



## Redescription of *Neanthes micromma* Harper, 1979 (Annelida: Nereididae) based on types and additional material from Tampa Bay, Florida, USA, with a discussion of ontogenetic morphological variation

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### Abstract

Small specimens of a seemingly undescribed nereidid polychaete species from Tampa Bay, Florida, USA lacked notopodial falcigers, paragnaths and papillae on the pharynx, and dorsal ligules. Quantitative analysis of a larger size range of material showed that all specimens could be referred to *Nereis* (*Neanthes*) *micromma* Harper, 1979. The use of *Neanthes* Kinberg, 1865 as a subgenus of *Nereis* Linnaeus, 1758 is no longer accepted and this species is now formally referred to *Neanthes micromma* Harper, 1979, which is here redescribed to better account for the observed size-related variation. Contrary to the original description, in this species, notaciculae are present in chaetigers 1 and 2, but difficult to observe. Given that earlier studies have identified the potential phylogenetic significance of presence of notaciculae, it is suggested that re-evaluation of this character in similar Nereididae may assist in revising the status of the polyphyletic genus *Neanthes*.

**Key words:** dorsal ligule, morphometric, paragnath, Polychaeta, Texas

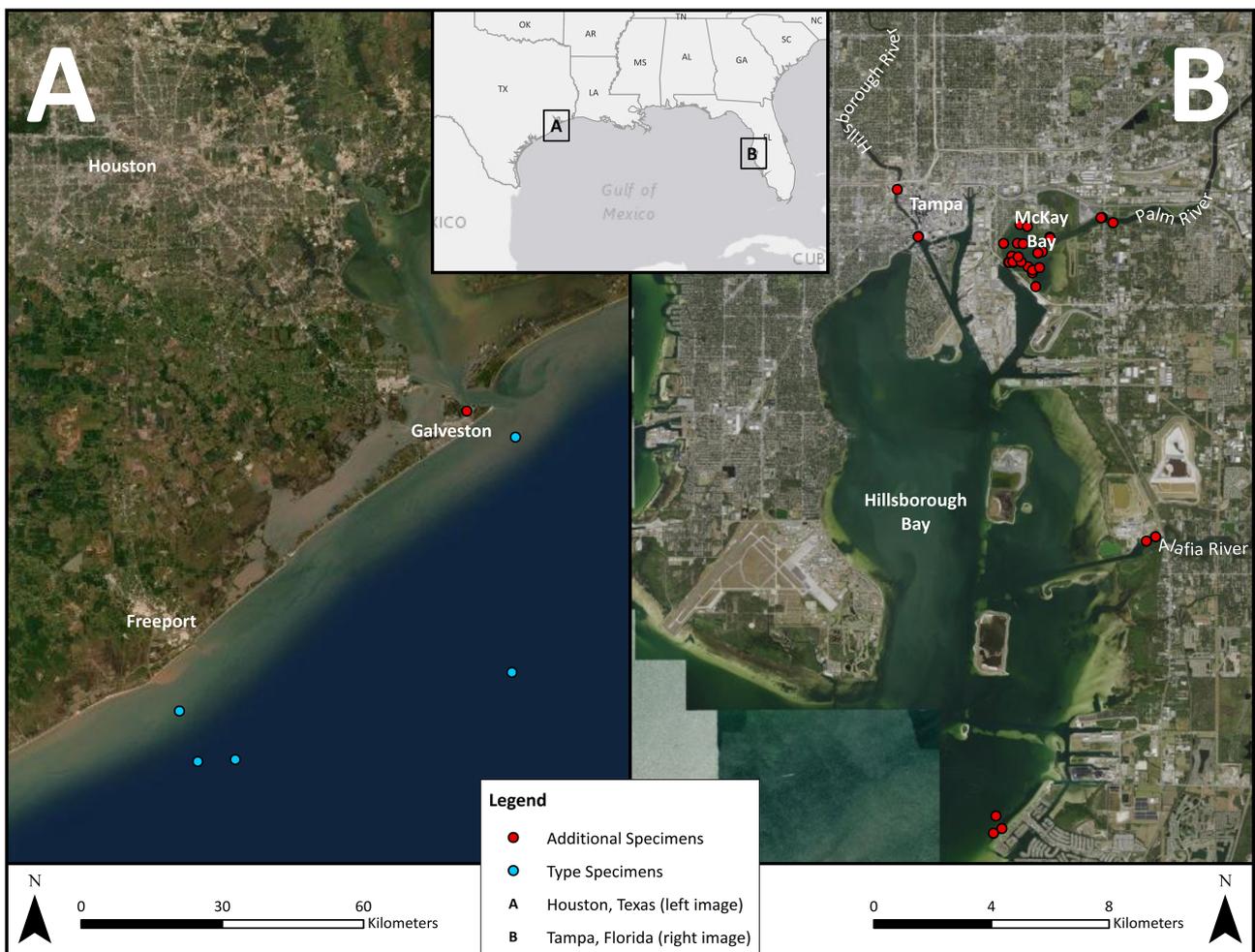
### Introduction

Long-term hydrobiological monitoring programs have been ongoing in the Tampa Bay area since 2000 by the regional water authority, Tampa Bay Water (TBW) to assess environmental impacts of surface water withdrawals and discharge from a desalination facility. Benthic macroinvertebrate samples were collected from 2000–2016 as part of these comprehensive environmental monitoring programs to assess potential impacts upon benthic community structure in several tributaries of, and areas within, Tampa Bay including the Alafia River, the Hillsborough River, McKay Bay, the Tampa Bypass Canal and just offshore of Apollo Beach near the desalination facility outfall (Fig. 1).

In many of these samples, several small polychaetes belonging to the family Nereididae were initially thought to be an undescribed species of *Nicon* Kinberg, 1865 due to the absence of paragnaths and papillae on the pharynx, dorsal ligules and notopodial falcigers. However, slightly larger specimens from subsequent collections possessed small, developing dorsal ligules and a few paragnaths on the pharynx. Comparison with common nereidid polychaetes from this area yielded an identification of *Nereis* (*Neanthes*) *micromma* Harper, 1979 originally described from offshore of Galveston, Texas. Eyes, tentacular cirri length, prostomial shape, chaetal characteristics and the neuropodial lobes all resembled *N. (Neanthes) micromma*. As the size-related variation observed in parapodial morphology and paragnath number and arrangement had not previously been reported, a redescription of *N. (Neanthes) micromma* was undertaken.

