Zelinkaderidae, a New Family of Cyclorhagid Kinorhyncha

ROBERT P. HIGGINS

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 500

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1990

ABSTRACT

Higgins, Robert P. Zelinkaderidae, a New Family of Cyclorhagid Kinorhyncha. *Smithsonian Contributions to Zoology,* number 500, 26 pages, 79 figures, 1990.—A new species, genus, and family are described from marine sediment collected east of Fort Pierce, Florida, USA, at a depth of 140 meters. *Cateria submersa* Gerlach, 1969, is placed in the new genus as *Zelinkaderes submersus* and is redescribed. Included is a review of classification of the phylum and a key to the orders, suborders, families, and genera of Zelinkaderidae, based upon adult characters. The complex head structure of *Zelinkaderes floridensis,* new species, is described and a new scheme of nomenclature is proposed for the arrangement of scalids. Collections of the new species were taken bimonthly for 12 months. Length/frequency study of the adults indicated only minor variation in size and abundance during the 12-month collecting period. All stages of the life history are included in the description of the new species. Molting of an adult is recorded for the first time. The new taxon may represent the most primitive kinorhynch so far discovered.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Higgins, Robert P.
Zelinkaderidae, a new family of cyclorhagid Kinorhyncha / Robert P. Higgins
p. cm. – (Smithsonian contributions to zoology ; no. 500)
Includes bibliographical references.
Supt. of Docs. no.: SI 1.27:500
1. Kinorhyncha—Classification. 2. Zelinkaderidae—Classification. I. Title. II. Series.
QL1.S54 no. 500
[QL391.K5]
591 s–dc20
[595.1'85]

89-600319
CIP

Contents

Zelinkaderidae, a New Family of Cyclorhagid Kinorhyncha

Robert P. Higgins

Introduction

In 1956, Gerlach described a new genus and species of cyclorhagid kinorhynch, *Cateria styx* from the coast of Brazil. The following year, Delamare Debouteville (1957) reported the same species from Angola. Five years later, while studying the interstitial invertebrates of beaches near Waltair, India, Rao and Ganapati (1966) found specimens of what they later identified as *C. styx*. This identification was almost certainly erroneous. After comparing specimens that I collected in 1964 from Waltair with the holotype and topotypes of *C. styx*, their record was placed in synonymy with the latter species (Higgins, 1968). In that publication, a new suborder, Cryptorhagae Higgins, 1968, was proposed to receive the family Cateriidae Gerlach, 1956, which consisted of the two species assigned to the genus *Cateria*.

Subsequently, *C. gerlachi* has been reported from the Andaman Islands (Higgins and Rao, 1979), *C. styx* from the coast of Chile (Brown and Higgins, 1983), and a third species, *C. submersa* Gerlach, 1969, from the North Sea. Until the latter was discovered, members of *Cateria* were considered to be obligate intertidal, tropical, high-energy-beach kinorhynchs; however, the North Sea species was found subtidally in medium to coarse sand, and at depths of between 30 and 46 meters.

During the past several years, collections of meiobenthos from subtidal muddy sand at a site 140 m deep, 33 km east of Fort Pierce, on the Atlantic Coast of Florida, have contained an undescribed kinorhynch about half the size of, but similar to, *Cateria submersa*. Subsequent study of both the North Sea and Florida species has led me to conclude that their affinities would be better recognized by assigning them to a new genus and new family for these taxa.

While reviewing the criteria used in the classification above that of the species group, I concluded that it was necessary to re-evaluate the characters that have been used. Consequently, I have prefaced the description of the new family with an emended series of diagnoses. Comments on some of the criteria used in the higher classification of the Kinorhyncha are included in the remarks following the description of the new species.

METHODS.—Sediment samples were collected by an anchor dredge at 2-month intervals for one year, 1982–1983. These samples included RH 1532 (5 Apr 82), RH 1598 (2 Jun 82), RH 1625 (2 Aug 82), RH 1630 (4 Oct 82), RH 1653 (6 Dec 82), and RH 1661 (31 Jan 83). The holotype (female) and allotype (male) of the new species were selected from the collection made in August. The statistical data presented are based only on this collection and conform to the presentation format of Higgins and Kristensen (1988). Kinorhynchs were extracted from the sediment by the bubbling technique described by Higgins (1983:4) and Higgins and Thiel (1988:137), sorted live using an Irwin Loop and the ×50 magnification of a stereomicroscope, fixed in 10% formalin, and transferred to 70% ethanol. Some specimens were selected for scanning electron microscope (SEM) study, but most were placed in a solution of 2% glycerin in 70% alcohol, which was slowly evaporated to glycerin. Specimens were mounted individually in Hoyer's-125 mounting medium following the technique prescribed by Higgins, 1983:4, 1988:330).

The kinorhynchs from the North Sea originally described as *Cateria submersa* were extracted from core samples of subtidal sand taken during two expeditions of the R/V *Anton Dohrn* north of Helgoland between 1967 and 1968. Specimens used for taxonomic description were fixed in formalin and mounted in glycerin (Gerlach, 1969).

Specimens mentioned in this paper, including the type material of *Cateria submersa*, are deposited in the National Museum of Natural History, Smithsonian Institution, and referred to by both catalog number (USNM) and author's reference number (RH).

MEASUREMENTS AND ABBREVIATIONS.—Analytical procedures follow those described by Higgins (1983:4). Measurements in text and on illustrations are given in micrometers

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(μm); ratios (e.g., SW/TL) are expressed in percent of the total length measured on the midline, from the anterior margin of segment 3 (first trunk segment, see the "Diagnosis" for Zelinkaderidae for special circumstances unique to the new taxon) to the posterior margin of segment 13, exclusive of spines. Maximum sternal width is not measured due to the unique morphology of this taxon. Standard width (or sternal width at segment 12) is measured across the anteroventral margin of the 12th sternal plates which, in the new family is considered equivalent to the distance between the lateral margin of the basal socket of the cuspidate spines of segment 11. All spines (except the midterminal spine) are numbered by segment.

Abbreviations used in this publication are as follows:

ar	arthrocorium
ch1	cuticular hair
ch2	bifid cuticular hair
cp	patch of less hirsute cuticle
cs	cuticular scar
cs(1)	cuticular scar of old exoskeleton
cs(2)	cuticular scar of new exoskeleton
d	middorsal spine (of segment number indicated)
di	diatom
go	gonopore
go(1)	gonopore of old exoskeleton
go(2)	gonopore of new exoskeleton
gu	midgut
l	lateral spine (of segment number indicated)
la	lateral accessory spine (of segment number indicated)
lf	lateral flange of oral style
ltas	lateral terminal accessory spine
lts	lateral terminal spine
mp	midventral placid
mts	midterminal spine
mv	midventral line
oo	oocyte
os	oral style
os1	oral style, prototype 1
os2	oral style, prototype 2
pf	pectinate fringe
pl	placid
po	pore
ps	pharyngeal style (followed by number)
s	segment (followed by number)
sc	scalid (followed by ring number)
sr	seminal receptacle
ss	sensory spot
st	striations
te	testis
tr	trichoscalid
x	anlage of middorsal spine

ACKNOWLEDGMENTS.—I am most grateful to Prof. Dr. S. Gerlach for his gift of the North Sea specimens to the Smithsonian Institution. During the several years of field work, I have received generous assistance from Marie Wallace, Cate Drew, and Susann Braden of the National Museum of Natural History; and Sherry Reed, Hugh Reichardt, William Lee, and other personnel at the Smithsonian Marine Station at Link Port. The patient and scholarly review of this manuscript by my colleagues Horton H. Hobbs, Jr., Reinhardt M. Kristensen, and Birger Neuhaus is also gratefully acknowledged. This study has been funded by grants from the Smithsonian Marine Station at Link Port and this publication is contribution number 252 of this facility.

Classification of the Kinorhyncha

Key to Orders, Suborders, Families, and Genera of Kinorhyncha

(based on adult morphology)

1. Second segment, or neck region, consisting of a ring of 14–16 placids; at least some trunk segments, excluding terminal segment, with lateral and middorsal spines [note: if the placids cannot be seen, lateral and middorsal spines constitute an alternative key character]; trunk segments round to oval or triangular in transverse section, rounded to vaulted dorsally, flattened ventrally (order Cyclorhagida) 2

   Second segment, or neck region, consisting of 2 or 4 dorsal placids and 2 or 4 ventral placids; trunk segments, excluding terminal segment, devoid of lateral and middorsal spines; all trunk segments triangular in transverse section, vaulted dorsally, flattened ventrally (order Homalorhagida, suborder Homalorhagae) 9

2. First trunk segment (segment 3) consisting of complete ring of cuticle (suborder Cyclorhagae) 3

   First trunk segment (segment 3) consisting of bilateral clamshell-like plates with or without wedge-shape plate dorsally and ventrally, trunk strongly triangular in transverse section; or with first trunk segment consisting of a rounded tergal plate with only incised margins indicating each lateroventral articulation zone but articulating with single midsternal plate, sometimes poorly defined or incompletely delineated anteriorly 7

3. First and second trunk segments consisting of complete bands of cuticle; midventral placid usually wider than other placids which are uniform in width 4

   First trunk segment consisting of a complete band of cuticle, second trunk segment of single tergal plate and 2 sternal plates; midventral placid usually wider than other placids, other placids, which are not uniform in width, usually alternating narrow and wide (family Centroderidae) 5

4. Midterminal spine present (Zelinkaderidae, new family) . . . . ***Zelinkaderes*,** new genus

   Midterminal spine absent (family Echinoderidae) . . . . ***Echinoderes***

5. Posterior margin of first trunk segment with two prominent ventral spines . . . 6

   Posterior margin of first trunk segment without spines . . . . ***Condyloderes***

6. Two prominent ventral spines extending nearly length of 4 segments; middorsal spine present on segment 12 . . . . ***Campyloderes***

   Two prominent ventral spines extending nearly length of 2 segments; middorsal spine absent on segment 12 . . . . ***Centroderes***

7. First trunk segment consisting of bilateral clamshell-like plates with or without inserted wedge-shape plate dorsally and ventrally, trunk strongly triangular in transverse section (suborder Conchorhagae, family Semnoderidae) 8

   First trunk segment consisting of rounded tergal plate with only incised margins indicating each lateroventral articulation zone but articulating with single midsternal plate sometimes poorly defined or incompletely delineated anteriorly (suborder Cryptorhagae, family Cateriidae) . . . . ***Cateria***

8. First trunk segment consisting of bilateral clamshell-like plates separated basally by midventral and middorsal wedge-shape plates . . . . ***Sphenoderes***

   First trunk segment consisting of bilateral clamshell-like plates without separation basally by midventral and middorsal wedge-shape plates . . . . . . ***Semnoderes***

9. First trunk segment with 3 sternal plates (2 episternal and midsternal plate); remaining trunk segments with 2 sternal plates clearly separated from and articulating with lateroventral margins of tergal plate; midterminal spine present in J-1 to J-3 stages of *Pycnophyes* only; trunk segments occasionally with middorsal spinose marginal projections only (family Pycnophyidae) 10

   First trunk segment lacking series of sternal plates; remaining trunk segments with 2 sternal plates not clearly separated from and articulating with lateroventral margins of tergal plate; midterminal spine present in *Paracentrophyes* only; trunk segments with middorsal and posterolateral spinous marginal projections (family Neocentrophyidae) 11

10. Terminal segment with lateral spines . . . . ***Pycnophyes***

    Terminal segment without lateral spines . . . . ***Kinorhynchus***

11. Terminal segment with lateral spines . . . . ***Paracentrophyes***

    Terminal segment without lateral spines . . . . ***Neocentrophyes***

Order CYCLORHAGIDA Zelinka, 1896

DIAGNOSIS.—Second segment consisting of a ring of 14–16 placids articulating with, or fused to the anterior margin of segment 3 (first trunk segment), placids sometimes distinguished only by a thin outline of cuticle in the neck region. Middorsal spines present in adults or, if absent, present in juvenile stages. Oral styles with 2 or 3 segments or unsegmented.

INCLUDED SUBORDERS.—Three: Cyclorhagae Zelinka, 1896; Conchorhagae Zelinka, 1907; and Cryptorhagae Higgins, 1968.

Suborder CYCLORHAGAE Zelinka, 1896

DIAGNOSIS.—Midventral placid of second segment usually wider than remaining placids. Segment 3 (first trunk segment), and sometimes segment 4, consisting of complete ring of cuticle. Segments 5–12 or 13 each consisting of rounded tergal plate articulating with 2 sternal plates at lateroventral articulation zones, and sternal plates articulating midventrally. Midterminal spine present in adults of some genera and at least some juvenile stages of all genera. Middorsal spines present in all juveniles and in adults with exception of a few species of *Echinoderes*. Subdorsal spines present in some. Cuspidate lateral spines present in some families. Oral styles with 2 segments or unsegmented.

INCLUDED FAMILIES.—Three: Echinoderidae Bütschli, 1876; Zelinkaderidae, new family; Centroderidae Zelinka, 1896.

Family ECHINODERIDAE Bütschli, 1876

DIAGNOSIS.—Segment 2 consisting of 16 distinct placids articulating with segment 3, all of similar width except for larger midventral placid. Segments 3 and 4 consisting of complete ring of cuticle. Segments 5-12 or 13 with 2 sternal plates articulating midventrally, and laterally with single rounded tergal plate. Midterminal spine absent in adult and present in at least some juveniles. Middorsal spines on some adults and all juvenile stages. Subdorsal spines, if present, on segment 4 only. Cuspidate lateral spines absent. Oral styles with 2 segments.

INCLUDED GENERA.—One: *Echinoderes* Claparède, 1863.

Family ZELINKADERIDAE, new family

DIAGNOSIS.—Segment 2 consisting of 16 indistinct placids, all of similar width except for wider midventral placid; placids basally fused with segment 3 (first trunk segment) and not clearly separated from each other (with weakly defined lateral margins visible only in SEM preparations). Segments 3 and 4 consisting of complete rings of cuticle. Segments 5-13 with lateral margins of single rounded tergal plate articulating midventrally, without indication of lateroventral articulation zones or incised posterior margins at such zones. Midterminal spine present in adult and juveniles. Middorsal spines present on segments 6, 8, 10-13. Subdorsal spines present on segment 12. Cuspidate lateral spines present. Oral styles with 2 segments.

INCLUDED GENERA.—One: *Zelinkaderes*, new genus.

Zelinkaderes, new genus

DIAGNOSIS.—Identical with family diagnosis.

TYPE SPECIES.—*Zelinkaderes floridensis*, new species.

