

PHYLOGENY AND ECOLOGY OF A KELP-BORING AMPHIPOD,  
*PERAMPHITHOE STYPTORUPETES*, NEW SPECIES  
 (COROPHIOIDEA: AMPITHOIDEA)

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A B S T R A C T

A new species of amphithoid amphipod has been found which bores into and occupies the interior of abraded stipes of kelps on the Pacific coast of North America. Adult bisexual pairs cohabit the stipes with their offspring of several generations. *Peramphithoe stypotrumpetes*, new species, is diagnosed, illustrated, and its boring habits are described. The type for the genus, *Peramphithoe femorata* (Krøyer, 1845), is redescribed and illustrated, and compared with the new species. *Peramphithoe stypotrumpetes* can be distinguished from *P. femorata* and other eastern Pacific species of the genus by its shorter pair of first antennae and narrower pereopod 3 and 4 bases. Relationships are compared cladistically and biogeographically, and presented in a key.

A new species of amphithoid amphipod, *Peramphithoe stypotrumpetes*, has been discovered by one of us (JRC) inhabiting the stipes of laminarian phaeophytes on the exposed coasts of California and southeastern Alaska. This is the first record of kelp-boring for this genus and the second record for the family Ampithoidae. The purpose of this paper is to describe this new species, to compare it with the type for the genus, *Peramphithoe femorata* (Krøyer, 1845), and other eastern Pacific members of the genus, and to set a hypothesis for its phylogeny and biogeography.

MATERIALS AND METHODS

Type specimens were illustrated, using a camera lucida, from the undissected body stained with methylene blue, and from individual appendages mounted in polyvinyl lactophenol and stained with lignin pink. Body lengths were measured by eyepiece micrometer, from the tip of the rostrum to the base of the telson. The diagnoses encompass characters that distinguish *Peramphithoe stypotrumpetes* from other eastern Pacific species of the genus described in Conlan and Bousfield (1982). Cladistic analyses were conducted on all species of *Peramphithoe* occurring in the eastern Pacific (*P. tea* (Barnard, 1965), *P. plea* (Barnard, 1965), *P. lindbergi* (Gurjanova, 1938), *P. mea* (Gurjanova, 1938), *P. humeralis* (Stimpson, 1864), *P. femorata* (Krøyer, 1845), *P. stypotrumpetes*, new species, and *P. lessoniophila* Conlan and Bousfield, 1982). The outgroup species was *Ampithoe lacertosa* Bate, 1858. All external characters that exhibited discontinuities within the species-group were selected for analysis. Quantitative characters were regressed against characters that were isometric with body size. Scores for the quantitative characters were

derived from the residuals by plotting each value and assigning a score to each cluster of residuals. The cluster containing the outgroup residual was assigned a score of zero in all cases. Cladistic analyses were run on the programs Hennig86 and PAUP version 2.4. Since the data set was small, the ie option was invoked for Hennig86 and the ALLTREES option for PAUP, in order to ensure trees of minimal length. Nelson consensus trees were computed for multiple trees generated by each program.

RESULTS

Species Descriptions

*Peramphithoe stypotrumpetes*,  
 new species

Figs. 1-3

*Adult Female*.—Holotype: Length 19.6 mm. Body moderately stout, head dorsally bulbous. Eye moderately large. Antenna 1, peduncle overlapping only first 25% of antenna 2 peduncular article 4; peduncle article 1 without spine at posterodistal corner; article 2 75% of length of article 1. Antenna 2, flagellum moderately setose, proximal articles fused. Mandible, lacinia mobilis with 5 teeth left, 7 teeth right, raker spines 10 left, 10 right; palp article 3 with setae on distal and distoventral margins. Maxilliped, palp article 4, width 52% of article 3 width. Gnathopods 1 and 2 and pereopods 3 and 4, bases densely setose posteriorly and medially. Gnathopod 1, carpus 94% of propodus length; dactyl extending beyond palm of propodus by 40% of its length. Gnathopod 2, propodus maximally 160% of width of propodus of gnathopod 1; palm shallowly concave. Pereiopod 3, basis 152% of width of basis of gnathopod 2, width 52% of length;

Dedicated to Dr. J. L. Barnard of the Smithsonian Institution, who died 16 August 1991.