The secondary purpose of this study was to evaluate the generic placement of *N. (Neanthes) micromma*. The use of *Neanthes* Kinberg, 1865 as a subgenus of *Nereis* Linnaeus, 1758 is no longer widely accepted. In

the mid-nineteenth century, Kinberg (1865) described *Neanthes* and differentiated it from *Nereis* on the basis of having similar parapodia throughout and the presence of paragnaths on all areas of the pharynx. Other early authors preferred to include all species with conical paragnaths in *Nereis* and used informal groupings or subgenera, such as *Neanthes*, to group species sharing similar paragnath numbers and arrangement and parapodial morphology (e.g. Ehlers 1868, Claparède 1870, Grube 1874, de Saint-Joseph 1898, and Gravier 1901). Grube in Peters (1881) described a new species of *Nereis* and designated it as “*Nereis Larentukana* Grube n. sp. (Gatt. *Neanthes* KBG.)”. It is unclear from this designation whether Grube intended *Neanthes* to be the subgenus, given that he used the abbreviation of Gatt. (Gattung which translates to genus). De Saint Joseph (1898) was the earliest author we could find who more precisely indicated *Neanthes* as a subgenus of *Nereis*, and this classification was based on *Neanthes* species having paragnaths on all areas of the pharynx. Many authors followed the subgeneric designation of *Neanthes* well into the late twentieth century (e.g. Fauvel 1923, Uschakov 1965, Day 1967, Hartmann-Schröder 1971, 1975), including Harper (1979) when he originally described *N. (Neanthes) micromma*; however, a growing opposition arose to the subgeneric designation of *Neanthes* (e.g. Chamberlin 1919, Treadwell 1928, Hartman 1940, Fauchald 1977a). Hartman (1940) regarded *Nereis* and *Neanthes* as two distinct genera based on the presence (*Nereis*) and absence (*Neanthes*) of homogomph falcigers in the posterior notopodia and whether or not the notopodial preacicular lobes are elongated in the posterior chaetigers (*Neanthes*). Since Hartman’s (1940) distinction, all but four of the species with former subgeneric designations under *Nereis* have been reassigned to *Alitta* Kinberg, 1865, *Nereis*, *Neanthes*, or other genera. These four species are *N. (Neanthes) bioculata* Hartmann-Schröder, 1975; *N. (Neanthes) heteroculata* Hartmann-Schröder, 1981; *N. (Neanthes) mancorae* Berkeley & Berkeley, 1961; and *N. (Neanthes) micromma* Harper, 1979 (Read & Fauchald 2019).



**FIGURE 1.** Sample collection locations for: A, type material and additional material from Texas; B, additional material from Tampa Bay, Florida.

Upon examination of the types and additional material from Texas and Florida, *N. (Neanthes) micromma* was confirmed as a member of the genus *Neanthes* as currently defined by Sato (2013) and will be referred to herein as *Neanthes micromma* (Harper, 1979). Previous authors have followed this designation, and further support for this generic assignment is provided herein (de León-González *et al.* 1999; Dean 2001). Furthermore, the parsimony analysis conducted by Bakken & Wilson (2005) indicated that *Neanthes* is polyphyletic with characters exhibiting high levels of homoplasy. Phylogenetic and revisionary studies of the genus *Neanthes* are currently underway and the generic assignment of *N. micromma* could possibly change in the near future (Villalobos-Guerrero pers. comm. 2019).

## Materials and Methods

Benthic macroinvertebrate samples for the long-term hydrobiological monitoring programs were collected by Atkins Global (subcontractor to TBW) staff with a Young-modified Van Veen grab at multiple locations throughout Tampa Bay and its tributaries (Fig. 1). The samples were sieved with a 0.5 mm mesh sieve, fixed in 10% buffered formalin, stained with Rose Bengal, and preserved in 70% isopropyl alcohol. All macroinvertebrates were identified to the lowest possible taxonomic level and enumerated. The following physicochemical parameters were collected at each sampling station: salinity (psu), water temperature (°C), dissolved oxygen (mg/L), specific conductivity (µS/cm), pH, water depth (m), Secchi depth (m) and percent sand, silt and clay. Any polychaetes identified as *N. micromma* or possible juveniles of *N. micromma* in samples collected from 2005–2010 were reserved for this study. A total of 161 specimens from Tampa Bay were examined, along with the holotype and 31 of the 94 paratypes. The holotype and paratypes were borrowed from the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Texas A&M Marine Laboratory, Galveston, Texas (AMML); and the Allan Hancock Foundation Polychaete Collection, Natural History Museum of Los Angeles County (LACM-AHF). Only a portion of the paratypes from USNM were observed for this study. Additionally, the first author was unable to locate any of the paratype material deposited in the collections at Texas A&M University, College Station, Texas (TAMU), and only 11 of the 25 paratypes were found in the Texas A&M Marine Laboratory in Galveston, Texas (AMML).

*Neanthes micromma* specimens were examined under a Nikon stereomicroscope (SMZ800) and a Leica compound microscope (DM2000) equipped with Nomarski differential interference contrast optics (DIC). Several parapodia were removed from selected specimens, dehydrated through an ethanol series and mounted on slides in Canada Balsam thinned with xylene. Photos of these parapodia were taken with a QImaging MicroPublisher 5.0 RTV CCD camera, and depth of field was improved where necessary using Helicon Focus v6.7, for illustration purposes.

A few juvenile and adult specimens from Tampa Bay along with four of the paratypes were selected for Scanning Electron Microscopy (SEM) analysis. Specimens were dehydrated in an ethanol series ending with acetone and critically point dried with a Samdri® PVT-3B. They were mounted on stubs and coated with gold palladium in a Cressington Sputter Coater 180 Auto. Specimens were examined with a Jeol JSM-6010LA scanning electron microscope.

In order to assess ontogenetic morphological variation in *N. micromma*, specimen widths were compared to several morphological characteristics (Table 1). Widths were measured at chaetiger 5 from photos taken with SPOT 4.6 and this character will be abbreviated as W5 from this point forward. Because approximately 10% of the specimens examined from Tampa Bay were anterior fragments and had total lengths less than 20 chaetigers, the width of a more anterior chaetiger was chosen than what is typically used (chaetiger 10 or 15) in morphometric analyses (*e.g.* Orrhage & Sundberg 1990; Glasby *et al.* 2011; Villalobos-Guerrero & Carrera-Parra 2015). SigmaPlot 13 was used to conduct nonparametric Spearman's rank order correlation analyses between body width and the various morphological characteristics in order to determine which pairwise correlations were significant. Significant pairwise correlations were plotted with PRIMER v7 to further illustrate the positive or negative relationships between body width and the various morphological characteristics.

**TABLE 1.** Nonparametric Spearman's rank order correlation analyses used to assess size-related variation in various morphological characters for *Neanthes micromma* Harper. Significant correlations ( $p < 0.05$ ) are in bold.

Morphological Characters	Chaetiger 5 Width (mm)		
	Correlation Coefficient ( $\rho$ )	p-value	Number of Individuals (N)
Presence/Absence of eyes	0.0732	0.299	203
Chaetiger number that dorsal tentacular cirri extend to	0.431	<b>1.95E-10</b>	203
Presence/Absence of dorsal ligule	0.809	<b>0.000002</b>	204
Chaetiger number that dorsal ligule becomes enlarged	0.524	<b>0.000002</b>	204
Total paragnaths in Area I	0.0316	0.654	204
Total paragnaths in Area II	0.522	<b>0.000002</b>	179
Total paragnaths in Area IV	0.801	<b>0.000002</b>	180
Total paragnaths in Area VI	0.799	<b>0.000002</b>	201
Total paragnaths in Areas VII–VIII	0.755	<b>0.000002</b>	201
Presence/Absence of notacacula in far posterior chaetigers	0.144	0.311	51
Total number of chaetigers present	0.579	<b>0.0000101</b>	51

