PELAGIC POLYCHAETES OF THE PACIFIC OCEAN

BY

R. PHILLIPS DALES

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PELAGIC POLYCHAETES OF THE PACIFIC OCEAN

BY

R. PHILLIPS DALES

INTRODUCTION

VERY LITTLE is known about the distribution of the pelagic polychaetes in the Pacific Ocean. Nearly all the expeditions that have collected pelagic polychaetes have been made in the Mediterranean, Atlantic, and Antarctic regions. Only three published works have dealt in any detail with collections made in the Pacific. The earliest of these was Izuka's (1914) short account of the species found near the Misaki Marine Station in Japan. Chamberlin's (1919) report of the polychaetes brought back by the *Albatross* expedition provides the most substantial contribution to our knowledge of the Pacific forms, and Treadwell's (1943) account of those collected during the last cruise of the *Carnegie* has extended our knowledge of the distribution of some of these species. Treadwell (1928) also records some Pacific species from the earlier, but much smaller collection made during the *Arcturus* expedition. Kinberg (1866), Claparède (1870), McIntosh (1885), and Rosa (1907, 1908*b*), while describing specimens collected mainly in Atlantic waters, also give a few records of pelagic species from the Pacific.

In this paper an attempt has been made to review all those species of pelagic polychaetes that have been found in the Pacific Ocean, and to provide keys and illustrations to aid in their identification. Included in the keys are species that occur elsewhere but have not yet been recorded from the Pacific.

Most of the animals described and illustrated in this paper were sorted from the plankton samples taken in the northeast Pacific as part of the Marine Life Research Program of the University of California, Scripps Institution of Oceanography. The Marine Life Research (MLR) Program is the Scripps Institution's component of the California Coöperative Oceanic Fisheries Investigations, a project sponsored by the Marine Research Committee and carried out coöperatively by the Scripps Institution, the Bureau of Marine Fisheries of the California Department of Fish and Game, the South Pacific Fishery Investigations of the United States Fish and Wildlife Service, the Hopkins Marine Station of Stanford University, and the California Academy of Sciences. All the samples which form the basis of the present work were collected during the first year's cruises (1949–1950) of the MLR Program.

The plankton samples were taken over a wide area, during the early part of the investigations from Cape Disappointment, Oregon (about 47° N.), to Pt. San Eugenio, Mexico (about 27° N.), a distance of about 3,000 km. and offshore for about 800 km. Usually three ships were used simultaneously over adjacent sections of the area explored so that for each cruise the plankton samples were collected over this area in a relatively short time. Each ship worked along equally spaced lines, which ran approximately at right angles to the coast, and took

plankton samples at ten equally spaced positions on each line. The distance between lines was about 250 km. Each operation with three coöperating research vessels took about a fortnight and was repeated monthly.

These plankton hauls were primarily intended to measure quantitatively the amount of animal life within 75 m. of the surface. Many species of pelagic polychaetes are known to be quite numerous at greater depths, or to occur only below 75 m., so that the idea of the distribution of some species obtained in this work is necessarily incomplete. That the sampling was repeated at intervals over the same area, however, makes the present survey unique, and since many night hauls were made, some of the deeper living and vertically migrating species were also likely to be collected. Oblique net-tows were taken from a depth of about 75 m., using a net 5 m. long supported by a ring 1 m. in diameter, and with mesh-apertures nominally 0.65 mm. across. The volume strained at each haul varied from 500–1,000 m^3, as measured by a current meter suspended in the center of the opening of the net. Physical data were taken also at each position.

Much additional information incorporated in this paper has been obtained from a study of collections made by members of the Hopkins Marine Station, Pacific Grove, California, in connection with work on Office of Naval Research contract No. N6onr-25127, project NR 163-901, in Monterey Bay. Much deeper hauls were taken in this work and many species were found in these collections which are not represented in the MLR samples (Dales, 1955*b*, 1956).

The whole collection of polychaetes, together with labeled specimens of all species found in the MLR samples, has been deposited in the British Museum (Natural History) in London. As far as possible, duplicate sets of representative specimens of each species have been deposited also in the U.S. National Museum, Washington, D.C., the Allan Hancock Foundation, University of Southern California, and the Scripps Institution of Oceanography, La Jolla.

All the preliminary sorting was done at the Scripps Institution of Oceanography in the laboratory of Professor Martin W. Johnson, whom I wish to thank for making the samples available to me for study, and for many other courtesies during my stay in La Jolla. I am grateful to the institutions engaged in the MLR Program for kindly supplying the collecting data. I am also greatly indebted to Dr. C. Støp-Bowitz for many helpful discussions concerning the taxonomy of pelagic polychaetes. Thanks are also due to Miss J. Kjennerud for kindly allowing me to examine, when in Bergen, the type-specimen of the Støp-Bowitz genus *Watelio,* and to Mr. Norman Tebble, of the British Museum (Natural History), for help in many ways. Finally, I wish to thank Dr. Remington Kellogg and Dr. Fenner Chace, of the Smithsonian Institution, U.S. National Museum, Washington, D.C., for kindly sending me many of Treadwell's type-specimens, and Dr. Olga Hartman of the Allan Hancock Foundation for most helpful criticism of the typescript.

DESCRIPTION OF PELAGIC POLYCHAETES OCCURRING IN THE PACIFIC

FAMILY PHYLLODOCIDAE Grube

All the pelagic phyllodocids are small, ranging in length from 1 mm. to 3 cm. The prostomium bears four short antennae and at most a single pair of eyes. The latter tend to be reduced in the genus *Lopadorhynchus*. The proboscis is eversible, and is either simple or provided with a pair of small lateral digitiform papillae. *Phalacrophorus* is exceptional in having jaws. The first two or three segments bear tentacular cirri, and the more posterior segments bear uniramous parapodia with foliaceous dorsal and ventral cirri. The chaetae are mostly compound, but heavy acicular chaetae may also occur, especially in the anterior segments. The pygidium bears two anal cirri.

Of the three groups of pelagic phyllodocids only the Lopadorhynchinae are represented in the MLR collections. Most of the species belonging to the other subfamilies, the Iospilinae and the Pontodorinae, are very small and probably frequently overlooked. Treadwell (1943) has found *Iospilus* and *Phalacrophorus* in the Pacific, and it seems quite likely that the other genera may be found there as well.

Genus *Lopadorhynchus* Grube

Prostomium broad, with two eyes and four antennae, but without palps. Two pairs of well-developed tentacular cirri and a third pair of smaller cirri sometimes also present. Parapodia uniramous; chaetae of two kinds: a simple, often heavy, acicular type, mostly restricted to the anterior segments of which the first two or three may bear only this kind, and longer compound chaetae with flattened, lanceolate endpieces. Parapodial cirri foliaceous, but ventral cirri absent from the first two chaetigerous segments in the subgenus *Lopadorhynchus*, although present in subgenus *Prolopadorhynchus*. Proboscis with two small papillae arising from the sides and provided with at least three large glands.

Lopadorhynchus (*Lopadorhynchus*) *uncinatus* Fauvel

(Figs. 1–5)

Lopadorhynchus uncinatus Fauvel, 1915, 1916, 1923, 1932, 1936; Monro, 1936, 1937; Treadwell, 1936; Wesenberg-Lund, 1939; Støp-Bowitz, 1948; Dales, 1955*b*; *Lopadorhynchus varius* Treadwell, 1943.

Specimens up to 25 mm. in length but mostly 12 mm. or less. Prostomium very broad, and extended laterally into a pair of antennae. A second, much-shorter pair arise ventrally, and may be seen only from the ventral side lying on either side of the mouth. Two eyes and three pairs of tentacular cirri, the two more anterior pairs of similar length and projecting beyond the tips of the antennae; third pair arising ventrally and much shorter than the others. First two chaetigerous segments swollen, with simple chaetae only, unlike the following segments which bear compound chaetae only; four to six simple, thick, curved chaetae in each parapodium of first two segments, bases of chaetae partly surrounded by a membranous collarlike expansion of the chaetigerous lobe. Compound chaetae with broad bladelike endpiece slightly serrated toward base of thicker edge. Ventral cirri absent from first two segments; third and following segments with both dorsal and ventral cirri.

Treadwell's (1943) *Lopadorhynchus varius* is certainly a young *L. uncinatus;* the prostomium has the shape characteristic of this species, and in his type-speci-

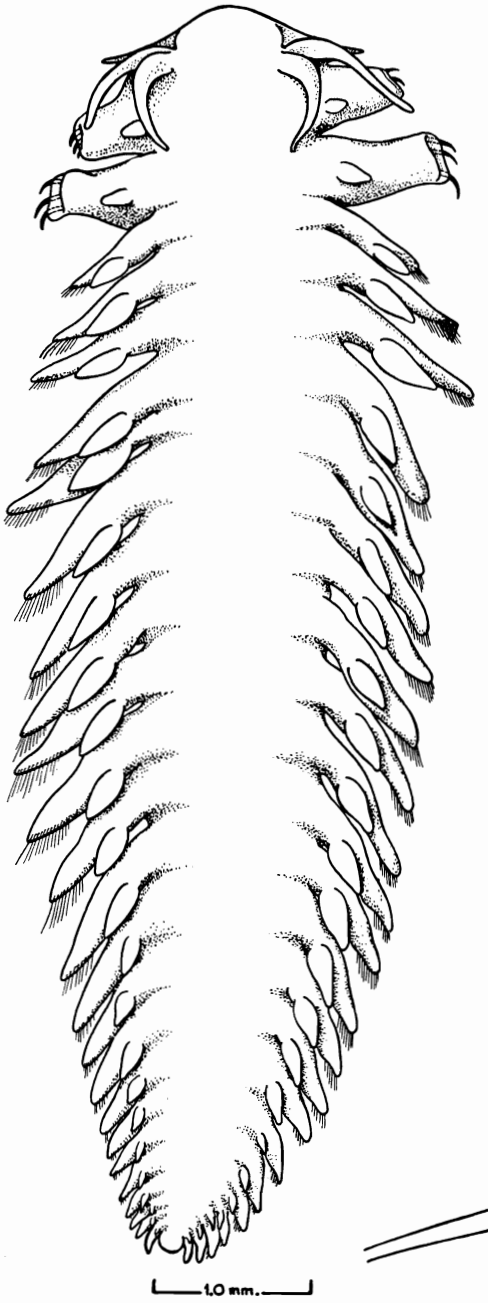

Fig. 1. *Lopadorhynchus uncinatus*, dorsal view.

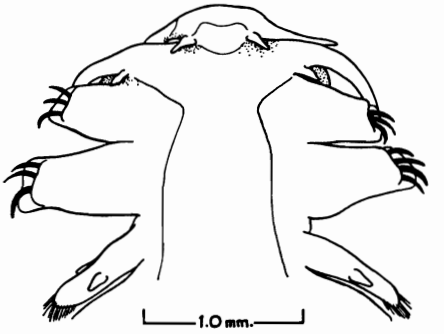

Fig. 2. *Lopadorhynchus uncinatus*, ventral view of the anterior region of the body.

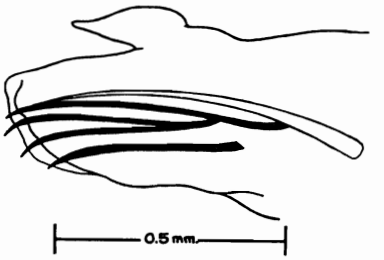

Fig. 3. *Lopadorhynchus uncinatus*, parapodium from the first chaetigerous segment.

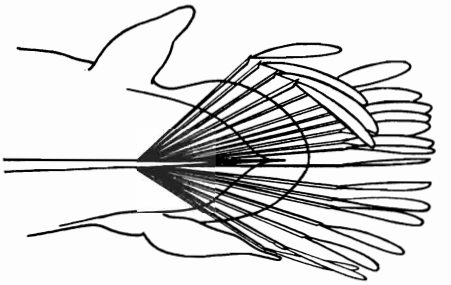

Fig. 4. *Lopadorhynchus uncinatus*, parapodium from the posterior region of the body.

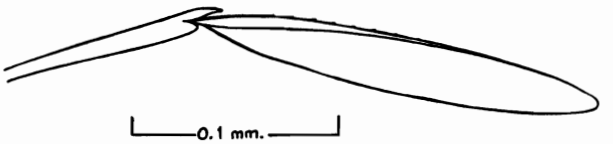

Fig. 5. *Lopadorhynchus uncinatus*, compound chaeta.

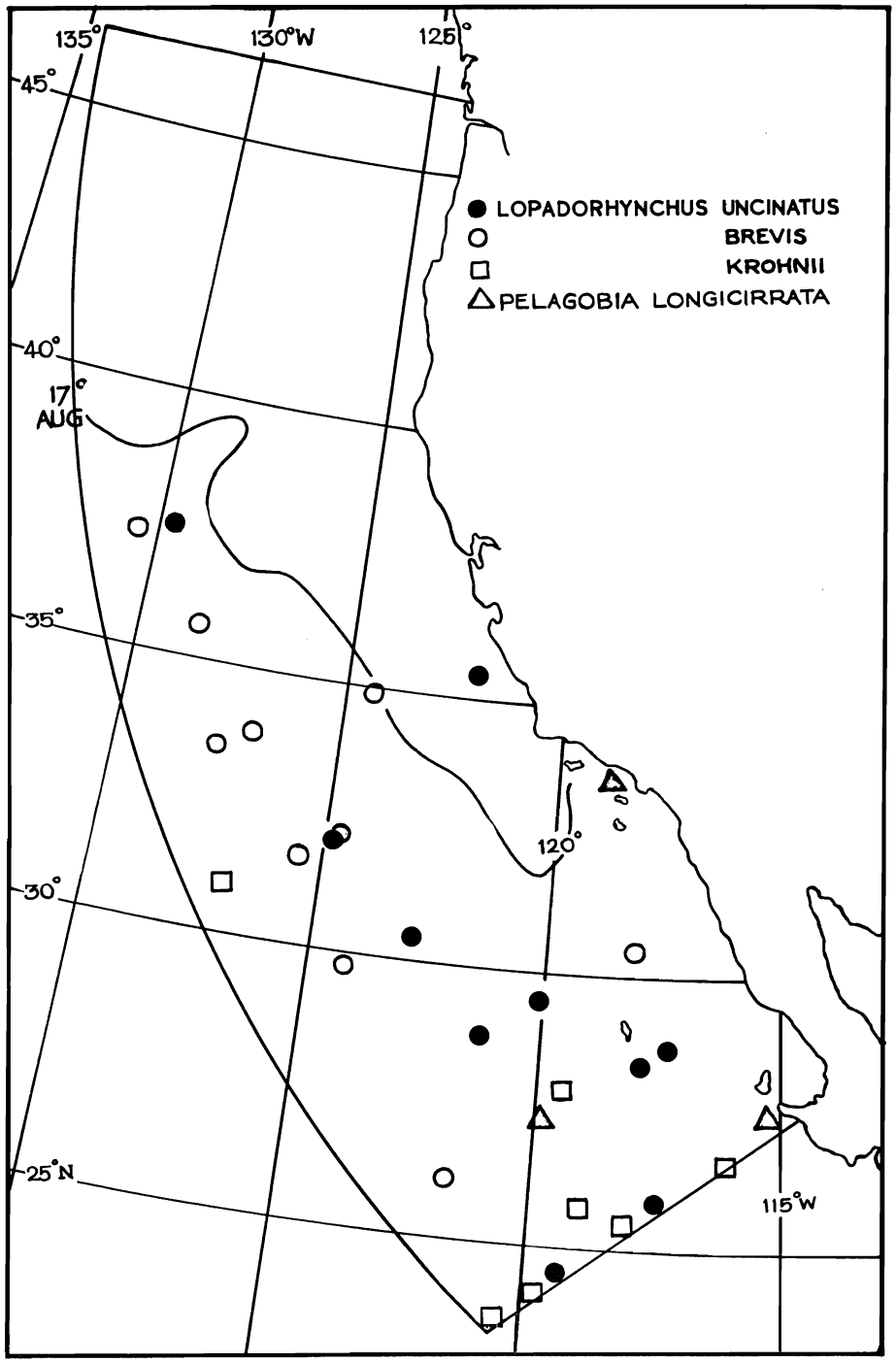

Fig. 6. Locality records of *Lopadorhynchus uncinatus, L. brevis, L. krohnii,* and *Pelagobia longicirrata.* Surface isotherm.

men the collars embracing the bases of the thick, simple chaetae of the first two segments can be clearly seen.

Distribution.—Treadwell collected his specimens from various localities in the Pacific, both north and south of the equator, as well as from the Atlantic. His type-specimen of *L. varius* was collected at 21° 18′ N., 138° 36′ W. The locality records off the coast of California are shown in figure 6. All the ten specimens collected were taken singly on different occasions between July and November in water of maximum surface temperature of 24° C., and a minimum temperature at a depth of 75 m. of about 10° C. Dales (1955*b*) found it occasionally in the deeper hauls made in Monterey Bay. Wesenberg-Lund (1939) found *L. uncinatus* to be the commonest species of *Lopadorhynchus* in the Medi-

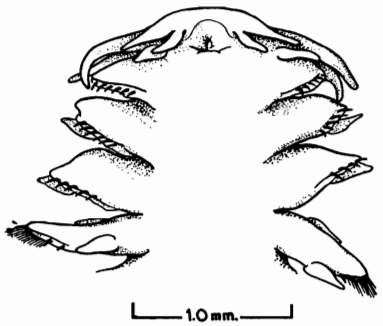

Fig. 7. *Lopadorhynchus brevis*, ventral view of the anterior region of the body.

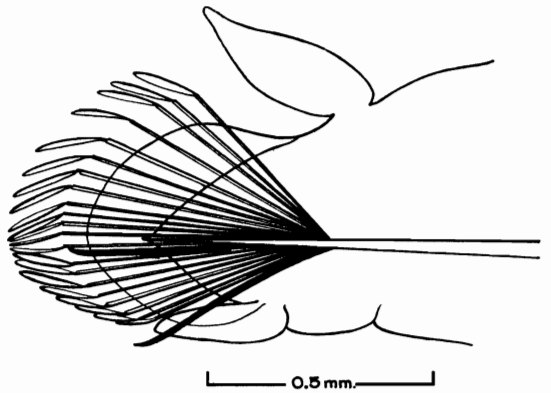

Fig. 8. *Lopadorhynchus brevis*, parapodium from the 7th segment.

terranean, and Støp-Bowitz (1948) found it widely distributed in the North Atlantic. Monro (1936) previously described it from the South Atlantic and Fauvel (1915, 1916, 1932) collected it from the Indian Ocean, so that the species seems to be cosmopolitan. In the Pacific, Treadwell (1943) found it in Japanese waters, off the Gilbert and Ellice Islands, in the Peruvian basin, and off central Mexico.

Lopadorhynchus (*Lopadorhynchus*) *brevis* Grube

(Figs. 7 and 8)

Lopadorhynchus brevis Grube, 1855; Levinsen, 1885; Lo Bianco, 1904; Ehlers, 1913; Bergström, 1914; Fauvel, 1923; Monro, 1930, 1937; Wesenberg-Lund, 1939; Støp-Bowitz, 1948; *Lopadorhychus parvum* Chamberlin, 1919.

About 17 mm. in length; shape of head much the same as *L. uncinatus*, and prostomium with two pairs of antennae characteristic of genus; ventral pair much smaller than dorsolateral. Three pairs of tentacular cirri; the most anterior, longest; third pair much shorter and visible only fom ventral side. Eyes more or less obscured in many specimens. First three segments rather stouter and also a little narrower than the following, and without ventral cirri, but with simple, curved chaetae only, these occurring in diminishing numbers in each of the segments following, usually two, widely separated, in the ventral part of the sheaf of chaetae in each segment behind the sixth.

Distribution.—Eleven specimens were collected during June to September cruises, in water ranging from a minimum temperature at 75 m. depth of about

11° C. to a maximum surface temperature of 22° C. (fig. 6). A further series was collected during the investigation of diurnal variation in quantity of plankton collected at one station (34° 53′ N., 124° 30′ W.), during October; all were taken at night in water with temperatures between 9.6° C. and 17.6° C. Wesenberg-Lund (1939) found this species in the Mediterranean and in the Bay of Biscay, but Støp-Bowitz (1948) did not find it in the collections brought back by the *Michael Sars* from the North Atlantic. However, Lo Bianco (1904) found it off the Spanish coast, and Ehlers (1913) and Monro (1930) took specimens from the tropical parts of the Atlantic. Chamberlin's *L. parvum* may be a young *L. brevis* as Støp-Bowitz (1948) suggests, since Chamberlin's specimens were all very small (4–5 mm.), and differed from *L. brevis* only in the absence of eyes. These specimens were found off the Mexican coast (15° 58′ N., 98° 13′ W.), but apart from this there are no previous records from the Pacific.

Lopadorhynchus (*Lopadorhynchus*) *errans* (Chamberlin)

Mastigethus errans Chamberlin, 1919; Støp-Bowitz, 1948.

Resembling *L. brevis*, but differing in the absence of ventral cirri from the fourth as well as from the first three chaetigerous segments.

Chamberlin (1919) excluded his single specimen from the genus *Lopadorhynchus* on the basis of two characters: (1) the presence of papillae on the sides of the proboscis (a character certainly characteristic of the genus *Lopadorhynchus*), and (2) the presence of branched outgrowths, which he described as nuchal organs. The presence of such complicated nuchal organs seems unlikely, and Chamberlin's drawing is very reminiscent of *Lopadorhynchus* parasitized by a copepod (see, for instance, Støp-Bowitz, 1948, fig. 11).

Distribution.—Chamberlin collected his single specimen at 0° 04′ S., 117° 07′ W.

Lopadorhynchus (*Lopadorhynchus*) *krohnii* (Claparède)

(Figs. 9 and 10)

Hydrophanes Krohnii Claparède, 1870; Viguier, 1886; *Lopadorhynchus Viguieri* Reibisch, 1895; Ehlers, 1913; *L. krohnii* Kleinenberg, 1886; Bergström, 1914; Fauvel, 1923; Wesenberg-Lund, 1939; *L. krohnii* var. *simplex* Monro, 1930.

Mostly about 3 mm. long; some 7 or 8 mm. in length. Front of prostomium more rounded than in *L. uncinatus* and eyes relatively prominent. Antennae and tentacular cirri with arrangement typical for genus. Species distinguished by rather stouter and narrower first two chaetigerous segments, which are provided with simple chaetae only, and without ventral cirri; third chaetigerous segment with ventral cirri and compound chaetae.

Fauvel (1923) and Wesenberg-Lund (1939) mention that the third segment and the segments following have a single simple chaeta in the ventral part of the parapodium, but the third parapodium of these specimens seems to bear only compound chaetae. These specimens, therefore, correspond with Monro's (1930) variety *simplex*, he also having found specimens without simple chaetae in the third and more posterior segments, from the South Atlantic. Monro's specimens also attained a length of 8 mm.

This species is easily confused with young *L. uncinatus*, but differs in the more rounded prostomium and the absence of the collars embracing the heavy chaetae

of the first two segments so distinctive of *L. uncinatus*. The first two chaetigerous segments of *L. krohnii* are also distinctly narrower than the following, which is generally not so in *L. uncinatus*.

Distribution.—Only seven specimens were collected, singly, and at all seasons, but only where the temperatures were fairly high; minimum 12.2° C. at 75 m. depth, maximum 23.0° C. at the surface (fig. 6). This species has been found on several occasions in the Mediteranean, most recently by Wesenberg-Lund (1939). Outside the Mediterranean it has been found in the equatorial Atlantic (Reibisch, 1895), and in the Indian Ocean (Ehlers, 1913). It does not appear to have been collected previously from the Pacific.

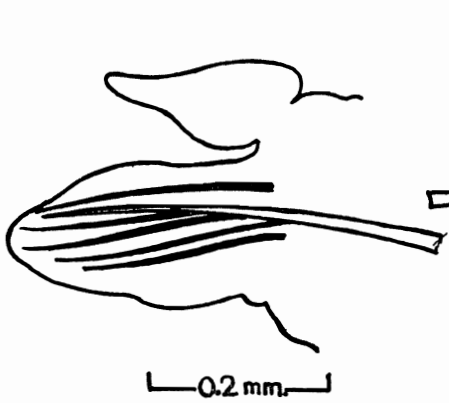

Fig. 9. *Lopadorhynchus krohnii*, parapodium from the 1st chaetigerous segment.

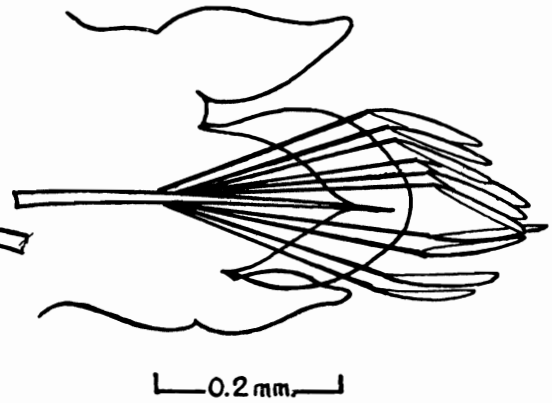

Fig. 10. *Lopadorhynchus krohnii*, parapodium from the posterior region of the body.

Lopadorhynchus (*Prolopadorhynchus*) *nationalis* Reibisch

Lopadorhynchus nationalis Reibisch, 1895; Ehlers, 1913; Fauvel, 1916, 1923, 1951; Wesenberg-Lund, 1939; Støp-Bowitz, 1948; *Prolopadorhynchus nationalis* Bergström, 1914; *Lopadorhynchus nans* Chamberlin, 1919; Treadwell, 1936, 1943.

7–11 mm. in length, with about twenty-five chaetigerous segments. First three pairs of parapodia stouter and narrower than those following, with simple acicular chaetae only, and provided with ventral, as well as dorsal cirri. Fourth chaetigerous segment with many simple chaetae in the ventral part of the sheaf, and in the fifth and more posterior segments one or two simple chaetae among the compound chaetae.

Støp-Bowitz (1948) thinks that Chamberlin's (1919) species *L. nans* found off Peru may be conspecific with *L. nationalis*. Treadwell found specimens, which he attributed to Chamberlin's species, widely distributed in the South Pacific.