ETYMOLOGY.—The generic name is masculine, based on the surname of Carl Zelinka (1859-1946), hereby recognized for his pioneering work on the biology of the Kinorhyncha. The suffix is from the Greek *deres* (neck), one employed in the naming of all of the generic taxa of the Cyclorhagae.

Family CENTRODERIDAE Zelinka, 1896

DIAGNOSIS.—Segment 2 consisting of 14-16 distinct placids; midventral placid widest, others alternating in lesser and approximately same widths. Segment 3 consisting of complete ring of cuticle. Segments 4-13 consisting of two sternal plates articulating midventrally, and laterally with single rounded tergal plate. Midterminal spine present in adults and juveniles. Middorsal spines present on segments 3-11 and segment 12 of juveniles and adults, except for one genus where present in juvenile only. Subdorsal spines present on segment 12 of juveniles and all adults except for males of *Centroderes*. Cuspidate lateral spines present only in *Condyloderes*. Oral styles with two segments or unsegmented, possibly fused to form extended mouth cone in *Campyloderes*.

INCLUDED GENERA.—Three: type-genus *Centroderes* Zelinka, 1907; *Campyloderes* Zelinka, 1913; and *Condyloderes* Higgins, 1969a.

Suborder CONCHORHAGAE Zelinka, 1907

DIAGNOSIS.—Segment 2 consisting of 16 placids, similar in width except for wider midventral placid, placids barely distinguishable in *Semnoderes*. Segment 3 bilaterally divided into clamshell-like closing apparatus, with wedge-shape midventral and middorsal plates in *Sphenoderes*. Segments 4-13 each consisting of vaulted tergal plate articulating with 2 sternal plates at lateroventral articulation zones, and sternal plates articulating midventrally. Midterminal spines present. Middorsal spines present on all trunk segments. Cuspidate lateral spines present. Subdorsal spines on segment 12. Oral styles with 3 segments.

INCLUDED FAMILIES.—One: Semnoderidae Remane, 1936.

Family SEMNODERIDAE Remane, 1936

DIAGNOSIS.—Same as suborder.

INCLUDED GENERA.—Two: type-genus *Semnoderes* Zelinka, 1907, and *Sphenoderes* Higgins, 1969a.

Suborder CRYPTORHAGAE Higgins, 1968

DIAGNOSIS.—Segment 2 consisting of 14 barely distinguishable placids. Segments 3-8 each consisting of a rounded tergal plate with only incised margins indicating each lateroventral articulation zone and single midventral or sternal plate, which may be poorly defined or incompletely separated at the anterior margin. Segments 9-12 with edges of tergal plate articulating midventrally, otherwise incised at each lateroventral articulation zone and on either side of ventral midline. Segment 13 with midventral tergal articulation and less distinct incisions at lateroventral articulation zones. Midterminal spine present. Middorsal spines present on segments 4-6, 8, 10-12 in adults. Cuspidate lateral spines absent. Oral styles with 3 segments.

INCLUDED FAMILIES.—One: Cateriidae Gerlach, 1956.

Family CATERIIDAE Gerlach, 1956

DIAGNOSIS.—Same as suborder.

INCLUDED GENERA.—One: *Cateria* Gerlach, 1956.

Order HOMALORHAGIDA Zelinka, 1896

DIAGNOSIS.—Second segment consisting of 2 to 4 dorsal placids and 3 or 4 ventral placids. Middorsal spines absent. Oral styles with 3 segments or unsegmented.

INCLUDED SUBORDER.—One: Homalorhagae Zelinka, 1896.

Suborder HOMALORHAGAE Zelinka, 1896

DIAGNOSIS.—Same as for order.

INCLUDED FAMILIES.—Two: Pycnophyidae Zelinka, 1896; and Neocentrophyidae Higgins, 1969b.

Family PYCNOPHYIDAE Zelinka, 1896

DIAGNOSIS.—Segment 2 consisting of 2–4 dorsal placids and 2–4 ventral placids. Segment 3 consisting of single arched tergal plate articulating with two episternal plates, which articulate with single midsternal plate. Segments 4–13 with single arched tergal plate and 2 sternal plates; lateral margin of tergal plate usually with pachycyclar peg inserted into socket at lateral edge of each sternal pachycyclus. Midterminal spine present only in early juvenile stages of *Pycnophyes*. Oral styles unsegmented.

INCLUDED GENERA.—Two: type-genus *Pycnophyes* Zelinka, 1907; and *Kinorhynchus* (Sheremetevskij, 1974).

Family NEOCENTROPHYIDAE Higgins, 1969

DIAGNOSIS.—Segment 2 consisting of 4 dorsal placids and 3 ventral placids. Lateroventral articulation zone of trunk segments indistinct. Segment 3 appearing as single band of cuticle arched dorsally and flattened ventrally with only slight indication of midsternal plate anteroventrally. Segments 4–12 similar to segment 3 but with lateral edges articulating at midventral line. Midterminal spine present in both adult and juvenile stages. Oral styles with 3 segments.

INCLUDED GENERA.—Two: type-genus *Neocentrophyes* Higgins, 1969b; and *Paracentrophyes* Higgins, 1983.

Descriptions of Two Species of the New Family Zelinkaderidae

Zelinkaderes floridensis, new species

FIGURES 1–68

DIAGNOSIS.—*Zelinkaderes*, adult trunk length 300–435 µm, trunk width 42–60 µm, about 14 percent of trunk length, with middorsal spines on segments 6, 8, 10–13, length of each nearly equal to that of segment of origin; cuspidate spines present laterally on segments 7, 10, 11; aciculate spines present laterally on segments 1–13; middorsal gland (cuticular scar) on segment 3, none evident on segment 4, subdorsal glands (cuticular scars) on segment 12; Lateral terminal spines shorter than lateral terminal accessory spines.

DESCRIPTION.—*Trunk:* Adult (Figures 1–68) trunk length 355–420 µm; $\bar{x}$ 17 (mean of 17 measurements) = 392.1 ± 20.7 µm. The maximum sternal width is indeterminable because the lateral tergal-sternal junctions are not evident; however, an estimate of this width is 42–60 µm, about 14 percent of the trunk length. The standard width, normally defined as the distance between the anterolateral margins of the sternal plates of segment 12, cannot be determined for the same reason given above. A substitute standard width measurement, based on the distance between the lateral margins of the cuspidate spines of segment 11, is 46–58 µm, $\bar{x}$ 17 = 52.0 ± 3.5 µm, 12.4–14.5 percent of the trunk length.

Segment 2 measurements are difficult to assess by light microscopy because of the segment's apparent basal fusion with segment 3. Estimates of the length of this segment are 16–24 µm, $\bar{x}$ 14 = 21.4 ± 2.0 µm. The midventral placid (Figures 1, 18) is about twice as wide as each of the remaining 15 placids.

Segment 3 is 22–30 µm in length, $\bar{x}$ 16 = 25.8 ± 2.6 µm. The anterior margin, adjacent to the placids, lacks cuticular hairs; the posterior two-thirds of the segment is evenly hirsute. When the cuticle is viewed with phase contrast optics, there is a distinctive internal striate pattern (see Figure 77). Cuticular hairs at the posterior margin of the segment extend beyond the intersegmental junction as a pectinate fringe. The arthrocorium, as in all of the following segments, often is expanded, more widely separating the adjacent segments (Figures 1, 2). The surface of the arthrocorium typically has transverse rows of minute tubercles (Figure 23). A distinct pachycyclus is absent; the cuticle appears to be uniformly thin. An exception to this is the thickened anteroventral margin of segment 13 in the female (see description of segment 13).

Segment 4 is 24–30 µm in length, $\bar{x}$ 16 = 27.4 ± 1.9 µm. A prominent middorsal cuticular scar (pore leading to a dorsal gland) is present (Figures 2, 21). Laterally, two in-line, less hirsute patches of cuticle appear as interruptions in the otherwise uniformly hirsute cuticle (Figure 14).

Segment 5 is 24–32 µm in length, $\bar{x}$ 16 = 26.7 ± 2.8 µm. The middorsal cuticular scar is absent, and only a single patch of less hirsute cuticle is present laterally. Beginning with this segment, and continuing through segment 13, there is a midventral fissure where the morphological lateral edges of the tergal plate meet. The cuticle in this area appears slightly thicker than elsewhere (Figure 1).

Segment 6 is 24–30 µm in length, $\bar{x}$ 16 = 27.5 ± 2.0 µm. A transverse row of three paired patches of less hirsute cuticle are situated anterodorsally. As in segment 5, a single patch is present laterally at midlength, and an additional sensory spot is present slightly more posteroventrally (Figure 14). A middorsal spine 20–29 µm in length, $\bar{x}$ 17 = 24.4 ± 2.4 µm, extends from the incised posterior margin of the segment. A sensory spot is present on each side of this spine (Figures 22, 23) and all other middorsal spines. As in all other spines, the cuticular surface is covered basally with minute tubercles (Figure 23) and distally with imbricate, short cuticular hairs (Figures 22, 23, 28–31).

Segment 7 is 26–32 μm long, $\bar{x}$ 16 = 28.9±2.9 μm. It is similar to segment 6 but with two, in-line, sensory spots and no lateral sensory spot (Figure 14). A cuspidate spine, 21–28 μm long, $\bar{x}$ 17 = 24.5±2.0 μm, is present ventrolaterally (Figures 1, 2, 14, 18). The basal half of a cuspidate spine is broad, narrowly oval in cross-section, and hirsute; the distal portion is narrow, round in cross-section, and terminates with a pore similar to that shown in Figure 29. Similar spines are present on segments 10 and 11.

Segment 8 is 28–33 μm long, $\bar{x}$ 16 = 30.1±1.5 μm. As in segment 6, there is a middorsal spine, which is 27–35 μm long, $\bar{x}$ 17 = 31.2±1.5 μm. Also, in all other respects it is similar to segment 6.

Segment 9 is 30–36 μm long, $\bar{x}$ 16 = 32.0± 1.9 μm. This segment lacks a middorsal spine, but otherwise is like segment 8.

Segment 10 is 28–36 μm long, $\bar{x}$ 16 = 32.6±2.4 μm. It is similar to segments 6 and 8 in having a middorsal spine, which is 32–40 μm long, $\bar{x}$ 16 = 22.5±2.2 μm. A transverse row of three paired-patches of less hirsute cuticle are situated anterodorsally, and there is a lateral patch as on segment 9, but no sensory spot is present: two lateral spines are situated in its place. The dorsalmost of the two spines is cuspidate, similar to those of segment 7 and 11, and measures 26–34 μm, $\bar{x}$ 17 = 29.3 ± 2.7 μm. Ventral to the cuspidate spine is an acicular spine, 18–28 μm long, $\bar{x}$ 17 = 22.5±2.2 μm. Although in ventral aspect, these two spines appear to be in positions equivalent to those of the following segment, they clearly are more elevated as can be seen in lateral view (Figures 14, 27). In ventral aspect, females have paired single pores situated anteromesial to the ventrolateral acicular spine.

Segment 11 is 32–42 μm long, $\bar{x}$ 16 = 37.0±2.9 μm. It also has a middorsal spine 40–50 μm long, $\bar{x}$ 17 = 43.5±2.8 μm. The anterodorsal margin of this segment is similar to those preceding it, but unlike segment 10, there are two, in-line, patches as in segments 4 and 7 (Figure 14, 27), and a sensory spot (Figures 14, 27, 30) ventral to the posteriormost lateral patch. This sensory spot appears to be in the same relative position as the cuspidate spine of the preceding segment. Below and slightly posterior to this sensory spot are two lateral spines. The most dorsal of the two spines is acicular, measuring 24–28 μm, $\bar{x}$ 17 = 26.3±1.2 μm. The most ventral of the two spines is cuspidate, measuring 26–37 μm, $\bar{x}$ 17 = 30.1±2.5 μm. As in the preceding segment, the ventral aspect shows paired single pores positioned anteromesial to the spines in the female (Figure 1).

Segment 12 is 30–40 μm long, $\bar{x}$ 16 = 34.9±3.1 μm. As in segments 6–11 three patches of less hirsute cuticle are present in a transverse row anterodorsally. A lateral patch is posterior to the ventralmost of the former patches and a sensory spot is located both dorsally and ventrally to the lateral patch (Figure 14). This segment has a middorsal spine 33–44 μm long, $\bar{x}$ 17 = 37.4±3.6 μm. In the male this and the 2 lateral spines on the segment, are flexible (Figures 3, 4, 14, 38), and distally segmented or moniliform in appearance. The middorsal spine also may be slightly shorter in males, 32–40 μm, $\bar{x}$ 12 = 36.1 ±2.5 μm, than in females, 34–44 μm, $\bar{x}$ 5 = 40.6 ±4.0 μm. The lateral spine on segment 12 is slightly elevated to nearly a midlateral position (Figure 14) and its length is 24–38 μm, $\bar{x}$ 17 = 33.2±3.0 μm. Although this spine may tend to be slightly longer (and flexible, as noted previously) in the male 30–38 μm, $\bar{x}$ 12 = 33.8±2.3 μm, than in the female 24–34 μm, $\bar{x}$ 5 = 31.8±4.4 μm, the differences are not significant. Subdorsally, near the posterior margin, on each side of the middorsal spine of both males and females, there is a unique cuticular scar. No evidence of any surface structure could be seen by scanning electron microscopy, but light microscopy revealed a series of four pores within this scar (Figures 2, 4).

Segment 13, the terminal segment, is 30–35 μm long, $\bar{x}$ 16 = 32.6±1.8 μm and strongly tapers to the base of the midterminal spine 230–290 μm long, $\bar{x}$ 16 = 262.4±18.3 μm. The length of the midterminal spine tends to be larger in males, 240–290 μm, $\bar{x}$ 11 = 270.7±14.8 μm, than in females, 230–255 μm, $\bar{x}$ 5 = 244±9.6 μm. The MTS/TL (ratio of midterminal spine length to trunk length expressed as percent) is 55.4–77.0 percent, $\bar{x}$ 16 = 67.4±7.4 percent. A middorsal spine 64–80 μm long, $\bar{x}$ 17 = 72.1±4.0 μm is present, extending well beyond the margin of the terminal segment. Lateral terminal spines are 44–54 μm long, $\bar{x}$ 17 = 48.4±2.9 μm. The LTS/TL (ratio of lateral terminal spine length to trunk length expressed as percent) is 11.1–13.8 percent, $\bar{x}$ 17 = 12.4±0.7 percent. Prominent sensory spots are present mesial to each lateral terminal spine (Figures 14, 31). Lateral terminal accessory spines, are slightly longer than, and lie dorsally adjacent to, the lateral terminal spines, 64–76 μm long, $\bar{x}$ 17 = 68.1±3.4 μm. The LTAS/LTS (ratio of lateral terminal accessory spines to length of lateral terminal spines expressed in percent) is 124.5–155.1 percent. Although there still appears to be no separation between the tergal and sternal plates, there is a distinct ventral margin separated from the remainder of the segment's cuticle (Figures 1, 3), giving the appearance of sternal plates much shorter than the presumptive tergal plate.

