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A revision of the genus *Pandalus* (Crustacea: Decapoda: Caridea: Pandalidae)

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The genus *Pandalus* Leach, 1814, is revised based upon the abundant material from collections in various museums or institutions in the world. Altogether 20 species are recognized which appear to form five groups. Nineteen species are recognized in *Pandalus*, three of which are described as new: *P. curvatus* from southern Japan, and *P. chani* and *P. formosanus* from Taiwan. Four informal species groups are also recognized within the genus: *P. montagui* group (*P. montagui* Leach, 1814; *P. borealis* Krøyer, 1838; *P. goniurus* Stimpson, 1860; *P. jordani* Rathbun, 1902; *P. tridens* Rathbun, 1902; and *P. eous* Makarov, 1935); *P. stenolepis* group (*P. stenolepis* Rathbun, 1902; *P. curvatus* sp. nov.); *P. hypsinotus* group (*P. hypsinotus* Brandt, 1851; *P. danae* Stimpson, 1857; *P. prensor* Stimpson, 1860; *P. gracilis* Stimpson, 1860; *P. gurneyi* Stimpson, 1871; *P. nipponensis* Yokoya, 1933; *P. teraoi* Kubo, 1937; *P. chani* sp. nov.; and *P. formosanus* sp. nov.); and *P. platyceros* group (*P. platyceros* Brandt, 1851; and *P. latirostris* Rathbun, 1902). The *P. platyceros* group appears to be most closely related to the genus *Pandalopsis* Bate, 1888, but *Pandalus* is retained as a possible paraphyletic group. Protandrous hermaphroditism is known in all but two species of the genus (*P. curvatus* and *P. formosanus*), for which only specimens of either male or female have been available. *Pandalus propinqvus* G. O. Sars, 1870, is transferred to a new monotypic genus *Atlantopandalus*, because of its lack of hermaphroditism and possession of some unique morphological characters, including one indicating a close relationsip to *Dichelopandalus* Caullery, 1896. All species are fully described and illustrated. The affinities and important morphological variations of the species are discussed. A key for adults is presented for the identification of the species. Biogeography of the genus is briefly discussed.

Keywords: Crustacea, Caridea, Pandalidae, *Pandalus*, *Atlantopandalus*, new genus, new species, key, taxonomy.

Introduction

The genus *Pandalus* Leach, 1814, currently represented by about 16 recognized species, is restricted to the northern hemisphere, occurring higher than 30° north latitude, and contains a number of large shrimps of current or potential economic importance (Holthuis, 1980). They have also been subjects of numerous biological

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or fishery studies. In spite of its economical and biological importance, however, there has been no comprehensive taxonomic study of the genus.

In this paper, all the known species of *Pandalus* are reviewed. Christoffersen (1989) and Komai (1994a) have commented that the genera *Pandalus* and *Pandalopsis* Bate, 1888, form a monophyletic group that includes *Pandalopsis* as a subordinated clade within *Pandalus*, and the results of the present study do not contradict this hypothesis. However, in this study, it is proposed that *Pandalopsis* is retained as a monophyletic genus and that *Pandalus* is a possibly paraphyletic genus (see 'Remarks' under account of the genus *Pandalus*). Moreover, it has been revealed that *Pandalus propinqvus* has several important morphological differences that set apart this species from other species of *Pandalus* and *Pandalopsis*, and a new genus is herein proposed to accommodate it. Within the genus *Pandalus*, four informal species groups are recognized: *P. montagui* group; *P. stenolepis* group; *P. hypsinotus* group; and *P. platyceros* group. Three new species of *Pandalus* are also described: *P. curvatus* from southern Japan; *P. chani* and *P. formosanus* from Taiwan. The discovery of the new species from the subtropical region in the northwest Pacific is remarkable as the previously described species in the region are temperate or subarctic inhabitants.

Detailed examination of the present extensive material has made it possible to recognize reliable diagnostic characters and to evaluate the range of morphological variations. A diagnosis is provided for each species group, and a description, including only differential characters, is provided for each species. Measurements were made by using a caliper or by using an image made with a stereomicroscope equipped with a drawing tube. The postorbital carapace length (CL) was used as an indication of the size of specimens. Drawings were made with a drawing tube mounted on Olympus SZH, Wild 308700 or Leica MZ8 stereomicroscopes. Specific names are arranged in chronological order within respective species group. Polarity of characters is assumed by comparison with closely related genera, *Austropandalus* Holthuis, 1952, *Pandalina* Calman, 1899 and *Dichelopandalus* Caullery, 1896 (cf. Christoffersen, 1989; Komai, 1994a).

It has been well known that the members of *Pandalus* are protandrous hermaphrodites (e.g. Berkeley, 1930; Butler, 1980; Williams, 1984; Komai, 1994a, 1994b). The term 'functional male' is used for a male which has a fully developed, spinose, appendix masculina of the second pleopod and a well-developed appendix interna of the first pleopod, and the term 'transitional male' is used for a male which has a reduced, less spinose, appendix masculina of the second pleopod and a reduced, subterminal appendix interna of the first pleopod. The female is recognizable by the complete absence of the appendix interna from the first pleopod, as well as the enlargement of the abdominal pleura. In females, the appendix masculina may be absent or remain rudimentary.

The specimens examined in this study are deposited in the institutions indicated by the following abbreviations: CBM: Natural History Museum and Institute, Chiba; HUMZ: Laboratory of Marine Zoology, Faculty of Fisheries, Hokkaido University, Hakodate; KMNH: Kitakyushu Museum of Natural History, Kitakyushu; MNHN: Muséum National d'Histoire Naturelle, Paris; MSMTU: Marine Science Museum, Tokai University, Shimizu; MZS: Musée Zoologique, Strasbourg; NFUS: National Fisheries University, Shimonoseki; NHM: Natural History Museum, London; NTOU: National Taiwan Ocean University, Keelung; TUF: Tokyo University of Fisheries, Tokyo; USNM: National Musem of Natural History, Smithsonian Institution, Washington, DC; ZMUO: Zoologisk Museum, Universitetet i Oslo.

Species of *Pandalus* are fished commercially and their biology has been the subject of active investigation during much of this century, and studies of larval development are no exception (see review by Haynes, 1985). However, I have not tried to review information on larval taxonomy, because the main purpose of this study is to present a taxonomic revision of the genus based upon adult morphology.

Systematic account

Family Pandalidae
Genus *Pandalus* Leach, 1814

Pandalus Leach, 1814: 432 [type species, by monotypy: *Pandalus montagui* Leach, 1814]; Calman, 1899: 29 (part); Holthuis, 1955; 123 (part); 1993: 272 (part); Christoffersen, 1989: 265 (part).

Description. Protandrous hermaphrodite. Integument devoid of scales.

Rostrum well developed, reaching or over-reaching scaphocerite, armed with spines with distinct basal suture dorsally and with teeth ventrally. Carapace with moderately strong antennal and small brachiostegal spines, lacking lateral carinae; dorsal surface carinate anteriorly, rounded posteriorly; orbital margin concave, with little developed lobe at infraorbital angle.

Abdomen usually without distinct median carina on any somites, third somite sometimes with hump-like projection or obtuse short carina; pleura of first to third somites rounded ventrally, those of fourth to sixth somites with acute posteroventral tooth; sixth somite with moderately strong posterolateral process. Telson longer than sixth somite, with dorsal tuft of setae near base; posteriormost pair of dorsolateral spines situated dorsolateral to base of long, lateral spine of posterior two pairs.

Eye with cornea wider than eyestalk, with distinct ocellus broadly attached to cornea.

Antennule (figure 1G) with intermediate segment of peduncle bearing few spinules on anterodorsal margin; stylocerite short, usually rounded, with rudimentary lateral protuberance; basal segment with well-developed ventromesial expansion; outer flagellum with aesthetasc-bearing portion comprising more than 20 articles, not exceeding twice carapace length; inner flagellum longer than outer flagellum, composed of numerous articles. Antennal scaphocerites (figure 1H) relatively long and narrow (ratio of scaphocerite length/carapace length decreasing with growth); basicerite with ventrolateral spine.

Mandible (figure 2B) with stout incisor process; palp (figure 2C) three-articulated, relatively broad, basal article with prominent expansion. Maxillule (figure 2D) with palp distally bilobed, inner lobule with one stout apical seta; distal endite subovate, with two rows of corneous spines on mesial margin; proximal endite thickly setose. Maxilla (figure 2E) with distal endite well developed, subequally bilobed; proximal endite less developed, anterior lobe strongly reduced to small process; posterior lobe of scaphognathite produced, fringed posteriorly and mesially with very long setae. First maxilliped (figure 2F) with three-articulated palp, endopod bilobed. Second maxilliped (figure 2G) with dactyl wider than long, usually with shallow mesial excavation; epipod with well-developed podobranch. Third maxilliped (figure 2H) with ultimate segment distinctly longer than penultimate segment; antepenultimate segment with dorsal surface inflated at mid-length, bearing conspicuous tubercle near base; ventral margin rounded; exopod absent.

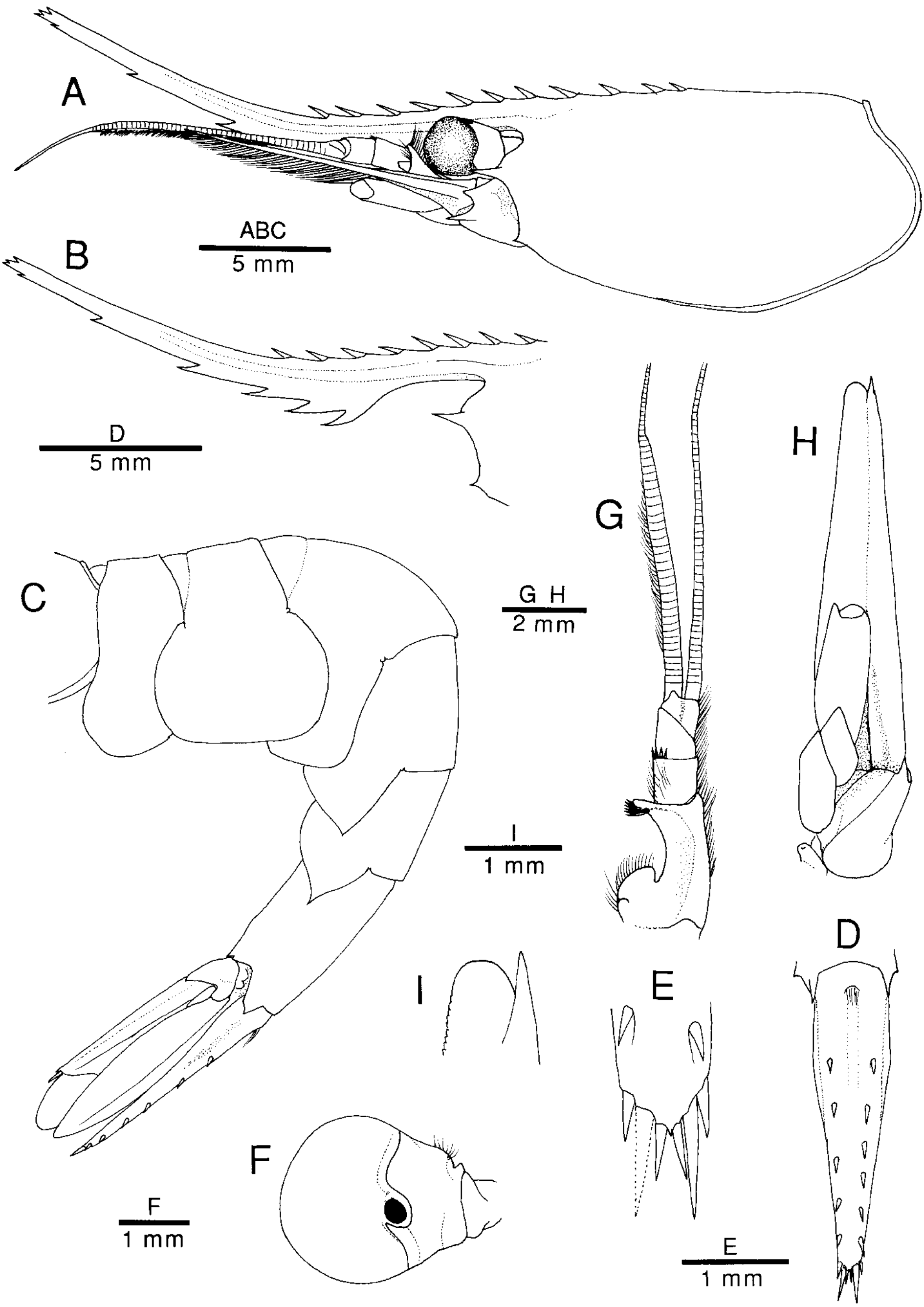


FIG. 1. *Pandalus montagui* Leach, 1814. (A)–(E) Male (CL 13.0 mm), Mull of Kintyre, Scotland, NHM 1894.9.26.60–75; F–H, transitional male (CL 10.5 mm), Texel Stroom, Netherlands, CBM-ZC 3422. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) abdomen, telson and uropod, lateral, pleopods omitted; (D) telson, dorsal; (E) posterior part of telson, dorsal; (F) eye, dorsal; (G) antennule, dorsomesial; (H) antenna, ventral; (I) distal part of scaphocerite.

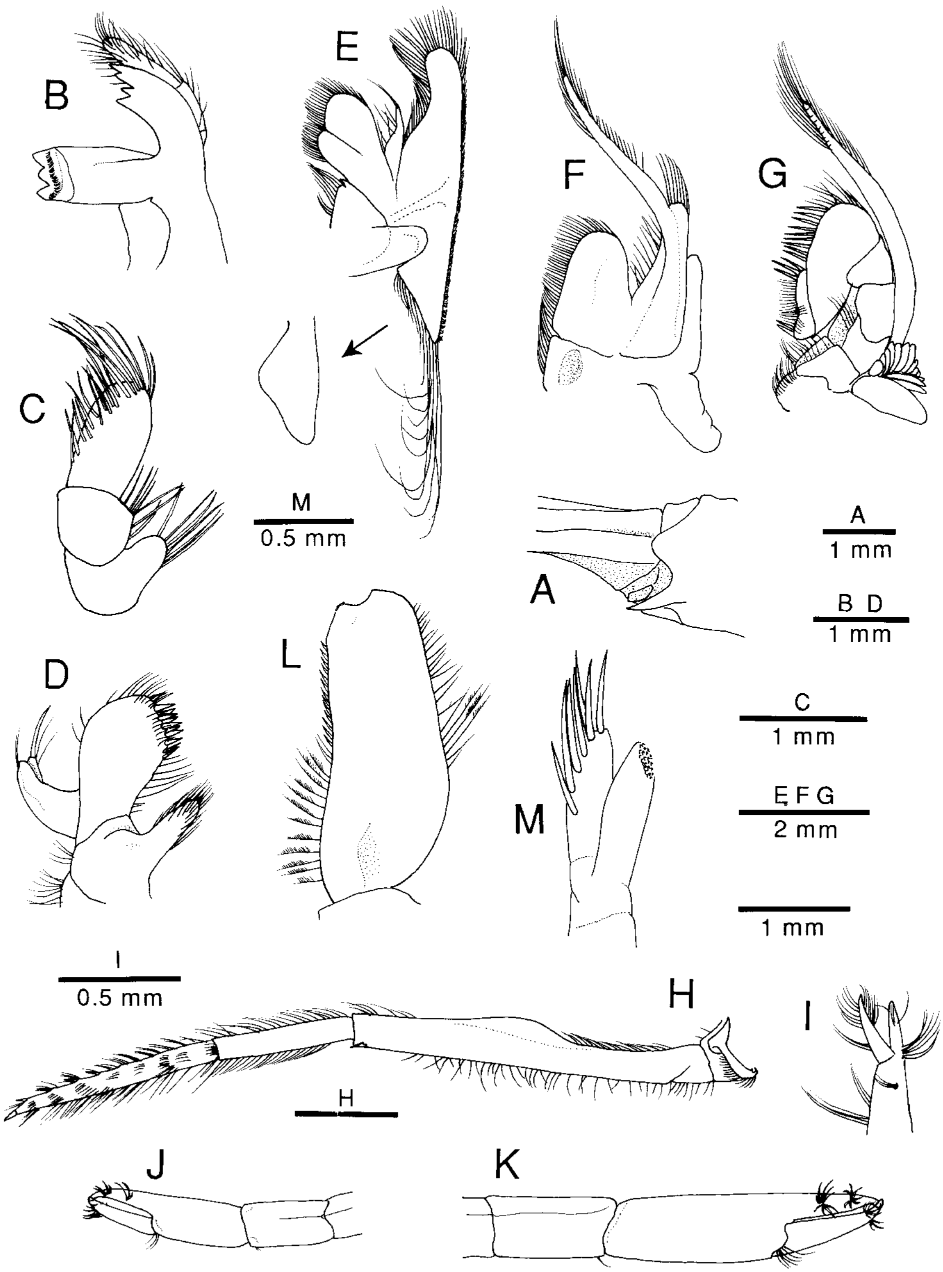


FIG. 2. *Pandalus montagui* Leach, 1814. (A)–(K) Transitional male (CL 10.5 mm), Texel Stroom, Netherlands; CBM-ZC 3422; L, M, functional male (CL 13.0 mm), Mull of Kintyre, Scotland, NHM 1894.9.26.60–75. (A) Anterior part of basicerite and basal part of scaphocerite, lateral; (B) left mandible, external; (C) same, palp, lateral; (D) right maxillule, external; (E) left maxilla, external; inset, posterior lobe of scaphognathite, mesial; (F) left first maxilliped, external; (G) left second maxilliped, external; (H) left third maxilliped, lateral; (I) chela of first pereopod, extensor; (J) chela of left second pereopod; (K) chela of right second pereopod; (L) endopod of first pleopod, ventral; (M) appendix masculina and interna of left second pleopod, mesial.

First pereopod minutely chelate (figure 2I), relatively slender; propodus not flattened, conical; ischium obliquely articulated to merus, only weakly laminate ventrally, with row of spinules and scattered short setae. Second pereopods very unequal, left longer and more slender than right; dactylus shorter than palm; left carpus divided into more than 10 articles, right carpus divided into more than six articles, number of articles considerably variable inter- or intraspecifically; left merus distinctly shorter than ischium, annulated; right merus subequal in length to ischium, usually annulated distally; ischia usually with annulations distally in left, proximally with weak ventral expanion bearing row of mesially curved setae. Posterior three pairs of pereopods moderately stout or slender, not extremely elongate, ischia always each with one ventral spine; dactyls with accessory spinules and one subterminal spinule closely appressed to terminal claw on flexor margin; carpi distinctly shorter than propodi, with lateral spines; meri with lateral and ventral or vetromesial rows of spines.

Branchial formula shown in table 1; epipods on third maxilliped to fourth pereopod each with terminal hook.

Endopod of first pleopod and appendix masculina of second pleopod showing sequential reduction associated with sex change; endopod of first pleopod in functional males with prominent appendix interna. Exopod of uropod with spine mesial to distolateral tooth on lateral margin.

Distribution. North Atlantic; North Pacific southward to Baja California in eastern part, southward to Taiwan in western part; intertidal to 1380 m.

Remarks. The usual presence of hermaphroditism is confirmed in all but two species here assigned to *Pandalus*. It is not possible to confirm its presence in the two species here described as new, *P. curvatus* and *P. formosanus*, because of lack of a sufficient series of specimens. Nevetheless, from the morphological similarities, I believe that the two species are probably hermaphrodites as well. As mentioned before, the presence of hermaphroditism can be verified from a sequential morphological change of the anterior two pairs of pleopods (Butler, 1980; Komai, 1994b).

The usual presence of protandric hermaphroditism is so far known only for two genera, *Pandalus* and *Pandalopsis*, within the superfamily Pandaloidea (King and Moffit, 1984; Chace, 1985; Christoffersen, 1989; Komai, 1994a), in spite of the rather widespread occurrence of hermaphroditism in the decapod Crustacea (Bauer, 1986). In external morphology, these two genera share several important features, such as the presence of the ventral laminar expansion on the ischium of the first pereopod (the expansion is much more developed in *Pandalopsis* than in *Pandalus*), extremely elongate setae on the posterior lobe of the scaphognathite and the absence of the

Table 1. Branchial formula of *Pandalus*.

	Maxillipeds			Pereopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	+	+	+	+	+
Arthrobranchs	–	–	2	1	1	1	1	–
Podobranch	–	+	–	–	–	–	–	–
Epipods	+	+	+	+	+	+	+	–
Exopods	+	+	–	–	–	–	–	–

exopod from the third maxilliped. However, *Pandalus* is immediately distinguishable from *Pandalopsis* in the less developed ventral laminar expansion of the ischium of the first pereopod, which bears spinules ventrally, the slender, conical propodus of the first pereopod, and the greatly unequal second pereopods. In *Pandalopsis*, the ventral laminar expansion on the ischium of the first pereopod is very broad, with numerous stiff setae on the ventral margin, but no spinules; the propodus of the first pereopod is somewhat compressed laterally; the second pereopods are subequal or equal; the first two character states appear to be autapomorphic for *Pandalopsis*. However, it has been suggested that *Pandalopsis* is a subordinated clade within the genus *Pandalus* (Christoffersen, 1989; Komai, 1994a). The strongly elongate posterior lobe of the scaphognathite, which represents a presumably autapomorphic state, suggests a sister relation between *Pandalopsis* and *Pandalus platyceros* group. Despite having such a problem, I have not tried to split *Pandalus* into several genera, because monophyly of the two of four informal groups recognized in *Pandalus* (*P. montagui* and *P. stenolepis* groups) has still not been established. Since *Pandalopsis* has been generally considered as a well-established taxon (Kobjakova, 1936; Holthuis, 1955, 1993; Komai, 1994b), it is better to retain it as a full genus. Following the evolutionary taxonomy (e.g. Mayr and Ashlock, 1991), both *Pandalus* and *Pandalopsis* can be recognized as good genera.

During this study, the absence of hermaphroditism in *P. propinqvus* was confirmed. Further examination has disclosed that the species has some unique morphological characters that set it apart from *Pandalus*. Thus, a new monotypic genus, *Atlantopandalus*, is proposed to accommodate *P. propinqvus*. The new genus appears more closely related to *Dichelopandalus* than to *Pandalus* is (see 'Remarks' under account of *Atlantopandalus* gen. nov.).

The following characters are important to differentiate the four species groups of *Pandalus* recognized herein: relative size of the posteriormost ventral tooth of the rostrum; presence or absence of a deep transverse groove on the tergum of the second abdominal somite; shape of the antennular stylocerite; development of the posterior lobe of the scaphognathite of the maxilla; armament of the carpi of the third and fourth pereopods; structure and function of the third and fourth pereopods; structure of the endopod of the first pleopod in functional males; and development and armament of the appendix masculina in functional males. The four informal groups are classified as follows: *P. montagui* group (with six species: *P. montagui* Leach, 1814; *P. borealis* Krøyer, 1838, *P. goniurus* Stimpson, 1860, *P. jordani* Rathbun, 1902a, *P. tridens* Rathbun, 1902a and *P. eous* Makarov, 1935); *P. stenolepis* group (with two species: *P. stenolepis* Rathbun, 1902a and *P. curvatus* sp. nov.); *P. hypsinotus* group (with nine species: *P. hypsinotus* Brandt, 1851, *P. danae* Stimpson, 1857, *P. prensor* Stimpson, 1860, *P. gracilis* Stimpson, 1860, *P. gurneyi* Stimpson, 1871, *P. nipponensis* Yokoya, 1933, *P. teraoi* Kubo, 1937, *P. chani* sp. nov. and *P. formosanus* sp. nov.); and *P. platyceros* group (with two species *P. platyceros* Brandt, 1851 and *P. latirostris* Rathbun, 1902b).

The present classification is considerably different from the phylogenetic hypothesis proposed by Christoffersen (1989). Presumed apomorphic characters supporting the sister relation between *P. platyceros* and *P. latirostris* pertain to such characters as distally tapering anntennular stylocerite, the presence of a prominent intercalated process on the antennal basicerite, the strongly elongate posterior lobe of the scaphognathite and the presence of a deep transverse groove on the second abdominal somite. There would seem to be little doubt that the *P. hypsinotus* group is monophyletic, characterized by the prehensile structure of the third and fourth pereopods in functional males and the spinose appendix interna of the first pleopod in functional males. The presence of the mesial spine on the carpi of the third and fourth pereopods and elongate appendix masculina of the male second pleopod, which also represent apopmorphic states, suggest a close relationship of the *P. stenolepis* group to the *P. hypsinotus* group. However, monophyly of the former group remains unknown because no unqiue feature for it could be found. The *P. montagui* group appears to be an assemblage of presumably ancient species and also lacks a synapomorphy.

The following characters are considered useful to distinguish closely related species: relative length of the rostrum, though ratios may partially overlap; number of teeth or spines of the rostrum; position of the posteriormost spine on the carapace; number of dorsolateral spines on the telson; relative length and armament of the dactyl of the third and fourth pereopods; relative length of the merus of the third pereopod. In addition, the colour patterns of the living animals appear to be very constant and diagnostic.

Other than the usual growth change of the anterior two pairs of pleopods, the third and fourth pereopods show noticeable sexual dimorphism in the *P. hypsinotus* group. Species of the group have a noticeably prehensile third pereopod and a weakly prehensile fourth pereopod in functional males; the third pereopod exhibits more noticeable morphological difference than the fourth pereopod. The propodi bear a set of numerous spinules, arranged irregularly in two to five rows, on at least the distal third of the flexor surface; the propodus of the third pereopod is often weakly curved, with a convex flexor margin. In females, the third pereopod is only weakly prehensile and the fourth pereopod is nearly simple or weakly prehensile; the propodus is straight, bearing fewer spinules than in functional males. Further, the propodi of the third and fourth pereopods in females sometimes have scattered spinules on the lateral, dorsal and mesial surfaces. The dactyls of the third pereopod may become proportionally shorter from male to female.

Key to species of *Pandalus*

In the following key, non-dichotomous characters, that help to identify the species, are inserted with brackets.

1a Integument of carapace partially or entirely pubescent; stylocerite of antennule triangular; [carpi of third to fifth pereopods without mesial spine] 2

1b Integument of carapace naked (except for *P. stenolepis*); stylocerite of antennule rounded 3

2a Stylocerite acutely pointed, reaching distal margin of proximal segment of antennular peduncle; scaphocerite with distolateral tooth reaching or over-reaching distal margin of blade . . . . *P. platyceros*
[Northeastern Pacific: from Unalaska, Alaska to San Diego, California]

2b Stylocerite triangular with blunt apex, falling far short of distal margin of proximal segment of antennular peduncle; scaphocerite with distolateral tooth far exceeded by distal margin of blade . . . . *P. latirostris*
[Northwestern Pacific: from Southeast Siberia to northern Japan and Korea]

3a Carpi of third and fourth pereopods without mesial spine; rostrum with posteriormost ventral tooth weaker or subequal in size to preceding tooth 4

3b Carpi of third and fourth pereopods with mesial spine; rostrum with posteriormost ventral tooth distinctly stronger than preceding tooth 9

4a Third abdominal somite obtusely carinate or with prominent median projection on dorsal surface 5
4b Third abdominal somite smooth on dorsal surface 8

5a Rostrum with movable dorsal spines distal to mid-length, ventral blade little developed with peak at second posteriormost tooth; dactyls of the third and fourth pereopods slender, slightly twisted, without accessory spinules on distal half of flexor margin
5b Rostrum without movable dorsal spine distal to midlength, ventral blade well developed with peak at posteriormost tooth; dactyls of third and fourth pereopods not twisted, with accessory spinules on distal half of flexor margins; [third abdominal somite with prominent median projection . . . . *P. goniurus*
[Northern North Pacific including Chukchi Sea, Vladivostok in Sea of Japan to Puget Sound, Washington State]

6a Third abdominal somite without prominent median projection; fourth abdominal somite with posterodorsal margin unarmed . . . . *P. jordani*
[Northern Pacific: from Unalaska, Aleutian to San Nicholas Island, California]
6b Third abdominal somite with prominent median projection; fourth abdominal somite with posterodorsal margin bearing median tooth 7

7a Rostrum usually less than 1.6 times as long as carapace; median projection on third abdominal somite obtuse . . . . *P. borealis*
[North Atlantic: Barents Sea to North Sea; western Greenland to Gulf of Maine]
7b Rostrum usually more than 1.6 times as long as carapace; median projection of third abdominal somite acute or subacute . . . . *P. eous*
[Northern North Pacific: from Sea of Japan to off Columbia River mouth, North America]

8a Rostrum usually less than 1.5 times as long as carapace; dactyls of third and fourth pereopods more than 0.25 times as long as propodi; body with red stripes in life . . . . *P. montagui*
[North Atlantic]
8b Rostrum more than 1.5 times as long as carapace; dactyls of third and fourth pereopods less than 0.25 times as long as propodi; body without red stripes in life . . . . *P. tridens*
[Northern North Pacific: from Hokkaido, Japan to San Nicholas Island, California]

9a Carapace with patch of pubescence on cardiac region; scaphocerite with distal blade narrow, obliquely truncate . . . . *P. stenolepis*
[Northeastern Pacific: from Unalaska Island, Alaska to Hecata Bank, Oregon]
9b Carapace without patch of pubescence on cardiac region; scaphocerite with distal blade relatively broad, rounded distally 10

10a Dactyl of third and fourth pereopod slender, without accessory spinules on distal half of flexor margin . . . . *P. curvatus* sp. nov.
[Northwestern Pacific: Amakusa-nada, southern Japan]
10b Dactyl of third and fourth pereopod moderately stout, with accessory spinules on distal half of flexor margin 11

11a Dorsal spines on carapace and rostrum not elongate 12
11b Dorsal spines on carapace and rostrum noticeably elongate, giving comb-like appearance; [postrostral ridge of carapace highly elevated with strongly convex dorsal profile in lateral view] 18

12a Rostrum and carapace with 14 or less dorsal spines 13
12b Rostrum and carapace with more than 14 dorsal spines 16

13a Rostrum with posterior three ventral teeth noticeably elongate; left second pereopod over-reaching distal margin of scaphocerite by full length of carpus; right second pereopod over-reaching distal margin of scaphocerite by length of chela and half of carpus . . . . *P. formosanus* sp. nov.
[Northwestern Pacific: NE Taiwan]

13b Rostrum with posterior three ventral teeth moderately long; left second pereopod over-reaching distal margin of scaphocerite only by part of carpus; right second pereopod over-reaching distal margin of scaphocerite by length of chela . . . 14

14a Posteriormost dorsal spine on carapace arising anterior to level of mid-length of carapace; merus of third pereopod 1.0–1.3 times as long as carapace . . *P. prensor*
[Northwestern Pacific: Russian Far East, Korea, northern Japan]
14b Posteriormost dorsal spine on carapace arising posterior to level of mid-length of carapace; merus of third pereopod 0.9–1.0 times as long as carapace 15

15a Rostrum less than 1.6 times as long as carapace, ventral margin with six or less than six teeth; scaphocerite 5.3–5.7 times as long as wide . . . . *P. danae*
[Northeastern Pacific: from Resurrection Bay, Alaska, to Point Loma, California]
15b Rostrum more than 1.6 times longer than carapace, ventral margin with more than six teeth; scaphocerite 6.4–7.3 times as long as wide . . . . *P. gurneyi*
[Eastern Pacific: California to Baja California]

16a Carapace with five to seven dorsal spines posterior to level of orbital margin, posteriormost spine arising anterior to level of mid-length of carapace; [large species, attaining 35 mm in CL] . . . . *P. nipponensis*
[Northwestern Pacific: Pacific coast of Honshu to Kyushu, Japan]
16b Carapace with eight or more dorsal spines posterior to level of orbital margin, posteriormost spine arising posterior to level of mid-length of carapace 17

17a Rostrum usually less than 1.3 times as long as carapace, with seven or less ventral teeth; postrostral ridge on carapace not crested in adults; relatively small species attaining 17.3 mm in CL . . . . *P. gracilis*
[Northwestern Pacific: Sea of Japan, Pacific coast of northern Japan]
17b Rostrum more than 1.3 times as long as carapace, with more than seven ventral teeth; postrostral ridge on carapace highly crested in adults; large species attaining 48.0 mm in CL . . . . *P. hypsinotus*
[Northern North Pacific: from Korean Strait to Puget Sound, including Bering Sea]

18a Rostrum and carapace with 17–21 dorsal spines, 8–11 of them posterior to level of orbital margin; intermediate segment of antennular peduncle armed with some slender spines on dorsal surface . . . . *P. teraoi*
[Northwestern Pacific: Southwestern Japanese Pacific coast]
18b Rostrum and carapace with 10–12 dorsal spines, seven of them posterior to level of orbital margin; intermediate segment of antennular peduncle unarmed on dorsal surface . . . . *P. chani* sp. nov.
[Northwestern Pacific: NE Taiwan]

***Pandalus montagui* group**

Diagnosis. Body slender, integument thin, glabrous. Rostrum with posteriormost ventral tooth not stronger than preceding teeth. Second abdominal somite with shallow transverse groove on tergum. Antennule with broadly rounded, semicircular stylocerite. Antennal basicerite without intercalated process. Posterior lobe of scaphognathite produced, but not noticeably elongate. Right second pereopod with carpus divided into more than 15 articles; merus with few annulations distally. Third to fifth pereopods slender, fourth and fifth pereopods subequal in length to third pereopod; third and fourth pereopods never prehensile in either sex, propodus each with single row of spinules flanked by rows of moderately long or long spines on flexor surface; carpi of third to fifth pereopods lacking mesial spine, mesial surface with two rows of spinules in third pereopod. Endopod of first pleopod in functional male with appendix interna not inflated, unarmed. Appendix masculina in functional males shorter than appendix interna, with several long spines distally.

Remarks. No apomorphic character state has been identified for this group. Although this group appears to be paraphyletic, it is established for convenience of discussion. This group contains the following six species: *P. montagui* Leach, 1814; *P. borealis* Krøyer, 1838; *P. goniurus* Stimpson, 1860; *P. jordani* Rathbun, 1902; *P. tridens* Rathbun, 1902; and *P. eous* Makarov, 1935.

Pandalus montagui Leach, 1814
(figures 1–3)

Pandalus montagui Leach, 1814: 432 [type locality: Shetland Islands]; Calman, 1899: 30, pls 1–4, fig. 1; Kemp, 1910; 86, pl. 10, fig. 8; Dons, 1915: 20; De Man, 1920: 103.

Pandalus annulicornis Leach, 1815: pl. 11; Latreille, 1818: pl. 322, fig. 1–4; Lamarck, 1818: 203; Desmarest, 1825: 220, pl. 38, fig. 2; H. Milne Edwards, 1837: 384; Krøyer, 1845: 469; 1846: pl. 6, fig. 3a–e; Bell, 1853: 297, unnumbered fig.; Ortmann, 1890: 491; Doflein, 1900: 320 (part); Appellöf, 1906: 117; Brashnikov, 1907: 103, fig. 11k, 1; Wollebaek, 1908: 63, figs 5 and 6.

?*Pandalus levigatus* Stimpson, 1854: 58 [type locality: Grand Manan, New Brunswick].

Pandalus leptorhynchus Kinahan, 1858: 80, fig. [type locality: Dublin Bay]; Ortmann, 1890: 492; Sars, 1882: 47, pl. 1, figs 8–10. [Not *Pandalus leptorhynchus* Stimpson, 1860].

Pandalus montagui: Hansen, 1908: 72; Grieg, 1926: 10; Rathbun, 1929: 8; Stephensen, 1939: 21; Holthuis, 1950: 28, fig. 8; Squires, 1957: 470; Holthuis and Rosa, 1965: 14; Squires, 1965: 62; Couture and Trudel, 1968: 863, fig. 4; Simpson *et al.*, 1970: 1230; Scrivener and Butler, 1971: 37 (bibliography); Smaldon, 1979: 94, fig. 39; Holthuis, 1980: 141; Rothlisberg, 1980: 19; Williams, 1984: 154, fig. 108; Williams *et al.*, 1989: 19; Squires, 1990: 245, figs 133 and 134, pl. 5a; Smaldon, 1993: 106, fig. 40; Komai, 1995: 258, fig. 190.

Not *Pandalus annulicornis*: Brandt, 1851: 124; Richters, 1884: 405; Doflein, 1902: 635. [= *Pandalus tridens* Rathbun, 1902].

Material examined. **Greenland**. Baffin Bay, 68°05.7′N, 54°55.7′W, 45–47 m; RV *Shinkai-Maru*, stn T-136; 30 August 1991; trawl; coll. H. Endo; 1 juvenile (CL 4.5 mm), 1 male (CL 7.8 mm); HUMZ-C 1299.

Netherlands. Texel Stroom; 8 April 1991; 5 transitional males (CL 9.8–10.8 mm); CBM-ZC 3422.

British Isles. Mull of Kintyre, Scotland, 117 m; 21 March 1888; coll. J. Murray; 1 functional male (CL 12.1 mm), 21 transitional males (CL 8.2–13.2 mm), 9 females (CL 10.9–15.0 mm), 7 ovigerous females (CL 10.0–15.2 mm); NHM 1894.9.26.60–75.

Type material. The lectotype from Zetland (Shetland Islands) is deposited in the Natural History Museum, London (Dry 267d, Leach cabinet no. 29) (Simpson *et al.*, 1972). Not examined.

Description. Rostrum (figure 1A, B) moderately curving dorsally, distinctly over-reaching scaphocerite, 1.02–1.55 times longer than carapace; dorsal margin nearly straight over eyes, armed with 10–12 spines, including four to six on carapace posterior to level of orbital margin, and one or two teeth near apex of rostrum, subdistal 0.5–0.6 length unarmed, anteriormost spine arising from anterior to level of distal margin of antennular peduncle, posteriormost spine arising from 0.43–0.50 of carapace length; ventral margin armed with five to seven teeth, posteriormost tooth subequal in size to preceding tooth, blade well developed, with peak at posteriormost tooth; lateral carina rather blunt over entire length, not extending posteriorly to gastric region. Carapace (figure 1A) with postrostral ridge low, extending to 0.6 length of carapace; dorsal margin of carapace nearly straight or faintly convex in lateral view.

Abdomen (figure 1C) with third somite devoid of median projection, postero-dorsal margin moderately produced posteriorly, rounded; fourth somite unarmed

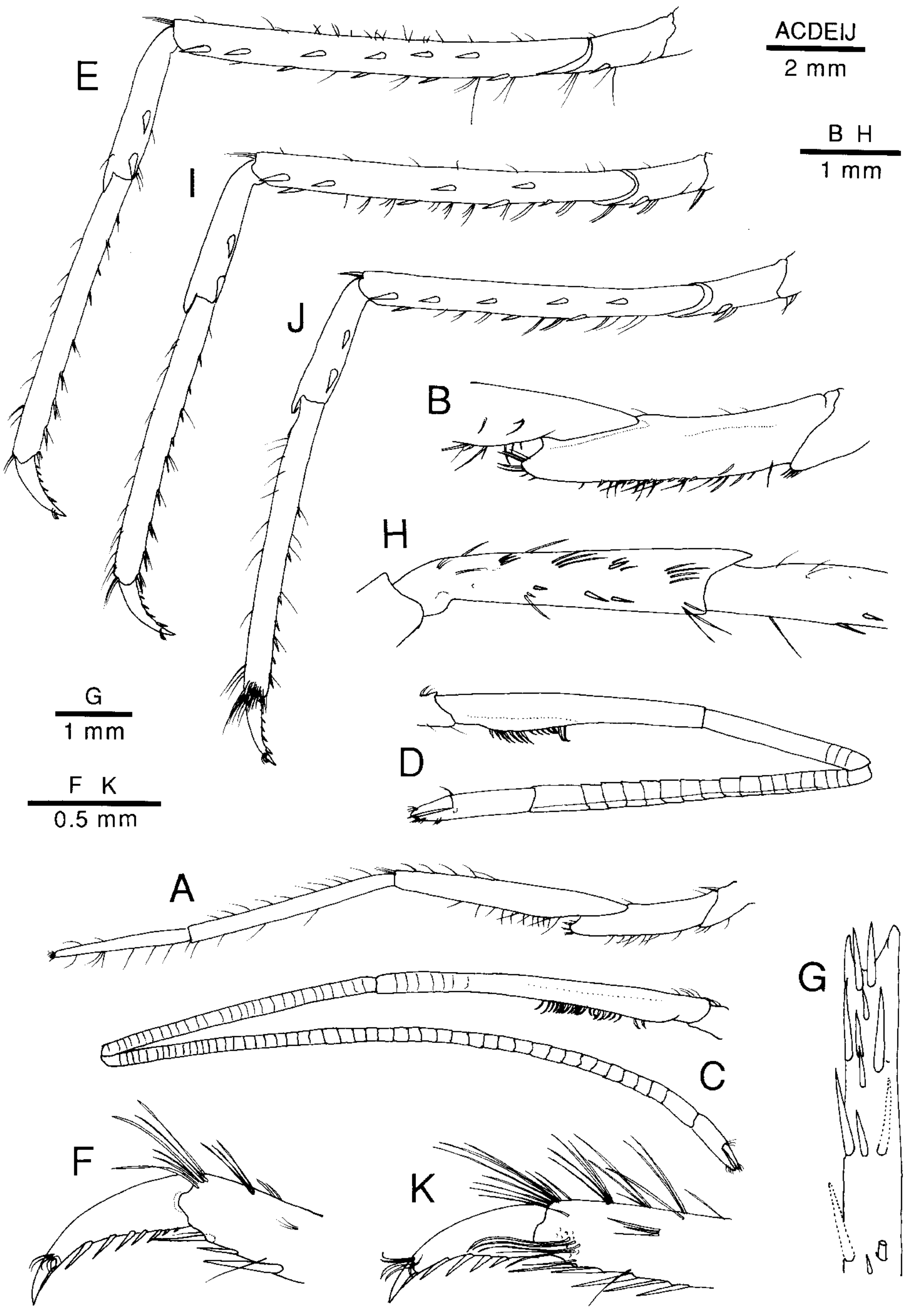


FIG. 3. *Pandalus montagui* Leach, 1814. Transitional male (CL 10.5 mm), Texel Stroom, Netherlands; CBM-ZC 3422. (A) Left first pereopod, lateral; (B) same, ichium, lateral; (C) left second pereopod, lateral; (D) right second pereopod, lateral; (E) left third pereopod, lateral; (F) same, dactyl, lateral; (G) same, distal part of propodus, flexor; (H) same, carpus and proximal part of propodus, mesial; (I) left fourth pereopod, lateral; (J) left fifth pereopod, lateral; (K) same, dactyl, lateral.

posterodorsally; sixth somite 0.6–0.7 times as long as carapace and 1.8–2.4 times as long as proximal depth. Telson (figure 1D) moderately broad, armed with six dorsolateral spines on either side.

Eye (figure 1F) broadly subpyriform.

Antennular peduncle (figure 1G) reaching mid-length of scaphocerite; intermediate segment without spines on dorsal surface. Scaphocerite (figure 1H) 0.9–1.0 times as long as carapace and 4.7–5.3 times as long as wide, lateral margin nearly straight, distolateral tooth just reaching or slightly over-reaching distal margin of moderately broad, rounded blade.

Third maxilliped (figure 2H) reaching or slightly over-reaching distal end of scaphocerite.

First pereopod (figure 3A) slightly falling short of or reaching beyond scaphocerite. Left second (figure 3C) pereopod over-reaching scaphocerite by length of chela and distal 0.6 of carpus; carpus divided into about 60–80 articles; dactyl distinctly shorter than palm. Right second pereopod (figure 3D) over-reaching scaphocerite by length of chela; carpus divided into 18–25 articles; dactyl distinctly shorter than palm. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 3E) over-reaching scaphocerite by length of dactyl and distal 0.3 of propodus; dactyl (figure 3F) moderately short, 0.23–0.29 times as long as propodus, not twisted, with five to seven accessory spinules over entire length of flexor margin; propodus (figure 3G) with moderately long flexor spines, lateral surface not spinose in either sex; carpus (figure 3H) with two or three (rarely four) lateral spines, mesial surface with few scattered spinules; merus 0.9–1.0 times as long as carapace, armed with five to seven lateral spines and four to seven (usually five or six) ventral or ventromesial spines. Fourth pereopod (figure 3I) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus with fewer spinules; merus 0.8–0.9 times as long as carapace, armed with six or seven lateral and four to six ventral or ventromesial spines. Fifth pereopod (figure 3J) slightly falling short of anterior margin of scaphocerite; dactyl (figure 3K) 0.14–0.22 times as long as propodus, armed with five or six (rarely seven) accessory spinules on flexor margin; carpus with two or three lateral spines; merus 0.8 times as long as carapace, with five to eight lateral and two to four ventral or ventromesial spines.

Endopod of first pleopod of functional males (figure 2L) with only weakly produced appendix interna, not reaching distal margin of distal lobe; mesial margin weakly sinuous, with row of small spines distal to mid-length; lateral margin generally convex. Appendix masculina of second pleopod in functional males (figure 2M) nearly equal in length to appendix interna, armed with about six to nine long spines dorsally and distally.

Colour. Smaldon (1979) described as follows: 'Usually semi-translucent, with red chromatophores giving overall pink colour, often with oblique red lines on carapace, becoming more horizontal on abdomen.' In addition, according to Squires's colour photograph (1990: pl. 5, figure a), the antennal flagellum is banded with red and white.

Distribution. Boreo-arctic: Greenland to Rhode Island; Iceland; northern Europe including British Isles; 5–790 m.

Remarks. This species is very similar to *P. tridens*. The number of subdistal teeth of the rostrum, used by Rathbun (1902a, 1904) and Butler (1980) to distinguish *P. tridens* from *P. montagui*, is found to be variable in the present specimens of both species. Nevertheless, as discussed by Butler (1980), *P. montagui* differs from

P. tridens in the relatively shorter rostrum and the relatively longer dactyls of the third and fourth pereopods, as well as the live coloration (see 'Remarks' under account of *P. tridens*).

Pandalus levigatus Stimpson, 1854, described from Grand Manan, New Brunswick, has generally been considered as a junior subjective synonym of *P. montagui* (see Ortmann, 1890; Holthuis, 1980; Williams, 1984). The type was perhaps destroyed in the Chicago fire of 1871 (Evans, 1967). From the brief original description, the colour pattern of *P. levigatus* appears to be similar to that of *P. montagui*, though the colour of stripes is different. Stimpson (1854) described the colour of *P. levigatus* as 'usually very pale yellow, with narrow blue lines on the back'. *Pandalus montagui* has red stripes on translucent background. So far, it is impossible to know what species was actually represented by the type specimen of *P. levigatus*, and therefore, *P. levigatus* is questionably considered conspecific with *P. montagui*. *Pandalus leptorhynchus* Kinahan, 1858, was considered to be founded on a specimen of *P. montagui* with an abnormally short rostrum (Calman, 1899; Kemp, 1910). No information about the type of this taxon has been obtained. From the original description, there is little doubt that *P. leptorhynchus* is conspecific with *P. montagui*, and I follow the previous authors in regarding *P. leptorhynchus* as a junior subjective synonym of *P. montagui*.

