Amphipoda of the Northeast Pacific (Equator to Aleutians, intertidal to abyss): XXVIII. Ampeliscoidea – an updated review.
Donald B. Cadien, LACSD 22Jul2004 (revised 2Mar2015)

Preface

The purpose of this review is to bring together information on all of the species reported to occur in the NEP fauna. It is not a straight path to the identification of your unknown animal. It is a resource guide to assist you in making the required identification in full knowledge of what the possibilities are. Never forget that there are other, as yet unreported species from the coverage area; some described, some new to science. The natural world is wonderfully diverse, and we have just scratched its surface.

Introduction to the Ampeliscoidea

The superfamily Ampeliscoidea consists solely of the family Ampeliscidae. It is well represented in the NEP, with about 50 species distributed among three genera. There has been at least one species introduced into California waters from the North Atlantic (Chapman 1988), *Ampelisca abdita*, which forms dense aggregations within San Francisco Bay. It is also distributed outside the bay, but penetration of non-embayment waters has not been extensive. The superfamily was established by Bousfield (1979) when he broadened the scope of his phyletic reevaluations beyond the limits of the Gammaridae s. l. addressed previously (Bousfield 1977). In addition to his diagnosis he characterized the Ampeliscoidea as "world-wide, marine coastal and abyssal: building sac-like tubes in soft stable sediments." He considered the group to be relatively recent in appearance; not earlier than the Tertiary (Bousfield 1982).



Ampelisca abdita from San Francisco Bay (www.calacademy.org/research/izg/sfbay2k)

Diagnosis of the Ampeliscoidea

"Apomorphic, arostrate, tube-building, fossorial gammarideans, having strongly dimorphic terminal male stage; peduncles of antenna 1 and 2 and basal flagellar segments of 1 bear brush setae but lack calceoli; antenna 2 peduncle elongate, antenna 1 usually short, lacking accessory flagellum; eyes consisting of two (or one) pairs of facets with corneal lenses; mouthparts somewhat modified; upper lip with distinct median notch, lower lip broad, inner lobes well developed; mandibular molar and palp strong; maxilla 1 inner plate bare, outer with 11 apical spine teeth; maxilla 2, inner plate moderately setose; maxilliped plates normal, palp slightly reduced. Coxal plates deep, regular, 4th strongly excavate; coxae 5-7 anteriorly lobate; gnathopods 1 and 2 nonamplexing, rather dissimilar, weakly subchelate or simple; peraeopods 3 and 4 glandular, dactyls simple, with ducts; peraeopods 5-7 strongly heteropodous, bases variously expanded; brood plates linear; coxal gills pleated, lacking on peraeopod 7; pleopods normal; urosome segment 1 carinate, 2 and 3 coalesced; uropods lanceolate, rami subequal; uropod 3 foliaceous, outer ramus 1-segmented; telson lobes deeply and narrowly separated, apices with minute notch and spine." (from Bousfield 1979).

Ecological Commentary

Ampeliscoids are primarily, although not exclusively, tube-dwellers. They build soft elastic amphipod-silk tubes with the glandular secretions from their third and fourth pereopods. The silk is combined with carefully selected materials from the surrounding sediments to construct a composite tube of silk and sediment. A few species, including the local *Ampelisca lobata*, seem associated with fouling growth or other "hard" substrate rather than the soft bottoms occupied by the vast majority of the superfamily members. These species do not appear to create and occupy tubes, being instead denizens of crevices and interstices in complex fouling growth. Dauvin has produced a series of papers describing the population biology of several North Atlantic *Ampelisca* species (Dauvin 1988a, b, c, 1989). None of these forms occur in the NEP, but similar forms which are assumed to have similar life histories are present in our fauna.

Enequist (1950), as he did with so many amphipods, made detailed aquarium observations of several different ampeliscoids. In the species observed tube construction began at the surface, and progressed downwards into the sediments for several centimeters, until the animal had a subsurface safe haven. The animal then returned to the surface and began constructing upwards, eventually terminating the tube when the surface of the sediments could no longer be reached by the extended antennae.

Feeding position in both the genera *Ampelisca* and *Haploops* was observed as lying at the mouth of the tube ventral side up, with the pereopods grasping the tube edge. In many taxa the dactyls of the posterior pereopods are slightly recurved at the end to facilitate control of the tube lip. Here the animal captured suspended particulates from the water column, and also scraped the surface of the mud to gather detrital aggregates with the antennae. Both scraped and filtered material accumulated on the antennae, and was combed from them by the gnathopods, then ingested. Gut analysis confirmed the diet of *Ampelisca richardsoni* as primarily phytoplankton, with undefinable organic matter second, and small admixtures of zooplankton fragments and sponge spicules (Graeve et al 2001). This assessment was further supported by stable isotope analysis which demonstrated that A. richardsoni differed significantly in diet from other benthic

species considered (Nyssen et al. 2002). Analysis of gut contents of *Ampelisca byblisoides* (J. L. Barnard 1962) showed mixtures of sediment particles and foraminifers, along with the undefined organic material found by Graeve et al (2001). He interpreted this as representing a mixture of bottom deposits and organics captured from the water column and termed it "semi-suspension feeding".

All the species observed by Enequist could be classified as detritivores, and all were also suspension-feeders/surface deposit feeders. The balance of these two types of source utilization varied with the availability of particulates in the water, and the length of time of residence in the tube. Surface deposit feeding was more common during the early period of tube occupation, but surface within the range of antennal scraping was eventually fully processed, and the animal relied to much larger extent on suspended particulates for its food. Antennal movement was often vigorous, especially when current movement of water was low or absent. The antennae were swung about in multiple planes above and below the body and to both sides, generating water movement which brought suspended particulates to and through them. When adequate current movement was present, the animal always adopted a position with the head away from the current, and the antennae extended forward into it. If the current reversed, the animal dove down into the tube and somersaulted, to reverse position and remain with the head away from the current direction. (Enequist 1950). Some species, typified by Ampelisca gibba in the North Atlantic, did not build tubes, but excavated into the sediment to form a shallow gallery from which it fed on surface deposits. They frequently abandoned these constructions to look for new feeding areas. Even though no true tube was constructed, the amphipod silk from the pereopodal glands was used to stabilize the walls of their constructed galleries.

