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Sinkhole and brackish water nereidid polychaetes: Revision of *Stenoninereis* Wesenberg-Lund, 1958 (Annelida)

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Abstract

Stenoninereis species are nereidids with a small body (ca. 35 chaetigers), dorsal cirri with conspicuous cirrophores and cirrostyles, bare pharynx, and lack of neuropodial ventral ligules throughout the body. Currently, there are two valid species, *S. martini* Wesenberg-Lund, 1958 from the Lesser Antilles and *S. tecolutlensis* de León-González & Solís-Weiss, 1997 from Eastern Mexico. *Nicon lackeyi* Hartman, 1958 has been regarded as a junior synonym of *S. martini*. The examination of type and topotype specimens indicated that *N. lackeyi* is a distinct species and both species are redescribed, *S. martini* is restricted to the Caribbean islands, and *N. lackeyi* is reinstated and transferred to *Stenoninereis*. Further, Puerto Rican specimens differ from these known species and a new species, *S. elisae* is also described, featured mainly by large cirrophores and short cirrostyles in anterior and middle chaetigers. Further discussions about their morphology and phylogenetic affinities and a key to identify all known *Stenoninereis* species are also included.

Keywords

Notopodial dorsal ligules, morphology, ecology, blood vessels, innervation, cirrophores

Introduction

The nereidid genus *Stenoninereis* was established by Wesenberg-Lund (1958) for a new species, *S. martini,* discovered in a sinkhole from Sint Maarten, the Caribbean Sea, featured by having a small body of about 35 chaetigers, and large dorsal cirri with

distinct cirrophores and cirrostyles, pharynx without papillae or paragnaths, and a progressive reduction and disappearing of notopodial dorsal ligules in the posterior end (Wesenberg-Lund 1958). Wesenberg-Lund (1958) argued that the set of features presence of antennae, lacking pharyngeal ornamentation, biramous parapodia but lacking hypertrophied dorsal ligules, separate the new species from genera with similar morphology such as *Micronereis* Claparède, 1863 or *Leptonereis* Kinberg, 1865. Later works have found morphological affinities among *Stenoninereis* and other plesiomorphic genera such as *Namalycastis* Hartman, 1959, *Namanereis* Chamberlin, 1919, and *Profundilycastis* Hartmann-Schröder, 1977 (Fitzhugh 1987; Santos et al. 2005), which have smooth pharynx and parapodia with few or no ligules.

At the same year, Hartman (1958) described *Nicon lackeyi* from a spring in Sarasota, Florida. She concluded it should belong to *Nicon* Kinberg, 1865 because it had a bare pharynx, biramous parapodia, notochaetae spinigers, and neurochaetae as spinigers and falcigers. Hartman (1958) also included a list and a key to species of all then known *Nicon*, but relevant features such as having dorsal cirri with distinct cirrophores and cirrostyles, the disappearing of notopodial dorsal ligules toward posterior end of body, and the lack of neuropodial ventral ligules throughout body, were disregarded as diagnostic at generic level. Pettibone (1971) studied the type material of *N. lackeyi* and *S. martini* and regarded them as synonyms because of their high resemblance. Consequently, *S. martini* has been reported along the Gulf of Mexico, the Caribbean Sea and the Eastern coasts of United States of America, especially in ecological studies, and even used as a bioindicator of hypoxic or anoxic conditions. Only another species has been described after *S. martini*, *S. tecolutlensis* de León-González & Solís-Weiss, 1997. This was found in oysters shells attached to mangrove roots from the Estero de Larios, Veracruz, Mexico (de León-González and Solís-Weiss 1997).

After a prospective examination of available material of *Stenoninereis* species in the National Museum of Natural History, Smithsonian Institution (USNM) from several localities, some doubts arose about if *Nicon lackeyi* is a synonym of *Stenoninereis martini*, and if some records of *S. martini* really correspond with it. With the aim to clarify the status of these species, all type, topotypes and additional specimens available of the involved species were revised. As a result of the revision, the type species is redescribed, *N. lackeyi* is reinstated and transferred to *Stenoninereis*, and a new species is proposed. Further, a key to identify all known species is also given.

Material and methods

Type and non-type specimens are deposited in the Museum of Natural History of Los Angeles County, California, United States of America (LACM-AHF); and the National Museum of Natural History, Smithsonian Institution, Washington D.C., United States of America (USNM). The holotype of *S. tecolutlensis* (USNM 174870) was examined for comparison.

All specimens were whole-mounted and observed under stereomicroscope and compound microscopes for observing parapodial and chaetal modifications along the body. Some parapodia were removed and mounted on semi-permanent slides with ethanol-glycerol, and examined under the compound microscope. Parapodia from first or two chaetiger were revised and sometimes dissected, and three to four additional parapodia were removed throughout the body. Due to the delicate tissues of the anterior end of specimens, dissection of the pharynx was avoided. The photographs were made with a digital camera with adaptor for both microscopes. In some cases, a set of photographs were made and combined manually to improve composition. Some contrast and brightness adjustments were performed in photographs to improve the visibility of structures. For describing parapodia, Bakken and Wilson's (2005) terminology was followed, and terms 'achaetous ring' and 'anterior cirri' were used instead of 'peristomium' and 'tentacular cirri', respectively, as suggested by Santos et al. (2005).

Results

Systematics
Order Phyllodocida Dales, 1962
Family Nereididae de Blainville, 1818

Genus *Stenoninereis* Wesenberg-Lund, 1958

Stenoninereis Wesenberg-Lund 1958: 12.

Type species. *Stenoninereis martini* Wesenberg-Lund, 1958, by monotypy.

Diagnosis (modified from León-González and Solís-Weiss 1997, additions are highlighted in boldface). Prostomium with anterior margin cleft. Antennae and eyes present. Four pairs of **anterior cirri**. Pharynx bare. First two chaetigers with neuroacicular ligules and ventral cirri only. **Anterior chaetigers with dorsal cirrophores and notopodial dorsal ligules ciliated.** Dorsal cirri with distinct cirrophores and cirrostyles throughout body. Notopodial dorsal ligules present in anterior and middle chaetigers, disappearing in posterior-most ones; neuropodial ventral ligules absent throughout body. **Notochaetae sesquigomph spinigers; neurochaetae sesquigomph spinigers and falcigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles.** Pygidium with two plate-like lobes.

Remarks. Main morphological features of *Stenoninereis* species are depicted in Figure 1. The species *S. tecolutlensis* was described as having two notopodial fascicles, the superior one bearing homogomph spinigers and the inferior one with sesquigomph spinigers. However, after the examination of the holotype (USNM 174870), there are no notopodial homogomph spinigers, likely being that indication an artifact due to the position of the shaft, and therefore this feature is deleted from the emended diagnosis.

