New Loricifera from Southeastern United States Coastal Waters

ROBERT P. HIGGINS
and
REINHARDT MØBJERG KRISTENSEN

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 438

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the Institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Folklife Studies
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 438

New Loricifera from Southeastern United States Coastal Waters

Robert P. Higgins
and Reinhardt Møbjerg Kristensen

SMITHSONIAN INSTITUTION PRESS
City of Washington
1986

ABSTRACT

Higgins, Robert P., and Reinhardt Møbjerg Kristensen. New Loricifera from Southeastern United States Coastal Waters. *Smithsonian Contributions to Zoology,* number 438, 70 pages, 87 figures, 1 map, 1986.—Eight new species, comprising two new genera and a new family of Loricifera, are described from the meiobenthos of medium to coarse sandy subtidal habitats, 289–439 m deep, off the coast of North and South Carolina. Five of the new species are placed in the new genus *Pliciloricus* and three are placed in the new genus *Rugiloricus*. A new family Pliciloricidae is established for the two new genera. The diagnosis of the phylum Loricifera is emended to include the new taxa. The morphology of loriciferans is re-evaluated and new terminology is established. A discussion of the biology and systematic relationships of the phylum is included.

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.
New Loricifera from southeastern United States coastal waters.
(Smithsonian contributions to zoology ; no. 438
Bibliography: p.
Supt. of Docs. no.: SI 1.27:438
1. Loricifera—Southern States—Classification. 2. Loricifera—Atlantic Coast (U.S.)—Classification. I. Kristensen, Reinhardt Møbjerg. II. Title. III. Series.
QL1.S54 no. 438 591 s [595.1'85] 85-60024
[QL391.L67]

Contents

New Loricifera from Southeastern United States Coastal Waters

Robert P. Higgins
and Reinhardt Møbjerg Kristensen

Introduction

The Loricifera Kristensen, 1983, is a phylum of marine microscopic metazoans recently described from the meiobenthos of subtidal coarse sediments. The phylum, one of three described during this century (Pogonophora: Caullery, 1914; Johansson, 1937; Ivanov, 1963; Gnathostomulida: Ax, 1956; Riedl, 1969), brings the total number of living animal phyla to 39, a figure that includes seven unicellular eukaryotic protists (Parker, 1982), and continues recognition of the Pogonophora as a separate phylum, not as a class in the phylum Annelida as proposed by van der Land and Nørrevang (1977). The known existence of the Loricifera dates back to May 1974, when a single adult male was found in a coarse-sand sample taken off the coast of North Carolina by the Senior author in collaboration with several colleagues (Coull, et al., 1977). Originally, the specimen was assumed to be a juvenile stage of an undescribed priapulid, a phylum that, at that time, was undergoing significant redefinition because of the discoveries of *Tubiluchus corallicola* van der Land, 1968, and *Maccabaeus tentaculatus* Por, 1973. Ironically, *Tubiluchus*, a common inhabitant of coarse sediments, is represented by a yet unidentified species in the same habitat as the loriciferans described in this paper.

The year following the appearance of the single, then unidentified, specimen from the coast of North Carolina, the junior author found a similar aberrant invertebrate near Helsingør, Denmark while he was engaged in a study of gnathostomulids. This specimen was more rotifer-like, about 80 μm in length, and came from coarse sediments, 10–12 m deep. Unfortunately, it was lost during preparation for transmission electron microscope examination (Kristensen, 1983). Between 1976 and 1979, and again in 1982, additional specimens, not necessarily the same species, were found by the junior author while investigating meiofauna from coarse sediments (100–110 m depth) outside the harbor of Godhavn, Greenland. Because these specimens exhibited no evidence of reproductive organs, they, also, were thought to be larval stages, perhaps larval stages of a priapulid considering, again, the recent discoveries by van der Land (1968) and Por (1973).

In 1980, a specimen found in coarse coralline sand from the Chesterfield Reefs (Coral Sea), was sent to the junior author, who recognized it as another larva of the yet undetermined taxon. So far, only larval stages were available for study. The mystery of the identity of these aberrant invertebrates, among the smallest metazoans

Robert P. Higgins, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. Reinhardt Møbjerg Kristensen, Institute of Cell Biology and Anatomy, University of Copenhagen, DK-2100 Copenhagen, Denmark.

known, finally was solved when the junior author found both larva and adults together in coarse sediment dredged up near Roscoff, France, in April 1982 (Kristensen, 1983). Since then, the known distribution of loriciferans has been expanded to include the Azores Islands (one specimen from the Barlett Expedition, 1975), the east coast of Florida (Kristensen, 1983), the Gulf of Mexico (USNM Accession 360974), the Mediterranean Sea (Soetaert, Heip, and Vincx, 1984, and pers. comm.—photograph of adult), and the Pacific Ocean (B. Burnett, pers. comm.—photograph of Higgins-larva; Y. Shirayama, pers. comm.—photograph of adult). For a more complete history of the events leading to the description of this new phylum, the reader should consult Kristensen, 1983.

METHODS.—The specimens upon which this study is based were from five samples of coarse sand from depths of 289 m and 439 m on the continental shelf of the coast of North Carolina and South Carolina. The sample from which the first loriciferan was extracted was from material considered unacceptable for the qualitative study being conducted during cruise E-5-74 of the R/V *Eastward,* 14 May 1974 (Coull et al., 1977). This sample was made using a Reinick Box Corer (10 cm × 20 cm). The coarse sand, about 1 liter in volume, was processed. The single specimen was preserved in 70% ethanol.

A second series of four samples was made during a cruise of the R/V *Cape Hatteras,* 16–19 November 1983. These samples were taken by an anchor dredge designed by the senior author to remove a layer of sediment 450 cm wide and up to 10 cm deep. When filled, about 50 liters of sediment are collected by the 120 μm mesh net of this apparatus. The sediment was released from the net into two large containers, one of which was used for the extraction of macrofauna and sediment analysis, the other processed similar to that described by Kristensen and Higgins, 1984, which was repeated here as follows.

Several handfuls of sediment were placed in a container with about 5–8 liters of fresh water. The treatment of coarse marine sediment with fresh water (Kristensen and Higgins, 1984) has been found to be a more effective extraction technique for hard-bodied meiofauna than the use of an isotonic solution of magnesium chloride (Hulings and Gray, 1971). The sediment was gently agitated in the fresh water for about 10–15 seconds, then it was decanted through a 62 μm mesh nylon sieve. This process was repeated twice for each unit of sediment preserved. The material retained by the conical-shaped sieve was washed with additional fresh water into the bottom of the sieve, which was quickly emptied into a container of 6% buffered (sodium borate) formalin to which a tincture of rose bengal was added in sufficient quantities to stain all organisms in order to facilitate sorting. This procedure was repeated until the entire sediment sample had been preserved.

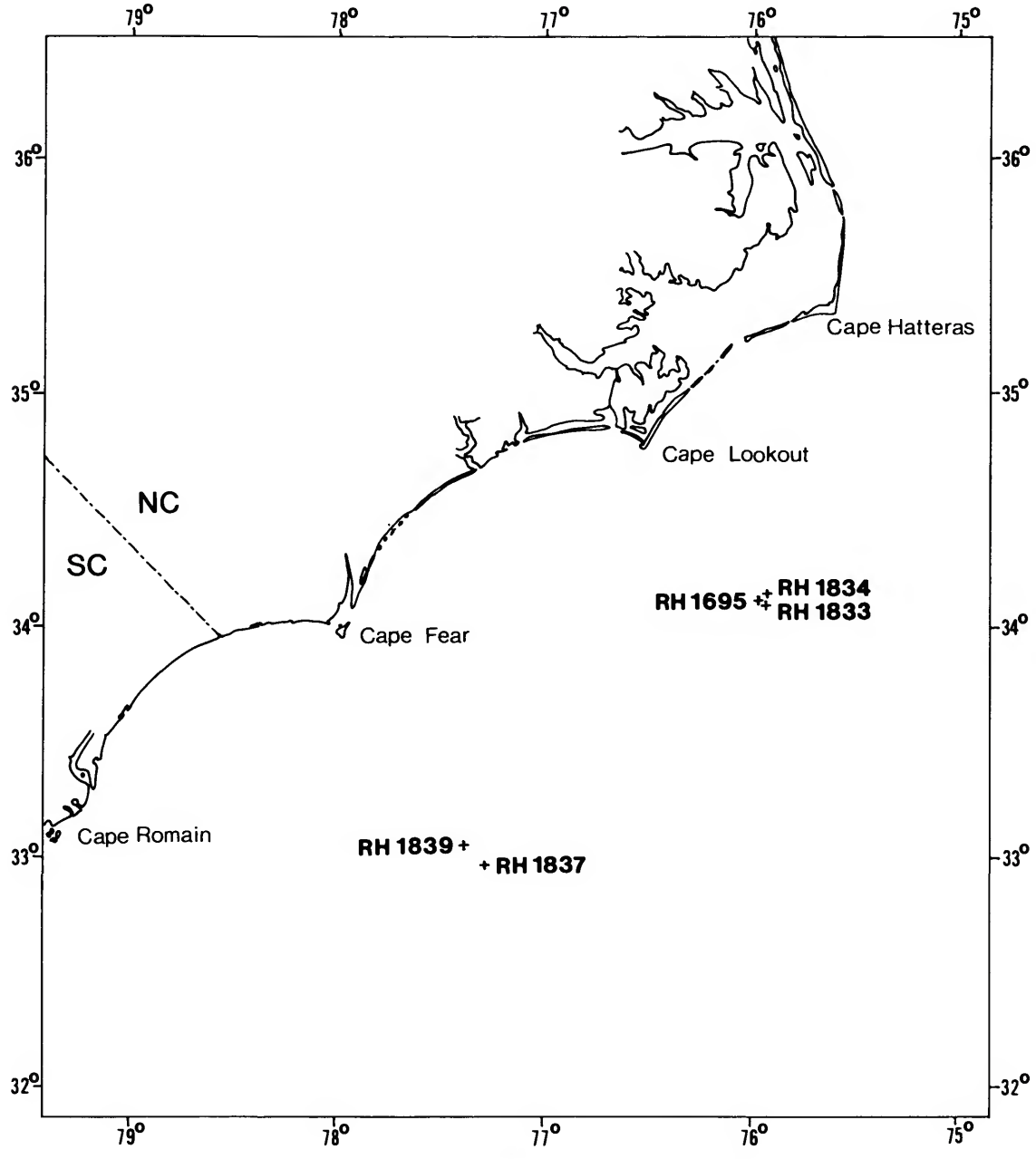
Sorting was conducted using 50× magnification of a stereomicroscope. Specimens of loriciferans were placed in either a solution of distilled water containing 2% glycerin that was slowly evaporated to glycerin over 5 to 7 days or to a special tube, sealed with 40 μm mesh nylon net, and placed in a small vessel of distilled water. Ethanol was added slowly to the distilled water over a period of 48 hours to affect a 100% ethanol medium. The tube and its contents were dried in a critical point depression apparatus using carbon dioxide. Specimens were mounted on 12 mm glass coverslips covered with Elmer's glue that were affixed to aluminum SEM stubs and coated with gold-platinum. SEM examinations were made with a Cambridge Stereoscan 250 MK2 and Stereoscan MK2.

Glycerin-impregnated specimens were mounted in this same medium or in a modified Hoyer's medium on glass microslides or on Cobb aluminum slide frame mounts (Higgins, 1983). Microslide preparations were sealed with Murrayite. Illustrations were made with the aid of a camera lucida. Some observations seen only by SEM were added to the illustrations. Photographs were taken through a Zeiss Universal Microscope equipped with phase and interference contrast optics.

Specimens of new species have been deposited in the Zoological Museum of Copenhagen, Den-

mark, and in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the former United States National Museum (USNM).

LOCALITIES.—Five sampling sites (Map 1) involving two general areas of the continental shelf of North and South Carolina, both under the influence of the Gulf Stream, provided the ma-



MAP 1.—Sampling localities for plicilorid loriciferans.

terial for this study. The collecting data for material examined will be referred to by the senior author's collection numbers (RH). These data are as follows:

RH 1695 14 May 1974; col. R.P. Higgins; from medium (quartz) sand, 400 m depth, ~195 km east of Cape Fear, North Carolina, USA (34°07.2′N, 75°58.6′W).

RH 1833 16 Nov 1983; col. R.P. Higgins; from medium (quartz) sand, 430 m depth, ~195 km east of Cape Fear, North Carolina, USA (34°06.9′N, 75°58.4′W).

RH 1834 16 Nov 1983; col. R.P. Higgins; from medium (quartz) sand, 439 m depth, ~195 km east of Cape Fear, North Carolina, USA (34°07.4′N, 75°57.0′W).

RH 1837 19 Nov 1983; col. R.P. Higgins; from medium (oolytic) sand, 294 m depth, ~195 km east of Cape Romain, South Carolina, USA (32°58.8′N, 77°18.1′W).

RH 1839 19 Nov 1983; col. R.P. Higgins; from medium (phosphorite) sand, 289 m depth, ~195 km east of Cape Romain, South Carolina, USA (33°03.7′N, 77°22.07′W).

ABBREVIATIONS.—The following abbreviations are used in the illustrations.

ac	anal cone
ad	apodeme on the mouth cone
af	anal field
an	anus
ap	anal plate
ar	anal ridge
at	accessory tooth (cl)
ba	bar-shaped structure of midventral plica
bc	buccal canal
bg	buccal canal gland
br	brain
bt	basal plate of toe
cl	claw-tipped spinoscalid (sr_4)
co	collar
cp	collar pore
cs	clavoscalid (sr_1)
cs_1	ventral clavoscalid
cs_2	dorsal clavoscalid
ct	claw-tip
D	dorsal
do	double-organ
ed	edge of lorica
ed_1	edge of larval lorica
ed_2	edge of adult lorica
es	esophagus
ex	larval exuvium
fl	flosculus (*Pliciloricus*-type)
fl_1	anterior flosculus
fl_2	posterior flosculus
gu	gut
ha	hair
ho	hook-shaped scalid of larval exuvium
ia	internal armature of larval buccal canal
in	introvert
in_1	introvert of larval exuvium
in_2	introvert of adult exuvium
lc	larval closing apparatus
lo	lorica
lo_1	lorica of larval exuvium
lo_2	lorica of adult exuvium
lr_1	primary double ridge of lorica
lr_2	secondary double ridge of lorica
ls_1	anterolateral seta
ls_2	anteroventral seta
mc	mouth cone
mc_1	first region of mouth cone
mc_2	second region of mouth cone
mc_3	third region of mouth cone
mh	middorsal hook (modified sr_9)
mo	molting body
mp	middorsal plate
mr	mucro
ms	midventral setae of mouth cone
mt	mouth tube
mu	muscle
mv	midventral scalid
nf	flosculus (*Nanaloricus*-type)
ne	nephridiopore(?)
or	oral ridge
os	oral stylet
ot	oral tooth
ph	pharynx bulb
pl_1	plica
pl_2	midventral modified plica
po	pore on trichoscalid plate
ps	penile spine(?)
pt	toe gland pore
re	ridge
ri	transverse ridge of lorica
ro	rosette structure
ru	ruff
sc	scalid
se_1	posterodorsal seta
se_2	posterolateral seta
se_3	posteroterminal seta
sp	spine on spinoscalid
sr_1–sr_9	scalid row 1–9
ss	spinoscalid
su	sculpture of lorica
te	testis
th	thorax

th_1	thorax of larval exuvium
th_2	thorax of adult
tl	telescopic region of mouth cone
to	toe
tp_1–tp_3	trichoscalid plates 1–3
tr	trichoscalid
tr_1	primary trichoscalid
tr_2	secondary trichoscalid
ts	trichoscalid plate spine
V	ventral

ACKNOWLEDGMENTS.—The authors were most grateful for the collecting opportunities made possible by the National Science Foundation's grant GA-42792 to B.C. Coull, University of South Carolina, grant GC-00005 to Duke University for R/V *Eastward* operations, and grant DPP-8026535 to R.Y. George, University of North Carolina at Wilmington, and for the generous cooperation of these two colleagues. We have received valuable technical assistance from S. Braden, G. Møbjerg Kristensen, S.A. Petry, M.L. Wallace and H. Wolf, as well as the captains and crews of the R/V *Eastward* (1974) and R/V *Cape Hatteras* (1983). The carbon dust illustrations were created by the Smithsonian's C. Gast and M. Ryan. Our colleagues B.C. Coull and E.E. Ruppert have critically reviewed this manuscript and made many valuable suggestions. This research was supported financially in part by project funds to the senior author from the Smithsonian Marine Station at Link Port and by a grant from the Sumner Gerard Foundation. The participation of the junior author in this work was supported by portions of the senior author's funds in addition to a NATO Science Fellowship, the Danish Natural Science Research Council, and a Smithsonian Postdoctoral Fellowship.

Phylum LORICIFERA Kristensen, 1983

EMENDED DEFINITION.—Adults 225–383 μm long, bilaterally symmetrical marine metazoans. Body consisting of a spherical, eversible head or "introvert," a neck and thorax, all retractable into a loricate abdominal region. Prominent mouth cone with 8–9 oral stylets or 6–16 oral ridges, and an extrusible cuticularized buccal canal centered in the head; head armed with up to 9 variably distinct rows of appendages or scalids. Sexual dimorphism may be apparent in the structure of the first row of scalids or clavoscalids. Thorax (sensu Kristensen, 1983) appears to consist of 2 "segments," the anterior portion, now called the neck, with appendages consisting of trichoscalids with basal plates, and a posterior portion, which retains the name thorax and lacks appendages. Abdomen covered by sclerotized lorica, consisting of 6 plates with hollow spines along anterior margin or 22 or more folds of plica. Flosculi, when present, located posteriorly on lorica. Saccate gonads open terminally. One pair of protonephridia present. Myoepithelial pharynx bulb with or without placoids.

Higgins-larva 80–385 μm long, with same body regions as adult. Mouth cone unarmed or with 6–12 oral stylets; internal armature may be present. Head always with 8 clavoscalids and up to 7 rows of spinoscalids, a single middorsal spinoscalid always modified. Sometimes with collar-like area, between seventh row of scalids and thorax, presumed to be a closing apparatus; sometimes double ventral plates formed from same area act as a closing apparatus. Thorax with 5–6 rows of plates formed from transverse and longitudinal folds. Lorica longitudinally folded, 2–3 locomotory and/or sensory setae present on anterior margin of lorica. Two toes located caudally; 2 or 3 sensory setae present on posterior margin of lorica. Development by series of several larval stages; postlarval stage precedes definitive adult stage or larva molts directly into adult.

Order NANALORICIDA Kristensen, 1983

EMENDED DEFINITION.—Same as phylum.

PLICILORICIDAE, new family

DEFINITION.—Adults 330–383 μm long. Tripartite mouth cone surrounded by 6–12 thin oral ridges; no annulation in the thin buccal canal;

placoids lacking in the pharyngeal bulb. Two kinds of unbranched clavoscalids; 2 second row midventral spinoscalids variously united to form "double-organ," occasionally well sclerotized; no gap between the spinoscalids on the head and the trichoscalids on the neck. Lorica only slightly sclerotized, with 22 or more longitudinal folds; flosculi present or absent (in one of two genera). Anus-gonopore complex apparently positioned ventroterminally.

Higgins-larva 110–375 μm long, some late stages larger than adults. Mouth cone with oral stylets; single ventral oral seta may be present. Internal armature posterior to pharynx sometimes present. Only 2 pairs of locomotory/sensory setae on anterior edges of lorica; 2–3 pairs of sensory setae on the posterior edges of lorica. Toes with large glands, smooth margined. No flosculi.

TYPE GENUS.—*Pliciloricus,* new genus.

Key to the Genera of Pliciloricidae

Adult with 15 single trichoscalids [Figure 76], lorica not well defined (cuticle thin); with 30–60 longitudinal folds or plica; larva with small, ventrally oriented toes if present, 4 pairs lorical setae if present [Figure 77] . . . . . ***Rugiloricus,*** new genus

Adult with 8 single and 7 double trichoscalids [Figure 1], lorica well defined (cuticle thick); with 22 longitudinal folds or plica; larva with straight, terminal toes, five pairs of setae [Figure 4] . . . . . ***Pliciloricus,*** new genus

Pliciloricus, new genus

DIAGNOSIS.—Adults 185–310 μm long, with a well-defined tripartite mouth cone, with 8 strongly cuticularized oral ridges and 4 thinner oral ridges; buccal canal weakly cuticularized, telescopically retractable to only slight extent; pharyngeal bulb glandular, without placoids. With 8 more or less pod-like clavoscalids. Complex cuticular formation of 14–30 thin fibers surrounding base of the mouth cone as a ruff. Double trichoscalids present. Lorica well defined, with 22 slightly sclerotized plicae. Two or more pairs of two different kinds of flosculi on posterior region of lorica.

Higgins-larva 130–305 μm long, with 6 oral stylets in mouth cone; buccal canal with internal armature consisting of a tri- or hexaradially symmetrical structure connected to pharyngeal bulb. Eight clavoscalids present, may be one of two types; area between last row of scalids and thoracic plates forming collar-like closing apparatus. Two pairs of locomotory/sensory setae at anterior edge of lorica; lorica consisting of only one piece with many longitudinal folds; 3 pairs of lorical setae. Toes short to very long, may reach anterior edge of lorica, hollow with glandular tissue inside. Anus dorsoterminal.

TYPE-SPECIES.—*Pliciloricus enigmaticus,* new species.

COMPOSITION.—*Pliciloricus enigmaticus,* new species; *P. dubius,* new species; *P. gracilis,* new species; *P. orphanus,* new species; *P. profundus,* new species.

ETYMOLOGY.—From the Latin *plica* (fold) plus *lorica* (corset); masculine gender.

Key to Adults of *Pliciloricus*

1. Two spinoscalids adjacent to ventral midline, row 2, fused except for terminal region (double-organ) [Figure 1]. 2

   Two spinoscalids adjacent to ventral midline in row 2 not fused or only fused near their base. 3

2. The lorica with two pairs of P-flosculi and a rosette structure; claw-tipped spinoscalids in row 3 with single claw-tip and 4–5 subterminal accessory teeth [Figure 1] ..... ***P. enigmaticus,*** new species
   The lorica with a single pair of P-flosculi and 3 pairs of lateral N-flosculi; claw-tipped spinoscalids with single claw-tip and a single subterminal accessory tooth [Figure 29] ..... ***P. dubius,*** new species
3. The lorica with a single pair of P-flosculi; claw-tipped spinoscalid with double terminal, strongly curved claw-tip; mouth cone without tube [Figure 48] ..... ***P. profundus,*** new species
   The lorica with a single pair of P-flosculi and at least one pair of N-flosculi; claw-tipped spinoscalid without accessory teeth; mouth cone with a long tube [Figure 37] ..... ***P. gracilis,*** new species

Key to Larvae of *Pliciloricus*

1. Toes shorter than the lorica. 2
   Toes same length or longer than the lorica. 3
2. Mouth opening with 6 oral teeth and 6 oral stylets; collar well defined with 7 pores; toes with mucros [Figure 39]. . . . ***P. gracilis,*** new species
   Mouth opening with a valvate structure; collar indistinct; toes short and setae-shaped [Figure 4]. ..... ***P. enigmaticus,*** new species
3. Mouth opening with a valvate structure; collar well defined with 7 thin areas; toes very long and thin [Figure 49]. . . ***P. profundus,*** new species
   Mouth opening surrounded by hairs; collar not well defined; toes long and robust [Figure 47]. ..... ***P. orphanus,*** new species

Pliciloricus enigmaticus, new species

FIGURES 1–28

DIAGNOSIS.—Adults 160–268 μm long (not including mouth cone), with double-organ consisting of 2 second-row midventral spinoscalids fused the basal half of their length, highly modified, strongly sclerotized, rigid; 15 third-row spinoscalids claw-tipped with 4–7 teeth, alternating with 15 unmodified spinoscalids. Lorica with 7 transverse cuticular ridges and longitudinal double ridges; 2 lateroventral plates of caudal region each with 2 papillate flosculi ("*Pliciloricus*-flosculi"); large rosette structure, consisting of 6 cells with central pore (gonopore?) on midventral caudal plate. Terminal anus.

Higgins-larva 200–305 μm long, mouth cone apparently without ventral oral setae (only the larval exuvium was found). Internal mouth armature hexaradially symmetrical, with 6 stylet-like structures, each with a furca joining the pharyngeal bulb; mouth opening surrounded by 6 valves; cuticular lining in anterior part of mouth cavity supported by 6 cuticular rods. Four ventral clavoscalids broad with terminal spine; 4 dorsal clavoscalids slightly narrower; spinoscalids relatively long, 15–22 μm (scalids were difficult to see in the larval exuvium). Collar not well defined and nearly continuous with posteriorly adjacent rows of thoracic plates; with 2 pairs of relatively short anterior setae, with small hairs; lorica sculptured, with midtransverse constriction, and 5–6 transverse ridges. Toes straight, small (40–58 μm), each with pointed tip; with 2 pairs of sensory setae, each with an enlarged base, at posterior end of lorica; 2 short spines present on anal plate. Flosculi not observed, but could be present.

MATERIAL EXAMINED.—*Type Material:* The holotype is an adult female, 238 μm long (Figures 1, 6) from station RH 1834. The allotype is an adult male (224 μm long) (Figure 7) also from

station RH 1834. Paratypes include 1 adult male from station RH 1695 (Figures 2, 5); 3 larvae molting to adults, 1 adult male and 1 adult exuvium from station RH 1833; 1 adult female (squash-preparation), 1 newly molted female, 1 female(?) (presumed dead at the time of collection), 1 newly molted male, 12 larvae molting to adults, 2 larval exuvia with newly molted adults, 5 adult exuvia (Figure 8), 1 adult female(?) (unmounted) from station RH 1834. SEM preparations include 1 adult male(?) mounted on stub 83 and 1 larva molting to adult (Figures 23–28) mounted on stub 84, both from station RH 1837. A total of 34 specimens were examined.

In addition to the holotype (USNM 98556) and allotype (USNM 98557), 16 paratypes (USNM 98558) and the SEM specimens have been deposited in the National Museum of Natural History, Washington, D.C.; all other paratypes have been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—From the Latin *enigmaticus* (puzzle); masculine gender.

DESCRIPTION.—The holotypic female (Figures 1, 16) is 238 μm long. The mouth cone, not completely extended in the holotype, is 38 μm long and consists of three regions (Figures 11, 12). The basal portion of the mouth cone has eight retractor muscles, each attaching distally to a cuticular apodeme. The second region, the broadest part of the mouth cone, has 16 thin cuticular plates, with eight double ridges, 10 μm long. The internal structure of the third region consists of a cuticularized tubular extension of thin, flexible buccal canal, about 2 μm in diameter, which can be withdrawn telescopically into the second region of the mouth cone. Eight primary and four secondary ridges are visible at the surface of the third region. Each of the eight primary ridges is continuous with those of the second region of the mouth cone, which attaches to an apodeme (Figure 11, ad), which, in turn, is continuous with one of the eight retractor muscles of the first region. The four secondary ridges are difficult to observe and appear to be thickenings of the internal cuticular surface. Although the third region varies in length depending upon the amount of extrusion, the 12 ridges appear to be a consistent 20 μm in length, twice as long as the eight double ridges of the second region of the mouth cone.

A complex cuticular formation of 14–16 very thin fibers surrounds the base of the mouth cone as a "ruff" (Figure 17, ru), hence we have so named it. These fibers are continuous with an internal ring-shaped structure behind the pharynx bulb. As part of the introvert, the ruff probably functions in the retraction of the mouth cone. In one specimen (RH 1834) the ruff was fully everted and the mouth cone fully extended. Each of the 14–16 fibers was coiled near the base of the first two rows of scalids; each coiled portion was associated with a small plate.

The head (introvert) has nine rows of appendages. The first row consists of eight very large, pod-shaped clavoscalids, identical in both female (Figure 1) and male (Figures 2, 7). One margin of each clavoscalid is heavily reinforced for support and projects slightly beyond the otherwise blunt tip. Each clavoscalid is compartmentalized by 12–13 internal transverse walls, resembling a leguminous pod. The second row of appendages consists of seven leg-like scalids; two, at the ventral midline, are partially fused basally and form the double-organ, ~90 μm long (Figure 17, do). This specialized appendage is more sclerotized than other head appendages and stiff hairs occur near its base. The mouth cone, when extruded, lies between the two rami of the double-organ. Inside the two rami of this appendage, ~40 μm from the base, are two crescent-shaped cuticular structures. The seven scalids of the dorsal half of this row are much larger (~120 μm) than those on the ventral half (~100 μm). In a partially extended specimen (Figure 2), two dorsal leaf-like structures were apparent, but could not be seen in any other specimens.

The third row of scalids consists of 15 smaller "leg-like" appendages with a double basal swelling. Each spinoscalid is jointed about 20 μm from the base; two stiff hairs are on each side of this tubercular joint.

The fourth row of scalids consists of 15 spinoscalids alternating with 10–15 shorter claw-tipped spinoscalids, each with a slightly bulbous based proximal segment and a serrate terminal segment with 4–7 subterminal teeth (Figures 15, 18).

The fifth through seventh rows of head appendages are very uniform in appearance; each appendage consists of a short basal segment and elongate terminal segment; there are 30 of these spinoscalids in each row. The eighth row also has 30 spinoscalids, but these differ in having a slightly spinose basal plate and an elongate terminal segment with small spines arranged as barbs of a feather. The ninth row consists of 30 small, beak-like appendages, each with a tricuspid tip.

The next row of appendages, eight single trichoscalids alternating with seven double trichoscalids, is situated on an area intermediate between the head and thorax that we have called the "neck," an area more clearly recognizable in this family than in the Nanaloricidae. The neck has two single midventral trichoscalids and one double middorsal trichoscalid as in all Pliciloricidae. The double trichoscalids each have a single base from which the larger or primary element extends; the smaller or secondary element originates on the shaft of the primary element. In cross-section, the trichoscalids appear flat with a central canal in which lies a cilium. The margins of the trichoscalids have widely separated serrations that, at the distal end, form a slight tuft (Figure 19). The double trichoscalids have a large basal plate with a crescentic depression. Two accessory basal plates (Figure 27) are situated above the main or lower basal plate. The middle basal plate has a small spine (Figure 27, tp_2) and a large pore. The upper basal plate is triangular. The single trichoscalid only has the lower basal plate; the middle basal plate is missing and, instead of the upper basal plate, a small tricuspid tooth is present. Superficially, the insertion of the trichoscalid on the lower basal plate makes it appear as though the trichoscalid emerges from a hole in the plate.

The thorax has no appendages; its cuticle is very thin and consists of three rows of folds or plates (only the first row is easily seen). The entire thoracic region, along with the neck, is capable of being withdrawn into the loricated abdomen.

The lorica on the abdomen is well developed. Its edge is separated from the thorax by 22 more or less crescent-shaped structures (Figures 1, 3), which correspond with 22 primary longitudinal double ridges of the lorica. The area between the longitudinal double ridges is called the plica (Figures 1, 13). In the middle of each plica is an elevation called the secondary double ridge. The midventral plica (Figures 1, 14, pl_2) is twice as broad as the others, and the anterior part has a characteristic sculpture that suggests that the midventral plica consists of two fused plicae.

The midventral plica is divided into anterior and posterior portions by a transverse line. The posterior region has a large rosette structure consisting of six cells surrounding a pore (Figures 1, 16, 21, ro), which we suspect may be a gonopore, but no other loriciferans have a ventral gonopore. Three to four anal ridges (Figure 21, ar) extend from the rosette to the caudal end. Two pairs of papillate flosculi are located lateral to the midventral plate (Figures 1, 21, 22). These sense organs are very different from the flosculi described in *Nanaloricus*. To differentiate between the two types we have named the *Nanaloricus*-type flosculus the "N-flosculus" and the *Pliciloricus*-type flosculus the "P-flosculus." The former type consists of a cluster of micropapillae surrounding a pore; the latter type consists of a single large papillate unit that, by light microscopy, seems to have a central pore, but cannot be demonstrated by SEM. However, the two caudal papillae seen by SEM (Figure 20) could be the nephridiopores, or perhaps they constitute two additional sensory structures.

