POLYNOID POLYCHAETES ASSOCIATED WITH A WHALE SKELETON IN THE BATHYAL SANTA CATALINA BASIN

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Abstract. — A whale-fall community dominated by microbial mats of sulfur-oxidizing bacteria in the Santa Catalina Basin is inhabited by species similar to those associated with hydrothermal vents in the northeast Pacific. Polynoid polychaetes associated with the skeleton include: Bathykurila guaymasensis (Macellicephalinae); Peinaleopolynoe santacatalina, new species (Branchinotogluminae, emended); and Harmothoe craigsmithi, new species, and Subadyte mexicana (Harmothoinae). Both the holotype of Peinaleopolynoe sillardi Desbruyères & Laubier and additional specimens of Subadyte mexicana Fauchald, were examined and descriptions supplemented.

Oceanographers aboard the deep submergence research vessel (DSRV) Alvin discovered an intact, 20 m long skeleton of a blue or fin whale at a depth of 1240 m in the Santa Catalina Basin (33°14'N, 118°30'W) during November, 1987. Subsequent collections revealed a characteristic "whale-fall" community associated with the skeleton (Smith et al. 1989, Allison et al. 1991, Smith 1992). The skeleton was partially buried and the bone surfaces were covered by a white "furry" microbial mat consisting of large filamentous sulfur-oxidizing bacteria (Beggiatoa sp.). The site was a sulfide rich, reducing habitat similar to those associated with hydrothermal vents. In addition, numerous invertebrate species, including large clams, mussels, limpets and snails, were associated with the bones in ways that were similar to those of hydrothermal vent faunas of the Galapagos Rift, Guaymas Basin and Juan de Fuca Ridge. These species were unreported from the Santa Catalina Basin (Smith & Hamilton 1983, Smith 1985, Kukert & Smith 1992). Additional Alvin dives to the whale-fall site were made in February 1991.

Polynoid polychaetes collected on or within 0.5 m of the bones were sent to me for identification by Dr. Craig R. Smith, University of Hawaii, Manoa. Included are four species in three subfamilies: Bathykurila guaymasensis Pettibone, 1989 (Macellicephalinae), originally described from the Guaymas Basin hydrothermal mounds; Peinaleopolynoe santacatalina, new species (Branchinotogluminae Pettibone, 1985a, emended); Harmothoe craigsmithi, new species, and Subadyte mexicana Fauchald, 1972 (Harmothoinae). The subfamily Branchinotogluminae is emended to include Peinaleopolynoe sillardi Desbruyères & Laubier, 1988, obtained from artificially enriched substrates placed at a depth of 4800 m in the northeast Atlantic off Spain. The original description of P. sillardi is supplemented, based on an examination of the holotype kindly sent on loan from the Muséum National d'Histoire Naturelle, Paris (MNHN). Harmothoe craigsmithi is similar to H. tenebricosa Moore, 1910, which was described from southern California in 914–1463 m. Subadyte mexicana was originally described from western Mexico in 567–844 m. Its description is also supplemented based on additional specimens from the Santa Catalina Basin and Channel Islands.
The larger polynoids, collected by the Alvin, were part of the epifauna on the whale bones and designated by Bone Implant number (1 or 2) or Vertebra (V) number. The smaller polynoids, part of the infauna, were collected by Ekman cores (E), and separated into subcores (A-D) and from 0–1, 1–5, and 5–10 cm below the sediment surface.

Types and additional specimens are deposited in the collections of the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution (USNM), the Natural History Museum of Los Angeles County (AHF-LACM), and with the donor of the collection, Dr. Craig R. Smith (CRS), of the Department of Oceanography, University of Hawaii at Manoa.

**Family Polynoidae**

**Subfamily Macellicephalinae**

Hartmann-Schröder, 1971, emended Pettibone, 1976

Genus *Bathykurila* Pettibone, 1976

*Bathykurila guaymasensis* Pettibone, 1989

*Bathykurila guaymasensis* Pettibone, 1989: 159, figs. 1, 2.

