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A new *Echinoderes* (Kinorhyncha: Cyclorhagida) from a submarine cave in New South Wales, Australia.

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Abstract: The cyclorhagid kinorhynch *Echinoderes cavernus* sp. nov. is described from a submarine cave in New South Wales, Australia. This finding represents the first kinorhynch, which probably lives in caves, exclusively. The usual sexual dimorphism in *Echinoderes* is absent in the new species, i.e. lateral terminal accessory spines are present in both sexes. Further sexually peculiar characters in *E. cavernus* sp. nov. are genital setae on the arthrocorium between segments 12 and 13 in both sexes, and the presence of only two penile spines in the males. The new species has interstitial placids and blunt (short and broad) lateral terminal spines. The blunt lateral terminal spines are proposed to be an autapomorphic character for a monophyletic clade consisting of *Echinoderes abbreviatus, E. brevicaudatus* and *E. cavernus* sp. nov. which all inhabit coarse coralligenous sand.

Résumé : *Une nouvelle espèce de* Echinoderes *(Kinorhyncha: Cyclorhagida) d'une grotte sous-marine des Nouvelle-Galles du Sud, Australie. Echinoderes cavernus* sp. nov. est décrit d'une grotte sous-marine des Nouvelle-Galles du Sud. Cette découverte signale pour la première fois un Kinorhynque qui vit probablement exclusivement dans ce milieu particulier. Le dimorphisme sexuel habituel des *Echinoderes* est absent chez la nouvelle espèce, les épines terminales accessoires latérales étant présentes dans les deux sexes. Les autres caractères sexuels particuliers à *E. cavernus* sp. nov. sont : la présence de soies génitales sur l'arthrocorium, entre les segments 12 et 13, chez les deux sexes et la présence de deux soies péniales chez le mâle. La nouvelle espèce a des placides interstitiels et des épines latérales terminales émoussées (courtes et larges). Ces épines latérales terminales émoussées sont envisagées comme des caractères autapomorphiques dans un clade monophylétique comprenant les espèces *Echinoderes abbreviatus, E. brevicaudatus* et *E. cavernus* sp. nov.

Keywords : Australia, caves, coralligenous sand, *Echinoderes* sp. nov., Kinorhyncha, new species.

Introduction

Recently marine caves have been objects of intensive macrofaunal investigations. These have resulted in the discovery of major new groups of crustaceans, e.g. Remipedia described from a cave in the Bahamas (Yager, 1981) and Mictacea from a marine cave in Bermuda (Bowman et al., 1985). Subsequently, remipeds have been found nearly world-wide, but only in marine caves or in inland caves with marine groundwater. More recently, remipeds have been found in Australian caves (Yager & Humphreys, 1996). Mictacea descriptions are based on materials both from caves (Bowman & Iliffe, 1985) and

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from the deep-sea (Sanders et al., 1985). Just & Poore (1988) later found mictaceans in the Australian deep-sea. This remarkable distribution of closely related crustaceans in anchialine caves and in the deep-sea gave rise to the theory that the caves functioned as biota for Mesozoic relicts now tied to the deep-sea (Hart et al., 1985; Manning et al., 1986). In fact, an old theory of Riedl (1966) stated that the environmental features of submarine caves are considered very similar to those of the deep-sea habitat.

Very few meiofauna investigations from eumarine caves have been published. A marine cave study on tardigrades was carried out on the Italian coast, where Grimaldi De Zio et al. (1982) described four new species of Arthrotardigrada, and Villora-Moreno (1996) more recently described the new genus *Trogloarctus* of the deep-sea family Coronarctidae from a submarine cave in the French Mediterranean Sea. This last finding supports the theory that the marine caves served as refuges for an old Tethyan fauna.

Until now, only one kinorhynch has been recorded from a marine cave. This was done by Riedl (1966), who found *Echinoderes dujardini* Claparède, 1863 in two Mediterranean submarine caves close to Napoli in Italy and Banyuls in Spain, respectively. However, *E. dujardini* has been recorded from bottom sediments at several localities in Europe (Higgins, 1977a), thus it cannot be considered as specialized for caves.

The present account reports the first kinorhynch, which probably lives in caves, exclusively. Several caves in Australia have been investigated for meiofauna, and this paper is the first in a series dealing with meiofauna in submarine caves and inland anchialine caves.

The Australian specimens of cave kinorhynchs were collected from sediments consisting of coral sand mixed with shell gravel. Previously only *E. krishnaswamyi* Higgins, 1985, *E. kristenseni* Higgins, 1985, and *E. nybakkeni* Higgins, 1986 were recorded to inhabit coarse calcareous sand environments (Higgins, 1985, 1986). *Echinoderes horni* Higgins, 1983 and *E. wallaceae* Higgins, 1983 were recorded from mixed coral sand, shell and rubble habitats (Higgins, 1983). Two very aberrant species of echinoderids, *Echinoderes brevicaudatus* Higgins, 1966 from the Red Sea (Higgins, 1966) and *Echinoderes abbreviatus* Higgins, 1983 from Belize (Higgins, 1983) were collected from fine calcareous sand with detritus.

The only Australian kinorhynch described today is *Kinorhynchus phyllotropis* Brown and Higgins, 1983. It was found in muddy sand in Sydney Harbour (Brown & Higgins, 1983). In Brown's unpublished thesis (Brown, 1985), she gave a detailed description of a species of *Pychnophyes* and a species of *Echinoderes* also from the East Coast of Australia. In addition, several other species of kinorhynchs have been found in an ABRS-project (Australian Biological Resources Study) by R. M. Kristensen in Queensland and New South Wales from 1995-96 (pers. comm. R. M. Kristensen) and by R. P. Higgins (pers.comm. R. P. Higgins) in Australian waters, but none of the recorded species resembled *E. cavernus* sp. nov..

The kinorhynchs from adjacent waters are *Campyloderes macquarie* Johnston, 1938, *Echinoderes newcaledoniensis* Higgins, 1967 and *Semnoderes pacificus* Higgins, 1967 from New Caledonia (Higgins, 1967). *Condyloderes paradoxus* Higgins, 1969 and *Sphenoderes indicus* Higgins, 1969 were collected from the Indian Ocean (Higgins, 1969). *Cateria gerlachi* Higgins, 1968, *E. andamanensis* Higgins & Rao, 1979 and *E. ehlersi* Zelinka, 1913 were collected from the Andaman Islands, Bay of Bengal (Higgins & Rao, 1979). *Echinoderes* cf. *coulli* Higgins, 1977 has been reported from New Zealand (Coull & Wells, 1981).

Material and methods

Locality description

Jim's Cave is located close to Seal Rocks south of Tuncurry (32°17'S, 152°29'E), New South Wales, Australia (Fig. 1). The cave was discovered by Denis Kemp but is named after its explorer the diving veteran Jim Gallegos. The cave is part of a large rock oriented in an East-West direction 3 km off the coast. The rock is 30 m tall, and at low tide the top of the rock is just 10 m below water. The bottom outside the cave is covered with large rocks and stones. The cave is located on the North side of the rock. It is an approximately 50 m long narrow tunnel cave with narrow appendices (Fig. 2). The entrance of the cave at 24 m depth is a tight circular hole with a diameter of 1.5 m. Huge amounts of fish

Figure 1. Maps showing the location of the sampling site (Jim's Cave). Left: Australia. Right: Close up of the sampling area south of Seal Rocks.

Figure 1. Cartes montrant l'emplacement du lieu de récolte (Grotte de Jim). A gauche : l'Australie ; à droite agrandissement de la région prospectée, au sud de Seal Rocks.

