

Original Article

*These authors contributed equally to this work.

Cite this article: Villalobos-Guerrero TF, Park T, 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. <https://doi.org/10.1017/S0025315421000126>

Received: 11 August 2020

Revised: 11 January 2021

Accepted: 28 January 2021

First published online: 10 March 2021

Key words:

DNA; morphology; *Neanthes*; new combination; *Perinereis aibuhitensis*; pharynx; semi-terrestrial; synonymy; taxonomy

Author for correspondence:

Tulio F. Villalobos-Guerrero,
E-mail: tulio1786@msn.com

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

Tulio F. Villalobos-Guerrero^{1,2,*} , Taeseo Park^{3,*} and Izwandy Idris¹

¹South China Sea Repository & Reference Centre, Institute of Oceanography & Environment, Universiti Malaysia Terengganu, 21030, Kuala Nerus, Terengganu, Malaysia; ²Departamento de Sistemática y Ecología Acuática, El Colegio de la Frontera Sur, Chetumal, Quintana Roo, 77000, Mexico and ³Overseas Biological Resources Team, National Institute of Biological Resources, Incheon, 22689, Korea

Abstract

The present study reviews *Perinereis* Group 2 species from the Eastern and South-eastern Asian seas based on morphological analysis of the types, non-types and original descriptions, and the use of molecular evidence (COI and 16S rDNA) from newly collected material. These species are characterized by having two bar-shaped paragnaths on pharyngeal area VI, which are often deemed conical when small and pointed, triggering misidentifications as to *Neanthes* species. New terminology and definition for this particular type of bars are proposed, and the generic position of some resembling *Neanthes* species is also re-assessed. Five species are transferred to *Perinereis*: *Perinereis babuzai* comb. nov., *P. belawanensis* comb. nov., *P. kinmensis* comb. nov., *P. shigungensis* comb. nov. and *P. vitabunda* comb. nov. ‘*Perinereis aibuhitensis*’ species group is newly proposed by encompassing species having proximal dorsal ligule similar throughout the body, dorsal cirri short, and blades of heterogomph falcigers straight with long terminal tooth forming a distinct tendon. *Perinereis belawanensis* comb. nov., *P. linea* and *P. vitabunda* comb. nov. are redescribed. *Perinereis linea* is regarded as a senior synonym of *Nereis* (*Neanthes*) *orientalis* and *Perinereis vancaurica tetradentata* based on type material, whereas its exotic status in the Mediterranean Sea is questioned. An identification key to all currently valid species within *Perinereis* Group 2 is also provided.

Introduction

Among Nereididae de Blainville, 1818, *Perinereis* Kinberg, 1865 is the second most species-rich genus with 89 valid taxa (Bonyadi-Naeini *et al.*, 2017; Park & Kim, 2017; Read & Fauchald, 2018a; Villalobos-Guerrero, 2019). The species have a broad ecological distribution ranging from supra-littoral (Wu *et al.*, 1985) to abyssal zones (deepest record about 3900 m depth; Faulwetter *et al.*, 2017), although they mainly inhabit shallow waters with sandy to muddy bottoms, dwelling among sessile organisms, rock crevices (Hutchings *et al.*, 1991; Tanaka, 2016), and fouling communities (Villalobos-Guerrero & Tovar-Hernández, 2014).

Perinereis is a polyphyletic genus and cannot currently be accurately diagnosed (Bakken & Wilson, 2005). Many authors have provided instead artificial groupings to assist identification of species. The number and type of paragnaths on areas V, VI, or both, were the primary characters proposed for groups in *Perinereis*, followed by the dorsal ligule development in posterior parapodia, the size of dorsal cirri, or the number of paragnaths on area I (e.g. Kinberg, 1865; Grube, 1878; Horst, 1889). Nonetheless, the most recent proposal on *Perinereis* species groups considered the number of transverse bars on area VI (Groups 1–3) and the expansion of the dorsal ligule in posterior chaetigers (subgroups A and B) (Hutchings *et al.*, 1991). These groupings by Hutchings *et al.* (1991) have been followed ever since (e.g. Wilson & Glasby, 1993; de León-González & Goethel, 2013; Darbyshire, 2014).

Perinereis species in Groups 2 and 3 *sensu* Hutchings *et al.* (1991) (hereafter abridged as G2 and G3, respectively) present more distinct differences to the type species *P. novaeollandiae* Kinberg, 1865 [= *P. amblyodonta* (Schmarda, 1861) *fade* Ehlers, 1904]. Those species in G3, viz. the ‘*Perinereis nuntia*’ species complex, have been pointed out in detail (Wilson & Glasby, 1993; Glasby & Hsieh, 2006; Villalobos-Guerrero, 2019). G2 is characterized by having species with two bar-shaped paragnaths on area VI and dorsal ligules either not greatly (subgroup 2A) or greatly (subgroup 2B) expanded in posterior parapodia (Hutchings *et al.*, 1991). Subgroup 2A species is the best represented in G2 and more widely distributed, in contrast to subgroup 2B initially proposed without members (Hutchings *et al.*, 1991) but encompassing a few species known nowadays only from Tropical America (see de León-González *et al.*, 2020). In the Eastern and South-eastern Asian seas, four G2 species were proposed: *Perinereis aibuhitensis* (Grube, 1878) from the Philippines, *P. linea* (Treadwell, 1936) from China, *P. singaporiensis* (Grube, 1878) from Singapore, and *P. vancaurica* (Ehlers, 1868) from the Nicobar Islands.



The present study aims to review the *Perinereis* species of artificial group G2 *sensu* Hutchings *et al.* (1991) from the Eastern and South-eastern Asian regions and identify additional species of *Perinereis* and *Neanthes* Kinberg, 1865 which belong in this group. Several species have been redescribed and their generic classification re-assessed. Where molecular data were available, the species identity of some problematic taxa have also been re-evaluated.

Materials and methods

Morphological observation

The type material examined in this study are deposited in the following zoological museums or institutions: Museum für Naturkunde, Berlin, Germany (ZMB); National Institute of Biological Resources, Incheon, Korea (NIBR); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); National Museum of Nature and Science, Tsukuba Research Departments, Tsukuba, Japan (NSMT); Phyletisches Museum Jena, Friedrich-Schiller-Universität, Jena, Germany (PMJ).

Total length (LT), length from the distal end of prostomium to chaetiger 15 (L15), and body width at chaetiger 15 excluding parapodia (W15) were measured, and the total number of chaetigers was counted for complete specimens. Paragnaths of paired and unpaired areas in the pharynx and the number of teeth on the jaws were counted. Paired areas in pharynx were indicated as 'a' for left and 'b' for right. The observation of features on non-everted pharynx required, when permitted, a longitudinal dissection in the mid-ventral oral region. Parapodia were dissected and mounted on glass slides to examine parapodial features. Decimal numbers were used for practical purposes when measurements between two structures exceeded one unit (e.g. 1.2 times, 2.5 times, twice); whereas, written fractions were used when those measurements were less than one unit (e.g. half, two-thirds, four-fifths).

Light microscopy observations were made using both stereo and compound microscopes. Specimens were photographed using a digital camera (Canon EOS T6i), which was mounted on each of the microscopes with a portable microscope adaptor; around 15–20 photos were stacked to improve the depth of field using Helicon Focus® 6 (Method C). The figures' background was cleaned, darkened or lightened, and the final figures were assembled in plates using Adobe Photoshop® CS6. Drawings were prepared with a camera lucida attached to a stereoscopic microscope (Nikon SMZ1500). Parapodia were shown in anterior views unless otherwise stated.

In the descriptions, the described specimen's character information was given first, followed by variation values in parentheses for the remaining examined material. The relative extension of parapodial structures and the relative width of ligules and lobes were described following recent studies (Conde-Vela & Salazar-Vallejo, 2015; Villalobos-Guerrero & Carrera-Parra, 2015; Conde-Vela, 2018). However, the length of dorsal cirri was measured in comparison with the full length of the proximal lobe of dorsal ligules (hereinafter proximal dorsal ligule); whereas, the length of the distal lobe of dorsal ligules (hereinafter distal dorsal ligule) was measured regarding the length of proximal dorsal ligules (Villalobos-Guerrero, 2019).

The atoke and epitoke nereidid parapodial terminology by Villalobos-Guerrero & Bakken (2018), which was modified from Hylleberg *et al.* (1986) and Bakken & Wilson (2005), is followed. The standardized definitions of the articulations of chaetae proposed by Villalobos-Guerrero & Bakken (2018) were used. The size of falcigers' blade (*b/a* ratio) and the length of its serrated edge concerning the total blade length were described following

Bakken & Wilson (2005) and Glasby & Hsieh (2006), respectively. In epitoke specimens, when available, the first natatory chaetiger was determined by the starting chaetiger with an additional parapodial lobe, particularly the lower lobe of ventral cirri cirrophore; other structures such as the natatory chaetae or the expanded neuropodial postchaetal lobe appear later.

The ridges' arrangement at dorsal areas of the oral ring of pharynx, i.e. areas VI–V–VI ridge pattern, is based from Villalobos-Guerrero (2019). Jansonius & Craig's (1971) nomenclature terminology of jaws and paragnaths by Bakken *et al.* (2009) were used. The scheme of describing the paragnaths' arrangement on areas VII–VIII, and the partially readapted terminology of bar-shaped paragnaths proposed by Conde-Vela (2018) is followed. Four types of rectangular-base paragnaths are recognized: (1) Smooth bars, (2) shield-shaped bars, (3) pointed bars (P-bars) and (4) crescent-shaped bars (Bakken *et al.*, 2009; Conde-Vela, 2018). We adopt the improved terminology of paragnaths' parts (Conde-Vela, 2018) but propose an additional term for describing the different shapes and stoutness of bars on area VI of the *Perinereis* G2 members exclusively, the (5) broad-petite bars (Figures 1A–L). This bar-shaped paragnath is stout, with a base ovoid to ellipsoid (up to 3 times wider than long; Figure 1B, E, F, H, K, L) and straight in its inferior edge (Figure 1A, C, D, G, I, J); the body has adjacent sides of similar size (Figure 1A, D, G, J) or sometimes slightly skewed to a flank; and the tip can be pointed (Figure 1B, C) or blunt (Figure 1E, F, H, I, K, L). This broad-petite bar sometimes has a conical appearance in anterior view (Figure 1A, C) with an ovoid base in superior view (Figure 1B). It has been usually confused with the conical paragnaths of *Neanthes* species (see Horst, 1924; Wu *et al.*, 1985; Hutchings *et al.*, 1991; Lee *et al.*, 1992), which has rendered genus misplacements and species misidentifications. It is likely that variations of these paragnaths, such as the wear of tip, depend on the specimens' maturity or the utilization of the paragnaths themselves during feeding or digging behaviour. The broad-petite bars may have a melted base (Figure 1F, L) similar to that described by Bakken *et al.* (2009) and redefined by Glasby *et al.* (2011); both atoke and epitoke individuals may present this melting, and it is thus unrelated to the reproductive stage.

DNA extraction, PCR amplification and molecular analysis

Partial sequences of two DNA barcoding gene regions: mitochondrial cytochrome *c* oxidase subunit I (COI) and mitochondrial 16S ribosomal DNA (16S rDNA), were obtained to examine the genetic distance between *Perinereis lineata* and *P. aibuhitensis*. Topotype specimens of *P. aibuhitensis* and non-type specimens of *P. lineata* were used for DNA sequencing. Another four *Perinereis* species were also included for in-group comparison: *Perinereis anderssoni* Kinberg, 1865 from Brazil, *P. euiini* Park & Kim, 2017 from Korea, *P. vallata* (Grube & Kröyer in Grube, 1858) from Australia and *P. vancaurica* (Ehlers, 1868) from Australia, whereas *Hediste atoka* Sato & Nakashima, 2003 from Japan was utilized as outgroup. Several sequences of COI and 16S rDNA genes utilized in the present study are newly sequenced from specimens deposited in NIBR (Table 1). In contrast, a few others were mined from GenBank based upon the following criteria: (1) DNA sequence was obtained from type locality or at least close to the type locality of each species, (2) DNA sequence was obtained from specimens identified by nereidid taxonomists (Table 1).

