Revista Mexicana de Biodiversidad

Revista Mexicana de Biodiversidad 93 (2022): e934052

Taxonomy and systematics

Redescriptions of four nereidid species (Annelida: Phyllodocida: Nereididae) from the Atlantic Ocean described by Aaron Louis Treadwell

Redescripciones de cuatro especies de neréididos (Annelida: Phyllodocida: Nereididae) del océano Atlántico descritos por Aaron Louis Treadwell

Víctor Manuel Conde-Vela [a, b]

[a] *Universidad Autónoma de Nuevo León, Facultad de Ciencias Biológicas, Av. Pedro de Alba y Av. Manuel L. Barragán 66450, San Nicolás de Los Garza, Nuevo León, Mexico*

[b] *El Colegio de la Frontera Sur, Departamento de Ecología Acuática, Av. Centenario Km. 5.5, 77014 Chetumal, Quintana Roo, Mexico*

*Corresponding author: victorconde2323@gmail.com (V.M. Conde-Vela)

Received: 25 May 2021; accepted: 22 November 2021

Abstract

Aaron Louis Treadwell proposed a large number of new taxa, and several of them are regarded as synonyms. Treadwell proposed 32 new species in the family Nereididae, and a few of them have been re-evaluated. Here, the validity of 4 species is reassessed based on the examination of type material of 3 *Nereis* species and 1 *Perinereis*: *N. arroyensis*, *N. largoensis*, and *P. diversidentata* are regarded as valid species, and the synonymy of *Nereis disparsetosa* Treadwell, 1932 with *Pseudonereis palpata* (Treadwell, 1923) is confirmed. A commented table of the nereidid species proposed by Treadwell is also included.

Keywords: Morphology; Systematics; New combination; Synonymy

Resumen

Aaron Louis Treadwell propuso una gran cantidad de nuevos taxones y varios de ellos se consideran sinónimos. Treadwell propuso 32 especies nuevas de la familia Nereididae y algunas de ellas han sido reevaluadas. Aquí se analiza la validez de 4 especies con base en el examen del material tipo de 3 especies de *Nereis* y 1 de *Perinereis*. *N. arroyensis* Treadwell, 1901, *N. largoensis* Treadwell, 1931 y *P. diversidentata* Treadwell, 1943 se consideran especies válidas, y la sinonimia de *Nereis disparsetosa* Treadwell, 1932 con *Pseudonereis palpata* (Treadwell, 1923) se confirma. Se incluye una tabla comentada de los neréididos propuestas por Treadwell.

Palabras clave: Morfología; Sistemática; Nueva combinación; Sinonimia

ISSN versión electrónica: 2007-8706; Universidad Nacional Autónoma de México, Instituto de Biología. https://doi.org/10.22201/ib.20078706e.2022.93.4052

Introduction

Aaron Louis Treadwell was a prolific polychaetologists with a long series of publications describing polychaetes with the proposal of many new species, of which 36 were nereidids proposed from 1901 to 1943 (Hartman, 1956). Hartman (1956) highlighted that Treadwell had scarce laboratory equipment and limited access to bibliography, and along with his schematic freehand drawings from memory, explained his purported problems when describing species and why most of his species were regarded as junior synonyms by herself and other. It is comprehensible that a large number of names were synonymized due to the prevalence at that time of preserving the oldest name (mainly European) and the idea of the existence of few cosmopolitan species with large ranges of morphological variation promoted by prominent colleagues (Hutchings & Kupriyanova, 2018), coinciding with a period (1930-1960) with few proposals for new names (Pamungkas et al., 2019).

Although Treadwell's species descriptions are sometimes succinct and the figures schematic, at least in nereidids they are accurate in most cases when compared to the original material. Some problems found in the works describing nereidids are the proposal of replacement for preoccupied names, and the lack of comparison of his new species with pre-existent ones in several cases, even with their own. Some nereidids described by Treadwell have already been redescribed and accepted as valid; however, the validity of most of them is pending to be re-assessed. Some examples are the species *Nereis arroyensis* Treadwell, 1901, *Nereis disparsetosa* Treadwell, 1932, *Nereis largoensis* Treadwell, 1931, and *Perinereis diversidentata* Treadwell, 1943.

In one of his early works, Treadwell (1901) proposed *Nereis arroyensis* based on specimens from Arroyo, Puerto Rico. The description is succinct and included 2 drawings of the head and a parapodium, presumably an anterior one but not clearly stated (Treadwell, 1901), avoiding giving more details in a later work (Treadwell, 1939). Hoagland (1919) recorded the species from Cayo María Langa, Puerto Rico. Hartman (1956) examined the holotype and described the pharyngeal features for the first time but no additional features or figures were included, and Rullier (1974) recorded *Nereis arroyensis* from La Habana Bay based on the original description. Although its validity is not in doubt, some key features used in current descriptions are missing from these descriptions, requiring further evaluation of their morphology.

Nereis brevicirrata Treadwell, 1929 was described based on a single specimen from Key Largo, Florida, but later Treadwell (1931) proposed *Nereis largoensis* as a replacement name because the homonymy with *N. brevicirrata* Treadwell, 1920. Hartman (1956) regarded it as a subspecies of the stem species *Nereis pelagica* Linnaeus, 1758, but recognizing some differences such as the presence of paragnaths in area V and larger notopodial lobes in posterior chaetigers in *N. pelagica largoensis*, and by having a different shape of blades of notopodial homogomph falcigers than another regional subspecies *Nereis pelagica occidentalis* Hartman, 1945. In the same year, Pettibone (1956) examined the type material of *N. largoensis*, synonymized the subspecies *Nereis pelagica largoensis* with *N. pelagica*, but regarded *Nereis pelagica occidentalis* as distinct from *N. pelagica* and gave it the status of species; *N. occidentalis* has been recently redescribed based on type material (Salazar-Vallejo et al., in press) to distinguish it from the *Nereis falsa* species complex, while *N. largoensis* remained as a junior synonym of *N. pelagica*. *Nereis largoensis* has been recorded from Isla de Providencia in the Colombian Caribbean (Báez & Ardila, 2003; Dueñas, 1999).

Treadwell (1932) described *Nereis disparsetosa* from São Paulo, Brazil based on 2 complete specimens, and included a comprehensive description and 5 line drawings of the head, parapodia, and chaetae. As in other several cases, Treadwell did not contrast this new species with another one described by himself, *Nereis* (*Neanthes*) *palpata* Treadwell, 1923, or *Nereis coerulea, N. microphthalma*, and *N. obscura*, proposed by Hansen (1882). Hartman (1938) examined the type material of both Treadwell's species, transferred *Nereis* (*Neanthes*) *palpata* to *Pseudonereis*, and regarded *N. disparsetosa* and *Pseudonereis atopodon* Chamberlin, 1919 as junior synonyms of *P. palpata*, but the additional features included and explanations of the synonymies are somewhat scarce. Bakken (2007) redescribed *P. palpata* and *P. atopodon* in detail, but overlooked the synonymy with *N. disparsetosa*.

Treadwell (1943) proposed *Perinereis diversidentata* from Cape Cross, Namibia, and included a comprehensive description and 7 figures describing the head, shape, and arrangement of the paragnaths of some areas, parapodia, and chaetae. Day (1953) regarded *P. diversidentata* as a junior synonym of *Pseudonereis variegata* (Grube & Kröyer, in Grube, 1857) from Chile, and Hartman (1956) agreed with Day's decision. Later, Bakken (2007) and Conde-Vela (2018) overlooked this synonymy in their respective works when redescribing *P. variegata*, as for Kara et al. (2018) that reinstated a similar species from southern Africa, *P. podocirra* (Schmarda, 1861), without mentioning Treadwell's species. Therefore, a re-assessment of the validity and a redescription of *Perinereis diversidentata* is needed.

The aim of this work is to redescribe *Nereis arroyensis* Treadwell, 1901, *Nereis disparsetosa* Treadwell, 1932,

Nereis largoensis Treadwell, 1931, and *Perinereis diversidentata* Treadwell, 1943, based on the examination of type material, to present more details on their morphology. Moreover, a commented table including all nereidids described by Treadwell is also provided.

Material and methods

Type specimens examined are deposited in the American Museum of Natural History, New York, USA (AMNH), and the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM).

Specimens were examined under stereomicroscope and compound microscopes for observing parapodial and chaetal features. Some parapodia along the body were removed and mounted in semi-permanent slides with ethanol-glycerol and examined under the compound microscope. Photographs were made using a Sony Alpha-6000 provided with an adapter for both microscopes. A set of photographs were digitally stacked to improve the depth of visual field with Zerene Stacker and post-processed with Adobe Photoshop.

The terminology proposed by Villalobos-Guerrero and Bakken (2018), Villalobos-Guerrero (2019), and Conde-Vela (2018), for parapodial and pharyngeal features was followed; whereas the description of chaetal shafts and the measuring of parapodial structures followed Conde-Vela (2021a).

Descriptions

Order Phyllodocida Dales, 1962
Family Nereididae de Blainville, 1818
Genus *Nereis* Linnaeus, 1758
Type species. *Nereis pelagica* Linnaeus, 1758, by subsequent designation (Hartman, 1948).
Diagnosis followed: Bakken and Wilson, 2005.

Nereis arroyensis Treadwell, 1901
Figs. 1, 2
Nereis arroyensis Treadwell, 1901: 193-194, Figs. 30-31. Hoagland, 1919: 574 (list only). Treadwell, 1939: 223, Fig. 48. Hartman, 1956: 280. Rullier, 1974: 37.

Description. Syntypes (USNM 16005) in good condition, one small, incomplete. Largest complete, 43 mm long, 2 mm wide at chaetiger 10 excluding parapodia, 70 chaetigers. Body pale, pigmentation absent, body tissue translucent toward posterior end (Fig. 1A, B).

Prostomium subpentagonal, as long as wide; anterior region distally entire, subtriangular, slightly longer than posterior region (Fig. 1A); anterolateral gap between antenna and palpophore as long as diameter of antennae (Fig. 1A). Antenna of left side distally incomplete, right one digitiform; antennae not passing the palps, gap between antennae very small (Fig. 1A). Palpophores ovoid, swollen, 1.5 longer than wide, shorter than prostomium, subdistal transverse groove present (Fig. 1A). Palpostyles subconical (Fig. 1A). Eyes almost entirely faded, reddish, anterior and posterior pairs rounded, subequal, in trapezoidal arrangement, eyes diameter slightly shorter than basal width of antennae, lenses visible, anterior big, covering almost all eye (Fig. 1A). Tentacular belt 1.5 times longer than chaetiger 1, partially covering posterior pair of eyes (Fig. 1A), with a small ventral flap (Fig. 1D). Tentacular cirri smooth, cirrophores ring-shaped, cirrostyles cirriform; posterodorsal tentacular cirri missing in larger specimen (Fig. 1A), in smaller syntype reaching chaetiger 4. Pharynx everted corrugated, partially dehydrated, oral ring 1.5x wider than maxillary ring (Fig. 1C, D). Jaws with inner margin dentate, more than 8 teeth (not extracted) (Fig. 1C, D). Maxillary ring: I = 3 cones in a vertical row; II = 17-18 cones in arc; III = 42 in a large rectangle; IV = 32-38 cones in round (Fig. 1C-D), merged paragnaths absent. Oral ring: V = 0; VI = 6-7 in a rectangle; VII-VIII = 98 small cones in 2 bands, anterior band with 32 paragnaths placed in ridge regions A-C and furrow regions a-c; posterior band with 66 paragnaths placed in ridge regions A-E and furrow regions a-e (Fig. 1C-E). Furrow pattern of areas VI-V-VI, λ-shaped (Fig. 1C). Dorsal cirrus digitiform in first 2 chaetigers, filiform thereafter, attached basally to dorsal ligule in anterior chaetigers, medially thereafter (Fig. 2A-D); 0.8x length of distal region of dorsal ligules in anteriormost chaetigers (Fig. 2A), 1.3-1.4x longer in anterior and middle chaetigers (Fig. 2B, C), 2.5x in posterior chaetigers (Fig. 2D). Dorsal ligule with distal region longer than proximal ones in anterior chaetigers, becoming shorter toward middle and posterior chaetigers (Fig. 2A-D). Distal region of dorsal ligule subconical throughout; 1.8x longer than median ligule in anterior chaetigers (Fig. 2B), 1.2x in middle chaetigers (Fig. 2C), 0.8x length in posterior chaetigers (Fig. 2D). Median ligule subconical with blunt tip in anteriormost chaetigers, slightly lanceolate in anterior and middle chaetigers, subconical with pointed tip in posterior ones (Fig. 2A-D); 1.8x longer than neuroacicular ligule in anterior chaetigers (Fig. 2B), 1.5x in middle chaetigers (Fig. 2C), 2.5x in posterior chaetigers (Fig. 2D). Neuroacicular ligule subconical throughout, superior and inferior lobes absent (Fig. 2A-D). Neuropodial postchaetal lobe rounded, shorter than neuroacicular ligule throughout (Fig. 2A-D). Ventral ligule subconical with blunt tip throughout; 3.4x longer than neuroacicular ligule in anteriormost chaetigers (Fig. 2A), as long as in anterior chaetigers (collapsed in Fig. 2B), 1.4x

in middle chaetigers (Fig. 2C), 2x in posterior chaetigers (collapsed in Fig. 2D). Ventral cirrus digitiform in first chaetigers, filiform thereafter (Fig. 2A-D); 0.5x length of ventral ligule in anteriormost chaetigers (Fig. 2A), 0.8x in anterior chaetigers (Fig. 2B), 0.5x in middle chaetigers (Fig. 2C), 0.7x in posterior chaetigers (incomplete in Fig. 2D). Aciculae amber throughout, becoming lighter toward posterior chaetigers (Fig. 2A-D); notoaciculae absent in first 2 chaetigers (Fig. 2A); both noto- and neuroaciculae of similar thickness throughout. Most chaetae broken or blades missing. Notochaetae consisting of homogomph symmetrical spinigers and falcigers. Spinigers with blades pectinate, teeth minute, decreasing in size toward blade tip, replaced by homogomph falcigers in posterior chaetigers. Falcigers with symmetrical rim of shaft; blades slightly falcate, 6 coarse teeth, one third of inner margin edentulate, blade tip stout, tendon not observed (Fig. 2E). Neurochaetae consisting of homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in infra-acicular ones, most blades detached or broken. Spinigers with blades as in notopodial ones. Infra-acicular falcigers with blades pectinate, teeth increasing in size toward distal end, blade tip stout, tendon not observed (Fig. 2F).

