Redescription and ecology of *Liponema brevicornis* (McMurrich, 1893), with definition of the family Liponematidae (Coelenterata, Actiniaria)

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Dunn, D. F. & Bakus, G. J. 1977. Redescription and ecology of *Liponema brevicornis* (McMurrich, 1893), with definition of the family Liponematidae (Coelenterata, Actiniaria). *Astarte 10*, 77–85.

The sea anemone *Liponema brevicornis* (McMurrich, 1893), which is recorded from depths of approximately 100–1000 m and lives unattached on sand, mud, and gravel bottoms, was the dominant benthic organism by number and weight at a site 135 m deep in St. George Basin, Bering Sea, Alaska. Its approximate density there was 4.2 individuals/m^2 and its distribution was nearly random. Oceanographic and sediment characteristics of this habitat are discussed. *Liponema brevicornis* is redescribed from specimens collected in Alaska, off Oregon, and in the northwest Pacific. Its singular appearance results from its reflexed, tentacle-covered oral disc. Multiple exocoelic and single endocoelic tentacles warrant its removal from family Actiniidae to family Liponematidae, defined here for the first time. It is known to contain only the genus *Liponema*, which has four nominal species.

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A survey associated with a Continental Offshore Stratigraphic Test (C. O. S. T.) was conducted 29–31 May 1976 in St. George Basin, approximately 100 nautical miles north of Dutch Harbor, Unalaska Island (Aleutian Islands), Alaska, at a depth of 135 m. The objective of the survey was to study the oceanography and marine biology of a potential drill site located at 55° 30′ 40″ N latitude, 166° 40′ 50″ W longitude. The M. V. *Mediterranean Seal,* a 50 m drillship, was used to carry out the study, which was sponsored by the Atlantic Richfield Company, North American Producing Division, South Alaska District. Chief Scientist was Dr. Gerald J. Bakus, and the Atlantic Richfield Company was represented by Mr. Dilworth W. Chamberlain, an Associate Scientist.

The most conspicuous benthic organism collected was the sea anemone *Liponema brevicornis* (McMurrich, 1893). According to Carlgren (1949), the genus *Liponema* contains four species of deep-water, high-latitude actinians. *Liponema multiporum* Hertwig, 1888, is recorded from the seas off southernmost Chile and Argentina, *L. multicornis* (Verrill, 1880) from the North Atlantic, *L. brevicirrata* Carlgren, 1928, from off South Africa, and *L. brevicornis* (McMurrich, 1893) from off California. The only published mention of *L. brevicornis* aside from its description and its listing in Carlgren's (1949) catalogue, are passing references by McMurrich (1898, 1904) and Verrill (1922).

MATERIAL AND METHODS

Oceanographic and biological data were gathered as described by Bakus (1976, 1977). Black and white (Kodak Plus X) and color (Ektachrome ER 404 Daylight) photographs of the bottom were taken.

The maximum diameter of each of 20 randomly selected preserved specimens of *Liponema brevicornis* from the C. O. S. T. survey was measured. One in every 30 color negatives of the seafloor was selected, for a total of 20 frames, and the sea anemones were counted and measured in each frame in which they appeared. Measurements in the photographs were converted into approximate real dimensions by employing known diameters of small, average, and large preserved actinians. The anemones were used as scales to figure the total area of each frame, and from this the approximate mean density of *L. brevicornis* at the C. O. S. T. site was calculated.

The redescription of *L. brevicornis* is based on a study of 14 preserved specimens collected by otter trawl at a depth of 135 m in the C. O. S. T. survey, one from 256 m off Newport, Oregon (U. S. National Museum specimen no. 53305), and 11 specimens in six lots dredged by the U. S. Fisheries Steamer *Albatross* in 1906 and now in the collection of the Department of Invertebrate Zoology, California Academy of Sciences (two from 933 m near southern Sakhalin; one from 1,019 m on Bowers Bank, Bering Sea; one from 103 m off the east coast of Kamchatka; one from 732 m between Korea and Japan; one from 549 m just north of Hokkaido; and five from 487 m just off the east coast of northern Honshu). Nematocyst measurements were taken from 12 animals of various sizes, four were dissected, and histological sections were made from seven.

