interstitial molluscs may be conservative forms, and there is some evidence for this in the fossil record. "The unique specimen of Bunyerichnus from the Bunyeroo Gorge has been interpreted as the trail of a shell-less mollusc, perhaps like a nudibranch or sea slug, and is one of the oldest trace fossils known. It is separated from the first true fossils of animal origin (body fossils) in the Flinders Ranges by some 1 800 metres or more of sediment, and therefore is considerably older" (Pledge 1974). It would seem feasable to consider sachitid affinity with the radulate acochlids, and perhaps also to small, spiculiferous turbellarians.

The Burgess Shale fossil Ottoia prolifica was a worm-like animal. It apparently was soft-bodied for the viscera are revealed in many of these compression fossils. Ottoia was apparently capable of considerable extension. The smallest specimens are 3 cm long, and the largest approach 25 cm, with the average length between 3-5 cm (Banta and Rice 1976). There were three body regions, called a proboscis, a collar and a soma. The proboscis was an evaginable spiny tube. It consisted of a smooth basal portion succeeded by a dilated section bearing multi-pointed spines resembling "a bear's foot print" (Banta and Rice 1976). The smooth distal section is usually so poorly preserved that the anterior termination of the gut, which passed into the proboscis, has not been observed. Between the proboscis and the collar there were two rings of setiform spines. The collar bore an array of robust spines and hooks arranged in rows. The soma formed ninety percent of the body length. It had corrugations resembling superficial cuticular annulations. The gut can be traced to the tip of the soma, which bore a sub-terminal cluster of hooks. The body cavity was spacious, and the gut can be seen to be surrounded by membranous material.

Ottoia prolifica has been accepted as a priapulid (van der Land 1968; Conway Morris 1977; Por 1983). In fact Conway Morris (1977) described seven Burgess Shale fossils as "archaeopriapulids", but in 1982 Conway Morris and Crompton reconsidered one of them, Ancalagon and referred it to the Acanthocephala. The remaining six are Ottoia prolifica, Selkirkia columbia, Louisella pedunculata, Fieldia lanceolata, Scolecofurca rara, and Lethioscopa simplex. Ottoia prolifica is the most numerous and best documented of the archaeopriapulids. Walcott collected over a thousand specimens and described it in 1911 as a gephyrean, citing Parker and Haswell's textbook (1897) for this classification. In 1953 Lang recognised Ottoia as being related to kinorhynchs and acanthocephalans (in Phylum Rhynchohelminthes, Lang 1953). He did not consider Ottoia to be a priapulid because it possessed anal hooks. Banta and Rice (1976) pointed out that the priapulid Halicryptus does possess anal hooks. They restudied Ottoia in detail but did not assign the fossil to any phylum, considering it to be "an early aschelminth-like animal". They noted priapulid features in Ottoia - in shape and body form, spacious body cavity, superficial annulations, straight gut with terminal mouth and anus, morphology and distribution of anterior spines and hooks. Banta and Rice remarked on the similarity between Ottoia pharyngeal teeth and the pharyngeal teeth of contemporary priapulids. Some priapulid features are lacking in the fossil - papillae on the trunk, and differentiation into a presoma and trunk. Ottoia possesses features lacking in priapulids - anterior rows of spine-hooks and anteriorly-directed collar setae. Banta and Rice acknowledged that "these differences seem to us to be relatively small". Conway Morris (1977) assessed them as too small to disqualify Ottia from being considered as an archaeopriapulid. Por (1983) accepted the priapulid status of Ottoia, and argued that Conway Morris' six archaeopriapulids should be referred to the seticoronarian priapulids. Por reappraised the errant Ancalagon as an ancestral form of the free-living priapulomorph priapulids.

What is the present status of the aschelminth classes?

