Zoologica Scripta, Vol. 18, No. 2, pp. 211–221, 1989
Printed in Great Britain

0300-3256/89 $3.00 + .00
Maxwell Pergamon Macmillan plc


# *Echinoderes higginsi* sp.n. (Kinorhyncha, Cyclorhagida) from the southern North Sea with a key to the genus *Echinoderes* Claparède

RONY HUYS and AUGUST COOMANS

*Accepted* 12 *April* 1988

Huys, R. & Coomans, A. 1989. *Echinoderes higginsi* sp.n. (Kinorhyncha, Cyclorhagida) from the southern North Sea with a key to the genus *Echinoderes* Claparède.—*Zool. Scr. 18:* 211–221.

*Echinoderes higginsi* sp.n. is described from shallow subtidal sand north of the mouth of the Westerscheldt estuary, The Netherlands. The species is compared with other species having the same spine formulae. It appears to be most closely related to *E. kristenseni* Higgins, 1983 and, to a lesser extent, to *E. riedli* Higgins, 1966. *Condyloderes multispinosus* (McIntyre, 1962) is reported from the same locality, the first report of this centroderid kinorhynch since the original description. Some additional information on *E. levanderi* Karling, 1954 is presented. The presence of lateroventral adhesive tubes on the fourth segment, lateral spines on segment 7 and small additional setae on segment 12 in the male is noted. *Echinoderes canariensis* Greeff, 1869 and *E. agigens* Băcescu, 1968 are considered *species inquirendae*. The distribution of adult North Sea Kinorhyncha is reviewed. Finally, an up-dated key, covering 43 valid species of *Echinoderes*, is presented.

*Rony Huys & August Coomans, Zoology Institute, State University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium.*

## Introduction

Although the North Sea is one of the most intensively investigated regions of the world, and despite numerous surveys of the meiofauna (see Heip *et al.* 1983 for a review), kinorhynchs have scarcely been mentioned in the literature since the discovery of the phylum in 1841 by the French naturalist Félix Dujardin. North Sea records were until now limited to 10 valid species (based on adults), mainly belonging to the Cyclorhagida (Fig. 1). *Kinorhynchus* Sheremetevskij, 1974 (= *Trachydemus* Zelinka, 1907) and representatives of the neotenic Neocentrophyidae have thus far not been recorded in North Sea waters.

The first record is that of Leuckart (1854), who mentioned 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 and since then has been reported from several other localities (Higgins 1977*b*). Metschnikoff (1865) also reported *E. dujardinii* from Helgoland, but Zelinka (1928) considered it to represent a new species *E. subfuscus* Zelinka, 1928. A second species *E. monocercus* Claparède, 1863 was based on immature stages and regarded as *incerta sedis* by Zelinka (1928).

The only published observation of kinorhynchs along the Belgian coast is that of Greeff (1869), who found five species in the vicinity of Ostend and Nieuwpoort: *E. dujardinii*, *E. monocercus* and three new species *E. borealis* Greeff, 1869, *E. setiger* Greeff, 1869 and *E. lanuginosa* Greeff, 1869. Both *E. monocercus* and *E. lanuginosa* were based on immature stages and assigned to a 'larval genus' as *Centropsis greeffi* Zelinka, 1928 and *C. lanuginosa* (Greeff, 1869), respectively (Zelinka 1928). *Echinoderes borealis* was considered a *nomen dubium* by Higgins (1966*b*).

Zaneveld (1938), working at the beach of Scheveningen, The Netherlands, found two species—*E. dujardinii* and *Pycnophyes dentatus* (Reinhard, 1881).

Along the east coast of Great Britain Kinorhyncha have been recorded by Brady (1903), Zelinka (1928), McIntyre (1962) and Moore (1973). Brady (1903) provisionally identified six specimens of *E. pellucidus* Reinhard, 1881 from muddy sand at 4–6 fathoms depth off the Yorkshire coast, and recorded an unidentified individual of another species from the north shore of the Solway Firth. According to Zelinka (1928), *E. pellucidus* is a juvenile homalorhagid (Hyalophyes stage). In his monograph published in 1928 Zelinka lists *P. dentatus*, *P. calmani* Southern, 1914 and the larval *Hyalophyes calmani* Zelinka, 1928 from the St Andrews–Dundee area, Scotland. McIntyre (1962) identified 33 specimens from the deep subtidal mud of Fladen Ground, Scotland. In addition to *E. setiger* he noted the sole North Sea record for *Condyloderes multispinosus* (McIntyre, 1962), *Semnoderes armiger* Zelinka, 1928 and *P. zelinkaei* Southern, 1914. His find of *Centrophyes denticulatus* Zelinka, 1928 is nothing more than a larva. Moore (1973) found *Campyloderes macquariae* Johnston, 1938 associated with holdfasts of the sublittoral kelp *Laminaria hyperborea* in various localities along the east coast of Britain.

Except for the data expressed in a personal letter from Dr R. P. Higgins, no information on kinorhynchs is available from the central North Sea. *Pycnophyes calmani* and an unknown *Semnoderes* species were identified from

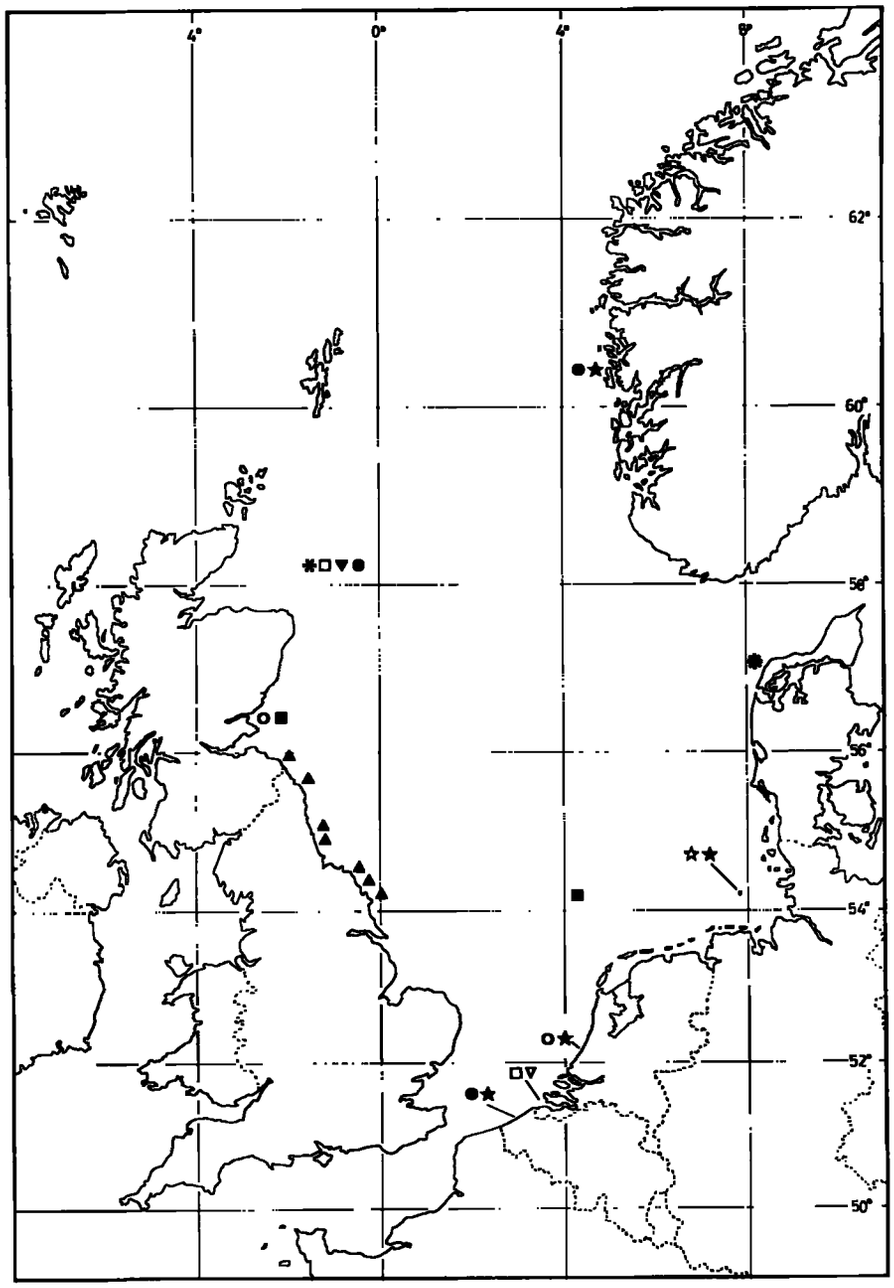


*Fig. 1.* Distribution records of adult North Sea Kinorhyncha: *Echinoderes dujardinii* Claparède, 1863 (★); *E. setiger* Greeff, 1869 (●); *E. subfuscus* Zelinka, 1928 (☆); *E. higginsi* sp.n. (▽); *Condyloderes multispinosus* (McIntyre, 1962) (□); *Campyloderes macquariae* Johnston, 1938 (▲); *Semnoderes armiger* Zelinka, 1928 (∗); *Cateria submersa* Gerlach, 1969 ( ● ); *Pycnophyes calmani* Southern, 1914 (■); *P. zelinkaei* Southern, 1914 (▼); *P. dentatus* (Reinhard, 1881) (○).