Since ampeliscoids are not dependent either on hunting, or, under normal conditions, local nutrient supply, they can exist in dense aggregations in areas of reliable current flow. In the shallow sublittoral and intertidal of embayments, the presence of dense tube arrays is a major influence on particle resuspension, stabilizing bedforms and leading to extensive accumulation of particles (Lynch and Harrison 1970). Similar density can be maintained offshore (Soliman and Wicksten 2007) in areas of consistent current flow and particle supply.

In the Bering Sea, ampeliscid accumulations are dense enough, and cover a large enough portion of the bottom that they are routinely fed upon by grey whales (Oliver et al 1984, Coyle et al 2007). Dense aggregations seem to attract predators, and ampeliscids are also known to be important in the diets of fish (Franz and Tanacredi 1990), and smaller predators such as nemerteans (McDermott 1993). Non-lethal predation results in damage to significant proportions of some populations of *Ampelisca tenuicornis*, usually loss of entire or partial antennae (Sheader 1988). Parasites as well as predators are favored when dense aggregations make host location effortless, and at least one species of turbellarian is known from *Ampelisca* (Christensen and Kanneworff 1964).

Even in these dense communities, however, more than one species of ampeliscid is usually present. In *Haploops* communities in the North Atlantic, populations of *Haploops tubicola* and *H. tenuis* are nearly always mixed (Kanneworff 1966). In SCB benthic samples it is common for a $1/10^{th}$ m² sample to contain between two and seven species of *Ampelisca* and *Byblis*. How these species subdivide the resources available is unknown.

Despite their benthic habitus, ampeliscoids are typically good swimmers. Saint-Marie and Brunel (1985), found that the family Ampeliscidae ranked second in frequency of animals captured swimming in the water column in their temperate Northwest Atlantic study area. Some of this activity is undoubtedly due to the need to find new feeding locations, while much of the swimming is probably associated with mate location (Mills 1967, Borowsky and Aiken-Ander 1991). The sexual molt of *Ampelisca* spp. includes expression of secondary sexual characters associated with swimming in the male (J. L. Barnard 1954). Modifications of the antennae, increased setosity of the body, and particularly development and elaboration of setation on the uropods are the major character states involved. There may also be some changes in the eyes, but this is less common than the other characters mentioned.

Conlan (1991) in her review of reproductive behavior in amphipods, characterized the ampeliscoids as non-mate guarding and with male pelagic searching behavior. This corresponds to the morphological modifications mentioned above, which are designed to reduce energy expenditure in the sexually mature male during his pelagic mate-searching period. Sainte-Marie (1991) summarized the literature on reproduction for ampeliscoids, and reported that roughly half of the species investigated produced only 1 brood per year. The other half produced two or perhaps more, although no firm reports of more than two broods per year were available. No data was presented for *Byblis*, and all reported *Haploops* had but a single brood per year.

NEP Ampeliscoidea from McLaughlin et al (2005) augmented by known provisionals. *= Taxa on SCAMIT Ed. 9 list (Cadien & Lovell 2014). Valid taxa **bolded**, synonyms not.

Family Ampeliscidae

Ampelisca abdita Mills 1964 – Temperate Western Atlantic; Introduced to San Francisco and Tomales Bays; 1-15m

Ampelisca agassizi (Judd 1896) – Western North Atlantic; NEP from Queen Charlotte Islands, British Columbia to Ecuador; 5-450m

Ampelisca amblyopsoides J. L. Barnard 1960 – Southern California Basins; 1123-1481m

Ampelisca articulata Stout 1913 (see Ampelisca lobata)

Ampelisca brachycladus Roney 1990 – Southern California Bight; 10-61m Ampelisca brevisimulata J. L. Barnard 1954 – Caribbean Sea; SE Alaska to Pacific Panama; 4-456m

Ampelisca cf. brevisimulata SCAMIT 1995 – SCB; 25-150m

Ampelisca careyi Dickinson 1982 – SE Alaska to Baja California; 0-200m

Ampelisca catalinensis J. L. Barnard 1954 (see Ampelisca eoa)

Ampelisca coeca Holmes 1908 - SCB;553-1168m

Ampelisca compressa Holmes 1905 (see Ampelisca agassizi)

Ampelisca cristata cristata Holmes 1908 – SE Alaska to Puerto Utria, Columbia: 0-152m

Ampelisca cristata microdentata J. L. Barnard 1954 – SE Alaska to Costa Rica 0-154m [not differentiable in literature records from nominate subspecies] **Ampelisca cristoides** J. L. Barnard 1954 – Caribbean Sea; NEP from Baja

