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The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha

Robert P. Higgins

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ABSTRACT

Higgins, Robert P. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. *Smithsonian Contributions to the Marine Sciences,* number 18, 131 pages, 343 figures, 23 tables, 1983.—Eighteen new species, including one new genus of Kinorhyncha, are described from the reef ecosystem at Carrie Bow Cay, Belize. *Pycnophyes neapolitanus* Băcescu, 1968, is considered a junior synonym of *P. ponticus* Zelinka. *Pycnophyes quadridentatus* Zelinka, 1928, and *P. flagellatus* Zelinka, 1928, are synonymized under the former taxon and placed in *Paracentrophyes,* new genus (Neocentrophyidae), represented by a new species from the study area. Other genera represented by the remaining new species are extensively reviewed, species names are corrected to agree in gender, distribution records and keys to adults are compiled, and phylogeny discussed. Species distribution and richness are discussed. A maximum of 13 species representing four genera were found in a single local sample. This is contrasted with similar data from other parts of the world. Certain local species appeared to prefer or were restricted to fine, organically rich, low energy mangrove sediments as opposed to the more heterogeneous sediments with *Thalassia* beds and the even higher energy sediments of the coral reef proper.

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The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha

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Introduction

Since their discovery in 1841 (Dujardin 1851), there have been 119 reports on the distribution of the Kinorhyncha, a phylum of marine meiobenthic invertebrates. Only a few dozen of these reports have involved tropical shallow-water ecosystems.

Five reports have been based on studies of coral reef ecosystems. The most extensive of these studies was conducted on the coral reefs of Baie St. Vincent, New Caledonia (Higgins, 1967). These resulted in the description of two new species, *Echinoderes newcaledoniensis* Higgins, 1967, and *Semnoderes pacificus* Higgins, 1967, and a new distribution record for *Campyloderes macquariae* Johnston, 1938, which was known originally only from Macquarie Island, in polar seas to the south. Three additional species have been reported from coralline sediments of the Red Sea; these include *Echinoderes riedli* Higgins, 1966a, *E. brevicaudatus* Higgins, 1966a, and *Pycnophyes egyptensis* Higgins, 1966a. *Centroderes spinosus* (Reinhard, 1881) has been found in the coralline sandy silt of Castle Harbor, Bermuda (Coull, 1968, 1970), and *Neocentrophyes intermedius* Higgins, 1969b, was reported from fine carbonate sediments of Nosy Bé, Madagasgar.

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Mangrove sediments, normally consisting of a fine mud, are a productive tropical shallow-water habitat for kinorhynchs. Kirsteuer (1964) was the first to make such a report in which he described *Echinoderes caribiensis* Kirsteuer, 1964, from the Bay of Mochima, Venezuela. Several years later, I described *Sphenoderes indicus* Higgins, 1969a, from mangrove mud in the Bay of Kutch, near Jamnigar, India.

Intertidal and subtidal sediments, not specifically identified as coralline in origin or associated with coral reef ecosystems, have accounted for the remaining tropical shallow-water kinorhynch distribution records. From the interstitial habitat of high energy sand beaches or subtidal sand, three species of *Cateria* have been described. Two of these species are restricted to tropical intertidal beaches. The first species, *Cateria styx* Gerlach, 1956, was described from Brazil and reported from Angola, on the opposite side of the South Atlantic, a year later (Delamare-Deboutteville, 1957). Since then it has been recorded from both the original locality and a second locality in Brazil (Higgins, 1968) as well as from several localities on the east coast of India (Ganapati and Rao, 1962; Rao and Ganapati, 1966, 1968; Nagabhushanam, 1972). A second species, *Cateria gerlachi* Higgins, 1968, was described from the east coast of India, reported again from the same locality by Rao and Ganapati (1968), and more recently reported from the Andaman Islands, on the opposite side of the Bay of Bengal (Higgins and Rao, 1979).

Echinoderes pacificus Schmidt, 1974, was reported from subtidal heterogenous sediments of the Galapagos Islands in the Pacific Ocean; all other records are from the Indian Ocean. *Echinoderes bengalensis* (Timm, 1958) was described from subtidal sand at Sonadia Island, near Cox Bazar, Bangladesh. A second species, *E. sonadiae* (Timm, 1958), was described from the same collection but has been synonymized with *E. bengalensis* (Higgins, 1977b) as a juvenile stage of the latter species. This species has also been found along with *Cateria styx* and *C. gerlachi* on the east coast of India (Rao and Ganapati, 1968). *Condyloderes paradoxus* Higgins, 1969a, *Sphenoderes indicus* Higgins, 1969a, and *Neocentrophyes satyai* Higgins, 1969b, were described from the east coast of India. Damodaran (1972) reported an unidentified species of *Echinoderes* from the southwest coast of India. *Echinoderes andamanensis* Higgins and Rao, 1979, *Echinoderes ehlersi* Zelinka, 1913 (originally found in sediment washed from an unidentified invertebrate collected in Zanzibar), and one species of *Pycnophyes* have been reported from the Andaman Islands (Higgins and Rao, 1979). Kinorhynchs have been collected from the Arabian Gulf near Bahrain (Basson et al., 1977) and the estuarine sediments of Shott-al-Arab, Iraq (Saad and Arlt, 1977), but were not identified further.

In April, 1977, I collected kinorhynchs in conjunction with the Smithsonian Institution's long-term study of the coral reef ecosystem at Carrie Bow Cay, Belize (Figure 1). Carrie Bow Cay (16°48.1′N, 88°04.7′W) is a small island, one of many that exist as part of the Belizian Barrier Reef which extends in a north-south direction and separates an extensive lagoon system from the open water of the Caribbean Sea. Two hundred meters north of Carrie Bow Cay, beginning at the edge of a *Thalassia* seagrass community in the shallowest part of the lagoon (1.5–2 m), is a study transect 50 m wide running eastward, 650 m to the open ocean. The lagoon area extends westward 20 km at Carrie Bow Cay. The western portion is as much as 20 m deep, but near the barrier reef, it rarely exceeds 5 m. Shallow seagrass bottoms (*Thalassia testudinium*), patch reefs, and mangrove cays are predominant on the outer barrier platform. A more complete description of this ecosystem has been compiled by Rützler and MacIntyre (1982).

For purposes of sampling in as many representative sediment types as practical within this ecosystem, the first station (RH 442) was established inside the shallow channel separating the two component mangrove cays, 2 km northwest of Carrie Bow Cay, which give Twin Cays (16°50.0′N, 88°06.0′W) its name. The meandering channel, especially near its southwestern limits, attains its maximum depth of 1–2 m where a fine gray calcareous sediment mixed with mangrove and seagrass detritus and sand accumulates. It represents the most minimal energy habitat of the series of stations established in this study.

The second station (RH 443) was 500 m southwest of the first, at a depth of 3.3 m. Here the bottom consisted of some scattered seagrass in a sediment made up of coralline mud mixed with sand and seagrass detritus. The sediment was detectably more coarse than the first station, suggesting a higher energy system.

The third station (RH 444) was located 500 m south of the previous station. The water depth was 3.0 m, the seagrass was more abundant, and the sediment, although similar to the previous station, was finer, suggesting a lesser energy level, possibly related to the increased amount of seagrass at this site.

The last three stations were established on the study transect, beginning with RH 446 at or near the zero point of the transect, 200 m north of Carrie Bow Cay. This station was located at a depth of 2.0 m in the *Thalassia* zone where sediment was mixed *Halimeda* sand and shell with some fine material. The second transect station (RH 447) was established in the sand and rubble zone of the lagoon, 1.5 m deep. Here the sediment consisted of *Halimeda* sand with broken shell and very little fine sediment. No areas of suitable sediments existed between this latter station and

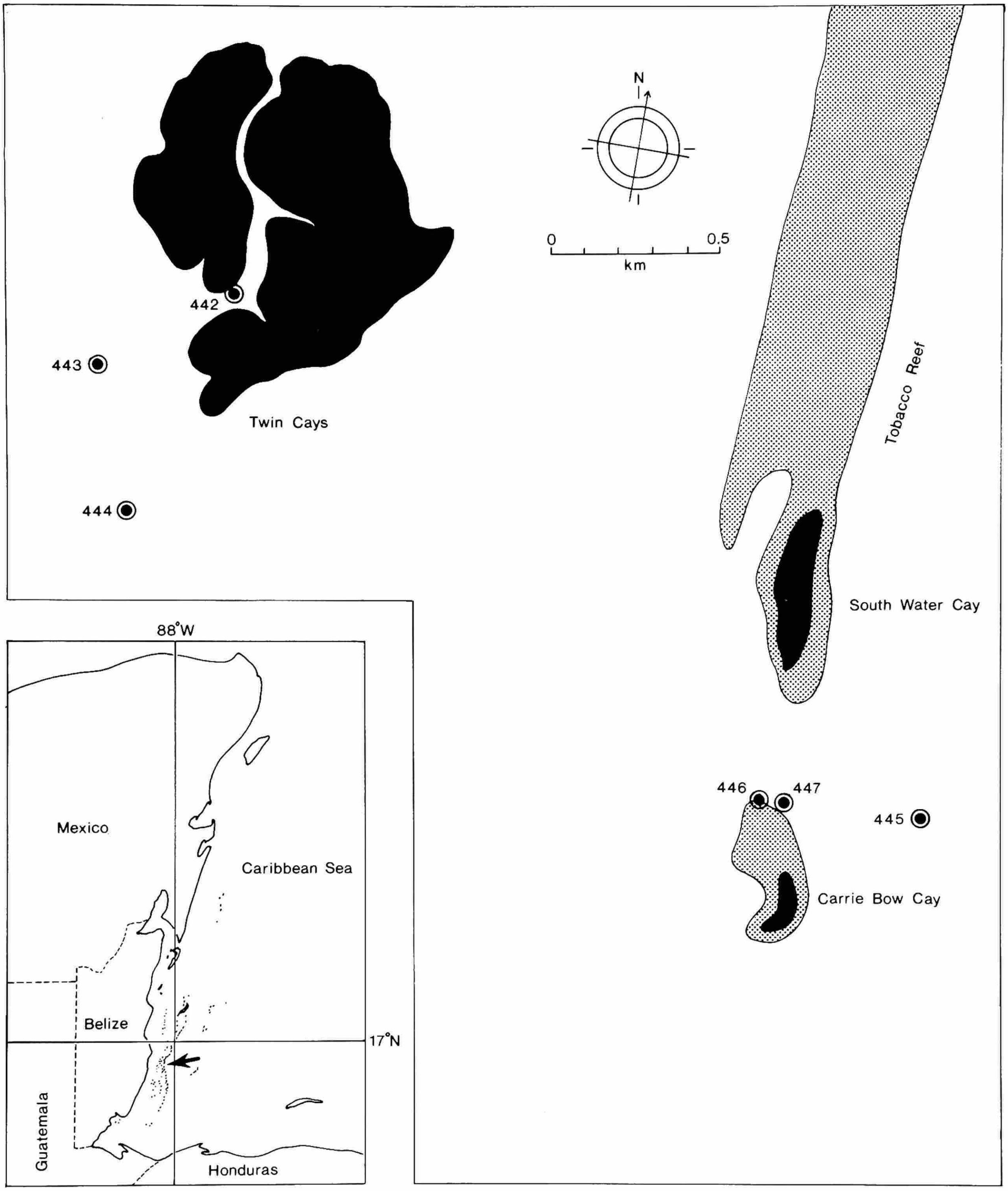


FIGURE 1.—Map of the study sites, Twin Cays and Carrie Bow Cay, Belize, showing the location of the six sampling stations (RH 442–447); area of larger map located on inset by arrow.

the sand trough station (RH 445) located at a depth of 25 m where very fine sand accumulated.

Although the *Thalassia* zone probably represented the lowest energy system within the study transect, all three stations were obviously subjected to periodically if not constantly higher levels of wave energy than the three stations 2 km further back in the lagoon.

METHODS.—In order to maximize the amount of kinorhynchs collected, a meiobenthic dredge was used to collect the surface few centimeters of sediment at each station. Insofar as it was possible, each sample consisted of a similar amount of sediment, about 10 liters, which probably represents a 4 m^2 minimum sample surface area, assuming the 25 cm wide dredge blade removed only the upper centimeter of sediment. Though by no means a quantitative method, samples taken in this manner probably offer a reasonable estimate of the relative abundance of kinorhynchs and their species diversity at a given station.

In the laboratory, sea water was added to each container of sediment in amounts sufficient to facilitate adequate mixing to produce a suspension into which fine air bubbles were introduced. Kinorhynchs have a hydrophobic exoskeleton which, as in several other meiobenthic taxa such as amphipods, taniads, nematodes, ostracodes, etc., transports the animals to the surface film where they remain trapped by the surface tension. After a few moments during which the suspended sediments settled away from the surface film, a half-sheet of standard commercial white inexpensive bond paper was allowed to lightly touch the surface film and was withdrawn quickly, thereby removing the animals trapped in the surface film.

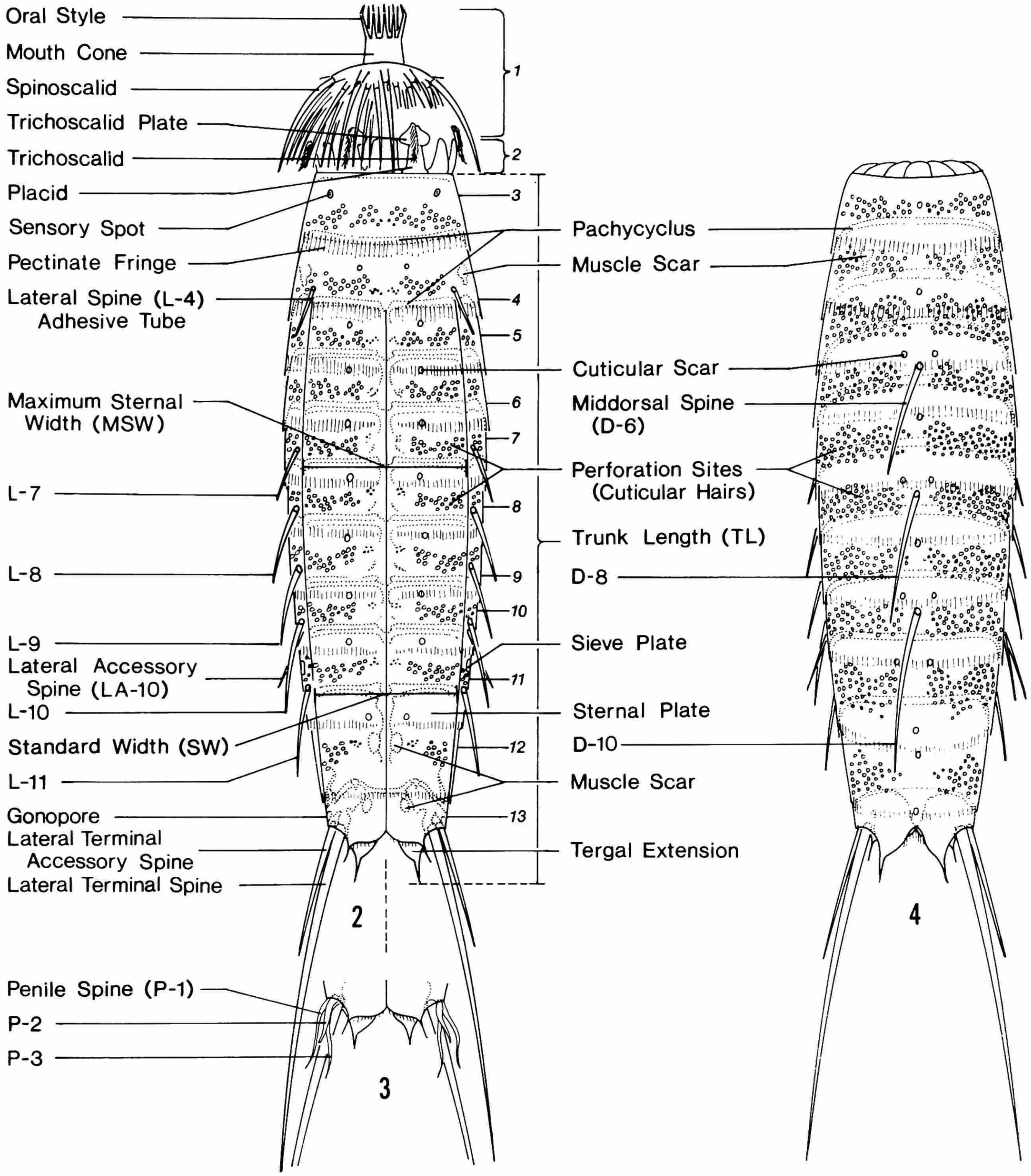
The attached meiobenthic organisms, mostly kinorhynchs and amphipods in this instance, were then washed off the paper onto a 62 μm mesh screen, and the bubbling process repeated until no further specimens were collected.

Specimens were preserved in 5 percent formalin and then transferred to 70 percent ethyl alcohol. A few specimens of what, under low magnification, appeared to be the most common species, were removed for SEM study; the remainder were transferred to a 70 percent ethyl alcohol–5 percent glycerin solution that was allowed to evaporate to glycerin. Most specimens were removed from the glycerin and individually placed in a modified Hoyer's mounting medium, between two coverslips, and positioned on Cobb aluminum slide frames. This mounting procedure allows the slide to be placed on either of its surfaces so that both dorsal and ventral aspects of the specimen can be observed.

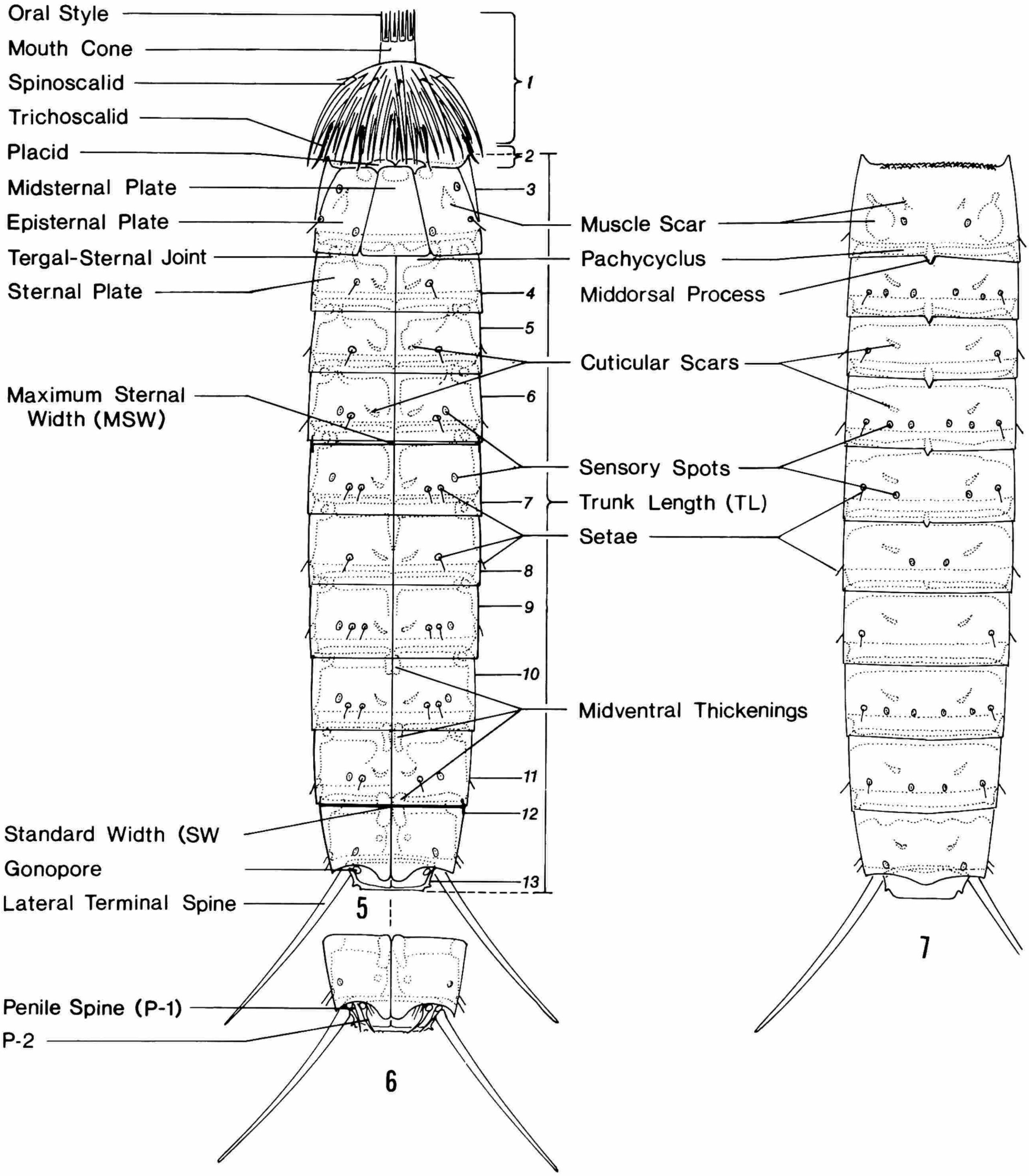
Hoyer's medium is necessary to soften the specimen so that, by judicious manipulation of the coverslip, the specimen will assume a dorsoventral position; this medium also clears the specimen, thus revealing the detailed structure of the exoskeleton.

A disadvantage of normal Hoyer's medium is its tendency to clear the specimen too much, especially over a period of several years. This may be partially overcome by using only 125 grams of chloral hydrate instead of the 200 grams normally required. Coverslips were sealed with an epoxy paint.

Each specimen was studied with the use of Zeiss differential interference contrast optics and analyzed. The resulting data are expressed in a standard format of abbreviations and terminology (Higgins, 1967, 1969a). Measurements are given in micrometers (μm); ratios (i.e., SW/TL) are expressed in percent of the total length (TL) measured on the midline, from the anterior margin of segment 3 (first trunk segment) to the posterior margin of segment 13, exclusive of spines. Maximum sternal width (MSW) is measured at the anteroventral margin of the widest pair of sternal plates as first encountered in measuring each segment from anterior to posterior. Sternal width at segment 12 (SW), or standard width, is measured at the anteroventral margin of the 12th sternal plates. Placids (neck plates of segment 2) and, where applicable, trichoscalid plates of cyclorhagid taxa are numbered beginning with the midventral placid as zero; therefore, those on either side of the midventral placid are each number 1, those next in sequence, number 2, etc.



FIGURES 2–4.—Cyclorhagid (*Echinoderes*) morphology: 2, ventral view, female; 3, same, male, terminal segment; 4, dorsal view, male.



FIGURES 5–7.—Homalorhagid (*Pycnophyes*) morphology: 5, ventral view, female; 6, same, male, terminal segment; 7, dorsal view, male.

Middorsal spines (D), lateral spines (L), and lateral accessory appendages (LA) are numbered by segment, and their cumulative mean length expressed by Dm, Lm, and LAm, respectively. Measurements are given for the lateral terminal spines (LTS), lateral terminal accessory spines (LTAS), midterminal spine (MTS), and penile-spines (P) in males. Some lateral spines are thinner than others, and before the mounting medium clears internal tissue, glandular material often can be noted at their base. They are hollow structures when viewed by SEM. On this basis they are assumed to be adhesive tubes. Thus the adhesive tubes of the fourth segment (L-4) are considered as homologues of other lateral spines. Appendages that function as adhesive tubes will be noted in the appropriate section of the text or tabular data. Figures 2–4 provide a reference to the morphological characters used in the description of a typical cyclorhagid kinorhynch (*Echinoderes*); Figures 5–7 provide the same for a typical homalorhagid kinorhynch (*Pycnophyes*).

Specimens mentioned in this paper are deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the former United States National Museum (USNM).

The following FAO sea area designations are used in tables and maps.

ANE	Atlantic Northeast
ANW	Atlantic Northwest
ASE	Atlantic Southeast
ASW	Atlantic Southwest
INE	Indo-Pacific Northeast
INW	Indo-Pacific Northwest
ISEW	Indo-Pacific Southeast-West
ISW	Indo-Pacific Southwest
MED	Mediterranean
PNE	Polar Northeast
PNW	Polar Northwest
PSE	Polar Southeast
PSW	Polar Southwest

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Order CYCLORHAGIDA Zelinka, 1896

Family ECHINODERIDAE Bütschli, 1876

Genus *Echinoderes* Claparède, 1863

Key to Adults of *Echinoderes*

1. Middorsal spines present 8
   Middorsal spines absent 2
2. Lateral spines (adhesive tubes) on segment 4 3
   Lateral spines (adhesive tubes) absent on segment 4 5
3. Additional lateral spines on segments 7–11; lateral accessory spine on segment 10 .... ***E. horni,*** new species
   Additional lateral spines on segments 10 and/or 11; none on segment 7; no lateral accessory spine 4

4. First 2 trunk segments enlarged, swollen; lateral spines on segments 4 and 10 with lateral seta on segment 12 .... ***E. capitatus*** (Zelinka, 1928)
   First 2 trunk segments not enlarged or swollen; lateral spines on segments 4, 10, and 11 .... ***E. andamanensis*** Higgins and Rao, 1979
5. Lateral spines on segments 7, 10, and 11 .. ***E. caribiensis*** Kirsteuer, 1964
   Lateral spines on segments 7 and 10 or absent 6
6. Lateral terminal spines longer than last 4 trunk segments (about one-half the trunk length) .... ***E. maxwelli*** (Omer-Cooper, 1957)
   Lateral terminal spines shorter than last 3 trunk segments 7
7. Lateral spines on segments 7 and 10 long (30–40 μm) and thin .... ***E. bengalensis*** (Timm, 1958)
   Lateral spines on segments 7 and 10 absent, not visible, or very short (10 μm) and thin .... ***E. coulli*** Higgins, 1977b
8. Middorsal spines on segments 6–10 17
   Middorsal spines otherwise 9
9. Middorsal spines on segments 6 and 9 only .... ***E. citrinus*** Zelinka, 1928
   Middorsal spines otherwise 10
10. Middorsal spines on 6, 8, and 10 only 11
    Middorsal spines otherwise 15
11. Lateral accessory spines present 12
    Lateral accessory spines absent .... ***E. arlis*** Higgins, 1966b
12. Lateral spines (adhesive tubes) present on segment 4 13
    Lateral spines (adhesive tubes) absent on segment 4 14
13. Lateral accessory spines on segments 4, 8–11 .... ***E. newcaledoniensis*** Higgins, 1967
    Lateral accessory spines on segment 10 only .... ***E. wallaceae,*** new species
14. Lateral terminal spines short (36–45 μm), stubby (LTS/TL 14–20 percent) .... ***E. abbreviatus,*** new species
    Lateral terminal spines long (140–172 μm), thin (LTS/TL 45–64 percent) .... ***E. riedli*** Higgins, 1966a
15. Middorsal spines on segments 6, 7, and 10 only.. ***E. druxi*** d'Hondt, 1973
    Middorsal spines otherwise 16
16. Middorsal spines on segments 6, 7 (possibly 8), and 9 .... ***E. setiger*** Greeff, 1968
    Middorsal spines on segments 7–10 only ..... ***E. tchefouensis*** Lou, 1934
17. Lateral spines (adhesive tubes) present on segment 4 27
    Lateral spines (adhesive tubes) absent on segment 4 18
18. Lateral spines on segments 6–12 .... ***E. agigens*** Băcescu, 1968
    Lateral spines otherwise 19
19. Lateral spines on segments 7–12 (12th spine may be very small in males) 20
    Lateral spines otherwise 21
20. Terminal tergal extensions truncate, with straight mesial border, middorsal spines relatively short, 13–30 μm, Dm/TL 5–8 percent .... ***E. truncatus,*** new species

Terminal tergal extensions pointed, bladelike, with curved mesial border; middorsal spines relatively long, 25–50 μm, Dm/TL 10 percent .... ***E. pilosus*** Lang, 1949

21. Lateral spines on segments 6–9 .... ***E. canariensis*** Greeff, 1869
    Lateral spines otherwise 22
22. Lateral spines on segments 7–11 23
    Lateral spines otherwise 26
23. Lateral terminal spines stubby, shorter than segment 12 .... ***E. brevicaudatus*** Higgins, 1977a
    Lateral terminal spines narrowly elongate, longer than segments 12 and 13 combined 24
24. Ventral surface of first and penultimate trunk segments hirsute, perforation sites (hairs) numerous and distinct; dorsolateral cuticular scars not prominent on segments 6–12 .... ***E. bookhouti*** Higgins, 1964a
    Ventral surface of first and penultimate trunk segments with few scattered hairs, perforation sites (hairs) not numerous but distinct; dorsolateral cuticular scars prominent on segments 6–12 25
25. LTS/TL nearly 40 percent; MSW/TL about 15 percent; prominent pectinate fringe on ventral margin of first trunk segment, LTAS/LTS of female 50–70 percent .... ***E. remanei*** (Blake, 1930)
    LTS/TL 24–31 percent; MSW/TL about 20 percent; moderate pectinate fringe on ventral margin of first trunk segment; LTAS/LTS of female 33 percent .... ***E. pennaki*** Higgins, 1960
26. Lateral spines on segment 11 twice the length of those on anterior segments .... ***E. levanderi*** Karling, 1954
    Lateral spines on segment 11 only slightly longer than those on anterior segments .... ***E. elongatus*** (Nyholm, 1947b)
27. Lateral spines on segments 3–12 (probably an error, no lateral spines likely on segments 3, 5, or 6) .... ***E. steineri*** (Chitwood, 1951)
    Lateral spines on segments 4 (adhesive tubes), 7–12 28
28. Lateral accessory spines on segment 10 29
    Lateral accessory spines not on segment 10 31
29. Prominent sensory spots on either side of ventral midline near anterior margin of segment 4 30
    Sensory spots not on either side of ventral midline near anterior margin of segment 4 .... ***E. dujardinii*** Claparède, 1863
30. Middorsal spines very short, 6–13 μm; Dm/TL 2.5–3 percent .... ***E. gerardi*** Higgins, 1978
    Middorsal spines long, 20–45 μm; Dm/TL 7–9 percent .... ***E. kozloffi*** Higgins, 1977a
31. Lateral spine on segment 12 short, distinct, 12–17 μm, curved away from body; LTS/TL 27–36 percent .... ***E. pacificus*** Schmidt, 1974
    Lateral spine on segment 12 similar to preceding lateral spines; LTS/TL 45 percent or more 32
32. Lateral spines on segment 12 same length or longer than those on segment 11 33

Lateral spines on segment 12 shorter than those on segment 11 34

33. Trunk segments hirsute, numerous perforation sites (hairs) in distinctive pattern; ventral border of segment 12 without distinct pectinate fringe .... ***E. ehlersi*** Zelinka, 1913
34. Lateral spines on segment 12 each with adjacent seta .... ***E. ferrugineus*** Zelinka, 1928

Lateral spines on segment 12 without adjacent setae 35

35. LTAS/LTS 23 percent .... ***E. worthingi*** Zelinka, 1928

LTAS/LTS 32 percent .... ***E. sublicarum*** Higgins, 1977b

Echinoderes abbreviatus, new species

FIGURES 8–19

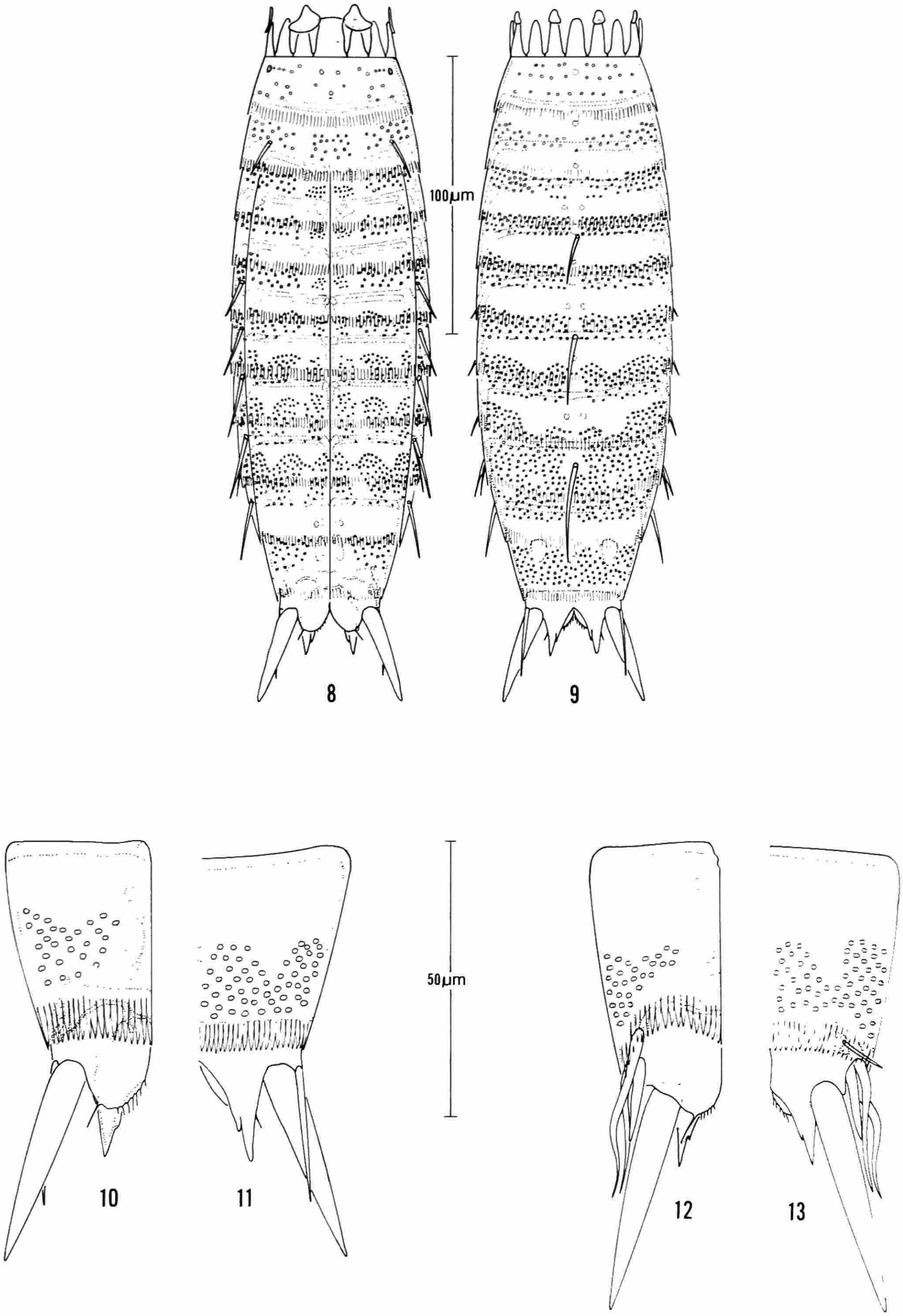
DIAGNOSIS.—Middorsal spines on segments 6, 8, and 10, increasing uniformly in length posteriorly; lateral spines on segments 4, 7–11 with what are thought to be adhesive glands at base of L-4; lateral accessory spine dorsally adjacent to L-10; lateral terminal spines short and stubby, 36–45 μm; 14.2–20.7 percent of trunk length.

DESCRIPTION.—Adults (Figures 8–19), trunk length 200–272 μm; MSW-8 48–61 μm, 19.4–29.0 percent of trunk length; SW 35–46 μm, 16.0–21.1 percent of trunk length. Second segment with 16 placids, about 14 μm long, wide posteriorly, narrow anteriorly; midventral placid wider (12 μm) than others (8–9 μm), anterior margin slightly expanded; trichoscalid plates 1 and 3 large, 10–11 μm wide at expanded portion overlapping placid (Figure 8); dorsal trichoscalid plates 5 and 7 small, about the same width as tip of placids (Figure 9).

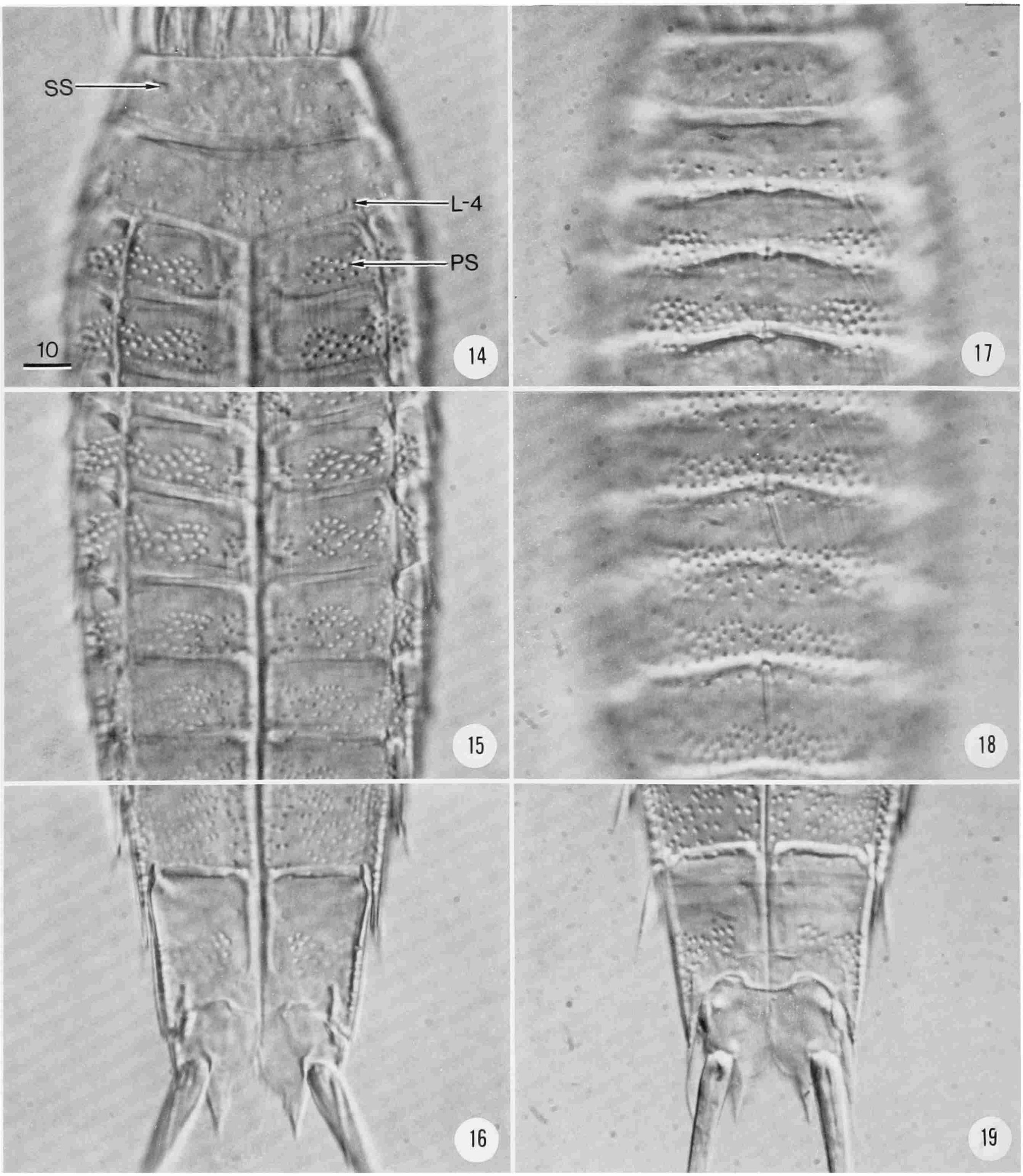
Trunk segments (Figures 14–19) with numerous cuticular perforation sites (where hairs emerge) producing a distinctive pattern on each segment (note: only the perforation sites are illustrated in Figures 8–13 to avoid masking other structural details); pectinate fringe on posterior tergal and sternal margins of segments 3–12; extensions of terminal tergal plate distinctive, narrowly elongate with primary and secondary points (Figures 11, 13); terminal sternal plates rounded, each with a small (5–6 μm) spinose process on the lateral margin and fringed on the mesial margin (Figures 10, 12).

Middorsal spines on segments 6, 8, and 10, 13–38 μm long, increasing in length posteriorly; lateral spines on segments 4, 7–11, 12–22 μm long, increasing in length posteriorly, those on segments 4 and 7 slightly thinner (adhesive tubes), each with basal adhesive gland; thin lateral accessory spines, 10–19 μm long dorsally adjacent to lateral spines on segment 10; lateral terminal spines short, stubby, 36–45 μm long, 14.2–20.7 percent of trunk length; lateral terminal accessory spines of female, 22–25 μm long, 9.5–12.0 percent of trunk length, males without lateral terminal accessory spines, each replaced by 3 penile spines; anteriormost penile spines (P-1), 25–26 μm long, mesially adjacent penile spines (P-2), 14–16 μm long, posteriorly adjacent penile spines (P-3), 24–26 μm long; male with setae, 9 μm long near anterolateral margins of terminal tergal plate (Figure 13).

Pachycycli well developed (Figures 14–19), forming a distinctive pattern at ventral midline, midventral thickenings (anteromesial portion of each sternal pachycyclus or "mittlewülste") appear especially thick and distinct; prominent muscle scars on either side of dorsal and ventral midlines of segment 12; sensory spots (appearing as circular or slightly oval thin cuticular areas about 2 μm diameter) near the anterolateral margins of segment 3 (Figure 8), others probably present but not easily distinguished; other cuticular spots noted middorsally on segments 3–5, 7, 9, and 12 and subdorsally on segments 6, 8, and 10; ventral cuticular spots on either side of ventral midline, anterior to muscle scars on segment 12 (note: the term cuticular spots is applied to thin areas of the cuticle which indicate unconfirmed sensory spots or possibly muscle scars). Sieve



FIGURES 8–13.—*Echinoderes abbreviatus*, new species: 8, neck and trunk segments, ventral view, holotypic female (USNM 69963); 9, same, dorsal view; 10, same, segments 12, 13, lateral half, ventral view; 11, same, dorsal view; 12, same, ventral view, allotypic male (USNM 69964); 13, same, dorsal view.


SS
L-4
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plate, 4 μm diameter, noted near posteroventral margin of tergal plate, segment 11 of one female only.

Males differ from females by presence of dorsolateral setae on segment 12, lack of lateral terminal accessory spines and presence of 3 pairs of penile spines.

Morphometric data for adult specimens are shown in Table 1.

HOLOTYPE.—Adult female, TL 216 μm (Figures 8–11, 14–18), Twin Cays, stat RH 442, Belize (16°50.0'N, 88°06.0'W), 8 Apr 1977, col. R.P. Higgins, USNM 69963.

ALLOTYPE.—Adult male, TL 216 μm (Figures 12, 13, 19), other data as for holotype, USNM 69964.

PARATYPES.—Eight females and 4 males, TL 200–272 μm, other data as for holotype, USNM 69965.

REMARKS.—*Echinoderes abbreviatus* most closely resembles *Echinoderes brevicaudatus* from the Red Sea. This new species is smaller (200–272 μm) than *E. brevicaudatus* (318–417 μm) but similar in trunk shape and other relative proportions including the short, stubby, lateral terminal spines that result in a LTS/TL of 17 percent in both species. *Echinoderes abbreviatus* differs from *E. brevicaudatus* by its middorsal spine formula 6, 8, 10 (as opposed to 6–10 in *E. brevicaudatus*), its longer middorsal spine length (12–18 μm in *E. brevicaudatus*, 13–38 μm in *E. abbreviatus*), the lack of notably coarse fringe on the ventral margin of segment 4 and lateroventral margins of segments 9 and 10, and the presence of a lateral accessory spine dorsally adjacent to each lateral spine on segment 10.

FIGURES 14–19.—*Echinoderes abbreviatus*, new species: 14, segments 2–6, ventral view, holotypic female (USNM 69963); 15, same, segments 6–9, ventral view; 16, same, segments 11 (lower half), 12, and 13, ventral view; 17, same, segments 2–6, dorsal view; 18, same, segments 6–9, dorsal view; 19, same, segments 11 (lower half), 12, and 13, ventral view, allotypic male (USNM 69964). (Interference contrast photographs all with same scale (in μm) as shown in Figure 14; SS = sensory spot, PS = perforation site.)

Three other species of *Echinoderes* share the same middorsal spine formula of 6, 8, and 10 with *E. abbreviatus*, but none share the same trunk-lateral terminal spine configuration, and all are much larger. *Echinoderes newcaledoniensis* has a more elongate trunk, 197–350 μm, and much longer lateroterminal spines, 104–267 μm, 30–80 percent of the trunk length depending upon its habitat (fine coralline mud—shorter spines, coarse coral detritus—longer spines). The New Caledonian species also differs in having lateral accessory spines on segments 4, 8–11 instead of only on segment 10 as in *E. abbreviatus*. Males of both species have a small seta situated dorsolaterally and slightly anterior to the penile spines.

Echinoderes riedli, a second species with a middorsal spine formula of 6, 8, 10, like *E. newcaledoniensis*, lacks the distinctive short, stubby, lateral terminal spines. Females of *E. riedli* share the same lateral spine formula including the presence of a lateral accessory spine on segment 10. In addition, males of *E. riedli* possess a small spine or seta situated dorsolaterally and slightly anterior to the penile spines as in both *E. newcaledoniensis* and *E. abbreviatus*. Like *E. newcaledoniensis*, *E. riedli* has a relatively long trunk (268–316 μm) and long lateral terminal spines, (148–172 μm, 64–52 percent of the trunk length). *Echinoderes riedli* was originally described from sandy coral mud from the Red Sea at Al-Ghardaqa, Egypt (Higgins, 1966a). Later (Higgins, 1978), *E. riedli* was found in the sediment covering stones in the very shallow Punic Port in Salammbo (Carthage), Tunisia.

The last species with the same middorsal spine formula of 6, 8, 10, *E. arlis* is the only one of this group not inhabiting tropical waters. *Echinoderes arlis* was found north of Pt. Barrow, Alaska, in the Arctic Ocean. It, too, lacks the relatively wide trunk and short, stubby, lateral terminal spines. It has, like *E. riedli* and *E. newcaledoniensis*, an elongated trunk (380–420 μm) and relatively long lateral terminal spines (210–238 μm, 50–60 percent of the trunk length).

ETYMOLOGY.—The name of this species is from the Latin *abbreviatus* (shortened).

TABLE 1.—Measurements (μm) and indices (%) for *Echinoderes abbreviatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	5	216–248	225.6	13.5	6.0	6.0
	♀	9	200–272	228.7	25.2	8.4	11.0
	♂♀	14	200–272	227.6	21.2	5.7	9.3
SW	♂	5	35–43	40.8	3.3	1.5	8.0
	♀	8	37–46	43.1	3.1	1.1	7.2
	♂♀	13	35–46	42.2	3.2	0.9	7.7
SW/TL	♂	5	16.0–19.3	18.0	1.4	0.6	7.7
	♀	8	16.0–21.1	19.0	2.3	0.8	12.1
	♂♀	13	16.0–21.1	18.6	2.0	0.6	10.7
MSW-8	♂	5	48–59	55.0	5.2	2.3	9.4
	♀	8	58–61	58.6	1.1	0.4	1.8
	♂♀	13	48–61	57.2	3.6	1.0	6.3
MSW/TL	♂	5	19.4–27.4	24.5	3.5	1.6	14.3
	♀	8	21.2–29.0	25.8	2.8	1.0	10.9
	♂♀	13	19.4–29.0	25.3	3.0	0.8	11.9
Dm	♂	4	21.7–24.7	23.4	1.6	0.8	6.8
	♀	9	21.0–28.0	25.4	2.4	0.8	9.5
	♂♀	13	21.0–28.0	24.8	2.3	0.7	9.4
Dm/TL	♂	4	9.0–11.2	10.3	1.0	0.5	10.1
	♀	9	9.6–12.7	11.2	1.3	0.4	11.6
	♂♀	13	9.0–12.7	10.9	1.3	0.4	11.5
D-6	♂	5	13–18	16.2	2.1	0.9	12.7
	♀	9	13–21	16.2	3.0	1.0	18.4
	♂♀	14	13–21	16.2	2.6	0.7	16.1
D-8	♂	4	18–24	21.5	2.5	1.26	11.7
	♀	9	18–29	23.9	3.7	1.2	15.6
	♂♀	13	18–29	23.2	3.5	1.0	15.1
D-10	♂	5	29–34	32.2	2.1	0.9	6.4
	♀	9	32–38	36.2	1.9	0.6	5.3
	♂♀	14	29–38	34.8	2.8	0.7	7.9
Lm	♂	2	16.9–17.3	17.1	0.3	0.2	1.7
	♀	6	16.9–17.8	17.5	0.6	0.2	3.2
	♂♀	8	16.9–17.8	17.4	0.5	0.2	3.0
Lm/TL	♂	2	7.8–8.0	7.9	0.1	0.1	1.8
	♀	6	6.2–8.5	7.2	0.9	0.4	12.4
	♂♀	8	6.2–8.5	7.4	0.8	0.3	11.1
L-4 (AT)	♂	5	12–14	13.2	0.8	0.4	6.3
	♀	8	12–15	13.3	0.9	0.3	6.7
	♂♀	13	12–15	13.2	0.8	0.2	6.3
L-7	♂	3	13–15	14.3	1.1	0.7	8.1
	♀	7	13–16	14.7	1.3	0.5	8.5
	♂♀	10	13–16	14.4	1.1	0.3	7.5
L-8	♂	5	16–19	18.2	1.3	0.6	7.2
	♀	8	13–21	18.6	2.6	0.9	14.0
	♂♀	13	13–21	18.5	2.2	0.6	11.6

TABLE 1.—Continued

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
L-9	♂	5	19–19	19.0	0.0	0.0	0.0
	♀	9	20–22	20.9	0.8	0.3	3.7
	♂♀	14	19–22	20.2	1.1	0.3	5.6
L-10	♂	5	19–21	19.6	0.9	0.4	4.6
	♀	9	19–22	21.1	1.1	0.4	5.0
	♂♀	14	19–22	20.6	1.2	0.3	5.9
LA-10	♂	2	16–19	17.5	2.1	1.5	12.1
	♀	5	10–11	10.4	0.6	0.2	5.3
	♂♀	7	10–19	12.1	3.4	1.2	28.4
L-11	♂	5	19–20	19.2	0.5	0.2	2.3
	♀	9	19–27	21.8	2.3	0.8	10.7
	♂♀	14	19–27	20.9	2.3	0.6	10.8
LTS	♂	4	38–45	41.3	3.0	1.5	7.2
	♀	9	36–41	37.9	1.4	0.5	3.6
	♂♀	13	36–45	38.9	2.5	0.7	6.3
LTS/TL	♂	4	16.8–20.7	18.1	1.8	0.9	9.6
	♀	9	14.2–19.2	16.8	1.8	0.6	10.7
	♂♀	13	14.2–20.7	17.2	1.8	0.5	10.5
LTAS	♀	9	22–25	23.9	0.8	0.3	3.3
LTAS/TL	♀	9	9.5–12.0	10.6	10.0	0.3	9.3
P-1	♂	5	25–26	25.8	0.5	0.2	1.7
P-2	♂	5	14–16	14.4	0.9	0.4	6.2
P-3	♂	5	24–26	25.0	1.0	0.5	4.0

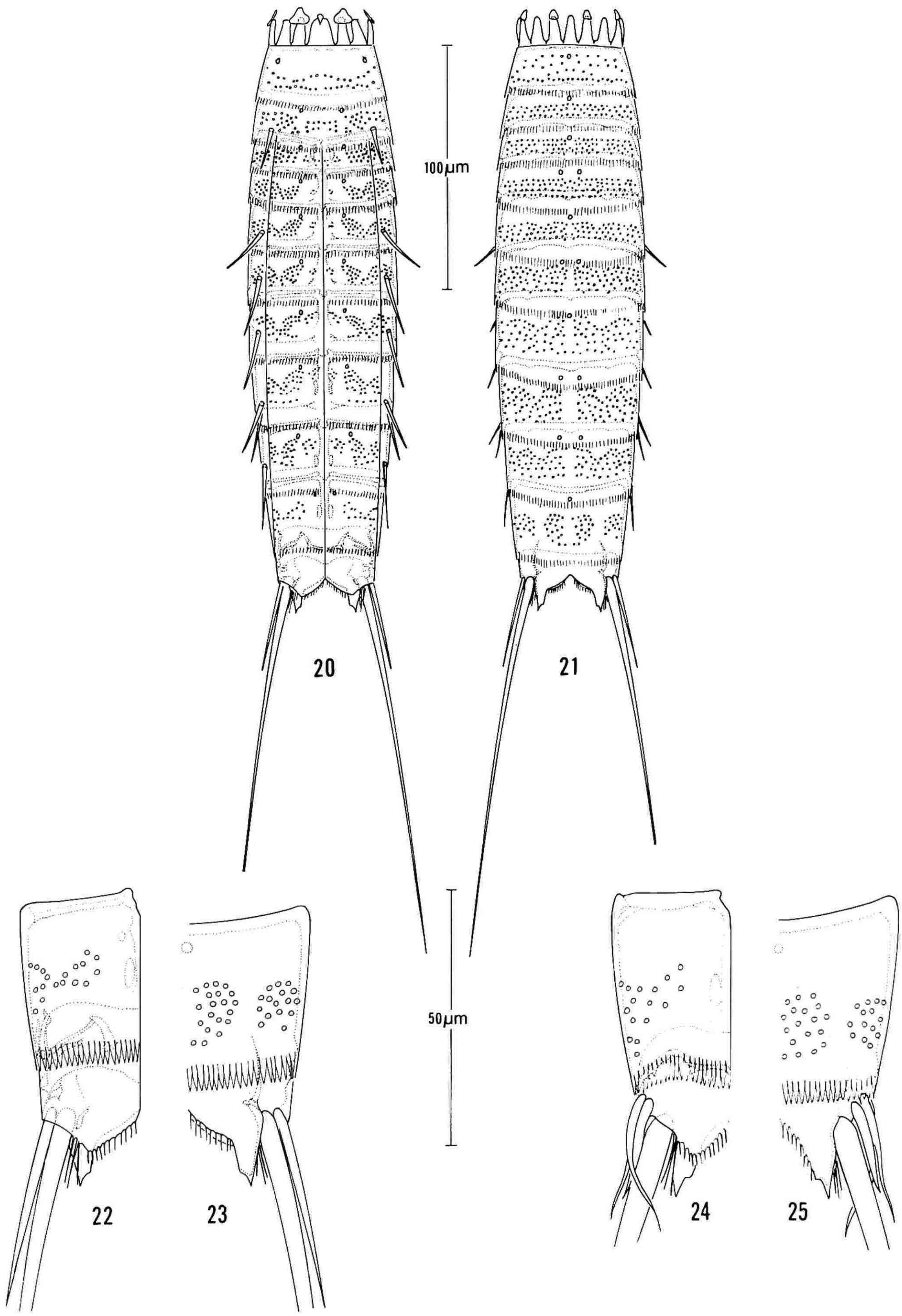
Echinoderes horni, new species

FIGURES 20–31

DIAGNOSIS.—Middorsal spines absent; lateral spines present on segments 4, 7–11 with adhesive glands at the base of L-4 and L-7; lateral accessory spines dorsally adjacent to L-10; lateral terminal spines very long, 140–176 μm, 62.5–89.8 percent of trunk length.

DESCRIPTION.—Adults (Figures 20–31), trunk length 196–268 μm; MSW-8 43–51 μm, 17.9–24.5 percent of trunk length; SW 38–45 μm, 14.3–22.0 percent of trunk length. Second segment with 16 placids, about 10 μm long, wide posteriorly, narrow anteriorly; midventral placid wider (12 μm) than others (6 μm), anterior margin of midventral placid slightly truncate with small, thin toothlike plate overhanging the margins (Figure 20), other placids expanded laterally to a slight point; ventral trichoscalid plates 1 and 3 large, 8 μm wide at expanded portion of overlapping placid (Figure 20); dorsal trichoscalid plates 5 and 7 small, no wider than tip of placids (Figure 21).

Trunk segments moderately pilose (Figures 20–31) with cuticular perforation sites producing a distinctive pattern on each segment; pectinate fringe moderately visible on posterior margin of segments 4–11, lighter on other trunk segments; extensions of terminal tergal plate distinct, relatively small, narrow, widely separated, with primary point only, slightly fringed (Figures 23–25); terminal sternal extensions slightly pointed with fringed mesial margins, several long bristles protrude from lateral margin adjacent to lateral terminal spine (Figures 21, 24). Middorsal spines absent; lateral spines on segments 4, 7–11, 13–27 μm long, increasing slightly in length posteriorly, those on segments 4 and 7 thinner (adhesive



FIGURES 20–25.—*Echinoderes horni*, new species: 20, neck and trunk segments, ventral view, holotypic female (USNM 69966); 21, same, dorsal view; 22, same, segments 12, 13, lateral half, ventral view; 23, same, dorsal view; 24, same, ventral view, allotypic male (USNM 69967); 25, same, dorsal view.