Distribution.—Chamberlin's (1919) single specimen was collected at 17° 55′ S., 87° 42′ W. Apart from Treadwell's (1943) subsequent finds, all records attributed directly to *L. nationalis* are from the warmer parts of the Atlantic where it seems to be confined to the surface waters; Wesenberg-Lund (1939) found it in the Mediterranean only during the summer months; that it has not been found in the cold waters of the northeast Pacific is not surprising.

Genus *Pelagobia* Greeff

Prostomium with two pairs of antennae. Two pairs of tentacular cirri clearly representing the dorsal and ventral cirri of the first segment, which is chaetigerous. Parapodia uniramous, with long digitiform dorsal and ventral cirri, except for the second segment in which the dorsal cirrus is reduced or absent. Chaetae all compound, with serrated and flattened endpieces. Proboscis simple.

Pelagobia longicirrata Greeff

(Figs. 11–13)

Pelagobia longicirrata Greeff, 1879*a;* Viguier, 1886; Reibisch, 1893, 1895, 1905; Southern, 1909; Bergström, 1914; Ehlers, 1912, 1913; Fauvel, 1916, 1923, 1936, 1951; Okuda, 1937, 1938; Augener, 1929; Monro, 1936; Støp-Bowitz, 1948, 1949; Williams, 1954; Dales, 1955*b;* *Pelagobia Viguieri* Gravier, 1911; Chamberlin, 1919; Benham, 1921, 1927; Treadwell, 1943; Uschakov, 1952.

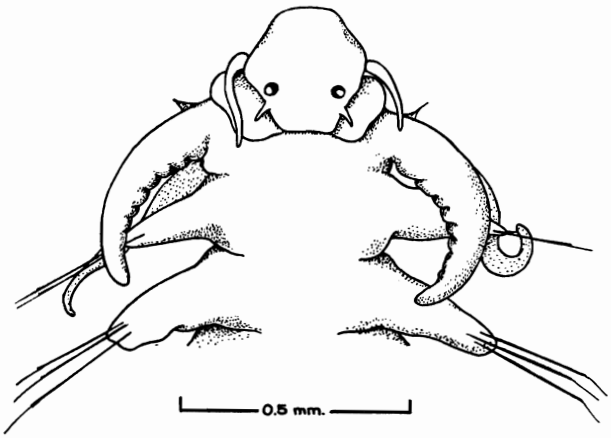

Fig. 11. *Pelagobia longicirrata,* dorsal view of the anterior region of the body.

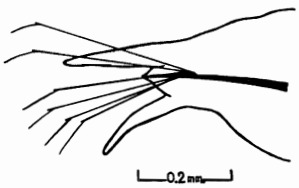

Fig. 12. *Pelagobia longicirrata,* parapodium.

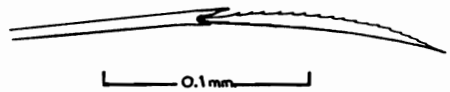

Fig. 13. *Pelagobia longicirrata,* chaeta.

Up to 12 mm. in length. Prostomium with two pairs of very short antennae, and closely applied to the first segment, which bears two pairs of cirri of equal length and some short chaetae. First two pairs of parapodia lack dorsal cirri, but the third and following pairs of parapodia with relatively long dorsal and ventral cirri. Each parapodium bears a sheaf of compound chaetae in which the distal part is clearly serrated.

Distribution.—This species has been found throughout the Atlantic from Greenland to the Antarctic, in the Mediterranean and Indian Ocean, as well as in the Pacific, where it seems to be widespread (Chamberlin, 1919; Okuda, 1937, 1938; Treadwell, 1943; Uschakov, 1952; Dales, 1955*b*). Only six specimens were found in the MLR collections, but this is probably due to others having been overlooked

in sorting (fig. 6). Dales (1955*b*) found it to be fairly numerous in Monterey Bay. These specimens were all collected during the summer in water temperatures ranging from 11° C. at 75 m. depth to 20° C. at the surface.

Genus *Maupasia* Viguier

Prostomium with four antennae, but without palps. Three pairs of tentacular cirri contributed by the first two segments both of which bear short chaetae, the third segment bearing long heterogomph chaetae. Parapodia uniramous with lanceolate or foliaceous dorsal cirri, and similar, though smaller, ventral cirri. All the chaetae are compound and have long, slender, simple endpieces. Proboscis simple.

Maupasia gracilis (Reibisch)

Haliplanes magna Southern, 1909; *H. gracilis* Reibisch, 1893, 1895; Bergström, 1914; *Maupasia magna* Bergström, 1914; *Haliplanella pacifica* Treadwell, 1943.

Prostomium rounded with four antennae of which the dorsal pair is slightly longer. Without eyes, and distinguished from other species by the very long dorsal cirri of the second segment, the collarlike form of the nuchal organs, and the foliaceous cirri of the more posterior segments.

The genus *Maupasia* includes rather broad, short-bodied worms seldom exceeding 3 or 4 mm. in length. *Maupasia gracilis* may be distinguished from *M. coeca* by the broader cirri and by the nuchal collar.

I can find no significant difference between Treadwell's (1943) type-specimen of *Haliplanella pacifica* and previous descriptions of *Maupasia gracilis*. Treadwell described his small specimen, which is less than 2 mm. long, as having only one pair of antennae, but there are actually two, the slightly shorter ventral pair being so closely applied to the dorsal that they can hardly be distinguished. Southern (1909) also found that the ventral antennae were hard to detect, and only one pair is shown in his drawing of the dorsal aspect of this species. Although one of the very long dorsal cirri of the second segment is missing, there is no doubt that Treadwell's specimen is conspecific with Southern's species.

Distribution.—Apart from Treadwell's (1943) specimens found in the South Pacific and the west-central Pacific, this species has not been found elsewhere in this region; all previous records are from the central Atlantic.

Genus *Iospilus* Viguier

Prostomium without antennae, but with two small palps. Two pairs of tentacular cirri, the hinder pair being the longer and related to the first chaetigerous segment. The following two chaetigerous segments have parapodia lacking dorsal and ventral cirri. Chaetae all compound. Proboscis simple.

Iospilus phalacroides Viguier

Iospilus phalacroides Viguier, 1886; Lo Bianco, 1904; Fauvel, 1916, 1923; *Phalacrophorus niger* Treadwell, 1943.

Closely resembling *Phalacrophorus*, but more robust and with dark chromatophores scattered over the dorsal surface of the body, and without jaws in the proboscis.

Treadwell's (1943) *Phalacrophorus niger* is certainly an *Iospilus*, and I can find no significant difference between his type-specimen and Fauvel's description of *I. phalacroides*. Treadwell's specimen has large dark chromatophores and is opaque, but the unarmed proboscis of *Iospilus* was clearly visible on clearing in cedarwood oil.

Distribution.—Most of Treadwell's (1943) specimens were collected off Peru and southeast of Easter Island, but one was found in equatorial waters off the Gilbert Islands.

Genus *Phalacrophorus* Greeff

Prostomium without antennae but provided with recognizable, although small, palps. Two pairs of tentacular cirri representing the dorsal cirri of the first two segments, the second bearing chaetae. Parapodial cirri small; the chaetae all compound, with simple endpieces. Proboscis unique in this family in bearing a pair of simple jaws.

Phalacrophorus pictus Greeff

Phalacrophorus pictus Greeff, 1879*a;* Viguier, 1886; Reibisch, 1895; Ehlers, 1913; Fauvel, 1916, 1923, 1936; Augener, 1929; Støp-Bowitz, 1951; ? *P. borealis* Reibisch, 1895; *P. maculatus* Treadwell, 1943.

Body long, slender, transparent when preserved, apparently in life with a thin scattering of reddish or brownish chromatophores. Most specimens 3–6 mm. long. *P. pictus* may be distinguished from *P. uniformis* by having only the first four segments with rudimentary parapodia.

Treadwell's (1943) *P. maculatus* collected during the *Carnegie* expedition is certainly conspecific with *P. pictus*. *P. borealis* Reibisch (1895) may well be merely a young *P. pictus*.

Distribution.—This species has been found in the Mediterranean and Atlantic, and has been collected more recently in the South Atlantic off Rio de Janeiro (Støp-Bowitz, 1951). Treadwell's (1943) specimens were found throughout the Pacific, in Japanese waters as well as off the coasts of California and Peru. His type-specimen (*P. maculatus*), which alone I have seen, was collected at 0° 52′ N., 81° 14′ W.

Phalacrophorus uniformis Reibisch

Phalacrophorus uniformis Reibisch, 1895; Ehlers, 1913; Fauvel, 1916, 1923; *P. attenuatus* Treadwell, 1943.

Very similar to *P. pictus* in appearance, although it may be rather longer (up to 10 mm. in length), and may be distinguished by the large number of anterior segments with rudimentary parapodia; there being 8–10 in *P. uniformis*.

Treadwell's (1943) type-specimen of *P. attenuatus* is identical with *P. uniformis*.

Distribution.—Treadwell (1943) found many specimens during the *Carnegie* expedition, mostly in samples from the equatorial and southern Pacific. His type-specimen (*P. attenuatus*) came from 8° 05′ N., 178° 48′ W.

Family ALCIOPIDAE Ehlers

All the members of this family are pelagic. Although typically transparent creatures, some have brownish pigment scattered over the dorsal parts of the body, especially in the anterior region. The eyes, which are usually very large, are red in life, but turn brown when preserved in formalin. Many species, which are otherwise colorless, have patches of brown pigment at the bases of the parapodia (the "segmental glands"). Alciopids are mostly very delicate, slender animals, and are rarely found complete; most of them may be identified from a head fragment. Some species, however, do not break up so easily. Many are very small,

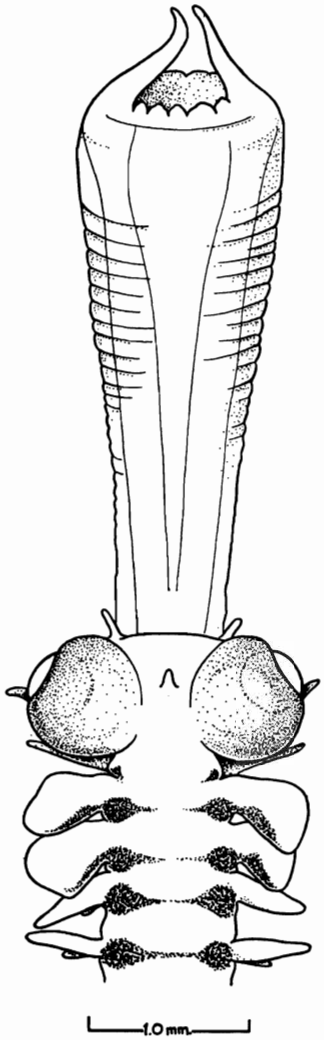

Fig. 14. *Torrea candida,* dorsal view of the anterior part of the body (female).

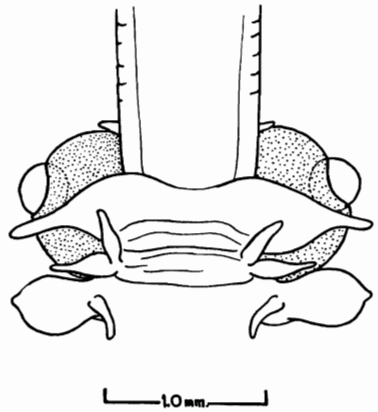

Fig. 15. *Torrea candida,* ventral view of the most anterior segments (female).

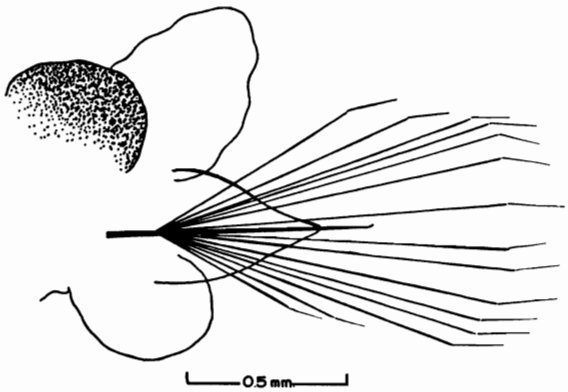

Fig. 16. *Torrea candida,* parapodium.

but others quite conspicuous. Unlike the pelagic phyllodocids they usually have five prostomial antennae. For a discussion of the evolution and relationships of the genera in this family, see Dales, 1955*a*.

Genus *Torrea* Quatrefages

Body long, slender; prostomium not projecting in front of the eyes, and with a single median antenna and two pairs of frontal antennae, the ventral pair longer. Eyes large and directed sideways. Three pairs of tentacular cirri corresponding to the first three segments, the first pair longest. The following two segments chaetigerous, although the parapodia reduced; in females the dorsal cirri of these segments enlarged to form receptacula seminis. Third and following chaetigerous segments with deeply pigmented segmental glands linked by bands of pigment

across the dorsal side of the body in each segment. Parapodia uniramous, with foliaceous dorsal and ventral cirri; chaetigerous lobe without a terminal cirriform appendage, and with slender compound chaetae only. Proboscis long, terminating in two simple hornlike processes, the rim between them papillate.

Torrea candida (Delle Chiaje)

(Figs. 14–16)

Alciopa candida Delle Chiaje, 1828; Krohn, 1845; *Alciopa vittata* Hering, 1860, 1892; *Liocapa vertebralis* Costa, 1864, 1867; Ehlers, 1864; Claparède, 1868; *L. candida* Levinsen, 1885; *Asterope candida* Claparède, 1870; Greeff, 1876; Apstein, 1900; Lo Bianco, 1904; Fauvel, 1907, 1916, 1923, 1932, 1939; Izuka, 1914; Fyfe, 1952; *Torrea vitrea* Quatrefages, 1850; *Torea vitrea* Quatrefages, 1865; *T. candida* Benham, 1929; Monro, 1930; Wesenberg-Lund, 1939; Støp-Bowitz, 1948; Dales, 1955*b*.

Up to 25 cm. long and 2–3 mm. broad. Distinguished by the dark segmental glands in each segment linked by dark pigment over the back, giving the species a striped appearance. Chaetigerous lobe without cirriform appendage and with long, slender, compound chaetae only. Proboscis long, with a pair of long horns at the end with papillae on the rim between, distinguishing the species from *T. pelagica*.

Distribution.—This species is widespread in the MLR area, although usually only one or two specimens were found in a single sample. The species has been found in the MLR samples collected throughout the year (fig. 17). The temperature of the water in which these specimens have been taken ranges from a minimum of about 10° C. at 75 m. depth to a maximum of 23° C. at the surface.

Torrea candida abounds in the Mediterranean and the Atlantic. It has been found also in the Indian Ocean and in Japanese waters, but Chamberlin (1919) did not find it in the collections made from the *Albatross* nor did Treadwell (1943) identify it in the collections brought back by the *Carnegie*.

Torrea pelagica Chamberlin

Torea pelagica Chamberlin, 1919; Treadwell, 1943.

Differing from *T. candida* in the form of the proboscis which has no papillae between the terminal horns. Parapodial cirri are also rather different in shape from those of *T. candida*, and the median prostomial antenna is longer.

Distribution.—Chamberlin (1919) found several specimens between Easter Island and Peru; his type-specimen was collected at 17° 55′ S., 87° 42′ W. Treadwell (1943) later found the species in the northwest Pacific.

Genus *Naiades* Delle Chiaje

Body relatively short, inflated, transparent. Prostomium not projecting in front of the eyes, which are not as large as in many alciopids and relatively widely separated. Two pairs of frontal antennae, and a median antenna between the eyes; three pairs of tentacular cirri contributed by the first three segments. Three segments following with reduced parapodia and with acicula only. The first of these segments in females with dorsal cirri, and to some extent the ventral cirri, modified as receptacula seminis. Segmental glands dark, small; parapodia with foliaceous cirri, the chaetigerous lobe without cirriform appendage and with simple capillary chaetae only. Proboscis short, bell-like, with two short lateral horns on the rim.

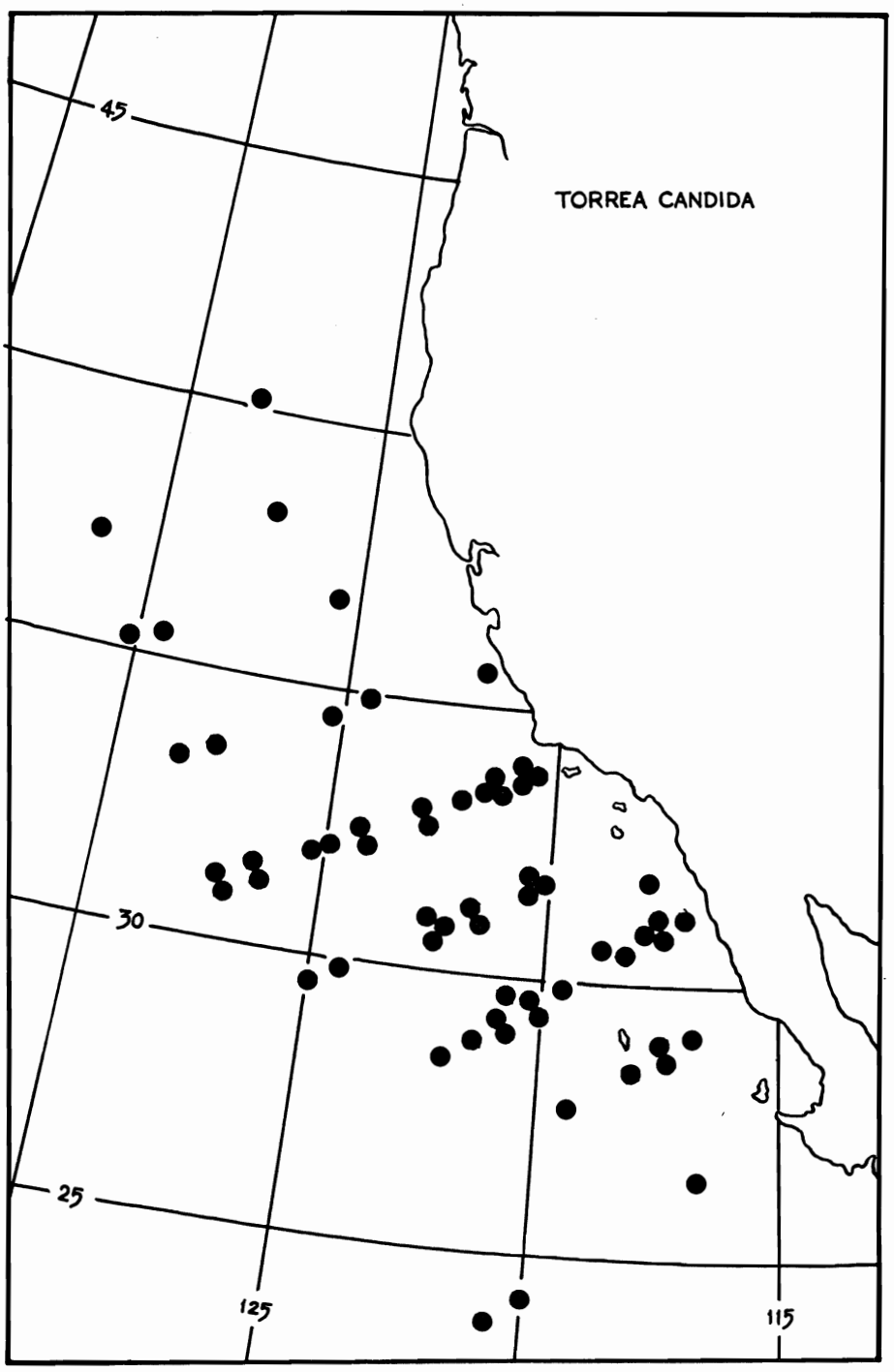

Fig. 17. Locality records of *Torrea candida*.

Naiades cantrainii Delle Chiaje

(Figs. 18 and 19)

Naiades Cantrainii Delle Chiaje, 1828; Støp-Bowitz, 1948; *Alciopa Reynaudii* Krohn, 1845; *A. Edwardsi* Krohn, 1847; Grube, 1850; Hering, 1860, 1892; *A. cantrainii* Greeff, 1876; Apstein, 1900; Lo Bianco, 1904; Izuka, 1914; Fauvel, 1916, 1923; Chamberlin, 1919; Benham, 1929; Monro, 1930, 1936; Wesenberg-Lund, 1939; Fyfe, 1952; *A. distorta* Treadwell, 1943; *Alciope microcephala* Viguier, 1886; *Krohnia Edwardsi* Quatrefages, 1865; *Liocapa vitrea* Costa, 1862.

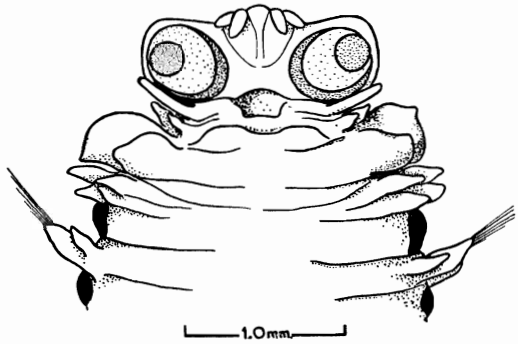

Fig. 18. *Naiades cantrainii,* ventral view of the anterior region of the body (female).

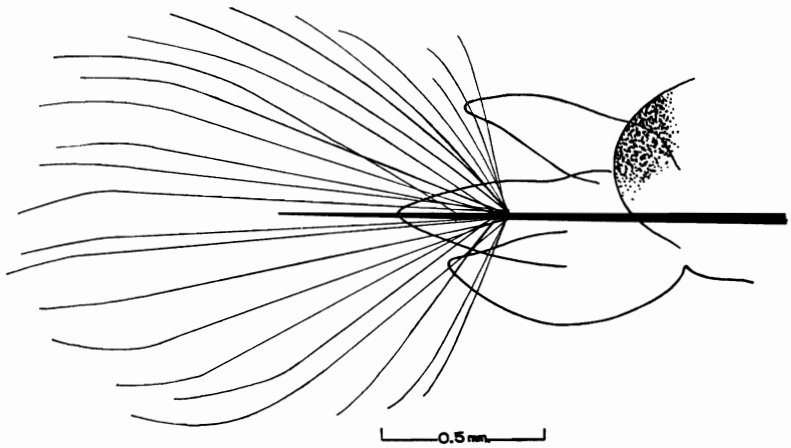

Fig. 19. *Naiades cantrainii,* parapodium.

Naiades cantrainii is the only known species belonging to this genus. The first pair of rudimentary parapodia has been interpreted as representing the second and third pairs of tentacular cirri by some early workers, since only the first pair of cirri is prominent, the following two pairs are exceedingly minute and easily overlooked. Treadwell's (1943) *Alciopa distorta* is certainly conspecific with this species. His type-specimen was collected from 24° 02′ N., 144° 33′ W.

Distribution.—Although one of the most numerous of the pelagic polychaetes found in the MLR samples, *Naiades cantrainii* has been rarely recorded before in the Pacific. Chamberlin (1919) found only one, and Treadwell (1943), only a few, one between California and Hawaii, the others over the Peruvian basin and

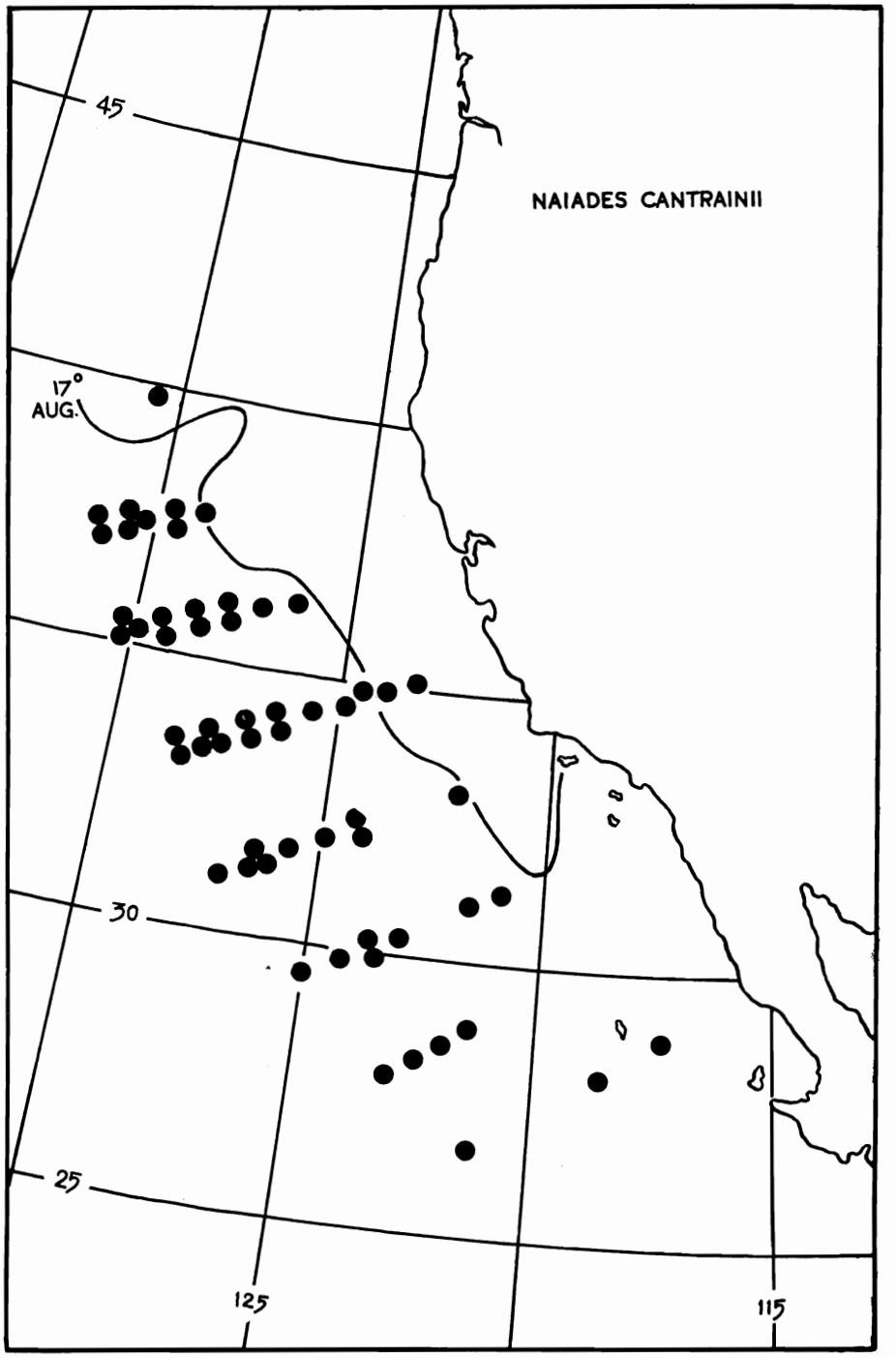

Fig. 20. Locality records of *Naiades cantrainii*. Surface isotherm.