**Material.**—Santa Catalina Basin, California, 33°12'N, 118°30'W, 1240 m, Alvin Dives in Whale-fall site, in Feb 1991, bucket washes: AD 2332, 20 Feb, Implant 1, 1 specimen (USNM 157592), Implant 2, 4 specimens (USNM 157593), 1 specimen (CRS); AD 2334, 22 Feb, Bone V21, 1 specimen (USNM 157594); AD 2336, 24 Feb, Bone V15, 5 specimens (USNM 157595).

**Description.**—The specimens agree with those previously described from the vents in the Guaymas Basin in 2004–2020 m. The largest specimen measures 10 mm long, 8 mm wide, with setae, with 15 segments, and 7 pairs of elytrophores; smaller specimens are 1.5–4 mm long, 1.5–3 mm wide, with 10–13 segments. Long ventral papillae on segment 11 (Fig. 1C, in Pettibone 1989) are present on 4 of the 12 specimens; 3 specimens have small ventral papillae on segments 10, 11, 12 (not reported previously).

**Remarks.**—The specimens have numerous filamentous sulfur-bacteria attached (*Beggiatoa* sp.), characterized by their gliding motility and internal globular elemental sulfur, described and figured by Nelson et al. (1989).


**Subfamily Branchinotogluminae**

Pettibone, 1985a, emended

The subfamily is emended to include *Peinaleopolynoe sillardi* Desbruyères & Laubier, 1988 and *P. santacatalina*, new species. Instead of 10 pairs of elytra and elytrophores on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, and dorsal cirri on the non-elytrigerous segments, including segments 20 and 21, there may be 9 pairs of elytra, with the elytra and elytrophores lacking on segment 19, but also lacking dorsal cirri and thus not a typical cirrigerous segment, as in *P. sillardi* or 10 pairs of elytra with the elytrophores and elytra extra small on segment 19, as in *P. santacatalina*. Notopodial bracts are not present on some or all of the elytrigerous segments, as in other members of the subfamily. Also the arborescent branchiae may begin on segment 2 and not on segment 3, as indicated previously.

**Genus Peinaleopolynoe**

Desbruyères & Laubier, 1988, emended

**Type species.**—*Peinaleopolynoe sillardi* Desbruyères & Laubier, 1988, by monotypy. Gender feminine.
The genus includes the type species, *P. sillardi*, and a new species, *P. santacatalina*.

**Diagnosis.**—Body short, with 21 segments. Elytra and elytrophores numbering 9 or 10 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, and 19 or lacking on 19. Elytra large, subreniform, overlapping, covering dorsum, without tubercles or papillae. Dorsal cirri with short cylindrical cirrophores and long distal styles; dorsal tubercles, in line with elytrophores, on non-elytrigerous segments. Arborescent branchiae attached on dorsal tubercles and bases of notopodia, beginning on segment 2 and continuing to near end of body. Prostomium bilobed, with triangular anterior lobes bearing minute frontal filaments, with median antenna in anterior notch and paired palps; without lateral antennae or eyes. First or tentacular segment not visible dorsally; tentacular cirrophores lateral to prostomium, each with small acicular lobe on inner side, dorsal and ventral tentacular cirri, without setae. Second or buccal segment with first pair of elytrophores, biramous parapodia, and ventral or buccal cirri attached to basal parts of neuropodia, lateral to ventral mouth; styles longer than following ventral cirri. Parapodia biramous, with notopodia almost as long as neuropodia. Notopodia without notopodial bracts, bulbous basally, extending distally into acicular processes; neuropodia with longer conical presetal lobes with acicular processes and shorter truncate postsetal lobes. Notosetae stouter than neurosetae, straight, acicular, smooth or with lateral spines. Neurosetae long, slender, finely spinous, with slightly hooked tips. Pharynx with 7 pairs of border papillae; jaws with lateral teeth. Ventral segmental papillae on segments 12–15. Pygidium with pair of anal cirri.

*Peinaleopolynoe sillardi*
Desbruyères & Laubier
Fig. 1

*Peinaleopolynoe sillardi* Desbruyères & Laubier, 1988:331, figs. 1, 2.