TABLE 2.—Measurements (μm) and indices (%) for *Echinoderes horni* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	12	208–268	241.7	18.0	5.2	7.5
	♀	15	196–268	228.0	16.6	4.3	7.3
	♂♀	27	196–268	234.1	18.3	3.5	7.8
SW	♂	12	40–43	41.9	1.2	0.4	3.0
	♀	12	38–45	42.0	2.6	0.7	6.1
	♂♀	24	38–45	42.0	2.0	0.4	4.7
SW/TL	♂	12	14.9–19.2	17.4	1.4	0.4	8.3
	♀	12	14.3–22.0	18.6	2.1	0.6	11.3
	♂♀	24	14.3–22.0	18.0	1.9	0.4	10.3
MSW-8	♂	12	48–51	49.8	1.1	0.3	2.3
	♀	12	43–48	47.4	1.5	0.4	3.2
	♂♀	24	43–51	48.6	1.8	0.4	3.6
MSW/TL	♂	12	18.5–23.1	20.6	1.3	0.4	6.3
	♀	12	17.9–24.5	20.9	1.6	0.5	7.5
	♂♀	24	17.9–24.5	20.8	1.4	0.3	6.7
Lm	♂	11	21.3–22.4	21.8	0.4	0.1	1.7
	♀	13	20.9–24.0	22.6	1.2	0.3	5.1
	♂♀	24	20.9–24.0	22.3	1.0	0.2	4.3
Lm/TL	♂	11	8.1–9.6	9.0	0.6	0.2	6.4
	♀	13	7.9–11.2	10.0	1.0	0.3	10.1
	♂♀	24	7.9–11.2	9.5	1.0	0.2	10.1
L-4 (AT)	♂	11	16	16.0	0.0	0.0	0.0
	♀	13	13–19	15.9	2.0	0.6	12.6
	♂♀	24	13–19	15.9	1.4	0.3	9.1
L-7	♂	11	16–18	17.1	1.0	0.3	6.1
	♀	14	16–26	19.9	3.9	1.1	19.7
	♂♀	25	16–26	18.6	3.3	0.7	17.6
L-8	♂	12	18–26	23.8	2.1	0.6	8.7
	♀	15	21–26	24.0	1.9	0.5	7.9
	♂♀	27	18–26	23.9	1.9	0.4	8.1
L-9	♂	12	22–26	24.8	1.2	0.3	4.8
	♀	15	22–27	25.1	1.4	0.4	5.7
	♂♀	27	22–27	25.0	1.3	0.3	5.3
L-10	♂	12	24–26	25.7	0.9	0.3	3.5
	♀	15	25–27	26.2	0.8	0.2	3.0
	♂♀	27	24–27	26.0	0.9	0.2	3.3
LA-10	♂	12	16–20	17.7	1.4	0.4	8.1
	♀	13	18–21	19.6	1.0	0.3	5.3
	♂♀	25	16–21	18.7	1.5	0.3	8.3
L-11	♂	12	21–27	26.2	1.7	0.5	6.5
	♀	14	25–27	26.5	0.7	0.2	2.5
	♂♀	26	21–27	26.4	1.2	0.2	4.7

TABLE 2.—Continued

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
LTS	♂	12	140–176	167.9	10.2	3.0	6.1
	♀	15	145–176	164.1	10.5	2.7	6.4
	♂♀	27	140–176	165.8	10.4	2.0	6.3
LTS/TL	♂	12	62.5–77.2	69.7	5.0	1.4	7.2
	♀	15	63.6–89.8	72.5	8.8	2.3	12.1
	♂♀	27	62.5–89.8	71.2	7.4	1.4	10.3
LTAS	♀	15	34–43	38.4	2.7	0.7	7.0
LTAS/TL	♀	15	12.5–19.6	16.9	1.9	0.5	11.2
P-1	♂	10	11–16	14.5	1.8	0.6	12.7
P-2	♂	11	14–20	17.0	1.7	0.5	10.2
P-3	♂	10	24–29	27.6	1.7	0.5	6.0

tubes), each with basal adhesive gland; thin lateral accessory spines, 12–21 μm long, dorsally adjacent to lateral spines on segment 10; lateral terminal spines very long, thin, 140–176 μm, 62.5–89.8 percent of trunk length, lateral terminal accessory spines of female, 34–43 μm long, 12.5–19.6 percent of trunk length; males without lateral terminal accessory spines, with 3 pairs of penile spines in same position; anteriormost penile spines (P-1) 11–16 μm long, mesially adjacent penile spines (P-2) 14–20 μm long, posteriorly adjacent penile spines 24–29 μm long (Figures 24, 25).

Pachycyli well developed (Figures 26–31), forming a distinctive pattern at ventral midline; oval muscle scars apparent ventrally near midline of segments 5, 10–12; cuticular spots anterolateral on ventral surface of segment 3, nearer to midline on segment 4–12 (Figure 20), small, round cuticular spots near anterior dorsal midline of segments 3–5, 7, 9, and 12, on either side of dorsal midline on segments 6, 8, 10, and 11 (Figure 21); few cuticular perforation sites on anterior and posterior segments but with consistently distinctive pattern (Figures 20, 21).

Males differ from females principally by lack of lateral terminal accessory spines and presence of 3 pairs of penile spines.

Morphometric data for adult specimens are shown in Table 2.

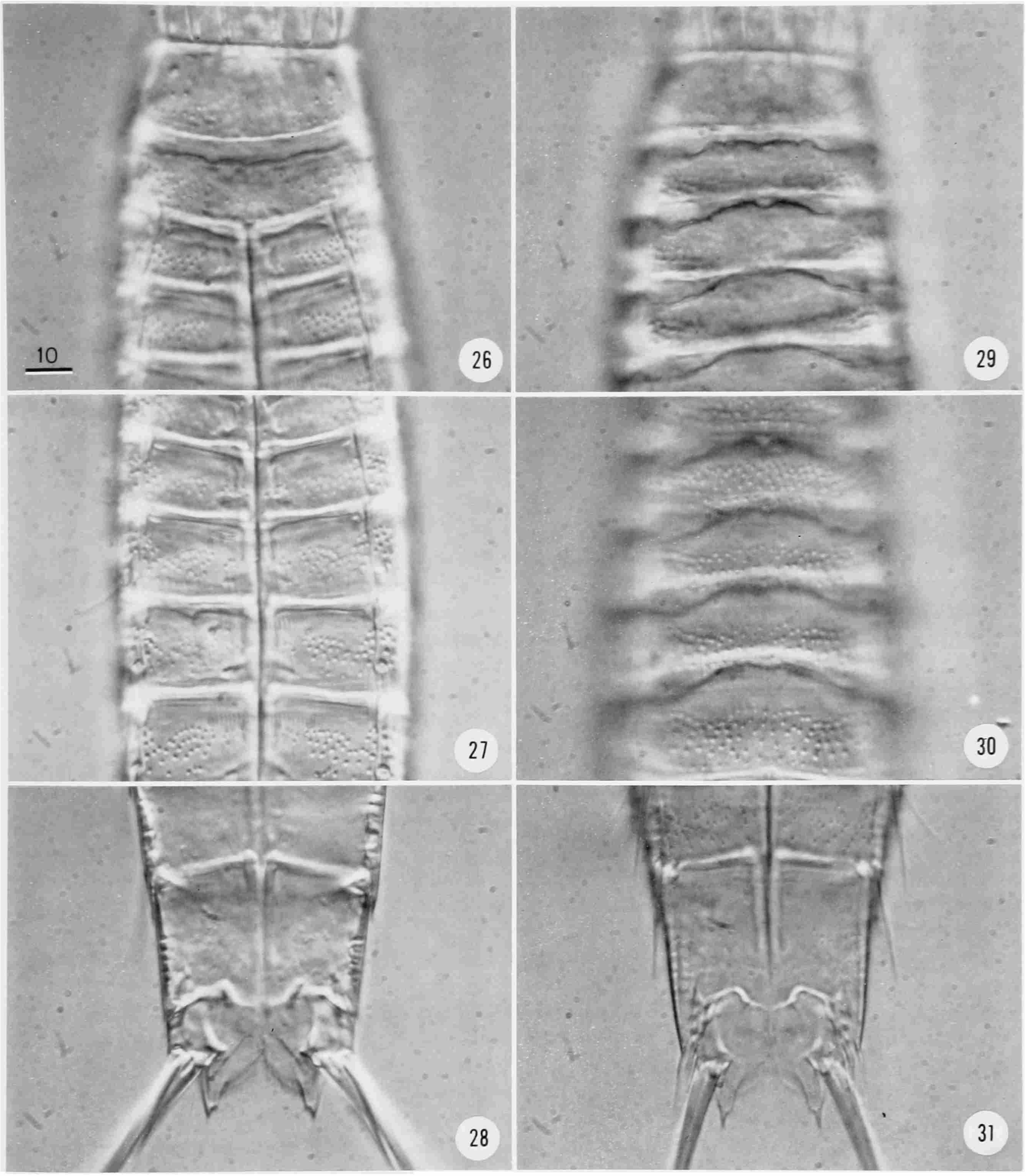
HOLOTYPE.—Adult female, TL 232 μm (Figures 20–23, 26–30), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69966.

ALLOTYPE.—Adult male, TL 228 μm (Figures 18, 19, 25), other data as for holotype, USNM 69967.

PARATYPES.—Eight females and 9 males, TL 212–268 μm, other data as for holotype, USNM 69968; 3 females and 1 male, TL 196–236 μm, Twin Cays, sta RH 444, other data as for holotype, USNM 69969; 3 females, TL 220–268 μm, Carrie Bow Cay, sta RH 446, Belize (16°48.1′N, 88°04.7′W), 10 Apr 1977, col. R.P. Higgins, USNM 69970; 1 male, TL 224 μm, Carrie Bow Cay, sta RH 447, Belize, 10 Apr 1977, col. R.P. Higgins, USNM 69971.

REMARKS.—*Echinoderes horni* shares its lack of middorsal spines with only six of the 33 species in the genus, none of which have the same lateral spine formula. The most similar species is *Echinoderes andamanensis*, but this latter species has thin

FIGURES 26–31.—*Echinoderes horni*, new species: 26, segments 3–6, ventral view, holotypic female (USNM 69966); 27, same, segments 6–9, ventral view; 28, same, ventral view, segments 11 (lower half), 12, and 13; 29, same, segments 3–6, dorsal view; 30, same, segments 6–9, dorsal view; 31, segments 11 (lower half), 12, and 13, ventral view, allotypic male (USNM 69967). (Interference contrast photographs all with same scale (in μm) as shown in Figure 26.)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lateral spines on segments 10 and 11 and, in males only, a small lateral setae more dorsally displaced on segment 12. In *E. andamanensis* the short lateral spine on segment 4 and those spines of segments 10 and 11 have basal adhesive glands. *Echinoderes horni* has very distinct lateral appendages on segments 4, 7–11 with a lateral accessory spine on segment 10. The latter spine, in addition to those appendages on segments 4 and 7, has basal adhesive glands. The LTS/TL of *Echinoderes horni* is 62.5–89.8 percent contrasted to the 41.0–50.1 percent in *E. andamanensis*. Additionally, the patterns of sensory and cuticular spots of the two species differ. *Echinoderes horni* has only a single round cuticular spot middorsally on segments 3–5, 7, 9, and 12 and subdorsal cuticular spots, one on either side of the dorsal midline of segments 6, 8, 10, and 11; *E. andamanensis* has middorsal cuticular spots on segments 3, 4, and 11 in addition to subdorsal cuticular spots on segments 3, 4, 6–12. The patterns of other cuticular spots and perforation sites in the two species are significantly different.

Among the other species lacking middorsal spines, *E. capitatus* is easily distinguished by its enlarged anterior two trunk segments which gives the species its name. In addition, *E. capitatus* has lateral spines only on segments 4 and 10, and a small lateral seta occurs on either side of segment 12 (male only?). The four remaining species all lack adhesive tubes on segment 4. *Echinoderes caribiensis* has retained the lateral spine on segment 7 as an adhesive tube, but others have lateral spines only on segments 10 and 11. Both *Echinoderes maxwelli* and *E. bengalensis* have lateral spines, both adhesive tubes, only on segments 7 and 10, and *E. coulli* has undergone further spine reduction to the extent that only in occasional adults can one detect very small, thin setae-like adhesive tubes on these same two segments.

Echinoderes horni has the same lateral spine formula as *E. newcaledoniensis*, but this latter species has lateral accessory spines on segments 4, 8–11 in addition to middorsal spines on segments 6, 8, and 10.

ETYMOLOGY.—This species is named in honor of Thomas D. Horn, who, as a student, had a brief romance with the Kinorhyncha until a career in medicine took precedence.

Echinoderes imperforatus, new species

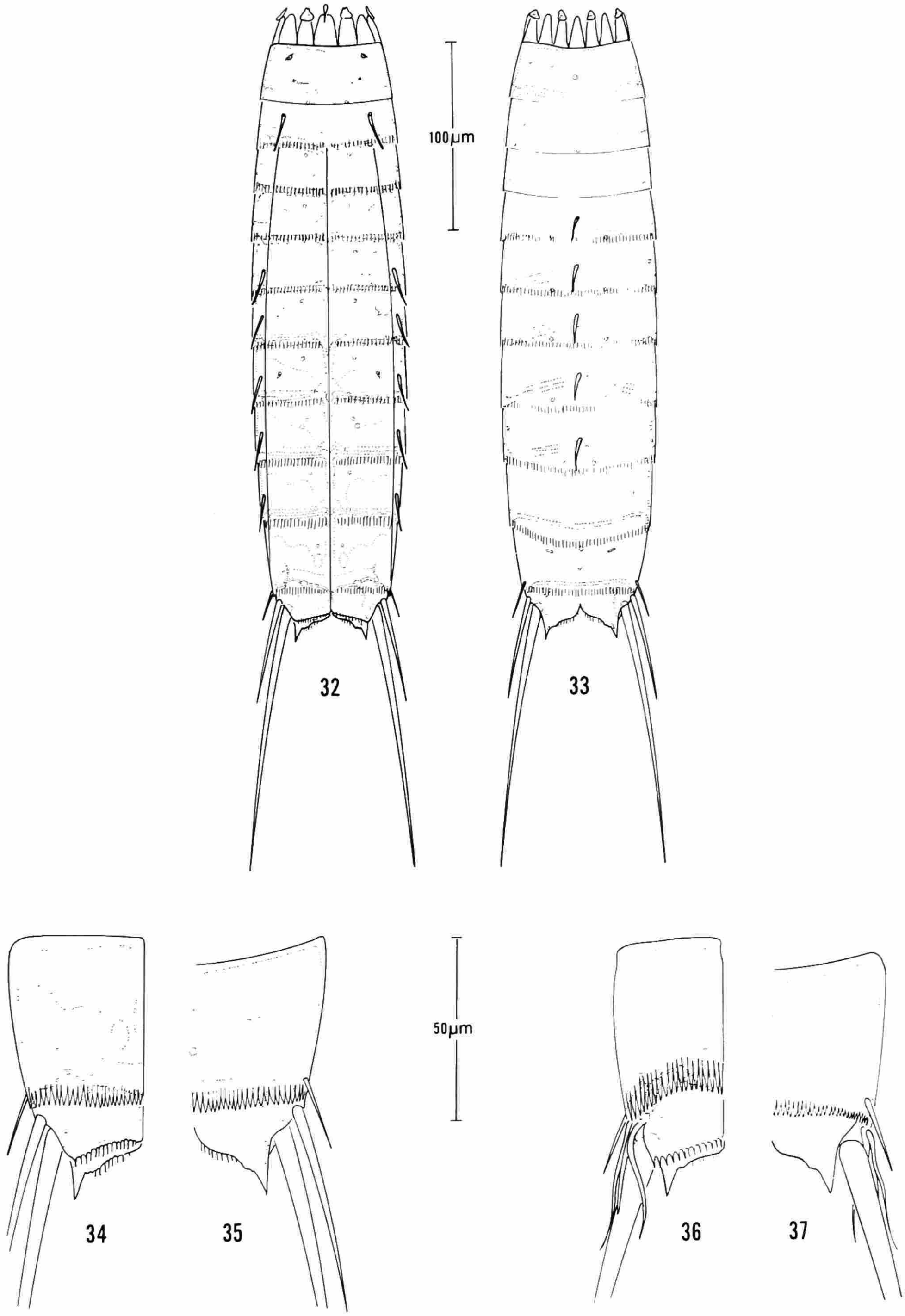
FIGURES 32–43

DIAGNOSIS.—Middorsal spines on segments 6–10, lateral spines on segments 4, 7–12 with adhesive glands at the base of L-4 and L-7; without lateral accessory spines; lateral terminal spines long, 164–192 μm, 53.8–66.7 percent of trunk length; fine cuticular hairs appear to be present but perforation sites are notably absent.

DESCRIPTION.—Adults (Figures 32–43), trunk length 288–320 μm; MSW-8 64–67 μm, 20.5–22.8 percent of trunk length; SW 61–67 μm, 20.5–22.8 percent of trunk length. Second segment with 16 placids, about 9 μm long, wide posteriorly, narrow anteriorly; posterior end of midventral placid only slightly wider (7 μm) than posterior ends of others (5 μm), anterior margin of all placids rounded, midventral placid overhung by small, narrow, toothlike plate (Figure 32); ventral trichoscalid plates 1 and 3 small, 4 μm wide at expanded portion overlapping placids; dorsal trichoscalid plates 5 and 7 very small, 3 μm wide at expanded portion overlapping placids (Figure 33).

Trunk segments appear to have fine cuticular hairs (Figures 39, 42) but without perforation sites; pectinate fringe moderately visible on ventral margins of segments 4–13 and dorsal margins of segments 6–13 (probably on other trunk segments but not visible under optics used); extensions of terminal tergal plate distinct, short, pointed, fringed mesially (Figures 34, 36); terminal sternal extensions nearly truncate, also fringed (Figures 35, 37).

Middorsal spines on segments 6–10 short, 8–24 μm long, increasing in length posteriorly; lateral spines on segments 4, 7–12, 17–26 μm long, increasing in length posteriorly, those on segments 4 and 7 thinner (adhesive tubes), each with basal adhesive gland; lateral spine on segment 12 dorsally displaced (Figure 35); lateral terminal spines long, 164–192 μm, 53.8–66.7 percent of trunk



FIGURES 32–37.—*Echinoderes imperforatus*, new species: 32, neck and trunk segments, ventral view, holotypic female (USNM 69972); 33, same, dorsal view; 34, same, segments 12, 13, lateral half, ventral view; 35, same, dorsal view; 36, same, ventral view, allotypic male (USNM 69973); 37, same, dorsal view.

TABLE 3.—Measurements (μm) and indices (%) for *Echinoderes imperforatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	2	292–304	298.0	8.5	6.0	2.9
	♀	4	288–320	304.0	16.3	8.2	5.4
	♂♀	6	288–320	302.0	13.6	5.5	4.5
SW	♂	2	61–62	61.5	0.7	0.5	1.2
	♀	4	66–67	66.3	0.5	0.3	0.8
	♂♀	6	61–67	64.7	2.5	1.0	3.9
SW/TL	♂	2	20.5–20.8	20.7	0.2	0.2	1.0
	♀	4	20.5–22.8	21.6	1.0	0.5	4.5
	♂♀	6	20.5–22.8	21.3	0.9	0.4	4.3
MSW-8	♂	2	64–66	65.0	1.4	1.0	2.2
	♀	4	66–67	66.3	0.5	0.3	0.8
	♂♀	6	64–67	65.8	1.0	0.4	1.5
MSW/TL	♂	2	21.6–21.9	21.8	0.2	0.2	1.0
	♀	4	20.5–22.8	21.6	1.0	0.5	4.5
	♂♀	6	20.5–22.8	21.7	0.8	0.3	3.6
Dm	♂	1	14.0	14.0	0.0	0.0	0.0
	♀	3	14.8–17.8	15.9	1.2	0.7	7.6
	♂♀	4	14.0–17.8	15.5	1.4	0.7	8.9
Dm/TL	♂	1	4.6	4.6	0.0	0.0	0.0
	♀	3	4.7–5.9	5.2	0.6	0.4	12.4
	♂♀	4	4.6–5.9	5.0	0.6	0.3	11.9
D-6	♂	2	10–12	11.0	1.4	1.0	12.9
	♀	4	8–14	11.8	2.9	1.4	24.4
	♂♀	6	8–14	11.5	2.4	1.0	20.4
D-7	♂	1	13	13.0	0.0	0.0	0.0
	♀	3	10–16	13.7	3.2	1.8	23.5
	♂♀	4	10–16	13.5	2.7	1.3	19.6
D-8	♂	1	14	14.0	0.0	0.0	0.0
	♀	4	12–16	14.5	1.9	1.0	13.2
	♂♀	5	12–16	14.4	1.7	0.8	11.6
D-9	♂	1	15	15.0	0.0	0.0	0.0
	♀	4	16–18	16.8	1.0	0.5	5.7
	♂♀	5	15–18	16.4	1.1	0.5	6.9
D-10	♂	2	16–18	17.0	1.4	1.0	8.3
	♀	4	17–24	19.5	3.1	1.6	15.9
	♂♀	6	16–24	18.7	2.8	1.2	15.0
Lm	♂	2	18.4–18.7	18.6	0.2	0.2	1.1
	♀	2	19.7–20.1	19.9	0.3	0.2	1.4
	♂♀	4	18.4–20.1	19.2	0.8	0.4	4.2
Lm/TL	♂	2	6.1–6.4	6.3	0.2	0.2	3.4
	♀	2	6.2–7.0	6.6	0.6	0.4	8.6
	♂♀	4	6.1–7.0	6.4	0.4	0.2	6.3

TABLE 3.—Continued

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
L-4 (AT)	♂	2	19–21	20.0	1.4	1.0	7.1
	♀	4	17–26	22.8	4.0	2.0	17.4
	♂♀	6	17–26	21.8	3.4	1.4	15.7
L-7 (AT)	♂	2	19	19.0	0.0	0.0	0.0
	♀	4	17–26	21.0	3.9	2.0	18.7
	♂♀	6	17–26	20.3	3.2	1.3	15.8
L-8	♂	2	16	16.0	0.0	0.0	0.0
	♀	4	16–17	16.3	0.5	0.3	3.1
	♂♀	6	16–18	16.2	0.4	0.2	2.5
L-9	♂	2	16–18	17.0	1.4	1.0	8.3
	♀	4	17–20	18.0	1.4	0.7	7.9
	♂♀	6	16–20	17.7	1.4	0.6	7.7
L-10	♂	2	19	19.0	0.0	0.0	0.0
	♀	4	12–21	15.3	4.3	2.1	28.0
	♂♀	6	12–21	16.5	3.8	1.6	23.2
L-11	♂	2	17–18	17.5	0.7	0.5	4.0
	♀	4	16–23	18.8	3.0	1.5	15.9
	♂♀	6	16–23	18.3	2.4	1.0	13.2
L-12	♂	2	21–22	21.5	0.7	0.5	3.3
	♀	4	22–24	23.5	1.0	0.5	4.3
	♂♀	6	21–24	22.8	1.3	0.5	5.8
LTS	♂	2	164–172	168.0	5.7	4.0	3.4
	♀	4	172–192	178.8	9.4	4.7	5.3
	♂♀	6	164–192	175.2	9.5	3.9	5.4
LTS/TL	♂	2	53.9–58.9	56.4	3.5	2.5	6.3
	♀	4	53.8–66.7	59.0	5.5	2.8	9.4
	♂♀	6	53.8–66.7	58.2	4.8	1.9	8.2
LTAS	♀	4	53–59	56.0	2.5	1.2	4.4
LTAS/TL	♀	4	17.5–20.3	18.5	1.3	0.6	6.9
P-1	♂	2	40–49	44.5	6.4	4.5	14.3
P-2	♂	2	22–23	22.5	0.7	0.5	3.1
P-3	♂	2	38–41	39.5	2.1	1.5	5.4

length; lateral terminal accessory spines of female 53–59 μm long, 17.5–20.3 percent of trunk length; males without lateral terminal accessory spines, with 3 pairs of penile spines in same position; anteriormost penile spines (P-1) 40–49 μm long, mesially adjacent penile spines (P-2) 22–23 μm long, posteriorly adjacent penile spines 38–41 μm long (Figures 36, 37).

Pachycycli simple, well developed (Figures 38–43), becoming more distinct at ventral midline; oval muscle scars near ventral midline on segment 12 (Figures 34, 36); brace-shaped muscle scar near lateral margin of sternal plates of segment 8; small transverse cuticular scars dorsally and ventrally on segment 3, dorsally on segment 12; small, round cuticular scars on either side of ventral midline, segments 3–12, widely separated anteriorly, becoming closer posteriorly; single cuticular scars middorsally on segments 3–5, 2 such scars apparently on segment 12 and on either side of dorsal midline on segments 6–11; no cuticular perforation sites although fine cuticular hairs appear to be present.

Males differ from females principally by lack of lateral terminal accessory spines and presence of 3 pairs of penile spines; the lateral terminal spines of males tend to be slightly shorter (164–172 μm, 53.9–58.9 percent of trunk length) than those of females (172–194 μm, 53.8–66.7 percent of trunk length).

Morphometric data for adult specimens are shown in Table 3.

HOLOTYPE.—Adult female, TL 320 μm (Figures 32–35, 38–42), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69972.

ALLOTYPE.—Adult male, TL 304 μm (Figures 36, 37, 43), other data as for holotype, USNM 69973.

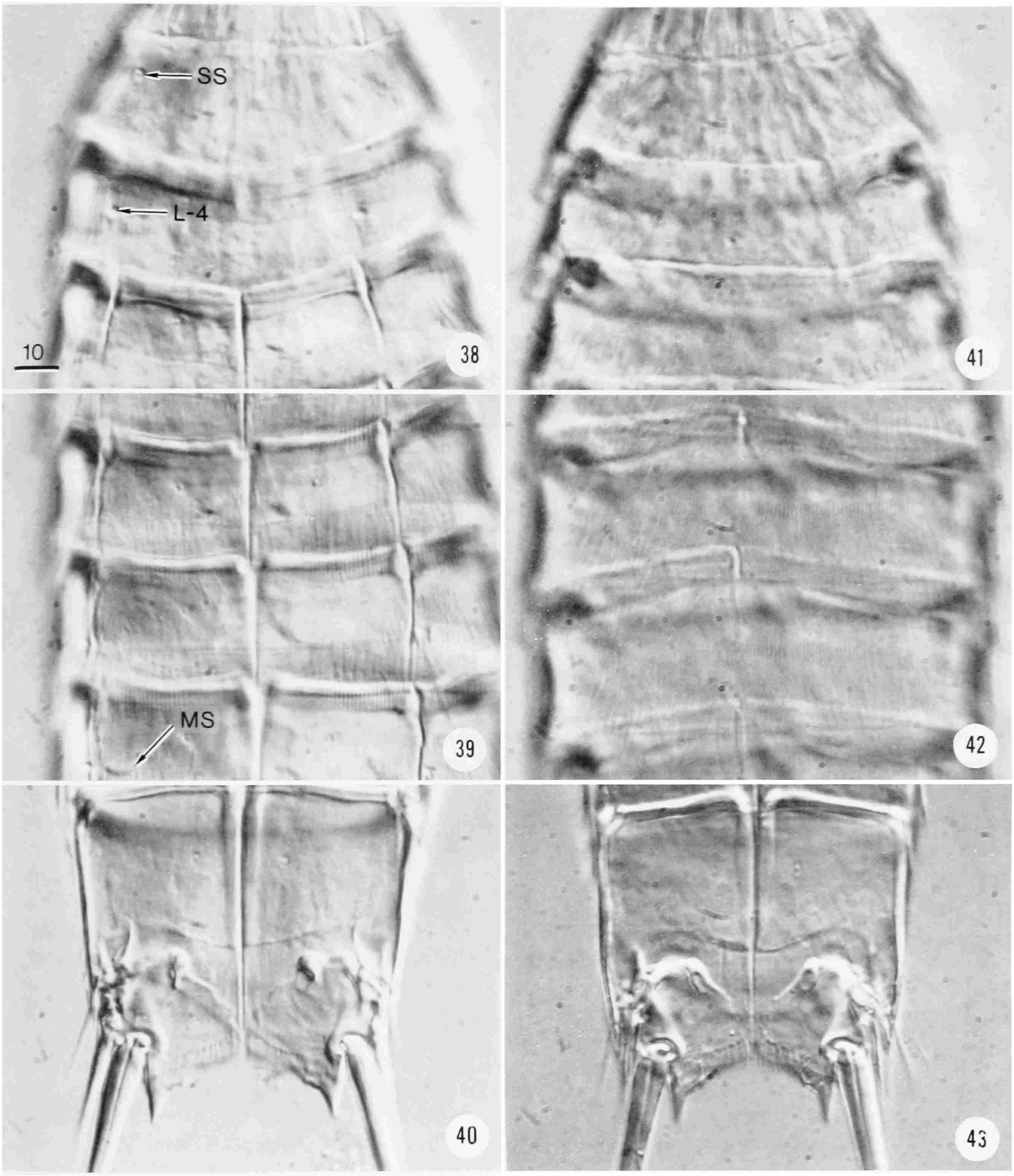
PARATYPES.—One female, TL 288 μm, other data as for holotype, USNM 69974. One male and 1 female, TL 292 μm, Twin Cays, sta RH 443, Belize, other data as for holotype, USNM 69975; 1 female, TL 316 μm, Twin Cays, sta RH 444, Belize, other data as for holotype, USNM 69976.

REMARKS.—The middorsal spine formula 6–10 is the most common one in *Echinoderes*, as is the lateral spine formula 4, 7–12. Thus, *Echinoderes imperforatus* shares these characteristics with nine other species. Aside from the lack of cuticular perforation sites that are associated with the trunk hair found in all other species having this same middorsal and lateral spine formula, *E. imperforatus* most closely resembles *E. gerardi* in general appearance. Both have relatively short dorsal and lateral spines but only when compared to other species and not to each other. *Echinoderes gerardi* has a mean middorsal spine length of 8.8–10.4 μm, 2.5–3.0 percent of the trunk length; in *E. imperforatus*, these measurements are 14.0–17.8 μm, 4.6–5.9 percent of trunk length. Both species have a brace-shaped muscle scar on the lateral margin of each sternal plate of segment 8 only, and their cuticular scar configuration is identical. Among the other differences separating *E. imperforatus* from *E. gerardi* is the presence of a lateral accessory spine on segment 10 of the latter species. This same lateral accessory spine is also found in *E. dujardinii* but is not present in any remaining species in this group.

Echinoderes imperforatus, like females of *E. ehlersi*, has relatively short middorsal spines. The mean length of these spines in the former species, for both males and females, is 14–18 μm, 4.6–5.9 percent of the trunk length. In the latter species, the mean female middorsal spine length is 11–12 μm, 4.0 percent of the trunk length. In the male, these figures are 26–29 μm, 10.1 percent of the trunk length. *Echinoderes ehlersi* has brace-shaped muscle scars on the sternal plates of segments 8–10, not just on segment 8 as in the new species, although the patterns of sensory spots and cuticular scars are identical in both species. The terminal tergal extensions of both *E. ehlersi* and *E. imperforatus* are similar, but the very large toothlike plate which overhangs the midventral placid (seen where the placids are extended) of *E. ehlersi* is a notable difference. This same plate is very narrow in *E. imperforatus* (Figure 32).

The relatively short middorsal spines of *E. imperforatus* (2.5–3.0 percent of the trunk length) are significantly different from those of *E. worthingi* (10 percent of the trunk length). Although *Echinoderes worthingi* is poorly described, it appears also to differ from *E. imperforatus* in that the middorsal spine on the tenth segment (45–50 μm long) is twice the length of that on the ninth segment (19–23 μm long); in the new species, these same spines are nearly similar in length, averaging 16 μm in the ninth middorsal spine and 19 μm in the tenth.

FIGURES 38–43.—*Echinoderes imperforatus*, new species: 38, segments 3–5, ventral view, holotypic female (USNM 69972); 39, same, segments 7, 8, ventral view; 40, same, segments 12, 13, ventral view; 41, same, segments 3–5, dorsal view; 42, same, segments 7, 8, dorsal view; 43, segments 12, 13, ventral view, allotypic male (USNM 69973). (Interference contrast photographs all with same scale (in μm) as shown in Figure 38; SS = sensory spot, MS = muscle scar.)


SS
L-4
10
38
MS
39
40
41
42
43

Echinoderes imperforatus differs from *E. pacificus* by having brace-shaped muscle scars only on the ventral plates of segment 8, much longer lateral terminal spines, 164–192 μm, 53–67 percent of the trunk length as opposed to 90–118 μm, 27–36 percent of the trunk length in *E. pacificus*, and in the presence of a distinctive, outward curving, robust lateral spine on segment 12 of *E. pacificus*. The latter species also has a small seta near this lateral spine but originating at the anterior lateral border of the terminal segment. As in all remaining species within this group, *E. pacificus* differs from *E. imperforatus* by its significantly longer middorsal spines. In *E. pacificus* these spines average 46–57 μm, 14–17 percent of the trunk length as opposed to 14–18 μm, 4.6–5.9 percent of the trunk length in the new species.

In addition to longer middorsal spines averaging 25–30 μm, 7–9 percent of the trunk length, *E. kozloffi* has brace-shaped muscle scars on the ventral plates of segments 8–10 and relatively shorter lateral terminal spines, 42.0–52.4 percent of the trunk length, all of which differ from these same characters in *E. imperforatus*. In *E. sublicarum* the middorsal spines are even longer, averaging 29–37 μm, 11–16 percent of the trunk length, and the brace-shaped muscle scars are only on ventral plates 9 and 10, none are present on segment 8. The mean length of the middorsal spines of *E. ferrugineus* is similar to that of *E. sublicarum*, hence also longer than those of *E. imperforatus*, and, like those of *E. worthingi*, the tenth middorsal spine is about twice the length of the one preceding it. In addition, the tergal terminal extensions of *E. ferrugineus* are of a significantly different shape than those of the new species.

Two other species that might be compared with *E. imperforatus* include *E. masudai* Abe, 1930, and *E. subfuscus* Zelinka, 1928. Neither species is adequately described. I believe *E. subfuscus* is conspecific with *E. dujardinii* and hence a junior subjective synonym. Tokioka (1949) considered *E. masudai* conspecific with *E. dujardinii* also, but I am reluctant to agree and prefer to relegate it to the status of species indeterminatum.

ETYMOLOGY.—The name of this species is from the Latin *im* (not) plus *perforatus* (perforated).

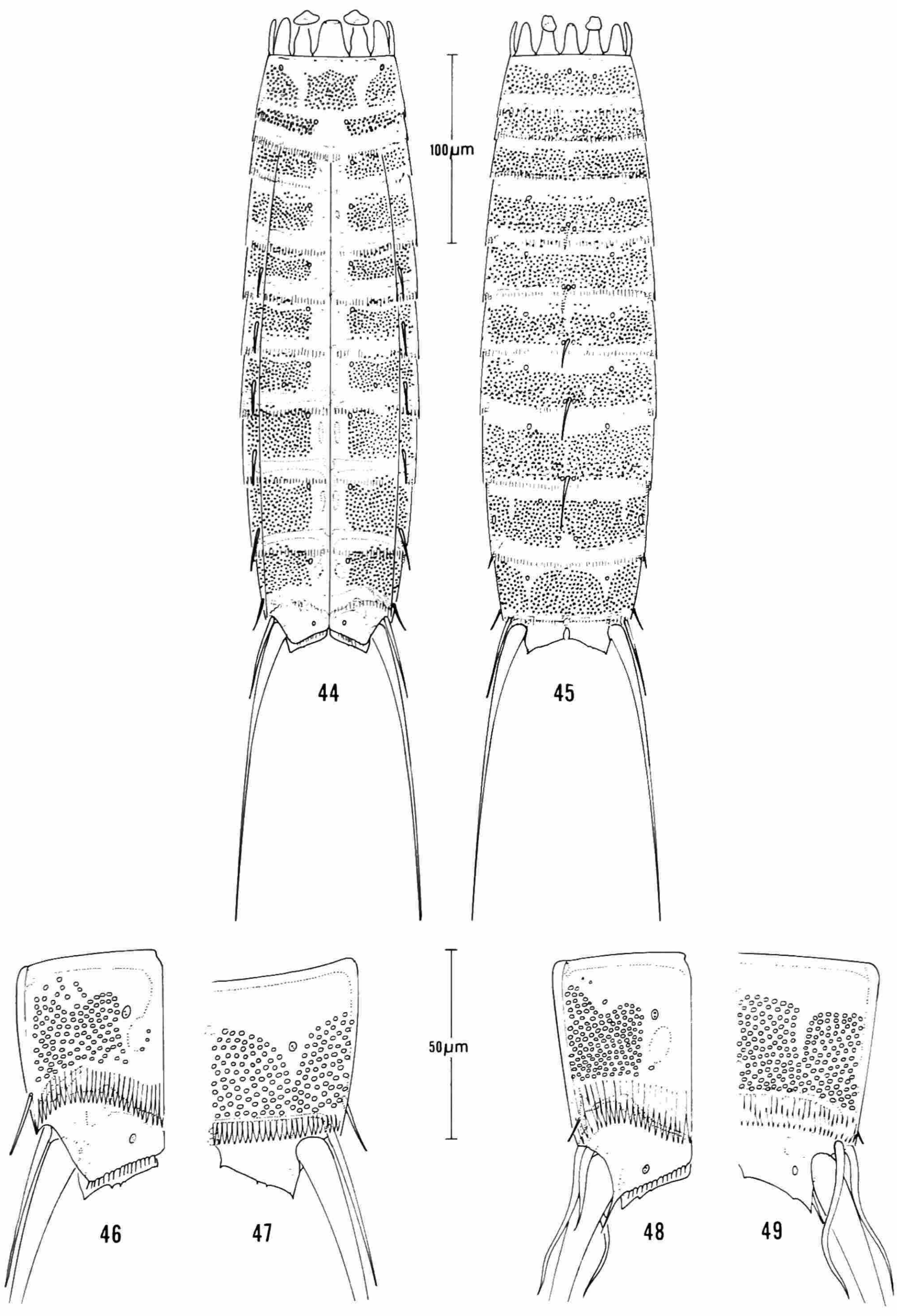
Echinoderes truncatus, new species

FIGURES 44–55

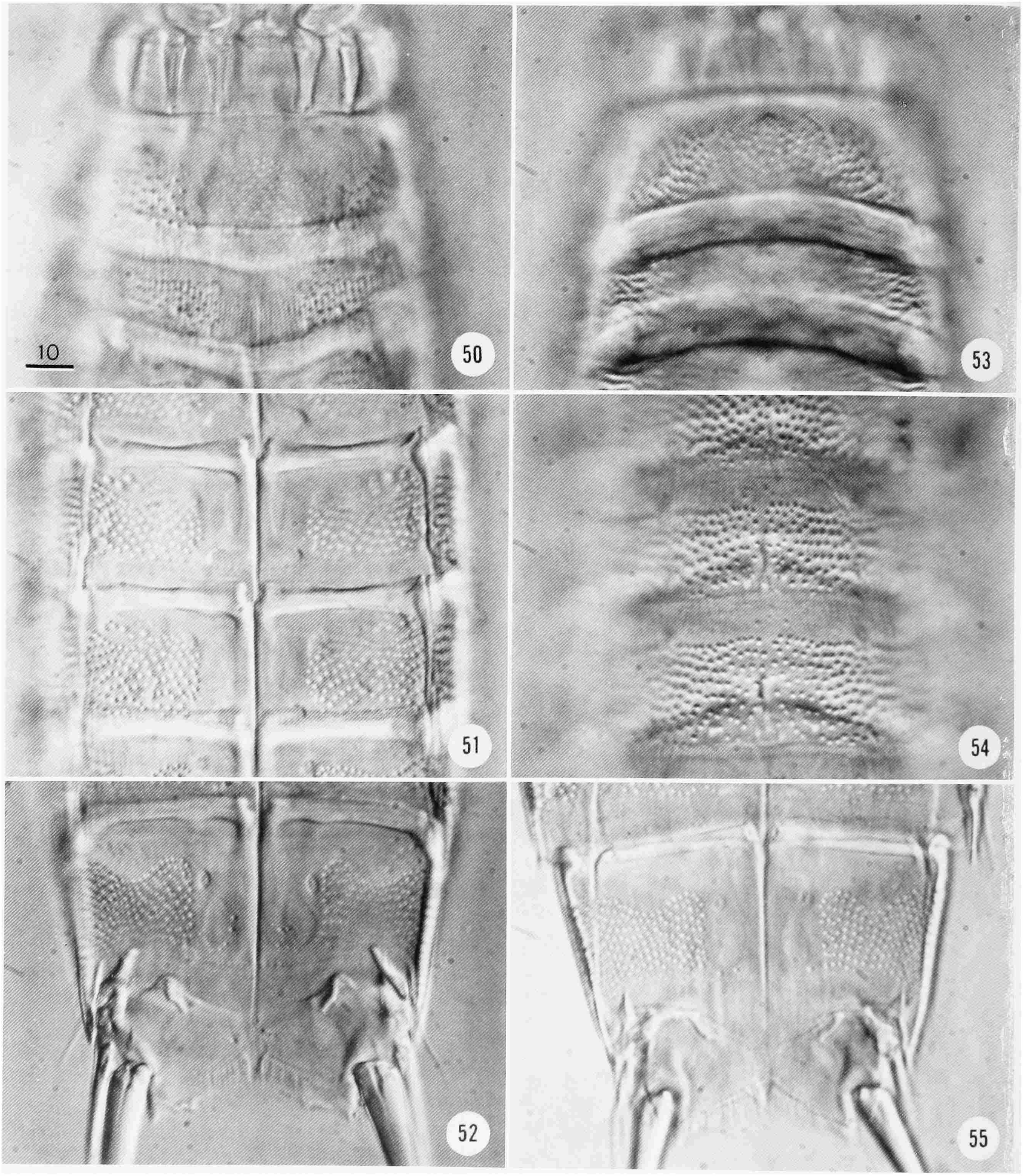
DIAGNOSIS.—Middorsal spines on segments 6–10, increasing uniformly in length posteriorly; lateral spines on segments 7–12 with adhesive glands at the base of L-4 and L-7; without lateral accessory spines; lateral terminal spines long, 152–168 μm, 42.2–61.7 percent of trunk length; cuticular perforation sites (indicating hair) prominent and abundant, arranged in distinctive pattern.

DESCRIPTION.—Adults (Figures 44–55), trunk length 270–372 μm, MSW-8 66–72 μm, 18.4–22.0 percent of trunk length; SW 66–75 μm, 18.4–24.1 percent of trunk length. Second segment with 16 placids, about 10 μm long, wide posteriorly, narrow anteriorly; midventral placid wider (10 μm) than others (5–6 μm), anterior margin of all placids rounded, placids adjacent to midventral placid with lateral margins slightly expanded in the middle; only 2 ventral trichoscalid plates evident (Figure 44), 7 μm wide at expanded basal portion which overlaps placid, only 2 dorsal trichoscalid plates evident (Figure 45), small, 4 μm, only slightly wider than long.

Trunk segments with cuticular perforation sites producing a distinctive pattern on each segment; pectinate fringe light, visible on dorsal and ventral margins of segments 3–12 and the terminal sternal plates; extensions of terminal tergal and sternal plates almost truncate (Figures 46–49), tapering with only slight interruption of margin, males with slight spinose extension of lateral sternal border, none seen in females. Middorsal spines on segments 6–10, short, thin, 13–30 μm long, increasing uniformly in length posteriorly; lateral spines on segments 7–12 in females (possibly 7 or 8–12 in males), 15–21 μm, L-12 spine shorter (16–18 μm) than preceding spine in females, L-12, seta-like (10 μm) in males (Figure 48), lateral spines (adhesive tubes) on segment 7 (seen only on females) thinner, each with basal adhesive gland; lateral terminal spines long, 152–168 μm,



FIGURES 44–49.—*Echinoderes truncatus*, new species: 44, neck and trunk segments, ventral view, holotypic female (USNM 69977); 45, same, dorsal view; 46, same, segments 12, 13, lateral half, ventral view; 47, same, dorsal view; 48, same, ventral view, allotypic male (USNM 69978); 49, same, dorsal view.


10
50
53
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54
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42.2–61.7 percent of trunk length; lateral terminal accessory spines of female 37–43 μm long, 11.1–13.8 percent of trunk length; males without lateral terminal accessory spines, with 3 pairs of penile spines in same position; anteriormost penile spines (P-1) 48 μm long, mesially adjacent penile spines (P-2) 24 μm long, posteriorly adjacent penile spines 48 μm long (Figures 48, 49, 55).

Pachycycli simple, well developed (Figures 50–55), becoming more distinct at ventral midline. Oval muscle scars near midline on sternal plates 5–12 (Figure 44) becoming longer in posterior progression to more rounded on segment 12; no brace-shaped muscle scars present; dorsal scars difficult to distinguish. Sensory spots on either side of ventral midline, widely separated, near anterior margin of segment 3. Small, round cuticular scars near midline on segments 4–13; middorsal and 2 subdorsal cuticular scars on segments 3, 4, 12, middorsal only on segment 5, widely subdorsal on segments 6–12 with similar cuticular scars on either side of spine on 6–10 and in same relative position on segment 11 (where juvenile spine is lost in final molt). Cuticular perforation sites form distinctive pattern (Figures 44, 45).

Males differ from females by possible lack of L-7 and the presence of short (10 μm) seta instead of L-12 spine as in female, otherwise males lack lateral terminal accessory spines and have 3 pairs of penile spines in their place.

Morphometric data for adult specimens are shown in Table 4.

HOLOTYPE.—Adult female, TL 320 μm (Figures 44–47, 50–54), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69977.

ALLOTYPE.—Adult male, TL 372 μm (Figures 48, 49, 55), other data as for holotype, USNM 69978.

PARATYPES.—Four females, TL 272–360 μm, other data as for holotype, USNM 69979.

REMARKS.—*Echinoderes pilosus* is the only other described species with the middorsal spine formula 6–10 and lateral spine formula of 7–12 (Lang, 1949). Because of this, it has been identifiable despite its inadequate description and diagrammatic illustration. Even the supplementary description by Pallares (1966) adds very little information; however, neither author observed any enlargement of the midventral placid, which contrasts with that of *E. truncatus*, nor did they note any distinct perforation site pattern for hairs, although there are numerous hairs in *E. pilosus* as the name suggests. As the name of the new species suggests, it has a truncated terminal segment margin which is not extended into pointed, bladelike structures as in *E. pilosus*.

These two species differ only slightly in size: *E. pilosus*, TL 400–460 μm, *E. truncatus*, TL 270–372 μm. Both have similar lateral terminal spine dimensions: 200–215 μm long, 51–56 percent of the trunk length in *E. pilosus* and 152–168 μm long, 42.2–61.7 percent of the trunk length in *E. truncatus*. The lateral terminal accessory spines of the female are shorter, 25–35 μm, about 7–8 percent of the trunk length, in *E. pilosus*, and 37–43 μm long, 11.1–13.8 percent of the trunk length, in *E. truncatus*.

Males of the *E. truncatus* may present a lateral spine formula of 7–11 since the L-12 spine is reduced, represented only by a very small seta (Figure 48), not a distinct spine as in the female (Figure 46). In this character, the male could be confused with other species with the same 6–10 middorsal spine formula but with a lateral spine formula of 7–11. Of these species, *E. brevicaudatus* is easily identified on the basis of its extremely short, stubby, lateral terminal spines. The remaining three species, *E. pennaki*, *E. bookhouti*, and *E. remanei*, all have distinct bladelike, pointed lateral extensions of the terminal tergal plate as opposed to the reduced or truncated appearance of *E. truncatus*.

FIGURES 50–55.—*Echinoderes truncatus*, new species: 50, segments 2–4, ventral view; holotypic female (USNM 69977); 51, same, segments 7, 8, ventral view; 52, same, segments 12, 13, ventral view; 53, same, segments 2–4, dorsal view; 54, same, segments 7, 8, dorsal view; 55, segments 12, 13, ventral view, allotypic male (USNM 69978). (Interference contrast photographs all with same scale (in μm) as shown in Figure 50.)

TABLE 4.—Measurement (μm) and indices (%) for *Echinoderes truncatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	1	372	372.0	0.0	0.0	0.0
	♀	5	272–360	318.4	31.7	14.2	10.0
	♂♀	6	272–372	327.3	35.8	14.6	10.9
SW	♂	1	69	69.0	0.0	0.0	0.0
	♀	5	66–75	70.4	4.0	1.8	5.7
	♂♀	6	66–75	70.2	3.7	1.5	5.2
SW/TL	♂	1	18.4	18.4	0.0	0.0	0.0
	♀	5	19.6–24.1	22.2	1.8	0.8	8.0
	♂♀	6	18.4–24.1	21.6	2.2	0.9	10.3
MSW-8	♂	1	69	69.0	0.0	0.0	0.0
	♀	5	66–72	69.2	2.8	1.2	4.0
	♂♀	6	66–72	69.2	2.5	1.0	3.6
MSW/TL	♂	1	18.4	18.4	0.0	0.0	0.0
	♀	5	20.0–22.0	21.8	1.5	0.7	6.8
	♂♀	6	18.4–22.0	21.3	1.9	0.8	8.9
Dm	♂	1	23.6	23.6	0.0	0.0	0.0
	♀	2	18.0–20.4	19.2	1.7	1.2	8.8
	♂♀	3	18.0–23.6	20.7	2.8	1.6	13.6
Dm/TL	♂	1	6.3	6.3	0.0	0.0	0.0
	♀	2	5.5–7.5	6.5	1.4	1.0	21.8
	♂♀	3	5.5–7.5	6.4	1.0	0.6	15.7
D-6	♂	1	18	18.0	0.0	0.0	0.0
	♀	3	13–14	13.7	0.6	0.3	4.2
	♂♀	4	13–18	14.8	2.2	1.1	15.0
D-7	♂	1	20	20.0	0.0	0.0	0.0
	♀	3	15–16	15.3	0.6	0.3	3.8
	♂♀	4	15–20	16.5	2.4	1.2	14.4
D-8	♂	1	24	24.0	0.0	0.0	0.0
	♀	5	16–25	18.2	3.9	1.7	21.9
	♂♀	6	16–25	19.2	4.2	1.7	22.0
D-9	♂	1	27	27.0	0.0	0.0	0.0
	♀	5	18–27	22.0	4.1	1.8	18.5
	♂♀	6	18–27	22.8	4.2	1.7	18.3
D-10	♂	1	29	29.0	0.0	0.0	0.0
	♀	4	27–30	28.8	1.3	0.6	4.4
	♂♀	5	27–30	28.8	1.1	0.5	3.8
Lm	♀	3	15.0–17.9	16.2	1.5	0.9	9.3
Lm/TL	♀	3	4.4–5.6	5.2	0.7	0.4	12.9
L-7 (AT)	♀	3	15–16	15.7	0.6	0.3	3.7
L-8	♂	1	14	14.0	0.0	0.0	0.0
	♀	3	14–18	15.3	2.3	1.3	15.1
	♂♀	4	14–18	15.0	2.0	1.0	13.3

TABLE 4.—Continued

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
L-9	♂	1	16	16.0	0.0	0.0	0.0
	♀	5	14–18	15.8	1.7	0.9	10.8
	♂♀	6	14–18	15.8	1.5	0.7	9.4
L-10	♂	1	16	16.0	0.0	0.0	0.0
	♀	5	14–18	15.4	1.7	0.8	10.9
	♂♀	6	14–18	15.5	1.5	0.6	9.8
L-11	♂	1	17	17.0	0.0	0.0	0.0
	♀	5	17–21	18.4	1.5	0.7	8.2
	♂♀	6	17–21				
L-12	♀	5	16–18	16.8	1.1	0.5	6.5
LTS	♂	1	168	168.0	0.0	0.0	0.0
	♀	5	152–168	161.0	5.8	2.6	3.6
	♂♀	6	152–168	162.2	6.0	2.4	3.7
LTS/TL	♂	1	45.2	45.2	0.0	0.0	0.0
	♀	5	42.2–61.7	51.1	7.0	3.1	13.6
	♂♀	6	42.2–61.7	51.2	8.0	4.0	15.7
LTAS	♀	5	37–43	47.0	14.7	6.6	31.3
LTAS/TL	♀	5	11.1–13.8	12.9	1.1	0.5	8.5
P-1	♂	1	48	48.0	0.0	0.0	0.0
P-2	♂	1	24	24.0	0.0	0.0	0.0
P-3	♂	1	48	48.0	0.0	0.0	0.0

ETYMOLOGY.—The name of this species is from the Latin *truncus* (cutoff).

Echinoderes wallaceae, new species

FIGURES 56–67

DIAGNOSIS.—Middorsal spines on segments 6, 8, and 10, increasing uniformly in length posteriorly. Lateral spines on segments 4, 7–11 with adhesive glands at the base of L-4 and L-7; lateral accessory spine with adhesive gland at base dorsally adjacent to L-10; lateral terminal spines long, 104–176 μm, 47.6–80.1 percent of trunk length. Cuticular perforation sites sparse but arranged in distinctive pattern. Prominent dorsolateral and ventrolateral muscle scars on segment 4.

DESCRIPTION.—Adults (Figures 56–67), trunk length 188–260 μm, MSW-7 45–56 μm, 17.8–26.4 percent of trunk length; SW 36–48 μm, 15.0–21.6 percent of trunk length. Second segment with 16 placids, about 11–12 μm long, wide posteriorly, narrow anteriorly; midventral placid wider (10–11 μm) than others (7–8 μm), anterior margin of all placids rounded, midventral placid slightly apiculate (Figure 56); ventral trichoscalid plates 1 and 3 prominent (Figure 56), about 7 μm long, 12 μm wide at expanded basal portion which overlaps placids, dorsal trichoscalid plates 5 and 7 small, 4×4 μm (Figure 57).

Trunk segments with relatively few cuticular perforation sites, forming a distinct pattern, extremely sparse on anterior 2 and posterior 2 trunk segments (Figures 56, 57); pectinate fringe moderate, visible on dorsal and ventral margins of all trunk segments. Bladelike extensions of terminal tergal plate long (20 μm), sharply pointed, terminal sternal plates evenly rounded, with fringed posterior margin but without spinose projections.

Middorsal spines on segments 6, 8, and 10, long, 21–56 μm, increasing uniformly in length posteriorly, D-10 long, 40–56 μm, particularly fragile, broken or missing in many specimens; lateral spines on segments 4, 7–11, 14–28 μm, those on segments 4 and 7 thinner (adhesive tubes), each with basal adhesive gland; lateral accessory spine (adhesive tube) dorsally adjacent to L-10; lateral terminal spines long, 104–196 μm, 47.6–80.1 percent of trunk length; lateral terminal accessory spines of female 29–43 μm long, 12.4–20.0 percent of trunk length, normally projecting straight back in contrast to lateral terminal spines that often extend more laterally; males without lateral terminal accessory spines, with 3 pairs of penile spines in same position, anteriormost penile spines (P-1) 22–26 μm long, mesially adjacent penile spines (P-2) 16–20 μm long, posteriorly adjacent penile spines 20–32 μm long (Figures 60, 61, 67).

Pachycycli well developed (Figures 62–67), becoming more distinct at ventral midline. Prominent oval-shaped muscle scars ventrally near midline on segment 12 and 13 (Figures 58, 60, 64, 67); large, prominent muscle scars dorsolateral and ventrolateral on segment 4 (Figures 56, 57, 62, 65). Sensory spots on either side of ventral midline, widely separated near anterior margin of segment 3; small, round cuticular scars near ventral midline on segments 4–12, especially close to midline on segment 12; middorsal round cuticular scars on segments 3–5, 7–9, 2 on 12, 1 on 13, subdorsal on segments 6, 8, and 10; cuticular perforation sites form distinctive pattern (Figures 57, 58, 62, 63, 65–67).

Males differ from females principally in the absence of lateral terminal accessory spines and presence of 3 pairs of penile spines.

Morphometric data for adult specimens are shown in Table 5.

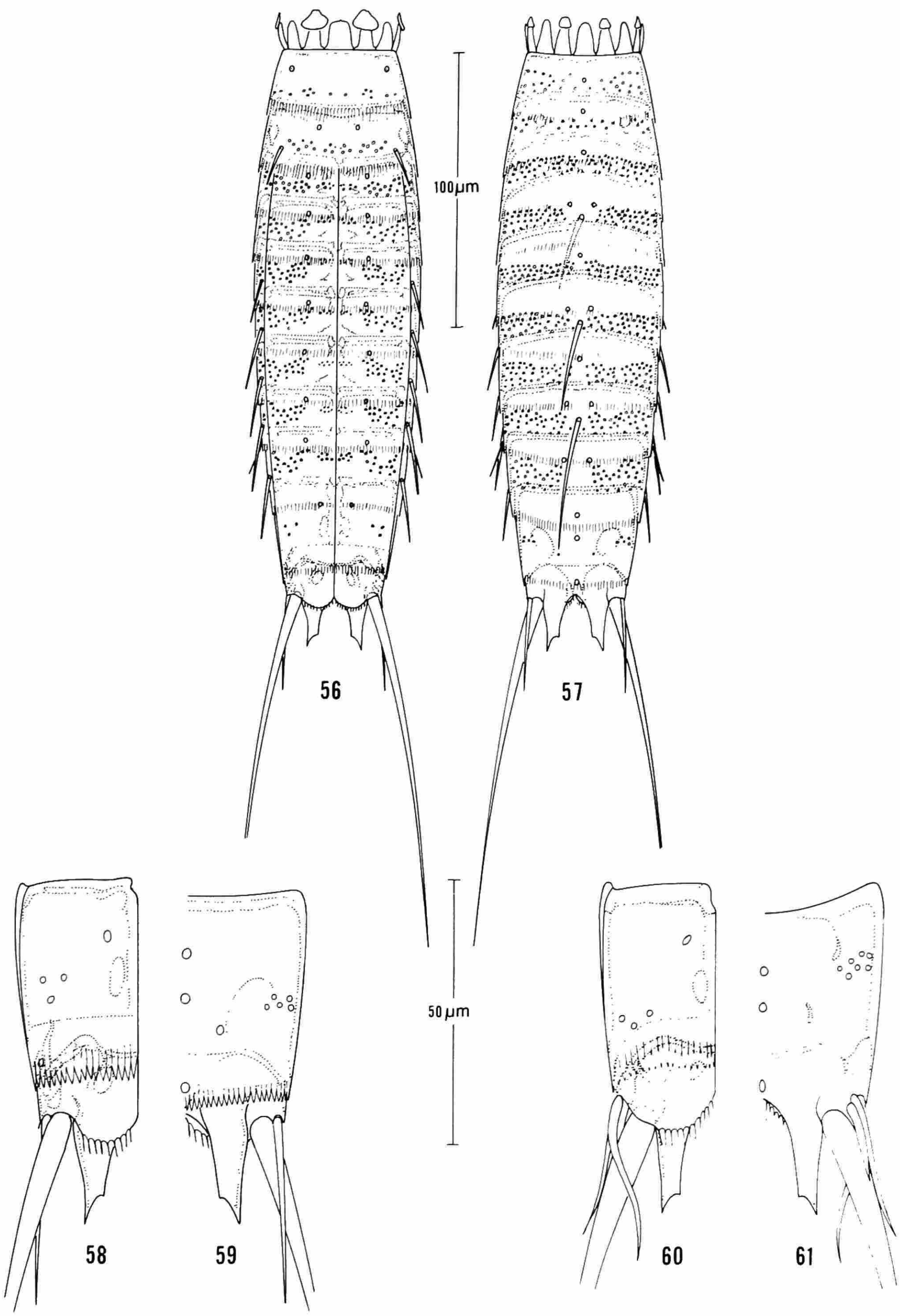
HOLOTYPE.—Adult female, TL 220 μm (Figures 56–59, 62–66), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69980.

ALLOTYPE.—Adult male, TL 216 μm (Figures 60, 61, 67), other data as for holotype, USNM 69981.

