Redescription of *Echinoderes dujardinii* (Kinorhyncha) with Descriptions of Closely Related Species

ROBERT P. HIGGINS
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*Robert P. Higgins*
ABSTRACT

Higgins, Robert P. Redescription of *Echinoderes dujardinii* (Kinorhyncha) with Descriptions of Closely Related Species. *Smithsonian Contributions to Zoology*, number 248, 26 pages, 31 figures, 2 tables, 1977.—A key to the adults of the genus *Echinoderes* is followed by a redescription of *E. dujardinii* from both adult and juvenile specimens. North American records for *E. dujardinii* are corrected by the description of *E. kozloffi*, new species. *Echinoderes pennaki*, a species sympatric with *E. kozloffi*, is redescribed, and the latter’s sibling species, *E. pacificus*, is discussed. Synonomies and distribution records are given for species mentioned.
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Introduction

The first published observation of a kinorhynch is that of the French naturalist Félix Dujardin (1851), who based his account on specimens found while examining material washed from algae collected near St. Malo on the coast of Normandy in 1841. In a manner not uncommon throughout the history of the study of meiofauna, Dujardin was unable to place the new invertebrate in an existing higher taxonomic category although he recognized its morphological affinities with acanthocephalans, rotifers, sipunculids, nematodes, tardigrades, and various crustaceans (“copepods without legs”). Ten years after his discovery, Dujardin (1851) introduced the first kinorhynch as “a tiny marine animal, l’Echinodère, constituting an intermediate form between the crustaceans and worms.” A few years later Leuckart (1854) noted that he had seen “l’Echinodère” at Helgoland in 1846 but had assumed that it was a dipteran larva.

“L’Echinodère” became Echinoderes dujardinii Claparède, 1863 when the latter author described specimens from St. Vaast la Hougue, not far from St. Malo where Dujardin made his discovery. The following year, Gosse (1864), apparently unaware of Claparède’s publication, also described this species from the same locality, naming it Echinoderes dujardini.

These descriptions suffered from the authors’ lack of experience with the taxon, as have many subsequent ones, including my own. Despite Zelinka’s (1928) more comprehensive description of E. dujardinii in his Monographie der Echinodera, certain taxonomic ambiguities have persisted. The lack of preserved specimens, especially types, has compounded the problem; consequently, the reported distribution of E. dujardinii, as well as other species, must be considered with due caution.

Since it was described, E. dujardinii has been reported from 26 localities including the northern and southern coasts of Europe, the Black Sea, Canary Islands, Japan, and the northwestern coast of the United States.

No specimens are available to confirm Chitwood’s (1964a) report of E. dujardinii from Tomales Bay, California, one of the two northwestern U.S. localities. Neither an unpublished photograph by Chitwood (pers. comm.) of one of the specimens, nor sketches of specimens collected at the same locality and time (1960) by Dr. Tor G. Karling (pers. comm.), indicate that the species from Tomales Bay is E. dujardinii. Specimens sent to me from San Juan Island, Washington, by Dr. Eugene N. Kozloff, resembled E. dujardinii sufficiently to
justify the tentative use of this name (Kozloff, 1972; Merriman and Corwin, 1973); however, both Kozloff and I expressed doubts that could be answered only by comparing the San Juan Island specimens with specimens from either the type-locality or localities (Naples and Trieste) where Zelinka (1928) obtained E. dujardinii from his redescription. My collection from the latter two localities failed to provide specimens of E. dujardinii but Kozloff, in 1973, was successful in collecting this species at Roscoff, not far from St. Vaast la Hougue.

The purpose of this paper is to redescribe E. dujardinii, clarifying both the original description by Claparède (1863) and the redescription by Zelinka (1928). In addition, this paper will correct the distribution record inasmuch as the San Juan Island specimens, reported as E. dujardinii, constitute a new species described below. Because of the co-occurrence of the new species with E. pennaki Higgins, 1960, the description of which reflects my own inexperience at the time, I shall redescribe it as well. The description of E. pacificus Schmidt, 1974 is included because it closely resembles the new species from San Juan Island. Finally, while studying the taxonomic history of E. dujardinii, I discovered that a name I proposed for a species from the Red Sea was preoccupied; therefore, a substitute name is offered for E. brevispinosus Higgins, 1966a.

METHODS.—Specimens were preserved in 70 percent ethyl alcohol, 5 percent formalin, or Duboscq and Brasil’s fluid, and then 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 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 the 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 reducing, by about 30 percent, the amount of chloral hydrate used in the medium and by sealing the preparation with Murrayite soon after the fluid has solidified. In this series of preparations, some specimens were re-mounted in glycerin once they had been oriented dorsoventrally. This is a procedure that should be used only when an adequate series of specimens are available, since in transferring them many dorsal spines are often broken. A few specimens were mounted in glycerin without first mounting them in Hoyer’s medium. In all instances, coverslips were sealed with Murrayite.

Each specimen was studied with the use of Zeiss differential interference contrast optics and metrically analyzed. The resulting data are expressed in a standard format of abbreviations and terminology (Higgins, 1967, 1969a). Measurements are given in microns (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.

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 penis spines (P) in males. The first penis spine (P–1) is usually the anteriormost of three such spines and is dorsally displaced; the second (P–2) is usually the shortest and often more truncate (probably the functional penis); the third (P–3) is usually adjacent to the second or slightly posterior to it. Both P–2 and P–3 are best observed in ventral aspect.

