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Echiniphimedia,
An Amphipod Genus
From the Antarctic Ocean

By J. Laurens Barnard
Associate Curator, Division of Crustacea

Echiniphimedia, a member of the Acanthonotozomatidae, is represented by three known species confined primarily to the sublittoral and upper bathval depths of antarctic seas. They are the most extraordinarily ornamented members of the family in their departure from the ordinary plan of paired dorsal teeth or low numbers of teeth. Two members of Echiniphimedia are virtually covered with medium to long spikelike fixed teeth and are rivalled in the density of their ornamentation only by a member of the Paramphithoidae, Uschakoviella Gurjanova, which has dense articulated spines covering the body. The degree of dorsal segmental ornamentation among benthic Amphipoda seems to increase directly with latitude, the tropics having few such species and the polar regions having large numbers of "spiny" amphipods. Ornamentation appears to be highly variable among polar species, differing in extent from youth to senility, from deme to deme, or within demes. The extent of intraspecific variations has scarcely been measured nor has it been identified with ecotypic and racial existence.

The purpose of this paper is to review the known species of the genus, report on variations among their individuals, elucidate a

nomenclatural problem, and determine whether the species have intrageneric affinities.

Materials were collected on the University of Southern California Eltanin (ET) Program and were made available through this office as well as that of Miss Patsy A. McLauglin of the Smithsonian Oceanographic Sorting Center. Dr. Donald F. Squires and Dr. David L. Pawson of the Smithsonian kindly provided specimens from their collections made aboard the icebreaker Eastwind (EW). Miss Naomi D. Manowitz of the Smithsonian, on NSF Grant GB-3285, inked my drawings.

Echiniphimedia K. H. Barnard

Echiniphimedia K. H. Barnard, 1930.

Type-species.—Iphimedia hodgsoni Walker 1906 (and 1907).

Diagnosis (revised).—Acanthonotozomatid with at least 2 or more coxal pairs obtaining submarginal fixed teeth in adulthood, some or all body segments becoming covered with rows or groups of erect cusps on lateral surfaces, teeth also occurring on dorsal surfaces and posterior margins of segments but not always distinct from ordinary dorsal and marginal cuspidation of other acanthonotozomatids; epistome broad from side to side, upper lip pendant from epistome and rounded or slightly truncate; mandibles of ordinary shape, neither extremely styliform nor bulky, but relatively simple; incisor of medium breadth, serrate or mostly entire; lacinia mobilis vermiform to subvermiform to spatulate, usually entire but occasionally serrate, molar absent; palp of maxilla 1 with 2 articles, reaching or exceeding apex of outer plate; palp of maxilliped 4-articulate, article 4 extremely small but articulate; both pairs of gnathopods minutely chelate (parachelate); telson deeply emarginate or truncate.

Remarks.—The relative consistency in mouthparts, despite minor variations among the three species and strong differences in ornamentation, suggests that the genus is internally homogeneous. Three other acanthonotozomatid genera (from a total of 21) have close affinities with Echiniphimedia and, presumably because of simpler ornamentation, may occur on the line of precursors to Echiniphimedia. Pariphimedialla Schellenberg (1931) seems to be the most primitive of the quartet of genera in that it has a lacinia mobilis in both mandibles. It was distinguished originally from Iphimediella Chevreux (1912) in the serrations of the mandibular incisors, but this character varies intraspecifically in Echiniphimedia and may be of no value as a generic character. Iphimediella, however, also lacks a lacinia mobilis in the left mandible like Echiniphimedia. The former differs from the latter in its vestigial mandibular hump (?molar), a slightly stouter mandible, and a thinner and narrower epistomal sclerite. Pseudiphimediella

Schellenberg (1931) has a deeply incised upper lip, a tendency toward which may be seen in one species of *Echiniphimedia*. Palp articles 1 and 2 of the maxilliped are broadened in *Pseudiphimediella*. The strong character difference between *Echiniphimedia* and the other three genera remains the acquisition of submarginal coxal teeth in adult *Echiniphmeidia* and the acquisition of pereonal and pleonal teeth supernumerary to the basic acanthonotozomatid plan.