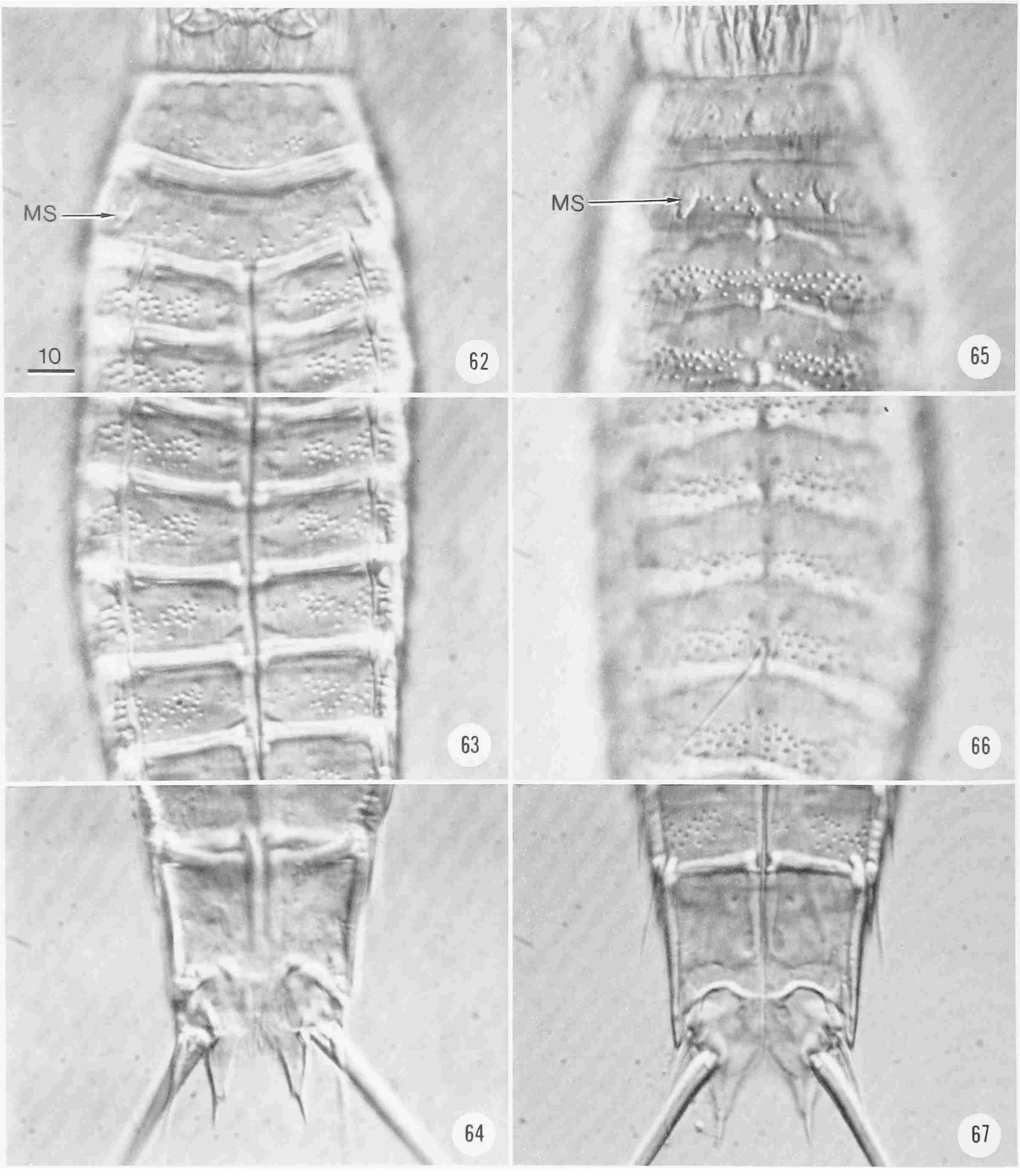
PARATYPES.—Six females and 8 males, TL 200–252 μm, other data as for holotype, USNM 69982; 1 female, TL 240 μm, Twin Cays, sta RH 442, other data as for holotype, USNM 69986; 10 females and 10 males, TL 208–260 μm, Twin Cays, sta RH 443, other data as for holotype, USNM 69983; 10 females and 10 males, TL 188–252 μm, Carrie Bow Cay, sta RH 445, Belize (16°48.1′N, 88°04.7′W), 9 Apr 1977, col. R.P. Higgins, USNM 69984; 2 females, TL 208–240 μm, Carrie Bow Cay, sta RH 446, 10 Apr 1977, col. R.P. Higgins, USNM 69985.

REMARKS.—*Echinoderes wallaceae* resembles *E. newcaledoniensis* in having the same middorsal (6, 8, 10) and lateral (4, 7–11) spine formulae and lateral accessory spines on segment 10; however, the latter species also has lateral accessory spines on segments 4, 8, 9, and 11 and subdorsal spines on segment 4. Both species have relatively long middorsal spines, although the first two (D-6 and D-8) of *E. newcaledoniensis* are relatively short (33–40 μm long) contrasted with the posteriormost spine (D-10) which is twice as long (85 μm); in *E. wallaceae* these three spines become longer in a posterior progression, although in some, the D-6 may be slightly larger than D-10. The relative length of the lateral terminal spines of *E. newcaledoniensis* may vary from 30–83 percent of the trunk length, those with longer spines generally associated with more coarse sediments (Higgins, 1967). Those of *E. wallaceae* are less variable, 47.6–80.1 percent of the trunk length, but no apparent correlation with sediment granulometry was suggested. The relative lengths of the lateral terminal spines of *E. newcaledoniensis* are also highly variable (7–22 percent of the trunk length); those of *E. wallaceae* vary less (12.4–20.0 percent of the trunk length). Noticeably different shapes of the long, pointed, bladelike tergal extensions, more pilose trunk segments, and extremely narrow trichoscalid plates of *E. newcaledoniensis* also help differentiate it from the new species.

Since the middorsal spines of *E. wallaceae* appear to be very fragile, it is conceivable that this species could be confused with *E. horni*. The latter species has the same lateral spine formula in addition to lateral terminal accessory spines on



FIGURES 56–61.—*Echinoderes wallaceae*, new species: 56, neck and trunk segments, ventral view, holotypic female (USNM 69980); 57, same, dorsal view; 58, same, segments 12, 13, lateral half, ventral view; 59, same, dorsal view; 60, same, ventral view, allotypic male (USNM 69981); 61, same, dorsal view.



FIGURES 62–67.—*Echinoderes wallaceae*, new species: 62, segments 2–6, ventral view, holotypic female (USNM 69980); 63, same, segments 6–9, ventral view; 64, same, segments 12, 13, ventral view; 65, same, segments 2–6, dorsal view; 66, same, segments 6–9, dorsal view; 67, segments 12, 13, ventral view, allotypic male (USNM 69981). (Interference contrast photographs all with same scale (in μm) as shown in Figure 62; MS = muscle scar.)

TABLE 5.—Measurements (μm) and indices (%) for *Echinoderes wallaceae* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	29	192–260	236.4	17.8	3.3	7.5
	♀	30	188–244	225.3	14.5	2.7	6.4
	♂♀	59	188–260	230.8	17.1	2.2	7.4
SW	♂	28	36–43	41.3	1.7	0.3	4.2
	♀	29	37–48	41.6	2.6	0.5	6.3
	♂♀	57	36–48	41.5	2.2	0.3	5.3
SW/TL	♂	28	15.0–20.8	17.6	1.5	0.3	8.8
	♀	29	16.3–21.6	18.6	1.3	0.2	6.9
	♂♀	57	15.0–21.6	18.0	1.5	0.2	8.3
MSW-7	♂	28	45–56	50.8	3.0	0.6	5.9
	♀	29	45–56	51.0	3.4	0.6	6.7
	♂♀	57	45–56	50.9	3.3	0.4	6.4
MSW/TL	♂	28	17.8–26.4	21.8	2.2	0.4	9.9
	♀	29	19.0–26.2	22.5	1.7	0.3	7.7
	♂♀	57	17.8–26.4	22.1	2.1	0.3	9.4
Dm	♂	7	39.5–52.5	45.6	4.4	1.7	9.6
	♀	6	39.0–47.0	43.0	3.6	1.5	8.3
	♂♀	13	39.0–52.5	44.4	4.1	1.1	9.2
Dm/TL	♂	7	17.7–24.8	19.4	2.7	1.0	13.8
	♀	6	18.3–22.8	19.9	1.6	0.7	8.0
	♂♀	13	17.7–24.8	19.6	2.2	0.6	11.1
D-6	♂	15	21–48	34.3	6.9	1.8	20.0
	♀	12	27–40	34.6	4.8	1.4	13.8
	♂♀	27	21–48	34.2	6.0	1.2	17.7
D-8	♂	15	28–57	46.4	8.6	2.2	18.5
	♀	18	35–64	46.2	7.8	1.8	16.8
	♂♀	33	28–64	46.4	7.8	1.4	16.7
D-10	♂	5	51–54	53.0	1.4	0.7	2.7
	♀	4	40–56	50.3	7.0	3.5	14.0
	♂♀	9	40–56	50.0	5.7	1.9	11.4
Lm	♂	6	19.0–21.3	20.1	0.8	0.3	3.8
	♀	6	19.6–21.6	20.0	0.8	0.3	4.0
	♂♀	12	19.0–21.6	20.1	0.7	0.2	3.7
Lm/TL	♂	6	7.8–9.9	8.8	0.8	0.3	8.5
	♀	6	8.4–10.8	9.5	1.0	0.4	10.5
	♂♀	12	7.8–10.8	9.2	0.9	0.3	10.1
L-4 (AT)	♂	19	16–19	16.4	1.1	0.3	6.6
	♀	16	14–16	15.6	0.8	0.2	5.2
	♂♀	35	14–19	16.0	0.9	0.2	5.7
L-7 (AT)	♂	20	14–19	17.5	1.3	0.3	7.6
	♀	17	16–19	17.5	1.0	0.2	5.8
	♂♀	37	14–19	17.4	1.2	0.2	6.8

TABLE 5.—Continued

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
L-8	♂	23	18–22	19.9	1.2	0.2	5.9
	♀	26	19–24	20.8	1.6	0.3	7.5
	♂♀	49	18–24	20.3	1.4	0.2	7.0
L-9	♂	24	18–24	21.1	1.3	0.3	5.9
	♀	26	19–25	21.5	1.4	0.3	6.5
	♂♀	50	18–25	21.3	1.3	0.2	6.3
L-10	♂	25	18–26	22.0	1.9	0.3	8.6
	♀	28	19–26	22.6	2.1	0.4	9.1
	♂♀	53	18–26	22.2	1.8	0.2	8.0
LA-10 (AT)	♂	9	17–20	18.7	1.1	0.4	6.0
	♀	8	18–20	18.9	0.6	0.2	3.4
	♂♀	17	17–20	18.8	0.9	0.2	4.8
L-11	♂	24	18–28	23.0	2.0	0.4	8.9
	♀	28	21–26	23.4	1.6	0.3	6.8
	♂♀	52	18–28	23.2	1.8	0.3	7.8
LTS	♂	28	120–170	126.9	9.8	1.9	7.7
	♀	30	104–176	133.1	15.8	2.9	11.9
	♂♀	58	104–176	130.1	13.5	1.8	10.4
LTS/TL	♂	28	47.6–80.1	54.4	6.4	1.2	11.8
	♀	30	49.1–72.1	59.1	6.2	1.1	10.5
	♂♀	58	47.6–80.1	56.8	6.7	0.9	11.8
LTAS	♀	30	29–43	30.7	3.2	0.6	8.8
LTAS/TL	♀	30	12.4–20.0	16.4	1.7	0.3	10.5
P-1	♂	7	22–26	24.3	2.1	0.8	8.8
P-2	♂	25	16–20	17.1	1.1	0.2	6.8
P-3	♂	24	20–32	26.2	3.6	0.7	13.7

segment 10 but lacks middorsal spines. These two species are very similar if one disregards the middorsal spine character. The most noticeable difference is the pattern and abundance of the cuticular perforation sites which are less abundant in *E. wallaceae* than in *E. horni*. The distinctive laterodorsal and lateroventral muscle scars on the fourth segment of *E. wallaceae* are a distinctive character.

ETYMOLOGY.—This species is named in honor of Marie Heller Wallace in gratitude for her assistance in both the field and laboratory work associated with this paper.

Discussion of *Echinoderes*

The genus *Echinoderes* was the first to be described (Claparède, 1863). It now consists of 66 described species, although only 38 are based on adults, and of these, four are species indeterminata, e.g., species not identifiable from the original description. In reality only 33 species are currently considered identifiable. *Echinoderes* is the most difficult of the kinorhynch genera to work with because of its relatively small size, usually 200–400 μm, and often cryptic taxonomic characters which can only be seen properly when the specimens are cleared and mounted in such a manner as to produce a dorso-ventral aspect.

The taxonomic history of this genus has been plagued by two general classes of problems: (1) 27 of the 66 species are described from juvenile stages in its seven-stage life history (Table 6) and (2) authors have not always been sufficiently experienced or careful in the interpretation of taxonomic characters either in their identification or description of species within this genus.

TABLE 6.—Composition of the genus *Echinoderes* incorporating the criteria of Zelinka, 1928, by which generic junior synonyms have arisen (species names originally feminine in gender have been corrected to agree with the masculine generic name *Echinoderes;* asterisk denotes species indeterminata based on inadequate description of the adult)

ADULTS		JUVENILES			
Echinoderes	(= *Echinoderella*)	(= *Habroderes*)	(= *Habroderella*)	(= *Centropsis*)	(= *Hapaloderes*)
No midterminal spine				Midterminal spine	
Eyespots	No eyespots	Eyespots	No eyespots	Eyespots	No eyespots
abbreviatus,	*bengalensis*	*erinaceus*	*ferox*	*arcticus*	*armatus*
new species	*capitatus*	*incertus*	*hyalinus*	*arcuatus*	*gracilis*
agigens	*elongatus*	*meridionales*	*trispinosus*	*erucus*	*kowalewskii*
andamanensis	*maxwelli*	*minax*		*greeffi*	*minimus*
arlis	*remanei*	*orientalis*		*languinosus*	*minutus*
bookhouti	* *steineri*	*splendidus*		*monocercus*	
* *borealis*				*pagenstecheri*	
brevicaudatus				*pallidus*	
canariensis				*parallelus*	
caribiensis				*pulchellus*	
citrinus				*pusillus*	
coulli				*rosaceus*	
druxi				*spinosus*	
dujardinii					
ehlersi					
ferrugineus					
gerardi					
horni,					
new species					
imperforatus,					
new species					
kozloffi					
levanderi					
* *masudai*					
newcaledoniensis					
pacificus					
pennaki					
pilosus					
riedli					
setiger					
sublicarum					
* *tchefouensis*					
truncatus,					
new species					
wallaceae,					
new species					
worthingi					

The first problem was created by the monographer of the Kinorhyncha, Carl Zelinka (1928), when he established a series of "larval genera" to accommodate the immature stages of *Echinoderes*. Zelinka's "adult genera" included *Echinoderella, Centroderes*, *Campyloderes*, *Semnoderes*, *Pycnophyes,* and *Trachydemus. Trachydemus* has been changed recently to *Kinorhychus* (Sheremetevskij, 1974). *Echinoderella* was nothing more than *Echinoderes* without pigmented eyespots, a character seen only in living animals—sometimes present, sometimes absent—and impossible to determine in preserved

TABLE 7.—Distribution of *Echinoderes* (see Figure 68; type-localities are in italics)

Species	FAO sea area	Locality	Authority
abbreviatus,	ASW	*Twin Cays,* Belize	Higgins, this study
new species	ASW	Carrie Bow Cay, Belize	Higgins, this study
agigens	MED	*Agigea,* Romania	Băcescu, 1968
andamanensis	ISW	*Andaman Is.*	Higgins and Rao, 1979
arcticus	PNE	*Barents Sea* (near White Sea) USSR	Steiner, 1919
arcuatus	MED	*Naples,* Italy	Zelinka, 1928
arlis	PNW	*Chukchi Sea* (Pt. Barrow, Alaska) USA	Higgins, 1966
armatus	MED	*Naples,* Italy	Zelinka, 1928
bengalensis	ISW	*Sonadia Is.* (Cox Bazar), Bangladesh	Timm, 1958
	ISW	Waltair, India	Rao and Ganapati, 1968
bookhouti	ANW	*Beaufort* (N.C.), USA	Higgins, 1964b
borealis	ANE	*Ostende,* Belgium	Greeff, 1869
brevicaudatus	ISW	*Al-Ghardaqa,* Egypt	Higgins, 1966a
canariensis	ASE	*Lanzarote,* Canary Is.	Greeff, 1869
capitatus	MED	Trieste, Italy	Zelinka, 1928
	MED	Naples, Italy	Zelinka, 1928
caribiensis	ASW	*Bay of Mochima,* Chile	Kirsteuer, 1964
citrinus	MED	*Naples,* Italy	Zelinka, 1928
coulli	ANW	*North Inlet Estuary* (S.C.), USA	Higgins, 1977b; Horn, 1978; Higgins and Fleeger, 1980
	ANW	Otaway (N.C.), USA	Higgins and Fleeger, 1980
	ASW	Sapelo Is. (Ga.), USA	Higgins and Fleeger, 1980
druxi	MED	*Sydra-Youcha Plage,* Algeria	d'Hondt, 1973
dujardinii	ANE	*St. Vaast la Hougue,* France	Claparède, 1863
	ANE	St. Malo, France	Dujardin, 1851
	ANE	Ostende, Belgium	Greeff, 1869
	ANE	Nieuwpoort, Belgium	Greeff, 1869
	ANE	Dieppe, France	Greeff, 1869
	ANE	Worthing (England), UK	Hartog, 1896
	ANE	Byfjord (Bergen), Norway	Schepotieff, 1907
	ANE	Clew Bay, Ireland	Southern, 1914
	ANE	Blacksod Bay, Ireland	Southern, 1914
	ANE	Scheveningen, Netherlands	Zaneveld, 1938
	ANE	Kadetrinne, GDR	Reimer, 1963
	ANE	Roskoff, France	Higgins, 1977a
	INW	Hoshiga ura Dalny, USSR	Zelinka, 1913
	INW	Misaki, Japan	Tokioka, 1949
	INW	Kasado Is., Japan	Sudzuki, 1976a,b
	MED	Salerno, Italy	Metschnikoff, 1869
	MED	Porto-Pi, Balearic Is.	Pagenstecher, 1875
	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
	MED	Brindisi, Italy	Zelinka, 1928
	MED	Bulgaria	Marinov, 1964
ehlersi	ISW	*Zanzibar*	Zelinka, 1913
	ISW	Andaman Is.	Higgins and Rao, 1979

TABLE 7.—Continued

Species	FAO sea area	Locality	Authority
elongatus	ANE	*Kristineberg*, Sweden	Nyholm, 1947b
	ANE	Loch Hourn, UK	McIntyre, 1962
erinaceus	MED	*Naples*, Italy	Zelinka, 1928
erucus	MED	*Naples*, Italy	Zelinka, 1928
ferox	MED	*Trieste*, Italy	Zelinka, 1928
ferrugineus	MED	*Naples*, Italy	Zelinka, 1928
	MED	Portorose, Yugoslavia	Zelinka, 1928
gerardi	MED	*Gulf of Tunis*, Tunisia	Higgins, 1978
gracilis	ANE	Gullmarfjord, Sweden	Nyholm, 1947b
	MED	*Naples*, Italy	Zelinka, 1928
greeffi	ANE	*Helgoland*, FRG	Zelinka, 1928
horni,	ASW	*Twin Cays*, Belize	Higgins, this study
new species	ASW	Carrie Bow Cay, Belize	Higgins, this study
hyalinus	MED	Trieste, Italy	Zelinka, 1928
imperforatus,	ASW	*Twin Cays*, Belize	Higgins, this study
new species	ASW	Carrie Bow Cay, Belize	Higgins, this study
incertus	MED	*Porto-Pi*, Balearic Is.	Reinhard, 1885
kowalewskii	MED	*Odessa*, USSR	Reinhard, 1885
kozloffi	INE	*San Juan Is.* (Wash.), USA	Higgins, 1977a; Kozloff, 1972; Merriman and Corwin, 1973
lanuginosa	ANE	*Ostende*, Belgium	Greeff, 1869
levanderi	ANE	*Tvarminne-Hangö*, Finland	Karling, 1954
	ANE	Stockholm Arch, Sweden	Karling, 1954
	ANE	Sandhamn, Sweden	Karling, 1954
	ANE	Åland-Helsinfors, Finland	Karling, 1954
	ANE	Southern Baltic	Drzycimski, 1975
	ANE	Askö-Landsort, Sweden	Anakr and Elmgren, 1976
masudai	INW	Gogoshima, Japan	Abe, 1930
	INW	Misaki, Japan	Abe, 1930
maxwelli	PSW	*Greater Kleinemonde Estuary*, South Africa	Omer-Cooper, 1957
meridionales	MED	*Cassamiccola* (Naples), Italy	Panceri, 1876
	MED	Salerno, Italy	Panceri, 1876
metschnikowii	MED	*Odessa*, USSR	Reinhard, 1885
minax	MED	*Naples*, Italy	Zelinka, 1928
minimus	ANE	Gullmarfjord, Sweden	Nyholm, 1947a
	MED	*Naples*, Italy	Zelinka, 1928
minutus	MED	Cassamiccola (Naples), Italy	Panceri, 1876
monocercus	ANE	*St. Vaast la Hougue*, France	Claparède, 1863
	ANE	Byfjord (Bergen), Norway	Schepotieff, 1907
	MED	Salerno, Italy	Panceri, 1876
newcaledoniensis	ISEW	*Baie St. Vincent*, New Caledonia	Higgins, 1967
pacificus	ISE	*Santa Cruz Is.* (Galapagos)	Schmidt, 1974
pagenstecheri	MED	*Porto-Pi*, Balearic Is.	Reinhard, 1885
pallidus	MED	*Naples*, Italy	Zelinka, 1928
parallelus	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
pennaki	INE	*East Sound* (Orcas Is., Wash.), USA	Higgins, 1960
pilosus	PSW	*Grytviken*, S. Georgia Is.	Lang, 1949
	PSW	Porto Deseado, Argentina	Pallares, 1966

TABLE 7.—Continued

Species	FAO sea area	Locality	Authority
	PSW	Sorrel, Argentina	Pallares, 1966
pulchellus	MED	*Naples,* Italy	Zelinka, 1928
pusillus	MED	*Trieste,* Italy	Zelinka, 1928
riedli	ISW	*Al-Ghardaqa,* Egypt	Higgins, 1966a
	MED	Carthage, Tunisia	Higgins, 1978
rosaceus	MED	*Naples,* Italy	Remane, 1936
setiger	ANE	*Ostende,* Belgium	Greeff, 1869
	ANE	Byfjord (Bergen), Norway	Schepotieff, 1907
	ANE	Fladden (Scotland), UK	McIntyre, 1962
spinosus	MED	*Cassimiccola* (Naples), Italy	Panceri, 1876
splendidus	MED	Naples, Italy	Zelinka, 1928
	MED	Portorose, Yugoslavia	Zelinka, 1928
steineri	ASW	*Aransas Bay* (Tex.), USA	Chitwood, 1951
sublicarum	ANW	*North Inlet Estuary* (S.C.), USA	Higgins, 1977b
tchefouensis	INW	*Tchefou,* People's Rep. China	Lou, 1934
trispinosus	MED	*Trieste,* Italy	Zelinka, 1928
truncatus,	ASW	*Twin Cays,* Belize	Higgins, this study
new species	ASW	Carrie Bow Cay, Belize	Higgins, this study
wallaceae,	ASW	*Twin Cays,* Belize	Higgins, this study
new species	ASW	Carrie Bow Cay, Belize	Higgins, this study
worthingi	ANE	*Blacksod Bay,* Ireland	Southern, 1914
	ANE	Worthing (England) UK	Zelinka, 1928
species	ANE	Plymouth (England), UK	Krishnaswamy, 1962
	ANE	Arcachon, France	Renaud-Debyser, 1963
	ANE	Kadetrinne, GDR	Reimer, 1963
	ANE	Loch Nevis (Scotland), UK	McIntyre, 1964
	ANE	Fladen (Scotland), UK	McIntyre, 1964
	ANE	Roskoff, France	d'Hondt, 1970
	ANW	Beaufort (N.C.), USA	Rieger and Ruppert, 1978
	INW	Seto, Japan	Tokioka, 1949
	INW	Irimote Is.	Sudzuki, 1976a
	INW	Okinawa Is.	Sudzuki, 1976b
	ISW	Narakal, India	Damodaran, 1972
	ISW	Malipuram, India	Damodaran, 1972
	ISW	Calicut, India	Damodaran, 1972
	ISW	Alleppey, India	Damodaran, 1972
	PSW	Isla Maillén, Chile	Lang, 1953
	PSW	Greater Kleinemonde Estuary, South Africa	Omer-Cooper, 1957

specimens. Thus, *Echinoderella* was synonomized with *Echinoderes* by Karling (1954). The last three juvenile stages of *Echinoderes* (with eyespots) were assigned to the "larval genus" *Habroderes;* the last three juvenile stages of *Echinoderella* (without eyespots) were assigned to the "larval genus" *Habroderella.*

The family Echinoderidae was defined on the basis of cyclorhagids (second segment with a radial series of placids closing off the retracted head) having only a single pair of lateral terminal spines, lateral terminal accessory spines in the female, and no midterminal spine! Kinorhynchs having two pairs of lateral terminal spines and a midterminal spine on the last segment were included in the family Centroderidae. Adult members of this family lacking eyespots were assigned to the genus *Centroderes,* juveniles with eyespots were placed in the "larval genus" *Centropsis,* and those lacking eyespots became *Hapaloderes.*

Remane (1936) recognized that Zelinka's larval genus *Centropsis* belonged to the family Echinoderidae, and that other than for the lack of eyespots, *Hapaloderes* was indistinguishable from *Centropsis.* Since then, life history studies by Nyholm (1947a,b), Higgins (1968, 1974, 1977a,b), Higgins and Fleeger (1980), and Kozloff (1972) have confirmed that *Centropsis* and *Hapaloderes* are, like *Habroderella, Habroderes,* and *Echinoderella,* junior synonyms of *Echinoderes.*

Fortunately, there are relatively few species indeterminata in *Echinoderes.* The oldest unresolved species, *Echinoderes borealis* Greeff, 1869, represents an example of a questionable segment count. Apparently, it had only 12 segments instead of 13, and, if so, it probably was a juvenile. This is further suggested by its alleged possession of middorsal spines on segments 5–10; 6–11 is more likely, since no species of *Echinoderes* adult or juvenile has middorsal spines anterior to segment 6. A spine on the 11th segment further corroborates the juvenile character of this species. The lateral spines further complicate the problem. They are reportedly on segments 8–11 but could be on 9–12; moreover, lateral spines (usually adhesive tubes) on segment 7 are often very difficult to observe, and considering the poorly rendered illustration of *E. borealis* and virtually useless description, one cannot be certain that other lateral spines were not present on this species, which as one might guess, has never been reported a second time.

Another common error in the taxonomic interpretation of *Echinoderes* is related to the lateral spines. It is very easy to mistake the optical-section view of a segment's thick cuticular wall for lateral spines. There are several examples of this error, the most obvious of which are *Echinoderes steineri* Chitwood, 1951, and *Echinoderes druxi* d'Hondt, 1973. The latter species, with its unique middorsal spine formula of 6, 7, 10, is easily identifiable on that single character alone, but the description and illustration of this species show lateral spines on all trunk segments. The author (d'Hondt, pers. comm.) has corrected a reprint of the illustration by crossing out lateral spines on segments 3 and 12, thereby making the formula 4–11, also unique and highly suspect. Even more unfortunate is the fact that of the three original specimens collected, two have been lost, and the author has refused permission to allow the remaining type specimen to be examined as a permanent whole mount (Higgins, 1978). *Echinoderes tchefouensis* Lou, 1934, illustrates another form of lateral spine confusion. Lou used a separate segment numbering system for the trunk (segments 1–11 instead of 3–13) and then reported middorsal spines on segments 5–8 (meaning trunk segments 5–8) which translates to body segments 7–10; more likely, the spines are really on body segments 6–10, and the one on segment 6 was lost.

Missing dorsal spines may also be a significant problem. If carefully mounted in a dorsal-ventral aspect and properly cleared, the site of a missing spine can be seen but only with extreme care. A single adult specimen of *Echinoderes* having anything other than a middorsal spine formula of 6–10 or 6, 8, 10 should be highly suspect and carefully examined. Where many specimens exist, the problem is usually resolved more satisfactorily, but with the exception of *E. druxi,* no data on number of specimens examined exist for species with such aberrant middorsal spine formulae as 7–10 (*E. tchefouensis*); 6, 7, 9 (*E. setiger*); 6, 7, 10 (*E. druxi*); or 6, 9 (*E. citrinus*). Similarly, lateral spines often create problems by breaking off or by being so small (especially the L-4 adhesive tube) as to be indistinguishable from surrounding cuticular hairs or by being arranged differently depending on sex. This latter instance may be seen in *E. gerardi, E. truncatus,* and *E. riedli,* where a shorter, seta-like spine replaces the normal lateral spine on the twelfth segment of the males.

The genus *Echinoderes* has been found throughout the world's oceans and far exceeds all other kinorhynch genera in the number of published distribution records. A summary of this distribution is found in Table 7 and portrayed graphically in Figure 68.

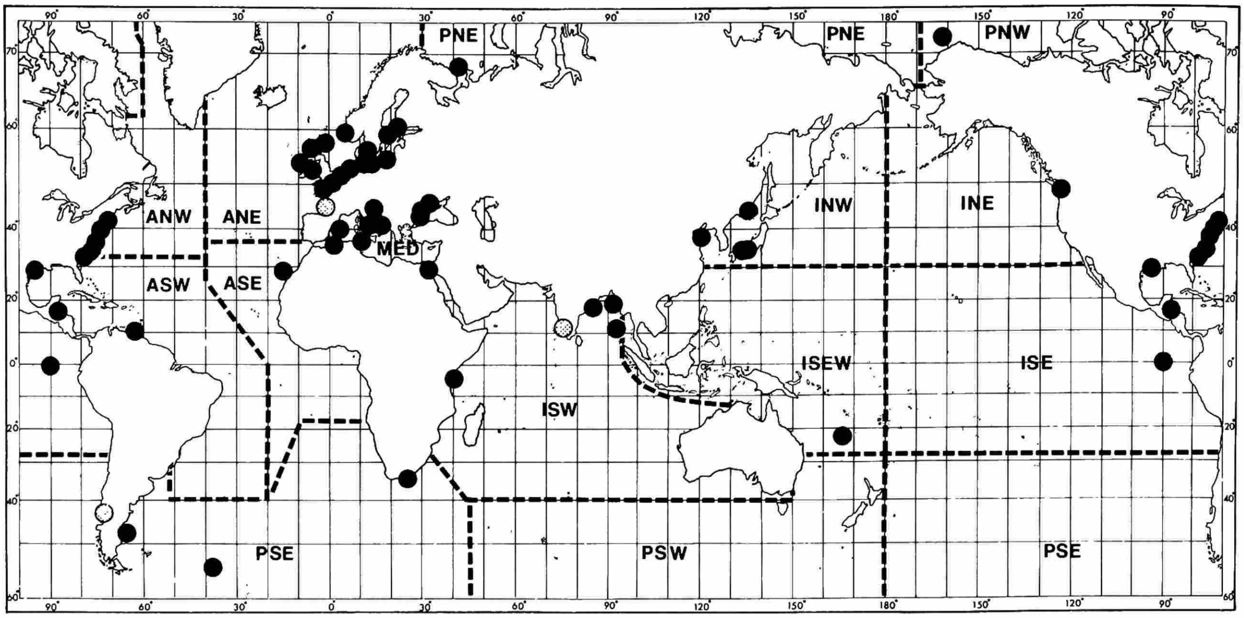


FIGURE 68.—Distribution of *Echinoderes* (solid circles indicate records of named species; stippled circles indicate genus records only).

Although its habitats vary, *Echinoderes* is usually an inhabitant of diatom-rich mud to muddy sand but may be found in sediments varying from fine organic material (Kozloff, 1972) to gravel (Krishnaswamy, 1962). Unlike most other kinorhynch genera, it is also a common inhabitant of algae, where it probably feeds on one or any combination of epiphytic diatoms, attached detritus, and bacteria. A few species have been found in association with other animals. *Echinoderes dujardinii,* the first kinorhynch found, was recorded from material adhering to oysters (Dujardin, 1851). *Echinoderes ehlersi* was found in association with an unknown invertebrate (Zelinka, 1913). The entire collection of kinorhynchs from the *Clare Island Survey* (Southern, 1914), including *E. dujardinii* and *E. worthingi,* was found in the debris at the bottom of bottles containing polychaetes. These examples probably represent no special relationship other than having been in the same sediment as their associated invertebrates, but the colonial hydroid *Eudendrium* species is the only known habitat for *Echinoderes sublicarum* (Higgins, 1977b), and *E. gerardi* has only been reported from a small, globose, red-orange sponge, *Tethya aurantium,* from the Bay of Tunis (Higgins, 1978a).

Data on the salinity and temperature of *Echinoderes* habitats are sparse, but the genus has been found throughout a wide range of both. *Echinoderes* is probably the common kinorhynch found in estuarine sediments. The more notable estuarine species include *E. bookhouti,* Newport River Estuary, Beaufort, N.C., USA; *E. maxwelli,* Greater Kleinemonde Estuary, South Africa; and *E. coulli,* North Inlet, estuarine system, Georgetown, S.C., USA; however, *E. bengalensis,* living in the Ganges Delta area is certainly estuarine, as are *E. levanderi* and *E. subfuscus,* both inhabitants of the eastern Baltic Sea, where salinities are extremely low. *Echinoderes levanderi* has been reported from the coast of Finland at salinities between 3.85‰ and 6.11‰ (Purasjoki, 1945). *Echinoderes coulli* has been reported from persistent salinities of 12‰ in the intertidal mud of *Spartina* marshes along the southeastern coast of the United States and is known to tolerate a salinity range from 1‰ to 42‰ (Horn, 1978).

Temperature data is even less frequently encountered. A minimum sea water temperature of 1.5°C was reported for *Echinoderes pilosus* by Lang (1949), which is not an unexpected low temperature for most north and south temperate localities as well as polar seas. *Echinoderes bookhouti* is commonly found in temperatures approaching 35°C in the shallow muddy areas of the Newport River Estuary. *Echinoderes coulli,* an obligate intertidal species, undoubtedly encounters temperatures equally as high or higher when its intertidal sediment is directly exposed to maximum solar radiation at low tide.

Most species of *Echinoderes* have been collected at shallow depths, usually less than 100 m. *Echinoderes arlis,* from 747 m (Higgins, 1966c), is the deepest record for the genus. Several species appear to be intertidal. *Echinoderes coulli* has never been found subtidally and appears to be restricted to the intertidal zone. *Echinoderes bengalensis* has been found in the intertidal sand at Sonadia Island, Bangladesh (Timm, 1958), and the sandy beaches near Waltair, India (Rao and Ganapati, 1968). *Echinoderes kozloffi* also appears to be intertidal but may or may not be restricted to this zone.

Echinoderes dujardinii is the most widely distributed species of kinorhynch. As noted previously (Higgins, 1977a), this species has been reported from 26 localities, including the northern and southern coasts of Europe, the Black Sea, the Canary Islands (incorrect), Japan, and the northwestern coast of the United States. The reports of *E. dujardinii* from the United States (Chitwood, 1964; Merriman and Corwin, 1973) are based on misidentifications, and there is considerable likelihood that the reports of this species from Japan (Tokioka, 1949; Sudzuki, 1976a,b) are likewise incorrect. The reports of *E. dujardinii* from the Black Sea (Băcescu et al., 1963; Marinov, 1964; Băcescu, 1968) in my opinion are questionable. Nonetheless, considering the length of the European coastline, the distribution of *E. dujardinii* is still extensive.

There are a few instances where other species of *Echinoderes* have been found over a wide geographic range. Recently, *E. ehlersi,* first described from Zanzibar (Zelinka, 1913), was found in the Andaman Islands on the opposite side of the Indian Ocean (Higgins and Rao, 1979). *Echinoderes riedli* whose type-locality is Al-Ghardaqa on the Egyptian coast of the Red Sea (Higgins, 1966a) has also been found on the Tunisian coast (Higgins, 1978). Along the east coast of the United States, *Echinoderes remanei* has been found in several localities north of Cape Hatteras (Wieser, 1960; Higgins, 1964a), while *E. bookhouti* is restricted to the southeastern coast (Higgins, 1964b). *Echinoderes coulli* is widely distributed in the marsh ecosystems of this latter region (Higgins, 1977b; Higgins and Fleeger, 1980). Most species of *Echinoderes* appear to be restricted to a relatively small geographic range, although this is likely an artifact of collection and identification.

Order HOMALORHAGIDA Zelinka, 1896

DEFINITION.—Kinorhyncha with second segment (neck) consisting of 6, 7, or 8 well-formed placids (neck plates); trunk segments flattened ventrally, vaulted dorsally, triangular or nearly so in cross-section; all trunk segments with single tergal (dorsal) plate, first trunk segment ventrally undivided, partially divided or completely divided longitudinally into 3 plates: 2 episternal (lateroventral plates) and a single midsternal plate (midventral); remaining trunk region with paired sternal plates articulating midventrally, sometimes with single, undivided terminal sternal plate; protonephridia without ligaments; gonads opening ventrolaterally or laterally near anterior margin of segment 13; pharynx musculature tripartite; oblique muscles absent; armor joints, if present, consisting of dorsal acetabulum and ventral condyle; with middorsal marginal processes or nonarticulate spinose processes both middorsally and laterally on tergal plates, if the latter, then with well-developed perispinal setae on either side of spinous processes; occasionally with midterminal and/or lateroterminal spines in early postembryonic stages or adult; surface of trunk segments porous with minute imbricate-adnate scales, minute hairs, or denticulate processes.

Family NEOCENTROPHYIDAE Higgins, 1969b

DEFINITION.—Homalorhagida with second segment (neck) consisting of 7 well-formed placids

(4 dorsal and 3 ventral); mouth cone with 4 short, thin, unjointed styles and 5 longer, two-jointed styles, all with a pectinate basal area; 6 rows of scalids present, first row with single elongate seta centered on basal plate, bordered by pectinate fringe; 14 trichoscalids present in posterior scalid row; first trunk segment not divided into 3 ventral plates, or with plate formation evidenced only at anterior margin; terminal segment may not be divided into 2 ventral plates; middorsal and lateral, nonarticulate spinous processes on all tergal plates; with well-developed perispinal setae on either side of most spinous processes; midterminal spine present, located between median terminal extensions of segment 13 so as to appear at the base of a notch in the terminal segment, flexible in males, rigid in females as is middorsal spine 13 preceding it; lateral terminal spines, when present, rigid in both sexes; 2 pairs of penile spines in male, generally long and flexible, attached lateroventrally near anterior margin of last segment.

TYPE GENUS.—*Neocentrophyes* Higgins, 1969b (type-species: *Neocentrophyes intermedius* Higgins, 1969b).

Paracentrophyes, new genus

DEFINITION.—Neocentrophyidae with lateral terminal spines and undivided terminal ventral plate.

TYPE-SPECIES.—*Paracentrophyes praedictus*, new species

COMPOSITION.—*Paracentrophyes praedictus*, new species, *Paracentrophyes quadridentatus*, new combination.

Paracentrophyes praedictus, new species

FIGURES 69–108

DIAGNOSIS.—Ventral portion of segment 3 with slight development of midsternal plate at anterior margin, midventral margin strongly dentate, remaining anterior margin of both ventral and dorsal plates minutely denticulate; sensory spots extremely prominent; perispinal setae on all trunk segments; lateral terminal spines short, 62–130 μm, 14.7–35.6 percent of trunk length.

DESCRIPTION.—Adults (Figures 69–108), trunk length 315–498 μm; MSW-8 112–130 μm, 24.0–37.5 percent of trunk length; SW 78–110 μm, 17.7–32.5 percent of trunk length. First segment (head) (Figure 79) with mouth cone surrounded by 5 two-jointed styles (Figures 79, 80, 103) the tips of which oppose 5 buccal teeth (Figures 79, 80, 97, 103) alternating with 4 nonjointed, thinner styles (middorsal unjointed style missing) (Figures 79, 80, 97), all with pectinate basal plate (Figures 97, 99, 100); 6 rows of scalids (Figure 80), 10 spinoscalids of first row blunt-tipped (Figure 79), ~90 μm long, with pectinate basal plate (Figures 79, 104) and single elongate seta, ~22 μm; second through fifth rows with pointed spinoscalids, ~70 μm, 60 μm, 50 μm, and 45 μm long; posteriormost row with 14 setate trichoscalids, 42 μm long (Figure 102).

Second segment (neck) with 3 ventral placids (Figures 71, 75), medial placid twice as wide (~56 μm) as lateral placids (~23 μm), and 4 dorsal placids (Figures 72, 76), ~20–22 μm wide.

Third segment (first trunk segment) with anterolateral margins projecting slightly as hornlike processes (Figures 71, 72); anterior margin of dorsal and ventral plates denticulate; midventral plate, defined only near anterior portion, with distinctly dentate margin; large dorso-ventral muscle scars evident laterally as thinner areas of tergal and sternal plates. Surface of cuticle with distinctive pattern of prominent sensory spots (Figures 69, 70, 95), cuticular hairs (Figures 92, 93) and few perforation sites not necessarily associated with cuticular hairs. Lateral and middorsal tergal margins extended posteriorly as spinose processes, ~30 μm long, with prominent perispinal setae, ~16 μm, adjacent to base (Figures 71, 75); additional setae anterior to perispinal setae on ventral plate; posterior margin of dorsal and ventral plates thin, finely striated.

Fourth segment with paired sternal plates, indistinctly articulating with dorsal plate, typical homalorhagid armor joints absent or poorly developed; perispinal setae near base of spinous processes; 3 (female) or 5 (male) sensory spots on either side of dorsal midline of tergal plate; single seta near lateral margin of each sternal plate; border without noticeable striations, otherwise similar to third segment.

Segments 5–11 similar to fourth segment ventrally, usually with 2–4 sensory spots on either side of dorsal midline of tergal plates (Figure 70); maximum sternal width at segment 8, 106–114 μm, 24.0–34.9 percent of trunk length in males, 112–130 μm, 25.9–37.5 percent of trunk length in females.

Segment 12 much narrower than anterior segments, narrower on male (78–88 μm, 17.7–27.9 percent of trunk length) than female (94–110 μm, 25.1–32.5 percent of trunk length), with only 1 sensory spot on each sternal plate and 1 (female) or 3 (male) on each side of tergal plate; lateral perispinal setae small; dorsal perispinal setae longer than lateral perispinal setae in males, absent in female. Middorsal spinous process of male flexible, longer (70–80 μm) than preceding processes, extending well beyond process of terminal segment (Figure 74); middorsal spinous process of female rigid, spinelike, shorter (18–20 μm) than preceding process.

Segment 13 slightly bifurcate terminally with tergal and sternal extensions terminating in a series of modified (probably glandular) sensory spots (Figures 73, 74, 77, 78, 108); no distinct midventral suture; midterminal spine of male short, 12–15 μm, situated ventral to long, flexible middorsal spinose process similar to but shorter (40–64 μm) than the preceding process of segment 12; midterminal spine of female long, 24–48 μm, without adjacent middorsal spine or process; prominent lateral terminal spines in both sexes, those of male shorter (62–80 μm) than those of female (98–130 μm). Males with 2 pairs of long, flexible penile spines, 52–60 μm, near anterolateral margins of terminal segment, anterior to lateral terminal spines.

Males differ from females principally in possession of more sensory spots; a long, flexible middorsal spinose process on segment 12 with perispinal setae; presence of 2 pairs of long, flexible penile spines on terminal segment; small midterminal spine ventral to the long, flexible middorsal spine; shorter lateral terminal spines, and slightly different structure of lateral extensions of terminal tergal and sternal plates; and narrower trunk (both MSW-8 and SW indices).

Morphometric data for adult specimens are shown in Table 8.

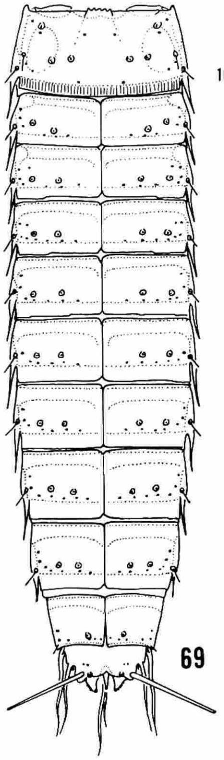
HOLOTYPE.—Adult male, TL 475 μm (Figures 69–74, 81–86), Twin Cays, sta RH 444, Belize (16°50.1′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69987.

ALLOTYPE.—Adult female, TL 495 μm (Figures 75–78, 87–90), other data as for holotype, USNM 69988.

PARATYPES.—Eight males and 13 females, TL 315–460 μm, other data as for holotype, USNM 69989.

JUVENILES.—Five with penile spines (therefore presumptive males) and 16 without penile spines, TL 130–360 μm, other data as for holotype, USNM 70073.

REMARKS.—*Paracentrophyes praedictus,* as its name infers, was not a surprise (Higgins, 1969b). This new taxon is similar to *Pycnophyes quadridentatus* Zelinka, 1928, a species represented by a single female, 370 μm long, and *P. flagellatus* Zelinka, 1928, a species represented by a single male, 590 μm long, which I now combine as one species and place in the new genus as *Paracentrophyes quadridentatus,* new combination. The *Paracentrophyes quadridentatus* male differs from males of *P. praedictus* in having a better defined midsternal plate on the first trunk segment, a uniform width throughout most of the trunk segments (none tapered as in *P. praedictus*), and an apparent! lack of sensory spots and small midterminal spine. The *Paracentrophyes quadridentatus* female was originally of undetermined sex, but based on the sexual dimorphic characters now apparent in this family, this latter specimen is female. Both of Zelinka's species were in the same sample collected from a muddy substrate at a depth of 15 m, Gulf of Baja, Naples, Italy; therefore, *Pycnophyes flagellatus* Zelinka (1928:311) becomes a junior synonym of *Paracentrophyes quadridentatus* (Zelinka, 1928:310). Thus, of the trilogy of aberrant species



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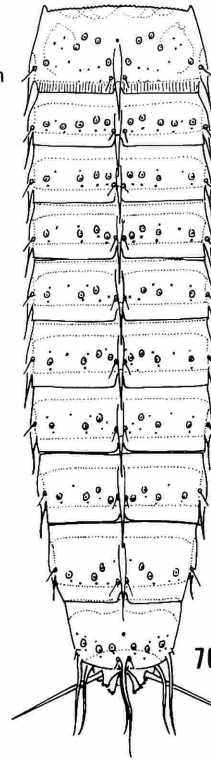

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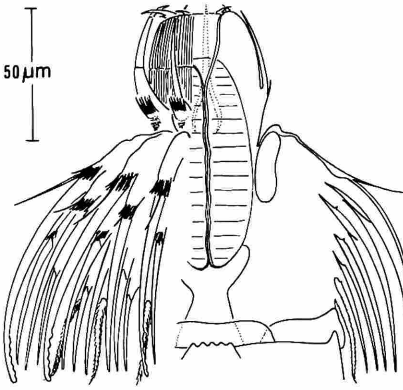

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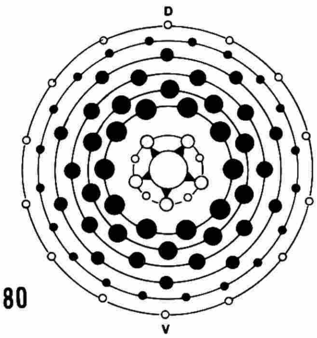

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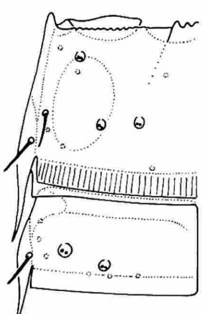

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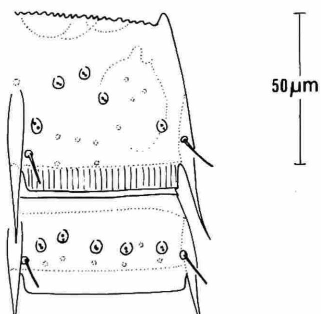

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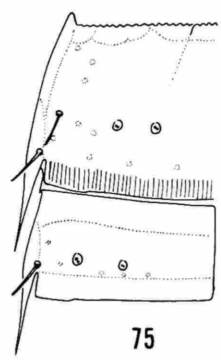

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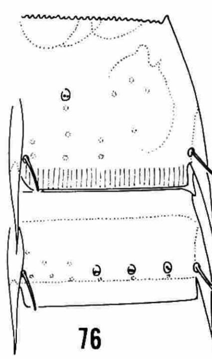

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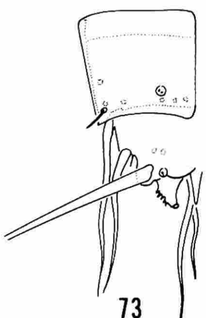

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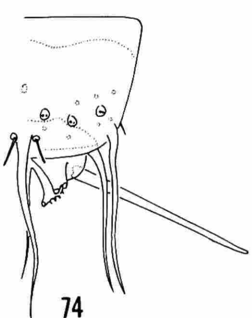

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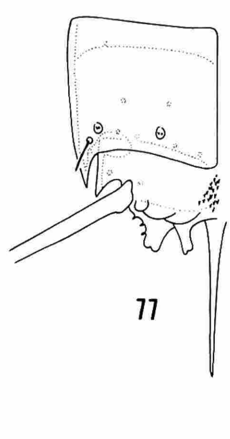

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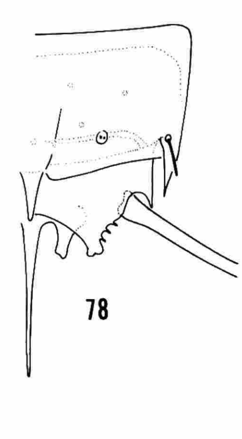

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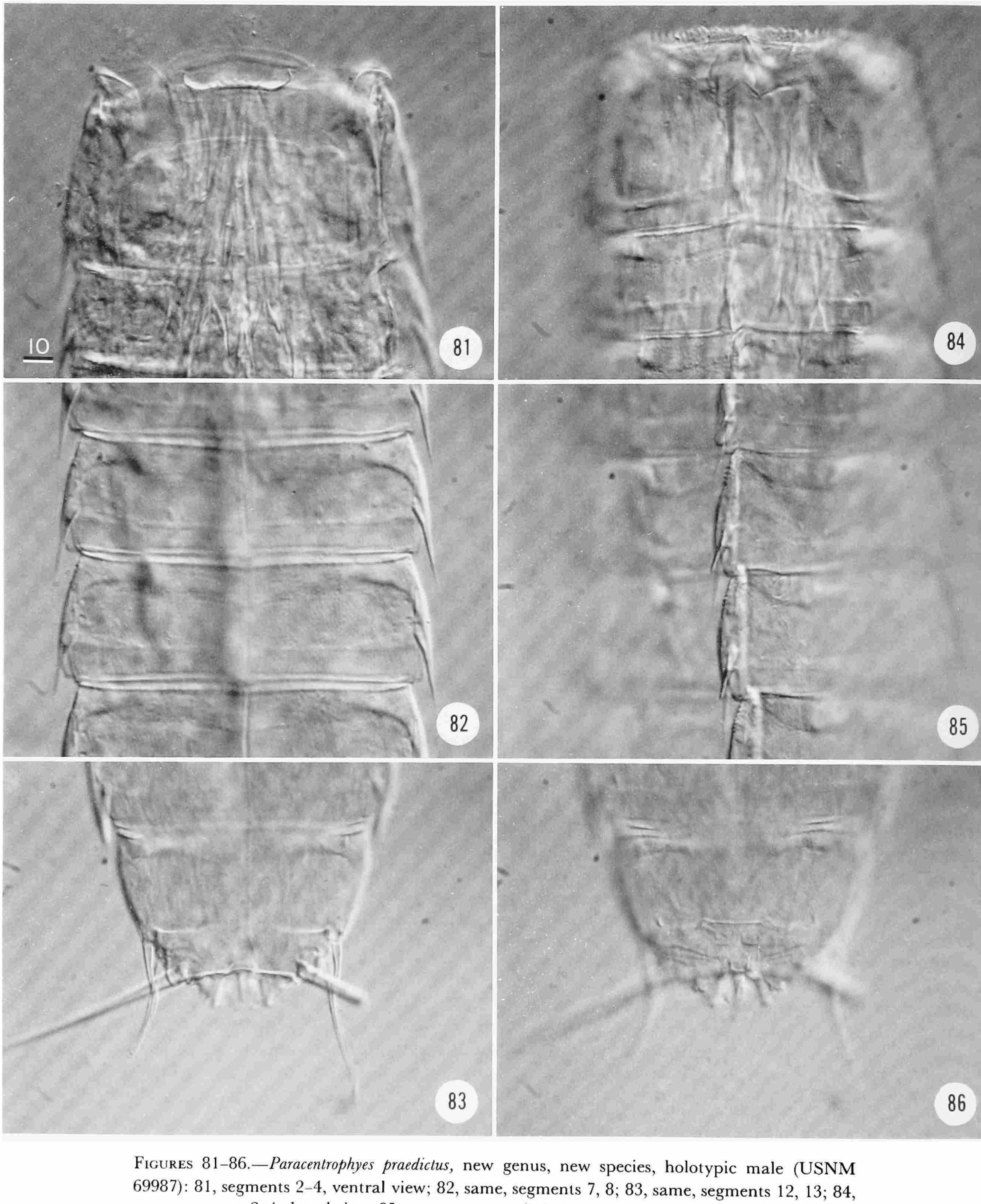
assigned to *Pycnophyes* by Zelinka, only *Pycnophyes echinoderoides* remains. A more complete review of these species is included in my discussion of the evolutionary significance of the Neocentrophyidae (Higgins, 1969b).

Considering the information obtained from this collection of *Paracentrophyes praedictus,* I now consider it possible that *Neocentrophyes satyai,* which I described from two adult females and a single juvenile collected at Visakapatnam (Bay of Bengal), India, may be conspecific and hence a junior synonym of *N. intermedius,* which I described from a series of eight adult males and a single juvenile from Nosy Bé, Madagascar. In the original discussion of these two species (Higgins, 1969b:123), I remarked that "I would not expect to find sexual dimorphism accounting for the differences between *N. intermedius* n. sp. of the West Coast of Madagascar and *N. satyai* n. sp. from the East Coast of India." I may have been in error.

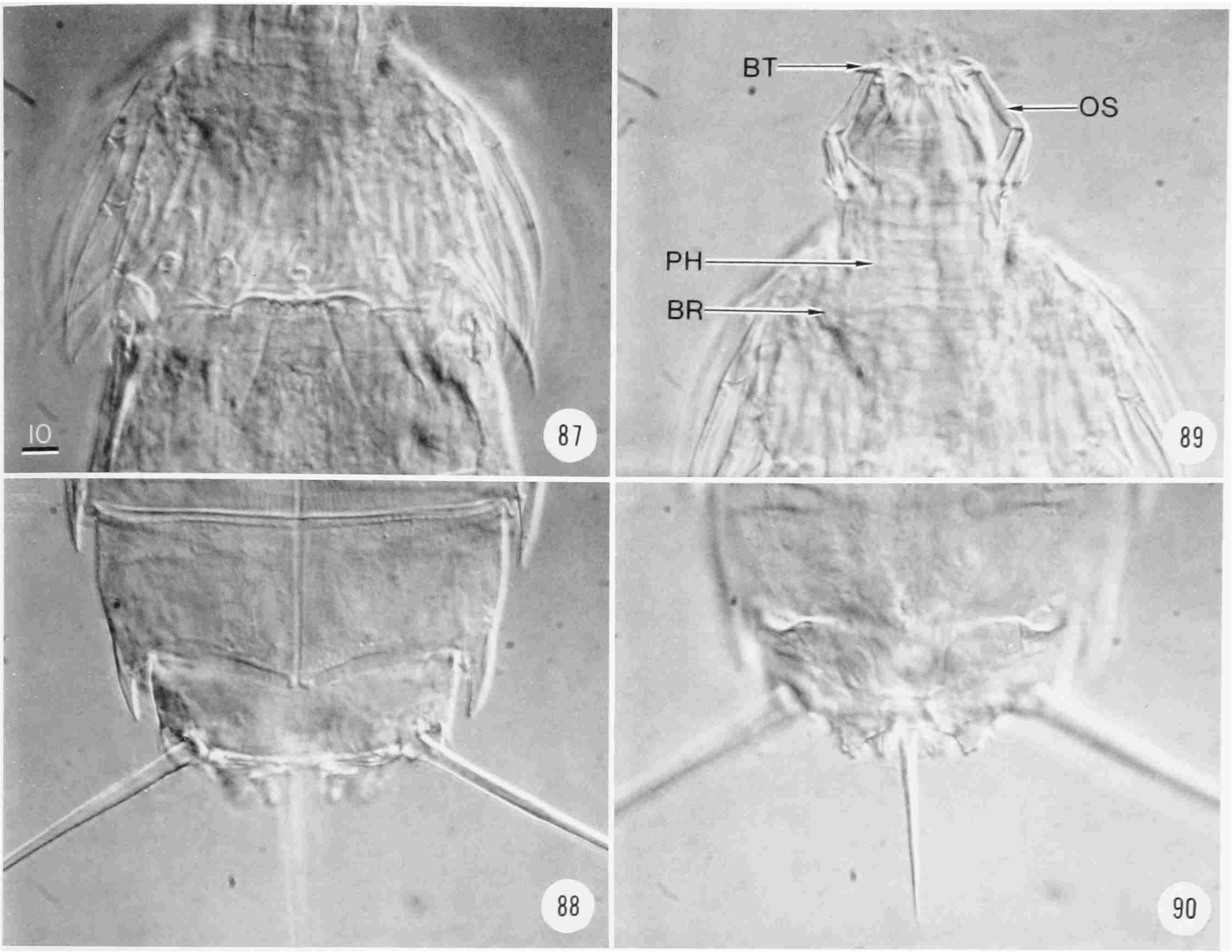
Of the total of 50 specimens of *Paracentrophyes praedictus* collected from the Twin Cays sta RH 444, six adults, three males and three females, were set aside for study using the scanning electron microscope (Figures 91–108). The remaining 44 specimens were prepared for light microscopy. Of these, 23 were adults and 21 were juveniles. Thirty-nine percent of the adults were males, and 61 percent were females. Five of the juveniles (24 percent) between 210 μm and 360 μm in length exhibited developing penile spines normally not seen until the final molt in a series of six juvenile stages (Higgins, 1974).