Several lateral spines appear to function as adhesive tubes. This study will introduce the adhesive tubes of the fourth segment (L–4) as homologues of other lateral spines. Appendages that function as adhesive tubes will be noted in the appropriate section of the text.
Specimens mentioned in this paper are deposited in the National Museum of Natural History, Smithsonian Institution, under the catalog numbers of the old United States National Museum (USNM).

Acknowledgments.—I am grateful to Mr. John C. Boykin, University of Washington, the first to collect the new species from San Juan Island and recognize its taxonomic problems; and to our mutual friend and colleague from this same institution, Dr. Eugene N. Kozloff, who accepted the challenge of culturing the new species, and provided me with specimens both of the new species and of *E. dujardinii* that have made this study possible. I also acknowledge the cooperation of Dr. Jean Merriman, California State College at Sonoma, whose recent doctoral dissertation and publication have contributed to the knowledge of the new species from San Juan Island. The personal communications of Dr. Tor G. Karling, University of Stockholm, and the late Dr. B. G. Chitwood were helpful in this study. Dr. Peter Schmidt, Institute für Zoologie der RWTH, Aachen, generously provided type specimens of *E. pacificus* for my use. Thanks also go to Prof. Peter Dohrn, Stazione Zoologica, Naples and to Dr. Jose Stirn, Marine Laboratory, Portoroz, Yugoslavia, for making their facilities available to me. Drs. Raymond B. Manning and Horton H. Hobbs, Jr., were generous in their advice and consultation during the preparation of this manuscript and, along with Dr. Richard S. Houbrick, in the reading of the final draft. I also wish to express my appreciation to Mrs. Eleanor Goldsmith, Mrs. Martha Brewster, and Mrs. Marie Wallace for their help in the preparation of this manuscript. Finally, I am pleased to acknowledge the Sumner Gerard Foundation and the Smithsonian Foreign Currency Program for their financial support.

Key to Adults of the Genus *Echinoderes*

1. Middorsal spines absent ............................................................... 2
   Middorsal spines present ......................................................... 5
2. Lateral spines (except for terminal segment) absent
   Lateral spines present .................................................................. 3
3. Lateral spines on segments 7, 10, and 12 only *Echinoderes bengalensis* (Timm, 1958)
   Lateral spines absent on segment 12 .............................................. 4
4. Lateral spines on segments 7, 10, and 11 only *Echinoderes caribieni*us Kirsteuer, 1964
   Lateral spines on segments 7 and 10 only, segments 3–4 expanded laterally .......................................................... *Echinoderes capitata* (Zelinka, 1928)
5. Middorsal spines on segments 6–10 only ........................................... 6
   Middorsal spines with other arrangement ..................................... 13
6. Lateral spines on segments 7–12 only ............................................. 7
   Lateral spines with other arrangement ............................................ 21
7. Lateral accessory spine on segment 10 ........................................... 8
   Lateral accessory spines absent on segments 3–11 .......................... 9
   Trunk length less than 300 μm ...................................................... 11
9. Lateral spine on segment 12 short (12–17 μm), less than half the length of lateral spine on segment 11 .................. *Echinoderes pacificus* Schmidt, 1974
   Lateral spines on segment 12 nearly equal to length of lateral spines on segment 11 .......... 10
10. Lateral terminal accessory spines 12%–15% of trunk length, midventral placid wider than adjacent placids ............................... *Echinoderes kozloffi*, new species
   Lateral terminal accessory spines about 8% of trunk length, midventral placid not wider than adjacent placids ........................................ *Echinoderes pilosus* Lang, 1949
11. Middorsal spine on segment 10 slightly longer than middorsal spine on segment 9 .................................................. 12
    Middorsal spine on segment 10 twice as long as middorsal spine on segment 9 .......................... *Echinoderes ehlersi* Zelinka, 1913
12. Lateral terminal accessory spines about 41% of trunk length, no lateral accessory spine on segment 12 ................................................. *Echinoderes worthingi* Zelinka, 1928
    Lateral terminal accessory spines about 23% of trunk length, lateral accessory spine adjacent to lateral spine ........................................ *Echinoderes ferruginosus* Zelinka, 1928
    Middorsal spine absent on segment 11 ........................................ 14
14. Middorsal spine on segment 7

15. Middorsal spine absent on segment 7

16. Middorsal spines on segments 6-9 only

17. Middorsal spines on segments 5-8 only

18. Middorsal spines on segments 6 and 9 only

19. Middorsal spines on segments 6, 8, and 10 only

20. Middorsal spines on segments 6, 7, and 9 only

Echinoderes setigera Greeff, 1869

Middorsal spine absent on segment 7

Middorsal spines on segments 6, 7, and 9 only

Echinoderes druxi d’Hondt, 1973

Middorsal spine on segment 5

Echinoderes newcaledoniensis Higgins, 1967

Middorsal spine on segment 10 or missing on all segments except terminal segment of female, terminal middorsal extensions with uneven margins

Echinoderes riedli Higgins, 1966a

Middorsal spine on segment 10 only, middorsal spines short, (15–18 \( \mu \text{m} \)). Terminal middorsal extensions mesially recurved and somewhat rectangular with small protuberances at corners

Echinoderes tchefouensis Lou, 1954

Middorsal spines on segments 5-8 only

Echinoderes borealis Greeff, 1869

Middorsal spines on segments 5-9 only

Echinoderes arlis Higgins, 1966b

Middorsal spines on segments 5-10 only

Echinoderes bookehouti Higgins, 1964b

Lateral accessory spine on segment 10 only, middorsal spines short, (15–18 \( \mu \text{m} \)). Terminal middorsal extensions evenly tapering to point