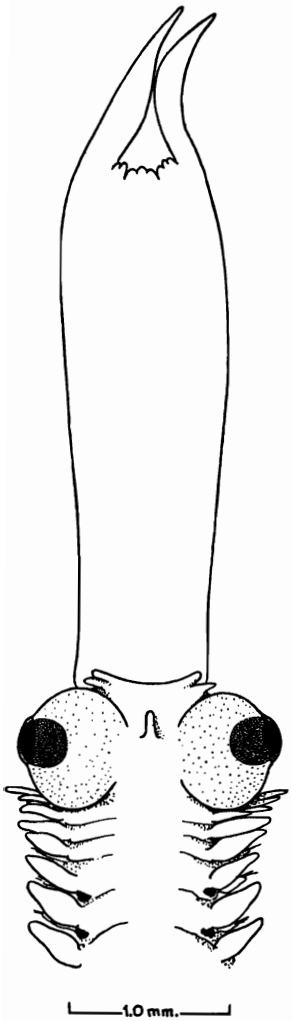

Fig. 21. *Vanadis formosa*, dorsal view of the anterior region of the body (male).

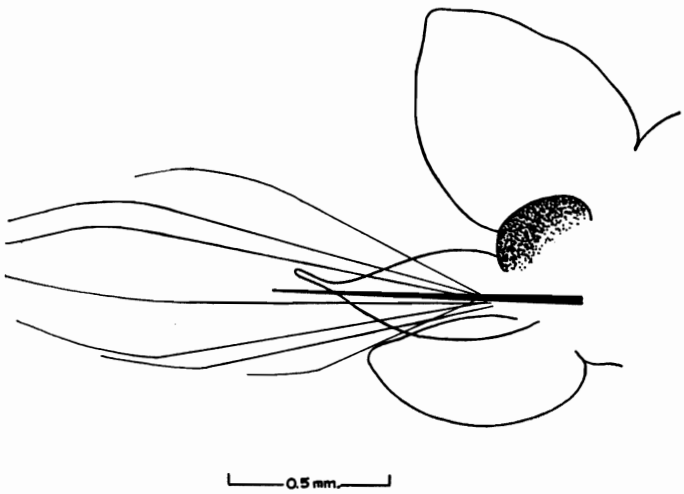

Fig. 22. *Vanadis formosa*, parapodium.

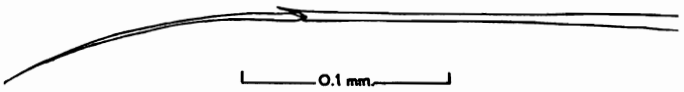

Fig. 23. *Vanadis formosa*, chaeta.

off the Tuamotu Islands. It is widely distributed in the Atlantic. In the MLR samples this species was found singly, or at most three or four specimens in any one sample, but it was found throughout the year in water with extreme surface temperatures of 12° to 20° C. (fig. 20).

Genus *Vanadis* Claparède

Body long, slender, often extremely so, and usually transparent. Prostomium not projecting in front of the eyes, and with two pairs of frontal antennae, the ventral somewhat longer than the dorsal; between the eyes, a single median antenna, which may be long, digitiform, or much reduced. Eyes large; often almost contiguous dorsally, with a tendency to be directed downward. There are usually three, sometimes four pairs of tentacular cirri. Females with second,

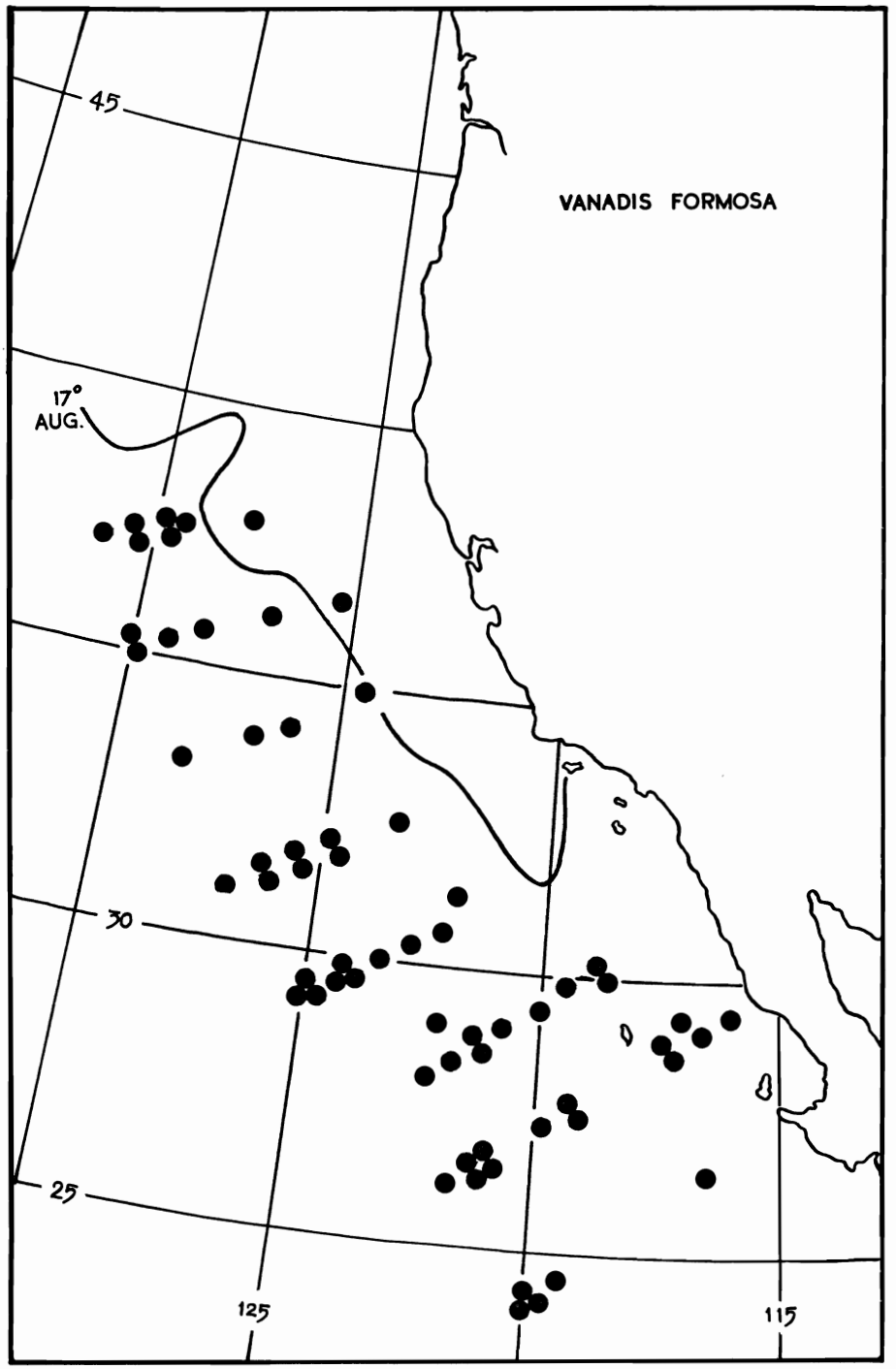

Fig. 24. Locality records of *Vanadis formosa*. Surface isotherm.

first and second, or second and third segments following those contributing the tentacular cirri, with dorsal cirri modified as receptacula seminis; parapodia of these and following segments otherwise greatly reduced or rudimentary. Segmental glands often dark, conspicuous; parapodia with foliaceous cirri, chaetigerous lobe terminating in a single cirriform appendage. Only slender, compound chaetae. Proboscis long.

Vanadis tagensis Dales

Vanadis tagensis Dales, 1955*b*.

Distinguished by the tentacular cirri, of which there are four pairs, two pairs apparently occurring on the third segment, and the proboscis, which is unique in having two pairs of short lateral horns on the rim.

Distribution.—None has been found in the MLR samples, which probably indicates that this species occurs only at depths greater than 75 m., the species having been described from samples taken in Monterey Bay from a depth of 500–1,000 m.

Vanadis formosa Claparède

(Figs. 21–23)

Vanadis formosa Claparède, 1870; Apstein, 1900; Lo Bianco, 1904; Southern, 1911; Fauvel, 1916, 1923, 1932, 1939; Chamberlin, 1919; Monro, 1930, 1936, 1937; Wesenberg-Lund, 1939; Støp-Bowitz, 1948, 1951; *V. Greeffiana* Grube, 1877; *V. pelagica* Greeff, 1876; *V. longicauda* Apstein, 1891; *V. uncinata* Treadwell, 1943; *Alciopa Krohnii* Hering, 1860, 1892.

Distinguished by the third parapodial segment with chaetae and normal dorsal and ventral cirri, although without a segmental gland, the first of which occurs on the segment following. First two parapodial segments in females with dorsal cirri modified as receptacula seminis; anterior to these, three pairs of tentacular cirri, the first of which is the longest. Prostomium with two pairs of frontal antennae; the more ventral slightly longer than dorsal, and a single median antenna between the eyes. Eyes looking obliquely downward. Proboscis long and terminating in two prominent horns; rim between raised into trilobed papillae.

I cannot find any significant difference between Treadwell's (1943) *V. uncinata* and Claparède's (1870) description of *V. formosa*. Chamberlin (1919) and Støp-Bowitz (1948) have suggested that Treadwell's (1906) *V. fusca punctata* is also conspecific with *V. formosa*, but Treadwell (1943) himself afterward regarded his *V. fusca punctata* as conspecific with *V. minuta*.

Distribution.—This is certainly one of the commonest alciopids off the coast of North America, and has been collected during the MLR investigations at all seasons (fig. 24). This species is never abundant, however, and usually only one or two specimens were found in any one sample. The temperature of the water in which specimens have been found ranges from 10° to 21° C., but few have been found in water at a temperature below about 12° C. None was found in Monterey Bay (Dales, 1955*b*). This species has been collected all over the world; Wesenberg-Lund (1939) found it the commonest alciopid in the Mediterranean. Chamberlin (1919) found many specimens in the *Albatross* collections, most of these having been collected off Peru. Treadwell's (1943) *V. uncinata* was taken at 14° 07′ S., 111° 50′ W., and most of his specimens also came from the Peruvian basin, but one was found between the Marianas and the Marshall Islands, and Claparède's original specimen was collected near Formosa, as the specific name implies.

Vanadis crystallina Greeff

(Figs. 25–27)

Vanadis crystallina Greeff, 1876; ? Apstein, 1900; Fauvel, 1916, 1923, 1932; Monro, 1936; Wesenberg-Lund, 1939; Støp-Bowitz, 1948; Chapman and Dales, 1954; *V. cristallina* Lo Bianco, 1904; Granata, 1911*a*; ? *V. augeneri* Benham, 1929; Fauvel, 1951; ? Fyfe, 1952; *V. collata* Treadwell, 1928.

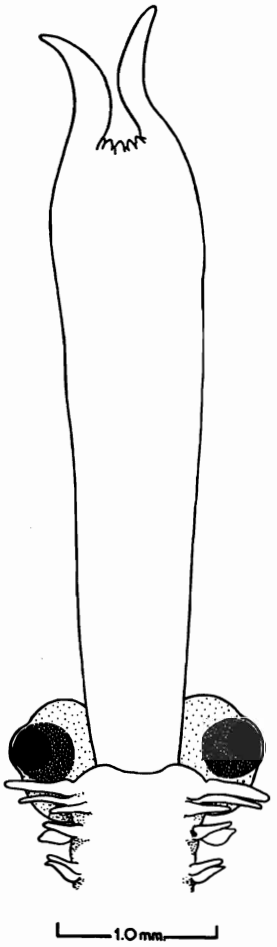

Fig. 25. *Vanadis crystallina*, ventral view of the anterior region of the body (male).

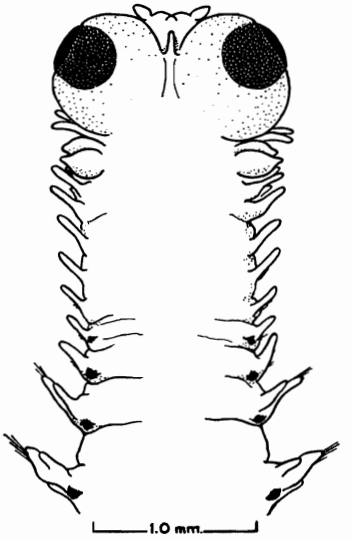

Fig. 26. *Vanadis crystallina*, dorsal view of the anterior region of the body (female).

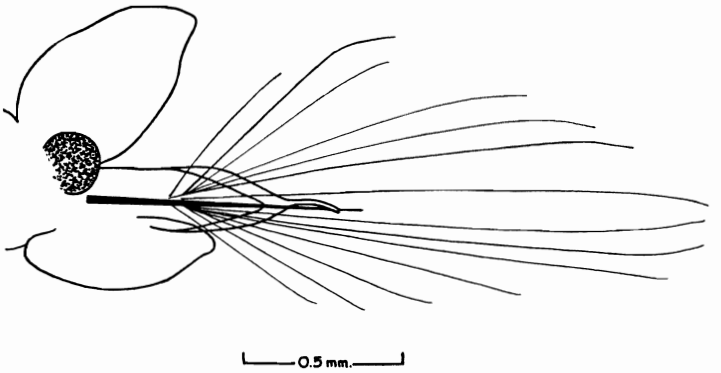

Fig. 27. *Vanadis crystallina*, parapodium.

Small; usually only 1–2 mm. across, sometimes as much as 3 mm. across and 8 cm. in length. Two pairs of small frontal antennae, the more ventral, longer, and a short digitiform antenna, often rather difficult to detect. Eyes very large and directed obliquely downward. Three pairs of tentacular cirri; the most posterior, smallest. First five parapodial segments with rudimentary parapodia; the dorsal cirri of the first two pairs modified as receptacula seminis in females; the ventral cirri also sometimes much swollen. Pigmented glands recognizable from the seventh parapodial segment posteriorly. Proboscis long, with terminal horns and trilobed papillae in-between, as in *V. formosa*, although often not as well developed as in this latter species.

Vanadis crystallina and *V. minuta* have probably been confused in the past, so that many of the earlier records of *V. crystallina* may actually refer to *V. minuta*. For example, Wesenberg-Lund's (1939) drawing (fig. 22) certainly refers to *V. minuta*, and this means that *V. minuta* occurs in the Mediterranean. Støp-Bowitz (personal communication) has since found it in the Atlantic, and it is widely distributed in the Pacific. Lo Bianco's (1904) drawing of *V. crystallina* might also be a *V. minuta*. Treadwell's (1928) description and illustrations of *V. collata* agree fairly well with *V. crystallina* Greeff; Treadwell's specimen was collected during the *Arcturus* expedition in the Galápagos region at 2° 0′ S., 89° 30′ W.

In view of the confusion between the two species, *V. minuta* and *V. crystallina*, a comparison of their contrasting characters is given below. I am indebted to Dr. Støp-Bowitz for originally drawing my attention to some of these differences.

Vanadis crystallina	*Vanadis minuta*
Median antenna digitiform.	Median antenna reduced or absent.
Receptacula seminis developed from dorsal cirri of first two parapodial segments.	Receptacula seminis developed from dorsal cirri of second parapodial segment only.
Pigmented segmental glands on 7th segment posteriorly; glands rounded.	Pigmented segmental glands on 4th segment posteriorly; anterior glands at least, vertically attenuated.
Proboscis long, with trilobed papillae between the horns.	Proboscis relatively much longer; without papillae between the horns.
Cirriform appendage of chaetigerous lobe relatively long.	Chaetigerous appendage small.

Distribution.—This species is by no means uncommon in the MLR samples, and has been collected at all seasons (fig. 28), although only one or two specimens were ever found in any one sample. Most have been collected in water with temperatures about 11° C. at 75 m. depth, and 20° C. at the surface. Apart from Treadwell's (1928) specimen mentioned above, this species has not been found elsewhere in the Pacific.

Vanadis minuta Treadwell

(Figs. 29 and 30)

Vanadis minuta Treadwell, 1906, 1943; Støp-Bowitz, 1948, 1951; ? *V. ornata* Greeff, 1876; *V. crystallina* Wesenberg-Lund, 1939 (in part); ? Apstein, 1900; *V. fusca punctata* Treadwell, 1906, 1936, 1943; ? *Alciopa longirhyncha* Greeff, 1885; ? *A. candida* Hering, 1892.

Mostly 1–2 mm. across; most striking feature perhaps dark segmental glands extending farther forward (first on the 4th parapodial segment) than in *V. crystallina*, giving the species a decidedly punctate appearance; number of rudimentary parapodia as in *V. crystallina*; proboscis-rim between lateral horns, simple.

Treadwell (1906) described two new species, *Vanadis minuta*, and *V. fusca punctata*, but later (1943) concluded that they were conspecific. In this later paper, Treadwell preferred the name *V. fusca punctata*, but as *V. minuta* has since been described by Støp-Bowitz (1948, 1951), and is a less cumbersome name, I think that *V. minuta* should be adopted as the specific name for this species. That *V. minuta* and *V. crystallina* have been previously confused has already been commented on above. Hering (1892) described a specimen as *Alciopa*

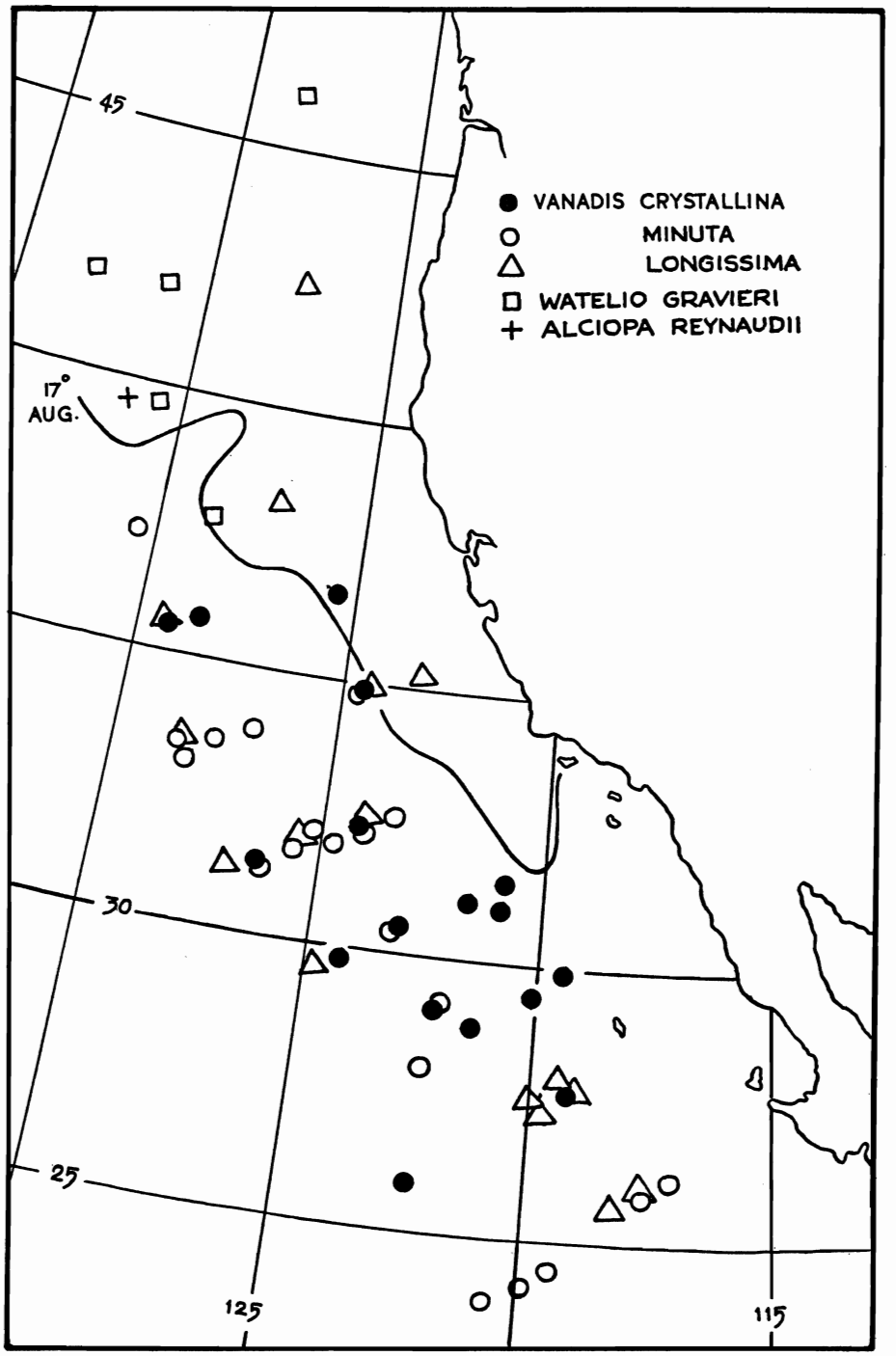

Fig. 28. Locality records of *Vanadis crystallina, V. minuta, V. longissima, Watelio gravieri,* and *Alciopa reynaudii.* Surface isotherm.

candida, which shows all the characters of *V. minuta,* although the median antenna is better developed than in any of the specimens I have seen; but it is still very short and could not be described as digitiform. As far as can be judged from illustrations, the specimens described by Greeff (1876, Taf. III, figs. 29–32), Apstein (1900, Taf. I, fig. 7), and Wesenberg-Lund (1939, fig. 22) are all more likely to be *V. minuta* than any other species.

Distribution.—Vanadis minuta has been found throughout the Pacific by Tread-

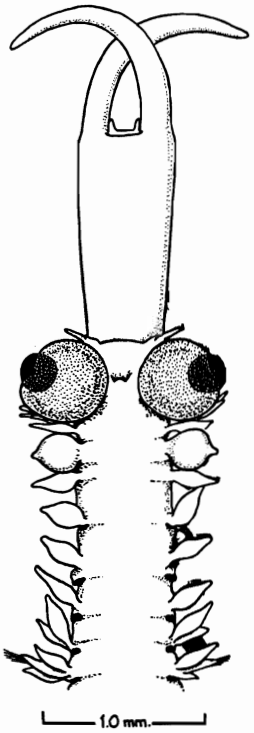

Fig. 29. *Vanadis minuta,* dorsal view of the anterior region of the body (female). The proboscis is only partly everted.

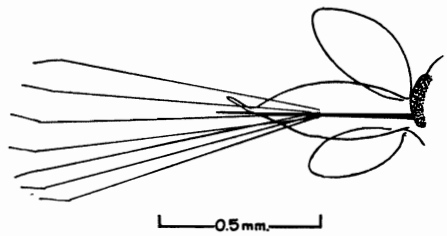

Fig. 30. *Vanadis minuta,* parapodium.

well (1943), and it is probably widely distributed in the Atlantic also. Treadwell's (1906) original specimens were collected in the Hawaiian region. Although collected at all seasons during the MLR investigations, this species is much less common than *V. crystallina* (fig. 28). The temperature of the water from which they have been taken ranges from 14° C. to 24° C.

Vanadis longissima (Levinsen)

(Figs. 31–33)

Rhynchonerella longissima Levinsen, 1885; *Vanadis fasciata* Apstein, 1890; *V. longissima* Apstein, 1900; Fauvel, 1916, 1923; Monro, 1930; Dales, 1955*b*; ? *V. grandis* Izuka, 1914; *Torea fasciata* Treadwell, 1943.

Eyes very large, directed downward, no part of the lens visible from above. Two pairs of frontal antennae short, but median antenna quite long and situated far forward on the pro-

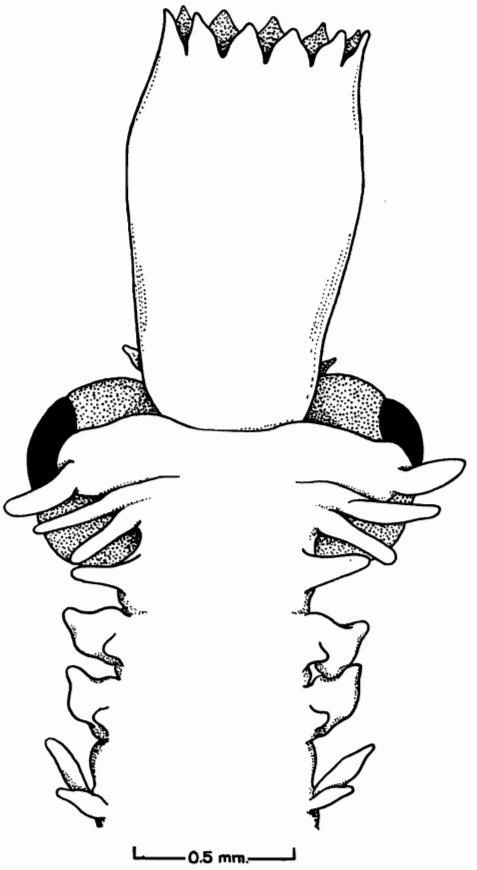

Fig. 31. *Vanadis longissima*, ventral view of the anterior region of the body (female).

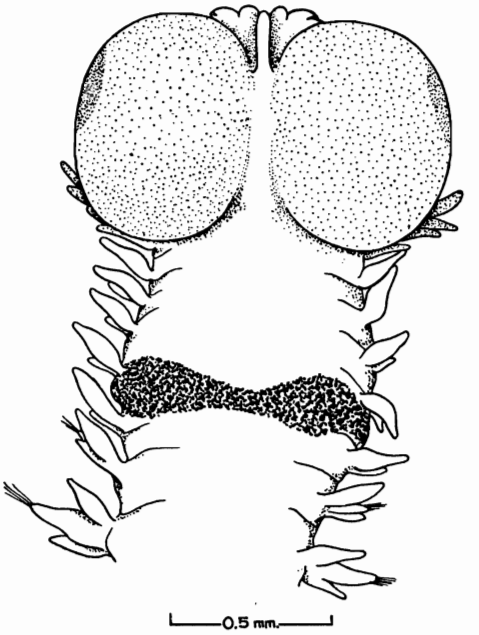

Fig. 32. *Vanadis longissima*, dorsal view of the anterior reigon of the body (male).