Although Gurney (1939) suggested that *Boreocaris moebiusi* Ortmann, 1893, might be the larva of *Pandalus montagui*, Pike and Williamson (1964) denied this possibility. They suggested affinities of the former with the larvae of *Caridion* (Hippolytidae) in the form of the rostrum, the expanded endopod of the first pereopod and the number of thoracic exopods. Despite the suggestion by Pike and Williamson, Holthuis (1993) still included *Boreocaris* in the synonymy of *Pandalus*, without comment. Review of the previously described larval forms is beyond the scope of this study, and I follow the opinion of Pike and Williamson (1964) in excluding *Boreocaris moebiusi* from the synonymy of *Pandalus montagui*.

Pandalus borealis Krøyer, 1838
(figures 4 and 5)

Pandalus borealis Krøyer, 1838: 254 [type locality: Sydprøven, Julianehaab and Fiskenaesset, Greenland]; 1846: pl. 6, fig. 2a–o; Smith, 1879: 86; Ortmann, 1890: 492; Doflein, 1900: 321; Sars, 1900: 31, pls 9, 10; Appellöf, 1906: 117; Hansen, 1908: 70; Wollebaek, 1908: 44, figs 3 and 4, pl. 11; Birula, 1910: 37; Dons, 1915: 22; De Man, 1920: 103 (part); Grieg, 1926: 9; Rathbun, 1929: 8, fig. 4; Stephensen, 1935: 27; 1939: 20; Holthuis, 1950: 31, fig. 9; Holthuis and Rosa, 1965: 13 (part); Squires, 1965: 54; Couture and Trudel, 1968: 863, fig. 3; Scrivener and Butler, 1971: 36 (part; bibliography); Christiansen, 1972: 29, fig. 25; Smaldon, 1979: 92, figs 35B and 38A; Holthuis, 1980: 138 (in part); Rothlisberg, 1980: 19 (part); Takeda, 1982: 18, fig. 52 (part); Williams, 1984: 151, fig. 107; Dore and Frimodt, 1987: 112, unnumbered fig.; Williams *et al.*, 1989: 19 (part); Squires, 1990: 239, figs 130–132; Komai, 1991: 73 (part), fig. 5; Squires, 1992: 257, figure 1a, c, e; Smaldon, 1993: 104, fig. 39; Komai, 1995: 254, fig. 189; Fransen *et al.*, 1997: 155.

Dymas typus Krøyer, 1861: 63 [type locality: ?].

Pandalus borealis v. *edenticulatus* Retowsky, 1946: 300, fig. 2 [type locality: Arctic Ocean].

Not *Pandalus borealis*: Brandt, 1851: 122; Thallwitz, 1891: 4; Rathbun, 1904: 35; Parisi, 1919: 69; Rathbun, 1929: 8, fig. 8; Berkeley, 1930: 5, figs 1B and 16A–E; Yokoya, 1933: 15; 1934; 14; 1939: 263; Yoshida, 1941: 23, pl. 5 fig. 2; Urita, 1942: 3; Kubo, 1960: 104, pl. 53 fig. 4; Miyake *et al.*, 1962: 123; Butler, 1964: 1419; Kubo, 1965: 610, fig. 955; Igarashi, 1969: 2, pl. 1, fig. 2, pl. 13, fig. 36; Kim and Park, 1972: 204; Motoh, 1972: 44, pl. 10 figs 3, 4; Squires and Figueira, 1974: 14; Miyake, 1975: 100, unnumbered fig. 309; Hayashi, 1976; 19; Kim, 1976: 144; 1977; 285, pl. 28 fig. 57a, b, text-figs 118, 121, 122; Butler, 1980;

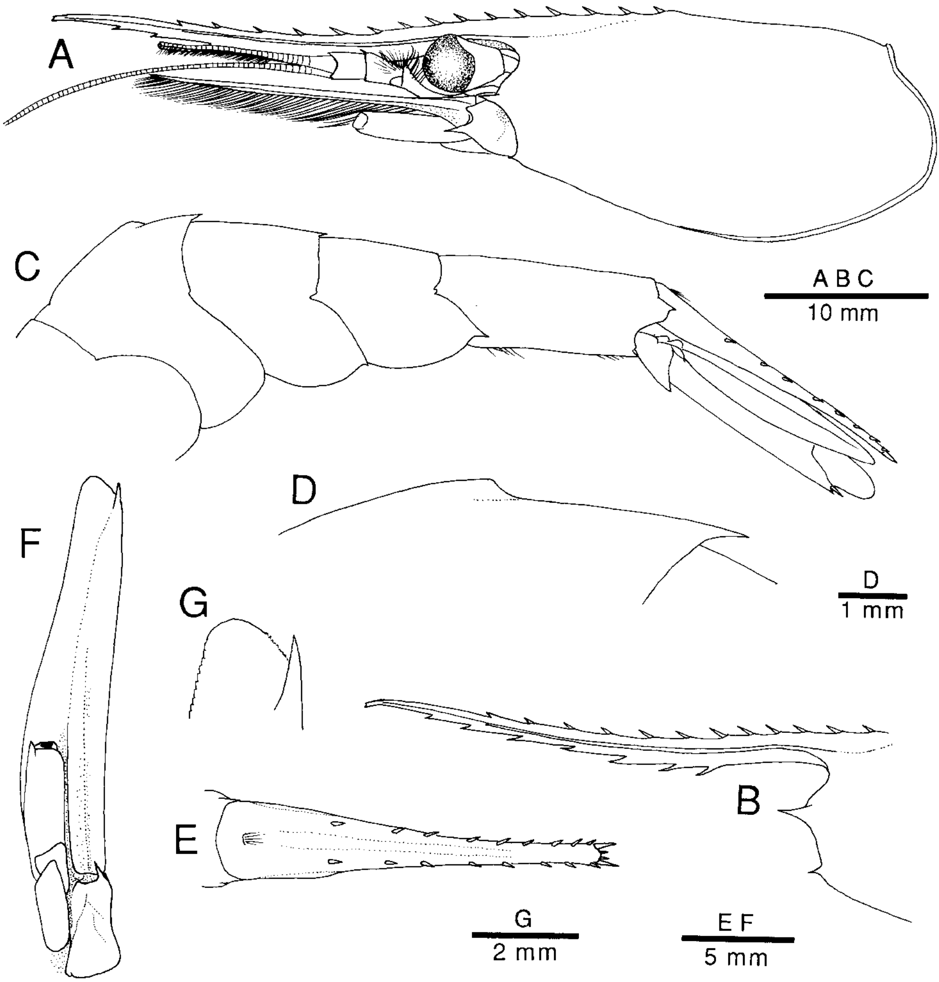


FIG. 4. *Pandalus borealis* Krøyer, 1838. Functional male (CL 21.0 mm), Baffin Bay, west of Greenland, HUMZ-C 1509. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropods, lateral, pleopod omitted; (D) median projection on third abdominal somite, lateral; (E) telson, dorsal; (F) left antenna, ventral, setae omitted; (G) distal part of scaphocerite, ventral, setae omitted.

128, unnumbered fig.; Miyake, 1982: 59, pl. fig. 1; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313. [=*Pandalus eous* Makarov, 1935].

Material examined. **Greenland**. Off east coast of Greenland, 71°35′N, 18°41′W, 560–575 m; 30 September 1989; trawl by RV *Shinkai-Maru*; coll. F. Muto; 1 female (CL 32.0 mm); HUMZ-C 1162. Baffin Bay, 64°58.5′N, 55°07.8′W, 698 m; September 1990; otter trawl by RV *Shinkai-Maru*; coll. E. Mihara; 10 males (CL 14.4–22.6 mm), 2 females (CL 26.0, 26.6 mm); HUMZ-C 1252. Baffin Bay, 66°26.6′N, 56°25.2′W, 338–350 m; 18 August 1991; trawl by RV *Shinkai-Maru*; coll. H. Endo; 4 males (CL 17.6–21.0 mm); HUMZ-C 1509.

Type material. The type could not be located in the collection of the Zoologisk Museum, University of Copenhagen (N. L. Bruce, personal communication). It is

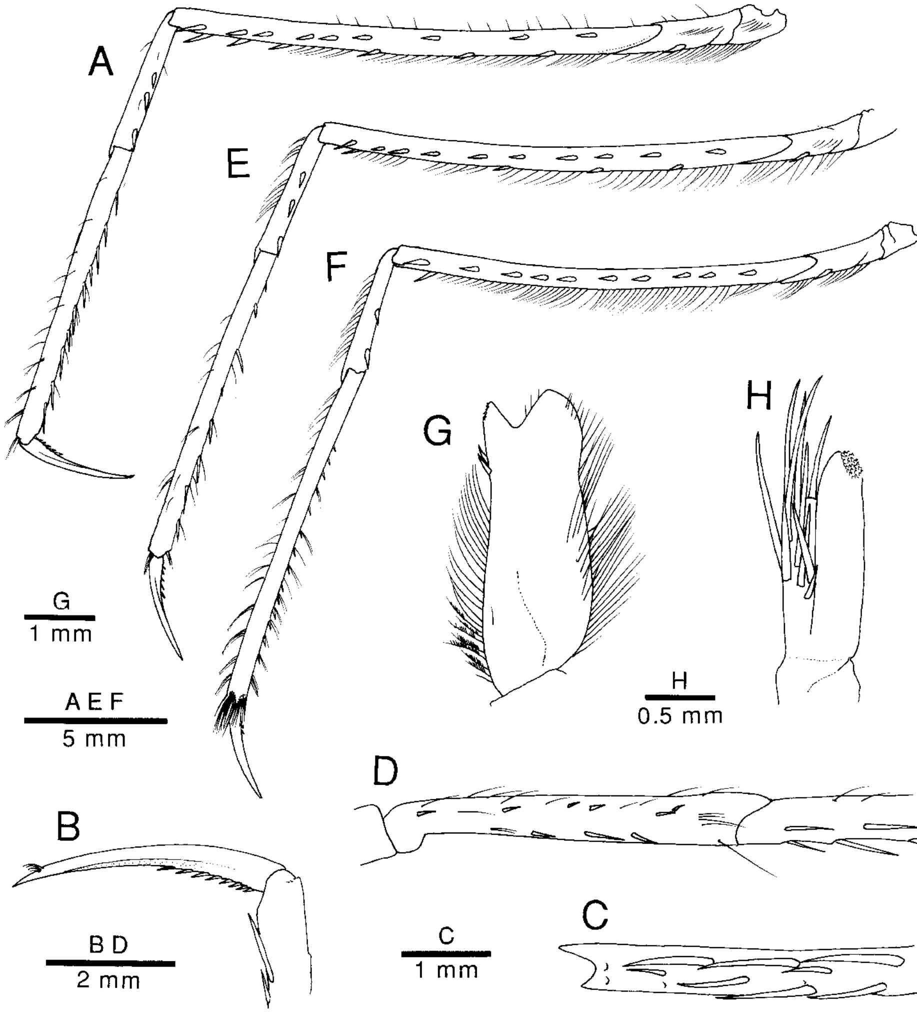


FIG. 5. *Pandalus borealis* Krøyer, 1838. Functional male (CL 21.0 mm), Baffin Bay, west of Greenland, HUMZ-C 1509. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) endopod of left first pleopod, ventral; (H) appendix masculina and interna of left second pleopod, mesial.

possible that the type deposited in the Zoologisk Museum was lost. Prof. L. B. Holthuis kindly informed me that there are two dry specimens of *Pandalus borealis* received from the Copenhagen Museum, under the name of '*Pandalus borealis* Krøyer', from Greenland, in the collection of the Nationaal Natuurhistorisch Museum, Leiden. This material was sent by D. F. Eschricht of the Copenhagen Museum to Leiden on 30 April 1838. As this is the same year when Krøyer described the species, it is highly possible that these specimens are syntypes, although they were not indicated as such (L. B. Holthuis, personal communication). From the photograph kindly provided by C. H. J. M. Fransen, I confirmed the identity of these putative types with *P. borealis*.

Description. Rostrum (figure 4A, B) weakly or moderately curving dorsally, far over-reaching distal end of scaphocerite, 1.13–1.60 (rarely 0.70) times longer than carapace; dorsal margin slightly convex over eyes, armed nearly throughout length with 15–17 spines or teeth, more widely spaced anteriorly, including three to five (usually four) on carapace posterior to level of orbital margin, subdistal one or two without complete basal suture, posteriormost spine arising from 0.34–0.39 of carapace length; one small tooth near apex; ventral margin armed with seven to nine teeth, posteriormost tooth subequal to or weaker than preceding one, ventral blade weakly developed; lateral carina conspicuous over entire length, not extending posteriorly to gastric region. Carapace (figure 4A) with postrostral ridge low, extending posteriorly to midlength of carapace; entire dorsal margin slightly convex in lateral view, with peak at posteriormost median spine.

Abdomen (figure 4C) with third somite bearing obtuse median projection, posterodorsal margin produced into acute tooth (figure 4D); fourth somite with small posterodorsal median tooth; sixth somite 0.6–0.7 times as long as carapace and 2.1–2.4 times longer than proximal depth. Telson (figure 4E) narrow, armed with 7–10 dorsolateral spines on either side.

Eye (figure 4A) broadly subpyriform.

Antennular peduncle (figure 4A) reaching mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antennal scaphocerite (figure 4F) 0.8–1.0 times as long as carapace and 4.7–5.3 times longer than wide, lateral margin nearly straight or slightly sinuous; distal blade (figure 4G) produced distomesially or rounded, usually exceeding distolateral tooth.

Third maxilliped reaching or slightly over-reaching anterior margin of scaphocerite.

First pereopod slightly falling short of or reaching distal end of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.6 of carpus; carpus divided into about 60–80 articles. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 25–30 articles. Third to fifth pereopods slender, subequal in length. Third pereopod (figure 5A) over-reaching scaphocerite by length of dactyl and distal 0.25–0.3 of propodus; dactyl (figure 5B) slender, 0.34–0.40 times as long as propodus, weakly twisted, somewhat flattened dorsoventrally in distal half of length, bearing 8–10 accessory spinules on proximal 0.4 of flexor margin; propodus (figure 5C) with elongate flexor spines, lateral surface not spinose in either sex; carpus (figure 5D) with two or three lateral spines, mesial surface with spinules arranged in double row; merus 0.8–0.95 times as long as carapace, armed with 7–11 lateral spines and five to seven ventral or ventromesial spines. Fourth pereopod (figure 5E) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus with fewer spinules. Fifth pereopod (figure 5F) over-reaching scaphocerite by tip of dactyl; dactyl 0.23–0.28 times as long as propodus, armed with six or seven accessory spinules on proximal 0.5 of flexor margin; carpus with one or two lateral spines; merus 0.7–0.9 times as long as carapace, with 7–11 lateral and one ventromesial spine.

Endopod of first pleopod of functional males (figure 5G) with well-differentiated appendix interna, separated from distal lobe of endopod by deep U-shaped notch, not reaching distal margin of distal lobe; mesial margin weakly sinuous, with few small spines somewhat proximal to base of appendix interna; lateral margin sinuous. Appendix masculina of second pleopod in functional males (figure 5H) distinctly shorter than appendix interna, armed with about 10 long spines dorsally and distally.

Colour. Entire body and appendages with fine red spots, closer on telson and uropods; antennular flagella obscurely banded with narrow white and broad red rings. Komai (1995: 254) published a colour photograph of this species.

Size. Functional males: 14.4–22.6 mm; females: 26.0–32.0 mm.

Distribution. Arctic boreal: Greenland southward to Martha's Vineyard, Massachusetts; Iceland; Novaya Zemlya, Franz Joseph Land and Spitzbergen, southward to northern Europe including British Isles; 30–1150 m.

Remarks. *Pandalus borealis* is very similar to the Pacific counterpart, *P. eous*. As Squires (1992) indicated, the relatively shorter rostrum, more obtuse median projection on the third abdominal somite and relatively smaller ventral teeth on the rostrum will distinguish *P. borealis* from *P. eous* (see 'Remarks' under account of *P. eous*).

Stephensen (1935) compared fragments of the unique type specimen of *Dymas typus* Krøyer, 1861, with larvae of *Pandalus borealis* from Greenland waters, and decided that Krøyer's specimen represented the fourth stage zoea of *P. borealis*. Following Stephensen, I treat *D. typus* as a junior subjective synonym of *P. borealis*. Retowsky (1946) recognized a new variety, *Pandalus borealis* var. *edenticulatus*, from the Arctic Ocean. No information about the type of this taxon has been obtained. From the original description, this form is characterized by the poorly developed ventral teeth of the rostrum and the fewer dorsal spines, which are absent from at least distal to the mid-length of the rostrum. However, such rostral armature is attributable to an abnormality in all probability, and Retowksy himself suggested that the morphology of the rostrum exhibited by his taxon possibly represents an aberration. Moreover, the specimens referred to the new variety were collected together with specimens of typical *P. borealis* (cf. Retowsky, 1946) from the same station (Ice-breaker 'G. Sedov', station 57). There would seem to be little doubt that Retowsky's taxon was founded on specimens of *P. borealis* with abnormal rostra.

Pandalus goniurus Stimpson, 1860
(figures 6 and 7)

Pandalus goniurus Stimpson, 1860: 105 [type locality: Avatska, Kamtchatka]; Rathbun, 1904: 38, pl. 1, fig. 3; Brashnikov, 1907: 103, fig. 11a–e; Rathbun, 1919: 3A; De Man, 1920: 103; Derjugin and Kobjakova, 1935: 142; Kobjakova, 1937: 102; Makarov, 1941: 113; Urita, 1941: 1, figs 1–5; 1942: 4, fig. 1; Kobjakova, 1955: 149, pl. 55, fig. 6; 1958: 222; Butler, 1964: 1441, fig. 27; Holthuis and Rosa, 1965: 14; Igarashi, 1969: 2, pl. 1, fig. 2, pl. 13, fig. 37; Scrivener and Butler, 1971: 37 (bibliography); Squires and Figueira, 1974: 15; Butler, 1980: 131, fig.; Holthuis, 1980: 139; Rothlisberg, 1980: 19; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al*., 1989: 19 (list); Komai *et al*., 1992: 192; Jensen, 1995: 54, fig. 100.

Pandalus dapifer Murdoch, 1884: 510 [type locality: 10 miles west of Point Franklin, Alaska]; 1885: 141, pl. 1, fig. 2–2c; Rathbun, 1899: 557.

Material examined. **Sakhalin**. Aniwa Bay, depth unknown; 17 October 1968; 9 females (CL 17.3–21.9 mm); HUMZ-C 438.

Siberia. Lebyazhiya Bay, Shantar Islands, nothern Okhotsk Sea, 10 m; 31 July 1995; beam trawl; coll. M. Yabe; 1 juv. (CL 5.8 mm); CBM-ZC 2413. Same locality, 23 m; 31 July 1995; beam trawl; coll. M. Yabe; 6 juv. (CL 11.0–11.5 mm), 4 males (CL 9.8–11.1 mm); CBM-ZC 2727.

Chukchi Sea. Off Cape Lisburne, depth unknown; July 1990; beam trawl by TS *Oshoro-Maru*; coll. M. Yabe; 15 males (CL 10.1–13.8 mm); CBM-ZC 952. Same locality, 69°40.8′N, 169°35.3′W; 26 July 1991; trawl by TS *Oshoro-Maru*; coll. M. Yabe; 1 male (CL 15.2 mm), 1 female (CL 18.1 mm); HUMZ-C 1367.

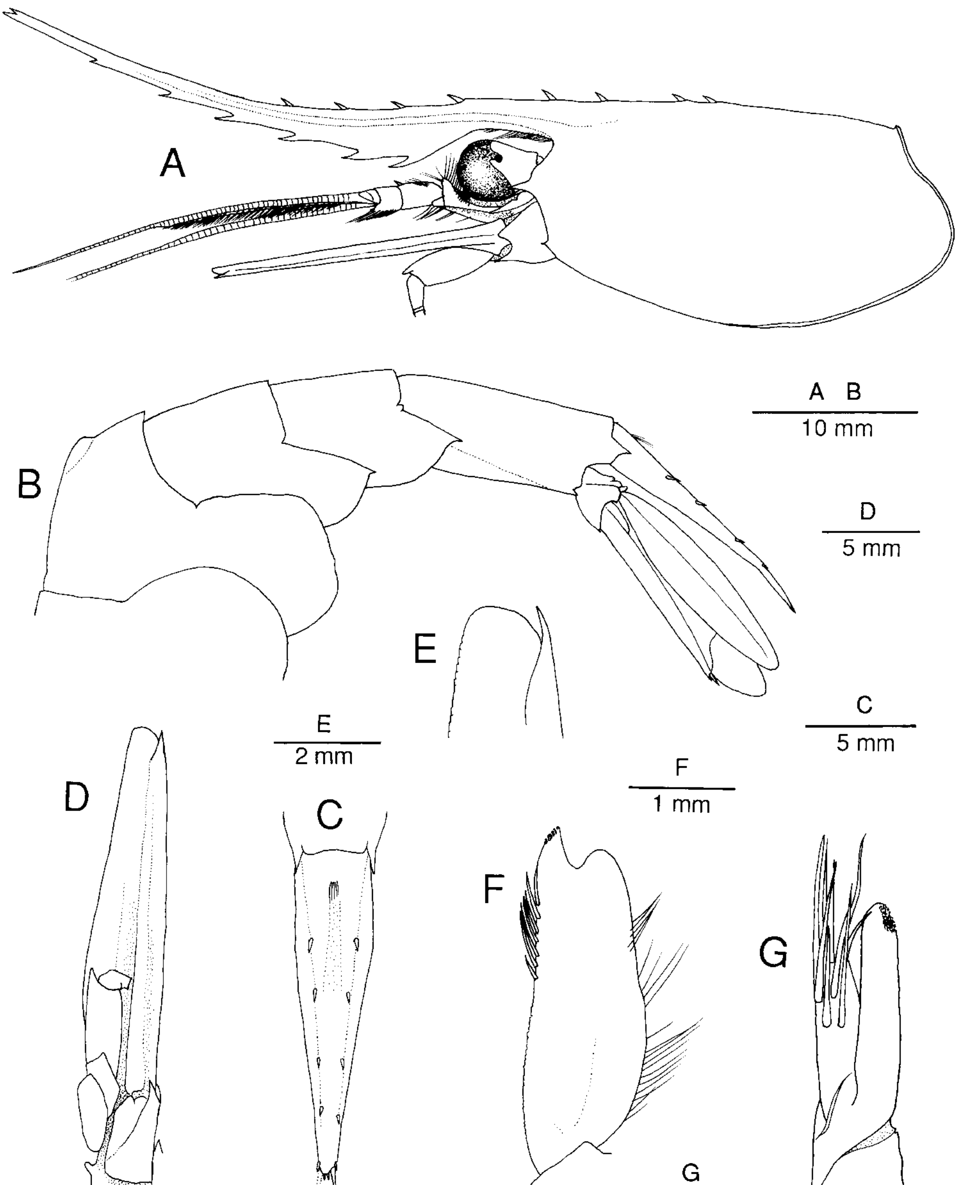


FIG. 6. *Pandalus goniurus* Stimpson, 1860. (A)–(E) female (CL 20.7 mm), Aniwa Bay, Sakhalin, HUMZ-C 438; (F)–(G) functional male (CL 7.9 mm), Shantar Islands, Okhotsk Sea, CBM-ZC 2727. (A) Carapace and cephalic appendages, lateral; (B) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (C) telson, dorsal; (D) left antenna, ventral, setae omitted; (E) distal part of scaphocerite, ventral, setae omitted; (F) endopod of left first pleopod, ventral; (G) appendix masculina and interna of left second pleopod, mesial.

Type material. The syntypes of *Pandalus goniurus* are still extant in the collection of the Natural History Museum, London: Avatska, Kamtchatka; two specimens; NHM No. 61.44 (Evans, 1967). Not examined.

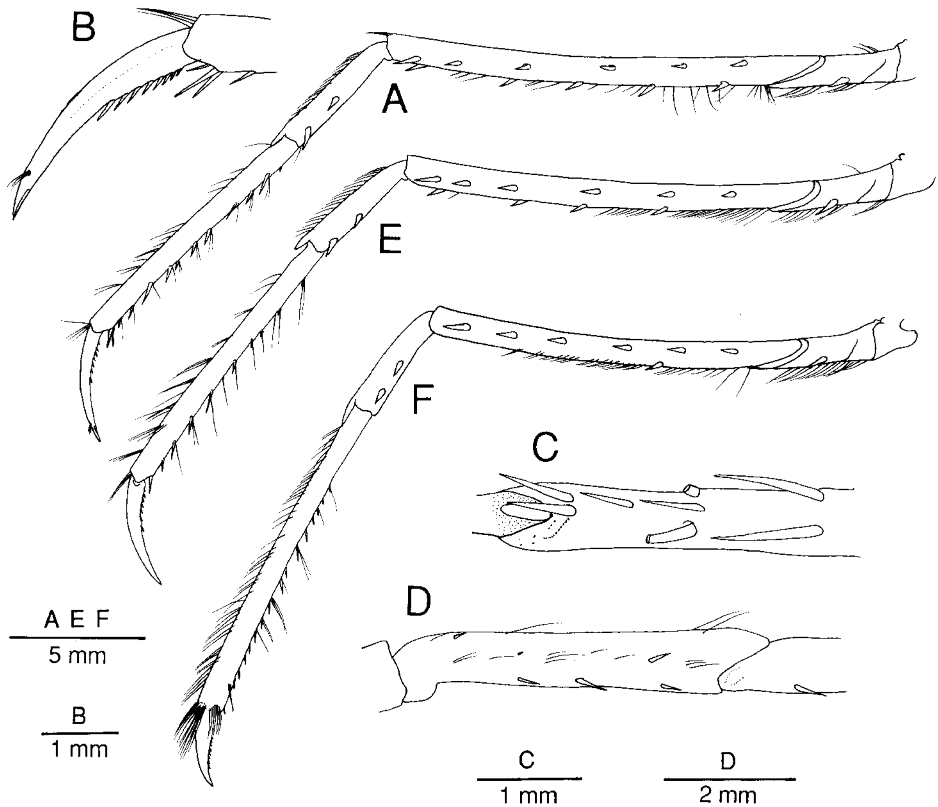


FIG. 7. *Pandalus goniurus* Stimpson, 1860. Female (CL 20.7 mm), Aniwa Bay, Sakhalin, HUMZ-C 438. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

Description. Rostrum (figure 6A) moderately curving dorsally, far over-reaching scaphocerite, 1.41–1.74 times as long as carapace; dorsal margin nearly straight over eyes, armed with 8–10 spines, including three (rarely four) on carapace posterior to level of orbital margin, and one tooth near apex of rostrum, subdistal 0.4–0.5 length unarmed, anteriormost spine arising from anterior to distal end of antennular peduncle, posteriormost spine arising from 0.43–0.46 of carapace length; ventral margin armed with six or seven teeth, posteriormost tooth subequal to or slightly weaker than preceding tooth; ventral blade well developed, becoming noticeably deeper with peak at posteriormost ventral tooth; lateral carina rather obtuse over entire length, not extending posteriorly to gastric region. Carapace (figure 6A) with postrostral ridge low, extending to midlength of carapace; dorsal margin slightly convex or nearly straight in lateral view.

Abdomen (figure 6B) with third somite bearing prominent but rounded median projection on strongly elevated dorsal surface in adults (> CL 15.2 mm), posterodorsal margin produced but rounded; fourth somite unarmed posterodorsally; sixth somite 0.6–0.7 times as long as carapace and 2.15–2.4 times as long as proximal depth. Telson (figure 6C) moderately broad, armed with five pairs of dorsolateral spines.

Eye broadly subpyriform (figure 6A).

Antennular peduncle (figure 6A) reaching mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antenna (figure 6D) with scaphocerite 0.8–1.0 times as long as carapace and 4.3–4.8 times as long as wide, lateral margin nearly straight, distolateral tooth (figure 6E) reaching distal margin of moderately broad, rounded blade.

Third maxilliped not reaching anterior margin of scaphocerite.

First pereopod somewhat falling short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.5–0.7 of carpus; carpus divided into about 50–60 articles. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 20–25 articles. Third to fifth pereopods relatively slender, subequal in length. Third pereopod (figure 7A) over-reaching scaphocerite by length of dactyl; dactyl (figure 7B) moderately stout, 0.35–0.41 times as long as propodus, not twisted, bearing six to eight accessory spinules on proximal 0.5–0.6 of flexor margin; propodus (figure 7C) with moderately long flexor spines, lateral surface not spinose in either sex; carpus (figure 7D) with two lateral spines, mesial surface with few spinules; merus 0.8–0.9 times as long as carapace, armed with six or seven (rarely eight) lateral spines and four to six ventral or ventromesial spines. Fourth pereopod (figure 7E) similar to third, reaching scaphocerite by tip of dactyl; mesial surface of carpus with few spinules. Fifth pereopod (figure 7F) not reaching scaphocerite; dactyl 0.2–0.3 times as long as propodus, armed with 6–10 accessory spinules on 0.6–0.7 of flexor margin; carpus with one or two lateral spines; merus 0.7–0.8 times as long as carapace, with six or seven lateral and one or two ventral or ventromesial spines.

Endopod of first pleopod of functional males (figure 6F) with well-differentiated appendix interna, separated from distal lobe of endopod by deep U-shaped notch, over-reaching distal margin of distal lobe; mesial margin weakly sinuous, with row of slender spines distal to mid-length; lateral margin slightly sinuous or generally convex. Appendix masculina of second pleopod in functional males (figure 6G) distinctly shorter than appendix interna, armed with about 10 long spines dorsally and distally.

Colour. Butler (1980) described it as follows: 'Background transparent to whitish; striping of red to orange dots on sixth abdominal somite dorsally and laterally, latter extending forward across lower parts of pleura of third to fifth somites; other oblique striping from dorsal surfaces of third to fifth somites extending to second pleuron; another stripe borders anterior margin of first somite. On carapace, red dots form oval outline on dorsal and lateral surfaces, dots of outline meet ventral margin adjacent to bases of all pereiopods, also along frontal margin from antennal spine to above orbit, along gastric region confluent with band of dots below six posterior dorsal spines on rostrum and carapace; another band extends along lower limb of rostrum from near base to tip; yellow patches on lateral surface. Groups of red dots on protopodites of pleopods; also scattered on telson and uropods, with large yellow spots on proximal parts of these appendages; yellow spots on each segment of third maxilliped, with red spots on distal segment; all pereiopods except II have red spots, with yellow spots on ischium of pereiopod I; also red banding on outer antennular flagellum; outer margin of antennal scale and basicerite marked with red'. The striped pattern of red dots is also observed in the material from the Chukchi Sea when preserved in formalin.

Size. Functional males: CL 10.1–15.2 mm; females: CL 17.3–21.8 mm.

Distribution. Chukchi Sea; Bering Sea to Puget Sound; Okhotsk Sea; Sea of Japan near Vladivostok; 5–450 m. There has been no certain record of this species from Japanese main islands, though Miyake (1982) listed it in his list of Japanese decapod Crustacea.

Remarks. The development of the median projection on the third abdominal somite changes with growth in this species. In young males or juvenile specimens examined (CL 5.8–13.8 mm), that projection is hardly discernible. It is distinct in the larger male and females (CL 15.2–21.9 mm), as illustrated (figure 6B).

The presence of a prominent median projection immediately separates *P. goniurus* from *P. montagui* and *P. tridens*. *Pandalus goniurus* further differs from *P. borealis*, *P. jordani* and *P. eous* in the relatively shorter, not twisted, dactyls of the third and fourth pereopods and the absence of dorsal spine or teeth from the distal half of the rostrum. It occupies an intermediate position between the two species, *P. montagui* and *P. tridens*, and the three species, *P. borealis*, *P. jordani* and *P. eous*, and will be easily recognized.

Rathbun (1904) reexamined the type material of *Pandalus dapifer* Murdoch, 1884, in the collection of the USNM, and synonymized that taxon with *P. goniurus*. From the original description, I am also confident that the two nominal taxa are conspecific. Therefore, *P. dapifer* should be treated as a junior subjective synonym of *P. goniurus*.

Pandalus jordani Rathbun, 1902
(figures 8 and 9)

Pandalus jordani Rathbun, 1902a: 900 [type locality: off Santa Cruz Island, California, 279 m]; 1904: 40, pl. 2, fig. 3; Schmitt, 1921: 41, pl. 14, fig. 1; Butler, 1964: 1414, fig. 11; Holthuis and Rosa, 1965: 14; Dahlstrom, 1970: 1382; Scrivener and Butler, 1971: 36 (bibliography); Holthuis, 1980: 140; Butler, 1980: 133, unnumbered fig., pl. 4D; Rothlisberg, 1980: 19; Wicksten, 1984: 136, 137; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19 (list).
Pandalus jordanii: De Man, 1920: 103 (list).

Material examined. **Alaska**. Exact data unknown; 3 females (CL 20.6–21.7 mm); HUMZ-C 484.

Northwest coast of North America. Off Grays Harbor, 90 m; *Albatross*, stn 3047; 2 transitional males (CL 15.0 mm), 3 females (CL 17.5–20.4 mm); USNM 27942.

California. Point Loma, San Diego, 241–279 m; *Albatross*, stn 4357; 15 March 1904; 1 ovig. female (CL 21.3 mm); USNM 51224.

Type material. Holotype: off Santa Cruz Island, 279 m; *Albatross*, stn 2949; ovigerous female (CL 21.5 mm); USNM 25277. Not examined.

Description. Rostrum (figure 8A) weakly or moderately curving dorsally, far over-reaching distal end of scaphocerite, 1.32–1.50 times longer than carapace; dorsal margin weakly convex over eyes, armed nearly throughout length with 15–18 spines or teeth, more widely spaced anteriorly, including four or five on carapace posterior to level of orbital margin, and distalmost two or three without basal suture, posteriormost spine arising from 0.34–0.37 of carapace length; ventral margin armed with five to seven teeth, posteriormost tooth usually weaker than preceding one, ventral blade weakly developed; lateral carina conspicuous over entire length, not extending posteriorly to gastric region. Carapace (figure 8A) with low postrostral

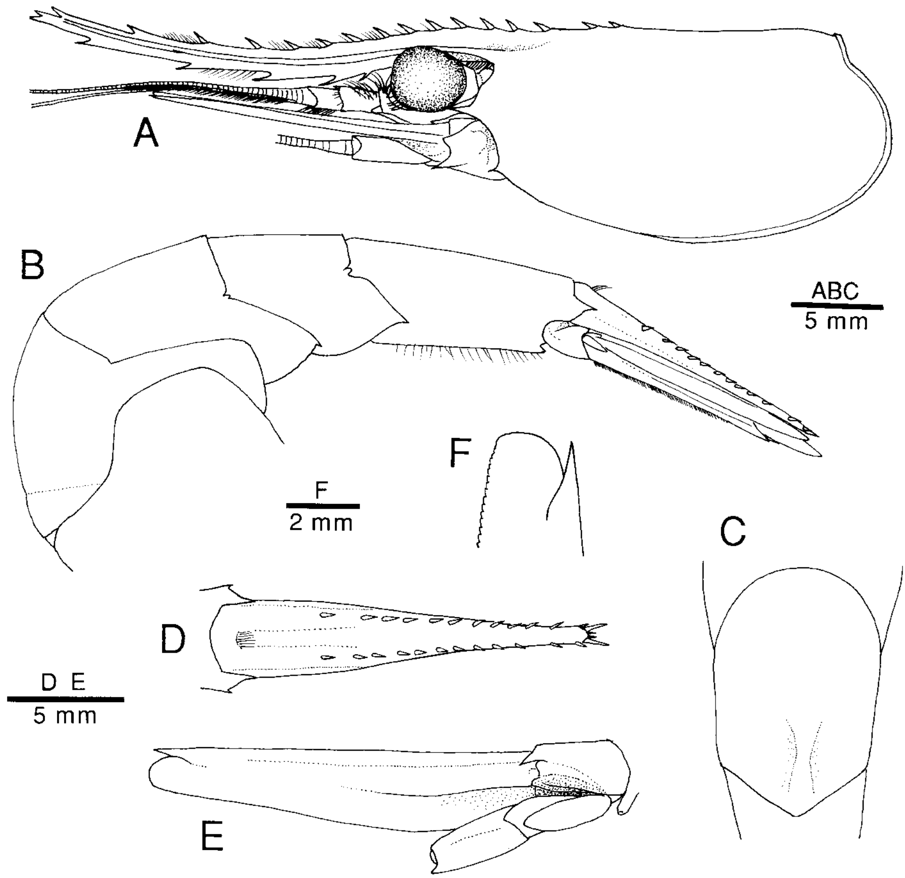


FIG. 8. *Pandalus jordani* Rathbun, 1902. Transitional male (CL 18.9 mm), off Grays Harbor, Washington State, USNM 27942. (A) Carapace and cephalic appendages, lateral; (B) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (C) third abdominal sormite, dorsal; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral, setae omitted.

ridge extending posteriorly to midlength of carapace; entire dorsal margin slightly sinuous in lateral view.

Third abdominal somite (figure 8B, C) with indistinct median boss in posterior part of tergite, posterodorsal margin produced posteriorly, terminating in blunt or subacute apex; fourth somite unarmed posterodorsally; sixth somite 0.6–0.7 times as long as carapace and 2.1–2.4 times longer than proximal depth. Telson (figure 8D) narrow, armed with 10–12 dorsolateral spines on either side.

Eye broadly subpyriform (figure 8A).

Antennular peduncle (figure 8A) reaching mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antennal scaphocerite (figure 8E) about 0.8 times as long as carapace and 3.8–4.8 times longer than wide, lateral margin nearly straight or slightly convex; distal blade (figure 8F) rounded distally, exceeding distolateral tooth.

Third maxilliped reaching or slightly falling short of anterior margin of scaphocerite.

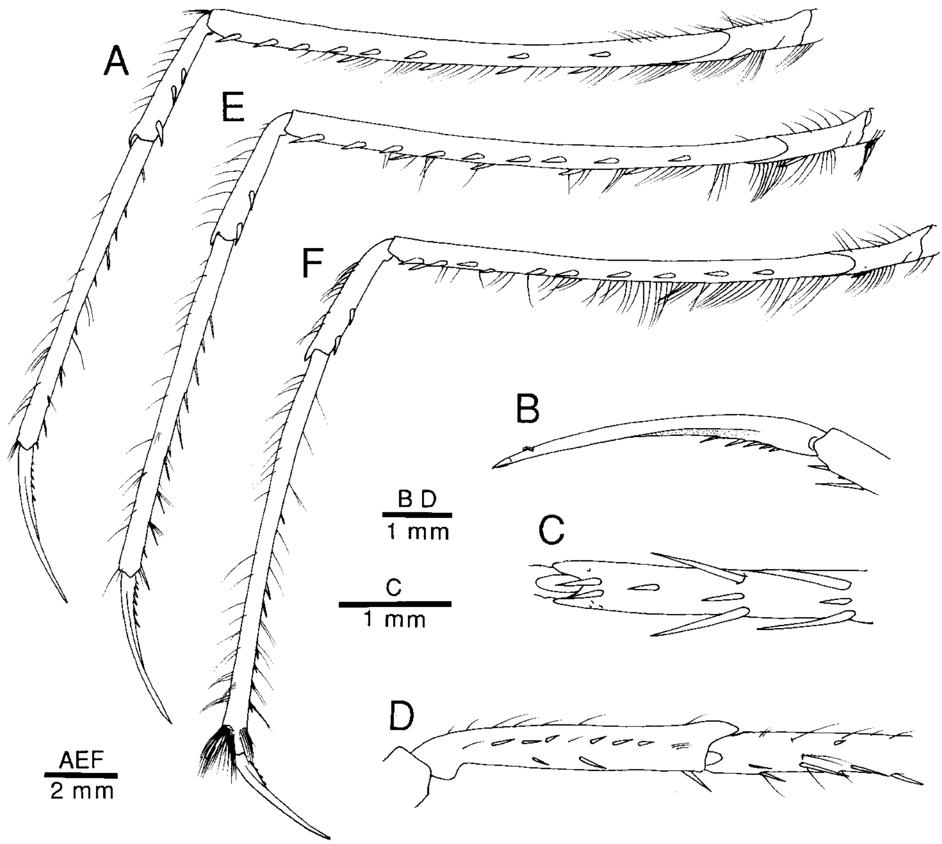


FIG. 9. *Pandalus jordani* Rathbun, 1902. Transitional male (CL 18.9 mm), off Grays Harbor, Washington State, USNM 27942. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

First pereopod falling short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.4 length of carpus; carpus divided into about 60–80 articles. Right second pereopod reaching scaphocerite by tip of chela; carpus divided into 21 or 22 articles. Third to fifth pereopods slender, subequal in length. Third pereopod (figure 9A) over-reaching scaphocerite by length of dactyl; dactyl (figure 9B) slender, 0.46–0.50 times as long as propodus, twisted, somewhat flattened dorsoventrally in distal half, bearing six accessory spinules in proximal 0.3 of flexor margin; propodus (figure 9C) with elongate flexor spines, lateral surface not spinose in either sex; carpus (figure 9D) with two or three (rarely four) lateral spines, mesial surface with spinules arranged in double row; merus 0.8 times as long as carapace, armed with 8–11 lateral spines and five to seven ventral or ventromesial spines. Fourth pereopod (figure 9E) similar to third, over-reaching scaphocerite by half of dactyl; mesial surface of carpus with few spinules. Fifth pereopod (figure 9F) reaching scaphocerite by tip of dactyl; dactyl 0.31–0.34 times as long as propodus, armed with four or five accessory spinules on proximal 0.3–0.4 of flexor margin; carpus with two lateral spines; merus 0.7 times as long as carapace, with 8–11 lateral and two ventral or ventromesial spines.

Coloration. After Butler (1980): 'Surface of shrimp almost entirely covered by fine red dots. These are distributed more densely on telson, posteroventral angle of sixth somite, branchial region of carapace and distal ventral margin of rostrum, giving a darker red. Proximal part of antennal flagellum pale pink.'

Size. Largest male: CL 21.0 mm; largest female: 29.3 mm (Butler, 1980).

Distribution. Iliuk Harbor, Unalaska Island, Aleutian Is., to San Nicholas Island, California; 36–457 m.

Remarks. The original and subsequent descriptions by Rathbun (1902a, 1904) and Butler (1980) are enough to recognize this species. *Pandalus jordani* is characterized by the third abdominal somite bearing a median boss, which never forms a prominent projection as in *P. borealis*, *P. goniurus* and *P. eous*. Like *P. borealis* and *P. eous*, the rostrum bears dorsal spines or teeth over the entire length and the dactyls of the third and fourth pereopods are slender and are weakly twisted in *P. jordani*. The absence of a posteromedian tooth from the fourth abdominal somite also immediately separates *P. jordani* from *P. borealis* and *P. eous*.

No functional male specimen of this species has been available to me during the present study. Dahlstrom (1970: figures 2 and 3) illustrated the sequential morphological change of the anterior two pairs of pleopods. According to Dahlstrom's illustration, the endopod of the first pleopod and appendix masculina of the second pleopods of *P. jordani* are generally similar to those of other species of the *P. montagui* group.

Pandalus tridens Rathbun, 1902
(figures 10 and 11)

Pandalus annulicornis: Brandt, 1851: 124; Richters, 1884: 5 (?part); Doflein, 1900: 320 (part); 1902: 635. Not *Pandalus annulicornis* Leach, 1815.

Pandalus montagui: Rathbun, 1899: 557. Not *Pandalus montagui* Leach, 1814.

Pandalus montagui tridens Rathbun, 1902a: 901 [type locality: off North Head, Aktan Island]; 1904: 41, pl. 2, fig. 2; De Man, 1920: 104; Schmitt, 1921: 42, pl. 13, fig. 2; Makarov, 1941: 115; Vinogradov, 1950: 194; Birshtein and Vinogradov, 1953: 216; Kobjakova, 1958: 223; Butler, 1964: 1436, fig. 23; Scrivener and Butler, 1971: 37 (bibliography); Squires and Figueira, 1974: 15; Rothlisberg, 1980: 19.

Pandalus tridens: Ivanov, 1971: 657; Butler, 1980: 136, unnumbered fig.; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19; Komai, 1991: 76, fig. 6; Komai *et al.*, 1992: 192; Jensen, 1995: 55, fig. 104.

Material examined. **Japan**. Off Hiroo, eastern Hokkaido, 42°10.4′N, 144°41.6′E, 115 m; 6 June 1990; sledge net by RV *Tanshu-Maru*; coll. T. Komai; 2 males (CL 10.0, 13.4 mm), 1 transitional male (CL 13.0 mm), 6 females (14.8–21.2 mm); HUMZ-C 1176. Off Esan, near mouth of Uchiura Bay, southern Hokkaido, 41°20′N, 141°15′E, 170–200 m; May 1992; commercial shrimp trap; coll. T. Komai; 1 male (CL 14.2 mm), 2 transitional males (CL 17.4, 19.0 mm), 8 females (19.6–23.7 mm); HUMZ-C 2050.

Bering Sea. Off Rat Island, Aleutian Islands, 99 m; 4 transitional males (CL 11.5–12.4 mm), 1 female (CL 14.0 mm); USNM 27920. North of Unalaska Island, 632 m; *Albatross*, stn 3331; 2 males (CL 11.3, 14.2 mm), 4 females (CL 16.7–18.3 mm); USNM 27889.

Gulf of Alaska. Off Trinity Islands, 286 m; *Albatross*, stn 2853; 3 males (CL 13.3–14.3 mm), 3 females (CL 17.7–21.4 mm); USNM 27861.

Type material. Holotype: off North Head, Akutan Island, 130 m; *Albatross*, stn 25278; holotype, female (CL 18.3 mm); USNM 25278 (cf. Rathbun, 1902a). Not examined.