Echinoderes canariensis Greeff, 1869

Lateral accessory spine on segment 10 only

Echinoderes setigera Greeff, 1869

Lateral accessory spine on segment 10 only, middorsal spines with other arrangement

Echinoderes canariensis Greeff, 1869

Lateral accessory spine on segment 10 only

Echinoderes citrinus Zelinka, 1928

Lateral accessory spine on segment 10 only

Echinoderes citrinus Zelinka, 1928

Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Lateral accessory spine on segment 10 only

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Lateral accessory spine on segment 10 only

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Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Lateral accessory spine on segment 10 only

Echinoderes brevispinus Houguet, 1966a

Habroderes meridionales Zelinka, 1928:254, pl. 2: figs. 11-15 [synonymy].—Remane, 1936:335 [noted as larval stage of Echinoderes dujardinii].

Centropsis parallela Zelinka, 1928:269, pl. 1: figs. 4, 5, 11, 12 [Naples, Trieste].—Remane, 1936:332, 335, fig. 273 [noted as larval stage of Echinoderes dujardinii].

Echinoderes Masudai Abe, 1930:42, 43, pl. 1: figs. 1, 2 [Hiroshima].—Remane, 1936:345, fig. 277.—Tokioka, 1949:87. Echinoderes sieboldii.—Lou, 1934:3 [erroneous spelling].


Not Echinoderes brevispinosus Higgins, 1966a:118-121, figs. 1, 2; 1966b:519.—Schmidt, 1974:14. [=Echinoderes brevicaudatus, substitute name].


Redescription.—Adults (Figures 1-6), trunk length, 328-405 μm; MSW-9, 78-85 μm, 19.9-24.9 percent of trunk length; SW, 70-85 μm, 18.9-24.9 percent of trunk length.

Second segment with 16 anteriorly rounded placids, midventral placid truncate, expanded slightly at anterior margin, distinctly larger than adjacent placids; trichoscalid plates on sides of midventral placid with medial indentation on anterior margin, posterior margin expanded laterally.

Segments 8-12 with short hairs, pattern distinctive (Figures 1, 2); posterior border of segments 5-11 with fine pectinate fringe ventrally, segments 6-11 with pectinate fringe dorsally; terminal segment with few hairlike processes along posterior margin, posterior margin expanded laterally.

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FIGURES 1-2.—Echinodera dujardini, adult female (USNM 55342, RH125.14), neck and trunk segments: 1, ventral view; 2, dorsal view.
spine (P-1) 23–33 μm in length, mesially adjacent penis spine (P-2) 24–36 μm, posteriorly adjacent penis spine (P-3) 26–39 μm in length.

Pachycycli (thickened anterior margins of trunk segments) well developed, forming a distinctive pattern at ventral midline and at attachments of lateral terminal spine muscles on segment 13; distinctive muscle scars on ventrolateral portion of first trunk segment, similar (but reversed orientation) lateral scars on eighth sternal plates; sensory spots, 2–3 μm in diameter, situated middorsally on segments 3–5, with two such spots on segment 12 (possibly one on each of segments 12 and 13), dorsolaterally on segments 6–11, and ventromesially on segments 5–12 (Figures 1, 2).

Morphometric data for adult specimens are shown in Table 1.

Juvenile Stages.—Preadult stage (J-6, “Habroderes-stage,” Figures 7, 8) trunk length, 320–328 μm; estimated MSW-9, 78–80 μm, 24.3–25.6 percent of trunk length; estimated SW, 65–72 μm, 19.8–23.5 percent of trunk length (estimated since tergal-ster nal junctions are not defined in juvenile stages).

Second segment similar to that of adult, both placids and trichoscalid plates less well developed.

Trunk segments with fewer hairs than adult, pattern less distinctive and more variable; posterior borders of segments without pectinate fringe, with hairs (stria tions?) along border, group of prominent hairs (stria tions?) at ventral midline, terminal segment slightly incised dorsally and ventrally, sternal area without spinous extensions, tergal area with small extensions 2–4 μm in length, not evenly tapered.

Middorsal spines on segments 6–11, increasing uniformly in length, 17–39 μm; lateral spines on segments 4 and 7–12, 17–26 μm in length; L-4, 7, 10 and 12 with poorly developed adhesive glands at base; L-10 and L-12 accompanied by a dorsally adjacent lateral accessory spine of nearly equal length, 21–25 μm, but thinner; L-4 more prominent than remaining lateral spines; lateral terminal spines long, 148–152 μm, 45.1–48.7 percent of trunk length; lateral terminal accessory spines 42–47 μm in length, sexes often indistinguishable in juvenile stages unless developing oocytes visible.
Table 1.—Measurements (μm) and indices (%) for Echinoderes dujardinii adults

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<td>0.2</td>
<td>6.3</td>
</tr>
<tr>
<td>L-TS/TL</td>
<td>26</td>
<td>160-198</td>
<td>175.5</td>
<td>6.1</td>
<td>1.2</td>
<td>3.5</td>
</tr>
<tr>
<td>SW</td>
<td>45</td>
<td>70-83</td>
<td>77.0</td>
<td>2.6</td>
<td>2.3</td>
<td>3.4</td>
</tr>
<tr>
<td>SW/TL</td>
<td>45</td>
<td>18.9-24.9</td>
<td>21.5</td>
<td>1.4</td>
<td>0.2</td>
<td>6.3</td>
</tr>
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Pachyacyli not well defined, muscle scars on ventrolateral areas of first trunk segment reduced, no scars on segment 8; sensory spots, 2–3 μm in diameter, situated middorsally on segments 4–5 and 12–13, laterodorsally on segments 6–15, mesially on sternal plates 4–11.