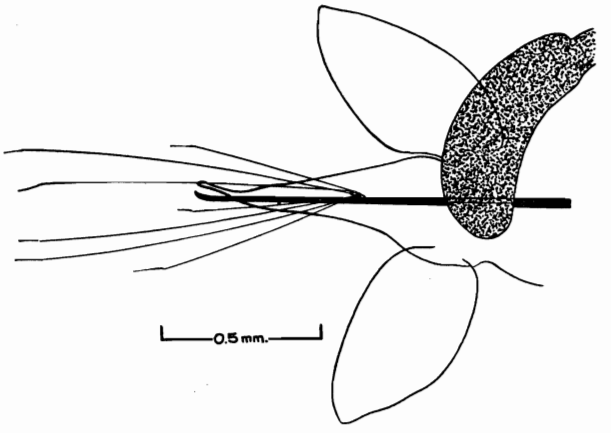

Fig. 33. *Vanadis longissima*, parapodium.

stomium. Three pairs of tentacular cirri, the first, longest; followed by four pairs of rudimentary parapodia; the first pigmented segmental gland situated on the fifth parapodium. Segmental glands joined across at intervals down the body, two or three adajcent segments may all be incorporated into a broad brown (when preserved) band; these bands separated by five or six segments without any pigment or pigmented segmental glands. In females the second and third pairs of dorsal cirri modified to form receptacula seminis. Proboscis without terminal horns; rim divided into eleven similar, broadly lanceolate papillae.

Only one female in the MLR collections was found with well-developed receptacula, and these clearly belonged to the second and third parapodial segments, and not to the first two segments as described by other workers. There is no doubt that Treadwell's (1943) *Torea fasciata* is a *Vanadis longissima;* not only are the distinctive brown bands present, but the parapodia have the short cirriform appendage characteristic of *V. longissima.* Izuka's (1914) description of *V. grandis* does not appear to differ significantly from the present species.

Distribution.—This is a much rarer species than other *Vanadis* species encountered, and although single specimens have been collected at all seasons, only nineteen were found in the whole collection sorted from the MLR samples (fig. 28). These usually occurred in water with temperatures between about 11° C. and 17° C. It appears to be widely distributed and has been found throughout the world, although Støp-Bowitz (1948) did not find it in the northern Atlantic in the *Michael Sars* collections. Monro (1930) found it as far south as 57° 16′ S. in the Atlantic. Treadwell's (1943) specimen was collected between California and Hawaii at 29° 21′ N., 132° 30′ W.

Vanadis nans (Chamberlin)

Mauita nans Chamberlin, 1919; ? *Mauita* sp. Treadwell, 1943.

First two pairs of tentacular cirri apparently arising from the same segment.

Chamberlin erected his new genus, *Mauita,* on the basis that the first two segments are coalesced, so that the first two pairs of tentacular cirri appear to arise from the same segment. His illustration does not show this very clearly, however, and since, apart from this, there is no difference from the genus *Vanadis,* it is probably better to retain his species within the genus *Vanadis.* Chamberlin's description and illustrations, although incomplete, do seem to indicate that his specimen differs from other *Vanadis* species, but a reëxamination of his type-specimen is desirable.

Distribution.—Chamberlin (1919) collected his specimen between the Galápagos and the Tuamotu Islands.

Genus *Alciopa* Audouin & Milne-Edwards

Body relatively short, broad, muscular, and opaque. Prostomium not projecting in front of the eyes, with two pairs of frontal antennae and a single median antenna dorsally, all somewhat reduced. Three pairs of tentacular cirri. Anterior parapodia well developed; dorsal and ventral cirri large, foliaceous; dorsal cirri imbricated over the back. Chaetigerous lobe with slender compound chaetae only, and terminating in two short appendages on either side of the aciculum. Segmental glands dark, and in males divided into a dorsal and ventral portion. Proboscis short, but provided with two terminal horns.

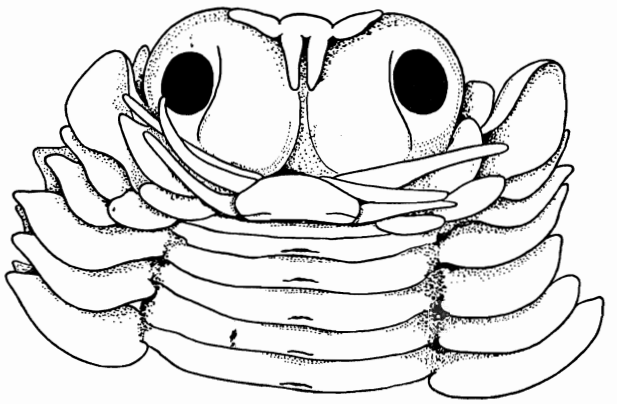

Fig. 34. *Alciopa reynaudii*, ventral view of the anterior region of the body (male).

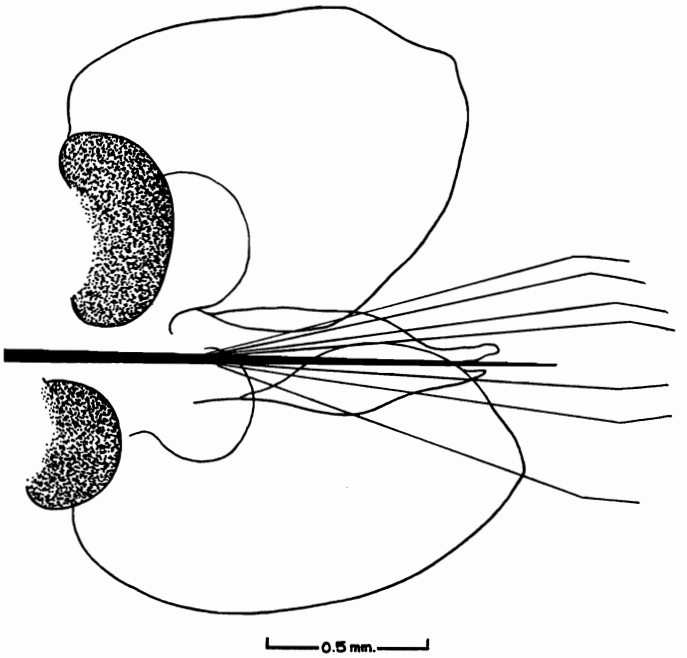

Fig. 35. *Alciopa reynaudii*, parapodium from the mid-body region (male).

Alciopa reynaudii Audouin & Milne-Edwards

(Figs. 34 and 35)

Alciopa Reynaudii Audouin & Milne-Edwards, 1833; Milne-Edwards, 1836; Grube, 1850; Quatrefages, 1865; Støp-Bowitz, 1948; *A. quadrioculata* McIntosh, 1885; *Halodora Reynaudii* Greeff, 1876; Chamberlin, 1919; *H. reynaudii* McIntosh, 1885; *Nauphanta spectabilis* Greeff, 1876; *N. celox* Greeff, 1876; Levinsen, 1882, 1885; *Greeffia celox* Apstein, 1891, 1900; Reibisch, 1905; Southern, 1911; Fauvel, 1916, 1923; *G. oahuensis* McIntosh, 1885; Treadwell, 1906, 1928; Benham, 1929; Monro, 1930, 1936; Wesenberg-Lund, 1939; Fyfe, 1952; *G. oahuensis* Apstein, 1900; *G. quadrioculata* Treadwell, 1906.

This genus includes a single species. This alciopid is, in contrast with most other genera, short and broad; one of the specimens found in the MLR collections was 13 mm. long and 4 mm. across. Støp-Bowitz (1948) has already discussed the previous descriptions of this species in some detail, and the use of the name *Alciopa* by earlier writers. McIntosh's (1885) specimen of *A. quadrioculata* from Honolulu is almost certainly conspecific with *A. reynaudii*. Treadwell (1906) was following McIntosh's description in identifying his specimen as *Greeffia quadrioculata,* and there is no reason for regarding his specimen as another species either.

Distribution.—Only two specimens were found in the MLR samples (fig. 28). Both were collected May 9, 1949, at 39° 37′ N., 131° 36′ W., during daylight, when the temperature at the surface was 13.25° C., and 12.23° C. at 75 m. depth. *Alciopa reynaudii,* although uncommon, appears to be widely distributed throughout the world. Treadwell (1906) found his specimens in the Pacific, off Peru.

Genus *Plotohelmis* Chamberlin

Body long, slender, transparent, small. Prostomium projecting forward in front of the eyes, which are very large and directed obliquely forward and slightly downward. Two pairs of frontal antennae, rather lanceolate in shape, and a digitiform median antenna between the eyes. Four or five pairs of tentacular cirri; the dorsal pairs of the second and third segments may be long and conspicuous; the segment following being the first chaetigerous segment. Anterior segments with acicular chaetae; the more posterior segments with slender compound chaetae alone, or with one or two simple acicular chaetae in the ventral part of the sheaf. Chaetigerous lobe without cirriform appendage; proboscis moderately long, swelling into a somewhat papillate terminal part, but without horns or other prominent processes on the rim.

This genus seems to be closely related to *Rhynchonerella* on the one hand, and to *Alciopina* and *Krohnia* on the other (Dales, 1955*a*); see Støp-Bowitz (1948) for a discussion of the status of this genus.

Plotohelmis tenuis (Apstein)

(Figs. 36–38)

Corynocephalus tenuis Apstein, 1900; *Plotohelmis tenuis* Dales, 1955*b*.

Small, slender; prostomium bulging forward; eyes large, directed forward and slightly sideways, the axes intersecting at right angles. Two pairs of lanceolate frontal antennae, and a digitiform antenna between the eyes. Four, possibly five, pairs of tentacular cirri; first pair short, related to first segment; second segment bearing a dorsal pair of long, slender cirri, and a pair of very short papilliform ventral cirri; third segment with a pair of fairly long dorsal cirri, and ventral cirri may also be just recognizable. Fourth segment the first chaetigerous segment, with simple acicular chaetae only. More posterior segments with only one such chaeta in each sheaf, the remainder compound, although the distal joint difficult to detect. Parapodia of distinctive shape, the large dorsal cirrus foliaceous, broadly lanceolate, contrasting with the small ventral cirrus, which is smaller than the chaetigerous lobe; chaetigerous lobe without a terminal appendage.

Apstein (1900) described this species from specimens collected near Naples in the Mediterranean, and from the equatorial Atlantic, but it has not been redescribed. The specimens in the MLR collections are identical with Apstein's description except in having compound chaetae. These chaetae are very slender and the distal joint difficult to see, especially in small specimens, and it seems likely that Apstein ascribed his species to *Corynocephalus* (= *Alciopina*) in error. Two

other species of *Plotohelmis* have been described, *P. alata* from the Pacific (Chamberlin, 1919), and *P. capitata* (as *Rhynchonerella capitata* Greeff, 1876), from the South Atlantic and Mediterranean, and later from Japan (Izuka, 1914). *P. tenuis* differs from these species most noticeably in the disposition of the eyes,

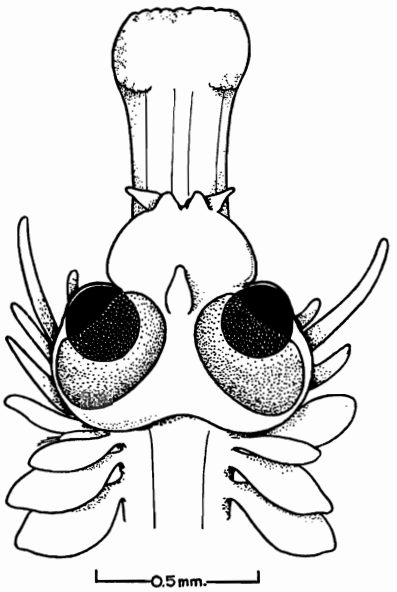

Fig. 36. *Plotohelmis tenuis,* dorsal view of the anterior region of the body.

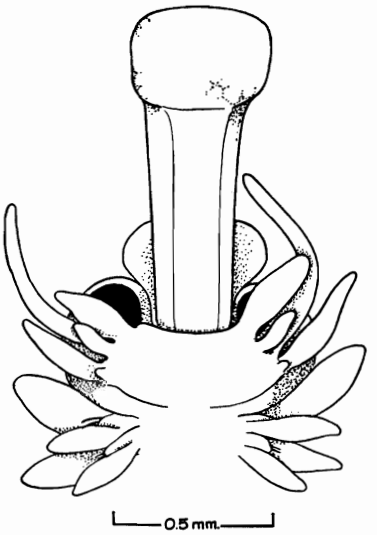

Fig. 37. *Plotohelmis tenuis,* ventral view of the anterior region of the body.

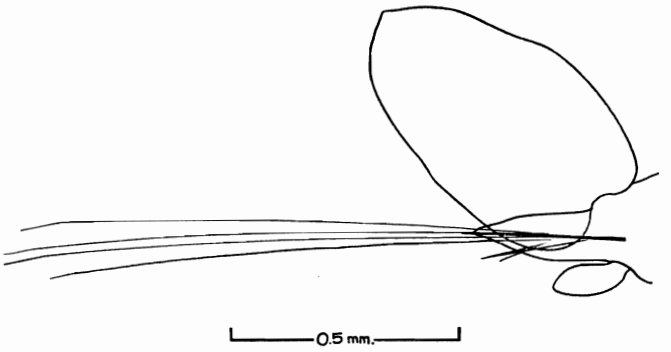

Fig. 38. *Plotohelmis tenuis,* parapodium.

but as these species have probably been confused in the past, the principal differences are tabulated below.

Plotohelmis tenuis	*Plotohelmis capitata*	*Plotohelmis alata*
2nd dorsal tentacular cirrus longest.	3rd dorsal tentacular cirrus longest.	2nd and 3rd dorsal tentacular cirri of equal length.
Axes of eyes at right angles.	Eyes directed sideways	
5th tentacular cirrus hardly detectable		5th tentacular cirrus small, but distinct and foliaceous.

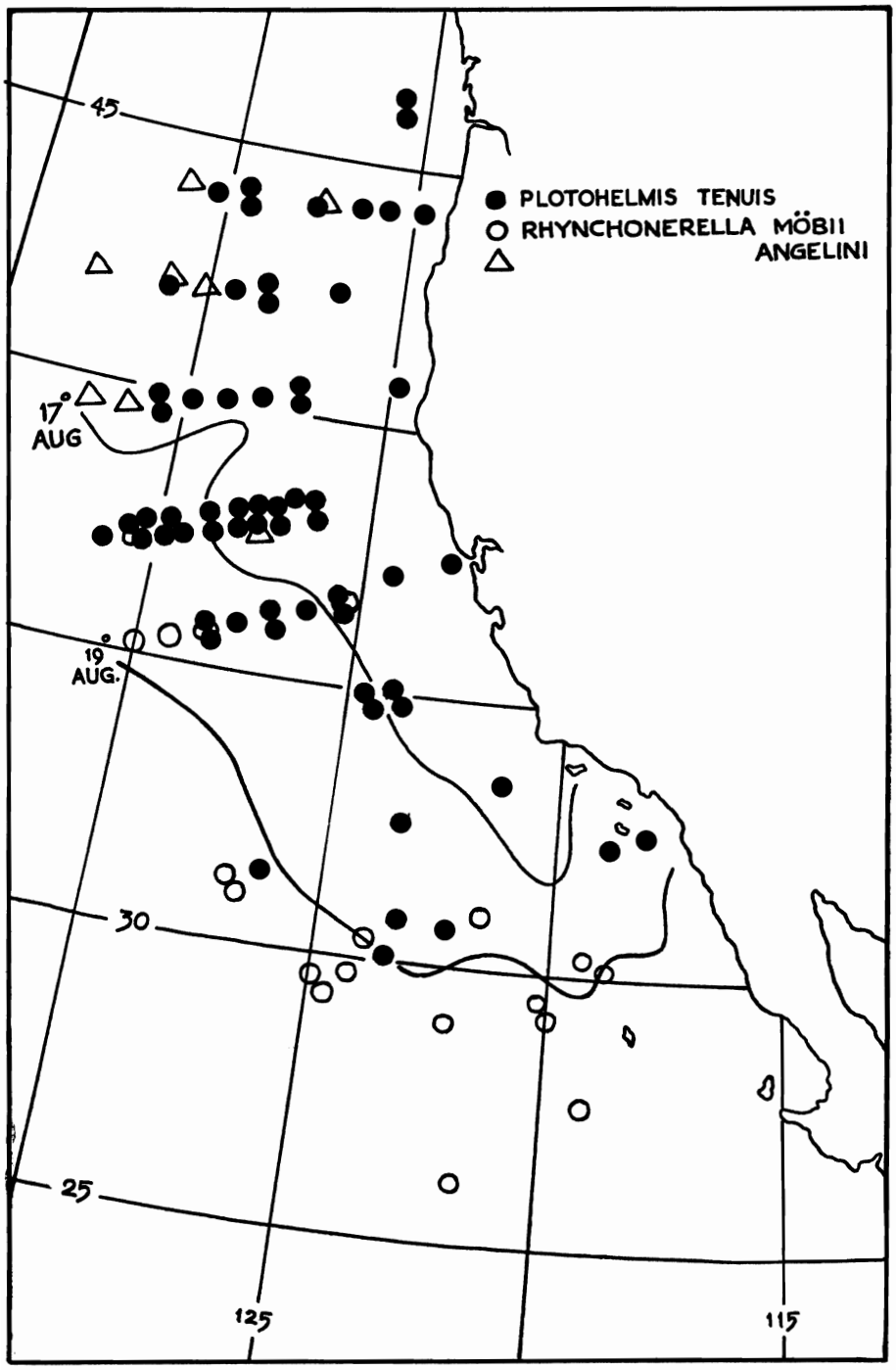

Fig. 39. Locality records of *Plotohelmis tenuis*, *Rhynchonerella möbii*, and *R. angelini*. Surface isotherms.

Distribution.—Plotohelmis tenuis may be widely distributed, but has not been previously recorded from the Pacific. Unlike most of the other alciopids that occur off the coast of California, it is almost confined to the cold-water stream in the north (fig. 39). This preference for colder water may account for this species not having been collected in the central Pacific. In the MLR samples it has been found at all seasons, normally only one or two in most samples, although as many as twenty have been found together, mainly in samples from water with temperatures between 10° C. and 15° C., but between extremes of 7.5° C. and 18.0° C. *P. tenuis* was found in Monterey Bay mainly during late summer and winter (Dales, 1955*b*). It has since been found in the Atlantic (Dales, unpublished).

Plotohelmis capitata (Greeff)

Rhynchonerella capitata Greeff, 1876; Viguier, 1886; Granata, 1911*a*; *R. fulgens* Greeff, 1885; Apstein, 1900; ? Izuka, 1914; Fauvel, 1923, 1951.

All the species of *Plotohelmis* resemble one another closely; the differences have been tabulated above. Izuka (1914) identifies his specimen as *Rhynchonerella fulgens,* but his illustration suggests *P. tenuis.*

Distribution.—This species is probably widely distributed, but, apart from Izuka's (1914) record, has not been found elsewhere in the Pacific; all the earlier records refer to the Mediterranean and Atlantic.

Plotohelmis alata Chamberlin

Plotohelmis alata Chamberlin, 1919; Treadwell, 1943.

For the differences between the species of *Plotohelmis,* see the table above.

Distribution.—Chamberlin (1919) found his type-specimen of the genus between Baja California and the Marquesas Islands (26° 18′ N., 128° 54′ W.). Treadwell (1943) found his specimens off the coast of California, and near the Phoenix Islands in the west equatorial Pacific.

Genus *Alciopina* Claparède

Body relatively short; prostomium projecting forward in front of the eyes, with two pairs of short frontal antennae. Median antenna represented by a carina with the tip prolonged into a short papilla. Eyes large, directed sideways; four or five pairs of tentacular cirri. First segment following those contributing tentacular cirri, chaetigerous, with well-developed foliaceous cirri; dorsal cirri imbricated over the back. Chaetae of two kinds, both simple: Heavy acicular chaetae, and slender capillaries. No cirriform appendage at the tip of the chaetigerous lobe.

Alciopina parasitica Claparède & Panceri

Alciopina parasitica Claparède & Panceri, 1867; Claparède, 1868; Granata, 1911*a*; Støp-Bowitz, 1948; ? *A. Pancerii* Buchholtz, 1869; *Corynocephalus albomaculatus* Levinsen, 1885; Apstein, 1900; Granata, 1911*b*; *C. albo-maculatus* Fauvel, 1916, 1923, 1951; Wesenberg-Lund, 1939; *C. paumotanus* Chamberlin 1919; Treadwell, 1943; ? *C. Gazellae* Apstein, 1893, 1900.

Four species have been described. Of these, Apstein's (1900) *Corynocephalus tenuis* has been thought to be an *Alciopina* by Støp-Bowitz (1948), though here it is interpreted as a *Plotohelmis.* The three species included in the list of synonyms above are all very similar as far as can be judged from published descriptions and illustrations. There certainly seems to be no difference between *A.*

parasitica and Chamberlin's (1919) species; Apstein's (1893) *C. gazellae* may be conspecific with this species, but it is desirable that the type-specimen be re-examined.

Distribution.—Treadwell (1943) found this to be one of the most widespread species in the Pacific, but it has not been found in the MLR samples. The earlier records all refer to the Atlantic and Mediterranean.

Genus *Krohnia* Quatrefages

Body elongate, transparent; with or without scattered patches of dark pigment. Prostomium extended in front of the eyes, with two pairs of lanceolate frontal antennae and a small median antenna. Eyes large, directed sideways and obliquely forward and slightly upward. Five pairs of tentacular cirri, of which the dorsal cirri of the third segment are somewhat foliaceous and extremely long, at least twice the length of the more anterior cirri. Parapodial cirri foliaceous and the chaetigerous lobe terminating in a cirriform appendage; with simple capillary chaetae, but some simple acicular chaetae also in the more anterior parapodia. Segmental glands dark, but not particularly conspicuous. Proboscis without long terminal horns; the rim divided into equal papillae.

Krohnia lepidota (Krohn)

Alciopa lepidota Krohn, 1845; Hering, 1860, 1892; Langerhans, 1880; *A. cirrata* Greeff, 1876; *A. krohnii* Greeff, 1879*b*; *Krohnia lepidota* Quatrefages, 1865; Granata, 1911*a*; Støp-Bowitz, 1948; *Callizonella lepidota* Apstein, 1900; Fauvel, 1916, 1923; Wesenberg-Lund, 1939; *C. pigmenta* Treadwell, 1943; *Callizona cincinnata* Greeff, 1876; *Rhynchonerella cincinnata* Chamberlin, 1919.

Of the two species that have been ascribed to this genus, *K. lepidota* is characterized by having dark chromatophores scattered over the body, and acutely pointed parapodial cirri. *K. bongraini* apparently has rather blunter-tipped cirri, and is without the scattered pigment spots so characteristic of *K. lepidota.*

Greeff's (1876) *Callizona cincinnata* is probably conspecific with *K. lepidota.* Greeff clearly did not regard, at that time, the possession of compound, as opposed to simple chaetae as a feature of primary importance, and although he has drawn his figures with compound chaetae, the description and illustrations are otherwise identical with *K. lepidota.* Also, his *Alciopa cirrata* was probably a young specimen of the same species. There is no doubt that Treadwell's (1943) type-specimen of *Callizonella pigmenta,* which I have examined, is conspecific with *K. lepidota.* Greeff's (1879*b*) *Alciopa krohnii,* and possibly also *A. bartelsii* (Hering, 1892), differ in having more pointed parapodial cirri, and may represent another species (see Fauvel, 1923).

Fauvel (1916) is of the opinion that this genus should be known by Apstein's name (*Callizonella*), as the name *Krohnia* has been applied to a chaetognath. However, Quatrefages used the name *Krohnia* long before it was used in the Chaetognatha, and Quatrefages' name is retained here (see the discussion by Støp-Bowitz, 1948).

Distribution.—Most of Chamberlin's (1919) specimens were collected between Peru and Easter Island, and northward across the equator to 19° 52′ N., off Mexico. Treadwell's (1943) specimen came from the same area, at 12° 40′ N., 137° 32′ W. Most other records are from the Atlantic.

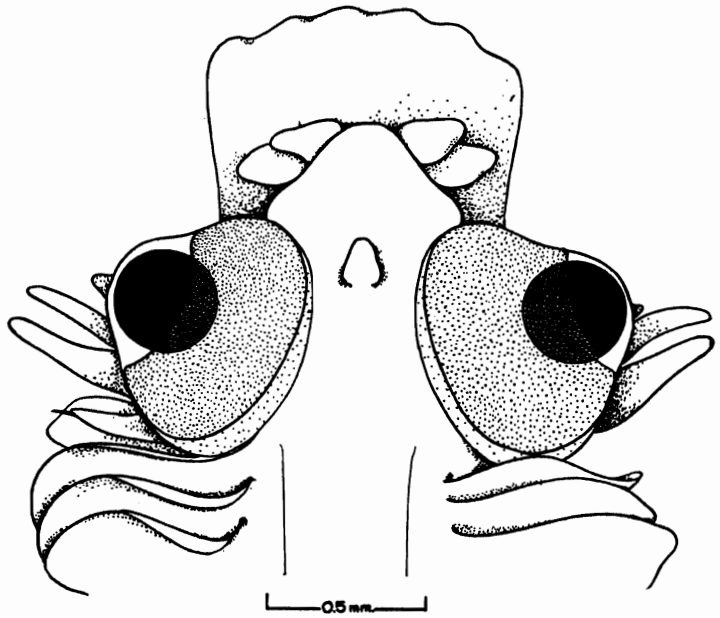

Fig. 40. ***Rhynchonerella möbii,*** dorsal view of the anterior region of the body.