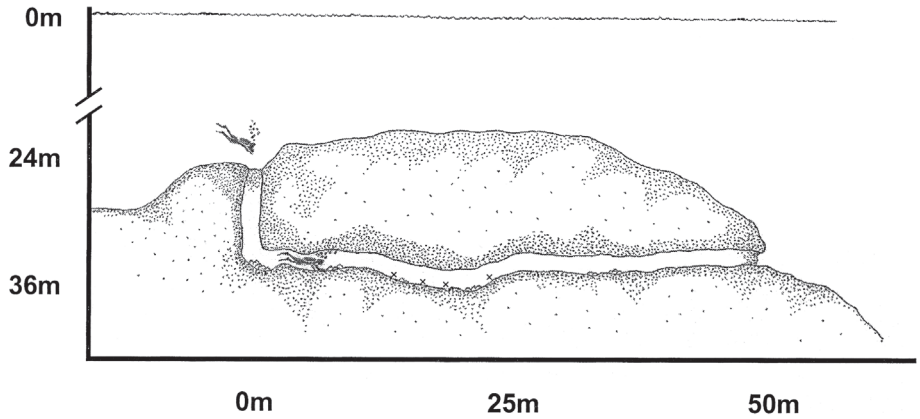

Figure 2. Longitudinal section showing Jim's Cave. The locations of the sampling sites are marked with crosses.
Figure 2. Coupe longitudinale de la grotte de Jim. Les croix indiquent l'emplacement des lieux de récolte.

gather at the entrance and just inside as well. Sponges and sea anemones are scattered on the walls and ceiling of the cave. The floor of the cave is reached at 34-36 m, and it is covered with a sediment of coarse coralligenous sand, rich in detritus. The darkness is complete 1-2 m after entering the entrance, and it is complete until a few meters from the narrow elliptical (1.5 m tall and 1 m broad) cave exit at 34 m. The salinity of the water in the cave is uniform from top to bottom, and the whole water column is similar to the sea water near the entrance. Almost no currents are present in the cave, and whirled material suspended in the water settles very slowly on the bottom. Thus, the exchange of small planktonic animals, such as larvae, must be considered as minimal.

Sampling and sorting

Sediment samples were collected by the senior author on the 13 January 1999 by SCUBA diving. For the sampling four plastic containers were used, each containing 3 l. Sampling were done in four different places on the cave floor, taking only the upper 5-10 cm of the sediment. The total amount of sediment taken from the cave was approximately 15 kg in wet weight. Each sample was fresh water "shocked" following the procedure set out by Kristensen & Higgins (1984). The meiofauna was extracted from the sediment by immersing the samples in 5 l buckets containing fresh water for 10 minutes, then swirling the bucket contents to suspend the osmotically incapacitated meiofauna. The supernatant was then decanted through a 50 µm mesh net. The meiofauna was stored in 7% formalin buffered with borax, and put in small plastic containers until the sorting at the Zoological Museum, University of Copenhagen, Denmark, using a dissecting microscope (40-80 x magnification). In the laboratory the samples were lightly stained with rose bengal in order to distinguish the "living" tissue from the unstained debris.

Preparation and examination of material

Specimens for light microscopy were washed in demineralised water and then postpreserved in 5% borax buffered formalin. After postpreservation specimens were dehydrated in graded glycerine by storing the specimens for about 1 h in dishes with 10%, 25%, 50%, 75%, and 100% glycerine, respectively. When fully dehydrated, each specimen was placed in a drop of Hoyer's solution (see Higgins, 1988) on a glass slide and covered with a cover slip. The cover slip was sealed with Glyceel®. The specimens mounted on slides were examined and drawn with a camera lucida mounted on a Leica DM-RXA Nomarski microscope. The LM photographs were taken with a Nikon Microphot-FX microscope.

Specimens for SEM were postpreserved in 5% borax buffered formalin, dehydrated through a graded ethanol series and afterwards transferred to acetone for critical point drying. The dried specimens were mounted on aluminium stubs and sputter coated with gold. All specimens for SEM were examined with a JEOL JSM-840 microscope.

The given measurements in the description are made in accordance with Higgins (1983), and the terms used in connection with the location of scars, spines, etc. are in accordance with Pardos et al. (1998).

Results

Order Cyclorhagida Zelinka, 1896
Family Echinoderidae Bütschli, 1876
Genus *Echinoderes* Claparède, 1863
Species *Echinoderes cavernus* sp. nov.

Material examined

Type material was obtained from samples taken 13 January 1999 by the senior author from coral sand with detritus in the cave "Jim's Cave", New South Wales, Australia (Fig. 1).

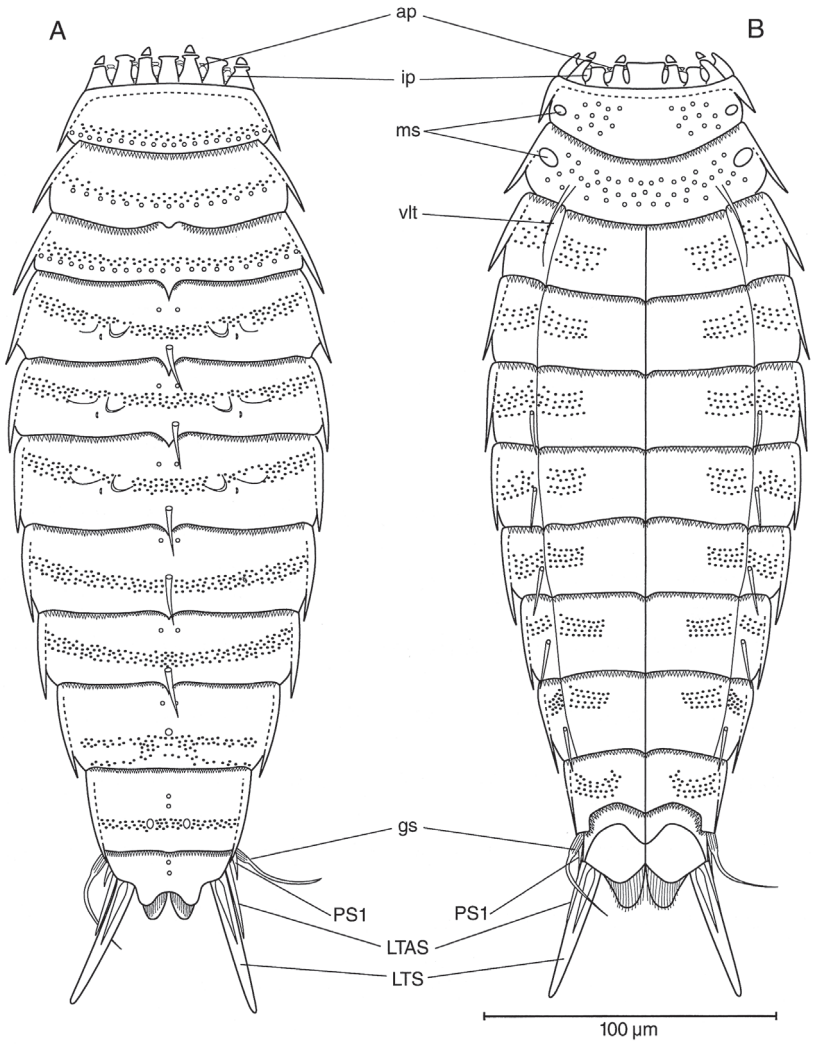

Figure 3. *Echinoderes cavernus* sp. nov. **A**. Neck and trunk segments, dorsal view, holotypic male (KIN-1). **B**. Holotypic male, ventral view; (ap) associated plate, (gs) genital seta, (ip) interstitial placid, (LTAS) lateral terminal accessory spine, (LTS) lateral terminal spine, (ms) muscle scar, (PS1) penile spine 1, (vlt) ventrolateral tubule.

Figure 3. *Echinoderes cavernus* sp. nov. **A**. Cou et segments du tronc, vue dorsale, holotype mâle (KIN-1). **B**. Holotype mâle, vue ventrale ; (ap) plaque associée, (gs) soie génitale, (ip) placide interstitiel, (LTAS) épine terminale latérale accessoire, (LTS) épine terminale latérale, (ms) empreinte musculaire, (PS1) épine pénienne 1, (vlt) tubule ventro-latéral.

Holotype: Adult male, KIN-1 (Figs. 3 A-B, 4 A), mounted in Hoyer's solution, deposited in the Zoological Museum, University of Copenhagen (ZMUC). Allotype: Adult female, KIN-2, mounted in Hoyer's solution, deposited in ZMUC. Paratypes: three adult females (KIN-3 to KIN-5), two adult males (KIN-6 and KIN-7), two juveniles, J-5, (KIN-8 and KIN-9), four juveniles, J-4, (KIN-10 to KIN-13), and one juvenile, J-1, (KIN-14), all mounted in Hoyer's solution. Furthermore, two adult males, and two adult females (KIN-15 and KIN-16) were mounted on aluminium stubs for SEM, and deposited in ZMUC.