Key to the Species of Echiniphimedia

Echiniphimedia hodgsoni (Walker)

FIGURES 1-3

Iphimedia Hodgsoni Walker, 1906, p. 152.
Iphimedia hodgsoni.—Walker, 1907, p. 30, pl. 11 (fig. 18).
Echiniphimedia hodgsoni.—K. H. Barnard, 1930, pp. 359-360, fig. 31.—Schellenberg, 1931, p. 123.—K. H. Barnard, 1932, p. 125.—Nicholls, 1938, pp. 82-84, figs. 43, 44.

DESCRIPTION.—Female, 38 mm, ET 428: Percon, coxae, second articles of pereopods 3-5 and pleonites 1-4 covered densely with fixed submarginal, acute teeth, on perconites and pleonites teeth arranged in crude vertical rows, generally 2 rows per segment or 3 rows on posterior metasomal segments; teeth on coxae arranged in rows to some extent; tubercles rarely occurring on ventrolateral margins of pereonites 2-5 and on dorsolateral margins of pleonites 2-3 (possibly representing scars of broken teeth); pleonite 5 with large dorsolateral tooth on each side with smaller cusp at its base, pleonite 6 with large mediodorsal tooth; pleonal epimeron 1 with slightly convex posterior margin, posteroventral corner with minute tooth extended from lateral ridge, epimera 2 and 3 with much larger posteroventral tooth and lateral ridge, epimeron 3 with large medioposterior tooth in addition to posteroventral tooth; head with stout rostrum of medium length, lateral planiform base produced laterally into large, hemispherical ocular bulge with pigmented ommatidial tissue, base with supraocular tooth, cheek below eye with 2 teeth, then, ventrally, cheek with deep incision bordered below by large tooth; articles 1 and 2 of antenna 1 extraordinarily palmate, resembling moose antlers, article 3 short and simple, accessory flagellum

small, 1-articulate, bearing 2 distal setules, barrel-like or mammilliform depending on aspect; antenna 2 basally palmate, article 1 with long ventral cusp appearing as gland cone might from lateral view

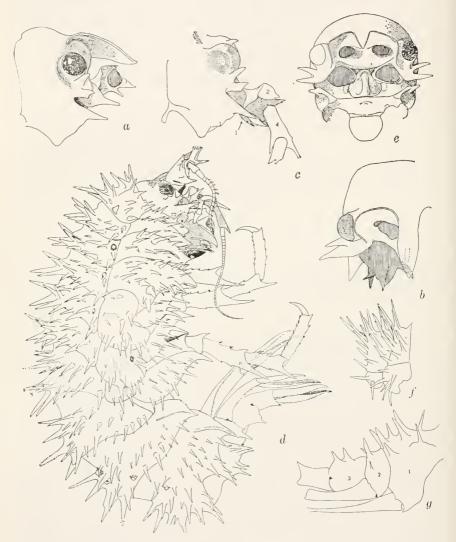


FIGURE 1.—Echiniphimedia hodgsoni (Walker), female, 38 mm, EW 66-022: a, head, lateral; b, half of head, anterodorsal. Female, 38 mm, ET 428: c, side of head and base of antenna 2; d, lateral view of body. Female, 29 mm, ET 1003: e, head, anterior; f, pereonites 6, 7, right side, right to left; g, urosome, right.

and occurring just medial to largest anteroventral cephalic tooth, article 2 with large, complex dorsal keel; epistome with weak anterior process from lateral view, process scarcely discernible from anterior

view, epistome with lateral alae clearly defined and forming ventral articulation sockets for mandible, epistome of this specimen possibly aberrant, having on right side (to left in drawing) a scale of chitin possibly not shed during latest ecdysis; upper lip slightly emarginate; mandibles broad, with flat, apically broad cutting edge, only right mandible with vermiform lacinia mobilis, molar absent; article 1 of mandibular palp with apicomarginal cusp on each extreme, article 3 falciform; outer lobes of lower lip scarcely incised; maxillae shown in figures; maxillipedal palp article 2 with small, poorly projecting mediodistal process scarcely extending along article 3, article 4 minute but distinctly articulate; gnathopod 1 scarcely setose, gnathopod 2 strongly setose, both minutely chelate; gnathopods and pereopods 1 and 2 in preserved condition held under coxae and not visible from lateral view; pereopods 3-5 similar to one another and successively slightly larger (3 broken distally), second articles complexly ornamented with teeth and lateral ridges; uropods without special features or distinctions but shown in figures; telson short, with medium-sized distal emargination, lateral lobes coniform.

