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Revision of Some Species Referred to Leptonereis, Nicon, and Laeonereis (Polychaeta: Nereididae)

ABSTRACT

Pettibone, Marian H. Revision of some species referred to Leptonereis, Nicon, and Laeonereis (Polychaeta: Nereididae). Smithsonian Contributions to Zoology, number 104, 53 pages, 27 figures. 1971.—Some 47 nereid species, which have been referred directly or indirectly to Leptonereis, Nicon, and Laeonereis, are reviewed and revised, based on examination of type-specimens, where available, and additional nereid material. Diagnoses are given for eight genera, two of them emended and two of them new. Sixteen species (including 16 synonyms) are referred to the eight genera, one of which is considered to be new. Supplementary descriptions and figures are given for fourteen of them. Four additional species are referred to Platynereis Kinberg, one of which is described and figured. Four species are considered to be indeterminable.

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Marian H. Pettibone

Revision of Some Species Referred to Leptonereis, Nicon, and Laeonereis (Polychaeta: Nereididae)

Introduction

A collection of heteronereids, found swarming in Tampa Bay, Florida, were sent to me for identification by Mr. John L. Taylor. In the process of attempting to identify them and comparing them with other nereid species, it appeared to me that a general review and revision of some of the genera and species of the family were needed. There has been no general agreement among polychaete systematists regarding the nereid genera Leptonereis, Nicon, and Laeonereis, as indicated by the following brief review.

Kinberg (1866:178) established three genera in a new family Niconidea, all characterized by the absence of paragnaths or soft papillae on the pharynx or proboscis. They were separated by differences in the parapodia: Nicon (six species), with the parapodia remaining uniform along the body, Leptonereis (single species), with the parapodia changing gradually, and Nicomedes (single species), with the parapodia changing abruptly and divided into three regions. Of the eight species, which were described very briefly by Kinberg, only Leptonereis laevis was figured in a subsequent publication. These differences were considered by Claparède (1870:454) to be of secondary value or associated with the sexual stages (i.e., heteronereids) and for this reason he selected Leptonereis (including Nicon and Nicomedes) to be retained. He ranked it as a subgenus of Nereis, emended it, and included within it a new

Marian H. Pettibone, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D. C. 20560 species, Nereis (Leptonereis) glauca, from the Mediterranean Sea.

The description of Claparède's species was supplemented by Ramsay (1914a:245), who observed minute papillae on the pharynx. The genus Leptonereis thus was further emended, resulting in a diagnosis that applied to L. glauca but not to L. laevis, the type-species of Leptonereis. Subsequently, Leptonereis generally was used to include nereids in which the pharynx lacks paragnaths and with soft papillae present or absent. This resulted in a heterogeneous grouping of species, placing together nereids having little affinity with one another or with the type-species, as pointed out by Hartman (1945:22). Some of these species were referred to two new genera: Laeonereis Hartman (1945:22; 1949:56) and Australonereis Hartman (1954b:19).

Based on examination of the type-specimens of Kinberg, Hartman (1949) proposed that Leptonereis Kinberg include only the type-species, L. laevis. She found the type-species of Nicomedes, N. difficilis Kinberg, to be indeterminable and therefore rejected the genus. Nicon Kinberg was retained by her and N. pictus was selected, from the six species included in the genus by Kinberg, as the type-species. Unfortunately, figures were not added nor was a clear generic diagnosis included.

After 1949, eight new species were added to *Nicon* by Knox (1951), Hartman (1953, 1958, 1965b, 1967) and Berkeley and Berkeley (1964). Two new species were added to *Laeonereis* by Day (1957) and Hartmann-Schröder (1959). Two new species were added to *Leptonereis* by Rullier (1963) and Fishelson and Rullier (1969). *Nicon* has come in turn to

include a heterogeneous grouping of species. Some of the species have been bandied about among the various genera, resulting in considerable confusion.

As shown in the list of species summarized on pages 2 to 5, there has been no general agreement regarding the composition of the genera Leptonereis, Nicon, and Laeonereis. The emphasis on the presence or absence of papillae on the pharynx has caused some of the difficulty. The papillae are sometimes difficult to detect, particularly on small specimens in which the pharynx is not extended. Some of the specimens examined were found to have minute denticles or pectinae on the pharynx, characteristic of Platynereis. Other sources of confusion have been incomplete or incorrect descriptions, inadequate figures, and confused terminology.

The purpose of this study, then, has been to review the various species that have been assigned either originally or subsequently to *Leptonereis*, *Nicon*, or *Laeonereis*, to seek additional characters that would serve to separate them in more meaningful ways, to supplement the original descriptions and figures, to clarify the terminology, and to include comparable generic diagnoses.

In addition to the abundant collections deposited in the Smithsonian Institution (USNM), some nereid material was available for study from the following Museums: Allan Hancock Foundation, Los Angeles (AHF), through K. Fauchald; American Museum of Natural History, New York (AMNH), through H. S. Feinberg; British Museum (Natural History), London (BMNH), through J. D. George; Museum National d'Histoire Naturelle, Paris (MNHNP). through J. Renaud-Mornant; Naturhistoriska Riksmuseet, Stockholm (NRS), through R. Oleröd; Universitetets Zoologiske Museum, Copenhagen (UZMC), through J. B. Kirkegaard; Zoologisches Museum, Berlin (ZMB), through G. Hartwich; Zoologisches Staats-museum, Hamburg (ZMH), through G. Hartmann-Schröder. Additional type material was obtained from the private collections of Professor F. Rullier at Angers, France, and from the Department of Zoology, Tel-Aviv University, Israel, through Ch. Lewinsohn. Additional nereids were sent in exchange by G. A. Knox from the University of Canterbury, New Zealand. Information concerning type-material deposited in the Museum of Comparative Zoology, Harvard, was obtained from H. W. Levi.

I take this opportunity to thank the above-mentioned individuals for their cooperation and help in arranging for the loans or exchanges of the nereid material on which this study is based. The manuscript benefited from the suggestions of Meredith L. Jones and Horton H. Hobbs, Jr., both of the Smithsonian Institution.

Of the 47 nereid species reviewed, 17 were originally assigned to Leptonereis [or Nereis (Leptonereis)], 15 to Nicon, three each to Nereis and Tylorrhynchus, two each to Leonnates [or Nereis (Leonnates)], Ceratocephale, and Laeonereis, and one each to Nicomedes, Chinonereis, and Stenoninereis.

The species of Nereididae, treated in this report, are listed below, along with indications of their type-localities, locations of the type-specimens (when known), and summaries of their subsequent and present designations.

ORIGINAL DESIGNATION
Nereis Linnaeus, 1758:

- N. heterocheta Quatrefages, 1865:552. Java. Holotype in Museum National d'Histoire Naturelle, Paris.
- 2. N. culveri Webster, 1880: 111. New Jersey and North Carolina, eastern North America. Syntypes in United States National Museum (US NM 541, 28178) and British Museum (Natural History) (BMNH ZB 1971.30).
- N. tridentata Webster, 1880:142. New Jersey, eastern North America. Type-specimens no longer exist.

Leonnates Kinberg, 1866 or Nereis (Leonnates):

1. L. pusillus Langerhans, 1880:279. Madeira.

SUBSEQUENT AND PRESENT DESIGNATIONS

Holotype examined and referred to Tylorrhynchus by Grube (1870:312). Referred to T. chinensis by Ramsay (1914b:231). Referred to T. heterochaetus [sic] by Gravier and Dantan (1932:671), see page 44.

Referred to Leptonereis by Fauvel (1923b:124). Referred to Laeonereis by Hartman (1945:21), see page

Referred to Ceratonereis by Hartman (1945:21). Specimens from Georgia and North Carolina examined; designated herein as typespecies of Websterinereis new genus, see page 21.

Questionably referred to Leptonereis glauca by Ramsay (1914a:251); same, without question, by Fauvel (1914:163). Referred to Laeonereis glauca by Hart-

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ORIGINAL DESIGNATION

2. N. (L.) ehlersi Augener, 1913:142. Australia.

Leptonereis Kinberg 1866, or Nereis (Leptonereis):

- L. laevis Kinberg, 1866: 179. Guayaquil, Ecuador. Syntypes in Naturhistoriska Riksmuseet, Stockholm (not found in 1970).
- N. (L.) glauca Claparède, 1870:454. Gulf of Naples.
- N. (L.) cebuensis Grube, 1878:61. Philippine Islands. Syntypes in Zoologisches Museum, Berlin (ZMB Q3465).
- N. (L.) vaillanti Saint-Joseph, 1888:246.
 France.

- 5. L. vasculosa Giard, 1890: 78. France.
- N. (L.) inermis Hoagland, 1920:608. Philippine Islands. Holotype in United States National Museum (USNM 18947).
- N. (L.) acuta Treadwell, 1923:1237. Brazil.
 Paratypes in United
 States National Museum
 (USNM 19030).

SUBSEQUENT AND PRESENT
DESIGNATIONS

man (1959a:244). Referred herein to Websterinereis glauca, see page 27. Referred to Leptonereis by Monro (1938:622). Referred to Laeonereis by Hartman (1949:56). Referred to Australonereis by Hartman (1954b:19).

Type-species of Leptonereis Kinberg, 1866, by monotypy. Syntypes examined by Hartman (1945, 1949), see page 6.

Referred to Leptonereis by Ramsay (1914a:244). Referred to Laeonereis by Hartman (1945:22). Specimens from England and France examined (BMNH, MNHNP, USNM) and referred herein to Websterinereis, see page 27.

Referred to Laeonereis by Hartman (1959a:243, 262). Syntypes examined and referred herein to Platynereis, see page 46.

Referred to N. (Leonnates) pusillus by Augener (1910: 236). Referred to Leptonereis glauca by Ramsay (1914a:245) and Fauvel (1914:163).

Referred to Laeonereis glauca by Hartman (1959a:245). Specimen from France, identified by Saint-Joseph, examined (MNHNP) and referred herein to Websterinereis glauca, see page 27.

Nomen nudum.

Possibly Nicon by Hartman (1949:55). Referred to Laeonereis by Hartman (1959a:
244, 262). Designated as
type-species of Kinberginereis new genus, see page 30.
Referred to Leptonereis culveri by Hartman (1938:14).
Referred to Laeonereis culveri by Hartman (1945:21),
see page 14.

ORIGINAL DESIGNATION

- L. egregicirrata Treadwell, 1924:13. Antigua,
 West Indies. Syntypes
 in United States National Museum (USNM 20324).
- L. foli Fauvel, 1930:520.
 New Caledonia. Holotype in Museum National d'Histoire Naturelle, Paris (MNHNP).
- N. (L.) distorta Treadwell, 1936:273. China. Holotype in United States National Museum (USNM 20118).
- L. pandoensis Monro, 1937:242. Uruguay (freshwater). Syntypes in British Museum (Natural History) (BMNH 1937: 4:22: 4-30) and United States National Museum (USNM 43474).
- 12. L. glauca moniloceras Hartman, 1940:217. Southern California and western Mexico.
- L. nota Treadwell, 1941:
 Texas, Gulf of Mexico. Holotype in American Museum Natural History (AMNH 2896).
- L. mexicana Treadwell, 1942:1. Lower California, western Mexico. Holotype and paratype in American Museum Natural History (AMNH 3222).
- L. punctata Wesenberg-Lund, 1949: 289. Persian Gulf. Syntypes in Universitetets Zoologiske Museum, Copenhagen (UZMC).
- L. zebra Rullier, 1963: 474. Mauritius, Indian Ocean. Syntypes in collection of F. Rullier (No. 16-10, W 92).
- 17. L. davidi Fishelson and

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Referred to Nereis by Treadwell (1939:233). Redescribed by Pettibone (1956:284): syntypes considered to include two species, N. egregicirrata (Treadwell) and N. allenae Pettibone (1956:287).

Referred to Laeonereis by Hartman (1949:55). Holotype examined and referred herein to Websterinereis, see page 23.

Considered questionable by Hartman (1956:255). Referred herein to Tylorrhynchus heterochetus, see page 44.

Referred to Laeonereis by Hartman (1959a:245). Syntypes examined and referred to Laeonereis culveri, see page 14.

Referred to Nicon monitoceras by Hartman (1958: 265). Referred herein questionably to Platynereis, see page 48.

Referred to Laeonereis culveri by Hartman (1951:44). Holotype examined, see page 14.

Types examined and referred to Nicon by Hartman (1956:253, 274, 279). Perhaps N. moniloceras by Hartman (1959a:245). Types examined and referred herein to Rullierinereis, see page 35.

Referred to *Nicon* by Hartman (1958:265). Syntypes examined and referred herein to *Websterinereis*, see page 25.

Perhaps Nicon by Hartman (1965a:36). Syntypes examined and designated herein as type-species of Rullierinereis new genus, see page 33.

Holotype examined and re-

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Rullier, 1969:62. Red Sea. Holotype in Department of Zoology, Tel-Aviv University, Israel (No. E 62/238).

Nicomedes Kinberg 1866:

 N. difficilis Kinberg, 1866:179. Rio de Janeiro, Brazil. Holotype in Naturhistoriska Riksmuseet, Stockholm (NRS 572).

Nicon Kinberg, 1866:

- N. eugeniae Kinberg, 1866:178. Magellan Strait, South America. Type-specimens in Naturhistoriska Riksmuseet, Stockholm.
- N. loxechini Kinberg, 1866:179. Magellan Strait, South America. Holotype in Naturhistoriska Riksmuseet, Stockholm.
- 3. N. maculata Kinberg, 1866:178. La Plata, Argentina. Holotype in Naturhistoriska Riksmuseet, Stockholm (NRS 493).
- N. pictus Kinberg, 1866:
 178. Brazil. Syntypes in Naturhistoriska Riksmuseet, Stockholm (NRS 486).
- N. tahitanus Kinberg, 1866: 178. Tahiti. Holotype in Naturhistoriska Riksmuseet, Stockholm (NRS 494).
- N. virgini Kinberg, 1866:
 179. Magellan Strait,
 South America. Holotype in Naturhistoriska
 Riksmuseet, Stockholm
 (NRS 576).
- N. aestuariensis Knox, 1951:225. New Zealand. Holotype in Canterbury Museum, New Zealand.
- N. ehlersi Hartman, 1953:29. Falkland Islands. Syntypes in Naturhistoriska Riksmuseet, Stockholm (NRS 3863).

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ferred herein to *Platynereis* species, see page 49.

Type-species of Nicomedes Kinberg, 1866, by monotypy. Holotype examined by Hartman (1949:57) and considered to be indeterminable. Holotype examined, see page 49.

Referred to Nereis by Ehlers (1897:67) and Hartman (1949:59).

Holotype examined by Hartman (1949:61) and referred to *Platynereis magalhaensis* Kinberg, 1866.

Holotype examined by Hartman (1949:58). Holotype examined and selected herein as type-species of *Nicon*, see pages 7, 8.

Syntypes examined by Hartman (1949:57) and selected as type-species of *Nicon*. Syntypes examined and considered to be indeterminable, see page 49.

Holotype examined by Hartman (1949:59). Holotype examined and considered to be indeterminable, see page 49.

Holotype examined by Hartman (1949:59). Holotype examined and considered to be indeterminable, see page 49.

Specimens from type-locality examined (USNM 43475, from G. A. Knox), see page 11.

Syntypes examined and referred to N. maculata, see page 8.

ORIGINAL DESIGNATION

- N. lackeyi Hartman, 1958: 263. Florida. Holotypes in United States National Museum (US NM 29627-8).
- N. peruviana Berkeley and Berkeley, 1964:128. Off Peru, pelagic. Holotype and paratype in United States National Museum (USNM 32821-2).
- 11. N. uncinatus Hartman, 1965b:86. Off New England.
- 12. N. abyssalis Hartman, 1967:66. Antarctic.
- 13. N. benhami Hartman, 1967:66. Antarctic.
- 14. N. polaris Hartman, 1967:68. Antarctic.
- N. maculatus.—Gallardo, 1968:65. South Viet Nam. In Allan Hancock Foundation (AHF 0252).

Ceratocephale Malmgren, 1867:

- C. osawai Izuka, 1903:
 Japan.
- C. corallicola Reish, 1968:215. Eniwetok, Marshall Islands. Holotype and paratypes in United States National Museum (USNM 38-392-3).

Tylorrhynchus Grube, 1868:

- 1. T. chinensis Grube, 1868:22. China (Shanghai).
- 2. T. sinensis.—Dawydoff, 1952:88. Indochina.

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Referred herein to Stenoninereis martini, see page 39.

Referred herein to Platynereis sp., see page 48.

Referred herein to Rullierinereis uncinata, see page 31.

Generic affinities doubtful.

Specimens from Benham's record of Nereis loxechini (BMNH 1928:2:29: 222-223, 226-228) from McMurdo Sound, the basis of N. benhami, examined and referred herein to N. maculata, see page 8.

Generic affinities doubtful.

Referred herein to Rullierinereis gallardoi new species, see page 39.

Referred to Tylorrhynchus chinensis by Ramsay (1914b: 231). Referred to T. heterochaetus [sic] by Gravier and Dantan (1932:671), see page 44.

Incorrect genus, according to Pettibone (1970:233). Referred to Websterinereis foli, see page 23.

Type-species of Tylorrhynchus Grube, 1868:22, by monotypy. Referred to T. heterochaetus [sic] by Gravier and Dantan (1932:671), see page 44.

Error for T. chinensis.— Hartman (1959a:280), see page 44. NUMBER 104

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2. T. bahamensis Hartmann-Schröder, 1958: 238. Bahamas.

Chinonereis Chamberlin, 1924:

 C. edestus Chamberlin, 1924:81. China (Canton), freshwater. Holotype not present in Museum of Comparative Zoology, Harvard.

Laeonereis Hartman, 1945:

- 1. L. ankyloseta Day, 1957: 83. South Africa.
- L. brunnea Hartmann-Schröder, 1959:135. El Salvador, Central America. Holotype and paratypes in Zoologisches Staats-museum, Hamburg (ZMH 143).

Stenoinereis Wesenberg-Lund, 1958:

 S. martini Wesenberg-Lund, 1958:9. West Indies (St. Martin). Syntypes in United States National Museum (US NM 29726). SUBSEQUENT AND PRESENT
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Referred herein to Rullierinereis, see page 31.

Type-species of Chinonereis Chamberlin, 1924, by original designation and monotypy. Referred herein to Tylorrhynchus heterochetus, see page 44.

Referred herein to Websterinereis punctata, see page 25. Type-specimens examined and referred herein to Laeonereis culveri, see page 14.

Type-species of Stenoninereis Wesenberg-Lund, 1958, by monotypy, see page 39.

Of the 47 species listed above, the following seven are not discussed further:

Leptonereis egregicirrata Treadwell [Referred to Nereis egregicirrata and N. allenae by Pettibone (1956)]

Leptonereis vasculosa Giard [nomen nudum]
Nereis (Leonnates) ehlersi Augener [Referred to
Australonereis by Hartman (1945b)]

Nicon eugeniae Kinberg [Referred to Nereis by Ehlers (1897)]

Nicon loxechini Kinberg [Referred to Platynereis magalhaensis by Hartman (1949)]

Nicon abyssalis Hartman [Generic affinities doubtful] Nicon polaris Hartman [Generic affinities doubtful]

The remaining 40 species are referred to Leptonereis Kinberg (single species), Nicon Kinberg, emended (two species, two synonyms), Laeonereis Hartman, emended (single species, four synonyms), Websterinereis new genus (four species, four synonyms), Kinberginereis new genus (single species), Rullierinereis new genus (five species, one of them new), Stenoninereis Wesenberg-Lund (single species, one synonym), Tylorrhynchus Grube (single species, five synonyms), Platynereis Kinberg (four species), and Indeterminable Nereididae (four species).

All of the genera discussed in this report (Leptonereis Kinberg, Nicon Kinberg, Laeonereis Hartman, Websterinereis new genus, Rullierinereis new genus, Stenoninereis Wesenberg-Lund, Tylorrhynchus Grube, and Kinberginereis new genus) show a number of characters in common, among which are the following. The prostomium is subpyriform, with paired frontal antennae, paired biarticulate palps, and usually two pairs of eyes (sometimes three pairs; sometimes lacking?). The tentacular segment is achaetous and apodous, bearing four pairs of tentacular cirri with distinct cirrophores. The first two setigerous segments have subbiramous parapodia, the notopodia lacking notosetae; the remaining segments have biramous parapodia. The ventral cirri are short, tapered, and single (not double). The pharynx lacks typical paragnaths (with or without soft papillae). The pygidium is provided with a pair of anal cirri. The eight genera may be separated according to the following Key.