**Material.**—Northeast Atlantic Ocean, 46°02'N, 16°40'W, 4800 m, from enriched module of colonization, 23 Jul 1985, holotype (MNHNP UB631).

**Supplementary description.**—The elytra and elytrophores are lacking on segment 19, thus there are 9 pairs of elytra, as originally indicated. However, segment 19 also lacks dorsal cirri, thus suggesting that it has secondarily lost the characteristic structure. The large elytra are subreniform, thick, white, opaque, without tubercles or papillae, except for some small posterior extensions, variable in size, shape, and number (Fig. 1A). The notopodia and neuropodia of the biramous parapodia are subequal in size, both with projecting acicular processes; the notosetae are short to longer, not as long as the neurosetae (Fig. 1C). The stout acicular notosetac, without spines, taper to rounded tips (Fig. 1D). The slender neurosetae have slightly hooked bare tips, with double rows of spines along one border; the upper neurosetae are more slender than the middle ones (Fig. 1E). Segmental ventral papillae are present on segments 12–15; they are short and curved laterally (Fig. 1B).

*Peinaleopolynoe santacatalina*,
new species

Fig. 2

**Material.**—Santa Catalina Basin, California, 33°14'N, 118°30'W, 1240 m, *Alvin* Dives in Whale-fall site, in Feb 1991, bucket washes: AD 2332, 20 Feb, Implant 1, paratype (USNM 157588), Implant 2, 2 paratypes (USNM 157589); paratype (CRS); (AD 2334, 22 Feb, Bone V21, holotype (USNM 157587).

**Description.**—Holotype (USNM 157587) 22 mm long, 14 mm wide with setae, 21 segments; paratype (USNM 157588) 20 mm long, 13 mm wide, 21 segments; 3 smaller paratypes (USNM 157589) 9–12 mm long, 7–10 mm wide, 21 segments, last 2 very small. Dorsum with ciliated transverse bands, 2 per segment, extending onto bases of elytrophores and dorsal tubercles (Fig...
2A, B). Elytrophores large, bulbous, 10 pairs, on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, smaller on segment 19 (Fig. 2A, B, F); elytra all missing, except for minute elytron on left 19th elytrophore of one paratype. Dorsal tubercles and dorsal cirri on non-elytrigerous segments; cirrophores rather long, cylindrical, on posterior sides of notopodia; styles long, filiform, extending beyond setae, shorter on segment 21 (Fig. 2B, G). Branchiae compact, arborescent, with numerous short bulbous terminal filaments, beginning on segment 2 and continuing to near posterior end, small on segment 20, lacking on segment 21; on elytrigerous segments, branchiae forming single large groups between elytrophores and bases of notopodia; on cirrigerous segments, branchiae in small groups attached to dorsal tubercles and larger groups near bases of notopodia (Fig. 2A, B, F, G).

Prostomium oval, deeply bilobed, forming triangular anterior lobes with delicate frontal filaments; median antenna with bulbous ceratophore in anterior notch, style short, only slightly surpassing prostomium; without eyes; palps stout, tapering, about twice length of prostomium; tentaculo-
Fig. 2. Peinaleopolynoe santacatalina, A–C, F–I, holotype (USNM 157587); D, E, paratype (USNM 157589): A, Dorsal view of anterior end, left dorsal tentacular cirrus missing; B, Dorsal view of posterior end, including segments 17–21, styles of dorsal cirri of segment 20 and anal cirri missing; C, Ventral view of left side of segments 12–15, showing ventral segmental papillae; D, Dorsal border papillae of pharynx; E, Jaw; F, Right elytrigerous parapodium from segment 9, anterior view, acicula dotted; G, Right cirrigerous parapodium from segment 10, posterior view; H, Long notoseta from same; I, Supraacicular neuroseta from same, with detail of parts; J, Subacicular neuroseta from same, with detail of parts. Scales = 1.0 mm for A, B; 2.0 mm for C; 0.2 mm for D, E; 1.0 mm for F, G; 0.1 mm for H, I.
phores of segment 1 lateral to prostomium and palps, achaetous, each with small acic-ular process on medial side, long dorsal tentacular cirrus about as long as palp and slightly shorter ventral tentacular cirrus, and forming anterior and lateral lips of ventral mouth (Fig. 2A). Segment 2 or buccal segment with first pair of large elytrophores, branchiae, biramous parapodia, and ventral buccal cirri inserted basally and extending beyond tips of neuropodia, with contributions to posterior lip of ventral mouth (Fig. 2A). Pharynx (dissected) with 7 pairs of dorsal and ventral border papillae; hooked jaws with small and larger teeth on inner borders (Fig. 2D, E).