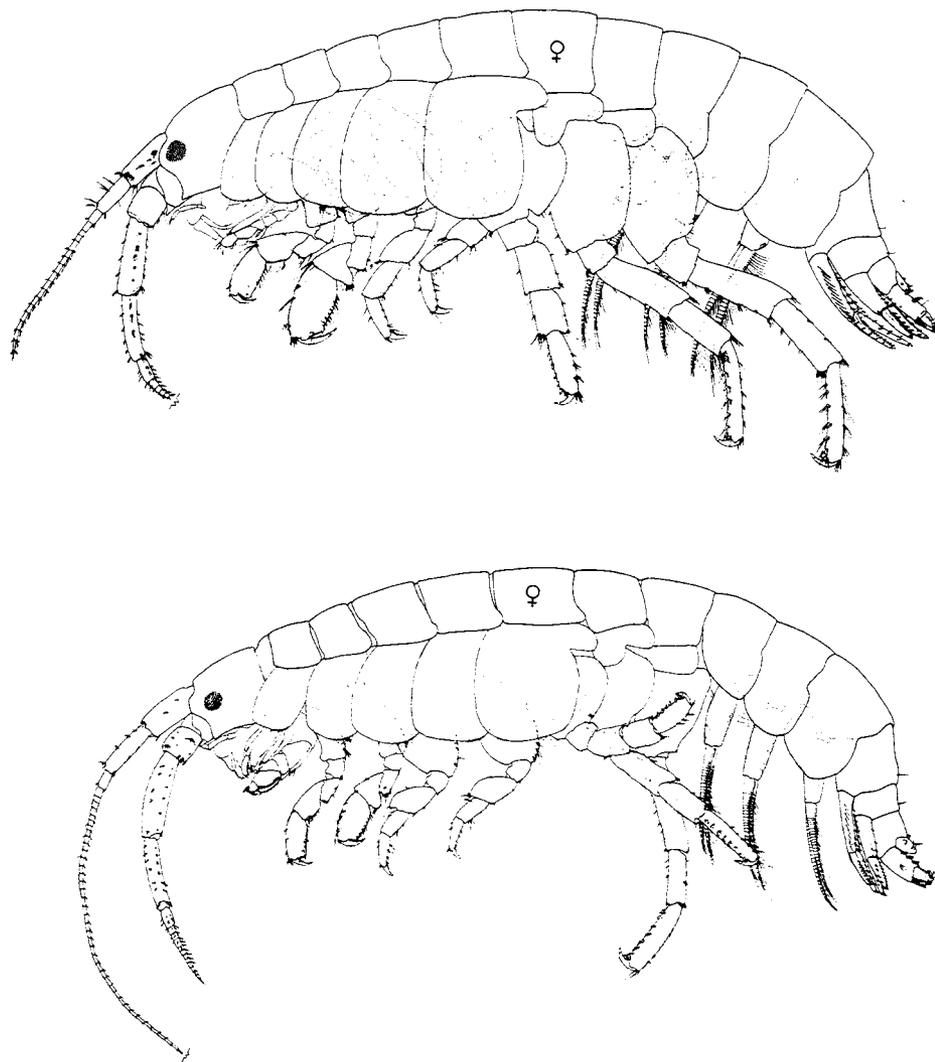


Fig. 1. Above: *Peramphithoe stypotrumpetes*, new species. Holotype, female, 19.6 mm, Whitesboro Cove, Mendocino County, California, 28 February 1985, J. R. Chess, collector. The first antenna is taken from a paratype, female, 16.1 mm, Bird Rock, Santa Catalina Island, Los Angeles County, California, 13 May 1980. Below: *Peramphithoe femorata* (Krøyer). Lectotype, female, 20.8 mm, Valparaiso, Chile.

merus, width 150% of width of carpus. Pereiopod 5, basis, width 118% of length. Pereiopod 7, length 103% of pereiopod 6; bases posteriorly convex; propodus with 8 spine groups. Uropods 1 and 2, rami slender and densely spinose. Uropod 3, peduncle more than twice length of rami.

*Condition.*—Brooding hatchlings. Both antennae 1 and 2 lack flagellar tips. Right ap-

pendages, telson, and mouthparts slide-mounted; other appendages with carcass.

*Adult Male.*—Allotype: Length 13.1 mm. Gnathopod 2, propodus, palm with shallow tubercle proximal to dactyl insertion and indentation proximal to tubercle; dactyl extending through half length of propodus, palmar defining spine absent.

*Condition.*—Missing right pereiopods 3, 5,

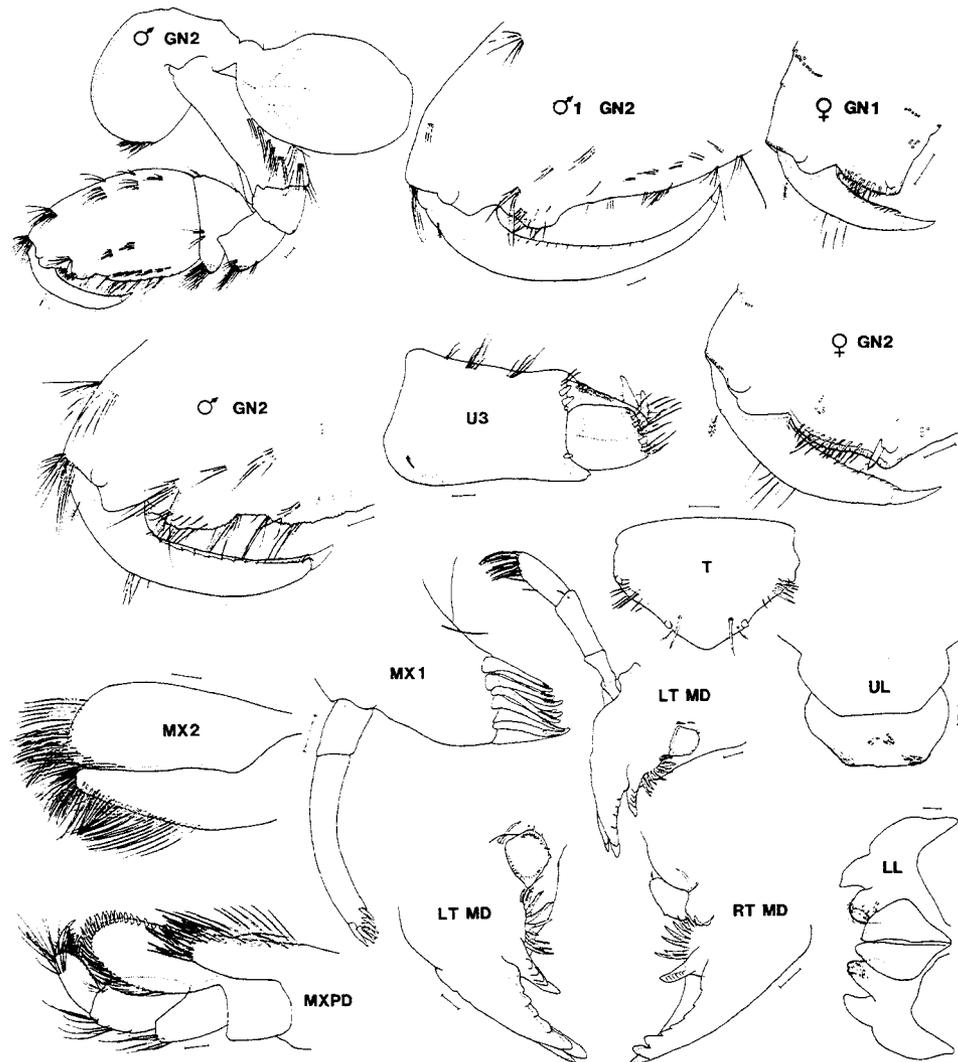


Fig. 2. *Peramphithoe stypotrumpetes*, new species. Holotype, female, 19.6 mm, Whitesboro Cove, Mendocino County, California, 28 February 1985, J. R. Chess, collector. Allotype, male, 13.1 mm, same location. Paratype, male 1, 15.8 mm, Big Branch Bay, Baranof Island, Alaska, 27 July 1980, J. R. Chess, collector. UL, upper lip; MD, mandible; LL, lower lip; MX, maxilla; MXPd, maxilliped; GN, gnathopod; U, uropod; T, telson; RT, right; LT, left. Some gnathopod setae are not shown; their insertions are marked by a circle. Mouthparts are of the female. Scale bars 0.1 mm.

and 7, and left pereopods 5–7. Right gnathopod 2 slide-mounted; other appendages with carcass.