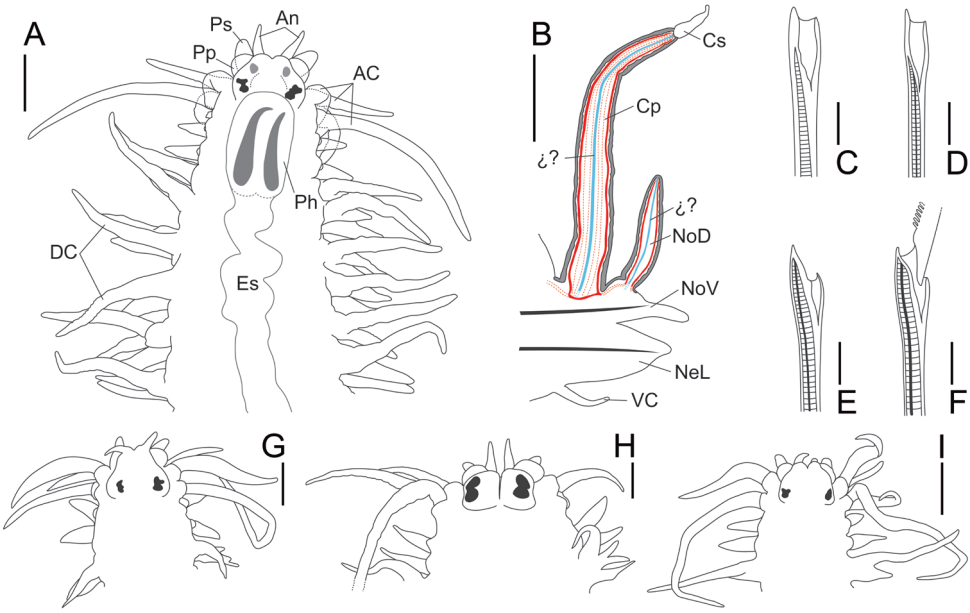

Figure 1. Morphology of *Stenoninereis* species **A** non-type of *S. lackeyi* comb. n. (USNM 53273) **B, I** syntypes of *S. elisae* sp. nov. (USNM 55366) **C–F** non-type of *S. elisae* sp. nov. (USNM 55360) **G** non-type of *S. martini* Wesenberg-Lund 1958 (USNM 61623) **H** holotype of *S. tecolutlensis* de León-González & Solís-Weiss, 1997 (USNM 174870) **A** anterior end, dorsal view **B** chaetiger 6, left parapodium (solid and dashed red lines: vessels; solid and dashed light blue lines: unknown structures, likely nerves) **C** shaft of notopodial sesquigomph spinigers, chaetiger 20 **D** shaft of neuropodial supra-acicular sesquigomph spiniger, same chaetiger **E** shaft of neuropodial sub-acicular heterogomph spiniger, chaetiger 20 **F** Shaft of neuropodial sub-acicular heterogomph falciger, chaetiger 20 **G–I** anterior ends, dorsal view. Abbreviations: AC, anterior cirri; An, antennae; Cp, cirrophore; Cs, cirrostyle; DC, dorsal cirrus; Es, esophagus; NeL, neuroacicular ligule; NoD, notopodial dorsal ligule; NoV, notopodial ventral ligule; Ph, pharynx; Pp, palpophore; Ps, palpostyle; VC, ventral cirrus; ¿?, unknown structures, likely nerves by their position. Scale bars: 0.2 mm (**A, G–I**); 0.1 mm (**B**); 5 μm (**C–F**).

Stenoninereis martini Wesenberg-Lund, 1958, restricted

Figures 1G, 2–3

Stenoninereis martini Wesenberg-Lund 1958: 9–12, figs 2, 3, 4a–c. Pettibone 1971: 39–41, figs 23a–n (partim).

Material examined. Syntypes. CARIBBEAN SEA, NETHERLANDS ANTILLES • 2; Sint Maarten, Devil's Hole; 26 Jul. 1955; P.W. Hummelinck leg.; 20x5x1.5 m, water almost clear and slightly greenish brown, 10900 mg Cl/l; USNM 29726.

Additional material. CARIBBEAN SEA, PUERTO RICO • 21; Laguna Joyuda, off Inlet canal; 18°7'30"N, 67°10'0.12"W; 9 Oct. 1979; R. Castro leg.; mud and shells, host gastropods; USNM 61623.

Description. Two syntypes (USNM 29726) in poor condition, dissections previously performed (Figs 2D–E). One syntype posteriorly incomplete, some anterior pa-

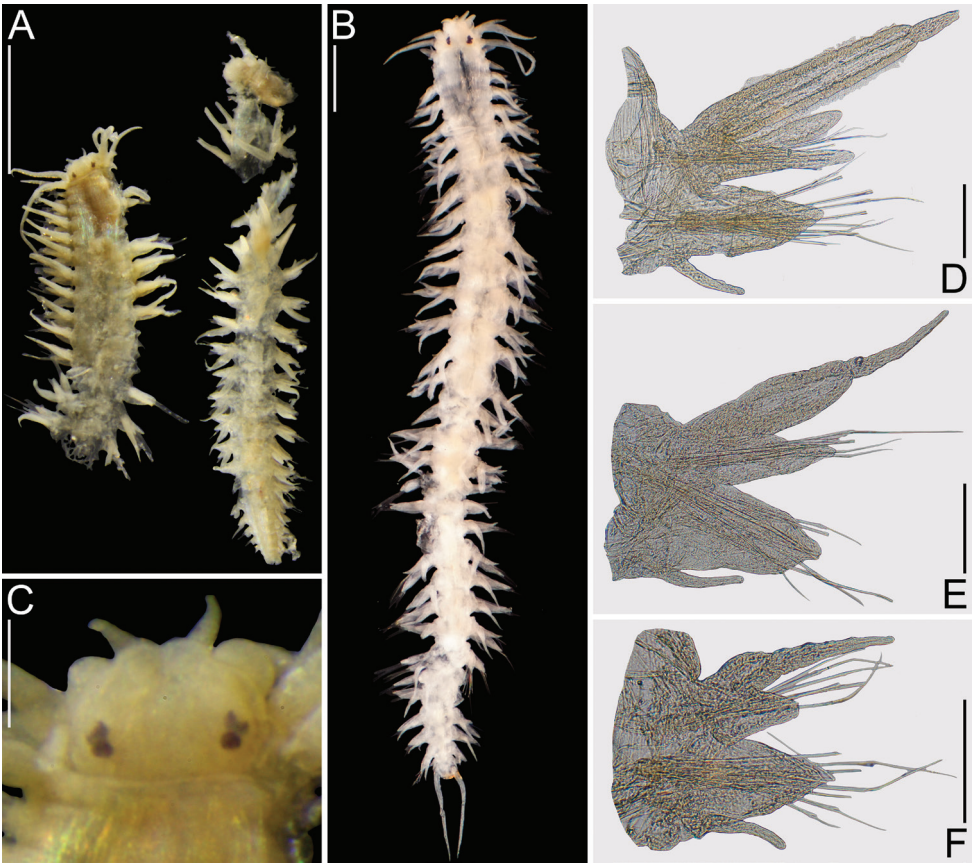

Figure 2. *Stenoninereis martini* Wesenberg-Lund, 1958 **A, C–F** syntypes (USNM 29726) **B** non-type (USNM 61623) **A** whole specimens, dorsal view **B** whole specimen, dorsal view **C** close-up of prostomium, dorsal view **D** chaetiger 6, left parapodium, anterior view (dorsal cirrostyle incomplete) **E** chaetiger 13, left parapodium, anterior view **F** chaetiger 18, left parapodium, anterior view. Scale bars: 0.5 mm (**A–B**); 0.1 mm (**C–F**).

rapodia previously dissected, 2.4 mm long, 0.4 mm wide at chaetiger 10, 16 chaetigers (Fig. 2A). The other syntype in two portions, anterior end very damaged, 3.5 mm long, 0.3 mm wide, 21 chaetigers, some posterior chaetigers previously dissected (Fig. 2A). Non-type material (USNM 61623) complete, 5 mm long, 0.3 mm wide, 32 chaetigers (Fig. 2B). All specimens pale, no pigmentation remaining.

Prostomium wider than long, anterior margin shallowly cleft (Figs 1G, 2C); antennae subulate, half as long as prostomium; eyes black, subequal, anterior eyes reniform, twice larger than posterior rounded eyes, anterior and posterior pairs slightly overlapped (Figs 1G, 2B–C). Achaetous ring half as long as first chaetiger; four pairs of anterior cirri, longest one reaching chaetiger 8 (Figs 1G, 2A–B).