Diagnosis

Middorsal spines on segments 6-10; a pair of ventrolateral tubules on segment 4; a pair of lateroventral tubules on segment 7; lateroventral spines on segments 8-11; both sexes with a pair of genital setae on the arthrocorium between segments 12 and 13 and lateral terminal accessory spines on segment 13; lateral terminal spines short, blunt, stout, 21-26 µm long (mean = 24.2 µm), 8.2-9.3 percent of trunk length. No eyespot present. Males with two pairs of penile spines; posterior edges of sternal plates on segment 12 concave, laterally twisting into ventrally pointed edges

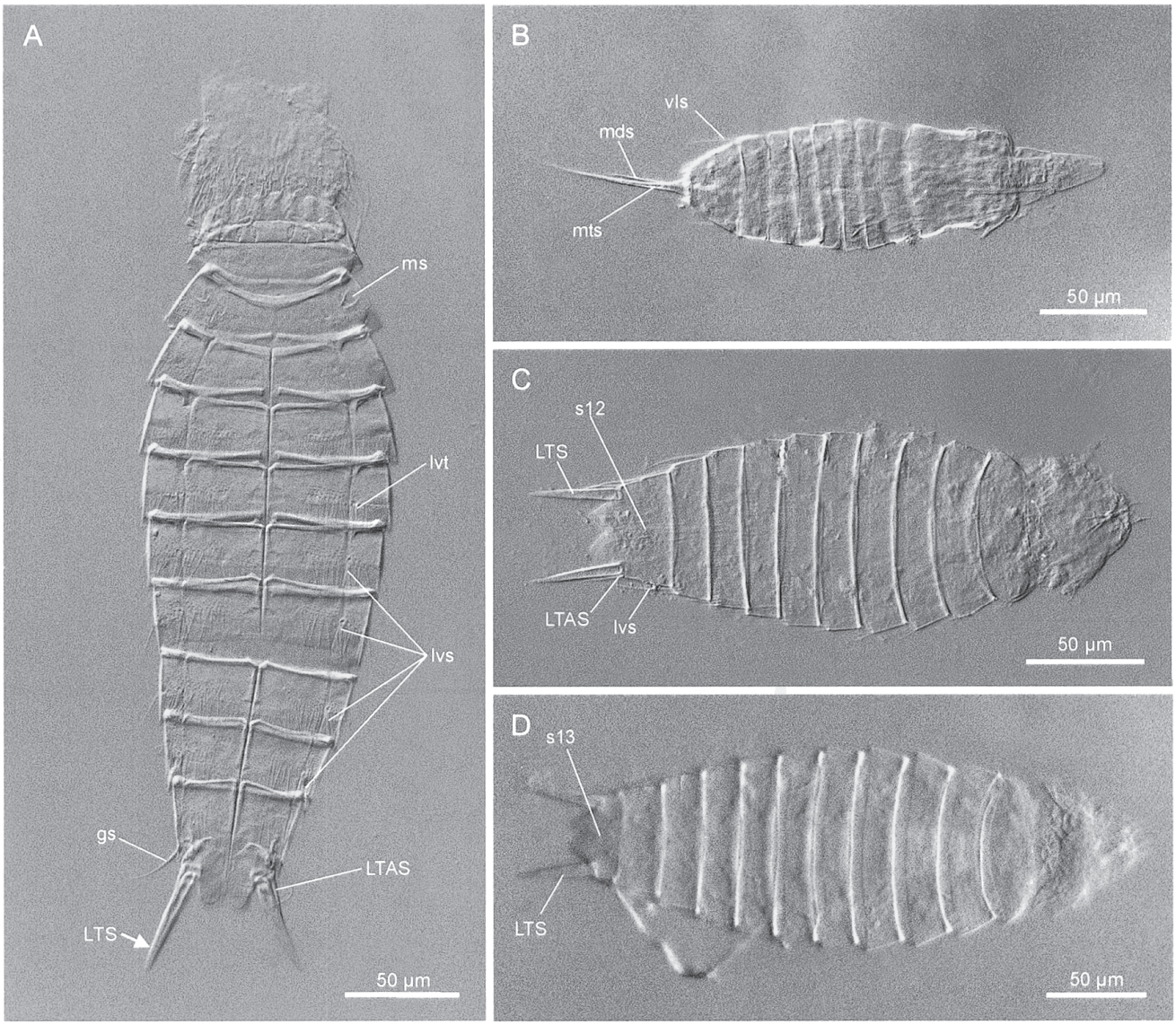

Figure 4. *Echinoderes cavernus* sp. nov. **A.** Holotypic male (KIN-1), ventral view. **B.** J-1, dorsal view, paratype (KIN-14). **C.** J-4, ventral view, paratype (KIN-10). **D.** J-5, ventral view, paratype (KIN-8); (gs) genital seta, (LTAS) lateral terminal accessory spine, (LTS) lateral terminal spine, (lvs) lateroventral spine, (lvt) lateroventral tubule, (ms) muscle scar, (mds) middorsal spine, (mts) midterminal spine, (s12) segment 12, (s13) segment 13.

Figure 4. *Echinoderes cavernus* sp. nov. **A.** Holotype mâle (KIN-1), vue ventrale. **B.** J-1, vue dorsale, paratype (KIN-14). **C.** J-4, vue ventrale, paratype (KIN-10). **D.** J-5, vue ventrale, paratype (KIN-8) ; (gs) soie génitale, (LTAS) épine terminale latérale accessoire, (LTS) épine terminale latérale, (lvs) épine latéro-ventrale, (lvt) tubule latéro-ventral, (ms) empreinte du muscle, (mds) épine médio-dorsale, (mts) épine médio-terminale, (s12) segment 12, (s13) segment 13.

(Figs. 5 C-D, 6 C-D, 7 B). Females with no unique sexual spines or tubules; posterior edges of sternal plates almost straight (Figs. 5 A-B, 6 A-B, 7 C).

Segment and spine/tubule/seta lengths are outlined in Tables 1 and 2, respectively. Location of scars, spines, and tubules are outlined in Table 3.

Description of adults (Figs. 3 A-B, 4 A, 7 A)

Trunk length 259-293 µm; MSW-7 (maximum sternal width of segment 7), 71-87 µm, 24.5-31.4 percent of trunk length; SW (standard width) at segment 12, 47-51 µm, 16.2-18.7 percent of trunk length.

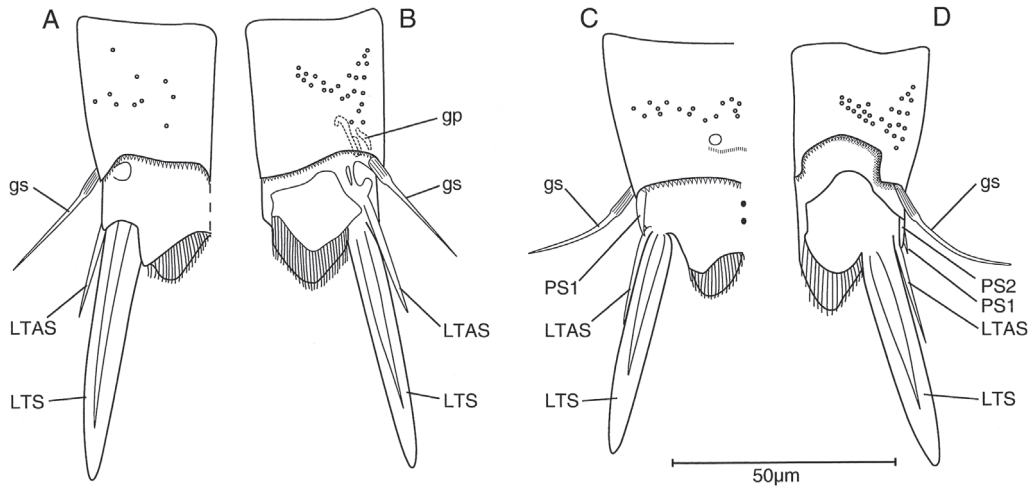

Figure 5. *Echinoderes cavernus* sp. nov. **A**. Segments 12 and 13, dorsal view, allotypic female (KIN-2). **B**. Allotypic female, ventral view. **C**. Segments 12 and 13, dorsal view, holotypic male (KIN-1). **D**. Holotypic male, ventral view; (gp) gonopores, (gs) genital seta, (LTAS) lateral terminal accessory spine, (LTS) lateral terminal spine, (PS1) penile spine 1, (PS2) penile spine 2.