A unique feature of the lorica of *Pliciloricus enigmaticus* are the seven transverse cuticular ridges (Figures 1, 13, ri), which are easily seen on the anterior part of the lorica.

Higgins-larva (Figures 3, 4) (description based

on 13 specimens in molt) 200–305 μm long; the mouth opening is surrounded by six valves. The dorsal clavoscalids are broader than those on ventral surface; the spinoscalids of the first two rows are fringed and covered with fine hairs. A collar is followed by a thorax consisting of five rows of plates formed in an accordion-like manner. The lorica has both transverse and longitudinal ridges. The anterior margin is not prominent; the accordion-like appearance is continued into the lorica.

Two pairs of hairy sensory setae are present at anteroventral region of lorica. The lorica's sculpture (Figure 28) consists of a polygonal pattern formed by small, round tubercles; no such sculpture is present on the thorax. The toes (Figure 9) are short (40–58 μm), terminally spinous, with the openings of the presumptive adhesive glands at the base of spinous portion (Figure 26). Three pairs of setae are present at the posterior end of the lorica; two pairs, with an enlarged basal area, apparently have a sensory function; the third pair, near the ventrally situated anus, are hollow and rigid.

REMARKS.—Some internal structures of *P. enigmaticus* are much different than those of *Nanaloricus mysticus.* In this new taxon, a glandular, triradiate pharynx bulb is located in the mouth cone when the introvert and mouth cone are fully extruded. The brain (Figures 7, 10) occupies most of the introvert.

Pliciloricus enigmaticus also differs from *Nanaloricus mysticus* by the presence of two very large circular muscles in the abdomen of the former species; one set of muscles is near the edge of the lorica and the other is near the caudal end of the lorica. The epidermal cells that form the lorica appear to be constant in number. The nuclei are placed in longitudinal rows in the elevated areas of the secondary double ridges of the lorica. There also are a fixed number of cells in the scalids, the pharynx bulb, and perhaps also in the gut. However, eutely appears limited to these organs; it is not present in the gonads as might be expected. Gametes are more numerous in larger animals than in smaller ones. Spermatozoa are filiform, but often coiled. Oocytes are very large; usually only one of the two ovaries is prominent, and a single egg is present at one time.

One paratypic male from station RH 1833 had a single midventral spinoscalid instead of the double-organ, but was normal in all other respects.

Because all larval specimens were in molt, certain features of this life-history stage remain undescribed.

Pliciloricus dubius, new species

FIGURES 29–34

DIAGNOSIS.—Adults 163–185 μm long; mouth cone with short mouth tube; two elements of double-organ joined basally. Fifteen third-row spinoscalids claw-tipped, each with single claw-tip and prominent subterminal accessory tooth. Lorica with single pair of P-flosculi, 1 on either side of ventral midline, and 3 pairs of lateroventral N-flosculi. Midventral plica of lorica very large and plate-like, with 5 transverse ridges. Secondary trichoscalids very thin and spine-like (easily overlooked); primary trichoscalids very broad, short, with undulating midventral canal inside. No larvae found.

MATERIAL EXAMINED.—*Type Material:* The holotype is a young female, 185 μm long (Figures 29–34) from station RH 1837; a single paratype, female, 163 μm long, from the same station, was lost during SEM preparation. The holotype (USNM 98559) has been deposited in the National Museum of Natural History, Smithsonian Institution. A total of two specimens were examined.

ETYMOLOGY.—From the Latin *dubius* (uncertain, doubtful); masculine gender.

DESCRIPTION.—The holotypic female is 185 μm long. The mouth cone, 43 μm long, is completely extended, with a relatively short terminal mouth surrounded by three small teeth (Figures 29, 32). The three sections of the mouth cone lack oral ridges. The proximal section attaches to the head by a narrow stalk-like region that

expands into a prominently bulbous section and contains eight retractor muscles, each attached to a small, distinct apodeme. The second section of the mouth cone is enlarged basally and nests within the distal limits of the bulbous expansion of the proximal section. Within the bulbous expansion created by the two sections is the pharynx. The third section is a narrow tube that contains a thin, flexible buccal canal less than 1 μm in diameter. There is no evidence for the elements of the mouth cone being telescopic. The mouth cone appears to be retractable into the head.

A complex, cuticularized ruff (Figure 30) is located at the base of the mouth cone. It consists of 14 relatively thick fibers, each ending in a small cuticular plate and 16 very thin fibers or ridges located between the thicker fibers. The 30 fibers terminate in a cuticular ring situated on the stalk of the proximal section of the mouth cone.

The head (introvert) has nine rows of appendages: one row of clavoscalids and eight rows of spinoscalids. The eight clavoscalids are short (~50 μm long) and broad (15 μm). All appear broken. The single paratype lost in SEM preparation had the same type of seemingly broken clavoscalids, suggesting the possibility that this character is not an artifact. The second row of scalids consists of seven leg-like spinoscalids (~65 μm long) and the double-organ (~50 μm long). The double-organ (Figures 29–32), as in *P. enigmaticus*, consists of two partially fused midventral scalids. The basally fused proximal portion is short and rapidly expands into a broad middle region with several stiff hairs. Beyond this region the double-organ consists of two unfused rami, each with a row of stiff hairs along the mesial margins. The seven remaining spinoscalids of the second row of head appendages are more leg-like. Each consists of a proximal element, slightly enlarged basally and with a small spine arising half its length. The proximal section articulates with a more elongate, flexible distal section.

The third row of head appendages consists of 15 smaller leg-like spinoscalids (Figures 29, 30). Each of these has a large, double base, which elongates and then articulates with the first of three other sections. The terminal section is thin and pointed; the second section has two small hairs or spines at its base.

The fourth row of head appendages consist of 30 spinoscalids; 15 of these long (~70 μm) and alternate with 12 (or 14?) claw-tipped spinoscalids (~50 μm long). The claw-tipped spinoscalids are more complex than others; the slightly bulbous basal section (~10 μm long) is slightly constricted in the middle. It is followed by a very short (~2 μm), narrow second element. The last two sections are more swollen; the last has a slightly enlarged midsection from which a single tooth protrudes; the element then terminates with a claw-like tip. Two distinct points of articulation are evident, one at the distal end of the first element and one at the proximal end of the last element.

The fifth to seventh rows of head appendages are very uniform in appearance; each row consists of 30 thin, elongate spinoscalids as in all Pliciloricidae. The eighth row consists of 30 elongate spinoscalids, each with a basal plate with one or two small projections. The ninth row has 30 highly modified, relatively short spine-like appendages without cusps.

The neck of *P. dubius* is not a constricted area. It bears seven double and eight single trichoscalids (Figure 33); the secondary trichoscalids are very difficult to see by light microscopy. The primary scalids are very broad and relatively short (~45 μm). The internal canal running the length of trichoscalid and containing a single cilium appears undulant. The edges of the trichoscalid are difficult to see, only a slight, widely spaced serration pattern is visible. The lower basal plate of the double trichoscalids is strongly ornamented, the middle basal plate has a pore, and the upper basal plate is lacking. The eight single trichoscalids have indistinct lower basal plates and each appears to have an even less distinct upper basal plate.

The cuticle of the thorax is very thin and wrinkled, possibly because of the underlying cir-

cular muscles. The posterior part of the thorax has very thin, divergent folds oriented somewhat transversely from midventral to lateral.

The lorica is a typical *Pliciloricus*-type with 22 plica. The cuticle has a distinctive honeycomb sculpturing. Two constrictions are present in the posterior region of the lorica. The anterior margin of the lorica has a scalloped pattern formed by two arch-like structures associated with each of the 22 plica, except for the midventral plica, which has a three-arch configuration. The midventral plica (Figure 34) is more or less plate-like as in *Nanaloricus*. This structure has five narrow cuticular ridges of different lengths. A triangular anal plate is present dorsally and a large anal field of thin cuticle is present on the ventral surface.

A single P-flosculus is located on either side of the ventral midline, near the posterior limits of the second abdominal region (defined by the two abdominal constrictions). Three N-flosculi (Figure 33, nf) are present more laterally on the third or terminal abdominal region. The N-flosculi consist of eight micropapillae surrounding a single pore from which a free cilium may protrude. The position of gonopores, nephridiopores, and anus could not be determined.

REMARKS.—The holotype is a young female. Gametes consist of single clusters of oocytes in the posterior region of the abdomen. No Higgins-larva was found. The adult clearly is related to *P. enigmaticus* and, to a lesser extent, to *P. gracilis*. We postulate that the larva of *P. dubius* will closely resemble that of *P. enigmaticus*, but with a stronger cuticular sculpturing.

Pliciloricus gracilis, new species

FIGURES 35, 37–46

DIAGNOSIS.—Adult 227 μm long with a very long mouth tube extending from the mouth cone. Two elements of double-organ with separate enlarged bases partially fused soon after, not sclerotized more than remaining spinoscalids. Claw-tipped spinoscalids of third row of head appendages without accessory teeth. Thorax well defined from lorica. Lorica with transverse constriction two-thirds posterior, a zig-zag suture terminally, 22 longitudinal folds, and sculpture only seen with interference contrast optics. Two P-flosculi and possibly 2 small N-flosculi present.

Higgins-larvae 130–238 μm long, with single midventral oral seta on mouth cone; internal mouth armature both tri- and hexaradially symmetrical, with 6 teeth and 6 small stylets near mouth opening; 6 stylets surround cuticular buccal tube; base of stylets join 2 cuticular rings; posterior part of mouth armature continuing inside pharyngeal bulb; 3 pairs of trumpet-shaped placoids in anterior end of pharyngeal bulb. Four ventral clavoscalids large, consisting of 2 large segments and a spinous tip; 4 dorsal clavoscalids similar, but more rounded. Appendages of second through fifth rows distinctly spine-shaped, remaining rows of scalids reduced, scale-like or papillate. Thorax well defined, anterior 2 rows of plates form a collar. Lorica with 2 pairs of three-segmented anterior setae, with many thin hairs; lorica constricted midway, with sculpture that can be seen by normal light microscopy. Toes straight, shorter than length of lorica, with serrate margin (small mucros) near base, articulated with lorica by ball-and-socket joint. Anal plate with single pair of stiff, relatively long, spines.

MATERIAL EXAMINED.—*Type Material:* The holotype (Figures 35, 37, 38) is an adult male, 227 μm long, from station RH 1839. Paratypes include 4 larvae from station RH 1839, 5 larvae from station RH 1834, 12 larvae from station RH 1837, and 1 larva from station RH 1833. SEM preparations include 3 larvae (stubs 83, 84) from station RH 1837. A total of 25 specimens were examined.

The holotype (USNM 98560) and 14 paratypes, including SEM preparations (USNM 98561), have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. All other paratypes have been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—From the Latin *gracilis* (thin); masculine gender.

DESCRIPTION.—The holotypic male (Figures 35, 37, 38) is 227 μm long. The oral cone, including the mouth tube, is 78 μm long. It is totally extended from the head, resulting in an overall total length of 295 μm. The mouth cone consists of three sections. The first section (nearest the head) has eight ridges, and a cross-striated muscle lies beneath each ridge and has prominent cuticular apodemes distally, marking the limits of the first section. The base of the first section, continuous with the pharynx bulb, is narrowly restricted as the apex of a cone; the proximal portion is much wider. The second section also is conical and has eight ridges; its base joins with the wide proximal portion of the first section and may, in a fully retracted mode, fold over the first section. The proximal end, or apex of the second section of the cone, is narrowly restricted. The third section, the mouth tube, consists of an extruded portion of the cuticularized buccal canal that can be withdrawn inside the mouth cone. The inner cuticular lining of the third section protrudes slightly (hyperextended?) at the distal end of the third section.

The limits of the head and adjoining trunk region are not well defined. A definite gap does not exist between the last rows of head scalids and the basal plates of the trichoscalids, but below the ninth row of head appendages is a horizontal cuticular fold, which is interrupted in line with the trichoscalids of the neck, the area between the head and the thorax. Both adult and larval stages have a thin unsculptured cuticle in the thoracic region.

The first row of head appendages consists of eight clavoscalids, ~95 μm long. In the male, the clavoscalids are slightly modified on either side of the ventral midline; they are thinner and appear more flexible than the remaining six more broadly flattened, apiculate-tipped clavoscalids (Figure 37). Each of the latter clavoscalids appears to have transverse septa in the form of seven or eight lines of punctations. A heavily cuticularized supporting axis as in the clavoscalids of *P. enigmaticus* was not observed.

The second row of head appendages consists of nine large leg-like spinoscalids, ~95 μm long. Two of these are slightly smaller, ~65 μm long, and fused near their separate origins on either side of the midline to form the double-organ (Figure 37), which appears no more cuticularized than the remaining seven separate spinoscalids of the second row. Each of these seven spinoscalids has a bulbous basal region and three other indistinct sections bending at two joints. A fringe of hairs is on the oral surface of the first element and another fringe defines the limits of the second element.

The third row consists of 15 leg-like spinoscalids ~70 μm long. Each has a double base and a knee-like swelling midway the length of the first element; no fringe is evident, but two stiff lateral hairs are present.

The fourth row of head appendages consists of 30 spinoscalids of two different kinds. Fifteen of these are very long, ~100 μm long, each consisting of a long bulbous shaft (30 μm) and a thinner distal segment. The remaining 15 spinoscalids of the fourth row, ~60 μm long, consist of two segments and alternate with the longer spinoscalids. The distal segment is claw-tipped but lacks any subterminal accessory teeth. A fringe of small hairs is present in the joint between the two elements.

The fifth, sixth, and seventh rows each have 30 long (~70 μm) uniformly filiform spinoscalids with smooth bulbous bases mounted on small triangular plates. The eighth row of head appendages are similar to those on rows 5–7 but are longer, ~100 μm, and their bulbous bases have a slight fringe.

The ninth row consists of rounded basal plates with only a beak-like appendage, ~3–5 μm long. Inside the cuticle in this area there are about 30 clusters of glandular cells.

The posterior margin of the neck has a row of 15 feather-like trichoscalids, each relatively short (~50 μm) and thin (~2–4 μm). Seven of the 15 trichoscalids are double; the secondary trichoscalid is attached to the upper surface of the primary trichoscalid ~10–15 μm from the base. The double unit has a common shaft with one lower basal plate as in all Pliciloricidae. Only one accessory basal plate is present in the single tri-

choscalid. The trichoscalids on either side of the ventral midline are single; thereafter there is an alteration of single and double trichoscalids, with the result that the middorsal trichoscalid is a single one.

The thorax appears to be hyperextended, because those specimens of this same genus not subjected to the osmotic shock of processing in fresh water have the row of trichoscalids positioned just anterior to the loricated abdomen, and the whole thorax is retracted inside the lorica, as was the case in *Nanaloricus mysticus*. The thorax of *P. gracilis* is divided into five parts; the three anterior parts have the same accordion-like structure as found in all Higgins-larvae.

The abdomen is divided into two areas. The more prominent anterior region has a slight constriction about midlength. The smaller posterior region is capable of being retracted into the anterior region. Both areas have 22 primary and 22 secondary vertical folds arranged uniformly around the abdomen. The lorica has a fine, honeycomb-like sculpture, which, through refraction of light, makes it appear much more distinctive than the remaining cuticularized areas. The anterior edge of the lorica is scalloped in a pattern coordinating with the longitudinal ridges of the lorica; it bends outward slightly giving this lorica a distinctive margin. A small posterior region of the abdomen is less cuticularized and may be withdrawn totally or in part into the anterior region; however, the caudal region of the lorica has fewer (20) folds. At least a single pair of P-flosculi and 2–4 small N-flosculi are present; these are the only sense organs present on the lorica. Two or three other pores are located terminally and probably are part of the nephridiopore-gonopore complex.

The holotypic male has very small, dorsally arranged gonads in the posterior region of the abdomen. Gametes consist of a single cluster of spermatocytes, suggesting that this is a very young male. The buccal canal is very thin, without any spiral thickening of the cuticle. The pharynx bulb is situated close to the anterior margin of the head and lacks placoids. The eight retractor muscles in the mouth cone are cross-striated and easily seen. The prominent dorsolateral muscle complex of other species was not visible in *P. gracilis;* only single circular muscles, clearly cross-striated, were observed. No adult females were found.

Only indirect evidence supports our contention that the description of the following Higgins-larva is that of *Pliciloricus gracilis*. No specimens were found molting from the larva of the preadult stage as in the case of *P. enigmaticus*. However, the larva is assumed to be that of *P. gracilis*, because two larvae, *P. enigmaticus* and *P. profundus*, are clearly identifiable with adults and they, like the adult, have similar sculpturing on the lorica. A potential problem exists, because no adult of *P. orphanus*, only two larvae, was found. The following description is based on a single first instar of the larva (RH 1839.13) and 3 specimens prepared for SEM.

Higgins-larvae of *P. gracilis* (Figures 39–46) are 130–238 μm long. In the single specimen where the anterior portion of the mouth cone was fully extended, a single midventral oral seta, six oral stylets, and six oral teeth (Figure 44) were observed.

The appendages of the head (introvert) are arranged in only seven rows. Those of the first row consist of eight characteristic clavoscalids, approximately 43 μm long. Each of the four ventralmost clavoscalids has a smooth, constricted base supporting an expanded, broadly flattened double-segmented blade with a strongly spinose tip. The four dorsalmost clavoscalids are similar, except the two major sections are more round, not so flattened. The second row consists of typical spinoscalids, approximately 25 μm long, six dorsal, four ventral; the two on either side of the ventral midline are smaller. The third row consists of six dorsal and eight ventral spinoscalids ~25 μm long; the ventral ones become thicker and shorter as they approach the midline.

The fourth row has 16 spinoscalids, eight dorsal and eight ventral. The two midventral scalids are longer (~20 μm) than the other 14 (~10–15 μm). The fifth row has, as in all *Pliciloricus* larvae, seven spinoscalids, 10–15 μm long, each with a hooked accessory spine projecting from the distal

end of the basal segment over the tip of the proximal end of the terminal segment. The middorsal spinoscalid of the fifth row has a triangular basal segment; the terminal segment is filiform.

The sixth row of head appendages consists of eight double, short, triangular projections, ~4 μm long. The double structure is totally separated at the base and consists of scale-like "protoscalids." Four of these protoscalids are found in a cluster at the midventral line in all *Pliciloricus* larvae.

The seventh row has two kinds of scalids, seven double protoscalids alternating with eight very small papillae situated on basal plates. The double protoscalids are only 3–4 μm long and fused at the base, forming a "W-shaped" structure. The protoscalids of the sixth row and seventh row alternate, suggesting their pattern of formation.

Between the head and thoracic regions is a longitudinally ridged closing apparatus, the collar (Figures 39, 40, 42), defined by an anterior horizontal line, middle horizontal constriction, and posterior line. Beneath each of these lines are circular muscles, which, like three purse strings, contract when the head is withdrawn. The collar appears to have its own double ventral ganglion similar to one more central in the thoracic region, one in the central abdominal region, and another in the caudal region of the abdomen. The collar has four dorsal and three ventral pores, each with a minute hook at its anterior margin.

The remaining, more extensive region of the thorax consists of at least five distinct horizontal rows with about 30 longitudinal ridges. This region is capable of being shortened slightly as the head is withdrawn, but does not close tightly over the lorica. The larval lorica consists of a much thicker cuticle than found on the head or thorax. It has some sculpturing, which is seen as very fine punctations under light microscopy, and a honeycomb pattern under SEM (Figure 46). The lorica has about 20 longitudinal ridges. A transverse constriction is visible, especially in dorsal view, in the midregion of the lorica.

A distinctive, somewhat inverted cordate anal plate is present dorsoterminally. Part of this plate is visible ventrally as well. The anus is positioned near the terminal limits of this plate.

Two elongate, straight, rigid toes, ~71 μm long, extend from the lateroventral region of the caudal end. About 85% of the length of these toes is uniformly wide, approximately 5 μm, and hollow; the tip is a narrow, solid spine with a pore near the base. Prominent glands, presumed to be adhesive organs, are present at the base of each toe. The lateral margin of each toe appears serrate (small mucros?) for at least half of its length (Figure 45, mr). The toes appear to be capable of moving both laterally and ventrally.

Other appendages of the lorica include paired setae. Two pair of ventral setae, ~40 μm long, are located on the anterior margin of the lorica; these are jointed about midlength and lack hairs. Two lateroventral setae, ~55 μm long, also jointed about midlength, have many small hairs near the base and a few scattered hairs along the remaining portion. The remaining three pairs of setae are located dorsally on the caudal region. Two of them have a small basal segment supporting the singular elongate element. No hairs are visible. The longer (~112 μm) pair of dorsocaudal setae are located more anteromesial than the slightly shorter dorsolateral pair (~105 μm). The third pair of setae, near the anus, are short (~15 μm), stiff, and without joints.

Several features of the larval internal morphology have not been seen in any other species. The buccal canal is lined with cuticle and forms a buccal tube. At the anterior end of the buccal tube are six oral stylets (Figure 44). Posterior to the stylets, encircling the buccal tube, are a series of cuticular structures. The anteriormost of these consists of six tooth-like structures with a single prominent central cusp and two smaller lateral cusps that join with the lateral cusps of each adjacent tooth. A tooth-like projection extends posteriorly from each central cusp. Other elements closely articulating with the six teeth include stylet-like structures, the bases of which extend posteriorly and project into the anterior portion of the pharynx bulb. About midway, two cuticularized rings envelop the stylets. Light microscopy has not resolved the critical structure

of these elements nor is their function apparent. Anteriorly, within the pharyngeal bulb, there is a complex series of cuticular lamellae and three pairs of trumpet-shaped placoids associated with the triradiate lumen of the pharyngeal bulb. The pharynx bulb consists of myoepithelial cells and, in the posterior portion, there are three large glands.

A short, cuticle-lined esophagus is present. The midgut appears to contain the band of vesicles seen in other loriciferan species, but the midgut does not appear to fill the entire abdominal area. The anus is terminal, but its exact position on the caudal cuticularization is not evident. Adhesive glands appear to extend into the toes a short distance and are presumed to open via a small duct near the base of the spinose terminal end.

REMARKS.—The adult of *Pliciloricus gracilis* shares only a few apomorphic characters with *P. dubius;* among these are eight single and seven double trichoscalids and 22 plicae in the lorica. These characters, however, are found also in at least one additional species to be described later. Although *P. gracilis, P. dubius,* and *P. enigmaticus* all have two modified second-row scalids partially fused at the ventral midline, the two components of this double-organ are fused to a greater extent in the latter two species than in the more elongate double-organ of *P. gracilis.*

Unique to *P. gracilis* is its mouth cone with a long tube, its only slightly sculptured lorica, and the presence of a single pair of P-flosculi and at least one pair of N-flosculi.

The Higgins-larva of this species has a scalid formula, which differs from either *P. dubius* or *P. enigmaticus,* but could be similar to that of an undescribed species found at a depth of 305 m off the west coast of Corsica (Soetaert, Heip, and Vincx, 1984).

Pliciloricus orphanus, new species

FIGURES 47, 55

DIAGNOSIS.—Higgins-larva 298 μm long, mouth cone without oral ventral setae, minute hairs surrounding mouth opening. Internal mouth armature hexaradially symmetrical. Each of 8 clavoscalids 3-segmented, only lateroventral pair club-shaped, other clavoscalids more or less spinose. Spinoscalids long (15–35 μm, protoscalids triangular-shaped; collar well defined, but irregular. Lorica with 2 pairs of long anterior setae, branched without hairs; sculpturing indistinct; with mid-transverse constriction. Toes straight and long (106 μm), pointed terminally. Two pairs of sensory setae present at posterior end of lorica in addition to a pair of hollow stiff spines near anus; anal plate triangular.

MATERIAL EXAMINED.—*Type Material:* No adults were found; the holotype (Figure 47) is a large larva, 298 μm long, from station RH 1834. One small paratype (Figure 55), ~150 μm long, mounted on SEM-stub 78, is from station RH 1839. The holotypic larva (USNM 98562) has been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC. The single paratype has been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—From the Latin *orphanus* (bereft); masculine gender.

DESCRIPTION.—The holotypic larva (Figure 47) is 298 μm long. The mouth cone is tripartite with the terminal portion slightly retracted telescopically. The thorax and abdomen are extended fully. The terminal portion of the mouth cone has six valves, and the mouth opening is surrounded by very fine hairs. The internal mouth armature is hexaradially symmetrical, but its detailed structure could not be resolved by light microscopy.

The appendages of the head (introvert) are arranged in seven rows. The scalids are of the *Pliciloricus*-type seen in all other larvae of this genus, but the first row consists of eight more or less spine-shaped clavoscalids. These three-segmented appendages are approximately 45–50 μm long. The first two segments of the lateroventral pair are slightly broader than those of the remaining six clavoscalids; the terminal segment is spinous. The basal segment has a few stiff hairs. The second row of head appendages

consists of typical two-segmented spinoscalids, ~25–40 μm long, six dorsal, four ventral. The ventral spinoscalids are longer and more robust than the dorsal ones. No hairs were seen on any of the spinoscalids. The basal segment of the spinoscalid is triangular in cross-section and has a slight lateral projection on two lateral surfaces. The spinose terminal segment is more oval in cross-section.

The third row of head appendages consists of spinoscalids ~25 μm long, eight dorsal and seven ventral. The fourth row has 14 spinoscalids, six dorsal and eight ventral; the two midventral spinoscalids have very broad basal segments and articulate with the terminal segments by a well-defined joint. A similar two-segmented spinoscalid is found in the Kinorhyncha. The two ventralmost spinoscalids of the second, third, and fourth row are nearly fused midventrally, but they characteristically diverge from the midline. The fifth row has seven spinoscalids, each with a hooked accessory spine on the basal segment, similar to that noted for the larva of *P. gracilis*. The middorsal spinoscalid of this same row has a large triangular basal segment with a prominent filiform proximal segment (Figure 47). The sixth row of head appendages consists of eight double protoscalids; each projection has a serrulate margin and central keel that continues beyond the margin as a very small spinose tip, a condition most prominent in the dorsal protoscalids. One of the diagnostic characters of the genus *Pliciloricus* is the presence of four clusters of protoscalids found along the midventral line. In *P. orphanus*, these four protoscalids are smaller (5 μm) than the remaining 12 protoscalids (7 μm) of the sixth row.

The seventh row of appendages consists of seven double protoscalids alternating with 8 single papillae; each papilla has a small terminal spine. These double protoscalids are more or less fused basally, forming a "W-shaped structure. One double protoscalid is middorsal, with a single papilla located lateral to it.

The collar is not so regularly folded as in *P. gracilis* and lacks collar pores. The thorax has five horizontal rows of 15–30 plates, separated by distinct ridges in the manner of an accordion. The first row of thoracic plates has 15 ridges, similar to the pattern of folds in the collar. The last row of thoracic plates has about 30 ridges that are continuous with those of the lorica. The last row of thoracic plates on the ventral surface is nearly divided into two separate rows of plates, giving the appearance of an extra "sixth" row of plates ventrally, but only five rows dorsally. The larval lorica has a very thick, unsculptured cuticle with ~20 primary longitudinal ridges beginning at its anterior edge and ending at the anal plate. Ten secondary ridges are present ventrally, but they extend just short of the middle of the lorica, where a transverse constriction is visible. A distinctive triangular anal plate is present dorsoterminally. Three additional pairs of cuticular plates are present lateral to the anal plate; the anus is terminal on the anal plate (Figure 47, an).

Two long, rigid toes (~106 μm long) extend from the lateroventral region of the caudal end. About 70% of the length of the toes is hollow (~8 μm wide); the other terminal 30% of the length narrows to a solid spine. Two prominent glands are present in the posterior abdomen at the base of each toe.

The two anterior pairs of lorical setae are branched; each begins with a swollen base, which gives rise to a mesial ramus; the lateral ramus continues, then branches again in a similar fashion, resulting in three units (Figure 47, ls_2). The lateroventral setae also have a large base, but have only a slight branch coming off the primary element. No hairs are visible on any setae.

The posterior three pairs of setae are similar to what have been described for *P. gracilis*, but the ball-and-socket joints of the dorsolateral pair are very large and project beyond the lateral margins of the lorica at the caudal end.

REMARKS.—The larva of *P. orphanus* is very large and is somewhat similar to the *Nanaloricus* larva in that both have more or less spine-shaped clavoscalids. The anterior midventral setae are stiff and could have a locomotory function as in those of the Higgins-larva of *Nanaloricus mysticus*.

The head appendage formula (spinoscalids and protoscalids) is similar to that of other species of *Pliciloricus,* especially *P. gracilis.* The toes clearly are of the *Pliciloricus*-type.

Pliciloricus profundus, new species

FIGURES 48–54

DIAGNOSIS.—Adult 200 μm long. Large mouth cone (48 μm long) without mouth tube. Eight clavoscalids present, midventral clavoscalid spinose; remaining clavoscalids very broad, especially in the middle of four distinct segments, distalmost segment spinose. Two short, adjacent second row spinoscalids perhaps only partially fused to form a double-organ. Fourth row of head appendages consists of 15 long, filiform spinoscalids alternating with 15 short claw-tipped spinoscalids. Lorica with single pair of P-flosculi. Secondary trichoscalid of 7 double trichoscalids nearly same size as primary trichoscalids. Midventral plicae of lorica differ only slightly from other 20 plicae.

Higgins-larvae 168–232 μm long, slender. Mouth cone with prominent midventral oral seta. Terminal oral field with 6 valves and hexaradially symmetrical internal mouth armature. First row of appendages consisting of 8 clavoscalids each with 2 laterally compressed segments and terminal spinose segment; second and third rows of appendages with fringed spinoscalids minutely double claw-tipped; protoscalids with small lateral teeth. Collar symmetrical, with 7 oval sensory spots. Lorica with 2 pairs of filiform anterior setae each with a row of widely dispersed hairs; 2 pairs of sensory setae at posterior end of lorica and pair of hollow stiff spinose setae near anus, all without hairs; surface of lorica pustulate. Anal plate dorsal, rectangular, joined to lorica by an indistinct heart-shaped plate; lateral anal plate on either side of anal plate. Toes long (75–107 μm), spinose.

MATERIAL EXAMINED.—*Type Material:* The holotype (Figure 48) is an adult male, 200 μm long, from station RH 1833. Paratypes include 7 larvae and 1 larval exuvium from station RH 1833 and 40 larvae from station RH 1834. SEM preparations include 1 decapitated larva mounted on stub 84 and 1 complete larva mounted on stub 85 (Figures 50–53), both specimens from station RH 1837. A total of 51 specimens were examined.

In addition to the holotype (USNM 98563), 3 paratypic larvae (USNM 98564), including the SEM materials, have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. All other paratypes have been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—From the Latin *profundus* (deep); masculine gender.

DESCRIPTION.—The holotypic male (Figure 48) is 200 μm long. The mouth cone (48 μm) is completely extended and the ruff on the head is everted. The three sections of the mouth cone are similar to those of *P. enigmaticus.* The first section (nearest the head) is large and expands in a cup-like manner at its junction with the second section. Within the first section are eight retractor muscles, each attached to an indistinct apodeme located at the distal limits of the sections, where it appears to telescope with the second section. The second section has eight oral ridges, which extend to the third section. The third section lacks a mouth tube; the internal buccal canal is very thin and apparently cannot be extruded as in *Nanaloricus.* The pharynx bulb is glandular and may not have a myoepithelium.