RESULTS

Oceanography and ecology

Water near the seafloor (depth 135 m) had a temperature of 6.5° C, salinity of 32 ppt, and dissolved oxygen concentration of 6.0 ml O_2/l. Current speed (at 122 m) was 6.4 cm/sec and current direction was 63° magnetic. The seafloor was flat. The grey-colored sediment was 12% clay, 21% sand and 67% silt, with a mean grain diameter of 18.9 μm. Total hydrocarbon saturates recovered from sediments ranged from 0.22 μg/g-sed to 1.7 μg/g-sed, and total oils from 0.31 μg/g-sed to 2.1 μg/g-sed. There was a relatively low quantity of unresolved materials.

Liponema brevicornis was by far the dominant benthic organism, on the bases of number and weight, taken in two one-hour otter trawls. The first yielded 1,950 individuals weighing a total of 22.82 kg (11.7 g average formalin weight per individual). The second yielded 1,863 individuals weighing a total of 18.04 kg (9.7 g average formalin weight per individual). The next most abundant organisms were the seastar *Ctenodiscus crispatus*, which is common throughout the Gulf of Alaska and the Bering Sea, the commercial pink shrimp *Pandalus borealis*, and the flathead sole *Hippoglossoides elassodon*.

Liponema brevicornis also ranked first in numerical abundance in videotapes and bottom photographs. Its density in the 11 selected color negative frames in which it appeared was 7.4 individuals/m^2. Averaging that over all 20 selected frames gave a corrected approximate density of 4.2 individuals/m^2. Surprisingly, no actinians were collected by the van Veen grab sampler.

Description

Liponema brevicornis (McMurrich, 1893, p. 158)

1893. *Bolocera brevicornis* McMurrich, p. 158.
1898. *Bolocera brevicornis* McMurrich, p. 231.
1904. *Bolocera brevicornis* McMurrich, p. 257.
1922. *Bolocera brevicornis* Verrill, p. 117.
1949. *Liponema brevicornis* Carlgren, p. 55.

Habitat: This sea anemone lives unattached on the surface of sand, mud, and gravel bottoms at depths of 103–1,019 m.

Body Form and Size: This species assumes a shape unusual among actinians, but apparently characteristic of members of the genus *Liponema*. When the animal is upright, the oral disc, which is normally densely covered with tentacles, flares to twice or more the diameter of the column and overhangs the short column so that its edge is at the level of the base and substratum. The animal thus resembles a low, tentacle-covered dome (Fig. 1; see also figs. 1 and 2, Plate 3 in Carlgren 1902, and fig. 2, Plate 23 in Verrill 1922). Its

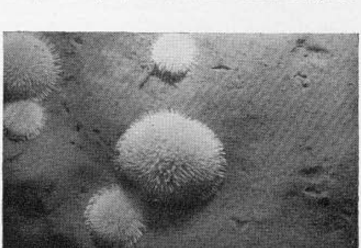

Fig. 1. *Liponema brevicornis* (McMurrich, 1893) *in situ* at –135 m, St. George Basin, Bering Sea.

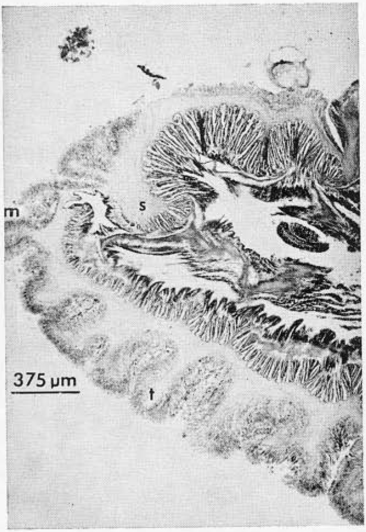

Fig. 2. Radial section through the upper column, margin and outer oral disc of *Liponema brevicornis*. m = margin, s = sphincter, t = tubercle.

height varied from 5 to 35 mm in those studied. The convex oral disc is generally flared to its edge, but in a few specimens the margin had contracted so that the greatest diameter of the animal was slightly above the margin. Maximum diameter at or just above the margin of the 26 anemones examined ranged from 11 to 105 mm. The mean diameter of the 20 randomly selected individuals used for estimating density was 37 mm, and the range was 20–69 mm. All body dimensions are probably underestimates since they were obtained from preserved animals.