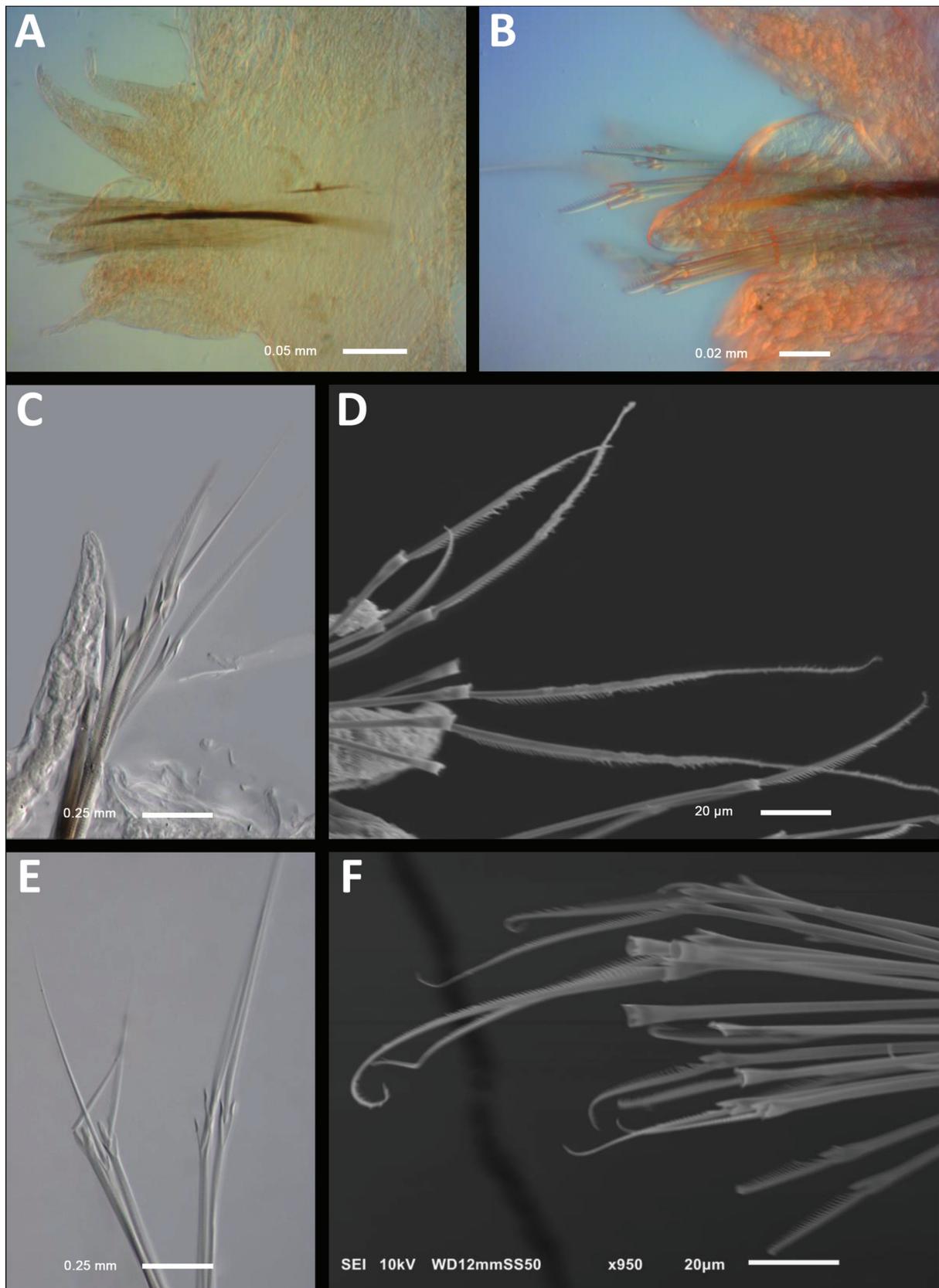
Standardized terminology of nereidid parapodial features follows Villalobos-Guerrero & Bakken (2018), while chaetal types follow those figured in Bakken & Wilson (2005, Figure 4A–R). A few of the morphological characteristics were difficult or impossible to observe in some of the specimens, so these data were not included in correlation analyses. For example, specimens from the type series of *N. micromma* with a retracted pharynx, were not dissected to preserve their integrity. Therefore, the arrangement and number of only the visible paragnaths were noted. Particularly small or damaged specimens in which the pharynx could not be dissected were also not included in the correlation analyses between paragnath number and body width.

Specimens of *N. micromma* from the Tampa Bay area were deposited at the Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM); Allan Hancock Foundation Polychaete Collection, Natural History Museum of Los Angeles County (LACM-AHF); University of Florida Museum of Natural History (FLMNH); and the first author's personal collection (JSD). Because the AMML collections are no longer being maintained, the paratype material that we used in this study was transferred to the Texas A&M University Biodiversity Research and Teaching Collection (BRTC) where it can be properly cared for. New catalog numbers are listed in the materials examined section as TAMU #-#####.