Juveniles appear very similar to the adults but do not have mature gonads and tend to reach their maximum sternal width at segment 5 instead of segment 8. The five juveniles with developing penile spines differed from adult males primarily in the greater length of their lateral terminal spines (Figure 109). Whereas adult males had lateral terminal spines 62–80 μm long, 14.7–22.8 percent of the trunk length, these measurements on the five juvenile males were 90–110 μm, 25.0–52.3 percent of the trunk length. These measurements closely approximate those of the adult females, i.e., 98–130 μm, 23.4–35.6 percent of the trunk length. The remaining 16 juveniles of undeterminable sex, on the other hand, had lateral terminal spines 96–122 μm long, 35.3–73.9 percent of the trunk length; five of these, less than 200 μm in length, were set off from the others by a significant increase in the relative length of their lateral terminal spines: the larger of these juveniles had lateral terminal spines 35.3–56.0 percent of the trunk length, the smaller size class (below 210 μm) had lateral terminal spines 63.1–73.9 percent of the trunk length. In a similar fashion, these five smallest juveniles differed in the standard width (SW) measurements and indices (Figure 110). Those juveniles 210 μm or longer had SW/TL indices of 24.6–34.0, those less than 210 μm had SW/TL indices of 36.6–41.5. The special morphometry of the five specimens, e.g., SW/TL indices and LTS/TL indices, are evidenced in both Figures 109 and 110. The cluster of the first five juveniles in each figure contrasts well with the remaining cluster of juveniles, including the inferred cluster of juveniles showing maleness.

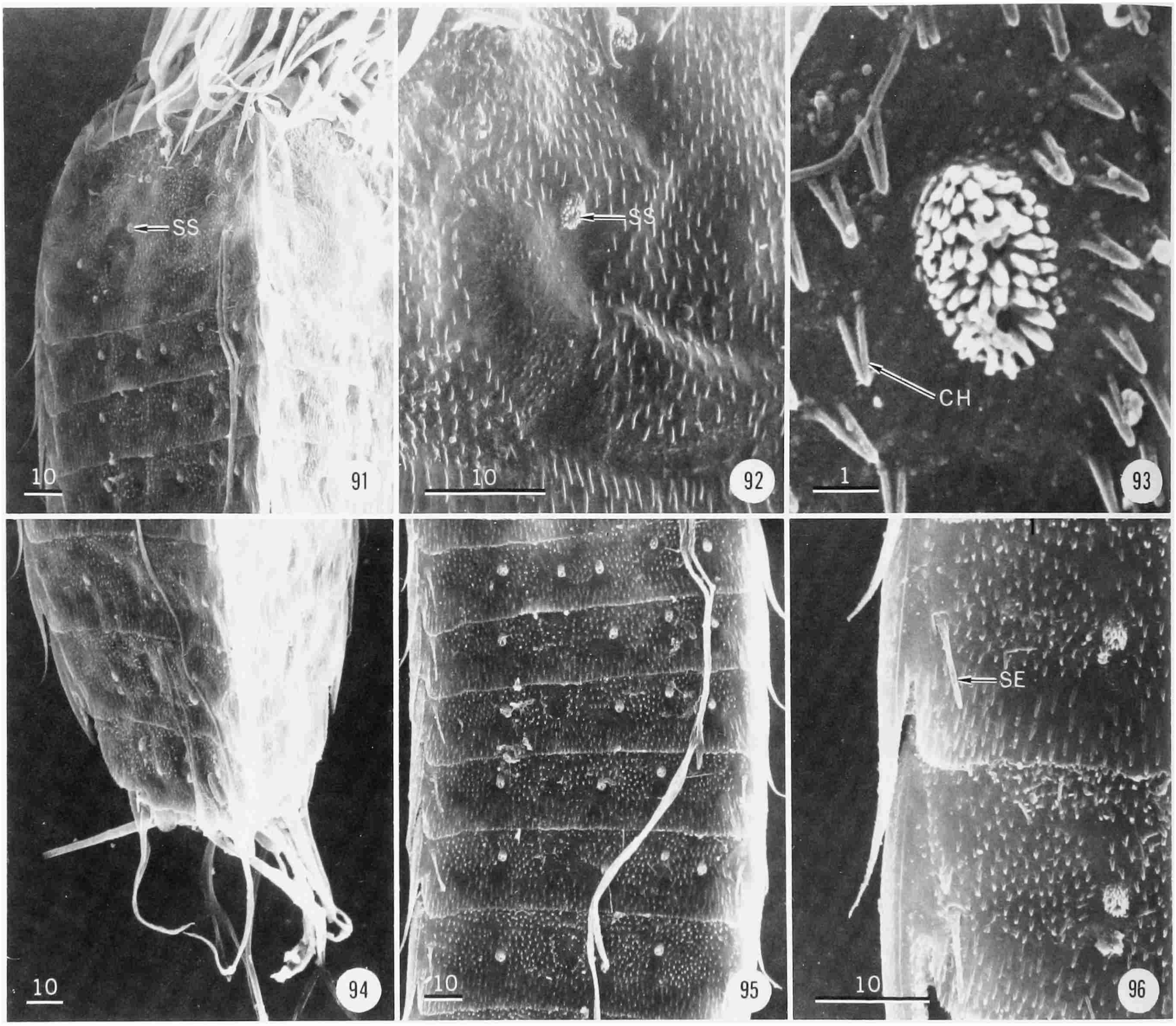
FIGURES 69–80.—*Paracentrophyes praedictus,* new genus, new species: 69, holotypic male (USNM 69987), neck and trunk segments, ventral view; 70, same, dorsal view; 71, same, segments 2–4, ventral view, lateral half; 72, same, dorsal view; 73, same, segments 13, 14, ventral view; 74, same, dorsal view; 75, allotypic female (USNM 69988), segments 2–4, ventral view, lateral half; 76, same, dorsal view; 77, same, segments 12, 13, ventral view; 78, same, dorsal view; 79, paratypic adult male (USNM 69989, RH 444.70), TL 330 μm, diagrammatic perspective, segments 1 (head) and 2 (neck) showing surface on left and optical section on right—note outline of brain (adjacent to muscular pharynx) and thickened cuticle (lens?) adjacent to forebrain; 80, anterior view (diagrammatic) of head appendage arrangement—the innermost ring consists of 5 buccal teeth (triangles) followed by a ring of alternating primary (two-jointed) styles and secondary (unjointed) styles followed by five rings of spinoscalids (black circles) and outer ring of trichoscalids (open circles).



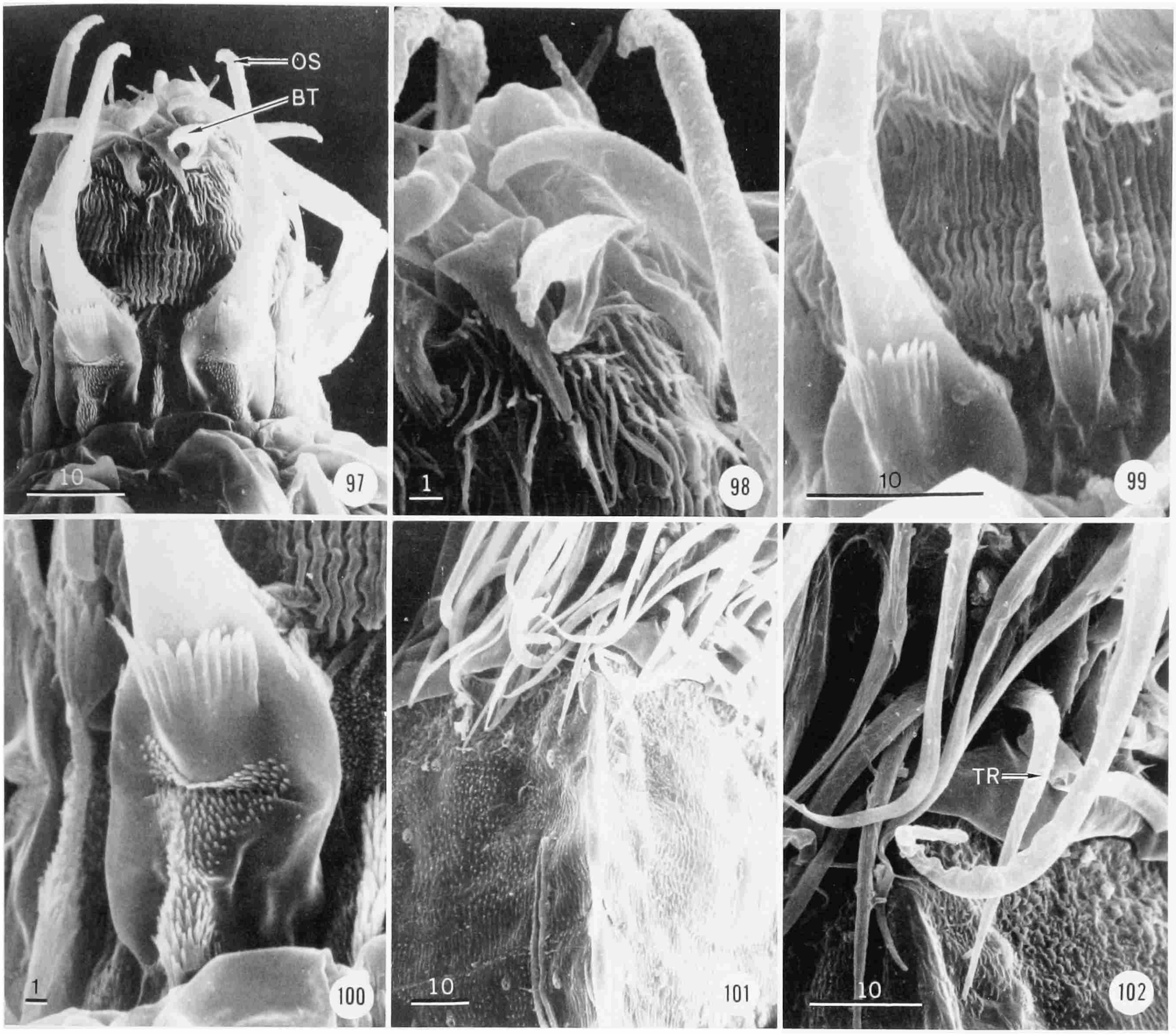
FIGURES 81–86.—*Paracentrophyes praedictus,* new genus, new species, holotypic male (USNM 69987): 81, segments 2–4, ventral view; 82, same, segments 7, 8; 83, same, segments 12, 13; 84, same, segments 2–4, dorsal view; 85, same, segments 7, 8; 86, same, segments 12, 13. (Interference contrast photographs all with same scale (in μm) as shown in Figure 81.)



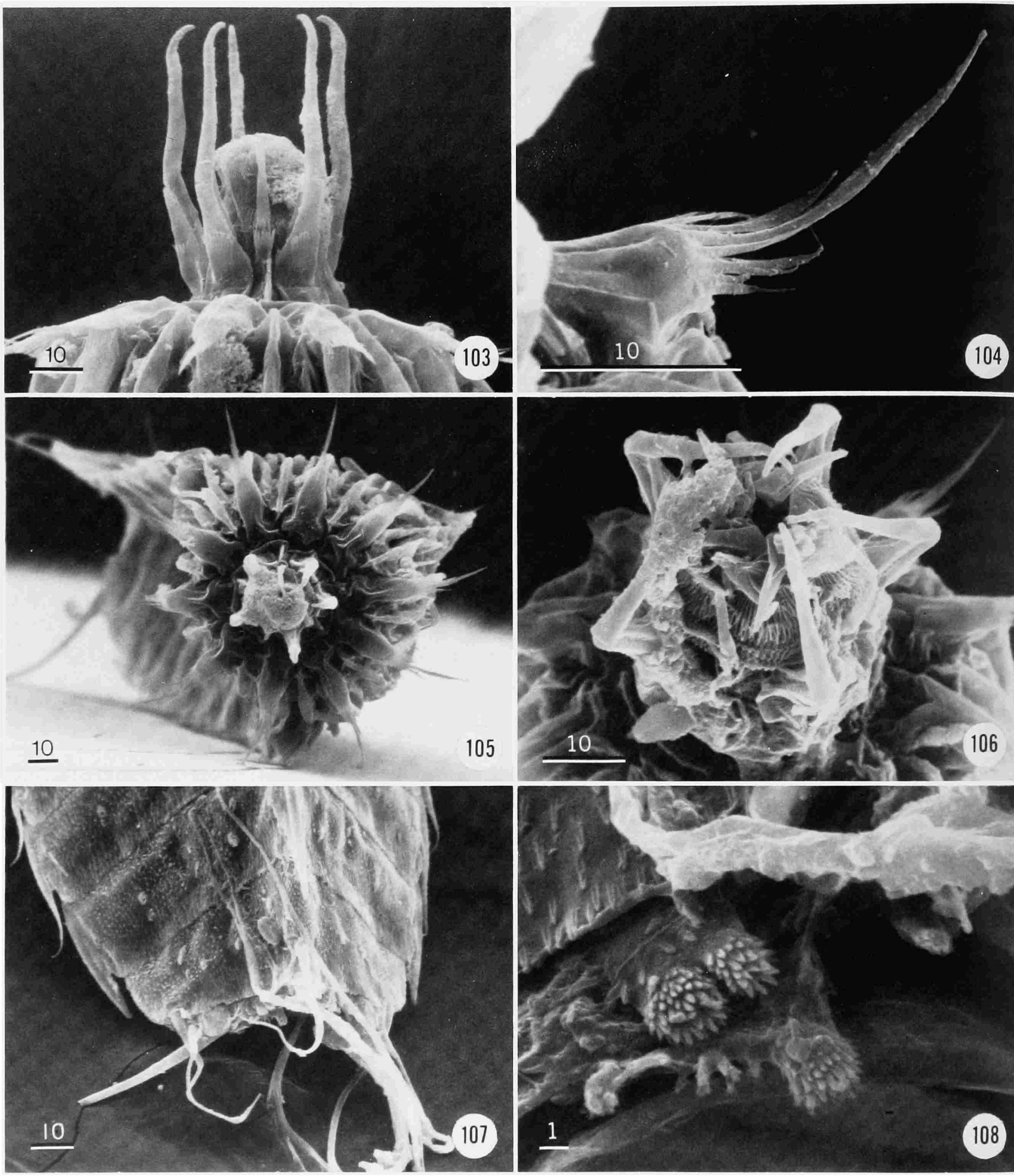
FIGURES 87–90.—*Paracentrophyes praedictus,* new genus, new species: 87, segments 1 (head) and 2 (neck), ventral view, paratypic male (USNM 69989, RH 444.70); 88, segments 12, 13, allotypic female (USNM 69988); 89, same adult as shown in Figure 88, segment 1 (head), dorsal view; 90, same adult as shown in Figure 88, segments 13, 14, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 87; BT = buccal tooth, OS = oral style, PH = pharynx, BR = brain.)



FIGURES 91–96.—*Paracentrophyes praedictus,* new genus, new species, male: 91, segment 1 (head) to segment 6, dorsal view; 92, enlarged view of Figure 91 showing cuticular depression in vicinity of dorso-ventral muscle attachment with cuticular hairs and sensory spots; 93, enlarged view of Figure 92 showing cuticular hairs and sensory spot with two pores surrounded by micropapillae; 94, segments 10–13, dorsal view, showing penile spines and elongated flexible middorsal spinous processes of segments 12 and 13; 95, segments 4–9, dorsal view showing sensory spots on left half of trunk; 96, segments 10, 11, ventral view of lateral margin showing cuticular hair pattern, sensory spot, and perispinal setae. (SEM photographs, each to scale (in μm) indicated; SS = sensory spot, CH = cuticular hair, SE = seta.)



FIGURES 97–102.—*Paracentrophyes praedictus*, new genus, new species: 97, extended mouth cone with primary and secondary styles and buccal teeth, dorsal view; 98, enlarged view of Figure 97 showing buccal tooth; 99, enlarged view of Figure 97 showing pectinate basal portion of primary (left) and secondary (right) styles; 100, enlarged view of Figure 97 showing greater detail of pectinate basal portion of primary style; 101, segments 1–4, dorsal view showing middorsal ridge and spinous processes; 102, enlarged view of Figure 101, showing detail of trichoscalid (center) and lower portion of primary spinoscalid (right). (SEM photographs, each to scale (in μm) indicated; OS = primary oral style, BT = buccal tooth, TR = trichoscalid.)



FIGURES 103–108.—*Paracentrophyes praedictus*, new genus, new species: 103, mouth cone, lateral view; 104, basal pectinate fringe and seta of primary scalid, lateral view; 105, extended head, anterior view; 106, mouth cone and oral styles, anterior view; 107, terminal segments of male, dorso-posterior view; 108, enlarged view of Figure 107 showing cluster of three modified sensory spots (probably secretory). (SEM photographs, each to scale (in μm) indicated.)

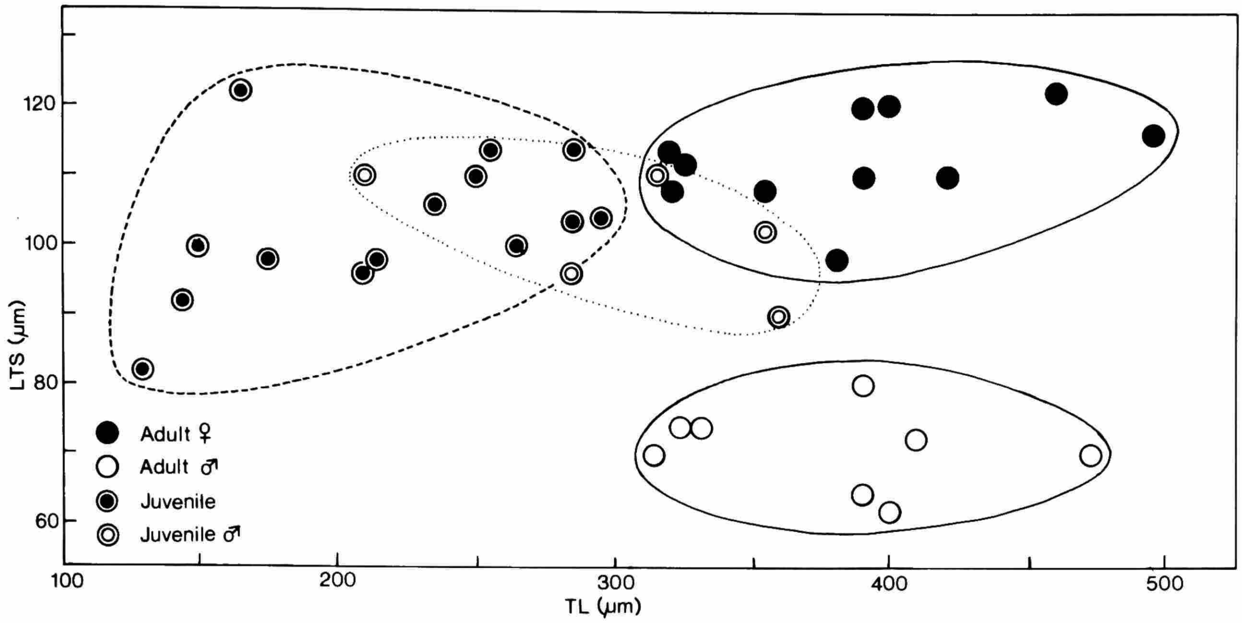


FIGURE 109.—*Paracentrophyes praedictus,* new genus, new species, adult males, females, and juveniles compared for relationships between length of lateral terminal spines (LTS) and total length (TL).

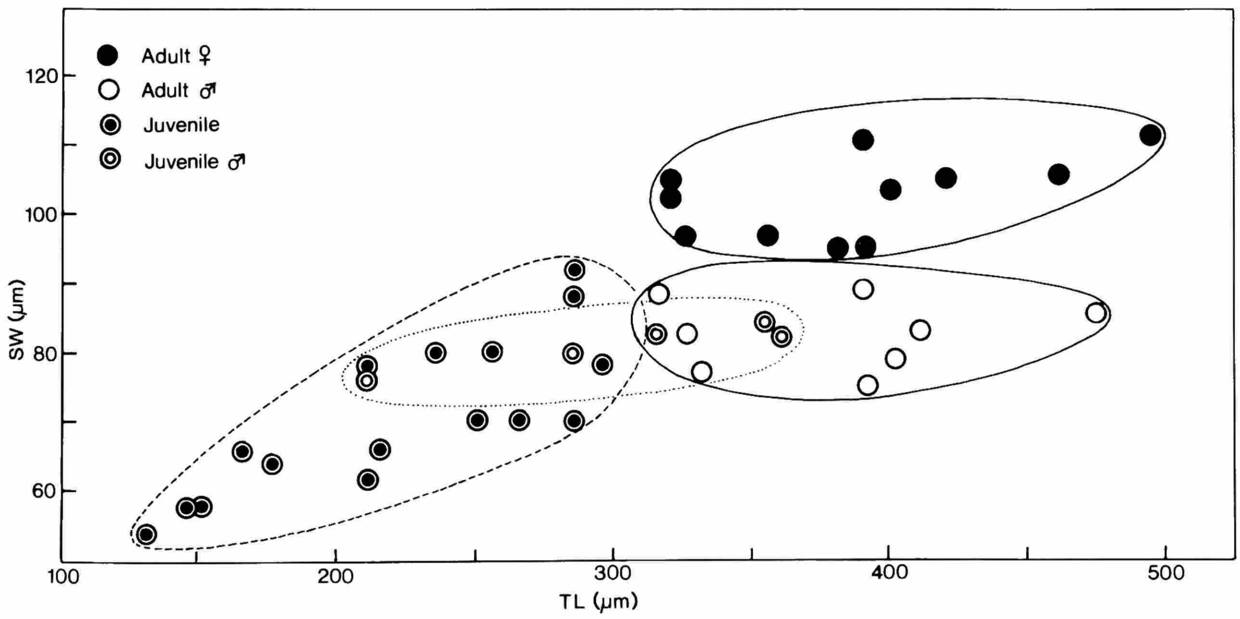


FIGURE 110.—*Paracentrophyes praedictus,* new genus, new species, adult males, females, and juveniles compared for relationships between standard width (SW) and total length (TL).

TABLE 8.—Measurements (μm) and indices (%) for *Paracentrophyes praedictus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	9	315–475	385.6	53.6	17.9	13.9
	♀	14	320–495	391.8	54.9	14.7	14.0
	♂♀	23	315–495	389.4	53.3	11.1	13.7
SW	♂	8	78–88	84.0	3.4	1.2	4.0
	♀	12	94–110	101.8	6.1	1.8	6.0
	♂♀	20	78–110	94.8	10.3	2.3	10.9
SW/TL	♂	8	17.7–27.9	22.6	3.6	1.3	15.8
	♀	12	25.1–32.5	26.5	3.4	1.0	12.7
	♂♀	20	17.7–32.5	25.0	3.9	0.9	15.7
MSW-8	♂	8	106–114	113.3	12.7	4.5	11.3
	♀	12	112–130	120.0	6.0	1.7	5.0
	♂♀	20	106–130	30.5	3.9	0.9	12.8
MSW/TL	♂	8	24.0–34.9	29.3	3.9	1.4	13.2
	♀	12	25.9–37.5	31.2	4.0	1.1	12.7
	♂♀	20	24.0–37.5	30.3	3.4	0.7	11.3
LTS	♂	9	62–80	71.6	5.9	2.0	8.4
	♀	14	98–130	113.7	7.8	2.1	6.9
	♂♀	23	62–130	97.2	22.2	4.6	22.8
LTS/TL	♂	9	14.7–22.8	18.9	3.1	1.0	16.6
	♀	14	23.4–35.6	29.4	3.8	1.0	12.9
	♂♀	23	14.7–35.6	25.3	6.3	1.3	24.9

Family PYCNOPHYIDAE Zelinka, 1896

Genus *Pycnophyes* Zelinka, 1907

Key to Adults of *Pycnophyes*

1. Posterior margin of tergal plate 3 with middorsal processes 2
   Posterior margin of tergal plate 3 even, without middorsal processes . . 11
2. Middorsal process of tergal plate 3 rounded 3
   Middorsal process of tergal plate 3 spinose, pointed 4
3. Midsternal plate of segment 3 elongate, apex of plate twice the width of base; length of plate two-thirds the width of posterior margin of segment 3 .... ***P. communis*** Zelinka, 1908
   Midsternal plate of segment 3 short, apex of plate three times the width of base; length of plate one-half the width of posterior margin of segment 3 .... ***P. maximus*** Reimer, 1963

4. Patches of punctations near lateral margins of sternal plates 4–12 .... ***P. iniorhaptus,*** new species
   No patches of punctations on sternal plates 4–12 5
5. Thin area of cuticle at anteromesial margin of episternal plates double or longitudinally divided 6
   Thin area of cuticle at anterior margin of episternal plates single or not present 8
6. Anteromesial thickenings of pachycycli ("Mittelwülste") of sternal plate 12 adjacent at ventral midline .... ***P. calmani*** Southern, 1914
   Anteromesial thickenings of pachycycli of sternal plate 12 ("Mittelwülste") widely separated, not adjacent at ventral midline 7
7. Vertical cuticular striations near lateral margin of sternal plate 12 .... ***P. dentatus*** (Reinhard, 1881)
   Sternal plate 12 without vertical cuticular striations .... ***P. flaveolatus*** Zelinka, 1928
8. Anterior margin of midsternal plate projecting well beyond anteromesial margins of episternal plates .... ***P. carinatus*** Zelinka, 1928
   Anterior margin of midsternal plate even with, not projecting beyond, anteromesial margins of episternal plates 9
9. Single laterodorsal placid on either side of single middorsal placid .... ***P. odhneri*** Lang, 1949
   Two laterodorsal placids on either side of midline, no middorsal placid 10
10. Prominent, elongate middorsal processes on tergal plates 4–11; tergal plate 12 pointed .... ***P. chiliensis*** Lang, 1953
    Middorsal processes not prominent, very short, tergal plate 12 rounded .... ***P. frequens*** Blake, 1930
11. Anterior margin of tergal plate 3 scalloped, with middorsal and laterodorsal projections conforming to lateral margins of dorsal placids .. 12
    Anterior margin of tergal plate 3 dentate, coronate, or even 13
12. Posterior margins of tergal plates 4 and 5 without middorsal processes .... ***P. kielensis*** Zelinka, 1928
    Posterior margins of tergal plates 4 and 5 (4–11) with middorsal processes .... ***P. ponticus*** (Reinhard, 1881)
13. Anterior margin of tergal plate 3 dentate-coronate with prominent middorsal projection and 3 lateral projections on either side; margin otherwise denticulate .... ***P. rugosus*** Zelinka, 1928
    Anterior margin of tergal plate even or evenly denticulate or otherwise sculptured 14
14. Thin area of cuticle at anteromesial margin of episternal plates double 15
    Thin area of cuticle at anteromesial margin of episternal plates single or otherwise undefined 16
15. Anteromesial thickenings of pachycyli ("Mittelwülste") of sternal plates 10 and 11 prominent; lateral terminal spines thick, robust; anterior margin of tergal plate 3 denticulate ... ***P. sanjuanensis*** Higgins, 1961

Anteromesial thickenings of pachycycli ("Mittelwülste") not prominent on any sternal plate; lateral terminal spines thin, not robust; anterior margin of tergal plate 3 smooth, without sculpturing .... ***P. sculptus*** Lang, 1949

16. Lateral terminal spines nearly equal to combined length of segments 12 and 13 17
    Lateral terminal spines nearly equal to or longer than combined length of segments 11, 12, and 13 18
17. Anterior margin of tergal plate 3 strongly denticulate; midsternal plate long and narrow .... ***P. zelinkaei*** Southern, 1914
    Anterior margin of tergal plate 3 even, unsculptured; midsternal plate short and wide .... ***P. beaufortensis*** Higgins, 1964b
18. Middorsal processes rounded on tergal plates 4–11; anterior margin of tergal plate 3 strongly denticulate, almost pectinate .... ***P. robustus*** Zelinka, 1928
    Middorsal processes absent or pointed on tergal plates 4–11; anterior margin of tergal plate 3 even or slightly denticulate 19
19. Middorsal processes pointed on tergal plates 4–11 .... ***P. longicornis,*** new species
    Middorsal processes absent on tergal plates 4–11 20
20. Posterior margin of tergal plate 13 with lateral bulbous protrusions and slight median notch; 2 lateral setae on either side of segment 12 .... ***P. emarginatus,*** new species
    Posterior margin of tergal plate 13 even or slightly roughened; single lateral seta on either side of segment 12 21
21. Sternal plates 11 and especially 12 with strong vertical cuticular ridges near lateral margins .... ***P. corrugatus,*** new species
    Sternal plates without vertical cuticular ridges near lateral margins .. 22
22. Midsternal plate broad at apex, about one-half the basal width; terminal segment often withdrawn beneath penultimate segment .... ***P. ecphantor,*** new species
    Midsternal plate very narrow at apex, one-fourth to one-third the basal width; terminal segment prominently broad, rounded and exposed .... ***P. egyptensis*** Higgins, 1966a

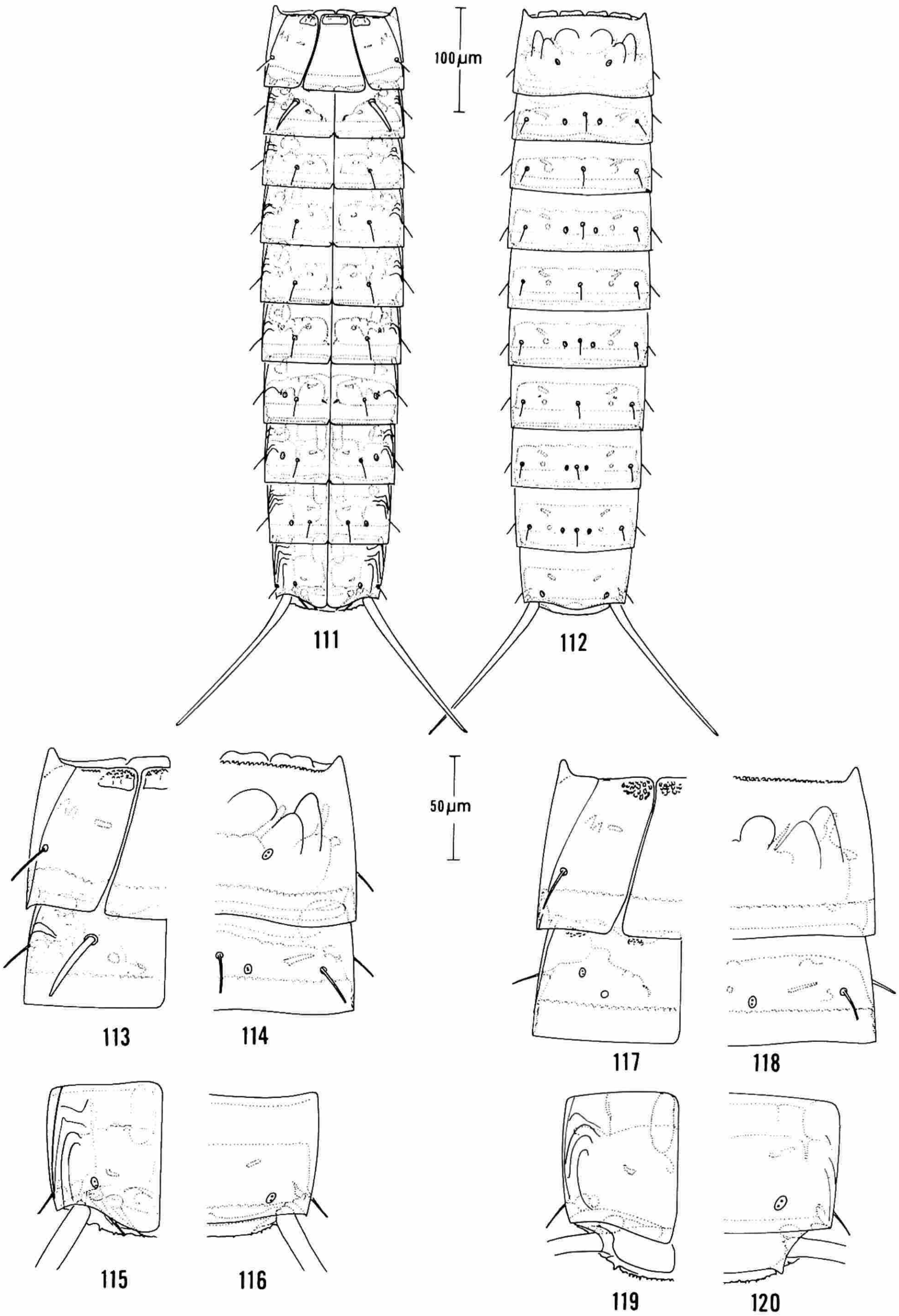
Pycnophyes corrugatus, new species

FIGURES 111–126

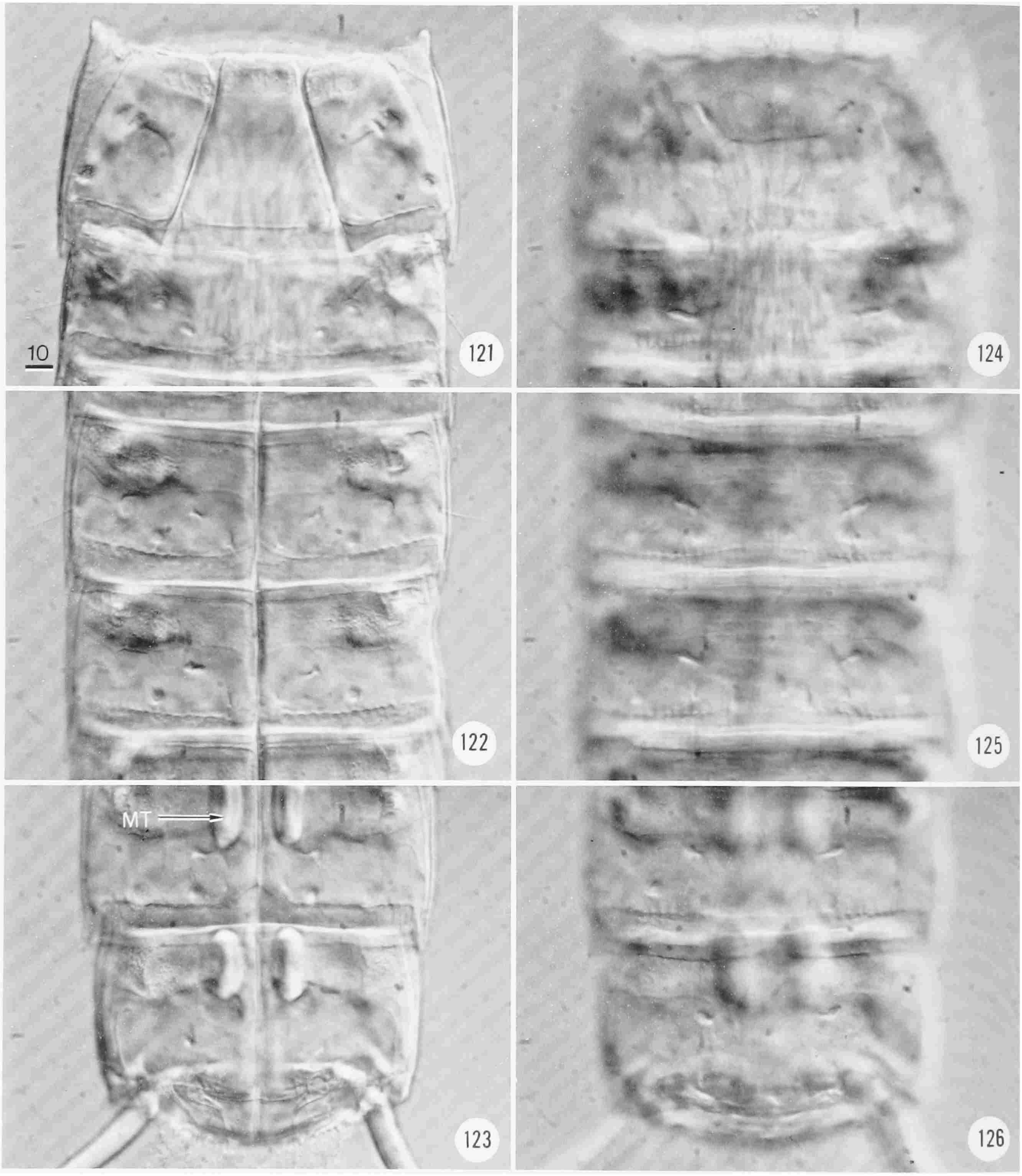
DIAGNOSIS.—Trunk segments 3–12 nearly uniform in width, tapering only slightly; lateral terminal spines long, 136–196 µm, 17.4–32.5 percent of trunk length, bent slightly outward about one-fourth distance from base; prominent cuticular ridges on either side of dorsal midline of first trunk segment and near ventrolateral margins of segments 4–12, reaching greatest prominence on segment 12.

DESCRIPTION.—Adults (Figures 111–126), trunk length 500–780 µm; trunk segments nearly uniform in width tapering only slightly, MSW-6 116–180 µm, 20.8–25.9 percent of trunk length; SW 104–128 µm, 16.4–22.0 percent of trunk length. Second segment consisting of 4 slightly incised dorsal placids and 2 even-margined ventral placids (Figures 113, 114).

Trunk segments (Figures 111, 112) without middorsal spinous processes; prominent setae, 20–23 µm long, situated middorsally and dorsolaterally on segments 4–11, laterally on segments 3–



FIGURES 111–120.—*Pycnophyes corrugatus,* new species: 111, neck and trunk segments, ventral view, holotypic male (USNM 69990); 112, same, dorsal view; 113, same, segments 2–4, lateral half, ventral view; 114, same, dorsal view; 115, same, segments 12, 13, lateral half, ventral view; 116, same, dorsal view; 117, segments 2–4, lateral half, ventral view, allotypic female (USNM 69991); 118, same, dorsal view; 119, same, segments 12, 13, lateral half, ventral view; 120, same, dorsal view.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12, and ventrolaterally on segments 5–11; sensory spots lateral to ventrolateral setae on sternal plates 9–12 and on either side of dorsal midline of segments 4, 5, 7, 9–11, more posterior and widely separated on segment 12. Pachycycli well developed on all trunk segments; midventral thickenings near anteromesial margins of ventral plates 10–12; prominent cuticular ridges in the form of rounded and ellipsoidal arches on dorsal plate of segment 3, slightly anterior to muscle scars (Figures 112, 114, 118); similar lateral cuticular ridges with prominent ridges parallel to lateral margin of segment on sternal plates 4–12, especially distinctive on segment 12 (Figures 111, 115, 119); large muscle scars middorsal and dorsolateral on tergal plate 3 (Figures 114, 118), slight evidence of anterior portion of 2 muscle scars near lateral margins of episternal plates. Elongate cuticular scars (with long axis oriented horizontally) on episternal plates of segment 3, oval cuticular scars (with long axis oriented horizontally) on sternal plates 4–12, similar elongate cuticular scars (with long axis oriented toward the anterolateral margin) dorsolateral on tergal plates 4–12.

First trunk segment (segment 3) with anterolateral margins of tergal plate extending to form slightly rounded to pointed projections, anterior tergal margin denticulate (Figures 114, 118); episternal plates with slight denticulate margin near junction with tergal plate and on small patch of thin cuticle near junction of midsternal plate (Figures 113, 117), midsternal plate with similar denticulate thin cuticular area; midsternal plate trapezoidal, about 73 μm long, 60 μm basal width tapering evenly to 22 μm about one-fourth distance from anterior margin and remaining this width to margin.

Segment 4 of males with prominent adhesive tubes, 35–39 μm long (Figure 115); females with sensory spot (Figure 114) in same area; pachycycli extensive. Segments 5–11 similar, differences already noted in distribution of setae, sensory spots and lateral cuticular ridges.

Sternal plates of segment 12 with posterior margin extending nearly to terminal margin of segment 13, rounded at midline; distinctive series of cuticular ridges near lateral margin (Figures 115, 120, 123); tergal plate evenly rounded and slightly extended near midline (Figures 116, 120). Sternal plates of segment 13 evenly rounded, parallel with margin of dorsal plate. Males with 2 pairs of penile spines at anterolateral margins of terminal sternal plates; single gonopore in female. Terminal tergal plate with uneven margin, slight protuberance near lateral terminal spines.

Lateral terminal spines long, 148–196 μm, 26.4–32.5 percent of trunk length in males, slightly shorter, 136–144 μm, 17.4–28.3 percent of trunk length in females; lateral terminal spines bent slightly outward about one-fourth distance from base.

Males differ from females by presence of adhesive tubes on sternal plates of segment 4 (Figure 113), 2 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 115), and slightly longer lateral terminal spines, which is common in this genus.

Morphometric data for adult specimens are shown in Table 9.

HOLOTYPE.—Adult male, TL 576 μm (Figures 111–116, 121–126), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69990.

ALLOTYPE.—Adult female, TL 614 μm (Figures 117–120), other data as for holotype, USNM 69991.

PARATYPES.—Four males and 3 females, TL 509–780 μm, other data as for holotype; 1 male, TL 603 μm, Twin Cays, sta RH 443, other data as for holotype, USNM 69992.

REMARKS.—*Pycnophyes corrugatus* differs from all other members of this genus by the presence of the prominent cuticular ridges on the lateral sur-

FIGURES 121–126.—*Pycnophyes corrugatus*, new species, holotypic male (USNM 69990); 121, segments 3, 4, ventral view; 122, segments 7, 8, ventral view; 123, segments 11–13, ventral view; 124, segments 3, 4, dorsal view; 125, segments 7, 8, dorsal view; 126, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 121; MT = midventral thickenings.)

TABLE 9.—Measurements (μm) and indices (%) for *Pycnophyes corrugatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	6	500–603	577.0	36.6	14.9	6.6
	♀	4	509–780	608.3	123.2	61.6	20.3
	♂♀	10	500–780	577.5	80.6	25.5	14.0
SW	♂	6	104–116	108.7	5.3	2.2	4.9
	♀	4	112–128	116.0	8.0	4.0	6.9
	♂♀	10	104–128	111.6	7.2	2.3	6.4
SW/TL	♂	6	18.2–21.1	19.5	1.2	0.5	6.1
	♀	4	16.4–22.0	19.4	2.6	1.3	13.3
	♂♀	10	16.4–22.0	19.5	1.7	0.6	8.9
MSW-6	♂	6	116–140	126.7	8.3	3.4	6.5
	♀	4	128–180	142.0	25.4	12.7	17.9
	♂♀	10	116–180	132.8	17.8	5.6	13.4
MSW/TL	♂	6	21.0–24.2	22.8	1.0	0.4	4.5
	♀	4	20.8–25.9	23.5	2.1	1.1	9.1
	♂♀	10	20.8–25.9	23.1	1.5	0.5	6.6
LTS	♂	6	148–196	165.3	16.9	6.9	10.2
	♀	4	136–144	139.0	3.8	1.9	2.8
	♂♀	10	136–196	154.8	18.7	5.9	12.1
LTS/TL	♂	6	26.4–32.5	29.7	2.1	0.9	7.1
	♀	4	17.4–28.3	23.6	4.7	2.3	19.9
	♂♀	10	17.4–32.5	27.2	4.5	1.4	16.3

face of the sternal plates, especially those of segments 11 and 12. It resembles *P. flaveolatus, P. sculptus, P. egyptensis, P. kielensis*, and *P. rugosus* in that all lack evidence of any middorsal spinous processes.

The series of parallel cuticular ridges near the lateral margin of sternal plates 4–12 somewhat resembles the series of parallel cuticular striations near the lateral margins on the sternal plates of segment 12 of *P. dentatus*. No other described species of *Pycnophyes* exhibits such a character.

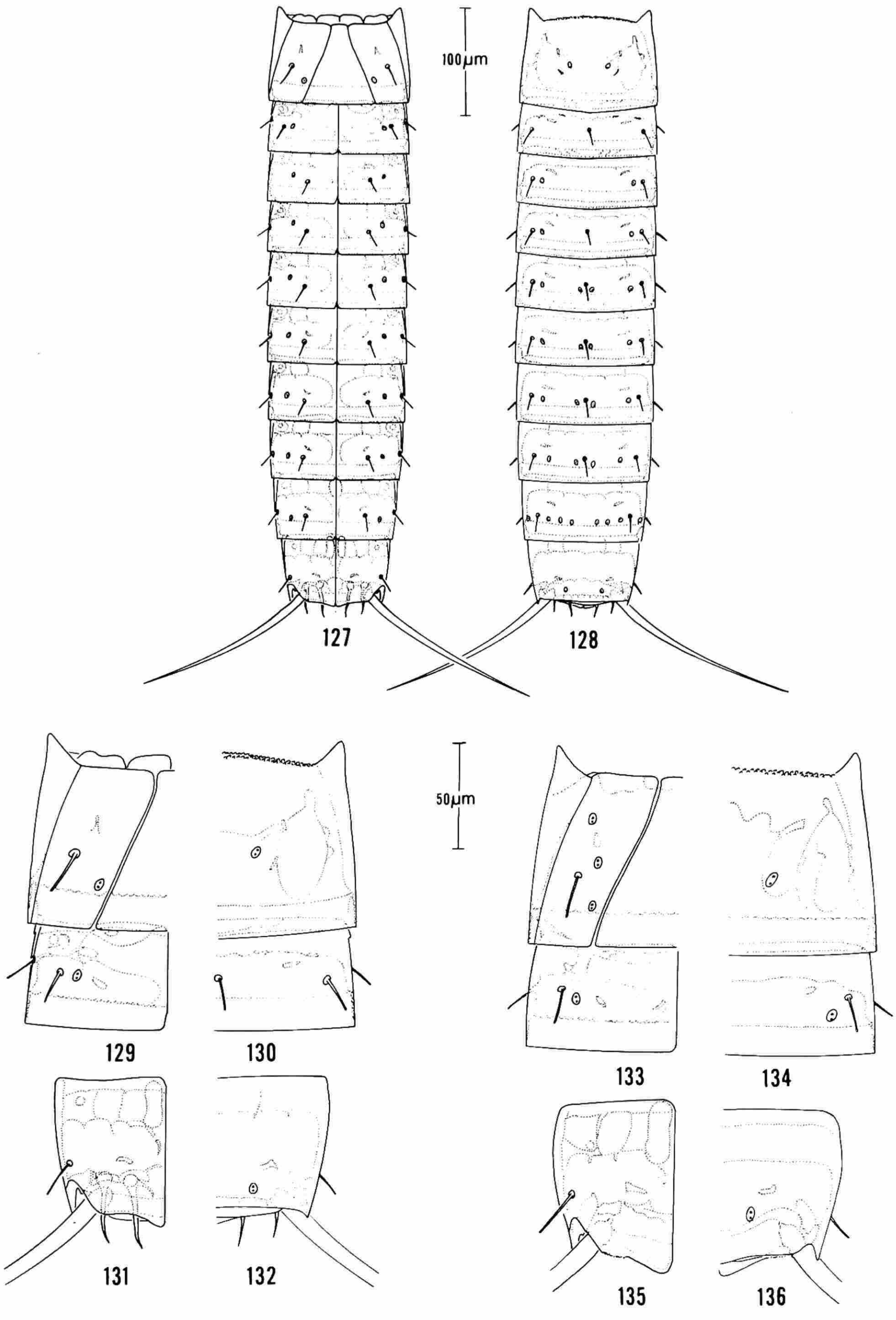
In general, *P. corrugatus* most resembles *P. flaveolatus*, although the latter species is much smaller, TL 460–520 μm; has smaller lateral terminal spines, 88 μm in the female and 111–120 μm in males, about 23 percent of the trunk length; and a different pattern of setae, muscle scars and sensory spots. With regard to "general shape" and these last characteristics, the new species resembles *P. egyptensis*, although the latter has much shorter setae, apparently no adhesive tubes in the male, and a much different pattern of cuticular sculpturing on the tergal plate of the first trunk segment.

ETYMOLOGY.—The name of this species is from the Latin *corrugatus* (wrinkled), referring to the series of parallel cuticular ridges on the sternal plates.

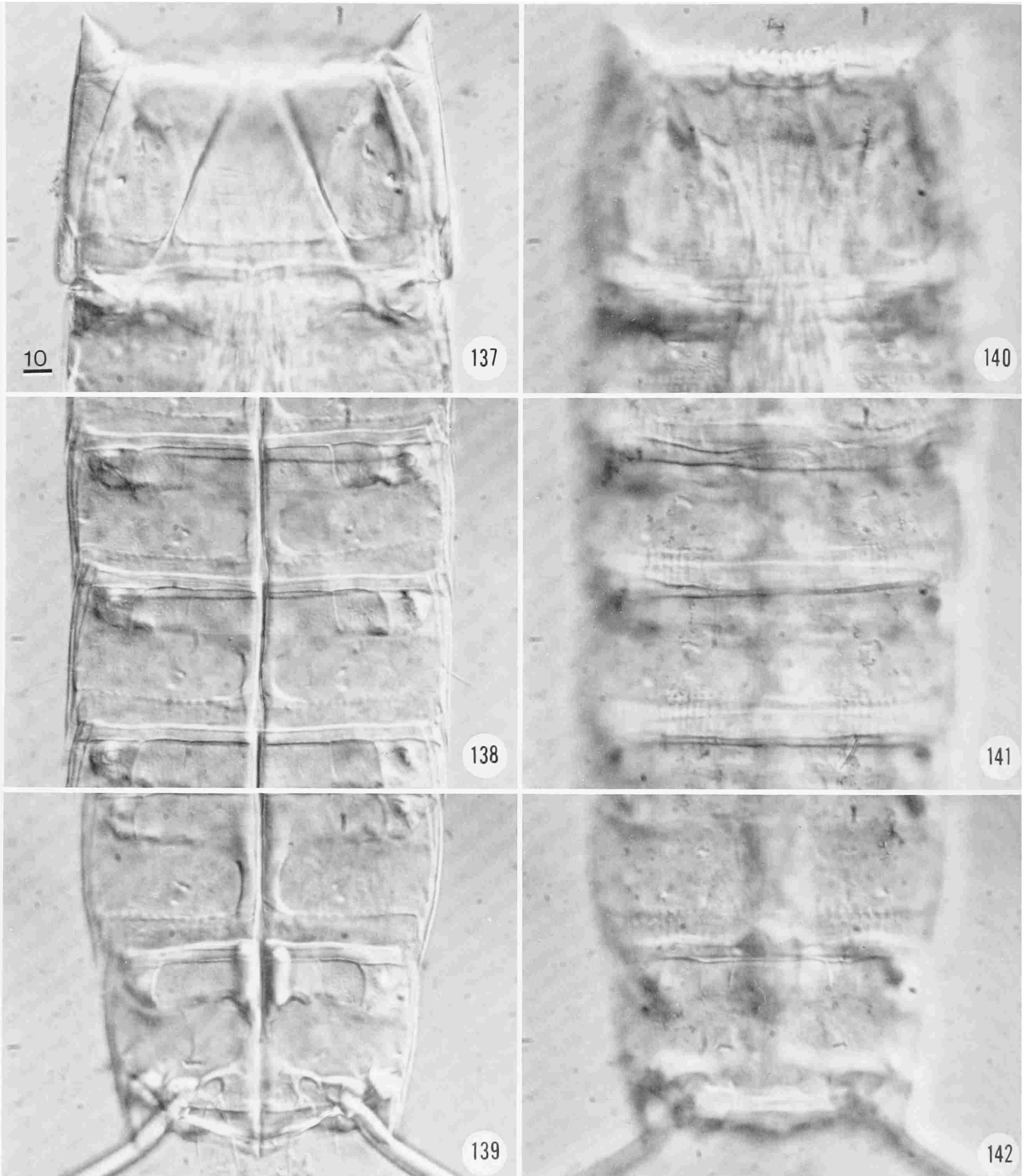
Pycnophyes ecphantor, new species

FIGURES 127–142

DIAGNOSIS.—Trunk segments 3–12 nearly uniform in width, tapering only slightly; lateral terminal spines very long, 188–192 μm, 33.0–33.5 percent of trunk length, slightly recurved; lateral posterior margin of twelfth sternal plates deeply incised to accommodate lateral terminal spine; segment 13 short, generally covered by penultimate segment; midsternal plate of first trunk segment wide at base, very narrow at apex; lateral



FIGURES 127-136.—*Pycnophyes ecphantor,* new species: 127, neck and trunk segments, ventral view, holotypic male (USNM 69993); 128, same, dorsal view; 129, same, segments 2-4, lateral half, ventral view; 130, same, dorsal view; 131, same, segments 12, 13, lateral half, ventral view; 132, same, dorsal view; 133, segments 2-4, lateral half, ventral view, allotypic female (USNM 69994); 134, same, dorsal view; 135, same, segments 12, 13, lateral half, ventral view; 136, same, dorsal view.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dorsal and ventral placids incised, mesial placids entire; trunk setae prominent.

DESCRIPTION.—Adults (Figures 127–142), trunk length 565–582 μm; trunk segments nearly uniform in length, tapering only slightly; MSW-6 124–128 μm, 22.0–22.1 percent of trunk length; SW 104–112 μm, 18.5–19.2 percent of trunk length. Second segment consisting of 4 dorsal and 4 ventral placids, lateral ventral placids incised, mesial ventral placids entire (Figures 129, 133).

Trunk segments (Figures 127, 128) without middorsal spinose processes. Prominent setae, 20–22 μm long, situated middorsally on segments 4, 6–10, dorsolaterally on segments 4–11, laterally on segments 4, 6–12, and ventrolaterally on segments 4–11. Sensory spots present near posteromesial margin of episternal plates on segment 3 of male (Figure 129), 2 additional spots more anteriorly situated in female (Figure 133), sensory spots mesial to ventrolateral setae on segment 4, lateral to ventrolateral setae on segments 5–12, subdorsally on segments 3, 7–12, mesial to dorsolateral setae on segments 5–12 with an additional sensory spot lateral to dorsolateral setae on segment 11 and still another spot situated more mesially (4 sensory spots on each lateral tergal surface). Pachycycli well developed on all trunk segments; midventral thickenings near anteromesial margins of sternal plates 11, 12, best developed on segment 12 (Figures 131, 135). Muscle scars on episternal plates of segment 3; cuticular scars on sternal plates 4–12, small, oval to crescentic with long axis oriented toward anterolateral margin of each sternal plate, similar scars situated dorsolaterally on segments 4–12; series of large muscle scars dorsolateral on segment 3 (Figures 130, 134).

First trunk segment (segment 3) with anterolateral margins extending to form pointed projection, anterior tergal margin denticulate (Figures 129, 134); episternal plates even, no thin cuticular areas; midsternal plate nearly triangular, about 78 μm long, 78 μm basal width, tapering evenly to 14 μm at apex (Figure 127).

Segment 4 of males lacking adhesive tubes, similar to female (Figures 129, 133); ventral pachycycli broad; segments 5–11 similar, differences already noted in distribution of setae and sensory spots.

Sternal plates of segment 12 extending beyond terminal margin of segment 13, deeply incised laterally to accommodate movement of lateral terminal spines, otherwise with shallowly incised truncate margins (Figures 131, 135); tergal plate similar, extending more posterior at midline, also parallel with last segment (Figures 132, 136); segment 13 withdrawn beneath penultimate segment, 2 pairs of penile spines at anterolateral margins of terminal sternal plates in males, single gonopore in females. Lateral terminal spines long, robust, slightly recurved, 188 μm long in male specimen, 33.5 percent of trunk length, 192 μm long in female, 33.0 percent of trunk length.

Male differs from female by the presence of 2 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 131) and 2 less sensory spots on the episternal plates of segment 3.

Morphological data for adult specimens are shown in Table 10.

HOLOTYPE.—Adult male, TL 565 μm (Figures 127–132, 137–142), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69993.

ALLOTYPE.—Adult female, TL 582 μm (Figures 133–136), other data as for holotype, USNM 69994.

REMARKS.—*Pycnophyes ecphantor* is unique in having incised lateral ventral placids, while the mesial ventral placids remain even margined. This character is often indicated, as in the type material, by the outline of these structures when in a retracted position; the head need not be everted in order to see this character. Another

FIGURES 137–142.—*Pycnophyes ecphantor*, new species, holotypic male (USNM 69993): 137, segments 3, 4, ventral view; 138, segments 7, 8, ventral view; 139, segments 11–13, ventral view; 140, segments 3, 4, dorsal view; 141, segments 7, 8, dorsal view; 142, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 137.)

TABLE 10.—Measurements (μm) and indices (%) for *Pycnophyes ecphantor* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂♀	2	561–582	571.5	14.9	10.5	2.6
SW	♂♀	2	104–112	108.0	5.7	4.0	5.2
SW/TL	♂♀	2	18.5–19.2	18.9	0.5	0.4	2.6
MSW-6	♂♀	2	124–128	126.0	2.83	2.0	2.24
MSW/TL	♂♀	2	22.0–22.1	22.0	<0.1	<0.1	0.3
LTS	♂♀	2	188–192	190.0	2.8	2.0	1.5
LTS/TL	♂♀	2	33.0–33.5	33.3	0.4	0.3	1.1

distinct feature is the almost triangular shape of the midsternal plate of the first trunk segment. *Pycnophyes chiliensis* approaches this state, but its plate has slightly recurved lateral margins. This species also resembles *P. ecphantor* in that the latter's penile spines are very long, and, like *P. ecphantor*, extend well beyond the terminal segment. *Pycnophyes chiliensis* has distinctly spinose middorsal tergal processes, the largest of any species in the genus, and in this way alone, differs significantly from *P. ecphantor*.

The distribution of setae and sensory spots on the new species appears to be unique. Unfortunately, some authors have not included these characters in their descriptions or illustrations.

ETYMOLOGY.—This species name is from the Greek *ekphantor* (revealer).