Genomic DNA was extracted from the ventral part of the worm's soft tissue using the DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. PCR amplifications were conducted using gene-specific primer sets (Table 2). PCR thermal cycling condition for COI

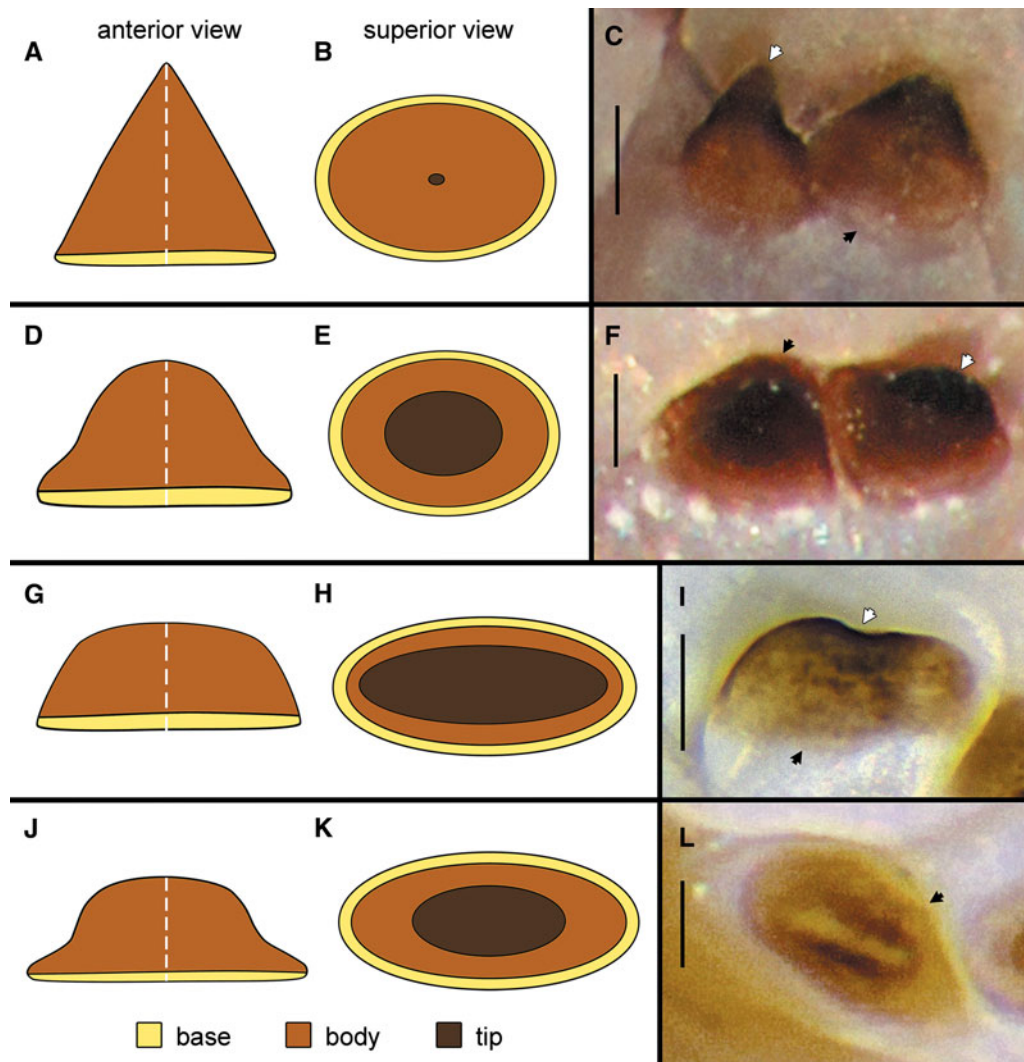


Fig. 1. Different broad-petite bar-shaped paragnaths on area VI of some *Perinereis* species belonging to Group 2A: (A–C) *P. belawanensis* (Pflugfelder, 1933) comb. nov.; (D–F) *P. vitabunda* (Pflugfelder, 1933) comb. nov.; (G–L) *P. linea* (Treadwell, 1936) ((G–I), holotype of *Nereis (Neanthes) orientalis* Treadwell, 1936; (J–L) holotype of *Nereis (Neanthes) linea*). (A, C, D, G, I, J) Anterior view of broad-petite paragnaths; (B, E, F, H, K, L) superior view of broad-petite paragnaths. Drawings indicate the tip (dark brown), body (light brown) and base (yellow) of broad-petite paragnaths. Arrows: white, tip of bar; black, base of bar. Scale bars: (C) 0.3 mm; (F) 0.2 mm; (I, L) 1 mm; remaining figures without scales.

followed Park & Kim (2017) and 16S rDNA followed Tosuji *et al.* (2019). Amplified PCR products were purified using the QIAquick PCR purification Kit (Qiagen, Valencia, CA, USA). The sequencing reaction was conducted with BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) using each of the same primers. The product was then analysed using an ABI 3730 sequencer (Applied Biosystems, Foster City, CA, USA). Sequences obtained were aligned using MUSCLE implemented in Geneious Prime 2020.1.2. Pairwise distances were calculated using the Kimura-2-parameter model (Kimura, 1980). Dendrograms were constructed using neighbour-joining (NJ) with 1000 times bootstrap resampling in MEGA ver. 10.1.8. for macOS (Stecher *et al.*, 2020).

Literature review

The list of valid species of *Neanthes* Kinberg, 1865 available in the World Polychaeta Database (Read & Fauchald, 2018b) was examined and compared with those lists formerly performed (Hartman, 1959; Fauchald, 1972; Wilson, 1984) or with other more recent literatures to discover those *Perinereis* G2 species currently hidden in *Neanthes*. The original descriptions, redescrptions, or both, of the 79 currently valid species of *Neanthes*

were gathered and analysed. These literatures were only taken into account to disregard possible misidentifications based upon non-type materials.

Results

The definition of a novel type of short bar-shaped paragnath in this study, i.e. broad-petite bars, has permitted a re-evaluation of some *Neanthes* species' generic placement traditionally considered as having two 'conical' paragnaths on area VI in a single transverse row.

Two semi-terrestrial *Neanthes* species from the Strait of Malacca, *N. belawanensis* (Pflugfelder, 1933) and *N. vitabunda* (Pflugfelder, 1933), and three marine species recently described from Taiwan, *N. babuzai* Hsueh, 2019, *N. kinmenensis* Hsueh, 2019 and *N. shigungensis* Hsueh, 2019, were found with the features of the *Perinereis* subgroup 2A *sensu* Hutchings *et al.* (1991): two bar-shaped paragnaths on area VI and proximal dorsal ligule not expanded. Interestingly, all these species also resemble each other by sharing (1) proximal dorsal ligule subequal or becoming shorter towards posterior end, (2) dorsal cirri short, and (3) blades of heterogomph falcigers straight with long terminal tooth forming a tendon. Therefore, *P. babuzai* comb. nov., *P.*

Table 1. Information on voucher specimens and GenBank accession numbers for molecular analysis

Species	Abbreviation	Voucher No.	Locality	Reference	GenBank accession	
					COI	16S rDNA
<i>Perinereis linea</i> (Treadwell, 1936)	Pljeongok2	NIBRIV0000810291	Korea	Present study	MT511711	MT540476
	Pljeongok3				MT511712	MT540477
	Paja1	NIBRIV0000810299	Possibly Korea or China (purchased, fishing-bait shop in Japan)	Present study	MT511713	MT540478
	Paja3				MT511714	MT540479
	Paja4				MT511715	MT540480
<i>Perinereis aibuhitensis</i> (Grube, 1878)	PaPaM1	NIBRIV0000787926	Palau (type locality)	Present study	MT511716	MT540481
	PaPaM2				MT511717	MT540482
	PaPaM3				MT511718	MT540483
<i>Perinereis vancaurica</i> (Ehlers, 1868)	PvD1	NIBRIV0000810300	Australia	Present study	MT511719	MT540484
	PvD2				MT511720	MT540485
<i>Perinereis anderssoni</i> Kinberg, 1865	Pander1	–	Brazil	Paiva <i>et al.</i> (2019)	MH143520	–
	Pander2	–			MH143522	–
	Pander4	–			–	MH128343
	Pander5	–			–	MH128340
<i>Perinereis euiini</i> Park & Kim, 2017	Peuiini1	NIBRIV0000502105-Pcgeoje1	Korea	Park & Kim (2017), present	KY249122	MT540486
	Peuiini2	NIBRIV0000502105-Pcgeoje2			KY249124	MT540487
<i>Perinereis vallata</i> (Grube & Kröyer in Grube, 1858)	Pval1	NIBRIV0000810301	Australia	Present study	MT511721	MT540488
	Pval2				MT511722	MT540489
* <i>Hediste atoka</i> Sato & Nakashima, 2003	Hatoka	–	Japan	Tosuji & Sato (2010)	AB603887	–
		–		Tosuji & Sato (2012)	–	AB703096

*Taxon used as outgroup for rooting the tree.

Table 2. Information on primers used in this study

DNA region	Name	Sequence (5'–3')	Reference
COI	polyLCO	GAYTATWTTCAACAATACATAAAGATATTGG	Carr <i>et al.</i> (2011)
	polyHCO	TAMACTTCWGGGTGACCAARAATCA	
16S rDNA	16SarL	CGCCTGTTTATCAAAAACAT	Palumbi (1996)
	16SbrH	CCGGTCTGAACTCAGATCACGT	

belawanensis comb. nov., *P. kinmenensis* comb. nov., *P. shigunensis* comb. nov. and *P. vitabunda* comb. nov. are thus transferred to *Perinereis* and placed within the newly proposed '*P. aibuhitensis*' species group, which also comprises other species, particularly the stem species *P. aibuhitensis* and *P. lineata*. They were all compared with other *Perinereis* species of the subgroup 2A based upon several pharyngeal and parapodial features. *Perinereis belawanensis* comb. nov. and *P. vitabunda* comb. nov. are redescribed in detail and distinguished from the similar

species *P. aibuhitensis*; whereas a diagnosis of Hsueh's species transferred to *Perinereis* is provided based on the original descriptions.

Moreover, *P. lineata* that has been misidentified in the literature with *P. aibuhitensis* was also redescribed. Morphological comparisons based on the type specimens, non-type materials, or both, reveal that the species can be distinguished from *P. aibuhitensis* by the patterns of the ridge of areas VI–V–VI, the arrangement of bands of paragnaths on areas VII–VIII, the presence of lateral

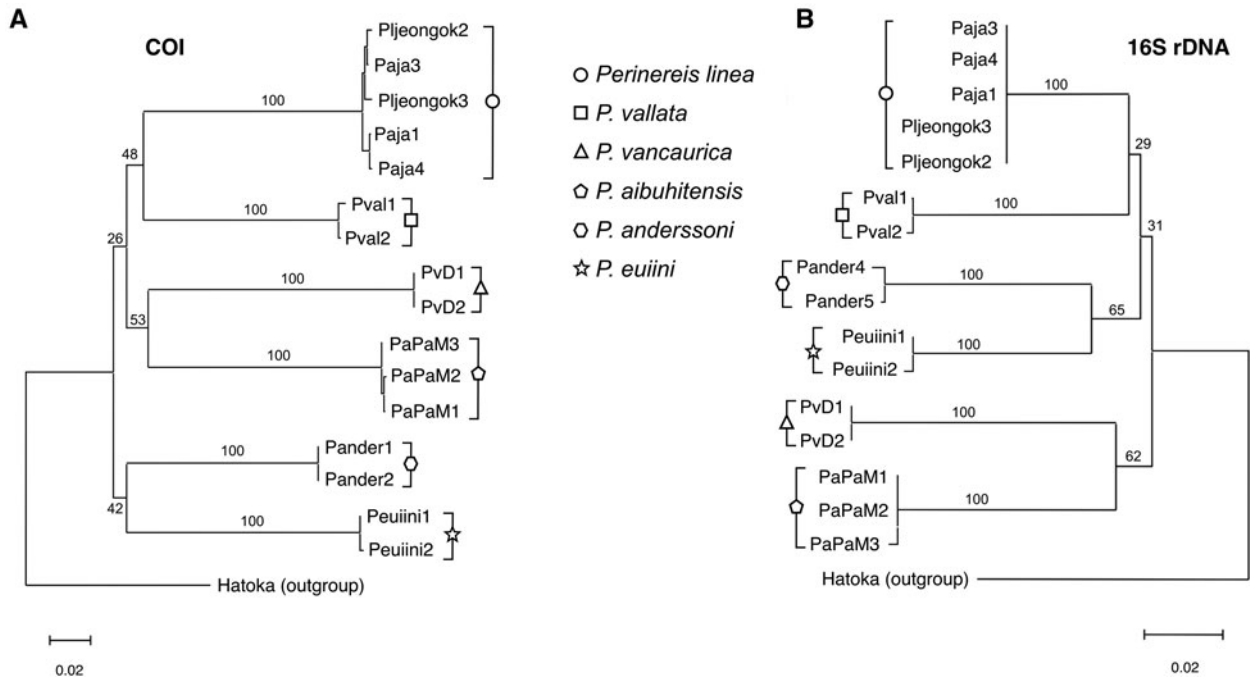


Fig. 2. Neighbour-joining (NJ) tree using partial sequences of COI (A) and 16S rDNA (B) genes for six *Perinereis* species. *Hediste atoka* (Hatoka) used as outgroup for rooting the tree. The numbers next to the branches indicate bootstrap support with 1000 replications.

Table 3. Pairwise sequence divergence (%) ranges of partial COI (below diagonal) and 16S rRNA (upper diagonal) among six *Perinereis* species

Species	<i>P. linea</i> ^a 0	<i>P. aibuhitensis</i> ^a 0–0.21(0.14)	<i>P. vancaurica</i> ^a 0	<i>P. vallata</i> ^a 0.21	<i>P. anderssoni</i> ^a 0.42	<i>P. euiini</i> ^a 0.21
<i>P. linea</i> , N = 5 ^a 0.16–0.97(0.65)	–	10–10.24 (10.08)	11.47	8.55–8.79 (8.67)	10.29–10.54 (10.42)	9.01–9.25 (9.13)
<i>P. aibuhitensis</i> , N = 3 ^a 0.16–0.32(0.21)	25–25.73 (25.41)	–	12.23–12.48 (12.31)	12–12.25 (12.09)	13.85–14.63 (14.2)	12.46–12.96 (12.67)
<i>P. vancaurica</i> , N = 2 ^a 0	25.8–26.79 (26.29)	24.71–24.95 (24.79)	–	13.21–13.47 (13.34)	15.35–15.63 (15.49)	13.99–14.25 (14.12)
<i>P. vallata</i> , N = 2 ^a 0.48	20.98–21.44 (21.23)	22.98–23.67 (23.36)	24.72–24.96 (24.84)	–	11.01–11.76 (11.39)	11.72–12.22 (11.97)
<i>P. anderssoni</i> , N = 2 ^a 0	23.8–24.47 (24.21)	22.19–22.64 (22.41)	25.41	22.75	–	9.83–10.33 (10.08)
<i>P. euiini</i> , N = 2 ^a 0.16	24.1–25.05 (24.65)	25.60–26.08 (25.88)	26.99–27.23 (27.11)	22.16–22.38 (22.27)	20.98–21.21 (21.09)	–

^a, intraspecific divergence; N, number of specimens; numbers in parentheses indicate ranges of mean divergence. Nucleotide sequence divergence were based on Kimura 2-parameter model.

groups of paragnaths on area III, and the arrangement of paragnaths on area II. Both sequences of COI and 16S rDNA genes newly obtained or mined from GenBank for six *Perinereis* species demonstrate distinctive clusters for each species in the neighbour-joining tree construction (Figure 2; Table 1, 3). *Perinereis linea* forms a genetically different cluster with interspecific distances ranging from 20–26.8 for COI and 8.5–15.6 for 16S rDNA (Table 3), supporting it as a distinct species. Hence, we confirm *P. linea* as a valid species based on this morphological and molecular evidence, and regard *N. (Neanthes) orientalis* and *P. vancaurica tetradentata* as junior synonyms of *P. linea* instead of *P. aibuhitensis* because of the similar morphology of the type material.