Pharynx dissected; jaws light brown, translucent, 13 teeth (Fig. 3J). Pharynx surface bare.

All chaetigers having both noto- and neuroaciculae; dorsal cirri cirrophores and notopodial dorsal ligules of anterior chaetigers ciliated. In first two chaetigers (Fig. 3A), no-

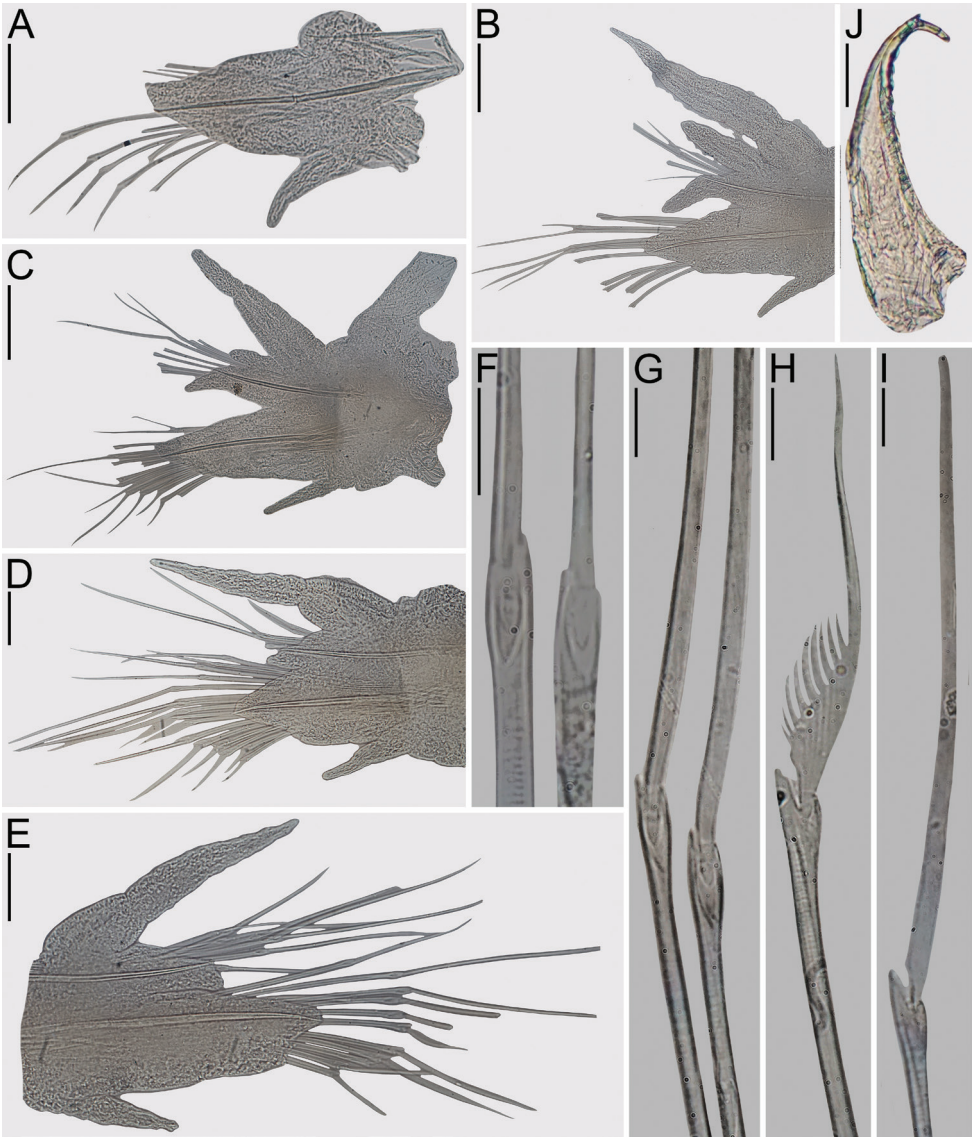

Figure 3. *Stenonereis martini* Wesenberg-Lund, 1958 **A–J** non-type specimens (USNM 61623) **A** chaetiger 2, right parapodium, anterior view **B** chaetiger 9, right parapodium, anterior view **C** chaetiger 21, right parapodium, anterior view **D** chaetiger 27, right parapodium, anterior view **E** chaetiger 28, left parapodium, anterior view **F** notopodial sesquigomph spinigers, chaetiger 28 **G** supra-acicular sesquigomph spinigers, chaetiger 28 **H** sub-acicular heterogomph spiniger, chaetiger 28 **I** sub-acicular heterogomph spiniger, chaetiger 28 **J** left jaw, dorsal view. Scale bars: 50 μm (**A, D**); 0.1 mm (**B–C**); 10 μm (**F–I**); 50 μm (**J**).

topodia small, rounded lobe with notoaciculum. Neuroacicular ligule subconical, twice longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In anterior chaetigers (Figs 2D, 3B), dorsal cirrus as long as chaetiger width, excluding parapodia; cirrophore 2–3 times longer than cirrostyle, 1.6–2.0 times longer

than notopodial dorsal ligule, twice longer than notopodial ventral ligule. Notopodial dorsal ligule digitiform, basally attached to, and slightly shorter than, notopodial ventral ligule; notopodial ventral ligule subconical to digitiform, 2.8–3.0 times longer than wide, 1.0–1.3 times longer than neuroacicular ligule. Neuroacicular ligule subconical, 1.8–2.0 times longer than wide, 2.0–2.5 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In middle chaetigers (Figs 2E, 3C), dorsal cirrus shorter than wide of chaetiger excluding parapodia; cirrophore 1.5 times longer than cirrostyle, 1.5 times longer than notopodial ventral ligule. Notopodial dorsal ligule absent in dissected syntype, digitiform in non-type specimen, 0.4 times as long as notopodial ventral ligule; notopodial ventral ligule subconical, 1.8–2.0 times longer than wide, as long as neuroacicular ligule. Neuroacicular ligule subconical, 1.4–1.8 times longer than wide, 1.7 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In posterior chaetigers (Figs 2F, 3D–E), dorsal cirrus shorter than chaetiger width, excluding parapodia; cirrophore 0.6 times as long as cirrostyle, half as long as notopodial ventral ligule. Notopodial dorsal ligule absent; notopodial ventral ligule subconical, 1.3–1.4 times longer than wide, half as long as neuroacicular ligule. Neuroacicular ligule subconical, 1.4–1.5 times longer than wide, 1.7 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

Notochaetae sesquigomph spinigers. Neurochaetae sesquigomph spinigers in supra-acicular fascicles, heterogomph spiniger and falcigers in sub-acicular fascicles.

Notopodial and neuropodial supra-acicular sesquigomph spinigers with blade smooth (Figs 3F–G). Neuropodial heterogomph spinigers with blades basally serrate, coarse teeth, larger teeth longer than blade width, 2/3 of the blade edentate and subulate (Fig. 3H). Neuropodial heterogomph falcigers with very long blades (Fig. 3I), increasing their length from upper to lower positions in the same fascicle; falcigers with blades smooth (Fig. 3I).

Pygidium with two anal plate-like lobes; anal cirri missing in types (Fig. 2A), as long as last five chaetigers in a non-type specimen (Fig. 2B).