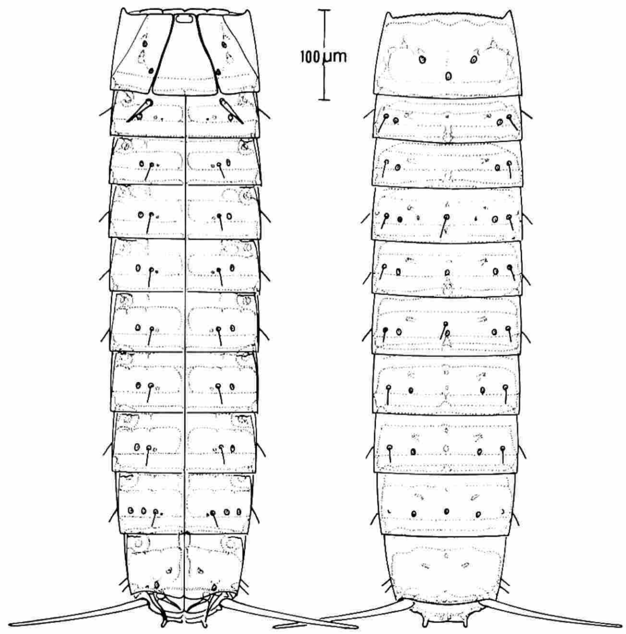
Pycnophyes emarginatus, new species

FIGURES 143–158

DIAGNOSIS.—Trunk segments 3–12 nearly uniform in width; lateral terminal spines long, robust, almost straight, 124–180 μm, 22.7–29.9 percent of trunk length; posterior margin of terminal segment slightly incised, terminal tergal plate with distinct lateral protuberances; anterior margin of tergal plate of first trunk segment denticulate, anterior margin of midsternal plate of same segment with area of thin cuticle.

DESCRIPTION.—Adults (Figures 143–158), trunk length 530–676 μm, trunk segments nearly uniform in width; MSW-7 144–160 μm, 22.5–27.5 percent of trunk length; SW 120–140 μm, 18.9–23.4 percent of trunk length. Second segment with 4 dorsal and 4 ventral placids with even margins (Figures 145, 149).

Trunk segments (Figures 143, 144) without middorsal spinose processes but with slight subcuticular spinose structure on tergal plates 4–8 (Figure 144). Prominent setae, 20–22 μm long, situated middorsally on segments 6 and 8 only, dorsolaterally on segments 4–10, laterally on segments 4, 6–8, 10, and 11 and 2 laterally on segment 12 of male only (Figures 147, 148); females have none on segment 12 (Figures 151, 152), lateroventrally on segments 5–11. Sensory spots (Figures 143, 144) middorsally on segments 3, 7, 8, and 11, possibly on others, dorsolaterally on segments 3 and mesial to dorsolateral setae on segments 4–10, ventrolateral on segments 4–10 with 2 on segment 11 and 1 near posterior margin of segment 12; 2 sensory spots, 1 centered on each sternal plate and 1 near posteromesial margin of segment 3. Posterior tergal margin with subcuticular interruptions middorsally, not appearing as either distinct spinose or rounded processes. Pachycycli broad, distinct, on all trunk segments; midventral thickenings slightly developed, apparent on segments 11–12 only; muscle scars of tergal plate of segment 3 broadly rounded (Figures 144, 146–150), those of sternal plate of same segment very small, situated anterior and posterior to central sensory spot; cuticular scars dorsoventral on trunk segments 4–12, mesial to ventrolateral setae and anteromesial to dorsolateral sensory spots; small, round cuticular scars on sternal plates 4–12, mesial to setae.



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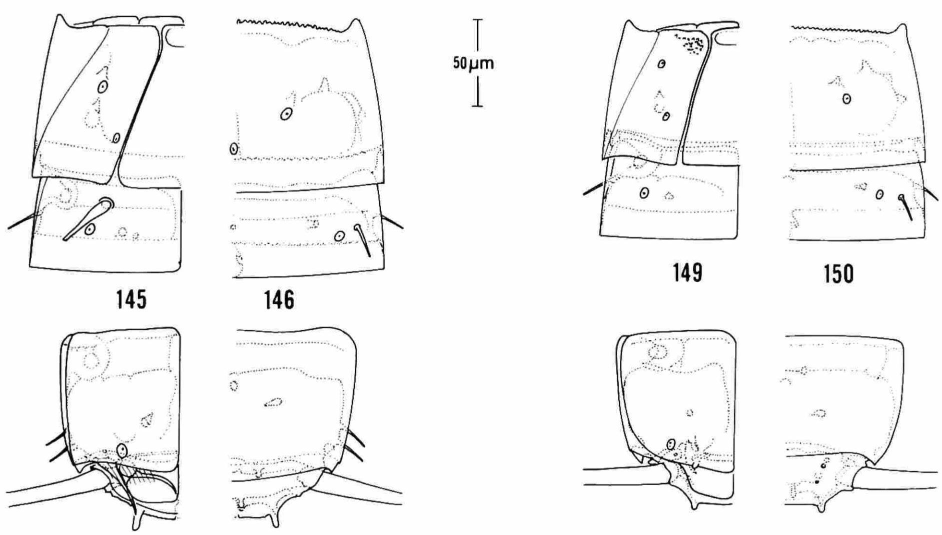

FIGURES 143–152.—*Pycnophyes emarginatus,* new species: 143, neck and trunk segments, ventral view, holotypic male (USNM 69995); 144, same dorsal view; 145, same, segments 2–4, lateral half, ventral view; 146, same, dorsal view; 147, same, segments 12, 13, lateral half, ventral view; 148, same, dorsal view; 149, segments 2–4, lateral half, ventral view, allotypic female (USNM 69996); 150, same dorsal view; 151, same, segments 12, 13, lateral half, ventral view; 152, same, dorsal view.

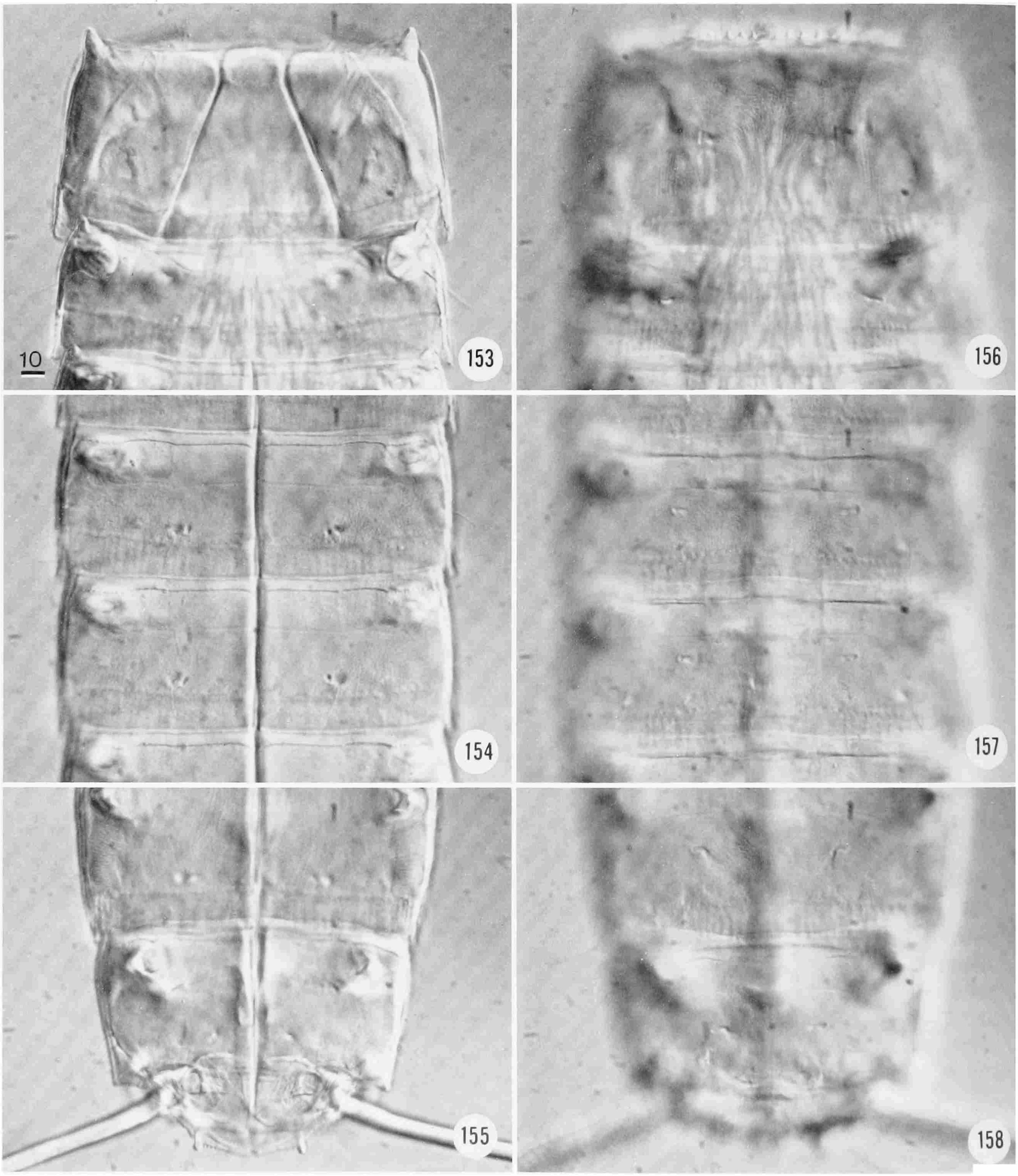
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TABLE 11.—Measurements (μm) and indices (%) for *Pycnophyes emarginatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	6	582-676	643.0	43.9	17.9	6.8
	♀	4	530-603	574.3	31.1	15.6	5.4
	♂♀	10	530-676	615.5	51.5	16.3	8.4
SW	♂	6	120-140	129.3	6.5	2.7	5.1
	♀	4	124-132	128.0	4.6	2.3	3.6
	♂♀	10	120-140	128.8	5.6	1.8	4.3
SW/TL	♂	6	18.9-21.5	20.1	1.0	0.4	4.8
	♀	4	21.3-23.4	22.3	0.9	0.5	4.1
	♂♀	10	18.9-23.4	21.0	1.5	0.5	6.9
MSW-7	♂	6	144-160	153.3	5.5	2.2	3.6
	♀	4	144-160	153.0	8.3	4.1	5.4
	♂♀	10	144-160	153.2	6.3	2.0	4.1
MSW/TL	♂	6	22.5-25.6	23.9	1.1	0.5	4.7
	♀	4	25.4-27.5	26.7	0.9	0.5	3.5
	♂♀	10	22.5-27.5	25.0	1.7	0.6	6.9
LTS	♂	6	140-172	158.7	12.3	5.0	7.8
	♀	4	124-180	146.0	24.8	12.4	17.0
	♂♀	10	124-180	153.6	18.2	5.8	11.9
LTS/TL	♂	6	23.7-25.6	24.7	0.8	0.3	3.1
	♀	4	22.7-29.9	25.4	3.2	1.6	12.8
	♂♀	10	22.7-29.9	25.0	2.0	0.6	8.0

First trunk segment (segment 3) with only slight extensions of anterolateral margins of tergal plate; anterior margin of tergal plate denticulate (Figures 146, 150, 156); clear area of nonperforated cuticle forms distinct, uneven anterior marginal band (limited by dotted line, Figures 144, 146, 150, 156); episternal plates without areas of thin cuticle although some sculpturing may occur near anteromesial border in females (Figure 149); midsternal plate trapezoidal, about 90 μm long, 76 μm basal width tapering evenly to 28 μm about one-fifth distance from anterior margin (Figure 153) and then becoming even or slightly enlarged; with area of thin cuticle near anterior margin (Figures 145, 149, 153).

Segment 4 of male with prominent adhesive tubes, about 35 μm long (Figure 145); segments 5–11 similar, differences already noted in distribution of setae, sensory spots, and cuticular scars.

Segment 12 with margin of ventral plates extending slightly posterior at the ventral midline; margin of each ventral plate of terminal segment evenly rounded, 2 pairs of penile spines at anterolateral margins of sternal plates, simple gonopores present in female; margin of terminal tergal plate with median notch and posteriorly directed submedial protuberances (Figures 143, 155), protuberances appear longer in males (Figure 147) than in females (Figure 151). Lateral terminal spines long, robust, almost straight, 140–172 μm, 23.7-25.6 percent of trunk length in males, 124–180 μm, 22.7-29.9 percent of trunk length in females.

Males differ from females by presence of ad-

FIGURES 153–158.—*Pycnophyes emarginatus*, new species, holotypic male (USNM 69995): 153, segments 3, 4, ventral view; 154, segments 7, 8, ventral view; 155, segments 11–13, ventral view; 156, segments 3, 4, dorsal view; 157, segments 7, 8, dorsal view; 158, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 153.)

hesive tubes on segment 4 (Figure 145), 2 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 147), and, possibly, the lack of 2 lateral setae on segment 12 (Figures 151, 152).

Morphometric data for adult specimens are shown in Table 11.

HOLOTYPE.—Adult male, TL 676 μm (Figures 143–148, 153–158), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 69995.

ALLOTYPE.—Adult female, TL 582 μm (Figures 149–152), other data as for holotype, USNM 69996.

PARATYPES.—Two males and 1 female, TL 530–676 μm, other data as for holotype, (USNM 69997); 3 males and 1 female, TL 593–676 μm, Twin Cays, sta RH 443, other data as for holotype (USNM 69998); 1 female, TL 603 μm, Twin Cays, sta RH 442, other data as for holotype (USNM 69999).

REMARKS.—*Pycnophyes emarginatus* and *P. rugosus* are the only two members of this genus with an area of thin cuticle present at the anterior margin of the midventral plate of the first trunk segment. Other species will have these areas limited to the episternal plates or in other combinations. The uniformly clear area along the anterior margin of the dorsal plate of the first trunk segment may be unique; it has not been noted in other species, but many species descriptions are inadequate. Furthermore, no other species have muscle scars as round as those appearing on this latter plate.

Protuberances commonly occur on the border of the terminal tergal plate, but no other species have the slight medial notch which gives this species its name.

ETYMOLOGY.—This species name is from the Latin *emarginatus* (notched at apex), referring to the medial notch on the terminal tergal plate.

Pycnophyes iniorhaptus, new species

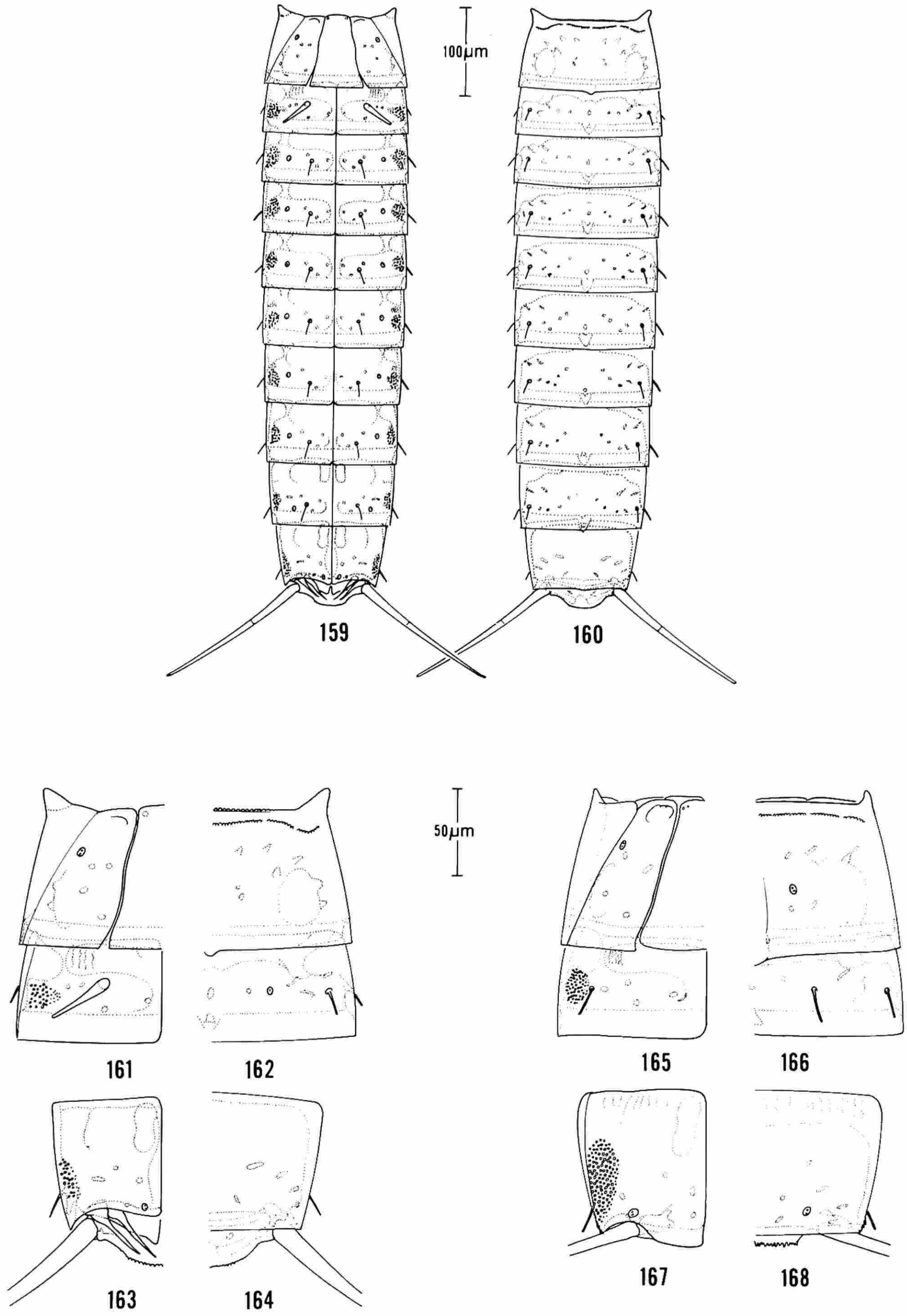
FIGURES 159–174

DIAGNOSIS.—Trunk segments 3–12 tapering slightly beginning with segment 6; lateral terminal spines long, slightly recurved, with transverse mark about one-third distance from base; line of punctate sculpturing parallel to a slightly denticulate dorsoanterior margin of first trunk segment; areas of distinctive punctate cuticle lateroventral on segments 4–12.

DESCRIPTION.—Adults (Figures 159–174), trunk length 572–686 μm, trunk segments tapering slightly in posterior progression beginning with segment 6; MSW-6 144–156 μm, 21.0–24.8 percent of trunk length; SW 120–144 μm, 17.8–22.7 percent of trunk length. Second segment with 4 dorsal and 4 ventral, even-margined placids (Figures 165, 166).

Trunk segments (Figures 159, 160) with subcuticular interruptions middorsally, spinose in appearance, forming slight external processes at the posterior margin of segment 3 (Figures 162, 166), less evident and probably only subcuticular on segments 4–11. Prominent setae, 20–23 μm long, situated dorsolaterally on segments 4–11, laterally on segments 4–12, with subdorsal setae in females, absent in males, and ventrolaterally on segments 5–11 in males, 4–11 in females; areas of punctate cuticular sculpturing ventrolateral on segments 4–12 (Figure 169); sensory spots (Figures 159, 160) dorsolateral on segments 3 (female) or 4–9, 11 along with several other cuticular perforation sites of unknown function; other sensory spots probable but not clearly visible, ventrolateral on episternal plate of segment 3, apparently missing from segment 4, lateral to setae on segments 5–11 and near the posteromesial margin on sternal plates of segment 12; pachycycli well developed with broad ventral areas (Figure 159) on segments 4–12; prominent midventral thickenings on segments 11, 12 (Figures 159, 171). Large muscle scars dorsolateral on tergal plate of first trunk segment, similar muscle scars on episternal plates; paired cuticular scars dorsolateral with long axis oriented toward anterolateral tergal margin on segments 4–12, ventrolateral cuticular scars, circular to oval, near midline but not always discernible from several other cuticular scars or perforations.

First trunk segment (segment 3) with prominent, hornlike extensions of the anterolateral margins of the tergal plate, (Figures 159–161, 165,



FIGURES 159-168.—*Pycnophyes iniorhaptus*, new species: 159, neck and trunk segments, ventral view, holotypic male (USNM 70000); 160, same, dorsal view; 161, same, segments 2-4, lateral half, ventral view; 162, same, dorsal view; 163, same, segments 12, 13, lateral half, ventral view; 164, same, dorsal view; 165, segments 2-4, lateral half, ventral view, allotypic female (USNM 70001); 166, same, dorsal view; 167, same, segments 12, 13, lateral half, ventral view; 168, same, dorsal view.

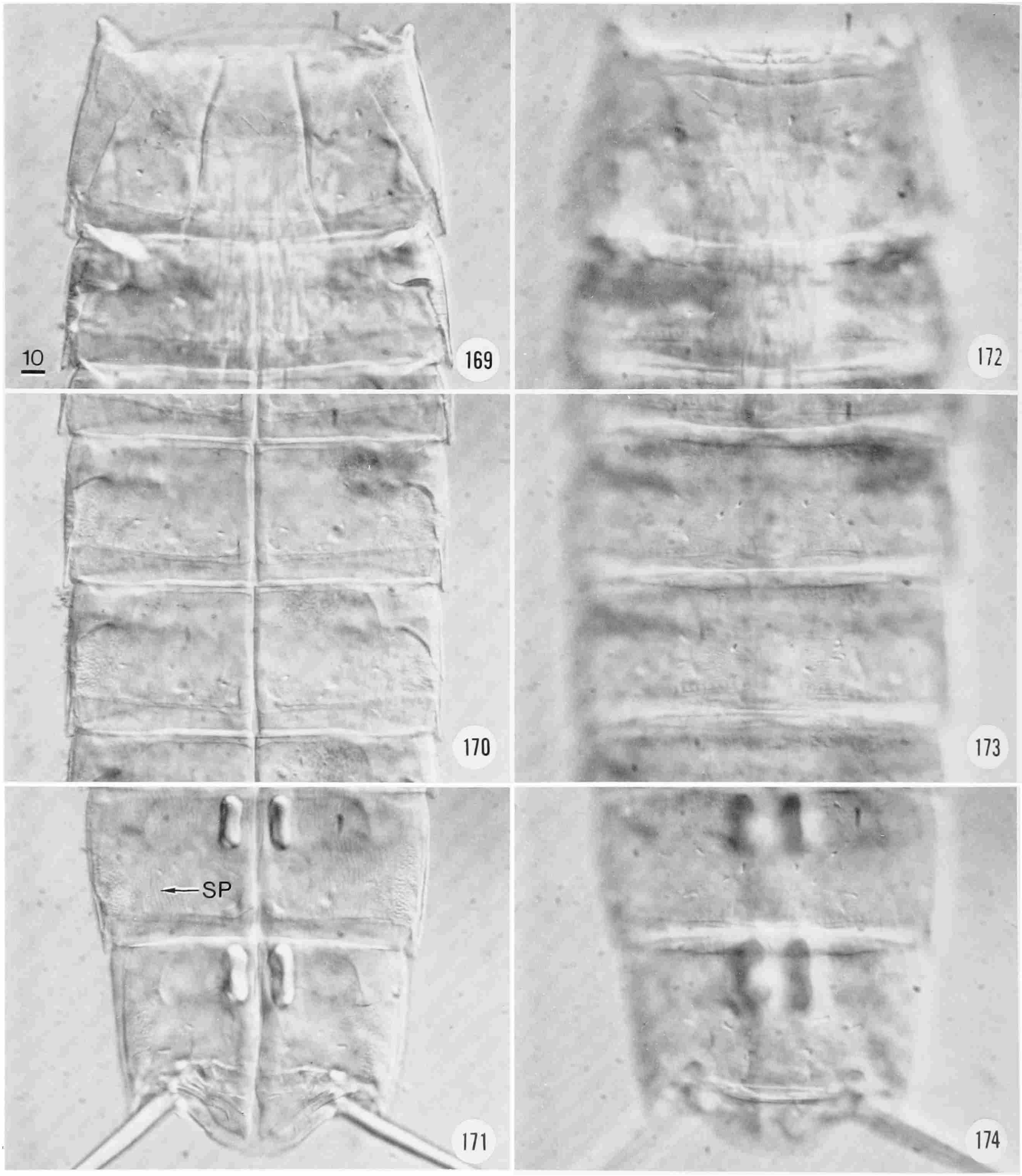

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TABLE 12.—Measurements (μm) and indices (%) for *Pycnophyes iniorhaptus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	7	572–686	631.4	39.1	14.8	6.2
	♀	2	634–676	655.0	29.7	21.0	4.5
	♂♀	9	572–686	636.7	36.9	12.3	5.8
SW	♂	7	120–132	126.3	4.5	1.7	3.6
	♀	2	140–144	142.0	2.8	2.0	2.0
	♂♀	9	120–144	129.8	8.0	2.7	6.2
SW/TL	♂	7	17.8–21.6	20.1	1.4	0.5	7.0
	♀	2	20.7–22.7	21.7	1.4	1.0	6.5
	♂♀	9	17.8–22.7	20.4	1.5	0.5	7.4
MSW-6	♂	7	144–152	148.0	4.0	1.5	2.7
	♀	2	152–156	154.0	2.8	2.0	1.8
	♂♀	9	144–156	149.3	4.5	1.5	3.0
MSW/TL	♂	7	21.0–24.8	23.5	1.5	0.6	6.2
	♀	2	22.4–24.6	23.5	1.6	1.1	6.6
	♂♀	9	21.0–24.8	23.5	1.4	0.5	5.8
LTS	♂	7	152–180	170.3	9.2	3.5	5.4
	♀	2	108–112	110.0	2.8	2.0	2.6
	♂♀	9	108–180	156.9	27.8	9.3	17.7
LTS/TL	♂	7	24.4–29.3	27.1	2.3	0.9	8.4
	♀	2	16.0–17.7	16.9	1.2	0.9	7.1
	♂♀	9	16.0–29.3	24.8	4.9	1.7	19.9

166); anterior margin of tergal plate of segment even, line of punctate sculpturing parallel to margin; episternal plates with small area of thin cuticle at anterior margin, no such area on midsternal plate; midsternal plate trapezoidal, about 83 μm long, 60 μm basal width with uneven margin tapering to 30 μm at apex (Figures 161, 165).

Sternal plate 4 of male with prominent adhesive tubes; about 40 μm long (Figure 161), no setae near lateral margin but present in female (Figure 165); areas of punctate cuticular sculpturing already noted previously. Segments 5–11 similar; segment 12 with margin of sternal plates extending slightly posterior at the ventral midline; tergal margin even. Posterior margin of each sternal plate of terminal segment angular (Figure 163) at least in males, structure not clearly evident in females. Tergal margin rounded with slightly fringed edge. Two pairs of penile spines at anterolateral margins of 12th sternal plates; single gonopore in female. Lateral terminal spines long, 152–180 μm, 24.4–29.3 percent of trunk length in males, slightly shorter, 108–112 μm, 16.0–17.7 percent of trunk length in females, slightly recurved with transverse mark about one-third distance from base (Figures 159, 160).

Males differ from females by presence of adhesive tubes and lack of setae on segment 4 (Figure 161), 2 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 163), no subdorsal setae, shorter lateral terminal

FIGURES 169–174.—*Pycnophyes iniorhaptus*, new species: 169, segments 2–4, ventral view; 170, segments 7, 8, ventral view; 171, segments 11–13, ventral view; 172, segments 2–4, dorsal view; 173, segments 7, 8, dorsal view; 174, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 169; SP = spermatozoa.)

spines, slight differences in number and position of cuticular markings, scars, etc., and a slightly denticulate anterodorsal margin on the first trunk segment.

Morphometric data for adult specimens are shown in Table 12.

HOLOTYPE.—Adult male, TL 676 μm (Figures 159–164, 169–174), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70000.

ALLOTYPE.—Adult female TL 676 μm (Figures 165–168), other data as for holotype, USNM 70001.

PARATYPES.—Six males and 1 female, TL 572–686 μm, other data as for holotype, USNM 70002.

REMARKS.—The presence of the areas of distinctive punctate cuticle located laterally on each sternal plate of segments 4–12 of *Pycnophyes iniorhaptus* is unique to this genus or any other kinorhynch taxon. A second important character is the line of cuticular punctations near the anterior tergal margin of the first trunk segment. Most sculpturing of this margin involves a toothed or toothlike pattern restricted to the anteriormost edge without a second pattern more posterior as in *Pycnophyes emarginatus* or *P. sanjuanensis*. Others, such as *P. corrugatus*, have various geometrically arranged cuticular ridges near the lateral edges of the sternal plates. *Pycnophyes egyptensis* has a band of punctate cuticle on either side of the dorsal midline of the first trunk segment.

Pycnophyes egyptensis is similar to *P. iniorhaptus* in that the former species has a similar shaped midsternal plate but with a thin area of cuticle near its anterior margins. *Pycnophyes egyptensis* also has a similar trunk shape, long lateroterminal spines, and distinctive midventral thickenings on segments 11 and 12 only; however, its lateral terminal spines do not have the transverse mark, nor are they slightly recurved; it has middorsal setae on most trunk segments and lacks the distinctive areas of punctate cuticle on the sternal plates.

ETYMOLOGY.—This species name is from the Greek *inion* (nape of neck) plus *rhaptos* (stitched), referring to the transverse line of cuticular punctations near the anterior margin of the first trunk segment.

Pycnophyes longicornis, new species

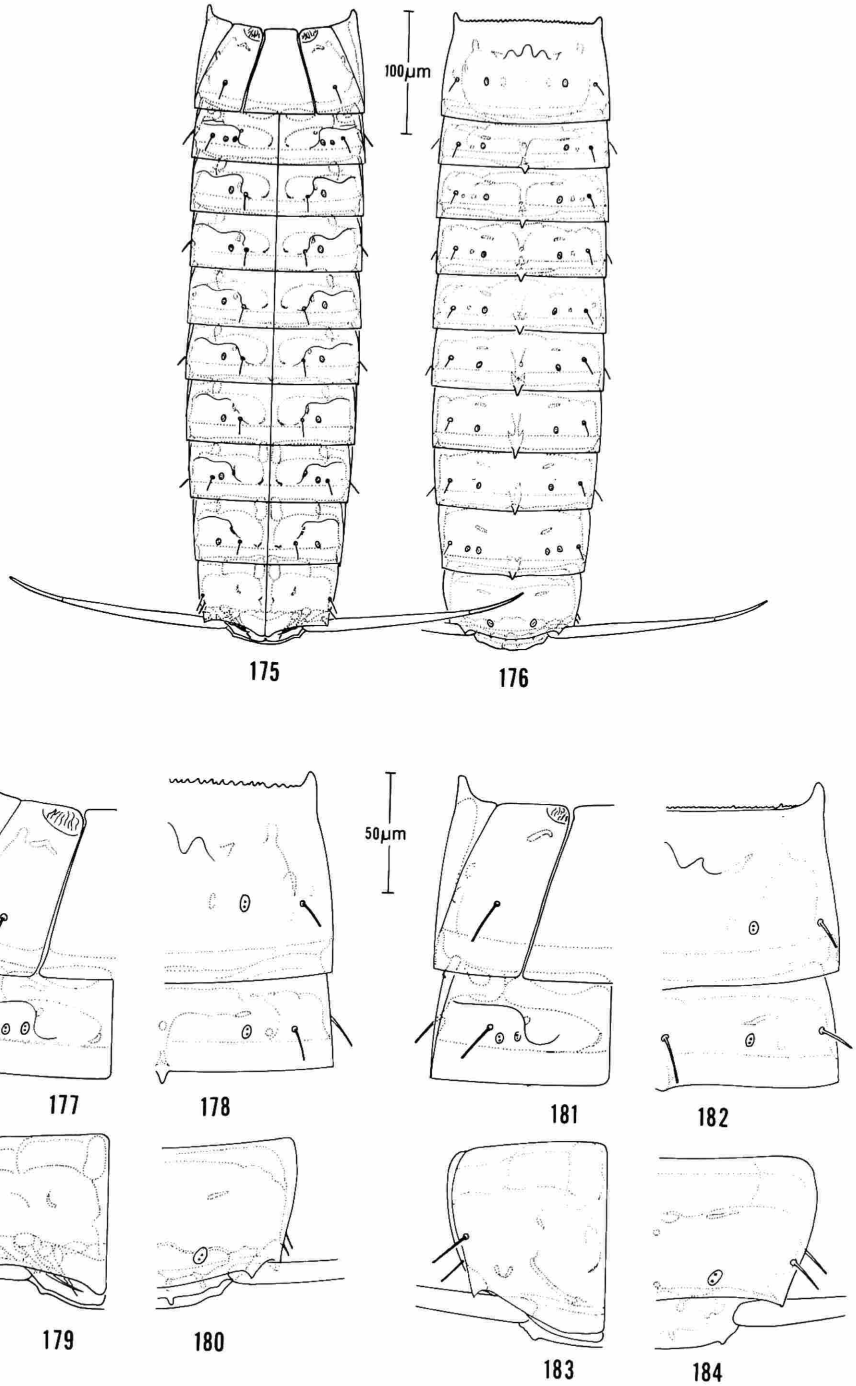
FIGURES 175–190

DIAGNOSIS.—Trunk tapering slightly beginning with segment 7; lateral terminal spines long, recurved at tip which is defined by transverse mark about three-fourths distance from base, lateral terminal spines usually perpendicular to trunk upon fixation; middorsal spinous processes at the posterior tergal margins; anterior margin of tergal plate of first trunk segment denticulate; lateral setae on every other segment beginning with segment 4; adhesive tubes absent in males.

DESCRIPTION.—Adults (Figures 175–190), trunk length 478–572 μm, trunk segments tapering slightly in posterior progression beginning with segment 7; MSW-7 120–140 μm, 23.7–28.5 percent of trunk length; SW 108–125 μm, 20.8–25.4 percent of trunk length. Second segment with 4 dorsal and 4 ventral, even placids.

Trunk segments (Figures 175, 176) with some middorsal setae present on females, absent on males, dorsolateral setae, 20 μm long, on segments 3–11, lateral setae at margin of segments 4, 6, 8, 10, with 2 on segment 12, ventrolateral setae on segments 3, 4, 10 with mesial setae on segments 5–9, 11; sensory spots dorsolateral on segments 3–10, 12, double, on 11, double ventrolateral on segment 4 only, ventrolateral on segments 5–11. Posterior margins of tergal plates 4–11 with prominent middorsal spinose processes. Pachycycli well developed; midventral thickenings on segments 10–12 (Figures 175, 187). Muscle scars prominent dorsolaterally and ventrolaterally on first trunk segment (Figures 175, 176, 185, 188), inverted V-shaped scar especially noticeable near anteromesial area of thin cuticle on episternal plate of first trunk segment in males (Figure 177); elongate cuticular scars on tergal plates 4–12 transversely oriented in anterior segments, becoming more angular posteriorly, those on ventral plates oval to crescentic, situated mesial to sensory spots (Figures 175, 176).

First trunk segment (segment 3) with prominent hornlike extensions of the anterolateral margins of tergal plate (Figures, 175, 176); anterior margin of segment denticulate (Figures 178, 182), undulant median ridge of cuticle about one-third



FIGURES 175–184.—*Pycnophyes longicornis*, new species: 175, trunk segments, ventral view, holotypic male (USNM 70003); 176, same, dorsal view; 177, same, segments 3, 4, lateral half, ventral view; 178, same, dorsal view; 179, same, segments 12, 13, lateral half, ventral view; 180, same, dorsal view; 181, segments 3, 4, lateral half, ventral view, allotypic female (USNM 70004); 182, same, dorsal view; 183, same, segments 12, 13, lateral half, ventral view; 184, same, dorsal view.

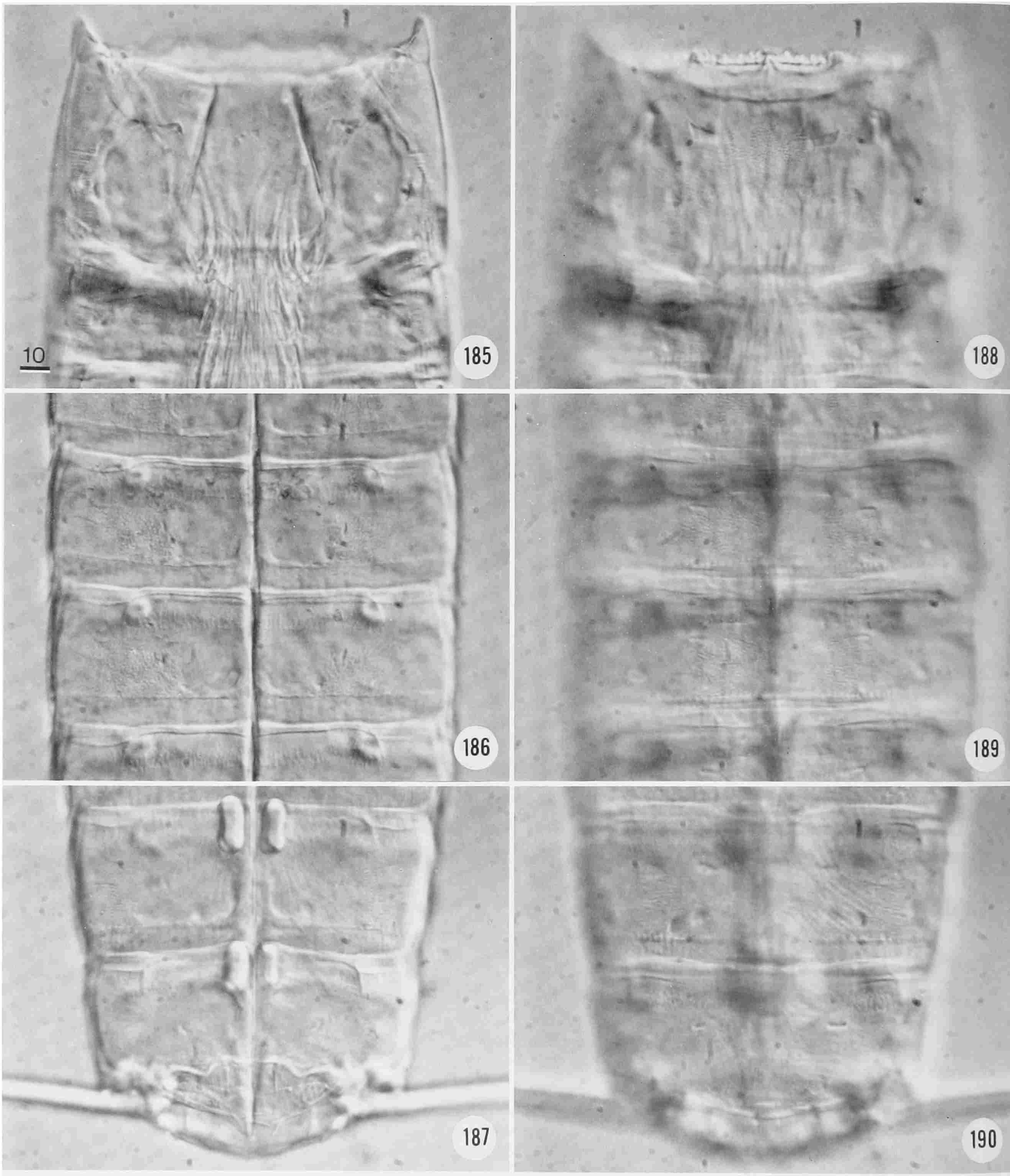

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TABLE 13.—Measurements (μm) and indices (%) for *Pycnophyes longicornis* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	19	478–551	511.1	20.8	4.8	4.07
	♀	15	489–572	522.7	26.6	6.9	5.1
	♂♀	34	478–572	516.2	23.9	4.1	4.6
SW	♂	19	108–124	116.6	4.1	0.9	3.5
	♀	15	120–125	122.2	2.1	0.6	1.8
	♂♀	34	108–125	119.1	4.3	0.7	3.6
SW/TL	♂	19	20.8–24.3	22.8	1.2	0.3	5.1
	♀	15	21.6–25.4	23.4	1.3	0.3	5.4
	♂♀	34	20.8–25.4	23.1	1.2	0.2	5.3
MSW-7	♂	19	128–136	132.5	2.3	0.5	1.7
	♀	15	120–140	133.2	4.4	1.1	3.3
	♂♀	34	120–140	132.8	3.3	0.6	2.5
MSW/TL	♂	19	24.2–28.5	26.0	1.25	0.3	4.8
	♀	15	23.7–27.1	25.6	1.4	0.4	5.3
	♂♀	34	23.7–28.5	25.8	1.3	0.2	5.0
LTS	♂	18	148–188	171.3	10.7	2.5	6.2
	♀	15	140–176	160.3	8.5	2.2	5.3
	♂♀	33	140–188	166.3	11.1	1.9	6.7
LTS/TL	♂	18	29.4–37.7	33.6	2.2	0.5	6.6
	♀	15	25.9–34.4	30.8	2.3	0.6	7.3
	♂♀	33	25.9–37.7	32.3	2.6	0.5	8.1

distance posterior (Figure 176); episternal plates with small area of thin, wrinkled cuticle at anteromesial margin, no such area on midsternal plate; midventral plate trapezoidal, about 70 μm long, 62 μm basal width with anterior margin slightly expanded, 30 μm wide at apex (Figure 175).

Segment 4 of male similar to that of female (Figures 177, 178, 181, 182), adhesive tubes absent in both sexes, with middorsal seta in female, absent in male, each sternal plate with ventrolateral setae and 2 mesial sensory spots; tergal plate with lateral setae and subdorsal sensory spots.

Segments 5–9, 11 similar except lateral setae

FIGURES 185–190.—*Pycnophyes longicornis*, new species: 185, segments 3, 4, ventral view; 186, segments 7, 8, ventral view; 187, segments 11–13, ventral view; 188, segments 3, 4, dorsal view; 189, segments 7, 8, dorsal view; 190, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 185.)

on segments 6 and 8. Setae on sternal plates 5–9, 11 ventromesial (mesial to sensory spot, Figure 175); seta on sternal plates 10 ventrolateral (lateral to sensory spot, Figure 175). Segment 11 with 2 dorsolateral sensory spots on each side. Segment 12 without lateroventral sensory spots or setae; 2 lateral setae and prominent dorsolateral sensory spots present; posterior margin of sternal plates subacute at midline. Terminal segment rounded with slightly angular lateroterminal margins, 2 pairs of penile spines at anterolateral margins of sternal plates, simple gonopores in females.

Lateral terminal spines long, 148–188 μm, 29.4–37.7 percent of trunk length in males, 140–176 μm in females; usually perpendicular to trunk upon fixation and with a slight bend near transverse mark about 3/4 distance from base.

Males differ from females by the presence of 2 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 179); lack of middorsal setae and slightly smaller and different shaped penultimate segment.

Morphometric data for adult specimens are shown in Table 13.

HOLOTYPE.—Adult male, TL 530 μm (Figures 175–180, 185–190), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70003.

ALLOTYPE.—Adult female, TL 572 μm (Figures 181–184), other data as for holotype, USNM 70004.

PARATYPES.—Nine females and 9 males, TL 489–556 μm, other data as for holotype, USNM 70005; 4 females and 2 males, TL 489–551 μm, Twin Cays, sta RH 443, Belize, other data as for holotype, USNM 70006; 7 males and 1 female, TL 478–530 μm, Twin Cays, sta RH 444, Belize, other data as for holotype, USNM 70007.

REMARKS.—Of the five new species of *Pycnophyes* described in this paper, *P. longicornis* has the broadest relative trunk length; this is especially noticeable when the first trunk segments are compared. This new species is similar to *P. zelinkaei* and *P. odhneri* in number and position of lateral setae but differs significantly in the number and arrangement of other setae. Like *P. zelinkaei*, its lateral terminal spines may tend to fix perpendicular to the trunk. This assumes that the original illustration of *P. zelinkaei* was typical of this species as well as accurate. In addition, both species have a dentate anterior margin on the tergal plate of the first trunk segment. In *P. zelinkaei* this border appeared much different to Zelinka (1928, fig. 64) than to Southern (1914, fig. 33E). The former author's illustration would suggest a row of longitudinal bars forming the dentate appearance. In *P. longicornis* this area is clearly denticulate, not the same as in *P. zelinkaei*.

The absence of adhesive tubes on the sternal plates of segment 4 in *P. longicornis* males is similar to *P. ecphantor* and *P. egyptensis*. *Pycnophyes longicornis* has a trunk shape similar to the latter species but has very few other similarities.

ETYMOLOGY.—This species name is from the Latin *longus* (long) plus *cornus* (horn), referring to the lateral terminal spines which, as typically extended, suggest the appearance of the "longhorn" cattle of the southwestern United States.

Discussion of *Pycnophyes*

Until 1896, all kinorhynchs were assigned to a single family, Echinoderidae Bütschli, 1876, with its monotypic genus, *Echinoderes* Claparède, 1863. Between 1888 and 1908, Zelinka published a series of papers that were "previews" of his monograph on kinorhynchs (Zelinka, 1928). Zelinka's first comments on kinorhynch classification were directed at a previous attempt (Reinhard, 1885) to divide the Kinorhyncha into three groups of undesignated rank—there is no basis for assuming that these were generic names as stated in a recent paper by Sheremetevskij (1974). In short, Zelinka (1894) stated that "a division of the *Echinoderes* into Bicerca, Monocerca and Acerca is untenable; the essential reason for dividing the species must be based on the closing apparatus of the anterior end." Thus, he laid to rest Reinhard's artificial divisions that were based on the spine character of the terminal segment. In 1896, Zelinka (1896:198 not 1894 as cited by Sheremetevskij, 1974) erected the family Pycnophyidae but did not establish the genus *Pycnophyes* until 11 years later (Zelinka, 1907). The first species assigned to this genus was *Pycnophyes communis* Zelinka, 1908. Although this latter species was not described by Zelinka until 1928, these rules for "indication" were satisfied by the earlier paper.

In 1928, Zelinka described 10 new species of *Pycnophyes: P. quadridentatus, P. flagellatus, P. echinoderoides, P. rugosus, P. robustus, P. calmani, P. flaveolatus, P. communis, P. carinatus*, and *P. kielensis*. *Pycnophyes calmani* was, in fact, described earlier by Southern, 1914. In addition, Zelinka reassigned *Echinoderes dentatus* Reinhard, 1881, and *E. ponticus* Reinhard, 1881, to the genus *Pycnophyes*. With the addition of *P. zelinkaei* Southern, 1914, the number of species assigned to *Pycnophyes* totaled 12. At this same time, Zelinka (1928) described larval species, life history stages known to be *Pycnophyes* but assigned to new larval genera.

These included *Hyalophyes longisetosus, H. solidus, H. conspicuus, Centrophyes curvatus, C. rectilineatus, C. moderatus, C. longihastatus, C. denticulatus, C. diffusus, C. validus, C. tenuis*, and *C. biserratus*. Thus, the genus *Pycnophyes* actually had a total of 24 nominal species.

Hyalophyes Zelinka (1907) consisted of the last three stages prior to the adult, and, aside from having a thin cuticle and no secondary sex characters, species assigned to this genus were similar to *Pycnophyes*. *Centrophyes* Zelinka (1907) consisted of the three stages that precede the *Hyalophyes* stages. Although they possessed the precursors of the lateral terminal spines, the presence of a midterminal spine dominated their morphology.

The larval genus *Leptodemus* Zelinka, 1907, was assigned to the family Trachydemidae Zelinka (1896), as was the nominal genus *Trachydemus* (now *Kinorhynchus* Sheremetevskij, 1974). In his monograph, Zelinka described *L. serratus, L. forceps, L. forficulus, L. perlatus, L. vitreus*, and *L. naviculus* in addition to reassigning *Echinoderes acercus* Reinhard, 1881 (considered "unidentifiable" by both Zelinka, 1928:360, and Remane, 1936:362), and *E. dubius* Reinhard, 1887, to this latter genus. These eight species, based on juveniles lacking all caudal spines (= Acerca sensu Reinhard, 1885) were subject to reinterpretation first by Remane (1929) who stated that *L. naviculus, L. perlatus, L. forficulus, L. dubius*, and *L. vitreus* were members of the genus *Pycnophyes* and later by Băcescu, 1968, who added *L. metschnikowii* and *L. acercus* to this same genus. Two remaining species assigned to *Leptodemus, L. forceps* and *L. serratus*, appear to have been ignored.

Despite the report of Nyholm (1947b) that *Leptodemus* can change into a *Centrophyes*, therefore implying that both the latter two genera are synonyms of *Pycnophyes*, there is contradictory evidence (Higgins, 1974) that *Leptodemus* stages are, in fact, juveniles of *Kinorhynchus* and that the Zelinkian species of *Leptodemus* are, at best, species incertae sedis.

Since 1928, nine additional species of *Pycnophyes* have been described. These include *P. beaufortensis* Higgins, 1964b, *P. chiliensis* Lang, 1953, *P. egyptensis* Higgins, 1966a, *P. frequens* Blake, 1930, *P. maximus* Reimer, 1963, *P. neapolitanus* Băcescu, 1968, *P. odhneri* Lang, 1949, *P. sanjuanensis* Higgins, 1961, and *P. sculptus* Lang, 1949.

In 1963, *Hyalophyes pellucidus* was synonymized (Reimer, 1963:443) with *P. kielensis* and supported by Băcescu (1968:243). The latter author, in the same publication, synonymized *P. ponticus* sensu Băcescu and Băcescu, 1956 (partim) and *P.*

TABLE 14.—Composition of the genus *Pycnophyes* incorporating the criteria of Zelinka, 1928, by which generic junior synonyms have arisen (asterisk denotes species indeterminata based on inadequate description of the adult)

ADULTS *Pycnophyes*	JUVENILES (= *Hyalophyes*)	JUVENILES (= *Centrophyes*)
Lateral terminal spines only		Midterminal spines
beaufortensis	*conspicuus*	*bisseratus*
calmani[1]	*longisetosus*	*curvatus*
carinatus	*solidus*	*denticulatus*
chiliensis		*diffusus*
communis		*longihastatus*
corrugatus, new species		*moderatus*
dentatus		*rectilineatus*
* *echinoderoides*		*tenuis*
ecphantor, new species		*validus*
egyptensis		
emarginatus, new species		
flaveolatus		
frequens		
iniorhaptus, new species		
kielensis[2]		
longicornis, new species		
maximus		
odhneri		
ponticus[3]		
robustus		
rugosus		
sanjuanensis		
sculptus		
zelinkaei		

[1] = *P. communis* according to Nyholm (1947b:10) and Lang (1949:12).
[2] Includes *Hyalophyes pellucidus*.
[3] Includes *P. neapolitanus*.

TABLE 15.—Distribution of *Pycnophyes* (see Figure 191; type-localities are in italics; asterisk denotes species indeterminata based on inadequate description of the adult)

Species	FAO sea area	Locality	Authority
beaufortensis	ANW	*Beaufort* (N.C.), USA	Higgins, 1964b
	ASW	Bears Bluff (S.C.), USA	Higgins, 1964b
	ASW	Marineland (Fla.), USA	Higgins, 1964b
biserratus	ANE	W. Sweden	Nyholm, 1947b
	MED	*Naples,* Italy	Zelinka, 1928
	MED	Sukhumi, USSR	Sheremetevskij, 1974
calmani	ANE	*Clew Bay,* Ireland	Southern, 1914
	ANE	St. Andrews Bay, UK	Zelinka, 1928
	ANE	Oresund, Denmark	Lang, 1936
carinatus	MED	Trieste, Italy	Zelinka, 1928
MED	Naples, Italy	Zelinka, 1928	
chiliensis	PSW	*Quellin Is.,* Chile	Lang, 1953
communis	ANE	Gullmarfjord, Sweden	Nyholm, 1947b
	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
conspicuus	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
corrigatus, new species	ASW	*Twin Cays,* Belize	Higgins, this study
curvatus	ANE	W. Sweden	
	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
dentatus	ANE	Clew Bay, Ireland	Southern, 1914
	ANE	Kiel, FRG	Zelinka, 1928
	ANE	Scheveningen, Netherlands	Zaneveld, 1938
	ANE	SW Isle of Man, UK	Bruce et al., 1963
	MED	*Odessa,* USSR	Reinhard, 1881, 1885, 1887, Băcescu, 1968
	MED	Rumania	Băcescu and Băcescu, 1956; Băcescu, 1968
	MED	Caucasus and Crimea Coast, USSR	Sheremetevskij, 1974
denticulatus	ANE	Fladden, UK	McIntyre, 1962
	MED	*Naples,* Italy	Zelinka, 1928
diffussus	MED	*Trieste,* Italy	Zelinka, 1928
* *echinoderoides*	MED	*Naples,* Italy	Zelinka, 1928
ecphantor, new species	ASW	*Twin Cays,* Belize	Higgins, this study
egyptensis	ISW	*Al-Ghardaqa,* Egypt	Higgins, 1966a
emarginatus, new species	ASW	*Twin Cays,* Belize	Higgins, this study
flaveolatus	ANE	Oresund, Denmark	Lang, 1936
	ANE	Gullmarfjord, Sweden	Nyholm, 1947b; Nyholm and Nyholm, 1976
	MED	Trieste, Italy	Zelinka, 1928
	MED	Naples, Italy	Zelinka, 1928

TABLE 15.—Continued

Species	FAO sea area	Locality	Authority
frequens	ANW	*Mt. Desert Is.* (Me.), USA	Blake, 1930; Hyman, 1951; Higgins, 1965
		Buzzards Bay (Mass.), USA	Wieser, 1960; Higgins, 1965
iniorhaptus, new species	ASW	*Twin Cays,* Belize	Higgins, this study
kielensis	ANE	*Kiel,* FRG	Zelinka, 1928
	ANE	Oresund, Denmark	Lang, 1936
longicornis, new species	ASW	*Twin Cays,* Belize	Higgins, this study
longihastatus	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
maximus	ANE	*Kadetrinne,* GDR	Reimer, 1963
moderatus	ANE	W. Sweden	Nyholm, 1947b
	MED	*Naples,* Italy	Zelinka, 1928
odhneri	PSE	*Cumberland Bay,* S. Georgia Is.	Lang, 1949
ponticus	MED	*Odessa,* USSR	Reinhard, 1881, 1885, 1887
	MED	Naples, Italy	Zelinka, 1928
	MED	Constanta, Rumania	Băcescu and Băcescu, 1956
	MED	Tusaul, Rumania	Băcescu and Băcescu, 1956
	MED	Chitic, Rumania	Băcescu and Băcescu, 1956
	MED	Bulgarian coast	Marinov, 1964
	MED	Danube Delta, Rumania	Băcescu, 1968
	MED	Caucasus coast, USSR	Sheremetevskij, 1974
rectilineatus	ANE	W. Sweden	Nyholm, 1947b
	MED	*Naples,* Italy	Zelinka, 1928
robustus	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
rugosus	MED	*Naples,* Italy	Zelinka, 1928
sanjuanensis	INE	*Orcas Is.* (Wash.), USA	Higgins, 1961
sculptus	PSE	*Berkeley Sound,* Falkland Is.	Lang, 1949
solidus	MED	*Naples,* Italy	Zelinka, 1928
tenuis	MED	*Naples,* Italy	Zelinka, 1928
validus	MED	*Trieste,* Italy	Zelinka, 1928
zelinkaei	ANE	*Clew Bay,* Ireland	Southern, 1914
	ANE	Fladden, UK	McIntyre, 1962
species	ISW	Andaman Is.	Higgins and Rao, 1979

ponticus Marinov, 1964, with *P. kielensis*, separating *P. ponticus* sensu Zelinka from *P. ponticus* Reinhard, 1881, and then renaming *P. ponticus* sensu Zelinka *P. neapolitanus*.

It is unfortunate that Reinhard's (1881, 1885, 1887) descriptions and particularly his illustrations (1885, figs. 19–42) and those of Băcescu (1968) and Marinov (1964) are of such limited use. Zelinka could only have been frustrated by Reinhard's illustrations and must have used the peculiar subcuticular scars of the penultimate sternal plates as an important criterion for considering Reinhard's species conspecific with his own specimens, which were the basis for his description and illustrations (Zelinka, 1928, pl. 11: fig. 11; pl. 13: figs. 5, 6). Băcescu's (1968, pl. 6) illustrations of *P. neapolitanus* are no more than a crude copy of Zelinka's excellent illustrations and, therefore, cannot be based on material seen by Băcescu.

In his attempt to improve on Băcescu's description and illustrations of *P. neapolitanus*, Sheremeteveskij (1974) produced illustrations (pl. 2: fig. 8–12) that are no better than those of Reinhard, and it seems inconceivable that the former author's illustrations represent the same species considered *P. ponticus* by Zelinka. In particular, there is no agreement in the number and position of sensory setae, nor do the shapes of either the entire trunk or the midventral plates bear any resemblance to one another.

Until more convincing evidence emerges, I

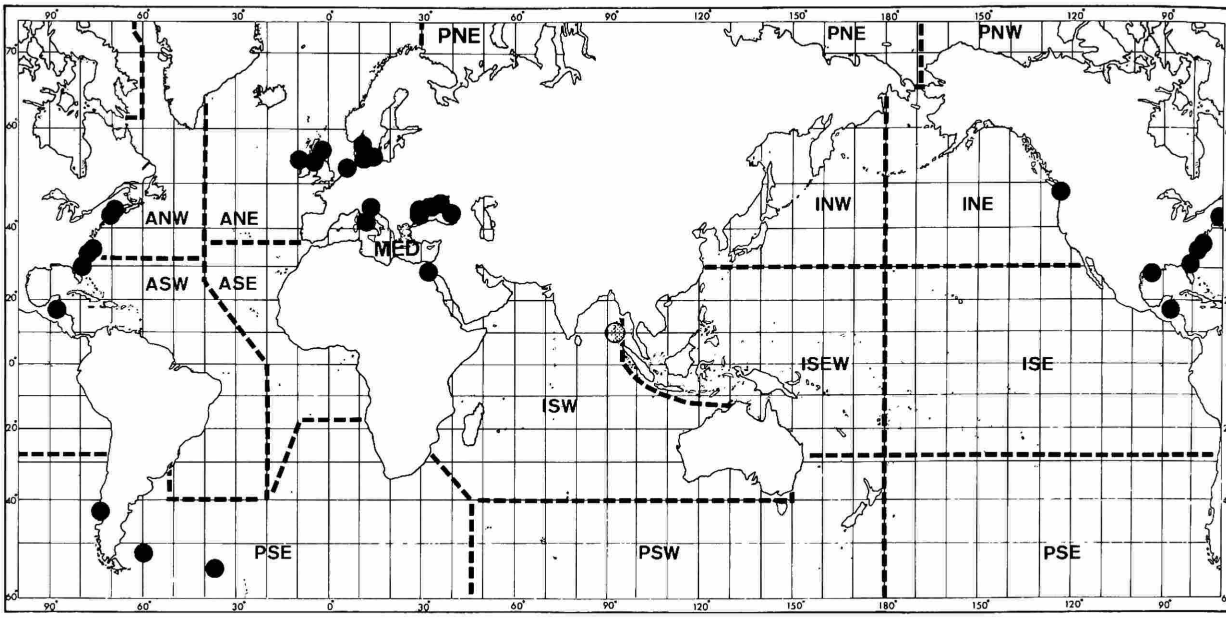


FIGURE 191.—Distribution of *Pycnophyes* (solid circles indicate records of named species, stippled circle indicates genus records only).

shall consider *P. neapolitanus* Băcescu, 1968, including the interpretation by Sheremetevskij (1974), a junior synonym of *P. ponticus* Zelinka, 1928.