Key to the Genera

- Dorsal cirri at base of upper notopodial ligules; neuropodia with lower ligules (Figures 1a, b; 6e,f; 17d,e; 18c,d)
- 2. Notopodia bilobed, with lower acicular lobes continuous with presetal distal lobes and upper notopodial ligules (latter diminishing posteriorly); neuropodia distally with diagonal anterior acicular lobes and shorter postsetal lobes (Figure 23h,i,n). Notosetae homogomph spinigers (Figure 23j). Neurosetae arranged in fan-shaped bundles and composed of homogomph and heterogomph spinigers and heterogomph falcigers (Figure 23h-m). Pharynx without papillae
 Stenoninereis Wesenberg-Lund
- 2'. Notopodia with low rounded lobes and subacicular ligules; neuropodia thick, bilobed distally with neuroaciculum between (Figure 25c-e). Notosetae hemigomph spinigers (Figure 25f), Neurosetae nearly encircling bilobed neuropodial lobes, arranged in form of "3" and

composed of hemigomph and heterogomph spinigers and heterogomph falcigers (Figure 25c-i). Pharynx with soft papillae on both maxillary and oral rings Tylorrhynchus Grube 3. Notosetae homogomph spinigers and homogomph falcigers posteriorly (Figure 18g,j). [Notopodia with two notopodial ligules (Figure 18c,d). Pharynx without papillae]. Rullierinereis new genus 4. Neurosetae all spinigerous—homogomph and hemigomph, without falcigers (Figure 17h-k). [Neuropodia with bilobed presetal lobes and short rounded postsetal lobes in addition to 5. Neurosetae only homogomph spinigers and homogomph falcigers with rather long blades (Figure 6g,h). Dorsal cirri very small—shorter than notopodial ligules (Figure 6b-f). Pharynx with tufts of papillae on maxillary ring (Figure 5c-e,g). [Notopodia with presetal lobe in addition to two notopodial ligules and neuropodia with presetal and postsetal lobes 5'. Some neurosetae heterogomph falcigers with relatively long blades (Figures 2i, 5f). Dorsal cirri longer than notopodial ligules (Figure 2b-e). Pharynx without papillae on maxillary ring 6 6. Pharynx with papillae on basal or oral ring: pair of larger papillae on area VI, single row of small papillae on areas VII-VIII (Figures 8a,b; 11b; 12a; 16a,b). Websterinereis new genus 7. Upper notopodial ligules in middle and posterior segments large, scale-like, with minute terminal dorsal cirri. Neuropodia without postsetal lobes Leptonereis Kinberg 7'. Upper notopodial ligules not enlarged, scale-like. Neuropodia with digitiform to conical

Abbreviations Used in the Figures

I-VIII, areas of pharynx acL, acicular lobe aL, anterior lobe an, anus anC, anal cirrus cph, cirrophore dC, dorsal cirrus dLa, dorsal lamella dLo, dorsal lobe fAn, frontal antenna mR, maxillary or distal ring of pharynx neLi, neuropodal ligule noLi, notopodial ligule oR, oral or basal ring of pharynx pa, palp pGl, parapodial gland pL, posterior lobe poL, postsetal lobe poLa, postsetal lamella prL, presetal lobe tC, tentacular cirrus tS, tentacular segment vC, ventral cirrus vLa, ventral lamella

Leptonereis Kinberg, 1866; emended Hartman, 1945

Type-species.—L. laevis Kinberg, 1866, by monotype. Gender: feminine.

REMARKS.—Leptonereis was proposed to receive a single species, L. laevis Kinberg, from Guayaquil, Ecuador. The original description was very sketchy. Subsequently, figures were added by Kinberg (1910, pl. 20: fig. 7), including dorsal and ventral views of the anterior end with the pharynx extended, a parapodium from setiger 10, and upper and lower neurosetae. Based on examination of the syntypes, deposited in the Naturhistoriska Riksmuseet, Stockholm, Hartman (1945, 1949) supplemented the description and included figures of anterior and posterior parapodia, the latter showing the characteristic greatly enlarged upper notopodial ligule with a minute terminal dorsal cirrus (pl. 3: figs. 5, 6, in Hartman, 1945). Hartman also pointed out that the types were atokous individuals and not epitokes, as Grube (1878:62) had supposed, and that L. laevis was the only known nereid which could be referred to Leptonereis, as defined in her revision of the genus. Unfortunately, the syntypes could not be found recently in the Stockholm Museum, according to Mr. Oleröd (in correspondence), and were not available

for the present study. The following diagnosis is based on the descriptions and figures given by Kinberg (1866:179; 1910:53, pl. 20: fig. 7) and Hartman (1945:21, pl. 3: figs. 5, 6; 1949:56, pl. 8: figs. 5, 6).

DIAGNOSIS.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Dorsal cirri at bases of upper notopodial ligules in anterior region. Notopodia with two ligules, upper one gradually increasing in size, becoming greatly enlarged, oval, scalelike, with minute dorsal cirri inserted terminally in middle and posterior parapodia. Neuropodia with setigerous lobe and lower ligule. Ventral cirri short, tapered. Notosetae [homogomph?] spinigers only. Neurosetae homogomph [?] and heterogomph spinigers and heterogomph falcigers with rather long blades. Pharynx with paired jaws, without paragnaths or papillae.

Following Hartman (1945, 1949), Leptonereis Kinberg is considered to include the single type-species: L. laevis Kinberg from Ecuador. The other 16 species (pages 3-4), described originally under Nereis (Leptonereis) or Leptonereis, are referred to seven other genera, including Kinberginereis (1) Laeonereis (3), Nereis (1), Platynereis (3), Rullierinereis (2), Tylorrhynchus (1), Websterinereis (4), and one nomen nudum.

Nicon Kinberg, 1866; emended

Type-species.—N. maculata Kinberg, 1866, selected herein. Gender: feminine.

DIAGNOSIS.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous, notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at bases of upper notopodial ligules. Notopodia with two ligules and small supraacicular or presetal lobe between them. Neuropodia with conical or bilobed acicular lobes, digitiform or conical postsetal lobes, and lower ligules. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae homogomph spinigers, heterogomph falcigers, and with or without heterogomph spinigers. Pygidium with paired anal cirri. Pharynx with paired jaws, without paragnaths or papillae.

REMARKS.—Nicon Kinberg was established for six

new species: N. eugeniae, N. loxechini, and N. virgini from the Magellan Strait, N. maculata from Argentina, N. pictus from Brazil, and N. tahitanus from Tahiti. The species were only briefly described and figures were lacking. No type-species for Nicon was designated. The genus was characterized by the pharynx lacking paragnaths and papillae and by having parapodia uniform along the body. Claparède (1870:454) placed Nicon under Leptonereis Kinberg. Nicon eugeniae was referred to Nereis by Ehlers (1897:67) and has been so recorded by various polychaete workers. Nicon loxechini was subsequently assigned by Ehlers (1908:73) and Benham (1921:65) to Nereis, and by Monro (1930:107) to Leptonereis. As pointed out by Hartman (1949:61), however, these records are confused and are referred herein to Nicon maculata. Nicon loxechini Kinberg was referred to Platynereis magalhaensis Kinberg by Hartman (1949:61). The other four species were not recorded in the literature until 1949 when Hartman examined Kinberg's type-specimens, supplemented their descriptions to some extent and, for some of them, added figures. For Nicon Kinberg, Hartman selected N. pictus as the type-species without, however, figuring it or giving a clear diagnosis. In order to clarify its identity, I examined the syntypes of N. pictus. As indicated on page 49, I found the specimens to be in such poor condition that no adequate diagnosis could be prepared. This was true also for the holotypes of N. tahitanus and N. virgini. Thus, all three species are to be considered indeterminable. The syntypes of Nicon maculata are better preserved, and, for this reason, I have selected N. maculata as the type-species of Nicon. The diagnosis of the genus and the redescription of the typespecies are based on the syntypes of N. maculata, as well as on additional material that was compared with the syntypes.

In addition to the 15 species originally assigned to *Nicon* Kinberg (page 4), three additional species were referred to it by Hartman (1958:265), including the following:

- N. moniloceras (Hartman, 1940), as Leptonereis glauca moniloceras. Southern California and western Mexico.
- N. mexicana (Treadwell, 1942), as Leptonereis. Lower California, western Mexico.
- N. punctata (Wesenberg-Lund, 1949), as Leptonereis. Persian Gulf.

Of the 18 species, which were originally placed in *Nicon* or subsequently referred to it, four species are retained in the genus as revised, including *N. maculata* (with synonyms *N. ehlersi* and *N. benhami*) and *N. aestuariensis*; nine species are referred to five

other genera, including Nereis (1), Platynereis (3), Rullierinereis (3), Stenoninereis (1) and Websterinereis (1); three species are considered to be indeterminable and two species to have doubtful generic affinities (N. abyssalis, N. polaris).

Key to the Species of Nicon

Nicon maculata Kinberg

FIGURES 1, 2

Nicon maculata Kinberg, 1866:178.

Nereis loxechini.—Ehlers, 1908:73, pl. 8: figs. 8-12.—Benham 1921:65, pl. 8: figs. 67-75; 1927:50. [Not Nicon loxechini Kinberg, 1866]

Not Leptonereis maculata.—Treadwell 1928:469. [=Rulli-erinereis mexicana (Treadwell)]

Leptonereis loxechini.—Monro 1930:107; 1936:138. [Not Nicon loxechini Kinberg 1866]

Nicon maculatus.—Hartman 1949:58.—Not Gallardo 1968: 65. [= Rullierinereis gallardoi new species]

Nicon ehlersi Hartman, 1953:29.

Nicon benhami Hartman, 1967:66, pl. 18: figs. A-C.

MATERIAL EXAMINED.—Off La Plata, Argentina, Eugenie Expedition—holotype of Nicon maculata (NRS 493). Antarctic: Falkland Islands, Burdwood Bank, 53°45′S, 61°10′W, shell fragments and stones, 137–150 meters, Swedish Antarctic Expedition, station 59, 12 September 1902—3 syntypes of Nicon ehlersi (NRS 3863).

Off Falkland Islands: 49°S, 62°W, sand, gravel, stones, 146 meters, *Discovery* Expedition, station WS 97, 18 April 1927—2 specimens (USNM 43445, from BMNH); 49°S, 59°14′W, fine dark sand, 251–225 meters, *Discovery* Expedition, station WS 99, 19 April 1927—1 specimen (USNM 43446, from BMNH). [as Leptonereis loxechini, by C. Monro]

McMurdo Sound off Glacier tongue, about 8 miles north of Hut Point, mud and undecomposed animal remains, 347–457 meters, *Terra Nova* Expedition, 1910, station 316—1 specimen (BMNH 1928: 2: 29: 226–228). 5 miles north of Inaccessible Island, mud, 406–441 meters, *Terra Nova* Expedition, 1910, station 314—1 specimen (BMNH 1928: 2: 29:

222-223). [as Nereis loxechini Kinberg by W. B. Benham]

McMurdo Sound near Cape Hallett, 72°05.8'S, 172°15.2'E, 392 meters, Deep Freeze III, USS "Atka," station 23, 12 January 1958—16 specimens (USNM 43395). McMurdo Sound east of Cape Hallett, 72°08'S, 172°10'E, 434 meters, Deep Freeze III, USS "Burton Island," station 3, 13 January 1958—2 specimens (USNM 43396). Davis Sea, 66°32.84'S, 93°90'E, 146 meters, Deep Freeze III, USS "Burton Island," station 5, 29 January 1958—1 specimen (USNM 43394). Nansen Island, Palmer Peninsula, 66°20'S, 67°47'W, 326 meters, Deep Freeze IV, USS "Edisto," station 31, 24 March 1959—3 specimens (USNM 43393).

Type-material.—The holotype of *Nicon maculata* (NRS 493) consists of three fragments, an anterior one of 8 setigers, a middle one of 19 setigers, and a posterior one of about 25 setigers with a narrow posterior growth zone, with a total length of about 15 mm and a width of 1.5 mm, including setae. The pharynx was extended and the jaws had been removed and are now missing, as noted by Hartman (1949:58) when she examined the type.

The three syntypes of *Nicon ehlersi* Hartman (NRS 3863) consist of a larger anterior fragment of 47 setigers, 62 mm in length and 8 mm in width, including setae, and two smaller specimens, one of which is complete. The pharynx was not extended but two of the syntypes had been slit open, revealing the absence of paragnaths and papillae.

Description.—Length up to 120 mm, width up to 10 mm, including setae, segments up to 140. Prostomium (Figure 2a) with more or less conspicuous middorsal depression on anterior half, with tapered

frontal antennae, stout biarticulate palps; eyes large, anterior pair larger than posterior. Tentacular segment nearly twice length of following segment; tentacular cirri of different lengths, longest extending to setiger 5–9, sometimes indistinctly annulated distally. Parapodia of first two setigers (Figure 2b,c) with dorsal cirrus and single notopodial ligule; neuropodia similar to those of following setigers; neurosetae homogomph spinigers and heterogomph falcigers.

Parapodia of anterior region (Figures 1a.b: 2d.e) with cirriform dorsal cirri extending beyond parapodial ligules, two bluntly conical notopodial ligules and more or less developed small supraacicular lobe between them; neuropodium with conical acicular lobe and digitiform postsetal lobe (ovate process referred to and figured by Benham, 1921, on pl. 8: figs. 69, 70, 72), thick rounded to bullet-shaped lower neuropodial ligule; ventral cirri short, tapered. Notosetae all homogomph spinigers, blades spinous, tapering rather abruptly to slender tips (Figures 1d;2h). Both upper and lower bundles of neurosetae homogomph spinigers similar to notosetae and heterogomph falcigers with rather long blades (Figures 1c; 2i; no heterogomph spinigers). Parapodia of middle (Figure 2f,g) and posterior (Figure 2i) regions with rami more widely separated; dorsal cirri becoming more elongate posteriorly; notopodial ligules more

sharply conical; postsetal neuropodial lobes less conspicuous than in anterior region; lower neuropodial ligules smaller, subconical. Setae similar to anterior region except heterogomph falcigerous neurosetae of upper bundles much stouter, darker, and with shorter blades (Figure 2k; usually two in number); blades often missing and stems somewhat worn, appearing as simple stout spines (Figure 2l).

Pygidium prominent, with long anal cirri. Pharynx lacking paragnaths or papillae; jaws dark ambercolored, each with about 16 oblique teeth along cutting edge (pl. 7: fig. 8, in Ehlers, 1908; pl. 8: fig. 75, in Benham, 1921).

Remarks.—The species is characterized by the absence of paragnaths and papillae on the pharynx, the relatively large eyes, the conical or digitiform postsetal neuropodial lobes, the relatively large, thick lower neuropodial ligules, especially in the anterior region, and the neurosetae composed of only homogomph spinigers and heterogomph falcigers [no heterogomph spinigers, as stated by Monro (1936:139) and Hartman (1949:58)]. In the middle and posterior parapodia, a few neuropodial heterogomph falcigers in the upper bundles are much thicker than the others; the blades are often broken off, thus appearing as simple setae.

Nicon loxechini Kinberg was found by Hartman (1949:61) to have denticles on the pharynx and was

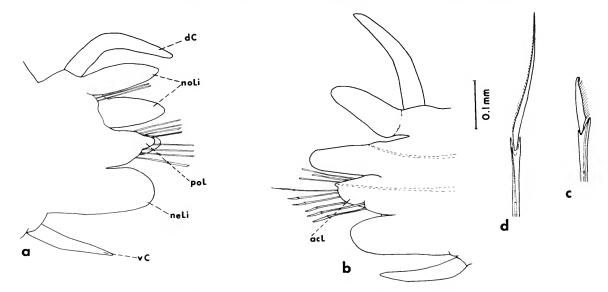
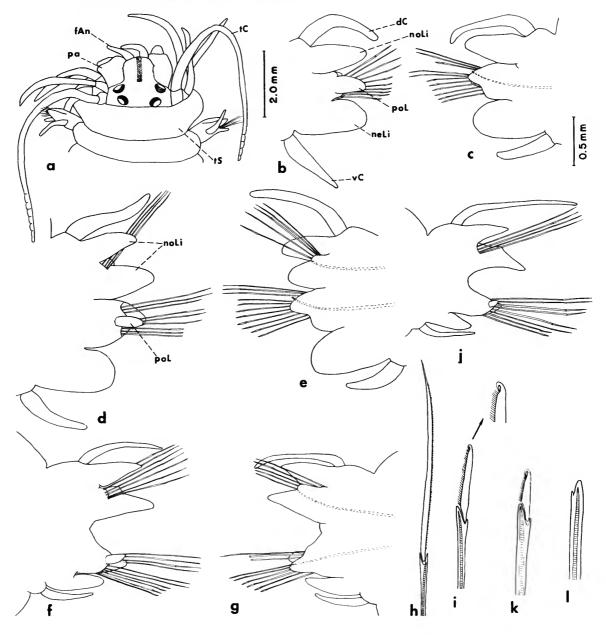


FIGURE 1.—Nicon maculata (holotype of N. maculata, NRS 493): a, Parapodium from anterior region, posterior view; b, same, anterior view; c, neuropodial heterogomph falciger from same; d, homogomph spiniger from same. [Figures c, d, not to scale]

FIGURE 2.—Nicon maculata (USNM 43394): a, Anterior end, dorsal view; b, first parapodium, posterior view; c, second parapodium, anterior view; d, parapodium from anterior region, posterior view; e, same, anterior view; f, parapodium from middle region, posterior view; g, same, anterior view; h, notopodial homogomph spiniger from same; i, neuropodial heterogomph falciger from same; j, parapodium from posterior region, posterior view; k, stout heterogomph falciger from upper neuropodial bundle of same; l, same, with blade broken off and stem somewhat worn. [Figures h, i, k, l, not to scale]



referred to Platynereis magalhaensis Kinberg. The specimens described and figured by Ehlers (1908) and Benham (1921), as Nereis loxechini, were not the same as Kinberg's species. Hartman (1953) gave the new name Nicon ehlersi for Ehlers' record and included Benham's record. Later, Hartman (1967) proposed the new name Nicon benhami for Benham's record. The presence of thick supraacicular heterogomph falcigers in the neuropodia of N. benhami was given as one of the distinguishing characters between N. benhami and N. ehlersi. However, examination of the syntypes of the latter species revealed their presence and both species are herein considered to be synonyms of N. maculata. The other distinguishing character mentioned by Hartman was the presence of prolonged dorsal cirri in N. benhami. These occur in the posterior parapodia of N. ehlersi also. Two of the specimens from McMurdo Sound, identified by Benham (1921) as N. loxechini, were examined (BMNH); they were found to agree with N. maculata, as described herein.

Gravid females with no sign of epitoky have been found. Monro (1930:108, as Leptonereis loxechini) described a male heteronereid.

DISTRIBUTION.—Common Antarctic and subantarctic species. In 92 to 1153 meters.

Nicon aestuariensis Knox

Figures 3, 4

Nicon aestuariensis Knox, 1951:225, pl. 50: figs. 41-46.— Estcourt 1966:179, figs. 1-4, pl. 1: figs. 1-3; 1967a:70; 1967b:390.

MATERIAL EXAMINED.—Heathcote estuary, New Zealand, I. N. Estcourt, collector, from G. A. Knox.—16 atokous specimens and 1 partially metamorphosed male heteronereid (USNM 43475).

Description.—Length up to 250 mm, width up to 6 mm, segments numerous. Prostomium (Figure 3a,c) with faint middorsal depression on anterior half, tapered frontal antennae, stout biarticulate palps; eyes moderately large, anterior pair larger than posterior (eyes much larger on heteronereids). Tentacular segment nearly twice length of following segment; tentacular cirri of different lengths, longest extending to about setiger 5 (4–6). Parapodia of first two setigers (Figure 3d,e) with dorsal cirrus and single notopodial ligule; neuropodium similar to those of following setigers; neurosetae homogomph and

heterogomph spinigers and heterogomph falcigers.