**Variation.**—Body length at maturity: male 12.1–13.1 mm, female 15.9–19.6 mm. The maturation length for the male is an assumption, because growth of the secondary

sexual characters is indeterminate and presence of penial papillae is not a reliable indicator of sexual maturity. Males of the sizes given above were found present with adult females and young. They are accordingly assumed to be the offsprings' parents, and therefore sexually mature. Second gnatho-

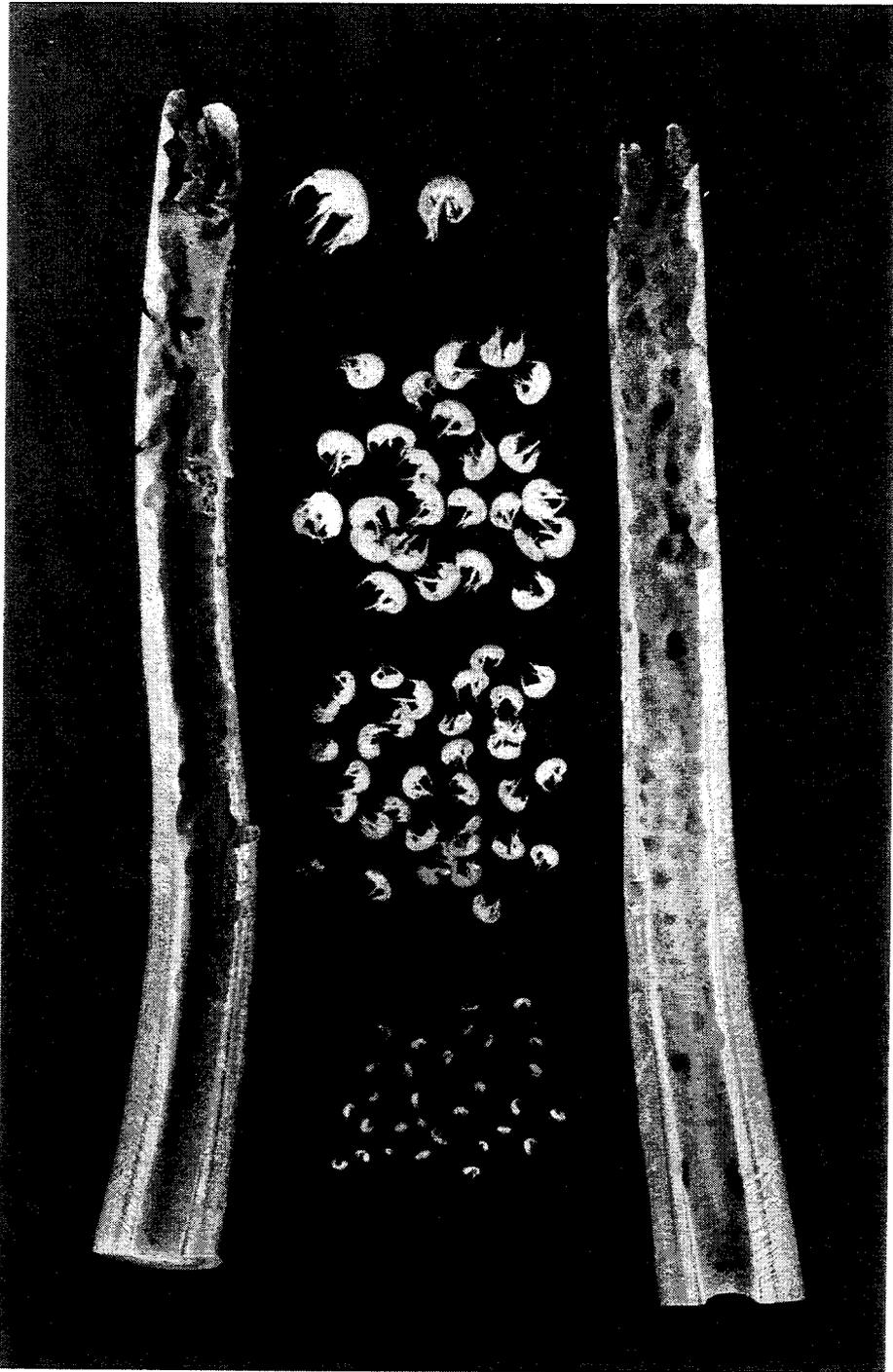


Fig. 3. Interior of a kelp stipe bored by *Peramphithoe stypotruripes*, showing the adult pair at top and three cohorts of offspring.

pod growth is indeterminate in all species of *Peramphithoe*; thus in males larger than those available for study here the dactyl may extend a greater distance along the posterior margin of the propodus.

Setae may be present or absent from the distolateral margin of the maxilla 1 palp.

*Type Material.*—HOLOTYPE, ♀ (Canadian Museum of Nature), catalogue no. NMCC1991-2120, and paratypes, 102 juveniles, catalogue no. NMCC1991-2123, Whitesboro Cove, Mendocino County, California, U.S.A. (39°13'N, 123°46.5'W), 28 February 1985, in 10-cm chamber bored in the stipe of *Laminaria dentigera* Kjellman, 1889, J. R. Chess, collector. ALLOTYPE, ♂ (Canadian Museum of Nature), catalogue no. NMCC1991-2121, and paratypes, 1 subadult ♀ and 1 juvenile, catalogue no. NMCC1991-2122, Point Cabrillo, Mendocino County, California (39°21'N, 123°49.5'W), 27 June 1980, in 3-cm chamber of *Laminaria dentigera*, J. R. Chess, collector. PARATYPES, 1 ♂, 1 adult ♀, and 156 juveniles, catalogue no. NMCC1991-2124, Santa Catalina Island, Los Angeles County, California (33°27'N, 118°29'W), 13 May 1980, in 31-cm chamber bored in the stipe of *Eisenia arborea* Areschoug, 1876, J. R. Chess, collector; paratype, 1 ♂, catalogue no. NMCC1991-2125, Whitesboro Cove, Mendocino County, 20 April 1981, from a stipe of *Laminaria dentigera*; paratypes, 1 ♂ and 1 adult ♀ brooding hatchlings, catalogue no. NMCC1991-2126, Big Branch Bay, Baranof Island, Alaska (56°03'N, 134°20'W), 27 July 1980.

