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A study on amphipods from the superfamily Stegocephaloidea Dana 1852 from the northeastern Pacific region: systematics and distributional ecology

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Nine species (including five new to science) of non-lafystiid stegocephaloid amphipods have been recognized within the collections of the Canadian Museum of Nature from the NE Pacific (Alaska to Oregon), *viz. Acanthonotozoma rusanovae* Bryazgin 1974 (Acanthonotozomatidae), *Iphimedia rickettsi* Shoemaker 1931 (Iphimediidae), *Parandania boecki* (Stebbing 1888), *Phippsiella cascadiensis* n.sp., *Stegocephalexia penelope* n. gen., n. sp., *Stegocephalopsis mamillidacta* n. sp. (Stegocephalidae). *Odius kelleri* Bruggen 1907 is reallocated to *Cryptodius* n. gen., and *C. unguidactylus* n. sp. and *Imbrexodius oclairi* n. gen., n. sp. (Odiidae) are also described. Keys are presented which allow the genera of Odiidae of the world, and of this collection of species, to be distinguished.

KEYWORDS: Amphipoda, Stegocephaloidea, *Stegocephalexia*, *Cryptodius*, *Imbrexodius*, taxonomy, NE Pacific.

Introduction

The amphipod superfamily Stegocephaloidea Dana 1852, as envisaged by Bousfield (1979) included the following families: Stegocephalidae Dana 1852, Acanthonotozomatidae Stebbing 1906, Ochlesidae Stebbing 1910 and Lafystiidae Sars 1893 (but see Discussion). The first three families are free-swimming or benthic gammarideans (Enequist, 1949), but lafystiids are external parasites of groundfishes.

More recently it has been suggested (Barnard and Karaman, 1991) that the Acanthonotozomatidae be submerged within a family Iphimediidae Boeck 1871 (redefined there to include Paramphithoidae Stebbing 1906 also, although the latter family has been submerged within the Epimeriidae by Coleman and Barnard, 1991). Coleman and Barnard (1991) reconsidered the relationships of the Iphimediidae and found it necessary to resurrect the Acanthonotozomatidae and to split from it a new family, the Odiidae. The Ochlesidae which were submerged within the Acanthonotozomatidae by Barnard and Karaman (1987), have once again been accorded family status by Coleman and Barnard (1991) (cf. treatment in Barnard and Karaman, 1991).

The following contribution deals with material referable to the families Acanthonotozomatidae, Iphemidiidae, Odiidae and Stegocephalidae in the collections of the Canadian Museum of Nature (formerly the National Museum of Natural Sciences,

This paper is dedicated to the memory of the late Dr J. L. Barnard.

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Ottawa). Bousfield (1987) and Bousfield and Kabata (1988) have recently published on the remaining stegocephaloid family, the Lafystiidae from Canadian waters. No ochlesids exist within the NE Pacific material of the Canadian Museum collections.

The following contribution therefore completes the systematic treatment of the superfamily from the region.

Little has been published on the biology of species within this superfamily. Their conically projecting mouthpart bundle has been referred to in shorthand as 'parasitic' (Barnard and Karaman, 1991). It is more likely, in the light of recent researches by Moore and Rainbow (1984, 1989, 1992) and by Coleman (1989a, b, 1990), that most stegocephaloids are carnivorous, existing on diets of coelenterates, sponges or bryozoans. Many years ago, Enequist (1949) showed in the laboratory that *Stegocephalus inflatus* and *Phippsiella similis* did not deposit-feed and exhibited no tendency to burrow. More recently, although Moore and Rainbow (1984) reported mineral grains (*inter alia*) in the gut of *Stegocephaloides christianiensis*, these were interpreted as having been ingested incidentally during feeding on sessile, benthic coelenterates (e.g. sea pens). Coleman (1989a) has also shown that the iphimediid *Maxilliphimedia longipes* feeds on coelenterates. Other iphimediids feed on sponges (*Echiniphimedia hodgsoni*, see Coleman, 1989a) and bryozoans (*Gnathiphimedia mandibularis*, see Coleman, 1989b).

The reproductive biology of stegocephalids is of particular interest. Most species are known only from females. Steele (1967a) provided evidence for *Stegocephalus inflatus* being a protandrous hermaphrodite, a possibility also admitted (along with parthenogenesis) by Powell and Moore (1991) in connection with the smaller *Stegocephaloides christianiensis*. Judging from Just's work (1978) on *Acanthonotozoma*, however, acanthonotozomatids may be more conventionally dioecious.

Materials

This study is based on material emanating principally from Alaska and British Columbia. The collections were made by Dr E. L. Bousfield and associates at the (then) National Museum of Natural Sciences. Station data for expeditions to southern Vancouver Island (1955), Queen Charlotte Islands (1957), northern Vancouver Island (1959), southeastern Alaska (1961) and north-central British Columbia (1964) have been published by Bousfield (1957, 1963, 1968) and by Bousfield and McAllister (1962). Station data for other collecting expeditions to Washington and Oregon (1966), southern Vancouver Island and Burrard Inlet (1970, 1975 and 1978), and southeastern Alaska (1980) have been published by Bousfield and Jarrett (1981). Deep-sea material from off Oregon was derived from collections made by personnel from Oregon State University.

All material referred to is housed in the Canadian Museum of Nature.

Systematic section

Superfamily **STEGOCEPHALOIDEA** Dana 1852

Diagnosis. Body smooth or variously processiferous. Rostrum well developed. Antenna 1, peduncle segment 1 may be enlarged, basal segments of flagellum may be conjoint (male), accessory flagellum small or lacking. Antennae lacking calceoli. Mouthparts in conical bundle. Upper lip incised. Lower lip lacking inner lobes. Mandible, with or without molar, palp slender or lacking. Plates of maxillae rather strongly setose and normally spinose. Coxal plates deep, often acuminate. Coxa 4

posterior margin very strongly excavate. Coxae 5–7 lobate posteriorly. Gnathopods non-sexually dimorphic, non-amplexing, somewhat dissimilar, chelate or weakly subchelate. Peraeopods 5–7 homopodous, bases variously expanded. Oostegites broad. Coxal gills simple, present on peraeopod 7. Pleopods normal. Uropods lanceolate, rami slightly unequal. Uropod 3 foliaceous or lanceolate-spinose, outer ramus basically 2-segmented. Telson incised, weakly (bilobate), or entire.

Family **ACANTHONOTOZOMATIDAE** Stebbing 1906

Diagnosis. Body robust, usually with dorsal teeth. Eyes large. Antennae elongate, subequal; accessory flagellum absent. Mandibles with 3-segmented palp, molar typically reduced, raker row absent. Lower lip, outer lobe often incised apically. Coxal plates usually acute, tapering. Coxa 4 expanded posteriorly to form large acuminate lobe. Gnathopods 1 and 2 weakly subchelate or parachelate, elongate. Peraeopods 5–7 basis broadly expanded behind, posterior margin (especially of 7) often acutely produced. Epimeral plate 3 posterior margin with 2 large cusps. Urosomites free. Uropods 1–3 biramous. Uropod 3 rami lanceolate, longer than peduncle, outer ramus 1-segmented. Telson weakly incised.

Genus ***Acanthonotozoma*** Boeck

Antenna 1 peduncle segment 2 shorter than 1. Maxilla 1 palp 2-segmented. Maxilla 2, inner plate without facial row of setae. Maxilliped, inner plate narrower but as long as outer plate, palp segment 2 generally unproduced, palp segment 4 small. Gnathopods diverse, simple, carpi and propodi elongate. Gnathopod 2 stouter than gnathopod 1.

Type species. Acanthonotus cristatus Ross 1835 (original designation).

Key to N. Pacific *Acanthonotozoma* (modified after Just, 1978)

1 Elevated dorsal teeth present . . . . . *A. rusanovae* Bryazgin
– Elevated dorsal teeth absent 2

2 Cephalon with lateral front margin entire . . . . . *A. dunbari* Just
– Cephalon with lateral front margin incised below produced interantennal lobe . . 3

3 Interantennal lobe of cephalon triangular, bluntly pointed; telson cleft 20% of length or more 4
– Interantennal lobe of cephalon evenly rounded; telson cleft 12·5% of length or less *A. gurjanovae* Just

4 Coxal plate 3 evenly tapering towards pointed apex, apical angle < 75°; peraeopod 5 and 6 basis with posterodistal angle acute . . . . . *A. inflatum* (Kröyer)
– Coxal plate 3 with nearly parallel margins, abruptly tapering towards blunt apex; apical angle obtuse; peraeopod 5 and 6 basis with posterodistal angle obtuse *A. monodentatum* Kudrjaschov

Acanthonotozoma rusanovae Bryazgin 1974
(Fig. 1)

A rusanovae Bryazgin 1974, pp. 1417–1420, fig. 1; Just 1978, pp. 23–28, figs 9–12, 23B.

Material examined. Alaska, Erlington Is., bar at head North Twin Bay, 59°58′N: 148°11′W, stones, hand-collected MW–HW, 28·0°C, 8 July 1961, E. L. Bousfield, Acc. 1961–123, Sta A118, single damaged specimen.

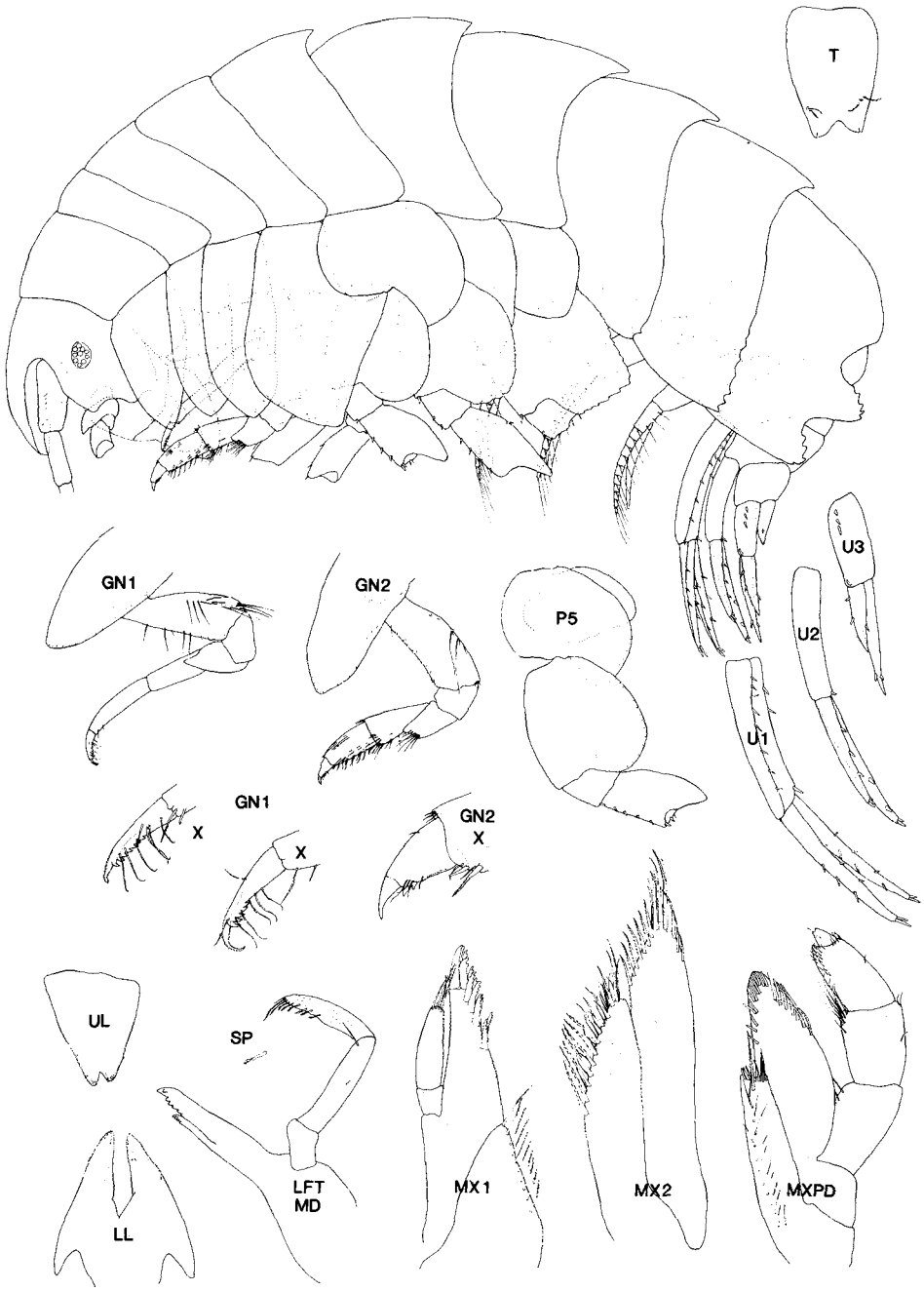

FIG. 1. *Acanthonotozoma rusanovae* Bryazgin (sex undetermined, 4·5 mm, Alaska). Gn1 = gnathopod 1, Gn2 = gnathopod 2, Lft = left, Ll = lower lip, Md = mandible, mx1 = maxilla 1, mx2 = maxilla 2, mxpd = maxilliped, P5 = peraeopod 5, SP = palp spine, T = telson, U1–3 = uropods 1–3, UL = upper lip, X = enlargement.