1. Rotifera

Rotifers have been considered as neotenous trochophores on the basis of the presence of circles of cephalic cilia (Hatschek 1878), but primitive rotifers show that the corona of cilia was originally ventral, suggesting a affinity with bilateral, creeping planarians (Remane 1929) which, however, do not have the persistent blastocoel of adult rotifers (Hyman 1951). Rotifer-gastrotrich affinity was promoted by Zelinka (1889) who designated both groups as trochelminthes. Van der Land (1970) compared the loricate rotifers with loricate priapulid larvae, and commented on similarity between caudal appendages ("toes") of rotifers and priapulids. A similarity of retractible corona-like heads in rotifers and kinorhynchs was observed by Dujardin (1851).

The separation of rotifers from gastrotrichs is supported by embryological studies (Teuchert 1968) and by ultrastructural studies of the rotifer mastax and gastrotrich jaw (Rieger and Mainitz 1977). The separation of rotifers from kinorhynchs is supported by biochemical study of the scleroprotein composition (Piavaux and Magis 1970) of the rotifer mastax and the chitinous composition of kinorhynch cuticle, scalids and spines (Jeuniaux 1975). The rotifer integument consists of an intracellular rigid lamina located within the epidermal syncytium, a layer formed of cellular inclusions (Clément 1969; Koehler 1965, 1966). The integument of endoparastic acanthocephalans also contains an intrasyncytial lamina, especially in the acanthor larva (Byram and Fisher 1974). As most parasitic platyhelminths (trematodes and cestodes) are covered with a continuous layer of cytoplasm connected to nuclei below the basement membrane, it has been suggested that rotifers, acanthocephalans and parasitic platyhelminths may share a common ancestor (Lyons 1977; Storch 1979).

2. Gastrotricha and Nematoda

The presence of a muscular triradial sucking pharynx in nematodes has promoted suggestion of nematode affinity with gastrotrichs (Ludwig 1875, cited Hyman 1951) and kinorhynchs (Bütschli 1876; Zelinka 1928).

However kinorhynch pharynx structure differs fundamentally from other comparable organs by the presence of a basement membrane between myofibrils and lining epithelium (Marcus 1958).

In both gastrotrichs and nematodes there is a myoepithelial pharynx with a Y-shaped lumen (Remane 1936; Teuchert 1974; Rieger and Ruppert 1974). There is cuticular similarity between chaetonotid gastrotrichs and nematodes in the position of a single trilaminar cortical membrane (Rieger and Rieger 1977). Teuchert (1977) argued for a close relationship between gastrotrichs and nematodes on the basis of construction of the pharyngeal nerve plexus, peripheral and central nerve systems and amphid-like sense organs. Ruppert (1982) argued that a myoepithelial foregut is a primitive (symplesiomorphic) character, with significant homology of construction (cross striated monofilaments possessing a T-system of muscle-sheath coupling) in gastrotrichs and nematodes.

Gastrotrichs and nematodes show common features in the production of eggshell and egg cuticle. Neither organism utilises nurse cells, follicle cells or secretory organs of the reproductive system. Both incorporate eggshell precursors into the egg, so that the egg itself produces the shell, whereas cuticle is secreted independently around the shell, a distinct difference from the penetrating microvilli of annelid eggs (Rieger and Rieger 1980).

3. Nematomorpha

Larval nematomorphs are parasitic and adults are reproductive non-feeding stages. However it is assumed that parasites have descended from free-living forms and that their anatomy must reflect this ancestry (Baer 1951; Rogers 1962). Similarity of the spiny eversible proboscis of kinorhynchs and larval nematomorphs has been noted (Bütschli 1876; Schepotieff 1907). Meglitsch (1972) speculated that nematomorphs arose from forms ancestral to both kinorhynchs and priapulids. Hyman (1951) noted similarities of longitudinal muscles in nematodes and nematomorphs. Homologies between nematomorphs, priapulids and kinorhynchs have been claimed (Conway Morris 1977; Malakhov 1980). Kristensen (1983) discussed possible homologies

between nematomorph larvae and loriciferans in the similarities between nematomorph oral stylets and loriciferan buccal canal, and the mutual possession of a ligament or diaphragm separating neck from trunk.