*Remarks.*—All stages and both sexes of *Peramphithoe stypotruripes* can be distinguished quickly from *P. femorata* and other eastern Pacific species of *Peramphithoe* by the shorter first antenna. In *P. stypotruripes* the propodus of the female second gnathopod is larger relative to that of gnathopod 1 than it is in *P. femorata*. The palm of the second gnathopod propodus is shallowly concave in *P. stypotruripes* and transverse in *P. femorata*. In *P. stypotruripes* the bases of the third and fourth pereopods are narrower than those of other eastern Pacific species, and are very setose.

Four males, of 15.8, 13.9, 13.1, and 12.1-mm body length, were available for study, along with numerous small juveniles. Since two of these males were found cohabiting chambers with adult females and young, it is probable that they were sexually mature. However, their small size relative to that of the adult females suggests that they were not fully grown, since in other species of *Peramphithoe* the adult male achieves a larger size than the adult female.

*Etymology.*—The name is formed from the Greek words “*stypos*,” meaning stalk, and

“*trupetes*,” meaning borer, referring to the species' habit of boring in kelp stipes.

*Habits of Peramphithoe stypotruripes.*—Ecological observations were made by one of us (JRC) along exposed parts of the Pacific coast of North America. *Peramphithoe stypotruripes* was found in the stipes of *Eisenia arborea* in southern California (Santa Catalina Island) and in stipes of *Laminaria dentigera* in northern California (Mendocino County) and southeastern Alaska (Baranof Island). Specimens probably referable to this species have been found in the stipes of *Pterygophora californica* Ruprecht, 1852, in southern California (Steve Schoeter, University of California, Santa Barbara, personal communication).

*Peramphithoe stypotruripes* feeds on the inner stipe tissues, as shown by microscopic examination of gut contents. The amphipod consumes tissues of the transition zone, medulla, and cortex of a stipe, which destroys the plant's ability to regenerate fronds and eventually leads to its death.

Infestation of the algae occurs when a single *Peramphithoe stypotruripes*, male or female, bores into the stipe at its distal end (refer to Fig. 3). Every observed entry was into a stipe whose fronds had been abraded away by physical or biotic forces. The following summary is based on examination of 74 stipes in various stages of infestation. After hollowing the stipe to a depth of 2–6 cm, the original invader is joined by another of the opposite sex. These mate and continue to bore deeper into the stipe, hollowing it as they go. By the time the first brood of juveniles is released, the adults have bored out a chamber of 4–8 cm depth. Often by the time the first cohort has grown to 2 mm, a second cohort is being brooded by the female. Successive cohorts remain in the chamber, all grazing on the stipe's interior. Usually by the time the chamber is 5–10 cm deep, the amphipods have bored small pores (1–3 mm diameter) through the stipe wall. As the amphipods continue to multiply, their chamber grows larger and the number of perforations increases. During this time the distal end of the stipe begins to disintegrate, so that as the chamber lengthens the stipe shortens. The amphipods leave the stipe when it has been completely hollowed out or when its inner tis-

sues have begun to decompose. Often in northern California a few *Jassa staudei* Conlan, 1990, occur among *P. stypotrurpetes* in the chambers of the older, disintegrating stipes.

In most of the infested stipes examined, the larger chambers contain more amphipods than do the smaller, but this relation fails to hold with extremes of either variable. Thus, the deepest chamber, 52 cm, contained only three subadults, and the largest number of amphipods, 208, occurred in a chamber only 14 cm deep. This larger group included two adults (a 19-mm male and a 24-mm female) and three distinct sibling cohorts, 103 individuals 2–3 mm long, 49 at 5–7 mm, and 54 at 9–11 mm (refer to Fig. 3).

*Peramphithoe femorata* (Krøyer, 1845)  
Figs. 1, 4

*Ampithoe femorata* Krøyer, 1845, 335, pl. 3, fig. 4.  
*Peramphithoe femorata*: Conlan and Bousfield, 1982,  
68, 69, fig. 16.  
*Ampithoe brevipes* Dana, 1852, 216.

**Adult Female.**—Lectotype (here designated): Body length 20.8 mm. Body stout, head not bulbous. Eye small. Antenna 1, peduncle overlapping 75% of antenna 2 peduncular article 4; peduncular article 1 without spine at posterodistal corner; article 2 98% of length of article 1. Antenna 2, flagellum moderately setose, proximal articles fused. Mandible, lacinia mobilis with 7 teeth left, 13 teeth right, raker spines 12 left, 14 right; palp article 3 with setae on distal margin only. Maxilliped, palp article 4, width 76% of article 3 width. Gnathopods 1 and 2 and pereopods 3 and 4, bases moderately setose posteriorly only. Gnathopod 1, carpus 93% of propodus length; dactyl extending beyond palm of propodus by 40% of its length. Gnathopod 2, propodus maximally 140% of width of propodus of gnathopod 1, palm transverse. Pereiopod 3, basis 220% of width of basis of gnathopod 2, width 60% of length; merus, width 175% of width of carpus. Pereiopod 5, basis, width 114% of length. Pereiopod 7, length 117% of pereiopod 6; bases posterodistally concave; propodus with 9 spine groups. Uropods 1 and 2, rami slender and densely spinose. Uropod 3, peduncle 1.5 times length of rami.