The ruff consists of 15 fibers attached to a terminal ring; the ruff is everted in the holotype and can be seen as an external cuticular structure at the anteriormost part of the head. The ring-shaped structure has a very small diameter and surrounds the basal part of the mouth cone. The 15 fibers attach to the cuticular ring and are not coiled at the free end, which is situated between the bases of the eight clavoscalids. As in all species where it is present, the ruff probably functions as a kind of sphincter in the extrusion and withdrawal of the mouth cone as mentioned in the description of *P. enigmaticus.* The ring-shaped structure marks the limit beyond which the

mouth cone cannot be extruded. It is obvious that the mouth cone cannot pass through the small diameter of the ring unless the ring can be enlarged. Thus, it acts as a kind of closing apparatus for the mouth cone.

The head (introvert) has the typical nine rows of appendages. The first row has eight clavoscalids; the two ventralmost are narrow, more spine-like; the two remaining clavoscalids, especially the dorsal ones, are very broad, laterally flattened scalids. The dorsal scalids have three distinct segments in addition to a spinose tip.

The second row of head appendages consists of seven very long, leg-like spinoscalids (~110 μm long), and short (~50 μm long) spinoscalids may be only partially joined along the ventral midline; the bases and the tips are separated, and the unsegmented double-organ appears to have a thin cuticle, quite different from the double-organ of *P. enigmaticus*. The seven other spinoscalids of the second row each have two distinct segments in addition to a small basal stalk. The proximal segment, largest of the two segments, is broad with two small, stiff hairs along the anterior margin. The distal segment is spinose. The third row of appendages consists of 15 small (70 μm) leg-shaped appendages, each with slightly enlarged double base. About one-third the length of each appendage there is a tubercular joint with a stiff hair projecting from its side. The fourth row of appendages consists of 15 long spine-shaped scalids (100 μm) alternating with 15 short claw-tipped scalids (45 μm). All appendages of the fourth row consist of two segments. The terminal segment of the claw-tipped spinoscalids is minutely serrated. The next three rows of appendages are nearly uniform, with each row consisting of 30 non-segmented spinoscalids. The 30 spinoscalids of the eighth row possess a basal plate that supports the finely serrate filiform single element. The ninth row consists of 30 very short, beak-like spinoscalids, ~10 μm long.

The neck is moderately extensive; the limits of the thorax are marked by a constriction. The limits of the head are less distinct. The seven double trichoscalids have well-developed lower (tp_1) and middle basal plates (tp_2). The upper basal plate (tp_3) is lacking. The large middle basal plate has a distinct spine. Both secondary and primary trichoscalids are serrated, and both elements are nearly equal in length. The eight single trichoscalids lack middle basal plates and each upper basal plate has a tooth-like projection.

The thorax is partly withdrawn into the lorica and is not entirely visible; however, there is only a slight separation of the lorica and thorax. The lorica lacks sculpturing; its midventral plica differs only slightly from the other plicae, and the middle of each plica is not elevated. The posterior part of the lorica has a thinner cuticle than that in the anterior region. It is separated from the latter by a zig-zag line. A single pair of P-flosculi is present ventrally. Two laterocaudal spines, each with a small basal pore, may be penile spines. Sperm are filiform with a slightly coiled head region.

The description of the Higgins-larva was facilitated by the large number of specimens, 49 total, most in excellent condition. The smallest specimen (130 μm), in a retracted configuration, had an ovoid structure attached caudally; this could be a remnant of the egg cuticle of the newly hatched first stage larva. No differences in the external structure were noted from the smallest (130 μm) to the largest (232 μm) larva.

The typical Higgins-larva of *P. profundus* (Figure 49), illustrated from specimen number RH 1834.72, is 224 μm long with toes 105 μm long. The mouth cone of the glycerin-mounted specimen is tripartite and the terminal part is slightly retracted telescopically. The terminal portion of the mouth cone has six pincer-like valves. The internal mouth armature is hexaradially symmetrical and superficially resembles the mastax of a rotifer. The exact structure of the armature is beyond the resolution of the light microscope; only a limited amount of detail could be seen. The anterior portion resembles an umbrella with six ribs; the umbrella surrounds six internal stylets that are jointed. The posterior portions of these stylets are embedded in the ovoid pharynx

bulb, where each terminates as a furcate base. In the middle of the whole structure there is a thin cuticular lining indicating the buccal canal. The buccal canal continues through the pharynx bulb as a triradiate lumen. The pharynx bulb appears to consist primarily of glandular tissue. On the posterior part of the mouth cone, there is a single prominent midventral seta (Figure 49, ms).

The appendages of the head (introvert) are of the *Pliciloricus*-type, but they appear to be arranged in only six rows. The first row of appendages consists of the eight clavoscalids, ~35–40 μm long. The four ventral clavoscalids are slightly narrower than the four dorsal ones; otherwise, all are broad, flat appendages with two segments and a spinose tip. At the base of the tip there is a fringe of hair. A few hairs are present at the junctions of the other segments, but these can be seen only by SEM.

The second and third rows of appendages consist of the typical 15 2-segmented spinoscalids, ~30–40 μm long. The seven dorsal scalids appear narrow and somewhat inflexible; the eight ventral are more robust and have small double-claw tips. The proximal segments of these appendages, particularly those on the ventral surface, have a broad base. The joint between the two segments is very distinct. The lateral edges of the proximal segments have a small keel with minute hairs. On the distal segments, the hair is arranged in a comb-like structure. The fourth row of appendages is similar to the fifth row in *P. gracilis* and *P. orphanus,* thereby suggesting that the Higgins-larva of *P. profundus* may lack one of the more anterior rows, perhaps the fourth row, but this is difficult to assess. The last three rows, 4, 5, and 6, are similar to other *Pliciloricus*-larva. The seven scalids of the fourth row have triangular or beak-like proximal segments. Both the single middorsal and the two midventral appendages have a triangular proximal segment with two sharp edges and are covered uniformly with minute hairs. The tip of the more or less triangular appendage is spine-like. The joint between the two segments is hidden below the spine. The distal segment is rhomboidal in cross-section, with four rows of hairs corresponding to the four angles.

The fifth row of appendages consists of eight protoscalids. The two midventral protoscalids are very small, and the two pairs of middorsal protoscalids are large, each with two elements and a fused base. The sixth row has seven double protoscalids alternating with eight small papillae, each with a basal plate. The triangular protoscalids have serrated lateral surfaces.

The collar (Figures 49–51) consists of 48 folds. Seven presumptive sensory spots are present, as in *P. gracilis.* Four such spots are dorsal (two near the dorsal midline, two more lateral) and three are on the ventral surface (one midventral and two lateral). Four folds in the collar corresponded with a single plate in the thorax; this could indicate that the collar is homologous with the neck area of the adult. These sensory spots (*P. profundus*) or oval pores (*P. gracilis*) could be seven prototrichoscalids, but this is only speculation. The collar is a closing apparatus with three circular muscles as mentioned under the description of *P. gracilis.*

The thorax has five distinct horizontal rows of plates; the first row consists of 13 plates, the second and third rows each have 14 plates, and the fourth and fifth rows each have ~20 plates. The lorica has ~20 longitudinal ridges. A transverse constriction divides the lorica about midway. A circular muscle is present beneath the cuticle at the site of the constriction. Sculpturing of the lorica could be seen only by SEM. The cuticular surface of the lorica is densely papillate in contrast with the honeycomb-structure pattern made up of this same material in *P. gracilis.* The thick cuticle of the dorsal lorica terminates ~10–15 μm from the caudal end; the caudal end has a distinctive rectangular anal plate and two lateral accessory anal plates. The anal plate is united with the anterior portion lorica by a more or less cordate cuticular structure. The anus is terminal.

Two very long, straight toes (Figures 49, 50, 53) (106 μm long) originate ventrolaterally near the caudal margin of the lorica and bend ventrally, away from the animal's body. About 65%

of the length of the toes is of uniform width (3–4 μm) and hollow; the tip is a narrow solid spine with a large pore near its base. A triangular basal plate (Figures 53, 54) covers the insertion of the toes on the ventral side of the lorica.

The two pairs of ventral setae originate at the anterior margin of the lorica. These are unsegmented, long and filiform (~55 μm) with 5–6 long hairs projecting from the surface. Several very small hairs were apparent by SEM. The remaining three pairs of setae are located caudally; none have any evidence of hairs, but SEM examination showed that three pairs have a serrated edge. The two dorsal pairs (~75 μm long), have a ball-and-socket articulation with the trunk; the third pair (~25 μm long), located on either side of the anus, are stiff and appear to have a terminal pore.

REMARKS.—*Pliciloricus profundus,* based on its larval characters, is closely related to *P. orphanus,* and to a lesser extent *P. enigmaticus* and *P. gracilis.* The presence of only six rows of head appendages is unique to *P. profundus.* The adult is notable in that its lorical structure is not so specialized as the other species of *Pliciloricus* and the double-organ is only slightly fused. These two characters suggest that *P. profundus* may be more closely related to the genus *Rugiloricus,* especially *R. ornatus;* however, the double trichoscalids and the typical *Pliciloricus*-larva clearly indicate that *P. profundus* belongs to the genus *Pliciloricus.*

Rugiloricus, new genus

DIAGNOSIS.—Adults 115–264 μm long, with a small mouth cone. Male with 4 large dorsal clavoscalids and 4 small ventral clavoscalids or with 8 uniform clavoscalids as in female. Glandular pharyngeal bulb without armature. Fifteen single trichoscalids on neck. Separation of thorax and loricated abdomen not well defined; lorica with 30–60 longitudinal folds, single transverse constriction about midway from anterior margin; cuticle very thin, without sculpture, without flosculi or with single pair of P-flosculi; posterior end of lorica may be constricted abruptly into a round pedicle-like structure with 2–4 small pores. The anus-gonopore complex appears dorsally displaced.

Higgins-larvae 114–345 μm, with a mouth cone consisting of three telescopic segments. External armature of the mouth cone hexaradially symmetrical, armature consisting of 6 primary teeth and 6 very small accessory teeth, 12 double oral stylets and 6 leaf-shaped structures; buccal tube very short, without internal armature; pharyngeal bulb long, without placoids. Eight clavoscalids, with a "swollen" tip, without hair; first 2 rows of spinoscalids elongate and pointed, remaining rows strongly modified; middorsal spinoscalid in last row peg-shaped. No collar area apparent. Thorax with 5–6 rows of plates. Lorica with both longitudinal and transverse folds; with 2 paris of anterior setae, each with many small, stiff hairs; only 2 paris of stiff posterior setae, each with swollen base; no flosculi observed; toes short, anal plate located ventrally. Note: In two of the three species of *Rugiloricus,* typical Higgins-larvae were not observed, only aberrant larvae (postlarvae?) without toes on the abdomen and without lorical setae were found.

TYPE-SPECIES.—*Rugiloricus cauliculus,* new species.

COMPOSITION.—*Rugiloricus carolinensis,* new species; *R. cauliculus,* new species; *R. ornatus,* new species.

ETYMOLOGY.—From the Latin *ruga* (wrinkle) plus *lorica* (corset); masculine gender.

Key to Adults of *Rugiloricus*

1. Lorica without flosculi; anal cone present; mouth cone very small (~16 μm long) with 4–6 oral stylets (or papillae). ***R. cauliculus,*** new species

Lorica with one pair of P-flosculi; mouth cone small (~25–40 μm long); anal field flat 2

2. Lorica with a delicate thin horizontal zig-zag pattern, claw-tipped spinoscalids of third row with terminal double claw; mouth cone with ventral mouth seta [Figure 84] ..... ***R. ornatus,*** new species

Lorica with regular plicae, long claw-tipped spinoscalids of third row without teeth; mouth cone with mouth tube [Figure 56] ..... ***R. carolinensis,*** new species

Key to Larvae/Post-larvae of *Rugiloricus*

1. With toes and 4 pairs of lorical setae [Figure 63] ..... ***R. carolinensis***, new species

Without toes or lorical setae 2

2. Fifteen large hook-shaped scalids on the anterior part of the head [Figure 77] ..... ***R. cauliculus***, new species

Six to nine very thin, straight spines on the anterior part of the head [Figure 86] ..... ***R. ornatus***, new species

Rugiloricus carolinensis, new species

FIGURES 56, 57, 63–75

DIAGNOSIS.—Adult about 205 μm long. Small mouth cone with long mouth tube (combined length ~40 μm). Eight uniform clavoscalids present in first row, 9 in second row, no double-organ present; fourth row with 30 filiform spinoscalids. Neck with 15 short, single trichoscalids. Lorica unsculptured, small, with single pair of P-flosculi. Anal field large, flat, with at least 2 pores.

Higgins-larva same as generic diagnosis, which is based only on *R. carolinensis*, because a typical Higgins-larva was found only in this species.

MATERIAL EXAMINED.—*Type Material*: The holotypic adult female(?) within a larval exuvium from station RH 1839. Paratypes include only larvae; 70 mounted and 129 unmounted larvae from RH 1839; 29 mounted larvae from station RH 1834; 4 mounted larvae from station RH 1837; and 1 mounted larva from station RH 1833. SEM preparations include 4 larvae mounted on stub 77 and 1 larva mounted on stub 78, all from station RH 1839. A total of 241 specimens were examined.

The holotype (USNM 98565) and 87 mounted and 129 unmounted larvae (USNM 98566) have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. All other paratypes including the SEM preparations have been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—Named after the states of North and South Carolina.

DESCRIPTION.—The holotype (Figures 56, 57) is an adult female(?) still in the exuvium of the Higgins-larva or postlarval stage. The adult appears to have been in the process of leaving the exuvium, because most of the head protrudes from the larval thorax. The specimen is mounted with the adult in ventral aspect from a lateral view. Because of the exuvium, several of the adult characters cannot be described.

Although not fully extended, the length of the adult is ~205 μm. The small oral cone (15 μm) is totally retracted inside the head. The oral cone is without armature outside. A long mouth tube (25 μm) with six ridges is present. A ruff, present in all *Pliciloricus* species, is not present in *R. carolinensis*. The head has the typical nine rows of appendages; they appear to be less specialized

than in other Pliciloricidae. The first row contains the typical eight clavoscalids, all nearly the same in appearance and size, although they are still wrinkled from the molting process; they are unsegmented and have a small spinose tip. The second row of head appendages consists of nine elongate spinoscalids; the two spinoscalids adjacent to the ventral midline are not fused to form a double-organ. The third row consists of ~15 similar, but smaller spinoscalids. The 30 appendages of the fourth row are more spine-like as are those of the next four rows. The ninth row consists of 30 small beak-like scalids.

The neck is extensive and set off from the head and thorax by constrictions. In addition, a slight constriction is present just about the insertion of the 15 single trichoscalids. The trichoscalids are small (~30 μm); seven of them (these correspond with the double trichoscalids in *Pliciloricus*) have typical well-defined lower basal plates, the other eight (these correspond with the single trichoscalids in *Pliciloricus*) have poorly formed lower basal plates. Upper basal plates, each with a distinct spine, are situated slightly above the lower basal plates. Middle basal plates were not seen.

The thorax is without sculpture, and the cuticle is very thin, revealing 15 underlying cross-striated muscles. These muscles attach near the anterior and the posterior limits of the thorax.

The lorica has about 30 longitudinal folds, corresponding to the plicae in *Pliciloricus*. One transverse constriction is present about midway from the distinctive anterior margin of the lorica. The constriction is formed by a system of circular muscles within the abdomen. The posterior end is not constricted abruptly, but a transverse fold is present; two ventrally situated P-flosculi are near this transverse fold. Two very small pores are situated laterally and slightly more posterior; two others are near the ventral midline. The posteriormost region has a large anal field or plate with two distinct pores (gonopores?). Close to the edge of the anal field there are two very small pores; these could be the nephridiopores. The anus was not easily observed, but the rectum was seen terminating dorsally in the vicinity of the anal field.

We suspect that the adult animal inside the larval cuticle is a young female, because the two clusters of very large gametes are present in the gonadal tissue, and because the spermatocytes and spermatids observed in other species of *Rugiloricus* are much smaller. The larval exuvium has all the characters of Higgins-larvae from this geographic area. Assuming the exuvium is that of a larva and the molting animal is an adult, a postlarval stage may not be present in the life-cycles of *R. carolinensis*.

The Higgins-larva of *R. carolinensis* is very different from the other larvae described in this paper, and without the holotypic specimen, an adult within the larval exuvium, it would have been difficult to relate the immature stage to the Pliciloricidae. The larvae varied from 114–345 μm in total length. Length-frequency measurements suggest that as many as five instars may exist, but such data are questionable, because length measurements seem highly subject to error because of preservation. The description of the larva is based on a last instar larva (RH 1839.5), but additional data from SEM specimens are included.

The total length of the larva illustrated in Figure 63 is 322 μm (measured from the mouth cone to the posterior edge of the lorica). The animal has the mouth cone (Figure 71), head, and thorax almost totally extended. The protruded mouth cone consists of three telescopic portions and has a very characteristic external armature. The first region (nearest the head) is unarmed, and a slight suture suggests an octaradial symmetry as contrasted with the hexaradial symmetry of the second region. The second region has six-valve like structures, which close off the oral opening when the mouth cone is retracted (as in the tardigrade *Milnesium*). Only in hyperextended animals can the third part of the mouth cone be seen and even then it can easily be overlooked by conventional light microscopy. The third part appears to have 12 very small (~3–4 μm) oral stylets (Figure 72), two located

on each of six basal plates. Each stylet is a double structure, so in all, 24 very thin stylets are present. In addition, six large primary teeth and six very small secondary teeth surround the mouth opening.

The appendages of the head consist of seven rows of scalids and two naked segments with only folds or wrinkles, probably homologous to the collar of *Pliciloricus*. The last row of scalids are so modified that they looked more like the "antennae" found in the coronal region of the Rotifera. The first row of scalids consists of eight clavoscalids. The four ventral clavoscalids have a slightly thicker base, but are not markedly different from the remaining four. The recurved tips of the clavoscalids are slightly claw-like. The second and third rows of head appendages are the only two rows that can be compared directly with the rows of spinoscalids in the other loricifera larvae. The second row has 15 scalids; the third row has seven elements. The two rows are not well separated and could be interpreted as a single row with 15 elements, seven double and eight single. This pattern is found several times in the arrangement of head and neck appendages, e.g., 15 trichoscalids in the adult of *P. enigmaticus*. The same adult pattern of one middorsal double scalid and two single ventral scalids is also present. Both scalids nearest the ventral midline of the second and third rows are recurved, almost claw-like. The fourth row consists of 8 single scalids similar to but smaller than the seven elements in the third row. In addition to the scalids situated on either side of the ventral midline, as those of row two directly anterior to it, two others are more laterally situated. On the dorsal surface, the four scalids are arranged similarly, but there is what could be interpreted as a middorsal double scalid (a middorsal of row 3 and posteriorly adjacent middorsal of row 4).

The fifth scalid row has seven more modified spinoscalids, each with a large basal plate with a fringe of small spines, and a short spinose projection. Three of these are dorsal, one on the midline, the other four are ventral, none on the midline. The shapes of the dorsal and ventral spinoscalids are slightly different. The middorsal scalid (Figure 69, sr_5) has a large pore and middorsal keel on the basal plate; the spinose projection is a single filiform element protruding from an opening in the basal plate, which is triangular and has a small spinose fringe. The two dorsolateral scalids have slightly longer fringe elements; the basal plate is also triangular, but the keel is lacking. The spinose projection is slightly broader, more flattened, and divides distally into two or three filiform elements. The four ventral scalids of the fifth row have a rectangular basal plate, and the spinose fringe is long and covers the edge of the basal plates (Figure 66). The proximal part of the spinose projection is hidden under the fringe. The distal part of the seta is stiff and slightly claw-shaped (Figure 70).

The sixth row of scalids consists of eight elements. Four of these, two lateroventral and two laterodorsal, are single and have asymmetrical basal plates (Figure 68, sr_6); the two ventral-most elements appear double (one on either side of the midline) and are highly modified; their lateral margins are strongly sclerotized and have five posteriorly directed teeth on each side (Figure 70, mv). The two asymmetrical lateroventral elements have serrate mesial margins, and their dorsolateral counterparts have serrate lateral margins; the elements on either side of the dorsal midline also appear double, with both lateral and mesial margins serrate. The seventh row of appendages consists of eight small papillae, superficially resembling the "antennae" in the Rotifera, alternating with seven elements of different shape. Of these, the middorsal element (Figure 67) is hook-shaped, i.e., it projects anteriorly before recurving posteriorly, and is associated with an arched cuticular plate (Figure 66, mp). The two lateral elements on the dorsal surface have an anteriorly directed lip-like structure with a very long, thin filament (cilium?) and many small cuticular hairs; the remaining four elements, two ventral and two dorsal, are tuft-like with many small filaments. The last two "seg-

ments" of the head, the eighth and ninth or collar region have no appendages or sensory structures and we assume this region normally is withdrawn into the thoracic region.

The thorax consists of five rows of plates. They are arranged as the folds of an accordion, but the plates are irregular and less distinct than those found in other Higgins-larvae. The plates are best developed on the ventral side; the presence of a few extra plates indicates that a sixth, but incomplete, row may exist in the last instar larva.

The larval lorica consists of a thin, very flexible cuticle. In well-fed larvae the lorica can expand enormously as an inflated balloon; in larvae lacking gut contents the lorica has deep longitudinal folds. The lorica consists of a single piece, but only few transverse folds are found as in *Nanaloricus mysticus*. The surface of the lorica has no sculpturing. On the posteroventral end, a large, slightly invaginated anal plate is present. The small toes, ~60 μm long, are attached ventrally on the anterior margin of the anal plate (Figure 75). The toes are smooth without mucros or any other structures. They consist of basally hollow tubes, which become solid near the terminal ends. The basal portion of the toes are slightly enlarged, and the margins are slightly undulant, not so straight and parallel as in *Pliciloricus*. In a few larvae, the toes were oriented backwards, but in at least 70 others the toes were oriented forward. The orientation of the toes could depend on how the pedal muscles were affected by the fresh-water shock treatment and subsequent fixaton.

Ventrally, at the anterior margin of the lorica, two pairs of setae are present. These anterior setae have many small stiff hairs, and their function may be only sensory and not locomotory as in the anterior setae of *Nanaloricus*. The setae on either side of the ventral midline are slightly smaller (~60 μm) than the two more laterally displaced setae (~75 μm). Two pairs of posterior setae are present: the longest pair is located dorsally (Figures 73, 74); the small pair, with many hairs, is more ventrolateral. Both pairs of setae are rigid with swollen bases, and lack a jointed basal area. Flosculi were not observed.

Internally, a smooth, short, straight, cuticular buccal canal extends posterior from the mouth opening to the pharynx bulb. The pharynx bulb is glandular and very long, about three times longer than broad; no placoids could be seen in the pharynx bulb. The esophagus is short and connects directly to the midgut. In well-fed larvae, the midgut expands enough to fill the entire abdomen with a white vesicular material. These vesicles very easily can be misinterpreted as coelomocytes, but such structures are absent in the larval stages. When the animals have been subjected to osmotic stress, the vesicles are found in the body cavity (Kristensen, 1983). The anus is hidden behind the anal plate. The attachments to the two pedal muscles on the anal plate appear as two punctated circular depressions.

Two very large glands are present in the posterior region of the head. The most notable internal structures (when the animals are not filled with gut material) are a pair of large toe glands. They open into the hollow toes, but no openings from the toes to the external surface were seen. We suspect that an opening does exist at the tip of the toes, and that the toes are adhesive organs.

REMARKS.—*Rugiloricus carolinensis* was the most abundant species collected. However, of the 240 Higgins-larvae found, only one was molting into an adult, which suggests that *R. carolinensis* may have a strong seasonal variation in its life cycle. Without the holotype, a specimen consisting of a larval exuvium and newly molted adult inside, it would not have been possible to relate this otherwise aberrant larva to the genus *Rugiloricus*. The adult has 15 single trichoscalids, one of the diagnostic characters for *Rugiloricus*. However, in other characters, e.g., the mouth cone with mouth tube, *R. carolinensis* appears more aligned with the genus *Pliciloricus*. The Higgins-larva of *R. carolinensis* is clearly not related to *Pliciloricus*. Until the Higgins-larva of

both *R. cauliculus* and *R. ornatus* are found, the systematic position of the *R. carolinensis* will remain unclear.

Rugiloricus cauliculus, new species

FIGURES 58–60, 76–83

DIAGNOSIS.—Adults 180–264 μm long, with very small mouth cone (~16 μm long) consisting of three sections. Males with 4 large dorsal clavoscalids and 4 small ventral clavoscalids; females with 8 uniformly large clavoscalids; double-organ present, consisting of two partially fused spinoscalids of the second row of head appendages, with blunt terminal segment; fourth row of head appendages with 15 very long filiform spinoscalids alternating with 15 very short claw-tipped spines. Fifteen single broad trichoscalids on neck. Lorica with 60 irregular longitudinal folds; one transverse constriction about midway from anterior margin; prominent terminal constriction forming a pedicle or small stem-like structure.

Higgins-larva (or postlarva?) 275 μm long, head without clavoscalids; first row of scalids replaced by 15 claw-tipped spines alternating with 9 slightly bulbous papillae; next six rows of appendages reduced to small scales. Neck with two rows of basal plates or prototrichoscalids. Lorica without toes or setae.

MATERIAL EXAMINED.—*Type Material*: The holotype is a young male(?), 264 μm long from station RH 1839. Paratypes include a male in molt within a larval (or postlarval) exuvium from station RH 1839, a "dead adult" from station RH 1834, and two adult females from station RH 1837; SEM preparations include a single adult male from station RH 1839 mounted on stub 79. A total of six specimens were examined.

The holotype (USNM 98567) and two paratypes (male in molt from station RH 1839 and adult female from station RH 1837) (USNM 98568) have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. The other paratypes have been deposited in the Zoological Museum, Copenhagen.

ETYMOLOGY.—From the Latin *cauliculus* (little stem); masculine gender.

DESCRIPTION.—The holotypic male (Figures 58, 76) is 273 μm long. The small oral cone, 16 μm long, is not totally extruded from the head and not included in the total length measurement given. The structure of the mouth cone cannot be described well enough from the holotype alone; SEM photos of a paratypic male show that it consists of three sections (Figures 78, 81). The two sections nearest the head have eight ridges; the anterior part of the second section is ruff-like, with at least 16 irregular folds. The third section is not fully extruded in any of the animals studied, making it hazardous to interpret its symmetry; however, at least one SEM photo (Figure 81) suggests that it has a tri- or hexaradial symmetry, with three large ridges terminating with six small oral stylets surrounding the mouth opening. The mouth cone is separated from the head by a prominent almost stalk-like constriction. The head, the neck, and thoracic regions merge without a clear separation. All rows of scalids including the row of trichoscalids of the neck are equally spaced.

The first row of head appendages consists of eight clavoscalids, ~108–137 μm long, which usually project anteriorly. In the holotypic male the four clavoscalids, two on either side of the ventral midline, are thinner than the other four and have a club-shaped terminal section, ~100 μm long. In a paratypic female only two ventral clavoscalids are slightly modified; six others are broadly flattened with apiculate distal ends. Each of the large clavoscalids has a mid-rib and a series of 4–8 cross-walls formed by very fine punctations.

The second row of head appendages consists of nine very large leg-like spinoscalids, ~150 μm long (Figure 78). Two of these at the ventral midline are fused near the base and form a double-organ (Figure 76). However, each is attached to the head separately as in *Plicilloricus gracilis*. The seven other scalids in the second row lie between the bases of the clavoscalids. The almost leg-like spinoscalids are very complex or-

gans with many small hairs, especially at the base. They are multicellular with basal muscles; each consists of a basal stalk joined to three additional elements. The first element is slightly swollen at its base and has a spinose projection extending from the base over the dorsal surface and an area of small hairs about midway to its distal end; a second element begins here and bends after a short distance; the third section continues farther as a flexible sensory tip.

The third row of head appendages consists of 15 spinoscalids, similar to, but shorter (~100 μm long) than, the appendages of the second row. Third row scalids have a double bulbous base (Figure 79) and a tubercular joint about 20 μm from the base. Two small spines are located on either side of the joint. The segment preceding the prominent joint has many hairs; the segment beyond the joint is filiform and flexible. The fourth row has 15 long spinoscalids (~100 μm long) alternating with 15 short claw-tipped appendages (~30 μm long). All 30 scalids of the fourth row have two segments; a second segment terminates as a small claw-like tip on the shorter scalids. Scalid rows five to seven have uniformly long (~120 μm) filiform appendages. Each row consists of 30 spinoscalids with a smooth, bulbous base situated on a small plate with irregular teeth. Between each appendage is a small triangular cuticular point, reflecting light in such a manner as to make the scalids of rows 4–6 very evident. The bulbous bases are relatively long (15 μm) and separated from the filiform part of the spinoscalid by a constriction.

The eighth row of scalids (Figures 82, 83) are the longest appendages (~140 μm) in the entire animal and have a serrate margin. The bulbous base (5 μm) is smooth and is situated on a large ovoid basal plate with two lateral teeth. The ninth row of appendages consists of 30 short, robust, beak-like spines. Between the seventh and eight rows are 30 poorly defined round areas on the cuticle, which could represent glandular areas just below the cuticle.

The posterior limit of the head is only slightly set off from the next region, the neck. Just below the cuticle is a band of circular muscle; a cuticular line is formed where the muscles attach to the cuticle (Figure 76). The neck normally is a transitional zone between the head and the thorax, but in *R. cauliculus,* the neck has many structural characters, more closely relating to the head. For example, there are 15 upper basal plates above the trichoscalids, eight of which have a small tooth-like spine. The arrangement of these plates follows the pattern of neck appendages, not the pattern of appendages of the head, but the morphology of the plates is nearly similar to the ovoid plate present in the eighth row or the beak-like scalids of the ninth row of head appendages.

The appendages of the neck consist of 15 single trichoscalids; seven of these originate on a shield-like lower basal plate (tp_1) in association with two anterior accessory basal plates for the insertion of the trichoscalids. The middle basal plate (tp_2) is nearly oval and has a small spine and a large pore (Figure 83). This structure associated with these seven single trichoscalids may represent the modified, otherwise missing, trichoscalids found in *Pliciloricus*. The upper basal plate (tp_3) is an indistinct rectangular plate with a V-shaped suture. The remaining eight trichoscalids have a crescent-shaped lower basal plate, the middle basal plate is missing, and the upper basal plate is as mentioned, a plate with a small toothlike spine. The trichoscalids are arranged in the same pattern as those of *Nanaloricus* and *Pliciloricus*. The two midventral trichoscalids have two basal plates; the middle basal plate is missing. The remaining scalids alternate between three basal plates and two basal plates. The middorsal trichoscalid always has three basal plates. The trichoscalid itself is very long (75 μm) and broad (4 μm) with a prominent midrib (Figure 83). The entire structure has a feather-like appearance and is more rigid than those of other pliciloricids. The two females from station RH 1837 appear to have slightly different single trichoscalids in that the length of the eight scalids with two basal plates are almost twice as long (80 μm) as the seven scalids (45 μm) with three basal plates. This suggests that it may be a step farther

in the reduction of the double trichoscalids found in *Pliciloricus*. The secondary trichoscalids may disappear first, followed by a reduction (in length) of trichoscalids.

The region of the thorax just posterior to the trichoscalids is sculptured with poorly defined cuticular plates. In the holotype, fresh-water immersion likely has hyperextended the remaining, unsculptured part of the thorax, which, in live animals, would ordinarily be retracted into and protected by the loricated abdomen. Consequently, the length of the thorax (~40 μm) as illustrated, may be exaggerated considerably. The boundary between the thorax and the lorica is not so well defined as in the other pliciloricids. The cuticular ridges of the lorica are numerous, about 60, and can be separated into 30 primary and 30 secondary folds. The primary folds continue the entire length of the lorica, including the anal cone. The lorica has a single constriction near the middle of the lorica. Light microscopy reveals that the anal cone has 2–4 small pores. When viewed from a posterior aspect (Figure 80), the anal cone has a longitudinal and two transverse lines, which define six plates. In a paratypic female, a system of three dorsal pores were apparent; these could constitute two gonopores and an anus. No flosculi, tubuli, or other sense organs were found on the lorica.