Systematics

Phylum ANNELIDA Lamarck, 1802
Class PLEISTOANNELIDA Struck, 2011

Subclass ERRANTIA Audouin & Milne-Edwards, 1832
Order PHYLLODOCIDA Dales, 1962
Family NEREIDIDAE de Blainville, 1818

Genus *Perinereis* Kinberg, 1865
Perinereis Kinberg, 1865: 175; 1910: 52.

Type species

Perinereis novaehollandiae Kinberg, 1865, by subsequent designation (fide Hartman, 1949). Currently regarded as a junior synonym of *P. amblyodonta* Schmarda, 1861 (Ehlers, 1904; Hartman, 1959).

Remarks

Perinereis is considered a non-monophyletic genus (Bakken & Wilson, 2005; Glasby et al., 2013; Liu et al., 2013). The presence of transverse bars on area VI, or more restrictively smooth bars as

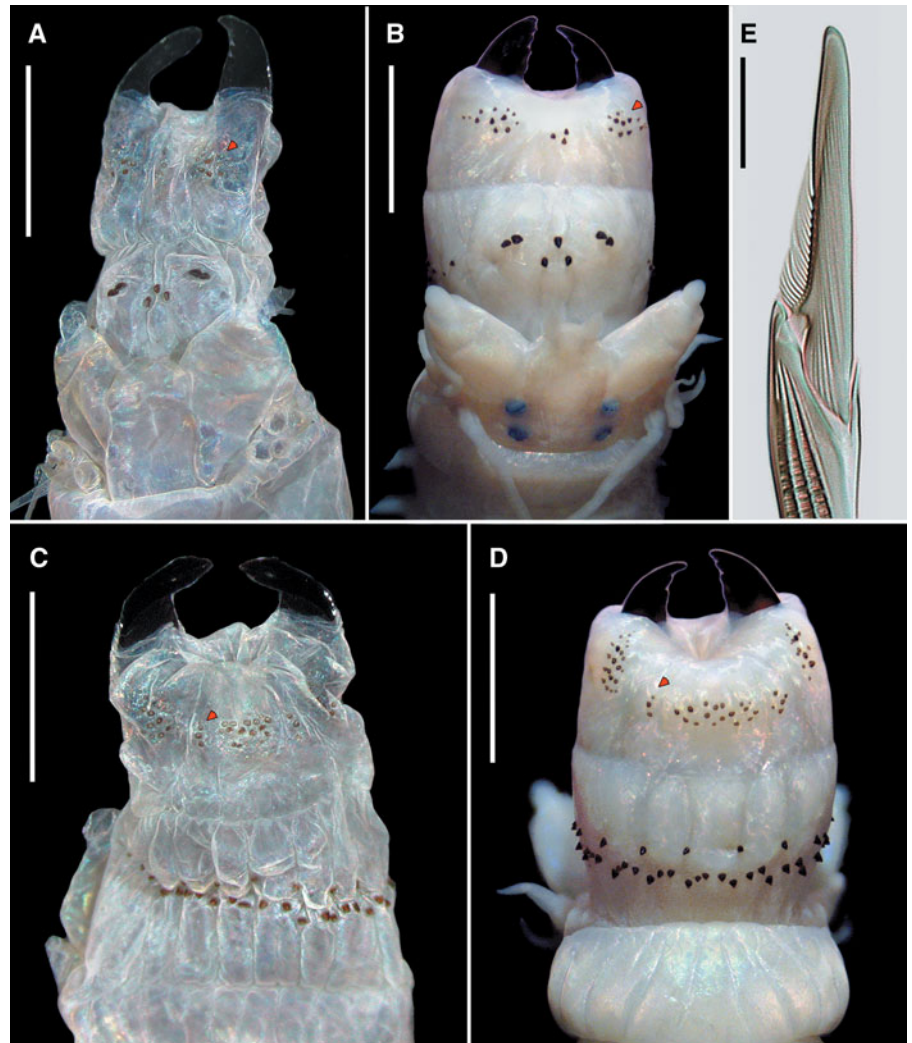


Fig. 3. *Perinereis aibuhitensis* (Grube, 1878). (A, C, E) Paralectotype of *Nereis* (*Perinereis*) *aibuhitensis* (ZMB Q.3440), Aibukit village, Palau, atoke; (B, D) toptype of *P. aibuhitensis*, Melekeok, Palau, atoke. (A, B) Anterior region in dorsal view (arrows pointing distal edge of rows on area II); (C, D) anterior region in ventral view (arrows pointing lateral isolated paragnaths on area III); (E) heterogomph falciger from neuropodial supracular fascicle (anterior chaetiger). Scale bars: A–D, 2 mm; E, 20 μ m.

stated in subsequent studies (Hutchings *et al.*, 1991; Bakken *et al.*, 2009), has been traditionally regarded as the main feature to recognize *Perinereis* species (e.g. de Saint-Joseph, 1898; Gravier, 1902; Fauvel, 1923; Fauchald, 1977). This feature is not unique in the genus since it is also shared with species of *Eunereis* Malmgren, 1865 (Bakken & Wilson, 2005). Furthermore, the type species *P. novaehollandiae* Kinberg, 1865 [= *P. amblyodonta* (Schmarda, 1861) *fide* Ehlers, 1904] has different bars on area VI – shield-shaped (*sensu* Bakken *et al.*, 2009) or crescent-shaped (*sensu* Conde-Vela, 2018) (see Knox, 1951). *Perinereis* differs from the polyphyletic genus *Neanthes* Kinberg, 1865 by the presence of bars on area VI (absent in *Neanthes sensu* Bakken & Wilson, 2005), *Pseudonereis* Kinberg, 1865 by the absence of both P-bars and comb-like rows on areas II–IV (present in *Pseudonereis sensu* Conde-Vela, 2018 and Villalobos-Guerrero & Idris, 2020), and *Eunereis* by the presence of paragnaths on the maxillary ring (absent in *Eunereis sensu* Bakken & Wilson, 2005). In the broad sense, the members of *Perinereis* are characterized by having paragnaths well-separated and mostly conical on both pharyngeal rings and bar-shaped paragnaths on area VI. However, a comprehensive revision of this polyphyletic genus is needed to restrict the genus definition, detect reliable generic features, and remove disparate species. The genus definition followed here is based on the phylogenetic study of Nereidinae *sensu* Fitzhugh (1987) by Bakken & Wilson (2005).

'*Perinereis aibuhitensis*' species group

Perinereis subgroup 2A: Hutchings *et al.*, 1991: 271–273 (*partim*).

Diagnosis

Prostomium with anterior margin complete. Four eyes, lenticulate. Antennae present. Palpophores with marked transverse groove. Four pairs of tentacular cirri with distinct cirrophores. Apodous anterior segment greater than length of chaetiger 1. Jaws denticulate, two canals emerging from pulp cavity. Maxillary and oral pharyngeal rings with paragnaths only (Figure 3A–D), rarely absent on area V. Conical paragnaths on all areas, except on area VI (rarely one); bar-shaped paragnaths only on area VI, two (rarely one, occasionally 3–4) in a transverse row on each side (Figure 3A, B); area IV without merged paragnaths. Pharyngeal areas VI–V–VI ridge pattern λ -shaped or π -shaped. Paired oesophageal caeca present. Glandular patches present in dorsal ligule. Notopodia well-developed. Dorsal cirri short, conical at least in middle and posterior parapodia, attached medially to dorsal ligule. Proximal dorsal ligule similar in size throughout body, or slightly enlarged in posterior parapodia. Distal dorsal ligule subequal throughout or becoming shorter towards posterior end. Notopodial prechaetal lobe absent, sometimes as acicular process in anterior chaetigers. Neuropodial postchaetal lobe absent. Neuropodial superior and inferior lobes blunt, present at least in anterior parapodia. Ventral ligule present throughout. Ventral cirri single. Notoaciculae absent in first two chaetigers, thereafter present. Aciculae black. Notochaetae all homogomph spinigers, throughout. Supracular neurochaetae with homogomph spinigers and heterogomph falcigers, both throughout. Subacicular neurochaetae with heterogomph spinigers and heterogomph falcigers, both throughout. Blades of

falcigers straight, with incurved terminal tooth markedly elongated forming distinct tendon (Figure 3E). Anal cirri with cirrophore.

Remarks

According to Hutchings *et al.* (1991), *Perinereis* species of the subgroup 2A are characterized by having area VI with two bar-shaped paragnaths and dorsal ligules not greatly expanded in posterior parapodia. In the present study, we noticed that most subgroup 2A species also share short dorsal cirri (not projecting beyond the end of distal dorsal ligule in medial parapodia) and blade of heterogomph falcigers straight with incurved terminal tooth markedly elongated forming a distinct tendon.

A major morphological species group is, therefore, here proposed for 11 species that share all the morphological features mentioned above: *Perinereis aibuhitensis*, *P. brevicirrata* (Treadwell, 1920), *P. linea*, *P. rookeri* de León-González & Goethel, 2013, *P. singaporiensis* (Grube, 1878), *P. vancaurica* (Ehlers, 1868), and other five species previously in *Neanthes* but here transferred: *Perinereis babuzai* comb. nov., *P. belawanensis* comb. nov., *P. kinmenensis* comb. nov., *P. shigungensis* comb. nov. and *P. vitabunda* comb. nov. The remaining species of the subgroup 2A have long dorsal cirri, extending further beyond distal dorsal ligule in medial parapodia, and blades of heterogomph falcigers with incurved terminal tooth short and inconspicuous tendon. These species are *P. camiguinoides* (Augener, 1922), *P. horsti* Gravier, 1899, *P. jascooki* Gibbs, 1972, *P. kuwaitensis* Mohammad, 1970 and *P. variodentata* (Augener, 1913). All these species can be morphologically distinguished as stated in the key (see below).

The most representative species in subgroup 2A is *P. aibuhitensis* (Grube, 1878), originally described from Palau. This species is widely studied due to its commercial value in both aquaculture and recreational fisheries (Gu *et al.*, 2002; Deng *et al.*, 2007), as a biological indicator of marine pollution (Wang *et al.*, 2008; Yang *et al.*, 2012; Tian *et al.*, 2014), as a model in ecotoxicology studies (Yuan *et al.*, 2010; Leung & Chan, 2018), and even applications in traditional and modern medicine (Gu *et al.*, 2002; Pan *et al.*, 2004; Li *et al.*, 2017). The species has also been subjected to several taxonomic studies using specimens from different geographic regions (e.g. Horst, 1924; Fauvel, 1932, 1953; Wu *et al.*, 1985; Hylleberg *et al.*, 1986; Lee *et al.*, 1992; Khlebovich, 1996; Sun & Yang, 2004), and combining them in a single redescription with the type material (Hutchings *et al.*, 1991). Hence, we have selected *P. aibuhitensis* to name the species group.

Perinereis babuzai (Hsueh, 2019) comb. nov.

Neanthes babuzai Hsueh, 2019: 174–177, figs 1, 2, table 2.

Diagnosis (based upon Hsueh, 2019)

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with broad-petite bars on area VI; areas VI–V–VI ridge pattern λ -shaped; distal dorsal ligule anteriorly conical, posteriorly distinctly short; neuroacicular ligule posteriorly subequal to median ligule; falcigers with camerated shaft divided into two partitions; postero-dorsal tentacular cirri extending to chaetigers 5–9.

Remarks

Neanthes babuzai Hsueh, 2019 is here transferred to *Perinereis* based on having bar-shaped paragnaths on area VI. The species resembles *P. linea* by having broad-petite bars on area VI, distal dorsal ligule conical in anterior parapodia, and areas VI–V–VI ridge pattern λ -shaped. Some relevant characters such as the presence of laterally isolated paragnaths on area III and the number of rows in the anterior band of areas VII–VIII were not mentioned nor illustrated in the original description, and the number of divisions in the camerated shaft of falcigers is unclear, and thus

remain unknown. However, the length of distal dorsal ligule in posterior parapodia can distinguish both species. In *P. babuzai* comb. nov., the distal dorsal ligule is distinctly short in posterior parapodia, projecting barely beyond notoaciculæ; whereas, in *P. linea* the distal dorsal ligule is of medium length in posterior parapodia, projecting markedly beyond notoaciculæ.

Habitat

Intertidal muddy bottom.

Reproduction

Unknown.

Type locality

Xianxi, Changhua County, Taiwan.

Distribution

The species is known only from the type locality in Changhua County (Taiwan).

Perinereis belawanensis (Pflugfelder, 1933) comb. nov.
(Figures 1A–C, 4)

Nereis belawanensis Pflugfelder, 1933: 72–73, fig. 13A–D; Harms, 1934: 29–30 (habitat); Wesenberg-Lund, 1958: 29 (species list); Salazar-Vallejo *et al.*, 2014: 23 (species list).

Neanthes belawanensis: Hartman, 1959: 250; Fauchald, 1972: 409; Wilson, 1984: 225 (all species list).

Neanthes succinea: Hartman, 1974: 618 (*non* Leuckart, 1847).

Neanthes belewanensis (sic): Glasby *et al.*, 2009: 14.

Type material

Holotype: PMJ Ann-168, Belawan, Sumatra, Indonesia, coll. J. W. Harms, 1927 or 1929.

Material examined

One specimen: PMJ Ann-167a, Belawan, Sumatra, Indonesia, coll. J. W. Harms, 1927 or 1929, atoke, in good condition.

Diagnosis

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with broad-petite bars on area VI; areas VI–V–VI ridge pattern π -shaped; area III with laterally isolated paragnaths; areas VII–VIII with anterior band of paragnaths consisting of two rows; neuroacicular ligule markedly projected; distal dorsal ligule distinctly short; falcigers with camerated shaft divided into two partitions; postero-dorsal tentacular cirri extending to chaetiger 4.