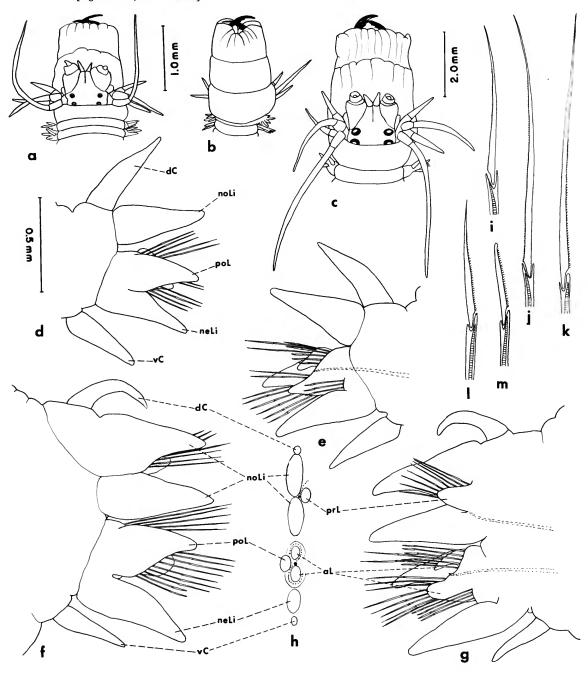
Parapodia of anterior region (Figure 3f-h) with subulate dorsal cirri shorter than notopodial ligules, two conical notopodial ligules, and shorter presetal lobe between them; neuropodium with bilobed anterior lobe-smaller digitiform one above and larger rounded one below neuroaciculum, longer conical postsetal lobe, and conical lower neuropodial ligule; ventral cirri short, subulate. Notosetae all homogomph spinigers, with blades finely spinous, shorter (few upper ones, Figure 3i) and longer (Figure 3j). Neurosetae arranged in S-shaped bundle nearly encircling bilobed anterior lobe (Figure 3h). Supraacicular bundle neurosetae homogomph spinigers with long blades (posterior and upper part bundle, Figure 3i), heterogomph spinigers with short blades (anterior part bundle, Figure 31), and heterogomph falcigers with relatively long blades (anterior part bundle, Figure 3m). Subacicular bundle of neurosetae heterogomph spinigers with long blades (posterior part bundle, Figure 3k), heterogomph spinigers with short blades (lower and anterior part bundle, Figure 31), and heterogomph falcigers (anterior part bundle, Figure 3m). Parapodia of posterior region (Figure 4c,d) somewhat modified: dorsal cirri extending beyond notopodial lobes; presetal notopodial and neuropodial lobes smaller; notopodial ligules with conspicuous coiled glands; notosetae few homogomph spinigers; upper bundle neurosetae few, slightly stouter heterogomph falcigers (Figure 4e); lower bundle neurosetae few heterogomph spinigers.

Parapodia of middle region of slightly modified male heteronereid (Figure 4a,b) showing early stages of extra lamellae: dorsal lamellae medial to dorsal cirri, large rounded neuropodial postsetal lamella and ventral lamella on bases of ventral cirri; notosetae homogomph spinigers; upper bundle neurosetae homogomph spinigers with long blades and heterogomph spinigers with short blades; lower bundle neuropodia heterogomph spinigers with long and short blades (usual type setae completely replaced by swimming setae in fully developed heteronereids, according to Knox, 1951: 226).

Pygidium with pair long anal cirri. Pharynx lacking paragnaths or papillae, dark brown jaws, each with about 10 oblique teeth along cutting edge (Figure 3a-c).

BIOLOGY.—N. aestuariensis is known from estuaries in New Zealand. Additional contributions to its life history, breeding biology, and habits have

FIGURE 3.—Nicon aestuariensis (USNM 43475: a, small complete specimen; b, slightly larger specimen; c-m, larger, partially metamorphosed male heteronereid): a, Anterior end, with pharynx extended, dorsal view; b, same, ventral view; c, same, dorsal view; d, first parapodium, posterior view; e, second parapodium, anterior view; f, parapodium from anterior region, posterior view; g, same, anterior view; h, diagrammatic end view of same showing arrangement of setae; i, homogomph spiniger with relatively short blade; j, same, with long blade; k, heterogomph spiniger with long blade; l, same, with relatively short blade; m, heterogomph falciger. [Figures i-m, not to scale]



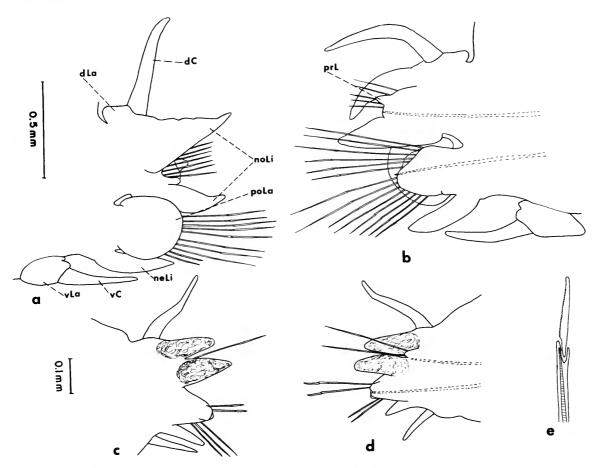


FIGURE 4.—Nicon aestuariensis (USNM 43475: a, b, partially metamorphosed male heteronereid; c-e, small complete specimen): a, Parapodium from middle modified region, posterior view; b, same, anterior view; c, parapodium from posterior region, posterior view; d, same, anterior view; e, heterogomph falciger from same. [Figure e, not to scale]

been reported by Estcourt (1966:179; 1967a:70; 1967b:390). It burrows in the mud, where it is a bottom-deposit feeder, and is able to tolerate wide variations in salinity (from 0 to 29‰). It is one of the most abundant animals in the upper reaches of Heath-cote Estuary. N. aestuariensis is one of the few nereid species that has become well adapted to the estuarine environment that reproduces as epitokes and not in the atokous stage. It appears to have a two-year life cycle. At sexual maturity it forms heteronereids and undergoes a typical swarming periodicity, spawning at the surface. The spent adults die after spawning. The eggs are moderate in size (about 150μ) and

demersal, developing into ciliated larvae. Early development presumably takes place in the surface layers of the mud, the larvae being absent from the plankton. Small specimens were found near the surface of the sediment, with large specimens occupying burrows as deep as 40 centimeters.

DISTRIBUTION.—New Zealand.

Laeonereis Hartman, 1945; eniended

Type-species.—Nereis culveri Webster, 1880, by original designation. Gender: feminine.

DIAGNOSIS.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous, notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at bases of upper notopodial ligules. Notopodia with two ligules and additional presetal lobe in anterior parapodia. Neuropodia with lower ligules and additional presetal and postsetal lobes in anterior parapodia. Ventral cirri very short. Notosetae homogomph spinigers only. Neurosetae homogomph spinigers and, more posteriorly, some homogomph falcigers with rather long blades. Pygidium with paired anal cirri. Pharynx with paired jaws, without paragnaths; with tufts of papillae on maxillary or distal ring and pair of large papillae on oral ring (area VI).

REMARKS.—In addition to L. culveri (Webster) as type-species, Hartman (1945:21) included Nereis (Leptonereis) glauca Claparède (1870) in Laeonereis. The latter species is referred herein to Websterinereis. In the brief diagnosis of Laeonereis given by Hartman, she indicated the presence of heterogomph falcigerous setae. On the contrary, the only falcigers present are homogomph, with rather long blades, as shown in the figures of Webster (1886, pl. 7: fig. 32), Fauvel (1923b, fig. 5e), Monro (1937, fig. lf), and Hartmann-Schröder (1959, fig. 98). Also Hartman indicated that the soft papillae were arranged in tufts on both the oral and maxillary rings of the pharynx. As shown in the figure of Webster (1886, pl. 6: fig. 24), the tufts of papillae are confined to the maxillary ring; the oral ring has a pair of triangular dorsal papillae (area VI).

Subsequently two additional species were added to Laeonereis—L. ankyloseta from South Africa by Day (1957) (referred herein to Websterinereis punctata) and L. brunnea from El Salvador by Hartmann-Schröder (1959) (referred herein to L. culveri). Nereis (Leptonereis) acuta Treadwell (1923) and Leptonereis nota Treadwell (1941) were both synonymized with L. culveri by Hartman (1938:14; 1951:44). Four additional species were referred to Laeonereis by Hartman (1959a, in Catalogue): Nereis (Leptonereis) cebuensis Grube (1878) from the Philippine Islands (referred herein to Platynereis), Nereis (Leptonereis) inermis Hoagland (1920) from the Philippine Islands (referred herein to Kinberginereis), Leptonereis foli Fauvel (1930) from

New Caledonia (referred herein to Websterinereis), and Leptonereis pandoensis Monro (1937) from Uruguay (referred herein to Laeonereis culveri).

Laeonereis culveri (Webster)

FIGURES 5-7

Nereis culveri Webster, 1880:111 [plates referred to but not published]; 1886:140, pl. 6: figs. 23-30, pl. 7: figs. 31, 32 [reprinting of 1880 with addition of figures].—Ferguson and Jones 1949:440.

Leptonereis culveri.—Fauvel 1923b:124, fig. 5.—Hartman 1938:14.

Nereis (Leptonereis) acuta Treadwell, 1923:1237, figs. 1-5. Leptonereis pandoensis Monro, 1937:242, fig. 1a-f.

Laeonereis culveri.—Hartman 1945:21; 1951:44, pl. 13: figs. 3, 4; 1954a:415; 1956:253; 1959a:243, 245, 262; 1959b:539, 540.—Behre 1950:12.—Hedgpeth 1950:111.

—Carpenter 1956:93, 101.—Rioja 1958:257.—Frankenberg and Burbanck 1963:87.—Wells and Gray 1964:72.

—Oglesby 1965:621.—Mazurkiewicz 1969:1146; 1970:1, figs. 1-27.

Leptonereis nota Treadwell, 1941:1, figs. 7-10.

Laeonereis brunnea Hartmann-Schröder, 1959:135, figs. 92-99.

MATERIAL EXAMINED. — CONNECTICUT: Mystic River estuary, 41°22'10"N, 71°59'42"W, depth less than 1 meter, salinity on bottom 31%, 24 August 1964, M. Mazurkiewicz, collector-60 specimens (USNM 33288). New Jersey: Beesley's Point, Great Egg Harbor, coarse sand and gravel, about half tide, H. E. Webster, collector—10 syntypes of Nereis culveri (USNM 541; BMNH). MARYLAND: Broom's Island, about 10 miles from mouth of Patuxent River, 30 May 1939, J. P. E. Morrison, collector—3 specimens (USNM 22244). Patuxent River at Long Point, 1 mile south of Benedict and N.E. of St. Leonard, Calvert County, August 1968, S. L. H. Fuller, collector-3 specimens (USNM 40127-8). Upper Chesapeake Bay in Fox Creek, tributary of Rhode River, 22 August 1969, J. Vogel, collector-5 specimens (USNM 41604). VIRGINIA: Norfolk peninsula in Willoughby Bay and off Hampton Bar, August 1940, F. F. Ferguson, collector—12 specimens (USNM 22245-6). North Carolina: Beaufort, summer 1877, Mr. C. L. Culver, collector-11 syntypes of Nereis culveri (USNM 28178). Cape Hatteras area in Sandy Bay, 12 July 1959, J. L. Taylor, collector-1 specimen (USNM 43400). Currituck Sound, 19 October 1960, J. A. Kerwin, collector-5 specimens

(USNM 33292). Beaufort, 1967, W. B. Vernberg, collector—24 specimens (USNM 38742). South CAROLINA: Charleston, March 1960, R. Lunz, collector-4 specimens (USNM 33291). Georgia: Sapelo Island on Raccoon Bluff Beach, Marsh at high tide, and Blackbeard Creek, sand and mud flat, 1961, M. Gray, collector—10 specimens (USNM 33294-6). High Point, Sapelo Island, muddy sand and Spartina, 1962, D. Frankenberg, collector — 4 specimens (USNM 33297). FLORIDA: East coast in St. John's River drainage system, Brevard County, taken on surface after using Rotenone, 13 May 1956, W. McLane, collector-numerous specimens (USNM 28083). West coast at Seahorse Key near Cedar Key, sand, 1959, 1960, J. L. Taylor, collector-65 specimens (USNM 30045, 33289-90). Gulf coast at Apalachicola and Bald Point, 1960, L. Oglesby, collector-17 specimens (USNM 39640-1). Missis-SIPPI: Biloxi, sandy-mud flat, October 1943, M. W. Williams, collector—2 specimens (USNM 22242). East Ocean Springs at Davis Bay, about 2 feet, brackish water on sheltered shore of sandy mud, 17 August 1949, R. L. Caylor, collector-5 specimens (USNM 22093). Ocean Springs east of Henderson Point, 30°18'N, 89°17'W, 21 March 1968, W. Langley, collector-1 specimen (collection Gulf Coast Laboratory). Louisiana: Grand Isle, sandy beach, E. H. Behre, collector—3 specimens (USNM 22243). Texas: Offats Bayou, Galveston—holotype of Leptonereis nota (AMNH 2896). Upper part Galveston Bay, center of Trinity Bay, mud, 18 December 1969, G. E. Williams, collector—1 specimen (USNM 43401). Brazil: Santos, February 1914, H. Lüderwaldt, collector—3 paratypes of Nereis (Leptonereis) acuta (USNM 19030). URUGUAY: Arroyo de Pando, Canelones, in freshwater, E. H. Cordero, collector-6 syntypes of Leptonereis pandoensis (BMNH 1934:4: 22:4-30; USNM 43474). EL SALVADOR, CENTRAL AMERICA: Gulf of Fonseca, Isla Perrico, G. Hartmann-Schröder, collector-holotype of Laeonereis brunnea (ZMH 143). Gulf of Fonseca—Isla Perrico, Jaltepeque and Jiquilisco estuaries, G. Hartmann-Schröder, collector-numerous paratypes of Laeonereis brunnea (ZMH 143; USNM 43403).

Type Material.—The syntypes of *Nereis culveri* from Great Egg Harbor, New Jersey (USNM 541) include nine complete specimens and one anterior fragment. One of them has a length of 55 mm, a width of 4 mm, including setae, and 110 segments.

The syntypes from Beaufort, North Carolina (USNM 28178) include four complete specimens and seven anterior fragments. The pharynx was not extended on any of the syntypes.

The three paratypes of Nereis (Leptonereis) acuta Treadwell (USNM 19030) are incomplete posteriorly, from 19 to 25 mm in length, 4 mm in width, including setae, and up to 72 segments. None of them had the pharynx extended, but dissection showed the presence of the paired triangular papillae on the oral ring and some tufts of papillae on the maxillary ring; being colorless, they are difficult to see (not mentioned by Treadwell). The more posterior parapodia are modified as in L. culveri; some of the lower neurosetae are homogomph falcigers with rather long blades (not described by Treadwell).

The syntypes of Leptonereis pandoensis (BMNH 1934:4:22:4-30; USNM 43474) include three smaller complete specimens, one of which has a length of 42 mm, a width of 4 mm, including setae, with about 125 segments, and three larger specimens incomplete posteriorly; one with 51 anterior segments has a length of 32 mm and a width of 5 mm, including setae. None of the syntypes had the pharynx extended, as noted by Monro; one of them had been dissected.

The holotype of Leptonereis nota Treadwell (AMNH 2896) is incomplete posteriorly, with a length of 55 mm, a width of 2 mm, including parapodia, and composed of 86 segments. It is rather dark, showing the transverse banding posteriorly. The setae are mostly broken. It is a female having large yolky eggs. The pharynx was partially extended, showing the characteristic tufts of papillae (Figure 5c,d; not mentioned by Treadwell).

The holotype of Laeonereis brunnea from the Gulf of Fonseca (ZMH 143) consists of anterior and middle fragments totaling 41 segments (67, according to Hartmann-Schröder), 14 mm in length (about 20 mm—Hartmann-Schröder), and 2 mm in width, including setae. The numerous paratypes vary in size from small specimens of 21 segments with posterior growth zone, 2 mm in length and 0.5 mm in width, to one of 55 segments with posterior growth zone, 12 mm in length and 1 mm in width. The types of L. brunnea all appear to be juveniles.

DESCRIPTION.—Length up to 60 mm, width up to 5 mm, including setae, segments up to 140. Body widest about segment 8, diminishing rapidly an-

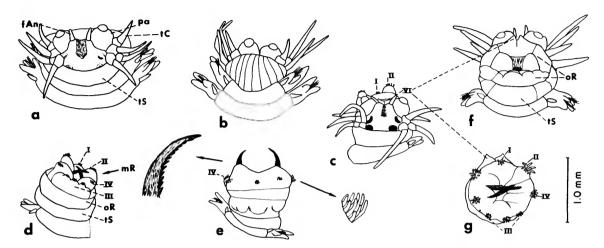


FIGURE 5.—Laeonereis culveri (a,b, syntype of Nereis culveri from New Jersey, USNM 541; c,d, holotype of Leptonereis nota from Texas, AMNH 2896; e, specimen from North Carolina, USNM 38742; f,g, specimens from Florida, USNM 28083): a, Anterior end, dorsal view, prostomium partially withdrawn into tentacular segment; b, same, ventral view; c, anterior end, dorsal view, with pharynx partially extended; left parapodium missing; d, same, ventral view; e, ventral view anterior end with pharynx fully extended; f, ventral view anterior end with pharynx partially extended showing basal or oral ring; g, frontal view of extended pharynx.

teriorly and gradually posteriorly. Variable in coloration: iridescent whitish to yellowish or reddish brown; posterior region sometimes with two broken bands per segment; conspicuous dark glandular areas in dorsal ligules and bases of dorsal and ventral cirri. Prostomium relatively small compared with broad body, with deep anterior notch, sometimes appearing as triangular depression on anterior half; frontal antennae and biarticulate palps short; eyes subequal, moderately large (Figures 5a-c; 6a; 7a). Tentacular segment about twice as long as following segment; tentacular cirri relatively short, longest extending to about setiger 2 (1–3). First two setigers (Figures 6b,c) with dorsal cirri and single notopodial ligule; neuropodia similar to those of following segments.

Parapodia of anterior region (Figures 6d-f; 7c,d) larger, with more numerous lobes. Dorsal cirri much shorter than ligules. Notopodia with larger triangular upper ligules, much smaller lower ligules, and still smaller presetal lobes between them. Neuropodia with rounded presetal and postsetal lobes and oval lower ligules. Ventral cirri very small. Notosetae and neurosetae only homogomph spinigers (Figure 6g). Parapodia of middle and posterior segments smaller,

with fewer lobes (Figure 6i-l; 7e-h). Presetal notopodial and both presetal and postsetal neuropodial lobes inconspicuous; neuropodial ligules much smaller. Upper bundles of neurosetae homogomph spinigers; lower bundles with homogomph spinigers and falcigers with rather long blades (Figure 6h).

Pygidium with paired anal cirri. Jaws of pharynx with 12 or more teeth extending to near tip; oral or basal ring bare except for pair of conical papillae or triangular areas on middorsal side (area VI); maxillary or distal ring with tufts of cylindrical hooked papillae on all areas as follows: middorsal group (area I) with about 5 papillae (3–6); dorsolateral groups (area II) with about 12 papillae (10–14); ventrolateral groups (area IV) with about 10 papillae (8–12), 3 midventral tufts (area III) of smaller papillae (Figures 5c-g; 7b). Juveniles with fewer papillae (Hartmann-Schröder, 1959, for L. brunnea).