Internal structure that can be seen in the holotype includes two different clusters of spermatids in the dorsal testes, indicating that the holotype is a young male, but all internal tissue has suffered from the osmotic effects of the fresh-water processing. The buccal canal is very thin and short. The pharynx bulb is large, lacks placoids, and is totally filled with glandular tissue. The muscular system (Figure 59) seems to be very similar to that of *Pliciloricus*, with eight small retractor muscles in the mouth cone itself and two very large retractor muscles in the head. These muscles are cross-striated, similar to those in the Kinorhyncha. A large diaphragm can be seen between the thorax and the abdomen. Two dorsolateral muscle sacs, found also in *Pliciloricus*, are present; all other muscles consist of single muscle fibers.

We cannot be certain that the Higgins-larva of this species was found. One (RH 1839.79) (Figure 77) is either a very large Higgins-larva or a postlarva, molting to an adult male. Its exuvium is 275 μm long, and the anterior part of the exuvium was clearly visible because the adult inside was retracted. The external characters of the exuvium included structures not observed in any other Pliciloricidae; however, some of these resembled structures found in the postlarva of *Nanaloricus* (Kristensen, 1983). New character states included the lack of the toes and lorical setae. In addition, the old larval mouth opening is closed by a rosette-like cuticular structure and the larval armature of the buccal canal is missing; normally, this armature can be seen lying inside the exuvium, as has been discussed in the descriptions of *P. enigmaticus* and *R. ornatus*. The head has seven rows of appendages in addition to two rows of basal plates, which we have interpreted as appendages of the neck; possible they are basal plates of the trichoscalids or a kind of "prototrichoscalid."

The first row of head appendages does not conform to the normal eight clavoscalid pattern; instead the first row consists of 15 claw-tipped spines (~30 μm long), alternating with nine slightly bulbous papillae. The second through sixth rows of the scalids are reduced or not well-defined. The third and fourth rows appear as a zig-zag line. The seventh row has eight beak-like scalids alternating with seven small papillae.

A clear view of the thorax region of the larval or postlarval exuvium is not possible, because of the underlying adult trichoscalids. These appendages have penetrated into the larval or postlarval cuticle. The lorica is totally free of any sculpture or appendages.

REMARKS.—The adult inside the exuvium has the same diagnostic characters as the holotype of *R. cauliculus*. However, the testes are better developed in the molting animal than in the holotypic adult. An alternate interpretation of this specimen is to consider it a postlarval stage molting to an adult, or it could be a kind of resting or cyst-like stage wherein the gonadal development occurs in the life cycles for *R. cauliculus*.

This specimen of *R. cauliculus* is a puzzle, because *R. carolinensis* appears to have direct metamorphosis from larva to adult, as *Pliciloricus enigmaticus*. Furthermore, the third species, *R. ornatus*, although having a larva (or postlarva) similar to *R. cauliculus*, has more normal loriciferan characters.

Rugiloricus ornatus, new species

FIGURES 61, 62, 84–86

DIAGNOSIS.—Adults 115–180 μm long; mouth cone small (~25 μm long) with single ventral setae. With 8 uniform clavoscalids; double-organ small, with double-claw tip on each element; fourth row of appendages consisting of 15 long spinoscalids alternating with 15 short double-claw tipped spinoscalids, fifteen single serrated trichoscalids present on neck. Lorica consisting of three sections: an anterior part with thick cuticle and about 20 plicae (double folds or ridges), a thinly cuticularized middle part set off by a zig-zag line formed by junction with a different plical pattern, and a posterior part with a very thick cuticle and about 20 longitudinal single folds or ridges; posterior part of lorica with single pair P-flosculi and large anal field with several pores.

Higgins-larvae (postlarvae?) 170–232 μm long without lorical setae. Immature stages have 8–9 thin oral stylets, but lack scalids.

MATERIAL EXAMINED.—*Type Material:* The holotype is an adult female (174 μm long), with well-developed ovaries, from station RH 1834. The allotype is a young male leaving the old larval exuvium, also from station RH 1834. Paratypes include 1 adult female, 2 larvae (or postlarvae) molting to an adult; a larva (or postlarva) in early metamorphosis, from station RH 1834; and a single larva (or postlarva) molting to an adult female from station RH 1833.

The holotype (USNM 98569), the allotype (USNM 98570), and one paratype (USNM 98571) have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. The other four paratypes have been deposited in the Zoological Museum, Copenhagen. A total of 7 specimens were examined.

ETYMOLOGY.—From the Latin *ornatus* (ornate); masculine gender.

DESCRIPTION.—The holotypic female (Figure 84) is 174 μm long. The oral cone, 25 μm long, is slightly retracted in the head and has not been included in the total length measurement. The mouth cone has three sections. The first section (nearest the head) has the eight retractor muscles and unites with the head by a narrow stalk. The stalk has three concentric rings and is attached to the head via the ring structure from the ruff. The second section is the broadest part of the mouth cone. It has eight double ridges, each mounted to the apodeme from the first section. The eight double ridges are continuous with the third section, which can be slightly withdrawn telescopically into the second section of the mouth cone; the eight ridges terminate about 10 μm from the mouth opening. The third section has a ventral oral setae, not found in any other adult Loriciferan, only in Higgins-larvae of *Pliciloricus*.

The ruff at the base of the mouth cone consists of 15 very thin cuticular lines and not a complex of cuticular fibers as in the *Pliciloricus*. The head has nine rows of appendages. The first row consists of eight uniform, relatively short (~70 μm) clavoscalids; all are broadly flattened with indistinct apiculate distal ends. Each of the clavoscalids has a supporting axis extending only 20 μm from the clavoscalid base. Two cross-walls, formed by fine cuticular punctations, are present. The distal cross-wall (~15 μm from the tip) is always present; the proximal cross-wall is lacking in the two ventral scalids and in all eight scalids of the male.

The second row of head appendages consists of nine large leg-like spinoscalids. The three dorsalmost scalids (Figure 84) are long (~100 μm) and spine-shaped. The dorsolateral pair (~90 μm long) have a broad proximal segment with a large spine (~10 μm long) and a filiform distal segment. The ventrolateral pair are spine-shaped (70 μm long), and the proximal segment has a short spine (~5 μm long). The midventrally

situated double-organ consists of two short (55 μm long) spinoscalids partly fused near their bases; each component is undivided and has a very short spine about 20 μm from the base and a double-clawed tip. The third row of scalids consists of 15 smaller distinctive spinoscalids each with a slightly enlarged double base and a swollen joint about 10 μm from the base. The fourth row of scalids has 15 long spinoscalids (~70 μm) each consisting of a proximal serrated segment and a filiform distal segment. These 15 scalids alternate with 15 short (~40 μm) double-claw tipped scalids, also consisting of two segments. The fifth to seventh rows are uniformly unsegmented spinoscalids, each row consists of 30 elements (~70 μm long). The eighth row of head appendages consists of 30 serrated spinoscalids (80 μm) with very small basal plates. The ninth row consists of 30 beak-like scalids (~15 μm long).

The head is separated from the neck by the slight constriction. The neck appendages consist of 15 single trichoscalids (~55 μm long). Seven of the trichoscalids have three basal plates and eight have two basal plates arranged in the same pattern described in *R. cauliculus*. The lower basal plates of the seven trichoscalids are very small, the middle basal plates have a long spine (15 μm), and the upper basal plates are indistinct. The lower basal plate is very large in the 8 trichoscalids where the middle basal plate is lacking, and the upper basal plates have a spine (10 μm). The trichoscalids are about 55 μm long and appear serrated.

The neck is well separated from the thorax, which consists of three parts, the anterior part is sculptured and has 30 double ridges, the middle part consists of a thin, unsculptured cuticle without ridges, and the posterior part is sculptured, but has fewer (~20) double ridges. The posterior part of the thorax is not well separated from the lorica; the double ridges continue on the lorica, but the ridges are slightly displaced.

The lorica has a very geometric ornamentation, a distinctive shape, and it consists of three regions. The anterior region has a thick cuticle, with the 20 double ridges similar to those found in *Pliciloricus*. The middle part has a thin cuticle, with five transverse lines. The middle part is built in an accordion-like system with a zig-zag sculpture near the anterior margin. The posterior region has about 20 longitudinal single folds with a single pair of P-flosculi on the ventral surface. The posteriormost area of the lorica consists of an anal field, a large plate surrounded by 12 smaller plates, four of them with pores. The two ventral pores are presumed to be gonopores; the other two, more laterally positioned, could be the nephridiopores. An anal opening could not be seen.

The Higgins-larva of *Rugiloricus ornatus* may not have been found. The immature stage associated with the adult of this species was possibly a postlarva. This immature stage has no toes or lorical setae. The following description is based on the specimen RH 1834.19 (Figure 86). The specimen consists of a larval exuvium with a metamorphosed young male inside.

Eight or nine thin oral stylets surround the larval mouth opening. No scalids are present. The internal mouth armature and the collar are of the *Pliciloricus*-type. The internal mouth armature remains inside the larval exuvium as seen in *P. enigmaticus* (RH 1834.20) and its structure is very similar to that of the latter species. The thorax of the exuvium has at least six rows of plates, but they are difficult to see. The lorica appears to be divided into rows of five plates as in *P. enigmaticus*. The metamorphosed adult inside the exuvium is surrounded by a thin membrane. This membrane was broken in the allotypic male (Figure 85) as it was emerging from the exuvium. The adult shown in Figure 86 already has well-developed testes with spiral-headed sperm, gut, and two large circular muscle bands in the abdomen. The scalids are characteristically oriented forward and the mouth cone is retracted inside the head. The adult inside the larval exuvium is smaller than the larva that produced it. When the adult emerges from the exuvium (Figure 85) the mouth cone will be extruded, most of the scalids will be directed posteriorly, and the length of the newly molted adult will increase.

REMARKS.—The systematic position of *R. or-*

natus is very difficult to determine. We have decided to place the species close to *R. cauliculus*, because the larval or postlarval stage lacks both the toes and setae of the normal Higgins-larva. The presence of 15 single trichoscalids clearly places it in the genus *Rugiloricus*, but *R. ornatus* has many more characters than we can account for, e.g., the larval internal armature, larval collar, and the lorica with P-flosculi. Only when the immature life history stages of both *R. cauliculus* and *R. ornatus* are found will a re-evaluation of the genus *Rugiloricus* be possible.

Morphology and Terminology in the Loricifera

Although some refinement and redefinition has been necessary, we have continued the terminology used in the original publication on the phylum Loricifera (Kristensen, 1983). The basis for the use of some of the terms was and still is the hypothesis that this new phylum has its closest affinities with the phylum Kinorhyncha, phylum Priapulida, and, to a much lesser extent, phylum Rotifera. With a quantum increase in the number of component taxa within the phylum, e.g., eight new species comprising two new genera and a new family, the major morphological features should be reviewed and current terminology clarified.

The body of Loricifera, both in larvae and adults, consists of the following regions: (1) a mouth cone; (2) a head (introvert); (3) an intermediate area, neck or collar, between the head and the thorax; (4) a thorax; and (5) a loricated abdomen. The thorax and the abdomen together constitute the trunk region. Some terms used for more specific lorificeran characters also have been applied to the Priapulida and/or the Kinorhyncha. For example, certain scalid terms were taken from *Monographie der Echinodera* (Zelinka, 1928). However, although these terms are based currently on superficial similarities of structure, position, and function among the phyla in question, they are not intended to convey evidence of homology. In particular, studies of the ultrastructure of the scalids and other morphological features of all three phyla will be of paramount importance in the determination of homologies.

MOUTH CONE.—The adults have a more or less pronounced tripartite mouth cone. The first section (closest to the head or introvert) has eight retractor muscles, each attaching to a cuticular apodeme at the distal limits of this section. The next two sections of the mouth cone vary from species to species; however, the main difference between Nanaloricidae and Pliciloricidae is that *Nanaloricus* has eight stylet-like structures, each with a free tip, whereas *Pliciloricus* has only 8–12 ridges and *Rugiloricus* has 6–8 ridges. In *Rugiloricus cauliculus*, six of the ridges are continuous with six small stylets.

The terminal mouth opening of *Nanaloricus* is at the end of a telescopic mouth tube. The mouth tube contains the buccal canal and is hexaradially symmetrical with a series of buccal teeth inside. Within the Pliciloricidae, in *P. gracilis* and *P. dubius*, the mouth tube does not appear to be telescopically retractable. The mouth tube cannot be seen in *P. enigmaticus*, *P. profundus*, *R. cauliculus*, or *R. ornatus*, but may be present in *R. carolinensis*. The buccal canal in all Pliciloricidae is so thin that it is difficult to see even with interference contrast optics.

The Higgins-larva of *Nanaloricus mysticus* has an unarmed mouth cone. All larvae of the Pliciloricidae have oral stylets and/or oral teeth surrounding the mouth opening. The armature of the mouth cone continues inside the larva as a structure that superficially looks as the mastax of the Rotifera. Both the external armature and internal armature are hexaradially symmetrical. In some species of *Pliciloricus*, the larva has a small ventral setae on the mouth cone; a similar seta occurs on the adult mouth cone of *Rugiloricus ornatus*.

HEAD (Introvert).—The mouth cone of *Nanaloricus mysticus* is slightly separated from the introvert by a naked, unarmed area. This area is transformed to a ruff, a series of wrinkles surrounding the base of the mouth cone in the genus *Pliciloricus*. In the genus *Rugiloricus* the cuticular fibers of the ruff are not so prominent. The

number of fibers varied from 14 to 30 in the different species of the *Pliciloricus*.

The head has nine rows of appendages in all adult Loricifera and seven, sometimes eight rows in the larvae. In the Kinorhyncha, up to seven rows (including a final row of trichoscalids) are present at least in the adult; fewer rows, usually no less than four, exist in the juvenile stages. The first row of appendages were given the new term clavoscalids by Kristensen (1983) because of the club-like distal end. In both Kinorhyncha and Lorificera, the first row of scalids are morphologically distinct from the remaining rows. In all known Loricifera (including five undescribed species) there are eight flat to club-shaped clavoscalids. The only significant divergence of this basic plan occurs in the male of *Nanaloricus mysticus,* where six of the eight clavoscalids are secondarily branched. In the Kinorhyncha, the first row of 10 scalids also can be club-shaped (blunt-tipped) as in the Loricifera. And, as in the Loricifera, especially *Pliciloricus,* these scalids can appear partitioned; examples include *Semnoderes pacificus* (Higgins, 1967, fig 11) and *Paracentrophyes praedictus* (Higgins, 1983, figs. 79, 102).

In *Pliciloricus* there are some indications that the clavoscalids are adhesive. One specimen of *P. enigmaticus* was still sticking to the sand grains after processing. In the Kinorhyncha, the first row of scalids of *Cateria styx* may be retractable and the blunted, swollen tips of some of these may be adhesive (Gerlach, 1956, fig. 9). The first row of 10 scalids in the Kinorhyncha as well as the subsequent rows have a single, very well-formed joint where the basal segment articulates with the distal segment. Although Zelinka (1928) used the term spinoscalids for all but the most posterior row of kinorhynch head appendages because of the spines associated with the basal segment of the scalid, Kristensen (1983) used the term for the second through ninth rows of loriciferan scalids because they were spine-shaped. The ultrastructure of both kinorhynch and at least *Nanaloricus* spinoscalids is similar. Both consist of a sensory ciliary structure with one to few enveloping cells.

The first two rows of spinoscalids in *Pliciloricus* are almost leg-like organs consisting of up to 10–12 cells. A good autapomorphic character for the family Pliciloricidae is that the two spinoscalids at the midventral line of the second row are modified, and variously fused. In *Rugiloricus* these spinoscalids may function independently and appear nearly the same as the other seven spinoscalids of that row. Based on the status of this double-organ, we postulate the following evolutionary sequence: *P. gracilis—P. profundus—P. dubius—P. enigmaticus.* In both *P. gracilis* and *P. profundus,* the two spinoscalids still have a sensory function and are separated as in *Rugiloricus.* In *P. dubius,* the two spinoscalids are fused to work as a double-organ. The elements of the double-organ are even more fused in *P. enigmaticus;* in this case, they are separated only at their bases and at or near the distal ends. Also, these are the most cuticularized elements of the loriciferan. There is some evidence that the double-organ may function some way in the support of the mouth cone; it may also function in molting. In at least five molting specimens, the double-organ had penetrated the old larval exuvium.

The fourth row of head appendages consists of two types, a normal, usually elongate spinoscalid alternating with a shorter, claw-tipped spinoscalid. This autapomorphic character for the family Pliciloricidae is very useful for the separation of the different species in the family. There are always a fixed number of 30 scalids from the fifth to ninth rows of spinoscalids. The eighth row has a basal plate and a long spinous element; the ninth row always consists of 30 robust, beak-like scalids.

The scalids of the loriciferan larvae are very difficult to compare with the scalids of the adults. We call attention to the fact that the spinoscalids of the fifth and seventh rows are short, triangular projections ("protoscalids") in all *Pliciloricus*-larvae. Similar protoscalids are found in at least two genera of Kinorhyncha (*Pycnophyes* and *Kinorhynchus*); furthermore, the scalids of both the larva and adult of the priapulid *Tubiluchus corallicola* are equally simple, unmodified, not too unlike

the protoscalids of the kinorhynchs and loriciferans. The larval spinoscalids of *R. carolinensis* are extremely modified compared with other Higgins-larvae. Scalids vary from very thin plates to hooks with many fine hairs.

NECK AND THORAX.—In the adults of Pliciloricidae there is an intermediate area or neck between the introvert and the thorax. Although this area is naked in *Nanaloricus,* in *Pliciloricus* there are two rows of small plates associated with the trichoscalids and the basal plates. These two rows of plates can be interpreted as accessory trichoscalid basal plates that have equivalent structures in the Kinorhyncha or they could be two separate rows of plate-shaped scalids. The structures are not always well developed. In the same way, the larvae of Pliciloricidae have an intermediate area between the introvert and the thorax. In all known species of *Pliciloricus,* the area is modified to a closing apparatus, called the collar. The closing apparatus in the larvae of *Nanaloricus* consists of two prominent thoracic plates. The larval closing apparatus in pliciloricid larvae is "not" homologous with the closing apparatus in nanaloricid larvae.

The use of the term trichoscalid is perhaps questionable, because it infers that it is a "hairy" scalid as in the Kinorhyncha (Zelinka, 1928). Zelinka applied the term to the last row of kinorhynch scalids, which were, like those in the loriciferans, highly modified. Similarities may be viewed as homologous if they have similarities in positional hierarchy; however, the problem is that we are not sure that the region where kinorhynch trichoscalids are found is the same region in the Loricifera. Although Kristensen (1983) first assumed that the trichoscalids of *Nanaloricus* were situated on the first part of the thorax, we have now come to the conclusion that they are situated on an intermediate area between the introvert and the thorax. In the Pliciloricidae it is difficult to determine what part of the body bears the trichoscalids, because there is no gap between the last row of spinoscalids and the accessory basal plates of trichoscalids; only the number of elements in each row differ. Furthermore, if we compare the loriciferan larva with the adult, it seems that the thorax of the larva is only homologous with the region posterior to the trichoscalids. Adults of *Nanaloricus* have this part of the body more or less retracted in the lorica, and it is always unsculptured. The situation is quite different in Pliciloricidae. The region after the trichoscalids may have thin plates in 1–3 rows, formed in a manner of the accordion system found in the thorax of the larva. The region where the trichoscalids are located could be homologous with the neck region of Kinorhyncha and the collar region of the larva of the Loricifera. The thorax of Loricifera, therefore, would be homologous with the first part of the trunk of the Kinorhyncha and not with the neck. Indeed, the first trunk segment of the Kinorhyncha generally differs from the successive trunk segments. The intermediate area between the head and the thorax in the Loricifera could be homologous with the neck in the Kinorhyncha. The rationale for this interpretation of the different regions of the body in the Loricifera relates to the special pattern in which the trichoscalids and their basal plates are formed in both Kinorhyncha and Loricifera. In at least *Rugiloricus cauliculus,* the upper basal plate (tp_3), middle basal plate (tp_2) and lower basal plate (tp_1) are arranged as in Kinorhyncha (Zelinka, 1928; pl. 10: figs. 8, 20). However, the kinorhynch tricholscalid originates from the middle of the three plates (= tp_2) rather than the lower plate (= tp_1).

The hypothesis that the region following the trichoscalids, the thorax, and the loricated abdomen are homologous with the trunk of the Kinorhyncha is also supported by the fact that the accordion-like structure on the thoracic region in both larvae and adults of *P. enigmaticus* continues on the lorica. The anterior part of the adult lorica has 6–7 transverse ridges, which are absent in the posterior half of the loricated abdomen; the posterior part lacks these ridges. The larva has six of these transverse ridges, resulting in the whole lorica being split up into small plates as in the thorax. The trunk of the larva consists of exactly five thoracic "segments" and six lorical

segments, giving total numbers of 11 segments, the same numbers as the trunk segments in the Kinorhyncha. Nonetheless, the empty larval exuvium of *P. enigmaticus* bears only some minor resemblance to the exuvium of cyclorhagid kinorhynchs, especially the genus *Echinoderes*. In the Kinorhyncha, however, there is a segment preceding the trunk, the neck, which has a series of plates. It is this segment that provides the closing apparatus for the withdrawn head.

Even greater resemblances are obvious when the body regions of the pliciloricid larvae are compared with the larval stage of *Tubiluchus corallicola* (van der Land, 1970, figs. 75, 76). The larva of this species of meiobenthic Priapulida has a pharynx that appears to be homologous with the loriciferan mouth cone; a head with five rows of scalids, which look like the protoscalids of both kinorhynchs and loriciferans; a neck whose seven rings of cuticle are interupted with longitudinal folds or ridges; and a loricated abdomen, longitudinally folded or ridged in the same manner as the neck region. The anteriormost ring bears flosculi and thus bears a remarkable resemblance to the Higgins-larva of *Pliciloricus gracilis*.

LORICATED ABDOMEN.—The folds in the lorica of Pliciloricidae has given the family its name. Its lorica is quite different from that of the Nanaloricidae in that it consists not of six heavy cuticularized plates as in *Nanaloricus*, but of many longitudinally folds, both in the adults and larvae. In *Rugiloricus*, the adults may have up to 40 irregular folds, but in *Pliciloricus* the lorica consists of 22 elements called plicae. A plica consists of the area from one primary double ridge of the lorica to the next primary double ridge. The middle of each plica is usually elevated to form the secondary double ridge of the lorica (Figure 19). The midventral plica is twice as wide as the others in *P. enigmaticus, P. dubius,* and *P. gracilis*. In *P. dubius* the midventral plica is heavily cuticularized and plate-like, more like *Nanaloricus*. In *P. enigmaticus,* a rosette structure is located caudally on the midventral plica. The function of the rosette structure is not clear, but it could be part of the anal and/or nephridiopore systems. If a cloaca is present, we remain faced with the question of the function of the dorsal opening on the terminal end of the lorica in *Nanaloricus,* where the anus is placed dorsally in both the larvae and the adults.

The sense organs on the adult lorica are called flosculi as in Priapulida (van der Land, 1970). The *Nanaloricus*-flosculus (N-flosculus) superficially looks like the flosculi in *Tubiluchus*. Transmission electron microscopic investigation of the N-flosculus has shown that it is a collar-receptor, characterized by a cilium with a collar of modified microvilli. The same type of receptor is also found in the sensory spot of Kinorhyncha (Higgins, 1983, fig. 253), but the collar-receptor is found also in other phyla such as the Rotifera, Nematoda, and Arthropoda. In the Pliciloricidae, only *P. dubius* and perhaps *P. gracilis* have N-flosculi (the type found in *Nanaloricus* and which closely resembles the flosculi of *Tubiluchus*) together with a quite different sense organ called *Pliciloricus*-flosculus (P-flosculus). The P-flosculus is best developed in *P. enigmaticus,* which has two pairs on the lateroventral side of the lorica (Figures 20, 21). The P-flosculus consists of a small round papilla with a very thin cuticle. Using phase contrast optics, one sees a large pore in the middle of the P-flosculus, but no such structure is apparent by SEM examination. P-flosculi are present in all Pliciloricidae, except for *R. cauliculus,* which has a very thin and delicate cuticle. Recently the same kind of sense organs were described in *Macrotrachela quadricornifera* (Rotifera, Bdelloidea) by an SEM-study (Ricci and Melone, 1984), but it is also found in other Rotifera. Although the Higgins-larva of *Nanaloricus mysticus* has N-flosculi, they are absent in the larvae of the Pliciloricidae. The sense organs of larval lorica are located at the anterior and posterior margin.

In *Nanaloricus mysticus* there are three pairs of ventral spines between the thorax and the abdomen. The ventral spines were postulated to have a sensory as well as a locomotory function. In Pliciloricidae there are two pairs of setae in the same area of the body. One pair is placed ventrally, the other laterally. All four are very thin

and probably have only a sensory function. The Higgins-larva of *N. mysticus* has two pairs of dorsal sensory setae at the caudal part of the abdomen. In *Pliciloricus* larvae there are three pairs of sensory setae in this same area. The dorsal (se_1) and lateral (se_2) pairs of setae articulate with a basal element as in the setae of *Nanaloricus*. The posterior pair of setae (se_3) are stiff and lack the basal element.

The most prominent structures seen on the Higgins-larva are the two caudal appendages or toes. The toes of the *Nanaloricus* larva have a series of leaf-like structures (mucros), which change direction in unison and function in swimming. The toes of Pliciloricidae differ significantly in that they appear to be adhesive toes only. A pair of very large toe glands are located ventrally in the caudal part of the abdomen, suggesting that the larva adheres to the substrate with a duo-gland system. The toes in *Pliciloricus* larvae are straight, with a terminal solid spine. The gland opening is found at the base of the spine. In *P. gracilis*, the larva has very small mucros on the lateral margins of the toes similar to those found in the larva of *Nanaloricus*. The larva of *P. enigmaticus* has spine-like toes, which superficially look like the lateral terminal spine of some homolorhagid kinorhynchs. They appear to articulate with the abdomen in such a way as to move only in a lateral motion. In the other *Pliciloricus* larvae, the toes are pointed forward or in a few cases backwards. The more ventrally positioned toes of *Rugiloricus carolinensis* are only seen pointing forward and there appears to be no basal articulation. No toes (or lorical setae) are found in *R. cauliculus* or *R. ornatus;* however, the exuvium upon which this information is based may have belonged to a postlarva, as found in *Nanaloricus mysticus,* and not the larva.

Biology of the Pliciloricidae

The 368 pliciloricid loriciferans studied in this investigation were found in three separate medium to coarse sand habitats on the continental shelf at the western limits of the influence of the Gulf Stream (Map 1). The substrate at the most northern site (RH 1695, RH 1833, RH 1834) consisted of coarse quartz sand at a depth of 400–437 m. This site appears to have had the greatest diversity of the three sites, because seven of the eight species were found there. However, the impreciseness of the collecting method, e.g., the use of an anchor dredge, which may indiscriminately collect sediment over as much as a kilometer before it has filled, makes diversity statements suspect at best. Of the two samples taken concurrently, RH 1833 and RH 1834, the former had five species *P. enigmaticus* (5 specimens), *P. gracilis* (1 specimen), *P. profundus* (9 specimens), *R. carolinensis* (1 specimen), and *R. ornatus* (1 specimen). The latter sample contained *P. enigmaticus* (26 specimens), *P. gracilis* (4 specimens), *R. profundus* (40 specimens), *R. carolinensis* (29 specimens), and *P. ornatus* (6 specimens) in addition to *P. orphanus* (1 specimen) and *R. cauliculus* (1 specimen), two of the four species represented by less than seven specimens. Seventeen specimens were found in RH 1833, whereas 107 specimens were found in RH 1834. Although the volume of sand was the same, there was a considerable difference in the number of loriciferans in the two samples, which could account for the lower diversity in RH 1833.

Two other sites farther south (Map 1) were sampled. Although these sites were about 20 km apart and nearly at the same depth (289–294 m), the 294 m station (RH 1837) was composed of a coarse oolytic sand and the 89 m station was composed of a black phosphorite sand. The loriciferan population in the former station (oolytic sand) had representatives of six of the eight species described; these included *P. enigmaticus* (2 specimens), *P. gracilis* (25 specimens), *P. profundus* (25 specimens), *R. carolinensis* (4 specimens), and *R. cauliculus* (2 specimens), also found at the first site, and *P. dubius* (2 specimens), one of the four rare species and one found only at this site. The total number of specimens from the coarse oolytic sand habitat was only 27.

Perhaps the most interesting site sampled was that having a substrate composed of black phosphorite sand (RH 1839). This single sample con-

tained 216 loriciferans of which 207 were a single species, *R. carolinensis*. The three other species, not well represented, included *P. gracilis* (5 specimens), *P. orphanus* (1 specimen), and *R. cauliculus* (3 specimens).

We know very little about the life cycle of the Loricifera, but our cumulative data suggest that the species of the Pliciloricidae may exhibit a strong seasonal variation. For example, no larvae of *P. enigmaticus* were found. Out of the 33 specimens collected from 16 to 19 November 1983, 19 of them were molting from larva to adult. Only eight mature animals were found, but the presence of six adult exuvia seems to indicate that ecdysis may take place in this stage of the life history. We suspect that at least half of the animals in molt were ready to leave the old larval exuvium within the next few days. The other animals in molt appeared to be in early stages in the metamorphosis. If our assumptions are correct, only adults of *P. enigmaticus* might be found during the winter. In the case of *R. carolinensis* no free adults were found, only 240 larvae and one adult still in the larval exuvium. These larvae varied in size from 117–340 μm. The smallest animals probably were the first instar. They have also relatively smaller toes than the larger larvae. The length of the larvae appeared to fall into five different clusters, indicating that *R. carolinensis* could have five instars of larvae. These data, however, are not reliable, because the animals are not always equally extended.

Pliciloricus gracilis and *P. profundus* show the same pattern in their life cycle as *R. carolinensis*. Many larvae were found in November, but only a single adult of each species was found. No larvae of either *R. cauliculus* or *R. ornatus* were collected, only larvae or postlarvae in the process of molting to the adult, and few adults. We did not find the adult of *P. orphanus* and have only two adults and no larvae of *P. dubius*. The last two species were very rare in the samples.

Systematic Relationships in the Pliciloricidae

The evolutionary lines that we postulate for the family Pliciloricidae are shown in Figure 87. The numbers on the various branches of this simplified cladogram indicate the apomorphic characters for Pliciloricidae relevant to Nanaloricidae and another undescribed family of Loricifera.

With respect to the species in the family Pliciloricidae, however, this same number represents the greatest number of plesiomorphic characters in the same way "2" represents the autapomorphic characters for the genus *Pliciloricus* and "3" represents the autapomorphic characters for the genus *Rugiloricus*. Other numbers (4–16) relate to apomorphic characters within the genus for the different branches of the cladogram. The greatest number being the most apomorphic. The letter "a" following a number indicates an adult character and "b" a larval or postlarval character. The numbered character states are as follows:

1a. Mouth cone with 12–16 ridges, terminating with 3–6 oral stylets; ruff at the base of the mouth cone; 8 clavoscalids, at least the dorsal ones very broad and flattened; 8 rows of spinoscalids, first two rows leg-like, second row with two adjacent midventral spinoscalids; third row with claw-tipped spinoscalids alternating with long thin pointed spinoscalids; lorica with thin cuticle folded in many ridges (plicae); single pair of P-flosculi.

1b. Valvate oral field, with an umbrella-like supporting structure; 5 pairs of lorical setae, 2 anterior, 3 posterior; toes tubular to spine-like.

2a. Eight single and 7 double trichoscalids, all with single base; 22 plicae in the lorica.

2b. Larva with collar as a closing apparatus for the retracted head; single ventral seta on the mouth cone; toes terminally spinose.