- California to Colombia; 3-80m
- **Ampelisca cucullata** J. L. Barnard 1954 Tenacatita Bay, Nayarit, Mexico; 4-16m
- **Ampelisca eoa** Gurjanova 1951 Bering Sea to Baja California; 230-3718m
- **Ampelisca eschrichti** Krøyer 1842 North Atlantic; NEP south to Morro Bay; 0-1375m
- **Ampelisca fageri** Dickinson 1982 Vancouver Island, British Columbia to the Gulf of California; 0-40m
- **Ampelisca furcigera** Bulycheva 1936 Okhotsk and Japan Seas in NWP; NEP south to the San Pedro Basin; 212-1248m
- Ampelisca gnathia J. L. Barnard 1954 (see Ampelisca pugetica)
- **Ampelisca hancocki** J. L. Barnard 1954 British Columbia to Costa Rica; 9-200m
- **Ampelisca hermosa** J. L. Barnard 1961 Gulf of Panama; 500m
- Ampelisca hessleri Dickinson 1982 British Columbia; 150-325m
- **Ampelisca indentata** J. L. Barnard 1954 Pt. Conception to the Gulf of California; 33-98m
- Ampelisca isocornea J. L. Barnard 1954 (see Ampelisca romigi)
- **Ampelisca lobata** Holmes 1908 Caribbean Sea; NEP from Queen Charlotte Ids., British Columbia to Peru; 0-234m
- **Ampelisca macrocephala** Liljeborg 1852 Circumboreal in the North Atlantic and North Pacific, south to the Aleutians; 10-280m
- Ampelisca mexicana J. L. Barnard 1954 SCB to Peru; 9-73m
- **Ampelisca milleri** J. L. Barnard 1954 Tomales Bay, Northern California to Ecuador; 0-187m
- **Ampelisca pacifica** Holmes 1908 Caribbean Sea; NEP from Monterey, California to Panama; 20-1821m
- Ampelisca panamensis J. L. Barnard 1954 Pacific Panama: 10-16m
- **Ampelisca plumosa** Holmes 1908 off Palos Verdes to Baja California; 553-2667
- **Ampelisca pugetica** Stimpson 1864 Caribbean Sea; NEP from SE Alaska to Peru; 0-225m
- **Ampelisca romigi** J. L. Barnard 1954 Caribbean Sea; NEP from Monterey, California to Ecuador; 3-504m
- **Ampelisca schellenbergi** Shoemaker 1933 Tropical West Atlantic; NEP from Cavucos, California to Peru; 1-128m
- **Ampelisca shoemakeri** J. L. Barnard 1954 Bahia San Cristobal, Baja California to Peru; 7-76m
- **Ampelisca unsocalae** J. L. Barnard 1960 Queen Charlotte Islands, British Columbia to Baja California; 50-1720m
- **Ampelisca venetiensis** Shoemaker 1916 Laguna Beach, California to Ecuador; 0-84m
- Ampelisca vera J. L. Barnard 1954 (see Ampelisca agassizi)
- Ampelisca sp A Dickinson 1976 Tanner Basin, Southern California Borderland; 1298-1353m

- Ampelisca sp B Dickinson 1976 Tanner Basin, Southern California borderland; 1317m
- **Byblis barbarensis** J. L. Barnard 1960 Oregon to Santa Catalina Basin Southern California; 496-1225m
- **Byblis bathyalis** J. L. Barnard 1966 Oregon to Tanner Submarine Canyon, Southern California; 400-950m
- **Byblis brevirama** Dickinson 1983 Arctic Alaska to Vancouver, British Columbia; 40-150m
- Byblis breviramus Dickinson 1983 (see Byblis brevirama)
- Byblis crassicornis Metzger 1875 record of J. L. Barnard 1971 (= Byblis n. sp. fide Dickinson 1983)
- Byblis gaimardi (Krøyer 1846) Circumboreal; NEP to Aleutian Ids.; 5-575
- Byblis longispina Dickinson 1983 Gulf of Alaska; 21-24m
- **Byblis millsi** Dickinson 1983 Queen Charlotte Ids., British Columbia to San Diego, California; 0-100m
- **Byblis mulleni** Dickinson 1983 Queen Charlotte Ids., British Columbia to Newport, Oregon; 175-270m
- Byblis pearcyi Dickinson 1983 Bering Sea to Aleutian Ids.; 40-50m
- **Byblis tannerensis** J. L. Barnard 1966 Tanner Submarine Canyon, southern California; 813m
- Byblis teres J. L. Barnard 1967 Baja California; 791-842m
- **Byblis thyabilis** J. L. Barnard 1971 Queen Charlotte Ids., British Columbia to Oregon; 200-800m
- **Byblis veleronis** J. L. Barnard 1954 Queen Charlotte Ids., British Columbia to Islas Revillagigedos, Mexico; 31-422m
- Byblis sp 1 Dickinson 1976 San Diego Trough, Southern California Borderland; 1229-1238m
- Byblis sp 2 Dickinson 1976 Tanner Basin, Southern California Borderland; 1302-1324m
- **Byblis sp**. Dickinson 1983 [recorded as B. crassicornis by J. L. Barnard 1971] Oregon; 600-2798m
- **Haploops lodo** J. L. Barnard 1961 North Atlantic bathyal; Cascadia Abyssal Plain, Oregon to Panama; 1200-3570m
- Haploops spinosa Shoemaker 1931 (see Haploops tubicola)
- **Haploops tubicola** Liljeborg 1855 Circumboreal, NEP to Pt. Conception, southern California; 1-2295m

Family Ampeliscidae

The family, while having many species level taxa, contains but four genera (J. L. Barnard and Karaman 1991). Three of these occur in the NEP, with the fourth, *Byblisoides*, occurring primarily in the Atlantic. Margulis (1967) reported the genus from the western North Pacific, but it remains unknown in the NEP. The three remaining genera are represented in the NEP, although *Haploops* not as well as either *Byblis* or *Ampelisca*. Because so few genera occur in the superfamily, a separate key to genera is not required. One is provided by Dickinson (1983), and at the beginning of the key to *Ampelisca* by Lisa Haney (2005).

Description: "Head free, not coalesced with peraeonite 1; exposed; as long as deep, or longer than deep; anteroventral margin moderately recessed or oblique or rounded, anteroventral margin deeply excavate, anteroventral corner hooked; rostrum present or absent, short; eyes present, well developed or obsolescent, or absent; not coalesced; 1 pair, or 2 or 3 pairs; not bulging. Body laterally compressed; cuticle smooth.

Antenna 1 shorter than antenna 2, or subequal to antenna 2, or longer than antenna 2; peduncle with sparse robust and slender setae; 3-articulate; peduncular article 1 shorter than article 2, or subequal to article 2, or longer than article 2; antenna 1 article 2 longer than article 3; peduncular articles 1-2 not geniculate; accessory flagellum absent; antenna 1 callynophore present, or absent. Antenna 2 present; medium length, or long, or greater than body length; articles not folded in zigzag fashion; without hook-like process; flagellum shorter than peduncle, or as long as peduncle, or longer than peduncle; 5 or more articulate; not clavate; calceoli absent.