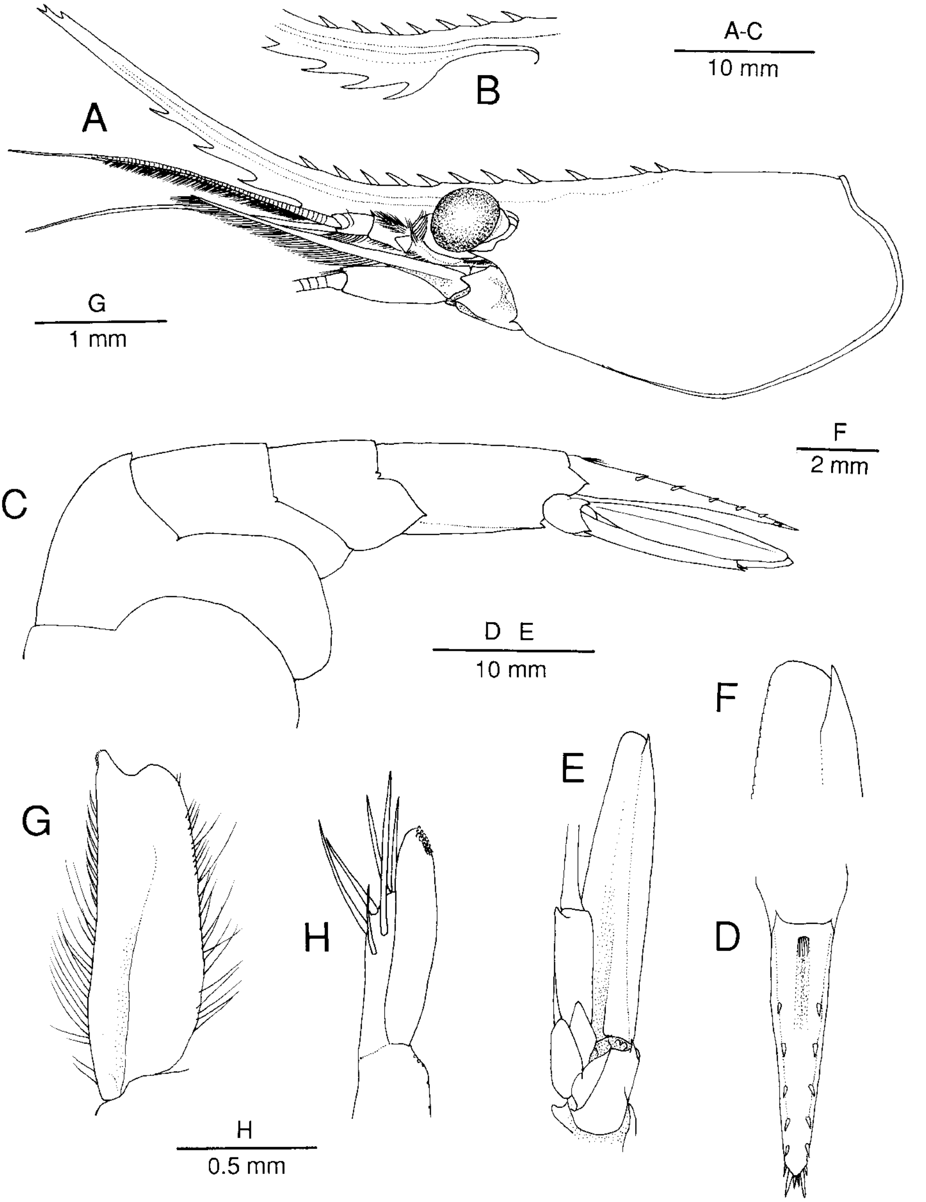


FIG. 10. *Pandalus tridens* Rathbun, 1902. (A)–(F) female (CL 22.0 mm), off Esan, southern Hokkaido, HUMZ-C 2050; (G), (H) functional male CL 13.4 mm, off Hiroo, eastern Hokkaido, HUMZ-C 1171. (A) Carapace and cephalic appendages, lateral; (B) proximal part of rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral, setae omitted; (G) endopod of left first pleopod, ventral; (H) appendix masculina and interna of left second pleopod, mesial.

Description. Rostrum (figure 10A, B) rather strongly curving dorsally, far overreaching scaphocerite, 1.49–1.76 times as long as carapace; dorsal margin nearly straight over eyes, armed with 10–12 spines, including four to six (usually four) on

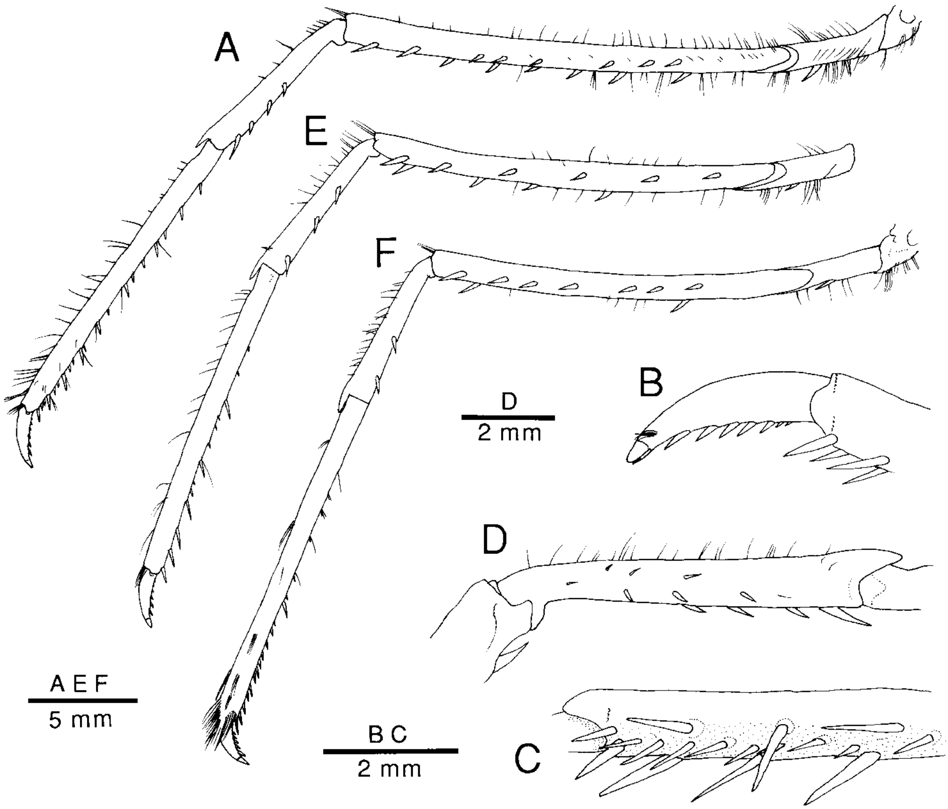


FIG. 11. *Pandalus tridens* Rathbun, 1902. Female (CL 22.0 mm), off Esan, southern Hokkaido, HUMZ-C 2050. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, ventrolateral; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

carapace posterior to level of orbital margin, and one or two teeth near apex of rostrum, subdistal 0.6 length unarmed, anteriormost spine arising from anterior to level of distal margin of antennular peduncle, posteriormost spine arising from 0.43–0.50 of carapace length; ventral margin armed with five to seven teeth, posteriormost tooth subequal in size to preceding tooth; ventral blade well developed, with peak at posteriormost tooth; lateral carina rather blunt over entire length, not extending posteriorly to gastric region. Carapace (figure 10A) with postrostral ridge low, extending to 0.6 length of carapace; dorsal margin nearly straight or faintly convex in lateral view.

Abdomen (figure 10C) with third somite devoid of median projection, posterodorsal margin moderately produced posteriorly, rounded; fourth somite unarmed posterodorsally; sixth somite 0.6–0.7 times as long as carapace and 1.8–2.4 times as long as proximal depth. Telson (figure 10D) moderately broad, armed with six dorsolateral spines on either side.

Eye broadly subpyriform (figure 10A).

Antennular peduncle (figure 10A) reaching mid-length of scaphocerite; intermediate segment without spines on dorsal surface. Antennal scaphocerite (figure 10E) 0.9–1.0 times as long as carapace and 4.7–5.3 times as long as wide, lateral margin nearly straight or slightly convex, distolateral tooth (figure 10F) just reaching or slightly falling short of distal margin of moderately broad, rounded blade.

Third maxilliped reaching or slightly over-reaching distal end of scaphocerite.

First pereopod slightly falling short of or reaching beyond scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.6 of carpus; carpus divided into about 60–80 articles. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 22–25 articles. Third to fifth pereopods relatively slender, becoming slightly shorter successively. Third pereopod (figure 11A) over-reaching scaphocerite by length of dactyl and distal 0.3 of propodus; dactyl (figure 11B) short, 0.18–0.22 times as long as propodus, not twisted, with five to seven accessory spinules over entire length of flexor margin; propodus (figure 11C) with moderately long flexor spines, lateral surface not spinose in either sex; carpus (figure 11A, D) with two or three (rarely four) lateral spines, mesial surface with scattered spinules; merus 0.9–1.0 times as long as carapace, armed with five to seven lateral spines and four to seven (usually five or six) ventral or ventromesial spines. Fourth pereopod (figure 11E) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus with fewer spinules; merus 0.8–0.9 times as long as carapace, armed with six or seven lateral and four to six ventral or ventromesial spines. Fifth pereopod (figure 11F) slightly falling short of anterior margin of scaphocerite; dactyl 0.14–0.22 times as long as propodus, armed with five or six (rarely seven) accessory spinules on flexor margin; carpus with two or three lateral spines; merus 0.8 times as long as carapace, with five to eight lateral and two to four ventral or ventromesial spines.

Endopod of first pleopod of functional males (figure 10G) with well-produced appendix interna, separated from distal lobe of endopod by shallow U-shaped notch, over-reaching distal margin of distal lobe; mesial margin nearly straight or weakly sinuous, with row of slender spines distal to mid-length; lateral margin generally convex. Appendix masculina of second pleopod in functional males (figure 10H) distinctly shorter than appendix interna, armed with about six to nine long spines dorsodistally and distally.

Coloration in life. Fine red dots covering entire body on translucent background; darker red on cardiac region, branchiostegite and orbital region of carapace, ventral part of rostrum and most of sixth abdominal somite, darker region on carapace sometimes reticulated. Abdomen with red spots on lateral face of second to fifth somites; first somite with four blue spots along anterodorsal margin. Antennular and antennal flagella banded by red and white or transparent. Third maxilliped and ambulatory pereopods with red bands on translucent background, ischia of ambulatory pereopods with dense yellow chromatophores. Jensen (1995: 55) published a colour photograph of this species.

Size. Functional males: 10.0–17.4 mm; transitional males: 11.5–19.0 mm; females: 14.0–23.7 mm.

Distribution. Widely distributed in the northern North Pacific: Pribilof Islands, Bering Sea, to San Nicholas Island, California; Cape Oyutorsky; southern Kurile Islands; Pacific coast of Hokkaido, Japan; 5–1984 m.

Remarks. The fact that the earlier authors (e.g. Rathbun, 1902a; Vinogradov, 1950) treated *P. tridens* as a subspecies of *P. montagui* shows that these two species are very similar. The present examination found that the number of subdistal teeth on the rostrum, used by Rathbun (1902a, 1904) and Butler (1980) to distinguish *P. tridens* from *P. montagui*, is variable in both species. Nevertheless, as Butler (1980) noticed, *P. tridens* is distinguishable from *P. montagui* in the relatively longer rostrum (1.49–1.76 times longer than the carapace versus 1.02–1.55 times) and relatively shorter dactyls of the third and fourth pereopods (0.18–0.22 versus 0.23–0.29 times as long). In addition, the ambulatory pereopods are relatively more slender in *P. tridens* than in *P. montagui* (cf. figure 3E, I, J and figure 11A, E, F). The live coloration is quite different between the two species, as mentioned by Butler (1964, 1980). *Pandalus montagui* has red stripes on the body, but *P. tridens* does not have such a striped colour pattern on the body (see 'Coloration in life').

Pandalus tridens appears to be restricted to the northern part of the North Pacific Ocean, including the Bering Sea. Therefore, the records of *Pandalus annulicornis* or *P. montagui* from the North Pacific (Brandt, 1851; Richters, 1884; Rathbun, 1899; Doflein, 1902) are in fact, referable to the present species. Richters (1884) suggested that *Pandalus lamelligerus* Brandt, 1851, might represent a large example of *Pandalus annulicornis* (=*P. tridens*). In his general account of *Pandalus annulicornis*, Doflein (1900) also concluded that *Pandalus lamelligerus* was synonymous with *P. annulicornis*. However, as shown by several authors (Urita, 1942; Kobjakova, 1936b; Komai, 1994b, 1997) Brandt's taxon is a good species of *Pandalopsis*.

Pandalus eous Makarov, 1935
(figures 12 and 13)

Pandalus borealis: Brandt, 1851: 122; Thallwitz, 1891: 4; Rathbun, 1904: 35; Parisi, 1919: 69; De Man, 1920: 103 (part); Rathbun, 1929: 8, fig. 8; Berkeley, 1930: 5, figs 1B and 16A–E; Yokoya, 1933: 15; 1934; 14; 1939: 263; Yoshida, 1941: 23, pl. 5 fig. 2; Urita, 1942: 3; Kubo, 1960: 104, pl. 53, fig. 4; Miyake *et al.*, 1962: 123; Butler, 1964: 1419; Kubo, 1965: 610, fig. 955; Holthuis and Rosa, 1965: 13 (part); Igarashi, 1969: 2, pl. 1, fig. 2, pl. 13, fig. 36; Scrivener and Butler, 1971: 37 (part; bibliography); Kim and Park, 1972: 204; Motoh, 1972: 44, pl. 10, figs 3 and 4; Squires and Figueira, 1974: 14; Miyake, 1975: 100, unnumbered fig. 309; Hayashi, 1976; 19; Kim, 1976: 144; 1977; 285, pl. 28 fig. 57a, b, text-figs 118, 121 and 122; Butler, 1980; 128, unnumbered fig.; Holthuis, 1980: 138 (part); Rothlisberg, 1980: 19 (part); Miyake, 1982: 59, pl. 20, fig. 1; Takeda, 1982: 18, fig. 52 (part); Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19 (in part); Komai, 1991: 73, fig. 5; Komai *et al.*, 1992: 192. [Not *Pandalus borealis* Krøyer, 1838]

Pandalus borealis var. *eous* Makarov, 1935: 321, figs 2 and 3 [type locality: the type series consists of specimens from three different locations: Bering Sea near Cape Navarin, 61°33′N, 179°09′W, 128 m; Bering Sea off Cape Oljutorsky, 59°48′N, 170°42′E, 142 m; near Bering Island, 52°25′N, 165°44′E, 234 m].

Pandalus borealis eous: Derjugin and Kobjakova, 1935: 142; Kobjakova, 1936: 211, pl. 3 fig. 41; 1937: 104, pl. 1 fig. 2; Makarov, 1941: 114; Vinogradov, 1950: 194, pl. 4 fig. 20A, V; Kobjakova, 1955: 148, pl. 35, fig. 5; 1958: 223; Zarenkov, 1960: 343, fig. 2.

Pandalus eous: Squires, 1992: 257, fig. 1b, d, f; Jensen, 1995: 54, fig. 99; Hayashi, 1995: pl. 90 fig. 3, 332.

Material examined. **Japan**. South of Kashima-nada, 300–400 m; 20 February 1995; commercial trawler; coll. T. Komai; 1 female (CL 23.0 mm); CBM-ZC 1065 Off Sakata, Yamagata, Sea of Japan, 38°51.4′N, 139°20.3′E, 623–626 m; 4 September 1994; trawl; 4 females (CL 27.0–29.5 mm); CBM-ZC 2365. Uchiura, Noto Peninsula, Sea of Japan, 38°51.1′N, 139°28.5′E, 311–319 m; 6 September 1994; trawl; 2 males (CL 20.3, 24.4 mm), 2 ovig. females CL 27.0, 28.0 mm; CBM-ZC. Sea of Japan off Rishiri Island, northern Hokkaido; September 1990; otter trawl by TS *Oshoro-Maru*; coll. M. Yabe; 4 males (CL 16.0–25.7 mm), 5 females (CL 25.4–29.1 mm); CBM-ZC 2992. Off Miyako, Iwate, Honshu mainland; 300–400 m; 8 March 1985; commercial trawler; coll. T. Komai; 1 male (CL 23.9 mm), 3 females (CL 30.7–35.6 mm);

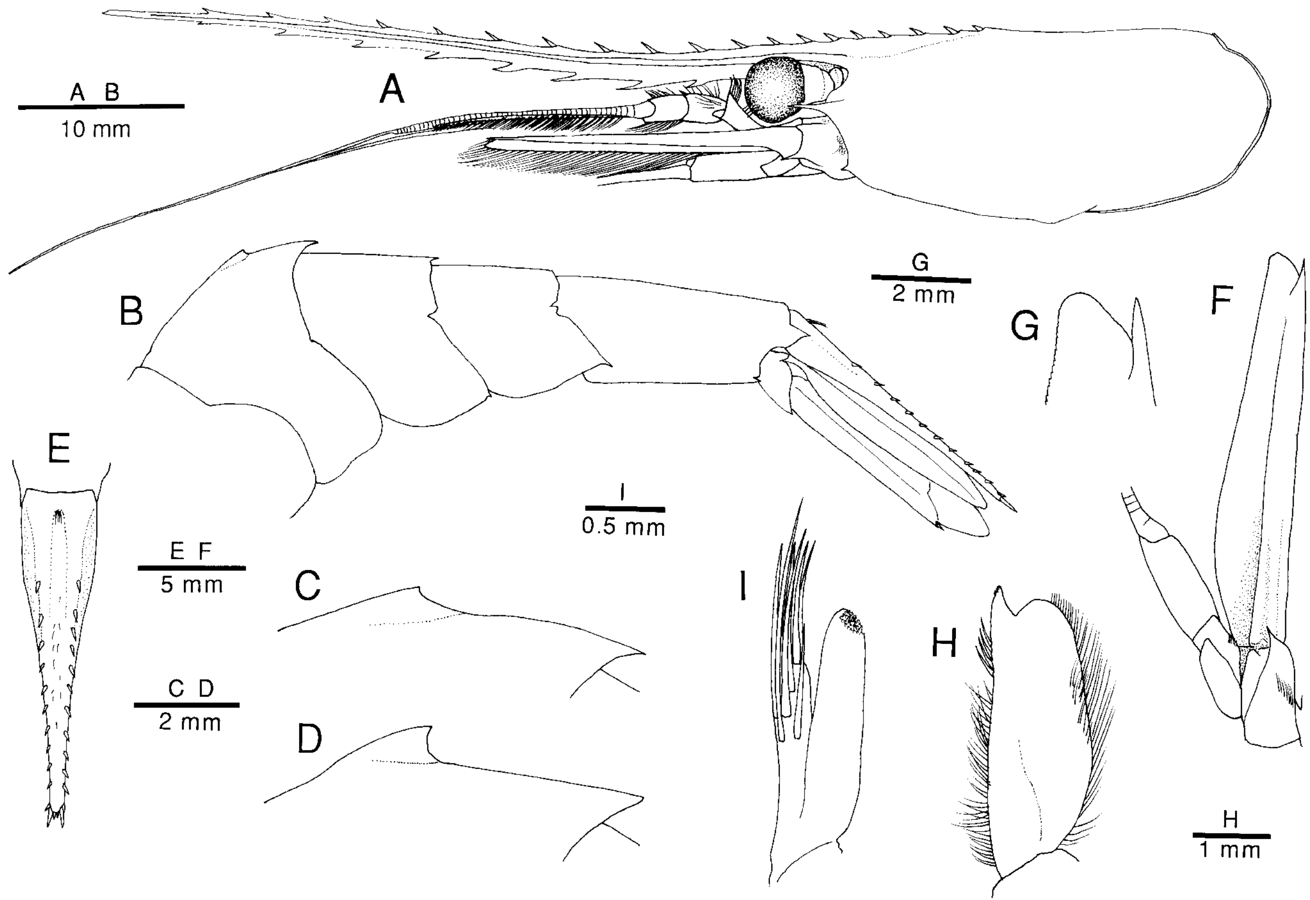


FIG. 12. *Pandalus eous* Makarov, 1935. (A)–(C), (E)–(I) Functional male (CL 20.8 mm), off Esan, southern Hokkaido, HUMZ-C 2051; D, ovig. female (CL 33.2 mm), Peter the Great Bay, Sea of Japan, CBM-ZC 3819. (A) Carapace and cephalic appendages, lateral; (B) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (C) median projection on third abdominal somite, lateral; (D) same; (E) telson, dorsal; (F) left antenna, ventral, setae omitted; (G) distal part of scaphocerite, ventral, setae omitted; (H) endopod of left first pleopod, ventral; (I) appendix masculina and interna of left second pleopod, mesial.

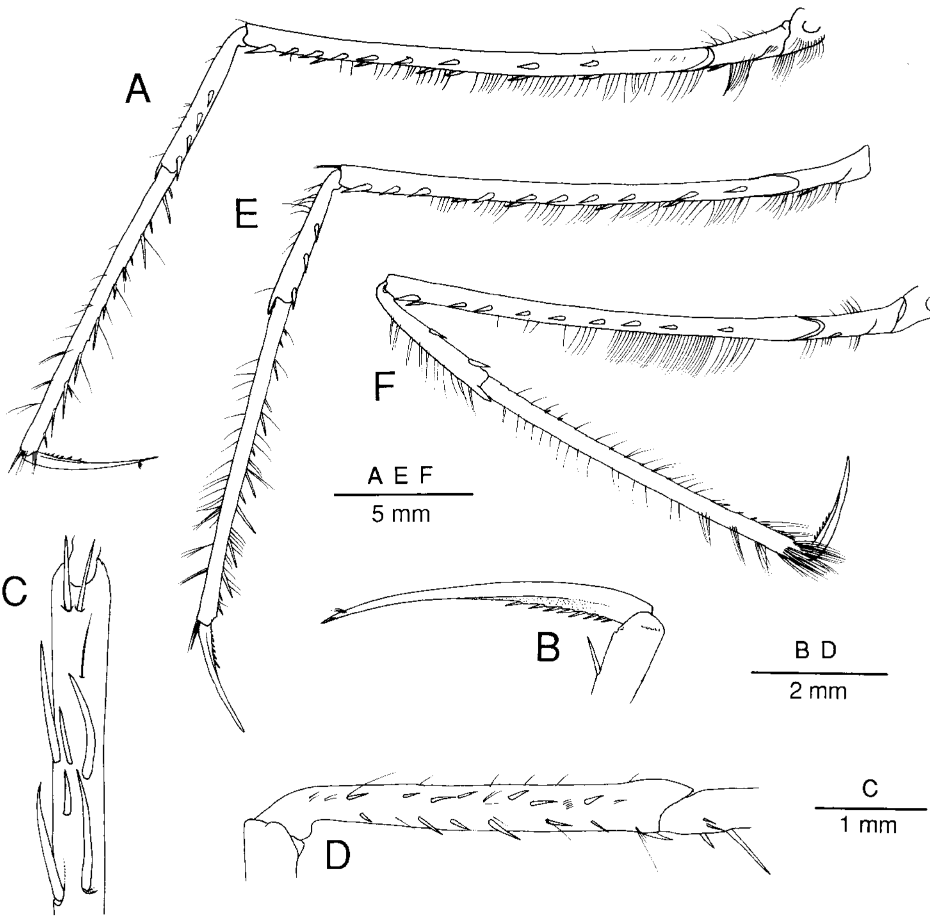


FIG. 13. *Pandalus eous* Makarov, 1935. Functional male (CL 20.8 mm), off Esan, southern Hokkaido, HUMZ-C 2051. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

HUMZ-C 76. Off Miyako, Iwate, 300–400 m; September 1985; commercial trawler; coll. T. Komai; 1 ovig. female (CL 22.7 mm); HUMZ-C 203 East of Cape Erimo, eastern Hokkaido, 41°42.34′N, 143°39.45′E, 265 m; 29 May 1990; otter trawl by RV *Tanshu-Maru*; coll. T. Komai; 3 males (CL 16.0–18.0 mm), 5 females (CL 24.0–29.0 mm); HUMZ-C 1048. Off Hamanaka, eastern Hokkaido, 42°49.43N, 145°19.31E, 429 m; 1 June 1990; otter trawl by RV *Tanshu-Maru*; coll. T. Komai; 1 male (CL 19.0 mm), 3 females (CL 26.7–28.0 mm); HUMZ-C 1074. Off Esan, near mouth of Uchiura Bay, southern Hokkaido, 41°20′N, 141°15′E, 170–200 m; May 1992; shrimp trap; coll. T. Komai; 5 males (CL 14.0–23.3 mm); HUMZ-C 2051.

Continental coast of Russian Far East. Near Vladivostok, Peter the Great Bay, depth unknown; coll. Y. M. Yakovlev; 1 female (CL 28.3 mm), 1 ovig. female (CL 33.2 mm); CBM-ZC 3819.

Bering Sea. Chernofski Harbor, Unalaska, 196 m; *Albatross*, stn 3324; 1 male (CL 15.6 mm), 1 transitional male (CL 16.7 mm), 4 females (CL 21.0–23.4 mm); USNM 28101.

Alaska. Off Kodiak; 4 August 1963; trawl by TS *Oshoro-Maru*; 1 male (CL 18.0 mm), 12 females (CL 20.4–25.0 mm); HUMZ-C 1078.

Type material. The type could not be located in the collection of the Zoological Institute, Akademie Nauk, St. Petersburg (S. Vassilenko, in litt). It was presumably lost. According to Makarov (1935), the type series consisted of 31 specimens from three different locations in the Bering Sea (see synonymy). He did not designate a holotype, and therefore the specimens should all be syntypes.

Description. Rostrum (figure 12A) weakly or moderately curving dorsally, far over-reaching distal end of scaphocerite, 1.61–1.96 times longer than carapace; dorsal margin nearly straight or slightly convex over eyes, armed nearly throughout length with 15–23 spines or teeth, more widely spaced anteriorly, including three to five (usually four) on carapace posterior to level of orbital margin, and one small tooth near apex of rostrum, anterior two to four without complete basal suture, posteriormost spine arising from 0.34–0.39 of carapace length; ventral margin armed with eight or nine teeth, posteriormost tooth weaker than preceding one, ventral blade weakly developed; lateral carina conspicuous over entire length, not extending posteriorly to gastric region. Carapace (figure 12A) with low postrostral ridge extending posteriorly to midlength of carapace; entire dorsal margin slightly sinuous in lateral view.

Abdomen (figure 12B–D) with third somite bearing acute or subacute median projection, posterodorsal margin produced into acute tooth; fourth somite with small posterodorsal median tooth; sixth somite 0.6–0.7 times as long as carapace and 2.1–2.4 times longer than proximal depth. Telson (figure 12E) narrow, armed with 7–13 dorsolateral spines on either side.

Antennular peduncle (figure 12A) reaching mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antennal scaphocerite (figure 12F) 0.8–1.0 times as long as carapace and 4.7–5.3 times longer than wide, lateral margin nearly straight; distal blade (figure 12G) produced distomesially, rounded, usually exceeding distolateral tooth.

Third maxilliped reaching or slightly over-reaching anterior margin of scaphocerite.

First pereopod falling slightly short of or reaching distal end of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.4 of carpus; carpus divided into about 60–80 articles. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 27–34 articles. Third to fifth pereopods slender. Third pereopod (figure 13A) over-reaching scaphocerite by length of dactyl and 0.2–0.3 of propodus; dactyl (figure 13B) slender, 0.40–0.47 times as long as propodus, slightly twisted, somewhat flattened dorsoventrally in distal half of length, bearing six to nine accessory spinules on proximal 0.5 of flexor margin; propodus (figure 13C) with elongate flexor spines, lateral surface not spinose in either sex; carpus (figure 13A, D) with two or three (rarely four) lateral spines, mesial surface with spinules arranged in double row; merus 0.8–0.95 times as long as carapace, armed with seven to nine (rarely six) lateral spines and five to eight (usually five or six) ventral or ventromesial spines. Fourth pereopod (figure 13E) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus with double row of spinules, fewer than in that of third pereopod. Fifth pereopod (figure 13F) over-reaching scaphocerite by tip of dactyl; dactyl 0.28–0.36 times as long as propodus, armed with five to seven accessory spinules on proximal half of flexor margin; carpus with two (rarely one) lateral spines; merus 0.7–0.9

times as long as carapace, with six to ten lateral and one to five (usually one or two) ventral or ventromesial spines.

Endopod of first pleopod of functional males (figure 12H) with well-differentiated appendix interna, separated from distal lobe of endopod by moderately wide V-shaped notch, over-reaching distal margin of distal lobe; mesial margin slightly sinuous, with row of few slender spines somewhat proximal to base of appendix interna; lateral margin slightly sinuous or generally convex. Appendix masculina of second pleopod in functional males (figure 12I) distinctly shorter than appendix interna, armed with about ten long spines dorsodistally and distally.

Colour. Entire body covered by fine red dots, without distinct stripes or bands; uropods and telson darker. Antennal flagella uniformly red. Ambulatory pereopods red, proximal portion of meri of ambulatory pereopods sometimes whitish. Miyake (1975: 100; 1982: pl. 20, fig. 1) and Jensen (1995: 54) gave colour photographs of this species.

Size. Largest functional male: CL 25.7 mm; females: CL 22.7–35.6 mm.

Distribution. Widely distributed in the northern North Pacific, including Chukchi Sea, from the Sea of Japan to Puget Sound, Washington State; 16–1380 m.

Remarks. The present form was always thought to be closely related to *P. borealis*. Makarov (1935) originally described it as a variety of *P. borealis*, and subsequent Russian authors (e.g. Kobjakova, 1936, 1937; Makarov, 1941; Vinogradov, 1947, 1950; Zarenkov, 1960) accepted the subdivision. On the other hand, other authors (e.g. Urita, 1942; Kubo, 1965; Butler, 1980; Miyake, 1982) did not accept such a subdivision. By arguing that there are several morphological differences between British Columbia and Newfoundland materials, Squires (1992) recognized it as a good species, *P. eous*.

Squires (1992) used the following characters to separate *P. eous* from *P. borealis*: relative length of the rostrum; movability of the second anteriormost dorsal spine on the rostrum; development of the rostral tip; relative size of the posteriormost spine on the carapace and distance between the posteriormost and preceding spines of the dorsal series of rostral spines; development of the median projection on the third abdominal somite; relative size of the lateral proximal lobe on the stylocerite; armament of the intermediate segment of the antennular peduncle; proportion of the scaphocerite; arrangement of the spines of the appendix masculina; and armament of the mandible. However, the present study found that many of these characters are not reliable because of individual variations exhibited by both forms. Nevertheless, *Pandalus eous* is distinct from *P. borealis* in the following particulars: the rostrum is longer in *P. eous* than in *P. borealis* (1.6–2.0 times as long as carapace versus 1.1–1.6 times as long), and the median projection of the third somite is usually more prominent with an acute or subacute apex in *P. eous*. As Squires (1992) suggested, the ventral teeth of the rostrum are slightly larger in *P. eous* than in *P. borealis*, though this feature is rather subjective. The number of subdistal fixed teeth on the dorsal margin of the rostrum seems to be greater in *P. eous* than in *P. borealis* (two to four versus one or two).

The material from different localities is generally similar in morphology and coloration, except for the number of dorsolateral spines on the telson. The Japanese specimens have 10–13 spines on either side of the telson, but there are 7–10 spines in the specimens from the Bering Sea and Alaska. This difference is often useful to separate the western and eastern populations. However, the two populations are treated as a single species at present. Future study may eventually reveal that the two populations are separate subspecies or species. The difference in the shape of the distal blade of the scaphocerite, mentioned by Makarov (1935), between the Pacific and Atlantic populations, is known to be a part of individual variations displayed by both species (cf. Zarenkov, 1960).

Pandalus stenolepis group

Diagnosis. Body slender or rather robust; integument thin or moderately firm. Rostrum with posteriormost ventral tooth distinctly stronger than preceding teeth. Second abdominal somite with shallow transverse groove on tergum. Antennule with broadly rounded, semicircular stylocerite. Antennal basicerite without intercalated process. Posterior lobe of scaphognathite produced, but not noticeably elongate. Right second pereopod with carpus divided into more than 15 articles; merus with few annulations distally. Third to fifth pereopods slender, becoming shorter successively; third and fourth pereopods never prehensile in either sex, propodus each with single or double row of spinules flanked by rows of moderately long spines on flexor surface; carpi of third to fifth pereopods armed with mesial spine; mesial surface of carpus of third pereopod with two rows of spinules and occasionally with row of spinules along with dorsal margin. Endopod of first pleopod in functional male with appendix interna not inflated, unarmed (uncertain in *P. curvatus*). Appendix masculina in functional male much longer than appendix interna, with spines becoming longer distally on dorsal surface and distal margin.

Remarks. This group contains *P. stenolepis* Rathbun, 1902, and *P. curvatus* sp. nov. The presence of a mesial spine on the carpi of the third to fifth pereopods, noticeably enlarged posteriormost tooth of the ventral series of the rostrum, and elongate appendix masculina in males, certainly indicate the close relationship between this group and the *P. hypsinotus* group. However, such characters as the simple third and fourth pereopods and the non-spinose appendix interna of the first pleopod in functional males places this group in an intermediate position between the *P. montagui* group and the *P. hypsinotus* group.

Pandalus stenolepis Rathbun, 1902
(figures 14 and 15)

Pandalus stenolepis Rathbun, 1902a: 901 [type locality: Straits of Juan de Fuca]; 1904: 49, fig. 14, pl. 2, fig. 4; De Man, 1920: 104; Butler, 1964: 1439, fig. 25; Scrivener and Butler, 1971: 38 (bibliography); Squires and Figueira, 1974: 17; Butler, 1980: 145, unnumbered fig., pl. 2C; Rothlisberg, 1980: 19; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19 (list); Jensen, 1995: 55, fig. 103.

Material examined. **Northwest coast of North America**. Straits of Juan de Fuca, Washington State, 221 m; 4 females CL 13.4–15.0 mm; USNM 28058.

Type material. Holotype: Straits of Juan de Fuca, Washington State, 72 m; *Albatross*, stn 3464; female (CL 16.2 mm); USNM 25279. Not examined.

Description. Rostrum (figure 14A, B) noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.10–1.25 times longer than carapace; dorsal margin not concave over eyes, armed with nine to 11 spines, including four or five on carapace posterior to level of orbital margin, and one or two teeth near apex of rostrum, subdistal half unarmed, posteriormost spine arising from 0.50–0.54 of carapace length; ventral margin armed with six teeth, noticeably increasing in size posteriorly, posteriormost tooth much stronger than preceding tooth; ventral blade well

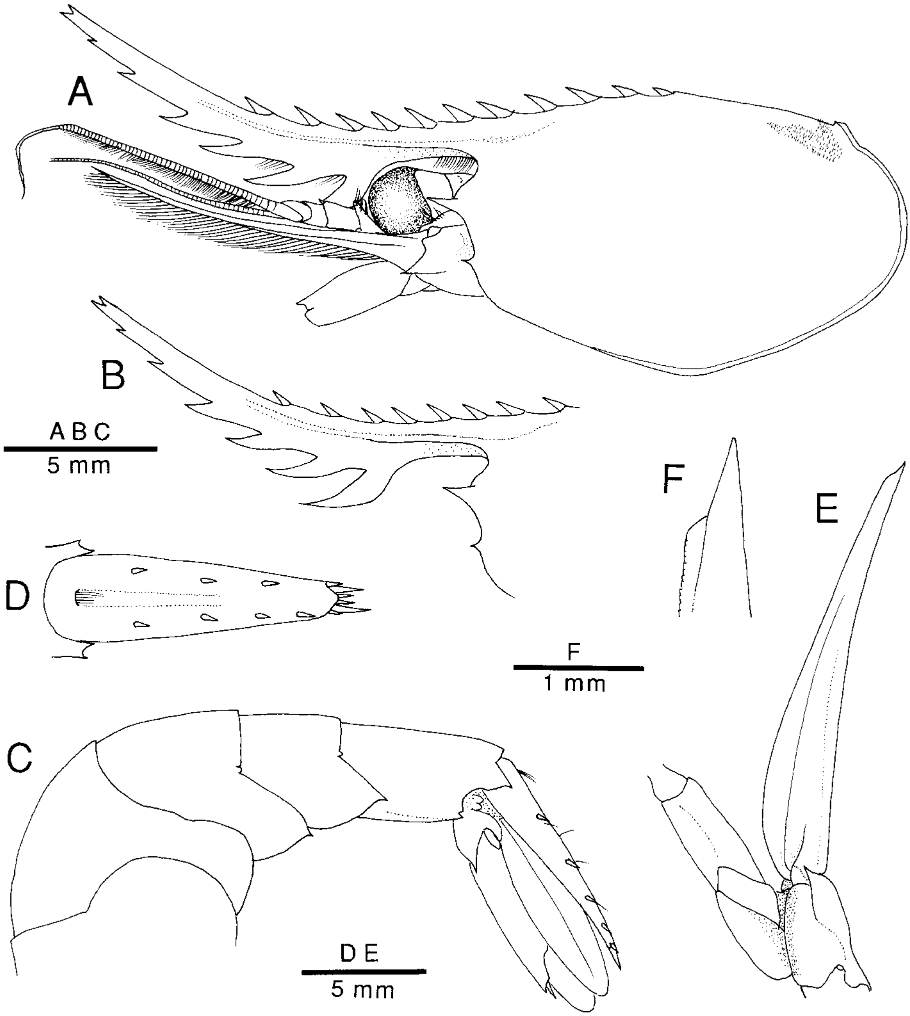


FIG. 14. *Pandalus stenolepis* Rathbun, 1902. Female (CL 14.6 mm), Straits of Juan de Fuca, Washington State, USNM 28058. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral, setae omitted.

developed; lateral carina obtuse throughout length, not extending posteriorly to gastric region. Carapace (figure 14A) with postrostral ridge low, extending beyond midlength of carapace; dorsal margin slightly convex in lateral view; cardiac region with patch of pubescence.

Abdomen (figure 14C) with third somite lacking median projection, postero-dorsal margin rounded; fourth somite without posterodorsal median tooth; sixth somite about 0.5 times as long as carapace and 1.5–1.75 times longer than proximal depth. Telson (figure 14D) relatively broad, armed with four or five dorsolateral spines on either side.

Eye broadly subpyriform (figure 14A).

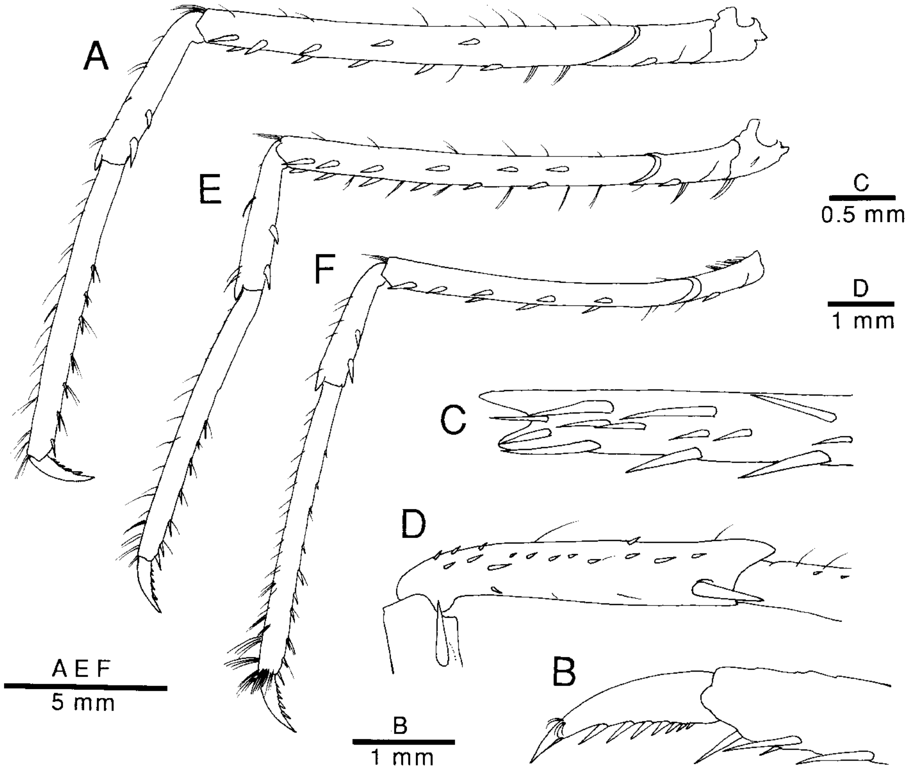


FIG. 15. *Pandalus stenolepis* Rathbun, 1902. Female (CL 14.6 mm), Straits of Juan de Fuca, Washington State, USNM 28058. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

Antennular peduncle (figure 14A) falling short of mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antennal scaphocerite (figure 14E) 0.9–0.95 times as long as carapace and 5.6–6.1 times longer than wide, tapering distally to an acute distolateral tooth, lateral margin slightly concave; distal blade (figure 14E) poorly developed, obliquely truncate.

Third maxilliped nearly reaching base of distolateral tooth of scaphocerite.

First pereopod falling somewhat short of base of distal tooth of scaphocerite. Left second pereopod over-reaching base of distolateral tooth of scaphocerite by 0.7–0.8 length of carpus; carpus divided into about 50 articles; merus annulated entirely; ischium annulated in distal 0.3. Right second pereopod over-reaching scaphocerite by dactyl; carpus divided into 11–15 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 15A) over-reaching scaphocerite by length of dactyl and more than 0.5 of propodus; dactyl (figure 15B) moderately stout, 0.21–0.23 times as long as propodus, not twisted, with six to eight accessory spinules on proximal 0.6 of flexor margin; propodus (figure 15C) straight, with single row of small spines or spinules flanked by row of moderately long spines on distal 0.5 of flexor surface, lateral surface not spinose in either sex; carpus (figure 15A, D) with two lateral and one mesial spines, mesial surface with row of spinules dorsally, dorsal surface with few spinules; merus 1.0–1.1 times as long as carapace, armed with five or six lateral spines and six to eight ventral or ventromesial spines. Fourth pereopod (figure 15E) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus with row of fewer spinules dorsally; dactyl with six or seven accessory spinules; merus about 0.9 times as long as carapace, with six or seven lateral and six ventral or ventromesial spines. Fifth pereopod (figure 15F) reaching 0.6 length of scaphocerite by tip of propodus; dactyl 0.21–0.24 times as long as propodus, armed with six or seven accessory spinules on proximal 0.6 of flexor margin; carpus with only two lateral spines; merus 0.7–0.8 times as long as carapace, with five lateral and four or five ventral or ventromesial spines.

Colour. Butler (1980) described the colour of *P. stenolepis* as follows: 'Background white to gray. On carapace, red dots form patches from cardiac region to posterior branchial region, in mid branchial and hepatic regions, and from gastric to orbital region; band of closely spaced dots on anterolateral margin from pterygostomian spine, past orbit to lower base of rostrum; also red patches along dorsal surface at bases of spines on carapace and rostrum; also on rostrum, several small red patches mainly near distal ventral spines; large yellow dots on mid-branchial and posterior branchial regions; 2 blue spots on each side in cardiac region, posterior to pubescent patch. On abdomen, red dots, closely spaced in patches, on dorsal and upper lateral surfaces of first and fifth somites, on anterior parts of second to fourth somites; more patches scattered on lower parts of pleura and protopodites of pleopods; yellow dots and patches on lower anterior part of first somite, over most of lower half of second pleuron; red patch on anterior lateral surface of sixth somite; blue spots, 2 on anterior dorsal surface of first somite; 2 on each side, one above the other, posterior to sulcus of second somite; 2 on anterior upper lateral surface of third somite; on fourth somite, 2 on each side, 1 on anterior upper lateral surface, the other near posterolateral margin, below articular knob. Anterior appendages, patch of red dots on eyestalk; patches form banding on all segments of pereiopods, except dactyli of pereiopods III–V, but sparse on carpus of II, merus of IV, and propodus of V; third maxilliped colored similarly, with reddish setae on 2 more distal segments; banding on outer antennular flagellum; almost solid light red to pinkish on antennal flagellum, darker red on peduncle and basicerite; and setae of scale and outer margin pinkish.' Jensen (1995: 55) published a colour photograph of this species.

Size. Functional males: 8.0–14.4 mm; transitional males: 9.4–11.8 mm; females: 9.9–18.2 mm (Butler, 1964; 1980).

Distribution. Unalaska Island, Aleutian Islands, to Hecata Bank, Oregon; 49–229 m (Butler, 1980).

Remarks. No male specimen of this species has been available to me during this study. According to the figure of Butler (1964: fig. 25), the appendix interna of the first pleopod appears to be rather elongate, unarmed on surfaces; the appendix masculina of the second pleopod is elongate, being about twice longer than appendix interna; the dorsal surface and terminal margin of the appendix masculina bear a few rows of spines that become longer distally. The morphology of these structures appears to be intermediate between those of the *P. montagui* group and *P. hypsinotus* group.

This species has been well diagnosed by the original description (Rathbun, 1902a) and subsequent descriptions (Rathbun, 1904; Butler, 1980). It is quite distinctive among *Pandalus* in the combination of the possession of a patch of pubescence on the cardiac region of the carapace and the narrow, obliquely truncate distal blade of the scaphocerite.

Pandalus curvatus sp. nov.
(figures 16 and 17)

Type material. **Japan**. Amakusa-nada, western Kyushu, southern Japan, 32°08.6′N, 129°41.2′E, 501 m; 4 October 1994, beam trawl by RV *Yoko-Maru* of the Seikai National Fisheries Research Institute, Nagasaki; coll. T. Kosuge; holotype, male (CL 11.8 mm); CBM-ZC 2993.

Description. Rostrum (figure 16A, B) strongly curving dorsally, far over-reaching scaphocerite, 2.14 times as long as carapace; dorsal margin weakly convex over eyes, armed with 14 spines, including six on carapace posterior to level of orbital margin, and one tooth near apex of rostrum, subdistal 0.6 unarmed, posteriormost spine arising from 0.45 of carapace length; ventral margin armed with 12 teeth, posteriormost tooth distinctly stronger than preceding tooth, strongly curved anteriorly, blade becoming noticeably deeper at position of posteriormost ventral tooth; lateral carina blunt, not extending posteriorly to gastric region. Carapace (figure 16A) with postrostral ridge low, extending beyond mid-length of carapace; dorsal margin nearly straight in lateral view.

Abdomen (figure 16C) with third somite lacking median projection, posterodorsal margin rounded; fourth somite without posterodorsal median tooth; sixth somite 0.52 times as long as carapace and 1.5 times as long as proximal depth. Telson (figure 16D) moderately broad, 1.58 times as long as sixth somite, armed with five dorsolateral spines on either side.

Eye (figure 16E) broadly subpyriform, with corneal region strongly dilated; ocellus present.

Antennular peduncle (figure 16A) reaching 0.4 of scaphocerite; stylocerite (figure 16E) broadly rounded; intermediate segment armed with few spinules on dorsodistal margin, but unarmed on dorsal surface; distal segment without spinule on dorsodistal margin. Antennal scaphocerite (figure 16F) 1.07 times as long as carapace and 5.7 times as long as wide, lateral margin slightly concave, distolateral tooth (figure 16G) slightly over-reaching distal margin of moderately broad, rounded blade.

Mouthparts typical of genus. Maxilla with posterior lobe of scaphognathite produced, but not noticeably elongate. Third maxilliped (figure 17A) nearly reaching distal end of scaphocerite.