The cuticle at the anteroventral margin of segment 12 in the female is thickened as a pachycyclus and has a distinctive morphology (Figure 1). Near the lateral margins, there is an arched region (Figures 33–35), which appears to form the anterior margin of a flap of cuticle covering an opening presumed to be a gonopore. A sensory spot lies lateral to each flap (Figures 34, 35). In the male (Figure 3), the cuticle is not thickened to form a distinctive structure, which can be seen in light microscopy; but SEM photographs (Figures 36, 37) reveal a modification of the cuticular surface in the position comparable to the cuticular flap of the female. A gonopore is assumed present in this area of cuticle in the male.

Head: Segment 1 is not always described in taxonomic publications, but in the case of *Zelinkaderes floridensis* sufficient material is available to present the following information. The kinorhynch head consists of two parts: an evertable, spherical region bearing up to 7 rings of scalids, and a mouth cone centered within the spherical head from which it is protruded anteriorly through the everted head in order to feed. The determination of the ring in which the scalid is located is complicated, at least in *Zelinkaderes*, by the extent of the attachment area. If, for example, the ring assignment is based on the anteriormost point of a scalid's origin, this may not be commensurate with the ring assignment based on the posteriormost point of the scalid's attachment, where it becomes free from the head, and usually where the second of the two elements begins. In this paper, the assignment of scalids to a ring has been determined by the point at which the posterior margin of the basal segment attaches to the article of the head or introvert.

As in all members of the phylum Kinorhyncha, the primary scalids are the largest scalids. Insofar as they are the organizers of the scalid pattern, they are the directive scalids, and with reference to the diagram (Figures 5, 6) constitute the first row of spinoscalids (indicated by solid triangles pointed radially to indicate their posteriorly directed orientation when the head is everted). Scalid arrangement is organized into 5 odd (shaded) and 5 even (unshaded) sectors as shown in Figures 5, 6. Each sector is divided into radii designated A,B,C, and D. D-radii are the directive radii established by each of the 10 primary scalids and which delimit each sector. The middle radius of each sector is referred to as the B (basal)-radius. On the sides of the basal radius are the A- and C-radii. As just noted, scalid ring 1 contains the 10 largest scalids. Their polar-coordinate position is "1-1-D through 10-1-D" which indicates first, the sector number (1-10), second, the ring number (1), and last, the radius (D). Sometimes the radius designation(s) may be replaced by the terms "odd" or "even." The directive (position of primary scalid) D-radius follows the C-radius of a given sector (on the clock-wise sequence of the four letters (A-B-C-D).

The 10 primary spinoscalids of the first ring (anteriormost) (Figure 7) (shown as solid triangles in Figures 5 and 6) are about 55-65 μm long, a multi-element basal fringe (Figures 5, 7, 16) extends as much as one third the spinoscalid length. The distal portion of the spinoscalid appears partially septate along its inner margin and terminate in a blunt tip with a pore (Figure 7). These and at least some other spinoscalids consist of a basal unit and an articulating distal unit. The basal unit is provided with a pectinate fringe at its origin.

Superficially, there appear to be 10 spinoscalids in the second ring. Five of these, located on the B-radii of odd sectors (1, 3, 5, 7, 9), are indicated by solid circles, assigned to the second ring (Figures 5, 6), have short attachment planes (Figure 8), and extend freely from the head more anteriorly than do those of a second set. The second set of 5, located on the B-radii of even sectors (2, 4, 6, 8, 10), are indicated by solid ovals, have longer attachment planes (Figure 11), and extend freely from the head more posteriorly (at the same level as the A- and C-radii scalids of the odd sectors); therefore, they are assigned to the fourth ring along with the A- and C-radii spines of the odd sectors. Both sets of 5 scalids are extremely similar (Figures 8, 11), appear to originate immediately posterior to the primary scalids of the first row, have a prominent 3-element basal fringe (Figures 5, 8, 11, 19), and smooth distal elements with pointed tips. The length of the odd-sector scalids is about 35-40 μm, the even-sector scalids are slightly shorter, 30-35 μm.

The 10 spinoscalids (Figure 11) of the third ring (shown as solid squares in Figures 5 and 6) are located on the A- and C-radii of even sectors (2, 4, 6, 8, 10). These spinoscalids are about 30-35 μm long, have a single-element basal fringe and fringed inner margins (Figures 5, 11, 16) as in A- and C-radii, odd-sector scalids of the fourth ring. Like the scalids of the second ring, the third-ring scalids are pointed at the tip.

The 15 spinoscalids of the fourth ring (shown as solid ovals in Figures 5 and 6) consist of 5 spinoscalids located on the B-radii of even-numbered sectors (see the paragraph concerning the second ring), and 10 additional spinoscalids occupying positions on the A- and C-radii of odd sectors. The latter 10 spinoscalids (Figure 12) are extremely similar to the 10 spinoscalids of the A- and C-radii, even-sector spinoscalids of ring 3 (Figure 11).

In those genera (*Pycnophyes, Kinorhynchus,* and *Echinoderes*) more carefully studied, 7 rings appear to be present in adults and as few as 4 rings in the earliest juvenile stage. Trichoscalids, typically 14 in number, occupy the posteriormost ring (ring 7) in kinorhynchs. Although classically (Zelinka, 1928:23) these sensory structures are hirsute, juvenile-stage trichoscalids typically lack this character, remaining simply smooth and highly flexible. The 14 simple, smooth, highly flexible scalids (Figures 10, 12) in the posteriormost ring of *Zelinkaderes floridensis* (indicated by open circles with short radii in Figures 5 and 6), are assumed to be homologous with the juvenile protrichoscalids and, therefore, are assigned to ring 7. Nine of the 14 trichoscalids (one on each of the A- and C-radii of sectors 2, 4, 8, and 10, and a single trichoscalid on the B-radius of sector 6 (Figure 13) are slightly elevated from the remaining 5 trichoscalids on the B-radii of sectors 1, 3, 5, 7, and 9 (Figure 10). The 9 even-sector trichoscalids are about 20 μm in length, have a modest amount of basal fringe, and an elongate, flexible distal element, which is pointed. The 5 odd-sector trichoscalids are slightly longer and more robust. Thus, the general appearance of the scalid pattern in *Z. floridensis* is (1) an anteriormost (ring 1) series of 10 primary spinoscalids, which define 10 sectors; (2) each sector with a (median) secondary and two (lateral) tertiary spinoscalids centered between the primary scalids apparently successive rows; and (3) a quaternary ring of 14 juvenile-like protrichoscalids, 9 of them elevated slightly with respect to the remaining 5. Superficially, if not actually, there appears to be only 4 rings of scalids in this genus.

There are 9 anteriorly directed, oral styles surrounding the mouth cone, the terminus of which is the mouth (Figures 5, 14, 16, 39–43). In the polar-coordinate diagram of the head (Figure 6), the positions of the 9 oral styles are indicated by the short, broad arrows, pointing toward the center of the circle, located on all B-radii except that of sector 1 (the middorsal oral style is missing); thus, they alternate with the positions of the 10 primary scalids located on all D-radii. Each oral style of *Zelinkaderes floridensis* has two segments, a basal element, about 25 µm long and a distal element about 5 µm long. The basal element of the style bears a pectinate fringe similar to the basal element of a spinoscalid (Figures 7–13), and the pectinate fringe typical of the posterior margin of most trunk segments. Near the base, each style is oval in transverse section; at about midlength the lateral edge forms what appears to be a hollow flange leading to the distal element (Figures 5, 16, 17). Since there is a pore (Figure 17) at the terminus of the distal element, these lateral flanges may be ducts leading to the pore.

Within the mouth cone are 20 pharyngeal styles arranged in 3 (possibly 4) rings. The innermost ring (ring 1) consists of 5 long, strongly cuticularized, longitudinally ridged pharyngeal styles (Figures 39–41, ps1) that may be partially extruded during the protrusion of the mouth cone. These originate in the epithelium of the pharynx near the cuticularized oral crown at the anterior end of the pharyngeal bulb. The midventral pharyngeal style of ring 1 appears to oppose an oral style (Figures 6, 40); therefore, it is assumed to be on the B-radius of sector 6, and the remaining 4 pharyngeal styles of ring 1 occupy B-radii positions on other even sectors. This assumption is supported by TEM studies of *Echinoderes aquilonius* Higgins and Kristensen, 1988, and *Pycnophyes greenlandicus* Higgins and Kristensen, 1988 (Kristensen and Higgins, in press). First ring pharyngeal styles are indicated on the first ring mouth cone (Figure 6) by asterisks.

Alternating with the first ring are 5 weakly cuticularized pharyngeal styles (Figure 39, ps2) of ring 2. These apparently are on B-radii of odd sectors, and are indicated in the diagram (Figure 6) by larger arrowheads.

The remaining 10 pharyngeal styles (ps3) occur in pairs, each pair originates between the pharyngeal styles of ring 2 (ps2) and are indicated by narrow arrowheads. One of each pair has its origin closer to the origin of ring-2 pharyngeal style, the other originates farther away. The result is a slight off-set of these paired oral styles so that they appear to be in separate rows (which is a possibility, but they appear to be morphologically identical). Hence, when the pharyngeal epithelium is hyper-extended, pharyngeal styles of the ps3 units are on either side of each ps2 unit (Figure 39), one appearing slightly posterior to the other.

JUVENILE STAGES.—Juvenile stages are rarely described in taxonomic publications. The quality and quantity of material of *Zelinkaderes floridensis*, however, permits an analysis of the entire life history of this species. A total of 62 juvenile specimens were studied, and among them were at least one representative of each of six stages (J-1 through J-6, Figures 45–62), which are included below as a part of the species description.

J-1 Stage: The first stage in the life history of *Zelinkaderes floridensis* (Figures 45, 46, 57–59) juvenile development is represented by a specimen 165 µm long (RH 1561.21, USNM 235451). Its estimated standard width is 40 µm, the SW/TL 21.1 percent. Middorsal spines (Figures 46, 59) are present on segment 6 (42 µm long), segment 8 (41 µm long), segment 10 (40 µm long), and segment 11 (110 µm long); the midterminal spine is 170 µm long, 73.9 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (20 µm long) and acicular lateral spines on segment 10 (42 µm long). The slightly protruding spines at the lateral margins of segment 11 may be the anlagen of the lateral terminal accessory spines, based on the observation that these, the more dorsally displaced lateral spines of the terminal segment, are also the most prominent throughout the life history, including the adult stage. The only other distinguishing feature of this stage is the presence of a cuticular scar middorsally on segment 4. Placids are apparent and commensurate with their distribution in the adult. Four rings of spinoscalids are present (Figure 57) although the disposition of the fourth row is not clear. Oral styles appear to begin as two types (Figure 57, os1, os2). The first and most prominent are 5 moderately large and distinct oral styles (os1) alternating with 4 smaller, less distinct oral styles (os2). The middorsal os2 style is missing.

J-2 Stage: The second stage (Figures 47, 48) of juvenile development is represented by a specimen 205 µm long (RH 1661.26, USNM 235460). Its estimated standard width is 34 µm, the SW/TL 16.5 percent. Middorsal spines (Figure 48) are present on segment 6 (30 µm long), segment 8 (40 µm long), segment 10 (36 µm long), segment 11 (56 µm long), and a newly added segment 12 (132 µm long; the midterminal spine is 146 µm long, 71.2 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (21 µm long); acicular lateral spines are on segment 10 (22 µm long) with cuspidate lateral accessory spines (24 µm long) dorsally adjacent. Acicular lateral spines (20 µm long) are now present on segment 11 and the newly added segment 12 (49 µm long). Lateral terminal accessory spines (20 µm long) appear at the lateral margins of the terminal segment, and lateral terminal spines are represented by very small (4 µm long) protuberances mesial to the lateral terminal accessory spines. The LTS/TL is 1.9 percent, the LTAS/TL is 9.7 percent, and the LTAS/LTS is 500 percent. The cuticular scar noted in the first stage remains middorsally on segment 4. Placids are proportionally larger.

J-3 Stage: The third juvenile stage (Figures 49, 50, 60–62) is represented by a specimen 225 µm long (RH 1661.25, USNM 235460). Its estimated standard width is 37 µm, the SW/TL 16.4 percent. Middorsal spines (Figures 50, 62) are present on segment 6 (30 µm long), segment 8 (38 µm long), segment 10 (34 µm long), segment 11 (42 µm long), and segment 12 (96 µm long); although segment 13 now appears to be at least partly differentiated, there is no evidence of a middorsal spine on this segment. The midterminal spine is 170 µm long, 75.5 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (20 µm long); acicular lateral spines are on segment 10 (24 µm long) with cuspidate lateral accessory spines (22 µm long) dorsally adjacent. Acicular lateral spines (21 µm long) are present on segment 11 and cuspidate lateral accessory spines (24 µm long) have been added. Segment 12 has a single acicular lateral spine (36 µm long). Lateral terminal accessory spines (40 µm long) appear at the lateral margins of the now more distinct terminal segment; lateral terminal spines (12 µm long) are present mesial to the lateral terminal accessory spines. The LTS/TL is 5.3 percent, the LTAS/TL is 17.7 percent, and the LTAS/LTS is 333 percent. The cuticular scar (dorsal gland) noted in the first and second stages remains middorsally on segment 4. Placids are proportionately larger.

J-4 Stage: The fourth juvenile stage (Figures 51, 52) is represented by a specimen 255 µm long (RH 1661.33, USNM 235460). Its estimated standard width is 44 µm, the SW/TL 17.2 percent. Middorsal spines (Figure 52) are present on segment 6 (24 µm long), segment 8 (30 µm long), segment 10 (32 µm long), segment 11 (40 µm long), segment 12 (60 µm long), and for the first time on segment 13 (126 µm long). The midterminal spine is 116 µm long, 62.7 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (20 µm long). Acicular lateral spines are on segment 10 (20 µm long) and the adjacent cuspidate lateral accessory spines are 22 µm long. Acicular lateral spines on segment 11 (20 µm long) are accompanied by cuspidate lateral accessory spines (21 µm long). Segment 12 has a single lateral spine (30 µm long). Lateral terminal accessory spines (42 µm long) of segment 13 are dorsally adjacent to lateral terminal spines (40 µm long). The LTS/TL is 15.6 percent, the LTAS/TL is 16.4 percent, and the LTAS/LTS is 105 percent. The cuticular scar (dorsal gland) noted in the first three stages remains middorsally on segment 4. Placids are proportionately larger.