Figure 5. *Echinoderes cavernus* sp. nov. **A**. Segments 12 et 13, vue dorsale, allotype femelle (KIN-2). **B**. Allotype femelle, même spécimen, vue ventrale. **C**. Segments 12 et 13, vue dorsale, holotype mâle (KIN-1). **D**. Holotype mâle, vue ventrale; (gp) gonopores, (gs) soie génitale, (LTAS) épine terminale latérale accessoire, (LTS) épine terminale latérale, (PS1) épine pénienne 1, (PS2) épine pénienne 2.

Segment 2, 8-9 µm long (mean = 8.8 µm), consisting of 16 placids, 8-9 µm tall, 5-6 µm wide; midventral placid (placid 1) wider (15-16 µm) than other placids (Figs. 3 B, 4 A). Ventral trichoscalid plates of head segment anterior to each 2nd placid, triangular-shaped. A row of smaller, 5 µm tall, 2 µm wide, interstitial placids located between placids each with a smaller associated plate, located anterior to interstitial placids (Fig. 3 A-B).

Segment 3, 24-26 µm long (mean = 24.9 µm). Dorsal side smooth with scattered perforation sites, posteriorly one row of perforation sites with cuticular hairs; lateral side anteriorly with a pair of small sublateral muscle scars (Fig. 3 B); two ventrolateral areas with small perforation sites, no cuticular hairs.

Segment 4, 22-24 µm long (mean = 22.5 µm). Dorsal perforation sites and cuticular hairs as segment 3; lateral side anteriorly with a pair of large sublateral muscle scars (Figs. 3 B, 4 A); perforation sites in three rows; a few cuticular hairs are scattered on the segment; one pair of ventrolateral tubules, 18-37 µm long (mean = 23.9 µm), broad and flattened at bases, tapering to thin and flagellate point (Fig. 7 D).

Segment 5, 22-25 µm long, (mean = 23.4 µm). Dorsal perforation sites and cuticular hairs as segment 4. Ventral side with perforation sites in four transverse rows laterally and at the lateral-most parts of sternal plates; pachycycli well developed.

Segment 6, 26-28 µm long (mean = 25.6 µm). Dorsal side with one posterior transverse row of cuticular hairs; two pairs of large subdorsal muscle scars; one pair of small paradorsal gland openings anterior on segment and one pair of elongate subdorsal cuticular scars, located between muscle scars (Fig. 3 A); one middorsal spine, 13-16 µm long (mean = 14.4 µm). Ventral and lateral cuticular hairs and perforation sites as segment 5. Pachycycli as segment 5.

Segment 7, 24-26 µm long (mean = 25.1 µm). One middorsal spine, 14-16 µm long (mean = 14.8 µm). A pair of lateroventral tubules, 8-21 µm (mean = 14.3 µm). All other characters similar to those on segment 6.

Segment 8, 24-32 µm long, (mean = 26.6 µm). One middorsal spine, 15-17 µm long (mean = 15.5 µm). A pair of lateroventral spines, 15-17 µm (mean = 15.8 µm). All other characters similar to those on segment 7.

Segment 9, 24-36 µm long (mean = 27.0 µm). One middorsal spine, 13-17 µm long (mean = 15.8 µm); no subdorsal muscle scars or cuticular scars. A pair of lateroventral spines, 16-22 µm (mean = 19.2 µm). All other characters similar to those on segment 8.

Segment 10, 25-26 µm long (mean = 25.6 µm). Cuticular hairs on dorsal side thicker and longer than those on segment 9; one middorsal spine, 11-17 µm long (mean = 15.4 µm). A pair of lateroventral spines, 17-25 µm (mean = 19.8 µm). Ventral and lateral perforation sites as on segment 9; cuticular hairs denser. All other characters similar to those on segment 9.

Segment 11, 25-28 µm long (mean = 26.6 µm). A few cuticular hairs are scattered on median part of segment; large middorsal cuticular scar; no middorsal spine (Fig. 3 A). A pair of mucus gland openings midlaterally; sublaterally, close to mucus gland openings, a pair of very small sieve

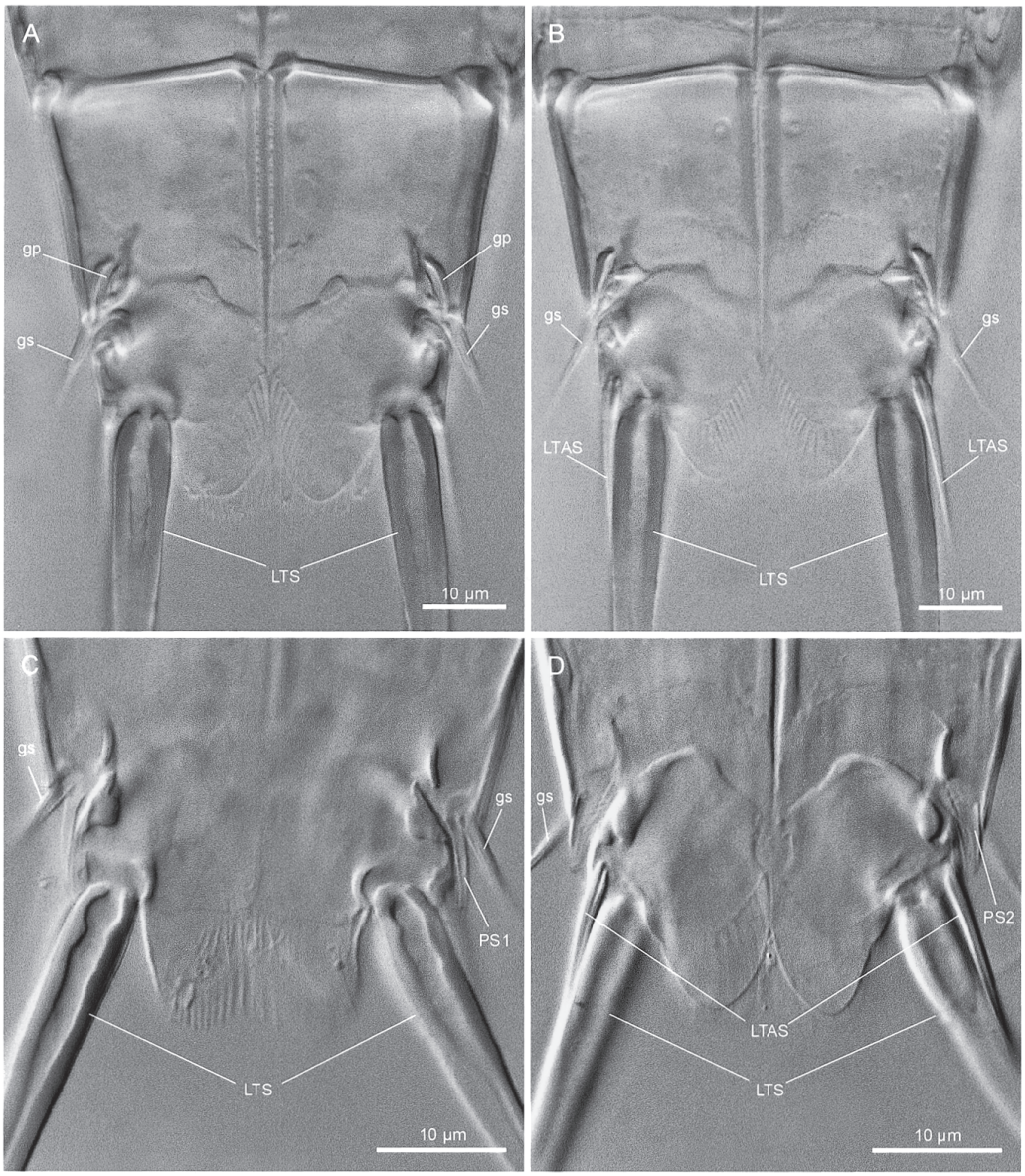

Figure 6. *Echinoderes cavernus* sp. nov. **A**. Segments 12 and 13, ventral view, allotypic female (KIN-2). **B**. Allotypic female, ventral view. **C**. Segments 12 and 13, dorsal view, holotypic male (KIN-1). **D**. Holotypic male, ventral view; (gp) gonopores, (gs) genital seta, (LTAS) lateral terminal accessory spine, (LTS) lateral terminal spine, (PS1) penile spine 1, (PS2) penile spine 2.