Pygidium swollen, as long as wide (Fig. 1B); anal cirri cirriform, long, as long as last 7 chaetigers (Fig. 1B).

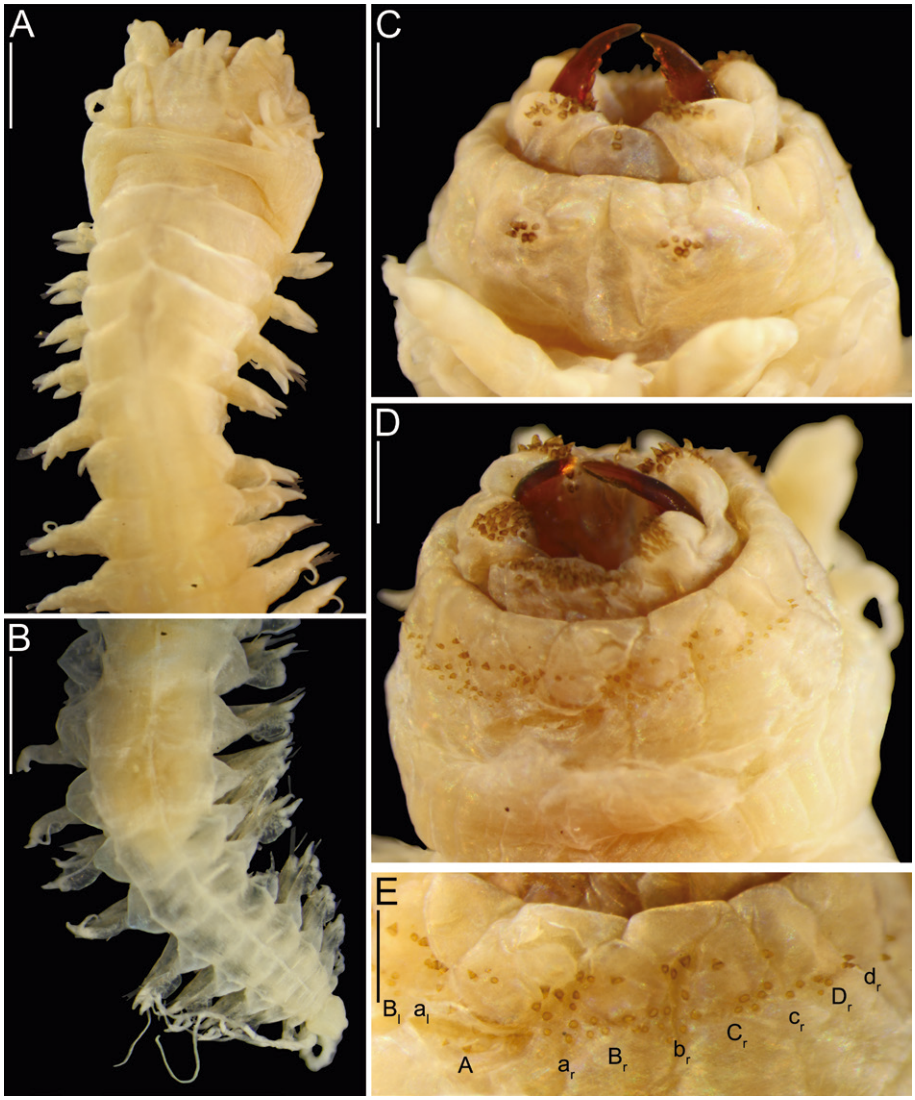

Figure 1. *Nereis arroyensis* Treadwell, 1901. Syntypes USNM 16005. A, Anterior end, dorsal view; B, posterior end, dorsal view; C, pharynx, dorsal view; D, same, ventral view; E, close-up of midventral region of oral ring (labels point ridge (uppercase) and furrow (lowercase) regions of the midventral region). Scale bars: A, B, 1 mm; C-E, 0.5 mm.

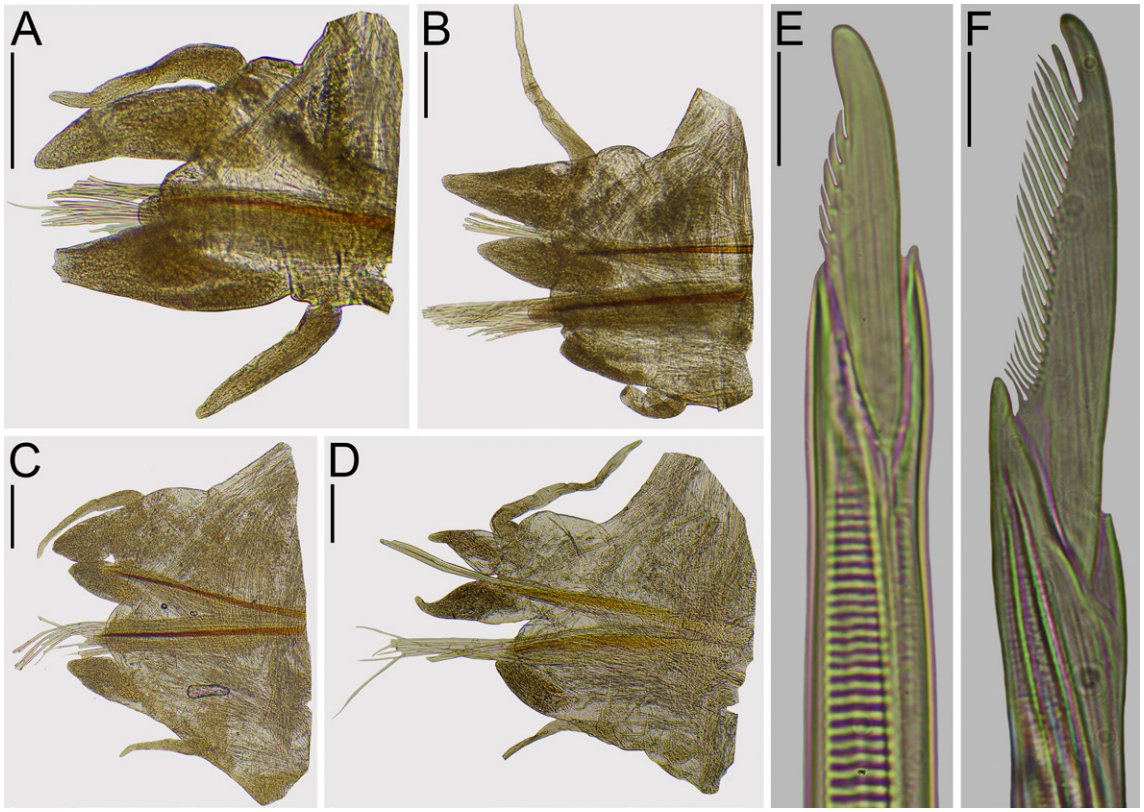

Figure 2. *Nereis arroyensis* Treadwell, 1901. Syntypes USNM 16005. A, Chaetiger 2, right parapodium; B, chaetiger 12, right parapodium; C, chaetiger 32, right parapodium; D, chaetiger 63, right parapodium; E, notopodial homogomph falciger, chaetiger 63; F, sub-acicular heterogomph falciger, chaetiger 12. A-D, 0.2 mm; E, F, 10 µm.

Taxonomic summary

Material examined. Syntypes USNM 16005 (2), San Juan, Puerto Rico, 567 m depth, 13 January 1899, Coll. R/V Fish Hawk.

Remarks

The original description is very brief and general and later Hartman (1956) detailed the paragnaths arrangement and jaw morphology and agreed with the current description. Some key features added are the arrangement of paragnaths in the furrow and ridge regions in pharyngeal areas VII-VII and the VI-V-VI furrow pattern, unambiguous descriptions of changes in the parapodia along the body, the presence of notopodial homogomph falcigers, and the description of the posterior end.

In their key to species of *Nereis* from the Grand Caribbean, Ramírez-Hernández et al. (2015) grouped *N. arroyensis* with species having longest tentacular cirri reaching chaetiger 6, but this feature was not provided in the original description. Moreover, Ramírez-Hernández et al. (2015) used the feature 'anterior pair of eyes crescent-shaped' based on the original description, but in the holotype they are rounded with big lenses, and the remaining reddish tissue is crescent-shaped. This feature separated *N. arroyensis* from *N. riisei* Grube & Ørsted in Grube, 1857, *N. lamellosa* Ehlers, 1868, and *N. rigida* Grube & Ørsted in Grube, 1857. However, *N. arroyensis* differs from *N. riisei* by having several paragnaths in areas VII-VIII arranged in 2 bands, whereas *N. riisei* has 5-6 paragnaths in a single band; and *N. arroyensis* differs from *N. arroyensis* differs from *N. lamellosa* and *N. rigida* by lacking paragnaths in area V. *Nereis arroyensis* has a very distinctive arrangement of paragnaths compared to the *Nereis* species recorded from the Caribbean Sea. The arrangement of paragnaths resembles *Nereis zonata* Malmgren, 1867 (sensu Chambers & Garwood, 1992) described from Great Britain, but they differ mainly in the following key features: in *N. arroyensis*, posterodorsal tentacular cirri reach chaetiger 4, whereas in *N. zonata* they reach chaetiger 2; in *N. arroyensis*, the paragnaths of both bands in areas VII-VIII are of similar size, whereas in *N. zonata* paragnaths of the anterior band are larger;

in *N. arroyensis*, dorsal ligules in anterior chaetigers are longer than median ligules, whereas in *N. zonata* they are subequal; in *N. arroyensis*, notopodial falcigers have dentate blades, whereas in *N. zonata* they are edentate.

Nereis largoensis Treadwell, 1931
Figs. 3, 4
Nereis brevicirrata Treadwell, 1929: 3-5, Figs.9-14 (preoccupied, non *Nereis brevicirrata* Treadwell, 1920).
Nereis largoensis Treadwell, 1931: 3 (replacement name).
Nereis pelagica largoensis Hartman, 1956: 280.

Description. Holotype (AMNH 1987) in good conditions, complete, 82 mm long, 5.5 mm wide at chaetiger 10 excluding parapodia, 63 chaetigers. Body pale, pigmentation absent (Fig. 3A, B).