mud samples taken at a depth of about 50 m south of Clay Deep (54°20′N, 04°20′E).

The only reference of northern North Sea Kinorhyncha is that of Schepotieff (1907), who found five *Echinoderes* species in a wide variety of habitats in Byfjord, Bergen, Norway. Of these, only *E. dujardinii* and *E. setiger* are valid species, whilst *E. lanuginosus* and *E. monocercus*—both assigned to the 'larval genus' *Centropsis* by Zelinka (1928)—and *?E. acerca* Reinhard, 1881—altered into *Leptodemus acercus* (Reinhard, 1881) Zelinka, 1928—are based on immature stages.

Finally, the sole North Sea cryptorhagid, *Cateria submersa* Gerlach, 1969, was discovered in subtidal medium coarse sand off the Jutland coast, Denmark.

A monthly survey of the harpacticoid copepod community in a subtidal sandy locality of the Southern Bight of the North Sea (Huys *et al.* 1986) produced several cyclorhagid kinorhynchs, one of which is new to science and ascribed to the genus *Echinoderes*.

## Material and methods

Samples of fine sand (Md: 0.235 mm; 0.39% mud) were collected from 7.5 m depth north of the mouth of the Westerscheldt estuary in the Southern Bight of the North Sea (51°28′25″N; 03°28′10″E) and fixed with neutralised 7% formaldehyde. Meiofauna was extracted by decantation and/or using a centrifugation–floatation technique based on Ludox, and stored in 7% formaldehyde.

Kinorhynchs were transferred to glycerine and individually placed in modified Hoyer's mounting medium (Higgins 1983) between two coverslips and positioned on Cobb aluminium slide frames in order to allow observation of both dorsal and ventral sides. Preparations were sealed with glyceel. Leitz differential interference contrast optics were used for examination. According to the standard format of abbreviations

and terminology (Higgins 1967, 1969) measurements are given in μm. Maximum sternal width (*MSW*) is measured at the anteroventral margin of the widest pair of sternal plates first encountered from anterior to posterior. Standard width (*SW*) is measured at the anteroventral margin of the sternal plates of segment 12. Placids and trichoscalid plates are numbered beginning with the mid-ventral placid as zero; those on either side are each number 1, those next in sequence number 2, etc. Adhesive tubes of zonite 4 are considered homologues of other lateral spines.

A few specimens were prepared for SEM examination by dehydration through graded ethanol, critical point drying, mounting on stubs and sputter coating with gold.

## Abbreviations

| | |
|---|---|
| *TL* | trunk length |
| *SW* | standard width = sternal width of segment 12 |
| *SW/TL* | ratio of standard width to trunk length |
| *MSW-9* | maximum sternal width at segment 9 |
| *MSW/TL* | ratio of maximum sternal width to trunk length |
| *Dm* | mean length mid-dorsal spines |
| *Dm/TL* | ratio of mean length mid-dorsal spines to trunk length |
| *D-(6, 8, 10)* | length of mid-dorsal spines (6, 8, 10) |
| *Lm* | mean length lateral spines |
| *Lm/TL* | ratio of mean length lateral spines to trunk length |
| *L-4(AT)* | length lateral spine segment 4 (adhesive tubes) |
| *L-(7–12)* | length lateral spines (7–12) |
| *LA-10* | length accessory lateral spine segment 10 |
| *LTS* | lateral terminal spine length |
| *LTS/TL* | ratio of lateral terminal spine length to trunk length |
| *LTAS* | lateral terminal accessory spine length |
| *LTAS/TL* | ratio of lateral terminal accessory spine length to trunk length |
| *P-(1, 2, 3)* | length penile spines (1, 2, 3) |

## Systematics

Order Cyclorhagida Zelinka, 1896

Family Echinoderidae Bütschli, 1876

### Genus *Echinoderes* Claparède, 1863

### *Echinoderes higginsi* sp.n. (Figs. 2–4)

*Material examined.* Holotype: adult female, TL 284 μm (Figs. 2A, B, 3B, D, E), north of Westerscheldt mouth, The Netherlands; coll. R. Huys, 26 Jan. 1983. Paratypes: allotypic male, TL 293 μm (Figs. 3F, G); other paratypes are 5 females and 2 males, locality data as for holotype. The type series is deposited in the collection of the Recent Invertebrates Section of the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels under no. IG 27226.

Associated kinorhynch fauna: 3 adult specimens of *Condyloderes multispinosus* (McIntyre, 1962) and 1 juvenile stage of *Pycnophyes* sp.

#### *Diagnosis*

*Echinoderes*. Mid-dorsal spines on segments 6, 8 and 10, increasing uniformly in length posteriorly, flexible; lateral spines on segments 4 (adhesive tubes) and 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 long, 128–143 μm, 42–47% of trunk length, smooth; fine cuticular hairs arranged in irregular pattern, but perforation sites notably absent; segment 13 with rounded tergal plates and prominent sternal extensions; male with minute dorsolateral seta on segment 12 and 3 pairs of penile spines.

#### *Description*

Adult female: trunk length 275–300 μm; MSW-9, 48–52 μm, 16.9–17.7% of trunk length; SW 44–46 μm, 16.0–16.6% of trunk length. Adult male: trunk length 282–293 μm; MSW-9, 48–50 μm, 16.5–17.3% of trunk length; SW 42–45 μm, 15.7–16.2% of trunk length. Posterior tergal and sternal borders of trunk segments with slight pectinate fringe. Trunk segments without perforation sites but with cuticular hairs (except segment 3) generally distributed over dorsal and ventral surfaces, being distinctly shorter in the medial region of the sternal plates (Figs. 3B, 4D).

Segment 1 (head) with 6 trichoscalid plates (Figs. 3A–C, 4B–D); ventral trichoscalid plates widest (9.5 μm), covering placids 1–3, articulating with placid 1; dorsal trichoscalid plates smallest (6 μm), subcircular, articulating with placid 7; lateral trichoscalid plates intermediary in size (8 μm) and covering placids 4 and 5, articulating with placid 5; each plate bearing one trichoscalid; small structures with bifurcated basis present between several placids (bearing spinoscalids).

Segment 2 (neck) with 16 placids, tapering anteriorly (Figs. 3A–C, 4B–D); mid-ventral placid widest (12 μm at base) and having 4 small rod-shaped plates at the top, others narrower (about 7 μm).

Segment 3 31 μm long; dorsal surface (Fig. 3A) with long cuticular hairs (no distinct pattern), a single mid-dorsal and 2 smaller subdorsal cuticular scars near anterodorsal margin; posterior half of ventral surface (Figs. 3B, 4D) with long cuticular hairs, 3 pairs of muscle scars and 2 small cuticular scars; anterior half with 2 ventrolateral sensory spots.

Segment 4 22 μm long (measured between anterior border and posterior fringe of segment); pachycyclus well developed; a single angular muscle scar on either side of ventral midline; 2 subventral cuticular scars near anterior margin and covered by the fringe of segment 3; small lateral spines (adhesive tubes), 15 μm long, midway in segment (Figs. 3B, 4D), in line with ventrolateral articulation zones of remaining segments (Fig. 2A); a single mid-dorsal cuticular scar near anterior margin.