3a. Fifteen single trichoscalids, 7 of them with an extra basal plate, with a hollow spine; lorica with more than 22 irregular folded plicae.

3b. Spinoscalids strongly modified, consisting of plates, hooks, etc.; larva without collar; lorica with irregular thin plicae; toes, if present, oriented ventrally.

4b. Larva with very long toes; lorica only slightly sculptured.

5b. Larva with medium-sized toes (shorter than lorica); lorica strongly sculptured.

6a. Clavoscalids segmented, the ventral ones spine-shaped; lorica thin, without clear secondary plical ridges.

6b. All appendages hairy; collar with 7 oval depressions (not pores); toes with a large gland opening near the base of the distal spinose region.

7a. (Adult not known.)

7b. Oral field with hairs; mouth cone seta lacking; anterior lorical setae branched.
8a. Two ventral spinsocalids largely fused to form a double-organ, which supports the extruded mouth cone.
9a. Two ventral spinoscalids long, only partially fused; mouth cone with a long tube; lorica with a single pair of P-flosculi, at least one pair of N-flosculi; lorica slightly sculptured.
9b. Larval mouth opening with 6 oral teeth and 6 oral stylets; toes with minute mucros.
10a. Lorica with 6–7 rows of transverse ridges, ventral rosette structure and 2 pairs of P-flosculi.
10b. Lorica with both transverse and longitudinal ridges; toes short and setae-like; valvate oral field.
11a. Lorica with a broad plate-like midventral plica; 1 pair of P-flosculi, 3 pairs of N-flosculi; mouth cone with a small tube; lorica strongly sculptured.
11b. (Larva not known.)
12a. Mouth cone with small tube; very short trichoscalids; flat anal plate with pores; 1 pair of small P-flosculi.
12b. Twelve double oral stylets; no mouth cone setae; single middorsal hook in the last row of spinoscalids; 4 pairs of lorical setae, lorica unsculptured.
13b. Larva (or postlarva?) without toes and lorical setae.
14a. Mouth cone with single ventral seta; lorica very thin with transverse zig-zag lines; one pair of P-flosculi; anal field surrounded by small plates.
14b. Larva (or postlarva?) with valvate oral field as in *Pliciloricus*, 6–9 very thin spines instead of spinoscalids.
15a. Lorica with more than 40 plicae; without flosculi; anal field on a small anal cone; mouth cone small with 4–6 stylets or papillae.
15b. Larva (or postlarva?) with 15 claw-tipped scalids around the mouth, other scalids modified to small plates in zig-zag pattern.

The genus *Rugiloricus* probably is a paraphyletic group; each of the three species may be related only through plesiomorphic characters. We have preferred not assigning these species to separate genera, especially because we have not found the larva of *R. cauliculus* or *R. ornatus*. We have only the larval or postlarval exuvium of animals in molt. These exuvia could be of a postlarva, as found in *Nanaloricus*. Both the larval exuvium of *R. cauliculus* and *R. ornatus* lack the toes and lorical setae, but these reductions could have happened independently in the two species. Furthermore, no real scalids were seen in the larval exuvium of *R. ornatus*, only 6–9 spines. The larval exuvium of *R. cauliculus* has very aberrant larval scalids, which cannot be compared with spinoscalids in any other larva of Loricifera.

It is noteworthy that the oral armature of the *R. ornatus* larva is structurally similar to the larva of both *P. enigmaticus* and *P. profundus*. This oral armature consists of three parts: (1) a valvate oral opening (with six valves), (2) a six-lobed umbrella-like structure supporting the valves, and (3) an armature within the buccal canal, which consists of a hexaradially symmetrical structure connected to the pharyngeal bulb by a structure with six furcae. In some respects, the oral armature is similar to that found in rotifers. The larvae of both *R. cauliculus* and *R. carolinensis* lack this very complex buccal structure.

Although the adults of *Rugiloricus* appear to have in common only plesiomorphic characters such as the 15 single trichoscalids and a thin lorica without a fixed pattern of 22 plicae as found in the genus of *Pliciloricus*, we have united these three species into one genus, *Rugiloricus*, only because we have no clear basis for separating them into two or three independent genera. The situation in the genus *Pliciloricus* is much different. Here the four known species are united into one genus by many autapomorphic larval and adult characters. Consequently, the genus *Pliciloricus* appears to be a monophyletic group, all of the species having a common larval form with a collar, five pairs of lorical setae, straight toes terminating as a spine, and an adult with a distinctive mouth cone and lorical plicae.

Literature Cited

Ax, P.

1956. Die Gnathostomulida, eine rätselhafte Wurmgruppe aus dem Meeressand. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse, Akademie der Wissenschaften und der Litteratur in Mainz,* 8:1–32, 48 figures.

Caullery, M.

1914. Sur les Siboglinidae, type nouveau d'invértebrés recueilli par l'expédition du Sibogo. *Comptes Rendus du Congrés des Societes Savantes de Paris et des Départments, Section des Sciences,* 158:2014–2017, 8 figures.

Coull, B.C., R.L. Ellison, J.W. Fleeger, R.P. Higgins, W.D. Hope, W.D. Hummon, R.M. Rieger, W.E. Sterrer, H. Thiel, and J.H. Tietjen

1977. Quantitative Estimates of the Meiofauna from the Deep Sea off North Carolina, U.S.A. *Marine Biology,* 39:233–240, 2 figures.

Gerlach, S.A.

1956. Über einen aberranten Vertreter der Kinorhynchen aus dem Küstengrundwasser. *Kieler Meeresforschungen,* 12(1):120–124, 3 plates.

Higgins, R.P.

1976. The Kinorhyncha of New-Caledonia. In *Expédition Française sur Récifs Coralliens de la Nouvelle Calédonia,* 2:75–90, 12 figures.

1983. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. *Smithsonian Contributions to the Marine Sciences,* 18:131 pages, 343 figures.

Hulings, N.C., and J.S. Gray, editors

1971. A Manual for the Study of Meiofauna. *Smithsonian Contributions to Zoology,* 78: xii + 84 pages, 13 figures.

Ivanov, A.V.

1963. *Pogonophora* (with Additional Material by E.C. Southward). xvi + 479 pages, 176 figures. London: Academic Press. [Translated from Russian by D.B. Carlisle.]

Johansson, K.E.

1973. Über *Lamellisabella zachsi* und ihre systematische Stellung. *Zoologischer Anzeiger,* 117:23–26, 4 figures.

Kristensen, R.M.

1983. Loricifera, a New Phylum with Aschelminthes Characters from the Meiobenthos. *Zeitschrift für Zoologische Systematik und Evolutionsforschung,* 21:163–180, 19 figures.

Kristensen, R.M., and R.P. Higgins

1984. Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with Descriptions of Two New Species from Disko Bay, West Greenland. *Smithsonian Contributions to Zoology,* 391: 40 pages, 51 figures.

Parker, S.P., editor

1982. *Synopsis and Classification of Living Organisms.* Volume 2. 1232 pages, 66 plates. New York: McGraw-Hill Book Company.

Por, F.D.

1973. Priapulida from Deep Bottoms near Cyprus. *Israel Journal of Zoology,* 21:525–528, 4 figures.

Ricci, C., and G. Melone

1984. *Macrotrachela quadricornifera* (Rotifera, Bdelloidea); a SEM Study on Active and Cryptobiotic Animals. *Zoological Scripta,* 13(3):195–200, 20 figures.

Riedl, R.

1969. Gnathostomulida from America: First Record of the New Phylum from North America. *Science,* 163:445–452, 12 figures.

Soetaert, K., C. Heip, and M. Vincx

1984. Meiofauna of a Deep-sea Transect off Corsica. *Annales de la Societe Royale Zoologique de Belgique,* 114:323–324. [Abstract of poster session.]

van der Land, J.

1968. A New Aschelminth, Probably Related to the Priapulida. *Zoologische Mededelingen* (Leiden), 42:237–250, 18 figures.

1970. Systematics, Zoogeography and Ecology of the Priapulida. *Zoologische Verhandelingen,* 12: v + 118 pages, 88 figures, 5 plates.

van der Land, J., and A. Nørrevang

1977. Structure and Relationships of *Lamellibrachia* (Annelida, Vestimentifera). *Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter,* 21(3):1–102, 127 figures.

Zelinka, C.

1928. *Monographie der Echinodera.* iv + 396 pages, 73 figures, 27 plates. Leipzig: Wilhelm Engelmann.

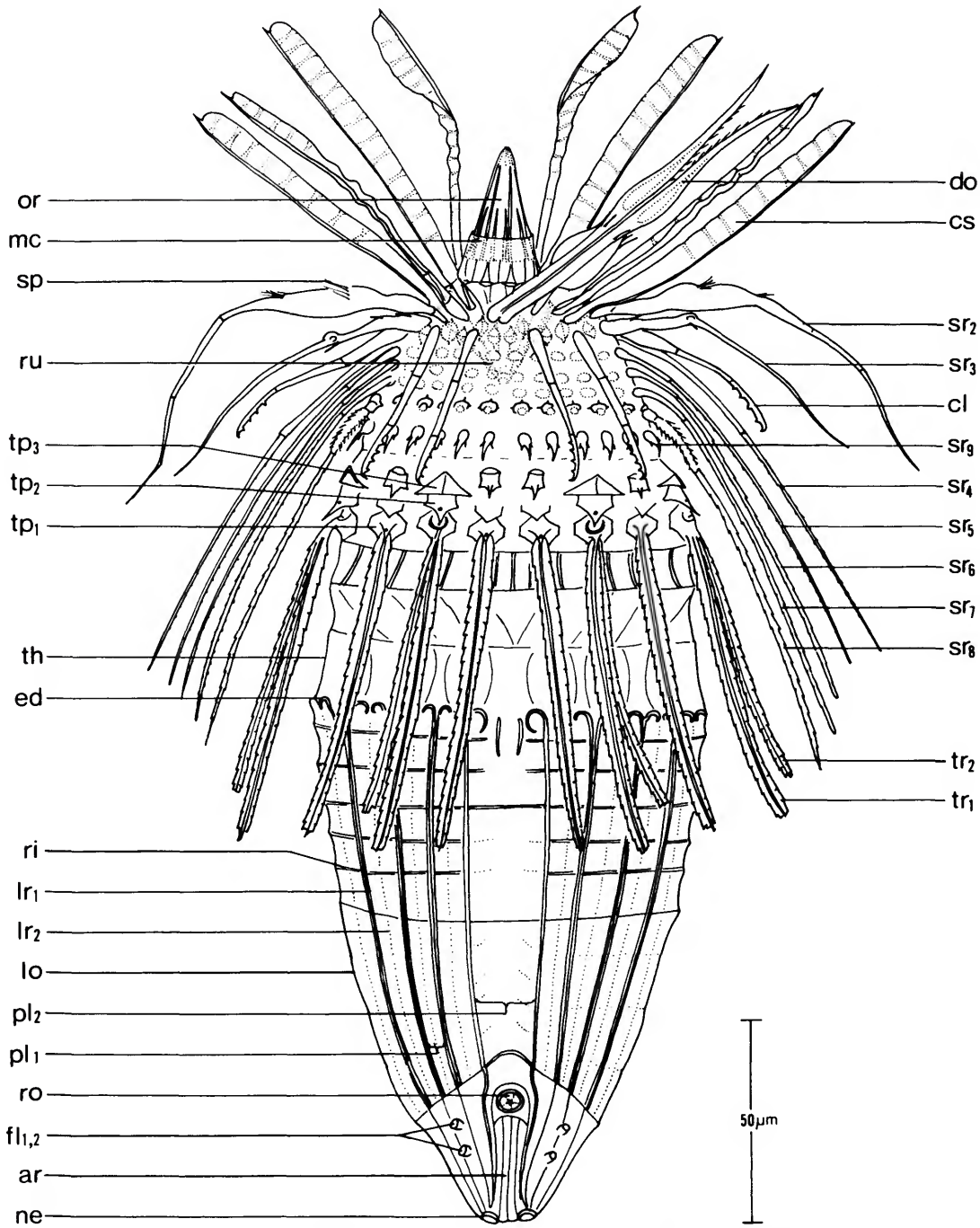


FIGURE 1.—*Pliciloricus enigmaticus*, new species, holotypic female, ventral view (scale in μm).

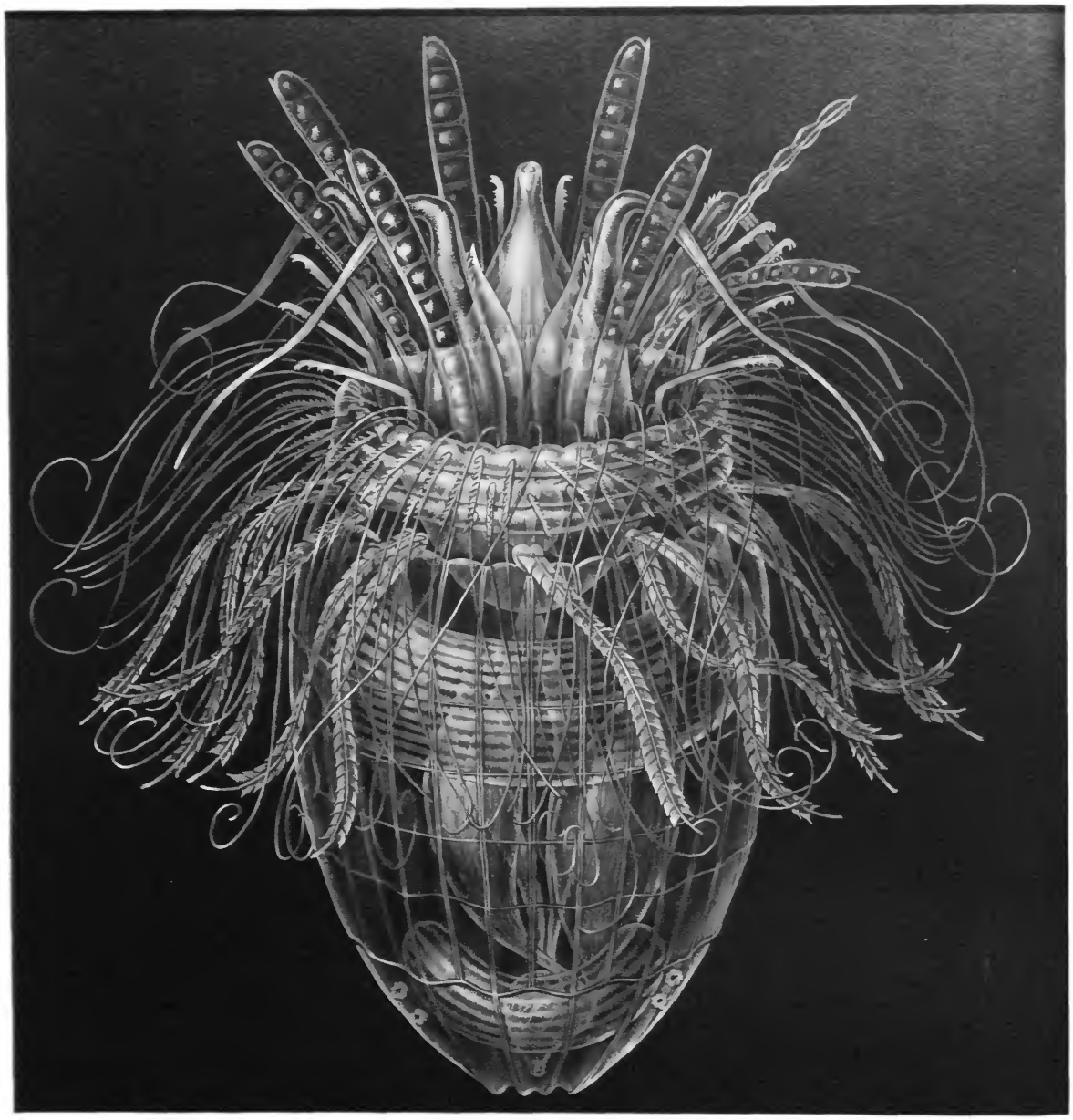


FIGURE 2.—*Pliciloricus enigmaticus,* new species, paratypic male (the first known loriciferan), RH 1695, retracted animal, dorsal view (see Figure 5 for scale).

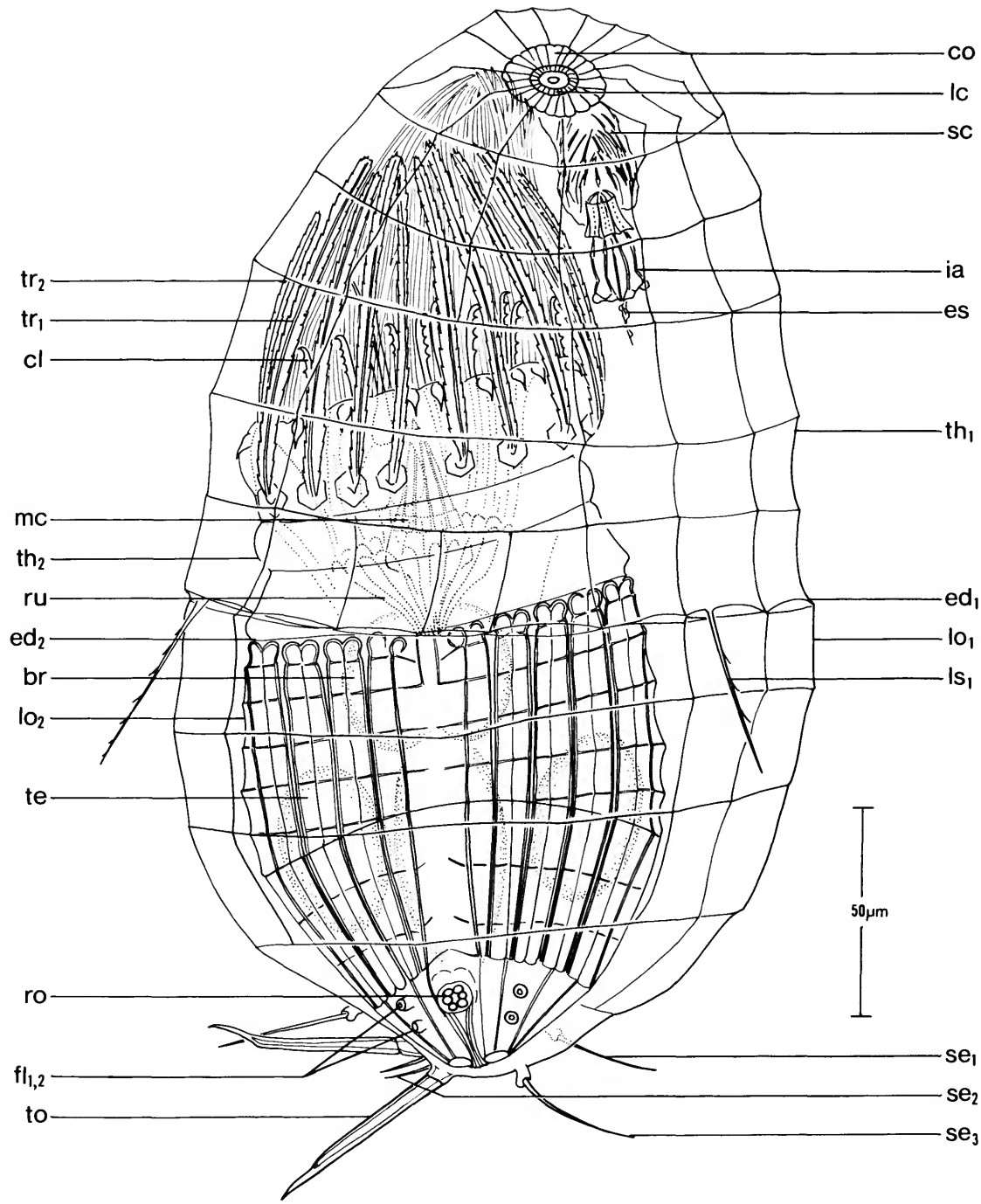


FIGURE 3.—*Plicilorícus enigmaticus*, new species, paratypic larva molting into an adult male, larval-exuvium in lateral view, adult in ventral view (scale in μm).

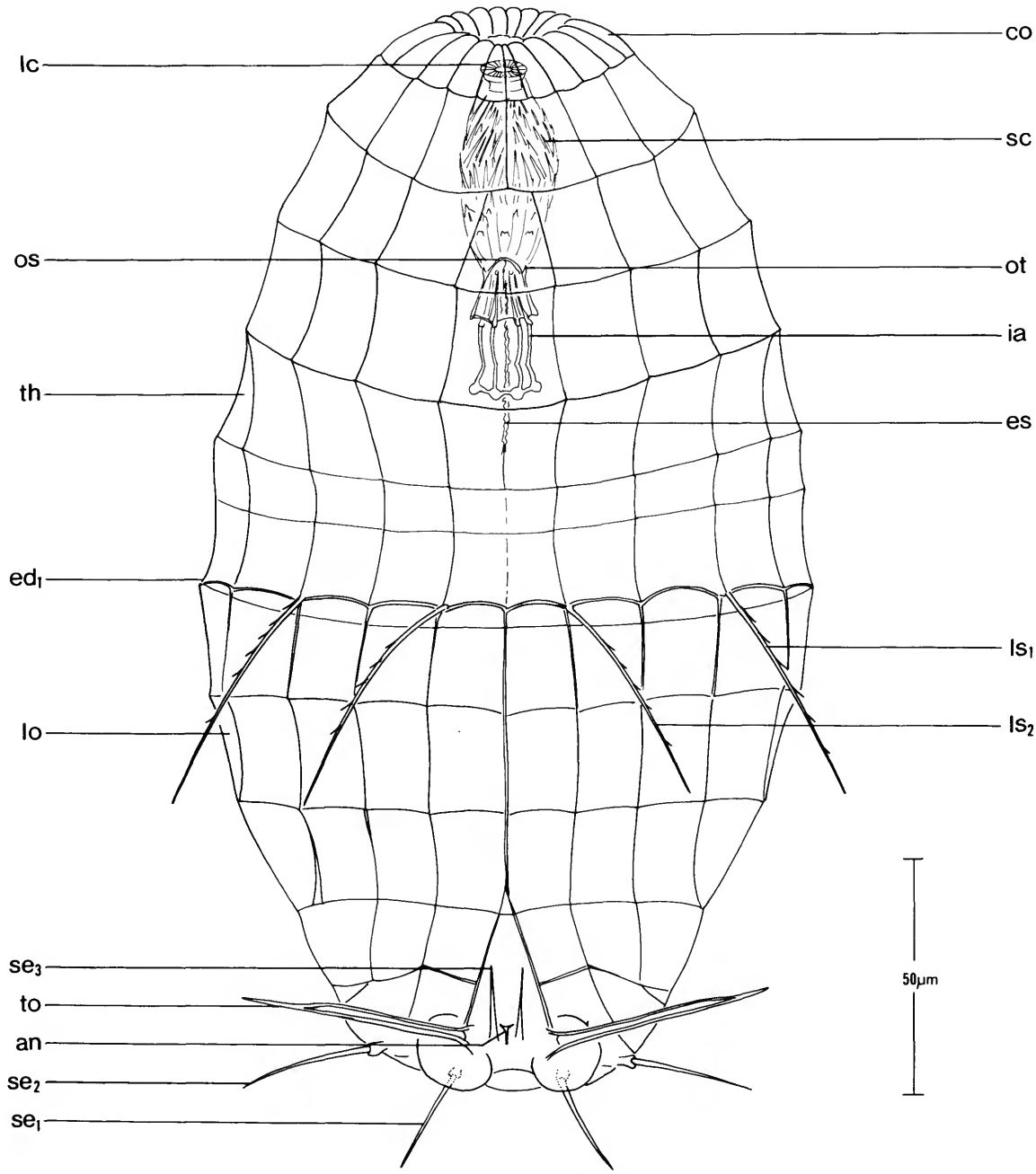
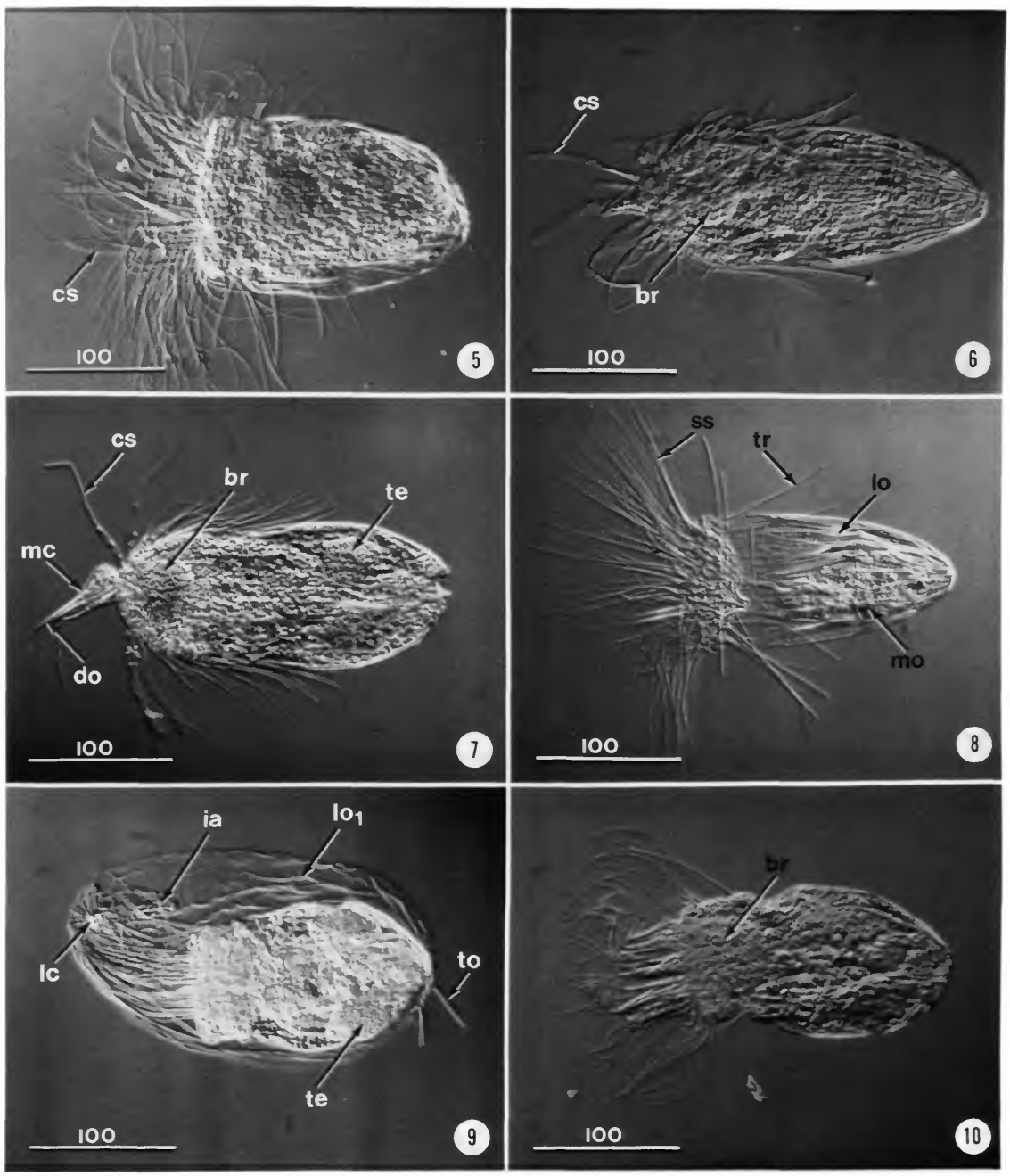
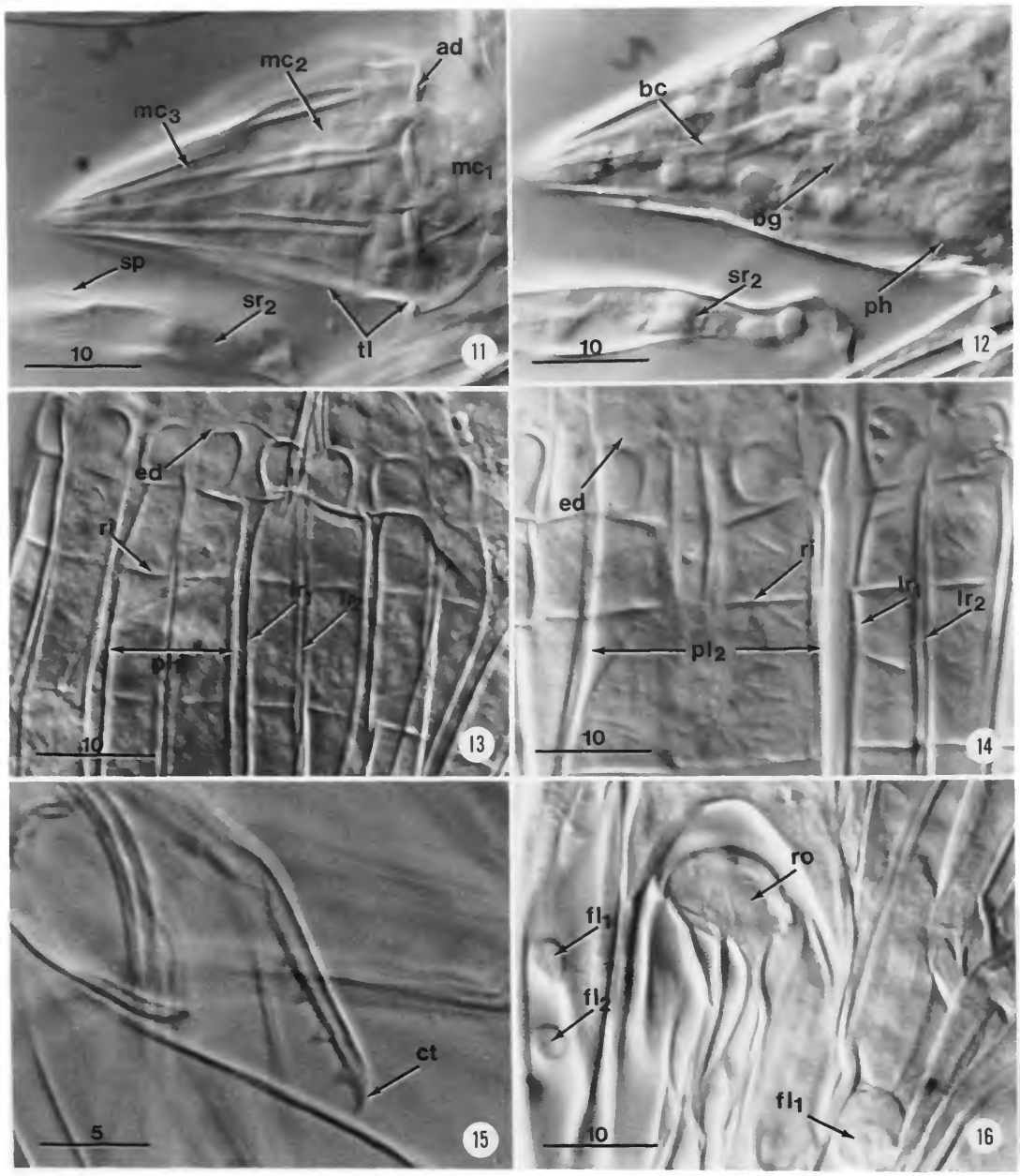


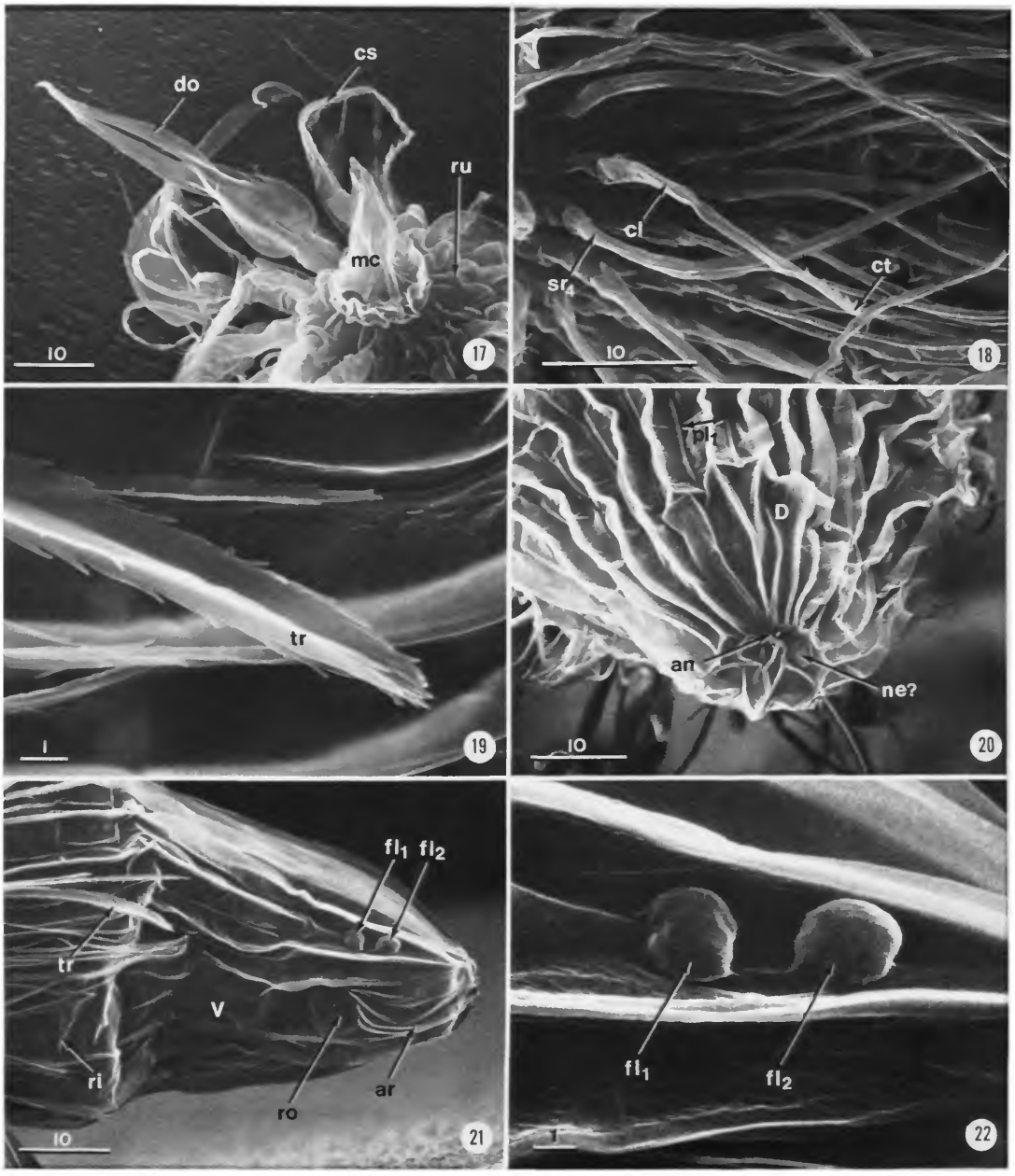
FIGURE 4.—*Pliciloricus enigmaticus*, new species, paratype, last larval exuvium after the adult has left, ventral view (scale in µm).