Fourth-stage juvenile (J-4, "Habroderes-stage," Figures 9, 10) trunk length, 224 μm; estimated MSW–9, 72 μm, 52 percent of trunk length; estimated SW, 65 μm, 29 percent of trunk length.

Second segment as in preadult, less well developed.

Trunk segments similar to those of preadult but not well defined posteriorly so that only 10 trunk segments apparent; series of medial hairs (stria-<tions?) both dorsally and ventrally indicating area of presumptive segment 12; corresponding area of segment 13 less distinct; hairs less obvious than in preadult, more scattered; terminal segment slightly incised ventrally with suggestions of pointed tergal extensions.

Middorsal spines on segments 6–11, D–6–10, 14–39 μm, increasing uniformly in length to segment 11, D–11, 79 μm, twice the length of D–10, extending slightly beyond terminal segment; lateral spines similar to preadult stage, 16–26 μm in length; lateral terminal spines 160 μm in length, 71.4 percent of trunk length; lateral terminal accessory spines 47 μm.

Third-stage juvenile (J-3, "Hapaloderes-stage," Figures 11, 12) trunk length, 200–208 μm; estimated MSW–9, 72 μm, 34.3 percent of trunk length; estimated SW, 51 μm, 24.5 percent of trunk length.

Second segment as in J–4 stage, less well developed.

Trunk segments similar to those of J–4 stage, less
FIGURES 7-8.—Echinoderes dujardinii, preadult (J-6) stage (USNM 53545, RH125.49), neck and trunk segments: 7, ventral view; 8, dorsal view.
FIGURES 9-10.—Echinoderes dujardinii, juvenile (J-4) stage (USNM 58344, RH125.53), neck and trunk segments: 9, ventral view; 10, dorsal view.
FIGURES 11-12.—Echinodera dujardini, juvenile (J-3) stage (USNM 53343, RH125.54), neck and trunk segments: 11, ventral view; 12, dorsal view.

well defined posteriorly, striations along posterior margins of segments 3–9 defining segments, striations incomplete on presumptive segment 10, restricted to midventral area, striations restricted to
middorsal and midventral areas of presumptive segment 11, striations apparent on midventral area of presumptive segment 12; terminal segment blunt, without extensions.

Middorsal spines on segments 6–12 (D–12 essentially midterminal), D–6–9, 17–29 μm, increasing uniformly in length to segment 10, D–10, 39–43 μm in length, D–11, 98–109 μm in length, D–12 (midterminal) 136–170 μm in length, 60.7–85.0 percent of trunk length; lateral spines similar to J–4 stage except LA–12 absent, 18–22 μm in length; lateral terminal spines 60–64 μm, 28.8–30.0 percent of trunk length; lateral terminal accessory spines 46 μm.

**Material Examined.**—46 adults (USNM 53342) consisting of 26 males and 20 females, 4 preadults (J–6, “Hapaloderes-stage”) (USNM 53345), one fourth-stage juvenile (J–4, “Hapaloderes-stage”) (USNM 53344), and 2 third-stage juveniles (J–3, “Hapaloderes-stage”) (USNM 53343); col. Dr. Eugene N. Kozloff, 19 October 1973, Roscoff, Nord-Finistère, France (from the surface of sandy mud in the port).

**Remarks.**—Dujardin (1851) and many subsequent authors prior to Zelinka (1928) introduced certain ambiguities into the description of *Echinoderes dujardinii*. The most common problems include the interpretation of the animal’s length and the position of the spines on the trunk segments. Dujardin, for example, probably included the head and neck and may have included some juvenile stages in his total length measurements (300–550 μm). Prior to Zelinka (1928), most authors were not consistent in numbering segments; consequently, one must carefully compare the illustrations with the text when assessing the correct position of middorsal and lateral spines.

The most accurate illustration of *E. dujardinii* published prior to Zelinka (1928) was that of Greeff (1869). One of the most important characteristics of this species, the presence of two lateral spines on segment 10, was noted by Dujardin (1851), but ignored by many subsequent authors.

Including *E. dujardinii*, the adults of seven species of *Echinoderes* have middorsal spines on segments 6–10 and lateral spines on segments 4, 7–12 (*E. pilosus* Lang, 1949 may have lateral spines or adhesive tubes on segment 4 although they are not included in the author’s description). *Echinoderes ehlersi* Zelinka, 1913 (from Zanzibar) is 228 μm long, much smaller than *E. dujardinii*, and has significantly longer lateral terminal spines in relation to the trunk length, 77 percent as contrasted with 41–55 percent in *E. dujardinii*. *Echinoderes ferrugineus* Zelinka, 1928 has been found with *E. dujardinii* at both Naples and Trieste (Zelinka, 1928). *Echinoderes ferrugineus* also is smaller than *E. dujardinii* and has longer lateral terminal spines relative to its trunk length, about 67–77 percent. *Echinoderes ferrugineus* differs from *E. ehlersi* in that D–10 in the former species is 55 μm, nearly twice the length of D–9; in *E. ehlersi*, the middorsal spines increase uniformly from 8–14 μm in length.