Pycnophyes flagellatus and *P. quadridentatus* have been synonymized herein and reassigned to *Paracentrophyes*, leaving *Pycnophyes echinoderoides* as a species indeterminatum. It is very doubtful that any of the remaining 13 species of *Pycnophyes*, which have been described only from juvenile stages, can be matched with an adult.

A compilation of the current status of the genus *Pycnophyes* is shown in Table 14. Table 15 and Figure 191 illustrate the reported distribution of these species. In number of described species, *Pycnophyes* with its total of 36, 24 of which are based on adults, is second only to *Echinoderes* with 65, 38 of which are based on adults. Because of both fewer records and number of species, little can be written about the distribution or ecology of this genus. Some, like *Pycnophyes beaufortensis*, have been found in estuaries (Higgins, 1964b) and the low salinities of the Black Sea and Baltic Sea (Sheremetevskij, 1974). Normally, members of this genus are associated with mud to sandy subtidal bottoms, rarely in algae. None have been found in association with other invertebrates.

Pycnophyes represents the largest kinorhynchs; their maximum trunk length reaches 980 μm in *P. sculptus*, and a minimum adult measurement is 380 μm for *P. ponticus*. On this basis one would assume them to be easier to see and hence more commonly reported. In part, the apparent disparity in numbers of the homalorhagid genus *Pycnophyes* versus the cyclorhagid genus *Echinoderes* is an artifact of my own research procedure, for my own collections include many additional undescribed species from the Arctic to the Antarctic, from intertidal estuarine mud, to high energy sandy beaches and abyssal sediments throughout the world.

Genus *Kinorhynchus* Sheremetevskij, 1974

Key to Adults of *Kinorhynchus*

1. Middorsal processes present on segment 11 2
   Middorsal processes absent on segment 11 8
2. Middorsal processes on segments 4–11, small, blunt or rounded; lateral protuberances of terminal segment bi- or trifurcate .... ***K. giganteus*** Zelinka, 1908
   Middorsal processes spinose; lateral protuberances of terminal segment bulbose or pointed 3
3. Segment 12 with single lateral seta on each margin; middorsal processes of anterior trunk segments blunt, bell-shaped .... ***K. ilyocryptus*** Higgins, 1961
   Segment 12 with 2 or 3 lateral setae on each margin; middorsal processes spinose 4
4. Segment 12 with 3 lateral setae on each margin .... ***K. trisetosus,*** new species
   Segment 12 with 2 lateral setae on each margin 5
5. First trunk segment with subdorsal setae ..... ***K. anomalus*** (Lang, 1953)
   First trunk segment without subdorsal setae 6
6. Lateral setae absent on segments 5, 7, and 9 only; terminal segment slightly pointed; margin of terminal segment pointed .... ***K. spinosus*** (Lang, 1949)
   Lateral setae absent on other combination of segments; margin of terminal segment not pointed 7
7. Lateral setae absent on segments 3, 5, 6, 8, 9, and 11; segment 12 sharply tapered; terminal segment very narrow ... ***K. stenopygus,*** new species
   Lateral setae absent on segments 5 and 11; segment 12 tapering only slightly; terminal segment broad .... ***K. cataphractus*** (Higgins, 1961)
8. Lateral setae absent on segment 11 9
   Lateral setae present on segment 11 13
9. Lateral setae present on segment 9 .... ***K. belizensis,*** new species
   Lateral setae absent on segment 9 10
10. Lateral setae absent on segment 10 .... ***K. paraneapolitanus*** Sheremetevskij, 1974
    Lateral setae present on segment 10 11
11. Lateral setae absent on segment 6; segment 12 very short, bulging lateroterminally .... ***K. distentus,*** new species
    Lateral setae present on segment 6 12
12. Lateroterminal margins of segment 12 distinctly spinose, extending well beyond terminal segment; anterior margin of first trunk segment much narrower than that of segment 7; middorsal spinous process on segment 10 .... ***K. mainensis*** Blake, 1930
    Lateroterminal margins of segment 12 spinose but not extending beyond terminal segment; anterior margin of first trunk segment about as wide

as that of segment 7; no middorsal process on segment 10 .... *K. langi* (Higgins 1964b)

13. Lateral setae missing on segment 12; diagonal buttresses extending from midlateral margins to pachycycli on segments 3–11 .... ***K. erismatus,*** new species

    Two lateral setae present on segment 11; no diagonal buttresses present 14

14. Middorsal setae on segments 4–11; segment 12 much longer than segment 11; 2 lateral setae of segment 12 very prominent, near posterior margin .... ***K. apotomus,*** new species

    Middorsal setae absent; segment 12 much shorter than segment 11; 2 lateral setae of segment 12 small, not near posterior margin .... ***K. deirophorus,*** new species

Kinorhynchus apotomus, new species

FIGURES 192–203

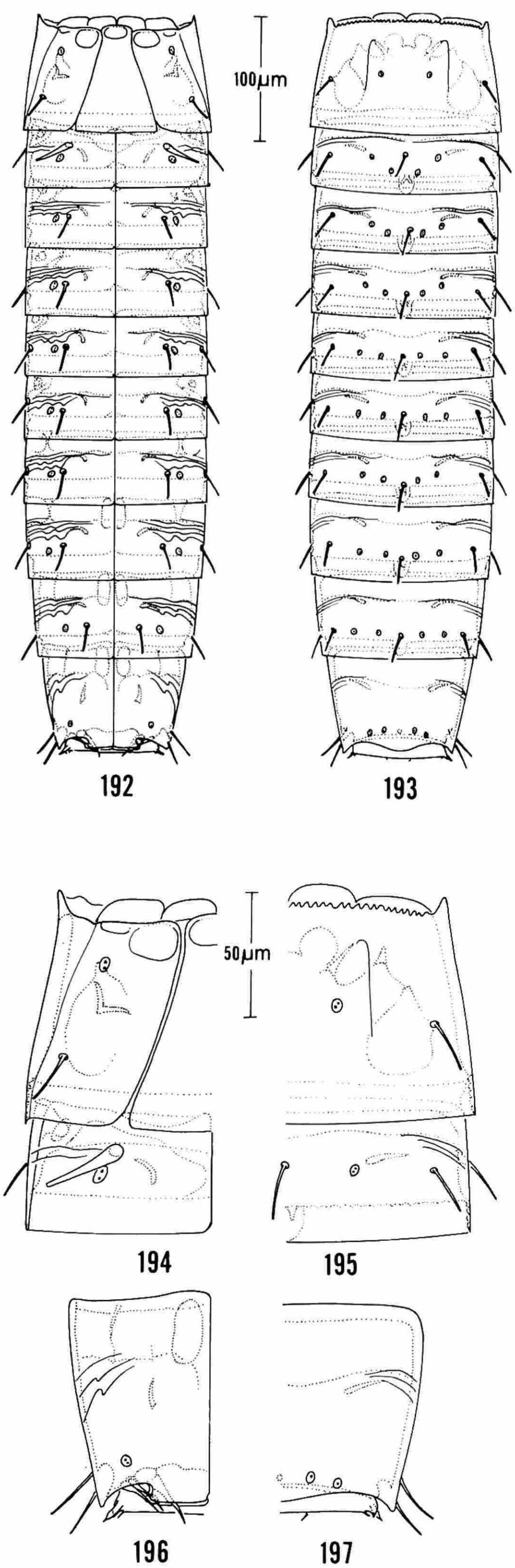
DIAGNOSIS.—Trunk segments 3–9 nearly equal in width, segments 10–13 tapering moderately; anterodorsal margin of first trunk segment evenly dentate; prominent midorsal setae on segments 4–11; lateral setae on segments 4, 6–11, 2 on either side of segment 12 near terminal margin; terminal segment truncate; L-shaped cuticular scars posteriorly adjacent to sensory spots on episternal plates.

DESCRIPTION.—Adults (Figures 192–203), trunk length 592 μm, segments 3–9 nearly equal in width, segments 10–13 tapering moderately; MSW-8 136–140 μm, 23.0–23.6 percent of trunk length; SW 112 μm, 18.6 percent of trunk length. Second segment with 4 dorsal and 4 ventral placids, margins even (Figures 194, 196).

Trunk segments (Figures 192, 193) without middorsal spinose processes, subcuticular rounded middorsal spinose structure present on segments 4–11. Prominent setae, 22–24 μm long, situated middorsally on segments 4–11, dorsolaterally on segments 3–11, laterally on segments 4, 6–11 with 2 on either side of segment 12 near terminal margin, ventrolaterally on sternal plate of segments 3 and lateral plates, mesial to sensory spots, segments 5–10, more mesial on segment 11. Sensory spots subdorsal on first trunk segment, 2 subdorsal sensory spots on segments 4–12, sensory spot near anterior margin of each episternal plate of first trunk segment or lateral to setae or setal position on lateral plates of segments 4–12. Pachycycli weakly developed; midventral thickenings at anteromesial margins of segments 10–12; series of cuticular ridges beginning with longitudinal subdorsal ridges on tergal plate of segment 3 (Figure 196), continuing as transverse ridges, becoming more uneven, beginning at anterolateral margins of tergal and sternal plates 4–12 (Figures 192, 193). Prominent muscle scars dorsolateral and ventrolateral on first trunk segment, prominent L-shaped cuticular scar (Figure 194) below sensory spot on each episternal plate; crescent-shaped cuticular scar near midline of sternal plates, beginning with 45° orientation on anterior segments, becoming more transverse on posterior segments changing to longitudinal orientation on segment 12, tergal plates with crescent-shaped cuticular scars anterior to lateralmost sensory spot, scars nearly transverse in orientation on all segments.

First trunk segment (segment 3) with anterolateral margins of tergal plate extending to form slightly pointed projections, anterior tergal margin evenly dentate (Figure 195), episternal plates with sculptured anteromesial area of thin cuticle, single such area at anterior margin of episternal plates (Figures 192, 194, 198); midsternal plate trapezoidal, about 86 μm long, 70 μm basal width tapering to a slightly expanded, rounded apex 26 μm in width.

Sternal plates of segment 4 of males with prominent adhesive tube, 35–37 μm long (Figure 194). Pachycyclus extensive, with granular surface sculpturing. Segments 5–11 similar except for differences already noted.



Segment 12 longer than segment 11, sternal plates incised near posterolateral margins (Figure 196), truncate at midline; tergal plate projecting slightly at midline.

Terminal tergal segment broadly truncate, extending slightly beyond penultimate segment, minutely pointed lateral terminal projections, about 8 μm long, at margin (Figures 196, 197); terminal sternal margin appears parallel with preceding sternal margin; 1 pair of prominent penile spines and 1 or 2 pairs of smaller penile spines near anterolateral margins of terminal sternal plates (cuticular hairs occasionally create the impression that more penile spines are present, requiring this character to be treated with caution).

Morphometric data for the second of two males were identical for TL, SW, SW/TL. Only the MSW measurement differed (MSW 140 μm, 23.6 percent of trunk length).

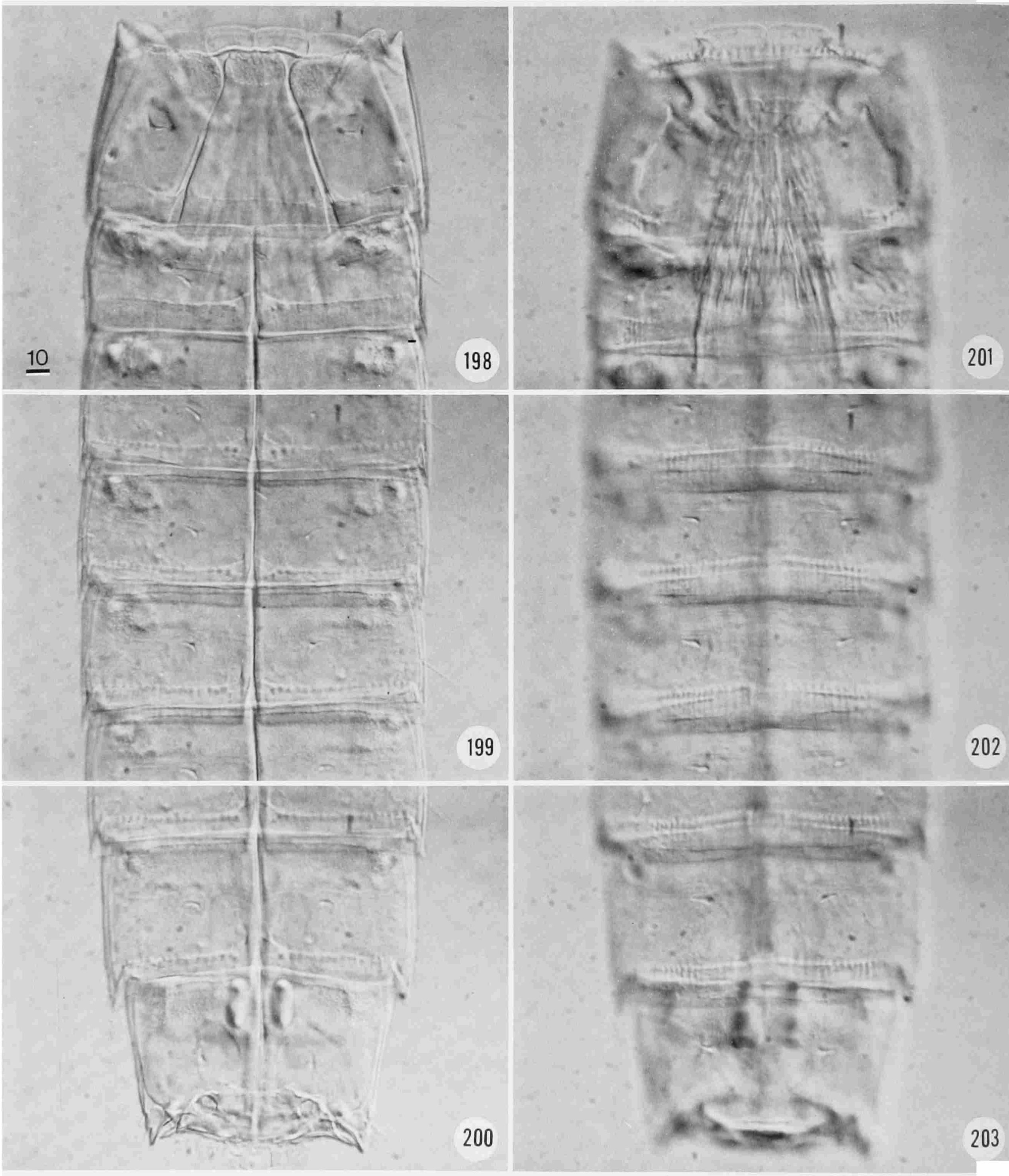
HOLOTYPE.—Adult male, TL 592 μm (Figures 192–203), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70008.

PARATYPE.—Adult male, TL 592 μm, other data as for holotype, USNM 70009.

REMARKS.—*Kinorhynchus apotomus* is unique in having middorsal setae. To be sure, setae are sometimes difficult to see, and previous descriptions could be faulty, but the middorsal setae on segments 4–11 are prominent as are all others on the trunk segments of this new species. With the exception of *K. ilyocryptus*, members of this genus have two lateral setae on segment 12. *Kinorhynchus apotomus* also has two, but they are located very close to the terminal margin, which emphasizes their prominence (Figures 195, 196).

No previously described species of *Kinorhynchus* has posterolaterally indented margins of the twelfth sternal plates (Figure 196) followed by the severely truncated terminal segment. The pointed

FIGURES 192–197.—*Kinorhynchus apotomus*, new species: 192, neck and trunk segments, ventral view, holotypic male (USNM 70008); 193, same, dorsal view; 194, same, segments 2–4, lateral half, ventral view; 195, same, dorsal view; 196, same segments 12, 13, lateral half, ventral view; 197, same, dorsal view.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lateral terminal protuberances of the terminal segment are similar to those described for several species, including *K. anomalus*. These structures, more commonly bulbous or accompanied by one or more additional minute protuberances, have led a few authors to speculate as to the validity of the separation of *Kinorhynchus* from *Pycnophyes*. Blake (1930) predicted the ultimate union of these two genera, and Lang (1949) referred to these structures as lateral terminal spines but defended the separation of the genera. These protuberances so far do not appear to be articulated in *Kinorhynchus* as contrasted with those of *Pycnophyes*.

The anterodorsal margin of *K. apotomus* is dentate (Figure 196), a feature shared with *K. giganteus*. No other species has demonstrated the series of transverse parallel cuticular ridges that occur near the lateral margins of both the tergal and sternal plates of this new species. These ridges are similar to those of *Pycnophyes corrugatus* as noted earlier. The thin cuticular areas of the episternal and midsternal plates are similar in number and position to *K. mainensis* and *K. ilyocryptus*. The L-shaped cuticular scars posteriorly adjacent to the sensory spots on the episternal plates have not been observed in other species.

ETYMOLOGY.—The name of this species is from the Greek *apotomus* (cut off, abrupt).

Kinorhynchus belizensis, new species

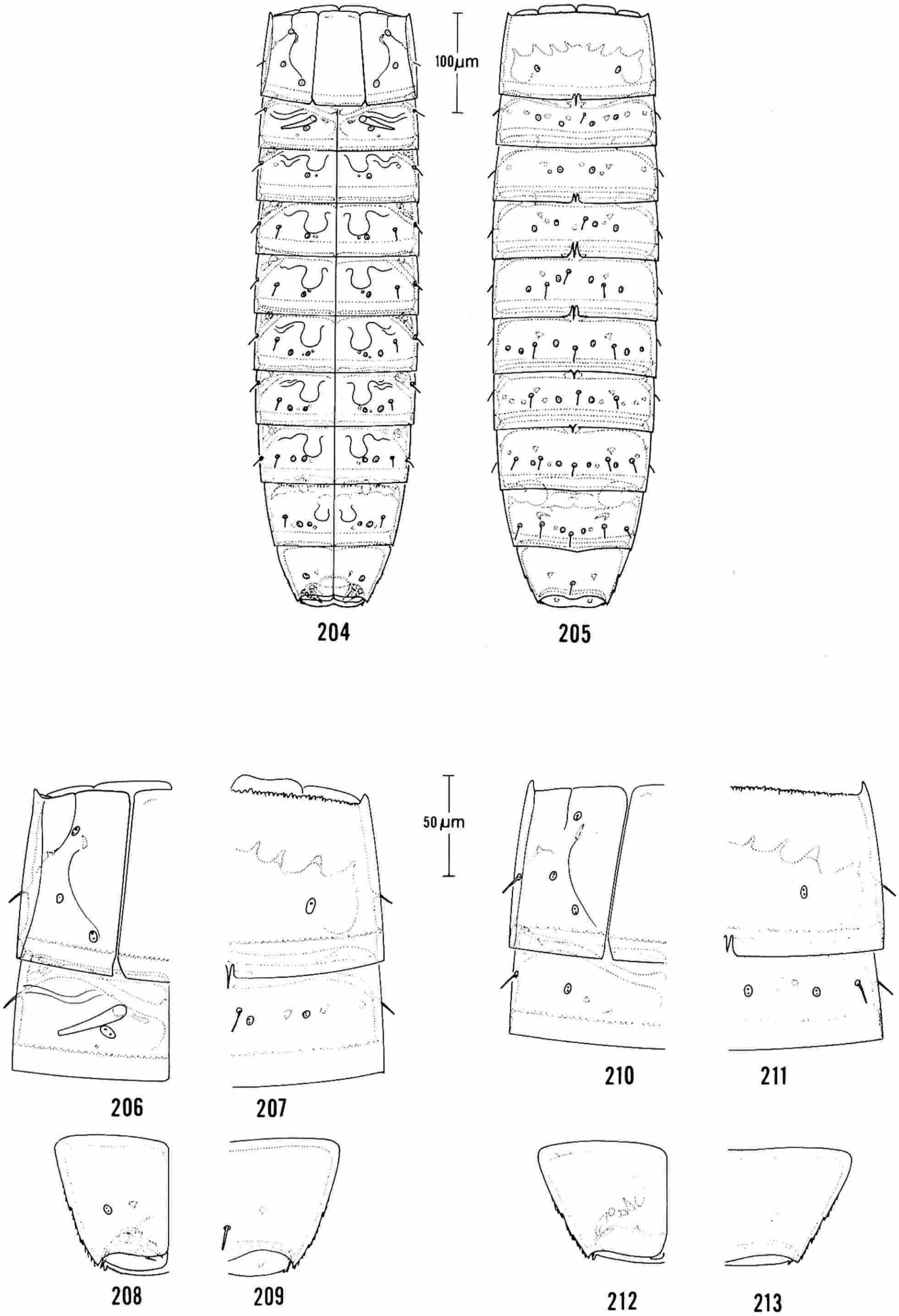
FIGURES 204–219

DIAGNOSIS.—First trunk segment slightly narrower than second trunk segment, maximum width at segment 7, tapering moderately thereafter, terminal segment slightly indented at midline; midsternal plate of first trunk segment with nearly parallel lateral margins; middorsal setae at least on segment 8–12; reduced middorsal spinose protuberances on segments 3, 5–9; no lateral setae on segment 12; buttress-like cuticular support present between lateral margin and pachycyclus of each sternal plate.

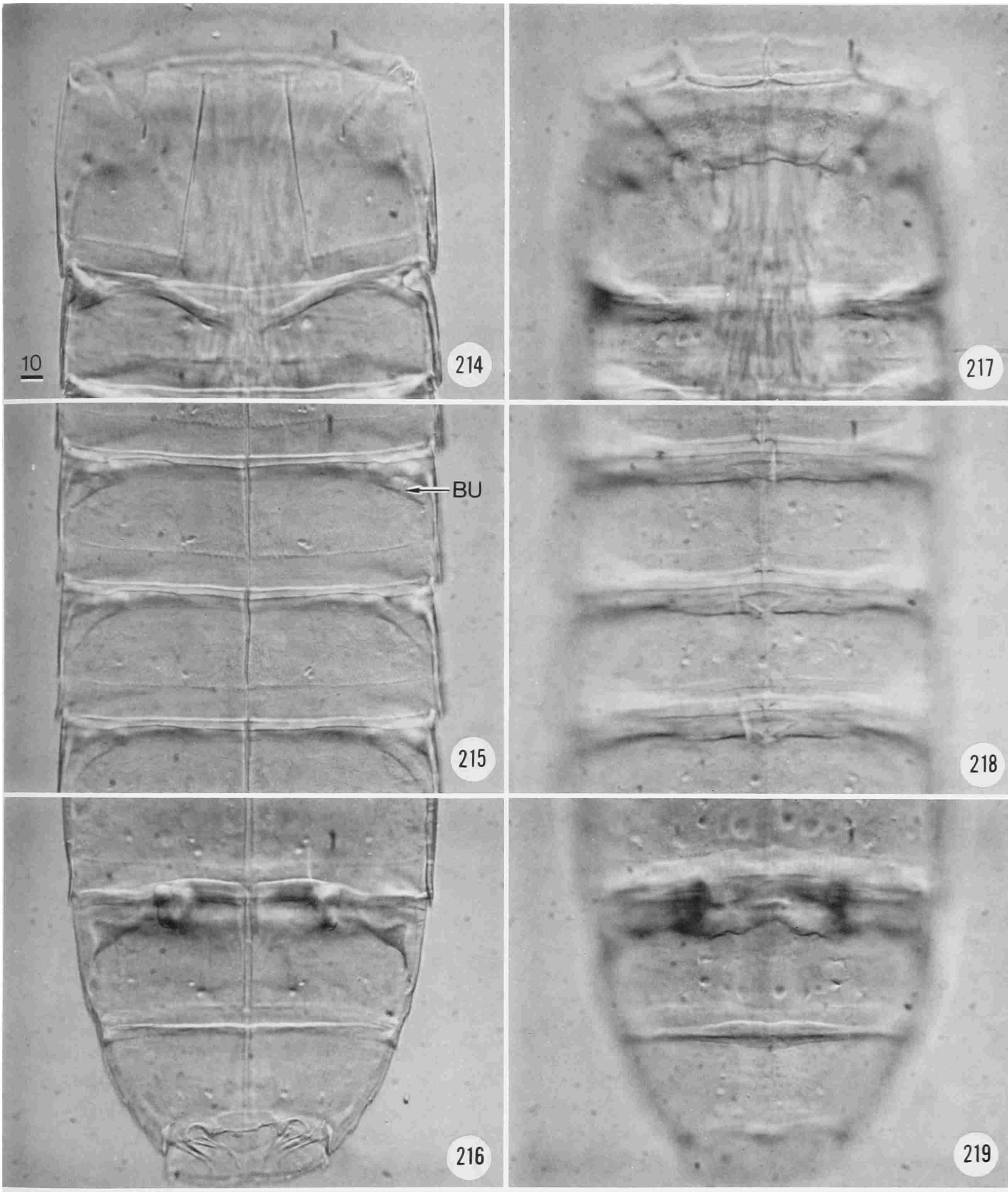
DESCRIPTION.—Adults (Figures 204–219), trunk length, 478–614 μm, first trunk segment slightly narrower than second trunk segment, MSW-7 136–168 μm, 22.2–33.5 percent of trunk length; trunk moderately tapered, SW 92–136 μm, 18.3–27.6 percent of trunk length. Second trunk segment with 4 dorsal and 2 ventral placids, dorsomesial placid with slightly indented margin (Figures 206, 207).

Trunk segments (Figures 204, 205) with small, 22–23 μm, middorsal spinose processes at posterior margins of segments 3, 5–9, slightly inset into margin on segments 3, 5–7. Setae, 20–21 μm long, situated middorsally on at least segments 8–12 (several specimens, including holotype, show off-centered setae on segments 4, 6, and 7; these may not occur in all specimens, see Figure 205); subdorsal setae on segments 7–11, laterodorsal setae on segments 10, 11, lateral setae on segments 3–10, none on 11 or 12, ventrolateral setae on segments 6–11; sensory spots subdorsal on segments 4–11, dorsolateral on segments 3, 4, 6–8, 10; additional sensory spots lateral to dorsolateral on segment 8; 3 sensory spots on each episternal plate; ventral sensory spots on each sternal plate 4–7; 2 ventral spots on sternal plates 8–11; single ventral spot on each sternal plate of segment 12. Pachycycli well developed, especially those of segment 11 (Figures 216, 219) where midventral thickenings appear to be laterally displaced. Slightly ridged, longitudinally oriented pattern evident on episternal plates (Figures 206, 210), 2 transverse, parallel ridges near pachycycli of sternal plates 4–5, 1 ridge diverting as a posterior loop evident on sternal plates 5–11 (Figure 204). Muscle scars lateral on tergal plate of segment 3; scars continuing across anterior third of plate in pattern shown in Figure 205; cuticular scars somewhat triangular in shape, lateral to subdorsal sensory spots on tergal plates 4–11, becoming more anteriorly situated in posterior segments, anterolateral to middorsal setae on segment 12, lateral to ventral midline on sternal plates, posteriorly adjacent to anterormost sensory spots of episternal plates.

FIGURES 198–203.—*Kinorhynchus apotomus*, new species: 198, segments 2–4, ventral view; 199, segments 7, 8, ventral view; 200, segments 11–13, ventral view; 201, segments 2–4, dorsal view; 202, segments 7, 8, dorsal view; 203, segments 12, 13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 198.)



FIGURES 204–213.—*Kinorhynchus belizensis*, new species: 204, neck and trunk segments, ventral view, holotypic male (USNM 70010); 205, same, dorsal view; 206, same, segments 2–4, lateral half, ventral view; 207, same, dorsal view; 208, same, segments 12, 13, lateral half, ventral view; 209, same, dorsal view; 210, segments 2–4, lateral half, ventral view, allotypic female (USNM 70011); 211, same, dorsal view; 212, same, segments 12, 13, lateral half, ventral view; 213, same, dorsal view.



FIGURES 214–219.—*Kinorhynchus belizensis*, new species: 214, segments 3, 4, ventral view; 215, segments 7, 8, ventral view; 216, segments 11–13, ventral view; 217, segments 3, 4, dorsal view; 218, segments 7, 8, dorsal view; 219, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 214; BU = buttress.)

TABLE 16.—Measurements (μm) and indices (%) for *Kinorhynchus belizensis* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	8	478–592	543.0	42.4	15.0	7.8
	♀	12	478–614	555.3	42.8	12.4	7.7
	♂♀	20	478–614	550.4	42.0	9.4	7.6
SW	♂	8	112–124	119.5	4.0	1.4	3.3
	♀	12	92–136	125.3	11.4	3.3	9.1
	♂♀	20	92–136	123.0	9.4	2.1	7.7
SW/TL	♂	8	18.3–24.9	22.4	2.3	0.8	10.11
	♀	12	19.2–27.6	22.6	2.2	0.6	9.7
	♂♀	20	18.3–27.6	22.5	2.2	0.5	9.6
MSW-7	♂	8	136–156	150.5	6.4	2.3	4.3
	♀	12	148–168	162.7	6.2	1.8	3.8
	♂♀	20	136–168	157.8	8.7	1.9	5.5
MSW/TL	♂	8	22.2–31.8	27.9	2.8	1.0	10.1
	♀	12	25.9–33.5	29.4	1.9	0.6	6.5
	♂♀	20	22.2–33.5	28.8	2.4	0.5	8.3

First trunk segment (segment 3) with only slight projection of the anterolateral tergal margins; anterior tergal margin roughly denticulate (Figures 207, 211). Midsternal plate long, 96 μm, narrow, 52 μm, lateral margins nearly parallel; episternal plates with apparent partial longitudinal division created by inner area of thicker cuticle. First trunk segment slightly shorter in female than in male (Figures 210, 211).

Sternal plates of segment 4 of males with adhesive tubes, 38 μm long (Figure 206); females lack adhesive tubes, have smaller sensory spots, and the elongated cuticular scars are in a more posterior position; ventral accessory pachycycli narrow, arching at primary pachycycli. Middorsal protuberance not evident on posterior margin. Segment 5 without ventral setae, occasionally with 1 or more subdorsal setae. Segment 6 with ventral setae and sensory spots as noted earlier, segments 7–10 similar, trunk begins to taper beginning with segment 7 or 8. Segment 11 with enlarged pachycycli and laterally displaced midventral thickenings. Segment 12 narrow at posterior margin, without lateral setae, only a serrate lateral margin partially caused by the distal ends of cuticular scales that appear like small hairs in lateral view.

Terminal tergal segment indented at midline, giving a slightly bilobed appearance to the margin, small bulbous projection at lateral margins, margins of terminal sternal plates parallel those of segment 12 (Figures 208, 209, 212, 213), males with 3 pairs of penile spines at anterolateral margins of terminal sternal plates (Figure 204), females with single gonopore (Figure 212).

Males differ from females by presence of 3 pairs of penile spines at the anterolateral margins of terminal sternal plates; adhesive tubes on sternal plates of segment 4; slightly longer first trunk segment; variable presence of middorsal and subdorsal setae, especially in the anterior region of the trunk; slightly narrower trunk.

Morphometric data for adult specimens are shown in Table 16.

HOLOTYPE.—Adult male, TL 592 μm (Figures 204–209, 214–219), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins USNM 70010.

ALLOTYPE.—Adult female, TL 572 μm (Figures 210–213), other data as for holotype, USNM 70011.

PARATYPES.—Six adult males and 10 females, TL 478–614 μm, other data as for holotype, USNM 70012; 1 male, TL 614 μm, Twin Cays, sta RH 443, other data as for holotype, USNM 70013; 1 female, TL 478 μm, Twin Cays, sta RH 444, other data as for holotype, USNM 70014.

DISCUSSION.—The most noticeable characters of *Kinorhynchus belizensis* are the slightly inset middorsal spinose projections at the posterior margins of segments 3, 5–7 (Figure 205), the prominent pachycycli of segment 11 (the latter character is coupled with distinct midventral thickenings which are laterally displaced from their normal position, Figures 216, 219), and the buttress-like reinforcements of the pachycycli of the sternal plates (Figure 204). Since all previously described species of *Kinorhynchus* have two, or less commonly one, lateral setae on segment 12, the absence of any such setae in *K. belizensis* is another character of note.

In general trunk shape, *K. belizensis* is similar to *K. langi;* the latter species also has poorly developed middorsal spinous projections, restricted to the first five or six trunk segments as in *K. belizensis,* and both have four dorsal and only two ventral placids. In this latter point, however, the presence of two or four ventral placids is a matter of some subjectivity, since the thickness of the cuticle may vary only slightly, and in cases where the lateral placid area is not as thick as the mesial placids, one may judge only the two thicker placids as the only ones present.

ETYMOLOGY.—This species is named after the country where it was discovered.

Kinorhynchus deirophorus, new species

FIGURES 220–235

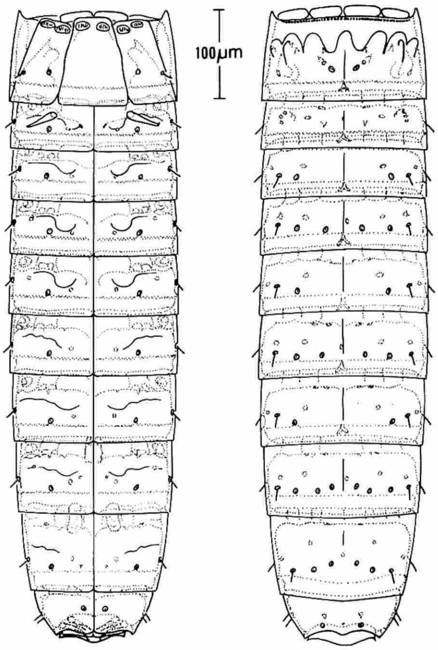
DIAGNOSIS.—First trunk segment almost of equal width, maximum width at segment 7, tapering moderately; anterodorsal margin even with row of punctate sculpturing followed by an undulating ridge of cuticle, anterior margin of episternal plates with 2 areas of sculptured, thin cuticle, lateral area slightly anterior to mesial area, 2 similar areas at margin of midsternal plates, middorsal ridge of cuticle prominent on anterior trunk segments; prominent ventral pachycycli and laterally displaced midventral thickenings on segment 11, segment 12 one-half as long as segment 11.

DESCRIPTION.—Adults (Figures 220–235), trunk length, 592 μm, segment 3 only slightly narrower at anterior margin than next few segments, MSW-7 128–180 μm, 23.3–28.5 percent of trunk length; trunk tapering moderately, SW 116–136 μm, 16.7–21.2 percent of trunk length. Second segment with 4 dorsal and 2 ventral placids, margins even (Figures 222, 223, 226, 227).

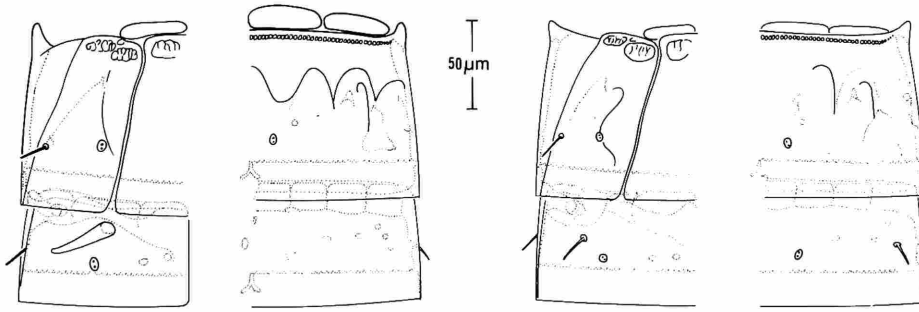
Trunk segments (Figures 220, 221) without middorsal projections. Slight cuticular ridge on segments 3–11 and slight indication of spinose subcuticular structure on segments 3–9. Setae, 20–23 μm long, situated dorsolaterally on segments 5–11, laterally on episternal plate, laterally on sternal plates 4–11, with 2 setae on either side of segment 12, ventral setae absent. Sensory spots subdorsal on segments 3, 6, 8, 10, 11, dorsolateral on segments 5–12 (mesial to setae), ventral on episternal plates and sternal plates 4–12. Pachycycli well developed, especially on segments 4 and 11 (Figures 230, 232, 233, 235); midventral thickenings of segment 11 laterally displaced (Figure 232); muscle scars with distinctive pattern on tergal plate (Figures 223, 227) and episternal plates (Figures 222, 226) of first trunk segment. Small, round to oval cuticular scars on either side of midline on sternal and tergal plates 4–11, (Figures 220, 221). Sternal plates 4–11 with single ridge of cuticle parallel with pachycycli laterally, extending posteriorly, a wide arc mesially, especially on anterior segments.

First trunk segment (segment 3) with distinct, somewhat blunt projections of the anterolateral tergal margins; anterior tergal margin even, with row of punctate sculpturing followed by an undulating ridge of cuticle (Figures 223, 227). Middorsal ridge of cuticle on posterior half of tergal plate; anterior margins of episternal plates with 2 areas of sculptured, thin cuticle, lateral area slightly anterior to mesial area, 2 similar areas at margin of midsternal plate; midsternal plate trapezoidal, lateral margins undulant, length about 100 μm, basal width 82 μm, 48 μm at apex.

Sternal plates of segment 4 of males each with adhesive tube, 34–36 μm long (Figure 227); fe-



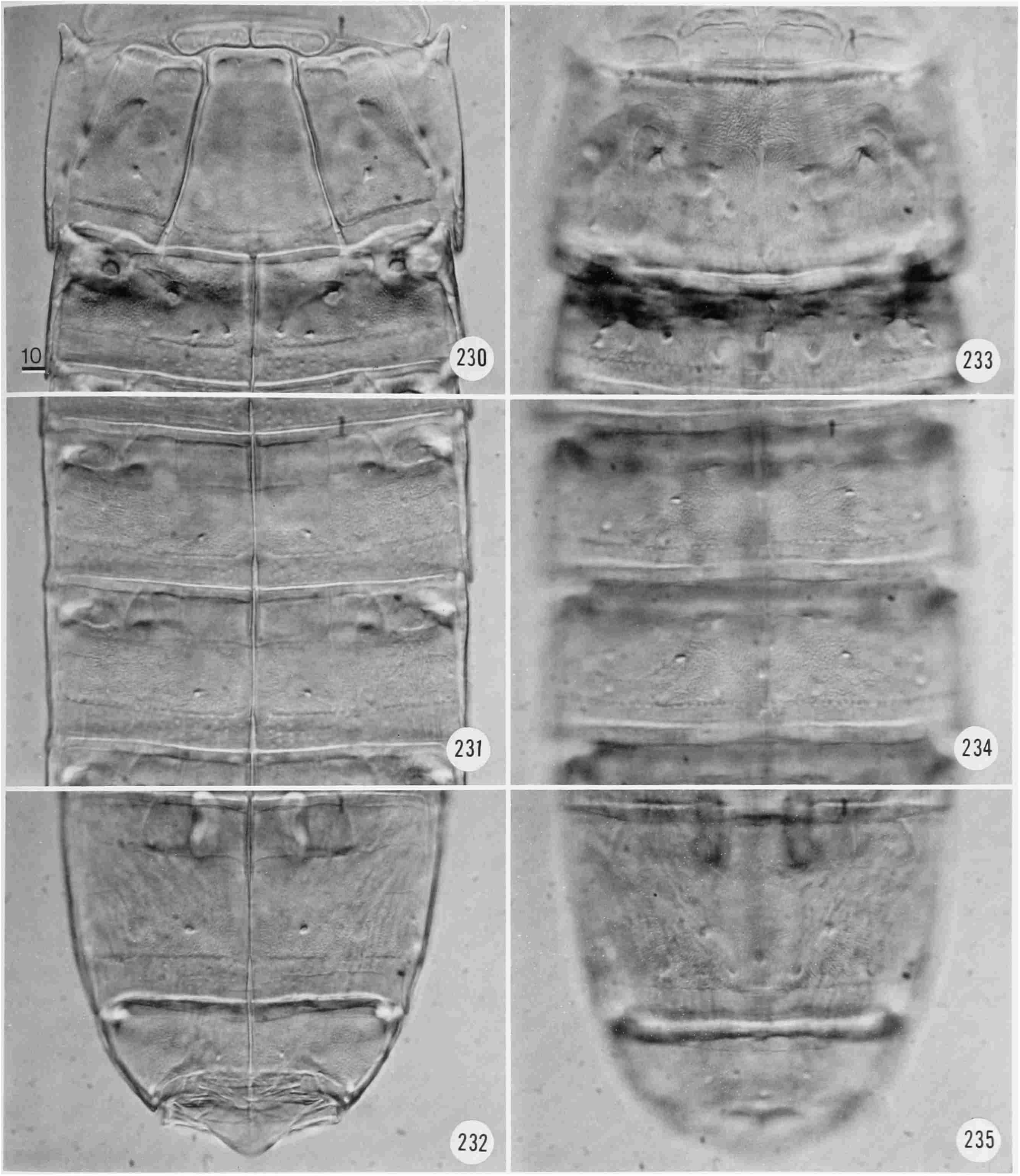
220 221



222 223 226 227

224 225 228 229

FIGURES 220–229.—*Kinorhynchus deirophorus,* new species: 220, neck and trunk segments, ventral view, holotypic male (USNM 70015); 221, same, dorsal view; 222, same, segments 2–4, lateral half, ventral view; 223, same, dorsal view; 224, same, segments 12, 13, lateral half, ventral view; 225, same, dorsal view; 226, segments 2–4, lateral half, ventral view, allotypic female (USNM 70016); 227, same, dorsal view; 228, same, segments 12, 13, lateral half, ventral view; 229, same, dorsal view.



FIGURES 230–235.—*Kinorhynchus deirophorus*, new species: 230, segments 3, 4, ventral view; 231, segments 7, 8, ventral view; 232, segments 11–13, ventral view; 233, segments 3, 4, dorsal view; 234, segments 7, 8, dorsal view; 235, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 230.)

TABLE 17.—Measurements (μm) and indices (%) for *Kinorhynchus deirophorus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	10	655–728	689.4	22.9	7.3	3.3
	♀	12	603–717	656.8	37.3	10.8	5.7
	♂♀	22	603–728	671.6	35.1	7.5	5.2
SW	♂	10	120–132	126.0	4.7	1.5	3.7
	♀	12	116–136	128.0	6.2	1.8	4.8
	♂♀	22	116–136	127.1	5.5	1.2	4.3
SW/TL	♂	10	16.7–19.5	18.3	0.9	0.3	4.9
	♀	12	18.4–21.2	19.6	0.9	0.3	4.8
	♂♀	22	16.7–21.2	19.0	1.2	0.3	6.2
MSW-7	♂	10	160–176	167.6	5.2	1.6	3.1
	♀	12	128–180	166.3	14.2	4.1	8.6
	♂♀	22	128–180	166.9	10.8	2.3	6.5
MSW/TL	♂	10	23.3–25.4	24.3	0.6	0.2	2.6
	♀	12	21.2–28.5	25.3	2.0	0.6	7.7
	♂♀	22	21.2–28.5	24.9	1.6	0.3	6.3

males lack adhesive tubes but have setae in the same location. Segments 5–11 similar except for characters already noted.

Segment 12 noticeably smaller than segment 11, about one-half the length of the latter; posterior margin of sternal plates nearly even, posterior margin of tergal plate slightly pointed at midline in male, less so in female (Figures 225, 229).

Terminal segment small, sternal margins even, tergal margin with lateral spinous projection in male (Figure 224), 1 or 2 additional marginal interruptions, more mesial in the female (Figure 228), broadly rounded in both sexes. One large and 2 small penile spines at anterolateral margin of each sternal plate (Figure 284); single gonopore in females (Figure 228).

Males differ from females by presence of 3 pairs of penile spines at anterolateral margins of terminal sternal plates, adhesive tubes on sternal plates of segment 4, and slightly more pronounced sculpturing on first trunk segment (Figures 223, 227).

Morphometric data for adult specimens are shown in Table 17.

HOLOTYPE.—Adult males, TL 697 μm (Figures 220–225, 230–234), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70015.

ALLOTYPE.—Adult female, TL 707 μm (Figures 226–229), other data as for holotype, USNM 70016.

PARATYPES.—Nine males and 11 females, TL 603–728 μm, other data as for holotype, USNM 70017.

DISCUSSION.—The pattern of cuticular sculpturing on the anterior margin of tergal plate 3 is the most obvious of the characters which separate *K. deirophorus* from all previously described members of this genus. This character resembles the tergal plate sculpturing of *Pycnophyes iniorhaptus* from this same locality. *Kinorhynchus paraneapolitanus* and *K. apotomus,* like *K. deirophorus,* lack middorsal processes at the posterior margin of at least some trunk segments.

A second unique character is the pattern of two thin, sculptured areas at the anterior margin of both the two episternal and single midsternal plates of the first trunk segment. The only other known species with two such areas on the episternal plates is *K. giganteus*. This latter species appears to have three less well-defined areas on the midsternal plate. The prominent pachycycli of segment 11 are similar to those previously described for *K. belizensis;* also similar are the laterally displaced midventral thickenings. Like the latter species, *K. deirophorus* has a ridge pattern on the sternal plates which suggests a further similarity.

ETYMOLOGY.—The name of this species is from the Greek *deiropedes* (necklace) plus *phoras* (bearing), in reference to the sculptured margin of the tergal plate of the first trunk segment.

Kinorhynchus distentus, new species

FIGURES 237-257

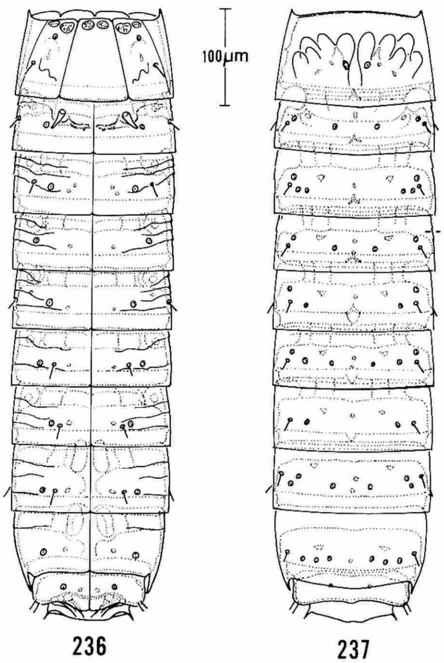
DIAGNOSIS.—Trunk only slightly narrowed both anteriorly and posteriorly; tergal plate of first trunk segment with 5 looped ridges on either side of midline; 2 thin cuticular areas at margin of episternal and midsternal plates; lateral margins of segment 11 extended posteriorly; penultimate segment short, one-half the length of the preceding segment, expanded and distended laterally, forming rounded margin; terminal segment with spinose lateral extensions of the margins; distinctive cuticular fringe pattern near midline of sternal plates on segment 4; series of 1 to 3 parallel cuticular ridges extending mesially from lateral margins of sternal plates 4–12.

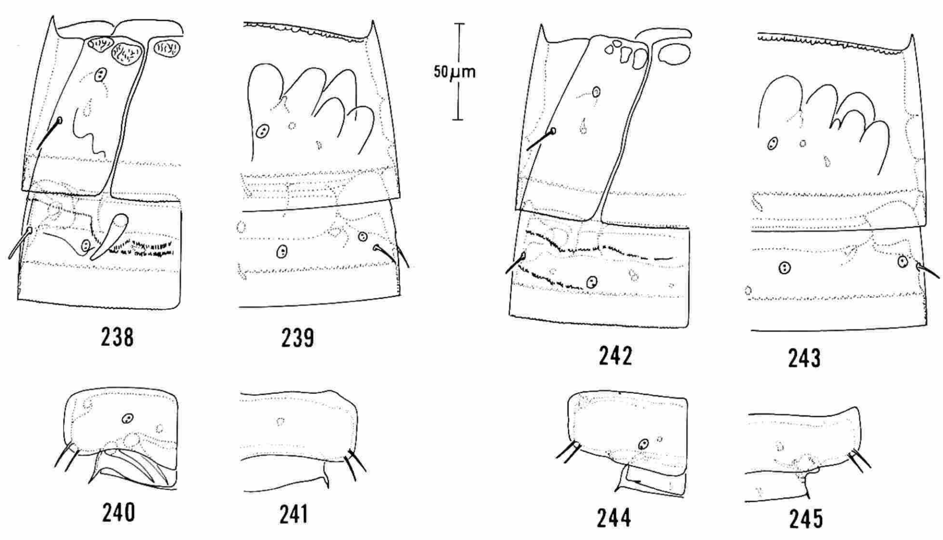
DESCRIPTION.—Adults (Figures 236–257), trunk length 540–665 μm, trunk only slightly narrowed both anteriorly and posteriorly; MSW-6 152–168 μm, 24.7–29.6 percent of trunk length; SW 112–120 μm, 18.0–20.7 percent of trunk length. Second segment with 4 dorsal and 2 ventral placids, margins even (Figures 236, 242, 246, 252).

Trunk segments (Figures 236, 237) without middorsal projections but with slight evidence of subcuticular spinose structure on segments 3–9. Setae, 20–22 μm long, situated dorsolaterally on segments 3–11, laterally on episternal plates and sternal plates 4, 7, 10, and 2 on lateral margins of segment 12; ventral setae near lateral margins of episternal plates and each sternal plate of segments 5, 8–10, those of segment 5 lateral to sensory spot, others mesial to sensory spot (Figure 236). Sensory spots subdorsal on segments 3, 4, 6, 8, 10, 11; 1 to 3 dorsolateral sensory spots on other segments; ventral sensory spot near anterior margin of episternal plate and on sternal plates 4–12. Series of 1 to 3 parallel cuticular ridges extending mesially from lateral margins of sternal plates 4–12. Pachycycli well developed, particularly on segments 4, 10, and 11, midventral thickenings on sternal plates of segments 10 and 11 (Figures 236, 248). Large muscle scars dorsolaterally on tergal plate and on episternal plates of segment 3; crescent-shaped cuticular scars, longitudinally oriented, posterior to sensory spot, mesial to setae of episternal plates; small, round to oval cuticular scars on sternal plates 4–12 near ventral midline, small, round to triangular-shaped cuticular scars on segments 4–12 near lateral margins of tergal plate 4, nearer to dorsal midline on tergal plates 5–12.

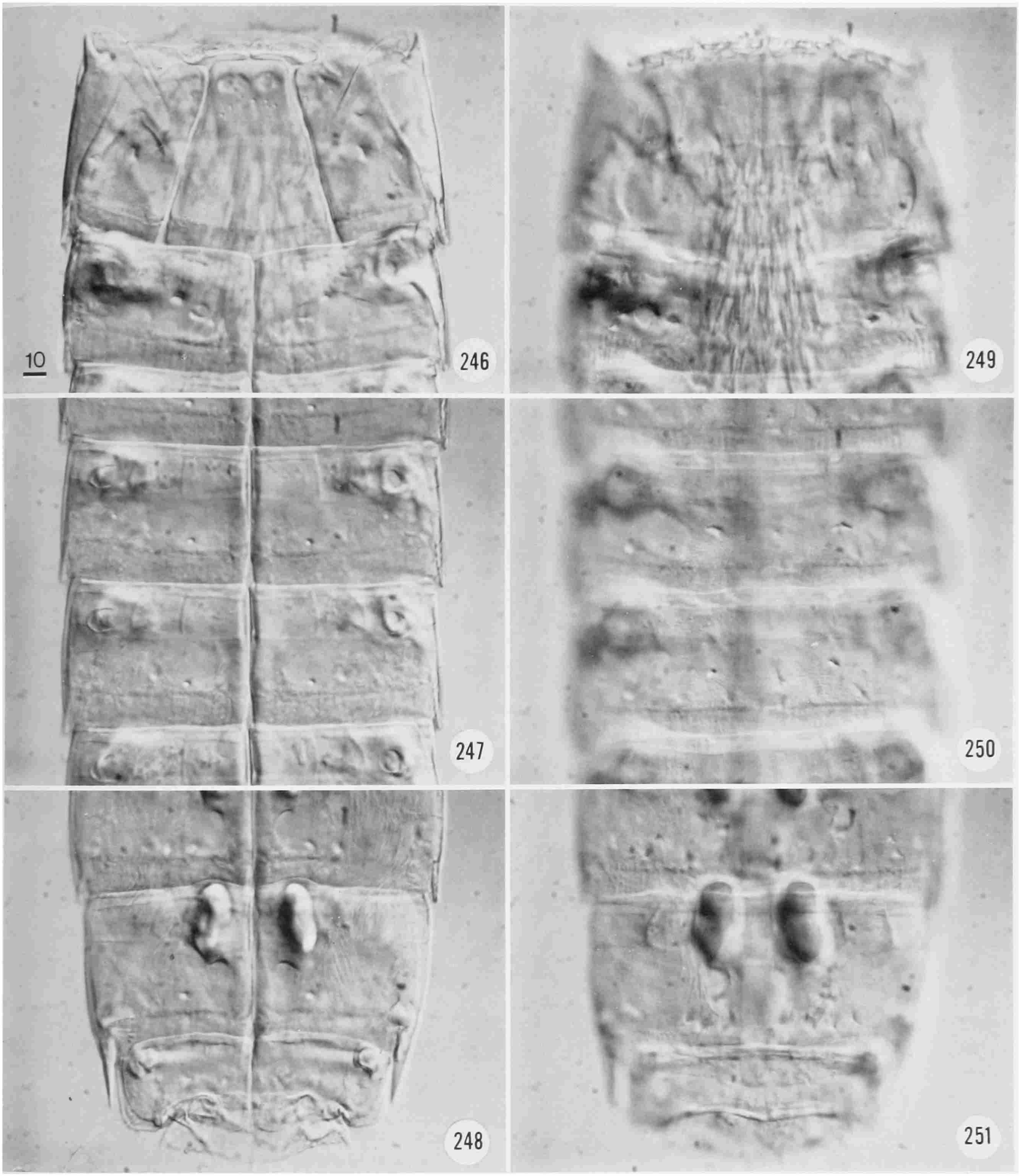
First trunk segment (segment 3) with moderate projections of the anterolateral tergal margins, anterior tergal margin with slightly roughened sculpture followed by series of 5 looped ridges on either side of midline (Figure 237). Anterior margin of episternal plates with 2 areas of sculptured, thin cuticle, lateral area slightly anterior to mesial area, 2 similar areas at margin of midsternal plate (Figures 236, 238, 252); midsternal plate trapezoidal, about 87 μm long, 68 μm basal width, 38 μm wide at apex.

Sternal plates of segment 4 of males with short, 25–30 μm, adhesive tubes (Figure 238); females lack adhesive tubes, and some lack dorsolateral setae on this segment (Figure 243). Two parallel ridges of fringe (Figures 238, 254) present, extending below adhesive tubes from lateral margins to midventral line. Segments 5–10 similar except for characters already noted. Segment 11 with distinctly projecting lateral margins (Figures 248, 257), margin fringed (Figure 256) but only visible through use of scanning electron microscope.

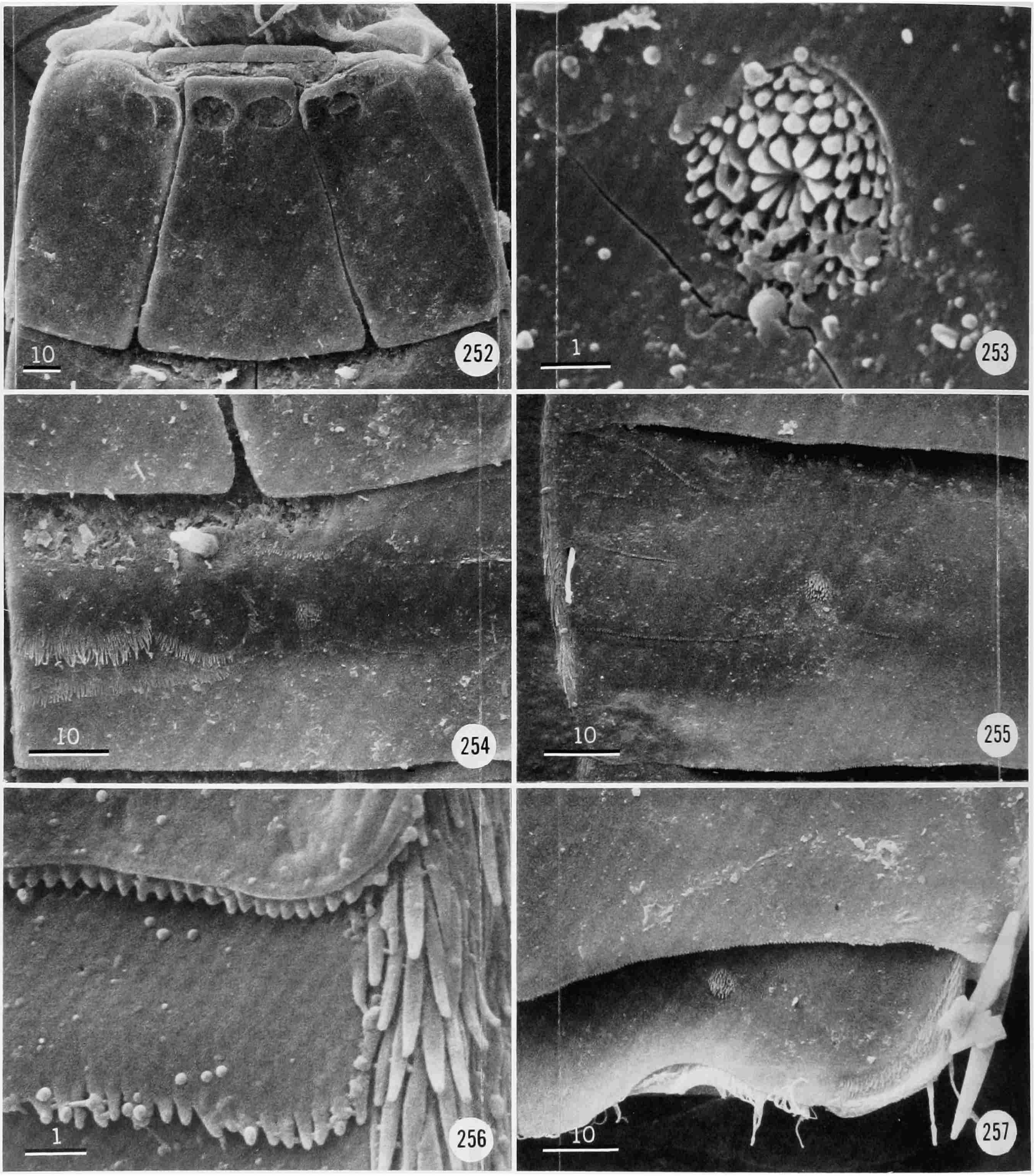




FIGURES 236–245.—*Kinorhynchus distentus,* new species: 236, neck and trunk segments, ventral view, holotypic male (USNM 70018); 237, same, dorsal view; 238, same, segments 2–4, lateral half, ventral view; 239, same, dorsal view; 240, same, segments 12, 13, lateral half, ventral view; 241, same, dorsal view; 242, segments 2–4, lateral half, ventral view, allotypic female (USNM 70019); 243, same, dorsal view; 244, same, segments 12, 13, lateral half, ventral view; 245, same, dorsal view.