Mouthparts well developed. Mandible incisor dentate; lacinia mobilis present on both sides; accessory setal row without distal tuft; molar present, medium, triturative; palp present. Maxilla 1 present; inner plate present, weakly setose apically or without setae; palp present, not clavate, 2 -articulate. Maxilla 2 inner plate present; outer plate present. Maxilliped inner and outer plates well developed or reduced, palps present, well developed or reduced; inner plates well developed, separate; outer plates present, small; palp 4-articulate, article 3 without rugosities. Labium smooth.

Peraeon. Peraeonites 1-7 separate; complete; sternal gills absent; pleurae absent.

Coxae 1-7 well developed, none fused with peraeonites. Coxae 1-4 longer than broad, overlapping, coxae not acuminate. Coxae 1-3 not successively smaller, none vestigial. Coxae 2-4 none immensely broadened.

Gnathopod 1 not sexually dimorphic; subequal to gnathopod 2; subequal to coxa 2; gnathopod 1 merus and carpus not rotated; gnathopod 1 carpus/propodus not cantilevered; longer than propodus; gnathopod 1 not produced along posterior margin of propodus; dactylus large. Gnathopod 2 not sexually dimorphic; simple; coxa subequal to but not hidden by coxa 3; ischium short; merus not fused along posterior margin of carpus or produced away from it; carpus/propodus not cantilevered, carpus elongate, longer than propodus, not produced along posterior margin of propodus.

Peraeopods homopodous (3-7 directed posteriorly), none prehensile. Peraeopod 3 well developed. Peraeopod 4 well developed. 3-4 with glandular meri; 3-7 without hooded dactyli, 3-7 propodi without distal spurs. Coxa well developed, longer than broad; carpus shorter than propodus, not produced; dactylus well developed. Coxa larger than coxa 3, not acuminate, with well developed posteroventral lobe; carpus not produced. Peraeopods 5-7 with few robust or slender setae; dactyli without slender or robust setae. Peraeopod 5 well developed; shorter than peraeopod 6, or subequal in length to peraeopod 6, or longer than peraeopod 6; coxa smaller than coxa 4, without posterior lobe; basis expanded, subovate, without posteroventral lobe; merus/carpus free; carpus linear; setae absent. Peraeopod 6 subequal in length to peraeopod 7, or longer than peraeopod 7; merus/carpus free; dactylus without setae. Peraeopod 7 with 6-7 well developed articles; shorter than peraeopod 5, or subequal to peraeopod 5;

different in structure to peraeopod 6; with 7 articles; basis expanded or slightly expanded, with long dense slender setae; dactylus without setae.

Pleon. Pleonites 1-3 without transverse dorsal serrations, without dorsal carina; without slender or robust dorsal setae. Epimera 1-3 present. Epimeron 1 well developed. Epimeron 2 without setae.

Urosome not dorsoventrally flattened; urosomites 1 free, 2 and 3 coalesced; urosome urosomite 1 carinate, or urosomites not carinate; urosomites 1-2 without transverse dorsal serrations. Uropods 1-2 apices of rami without robust setae. Uropods 1-3 similar in structure and size. Uropod 1 peduncle without long plumose setae, without basofacial robust seta, without ventromedial spur. Uropod 2 well developed; without ventromedial spur, without dorsal flange; inner ramus subequal to outer ramus. Uropod 3 sexually dimorphic; peduncle short; outer ramus longer than peduncle, 1-articulate, without recurved spines. Telson laminar; deeply cleft, or moderately cleft; longer than broad, or broader than long; apical robust setae present, or absent." (Lowry and Springthorpe 2001).



Ampelisca cristata microdentata (Photo Leslie Harris, NHMLAC)

Ampelisca - The largest genus in the family both world-wide, and in the NEP. J. L. Barnard and Karaman (1991) list over 150 species of *Ampelisca*, and 34 of these are known from the NEP. The majority of these forms are from continental shelf depths in either the temperate or boreal NEP, but a few range into tropical waters. Most of the *Ampelisca* from the Panamic province are deep dwelling rather than found in warm coastal waters. Foundation studies of the NEP ampeliscids were done by Stimpson (1854), who described *A. pugetica*, and continued by Holmes (1908) who described

several of the NEP taxa. Shoemaker (1942) added records of several species from western Mexico, including records of a trans-isthmic distribution of a species he had described from Florida (Shoemaker 1933). J. L. Barnard worked frequently on the group, publishing several major papers on regional faunas (J. L. Barnard 1954a, b, 1960, 1967b, 1971). While his remains the bulk of information on the family in the NEP, several other major contributions have been made. Shoemaker (1955) and Dickinson (1982) examined materials from Arctic and boreal waters, extending the range of many species, and describing a number of new taxa. Roney (1990) added one more species to the fauna. Another Ampelisca species was described by Coyle and Highsmith (1989), but it is restricted to waters north of the Aleutians and outside our study area.

Gurjanova (1951) monographed the ampeliscids of the Northwest Pacific, a number of which also range into the NEP. Margulis (1967) concentrated on the ampeliscid fauna of the deep North Pacific. Hirayama (1983) reported on that portion of the North West Pacific ampeliscid fauna which occurs in Japanese waters. Bousfield (1973), while dealing with the western Atlantic fauna, gave good descriptions and illustrations of several species which have either circumboreal distributions, or have been introduced to the NEP through human transport. Mills (1965) discussed distributions of both North Atlantic and North Pacific ampeliscids. Watling (1995) provided brief descriptions and records of *Ampelisca* species taken in the Santa Maria Basin and the Western Santa Barbara Channel. Most recently Chapman (2007) covered the ampeliscids occurring in the central and northern portions of California; providing a key to species, and valuable summary ecological information. *Triodos*, proposed as another genus of ampeliscids by K. H. Barnard, was submerged back into *Ampelisca* by Karaman and J. L. Barnard 1981).