**Condition.**—Not brooding. With all appendages. Antennae 1, flagellar tips absent.

**Adult Male.**—Not type. Canadian Museum of Nature, accession no. 70–218, station no. 27896, Cape Horn Island, Chile, J. Markham, collector, 1970. Length 15.8 mm. Gnathopod 2, propodus, palm with shallow tubercle proximal to dactyl insertion and indentation proximal to tubercle; dactyl extending through 68% of length of propodus, palmar defining spine absent.

**Condition.**—Without antennae 1 and 2 or pereopods 5–7. Right appendages, mouthparts, and telson slide-mounted. Left appendages with carcass.

**Variation.**—Body size at maturity: male 15.8 mm, female 20.8 mm. The maturation size for the male is an assumption, because growth of the secondary sexual characters is indeterminate and the presence of penial papillae is not a reliable indicator of sexual maturity. In the 11.5-mm male, the palm of the propodus of the second gnathopod lacks a tubercle proximal to the dactyl insertion. There is a defining spine at the palmar corner.

**Type Material.**—Lectotype (here designated), adult ♀, 20.8 mm, Universitets Zoologiske Museum København; Valparaiso, Chile (33°05'S, 71°40'W). Paralectotypes, 3 juveniles, same location.

**Other Material** (excluded from type series).—Two ♂♂ and 1 subadult ♀, Cape Horn Island, Chile (56°S, 67°W), 1970, Canadian Museum of Nature accession no. 70–218, station no. 27896; 4 juvenile ♂♂, 1 juvenile ♀, Banco de las Tacas, Isla Navarino, Chile (55°05'S, 67°04'W), 5 February 1970, Canadian Museum of Nature accession no. 70–218, station no. 27924, J. Markham, collector.

**Remarks.**—The 15.8-mm and 11.5-mm males illustrated in Fig. 4 were illustrated in Conlan and Bousfield (1982), but their body lengths were given erroneously as 18.0 mm and 12.5 mm, respectively. Like *Peramphithoe humeralis*, *Peramphithoe femorata* builds tubes among kelp fronds. The living habits of *P. femorata* are described by Kreibohm de Paternoster and Escofet (1976) and Kreibohm de Paternoster (1985).

#### Species Relationships

**Cladistic Analysis.**—Characters used for cladistic analysis are listed in Appendix Table 1. Their raw states are shown in Appendix Table 2, and the gap-coded states are given in Appendix Table 3. For nine

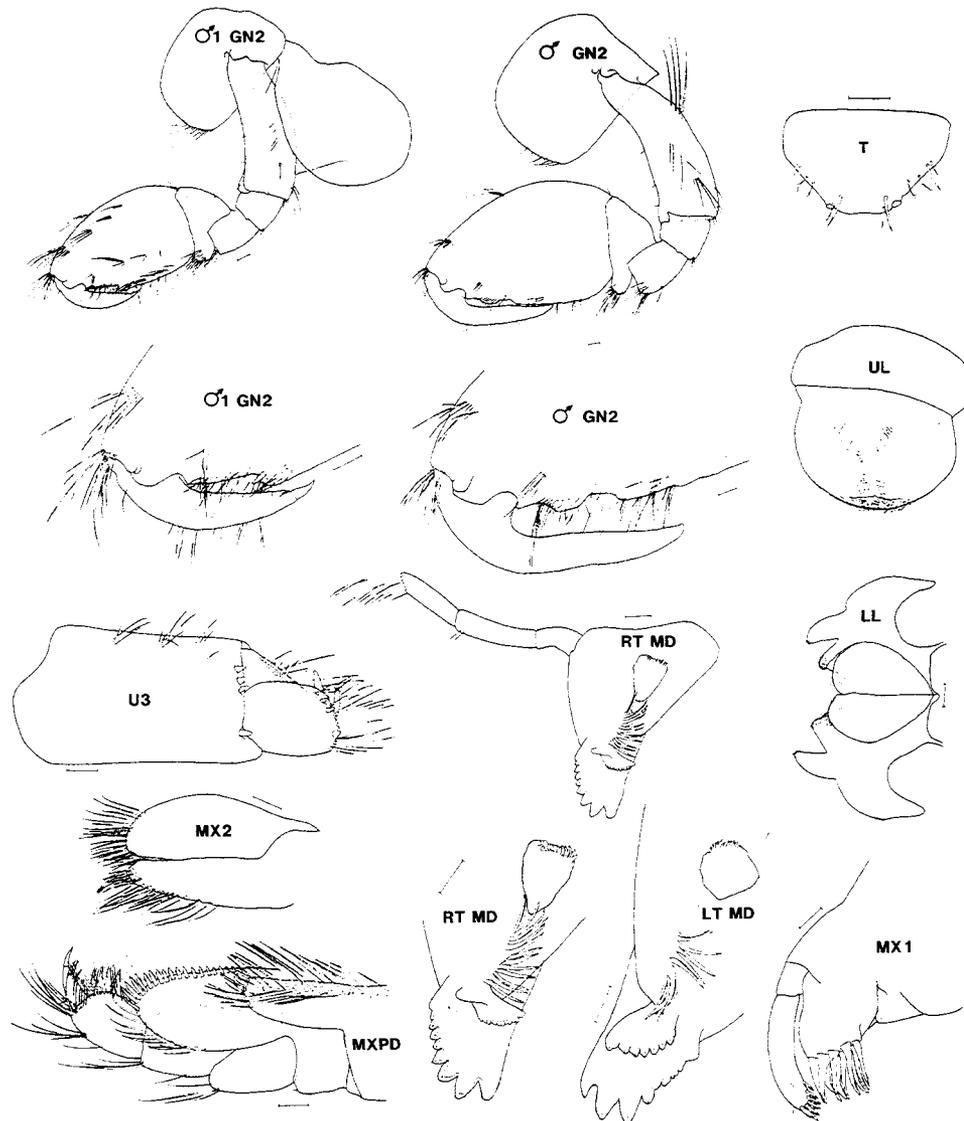


Fig. 4. *Peramphithoe femorata* (Krøyer). Lectotype, female, 20.8 mm, Valparaiso, Chile, 15.8 mm, Cape Horn Island, Chile, 1970, J. Markham, collector. Male 1, 11.5 mm, same location. UL, upper lip; MD, mandible; LL, lower lip; MX, maxilla; MXP, maxilliped; GN, gnathopod; U, uropod; T, telson; RT, right; LT, left. Some gnathopod setae are not shown; their insertions are marked by a circle. Mouthparts are of the male, 15.8 mm. Scale bars 0.1 mm.