Female, 29 mm, ET 1003: This specimen differs from the 38 mm female in many ways; grossly it resembles Walker's (1907) figure more strongly than does the 38 mm female because the segmental teeth are longer and seemingly more closely spaced even though slightly fewer in number than those on the 38 mm female. Possibly in adulthood the teeth do not elongate or thicken proportionally to body growth; however, many of the teeth on the 38 mm female are thicker than those on the 29 mm female. Drawings on two perconal segments and the urosome seem sufficient to demonstrate these differences (figs. 1f, g). Urosomite 3 resembles Walker's drawing in having 2 posterolateral and 2 middorsal teeth. Only the right-sided member of each pair of teeth is shown in the figure herein. Urosomite 3 of the 38 mm female has a single large posterolateral tooth as if the pair of teeth in the smaller female had become amalgamated in the larger female. The 29 mm female lacks the supraorbital tooth seen in both the 38 mm female and the 8 mm juvenile. The second articles of pereopods 3-5 are more slender, and the posteroventral cusps on the corners of the pleonal epimera are longer than in the 38 mm female. Article 2 of the maxillipedal palp of the 29 mm female, like Walker's figure, does not have a distinct distomedial process. The eye is fully developed and almost perfectly circular, with all of its ommatidia clearly delineated, whereas in the 38 mm female, the posterior margin of the eye is clouded, presumably with carbonate deposits. Female, 37 mm, EW 66-022: This specimen has no supraocular

Female, 37 mm, EW 66-022: This specimen has no supraocular tooth and the dorsolateral cephalic flange is extremely strong. The emargination is especially deep.

Male, 19 mm, EW 66-004: This specimen has essentially no teeth on pleonite 5, no supraocular tooth, the ventrolateral cephalic tooth forming the anterior boundary of the cheek notch is much longer than in other specimens, and the tooth of the posterior boundary is obsolete.

Male, 9 mm, ET 1003: This specimen is somewhat closer to Walker's portrayal of the species than are other specimens. The thin dorsal teeth are densely packed, the supraocular tooth is absent, and the coxae have the following number of teeth: coxa 1=3, 2=4, 3=5, 4=5, 5=8, 6=4 or 5 (left and right) and 7=2. The mandibular incisor is deeply serrate and the lacinia mobilis very broad. Pleonite 5 has one pair of dorsolateral erect cusps and pleonite 6, a small medial pair and a large posterolateral pair.

MATERIAL.—ET 428 (female, 38 mm); 993 (damaged juvenile, 8.0 mm); ET 1003 (female, 29 mm, and male, 9.0 mm). EW 66-004 (male, 19 mm); EW 66-022 (female, 37 mm).

Records.—ET 428, 62°41′S, 57°51′W, 662–1120 m; ET 993, 61°25′S, 56°30′W, 300 m; ET 1003, 62°40′S, 54°45′W, 210–219 m; EW 66–004, 67°49.8′S, 69°10.5′W, 119 m; EW 66–022, 60°26.5′S, 45°53.3′W, 146–168 m. Bransfield Strait; near Elephant Island; off Adelaide Island; South Orkney Islands.

DISTRIBUTION.—Coulman Island, 183 m; McMurdo Sound, 348-547 m; Oates Land, 329-366 m; Cumberland Bay, South Georgia Islands, 250-310 m, and South Georgia Islands, 110-401 m; South Shetland Islands, 200-342 m; Palmer Archipelago, 90-130 m; Commonwealth Bay, 82-730 m; Davis Sea, 200-595 m. Confirmed depth range, 119-662 m.