Diagnosis. Sex undetermined 4·5 mm. Rostrum prominent, overreaching antenna 1 peduncle segment 1. Eyes slightly reniform. Body with peraeonites 5–7 and pleonites 1 and 2 each with a single, compressed, backwards-pointing tooth dorsally; pleonite 3 with a rounded carina but no dorsal tooth. Upper lip incised somewhat asymmetrically. Mandible, incisors with 5 subapical teeth; laciniae mobiles elongate. Maxilla 2, outer plate parallel-sided. Maxillipedal palp segments 2 and 3 slightly produced distomedially, segment 4 very reduced. Coxal plates 1–3 tapering distally; coxal plate 4 with free posterior margin nearly straight, not insinuate. Gnathopod 1, dactylus elongate, polydentate with multiple complex setae and an apical whip-like setulose elongation. Gnathopod 2, dactylus squat, with 3 subapical teeth on posterior margin. Peraeopod 5 basis rounded posteriorly. Peraeopods 6 and 7 bases posterodistal angle subquadrate. Epimeral plates 1 and 2 acute with posterodistal serration; plate 3 with 2 posterior projections, both serrate apically and along upper margins. Uropod 1 rami 10% shorter than peduncle, inner ramus 10% longer than outer. Uropods 2 and 3 inner rami longer than outer.

Remarks. Just (1978) drew attention to the geographical variability of this species in terms of colour pattern and morphology. He noted a tendency for peraeopods 5 and 6 bases to become more rounded posterodistally in animals from the Bay of Fundy. The Alaskan specimen herein described also shows this tendency in peraeopod 5. The degree to which maxilliped palp segment 2 is produced may also be variable (cf. Just's fig. 9, illustrating a SW Greenland female). Just (1978) also noted variation in the degree of elevation of the dorsal teeth, particularly of peraeonite 5. He also gave the number of subapical teeth on the right mandible as 3: in the present specimen it is 5.

Distributional ecology. A widely distributed circumpolar species. In the Pacific Ocean, recorded from the Bering Sea.

Family **IPHIMEDIIDAE** *sensu* Coleman and Barnard 1991

IPHIMEDIIAE [*sic*] Coleman and Barnard 1991, p. 261

Diagnosis. Body compressed, generally with dorsal teeth. Rostrum well developed. Antennae elongate, accessory flagellum present or absent. Mandible, raker row absent, palp 3-segmented. Maxilla 1, palp 1- or 2-segmented. Maxilla 2, inner plate usually without facial row of setae. Maxilliped palp 3- or 4-segmented, segment 2 may be produced distomedially. Coxa 4 with large posteroventral lobe. Gnathopods weakly subchelate, or parachelate or simple, with carpi and propodi elongate. Gnathopod 1 simple or propodochelate. Gnathopod 2 propodochelate. Peraeopods 5–7 bases often with posterior cusps. Epimeral plate 3 usually with 2 large lateral cusps. Urosomites free. Uropods 1–3 biramous. Uropod 3 rami lanceolate, longer than peduncle, outer ramus 1-segmented. Telson entire or weakly incised.

Genus ***Iphimedia*** Rathke 1843

Microcheles Kröyer 1846, p. 58.
Panoploea Thompson 1880, p. 2.
Iphimediopsis Della Valle 1893, p. 585.
Cypsiphimedia K. H. Barnard 1955, p. 87.

Diagnosis. Body with dorsal processes or smooth. Antenna 1 peduncle segment 2 shorter than 1. Accessory flagellum absent. Upper lip entire or slightly emarginate.

Mandible, molar conical or simple. Lower lip, outer lobes may be notched. Maxilla 1, palp 2-segmented. Maxilla 2, inner plate without facial row of setae. Maxilliped, inner plate narrow, usually as long as outer plate, palp segment 2 distomedially produced, segment 4 lacking. Coxae 1–4 progressively deeper. Coxa 4 sometimes weakly polycuspidate. Gnathopods diverse, subequal, propodochelate.

Type species. *Iphimedia obesa* Rathke 1843.

Key to N. Pacific *Iphimedia*

1 Peraeonite 1 not longer than head; coxa 4 posterodistal angle serrated; peraeonite 7 and pleonites 1 and 2 posterior margin with lateral tooth . . *I. rickettsi* (Shoemaker)
– Peraeonite 1 longer than head; coxa 4 posterodistal angle not serrated; peraeonite 7 and pleonites 1 and 2 posterior margin lacking lateral tooth . . *I. mala* (Hirayama)

Iphimedia rickettsi (Shoemaker 1931)

(Fig. 2)

Panoploea rickettsi Shoemaker 1931, p. 1, figs 1 and 2. Barnard 1962, p. 79; 1964a, p. 212; 1966, p. 14. Karaman 1980, p. 64.

Material examined. N. end Banks Is., B.C., Sta H21, 40–60 m, 17 July 1964, coll. E. L. Bousfield, Acc. 1964–198, 15 individuals (incl. *ca* 8 mm female illustrated). Half a mile off Goose Is., Sta. H52; coll. E. L. Bousfield, 6 August 1964, 76 m, Acc. 1964–198, 4 individuals. Half a mile off N. end of Banks Is., Sta N22, 20 m, coll. E. L. Bousfield, 17 July 1964, 1964–198, 4 individuals. San Josef Bay, V.I., B.C., Sta 02c, coll. E.L. Bousfield, 18 July 1959, 1 individual. Bonilla Is., B.C., Sta JWS-35, coll. J. W. Scoggan, 6 August 1965, Acc. 1965–51, 1 individual. Just W. Amphitrite Rock, B.C., 44–48 m, coll. N. A. Powell, 22 August 1967, Sta 67-82APK, Acc. 1967–223, 1 individual.

Diagnosis. Female *ca* 8 mm (ovigerous, 24 eggs). Body well calcified. Head, lateral lobe with 2 pointed cusps, that ventrad strongly recurved medially and ventrally. Eye red/brown (in spirit). Peraeonite 7 and pleonites 1–3 with 2 pairs of cusps, 1 pair posterodorsal, lateral to the mid-line, the other pair lateral to the body. Urosomite 1, with low dorsal hump. Eyes reniform, red/brown (in spirit). Upper lip slightly emarginate. Mandible elongate, rapidly broadening proximally, incisor armed with few, blunt teeth; left lacinia mobilis elongate, with 2 broad, blunt teeth, right lacinia, slender, reduced; palp segment 2 with 4 long setae mediodistally, segment 3 slightly falcate, medial margin armed with stout, distally expanded and serrate, spines; molar simple, a broad sharp plate, non-triturative (based on condition of right mandible, left damaged at this position). Lower lip highly setose, outer plates distinctly notched. Maxilla 1, inner plate convexly conical, lateral margin setose, bearing 2 long setae terminally and 2 long setae subterminally on medial margin; outer plate, medial margin setose, bearing 10 strong spines distally (variously spatulate, nodular, falcate); palp segment 2 bearing 5 long setae distally. Maxilliped, inner plate not quite as long as outer, both plates with long marginal setae. Coxae 1–4 with posterodistal angle minutely serrate. Coxa 2 posterior margin with quadrate distal excavation. Coxa 4 with single cusp on posterior margin. Coxae 5–7 posterior margin drawn out into cusp. Coxae 6 and 7 ventral margin minutely serrate. Epimeral plate 1, posterodistal angle

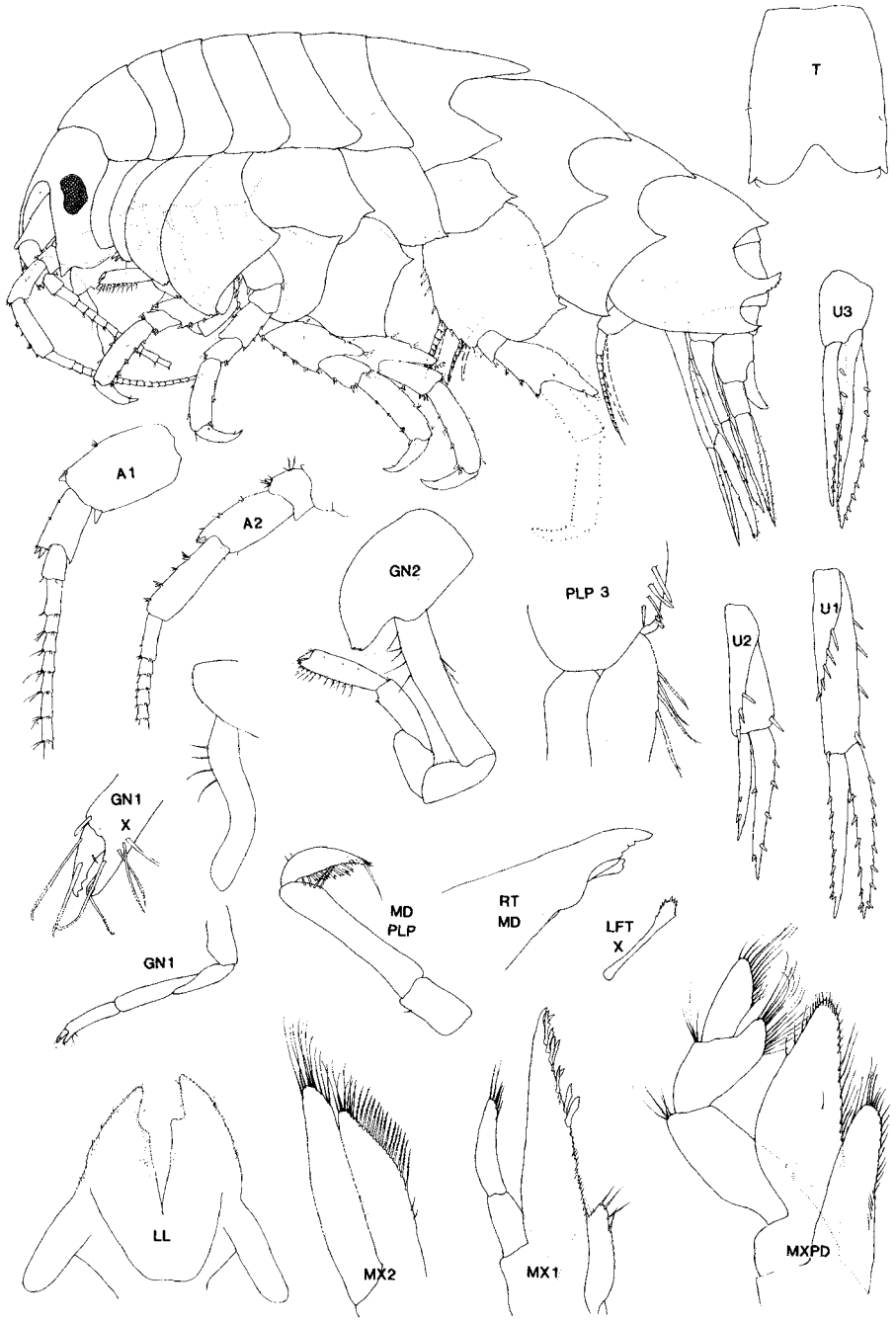

FIG. 2. *Iphimedia rickettsi* (Shoemaker) (female, 8 mm, Banks Is.). Abbreviations as in Fig. 1, also A1–2 = antenna 1–2, plp 3 = pleopod 3 (distal tip of peduncle), RT = right.

somewhat obtuse. Epimeral plate 2, posterodistal angle acute. Epimeral plate 3, posterior margin distally excavate, forming 2 ventrally serrate teeth (the dorsalmost more recurved than the ventralmost). Gnathopod 1, basis sinuous, anterior margin bearing line of 4 long setae proximally; carpus slightly longer than propodus; dactylus posterior margin with subdistal serrations, bearing 2 long plumose setae; propodal chelate spur subequal to dactylus, bearing 5 long, plumose setae. Gnathopod 2, basis sublinear with slight waist subdistally, both margins bearing a few long setae; propodus, posterior margin with even rank of moderately long setae, posterodistal angle produced into an acute lobe; dactylus reaching to tip of propodal posterodistal lobe, posterior margin minutely dentate subdistally. Peraeopods 5–7, basis posterior margin with respectively 1 (proximal), 2 (proximal + distal) and 1 (distal) cusp; P7 basis posterior margin minutely serrate. Pleopods 1–3, peduncle lateral margins distally setose (pleopod 3 least), distomedial angle with 2 locking spines, in addition to which pleopod 3 has 4 stout (3 long, 1 short) spines. Uropod 1, peduncle slightly longer than rami, rami subequal. Uropod 2, inner ramus longer than outer, peduncle longer than outer ramus but shorter than inner. Uropod 3 peduncle short, rami elongate, lanceolate; inner ramus slightly longer than other. Telson emarginate, hollow dorsally, slightly overreaching distal margin of uropod 3.

Distributional ecology. A species of the shallow, usually rocky, sublittoral (20–100 m+), British Columbia; Monterey Bay, California (Shoemaker, 1931; Barnard, 1962, 1964a, b, 1966).