J-5 Stage: The fifth juvenile stage (Figures 53, 54) is represented by a specimen 320 µm long (RH 1661.28, USNM 235469). Its estimated standard width is 50 µm, the SW/TL 15.6 percent. Middorsal spines (Figure 54) are present on segment 6 (22 µm long), segment 8 (28 µm long), segment 10 (34 µm long), segment 11 (40 µm long), segment 12 (42 µm long), and segment 13 (76 µm long). The midterminal spine is 214 µm long, 66.8 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (20 µm long). Acicular lateral spines (20 µm long) and cuspidate lateral accessory spines (20 µm long) are on segment 10. Acicular lateral spines on segment 11 (26 µm long) are accompanied by cuspidate lateral accessory spines (23 µm long). Segment 12 has a single lateral spine (30 µm long). Lateral terminal accessory spines (60 µm long) of segment 13 are dorsally adjacent to lateral terminal spines (48 µm long). The LTS/TL is 15.0 percent, the LTAS/TL is 18.7 percent, and the LTAS/LTS is 125 percent. The cuticular scar noted in the first four stages remains middorsally on segment 4. Placids are proportionately larger.

J-6 Stage: The sixth juvenile stage or pre-adult stage (Figures 55, 56) is represented by a specimen 350 µm long (RH 1661.34, USNM 235460). Its estimated standard width is 50 µm, the SW/TL 14.2 percent. Middorsal spines (Figure 56) are present on segment 6 (22 µm long), segment 8 (33 µm long), segment 10 (39 µm long), segment 11 (41 µm long), segment 12 (42 µm long), and segment 13 (72 µm long). The midterminal spine is 210 µm long, 60.0 percent of the trunk length. Cuspidate lateral spines occur on segment 7 (21 µm long). Acicular lateral spines are on segment 10 (22 µm long) adjacent to cuspidate lateral accessory spines (26 µm long). Acicular lateral spines on segment 11 (24 µm long) are accompanied by cuspidate lateral accessory spines (24 µm long). Segment 12 has a single lateral spine 30 µm long. Lateral terminal accessory spines of segment 13 are 60 µm long, lateral terminal spines are 50 µm long. The LTS/TL is 14.2 percent, the LTAS/TL is 17.1 percent, and the LTAS/LTS is 120 percent. The cuticular scar noted in all the earlier stages is still present middorsally on segment 4. Placids remain as in the adult.

HOLOTYPE.—Adult female, TL 400 µm (Figures 1, 2, 25 26), from muddy sand, 140 m depth, 33 km east of Fort Pierce, Florida, Southeastern Atlantic Ocean. Collected 2 Aug 82 by R. Higgins, RH 1626.10, USNM 235456.

ALLOTYPE.—Adult male, TL 395 µm (Figures 3, 4), same data as for holotype, RH 1626.12, USNM 235457.

PARATYPES.—All remaining paratypes with same data as for holotype, except for dates collected and include: 15 adult males, 8 adult females, and 18 juveniles, collected 5 Apr 82, RH 1561, USNM 235451; 9 adult males, 2 adult females, and 9 juveniles, collected 5 Apr 82, RH1562, USNM 235453; 9 adult males, 8 adult females, and 3 juveniles, collected 2 Jun 82, RH 1598, USNM 235454; 11 adult males, 4 adult females, and 6 juveniles, collected 2 Aug 82, RH 1626, USNM 235455. 10 adult males, 7 adult females, and 3 juveniles, collected 4 Oct 82, RH 1630, USNM 235458; 10 adult males, 6 adult females, and 11 juveniles, collected 6 Dec 1982, RH 1653, USNM 235459; 20 adult males, 2 adult females, and 12 juveniles, collected 31 Jan 83, RH 1661, USNM 235460.

REMARKS.—*Zelinkaderes floridensis* is similar in basic shape and terminal spine configuration to those species herein recognized as members of the genus *Cateria*. These resemblances, however, are for the most part superficial. The most notable difference between *Zelinkaderes* and *Cateria* is the arrangement of cuticular plates on the ventral surface. Although in both genera, only TEM sections will resolve the exact nature of the apparent lack of clearly defined articulation between tergal and sternal plates, this appearance is characteristic of nearly all known juvenile stages within the phylum. The articulation of the cuticle along the ventral midline with a ligament uniting the two areas of thicker cuticle, appears early in the juvenile development of the Cyclorhagida. The separation of sternal plates from the lateroventral margins of the tergal plates is not apparent until the final molt to the adult and the distinctiveness may be primarily a matter of how thick the cuticle becomes on either side of the zone of articulation.

In *Cateria*, some indication of the presence of the tergal-sternal junction is evidenced by the incised posterior margins of most segments at the area where this junction would be expected (Higgins, 1968). *Cateria* is also distinguished by the presence of midsternal plates on segments 3-8; the remaining segments exhibit a midventral junction, which, although having certain unique aspects, is a feature shared with all members of the phylum. In *C. styx*, the midsternal plates appear to be incompletely separated anteriorly, but in *C. gerlachi* the midsternal plates are completely separated (Higgins, 1968).

The two species of *Cateria* have acicular lateral spines only; both acicular and cuspidate ("club-shape" spine of Gerlach, 1956) spines are found in the families Zelinkaderidae and Centroderidae (*Condyloderes*), as well as in both genera (*Semnoderes* and *Sphenoderes*) of the family Semnoderidae, which comprises the suborder Conchorhagae (Higgins, 1969a). The highly derived condition of bivalved plates on the third segment of the conchorhagous kinorhyncha is conspicuously, and no doubt fundamentally, different from the two complete rings of cuticle making up the third and (in the case of both *Echinoderes* and *Zelinkaderes*) fourth segments of members of the other cyclorhagid suborder. The only homalorhagids having a third segment consisting of a complete ring of cuticle are members of the genus *Neocentrophyes*. Plesiomorphic characters of the latter genus include the presence of a midterminal spine, weakly developed cuticle, and both middorsal and lateral spinose processes.

With the exception of the last three juvenile stages and the adults of the genus *Echinoderes*, cyclorhagids possess a midterminal spine; and, with the exception of the male of the genus *Echinoderes* and at least the adults of both sexes of the genus *Condyloderes*, all have both lateral terminal and lateral terminal accessory spines.

Middorsal spines on all trunk segments represent the plesiomorphic state of the Kinorhyncha. Such spines are present on all trunk segments of the Conchorhagae and in the genus *Campyloderes* of the Cyclorhagae, on all trunk segments except segment 12 of the genus *Centroderes* (although this spine is present in the juvenile stages) and all but segment 13 of the genus *Condyloderes* in the suborder Cyclorhagae. In the other two families of the suborder Cyclorhagae (Echinoderidae and Zelinkaderidae), middorsal spines usually occur on segments 6 through the terminal segment of at least some if not all juvenile stages. The most common middorsal spine occurrence in *Echinoderes* is on segments 6–10. A moderately large number of members of this genus have middorsal spines missing on segments 7 and 9 of the adult; these spines usually are missing in the juveniles also (Higgins, 1978). Several species of *Echinoderes* lack middorsal spines in the adult, but at least some middorsal spines (usually including that on segment 11) are present in the juvenile stages. Members of the cryptorhagous genus *Cateria* have middorsal spines on segments 4–6, 8, 10–12, a pattern where, as in some *Echinoderes*, middorsal spines on segments 7 and 9 are missing and the retention of middorsal spines on the segments 4 and 5, and especially on segments 11–12, suggest the plesiomorphic state of the Cryptorhagae.

In *Zelinkaderes* the middorsal spine pattern, e.g., on segments 6, 8, 10–13, is similar to the early juvenile stages of several members the genus *Echinoderes*. The pattern of middorsal spine loss through the series of juvenile molts in this latter genus is in a progression from midterminal spine to the middorsal spine on segment 11; the latter is lost when the last juvenile stage (J-6) molts to the adult (Higgins, 1977a,b).

The appearance of the peculiar lateroventral pachycyclar rings on adult females of *Zelinkaderes floridensis* is not unique among the Cyclorhagida. Similar structures occur in females of the genus *Centroderes;* moreover, in the suborder Conchorhagae, the same structures are present in the females of both *Semnoderes* and *Sphenoderes*.

Although there is no evidence of two different types of oral styles in the adult of *Zelinkaderes*, two types of styles have been demonstrated in members of the family Neocentrophyidae, e.g., *Neocentrophyes intermedius* Higgins, 1969 (Higgins, 1969a, fig. 3) and *Paracentrophyes praedictus* Higgins, 1983 (Higgins, 1983, figs. 99, 103). In members of the family Pycnophyidae, the differences in the two oral styles are much less striking. In *Pycnophyes greenlandicus* Higgins and Kristensen, 1984 (see Kristensen and Higgins, in press), and *Kinorhynchus phyllotropis* Brown and Higgins, 1983 (see Brown, 1985) alternate oral styles have a single basal spine.

Based on the lack of a clearly defined lateroventral articulation between tergal and sternal plates, which may be a consequence of a poorly developed cuticle, the presence of a long midterminal spine throughout the life history of the species, the presence of five, and perhaps only four rings of scalids, and only four kinds of scalids, all arranged in a pattern nearly identical to that of the J-2 stage of *Pycnophyes greenlandicus* Higgins and Kristensen, 1988, *Zelinkaderes floridensis* probably represents a primitive group within the phylum.

NOTES ON LIFE HISTORY AND FEEDING.—Although I have conducted studies of kinorhynchs for over 30 years, I have never before encountered an instance of an adult kinorhynch molting. Along with other unique characteristics, *Zelinkaderes floridensis* is the first species in which molting has been observed in the adult. The definition of adult is based on the existence of either the flexible spines on segment 12, indicating the male, or the presence of the distinctive ventral pachycyclar development and the presence of the presumptive gonopores at or near the lateral margin or midventral junction on segments 10 and 11, indicating the female. The presence of mature gametes in the gonads of available adult specimens in molt could not be determined, although the gonads appeared to be mature. Figure 63 demonstrates a molt from J-5 to J-6 stage (juvenile to juvenile); Figure 64 depicts a J-6 (female) molting to the adult female (note the distinctive pachycyclar morphology and the singular distinctive pores on the ventral surface of the newly formed female cuticle); Figure 65 demonstrates a molt of an adult female into a second adult female (note the double internal pachycyclar morphology and double distinctive pores on the ventral surfaces of both the old and new cuticle of the molting individual). Three specimens of this kinorhynch considered to be adults, male (RH 1661.18, TL 300 μm, collected 31 Jan 83), female (RH 1653.1, TL 415 μm, collected 6 Dec 82), and female (RH 1598.11, TL 428 μm, collected 2 June 82) were found to be in molt at the time of their fixation for study.

The development of secondary sex characteristics in the manner described is consistent with previous observations (Higgins, 1977b) that juveniles of both sexes appear female relevant to spine character until the final molt into the adult. At that time, males of the genus *Echinoderes*, for example, lose the lateral terminal accessory spine and develop the penile spines in their place. At this time the gonopores also become established. As can be seen in Figure 69, females generally are larger than males throughout the year.

The small size of the male suggests that it may have developed secondary sexual characteristics in the J-5 stage and was in the process of its final molt when killed. The precocious development of adult characters has been suspected in several instances within the homalorhagid taxa (Higgins, 1961:186). The sizes of the molting females were within the normal upper range of adult females of the species; at least some mature oocytes could be identified in the ovaries, and moreover, the distinctive presence of sperm in the seminal receptacles was noted (Figure 66).

Throughout the year, most males and females exhibited well-developed gonads with many densely packed sperm in the testes (Figure 67) and even more densely packed sperm in the seminal receptacles of females (Figure 66), all of which had a single large oocyte in one of the two ovaries. Figure 67 also shows the presence of food in the gut; this species appears to be a bacterial feeder (Figure 67). On the other hand, at least five specimens had diatom frustules in the gut (Figure 68), which, however, were present in so few of the many specimens examined, I believe that the diatoms observed were accidentally ingested, or, at best, constitute only an occasional nutritional component.

A bimonthly study of a more temperate (and intertidal) species, *Echinoderes coulli* Higgins, 1977, demonstrated a significant variation in the size of a kinorhynch over a 12-month period (Higgins and Fleeger, 1980). In contrast, *Zelinkaderes floridensis* maintained a moderately uniform range of trunk length (Figure 69) throughout the year. The maximum length of the animal occurs in the summer months with some decline in size during the fall and early winter months.

Zelinkaderes submersus, new combination

FIGURES 70–79

Cateria submersa Gerlach, 1969:120.

DIAGNOSIS.—*Zelinkaderes*, adult trunk length 576–720 μm, general trunk width about 15 percent of trunk length, with middorsal spines on segments 6, 8, 10–13 each nearly one-third longer than length of segment of origin; middorsal cuticular scars on segments 3 and 4, subdorsal cuticular scars on segment 12; cuspidate spines ventrolaterally on segments 4, 6–9, and 11, elevated on segment 10; acicular spines ventrolaterally on segment 10 and as lateral terminal spines on segment 13; acicular spines lateroventrally on segments 11, 12, and as lateral terminal accessory spine on segment 13; lateral terminal spines longer than lateral terminal accessory spines.

REDESCRIPTION.—Adult, paratypic female (Figures 70, 71; original type designation (Gerlach's number "301g," RH 1225.3, USNM 063089) 665 μm long. The maximum sternal width is estimated to be about 15 percent of the trunk length. The standard width, based on the distance between the lateral margins of the cuspidate spines of segment 11 is 88 μm, 13.2 percent of the trunk length.

Segment 2 is estimated to be about 25 μm long and appears to have no distinct articulation with segment 3, individual placids (Figure 74, pl) are weakly developed; the midventral placid is about twice as wide as the remaining 15 placids.

Segment 3, 50 μm long, is surrounded by a complete ring of cuticle. The anterior margin, adjacent to the placids, lacks cuticular hairs and the internal striate pattern (visible only with phase contrast optics; Figure 77, st), typical of areas of cuticular hairs; the remaining portion of the segment is hirsute with a pectinate fringe at the posterior margin. No pachycyclar area is evidenced on any of the segments with the exception of the anteroventral margin of segment 12 of the female; the cuticle is uniformly thin except for the arthrocorium.

Segment 4 is 54 μm in length and, like segment 3, is surrounded by a complete ring of cuticle. A prominent middorsal cuticular scar (a pore leading to a middorsal gland) is present. A transverse row of three patches of less hirsute cuticle are located anterodorsally. On the ventral surface there are two small (25 μm) cuspidate spines.

Segment 5 is 60 μm in length. A middorsal cuticular scar is present as are three paired patches of less hirsute cuticle noted on segment 4. Beginning with this segment, there is a midventral fissure where the lateral edges of the cuticle meet. This area appears slightly thicker than the remainder of the cuticle (Figure 70).