Remarks.—This is probably the most strongly ornamented gammaridean amphipod. It is rivalled only by Uschakoviella echinophora Gurjanova (1955), on which the ornamental spines are articulate and small, and by Actinacanthus Stebbing (1888), on which the processes are fewer in number but so large that they dominate the body completely. The teeth of Echiniphimedia have been drawn in the accompanying figures exactly as they appear on the organism except for a few obviously bent or apically broken teeth that have been restored to their presumed original condition; a few large dorsal teeth have not been restored because one cannot determine their extent. The overall appearance of the in toto view of the 38 mm female differs strongly from that published by Walker (1907) mainly because the teeth and cusps are actually smaller than he represented them to be and more of the details of coxae and somites are truly visible. Of course, teeth projecting laterally are foreshortened. The pattern of teeth is not precisely symmetrical on bilateral comparison but is extremely similar from side to side. Surficial chitin between processes

often is marked with faint lines defining shallow basal bulges on the processes, similar to the texture of echinoids; most of these lines have been omitted from the drawings for the sake of clarity.



FIGURE 2.—Echiniphimedia hodgsoni (Walker), female, 38 mm, ET 428: a,b, gnathopods 1, 2; c, left antenna 1; d, anterior view of upper lip (u), epistome (E), and mandible (M); e, telson; f, left lateral view of head, pereonite 1, and base of antenna 1; g, base of antenna 2; h, right side of head, eye (E); i-k, uropods 1-3; l, accessory flagellum on antenna 1; m, end of gnathopod 2. Female, 37 mm, EW 66-022: n,o, antenna 1; left and right sides. Male, 19 mm, EW 66-004: p, head; τ, urosome, right side. Juvenile, 8.0 mm, ET 993: q, right mandible.

Ocular bulges, projecting strongly, are formed of very clear chitin having a microscopic, almost reticulate, polygonal pattern; ommatidia are extremely small and densely packed.

Walker (1907) wrote that the gnathopods are like those of *Iphimedia obesa* Rathke, but his drawing of gnathopod 1 shows it to be simple; presumably it had twisted in its mount. I therefore assumed Walker's statement was untrue and his figure correct when I erroneously moved *Echiniphimedia echinata* to *Pariphimediella* (see J. L. Barnard, 1964).

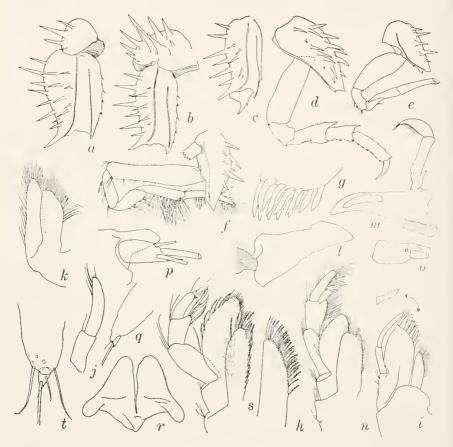


Figure 3.—*Echiniphimedia hodgsoni* (Walker), female, 38 mm, ET 428: a-d, pereopods 5, 4, 3, 1; e,f, gnathopods 1, 2; g-j, maxilla 1; k, maxilla 2; l,m, mandibles; n-q, maxillipeds; r, lower lip. Juvenile, 8.0 mm, ET 993: s,t, maxilliped.

A posterodistal tooth on epimeron 2 is not shown in Walker's (1907) figure but all specimens at hand have that tooth.

K. H. Barnard (1930) illustrates a much longer rostrum for *E. echinata* than seen in material at hand or in Nicholls' (1938) drawing. Nicholls' specimens did not have the supraocular tooth. Nicholls has already discussed the differences between his material and that of K. H. Barnard and the difficulty of matching various specimens to

the inadequate description of Walker. A wide variability in characters of *E. echinata* (Walker) is confirmed by Nicholls (1938) and this appears to be true also for *E. hodgsoni*.

Echiniphimedia echinata (Walker)

FIGURES 4, 5

?Iphimedia nodosa Dana, 1853, p. 928, pl. 63 (figs. 3, a, b).—Bate, 1862, p. 125 pl. 23 (fig. 1).—?Chevreux, 1912, pp. 118–119.