Segment 5 32 μm long; pachycyclus well developed; mid-ventral articulation of sternal plates clearly visible (Figs. 3B, 4D); dorsal surface with a mid-dorsal cuticular scar and 2 subdorsal sensory spots near anterior margin; ventral surface with a single angular muscle scar on either side of ventral midline and 2 subventral cuticular scars; ventral sensory spots absent.

Segment 6 35 μm long; pachycyclus similar to preceding one; mid-dorsal spine D-6 (27–34 μm) anteriorly displaced, near fringe of previous segment (Fig. 2B); a single cuticular scar on either side of dorsal midline, laterally adjacent and slightly anterior to D-6; angular muscle scar on either side of ventral midline; cuticular scars near middle of sternal plate in line with those of previous segments; neither ventral nor dorsal sensory spots present.

Segment 7 35 μm long; pachycyclus similar to preceding one; mid-dorsal spine absent; mid-dorsal cuticular scar near anterior margin; a single subdorsal sensory spot on either side of dorsal midline, in line with those of segment 5 (Fig. 2B); lateral spine L-7 (16–18 μm) on tergal plate

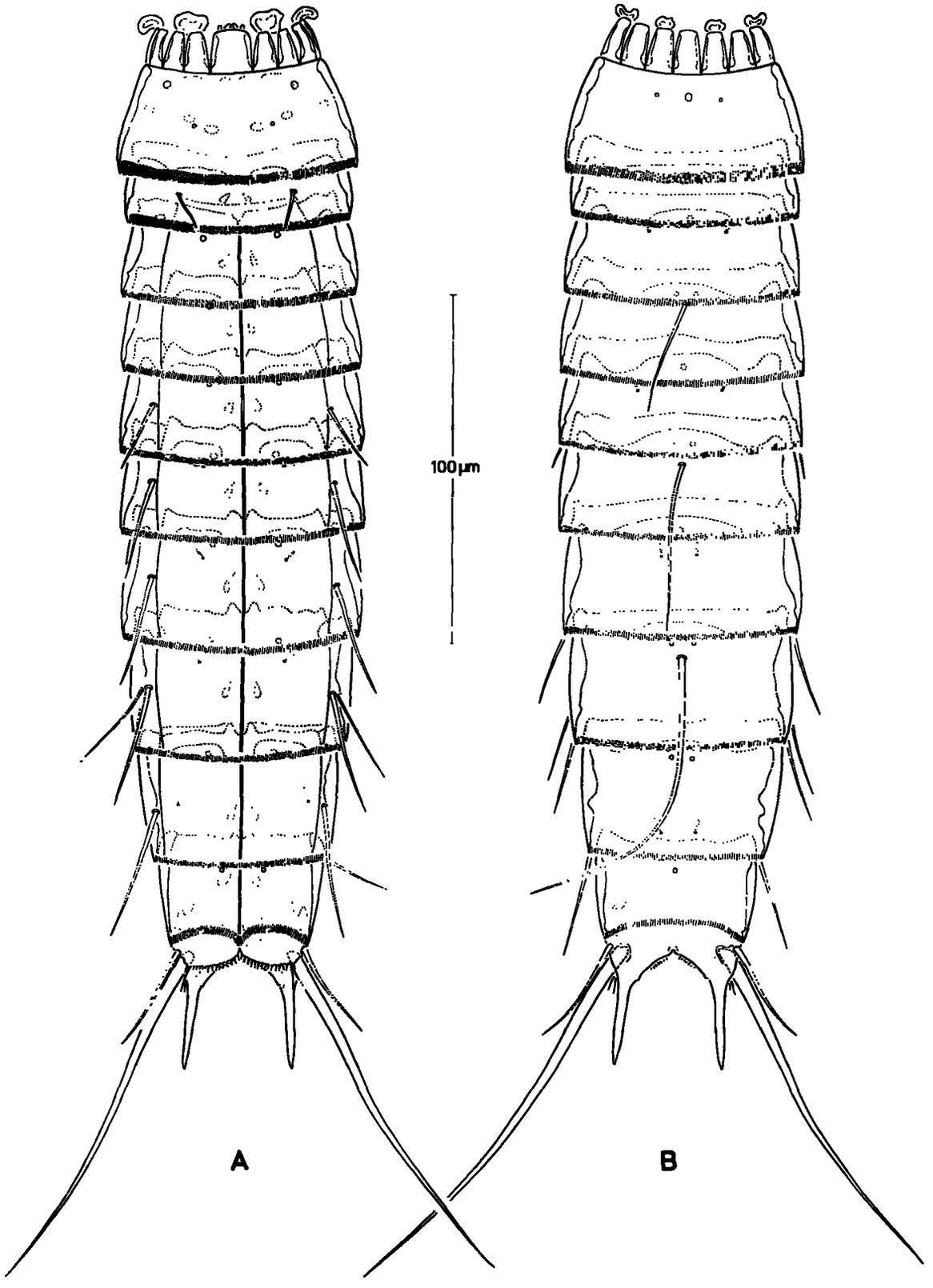


*Fig. 2. Echinoderes higginsi* sp.n., holotype female.—*A*. Habitus, ventral view.—*B*. Habitus, dorsal view.

adjacent to junction with each ventral plate; cuticular scar near middle of each sternal plate as in previous segment; angular muscle scar on either side of ventral midline; ventral sensory spots absent (Fig. 2A).

Segment 8 36 µm long; pachycyclus as in segment 7; mid-dorsal spine D-8 (39–43 µm) anteriorly displaced near fringe of preceding segment; a single cuticular scar on either side of dorsal midline, laterally adjacent and slightly anterior to D-8; dorsal sensory spots absent (Fig. 2B); lateral spines L-8 (24–26 µm) near junction with sternal plates; cuticular scars and muscle scars as in preceding segment; a single sensory spot on either sternal plate, laterally adjacent and slightly posterior to cuticular scar (Fig. 2A).

Segment 9 41 µm long; pachycyclus as in preceding segment; maximum sternal width (MSW) 48–52 µm; mid-dorsal spine absent; sensory spot on either side of dorsal midline, laterally adjacent and slightly posterior to single