Prostomium subpyriform, 1.3x longer than wide; anterior region distally entire, oblong, as long as posterior region, dorsal groove present (Fig. 3A); anterolateral gap between antenna and palpophore as long as diameter of antennae (Fig. 3A). Antennae digitiform, not passing the palps, gap between antennae very small (Fig. 3A). Palpophores ovoid, swollen, 1.5x longer than wide, 1.2x longer than prostomium, subdistal transverse groove present (Fig. 3A). Palpostyles subconical with rounded tips (Fig. 3A). Eyes blackish, rounded, anterior and posterior pairs subequal, eyes diameter shorter than basal width of antennae, in trapezoidal arrangement, lenses small (Fig. 3A). Tentacular belt 2.5x longer than chaetiger 1, covering posterior pair of eyes, anterior dorsal margin convex (Fig. 3A). Tentacular cirri smooth, cirrophores cylindrical, cirrostyles cirriform, left ventral cirri missing; posterodorsal tentacular cirri reaching chaetiger 2 (Fig. 3A). Pharynx not everted, previously dissected, oral ring longer than maxillary one (Fig. 3C). Jaws broad, inner margin dentate with about 7-8 rounded teeth (Fig. 3C). Maxillary ring: I = 2 cones in vertical row; II = 15-16 paragnaths with polygonal bases; III = 9-10 paragnaths with polygonal bases (perhaps incomplete because dissection); IV = 37-38 paragnaths with polygonal bases (Fig. 3C). Oral ring: V = 1 cone; VI =5 central cones in round (right VI with a hard irregular plate), merged paragnaths absent; 1-1 cone at the lateral margins bordering areas VII-VIII; VII-VIII = a broad belt with about 126 paragnaths covering all ridge and furrow regions, number of bands and rows unclear (midventral region missing); large paragnaths with polygonal bases in ridge regions forming a row, remaining ones much shorter and conical (Fig. 3C). Furrow pattern of areas VI-V-VI, λ-shaped (Fig. 3C). Dorsal cirrus digitiform and basally attached to dorsal ligule in first 2 chaetigers, filiform and medially attached thereafter (Fig. 4A-E); twice longer than distal region of dorsal ligule in anteriormost chaetigers (Fig. 4A), 2.3x in anterior chaetigers (Fig. 4B), 3.2-4.0x in middle chaetigers (Fig. 4C, D), 5x in posterior chaetigers (Fig. 4E). Dorsal ligule subconical with distal region longer than proximal ones in anteriormost chaetigers, becoming shorter since chaetiger 10 (Fig. 4A-E). Distal region of dorsal ligule 0.6x length of median ligule in anterior chaetigers (Fig. 4B), 0.8-1.2x in middle chaetigers (Fig. 4C, D), as long as in posterior chaetigers (Fig. 4E). Median ligule rounded in anterior chaetigers, subconical or digitiform from anterior chaetigers (Fig. 4A-E); 2.4x longer than neuroacicular ligule in anterior chaetigers (Fig. 4B), 1.3-1.4x in middle chaetigers (Fig. 4C, D), 2.5x in posterior chaetigers (Fig. 4E). Neuroacicular ligule rounded throughout, superior and inferior lobes absent (Fig. 4A-E). Neuroacicular postchaetal lobe rounded, shorter than neuroacicular ligule throughout. Ventral ligule digitiform in anterior chaetigers, subconical with blunt tip since chaetiger 15 (Fig. 4A-E); 2.3x longer than neuroacicular ligule in anterior chaetigers (Fig. 4B), 1.0-1.2x in middle chaetigers (Fig. 4C, D), as long as in posterior chaetigers (Fig. 4E). Ventral cirrus digitiform and long in first chaetigers, filiform thereafter (Fig. 4A-E); 0.8x length of ventral ligule in anterior chaetigers (Fig. 4A), 1.3x longer in middle chaetigers (Fig. 4C, D), 1.5x in posterior chaetigers (Fig. 4E). Aciculae dark brown throughout, becoming thicker toward posterior chaetigers (Fig. 4A-E); notoaciculae absent in first 2 chaetigers (Fig. 4A-E). Most chaetae broken or blades detached. Notochaetae consisting of homogomph symmetrical spinigers and falcigers. Blade of spinigers with basal pectinate, coarse teeth, becoming minute toward distal end. Notopodial homogomph falciger with symmetrical rim of shaft, inner edge edentate, blade fusiform with blunt ends in middle chaetigers and becoming sharp in posterior chaetigers (Fig. 4F-H). Neurochaetae consisting of heterogomph spinigers with short bosses and heterogomph falcigers with long bosses in supra-acicular fascicles, heterogomph spinigers and falcigers with long bosses in infra-acicular fascicles. Blade of spinigers with basal pectinate, coarse teeth, becoming minute toward distal end (Fig. 4I, J). Blades of falcigers falcate, pointed tips, with narrow teeth, infra-acicular ones with more teeth than supra-acicular ones (Fig. 4K, L).

Pygidium swollen, crenulated, wider than long (Fig. 3B); anal cirri missing (Fig. 3B).

Taxonomic summary

Material examined. Holotype of *Nereis brevicirrata* Treadwell AMNH 1987, Key Largo, Florida, no date, Coll. W Beebe.

Remarks

Hartman (1956) thought *Nereis largoensis* was similar to *Nereis pelagica* Linnaeus, 1758 and regarded it as a

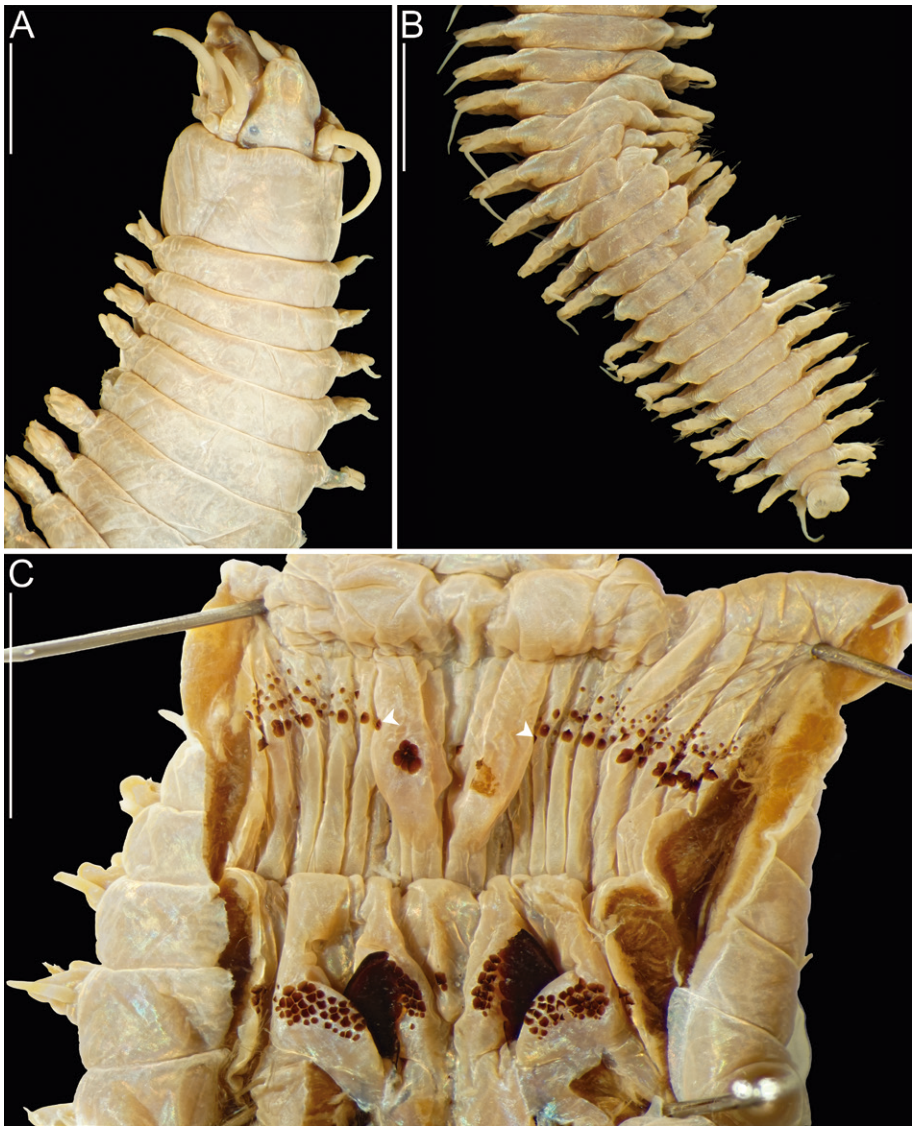

Figure 3. *Nereis largoensis* Treadwell, 1931. Holotype AMNH 1987. A, Anterior end, dorsal view; B, posterior end, dorsal view; C, anterior end dissected showing pharynx, ventral view (arrows point cones at the lateral margins of areas VI). Scale bars: A-C, 3 mm.

subspecies. Since a recent redescription of this supposed cosmopolitan species is not available, here the description by Chambers and Garwood (1992), and a specimen from England (ECOSUR P2840), were used for comparison. *Nereis largoensis* differs from *N. pelagica* in the following key features: in *N. largoensis*, the pharyngeal area V has paragnaths, which are lacking in *N. pelagica*; in *N. largoensis*, merged paragnaths in pharyngeal areas IV are absent, which are present in *N. pelagica*; in *N. largoensis*, the median ligules are longer than neuroacicular ligules in anterior chaetigers, whereas in *N. pelagica* they are subequal; in *N. largoensis*, the ventral ligules are longer than neuroacicular ligules in anterior and middle chaetigers, whereas in *N. pelagica* they are shorter or subequal; in *N. largoensis*, ventral cirri are longer than ventral ligules in posterior chaetigers, whereas in *N. pelagica* they are subequal.

Hartman (1956) separated *Nereis largoensis* from *N. occidentalis* by the shape of the blades of notopodial falcigers, here additional features are added: in *N. occidentalis*, the tentacular belt is slightly longer than chaetiger 1, whereas in *N. largoensis* it is 2.5 times longer than; in *N. occidentalis*,

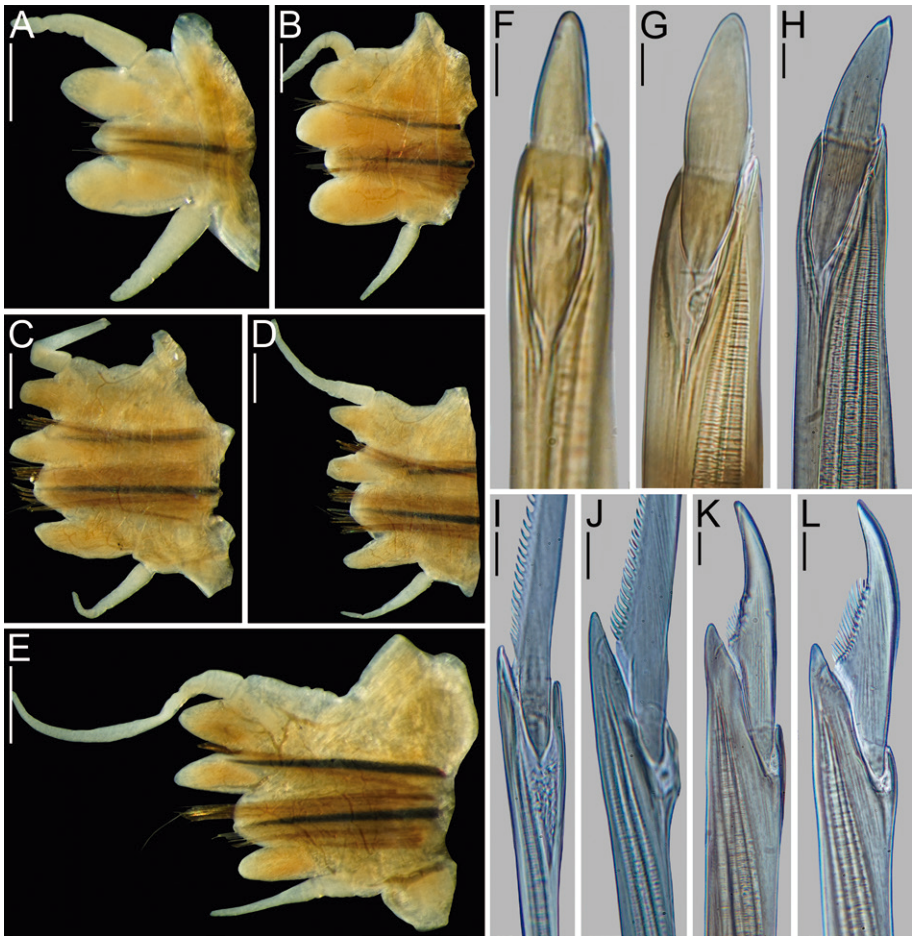

Figure 4. *Nereis largoensis* Treadwell, 1931. Holotype AMNH 1987. A, Chaetiger 1, right parapodium; B, chaetiger 11, right parapodium; C, chaetiger 25, right parapodium; D, chaetiger 38, right parapodium; E, chaetiger 55, right parapodium; F, notopodial homogomph falciger, chaetiger 25; G, notopodial homogomph falciger, chaetiger 38; H, notopodial homogomph falciger, chaetiger 60; I, shaft of supra-acicular, heterogomph with short boss spiniger, chaetiger 60; J, shaft of sub-acicular, heterogomph with long boss spiniger, chaetiger 60; K, supra-acicular heterogomph falciger, chaetiger 60; L, sub-acicular heterogomph falciger, chaetiger 60. Scale bars: A-E, 0.25 mm; F-L, 10 µm.

longest tentacular cirri reach chaetigers 7-8, whereas in *N. largoensis* they reach chaetiger 2; *N. occidentalis* has 2 bands of conical paragnaths, whereas *N. largoensis* has a wide band with several paragnaths; in *N. occidentalis*, ventral cirri are shorter than ventral ligules throughout, whereas in *N. largoensis* they are longer than in posterior chaetigers; in *N. occidentalis*, the blades of the notopodial homogomph falcigers are falcate with a distinct tendon and inner margin fully dentate, whereas in *N. largoensis* the blades are fusiform without a tendon and the margins are smooth. Therefore, *Nereis largoensis* is regarded as a valid species and different from its similar species *N. pelagica* and *N. occidentalis*.

Warren (1942) introduced the name *Nereis gracilicirrata* for material collected in Grand Isle, Louisiana, USA, but the description is so general that it is even difficult to ascertain the genus of the species, and the type material was not deposited. Hartman (1954, 1956) concluded that *N. gracilicirrata* is a synonym of *N. largoensis*, and Pettibone (1956) examined material from Grand Isle previously identified as *N. largoensis* by Behre (1950) and concluded they are *N. occidentalis* instead. However, after the very general description, it is not possible to assure such specimens are *N. gracilicirrata* and no other nereidid, so here *N. gracilicirrata* is considered to be an indeterminable species, and not a synonym of *N. largoensis*.

Genus *Perinereis* Kinberg, 1865
Type species. *Perinereis novaehollandiae* Kinberg, 1865, by subsequent designation (Hartman, 1948).
Diagnosis followed: Bakken and Wilson, 2005.

Perinereis diversidentata Treadwell, 1943
Figs. 5, 6
Perinereis diversidentata Treadwell, 1943: 1-2, Figs.1-7.
Pseudonereis variegata Day, 1953: 425-426 (partim, record only). Hartman, 1956: 281-282 (non Grube & Kröyer in Grube, 1857).

Description. Holotype (AMNH 3235) incomplete, body with soft tissue but in good conditions, previously dissected, pharynx damaged and incomplete (Fig. 5D, E), 140 mm long, 7 mm wide at chaetiger 10 excluding parapodia, 72 chaetigers (Fig. 5A). Body pale, pigmentation absent (Fig. 5A-C).