Segment 6 is 60 μm in length. There is no middorsal cuticular scar. A middorsal spine, 96 μm in length, extends from a slight indentation on the posterior margin of the segment. Sensory spots are present on either side of the base of the middorsal spine as are adjacent to all middorsal spines. Ventrolateral cuspidate spines, 30 μm long, are present.

Segment 7 is 62 μm long. No middorsal spine is present, ventrolateral cuspidate spines are 32 µm long.

Segment 8 is 65 µm long and similar to segment 6. The middorsal spine is 118 µm long, the ventrolateral cuspidate spines are 33 µm long.

Segment 9 is 70 µm long and similar to segment 7. The ventrolateral cuspidate spines are 36 µm long.

Segment 10 is 88 µm long. The middorsal spine is 102 µm long. Acicular spines (90 µm long) are present ventrolaterally with cuspidate spines (40 µm long) dorsally adjacent. Both spines are slightly elevated above those of anterior and posterior segments. On the ventral surface of the female there is a prominent pore anteromesial to the base of each acicular spine.

Segment 11 is 78 µm long. The middorsal spine is 115 µm long. Ventrolateral cuspidate spines (Figure 77), 34 µm in length, are in the position of the acicular spines of the previous segment and are accompanied by acicular spines, 91 µm long. The prominent pores on the ventral cuticle of the female are slightly more mesially situated than in segment 10.

Segment 12 (Figures 70, 71, 77, 79) is 70 µm long and has an acicular middorsal spine typical of the females of this genus. Lateral to the base of the middorsal spine on segment 12 are cuticular scars. Acicular spines, 70 µm long, also are present lateroventrally, in a slightly elevated position (Figure 79). Like the middorsal spine of this segment, this lateral spine is flexible in the male (Figures 72, 73, 78).

Segment 13 is 68 µm long. The middorsal spine is 220 µm long, extending over one-third the length of the midterminal spine directly posterior to it. The lateral terminal spines are 142 µm long, 21.4 percent of the trunk length, longer than the lateral terminal accessory spines. The lateral terminal accessory spines are 114 µm long, 17.1 percent of the trunk length. The LTAS/TL is 80.1 percent. The midterminal spine is 500 µm long, 75.2 percent of the trunk length. In the female, near the anterior margin on the ventral surface of segment 13, there is an area of thickened pachycyclar cuticle with a prominently arched configuration near the lateral margins (Figures 70, 77). This pachycyclar structure is not evident in males (Figures 72, 73).

The head cannot be described in detail; however, the oral styles (Figures 74–76) appear to be long (70–85 µm) and thin, and the pharyngeal styles are well developed.

The male appears to be similar to the female with the exception of those sexual dimorphic characters already noted.

REMARKS.—This redescription is largely based on a single female, remounted in Hoyer's in order to optimize the morphological characters necessary for taxonomic evaluation. One additional female and two male paratypes were also remounted for this purpose. Other type material remains in the original glycerin mounts. *Zelinkaderes submersus* is a larger species (adults 576–720 µm) than *Z. floridensis* (300–435 µm), its cuticle, although thin, is thicker and better developed than that of the Florida species. The diagnostic differences between these two species are easily recognized, making it virtually impossible to confuse the two. The acicular spines of both the middorsal and lateral areas of the two species follow the same spine pattern. A significant difference can be seen in both the actual and relative spine lengths, however. The relative length of the midterminal spine appears to be highly variable and this is complicated by its tendency to be broken, but the length of middorsal spine 13 in relation to the midterminal spine offers a reliable discriminating character. In *Z. floridensis* this spine is no longer than the length of the terminal segment, resulting in its extending less than one-fourth the length of the midterminal spine. In *Z. submersus* the middorsal spine on segment 13 is three times the length of the segment of origin and extends in excess of one-third the length of the midterminal spine.

Equally notable are the differences in the number and arrangement of the cuspidate spines. In *Z. submersus* these spines are present on segments 4, 6, 8, and 9 in addition to segments 7, 10, and 11, the only positions in which they occur in *Z. floridensis*. Although it is not so noticeable, the lateral terminal spine of *Z. floridensis* is shorter than the lateral terminal accessory spine lying dorsolateral to it in contrast to the opposite condition in *Z. submersus*.

The sediments in which the two species are found may offer some explanation as to the considerable size difference between the relatively large *Zelinkaderes submersus* (from medium to coarse sand at depths of 30–46 meters) and the smaller *Z. floridensis* (from muddy sand at depths of 145 meters). The size may be an adaptation to the available interstitial space within the sediment. Similarly, the additional cuspidate spines, which I suspect contain adhesive glands, on the European species may be commensurate with its presence in coarser sand, a product of stronger currents and a greater potential of being washed out of the habitat without such an adaptive feature. The presence of longer spines in the latter species is also an adaptation for existence in coarser sediment (Higgins, 1967).

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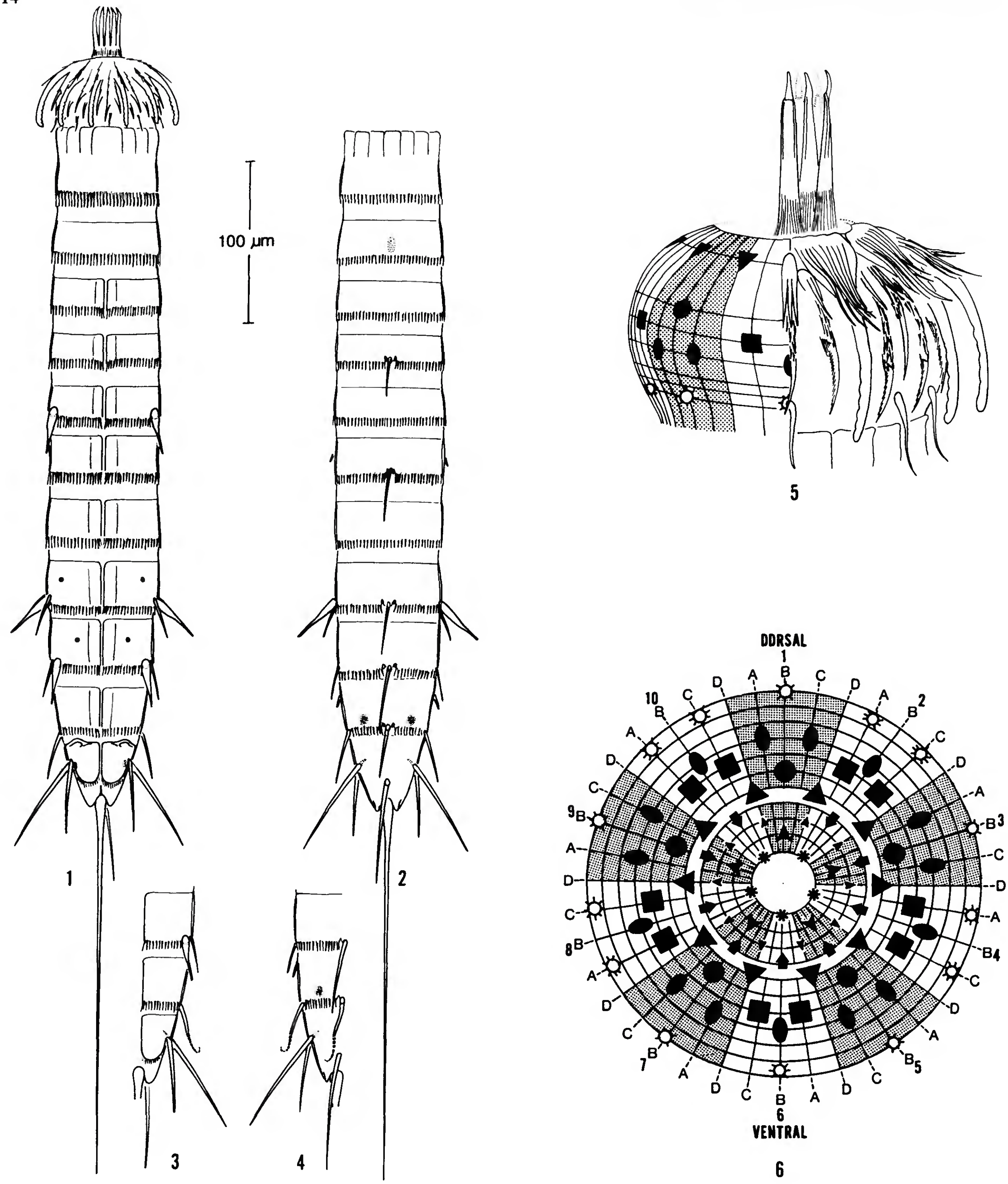
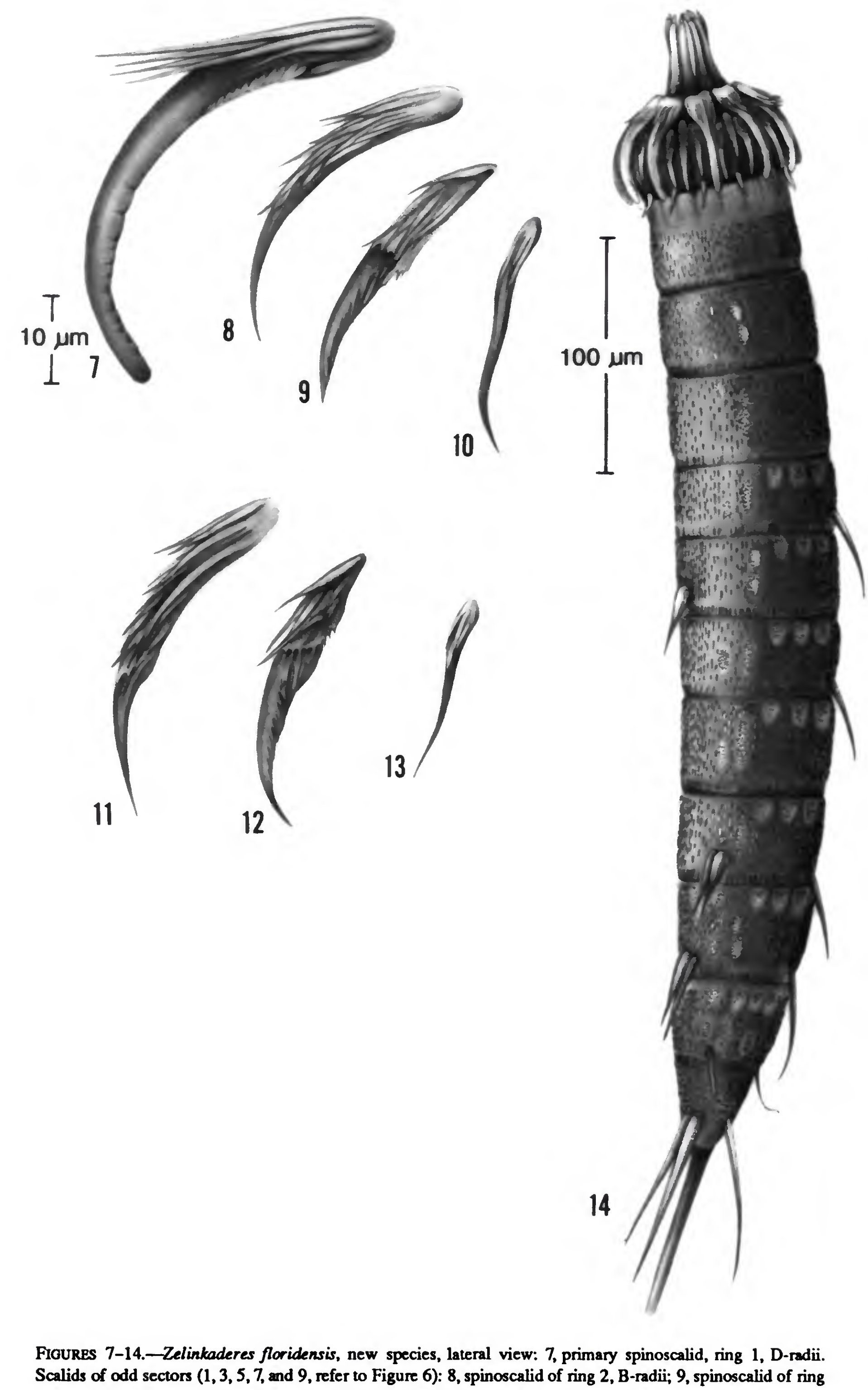
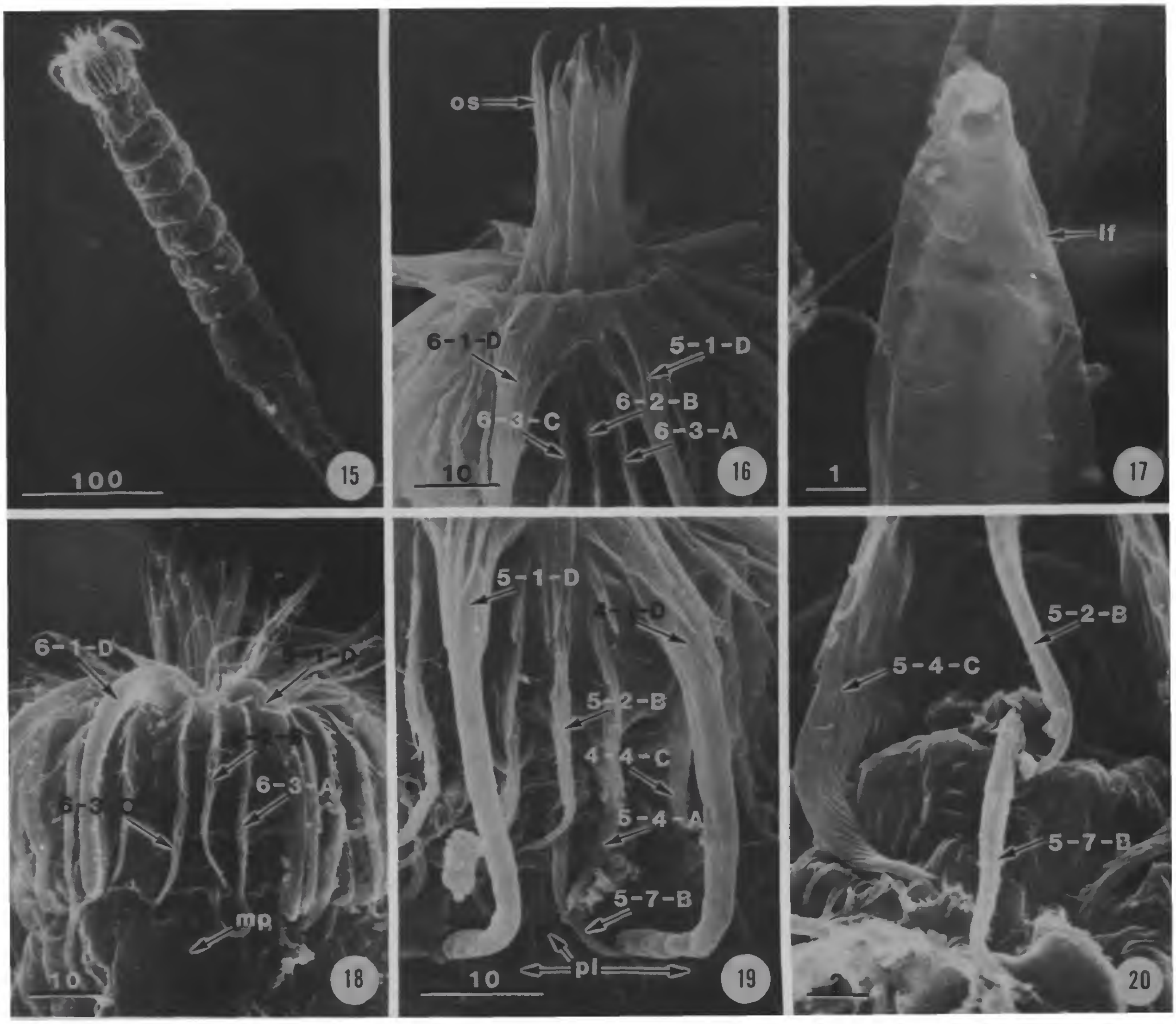