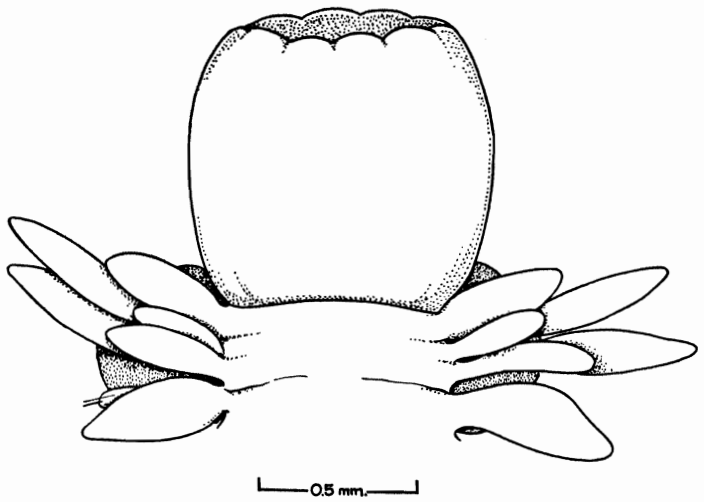

Fig. 41. ***Rhynchonerella möbii,*** ventral view of the anterior region of the body.

Genus *Rhynchonerella* Costa

Body long, slender, but relatively robust; prostomium with four frontal antennae and a median antenna, and extended forward in front of the eyes, which are large and generally directed sideways. Five pairs of tentacular cirri, the first related to the first segment; the other four representing dorsal and ventral cirri of the following segments. Fourth segment chaetigerous, and with well-developed foliaceous cirri. Chaetigerous lobe terminating in a cirriform appendage; with slender compound chaetae and acicular chaetae, which tend to be most numerous in the more anterior segments. Proboscis short with the rim divided into conical papillae of approximately equal size.

Rhynchonerella gracilis Costa

Rhynchonerella gracilis Costa, 1862; *Callizona nasuta* Greeff, 1876; Apstein, 1900; Fauvel, 1923; Wesenberg-Lund, 1939; *C. japonica* Izuka, 1914.

Club-shaped central part of prostomium projecting far in front of the eyes. Anterior parapodia with only one or two acicular chaetae, which, like those of *R. möbii*, are simple.

The frontal antennae seem to have papillate borders, although these are not shown in Izuka's (1914) or Wesenberg-Lund's (1939) illustrations, and are perhaps not distinctive. It seems to be generally held that this is a rare species. As far as can be judged from the description and illustration, Izuka's specimen is conspecific with *R. gracilis*, and this constitutes the only record from the Pacific. All other records are from the Mediterranean and Atlantic.

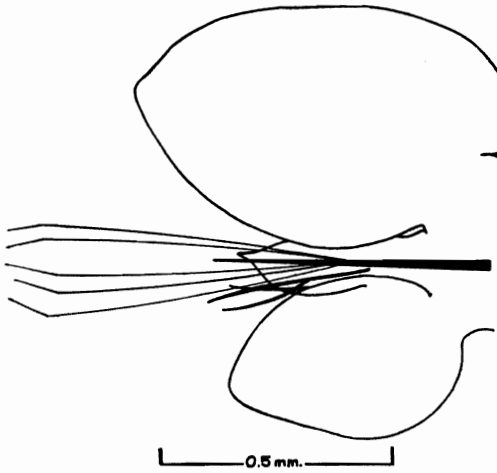

Fig. 42. *Rhynchonerella möbii*, parapodium.

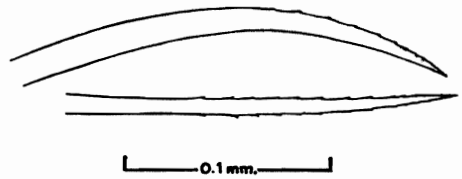

Fig. 43. *Rhynchonerella möbii*, acicular chaetae.

Rhynchonerella möbii (Apstein)

(Figs. 40–43)

Callizona Möbii Apstein, 1893, 1900; *C. Moebii* Fauvel, 1923; Wesenberg-Lund, 1939; *C. möbii* Støp-Bowitz, 1948.

Mostly 4–5 mm. in length and 1–2 mm. across; body opaque and yellowish in color when preserved in formalin; segmental glands rather variably developed, but often quite conspicuous. Prostomium large, with four fleshy frontal antennae and a small median antenna between the eyes, which are large and directed outward and forward. Five pairs of tentacular cirri, with one pair related to the first segment and two pairs representing the dorsal and ventral cirri of each of the following two segments, the dorsal cirri longer than the ventral, and much the same in length in each segment. Segments following provided with foliaceous dorsal and ventral cirri which become more or less imbricated over the back. Proboscis short and provided with terminal papillae. Chaetigerous lobe terminates in a short cirriform appendage, bears only slender compound chaetae in the more posterior segments, but many acicular chaetae in the anterior parapodia, unlike *R. gracilis*. Acicular chaetae simple.

Distribution.—This species is not numerous in the surface waters of the northeast Pacific, single specimens occurring occasionally in the MLR samples, but at all seasons (fig. 39). Nearly all these specimens are from samples taken at night,

so it may be found to be more numerous at greater depths, although Dales (1955*b*) did not find it in the deeper hauls taken in Monterey Bay. The temperature of the water in which the specimens have been found was usually between 12° C. and 18° C. *R. möbii* does not appear to have previously been collected from the Pacific.

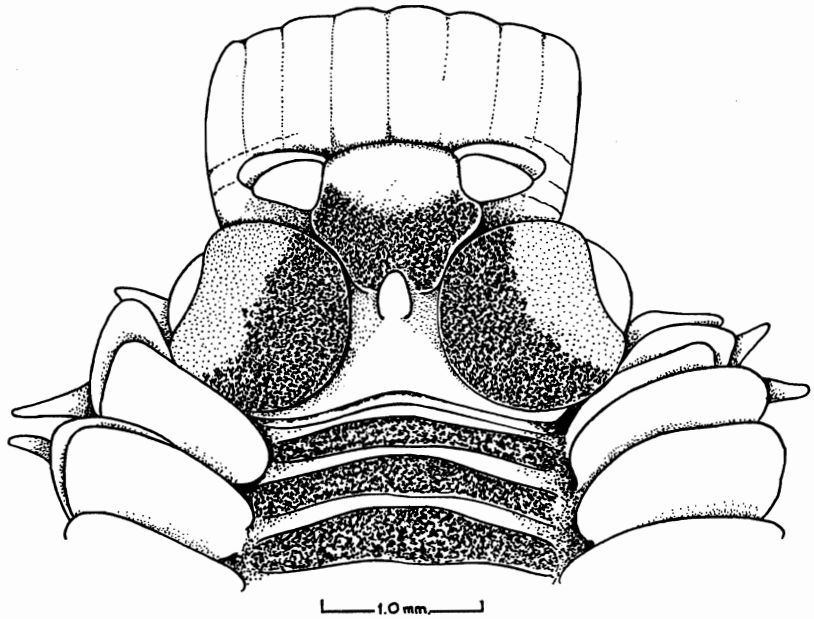

Fig. 44. *Rhynchonerella angelini,* dorsal view of the anterior region of the body.

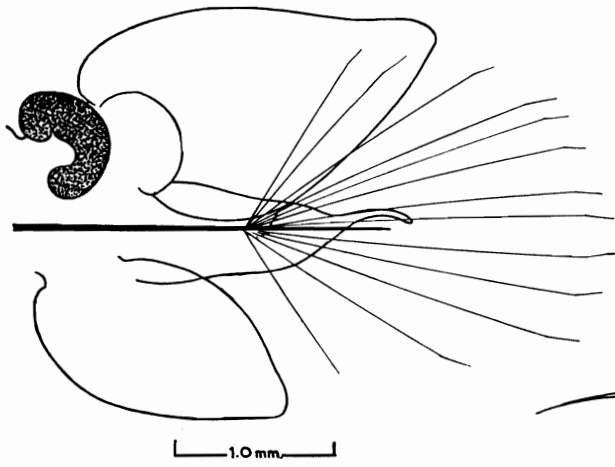

Fig. 45. *Rhynchonerella angelini,* parapodium.

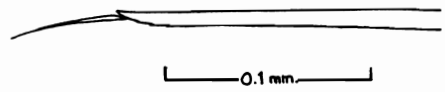

Fig. 46. *Rhynchonerella angelini,* acicular chaetae.

Rhynchonerella angelini (Kinberg)

(Figs. 44–46)

Kronia Angelini Kinberg, 1866; *Callizona Grubei* Greeff, 1876; Apstein, 1891, 1892, 1900; *C. Angelini,* 1900; Southern, 1911; Fauvel, 1916, 1923, 1932; Monro, 1930, 1936; Wesenberg-Lund, 1939; ? *C. Henseni* Apstein, 1900; *Rhynchonerella pycnocera* Chamberlin, 1919; Treadwell, 1928, 1943; *R. parva* Chamberlin, 1919; *R. Angelini* Greeff, 1876; Støp-Bowitz, 1948; Dales, 1955*b*.

Often of relatively large size, up to 11.5 cm. long, and 8.0 mm. across, but mostly 5–6 cm. long and 6 mm. broad; larger specimens yellowish or brown in color when preserved, with heavy deposits of dark pigment on the dorsal side of each segment and prostomium. Prostomium forming a cushion in front of the eyes and bearing four frontal antennae, all short and fat; median antenna more slender and arising posteriorly between the eyes. Proboscis short, with twelve similar papillae around the rim. Parapodia with large foliaceous dorsal and ventral cirri; ventral cirri often thick and stout; dorsal cirri more foliaceous and more or less imbricated over the back. Segmental glands dark and conspicuous, occurring from the 15th segment or thereabouts, posteriorly; chaetae borne on the first segment following that contributing the most posterior cirri; each sheaf consisting of long, slender, compound chaetae, and stout compound acicular chaetae with slender, simple endpieces. These are most numerous in the anterior segments, twelve to fifteen in the first few, but only one or two farther back.

Distribution.—About a dozen specimens have been found in the whole of the MLR samples, all in samples collected in rather cold water in the northern part of the area investigated (fig. 39), contrasting with *R. möbii,* which was found only in the warmer waters to the south. All the specimens were collected at night, but at all seasons. A single specimen was found in Monterey Bay (Dales, 1955*b*). This species has been found all over the world; Kinberg's (1866) type-specimen came from the China Sea, and Chamberlin's (1919) and Treadwell's (1928, 1943) specimens (*R. pycnocera,* and *R. parva*), were collected over a wide area in the Pacific.

Rhynchonerella petersii (Langerhans)

Alciope (*Halodora*) *Petersii* Langerhans, 1880; Ehlers, 1913; *Alciopa Cari* Hering, 1892; *Vanadis heterochaeta* Viguier, 1886; *V. setosa* Greeff, 1885; *Callizona setosa* Apstein, 1900; Southern, 1911; Fauvel, 1916, 1923; Wesenberg-Lund, 1939; *Corynocephalus magnachaetus* Treadwell, 1943; *Rhynchonerella Petersii* Støp-Bowitz, 1948.

Smaller and more delicate than other species of this genus, and easily recognized by the relatively large, rather curved and clearly serrated endpieces of the acicular chaetae.

There is no doubt that Treadwell's (1943) *Corynocephalus magnachaetus* refers to *R. petersii;* the large serrated endpiece of the acicular chaetae can be quite clearly seen in his type-specimen.

Distribution.—Treadwell's (1943) single specimen collected at 3° 47′ S., 172° 39′ W., is the only record from the Pacific; all other records are from the Atlantic and Mediterranean.

Genus *Watelio* Støp-Bowitz

Body long, transparent, somewhat flattened dorsoventrally. Prostomium projecting in front of the eyes, with two pairs of very small frontal antennae and a small median antenna between the eyes, which are spaced far apart. Four pairs of tentacular cirri, the segments following with strap-shaped dorsal and ventral cirri, particularly long in the most anterior segments, but more lanceolate farther back; ventral cirri exceptional in being longer than the dorsal cirri. Chaetigerous lobe with a short blunt appendage dorsal to the extremely long, stout

aciculum, which projects from the tip of the chaetigerous lobe to a distance equal to the length of the lobe itself. Chaetae numerous, mainly long, slender, compound; but some simple and also slender chaetae occur in the ventral part of the sheaf. Segmental glands dark but small. A large raised conical projection on the ventral side near the base of each parapodium. Proboscis provided with similar lanceolate papillae round the rim.

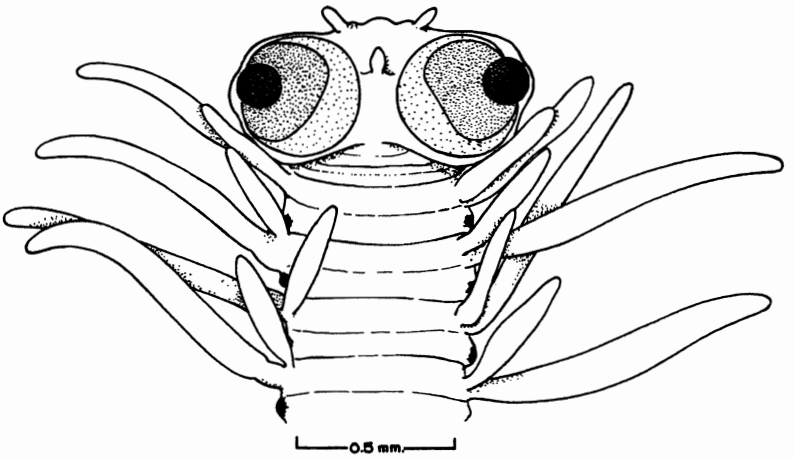

Fig. 47. *Watelio gravieri,* dorsal view of the anterior region of the body of a young individual.

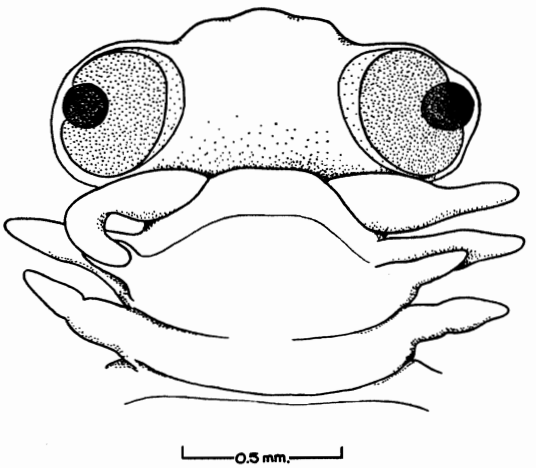

Fig. 48. *Watelio gravieri,* ventral view of the anterior region of the body of an older individual.

Watelio gravieri (Benham)

(Figs. 47–50)

Callizona gravieri Benham, 1929; *Watelio longifoliata* Støp-Bowitz, 1948.

The type-specimen of this genus described by Støp-Bowitz (1948) is 11 cm. long and 2 mm. across. The specimens found in the MLR collections were very variable in size; the smallest was about 2 cm. long and less than 1 mm. across, the largest 15 cm. long with a maximum breadth of 3 mm. The smallest specimen had much larger eyes relative to the size of the head than the older individuals,

and it seems that the absolute size of the eyes becomes only slightly larger and more widely spaced with increasing age of the individual. Støp-Bowitz (1948) regarded his species and Benham's (1929) *Callizona gravieri* as belonging to the same genus, but was unable to conclude whether they should be regarded as conspecific from Benham's description alone. I have had the opportunity of examining both specimens, and can find no difference between them, or the specimens found in the MLR collections.

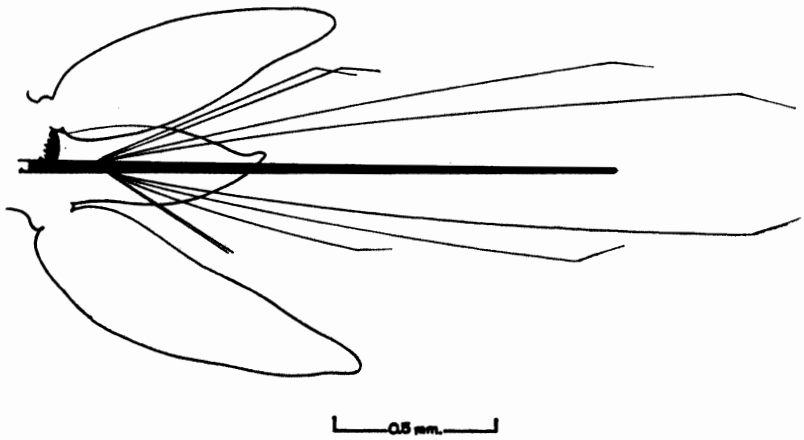

Fig. 49. *Watelio gravieri*, parapodium from the anterior region of the body.

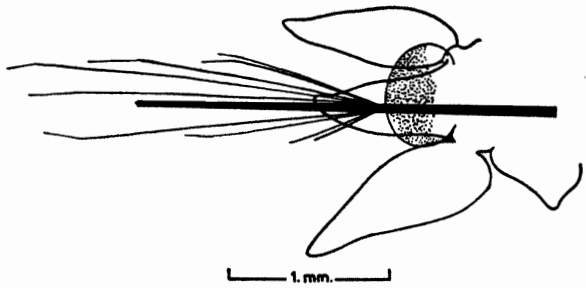

Fig. 50. *Watelio gravieri*, parapodium from the posterior region of the body.

Distribution.—The localities where these specimens have been taken in the MLR investigations are shown in fig. 28. They were collected singly, at all seasons, and in water ranging in temperature from 8° C. at 75 m. depth, to a maximum of 16.7° C. at the surface. Benham's (1929) specimen was found in New Zealand waters; Støp-Bowitz' (1948) specimen was collected in the North Atlantic, south of the Azores, so the species appears to be widely distributed.

Family TOMOPTERIDAE Grube

All the members of this family are pelagic and easily recognized. They are characterized by the reduction of the parapodia to biramous achaetous paddles, by the shape of the prostomium, which is produced laterally into hornlike antennae and fused to the first body segment; and by the extension of the acicula of the second segment into long streamers. In some species there is a pair of cirri,

representing the first segment, between these streamers and the prostomial horns. Most have a pair of eyes and ciliated epaulettes representing the nuchal organs. Most are small, but some species attain a large size, specimens with a length of 10 cm. or more occasionally being found.

Identification of tomopterids.—The great uniformity in appearance of the members of this group necessitates care and some practice in identification. The most important characters distinguishing the different species are (1) the presence or absence of the small cirrus between the prostomial horns and the large acicular streamers, (2) the disposition and occurrence of various glands in the parapodia, and (3) the presence or absence of reduced posterior segments forming a tail. The first character is most easily seen in ventral view. The parapodial glands may have to be stained to be certain of their distribution; staining in haematoxylin and examining the whole specimen in acid alcohol during differentiation was found to be the quickest and most satisfactory method, but with practice many details may be seen without staining by arrangement of the lighting.

There are four types of gland, but at most three occur in any one animal. The largest and usually most conspicuous consist of bunches of hyaline or yellowish tubes converging to a common opening near the ventral border of the pinnule of the ventral ramus. These are known as *chromophile glands,* and are most commonly present in the third or fourth parapodia posteriorly; in many species they may be seen with the naked eye, even in small specimens, but in others they are hard to detect. In a few species there is an additional gland situated distally to the chromophile gland, opening on a spurlike projection from the edge of the pinnule (*spur gland*). The other types of gland occurring in the parapodia are known as *hyaline glands* and *rosettes.* These are homologous (Malaquin & Carin, 1922) and only one form ever occurs in any species. Both rosettes and hyaline glands are often distinguished by a small mass of dark-brown or reddish pigment at the center. Rosettes are minute, and generally occur in the tailed forms; these glands are composed of a ring of eight cells derived from the coelomostomes as Meyer (1930) has shown. The first two pairs of parapodia usually bear these, not in the pinnules, but in the trunks of the parapodia where they may be seen through the muscle from the anterior side. In more posterior segments they occur at the tips of the parapodial rami, having become subdivided so that one is found at the base of each pinnule. Hyaline glands are apparently further modifications of these, and consist of a mass of transparent tubes; they may occur in either dorsal or ventral pinnule, or in both. Hyaline glands may have dark pigment at the center or not, this varying from one specimen to another in the same species.

Although it is hoped that the notes and the key given in this paper will assist in the identification of the species of *Tomopteris,* the reader is referred to the papers of Rosa (1908*b*) and Terio (1947*a, b,* 1950*b,* 1952*a, b*) for concise and useful descriptions of the species that have not so far been recorded from Pacific waters. The following list of equivalent terms may be found useful when referring to earlier texts.

Note on species with spur glands.—Rosa (1908*b*) described *Tomopteris apsteini* as lacking rosettes in the pinnules. His drawing (fig. 12) does, however, show clear areas at the tips of the rami where the rosettes are normally situated,

and Rosa mentions this in the text, but to account for the lack of rosettes, he described hyaline glands separate from, and just distal to, the spur glands. The spur gland is not homologous with the hyaline gland as Rosa himself realized (1912). Terio (1950*b*) has also described a species (*T. spartai*) without rosettes and with hyaline glands. Støp-Bowitz (1948), on the other hand, notes that the pigment of the rosettes disappears very easily in alcohol, when the clear areas described by Rosa would alone remain. Terio's species *T. spartai* is probably distinct from *T. apsteini* owing to the adnate pinnules in the former species, but

TERMS USED IN DESCRIPTIONS OF TOMOPTERIS, WITH ITALIAN AND GERMAN EQUIVALENTS USED BY EARLIER WRITERS

Prostomial horns, antennae	Corna	Kopflappen, Kopffühler, Kopfforsätze, Stirnfühler
Anterior cirrus, anterior or first cirriform appendage or chaetigerous appendage, anterior cirri, 2nd antennae	Primo cirro	Erstes Fühlercirre or Cirrenpaar, Retraktile Fühler
2nd cirriform appendage, acicular appendages, streamers	Secondo cirro	Zweites Fühlercirre or Cirrenpaar, 2nd Tentakel, Starre Fühler
Pinnule, membrane	Pinna	Flossen
Chromophile glands	Ghiandole chromofile	Flossendrüsen
Hyaline glands	Ghiandole jaline (G. chromofile + G. jaline = G. pinnale)	.....
Rosettes	Rosette	Rosetten Organ I (when in pinnule), Rosetten Organ II (when in ramus), Rosettenförmiges Organ
Spur gland	Aculeo	.....
Ramus	Remo	Ruderast
Trunk of parapodium	Tronco	Ruder
Ciliated epaulettes	Spalline vibratile	.....

the presence of hyaline glands in any of the species bearing spur glands is doubtful, and it seems more likely that these latter species have been described from specimens in which the rosettes have disappeared in preservation. There is no reason a priori why hyaline glands should not be present, but the illustrations of the spur gland in both these species do not lead one to suppose them to be different from those species with distinct rosettes as well. This does not mean that either *T. apsteini* or *T. spartai* has been incorrectly described as a separate species, since a combination of other characters differentiates both from other species bearing spur glands. No distinct hyaline glands, as found in most species of *Tomopteris, sensu stricto,* have been found in species bearing spur glands.

Parasites.—Young stages of the narcomedusan, presumably *Cunina lativentris* (Damas, 1936) frequently occur in the coelom of *Tomopteris.* In the MLR collections, *T. septentrionalis* and *T. elegans* have been found so parasitized, but not the other species.

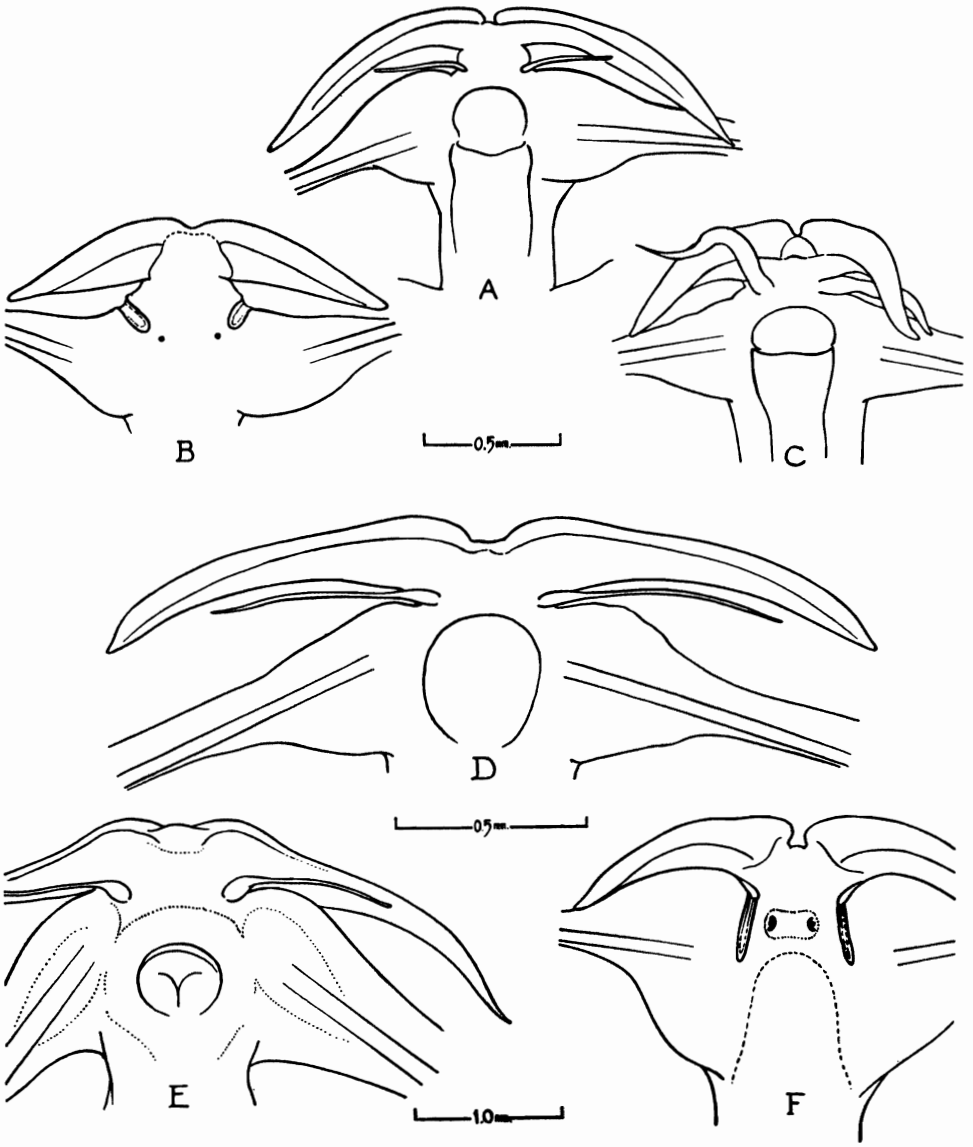

Fig. 51. Anterior region of the body of Pacific tomopterids: A, *Tomopteris elegans;* B, *T. cavallii;* C, *T. nationalis;* D, *T. krampi;* E, *T. pacifica;* F, *T. septentrionalis.*

Genus *Tomopteris* Eschscholtz

This genus differs from the only other genus included in the family (*Enapteris*) in having the parapodial rami bordered completely by the pinnules (in *Enapteris* the pinnules do not extend along the inner borders of the rami).