FIGURES 246–251.—*Kinorhynchus distentus,* new species: 246, segments 3, 4, ventral view, holotypic male (USNM 70018); 247, same, segments 7, 8, ventral view; 248, same, segments 11–13, ventral view; 249, same, segments 3, 4, dorsal view; 250, same, segments 7, 8, dorsal view; 251, same, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 246.)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252
1
253
10
254
10
255
1
256
10
257

TABLE 18.—Measurements (μm) and indices (%) for *Kinorhynchus distentus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	1	614	0.0	0.0	0.0	0.0
	♀	3	540–665	606.3	62.9	36.3	10.4
	♂♀	4	540–665	608.3	51.5	25.7	8.5
SW	♂	1	112	0.0	0.0	0.0	0.0
	♀	3	112–120	114.7	4.6	2.7	4.0
	♂♀	4	112–120	114.0	4.0	2.0	3.5
SW/TL	♂	1	18.2	0.0	0.0	0.0	0.0
	♀	3	18.0–20.7	19.0	1.5	0.9	7.8
	♂♀	4	18.0–20.7	18.8	1.3	0.6	6.8
MSW-6	♂	1	152	0.0	0.0	0.0	0.0
	♀	3	160–168	164.0	4.0	2.3	2.4
	♂♀	4	152–168	161.0	6.8	3.4	4.2
MSW/TL	♂	1	24.7	0.0	0.0	0.0	0.0
	♀	3	25.3–29.6	27.2	2.2	1.3	8.0
	♂♀	4	24.7–29.6	26.6	2.2	1.1	8.2

Segment 12 short, one-half the length of the preceding segment, expanded and distended laterally forming rounded margins. Midventral area of sternal plates projects posteriorly. Terminal tergal plate with distinct, thin projection of lateral margin (Figures 240, 244, 257); sternal plates with 2, possibly 3, pairs of penile spines near anterolateral margins in males, females with single gonopore.

Males differ from females by presence of 2 (or 3) pairs of penile spines at the anterolateral margins of terminal sternal plates, presence of adhesive tubes on sternal plates of segment 4, and some minor variation in dorsolateral setae presence or position.

Only one male and three females were available for type material (one specimen used for SEM study); morphometric data (Table 18) may not be meaningful.

FIGURES 252–257.—*Kinorhynchus distentus*, new species: 252, segments 2, 3, ventral view, male; 253, ventral sensory spot (enlarged from Figure 254), segment 4, left sternal plate, male; 254, segment 4, ventral view, left sternal plate, male; 255, segment 7, ventral view, right sternal plate, male; 256, segment 7, ventral view, portion of left sternal plates, male; 257, segments 11, 12, 13, ventral view, left sternal plates, male. (SEM photographs, each to scale (in μm) indicated.)

HOLOTYPE.—Adult male, TL 614 μm, (Figures 236–241, 246–251), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70018.

ALLOTYPE.—Adult female, TL 665 μm (Figures 242–245), other data as for holotype, USNM 70019.

PARATYPES.—Two females, TL 540–614 μm, other data as for holotype, USNM 70020.

DISCUSSION.—*Kinorhynchus distentus* resembles *K. deirophorus* in the character of its thin sculptured areas on the anterior margin of the episternal and midsternal plates and *K. apotomus* in that both have a similar series of parallel cuticular ridges which are especially distinct near the lateral margins of the anterior sternal plates. Furthermore, *K. distentus* shares the otherwise unique short penultinate segment character previously described for *K. deirophorus*; both of these latter species have marginal sculpturing on the tergal plate of the first trunk segment. This sculpturing is different in the two species but occurs in the same two areas and suggests a kinship. This species has very few characters which can be meaningfully compared with other species in the same genus.

ETYMOLOGY.—The name of this species is from the Greek *distentus* (swell out, distended), which reflects the character of the penultimate trunk segment.

Kinorhynchus erismatus, new species

FIGURES 258–273

DIAGNOSIS.—Trunk slightly tapered anteriorly, moderately so with rounded margin posteriorly; tergal plate of first trunk segment with minute projections of anterolateral margins, slightly denticulate at anterior margin; area of thin, sculptured cuticle across anterior margin of episternal plates, 2 such areas at anterior margin of midsternal plate; buttress-like reinforcement between lateral pachycycli of sternal plates 3–11; 1 to 3 parallel cuticular ridges along anterior half of sternal plates 4–11; 12th segment without lateral setae; terminal tergal plate with lateral bulbous projections.

DESCRIPTION.—Adults (Figures 258–273), trunk length 614–770 μm, trunk slightly tapered anteriorly, moderately so with rounded margin posteriorly; MSW-7 168–220 μm, 22.8–30.9 percent of trunk length; SW 140–180 μm, 18.7–27.4 percent of trunk length. Second segment with 4 dorsal placids with slightly dentate margins and 2 even margined ventral placids (Figures 260, 261, 264, 265).

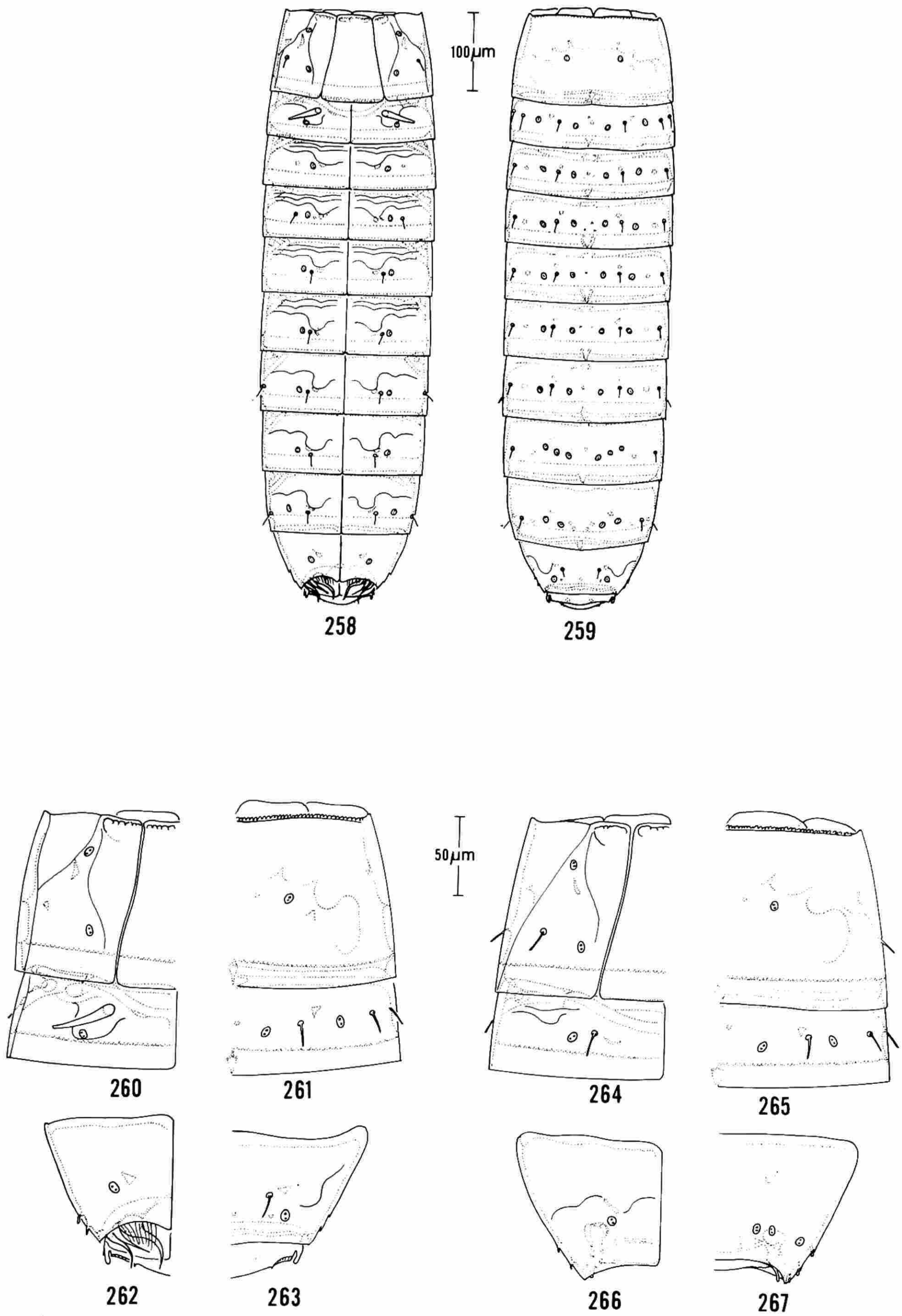
Trunk segments (Figures 258, 259) without middorsal marginal projections; slight evidence of subcuticular spinose structure on trunk segments 4–11. Setae, 20–22 μm long, situated subdorsally on segments 4–9, 12, dorsolaterally on segments 4–11, at extreme lateral margins of segments 3, 4 (but not always visible), laterally on episternal plates and sternal plates of segments 9 and 11, ventrally on sternal plates 6–11; setae lateral to ventral sensory spot on segment 6, mesial on segments 7–11; 1 to 3 parallel cuticular ridges along anterior half of sternal plates 4–11. Subdorsal sensory spots on segments 3–11; dorsolateral sensory spots on segments 4–12 with extra, more lateral, sensory spot on segment 10 (Figure 259); 2 additional sensory spots on the 12th tergal plate of female (Figure 267), 2 ventral sensory spots on episternal plates, 1 anterior, 1 posterior (Figure 264), single lateral sensory spot on each sternal plate of segments 4–12. Large muscle scars dorsolateral on tergal plate of first trunk segment, more visible on episternal plates; small, longitudinal cuticular scar posterior to anteriormost sensory spots of episternal plates; small, oval to triangular cuticular scars usually anteriorly adjacent to dorsolateral setae of tergal plates 4–12; small, oval cuticular scars posteriorly adjacent to cuticular ridge on sternal plates 3–11, slightly larger, slightly crescent-shaped cuticular scar anterior to ventral sensory spots of penultimate sternal plates. Pachycycli moderately developed, midventral thickenings absent. Buttress-like reinforcement between lateral margin and pachycycli of sternal plates 3–11.

First trunk segment (segment 3) with minute projections of the anterolateral tergal margins, anterior tergal margin slightly denticulate. Muscle scars as illustrated (Figure 261). Area of thin sculptured cuticle across anterior margins of episternal plates, 2 such areas at anterior margin of midsternal plate; midsternal plate trapezoidal, lateral margins slightly curved inward, length about 104 μm, basal width 80 μm, width at apex, 48 μm.

Sternal plates of segment 4 of males with adhesive tubes, about 43 μm long (Figure 260); females lack adhesive tubes but have setae in same area (Figure 264). Accessory pachycycli complex (Figure 260); cuticular ridge looping posteriorly around ventral sensory spot of each sternal plate; with exception of sternal plates of segment 4, segments 4–11 are similar except for details already noted.

Segment 12 tapering sharply, sternal margins bowed (Figure 262) occasionally obscuring terminal segment (Figure 266). Lateral setae lacking, replaced by 2 minute protuberances (possibly secretions) on either side of segment (Figure 262, 266).

Terminal segment with bulbous projection at lateroterminal margin of tergal plate. Sternal plates less rounded, with 3 pairs of penile spines at anterolateral margins in males (Figures 262, 270), single gonopore in females.



FIGURES 258–267.—*Kinorhynchus erismatus,* new species: 258, neck and trunk segments, ventral view; holotypic male (USNM 70021); 259, same, dorsal view; 260, same, segments 2–4, lateral half, ventral view; 261, same, dorsal view; 262, same, segments 12, 13, lateral half, ventral view; 263, same, dorsal view; 264, segments 2–4, lateral half, ventral view, allotypic female (USNM 70022); 265, same, dorsal view; 266, same, segments 12, 13, lateral half, ventral view; 267, same, dorsal view.

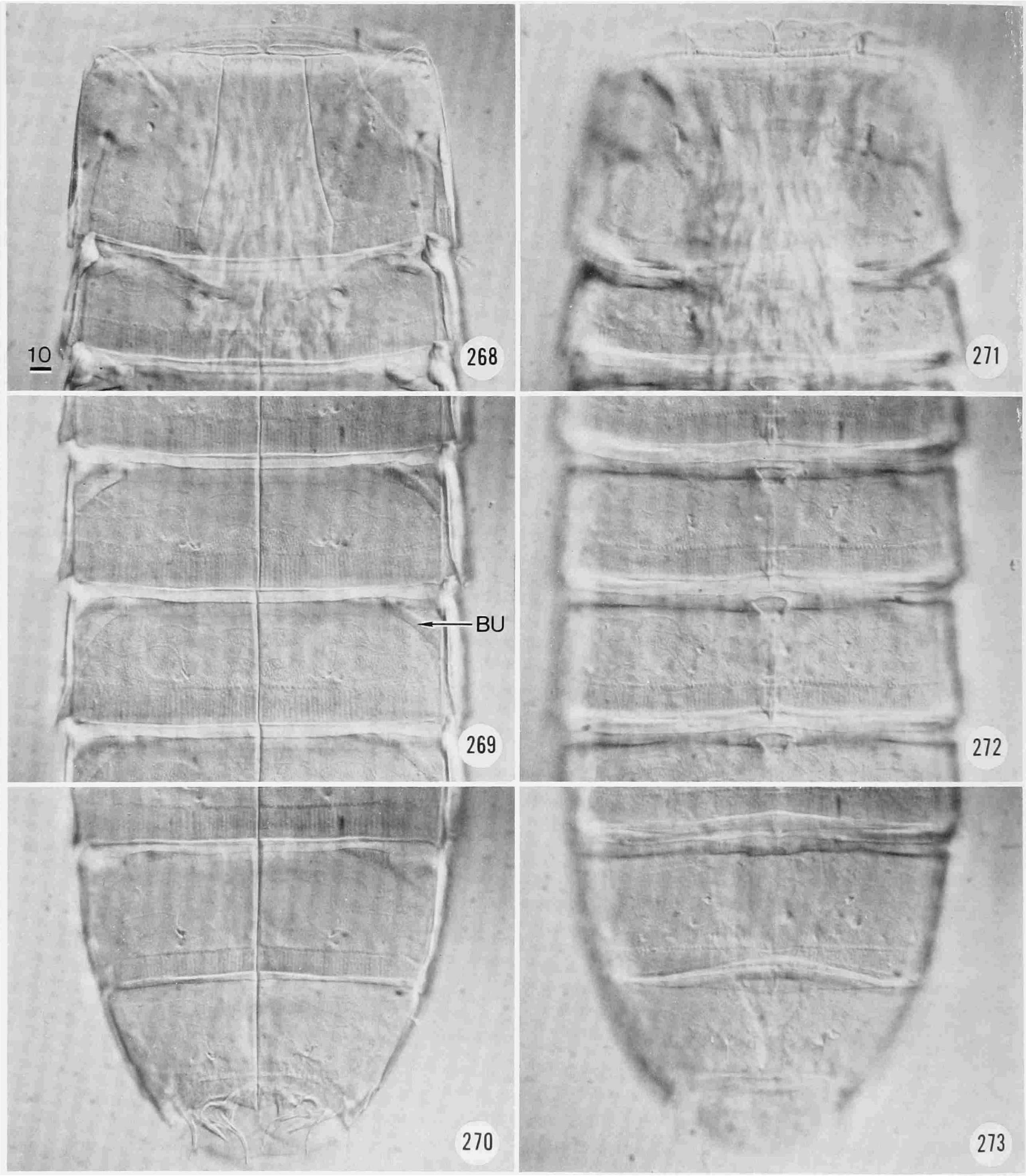

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TABLE 19.—Measurements (μm) and indices (%) for *Kinorhynchus erismatus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	25	624–770	718.8	37.9	7.6	5.3
	♀	19	614–760	698.6	40.6	9.3	5.8
	♂♀	44	614–770	710.4	39.8	6.0	5.6
SW	♂	25	140–172	159.4	6.7	1.3	4.2
	♀	19	164–180	170.3	6.3	1.5	3.7
	♂♀	44	140–180	164.1	8.5	1.3	5.2
SW/TL	♂	25	18.7–26.2	22.2	1.6	0.3	7.1
	♀	19	22.0–27.4	24.5	1.7	0.4	6.8
	♂♀	44	18.7–27.4	23.2	2.0	0.3	8.4
MSW-7	♂	25	168–220	190.0	11.0	2.2	5.8
	♀	19	172–204	195.3	7.2	1.7	3.7
	♂♀	44	168–220	192.1	9.8	1.5	5.1
MSW/TL	♂	25	22.8–30.2	26.4	1.7	0.3	6.5
	♀	19	23.6–30.9	28.0	1.7	0.4	6.1
	♂♀	44	22.8–30.9	27.1	1.9	0.3	6.9

Males differ from females by presence of 3 pairs of penile spines at anterolateral margins of terminal sternal plates, single sensory spot on the tergal plate of segment 12, presence of adhesive tubes on sternal plates of segment 4, and slightly narrower sternal width (Table 19).

Morphometric data for adults of *Kinorhynchus erismatus,* new species, are shown in Table 19.

HOLOTYPE.—Adult male, TL 749 μm (Figures 258-263, 268-273), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70021.

ALLOTYPE.—Adult female TL 728 μm (Figures 244-267), other data as for holotype, USNM 70022.

PARATYPES.—Eleven males and 8 females, TL 655–770 μm, Twin Cays, sta RH 443, other data as for holotype, USNM 70024; 10 males and 10 females, TL 614–749 μm, Twin Cays, sta RH 444, other data as fo: holotype, USNM 70025; 3 males, TL 697–730 μm, Twin Cays, sta RH 442, other data as for holotype, USNM 70023.,

FIGURES 268–273.—*Kinorhynchus erismatus,* new species: 268, segments 2–4, ventral view; 269, segments 7, 8, ventral view; 270, segments 11–13, ventral view; 271, segments 2–4, dorsal view; 272, segments 7, 8, dorsal view; 273, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 268; BU = buttress.)

DISCUSSION.—*Kinorhynchus erisimatus* most closely resembles *K. belizensis* on the basis of the buttress-like reinforcement of the pachycycli, a character unique to these two species. Another similarity exists in that, likewise, these two species uniquely lack lateral setae on the penultimate segment. Both have a similar trunk shape, both have a similar sternal cuticular sculpturing, and both exhibit similar muscle scars on the tergal plate of the first trunk segment. There are differences in accessory pachycycli structure between the two species, differences in the pachycycli of the 11th segment, as well as differences in setae and sensory spot arrangement, but these latter characters do not diminish the suggested close kinship.

Although it is not similar in the same sense as *K. belizensis, K. langi* partially resembles *K. erismatus* in general shape and accessory pachycycli structure. Like most of the new species of this genus being described in this paper, there are many unique taxonomic characters and only a few general similarities between the Belizian fauna and that of the remaining world.

Etymology.—This species name is from the Greek *erismatus* (buttressed), which reflects the structural reinforcement of the sternal pachycycli.

Kinorhynchus stenopygus, new species

Figures 274–301

Diagnosis.—Trunk slightly tapered anteriorly, strongly tapered posteriorly with narrow penultimate and slightly flaring terminal segments; well-developed middorsal spinose projections; sternal plates with prominent semicircular cuticular ridge; projections of the anterolateral tergal margins of the first trunk segment distinctly rounded; anterior tergal margin with 3 minute projections.

Description.—Adults (Figures 274–301), trunk length 509–603 μm, trunk slightly tapered anteriorly, strongly tapered posteriorly; MSW-8 132–152 μm, 24.5–28.8 percent of trunk length; SW 96–112 μm, 16.6–22.0 percent of trunk length. Second segment with 2 even-margined ventral placids, 4 dorsal placids suspected but not confirmed (Figures 276–280).

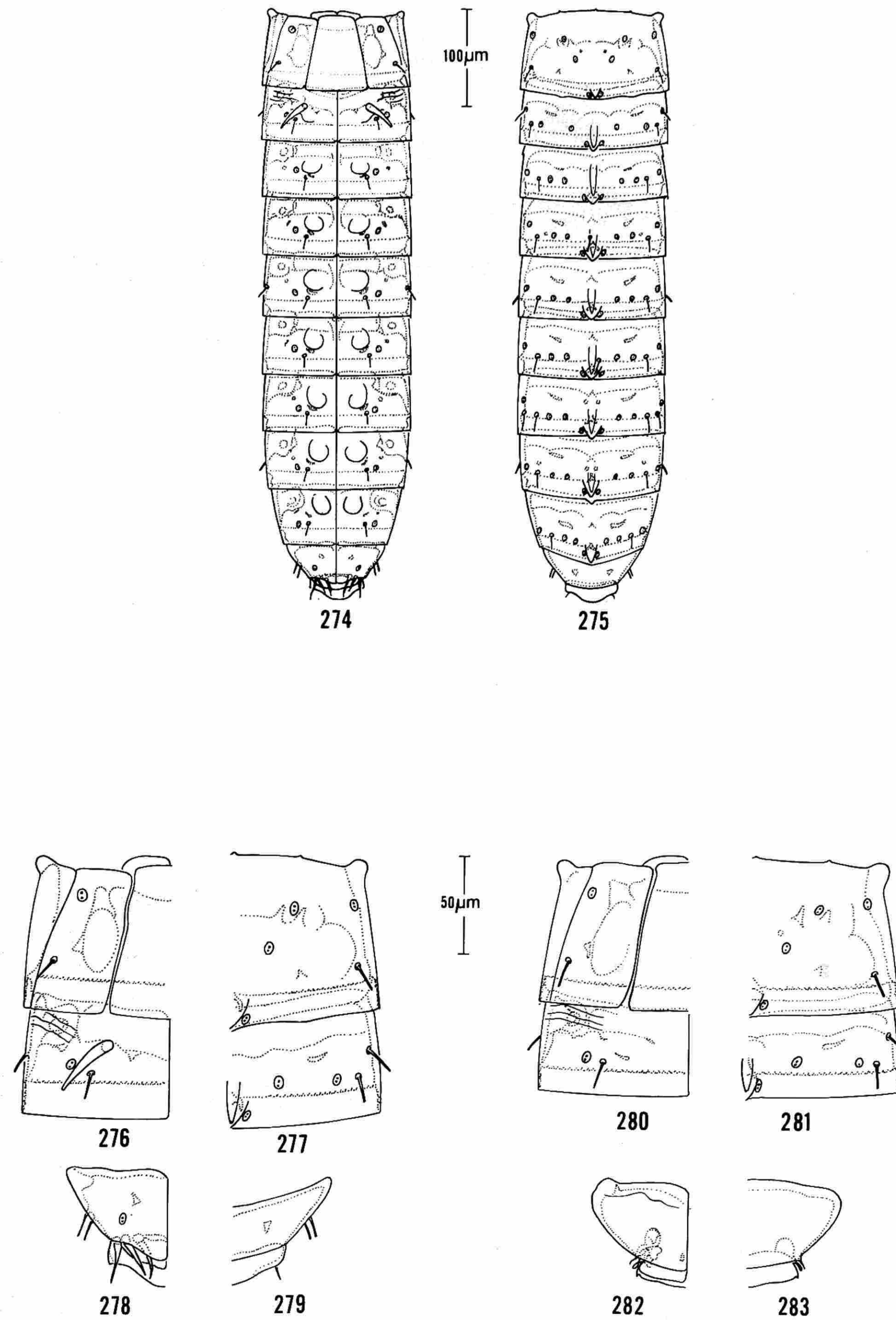
Trunk segments (Figures 274, 275) with spinose middorsal projections on posterior margins of segments 3–11. Setae, 19–22 μm long, situated middorsally (or slightly off center) on segments 6 and 8 (occasionally on other segments), occasionally subdorsally on segment 3 (Figure 298), dorsolaterally on segments 3, 2 on 4, 5–11, lateral on episternal plate of segment 3, lateral on segments 7, 10, and 2 on segment 12, ventrally, centered on sternal plates of segments 4–11. Several small cuticular ridges present near anterolateral margins of sternal plates on segment 4; prominent semicircular cuticular ridge centered on sternal plates of segments 3–11 (Figures 274, 292). Perispinal sensory spots on either side of middorsal marginal projections of segments 3–11 (Figures 274, 297, 299); 2 subdorsal sensory spots on segments 3–11, dorsolateral sensory spots near margin of segments 3, 5–11; ventral sensory spots anterolateral on episternal plates of segment 3 and near center of each sternal plate of segments 4–12, usually laterally adjacent to ventral setae but occasionally reversed, especially on segments 5 and 7. Prominent oval muscle scars on episternal plates (Figures 276, 280) and lateral on tergal plate of segment 3 (Figures 277, 281); elongate transverse cuticular scars dorsolateral on segments 4–11, same scars more triangular-shaped on segment 12; oval to crescent-shaped cuticular scars posterior to semicircular cuticular ridges of sternal plates 4–11, in same relative position (ridges absent) on segment 12. Pachycycli well developed, narrow midventral thickenings on segment 11.

Surface of trunk segments with prominent scales on tergal plates (Figure 301) and lateral surfaces of most sternal plates, scales becoming more hairlike mesially and on posterior segments (Figure 295) but clearly visible only when using a scanning electron microscope. First trunk segment (segment 3) with rounded projections of the anterolateral tergal margins, tergal margin even except for middorsal and lateral slightly protruding points (Figures 277, 281, 298). Muscle scars, setae, and sensory spots as previously noted. No areas of thin cuticle present on episternal or midsternal plates; midsternal plate trapezoidal, lateral margins straight, length about 78 μm, basal width 67 μm, 40 μm at apex, slight transverse line present one-fourth distance posterior.

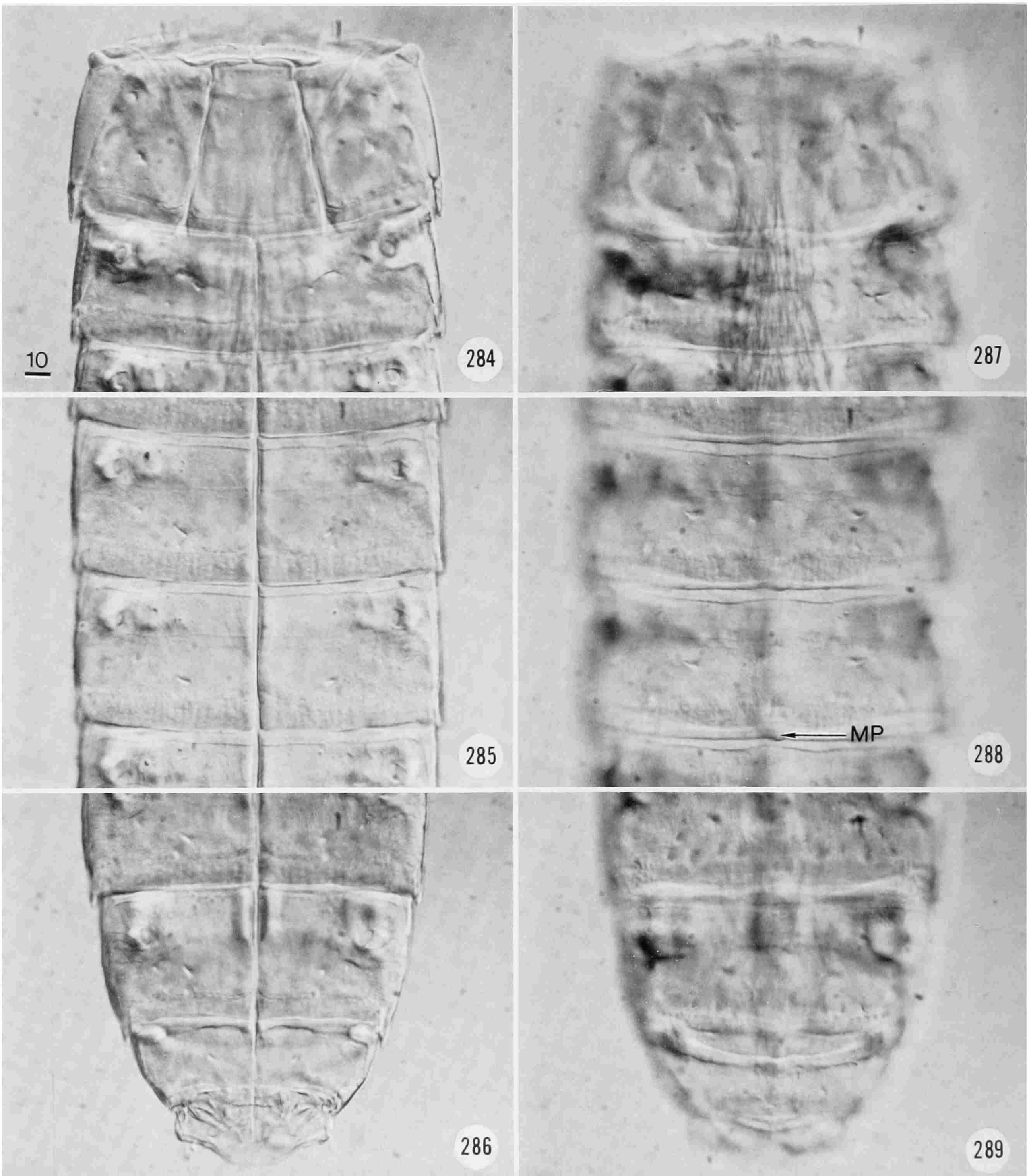
Sternal plates of segment 4 of males with adhesive tubes 37 μm long (Figures 276, 291, 292); females lack adhesive tubes; several small cuticular ridges present at anterolateral margins, with prominent semicircular cuticular ridge posteriorly adjacent to adhesive tubes (Figures 291, 292).

Segments 5–11 similar with exceptions as previously noted. Segment 12 strongly tapered, with rounded posterior margin. Lateral setae prominent in male, modified in female (Figures 278, 282, 294, 295).

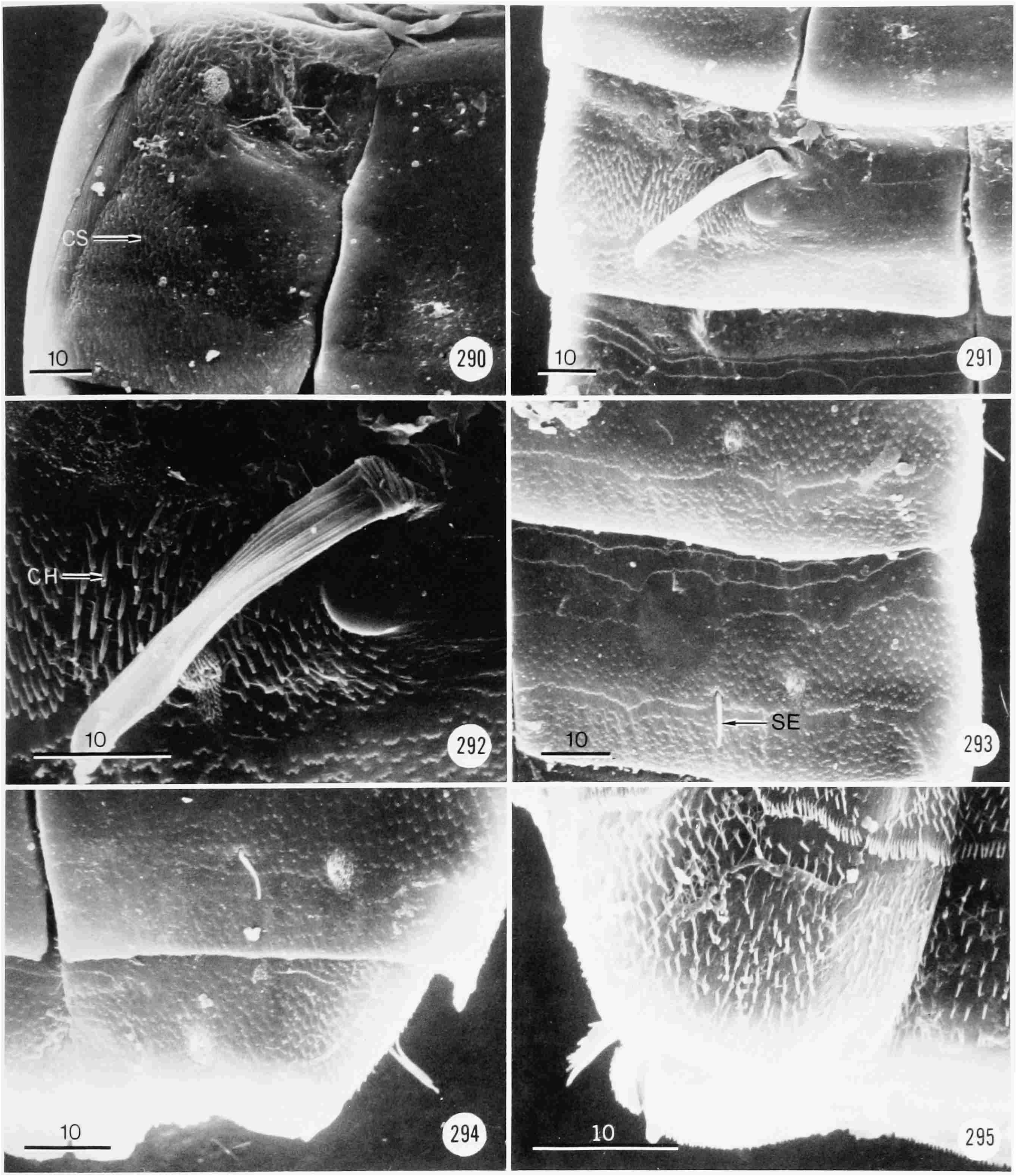
Terminal segment of both sexes small; female with lateral projection of tergal plate (Figures 282, 295), none in male (Figures 278, 294). Sternal plates small, often hidden; tergal plate prominent in most cases, flared with margin slightly ex-



FIGURES 274–283.—*Kinorhynchus stenopygus,* new species: 274, neck and trunk segments, ventral view, holotypic male (USNM 70026); 275, same, dorsal view; 276, same, segments 2–4, lateral half, ventral view; 277, same, dorsal view; 278, same, segments 12, 13, lateral half, ventral view; 279, same, dorsal view; 280, segments 2–4, lateral half, ventral view, allotypic female (USNM 70027); 281, same, dorsal view; 282, same, segments 12, 13, lateral half, ventral view; 283, same, dorsal view.



FIGURES 284–289.—*Kinorhynchus stenopygus,* new species: 284, ventral view, segments 2–4; 285, ventral view, segments 7, 8; 286, ventral view, segments 11–13; 287, dorsal view, segments 2–4; 288, dorsal view, segments 7, 8; 289, dorsal view, segments 11–13. (Interference contrast photographs all with same scale (in μm) as shown in Figure 284; MP = middorsal process.)



FIGURES 290–295.—*Kinorhynchus stenopygus,* new species: 290, episternal plate, segment 3, male; 291, adhesive tube, segment 4, male; 292, enlargement of Figure 291; 293, segments 7, 8, lateral half, ventral view, male; 294, segments 11, 12, lateral half, ventral view, male; 295, segments 12, 13, lateral half, ventral view, female. (SEM photographs, each to scale (in μm) indicated; CS = cuticular scale, CH = cuticular hair, SE = seta.)

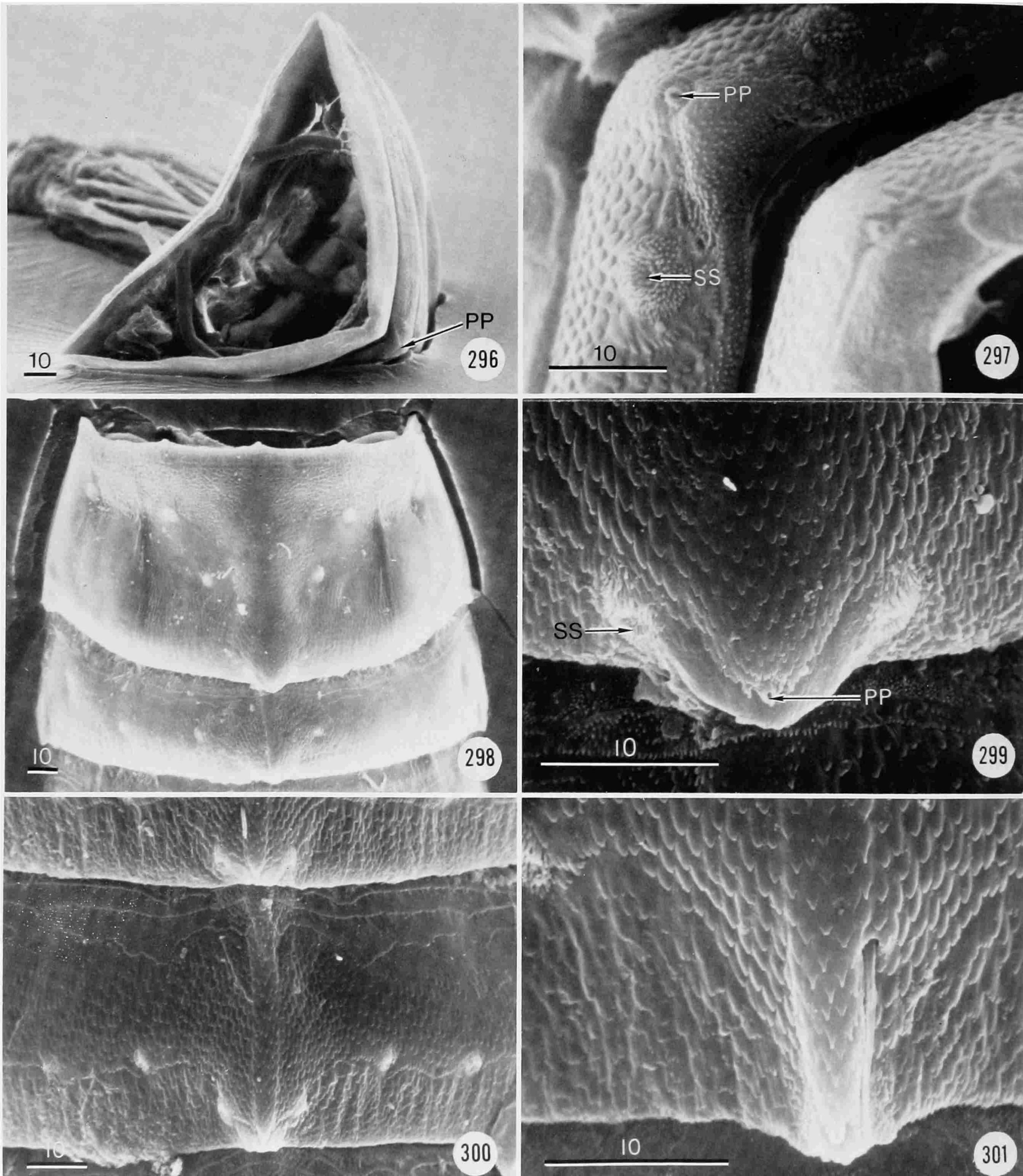

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TABLE 20.—Measurements (μm) and indices (%) for *Kinorhynchus stenopygus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	4	520–603	556.3	38.5	19.2	6.9
	♀	9	509–592	543.9	32.8	10.9	6.0
	♂♀	13	509–603	545.7	34.2	9.9	6.3
SW	♂	4	100–104	103.0	2.0	1.0	1.9
	♀	9	96–112	107.1	6.9	2.3	6.4
	♂♀	13	96–112	106.0	6.3	1.8	5.9
SW/TL	♂	4	16.6–20.0	18.6	1.5	0.8	8.3
	♀	9	17.8–22.0	19.7	1.8	0.6	9.0
	♂♀	13	16.6–22.0	19.5	1.8	0.5	9.1
MSW-8	♂	4	132–152	145.0	8.9	4.4	6.1
	♀	9	140–148	145.3	2.8	0.9	2.0
	♂♀	13	132–152	144.7	4.8	1.4	3.3
MSW/TL	♂	4	24.5–27.9	26.1	1.5	0.7	5.7
	♀	9	24.7–28.8	26.6	1.6	0.5	5.9
	♂♀	13	24.5–28.8	26.4	1.6	0.5	5.9

tended posteriorly at midline (Figure 278). Three pairs of penile spines at anterolateral margins of sternal plates in males (Figure 278), simple gonopores present in females.

Males differ from females by the presence of 3 pairs of penile spines at anterolateral margins of terminal sternal plates, presence of 2 unmodified lateral setae on segment 12, presence of adhesive tubes on sternal plates of segment 4, even lateral margin on terminal tergal plate, and slightly narower trunk segments.

Morphometric data for adults of *Kinorhynchus stenopygus,* new species, are shown in Table 20.

HOLOTYPE.—Adult male TL 603 μm (Figures 274-279, 284-289), Twin Cays, sta RH 444, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70026.

ALLOTYPE.—Adult female, TL 572 μm (Figures 280–283), other data as for holotype, USNM 70027.

PARATYPES.—Two adult males and 8 females, TL 509–582 μm, other data as for holotype, USNM 70028; 1 male, TL 572 μm, Twin Cays, sta RH 442, other data as for holotype, USNM 70029.

REMARKS.—Like *Kinorhynchus deirophorus* and *K. distentus, K. stenopygus* has unusually small penultimate and terminal segments. It differs from the former two species by its prominent middorsal marginal projections which are distinctly spinose, not unlike those of *K. anomalus.* In fact, the terminal segment of this latter species, with its slightly flaring margin, is also similar to this same segment of *K. stenopygus.*

The cuticular ridges of the sternal plates of *K. stenopygus* are similar to those of several other new species described from this same locality. Especially notable are the semicircular ridges which resemble those of *K. belizensis* and *K. erismatus.* The lack of thin areas of cuticle at the anterior margins of the episternal and midsternal plates is thus far distinctive among the Belizian material, and the three small points positioned middorsally and laterally on the anterior margin of the tergal

FIGURES 296–301.—*Kinorhynchus stenopygus,* new species: 296, cross-sectional view of broken trunk, male; 297, posterior margins of segments 4, 5, enlarged from Figure 296; 298, segments 3, 4, dorsal view; 299, middorsal marginal process, segment 3; 300, segment 9, dorsal view; 301, middorsal marginal process, segment 10. (SEM photographs, each to scale (in μm) indicated; PP = process pore, SS = sensory spot.)

plate of the first trunk segment are unique to the genus *Kinorhynchus;* similar tergal margins have been described for *Pycnophyes ponticus, P. keilensis,* and *P. neapolitanus.*

ETYMOLOGY.—This species name is from the Greek *steno* (narrow) plus *pygos* (rump), which reflects the morphology of the terminal segments.

Kinorhynchus trisetosus, new species

FIGURES 302–335

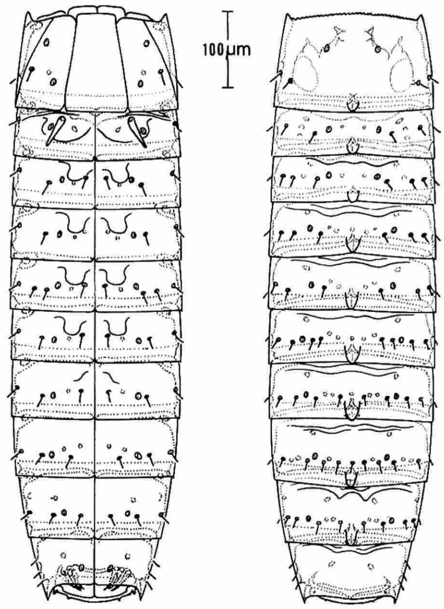
DIAGNOSIS.—Trunk slightly tapered anteriorly and posteriorly; anterolateral tergal projections pointed, similar projections situated lateroterminally at the tergal-sternal junction of the penultimate segment, extending beyond terminal segment; anterodorsal tergal margin denticulate; middorsal margin spinose processes on segments 3–11; 3 lateral setae on segment 12.

DESCRIPTION.—Adults (Figures 302–335) trunk length 676–832 μm; trunk slightly tapered anteriorly and posteriorly; MSW-8 204–236 μm, 26.8–32.5 percent of trunk length; SW 148–176 μm, 20.0–25.5 percent of trunk length. Second segment with 4 dorsal and 2 ventral even-margined placids (Figures 304, 319, 322).

Trunk segments (Figures 302, 303) with spinose middorsal marginal projections on segments 3–11. Setae, 20–22 μm long, situated middorsally on segment 10, perispinally on tergal plates of segments 9–11, subdorsally on segments 3–10, dorsolaterally on segments 3–11 with single seta lateral to each dorsolateral seta of segment 3; 1 seta between dorsolateral and subdorsal setae on segments 5–7, 9, 10, and 2 setae between the dorsolateral and subdorsal setae of segment 8; lateral setae on segments 4–11 with 3 lateral setae on segment 12 of males, sometimes not evident in females (Figure 332); single lateral setae on sternal plates of segments 5, 6, 8–11, 2 such setae on segment 7; mesial setae on segments 4, 6–11. Series of parallel cuticular ridges and cuticular ridge broadly looping posteriorly on sternal plates of segment 3; more narrow, smaller cuticular loops on sternal plates of segments 5–8 (Figures 302, 332, 333). Perispinal sensory spots on anterior 3–4 tergal plates (Figure 324); subdorsal sensory spots on segments 3–5 with 2 additional sensory spots on tergal plates of segment 3 (Figures 319, 321); dorsolateral sensory spots on segments 6–11; several smaller sensory spots (which are difficult to see without SEM) on segment 10 and more randomly on other tergal plates; 2 sensory spots, 1 anterior (Figures 330, 331) and 1 posterior (Figure 332), on episternal plates of segment 3; single sensory spot on each sternal plate of segments 4–10, 12 (Figures 330, 331) with 2 ventral sensory spots on sternal plates of segment 11 (Figure 334). Large oval muscle scars dorsolateral on first trunk segment (Figures 303, 305–309), more prominent on episternal plates; several triangular cuticular scars anteromesial to larger muscle scars, small oval cuticular scars subdorsal on segments 4–12 (Figure 303), small, round to oval scars on episternal plate of segment 3 and sternal plates of segments 3–12. Pachycycli well developed; no midventral thickenings observed. Cuticle with some elongate scales on tergal plates and lateral margins of sternal plates, forming hairlike processes at tergal-sternal junctions (Figure 323); cuticular surface over large oval muscle scars of tergal plate 3 with striations (Figure 322), short cuticular hairs appear to replace scaly cuticular surface on mesial portions of sternal plates, progressively more prominent on posterior segments.

First trunk segment (segment 3) with pointed anterolateral tergal projections (Figures 304, 309, 319, 322); anterodorsal margin denticulate (Figures 305, 309, 321). Muscle scars, setae, and sensory spots as previously noted; no areas of thin cuticle visible by light microscopy at anterior margins of episternal or midsternal plates although these areas are set apart by fine superficial sculpturing when viewed with SEM (Figure 330). Midsternal plate elongate-trapezoidal, lateral margins straight, 131 μm long, 86 μm basal width, 30 μm width at apex; apex slightly expanded at margin only.

Sternal plates of segment 4 of males with adhesive tubes 48 μm long (Figure 304); females lack adhesive tubes but have 2 setae, 1 on either



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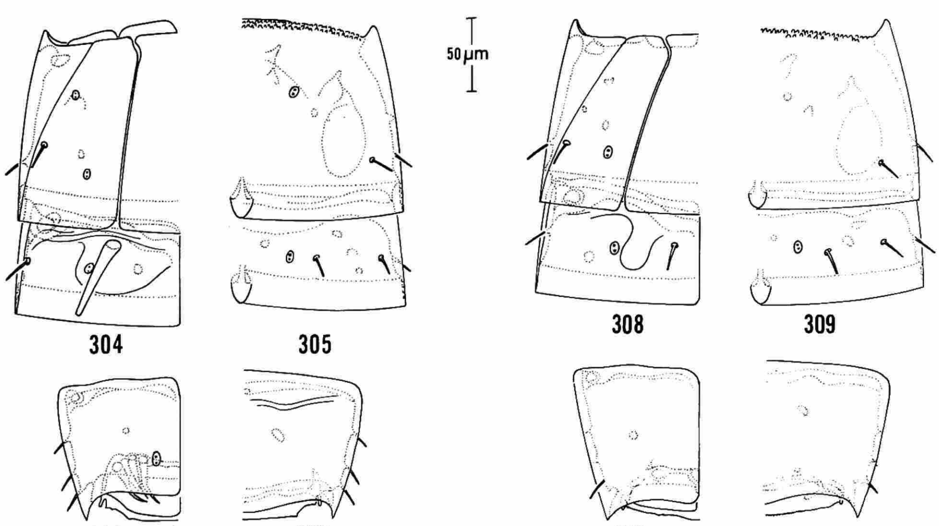

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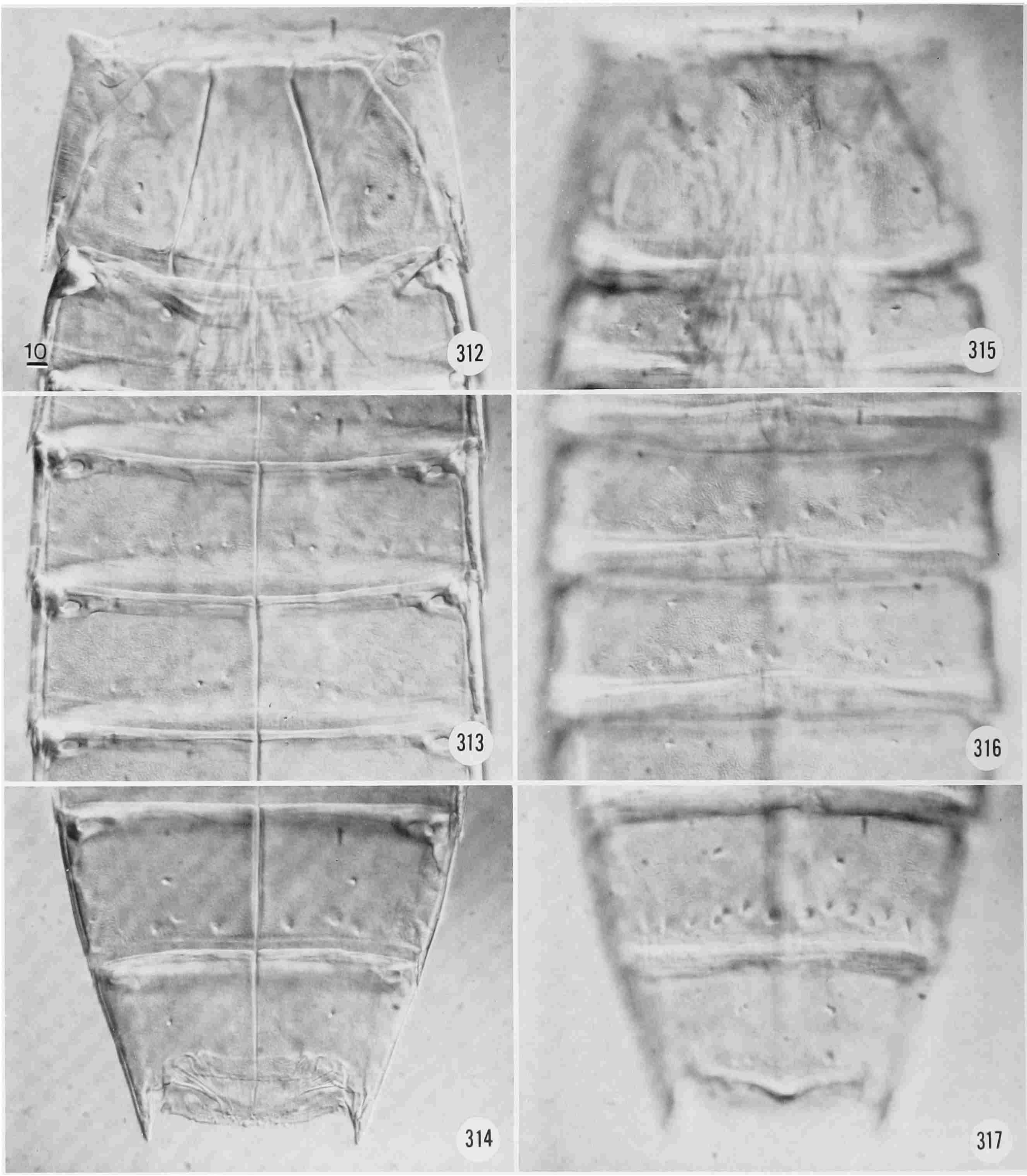
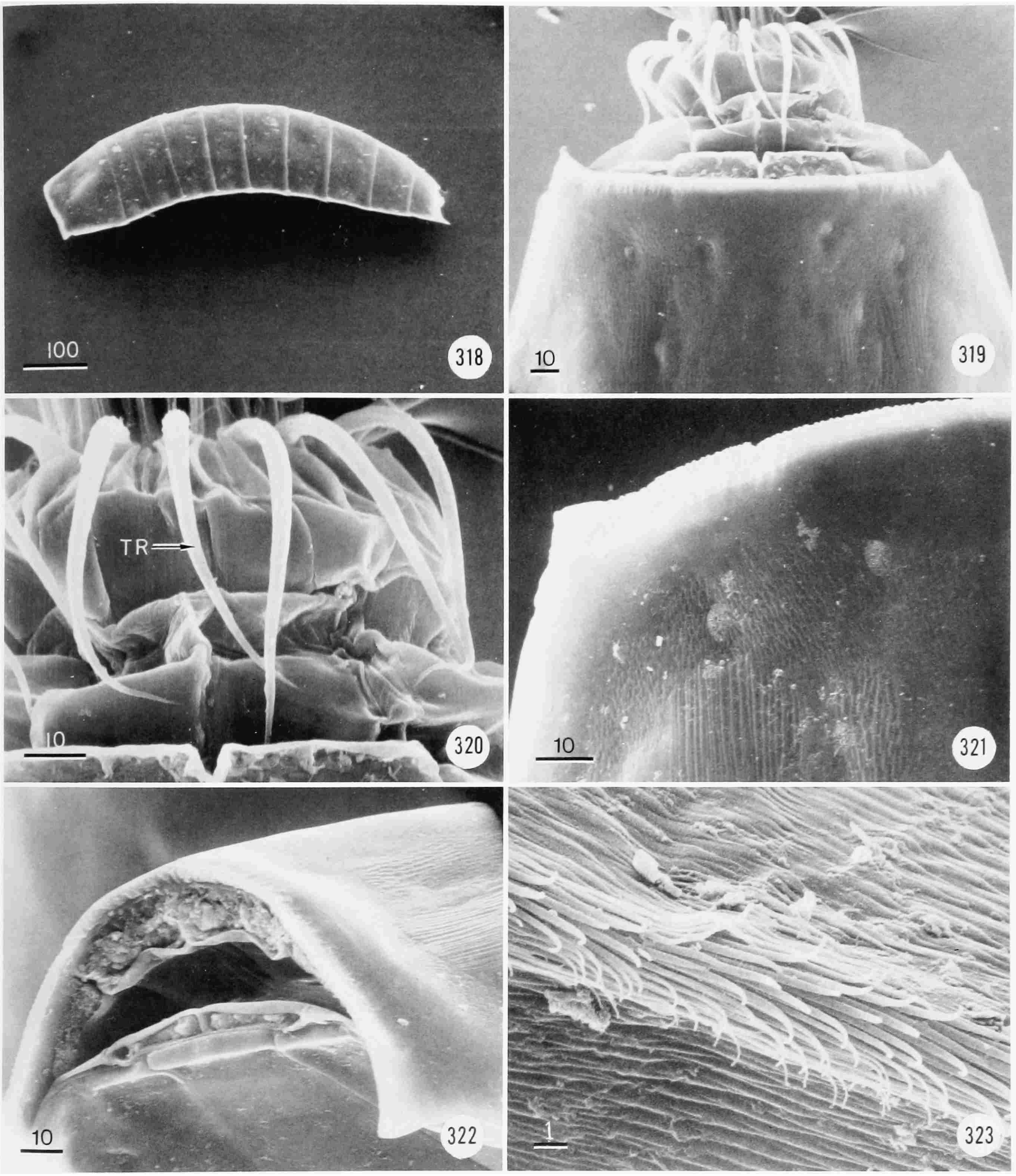
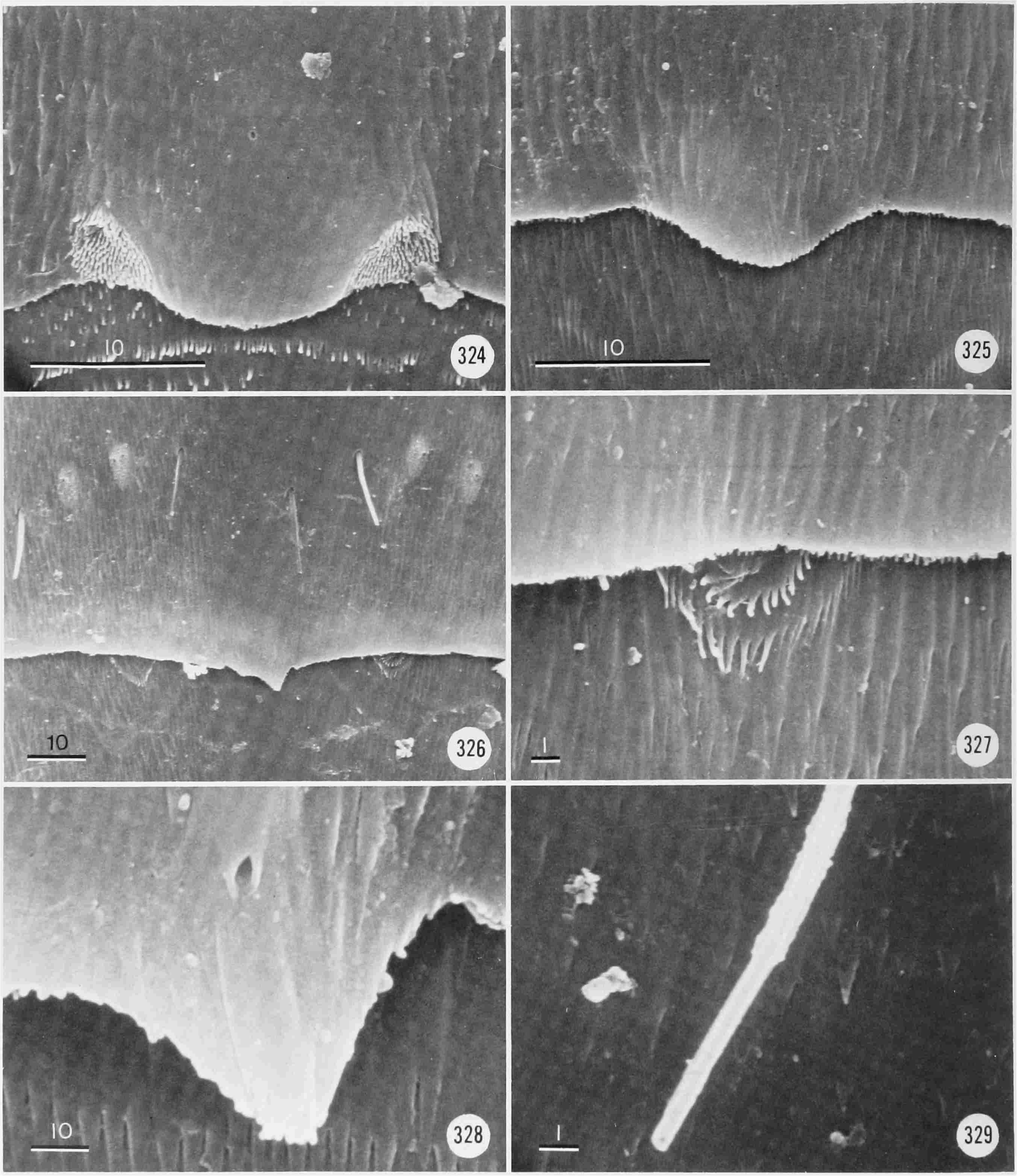
FIGURES 302–311.—*Kinorhynchus trisetosus,* new species: 302, neck and trunk segments, ventral view, holotypic male (USNM, 70030); 303, same, dorsal view; 304, same, segments 2–4, lateral half, ventral view; 305, same, dorsal view; 306, same, segments 12, 13, lateral half, ventral view; 307, same, dorsal view; 308, segments 2–4, lateral half, ventral view, allotypic female (USNM 70031); 309, same, dorsal view; 310, same, segments 12, 13, lateral half, ventral view; 311, same, dorsal view.