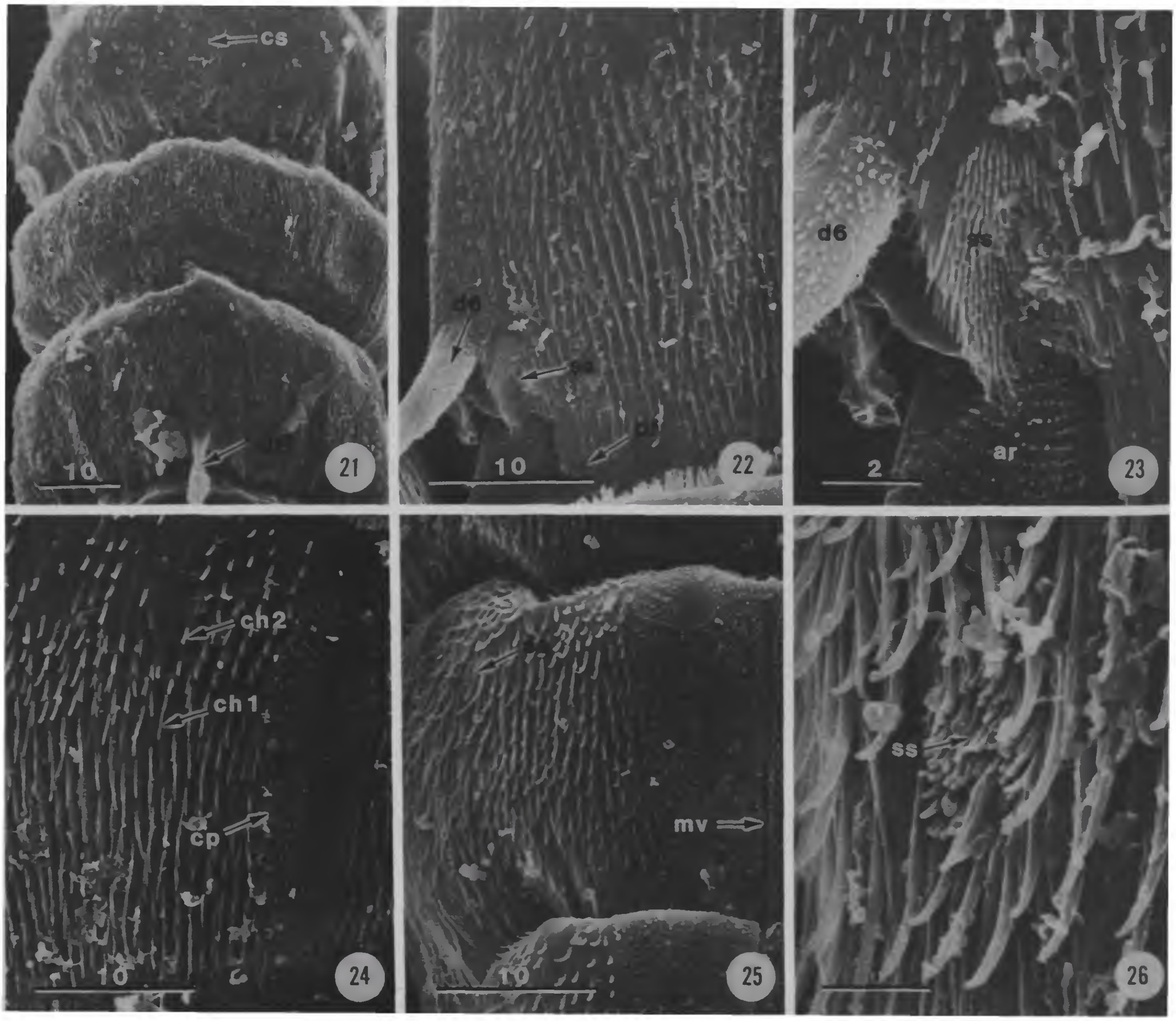
FIGURES 1–6.—*Zelinkaderes floridensis*, new species: 1, 2, holotypic female (USNM 235456), neck and trunk segments, ventral and dorsal views; 3, 4, allotypic male (USNM 235457), segments 11, 12, 13, left half, ventral and dorsal views; 5, head, diagramatic representation, ventral view, left half with symbols coded to Figure 6; 6, polar coordinate diagram showing arrangement of head and mouth cone appendages.



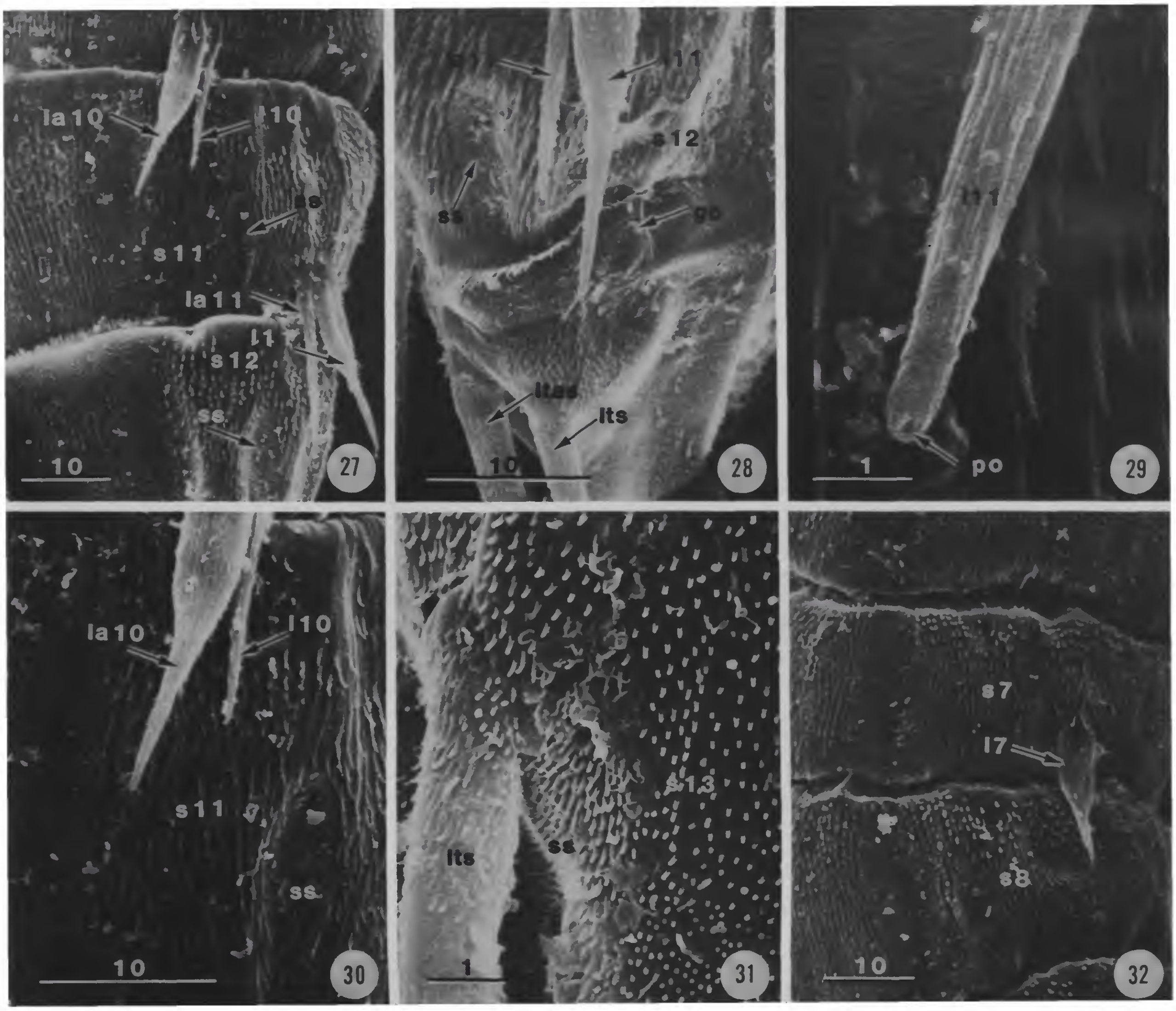
FIGURES 7–14.—*Zelinkaderes floridensis*, new species, lateral view: 7, primary spinoscalid, ring 1, D-radii. Scalids of odd sectors (1, 3, 5, 7, and 9, refer to Figure 6): 8, spinoscalid of ring 2, B-radii; 9, spinoscalid of ring 4, A- and C-radii; 10, trichoscalid of ring 7, B-radii. Scalids of even sectors (2, 4, 6, 8, and 10, refer to Figure 6): 11, spinoscalid of ring 4, B-radii; 12, spinoscalid of ring 3, A- and C-radii; 13, trichoscalid of ring 7, A- and C-radii of sectors 2, 4, 8, and 10, and B-radius of sector 6. 14, Entire animal, lateral view. (Illustrations by Charissa Baker-Lounibos.)



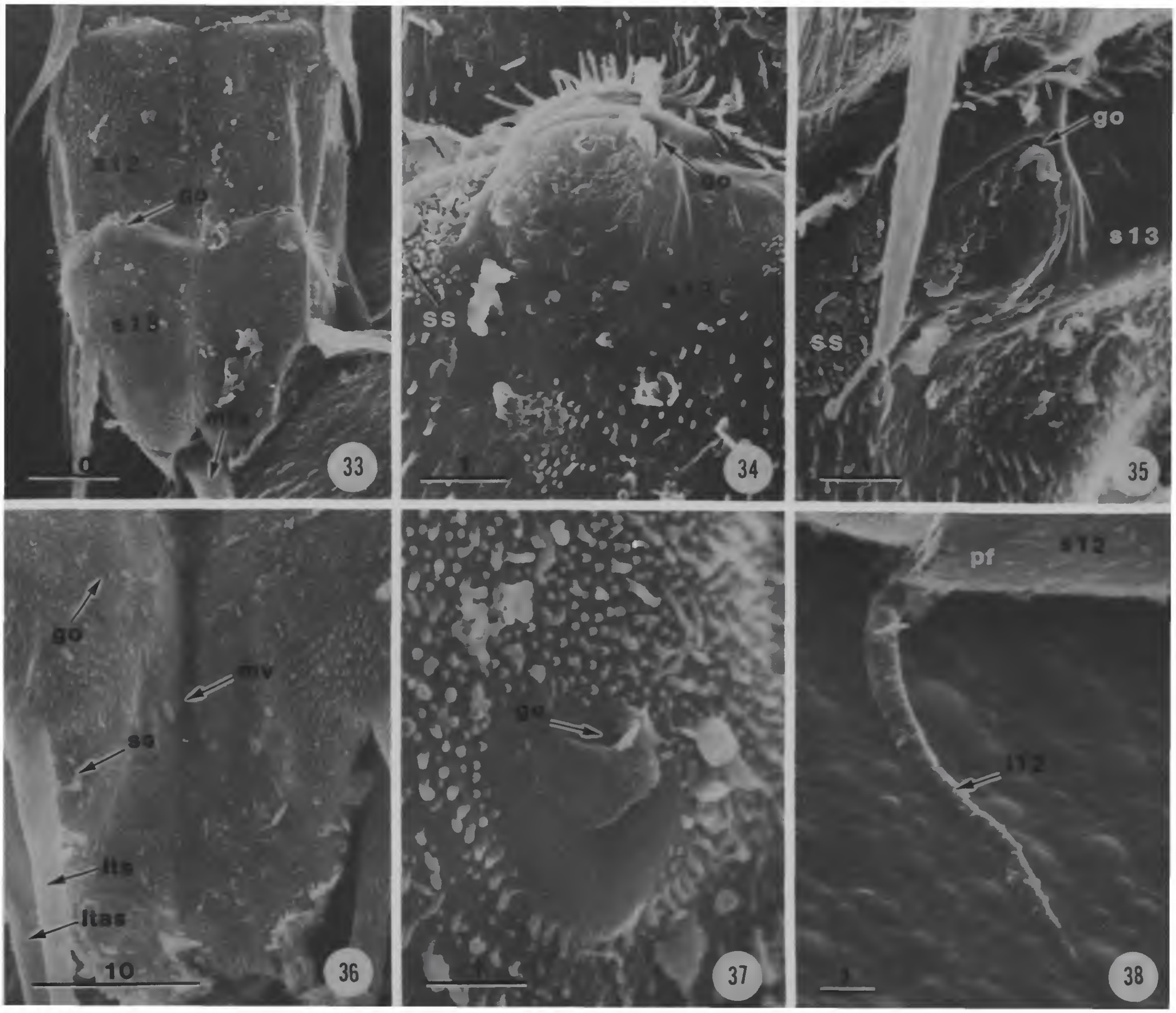
FIGURES 15-20.—*Zelinkaderes floridensis*, new species: 15, entire animal, ventral view; 16, mouth cone and adjacent head, ventral view; 17, apical part of oral style; 18, partially withdrawn mouth cone and adjacent head, ventral view; 19, 20, head, sector 5 scalids. (SEM photographs, scales in μm.)