First pereopod (figure 17B) somewhat falling short of scaphocerite; ischium (figure 17C) with weak ventral lamina. Left second pereopod (figure 17D) over-reaching scaphocerite by nearly full length of carpus; carpus divided into about 75 articles; merus annulated entirely; ischium annulated in distal 0.3. Right second pereopod (figure 17E) over-reaching scaphocerite by length of chela; carpus divided into 25 articles; merus with one complete annulation distally. Third to fifth pereopods slender, becoming shorter successively. Third pereopod (figure 17F) over-reaching scaphocerite by length of dactyl and half of propodus; dactyl (figure 17G) slender, 0.42 times as long as propodus, not twisted, with 10 accessory spinules on proximal half of flexor margin; propodus (figure 17H) straight, with double row of small spines or spinules flanked by row of elongate spines on distal 0.25 length of flexor surface; carpus (figure 17F, I) with two lateral and one mesial spines, mesial surface

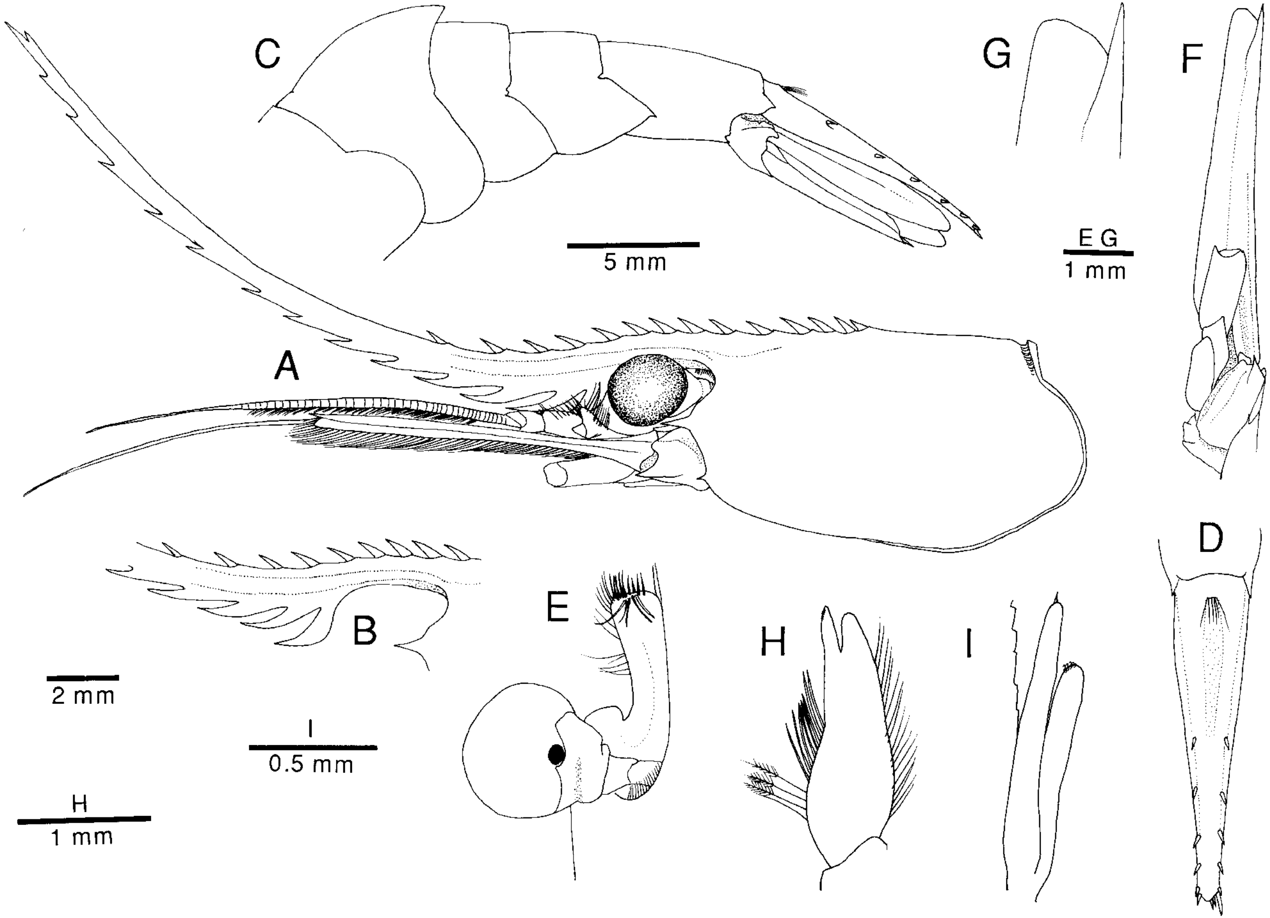


FIG. 16. *Pandalus curvatus* sp. nov. Holotype, subadult male (CL 11.8 mm), Amakusa-nada, Kyushu, Japan, CBM-ZC 2993. (A) Carapace and cephalic appendages, lateral; (B) proximal part of rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) eye and proximal segment of antennular peduncle, dorsal; (F) left antenna, ventral, setae omitted; (G) distal part of scaphocerite, ventral; (H) endopod of left first pleopod, ventral; (I) appendix masculina and interna of left second pleopod, mesial.

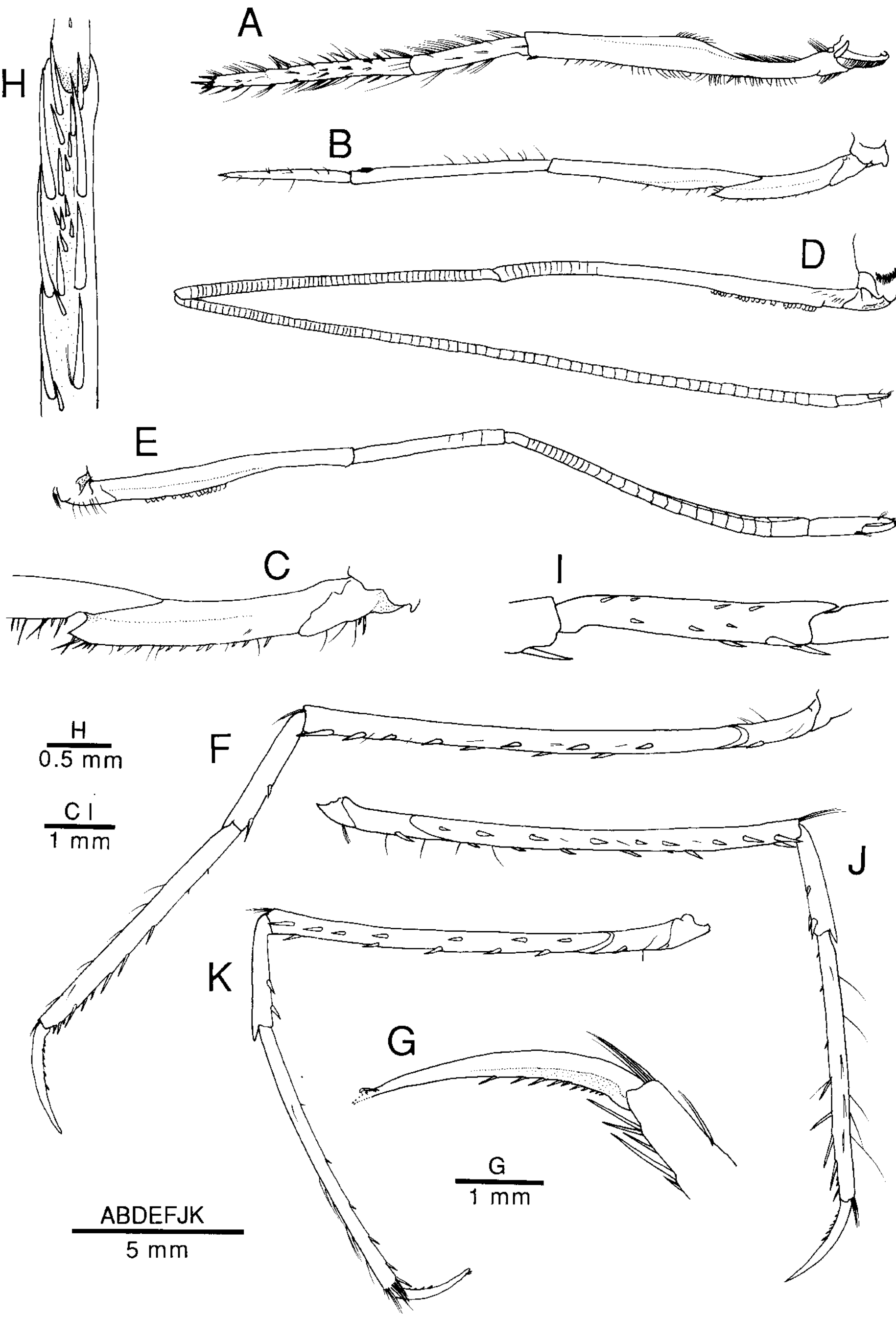


FIG. 17. *Pandalus curvatus* sp. nov. Holotype, subadult male (CL 11.8 mm), Amakusa-nada, Kyushu, CBM-ZC 2993. (A) Left third maxilliped, lateral; (B) left first pereopod, lateral; (C) same, ischium, lateral; (D) left second pereopod, lateral; (E) right second pereopod, lateral; (F) left third pereopod, lateral; (G) same, dactyl, lateral; (H) same, distal part of propodus, flexor; (I) same, carpus and proximal part of propodus, mesial; (J) right fourth pereopod, lateral; (K) left fifth pereopod, lateral.

with scattered spinules; merus 1.14 times as long as carapace, armed with seven lateral spines and six ventral or ventromesial spines. Fourth pereopod (figure 17J) similar to third, over-reaching scaphocerite by length of dactyl; mesial surface of carpus without spinules; dactyl with seven accessory spinules; merus 1.03 times as long as carapace, with nine lateral and seven ventral or ventromesial spines. Fifth pereopod (figure 17K) over-reaching scaphocerite by half length of dactyl; dactyl 0.39 times as long as propodus, armed with six accessory spinules on proximal half of flexor margin; propodus with double row of long spines on flexor face in distal half; carpus with only two lateral spines; merus 0.9 times as long as carapace, with seven lateral and five ventral or ventromesial spines.

Endopod of first pleopod (figure 16H) with sinuous mesial margin, bearing row of elongate spines proximal to level of mid-length; appendix interna separated from distal lobe of endopod by narrow V-shaped deep notch, over-reaching distal margin of distal lobe. Appendix masculina of second pleopod (figure 16I) distinctly longer than appendix interna, armed with one bristle distally.

Colour. Unknown.

Size. The holotype is a subadult male, measuring 11.8 mm in CL.

Type locality. Amakusa-nada, Kyushu, southern Japan (East China Sea).

Distribution. Known only from the type locality.

Etymology. The species is named from the Latin *curvatus* (bent), in reference to the strongly upturned rostrum.

Remarks. The development of the anterior two pairs of pleopods suggests that the holotype is a subadult. Although the armament of the appendix masculina seems to be not fully developed, the appendix masculina itself is elongate, being distinctly longer than the appendix interna.

The new species appears closest to *P. stenolepis* in having a mesial spine on the carpi of the third and fourth pereopods and a simple, non-prehensile, third pereopod. However, there is no evidence to support these two species belonging to sister groups. There are numerous characters to separate them: the rostrum is remarkably elongate and strongly curved in the new species; the ambulatory pereopods are more slender in *P. curvatus* than in *P. stenolepis*; the ambulatory dactyls are relatively longer, with accessory spinules on proximal 0.4 in the new species, rather than 0.75 in *P. stenolepis*; the carapace lacks a patch of pubescence on the cardiac region in *P. curvatus*; the distal blade of the scaphocerite is normally developed in the new species, while it is very narrow with an obliquely truncate blade in *P. stenolepis.*

***Pandalus hypsinotus* group**

Diagnosis. Body robust; integument firm, glabrous. Rostrum with posteriormost ventral tooth distinctly longer than preceding teeth. Second abdominal somite with shallow transverse groove on tergum. Antennule with broadly rounded, semicircular stylocerite. Antennal basicerite without intercalated process. Posterior lobe of scaphognathite produced, but not noticeably elongate. Right second pereopod with carpus divided into more than 15 articles; merus with few annulations distally. Third to fifth pereopods relatively stout, becoming shorter successively. Third and fourth pereopods prehensile in functional males, flexor surfaces of propodi with numerous spinules, sometimes arranged in two to four rows, flanked by two rows of moderately long spines, particularly well marked in third pereopod; in transitional males and females, third pereopod weakly prehensile, fourth pereopod sometimes simple, dactyls becoming shorter proportionally, spinules on flexor surface of propodus less numerous. Carpi of third to fifth pereopods armed with one mesial spine (carpus of fifth pereopods sometimes lacking mesial spine); mesial surface of carpus of third pereopod with scattered spinules. Endopod of first pleopod in functional males with appendix interna well differentiated, sometimes strongly inflated, spinose; mesial margin of endopod with shallow notch proximal to base of appendix interna, posterior half of mesial margin convex, with irregularly double row of long spines or spiniform setae; distal lobe fringed with bristles according to developmental stage. Appendix masculina in functional males elongate, attaining more than twice length of appendix interna, somewhat curved ventrally, terminating in acute basally articulated spine, armed with numerous spines or spinules arranged in one to four rows on dorsal and/or mesial surfaces; development of spines variable according to developmental stage.

Remarks. The prehensile third pereopod and spinose appendix interna of the first pleopod in functional males, representing derived conditions, indicate that this group is monophyletic.

This group is the most diverse among the four informal groups, including the following nine species: *Pandalus hypsinotus* Brandt, 1851; *P. danae* Stimpson, 1857; *P. gracilis* Stimpson, 1860; *P. prensor* Stimpson, 1860; *P. gurneyi* Stimpson, 1871; *P. nipponensis* Yokoya, 1933; *P. teraoi* Kubo, 1937; *P. chani* sp. nov.; and *P. formosanus* sp. nov.

Pandalus hypsinotus Brandt, 1851
(figures 18 and 19)

Pandalus hypsinotus Brandt, 1851: 125 [type locality: Unalaska]; Kingsley, 1878: 64; Doflein, 1900: 322; Rathbun, 1902b: 46; 1904: 46, pl. 2 fig. 5; Brashnikov, 1907: 114, fig. 13a–k, pl. 2 fig. 9; Balss, 1914: 29; Parisi, 1919: 69; De Man, 1920: 103; Berekeley, 1930: 5, fig. 1D; Yokoya, 1933: 16 (? in part); 1934: 14; Urita, 1934: 254, figs 1 and 2; Derjugin and Kobjakova, 1935: 142 (list); Kobjakova, 1936: 209; 1937: 102; Nishimura, 1939: 382; Yokoya, 1939: 263; Makarov, 1941: 115; Yoshida, 1941: 22, pl. 5 fig. 1; Urita, 1942: 6; Igarashi, 1951: 1, figs 1–3; Kobjakova, 1958: 222; Kubo, 1960: pl. 53 fig. 6; Miyake *et al.*, 1962: 123; Butler, 1964: 1428; Holthuis and Rosa, 1965: 14; Kubo, 1965: 609 (? in part), fig. 951; Kobjakova, 1967: 231; Igarashi, 1969: 2, pl. 2, fig. 4, pl. 8, fig. 38; Scrivener and Butler, 1971: 37 (bibliography); Kim and Park, 1972: 274; Motoh, 1972: 45, pl. 12 fig. 1; Squires and Figueira, 1974: 15; Miyake, 1975: 100, unnumbered fig., 277; Hayashi, 1976: 19; Kim, 1976: 144; 1977: 281, pl. 27, fig. 55a, b, text-figs. 118–120; Butler, 1980: 143; Holthuis, 1980: 140 (part); Rothlisberg, 1980: 19; Takeda, 1982: 18, fig. 53; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19; Komai, 1991: 75; Komai *et al.*, 1992: 192; Hayashi, 1995: pl. 90, fig. 4, 332; Jensen, 1995: 54, fig. 101.
Not *Pandalus hypsinotus*: Doflein, 1902: 635, pl. 4 figs 1 and 2. [=*Pandalus prensor* Stimpson, 1860].
Not *Pandalus hypsinotus*: Holthuis, 1976: 50, fig. 1. [=*Pandalus gracilis* Stimpson, 1860].
Not *Pandalus hypsinotus*: Miyake, 1982: 60, pl. 20 fig. 2. [=*Plesionika izumiae* Omori, 1971].

Type material. The four syntypes from Unalaska Island, collected by I. G. Voznesensky, are still extant in the collection of the Zoological Institute at St. Petersburg (registration number N 1453; S. Vassilenko, in litt). According to her, they are preserved in alcohol, but the condition is bad.

Material examined. **Japan**. Obira, Sea of Japan coast of Hokkaido, 45 m; 21 August 1991; beam trawl; coll. S. Maruyama; 2 juvs. (CL 8.0, 9.2 mm); CBM-ZC 505. Off Taneichi, Iwate, 40°24.9′N, 142°04.9′E, 223 m; 14 October 1994; trawl by RV *Wakataka-Maru*; coll. D. Tsutsui; 1 male (CL 11.4 mm); CBM-ZC 1123. Nemuro

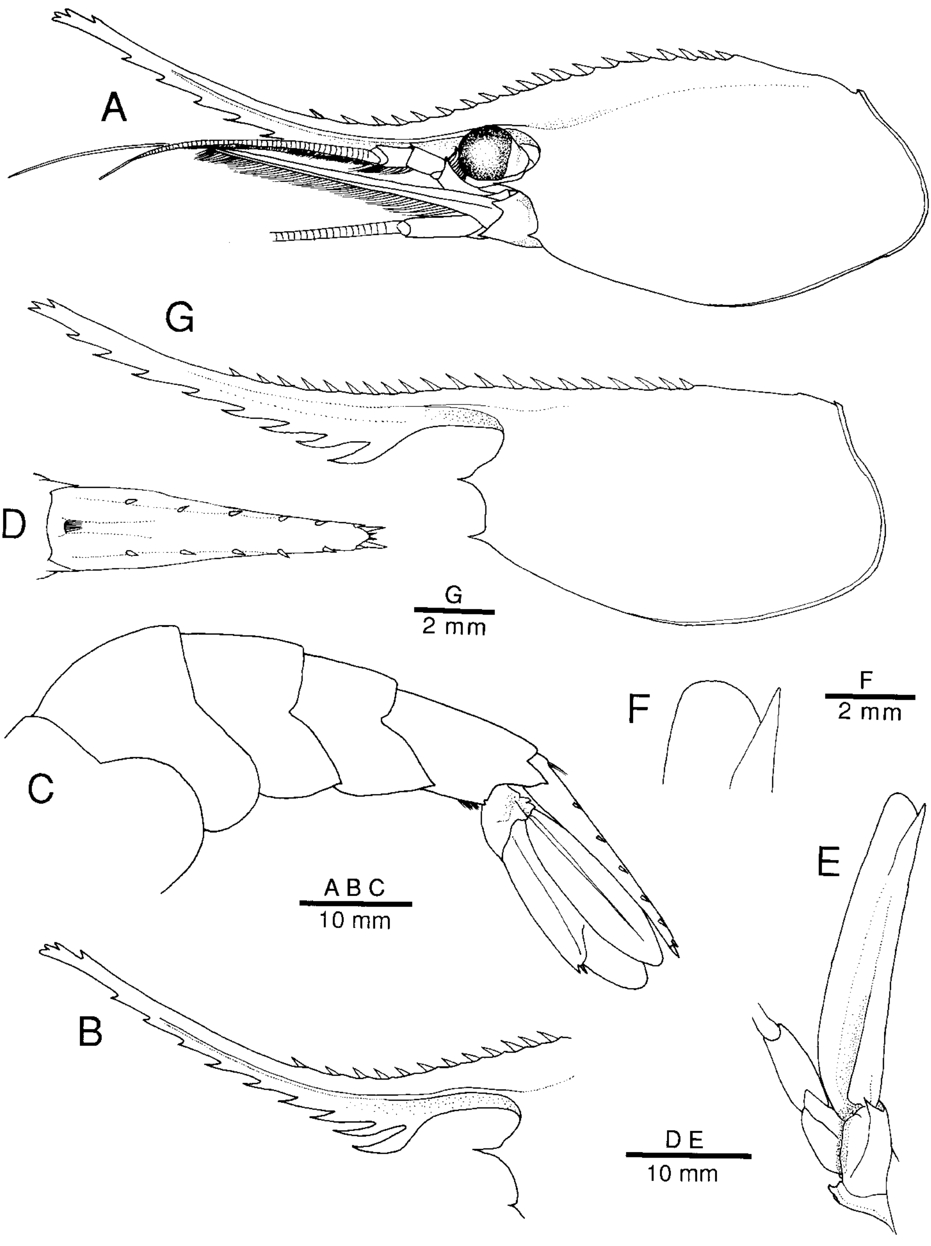


FIG. 18. *Pandalus hypsinotus* Brandt, 1851. (A)–(F) Functional male (CL 31.2 mm), off Miyako, Iwate, Japan, HUMZ-C 204; (G) juvenile (CL 8.6 mm), Usujiri, southern Hokkaido, HUMZ-C 145. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) same, distal part; (G) carapace and rostrum, lateral.

Bay, eastern Hokkaido, 43°21.4′N, 145°29.5′E, 15 m; 15 September 1995; dredge by RV *Tansei-Maru*; coll. T. Komai; 3 males (CL 8.0–9.8 mm); CBM-ZC 2437. Off Miyako, Iwate; 28–31 March 1987; commercial trawler; coll. T. Komai; 3 males

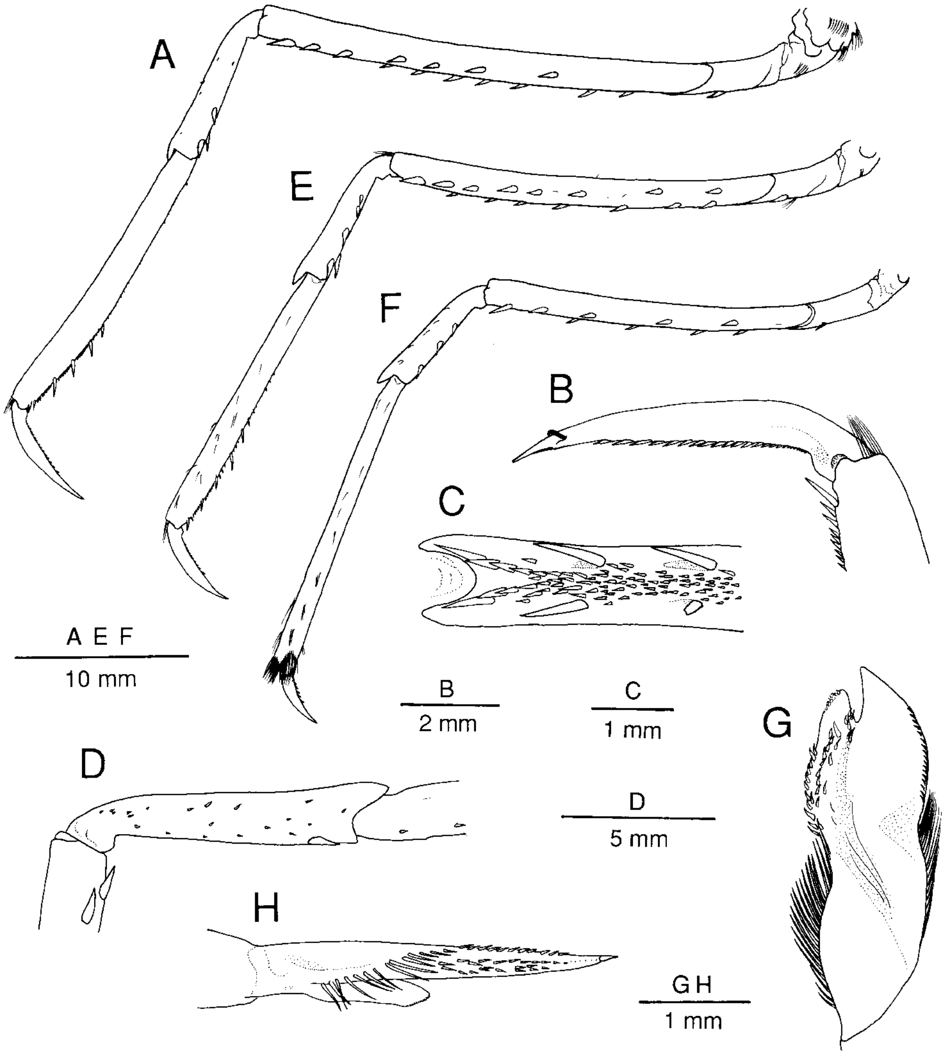


FIG. 19. *Pandalus hypsinotus* Brandt, 1851. (A)–(F) Functional male (CL 31.2 mm), off Miyako, Iwate, Japan, HUMZ-C 204; (G), (H) male (CL 28.7 mm), off Ojironai, Volcano Bay, southern Hokkaido, HUMZ-C 422. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) endopod of left first pleopod, ventral; (H) appendix masculina and interna of left second pleopod, dorsal.

(CL 19.8–23.2 mm); HUMZ-5. Off Hiroo, eastern Hokkaido, 42°16.2′N, 143°41.6′E, 217 m; 7 September 1986; otter trawl by T/S *Oshoro-Maru*; coll. T. Komai; 1 ovig. female (CL 46.2 mm); HUMZ-C 72. Usujiri, rocky intertidal; 15 July 1987; beach seine; coll. T. Komai; 1 juv. (CL 8.3 mm); HUMZ-C 145. Off Miyako, Iwate; January 1985; commercial trawler; coll. T. Komai; 1 male (CL 31.2 mm); HUMZ-C 204. Off Usujiri, Oshima Peninsula, southern Hokkaido; May 1987; set net; coll. T. Komai; 1 male (CL 15.8 mm); HUMZ-C 313. Off Tomakomai, southern Hokkaido; 28 June 1988; otter trawl by R/V *Ushio-Maru*; coll. F. Muto; 2 males

(CL 20.4, 21.3 mm); HUMZ-C 394. Off Ojironai, Volcano Bay, southern Hokkaido; 18 December 1968; coll. T. Igarashi; 1 male (CL 28.7 mm); HUMZ-C 422. Off Ojironai, Volcano Bay, 19 December 1968; coll. T. Igarashi; 5 males (CL 14.4–16.5 mm); HUMZ-C 423. Off Hachinohe, Aomori, 40°30.8′N, 145°18.4′E, 501 m; 3 April 1989; otter trawl by TS *Hokusei-Maru*; coll. O. Yamamura; 1 female (CL 35.0 mm); HUMZ-C 1075. Kitami Yamato Bank, southern Okhotsk Sea, 44°17.2′N, 144°16.3′E, 271–283 m; 7 September 1991; otter trawl; coll. T. Komai; 1 male (CL 26.8 mm), 3 females (CL 40.5–48.0 mm); HUMZ-C 2413.

Siberia. Lebyazhiya Bay, Shantar Islands, northern Okhotsk Sea, 23 m; 31 July 1995; beam trawl; coll. M. Yabe; 11 subadult males (CL 10.0–13.8 mm); CBM-ZC 2577. Near Vladivostok, Peter the Great Bay, depth unknown; coll. Y. M. Yakovlev; 1 ovig. female (CL 42.2 mm); CBM-ZC 3820.

Alaska. Southeastern Alaska; 1927; coll. F. W. Hynes; 1 male (CL 23.3 mm), 1 female (CL 29.4 mm), 1 ovig. female (CL 29.0 mm); USNM 61791.

Northwest coast of North America. Queen Charlotte Sound, 30–54 m; *Albatross*, stn 4203; 2 males (CL 16.6, 17.0 mm); USNM 31674.

Description. Rostrum (figure 18A, B) noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.33–1.84 times longer than carapace; dorsal margin nearly straight over eyes, armed with 17–22 spines, including 7–10 on carapace posterior to level of orbital margin, and two (rarely one) fixed teeth near apex of rostrum, subdistal 0.3–0.5 unarmed, posteriormost spine arising from 0.60–0.65 of carapace length in adults; ventral margin with 8–10 teeth, posterior two or three teeth somewhat elongate, posteriormost tooth strongest; lateral carina conspicuous in proximal half. Carapace (figure 18A) with postrostral ridge highly crested in adults, extending nearly to posterodorsal margin of carapace; dorsal profile in lateral view convex.

Abdomen (figure 18C) with third somite lacking median projection or carina, posterodorsal margin rounded; fourth abdominal somite without posterodorsal median tooth; sixth somite 0.5–0.6 times as long as carapace and 1.7–2.0 times as long as proximal depth. Telson (figure 18D) moderately broad, armed with five or six dorsolateral spines on either side.

Eye (figure 18A) broadly subpyriform.

Antennular peduncle (figure 18A) reaching mid-length of scaphocerite; intermediate segment unarmed dorsally. Antennal scaphocerite (figure 18E) 0.8–1.1 times as long as carapace and 4.8–5.5 times as long as wide, lateral margin weakly concave, distolateral tooth distinctly over-reaching distal margin of blade in juveniles and subadults, but just reaching or falling slightly short of that in adults (figure 18F).

Third maxilliped reaching or falling slightly short of distal margin of scaphocerite.

First pereopod falling somewhat short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.6–0.8 of carpus; carpus divided into about 50–80 articles; merus annulated entirely; ischium with annulation in distal 0.4. Right second pereopod over-reaching scaphocerite by length of chela and distalmost article of carpus; carpus divided into 19–24 articles; merus with few annulations in distal 0.3. Third to fifth pereopods moderately stout, noticeably becoming shorter successively. Third pereopod (figure 19A) over-reaching scaphocerite by length of dactyl and 0.5–0.8 of propodus; dactyl (figure 19B) 0.33–0.49 times as long as propodus in males and 0.30–0.38 times as long in females, with 16–27 accessory spinules on proximal 0.60–0.75 of flexor margin; propodus of functional males (figure 19C) compressed, weakly curved, flexor surface with numerous spinules, flanked by two rows of moderately long spines, in distal 0.7, lateral and dorsal surface nearly smooth, mesial face with few scattered spinules; propodus of females generally similar to that of functional males, but flexor surface with fewer spinules; carpus (figure 19A, D) with two or three lateral and one subdistal mesial spines, mesial surface with scattered spinules; merus 0.9–1.1 times as long as carapace, with 7–11 lateral and 7–10 ventral or ventromesial spines. Fourth pereopod (figure 19E) reaching distal margin of scaphocerite by tip of dactyl or over-reaching that by length of dactyl; dactyl 0.29–0.42 times as long as propodus in males and 0.31–0.36 times as long in females, with 13–23 accessory spinules on proximal 0.7 of flexor margin; carpus with two or three lateral and one mesial spines and with few mesial spinules dorsally; merus 0.8–0.9 times as long as carpus, with seven to nine lateral and six or seven ventral or ventromesial spines. Fifth pereopod (figure 19F) reaching mid-length of scaphocerite by tip of propodus or of dactyl; dactyl 0.26–0.31 times as long as propodus, with 8–11 accessory spinules; carpus with two or three lateral and one mesial spines; merus 0.7–0.8 times as long as carapace, with four to six lateral and four or five ventral or ventromesial spines.

Endopod of first pleopod in functional males (figure 19G) with appendix interna subterminal, moderately inflated, separated from endopod by deep V-shaped notch, armed with curved spinules on dorsal, mesial and ventral surfaces. Appendix masculina of second pleopod in functional males (figure 19H) elongate, armed dorsally with irregular three or four rows of numerous spines or spinules.

Colour. Base colour light tan or orange. Carapace with reddish or brownish area around orbital and cardiac regions; branchial region with scattered red spots; hepatic region with somewhat large white spots. Abdomen with reddish or chocolate brown transverse bands on third to fifth somites; reddish brown blotches or spots on dorsal and lateral surfaces of each somite. Miyake (1975: 100), Hayashi (1995: pl. 90, fig. 4) and Jensen (1995: 54) published colour photographs of this species.

Size. Largest male: CL 29.4 mm (Butler, 1980); females: CL 28.7–46.2 mm (present study).

Distribution. Widely distributed in the northern North Pacific: Alaska; Puget Sound; Bering Sea; Kamtchatka; Kurile Islands; Okhotsk Sea; Sea of Japan; continental coast southward to Korea; northern Japan; 5–501 m. Juveniles sometimes occur in intertidal zone in southern Hokkaido.

Remarks. The material from the various localities is generally very similar, though the species shows a wide geographical range in the northern North Pacific. The shape of the carapace is variable according to growth in this species. In young specimens (figure 18G), the postrostral ridge is low, and extends to the posterior 0.7 of the carapace length. In adults (figure 18A), the ridge is highly crested and extends near to the posterior end of the carapace, with a convex dorsal profile in lateral view. Additionally, the degree of extension of the distolateral tooth of the scaphocerite is subject to growth change in *P. hypsinotus*. In juveniles and subadult specimens, the tooth extends beyond the distal margin of the blade, while in adult specimens, it falls short of or just reaches that margin.

Morphology of the third pereopod is generally similar between functional males and females. Proportional ratio of 'dactyl length/propodus length' of the third and fourth pereopods greatly overlap between males and females, though the ratio may be greater in males than in females (0.33–0.48 versus 0.30–0.38).

The present species represents one of the largest known within the genus. The highly crested dorsal margin of the carapace with a convex profile characterizes this species. One of the closest relative is *P. gracilis*, but the largest *P. gracilis* is much smaller than the largest male of *P. hypsinotus*. Without determination of sex, the young of the present species may be easily mistaken for *P. gracilis*. Nevertheless, the relatively longer rostrum with more numerous ventral teeth will separate young of *P. hypsinotus* from adult *P. gracilis* (see 'Remarks' under account of *P. gracilis*).

Pandalus hypsinotus has often been confused with *P. prensor* or *P. gracilis* in the literature. Urita (1942) was the first to make clear distinction between *P. hypsinotus* and *P. prensor* (under the name of *P. meridionalis* Balss, 1914). Recently Hayashi (1988) clarified a serious confusion between *P. gracilis* and *P. hypsinotus*, showing the former to be a distinct species, not a synonym of the latter. Although De Man (1920) suggested that *P. stimpsoni* Thallwitz, 1891 was probably identical with *P. hypsinotus*, Thallwitz's taxon is interpreted to be a junior subjective synonym of *P. gracilis* Stimpson, 1860 (see 'Remarks' under account of *P. gracilis*). Yokoya (1933) reported *Pandalus hypsinotus* from 12 'Soyo-Maru' stations; all were from the Sea of Japan, including Tsugaru Strait. The specimens from the two stations (600 and 648) in the collection of the Kitakyushu Museum of Natural History were re-examined and it was found that they did not represent *P. hypsinotus*, but *P. prensor* instead. The photograph given by Miyake (1982) as *Pandalus hypsinotus* certainly shows a shrimp belonging to a genus other than *Pandalus*. In all probability, it represents *Plesionika izumiae* Omori, 1971, judging from the colour and the shape of the dactyls of the third to fifth pereopods.

Pandalus danae Stimpson, 1857
(figures 20 and 21)

Pandalus danae Stimpson, 1857: 87, pl. 21, figs 6 and 7 [type locality: opposite Fort Townsend in Puget Sound]; Walker, 1898: Holmes, 1900: 209, pl. 4, figs 61 and 62; Rathbun, 1904: 47, fig. 13; De Man, 1920: 103; Schmitt, 1921: 44, fig. 25, pl. 13, fig. 3; Berkeley, 1930: 5, figs 1D, 2, 14 and 15; Bousfield and McAllister, 1962: Scrivener and Butler, 1971: 37 (bibliography); Squires and Figueira, 1974: 15; Butler, 1980: 147, unnumbered fig., pl. 4A; Holthuis, 1980: 139; Rothlisberg, 1980: 19; Wicksten, 1984: 136, 137; Kozloff, 1987: 397 (key), fig. 19.5; Wicksten, 1989: 303, 313; Williams *et al.*, 1989: 19; Wicksten, 1991: 812–815 (part); Jensen, 1995: 53, fig. 98.

Pandalus franciscorum Kingsley, 1878: 94 [type locality: San Francisco]; De Man, 1920: 103.

Not *Pandalus danae*: Kim, 1985: 67, fig. 1A, B. [=*Pandalus prensor* Stimpson, 1860].

Material examined. **Northwest coast of North America**. Juan de Fuca Islands, Washington State, 81 m; 3 males (CL 13.3–15.4 mm), 2 females (CL 15.2, 19.6 mm); USNM 28033.

California. San Francisco Bay, California, 39–95 m; *Albatross*; 4 November 1912; 3 males (CL 15.0–20.0 mm); USNM 55520. San Francisco Bay, 31–34 m; *Albatross*; 30 January 1912; 2 males (CL 13.4, 16.4 mm); USNM 55535.

Type material. Presumably no longer extant. Material from the North Pacific Exploring Expedition (1853–56), studied by William Stimpson, was destroyed in the 1871 Chicago fire (Evans, 1967; Deiss and Manning, 1981).

Description. Rostrum (figure 20A, B) moderately to noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.28–1.54 times longer than carapace; dorsal margin nearly straight over eyes, armed with 9–11 spines, including four or five on carapace posterior to level of orbital margin, and two or three fixed teeth near apex of rostrum, subdistal 0.4–0.3 unarmed, posteriormost spine arising from 0.51–0.60 of carapace length; ventral margin with six teeth, posteriormost tooth more strongly erect and much stronger than preceding teeth; lateral carina conspicuous in proximal

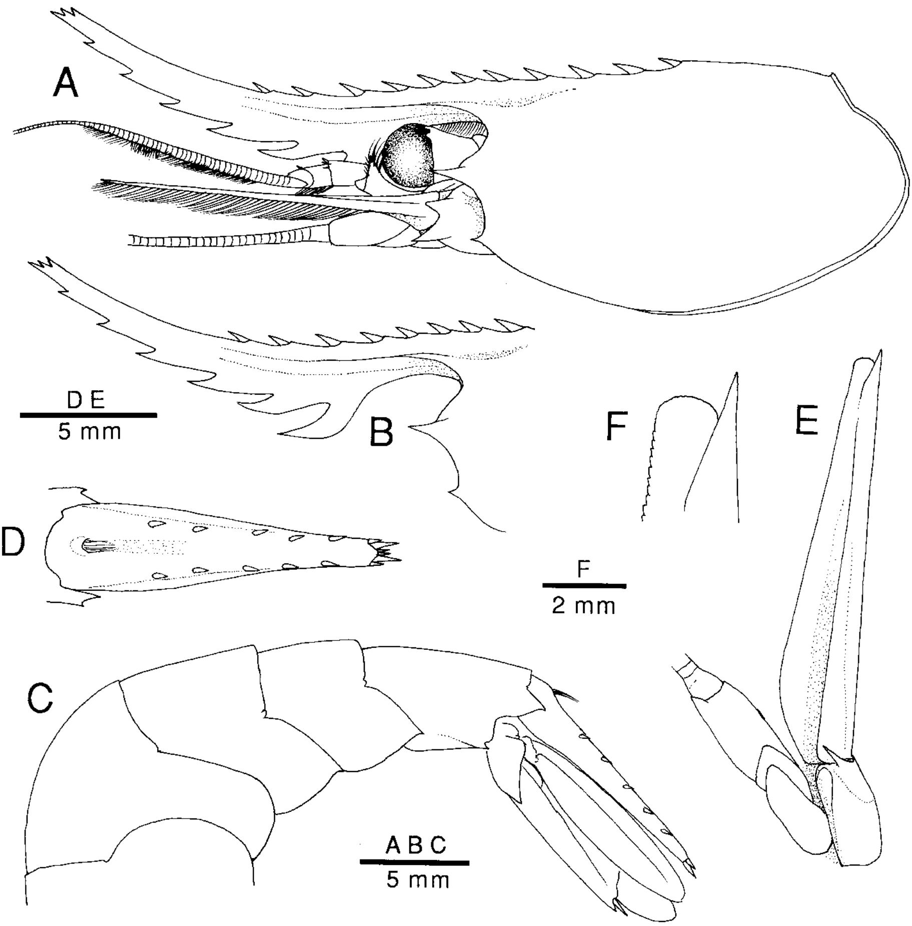


FIG. 20. *Pandalus danae* Stimpson, 1857. Female (CL 16.0 mm), Straits of Juan de Fuca, Washington State, USNM 28033. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral.

half. Carapace (figure 20A) with postrostral ridge low, extending beyond mid-length of carapace; dorsal profile in lateral view slightly sinuous with peak at level of posteriormost dorsal spine.

Abdomen (figure 20C) with third somite lacking median projection or carina; posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5–0.6 times as long as carapace and 1.7–1.9 times as long as proximal depth. Telson (figure 20D) moderately broad, armed with six (rarely five) dorsolateral spines on either side.

Eye (figure 20A) broadly subpyriform.

Antennular peduncle (figure 20A) reaching mid-length of scaphocerite; intermediate segment unarmed dorsally. Antennal scaphocerite (figure 20E) 0.8–1.0 times as long as carapace (ratio tending to decrease with growth) and 5.3–5.7 times longer than wide, lateral margin weakly concave, distolateral tooth (figure 20F) distinctly over-reaching distal margin of moderately narrow, rounded blade.

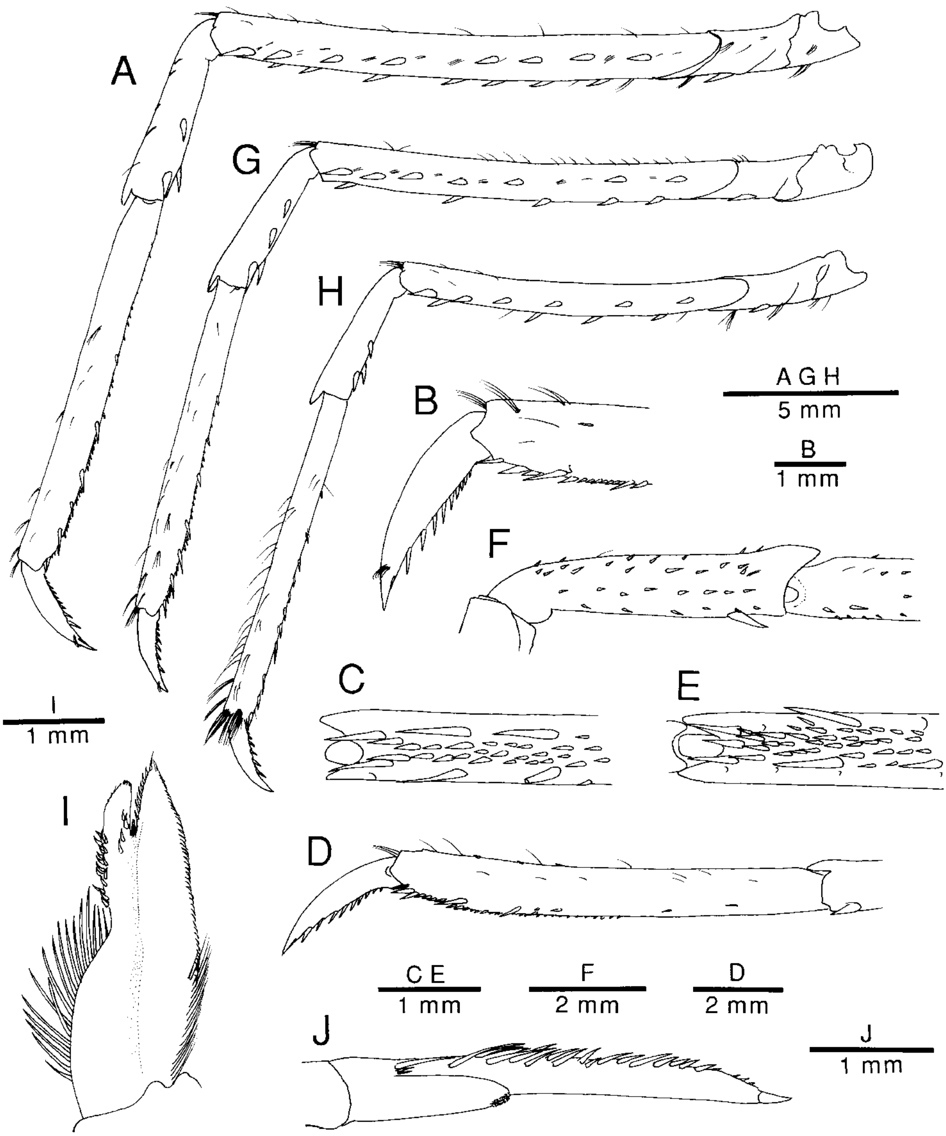


FIG. 21. *Pandalus danae* Stimpson, 1857. (A)–(C), (F)–(H) Female (CL 16.0 mm), Straits of Juan de Fuca, Washington State, USNM 28033; (D), (E), (I), (J) male (CL 14.4 mm), same lot. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C), (E) same, distal part of propodus, flexor; (D) same, dactyl and propodus, lateral; (F) carpus and proximal part of propodus, mesial; (G) left fourth pereopod, lateral; (H) left fifth pereopod, lateral; (I) endopod of left first pleopod, ventral; (J) appendix masculina and interna of left second pleopod, mesial.

Third maxilliped reaching or slightly over-reaching distal margin of scaphocerite. First pereopod falling somewhat short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.2–0.3 of carpus; carpus divided into about 60–70 articles; merus annulated entirely; ischium with annulation in distal 0.2. Right second pereopod over-reaching scaphocerite by length of chela;

carpus divided into 19–23 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 21A) over-reaching scaphocerite by length of dactyl and 0.2–0.5 of propodus; dactyl 0.35–0.54 times as long as propodus in males (figure 21D) and 0.28–0.31 times as long in females (figure 21A, B), with 12–14 accessory spinules on proximal 0.6–0.8 of flexor margin; propodus of functional males (figure 21D, E) somewhat compressed, slightly curved, flexor face with irregular three or four rows of spinules flanked by two rows of moderately long spines in distal 0.3–0.5, only mesial face with scattered spinules; propodus in females (figure 21A, C) less compressed, mesial surface with scattered spinules, but dorsal and lateral surfaces nearly smooth; carpus (figure 21A, F) with two lateral and one subdistal mesial spines and scattered spinules mesially and dorsally (in males, spinules present only on mesial surface); merus 0.87–1.04 times longer than carapace, with 7–10 lateral and five to eight ventral or vetromesial spines. Fourth pereopod (figure 21G) reaching distal margin of scaphocerite by tip of dactyl or over-reaching it by length of dactyl; dactyl 0.27–0.31 times as long as propodus in both sexes, with nine accessory spinules; carpus with two or three lateral and one mesial spines and with fewer spinules on mesial surface; merus 0.8–0.9 times as long as carpus, with seven to nine lateral and five to seven ventral or ventromesial spines. Fifth pereopod (figure 21H) reaching mid-length of scaphocerite by tip of propodus or dactyl; dactyl 0.22–0.30 times as long as propodus, with six or seven accessory spinules; carpus with two or three lateral and one mesial spines; merus 0.7–0.8 times as long as carapace, with five or six lateral and four or five ventral or ventromesial spines.

Appendix interna of first pleopod in functional males (figure 21I) subterminal, not strongly inflated, somewhat elongate, armed with irregular rows of spinules on mesial to dorsal surface and short single row of spinules on ventral surface. Appendix masculina of second pleopod in functional males (figure 21J) elongate, armed with about 15 long spines arranged in single or double row on dorsal and dorsomesial surfaces.

Colour. Butler (1980) described the colour of *Pandalus danae* as follows: 'The individual illustrated (Plate 4A) has a milky, translucent background, with irregular striping and spots of chocolate brown on lateral and dorsolateral surfaces of all abdominal somites and telson; lying between stripes, and especially along dorsal surface including uropods, are patches of fine brick-red dots. Pleopods have basipodites with scattered small brown patches, endopods and exopods mainly brick-red. On carapace, most small brown spots on hepatic and posterior branchial regions; on posterolateral surface, wide swath of fine brick-red dots. This coloration also seen in orbital and frontal regions, along lateral surface and at tip of rostrum, on basicerite and peduncle of antenna, and antennular peduncle. Eyestalk with outer red-brown patch; bands of much the same hue on all flagella. Brown spots and bands on third maxilliped and pereopods. Fine blue spots on cardiac region of carapace, on dorsal surfaces of first to third somites. On dorsolateral surfaces of first to third abdominal somites, striping and spots on other individuals vary in shades of brown and red, and some have white markings.' Jensen (1995: 53) published a colour photograph of this species.