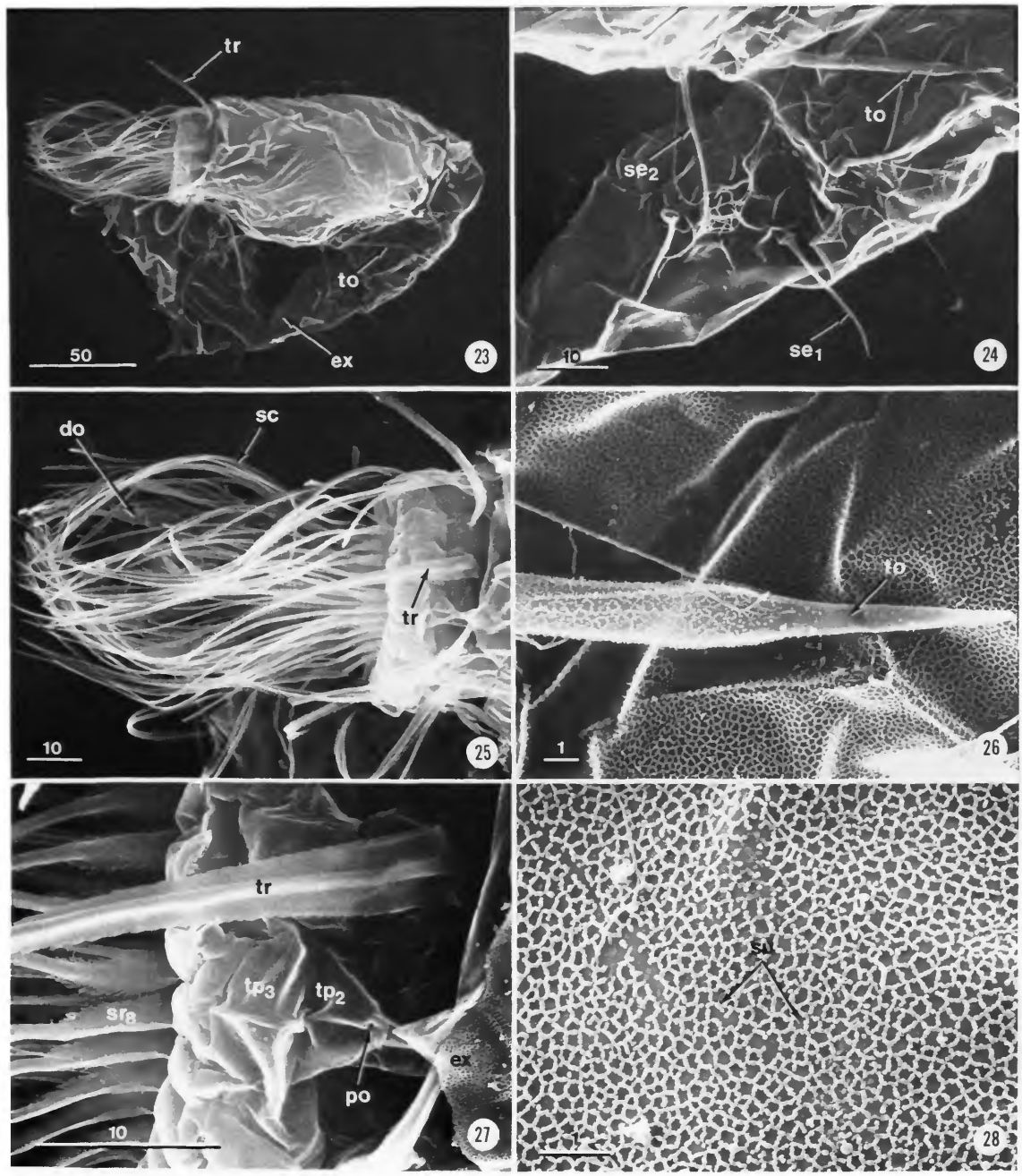
FIGURES 5–10.—*Pliciloricus enigmaticus,* new species: 5 (the first known loriciferan), RH 1695, paratypic male, dorsal view; 6, holotypic female, ventral view; 7, allotypic male, dorsal view; 8, exuvium of an adult animal; 9, paratypic larva molting to a mature male; 10, newly molted male. (Scales in μm.)



FIGURES 11–16.—*Pliciloricus enigmaticus,* new species: 11, mouth cone showing the three different parts, ventral view; 12, optic section of the mouth cone showing the buccal canal, buccal canal glands, and the pharynx bulb; 13, anterior part of the lorica, dorsal view; 14, anterior part of the lorica, ventral view; 15, modified spinoscalid, the claw-tipped scalid; 16, posteroventral part of lorica with the rosette structure and the floscula. (Scales in μm.)



FIGURES 17–22.—*Pliciloricus enigmaticus,* new species, adult male(?): 17, anterior part of the head and mouth cone, double-organ and ruff; 18, fourth row of scalids with modified claw-tipped spinoscalid and other spinoscalids; 19, tip of trichoscalid; 20, posterior part of animal, showing dorsal anus, two nephridiopores(?); 21, lorica showing rosette structure and a pair of flosculi, lateroventral view; 22, *Pliciloricus*-type flosculi. (SEM micrographs; scales in μm.)



FIGURES 23–28.—*Plicilloricus enigmaticus,* new species, larval exuvium with newly molted adult: 23, overall view; 24, larval toes and setae; 25, scalids of adult; 26, larval cuticle and toe; 27, base of the trichoscalids and spinoscalids; 28, fine structure of larval cuticle. (SEM micrographs; scales in μm.)

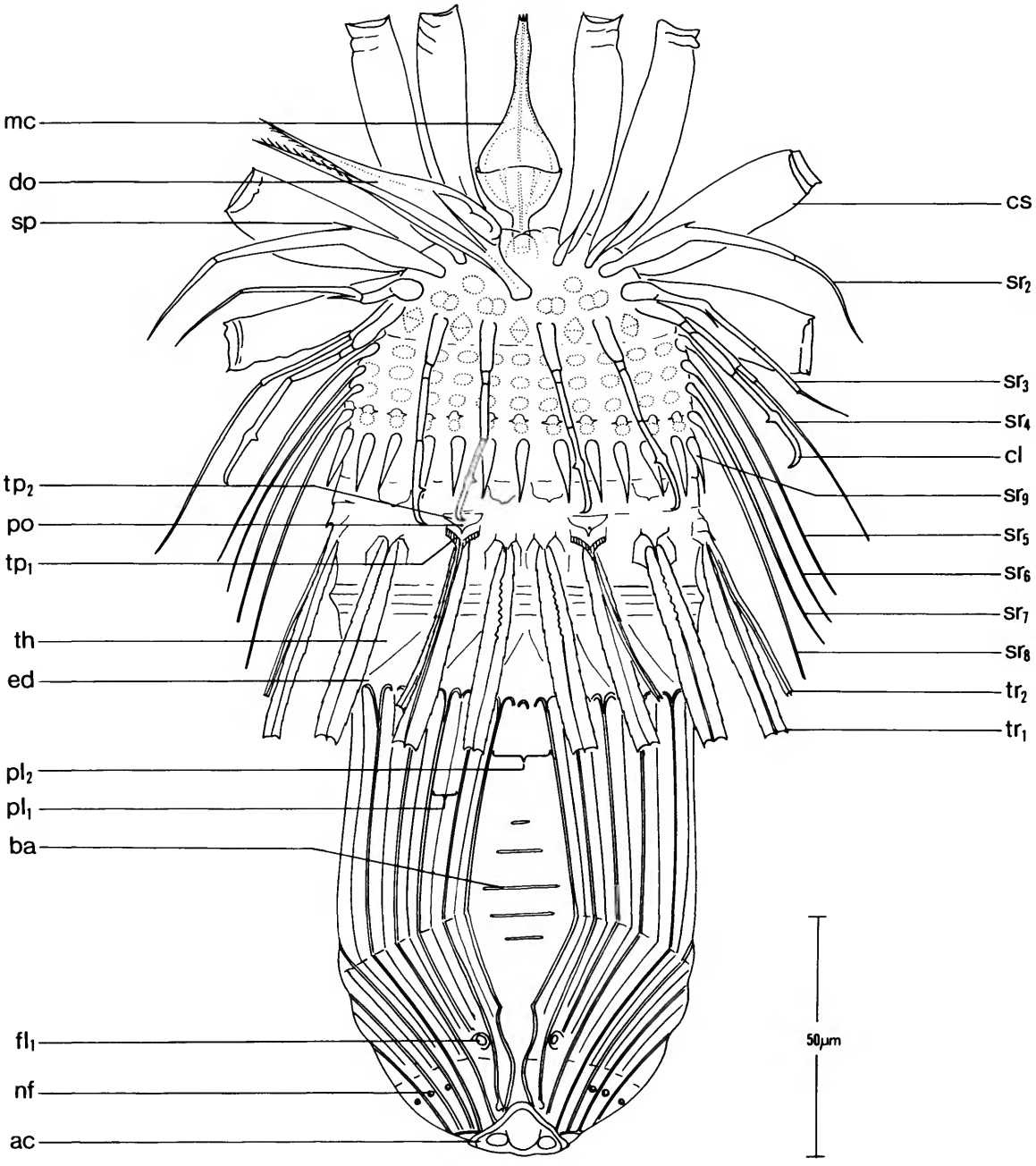


FIGURE 29.—*Pliciloricus dubius*, new species, holotypic female, ventral view (scale in µm.)

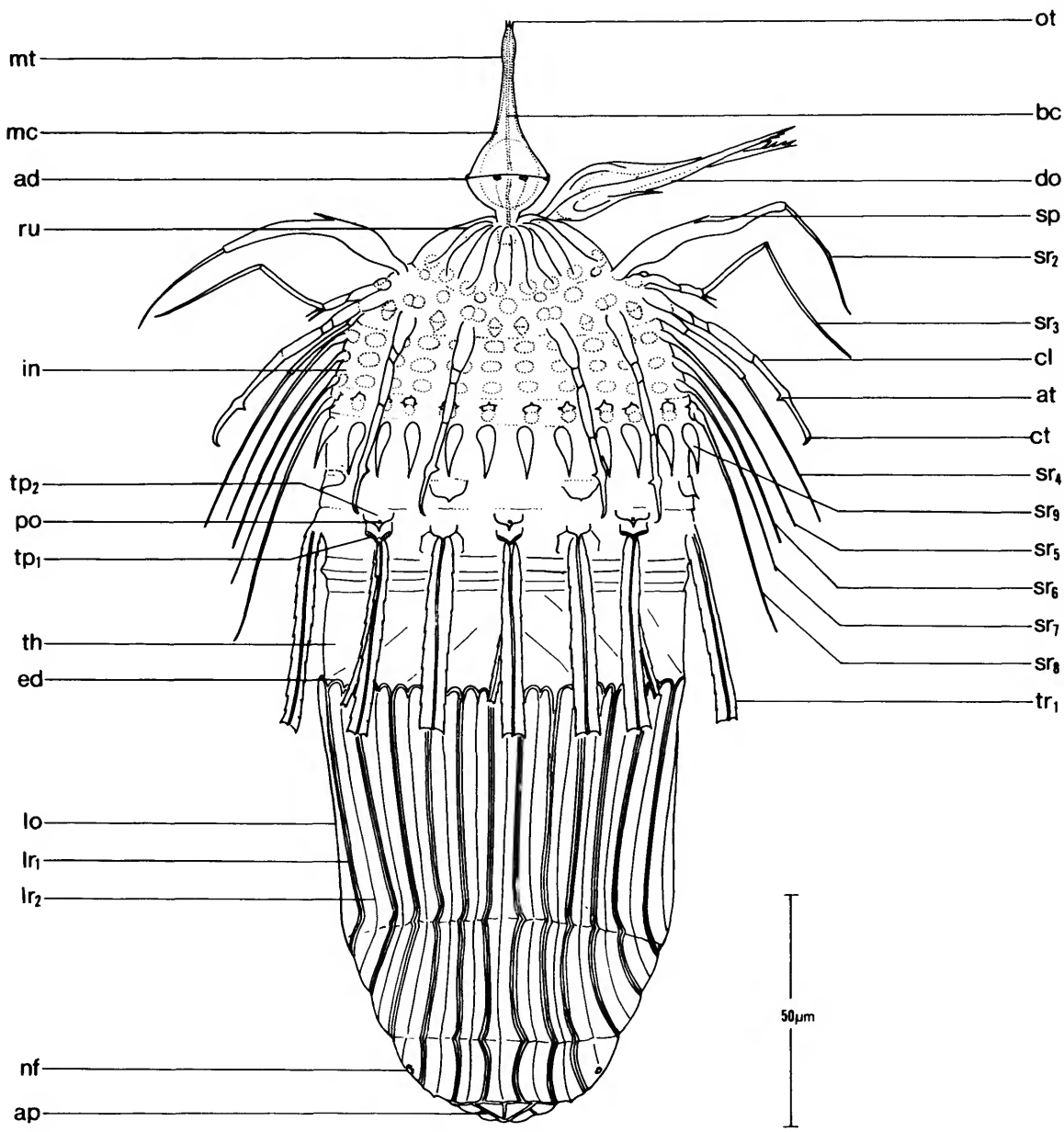
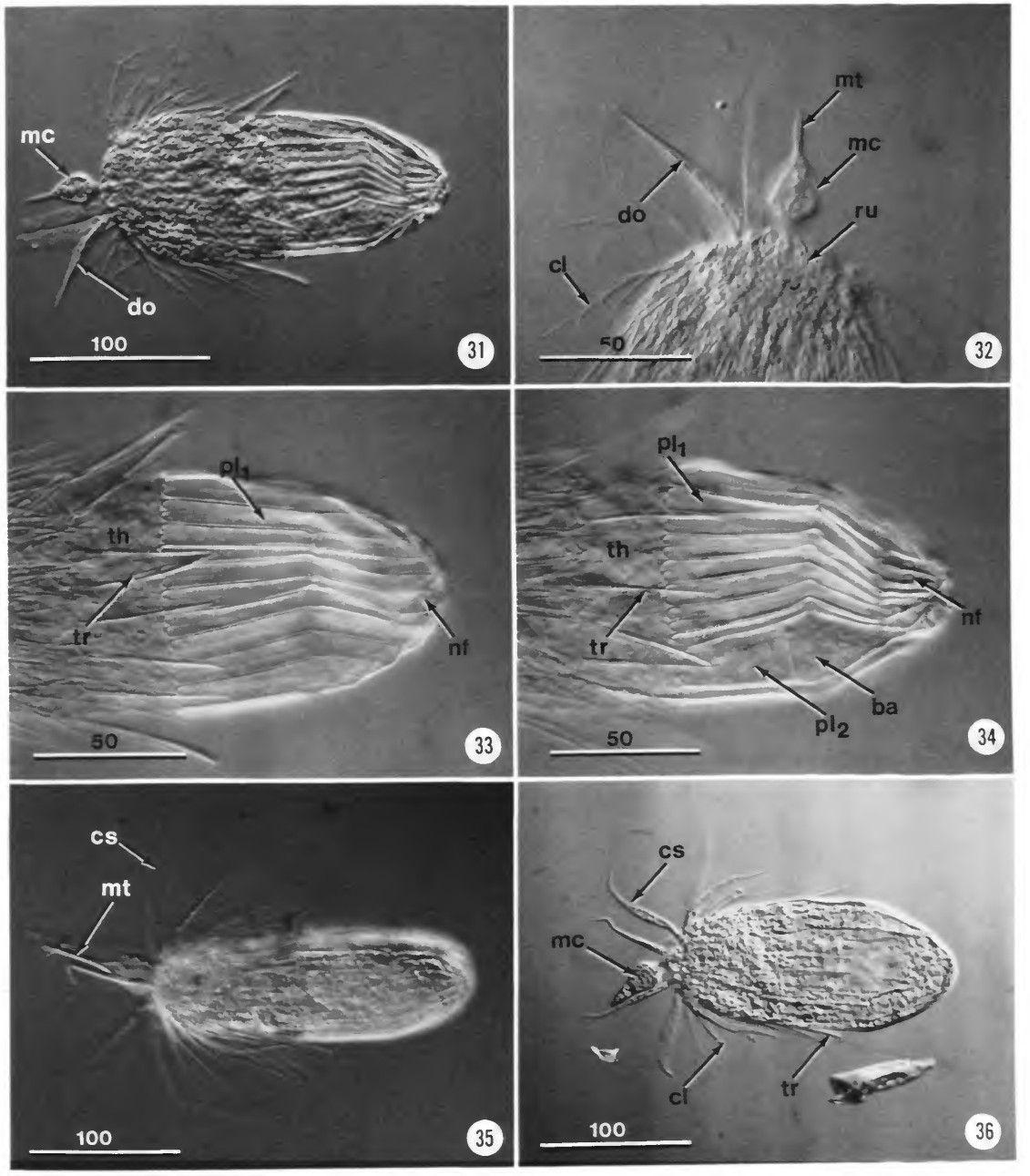


FIGURE 30.—*Pliciloricus dubius*, new species, holotypic female, dorsal view, note clavoscalids not illustrated (scale in µm.)



FIGURES 31–36.—*Pliciloricus*, new genus: 31, *P. dubius*, new species, holotypic female, lateroventral view; 32, same, anterior part showing mouth cone, double-organ and ruff; 33, same, lorica, dorsal view; 34, same, lorica, ventral view; 35, *P. gracilis*, new species, holotypic male, lateral view; 36, *P. profundus*, new species, holotypic male, ventral view. (Scales in μm.)

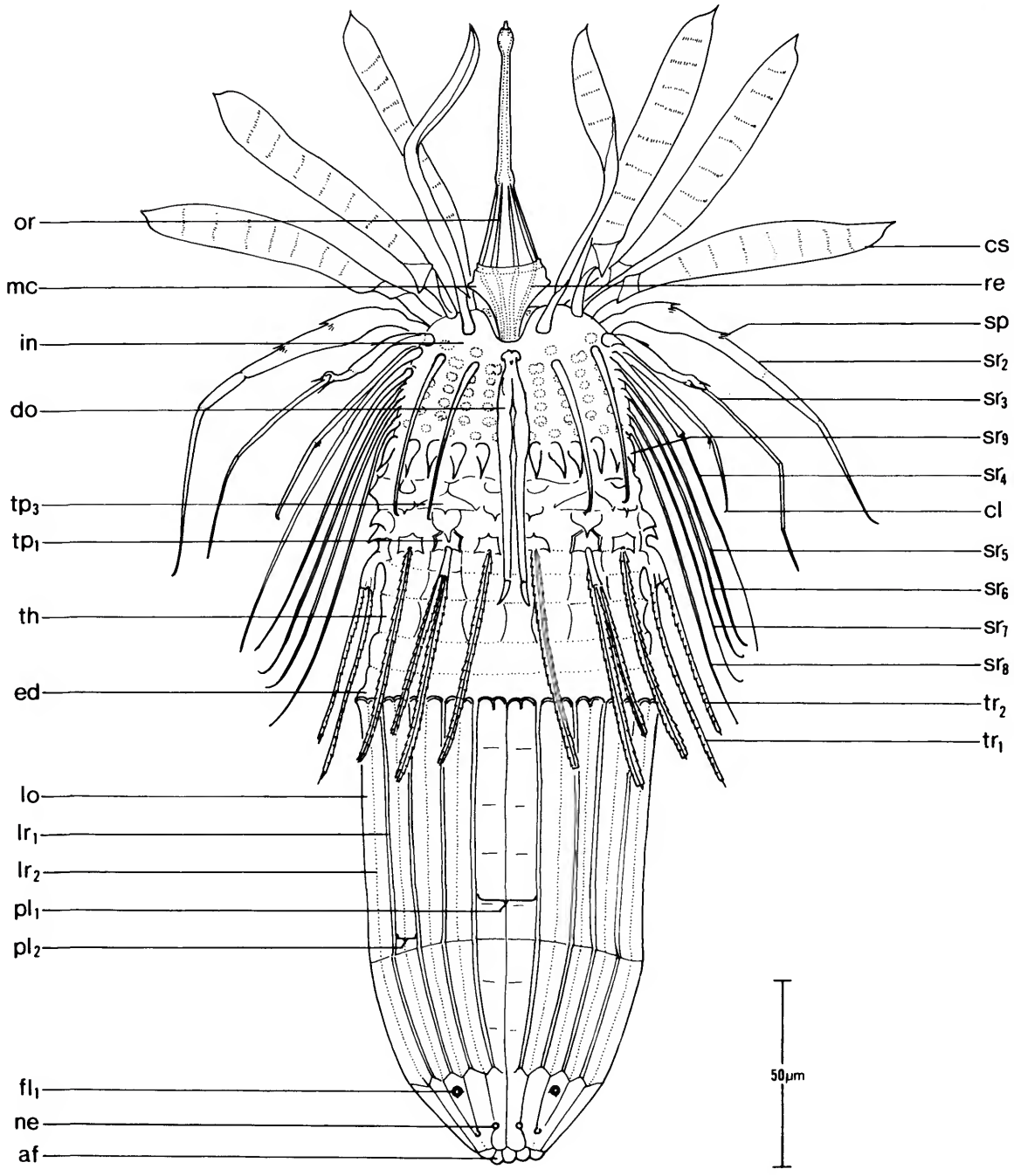


FIGURE 37.—*Plicilloricus gracilis*, new species, holotypic male(?), ventral view (scales in µm).

FIGURE 38.—*Pliciloricus gracilis*, new species, holotypic male(?), ventral view (see Figure 37 for scale).

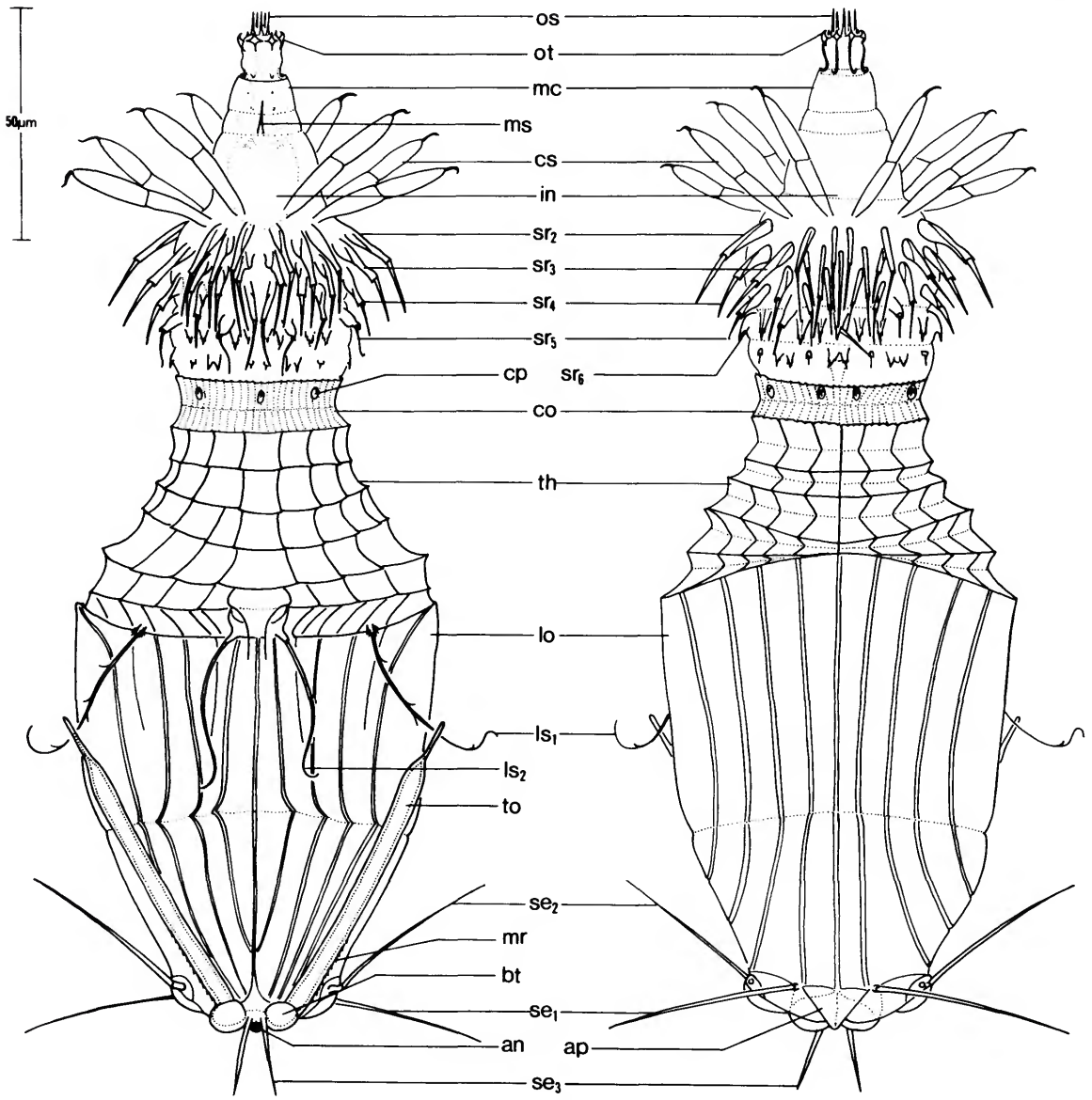
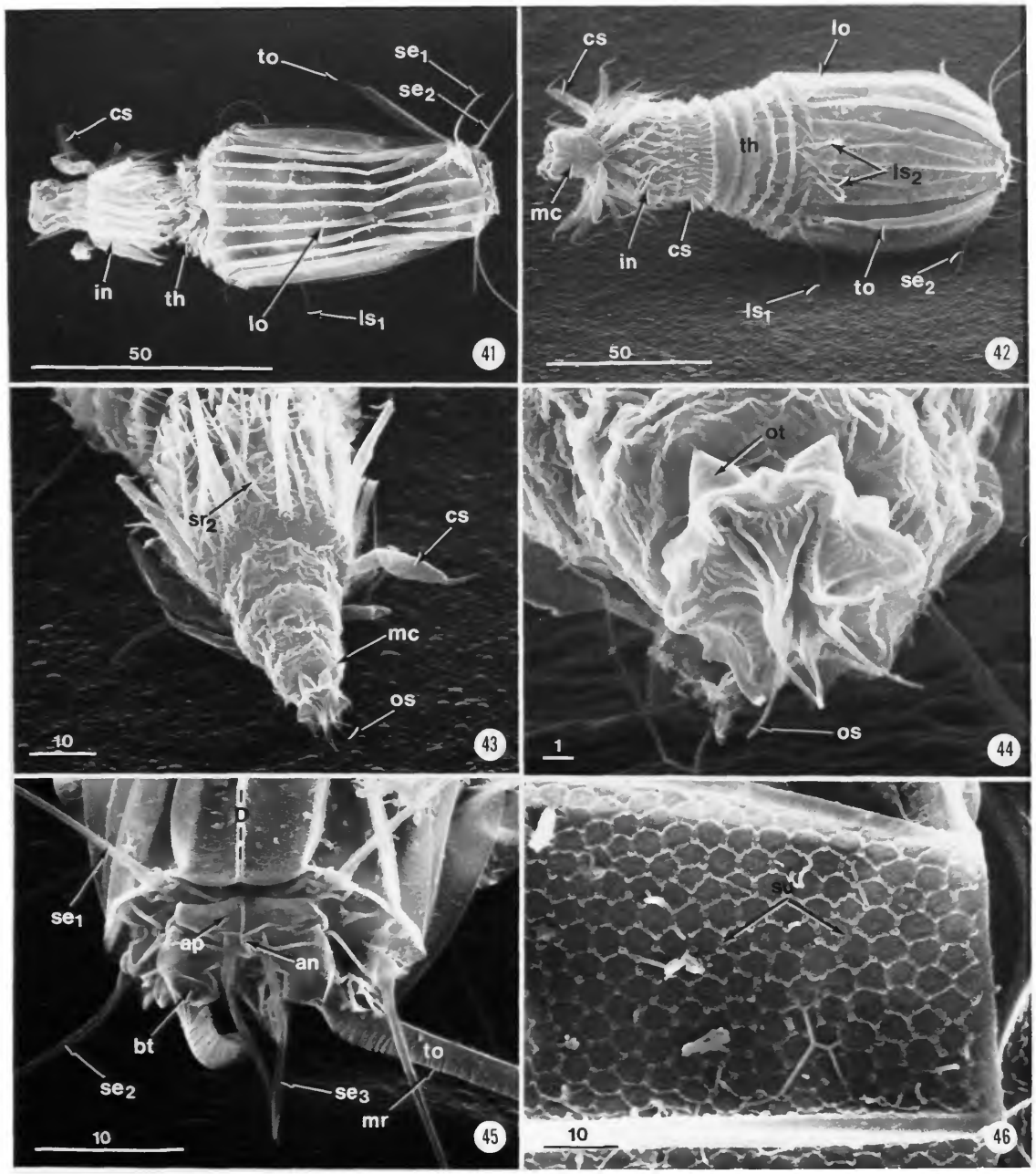


FIGURE 39.—*Pliciloricus gracilis*, new species, paratypic larva: *left*, ventral view; *right*, dorsal view (scale in µm).