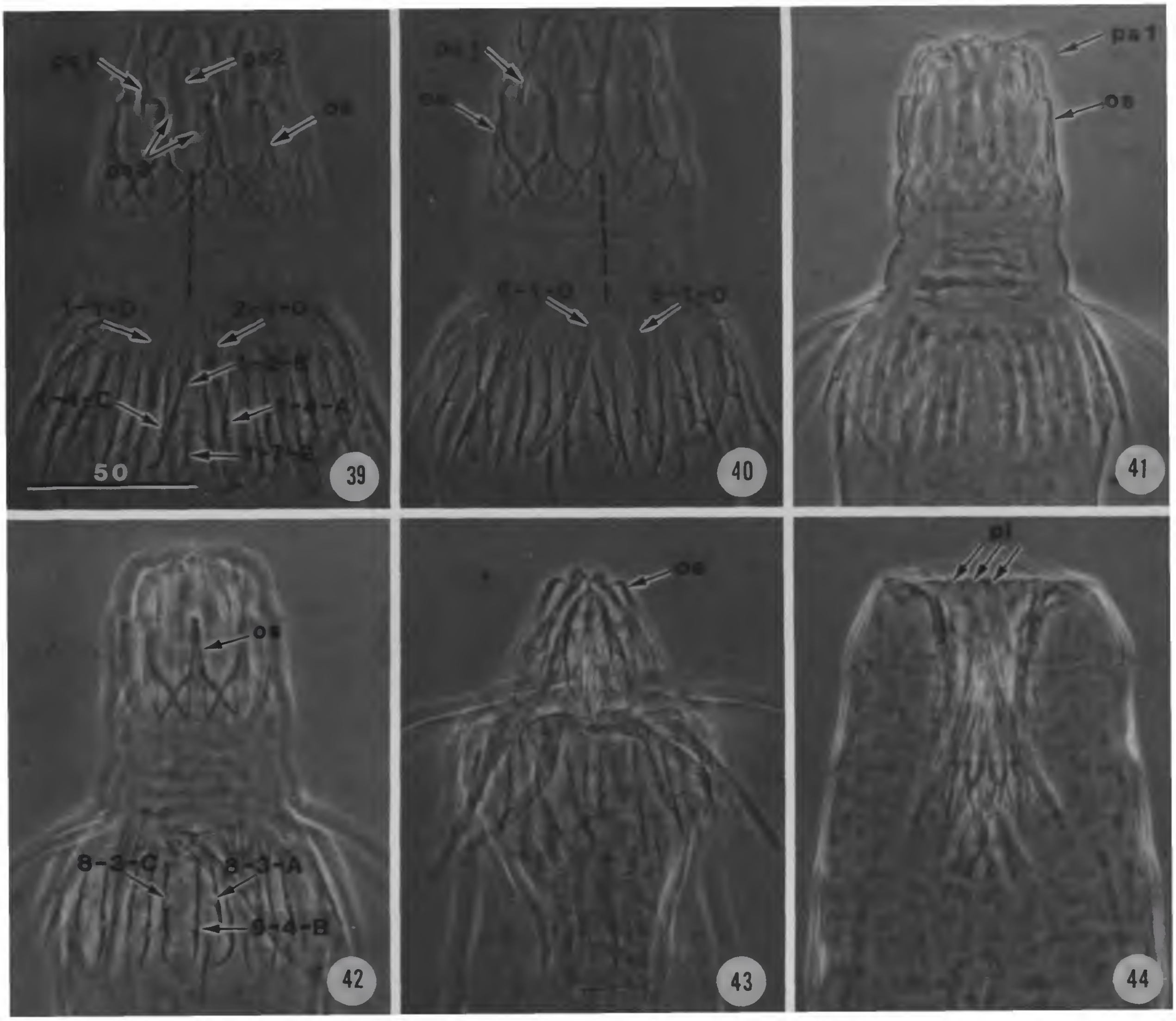
FIGURES 21-26.—*Zelinkaderes floridensis,* new species: 21, segments 4-6, dorsal view. 22, 23, Segment 6, origin of middorsal spine, dorsolateral and magnified views. Segment 9, cuticular surface: 24-26, lateral, ventral, and magnified views. (SEM photographs, scales in μm.)



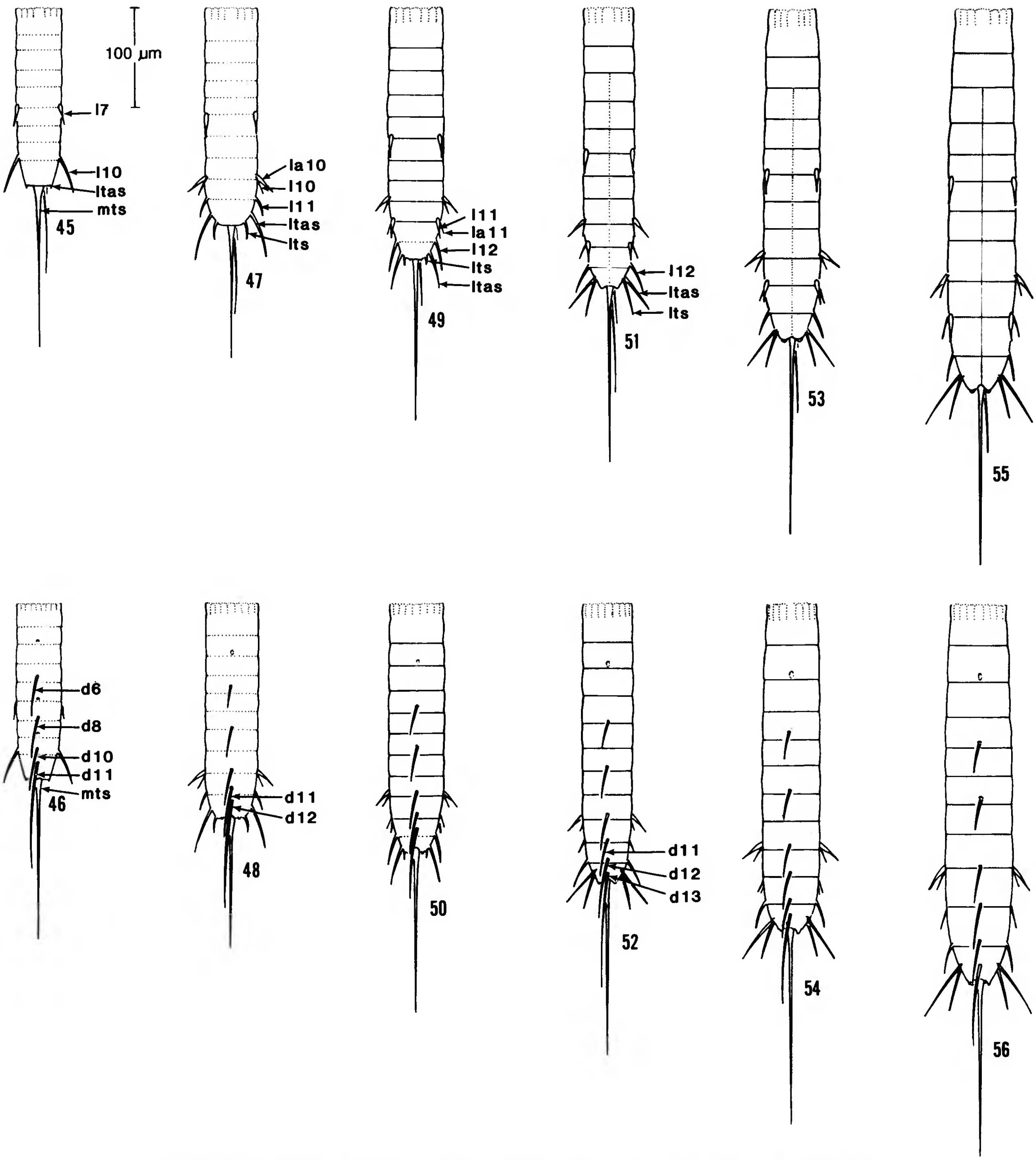
FIGURES 27–32.—*Zelinkaderes floridensis*, new species: 27, segment 11, ventrolateral view; 28, segments 12, 13, lateral view; 29, distal end of lateral spine of segment 11; 30, segment 11, magnified view of 27; 31, segment 13, ventrolateral view, base of lateral terminal spine; 32, segments 7, 8, lateroventral view. (SEM photographs, scales in µm.)



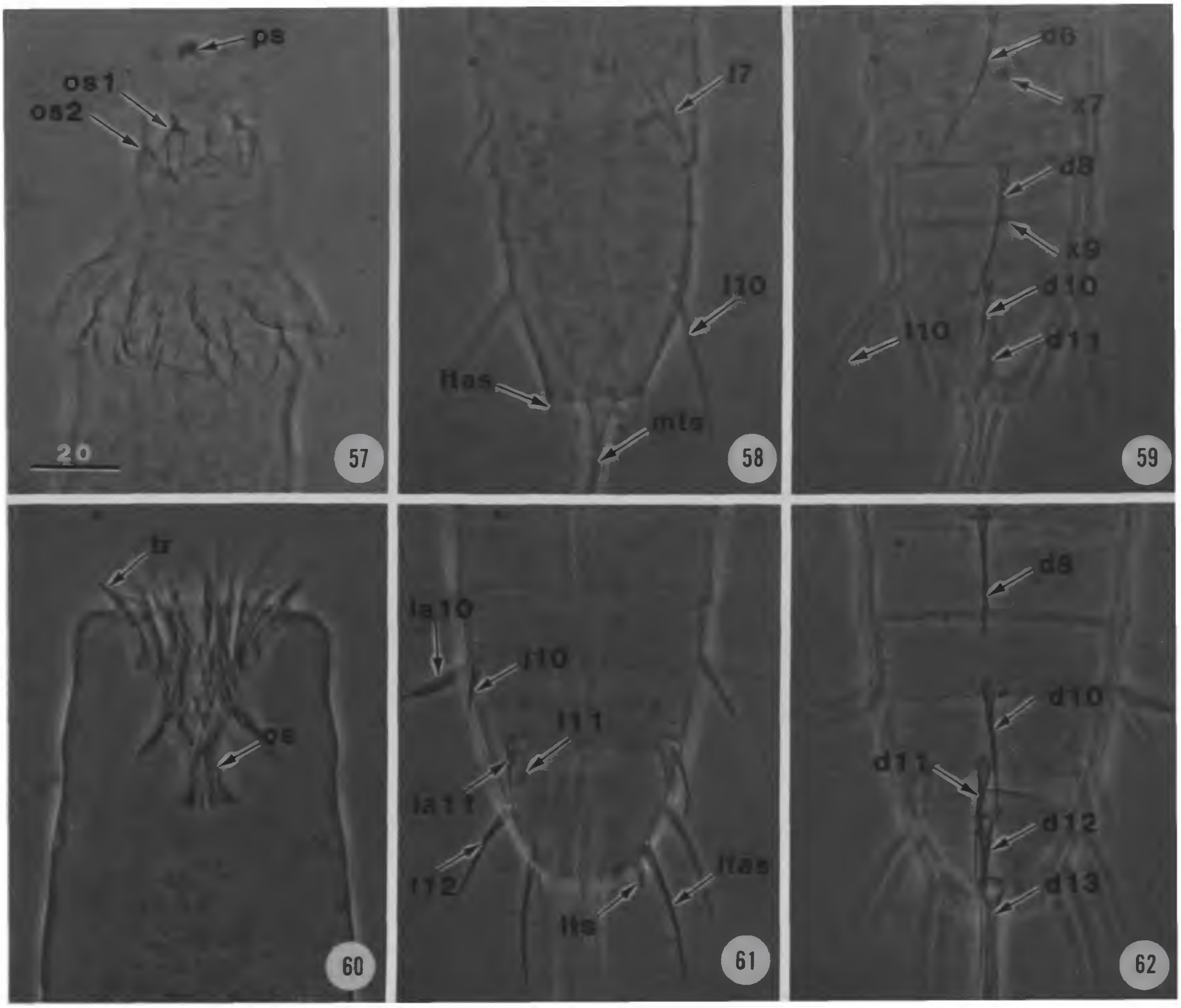
FIGURES 33-38.—*Zelinkaderes floridensis*, new species. Segments 12, 13 of female: 33, ventral view; 34, 35, anterolateral margin, lateral view, magnified and slightly more magnified. Segments 12, 13 of male: 36, ventral view; 37, anterolateral margin, magnified. 38, Lateral spine 12 of male. (SEM photographs, scales in µm.)



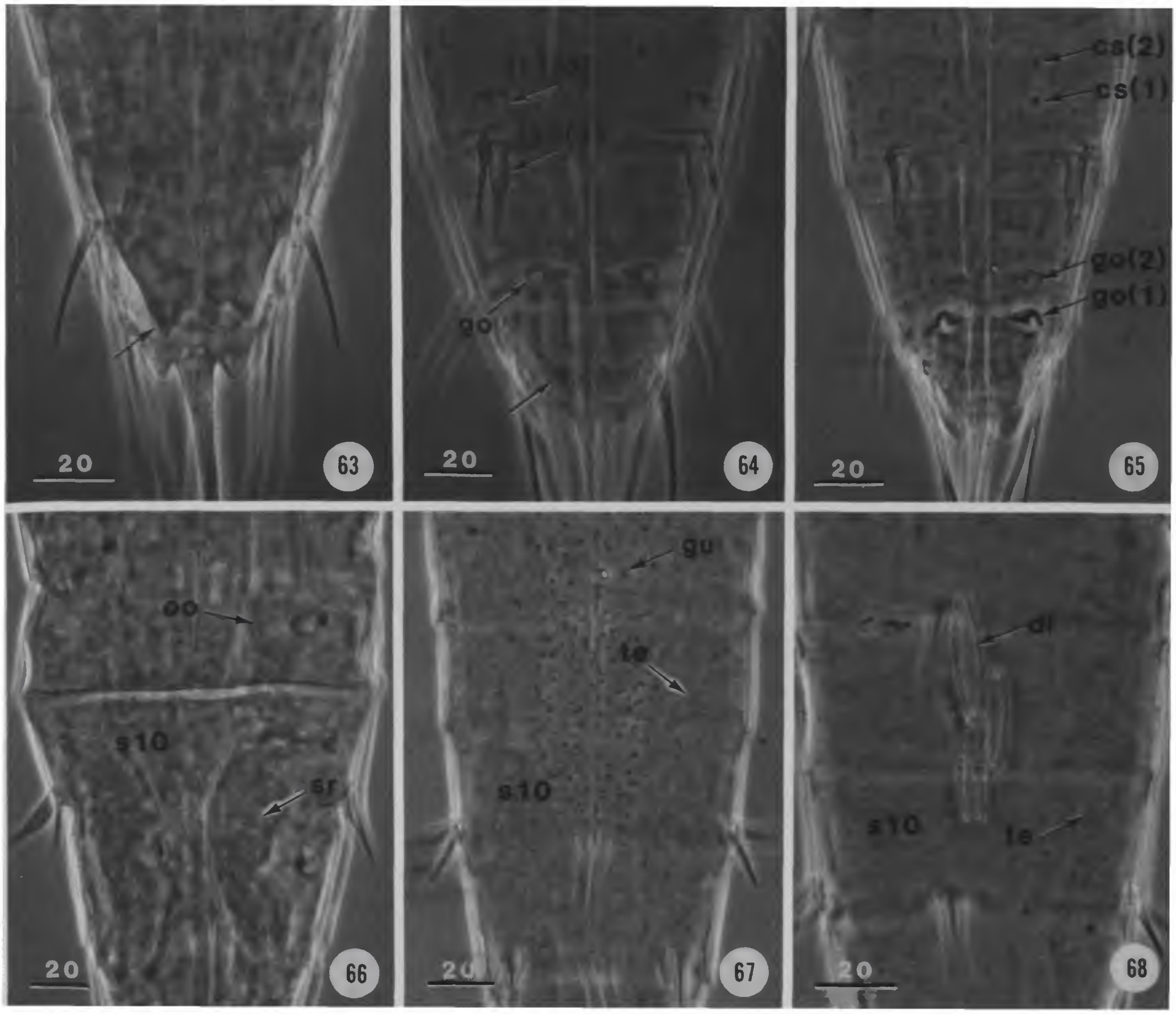
FIGURES 39–44.—*Zelinkaderes floridensis*, new species. Holotypic female, mouth cone and head: 39, dorsal view; 40, ventral view (dashed line indicates dorsal midline); 41, optical section view. Mouth cone and head: 42, female, lateral view; 43, male, ventral view, showing oral styles closed over mouth; 44, male, mouth cone and head withdrawn, showing limits of placids (pl). (Phase contrast photographs, scale in μm.)