Base: The firm pedal disc is circular in outline, slightly wider than the column, somewhat convex, apparently non-adhesive, and ranged in diameter from 4 to 55 mm in the animals studied. Mesenterial insertions may be visible in smaller specimens. Basilar musculature is strong. The ectoderm is rough.

Column: The texture is firm, and mesenterial insertions are not visible. The color of live and recently preserved animals is rusty orange-red. Those that have been preserved for some time may fade to a pinkish hue. The column lacks verrucae, but has radially-arranged rows of tubercles. At the margin there is a strongly thickened, smooth ridge, but no fosse. This thickening is produced by the diffuse endodermal sphincter, which appears to be weak. The endodermal circular musculature immediately below the sphincter is strong. These histological features are shown in Fig. 2.

Tentacles and Oral Disc: The color of the domed oral disc is the same as that of the column. The oval mouth is flanked by prominent ribbed lips which are the same color as the disc, but the tentacles obscure the mouth in live animals (Fig. 1). In preserved specimens, normally only a 1–2 mm wide ring of the oral disc immediately around the mouth is visible due to the dense covering of tentacles. The circular musculature of the oral disc is endodermal and the radial musculature is ectodermal (Fig. 3). The convex oral disc cannot be withdrawn and the tentacles cannot be covered.

The tentacles of preserved animals are furrowed longitudinally and are bluntly pointed. The terminal portion may be lighter in color than the rest, which is the same shade of orange as the oral disc, column, and pedal disc. Intermediate-sized anemones have inner tentacles 10–15 mm long and outer ones

Fig. 3. Radial section through the oral disc and tentacles of *Liponema brevicornis*. od = oral disc, ps = pore sphincter, ts = tentacle sphincter.

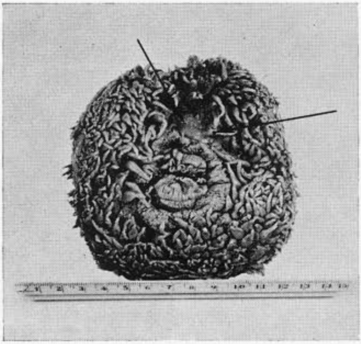

Fig. 4. Preserved specimen of *Liponema brevicornis*. Arrows indicate pores of cast-off tentacles.

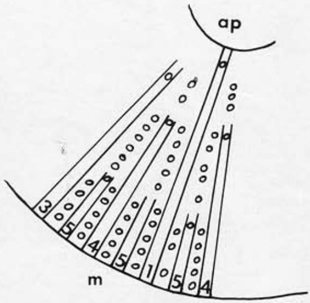

Fig. 5. Diagram of tentacle/mesentery arrangement in *Liponema brevicornis*. Circles represent tentacles, numbers refer to order of mesenteries forming the designated endocoel, ap = actinopharynx, m = margin.

4–6 mm long. The base of each tentacle is constricted to a diameter of 1–2 mm, while the maximum diameter of a long tentacle may be 4 mm. Some tentacles flare to their maximum diameter immediately above the base, then taper gradually to a point; some may be at their maximum diameter for the greater part of their length, constricting abruptly at the tips and thereby forming 'nipples'; or they might bulge only in the center, being constricted at both ends. The circular musculature is endodermal and the longitudinal ectodermal (Fig. 3).

The tentacles are deciduous (Fig. 4). Near the base of each one, just distal to the thinnest part of its wall, is a strong endodermal sphincter, which projects into the tentacle lumen (Fig. 3). Contraction of this sphincter presumably causes a break through the thin part of the tentacle about 1 mm above the surface of the disc. This proximal bit of tentacle wall remains around the opening after the tentacle is shed. There is also a strong endodermal sphincter in the oral disc around each tentacle opening (Fig. 3). When a tentacle is cast off, contraction of this muscle may constrict the pore so tightly that it is difficult to perceive.