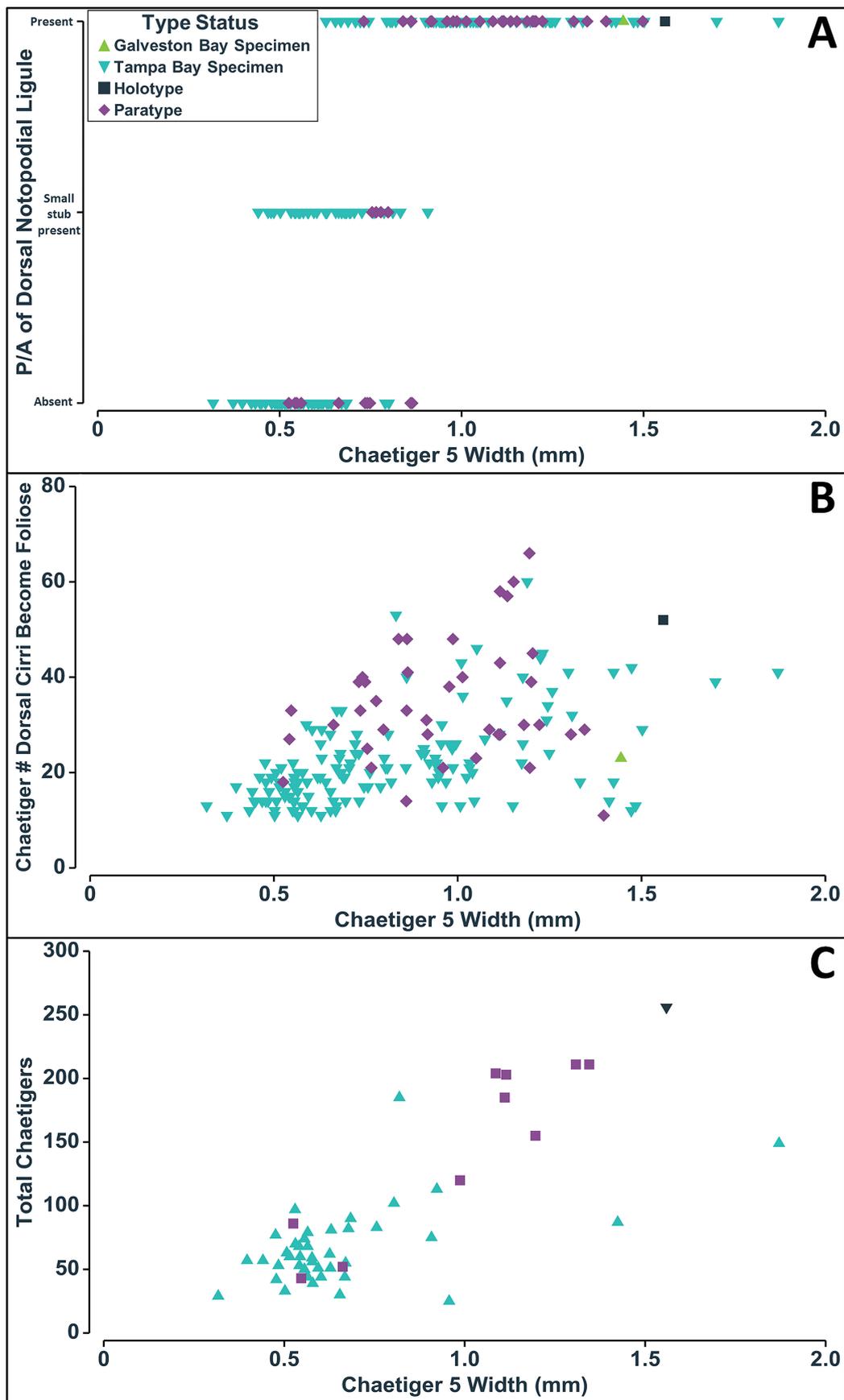
## Results

### Assessment of size-related morphological variation in *Neanthes micromma*

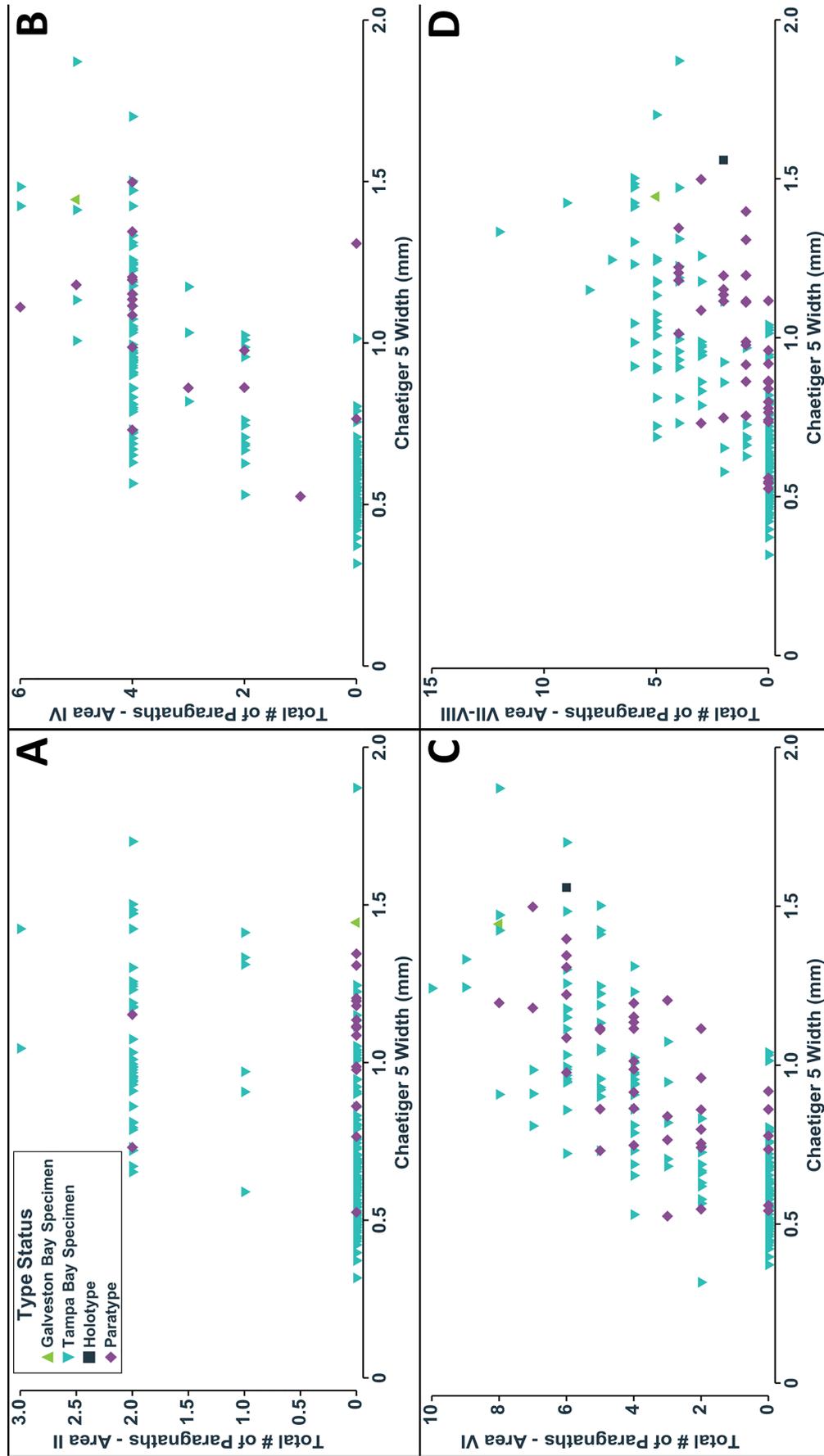
Harper (1979), Taylor (1984) and Dean (2001) reported notacaculae lacking in the first two chaetigers of *N. micromma*. This character was thought to be size-related, so it was initially included in the morphometric analysis. When examined under a dissecting microscope, notacaculae appeared absent in chaetiger 1 for all specimens; however, notacaculae could sometimes be observed deeply embedded in chaetiger 2 of the larger specimens. To further evaluate this character, first and/or second parapodia were dissected from all Tampa Bay specimens previously thought to lack notacaculae and examined under a compound microscope. Small, deeply embedded notacaculae were found consistently in chaetigers 1 and 2 for *N. micromma* (Fig. 2A); therefore, this character was excluded from further morphometric analyses. Similarly, no paragnaths were observed on Areas III and V of the pharynx for all specimens which corresponded with the original species description, so evaluation of these characteristics for size-related variation was not necessary (Harper 1979).



**FIGURE 2.** Parapodia and chaetae of *Neanthes micromma*. A, anterior view of chaetiger 1 from Alafia River specimen (JSD), DIC x20 obj.; B, anterior view of neurochaetae from chaetiger 1 of Alafia River specimen (JSD), DIC x40 obj.; C, notochaetae from paratype USNM 55576, DIC x40 obj. (2x magnification); D, SEM of notochaetae from paratype TAMU 1-3829 #6 (formerly AMML G1 #6); E, neurochaetae from paratype USNM 55576, DIC x40 obj. (2x magnification); F, SEM of neurochaetae from paratype LACM-AHF Poly 1251 #11.



**FIGURE 3.** Morphometric analyses illustrating significant correlations between body width at chaetiger 5 (W5) and: A, presence/absence of dorsal ligule; B, chaetiger number in which the dorsal ligule becomes foliose; C, total number of chaetigers in complete specimens.



**FIGURE 4.** Morphometric analyses illustrating significant correlations between body width at chaetiger 5 (W5) and: A, total number of paragnaths on Area II; B, total number of paragnaths on Area IV; C, total number of paragnaths on Area VI; D, total number of paragnaths on Area VII–VIII

Nonparametric Spearman's rank order correlation analyses indicated that the presence of eyes was not significantly correlated with size (Table 1). Eyes were absent in 37 of 203 specimens. Fading of eye pigment could be due to excessive fixation, staining or preservative as shown to occur in other polychaetes (Bick 2005).

The posterior pair of tentacular cirri varied in length, extending to chaetigers 2–6, and was significantly correlated with size, albeit slightly, given the modest correlation coefficient ( $\rho$  value) in Table 1. Variation observed in this character could be size-related, but could also be attributed to the extent of contraction of the tentacular cirri and/or the anterior chaetigers (Harper 1979).