additional characters a residuals plot showed no score clusters, or isolation of a single score. Accordingly, these characters were deleted from further analysis, and are not shown in the Appendix tables. Most char-

acters that exhibited discontinuities in variation were from the anterior of the animal. Few such characters could be found from the posterior of the body. This indicates that, for a predominantly tube-dwelling genus

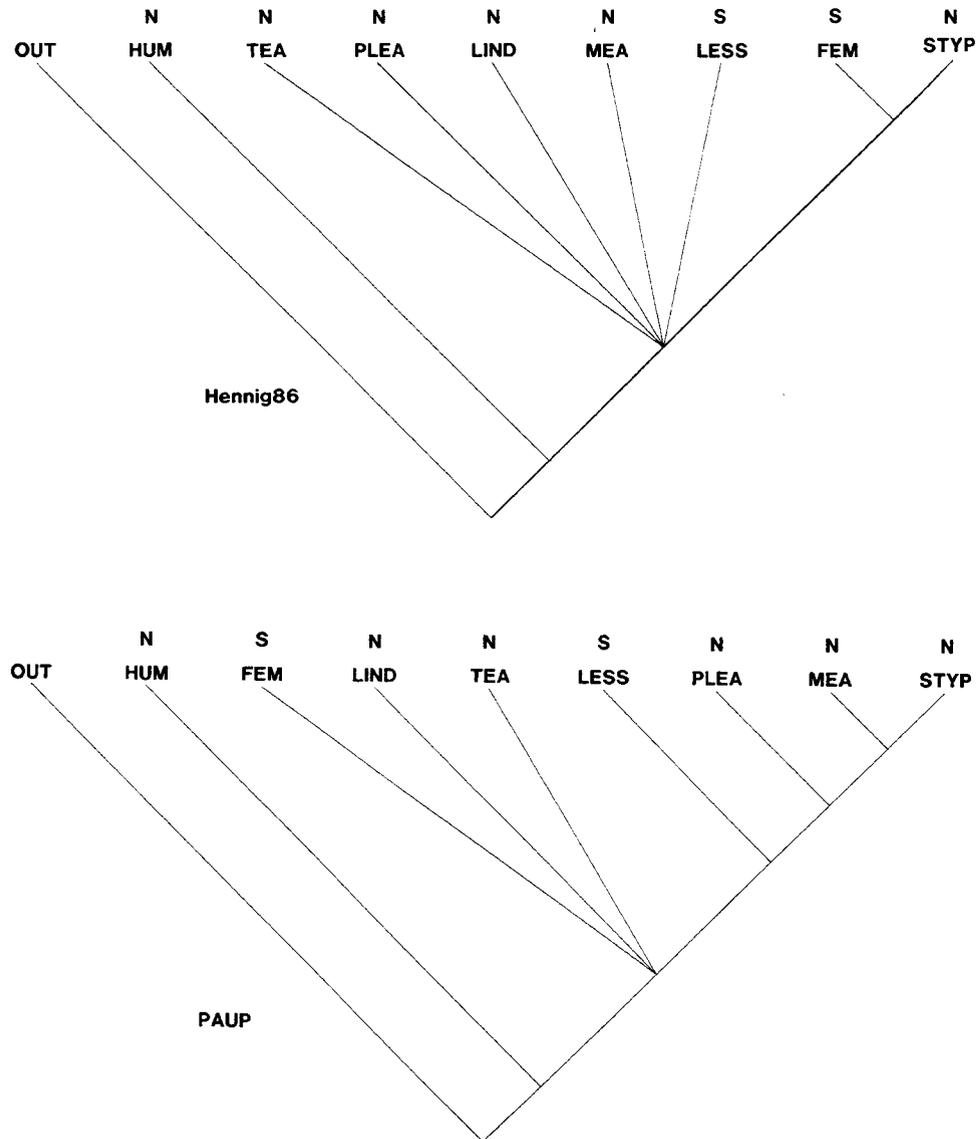


Fig. 5. Above: Nelson consensus tree produced by the cladistics program Hennig86. Below: Nelson consensus tree produced by the cladistics program PAUP. In each case the distribution is indicated as N, North America; S, South America. Abbreviations: OUT, outgroup (*Ampithoe lacertosa*); HUM, *P. humeralis*; TEA, *P. tea*; PLEA, *P. plea*; LIND, *P. lindbergi*; MEA, *P. mea*; LESS, *P. lessoniophila*; FEM, *P. femorata*; and STYP, *P. stypotrurpetes*.

such as *Peramphithoe*, the greatest evolutionary forces have been on the body appendages that extend from the tube.

Wagner analysis using Hennig86 produced 28 trees of length 46. The Nelson consensus tree for the eight species of *Per-*

*amphithoe* (outgroup species deleted) is shown in Fig. 5a. The character consistency index for the consensus tree is 60 and the retention index 33. The consensus tree shows an unresolved polychotomy for the north-eastern Pacific *Peramphithoe tea*, *P. plea*, *P.*

*lindbergi*, and *P. mea*, and the southeastern Pacific *P. lessoniophila*. *Peramphithoe stypotruripes* is grouped with *P. femorata*.

Wagner analysis using PAUP produced three trees of length 23.25. The Nelson consensus tree is shown in Fig. 5b. Rohlf's consistency index for the consensus tree is 0.679. The consensus tree is not fully resolved, with *P. femorata*, *P. lindbergi*, and *P. tea* forming a trichotomy. In this case, the sister species to *P. stypotruripes* is *P. mea*.

It is apparent from both cladistic analyses that the eastern Pacific species of *Peramphithoe* closely resemble each other, and that the fifteen characters found to differentiate the species are not very congruent. The only consistencies in the two consensus trees are the positions of *P. humeralis* and *P. stypotruripes*.