Remarks. The syntypes revised are damaged, but some parapodia in good conditions were dissected and examined. There are a few differences between the current description and the original one. The syntypes include about 25 specimens of a wide range of size, including juveniles having the larval eyes ("In young specimens there are 6 eyes arranged in two triangles of three each…") (Wesenberg-Lund 1958). Wesenberg-Lund (1958) noted that notopodial dorsal ligules disappear from chaetiger 26 in the specimen dissected, but there is no indication about the number of chaetigers of such specimen, likely being the largest one 6 mm long, and 34 chaetigers. In the specimens examined, the notopodial dorsal ligules disappear from anterior chaetigers (about chaetiger 12). Remaining parapodial features in the current redescription match the original description, and the redescription by Pettibone (1971). Pettibone (1971) described the notopodia of the first two chaetigers as having "slender notoaciculum with short, conical, basal cirrophore of dorsal cirrus; style short (sometimes missing)", and such dorsal cirrus was depicted in the anterior end and the second chaetiger draw-

ings (Pettibone 1971, Figs 23a and g, respectively). However, there are no dorsal cirri in first two chaetigers of the specimens of this and all other known species.

On the other hand, the holotype of *S. tecolutlensis* (USNM 174870) was examined for comparison, and differences are evident between it and *S. martini*. In *S. tecolutlensis*, the prostomial margin is deeply cleft and a median groove is present, reaching the anterior pair of eyes, whereas in *S. martini* the cleft is shallow, and there is no median groove. In *S. tecolutlensis*, the dorsal cirrophores are 1.5 times longer than cirrostyles and as long as notopodial dorsal ligules in anterior chaetigers, whereas in *S. martini* cirrophores are 2–3 times longer than cirrostyles and twice longer than notopodial dorsal ligules. Further, in *S. tecolutlensis* the cirrophores are as long as notopodial dorsal ligules in middle chaetigers and as long as them in posterior chaetigers, whereas in *S. martini* cirrophores are twice longer than notopodial dorsal ligules in middle chaetigers and half as long as them in posterior chaetigers. Both species are similar in other respects. The differences with *S. elisae* sp. nov. and *S. lackeyi* comb. n. are discussed in the remarks for these species.

The record of *S. martini* for the Gulf of Mexico by de León-González and Solís-Weiss (1997) is also different. The authors described specimens with 'trilobate' notopodia', i.e., with notopodial prechaetal lobes, a feature absent in all known species; also, the notopodial dorsal ligules are present throughout the body in specimens from the Gulf of Mexico, whereas in *S. martini* and other known species the notopodial dorsal ligules disappear in posterior chaetigers. Further, the cirrophores are several times longer than cirrostyles along the body in the specimens from the Gulf of Mexico (4 in anterior, 3.3 in middle, and 2.3 in posterior chaetigers), and shorter than cirrostyles in posterior chaetigers (0.5) in the syntypes of *S. martini*; this development of the dorsal cirri resembles the one found in *S. elisae* sp. nov. Furthermore, the cirrostyle/notopodial ventral ligule ratios in the specimens of *S. martini* from the Gulf of Mexico are almost the same along the body (1.4–1.5), whereas in the syntypes of *S. martini* the ratio decreases toward posterior chaetigers. Finally, the neuropodial sub-acicular spinigers in specimens from the Gulf of Mexico have 2/3 of the blade dentate, whereas in the syntypes of *S. martini* only 1/3 is dentate. These differences make doubtful the conspecificity of the specimens from the Gulf of Mexico with specimens from the Caribbean Sea, so a further study is needed to clarify their status.

***Stenoninereis lackeyi* (Hartman, 1958), reinst. comb. n.**
Figures 1A, 4, 5

Nicon lackeyi Hartman 1958: 263–265, figs 1–5.
Stenoninereis martini Pettibone 1971: 39–41, figs 24a–c (*partim, non* Wesenberg-Lund, 1958)

Material examined. Paratypes. GULF OF MEXICO, UNITED STATES • 8, paratypes of *Nicon lackeyi*; Florida, Sarasota County, Warm Mineral Springs; 27°02'43"N,

82°17'35"W; J. Lackey leg.; no date, 86 °F, 17000 ppm dissolved solids, 7.2±0.2 pH; LACM-AHF 806.

Additional material. GULF OF MEXICO, UNITED STATES • 60; Florida, Tampa Bay; 1963; J. L. Taylor leg.; USNM 45699 • 16; Halstead Bayou, Jackson County, Mississippi; Sep. 1975; R. Herd leg.; USNM 53273.

NORTHWESTERN ATLANTIC OCEAN, UNITED STATES • 6; North Carolina, Beaufort, Town Marsh; L. Cammen leg.; USNM 55619 • 7; North Carolina, Bogue Sound, Tar Landing Bay; Oct. 1976; R. T. Kneib leg.; USNM 55618.

Description. Paratypes (LACM-AHF 806) complete, some parapodia previously dissected; one complete paratype selected for description, 4 mm long, 0.5 mm wide at chaetiger 10, 31 chaetigers (Fig. 4A). Specimens from Florida (USNM 45699) most complete, some filled with large oocytes, two per segment (Fig. 5A); one paratype used for variation, complete, 4.8 mm long, 0.4 mm wide, 33 chaetigers (Fig. 5A). All specimens pale.

Prostomium wider than long, anterior margin shallowly cleft (Fig. 4B); antennae subulate, half as long as prostomium; eyes black, anterior eyes reniform, slightly larger than posterior rounded ones, anterior and posterior eyes slightly overlapped (Fig. 4B). Achaetous ring as long as first chaetiger; four pairs of anterior cirri, anterodorsal pair lanceolate, remaining ones subulate, longest one reaching chaetiger 7, (Figs 4A–B).

Pharynx previously removed in paratype. In non-type material, jaws light brown, 10 teeth restricted to half cutting edge (Fig. 5B). Pharynx bare.

All chaetigers with noto- and neuroaciculae; dorsal cirri cirrophores and notopodial dorsal ligules of anterior chaetigers ciliate. In first two chaetigers (Fig. 5C), notopodium consists in a small, rounded lobe bearing notoaciculum. Neuroacicular ligule subconical, 2.5 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In anterior chaetigers (Figs 4H, 5D–E), dorsal cirrus shorter than chaetiger width, excluding parapodia; cirrophore 1.5–2.0 times longer than cirrostyle, 1.3 times longer than notopodial dorsal ligule, 1.0–1.2 times longer than notopodial ventral ligule. Notopodial dorsal ligule digitiform, basally attached to, and half as long as, notopodial ventral ligule; notopodial ventral ligule subconical, 3.0–3.5 times longer than wide, 1.0–1.2 times longer than neuroacicular ligule. Neuroacicular ligule subconical, 2.3–2.5 times longer than wide, 2.8–3.0 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In middle chaetigers (Figs 4I, 5F), dorsal cirrus shorter than chaetiger width, excluding parapodia; cirrophore 1.2–1.4 times longer than cirrostyle, 4 times longer than notopodial dorsal ligule, 1.0-1.2 times longer than notopodial ventral ligule. Notopodial dorsal ligule digitiform, basally attached to, and 0.2 times as long as, notopodial ventral ligule; notopodial ventral ligule subconical, 2.2–2.4 times longer than wide, as long as notopodial ventral ligule. Neuroacicular ligule subconical, 2.5–2.7 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In posterior chaetigers (Figs 4J, 5G), dorsal cirrus shorter than wide of chaetigers excluding parapodia; cirrophore 0.6 times as long as cirrostyle, 0.7 times as long as