Presence of the dorsal ligule was positively correlated with size; however, for those worms that possessed the dorsal ligule, the chaetiger number in which this ligule first appeared was not correlated with size (Table 1). Dorsal ligules were completely lacking in specimens with W5 ranging between 0.3–0.9 millimeters (mm), and in complete specimens with total number of chaetigers ranging between 29–97 (Fig. 3A). Dorsal ligules began to appear as small stubs in specimens with W5 ranging between 0.4–0.9 mm (Fig. 3A). Fully developed dorsal ligules were observed in larger specimens with W5 ranging between 0.6–2.0 mm (Fig. 3A). The dorsal ligule arose somewhere between chaetigers 3–18 despite whether it was a small stub or fully developed. Furthermore, the first appearance of an enlarged, foliaceous dorsal ligule along the anterior-posterior axis of the worm varied widely (chaetigers 11–66) and was positively correlated with size (Table 1; Fig. 3B).

Total number of paragnaths on most of the remaining areas of the pharynx of *N. micromma* specimens was significantly correlated with worm size. Total number of paragnaths on Area I was not significantly correlated with size (Table 1). Only one specimen of width 0.9 mm had one paragnath on Area I. The presence of a paragnath in Area I has not previously been reported for this species. Total number of paragnaths on Area II was positively correlated with size (Table 1). The larger specimens had more paragnaths on each side of Area I (Fig. 4A). Similarly, total number of paragnaths on Area IV was positively correlated with size as larger specimens possessed more paragnaths on each side of Area III (Table 1; Fig. 4B). Total number of paragnaths on Area VI was also positively correlated with size as larger specimens had more paragnaths in the triangle, arc or row present on each side of Area V (Table 1; Fig. 4C). Lastly, total number of paragnaths on Areas VII–VIII was positively correlated with size (Table 1; Fig. 4D). Larger specimens had more paragnaths in the original row, occasionally possessed a second anterior row with 1–5 paragnaths, and on rare occasions, possessed one more paragnath in a third or fourth anterior row.

In complete specimens, two morphological characters were compared with W5. Presence of notaciculae in far posterior chaetigers was not significantly correlated with size (Table 1). Contrastingly, total number of chaetigers was positively correlated with size, which was expected given that chaetigers are added from a prepygidial growth zone as the worm matures (Table 1; Fig. 3C; Anderson 1961).

## Systematics

### Family Nereididae de Blainville, 1818

#### *Neanthes* Kinberg, 1865

*Neanthes* Kinberg, 1865: 171; Fauchald, 1977b: 89; Wilson, 1984: 210; 1988: 5; Wu *et al.*, 1985: 143–144; Bakken & Wilson, 2005: 527; Glasby *et al.*, 2011: 363; Sato, 2013: 35.

**Type species:** *Neanthes vaalii* Kinberg, 1865 by subsequent designation. Southern Australia.

**Diagnosis** (following Glasby *et al.* 2011 & Sato 2013). Prostomium with entire anterior margin, one pair of antennae, one pair of palps. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx with conical paragnaths and occasionally smooth bar-like paragnaths on Area IV. Oral ring with conical paragnaths; paragnaths may emerge from plate-like basement. Four pairs of tentacular cirri. Parapodia biramous, except first two pairs; notaciculae present or absent on chaetigers 1 and 2. Dorsal cirrus lacking basal cirrophore. Notochaetae: homogomph spinigers. Neurochaetae minimally include homogomph spinigers and heterogomph falcigers (both dorsally) and heterogomph falcigers (ventrally); heterogomph falcigers of posterior body may show varying degrees of anchyolisation, which is the fusion of chaetal shaft and blade.

*Neanthes micromma* (Harper, 1979)

Figs 2A–F and 5A–H

*Nereis* (*Neanthes*) *micromma* Harper, 1979: 91–103, figs 1–11; Taylor, 1984: 31–16–31–17, fig 31–14; Hernández-Alcántara & Solís-Weiss, 1991: 255; de León-González *et al.*, 1999: 673; Dean, 2001: 46–47, figs 18–21.

**Type Material Examined. Holotype:** Freeport, Texas, USA, 19 km offshore on muddy sand bottom of drowned Brazos-Colorado River delta, 28°44.5'N, 95°13.2'W, 21 m, 2 December 1977 (USNM 55575). **Paratypes:** Same location and date as holotype, 17 specimens (USNM 55576, 55578), 12 specimens including 2 on SEM stubs (LACM-AHF Poly 1251), and 5 specimens including 1 on SEM stub (TAMU 1-3830, formerly AMML). Freeport, 8 km offshore on clay bottom of Brazos River subaqueous delta, 28°49.4'N, 95°19.6'W, 17 m, 15 December 1977, 1 specimen (USNM 55577). Buccaneer Oil/Gas Field, about 50 km south of Galveston, sand-mud bottom, 28°53.3'N, 94°41.5'W, 21 m, 2 December 1977, 6 specimens including 1 on SEM stub (TAMU 1-3829, formerly AMML). **Additional material examined:** McKay Bay, Tampa, Florida, USA: 27°56.235'N, 82°25.24'W, Station M1833827, 27 September 2005 (1, JSD); 27°56.06'N, 82°25.776'W, Station M2310664, 7 August 2006 (2, JSD); 27°56.373'N, 82°25.697'W, Station M1030747, 10 May 2007 (1, FLMNH 8828 + parapodial slide); 27°56.062'N, 82°25.86'W, Station M2026285, 6 August 2007 (3, LACM-AHF 12705 + parapodial slide); 27°56.162'N, 82°25.801'W, Station M1706747, 6 September 2007 (2, FLMNH 8829 + parapodial slide); 27°55.991'N, 82°25.503'W, Station M2612709, 6 September 2007 (1, JSD); 27°55.89'N, 82°25.422'W, Station M2627912, 6 November 2007 (1, LACM-AHF 12706 + parapodial slide); 27°56.473'N, 82°25.101'W, Station M1516985, 13 December 2007 (1, JSD); 27°56.059'N, 82°25.845'W, Station M2028311, 9 January 2008 (2, NTM W030109, W030110 + parapodial slide; 15, FLMNH 8830); 27°56.072'N, 82°25.779'W, Station M2308214, 9 January 2008 (1, NTM W030116 + parapodial slide; 5 including 1 on SEM stub, LACM-AHF 12707); 27°56.678'N, 82°25.651'W, Station M0435507, 25 August 2008 (1, JSD; 1, NTM W030113); 27°56.059'N, 82°25.629'W, Station M2340916, 25 August 2008 (2, NTM W030114–030115; 3, JSD); 27°56.37'N, 82°25.952'W, Station M1319893, 5 September 2008 (1 on SEM stub, FLMNH 8831); 27°56.151'N, 82°25.683'W, Station M1729594, 5 September 2008 (29 including 3 on SEM stubs, FLMNH 8832; 6, NTM W030102 + parapodial slide, W030105 + parapodial slide, W030107–W030108 + parapodial slides, W030117–W030118 + parapodial slides); 27°56.212'N, 82°25.322'W, Station M1812234, 5 September 2008 (2, JSD); 27°55.937'N, 82°25.419'W, Station M2604564, 5 September 2008 (3, LACM-AHF 12708); 27°55.666'N, 82°25.363'W, Station M3113617, 5 September 2008 (1, LACM-AHF 12709); 27°56.644'N, 82°25.515'W, Station M0724560, 14 October 2008 (3, JSD); 27°56.456'N, 82°25.096'W, Station M1519000, 14 October 2008 (1, NTM W030101; 1, JSD); 27°55.634, 82°25.593'W, Station M1404821, 3 November 2008 (1, NTM W030111; 3, FLMNH 8833); 27°55.976'N, 82°25.292'W, Station M2419985, 3 November 2008 (2, LACM-AHF 12710); 27°56.524'N, 82°24.979'W, Station M0817427, 13 January 2009 (5, LACM-AHF 12711); 27°55.76'N, 82°25.062'W, Station M3215542, 13 January 2009 (1, JSD); 27°55.993'N, 82°25.233'W, Station M2434747, 10 February 2009 (3, JSD); 27°56.573'N, 82°25.822'W, Station M0619423, 4 March 2009 (3 including 1 on SEM stub, JSD); 27°56.562'N, 82°25.231'W, Station M1137341, 4 March 2009 (1, FLMNH 8834); 27°56.314'N, 82°25.944'W, Station M1322578, 4 March 2009 (9 including 1 on SEM stub, LACM-AHF 12712); 27°56.403'N, 82°25.67'W, Station M1036669, 17 April 2009 (1, JSD); 27°56.511'N, 82°24.962'W, Station M1200601, 17 April 2009 (1, FLMNH 8835); 27°56.348'N, 82°25.176'W, Station M1502012, 17 April 2009 (1, JSD); 27°55.89'N, 82°25.247'W, Station M2930759, 4 May 2009 (1, LACM-AHF 12713); 27°56.068'N, 82°25.318'W, Station M2414852, 9 June 2009 (1, LACM-AHF 12714); 27°56.55'N, 82°25.513'W, Station M0722869, 21 July 2009 (1, JSD); 27°55.941'N, 82°25.128'W, Station M2707213, 11 February 2010 (1, LACM-AHF 12715); 27°56.277'N, 82°25.639'W, Station M1742624, 20 August 2010 (2, LACM-AHF 12716); 27°56.06'N, 82°25.763'W, Station M2316218, 17 September 2010 (1, JSD). Apollo Beach, Florida, USA: 27°46.752'N, 82°26.136'W, Station Q1-07-C1, 18 December 2006 (1, JSD); 27°46.829'N, 82°25.981'W, Station Q4-07-C3, 25 September 2007 (1, JSD + parapodial slide); 27°47.032'N, 82°26.091'W, Station Q1-09-C5, 15 December 2008 (1, NTM W030103). Alafia River, Tampa, Florida, USA: 27°51.518'N, 82°23.333'W, Station AR101083, 3 October 2007 (1, FLMNH 8836 + parapodial slide); 27°51.488'N, 82°23.278'W, Station AR101119, 8 May 2008 (2, LACM-AHF 12717); 27°51.587'N, 82°23.164'W, Station AR101318, 6 October 2008 (1, JSD); 27°51.592'N, 82°22.992'W, Station AR101625, 12 January 2009 (1 on SEM stub, JSD); 27°51.498'N, 82°22.766'W, Station AR102129, 12 January 2009 (1,