**Biogeography.**—All species of *Peramphithoe* are restricted to cold temperate waters. An allopatric speciation event can be hypothesized for both phyletic scenarios for *Peramphithoe stypotruripes*. In the Hennig86 scenario the proposed sister species is *P. femorata*, a species that is endemic to southern Chile, and thus is well separated from *P. stypotruripes* by tropical waters. In the PAUP scenario, the proposed sister species is *P. mea*, the most northwesterly ranging species of the genus, occurring in the Aleutian Islands and the Sea of Japan. Undoubtedly *P. stypotruripes* will be found in other parts of the eastern Pacific within its currently documented range of California to southeastern Alaska. American endemic species with such ranges do not generally occur as far north as the Aleutian Islands, however (Bousfield, 1979, 1982; Conlan and Bousfield, 1982; Conlan, 1983). Thus, *P. stypotruripes* is probably well separated in its range from *P. mea*, and could have evolved allopatrically from a common ancestor.

#### KEY TO EASTERN PACIFIC SPECIES OF *PERAMPHITHOE*

(After Conlan and Bousfield (1982), in which all eastern Pacific species but *Peramphithoe stypotruripes* are illustrated.)

1. Antenna 2, flagellum, proximal articles not fused (first article twice or less length of following 2 articles, without any more setal clusters than on following articles). Adult male gnathopod 2, propodus, width less than twice width of propodus of gnathopod 1 ..... 2
  - Antenna 2, flagellum, proximal articles fused (first article more than twice length of following articles and with more setal clusters than on following articles). Adult male gnathopod 2, propodus, width more than twice width of propodus of gnathopod 1 ..... 3
2. Gnathopod 1, carpus longer than propodus. Gnathopod 2 (both sexes), propodus hardly larger than that of gnathopod 1, palm transverse; carpus longer than deep, and as long as propodus. Pereiopod 7 about 1.5 times length of pereiopod 6. Central Alaska to Baja California. .... *Peramphithoe humeralis* (Stimpson, 1864)
  - Gnathopod 1, carpus as long as propodus. Gnathopod 2 (both sexes), propodus larger than that of gnathopod 1, palm oblique; carpus shorter than deep and shorter than propodus. Pereiopod 7 less than 1.2 times length of pereiopod 6. Aleutian Islands, Alaska, and Japan Sea ..... *Peramphithoe mea* (Gurjanova, 1938)
3. Antenna 1 about as long as antenna 2. Pereiopods 3 and 4, bases, width 1.5 times width of basis of gnathopod 2. Boring into and inhabiting kelp stipes ..... *Peramphithoe stypotruripes*, new species
  - Antenna 1 about 25% longer than antenna 2. Pereiopods 3 and 4, bases, width more than 1.5 times width of basis of gnathopod 2. Tubicolous, in algal fronds ..... 4
4. Body length at adulthood 12–35 mm. Southern hemisphere ..... *Peramphithoe femorata* (Krøyer, 1845)
  - Body length at adulthood 6–13 mm. Mainly northern hemisphere ..... 5
5. Male gnathopod 2, propodus 2 times width of propodus of gnathopod 1, palm shallowly concave, dactyl less than half length of posterior margin. Southern hemisphere ..... *Peramphithoe lessoniophila* Conlan and Bousfield, 1982
  - Male gnathopod 2, propodus 3 times width of propodus of gnathopod 1, palm concave or transverse, dactyl half or more length of posterior margin. Northern hemisphere ..... 6
6. Antenna 1, peduncle article 3 without posterodistal spine. Antenna 2 slender and nearly as long as antenna 1. Gnathopod 1, propodus, dactyl overlapping palm by hardly more than length of unguis. Male gnathopod 2, propodus rectangular, palm with tubercle at dactyl hinge, dactyl sinuous ..... *Peramphithoe plea* (Barnard, 1965)
  - Antenna 1, peduncle with posterodistal spine in adults. Antenna 2 heavy, less than three-quarters length of antenna 1. Gnathopod 1, propodus, dactyl overlapping palm by more than length of unguis. Male gnathopod 2, propodus wider proximally than distally, palm with or without tubercle at dactyl hinge, dactyl evenly curved ..... 7
7. Antenna 2 about three-quarters length of antenna 1; flagellum about 1.5 times length of peduncular article 5, proximal articles of flagellum fused in pairs. Male gnathopod 2, prop-

odus, palm with tubercle at dactyl hinge, dactyl reaching length of palm in larger individuals  
 ..... *Peramphithoe tea* (Barnard, 1965)  
 Antenna 2 about half length of antenna 1; flagellum about as long as peduncular article 5, proximal 5 and 6 articles of flagellum fused. Male gnathopod 2, propodus, palm without tubercle at dactyl hinge, dactyl half or less length of palm  
 ..... *Peramphithoe lindbergi* (Gurjanova, 1938)

#### DISCUSSION

Although all species of the genus *Peramphithoe* are herbivorous, *P. stypotruripes* is the only species known to bore into kelp stipes. Other species of the genus colonize algae, living within tubes, channels gouged along tissue edges, or rolls of algal blades cemented together with self-produced "amphipod silk" (Griffiths, 1979; Gunnill, 1984). They eat the surrounding algae (as in *P. humeralis* (see Jones, 1971; Griffiths, 1979)), or consume drift and/or epiphytic algae (as in *P. tea* (see Gunnill, 1982)).

The living habits of *Peramphithoe stypotruripes* differ from other members of the genus and are reflected in a somewhat altered morphology. The head is rather bulbous, the antennae are short and about equal in length, the body is stout, and pereopod 3 and 4 bases, which house the silk-secreting glands, are not as expanded as in other (at least eastern Pacific) members of the genus. Species of *Peramphithoe* do not achieve as great a diversity of sexual dimorphism in the second gnathopods as do species of *Ampithoe*. This suggests that sexual habits differ between the genera, perhaps trending toward monogamy in some species of *Peramphithoe*. This appears to be the case, at least, for *P. stypotruripes*.