The six tentacles nearest the mouth communicate with the primary endocoels. Only one tentacle communicates with each endocoel, except perhaps for those of the highest order present which in some cases appear to lack tentacles altogether. There are numerous tentacles per exocoel, often as many as seven. Figure 5 illustrates the typical arrangement. A moderate-sized animal has several hundred tentacles. Mesenterial insertions are not visible through the oral disc, even in small animals that have lost their tentacles.

Mesenteries and Internal Anatomy: The mesenteries are arranged in a very regular manner (Fig. 6). However, the mesenteries of a new cycle, which are added at the margin, do not always develop in synchrony, and one member of a pair may appear before there is evidence of its partner. Newly formed mesenteries grow from the margin inward along the underside of the oral disc, initially appearing as bands about a millimeter deep. A moderate-sized animal typically has at least 96 pairs of mesenteries. Of these, the primaries and secondaries are complete and sterile. The next two cycles are incomplete and fertile, and the youngest mesenteries, which seem always to have mesenterial filaments, may be fertile. In very large animals, with as many as nine cycles of mesenteries, at least some of the third, fourth, and perhaps fifth order fertile mesenteries are also complete. The sexes are apparently separate; we have found only females (in which the endoderm along each oocyte is developed into a trophonema). The regularity of its internal anatomy suggests that *L. brevicornis* does not reproduce asexually.

Fig. 6. Cross section at mid-column level of *Liponema brevicornis.*

Retractor muscles are diffuse and weak, in higher orders the mesogleal lamellae generally being shorter than the width of the central mesogleal band (Fig. 6). There is no detached flap of retractor musculature, but the parietobasilar muscles have a short detached pennon. There are small marginal and moderate-sized oral stomata.

The two shallow siphonoglyphs are the same orange color as the body, while the rest of the pleated throat is darker in hue.

Cnidom: Spirocysts, basitrichs, microbasic p-mastigophores.

Distribution and size of Nematocysts:

Tentacle tips

Spirocysts (A) (24.7)26.8 – 53.3(65.9) × 3.1 – 4.5(5.2) μm n = 67
Spirocysts (B) 39.1 – 55.6(57.7) × 5.2 – 6.6 (7.2) μm n = 34
Basitrichs (C) (17.5)18.5 – 55.6 × 2.1 – 5.2 μm n = 57
Basitrichs (D) (35.0)41.0 – 68.0(70.0) × 2.5 – 4.1 μm n = 73

Tentacle bases

Spirocysts (A) 26.8 – 39.1(43.3) × 3.7 – 5.2 μm n = 73
Spirocysts (B) 26.8 – 51.5 × 4.5 – 6.6(7.8) μm n = 40
Basitrichs (C) (15.5)16.5 – 43.3(49.4) × 2.1 – 4.1 μm n = 65
Basitrichs (D) 53.6 – 63.9 × 3.1 – 3.7 μm n = 2 (rare)

Column

Spirocysts (A) 24.7 – 41.2(43.3) × 3.1 – 4.5 μm n = 33
Spirocysts (B) (26.8)33.0 – 49.4(51.5) × (4.5) 5.2 – 6.6 μm n = 17
Basitrichs (C) 14.4 – 33.0(37.1) × 2.1 – 3.7 (4.1) μm n = 77
Basitrichs (D) (35.0)39.1 – 61.8 × 3.1 – 4.1 μm n = 29

Actinopharynx

Basitrichs (C) (16.5)18.5 – 24.7 × 2.5 – 3.7 μm n = 24 (scarce)
Basitrichs (D) (26.8)28.8 – 53.6 × 2.5 – 4.5 μm n = 177
Microbasic p-mastigophores (E) 20.6 – 28.8 (33.0) × 3.5 – 5.2 μm n = 29 (scarce)

Mesenterial Filaments

Basitrichs (C) 16.5 – 30.9 × 2.1 – 4.1 μm n = 46
Basitrichs (C) 37.1 – 47.6 × 3.7 – 6.2 μm n = 50
Basitrichs (D) (33.0)35.3 – 55.6 × 3.1 – 4.1 μm n = 85

Microbasic p-mastigophores (E) (22.7)24.7 – 33.0(35.0) × 4.1 – 5.6 μm n = 75 (scarce)

Letters refer to illustrations in Fig. 7. Measurements in parentheses are from a single nematocyst which fell outside the usual range.