Size. Functional males: 13.3–26.0 mm; females: 15.2–29.2 mm (Butler, 1980; present study).

Distribution. Resurrection Bay, Alaska, to Point Loma, California; intertidal to 185 m.

Remarks. The species has rather a wide distributional range from Alaska to California. *Pandalus franciscorum*, described by Kingsley (1878) from San Francisco Bay, California, has been treated as a junior subjective synonym of the present species (e.g. Butler, 1980; Holthuis, 1980). The type of this taxon is no longer extant in the General Invertebrate Collection of the Academy of Natural Sciences, Philadelphia (N. S. Gilmore, in litt.). Since the material from San Francisco Bay is very similar to the specimens from Oregon, I have little hesitation in following the previous authors in regarding these two species as synonyms.

Wicksten (1991) concluded that *Pandalus gurneyi* Stimpson, 1871, described from Monterey, California, is a southern population of a single variable species, *P. danae*. However, the present study found that the constantly longer rostrum with more numerous ventral teeth, and more elongate scaphocerite separate the southern Californian form from the northern form. Therefore, *Pandalus gurneyi* is recognized as a good species (see 'Remarks' under account of *P. gurneyi*). The type materials of both species were presumably destroyed in the 1871 Chicago fire (Evans, 1967; Deiss and Manning, 1981). These two species are differentiated by external morphology, and are separated geographically with small overlapping at northern California. Therefore there is no necessity to designate neotypes for both taxa.

Pandalus danae is very similar to the western Pacific species, *P. prensor*. It can be best distinguished from the latter by the more posteriorly arising posteriormost median spine on the carapace and usually shorter merus of the third pereopod (see 'Remarks' under account of *P. prensor*). The present species appears to be restricted to the eastern part of the North Pacific Ocean. In all probability, the record of *P. danae* from Korea (Kim, 1985) was based on misidentification of *P. prensor*.

Pandalus prensor Stimpson, 1860
(figures 22 and 23)

Pandalus prensor Stimpson, 1860: 37 [type locality: Hakodate]; Holthuis and Rosa, 1965: 14; Holthuis, 1976: 52; Rothlisberg, 1980: 19; Mikurich *et al.*, 1982: 19, figs 1 and 2; Hayashi, 1988: 73, 74; 1995: pl. 90 fig. 5, 332; Komai *et al.*, 1992: 192; Okutani, 1994: 219, fig. 8.
Pandalus hypsinotus: Doflein, 1902: 635, pl. 4 figs 1 and 2; Yokoya, 1933: 16 (?part).
Pandalus hypsinotus meridionalis Balss, 1914: 29 (part); Urita, 1934: 254, fig. 3; Nishimura, 1939: 382.
Pandalus sp.: Yokoya, 1930: 539, pl. 16, figs 7–12.
Pandalus meridionalis?: Derjugin and Kobjakova, 1935: 142.
Pandalus meridionalis: Kobjakova, 1936: 209, pl. 3 fig. 23; 1937: 100, pl. 1 fig. 3; Urita, 1942: 7; Kobjakova, 1958: 223; 1967: 232; Igarashi, 1969: 3, pl. 2 fig. 5, pl. 13 fig. 39; Miyake, 1975: 100, unnumbered fig., 258; Takeda, 1986: 107, unnumbered fig.
?*Pandalus nipponensis*: Yokoya, 1939: 263.
Pandalopsis mitsukurii: Kim and Park, 1972: 205, pl. 4, fig. 8. Not *Pandalopsis mitsukurii* Rathbun, 1902b [=*Pandalopsis pacifica* (Doflein, 1902)].
Pandalus danae: Kim, 1985: 67, fig. 1A, B. Not *Pandalus danae* Stimpson, 1857.
?*Pandalus meridionalis*: Liu and Zhong, 1994: 560.
Not *Pandalus prensor*: Miyake, 1982: 60, pl. 20 fig. 3. [=*Pandalus gracilis* Stimpson, 1860].

Material examined. **Japan**. Cape Noshappu, Wakkanai, northern Hokkaido, intertidal; 28 September 1976; beach seine; 5 males (CL 7.7–9.1 mm), 1 transitional male (CL 9.7 mm), 2 females (CL 10.4, 12.2 mm); CBM-ZC 260. Soya, northern Hokkaido, 45 m; 18 June 1992; beam trawl; coll. S. Maruyama; 2 ovig. females (CL 14.3, 15.2 mm); CBM-ZC 507. Nemuro Bay, eastern Hokkaido, 43°43.3′N, 145°27.4′E, 8–13 m; 15 September 1995; beam trawl with 2 m opening by R/V *Tansei-Maru*; coll. T. Komai; 3 males (CL 10.4–11.8 mm), 8 females (CL 13.2–18.8 mm);

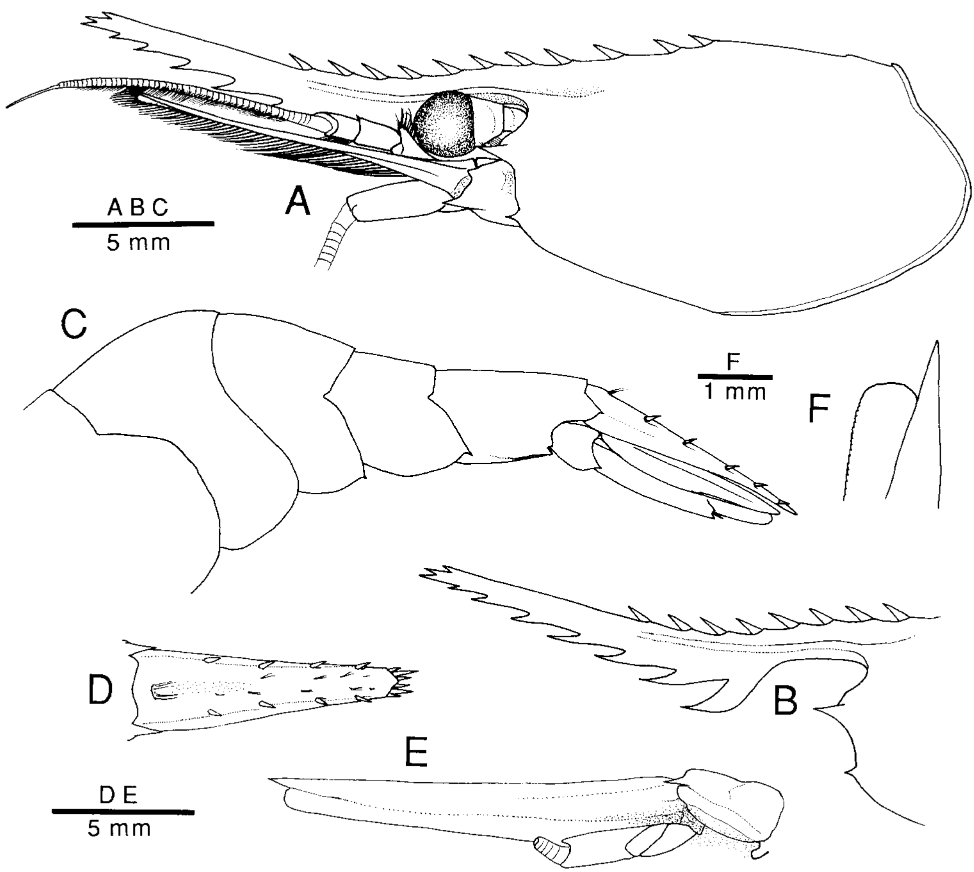


FIG. 22. *Pandalus prensor* Stimpson, 1860. Female CL 15.4 mm, Nemuro Bay, eastern Hokkaido, CBM-ZC 2426. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral.

CBM-ZC 2426. Lake Saroma, Okhotsk coast of Hokkaido, 5 m; 26 September 1990; beam trawl; coll. M. Yabe; 2 males (CL 8.0, 8.9 mm), 1 female (CL 11.8 mm); CBM-ZC 2439. Miyako Bay, Iwate, 3–4 m; 12 August 1994; trap; coll. T. Komai; 1 male (CL 9.0 mm); CBM-ZC 3032. Sokei, Miyako Bay, Iwate, 2 m; 15 June 1987; trap; coll. T. Komai; 1 juv. (CL 3.0 mm); HUMZ-C 94. Wakkanai, northern Hokkaido, grass beds; September 19871; 1 male (CL 11.8 mm); HUMZ-C 143. Sokei, Miyako Bay, Iwate, 2 m; 24 October 1987; trap; coll. T. Komai; 2 males (CL 11.6, 11.7 mm); HUMZ-C 158. Odaito, Okhotsk coast of Hokkaido; 30 May 1988; dip. net; coll. M. Yabe & F. Muto; 1 female (CL 15.7 mm); HUMZ-C 379. Off Kushiro, eastern Hokkaido, 54 m; trawl; coll. J. Sasaki; 1 female (CL 20.0 mm); HUMZ-C 1034. Off Yubetsu, Okhotsk coast of Hokkaido, depth unknown; 21 August 1990; beam trawl; coll. S. Goshima; 2 transitional males (CL 12.5, 13.0 mm); HUMZ-C 2146. Off Usujiri, Oshima Peninsula, southern Hokkaido, 10–15 m; 23 April 1993; dredge; coll. F. Muto; 1 male (CL 13.8 mm), 1 ovig. female (CL 11.6 mm); HUMZ-C 2157. North of Sado Island, 168 m; Soyo-Maru, stn 600; 9 August 1930;

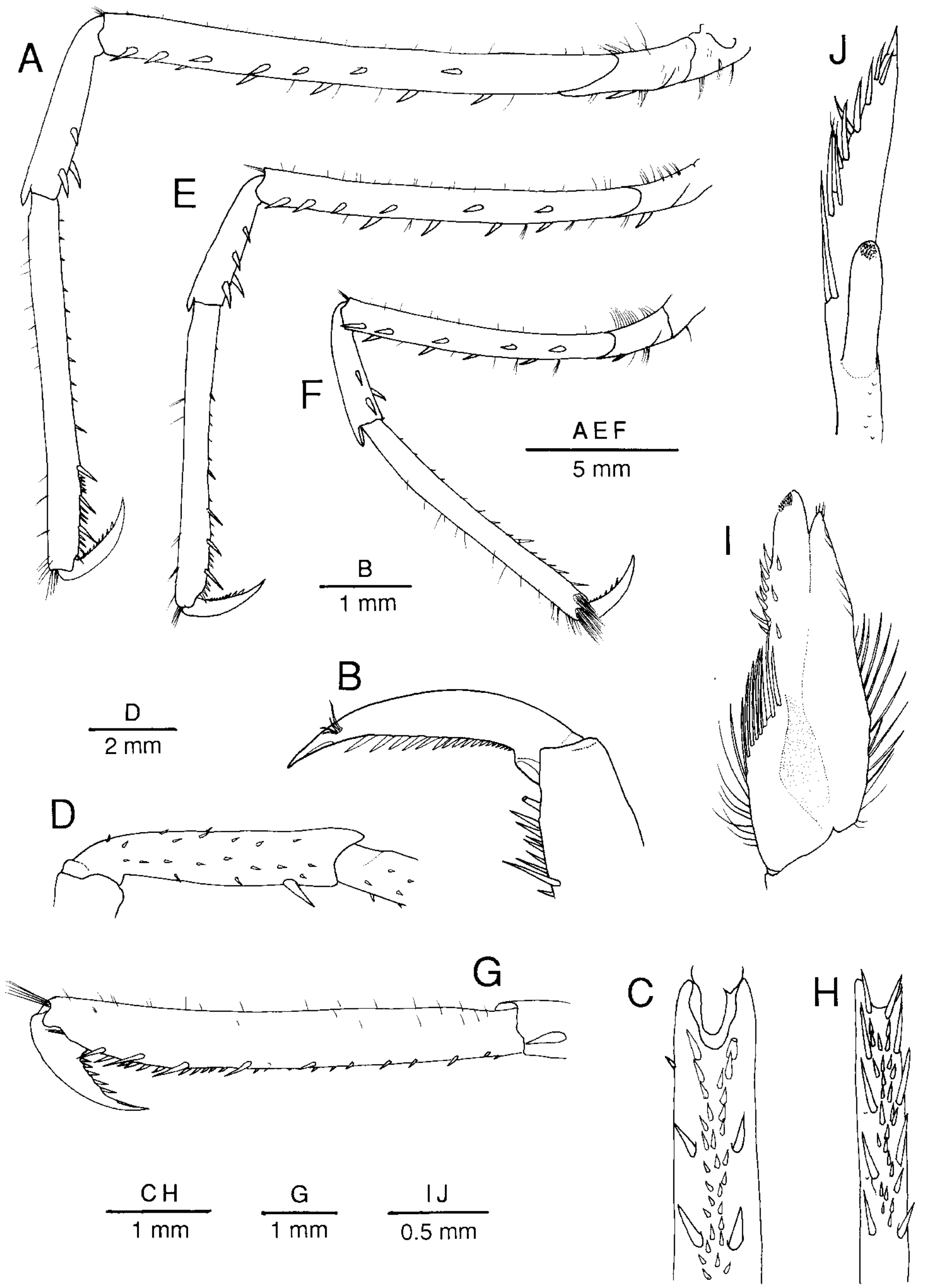


FIG. 23. *Pandalus prensor* Stimpson, 1860. (A)–(F) Female (CL 15.4 mm), Nemuro Bay, eastern Hokkaido, CBM-ZC 2426; (G)–(J) functional male (CL 8.0 mm), Noshappu-misaki, northern Hokkaido, CBM-ZC 260. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) dactyl and propodus of third pereopod, lateral; (H) distal part of propodus of left third pereopod, flexor; (I) endopod of left first pleopod, ventral; (J) appendix masculina and interna of left second pleopod, mesial.

1 male (CL 8.5 mm), referred to as *Pandalus hypsinotus* by Yokoya (1933); KMNH. West of Tsugaru Strait, 247 m; Soyo-Maru, stn 648; 23 August 1930; 3 males (CL 8.9–9.5 mm), 1 ovig. female (CL 13.7 mm), referred to as *Pandalus hypsinotus* by Yokoya (1933); KMNH.

Russian continental coast of Sea of Japan. Olga Bay, 2–5 m; 19 August 1994; beam trawl; coll. M. Yabe; 3 females (CL 15.2–18.5 mm); CBM-ZC 2443. Srednaya Bay, 1 m; 24 August 1994; beach seine; coll. M. Yabe; 1 female (CL 15.5 mm); CBM-ZC 2450.

Type material. The type of *Pandalus prensor* Stimpson is no longer extant (Holthuis, 1976). It was destroyed in the Chicago fire of 1871 (Evans, 1967; Deiss and Manning, 1981).

Description. Rostrum (figure 22A, B) moderately (females) or noticeably (males) curving dorsally, slightly or distinctly over-reaching scaphocerite, 0.92–1.44 times as long as carapace; dorsal margin nearly straight over eyes, armed with 10–14 spines, including four or five (rarely six) on carapace posterior to level of orbital margin, and two or three fixed teeth near apex of rostrum, subdistal 0.4–0.3 unarmed, posteriormost spine arising from 0.48–0.51 of carapace length; ventral margin with six or seven (rarely eight) teeth, posteriormost tooth more strongly erect and much stronger than preceding teeth; lateral carina conspicuous in proximal half. Carapace (figure 22A) with postrostral ridge low, extending beyond mid-length of carapace; dorsal profile in lateral view slightly sinuous with peak at level of posteriormost dorsal spine.

Abdomen (figure 22C) with third somite lacking median projection or carina; posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5 times as long as carapace and 1.7–1.9 times as long as proximal depth. Telson (figure 22D) moderately broad, armed with five or six dorsolateral spines on either side.

Eye (figure 22A) broadly subpyriform.

Antennular peduncle (figure 22A) reaching mid-length of scaphocerite; intermediate segment unarmed on dorsal surface. Antennal scaphocerite (figure 22E) 0.8–1.0 times as long as carapace (ratio tending to decrease with growth) and 4.8–5.5 times as long as wide, lateral margin weakly concave, distolateral tooth (figure 22F) distinctly over-reaching distal margin of moderately narrow, rounded blade.

Third maxilliped reaching or slightly over-reaching distal margin of scaphocerite.

First pereopod somewhat falling short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.2–0.3 of carpus; carpus divided into about 44–51 articles; merus annulated entirely; ischium with annulation in distal 0.2. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 17–20 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, becoming noticeably shorter successively. Third pereopod (figure 23A) over-reaching scaphocerite by length of dactyl and 0.5–0.8 of propodus; dactyl rather stout even in males, 0.27–0.36 times as long as propodus in males (figure 23G) and 0.22–0.30 times as long in females (figure 23A), with 8–15 accessory spinules on proximal 0.6 of flexor margin; propodus of functional males (figure 23G, H) somewhat compressed, straight or slightly curved, flexor face with irregularly double or triple row of spinules flanked by two rows of moderately long spines in distal 0.3–0.5, only mesial face with scattered spinules; propodus in females (figure 23A, C) less compressed, weakly curved or nearly straight, mesial surface with scattered spinules, but dorsal and lateral surface nearly smooth; carpus (figure 23A, D) with one to three (usually two) lateral and one subdistal mesial spines and scattered spinules mesially and dorsally (in males, spinules present only on mesial surface); merus 1.0–1.3 times as long as carapace, with five to eight lateral and six to nine ventral or ventromesial spines. Fourth pereopod (figure 23E) reaching distal margin of scaphocerite by tip of dactyl or over-reaching that by length of dactyl; dactyl 0.21–0.26 times as long as propodus in both sexes, with 6–10 accessory spinules; carpus with two or three lateral and one mesial spines and with fewer spinules on mesial surface; merus 0.8–1.0 times as long as carpus, with five to seven lateral and four to six ventral or ventromesial spines. Fifth pereopod (figure 23F) reaching mid-length of scaphocerite by tip of propodus or dactyl; dactyl 0.19–0.28 times as long as propodus, with 6–10 accessory spinules; carpus with two or three lateral and one mesial spines; merus 0.6–0.7 times as long as carapace, with four to six lateral and four or five ventral or ventromesial spines.

Appendix interna of first pleopod in functional males (figure 23I) subterminal, not strongly inflated, separated from endopod by V-shaped notch. Appendix masculina of second pleopod in functional males (figure 23J) elongate, attaining more than twice length of appendix interna, terminating in acute apex, armed with about 15 long spines dorsally or dorsomesially.

Colour. Base colour of body brown or reddish brown. Carapace with paler spots or faint stripes on lateral surface, with fine blue spots on cardiac region. Abdomen also with paler spots or irregular striping and scattered fine blue spots, and sometimes with white median markings. Scaphocerite entirely brown. Antennal flagellum banded with brown and white. Third maxilliped and ambulatory pereopods banded with brown, yellow and violet or blue-gray. Miyake (1975: 100), Takeda (1986: 107) and Okutani (1994: 219, figure 8) published colour photographs of this species.

Size. Largest functional male: 13.8 mm in CL; largest female: 20.0 mm.

Distribution. Restricted to Asian waters: northern Japan; continental coast of Russia; Sakhalin; southern Kurile Islands; Korea; subtidal to 247 m.

Remarks. The proportional length of the dactyl of the third pereopod in functional males is rather widely variable in *P. prensor*. The ratio of 'dactyl length/propodus length' ranges from 0.24 to 0.34. The ratio in females (0.22–0.30) is greatly overlapped by the variation range of males. In addition, even in females, the propodus of the third pereopod is nearly smooth on the lateral and dorsal surfaces. The degree of curvature of the rostrum seems to differ between males and females. In general, the rostrum is more strongly curved dorsally in males than in females.

The present species from the northwestern Pacific is very similar to *P. danae* from the northeastern Pacific in both external morphology and coloration, but, so far as I can determine, specimens from both sides of the Pacific have not been compared. The present study found several minor but notable differences between the specimens from the northwest and northeast Pacific. The posteriormost median spine on the carapace arises more anteriorly in *P. prensor* than in *P. danae*. The position where that spine arises is 0.48–0.51 of the carapace length in *P. prensor* and 0.53–0.60 in *P. danae*. The merus of the third pereopod is proportionally longer in *P. prensor* than in *P. danae* (1.0–1.27 as long as the carapace versus 0.94–1.04 times as long), though the ratios partly overlap. The dactyl of the third pereopod in functional males is proportionally shorter in *P. prensor* than in *P. danae* (0.27–0.36 times as long as propodus versus 0.36–0.43 times as long). In addition, the available material and literature records suggest that *P. danae* can attain much larger size than *P. prensor* (29.2 mm in CL versus 20.0 mm in CL).

As Holthuis (1976) demonstrated, there is little doubt that *Pandalus hypsinotus meriodionalis* Balss, 1914, is a junior synonym of *Pandalus prensor*. The pandalid shrimp reported from Mutsu Bay by Yokoya (1930) as '*Pandalus* sp.' might actually be *P. prensor*, as the figure given by Yokoya is very similar to that species. Later Yokoya (1933) reported *Pandalus hypsinotus* from 12 'Soyo-Maru' stations, all were from the Sea of Japan, including Tsugaru Strait. I re-examined the specimens from the two stations (600 and 648) in the collection of the KMNH, and found that they do not represent *P. hypsinotus*, but *P. prensor* instead. Yokoya (1939) reported *P. nipponensis* from near Kinkazan, Miyagi Prefecture (northeastern part of Honshu mainland, Japan), at a depth of 19 m. Yokoya's specimen may belong to the present species instead of *P. nipponensis*, because his material was obtained from a depth much shallower than those for *P. nipponensis* (shallowest depth 100 m in the present study). Record of *P. danae* from Korea (Kim, 1985) is probably based on the misidentification of specimens of *P. prensor*. There is little doubt that Miyake's (1982) specimen referred to as *P. prensor* actually belongs to *P. gracilis*. The record by Liu and Zhong (1984) from the Yellow Sea (under the name of *P. meridionalis*) needs to be verified.

Although Balss (footnote in De Man, 1920: 103) regarded *Pandalus robustus* Stimpson, 1860 as identical with *P. prensor*, the former taxon is here interpreted to be synonymous with *P. gracilis* Stimpson, 1860 (see under 'Remarks' of *P. gracilis*).

Pandalus gracilis Stimpson, 1860
(figures 24–26)

Pandalus gracilis Stimpson, 1860: 37 [type locality: Hakodati (=Hakodate), Hokkaido, Japan]; Miers, 1879: 56; De Man, 1920: 103; Kim and Park, 1972: 204; Hayashi, 1988: 72; Komai *et al*., 1992: 192.

Pandalus robustus Stimpson, 1860: 37 [type locality: Hakodati (=Hakodate), Hokkaido, Japan]; De Man, 1920: 104.

Pandalus stimpsoni Thallwitz, 1891: 3 [type locality: Japan or China].

Pandalus platyceros: Balss, 1914: (in part); Yokoya, 1933: 15. Not *Pandalus platyceros* Brandt, 1851.

Pandalus hypsinotus: Holthuis, 1976: 50, fig. 1. Not *Pandalus hypsinotus* Brandt, 1851.

Pandalus sp.: Tashiro *et al*., 1979: 53, fig. 8.

Pandalus prensor: Miyake, 1982: 60, pl. 20 fig. 3. Not *Pandalus prensor* Stimpson, 1860.

Material examined. **Japan**. Off Shiriya-zaki, Tsugaru Strait, 41°30′N, 141°32′E, 65 m; 1 July 1992, dredge by R/V *Soyo-Maru*; coll. H. Saito; 1 ovig. female (CL 10.4 mm), CBM-ZC 356. Off Hamada, Shimane Prefecture, Sea of Japan, 35°23.2′N, 132°20.2′E, 151 m, 11 September 1994, trawl; 5 males (CL 8.7–12.5 mm), 3 ovig. females (CL 12.2–14.0 mm), CBM-ZC 2576. Northwest of Tsushima, Sea of Japan, 34°38′N, 129°10′E, 153–204 m; 31 March 1978; trawl; 2 males (CL 12.7, 13.2 mm), 5 females (CL 14.0–17.3 mm); HUMZ-C 370. Sendai Bay, Pacific coast of northeastern Honshu, 37°49.2′N, 141–23.6′E, 106 m; 29 May 1989; otter trawl by RV *Tanshu-Maru*; coll. O. Yamamura; 1 ovig. female (CL 14.0 mm); HUMZ-C 991. South of Sado Island, Sea of Japan, 311 m; *Soyo-Maru*, station 591; 3 August 1930; 1 male, badly damaged, referred to as *Pandalus platyceros* by Yokoya (1933); KMNH.

Type material. Lectotype: Hakodate Bay, southern Hokkaido, Japan; female (CL 5 mm); NHM 61.44 (Evans, 1967; Holthuis, 1976). Not re-examined.

Description. Body moderately robust. Rostrum (figure 24A, B) moderately curving dorsally, somewhat over-reaching scaphocerite, 1.05–1.27 times as long as

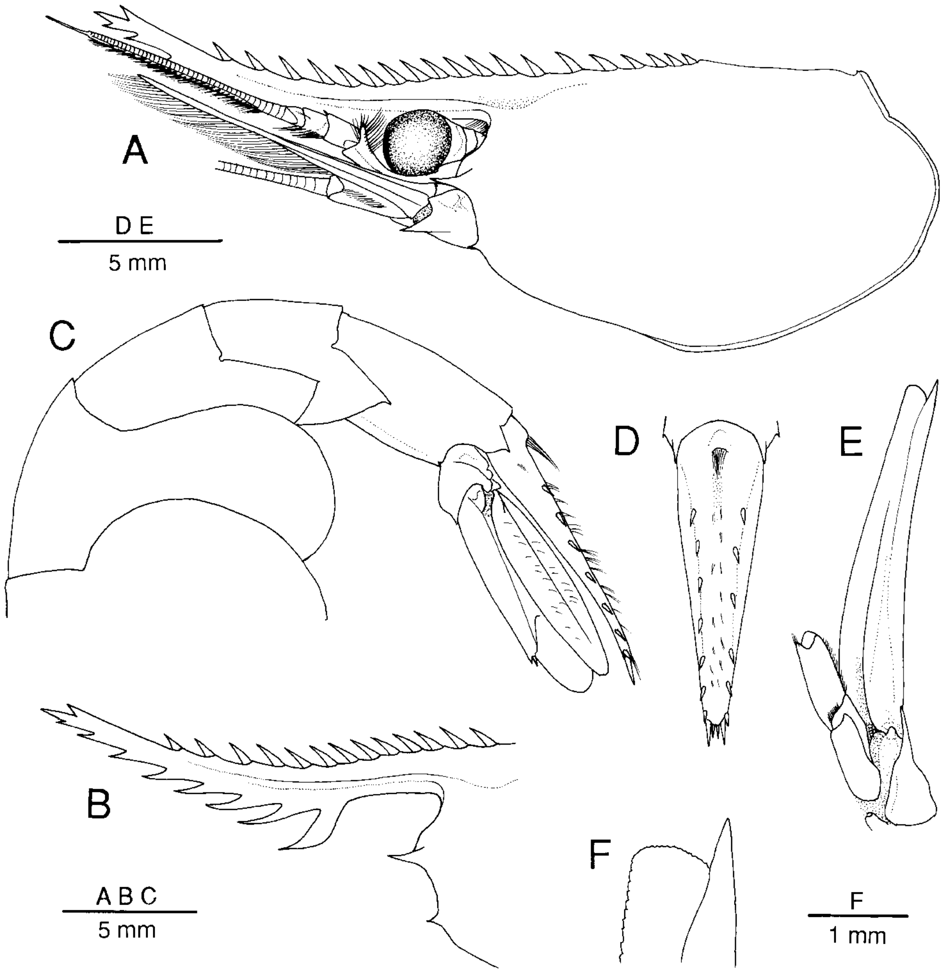


FIG. 24. *Pandalus gracilis* Stimpson, 1860. Ovig. female (CL 13.9 mm), off Hamada, Shimane, Sea of Japan, CBM-ZC 2576. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral.

carapace; dorsal margin nearly straight over eyes, armed with 14–21 moderately short spines, including seven to nine (rarely six) on carapace posterior to level of orbital margin, and one or two fixed teeth near apex of rostrum, subdistal 0.2–0.3 unarmed, anteriormost spine arising from anterior to level of distal end of antennular peduncle, posteriormost spine arising from 0.50–0.54 of carapace length; ventral margin with six or seven teeth, posteriormost tooth much stronger than preceding teeth; lateral carina conspicuous in proximal half. Carapace (figure 24A) with post-rostral ridge low, extending beyond mid-length of carapace; dorsal profile weakly sinuous, with peak at level of posteriormost dorsal spine.

Abdomen (figure 24C) with third somite lacking median projection or carina; posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5–0.6 times as long as carapace and 1.8–1.9 times as long as proximal depth. Telson

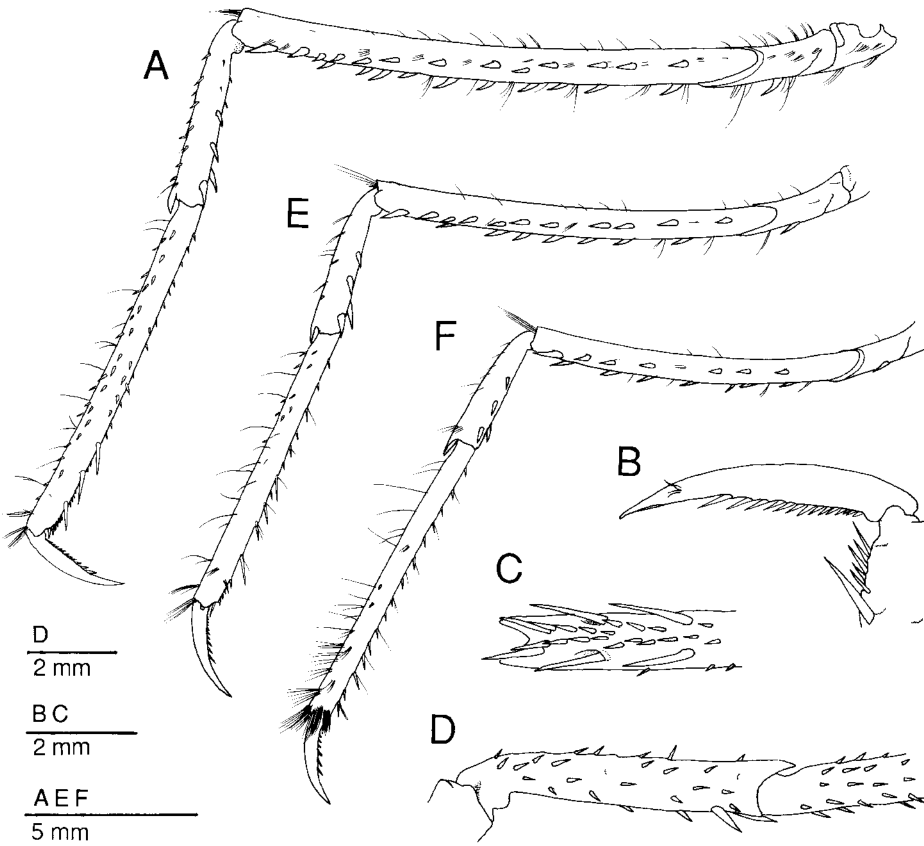


FIG. 25. *Pandalus gracilis* Stimpson, 1860. Ovig. female (CL 13.9 mm), off Hamada, Shimane, Sea of Japan, CBM-ZC 2576. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral.

(figure 24D) moderately broad, armed with five to eight (usually six) dorsolateral spines on either side.

Eye (figure 24A) broadly subpyriform.

Antennular peduncle (figure 24A) reaching mid-length of scaphocerite; intermediate segment without spines on dorsal surface. Antennal scaphocerite (figure 24E) 0.7–1.0 times as long as carapace and 5.3–5.7 times as long as wide, lateral margin weakly concave, distolateral tooth (figure 24F) distinctly over-reaching distal margin of moderately broad, rounded blade.

Third maxilliped reaching or slightly over-reaching distal margin of scaphocerite.

First pereopod falling slightly short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.6–0.8 of carpus; carpus divided into about 50–56 articles; merus annulated entirely; ischium with annulation in distal 0.2. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 15–20 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, noticeably becoming shorter successively. Third pereopod (figure 25A) over-reaching scaphocerite by length of dactyl and distal 0.8 to entire propodus; dactyl slender, 0.57–0.65 times as long as propodus in functional

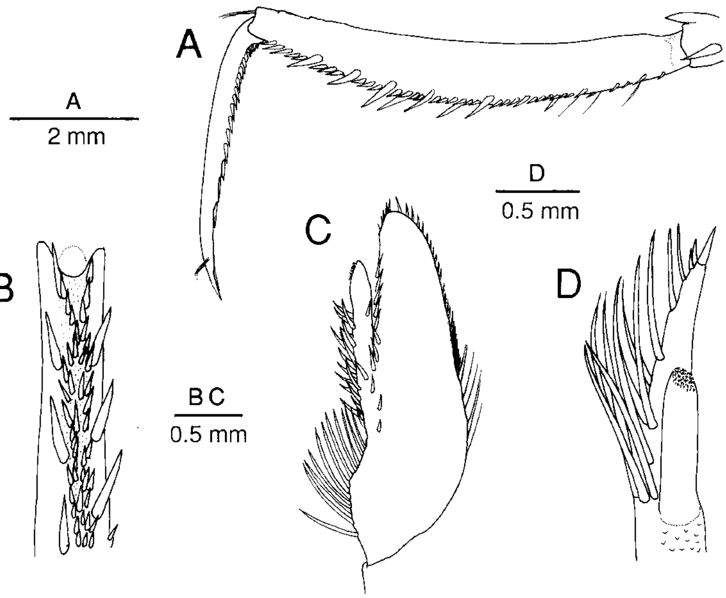


FIG. 26. *Pandalus gracilis* Stimpson, 1860. Functional male (CL 10.5 mm), off Hamada, Shimane, Sea of Japan, CBM-ZC 2576. (A) Dactyl and propodus of left third pereopod, lateral; (B) distal part of propodus of left third pereopod, flexor; (C) endopod of left first pleopod, ventral; (D) appendix masculina and interna of left second pleopod, mesial.

males (figure 26A), 0.22–0.33 times as long in females (figure 25A, B), with 11–19 accessory spinules on proximal 0.75 of flexor margin; propodus of functional males (figure 26A, B) strongly compressed, noticeably curved, flexor surface with numerous spinules arranged in two or three rows, flanked by two rows of moderately long spines, lateral and dorsal surfaces not spinose; propodus of females (figure 26A, C) straight, flexor surface with fewer spinules, lateral, dorsal and mesial surfaces spinose; carpus (figure 25A, D) with three lateral and one mesial spines and scattered spinules mesially and dorsally (in males, spinules present only on mesial surface); merus 1.2–1.3 times as long as carapace, with 9–16 lateral and 7–14 ventral or ventromesial spines. Fourth pereopod (figure 25E) over-reaching scaphocerite by length of dactyl and 0.25 of propodus; dactyl 0.46–0.48 times as long as propodus in functional males, 0.22–0.34 times as long in females, with 9–13 accessory spinules on proximal half of flexor margin; propodus of females with fewer spinules on lateral and mesial surfaces; carpus with two or three lateral and one mesial spines and with fewer spinules mesially and dorsally; merus 0.9–1.0 times as long as carpus, with 8–13 lateral and 7–10 ventral or ventromesial spines. Fifth pereopod (figure 25F) slightly falling short of or slightly over-reaching scaphocerite by dactyl; dactyl 0.25–0.36 times as long as propodus, with six to nine accessory spinules; carpus with two or three lateral and one mesial spines; merus 0.7–0.85 times as long as carapace, with five to eight lateral and five to eight ventral or ventromesial spines.

Endopod of first pleopod in functional males (figure 26C) with appendix interna arising from about mid-length of endopod, deeply separated from endopod proper, bearing numerous curved small spines mesially, ventral surface near base of appendix interna with row of spinules. Appendix masculina of second pleopod in functional males (figure 26D) attaining about twice length of appendix interna, tapering distally to basally articulated spine, armed with about 15 long spines dorsally or dorsomesially, becoming noticeably shorter distally.

Colour. Body generally pale brown, with scattered dark reddish brown spots on branchial region of carapace and entire abdomen. Antennal flagellum banded with brown and white. Third maxilliped and ambulatory pereopods with dark brown bands on paler background. Colour photograph of this species was published by Miyake (1982: pl. 20, figure 3; under the name of *Pandalus prensor*).

Size. Largest functional male: 13.2 mm; females: 10.4–17.3 mm.

Distribution. Sea of Japan; Tsugaru Strait; Korean Strait; Sendai Bay; sublittoral to upper bathyal depths of 30–311 m.

Remarks. *Pandalus gracilis* shows a stronger sexual dimorphism in the structure and armament of the third and fourth pereopods than any other species of the group. The ratios of the dactyl length/propodus length of the third pereopod are 0.57–0.65 in males and 0.22–0.33 in females; those of the fourth pereopod are 0.46–0.48 in males and 0.22–0.34 in females. The propodus of the third pereopod in males is noticeably curved; the flexor spinules are denser; and the lateral surface is not spinose. In females, the propodus is nearly straight with a spinose lateral surface.

Holthuis (1976) re-described the lectotype of *Pandalus gracilis*, kept in the collection of the Natural History Museum, London (Evans, 1967), and concluded that this taxon was a junior synonym of *P. hypsinotus*. However, Hayashi (1988) showed that it was a distinct species based upon comparison of Holthuis's re-description and the additional material from the Sea of Japan. As mentioned by Hayashi, accessory spinules on the ambulatory dactyls are more numerous in the present material than in the small lectotype of *P. gracilis* (11–19 in the third, 9–13 in the fourth and six to nine in the fifth versus seven in all three appendages in the lectotype; Holthuis, 1976). The lectotype, measuring 5 mm in the postorbital carapace length (Holthuis, 1976), is much smaller than any specimens in the present material. There is little doubt that this difference depends on the specimen size as increase of the accessory spinules with growth is usual in *Pandalus*. I am confident that the present material from the Sea of Japan and Tsugaru Strait (near the type locality) represents *P. gracilis*.

The differences between *P. gracilis* and *P. hypsinotus* are numerous. The rostrum is shorter in *P. gracilis* than in *P. hypsinotus* (1.05–1.27 as long as the carapace versus 1.33–1.84 times as long). The ventral teeth of the rostrum are fewer in *P. gracilis* than in *P. hypsinotus* (six or seven versus eight to ten). The postrostral ridge of the carapace is never highly crested in *P. gracilis*. The appendix interna of the first pleopod in functional males of *P. gracilis* is more slender, and separated from the endopod proper by a very deep, narrow incision. This appendage in *P. hypsinotus* is broad, somewhat inflated; the notch separating the appendix interna and endopod is widely V-shaped. *P. gracilis* attains a much smaller size than *P. hypsinotus*: females of *Pandalus gracilis* are equivalent to males of *P. hypsinotus*, and the males of *P. gracilis* are equivalent to the juveniles of *P. hypsinotus*. Without determination of sex, *P. gracilis* may be easily mistaken for the juveniles and young males of *P. hypsinotus*. Nevertheless, the form of the rostrum is still useful to distinguish *P. gracilis* from young *P. hypsinotus*.

Pandalus robustus Stimpson, 1860, was described on the basis of material from Hakodate, probably collected together with the lectotype of *P. gracilis*. The type material of *P. robustus* was presumably destroyed during the 1871 Chicago fire (Evans, 1967; Deiss and Manning, 1981). Balss (footnote in De Man, 1920: 103) regarded *P. robustus* as identical with *Pandalus hypsinotus meridionalis* (=*Pandalus prensor*) named by himself (Balss, 1914). No subsequent authors have tried to evaluate the taxonomic status of *P. robustus*. From the original description, *P. robustus* appears more similar to the present adult specimens of *P. gracilis*, rather than to *P. hypsinotus* or *P. prensor*, particularly in the number of dorsal spines on the rostrum and carapace (according to Stimpson, 19 spines on that margin) and in the length of the rostrum (Stimpson described as 'Rostrum carapacis longitudine'). The differences that led Stimpson to separate *P. gracilis* and *P. robustus* might be due to growth change, because the specimen of *P. robustus* was much larger than that of *P. gracilis*. I am now convinced that *P. gracilis* and *P.robustus* are the same species. On the same page of Stimpson's paper (1860: 37), both species were described as new, but the name *P. gracilis* was preceded by *P. robustus*. To ensure nomenclatural stability, it would be best to establish a neotype for *P. robustus*. As such, I hereby designate the lectotype of *P. gracilis* as the neotype of *P. robustus*. This would make the name *P. robustus* an objective synonym of *P. gracilis*. According to the Article 24 of the International Code of Zoological Nomenclature (1985), either name can be considered to be the senior synonym by the first reviews. In accordance with this, as a first reviser, I hereby choose *P. gracilis* as the senior synonym of *P. robustus*, because the former name has been generally accepted by recent authors (e.g. Hayashi, 1988; Komai *et al*., 1992).

Pandalus stimpsoni Thallwitz, 1891, was described on the basis of four specimens, with the indication of the type locality as 'Japan oder China'. Thallwitz compared his new species with *P. prensor*, *P. robustus* and *P. gracilis*, all described by Stimpson (1860). De Man (1920) suggested that Thallwitz's taxon was probably identical with *P. hypsinotus*. Unfortunately, the type material is no longer extant in the collection of the Staatliches Museum für Tierkunde in Dresden (K. Schniebs, personal communication). From the original description, Thallwitz's taxon appears rather more similar to *P. gracilis* than to *P. hypsinotus*, particularly in the relative shortness of the rostrum, as mentioned by Thallwitz, and therefore it is treated as a junior subjective synonym of *P. gracilis*.

Balss (1914) misinterpreted *P. gracilis* and considered it synonymous with *P. platyceros*. Yokoya (1933) reported *P. platyceros* from south of Sado Island, Sea of Japan. However, Yokoya's synonymy includes *Pandalus platyceros* sensu Doflein (1902) (=*P. latirostris*) and *P. robustus* Stimpson, 1860, which is incorrect. The specimen reported by Yokoya (1933) is still extant in the collection of the Kitakyushu Museum of Natural History, and an examination proved that it actually represents *P. gracilis*. Miyake's (1982) specimen from the Sea of Japan referred to as *P. prensor* does most certainly represent *P. gracilis*.

Pandalus gurneyi Stimpson, 1871
(figures 27 and 28)

Pandalus gurneyi Stimpson, 1871: 128 [type locality: Monterey, California]; Rathbun, 1904: 50, pl. 2, fig. 6; De Man, 1920: 103; Schmitt, 1921: 46: pl. 13, fig. 1; Rothlisberg, 1980: 19; Kozloff, 1987: 397 (key).
Pandalus danae: Wicksten, 1991: 812–815 (part).

Material examined. **California**. Palos Verdes, 117 m; 25 April 1974; coll. J. I. Word; 2 males (CL 10.4, 10.7 mm); USNM 222998. Southern part of California,

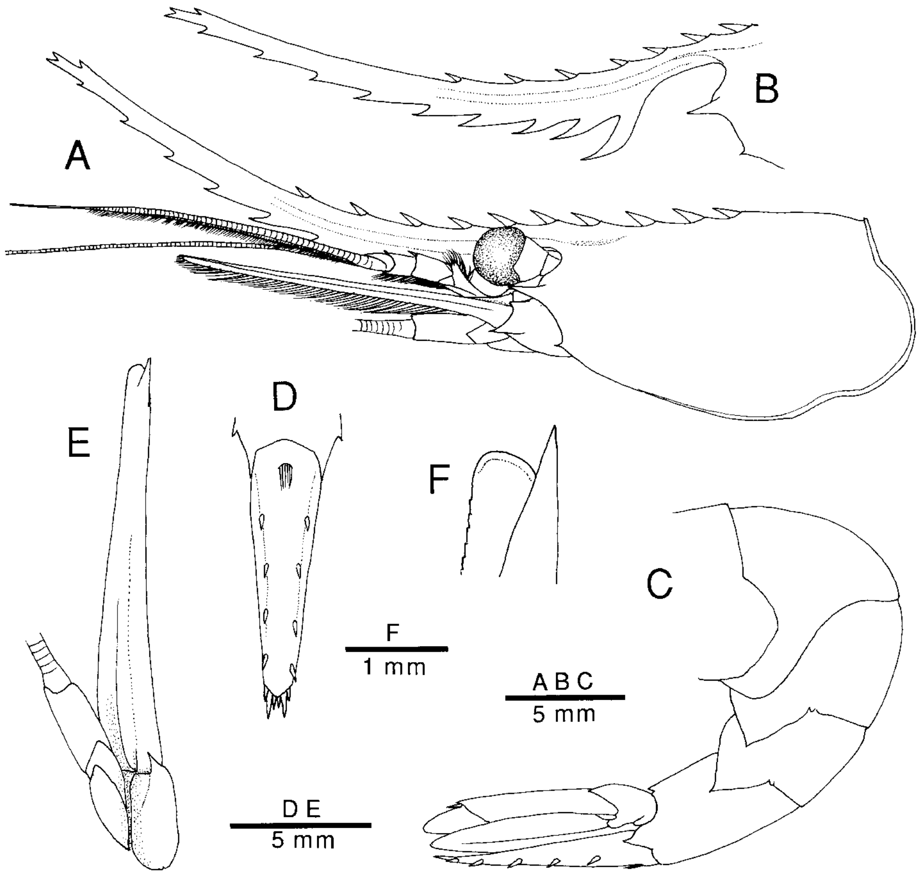


FIG. 27. *Pandalus gurneyi* Stimpson, 1871. Functional male (CL 12.8 mm), southern California, HUMZ-C 1567. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left antenna, ventral, setae omitted; (F) distal part of scaphocerite, ventral.

exact locality unknown; aquarium trade; 1992; coll. J. Okuno; 1 male (CL 13.4 mm); HUMZ-C 1567.

Type material. The type of *Pandalus gurneyi* Stimpson is no longer extant. It was probably destroyed in the 1871 Chicago fire.

Description. Body moderately stout. Rostrum (figure 27A, B) noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.70–1.88 times longer than carapace; dorsal margin nearly straight over eyes, armed with nine or 10 spines, including four on carapace posterior to level of orbital margin, and two fixed teeth near apex of rostrum, subdistal half unarmed, posteriormost spine arising from 0.52–0.60 of carapace length; ventral margin with nine teeth, posteriormost tooth more strongly erect and much stronger than preceding teeth; lateral carina less conspicuous. Carapace (figure 27A) with postrostral ridge low, extending beyond mid-length of carapace; dorsal profile in lateral view slightly sinuous with peak at level of posteriormost dorsal spine.