Figure 6. *Echinoderes cavernus* sp. nov. **A**. Segments 12 et 13, vue ventrale, allotype femelle (KIN-2). **B**. Allotype femelle, même spécimen, vue ventrale. **C**. Segments 12 et 13, vue dorsale, holotype mâle (KIN-1). **D**. Holotype mâle, vue ventrale ; (gp) gonopores, (gs) soie génitale, (LTAS) épine terminale latérale accessoire, (LTS) épine terminale latérale, (PS1) épine pénienne 1, (PS2) épine pénienne 2.

plates of protonephridia (Fig. 7 E). A pair of lateroventral spines, 13-18 µm (mean = 16.1 µm). All other characters similar to those on segment 10.

Segment 12, 22-30 µm long (mean = 25.8 µm). Dorsal side with one posterior transverse row of short cuticular hairs; two small middorsal gland openings; no paradorsal gland openings; a pair of large subdorsal cuticular scars posterior on segment (Fig. 3 A); no middorsal cuticular scar; posterior edges of tergal plate slightly fringed. Ventral perforation sites in two to three less well-defined rows; cuticular hairs in same area as perforation sites; no lateroventral spines. Posterior edges of sternal plates in males concave, laterally twisting into ventrally pointed corners (Figs. 3 B, 5 D); posterior edges of sternal plates in females almost straight (Fig. 5 B).

Segment 13, 24-32 µm long (mean = 26.7 µm). Gonopores on arthrocorium between segments 12 and 13 (Figs. 5 B, 6 A); both sexes with a pair of genital setae,

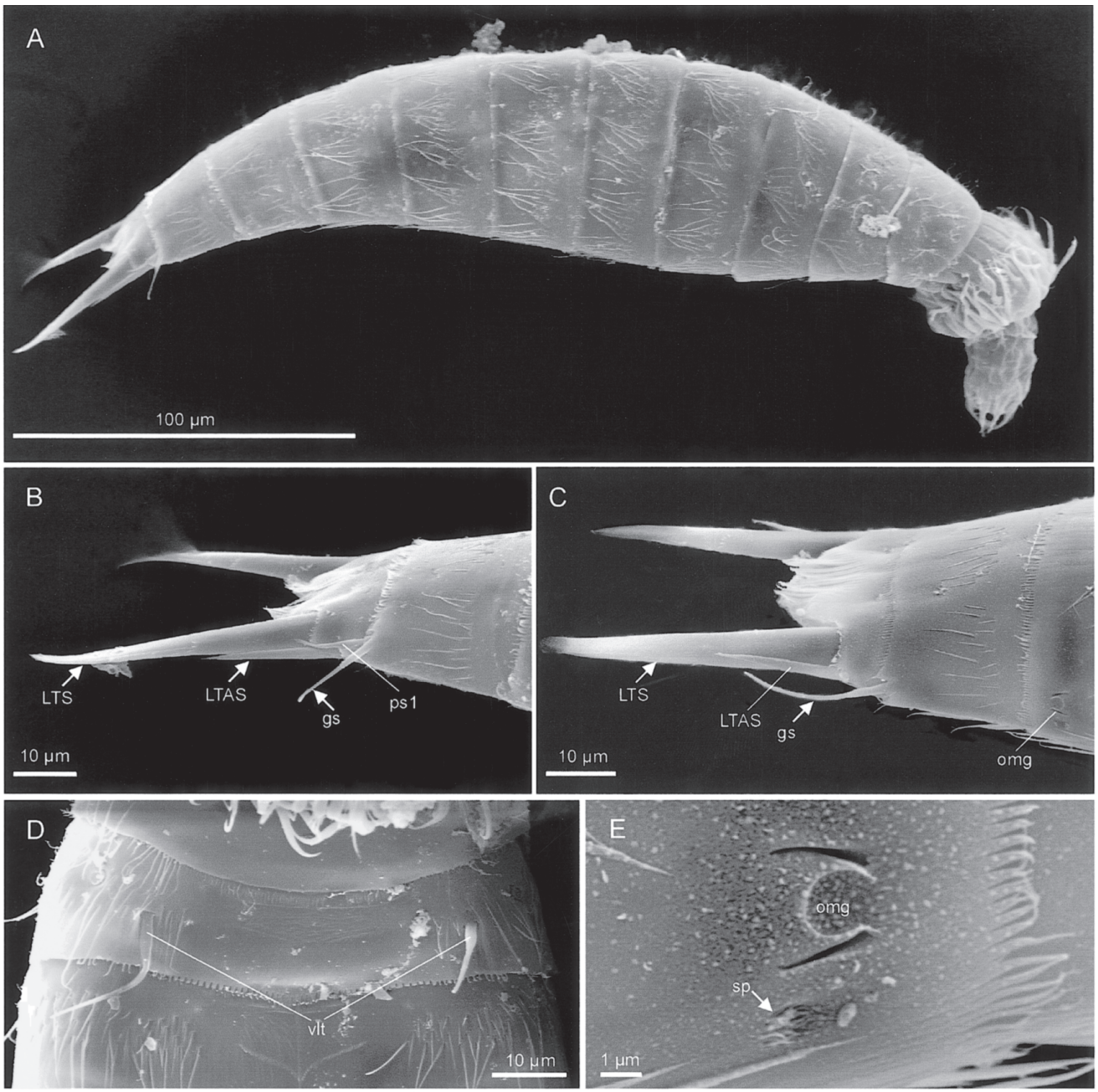

Figure 7. *Echinoderes cavernus* sp. nov.. SEM micrographs. **A**. Adult male, lateral view. **B**. Adult male, segments 12-13, lateral view. **C**. Adult female, segments 11-13, lateral view. **D**. Adult female, segment 4, sternal plate. **E**. Adult female, segment 11, lateral view; (gs) genital seta, (LTAS) lateral terminal accessory spine, (LTS) lateral terminal spine, (omg) opening from mucous gland, (ps1) penile spine 1, (sp) sieve plate, (vlt) ventrolateral tubules.

Figure 7. *Echinoderes cavernus* sp. nov. Microscopie électronique à balayage. **A**. Mâle adulte, vue latérale. **B**. Mâle adulte, segments 12 et 13, vue latérale. **C**. Femelle adulte, segments 11-13, vue latérale. **D**. Femelle adulte, segment 4, plaque sternale, vue ventrale. **E**. Femelle adulte, segment 11, vue latérale ; (gs) soie génitale, (LTAS) épine terminale latérale accessoire, (LTS) épine terminale latérale, (omg) orifice de la glande muqueuse, (ps1) épine pénienne 1, (sp) pores néphridiens, (vlt) tubules ventro-latéraux.