Prostomium subpyriform, as long as wide; anterior region distally entire, oblong, as long as posterior region, dorsal groove present (Fig. 5B); anterolateral gap between antenna and palpophore as long as diameter of antennae (Fig. 5B). Antennae subconical, not passing the palps, gap between them very small (Fig. 5B). Palpophores ovoid, swollen, 1.2x longer than wide, 0.8x length of prostomium, subdistal transverse groove present (Fig. 5B). Palpostyles subpyriform (Fig. 5B). Eyes blackish, rounded, anterior and posterior pairs subequal, eyes diameter half as long as antennae basal width, in trapezoidal arrangement, anterior pair placed on the dorsolateral margins of prostomium, lenses not visible, nuchal organs visible (Fig. 5B). Tentacular belt 1.3x longer than chaetiger 1, not covering posterior pair of eyes, anterior dorsal margin straight (Fig. 5B). Tentacular cirri smooth, cirrophores ring-shaped, cirrostyles cirriform; posterodorsal tentacular cirri reaching chaetiger 2 (Fig. 5B). Pharynx previously dissected, damaged, oral ring 1.6x longer than maxillary one (Fig. 5D). Jaws broad, inner margin with 7-8 rounded teeth (Fig. 6F). Maxillary ring: I = 1 cone; II = 14-16 cones in triangle; III = 27 cones in 4 rows (perhaps area incomplete); IV = 27-30 cones in 6-7 rows (perhaps areas incomplete), merged paragnaths absent. Oral ring: V = 0; VI = 1-1 central shield-shaped paragnaths, 1-1 cone at the lateral margins bordering areas VII-VIII; VII-VIII = anterior band with 1 furrow row with 8 cones and a ridge row with 10 cones; posterior band with 1 furrow region with 8 cones and a ridge row with 13 cones; furrow and ridge regions with 1 or 2 paragnaths each, perhaps midventral area incomplete (Fig. 5D, E). Furrow pattern of areas VI-V-VI, Π-shaped (Fig. 5D). Caecal glands present (Fig. 5E). Dorsal cirrus digitiform in first 2 chaetigers, subconical with blunt tip thereafter, attached basally to dorsal ligule in anteriormost chaetigers, medially in middle chaetigers, subdistally in posterior chaetigers (Fig. 6A-E); 1.6x longer than tip of distal region of dorsal ligule in anteriormost chaetigers (Fig. 6A), 3x in anterior and middle chaetigers (Fig. 6B-D), 2.5x in posterior chaetigers (Fig. 6E); 3.2x longer than proximal region of dorsal ligule in anteriormost chaetigers (Fig. 6A), 1.3-1.5x in anterior chaetigers (Fig. 6B), as long as in middle chaetigers (Fig. 6C, D), 0.4x length in posterior chaetigers (Fig. 6E). Dorsal ligule rounded in anterior chaetigers, becoming subcylindrical in middle chaetigers, and pennant-like in posterior chaetigers, with distal regions shorter than proximal ones throughout (Fig. 6A-E). Distal region of dorsal ligule as long as median ligule in anterior chaetigers (Fig. 6B), 2.0-2.2x in middle chaetigers (Fig. 6C, D), 3.8x in posterior chaetigers (Fig. 6E). Median ligule rounded in anterior chaetigers, digitiform thereafter; 2.5x longer than neuroacicular ligule in anterior chaetigers (Fig. 6B), 1.5x in middle and posterior chaetigers (Fig. 6C-E). Neuroacicular ligule subconical throughout (Fig. 6A-E); superior and inferior lobes present in anterior and middle chaetigers, both rounded, inferior one slightly longer than superior one throughout (Fig. 6A-E). Neuropodial postchaetal lobes rounded, lamelliform, half as long as neuroacicular ligule throughout (Fig. 6A-E). Ventral ligule subconical with blunt tip in anterior chaetigers, digitiform thereafter (Fig. 6A-E); as long as neuroacicular ligule throughout (Fig. 6A-E). Ventral cirrus digitiform in first chaetigers, subconical thereafter (Fig. 6A-E); as long as ventral ligule in anteriormost chaetigers (Fig. 6A), 0.7x length in anterior and middle chaetigers (Fig. 6B-D), half as long as in posterior chaetigers (Fig. 6E). Aciculae dark brown and neuroaciculae almost twice thicker than notoaciculae throughout (Fig. 6A-E); notoaciculae absent in first 2 chaetigers (Fig. 6A). Notochaetae consisting of homogomph symmetrical spinigers throughout, decreasing in number toward posterior chaetigers (Fig. 6A-E). Neurochaetae consisting of homogomph symmetrical spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in infra-acicular fascicles. Blades of heterogomph falcigers in both fascicles falcate, blades decreasing their size toward posterior chaetigers, narrow teeth, a half of the inner edge edentate (Fig. 6G-J).

Pygidium missing (Fig. 5C).

Taxonomic summary

Material examined. Holotype of *Perinereis diversidentata* AMNH 3235, Cape Cross, Namibia, Africa, 11 September 1925, Coll. H Lang & R Boulton.

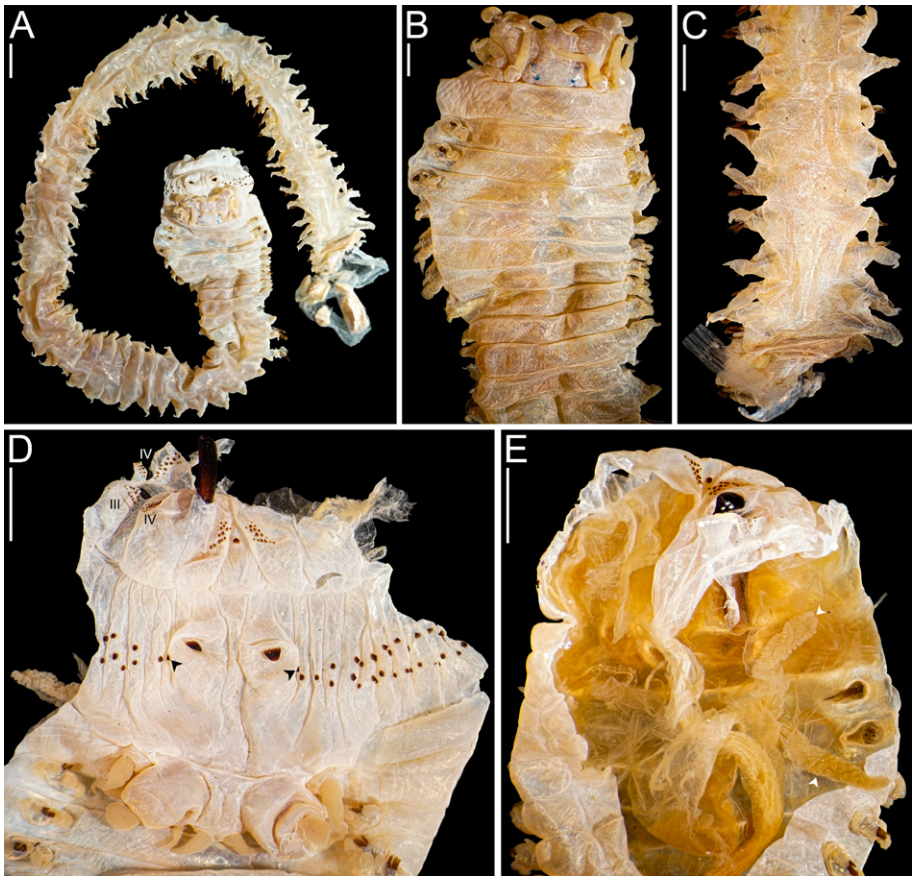

Figure 5. *Pseudonereis diversidentata* (Treadwell, 1943) n. comb. Holotype of *Perinereis diversidentata* AMNH 3235. A, Whole specimen, dorsal view; B, anterior end, dorsal view; C, posterior end, dorsal view; D, pharynx, dorsal view (arrows point cones at the lateral margins of areas VI); E, anterior end, ventral view (arrows point caecal glands). Scale bars: A, 4 mm; B-E, 2 mm.

Remarks

The current description agrees well with the original one, some features were added as the presence of the caecal glands, illustrations of the pharynx, the presence of both neuropodial superior and inferior lobes in anterior and middle chaetigers, and the description of posteriormost chaetigers. Treadwell (1943, Fig. 5) described a distorted parapodium from chaetiger 50 (aciculae are overlapped) perhaps because he misplaced the parapodium in the slide and the tissue of the parapodium from such region is delicate, so he described neuroacicular ligules broad and ventral cirri longer than ventral ligules, but neuroacicular ligules are narrower and ventral cirri are shorter than throughout the body. Treadwell (1943) mentioned the poor state of the pharynx when examined the specimens, suggesting previous damage.

Day (1953) examined type material of *Perinereis diversidentata* and considered it was a junior synonym of *Pseudonereis variegata* (Grube & Kröyer in Grube, 1857), although he highlighted differences in the arrangement of paragnaths in the maxillary ring. Hartman (1956) agreed with Day's decision. However, both species can be separated based on the following key differences (sensu Conde-Vela, 2018): *P. diversidentata* has a straight anterior margin of the tentacular belt, whereas in *P. variegata* it is convex; *P. diversidentata* lacks paragnaths in area V and has shield-shaped paragnaths in central areas VI and cones in lateral areas VI, whereas *P. variegata* has paragnaths in area V and has crescent-shaped paragnaths in central areas VI only; in *P. diversidentata*, ventral ligules are subequal than neuroacicular ligules throughout, whereas in *P. variegata* they are shorter throughout; in *P. diversidentata*, dorsal cirri are relatively shorter in middle and posterior chaetigers than in *P. variegata*.

Moreover, a crucial difference between *Perinereis diversidentata* and *P. variegata* is the lack of p-bars

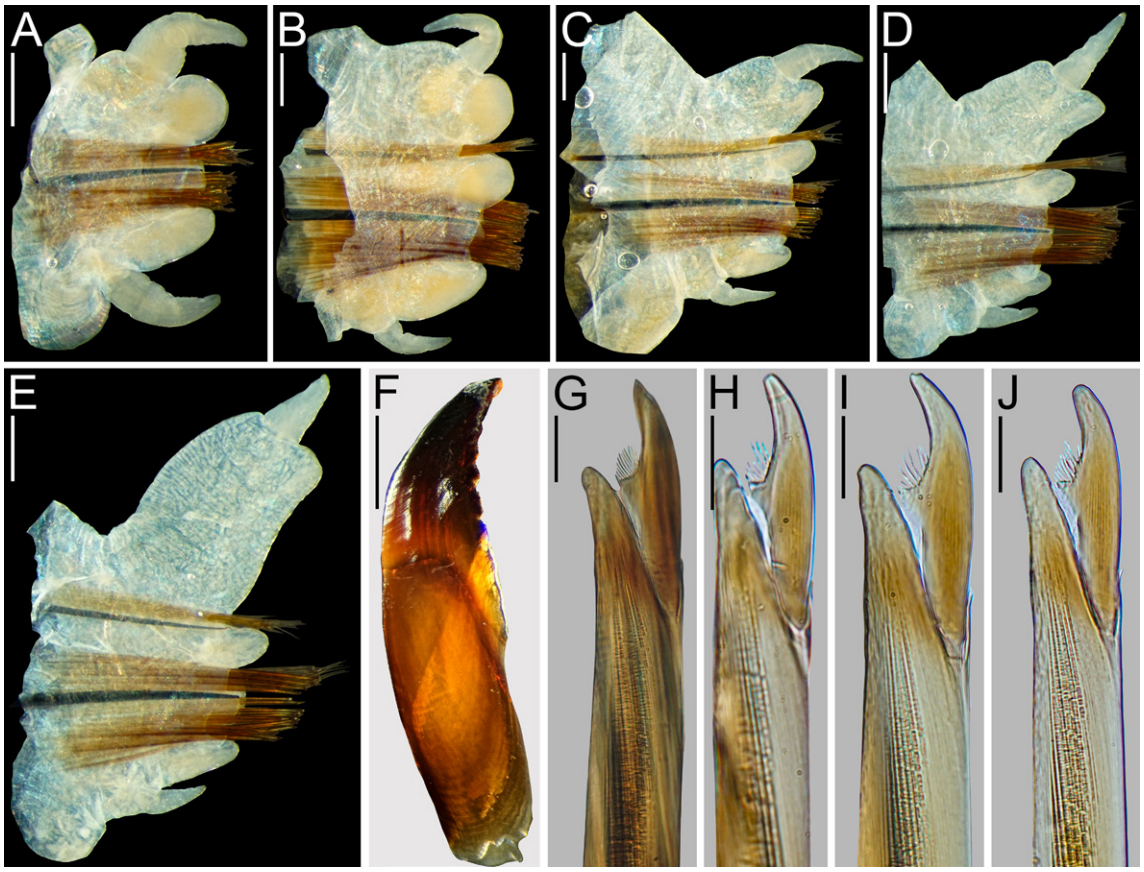

Figure 6. *Pseudonereis diversidentata* (Treadwell, 1943) n. comb. Holotype of *Perinereis diversidentata* AMNH 3235. A, Chaetiger 2, right parapodium, posterior view; B, chaetiger 11, right parapodium, posterior view; C, chaetiger 26, right parapodium, posterior view; D, chaetiger 44, right parapodium, posterior view; E, chaetiger 71, right parapodium, posterior view; F, left jaw, dorsal view; G, supra-acicular heterogomph falciger, chaetiger 44; H, sub-acicular heterogomph falciger, chaetiger 2; I, sub-acicular heterogomph falciger, chaetiger 11; J, sub-acicular heterogomph falciger, chaetiger 44. Scale bars: A-E, 0.25 mm; F, 0.1 mm; G-J, 10 µm.

arranged in comb-like rows in the former species, which is a key feature to separate *Pseudonereis* species from *Perinereis* (Villalobos-Guerrero et al., 2021). Therefore, here the original combination *Perinereis diversidentata* is used. This difference also separates *P. diversidentata* from the similar species *Pseudonereis podocirra* (Schmarda, 1861) (type locality: Cape of Good Hope, South Africa). Based on the *Perinereis* groups proposed by Hutchings et al. (1991), *P. diversidentata* belongs to the group 1B (areas VI with a single bar and dorsal ligules greatly expanded on posterior chaetigers). Some *Perinereis* species from the Eastern Atlantic coasts are *P. atlantica* (McIntosh, 1885) (type locality: Cape Verde Islands), *P. capensis* (Kinberg, 1865) (type locality: Cape of Good Hope, South Africa), *P. falsovariegata* Monro, 1933 (type locality: Preekstoel, South Africa), *P. majungaensis* Fauvel, 1921 (type locality: Madagascar), and *P. namibia* Wilson & Glasby, 1993 (type locality: Lüderitz, Namibia), but none of them belong to group 1B. Overlooking the differences in parapodial features, *P. diversidentata* differs mainly from *P. namibia* in having a single bar in areas VI rather than several bars in a row, and *P. diversidentata* differs from *P. capensis* (fide Monro, 1933) in having a single cone on the lateral margins of each area VI.