Nematocysts from the inner tentacles are generally larger than those from the outer tentacles. Thus the smaller nematocysts are mostly confined to the outer tentacles. The same is true of the smaller spirocysts, but the size range of robust spirocysts (Fig. 7B) is virtually identical in inner and outer tentacles. Smaller actinians tend to have somewhat smaller nematocysts.

DISCUSSION

Not only is the habitus of this actinian unusual, but its mode of getting about on the unconsolidated sediments of the seafloor is noteworthy. In order to move, it apparently draws the pedal disc up above the level of the margin, possibly while contracting the sphincter muscle which, because of the reflexed nature of the oral disc, tends to draw the margin downward and inward. This produces a barrel-shaped animal which can roll about on the sea bottom (Fig. 8). This was rarely seen in photographs, and the videotapes showing such specimens rolling suggest that they were being pushed by the pressure head

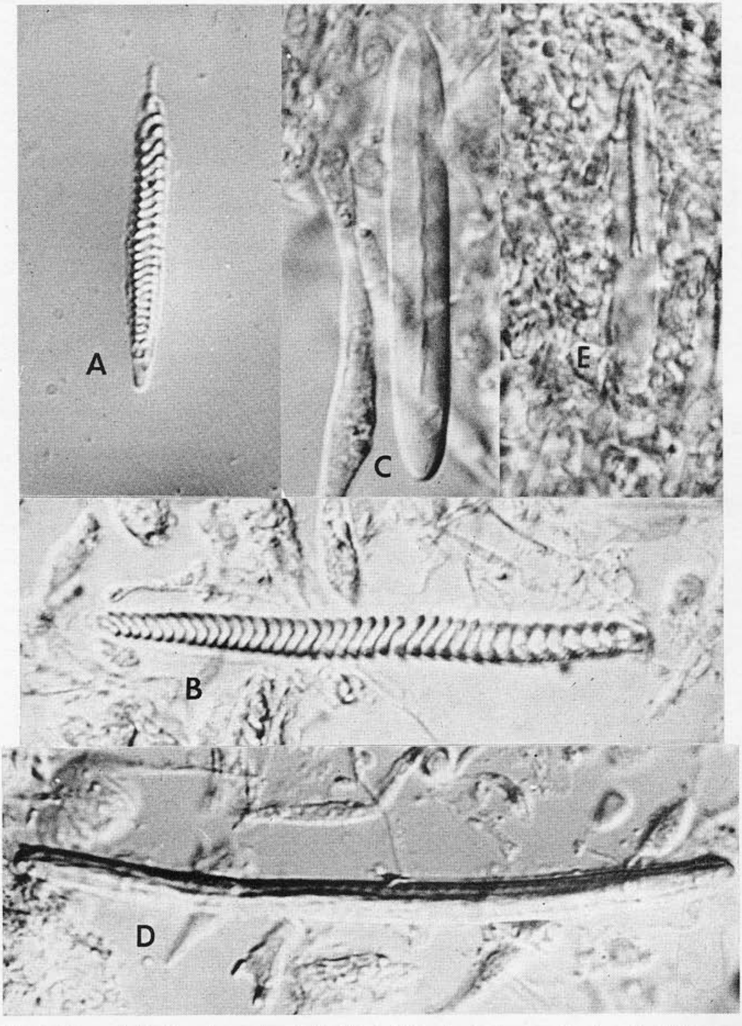

Fig. 7. Spirocysts (A, B) and nematocysts (basitrichs C, D; microbasic p- mastigophore E) of *Liponema brevicornis*. (Nomarski interference contrast).