SCAMIT has recently revisited the ampeliscid fauna of the SCB, and a key to *Ampelisca* was created for the meeting by Lisa Haney (CSDLAC). The key was not fully comprehensive for all ampeliscids included here. A large number of keys have been produced over the years, since this is such a diverse family in the NEP; however none have been comprehensive. The most inclusive was that of J. L. Barnard 1960, which covered the genus *Ampelisca* worldwide to the species level. Many species have been described since, but the key included all species known at publication. In support of that key J. L. Barnard produced a character state review that is of considerable value. It should be examined by all taxonomists dealing with *Ampelisca*.

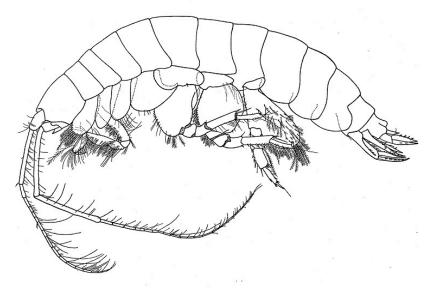
Controversy remains over the limits of morphological variability in several of the NEP *Ampelisca* species. Watling (1995), for instance, viewed *A. careyi* as inseparable from *A. unsocalae*. SCAMIT has debated for a number of years whether there is more than one taxon combined in the species *Ampelisca hancocki*. Differences in the

descriptions of the taxon by J. L. Barnard and J. J. Dickinson have led to these forms being keyed separately. In previous editions of the SCAMIT list we have maintained a taxon *Ampelisca hancocki* Complex, to indicate our perplexity in resolving the variability of this form. This was resolved at the recent Ampeliscidae meeting by dropping the "Complex" designation. This was prompted by findings that locally collected material had neither the toothed nor "slit" character of coxae 1 and 2 which was the difference in the Barnard and Dickinson descriptions. Reexamination of the type by Lisa Haney (CSDLAC) showed it lacked both teeth and slits as well. The discussion was reported in SCAMIT Newsletter Vol. 23(7) in November 2004. Somewhat similarly we have considered, and are still investigating the validity of the described *Ampelisca cristata microdentata* J. L. Barnard (1954). We currently consider this a subspecies, but efforts to gather distributional detail on the two forms of this species continue in the hope that we can find ecological characters that will help separate them. Since the two are sympatric, maintenance of them as subspecies is unwarranted. *Ampelisca microdentata* should be elevated to full specific rank, or dropped into the synonymy of a variable *A. cristata*.

The introduced *Ampelisca abdita* has been relatively well investigated on the east coast (Mills 1964, 1967; Borowski and Aiken-Ander 1991; Franz and Tanacredi 1992). Methods of distinguishing it from the very similar *A. milleri* (presumed endemic to the NEP) are provided by Chapman (1988). It seems to have been the only species in the family successfully introduced to NEP waters. The introduction is assumed to have been via ship ballast water, a process perhaps facilitated by the very small size of this species. *Ampelisca agassizi*, described from the North West Atlantic by Judd (1896), is either a circumboreal species, or as suspected by Chapman (2007) an undifferentiated species complex. In either case it does not seem to have been anthropogenically distributed.

Dickinson introduced several provisional taxa in his thesis (1976). These, unfortunately, cannot yet be recognized, although vouchers should reside in the Oregon State University collection. As there are currently no descriptions or diagnoses of these species they are included only to better approximate the diversity of ampeliscoids in the NEP. Dickinson did not address either of these provisionals in his publication on the taxonomy of *Ampelisca* (1982).

Diagnosis: "Head longer than deep, narrowing anteriorly with anteroventral corner unproduced. Eyes (when present) have lenses in both dorsofrontal and ventrofrontal pairs. Antenna 2, flagellum with more than 5 flagellar segments. Mandibular palp, segment 3 usually much shorter than segment 2. Maxilliped, inner plate short and broad. Anterior coxae much longer than broad. Peraeopods 3-4, segment 5 very short and often partially overhung by segment 4. Peraeopods 5-6, dactyls very short and hook like. Basal lobe of peraeopod 7 expanded distally, posterior margin oblique, and lacking setae on anterior margin near junction with segment 3. Peraeopod 7 with seven distinct segments, dactyl broad at base. Telson lobes elongated and fused only basally in both sexes." (from Dickinson 1982)

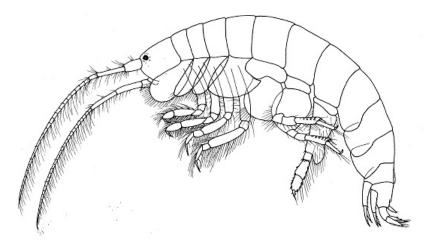


Byblis tannerensis (from J. L. Barnard 1966)

Byblis – Second of the three ampeliscid genera in the NEP in diversity, 15 species are known from the NEP. The genus world-wide contains at least 56 species (J. L. Barnard and Karaman 1991), so roughly one quarter of the world diversity is found in this region. Virtually all *Byblis* species have strikingly different eyes from *Ampelisca*. In Byblis the pigmented portion of the eye is brown to black, which in Ampelisca it is red to clear, with occasional species tending to a very dark reddish brown. In most respects the two genera are not that different, and Karaman and J. L. Barnard (1981) suggested they might be synonymized, pending further investigation of the type species. Neither of these authors has since suggested this, and it seems probable that the two will remain separated as they currently are for the foreseeable future. Reports of Byblis began with Holmes (1908) who reported B. gaimardi from Monterey (these specimens would now be differently identified). Additional species were created by J. L. Barnard (1954b, 1960, 1966, 1967, 1971), and by Dickinson (1983). Coyle and Highsmith (1989) described two species of Byblis, but both are Arctic forms not yet reported from the NEP below the Aleutians. NEP species in this genus can be separated using the key provided by Dickinson (1983, pp. 3-4). At least one form is viewed as a provisional. This was identified as *Byblis crassicornis* Metzger 1875 by J. L. Barnard 1971. Later review by Dickinson (1983), suggests that this is sufficiently different from the North Atlantic form to warrant erection of a new taxon. It remains as Byblis sp. for the moment, with no specific provisional designation.