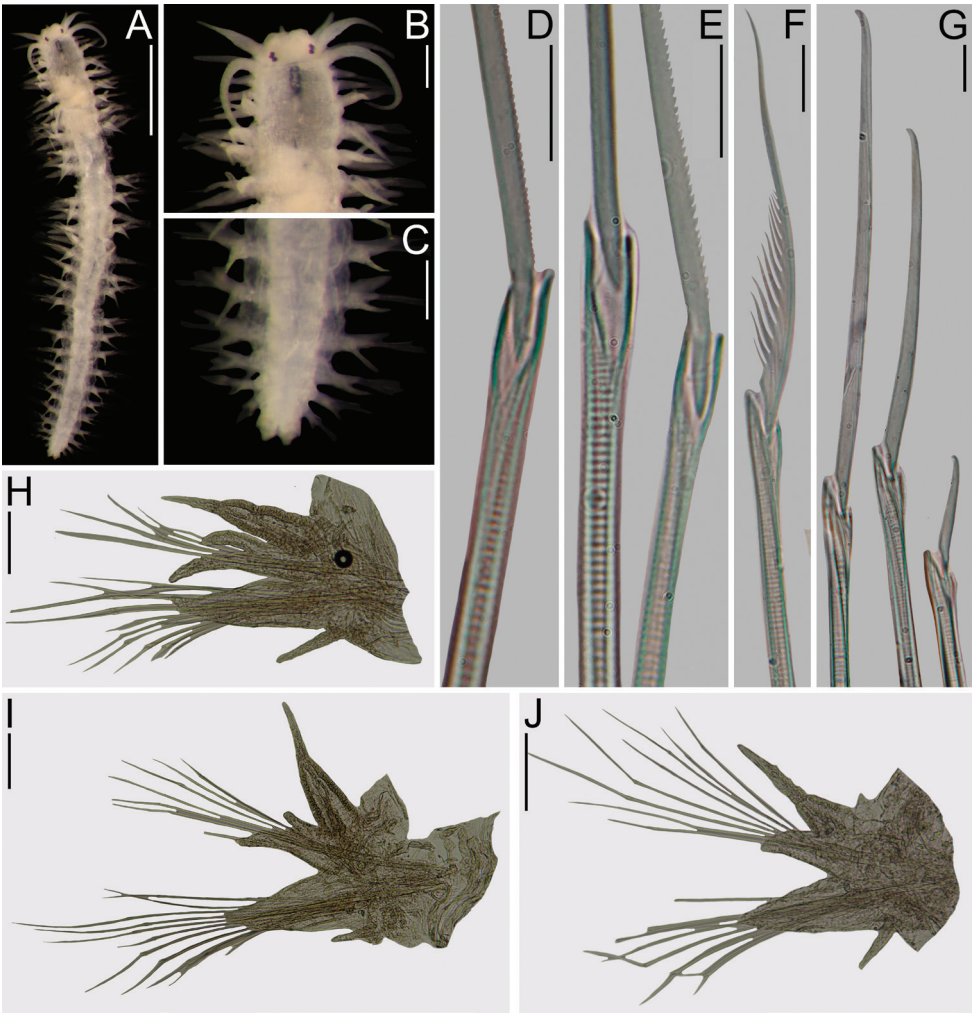

Figure 4. *Stenonereis lackeyi* (Hartman, 1958) comb. n. **A–J** paratype (AHF-POLY-806) **A** whole specimen, dorsal view **B** anterior end, dorsal view **C** posterior end, dorsal view **D** notopodial sesquigomph spiniger, chaetiger 27 **E** supra-acicular sesquigomph spinigers, chaetiger 27 **F** sub-acicular heterogomph spiniger, chaetiger 27 **G** sub-acicular heterogomph falcigers (uppermost one at the left), chaetiger 27 **H** chaetiger 7, right parapodium, anterior view **I** chaetiger 19, right parapodium, anterior view **J** chaetiger 26, right parapodium, anterior view. Scale bars: 1 mm (**A**); 0.25 mm (**B–C**); 10 μm (**D–G**) 0.1 mm (**H–J**).

notopodial ventral ligule. Notopodial dorsal ligule absent; notopodial ventral ligule subconical, 1.5–2.0 times longer than wide, 0.7–1.0 times as long as neuroacicular ligule. Neuroacicular ligule subconical, 2.0–2.1 times longer than wide, 2.5 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

Notochaetae sesquigomph spinigers. Neurochaetae sesquigomph spinigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles.

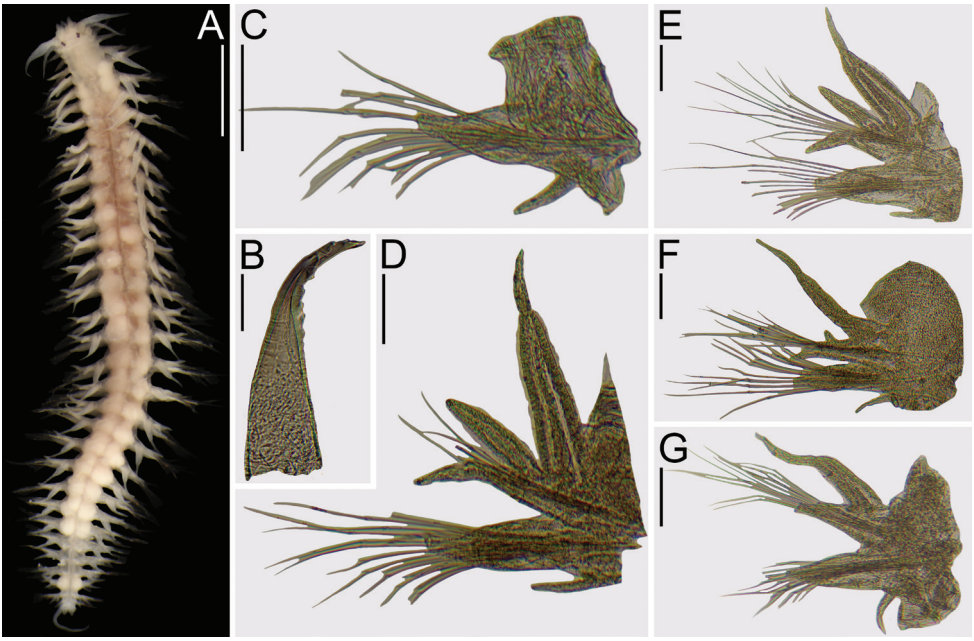

Figure 5. *Stenoninereis lackeyi* (Hartman, 1958) comb. n. **A–F** non-type specimen (USNM 45699) **A** whole specimen, dorsal view **B** left jaw, dorsal view **C** Chaetiger 2, right parapodium, anterior view **D** Chaetiger 6, right parapodium, anterior view **E** Chaetiger 17, right parapodium, anterior view **F** Chaetiger 23, right parapodium, anterior view **G** Chaetiger 29, right parapodium, anterior view. Scale bars: 1 mm (**A**); 50 μm (**B**); 0.1 mm (**C–G**).

Notopodial (Fig. 4D) and neuropodial (Fig. 5E) supra-acicular sesquigomph spinigers pectinate, very minute teeth, progressively disappearing distally. Neuropodial heterogomph spinigers (Fig. 4F) serrate, coarse teeth, longer teeth are longer than the wide of the blade, half of 1/3 of the blade edentate and subulate. Neuropodial heterogomph falcigers (Fig. 4G) with very long blades, blades increasing their length toward posterior chaetigers, blades with minute teeth throughout, often inconspicuous; blades increasing their length from upper to lower positions in the same fascicle (Fig. 4G).

Pygidium with two plate-like lobes; anal cirri subulate, as long as last four chaetigers (Figs 4C, 5A).

Remarks. Hartman (1958) described *Nicon lackeyi* with several specimens but the exact number of them was not stated; the specimens were supposedly deposited in a single lot (USNM 29627). Pettibone (1971) examined the lot and found the holotype and an additional lot with catalog number USNM 29628 containing two paratypes, but no further comments about the supposed splitting of the type material were added. These lots were not found during three research visits at the USNM (2015, 2016, and 2018). Some specimens, however, are deposited in the Los Angeles Museum; they were examined by Hartman, with identical field data as those recorded for the supposed

type specimens. LACM material was labeled as paratypes by Kristian Fauchald according to the collection records, but no further comments were found. Because the specimens belonged to the original set of specimens, and because the specimens previously regarded as holotype and remaining type specimens are currently missing, the species was redescribed with available specimens in the LACM.