REMARKS. — L. brunnea Hartmann - Schröder (1959) was based upon what appear to be juveniles of L. culveri. They have fewer papillae on the maxillary ring of the pharynx, probably associated with their smaller size. The fifth parapodium on Figure

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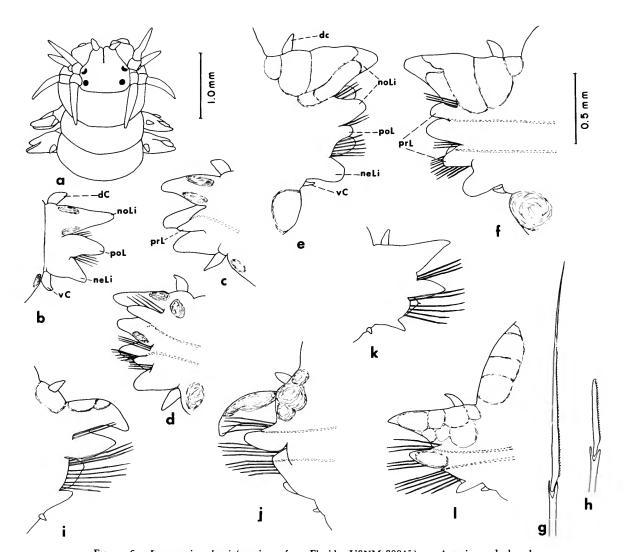


FIGURE 6.—Laeonereis culveri (specimen from Florida, USNM 30045): a, Anterior end, dorsal view; b, parapodium from setiger 1, posterior view; c, parapodium from setiger 2, anterior view; d, parapodium from setiger 3, anterior view, e, parapodium from anterior region, posterior view; f, same, anterior view; g, neuropodial homogomph spiniger from same; h, neuropodial homogomph falciger from same; i, parapodium from middle region, posterior view; j, same, anterior view; k, parapodium from posterior region, posterior view; l, same, anterior view. [Figures g,h, not to scale]

94 by Hartmann-Schröder incorrectly shows four neuropodial lobes instead of three.

Biology.—L. culveri is typically an intertidal, brackish, warm water species along much of the eastern and southeastern coasts of the United States

where it abounds in estuaries, brackish streams, coves, and sandy shoals. It occupies extensive sand flats and provides an important source of food for shore birds (Hartman, 1959b:539). It was found to be the most important burrowing form on the salt flats

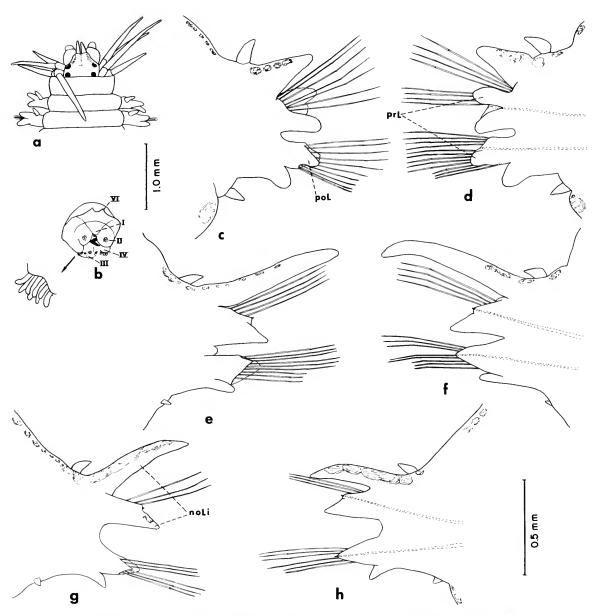


FIGURE 7.—Laeonereis culveri (specimens from Sapelo Island, Georgia, USNM 33294): a, Anterior end, dorsal view; b, frontal view extended pharynx; c, parapodium from anterior region, posterior view; d, same, anterior view; e, parapodium from middle region, posterior view; f, same, anterior view; g, parapodium from posterior region, posterior view; h, same, anterior view.

in the Aransas Refuge, Texas, being resistant to periods of low salinity and temporary droughts (Hedgpeth, 1950:111). In Salt Lake, Brevard County, Florida, in the St. John's River drainage, specimens were observed to emerge by the thousands after treatment with Rotenone on 13 May 1956 (observation of Wm. McLane, et al.). According to Carpenter (1956:101), L. culveri is one of the most

common annelids in the Alligator Harbor area, Florida, where it was found from mean high tide downward to below mean low tide. In the Mystic River estuary, Connecticut, *L. culveri* appeared to be distributed in aggregates and occurred in greatest abundance intertidally in the upper ten centimeters of soft, fine sediments in habitats where salinities fluctuated widely, with a maximum range per tidal cycle from 0.5 to 30% (Mazurkiewicz, 1970). Specimens have been maintained experimentally in freshwater (Webster, 1880:113). The species is euryhaline, known from freshwater (Uruguay, as *L. pandoensis*—Monro, 1937:242), from water of low salinity (1 to 6% in Florida—Oglesby, 1965:624), and higher salinities (Florida—Carpenter, 1956:93, 101).

They form tough tubes of mucoid-lined burrows, fitting the body very closely, often reddish brown or rustcolored (Webster, 1880:113; Mazurkiewicz, 1970). They are nonselective deposit feeders, with characteristic sinuous fecal strings being ejected and accumulating on the surface of the sediment around their burrow entrances (Mazurkiewicz, 1970).

The mature worms remain atokous, both sexes being identical in external morphology. They show no structural changes at the time of reproduction except that the eyes become a little larger, the body coloration changes from orange-brown to yellow, then to green, and the muscles of the body wall undergo histolysis, resulting in somewhat shorter and more fragile bodies. The reproduction and development of L. culveri in the Mystic River estuary, Connecticut, was followed by Mazurkiewicz (1970). Their life span includes a single spawning period and normally does not exceed one year. Spawnings occur during a period when the water temperature exceeds 20° C from June through August and possibly into September. While swimming, presumably along the bottom, the males shed their sperm through retractile pygidial papillae. The females spawn within their mucoid tubes, their eggs being extruded through rents in the body wall. The mature eggs are moderate in size $(135-162 \mu)$, demersal, and are found in clumps adhering to the walls of the tube. The aeration currents, produced by dorsoventral undulations of the females, presumably draw the sperm into the tubes, where fertilization takes place. The spent females remain in their tubes, the eggs and embryos being ventilated by the aeration currents produced by the females. The spent worms die ten to sixteen days after spawning. Developmental

stages include nonciliated embryos with three pairs of setal sacs, later developing into benthic larvae with ciliary bands and occupying burrows in the upper two centimeters of the sediment, being absent from the plankton. The ciliary bands are used to ventilate their burrows. Larvae of three to five setigers feed predominantly on benthic diatoms. All life history stages appear to tolerate rigorous environmental conditions.

According to Mrs. Winona Vernberg (in correspondence), L. culveri from North Carolina served as the second intermediate host for the trematode Zoogonus lasius. Mazurkiewicz (1969:1146; 1970) reported a high incidence of infection in L. culveri from Connecticut by parasitic sporozoans. The life cycle of the eugregarine sporozoan, Gonospora pilosa Mazurkiewicz, was found to be synchronized with the reproduction of the host, the parasite reproducing only after the host had spawned.

DISTRIBUTION.—East coast North America from Connecticut (Mystic River estuary) to Florida (east coast), Gulf of Mexico (Florida to Mexico), Central America (El Salvador), east coast South America from French Guinea (Fauvel, 1923b:124), Brazil, and Uruguay (freshwater).

Websterinereis new genus

Type-species.—Nereis tridentata Webster, 1880. Gender: feminine.

Diagnosis.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous, notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at bases of upper notopodial ligules. Notopodia with two ligules and usually additional presetal lobe in anterior parapodia (inconspicuous in W. glauca). Neuropodia with postsetal lobes and lower ligules; with or without presetal lobes distinct from acicular lobes. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae homogomph and heterogomph spinigers and heterogomph falcigers. Pygidium with paired anal cirri. Pharynx with paired jaws, without paragnaths; with papillae on basal or oral ring: large papillae dorsally (area VI) and single row of minute papillae ventrally (areas VII-VIII).

ETYMOLOGY.—The genus is named for Harrison Edwin Webster, pioneer worker on the Polychaeta.

Four species (together with four synonyms) are referred herein to Websterinereis, including the following:

W. glauca (Claparède) [including Leonnates pusillus Langerhans; Nereis (Leptonereis) vaillanti Saint-Joseph]

W. tridentata (Webster)

W. foli (Fauvel) [including Ceratocephala corallicola Reish]

W. punctata (Wesenberg-Lund) [including Laeonereis ankyloseta Day]

REMARKS.—A species, such as Nereis tridentata, does not fit into the more or less accepted scheme of the nereid genera. Webster (1880, 1886) reported and figured it as having three small paragnaths on the ventral surface of the basal or oral ring (area VII) of the pharynx; they were described as being circular or elliptical, flat, horny, and brown; in addition, two minute fleshy papillae on either side of the dorsal midline of the same basal ring (area VI) were observed on living specimens but not when preserved. Paragnaths were not observed on the pharynx by Hartman (1945: 21) when she referred the species to Ceratonereis (in the latter genus, the paragnaths are confined to the maxillary or distal ring and absent from the oral ring). Better choices would have been Eunereis (with paragnaths confined to the oral ring) or Leptonereis or Nicon (without paragnaths). The evanescent character of the so-called paragnaths of N. tridentata is due to the fact that they are not of the usual type of horny paragnaths found in the Neredidae. They are low, nodular papillae with thickened cuticle (Figure 8b). The three midventral ones. having a slightly thicker cuticular layer, may be brownish but fade on preservation. Thus they are easily overlooked, especially when the pharynx is withdrawn and observed only by dissection.

For Leptonereis foli, Fauvel (1930) described the slit pharynx as having an inflated rounded vesicle on area VI and a row of papillae on areas VII-VIII (exact number of papillae not stated; examination of the holotype revealed a row of seven papillae). For Ceratocephala corallicola, Reish (1968) described each area VI with a pair of conical papillae and areas VII-VIII with eight papillae in a single row (examination of the type-specimens revealed a single large papilla on area VI and a row of seven papillae on areas VII-VIII).

For Leptonereis punctata, Wesenberg-Lund (1949) observed two small papillae asymmetrically placed on the ventral side of the oral ring of the extended pharynx on one of the two syntypes (examination of the syntypes revealed a row of seven minute papillae). For Laeonereis ankyloseta, Day (1957) observed a truncate fleshy lobe on area VI and a single row of six [perhaps seven?], soft, rather indistinct papillae on areas VII-VIII, the three medial ones on area VII sometimes brown. The latter would correspond to the three "paragnaths" of N. tridentata.

Most of the above-mentioned species were included under *Laeonereis* by Hartman (1945, 1959a). *L. culveri*, the type-species *Laeonereis*, however, has tufts of papillae on the maxillary ring of the pharynx, in addition to parapodial differences.

In the upper neuropodial bundles of the middle and posterior parapodia, stout heterogomph falcigers appear. When the blades are broken off, they may appear as stout simple acicular setae. In *W. punctata* (and its synonym *ankyloseta*), the blades are fused to the stems, forming ankylosed setae. In the posterior tail regions of male heteronereids of *W. glauca*, stout simple setae occur in the uniramous parapodia.

Key to Species of Websterinereis

1. Anterior parapodia with presetal notopodial lobes small, inconspicuous (Figure 14d-f).

W. glauca

- 3'. Posterior parapodia without ankylosed simple setae in upper bundles of neuropodia.

W. tridentata

Websterinereis tridentata (Webster), new combina-

FIGURES 8, 9

Nereis tridentata Webster, 1880:113; 1886:142, pl. 7: figs. 33-40.

Ceratonereis tridentata.—Hartman 1945:21, pl. 3: figs. 3, 4; 1951:48.—Wells and Wells 1962:149.—Wells 1965:

MATERIAL EXAMINED.—GEORGIA, off Sapelo Island, M. Gray, collector: off Sea Buoy, 20 meters, 7 March 1961—4 specimens (USNM 33264); off Sapelo Whistle, 18 meters, 8 November 1961—2 specimens (USNM 33266); off Sapelo Whistle, 20 meters, 7 February 1962—1 specimen (USNM 33265). North Carolina: off Beaufort, 34°28′N, 76°07′W, 40 meters, sandy mud, 30 September 1965, J. H. Day, collector—6 specimens (USNM 43404). Off Beaufort, on coral in 10 meters, L. R. McCloskey, collector—1 specimen (USNM 43402).

DESCRIPTION.—Length up to 65 mm, width up to 3.5 mm, including parapodia, segments up to 105. Prostomium with faint to deep middorsal depression on anterior half, short tapered frontal antennae, and stout biarticulate palps; eyes large, anterior pair being larger than posterior pair (Figure 8a). Tentacular segment about twice length of following segment; tentacular cirri short, longest extending to about setiger 2 (1-4). Parapodia of first two setigers with dorsal cirrus, notopodial ligule, neuropodial postsetal lobe, lower ligule, and ventral cirrus (Figure 8c,d); upper bundle of neurosetae composed of homogomph spinigers with long blades, heterogomph spinigers with short blades, and heterogomph falcigers with relatively long blades (Figure 9d-f); lower bundle neurosetae all heterogomph spinigers with short blades. Third parapodium with two notopodial ligules, short presetal lobe, and fan-shaped bundle of homogomph spinigers with long blades; neuropodium similar to those of following setigers (Figure 8e).

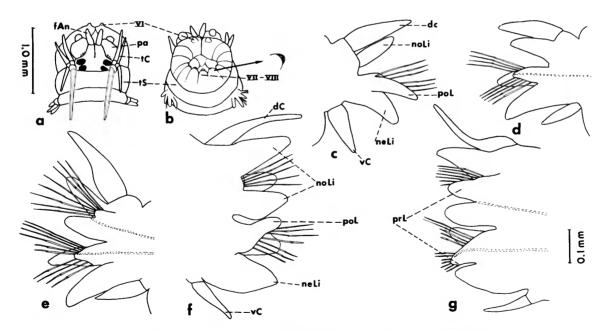


FIGURE 8.—Websterinereis tridentata (USNM 43403): a, Dorsal view anterior end, with pharynx partially extended; b, same, ventral view; c, parapodium from setiger 1, posterior view; d, parapodium from setiger 2, anterior view; e, parapodium from setiger 3, anterior view; f, parapodium from anterior region, posterior view; g, same, anterior view.

Parapodia of anterior region (Figure 8f,g) with dorsal cirri emerging from basal parts of upper notopodial ligules and extending slightly beyond them; notopodium with upper ligules large, subtriangular and lower ones smaller, subconical; presetal notopodial lobes, between them, somewhat smaller than lower ligules; presetal and postsetal neuropodial lobes subequal in size to notopodial presetal lobes; lower neuropodial ligules subequal to upper notopodial ligules; short subulate ventral cirri. Thus, anterior parapodia provided with six lobes in addition to dorsal and ventral cirri: three notopodial (two ligules and presetal lobe) and three neuropodial (presetal and postsetal lobes and lower ligule). Notosetae all homogomph spinigers with long blades (Figure 9d). Upper bundle of neurosetae composed of homogomph spinigers with long blades and heterogomph falcigers with relatively long blades (Figure 9f); lower bundle of neurosetae composed of heterogomph spinigers with short blades (Figure 9e) and heterogomph falcigers with relatively short blades (Figure 9g).

Parapodia of middle region (Figure 9a,b) with notopodia and neuropodia widely separated; notopodial presetal lobes diminished in size but still distinct; neuropodial presetal lobes indistinct from acicular lobes. Upper bundles of neurosetae homogomph spinigers with long blades; lower bundles of neurosetae with heterogomph spinigers with short blades and heterogomph falcigers with short blades (Figure 9h).

Parapodia of posterior region (Figure 9c) modified somewhat; both notopodial and neuropodial presetal lobes indistinct, resulting in four lobes: two notopodial ligules, postsetal neuropodial lobe and lower neuropodial ligule. Upper bundle of neurosetae

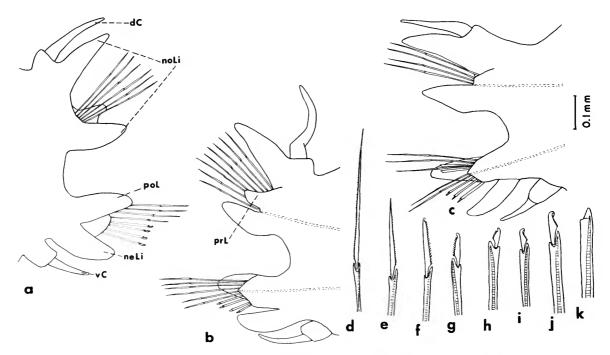


FIGURE 9.—Websterinereis tridentata (USNM 43403): a, Parapodium from middle region, posterior view; b, same, anterior view; c, parapodium from posterior region, posterior view; d, homogomph spiniger with long blade; e, heterogomph spiniger with short blade; f, heterogomph falciger with relatively long blade; g, heterogomph falciger from lower neuropodial bundle of anterior region; h, same, from middle region; i, same, from posterior region, j, stouter heterogomph falciger from upper neuropodial bundle of posterior region; k, same, with blade missing. [Figures d-k, not to scale]

homogomph spinigers with long blades and 1-2 stout heterogomph falcigers with short blades (Figure 9j); blades sometimes missing, then appearing as stout simple setae (Figure 9k); lower bundle of neurosetae heterogomph spinigers with relatively short blades and heterogomph falcigers with short blades (Figure 9i).

Pygidium with pair long anal cirri. Jaws of pharynx (Figure 8a,b) with numerous sharp teeth. Maxillary or distal ring bare, without paragnaths or papillae; basal or oral ring with subconical papillae on dorsal surface (area VI) and row of seven papillae on ventral surface (areas VII-VIII); papillae circular or elliptical, flat, horny, middle three (area VII) with thicker cuticle, sometimes brown in color but fading on preservation.

BIOLOGY.—W. tridentata forms compact tubes of sand grains and is associated with hard substrates, shelly bottoms and corals. In North Carolina and Florida, it was found by Wells and Wells (1962) and Wells (1965) to be a pest of the calico scallop Aequipecten gibbus where it penetrates areas between the shell and mantle, forming U-shaped tubes of fine sand grains loosely held together by mucus, and causing large oval or crescent-shaped mud blisters on the shells. The anterior ends of the worm may project into the mantle cavity. They appear to be facultative parasites, parasitizing the scallop but also occurring among the epifauna of the shells. Reproduction, as far as is known, occurs in the atokous condition.

DISTRIBUTION.—East coast North America from New Jersey to Florida, Gulf of Mexico (Mississippi, Texas).

Websterinereis foli (Fauvel) new combination

FIGURES 10, 11

Leptonereis foli Fauvel, 1930:520, fig. 3. Laeonereis foli.—Hartman 1949:55; 1959a:245. Ceratocephala [sic] corallicola Reish, 1968:215, fig. 4:1-5.

MATERIAL EXAMINED.—Ile des Pins, New Caledonia, 1928, Mm. A. Pruvot-Fol, collector—holotype of *Leptonereis foli* (MNHNP).

Bogen Island, Eniwetok Atoll, Marshall Islands, 12 September 1956, D. Reish, collector—holotype and 7 paratypes of *Ceratocephala corallicola* (USNM 38392-3).

Type material.—The holotype of L. foli consists of an anterior fragment of 62 segments, 17 mm long

and 1 mm wide, including setae. The pharynx was not extended but had been slit.

The holotype of *C. corallicola* consists of about 90 segments, 12 mm long and 1 mm wide, including setae. The pharynx was not extended. Of the seven paratypes, four are complete and three consist of anterior fragments. The pharynx is partially or completely extended on four of them.

DESCRIPTION.—Length up to 20 mm, width up to 1 mm, including parapodia, segments up to 112. Prostomium with faint to deep mid-dorsal depression on anterior half, short tapered frontal antennae, and stout biarticulate palps; eyes moderately large, anterior pair being larger than posterior pair (Figures 10a, 11a). Tentacular segment longer than following segment; tentacular cirri with styles short to long, longest extending to about setiger 4 (2-7). Parapodia of first two setigers with dorsal cirrus, notopodial ligule, neuropodial postsetal lobe, lower ligule and ventral cirrus (Figure 10b); upper bundle of neurosetae composed of homogomph spinigers and heterogomph falcigers with relatively long blades (Figure 10e); lower bundle of neurosetae heterogomph falcigers (no heterogomph spinigers).