Iphimedia echinata Walker, 1906, p. 150; 1907, pp. 28-29, pl. 10 (fig. 16).— Chevreux, 1912, p. 119.

Echiniphimedia nodosa.—K. H. Barnard, 1930, pp. 361-363, fig. 33.

Echiniphimedia echinata.—K. H. Barnard, 1932, p. 126.—Nicholls, 1938, pp. 80–82, fig. 42.

Not Iphimedia nodosa.—Stebbing, 1906, pp. 216-217.

Nomenclature.—K. H. Barnard (1930) synonymized Iphimedia echinata with I. nodosa but then reversed his position in 1932 after Schellenberg (1931) refuted the move. Both I. echinata and I. nodosa bear a strong resemblance to each other in several characters not found as yet in other acanthonotozomatids, and K. H. Barnard's conclusion that they were synonymous was probably correct. The absence of teeth on perconites 1-4 (or 5) but the presence of supernumerary submarginal teeth on pleonites (1) 2-3 are characteristic of both Dana's and Walker's material. Dana apparently did not completely understand the morphology of his species for he failed to account for some important characters such as the giant posterior teeth of pleonal epimeron 3 and the dorsal teeth of the urosome. As his material has long been presumed lost, one can only conjecture on how he failed to illustrate or describe these characters adequately unless an acanthonotozomatid fitting his description more closely than does I. echinata remains to be rediscovered. Until we can be sure that such does not exist, it is prudent to place Dana's and Walker's species together only in provisional status.

Schellenberg (1931) and K. H. Barnard (1932), in his retraction of the 1930 synonymy, apparently were both misled by Stebbing (1906), who appears to have based his monographic description of Dana's I. nodosa on a species only remotely related to Dana's. His interpretation of Dana's work was far too extreme, and we must presume he found in British Museum collections an undescribed acanthonotozomatid that seemed close to I. nodosa. I have made no attempt to trace that species to a taxon described later, but there is a strong possibility that such exists. It may indeed represent a specimen Schellenberg figured as "I. nodosa." The generic assignment is open to question also except that neither fits Echiniphimedia as diagnosed herein. K. H. Barnard's (1932) "Iphimediella nodosa" is yet another species but not an Echiniphimedia.

Group description of material at hand.—Pereonites 5-7 or 6-7 only, coxae 3-7 or 5-7 only, second articles of percopods 3-5 or 4-5 only, and pleonites 1-4 covered sparsely with fixed submarginal and marginal teeth, submarginally mainly on pleon and coxae 5-6, pereonites 1-4 always smooth except for one small posteroventral cusp also found on pereonites 5-7 and forming serially a small lateral carina, teeth of percopods and pleonites increasing in number with increased size of individual but also varying considerably among equal-sized individuals; thus an individual 22 mm long lacking submarginal teeth on coxae 3-4, whereas an individual 19 mm long having such teeth; small individuals 9 mm or smaller with dorsal midline teeth of pleonites 3-4 anteriorly reverted, becoming vertically erect in larger individuals; pleonite 5 with dorsal hump, 6 with posterolateral wings; pleonal epimeron 1 with slightly convex posterior margin, posteroventral corner lacking tooth, anteroventral corner with one spine, epimeron 2 with small tooth and lateral ridge, epimeron 3 with large posteroventral tooth, a larger posteromedial tooth; rostrum of medium length, weakly developed lateral planiform base of head with large hemispherical ocular bulge enclosing pigmented ommatidial tissue, no extraocular teeth, anteroventral margin of cheek with deep notch, its boundaries forming sharp teeth, anterior tooth essentially forming lateral cephalic lobe; articles 1-2 of antenna 1 moderately palmate, article 3 short and simple, accessory flagellum very small, 1-articulate, bearing several setules, barrel-like; antenna 2 basally palmate to moderate extent, article 1 with long ventral cusp appearing as gland cone; epistome with appearance of fleur-de-lis; upper lip rounded or nearly truncate below; mandibles broad, incisors either smooth or weakly serrate, lacinia mobilis in right mandible subvermiform, distally broadened and flattened and distolaterally serrate minutely and irregularly; article 1 of mandibular palp lacking conspicuous cusp, article 3 falciform; lower lip and maxillae generally as in E. hodgsoni but outer lobe of maxilla 2 with 2 distolateral marginal setae; emargination of telson narrower than in E. hodgsoni.