Pseudonereis palpata (Treadwell, 1923)
Figs. 7-9
Nereis (*Neanthes*) *palpata* Treadwell, 1923: 5-9, Figs.6-15.
Pseudonereis palpata Hartman, 1956: 255, 256, 264, 267 (list only). Bakken, 2007: 163-164, Figs.10A-C.
Nereis disparsetosa Treadwell, 1932: 13-15, Figs.1-5.

Description of paratype of Nereis (Neanthes) palpata. Paratype (USNM 19031) incomplete, in fair conditions, 85 mm long, 3.5 mm wide at chaetiger 10 excluding

parapodia, 70 chaetigers. Body pale, pigmentation absent, whitish glandular masses in parapodia of anterior and middle chaetigers, whitish in posterior chaetigers (Fig. 7A, B).

Prostomium subpyriform, as long as wide; anterior region distally entire, oblong, shorter than posterior region, dorsal groove present (Fig. 7A); anterolateral gap between antenna and palpophore half as long as diameter of antennae (Fig. 7A). Antennae subconical, not passing the palps, gap between them inconspicuous (Fig. 7A). Palpophores subcylindrical, 1.2x longer than wide, as long as prostomium, subdistal transverse groove absent (Fig. 7A). Palpostyles rounded (Fig. 7A). Eyes blackish, rounded, anterior pair slightly larger than posterior one, eyes diameter as long as antennae basal width, in trapezoidal arrangement, lenses not visible (Fig. 7A). Tentacular belt as long as chaetiger 1, not covering posterior pair of eyes, anterior dorsal margin straight (Fig. 7A). Tentacular cirri smooth, cirrophores ring-shaped, cirrostyles cirriform; posterodorsal tentacular cirri reaching chaetiger 5 (Fig. 7A). Pharynx everted in both specimens, oral ring 1.5x longer than maxillary one (Fig. 7E, F.). Jaws broad, inner margin with 8-10 rounded teeth (Fig. 7G). Maxillary ring: I = 1 cone; II = 41 p-bars arranged in 4 rows in triangle; III = 105 p-bars arranged in 4 rows in triangle; IV = 125-132 paragnaths in a sigmoidal patch, 84-86 p-bars arranged in 5 rows, 32-37 cones and 9 merged paragnaths arranged in arc. Oral ring: V = 1 cone; VI = 1-1 central shield-shaped paragnath with a cone on the right region; VII-VIII = anterior band with 1 furrow row with 12 p-bars and a ridge row with 9 cones in a single band, rows vertically displaced; furrow and ridge regions with 1 paragnath each (Fig. 7E, F). Furrow pattern of areas VI-V-VI, Π-shaped (Fig. 7F). Caecal glands not seen because the poor state of the specimen. Dorsal cirrus digitiform in first chaetigers, filiform in anterior, middle and posterior chaetigers, digitiform in posteriormost chaetigers, attached basally to dorsal ligule in anteriormost chaetigers, medially in anterior chaetigers, subdistally in middle and posterior chaetigers (Fig. 7C, D); 3.5x longer than tip of distal region of dorsal ligule in anterior chaetigers (Fig. 7C), 5.4x in posterior chaetigers (Fig. 7D); 2.7x longer than proximal region of dorsal ligule in anterior chaetigers (Fig. 7C), 0.3x in posterior chaetigers (Fig. 7D). Dorsal ligule subconical with rounded, broad tips in anterior chaetigers, becoming subcylindrical in middle chaetigers, and oblong in posterior chaetigers, with distal regions shorter than proximal ones throughout (Fig. 7C, D); distal region of dorsal ligule as long as median ligule in anterior chaetigers (Fig. 7C), 4.8x longer in posterior chaetigers (Fig. 7D). Median ligule rounded in in anterior chaetigers, digitiform thereafter; as long as neuroacicular ligule in anterior chaetigers (Fig. 7C), 3x longer in posterior chaetigers (Fig. 7D). Neuroacicular ligule subconical throughout (Fig. 7C, D); superior and inferior lobes present in anterior and middle chaetigers, both rounded, inferior one slightly longer than superior one throughout (Fig. 7C, D). Neuropodial postchaetal lobes rounded, lamelliform, half as long as neuroacicular ligule throughout. Ventral ligule rounded in anterior chaetigers, digitiform thereafter (Fig. 7C, D); half as long as neuroacicular ligule in anterior chaetigers (Fig. 7C), 0.3x length in posterior chaetigers (Fig. 7D). Ventral cirrus digitiform and broad in first chaetigers, narrower thereafter (Fig. 7C, D); 0.8x length of ventral ligule in anterior chaetigers (Fig. 7C), 0.7x in posterior chaetigers (Fig. 7D). Aciculae dark brown throughout (Fig. 7C, D); notoaciculae absent in first 2 chaetigers (Fig. 9A); neuroaciculae becoming thicker than notoaciculae toward posterior chaetigers. Notochaetae consisting of homogomph symmetrical spinigers throughout, decreasing in number toward posterior chaetigers (Fig. 7C, D). Neurochaetae consisting of homogomph symmetrical spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in infra-acicular fascicles (Fig. 7H, I). Heterogomph spinigers present from chaetiger 22. Blades of supra-acicular spinigers pectinate, teeth minute, decreasing in size toward distal end (Fig. 7I). Blades of heterogomph falcigers in both fascicles falcate, blades decreasing their size toward posterior chaetigers, narrow teeth, 2 third of the inner edge edentate (Fig. 7H, I).

Pygidium missing (Fig. 7B).

Description of syntypes of Nereis disparsetosa. Syntypes (USNM 19638) consisted in 2 specimens in excellent conditions, one selected for description, 32 mm long, 2.2 mm wide at chaetiger 10 excluding parapodia, 68 chaetigers. Body pale, pigmentation absent, whitish glandular masses in parapodia of anterior and middle chaetigers, orangish in posterior chaetigers (Fig. 8A, B).

Prostomium subpyriform, as long as wide; anterior region distally entire, oblong, shorter than posterior region, dorsal groove present (Fig. 8A); anterolateral gap between antenna and palpophore half as long as diameter of antennae (Fig. 8A). Antennae subconical, not passing the palps, gap between them inconspicuous (Fig. 8A). Palpophores subcylindrical, 1.2x longer than wide, as long as prostomium, subdistal transverse groove absent (Fig. 8A). Palpostyles rounded (Fig. 8A). Eyes blackish, rounded, anterior pair slightly larger than posterior one, eyes diameter as long as antennae basal width, in trapezoidal arrangement, lenses not visible (Fig. 8A). Tentacular belt as long as chaetiger 1, not covering posterior pair of eyes, anterior dorsal margin straight (Fig. 8A). Tentacular cirri

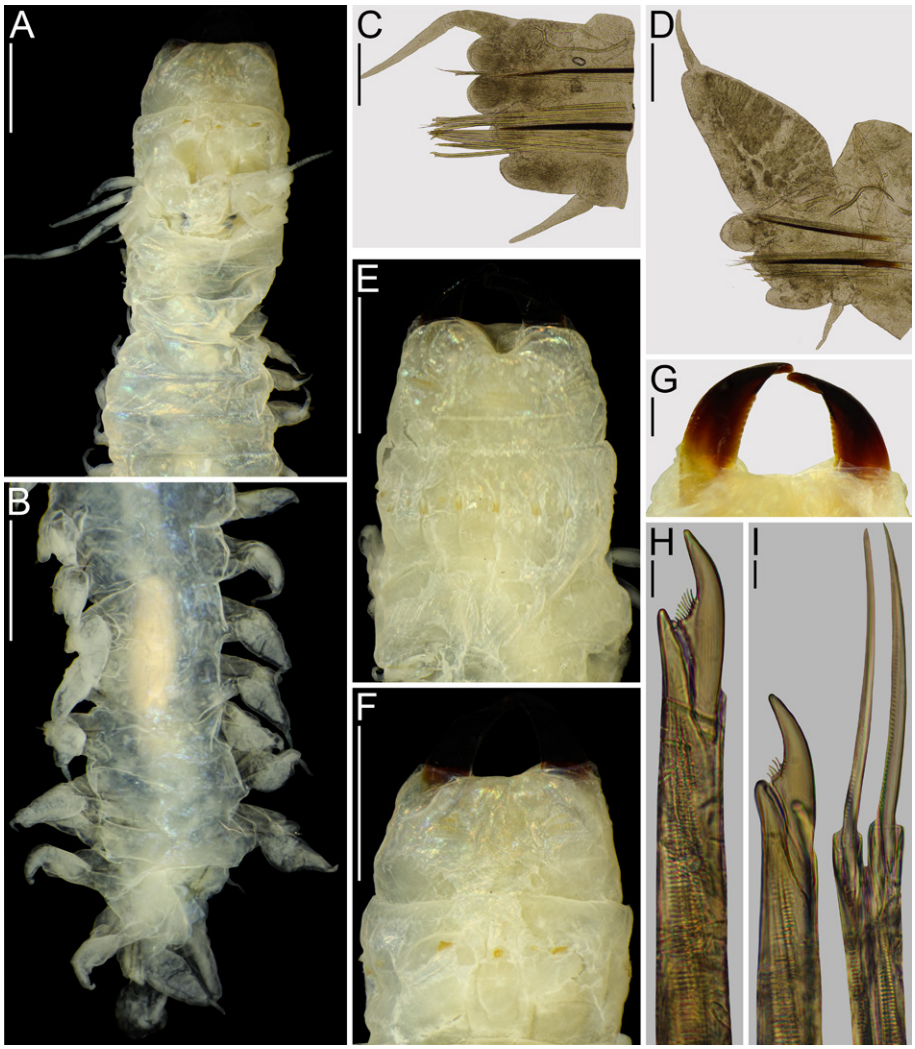

Figure 7. *Pseudonereis palpata* (Treadwell, 1923). Paratype of *Nereis* (*Neanthes*) *palpata* USNM 19031. A, Anterior end, dorsal view; B, posterior end, dorsal view; C, chaetiger 14, right parapodium, anterior view; D, chaetiger 70, right parapodium, anterior view; E, pharynx, ventral view; F, same, dorsal view; G, jaws, dorsal view; H, sub-acicular heterogomph falciger, chaetiger 70; I, supra-acicular heterogomph falciger (left) and homogomph spinigers (right), chaetiger 70. Scale bars: A, B, E, F, 2 mm; C-D, G, 0.4 mm; H, I, 10 μm.

smooth, cirrophores ring-shaped, cirrostyles cirriform; posterodorsal tentacular cirri reaching chaetiger 5 (Fig. 8A). Pharynx everted, oral ring as long as maxillary one (Fig. 8C, D). Jaws broad, inner margin with 8-10 rounded teeth (Fig. 8E). Maxillary ring: I = 0; II = 27-28 p-bars arranged in 3-4 rows in triangle; III = 67 p-bars arranged in 4 rows in triangle; IV = 81-94 paragnaths in a sigmoidal patch, 45-56 p-bars arranged in 5-6 rows, 31-32 cones and 5-6 merged paragnaths arranged in arc. Oral ring: V = 1; VI = 1-1 central smooth bar; VII-VIII = anterior band with 1 furrow row with 12 p-bars and a ridge row with 9 cones in a single band, rows vertically displaced; furrow and ridge regions with 1 paragnath each (Fig. 8C, D). Furrow pattern of areas VI-V-VI, Π-shaped (Fig. 8C). Dorsal cirrus digitiform in first chaetigers, filiform in anterior, middle and posterior chaetigers, digitiform in posteriormost chaetigers, attached basally to dorsal ligule in anteriormost chaetigers, medially in anterior chaetigers, subdistally in middle and posterior chaetigers, distally in posteriormost chaetigers (Fig. 9A-D); 3.2x longer than tip of distal region of dorsal ligule in anteriormost chaetigers (Fig. 9A), 3.5x in anterior chaetigers (Fig. 9B), 5x in