After a comparison between type material of *N. lackeyi* and *S. martini* led Pettibone (1971) to regard them as synonyms. However, there are relevant differences to separate them as two distinct species of the same genus. The main distinctive feature is the slender aspect of both notopodial ventral ligules and neuroacicular ligules and mainly observed in middle and posterior chaetigers, as seen when comparing the length/wide ratios in these ligules along the body. In anterior chaetigers, both species have similar ratios in notopodial ventral ligules, but *Stenoninereis lackeyi* comb. n. has larger ratios in the middle (2.2–2.4) and posterior (1.5–2.0) chaetigers than *Stenoninereis martini* (1.8–2.0 and 1.3–1.4, respectively). Likewise, in neuroacicular ligules, *S. lackeyi* comb. n. has larger ratios in anterior (2.3–2.5), middle (2.5–2.7), and posterior (2.0–2.1) chaetigers than *S. martini* (1.8–2.0, 1.4–1.8, and 1.4–1.5, respectively). Further, in anterior chaetigers, dorsal cirrophores in *S. lackeyi* comb. n. are 1.5–2.0 times longer than their respective cirrostyles, whereas in *S. martini* they are 2–3 times longer; in middle and posterior chaetigers, both species have similar ratios.

Stenoninereis lackeyi comb. n. is easily recognized from *S. tecolutlensis,* the other Gulf of Mexico species. In *S. lackeyi* comb. n., the prostomium is shallowly incised and the eyes are minute, whereas in *S. tecolutlensis* the prostomium is deeply incised and the eyes occupy a larger prostomial surface (Fig. 1H). In addition, in *S. lackeyi* comb. n. the neuroacicular lobes are blunt, whereas in *S. tecolutlensis* they are acuminate.

***Stenoninereis elisae* sp. nov.**
http://zoobank.org/C5EF40A3-DCE5-45DC-B804-A6A9D8A16585
Figures 1B–F, I; 6

Type material. Syntypes. CARIBBEAN SEA, PUERTO RICO • 5; Rio Grande, Espiritu Santo River, 50 m below Castanon confluent; Apr. 1977; W.R. Bhajan leg.; USNM 55366.

Additional material. CARIBBEAN SEA, PUERTO RICO • 3; Rio Grande, Espiritu Santo River, 50 m above Castanon confluent; W.R. Bhajan leg.; USNM 55360.

Type locality. Espiritu Santo River, Rio Grande, Puerto Rico.

Description. Five syntypes (USNM 55366) complete, in good condition. Specimen dissected complete, 62 mm long, 0.4 m wide at chaetiger 10, 27 chaetigers. All specimens pale (Figs 6A–B).

Prostomium wider than long, anterior margin shallowly cleft (Figs 1I, 6C); antennae subulate, half as long as prostomium; eyes black, anterior and posterior eyes

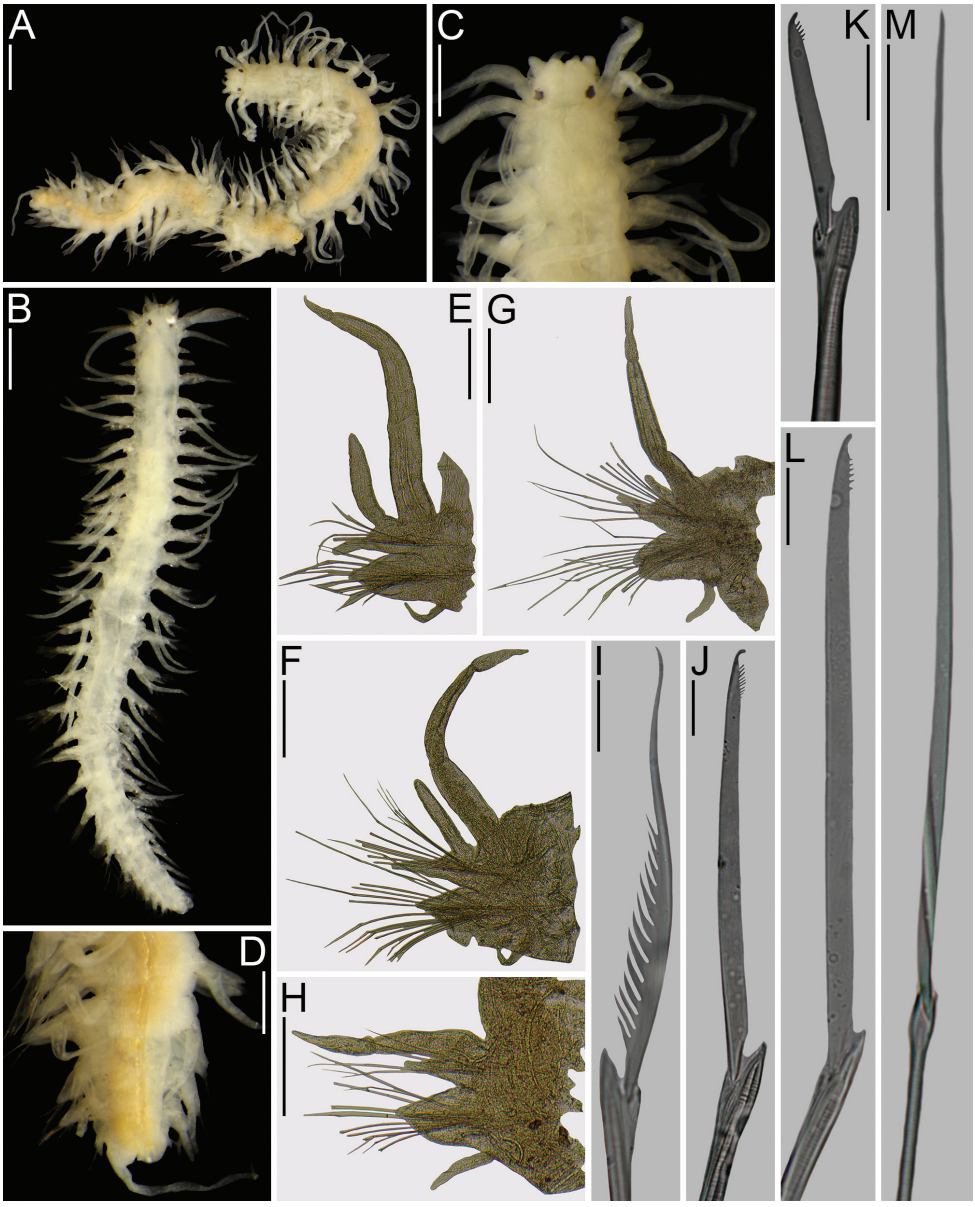

Figure 6. *Stenoninereis elisae* sp. nov. **A–M** Syntypes (USNM 55366) **A** whole specimen, dorsal view **B** whole specimens, dorsal view **C** anterior end, dorsal view **D** Posterior end, dorsal view **E** chaetiger 6, right parapodium, anterior view **F** chaetiger 16, right parapodium, anterior view **G** chaetiger 18, right parapodium, anterior view **H** chaetiger 24, right parapodium, anterior view **I** subacicular heterogomph spinigers, chaetiger 18 **J–L** subacicular heterogomph falcigers, chaetiger 18 **M** notopodial homogomph spiniger, chaetiger 49. Scale bars: 0.5 mm (**A–B**); 0.25 mm (**C**); 0.2 mm (**E–H**); 10 μm (**I–L**); 30 μm (**M**).

rounded, anterior eyes smaller than posterior ones, strongly overlapped, forming a pyriform spot (Figs 1I, 6A–C). Achaetous ring as long as first chaetiger; four pairs of anterior cirri, longest one reaching chaetiger 6, anterodorsal pair lanceolate, remaining ones subulate (Figs1I, 6A–C).