Abdomen (figure 27C) with third somite lacking median carina or projection;

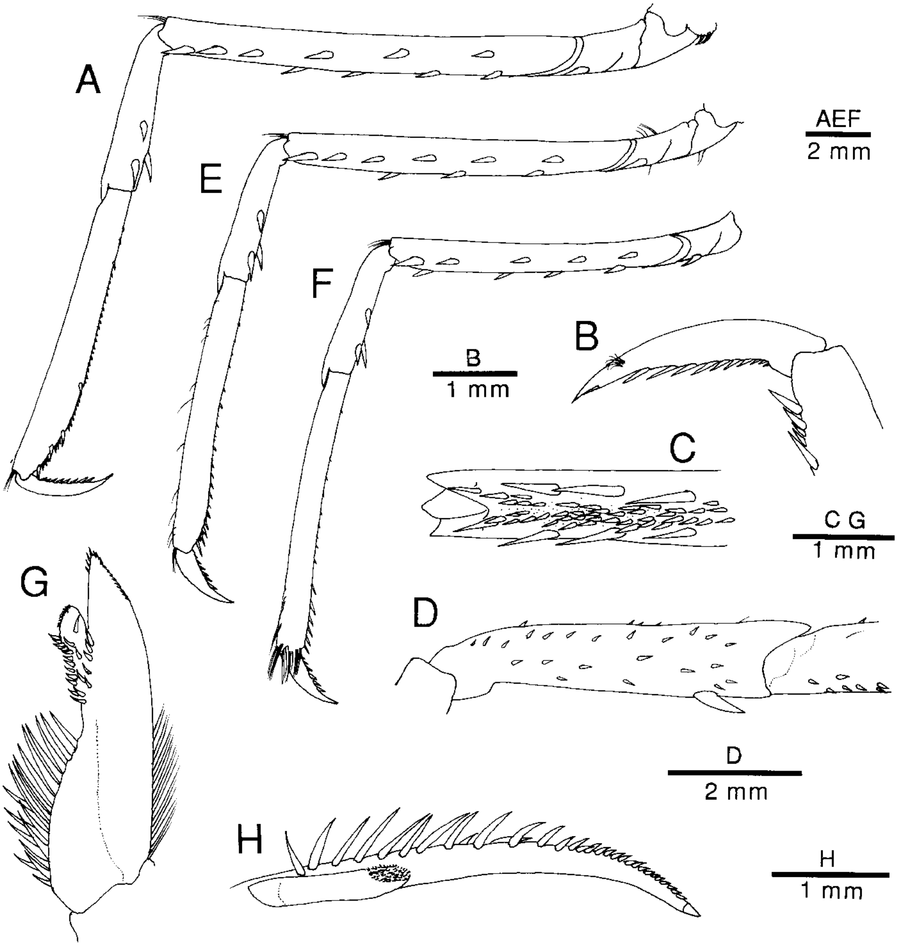


FIG. 28. *Pandalus gurneyi* Stimpson, 1871. Functional male (CL 12.8 mm), southern California, HUMZ-C 1567. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) endopod of left first pleopod, ventral; (H) appendix masculina and interna of left second pleopod, dorsal.

posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5–0.6 times as long as carapace and 1.7–1.9 times as long as proximal depth. Telson (figure 27D) moderately broad, armed with five dorsolateral spines on either side.

Eye (figure 27A) broadly subpyriform.

Antennular peduncle (figure 27A) not reaching mid-length of scaphocerite; intermediate segment unarmed dorsally. Antennal scaphocerite (figure 27A) 1.0–1.1 times as long as carapace and 6.4–7.3 times longer than wide, lateral margin weakly concave, distolateral tooth (figure 27F) distinctly over-reaching distal margin of moderately narrow, rounded blade.

Third maxilliped not reaching distal margin of scaphocerite.

First pereopod falling somewhat short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.4–0.5 of carpus; carpus divided into about 50 articles; merus annulated entirely; ischium with annulation in distal 0.2. Right second pereopod not reaching distal margin of scaphocerite; carpus divided into 15–17 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 28A) noticeably longer than fourth or fifth pereopods, over-reaching scaphocerite by length of dactyl and 0.2–0.5 of propodus; dactyl (figure 28B) 0.28–0.37 times as long as propodus in functional males, with 10 or 11 accessory spinules on proximal 0.75 of flexor margin; propodus of functional males (figure 28C) somewhat compressed, slightly curved, flexor face with irregularly double or triple row of spinules flanked by two rows of moderately long spines in distal 0.3–0.5, only mesial face with scattered spinules; carpus (figure 28A, D) with two or three lateral and one subdistal mesial spines and scattered spinules mesially and dorsally; merus 0.93–1.00 times longer than carapace, with six lateral and five ventral or ventromesial spines. Fourth pereopod (figure 28E) reaching distal margin of scaphocerite by tip of dactyl or falling slightly short of it; dactyl 0.27–0.31 times as long as propodus in functional males, with seven or eight accessory spinules; carpus with two or three lateral and one mesial spines and with fewer spinules on mesial surface; merus 0.8–0.9 times as long as carpus, with six or seven lateral and four ventral or ventromesial spines. Fifth pereopod (figure 28F) over-reaching mid-length of scaphocerite by length of dactyl; dactyl 0.22–0.30 times as long as propodus, with six accessory spinules; carpus with two lateral and one mesial spines; merus 0.7–0.8 times as long as carapace, with five or six lateral and two to four ventral or ventromesial spines.

Appendix interna of first pleopod in functional males (figure 28G) not strongly inflated or elongate, separated from endopod by deep notch. Appendix masculina of second pleopod in functional males (figure 28H) elongate, attaining about three times longer than appendix interna, terminating in acute apex, armed with numerous spines becoming shorter distally on dorsal and dorsomesial surfaces.

Coloration. Wicksten (1991) noted as follows: 'Shrimp from Monterey Bay and farther south tended to have brick red bands and bands of bright yellow on the appendages, as well as a few bright turquoise blue spots on the body. However, some larger individuals from Monterey Bay were translucent with very dark brown stripes, much like the animals from Puget Sound'.

Size. Rathbun (1904: 50) gave the following measurements of an ovigerous female of *P. gurneyi*: length 77.5 m, length of carapace and rostrum 38.5 mm, of rostrum 25 mm.

Distribution. Monterey, California, to Bahia San Quintin, Mexico; 16–117 m.

Remarks. The present species was thought to be closely related to *P. danae* (see Rathbun, 1904; Schmitt, 1921). After having compared materials from various localities in the northwest coast of North America, Wicksten (1991) came to the conclusion that *P. gurneyi* should be treated as a junior subjective synonym of *P. danae*. However, though rather few specimens have been available for comparison, the present study found that the southern California population is different from northern populations in the much longer rostrum (1.70–1.88 times longer than the carapace versus 1.28–1.54 times), more numerous ventral teeth on the rostrum (nine versus six) and shorter dactyl of the third pereopod in functional males (0.28–0.37 times as long as the propodus versus 0.35–0.54 times as long). Furthermore, the southern California form has a more elongate antennal scaphocerite than typical *P. danae*. Its proportional ratio of 'length/width' ranges from 6.4 to 7.3, rather than from 5.4 to 5.7 in *P. danae*. Thus, the third maxilliped and right second pereopod do not reach the distal margin of the scaphocerite in the southern California form, rather than reaching or over-reaching it in *P. danae*. The number of dorsolateral spines on the telson is found to be usually fewer in the southern Californian form than in the Oregon and northern California form (five versus six). In addition, despite her action, Wicksten (1991) noted a difference in the colour between typical *P. danae* and the southern California form. She noted as follows: 'As a general rule, coonstripe shrimp from Puget Sound and British Columbian waters had bands of dark chocolate brown on the body and appendages, and only white or translucent bands on the appendages. Shrimp from Monterey Bay and farther south tended to have brick red bands and bands of bright yellow on the appendages, as well as a few bright turquoise blue spots on the body.' With such significant differences, the name *gurneyi* is revived and warrants full specific status. These two species are clearly differentiated by external morphology, and are separated geographically with small overlapping at northern California. Moreover, from the original description of *P. gurneyi*, there is little possibility that the type of *P. gurney* actually represented *P. danae*. Therefore there is no necessity to designate neotypes for both taxa.

Pandalus gurneyi is also similar to *P. prensor*, but the characters separating *P. gurneyi* and *P. danae* are also useful to differentiate the two species.

Pandalus nipponensis Yokoya, 1933
(figures 29 and 30)

Pandalus nipponensis Yokoya, 1933: 16, text-fig. 5 [type locality: the type series consists of specimens from six different locations: near middle between Sioya-zaki and Inubo-zaki, 583 m, Soyo-Maru, stn 18; near Inubo-zaki, 76 m, Soyo-Maru stn, 157; north-east of Inubo-zaki, 208 m, Soyo-Maru stn, 159; off Owase, Mie Prefecture, 353 m, Soyo-Maru, stn 383; off Totomi, Sizuoka Prefecture, 100 m, Soyo-Maru, stn 386; off Owase, Mie Prefecture, 379 m, Soyo-Maru, stn 400.]; 1934: 16; Kubo, 1965: Scrivener and Butler, 1971: 38 (bibliography); Holthuis, 1980: 140; Toriyama and Hayashi, 1982: 90, 92; Miyake, 1982: 60, pl. 20 fig. 5; Takeda, 1982: 17, fig. 50; Hayashi, 1986: 126, fig. 80, 127, 270; 1995: pl. 90, fig. 7, 333.
Not *Pandalus nipponensis*: Yokoya, 1939: 263. [? = *Pandalus prensor* Stimpson, 1860].

Material examined. **Japan**. Suruga Bay, depth unknown; 25 October 1990; commercial trawler; coll. M. Osawa; 2 young males (CL 15.0, 15.6 mm); CBM-ZC 244. Off Choshi, Chiba, central Honshu, 300–400 m; 20 February 1995; commercial trawler; coll. T. Komai; 1 functional male (CL 22.6 mm); CBM-ZC 1074. Off Choshi, 200–300 m; 1990; commercial trawler; 1 ovig. female (CL 34.7 mm); CBM-ZC 2880. Off Kochi, Tosa Bay, Shikoku, 200–300 m, 22 November 1996; commercial trawler; coll. H. Endo; 2 females (CL 36.2, 40.2 mm); CBM-ZC 3411. Off Kochi, Tosa Bay, 200–300 m; 26 November 1996; commercial trawler; coll. T. Komai; 5 males (CL ? mm); CBM-ZC 3412. Off Kochi, Tosa Bay, 200–300 m; 28 November 1996; commercial trawler; 2 males (CL 24.8, 30.6 mm); CBM-ZC 3413. Off Onahama, Kashima-nada, 200–300 m; 14 November 1977; commercial trawler; coll. T. Kanayama and E. Yamamoto; 1 male (CL 26.7 mm); HUMZ-C 261. Off Tohtomi, Suruga Bay, 100 m; Soyo-Maru, stn 386; 11 December 1927; lectotype, ovig. female (CL 38.2 mm); KMNH. Off Yaizu, Suruga Bay, 250–350 m; 16 December 1977; shrimp trap; coll. Y. Maihara; 15 ovig. females CL 26.0–33.6 mm; MSMTU. Kagoshima Bay, southern Kyushu, 30°39.4′N, 129°55.1′E, 480 m; 9 September 1960; coll. Y. Tokutome; 1 ovig. female (CL 32.4 mm); NFU 530-2-1112. Tosa Bay, 375 m; 9 April 1960; coll. M. Toriyama; 1 functional male (CL 32.4 mm); NFU 530-2-1176.

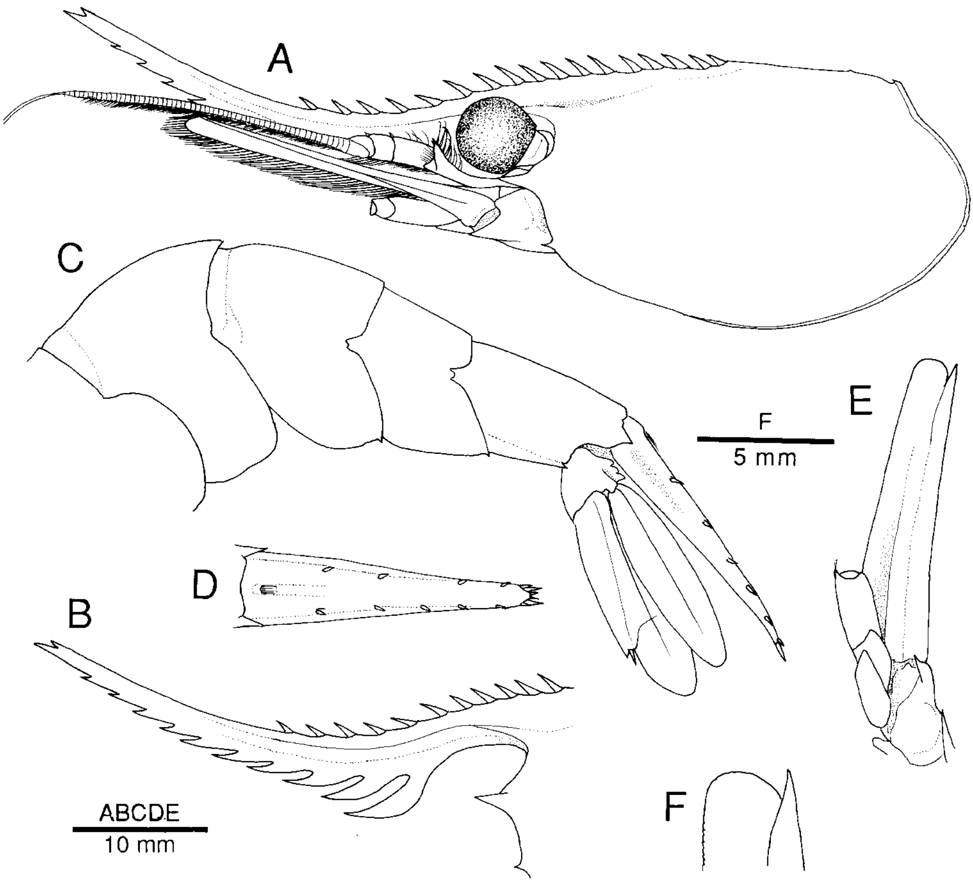


FIG. 29. *Pandalus nipponensis* Yokoya, 1933. Functional male (CL 24.2 mm), Tosa Bay, Shikoku, CBM-ZC 3413. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites and telson, lateral, pleopods and setae omitted; (D) left antenna, ventral, setae omitted; (E) same, distal part.

Type material. This species was described on the basis of nine specimens from six different *Soyo-Maru* stations (see synonymy). Yokoya (1933) did not designate a holotype, and therefore all specimens should be syntypes. Only a single specimen (from station 386, off Tohtohmi, Suruga Bay, at a depth of 100 m) was located in the collection of the KMNH, which is designated here as the lectotype (see 'Material examined').

Description. Body robust. Rostrum (figure 29A, B) noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.06–1.81 times as long as carapace; dorsal margin nearly straight over eyes, armed with 14–18 spines, including five to seven on carapace posterior to level of orbital margin, and one (rarely two) fixed teeth near apex of rostrum, subdistal 0.4–0.5 unarmed, posteriormost spine arising from 0.41–0.48 of carapace length; ventral blade well developed, with 9–12 teeth, posteriormost tooth much stronger than preceding tooth; lateral carina conspicuous in at least proximal half. Carapace (figure 29A) with postrostral ridge strongly compressed, but not crested, becoming blunt posteriorly, not extending nearly to

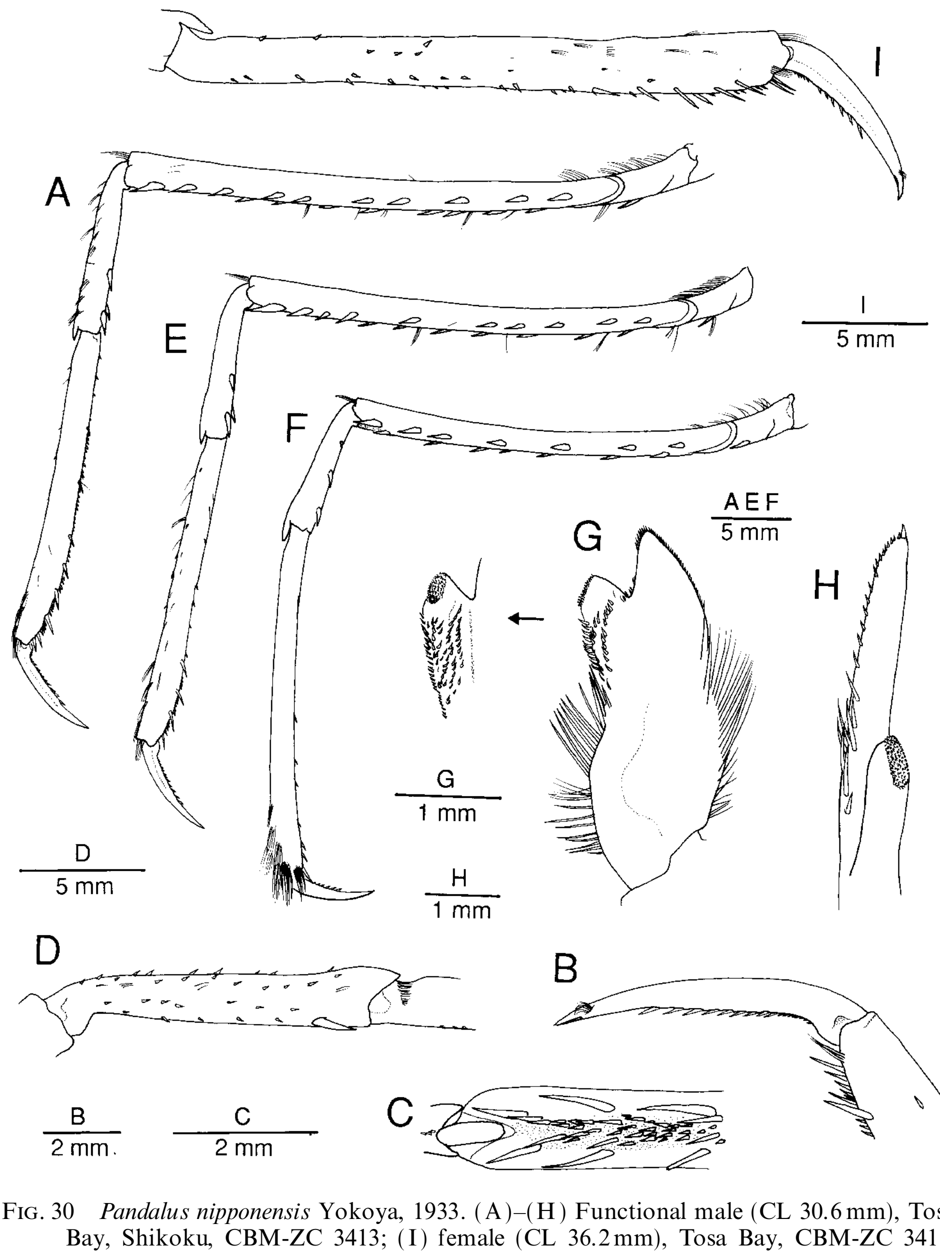


FIG. 30 *Pandalus nipponensis* Yokoya, 1933. (A)–(H) Functional male (CL 30.6 mm), Tosa Bay, Shikoku, CBM-ZC 3413; (I) female (CL 36.2 mm), Tosa Bay, CBM-ZC 3411. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) endopod of left first pleopod, ventral; (H) appendix masculina and appendix interna of left second pleopod, dorsal, mesial; (I) dactyl and propodus of right third pereopod, lateral.

posterodorsal end of carapace; dorsal profile in lateral view weakly convex, with peak at level of posteriormost dorsal spine.

Abdomen (figure 29C) with third somite lacking median projection or carina;

posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5–0.6 times as long as carapace and 1.7–1.9 times as long as proximal depth. Telson (figure 29D) moderately broad, armed with five or six dorsolateral spines on either side.

Eye (figure 29A) broadly subpyriform.

Antennular peduncle (figure 29A) reaching mid-length of scaphocerite; intermediate segment unarmed dorsally. Antennal scaphocerite (figure 29E) 0.8–1.0 times as long as carapace and 3.5–5.2 times longer than wide, lateral margin nearly straight, distolateral tooth reaching or falling slightly short of distal margin of moderately broad blade.

Third maxilliped slightly over-reaching or falling slightly short of distal margin of scaphocerite.

First pereopod reaching 0.7 of distal margin of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and 0.6–0.75 of carpus; carpus divided into 50–80 articles; merus annulated entirely; ischium with annulation in distal 0.4. Right second pereopod over-reaching scaphocerite by length of dactyl or length of chela and 0.3 of carpus; carpus divided into 21–32 articles; merus with few annulations in distal 0.3. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 30A) over-reaching scaphocerite by length of dactyl and half of propodus; dactyl (figure 30B, I) 0.35–0.49 times as long as propodus in either sex (not showing notable sexual dimorphism), with 11–18 accessory spinules on proximal 0.6–0.75 of flexor margin; propodus of functional males (figure 30C) somewhat compressed, slightly curved or straight, flexor face with three or four rows of spinules flanked by two rows of moderately long spines in distal 0.75, lateral, dorsal and mesial faces with few spinules; propodus in females (figure 30I) less compressed, nearly straight, lateral, mesial and dorsal surface with scattered spinules; carpus (figure 30A, D) with two or three ventrolateral and one subdistal ventromesial spines and few scattered spinules mesially and dorsally (in males, spinules present only on mesial surface); merus 0.9–1.1 times as long as carapace, with 8–11 lateral and 6–10 ventral or ventromesial spines. Fourth pereopod (figure 30E) reaching distal margin of scaphocerite by tip of dactyl or over-reaching it by length of dactyl and half of propodus; dactyl 0.30–0.37 times as long as propodus in either sex, with 12–18 accessory spinules; carpus with two or three ventrolateral and one ventromesial spines and with few mesial spinules dorsally; merus 0.8–1.0 times as long as carpus, with 7–11 lateral and 6–10 ventral or ventromesial spines. Fifth pereopod (figure 30F) over-reaching distal margin of scaphocerite by length of dactyl or reaching it by tip of dactyl; dactyl 0.21–0.32 times as long as propodus, with 9–14 accessory spinules; carpus with two or three lateral and one mesial spines; merus 0.8–0.9 times as long as carapace, with seven or eight lateral and five or six ventral or ventromesial spines.

Endopod of first pleopod in functional males (figure 30G) with appendix interna weakly inflated, separated terminally by deep V-shaped notch, armed with numerous curved spinules forming several rows on dorsal, mesial and ventral surfaces. Appendix masculina of second pleopod in functional males (figure 30H) greatly elongate, armed dorsally with three or four rows of spines or spinules.

Colour. Yellowish or orangish brown in ground colour of body, with fine red patches or spots on lateral surface of first to fifth abdominal somite; rostrum generally pale yellow with broad red band centrally; telson and uropods red; scaphocerite with broad band of red on nearly colourless background; meri of ambulatory pereopods pinkish, with tinge of yellow near articulation with carpi; carpi and propodi generally colourless, with tinge of yellow around articulations; dactyl deep red proximally, colourless distally. Colour photographs of this species were published by Miyake (1975: 100; 1982: pl. 20, fig. 5), and Hayashi (1986: 126, fig. 80; 1995: pl. 90, fig. 7).

Size. Largest functional male: CL 32.4 mm; females: 26.0–40.2 mm.

Distribution. Endemic to the Japanese Pacific coast from off Fukushima, Kashima-nada, to Kagoshima Bay, Kyushu; 100–480 m. It has been believed that *Pandalus nipponensis* occurs in northern Japan northward from Kinkazan, Miyagi, to southern Hokkaido (Kubo, 1965; Takeda, 1982; Hayashi, 1986), but no specimen referable to this species was collected in that area during my faunal survey between 1987 and 1993. My attempt to find a representative of this species from Hokkaido in collections of other Japanese museums or institutes has not been successful. Although the common Japanese name 'Toyama-ebi' should be applied to *P. hypsinotus*, local fishermen in northern Japan generally call *P. hypsinotus* 'Botan-ebi', which is a Japanese common name of *P. nipponensis*. It is highly probable that the previous records of *P. nipponensis* from Hokkaido was due to confusion of the common names.

Remarks. In this species, the proportional ratio of the dactyl length/propodus length of the third and fourth pereopods in females is included in the variation range of males.

In the number of the median spines on the rostrum and carapace, *P. nipponensis* appears to be rather close to *P. hypsinotus* and *P. gracilis*. In these three species, there are more than 13 spines. *P. nipponensis* differs from the other two species in the posteriormost dorsal spine on the carapace arising from or slightly anterior, rather than posterior, to the mid-length of the carapace. Furthermore, the dorsal spines on the carapace are still fewer in *P. nipponensis* than in *P. hypsinotus* and *P. gracilis* (five to seven versus seven to 10). The geographical range of *P. nipponensis* appears restricted to the Japanese Pacific coast from Kashima-nada to southern Kyushu, whereas *P. hypsinotus* and *P. gracilis* is distributed in the Sanriku coast of northeastern Honshu, Hokkaido, and the Sea of Japan; *P. hypsinotus* extends its range to Alaska and the northwest coast of North America. Only on the Sanriku coast and in the Kashima-nada region does the range of *P. nipponensis*, *P. gracilis* and *P. hypsinotus* possibly overlap. *Pandalus danae*, *P. prensor*, *P. gurneyi* and *P. formosanus* are distinguishable from *P. nipponensis* by having usually fewer (9–13) dorsal spines on the rostrum and carapace. However, *P. prensor* rarely has 14 dorsal spines. Nevertheless, the more strongly compressed postrostral ridge on the carapace and the relatively shorter dactyl of the third pereopod will separate *P. nipponensis* from *P. prensor*. In addition, like *P. hypsinotus*, *P. nipponensis* is one of the largest species among *Pandalus*. When fresh, *P. nipponensis* is readily recognized by its yellowish or orangish brown base colour, with fine red patches on the lateral surface of the abdomen and with fine red bands crossing the rostrum and scaphocerites.

Two female specimens referred to as *Pandalus nipponensis* from Koshikine, Onagawa, Miyagi Prefecture, by Yokoya (1939) might represent another species, as the specimens came from a depth of 19 m. *P. nipponensis* usually occurs to bathyal depths greater than 100 m. Considering the geographical and bathymetrical distributions, Yokoya's specimens might actually represent *P. prensor*.

Pandalus teraoi Kubo, 1937
(figures 31, 32 and 44A)

Pandalus teraoi Kubo, 1937: 96, figs 4–6 [type-locality: off Ohyama, Aichi Prefecture, 250–306 m]; Miyake, 1982: 187 (list).

Material examined. **Japan**. Off Choshi, Chiba, *ca* 300–400 m; 20 February 1995; commercial trawler; coll. T. Komai; 1 female (CL 30.4 mm); CBM-ZC 1075. Kumano-nada off Shionomisaki, Kii Peninsula, 320–350 m; 16 April 1990; dredge; coll. S. Nagai; 1 male (CL 27.9 mm); CBM-ZC 1142. SE of Katsuyama Ukishima Islet, Uchibo coast of Boso Peninsula, 140–220 m; 10 May 1995; gill net; coll. T. Komai and M. Miya; 1 female (CL 28.4 mm); CBM-ZC 1661. Off Shioyazaki, Fukushima, 36°51.4′N, 141°24.3′E, 310 m; 24 October 1994; trawl by RV *Wakataka-Maru*; coll. D. Tsutsui; 4 males (CL 25.4–26.6 mm); CBM-ZC 1136. Off Choshi, *ca* 200–300 m; 1990; commercial trawler; 1 ovig. female (CL 31.4 mm); CBM-ZC 2881.

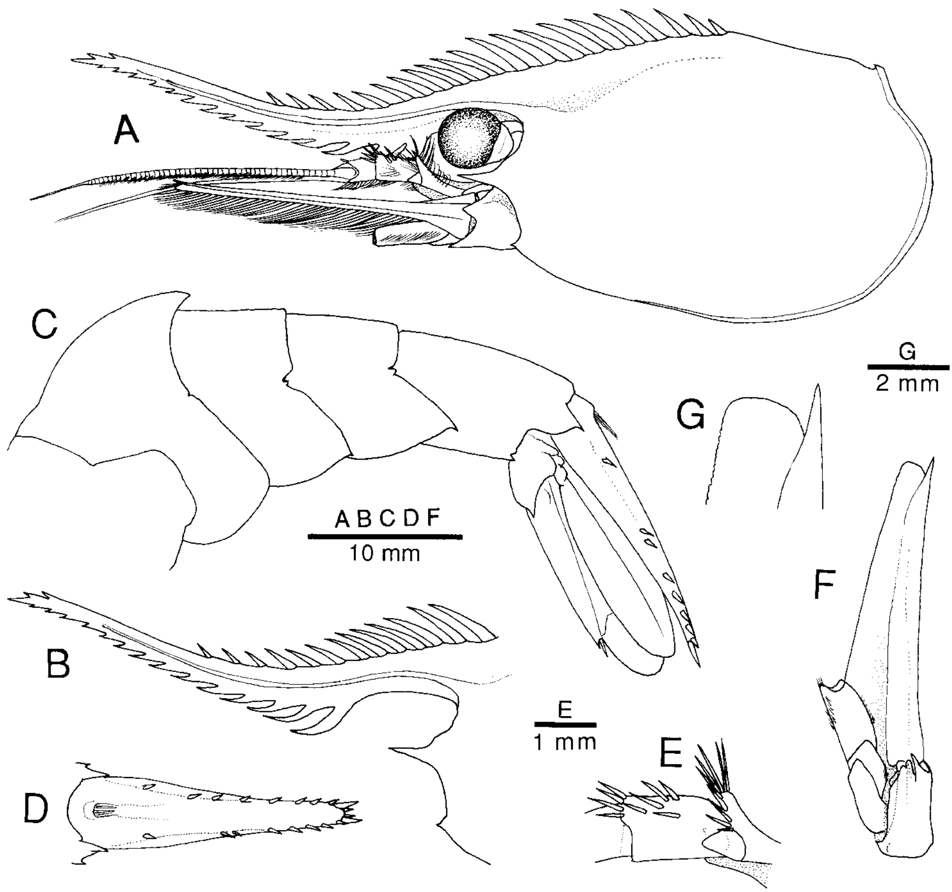


FIG. 31. *Pandalus teraoi* Kubo, 1937. Functional male (CL 25.4 mm), off Shioya-zaki, Fukushima, Kashima-nada, CBM-ZC 1136. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) intermediate segment of left antennular peduncle, lateral, setae omitted; (F) left antenna, ventral, setae omitted; (G) distal part of scaphocerite, ventral.

Kashima-nada off Onahama, Fukushima; 14 November 1977; commercial trawler; coll. T. Kanayama; 1 male (CL 24.0 mm, 1 female CL 34.0 mm); HUMZ-C 205. Off Ohyama, Aichi Prefecture, 250–360 m; spring of 1936; trawl; coll. G. Abe; holotype, male (CL 25.0 mm); paratypes, 3 males (CL 16.0–25.4 mm), 3 females (CL 26.0–29.3 mm); TUF.

Type material. Off Ohyama, Aichi Prefecture, 250–360 m; spring of 1936; trawl; coll. G. Abe; holotype, male (CL 25.0 mm); paratypes, 3 males (CL 16.0–25.4 mm), 3 females (CL 26.0–29.3 mm); TUF (see 'Material examined').

Description. Body robust. Rostrum (figure 31A, B) moderately curving dorsally, distinctly over-reaching scaphocerite, 1.03–1.44 times as long as carapace; dorsal margin nearly straight over eyes, armed with noticeably elongate 17–21 spines, including 8–10 on carapace posterior to level of orbital margin, becoming longer anteriorly to spines around orbital margin, thereafter gradually becoming shorter; two or three fixed teeth near apex of rostrum, subdistal 0.4 of dorsal margin unarmed; posteriormost spine arising from 0.50–0.56 of carapace length; ventral margin with 13 or 14 teeth, two or three posterior teeth somewhat elongate, posteriormost tooth strongest; lateral carina conspicuous in at least proximal half of rostrum. Carapace (figure 31A) with postrostral ridge strongly compressed laterally, crested, extending beyond 0.6 of carapace length, with strongly convex dorsal profile in lateral view.

Abdomen (figure 31C) with third somite lacking median carina or projection; posterodorsal margin of third and fourth somites unarmed; sixth somite 0.5–0.6 times as long as carapace and 1.6–1.8 times longer than proximal depth. Telson (figure 31F) moderately broad, armed with six or eight dorsolateral spines on either side.

Eye (figure 31A) broadly subpyriform.

Antennular peduncle (figure 31A) nearly reaching mid-length of scaphocerite; intermediate segment (figure 31E) with scattered long spines on anterodorsal margins and dorsal surface. Antennal scaphocerite (figure 31F) 0.7–0.8 times as long as carapace and 3.7–3.9 times longer than wide, lateral margin nearly straight, distolateral tooth (figure 31G) reaching or slightly over-reaching distal margin of moderately broad, rounded blade.

Third maxilliped slightly over-reaching anterior margin of scaphocerite; lateral surface of ultimate segment spinose.

First pereopod falling short of scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela and distal 0.6 of carpus; carpus divided into 63–66 articles; merus annulated entirely; ischium with few annulations in distal 0.2. Right second pereopod over-reaching scaphocerite by length of chela; carpus divided into 16–21 articles; merus with few annulations in distal part. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 32A) over-reaching scaphocerite by length of dactyl and distal 0.6–0.7 of propodus; dactyl 0.35–0.37 times as long as propodus in functional males (figure 32A, B), 0.25–0.30 times as long in females (figure 32J, K), with 12–16 accessory spinules on proximal 0.7–0.8 of flexor margin; propodus of functional males (figure 32A, C) strongly compressed, curved, flexor face with irregular three or four rows of spinules flanked by two rows of moderately long spines, mesial, dorsal and lateral faces spinose; propodus of females (figure 32J) less compressed, nearly straight, flexor spinules fewer than in functional males, lateral, dorsal and mesial surfaces spinose; carpus (figure 32A, D) with three to six lateral and one subdistal mesial spines, all faces spinose; merus 0.9 times as long as carapace, with 10 or 11 lateral and 9–14 ventral or ventromesial spines. Fourth pereopod (figure 32E) over-reaching scaphocerite by

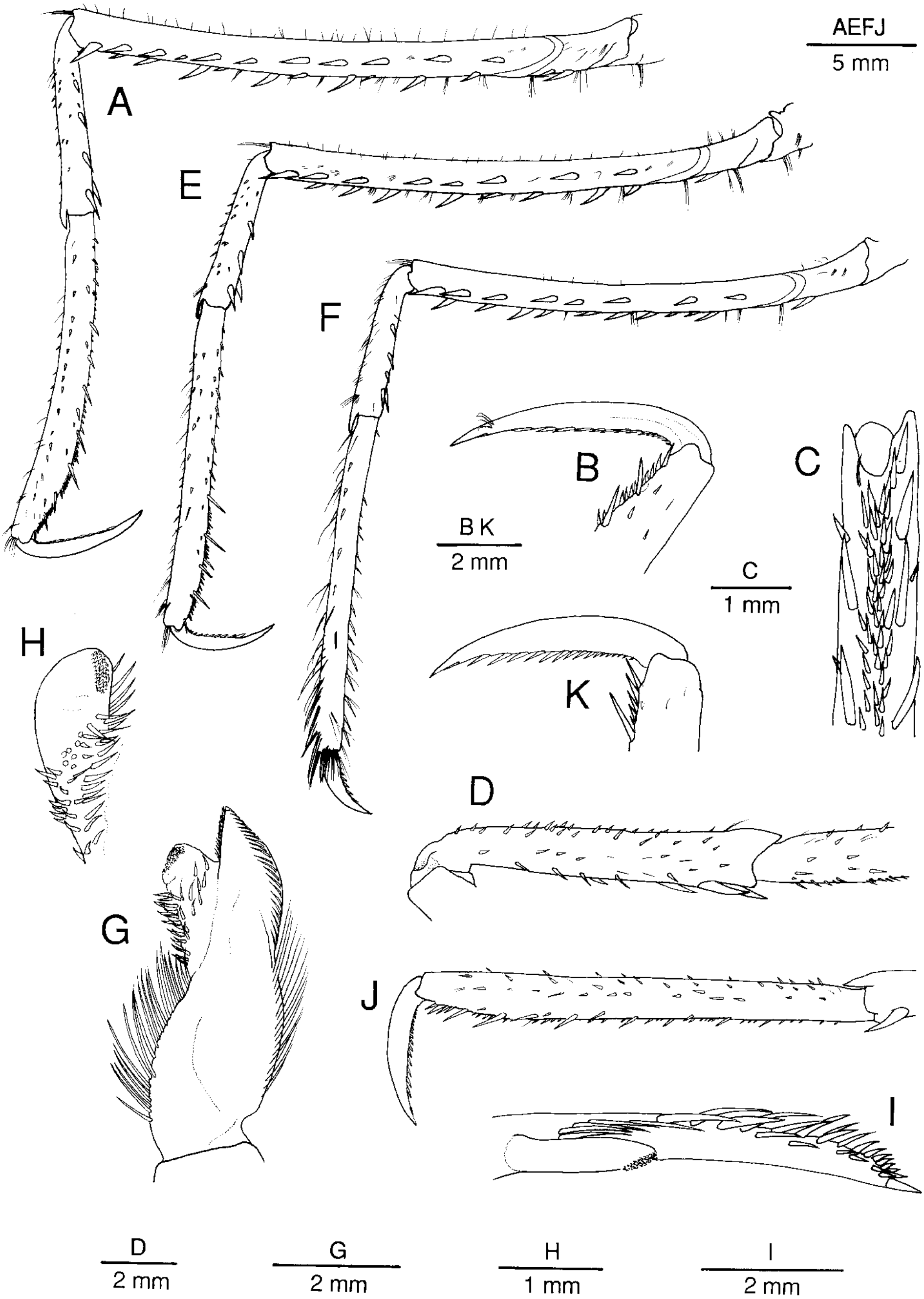


FIG. 32 *Pandalus teraoi* Kubo, 1937. (A)–(I) Functional male (CL 25.4 mm), off Shioya-zaki, Fukushima, Kashima-nada, CBM-ZC 1136; (J), (K) female (CL 30.4 mm), off Choshi, Chiba, CBM-ZC 1075. (A) Left third pereopod, lateral; (B) same, dactyl, lateral; (C) same, distal part of propodus, flexor; (D) same, carpus and proximal part of propodus, mesial; (E) left fourth pereopod, lateral; (F) left fifth pereopod, lateral; (G) endopod of left first pleopod, ventral; (H) same, appendix interna, mesial; (I) appendix masculina and appendix interna of left second pleopod, mesial; (J) dactyl and propodus of left third pereopod, lateral; (K) dactyl of left third pereopod, lateral.

length of dactyl and 0.25 of propodus; dactyl 0.30–0.33 times as long as propodus in males, 0.28 times as long in females, with 12 accessory spinules; carpus with three or four lateral and one mesial spines, mesial, dorsal and lateral faces less spinose than in third pereopod; merus 0.8–0.9 times as long as carapace, with 7–10 lateral and 7–10 ventral or ventromesial spines. Fifth pereopod (figure 32F) reaching or slightly over-reaching scaphocerite by dactyl; dactyl 0.22–0.26 times as long as propodus, with seven or eight accessory spinules on proximal 0.7 of flexor margin; carpus with three or four lateral and one flexor spines; merus about 0.7 times as long as carapace, with seven or eight lateral and five to nine ventral or ventromesial spines.

Appendix interna of first pleopod in functional males (figure 32G, H) separated distally by broad notch from endopod proper, strongly inflated, armed with numerous curved spinules mesially and ventrally, unarmed dorsally; lateral margin of endopod with shallow notch. Appendix masculina of second pleopod in functional males (figure 31I) strongly elongate, armed with about 30 long spines, arranged in irregular double row, on dorsal surface.

Colour. Generally yellow or light orange. Proximal half of rostrum pale yellow. Carapace with deep red patch on gastric region. Abdomen with double row of small or large deep red spots on lateral surface; third abdominal somite dorsally with pair of very large deep red spots circumscribed by white. Antennular flagellum with thickened aesthetascs-bearing portion white, distal slender portion deep red. Scaphocerite with broad transverse band of deep red. Distal two segments of third maxilliped tinged with dark red, antepenultimate segment pale orange. Meri of third to fifth pereopods tinged with orange; distal three segments generally paler, with tint of pale red on dactyl and distal portion of propodi. See figure 44A.

Size. Largest male: CL 27.9 mm; females: 26.0–34.0 mm.

Distribution. Endemic to Japanese Pacific coast from Kashima-nada to Kumano-nada; 140–310 m.

Remarks. The type material of *Pandalus teraoi*, which was borrowed from the Tokyo University of Fisheries, consists of seven specimens, including the holotype, as Kubo (1937) mentioned. The specimens are still in good condition, and agree well with Kubo's original description, except that the first pereopod is microscopically chelate.

This species is quite distinctive from all congeners in the unusually elongate dorsal spines on the carapace and rostrum, giving a comb-like appearance, the presence of long spines on the dorsal surface of the intermediate segment of the antennular peduncle, and the spinose propodus of the third pereopod in both males and females. Although *P. chani* sp. nov. also has elongate dorsal spines, the spines in *P. teraoi* are more slender and more numerous than *P. chani*. The coloration of *P. teraoi* is also quite distinctive in the genus. It can be easily recognized by a pair of large red spots encircled by white on the tergite of the third abdominal somite (figure 44A).

Pandalus chani sp. nov.
(figures 33–35 and 44B)

Type material. **Taiwan**. Su-Aou, I-Lan County, northeast of Taiwan, *ca* 400 m, sandy mud bottom; 16 June 1994; commercial trawler; coll. T.-Y. Chan: holotype, female (CL 21.2 mm); NTOU. Same data; paratypes, 1 male (CL 18.2 mm), 9 females (CL 19.5–25.0 mm); NTOU. Same data; paratypes, 3 females (CL 20.5–25.0 mm);

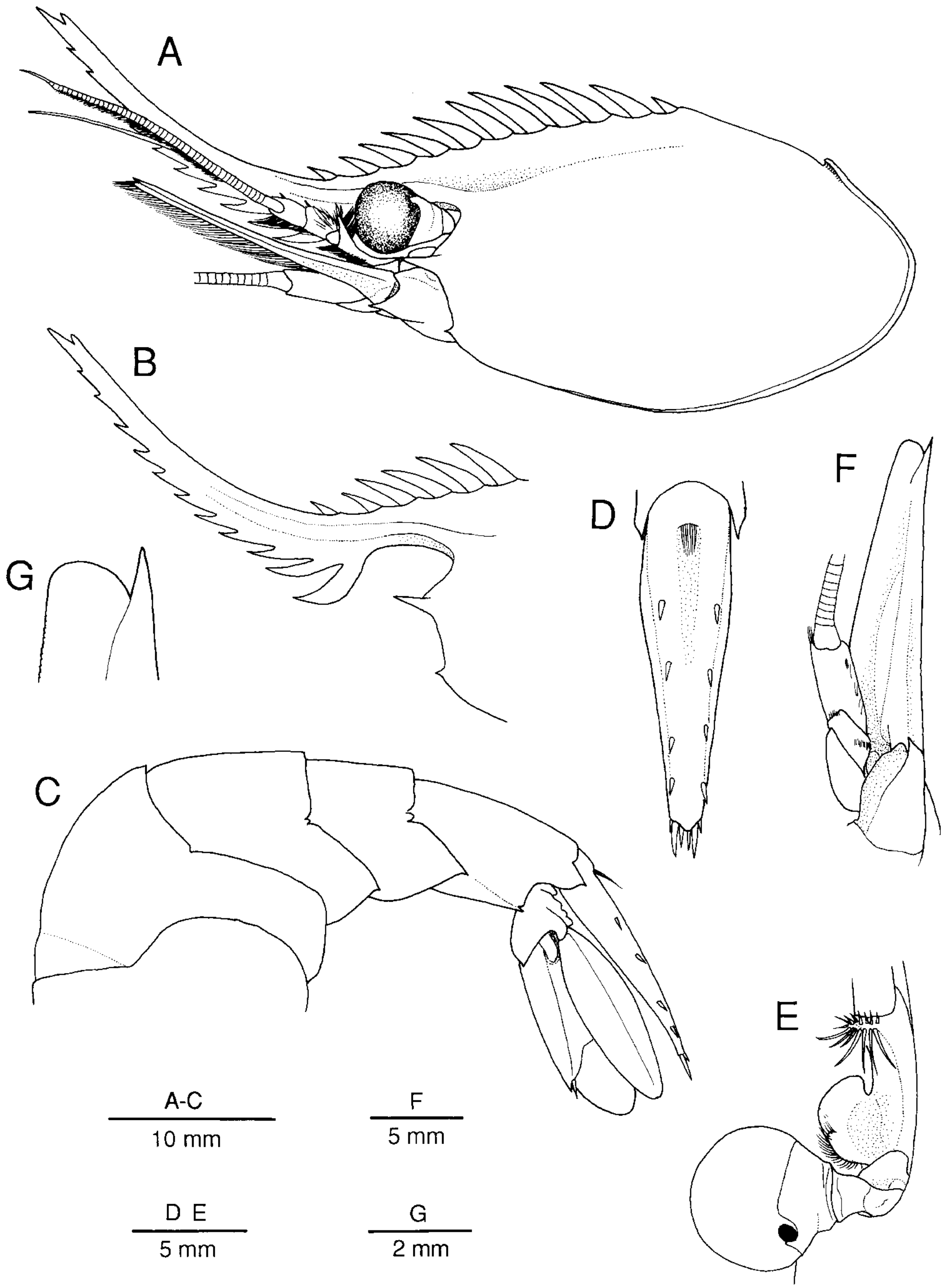


FIG. 33. *Pandalus chani* sp. nov. Holotype, female (CL 21.2 mm), Su-Aou, NE Taiwan, NTOU. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) eye and proximal segment of antennular peduncle, dorsal; (F) left antenna, ventral, setae omitted; (G) distal part of scaphocerite, ventral.

MNHN-Na 13275. Same locality, about 400 m; 17 June 1993; commercial trawler; coll. T.-Y. Chan; 2 males (CL 15.8, 18.5 mm), 3 females (CL 22.4–25.1 mm); NTOU. Same locality; 6 August 1996; coll. T. Komai and T.-Y. Chan; paratypes, 2 males (CL 13.9, 20.3 mm), 1 female (21.4 mm), 1 ovig. female (CL 20.4 mm); CBM-ZC 2954. Same data; paratypes, 5 males (CL 14.5–20.0 mm); NTOU. Same locality; 12 March 1997; commercial trawler; coll. T.-Y. Chan; 1 female (CL 25.7 mm); NTOU. Same locality; 11 November 1997; coll. T.-Y. Chan; 9 females (CL 19.8–25.8 mm), 1 specimen, sex could not be determined (CL 22.4 mm); NTOU. Same locality, about 400 m; 5 December 1997; commercial trawler; coll. T.-Y. Chan and T. Komai; 4 males (CL 13.7–17.1 mm), 2 transitional males (CL 16.5, 17.3 mm), 2 ovig. females (CL 22.1, 23.0 mm); NTOU. Ta-Shi, northeast of Taiwan, depth unknown; 15 August 1997; commercial trawler; 3 females (CL 22.2–24.9 mm); NTOU.