FIGURE 40.—*Pliciloricus gracilis*, new species, paratypic larva, ventral view (see Figure 39 for scale).



FIGURES 41–46.—*Pliciloricus gracilis,* new species, paratypic larva: 41, larva 2, dorsal view; 42, larva 3, ventral view; 43 fully extended mouth cone, larva 1; 44, same, oral stylets and oral teeth, polar view; 45, posterior part of larva 2 showing toes, anal plate, anus, and the posterior three pairs of setae; 46, fine structure of lorical cuticle of larva 2. (SEM micrographs; scales in μm.)

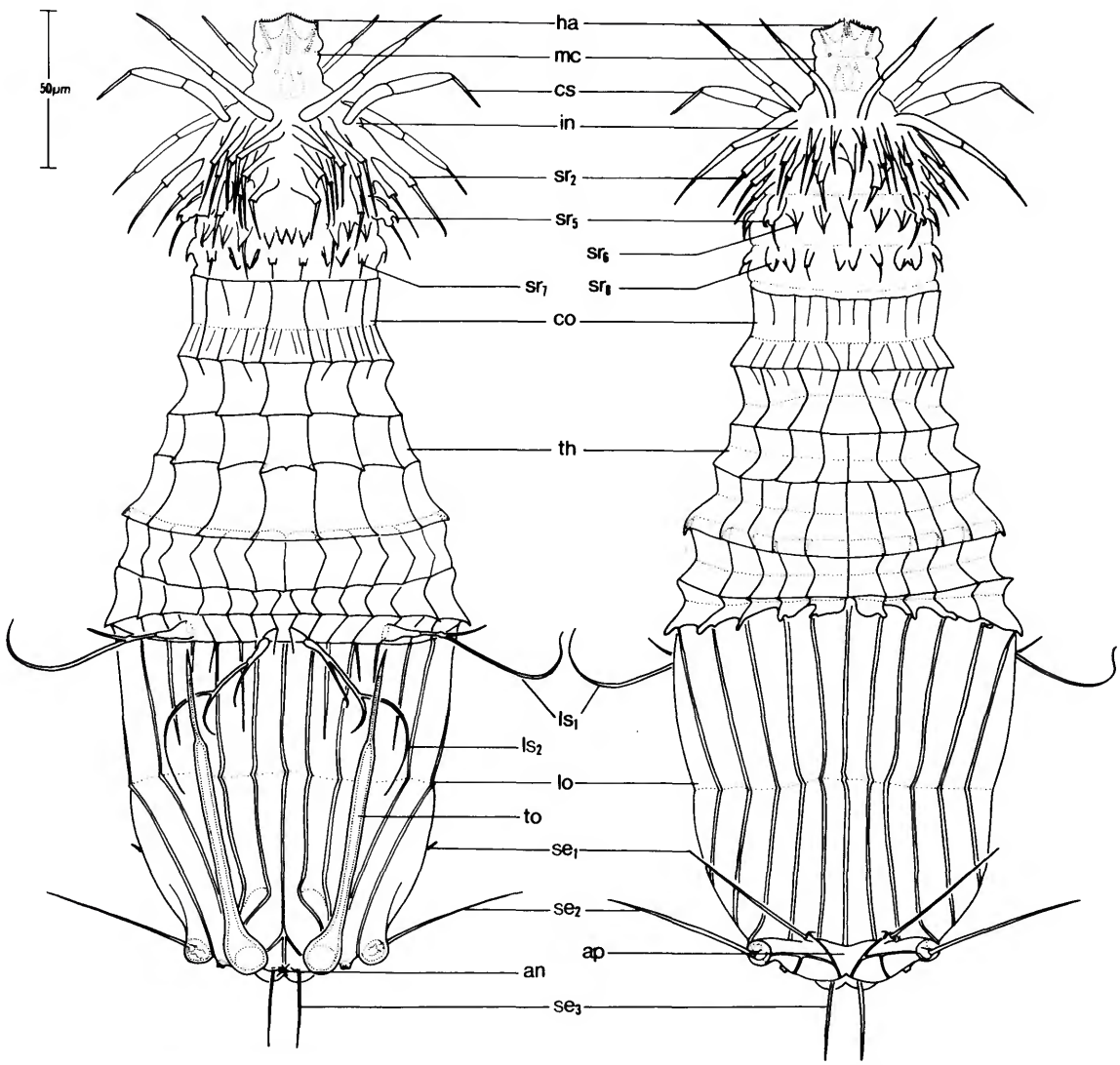


FIGURE 47.—*Pliciloricus orphanus,* new species, holotypic larva: *left,* ventral view; *right,* dorsal view (scale in µm).

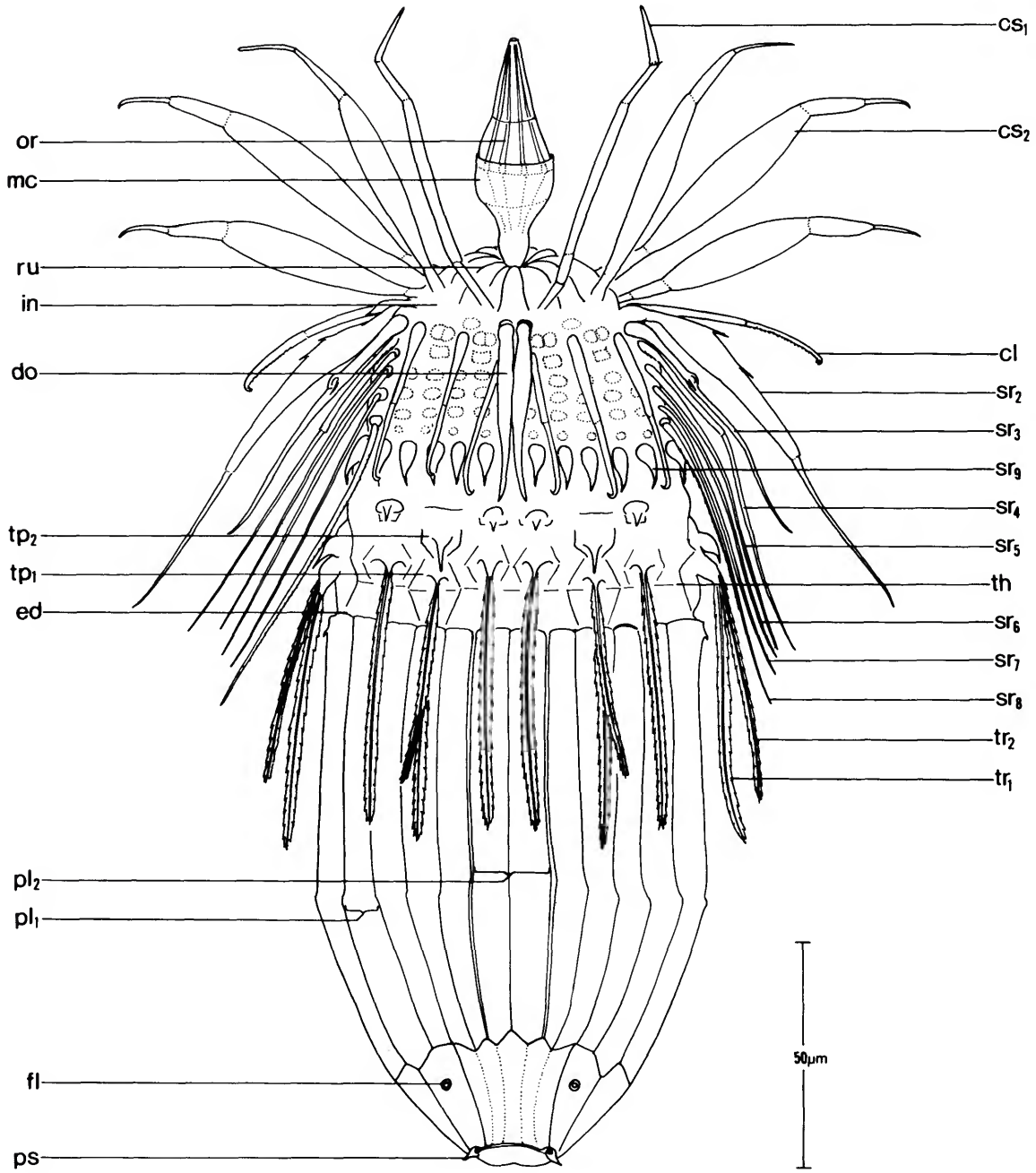


FIGURE 48.—*Plicilloricus profundus*, new species, holotypic male, ventral view (scale in µm).

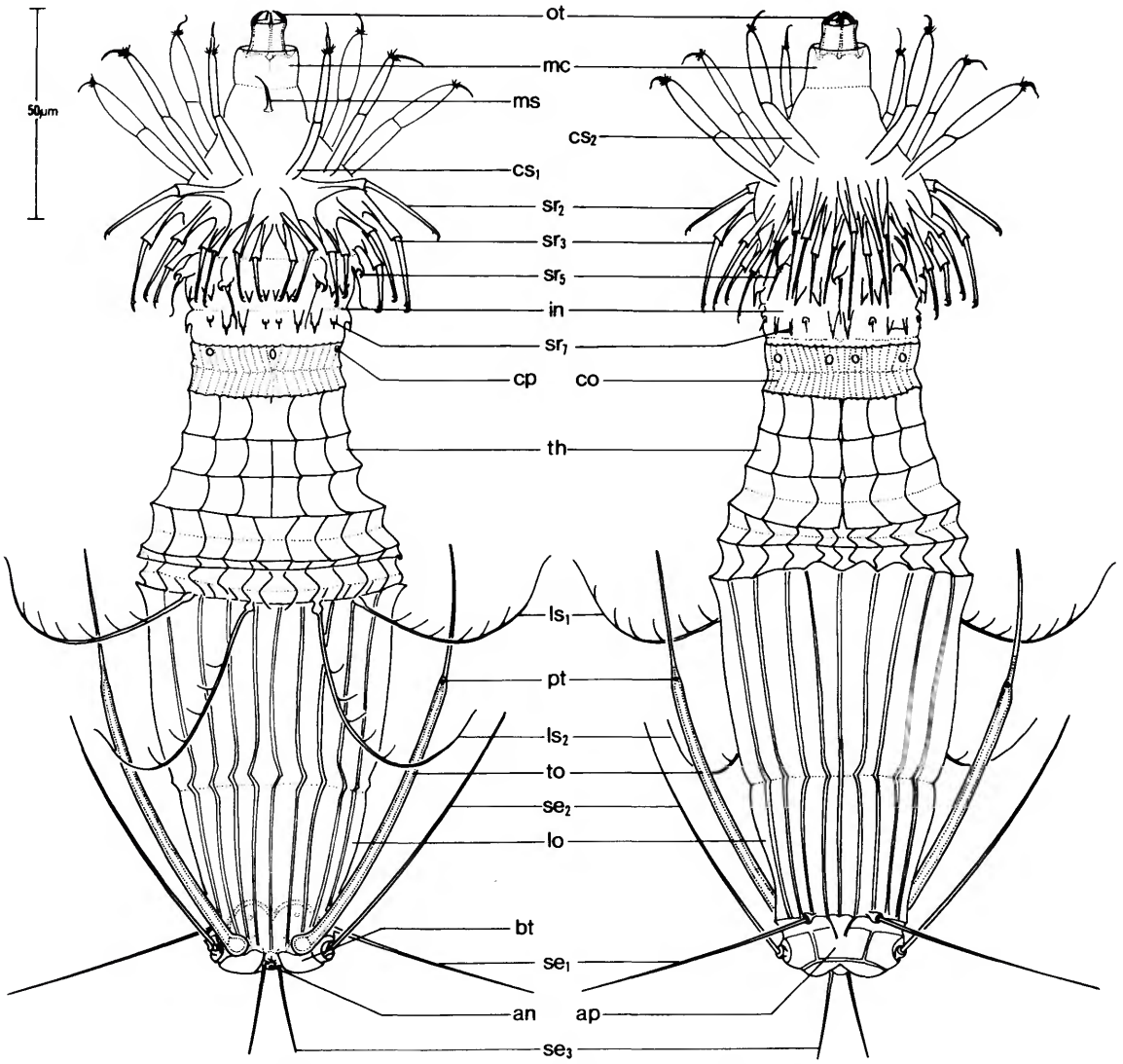
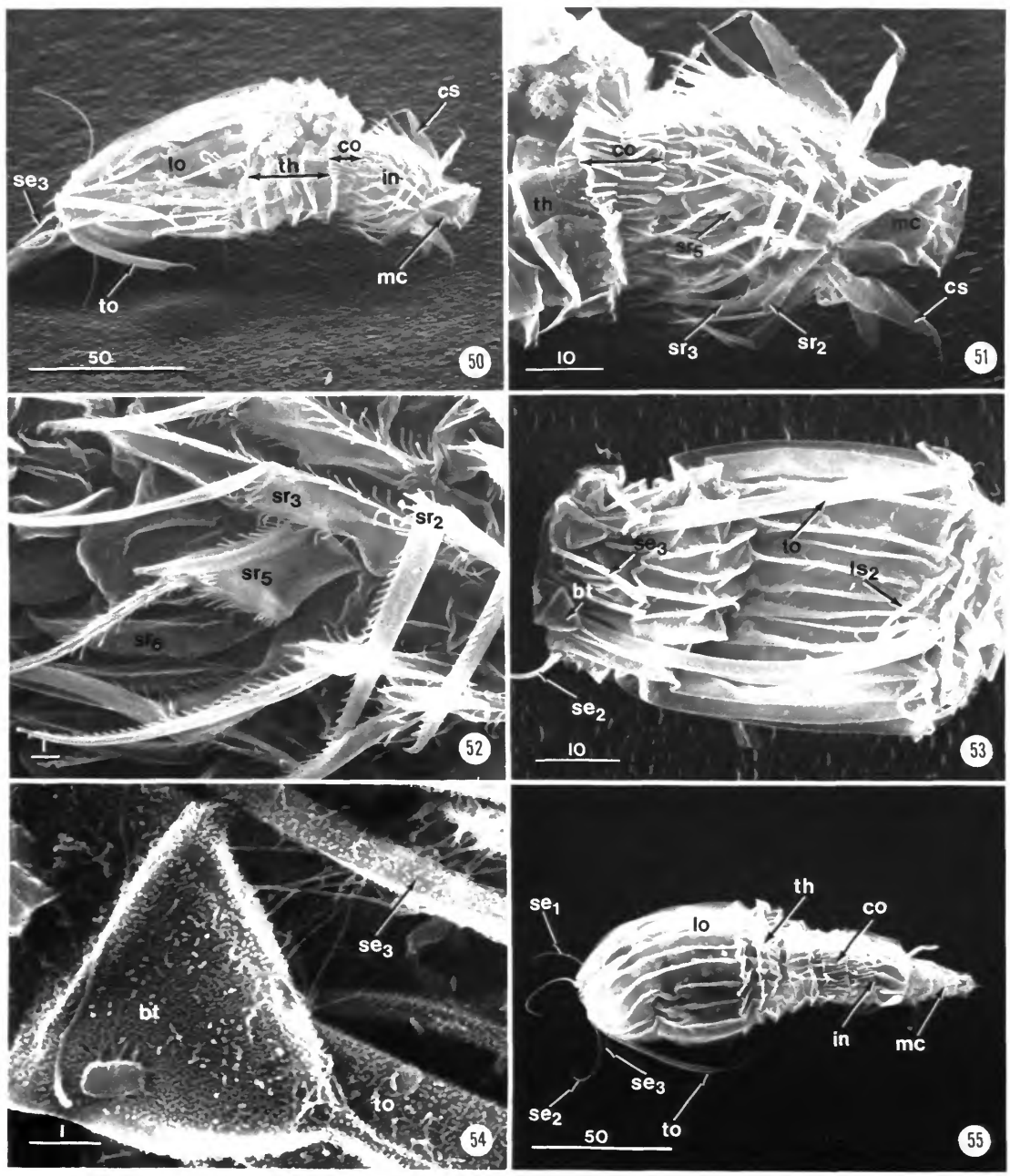


FIGURE 49.—*Pliciloricus profundus*, new species, paratypic larva: *left*, ventral view; *right*, dorsal view (scale in µm).



FIGURES 50–55.—*Pliciloricus*, new genus, larvae: 50, *P. profundus*, new species, larva 2, ventrolateral view; 51, same, head with scalids, collar, mouth cone with oral setae; 52, same, ventral spinoscalids; 53, same, larva 1, lorica and toes, ventral view; 54, same, cuticular surface, base of toe; 55, *P. orphanus*, new species lateral view. (SEM micrographs; scales in μm.)

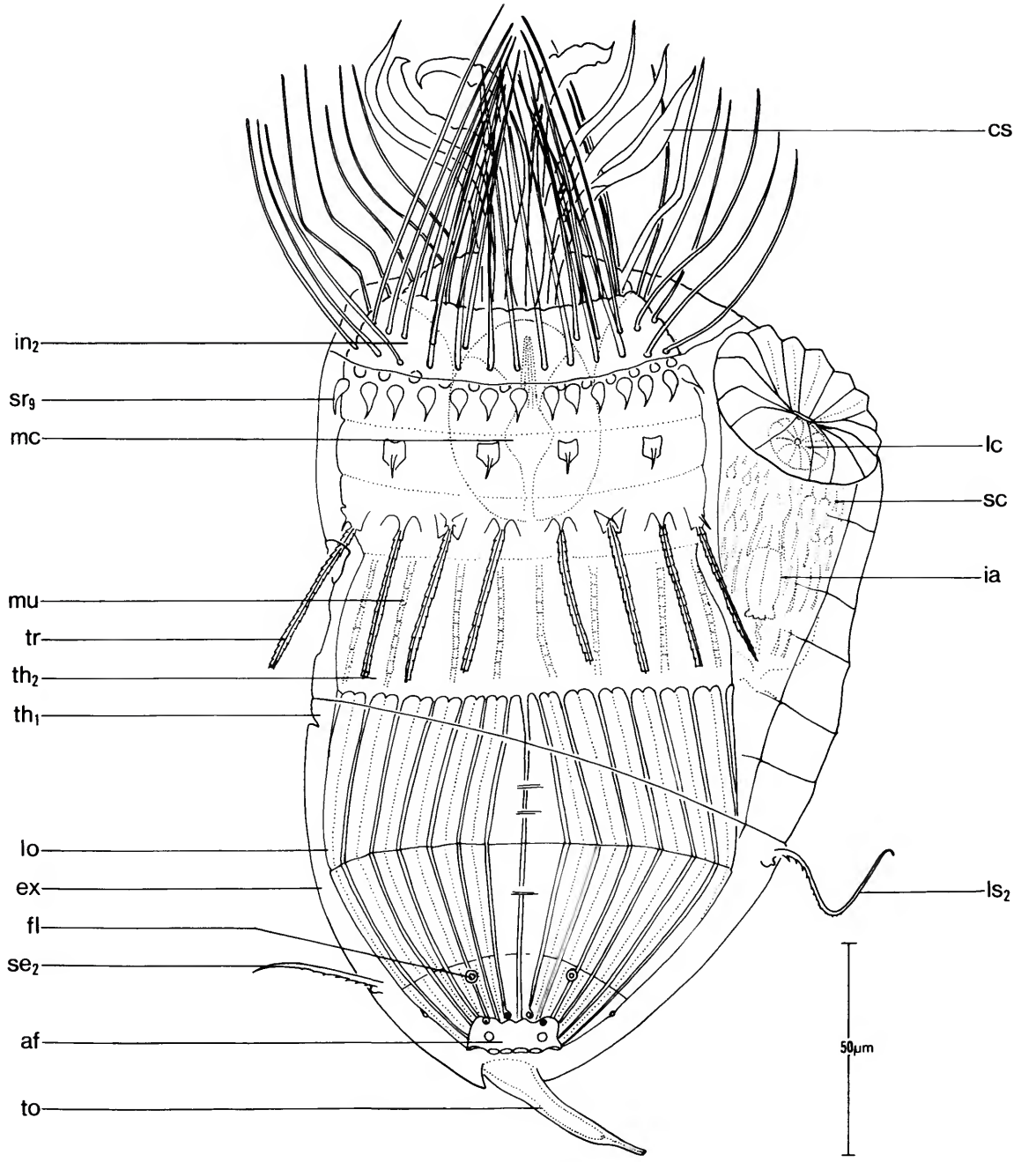
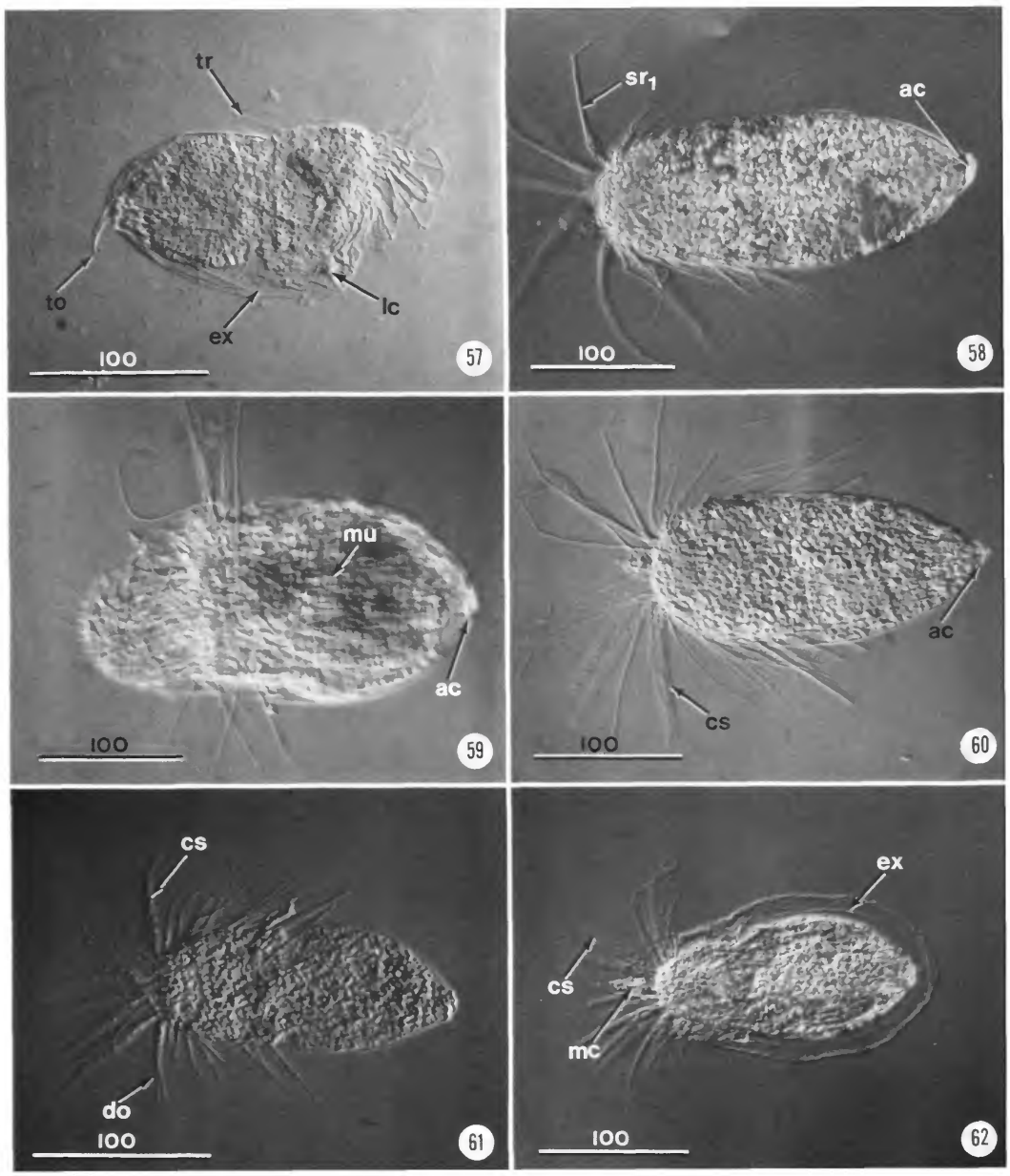


FIGURE 56.—*Rugiloricus carolinensis,* new species, holotypic adult female(?) in larval exuvium, lateral view of larval exuvium, ventral view of adult (scale in µm).



FIGURES 57–62.—*Rugiloricus,* new genus: 57, *R. carolinensis,* new species, holotypic adult female(?) in larval exuvium, lateral view of larval exuvium, ventral view of adult; 58, *R. cauliculus,* new species, holotypic adult male, lateral view; 59, same, allotypic adult male in larval (postlarval?) exuvium, ventral view; 60, same, paratypic adult female (variant) with eight large clavoscalids, lateroventral view; 61, *R. ornatus,* new species, holotypic female, lateral view; 62, same, allotypic adult male in larval (postlarva?) exuvium, lateral view. (Scales in μm.)

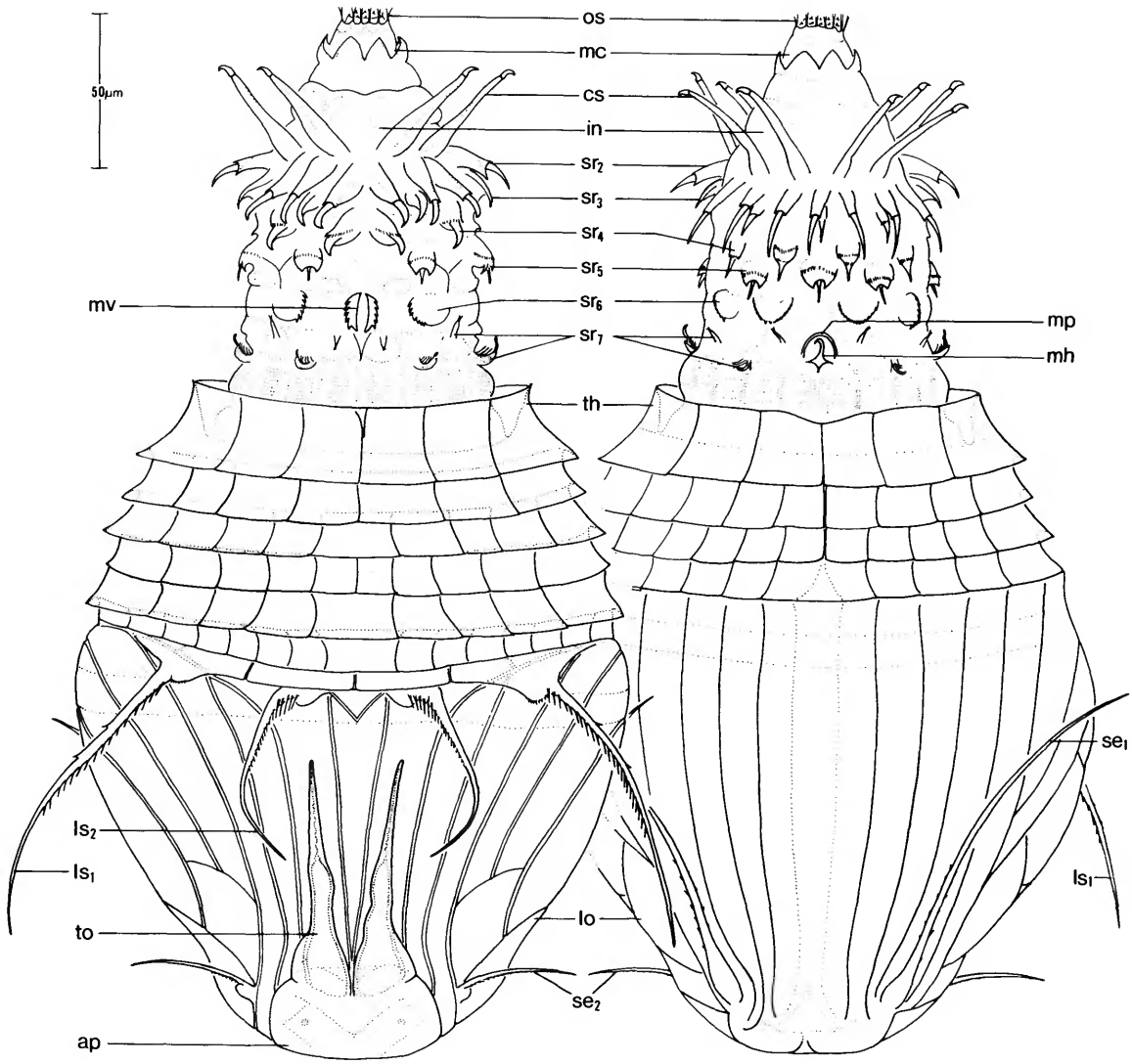
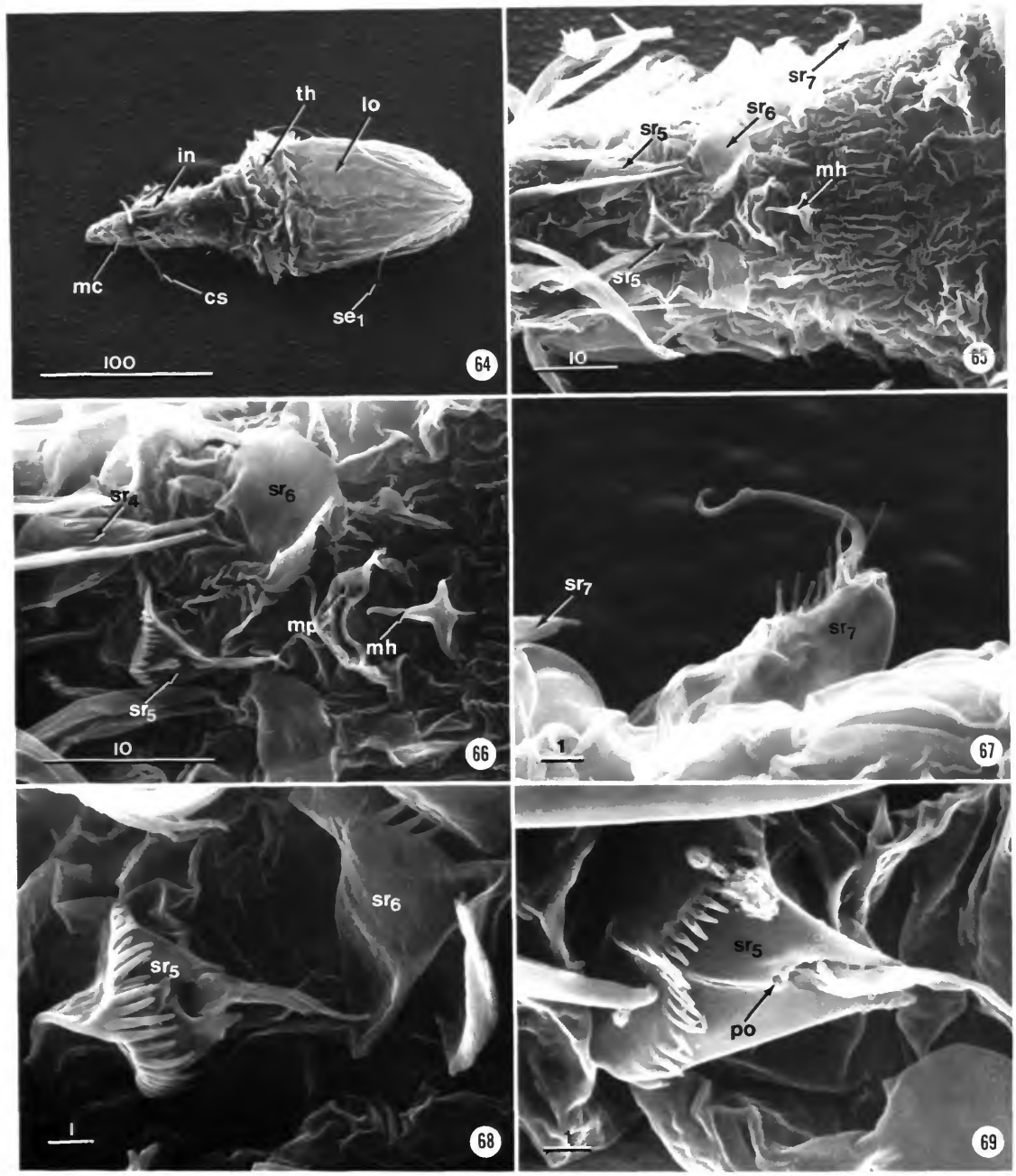
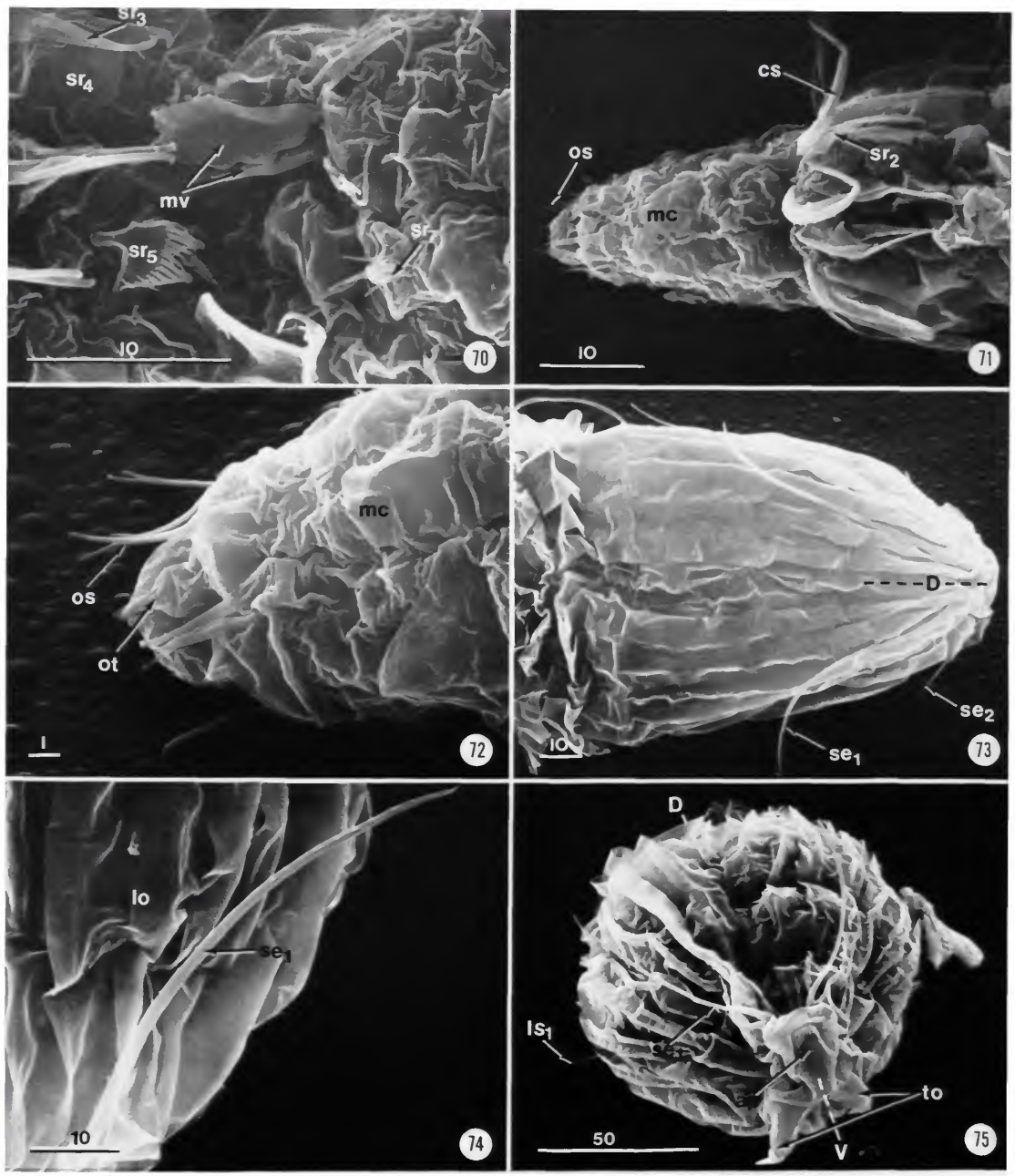