Description

Holotype atoke, incomplete, posterior part missing, in good condition except already cut off into two parts at level of third and fourth chaetigers, 75 (95) mm LT, 13 (13.8) mm L15, 3.5 (3.2) mm W15, with 133 (140) chaetigers. Body colour brownish (Figure 4A), with three darkish longitudinal lines of tegument on dorsum of segments: one mid-dorsal line and two dorsolateral lines present throughout; body covered by salt granules in mid-anterior dorsal part.

Prostomium campanulate, faintly stretching in middle, as long as wide; anterior end broad, distally complete; anterolateral gap aside palpophore broad, 1.5 times as wide as basal diameter of antennae (Figure 4B). Nuchal organs deeply embedded, medium size, subequal to diameter of posterior pair of eyes.

Palpophores sub-conical, thick, as long as wide, as long as three-quarters of entire prostomium; sub-distal transverse groove distinct, deeply embedded (Figure 4B, C). Palpostyles oval, one-quarter as wide as diameter of palpophore.

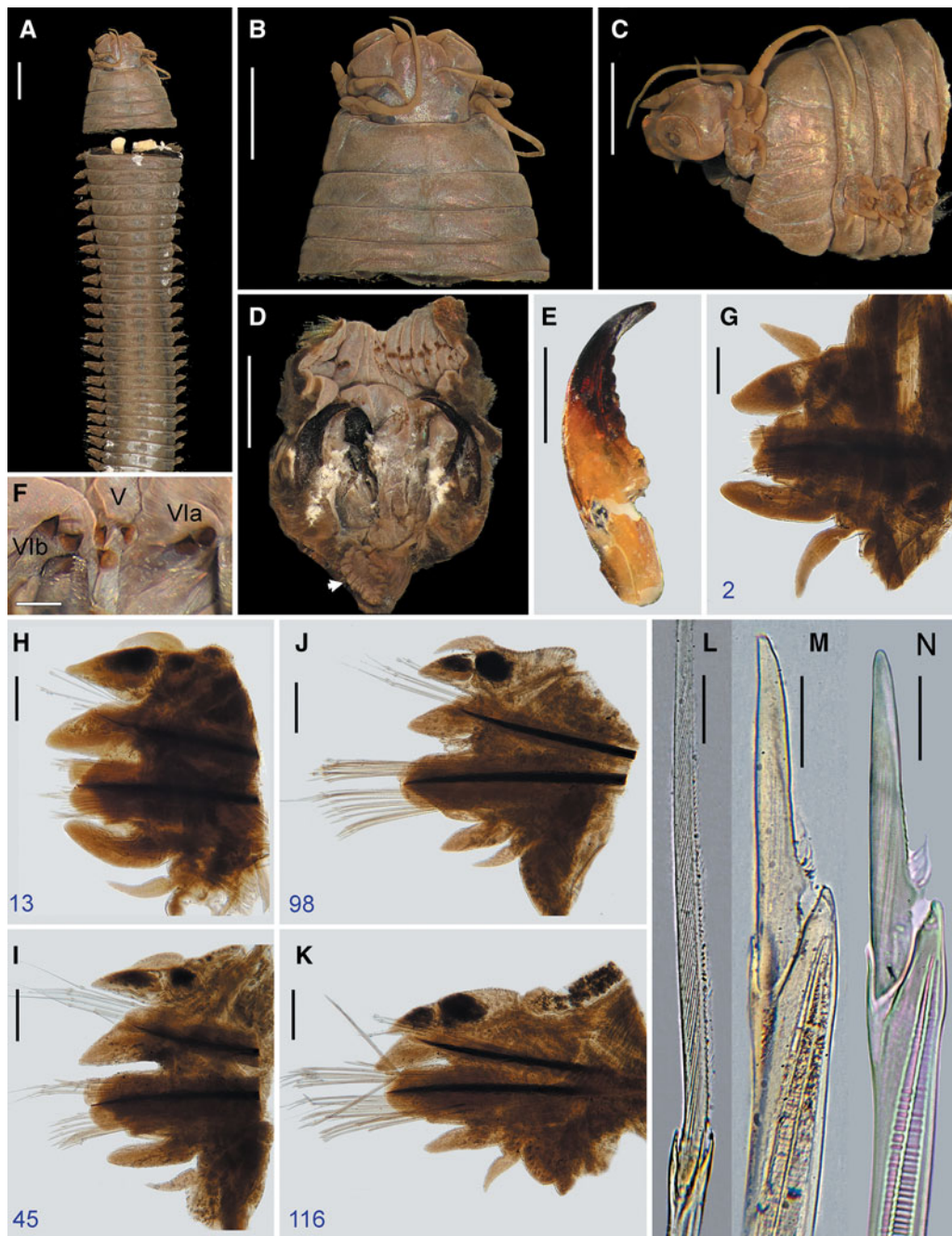


Fig. 4. *Perinereis belawanensis* (Pflugfelder, 1933) comb. nov. Holotype (PMJ Ann-168), Belawan, Sumatra, atoke: (A) anterior region in dorsal view; (B) prostomium in dorsal view; (C) anterior region in lateral view; (D) non-everted pharynx in ventral view (arrow pointing caecal gland); (E) right jaw in dorsal view; (F) oral ring in ventral view; (G–K) parapodia, numbers refer to the chaetiger; (L) homogomph spiniger from notopodia (chaetiger 60); (M) heterogomph falciger from neuropodial supracicular fascicle (chaetiger 116); (N) heterogomph falciger from neuropodial subacicular fascicle (chaetiger 98). Scale bars: A–D, 2 mm; E, 1 mm; F, 0.5 mm; G–K, 0.2 mm; L–N, 20 μ m.

Antennae tapered, thick, short; extending forwards to tip of palpophore and posteriorly to distal quarter of length of prostomium; antennae separated with gap as wide as basal diameter of antennae (Figure 4B).

Paired eyes blackish, arranged in a trapezoid form; gap between both pairs twice diameter of posterior pair of eyes (Figure 4B); anterior pair of eyes oval, subequal to basal diameter of antennae, gap between both eyes as wide as 5.5 times diameter of eyes, with lens distinct, whitish, covering 85% of eye; posterior pair of eyes rounded, three-quarters as wide as basal diameter of antennae, with lens distinct, purplish, placed in middle of eye and covering 50% of it.

Apodous anterior segment 3.5 times wider than long, 1.7 times as long as chaetiger 1 (Figure 4A–C), with even anterior margin, dorsum without marked transverse wrinkles.

Tentacular cirri slender, smooth (Figure 4B, C); postero-dorsal cirri extending posteriorly to chaetiger 4, 2.3 times as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to chaetiger 1; postero-ventral cirri extended over first quarter of prostomium; antero-ventral cirri as long as three-quarters of postero-ventral cirri and slightly smaller than palpophore; cirrophores cylindrical, postero-dorsal cirrophores longest, postero-ventral cirrophores narrowest.

Pharynx not everted, previously dissected with pharyngeal bulb and its surrounding muscle removed from body, separated in vial. Jaws (Figure 4D, E) reddish in distal half, remaining amber, with eight slightly developed and blunt denticles; pulp cavity as long as three-fifths of jaw, with two thick canals. Pharynx with paragnaths brownish on maxillary ring

(Figure 4D) and reddish paragnaths on oral ring (Figure 4D, F), consisting of uniform-base cones, except broad-petite bars on area VI; merged paragnaths and plate-like basements absent. Area I: 2, longitudinal row of cones, distal one smaller; areas IIa: 15 (10) and IIb: 12 (11), three irregular rows of uneven cones in ovoid slightly curved patch, medial cones larger; area III: 25 (18), four slightly regular rows of uneven cones in sub-rounded patch, distal cones larger, with distinct isolated lateral groups; areas IVa: 19 (16) and IVb: 15, five regular transverse rows of uneven cones in sub-oval patch, distal-most and most proximal cones shorter; area V: 3, triangular patch of coarse cones of similar size, two proximal cones in transverse row and single distal cone on same level as distal-most paragnath on area VI; areas VIa: 2 and VIb: 2, one oblique row of even, coarse broad-petite bars with pointed tip, barely separated (Figures 1A–C, 4F); areas VII–VIII: 36 (35), two well-separated bands of coarse and uneven cones, with anterior band consisting of two transversely aligned rows (furrow row with one stout paragnath on each region, ridge row with a slightly shorter cone only on ridge regions A and paired B), and posterior band with two transverse rows displaced from each other (furrow row proximal with one cone on each region, ridge row distal with two cones on each region). Areas VI–V–VI ridge pattern, π -shaped. Gap between area VI and areas VII–VIII broad, as wide as palpophore.

Paired oesophageal caeca present (Figure 4D).

Parapodia with blackish, glandular notopodial patches, more distinct in posterior chaetigers (Figure 4K).

Notopodia consisting of dorsal cirrus, dorsal ligule (distal and proximal), and median ligule in biramous parapodia; notopodial prechaetal lobe or notoacicular process not developed throughout.

Dorsal cirri conical, thick, short (Figure 4G–K), extending up to three-quarters of distal dorsal ligule throughout; dorsal cirri longer than proximal dorsal ligule in anteriormost parapodia (Figure 4F), subequal in anterior parapodia (Figure 4H), shorter in following parapodia (Figure 4I–K); dorsal cirri inserted basally to dorsal ligules in anteriormost parapodia, one-third in anterior parapodia, medially in following parapodia.

Proximal dorsal ligule even towards posterior end; subequal to distal dorsal ligule in anterior parapodia (Figure 4H), becoming longer than distal dorsal ligule from medial parapodia (Figure 4I), twice as long distal dorsal ligule in posterior parapodia (Figure 4J, K); one massive, sub-oval glandular patch throughout, larger in posterior parapodia (Figure 4K).

Distal dorsal ligule becoming gradually shorter towards posterior end, extending beyond end of notoaciculae throughout, slightly in posterior parapodia (Figure 4I–K); distal dorsal ligule conical throughout (Figure 4H–K), shorter than median ligule throughout, except in anteriormost parapodia; one massive, sub-oval glandular patch throughout, larger than that in proximal dorsal ligule in anterior parapodia, becoming smaller in medial and posterior parapodia (Figures 4J, K).

Median ligule bluntly conical in anteriormost and anterior parapodia (Figure 4H, I), conical and becoming slightly shorter and narrower in following parapodia (Figure 4J, K).

Neuropodia consisting of neuroacicular ligule with superior and inferior lobes, ventral ligule, and ventral cirrus; neuropodial postchaetal lobe reduced throughout.

Neuroacicular ligule shorter than ventral ligule in anteriormost parapodia (Figure 4G), subequal in anterior parapodia, distinctly longer in following parapodia (Figure 4I–K); neuroacicular ligule twice as wide as ventral ligule in anteriormost and anterior parapodia, 2.5 times as wide in medial and posterior parapodia.

Superior lobe rounded, subequal to inferior lobe and neuroacicular ligule in anterior and medial parapodia (Figure 4G–J), reduced in posterior parapodia from chaetiger 118.

Inferior lobe rounded, slightly longer than neuroacicular ligule in first 34 chaetigers (Figure 4G, H), becoming shorter and narrower in following parapodia.

Ventral ligule digitiform and subequal to median ligule in anteriormost and anterior parapodia (Figure 4G, H), slightly tapering and becoming shorter in following parapodia (Figure 4I–K).

Ventral cirri cirriform and thick in anteriormost and anterior parapodia (Figure 4G, H), becoming conical and narrower in following parapodia; ventral cirri as long as two-thirds of ventral ligule, except one-half of ventral ligule in posterior parapodia.

Pygidium missing but topotype with regenerating posterior end, anal cirri incomplete, as long as last two chaetigers.

Aciculae black, with basal end uncoloured. Notoaciculae absent in chaetigers 1 and 2 (Figure 4G). Neuroaciculae markedly extending beyond distal end of notoaciculae throughout (Figure 4H–K); neuroaciculae shorter than median ligule in anteriormost and anterior parapodia, subequal to median ligule in medial and posterior parapodia.

Notochaetae all homogomph spinigers; 11–13 spinigers present in anterior parapodia, 6–10 spinigers in medial parapodia, 3–5 spinigers in posterior parapodia.

Supracicular neurochaetae consisting of homogomph spinigers and heterogomph falcigers, both present throughout; 1–2 spinigers present in anteriormost and anterior parapodia, 3–4 spinigers in medial parapodia, 2–3 spinigers in posterior parapodia; 7–9 falcigers present in anteriormost and anterior parapodia, 5–7 falcigers in medial and posterior parapodia.

Subacicular neurochaetae consisting of heterogomph spinigers and heterogomph falcigers, both present throughout; 1–2 spinigers present in anteriormost parapodia, 3–4 spinigers in anterior parapodia, 1–2 spinigers in medial and posterior parapodia; 14–16 falcigers in anteriormost and anterior parapodia, 8–10 falcigers in medial parapodia, 11–13 falcigers in posterior parapodia.

Blades of both homogomph (Figure 4L) and heterogomph spinigers finely serrated towards toothed edge, evenly spaced, long with high b/a ratio (9–16.5). Blades of heterogomph falcigers long with low b/a ratio (2–2.5), slender, straight, distal end digitiform with incurved terminal tooth very long forming distinct tendon (equalling about two-fifths of total blade length: 0.42–0.47); blades of falcigers partially serrated, with serrations capilliform, curved, looking upwards, present in about half (0.49–0.52) of total blade length (Figure 4M, N); vertex between distal and basal end on serrated edge markedly prominent, sub-conical. Shaft of falcigers camerated, with cavity divided sub-distally into two distinct longitudinal partitions (Figure 4M, N).