Parapodia of anterior region (Figure 11c,d) with dorsal cirri emerging from basal parts of upper notopodial ligules and extending beyond them; upper notopodial ligules rather large, subtriangular; lower notopodial ligules smaller, subconical; presetal notopodial lobes, between them, smaller than lower ligules; presetal and postsetal neuropodial lobes subequal in size to notopodial presetal lobe; lower neuropodial ligules slightly smaller than upper notopodial ligules; short subulate ventral cirri. Notosetae all homogomph spinigers (Figure 11g). Upper bundle of neurosetae composed of homogomph spinigers and heterogomph falcigers with short blades; lower bundle of neurosetae composed of heterogomph falcigers (Figure 11h).

Parapodia of middle region (Figures 10c,d; 11e,f) with notopodial presetal lobes diminishing in size; neuropodial presetal lobes indistinct from acicular lobes; upper bundle of neurosetae homogomph spinigers (Figures 10f; 11i) and single stouter heterogomph falciger with short blade (Figures 10g; 11j); lower bundle of neurosetae with heterogomph falcigers bearing short blades (Figures 10h; 11k). Posterior parapodia sometimes with single heterogomph spiniger having relatively short blade in lower bundle of neurosetae.

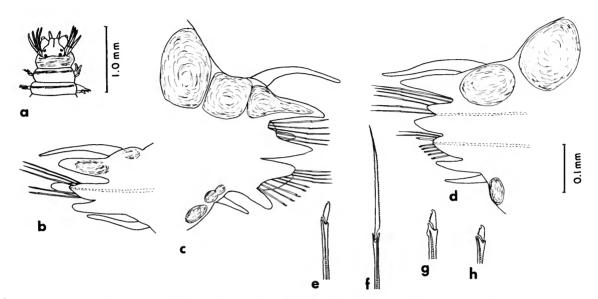


FIGURE 10.—Websterinereis foli (holotype of Leptonereis foli, MNHNP): a, Anterior end, dorsal view; b, first parapodium, anterior view; c, parapodium from middle region, posterior view; d, same, anterior view; e, heterogomph falcigerous neuroseta from first parapodium; f, homogomph spiniger; g, heterogomph falcigerous neurosetae from upper bundle of middle region; h, same, from lower bundle. [Figures e-h, not to scale]

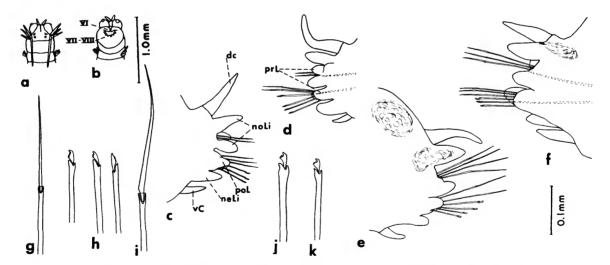


FIGURE 11.—Websterinereis foli (paratypes of C. corallicola, USNM 38393): a, Anterior end, dorsal view, pharynx partially extended; b, same, ventral view; c, parapodium from anterior region, posterior view; d, same, anterior view; e, parapodium from middle region, posterior view; f, same, anterior view; g, homogomph spiniger from anterior region; h, heterogomph falcigers from anterior region; i, homogomph spiniger from middle region; j, heterogomph falciger from upper bundle neuropodium; k, same, from lower bundle neuropodium. [Figures g-k, not to scale]

Pygidium with long anal cirri. Jaws of pharynx (Figure 11b) bearing numerous sharp teeth; maxillary or distal ring bare, without paragnaths or papillae; oral or basal ring with large subconical papilla on dorsal surface (area VI) and row of seven papillae on ventral surface (areas VII-VIII).

REMARKS.—Pettibone (1970:233) previously pointed out that *C. corallicola* was incorrectly assigned to *Ceratocephale*. *W. foli* is associated with corals, and is probably much more widely distributed than the two locality records might indicate. Due to its small size, it easily escapes notice.

DISTRIBUTION.—Central Pacific (New Caledonia, Marshall Islands). Associated with corals.

Websterinereis punctata (Wesenberg-Lund) new combination

FIGURES 12, 13

Leptonereis punctata Wesenberg-Lund, 1949:289, figs. 21-23.

Laeonereis ankyloseta Day, 1957:83, fig. 5a-j; 1960:321.— Hartman 1959a:243.

Nicon punctata.-Hartman 1958:265; 1959a:245, 274.

MATERIAL EXAMINED.—Persian Gulf, G. Thorson, collector: station 25A, 14 March 1937, 28°58′N, 49°30′E, 49 meters, sand with very little clay—larger syntype (UZMC); station 45D, 31 March 1937, 27°42′N, 51°25′E, 58 meters, clay mixed with sand, shells—smaller syntype (UZMC).

Type material.—The larger syntype from station 25A is incomplete posteriorly, 40 mm in length, 3 mm in width, including setae, and 70 segments; it is rather flaccid. The smaller syntype from station 45D is a complete specimen of about 90 segments, 30 mm in length and 2 mm in width, including setae; it is a female containing relatively large eggs; the eyes are larger than those in the other syntype. The pharynx is extended in both syntypes.

DESCRIPTION.—Length up to 50 mm, width up to

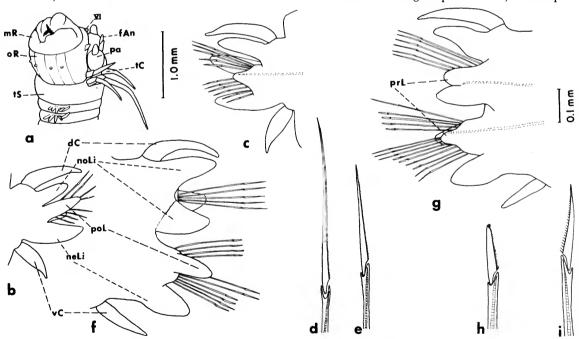


FIGURE 12.—Websterinereis punctata (smaller syntype of Leptonereis punctata from station 45D, UZMC): a, Anterior end, lateral view; b, first parapodium, posterior view; c, second parapodium, anterior view; d, homogomph spiniger from same; e, heterogomph spiniger from same; f, parapodium from anterior region, posterior view; g, same, anterior view: h, neuropodial heterogomph falciger from same; i, neuropodial heterogomph spiniger from same. [Figures d,e,h,i, not to scale]

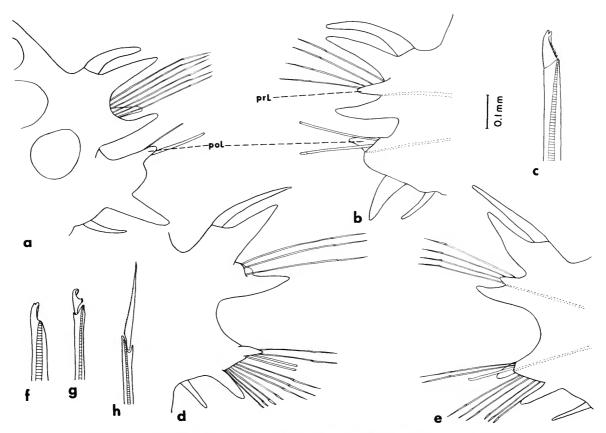


FIGURE 13.—Websterinereis punctata (smaller syntype of Leptonereis punctata from station 45D, UZMC): a, Parapodium from middle region, posterior view; neurosetae mostly missing; b, same, anterior view; c, stout heterogomph falciger from upper bundle neurosetae from same; d, parapodium from posterior region, posterior view; e, same, anterior view; f, stout simple seta from upper bundle neurosetae from same; g, heterogomph falciger from lower bundle neurosetae from same; h, heterogomph spiniger from lower part of lower bundle neurosetae from same. [Figures c,f-h, not to scale]

3 mm, including setae, segments up to 90. Prostomium with short tapered frontal antennae and stout biarticulate palps; moderately large eyes, anterior pair larger than posterior pair (Figure 12a). Tentacular segment about twice length of following segment; tentacular cirri with cylindrical cirrophores, longest extending to about setiger 6. Parapodia of first two setigers with dorsal cirrus and notopodial ligule; neuropodium with postsetal lobe, short presetal lobe, lower ligule, and ventral cirrus (Figure 12b,c); upper bundle of neurosetae composed of homogomph spinigers (Figure 12d) and heterogomph spinigers (Figure 12e); lower bundle of neurosetae hetero-

gomph spinigers with blades long (upper ones) to short (lower ones).

Parapodia of anterior region (Figure 12f,g) with dorsal cirri emerging from basal parts of upper notopodial ligules and extending slightly beyond them; upper and lower notopodial ligules subconical and subequal; presetal notopodial lobe, between ligules, rounded and somewhat smaller; postsetal neuropodial lobe elongate-conical; presetal neuropodial lobe short; lower neuropodial ligules subequal to notopodial ligules; short subulate ventral cirri. Notosetae all homogomph spinigers with long blades (Figure 12d). Upper bundle of neurosetae composed of few

homogomph spinigers with long blades and heterogomph falcigers with relatively long blades (Figure 12h); lower bundle of neurosetae composed of upper heterogomph spinigers with long blades, heterogomph falcigers with relatively long blades and lower heterogomph spinigers with short blades (Figure 12i).

Parapodia of middle region (Figure 13a,b) with notopodia and neuropodia more widely separated; notopodial presetal lobes diminishing in size; neuropodial presetal lobes indistinct from acicular lobes. Upper bundle of neurosetae homogomph spinigers with long blades and few (1-4) stout heterogomph falcigers with bifid tips, blades showing signs of fusion to stems (Figure 13c); lower bundle neurosetae with heterogomph spinigers and heterogomph falcigers, both bearing short blades.

Parapodia of posterior region (Figure 13d,e) with notopodial presetal lobes further diminished in size. Upper bundle of neurosetae homogomph spinigers with long blades and few (1-2) stout simple falcigers formed by complete fusion of blades to stems, their tips bifid, differing in appearance due to wear (Figure 13f). Lower bundle of neurosetae heterogomph spinigers with long blades, heterogomph falcigers with short blades (Figure 13g), and heterogomph spinigers with relatively short blades (Figure 13h).

Jaws of pharynx (Figure 12a) with about ten teeth. Maxillary or distal ring bare, without paragnaths or papillae; basal or oral ring with large subconical papillae on dorsal surface (area VI) and row of seven small papillae on ventrolateral surface (areas VII-VIII), middle three (area VII) somewhat larger.

Remarks.—Wesenberg-Lund observed only two small asymmetrically placed papillae on the ventral surface of the oral ring of the extended pharynx on the smaller syntype; seven papillae were observed by me on both syntypes. The stout simple neurosetae were found in both syntypes of *L. punctata*, not on just the larger one, as indicated by Wesenberg-Lund.

Day (1957:84) indicated that *L. ankyloseta* was closely allied to *L. punctata*. The two species were distinguished by the greater number of papillae on the pharynx of the former and by the form of the enlarged tips of the stout simple neurosetae. Examination of the syntypes of *L. punctata* obliterates these distinctions and the two are herein considered to be synonymous.

Biology.—In the Persian Gulf, W. punctata was collected in 49 to 59 meters on bottoms of sand, clay and shells. In South Africa, it was dredged in 2 to 55 meters on bottoms of sand, mud, rock, shells and coral and was found to be common in sheltered sand banks. Day (1960:321) collected a heteronereid in Mossel Bay in 9 meters (not described).

DISTRIBUTION.—Persian Gulf (northern and central part) and South Africa (False Bay to Natal and Mozambique). In 2 to 58 meters.

Websterinereis glauca (Claparède) new combination Figures 14-16

Nereis (Leptonereis) glauca Claparède, 1870:454, pl. 7: fig. 3.

Leonnates pusillus Langerhans, 1880:279, pl. 14: fig. 10.

Nereis (Leptonereis) vaillanti Saint-Joseph, 1888:246, pl. 10: figs. 113-123, pl. 11: fig. 124.

Nereis (Leonnates) pusillus.—Augener 1910:236.

Leptonereis glauca.—Ramsay 1914a:244, pl. 1: figs. 1-10.— Fauvel 1914:163, pl. 12: figs. 5-23; 1923a:333, fig. 129, a-d.—Fage and Legendre 1927:90, figs. 9, 10. Laeonereis glauca.—Hartman 1945:22; 1949:55; 1959a: 243, 262.

MATERIAL EXAMINED.—Plymouth, England, 6 December 1913, C. Crossland, collector—2 specimens (BMNH 1938:7:1:1-6).

Dinard, France, collection of M. le Baron de Saint-Joseph, no. 20, 1911 (as Leptonereis vaillanti)—atokous female with large eggs (MNHNP). Cherbourg, France, 25 May 1922, collection of P. Fauvel—2 male heteronereids (BMNH 1928:4:26:827-9).

Cape Pescade, near Algers, 5 December 1924—13 females (MNHNP; USNM 43399). Cape Matifou, Algeria, 22 April 1924, at night-light—numerous male heteronereids (MNHNP; USNM 43398).

Description.—Length up to 35 mm, width up to 3 mm, including setae, segments up to 65. Prostomium with short subulate frontal antennae and stout biarticulate palps; eyes moderately large (Figure 14a). Tentacular segment about twice length of following segment; tentacular cirri short, longest extending to about setiger 4 (3–7). Parapodia of first two setigers with dorsal cirrus, notopodial ligule, neuropodial postsetal lobe, ligule and ventral cirrus (Figure 14b,c); upper bundle neurosetae composed of homogomph spinigers and heterogomph falcigers; lower bundle with heterogomph spinigers and falcigers.

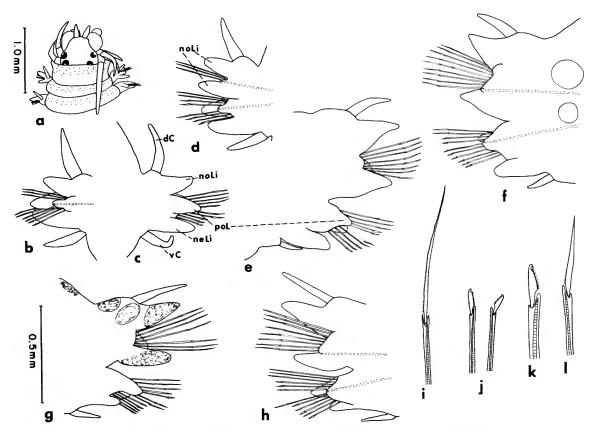


FIGURE 14.—Websterinereis glauca (atokous female with large eggs, from Dinard, MNHNP): a, Anterior end, dorsal view; b, first parapodium, anterior view; c, second parapodium, posterior view; d, third parapodium, anterior view; e, anterior parapodium, posterior view; f, same, anterior view; g, posterior parapodium, posterior view; h, same, anterior view; f, homogomph spiniger from anterior region; f, heterogomph falcigers from anterior region; f, same, from upper bundle posterior region; f, heterogomph spiniger with short blade from lower bundle neuropodium of posterior region. [Figures f-f, not to scale]

Parapodia of anterior region (Figure 14d-f) with dorsal cirri emerging from basal parts of upper notopodial ligules and extending slightly beyond them; upper and lower notopodial ligules subequal, subconical, with low presetal notopodial lobe between them; neuropodia with anterior subconical acicular lobe and slightly longer postsetal lobe; lower neuropodial ligule smaller than notopodial ligules; ventral cirri short subulate. Notosetae all homogomph spinigers with long blades; upper bundle of neurosetae homogomph spinigers with long blades (Figure 14i) and heterogomph falcigers (Figure 14j); lower bundle of neurosetae with or without heterogomph spinigers with long blades (Figure 14j)

igers with short blades; with heterogomph falcigers.

Parapodia of posterior region (Figure 14g,h) somewhat modified; upper notopodial ligules larger than lower ones; lower neuropodial ligules smaller than neuropodial postsetal lobes. Upper bundle of neurosetae homogomph spinigers and few stouter heterogomph falcigers (Figure 14k); lower bundle of neurosetae heterogomph spinigers with relatively short blades (Figure 14l) and heterogomph falcigers.

Pygidium with anal cirri (Figure 15c). Jaws of pharynx (Figure 16a,b) with numerous teeth (10-15). Maxillary or distal ring bare, without paragnaths or papillae; basal or oral ring with pair of large

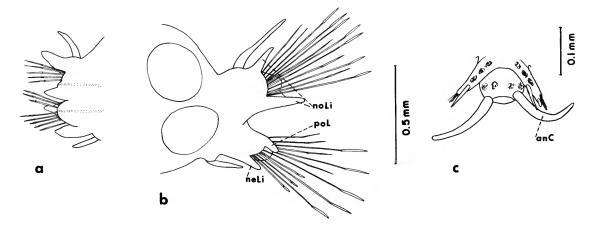


FIGURE 15.—Websterinereis glauca (female heteronereid from Cape Pescade, near Algers, MNHNP): a, Parapodium from anterior region, anterior view; b, parapodium from middle region, posterior view; with mixture of long swimming and usual type of setae; c, posterior end, dorsal view.

papillae on dorsal surface (area VI) and row of about seven (5-9) minute papillae on ventrolateral surface (areas VII-VIII).

Description of female heteronereid.—Body divided into three regions: anterior region of 15–18 setigers with parapodia unmodified, middle region of about 16 modified setigers, and posterior unmodified region of about 12 setigers. Parapodia of anterior region (Figure 15a), posterior region, and pygidium (Figure 15c) similar to those of atokous individuals. Parapodia of middle region (Figure 15b) enlarged, with long swimming setae in addition to usual shorter notosetae and neurosetae (not replacing them).

Description of male heteronereid.—Body divided into three regions: anterior region of 14–15 setigers, middle region of about 30 setigers (16–45), and posterior region of 10–12 setigers forming sort of tail. Prostomium with eyes enlarged (Figure 16a). Dorsal cirri of anterior seven setigers enlarged, clavate, increasing in size posteriorly (Figure 16c,d); ventral cirri of anterior seven setigers thicker than those of following setigers.

Parapodia of middle region enlarged and considerably modified (Figure 16f,g). Dorsal cirri cirriform (not lobulated); dorsal lamellae on medial bases of dorsal cirri; large foliaceous postsetal lamellae developed from postsetal neuropodial lobes, extending beyond ligules; winglike ventral lamellae on bases of

long cirriform ventral cirri. Usual type of notosetae and neurosetae completely replaced by numerous long swimming setae.

Parapodia of posterior tail region uniramous (Figure 16i); notopodia absent except for large subulate dorsal cirri; neuropodia with lower ligules and ventral cirri. Upper bundle of neurosetae composed of few homogomph spinigers and one to two stout dark simple acicular setae with hooked tips (Figure 16j); lower bundle of neurosetae consisting of one to two simple acicular setae. Pygidium with paired stout dorsal lobes and anal cirri (without papillated area around anus; Figure 16h).

REMARKS.—Claparède (1870) described and figured a female of the atokous form. Langerhans (1880) described and figured the male heteronereid (as Leonnates pusillus). The three forms of the species—atokous nereid, female and male heteronereids—were recognized by Saint-Joseph [1882, as N. (Leptonereis) vaillanti]. L. pusillus was questionably referred to Leptonereis glauca by Ramsay (1914a) and by Fauvel (1914) without question. Nereis (Leptonereis) vaillanti was referred to N. (Leonnates) pusillus by Augener (1910) and to L. glauca by Ramsay (1914a) and by Fauvel (1914).

BIOLOGY.—W. glauca has been found on pilings, among compound ascidians, sponges, and other sedentary forms, and on bottoms of mud and stones. Male heteronereids were found in large numbers in the

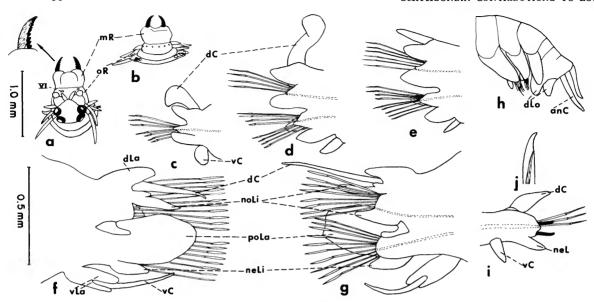


FIGURE 16.—Websterinereis glauca (male heteronereid from Cape Matifou, Algeria, MNHNP): a, Dorsal view of anterior end, with pharynx extended; b, same, ventral view; c, first parapodium, anterior view; d, parapodium from setiger 7, anterior view; e, parapodium from setiger 8, anterior view; f, modified parapodium from middle region, posterior view; g, same, anterior view; h, posterior end, lateral view; i, parapodium from posterior region; j, neuropodial hook from same. [Figures i,j, not to scale]

plankton but females were taken only rarely at the surface (Fage and Legendre, 1927). The females are only partly transformed to heteronereids—there may be no trace of swimming setae, or swimming setae may appear in addition to the usual setae but not replacing them. Large eggs are developed (up to 240 μ in diameter, according to Ramsay, 1914a) and laid in the tube. Development is presumably direct.