*Echinoderes worthingi* Zelinka, 1928 also occurs with *E. dujardinii*. One specimen was collected along with *E. dujardinii* in this study and Southern (1914) found both species at Blacksod Bay, Ireland. *Echinoderes worthingi* is similar in size and other characteristics to both *E. ehlersi* and *E. ferrugineus* as noted by Zelinka (1928). *Echinoderes worthingi* most closely resembles *E. ferrugineus* in that the length of D–10, 45–50 μm, is twice that of D–9, 19–23 μm. The two species appear to be distinguishable by the shape of the terminal segment, a slightly smaller lateral terminal spine, and the presence of a prominent sensory hair (spine?) posteriorly adjacent to the lateral spine on segment 12 in *E. ferrugineus*; a similar hair exists in *E. pacificus* (Figures 28, 30).

Three additional species with the D–6–10, L–4, 7–12 spine combination are also similar to *E. dujardinii* in size. *Echinoderes pilosus* (from South Georgia Island) is poorly described, and as mentioned previously, I am including it because there is a chance that Lang (1949) overlooked the lateral spines (= adhesive tubes) on segment 4. *Echinoderes pilosus* differs from *E. pacificus* Schmidt, 1974 (from the Galapagos) in that the former has relatively longer lateral terminal spines, about 52 percent of the trunk length compared with 27–36 percent in the latter. If Lang is correct, a distinguishing feature of *E. pilosus* is the uniform size of the placids. In the other species, however, the midventral placid is much wider than the adjacent ones. Both *E. pacificus* and the remaining species, *E. kozloffi*, new species, are discussed more extensively below.

All six species mentioned in the foregoing discussion differ from *E. dujardinii* by their lack of a lateral accessory spine on segment 10.

Two additional species of *Echinoderes* share with
E. dujardinii the presence of a lateral accessory spine on segment 10. These include E. riedli Higgins, 1966a (from the Red Sea) and E. newcaledoniensis Higgins, 1967. Echinoderes riedli is smaller, 238 μm in length. Echinoderes newcaledoniensis is the only member of this genus having lateral accessory spines on segments 8–11 and is unique in possessing dorsolateral spines on segment 4. Both E. riedli and E. newcaledoniensis differ from E. dujardinii by having middorsal spines on segments 6, 8, and 10 only.

**Distribution.**—Echinoderes dujardinii has been reported from 26 localities (Figure 13, also see annotations in synonymy). Most of the reports are European and include both the northern and southern coastal areas of the continent. These distribution records are probably reliable except for those from the Black Sea. Based on the evidence presented by Reinhard (1881), Băcescu et al. (1963), and Marinov (1964), I believe these records are questionable. Similarly, the reports of E. dujardinii from Japan (Tokioka, 1949) and the Pacific coast of the United States (Chitwood, 1964a; Merriman and Corwin, 1972) are based on misidentifications of E. kozloff, new species.

**Echinoderes kozloff, new species**

**Figures 14–21**

Echinoderes.—Kozloff, 1972:121, figs. 1–18.—Higgins, 1974:514, figs. 11–16.


Echinoderes sp.—Boykin, 1974:40.

**Diagnosis.**—Trunk length, 328–376 μm, middorsal spines on segments 6–10, increasing uniformly in length; lateral spines on segments 4, 7–12, with adhesive glands at base of L–4, 7, 10 and 12, lateral spine of segment 12, 20–30 μm in length; lateral extensions of terminal tergal plate tapering evenly to point protruding about 5 μm beyond extensions of tergal plate (exclusive of prominent spines on latter).

**Description.**—Adults (Figures 14–19), trunk length, 328–376 μm; MSW–9, 68–74 μm, 18.0–22.3 percent of trunk length; SW, 62–69 μm, 17.5–20.0 percent of trunk length.

Second segment with 16 anteriorly rounded placids; midventral placid truncate, not expanded laterally at anterior margin, distinctly larger than adjacent placids; trichoscalid plates on sides of
Figures 14-15.—Echinoderae kozloffi, new species, holotypic female (USNM 53337), neck and trunk segments: 14, ventral view; 15, dorsal view.
midventral placid indented at anteromedial margin, posterior margin expanded laterally, four trichoscalid plates on dorsal placids much smaller than those on ventral placids.

Segments 3–12 with short hairs, pattern distinctive (Figures 14, 15); posterior border of segments 4–11 with fine pectinate fringe dorsally and ventrally; terminal segment with few hairlike processes along posterior margin; posterior margin of tergal plate deeply incised, laterally forming pointed, evenly tapered extensions mesial to base of each lateral terminal spine; sternal plates broadly rounded with spinous extensions, 15–22 μm in length (Figures 16, 18).

Middorsal spines on segments 6–10, increasing uniformly in length posteriorly, 20–45 μm; lateral spines on segments 4 and 7–12, 24–82 μm in length; L-4, 7, 10 and 12 with adhesive gland at base; L-8 usually shorter (mean 22.9 μm) than L-7 (mean 27.5 μm) or L-9 (mean 26.1 μm); L-9–12 all similar in length, 22–32 μm; lateral terminal spines long, 144–180 μm, 42.0–52.4 percent of trunk length; lateral terminal accessory spines of female 46–59 μm in length; males without lateral terminal accessory spines but with penis spines in same position; anteriormost penis spine (P-1) 25–35 μm in length, mesially adjacent penis spine (P-2) 21–27 μm in length and distinctly broader, posteriorly adjacent penis spine (P-3) 35–42 μm in length, generally tending to curve mesially, crossing lateral terminal spine.