Remarks

Perinereis belawanensis (Pflugfelder, 1933) comb. nov. belongs to the *P. aibuhitensis* species group characterized by having short dorsal cirri throughout the body and blade of heterogomph falcigers straight with incurved terminal tooth markedly elongated and forming a distinct tendon. *Perinereis belawanensis* comb. nov. resembles *P. aibuhitensis*, *P. rookeri* and *P. vitabunda* comb. nov. by sharing areas VI–V–VI ridge pattern π -shaped, area VI with broad-petite bars, and area III with distinct laterally isolated paragnaths. Nonetheless, *P. belawanensis* comb. nov. is separated from *P. aibuhitensis* and *P. vitabunda* comb. nov. by having an anterior band of areas VII–VIII with two transverse rows on furrows and ridges (Figure 4D) and the camerated shaft of falcigers divided sub-distally into two partitions (Figure 4M) (only furrow row on the anterior band of areas VII–VIII and three partitions in the shaft of falcigers in the latter two species; Figure 3C–E). Likewise, *P. belawanensis* comb. nov. can be distinguished from *P. aibuhitensis* and *P. rookeri* because the neuroacicular ligule is projecting markedly beyond ventral ligule in posterior parapodia (Figure 4K), the distal dorsal ligule is

distinctly shorter than median ligule throughout the body (Figure 4H–K), and the proximal dorsal ligule is longer than distal dorsal ligule in medial and posterior parapodia (Figure 4J, K); whereas in *P. aibuhitensis* and *P. rookeri* the neuroacicular ligule is subequal to or slightly shorter than ventral ligule, the distal dorsal ligule is subequal to or barely shorter than median ligule, and both proximal and distal dorsal ligules are subequal in medial and posterior parapodia. *Perinereis belawanensis* comb. nov. can also be distinguished from *P. rookeri* because the blade of the heterogomph falciger is evenly slender towards the distal end, whereas in *P. rookeri* the proximal end of the blade is more expanded than the distal end.

Perinereis belawanensis comb. nov. is more similar to *P. vitabunda* comb. nov. in terms of habitat and locality; however, they are different in several respects. In *P. belawanensis* comb. nov., the distal dorsal ligules exceed the distal end of notoaciculae, whereas in *P. vitabunda* comb. nov. they are subequal to or slightly shorter than notoaciculae. In *P. belawanensis* comb. nov., the postero-dorsal tentacular cirri are longer (reaching chaetiger 4) than in *P. vitabunda* comb. nov. (reaching chaetiger 1). In *P. belawanensis* comb. nov., the camerated shaft of falcigers has cavity divided sub-distally into two longitudinal partitions, although in *P. vitabunda* comb. nov. it is divided into three partitions. In *P. belawanensis* comb. nov., the paragnaths on area VI are arranged obliquely, area III has 25 (18) paragnaths, and area IV has 15–19 paragnaths; whereas in *P. vitabunda* comb. nov., the paragnaths on area VI are arranged transversally, area III has 36 paragnaths, and area IV has 31 paragnaths. Finally, in *P. belawanensis* comb. nov., the nuchal organs are subequal to the diameter of posterior eyes, which in *P. vitabunda* comb. nov. are distinctly shorter than the diameter of the same eyes.

Perinereis belawanensis comb. nov. is a semi-terrestrial species from Sumatra originally described as a *Nereis* by Pflugfelder (1933). The species was transferred to *Neanthes* and recognized there without further information (Hartman, 1959; Fauchald, 1972; Wilson, 1984; Glasby et al., 2009). Moreover, Hartman (1974) synonymized the species with *Neanthes succinea* (Leuckart, 1847) (currently in *Alitta* Kinberg, 1865) from the North Sea with unknown justification. However, both species are markedly different, and the synonymy has prevailed ever since and listed as such in recent works either in *Neanthes* or in *Alitta* (e.g. Salazar-Vallejo et al., 2014; Villalobos-Guerrero & Carrera-Parra, 2015; Read & Fauchald, 2019). After re-examining the type material, the species is here transferred to *Perinereis*.

Perinereis belawanensis comb. nov. has not been recorded since the original description. The specimens used by Pflugfelder (1933) were collected by Jürgen W. Harms in 1927 or 1929, who provided a detailed description of the habitat of the species (Harms, 1934).

Habitat

Semi-terrestrial. Dwelling in burrows dug within almost-dried, sandy-clay soil in 20–30 cm depth, which are only partially rinsed by water when tides are high, usually living along with its congener *P. vitabunda* comb. nov. (Pflugfelder, 1933).

Reproduction

Unknown.

Type locality

Belawan, Sumatra, Indonesia.

Distribution

The species is known only from the type locality, Belawan (Indonesia).

Perinereis kinmenensis (Hsueh, 2019) comb. nov.

Neanthes kinmenensis Hsueh, 2019: 183–185, figs 9, 10, table 2.

Diagnosis (based upon Hsueh, 2019)

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with broad-petite bars on area VI; areas VI–V–VI ridge pattern π -shaped; area III with laterally isolated paragnaths; areas VII–VIII with anterior band consisting of one row; distal dorsal ligule anteriorly subulate, subequal in size throughout; neuroacicular ligule posteriorly subequal to median ligule; falcigers with camerated shaft divided into three partitions; postero-dorsal tentacular cirri extending to chaetiger 2.

Remarks

Neanthes kinmenensis Hsueh, 2019 is here transferred to *Perinereis* based on the presence of bar-shaped paragnaths on area VI. The species resembles *P. aibuhitensis* by having broad-petite bars on area VI, distal dorsal ligule projecting markedly beyond notoaciculae, areas VI–V–VI ridge pattern π -shaped, areas VII–VIII with the anterior band having only one furrow row, and area III with distinct laterally isolated paragnaths. However, both species can be distinguished by the shape of ligules in anterior parapodia, the division of camerated shaft of falcigers, and the length of postero-dorsal tentacular cirri. In *P. kinmenensis* comb. nov., the ligules in anterior parapodia are slender and acuminate, whereas those in *P. aibuhitensis* are thicker with a blunt tip. Finally, in *P. kinmenensis* comb. nov. the postero-dorsal tentacular cirri extend posteriorly to chaetiger 2, whereas in *P. aibuhitensis* they extend to chaetiger 4–5.

Habitat

Intertidal soft bottom.

Reproduction

Unknown.

Type locality

Yangshan, Kinmen County, Fujian, China.

Distribution

The species is known only from the type locality, Yangshan in Fujian (China).

Perinereis lineata (Treadwell, 1936)

(Figures 1G–L, 5–9)

Perinereis aibuhitensis: Fauvel, 1933: 25–26; Hartman, 1938: 15; Khlebovich & Wu, 1962: 39, 50–51; Wu et al., 1985: 189–193, figs 107–109 (*partim*, *non* records from Hainan Island); Lee et al., 1992: 1–10, figs. 2–3; Imajima, 1996: 131, fig. 104A–H; Khlebovich, 1996: 147, pl. 46, figs 1–7 (*partim*, only records from the Yellow Sea); Sun & Yang, 2004: 180–183, figs 101–103 (*partim*, *non* records from Hainan Island) (*non* Grube, 1878).

Nereis aibuhitensis: Monro, 1934: 361–362 (*non* Grube, 1878).

Nereis (*Neanthes*) *lineata* Treadwell, 1936: 268–270, figs 19A–E.

Nereis (*Neanthes*) *orientalis* Treadwell, 1936: 270–272, figs 19F–I.

Perinereis lineata: Wu, 1967: 68–69, figs 10a–d; Sato, 2017: 492–493, table 19.1 (*Perinereis vancaurica tetradentata* jun. syn.).

Perinereis vancaurica tetradentata Imajima, 1972: 86–88, fig. 23; Paik, 1975: 7, pl. 6, figs 44–46; 1977: 172–174, figs 16A–F; 1989: 309–311, text figs 72A–E, pl. 24, figs 62A (1–2), pl. 25, fig. 62A–3; Sato, 2017: 493.

Neanthes virens: Paik, 1975: 412–413, pl. 3, figs 16–24; 1977: 200–202, figs 29A–F; 1982: 789, pl. 14, figs J–L, 1989: 339–341, text figs 89A–H, pl. 32, figs 78(1–2), pl. 33, fig. 78–3 (*partim*, *non* figures in plates, *non* Sars, 1835).

Type material

Holotype: *Nereis* (*Neanthes*) *lineata* Treadwell, 1936, USNM 20115, Amoy (Xiamen), Fujian, China, coll. T. Y. Chen.

Holotype: *Nereis (Neanthes) orientalis* Treadwell, 1936, USNM 20116, Amoy (Xiamen), Fujian, China, coll. T. Y. Chen.

Holotype: *Perinereis vancaurica tetradentata* Imajima, 1972, NSMT-Pol-H78, Sumida-gawa River, Tokyo, Japan, coll. A. Izuka (?), 20 July 1908.

Comparative material examined

Nereis (Perinereis) aibuhitensis Grube, 1878. Paralectotype: ZMB Q.3440, Aibukit village, Ngebuked, Babeldaob Island, Palau, coll. C. G. Semper, any date between end of March 1862 to January 1863 (*sensu* Semper, 1873). Topotypes: Four specimens (NIBRIV0000787926), Melekeok, Palau (7°28'5"N 134°36'42"E), coll. T. Park, 5 August 2013, mangrove, fixed in 80% ethanol. Non-types: Twenty-four specimens (NIBRIV0000787927), Koh Kong, Cambodia, Gulf of Thailand, coll. T. Park, 6 September 2011, mangrove, fixed in 70% ethanol; one specimen (NIBRIV0000787924), Koh Rung Samloem Island, Cambodia (10°37'20"N 103°17'37"E), Gulf of Thailand, coll. T. Park, 29 April 2012, sandy beach, fixed in 80% ethanol.

Other material examined

Fourteen specimens (NIBRIV0000783811, 1 ind.; NIBRIV0000783812, 1 ind.; NIBRIV0000783813, 1 ind.; NIBRIV0000783814, 11 inds), Ganghwado Island, Dongmak-ri, Hwadomyeon, Ganghwa-gun, Incheon-si, Korea, coll. T. Park, 12 May 2013, muddy tidal flat, fixed in 10% formalin. Nine specimens (NIBRIV0000317216, 3 inds; NIBRIV0000317217, 2 inds; NIBRIV0000317218, 2 inds; NIBRIV0000317220, 2 inds), Daehang-ri, Byeonsan-myeon, Buan-gun, Jeollabuk-do, Korea (35°41'55.3"N 126°33'8.4"E), coll. H.-K. Choi, muddy tidal flat, 13 August 2014. Four specimens (NIBRIV0000129004), Sangam-ri, Buan-myeon, Gochang-gun, Jeollabuk-do, Korea, coll. Y. Eun & S.-S. Hong, muddy tidal flat, 24 July 2007. One specimen (NIBRIV0000262307), Songnim-ri, Janghang-eup, Seocheon-gun, Chungcheongnam-do, Korea, coll. S.-H. Kim, 9 August 2010. One specimen (NIBRIV0000521098), Dongho-ri, Haeri-myeon, Gochang-gun, Jeollabuk-do, Korea (35°31'18"N 126°29'8.84"E), coll. H.-K. Choi, 3 May 2015. One specimen (NIBRIV0000282343), Jungsan-dong, Jung-gu, Incheon-si, Korea (37°31'45.19"N 126°35'25.83"E), coll. S.-Y. Wang, 7 March 2012. Five specimens (NIBRIV0000810291), Jeongok Harbor, Jeongok-ri, Hwaseong-si, Gyeonggi-do, Korea (37°11'12"N 126°38'3"E), coll. P. G. Lee and H. P. Lee, 8 March 2012, muddy tidal flat, fixed in 80% ethanol. Seven specimens (NIBRIV0000866077), Dalian, Liaoning, China, coll. R. Sun, no further data. Five specimens (NIBRIV0000810299), fishing bait shop, Shirahama, Nishimuro-gun, Wakayama, Japan, 8 January 2006, fixed in 99% ethanol by Ko Tomikawa.

Diagnosis

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with broad-petite bars on area VI; areas VI–V–VI ridge pattern λ -shaped; area III without laterally isolated paragnaths; areas VII–VIII with anterior band consisting of two rows; distal dorsal ligule anteriorly conical, subequal in size throughout; falcigers with camerated shaft divided into three partitions; postero-dorsal tentacular cirri extending to chaetiger 5–6.

Description

Holotype of Nereis (Neanthes) linea Treadwell, 1936. Atoke, complete, in good condition, 172 mm LT, 17 mm L15, 4.5 mm W15, with 158 chaetigers. Body colour yellowish (Figure 5A), lacking pigmentation.

Prostomium campanulate (Figure 5B), 1.3 times longer than wide; anterior end broad, distally complete; anterolateral gap aside palpophore broad, twice as wide as basal diameter of

antennae. Nuchal organs deeply embedded, small, subequal to diameter of posterior pair of eyes.

Palpophores sub-conical, thick, 1.5 times longer than wide, as long as four-fifths of entire prostomium; sub-distal transverse groove distinct. Palpostyles oval, two-fifths as wide as diameter of palpophore.

Antennae tapered, thick, short; extending forwards to three-quarters of palpophore and posteriorly to distal quarter of length of prostomium; antennae separated with gap as wide as basal diameter of antennae.

Paired eyes blackish, arranged in trapezoid form; gap between both pairs 2.5 times as wide as diameter of posterior pair of eyes (Figure 5B); anterior pair of eyes reniform, as wide as basal diameter of antennae, gap between both eyes 5 times diameter of eyes, with lens distinct, whitish, covering 35% of eye; posterior pair of eyes rounded, three-quarters as wide as basal diameter of antennae, with lens distinct, whitish, placed mid-posteriorly in eyes and covering 60% of it.

Apodous anterior segment 5 times wider than long, 1.5 times as long as chaetiger 1 (Figure 5B), with even anterior margin, dorsum without marked transverse wrinkles.