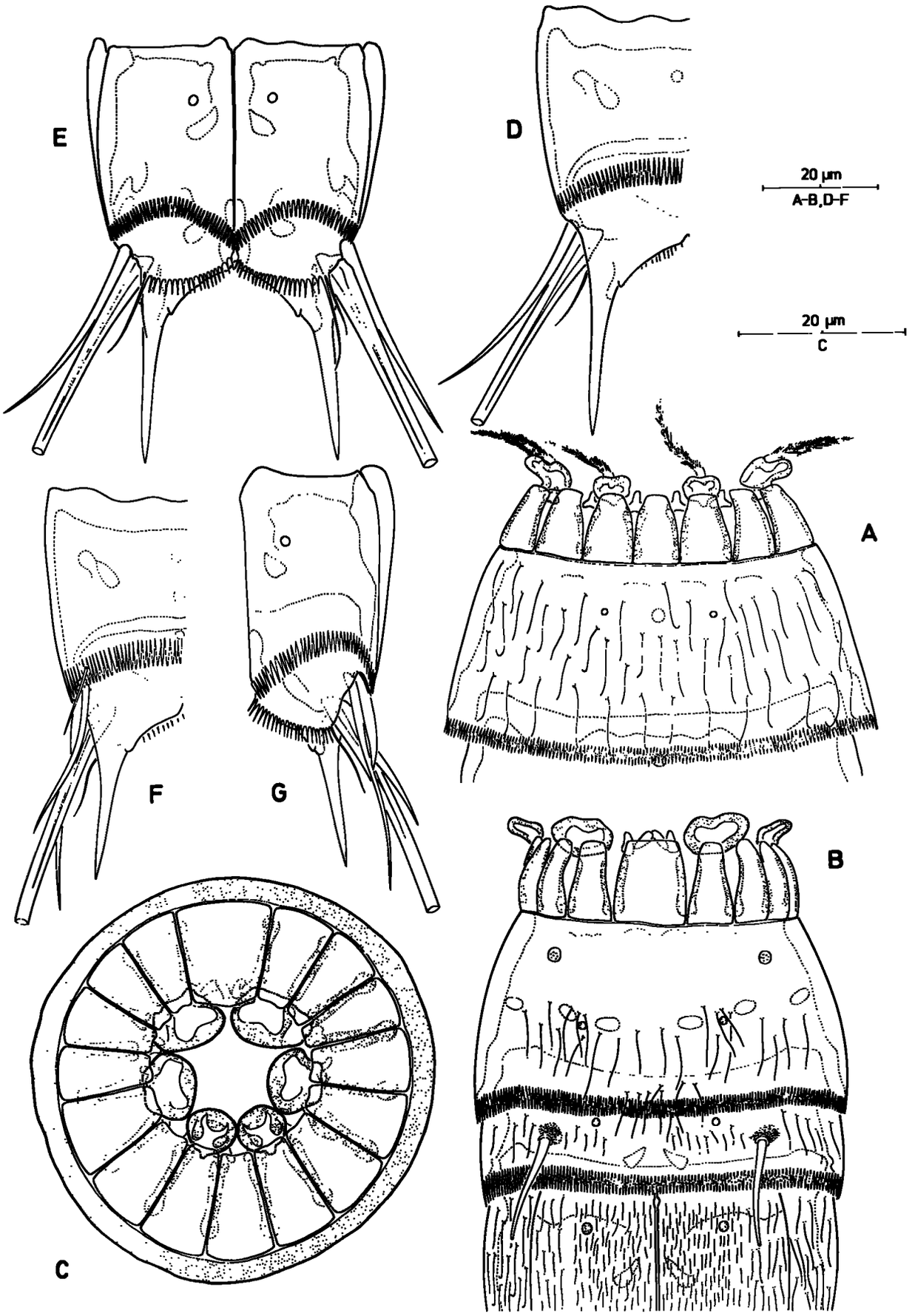


*Fig. 3. Echinoderes higginsi* sp.n.—*A*. Segments 2–3, including trichoscalid plates (paratype female), dorsal view.—*B*. Segments 2–4, including trichoscalid plates (trichoscalids not drawn; holotype female), ventral view.—*C*. Second segment and trichoscalid plates (paratype female), frontal view.—*D*. Segments 12–13 (holotype female), dorsal view.—*E*. Segments 12–13 (holotype female), ventral view.—*F*. Segments 12–13 (allotype male), dorsal view.—*G*. Segments 12–13 (allotype male), ventral view.

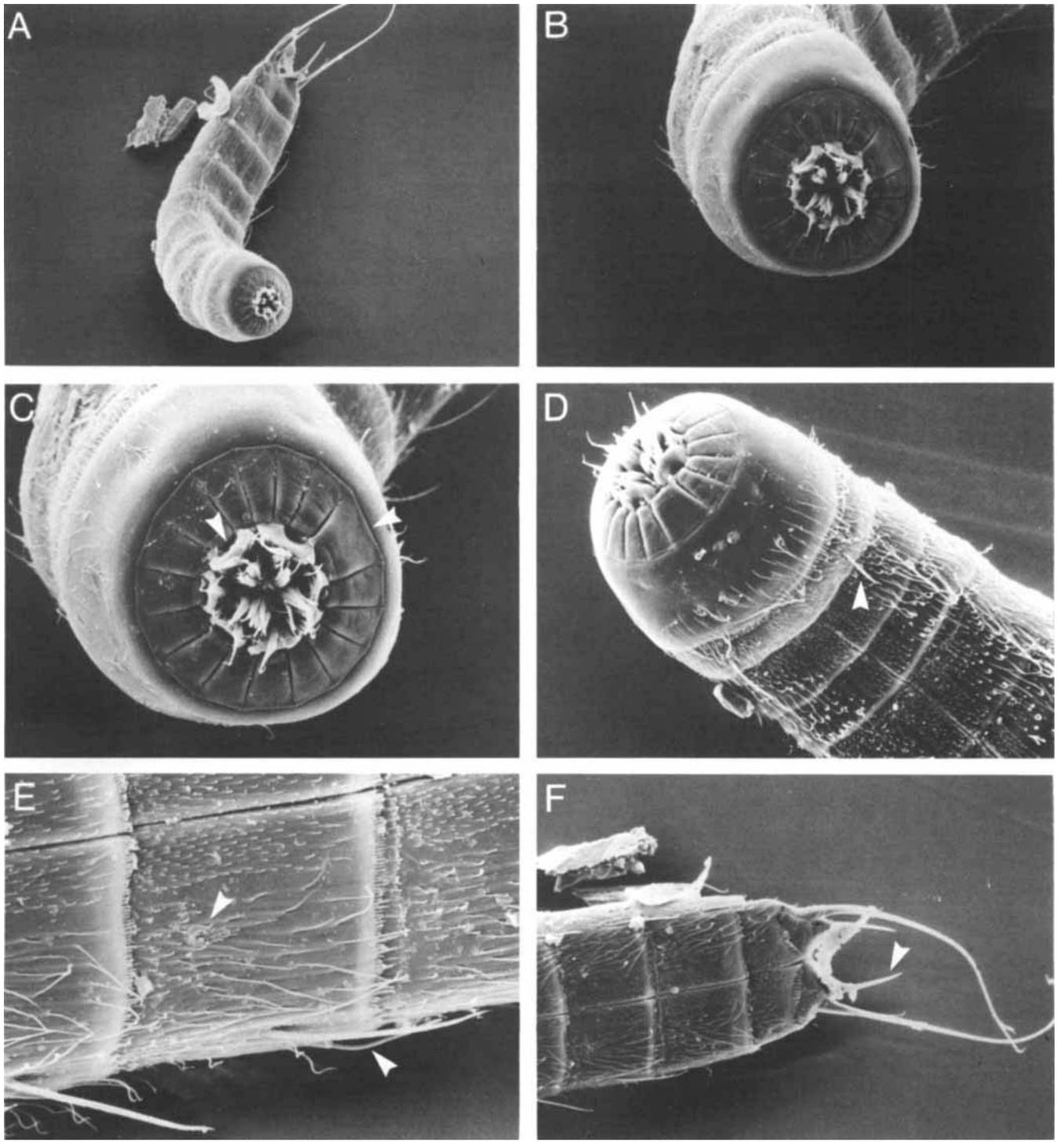


*Fig. 4. Echinoderes higginsi* sp.n., female (SEM photography)—*A*. Habitus, lateroventral view (×270).—*B*. Segments 2–3, anterior view (×670).—*C*. Segments 2–3, anterior view (*arrows* indicating mid-ventral placid and trichoscalid plate) (×1025).—*D*. Segments 3–7, ventral view (*arrow* indicating adhesive tube of segment 4) (×740).—*E*. Segments 9–11, ventral view (*arrows* indicating sensory spot and lateral accessory spine of segment 10) (×1580)—*E*. Segments 10–13, ventral view (*arrow* indicating long tergal extension) (×540).

mid-dorsal cuticular scar (Fig. 2B); lateral spine L-9 25–27 μm long; angular muscle scars and cuticular scars similar to those of segment 8; sensory spot near middle of either sternal plate and slightly posterior to cuticular scars (Fig. 2A).

Segment 10 41 μm long; pachycyclus similar to preceding one) mid-dorsal spine D-10 (70–82 μm) more flexible in appearance than preceding mid-dorsal spines; a single cuticular scar on either side of dorsal midline, laterally adjacent and slightly anterior to D-10; dorsal sensory spots absent (Fig. 2B); lateral spine L-10 (28–30 μm) near junction with each ventral plate; lateral accessory spine LA-10 (18–21 μm) slightly displaced dorsally, blunt at tip (Figs. 2A, 4E); ventral angular muscle scars, cuticular scars and sensory spots similar to segment 9.

Segment 11 40 μm long; pachycyclus well developed; cuticular scar on either side of dorsal midline near fringe of segment 10; subdorsal sensory spots in line with those of segment 9 but posteriorly displaced (Fig. 2B); lateral spine L-11 30–32 μm long; ventral cuticular scars and angular muscle scars similar to those of preceding

segment; a single sensory spot on either sternal plate, laterally adjacent to junction with tergal plate and slightly anterior to L-11 (Fig. 2A).