Remarks. The individual illustrated has right maxilla 1 with a 2-segmented palp, the left 1-segmented. This latter is interpreted as being the result of trauma to the living animal, since the left maxilla 1 of another has a 2-segmented palp consistent with expectation.

The recent submergence of several genera (see synonymy above) within an expanded concept of *Iphimedia* (see Karaman, 1980; Myers *et al.*, 1987; Coleman and Barnard, 1991) has produced a large genus currently standing at 43 species (Barnard and Barnard, 1990). The present record is this species' most northerly Pacific record. The species is characterized by having posterodistal angle of coxae 1–4 serrated (a condition otherwise seen, but to a much more extreme degree, in *I. pacifica* Stebbing).

Some differences of detail are apparent between the present material and that described and figured by Shoemaker (1931), which might be attributable to oversight, to the size difference in the individuals considered (4·5 mm by Shoemaker, cf. 8 mm above) or to geographical variation. Since the American and Canadian localities are not too distant one from another, these differences are not presently thought to be of species diagnostic significance. They relate to: (i) the dentation or otherwise of the posterior margin of the dactylus of gnathopods 1 and 2; (ii) the setation of the lateral margin of maxilla 1 inner plate; (iii) the somewhat different proportional length of peraeonite 1 to the following 3 segments (=2+3+4 in Shoemaker's material; =2+3+(1/2)4 above); (iv) gnathopod 2 palm was not armed with 'a row of forward-pointing bristles' in the present material; and (v) the absence of setae on the basis of gnathopods 1 and 2 in Shoemaker's material. This final condition is likely to be a consequence of small body size, since it obtained in a 3 mm individual examined from the present collection. In spite of the above reticence to split these entities, however, it should not be overlooked that species differentiating features in this genus can be quite subtle (see Myers *et al.*, 1987).

Family **ODIIDAE** Coleman and Barnard 1991

Diagnosis. Body compressed, all peraeonites dorsally flush, usually raised into a narrow keel. Pleon with or without dorsal projections. Eyes present. Antennae short, accessory flagellum absent. Upper lip incised. Mandible, incisor minutely toothed, spine row strong or absent, molar small, triturative, palp 3-segmented. Maxilla 1 inner plate with 1–3 apical setae, outer plate conical, palp 1-segmented. Maxilla 2, inner plate lacking facial row of setae. Maxilliped palp 4-segmented, segment 2 expanded medially or not. Coxa 1–3 tapering. Coxa 4 with large posteroventral lobe. Gnathopod 1 weak, chelate, carpus and propodus elongate. Gnathopod 2 subchelate, merus and carpus produced posterodistally. Peraeopods 5–7 bases expanded with or without posterior teeth. Epimeral plate 3 posterior margin with 2 cusps. Telson entire or weakly incised, usually keeled below.

Remarks. Two features in this diagnosis are especially worthy of note in modifying that of Coleman and Barnard (1991). Whilst typical, the dorsal keel may be lacking (see new genus immediately below) or only weakly developed (*Odius antarcticus* Watling and Holman). Typically also, the mandibular spine row is strong. In the second new genus following below, however, the spine (=raker) row is lacking. It should be noted that this renders inconclusive Key I in Coleman and Barnard (1991), the first couplet of which directs the reader to this feature in order to differentiate Iphimediidae and related families.

Key to genera of Odiidae of the world

1 Telson incised 2
– Telson entire 3

2 Maxilliped inner plate as long as, or longer than, outer plate; maxillipedal palp, segment 2 not expanded, segment 4 obsolescent . . . . . *Odius* Liljeborg
– Maxilliped inner plate shorter than outer plate; maxillipedal palp, segment 2 somewhat expanded, segment 4 well developed . . . . . *Imbrexodius* n. gen.

3 Upper lip entire; maxilliped, inner plate shorter than outer, palp segment 2 somewhat expanded, segment 4 lacking . . . . . *Postodius* Hirayama
– Upper lip incised; maxilliped, inner plate equal to or longer than outer, palp segment 2 distinctly expanded, segment 4 well developed . . . . *Cryptodius* n. gen.

Genus ***Cryptodius*** n. gen.

Diagnosis. Body smooth. Peraeon lacking a conspicuous narrow, mid-dorsal keel. Head telescoped into a peraeon segment 1. Rostrum overreaching antenna 1 peduncle segment 1. Eyes present, large. Antennae short. Antenna 1, peduncle segment 1 subequal to 2 and 3 together. Antenna 2, peduncle segments 4 and 5 subequal. Epistome raised in a median keel. Upper lip elongate, asymmetrically incised. Mandible elongate; spine row strong, molar on level with palp origin, well developed; mandibular palp, segment 1 small, segments 2 and 3 elongate, subequal. Maxilla 1, inner plate reduced, few setose; outer plate conical, medial margin with curved dentate spines distally, setose proximally; palp 1-segmented. Maxilla 2, inner plate with medial margin setulose, outer plate with lateral margin setulose. Maxilliped, palp, segment 2 produced medially, segment 4 not reduced (may be slender and obscured by setae), inner plate subequal to or longer than outer plate. Coxae 1–4 not shortened. Coxa 1 triangular. Coxae 2 and 3 distally truncate. Coxa 4 with posterodistal lobe truncated obliquely to produce an acute posterior tooth. Gnathopods and peraeopods 3–7,

dactylus with unguis. Gnathopod 1 flagellar, propodochelate; carpus and propodus elongate, subequal; dactylus bearing several long plumose setae and 2 unguinal spines distally. Gnathopod 2, broader than 1, propodus triangular, with long palm, dactylus with accessory tooth on posterior margin. Peraeopods 5–7, bases not bearing teeth or cusps. Epimeral plates 2 and 3 posterodistal angles acute. Uropod 1, rami subequal. Uropod 2, inner ramus longer than outer. Uropod 3, inner ramus longer than outer and subequal to peduncle. Telson, ventrally boat-keeled, apex acutely rounded, entire.

Etymology. The generic name is a derivative of *Odius*, alluding to this organism's hitherto hidden identity (L. *crypticus*—secret). Gender, masculine.

Type species. *Odius kelleri* Brüggen 1907.

Remarks. *Cryptodius* n. gen. resembles both *Odius* Liljeborg and *Postodius* Hirayama, but differs in important particular sufficiently from both to warrant recognition as a new genus. Thus the upper lip of *Odius* and *Cryptodius* is incised, that of *Postodius* is entire. The inner plate of the maxilliped is as long as, or longer than, the outer in *Odius*, in *Postodius* and *Cryptodius* it is as long as or shorter. The maxillipedal palp has segment 2 distomedially unproduced in *Odius*, but produced in *Cryptodius* and *Postodius* and segment 4 ranges in form from well-developed (in *Cryptodius*) to obsolescent (in *Odius*) or absent (in *Postodius*). (Note; my interpretation of the segmentation of the maxilliped palp of *Postodius* differs from that given by Hirayama (1983, p. 100), though his account is internally inconsistent (cf. p. 97).) Like *Postodius*, *Cryptodius* has telson entire, its condition in *Odius* is incised. The cuspidate form of peraeopod 7 basis posterior margin is seen to be a feature of most *Odius* spp. (although not *O. antarcticus* Watling and Holman) which is not shared by *Cryptodius* or *Postodius*.

Key to the genus *Cryptodius*

1 Gnathopod and peraeopod dactyli lacking prominent unguinal spines: pleon segments 3 and 4 (slight) midlines with gibbous hump, pleon segment 6 with single longitudinal ridge on either side of dorsal midline . . . . . *C. kelleri* (Brüggen)
– Gnathopod and peraeopod dactyli with prominent unguinal spines: pleon segments dorsally smooth . . . . . *C. unguidactylus* n. sp.

Cryptodius kelleri (Brüggen 1907)
(Fig. 3)

Odius kelleri Bruggen 1907, p. 660.

Material examined. Vancouver Is., Victoria region, British Columbia, 24 January 1981, coll. C. Low, Acc. 1982–34, 13 individuals (incl. female *ca* 5 mm, illustr.). Amchitka Is., Alaska (9 samples): 1 individual (broken), Rifle Range Pt, 51°23·7′N, 179° 10′E, rocky intertidal, *Laminaria*, coll. C. E. O'Clair, 12 August 1969, Sta. RT 006 R-10, Acc. 1976–30; individuals (mostly juv.), St Makarius Bay, in waters adjacent to *Laminaria*, coll. C. E. O'Clair, 5 August 1968, Sta. 68-PSC-8A-VII, Acc. 1976–30; 1 individual, St Makarius Bay, coll. C. E. O'Clair, 20 July 1968, Acc. 1976–30; 1 individual, St Makarius Bay, coll. P. A. Lebednik, 28 December 1968, Acc. 1976–30; 122 individuals, Constantine Harbour, dock, coll. P. N. Slattery, 21 September 1969, Acc. 1982–79; 1 individual, Constantine Harbour, 51°25′N, 179°18′W, coll. C. E. O'Clair, 8

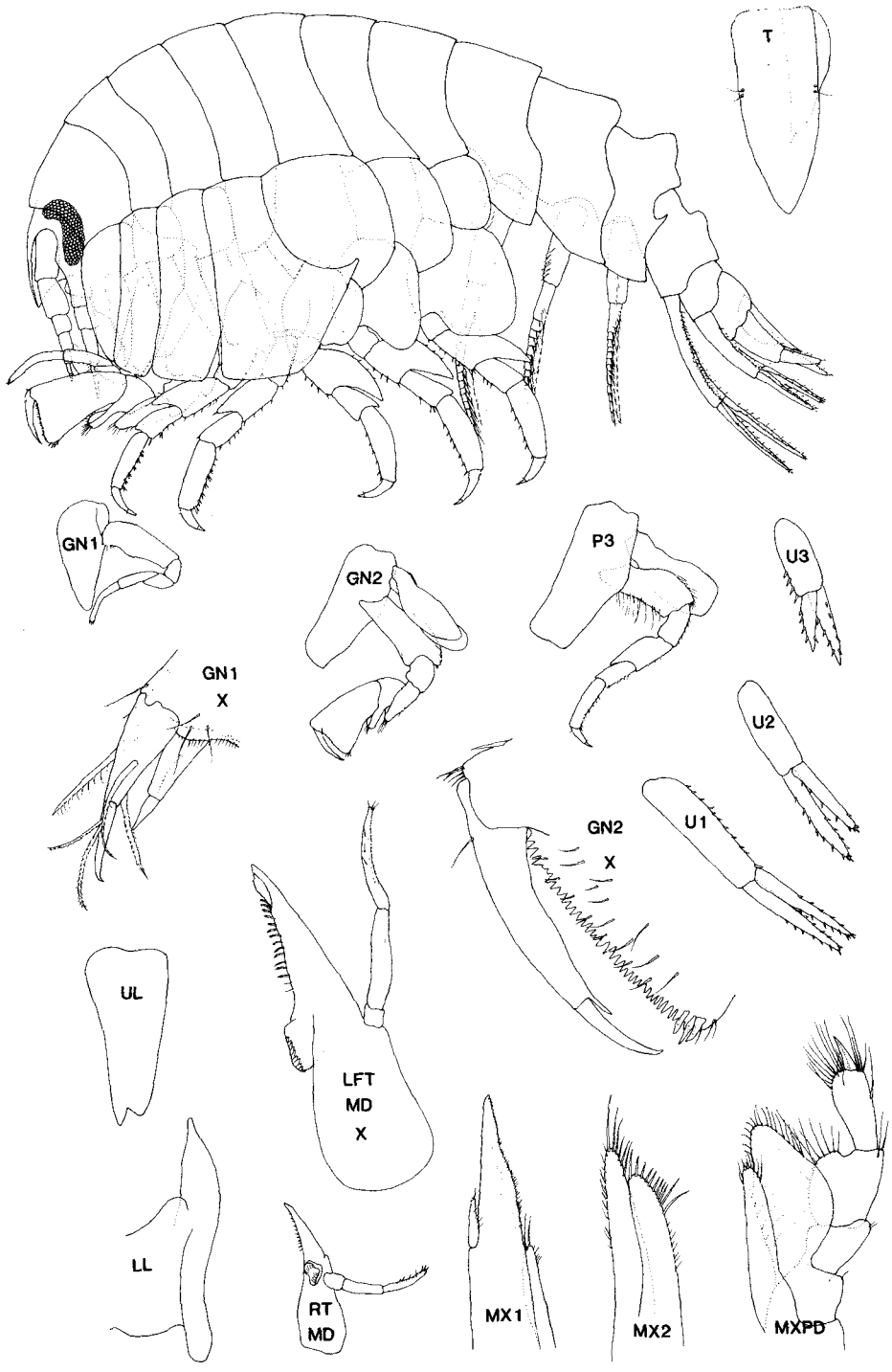

FIG. 3. *Cryptodius kelleri* (Brüggen) (female, 5 mm, Vancouver Is.). Abbreviations as in Figs 1 and 2.