FLMNH 8837); 27°51.442'N, 82°25.318'W, Station AR101093, 11 June 2009 (2, JSD). Hillsborough River, Tampa, Florida, USA: 27°56.485'N, 82°27.509'W, Station HR100034, 5 September 2007 (5, JSD + parapodial slide); 27°56.485'N, 82°27.512'W, Station HR100038, 15 February 2008 (1, NTM W030106 + parapodial slide); 27°57.248'N, 82°27.9'W, Station HR101635, 16 July 2008 (1, NTM W030104); 27°56.479'N, 82°27.517'W, Station HR100052, 11 September 2008 (10, LACM-AHF 12718; 1, NTM W030112 + parapodial slide); 27°57.424'N, 82°27.873'W, Station HR101948, 13 January 2009 (1, LACM-AHF 12719). Palm River/Tampa Bypass Canal, Tampa, Florida, USA: 27°56.708'N, 82°23.945'W, Station PR103512, 25 August 2008 (1, JSD); 27°56.794'N, 82°24.142'W, Station PR103191, 2 September 2008 (1, LACM-AHF 12720); 27°56.788'N, 82°24.167'W, Station PR103142, 3 November 2008 (1, FLMNH 8838).

**Diagnosis (emended).** Body slender, elongate. Prostomium with short antennae; eyes visible or not, if visible, two small pairs. Upper posterior tentacular cirri twice as long as others. Pharynx with few paragnaths on areas II, IV, VI and VII–VIII, may be absent in juvenile specimens. Dorsal ligule first appears anywhere between chaetigers 3–18, absent in juveniles ( $W5 < 0.8\text{mm}$ ); in posterior segments, dorsal ligule enlarged, foliaceous, vascularized, with small subterminal dorsal cirrus. Notaculacae present from first chaetiger, lacking in far posterior parapodia.

**Redescription.** Body long; cylindrical anteriorly, somewhat dorsoventrally flattened and tapering posteriorly. Prostomium with entire anterior margin and with short tapered antennae not extending beyond palpophores. Palps with palpophore tapered, distal halves mostly retract into proximal halves (Fig. 5A). Two pairs of small eyes; anterior pair slightly arcuate, posterior pair suboval. Tentacular cirri with cirrophores; anterior pairs and ventral posterior pair subequal, reaching to chaetiger 1 or 2; posterodorsal pair twice as long as the other tentacular cirri, reaching chaetiger 3–7 depending on state of contraction of anterior segments. Pharynx with pair of toothed jaws, 6–14 denticles. Pharynx with small conical paragnaths only, no bars on Area IV. Area I: 0, rarely 1. Area II: 0–2, on each side of Area I. Area III: 0. Area IV: 0–3 in oblique row on each side of Area III. Area V: 0. Area VI: 0–6 in triangle, arch or row. Area VII–VIII: 0–5, single transverse row, occasionally 1–5 in an additional row anterior to the first row, and rarely 1 in a third and/or fourth row anteriorly (Fig. 5A, B).

Subbiramous first and second chaetigers consisting only of dorsal cirrus, notaculacae (short, deeply embedded), median ligule, neuropodial postchaetal lobe; ventral ligule, neurochaetae, and ventral cirrus, thus lacking dorsal ligule and notochaetae (Fig. 5C, 2A, B). Remaining parapodia biramous.

Dorsal ligules absent in specimens with  $W5 = 0.3\text{--}0.9\text{ mm}$ , and total chaetigers = 29–97. Dorsal ligule beginning as small stub in specimens with  $W5 = 0.4\text{--}0.9\text{ mm}$  (Fig. 5D, E). Dorsal ligule appears from chaetiger 3–18 to end of body in adults with  $W5 = 0.6\text{--}1.9\text{ mm}$ . Dorsal ligule well-developed in larger adults; smaller than dorsal cirrus on chaetigers 5–8, subequal or slightly larger to about chaetiger 20; smaller than dorsal cirrus in chaetigers 21–50, and smaller, more cirriform than subtriangular ventral ligule (Fig. 5F). Bases of the dorsal ligules become enlarged, foliaceous and vascularized from chaetigers 11–66 to posterior end. Dorsal cirri subterminally to terminally attached on the enlarged dorsal ligules (Fig. 5G).

Neuropodial prechaetal lobes absent, inferior and postchaetal lobes present only in anterior chaetigers. Postchaetal lobes small, digitiform. Inferior lobe subequal to postchaetal lobe. Ventral ligules extend beyond tips of neuropodial inferior lobes throughout. Ventral cirri single throughout, extending beyond tips of ventral ligules, subequal in posterior chaetigers.