DISTRIBUTION.—Northeast Atlantic from Great Britain to Madeira, Mediterranean.

Kinberginereis new genus

TYPE-SPECIES.—Nereis (Leptonereis) inermis Hoagland, 1920. Gender: feminine.

DIAGNOSIS.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous; notopodium with dorsal cirrus, notopodial ligule and slender notoaciculum. Dorsal cirri at bases of upper notopodial ligules. Notopodia with two ligules. Neuropodia with bilobed presetal lobe, short rounded post-

setal lobe, and subsetal ligule. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae all compound spinigers — homogomph and slightly heterogomph or hemigomph. Pharynx with paired jaws and soft papillae on oral ring only.

ETYMOLOGY.—The genus is named for Johan Gustaf Hyalmar Kinberg, pioneer worker on the Polychaeta.

REMARKS.—Kinberginereis resembles Tylonereis Fauvel, with type-species T. bogoyawlenskyi Fauvel (1911:376) from the Persian Gulf and Indian Ocean. In Tylonereis, the neurosetae are homogomph spinigers only; the dorsal cirri are very short, much shorter than the notopodial ligules; notoacicula are absent on the first two setigers; the pharynx bears tufts of papillae on both maxillary and oral rings.

Kinberginereis inermis (Hoagland) new combination

FIGURE 17

Nereis (Leptonereis) inermis Hoagland, 1920:608, pl. 47: figs. 8-12.

Type-material.—Cliff Island, Philippine Islands, 13 meters, mud bottom, Albatross station D5346, 26 December 1908—holotype (USNM 18947). The holotype consists of an anterior fragment of 29 setigerous segments, 12 mm in length, and 5 mm in width, including Parapodia. The pharynx is not extended.

DESCRIPTION.—Body flattened dorsoventrally, segments much compressed. Prostomium partially withdrawn into achaetous tentacular segment, with deep anterior notch between bases of conical frontal antenna; stout palps more or less telescoped, appearing two to three segmented; eyes moderately large, on posterior half of prostomium (Figure 17a). Tentacular segment about equal in length to following segment but larger and inflated laterally and ventrally; tentacular cirri with long cylindrical cirrophores; styles of longest cirri extending to about setiger 13 (posterodorsal pair missing—perhaps even longer). Parapodia of first two setigers with dorsal cirrus, single notopodial ligule, and slender notoaciculum with curved distal tip; neuropodium similar to those of following segments (Figure 17b,c).

Anterior biramous parapodia (Figure 17d,e) with cirriform dorsal cirrus and two conical notopodial ligules subequal in length; small bundle of notosetae emerging between ligules; notosetae all homogomph spinigers with long blades, finely serrated along one side (Figure 17h). Neuropodium with bilobed presetal lobe-subequal conical lobes and shorter rounded postsetal lobe; subsetal neuropodial ligule similar in size and shape to notopodial ligules. Neurosetae very numerous; upper bundle all homogomph spinigers with long blades similar to notosetae (Figure 17h); lower bundle slightly heterogomph or hemigomph spinigers, upper few with blades shorter, curved, with long spines along basal part (Figure 17i), middle ones with blades longer, straight, and finely serrated along one side (Figure 17j), and lower ones with shorter blades (Figure 17k). Ventral cirri tapered, shorter than neuropodial ligule.

More posterior parapodia (Figure 17f,g) somewhat modified; cirriform dorsal cirri more elongated, extending far beyond notopodial ligules; upper notopodial ligules decreasing in size, becoming considerably smaller than lower notopodial ligules.

Pharynx (observed only when cut) without paragnaths or papillae except for fleshy knobs on areas VI of oral ring. Hooked jaws amber-colored, with serrations or teeth along most of concave border—about

20 teeth.

DISTRIBUTION.—Philippine Islands. In 13 meters.

Rullierinereis new genus

Type-species.—Leptonereis zebra Rullier, 1963. Gender: feminine.

Diagnosis.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of eyes. Tentacular segment apodous and achaetous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous; notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at bases of upper notopodial ligules. Notopodia with two ligules, upper one sometimes fused with dorsal cirri (in posterior notopodia of zebra; from setiger 3 on, in bahamensis). Neuropodia with acicular lobes and lower ligules. Ventral cirri short, tapered. Notosetae homogomph spinigers and, more posteriorly, homogomph falcigers. Neurosetae homogomph and heterogomph spinigers and heterogomph falcigers. Pygidium with paired anal cirri. Pharynx with paired jaws, without paragnaths or papillae (latter present on oral ring in bahamensis).

ETYMOLOGY.—The genus is named for François Rullier, eminent worker on the Polychaeta.

REMARKS.—The following nereid species are referred to Rullierinereis:

- R. mexicana (Treadwell, 1942), as Leptonereis. Lower California, western Mexico.
- R. bahamensis (Hartmann-Schröder, 1958), as Tylorrhynchus. Bimini, Bahamas.
- R. zebra (Rullier, 1963), as Leptonereis. Mauritius, Indian Ocean.
- R. uncinata (Hartman, 1965b), as Nicon uncinatus.

 Off New England.
- R. gallardoi new species, as Nicon maculatus.—Gallardo, 1968. South Viet Nam.

The five species lack paragnaths on the pharynx and are provided with one to two homogomph falcigers in the more posterior notopodia (not present in male heteronereids lacking posterior unmodified regions). R. mexicana is known only as sexual epitokes. The other four species are small and heteronereids have not been observed.

Hartman (1965a:36) indicated that *L. zebra* should perhaps be referred to *Nicon* because the proboscis is smooth. However, the species may be separated from members of the genus *Nicon* on other characters. *R. bahamensis* was incorrectly assigned

FIGURE 17.—Kinberginereis inermis [holotype of N. (L.) inermis, USNM 18947]: a, Anterior end, dorsal view, prostomium partially withdrawn in tentacular segment, posterior pair eyes visible through transparent integument dotted in; styles of two upper right and second upper left tentacular cirri missing; b, first parapodium, anterior view; c, second parapodium, posterior view; d, parapodium from anterior region, anterior view; e, same, posterior view; f, parapodium from middle region (about setiger 26), anterior view; g, same, posterior view; h, homogomph spinigerous notoseta; h, slightly heterogomph or hemigomph spiniger from upper part of lower neurosetal bundle; h, same, from middle of bundle; h, same, from lower part of bundle. [Figures h-h, not to scale]



to the genus *Tylorrhynchus* Grube by Hartmann-Schröder. In the latter genus, the neuropodia are provided with well-developed anterior and posterior lips but without lower neuropodial ligules.

R. bahamensis was reported as having two achaetous tentacular segments (perhaps distorted in connection with the extended pharynx?). Also, beginning with setiger 3, the upper notopodial ligules are fused with the dorsal cirri (this is true only in the posterior

notopodia of *R. zebra*). The maxillary ring of the pharynx is provided with some soft papillae in *R. bahamensis*; papillae were not observed in the other four species. This character, however, is difficult to observe on small specimens, especially when the pharynx is not extended.

R. uncinata was reported as having only heterogomph spinigers and falcigers in the neuropodia (no homogomph spinigers).

Key to the Species of Rullierinereis

- 1. Upper notopodial ligules fused with dorsal cirri from setiger 3 on (pl. 39: figs. 16, 17, in Hartmann-Schröder, 1958). Pharynx with papillae on oral ring. [Notopodial homogomph spinigers with blades short, with bifid tips, pl. 39: fig. 18, in Hartmann-Schröder].
- *R. bahamensis
 1'. Upper notopodial ligules distinct from dorsal cirri (except in posterior parapodia of R.
- zebra). Pharynx without papillae
 Upper notopodial ligules diminishing in size posteriorly and fused with dorsal cirri (Figure 18f). Neuropodial heterogomph falcigers with short blades (Figure 18h, i). [Notopodial homogomph falcigers with blades short, oval, Figure 18j]

 R. zebra
- 3. Neuropodial heterogomph falcigers with bifid tips (pl. 12: fig. c, in Hartman, 1965). Dorsal cirri shorter than notopodial ligules (at least on setiger 18, pl. 12: fig. a, in Hartman). [Notopodial homogomph falcigers elongate-oval, spinous, pl. 12: fig. b, in Hartman].

*R. uncinata

- 3'. Neuropodial heterogomph falcigers with entire tips (Figures 19k, 22g,k,n). Dorsal cirri extending beyond notopodial ligules (Figures 19f,g, 22d,i,l) 4
- 4'. Notopodial homogomph falcigers with blades short, elongate-oval, smooth (Figure 22j).

R. gallardoi

Rullierinereis zebra (Rullier) new combination

FIGURE 18

Leptonereis zebra Rullier, 1963:474, fig. 1: 1-12.—Hartman 1965a:36.

MATERIAL EXAMINED.—Mauritius, Indian Ocean, 1962, C. Michel, collector—2 syntypes (no. 16–10 and slide W–92, collection of F. Rullier).

Type-material.—One of the eight syntypes (no. 16–10) is a female, 9 mm in length, 1 mm in width, including setae, and 43 segments, containing very large eggs. A smaller syntype (on slide W–92) is 6 mm long, 1 mm wide, with 35 segments. The pharynx is withdrawn on both syntypes.

Description.—Length up to 10 mm, width up to 1 mm, including setae, segments up to 48. Anterior

segments banded with brown granular pigmentation. Anterior region (about 13 setigers) flattened dorsoventrally, segments short, with parapodia more conspicuous than those posterior. Posterior region cylindrical, inflated, with segments well delineated; body wall thin, transparent, dark parapodial acicula, ventral nerve cord and glands (three per parapodium) appearing prominently; sometimes filled with very large eggs-their diameter about half that of body (Figure 18f). Prostomium (Figure 18a) with short tapered frontal antennae, stout biarticulate palps, and small subequal eyes. Achaetous tentacular segment up to twice length of following segment, tentacular cirri rather short, longest extending to setiger 1-3. Parapodia of first two setigers (Figure 18b) with large, thick dorsal cirrus and single notopodial ligule; neuropodium similar to those of following setigers.

^{*}Specimens not examined in this study.

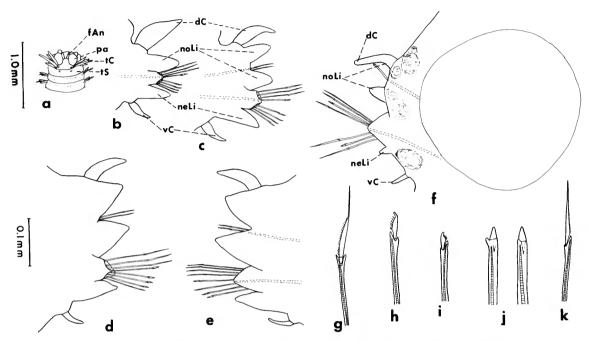


FIGURE 18.—Rullierinereis zebra (syntype no. 16-10 of L. zebra, collection of F. Rullier): a, Anterior end, dorsal view, prostomium partially withdrawn into tentacular segment, posterior pair eyes dotted in; b, first parapodium, posterior view; c, third parapodium, posterior view; d, parapodium from anterior region, posterior view; e, same, anterior view; f, parapodium from posterior region, anterior view, with single large egg; g, neuropodial homogomph spiniger from setiger 3; h, neuropodial heterogomph falciger from setiger 3; i, same, from anterior region; j, notopodial homogomph falcigers from posterior region; k, heterogomph spiniger from lower bundle neuropodium, from posterior region. [Figures g-k, not to scale]

Parapodia biramous from setiger 3 posteriorly (Figure 18c). Dorsal cirri subulate, extending beyond notopodial ligules. Upper and lower notopodial ligules subconical and subequal in size; notosetae homogomph spinigers, few in number (1-2). Neuropodial acicular lobes subtriangular, without prominent accessory lobes; neuropodial ligules subequal in size and shape to notopodial ligules. Ventral cirri short, subulate. Upper bundle of neurosetae (4-5) homogomph spinigers (Figure 18g) and single heterogomph falciger (Figure 18h); lower bundle of neurosetae heterogomph falcigers (4). Following parapodia of anterior region (Figure 18d,e) with notopodial ligules large, subtriangular; upper bundles of neurosetae with homogomph spinigers (4-5) and single heterogomph falciger; lower bundles with heterogomph falcigers (4-6) with somewhat shorter blades (Figure 18i).

Parapodia of middle and posterior regions gradually modified (Figure 18f); upper notopodial ligules and dorsal cirri somewhat fused; lower notopodial and neuropodial ligules much smaller. Notosetae a single homogomph falciger with short rounded blade (beginning about setiger 20); in far posterior region, blades of homogomph falcigers more or less fused to stems, forming simple setae (Figure 18j; not mentioned by Rullier). Upper bundle of neurosetae homogomph spinigers (5–6) and single heterogomph spinigers (2) with short blades (Figure 18k; not mentioned by Rullier) and single heterogomph falciger.

Pygidium with paired glands, ventral anal cirri and dorsal anus. Pharynx without paragnaths or papillae, basal ring (observed on slit pharynx) appearing indistinctly lobulated; jaws with 7-8 teeth. Repro-

duction in atokous condition, having huge eggs (300μ) in diameter, according to Rullier).

DISTRIBUTION.—Indian Ocean (Mauritius).

Rullierinereis mexicana (Treadwell), new combination

FIGURES 19-21

Leptonereis maculata.—Treadwell 1928:469. [Not Kinberg, 1866].

Leptoneris mexicana Treadwell, 1942:1, figs. 2-9. Nicon mexicana.—Hartman 1956:253, 279; 1958:265; 1959a:245, 274.—Berkeley and Berkeley 1958:402 (part; not smaller male heteronereid).

MATERIAL EXAMINED.—Lower California, outside Topolobampo Bay, 25°30'N, 109°12'W, 17 November 1935—holotype (male heteronereid) and paratype (female heteronereid) (AMNH 3222). Marina Madre Island, western Mexico, at night-light off shore, 20 September 1956, W. L. Klawe, collector—male heteronereid (USNM 35813).

Pacific side Panama, Balboa, Canal Zone, at oil dock, 4 February 1937, S. F. Hildebrand, collector—2 male heteronereids (USNM 24481).

Florida, Boca Ciega, Tampa Bay, swarming at 6 to 10 P.M., 3 April 1968, J. L. Taylor, collector—3 male (USNM 43406) and 28 female heteronereids (USNM 43405).

Galapagos, Arcturus Oceanographic Expedition: Seymour Bay, 0°27'N, 90°19'W—female and more than 60 male heteronereids (AMNH 2621; USNM 43407); 0°19'N, 89°57'W, on surface—1 male heteronereid (AMNH 2614).

Type-material.—The male heteronereid (holotype) has a length of about 50 mm, a width of 3 mm, including setae, and has very numerous segments; the pharynx is extended. The female heteronereid (paratype) is incomplete posteriorly, having a length of 26 mm and a width of 3 mm, including setae; the pharynx is not extended but, when slit, no paragnaths or papillae were observed, although the ridges may appear as indistinct large papillae; large eggs are present in the body cavity.

DESCRIPTION OF FEMALE HETERONEREIDS.—Length up to 70 mm, width up to 4 mm, including setae, segments up to 200. Body formed of three regions: anterior unmodified (about 50 segments), middle modified (about 55 segments) and posterior unmodified (up to 100 segments). Prostomium with short tapered frontal antennae, stout biarticulate palps,

and large eyes (Figure 19a). Tentacular segment about same length as following segment, with rather short tentacular cirri, longest extending to setiger 4–5. Parapodia of first two setigers with dorsal cirrus and single notopodial ligule; neuropodium similar to those of following segments (Figure 19d,e). Dorsal cirri on anterior five setigers slightly modified—thicker basally, with curved tips; ventral cirri of anterior two to four setigers slightly modified—thicker than those of following setigers.

Parapodia of anterior region (Figure 19f,g) with tapered dorsal cirri extending slightly beyond notopodial ligules, two conical notopodial ligules, conical anterior neuropodial acicular lobe, shorter truncate postsetal lobe, and lower conical neuropodial ligule; ventral cirri slightly shorter than dorsal cirri. Notopodia with relatively few homogomph spinigers having long spinous blades (Figure 19h). Upper bundle of neurosetae homogomph spinigers, similar to notosetae, and heterogomph falcigers with rather long blades (Figure 19k). Lower bundle of neurosetae heterogomph spinigers with relatively short blades (Figure 19i,j) and heterogomph falcigers similar to those of upper bundle.

Parapodia of middle modified region with numerous swimming setae completely replacing normal setae in both notopodia and neuropodia (Figure 20a-c). Conical dorsal lamella developed medial to base of dorsal cirrus; notopodial ligules more widely separated by enlarged, rounded supraacicular notopodial lobe bearing numerous modified swimming setae. Neuropodial acicular lobe paddle-shaped, bearing fan-shaped bundle of modified swimming setae; large oval postsetal lamella developed from postsetal neuropodial lobe and extending to about level of notopodial ligules; lower neuropodial ligule large, subconical; base of ventral cirrus enlarged, forming asymmetrical winglike ventral lamella.

Parapodia of posterior unmodified region similar to those of anterior region; dorsal cirri longer, more slender (Figure 20d). Notosetae few in number (sometimes absent), consisting of single homogomph spiniger and stouter homogomph falciger with spinous blade and blunt curved tip (Figure 20e). Upper bundle of neurosetae homogomph spinigers with long blades and single stout heterogomph falciger (Figure 20f). Lower bundle of neurosetae mostly heterogomph spinigers with blades long (upper ones) to short (lower ones); lowest neuroseta sometimes heterogomph falciger.

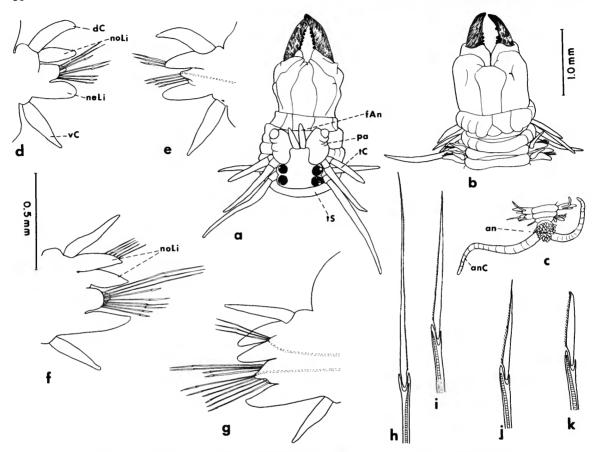


FIGURE 19.—Rullierinereis mexicana (female heteronereid from Tampa Bay, Florida, USNM 43405): a, Anterior end, dorsal view, pharynx extended; b, same, ventral view; c, posterior end, dorsal view; d, first parapodium, posterior view; e, second parapodium, anterior view; f, parapodium from anterior region, posterior view; g, same, anterior view; h, homogomph spiniger from same; i, heterogomph spiniger from upper part of lower bundle of neurosetae from same; j, same, from middle part of lower bundle; k, heterogomph falciger from lower part of lower bundle from same. [Figures h-k, not to scale]

Pygidium with papillated area around anal opening and ventral anal cirri (Figure 19c). Pharynx stout, muscular, without paragnaths or definite papillae; jaws dark amber-colored, each with about 11 teeth (Figure 19a,b).

Description of male heteronereids.—Length up to 55 mm, width up to 4 mm, including setae, segments up to 180. Body formed of two regions (posterior unmodified region lacking): anterior unmodified (about 50 segments) and posterior modified (about 135 segments). Prostomium and tentacular segment similar to those of female (Figure 21a,b).