September 1968, Acc. 1976–30; 1 individual (6·5 mm female, NMC slide mount), Constantine Harbour, coll. P. N. Slattery, 14 July 1970; 151 individuals, Constantine Harbour, night light 2 m below surface, plankton pump sample no. 349, coll. P. N. Slattery, id. Ulf Lie, 15 March 1969, Acc. 1982–79; 34 individuals, Constantine Harbour, 100 m SW of dock, 0–6 m, algae, coll. G. Simenstad, 14 July 1970, NMC 1982–79; 30 individuals, Constantine Harbour, algae from dock pilings, coll. P. N. Slattery, 7 September 1969, Acc. 1982–79. Five individuals (1 broken), A151, small island 1·4 mi. E of Johnstone Pt, D. E. McAllister, E. L. Bousfield, J. W. Scoggan, 15 June 1961, Acc. 1961–123. One individual, Holkam Bay, A32, E. L. Bousfield, D. E. McAllister, 12 June 1961, Acc. 1961–123. One individual, Malcolm Is., B.C., Pulteney Pt, SW tip, 50·6°N, 127·1°W, coll. E. Black/C. Low, 3 May 1980, id. N. Jarrett, Acc. 1981–168. Three individuals, British Columbia (no other locality data), coll. E. Black, 5, May 1981, id. E. L. Bousfield, Acc. 1982–300. One individual, Column Pt, SE Alaska, N end of Lisianski Str., 58°06·4′N, 136°27′W, Sta 511B1, coll. E. L. Bousfield, 30 July 1980, id. E. L. Bousfield, Acc. 1980–357. One individual, Sta A33, Halkam Bay, LW, 12 June 1961, E. L. Bousfield, D. E. McAllister, Acc. 1961–123. One individual, Becher Bay (at head), V.I., B.C., 48°20′N, 123°35′W, LW, Sta P718, coll. E. L. Bousfield, 31 July 1970, Acc. 1970–152. Fourteen individuals, near Victoria, British Columbia, coll. C. Low, 24 May 1981, NERC, Acc, 1982–16. One individual, Sta P17a, Diana Is., bay inside Kirby Pt, dredge, 3–8 m, sand, kelp, urchins, 6 August 1975, E. L. Bousfield, M. Haylock, Acc. 1975–205. One individual, Edward King Is., B.C., 48°49·08′N, 125°12·05′W, Sta B28, LW-HW, *ca* 12°C, *ca* 32 + ‰, 10 July 1976, E. L. Bousfield, Acc. 1976–157. Two (of 5) individuals, Deer Is., B.C., 50·6°N, 127·4°W, depth 10 m, sand, boulders, coll. E. A. Black/C. Low, 20 April 1980, id. E. L. Bousfield, Acc. 1981–168. One individual, Townsend Pt, St John Harbour, B.C., Sta H53, 52°12′N, 128°29′W, surf exposed bedrock, boulders, *Phyllospadix*, kelp, LW-MW, 14·2°C, 7 August 1964, E. L. Bousfield, Acc. 1964–198. Seven individuals, Sta H50, Goose Is., S. beach, HW, 6 August 1964, E. L. Bousfield, Acc. 1964–198. One individual, Sta H12, NW end Stephens Is., 13 July 1964, E. L. Bousfield, Acc. 1964–198. One individual, Sta H3, off Masset Sd, Q.C.I., B.C., dredge 3–20 m, sand, gravel, 27 August 1957, E. L. Bousfield, Acc. 1957–122. One individual, SE Alaska, Sitka region, Column Pt, N. Lisianski Str., 58°06·4′N, 136°27′W, coll. E. L. Bousfield, Sta S11B1, 30 July 1980, LW & subtidal bedrock + boulders, id. N. Jarrett, Acc. 1980–357. Three individuals, Sta F2, William Hd, Bentinck Is., V.I., B.C., rock + algae, E. L. Bousfield, 8 August 1955, Acc. 1955–104. Five individuals, Sta F4, N side Albert Hd, Victoria, B.C., steep rock, gravel, sand, E. L. Bousfield, 14 August 1955, Acc. 1955–104.

Diagnosis. Body surface ornamented with pattern of circular pores and tiny setae. Eyes large, reniform. Antenna 1, flagellum 6-segmented. Mandible, palp segment 3 bearing 3 pectinate spine-setae along concave margin. Maxilliped, inner plate longer than outer plate. Gnathopod 1, propodal spur with strong spine distally and several slender setae proximally; dactylus bearing 5 or 6 long plumose setae (emanation of one seta contentious, may arise from propodal spur). Gnathopod 2 propodus palm minutely serrate, defined by 3 stout spines. Oostegites on P2–P5 (non-setose in holotype). Peraeopods 3–7, dactyli with slender seta subdistally. Peraeopods 3 and 4, bases swollen posterodistally, anterior margins and distal portion of posterior margins setose; meri almost completely overreaching carpi posteriorly. Peraeopod 5 basis anterior margin with saddle-like concavity bearing few long setae proximally. Peraeopods 5 and 6 coxae with long setae medially at point of insertion of bases. Pleon

segments 1 (slightly) and 2 (more pronounced, bluntly) midlines with raised posterior tooth, pleon segment 3 midline with gibbous hump. Epimeral plate 1, posterodistal angle acute. Epimeron 3 posterior margin concave, sweeping up to a single, acute, slightly recurved tooth. Urosomite 1 with slight, angular dorsal gibbosity, urosomite 3 bearing a single longitudinal ridge on either side of the dorsal midline. Uropod 2, inner ramus subequal to peduncle. Uropod 3, inner ramus slightly longer than peduncle.

Remarks. Differences can be seen between the present material and that illustrated by Gurjanova (1951), *viz.* the numbers of flagellar segments in the antennae, the extent of the projection of the propodal chela on gnathopod 1, the shape of the anterior margin of gnathopod 1 basis and (less so) the shape of the basis of peraeopod 7. Given, however, the differences within Gurjanova's illustration between the basal shape of the two second gnathopods and the potential ambiguity over the segmentation of uropod 3 rami, the general precision of these figures must be doubted. So the differences alluded to above may be more apparent than real. Certainly the gross features of body form, carination and ornamentation are consistent with the Canadian material belonging to this species. The original descriptions did not dwell on the minutiae of mouthpart morphology, on the basis of which (*inter alia*) this species has here been removed from *Odius*. The type material of *O. kelleri* has not been traced, so some residual doubt must remain over the course of action here taken. Only collecting in the type locality (Vladivostok) can resolve all doubt.

Distributional ecology. A shallow-water species in the northern Pacific, occurring in low intertidal and down to *ca* 90 m, generally amongst algae, British Columbia, Alaska, Bering Sea, Sea of Okhotsk, Sea of Japan (see also Gurjanova, 1951).

Cryptodius unguidactylus n. sp.

(Fig. 4)

Material examined. HOLOTYPE, female (ovigerous, 24 eggs) *ca* 6 mm, Deer Is., 50·6°N, 127·4°W, depth 10 m, sandy boulders, coll. E. A. Black/C. Low, 20 April 1980, Cat. NMCC1990–1342.

Diagnosis. Head, lateral lobe anterodistal angle rounded truncate. Eye large, reniform. Epistome gibbous, raised into a bi-convex, notched keel, upper part broad. Antennae tapering. Antenna 1, flagellum 8-segmented, bearing slender aesthetascs. Antenna 2, peduncle segment 2 with gland cone truncated.

Mandible, molar triangular; lacinia mobilis broad, pectinate (left) or lacking (right); palp, segment 3 bearing 3 strong, plumospatulate spine-setae distally and 4 spaced along concave margin. Lower lip, outer lobe apex pointed, medial margin notched to form an obtuse shoulder, mandibular processes blunt. Maxilla 1, inner plate, margins setose; outer plate, medial margin densely spinose, terminating in 8 strong, curved dentate spines subdistally and 1 stout, falcate spine distally; palp, set on a bracket-like shoulder, lateral margin setulose. Maxilla 2, outer plate, both margins setulose. Maxilliped, inner plate subequal in length to outer plate, inner plate marginally setose, with 2 strong, apical spines; outer plate, densely setose submarginally; palp, segment 2 broadly expanded medially, expansion bearing numerous long setae, segment 3 densely setose apically (obscuring segment 4 from casual view), segment 4 slender, with oblique

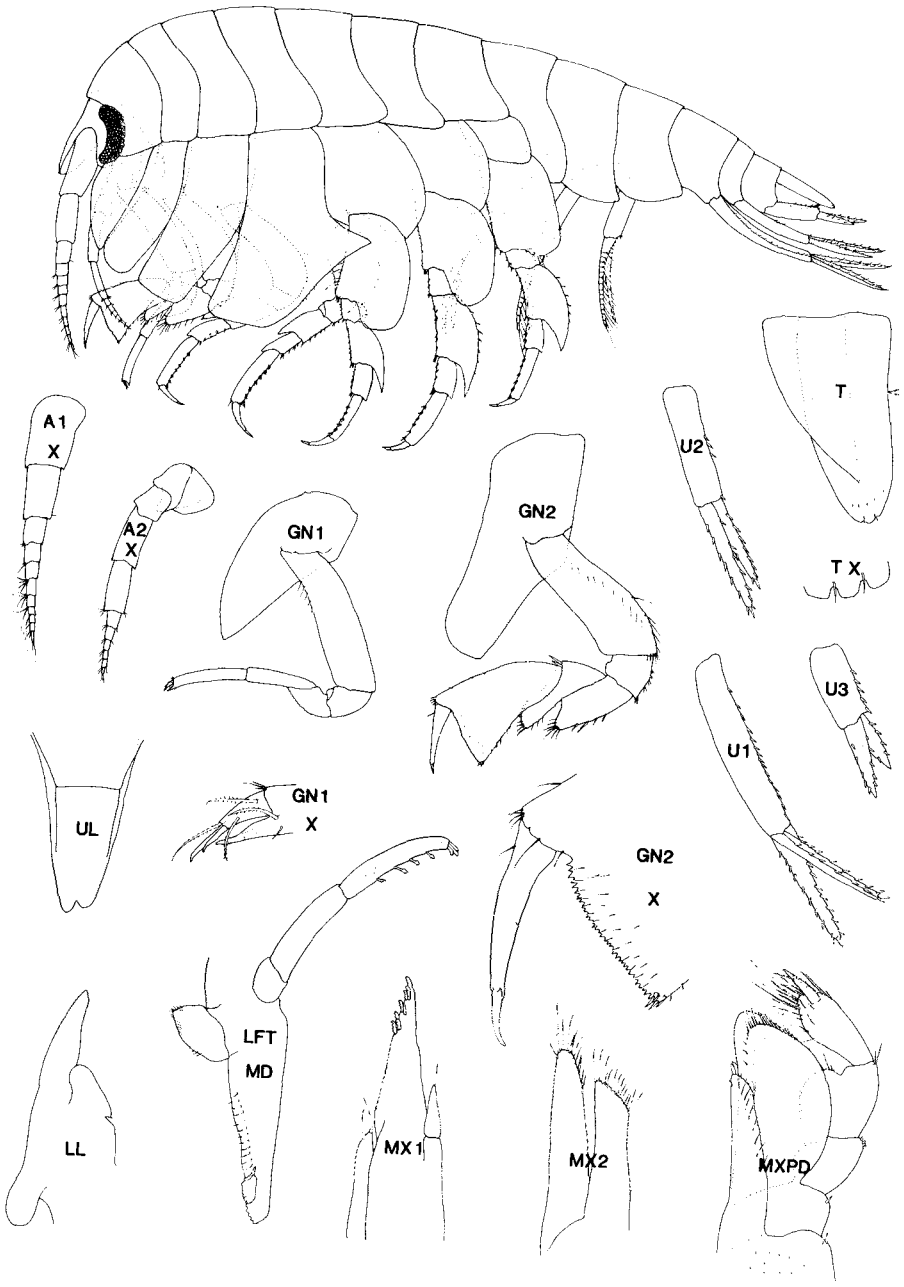

FIG. 4. *Cryptodius unguidactylus* n. sp. Holotype (female, 6 mm, Deer Is.). Abbrevations as in Figs 1 and 2.

ranks of setules and 2 long setae subdistally. Gnathopod 1, propodal chelation not reaching tip of dactylus, bearing single, long plumose seta basally and single strong spine distally; dactylus bearing 2 strong unguinal spines and 3 long, plumose setae. Gnathopod 2, coxa posterodistal angle oblique; basis, posterior margin with row of long setae; merus and carpus, posterodistal lobes strongly setose; propodus triangular, palm markedly serrate, with row of short setae subdistally, defined by 2 stout spines; dactylus with long unguis. Peraeopods 5–7 (possibly 3–7) dactyli with single seta subdistally (P3–4 setae missing on holotype?). Peraeopod 3, coxa truncate; basis, margins (posterior especially) sinuous, anterior margin bearing long setae, posterior margin with shorter setae (distally); dactylus, elongate with unguis. Peraeopod 4 spinose, coxa with pronounced acute posterior cusp; basis margins setose distally. Peraeopods 5 and 6 spinose, coxa rounded; basis, posterior lobes rounded, anterior margin setose distally; limb root at coxa with long setae medially; dactylus with unguis. Peraeopod 7, as 5 and 6 except basis anterior margin non-setose distally. Pleopod 3 peduncle with fewer long setae laterally than pleopods 1 and 2, each pleopod with pair of locking spines at distomedial angle. Pleosomites 1–6 dorsally smooth. Epimeral plate 1 obtuse ventrally, anterior margin bearing 3 setae distally. Epimeral plate 3, posterior margin lacking ornamentation. Uropod 2, inner ramus slightly shorter than peduncle. Uropod 3, rami short, peduncle longer than inner ramus. Telson, distal margin minutely tricuspid, each lateral excavation of the distal margin bearing a slender setule at its base.