Tentacular cirri markedly slender, smooth (Figure 5B); postero-dorsal cirri extending posteriorly to chaetiger 6, 1.5 times as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to chaetiger 3; postero-ventral cirri extended over half of prostomium; antero-ventral cirri as long as three-fifths of postero-ventral cirri and extending to two-thirds of palpophore; cirrophores of anterior cirri ring-shaped, those in posterior cirri cylindrical, postero-dorsal cirrophores 1.5 times as long as antero-dorsal cirrophores, antero-ventral cirrophores broadest, postero-ventral cirrophores narrowest.

Pharynx not everted, previously dissected. Jaws with 10 slightly developed and blunt denticles; pulp cavity with two canals. Pharynx with paragnaths dusky-yellow amber on maxillary ring and brownish paragnaths on oral ring (Figure 5D), consisting of uniform-base cones, except broad-petite bars on area VI; merged paragnaths and plate-like basements absent. Area I: 4, cones of similar size in sub-rhomboidal patch, except proximal cone slightly longer; areas IIa: 17 and IIb: 19, two irregular rows of uneven cones in crescent and markedly curved patch, distal cones curved and longer; area III: 48, four irregular rows of cones with similar size in rectangular patch, without distinct isolated lateral groups; areas IVa: 16 and IVb: 14, four two irregular rows of uneven cones in crescent and markedly curved patch, medial cones longer; area V: 3, linear oblique row of coarse cones with similar size, distal-most cone on same level as paragnaths on area VI; areas VIa: 2 and VIb: 2, one transverse row of uneven, coarse broad-petite bars with blunt tip and melted base (Figure 1J–L, 5D), separated, inner bar slightly longer; areas VII–VIII: 55, two well-separated bands of coarse cones, with anterior band consisting of two transversely aligned rows (furrow row and ridge row with one cone on each region), and posterior band with two transverse rows slightly displaced from each other (furrow row proximal with one cone on each region, ridge row distal with two cones on region A and one or two cones in remaining regions). Areas VI–V–VI ridge pattern, λ -shaped. Gap between area VI and areas VII–VIII broad, as wide as palpophore.

Paired oesophageal caeca present (Figure 5E).

Parapodia with barely distinct, whitish glandular notopodial patches.

Notopodia consisting of dorsal cirrus, dorsal ligule (distal and proximal), and median ligule in biramous parapodia; notopodial prechaetal lobe or notoacicular process not developed throughout.

Dorsal cirri digitiform, thick, short (Figure 5F–J), extending up to three-quarters of distal dorsal ligule throughout; dorsal

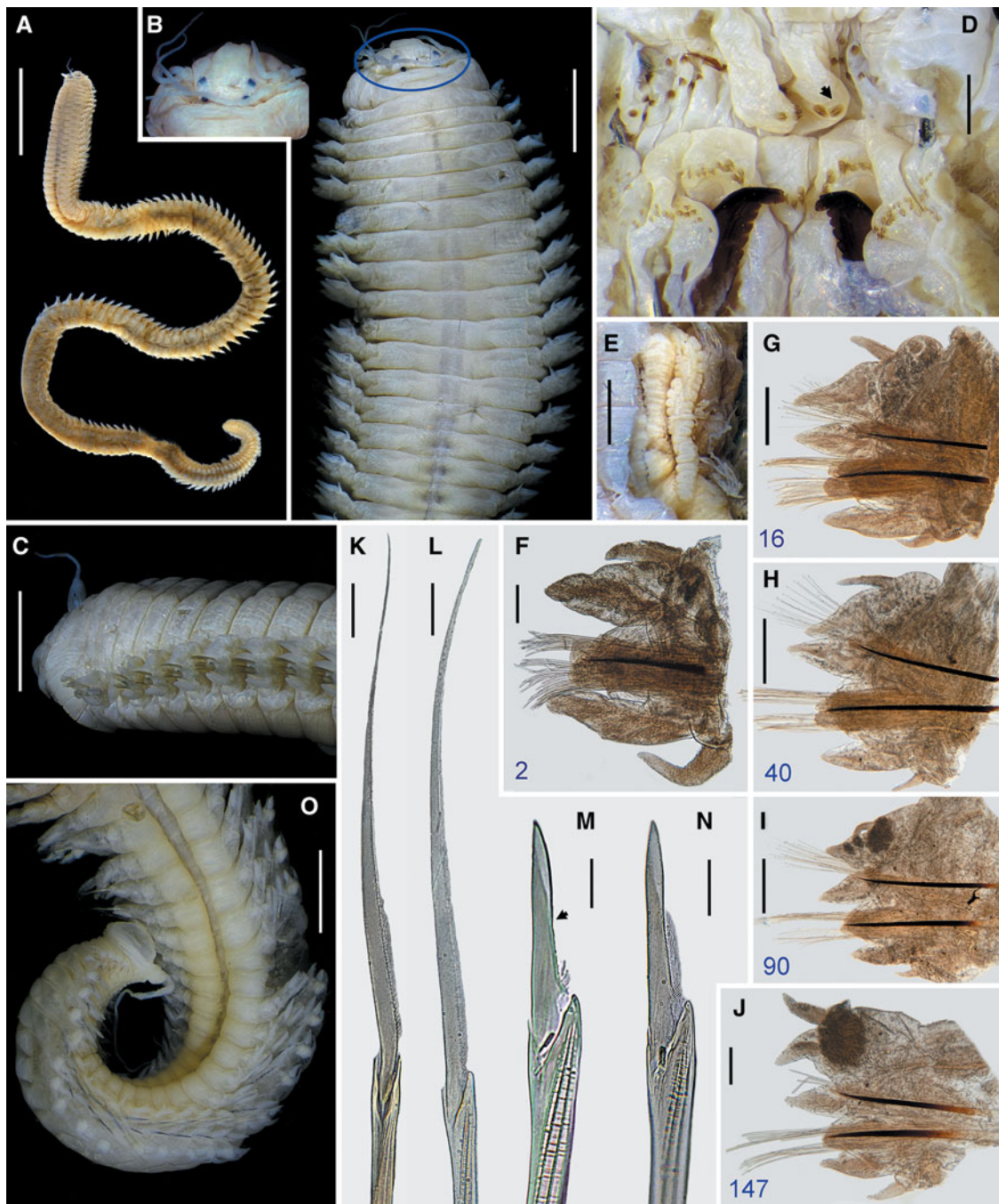


Fig. 5. *Perinereis lineata* (Treadwell, 1936). Holotype (USNM 20115), Amoy (Xiamen), Fujian, China, atoke: (A) whole body in dorsal view; (B) anterior region in dorsal view (frame showing prostomium); (C) anterior region in lateral view; (D) non-everted pharynx in ventral view (arrow pointing broad-petite bar); (E) paired oesophageal glands in ventral view; (F–J) parapodia, numbers refer to the chaetiger; (K) homogomph spiniger from neuropodial supracicular fascicle with medial and distal serrations broken (chaetiger 16); (L) heterogomph spiniger from neuropodial subacicular fascicle (chaetiger 40); (M) heterogomph falciger from neuropodial supracicular fascicle with most serrations broken (chaetiger 16, arrow indicates end of serration); (N) heterogomph falciger from neuropodial subacicular fascicle (chaetiger 16). Scale bars: A, 15 mm; B, C, F, J, O, 2 mm; D, G–I, 0.5 mm; E, 1 mm; K–N, 20 μ m.

cirri longer than proximal ligule in anteriormost parapodia (Figure 5F), subequal in anterior parapodia (Figure 5G), shorter in following parapodia (Figure 5J); dorsal cirri inserted basally to dorsal ligules in anteriormost parapodia, one-third in anterior parapodia (Figure 5G), medially in medial and posterior parapodia (Figure 5H, I), sub-distally in posteriormost parapodia (Figure 5J).

Proximal dorsal ligule even towards posterior end except slightly enlarged in posterior parapodia; shorter than distal dorsal ligule in anteriormost and anterior parapodia, becoming longer than distal dorsal ligule from medial parapodia, 1.3 times as

long as distal dorsal ligule in posterior parapodia (Figure 5I), twice as long as distal dorsal ligule in posteriormost parapodia (Figure 5J); glandular patch massive and sub-oval, more distinct in medial and posterior parapodia (Figure 5I, J).

Distal dorsal ligule extending markedly beyond end of notocaulae throughout (Figure 5G–J); conical (Figure 5C, F–J), subequal or slightly smaller than median ligule throughout (Figure 5G–I), except slightly longer in anteriormost parapodia (Figure 5J); one whitish glandular patch throughout, much smaller than that in proximal dorsal ligule of medial and posterior parapodia (Figure 5J).

Median ligule conical throughout, becoming slightly shorter and narrower from medial parapodia towards posterior end (Figure 5G–J).

Neuropodia consisting of neuroacicular ligule with superior and inferior lobes, ventral ligule, and ventral cirrus; neuropodial postchaetal lobe reduced throughout.

Neuroacicular ligule subequal and twice as wide as ventral ligule throughout (Figure 5F–H), except slightly longer in posterior parapodia.

Superior lobe rounded, subequal to inferior lobe in anterior-most parapodia, becoming shorter than inferior lobe in following ones (Figure 5G, H), reduced in posterior parapodia from chaetiger 87.

Inferior lobe rounded, longer than neuroacicular ligule in first 125 parapodia (Figure 5G, H), becoming shorter and narrower towards posterior end from chaetiger 32.

Ventral ligule conical, thick and subequal to median ligule in anteriormost parapodia (Figure 5C), becoming shorter and slightly narrower in following parapodia (Figure 5I, J).

Ventral cirri digitiform and thick in anteriormost parapodia (Figure 5C, F), becoming conical in following ones; ventral cirri as long as two-thirds of ventral ligule in anteriormost parapodia, as long as one-quarter of ventral ligule in following parapodia.

Pygidium with anal cirri elongated, as long as last 25 chaetigers, with small cirrophores.

Aciculae black, with basal end uncoloured. Notoaciculae absent in chaetigers 1 and 2 (Figure 5F). Neuroaciculae extending beyond distal end of notoaciculae throughout; neuroaciculae as long as two-thirds of median ligule in anterior and medial parapodia, as long as one-half of median ligule in following parapodia (Figure 5J).

Notochaetae all homogomph spinigers; 20–22 spinigers present in anterior and medial parapodia, 15–16 spinigers in posterior parapodia, 3–5 in posteriormost parapodia.

Supracicular neurochaetae consisting of homogomph spinigers and heterogomph falcigers, both present throughout; 3–4 spinigers in anteriormost, anterior and medial parapodia, 7–8 spinigers in posterior parapodia, 4–5 spinigers in posteriormost parapodia; 7–8 falcigers present in anteriormost parapodia, 12–13 falcigers in anterior parapodia, 8–9 falcigers in medial parapodia, 6–7 falcigers in posterior parapodia, 4–5 falcigers in posteriormost parapodia.

Subacicular neurochaetae consisting of heterogomph spinigers and heterogomph falcigers, both present throughout; 5–6 spinigers in anteriormost and anterior parapodia, 3–4 spinigers in medial and posterior parapodia, 1–2 spinigers in posteriormost parapodia; 21–24 falcigers in anteriormost parapodia, 15–18 falcigers in anterior parapodia, 12–14 falcigers in medial parapodia, 9–10 falcigers in posterior parapodia, 6–7 falcigers in posteriormost parapodia.

Blades of both homogomph (Figure 5K) and heterogomph (Figure 5L) spinigers finely serrated towards toothed edge, evenly spaced, long with high b/a ratio (8.5–13). Blades of heterogomph falcigers long with low b/a ratio (2.3–3.3), slender, straight, distal end club-shaped with incurved terminal tooth very long forming distinct tendon (equalling about two-fifths of total blade length: 0.36–0.38); blades of falcigers partially serrated, with serrations capilliform, curved, looking upwards, present in about one-third (0.34–0.35) of total blade length (Figure 5M, N); vertex between distal and basal end on serrated edge markedly prominent, sub-conical. Shaft of falcigers camerated, with cavity divided sub-distally into three longitudinal partitions (Figure 5N).

Holotype of Nereis (Neanthes) orientalis Treadwell, 1936. Epitoke male, incomplete, possibly only a few posterior chaetigers missing, relatively in good condition, anterior region almost detached,

strongly dissected at third and fourth chaetigers (parapodia missing), 74 mm LT, 15 mm L15, 6 mm W15, with 112 chaetigers. Body colour brownish (Figure 6A), with a transverse pale brown line on distal third of dorsum and venter of all chaetigers, whitish pigmentation in dorsum and venter of natatory chaetigers.

Prostomium campanulate, slightly wider than long (Figure 6B); anterior end broad, distally complete; anterolateral gap aside palpophore broad, twice as wide as basal diameter of antennae. Nuchal organs deeply embedded, small, subequal to diameter posterior pair of eyes.

Palpophores oval, thick (Figure 6C), slightly wider than long, as long as three-fifths of entire prostomium; sub-distal transverse groove distinct. Palpostyles oval, one-third as wide as diameter of palpophore.

Antennae tapered, thick, short (Figure 6C); extending forwards to tip of palpophore, posteriorly to distal quarter of length of prostomium; antennae separated, with gap as wide as basal diameter of antennae.

Paired eyes blackish, slightly enlarged, arranged in a trapezoid form; gap between both pairs as wide as diameter of posterior pair of eyes (Figure 6B); anterior pair of eyes rounded, 1.7 times as wide as basal diameter of antennae, gap between both eyes as wide as 3.5 times diameter of eyes, with lens distinct, whitish, covering 70% of eye; posterior pair of eyes rounded, as wide as diameter of anterior pair, with lens distinct, whitish, placed mid-posteriorly in eyes and covering 60% of it.

Apodous anterior segment 4 times wider than long, 1.5 times as long as chaetiger 1 (Figure 6B), with even anterior margin, dorsum without marked transverse wrinkles.

Tentacular cirri thickened, smooth (Figure 6B); postero-dorsal cirri extending posteriorly to chaetiger 5, 1.5 times as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to chaetiger 2; postero-ventral cirri extended over half of prostomium; antero-ventral cirri as long as four-fifths of postero-ventral cirri and extending beyond palpophore; cirrophores of anterior cirri ring-shaped, those in posterior cirri cylindrical, postero-dorsal cirrophores 1.3 times as long as antero-dorsal cirrophores, antero-ventral cirrophores broadest, postero-ventral ones narrowest.