26-30 µm long (27-29 µm in males; 26-30 µm in females), (mean = 28.2 µm), located close to gonopores (Figs. 5, 6, 7 B-C); genital setae long, flexible; proximal parts thickened with approximately 9 longitudinal wrinkles; 1/4 from proximal end setae taper abruptly towards distal end. Tergal furcae triangular, rounded at tips. LTS (lateral terminal spines) short, blunt, stout, 44-51 µm (mean = 48.8 µm), (47-50 µm in males; 44-51 µm in females), 16.4-18.5

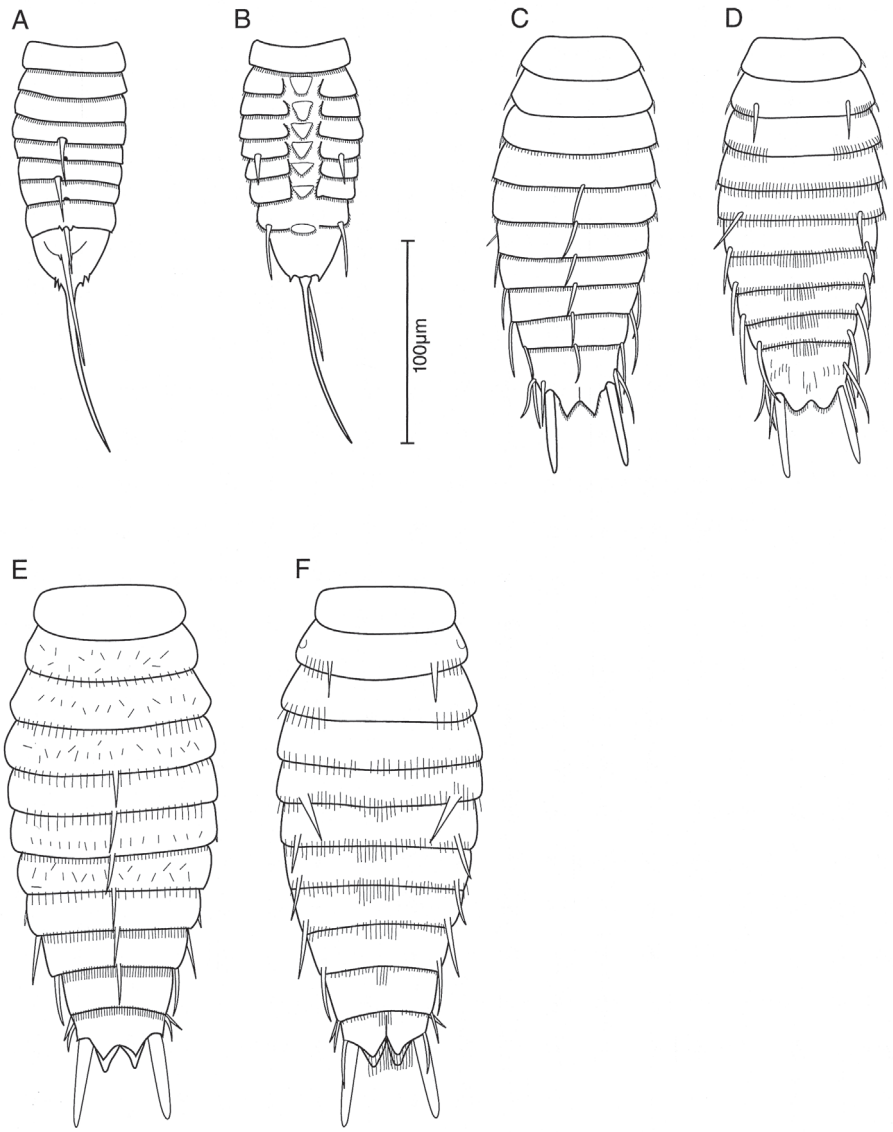

Figure 8. *Echinoderes cavernus* sp. nov., juvenile stages, all drawn to same scale. **A**. J-1, dorsal view, paratype (KIN-14). **B**. J-1, ventral view. **C**. J-4, dorsal view, paratype (KIN-10). **D**. J-4, ventral view. E. J-5, dorsal view, paratype (KIN-8). F. J-5, ventral view.

Figure 8. *Echinoderes cavernus* sp. nov., stades juvéniles, tous dessinés à la même échelle. **A**. J-1, vue dorsale, paratype (KIN-14). **B**. Même individu, J-1, vue ventrale. **C**. J-4, vue dorsale, paratype (KIN-10). **D**. Même individu, J-4, vue ventrale. E. J-5, vue dorsale, paratype (KIN-6). F. Même individu, J-5, vue ventrale.

percent of trunk length (Figs. 3, 4 A, 5, 6, 7 B-C). Both sexes with a pair of LTAS (lateral terminal accessory spines) located ventrolaterally to LTS (Figs. 5, 6 B, D, 7 B-C), 21-26 µm long (mean = 24.2 µm), (24-25 µm in males; 21-26 µm in females), 8.2-9.3 percent of trunk length. Dorsal posterior edge concave medially, extending laterodorsally into paired, rounded outgrowths; medial part of edge fringed; two small middorsal gland openings (Fig. 3 A). Ventral plates with rounded posterior margins, strongly fringed.

Males with two pairs of penile spines, originating from same site as genital setae (Figs. 5 C-D, 6 C-D, 7 B). Penile spine 1 short, 10-12 µm long (mean = 11.7 µm), pointed; penile spine 2 very short, 8-9 µm long (mean = 8.2 µm), hollow, truncate tube.

Females with no unique sexual spines or tubules (Figs. 5 A-B, 6 A-B, 7 C). Gonopores visible as bent interior cuticular thickenings anteriorly to ventrolateral spines (Figs. 5 B, 6 A). Oocytes and spermatozoa visible in several specimens.

Table 1. Measurements (in µm) of adult *Echinoderes cavernus* sp. nov. Abbreviations: MSW: maxium sternal width; SW: standard width; S2-13: segments 2-13; TL: trunk length.

Tableau 1. Mesures (en µm) des adultes de *Echinoderes cavernus* sp. nov. Abréviations : MSW : largeur sternale maximum ; SW : largeur standard ; S2-13 : segments 2-13 ; TL : longueur du tronc.

Character	n	Range	Mean	S.D.
TL	8	259-293	277.9	10.9
SW	7	47-51	49.8	1.3
MSW	7	71-87	75.2	5.6
S2	8	8-9	8.8	0.6
S3	7	24-26	24.9	1.2
S4	7	22-24	22.5	0.6
S5	7	22-25	23.4	1.2
S6	7	26-28	25.6	1.5
S7	7	24-26	25.1	1.1
S8	7	24-32	26.6	2.8
S9	7	24-36	27.0	4.2
S10	7	25-26	25.6	0.7
S11	7	25-28	26.6	0.9
S12	7	22-30	25.8	3.0
S13	7	24-32	26.9	2.9

Table 2. Spine/seta/tubule measurements (in µm) of adult *Echinoderes cavernus* sp. nov. Abbreviations: GS: genital seta; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; VL: ventrolateral;

Tableau 2. Mesures (en µm) des épines/soies/tubules de *Echinoderes cavernus* sp. nov. adulte. Abréviations : GS : soie génitale ; LTAS : épine terminale latérale accessoire ; LTS : épine terminale latérale ; LV : latéro-ventral ; MD : médio-dorsal ; VL : ventro-latéral.

Character	n	Range	Mean	S.D.
VL 4	8	18-37	23.9	6.1
LV 7	7	8-21	14.3	4.8
LV 8	6	15-17	15.8	0.8
LV 9	7	16-22	19.2	2.6
LV 10	6	17-25	19.8	3.0
LV 11	6	13-18	16.1	1.9
MD 6	5	13-16	14.4	1.2
MD 7	5	14-16	14.8	0.6
MD 8	6	15-17	15.5	1.3
MD 9	5	13-17	15.9	1.6
MD 10	7	11-17	15.4	1.9
GS	8	26-30	28.2	1.6
LTAS	8	21-26	24.2	1.5
LTS	8	44-51	48.8	2.4

Table 3. Summary of nature and location of scars, spines, and tubules arranged by series in *Echinoderes cavernus* sp.nov. Abbreviations: LA: lateral accessory; LTAS: lateral terminal accessory spine; LTS: lateral terminal spine; LV: lateroventral; MD: middorsal; PD: paradorsal; SD: subdorsal; SL: sublateral; VL: ventrolateral; # = cuticular scar; @ = gland opening; ¤ = muscle scar; + = spine; * = tubule.

Tableau 3. Résumé de la nature et de l'emplacement des empreintes, épines et tubules arrangés en série chez *Echinoderes cavernus* sp. nov. Abréviations : LA : latéral accessoire ; LTAS : épine terminale latérale accessoire ; LTS : épine terminale latérale ; LV : latéro-ventral ; MD : médio-dorsal ; PD : paradorsal ; SD : subdorsal ; SL : sub-latéral ; VL : ventro-latéral ; # = empreinte cuticulaire ; @ = orifice de la glande ; ¤ = empreinte du muscle ; + = épine ; * = tubule.