Pharynx dissected; jaws brown, translucent, 8 teeth. Pharynx surface bare.

All chaetigers with noto- and neuroaciculae; dorsal cirri cirrophores and notopodial dorsal ligules of anterior chaetigers with ciliate surface. In first two chaetigers, notopodium with a small, rounded lobe bearing notoaciculum. Neuroacicular ligule subconical, twice longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In anterior chaetigers (Figs 6E), dorsal cirrus longer than chaetiger width, excluding parapodia; cirrophore 5.5–6.0 times longer than cirrostyle, 2.6 times longer than notopodial dorsal ligule, 3 times longer than notopodial ventral ligule. Notopodial dorsal ligule digitiform, basally attached to, and 1.2 times longer than, notopodial ventral ligule; notopodial ventral ligule subconical, 2.3 times longer than wide, 1.3 times longer than neuroacicular ligule. Neuroacicular ligule subconical, 1.5 times longer than wide, 2.2 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In middle chaetigers (Figs 6F–G), dorsal cirrus longer than chaetiger width, excluding parapodia; cirrophore 2.5–3 times longer than cirrostyle, twice longer than notopodial dorsal ligule and becoming shorter toward posterior chaetigers, twice longer than notopodial ventral ligule. Notopodial dorsal ligule digitiform, as long as notopodial ventral ligule, rapidly decreasing in size toward posterior chaetigers and disappearing from chaetiger 23–25; notopodial ventral ligule subconical, twice longer than wide, 1.6 times longer than neuroacicular ligule. Neuroacicular ligule subconical, 1.2–1.4 times longer than wide, twice longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

In posterior chaetigers (Fig. 6H), dorsal cirrus as long as chaetiger width, excluding parapodia; cirrophore 1.4 times longer than cirrostyle, 1.5 times longer than notopodial ventral ligule. Notopodial dorsal ligule absent; notopodial ventral ligule subconical, twice longer than wide, as long as neuroacicular ligule. Neuroacicular ligule subconical, 1.3 times longer than wide, 1.3 times longer than ventral cirrus. Ventral cirrus subulate, cirrophore and cirrostyle indistinct.

Notochaetae sesquigomph spinigers. Neurochaetae sesquigomph spinigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial (Figs 1C, 6M) and neuropodial (Fig. 1D) supra-acicular sesquigomph spinigers pectinate, very minute teeth, disappearing toward distal end. Neuropodial heterogomph spinigers (Figs 1E, 6I) serrate, coarse teeth, larger teeth longer than blade width, 1/3 of blade edentate, subulate. Neuropodial heterogomph falcigers (Fig. 1F) with very long blades, blades increasing their length toward posterior chaetigers, blades with basal and medial teeth minute, often inconspicuous (Figs 6J–L), rarely some small teeth basally and distally (Fig. 1E); supra-acicular blades shorter than sub-acicular ones, blades of sub-acicular falcigers increasing their length from upper to lower positions in the same fascicle (Figs 6J–L).

Pygidium with two anal plate-like lobes; anal cirri as long as last five chaetigers (Fig. 6D).

Etymology. The name is after the late Dr. Elise Wesenberg-Lund, in recognition of her many works in polychaete taxonomy, especially freshwater ones, and by proposing the genus *Stenoninereis*. The name is a noun in apposition and was formed by the elision of the last vowel for euphony.

Remarks. Due to the morphological variability observed in specimens belonging to *Stenoninereis*, the designation of syntypes was preferred (ICZN 1999, Art. 72.3). *Stenoninereis elisae* sp. nov. is easily recognized by the enlarged dorsal cirri in anterior and middle chaetigers, being two or three times longer than the width of their respective segments, and by the size and proximity of the eyes resulting into a pyriform shape. The cirrophore/cirrostyle lengths ratio is also distinctive for this species because the cirrophore is longer than cirrostyle throughout the body, whereas in *S. lackeyi* comb. n., *S. martini*, and *S. tecolutlensis*, cirrostyles are longer than cirrophores in posterior chaetigers. Also, the cirrophore/cirrostyle lengths ratios in *S. elisae* sp. nov. are greater than in the other species, especially in anterior (5.5–6.0) and middle (2.5–3.0) chaetigers. Finally, the blades of the neuropodial heterogomph falcigers are denticulated, whereas in the remaining species they are smooth.

The notopodial dorsal ligules exhibit a high variation in their length as shown in the cirrophore/ notopodial dorsal and notopodial ventral ligules/notopodial dorsal ligules ratios in anterior (2.3–7.1 and 1.3–3.4, respectively) and middle (1.3–3.8 in both ratios) chaetigers. This variability in the size of the notopodial dorsal ligules was also observed in specimens of *S. lackeyi* comb. n., and *S. martini*, but the ratios are less variable.

Ecological notes

Stenoninereis species are known by living in unusual habitats and organically enriched or polluted environments. They live in inland waters such as sinkholes, marshes, mineral springs with tidal influences and freshwater inputs, often with high fluctuations in salinity and dissolved oxygen (McBee and Brehm 1979; Wenner and Beatty 1988). Also, *Stenoninereis* species have been recorded in bays associated with mangroves, reaching high population densities in some places (Ibárzabal 1997; McBee and Brehm 1979; Wenner and Beatty 1988; Williams et al. 1976); or in tidal creeks (Walton et al. 2013).

Williams et al. (1976) reported *S. martini* from Texas coasts and found some environmental differences regarding those previously reported as shown in Table 1. Hartmann-Schröder (1977) reported this species from Cuba in a sinkhole pond having brackish water with the proliferation of marine algae. Gillet (1986) reported several specimens of *S. martini* from Guadeloupe, in warm waters with low dissolved oxygen and found in places organically enriched with abundant mangrove leaves. Table 1 summarizes the environmental features where *Stenoninereis* species have been recorded; most of these records were under *S. martini*. The most remarkable ecological characteristics are the findings in warm waters, and in areas with low oxygen levels, or deprived of it, with high contents of hydrogen sulfide and solids. *Stenoninereis martini* has been

Table 1. Records and ecological notes of *Stenonereis* species. *= records in need of a new evaluation.

Species	Locality	Habitat	Inland distance	Temperature	pH	Salinity	Dissolved oxygen	Dissolved Hydrogen sulfide	Additional features	References
S. martini	Devil's Hole, Sint Maarten, Netherlands	Sinkhole pond	150 m	–	8	10.9– 13.8 ppt	–	–	Limestone area with tidal movements, *Batophora* and *Avicennia*	Wesenberg-Lund 1958
	Cenote Aerolito, Quintana Roo, Mexico*	Sinkhole	–	25–28 °C	7.25–7.42	15.8–20.41 ppt	–	–	Soft bottoms, in mangrove roots	Frontana-Uribe and Solís-Weiss 2011
S. lackeyi	Warm Mineral Springs, Florida, USA	Spring	18000 m	30 °C	7.2 ±0.2	17 ppt	0 ppt	0.162 ppm	No direct connection with the Gulf of Mexico	Hartman 1958
	Tampa Bay, Florida, USA	Bay	–	28.5 °C	7.9	24.2 ppt	–	–	Fine sand, at 0.3 m depth	Taylor 1971
	Cedar Bayou, Texas, USA (as *S. martini*)	Bay	0	30°C	8.6	17.2 ppt	3.5 ppm	–	Polluted with domestic and industrial waters	Williams et al. 1976

reported in association with *Sigambra bassi* (Gillet 1986) in Guadeloupe, and with and *Streblospio benedicti* (Ibárzabal 1997) in water with high organic enrichment in Cuba.