Pachycycli well developed, forming distinctive pattern at ventral midline and superficial to lateral terminal spine muscle attachments on segment 13; muscle scars on ventrolateral portion of first trunk segment almost indistinguishable, similar V-shaped scars on either side of ventral midline of segments 4–9; prominent scars on lateral margins of sternal plates 8–9, more centrally located on sternal plates of segment 10 (Figure 14); sensory spots, 2–3 μm in diameter, situated middorsally on segments 3–5 with two such spots on segment 12 (possibly one on each of segments 12 and 13), dorsolaterally on seg-

**Figures 16–19.—** *Echinoderes kozloffi*, new species, segments 12–13: 16, ventral view, lateral half, holotypic female (USNM 53337); 17, dorsal view, lateral half, holotypic female; 18, ventral view, lateral half, allotypic male (USNM 53338); 19, dorsal view, lateral half, allotypic male.
ments 3–11, ventromesially on segments 4–12, anterolaterally on ventral surface of segment 3, and possibly near lateral margin of sternal plates 5–7 (Figures 14, 15).

Morphometric data for adult specimens are shown in Table 2.

**Juvenile Stages.**—Preadult stage (J–6, “Habroderes-stage,” Figures 20, 21) trunk length, 276–300 μm; estimated MSW–9, 64–68 μm, 23–24 percent of trunk length; estimated SW, 62–64 μm, 22–23 percent of trunk length (estimated since tergal-sternal junctions not defined in juvenile stages).

Second segment similar to that of adult, both placids and trichoscalid plates less well developed.

Trunk segments with fewer hairs than adult although hairs as long as in adult (5–9 μm), pattern less distinctive and more variable; posterior borders of segments without pectinate fringe, with hairs (striations?) along border, group of prominent hairs (striations?) at ventral midline and second group lateral to midline; terminal segment slightly incised dorsally and ventrally, sternal area without spinous extensions, tergal area with evenly tapered extensions, 2–4 μm in length.

Middorsal spines on segments 6–11, increasing uniformly in length, 17–26 μm (mean 27.9–34.0 μm, 10.7–12.0 percent of trunk length), D–11 extending beyond terminal tergal borders; lateral spines on segments 4, 7–12, 17–26 μm in length; L–4, 7, 10, and 12 with poorly developed adhesive glands at base; L–12 accompanied by a lateral accessory spine situated dorsally to it, slightly longer (22–26 μm) and thinner; L–4 also thinner than other lateral spines; lateral terminal spines long, 152–160 μm, 50.7–56.5 percent of trunk length; lateral terminal accessory spines 35–40 μm in length.

Pachycyclid not well defined, muscle scars similar to those of preadult stage of *E. dujardini*.

Fifth-stage juvenile (J–5, “Habroderes-stage”) trunk length, 224–256 μm; other measurements similar to preadult stage described above.
FIGURES 20-21.—Echinoderes kozloffii, new species, preadult (J–6) stage (USNM 55341, RH145.43), neck and trunk segments: 20, ventral view; 21, dorsal view.
Middorsal spines on segments 6–11, increasing uniformly in length, 15–72 μm (mean 33.0–39.8 μm), 14.7–15.8 percent of trunk length. Note: This latter statistic distinguishes J–5 from J–6.

**Holotype.**—Adult female, TL 344 μm; North Bay, San Juan Island, Washington, USA (48°31.0'N, 123°01.0'W); 9 August 1975; col. E. N. Kozloff; USNM 53337.

**Allotype.**—Adult male, TL 348 μm; as holotype; USNM 53338.

**Paratypes.**—19 females and 19 males, TL 328–376 μm; data as for holotype; USNM 53339; 5 pre-adult juveniles, TL 224–300 μm, 5 J–5 juveniles, 224–256 μm; as holotype; USNM 53340; 4 females and 4 males, TL 328–364 μm; Reid Harbor, Stuart Island, Washington, USA (48°40.0'N, 123°11.0'W); 31 July 1968; col. J. C. Boykin; USNM 53347; 3 preadult juveniles, TL 280–292 μm; data as for above; USNM 53348.

**Remarks.**—*Echinoderes kozloffi*, new species, most closely resembles *E. pacificus* from the Galápagos Islands. I consider the two sibling species. A similar sibling relationship involving the two geographic areas has been noted for two species of otoplanid turbellarians: *Philosytis sanjuanensis* Ax and Ax, 1967 (from San Juan Island, Washington) is a sibling species of *P. sanctacruzensis* Ax and Ax, 1974 (from the Galápagos Islands) according to these authors. *Echinoderes kozloffi* is similar to *E. pacificus* in total length, standard width, maximum sternal width, and general appearance. The range of the mean lengths of middorsal spines in *E. kozloffi* (25.4–29.8 μm) and those of *E. pacificus* (46.5–56.5 μm) is one of the significant differences between the two species. Other differences include the longer (25–29 μm) lateral spine on segment 4 in *E. kozloffi*, which contrasts with the shorter (12–17 μm) lateral spine on segment 4 in *E. pacificus*; in the former species the lateral terminal spines, 144–180 μm, 42.0–52.4 percent of the trunk length, are longer than those of the latter species, 90–118 μm, 27.0–36.0 percent of the trunk length. The lateral terminal accessory spines of *E. kozloffi* are slightly longer (46–59 μm) than those of *E. pacificus* (34–41 μm).