Segment	3	4	5	6	7	8	9	10	11	12	13
MD				+	+	+	+	+	+	@@	@@
PD				@	@	@	@	@	@		
SD				¤#¤	¤#¤	¤#¤				#	
Dorsal series											
	¤	¤									
SL											
LA (incl. LTAS)											+
LV (incl. LTS)					*	+	+	+	+		+
Lateral series											
VL		+									
Ventral series											

Juvenile stages

First stage juvenile (Figs. 4 B, 8 A-B), J-1, 11 segments, trunk length 116 µm, MSW-7 11 µm, 9.5 percent of trunk length, SW-10 12 µm, 10.3 percent of trunk length. Placids barely visible; dorsal posterior edges of trunk segments 3-9 with pectinate fringes. Tergal plates with smooth surface. Middorsal spines on segments 6, 8, 10, and 11 (MD6: 25 µm, MD8: 22 µm, MD10: 22 µm, MD11: 57 µm long); middorsal spines originate from small cuticular elevations, which appear as small, terminal pointed hooks in the squeezed specimen; middorsal spines on segments 6, 8, and 10 at posterior edge of segments, middorsal spine on

segment 11 on medial elevated part of segment; posterior edges of segments 7 and 9 with cuticular middorsal scar, probably sensory spots, flanked by pair of small, terminal pointed hooks. Ventral side with one row of triangular sternal plates at segments 4 to 10 (note that the triangular shape may be due to an artefact caused be contraction during the fixation). Ventromedian tubules (15 µm long) at segment 7, ventrolateral spines (28 µm long) at segment 10. Unpaired midterminal spine 80 µm long; terminal spine flanked by two pairs of small hooks, probably sensory structures, 4 µm long. Ventral edge at segment 11 straight, pectinate; ventrolateral corners with undeveloped LTS appearing as small acute projections.

Fourth stage juvenile (Figs. 4, C, 8 C-D), J-4, 12 segments, trunk length 186 µm. Placids barely visible. Posterior edges of dorsal segments 5 to 12 with pectinate fringes. Middorsal spine on segments 6-11 (MD6: 20 µm, MD7: 18 µm, MD8-10: 16 µm, MD11: 18 µm); middorsal spines located at posterior edge of segments. Ventral side with no distinctive sternal plates; segments 4-5 with cuticular hairs laterally at posterior edges; segments 6-11 with row of cuticular hairs near posterior edges, cuticular hairs longer at median part of segment; segment 12 with lightly scattered cuticular hairs; pectinate fringe posterior on terminal furcae. Ventrolateral tubules (17 µm long) on segment 4, lateroventral tubules (18 µm long) on segment 7, lateroventral spines (21 µm long) on segment 8, lateroventral spines (26 µm long) on segment 9, lateroventral spines (34 µm long) on segments 10 and 11, midlateral spines (tubules?) (22 µm long) on segment 12, lateroventral spines (tubules ?) (25 µm) on segment 12; spines on segments 6-11 located posterior on segments, spines on segment 12 located medially. LTAS 21 µm, LTS 40 µm.

Fifth stage juvenile (Figs. 4 D, 8 E-F), J-5, 13 segments, trunk length 237 µm. Placids barely visible. Posterior edges of dorsal segments 4 to 12 with pectinate fringes. Middorsal spine (17 µm long) at segment 6, middorsal spines (18 µm long) on segments 7-11; middorsal spines located at posterior edge of segments. Ventral side with no distinctive sternal plates; segments 4-5 with cuticular hairs laterally at posterior edges; segments 6-12 with row of cuticular hairs near posterior edges, cuticular hairs longer at median part of segment; strong pectinate fringe posterior on terminal furcae. Ventrolateral tubules (20 µm long) on segment 4, lateroventral tubules (22 µm long) on segment 7, lateroventral spines (20 µm long) on segment 8, lateroventral spines (22 µm long) on segment 9, lateroventral spines (28 µm long) on segments 10 and 11, midlateral spines (tubules?) (11 µm long) on segment 12, lateroventral spines (tubules ?) (15 µm long) on segment 12; spines on segments 6-12 located posterior on segments. LTAS 17 µm, LTS 41 µm.

Etymology: The name of the species is from the Latin caverna, which means cave. The name refers to the species' habitat.

Discussion

Discussion of diagnostic features

Echinoderes cavernus sp. nov. holds a number of unique or rare diagnostic features. The interstitial placids, located internally between the placids of segment 2 have, in *Echinoderes*, only been described from *E. dujardini* see (Zelinka, 1928). However, the structures are known from other species of Kinorhyncha (Nebelsick, 1990; ref. Higgins pers. comm.). The interstitial placids in *E. dujardini* are elongate, anteriorly broadened and with a sinuate anterior margin, and they do not resemble those in *E. cavernus* sp. nov. Despite their minute size, the interstitial placids are easily recognized. In more recent descriptions, the structures have been neglected, but it is probable that they contain information of systematic importance. It should be noted that interstitial placids also are described from the species of *Antygomonas* (Nebelsick,1990; Bauer-Nebelsick, 1996). In this genus, two interstitial placids occur between the placids.

Several species with lateral or subdorsal spines or setae posterior on segment 12 have been described, but the presence of genital setae on the arthrocorium between segments 12 and 13, as it is found in *E. cavernus* sp. nov., have never been reported. The setae resemble the longest penile spines found in most other species in *Echinoderes*, but the presence of an identical seta in females rejects that it is a penile spine. Thus, it is tempting to suggest that the features in *E. cavernus* sp. nov. display a very basic pattern, and that the genital setae in other *Echinoderes* were modified to a penile spine in males and lost in females. However, other characters point toward a relationship between *E. cavernus* nov. sp., *E. brevicaudatus* and *E. abbreviatus* (see Phylogenetic notes below). Since both the two last mentioned species display the common *Echinoderes*-pattern with three pairs of penile spines, it is more likely that the pattern in *E. cavernus* nov. sp. is autapomorphic.

Another very divergent character in connection with the sex determination is the presence of LTAS in males. In all other *Echinoderes* species only females have LTAS (Higgins, 1974). Whether the presence of LTAS in both sexes in *E. cavernus* sp. nov. is a plesiomorphy or an specialisation is uncertain. However, it should be noted that some species in other cyclorhagid genera, i. e. *Semnoderes, Sphenoderes, Zelinkaderes* and *Antygomonas* actually have LTAS in males as well as females (Higgins, 1967, 1969, 1990; Nebelsick, 1990; Zelinka, 1928).

Phylogenetic notes

Within the genus *Echinoderes*, *E. abbreviatus* and *E. brevicaudatus* have short and blunt LTS (Higgins 1966, 1983) that resembles the LTS of *E. cavernus* sp. nov. Other *Echinoderes*, i.e. *E. aquilonius* Higgins & Kristensen, 1988, *E. caribiensis* Kirsteuer, 1964, *E. citrinus* Zelinka, 1928 and *E. coulli*, have also relatively short LTS, but these are considerably slender (Higgins, 1977b; Higgins & Kristensen, 1988; Kirsteuer, 1964; Zelinka, 1928). The form II-females of *E. coulli* have very short LTS (Higgins, 1977b), but those are gradually pointed toward the tips, and not blunt as in *E. cavernus* sp. nov.

Thus, the presence of short and broad LTS is evaluated as an synapomorphy for a monophylum consisting of *Echinoderes abbreviatus*, *E. brevicaudatus* and *E. cavernus* sp. nov. This relationship is probably supported by similarities in substrate, which are discussed below.

Ecological notes

Higgins (1985, 1986) has clearly indicated that psammophilic species of *Echinoderes* from subtidal coarse sediments have long spines (including the lateral terminal spines). *Echinoderes abbreviatus*, *E. brevicaudatus* and *E. cavernus* sp. nov. have short and blunt lateral terminal spines and inhabit fine to rather coarse coralligenous sand. Short and broad lateral terminal spines could be an adaptation to a specific sediment type, e.g. coral sand. *Echinoderes aquilonius*, *E. caribiensis*, *E. citrinus* and *E. coulli* with short but considerably slender lateral terminal spines inhabit softer sediments.