FIGURES 45–56.—*Zelinkaderes floridensis*, new species: 45, 46, J-1 stage, ventral and dorsal views; 47, 48, J-2 stage, ventral and dorsal views; 49, 50, J-3 stage, ventral and dorsal views; 51, 52, J-4 stage, ventral and dorsal views; 53, 54, J-5 stage, ventral and dorsal views; 55, 56, J-6 (pre-adult) stage, ventral and dorsal views.



FIGURES 57–62.—*Zelinkaderes floridensis*, new species: 57, mouth and head, J-1 stage, ventral view; 58, 59, segments 7–11, J-1 stage, ventral and dorsal views; 60, anterior segments, mouth cone and head retracted, J-2 stage, optical section; 61, 62, segments 9–13, J-2 stage, ventral and dorsal views. (Phase contrast photographs, scale in µm.)



FIGURES 63–68.—*Zelinkaderes floridensis*, new species: 63, 64, segments 11–13, J-6 stage in molt (arrows show new adult male and female, respectively, within juvenile exoskeletons); 65, segments 11–13, adult female molting to new adult female; 66, segments 9, 10, female with oocyte (oo), and spermatozoa in seminal receptacle (sr); 67, segments 9–11, male with bacteria in midgut and spermatozoa in testes; 68, segments 8–11, male with diatoms in midgut and sperm in testes. (Phase contrast photographs, scales in μm.)

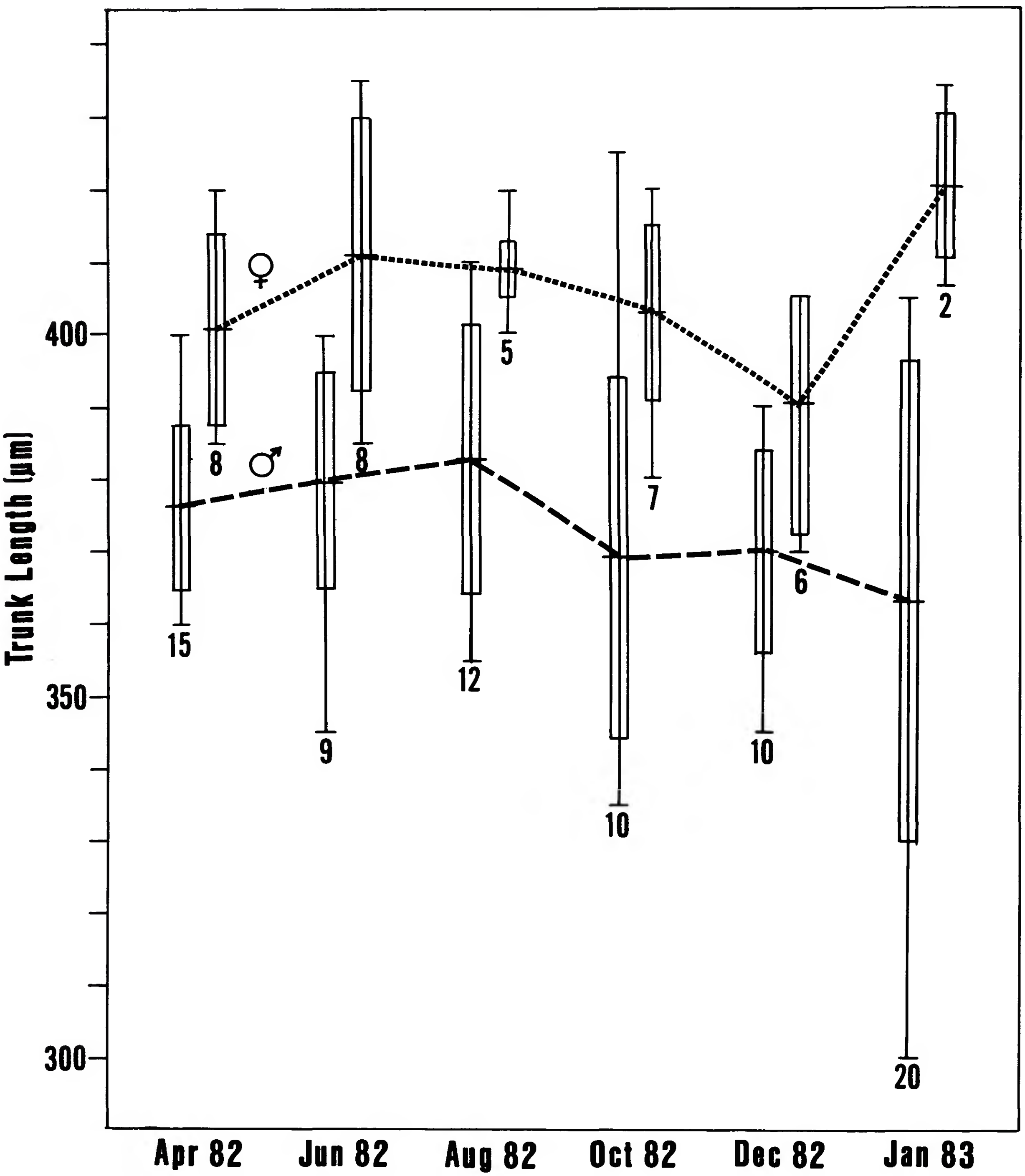
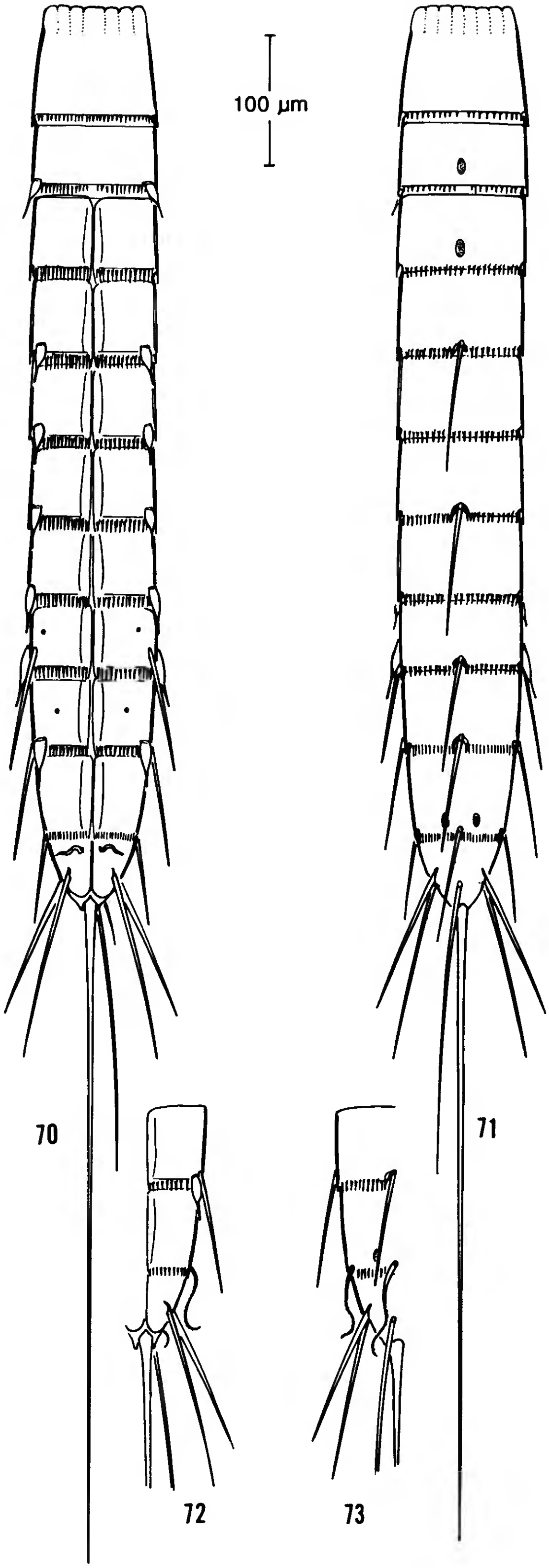
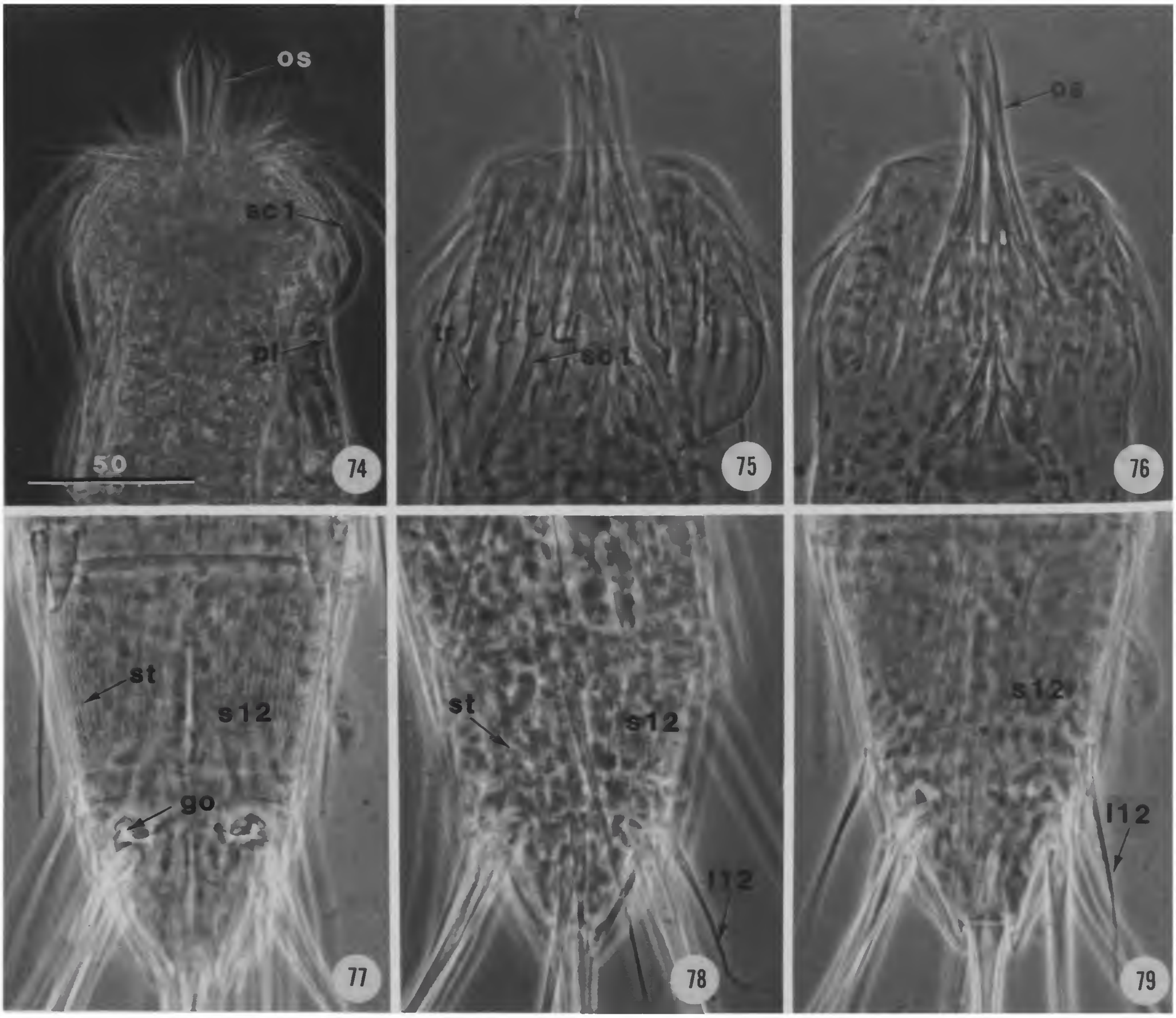


FIGURE 69.—Length/frequency graph of adult males and females of *Zelinkaderes floridensis* used in this study. Data are from bimonthly collections made during a 12-month sampling period. Ranges are indicated by single vertical lines, standard deviations of samples are indicated by double vertical lines, means are connected by large-broken lines for males and small broken lines for females.



FIGURES 70-73.—*Zelinkaderes submersus*. 70, 71, paratypic female (USNM 063090), neck and trunk segments, ventral and dorsal views; 72, 73, paratypic male (USNM 063090), segments 12, 13, left half, ventral and dorsal views.



FIGURES 74-79.—*Zelinkaderes submersus*, paratypes. Mouth cone, head, and first trunk segment: 74, female (USNM 063089); 75, 76, male (USNM 063090); optical sections. Segments 12, 13: 77, female (USNM 063090), ventral view; 78, male (USNM 063089), showing modified lateral spine of segment 12; 79, female (USNM 063090), showing acicular lateral spine on segment 12. (Phase constrast photographs, scale in μm.)

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