Pharynx not everted, previously dissected. Jaws with three barely developed denticles; pulp cavity with two canals. Pharynx with paragnaths dusky-yellow amber on maxillary ring (Figure 6D) and brownish paragnaths on oral ring (Figure 6D, E), consisting of uniform-base cones, except broad-petite bars on area VI; merged paragnaths and plate-like basements absent. Area I: 2, one longitudinal row of cones with similar size; areas IIa: 18 and IIb: 19, two irregular rows of uneven cones in crescent, markedly curved patch, distal cones curved and longer; area III: 47, four irregular rows of cones with similar size in rectangular patch, with distinct isolated lateral groups; areas IVa: 14 and IVb: 17, two irregular rows of uneven cones in crescent, markedly curved patch, medial cones longer; area V: 3, triangular patch of coarse cones of similar size, two proximal cones in transverse row and single distal cone on same level as paragnaths on area VI; areas VIa: 2 and VIb: 2, one oblique row of uneven broad-petite bars with rounded tip and melted base (Figure 1G–I, 6D, E), separated, inner bar slightly longer; areas VII–VIII: 39, two well-separated bands of coarse cones, with anterior band consisting of two transversely aligned rows (furrow row and ridge row with one cone on each region), and posterior band with two transverse rows slightly displaced from each other (furrow row proximal with one cone on each region, ridge row distal with two cones on region A and one cone in remaining regions). Areas VI–V–VI ridge pattern, λ -shaped. Gap between area VI and areas VII–VIII broad, as wide as palpophore (Figure 6D, E).

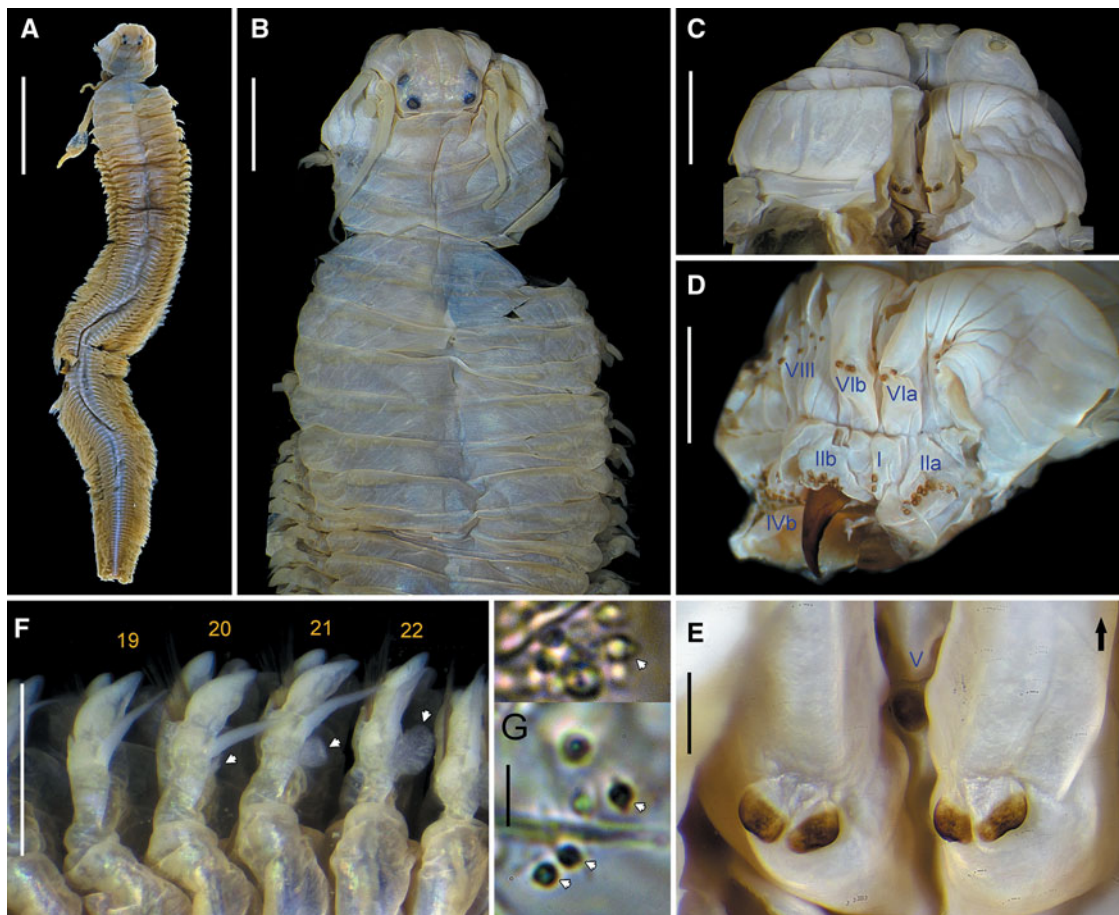


Fig. 6. *Perinereis lineata* (Treadwell, 1936). Holotype of *Nereis (Neanthes) orientalis* Treadwell, 1936 (USNM 20116), Amoy (Xiamen), Fujian, China, epitoke male: (A) whole body in dorsal view; (B) anterior region in dorsal view; (C) buccal region in ventral view; (D) everted pharynx in dorso-lateral view; (E) dorsal areas of oral ring of non-everted pharynx (arrow pointing orientation of prostomium); (F) right parapodia from chaetigers 19–22 in dorsal view (arrows pointing upper lobe of dorsal ligule); (G) mature sperm pointed by arrows. Scale bars: A, 10 mm; B, D, 3 mm; C, E, F, 2 mm; G, 5 μ m.

Paired oesophageal caeca present.

Parapodia with distinct, whitish glandular notopodial patches.

Body regionalized into two distinct sections (Figures 6A, F, 7A): 19 pre-natatory chaetigers and 93 natatory chaetigers but incomplete, becoming gradually slender towards posterior end.

Pre-natatory chaetigers with notopodia consisting of dorsal cirrus, dorsal ligule (distal and proximal), and median ligule in biramous parapodia; and neuropodia consisting of neuroacicular ligule with superior and inferior lobes, ventral ligule, and ventral cirrus. First eight dorsal and ventral cirri modified: dorsal cirri teardrop-shaped with distinctly convex upper edge, markedly longer than distal dorsal ligule in parapodia 1–2 (Figure 7B), becoming narrower and barely longer than dorsal ligule in parapodia 3–7, dorsal cirri broad and slightly papillated ventrolaterally in parapodia 8 (Figure 7C); ventral cirri tapering, thick, acuminate, subequal to ventral ligule in parapodia 1–2 (Figure 7B), becoming narrower and shorter than ventral ligule in parapodia 3–8 (Figure 7C). Dorsal and ventral cirri of parapodia 9–19 unmodified, cirriform (Figure 7D). Distal dorsal ligules digitiform in parapodia 1–2 (Figure 7B), conical in following parapodia; slightly longer than median ligule throughout.

Natatory chaetigers with notopodia consisting of dorsal cirrus, unilobate distal dorsal ligule, unilobate proximal dorsal ligule, notopodial prechaetal lobe, and unilobate median ligule; neuropodia consisting of neuroacicular ligule with superior and inferior lobes, neuropodial postchaetal lobe, unilobate ventral ligule, ventral cirrus, and tri-lobate cirrophore of ventral cirrus. Dorsal cirri elongated, 1.5 times as long as proximal dorsal ligule in anterior and medial parapodia (Figure 7E, F), subequal to proximal dorsal

ligule in following parapodia; dorsal cirri with ventrolateral papillae in parapodia 25–95 (Figure 7F), 3 papillae in first papillated parapodia, up to 8 papillae reached in medial parapodia. Ventral cirri elongated, longer than ventral ligule in anterior parapodia (Figure 7E), slightly shorter in following parapodia; ventral cirri with two sub-distal, barely developed papillae in anterior parapodia, absent in following parapodia. Ventral cirri cirrophore with reniform lower lobe present from parapodia 20 (Figure 7A) but markedly enlarged from parapodia 23 to posterior end, digitiform upper lobe present from parapodia 22 to posterior end, and digitiform upper secondary lobe present from parapodia 23 to posterior end, shorter than upper lobe. Proximal dorsal ligule with reniform upper lobe present from parapodia 20 but markedly enlarged from parapodia 25 to posterior end (Figure 7E–G). Distal dorsal ligule lanceolate, slightly elongated, lamellar, with a basal, knob-shaped upper secondary lobe. Notopodial prechaetal lobe enlarged, short, wider than long. Median ligule sub-oval, slightly elongated, barely lamellar, with a basal lower secondary lobe from parapodia 25 to posterior end, reniform in medial parapodia (Figure 7G), digitiform in anterior and posterior parapodia (Figures 7E, H). Neuroacicular ligule slightly elongated and slender, subequal or barely longer than ventral ligule throughout. Neuropodial postchaetal lobe with upper lamella in parapodia 24, enlarged in parapodia 26 but broad flabellate from about parapodia 28 towards posterior end (Figure 7F, G). Superior lobe rounded, not enlarged. Inferior lobe enlarged, rounded, lamellar. Ventral ligule slightly elongated, barely lamellar, sub-oval, with a bluntly conical and basal upper secondary lobe from parapodia 23 to posterior end, more distinct in

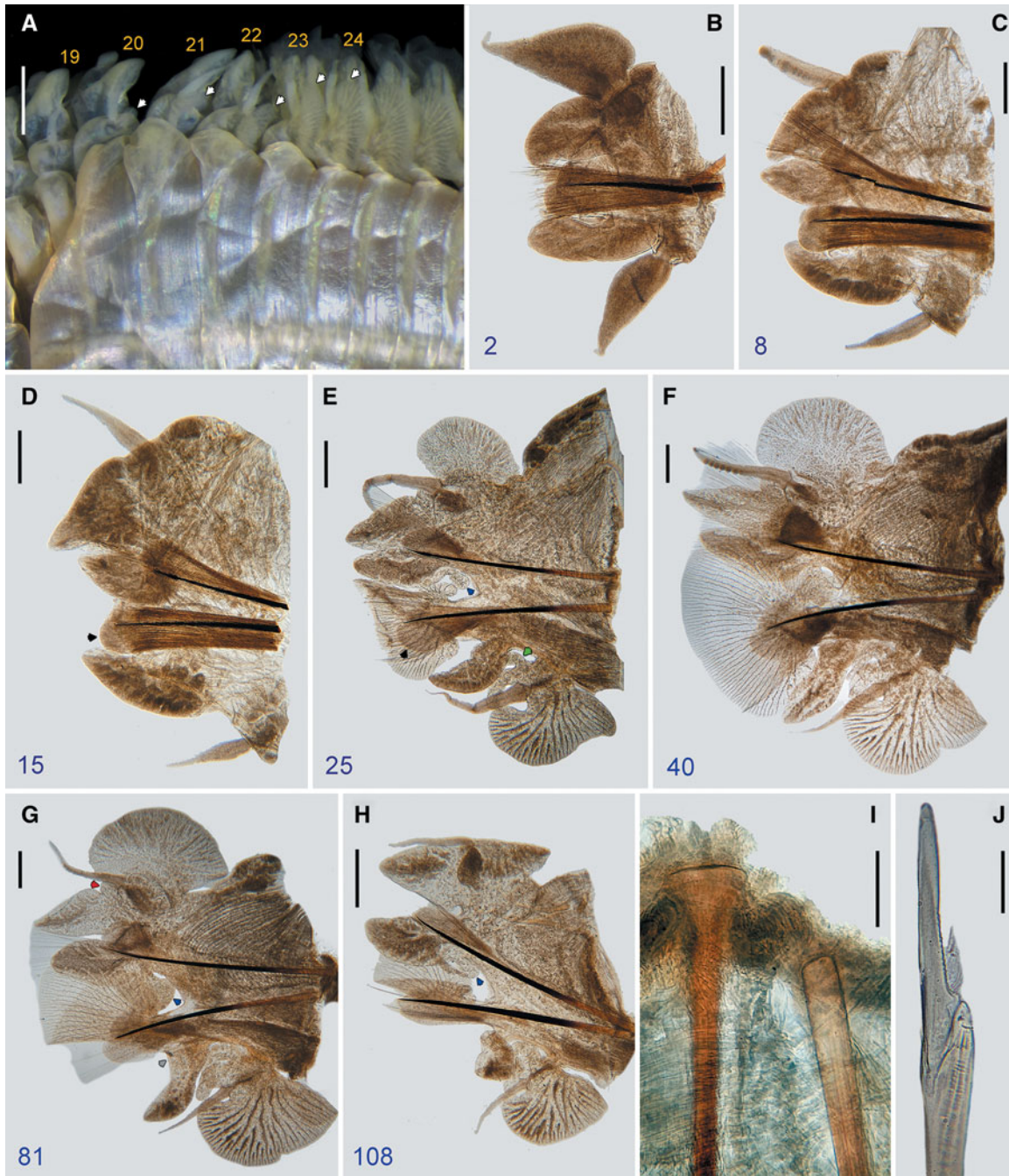


Fig. 7. *Perinereis linea* (Treadwell, 1936). Holotype of *Nereis (Neanthes) orientalis* Treadwell, 1936 (USNM 20116), Amoy (Xiamen), Fujian, China, epitoke male: (A) left parapodia from chaetigers 19–26 in ventral view (arrows pointing lower lobe of ventral cirri cirrophore); (B–H) parapodia, numbers refer to the chaetiger (black arrow pointing inferior lobe; blue arrow pointing lower secondary lobe of median ligule; green arrow pointing upper secondary lobe of ventral cirri cirrophore; grey arrow pointing upper secondary lobe of ventral ligule; red arrow pointing upper secondary lobe of distal dorsal ligule); (I) basal end of notoacicula (left) and neuroacicula (right) (chaetiger 40); (J) heterogomph falciger from neuropodial subacicular fascicle (chaetiger 2). Scale bars: A, 1 mm; B–G, 0.5 mm; H, I, 0.2 mm; J, 20 μ m.

medial parapodia (Figure 7F, G). Notoaciculae with expanded basal end (Figure 7I). Atoke chaetae not entirely replaced, only a few remain. Epitoke chaetae paddle-like, present in both noto-chaetae and neurochaetae from parapodia 25 to posterior end; spinigers and falcigers (Figure 7J) as atoke holotype of *N. (Neanthes) linea*.