Lie (1968, pp.408-417) reported on the population of *Byblis veleronis* in Puget Sound. Subsequent nomenclatural change suggest this was actually *Byblis millsi*. He found that individuals grew at a rate of 7mm/year, and had a life span of 2 years, with some individuals surviving into a third year. He found no significant seasonal trend in abundance in the population, so recruitment, and consequently reproduction, is expected to be relatively continuous. There is some suggestion of two cohorts in the size-frequency graphs, but they were not well separated. Growth rate appeared linear throughout the life span, not slowing as the organisms aged.

Diagnosis: "Head longer than deep, narrowing anteriorly with anteroventral corner excavate for insertion of antenna 2. Eyes (when present) have lenses in both dorsofrontal and ventrofrontal pairs. Antenna 2, flagellum with more than five segments. Mandibular palp, segment 3 much shorter than segment 2. Maxilliped, inner plate slender and slightly elongate. Anterior coxae slightly longer than broad. Coxa 4, broader than long, posterior lobe acutely produced. Peraeopods 3-4, segment 5 not greatly reduced in length. Peraeopods 5-6, dactyls medium length and simple. Basal lobe of peraeopod 7, expanded distally, posterior margin oblique, and anterior margin fully setose near junction with segment 3. Peraeopod 7, dactyl reduced to a spine. Uropod 3, medial margins of rami usually serrate. Telson, short in female and elongate in pelagic stage males, cleft varies from 1/4 to 3/4 length. "(from Dickinson 1983)



Haploops tubicola (from Lincoln 1979)

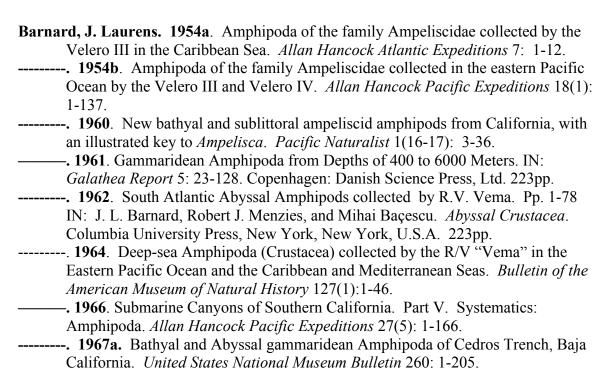
Haploops - Fewer species belong to this genus than to either of the other NEP genera; only two out of the world list of 14 species (J. L. Barnard and Karaman 1991). The genus was comprehensively reviewed by Dickinson (1983), and no new taxa have been added subsequently. His key (1983, p. 22) covers all known NEP species, and also includes three similar forms presently known only from Arctic and Northwest Pacific waters. Members of this genus, while similar in overall appearance to both *Ampelisca* and *Byblis*, have different structure to the last pereopod. In both the former genera the basis of the last leg is prolonged posteriorly into a large variously rounded lobe along the full length of the segment. In *Haploops* species, this lobe is quite narrow and posteriorly expanded only at the distal end of the segment to form a pendulous lobe drooping from the basis. The rest of the leg tends to be broad and powerful compared to the more gracile seventh pereopods of *Ampelisca* and *Byblis*. This genus, along with *Byblis*, tends to occur more deeply than most *Ampelisca* species. At the southern end of their distribution these species are virtually absent in waters shallower than 400m, while in the boreal portion of the NEP they may be taken as shallowly as 100m.

J. L. Barnard vacillated in his recording of *Haploops tubicola* in the NEP. He initially (1960) recorded specimens as this species, only to change his identification to *H. spinosa* (J. L. Barnard 1966, 1967). Kanneworff (1966) synonymized the two taxa, an action accepted by J. L. Barnard who returned to use of *H. tubicola* (1971). Descriptions and illustrations of *H. tubicola* are available in Sars (1895, plt. 67), Kanneworff (1966,

figs. 1, 2, and part of 5 and 6), and Lincoln (1979, figs. 53 and 54 in part). Sars' figure was reproduced by Watling (1995) who provided a brief description of the animal. *Haploops lodo* description and illustration are available in J. L. Barnard 1961 (Figure 38) with additional details provided in 1964 (Figure 13), and in 1971 (Figure 5), and by Bellan-Santini and Dauvin (2008).

Diagnosis: "Head as deep as long, narrowing only slightly anteriorly. Eyes (when present) usually have lenses only in dorsofrontal pair. Mandibular palp, segments 2-3 usually subequal in length. Maxilliped, inner plate slender and elongate tapering distally. Anterior coxae, medium length. Coxa 1, usually expanded distally. Coxae 2-3, truncated distally. Coxa 4, usually broader than deep with posterior lobe broadly rounded rather than acute. Peraeopods 3-4, segment 5 not greatly reduced in length. Peraeopods 5-6, dactyl medium length and simple. Basal lobe of peraeopod 7, not expanded distally, posterior margin vertical, anterior margin setose near its junction with segment 3. Peraeopod 7, segment 6 usually very reduced in size, dactyl spine-like. Telson, short in female and elongate in pelagic stage male." (from Dickinson 1983)