Subgenus *Johnstonella* Gosse

Rosettes present; hyaline glands absent; body usually terminating in a tail; gonads often present in both dorsal and ventral rami.

Tomopteris (*Johnstonella*) *nationalis* Apstein amend. Terio (1950*a*)

(Figs. 51, *c*; 52, *c*)

Tomopteris nationalis Apstein, 1900; *T.* (*Johnstonella*) *nationalis* Rosa, 1908*b*; Terio, 1947*a*, 1950*a*; *T. Apsteini* Malaquin & Carin, 1911, 1922 (in part); Støp-Bowitz 1948, 1951; ? *T. rosaea* Ehlers, 1917; ? *T.* (*Johnstonella*) *membranacea* Caroli, 1930; Terio, 1947*a*.

Small; long-tailed; with stout anterior cirri, which may be almost as long as the prostomial horns. Rosettes clearly present near the tips of the rami in the mid-body region; rosettes also on the trunks of the first two pairs of parapodia situated toward the ventral side at the base of the ventral rami.

Distribution.—Only one specimen has been recorded from the Pacific, and this was collected during the MLR investigations at 28° 40.5′ N., 122° 46′ W., in daylight on the 10th of February, 1950, when the surface temperature was 16.44° C. and 16.39° C. at 75 m. depth.

Tomopteris (*Johnstonella*) *apsteini* Rosa

Tomopteris onisciformis Grube, 1848 (in part); *T. scolopendra* Keferstein, 1861 (in part); Apstein, 1900; ? Greeff, 1879*a* (not *T. scolopendra* Gosse, 1855); ? *Briaraea scolopendra* Quoy & Gaimard, 1827; *Escholtzia Leuckartii* Quatrefages, 1865 (in part); *Tomopteris* (*Tomopteris*) *Apsteini* Rosa, 1908*b*; *T.* (*Johnstonella*) *Apsteini* Rosa, 1912; Caroli, 1928*b*, 1930; Terio, 1947*a*; *T. Apsteini* Izuka, 1914; Ehlers, 1917.

This species is very like *T. nationalis*, but may be distinguished by the chromophile glands being absent in the third pair of parapodia, and by the absence of rosettes.

Distribution.—Rosa (1908*b*) found this species off the Mexican coast; Izuka (1914) found it off Misaki Bay in Japan, so the species is probably widely distributed in the northern Pacific.

Tomopteris (*Johnstonella*) *aloysii sabaudiae* Rosa

Tomopteris Aloysii Sabaudiae Rosa, 1907; *T.* (*Johnstonella*) *Aloysii Sabaudiae* Rosa, 1908*b*; Caroli, 1930; Terio, 1947*a*.

This species may be distinguished from *T. nationalis* by the absence of the anterior cirri, and by the less well differentiated tail region.

Distribution.—Although this has not been found in the MLR collection, Rosa (1908*b*) found a specimen off Acapulco, Mexico.

Tomopteris (*Johnstonella*) *duccii* Rosa

Tomopteris Ducci Rosa, 1907; *T.* (*Johnstonella*) *Duccii* Rosa, 1908*b*; Terio, 1947*a*; Caroli, 1933; Treadwell, 1948.

This species is very similar to *T. nationalis*, from which it may be distinguished by having the most anterior chromophile gland on the fifth parapodial segment, not on the third as in *T. nationalis*.

Distribution.—This species has not been found in the MLR samples but is reported by Rosa (1908*b*) from the Pacific, off Mexico; other records are from the Atlantic and Red Sea.

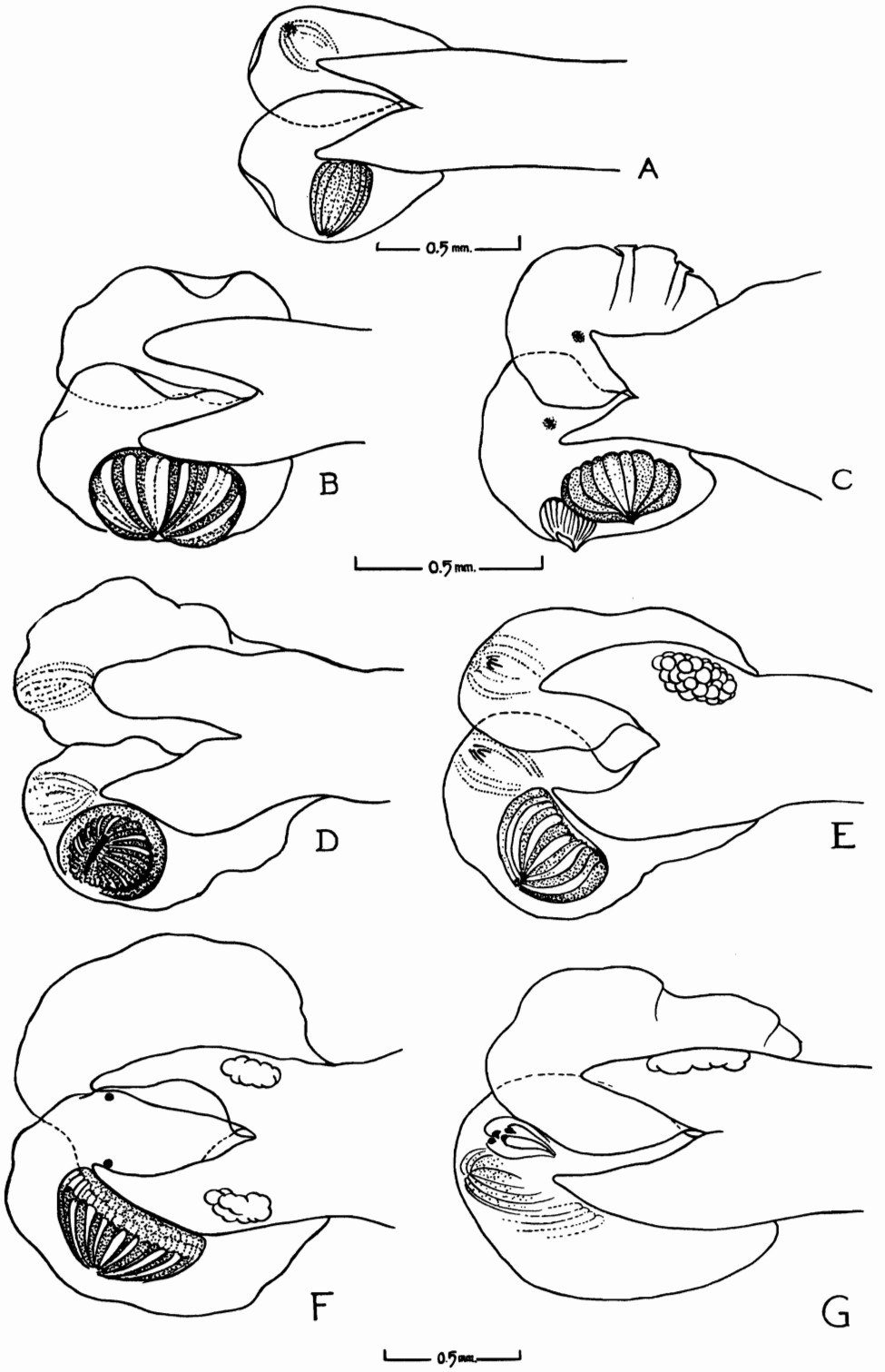

Fig. 52. Parapodia of Pacific tomopterids: A, *T. elegans* (4th); B, *T. cavallii*; C, *T. nationalis*; D, *T. nisseni*; E, *T. krampi*; F, *T. pacifica*; G, *T. septentrionalis*.

Tomopteris (*Johnstonella*) *pacifica* Izuka

(Figs. 51, *e*; 52, *f*)

Tomopteris pacifica Izuka, 1914; Dales, 1955*b*; *T. elegans* Berkeley, 1924; *T. renata* Berkeley & Berkeley, 1948; Uschakov, 1952; ? *T. eura* Chamberlin, 1919; Treadwell, 1943.

Up to 30–40 mm. in length. Anterior cirri present; rosettes on the trunks of the first two pairs of parapodia and at the tips of the rami of the third and following segments. Gonads in both dorsal and ventral rami. Chromophile glands in the third and more posterior segments; the glands large and broad at the base. Tail very long and slender and quite devoid of parapodia toward the tip.

The rosettes on the trunks of the first two pairs of parapodia are often difficult to detect, and the anterior cirri are sometimes broken off. Such specimens might easily be confused with Monro's species *T. kempi* were it not for the presence of gonads in both rami. The specimens found in Monterey Bay (Dales, 1955*b*) certainly resemble Berkeley's specimens in the British Museum, and Izuka's description of *T. pacifica*. Chamberlin's (1919) species *T. eura* may also be conspecific with *T. pacifica*, but this cannot be decided from the published description and illustrations.

Distribution.—*Tomopteris pacifica* has not been found in the MLR samples, so it probably does not occur near the surface, but it was found to be not uncommon in the deeper hauls taken in Monterey Bay (Dales, 1955*b*). As Izuka (1914) described the species from specimens collected off Japan, it would appear to be widely distributed in the colder waters of the North Pacific. Uschakov (1952) has recently found this species in the Kamchatka region.

Subgenus *Tomopteris sensu stricto* Eschscholtz

Rosettes absent; hyaline glands usually present; body usually without a tail, and gonads commonly restricted to the dorsal parapodial rami.

Tomopteris (*Tomopteris*) *nisseni* Rosa

(Fig. 52, *d*)

Tomopteris Nisseni Rosa, 1908*a*; *T.* (*Tomopteris*) *Nisseni* Rosa, 1908*b*; Southern, 1911; Malaquin & Carin, 1922; Fauvel, 1923; Wesenberg-Lund, 1935, 1951; Monro, 1930; Terio, 1947*a*; Støp-Bowitz, 1948; Dales, 1955*b*; ? *T. innatans* Chamberlin, 1919; ? *T. idiura* Chamberlin, 1919; ? *T. longisetis* Treadwell, 1936.

Often of large size; some specimens have been collected with a length of 100 mm. or more. Tail fairly short, with reduced parapodia; anterior cirri absent, but acicular streamers very long. Chromophile glands very large and globular and present in the fourth parapodia posteriorly; hyaline glands also large and conspicuous, present in the ventral pinnules of the third and more posterior segments; farther back equally large hyaline glands may be seen in the dorsal pinnules as well. Gonads in the dorsal rami only, the most anterior in the first or second parapodial segment.

Chamberlin's (1919) new species are indeterminable from the published description and figures, but both may be conspecific with *T. nisseni*.

Distribution.—No representatives of this species have been found in the MLR samples, but Dales (1955*b*) found it to occur occasionally in the deeper hauls taken in Monterey Bay, and these specimens were often of large size. *T. innatans* was found between California and the Marquesas Islands (4° 35′ N., 136° 54′ W.)

by Chamberlin (1919) who found others in the South Pacific between the Galápagos and Easter Island (4° 47′ S., 94° 05′ W.). *T. idiura* Chamberlin (1919) is represented by a single specimen collected near Hood Island in the Galápagos group.

Tomopteris (*Tomopteris*) *ligulata* Rosa

Tomopteris ligulata Rosa, 1908*a*; *T.* (*Tomopteris*) *ligulata* Rosa, 1908*b*; Malaquin & Carin, 1922; Ehlers, 1917; Caroli 1928*a*, *b*, 1933; Terio, 1947*a*, 1952*b*; Støp-Bowitz, 1948.

This species may be distinguished by the pinnules being adnate to the parapodial trunks. There are no anterior cirri; the most anterior chromophile glands occur on the fourth pair of parapodia, but the hyaline glands, which are rather indistinct, occur from the third pair of parapodia. Gonads in the dorsal rami only.

Distribution.—Rosa (1908*b*) reports this species from the South Pacific, but none has been found in the MLR samples, or in the deeper hauls made in Monterey Bay.

Tomopteris (*Tomopteris*) *krampi* Wesenberg-Lund

(Figs. 51, *d*; 52, *e*)

Tomopteris (*Tomopteris*) *krampi* Wesenberg-Lund, 1936; Støp-Bowitz, 1948; Dales, 1955*b*.

Reminiscent of *T. elegans*, but body more tapering in shape, and composition of parapodial glands different; *T. krampi* with hyaline glands in both dorsal and ventral pinnules of third and more posterior segments, although these glands rather indistinct. Anterior cirrus present. Body terminating in a short tail.

Distribution.—This species has not previously been found save in the North Atlantic. Dales (1955*b*) found *T. krampi* to be occasionally present in the deep hauls made in Monterey Bay, and the absence of this species from the superficial hauls made during the MLR investigations confirms Wesenberg-Lund's contention that this species is characteristic of deep water.

Tomopteris (*Tomopteris*) *elegans* Chun

(Figs. 51, *a*; 52, *a*)

Tomopteris elegans Chun, 1887; *Izuka*, 1914; Ehlers, 1917; Malaquin & Carin, 1911, 1922; Caroli, 1928*a*, *b*, 1930; Benham, 1929; *T.* (*Tomopteris*) *elegans* Rosa, 1908*b*, 1912; Fauvel, 1923; Caroli, 1933; Terio, 1947*a*; Støp-Bowitz, 1948, 1951; Fyfe, 1952; *T. onisciformis*, 1825; Quatrefages, 1865; *T. Kefersteinii* Apstein, 1900; Lo Bianco, 1901, 1904; Schwartz, 1905 (not *T. Kefersteini* Greeff 1879*a*).

Small, delicate; parapodia slender, with well-developed anterior cirri. Disposition of hyaline glands characteristic: these are restricted to the dorsal pinnules of the third and fourth pairs of parapodia. Gonads in the dorsal rami only; tail absent.

Distribution.—This species is evidently widespread in the Pacific, as the reports of Eschscholtz (1825), Rosa (1908*b*), and Izuka (1914) show. In Monterey Bay, Dales (1955*b*) found *T. elegans* to be present throughout the year, but to be commoner in winter. Analysis of the MLR samples has revealed that *T. elegans* is most numerous in the offshore waters of California, the highest density of population occurring about 400 km. from the coast, and extending from San Francisco Bay to Guadaloupe Island (fig. 53). Within this area in July (1949), for example, there were as many as 300–500 *T. elegans* in 1,000 m.^{3}, between

the surface and a depth of 75 m. Similar numbers were found in the winter in the same area, although rather more were found inshore. In January/February (1950) samples taken within 100 km. of San Francisco and Pt. Concepción

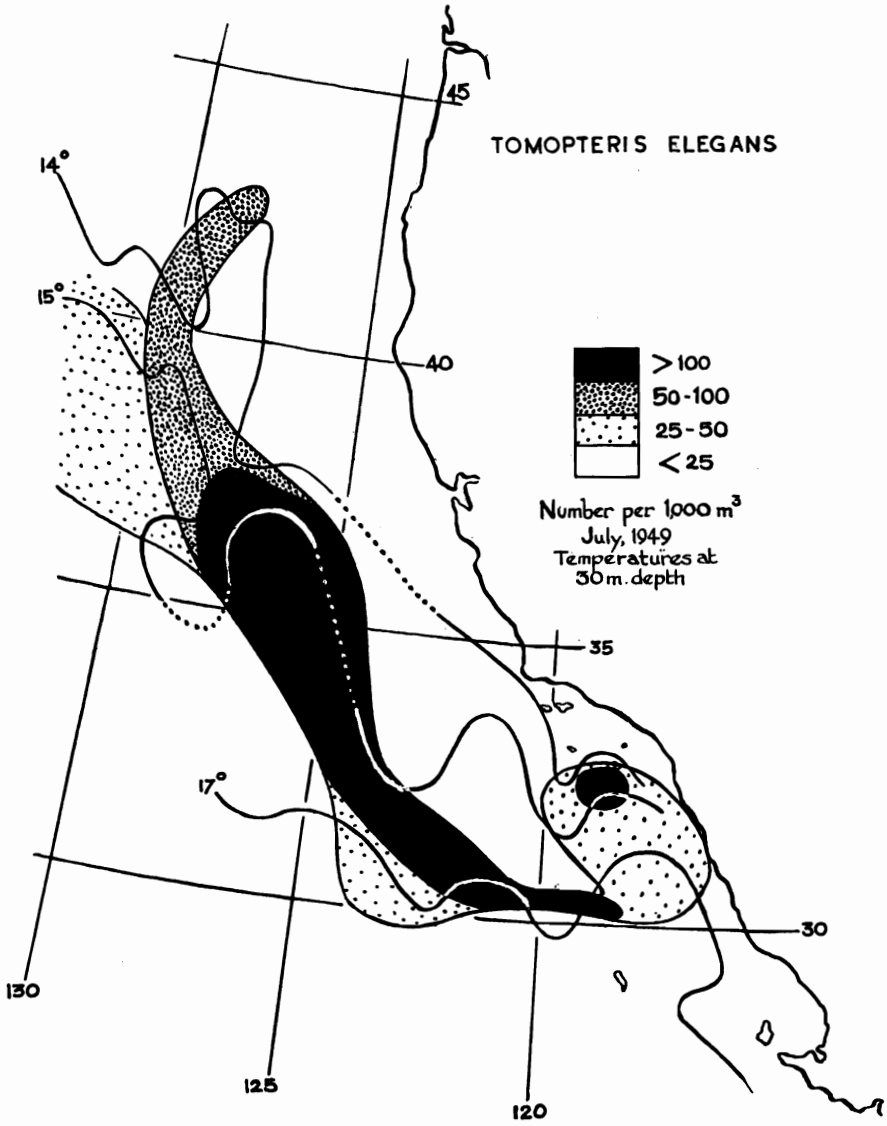

Fig. 53. Distribution of *Tomopteris elegans* off the Pacific Coast of North America.

included about 30 *T. elegans* in 1,000 m.^{3}, whereas ten times this density was found 500 km. off the coast. Figure 53 gives some idea of the distribution of this species in July (1949) and the temperature of the surface water at this time. In winter the maximum numbers were found where the surface temperature was 13° C. or more.

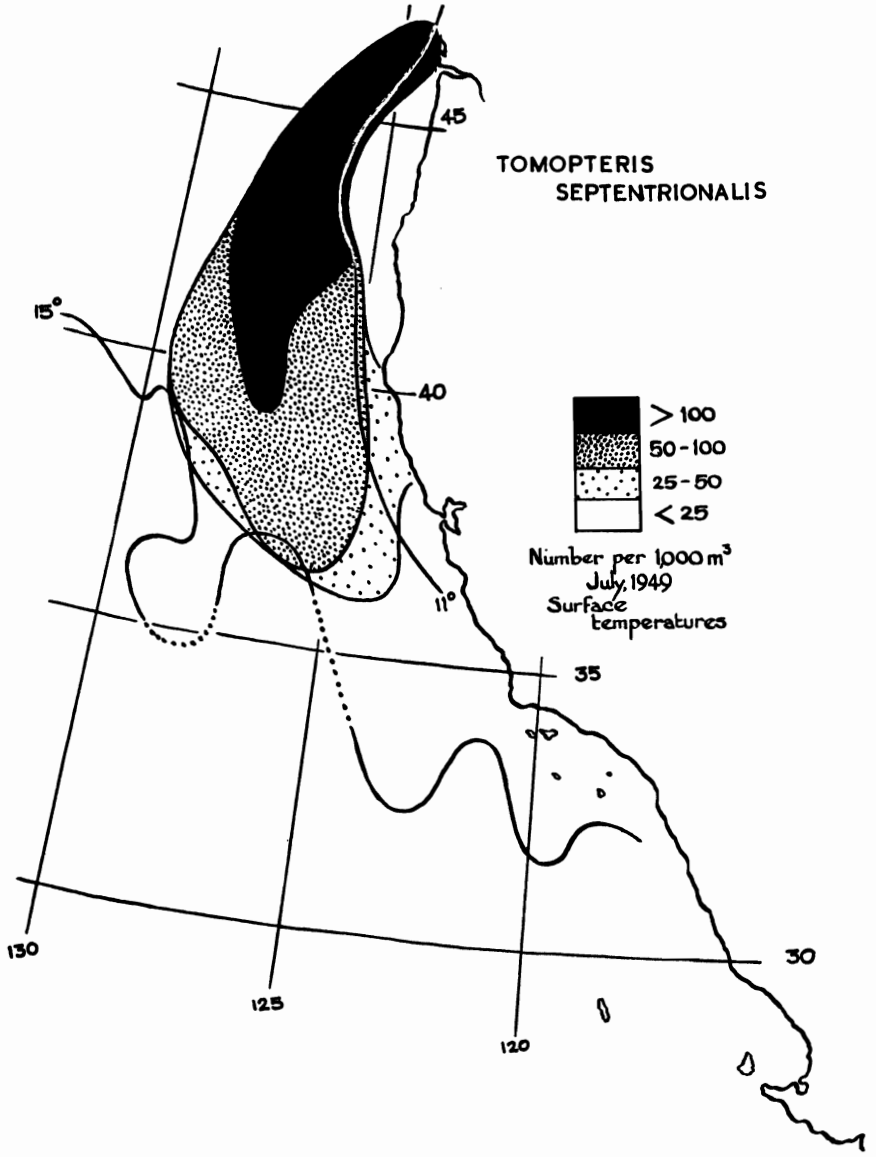

Fig. 54. Distribution of *Tomopteris septentrionalis* off the Pacific Coast of North America.

Tomopteris (*Tomopteris*) *cavallii* Rosa

(Figs. 51, *b*; 52, *b*)

Tomopteris Cavallii Rosa, 1907; *T.* (*Tomopteris*) *Cavallii* Rosa, 1908*b*; Southern, 1911; Ehlers, 1917; Fauvel, 1923; Caroli, 1928*a*, 1933; Benham, 1929; Monro, 1930, 1936; Wesenberg-Lund, 1935, 1936, 1951; Terio, 1947*a*; Dales, 1955*b*; ? *T.* (*T.*) *Colosii* Caroli, 1930; Terio, 1947*a*.

Usually rather small; shape characteristic, the hinder segments tapering toward the posterior end. Tail absent; no anterior cirrus. Prostomial horns short, usually curving backward. Chromophile glands large and conspicuous; no hyaline glands. First two pairs of parapodia with some

tubules in the dorsal pinnules of same appearance (when preserved) as those composing the chromophile glands, but these tubules irregular in arrangement, the third pair of parapodia without them, or with tubules less well developed. First chromophile gland on the fourth pair of parapodia; gonads in the dorsal rami only, the most anterior in the first or second pair of parapodia.

The appearance of the tubules in the most anterior pinnules is reminiscent of *T. pierantonii* Terio (1947*c*), but the arrangement is never as regular as Terio describes for that species.

Distribution.—Rosa (1907) found this in the Pacific near Valparaiso, Chile, and between New Zealand and New Caledonia. In the MLR investigations *T. cavallii* has been found to be sparsely distributed in the surface waters throughout the area investigated, although generally most common 400–500 km. offshore. In July (1949), for example, maximum numbers of 25–50 worms in 1,000 m.^{3} were found, but over most of the area surveyed this species has been found in much smaller numbers. In Monterey Bay, where deeper hauls were taken, *T. cavallii* was found to be more numerous (Dales, 1955*b*).

Tomopteris (*Tomopteris*) *septentrionalis* Steenstrup

(Figs. 51, *f*; 52, *g*)

Tomopteris septentrionalis Steenstrup, 1849; Quatrefages, 1865; Levinsen, 1883; Apstein, 1900; Reibisch, 1905; Berkeley, 1924; Treadwell, 1948; *T.* (*Tomopteris*) *septentrionalis* Rosa, 1908*b*; Izuka, 1914; Ehlers, 1913; Malaquin & Carin, 1922; Caroli, 1928*b*; Terio, 1947*a*; Monro, 1930; Fauvel, 1923; Benham, 1929; Støp-Bowitz, 1948; Berkeley & Berkeley, 1948; Wesenberg-Lund, 1936; Fyfe, 1952; Dales, 1955*b*; ? *T.* (*T.*) *Eschscholtzi* Greeff, 1879*a*; Apstein, 1900; Rosa, 1908*b*; Caroli, 1933.

Chromophile glands rather diffuse, situated toward the tips of the ventral rami; hyaline glands more distinct, and situated at the tips of the ventral rami; no glands in the dorsal pinnules, which have a characteristic oblong shape. Anterior cirri absent; gonads in the dorsal rami only.

Distribution.—In the Pacific, Izuka (1914) found *T. septentrionalis* in Misaki Bay, Japan, and Berkeley (1924) found it off Vancouver Island, British Columbia. Rosa (1908*b*) reports it from the Chilean coast. In the MLR investigations, *T. septentrionalis* was found to be by far the most abundant species of *Tomopteris*. Unlike *T. elegans,* however, *T. septentrionalis* was found to be abundant in the colder water region in the northern part of the survey area, extending from Cape Disappointment, Oregon, south to San Francisco Bay, and was found more inshore than the former species (fig. 54). In July, 1949, 200–600 worms in 1,000 m.^{3} were found about 300 km. from the Oregon coast; in winter as many as 2,000 were found in 1,000 m.^{3} in the same area. In February, 1950, these large numbers extended as far south as San Francisco, and as many as 500 were found in 1,000 m.^{3}, 400 km. off Monterey. In Monterey Bay itself the largest numbers of *T. septentrionalis* were found at this time (Dales, 1955*b*). This species seems to be less numerous in spring and autumn, and how far this is due to the coastal current system and how far to a breeding cycle, has been discussed elsewhere (Dales, 1955*b*). The distribution of *T. septentrionalis* off the coast of North America in July, 1949, is shown in figure 54. From these records, and from previous reports, it would appear that this tomopterid is a cold-water coastal form.