Other material. Off Ta-Shi, NE Taiwan, about 400 m; 15 December 1997; commercial trawler; coll. T.-Y. Chan; 3 males (CL 16.0–16.2 mm); NTOU.

Description. Body considerably robust. Rostrum (figure 33A, B) strongly curving dorsally, distinctly over-reaching scaphocerite, 1.04–1.49 times as long as carapace; dorsal margin generally nearly straight over eyes, armed with unusually strong 10–12 (usually 11) spines, including seven on carapace posterior to level of orbital margin, gradually decreasing in length anteriorly and posteriorly, with posterior fifth or sixth longest, and one or two fixed teeth near apex of rostrum, subdistal 0.6–0.7 unarmed, anteriormost spine arising from posterior to level of distal end of antennular peduncle, posteriormost spine arising from 0.56–0.63 of carapace length; ventral blade well developed, with 9–11 teeth, posteriormost tooth much stronger than preceding tooth; lateral carina conspicuous in at least proximal 0.3 length. Carapace (figure 33A) with postrostal ridge highly elevated with peak at posteriormost dorsal spine.

Abdomen (figure 33C) with third somite lacking median carina or projection, posterodorsal margin rounded; fourth somite unarmed on posterodorsal margin; sixth somite 0.5 times as long as carapace and 1.6–1.7 times as long as proximal depth. Telson (figure 33D) moderately broad, 1.3–1.5 times as long as sixth somite, armed with five or six (rarely four) dorsolateral spines on either side.

Eye (figure 33A, E) broadly subpyriform, corneal region strongly dilated; ocellus present.

Antennular peduncle (figure 33A) reaching mid-length of scaphocerite; intermediate segment armed with few spinules on dorsodistal margin, but unarmed on dorsal surface; distal segment without spine or spinule on dorsodistal margin; stylocerite short, rounded (figure 33E). Antennal scaphocerite (figure 33F) 0.7–0.85 times as long as carapace and 3.6–4.3 times as long as wide, lateral margin nearly straight, distolateral tooth (figure 33G) reaching or slightly over-reaching distal margin of moderately broad, rounded blade.

Mouthparts typical of genus. Maxilla with posterior lobe of scaphognathite not noticeably elongate. Third maxilliped (figure 34A) reaching distal end of scaphocerite; lateral surface of ultimate segment spinose.

First pereopod (figure 34B) falling somewhat short of distal margin of scaphocerite; ischium (figure 34C) with weak ventral laminar expression. Left second pereopod (figure 34D) over-reaching scaphocerite by length of chela and nearly whole of carpus; carpus divided into about 60–70 articles; merus annulated entirely; ischium with annulations in distal 0.3. Right second pereopod (figure 34E) over-reaching

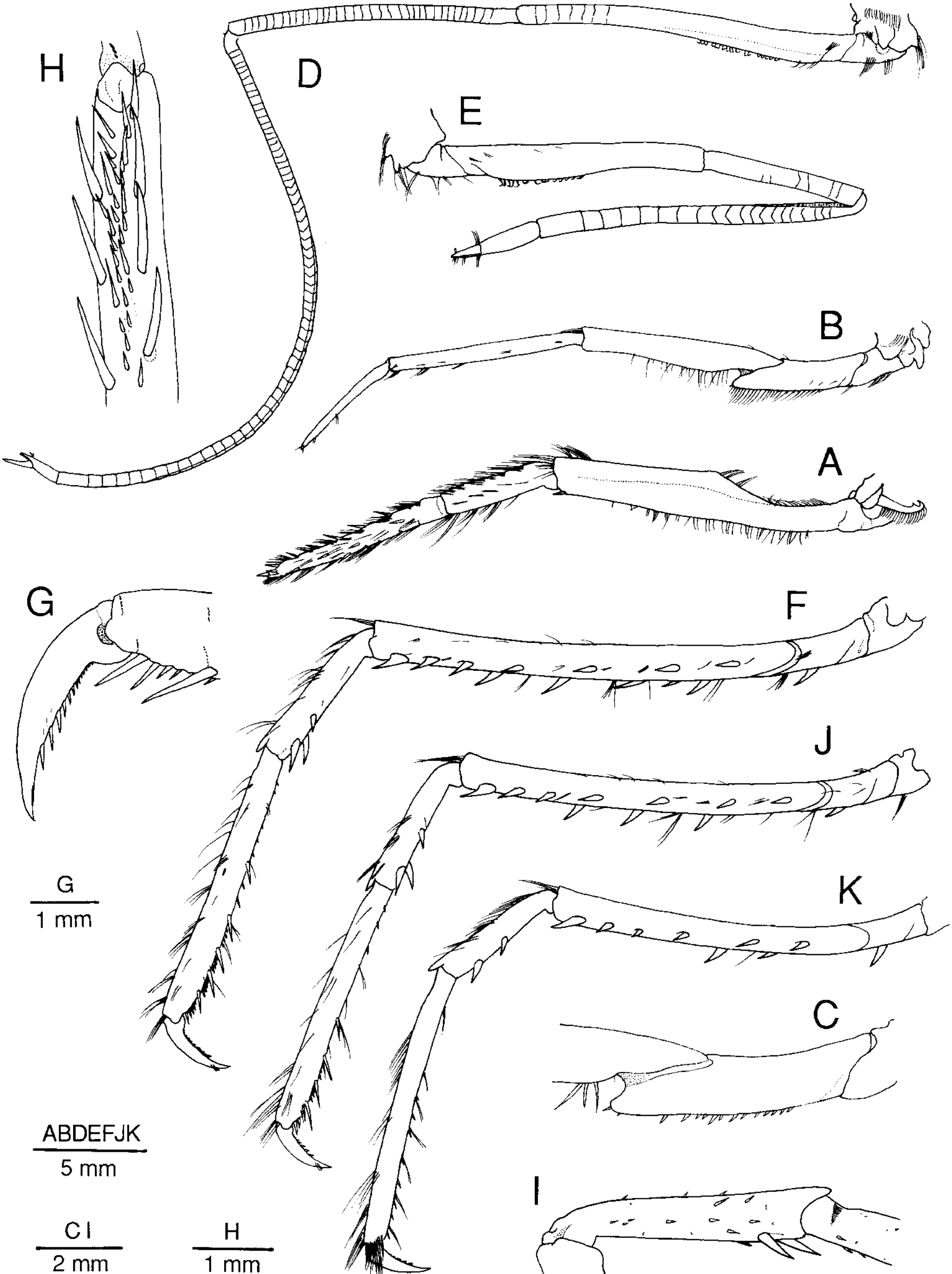


FIG. 34. *Pandalus chani* sp. nov. Holotype, female (CL 21.2 mm), Su-Aou, NE Taiwan, NTOU. (A) Left third maxilliped, lateral; (B) left first pereopod, lateral; (C) same, ischium, lateral; (D) left second pereopod, lateral; (E) right second pereopod, lateral; (F) left third pereopod, lateral; (G) same, dactyl, lateral; (H) same, distal part of propodus, flexor; (I) same, carpus and proximal part of propodus, mesial; (J) left fourth pereopod, lateral; (K) left fifth pereopod, lateral.

scaphocerite by length of chela; carpus divided into 17–20 articles; merus with few annulations in distal half of length. Third to fifth pereopods moderately stout, becoming shorter successively. Third pereopod (figure 34F) over-reaching scaphocerite by length of dactyl and half of propodus; dactyl 0.29–0.39 times as long as propodus in males (figure 34A), 0.27–0.30 times as long in females (figure 34F, G), with 9–13 accessory spinules on proximal 0.7–0.8 of flexor margin; propodus of males (figure 34A) somewhat compressed laterally, slightly curved, flexor face with many spinules arranged in three or four rows in distal half, lateral, dorsal and mesial faces with few spinules; propodus of females (figure 34H) less compressed, nearly straight, flexor surfaces with two or three rows of spinules; carpus (figure 34A, I) with one or two lateral and one mesial spines, dorsal and mesial surfaces with scattered spinules; merus 0.85–1.00 times as long as carapace, with five to seven lateral and four to seven ventromesial spines. Fourth pereopod (figure 34J) over-reaching scaphocerite by length of dactyl; dactyl 0.24–0.30 times as long as propodus in either sex, with 8–12 accessory spinules; carpus with one or two lateral and one mesial spines, mesial surface with few spinules, dorsal and lateral surface without spinules; merus 0.7–0.9 times as long as carapace, with six to eight lateral and five to eight ventral or ventromesial spines. Fifth pereopod (figure 34K) reaching scaphocerite by tip of dactyl; dactyl 0.22–0.26 times as long as propodus, with six to nine accessory spinules; carpus with five to seven lateral and one mesial spines (mesial spine sometimes absent), mesial surface without spinules; merus about 0.7 times as long as carapace, with five to six lateral and three to five ventral or ventromesial spines.

Appendix interna of first pleopod in functional males (figure 35A, B) separated from endopod by broad V-shaped notch, strongly inflated, armed with numerous curved spinules mesially and ventrally, unarmed dorsally; lateral margin of endopod with shallow notch. Appendix masculina of second pleopod in functional males (figure 35C) strongly elongate, weakly curved ventrally, armed with about 30 spines, arranged in irregularly double row on dorsal surface.

Colour. Carapace mottled with orange, reddish brown and white, without distinct bands or spots; rostrum nearly translucent; dorsal spines white with tinge of orange

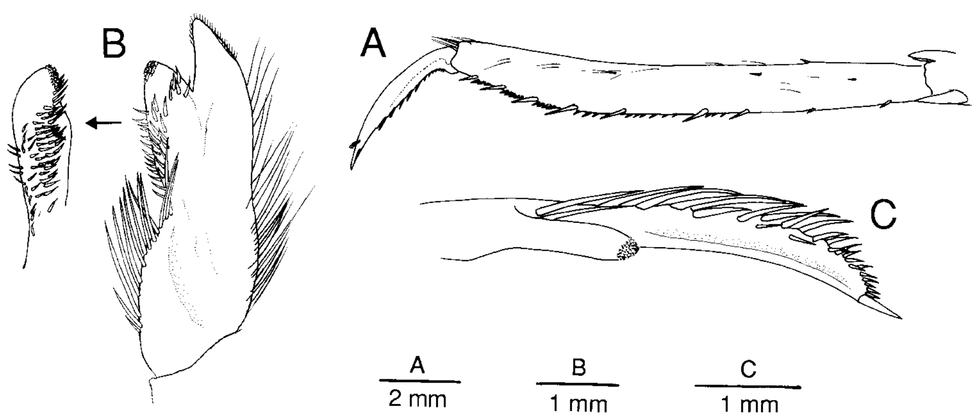


FIG. 35. *Pandalus chani* sp. nov. Paratype, male (CL 19.0 mm), Su-Aou, NE Taiwan, NTOU. (A) Dactyl and propodus of left third pereopod, lateral; (B) endopod of left first pleopod, ventral; inset, appendix interna, mesial; (C) appendix masculina and appendix interna of left second pleopod, mesial.

basally. Abdomen nearly translucent, with scattered orange or reddish brown spots; third abdominal somite with large median white spot. Antennular flagellum obscurely banded with white and reddish brown. Third maxilliped and first pereopod deep red. Meri of third to fifth pereopods deep red excepting colourless subdistal portion; distal three segments transparent with tinge of orange or reddish brown; pleopods same colour as abdomen; uropods with tinge of red distally. See figure 44B.

Size. Largest male: 20.3 mm; females: 19.5–25.0 mm; ovigerous female: CL 19.8–25.8 mm.

Type locality. Off Su-Aou, NE Taiwan.

Distribution. So far known only from northeastern Taiwan, southern East China Sea; 300–500 m.

Remarks. A total of 49 specimens, including 14 males, two transitional males and 33 females was examined, and there is an indication of protandry on the basis of the morphology of the anterior two pairs of pleopods. The two specimens from Su-Aou (NTOU, CL 16.5, 17.3 mm) show a typical transitional phase. In addition, the size distribution of the specimens (the males have CL 13.9–20.3 mm, while the females are usually larger, ranging from CL 19.8 to 25.7 mm) may suggest that *Pandalus chani* is protandrous. The third pereopod shows the clear sexual dimorphism of other species of the *P. hypsinotus* group. The rostrum is more strongly curved in males than in females.

The present new species from Taiwan appears closest to *P. teraoi* from Japan, particularly in having elongate median spines on the postrostral ridge of the carapace. Nevertheless, there are many features distinguishing the two species. The dorsal spines on the carapace and rostrum are 10 or 11 (rarely 12) in the new species and 17–21 in *P. teraoi*; the anteriormost spine arises from posterior, rather than anterior, to the distal end of the atennular peduncle in *P. chani*. Further, these spines are more stout in *P. chani* than in *P. teraoi*. The number of ventral teeth of the rostrum may be fewer in *P. chani* than in *P. teraoi* (9–11 versus 11–14). The absence of long spines on the dorsal surface of the intermediate segment of the antennular peduncle also distinguishes the new species from *P. teraoi*. The third pereopod of *P. chani* is not spinose in either sex. The coloration of *P. chani* is distinctive among the genus in the presence of a white spot on the tergite of the third abdominal somite (figure 44B).

The eggs of *Pandalus chani* are very large, ovate, measuring 1.85–1.93 mm × 2.37–2.74 mm in non-eyed stage. The number of eggs is relatively few, being 182 in the specimen from off Su-Aou (CL 20.4 mm; CBM-ZC 2954). Two females collected in 18 November 1997 bear eggs in a fairly advanced embryonic stage near hatching. The embryos removed from eggs are in a fairly advanced stage with supposedly functional pereopods, as in *P. prensor*, *P. nipponensis* and *P. latirostris* (cf. Mikurich and Ivanov, 1983; Yamamoto *et al.*, 1982; Kurata, 1955).

Pandalus formosanus sp. nov.
(figures 36, 37 and 44C)

Type material. **Taiwan**. Su-Aou, I-Lan County, NE Taiwan, about 500 m; 17 June 1993; commercial trawler; coll. T.-Y. Chan; holotype, ovig. female (CL 22.8 mm); NTOU. Same data; paratypes, 2 females (CL 22.8, 25.0 mm); NTOU. Same data; paratype, 1 ovig. female (CL 24.6 mm); MNHN-Na 13276.

Description. Body moderately robust. Rostrum noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.32 times as long as carapace; dorsal margin

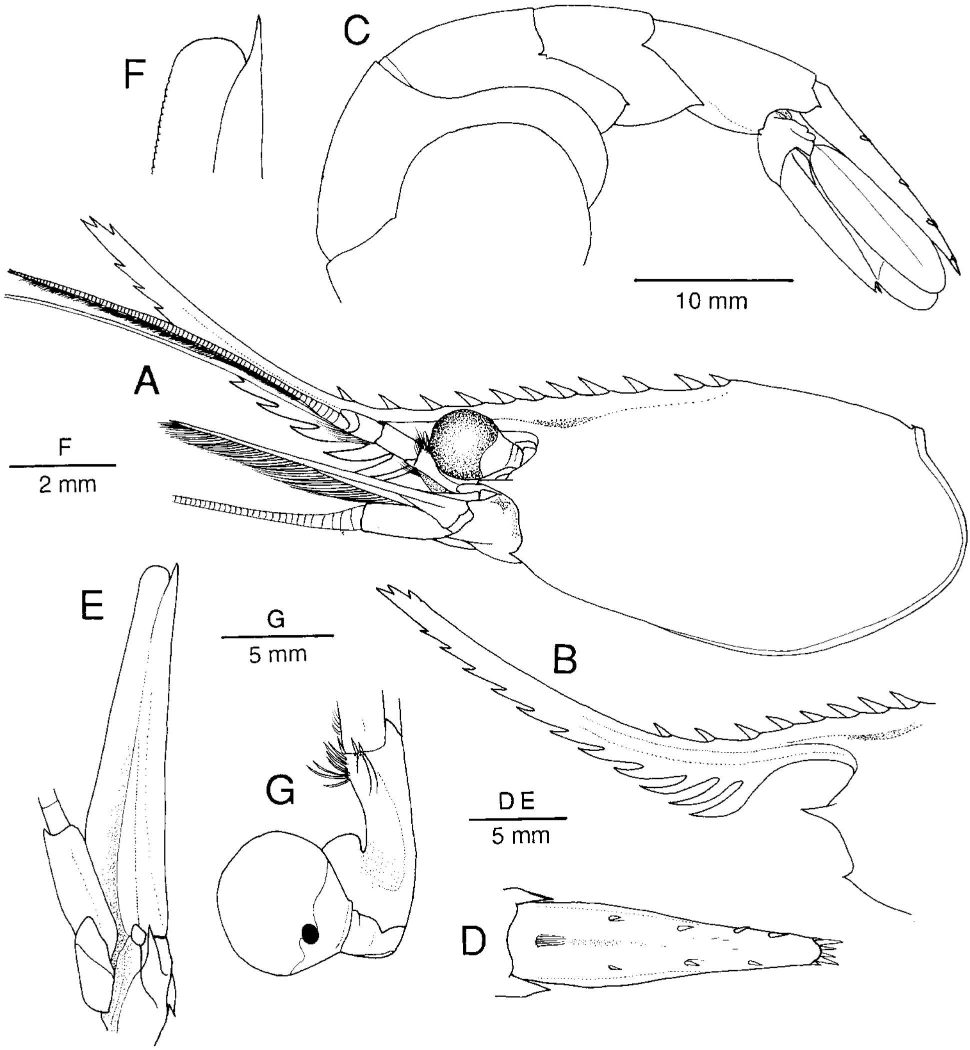


FIG. 36. *Pandalus formosanus* sp. nov. Holotype, female (CL 22.8 mm), Su-Aou, NE Taiwan, NTOU. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) third to sixth abdominal somites, telson and uropod, lateral, pleopod and setae omitted; (D) telson, dorsal; (E) eye and proximal segment of antennular peduncle, dorsal; (F) left antenna, ventral, setae omitted; (G) same, distal part.

nearly straight over eyes, armed with 11 moderately short spines, including five or six on carapace posterior to level of orbital margin, and two fixed teeth near apex of rostrum, subdistal 0.6 unarmed, anteriormost spine arising from level of distal end of antennular peduncle, posteriormost spine arising from 0.46–0.52 of carapace length; ventral blade well developed, with 11 teeth, posterior three teeth noticeably elongate, posteriormost tooth much stronger than preceding teeth; lateral carina rather obsolete. Carapace with postrostral ridge somewhat compressed, extending beyond 0.7 of carapace; dorsal profile weakly convex with peak at level of posteriormost dorsal spine.

Abdomen with third somite smooth dorsally, posterodorsal margin rounded;

fourth somite unarmed on posterodorsal margin; sixth somite about 0.5 times as long as carapace and 2.0 times longer than proximal depth. Telson moderately broad, 1.25–1.38 times as long as sixth somite, armed with four or five dorsolateral spines on either side.

Eye broadly subpyriform with cornea strongly dilated; ocellus distinct.

Antennular peduncle reaching mid-length of scaphocerite; intermediate segment without spinules on dorsal surface; distal segment without dorsodistal spinule. Antenna with scaphocerite about 0.8 times as long as carapace and 4.6 times as long as wide, lateral margin nearly straight, distolateral tooth over-reaching distal margin of moderately broad, rounded blade.

Third maxilliped over-reaching distal margin of scaphocerite.

First pereopod falling slightly short of or slightly over-reaching scaphocerite. Left second pereopod over-reaching scaphocerite by length of chela, carpus and distal 0.15 of merus; carpus divided into 73–78 articles. Right second pereopod over-reaching scaphocerite by length of chela and half of carpus; carpus divided into 23–27 articles; merus with several annulations. Third to fifth pereopods relatively slender. Third pereopod slightly longer than fourth pereopod, over-reaching scaphocerite by length of dactyl and entire propodus; dactyl 0.25 times as long as propodus, with 11 accessory spinules on proximal 0.7 of flexor margin; propodus straight, flexor surface with two or three rows of spinules flanked by two rows of moderately long spinules, lateral and mesial surfaces with few spinules; carpus with two lateral and one mesial spines and scattered spinules mesially and dorsally; merus 1.0–1.1 times as long as carapace, with five or six lateral and four or five ventral or ventromesial spines. Fourth pereopod over-reaching scaphocerite by length of dactyl and half of propodus; dactyl 0.22 times as long as propodus, with nine to 11 accessory spinules; carpus with two lateral and one mesial spines and with fewer spinules mesially and dorsally; merus 0.9–1.0 times as long as carpus, with six lateral and four ventral or ventromesial spines. Fifth pereopod over-reaching scaphocerite by length of dactyl; dactyl 0.21–0.22 times as long as propodus, with seven accessory spinules; carpus with one or two lateral spines, no mesial spine; merus about 0.8 times as long as carapace, with three or four lateral and zero to two ventral or ventromesial spines.

Colour. Body generally pale reddish brown, with patches or spots of darker reddish brown on abdomen. Antepenultimate segment of third maxilliped with tinge of red. First pereopod with tinge of red on propodus, carpus and merus; third to fifth pereopods generally transparent, with obscure band of red on each merus. Pleopods with protopods having same colour as body, but rami redder. Exopod of uropod white laterally, with red irregular band.

Size. Largest female: CL 25.0 mm.

Type locality. Off Su-Aou, NE Taiwan.

Distribution. Known only from the type locality in Taiwan; about 500 m.

Etymology. The species is named after its type-locality since it has only been found there at present.

Remarks. This species appears very rare in Taiwan (T.-Y. Chan, personal communication). Although no male specimen was obtained, morphological characters such as the weakly prehensile third pereopods and the presence of a mesial spine on the carpi of the third and fourth pereopods evidently place this species in the *P. hypsinotus* group. One of the three specimens (NTOU, CL 24.5 mm) has a presumably regenerated left second pereopod which is much shorter than the right second pereopod.

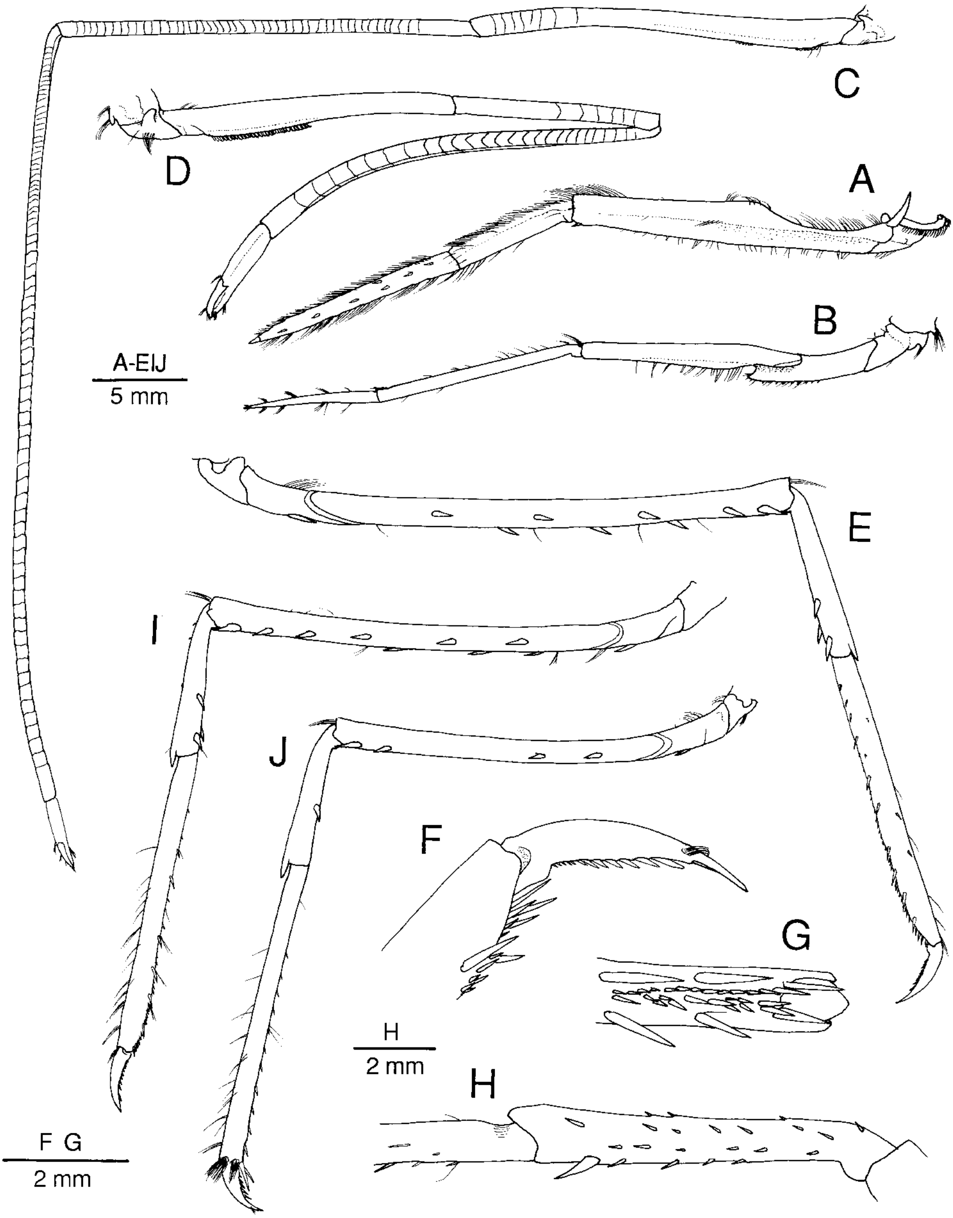


FIG. 37. *Pandalus formosanus* sp. nov. Holotype, female (CL 22.8 mm), Su-Aou, NE Taiwan; NTOU. (A) Left third maxilliped, lateral; (B) left first pereopod, lateral; (C) left second pereopod, lateral; (D) right second pereopod, lateral; (E) left third pereopod, lateral; (F) same, dactyl, lateral; (G) same, distal part of propodus, flexor; (H) same, carpus and proximal part of propodus, mesial; (I) left fourth pereopod, lateral; (J) left fifth pereopod, lateral.

Relatively few dorsal spines on the rostrum and carapace relates the present new species to *P. danae*, *P. prensor* and *P. gurneyi*. *Pandalus formosanus* differs from the latter three species in the following points. The posterior three ventral rostral teeth are noticeably elongate in the new species, but in the latter three species, the teeth are not particularly elongate. The second, fourth and fifth pairs of pereopods are much longer in the new species than in the latter three species. For example, the right second pereopod over-reaches the distal margin of the scaphocerite by the length of the chela and half of the carpus in *P. formosanus*, while it over-reaches that by the length of the chela in the three relatives. The presence of more numerous ventral rostral teeth (11 versus six to eight) is also useful to distinguish the new species from *P. danae* and *P. prensor*. In addition, the coloration of *P. formosanus* is quite distinct from the closely related species in the generally pale red colour of the body, with scattered darker patches or spots on the abdomen.

The eggs of *P. formosanus* are relatively large and few, though the egg size and number was not checked. This species is supposed to have an abbreviated pattern of larval development.

Pandalus platyceros group

Diagnosis. Body moderately robust; integument firm, with pubescence at least on carapace. Rostrum with posteriormost ventral tooth slightly stronger than preceding teeth. Second abdominal somite with deep transverse groove on tergum. Antennule with tapering stylocerite. Antennal basicerite with acute intercalated process. Posterior lobe of scaphognathite noticeably elongate, like *Pandalopsis*. Right second pereopod with carpus divided into less than 15 articles; merus without annulation distally. Third to fifth pereopods stout, similar in length. Third and fourth pereopods not prehensile in either sex, dactyls without convexity basally, propodi of each with single or double row of small spines flanked by rows of relatively strong spines on flexor surfaces; carpi of third to fifth pereopods armed only with lateral spines. Endopod of first pleopod in functional male with appendix interna not inflated, unarmed. Appendix masculina in functional male longer than appendix interna, with spines distally and dorsally.

Remarks. This group, containing two species, *P. platyceros* Brandt, 1851 and *P. latirostris* Rathbun, 1902, is characterized by a number of unique features among *Pandalus*: at least partially pubescent carapace; unusually strong lateral carina of the rostrum; the presence of a deep groove on the second abdominal somite; distally tapering stylocerite of the antennule; the presence of a prominent intercalated process on the antennal basicerite (figures 38F and 40G); and strongly elongate posterior lobe of the scaphognathite (figures 38G and 40H). Furthermore, the last character indicates the close phylogenetic relationship between the *P. platyceros* group and *Pandalopsis* (Komai, 1994a). Christoffersen's (1989) hypothesis that *P. latirostris* (under the name of *P. kessleri*) was a sister group of the genus *Pandalopsis* is falsified by the discovery of the presumably apomorphic characters enumerated above.

Pandalus platyceros Brandt, 1851
(figures 38 and 39)

Pandalus platyceros Brandt, 1851: 123 [type locality: Unalaska]; Stimpson, 1857: 501; Rathbun, 1904: 44; Brashnikov, 1907: 107–113; De Man, 1920: 104; Schmitt, 1921: 43, pl. 14 fig. 3; Berkeley, 1930: 85, fig. 1C; Yokoya, 1934: 15 (part); Holthuis and Rosa, 1965: 14; Butler, 1970: 1294 (part), fig. 1; Scrivener and Butler, 1971: 37 (bibliography); Squires and Figueira, 1974: 15; Butler, 1980: 139, unnumbered fig., pl. 2A; Holthuis, 1980: 142; Rothlisberg, 1980: 19 (part); Wicksten, 1980: 364; Kozloff, 1987: 397 (key); Wicksten, 1989: 303, 313; 397 (key); Williams *et al*., 1989: 19; Jensen, 1995: 55, fig. 102.

Pandalus pubescentulus Dana, 1853: 568 [type locality: Straits of Juan de Fuca]; 1855: pl. 36

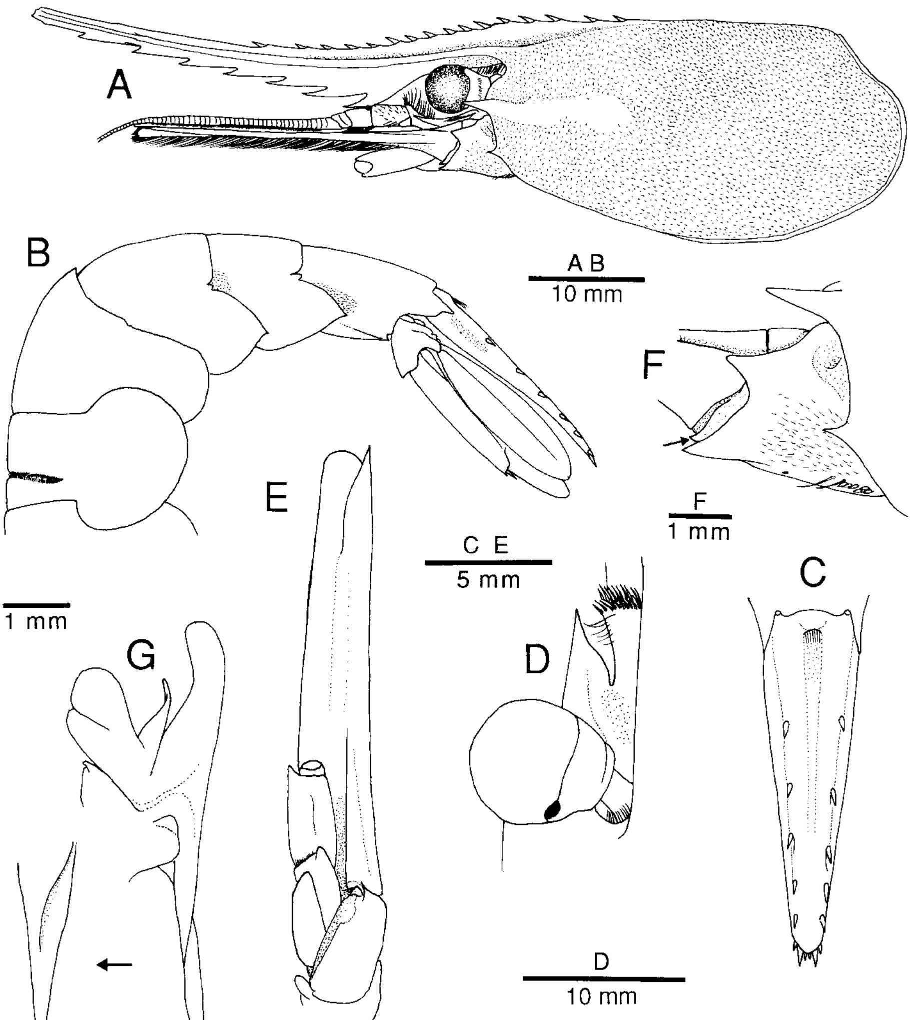


FIG. 38. *Pandalus platyceros* Brandt, 1841. (A)–(F) Female (CL 28.4 mm), Straits of Juan de Fuca, USNM 27994; (G) male (CL 22.2 mm), same lot. (A) Carapace and cephalic appendages, lateral; (B) second to sixth abdominal somites, telson and uropods, lateral, pleopods and setae omitted; (D) left eye and proximal segment of antennular peduncle, dorsal; (E) left antenna, ventral, setae omitted; (F) basicerite of left antenna, lateral, arrow indicating intercalated process; (G) left maxilla, external, setae omitted; inset, posterior lobe of scaphognathite, mesial.

fig. 8; Stimpson, 1857: 501; Kinglsey, 1878: 63; Smith, 1880: 214; Holmes, 1900: 210; De Man, 1920: 104.

Not *Pandalus platyceros*: Doflein, 1902: 635 (part), pl. 1, figs 1 and 2; Balss, 1914: 28 (part). [= *Pandalus latirostris* Rathbun, 1902].

Not *Pandalus platyceros*: Yokoya, 1933: 15. [= *Pandalus gracilis* Stimpson, 1860].

Material examined. **Northwest coast of North America**. Straits of Juan de Fuca, Washington State, 180 m; 1 male (CL 22.2 mm), 2 females (Cl 26.0, 28.4 mm); USNM 27994.

Type material. The type from Unalaska Island, collected by I. G. Voznesensky, is still extant in the collection of the Zoological Institute at St. Petersburg (registration number N 1452; S. Vassilenko, in litt.). According to her, it is still in good condition.

Description. Body moderately stout. Rostrum (figure 38A) weakly curving dorsally, distinctly over-reaching scaphocerite, ? times longer than carapace; dorsal margin weakly convex over eyes, armed with 14 spines, including five or six on carapace posterior to level of orbital margin, and one tooth near apex of rostrum, posteriormost spine arising from 0.32–0.34 of carapace length, anteriormost spine arising far anterior to distal end of antennular peduncle, subdistal half unarmed, without tuft of setae to subdistal tooth; ventral blade well developed, with 11 teeth, posteriormost tooth slightly longer than preceding teeth; lateral carina conspicuous over entire length, not extending posteriorly to gastric region. Carapace (figure 38A) entirely pubescent or partially naked on branchial region, with postrostral ridge compressed laterally, weakly convex over eyes, extending to mid-length of carapace; dorsal profile in lateral view nearly straight or slightly convex.

Abdomen (figure 38B) with pleura of first, fourth and fifth somites partially pubescent; second somite with deep transverse groove obscured by row of dense short setae; third somite lacking median carina or projection; posterodorsal margin of third and fourth somites unarmed; sixth somite 0.4–0.5 times as long as carapace and 1.6–1.7 times longer than proximal depth. Telson (figure 38C) moderately broad, armed with five or six dorsolateral spines on either side.

Eye (figure 38A, D) subpyriform, with corneal region moderately large, much longer than stalk.

Antennular peduncle (figure 38A) reaching 0.3 of scaphocerite; stylocerite (figure 38D) tapering distally into acute apex; intermediate segment unarmed on dorsal surface. Scaphocerite (figure 38A, D) 0.97–0.98 times as long as carapace and 4.7–4.8 times longer than wide, lateral margin nearly straight or slightly sinuous, blade rounded, slightly exceeded by distolateral tooth.

Third maxilliped falling somewhat short of distal margin of scaphocerite.

First pereopod reaching 0.7 of scaphocerite. Second pereopods relatively slender. Left second pereopod (figure 39A) over-reaching scaphocerite by length of chela and 0.3 of carpus; carpus divided into about 29 articles; merus annulated in distal 0.7; ischium with few annulations in distal 0.2. Right second pereopod (figure 39B) falling somewhat short of scaphocerite; carpus divided into nine articles. Third to fifth pereopods moderately stout. Third pereopod (figure 39C) over-reaching scaphocerite by length of dactyl; dactyl (figure 39D) moderately stout, 0.24 times as long as propodus, not twisted, with seven accessory spinules on proximal 0.7 of flexor margin; propodus straight, with single row of small spines flanked by two rows of moderately long spines on flexor surface (figure 39E), only mesial surface spinose (figure 39F); carpus with three lateral spines, mesial surface (figure 39F) with scattered spinules; merus 0.85 times as long as carapace, armed with seven to nine lateral spines and eight ventral or ventromesial spines. Fourth pereopod (figure 39G) similar to third in general, not reaching distal margin of scaphocerite; merus 0.8 times as long as carapace. Fifth pereopod (figure 39H) over-reaching mid-length of scaphocerite by length of dactyl; dactyl 0.16 times as long as propodus, armed with seven or eight accessory spinules; propodus with double row of long spines on flexor face over entire length, mesial surface with row of spinules ventrally; carpus with three lateral spines; merus about 0.7 times as long as carapace, with six or five lateral and five ventral or ventromesial spines.

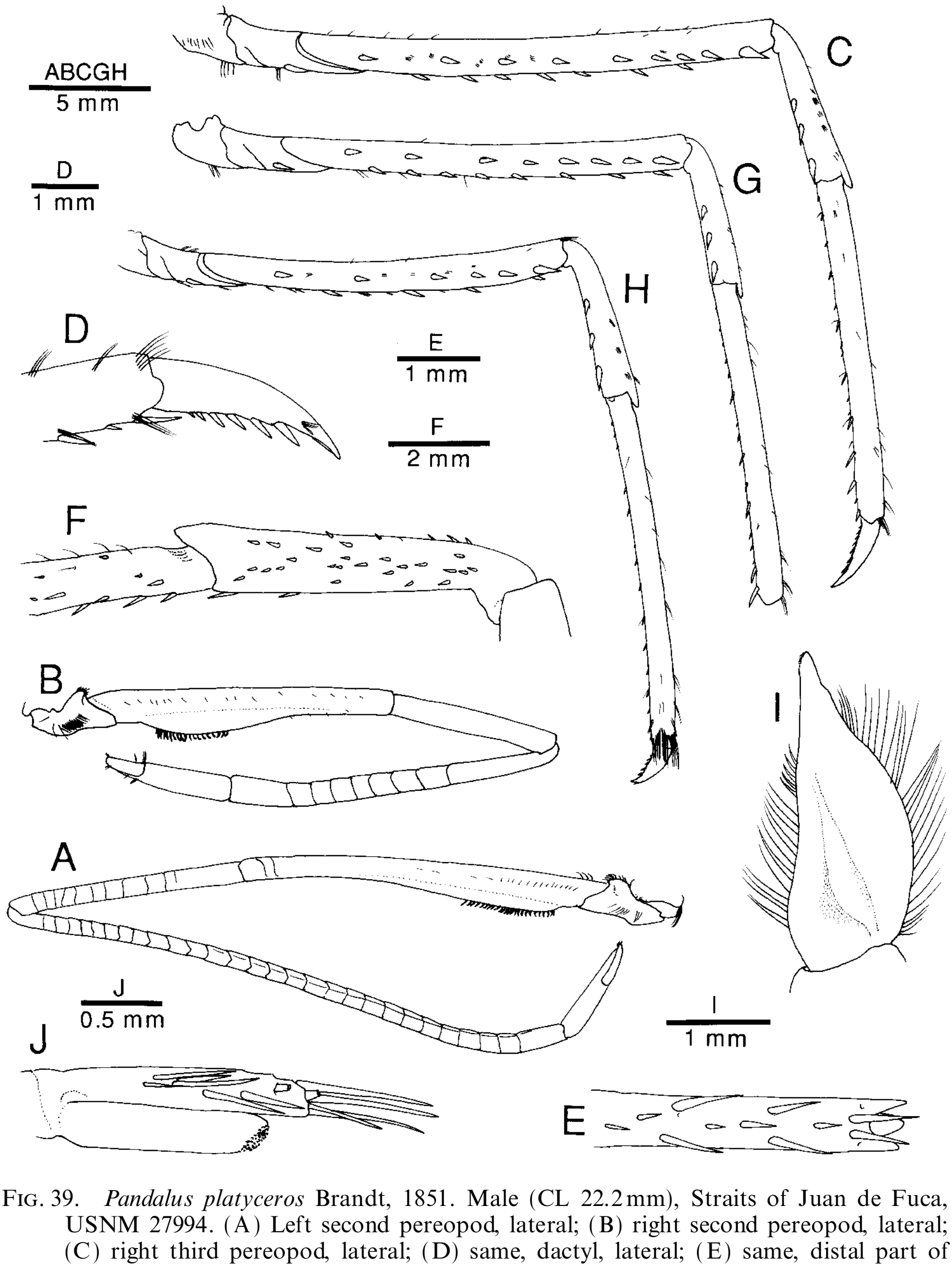


FIG. 39. *Pandalus platyceros* Brandt, 1851. Male (CL 22.2 mm), Straits of Juan de Fuca, USNM 27994. (A) Left second pereopod, lateral; (B) right second pereopod, lateral; (C) right third pereopod, lateral; (D) same, dactyl, lateral; (E) same, distal part of propodus, flexor; (F) same, carpus and proximal part of propodus, mesial; (G) right fourth pereopod, lateral; dactyl missing; (H) right fifth pereopod, lateral; (I) endopod of left first pleopod, ventral; (J) appendix masculina and interna of left second pleopod, mesial.

Endopod of first pleopod in functional males (figure 39I) with distal lobe strongly reduced, vestigial, thus appendix interna occupying distal portion of endopod; mesial margin sinuous, with short row of curved spines distal to 0.6 of endopod; lateral margin generally convex. Appendix masculina of second pleopod in functional males (figure 39J) slightly longer than appendix interna, with long spines on mesial surface and dorsal surfaces and terminal margin.

Colour. Butler (1980) described as follows: 'Color illustration (Plate 2A) of an adult shows a basis overall color of "washed out" red, darker on carapace due to pubescence; other adults are fawn or tan. Three or 4 lateral stripes prominent on carapace; longest and widest stripes extend from antennal and pterygostomian spines posteriorly for most of carapace length. Conspicuous round white spots, pair on dorsolateral surface of each of first and fifth abdominal somites give species common names in use elsewhere on the coast of North America. Alternating red and white bands on third maxilliped, pereiopods, and flagella of antennule and antenna. Juvenile specimens in shallow water, among eelgrass, sea lettuce (*Ulva*), apron kelp (*Laminaria*), and red algae are correspondingly green, brown, or red; white marking on body barely visible. Young animals normally have more white stripes and dots than adults; former appear on carapace, either medially or adjacent to dorsal spines; additional pairs of white dots occur on dorsolateral surface of second abdominal somite and membrane between first and second somites. Fine blue spots occur in pairs on anterior dorsal surface of first to third somites, also 2 or 3 spots along cardiac and gastric regions of carapace.' Jensen (1995: 55) published a colour photograph of this species.

Size. Largest functional male: CL 48.1 mm; largest female: CL 61.1 mm (Butler, 1980).

Distribution. Unalaska Island, Aleutian Islands, to off San Diego, California; intertidal to 487 m.

Remarks. This species is quite distinctive in the genus by the pubescent carapace, acutely pointed stylocerite of the antennule and the absence of a distolateral lobe from the endopod of the first pleopod in functional males. Although it is most closely related to *P. latirostris*, there are numerous characters to separate them (see 'Remarks' under account of *P. latirostris*).

Dana (1852), who seemed to be unaware of Brandt's (1851) work, described *Pandalus pubescentulus* from the Straits of Juan de Fuca, Washington State. The type of this taxon was presumably lost in the 1871 Chicago fire (Evans, 1967; Deiss and Manning, 1981). This name has generally been regarded as a junior synonym of *P. platyceros* (see Butler, 1970, 1980; Holthuis, 1980). From the original description, there is little doubt that Dana's taxon is identical with *P. platyceros*. I follow previous authors in regarding these two species as synonymous, and Brandt's name should have priority over Dana's name. The specimen from the Sea of Japan, referred to as *P. platyceros* by Yokoya (1933) is kept in the collection of the Kitakyushu Museum of Natural History. Re-examination of the specimen disclosed that it actually represented *P. gracilis*. From the given synonymy of *P. platyceros*, it is obvious that Yokoya (1933) confused *P. platyceros*, *P. latirostris* and *P. robustus* (here interpreted as a synonym of *P. gracilis*). Butler's (1970, 1980) summary of distribution of this species is partially based on the erroneous record of Yokoya. So far, *P. platyceros* has never been found in the northwestern Pacific.