Segment 12 (Figs. 3D, E) 26 μm long; standard width (SW) 44–46 μm; pachycyclus as in preceding segment; a single mid-dorsal cuticular scar anteriorly; 2 prominent dorsolateral muscle scars; ventral muscle scars situated closely to fringe of segment 11; cuticular scars closer to ventral midline than preceding ones; lateral spines absent; neither dorsal nor ventral sensory spots present.

Segment 13 (Figs. 3D, E) shortest; lateral terminal spines (LTS) long (128–140 μm), 46–50% of trunk length, smooth; lateral terminal accessory spines (LTAS) 34–37 μm long, 12–14% of trunk length; tergal plate without cuticular scars, bifurcated and forming 2 very elongated, pointed tergal extensions mesial to lateral terminal spines (inner margin with a small cusp); sternal plates rounded, each with 2 small hair-like processi on lateral margin, and fringed on mesial margin.

Mean length of mid-dorsal spines (Dm) 49–54 μm, 16.9–17.6% of trunk length; mean length of lateral spines (Lm) 22–25 μm, 7.4–8.5% of trunk length.

Adult males chiefly differing from females in the following respects (Figs. 3F, G): (1) presence of a small dorsolateral seta (13 μm) on segment 12; (2) lack of lateral terminal accessory spines; (3) tergal extensions are somewhat shorter; (4) lateral margin of sternal plates with only 1 hair-like processus; (5) presence of 3 pairs of penile spines—the first (P-1) the anterior-most of the three and dorsally displaced (29 μm), the second (P-2) the shortest (and probably the functional one), somewhat swollen and slightly truncate (17 μm) and the third (P-3) the longest (38 μm), situated adjacent to P-2.

*Etymology*. This species is named in honour of Dr Robert P. Higgins, Smithsonian Institution, Washington, D.C. who has studied kinorhynchs in all their facets for nearly 30 years.

## Discussion

Forty-eight species of *Echinoderes* have been described on the basis of adult specimens. In addition, 28 species are established on the basis of juvenile stages which are not likely to be attributed to any adult and must therefore be ranked as *nomina dubiae* (for a synopsis of the latter species, see Higgins 1983, table 6). The problematic species *E. borealis* Greeff, 1869 should be considered *nomen dubium* instead of *species inquirenda*, since it is based on immature stages, its juvenile character being corroborated by the presence of only 12 segments and of a mid-dorsal spine on segment 11.

Another species described by Greeff (1869), *E. canariensis* is, in our opinion, unidentifiable on the basis of the poorly rendered illustrations and the inadequate description. Its alleged possession of lateral spines on segments 3 and 6–9 is questionable, since it has never been found elsewhere, not even in juveniles. No information is given concerning lateral accessory spines in general and lateral spines (or setae) on segment 12. The only useful character apparent from the description is the presence of mid-dorsal spines on segments 6–10, being the most common spine formula and shared by 23 other *Echinoderes* species. Since there is no possibility of identifying any specimens from Greeff's description, the species should be ranked as a *species inquirenda*.

*Echinoderes agigens* Bărcescu, 1968 has a lateral spine configuration which is highly suspect. The presence of L-6 has thus far been recorded only in the unidentifiable species *E. steineri* (Chitwood, 1951) and in *E. druxi* d'Hondt, 1973. The questionable spine formula of the latter species has been scrutinized previously by Higgins (1978, 1983). In addition, Bărcescu's (1968) original description is merely diagrammatic and lacks sufficient detail to allow identification satisfactorily. The species must be redescribed and pending this can be considered only *species inquirenda* in the genus.

Of the 43 species (including *E. higginsi* sp.n.) based on adult specimens and identifiable on the basis of their description (Table I), nine share the mid-dorsal spine formula D-(6, 8, 10).

*Echinoderes arlis* Higgins, 1966, reported from the Arctic Ocean, differs from the new species by lacking lateral spines on segments 7 and 12 (in the male) and lateral accessory spines on segment 10. The big difference in trunk length (380–420 μm) also helps differentiating it from *E. higginsi* sp.n. Both species have elongated pointed tergal extensions, those of *E. arlis* being narrower.

The new species resembles *E. newcaledoniensis* Higgins, 1967 in having the same lateral spine formula (L-4, 7–11) and lateral accessory spines on segment 10. The New Caledonian species, however, is unique within the genus in its possession of additional lateral accessory spines on segments 4, 8, 9 and 11 and subdorsal spines on segments 4 and 10. Males of both species share a small lateral seta on segment 12, situated dorsolaterally and slightly anterior to the penile spines.

*Echinoderes peterseni* Higgins & Kristensen, 1988, described from West Greenland and being most closely related to *E. newcaledoniensis*, also exhibits lateral spines on segments 4 and 7–11. However, the Greenland species differs considerably from *E. higginsi* in the presence of paired subdorsal and lateral accessory spines on segment 4. Additional differences are found in the absence of the small lateral seta on segment 12 in males and in the outline of the terminal tergal plates.

Concerning the spine formulae, *E. wallaceae* Higgins, 1983, collected from Carrie Bow Cay, Belize, differs only in the lack of the small spine L-12 in the male. Noticeable differences are the long, pointed, blade-like tergal extensions and the abundance of cuticular perforations that usually accompany trunk hairs.

Among the other members of the species group, *E. bermudensis* Higgins, 1982 is easily distinguished by its absence of lateral accessory spines on segment 10 and of minute additional setae on segment 12 in the male. The species share many traits, e.g. the relative length of most of the spines and the lack of distinct perforation sites, however, the range of their body lengths do not overlap (200–240 μm contrasted with 275–300 μm).

*Echinoderes riedli* Higgins, 1966, *E. abbreviatus* Higgins, 1983 and *E. kristenseni* Higgins, 1985 all have exactly

Table I. *Spine formulae of valid* Echinoderes *species*

| | D | | | | | | L | | | | | | | | | | LA | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4 | 6 | 7 | 8 | 9 | 10 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 FM | 4 | 8 | 9 | 10 | 11 |
| *dujardinii* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | + | − |
| *setiger* | − | + | * | + | + | ? | − | + | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *ehlersi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *worthingi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *capitatus* | − | − | − | − | − | − | − | + | − | − | m | − | − | m | − | * + | − | − | − | − | − |
| *citrinus* | − | + | − | − | + | − | − | − | − | − | + | + | + | + | + | ? + | − | − | − | − | − |
| *ferrugineus* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *remanei* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *pilosus* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *elongatus* | − | + | + | + | + | + | − | − | − | − | − | + | + | + | + | − − | − | − | − | − | − |
| *levanderi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | − + | − | − | − | − | − |
| *maxwelli* | − | − | − | − | − | − | − | − | − | − | + | − | − | + | − | − − | − | − | − | − | − |
| *bengalensis* | − | − | − | − | − | − | − | − | − | − | + | − | − | + | − | − − | − | − | − | − | − |
| *pennaki* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *bookhouti* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *caribiensis* | − | − | − | − | − | − | − | − | − | − | + | − | − | + | + | − − | − | − | − | − | − |
| *arlis* | − | + | − | + | − | + | − | + | − | − | − | + | + | + | + | − − | − | − | − | − | − |
| *riedli* | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − + | − | − | − | + | − |
| *newcaledoniensis* | 2 | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − + | + | + | + | + | + |
| *druxi* | − | + | + | ? | ? | + | − | + | * | * | + | + | + | + | + | − − | − | − | − | − | − |
| *pacificus* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *coulli* | − | − | − | − | − | − | − | − | − | − | m | − | − | m | − | − − | − | − | − | − | − |
| *sublicarum* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *brevicaudatus* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *kozloffi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *gerardi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | + | − |
| *andamanensis* | − | − | − | − | − | − | − | + | − | − | − | − | − | + | + | − + | − | − | − | − | − |
| *bermudensis* | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *bispinosus* | − | + | − | + | − | − | − | + | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *abbreviatus* | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − + | − | − | − | + | − |
| *horni* | − | − | − | − | − | − | − | + | − | − | + | + | + | + | + | − − | − | − | − | + | − |
| *imperforatus* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *truncatus* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | + + | − | − | − | − | − |
| *wallaceae* | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − − | − | − | − | + | − |
| *krishnaswamyi* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + ? | − | − | − | − | − |
| *kristenseni* | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − + | − | − | − | + | − |
| *nybakkeni* | − | + | + | + | + | + | − | + | − | − | + | + | + | + | + | + ? | − | − | − | − | − |
| *angustus* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *aquilonius* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *eximus* | − | + | + | + | + | + | − | − | − | − | + | − | − | + | + | − − | − | − | − | − | − |
| *tubilak* | − | + | + | + | + | + | − | − | − | − | + | + | + | + | + | − − | − | − | − | − | − |
| *peterseni* | 2 | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − − | + | − | − | + | − |
| *higginsi* sp.n. | − | + | − | + | − | + | − | + | − | − | + | + | + | + | + | − + | − | − | − | + | − |