Notochaetae appear in chaetiger 3, arranged in a line slanting downward and posteriorly above median ligule. Upper fascicles of neurochaetae immediately above and behind neuropodial inferior lobe. Lower fascicles of neurochaetae arranged in a semicircle posteriorly and ventrally to neuropodial inferior lobe. Shafts of all chaetae canaliculated. Spiniger blades range from long (dorsally) to short (ventrally) within chaetal bundles; from chaetiger 3, short-bladed spinigers consistently occur in upper neuropodial fascicles, anterior part, and lower neuropodial semicircle fascicle, below neuropodial inferior lobe.

On chaetiger 1, upper neurochaetae consisting of heterogomph falcigers with rounded tips and coarse teeth at anterior position, and homogomph spinigers at posterior position; lower neurochaetae consisting of only heterogomph falcigers with rounded tips and coarse teeth (Fig. 2B). On chaetiger 2, upper neurochaetae consisting of heterogomph spinigers with short blades at anterior position and homogomph spinigers at posterior position; lower neurochaetae consisting of heterogomph falcigers with fine teeth at inferior position and heterogomph spinigers at posterior position. On remaining anterior and median segments, notochaetae

only with homogomph spinigers; upper neurochaetae consisting of hetero- and sesquigomph spinigers with short blades in anterior position and homogomph spinigers at posterior position; lower neurochaetae consisting of heterogomph spinigers with short blades at inferior position and hetero- and sesquigomph spinigers with long blades at posterior position (Fig. 2C–F). Blades of homo-, hetero- and sesquigomph spinigers finely serrated throughout body.

Chaetae become less numerous posteriorly; separation between upper and lower fascicles of neurochaetae less distinct. Notochaetae in posterior chaetigers with 2–3 homogomph spinigers; upper neurochaetae with 1–3 long-bladed homogomph spinigers and 1–3 short-bladed sesqui- and heterogomph spinigers; lower neurochaetae with 1–4 hetero- and sesquigomph spinigers with short blades and 1–2 heterogomph falcigers. Heterogomph falcigers serrated, teeth becoming slightly shorter toward distal end, totaling approximately 15–20 teeth. Far posterior parapodia lacking notaculacae; notopodium with only enlarged, foliaceous dorsal ligule and single homogomph spiniger. Neurochaetae as on preceding posterior segments but less numerous.

Pygidium bilobed with anal cirri (Fig. 5H).

Coloration and pigmentation patterns in living, preserved and Rose Bengal stained specimens as in Harper (1979).

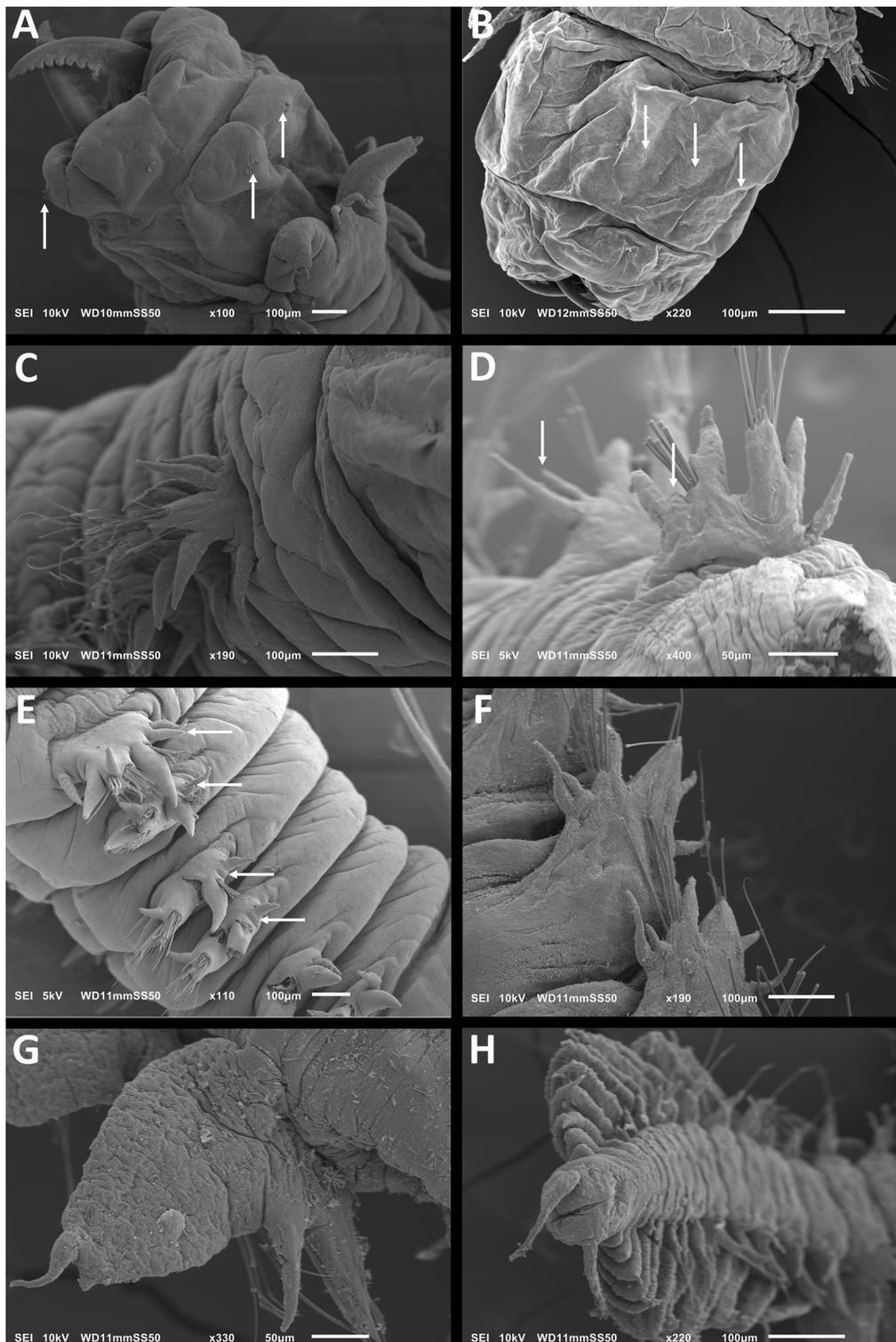
Female epitoke morphology (early stage). Only one specimen. Body regions: pre-natatory, chaetigers 1–16; natatory, chaetigers 17–48; post-natatory, chaetiger 49 to end of fragment. Eyes enlarged, anterior pair oval, posterior pair transversely teardrop shape. Dorsal ligule first present from chaetiger 3, longer than dorsal cirrus from approximately chaetiger 7–40, thereafter shorter than dorsal cirrus and enlarged, foliaceous toward posterior end. Neuropodial postchaetal lobe transitions from a conical lobe to an enlarged and rounded lobe from chaetigers 17–50, and then reverts to a small, indistinct conical lobe. Typical atoke chaetae present, epitoke chaetae absent. Eggs observed through body wall.

**Distribution.** This species is widely distributed throughout shallow waters of the Gulf of Mexico (Harper 1979; Taylor 1984; de León-González *et al.* 1999). In this study, *N. micromma* was collected from locations throughout Tampa Bay and across seasons (Fig. 1; Table 2). *Neanthes micromma* has also been reported from the Gulf of California and the Pacific coast of Costa Rica in similar depths and sedimentary conditions (Hernández-Alcántara & Solís-Weiss 1991; Dean 2001). Because *N. micromma* has been reported from both the Pacific and Gulf locations, it could be widespread, or endemic to either region; the presence of cryptic species should not be ruled out. Phylogenetic and more detailed morphological analyses of material from both locations are needed to determine if cryptic species are present and, if so, to what geographical extent.