Dorsal cirri of anterior seven setigers and ventral cirri of anterior five setigers thick, with terminal papillae or slender curved tips (Figure $21d_{e}$); dorsal cirri of setiger 7 slightly longer than preceding ones. Parapodia of anterior unmodified region similar to those of female heteronereids (Figure $21d_{e}$).

Parapodia of posterior modified region with numerous swimming setae completely replacing normal setae in both notopodia and neuropodia (Figure 21h,i). Bulbous dorsal lamella developed medial to base of dorsal cirrus; dorsal cirrus elongated, lobulated—about 6-8 rounded lobes along one side; noto-

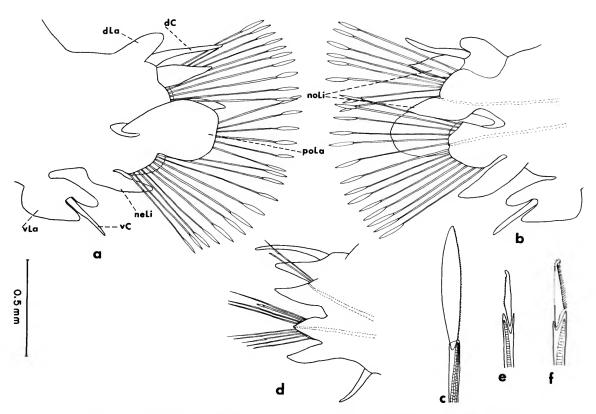


FIGURE 20.—Rullierinereis mexicana (female heteronereid from Tampa Bay, Florida, USNM 43405): a, Modified parapodium, posterior view; b, same, anterior view; c, swimming seta from same; d, parapodium from posterior region, anterior view; e, stout notopodial homogomph falciger from same; f, stout heterogomph falciger from upper bundle of neuropodia from same. [Figures c,e,f, not to scale]

podial ligules enlarged, with rounded supraacicular notopodial lobe bearing numerous modified swimming setae. Neuropodial acicular lobe paddle-shaped, bilobed distally in region of neuroaciculum, bearing fan-shaped bundle of modified swimming setae; very large postsetal lamella developed from postsetal neuropodial lobe and extending beyond level of notopodial ligules; lower neuropodial ligule large; subconical; base of ventral cirrus greatly enlarged, forming asymmetrical winglike ventral lamella.

Pygidium with large papillated area around anal opening (more extensive than in female) and anal cirri (Figure 21c). Pharnyx similar to that of female.

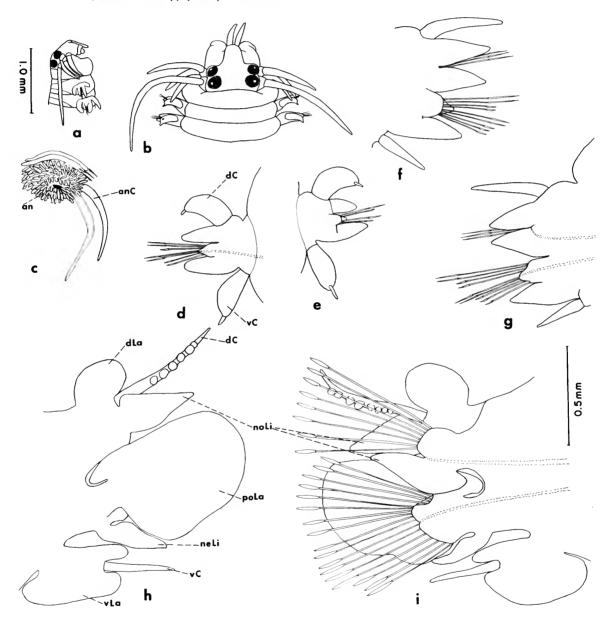
REMARKS.—The figure of the first parapodium by Treadwell (1942: fig. 3) was inverted. The first two

setigers have uniramous or subbiramous parapodia, not just the first setiger, as stated by Treadwell (1942: 3). The notopodial homogomph falcigers of the posterior unmodified parapodia in the female heteronereids were not noted in previous publications.

Leptonereis mexicana was referred to Nicon by Hartman (1956:279). Later, Hartman (1959a:245) indicated that N. mexicana was perhaps referable to N. moniloceras (Hartman); however, the two species do not have the same type of compound falcigerous neurosetae.

DISTRIBUTION.—Known only from epitokous stages. Galapagos, Lower California, western Mexico, Pacific side of Panama, Gulf of Mexico (Tampa Bay, Florida).

FIGURE 21.—Rullierinereis mexicana (a, male heteronereid from western Mexico, USNM 35813; b-i, male heteronereid from Tampa Bay, Florida, USNM 43406): a, Anterior end, lateral view; b, anterior end, dorsal view; c, posterior end, dorsolateral view; d, first parapodium, posterior view; e, second parapodium, anterior view; f, parapodium from anterior region, posterior view; g, same, anterior view; h, parapodium from modified region, posterior view (setae not shown); i, same, anterior view.



Rullierinereis gallardoi new species

FIGURE 22

Nicon maculatus.—Gallardo 1968:65, pl. 15: figs. 3-7. [Not Kinberg, 1866].

MATERIAL EXAMINED.—Nha Trang, South Viet Nam, 26 meters, coarse sand with shell and coral debris, station 164, 25 February 1960, V. A. Gallardo, collector—holotype (AHF 0252).

Description.—Length of holotype 40 mm, width 2 mm, including setae, segments about 64. Body colorless except for faint brownish wide band on setiger 3 and narrow bands on following anterior segments. Body cylindrical, tapering gradually posteriorly. Prostomium (Figure 22a) with short tapered frontal antennae and stout biarticulate palps; eyes moderately large, anterior pair slightly larger than posterior pair. Tentacular segment nearly twice length of following segment; tentacular cirri rather short, longest extending to setiger 2. Parapodia of first two setigers with large subulate dorsal cirri and single notopodial ligule; neuropodia similar to those of following setigers (Figure 22b).

Parapodia biramous from setiger 3 on (Figure 22c,d). Dorsal cirri subulate, extending beyond notopodial ligules. Upper and lower notopodial ligules subconical and subequal in size; notosetae few in number (1-2), homogomph spinigers with rather short blades (Figure 22e). Neuropodia with conical anterior acicular lobes and short rounded postsetal lobes (no conspicuous accessory lobes); neuropodial ligules subequal in size and shape to notopodial ligules. Ventral cirri short, subulate. Upper bundle neurosetae homogomph spinigers (3-4) with rather long blades (Figure 22f) and heterogomph falcigers (2) with moderately long blades (Figure 22g); lower bundle neurosetae heterogomph spinigers (1-2) with rather short blades (Figure 22h) and heterogomph falcigers (4-5).

Parapodia of middle and posterior regions slightly modified (Figure 22i,l); dorsal cirri longer and more slender, cirriform; lower neuropodial ligules smaller than notopodial ligules. Notosetae single stout homogomph falciger with short, elongate-oval blade (beginning about setiger 18; blades often missing; (Figure 22j,m). Upper bundle of neurosetae homogomph spinigers (7-8) and stouter heterogomph falcigers (1-2) with slightly shorter blades (Figure 22k,n); lower bundle of neurosetae heterogomph spinigers (3-5) and heterogomph falcigers (2-3).

Pygidium with ventral anal cirri and dorsal anus. Pharynx without paragnaths or papillae; horny jaws each with about 6 teeth (Figure 22a). Body cavity of holotype with moderately large eggs (Figure 22i).

ETYMOLOGY.—The species is named for Victor A. Gallardo, the collector and worker on the Polychaeta. DISTRIBUTION.—South Viet Nam.

Stenoninereis Wesenberg-Lund, 1958

Type-species.—S. martini Wesenberg-Lund, 1958, by monotypy. Gender: feminine.

Diagnosis.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two to three pairs of eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous; notopodium with dorsal cirrus and delicate notoaciculum. Dorsal cirri with elongate cirrophores and short subulate distal styles. Notopodia bilobed, forming lower acicular lobes continuous with presetal distal lobes and upper notopodial ligules present in anterior region but disappearing in posterior region. Neuropodia with acicular lobes but without ligules. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae homogomph and heterogomph spinigers and heterogomph falcigers. Pygidium with paired winglike lobes and anal cirri. Pharynx with paired jaws, without paragnaths or papillae.

A single species, S. martini, and one synonym, Nicon lackeyi Hartman, are referred to Stenoninereis. The genus is unique among the nereid genera in having dorsal cirri with elongate cirrophores and short distal styles. The parapodia have bilobed notopodia anteriorly and simple neuropodia, lacking extra neuropodial ligules.

Stenoninereis martini Wesenberg-Lund

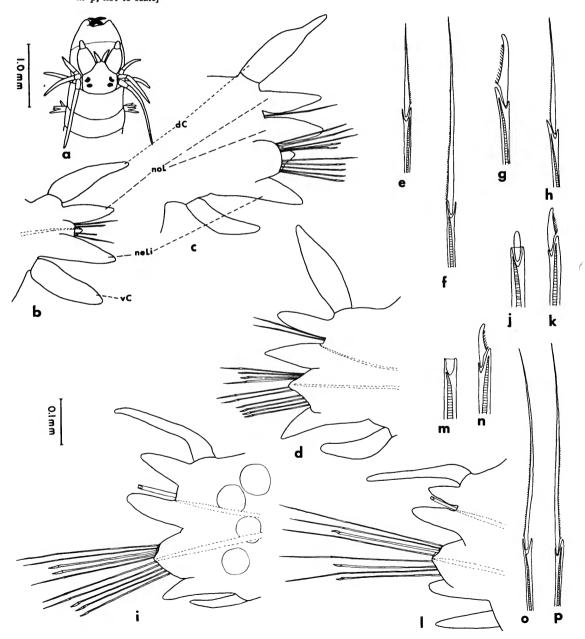
Figures 23, 24

Stenoninereis martini Wesenberg-Lund, 1958:9, figs. 2-4. [Published July 1958]

Nicon lackeyi Hartman, 1958:263, figs. 1-5. [Published August 1958]

MATERIAL EXAMINED.—Devil's Hole Swamp near Simson Bay Bridge, St. Martin Island, West Indies, 4 August 1949, P. W. Hummelinck, collector—2 syntypes of *Stenoninereis martini* (USNM 29726).

Warm Mineral Springs, Sarasota County, Florida,



J. Lackey, collector—holotype and 2 paratypes of Nicon lackeyi (USNM 29627-8).

Type-material.—One of the syntypes of S. martini (in two pieces) has a total length of 4 mm, a width of 1 mm, including setae, and 26 segments. The other syntype has a length of 3.5 mm, 1 mm in width, and 24 segments.

The holotype of *N. lackeyi* is a female filled with eggs, 6 mm in length, 2 mm in width, including setae, and 32 segments. The two paratypes are 3 and 4 mm in length, 1 mm in width, including setae, comprising 23 and 30 segments.

Description.—Length up to 6 mm, width up to 2 mm, including setae, segments up to 34. Prostomium (Figures 23a,b; 24a,b) with anterior medial notch, tapered frontal antennae, stout biarticulate palps, and moderately large eyes, anterior pair larger than posterior pair; sometimes additional small pair near posterior border. Tentacular segment shorter than following segments; tentacular cirri with long cylindrical cirrophores and filiform styles, longest extending to about setiger 7 (4-9). Parapodia of first two setigers with slender notoaciculum within short, conical, basal cirrophore of dorsal cirrus; style short (sometimes missing); neuropodia similar to those of following segments (Figure 23a,f,g).

Parapodia of anterior region with rami well separated (Figure 23h,i). Dorsal cirri with elongate, tapered basal cirrophores and short, subulate distal styles; notopodia elongate, distally bilobed, forming lower acicular lobe continuous with presetal distal lobe and upper notopodial ligule, lobes digitiform and subequal in length; notopodial lobes and lower border of dorsal cirrophores ciliated. Neuropodia with diagonally truncate anterior acicular lobes and shorter rounded postsetal lobes. Ventral cirri short, tapered. Notosetae homogomph spinigers with long, finely spinous blades (Figure 23j). Neuropodium with fanshaped group of neurosetae; upper few heterogomph spinigers with short blades (Figure 23k), supraacicular homogomph spinigers with long blades (Figure 23j), few subacicular heterogomph spinigers with blades relatively short, curved, with long basal spines (Figure 231), and heterogomph falcigers with blades long (upper ones) to short (lower ones; Figure 23m), finely spinous, and with hooked tips.

More posteriorly, dorsal cirrophores gradually shortened, upper notopodial ligules gradually diminishing and finally nearly absent (Figure 23n). Pygidium with flat winglike expansions lateral and

ventral to anus, with anal cirri attached laterally (Figures 23d,e; 24c). Pharynx without paragnaths or papillae; paired jaws each with about 9 teeth (6-10; Figure 23c).

REMARKS.—The descriptions of Stenoninereis martini Wesenberg-Lund and Nicon lackeyi Hartman were both published in 1958, the former in July, the latter in August. Examination of the type-specimens of both species indicates that the species are synonymous. The parapodial setae were incompletely described and not figured by Wesenberg-Lund. Hartman emended Nicon Kinberg to include N. lackeyi, as well as nine other nereid species. The only distinguishing character they have in common is an absence of paragnaths or papillae on the pharynx. In the present revision, some of these species are assigned to other genera.

BIOLOGY.—S. martini, a minute aberrant nereid, lives under unusual conditions. The type-locality of S. martini is Devil's Hole Swamp, a sinkhole pond of limestone area about 150 meters from shore on St. Martin Island. It is subject to tidal movements, with a bottom of rocks with mud, detritus, and algae, a pH of about 8 and salinity of 13.8% (Wesenberg-Lund, 1958: 6). The type-locality of N. lackeyi is Mineral Springs, Sarasota County, Florida, a large first magnitude spring emerging from a deep boil, having a constant temperature of 86° F, pH about 7.2, and salinity about 17% containing some hydrogen sulfide but no dissolved oxygen, and characterized by a unique flora and fauna (Lackey, 1957:255; Hartman, 1958:265). A flourishing population of N. lackeyi was found in this environment, which is unusual for its high temperature and concentration of certain minerals. The females have giant-size eggs. Development apparently is direct, without epitoky. Adults, kept alive in the laboratory by Dr. James Lackey, continued to give rise to young stages (Hartman, 1958:265).

DISTRIBUTION.—Florida (Warm Mineral Springs, Sarasota County), West Indies (Devil's Hole Swamp, St. Martin).

Tylorrhynchus Grube, 1868

Type-species.—T. chinensis Grube, 1868, by monotypy. Gender: masculine.=T. heterochetus (Quatrefages, 1865).

Chinonereis Chamberlin, 1924. Type-species: C. edestus

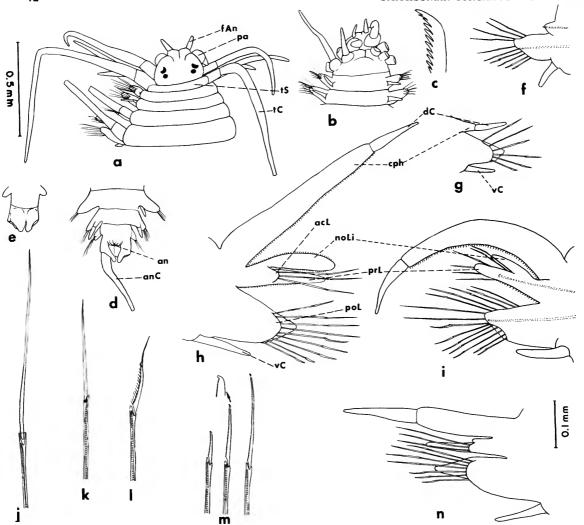


FIGURE 23.—Stenoninereis martini (syntypes of S. martini, USNM 29726): a, Anterior end, dorsal view, parapodia on right side not shown; tips of dorsal cirri of setigers 3 and 4 broken off; b, anterior end, ventral view; styles of all but two of tentacular cirri missing; c, tip of jaw; d, posterior end of female, dorsal view; right anal cirrus broken off and tip of left one broken; e, posterior end of male, ventral view; anal cirri broken off; f, first parapodium, anterior view; dorsal cirrus either absent or broken off; g, second parapodium, posterior view; h, parapodium from anterior region (setiger 5), posterior view; i, same (setiger 6), anterior view; j, homogomph spiniger from same; k, heterogomph spiniger from upper part of lower neuropodial bundle from same; m, heterogomph falcigers from lower neuropodial bundle from same; m, parapodium from posterior region, posterior view. [Figures c_i j-m, not to scale]

Chamberlin, 1924, by original designation and monotypy. Gender: feminine. = T. heterochetus (Quatrefages, 1865).

Diagnosis.—Prostomium subpyriform, with paired frontal antennae, biarticulate palps, and two pairs of

eyes. Tentacular segment achaetous and apodous; four pairs of tentacular cirri with distinct cirrophores. Parapodia of first two setigers subbiramous; notopodium with dorsal cirrus and ligule. Dorsal cirri with

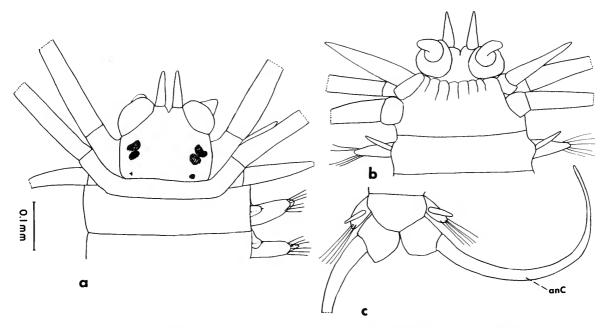


FIGURE 24.—Stenoninereis martini (paratype of Nicon lackeyi, USNM 29628): a, Anterior end, dorsal view; only bases of tentacular cirri shown; b, same, ventral view; c, posterior end, ventral view.

large thick cirrophores, enclosing large parapodial glands, and distal styles. Notopodia with low, rounded acicular lobes and subacicular ligules. Neuropodia thick, bilobed distally forming small rounded supraacicular and subacicular lobes; without ligules. Ventral cirri short and subulate. Notosetae hemigomph spinigers (homogomph, with accessory spine). Neurosetae hemigomph and heterogomph spinigers and heterogomph falcigers with relatively long blades. Pygidium with paired anal cirri. Pharynx with paired jaws, without paragnaths but with soft papillae on both maxillary and oral rings.

Remarks.—Tylorrhynchus differs in a number of ways from the usual pattern in the Nereididae. The following points may be mentioned: 1. single subacicular notopodial ligules (no neuropodial ligules); 2. dorsal cirri with large cirrophores, enclosing large parapodial glands with lateral openings, and distal styles (the cirrophores corresponding to the usual upper notopodial ligules); 3. thick neuropodia, bilobed distally, with circular arrangement of the neurosetae (not the usual fan-shaped upper and lower bundles); 4. all setae with articulations hemigomph or

heterogomph (none strictly homogomph); 5. sexual epitokes formed by transformation of the anterior part of the body, with the posterior part cast off.

The genus is represented by a single species, T. heterochetus (Quatrefages), and five synonyms. Quatrefages (1865) described Nereis heterocheta, based on a single epitoke from Java; the description was brief and no figures were provided. Grube (1868) described and figured Tylorrhynchus chinensis, based on a single male epitoke from Shanghai, China, and established the genus Tylorrhynchus. Grube (1870), after examining Quatrefages' holotype in the Paris Museum, indicated that Nereis heterochaeta [sic] belonged to his genus Tylorrhynchus. Izuka (1903) described Ceratocephale osawai from the west coast of Japan, including atokous and swarming epitokous stages of both males and females, the Japanese Palolo; he tentatively referred his species to Ceratocephale in preference to creating a new genus for it. Ramsay (1914b) synonymized the three species but chose to use T. chinensis because of Grube's more complete description, including figures. Based on a study of specimens from Indochina (Tonkin and Annam), Gravier and Dantan (1932) synonymized the three species and followed the law of priority by using *Tylorrhynchus heterochaetus* [sic] (Quatrefages). *T. sinensis* (error for *T. chinensis*) was introduced in the literature by Dawydoff (1952).