Pandalus latirostris Rathbun, 1902
(figures 40 and 41)

Pandalus kessleri Czerniavskii, 1878: 23 (*nomen nudum*); Brashnikov, 1907: 106, text-figs 12a, b, pl. 2 figs 7 and 8 [type locality: Olga Bay, continental coast of Sea of Japan]; Balss, 1914: 24; De Man, 1920: 103; Balss, 1924: 24; Urita and Nomura, 1938: 236, fig. 1;

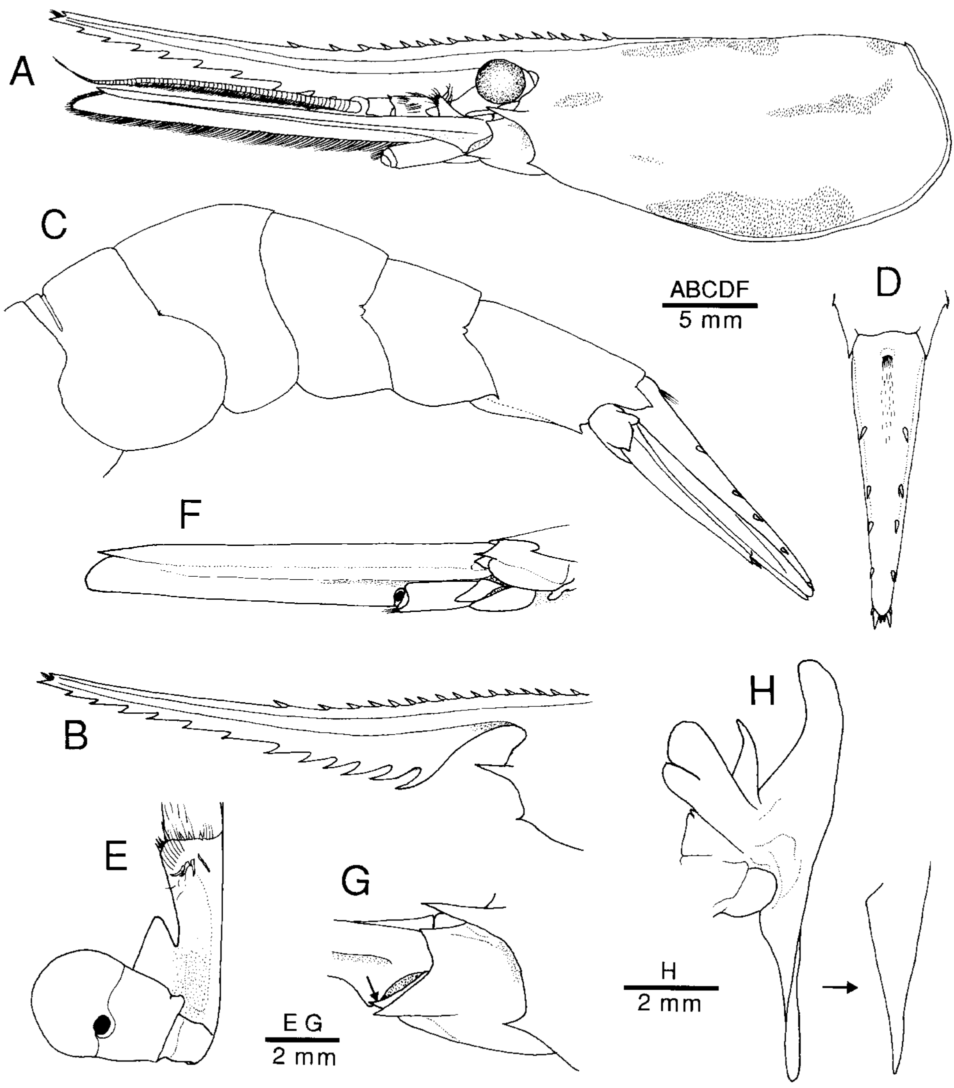


FIG. 40. *Pandalus latirostris* Rathbun, 1902. (A)–(G) Transitional male (CL 20.4 mm), Usujiri, southern Hokkaido, CBM-ZC 276; (H) male (CL 18.0 mm), Usu Bay, southern Hokkaido, HUMZ-C. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) second to sixth abdominal somites and telson, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left eye and proximal segment of antennular peduncle, dorsal; (F) left antenna, ventral, setae omitted; (G) basicerite of left antenna, lateral, arrow indicating intercalated process; (H) left maxilla, external, setae omitted; inset, posterior lobe of scaphognathite, mesial.

Nishumura, 1939: 382; Yoshida, 1941: 24, pl. 6 fig. 1; Urita, 1942: 8; Kubo, 1960: 106, pl. 53, fig. 7; 1965: 605, fig. 949; Igarashi, 1969: 3, pl. 2, fig. 2, fig. 6, pl. 14, fig. 40; Scrivener and Butler, 1971: 37 (part; bibliography); Kim and Park, 1972: 204; Miyake, 1975: 100, unnumbered fig., 309; Kim, 1976: 144; 1977: 284, pl. 53 fig. 56, text-fig. 118.; Holthuis, 1980: 141; Rothlisberg, 1980: 19; Miyake, 1982: 60, pl. 20 fig. 4; Takeda, 1982: 17, fig. 51; Takeda, 1986: 107, unnumbered fig.; Komai *et al.*, 1992: 192; Okutani, 1994: 219, fig. 7; Hayashi, 1995: pl. 90 fig. 6, 333.

Pandalus platyceros: Doflein, 1900: 321; 1902: 635, pl. 1 figs 1 and 2; Balss, 1914: 28; Schmitt, 1921: 43 (part).

Pandalus latirostris Rathbun, 1902b: 46, figs 20 and 21 [type locality: Mororan (=Muroran), Hokkaido, Japan]; De Man, 1920: 103 (footnote); Yokoya, 1930: 538; 1933: 16; 1934: 16; Derjugin and Kobjakova, 1935: 142; Kobjakova, 1936: 209; 1937: 103; Vinogradov, 1950: 193, 255, pl. 6, fig. 18; Kobjakova, 1955: 148, pl. 35 fig. 4; 1958: 223; 1967: 232; Holthuis, 1995: 150.

Material examined. **Japan**. Noshappu-misaki, Wakkanai, northern Hokkaido, *Zostera* beds in intertidal zone; 28 September 1976; dip net; 2 males (CL 11.3, 13.2 mm); CBM-ZC 261. Usujiri Fishery Port, southern Hokkaido, 0–1 m; May 1987; dip net; coll. T. Komai; 1 male (CL 20.4 mm); CBM-ZC 276. Lake Saroma, Okhotsk coast of Hokkaido, 5 m, *Zostera* beds; 26 September 1990; beam trawl; coll. M. Yabe; 1 male (CL 19.4 mm); CBM-ZC 2440. Takahama, Miyako Bay, Iwate; 30 December 1983; trap; coll. T. Komai; 1 male (CL 22.1 mm); HUMZ-C. Sokei, Miyako Bay, Iwate; 5 January 1986; trap; coll. T. Komai; 2 females (CL 29.3, 30.5 mm); HUMZ-C. Usu Bay, southern Hokkaido, subtidal; October 1970; dip net; coll. T. Igarashi; 1 male (CL 18.0 mm); HUMZ-C uncat.

Continental coast of Sea of Japan. Srednaja Bay, *Zostera* beds in subtidal zone; 24 August 1994; beach seine; coll. M. Yabe; 10 males (CL 10.2–22.6 mm), 1 juvenile (CL 9.2 mm); CBM-ZC 2451. Popov Island, 10 m; 25 August 1994; beam trawl; coll. M. Yabe; 1 male (CL 20.4 mm), 1 juvenile (CL 10.3 mm); CBM-ZC 2457. Tzoitsy Bay, 42°38′N, 131°13′E, intertidal; 29 August 1994; beach seine; coll. M. Yabe; 1 male (CL ? mm); CBM-ZC 2461.

Type material. Mororan (=Muroran), Hokkaido, Japan; coll. Jordan and Snyder; syntypes, 18 specimens; USNM 26160. Not examined.

Description. Body rather slender. Rostrum (figure 40A, B) slightly curving dorsally or nearly straight, reaching or slightly over-reaching scaphocerite, 0.95–1.42 times as long as carapace; dorsal margin nearly straight or slightly convex over eyes, armed with 16 or 17 spines, including four or five on carapace posterior to level of orbital margin, and one tooth near apex of rostrum, posteriormost spine arising from 0.16–0.17 of carapace length, anteriormost spine arising anterior to distal end of antennular peduncle, subdistal half unarmed, with tuft of setae distal to subdistal tooth; ventral blade well developed, with 10–12 teeth, posteriormost tooth slightly stronger than preceding teeth; lateral carina conspicuous over entire length, extending posteriorly to gastric region. Carapace (figure 40A) with patches of pubescence on dorsal and lateral surfaces; postrostral ridge low, extending beyond 0.3 of carapace length; dorsal profile in lateral view nearly straight or slightly convex.

Abdomen (figure 40C) glabrous; second somite with deep transverse groove on tergum, not obscured by setae; third somite lacking median carina or projection; postero-dorsal margin of third and fourth somites unarmed; sixth somite 0.4–0.5 times as long as carapace and 1.7 times longer than proximal depth. Telson (figure 40D) moderately broad, armed with five or six dorsolateral spines on either side.

Eye (figure 40E) subpyriform, corneal region relatively small, subequal in length to stalk.

Antennular peduncle (figure 40A) reaching 0.25–0.3 of scaphocerite; stylocerite (figure 40E) tapering but rounded distally; intermediate segment unarmed on dorsal surface. Scaphocerites (figure 40F) 1.2–1.3 times as long as carapace and 6.6–7.0 times as long as wide, rarely dissimilar, lateral margin nearly straight or faintly sinuous, blade rounded, strongly produced distally and far exceeding distolateral tooth.

Third maxilliped reaching or over-reaching mid-length of scaphocerite.

First pereopod reaching 0.2–0.4 of scaphocerite. Second pereopods relatively stout. Left second pereopod (figure 41A) over-reaching 0.6 length of scaphocerite by tip of chela; carpus divided into 14–21 articles; merus annulated in distal 0.7;

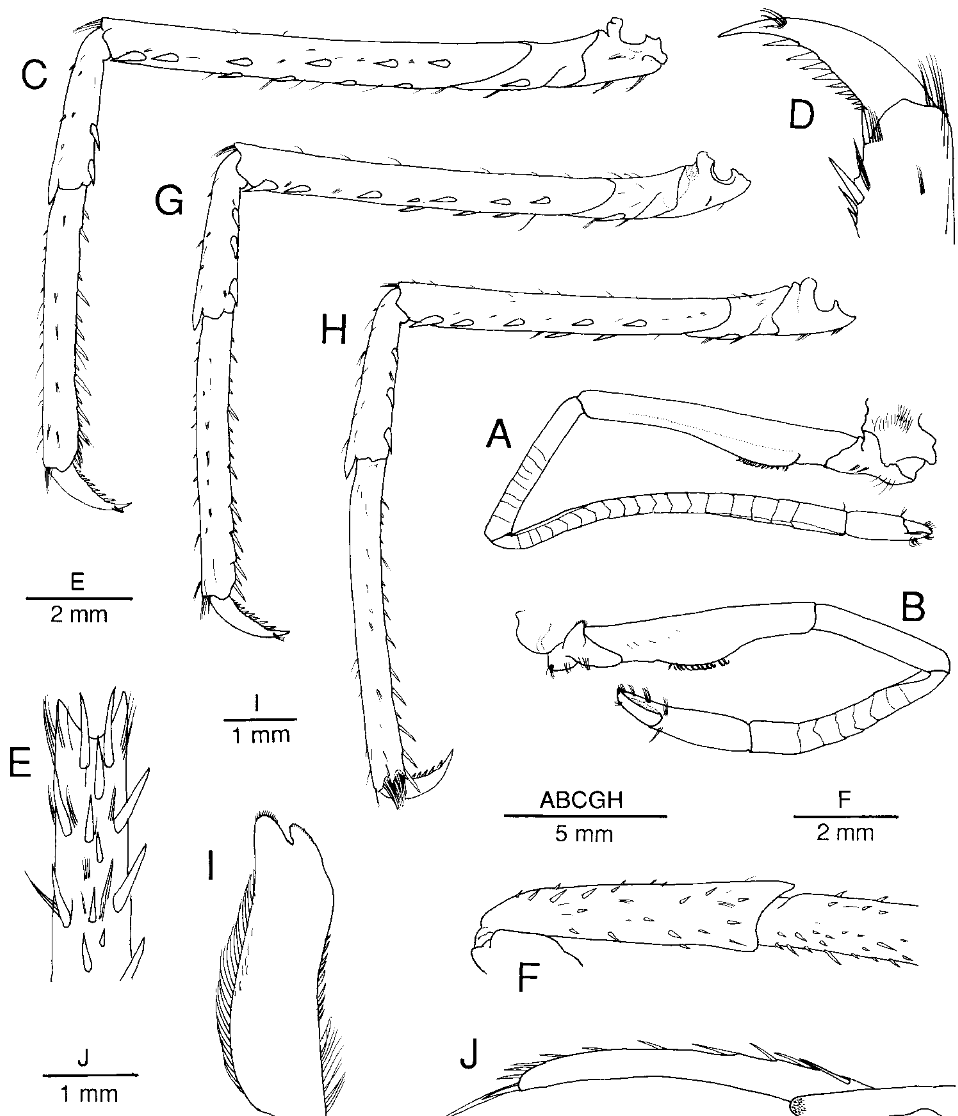


FIG. 41. *Pandalus latirostris* Rathbun, 1902. (A)–(H) Transitional male (CL 20.4 mm), Usujiri, southern Hokkaido, CBM-ZC 276; (I), (J) Functional male (CL 18.0 mm), Usu Bay, southern Hokkaido, HUMZ-C. (A) Left second pereopod, lateral; (B) right second pereopod, lateral; (C) left third pereopod, lateral; (D) same, dactyl, lateral; (E) same, distal part of propodus, flexor; (F) same, carpus and proximal part of propodus, mesial; (G) left fourth pereopod, lateral; (H) left fifth pereopod, lateral; (I) endopod of right first pleopod, ventral; (J) appendix masculina and interna of left second pleopod, mesial.

ischium entire. Right second pereopod (figure 41B) reaching 0.25–0.30 of scaphocerite by tip of chela; carpus divided into seven to nine articles. Third to fifth pereopods relatively short and stout. Third pereopod (figure 40C) nearly reaching mid-length of scaphocerite by tip of propodus; dactyl (figure 40D) relatively stout, 0.30–0.34 times as long as propodus, not twisted, with 5–12 accessory spinules on proximal 0.75 of flexor margin; propodus straight, with single or double row of small spines flanked by row of moderately long spines on flexor surface (figure 41E), mesial surface spinose (figure 41F), dorsal surface with row of spinules; carpus with one to four lateral spines, mesial surface (figure 41F) with scattered spinules; merus 0.7 times as long as carapace, armed with six or seven lateral spines and four to six ventral or ventromesial spines. Fourth pereopod (figure 41G) similar to third in general, reaching mid-length of scaphocerite by tip of dactyl; merus 0.55–0.60 times as long as carapace. Fifth pereopod (figure 41H) reaching 0.3 length of scaphocerite by tip of propodus; dactyl 0.27–0.31 times as long as propodus, armed with 7–11 accessory spinules; propodus with double row of long spines on flexor face over entire length, mesial surface with row of spinules ventrally; carpus with two or three lateral spines; merus about 0.5 times as long as carapace, with four or five lateral and one to four ventral or ventromesial spines.

Endopod of first pleopod in functional males (figure 41I) with well-developed distal lobe; appendix interna separated from distal lobe by deep V-shaped notch; mesial margin strongly sinuous, with short row of curved spines around mid-length of endopod; lateral margin also sinuous. Appendix masculina of second pleopod in functional males (figure 41J) strongly elongate, attaining more than three times as long as appendix interna, with scattered spinules or long spines on dorsal surface and distal margin.

Colour. Base colour of body greenish brown or brown, with several white stripes running on carapace and abdomen; mesial margin of scaphocerite and distal lamina of exopod of uropod deep blue; rami of uropods with tinge of red distally. Third to fifth pereopods green, sometimes reddish on meri. Colour photographs of this species are available from Miyake (1975: 100; 1982: pl. 20, fig. 4) and Hayashi (1995).

Size. Largest functional male: CL 22.6 mm; largest female: CL 30.3 mm.

Distribution. Southeast Siberia, Korea, Sakhalin, northern Japan; intertidal to 9 m. Around 1959 this species was introduced into the Black Sea (Holthuis, 1980).

Remarks. *Pandalus latirostris* is very distinctive among *Pandalus* species, though it appears closest to the eastern Pacific *P. platyceros*. It differs from *P. platyceros* in the following points: the carapace is only partially pubescent, rather than entirely pubescent; the rostrum has fewer ventral teeth; the transverse groove on the tergum of the second abdominal somite is naked, not setose; the eye is distinctly smaller, with the corneal region being subequal to the stalk; the stylocerite of the antennule is triangular with a rounded apex, rather than acutely pointed; the distal blade of the scaphocerite is strongly produced distally, and thus far overreaches the distolateral tooth; the pereopods are much shorter; the distolateral lobe of the endopod of the first pleopod is well differentiated in functional males; the appendix masculina of the second pleopod is strongly elongate in functional males, attaining more than three times longer than the appendix interna, rather than only slightly longer than it. The coloration of *P. latirostris* is also unique in the genus. It can be easily recognized by several white stripes on a greenish brown background of the body.

Like *P. hypsinotus* group, the appendix masculina is strongly elongate in this species. However, considering the presence of numerous apomorphic character states shared by this species and *P. platceros*, this phenomenon is attributable to character convergence. Sequential developmental change of the appendix masculina of the second pleopod in this species has been described and illustrated in detail (Kubo, 1951; Kashigawa, 1974). For a discussion on the nomenclature of this species see Kobjakova (1937) and Holthuis (1995).

Atlantopandalus gen. nov.

Pandalus: Calman, 1899: 29 (part); Holthuis, 1955: 123 (part); 1993: 272 (part); Christoffersen, 1989: 265 (part).

Type species. *Pandalus propinqvus* G. O. Sars, 1870, by the present designation.

Species included. *Atlantopandalus propinqvus* (G. O. Sars, 1870), comb. nov.

Diagnosis. Dioecious. Integument devoid of scales. Rostrum well developed, distinctly over-reaching scaphocerite. Eye semi-spherical with well-developed cornea, without ocellus. Stylocerite of antennule short, rounded. Posterior lobe of scaphognathite produced, but not strongly elongate. Second maxilliped with dactyl shallowly notched mesially. Third maxilliped lacking exopod. Ischium of first pereopod with weak ventral lamina, bearing spinules on ventral margin. Second pereopods greatly unequal; carpus of right leg divided into nearly exclusively five articles, proximal article longest, occupying about half length of carpus. Carpi of third and fourth pereopods distinctly shorter than propodi, armed with moderately small spines on lateral and flexor surfaces; mesial surfaces with scattered spinules, but without spines. First pleopod in males with appendix interna not produced, separated from distolateral lobule by prominent notch. Male second pleopod with appendix masculina subequal in length to appendix interna, armed with several long spines distally or dorsodistally.

Distribution. See 'Distribution' of *Atlantopandalus propinqvus.*

Etymology. From Atlantic and the generic name *Pandalus*, in reference to the exclusive Atlantic distribution of this genus. Gender: masculine.

Remarks. It is known that *Pandalus propiqvus* is not hermaphroditic (Squires, 1965; Williams, 1984) and the present study confirms that this species is dioecious. The absence of hermaphroditism excludes *P. propinqvus* from the *Pandalus* and *Pandalopsis* clade. Other differences that set it apart from *Pandalus* include the following features: the carpus of the right second pereopod is divided into nearly exclusively five (very rarely six) articles, with the proximalmost article occupying half the length of the carpus; the carpi of the third and fourth pereopods are armed with relatively small spines, usually forming a row, on each lateral and flexor surface; and the eye lacks an ocellus. The structure of the carpus of the right second pereopod, which represents a presumably derived condition, links *Atlantopandalus* to the genus *Dichelopandalus* Caullery, 1896. In addition to the characters of the eyes and carpi of the third and fourth pereopods mentioned above, *Atlantopandalus* differs from *Dichelopandalus* in the absence of an exopod from the third maxilliped.

Atlantopandalus propinqvus (G. O. Sars, 1870), new comb.
(figures 42 and 43)

Pandalus propinquus G. O. Sars, 1870: 148 [type locality: Lofoten near Skrava, Guldbrandsøy or Brettesnes]; 1871: 259; 1882: 47.

Pandalus propinquus: Smith, 1881: 437; 1882: 58; A. Milne Edwards, 1883: pl. 22; Smith, 1886: pl. 13, fig. 1; Ortmann, 1890: 492; Calman, 1899: 32, pls 1–4, fig. 2; Doflein, 1900: 321;

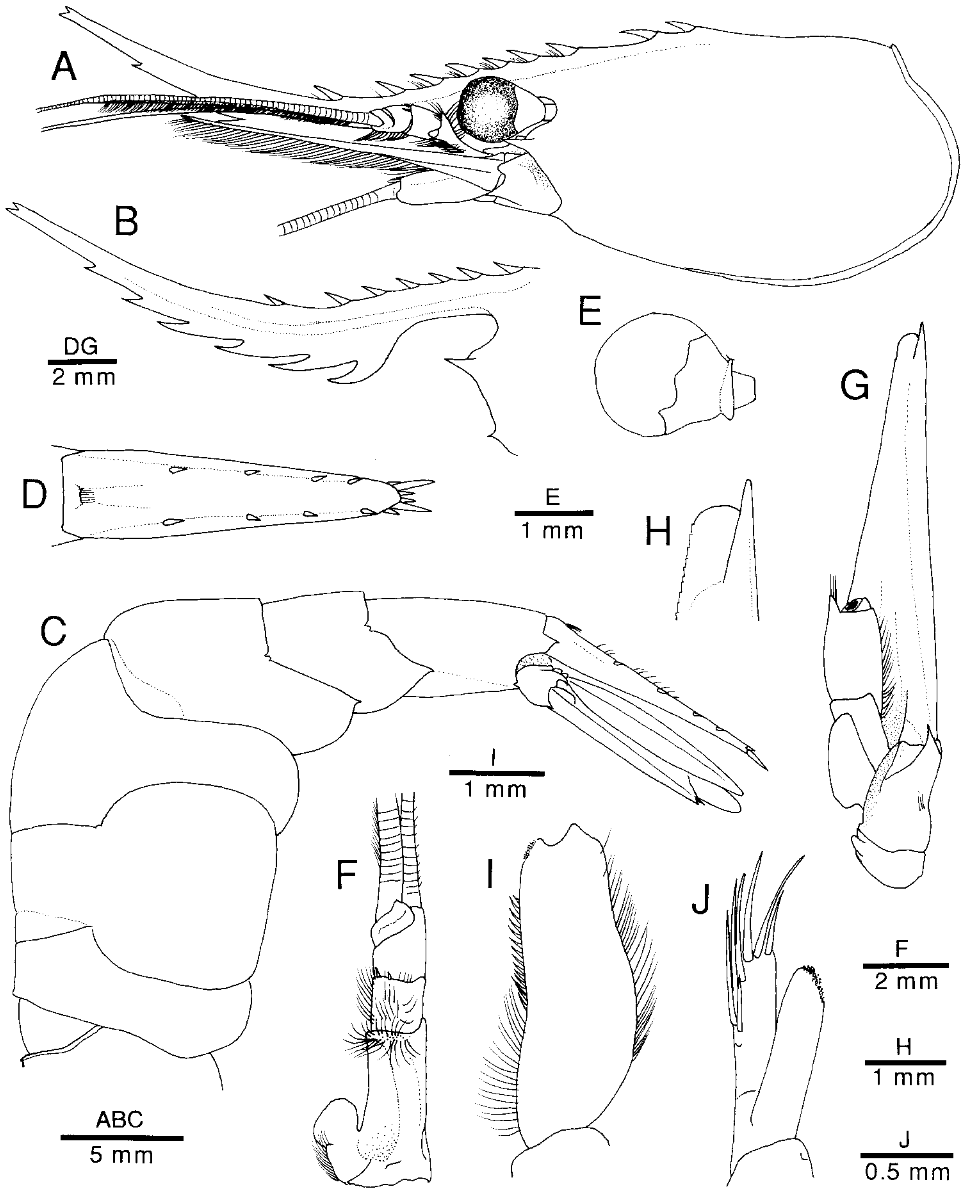


FIG. 42. *Atlantopandalus propinqvus* (G. O. Sars, 1870), comb. nov. (A)–(D) Female (CL 13.9 mm), Norwegian Sea, CBM-ZC 3420; (E)–(J) male (CL 13.8 mm), same lot. (A) Carapace and cephalic appendages, lateral; (B) rostrum, lateral; (C) abdomen, lateral, pleopods and setae omitted; (D) telson, dorsal; (E) left eye, dorsal; (F) left antennule, dorsal; (G) left antenna, ventral, most setae omitted; (H) distal part of scaphocerite, ventral; (I) endopod of left first pleopod, ventral; (J) appendix masculina and interna of left second pleopod, mesial.

Appelöff, 1906: 119; Hansen, 1908: 72; Wollebaek, 1908: 67, fig. 7; Kemp, 1910: 89, pl. 11, figs 1–4; Wedemeyer, 1912: 126; Stephensen, 1913: 44; Dons, 1915: 24; De Man, 1920: 104; Balss, 1926: 13; Grieg, 1926: 12; Rathbun, 1929: 9, fig. 6; Stephensen, 1935: 28; 1939: 21; Sivertsen and Holthuis, 1956: 36; Squires, 1965: 65; 1990: 251, figs 136–138; Couture and Trudel, 1968: 864, fig. 5; Scrivener and Butler, 1971: 37 (bibliography); Williams, 1974: 13, fig. 33; Smaldon, 1979: 96, fig. 40; Rothlisberg, 1980: 19; Williams, 1984: 156, fig. 109; Smaldon, 1993: 108, fig. 41; Komai, 1995: 259, fig. 191; Forest and Holthuis, 1997: pl. 22.

Material examined. **Norway**. Lofoten near Skrava, Guldbrandsøy, 360–540 m; 1 juvenile (CL 6.8 mm), lectotype (herein designated); ZMUO F16448. Norwegian Sea, 63°39′N, 9°49′E, 50–300 m; 27 August 1965; 3 males (CL 13.0–14.2 mm), 2 females (CL 13.9m 16.6 mm); CBM-ZC 3420, on exchange from RMNH. Trondhjeimsfjord; 1888; 1 female (CL 21,5 mm); examined by Ortmann (1890); MZS no. 93.

Greenland. Baffin Bay, depth unknown; 5 December 1992; otter trawl by RV *Shinkai-Maru*; 1 female (CL 17.8 mm); CBM-ZC 3419. Baffin Bay, 65°20′N, 55°10′W, 583 m; *Shinkai-Maru*, stn 3-65; 6 September 1990; otter trawl; coll. E. Mihara; 2 females (CL 16.4, 16.8 mm); HUMZ-C 1228. Baffin Bay, 64°13.2′N, 57°41.1′W, 884 m; RV *Shinkai-Maru*, stn 3-36; otter trawl; coll. E. Mihara; 1 male (CL 15.5 mm); HUMZ-C 1241. Baffin Bay, 69°34.8′N, 58°48.7′W, 577–580 m; *Shinkai-Maru*, stn T-109; 25 August 1991; otter trawl; coll. H. Endo; 1 male (CL 15.3 mm); HUMZ-C 1291.

British Isles. Loch Tyne, 162–180 m; June 1885; coll. A. M. Norman; 3 males (CL 13.1–17.0 mm), 5 females (CL 13.4–21.4 mm); NHM 1898.5.7.584–590. Kilchattan Bay, Clyde area; 6 October 1948; 1 male (CL 13.1 mm), 4 females (CL 13.7–19.2 mm); NHM 1949.1.18.46–48.

East coast of North America. Off Martha's Vineyard, 39°54.45′N, 69°25.45′W, 450 m; *Albatross*, stn 2262; 28 September 1884; 1 male (CL 13.3 mm), 3 females (CL 15.5–21.2 mm); examined by Smith (1886); USNM 8673.

Type material. Lectotype (here designated); Lofoten near Skrava, Guldbrandsøy, 360–540 m; 1 juv. (CL 16.8 mm); ZMUS F16448 (see 'Material examined'). See 'Remarks'.

Description. Rostrum (figure 42A, B) noticeably curving dorsally, distinctly over-reaching scaphocerite, 1.12–1.60 times longer than carapace; dorsal margin armed with 8–10 spines, including two or three on carapace posterior to level of orbital margin; and one tooth near apex of rostrum, subdistal 0.5–0.6 length unarmed, anteriormost spine arising from anterior to level of distal margin of antennular peduncle, posteriormost spine arising from 0.37–0.42 of carapace length; ventral margin armed with six to eight teeth, posteriormost tooth subequal to or somewhat stronger than preceding tooth, blade well developed, widest at posteriormost tooth; lateral chain blunt over entire length. Carapace (figure 42A) with post-rostral ridge weakly elevated, extending to 0.4–0.5 of carapace length; dorsal margin slightly convex, highest at posteriormost dorsal spine.

Abdomen (figure 42C) with third somite devoid of median projection, posterodorsal margin moderately produced posteriorly, rounded; fourth somite unarmed posterodorsally; sixth somite 0.5–0.6 times as long as carapace and 1.7–1.8 times as long as proximal depth. Telson (figure 42D) moderately broad, 1.2–1.3 times longer than sixth somite, armed with five (rarely four) dorsolateral spines on either side.

Eye (figure 42E) broadly subpyriform; ocellus absent.

Antennular peduncle (figure 42F) not reaching mid-length of scaphocerite; intermediate segment without spines on dorsal surface. Scaphocerite (figure 42G) 0.76–0.94 times as long as carapace and 3.7–8.,4 times as long as wide, markedly narrowed distally; lateral margin nearly straight, distolateral tooth far over-reaching distal margin of rounded blade.

Third maxilliped (figure 43A) reaching or slightly over-reaching distal end of scaphocerite.

First pereopod (figure 43B) reaching 0.7 of scaphocerite; ischium with weak ventral lamina bearing row of stiff setae and minute spinules on its ventral margin. Left second pereopod (figure 43C) over-reaching distal margin of scaphocerite by length of chela and distalmost article of carpus; carpus divided into 25–29 articles; dactyl distinctly shorter than palm. Right second pereopod (figure 43D) not reaching distal margin of scaphocerite; carpus divided constantly into five (very rarely six) articles, proximal article occupying about half length of carpus; dactyl distinctly shorter than palm. Third to fifth pereopods relatively slender, becoming slightly shorter successively. Third pereopod (figure 43E) over-reaching scaphocerite by length of dactyl and distal 0.5 of propodus; dactyl (figure 43F) moderately stout, 0.23–0.25 times as long as propodus, not twisted, with relatively long five to nine accessory spinules over entire length of flexor margin; carpus (figure 43H) with five or four relatively small spines on lateral surface and row of one to five spines on flexor surface, mesial surface (figure 43I) with scattered spinules; merus 0.9–1.0 times as long as carapace, armed with six to nine lateral spines and six to eight ventral or ventromesial spines. Fourth pereopod (figure 43J) similar to third, reaching distal margin of scaphocerite by tip of dactyl; dactyl with four to seven accessory spinules; carpus with three or four spines on lateral surface and one or two spines on flexor surface (rarely unarmed on flexor surface), mesial surface with fewer spinules; merus 0.8–0.9 times as long as carapace, armed with six to eight lateral and three to six ventral or ventromesial spines. Fifth pereopod (figure 43K) falling short of distal margin of scaphocerite; dactyl 0.19–0.20 times as long as propodus, with four to six accessory spinules on flexor margin; carpus with two to four lateral spines, flexor surface unarmed; merus 0.7–0.8 times as long as carapace, with only five or six lateral spines.

Endopod of first pleopod (figure 42I) with less produced appendix interna, separated from distal lobe of endopod by broad notch; mesial margin slightly sinuous, with row of short spines distal to mid-length; lateral margin generally convex, with rows of setae. Appendix masculina of second pleopod (figure 42J) subequal in length to appendix interna, armed with about 10 long spines distally and dorsodistally.

Coloration. Carapace generally pale red, posterior part sometimes colourless; rostrum bright red distally, proximally paler with red dots. Abdomen with transverse bands of red on first somite, on anterior parts of second and third, and on posterior parts of second, third, fourth and fifth somites; sixth somite, telson and uropods darker red. Eyes darkly pigmented. Antennular peduncle pale red with darker spots; flagella uniformly red. Scaphocerite distally red, proximally paler; flagellum uniformly red. Third maxilliped with distal two segments white; antepenultimate segment dark red. Third to fifth pereopods with carpi and greater part of propodi white, distal extremity of propodi, dactyli and meri dark red (based on fresh specimens from Baffin Bay). Komai (1995: fig. 191) published a colour photograph of this species.

Size. Largest male: CL 19 mm (Squires, 1990); largest female: CL 21.5 mm (present study).

Distribution. North Atlantic: Davis Strait to Delaware Bay including the Gulf of St. Lawrence and Gulf of Maine in America; Greenland, Iceland and Norway to the British Isles and Bay of Biscay in Europe; 20–2180 m.

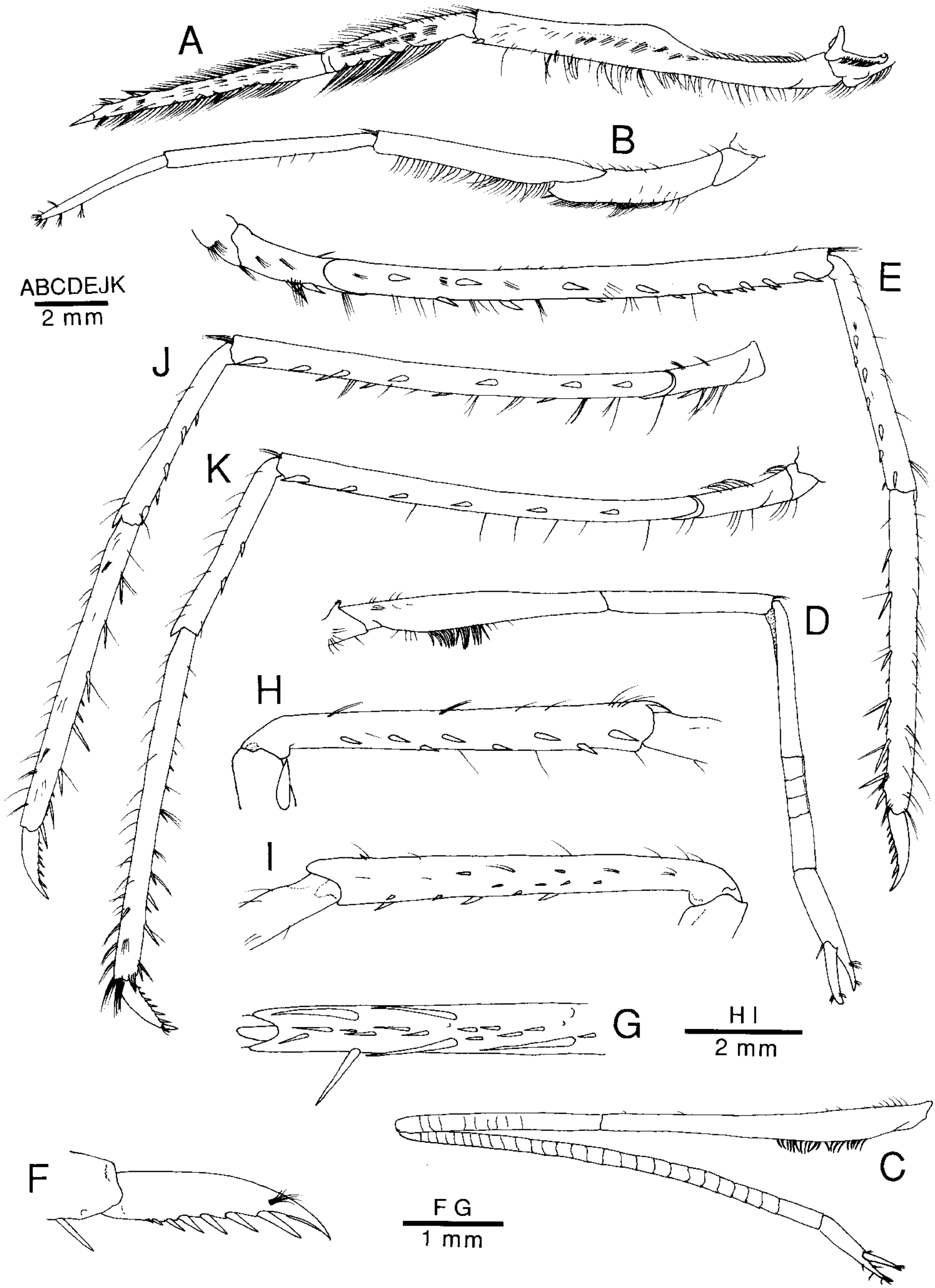
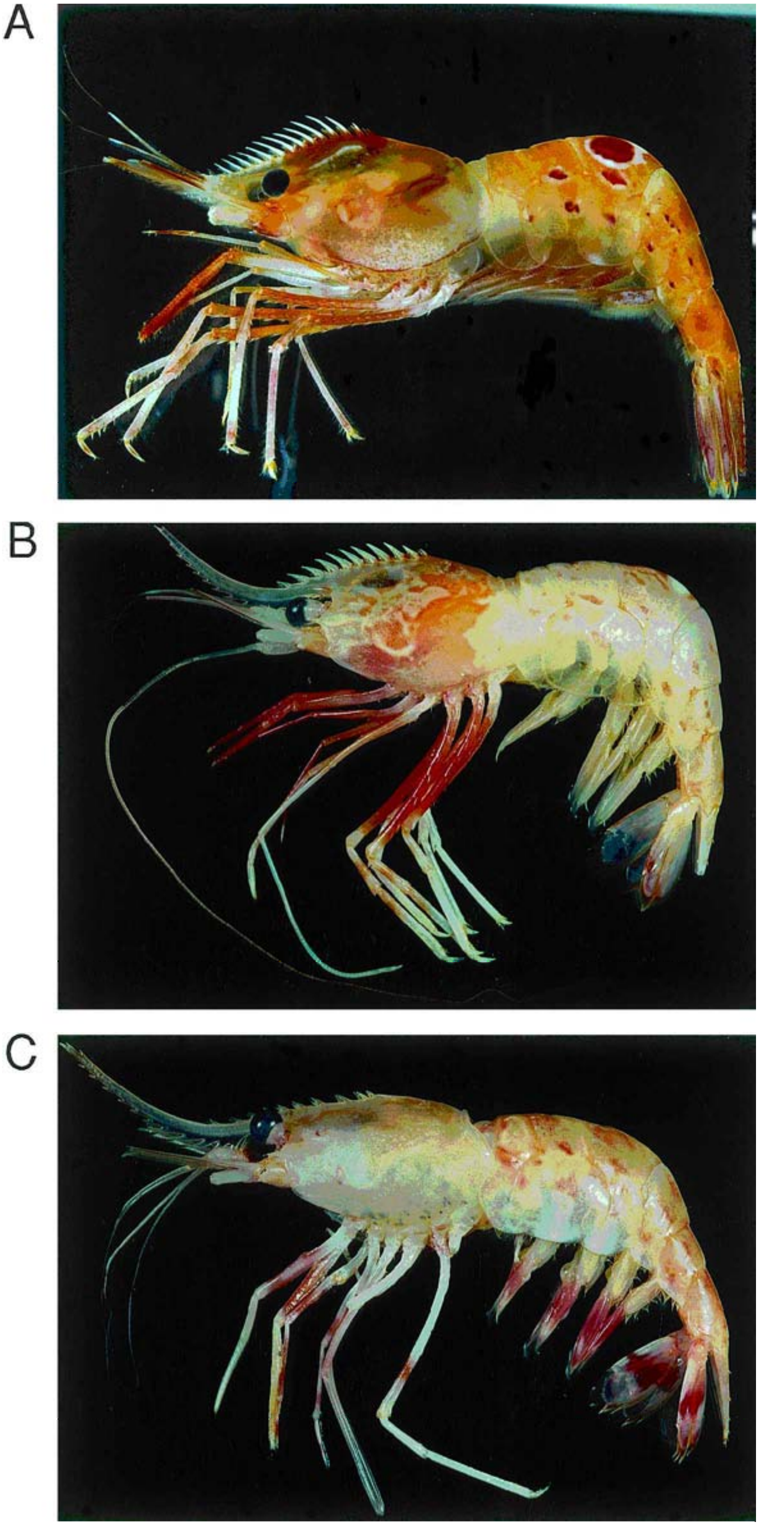


FIG. 43. *Atlantopandalus propinqvus* (G. O. Sars, 1870), comb. nov. Male (CL 13.8 mm), Norwegian Sea, CBM-ZC 3420. (A) Left third maxilliped, lateral; (B) left first pereopod, lateral; (C) left second pereopod, lateral; (D) right second pereopod, lateral; (E) right third pereopod, lateral; (F) same, dactyl, lateral; (G) same, distal part of propodus, flexor; (H) same, carpus, lateral; (I) same, carpus and proximal part of propodus, mesial; (J) left fourth pereopod, lateral; (K) left fifth pereopod, lateral.


A
B
C

Remarks. G. O. Sars (1870) described *Pandalus propinqvus* from Lofoten, Norwegian Sea, but he did not designate a type. Through the kind co-operation of A. Willhelmsen of the Zoological Museum, University of Oslo, a specimen from Lofoten in the Sars collection kept in the museum (ZMUO F16448) was made available for examination. According to Mr Willhelmsen, the specimen was not labelled as type, but it was usual that G. O. Sars did not indicate a type. Careful examination has revealed that the Sars specimen agrees well with the original description, particularly in the counts of the spines or teeth on the rostrum and the carpal articles of the second pereopods. It is noteworthy that the number of the carpal articles of the right second pereopod is aberrant in the Sars specimen (six rather than five in the other specimens examined), and it gives good evidence that this specimen represents that described by G. O. Sars. Therefore, this specimen is here designated as the lectotype of *Atlantopandalus propinqvus*.

In his original description, G. O. Sars (1870) consistently spelled the name of this species as '*propinqvus*'. Although the latter authors usually used the spelling '*propinquus*' (see synonymy), the original spelling has to be used.

Kemp (1910) noted that the specimens from deeper water (756–1129 m) off the west coast of Ireland were different from those from shallower water (61–234 m) of the north and east coasts of the same country in the longer rostrum, more slender pereopods and larger eyes. However, the present material from various localities, covering a wide bathymetric range (50–884 m), are generally very similar. The relative length of the rostrum is rather variable even in specimens from the same location. For example, the proportional ratio of 'rostrum length/carapace length' ranges from 1.12 to 1.51 of the material from Kilchattan Bay, England (NHM 1949.1.18: 46–48). The third pereopod seems to become more stout with growth. Size and form of the eye are easily affected by preservation condition, and therefore I could not evaluate the difference of the eye size. Coloration of the present specimens from Baffin Bay agrees well with that of the shallow water specimens of Kemp (1910). At present, only a single species, *A. propinqvus*, is recognized in the genus *Atlantopandalus*.

Biogeography

Horizontal distribution. The present material enables a rough description of the distribution of the species of *Pandalus* (table 2). It is remarkable (1) that the genera closely related to the *Pandalus*+*Pandalopsis* clade, i.e. *Pandalina* Calman, 1899, *Dichelopandalus* Caullery, 1896 and *Atlantopandalus* gen. nov. (cf. Christoffersen, 1989; Komai, 1994a) show nearly exlusively Atlantic distribution (only *Pandalina nana* Burukovsky, 1990, is known from the Eastern Pacific) and (2) that one of presumably most ancient species of *Pandalus*, *P. montagui* occurs also in the North Atlantic. These suggest that the common ancestor of *Pandalus* (including *Pandalopsis*) originated from the North Atlantic Ocean and its descendants later spread into the North Pacific. Despite its origin, the genus *Pandalus* is much more highly diverse in the Pacific than in the Atlantic. Such a distributional pattern seems

FIG. 44. (A) *Pandalus teraoi* Kubo, 1937, off Choshi, central Japan, female (CL 30.4 mm), CBM-ZC 1057; (B) *Pandalus chani* sp. nov., paratype, female, off Su-Aou, NE Taiwan, female, NTOU; (C) *Pandalus formosanus* sp. nov., paratype, ovig. female (CL 22.8 mm), MNHN-Na 13276. (A) Photograph by T. Komai; (B, C) photograph by T.-Y. Chan.

Table 2. Summary of geographical range of *Pandalus*.

	North Sea	Barents Sea	Greenland	Arctic Canada	East coast of North America	Chukchi Sea	Gulf of California	California	British Columbia	Unalaska Island	Western Bering Sea	Sea of Okhotsk	Sea of Japan	Pacific coast of northern Japan	Pacific coast of southern Japan	East China Sea (Japan)	East China Sea (Taiwan)
P. montagui	●	●	●	●	●												
P. borealis	●	●	●	●	●												
P. goniurus						●			●	●	●	●	●				
P. jordani								●	●	●							
P. tridens								●	●	●	●			●			
P. eous						●		●	●	●	●	●	●	●			
P. stenolepis									●	●							
P. curvatus																●	
P. hypsinotus									●	●	●	●	●	●			
P. danae								●	●	●							
P. prensor												●	●	●			
P. gracilis													●	●			
P. gurneyi							●	●									
P. nipponensis															●		
P. teraoi															●		
P. chani																	●
P. formosanus																	●
P. platyceros								●	●	●							
P. latirostris												●	●	●			
No. of species	2	2	2	2	2	2	1	6	8	8	4	5	6	6	2	1	2

to fit the progression rule in the context of phylogenetic biogeography (see Cracraft, 1975; Wiley, 1980). Among the 19 recognized species of *Pandalus*, only two, *P. borealis* and *P. montagui*, are distributed in the North Atlantic with great overlapping, while the remaining 17 species occur exclusively in the North Pacific. Of the 17 species from the Pacific, *P. tridens*, *P. eous*, *P. goniurus* and *P. hypsinotus* show wide northern North Pacific distribution from East Asia to the west coast of North America, though *P. goniurus* is rather scattered in this region. It is also remarkable that the genus is highly diverse in the western Pacific with members having a very restricted geographical range. *Pandalus chani* and *P. formosanus* occur so far only in the northeastern part of Taiwan, southern East China Sea; *P. curvatus* only in western Kyushu, northern East China Sea, *P. gracilis* in the Sea of Japan and the Pacific coast of Tohoku district of Japan, *P. latirostris* and *P. prensor* in northern Japan, southern Kurile Islands, Sakhalin and cool temperate contintental coasts, and *P. nipponensis* and *P. teraoi* only on the Pacific coast of southern Japan southward from Kashima-nada. Further, *P. latirostris* is restricted to sea grass beds in the coastal region. The occurrence of many endemic forms suggests that the Japanese Archipelago, including Taiwan, is a distinct geographical subregion. On the other hand, interestingly, four of five Eastern Pacific members, i.e. *P. danae*, *P. jordani*, *P. platyceros* and *P. stenolepis* have greatly overlapping, rather wide geographical ranges from Unalaska to California (though *P. stenolepis* does not occur in California); only *P. gurneyi* shows a very restricted distribution from southern California to Mexico. It can be said that the members of the *P. montagui* group, which contains presumably early derived members of the genus, tend to have rather wide geographic ranges, while the other groups, showing derived morphological features, have limited or restricted distributions. *Pandalus hypsinotus* is the sole representative of the *P. hypsinotus* group showing a wide distribution in the North Pacific. It is also remarkable that *Pandalopsis*, which is considered to form a subordinated clade within *Pandalus* (Christoffersen, 1989; Komai, 1994a), is also more highly diverse in the western Pacific than in the eastern Pacific (Komai, 1994b), showing a parallel case with *Pandalus*.

Vertical distribution. Most species of *Pandalus* are commonly found on the continental shelf and the upper part of the continental slope from the subtidal to about 500 m. Although *Pandalus montagui*, *P. borealis*, *P. tridens* and *P. eous* occur at bathyal depths greater than 700 m, the main habitats of these species are sublittoral to upper bathyal zones at depths of 100–300 m. Although most species do not occur in the intertidal zone, three species, *P. danae*, *P. prensor* and *P. latirostris*, have been collected in the intertidal zone. In addition, juveniles of *P. hypsinotus* sometimes occur intertidally. The species distributed in warm temperate or subtropical regions, such as *P. nipponensis*, *P. curvatus* sp. nov., *P. chani* sp. nov. and *P. formosanus* sp. nov., tend to inhabit mainly the continental slope at depths of 200–500 m. As mentioned previously, habitats of *Pandalus latirostris* are nearly exclusively limited to sea grass beds in the coastal region, and thus its vertical range is very narrow. Although *Atlantopandalus propinqvus* is generally said to be a bathyal species, its bathmetrical range is very wide, ranging from 20 to 2180 m.

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