4. Kinorhynchs and priapulids

Kinorhynch-priapulid homologies have been suggested by many authors (Hammarsten 1915; Lang 1953, 1963; Marcus 1958; van der Land 1968, 1970) on the basis of similarities of spiny eversible heads and peripharyngeal musculature. Kinorhynchs and priapulids were united with acanthocephalans in Phylum Rhynchohelminthes (Lang 1953). Van der Land (1968) accepted this taxon, except for the inclusion of the acanthocephalans. Por (1983) suggested that the loricate priapulid larva represented "an ontogenetic repetition of what must have been the Precambrian priapulid" and suggested that this is the stage with which kinorhynchs, nematomorphs and rotifers should be compared.

Functional similarities between priapulids and kinorhynchs have been observed. Beklemischev (1969) discussed similarity of the mechanisms of head eversion in kinorhynchs and larval priapulids. Both use cuticular plate adductors to increase internal body pressure through the fluid of the body cavity.

What is the present understanding of phylogenetic relationships between Loricifera and aschelminths?

In 1983 Kristensen erected a new phylum, the Loricifera - microscopic metazoans recovered from sediments collected from the coasts of Brittany, Greenland, the Coral Sea Chesterfield Reefs, the Azores and Florida. Kristensen (1983) said that loriciferans resemble loricate rotifers in appearance, and in the possession of a caudal floscula (epidermal sensory spot). He discussed similarity between loriciferan and kinorhynch spinoscalids, as well as possible homology between the floscula of loriciferans and priapulids and possibly of kinorhynchs. He pointed out that growth involves moulting in these three groups as well as in nematodes. The priapulid larva is encased in a lorica, as is the larva and adult of Nanaloricus mysticus. Kristensen noted that the morphology of loriciferan oral stylets resembles that of

nematomorph larvae, and that both have a ligamentous diaphragm separating the neck from the trunk.

The present study describes two new types of kinorhynch external scalid. Homology of these scalids with loriciferan head structures is suggested - homology of the tooth-like scalids of loriciferans and proscalids of kinorhynchs, and homology of loriciferan hook scalids and kinorhynch protrichoscalids. There is also possible homology of trunk epidermal sense organs or floscula in both groups, for both show similar cuticular elaboration. Kinorhynchs and loriciferans appear to have primary bilateral symmetry of the basic body plan, for even the radial elements of the kinorhynch head have been shown to have bilateral origins. These are the oral scalids, and the protrichoscalids.

The internal structure of kinorhynch and priapulid floscula have marked similarity in the structure of this ciliated sense organ. The earliest juvenile stage of Kinorhynchus phyllotropis appears to show a developmental separation of the radial myofibrils from the lining epithelium. This arrangement resembles the pharyngeal bell of the seticoronarian priapulid Maccabeaus tentaculatus in which there are two layers of circular myofibrils separated by a few longitudinal strands.

What conclusions about aschelminth phylogeny can be derived from present data?

Present understanding of the aschelminth concept is that the group is likely to be reconstituted and redefined in terms of characters other than those listed in Hyman's definition. There are now ultrastructural data giving grounds for considering relationship between rotifers, acanthocephalans and platyhelminths. There is evidence supporting phylogenetic relationships between gastrotrichs and nematodes and between priapulids, loriciferans, kinorhynchs and possibly nematomorphs. Rieger and Rieger (1980) noted that "the Acanthocephala-Rotifera line and the Nematoda-Gastrotricha line may be connected through the Gnathostomatulida because this group shows possible special homolog similarities to the Rotifera (jaw fine

structure) and to the Gastrotricha (nephridial fine structure)."

Confident postulation of homology requires detailed study of organisms, their organ systems, and the relationship between the components of the organ systems. An attempt has been made to carry out such a study on the development of kinorhynch head processes. However a study which has been carried out on one species can only offer educated guesses as to potential variation of these characters in other groups. Nevertheless the study should provide a basis for future evaluation of homology between the scalids of kinorhynchs and of other scalid bearers, especially the new loriciferan species and the loricate larvae of priapulids. It is hoped that future studies will be facilitated by the techniques for revealing and describing kinorhynch head processes which have been evolved during the present study. This study has also provided means enabling the inclusion of information on scalid arrangement in taxonomic descriptions, even when that information is incomplete.

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