The relatively long (22–30 μm) lateral spine on segment 12 of *E. kozloffi* is a particularly noticeable feature that contrasts with the short (12–17 μm), blunt lateral spine on segment 12 of *E. pacificus*. The posterior margins of both tergal and sternal plates of the terminal segment distinguish the two species. The mesial margins of the terminal sternal extensions of *E. pacificus* are interrupted and beset with a series of prominent hairs (Figure 28); in *E. kozloffi* these margins are even and have a less obvious series of hairs. Both species have hairs along the mesial margins of the terminal sternal extensions but, again, those of *E. pacificus* are more distinct, each hair associated with a steplike interruption of the margin. Also, the sternal extensions of both species have a spinous process. The processes in *E. pacificus*, however, are half the length (8–12 μm) of those in *E. kozloffi* (17–25 μm). *Echinoderes pacificus* is discussed later in this paper.

*Echinoderes kozloffi* is similar to *E. pilosus*. As noted above, *E. pilosus* is not well described but has the same general trunk length and spination formula as both *E. kozloffi* and *E. pacificus*. *Echinoderes pilosus* appears to differ from *E. kozloffi* in only two principal characters: *E. pilosus* has shorter lateral terminal accessory spines, about 35 μm, about 8 percent of the trunk length, and the midventral placid is the same width as adjacent placids. This latter character is unique within the genus.

*Echinoderes kozloffi* is sympatric with *E. pennaki* Higgins, 1960 but differs in that the latter species lacks a lateral spine on segment 12, has conspicuously longer lateral spines (mean 58.1 μm, 14 percent of the trunk length), a prominent ventral spinous fringe on the posterior border of the first trunk segment, lacks spinous processes on the terminal sternal plates, and has slightly longer, more pointed terminal tergal extensions. Other differences are mentioned in the discussion of *E. pennaki* that follows.

**Etymology.**—This species is named in honor of Eugene N. Kozloff, a fellow student of the Kinorhyncha.

*Echinoderes pennaki* Higgins

**Figures** 22–25


**Redescription.**—Holotypic adult female (Figures 22–25), trunk length, 40± μm; MSW–8, 62 μm, 15
FIGURES 22–23.—Echinoderes pennaki, holotypic female (USNM 29746), neck and trunk segments; 22, ventral view; 23, dorsal view.
percent of trunk length; SW, 56 μm, 14 percent of trunk length.

Second segment with 16 anteriorly rounded placids; midventral placid slightly truncate, distinctly larger than adjacent placids; trichoscalid plates on sides of midventral placid indented slightly on anterior margin, short and broad, trichoscalid plates on dorsal surface similar but equally as broad as long.

Segments 3–12 with prominent hairs (10–15 μm), pattern distinctive (Figures 22–23); posterior border of segments 3–11 with pectinate fringe both dorsally and ventrally, fringe on ventral surface of segment 3 almost spinose, more finely pectinate on remaining segments, slightly evident near posterior border of 12th sternal plates; terminal segment with minute hairs on border of tergal and sternal plates, posterior margin of tergal plate deeply incised forming pointed extensions mesial to base of each lateral terminal spine, sternal plates broadly rounded without spinous extensions (Figures 24, 25).

Middorsal spines on segments 6–10, increasing uniformly in length, 48–70 μm, mean length 59.6 μm, 15 percent of trunk length; lateral spines on segments 7–11, L–4 (=adhesive tube) absent although a scar, or perhaps a sensory spot, located slightly mesial to usual position of L–4; L–7 shorter (14 μm) than remaining lateral spines (32–36 μm) subequal in length, mean length of lateral spines 29.8 μm, 7 percent of trunk length; lateral terminal spines long, 156 μm, 39 percent of trunk length; lateral terminal accessory spines 52 μm in length.

Pachycycli well developed, forming distinctive pattern at ventral midline and superficial to attachment of lateral terminal spine muscles on segment 13; small muscle scars visible near midventral line of segments 3–4, 7, 11, and 12, more prominent scars dorsolaterally on segments 3, 5–12; sensory spots situated ventrolaterally on segment 3 and possibly on segment 4 (possibly adhesive tube openings?).

Material Examined.—4 adult females including holotype (USNM 29746) and 3 paratypes (USNM 29747); col. P. L. Illg, 16 July 1958, East Sound, Orcas Island, Washington, USA, from a depth of 32 meters.

Remarks.—Eighteen years of research on the Kinorhyncha has prompted me to reexamine my first species descriptions with better experience to guide me. The combination of this experience and better optical instruments has allowed me to illustrate and describe E. pennaki more accurately. For example, the range of “total length” given in my original description (Higgins, 1960) is “390–430 μm (taken along dorsal surface between anterior edge of second zonite and posterior edge of zonite 13).” More standard measurements are now taken from the anterior edge of segment 3 to the posterior edge of segment 13. Similarly, the maximum width of 80–90 μm originally given for this species differs from the more precise and standardized measurement of maximum sternal width as noted in previous publications (Higgins, 1967).

Echinoderes pennaki most closely resembles E. remanei (Blake, 1930) redescribed by me (Higgins, 1964a). The two species differ in size: E. pennaki is larger (380–404 μm) than E. remanei 282–358 μm) yet both have the same spination formula (D–6–10, L–4? 7–11). Both have a prominent spinous fringe on the posteroventral border of segment 3; this feature is more prominent in E. remanei and also occurs on the fourth segment. The midventral
placid of *E. remanei* is expanded laterally along its anterior margin, and the border of the terminal sternal plates is pointed, not rounded as in *E. pennaki* (Figure 24). Our understanding of both species would benefit from an expanded study of their taxonomic characters based on larger numbers of individuals in a given sample.