Material.—ET 435 (female, 22 mm, figured); ET 436 (12 specimens, some figured).

RECORDS.—ET 435, 63°14'S, 58°40'W, 73-92 m; ET 436, 63°14'S, 58°45'W, 73 m.

Distribution.—Tierra del Fuego; Cape Virgins; Straits of Magellan; south of Graham Land; Commonwealth Bay, 46–732 m; McMurdo Sound, 175–547 m; South Georgia Islands, 122–234 m; Palmer Archipelago, 90–132 m; Marguerite Bay, 200 m; Ile Jenny, 230 m; near King George Island, 73–92 m.

Remarks.—Dana's *Iphimedia nodosa* would appear to be a younger individual than any in this collection, the smallest at hand being 6.4

mm. A recognizable male is only 7.8 mm long; thus, considerable growth occurs after sexual maturity: the largest individual reported is 45 mm long. The 6.4 mm specimen, however, is better developed in some characters than the largest adults for it has 1 dorsal, 2 lateral,

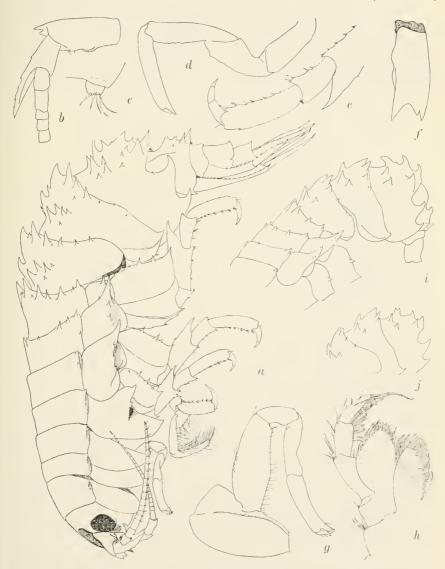


FIGURE 4.—Echiniphimedia echinata (Walker), female, 22 mm, ET 435: a, lateral view of body; b, left lateral antenna 1; c, accessory flagellum; d, gnathopod 2, setae removed; e, distal end of pereopod 3; f, dorsal article 1 of antenna 1; g, gnathopod 1; h, maxilliped. Juvenile, 6.4 mm, ET 436: i, pereonite 4 through pleonite 6, left to right. Male, 7.8 mm, ET 436: j, pleonites 1-3, left to right.

and 2 posteroventral teeth on perconite 5, whereas the 22 mm female has only 2 posteroventral and 2 ventral supernumerary teeth on that segment. Considerable phenotypic differences are seen, therefore,

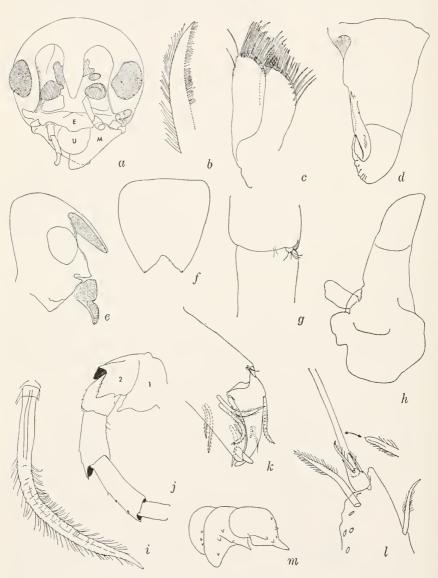


FIGURE 5.—Echiniphimedia echinata (Walker), female, 22 mm, ET 435: a, head, anterior view (E=epistome, U=upper lip, M=mandible, hatching=antennal socket); b, seta of maxilla 2; c, maxilla 2; d, right mandible; e, head and epistomal-labral complex; f, telson; g, accessory flagellum; h, left mandible; i, seta of gnathopod 1; j, medial antenna 2; k, end of gnathopod 1; l, apex of maxillipedal palp. Female, 19.5 mm, ET 436: m, coxae 3-5, left to right.

and these have been mentioned in detail by K. H. Barnard. Teeth may be added to the pleon but perhaps lost from the pereon with increase in age.