Etymology. The specific epithet alludes to the prominent dactylar nails on the limbs of this species (L. *unguis*—a fingernail).

Remarks. This individual was severely squashed and misshapen on the left side (as received). In order to represent (for consistency) the animal's appearance from the left side (Fig. 4) a reconstruction had, therefore, to be made based on limbs dissected from the animal's right side. The representation of body depth as shown may not be entirely accurate, but it is not thought that the species has any appreciable peraeonite dorsal keel (cf. the new taxon following).

Distributional ecology. Alaska, a shallow-water species known only from the type locality.

Genus ***Imbrexodius*** n. gen.

Diagnosis. Body smooth. Peraeon raised into a narrow, mid-dorsal keel. Head retractable under cowl-like peraeonite 1 (to extent of obscuring eye). Rostrum well developed, reaching distal margin of antenna 1 peduncle segment 1. Eyes reniform. Antennae short. Antenna 1 tapering, peduncle segment 1 subequal to 2 and 3 together. Antenna 2, segments 4 and 5 subequal. Epistome raised in a median keel. Upper lip elongate, asymmetrically incised. Mandible elongate; spine row lacking; molar on level with palp origin, weak; mandibular palp, segment 1 small, segments 2 and 3 elongate, subequal. Lower lip, with outer lobe acute. Maxilla 1, inner plate reduced, few setose; outer plate conical, medial face setulose with strong spines subdistally; palp 1-segmented. Maxilla 2, inner plate medial margin setulose, outer plate with lateral margin setulose. Maxilliped, palp segment 2 slightly expanded medially, segment 4 prominent; inner plate shorter than outer plate. Coxae 1–4 not shortened. Coxa 1

tapering, bluntly rounded ventrally, anterior margin concave, obscuring lateral lobe of head. Coxa 2 hardly tapering, distally truncate, anterior margin concave. Coxa 4 posterior margin, with prominent, acute cusp. Gnathopod 1 flagellar, propodochelate; propodus longer than carpus. Peraeopods 5–7 stout. Peraeopod 7 basis with posterior margin drawn out into a blunt cusp. Pleon segment 2 with mid-dorsal gibbous hump distally. Pleon segment 3 with wedge-shaped, mid-dorsal hump (planar face anteriorwards). Epimeral plates acute, with posterior margins broadly excavate distally. Pleopod rami particularly strongly developed. Urosomite 1 with small mid-dorsal hump, urosomites 2 and 3 with dorsal margins smooth. Uropods 1–3 slender. Uropod 1, rami subequal. Uropod 2, inner ramus longer than outer. Uropod 3 rami lanceolate, inner ramus more than twice as long as outer ramus, peduncle longer than outer ramus. Telson, apex moderately incised.

Etymology. The generic name is a derivative of *Odius*, alluding to this organism's conspicuous, ridge-backed form (L. *imbrex*—a ridge tile). Gender, masculine.

Imbrexodius oclairi n. sp.

(Fig. 5)

Material examined. HOLOTYPE *ca* 3 mm, sex indet. (no oostegites), Banjo Pt, Amchitka Is., Alaska, 51°28·8′N, 179°08·3′E, Sta. BIG I, 14 August 1971, coll. C. E. O'Clair, Cat. NMCC1990–1343. PARATYPES 13 individuals, same data, NMCC1990–1344. One individual, Amchitka Is., Alaska, Sta, 1A-2, 22 May 1974, coll. C. E. O'Clair, Cat. NMCC1990–1345. One individual, Square Bay, Amchitka Is., Alaska, 51°27·2′N, 179°11·5′E, Sta CT 018 69, M-48, intertidal, rocky, water temp. 7·2°C, coll. C. E. O'Clair, Cat. NMCC1990–1346.

Diagnosis. Eyes reniform. Gnathopod 1 basis swollen proximally, anterior margin with row of very short setae, dactylus bearing 6 long plumose setae, overreaching chelate extension of propodus. Gnathopod 2, carpal lobe bearing stiff, pectinate setae, propodus with palm minutely serrate, with row of 5 spines around posterodistal angle. Peraeopods with strong dactyli. Peraeopods 5–7 bases, anterior margins slightly setose. Epimeral plate 3, posterior margin concave excavation terminating proximally in strong, upturned tooth forming a hook halfway along posterior margin.

Etymology. Named for its collector, Charles E. O'Clair.

Distributional ecology. A shallow-water species from rocky substrata, presently known only from Amchitka Is., Alaska.

Remarks. Although bearing some superficial resemblance to *Cryptodius kelleri*, with which it co-occurs, this species can be distinguished immediately with reference to the following externally visible features; the ridged form of the dorsum, the shape of the pleosomal dorsal projections and the prominent pleopods. Other distinguishing features are the relative lengths of the rostrum and antenna 1 peduncle segment 1, the lack of a mandibular spine row, the weak molar, the short maxillipedal inner plate, the shape of coxa 2 and P7 basis, the smoothly curved transverse section to urosomite 3 and the incised telson.

Imbrexodius resembles *Odius* in having telson incised and having peraeopod 7 basis posterior margin cuspidate, cf. *Postodius* and *Cryptodius*.

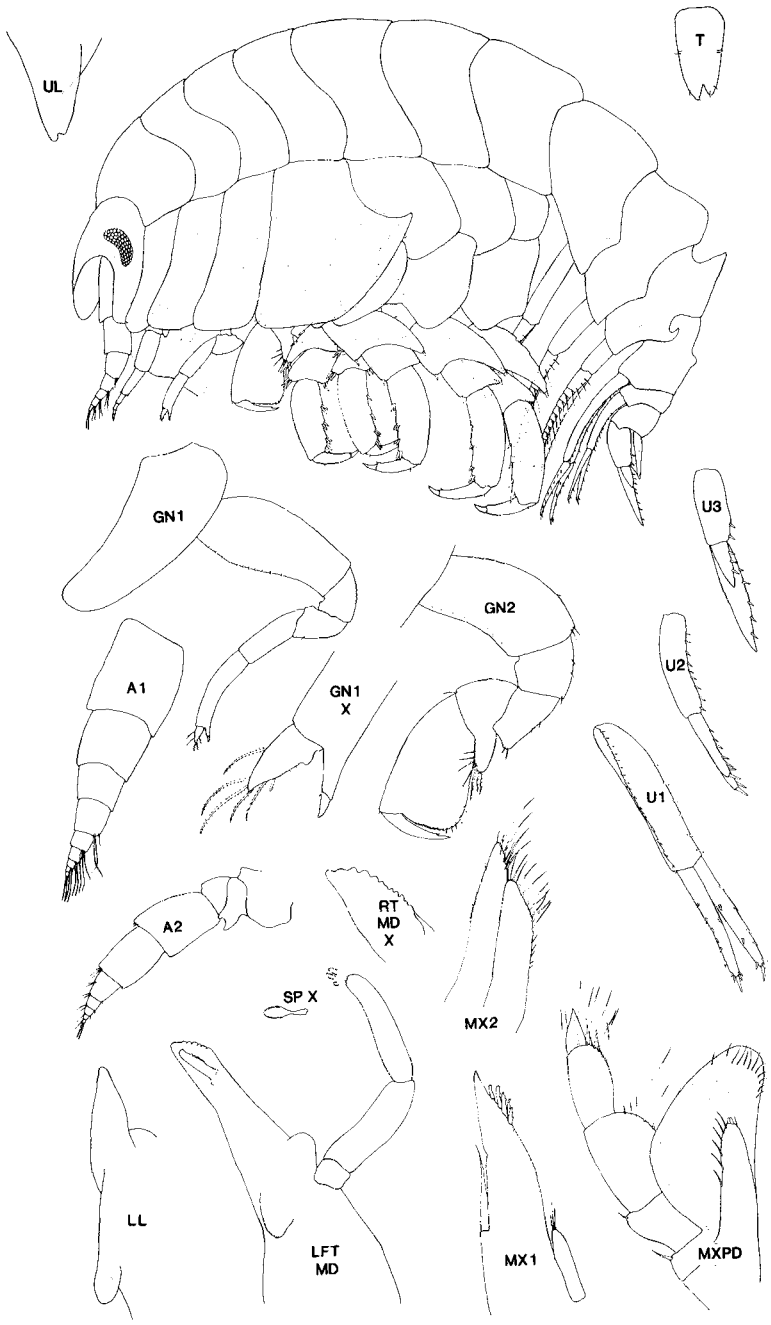

FIG. 5. *Imbrexodius oclairi* n. gen., n. sp. Holotype (sex undet., 3 mm, Alaska). Abbreviations as in Figs 1 and 2.

Family **STEGOCEPHALIDAE** Dana 1852

Diagnosis. Body stout, globular, generally non-processiferous. Rostrum strongly deflexed. Head generally 'telescoped' back into first peraeonal segment. Cuticle slick. Coxae 1–4 attached directly to corresponding segments (lateral view), forming a deep, convex lateral shield. Coxa 1 acuminate, not covered by following coxae. Antennae short. Antenna 1 peduncle short, swollen, accessory flagellum 1–2-segmented, flagellum callynophorate. Mandible without molar or palp. Maxilla 1 strong, inner plate large, palp variable, large or small, 1–2-segmented. Maxilla 2 inner plate large, outer plate smaller or absent, sometimes attached in geniculate fashion, apical spine-setae often hooked. Maxilliped inner plate usually short, outer plate very large, palp 3–4-segmented. Gnathopods not strongly developed, non-sexually dimorphic, simple. Peraeopod 5 basis hidden behind coxae, rectolinear. Peraeopods 5–7 generally unlike (note should also be taken of the following non-diagnostic features: eyes usually lacking; uropod 3, outer ramus usually 2-segmented, or rami vestigial or absent).

Key to genera of Stegocephalidae of the NE Pacific

1 Maxilla 1 palp, 1-segmented 2
– Maxilla 1 palp, 2-segmented 3

2 Uropod 3, peduncle shorter than rami 4
– Uropod 3, peduncle longer than, or subequal to, rami 5

3 Maxilla 2, outer plate ordinary, spines without hooks; mandibular incisor smooth
Andaniexis Stebbing†
– Maxilla 2, outer plate geniculate, spines usually with hooks; mandibular incisor toothed
Phippsiella Schellenberg

4 Maxilla 2, outer plate, spines with hooks; maxilliped, inner plate reaching palp segment 2
Stegocephalus Krøyer†
– Maxilla 2, outer plate, spines without hooks; maxilliped, inner plate not reaching palp segment 2 . . . . . *Stegocephalexia* n. gen.

5 Uropod 3, peduncle longer than rami; mandibular incisor smooth *Parandania* Stebbing
– Uropod 3, peduncle subequal to rami; mandibular incisor toothed
Stegocephalopsis Schellenberg

Genus ***Parandania*** Stebbing 1899

Diagnosis. Body smooth. Antenna 1 proximal segment of flagellum conjoint, longer than peduncle. Antenna 2 peduncle segment 4 shorter than 5. Upper lip weakly incised, somewhat asymmetrical. Mandible, incisor with smooth cutting edge, subdistal transverse ridge running parallel to cutting edge terminating in a toothed projection of the left mandible. Lower lip forming a deep-throated collar lining to the mandibles, outer lobe setose with prominent tooth-like papilla distally, mandibular processes short and blunt. Maxilla 1, palp 1-segmented, orientated at right angles to the plane of the inner and outer plates. Maxilla 2, outer plate at right angles to inner, not gaping or geniculate, with unhooked spines distally. Maxilliped, inner plates fleshy, triangular in section reaching base of palp segment 2, distal truncate face bearing 2 slender setae and 2 stylet-like spines emanating from conical bases; palp 4-segmented, segment 2 unproduced mediodistally, segment 4 lanceolate. Gnathopods simple,

† Since this manuscript was finalized, Dr Bousfield informs me that representatives of these genera have been found in recent N. Pacific collections, hence their inclusion in this key.

dactyls slender, straight. Peraeopod 5, basis slender. Peraeopods 6 and 7 bases expanded. Uropod 3, peduncle longer than rami, outer ramus 2-segmented. Telson triangular, entire.

Type species. *Parandania boecki* (Stebbing 1888)

Remarks. Stebbing's original description (1888) and figures of *Andania boecki* showed no articulation to the outer ramus of uropod 3. J. L. Barnard (1961) described a small second segment on this appendage. This feature is apparent in the present material and also in material from the deep Atlantic which I have examined (for Station details, see Moore and Rainbow, 1989). The demarcating suture is, however, easily missed. Such a 2-segmented condition occurs in *Andaniella*, *Andaniexis*, *Andaniopsis*, *Andaniotes* (some), *Stegosoladidus* (?) and *Tetradeion*, as well as in *Parandania*, and is typical of the family.