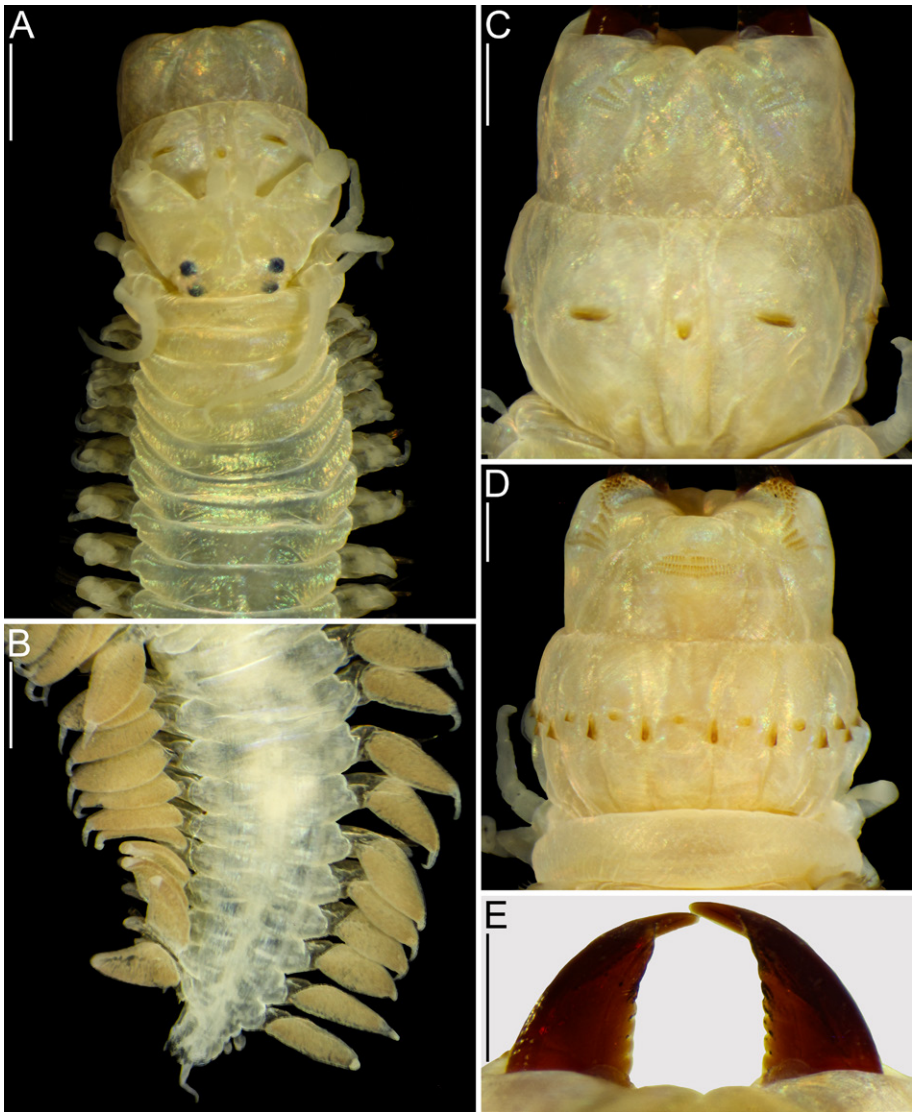

Figure 8. *Pseudonereis palpata* (Treadwell, 1923). Holotype of *Nereis disparsetosa* Treadwell USNM 19638. A, Anterior end, dorsal view; B, posterior end, dorsal view; C, pharynx, dorsal view; D, same, ventral view; E, jaws, dorsal view. Scale bars: A, 1 mm; B- E, 0.5 mm.

middle chaetigers (Fig. 9C), 11x in posterior chaetigers (Fig. 9D); 3.2x longer than proximal region of dorsal ligule in anteriormost chaetigers (Fig. 9A), 2.7x in anterior chaetigers (Fig. 9B), 1.2x in middle chaetigers (Fig. 9C), 0.3x length in posterior chaetigers (Fig. 9D). Dorsal ligule subconical with rounded, broad tips in anterior chaetigers, becoming subcylindrical in middle chaetigers, and oblong in posterior chaetigers, with distal regions shorter than proximal ones throughout (Fig. 9A-D); distal region of dorsal ligule as long as median ligule in anterior chaetigers (Fig. 9B), 2x longer in middle chaetigers (Fig. 9C), 3.4x in posterior chaetigers (Fig. 9D). Median ligule rounded in in anterior chaetigers, digitiform thereafter; as long as neuroacicular ligule in anterior chaetigers (Fig. 9B), 1.5x longer in middle chaetiger 31 (Fig. 9C), 2.7x in posterior chaetigers (Fig. 9D). Neuroacicular ligule subconical throughout (Fig. 9A-D); superior and inferior lobes present in anterior and middle chaetigers, both rounded, inferior one slightly longer than superior one throughout (Fig. 9A-D). Neuropodial postchaetal lobes rounded, lamelliform, half as long as neuroacicular ligule throughout. Ventral ligule rounded in anterior chaetigers, digitiform thereafter

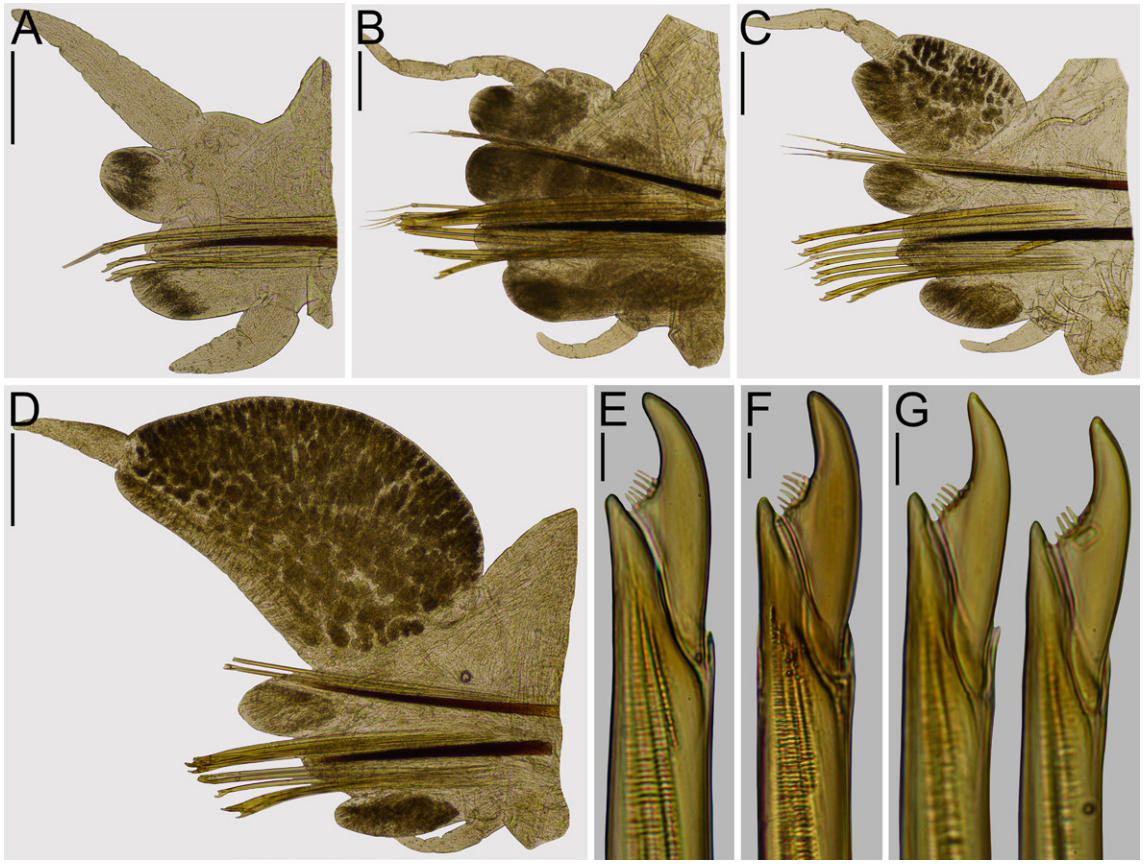

Figure 9. *Pseudonereis palpata* (Treadwell, 1923). Holotype of *Nereis disparsetosa* Treadwell USNM 19638. A, Chaetiger 1, right parapodium, anterior view; B, chaetiger 12, right parapodium, anterior view; C, chaetiger 31, right parapodium, anterior view; D, chaetiger 65, right parapodium, anterior view; E, supra-acicular heterogomph falciger, chaetiger 31; F, sub-acicular heterogomph falciger, chaetiger 12; G, sub-acicular heterogomph falciger, chaetiger 31. Scale bars: A-D, 2 mm; E-G, 10 µm.

(Fig. 9A-D); twice longer than neuroacicular ligule in anteriormost chaetigers (Fig. 9A), half as long as in anterior and middle chaetigers (Fig. 9B, C), 0.3x length in posterior chaetigers (Fig. 9D). Ventral cirrus digitiform and broad in first chaetigers, narrower thereafter (Fig. 9A-D); 0.8x length of ventral ligule in anterior chaetigers (Fig. 9A, B), 0.7x in middle and posterior chaetigers (Fig. 9C, D). Aciculae dark brown throughout (Fig. 9A-D); notoaciculae absent in first 2 chaetigers (Fig. 9A); neuroaciculae becoming thicker than notoaciculae toward posterior chaetigers. Notochaetae consisting of homogomph symmetrical spinigers throughout, decreasing in number toward posterior chaetigers (Fig. 9A-D). Neurochaetae consisting of homogomph symmetrical spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in infra-acicular fascicles (Fig. 9E-G). Heterogomph spinigers present from about chaetiger 30. Blades of supra-acicular spinigers pectinate, teeth minute, decreasing in size toward distal end. Blades of heterogomph falcigers in both fascicles falcate, blades decreasing their size toward posterior chaetigers, narrow teeth, two third of the inner edge edentate (Fig. 9E-G).

Pygidium swollen, as long as wide (Fig. 8B); anal cirri cirriform, as long as pygidium (Fig. 8B).

Taxonomic summary

Material examined. Paratype of *Nereis* (*Neanthes*) *palpata* USNM 19031 (1), Ilha de Alcatrazes, São Paulo, Brazil, Coll. H Leuderwaldt (2 specimens in the vial, one is a *Perinereis* in bad conditions, disposed separately in a vial and labeled as *Perinereis* sp.). Syntypes of *Nereis disparsetosa* USNM 19638 (2), Villa Bella, Ilha de São Sebastião, São Paulo, Brazil, Coll. H Leuderwaldt, 1925.

Remarks

The current description matches with the original one in most features (Treadwell, 1923; 1932), but some differences are detailed below. Treadwell (1923) detailed for *P. palpata* the presence of brownish pigmentation in prostomium, palps, tentacular belt, and dorsum of chaetigers up to the posterior end of the body, but the paratype examined lacked such pigments. Also, the author described edentate jaws, but teeth are present, although they are almost wholly ensheathed. Treadwell (1932, Fig. 4) detailed the presence of heterogomph falcigers in the notopodia, but they were not found in the types specimens examined, and after the illustration clearly describes typical neuropodial heterogomph falcigers in *Pseudonereis* species, so the discrepancy is attributed to confusion in the words.

Treadwell originally placed *Nereis palpata* in the subgenus *Neanthes* after the presence of paragnaths in all pharyngeal areas, but Hartman (1938) transferred it to *Pseudonereis*, and believed *Nereis disparsetosa* and *Pseudonereis atopodon* Chamberlin, 1919 (type locality: Nomuka, Tonga) were synonyms of it. After the examination of the type material of *Nereis palpata* and *N. disparsetosa*, the synonymy of the latter is retained after no relevant differences were found between them. Curiously, the type localities from both species are very near each other, but Treadwell overlooked this fact and failed in comparing *N. disparsetosa* with his previous species *N. palpata*. *Pseudonereis palpata* differs from *P. atopodon* in the following key features (sensu Bakken 2007): in *P. palpata*, median ligules are subequal to slightly longer than neuroacicular ligules in anterior chaetigers and longer than in middle chaetigers, whereas in *P. atopodon* they are shorter than in such chaetigers; in *P. palpata*, dorsal ligules are much broader and larger in chaetiger 30 than in *P. atopodon* in such chaetiger; in *P. palpata*, the distal region of dorsal ligules are twice longer than median ligules in chaetiger 30, whereas in *P. atopodon* they as subequal; in *P. palpata*, dorsal ligules in posteriormost chaetigers become very broad, with a high convex dorsal surface, and up to 5x longer than median ligules, whereas in *P. atopodon* they are less broad, lack a convex dorsal surface, and are 2.5x longer than median ligules.

Discussion

Three of the 4 species examined here were regarded as valid species. To facilitate future studies of Nereididae described by Treadwell, they are summarized in the Table 1 with additional comments. Of the 34 nereidid names proposed by Treadwell, 2 are replacement names, 16 are junior synonyms of other, 6 are valid and retain their original combination, and 10 are valid but they were transferred to another genus (Table 1).