D (mid)dorsal spine; L Lateral spine; LA lateral accessory spine; F female; M male; m not visible or very short; + present; − absent; * doubtful; ? unknown.

the same spine formulae (in both sexes) as the new species. *Echinoderes abbreviatus*, from the Caribbean coast of Central America, however, differs profoundly in the general trunk shape and other relative proportions, including the short stubby, lateral terminal spines (LTS/TL 17%). Like *E. higginsi*, *E. riedli* has a relatively long trunk (268–316 μm), long lateral terminal spines (LTS/TL 52–64%) and lacks cuticular hairs in the anterior half of the ventral surface of segment 3. In the latter species, inhabiting tropical waters and originally described from sandy coral mud from the Red Sea at Al-Ghardaqa, Egypt, the mid-dorsal spines are much shorter and nearly equal in size. The dense pattern of cuticular perforation sites and the blade-like tergal extensions of *E. riedli* are additional distinctive characters. *Echinoderes higginsi* most closely resembles *E. kristenseni*, the most recently described species, with the same spine arrangement and also zoogeographically the closest relative; it is known from *Dentalium* sand from Roscoff, France. Like *E. riedli*, *E. kristenseni* displays abundant cuticular perforations. In addition, it can be distinguished from the new species by the more flexible and longer (LTS 170–214 μm; LTS/TL 61.8–88.5%) lateral terminal spines and by the general outline of the terminal tergal extensions. The mean length of the dorsal spines is also smaller in *E. higginsi*, 49–54 μm contrasted with 74–79 μm.

At the time of its description *E. levanderi* Karling, 1954 needed only to be compared with a few species. In connection with the construction of an up-dated key to the genus, the latter species has been re-examined on the basis of the holotype female (coll. T. Karling) and of material collected south of the Tvärminne Zoological Station, Finland (the Baltic), by Dr J. Sarvala, University of Turku. Karling's original description apparently yielded several errors, which should be rectified as follows: (1) although not clearly visible, adhesive tubes are present on segment 4; (2) the lateral spine formula is not L-(8–11), because of the presence of apparent lateral spines on segment 7 it should be L-(4, 7–11); (3) a small dorsolateral spine is present on segment 12 in the male; (4) L-11 is not twice the length of the preceding lateral spines, yet the lateral spine series increases uniformly in length posteriorly. In addition, the complete absence of lateral accessory spines is noteworthy.

**An up-dated key to the species of *Echinoderes***

Due to the relatively small size and often cryptic characters, a simple key to the genus *Echinoderes* cannot easily be constructed. Previous keys have been published, particularly by Higgins (1960, 1977*b*, 1983) and Higgins & Kristensen (1988).

Re-examining Higgins & Kristensen's (1988) key it attracted our attention that some couplets may cause confusion and consequently the following remarks have to be borne in mind.

(1) According to couplet 9, all species (except *E. krishnaswamyi*) having the spine formula D-(6–10), L-(4, 7–12) and lacking lateral accessory spines should have ". . . ventral plates with more than single row of perforation sites . . .". In *E. imperforatus,* however, fine cuticular hairs appear to be present but perforation sites are notably absent on all segments (Higgins 1983). Moreover, this unusual character was used in couplet 15 to differentiate the latter species from *E. ehlersi, E. sublicarum* and *E. kozloffi.* Higgins' (1986) text (p. 268) and drawings (figs. 1, 2) clearly illustrate that cuticular hairs, as well as associated perforation sites, are absent in *E. nybakkeni.* According to Higgins' (1985) redescription, there is no evidence of perforation sites in *E. worthingi* either; in the latter, cuticular hairs are present, but without distinct pattern.

(2) Couplet 11 may cause some confusion. The statement "Middorsal spine on segment 10 equal or only slightly longer than that on segment 9" is without doubt true for *E. imperforatus, E. pacificus* and *E. ehlersi.* However, in *E. sublicarum, E. kozloffi* and *E. pilosus* the mid-dorsal spine D-10 is 1.5 times longer than D-9 and the measurements (see range) of *E. sublicarum* (Higgins 1977*a*, table II) and *E. kozloffi* (Higgins 1977*b*, table 2) suggest that in some cases D-10 may be twice the length of D-9, as in *E. worthingi* and *E. ferrugineus.*

(3) Following couplet 37, *E. capitatus* should lack lateral spines on segment 4 (adhesive tubes). Zelinka's (1928) illustration of the ventral view (Taf. 3, fig. 5), however, clearly indicates adhesive tubes (reported as 'Klebröhre') on segment 4 and additional lateral spines on segments 7, 10 and 12 (male only?). Higgins (1983), in discussing the relationships of *E. horni* (p. 20), alluded to this configuration as a differentiating character.

(4) Although considered *nomen dubium* by Higgins (1960, 1964), and for that reason worthless for identification purposes, *E. tchefouensis* Lou, 1934 was incorporated in their key.

(5) For the reasons mentioned above, *E. canariensis* and *E. agigens* must rank as *species inquirendae*.

Based on these considerations and on the additional information on *E. levanderi,* an up-dated key to the genus *Echinoderes* is proposed, now covering 43 valid species and applicable to both sexes.