FIGURE 63.—*Rugiloricus carolinensis*, new species, paratypic larva: *left*, ventral view; *right*, dorsal view (scale in µm).



FIGURES 64–69.—*Rugiloricus carolinensis,* new species, larvae: 64, larva 1, dorsal view; 65, same, posterior part of head with middorsal hook, dorsal view; 66, same, spinoscalids, dorsal view; 67, same, modified lateral spinoscalids of row 7; 68, larva 2, fifth and sixth row spinoscalids, lateral view; 69, larva 4, fifth row spinoscalids with pore, dorsal view. (SEM micrographs; scales in μm.)



FIGURES 70–75.—*Rugiloricus carolinensis,* new species, larvae: 70, larva 2, midventral double scalids; 71, same, anterior part of head with mouth cone; 72, same, double oral stylets and oral teeth; 73, larva 1, lorica, dorsal view; 74, same, large dorsal setae and smooth cuticle of lorica; 75, larva 5, anal plate and small ventral toes, posterior view. (SEM micrographs; scales in μm.)

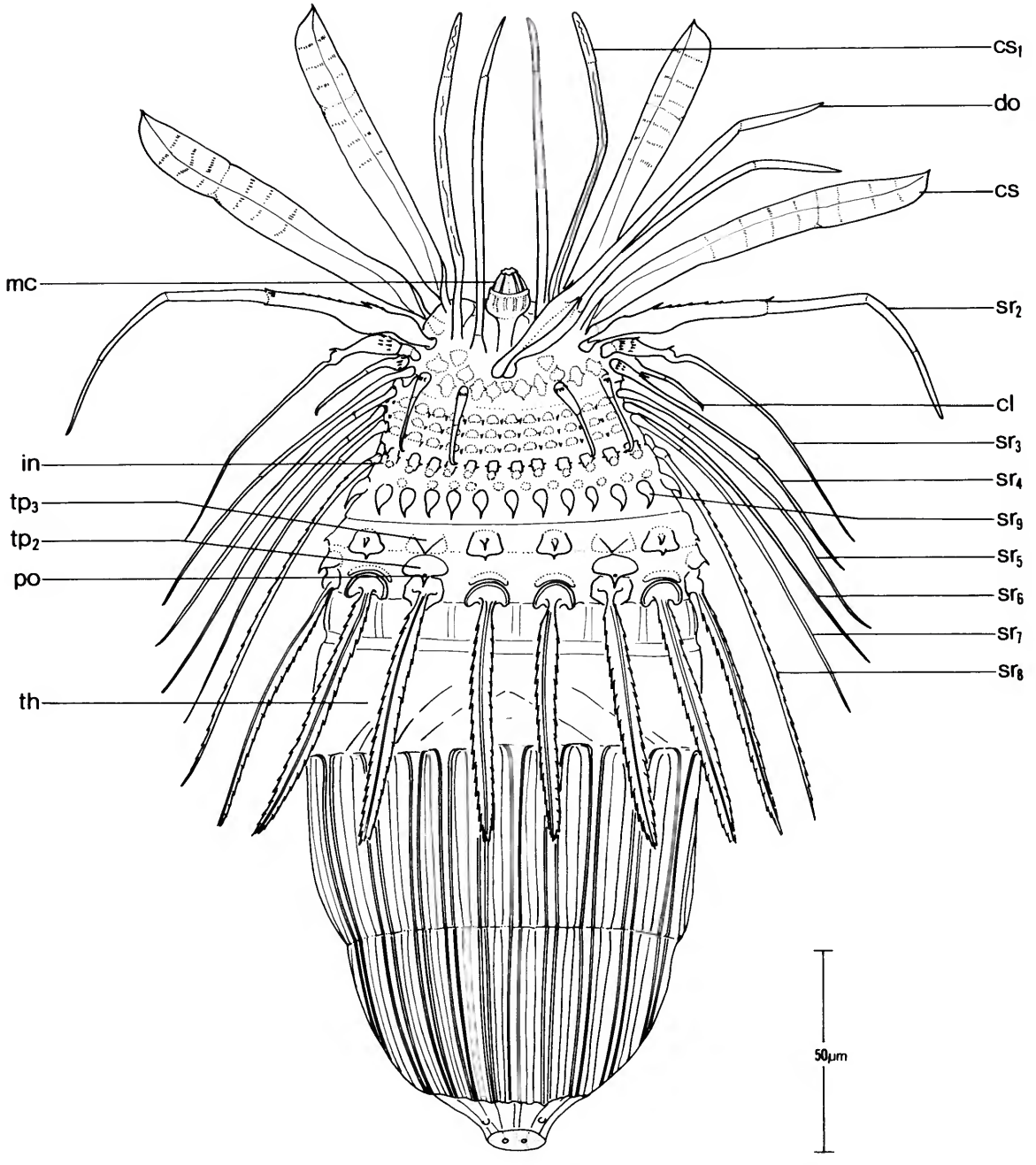


FIGURE 76.—*Rugiloricus cauliculus*, new species, holotypic adult male(?), ventral view (scale in µm).

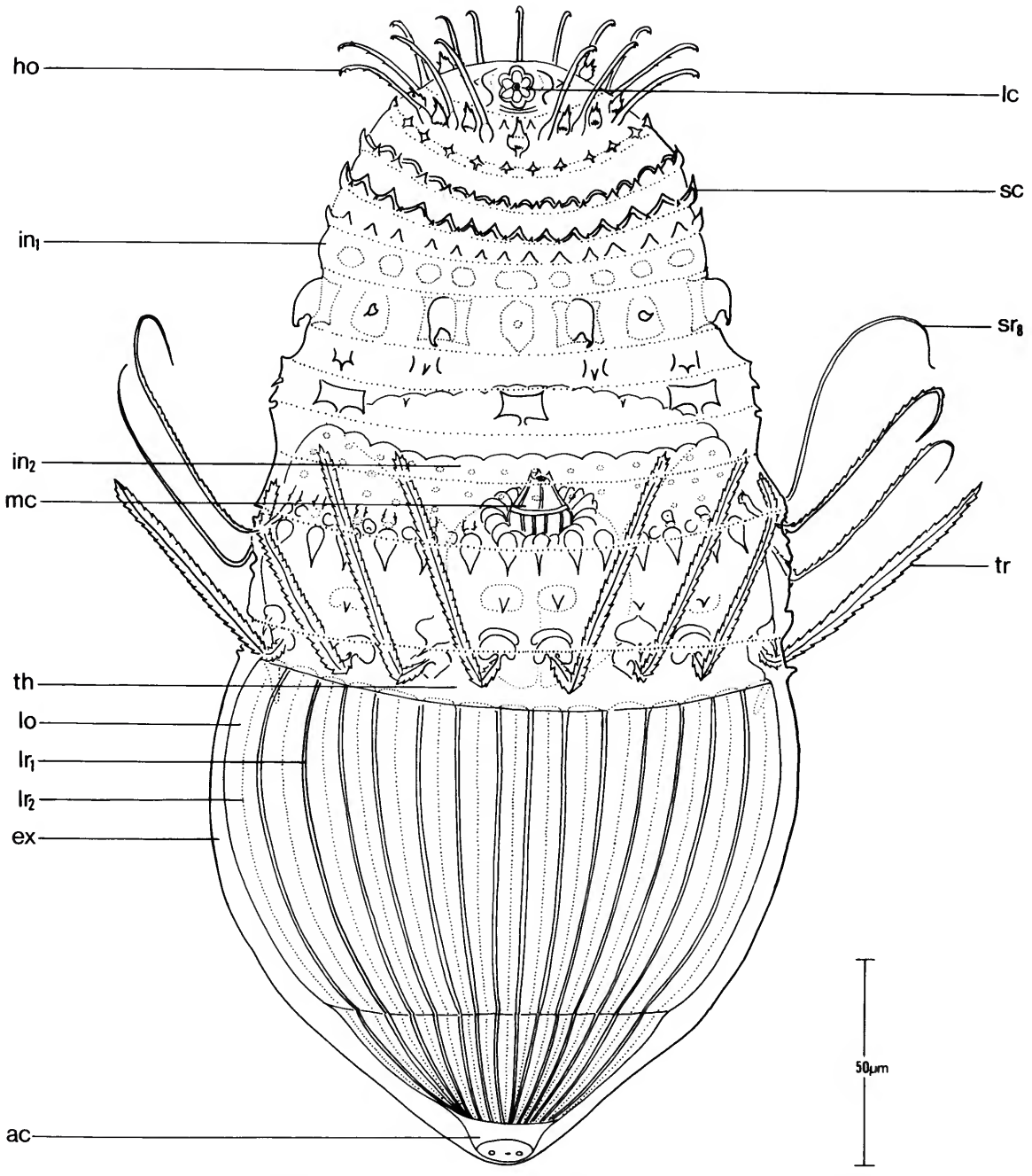
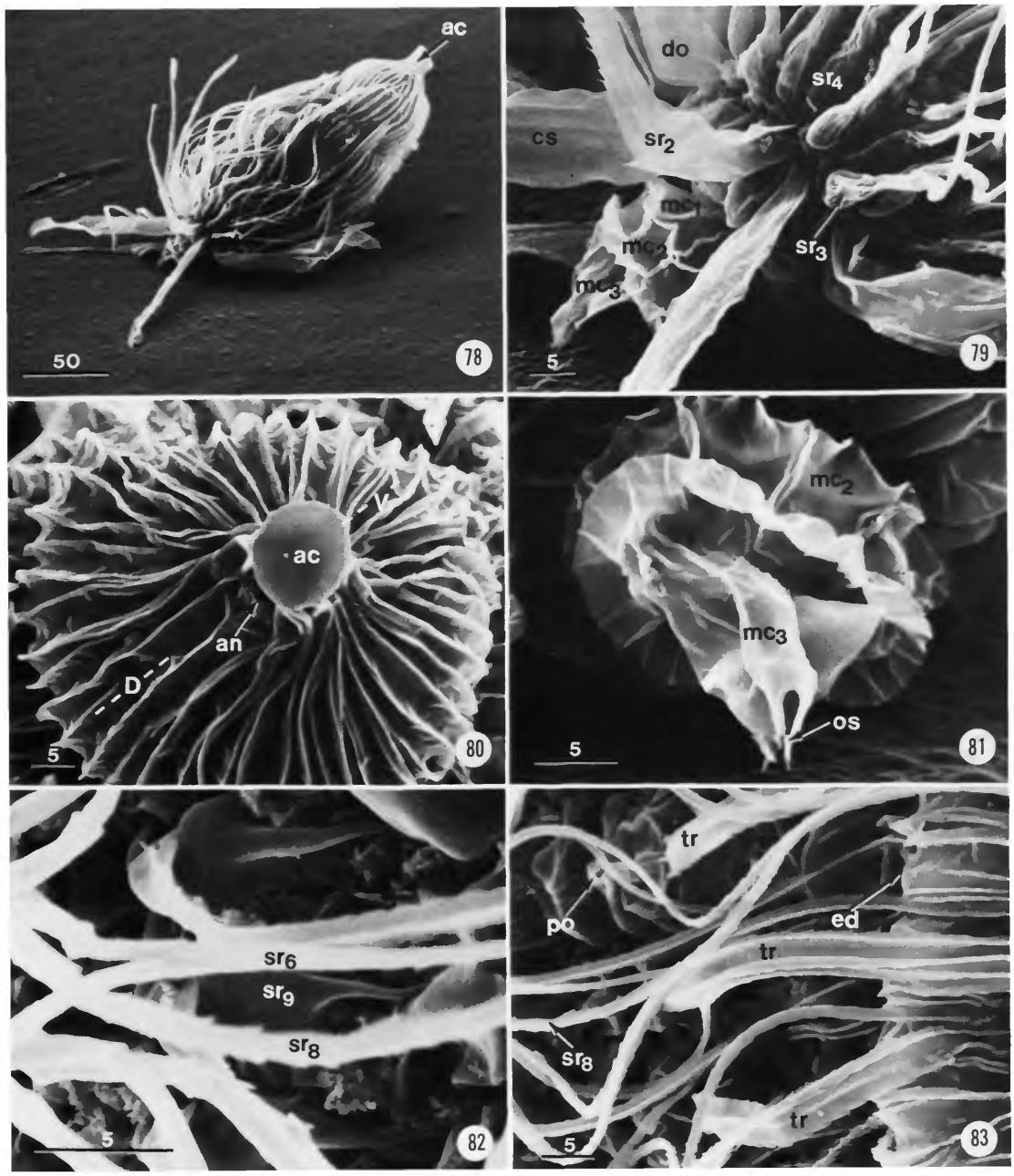


FIGURE 77.—*Rugiloricus cauliculus,* new species, allotypic adult male(?) in larval (postlarval?) exuvium, ventral view (scale in µm).



FIGURES 78–83.—*Rugiloricus cauliculus,* new species, paratypic adult male(?): 78, lateral view; 79, mouth cone and first few scalid rows; 80, anal cone, dorsal anus, and lorica, posterior view; 81, mouth cone with oral styles, polar view; 82, last row of spinoscalids; 83, single trichoscalids with the trichoscalid plate and pore. (SEM micrographs, scales in μm.)

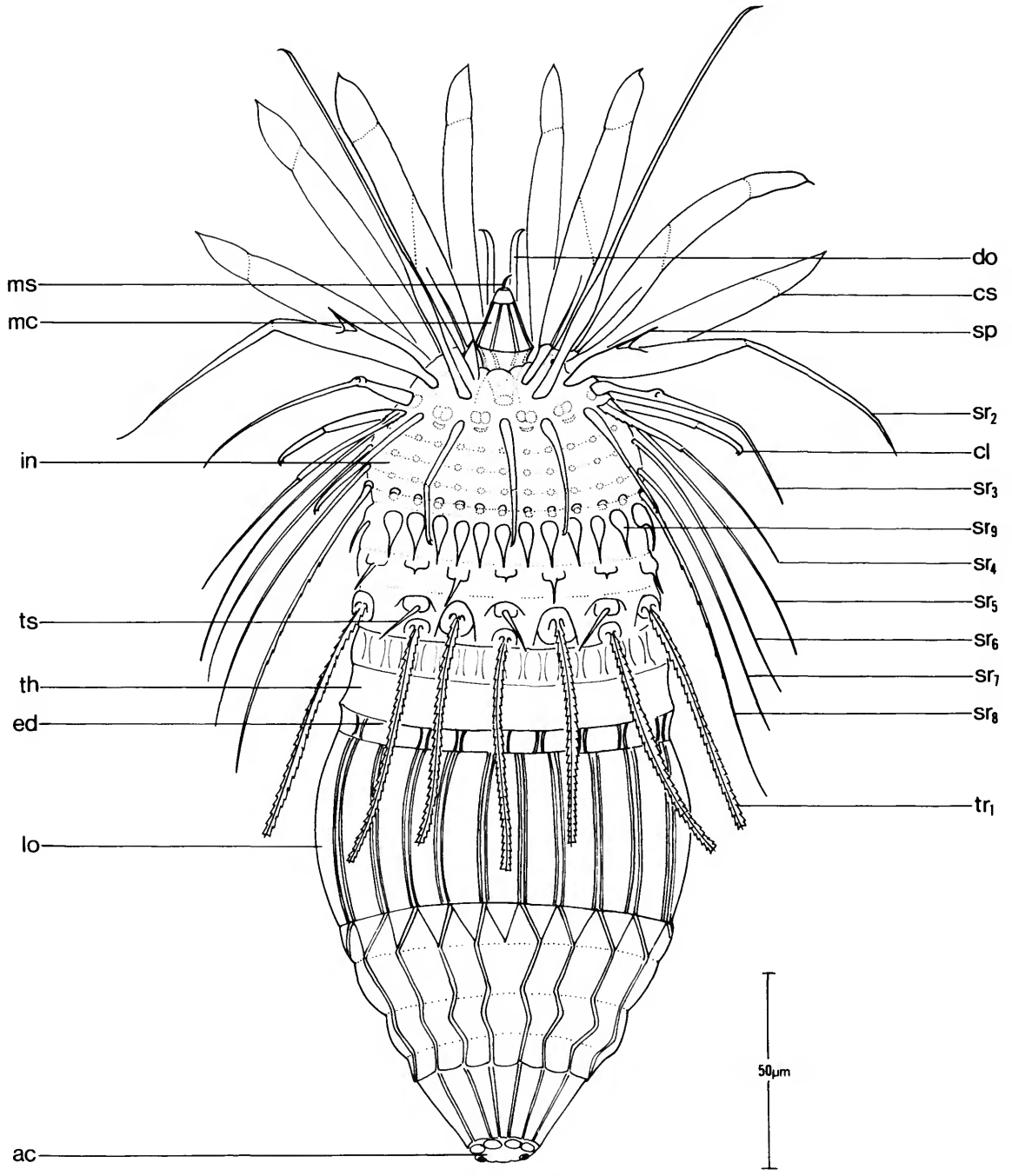


FIGURE 84.—*Rugiloricus ornatus,* new species, holotypic female, dorsal view (scale in µm).

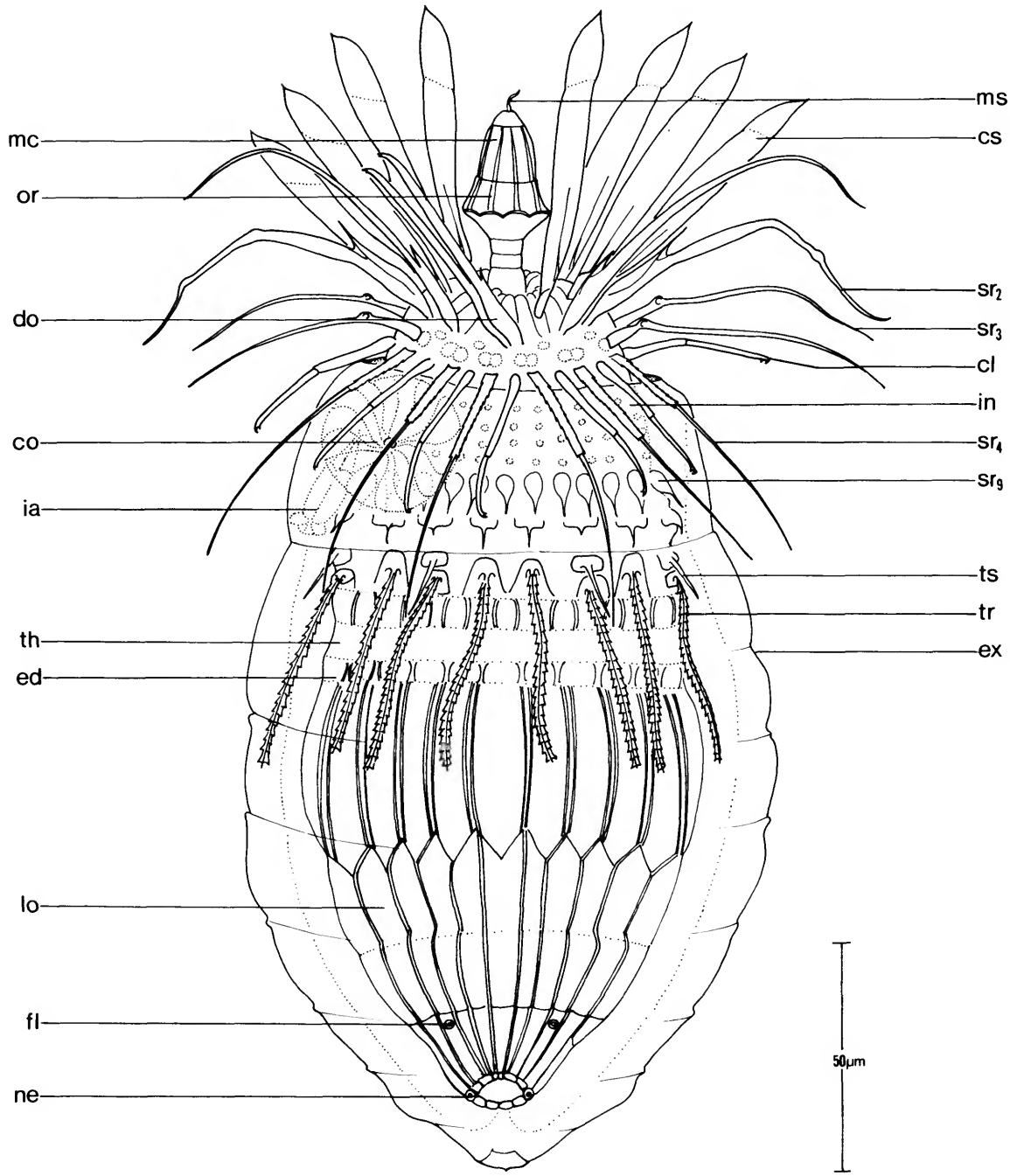


FIGURE 85.—*Rugiloricus ornatus*, new species, allotype, adult male in larval exuvium, ventral view (scale in µm).

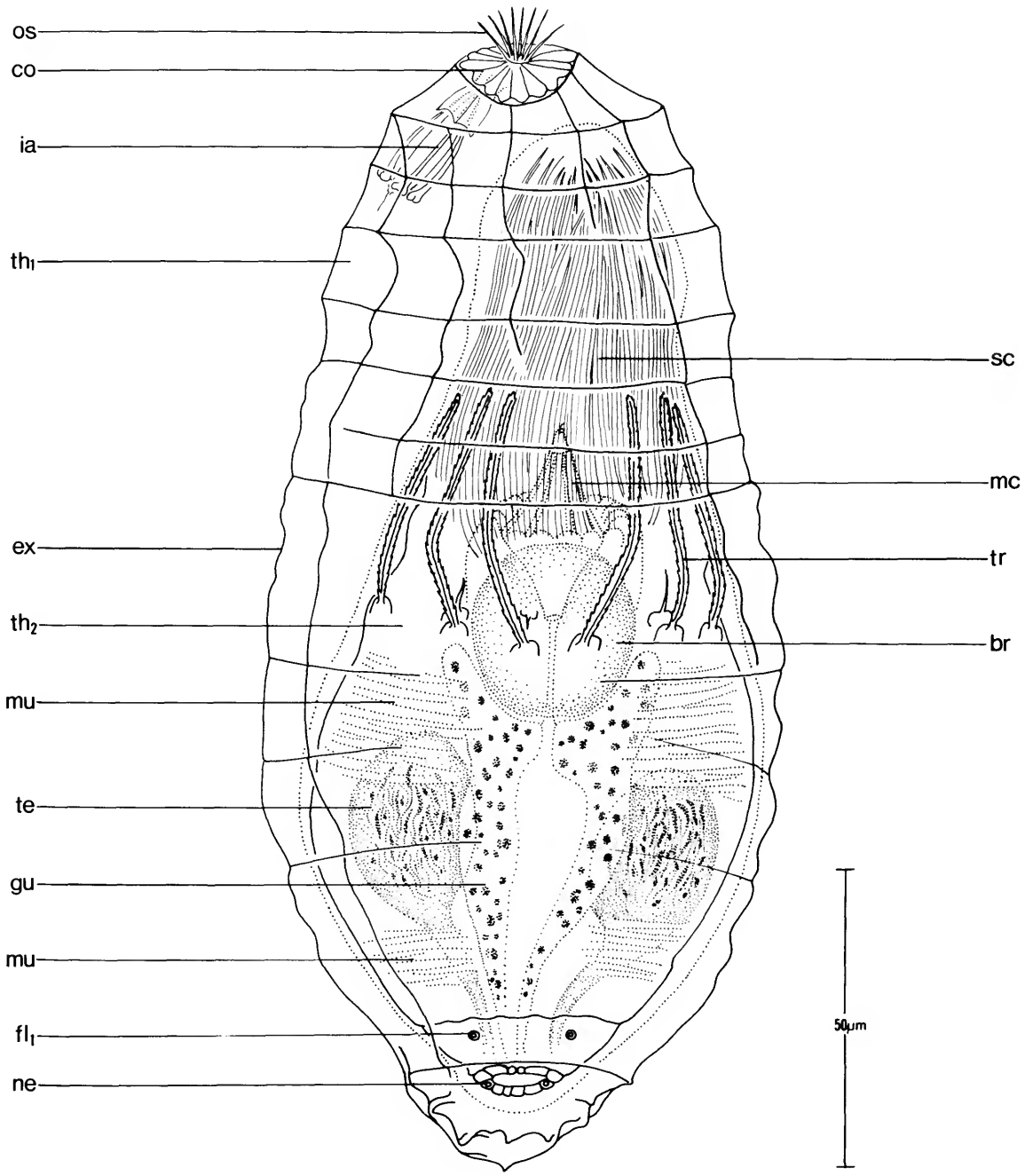


FIGURE 86.—*Rugiloricus ornatus*, new species, paratypic adult male in larval (postlarva?) exuvium, ventral view (scale in µm).

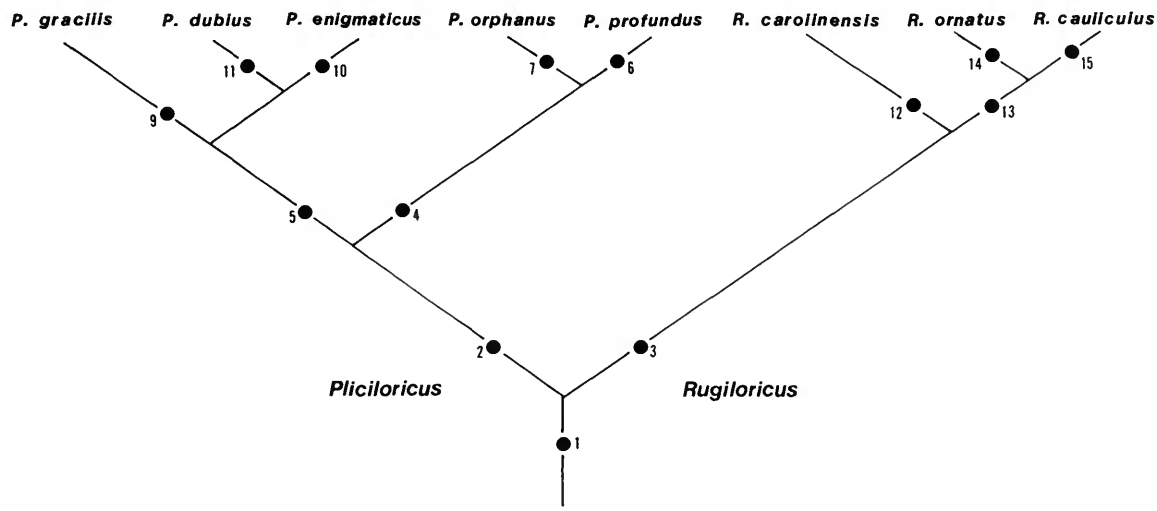


FIGURE 87.—Cladogram of the family Pliciloricidae.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼″ margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title page** with only title and author and no other information, **abstract** page with author, title, series, etc., following the established format; table of **contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number): pagination: "10(2):5–9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9*b*." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9*b*." Keys to any symbols within an illustration should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendixes, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when manuscript is submitted.