A unique feature for *E. cavernus* sp. nov. is that it seems to be restricted to the submarine caves. Naturally, it cannot be rejected à priori that the species occurs outside the caves as well, but it has not been observed, despite the coast of New South Wales have been sampled rather intensively by the senior author and R. M. Kristensen (Kristensen, pers. comm.). As noted in the locality description, the bottom right outside the cave was covered with rocks and large stones, which made sediment sampling impossible.

Very few deep-sea kinorhynchs have been described (Bauer-Nebelsick, 1996) and unfortunately none of the echinoderid records from the deep-sea (Shirayama, pers.comm.) have been published. Thus, it remains uncertain whether there is a relationship between the deep-sea and cave kinorhynchs. The closest relationship to the first described submarine cave kinorhynch, *Echinoderes cavernus* sp. nov. from Australia is the Caribbean species, *E. abbreviatus* and the Red Sea species *E. brevicaudatus*.

The associated meiofauna in Jim's Cave

Jim's Cave has a very rich meiofauna especially compared to the relatively small amount of sediment sampled. Additionally to *Echinoderes cavernus* sp. nov., several species of nematodes, gastrotrichs, polychaetes, tardigrades, crustaceans, aplacophorans, and loriciferans were found. The finding of loriciferans was expected, but it is the first record from Australian waters. The loriciferans, tardigrades and aplacophorans are subject to further investigation. No other kinorhynch species were found in this cave.

Conclusions

The new species, *E. cavernus* belongs to a group of small and broad species in *Echinoderes*, with distinctive short, stubby, lateral terminal spines. The group consist of *E. abbreviatus*, *E. brevicaudatus* and *E. cavernus* sp. nov., which all inhabit tropical waters. Furthermore, all three species are found in calcareous sediment (coral sand) mixed with detritus. *Echinoderes cavernus* sp. nov. most closely resembles *E. abbreviatus* from Carrie Bow Cay, Belize. Their relationship with or within the D-(6-10), L-(7-11) group is not resolved.

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References

Bauer-Nebelsick M. 1996. *Antygomonas oreas* sp.n., a new deep sea kinorhynch from the Pacific Ocean. *Annalen des Naturhistorischen Museum in Wien*, **98:** 5-22.

Bowman T. E. & Iliffe T. M. 1985. *Mictocaris halope*, a new unusual peracaridean crustacean from marine caves on Bermuda. *Journal of Crustacean Biology*, **5:** 58-73.

Bowman T. E., Garner S. P., Hessler R. R., Iliffe T. M. & Sanders H. L. 1985. Mictacea, a new order of Crustacea Peracarida. *Journal of Crustacean Biology*, **5:** 74-78.

Brown R. 1985. Developmental and taxonomic studies of Sydney Harbour Kinorhyncha. Unpublished Ph.D thesis. 193 pp. Macquarie University.

Brown R. & Higgins R. B. 1983. A new species of *Kinorhynchus* (Homalorhagida, Pycnophyidae) from Australia with a redescription and range extension of other Kinorhyncha from the South Pacific. *Zoologica Scripta*, **12:** 161-169.

Coull B. C. & Wells J. B. J. 1981. Density of mud-dwelling meiobenthos from three sites in the Wellington region. *New Zealand Journal of Marine and Freshwater Research*, **15:** 411-415.

Grimaldi De Zio S., D'Addabbo Gallo M., Morone De Lucia R. M., Vaccarella R. & Grimaldi P. 1982. Quattro nuove specie di Halechiniscidae rinvenute in due grotte sottomarine dell'Italia meridionale. (Tardigrada: Heterotardigrada). *Cahiers de Biologie Marine*, **23:** 415-426.

Hart C. W., Manning R. B. & Iliffe G. T. M. 1985. The fauna of Atlantic marine caves: Evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proceedings of the Biological Society of Washington*, **98:** 288-292.

Higgins R. P. 1966. Faunistic studies in the Red Sea (in Winter, 1961-62). *Zoologisches Jahrbücher, Systematik, Oekologie und Geographie der Tiere*, **93:** 118-126.

Higgins R. P. 1967. The Kinorhyncha of New Caledonia. In: *Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie*, pp. 75-90. Éditions de la fondation Singer-Polignac: Paris.

Higgins R. P. 1969. Indian Ocean Kinorhyncha: 1, *Condyloderes* and *Sphenoderes*, new cyclorhagid genera. *Smithsonian Contributions to Zoology*, **14:** 1-13.

Higgins R. P. 1974. Kinorhyncha. In: *Reproduction of Marine Invertebrates* (A. G. Giese & J. S. Pearce eds), vol. 1., pp. 507-518. Academic Press: New York.

Higgins R. P. 1977a. Redescription of *Echinoderes dujardinii* (Kinorhyncha) with descriptions of closely related species. *Smithsonian Contributions to Zoology*, 248**:** 1-26.

Higgins R. P. 1977b. Two new species of *Echinoderes* (Kinorhyncha) from South Carolina. *Transactions of the American Microscopical Society,* **96:** 340-354.

Higgins R. P. 1983. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, II: Kinorhyncha. *Smithsonian Contributions to the Marine Sciences*, **18:** 1-131.

Higgins R. P. 1985. The genus *Echinoderes* (Kinorhyncha: Cyclorhagida) from the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **65:** 785-800.

Higgins R. P. 1986. A new species of *Echinoderes* (Kinorhyncha: Cyclorhagida) from a coarse-sand California Beach. *Transactions of the American Microscopical Society*, **105:** 266-273.

Higgins R. P. 1988. Kinorhyncha. In: *An Introduction to the Study of Meiofauna* (R. P. Higgins & H. Thiel eds), pp. 328-331. Smithsonian Institution Press: Washington.

Higgins R. P. 1990. Zelinkaderidae, a new family of Cyclorhagid Kinorhyncha. *Smithsonian Contributions to Zoology*, **500:** 1-13.

Higgins R. P. & Kristensen R. M. 1988. Kinorhyncha from Disko Island, West Greenland. *Smithsonian Contributions to Zoology*, **458:** 1-56.

Higgins R. P. & Rao G. C. 1979. Kinorhynchs from the Andaman Islands. *Zoological Journal of the Linnean Society*, **67:** 75-85.

Just J. & Poore G. C. B. 1988. Second record of Hirsutiidae (Peracarida: Mictacea): *Hirsutia sandersetalia*, new species, from southeastern Australia. *Journal of Crustacean Biology*, **8:** 483-488.

Kirsteuer E. 1964. Zur Kenntnis der Kinorhynchen Venezuelas. *Zoologischer Anzeiger,* **173:** 388-393.

Kristensen R. M. & Higgins R. P. 1984. Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with descriptions of two new species from Disko Bay, West Greenland. *Smithsonian Contributions to Zoology*, **391:** 1-40.

Manning R. B., Hart C. W. & Iliffe T. M. 1986. Mesozoic relicts in marine caves of Bermuda. *Stygologia*, **2:** 156-66.

Nebelsick M. 1990. *Antygomonas incomitata* gen. et sp.n. (Cyclorhagida, Kinorhyncha) and its phylogenetic relationships. *Zoologica Scripta*, **19:** 143-152.

Pardos F., Higgins R. P. & Benito J. 1998. Two new *Echinoderes* (Kinorhyncha, Cyclorhagida) from Spain, including a reevaluation of kinorhynch taxonomic characters. *Zoologischer Anzeiger*, **237:** 195-208.

Riedl R. 1966. *Biologie der Meereshöhlen*. Verlag Paul Parey: Hamburg. 636 pp.

Sanders H. L., Hessler R. R. & Garner S. P. 1985. *Hirsutia bathyalis*, a new unusual deep-sea benthic peracaridan crustacean from the tropical Atlantic. *Journal of Crustacean Biology*, **5:** 30-57.

Villora-Moreno S. 1996. A new genus and species of the deep-sea family Coronarctidae (Tardigrada) from a submarine cave with a deep-sea like condition. *Sarsia*, **81:** 275-283.

Yager J. 1981. Remipedia, a new class of Crustacea from a marine cave in the Bahamas. *Journal of Crustacean Biology*, **1:** 328-333.

Yager J. & Humphreys W. F. 1996. *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. *Invertebrate Taxonomy*, **10:** 171-187.

Zelinka K. 1928. Monographie der Echinodera. Verlag von Wilhelm Engelmann in Leipzig: Leipzig. 393 pp.