Notopodia of biramous parapodia bulbous basally, extending into long acicular processes on lower sides; neuropodia with subtriangular presetal lobes extending into long acicular processes, postsetal lobes shorter, truncate (Fig. 2F, G). Notosetae forming radiating bundles, short to long, almost as long as neurosetae, stout, acicular, tapering to blunt tips, with double alternating rows of short spines on one side, 3–4 pairs on shorter notosetae and up to 11 pairs on longer ones (Fig. 2F–H). Neurosetae forming fan-shaped bundles, very numerous, slender, with slightly curved tips and double rows of spines; supraacicular neurosetae with more prominent spines than in subacicular neurosetae (Fig. 2F, G, I, J). Ventral cirri with small cirrophores on middle of neuropodia, styles short, tapering, often curved distally on posterior sides of neuropodia (Fig. 2F, G). Ventral segmental papillae 4 pairs, on segments 12–15, rather long, curved laterally (Fig. 2C); ventral segmental papillae small, rounded, on smaller paratype. Pygidium enclosed in parapodia of segments 19–21, last 2 smaller, with pair of anal cirri (sometimes missing, Fig. 2B).

**Etymology.—**The new species is named for the collecting site, Santa Catalina Basin.

**Remarks.—**Peinaleopolynoe santacatalina differs from *P. sillardi* in having small elytrophores and elytra on segment 19, making 10 pairs of elytra, instead of lacking elytrophores, elytra and dorsal cirri, and 9 pairs of elytra. The stout acicular notosetae have double rows of spines on one side in *P. santacatalina* and are smooth in *P. sillardi*.

Subfamily Harmothoinae Willey, 1902
Genus *Harmothoe* Kinberg, 1856
*Harmothoe craigsmithi*, new species

**Material.**—Santa Catalina Basin, California, 33°12'N, 118°30'W, 1240 m, *Alvin* Dives in Whale-fall site, in Nov 1988: AD 2138, 11 Nov, E2 A 0–1, holotype (USNM 157590), E6 B 0–10, paratype (CRS); AD 2133, 6 Nov, WS-6, bone scrapings, paratype (USNM 157591).

**Description.**—Holotype 22 mm long, 8 mm wide with setae, 37 segments. Complete paratype (USNM 157591) 24 mm long, 8 mm wide, 37 segments. Dorsum darkly pigmented, with low ciliated transverse bands, 2 per segment, continuing on bases of elytrophores and dorsal tubercles. Elytra 15 pairs, on bulbous elytrophores, on segments 2, 4, 5, 7, alternate segments to 23, 26, 29, 32. First elytra round, with long papillae on border and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B). Following elytra subreniform, with long papillae on lateral and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B). Following elytra subreniform, with long papillae on lateral and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B). Following elytra subreniform, with long papillae on lateral and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B). Following elytra subreniform, with long papillae on lateral and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B). Following elytra subreniform, with long papillae on lateral and scattered on surface, with conical microtubercles throughout but more concentrated near borders (Fig. 3B).
bulbous ceratophore in anterior notch, style missing; lateral antennae with ceratophores inserted ventrally, styles short, subulate, papillate; palps stout, tapering about twice length of prostomium; tentaculophores of segment I lateral to prostomium, each with small acicular lobe and 3 notosetae on inner side and dorsal and ventral tentacular cirri (missing) (Fig. 3A). Second segment with first pair of large elytrophores, biramous parapodia and long ventral buccal cirri lateral to ventral mouth (Fig. 3A).
Notopodium of biramous parapodium almost as long as neuropodium, rounded, with long acicular process on lower side; neuropodium with subconical presetal acicular lobe with digitiform supraacicular process, postsetal lobe shorter, rounded (Fig. 3D, E). Notosetae numerous, forming radiating bundle, stouter than neurosetae, shorter, slightly curved to longer, nearly straight, with numerous spinous rows and short, bare tips; longer ones mostly faint split tips (Fig. 3F). Neurosetae numerous, forming fan-shaped bundle, with numerous spinous rows and bare, slightly hooked tips; middle and upper ones with slender secondary tooth and more prominent spinous rows; lower ones with shorter spinous regions and entire tips (Fig. 3G). Ventral cirri with cirrophores on middle of neuropodia; styles short, tapered (Fig. 3D, E).