Family TYPHLOSCOLECIDAE Uljanin

All the members of this family are pelagic. They are highly specialized, fusiform, transparent worms with the prostomium prolonged forward into a papilla, and posteriorly merging into the anterior segments. Eyes are always absent, but the nuchal organs are, on the contrary, well developed and conspicuous. Dorsal to the pharynx is a large gland (the retort organ). The parapodial cirri are large and foliaceous, but the chaetigerous lobes are rudimentary; simple chaetae are usually recognizable only in the most posterior segments, in which the chaetigerous lobes are also best developed. There is a pair of anal cirri, generally foliaceous and similar to the parapodial cirri.

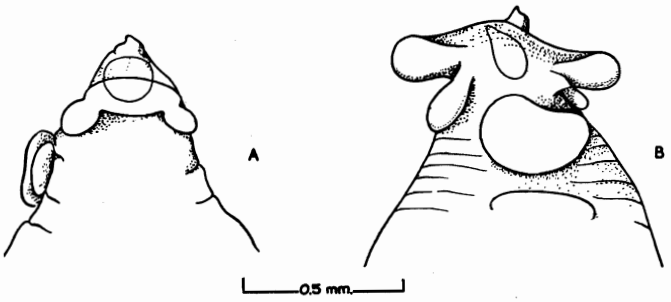

Fig. 55. *Typhloscolex mülleri; A,* dorsal view of the anterior region of the body; *B,* view of the same region from the right side.

Genus *Typhloscolex* Busch

Small or very small; body short, fusiform, transparent. Prostomium prolonged forwards into a papilla, and raised dorsally and ventrally into ciliated lobes, the dorsal lobe being connected with the nuchal organs. Segments not clearly differentiated, bearing dorsal and ventral cirri, and a few simple chaetae in the most posterior segments.

Typhloscolex mülleri Busch

(Fig. 55, *a* and *b*)

Typhloscolex mülleri Busch, 1851; Reibisch, 1895; Ehlers, 1913; Chamberlin, 1919; Fauvel, 1923; Augener, 1929; Monro, 1930; Treadwell, 1943; Berkeley & Berkeley, 1948; Uschakov, 1952; Dales, 1955*b*; *Acicularia Vachowii* juv. Greeff, 1879*a*; *Sagitella Kowalevskii* forme B Wagner, 1872; ? *S. Bobretskii* Wagner, 1872; ? *S. barbata* Uljanin, 1878; ? *S. praecox* Uljanin, 1878.

Friedrich (1950) has given some attention to the features separating the different species of *Typhloscolex,* and has placed special emphasis on the form of the prostomial lobes and the position of the nuchal organs, but more study of the known specimens must be made before even the validity of the species that have been described can be shown. I can find no significant difference between the specimens in the MLR collections and the various descriptions of *T. mülleri,* and the ciliated lobe pattern corresponds closely with that illustrated for this species by Friedrich (1950).

Distribution.—Only five specimens have been found in the MLR collections, in samples taken at all seasons, but all in water with a temperature of about 15° C. (fig. 60); a further specimen was found in the Monterey Bay samples

(Dales, 1955*b*). *Typhloscolex* has been found all over the world. Chamberlin (1919) described his specimen collected off the Gilbert Islands as *T. mülleri,* but he did not illustrate the specimen. Treadwell's (1943) specimens were also ascribed to this species, and these were collected from widely different localities in the Pacific as well as in the equatorial Atlantic. Berkeley and Berkeley (1948) have also found *T. mülleri* in the plankton off the west coast of Vancouver Island, and Uschakov (1952) in the Kamchatka region.

Genus *Sagitella* Wagner

Body short, slender, fusiform, transparent. Prostomium prolonged anteriorly into a slender papilla, but not raised into ciliated lobes as in *Typhloscolex.* Nuchal organs conspicuous, forming two boomerang-shaped ridges on the posterior part of the prostomium. No caruncle as in *Travisiopsis,* but the large retort-shaped organ may be seen by transparency of the body wall. Parapodial cirri large and foliaceous, the two anal cirri being particularly well developed and reminiscent of the terminal fin of the chaetognath, *Sagitta.*

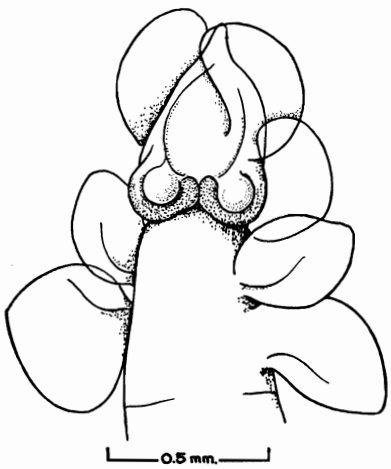

Fig. 56. *Sagitella kowalevskii,* dorsal view of the anterior region of the body. Some of the cirri have been removed to reveal the nuchal ridges.

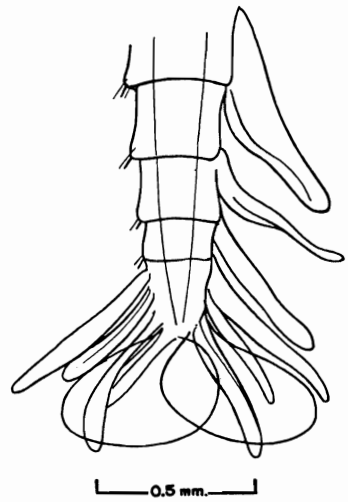

Fig. 57. *Sagitella kowalevskii,* posterior region of the body showing the form of the anal cirri.

Sagitella kowalevskii Wagner

(Figs. 56 and 57)

Sagitella Kowalevskii forme A Wagner, 1872; *S. Kowalevskii* Uljanin, 1878; Reibisch, 1895; Southern, 1910, 1911; Gravier, 1911; Fauvel, 1916, 1923; Støp-Bowitz, 1948; Uschakov, 1952; Dales, 1955*b*; *S. kowalewskii* Ehlers, 1913; Chamberlin, 1919; Benham, 1927, 1929; Okuda, 1937, 1938; Berkeley & Kerkeley, 1948; Fyfe, 1952; *Acicularia Virchowi* Langerhans, 1877; Greeff, 1878, 1879*a*; *Typhloscolex Mülleri* Greeff, 1879*c*; *Plotobia paucichaeta* Treadwell, 1943.

Usually 1 mm. across and about 15 mm. in length; distinguished from other typhloscolecids by the absence of the caruncle and ciliated cushions, and by the characteristic shape of the nuchal organs.

Distribution.—Although usually occurring singly in the samples taken during the MLR investigations, this species has been found throughout the year, and seems to be widely distributed in the southern part of the area (fig. 60). Samples from this collection in which it has been found have been taken from water with temperatures between 10° C. and 24° C., most commonly between 15° C. and 18° C. Chamberlin (1919) collected his specimens between the Galápagos and the Tuamotu Islands; Okuda (1937, 1938) near the Mitsui Marine Station in Japan. Treadwell's (1943) *Plotobia paucichaeta* does not differ in any respect from *Sagitella kowalevskii,* and his specimens were collected throughout the Pacific and central Atlantic. Dales (1955*b*) found it not uncommon in Monterey Bay.

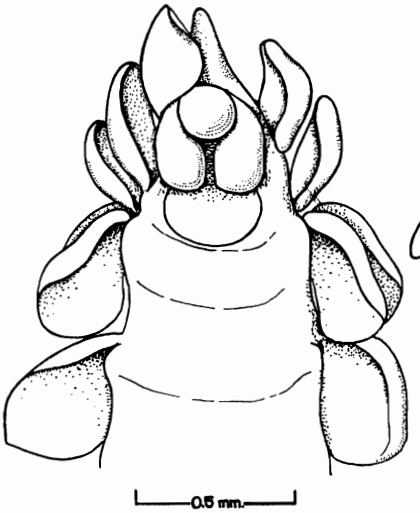

Fig. 58. *Travisiopsis lobifera,* dorsal view of the anterior region of the body. Some of the cirri have been removed to reveal the nuchal organs.

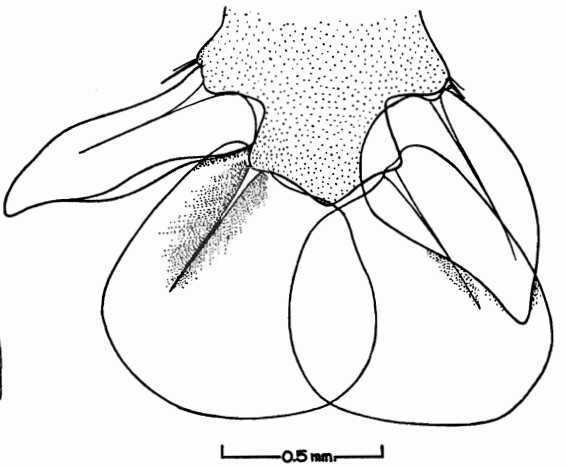

Fig. 59. *Travisiopsis lobifera,* posterior region of the body showing the anal cirri.

Genus *Travisiopsis* Levinsen

Body short, fusiform, transparent, usually more plump than in the preceding genera. Prostomium without ciliated lobes, but with prominent nuchal ridges encompassing a raised caruncle. Parapodial cirri large and foliaceous; only a single pair on the first two segments, but the chaetigerous lobe reduced. Anal cirri large, but comparable in size to the most posterior parapodial cirri.

Travisiopsis lobifera Levinsen

(Figs. 58 and 59)

Travisiopsis lobifera Levinsen, 1885; Reibisch, 1895; Fauvel, 1916, 1923; Støp-Bowitz, 1948, 1951; Dales, 1955*b*; *Plotobia simplex* Chamberlin, 1919; Treadwell, 1943.

Relatively large, up to 25–30 mm. in length and 2–3 mm. across. Parapodial cirri large, cordate or broadly lanceolate in shape; anal cirri almost triangular, broadly overlapping, and each with a transparent supporting rib. This species may be distinguished by the rounded caruncle and the short, parallel, backwardly projecting nuchal processes.

Distribution.—Although rarely occurring in large numbers, this species was one of the most constantly represented in all the samples sorted during the MLR

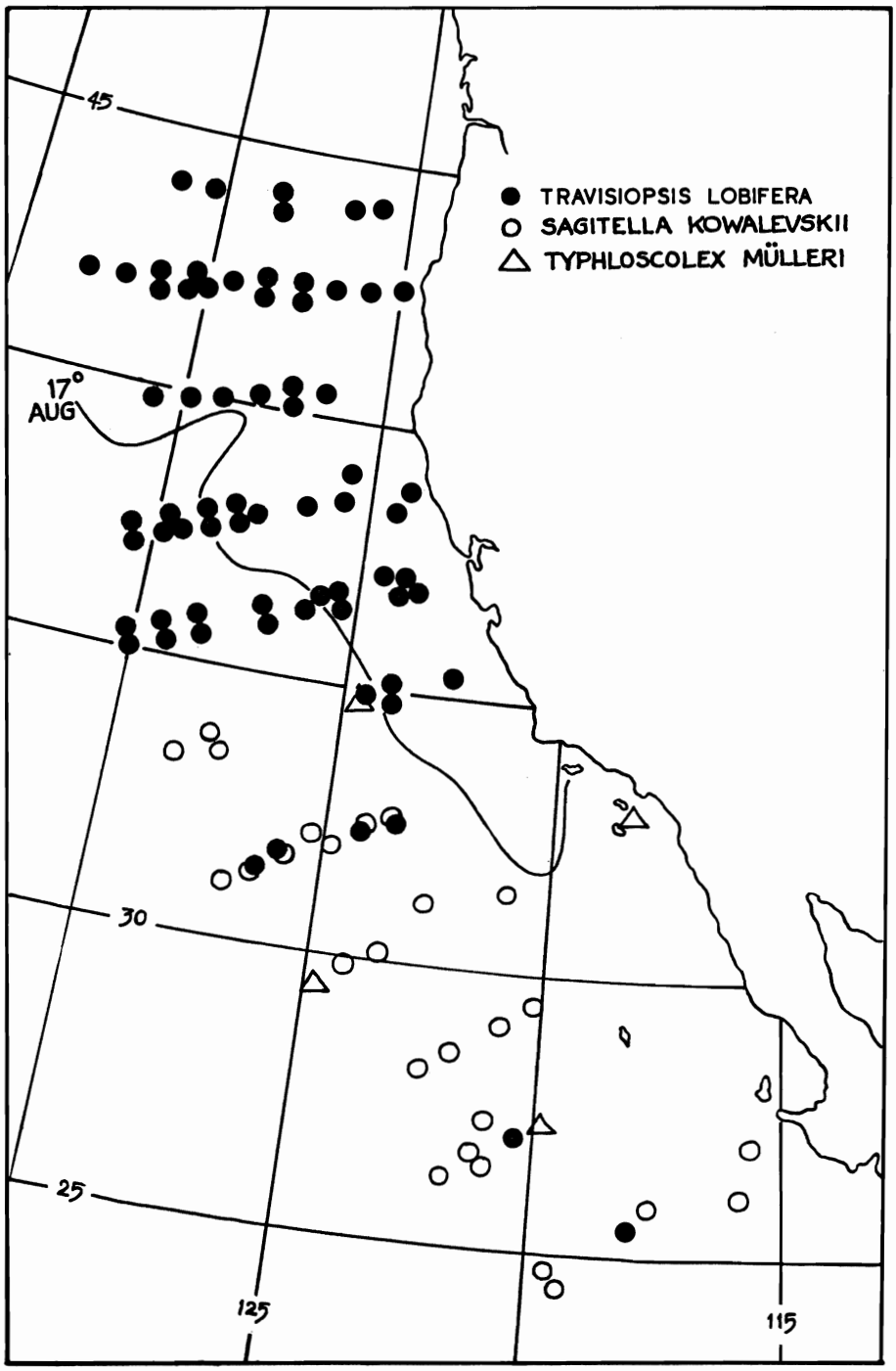

Fig. 60. Locality records of *Travisiopsis lobifera, Sagitella kowalevskii,* and *Typhloscolex müller*i. Surface isotherm.

investigations (fig. 60). It occurred at all seasons within a fairly wide temperature range, but was most commonly found in the colder water region in the north of the survey area in temperatures of 10°–17° C. Apart from Chamberlin's (1919) and Treadwell's (1943) specimens from the Pacific, this species has been recorded mainly from the North Atlantic. Chamberlin's (1919) *Plotobia simplex* is clearly conspecific with *Travisiopsis lobifera,* and his specimens were collected around the Tuamotu Islands, and between these islands and the Galápagos. The specimens collected by Treadwell (1943) were found in the northern and western Pacific. Dales (1955*b*) found it in Monterey Bay.

Travisiopsis levinseni Southern

Travisiopsis levinseni Southern, 1910, 1911; Fauvel, 1916, 1923; Wesenberg-Lund, 1935, 1936, 1939, 1951; Dales, 1955*b*; *T. benhami* Monro, 1936; *Sagitella kowalevskii* Monro, 1930; *S. Kowalewskii* Gravier, 1911; Benham, 1927, 1929; ? *S. opaca* Ehlers, 1913.

Small, rather delicate, deep-water species most readily distinguished from *T. lobifera* by the nuchal processes, which, although resembling those of the latter species in shape, project obliquely outward, and are not parallel as in *T. lobifera.*

Distribution.—Only three specimens have so far been collected from the Pacific, these having been found in the deep hauls taken in Monterey Bay (Dales, 1955*b*).

Travisiopsis coniceps (Chamberlin)

Plotobia coniceps Chamberlin, 1919; *Sagitella lobifera* Ehlers, 1912; Monro, 1930, 1936; *Travisiopsis coniceps* Støp-Bowitz, 1948; Dales, 1955*b*.

This species is at once distinguished by the branched nuchal organs, although in other characters apparently resembling *T. lobifera.*

Distribution.—The records of Monro (1930, 1936) and Ehlers (1912) are from the Atlantic; those of Chamberlin (1919) from the Peruvian coast, and all between 5° S. and 12° S. Dales (1955*b*), however, found the species in Monterey Bay, so it probably occurs elsewhere in deeper water off the coast of North America.

DISTRIBUTION OF PELAGIC POLYCHAETES IN THE PACIFIC OCEAN

Introduction

Few oceanographical expeditions in the Pacific have collected pelagic polychaetes in any great amount, thus a very detailed map of their distribution is not at present possible. However, a more detailed account can now be made within the area explored during the MLR investigations.

The prevailing current off the west coast of the United States is from the north, and in the coastal region is associated with strong centers of upwelling which are particularly well marked at some localities from Cape Mendocino to Baja California, Mexico. This upwelling is mainly responsible for the cold spring and summer temperatures of California. In late summer, when the upwelling diminishes, there is a strong incursion of oceanic water into coastal regions, and much larger numbers of pelagic polychaetes were found at this time. In winter there is less upwelling. This combination of factors is responsible for the remarkably

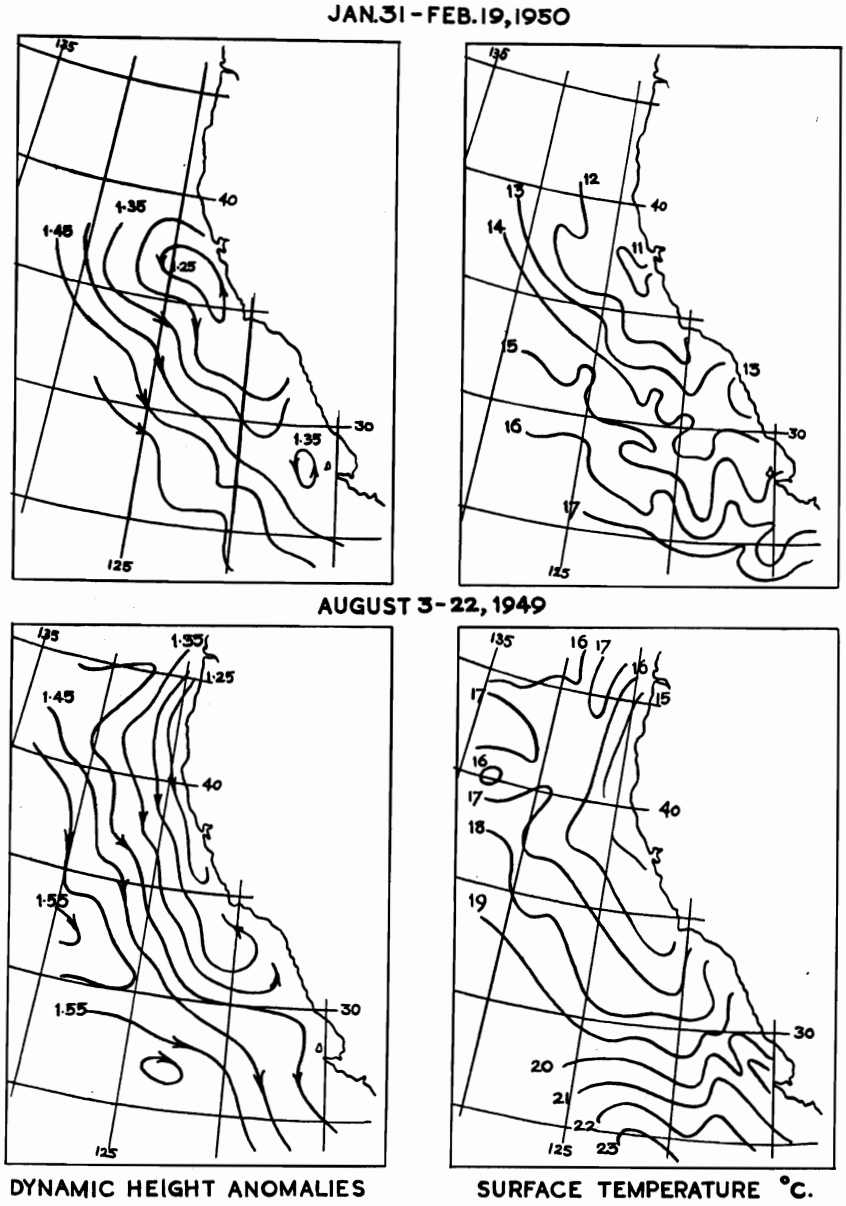

Fig. 61. Currents and surface temperatures over the area studied.

uniform and cool temperatures along the coast of California. The surface temperatures and current pattern over the area surveyed in January-February, and in August, are shown in figure 61, which gives some idea of the winter and summer conditions prevailing over the period during which polychaetes have been collected and identified.

As is well known, salinities are lower in the Pacific than in the Atlantic. Over

the area investigated during the MLR Program, the salinity varied between extremes of 32.5 ‰ in the north and 34.5 ‰ in the south.

The reader is referred to the interesting papers of Gislén (1943, 1944), and to the volume of Sverdrup *et al.* (1942) for information on the physiographical conditions in the Pacific.

The known locality records of most of the species of pelagic polychaetes that have been found so far in the Pacific are shown in figures 62–64. The apparent abundance of species in the Peruvian basin is probably due to the more intensive investigations of this area, and the course of the two major expeditions, the *Albatross,* and the last cruise of the *Carnegie,* is clearly reflected by the records of pelagic polychaetes.

Family PHYLLODOCIDAE

It will be seen from the map (fig. 62) that of all the pelagic phyllodocids, *Pelagobia longicirrata* appears to be both the most abundant and the most widely distributed, for it occurs in the cold waters off the Aleutians, in the equatorial region, and off southern Chile. *Lopadorhynchus uncinatus* also appears to be widespread, although few specimens have been collected. *L. brevis* and *L. krohnii,* on the other hand, are either less widely distributed or rare, and although found off the coast of California in the MLR collections, neither of these species has been found by earlier workers in the Pacific. *L. nationalis,* although not occurring in the MLR collections, was found both by Chamberlin and by Treadwell to be widely distributed in the Pacific. Only two specimens of *Maupasia gracilis* have been found there (Treadwell, 1943), both in equatorial waters. Treadwell also found both species of *Phalacrophorus* to be widely distributed, especially *P. pictus;* although this species has been found off California and Oregon by Treadwell (1943), it has not been found identified in the MLR collections, but it is a very small species and easily overlooked. *Iospilus* has so far been found only off the Gilbert Islands and in the southeast Pacific (Treadwell, 1943).

Family ALCIOPIDAE

Off California the most abundant species were found to be *Torrea candida, Naiades cantrainii, Vanadis formosa,* and *Plotohelmis tenuis. T. candida* has not previously been found in the Pacific, although another species, *T. pelagica,* which has not been found during these investigations, was collected by Chamberlin (1919) and Treadwell (1943) in the southwest Pacific. The most widespread species found by earlier workers are *Vanadis minuta, Alciopina parasitica,* and *Rhynchonerella angelini.* Of these three, only the first and the last have been collected off California, but it should be borne in mind that only superficial hauls have been taken. This is probably the explanation of the predominance of species such as *Vanadis formosa* and *Naiades cantrainii,* both of which are certainly surface-living forms. The distribution of *Plotohelmis tenuis* is interesting as it is almost confined to the cold-water stream from the north, off the coasts of northern California and Oregon. Both *Alciopa reynaudii* and *Watelio gravieri* were found also only in this colder water off Oregon. The

salinity in this region is usually below 33 ‰. Treadwell (1943) found *Alciopa* off the Peruvian coast—another cold-water region—but one specimen has been collected in the warmer water off the Marquesas Islands (fig. 63). The two commonest species of *Rhynchonerella,* also show an interesting difference in their distribution: *R. angelini* occurring only in the colder northern waters; *R. möbii* only in the south (fig. 39).

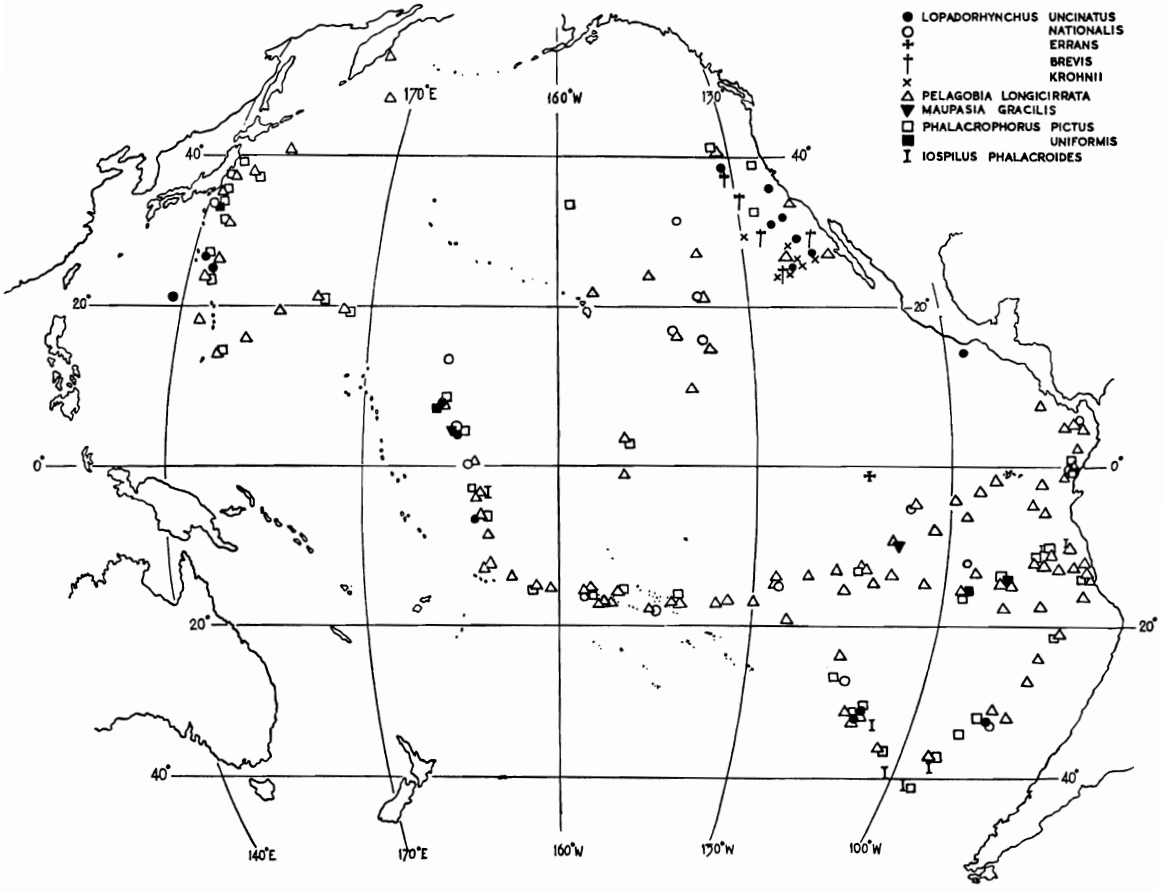

Fig. 62. Locality records of pelagic phyllodocids in the Pacific.