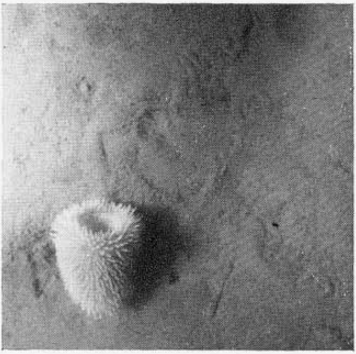

Fig. 8. *Liponema brevicornis* rolling on the sea-floor at –135 m.

created by the frame holding lights and cameras.

Although *Liponema brevicornis* may have a mean density approximating four individuals per square meter, its distribution is patchy since only about half of the examined negatives showed this species. Using Morisita's distribution index, $\frac{\Sigma ni\,(ni-1)}{N(N-1)}$, it was found that the distribution of *L. brevicornis* (+0.12) is near the borderline between random and slight aggregation. The variance to mean ratio (+1.94), although sensitive to sample size, indicates the same distribution pattern (see Grassle *et al*. 1975). Bottom photographs and videotape records show no consistent grouping of individuals by size. Videotapes occasionally show a shallow circular imprint in the sediments, indicating the former position of a sea anemone. No anemones were observed feeding on macroscopic prey.

Data from the National Marine Fisheries Service (1948–1975), listing the four dominant species at each station by catch weight, suggest that *Liponema brevicornis* occurs in relatively large numbers in the area 55°–58° N, 164°–170°W, at depths of 46–152 m. The rank occurrence of an unspecified actinian with other benthic organisms, in decreasing order based on number of stations, included the tanner crab and eelpouts, flathead sole, seastar (probably *Ctenodiscus crispatus*), pollock, rock sole, king crab, Pacific cod, whelks, yellow-fin sole and sculpins. Our collections of species associated with *L. brevicornis* conform very closely with this list. Therefore, based on these data as well as depth and abundance, we believe that most of the sea anemones recorded from this area by the National Marine Fisheries Service were *Liponema brevicornis*.

McMurrich's (1893) description of *L. brevicornis* was accurate in most respects. He described the pedal disc as 'adherent', but there was no indication that the two specimens he studied were in fact attached to anything. He speculated that verrucae might be present on the upper column, but the irregularities are actually tubercles. There is no second sphincter although the upper column muscle processes are long. In order to fit the unique anatomy of this species into the common actinian pattern, McMurrich (p. 159) suggested that 'abortive (or incipient?) mesenteries' occur between normal pairs of mesenteries in 'an attempt . . . to preserve the relation of mesenteries to tentacles which is usually found'. He was thereby able to reconcile this species with the genus *Bolocera*. Actually, the 'abortive' mesenteries were probably the beginnings of the highest order mesenteries that extend along the underside of the oral disc.

Verrill (1880) also originally described *Liponema multicornis* as a species of *Bolocera*, probably because of the deciduous tentacles. However, the distinctive external anatomy soon led him (1922) to propose the new genus *Eubolocera* for *Bolocera multicornis*, and he suggested that *Bolocera brevicornis* was similar. The tentacle-covered disc was also recognized as unusual by D. C. Fish who, in 1913, labeled the *Albatross* specimens that we studied as *Discosoma anemone* (a synonom for *Stoichactis helianthus*). In fact, the arrangement of tentacles in *L. brevicornis*, with one per endocoel and many in most exocoels, is just the converse of that in stoichactids, which have one per exocoel and many per endocoel.

Hertwig (1888) described the genus *Liponema* for the species *L. multiporum* (erroneously listed by Carlgren [1949] as *L. multipora*) which he believed to have tentacles that were extraordinarily reduced in length and in which the terminal pore was disproportionately large. McMurrich (1893) recognized that Hertwig had been dealing with individuals which had lost all their tentacles, and that what he had called tentacles were actually the raised rims about each opening through the oral disc. McMurrich therefore called Hertwig's species *Bolocera multipora*.

Carlgren (1928) stated that *Liponema brevicirrata* has only single exocoelic tentacles. This explains his placement of the genus *Liponema* among the Actiniidae (e.g. 1928, 1933, 1949). However, it is clear from our study and Hertwig's (1888) description of *L. multiporum*, type species of the genus, that the tentacular arrangement of members of this genus does not conform to that of any currently recognized family of endomyarian actinians.