Literature Cited



- ------. **1967b**. New species and records of Pacific Ampeliscidae (Crustacea: Amphipoda). *Proceedings of the united States National Museum* 121(3576): 1-20.
- ———. **1971**. Gammaridean Amphipoda from a Deep-Sea Transect off Oregon. *Smithsonian Contributions to Zoology* 61: 1-86.
- ----- **1979**. Littoral gammaridean Amphipoda from the Gulf of California and the Galapagos Islands. *Smithsonian Contributions to Zoology* 271: 1-149.
- -----, and Gordan S. Karaman. 1991 The Families and Genera of Marine Gammaridean Amphipoda (except marine gammaroids). Records of the Australian Museum Supplement 13 (Parts 1 and 2): 1-866.
- **Bellan-Santini, Denise, and Jean Claude Dauvin. 2008.** Contribution to the knowledge of the genus *Haploops*, a new location of *Haploops lodo* (Crustacea: Amphipoda: Ampeliscidae) from the bathyal North Atlantic Ocean with a complement to the description of the species. *Journal of Natural History* 42(13-14): 1065-1077.
- **Borowsky, Betty, and P. Aitken-Ander. 1991.** Sexually dimorphic free-swimming behaviour in the amphipod crustacean *Ampelisca abdita. Journal of the Marine Biological Association of the United Kingdom* 71: 655-663.
- **Bousfield, Edward L. 1973.** *Shallow-water gammaridean Amphipoda of New England.* Comstock Publishing Associates/Cornell University Press. Ithaca, New York, U.S.A. 312pp.
- ----- **1977**. A new look at the systematics of gammaroidean amphipods of the world. *Crustaceana* Supplement 4: 282-316.
- **Transactions of the Royal Society of Canada** 4(14): 343-390.
- -----. **1982**. Amphipoda (Palaeohistory), pp. 96-100 IN: *McGraw-Hill Yearbook of Science & Technology 1982/1983*. McGraw-Hill Book Company. New York, New York, U.S.A.
- **Chapman, John W. 1988**. Invasions of the Northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. *Journal of Crustacean Biology* 8(3): 364-382.
- ------ **2007.** Gammaridea. Pp. 545-618 IN: Carlton, James T. (ed.). The Light and Smith Manual: intertidal invertebrates from Central California to Oregon. 4th edition. University of California Press, Berkeley, California, U.S.A. 1001pp.
- Christensen, Aage M., and Birgitte Kanneworff. 1964. *Kronborgia amphipodicola* gen. et sp. nov., a dioecious turbellarian parasitizing ampeliscid amphipods. *Ophelia* 1(1): 147-166.
- **Conlan, Kathleen E. 1991**. Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea. *Hydrobiologia* 223: 255-282.
- Coyle, Kenneth O., Bodil A. Bluhm, Brenda Konar, Amy Blanchard and Raymond C. Highsmith. 2007. Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002-2003. *Deep Sea Research Part II Topical Studies in Oceanography* 54(23-26): 2906-2918.
- ----- and Raymond C. Highsmith. 1989. Arctic ampeliscid amphipods: three new species. *Journal of Crustacean Biology* 9(1): 157-175.

- **Dauvin, Jean-Claude. 1988a**. Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 1. *Ampelisca tenuicornis* Liljeborg. *Journal of Experimental Marine Biology and Ecology* 118: 55-84.
- **. 1988b**. Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 2. *Ampelisca brevicornis* (Costa). *Journal of Experimental Marine Biology and Ecology* 119: 213-233.
- **. 1988c**. Biologie, dynamique, et production de populations de crustacés amphipodes de la Manche occidentale. 3. *Ampelisca typica* (Bate). *Journal of Experimental Marine Biology and Ecology* 121: 1-22.
- ------ **1989**. Life cycle, dynamics and productivity of Crustacea-Amphipoda from the western English Channel. 5. *Ampelisca sarsi* Chevreux. *Journal of Experimental Marine Biology and Ecology* 128: 31-56.
- -----, and Souaad Zouhiri. 1996. Suprabenthic crusteacean fauna of a dense *Ampelisca* community from the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 76: 909-929.
- **Dickinson, John J. 1976.** Two zoogeographic studies of deep sea benthic gammarid amphipods. <u>Oceanography</u>. Corvallis, Oregon, Oregon State University. Ph.D. Thesis, 127pp.
- The systematics and distributional ecology of the family Ampeliscidae (Amphipoda: Gammaridea) in the Northeastern Pacific region. I. The genus *Ampelisca*. *National Museums of Canada*, *Publications in Biological Oceanography* 10: 1-39.
- **Enequist, Paul. 1950**. Studies on the soft-bottom amphipods of the Skagerak. *Zoologische Bidrag Fran Uppsala* 28: 297-492.
- **Franz, David R., and John T. Tanacredi. 1992**. Secondary production of the amphipod *Ampelisca abdita* Mills and its importance in the diet of juvenile winter flounder (*Pleuronectes americanus*) in Jamaica Bay, New York. *Estuaries* 15(2): 193-203
- García Madrigal, Maria d. S. 2007. Annotated checklist of the amphipods (Peracarida: Amphipoda) from the tropical eastern Pacific. *Contributions to the Study of East Pacific Crustaceans* 4(2): 63-195.
- **Graeve, M., Patrick Dauby, and Yves Scailteur. 2001**. Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. *Polar Biology* 24(11): 853-862.
- **Gurjanova**, **Eupraxie F. 1951**. Bokoplavy morey SSSR i sopredel'nykh vod (Amphipoda Gammaridea). *Opredeliteli Po Faune SSSR* 41: 1-1029.
- **Hirayama, Akira. 1983.** Taxonomic studies on the shallow water gammaridean Amphipoda of west Kyushu, Japan. I. Acanthonotozomatidae, Ampeliscidae, Ampithoidae, Amphilochidae, Anamixidae, Argissidae, Atylidae and Colomastigidae. *Publications of the Seto Marine Biological Laboratory* 28(1-4): 75-150.