Parandania boecki (Stebbing 1888)

(Fig. 6)

Andania boecki Stebbing, 1888, 735, pl. 36.
Parandania boecki Stebbing, 1899, p. 206; 1906, 95, figs 19, 20.
P. boecki Schellenberg, 1926, 223. J. L. Barnard, 1961, 57–58, fig. 27 (incl. full bibliography); 1964b, 320. Gurjanova, 1962, 382–383, fig. 132. Birstein and Vinogradov, 1970, Thurston, 1976, 374, fig. 8. Watling and Holman, 1981, 225, fig. 27e. Andres, 1985, 133–134. Moore and Rainbow, 1989, 4–7, fig. 1. Coleman, 1990, fig. 1.

Material examined. British Columbia, Skidgate Channel, 53°01'N, 132°45·5'W, 1300 m, 12 August 1967, coll. N. A. Powell, Acc. 1967–223, single damaged individual, male? 9·5 mm (illustr.). Same details, Acc. 1967–223, St 65-52GBR, 6 individuals. (Note: upper lip in Fig. 6 is from one of these individuals.)

Diagnosis. With the genus, genus monotypic.

Remarks. Barnard (1961) noted that several discrepancies existed between Stebbing's original drawings (1888) of *P. boecki* and his own material (Barnard's had longer uropod rami and a less well-developed accessory flagellum). He was also surprised that, despite its common occurrence, only two groups of figures had, to that time, been published and no-one had worked out the morphological variation of this cosmopolitan species. This latter comment remains pertinent. In this connection it may be noted that the present material showed peraeopod 6 basis posterior margin to be rather more convex, and peraeopod 7 anterior margin to be distinctly less convex proximally than those limbs illustrated either by Stebbing or Barnard. This species has been described by Moore and Rainbow (1989) as feeding on mesopelagic medusae (see also Coleman, 1990).

Distributional ecology. Coldwater cosmopolitan in both hemispheres, mesopelagic or deeper, usually 550–960 m, but records from 0–3970 m exist (see Schellenberg, 1926). J. L. Barnard (1961) confirmed records between 300 and 2200 m (based on closed hauls). Scrutiny of the literature reveals some tendency, as would be expected, for this species to occur deeper in samples taken from lower latitudes, but the reliability of depths quoted (probably often based on open-net oblique tows) makes detailed analysis of this relationship impossible.

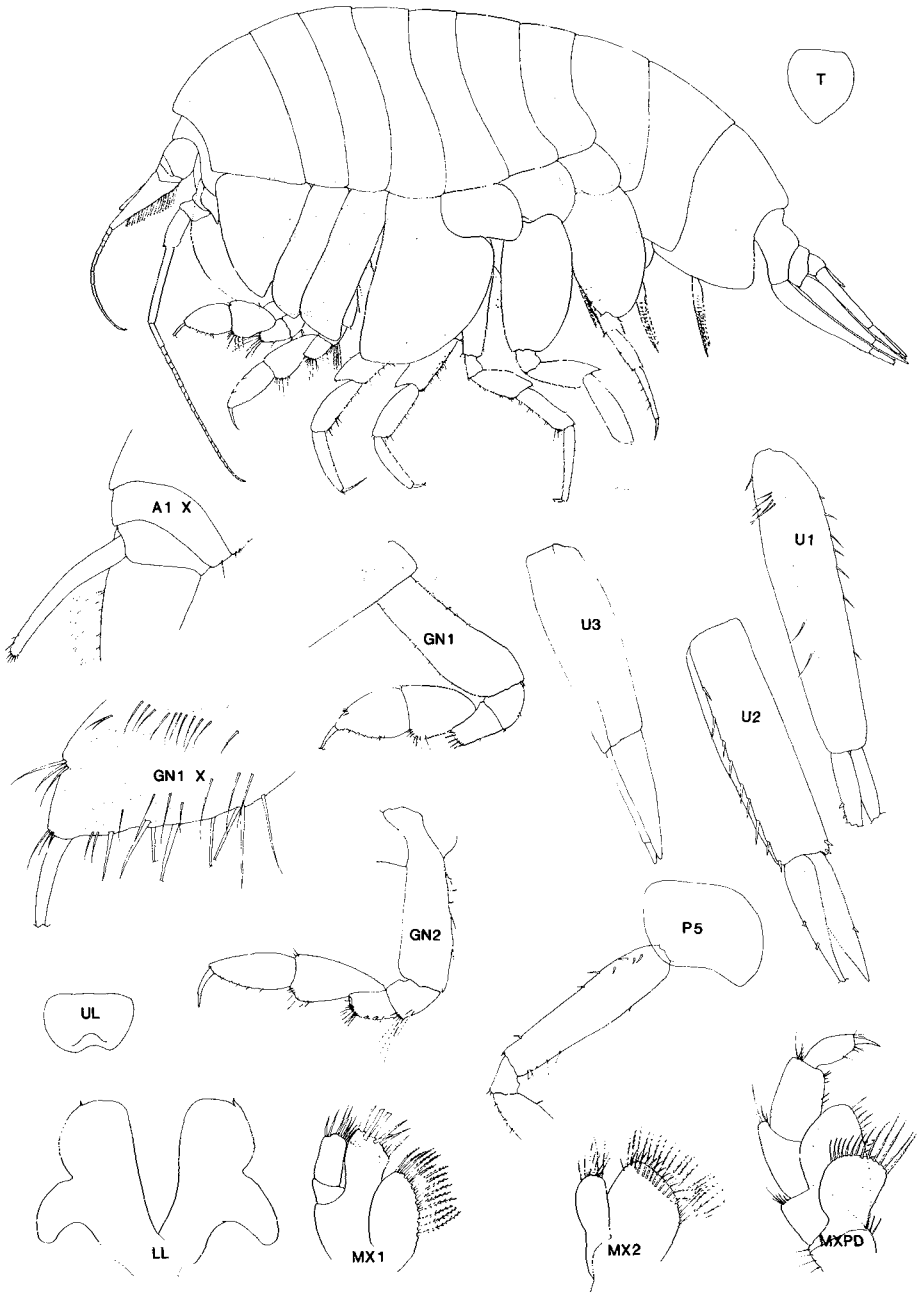

FIG. 6. *Parandania boecki* (Stebbing) (male?, 9·5 mm, British Columbia). Abbreviations as in Figs 1 and 2.

Genus *Phippsiella* Schellenberg 1924

Diagnosis. Antenna 2, segment 4 slightly longer than 5. Upper lip incised symmetrically or asymmetrically. Mandible with toothed incisor. Maxilla 1, palp 2-segmented. Maxilla 2, outer plate geniculate, apical spines usually with hooks. Maxilliped, palp 4-segmented, segment 2 unproduced. Gnathopods simple. Peraeopod 6 basis expanded. Peraeopod 7 basis usually with rounded posterodistal lobe. Uropod 3 biramous, peduncle subequal to or shorter than rami, outer ramus 1-segmented. Telson longer than broad, cleft.

Type species. *Stegocephalus similis* Sars 1895.

Key to N. Pacific *Phippsiella*

1 Antenna 1, accessory flagellum 2-segmented . . . *P. longicornis* Gurjanova 1962
– Antenna 1, accessory flagellum 1-segmented 2

2 Left lacinia mobilis well developed; gnathopod 1 basis, anterior margin densely setose; peraeopod 7 basis posterior margin smooth . . . . *P. cascadiensis* n. sp.
– Left lacinia mobilis absent; gnathopod 1 basis, anterior and posterior margins densely setose; peraeopod 7 basis posterior margin slightly serrate
P. nipoma J. L. Barnard 1961

Phippsiella cascadiensis n. sp.

(Fig. 7)

Materials examined. HOLOTYPE male (?) (18 mm, figured), Cascadia Abyssal Plain, off Oregon, 45°10·8′N, 126°43·0′W, Sta BMT 160, 18 January 1970, coll. Oregon State University, Cat. NMCC1992–0193; PARATYPES female (28 mm, setose oostegites) 44°44·15′N, 127°29·0′W, depth 2818 m, Sta BMT 317, 3 February 1973, R/V 'Yaquina', coll. Oregon State University, Cat. NMCC1992–0194; sex indet. (17 mm), 45°21·6′N, 127°35·7′W, Sta BMT 280, 18 May 1971, coll. Oregon State University, Cat. NMCC1992–0195; female (23 mm, setose oostegites), 44°38·55′N, 127°39·05′W, Sta BMT 281, 19 May 1971, coll. Oregon State University, Cat. NMCC1992–0196; 1 male (?, 18 mm), 1 female (19 mm, setose oostegites), 46°02·0′N, 127°31·8′W, 2740 m, Sta BMT 322, 12 March 1973, coll. Oregon State University, Cat. NMCC1992–0197.

Diagnosis. *Male* (?) holotype (18 mm, apparent penile papillae medial to gill in P7). Head, retractable (near totally) under cowl-like anterior dorsal margin of peraeon segment 1. Eyes lacking. Antenna 1, segment 1 of flagellum longer than peduncle, flagellum with 7 segments, accessory flagellum longer than peduncle, flagellum with 7 segments, accessory flagellum 1-segmented. Antenna 2, flagellum with 16 segments. Epistome somewhat gibbous distally. Upper lip cleft asymmetrically. Mandible, left lacinia mobilis well developed and toothed, right lacinia lacking. Lower lip gaping, outer lobe with single distal finger, inner lobes lacking. Maxilla 1, outer plate with 9 spines distally, palp segment 2 with 7 long and 7 short setae distally. Maxilla 2, outer plate, bearing 8 unhooked spines distally. Maxilliped, inner plate reaching less than half-way along palp article 1. Gnathopod 1, basis, anterior margin densely setose. Gnathopod 2, basis, posterior margin bearing many long setae. Dactyli of gnathopods and peraeopods simple. Peraeopod 6, basis moderately expanded, subrectangular. Peraeopod 7, basis expanded, posterodistal lobe distal margin rather straight, angle

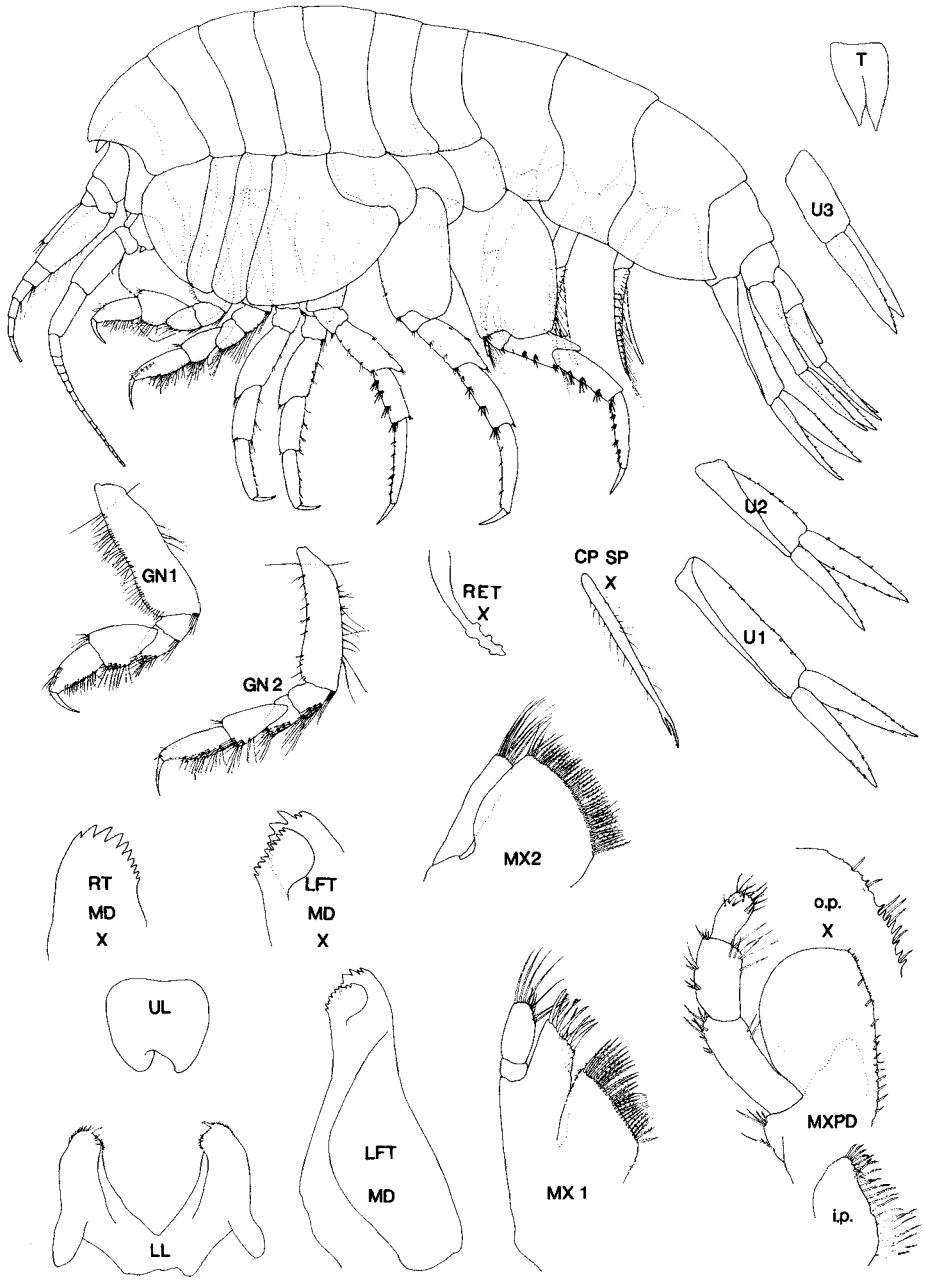

FIG. 7. *Phippsiella cascadiensis* n. sp. Holotype (male?, 18 mm, off Oregon). Abbreviations as in Figs 1 and 2, also CPSP = 'clothespin' spine (pleopod 3 base of inner ramus), i.p. = inner plate, o.p. = outer plate, RET = spine from base of pleopod 2 inner ramus.

sub-quadrate. Epimeral sideplate 3 posterodistal angle produced, posterior margin smooth. Uropod 1, rami subequal. Uropod 2, inner ramus longer than outer. Uropod 3 outer ramus slightly longer than inner. Telson, two-thirds cleft.