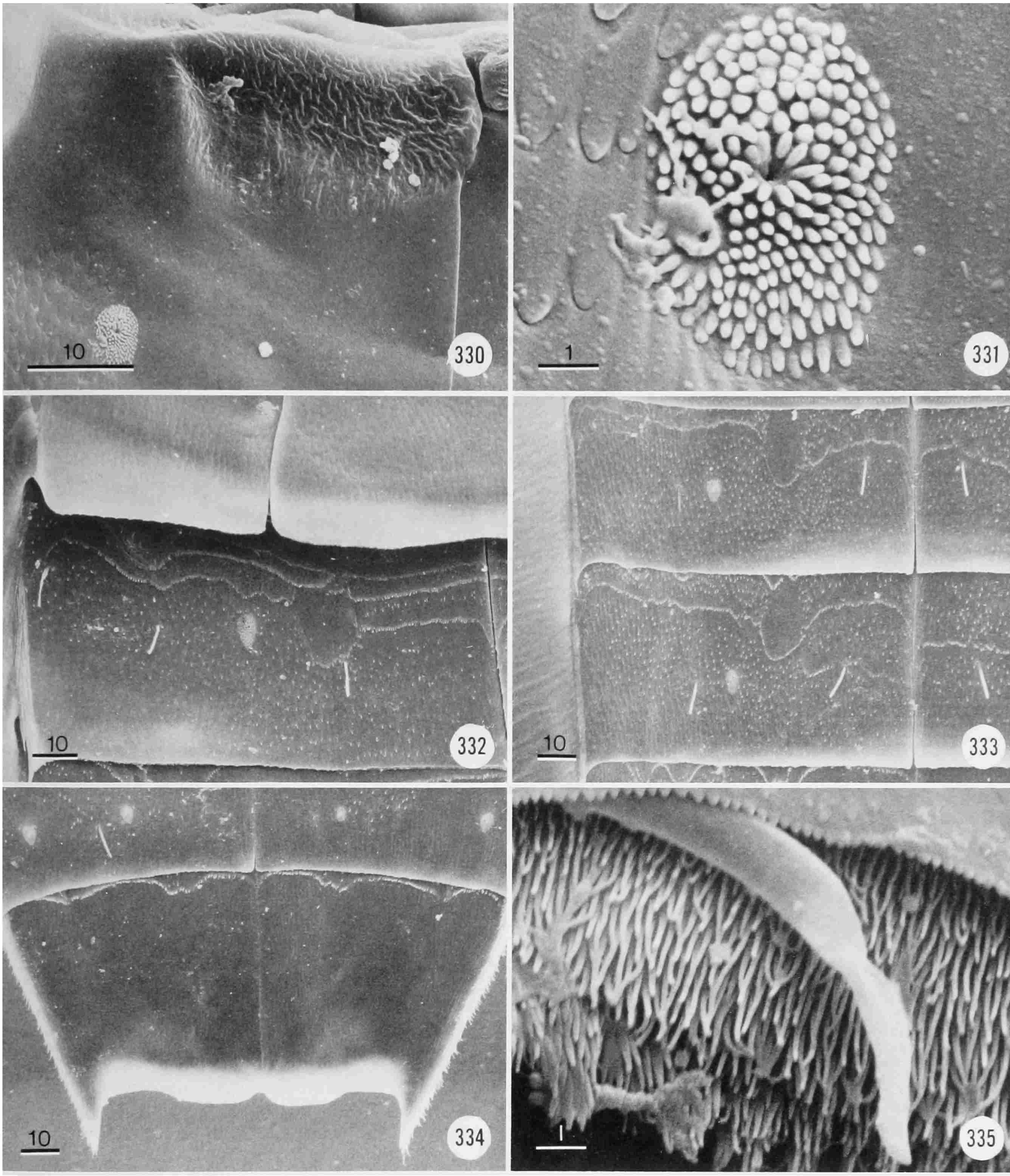
FIGURES 312–317.—*Kinorhynchus trisetosus*, new species: 312, segments 3, 4, ventral view; 313, segments 7, 8, ventral view; 314, segments 11–13, ventral view; 315, segments 3, 4, dorsal view; 316, segments 7, 8, dorsal view; 317, segments 11–13, dorsal view. (Interference contrast photographs all with same scale (in μm) as shown in Figure 312.)



FIGURES 318–323.—*Kinorhynchus trisetosus*, new species: 318, trunk segments, lateral view; 319, neck and first trunk segment, dorsal view; 320, neck with trichoscalids, dorsal view; 321, anterolateral surface of first trunk segment; 322, neck and first trunk segment showing closed position, anterior view; 323, tergal-sternal junction. (SEM photographs, each to scale (in μm) indicated; TR = trichoscalid.)



FIGURES 324–329.—*Kinorhynchus trisetosus,* new species: 324, segment 4, middorsal marginal protuberance; 325, same, segment 9; 326, same, segment 10; 327, portion of intersegmental area from Figure 326 (enlarged); 328, same, segment 10 (enlarged); 329, tip of hollow seta. (SEM photographs, each to scale (in μm) indicated.)



FIGURES 330-335.—*Kinorhynchus trisetosus,* new species: 330, segment 3, anterolateral view, episternal plate (female); 331, sensory spot, episternal plate (enlarged from Figure 330); 332, segment 4, sternal plate (female); 333, segments 7, 8, sternal plates, right half (female); 334, segment 12, sternal plates (female); 335, terminal margin with exposed penile spine. (SEM photographs, each to scale (in μm) indicated.)

TABLE 21.—Measurements (μm) and indices (%) for *Kinorhynchus trisetosus* adults (see "Methods" for character abbreviations)

Character		Number	Range	Mean	Standard deviation	Standard error	Coefficient of variability
TL	♂	22	697–801	757.8	33.3	7.1	4.4
	♀	13	676–832	760.9	39.1	10.8	5.1
	♂♀	35	676–832	758.9	35.0	5.9	4.6
SW	♂	22	148–168	161.3	4.8	1.0	3.0
	♀	13	156–176	167.1	6.8	1.9	4.1
	♂♀	35	148–176	163.4	6.2	1.1	3.8
SW/TL	♂	22	20.0–23.0	21.3	0.9	0.2	4.3
	♀	13	20.0–25.5	22.0	1.5	0.4	6.9
	♂♀	35	20.0–25.5	21.6	1.2	0.2	5.6
MSW-8	♂	22	204–236	216.7	9.4	2.0	4.3
	♀	13	212–236	221.4	5.9	1.6	2.6
	♂♀	35	204–236	218.5	8.5	1.4	3.9
MSW/TL	♂	22	26.8–30.3	28.6	1.3	0.3	4.6
	♀	13	27.7–32.5	29.1	1.3	0.4	4.3
	♂♀	35	26.8–32.5	28.8	1.3	0.2	4.6

side of each adhesive tube site (Figures 308, 330). Several cuticular ridges with posterior loops present on sternal plates. Segments 5–11 similar with exceptions as previously noted. Segment 12 tapered with slightly uneven posterior tergal and sternal margins (Figures 306, 311, 334); 3 lateral setae present in males, more variable in females but usually indicated by setal pores in cuticle. Lateroterminal margins projecting beyond margin of terminal segment.

Terminal tergal segment with minute bulbous protuberance at lateroterminal margin, otherwise with even margin. Sternal plates even, generally with margins paralleling that of terminal tergal plate (Figures 306, 310). Three pairs of penile spines at anterolateral margins of terminal sternal plates in males (Figures 306, 335); single gonopore in females (Figure 310).

Males differ from females by presence of 3 pairs of penile spines at anterolateral margins of terminal sternal plates, presence of adhesive tube on each sternal plate of segment 4, slightly narrower trunk, and some variation in sensory spots and setae.

Morphometric data for adults of *Kinorhynchus trisetosus* are shown in Table 21.

HOLOTYPE.—Adult male, TL 790 μm (Figures 302-307, 312-317), Twin Cays, sta RH 442, Belize (16°50.0′N, 88°06.0′W), 8 Apr 1977, col. R.P. Higgins, USNM 70030.

ALLOTYPE.—Adult female, TL 754 μm (Figures 308–311), other data as for holotype, USNM 70031.

PARATYPES.—Seventeen males and 9 females, TL 676–832 μm, other data as for holotype, USNM 70032; 4 males and 3 females, TL 749–801 μm, Twin Cays, sta RH 443, other data as for holotype, USNM 70033.

DISCUSSION.—*Kinorhynchus trisetosus* is the largest and most abundant of the kinorhynchs in the area of Carrie Bow Cay. On the basis of its size alone, it can easily be distinguished from other species. Because of the character of the extended-lateral margin of the penultimate segment which often exceeds the terminal margin of the last segment, *K. trisetosus* most closely resembles *K. mainensis*. Several other characters are similar, including the bulbous projection situated posterolaterally on the terminal tergal plate, the general shape and dimensions of the midsternal plate, the setae of the episternal plate, and the relatively large number of sensory spots.

The episternal and midsternal plates of *K. mainensis* have distinct areas of thin, sculptured cuticle readily apparent in all specimens when viewed by light microscopy; this is not the case in *K. trisetosus*. *Kinorhynchus mainensis* does not have a denticulate margin on the tergal plate of the first trunk segment nor does it have middorsal spinous marginal projections on the margins of most trunk segments as in *K. trisetosus*. Furthermore, those spinose projections are much smaller, less distinctive in *K. mainensis*. This latter species has lateral setae on segments 3, 4, 6, 8, 10 and two on 12 as opposed to 4–11 and three on 12 (occasionally absent or less apparent in females) in the new species. Altogether, the two species are distinct.

Kinorhynchus giganteus, heretofore the largest of the genus *Kinorhynchus*, is easily distinguished from *K. trisetosus* on the basis of the crescent-shaped cuticular scars on the sternal plates of *K. giganteus* and its bi- or trifid lateroterminal projections and lateral setation pattern differences.

ETYMOLOGY.—The name of this species is from the Latin *tres* (three) plus *seta* (bristle), reflecting the three lateral setae condition of the penultimate segment.

Discussion of *Kinorhynchus*

As a kind of progress report on his preparation of *Monographie der Echinodera*, Carl Zelinka, in 1895, demonstrated his illustrations to an audience of the Deutsches Zoologisches Geselschaft. The following year, when the proceedings were published (Zelinka, 1896), several new taxa and their descriptions were in print for the first time. Included in this publication was the family Trachydemidae but not its nominal genus *Trachydemus*. In 1907, under the title *Zur Kenntnis der Echinoderen*, Zelinka (1907:135) established the genus *Trachydemus* and the "larval genus" *Leptodemus* that in part, along with the "larval genus" *Centrophyes*, contained juveniles that later comprised the "larval genus" *Hyalophyes*. Specimens of the latter genus are juveniles of *Pycnophyes*. Other forms of *Leptodemus* are juveniles of *Trachydemus*. Thus, at that time, the order Homalorhagida consisted of two families: Pycnophyidae with its nominal genus *Pycnophyes* and three "larval genera" (synonyms) *Hyalophyes*, *Centrophyes*, and *Leptodemus* (part), and Trachydemidae with its nominal genus *Trachydemus* and "larval genus" (synonym) *Leptodemus* (part).

Remane (1936:352, 353) first suggested that the two homalorhagid families be united; Lang (1949:11–14) formalized this union. It was not until 1974 that Sheremetevskij discovered that the name "*Trachydemus*" and its junior synonym *Leptodemus* were preoccupied by *Trachydemus* Chevrolat, 1873 (Coleoptera), and *Leptodemus* Reuter, 1900 (Hemiptera), respectively. Consequently, Sheremetevskij substituted the generic name *Kinorhynchus* Sheremetevskij, 1974, for *Trachydemus* Zelinka, 1907.

For many years, the only described species of adult *Kinorhynchus* was *K. giganteus*. This species was found on both the northern and Mediterranean coasts of Europe (Table 22). Nine other species, probably of *Kinorhynchus*, include: *Leptodemus acercus* and *L. metschnikowii* (considered *Pycnophyes acercus* by Băcescu, 1968), *L. dubius*, *L. forficulus*, *L. parvulus*, *L. perlatus*, and *L. vitreus* (considered *Pycnophyes* by Remane, 1929), *L. forceps*, and *L. serratus*. As noted previously in my discussion of *Pycnophyes*, I prefer to assume that without greater evidence than currently available, these species should be in the genus *Kinorhynchus*, although it is doubtful that any will be united with a given adult.

The second species of *Kinorhynchus* based on an adult was *K. mainensis*, which was redescribed from material collected at the type-locality, Mt. Desert Island, Maine, USA (Higgins, 1965). The third such species of *Kinorhynchus* was *K. spinosus* from the Falkland Islands (Lang, 1949). The next species, *K. anomalus*, was collected from the coast of Chile (Lang, 1953). *Kinorhynchus ilyocryptus* and *K. cataphractus* were described from the San Juan Archipelago, Washington, USA (Higgins, 1961). *Kinorhynchus langi* was described from Beaufort, North Carolina, USA (Higgins, 1964b). The most recently published species, *K. paraneapolitanus*, was described by Sheremetevskij (1974) from the Black Sea.

Considering the number of collections made over the past hundred or so years, it is noteworthy that only eight species of *Kinorhynchus* (based on adults) have been described compared to the closely related genus *Pycnophyes* with its 18 species published on the basis of adults. More important, perhaps, is the frequency by which *Pycnophyes* (Table 15) is encountered as compared to that of *Kinorhynchus* (see Table 22). The genus *Kinorhynchus,* like *Pycnophyes,* is found in a wide variety of habitats but appears to have a limited distribution in the world oceans (Figure 336), and very little can be construed from the published distribution records.

Many authors have commented on the validity of maintaining the separation of the two genera of Pycnophyidae. Remane (1936) was the first to question the propriety of the two genera, while Lang (1949) defended the continual separation of the two genera, and this has persisted to date. The only character separating these two genera is the presence of lateral terminal spines in *Pycnophyes.* So far, whenever an appendage appears in the equivalent position in the genus *Kinorhynchus,* it appears to be an unarticulated extension of the lateral or lateroterminal margin of the terminal tergal plate. This protuberance has been described as a bifid (male) or flaring (female) portion of the tergal plate in *K. giganteus* (Zelinka, 1928), as a bulbous projection in *K. mainensis* (Blake, 1930), or as stunted lateral terminal spines in *K. spinosus.* Until it can be demonstrated that these structures are articulated and attached to muscles as in the case of all known species of *Pycnophyes,* the genus *Kinorhynchus* should, in my opinion, remain distinct.

To date, there has been no concerted effort to conduct a contemporary comparative study of the two genera. In addition to developing culture methods to enhance the study of the life histories of members of the two genera, ultrastructural studies of various organs, such as adhesive glands, sensory spots, setae, and careful observations on the detailed structure of the head should be pursued for additional data to better understand their relationships.

Meanwhile, another important task remains: that of carefully redescribing most of the previously described species, including *K. giganteus,* in order to more carefully assess the number and position of characters such as sensory spots and setae. In several species such as *K. spinosus,* only lateral setae were noticed, and no sensory spots were evident. Certainly more detailed illustration of the trunk segments of this and other species, including *K. ilyocryptus, K. cataphractus,* and *K. langi* originally described by me, will be necessary in the near future. In my opinion, however, only *Kinorhynchus paraneapolitanus* is so poorly described and illustrated as to prevent its accurate identification.

Species Distribution and Richness

Prior to this publication, 119 papers by 52 different authors have included distribution records. Of these, 80 papers have included species identifications. These 80 papers have involved, as best as I can determine, 182 samples, stations, or localities. Regardless of the limits of the collecting unit involved, the resulting data give one the overwhelming impression that rarely does one encounter more than one or two genera or more than three or four species within the collecting units (Table 23).

The greatest recorded species richness was reported from Naples, Italy (Figure 337), by Zelinka (1928). From his Pallazzo Domano station (sta 5) at 35 m depth, Zelinka found seven species representing three genera (Figure 338). Altogether, Zelinka sampled 18 stations, 13 of which produced at least one kinorhynch. His habitats ranged from algae to mud, or combinations of the two, and depths of 1–65 meters. Data concerning the specimens from seven of the productive stations are incorporated into Figure 338 to illustrate both species distribution and richness within the study area (about 14 km of coastal water) in the Bay of Naples. Relative abundance indications in the figure are not based on real numbers, but on Zelinka's commentary.

Zelinka's study of 19 stations in the Gulf of

TABLE 22.—Distribution of *Kinorhynchus* (see Figure 336); type-localities are in italics)

Species	FAO sea area	Locality	Authority
anomalous	PSW	*W. Estero Reconcavi*, Chile	Lang, 1953
	PSW	W. Canal Moraleda, Chile	Lang, 1953
apotomus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
belizensis, new species	ASW	*Twin Cays*, Belize	Higgins, this study
cataphractus	INE	*Sucia Is.* (Wash.), USA	Higgins, 1961
	INE	Orcas Is. (Wash.), USA	Higgins, 1961
	INE	Stuart Is. (Wash.), USA	Higgins, 1961
deirophorus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
distentus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
erismatus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
giganteus	ANE	Kiel, FRG	Zelinka, 1928
	MED	Naples, Italy	Zelinka, 1928
	MED	Trieste, Italy	Zelinka, 1928
ilyocryptus	INE	*Orcas Is.* (Wash.), USA	Higgins, 1961
	INE	Sucia Is. (Wash.), USA	Higgins, 1961
	INE	Stuart Is. (Wash.), USA	Higgins, 1961
	INE	Tomales Bay (Calif.), USA	Higgins, 1964b
langi	ANW	*Beaufort* (N.C.), USA	Higgins, 1964b
	ANW	Marineland (Fla.), USA	Higgins, 1964b
mainensis	ANW	*Mt. Desert Is.* (Me.), USA	Blake, 1930; Higgins, 1965
	ANW	Buzzards Bay (Mass.), USA	Wieser, 1960; Higgins, 1965
	ANW	Lewes (Del.), USA	Higgins, 1965
paraneapolitanus	MED	*Lazarevskoye*, USSR	Sheremetevskij, 1974
spinosus	PSW	*Barkley Sound*, Falkland Is.	Lang, 1949
stenopygus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
trisetosus, new species	ASW	*Twin Cays*, Belize	Higgins, this study
species	INW	Kasado Is., Japan	Sudzuki, 1976a,b
species	MED	Bulgaria	Marinov, 1964

Trieste (Figures 339, 340) produced similar results. Here again, a maximum of seven species (three genera) were found at stations 2, 3, and 9; 10 species representing four genera were found in this overall area, which included the smaller Bay of Piran south of Trieste. The most meaningful data came from samples taken along a seven-mile transect from station 1 (17 m) to station 4 (24 m) off the coast of Barcola (Figure 339). Two of Zelinka's Trieste stations, stations 2 and 9, had the same seven species present. One additional station, station 7, had seven species; six of which were the same as those found in stations 2 and 9. Zelinka's studies in these two Mediterranean localities, the Bay of Naples and Gulf of Triste, account for most of the highest records of species richness shown in Table 23. Unlike the majority of these records, Zelinka's work was the product of research directed toward only the kinorhynch fauna of his study sites, which may account for some of his results; however, where the few other similar intensive studies of a given locality have

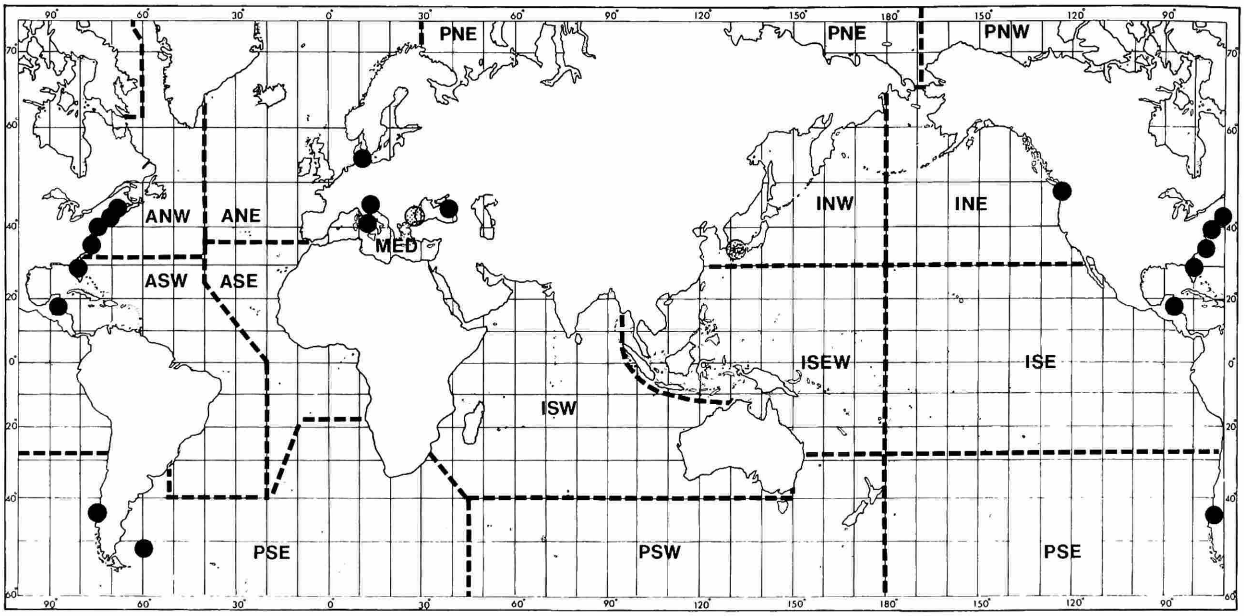


FIGURE 336.—Distribution of *Kinorhynchus* (solid circles indicate records of named species, stippled circles indicate genus records only).

TABLE 23.—Summary of frequency of species and genera reports per sample site (* = this study)

Maximum number of genera/site	Number of sample sites	Maximum number of species/site	Number of sample sites
1	127	1	119
2	34	2	25
3	17	3	17
4	4 + 1*	4	10
		5	5
		6	3
		7	2
		8	1
		13	1*

been conducted (Higgins, 1960, 1961, 1964b; Nyholm, 1947b; Wieser, 1960; McIntyre, 1962, 1964; Sheremetevskij, 1974; Băcescu, 1968), the results have indicated that the meiobenthic community generally accommodates three genera or less with four species or less, if the samples are restricted to subtidal sediments only. A series of collections made in the San Juan Archipelago (Figure 341), Washington, USA (Higgins, 1960, 1961; Kozloff, 1972), illustrates a typical community structure of five species representing three genera (Figure 342).

Considering the previous records of relatively low kinorhynch species richness within given restricted localities, most of them at temperate latitudes, the results of the limited sampling in the Carrie Bow Cay study area are exceptional although, perhaps, in keeping with our general concept of high species richness in tropical ecosystems. Although this study was not designed to support such ecological conclusions, possibly the greater environmental heterogeneity in this tropical reef ecosystem is the reason for the accommodation of the unprecedented number of kinorhynch species found.

Eighteen new species representing four genera, one of these new, were the product of a single dredge sample at each of six stations. The two richest stations included RH 442, located in the mangrove channel system of Twin Cays, and RH 444, located 1 km to the southwest in a typical area of seagrass. Each station produced 13 species (Figure 343). The mangrove station with its very fine gray-brown mud at a depth of 1–2 meters had 13 species representing three genera: *Kinor-*

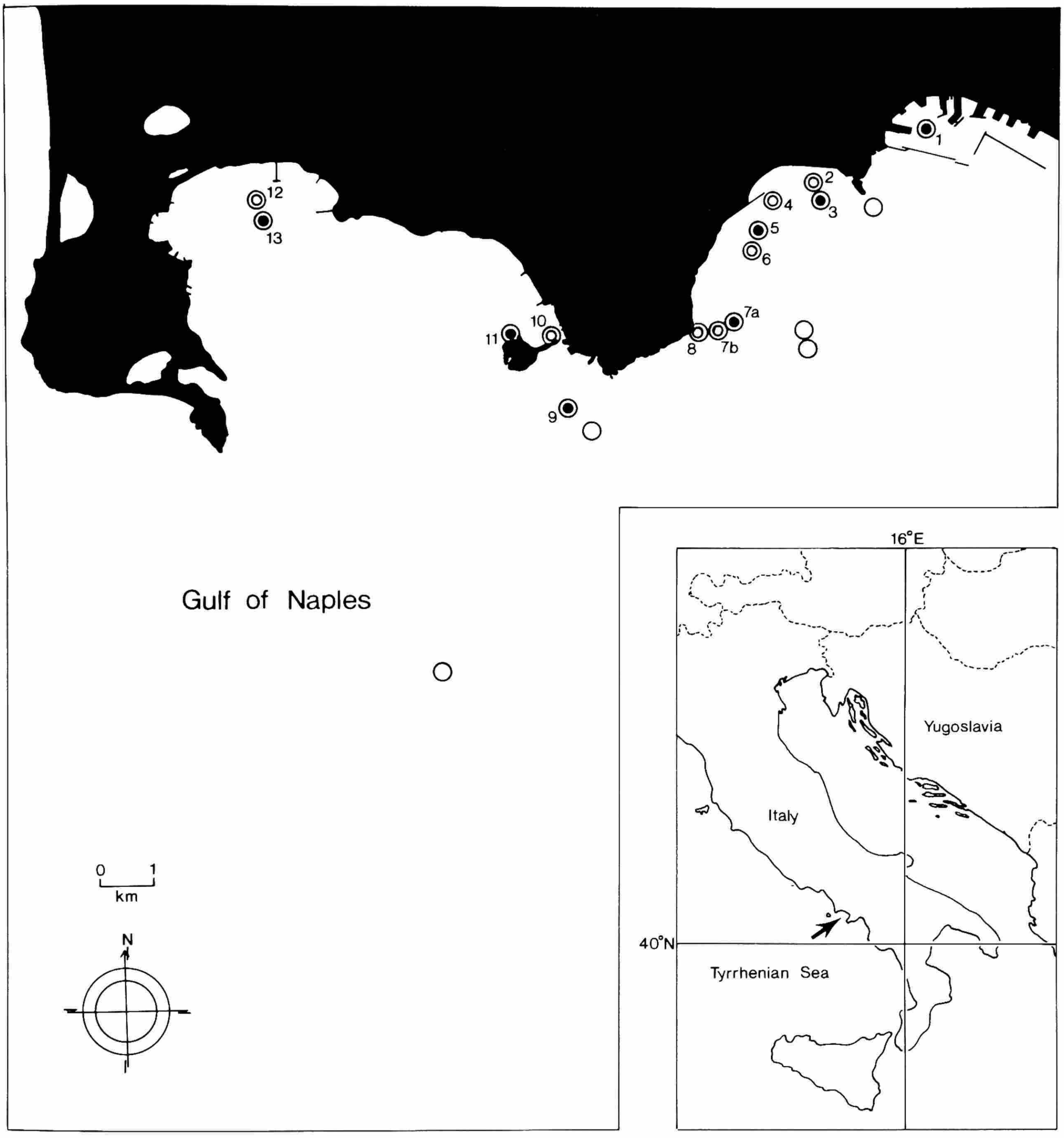


FIGURE 337.—Map showing Gulf of Naples sample stations (Zelinka, 1928) (open circles indicate negative sample, circles with solid inner circles indicate selected stations referred to in Figure 338, circles with open inner circles indicate other stations where kinorhynchs were collected; area of larger map located on inset by arrow).

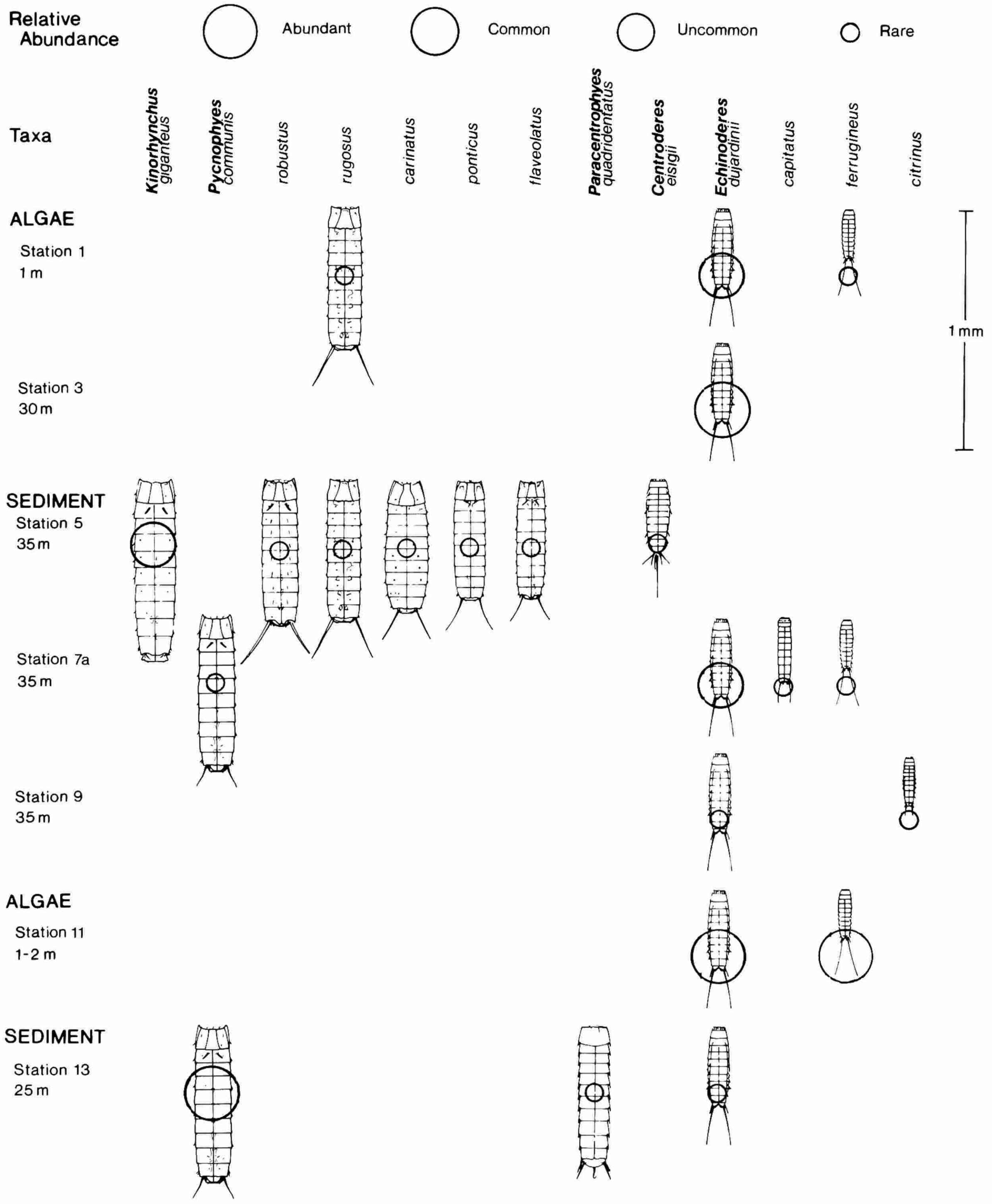


FIGURE 338.—Diagrammatic representation of selected Gulf of Naples stations (Zelinka, 1928), their species composition and relative abundance. All stations were sampled within the same month, and the results are assumed to be the product of a single sample.

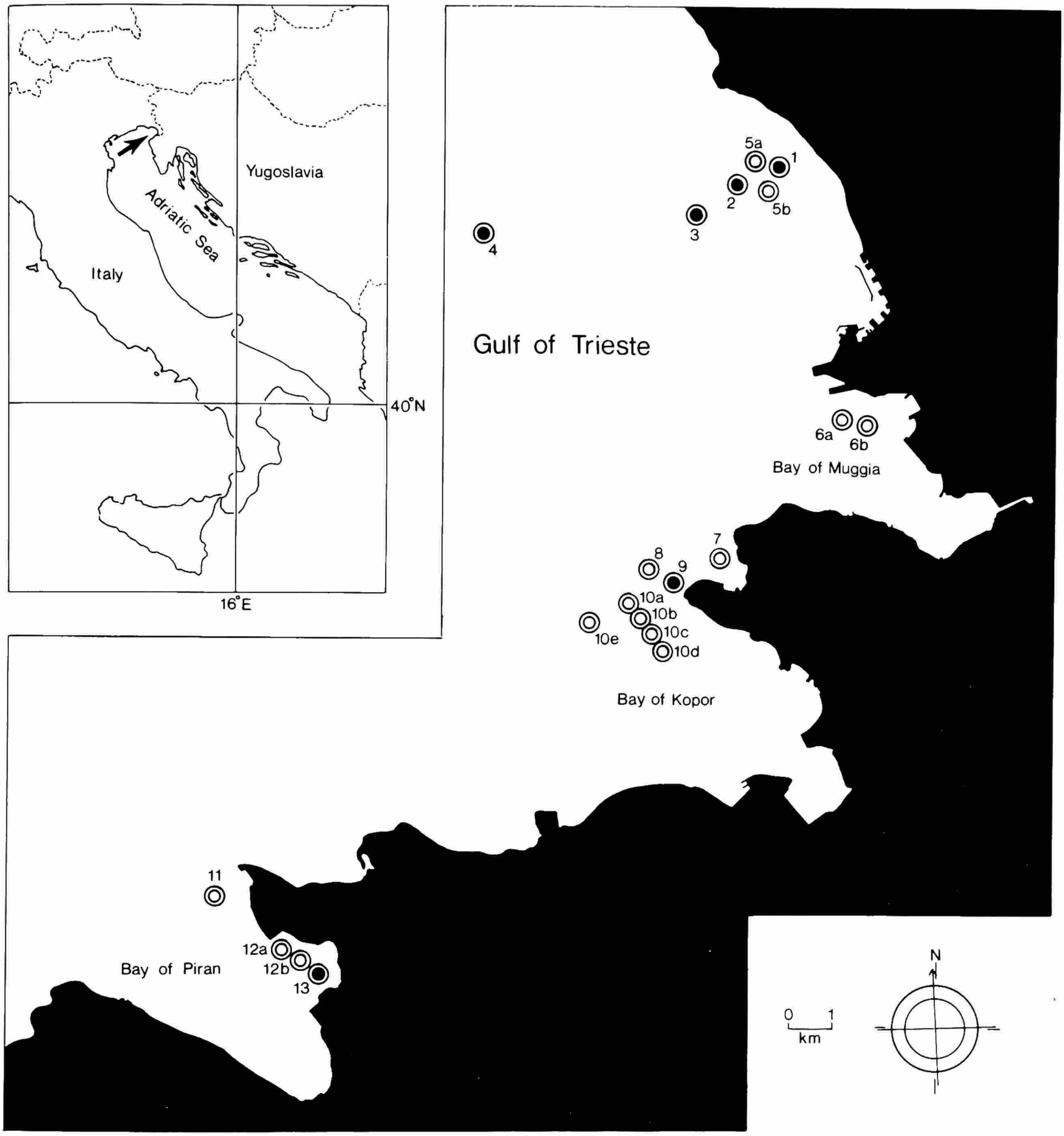


FIGURE 339.—Map showing Gulf of Trieste sample stations (Zelinka, 1928) (circles with solid inner circles indicate selected stations referred to in Figure 340, circles with open inner circles indicate other stations where kinorhynchs were collected; area of larger map located on inset by arrow).

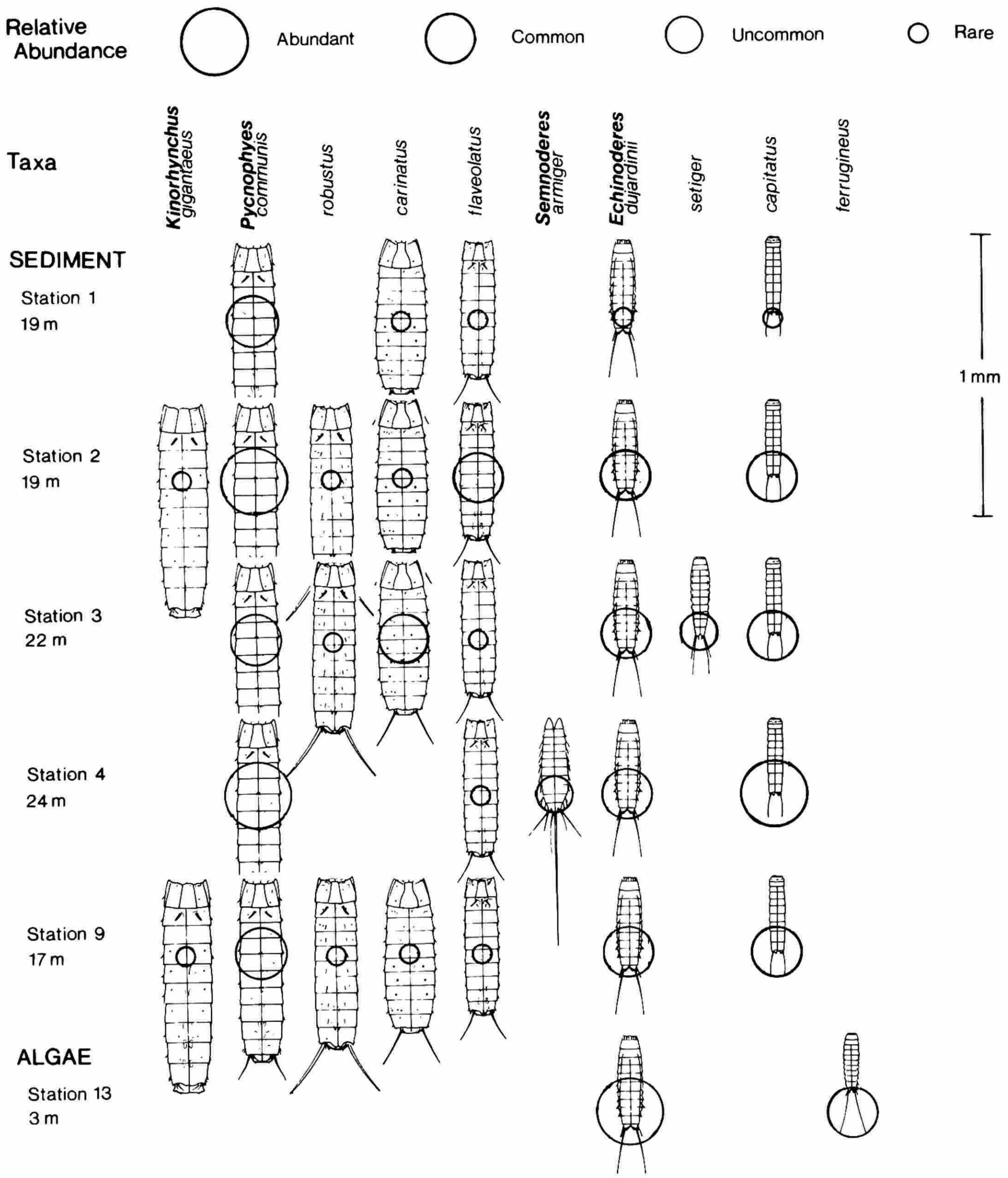


FIGURE 340.—Diagrammatic representation of selected Gulf of Trieste stations (Zelinka, 1928), their species composition and relative abundance. All stations were sampled within the same month, and the results are assumed to be the product of a single sample.

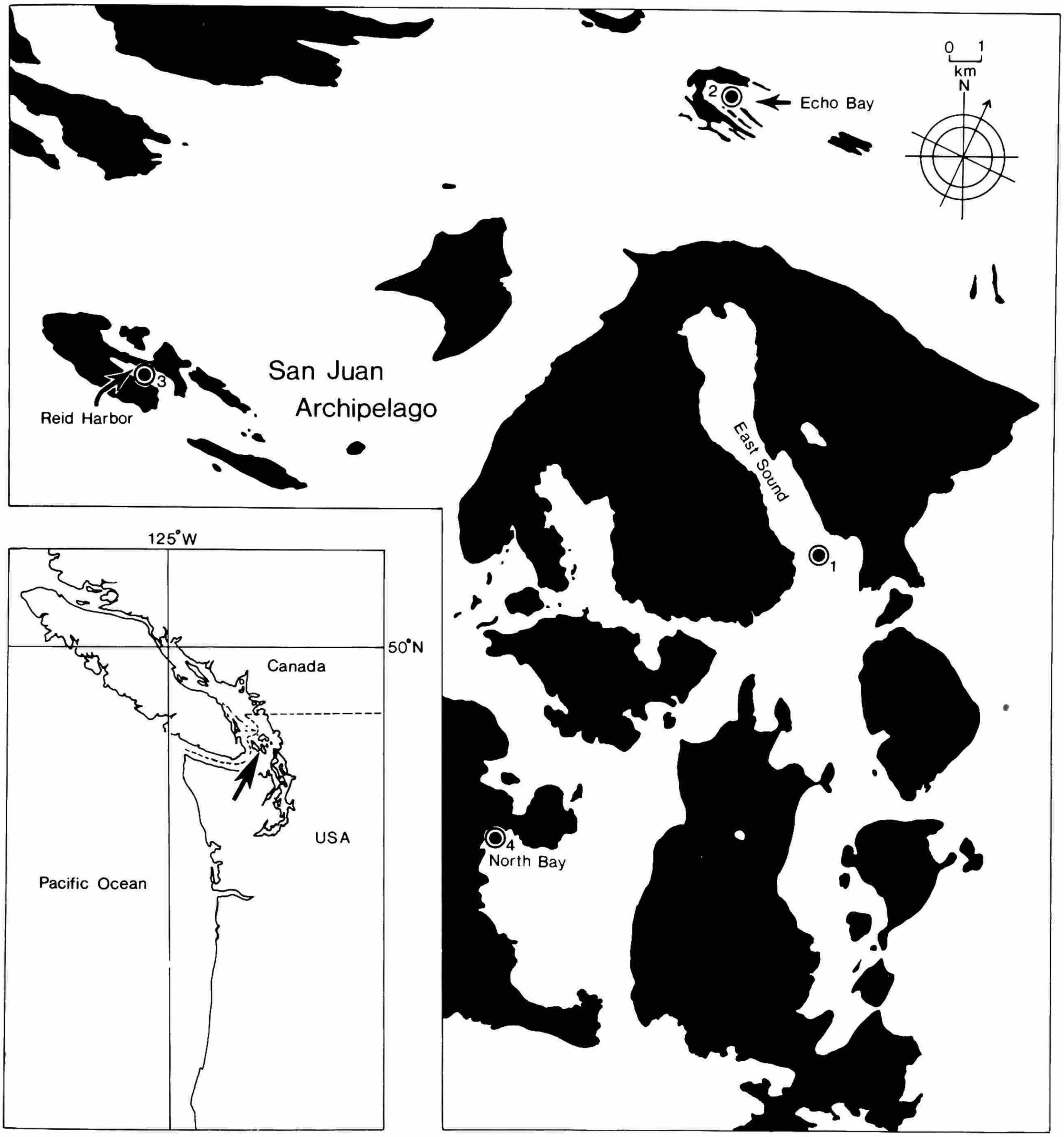


FIGURE 341.—Map showing islands of the San Juan Archipelago (Washington, USA) sample stations (Higgins, 1960, 1961; Kozloff, 1972) (area of larger map located on inset by arrow).

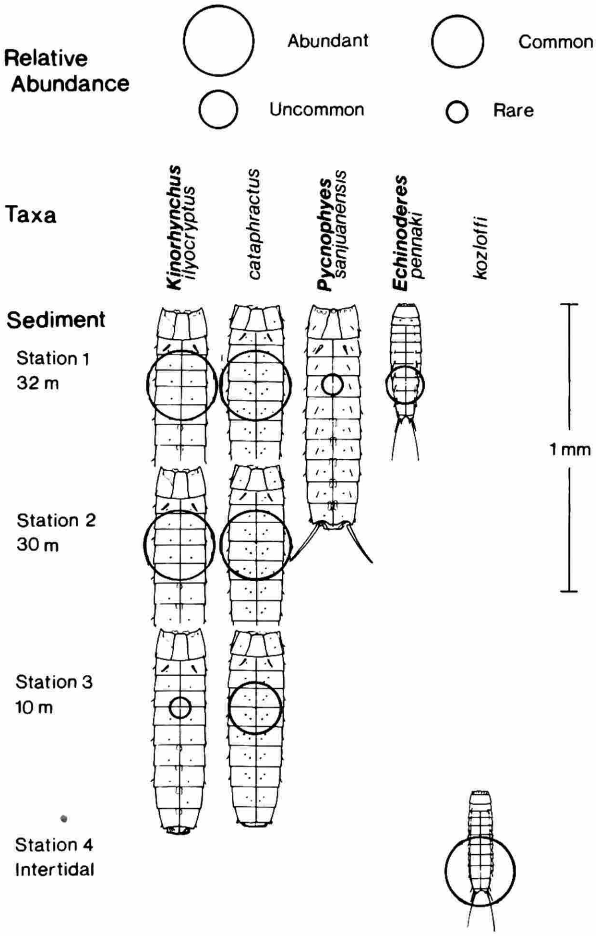


FIGURE 342.—Diagrammatic representation of San Juan Archipelago stations (Higgins, 1960, 1961; Kozloff, 1972), their species composition and relative abundance. Stations 1-3 were sampled during the same month, station 4 was sampled at various periods of time, not in the same year.

hynchus, Pycnophyes, and *Echinoderes.* The seagrass station, RH 444, had 13 species representing four genera: *Kinorhynchus, Pycnophyes, Paracentrophyes,* and *Echinoderes.*

Eight of the 18 species were found at both the mangrove and seagrass stations noted above (Figure 343), seven of these were also found at the intermediate station, RH 443, a less stable site as indicated by the slightly coarser sediment and less dense, more patchy *Thalassia* growth. Within the group of species found at both the mangrove (RH 442) and seagrass (RH 444) sites, their relative abundance indicates that while they may be found in both habitats, one habitat apparently is preferred over the other in at least a few cases. This is illustrated by *Kinorhynchus erismatus* and *K. stenopygus,* which are more abundant in the seagrass habitat, whereas *K. trisetosus* and *K. belizensis* and possibly *Pycnophyes longcornis* appear to prefer the mangrove habitat. Only two of the five species of *Echinoderes, E. horni* and *E. wallaceae,* were found in any of the three stations along the reef transect where conditions reflected the higher energy, less stable sediment of this ecosystem.

Nine (representing all four genera) of the area's 18 species were found at only one station. These included *Kinorhynchus deirophorus, K. distentus, K. apotomus, Pycnophyes iniorhaptus, P. corrugatus, P. ecphantor, Paracentrophyes praedictus, Echinoderes truncatus,* and *E. abbreviatus.* Although the evidence is limited, it suggests that these species are probably restricted to one of the two habitats, mangrove or seagrass. No species was restricted to the intermediate, less stable habitat (sta RH 443) between the two other stations.

Although *Echinoderes wallaceae* was not present in the sand rubble sample, and *E. horni* was absent from the reef trough sample, I suspect both *E. wallaceae* and *E. horni* would have been found in these stations if a larger number of samples could have been taken. Of the five local species in the genus, *E. wallaceae* and *E. horni* have the longest lateral terminal spines in relation to the trunk length.

Both *E. truncatus* and *E. abbreviatus* were found at a single station each. The latter species, with its relatively short lateral terminal spines as contrasted with *E. wallaceae* and *E. horni* with their very long lateral terminal spines, would appear to support the hypothesis (Higgins, 1967) that short-spined species are adapted to fine sediments and longer spines to coarser sediments.

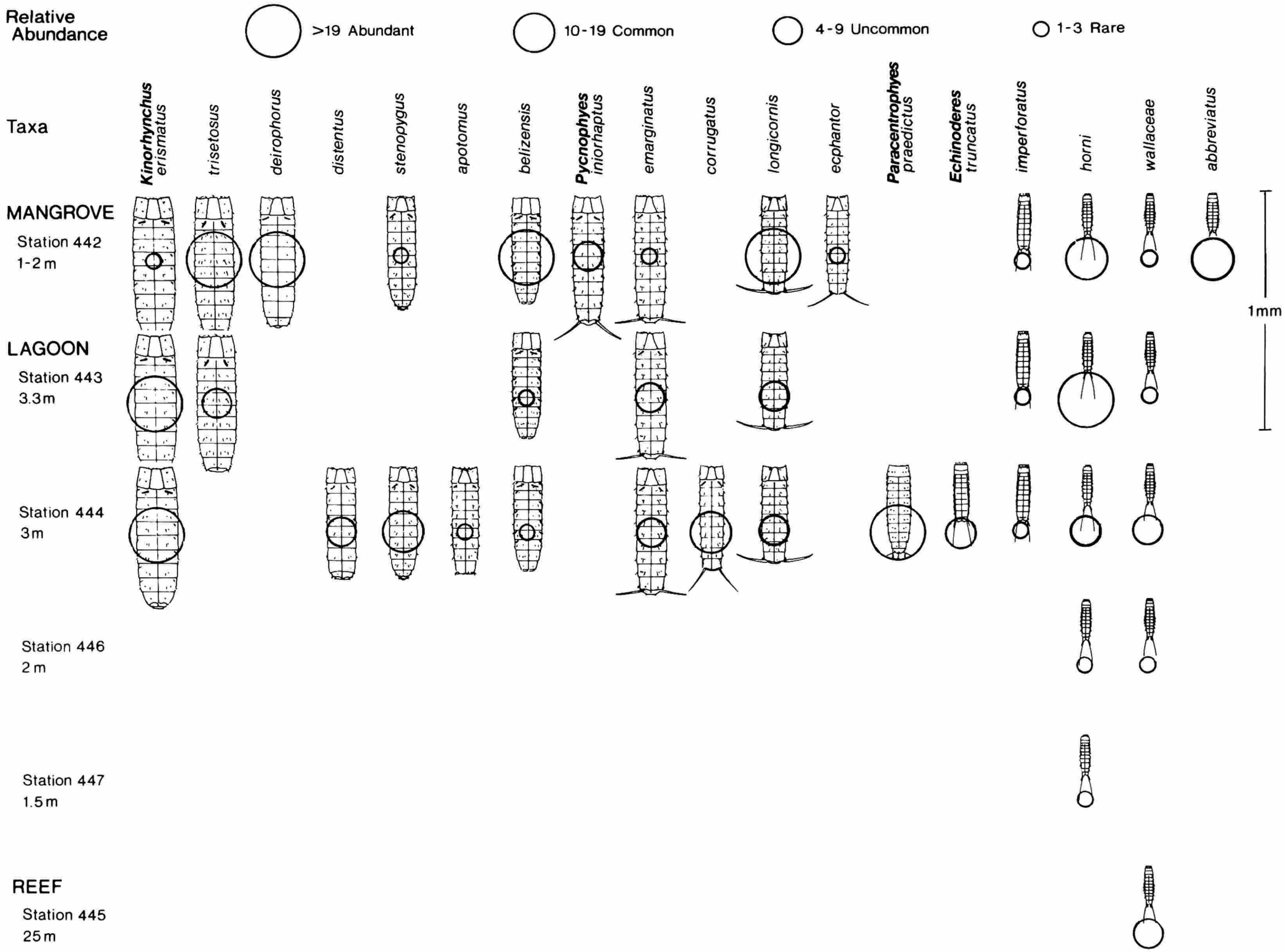


FIGURE 343.—Diagrammatic representation of the Belize stations (see Figure 1), their species composition and relative abundance.

Phylogenetic Relationships

Apart from the phylogenetic relationships discussed in connection with *Paracentrophyes praedictus,* several observations should be made concerning other kincrhych taxa found in Belize. Perhaps the most unexpected find was the seven new species of *Kinorhynchus.* Only once have more than two species of this genus been found in a single station or even within a several hundred square kilometer area (Higgins, 1960, 1961). The previous total number of species of this genus was only eight; seven new species from one area has nearly doubled the number of known species of this genus.

Excluding any relationship with *Kinorhynchus paraneapolitanus,* which is so poorly described that no comparison is practical, there seems to be no close phylogenetic relationships between the Belizian material and the remaining species; however, two pairs of Belizian species show distinct relationships that should be noted.

The first two species that are remarkably similar are *Kinorhynchus deirophorus* and *K. distentus.* Both have reduced penultimate segments, a character also shared with *K. stenopygus* but with no other species in the genus. The structure of the first trunk segment is a second important shared character. Both species have a similar pattern of thin cuticular areas, two on each episternal plate and two on each midsternal plate, and the shape of the midsternal plates is nearly identical. Some similarity can be found between this condition and that of *K. giganteus* from both the north and south coasts of Europe, but this latter species appears to have three thin cuticular areas on the midsternal plate rather than two. Therefore, this character state in the species from Belize appears to be unique. Likewise the tergal plates of the first trunk segment of *K. distentus* and *K. deirophorus* are similar, especially in the pattern of cuticular ridges and the close proximity of the two prominent sensory spots on either side of the dorsal midline. Other, less obvious, shared character states include the structure of the pachycycli of the sternal plates of segments 10 and 11. This is especially noticeable when one compares the midventral thickenings of the two species. Also, the cuticular ridge pattern of the sternal plates of the fourth segment appear remarkably similar. Neither species has middorsal marginal processes.

The second pair of species that share character states, some of which are unique to the genus, include *K. erismatus* and *K. belizensis.* The most obvious, as well as uniquely, shared character state is the structural element between the lateral margins and pachycycli of the sternal plates of segments 4–10 or 11. This "buttressing" feature has not been seen in other species of kinorhynch. A second shared unique character state is the lack of any lateral setae on the penultimate segment. In fact, the margin appears to have two cuticular interruptions in the area where setae are usually found. Some additional similarities include the pattern of muscle scars on the tergal plates of the first trunk segment and some similarities between the episternal plate structure and cuticular ridges of the sternal plates.

Kinorhynchus deirophorus and *K. distentus* appear to occupy separate habitats (Figure 343); however, both *K. erismatus* and *K. beliziensis* are found in all three Twin Cays sites, although the latter species appears to be distinctly more abundant in the mangrove habitat (Figure 393). These two pairs of *Kinorhynchus* species appear to have evolved, each from the same common ancestor, which may or may not include an extant species, or one from the other, but only one pair appears to have persisted in both seagrass and mangrove habitats.

Within the genus *Pycnophyes,* two of the five Belizian species lack the adhesive tubes found in all other males of the genus except for *P. egyptensis.* The two local species are *P. longicornis* and *P. ecphantor.* Aside from the lack of adhesive tubes, the only other notable similarities between the two species include the arrangement of setae and sensory spots on the sternal plates, the denticulate margin of the tergal plate of segment 3 (common to other species as well), and the length and shape of the lateral terminal spines.

Pycnophyes corrugatus has a unique series of ridges near the lateral margins of the sternal plates. This character state is slightly suggestive of a similar pattern of striations in this same area in *P. dentatus*. *Pycnophyes corrugatus*, with regard to this character state, is most similar to *Kinorhynchus apotomus*. Moreover, the two species share several other characters such as a general similarity of seta distribution, a single, thin cuticular area on each episternal and midsternal plate, a denticulate anterodorsal margin of the first trunk segment, and some similar cuticular ridges on the same tergal region. Both are restricted to the more stable *Thalassia* station (RH 444) of the Twin Cays area.

In addition to the previously mentioned unique character states found in these Belizian species, the unusual patches of pores near the lateral margins of the sternal plate of *K. iniorhaptus* should also be mentioned. This character is found in no other known kinorhynch.

The species of *Echinoderes* from Belize show no clear relationships to each other as far as I can determine. Perhaps the most noteworthy relationship between any known species of *Echinoderes* from Belize to any other member of this genus is that between *E. abbreviatus* and *E. brevicaudatus* from the Egyptian Red Sea. Both have notably short lateral terminal spines, and both have been found in coral-derived fine sediments.

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