The urosome folds toward the metasome in such a way that the dorsal teeth of pleonite 4 become nearly congruent with those of pleonal epimeron 3. Dana, therefore, with inferior microscopy, may have thought he was seeing the opposite epimeron projecting from behind and thus illustrated the urosome as dorsally smooth.

Nicholls had juvenile and adult specimens with dentations commencing on pereonite 2 instead of pereonites 5 or 6.

Echiniphimedia scotti K. H. Barnard Figure 6

Echiniphimedia scotti K. H. Barnard, 1930, pp. 360-361, fig. 32.

Description.—Male, 22 mm: Pereon, coxae, second articles of pereopods 3-5 and pleonites 1-4 covered with acute or blunt submarginal teeth, teeth especially blunt on anterior perconites, arranged in crude vertical rows on pereonites and pleonites, generally 2 rows except on pereonites 2-6 with 1 row, teeth on coxae, though sparse, generally arranged in rows; pleonite 5 smooth, pleonite 6 with weak dorsolateral tooth on each side; pleonal epimeron 1 with slightly convex posterior margin, posteroventral corner simple but lateral face with weak ridge, epimeron 2 with small posteroventral tooth, epimeron 3 with large posteroventral tooth, both epimera with strong lateral ridges, epimeron 3 with large medioposterior tooth in addition to posteroventral tooth; stout rostrum of medium length, lateral subplaniform base of head produced laterally into large hemispherical ocular bulge, faintly gray pink in alcohol, without supra- and subocular teeth, cheek below eye with deep incision, its borders asymmetrically cuspidiform; articles 1 and 2 of antenna 1 extraordinarily palmate, resembling moose antlers, article 3 short and simple; accessory flagellum small, 1-articulate, barrel-like or mammilliform depending on aspect; antenna 2 basally palmate like E. hodgsoni; epistome weak, upper lip rounded below; mandibles broad, incisors serrate, lacinia mobilis on right mandible slender, thin, short, apex broad but obliquely and weakly serrate, palp article 1 scarcely cuspidate distally, article 3 falciform; outer lobes of lower lip not incised; maxillae and maxillipeds, gnathopods, pereopods and uropods like those of E. hodgsoni.

MATERIAL.—ET 1003 (male, 22 mm).

RECORD.—Near Joinville Island, 62°40′ S, 54°45′ W, 210-219 m.

DISTRIBUTION.—McMurdo Sound, 348-457 m.

Remarks.—This individual differs from the type-specimen (female, 23 mm) described by K. H. Barnard in the following characters: (1) the asymmetrical boundaries of the subocular notch; (2) the more abundant but shorter anterior pereonal teeth; (3) one more tooth on coxa 1 and one less on coxa 3; (4) pleon segment 3 with only 2 instead of 3 rows of teeth; (5) the unincised, truncate telson.

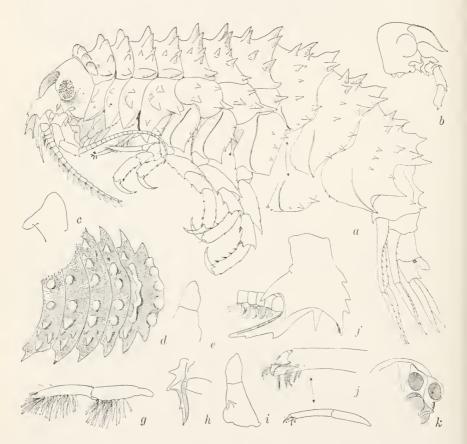


FIGURE 6.—Echiniphimedia scotti K. H. Barnard, male, 22 mm, ET 1003: a, lateral view of body; b, head and peduncle of antenna 2; c, half of lower lip; d, dorsal view of pereonites 1-5, right to left; e, obverse side of right mandible; f, right dorsal antenna 1; g, left gnathopod 2; h, left coxa 4, view from posterior end; i, left mandible; j, right gnathopod 1; k, left side of head, anterior view (hatching=antennal sockets).

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