Family TOMOPTERIDAE

Tomopteris septentrionalis, T. elegans, and *T. cavallii* are the three commonest species in the surface waters off the North American coast. Of these, *T. cavallii* is the least numerous, although often more common than *T. elegans* in coastal waters, this species being most abundant 400–500 km. offshore. *T. septentrionalis* appears to be characteristic of the cold-water region with surface temperatures of about 13° C. or less, whereas *T. elegans* is found in larger numbers only in water warmer than this (figs. 53 and 54). *T. pacifica, T. nisseni,* and *T. krampi* have been found only in the deeper hauls taken in Monterey Bay.

Family TYPHLOSCOLECIDAE

Travisiopsis lobifera is not only the most numerous member of this family in North American waters, but also one of the most widespread members of the pelagic polychaete fauna (fig. 64). *T. lobifera* seems to be confined to the colder waters off northern California, although a few specimens were found farther

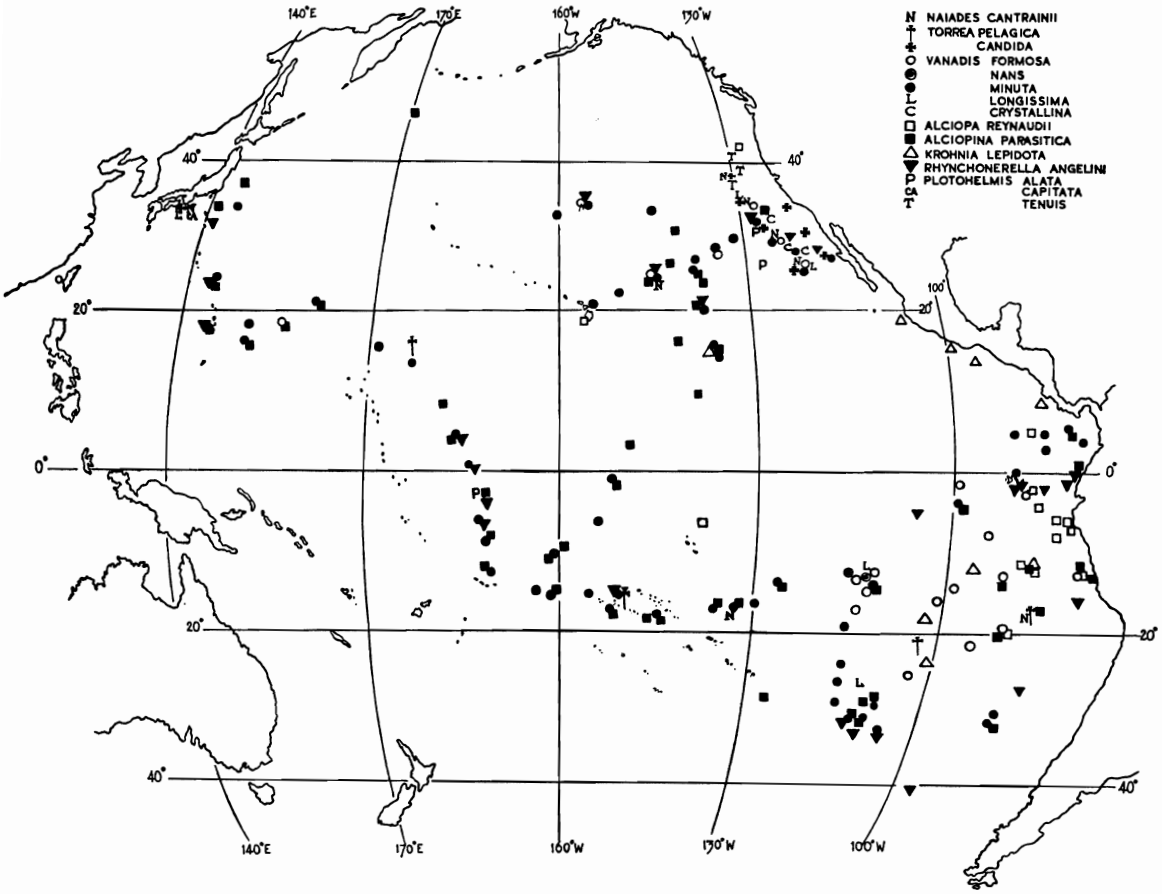

Fig. 63. Locality records of alciopids in the Pacific.

south. Treadwell (1943) found some specimens off the Aleutians, and Chamberlin (1919) found the species between the Galápagos and the Marquesas Islands, and off Chile, but not in the western Pacific. *Sagitella kowalevskii* and *Typhloscolex mülleri* are widely distributed throughout the Pacific; near the coast of North America both species are confined to the warmer waters off southern California and Mexico. *Travisiopsis levinseni* and *T. coniceps* are probably also widely distributed in the colder waters of the Pacific, but have been collected less frequently because of the greater depths at which these animals live.

Vertical Distribution

Although the plankton samples taken during the MLR investigations were taken from a depth of about 75 m., some idea of the vertical distribution of a few of the species was obtained at a position established off central California at about 34° 53′ N., 124° 30′ W. Oblique hauls were taken at three-hour intervals from

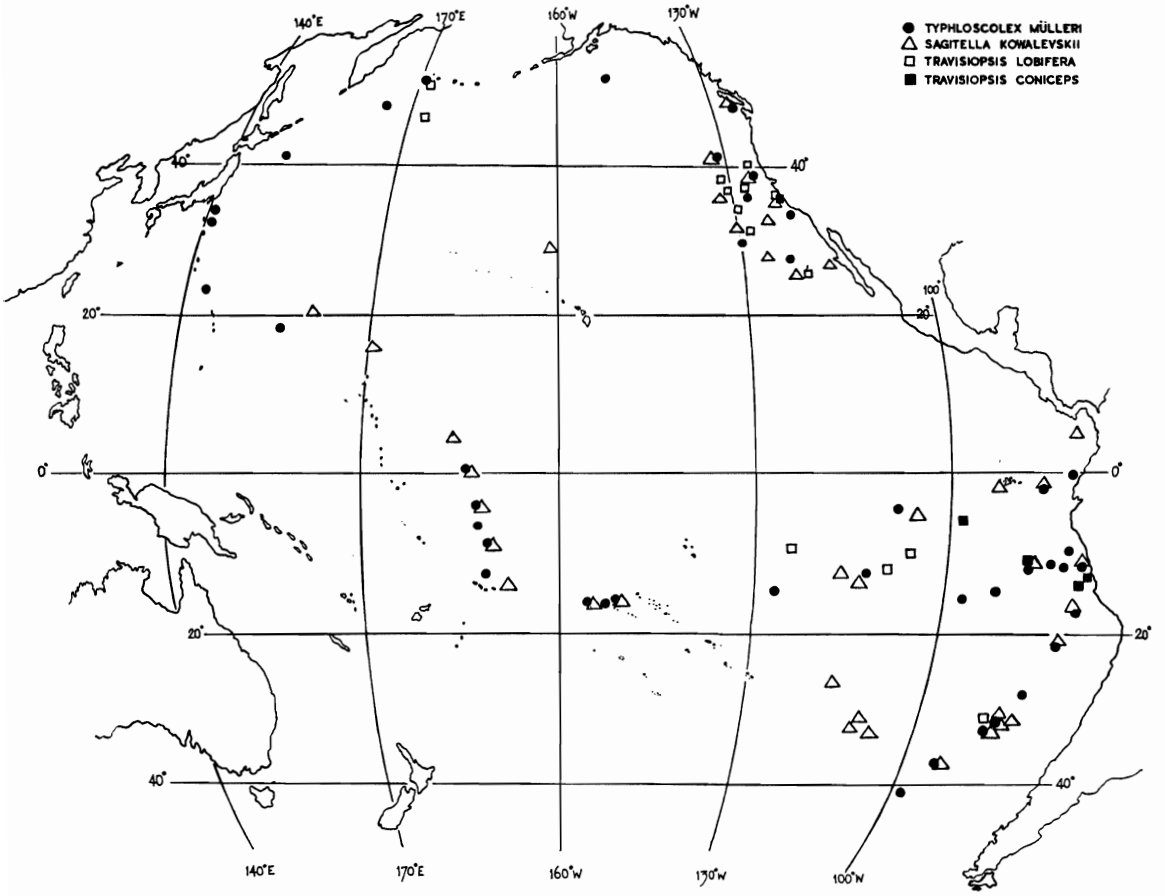

Fig. 64. Locality records of typhloscolecids in the Pacific.

a depth of 75 m. over a period of eight days in mid-October. Seven species of polychaetes were found in this series of samples. Of these, *Lopadorhynchus brevis* was collected only at night, so it may well be that this animal lives at a depth greater than 75 m. during the day. Some species, such as *Travisiopsis lobifera,* seem to be quite as numerous during the day, but rather more numerous at night, whereas others, such as *Naiades cantrainii,* were found to be equally numerous during day and night. In most previous work in which deeper hauls have been taken with open nets, it is quite impossible to tell the depths at which species

live when they occur in such small numbers, but it is clear, from the results of the work on the deeper hauls taken in Monterey Bay, that species such as *Travisiopsis levinseni, T. coniceps,* and *T. krampi* really are deep-water forms, as these species were never found in the MLR collections.

Seasonal Distribution

As the plankton samples were taken over the area studied during the MLR investigations throughout the year, an indication of the seasonal abundance of the different species may be obtained. All the species are most numerous during the late summer and autumn. Many species, such as *Vanadis minuta, V. crystallina, V. formosa, Rhynchonerella möbii,* and *Sagitella kowalevskii,* seem to prefer waters with a temperature of not less than about 17° C., and since the surface isotherm for 17° C. moves south in winter and early spring to the southern limit of the area studied in this work, it is perhaps not surprising that few species of these species were found between December and the beginning of May. On the other hand, cold-water forms, such as *Travisiopsis lobifera* and *Tomopteris septentrionalis,* are much more abundant in winter, so that it may be that even larger numbers of these species occur to the north of the region studied. The number of specimens of most of the species was insufficient to associate any seasonal variation in number with life cycle. The larger number of *Tomopteris septentrionalis* occurring in midwinter and midsummer may indicate a half-yearly reproductive cycle (Dales, 1955*b*), but much of this variation may be due to the varying incursion of ocean water into coastal regions.

KEYS FOR THE IDENTIFICATION OF GENERA AND SPECIES

Family PHYLLODOCIDAE

1. With antennae 2
   Without antennae; palps rudimentary; two pairs of tentacular cirri ..... 3 (Iospilinae)
2. Four antennae; two or three pairs of tentacular cirri ..... 6 (Lopadorhynchinae)
   Two antennae; two pairs of tentacular cirri; parapodia very long, cirriform
   Pontodora pelagica Greeff, 1879*a* (Pontodorinae)
3. Proboscis with jaws 4
   Proboscis unarmed 5
4. First three chaetigerous segments reduced ..... *Phalacrophorus pictus* Greeff, 1879*a*
   First seven chaetigerous segments reduced ..... *Phalacrophorus uniformis* Reibisch, 1895
5. Third and fourth segments without cirri ..... *Iospilus phalacroides* Viguier, 1886
   Third and fourth segments with cirri ..... *Pariospilus affinis* Viguier, 1911
6. Parapodial cirri short, lanceolate, much shorter than the chaetigerous lobe; first three chaetigerous segments modified, often larger than the segments following, and with simple chaetae only 12
   Parapodial cirri foliaceous or cylindrical, if shorter than the chaetigerous lobe, then the first few segments not with simple chaetae alone 7
7. Dorsal parapodial cirri foliaceous, the ventral cirri cylindrical
   Pedinosoma curtum Reibisch, 1895
   Dorsal and ventral cirri essentially similar 8

8. Cirri more or less cylindrical 9
   Cirri foliaceous, usually larger than the chaetigerous lobe, if not, then the dorsal cirri of the second chaetigerous segment prolonged 10
9. Prostomium with eyes; shafts of the chaetae smooth distally
   Pelagobia longicirrata Greeff, 1879*a*
   Prostomium without eyes; chaetal shafts serrated toward the distal end
   Pelagobia serrata Southern, 1909
10. Dorsal cirri cylindrical, rather small except for those of the second chaetigerous segment which are very long ..... *Maupasia isochaeta* (Reibisch, 1895)
    Dorsal cirri foliaceous 11
11. Dorsal cirri of the second segment much longer than those of the first; ventral cirri obtusely pointed ..... *Maupasia gracilis* (Reibisch, 1895)
    Dorsal cirri of the second segment not longer than those of the first; ventral cirri subulate
    Maupasia coeca Viguier, 1886
12. First two chaetigerous segments with ventral cirri ..... 13 (*Prolopadorhynchus*)
    First two chaetigerous segments without ventral cirri ..... 16 (*Lopadorhynchus*)
13. Ventral cirri with a filiform extension at the tip
    Lopadorhynchus appendicularis Southern, 1909
    Ventral cirri simple 14
14. Parapodia in the mid-body region with simple chaetae
    Lopadorhynchus nationalis Reibisch, 1895
    Parapodia in the mid-body region with compound chaetae only 15
15. Eyes prominent ..... *Lopadorhynchus macrophthalmus* Reibisch, 1895
    Without eyes ..... *Lopadorhynchus henseni* Reibisch, 1895
16. First ventral cirri on the third or fourth chaetigerous segment 17
    First ventral cirri on the fifth chaetigerous segment
    Lopadorhynchus errans (Chamberlin, 1919)
17. First two chaetigerous segments very large and with heavy, simple, chaetae partly surrounded at the base by a collarlike expansion of the chaetigerous lobe; prostomium rather square in front; no simple chaetae in the third and more posterior segments; first ventral cirrus on third chaetigerous segment ..... *Lopadorhynchus unicinatus* Fauvel, 1915
    If the first two chaetigerous segments larger than the following, then the simple chaetae not as well developed and never partly surrounded at the base by a collar 18
18. First two pairs of parapodia stouter and shorter than those following; only one, or no simple chaetae in the more posterior segments; first ventral cirrus on the third segment
    Lopadorhynchus krohnii (Claparède, 1870)
    First three pairs of parapodia stouter than the following; usually two simple chaetae in the more posterior segments; first ventral cirrus on the fourth segment
    Lopadorhynchus brevis Grube, 1855

Family ALCIOPIDAE

1. All the chaetae of one kind, either all compound or all simple 2
   More than one kind of chaeta 13
2. All the chaetae simple capillaries ..... *Naiades cantrainii* Delle Chiaje, 1828
   All the chaetae compound 3
3. Chaetigerous lobe terminating in one (usually) or two cirriform appendages 4
   Chaetigerous lobe without a terminal appendage, the aciculum protruding from the apex of the lobe 23
4. Chaetigerous lobe with one cirriform appendage 5
   Chaetigerous lobe with two cirriform appendages
   Alciopa reynaudii Audouin & Milne-Edwards, 1833

5. Pigmented segmental glands on every segment in the mid-body region.....6
   Pigmented segmental glands not on every segment, several consecutive segments with glands alternating with several segments without any pigment (body striped)
   Vanadis longissima (Levinsen, 1885)
6. First two segments coalesced so that the first two pairs of tentacular cirri appear to arise from the first segment .....*Vanadis nans* (Chamberlin, 1919)
   First two segments distinct, the first segment with a single pair of cirri, usually the larger 7
7. Prostomium with a deep incision .....*Vanadis studeri* Apstein, 1893
   Prostomium simple 8
8. Median antenna short, represented by a rounded knob or entirely absent; rim of proboscis simple between the horns .....*Vanadis minuta* Treadwell, 1906
   Median antenna digitiform 9
9. Proboscis with a single pair of terminal horns 12
   Proboscis without a single pair of horns, either with two pairs of lateral horns, or rim divided into subequal papillae 10
10. Proboscis with two pairs of short lateral horns; first five parapodial segments with reduced parapodia .....*Vanadis tagensis* Dales, 1955*b*
    Proboscis with the rim divided into papillae of similar length; only 2–3 pairs of reduced parapodia 11
11. Body purplish-brown in color, without brown transverse bands anteriorly; two pairs of rudimentary parapodia .....*Vanadis violacea* Apstein, 1893
    Body not with this color, but with brown transverse bands anteriorly; three pairs of rudimentary parapodia .....*Vanadis antarctica* (McIntosh, 1885)
12. First two segments following those contributing tentacular cirri with rudimentary parapodia; body often of large size .....*Vanadis formosa* Claparède, 1870
    First 5–6 segments following those contributing tentacular cirri with rudimentary parapodia; slender, delicate worms usually of small size.....*Vanadis crystallina* Greeff, 1876
13. Simple capillary chaetae and simple acicular chaetae 14
    Slender compound chaetae and simple or compound acicular chaetae 16
14. Chaetigerous lobe terminating in a cirriform appendage 15
    Chaetigerous lobe without a terminal cirriform appendage
    Alciopina parasitica Claparède & Panceri, 1867
15. Body with scattered spots of dark pigment; tips of the parapodial cirri acute
    Krohnia lepidota (Krohn, 1845)
    Body without such dark spots; tips of parapodial cirri obtuse
    Krohnia bongraini (Gravier, 1911)
16. Chaetigerous lobe terminating in a cirriform appendage 19
    Chaetigerous lobe without a cirriform appendage 17
17. Eyes directed partly forward, their axes intersecting at right angles as seen from above; second pair of dorsal tentacular cirri longest .....*Plotohelmis tenuis* (Apstein, 1900)
    Eyes directed sideways, the angle between their axes much greater than a right angle when viewed from above; second pair of dorsal tentacular cirri not the longest 18
18. Third pair of dorsal tentacular cirri longer than the second; fifth pair of tentacular cirri hardly detectable .....*Plotohelmis capitata* (Greeff, 1876)
    Second pair and third pair of dorsal tentacular cirri of equal length; fifth pair small but foliaceous .....*Plotohelmis alata* Chamberlin, 1919
19. Parapodial cirri ribbon shaped, the ventral longer than the dorsal; eyes wide apart
    Watelio gravieri (Benham, 1929)
    Parapodial cirri broadly foliaceous, the dorsal longer than the ventral; eyes usually not widely separated 20
20. Acicular chaetae simple, without a small endpiece 21
    Acicular chaetae compound 22

21. 1–2 acicular chaetae in the anterior parapodia ..... *Rhynchonerella gracilis* Costa, 1862
    More than two acicular chaetae in the anterior segments
    Rhynchonerella möbii (Apstein, 1893)
22. Distal endpiece of the acicular chaetae small and simple
    Rhynchonerella angelini (Kinberg, 1866)
    Distal endpiece of the acicular chaetae large and clearly serrated
    Rhynchonerella petersii (Langerhans, 1880)
23. Proboscis with papillae between the horns..... *Torrea candida* (Delle Chiape, 1828)
    Proboscis without papillae between the horns ..... *Torrea pelagica* Chamberlin, 1919

Family TOMOPTERIDAE

1. Parapodia with rectangular pinnules which do not border the inner edges of the rami
   Enapteris euchaeta (Chun, 1887)
   Parapodia with rounded pinnules bordering both inner and outer edges of the rami 2
2. With a distinct tail, or with a short taillike region, bearing reduced parapodia 3
   Without a tail 18
3. Anterior cirrus present 4
   Anterior cirrus absent 10
4. With spur glands 5
   Without spur glands.....13
5. With gonads in both dorsal and ventral rami 6
   With gonads in dorsal rami only 9
6. With rosettes near the tips of the rami in the mid-body region, and on the parapodial trunks of the first two pairs of parapodia 8
   Apparently without rosettes, either on the trunks of the first two pairs of parapodia or in the pinnules in the mid-body region 7
7. Pinnules adnate to the parapodial trunks ..... *Tomopteris spartai* Terio, 1950*b*
   Pinnules not adnate ..... *Tomopteris apsteini* Rosa, 1908
8. Most anterior chromophile gland on the first parapodium
   Tomopteris partenopea Caroli, 1928*b*
   Most anterior chromophile gland on the third parapodium
   Tomopteris nationalis Apstein, 1900, amend. Terio, 1950*a*
   Most anterior chromophile gland on the fourth parapodium
   Tomopteris espansa Caroli, 1932
9. Most anterior chromophile gland on the third parapodium
   Tomopteris membranacea Caroli, 1930
   Most anterior chromophile gland on the fifth parapodium .... *Tomopteris duccii* Rosa, 1907
10. With spur glands 11
    Without spur glands 15
11. Pinnules adnate to the parapodial trunks ..... *Tomopteris marginata* Caroli, 1932
    Pinnules not adnate 12
12. Ciliated epaulettes large; tail well differentiated from the body
    Tomopteris dunckeri Rosa, 1908*b*
    Ciliated epaulettes normal; body gradually tapering toward the tail
    Tomopteris aloysii sabaudiae Rosa, 1907
13. With rosettes in the pinnules 14
    Without rosettes ..... *Tomopteris krampi*
14. Gonads in the dorsal rami only ... *Tomopteris sanzoi* Caroli, 1930 and *T. ehlersi* Caroli, 1930
    Gonads in both dorsal and ventral rami..... *Tomopteris pacifica* Izuka, 1914
15. Gonads present in both dorsal and ventral rami; chromophile glands from first parapodium
    Tomopteris helgolandica Greeff, 1879*a* and *T. nessania* Terio 1952*a*
    Gonads present in the dorsal rami only.....16

16. Rosettes present on the trunks of the first two pairs of parapodia
Tomopteris erythrea Caroli, 1930
Rosettes absent from the trunks of the first two pairs of parapodia.....17
17. Hyaline glands very large; chromophile glands globular; body rather inflated, often large
Tomopteris nisseni Rosa, 1908*b*
Hyaline glands not recognizable; rosettes only, at the tips of the pinnules (from third parapodium) .....*Tomopteris kempi* Monro, 1930
18. Anterior cirri present 19
Anterior cirri absent 27
19. Hyaline glands in the dorsal pinnules of the 3rd and 4th pairs of parapodia only; small delicate worms with slender parapodia.....26
Hyaline glands not only in the 3rd and 4th pairs of dorsal pinnules.....20
20. Chromophile glands normal, compact.....22
Chromophile glands represented by a number of separate tubules or groups of tubules...21
21. Chromophile gland represented by 8–9 groups of tubules
Tomopteris poliglandulata Caroli, 1932
Chromophile glands represented by about 15 simple tubules
Tomopteris miriaglandulata Terio, 1947*b*
22. Gonads present in both dorsal and ventral rami
Tomopteris mariana Greeff, 1882, and *T. rolasii* Greeff, 1882
Gonads present in the dorsal rami only.....23
23. With a small rosette at or near the tip of the ventral ramus in the 2nd pair of parapodia..24
Without rosettes 25
24. Gonads in the dorsal rami of the 3rd–6th pairs of parapodia
Tomopteris stefanellii Terio, 1947*c*
Gonads in the dorsal cirri of the 3rd–10th pairs of parapodia
Tomopteris biancoi Terio, 1947*c*
25. Anterior cirri well developed, at least half as long as the prostomial horns, which are much like those of *T. elegans* .....*Tomopteris carolii* Terio, 1947*c*
Anterior cirri short, not more than a quarter the length of the prostomial horns, which do not resemble those of *elegans* .....*Tomopteris pediculosa* Terio, 1947*c*
26. Gonads present in the 3rd–8th pairs of parapodia.....*Tomopteris elegans* Chun, 1887
Gonads present in the 3rd–9th pairs of parapodia .....*Tomopteris kefersteini* Greeff, 1879*a*
27. Pinnules adnate to the trunks of the parapodia.....*Tomopteris ligulata* Rosa, 1908*b*
Pinnules not adnate 28
28. Chromophile glands not clearly differentiated; hyaline glands more distinct and situated at the tips of the ventral rami; no glands in the dorsal rami
Tomopteris septentrionalis Steenstrup, 1849
Chromophile glands more or less clearly differentiated and compact.....29
29. Four simple tubules similar to those composing the chromophile gland at the apex of the dorsal pinnules of the first parapodium .....*Tomopteris pierantonii* Terio, 1947*c*
If chromophile glandlike tubules in the first dorsal pinnules, not with this constant arrangement 30
30. Gonads in both dorsal and ventral rami.....*Tomopteris carpenteri* Quatrefages, 1865
Gonads in dorsal rami only.....31
31. Base of the ventral ramus not bordered by the pinnule that terminates at the proximal end of the chromophile gland .....*Tomopteris planktonis* Apstein, 1900
Pinnule extending to the base of the ventral ramus
Tomopteris cavallii Rosa, 1907 and *T. colosii* Caroli, 1930

Family TYPHLOSCOLECIDAE

1. Prostomium with prominent ciliary lobes on the dorsal and ventral sides; animals usually of very small size ..... *Typhloscolex* sp.
   Prostomium without such raised ciliary lobes, with or without a median dorsal caruncle, flanked by nuchal ridges or digitiform projections 2
2. Prostomium with a raised caruncle more or less encompassed by the nuchal organs which commonly extend backward in the form of two digitiform lobes 3
   Prostomium without a raised caruncle, although with slightly raised nuchal ridges; long, slender spindle-shaped animals ..... *Sagitella kowalevskii* Wagner, 1872
3. Caruncle T-shaped, or roughly triangular 4
   Caruncle rounded or rectangular 5
4. Nuchal organs extended backward as digitiform processes which are long and almost parallel *Travisiopsis lanceolata* Southern, 1910
   Processes of nuchal organs branched ..... *Travisiopsis coniceps* (Chamberlin, 1919)
5. Nuchal organs directed obliquely outward behind the caruncle *Travisiopsis levinseni* Southern, 1910
   Nuchal organs directed backward and more or less parallel *Travisiopsis lobifera* Levinsen, 1885

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