A trend of Treadwell making better and more complete descriptions of nereidids over time was observed. A common practice in the works of Treadwell consulted is the lack of comparisons between his new species and the pre-existent ones. This is the case of *Nereis* (*Neanthes*) *palpata* and *Nereis disparsetosa*. Furthermore, these species by themselves are evidence that Treadwell did not have a consistent scheme on the use of genera or subgenera in nereidids: *Nereis palpata* was placed in the subgenus *Neanthes*, whereas *Nereis disparsetosa* was not, even though it is very similar. Other examples are when he recognized *Leptonereis* as a subgenus of *Nereis* in *Nereis* (*Leptonereis*) *distorta* Treadwell, 1936 but as valid genus for *Leptonereis egregicirrata* Treadwell, 1924 or *Leptonereis mexicana* Treadwell, 1942. Regardless of this inconsistency throughout his work, Treadwell made a remarkable effort in the description of several new species, and his proposed species are therefore encouraged to be reevaluated.

Acknowledgments

To Geoff Keel (USNM), Karen Osborn (USNM), Kathryn Ahlfeld (USNM), and Lily Berniker (AMNH), for the attention offered in their collections. The author appreciates the relevant suggestions made by the reviewer Tulio F. Villalobos-Guerrero and an anonymous reviewer. I thank TFVG for providing additional details of *P. palpata*. The author was first supported with a scholarship from Conacyt (586685) and currently with a postdoctoral grant from the same institution, and had additional support from the Kenneth Jay Boss Fellowship awarded by the Smithsonian Institution, and from a Collection Study Grant awarded by the American Museum of Natural History.

Table 1

Original nereidid names proposed by Treadwell from 1901 to 1943 (excepting *Leptonereis maculata*, see below), including their current status. Names are sorted first by year and later alphabetically.

Original name	Type locality	Current combination or synonymy	Type locality of senior synonym (if apply)	Observations
Nereis arroyensis Treadwell, 1901	Arroyo, Puerto Rico	*Nereis arroyensis* Treadwell, 1901	--	Regarded as valid species by Hartman (1956), redescribed here and retained as valid species.
Nereis notomacula Treadwell, 1914	San Francisco Bay, California, USA	*Platynereis bicanaliculata* (Baird, 1863)	Vancouver Island, Canada.	Hartman (1936) proposed *N. notomacula* and *Uncinereis subita* are synonyms of *U. agassizi* (Ehlers, 1868). After, Hartman (1951) proposed the synonymy with *P. bicanaliculata* without further comments, requiring examination of types to reassess its status.
Nereis (*Platynereis*) *integer* Treadwell, 1920	Romblon, Philippines	*Platynereis polyscalma* Chamberlin, 1919	Ellice Island, Tuvalu.	Hartman (1938) synonymized the species without further explanation. Examination of type material is needed to reassess its status.
Nereis brevicirrata Treadwell, 1920	Santos, Brazil	*Perinereis brevicirrata* (Treadwell, 1920)	--	Hartman (1938) transferred this species to *Perinereis* Kinberg, 1865 based on the pharyngeal arrangement and kind of paragnaths. Belonging to *P. aibuhitensis* (Grube, 1878) species group fide Villalobos-Guerrero et al. (2021).
Nereis (*Ceratonereis*) *alaskensis* Treadwell, 1921	Valdez Harbor, Alaska	*Composetia paucidentata* (Moore, 1903)	Aleutian Islands, Bering Sea.	Hartman (1938) synonymized the species without further explanation. Revision of type material is needed to reassess its status.
Nereis (*Leptonereis*) *acuta* Treadwell, 1923	Santos, Brazil	*Laeonereis acuta* (Treadwell, 1923)	--	Hartman (1956) and later Pettibone (1971) synonymized it with *Laeonereis culveri* (Webster, 1879), but some authors regarded them as distinct. Conde-Vela (2021a) regarded *L. acuta* as valid after the examination of type material.
Nereis (*Neanthes*) *australis* Treadwell, 1923	Maldonado, Uruguay	*Alitta succinea* (Leuckart, 1847)	Helgoland, Germany.	Villalobos-Guerrero and Carrera-Parra (2015) highlighted this and other species are in need of further revision to reassess its synonymy with *A. succinea*.
Nereis (*Neanthes*) *palpata* Treadwell, 1923	São Paulo, Brazil	*Pseudonereis palpata* (Treadwell, 1923)	--	Bakken (2007) redescribed the species. Here is retained as valid species and includes *N. disparsetosa* Treadwell, 1932.
Leptonereis egregicirrata Treadwell, 1924	Antigua Island, Antigua and Barbuda	*Neanthes egregicirrata* (Treadwell, 1924)	--	Hartman (1956) regarded it as questionable and Pettibone (1956) redescribed it and regarded as valid. De León-González et al. (1999) transferred it to *Neanthes* Kinberg, 1865. Since *Neanthes* species exhibit several epitokal patterns (Villalobos-Guerrero & Idris, 2021), further revisions of this and other species in the genus are needed.
Namonereis (sic) *kartaboensis* Treadwell, 1926	Kartabo Point, Guyana	*Namalycastis kartaboensis* (Treadwell, 1926)	--	Glasby (1999) redescribed and transferred it to *Namalycastis* Hartman, 1959 based on material from Surinam because type material is dried out.

Table 1. Continued

Original name	Type locality	Current combination or synonymy	Type locality of senior synonym (if apply)	Observations
Leptonereis maculata (Kinberg, 1865) sensu Treadwell (1928) (combination proposed for *Nicon maculata* Kinberg, 1865)	Galapagos Islands, Ecuador (not type locality of *N. maculata*)	*Rullierinereis mexicana* (Treadwell, 1942)	Topolobampo Bay, Mexico.	Treadwell (1928) examined several epitokes collected in the Arcturus Expedition, and following Grube (1878), he transferred *Nicon maculata* to *Leptonereis* Kinberg, 1865, instead of proposing the new name *L. maculata* as Hartman (1956) suggested. Pettibone (1971) identified the Arcturus Expedition specimens as *Rullierinereis mexicana* (Treadwell, 1942), but needs to be re-assessed to ensure they belong to the same species.
Neanthes obscura Treadwell, 1928	Off Cocos Island, Costa Rica	*Perinereis helleri* (Grube, 1878)	Bohol Island, Philippines.	Hartman (1956) regarded this species as a typical representative of *Perinereis helleri*. Hutchings et al. (1991) redescribed *P. helleri* but overlooked this synonymy, so further revision is needed.
Uncinereis lutea Treadwell, 1928	Sargassum Sea, Atlantic Ocean	*Platynereis dumerilii* (Audouin & Milne-Edwards, 1833)	La Rochelle, France.	Hartman (1951) synonymized the species with *P. dumerilii* without further explanation. Species similar to *Platynereis mucronata* de León-González et al., 2001.
Ceratonereis singularis Treadwell, 1929	Gulf of California, Mexico	*Ceratonereis singularis* Treadwell, 1929	--	Perkins (1980) redescribed this species but regarded it as amphiamerican. Conde-Vela (2021b) redescribed the species and restrict its distribution to the Tropical Eastern Pacific.
Nereis spinifera Treadwell, 1929	Puget Sound, Washington, USA	*Perinereis monterea* (Chamberlin, 1918)	Monterey Bay, California, USA.	Hartman (1936) transferred *Nereis* (*Neanthes*) *monterea* to *Perinereis* and later Hartman (1940) regarded *N. spinifera* as its junior synonym. Examination of type material is needed to reassess the synonymy.
Nereis heterocirrata Treadwell, 1931	Takami Island, Japan	*Nereis heterocirrata* Treadwell, 1931	--	Imajima and Hartman (1964) noted it is similar to *Nereis pelagica*. Imajima (1972) added illustrations of the pharynx, parapodia, and chaetae, of both atokes and epitokes.
Nereis largoensis Treadwell, 1931 (replacement name for *Nereis brevicirrata* Treadwell, 1929)	Key Largo, Florida	*Nereis largoensis* Treadwell, 1931	--	Hartman (1956) regarded *N. largoensis* as a subspecies of *N. pelagica*. Here the former species is redescribed and distinguished from *N. pelagica*.
Nereis decora Treadwell, 1932	São Paulo, Brazil	*Nereis riisei* Grube & Ørsted in Grube, 1857	Saint Croix, US Virgin Islands	Hartman (1956) synonymized this species with *N. riisei* without further explanation, requiring examination of type material to reassess its status.
Nereis disparsetosa Treadwell, 1932		*Pseudonereis palpata* (Treadwell, 1923)		Hartman (1938) proposed this synonymy without further comments. Here the synonymy is retained after the examination of type material.

Table 1. Continued

Original name	Type locality	Current combination or synonymy	Type locality of senior synonym (if apply)	Observations
Nereis (*Leptonereis*) *distorta* Treadwell, 1936	Xiamen, China	*Tylorrhynchus heterochetus* (de Quatrefages, 1866)	Shanghai, China.	Pettibone (1971) examined the type material and synonymized it with *T. heterochetus*. Recently, Xing-Han et al. (2020) found at least 3 genetic geographic lineages of *T. heterochetus* are present in the China Seas, so further revision is needed to reassess its status.
Nereis (*Neanthes*) *amoyensis* Treadwell, 1936	Xiamen, China	*Nereis amoyensis* Treadwell, 1936	Yellow Sea, China.	Hartman (1956) transferred it to *Nereis* because the presence of notopodial homogomph falcigers. Sun and Yang (2004) subjectively regarded it as a junior synonym of *Nereis longior* Khlebovich &Wu, 1962 from the Yellow Sea. However, Treadwell's name has priority (ICZN 1999, Art. 23), so *N. longior* becomes a junior synonym of *N. amoyensis*.
Nereis (*Neanthes*) *orientalis* Treadwell, 1936	Xiamen, China	*Perinereis linea* (Treadwell, 1936)	Xiamen, China.	Arias et al. (2013) made a taxonomic summary of *P. linea*, and suggested *N.* (*Neanthes*) *orientalis* as its synonym. Villalobos-Guerrero et al. (2021) redescribed the types of both species and confirmed the synonymy.
Nereis (*Perinereis*) *linea* Treadwell, 1936	Xiamen, China	*Perinereis linea* (Treadwell, 1936)	--	Villalobos-Guerrero et al. (2021) redescribed and retained this species as valid.
Nereis (*Ceratonereis*) *bartletti* Treadwell, 1937	Off Greenland, Denmark	*Composetia hircinicola* (Eisig, 1870)	Balearic Islands, Spain.	Hartman (1938) synonymized this species with *C. hircinicola*. Villalobos-Guerrero et al. (2022) overlooked this species in their review of *Composetia*. Further revision is needed to ensure they are identical.
Nereis ambiguus Treadwell, 1937	Islas Revillagigedo, Mexico	*Nereis ambigua* Treadwell, 1940	--	Hartman (1956) synonymized it with *Nereis riisei*. Salazar-Vallejo et al. (2021) proposed fixing the declination of the original specific name and regarded it as a valid species.
Uncinereis trimaculosa Treadwell, 1940	Galveston, Texas, USA	*Platynereis dumerilii* (Audouin & Milne-Edwards, 1833)	La Rochelle, France.	Hartman (1951) synonymized the species with *P. dumerilii* without further explanation. Species similar to *Platynereis mucronata* de León-González, Solís-Weiss & Valadez-Rocha, 2001.
Leptonereis nota Treadwell, 1941	Galveston, Texas, USA	*Laeonereis nota* (Treadwell, 1941)	--	Hartman (1956) and Pettibone (1971) considered the species as synonym of *Laeonereis culveri* (Webster, 1879). However, Conde-Vela (2021a) retained *L. nota* as valid species after the examination of type material.
Nereis (*Neanthes*) *varia* Treadwell, 1941 (replacement name for *Nereis* (*Neanthes*) *paucidentata* Treadwell, 1939)	Charlestown, Massachusetts, USA	*Alitta virens* (Sars, 1835)	Norway.	Hartman (1956) placed the species in *Nereis riisei*, and Pettibone (1963) transferred it to *Alitta virens*. No further comments about synonymies were made, so a revision is needed.

Table 1. Continued

Original name	Type locality	Current combination or synonymy	Type locality of senior synonym (if apply)	Observations
Leptonereis mexicana Treadwell, 1942	Topolobampo Bay, Mexico	*Rullierinereis mexicana* (Treadwell, 1942)	--	Pettibone (1971) redescribed this species and transferred it to *Rullierinereis*, but regarded it as an amphiamerican species. Further examination of type and additional materials is needed to ensure its wide distribution.
Ceratonereis longicauda Treadwell, 1943	Padada, Davao del Sur, Philippines	*Neanthes pachychaeta* (Fauvel, 1918)	Sarodrano, Madagascar.	Glasby et al. (2011) subjectively retain the synonymy of this species with *N. pachychaeta*. Examination of type material is needed to reassess its status.
Eunereis africana Treadwell, 1943	Lobito, Angola	*Platynereis dumerilii* (Audouin & Milne-Edwards, 1833)	La Rochelle, France.	Hartman (1951) synonymized it with *P. dumerilii* without further explanation, requiring examination of type material to ensure they are identical.
Nereis singularis Treadwell, 1943	Newfoudland Basin, Northern Atlantic Ocean	*Platynereis singularis* (Treadwell, 1943)	--	Hartman (1956) suggested this species could be the same as *Ceratonereis singularis*. Conde-Vela (2021b) transferred it to *Platynereis* after the examination of type material.
Perinereis diversidentata Treadwell, 1943	Cape Cross, Namibia	*Perinereis diversidentata* (Treadwell, 1943)	--	Day (1953) synonymized it with *P. variegata*. Here it is redescribed and regarded as a *Perinereis* valid species.