**Etymology.**—The species is named for Dr. Craig R. Smith, the collector of the polygnoids from the whale-fall site, sent for identification.

**Remarks.**—*Harmothoe craigsmithi* is close to *H. tenebricosa* Moore (1910:351-353), which was described from off California in 1914-1916 m (also see Pettibone 1969b:31-42) and is widely distributed from Japan and the Bering Sea to Lower California, in 203-1990 m. *Harmothoe craigsmithi* differs from *H. tenebricosa* in the following: the elytra have marginal and surface papillae and microtubercles, instead of lacking them; the eyes are rather large, instead of small or absent; the notopodia are almost as long as the neuropodia, instead of shorter; the neuropodial presetal acicular lobe has a long digitiform supraacicular process, instead of a small rounded process; the notosetae have distinct spinous rows, instead of nearly smooth or faint spinous rows.

**Genus Subadyte** Pettibone, 1969a

*Subadyte mexicana* Fauchald, 1972

Figs. 4, 5

*Subadyte mexicana* Fauchald, 1972:27, pl. 1:figs. a–e.

**Subadyte sp.** A. Jones & Thompson, 1987: 128, fig. 3a (list).

**Material.**—Baja California, vicinity of Cedros Island, 27°28'N, 115°16'W, 792-844 m, mud and glauconitic sand, holotype (LACM-AHF 1008).

Santa Catalina Basin, California, 33°12'N, 118°30'W, 1240 m, *Alvin* Dives in Whalebone habitat, Nov 1988: 0 m distance from whale bones; AD 2133, 6 Nov, E2 A 0-2, 1 specimen (USNM 157601); AD 2138, 11 Nov, E6 A 0-10, E6 C 0-10, E6 D 0-10; E7 D 0-5, 4 specimens (USNM 157602–5). 0.5 m distance from whale bones: AD 2133, 6 Nov, E11 B 0-1, 1 specimen (USNM 157600); AD 2135, 8 Nov, E10 C 0-1, 1 specimen (USNM 157596); AD 2137, 10 Nov, E6 D 0-1, E9 B 5-10, E9 C 5-10, 3 specimens (USNM 157597–9); AD 2138, 11 Nov, E1 A 0-1, E2 C 0-1, 2 specimens (CES).

Channel Islands, California, *R/V Velero IV*, (as *Subadyte sp. A*): AHF 22970, Santa Rosa Island, 33°51'N, 120°08'W, 368 m, 1 specimen (LACM): AHF 23000, Santa Rosa Island, 33°48'N, 120°04'W, 127 m, 1 specimen (LACM); AHF 23093, Santa Rosa Island, 33°39'N, 119°58'W, 113 m, 1 specimen (USNM 157610); AHF 23182, San Miguel Island, 33°57'N, 120°22'W, 118 m, 2 specimens (USNM 157611); AHF 24241, San Miguel Island, 33°57'N, 120°23'W, 139 m, 2 specimens (LACM).

Southern California, *R/V Thomas G. Thompson* Cruise 113, 1977 (as *Subadyte sp. A*): AHF 82801, off Huntington Beach, 33°23'N, 117°54'W, 536-543 m, 2 specimens (LACM); AHF 80201, off Santa Barbara, 34°22'N, 119°57'W, 329-340 m, 1 specimen (LACM); AHF 80546, San Miguel Island, 33°57'N, 120°22'W, 444-500 m, 3 specimens (LACM); AHF 81735, Tanner Bank, 32°47'N, 119°15'W, 511-530 m, 1 specimen (LACM).