**Echinoderes pacificus** Schmidt

*Figures 26–31*


This species has been described with considerable accuracy by my colleague, Dr. Peter Schmidt (1974). In studying the holotype and paratype material sent to me by him, however, certain additional information was revealed by mounting specimens in Hoyer's and observing them with differential interference contrast optics. I have reillustrated *E. pacificus* (Figures 26–31) in order to facilitate the comparison of this species with others that might be confused with it.

Segments 3–12 are covered with short hairs in a distinctive pattern (Figures 26, 27). A fine pectinate fringe is evident ventrally on the posterior border of segments 4–13 although it is much less distinct on segment 12; segments 6–13 exhibit this fringe dorsally.

As noted in the discussion of *E. kozloffi*, the short (12–17 μm) lateral spine on segment 12 of *E. pacificus* is diagnostic. This spine tends to curve away from the trunk. Slightly posterior to it, at the junction of segments 12 and 13, there is a sensory hair (Figures 29–31) not reported in the original description.

Small muscle scars (2–3 μm in diameter), similar to sensory spots, are present anterolaterally on the ventral surface of the first trunk segment. Narrow, slitlike scars occur posterior to the sensory spots on sternal plates 7–9. More distinctive muscle scars (Figure 26) occur near the lateral margin of the sternal plates of segment 9; similar scars are situated near the sensory spots of the 10th sternal plates. Sensory spots occur on either side of the ventral midline of segments 4–12. Three spots are present on the dorsal surface of the first trunk segment; only the median spot persists on the following two trunk segments (segments 4–5). Sensory spots on the segments bearing middorsal spines are on both sides of the midline. Two middorsal sensory spots appear to be on segment 12; one of these may be associated with segment 13.

**Material Examined.**—Holotypic male, TL 372 μm (USNM 55335); 8 paratypic females and 7 paratypic males (USNM 55336); col. P. Schmidt, July–September 1972, Academy Bay, Station IX, 5c, upper subtidal sediments.

**Remarks.**—As noted in the discussion of *E. kozloffi*, this species closely resembles *E. pacificus*. Both species share the same spination formula with *E. pilosus, E. ehlersi, E.worthingi,* and *E. ferrungineus* (*E. dujardinii* is similar but has a lateral accessory spine on segment 10).

*Echinoderes ehlersi, E. worthingi,* and *E. ferrungineus* are smaller, 210–260 μm trunk length, although the latter species shares with *E. pacificus* the presence of a sensory hair posterior to the lateral spine on segment 12. *Echinoderes pacificus* is most easily distinguished from all species having the same spination formula by its short lateral spine on segment 12 and the prominent border of hairs on the terminal sternal plates.

**Echinoderes brevicaudatus, substitute name for E. brevispinosus** Higgins

During the course of the present investigation, I discovered that the name *E. brevispinosus* was first used by Metschnikoff (1869:190), corrected to *E. brevispinosus* by Panceri (1876:4), and synonymized with *E. dujardinii* by Zelinka (1928:228). Since I inadvertently applied this preoccupied name to a species from the Red Sea (Higgins, 1966a), I now propose that it be replaced by the substitute name, *Echinoderes brevicaudatus.*
FIGURES 26-27.—Echinoderes pacificus, paratypic female (USNM 53336 RH162.1), neck and trunk segments: 26, ventral view; 27, dorsal view.
FIGURES 28-31.—Echinoderes pacificus, segments 12-15: 28, ventral view, lateral half, paratypic female (USNM 53336, RH162.1); 29, dorsal view, lateral half of same paratypic female; 30, ventral view, lateral half, paratypic male (USNM 53336, RH162.9); 31, dorsal view, lateral half of same paratypic male.
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Bibliography, depending upon use, is termed “References,” “Selected References,” or “Literature Cited.” Spell out book, journal, and article titles, using initial caps in all major words. For capitalization of titles in foreign languages, follow the national practice of each language. Underline (for italics) book and journal titles. Use the colon-parentheses system for volume/year/page citations: “10(2):5-9.” For alignment and arrangement of elements, follow the format of the series for which the manuscript is intended.

Legends for illustrations must not be attached to the art nor included within the text but must be submitted at the end of the manuscript—with as many legends typed, double-spaced, to a page as convenient.

Illustrations must not be included within the manuscript but must be submitted separately as original art (not copies). All illustrations (photographs, line drawings, maps, etc.) can be intermixed throughout the printed text. They should be termed Figures and should be numbered consecutively. If several “figures” are treated as components of a single larger figure, they should be designated by lowercase italic letters (underlined in copy) on the illustration, in the legend, and in text references: “Figure 9b.” If illustrations are intended to be printed separately on coated stock following the text, they should be termed Plates and any components should be lettered as in figures: “Plate 9b.” Keys to any symbols within an illustration should appear on the art and not in the legend.

A few points of style: (1) Do not use periods after such abbreviations as “mm, ft, yds, USNM, NNE, AM, BC.” (2) Use hyphens in spelled-out fractions: “two-thirds.” (3) Spell out numbers “one” through “nine” in expository text, but use numerals in all other cases if possible. (4) Use the metric system of measurement, where possible, instead of the English system. (5) Use the decimal system, where possible, in place of fractions. (6) Use day/month/year sequence for dates: “9 April 1976.” (7) For months in tabular listings or data sections, use three-letter abbreviations with no periods: “Jan, Mar, Jun,” etc.

Arrange and paginate sequentially EVERY sheet of manuscript—including ALL front matter and ALL legends, etc., at the back of the text—in the following order: (1) title page, (2) abstract, (3) table of contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes, (8) glossary, (9) bibliography, (10) index, (11) legends.