The presence of *Stenoninereis* species in low oxygen environments could be possible after the high vascularization shown in the dorsal cirri and notopodial dorsal ligules. Also, it is remarkable the presence of long-bladed chaetae (especially falcigers) because they can be as long as the ligules, and the enlarged dorsal cirri, which are unusual in most nereidids. These elongations could be related to a cryptic life and be regarded as troglomorphic features developed in these aphotic environments, including the almost transparent body wall, linked to living in habitats with low or no light. Moreover, the presence of *Stenoninereis* species in karstic inland environments very likely corresponds to a secondary invasion from the ocean, likely through subterranean connections, because specimens belonging to the same species found in the coasts are almost identical to inland specimens. Therefore, elongation of chaetal blades and dorsal cirri are features developed beyond subterranean environments, but aphotic ones, as already suggested for namanereidins (Conde-Vela 2017). The secondary invasion is also possible because of the high endurance to drastic changes of temperature, salinity, and oxygen availability shown by these species.

Discussion

The strongly reduced notopodia lacking dorsal cirri and dorsal ligules in the first two chaetigers is a distinctive feature of species belonging to *Stenoninereis* and *Micronereis* Claparède, 1863. They also have small body with few chaetigers, parapodial surfaces ciliated, and the absence of several parapodial structures such as the neuropodial ventral ligules. In fact, the parapodia of *Micronereis* species consist of two main acicular ligules with their respective cirri, resembling the posterior parapodia of *Stenoninereis* species. The main differences between these two genera are the presence of notopodial dorsal ligules, and that ciliated surfaces are restricted to dorsal cirrophores and notopodial dorsal ligules in *Stenoninereis*, whereas in *Micronereis* both parapodial lobes have cilia in ventral and dorsal surfaces, and notopodial dorsal ligules are absent throughout body.

The clear distinction between cirrophores and cirrostyles is also remarkable in *Stenoninereis* species, where the gymnonereidins *sensu stricto* (Santos et al. 2005) such as *Ceratocephale* Malmgren, 1865, *Gymnonereis* Horst, 1919, and *Tambalagamia* Pillai, 1961, have very similar development (pers. obs.). The cirrophores in gymnonereidins and in *Stenoninereis* species are strongly vascularized, with two main vessels running longitudinally the structure and a thick superficial tissue. Moreover, gymnonereidins and *Stenoninereis* species share the presence of cilia in cirrophores. Sometimes, the cilia are missing perhaps as a consequence of fixation, but when visible, the cilia in gymnonereidins are present in anterior and middle parapodia and even form tufts of cilia in the dorsal surface that cross each segment (Banse 1977). *Stenoninereis* species and gymnonereidins are similar in other respects such as the cleft anterior prostomial margin, and the progressive reduction of cirrophores toward posterior chaetigers.

Gymnonereidins show some relevant differences such as the presence of papillae in the pharynx oral ring, presence of neuropodial ventral ligules, double ventral cirri throughout the body, and remarkable chaetal bundles with abundant homogomph spinigers in anterior chaetigers. These features are not present in *Stenoninereis* species.

The notopodial structures are worth further comments. The vascularization of the cirrophores in *Ceratocephale*, *Gymnonereis*, and *Stenoninereis* consists in at least two thick vessels running close to the cirrophore wall, and also some slender vessels running parallel to the main ones (Fig. 1B). The inner structure of the notopodial dorsal ligules is almost identical to the one seen in cirrophores, and in both cases, a second structure running along the ligule is sometimes visible (Fig. 1B). The linking among cirrophore and notopodial dorsal cirri vessels and nerves are not clear because of the high transparency of the tissues. By its central position, the second structure shown by the cirrophores and the notopodial dorsal ligules in *Stenoninereis* could be the parapodial and notopodial dorsal ligule nerves, respectively, as observed in other nereidids (e.g. Winchell et al. 2010), but further studies are needed to elucidate the blood vessels and nerves patterning in *Stenoninereis*. A second particular feature is that the length of notopodial dorsal ligules is the most variable feature in parapodia, which could mean that this structure is muscular and contractile. Because of this, the cirrophores/notopodial dorsal ligules ratio are not used as diagnostic for these species.

Another relevant feature is the absence of neuropodial ventral ligules, which is shared with *Lycastonereis* Rao, 1981 and *Tylorrhynchus* Grube, 1866 (Conde-Vela 2019; Pettibone 1971). *Tylorrhynchus* species also lack notopodial dorsal ligules throughout the body, and both *Lycastonereis* and *Stenoninereis* species lack such ligules toward posterior chaetigers, such that the posterior parapodia are similar to those present in the posterior end of the body. Main differences and similarities among these genera are: *Lycastonereis* and *Tylorrhynchus* species have notopodial structures in chaetigers 1 and 2, papillae in pharynx, and neuroacicular ligules distally bilobated (i.e. superior and inferior lobes) in anterior chaetigers, but *Stenoninereis* species lack such features; *Stenoninereis* and *Tylorrhynchus* species have dorsal cirri with distinct cirrophores and cirrostyles, whereas in *Lycastonereis* species articulations are inconspicuous.

The phylogenetic affinities among *Ceratocephale*, *Gymnonereis*, and *Stenoninereis* was addressed by Fitzhugh (1987), and he concluded that *Stenoninereis* could be regarded as part of Gymnonereidinae by having bare pharynx and both noto- and neuroacicular in independent lobes (i.e. biramous parapodia). In the same analysis, namanereidins occupied the most basal positions in the cladogram because the character 'uniramous parapodia' was regarded as plesiomorphic, followed by *Tylorrhynchus* and *Stenoninereis* as the most basal genera with biramous parapodia and no directly related with gymnonereidins. The study by Glasby (1991) had a similar conclusion, where *Stenoninereis* was the most basal taxon with biramous parapodia, but in this case, gymnonereidins taxa were excluded. In the phylogenetic analysis by Santos et al. (2005), *Stenoninereis* appeared as the most plesiomorphic nereidid, even basal to namanereidins, whereas gymnonereidins are the most derived taxa and the sister group of the clade containing *Kinberginereis* Pettibone, 1971 and *Paraleonnates*

Khlebovich & Wu, 1962, both genera with several parapodial processes. Futures studies should be focused on clarifying the blood vessel and innervation patterning in *Stenoninereis* and allied genera, as a means to reach a better understanding of their phylogenetic affinities.

Key to species of *Stenoninereis* Wesenberg-Lund, 1958

1 Anterior prostomial margin deeply incised, dorsal prostomial groove reaching posterior pair of eyes; eyes large, covering half prostomial surface ..... ***S. tecolutlensis* de León-González & Solís-Weiss, 1997 (Tecolutla, Mexico, Gulf of Mexico)**

– Anterior prostomial margin shallowly incised, dorsal prostomial groove prostomium often inconspicuous, or not reaching anterior eyes **2**

2 Anterior chaetigers with dorsal cirrophores as long as notopodial ventral ligules ... . ***S. lackeyi* (Hartman, 1958) comb. n. (Florida, USA, Gulf of Mexico)**

– Anterior chaetigers with dorsal cirrophores at least twice longer (>2) than notopodial ventral ligules **3**

3 In anterior chaetigers, cirrophores of dorsal cirri are 2–3 times longer than cirrostyles ..... ***S. martini* Wesenberg-Lund, 1958 (Sint Maarten, Netherlands, Caribbean Sea)**

– In anterior chaetigers, cirrophores of dorsal cirri are 5.5–6.0 times longer than cirrostyles ..... ***S. elisae* sp. nov. (Rio Grande, Puerto Rico, Caribbean Sea)**

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