**Type material.**—The holotype consists of an anterior fragment 4, 5 mm long, 2 mm
Fig. 4. *Subadyte mexicana*. A, B (USNM 157601), C (USNM 157603), D–F (USNM 157597): A, Dorsal view of anterior end, left tentacular cirri and left dorsal cirrus of segment II missing; B, Ventral view of lateral antennae and facial tubercle (not to scale); C, Left 1st elytron from segment II; D, Right middle elytrigerous parapodium, anterior view, acicula dotted; E, Short and longer notosetae, from same, with detail of parts; F, Neuroseta, from same, with detail of parts. Scales = 0.2 mm for A, C; 0.1 mm for D–F.

wide without setae, and 12 segments. Most of the parapodia are broken off, with elytra missing.

**Supplementary description.**—All 12 specimens from Whale-bone site incomplete, some with developing posterior ends; figured specimen (USNM 157601) 2.5 mm long, 3 mm wide with setae, and 9 segments; largest specimen with 16 segments, plus posterior end of 3 developing segments (USNM 157597), 2.5 mm long, 2 mm wide with setae. Of 15 specimens from Channel Islands, largest specimen incomplete (USNM 157610), 8.5 mm long, 4 mm wide with setae and 25 segments.

Body flattened, with long parapodia and setae, giving aspect of pelagic form (Fig. 4A, D). Elytrophores large, bulbous, on segments 2, 4, 5, 7, continuing on alternate segments to 23, or more? Elytra mostly missing; remaining left elytron on specimen from Santa Catalina Basin, oval, with long papillae on surface (Fig. 4C), covered with foreign material, including filamentous bacteria (*Beggiatoa* sp.). Elytra remaining on specimens from Channel Islands more numerous: large, delicate, oval, with papillae scattered on surfaces and near borders, variable in size and shape, some short with clavate tips and some longer, bulbous basally, with clavate tips (Fig. 5A, B). Cirriferous segments with inconspicuous dorsal tubercles; cirrophores of dorsal cirri short, cylindrical, on posterior sides of notopodia, with styles long, extending beyond setae, papillate, with filamentous tips (Fig. 4A).

Prostomium (Fig. 4A, B) oval, deeply bilobed, wider than long, with small anterior peaks; 2 pairs of small eyes on posterior half of prostomium; median antenna with bulbous ceratophore in anterior notch of prostomium, style long, papillate, with long fil-
amentous tip; lateral antennae with bulbous ceratophores, inserted ventrally and nearly hidden from view dorsally, styles short, subulate, papillate.

Tentaculophores of segment I (Fig. 4A) lateral to prostomium, projecting anteriorly, each with small projecting acicular lobe and 2 curved notosetae on inner side, long dorsal tentacular cirrus, similar to median antenna, and shorter ventral tentacular cirrus; small rounded facial tubercle (Fig. 4B) between bases of ceratophores of lateral antennae. Segment II (Fig. 4A) with first pair of large elytrophores, biramous parapodia, and long ventral buccal cirri, attached basally lateral to ventral mouth, similar to ventral tentacular cirri.

Biramous parapodium (Fig. 4D) with notopodium shorter than neuropodium, bulbous basally, with tapering acicular process on lower side; neuropodium subconical, presetal lobe tapering to pointed acicular process, postsetal lobe shorter, rounded. Notosetae (Fig. 4D, E) numerous, forming radiating bundle, stouter than neurosetae, shorter, curved to longer, nearly straight, and nearly as long as neurosetae; shorter notosetae with up to 15 spinous pockets on curved borders and entire tips; longer notosetae with spinous pockets basally and more distally with smaller close-set spines and bifid split tips. Neurosetae (Fig. 4D, F) numerous, very long, forming fan-shaped bundles; neurosetae slender, with basal spinous pockets or spurs, finely spinous distally, tapering to slender bifid split tips. Ventral cirri (Fig. 4D) on middle of neuropodia, short, subulate, smooth.

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