References

Arias, A., Richter, A., Anadón, N., & Glasby, C. J. (2013). Revealing polychaetes invasion patterns: Identification, reproduction and potential risks of the Korean ragworm, *Perinereis linea* (Treadwell), in the Western Mediterranean. *Estuarine, Coastal and Shelf Science*, *131*, 117–128. http://doi.org/10.1016/j.ecss.2013.08.017

Báez, D. P., & Ardila, N. E. (2003). Poliquetos (Annelida: Polychaeta) del Mar Caribe colombiano. *Biota Colombiana*, *4*, 89–109.

Bakken, T. (2007). Revision of *Pseudonereis* (Polychaeta, Nereididae). *Zoological Journal of the Linnean Society*, *150*, 145–176. https://doi.org/10.1111/j.1096-3642.2007.00289.x

Bakken, T., & Wilson, R.S. (2005). Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta*, *34*, 507–547. https://doi.org/10.1111/j.1463-6409.2005.00200.x

Behre, E. (1950). Annotated list of the fauna of the Grand Isle region. *Occasional Papers of the Louisiana State University Marine Laboratory*, *6*, 1–66.

Chambers, S. J., & Garwood, P. (1992). *Polychaetes from Scottish waters. A guide to identification*. 3. Family Nereidae. Edinburgh: National Museums of Scotland.

Conde-Vela, V. M. (2018). New species of *Pseudonereis* Kinberg, 1865 (Polychaeta: Nereididae) from the Atlantic Ocean, and a review of paragnath morphology and methodology. *Zootaxa*, *4471*, 245–278. http://doi.org/10.11646/zootaxa.4471.2.2

Conde-Vela, V. M. (2021a). Revision of *Laeonereis* Hartman, 1959 (Annelida: Phyllodocida: Gymnonereidinae), with a review of shaft morphology in nereidids. *Journal of Natural History*, *55*, 381–455. http://doi.org/10.1080/00222933.2021.1903601

Conde-Vela, V. M. (2021b). Revision of *Ceratonereis* Kinberg, 1865 recorded from the Caribbean Sea, with description of two new *Ceratonereis* species and a new combination of *Platynereis* Kinberg, 1865. *Zootaxa*, *5026*, 301–343. http://doi.org/10.11646/zootaxa.5026.3.1

Conde-Vela, V. M., Wu, X., & Salazar-Vallejo, S. I. (2018). Reevaluation and new species of *Kainonereis* Chamberlin, 1919 (Annelida: Polychaeta: Nereididae). *Zoological Studies*, *57*, e6. http://doi.org/10.6620/ZS.2018.57-06

Day, J. H. (1953). The Polychæt fauna of South Africa. Part 2. Errant species from Cape shores and estuaries. *Annals of the Natal Museum*, *12*, 397–441.

de León-González, J. A., Solís-Weiss, V., & Ochoa-Rivera, V. (1999). Nereidids (Polychaeta) from the Caribbean Sea and adjacent coral islands of the southern Gulf of Mexico.

Proceedings of the Biological Society of Washington, *112*, 667–681.

Dueñas, P. R. (1999). Listado de poliquetos colectados durante los años 1979-1999 en la bahía de Cartagena y Golfo de Morrosquillo. *Revista Milenio*, *1*, 9–18.

Glasby, C. J. (1999). The Namanereidinae (Polychaeta: Nereididae). Part 1, Taxonomy and Phylogeny. *Records of the Australian Museum, Supplement*, *25*, 1–129. http://dx.doi.org/10.3853/j.0812-7387.25.1999.1354

Glasby, C. J., Wilson, R. S., & Bakken, T. (2011). Redescription of the Indo-Pacific polychaete *Neanthes pachychaeta* (Fauvel, 1918) n. comb. (Annelida, Phyllodocida, Nereididae) and its synonyms. *Zoosystema*, *33*, 361–375. http://doi.org/10.5252/z2011n3a5

Grube, A. E. (1878). Annulata Semperiana. Beitrage zur Kenntnis der Annelidenfauna der Philippinen nach den von Herrn Prof. Semper mitgebrachten sammlungen. *Memoires De L'Académie Impériale Des Sciences De St. Pétersbourg, 7ème Série*, *25*, 1–300.

Hansen, G. A. (1882). Recherches sur les Annélides Recueillies par M. le professeur Édouard Van Beneden pendant son Voyage au Brésil et à La Plata. *Memoires Couronnes Et Memoires Des Savants Etrangers Publies Par L'Academie Royale Des Sciences, Des Lettres Et Des Beaux-Arts De Belgique*, *44*, 1–29.

Hartman, O. (1936). Nomenclatorial changes involving California polychaete worms. *Journal of the Washington Academy of Sciences*, *26*, 31–32.

Hartman, O. (1938). Nomenclatorial changes involving types of polychaetous annelids of the family Nereidae in the USA National Museum. *Journal of the Washington Academy of Sciences*, *28*, 13–15.

Hartman, O. (1940). Polychaetous annelids. Part II. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions*, *7*, 173–287.

Hartman, O. (1948). The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Arkiv för Zoologi*, *42A*, 1–137.

Hartman, O. (1951). The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science*, *2*, 7–124.

Hartman, O. (1954). Polychaetous annelids of the Gulf of Mexico. *Fishery Bulletin of the Fish and Wildlife Service*, *55*, 413–420.

Hartman, O. (1956). Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. *Bulletin of the American Museum of Natural History*, *109*, 239–310.

Hoagland, R. A. (1919). Polychaetous annelids from Porto Rico, the Florida Keys, and Bermuda. *Bulletin of the American Museum of Natural History*, *41*, 571–591.

Hutchings, P. A., & Kupriyanova, E. K. (2018). Cosmopolitan polychaetes – fact or fiction? Personal and historical perspectives. *Invertebrate Systematics*, *32*, 1–9. http://doi.org/10.1071/IS17035

Hutchings, P. A., Reid, A., & Wilson, R. S. (1991). *Perinereis* (Polychaeta, Nereididae) from Australia, with redescriptions of six additional species. *Records of the Australian Museum*, *43*, 241–274. http://doi.org/10.3853/j.0067-1975.43.1991.47

ICZN. (1999). *International Code of Zoological Nomenclature (4 Ed.)*. London: International Trust for Zoological Nomenclature (The Natural History Museum).

Imajima, M. (1972). Review of the annelid worms of the family Nereidae from Japan, with descriptions of five new species or subspecies. *Bulletin of the National Science Museum, Tokyo*, *15*, 37–153.

Imajima, M., & Hartman, O. (1964). The polychaetous annelids of Japan. Part I. *Allan Hancock Foundation Publications, Occasional Paper*, *26*, 1–237.

Kara, J., Macdonald, A. H. H., & Simon, C. A. (2018). Integrative taxonomic methods reveal an incorrect synonymisation of the South African *Pseudonereis podocirra* (Schmarda) as the widespread *Pseudonereis variegata* (Grube) from Chile. *Invertebrate Systematics*, *32*, 1282–1297. http://doi.org/10.1071/IS18016

Monro, C. C. A. (1933). Notes on a collection of Polychæta from South Africa. *Journal of Natural History*, *11*, 487–509. http://dx.doi.org/10.1080/00222933308673679

Pamungkas, J., Glasby, C. J., Read, G. B., Wilson, S. P., & Costello, M. J. (2019). Progress and perspectives in the discovery of polychaete worms (Annelida) of the world. *Helgoland Marine Research*, *73*, 413–10. http://doi.org/10.1186/s10152-019-0524-z

Perkins, T. H. (1980). Review of species previously referred to *Ceratonereis mirabilis*, and descriptions of new species of *Ceratonereis*, *Nephtys*, and *Goniada* (Polychaeta). *Proceedings of the Biological Society of Washington*, *93*, 1–49.

Pettibone, M. H. (1956). Some polychaete worms of the families Hesionidae, Syllidae, and Nereidae from the east coast of North America, West Indies, and Gulf of Mexico. *Journal of the Washington Academy of Sciences*, *46*, 281–294.

Pettibone, M. H. (1963). Marine polychaete worms of the New England Region. I. Families Aphroditidae through Trochochaetidae. *Bulletin of the USA National Museum*, *227*, 1–356.

Pettibone, M. H. (1971). Revision of some species referred to *Leptonereis*, *Nicon*, and *Laeonereis* (Polychaeta: Nereididae). *Smithsonian Contributions to Zoology*, *104*, 1–53.

Ramírez-Hernández, A., Hernández-Alcántara, P., & Solís-Weiss, V. (2015). *Nereis alacranensis*, a new species of polychaete (Annelida, Nereididae) from Alacranes Reef, southern Gulf of Mexico, with a key to *Nereis* from the Grand Caribbean. *Zootaxa*, *4012*, 156–166. http://dx.doi.org/10.11646/zootaxa.4012.1.8

Rullier, F. (1974). Quelques annélides polychetes de Cuba recueillies dans des éponges. *Travaux Du Muséum National d'Histoire Naturelle Grigore Antipa*, *14*, 9–77.

Salazar-Vallejo, S. I., de León-González, J. A., & Conde-Vela, V. M. (2021). Revision of the species confused with "*Nereis falsa*" de Quatrefages, 1866 (Annelida, Nereididae). *European Journal of Taxonomy*, *779*, 1–70. https://doi.org/10.5852/ejt.2021.779.1579

Sun, R., & Yang, D. J. (2004). Annelida. Polychaeta II. Nereidida (= Nereimorpha). Nereididae, Syllidae, Hesionidae, Pilargidae, Nephtyidae. In C. Huo, & G. Zhao (Eds.), *Fauna Sinica, Invertebrata, Vol. 33* (pp. 1–520). Beijing: Science Press.

Treadwell, A. L. (1901). The polychaetous annelids of Porto Rico. *Bulletin of the USA National Fish Commission*, *20*, 181–210.

Treadwell, A. L. (1923). Two new species of polychaetous annelids of the genus *Nereis* from Brazil. *Revista Do Museu Paulista*, *13*, 3–9.

Treadwell, A. L. (1928). Polychaetous annelids from the Arcturus Oceanographic Expedition. *Zoologica: Scientific Contributions of the New York Zoological Society*, *8*, 449–485.

Treadwell, A. L. (1929). New species of polychaetous annelids in the collections of the American Museum of Natural History, from Porto Rico, Florida, Lower California, and British Somaliland. *American Museum Novitates*, *392*, 1–13.

Treadwell, A. L. (1931). New species of polychaetous annelids from California, Mexico, Porto Rico, and Jamaica. *American Museum Novitates*, *482*, 1–7.

Treadwell, A. L. (1932). New species of polychaetous annelids from Ihla de São Sebastião, together with a list of other annelids determined from Brasil. *Revista Do Museu Paulista*, *17*, 13–20.

Treadwell, A. L. (1939). Polychaetous annelids of Porto Rico and vicinity. *Scientific Survey of Porto Rico and the Virgin Islands*, *16*, 1–319.

Treadwell, A. L. (1943). Polychaetous annelids form Africa in the collections of the American Museum of Natural History. *American Museum Novitates*, *1221*, 1–6.

Villalobos-Guerrero, T. F. (2019). Redescription of two overlooked species of the *Perinereis nuntia* complex and morphological delimitation of *P. nuntia* (Savigny in Lamarck, 1818) from the Red Sea (Annelida, Nereididae). *Zoosystema*, *41*, 465–496. http://doi.org/10.5252/zoosystema2019v41a24

Villalobos-Guerrero, T. F., & Bakken, T. (2018). Revision of the *Alitta virens* species complex (Annelida: Nereididae) from the North Pacific Ocean. *Zootaxa*, *4483*, 201–257. http://doi.org/10.11646/zootaxa.4483.2.1

Villalobos-Guerrero, T. F., & Carrera-Parra, L. F. (2015). Redescription of *Alitta succinea* (Leuckart, 1847) and reinstatement of *A. acutifolia* (Ehlers, 1901) n. comb. based upon morphological and molecular data (Polychaeta: Nereididae). *Zootaxa*, *3919*, 157–178. https://doi.org/10.11646/zootaxa.3919.1.7

Villalobos-Guerrero, T. F., & Idris, I. (2021). Reproductive morphology and redescriptions of some *Neanthes* Kinberg, 1865 (Annelida: Nereididae) species from the southeastern Asian seas, with comparative synoptic tables of accepted species. *The European Zoological Journal*, *88*, 556–594. http://doi.org/10.1080/24750263.2021.1899318

Villalobos-Guerrero, T. F., Park, T. S., & Idris, I. (2021). Review of some *Perinereis* Kinberg, 1865 (Annelida: Nereididae) species of Group 2 *sensu* Hutchings, Reid & Wilson, 1991 from the Eastern and South-eastern Asian seas. *Journal of the Marine Biological Association of the United Kingdom*, *101*, 279-307. http://doi.org/10.1017/S0025315421000126

Villalobos-Guerrero, T. F., Conde-Vela, V. M., & Sato, M. (2022). Review of *Composetia* Hartmann-Schröder, 1985 (Annelida: Nereididae), with the establishment of two new genera. *Journal of Natural History*, *55*, 2313–2397. https://doi.org/10.1080/00222933.2021.1976295

Warren, W. S. (1942). A survey of the annelid worms of the Grand Isle Region. *Bios*, *13*, 39–46.

Xing-Han, C., Sen, Y., Wei, Y., Yuan-Yuan, S., Rui-Wen, X., Bin, F. et al. (2020). First genetic assessment of brackish water polychaete *Tylorrhynchus heterochaetus*: mitochondrial COI sequences reveal strong genetic differentiation and population expansion in samples collected from southeast China and north Vietnam. *Zoological Research*, *41*, 61–69. http://doi.org/10.24272/j.issn.2095-8137.2020.006