In 1882, Hertwig (a, b) erected a family Liponemidae for the anemones *Polysiphonia tuberosa* and *Polystomidia patens*, both of which were new genera and species, taken by the *Challenger*. These species have since been placed in families Exocoelactiidae and Actiniidae, respectively (Carlgren 1949). It was not until 1888 that Hertwig defined the genus *Liponema*, although he referred to it in 1885 without a specific epithet. Carlgren (1949) gave a date of 1882 for that genus, but there is no mention of the name on the page cited nor in any of Hertwig's 1882 papers based on *Challenger* material (a, b, c). Volume 4 of *Nomenclator Zoologicus* (Neave 1940) listed Hertwig's 1888 supplement to his earlier report on *Challenger* material as the source of the name *Liponema*. Therefore, the family name Liponemidae was unavailable when proposed, not having been based on a then-valid name of a contained genus (Article 11e, International Code of Zoological Nomenclature). It became available with Hertwig's (1888) listing of the generic name *Liponema* under family Liponemidae, but lacks an explicit definition since the 1882 description is without standing.

Although it has no bearing on the question of availability, Hertwig's family name Liponemidae was incorrectly derived, according to Article 29 of the International Code of Zoological Nomenclature. The genitive singular of the ending of the name of the type genus *Liponema* is 'nematos', the stem of which is 'nemat-', and so the family name must be Liponematidae. Since the incorrect family-group name is not in general current use, it may be corrected (Article 29d, International Code of Zoological Nomenclature).

We therefore propose recognition of the family Liponematidae, of which *Liponema* is the only currently included genus, and define it as follows:

Thenaria (Endomyaria) with well-developed pedal disc. Column smooth or with tubercles. Endodermal sphincter diffuse to circumscribed, not very strong. Tentacles many, simple, with an endodermal sphincter allowing them to be cast off, usually more than one communicating with each exocoel, one with each endocoel (or none in the highest order?). Two siphonoglyphs. Mesenteries not divisible into macro- and microcnemes.

Detailed taxonomic study of the three other nominal species of *Liponema* would be very interesting, particularly from a zoogeographical standpoint. One species is recorded from off South Africa, one from off South America, one from the North Pacific and one from the North Atlantic. The genus thus exhibits taxonomic bipolarity *sensu* Ekman (1953). Carlgren (1933) implied that there may be only a single species in the northern hemisphere, but he did not explain the source of his data for a map showing a circumpolar distribution for *Liponema multicornis*. The same could also be true of the southern hemisphere, or it might even be that a single species is distributed antipodally. Possible support for the last hypothesis is the curious fact that the station list (Murray 1895), but not Hertwig's (1888) description, identified a third *Challenger* specimen as *Liponema multiporum* – this one from the North Pacific.

ACKNOWLEDGEMENTS

The following companies are acknowledged for support of this study: Ameralda Hess, Atlantic Richfield Co., Cities Service, Exxon USA, Gulf Energy and Minerals, Mobil Exploration, Phillips Petroleum, Skelly Oil Co., Sun Co., Inc., Texaco, Inc., AMOCO Production Co., BP Alaska Exploration, Continental Oil Co., Getty Oil Co., Marathon Oil Co., Penzoil Co., Shell Oil Co., Standard of California, Tenneco Oil Co., Union Oil. Co. of California. We thank Mr. Dilworth W. Chamberlain (Atlantic Richfield Co., Los Angeles), Dr. Edward Noda, Mr. Gregory Smith, Mr. Nick Mueller (Tetra Tech, Inc.), Mr. Pete Sloan (U. S. Geological Survey, Anchorage), and Capt. Maurer and the crew of the M. V. *Mediterranean Seal* for helping with the collections. We are grateful to Dr. Frederick M. Bayer, U. S. National Museum, for loan of a specimen, and Drs. Arthur Furst and Thomas S. Acker, University of San Francisco, and Kian-Joe Lie, University of California, San Francisco, for use of facilities and equipment. We thank Mr. Chamberlain, Dr. June Lindstedt-Siva, Atlantic Richfield Co., Los Angeles, Dr. Paul Falls, Atlantic Richfield Co., Anchorage, Dr. Cadet Hand, University of California, Berkeley, and Dr. Frederick L. Dunn for reading the manuscript. This research was supported in part by NSF grant DEB 76-82277 to DFD.