Chamberlin (1924) described Chinonereis edestus, based on a gravid female (not epitokous) from freshwater in Canton, China, collected by Mr. Arthur S. Campbell who reported that the worms were common in the rice-fields surrounding Canton and in the low-lands as far as Hongkong and were used as food. Chamberlin's description was brief, incomplete, and confusing in some respects; there were no figures. The type-specimen is not present in the Museum of Comparative Zoology, Harvard, where it was supposed to have been deposited (H. W. Levi, in correspondence). Chinonereis is herein referred to Tylorrhynchus and C. edestus to T. heterochetus. The latter species was reported from Canton, Amoy, and Shanghai, China, by Wu and Chen (1963), where it is known as a mixohaline and freshwater species; they suspected that the two species were synonymous.

Treadwell (1936) described Nereis (Leptonereis) distorta from Amoy, China, based on a single male epitoke collected by T. Y. Chen. Examination of the holotype, deposited in the United States National Museum, showed it to be the same as T. heterochetus and is described below. It is of interest to note that Monro (1934) identified a specimen, also from Amoy by the same collector, as T. heterochaetus [sic].

T. bahamensis Hartmann-Schröder (1958) from the Bahamas was incorrectly referred to Tylorrhynchus, as shown by the presence of lower neuropodial ligules, notopodial homogomph falcigers, and neuropodial heterogomph falcigers with short blades. The species is herein referred to Rullierinereis (see page 31).

Tylorrhynchus heterochetus (Quatrefages)

FIGURE 25

Nereis heterocheta Quatrefages, 1865:552.

Tylorrhynchus chinensis Grube, 1868:22, pl. 2: fig. 3.—
Ramsay 1914b:231 (synonymy).

Nereis heterochaeta [sic].—Grube 1870:312.

Ceratocephale osawai Izuka, 1903:1, pls. 1, 2.

Chinonereis edestus Chamberlin, 1924:81.

Tylorrhynchus heterochaetus [sic].—Gravier and Dantan 1932:671, figs. 1-3 (synonymy).—Monro 1934:363.—Wu and Chen 1963:20, 31, pl. 2: figs. B-G.

Nereis (Leptonereis) distorta Treadwell, 1936:273, fig. 20a-f.

Tyllorhynchus [sic] sinensis.—Dawydoff 1952:88 (error for T. chinensis]

Tylorrhynchus heterochetus.-Hartman 1959a: 260, 280.

MATERIAL EXAMINED.—Near Amoy, China, T. Y. Chen, collector.—holotype of Nereis (Leptonereis) distorta (USNM 20118).

Type-material.—The holotype of *Nereis (Leptonereis) distorta* consists of a male epitoke, 70 mm in length, 8 mm in width, including parapodia, and 61 setigers, with posterior end missing (characteristic of epitokes). The pharynx was not extended but had been slit open, the pharynx removed and is now missing. Modified parapodia with swimming setae begin on setiger 25.

Description of male heteronereid.—Prostomium with deep middorsal depression on anterior half, subulate frontal antennae, and stout biarticulate palps; eyes large, anterior pair much larger than posterior pair (Figure 25a). Tentacular segment longer than following segment; tentacular cirri with styles relatively short, longest extending to about setiger 5. Parapodia of first two setigers with dorsal cirrus and ligule only; neuropodium similar to those of following segments (Figure 25b).

Parapodia of anterior unmodified segments (Figure 25c-e) with rami indistinctly separated, thick, opaque, only tips of the acicula evident externally. Dorsal cirri with thick subrectangular cirrophores and short subulate distal styles; parapodial glands in basal part, with openings laterally. Notopodia with low rounded postsetal lobe and shorter presetal lobe continuous with lower conical ligule. Neuropodia thick, with subtriangular posterior and bilobed anterior lobes, above and below neuroaciculum. Ventral cirri short, subulate. Notosetae relatively few, short, arranged in vertical row above notoaciculum. Notosetae slightly heterogomph or hemigomph spinigers, with blades rather short (Figure 25f). Neurosetae nearly encircling upper and lower neuropodial lobes with gap in middle anteriorly, setal bundle arranged in form of "3". Dorsoposterior neurosetae hemigomph spinigers with long, finely spinous blades (Figure 25g); ventroposterior neurosetae heterogomph spinigers with long blades, with more prominent spines basally (Figure 25h); upper and lower anterior neurosetae heterogomph falcigers with relatively long blades (Figure 25i).

Parapodia of modified region somewhat enlarged

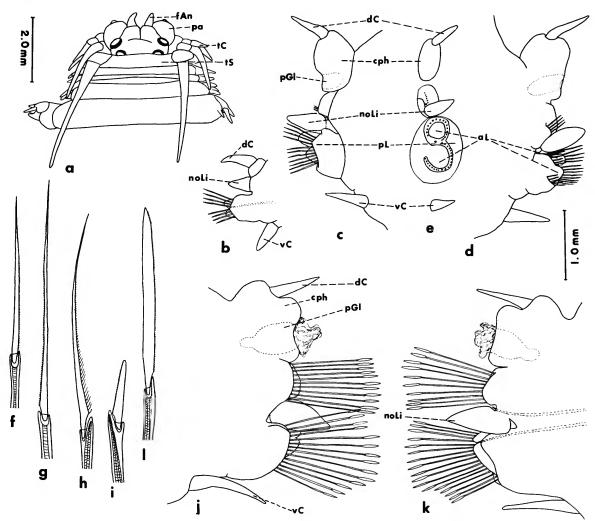


FIGURE 25.—Tylorrhynchus heterochetus, male heteronereid [holotype of Nereis (Leptonereis) distorta, USNM 20118]: a, Anterior end, dorsal view; first three setigerous segments compressed unnaturally; b, first parapodium, posterior view; c, parapodium from anterior region (setiger 16), posterior view; d, same, anterior view; e, diagrammatic cross-section of same, showing arrangement of setae; f, hemigomph spinigerous notoseta; g, hemigomph spinigerous neuroseta; h, heterogomph spinigerous neuroseta; i, heterogomph falcigerous neuroseta; j, parapodium from middle modified region, posterior view; k. same, anterior view; l, heterogomph swimming seta from same. [Figures f-i, l, not to scale]

and flattened but similar to anterior parapodia, without addition of extra lamellae (Figure $25j_{,k}$). Cirrophores of dorsal cirri wider, with more prominent parapodial glands; notopodial ligules more pointed; usual setae replaced by numerous heterogomph swimming setae (Figure 25l). Pharynx with denticulate

jaws and soft papillae on both maxillary and oral rings, papillae somewhat variable in number and size (pl. 2: fig. 3a,b, in Grube, 1868; pl. 2: figs. 10, 11, in Izuka, 1903; pl. 2: figs. B,C, in Wu and Chen, 1963).

Biology.—T. heterochetus is a shallow water,

brackish and freshwater nereid found burrowing in the bottom mud of the mouths and tributaries of rivers, including canals, ditches and marshes. They burrow in the bottom mud and move about on the surface of the substrate during flood tides. They are active and voracious, feeding on various aquatic animals and plants. Sometimes they have become pests in the rice fields. This atokous stage has been variously called "saltwater millepede," "Itomé" by the Japanese (meaning thread worm), and "Wohchung" by the Chinese (meaning rice or field worm). The atokous forms have been reported up to 250 mm in length, 4 mm in width, and 300 segments.

At sexual maturity, the anterior portions of the worms, representing about a third of the total body segments, become filled with eggs or sperm and transformed into heteronereids or epitokes, modifications including the enlargement of the eyes, expansion of the parapodia, enlargement of the segments, and development of swimming setae. The posterior two-thirds of the body takes no part in the transformation and undergoes degeneration. These transformed adults with their shrunken tail regions, when still on the bottom, are referred to as "Hori-Bachi" (meaning dug-out Bachi).

During reproduction, in a lunar periodicity, the anterior modified portions break away from the posterior regions, leave the bottom and swarm in large numbers near the water surface, when they are called "Bachi" or Japanese Palolo. They vary in length from 33 to 130 mm, with a width of 3 to 11 mm, and consist of 60–78 segments. The swimming setae begin about setiger 24. The posterior ends are missing except sometimes remnants may remain.

DISTRIBUTION.—Indo-Pacific: Java, China, Indo-china, Japan. Estuarine and freshwater.

Platynereis Kinberg, 1866 Platynereis cebuensis (Grube) new combination

FIGURES 26, 27

Nereis (Leptonereis) cebuensis Grube, 1878:61. Laeonereis cebuensis.—Hartman 1959a:243, 262.

MATERIAL EXAMINED.—Cebu, Philippine Islands, Semper, collector—2 syntypes (ZMB Q3465).

Type-material.—The larger syntype is a partially metamorphosed male heteronereid of about 83 setigers, 24 mm in length and 4 mm in width, including setae; the pharynx is extended. The smaller syn-

type is atokous, with about 40 setigers, a length of 13 mm and a width of 2 mm, including setae.

DESCRIPTION.—Body pigmented with brown dots on prostomium and anterior segments, forming transverse bands; more posteriorly, pigmented areas confined to lateral parts of body medial to parapodia, notopodial and neuropodial ligules. Prostomium (Figure 26a,b) suboval, with paired subulate frontal antennae, stout biarticulate palps; two pairs of eyes moderately large (small atokous syntype) to large (partially metamorphosed male syntype). Tentacular segment subequal in length to following segment; four pairs of tentacular cirri, upper two pairs conspicuously long, extending beyond setiger 11 (tips broken). Parapodia of anterior two setigers subbiramous, notopodium represented by subulate dorsal cirrus and single notopodial ligule (Figure 26e,f); neuropodium with anterior conical acicular lobe and prominent postsetal lobe and neuropodial ligule; ligules and postsetal lobe elongate-conical. Upper bundle of neurosetae homogomph spinigers; lower bundle of neurosetae heterogomph spinigers with long (upper ones) to short (lower ones) blades. Ventral cirri subulate.

Dorsal cirri of anterior seven and ventral cirri of anterior five setigers slightly modified—thicker, cylindrical on basal halves, with curved tips (Figure 26 e-h). Biramous parapodia of more anterior setigers (Figure 26g,h) with two thick, rounded notopodial ligules, conical anterior neuropodial acicular lobe, shorter postsetal lobe, and thick, rounded neuropodial ligule. Notosetae homogomph spinigers (Figure 26i). Upper bundle of neurosetae consisting mostly of homogomph spinigers and few heterogomph falcigers (Figure 26j); lower bundle of neurosetae with few heterogomph spinigers and mostly heterogomph falcigers. More posterior parapodia of anterior region (Figure 27a,b) with dorsal cirri more elongate, cirriform; two notopodial ligules elongate-conical, widely separated, with low rounded notopodial acicular lobe between them; neuropodium with subequal anterior acicular and postsetal lobes; neuropodial ligules subconical; ventral cirri tapered. Setae similar to those of more anterior parapodia.

Middle and posterior parapodia of partially metamorphosed male heteronereid showing beginning stages of developing extra lamellae (Figure 27c,d): dorsal cirri slightly scalloped along one margin, exhibiting early development of lobulated dorsal cirri characteristic of male heteronereids; dorsal lamella

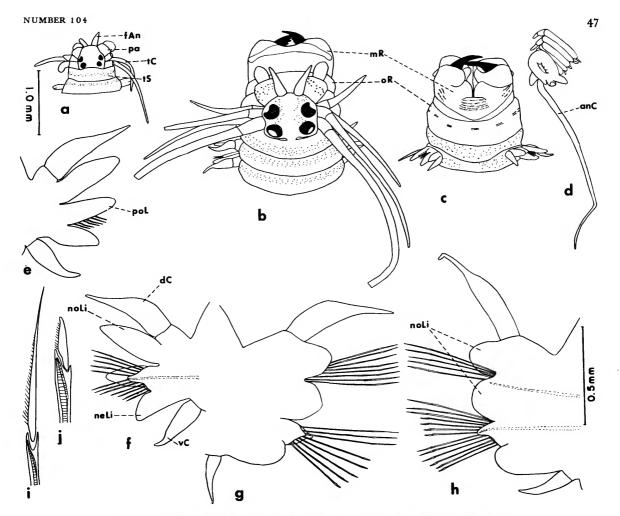


FIGURE 26.—Platynereis cebuensis [syntypes of Nereis (Leptonereis) cebuensis, ZMB Q3465: a, smaller syntype; b-j, larger syntype—partially metamorphosed male heteronereid]: a, Anterior end, dorsal view; part of tentacular cirri missing or regenerating; b, dorsal view of anterior end with pharynx extended; some of tentacular cirri with tips broken; c, same, ventral view; d, posterior end, dorsolateral view, right anal cirrus missing; e, first parapodium, posterior view; f, second parapodium, anterior view; g, parapodium from setiger 6, posterior view; h, parapodium from setiger 7, anterior view; i, homogomph spiniger from same; j, heterogomph falciger from same. [Figures i,j, not to scale]

medial to base of dorsal cirrus somewhat enlarged; neuropodial postsetal lamella paddle-shaped, and winglike ventral lamella on base of ventral cirrus somewhat enlarged. None of setae replaced by swimming setae. Notosetae consisting of numerous homogomph spinigers and few homogomph falcigers, blades with hooked tips (Figure 27e). Upper bundle of neurosetae homogomph spinigers and heterogomph falcigers (Figure 27f); lower bundle of neurosetae

heterogomph spinigers and falcigers.

Pygidium with conical lateral lobes and long anal cirri (Figure 26d). Pharynx (Figure 26b,c) with pair of jaws each with four subterminal teeth; faint denticles, characteristic of *Platynereis*, present on both rings; maxillary or distal ring: dorsally (areas I and II) with transverse ridge, without denticles; midventrally (area III) elongate-oval area of five transverse rows; ventrolaterally (area IV) arched groups

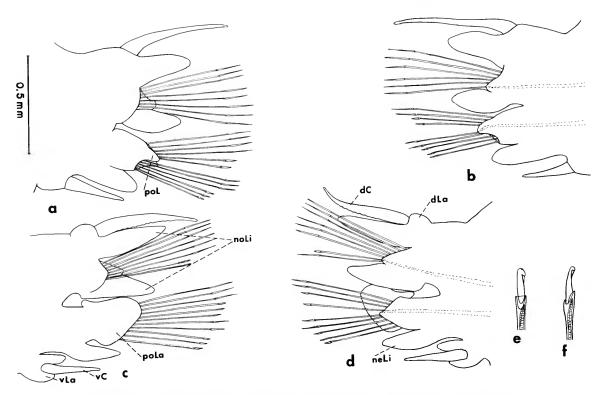


FIGURE 27.—Platynereis cebuensis (larger syntype—partially metamorphosed male heteronereid, ZMB Q3465): a, Parapodium from setiger 11, posterior view; b, parapodium from setiger 12, anterior view; c, parapodium from middle region, posterior view (partially modified, showing partial development of enlarged lamellae); d, same, anterior view; e, notopodial homogomph falciger from same; f, neuropodial heterogomph falciger from same. [Figures e,f, not to scale]

of three rows; basal or oral ring: middorsally (area V) bare; dorsolaterally (area VI) two faint rows; ventrally (areas VII-VIII) 7 groups of two rows each.

REMARKS.—The pharynx is extended on the larger syntype but the minute denticles of the *Platynereis* type were overlooked by Grube. The pharynx of the smaller syntype is not extended; when dissected, it also revealed the characteristic denticles. Grube (1878) described *Nereis (Platynereis) fusco-rubida* from the Philippines in the same publication in which *N. (Leptonereis) cebuensis* was named. Neither species was figured. Unfortunately, types of the former species were not found in the Zoologisches Museum, Berlin (according to G. Hartwich, in correspondence) and the species must be considered questionable.

DISTRIBUTION.—Philippine Islands.

[?] Platynereis sp.

Leptonereis glauca moniloceras Hartman, 1940:217, pl. 34: figs. 42-46.

Nicon moniloceras.—Hartman 1958:265; 1959a:245, 274.

Remarks.—The species, described from a female heteronereid dredged in 73 meters off Catalina Island, Southern California, and associated with brachiopod and sponge clusters, is questionably referred to *Platynereis*. The necessity for this reassignment is suggested by the oval prostomium, conspicuously long tentacular cirri, the parapodial lobes and setae—all agreeing with *Platynereis*. Perhaps the minute pharyngeal denticles were overlooked.

Platynereis sp.

Nicon peruviana Berkeley and Berkeley, 1964:128, figs. 1, 2.

MATERIAL EXAMINED.—South Pacific off Peru, approximately 5°S, 81°W, at night-light, 10 April 1959, P.N. Sund, collector—holotype and paratype (USNM 32821-2).

Remarks.—The types are male heteronereids. The pharynx of the holotype had been dissected and is now missing. The pharynx of the paratype was dissected but the denticles are not clearly visible. The specimens appear, however, to be a typical *Platynereis*.

Platynereis sp.

Leptonereis davidi Fishelson and Rullier, 1969:62, fig. 1A-D.

MATERIAL EXAMINED.—Bay of David, Entedebir Island, Red Sea, on *Sargassum*, 13 March 1962—holotype (No. E62/238, Department of Zoology, Tel-Aviv University, Israel).

Remarks.—The holotype consists of a small specimen, 8 mm in length, 1 mm in width, including setae, and about 55 segments with a posterior growing zone. The pharynx was not extended but had been dissected; however, no denticles were observed. Since the specimen is small and the pharynx was not extended, this character would be difficult to observe. Nevertheless, the parapodial lobes, setae, and prominent glandular masses are of the typical *Platynereis* type.

Indeterminable NEREIDIDAE

1. Nicomedes difficilis Kinberg

Nicomedes difficilis Kinberg, 1866:179.—Hartman 1949:57.

MATERIAL EXAMINED.—South Atlantic off Rio de Janeiro, Brazil, 55–73 meters, *Eugenie* Expedition—holotype (NRS 572).

REMARKS.—The holotype consists of the posterior end of a heteronereid. As indicated earlier by Hartman (1949:57), both the genus and species must be considered indeterminable because of the brevity of the original description, absence of figures, and the poor condition of the holotype.

2. Nicon pictus Kinberg

Nicon pictus Kinberg, 1866:178.-Hartman 1949:57.

MATERIAL EXAMINED.—South Atlantic off Rio de Janeiro, Brazil, 20°30'S, 40°55'W, 40–55 meters, Eugenie Expedition—4 syntypes (NRS 486).

Remarks.—The syntypes consist of two complete specimens, 19 and 12 mm in length, 1 mm in width, and about 50 segments, and two anterior fragments. They are in poor condition, transparent, and covered with crystals and fibers. Since the species has not been, nor can it now be, adequately described or figured, *N. pictus* should be considered indeterminable.

3. Nicon tahitanus Kinberg

Nicon tahitanus Kinberg, 1866:178.—Hartman 1949:59, pl. 8: figs. 7, 8.

MATERIAL EXAMINED.—Tahiti near Papeete, in sand and corals, 16.5 meters—holotype (NRS 494).

REMARKS.—The holotype consists of anterior and middle fragments totaling 36 segments, 8 mm in length and 1 mm in width. Accompanying the specimen is a thin tube covered with debris. The pharynx had been removed and is now missing. Eggs are present in the body cavity, indicating that it was not a juvenile, as stated by Hartman (1949:59). The type material is too poor for an adequate description. For the present, N. tahitanus should be considered indeterminable.

4. Nicon virgini Kinberg

Nicon virgini Kinberg, 1866:179.-Hartman 1949:59.

MATERIAL EXAMINED.—York Bay, Magellan Strait, C. A. Virgin collector, *Eugenie* Expedition—holotype (NRS 576). Port Famine, Magellan Strait, 14.6 meters, *Eugenie* Expedition—4 specimens (NRS 575). Magellan Sound, South America, *Eugenie* Expedition—1 specimen (NRS 1647).

REMARKS.—Of the three lots collected by the Eugenie Expedition and identified by Kinberg as N. virgini, only NRS 576 was apparently collected in the type-locality. The holotype consists of about 70 segments, 20 mm long and 1 mm wide. It is in poor condition being covered with crystals and with the blades of the setae mostly broken. NRS 575 contains four anterior fragments in poor shape. NRS 1647 contains anterior and middle fragments of a larger specimen; the pharynx is extended and paragnaths are present. In the absence of figures, an adequate

description, and the poor condition of the holotype, N. virgini should be considered indeterminable.

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