Female. Apparently bigger than male, otherwise no major differences. Peraeopod 7 basis, distal margin slightly more convex than in male. Oostegites broad, anteriormost (P2) narrower than posteriormost (P5). Eggs (size 1·4 × 1·2 mm) were present loose in one sample tube (12 March 1973) containing a mature female (*ca* 19 mm) which had been partially dissected by another.

Distributional ecology. Off Oregon, *P. cascadiensis* has been collected only from bathyal depths at the type locality.

Associate. A single cryptoniscid (?) isopod (unidentified) was recovered from the dissected holotype.

Remarks. A noteworthy feature of the material is that the telson lobes are symmetrical in some individuals, asymmetrical in others. *Phippsiella cascadiensis* resembles *P. longicornis*, *P. abyssicola*, *P. minima*, *P. pajarella*, *P. nipoma*, *P. pseudophippsia* and *P. viscaina* in having the basis of peraeopod 6 only moderately expanded (cf. broad in *P. similis*). The left lacinia mobilis is well developed (cf. absent in *P. nipoma*). Although the usual condition of the outer plate of maxilla 2 in *Phippsiella* is for distal spines to terminate in hooks, *P. cascadiensis* exhibits the unhooked condition (like *P. minima*). The shape of the distal margin of peraeopod 7 approaches that in some *Stegocephalus* spp. However, in possessing a 2-segmented maxilla 1 palp (even in the biggest female), the new species is clearly referable to *Phippsiella*. (Note: young *Stegocephalus inflatus* Kröyer have a 2-segmented maxilla 1 palp which fuses to 1-segmented in adulthood, so immature animals require special scrutiny—see Steele, 1967b.)

Genus ***Stegocephalexia*** n. gen.

Diagnosis. Antenna 1, proximal segment of flagellum, shorter than peduncle. Antenna 2 peduncle segment 4 shorter than 5. Upper lip incised, asymmetrical, Mandible, incisor serrate, left mandible with large serrate lacinia mobilis, right mandible lacking lacinia but with blunt projection. Lower lip, outer lobe terminally setose with prominent tooth-like papilla subdistally. Maxilla 1, palp 1-segmented. Maxilla 2, outer plate approaching the geniculate condition borne on blunt projection of inner plate, outer plate with 6 long, slightly curved spines (not hooked), inner plate bearing stiff seta halfway along lateral margin. Maxilliped, inner plate hardly reaching distal end of palp segment 1, outer plate setose overreaching palp segment 3, distal margin smooth, palp 4-segmented, segment 2 unproduced mediodistally, segment 4 lanceolate. Gnathopods simple, coxa 1 triangular. Gnathopod 2, basis proximally sharply geniculate. Coxa 4 deep, rudder-shaped. Peraeopod 5 basis slender, Peraeopods 6 and 7 bases expanded. Epimera 1–3 subquadrate. Uropod 1 reaching beyond uropods 2 and 3, peduncle longer than rami, rami subequal. Uropod 2 peduncle longer than rami, rami subequal. Uropod 3 peduncle shorter than rami, rami subequal, outer ramus 1-segmented. Telson, tear-drop shaped, deeply cleft, bilobate, not reaching distal margin of uropod 3 peduncle.

Gender. Feminine.

Stegocephalexia penelope n. sp.

(Fig. 8)

Material examined. HOLOTYPE, female (damaged), 3·5 mm (with 2 eggs), British Columbia, Swanson Bay 53°00′N: 128°30′W, 38 m, 11 April 1973, C. Levings, Sta K, Cat. NMC1990–0363 (illstr.). PARATYPES, 2 individuals (4·5 mm female with 1 juvenile) same site, 52°00′N, 128°30′W, 45 m, 18 November 1975, C. Levings, Sta. M, Cat. NMCC1990–0364. One immature individual (2·5 mm), same site, 45 m, 18 November 1975, Sta M, Cat. NMCC1990–0365.

Diagnosis. With the genus.

Description. Antennae subequal. Antenna 1, peduncle segment 1 with rank of 5 long setae medially; flagellum segment 1, conjoint, with callynophore, flagellum 5-segmented, segments 1, 2 and 3 bearing a long stout seta distally; accessory flagellum, not reaching distal end of flagellum segment 1, terminating in one long stout and 3 short setae. Antenna 2 tapering, flagellum 6-segmented. Upper lip, asymmetrical incision more pronounced on smaller individuals (slides of holotype upper lip and left peraeopod 6 broken by accident). Mandible, incisors with 10 (right) or 13 teeth (left), lacinia mobilis (left) broad with 17 teeth. Gnathopod 1 basis with short setae along anterior margin and rank of 4 long setae midway along posterior margin; ischium, merus and carpus posterior margins with long setae; carpus and propodus subequal; propodus tapering with numerous long, thin setae and fewer longer plumose setae along posterior margin; dactylus with subapical cusp. Gnathopod 2, coxa elongate with posterodistal angle acute; basis with long setae along posterior margin; ischium with long plumose setae at posterodistal angle; propodus tapering, subequal to merus and carpus together, bearing thin, long setae and stouter pectinate setae along posterior margin; dactylus with subapical cusp. Peraeopods 3 and 4 simple, basis (P4) with numerous slender setae along posterior margin. Coxa 5 rounded diamond-shaped. Coxa 6 elongate ovoid. Oostegites strap-like. Coxa 7 with posterodistal lobe rounded, anterior margin with few spines. Epimeral plates 2 and 3 with few slender setae along ventral margins. Pleopod 1 penduncle with pair of locking spines (situation in 2 and 3 uncertain). Uropod 3 aspinose. Telson somewhat asymmetrical. Coloration (paratype), body closely punctate dark olive/brown (in alcohol), denser pigmentation at posterolateral angles of peraeon segments and middle of coxa 3.

Etymology. Named for my daughter, Penelope Moore.

Remarks. The new genus is close to *Stegocephalopsis* Schellenberg and *Steleuthera* J. L. Barnard, depending upon the interpretation given to the condition of maxilla 2, i.e. geniculate or otherwise. It differs from the usual condition of *Stegocephalopsis* in not having hooked spines on maxilla 2 outer plate, in the inner plate of the maxilliped not reaching article 2 of the maxilliped palp, in the basis of peraeopod 6 not being rectolinear and in uropod 3 peduncle not being subequal to rami. From *Steleuthera*, it differs in not having antenna 1 flagellum segment 1 longer than peduncle, in not having a 2-segmented accessory flagellum and in having a deeply cleft telson.

Distributional ecology. British Columbia, shallow water. Presently known only from the type locality.

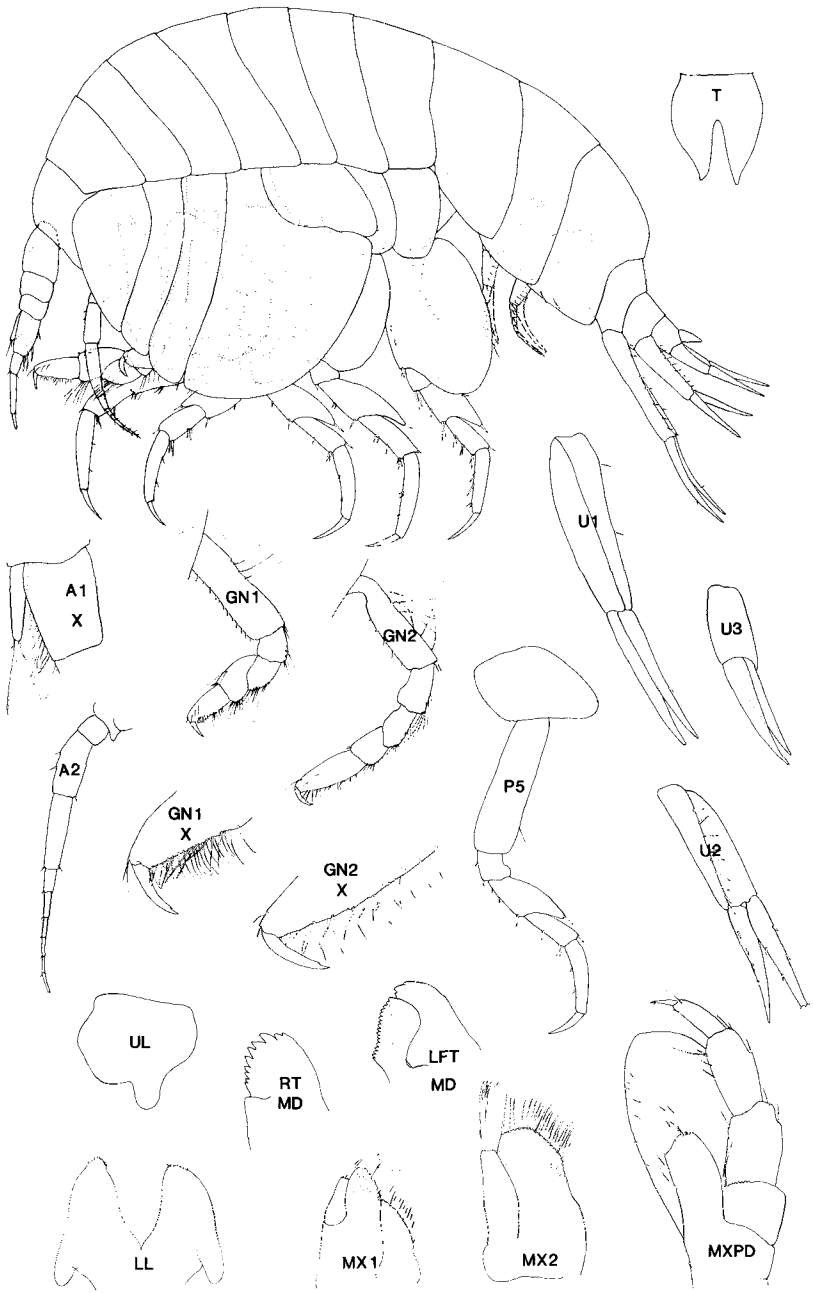

FIG. 8. *Stegocephalexia penelope* n. gen., n. sp. Holotype (female, 3·5 mm, British Columbia). Abbreviations as in Figs 1 and 2.

Genus ***Stegocephalopsis*** Schellenberg 1924

Diagnosis. Body smooth. Antenna 1, flagellum weakly or not callynophorate. Antenna 2, peduncle article 4 scarcely longer than segment 5. Upper lip incised. Mandibular incisor toothed. Maxilla 1, palp 1-segmented. Maxilla 2, outer plate geniculate, distal spines usually with hooks. Maxilliped, palp segment 2 not produced. Gnathopods 1 and 2, simple. Peraeopod 6 basis usually rectolinear. Peraeopod 7, basis usually produced into a posterodistal lobe. Uropod 3 biramous, outer ramus 1-segmented, peduncle usually subequal to rami. Telson, longer than broad, bilobate.

Type species. *Stegocephalopsis ampulla* (Phipps 1774)

Key to N. Pacific *Stegocephalopsis*

1 Maxilliped palp 4-segmented	*S. mamillidacta* n. sp
– Maxilliped palp 3-segmented	*S. pacifica* (Bulycheva 1952)

Stegocephalopsis mamillidacta n. sp.

(Fig. 9)

Material examined. HOLOTYPE 3 mm (sex indet.), Amchitka Is., Alaska, off Banjo Point (Bering Sea), from RV 'Commander' using otter trawl, 100 m, 14 September 1971, coll. P. N. Slattery, Cat. NMCC1990–0366. PARATYPE 3 mm (sex indet.), same details, Cat. NMCC1990–0367.