REFERENCES

Bakus, G. J. 1976. Oceanography and marine biology of St. George Basin, Bering Sea. *Tetra Tech Report TC-683* (October 1976). 189 pp.

Bakus, G. J. 1977. Marine Research in Alaska (1975–1976). V. 4. Current Research, pp. 39–49. 28th Alaska Science Conference, Alaska Division. AAAS. Anchorage, Alaska. September 22–24, 1977.

Carlgren, O. 1902. Die Actiniarien der Olga-Expedition. *Wiss. Meeresunters. Helgoland n. f. 5*, 33–56.

Carlgren, O. 1928. Actiniaria der Deutschen Tiefsee-Expedition. *Deutsche Tiefsee-Exped. 1898–1899* 22, 125–266.

Carlgren, O. 1933. The Godthaab Expedition 1928. Zoantharia and Actiniaria. *Meddr. Grønland 79* (8), 1–55.

Carlgren, O. 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. *K. svenska VetenskapsAkad. Handl.* Ser. 4, *1* (1), 1–121.

Accepted 1 October 1977

Ekman, S. 1953. *Zoogeography of the Sea.* Sidgwick and Jackson, Ltd., London. 417 pp.

Grassle, J. F., Sanders, H. L., Hessler, R. R., Rowe, G. T. & McLellan, T. 1975. Pattern and zonation: a study of the bathyl megafauna using the research submersible *Alvin. Deep-Sea Res. 22*, 457–481.

Hertwig, R. 1882a. *Die Actinien der Challenger-expedition.* Gustav Fischer, Jena. 119 pp.

Hertwig, R. 1882b. Report on the Actiniaria dredged by H. M. S. Challenger during the years 1873–1876. *Sci. Res. Voy. H. M. S. Challenger, Zool. 6* (1), 1–136.

Hertwig, R. 1882c. Die Tiefseeactinien des Challenger. *Sitzungsber. jenaischen Ges. Med. Naturwiss.* 1881, 10–13.

Hertwig, R. 1885. Deep-sea Actiniaria. *Sci. Res. Voy. H. M. S. Challenger, Narrative 1*, 574–576.

Hertwig, R. 1888. Report on the Actiniaria dredged by H. M. S. Challenger during the years 1873–1876, supplement. *Ibid., Zool. 26* (3), 1–56.

McMurrich, J. P. 1893. Report on the Actiniae collected by the United States Fish Commission steamer Albatross during the winter of 1887–1888. *Proc. U. S. natn Mus. 16*, 119–216.

McMurrich, J. P. 1898. Report on the Actiniaria collected by the Bahama Expedition of the State University of Iowa, 1893. *Bull. Lab. nat. Hist. State Univ. Iowa 4*, 225–249.

McMurrich, J. P. 1904. The Actiniae of the Plate Collection. *Zool. Jahrb.*, Suppl. 6, 215–306.

Murray, J. 1895. A summary of the scientific results, parts 1 and 2. *Rpt. Sci. Res. Voy. H. M. S. Challenger.* 1608 pp.

National Marine Fisheries Service. 1948–1975. Alaska NMFS exploratory fishing drags. Part 4. Bering Sea. U. S. Department of Commerce. Continuing series.

Neave, S. A. (ed.) 1940. *Nomenclator Zoologicus*, vol. 4. Zoological Society of London, London. 758 pp.

Verrill, A. E. 1880. Notice of recent additions to the marine invertebrates of the northeastern coast of America, with descriptions of new genera and species, and critical remarks on others. Part I. *Proc. U. S. natn Mus. 2*, 165–205.

Verrill, A. E. 1922. The Actiniaria of the Canadian Arctic Expeditions, with notes on interesting species from Hudson Bay and other Canadian localities. *Rpt. Can. Arct. Exped. 1913–1918 7* (G), 89–164.