Densities ranged between 25 and 875 individuals per square meter. Higher densities were observed during late summer and early fall which corresponded to the conclusion of the local wet season (Table 2). A single heteronereid was observed during late summer. A secondary peak in densities occurred during the spring and this bimodal annual trend was also observed by Harper (1979). As with Harper's study, no heteronereids were observed prior to the spring peak in population numbers, but heteronereids were observed prior to the late summer/early fall peak in densities. Harper (1979) speculated that the lower densities observed during the winter could be due to the worms burrowing deeper into the sediment to avoid the colder temperatures of the upper sediment layers, thus becoming inaccessible to the sampling gear.

**TABLE 2.** Densities of *Neanthes micromma* Harper and sediment and bottom water quality data for the Tampa Bay sampling locations.

Descriptive Statistics	Density (# individuals/m <sup>2</sup> )	% Sand	% Silt	% Clay	Depth (m)	Secchi Depth (m)	Dissolved Oxygen (mg/L)	pH	Salinity (psu)	Water Temperature (°C)
Minimum	25	52.2	3	0.8	0.2	0.2	0.35	6.41	22.84	14.06
Maximum	875	96.3	41.8	6.9	4.8	2.5	9.05	8.12	32.67	31.78
Mean	75.94	82.04	14.07	3.90	2.10	1.15	5.08	7.80	28.17	24.64
Standard Deviation	133.19	9.49	8.15	1.57	1.22	0.46	2.19	0.26	2.57	5.28



**FIGURE 5.** SEM of various structures of *Neanthes micromma*. A, dorsolateral view of everted pharynx and prostomium in paratype TAMU 1-3830 #4 (formerly AMML 10B3 #4) with arrows pointing to paragnaths; B, ventral view of everted pharynx from a Tampa Bay specimen with arrows pointing to paragnaths (FLMNH 8832); C, anterior view of chaetigers 1–4 in paratype LACM-AHF Poly 1251 #7; D, anterior view of developing dorsal ligule in chaetigers 8–9 of a juvenile specimen from Tampa Bay (JSD) with arrows pointing to dorsal ligules; E, lateral view of chaetigers 9–14 from a Tampa Bay specimen illustrating development of a dorsal ligule from right to left along anterior-posterior axis of worm (FLMNH 8832) with arrows pointing to developing dorsal ligules; F, posterior view of mid-body chaetigers in paratype LACM-AHF Poly 1251 #7; G, anterior view of enlarged dorsal ligule from posterior end of paratype TAMU 1-3830 #4 (formerly AMML 10B3 #4); H, posterior end and pygidium of paratype LACM-AHF Poly 1251 #7.

**Habitat.** In this study, *N. micromma* resided in shallow (<5 m), polyhaline waters throughout Tampa Bay. This species tolerated a wide range of bottom dissolved oxygen levels (0.35–9.05 mg/L), and seasonal fluctuations in bottom water temperatures (14.1–31.8°C). Secchi depth (m) and pH were relatively stable across seasons (Table 2). Sediments consisted mostly of sand and silt with a fine percentage of clays (Table 2).

## Discussion

On average, parapodial lobes and ligules of *N. micromma* reached the adult complement at the 62-chaetiger stage which is much later than reports for other nereidid species. Dorsal ligules appeared at the 11-chaetiger stage in *Laeonereis culveri* (Webster, 1879) and the parapodial lobes matched the adult complement at the 19-chaetiger stage (Mazurkiewicz 2009). Similarly, *Nereis pelagica* Linnaeus, 1758 possessed all parapodial lobes at the 21-chaetiger stage (Wilson 1932). Developmental studies on *Alitta virens* (Sars, 1835) (as *Nereis virens*) indicated that the dorsal cirri appeared earlier than the dorsal ligules, the latter arose during the 11-chaetiger stage, and all parapodial lobes were fully developed by the 40-chaetiger stage (Bass & Brafield 1972). *Nereis grubei* (Kinberg, 1865) exhibited a slightly later development of the dorsal ligule at the 36-chaetiger stage (Reish 1954). *Neanthes bassi* Wilson, 1984, *N. flindersi* Wilson, 1984, *N. kerguelensis* (McIntosh, 1885) and *N. vaalii* Kinberg, 1865 exhibited late development of prechaetal notopodial and postchaetal neuropodial lobes for body widths < 1–2 mm (Wilson 1984). These body widths are similar to the widths attained by *N. micromma* at the stage when the dorsal ligule was fully developed. Late development of the dorsal ligule in *N. micromma* has previously been unreported and is an important feature to consider when identifying juvenile specimens in order to avoid misidentifications.

*Neanthes micromma* also exhibited late development of paragnaths on the pharynx. In this study, the minimum W5 in which paragnaths were visible with standard light microscopy was 0.4 mm. This specimen was not complete, so the total number of chaetigers corresponding with this width could not be determined. Of the complete specimens observed in this study, the smallest W5 that paragnaths were observed was 0.4 mm, and this specimen had a total length of 57 chaetigers. Development of paragnaths in *A. virens* occurred at the 13-chaetiger stage and reached the adult complement at the 40-chaetiger stage (Bass & Brafield 1972). Paragnaths began to appear in *Nereis riisei* Grube & Ørsted in Grube, 1858 at the 24-chaetiger stage (Zottoli & Long 1998). Variation observed in paragnath development across species could be due to several factors including size and age of the worm, feeding mode, environmental effects, and genetic determination (Barnes & Head 1977; Barnes 1978). While no other ecological, environmental or genetic factors were tested in this study, the total number of paragnaths in various areas of the pharynx for *N. micromma* was strongly correlated with size, thereby indicating level of maturity was a primary factor in paragnath development.

*Neanthes* as a subgenus of *Nereis* is no longer widely accepted, so the generic placement of *N. (Neanthes) micromma* was evaluated herein. Bakken & Wilson (2005) provided a broad diagnosis for *Neanthes* but recognized that it is polyphyletic as currently defined. Sato (2013) revised the diagnosis of *Neanthes* to allow for the presence of notacaculae in chaetigers 1 and 2 based on what he observed in *Neanthes succinea* (Leuckhart, 1847). All of the morphological characteristics of this species fit the current diagnosis for *Neanthes* provided by Sato (2013); however, it differs substantially from the type species, *N. vaalii* Kinberg, 1865 in the form and arrangement of notopodial lobes and possession of notacaculae in chaetigers 1 and 2. The enlarged, foliaceous dorsal ligules in the posterior segments of *N. micromma* are similar to those in the genus *Alitta*, but it differs from the diagnosis of *Alitta* given by Villalobos-Guerrero & Carrera-Parra (2015) in lacking a well-developed notopodial prechaetal lobe and neuropodial postchaetal lobe, and possessing notacaculae in chaetigers 1 and 2. As shown in this study, parapodia should be dissected and examined under high magnification in order to reliably assess whether notacaculae are present. Notacaculae were deeply embedded, especially in chaetiger 1, in the parapodia of *N. micromma* (Fig. 2A). Re-evaluating this character for the type species and other species within *Neanthes*, and even across genera within Nereididae, should assist in resolving the polyphyletic status of *Neanthes*. Until the polyphyletic status is resolved, this species is confirmed herein as a member of the genus *Neanthes* Kinberg, 1865, and thus properly cited as *Neanthes micromma* (Harper, 1979).

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