- **Holmes, Samuel J. 1908**. The Amphipoda Collected by the U. S. Bureau of Fisheries Steamer 'Albatross' off the West Coast of North America, in 1903 and 1904, with Descriptions of a New Family and Several New Genera and Species. *Proceedings of the United States National Museum* XXXV(1654): 489-543.
- **Judd, Sylvester D. 1896**. Descriptions of three species of sand fleas (Amphipoda) collected at Newport, Rhode Island. *Proceedings of the United States National Museum* 18(1084): 593-603.
- **Kanneworff, Ebbe**. **1966**. On some amphipod species of the genus *Haploops*, with special reference to *H. tubicola* Liljeborg and *H. tenuis* sp. nov. from the Oresund. *Ophelia* 3: 183-207.
- **Karaman, Gordan S., and J. L. Barnard. 1981**. The synonymization of *Triodos* K. H. Barnard with *Ampelisca* Krøyer (Crustacea, Amphipoda). *Annals of the South African Museum* 84(7): 255-264.
- **Lie, Ulf. 1968.** A quantitative study of benthic infauna in Puget Sound, Washington, USA, in 1963-1964. *Fiskeridirektoratets Skrifter, Serie Havundersokelser* 14(5): 229-556
- **Lincoln, Roger J. 1979**. *British Marine Amphipoda: Gammaridea*. British Museum (Natural History); London, England. 658pp.
- Lowry, James K., and Roger T. Springthorpe (2001 onwards). Amphipoda: Families and Subfamilies. Version 1: 1 September 2001. http://crustacea.net/.
- **Lynch, M. P., and W. Harrison. 1970**. Sedimentation caused by a tube-building amphipod. *Journal of Sedimentary Petrology* 40: 434-436.
- **Margulis, R. J. 1967**. Deep-sea Ampeliscidae (Amphipoda, Gammaridea) from the Pacific Ocean. *Crustaceana* 13(3): 299-309.
- **McDermott, John J. 1993**. Nemertea inhabiting the *Haploops* (Amphipoda) community of the northern Oresund with special reference to the biology of *Nipponemertes pulcher* (Hoplonemertea). *Hydrobiologia* 266: 15-28.
- McLaughlin, P. A., D. K. Camp, M. V. Angel, E. L. Bousfield, P. Brunel, R. C. Brusca, D. B. Cadien, A. C. Cohen, K. Conlan, L. G. Eldredge, D. L. Felder, J. W. Goy, T. A. Haney, B. Hann, R. W. Heard, E. A. Hendrycks, H. H. Hobbs III, J. R. Holsinger, B. Kensley, D. R. Laubitz, S. E. LeCroy, R. Lemaitre, R. F. Maddocks, J. W. Martin, P. Mikkelsen, E. Nelson, W. A. Newman, R. M. Overstreet, W. J. Poly, W. W. Price, J. W. Reid, A. Robertson, D. C. Rogers, A. Ross, M. Schotte, F. R. Schram, C.-T. Shih, L. Watling, and G. D. F. Wilson. 2005. Common and Scientific Names of Aquatic Invertebrates from the United States and Canada Crustaceans. Bethesda, Maryland, U. S. A.: American Fisheries Society. 565pp.
- Mills, Eric L. 1964. *Ampelisca abdita*, a new amphipod crustacean from Eastern North America. *Canadian Journal of Zoology* 42: 559-575.
- **----- 1965**. The zoogeography of North Atlantic and North Pacific ampeliscid amphipod crustaceans. *Systematic Zoology* 14(2): 119-130.
- ------- **1967**. The biology of an ampeliscid amphipod crustacean sibling species pair. *Journal of the Fisheries Research Board of Canada* 24(2): 305-355.

- Nyssen, Fabienne, Thomas Brey, Gilles Lepoint, Jean-Marine Bouquegneau, Claude De Broyer, and Patrick Dauby. 2002. A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods. *Polar Biology* 25: 280-287.
- Oliver, John S., James M. Oakden, M. A. Silberstein, and E. F. O'Connor. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. *Canadian Journal of Zoology* 62(1): 41-49.
- **Roney, James D. 1990**. A new species of marine amphipod (Gammaridea: Ampeliscidae) from the sublittoral of southern California. *Bulletin of the Southern California Academy of Sciences* 89(3): 124-129.
- **Sainte-Marie, Bernard. 1991**. A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia* 223: 189-227.
- -----, **and Pierre Brunel. 1985**. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. *Marine Ecology Progress Series* 23: 57-69.
- **Sars, George O. 1895**. Amphipoda. An Account of the Crustacea of Norway, with Short Descriptions and Figures of all the Species 1: 1-711.
- **Sheader, M. 1998**. Grazing predation on a population of *Ampelisca tenuicornis* (Gammaridae: Amphipoda) off the south coast of England. *Marine Ecology Progress Series* 164: 253-262.
- **Shoemaker, Clarence R. 1933**. Amphipoda from Florida and the West Indies. *American Museum Novitates* 598: 1-24.
- ----- **1942**. Amphipod Crustaceans Collected on the Presidential Cruise of 1938. *Smithsonian Miscellaneous Collections* 101(11): 1-52.
- -----. **1955.** Amphipoda collected at the Arctic Laboratory, Office of Naval Research, Point Barrow, Alaska, by G. E. MacGinitie. *Smithsonian Miscellaneous Collections* 128(1): 1-78.
- **Soliman, Yousria, and Mary K. Wicksten. 2007**. *Ampelisca mississippiana*: a new species (Crustacea: Amphipoda: Gammaridea) from the Mississippi Canyon (Northern Gulf of Mexico). *Zootaxa* 1380: 45-54.
- **Stimpson, William. 1864**. Descriptions of new species of marine invertebrata from Puget Sound, collected by the naturalists of the North-west Boundary Commission, A. H. Campbell, Esq., Commissioner. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1864(3): 153-161.
- Watling, Les. 1995. The Families Ampeliscidae, Amphilochidae, Liljeborgiidae, and Pleustidae. Chapter 3, Pp. 137-176 IN: Blake, James A., Les Watling, and Paul H. Scott (eds.) *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. The Crustacea Part 3 The Amphipoda*. Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A. 251pp.
- Wesławski, Marcin, and Joanna Legezynska. 2002. Life cycles of some Arctic amphipods. *Polish Polar Research* 23(3-4): 253-264.