1. Mid-dorsal spines absent . . . . . 2
   Mid-dorsal spines present . . . . . 8
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 . . . . . ***horni*** Higgins, 1983
   Additional lateral spines otherwise; no lateral accessory spine on segment 10 . . . . . 4
4. First two trunk segments enlarged, swollen; additional minute, lateral spines or setae on segments 7 and 10; lateral terminal accessory spines absent in female . . . . . ***capitatus*** (Zelinka, 1928)
   First two trunk segments not enlarged or swollen; additional lateral spines on segments 10 and 11; lateral terminal accessory spines present in female . . . . . ***andamanensis*** Higgins & Rao, 1979
5. Lateral spines on segments 7, 10 and 11 . ***caribiensis*** Kirsteuer, 1964
   Lateral spines on segments 7 and 10 or absent . . . . . 6
6. Lateral terminal spines longer than last 4 trunk segments combined (more than 50% of trunk length) . ***maxwelli*** (Omer-Cooper, 1957)
   Lateral terminal spines shorter than last 3 trunk segments combined (less than 30% of trunk length) . . . . . 7
7. Lateral spines on segments 7 and 10 long (30–40 $\mu$m) and thin . . . . . ***bengalensis*** (Timm, 1958)
   Lateral spines on segments 7 and 10 absent, not visible or very short (10 $\mu$m) and thin . . . . . ***coulli*** Higgins, 1977*a*
8. Mid-dorsal spines on segments 6–10 . . . . . 21
   Mid-dorsal spines otherwise . . . . . 9
9. Mid-dorsal spines on segments 6 and 9 only . ***citrinus*** Zelinka, 1928
   Mid-dorsal spines otherwise . . . . . 10
10. Mid-dorsal spines on segments 6 and 8 only . . . . . ***bispinosus*** Higgins, 1982
    Mid-dorsal spines otherwise . . . . . 11
11. Mid-dorsal spines on segments 6, 7 and 10 only . . . . . ***druxi*** d'Hondt, 1973
    Mid-dorsal spines otherwise . . . . . 12
12. Mid-dorsal spines on segments 6, 7 (possibly 8) and 9 only . . . . . ***setiger*** Greeff, 1869
    Mid-dorsal spines on segments 6, 8 and 10 only . . . . . 13
13. Lateral accessory spines absent . . . . . 14
    Lateral accessory spines present . . . . . 15
14. Lateral spines on segment 4 (adhesive tubes), 7–11 . . . . . ***bermudensis*** Higgins, 1982
    Lateral spines on segment 4 (adhesive tubes), 8–11 . . . . . ***arlis*** Higgins, 1966*a*
15. Segment 4 with subdorsal and lateral accessory spines . . . . . 16
    Segment 4 without subdorsal and lateral accessory spines . . . . 17
16. Additional lateral accessory spines on segments 8–11; subdorsal spines on segment 10 . . . . . ***newcaledoniensis*** Higgins, 1967
    Additional lateral accessory spines on segment 10 only; subdorsal spines on segment 10 absent ***peterseni*** Higgins & Kristensen, 1988
17. Lateral terminal spines short (36–45 $\mu$m), stubby (LTS/TL 14–20%) . . . . . ***abbreviatus*** Higgins, 1983
    Lateral terminal spines long (>104 $\mu$m), thin (LTS/TL >45%) . . . . . 18
18. Trunk segments hirsute, but without associated cuticular perforations; terminal tergal extensions nearly as long as lateral terminal accessory spines . . . . . ***higginsi*** sp.n.
    Trunk segments hirsute with associated cuticular perforations; terminal tergal extensions distinctly shorter than lateral terminal accessory spines . . . . . 19
19. Terminal sternal plate devoid of spinus projection in female; male without minute additional seta on segment 12; segment 11 with 2 subdorsal cuticular scars (sensory spots?) ***wallaceae*** Higgins, 1983
    Terminal sternal plate with spinous projection in female; male with minute additional seta on segment 12; segment 11 with 1 mid-dorsal cuticular scar (sensory spot?) . . . . . 20
20. Mid-dorsal spine D-10 short (18 $\mu$m), not extending to caudal margin of trunk; segment 3 with perforation sites on ventral surface; no prominent ventro- and dorsolateral muscle scars on segment 4 . . . . . ***riedli*** Higgins, 1966*b*
    Mid-dorsal spine D-10 long (84–92 $\mu$m), extending to caudal margin of trunk; segment 3 devoid of perforation sites on ventral surface; prominent ventro- and dorsolateral muscle scars on segment 4 . . . . . ***kristenseni*** Higgins, 1985
21. Lateral spines (adhesive tubes) present on segment 4 . . . . . 30
    Lateral spines (adhesive tubes) absent on segment 4 or indicated by either a pore or a cuticular scar in the L-4 position . . . . . 22
22. Lateral spines on segments 7–12 (12th spine may be very small in males) . . . . . 23
    Lateral spines otherwise . . . . . 24
23. Terminal tergal extensions truncate, with straight mesial border, mid-dorsal spines relatively short (13–30 $\mu$m) . . . . . ***truncatus*** Higgins, 1983
    Terminal tergal extensions pointed, with curved, fringed mesial border; mid-dorsal spines relatively long (30–50 $\mu$m) . . . . . ***bookhouti*** Higgins, 1964*a*
24. Lateral spines on segments 7–11 . . . . . 26
    Lateral spines otherwise . . . . . 25
25. Lateral spines on segments 8–11 . . . . ***elongatus*** (Nyholm, 1947)
    Lateral spines on segments 7, 10 and 11 . . . . . ***eximus*** Higgins & Kristensen, 1988

26. Border of sternal plates pointed; round pore or cuticular scar not at site of missing lateral spine on segment 4 ***remanei*** (Blake, 1930)
Border of terminal sternal plates rounded; round pore or cuticular scar replacing lateral spine on segment 4 ..... 27
27. Pectinate fringe on sternal plates of segment 3 shorter on either side of midline ..... ***tubilak*** Higgins & Kristensen, 1988
Pectinate fringe on sternal plates of segment 3 uniform in length 28
28. LTS/TL generally less than 30% ..... ***aquilonius*** Higgins & Kristensen, 1988
LTS/TL generally more than 30% ..... 29
29. Segment 4 with almost completely developed mid-ventral suture; combined length of ventral plates of segments 12 and 13 less than sternal width of segment 12 ***angustus*** Higgins & Kristensen, 1988
Segment 4 without such suture; combined length of ventral plates of segments 12 and 13 more than sternal width of segment 12 ..... ***pennaki*** Higgins, 1960
30. Lateral accessory spines present on segment 10 ..... 31
Lateral accessory spines absent on segment 10 ..... 32
31. Prominent sensory spots on either side of ventral midline near anterior margin of segment 4; mid-dorsal spines very short (6–13 μm, Dm/TL 2.5–3%) ..... ***gerardi*** Higgins, 1978
Sensory spots not on either side of ventral midline near anterior margin of segment 4; mid-dorsal spines relatively short (14–22 μm, Dm/TL 4.0–5.6%) ..... ***dujardinii*** Claparède, 1863
32. Lateral terminal spines stubby, shorter than segment 12; lateral spine (or setae if male) absent on segment 12 ..... ***brevicaudatus*** Higgins, 1977*b*
Lateral terminal spines narrowly elongate, longer than segments 12 and 13 combined; lateral spines (or setae if male) present on segment 12 ..... 33
33. Cuticular perforations associated with the trunk hair absent on all segments ..... 34
Cuticular perforations associated with the trunk hair present on at least some of the segments ..... 36
34. Segment 13 with apparent mid-dorsal articulation zone establishing 2 bilateral terminal tergal plates; D-7 much longer than other mid-dorsal spines; cuticular hairs absent ***nybakkeni*** Higgins, 1986*a*
Segment 13 without mid-dorsal articulation zone on segment 13; mid-dorsal spines increasing in length posteriorly; cuticular hairs present ..... 35
35. Mid-dorsal spines short (8–24 μm), increasing evenly in length posteriorly: posterior end of mid-ventral placid (7 μm) only slightly wider than that of others (5 μm) .... ***imperforatus*** Higgins, 1983
Anterior 4 mid-dorsal spines nearly equal in length (18–26 μm), D-10 nearly 3 times longer; mid-ventral placid apparently wider (13 μm) than others ..... ***worthingi*** Southern, 1914
36. Length D-10 at least 2.5 times the length of D-6 ..... 37
Length D-10 at most 1.5 times the length of D-6 ..... 40
37. Lateral spine on segment 12 short (12–17 μm), blunt, curved away from body; LTS/TL 27–36% ..... ***pacificus*** Schmidt, 1974
Lateral spine on segment 12 similar to preceding lateral spines; LTS/TL at least 45% ..... 38
38. Lateral spines on segment 12 each with adjacent seta ..... ***ferrugineus*** Zelinka, 1928
Lateral spines on segment 12 without adjacent seta ..... 39
39. Dorsal, lateral and lateral terminal spines bi-laterally spinulose ..... ***levanderi*** Karling, 1954
Dorsal, lateral and lateral terminal spines smooth ..... ***sublicarum*** Higgins, 1977*a*
40. Lateral and mid-dorsal spines flexible, reaching their greatest length in the middle of each series; terminal tergal extensions not projecting beyond sternal margins ..... ***krishnaswamyi*** Higgins, 1985
Lateral and mid-dorsal spines not flexible, reaching their greatest length proximally; terminal tergal extensions projecting beyond sternal margins ..... 41
41. Lateral margins of terminal spines minutely serrulate; segment 3 with 2 mid-dorsal and 2 subdorsal sensory spots ***pilosus*** Lang, 1949
Lateral margins of terminal spines smooth; segment 3 with at most 3 (1 mid-dorsal, 2 subdorsal) sensory spots ..... 42
42. Segments 3–5 with 1 mid-dorsal sensory spot; terminal sternal plates evenly rounded; inner margin of terminal tergal extensions distinctly interrupted by a secondary cusp ..... ***ehlersi*** Zelinka, 1913
Segments 3–5 with 1 mid-dorsal and 2 subdorsal sensory spots; terminal sternal plates somewhat pointed; inner margin of terminal tergal extensions relatively smooth ..... ***kozloffi*** Higgins, 1977*b*

## Acknowledgements

Grateful thanks are due to Mrs S. Wellekens for help in SEM photography and to Prof. Tor Karling, Swedish Museum of Natural History, Stockholm, Sweden, for the loan of the holotype of *Echinoderes levanderi*. We also thank Dr Jouko Sarvala, University of Turku, Finland, for providing material of *E. levanderi* and Mr R. Herman for assistance in the field. The first author acknowledges a grant from the Belgian Institute for the encouragement of Scientific Research in Industry and Agriculture (IWONL). Part of the work was carried out under research grant 2.0009.81 of the Fund for Collective Fundamental Research.