Generally, species of *Peramphithoe* have larger pereopod bases which house the web-spinning glands than do species of *Ampithoe*. Species of *Ampithoe* build their tubes among eelgrass, kelp holdfasts, coralline algae, and such green, brown, and red algae as *Ulva*, *Enteromorpha*, *Monostroma*, *Spongomorpha*, *Codium*, *Chordaria*, *Ralfsia*, *Dictyota*, *Sargassum*, *Fucus*, *Pelvetia*, *Leathesia*, *Halidrys*, *Cystoseira*, *Padina*, *Desmarestia*, *Polysiphonia*, *Chondrus*, *Gracillaria*, *Gracillariopsis*, *Neoagardhiella*, *Polyneura*, *Callophyllis*, *Prionitis*, *Antihamnion*, *Amphiroa*, *Rhodomenia*, *Rhodomela*, *Ceramium*, *Iridaea*, *Schizymeria*,

*Cladophora*, *Halosaccion*, *Jania*, *Laurencia*, *Peyssonellia*, *Cryptonemia*, *Calonitophyllum*, *Chondria*, and *Hypnea* (Holmes, 1901; Skutch, 1926; Shoemaker, 1938; Heller, 1968; Barnard, 1969, 1970; Nicotri, 1977; Bellan-Santini *et al.*, 1982; Conlan and Bousfield, 1982; Moore, 1984; Myers, 1985; Hay *et al.*, 1987; Duffy and Hay, 1991). Species of *Peramphithoe* occur on the branching brown alga *Pelvetia* and the blades and holdfasts of such large kelps as *Laminaria*, *Macrocystis*, *Agarum*, *Egregia*, *Lessonia*, and *Ecklonia* (Barnard, 1969; Jones, 1971; Griffiths, 1979; Conlan and Bousfield, 1982; Gunnill, 1982, 1983, 1984; Kreibohm de Paternoster, 1985), or in the stipes of *Eisenia*, *Laminaria*, and *Pterogophora* (*Peramphithoe stypotruripes*, this study). This affinity for larger and tougher algae suggests that species of *Peramphithoe* are more powerful algal manipulators than are species of *Ampithoe*.

*Peramphithoe stypotruripes* is not unique within the family Ampithoidae in its burrowing habits. In Britain, *Amphitholina cuniculus* (Stebbing, 1874) burrows into the medullary region of stipes of the kelp *Alaria esculenta* (Linnaeus) Greville, 1830 (Myers, 1974). Like *P. stypotruripes*, *A. cuniculus* burrows extensively and perforates the stipe in numerous places. *Amphitholina cuniculus* has never been found with more than six conspecifics in a stipe chamber, however. *Amphitholina cuniculus* is much more modified for burrowing than is *P. stypotruripes*. Its mouthparts are prognathous and styliform. The head is beaked in appearance, and dorsally grooved, presumably to accommodate the antennae during burrowing. There are several taxa of amphipods outside the family Ampithoidae that burrow. Members of the corophioidean family Cheluridae burrow into timber and can be destructive to pilings and moorings (Holmes, 1905). Members of the corophioidean family Biancolinidae burrow into kelp stipes in tropical and semitropical waters. As with *Amphitholina*, their heads are globose and their mouthparts prognathous (Myers, 1985). Members of the talitrid families Najnidae, Phliantidae, and Eophliantidae burrow into kelp stipes in a fashion similar to *P. stypotruripes*.

In tube-building corophioidean amphipods, with which *Peramphithoe stypotru-*

*petes* is classified, the adult male usually leaves his mate's tube following mating, and the activities of the mother and her new partner cause the young to leave as well (Borowsky, 1983; Shillaker and Moore, 1987). In *P. stypotruripes*, the regular collection of a mating pair with offspring suggests a prolonged period of residency for all concerned, at least until the chamber erodes sufficiently for it to be abandoned. The difference in living habit may be related to the substance of the housing structure. In most other tubicolous amphipods the housing material consists of detritus, wood debris, shells, algal cuttings, or fronds wrapped around the body and glued in place with "amphipod silk." For *P. stypotruripes* the housing is also the food source, and consumption of the stipe interior generates added space for new offspring. There is, therefore, not as immediate a housing-size limitation as might be experienced by tube-dwellers whose housing does not enlarge on demand.

Brood care and prolonged cohabitation are not common among amphipods, but do occur in a few other species. Bate and Westwood (1863) found cohorts of two sizes of *Podocerus variegatus* Leach, 1814, cohabiting a tube. Mothers and their offspring of the podocerids *Dulichia rhabdoplastis* McCloskey, 1970, *Dyopedos porrectus* Bate, 1857, and *Dyopedos monacanthus* (Metzger, 1875) live on self-built rodlike structures attached to the ends of sea urchin spines, hydroids, bryozoans, or shells (McCloskey, 1970; Moore and Earll, 1985; Mattson and Cedhagen, 1989). Females of *Caprella monoceros* Mayer, 1890, carry their young with them after release from the brood pouch, grooming them and defending them from other caprellids (Aoki and Kikuchi, 1991). Young *Leptocheirus pilosus* Zaddach, 1844, remain in the mother's tube until at least the second molt (Goodhart, 1939). *Phronima sedentaria* Forskål, 1775, rears young in hollowed out salp or pyrosome barrels (Hardy, 1956; Laval, 1980). *Peramphithoe humeralis*, which rolls kelp fronds and occupies the chambers so formed, lives in a manner similar to *P. stypotruripes*. Young cohabit the chamber and feed on the inner wall of the distal end, progressively extending the chamber backward as the walls are eaten (Griffiths, 1979), or leave en masse on foraging forays elsewhere (Jones, 1971).

*Peramphithoe tea*, found in the fucoid alga *Pelvetia fastigiata* (J. Agardh, 1841) DeToni, 1895, also appears to reproduce as a colony (Gunnill, 1982).

The phyletic relationship of *Peramphithoe stypotruripes* to eastern Pacific members of the genus is not well resolved. The phyletic scenarios developed by the cladistics programs employed here set closest relationships to species that are well separated from *P. stypotruripes* geographically. Species of *Peramphithoe* are not as highly sexually dimorphic as are species of *Ampithoe*, and somatic characters are not highly variable. The greatest differences between the species of *Peramphithoe* may be in their feeding habits and substrate preferences, both of which require further investigation.

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