Diagnosis. Antenna short, subequal. Antenna 1 stouter than 2, peduncle segment 1 shorter than peduncle (? a female characteristic), weakly callynophorate, flagellum 4-segmented, accessory flagellum 1-segmented. Antenna 2 flagellum 4-segmented. Head lacking cowl-like rostrum, lateral lobe acutely produced ventrally. Upper lip somewhat longer than broad, cleft asymmetrically. Mandibles with serrate incisors, right mandible lacking lacinia mobilis, lacinia of left mandible strongly developed, serrate, not sheathed. Lower lip, outer lobes with simple distal finger. Maxilla 1, palp 1-segmented, outer plate with 9 spines distally, inner plate with 6 stout, spatulate spines distally. Maxilla 2, outer plate with 2 blunt, elongate, spatulate spines and 1 slender seta distally. Maxilliped, palp 4-segmented, inner plate reaching distal margin of palp segment 2, armed with stout spines; outer plate margin unadorned. Gnathopod 1, coxa triangular, basis with 3 long setae spaced along posterior margin; ischium longer than merus; carpus and propodus short, propodus slightly longer than carpus, bearing row of 5 stout spines along posterior margin; dactylus short and stout, minutely serrate along posterior margin and generally mamillate in shape. Gnathopod 2, basis slightly geniculate, distal half of posterior margin bearing sparse fringe of long setae; propodus more elongate than that of gathopod 1, with spinose posterior margin and dactylus of similar form. Peraeopods 3 and 4 dactyli squat, mamillate. Peraeopod 5, coxa ovoid. Peraeopod 6, coxa triangular, basis very slightly expanded. Peraeopod 7 squat, basis not produced into a posterodistal lobe; all distal segments short. Gills present on P2–P6. Epimeral plates 1 and 2 acutely rounded at posterodistal angle. Epimeron 3 posterior margin unadorned, posterodistal angle rounded quadrate. Pleopod 1 peduncle with 2 stout, tapering plumose setae at distomedial angle. Pleopods 2 and 3 with 1 such seta and 2 sub-distally knobbed locking spines at this position. Uropods 1–3 progressively shorter, rami squat, shorter than peduncles. Inner margins of outer rami

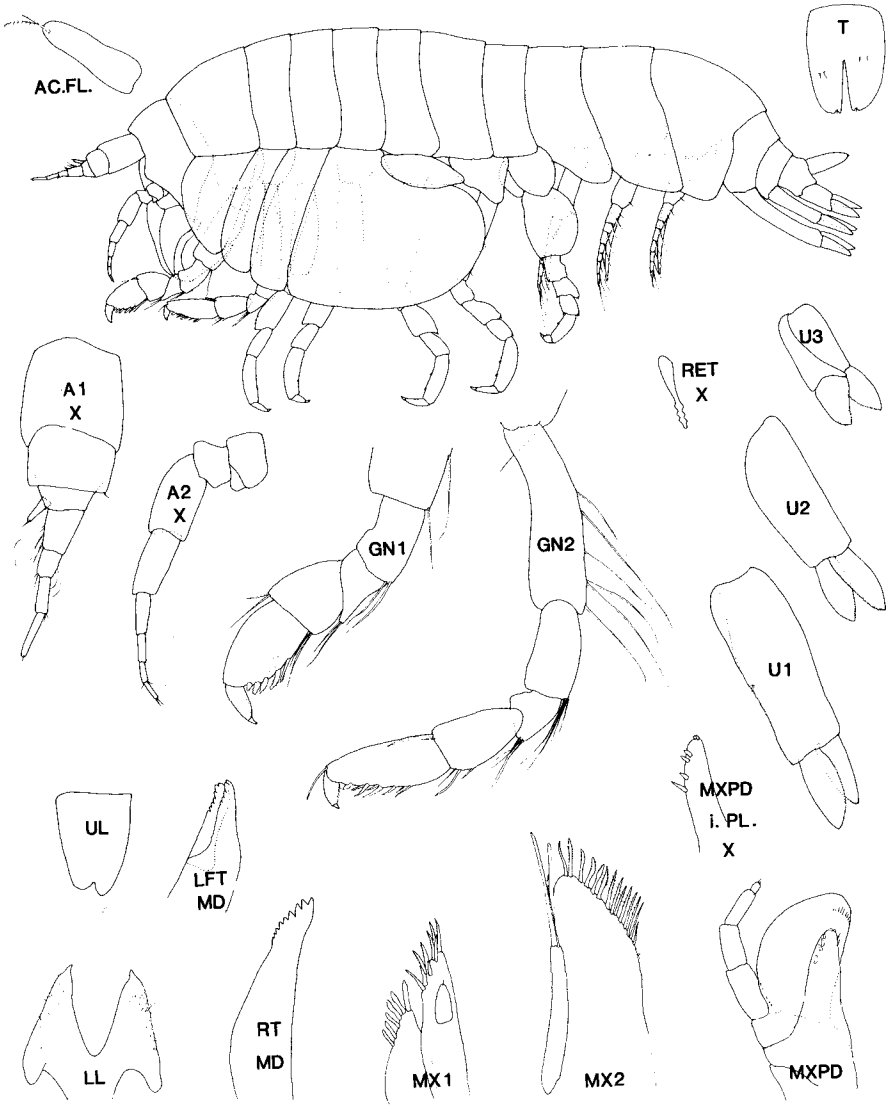

FIG. 9. *Stegocephalopsis mamillidacta* n. sp. Holotype (sex undet., 3 mm, Alaska). Abbreviations as in Figs 1 and 2, also AC FL = accessory flagellum.

and outer margins of inner rami minutely serrulate, as also outer margin of uropod 1 peduncle. Telson, overreaching uropod 3 peduncle, cleft halfway, with single apical seta on each lobe.

Etymology. The specific epithet refers to the distinctive shape of the peraeopodal dactyli (from *mamilla* (L)—a little teat).

Remarks. The protuberant condition of the head and the erect appearance of the telson in the holotype are probably artifacts (of fixation?), since they are not witnessed in the paratype. The general condition of the paratype individual, however, was not as good as the 'aberrant' individual which, in spite of these characteristics, was selected as holotype.

The genus *Stegocephalopsis*, as constituted by Barnard and Barnard (1990), contains 6 rather poorly known species. The new taxon herein described differs (*inter alia*) from *S. vegae* (Oldevig) in possessing a 1 (not 2)-segmented accessory flagellum; from *S. vanhoffeni* (Schellenberg) in the shape of the basis and proportions of the propodus of gathopod 1, in lacking ornamentation on the posterior margin of epimeral plate 3 and in the stubby form of peraeopod 7; from *S. pacifica* (Bulycheva) which has a 3-segmented maxillipedal palp; from *S. latus* (Haswell) in the form of gnathopods 1 and 2; from *S. ampulla* (Phipps) in the shape of the head and of the posterior margin of epimeron 3.

Stegocephalopsis mamillidacta n. sp. is perhaps closest to *S. katalia* (J. L. Barnard) in also possessing a large left lacinia mobilis (but it is not basally sheathed). Both these species have simple, spatulate spines on the outer plate of maxilla, 2, i.e. they are not hooked. The peduncle of uropod 3 is also rather elongate in *S. mamillidacta* and *S. katalia* (see also *S. pacifica*), though the rami of the new species are much stubbier than those of *S. katalia*. The basis of peraeopod 6 is somewhat expanded in both *S. katalia* and *S. mamillidacta*, cf. the rectolinear norm for the genus.

Distributional ecology. Shallow water, Bering Sea, Alaska; known only from the type locality.

Key to non-lafystiid stegocephaloid amphipods of the NE Pacific

(but see footnote to p. 922)

1 Peraeonite 7 with mid-dorsal or dorsolateral cusp or cusps 2
– Peraeonite 7 dorsally smooth 3

2 Peraeonite 7 and pleonites 1 and 2 with single, mid-dorsal cusp posteriorly
Acanthonotozoma rusanovae Bryazgin
– Peraeonite 7 and pleonites 1–3 with 1 pair of dorsolateral and 1 pair of lateral cusps
Iphimedia rickettsi (Shoemaker)

3 Gnathopods feeble, simple or weakly subchelate; mandible lacking palp and molar; accessory flagellum 1- or 2-segmented 4
– Gnathopod 1 feeble, gnathopod 2 subchelate; mandible with palp and molar; accessory flagellum lacking 7

4 Maxilla 1, palp 1-segmented 5
– Maxilla 1, palp 2-segmented . . . . . *Phippsiella cascadiensis* n. sp.

5 Telson entire . . . . . *Parandania boecki* (Stebbing)
– Telson cleft 6

6 Uropod 3, peduncle shorter than rami . . *Stegocephalexia penelope* n. gen., n. sp.
– Uropod 3, peduncle longer than rami . . . *Stegocephalopsis mamillidacta* n. sp.

7 Telson incised . . . . . *Imbrexodius oclairi* n. gen., n. sp.
– Telson entire 8

8 Pleonites 3, 4 and 6 with raised dorsal ornamentation . *Cryptodius kelleri* (Brüggen)
– Pleonites 3, 4 and 6 dorsal surfaces smooth. . . . . *C. unguidactylus* n. sp.

Discussion and conclusions

Biogeography

Little biogeographical information can be gleaned on the new species of northern Pacific Stegocephaloidea herein described, since they are all known only from their type localities. Thus whether *Cryptodius unguidactylus*, *Imbrexodius oclairi*, and *Stegocephalopsis mamillidacta* prove to be Alaskan endemics awaits further research.

The remaining species can be divided into the following categories: (1) coldwater cosmopolitan species, e.g. *Parandania boecki*—a mesopelagic species which no doubt explains its transhemispheric distribution; (2) northern circumpolar species, e.g. *Acanthonotozoma rusanovae*; (3) North Pacific coldwater species, e.g. *Cryptodius kelleri* and (4) American endemic, boreal species, e.g. *Iphimedia rickettsi*, occurring from British Columbia to California.

Ecology

Consistent with the view that acanthonotozomatid, iphimediid and odiid species are carnivorous on sessile colonial organisms of one sort or another is finding that *A. rusanovae*, *I. rickettsi*, *C. kelleri*, *C. unguidactylus* and *I. oclairi* occur predominantly in association with shallow rocky grounds. It is interesting that *C. kelleri* can be collected in a light trap (something which the stegocephalids, lacking eyes, presumably could not be).

The globular body shape of stegocephalids betokens an active swimming lifestyle (reminiscent of hyperiids). Bousfield and Shih (in preparation) are currently finalizing a cladistic analysis that puts hyperiids closer to stegocephalids than to any other gammaridean group (somewhere between stegocephalids, pardaliscids and lysianassids), but convergent morphology may be involved.

The habitat requirements of *Stegocephalexia penelope* and *Stegocephalopsis mamillidacta* are presently unknown. *Parandania boecki* is a predator on mesopelagic medusae (primarily of the genus *Atolla*), but whether the other deep-water species in this collection, *viz. Phippsiella cascadiensis*, feeds on pelagic or benthic prey has not been ascertained.

Systematic relationships

The superfamilial and familial relationships within the Amphipoda remain a hotly debated subject. Resolution of these issues as they relate to taxa under present consideration remains as far away as ever (see Introduction), as witness the counter-schemes of Barnard and Karaman (1991) and Coleman and Barnard (1991) published—if not conceived—in the same year. Thus, Bousfield (personal communication, 1991) is critical of the latter authors' break-up of the Acanthonotozomatidae, and doubts the validity of the Odiidae. Bousfield (personal communication, 1991) is now less convinced that acanthonotozomatids are closest to stegocephalids, but rather belong somewhere between the advanced eusiroideans (e.g. paramphithoids) and

primitive leucothoideans (e.g. pleustids). Bousfield would question the validity of the Barnardian break-up of the Acanthonotozomatidae (at family level) based on a few character states that elsewhere (e.g. in Stenothoidae, Phoxocephalidae) appear significant at genus or subfamily level only.

Whereas acanthonotozomatids and lafystiids seem closely related to pleustids (e.g. Bousfield, 1987), their links with paramphithoids and other eusiroideans, as well as with leucothiodeans, remain formally unresolved. The stegocephalids, on the other hand, seem more securely related to lysianassids, synopiids and even hyperiids.

Did hyperiids evolve from stegocephalid ancestral types? Ecologically the two groups have much in common, e.g. an exclusively marine distribution, predominantly coelenterophagous diet (though stegocephalids seem more usually to inhabit sessile hosts, cf. typical planktonic hosts of hyperiids), and significant penetration into the deep-sea. Morphological features of the hyperiid infraorder Physosomata Pirlot 1929 are certainly reminiscent of stegocephalids, *viz.* the rather swollen body and reduced mouthparts, and frequency of reduction of peraeopod 7 in both groups. On the other hand, other equally fundamental points differ, notably the absence of an accessory flagellum, the possession of eyes (if usually small in Physosomata), small coxae and (perhaps) broader oostegites in hyperiids. In the absence (largely) of detailed knowledge on the functional significance of these characters in different groups, i.e. the extent to which each is adaptive, it is difficult to assess which similarities may be the outcome of independent convergence in response to ecological pressures brought about by similar lifestyles, or the reflection of shared ancestry. Given the plasticity of amphipod morphological solutions to functional problems, e.g. gills serving as oostegites (*Rhabdosoma*) and peraeopod bases as a lateral shield (Platyscelidae), it is merely speculative to launch phylogenetic schemes based on characters whose adaptive significance is unappreciated (note Steele, 1991).

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