## References

Abe, Y. 1930. Das Vorkommen von *Echinoderes* in den japanischen Gewässern.—*J. Sci. Hiroshima Univ.* (ser. B) *1:* 39–44.

Băcescu, M. 1968. Class Kinorhyncha: Determination of fauna of the Black and Azov Seas.—*Naukova Dumka 1:* 237–250.

Blake, C. H. 1930. Three new species of worms belonging to the order Echinodera.—*Biol. Surv. Mt. Desert Reg. 4:* 3–10.

Brady, G. S. 1903. *Echinoderes.—Nat. Hist. Trans. Northumb. 14:* 102–103.

Chitwood, B. G. 1951. *Echinoderella steineri* new species (Scolecida: Echinodera).—*Tex. J. Sci. 3:* 113–114.

Claparède, 1863. *Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Tiere an der Kuste der Normandie angestellt.* Wilhelm Engelmann, Leipzig.

Gerlach, S. A. 1969. *Cateria submersa* sp.n., ein cryptorhager Kinorhynch aus dem sublittoralen Mesopsammal der Nordsee.—*Veröff. Inst. Meeresforsch. Bremerh. 12:* 161–168.

Greeff, R. 1869. Untersuchungen über einige merkwürdige Formen des Arthropoden- und Wurm-Typus.—*Arch. Naturgesch. 35:* 71–100.

Heip, C., Herman, R. & Vincx, M. 1983. Subtidal meiofauna of the North Sea: a review.—*Biol. Jb. Dodonaea 51:* 116–170.

Higgins, R. P. 1960. A new species of *Echinoderes* (Kinorhyncha) from Puget Sound.—*Trans. Am. microsc. Soc. 79:* 85–91.

Higgins, R. P. 1964. Three new kinorhynchs from the North Carolina coast.—*Bull. mar. Sci. 14:* 479–493.

Higgins, R. P. 1966*a*. *Echinoderes arlis*, a new kinorhynch from the Arctic Ocean.—*Pacif. Sci. 20:* 518–520.

Higgins, R. P. 1966*b*. Faunistic studies in the Red Sea (in winter, 1961–1962), Part II: Kinorhynchs from the area of Al-Ghardaqa.—*Zool. Jb.* Syst. Ökol. Geogr. Tiere *93:* 118–126.

Higgins, R. P. 1967. The Kinorhyncha of New-Caledonia. In *Expédition française sur récifs coralliens de la Nouvelle Caledonia 2:* 75–90. Éditions de la Fondation Singer-Polignac, Paris.

Higgins, R. P. 1969. Indian Ocean Kinorhyncha: 1, *Condyloderes* and *Sphenoderes*, new cyclorhagid genera.—*Smithson. Contr. Zool. 14:* 1–13.

Higgins, R. P. 1977*a*. Two new species of *Echinoderes* (Kinorhyncha) from South Carolina.—*Trans. Am. microsc. Soc. 96:* 340–354.

Higgins, R. P. 1977*b*. Redescription of *Echinoderes dujardinii* (Kinorhyncha) with descriptions of closely related species.—*Smithson. Contr. Zool. 248:* 1–26.

Higgins, R. P. 1978. *Echinoderes gerardi* n.sp. and *E. riedli* (Kinorhyncha) from the Gulf of Tunis.—*Trans. Am. microsc. Soc. 97:* 171–180.

Higgins, R. P. 1982. Three new species of Kinorhyncha from Bermuda.—*Trans. Am. microsc. Soc. 101:* 305–316.

Higgins, R. P. 1983. The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha.—*Smithson. Contr. mar. Sci. 18:* 1–131.

Higgins, R. P. 1985. The genus *Echinoderes* (Kinorhyncha: Cyclorhagida) from the English Channel.—*J. mar. biol. Ass. U.K. 65:* 785–800.

Higgins, R. P. 1986*a*. A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from a coarse-sand California beach.—*Trans. Am. microsc. Soc. 105:* 266–273.

Higgins, R. P. 1986*b*. Redescription of *Echinoderes pilosus* (Kinorhyncha: Cyclorhagida).—*Proc. biol. Soc. Wash. 99:* 399–405.

Higgins, R. P. & Kristensen, R. M. 1988. Kinorhyncha from Disko Island, West Greenland.—*Smithson. Contr. Zool. 458:* 1–56.

Higgins, R. P. & Rao, G. C. 1979. Kinorhynchs from the Andaman Islands.—*Zool. J. Linn. Soc. 67:* 75–85.

Hondt, J. L. d' 1973. Contribution a l'étude de la microfaune interstitielle des plages de l'Ouest Algérien.—*Vie Milieu 23:* 227–241.

Huys, R., Herman, R. & Heip, C. 1986. Seasonal fluctuations in vertical distribution and breeding activity of a subtidal harpacticoid community in the Southern Bight, North Sea.—*Neth. J. Sea Rs. 20:* 375–383.

Karling, T. G. 1954. *Echinoderes levanderi* n.sp. (Kinorhyncha) aus der Ostsee.—*Ark. Zool.* (2) *7:* 189–192.

Kirsteuer, E. 1964. Zur Kenntnis der Kinorhynchen Venezuelas.—*Zool. Anz. 173:* 388–393.

Lang, K. 1949. Echinoderida. *Further zool. Results Swed. Antarct. Exped. 4:* 1–22.

Leuckart, R. 1854. Bericht über die Leistungen in der Naturgeschichte der niederen Tiere während der Jahre 1848–1853.—*Arch. Naturgesch. 20:* 289–473.

Lou, T.-H. 1934. Sur la présence d'un nouveau Kinorhynque a Tchéfou: *Echinoderes tchefouensis* sp. nov.—*Contr. Lab. zool. Acad. natn. Peiping 1:* 1–9.

McIntyre, A. D. 1962. The class Kinorhyncha (Echinoderida) in British waters.—*J. mar. biol. Ass. U.K. 42:* 503–509.

Metschnikoff, E. 1865. Ueber einige wenig bekannte niedere Thierformen.—*Z. wiss. Zool. 15:* 450–461.

Moore, P. G. 1973. *Campyloderes macquariae* Johnston, 1938 (Kinorhyncha: Cyclorhagida) from the northern hemisphere.—*J. nat. Hist. 7:* 341–354.

Nyholm, K.-G. 1947. Studies in the Echinoderida.—*Ark. Zool. 39A* (14): 1–36.

Omer-Cooper, J. 1957. Deux nouvelles espèces de Kinorhyncha en provenance de l'Afrique du Sud.—*Bull. mens. Soc. linn. Lyon 26:* 213–216.

Pallares, R. 1966. Nota sobre *Echinoderes pilosus* Lang, 1949 (Aschelminthes, Kinorhyncha).—*Physis 26:* 101–106.

Schepotieff, A. 1907. Zur Systematik der Nematoideen.—*Zool. Anz. 31:* 132–161.

Schmidt, P. 1974. Interstitielle Fauna von Galapagos, X: Kinorhyncha.—*Mikrofauna Meeresboden 43:* 1–15.

Southern, R. 1914. Nemathelmia, Kinorhyncha, and Chaetognatha. Clare Island Survey, Part 54.—*Proc. R. Ir. Acad. 31:* 1–80.

Timm, R. W. 1958. Two new species of *Echinoderella* (Phylum Kinorhyncha) from the Bay of Bengal.—*J. Bombay nat. Hist. Soc. 55:* 107–109.

Zaneveld, J. S. 1938. Marine Gastrotricha and Kinorhyncha from Scheveningen.—*Zoöl. Meded., Leiden 20:* 257–262.

Zelinka, C. Die Echinoderen der Deutschen Südpolarexpedition 1901–1903.—*Dt. Südpol.-Exped. 14* (Zool. 6): 419–436.

Zelinka, C. 1928. *Monographie der Echinodera.* Wilhelm Engelmann, Leipzig.