Pygidium missing.

Spermatozoa with spherical head, somewhat-inflated conical acrosome, and long flagellum (ect-aquasperm type) (Figure 6G).

Holotype of *Perinereis vancaurica tetradentata* Imajima, 1972. Atoke, complete but regenerating posterior end, in good condition, 192 mm LT, 16.5 mm L15, 5 mm W15, with 172 chaetigers.

Body colour greyish brown (Figure 8A, B), pigmentation completely faded, except brownish posterior dorsum of prostomium.

Prostomium campanulate (Figure 8A), slightly longer than wide; anterior end broad, distally complete; anterolateral gap aside palpophore broad, twice as wide as basal diameter of antennae.

Palpophores sub-conical, thick (Figure 8A), 1.5 times longer than wide, as long as entire prostomium; sub-distal transverse groove distinct. Palpostyles oval, one-third as wide as diameter of palpophore.

Antennae tapered, thick, short (Figure 8A); extending forwards to tip of palpophore and posteriorly to distal third of length of prostomium; antennae separated with gap as wide as basal diameter of antennae.

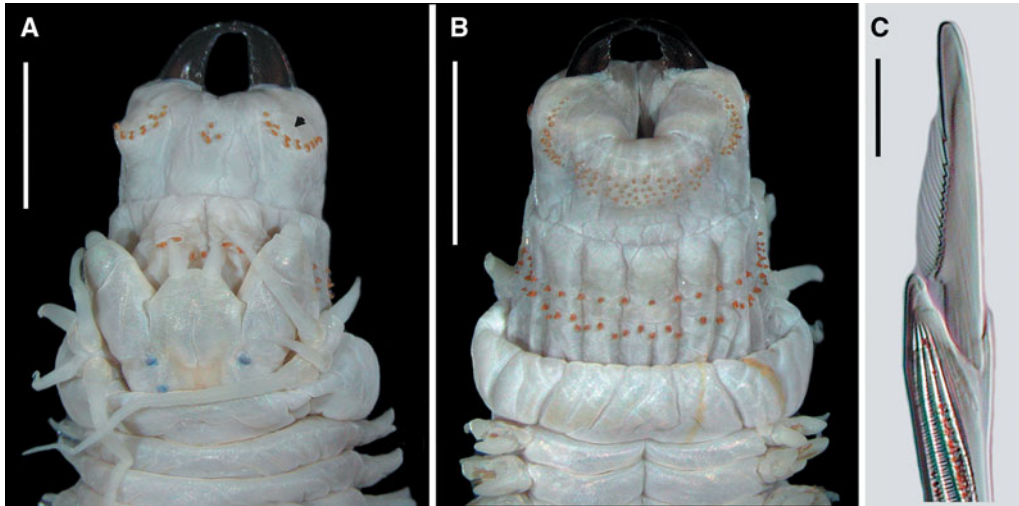


Fig. 8. *Perinereis linea* (Treadwell, 1936). (A–C) Holotype of *P. vancaurica tetradentata* Imajima, 1972 (NSMT-Pol-H78), Tokyo, Japan, atoke. (A) Anterior region in dorsal view (arrows pointing concave edge of rows on area II); (B) anterior region in ventral view; (C) heterogomph falciger in neuropodial supracircular fascicle (anterior chaetiger). Scale bars: A, B, 2 mm; C, 20 μ m.

Paired eyes blackish, arranged in trapezoid form (Figure 8A); gap between both pairs 2.3 times as wide as diameter of posterior pair of eyes; anterior pair of eyes reniform, two-thirds as wide as basal diameter of antennae, gap between both eyes as wide as 6 times diameter of eyes, with lens distinct, whitish, covering 75% of eye; posterior pair of eyes rounded, two-thirds as wide as basal diameter of antennae, with lens distinct, whitish, placed mid-posteriorly in eyes and covering 60% of it.

Apodous anterior segment (Figure 8A) 6 times wider than long, 1.5 times as long as chaetiger 1, with even anterior margin, dorsum without marked transverse wrinkles.

Tentacular cirri smooth (Figure 8A); postero-dorsal cirri extending posteriorly to chaetiger 6, twice as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to chaetiger 2; postero-ventral cirri extended over first quarter of prostomium; antero-ventral cirri as long as one-third of postero-ventral cirri and extending to three-quarters of palpophore; cirrophores cylindrical, except ring-shaped postero-ventral one, postero-dorsal cirrophores 1.5 times as long as antero-dorsal cirrophores, antero-ventral cirrophores broadest, postero-ventral ones narrowest.

Pharynx everted (Figure 8A, B). Jaws with 7 well-developed and blunt denticles; pulp cavity with two canals. Pharynx with paragnaths orange-amber on maxillary and oral rings (Figure 8A, B), consisting of uniform-base cones, except broad-petite bars on area VI; merged paragnaths and plate-like basements absent. Area I: 4, cones of similar size in sub-rhomboidal patch, except proximal cone slightly longer; areas IIa: 19 and IIb: 21, two irregular rows of uneven cones in crescent and markedly curved patch, distal cones curved and longer; area III: 55, four irregular rows of cones with similar size in sub-rectangular patch, without distinct isolated lateral groups; areas IVa: 23 and IVb: 24, three irregular rows of uneven cones in crescent, markedly curved patch, medial cones longer; area V: 3, triangular patch of coarse cones of similar size, two proximal cones in transverse row and single distal cone slightly behind paragnaths on area VI; areas VIa: 2 and VIb: 2, one row of even broad-petite bars with slightly pointed tip, separated; areas VII–VIII: 69, two well-separated bands of cones, with anterior band consisting of two transversely aligned rows (furrow row and ridge row with one cone on each region, former with cones slightly stouter), and posterior band with two transverse rows slightly displaced from each other (furrow row proximal with one cone on each region, ridge row distal with three cones on region A and one

or three cones in remaining regions). Areas VI–V–VI ridge pattern, λ -shaped. Gap between area VI and areas VII–VIII broad, as wide as palpophore.

Notopodia consisting of dorsal cirrus, dorsal ligule (distal and proximal), and median ligule in biramous parapodia; notopodial prechaetal lobe or notoacicular process not developed throughout.

Dorsal cirri from cirriform to conical, thick, short, extending up to three-quarters of distal dorsal ligule throughout; dorsal cirri longer than proximal ligule in anteriormost parapodia, subequal in anterior parapodia, shorter in following parapodia; dorsal cirri inserted basally to dorsal ligules in anteriormost parapodia, one-third in anterior parapodia, medially in medial and posterior parapodia, sub-distally in posteriormost parapodia.

Proximal dorsal ligule even towards posterior end except slightly enlarged in posterior parapodia; shorter than distal dorsal ligule in anterior parapodia, becoming longer than distal dorsal ligule from medial parapodia to end of body.

Distal dorsal ligule extending markedly beyond end of notoacicular throughout; conical, subequal or slightly smaller than median ligule throughout.

Median ligule conical throughout, becoming slightly shorter and narrower from medial parapodia towards posterior end.

Neuropodia consisting of neuroacicular ligule with superior and inferior lobes, ventral ligule, and ventral cirrus; neuropodial postchaetal lobe reduced throughout.

Neuroacicular ligule shorter than ventral ligule in anterior parapodia, becoming slightly longer in following chaetigers, subequal to ventral ligule in posterior parapodia; neuroacicular ligule twice as wide as ventral ligule throughout.

Superior lobe rounded, slightly shorter than inferior lobe in anterior parapodia, reduced from medial parapodia towards posterior end.

Inferior lobe rounded, longer than neuroacicular ligule in anterior and medial parapodia, becoming shorter and narrower towards posterior end.

Ventral ligule bluntly conical, thick and as long as three-quarters of median ligule in anterior parapodia, becoming conical and shorter in following parapodia.

Ventral cirri conical, thick and as long as one half of ventral ligule in anterior parapodia, becoming narrower and distinctly shorter, barely reaching base of ventral ligule in medial parapodia, shorter in posterior parapodia.

Pygidium regenerating, anal cirri missing.

Aciculae black, with basal end uncoloured. Notoaciculae absent in chaetigers 1 and 2. Neuroaciculae extending beyond distal end of notoaciculae throughout body.

Notochaetae all homogomph spinigers, present throughout. Supracicular neurochaetae consisting of homogomph spinigers and heterogomph falcigers, both present throughout. Subacicular neurochaetae consisting of heterogomph spinigers and heterogomph falcigers, both present throughout.

Blades of both homogomph and heterogomph spinigers finely serrated towards toothed edge, evenly spaced, long with high *b/a* ratio. Blades of heterogomph falcigers long with low *b/a* ratio, slender, straight, distal end club-shaped with incurved terminal tooth forming very long tendon (equalling about one-third of total blade length); blades of falcigers partially serrated, with serrations capilliform, curved, looking upwards, present in about two-fifths of total blade length (Figure 8C); vertex between distal and basal end on serrated edge markedly prominent, sub-conical. Shaft of falcigers camerated, with cavity divided sub-distally into three longitudinal partitions (Figure 8C).

Non-type material from Korea. Atoke, complete, in good condition (NIBRIV0000783811), 154 mm LT, 21.8 mm L15, 5.2 mm W15, with 148 chaetigers. Body colour cream in preserved specimens, living individuals with dark green dorsum. Prostomium campanulate (Figure 9A), as long as wide; anterior end broad, distally complete; anterolateral gap aside palpophore broad. Palpophores sub-conical, thick (Figure 9A), longer than wide; sub-distal transverse groove distinct. Palpostyles oval. Antennae tapered, thick, short (Figure 9A), distinctly separated from each other. Paired eyes blackish, arranged in trapezoid form, medium sized; anterior pair of eyes reniform, posterior pair rounded, both pairs well-separated from each other (Figure 9A), with lens distinct, whitish, large (Figure 9A), placed mid-posteriorly in posterior pair of eyes. Apodous anterior segment longer than chaetiger 1 (Figure 9A). Tentacular cirri smooth, medium-sized (Figure 9A); postero-dorsal cirri extending posteriorly to chaetiger 6, twice as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to chaetiger 4; postero-ventral cirri extended over two-thirds of prostomium antero-ventral cirri as long as three-fourths of postero-ventral cirri and extending to three-fourths of palpophore; cirrophores of anterior cirri ring-shaped, those in posterior cirri cylindrical, postero-dorsal cirrophores 1.5 times as long as antero-dorsal cirrophores, antero-ventral cirrophores broadest, postero-ventral ones narrowest.

Pharynx with dark brown jaws, 9 denticles; pulp cavity with two canals. Paragnaths on maxillary and oral rings (Figures 9A–C) consisting of uniform-base cones, except broad-petite bars on area VI (Figure 9A); merged paragnaths and plate-like basements absent. Area I: 5 (2–8) in rhombus patch; areas IIa: 23 (8–25) and IIb: 20 (10–25), 2–3 rows of uneven cones in crescent patch, distal cones curved and longer; area III: 48 (32–70), 4–5 rows of cones with similar size in sub-rectangular patch, without lateral isolated groups; areas IVa: 23 (11–26) and IVb: 21 (13–31), three rows of uneven cones in crescent patch, medial cones longer; area V: 2 (2–5), coarse cones in triangular patch; areas VIa: 2 (seldom 1–3) and VIb: 2 (seldom 1–3), one row of broad-petite bars with tip slightly pointed or rounded (seldom one conical paragnath instead of a bar), separated, inner bars sometimes slightly longer; areas VII–VIII: 58 (43–81), two well-separated bands of cones, with anterior band consisting of two transversely aligned rows (furrow row and ridge row with one cone on each region, former with cones slightly stouter), and posterior band with two transverse rows slightly displaced from each other (furrow row proximal with one stout cone on each region, ridge row distal with 1–2 cones on region A and 1–3 cones in remaining regions). Areas VI–V–VI

ridge pattern, λ -shaped. Gap between area VI and areas VII–VIII subequal or as broad as three-quarters of palpophore.

Dorsal cirri from cirriform to conical, thick, short, extending up to three-quarters of distal dorsal ligule throughout, sub-distally inserted to dorsal ligule in posterior parapodia. Proximal dorsal ligule slightly enlarged in posterior parapodia; distal dorsal ligule conical, subequal to median ligule throughout. Notopodial prechaetal lobe reduced, sometimes notoacicular papillae in anterior parapodia of large specimens. Median ligule conical. Neuroacicular ligule shorter than ventral ligule in anterior parapodia, becoming longer towards posterior end. Superior and inferior lobes present in anterior and medial parapodia, subequal in length. Neuropodial postchaetal lobe reduced. Ventral ligule conical, shorter than median ligule throughout, as long as one-half of median ligule in posterior parapodia. Ventral cirri conical, thick, distinctly shorter than ventral ligule.

Pygidium with tapering cylindrical anal cirri.

Aciculae black, with basal end uncoloured. Notoaciculae absent in chaetigers 1 and 2. Neuroaciculae extending beyond distal end of notoaciculae throughout. Notochaetae all homogomph spinigers, present throughout. Supracicular neurochaetae consisting of homogomph spinigers and heterogomph falcigers, both present throughout. Subacicular neurochaetae consisting of heterogomph spinigers and heterogomph falcigers, both present throughout. Blades of both homogomph (Figure 9K) and heterogomph spinigers (Figure 9J) finely serrated, long. Blades of heterogomph falcigers long, slender, straight, distal end club-shaped with incurved terminal tooth very long forming distinct tendon (equalling about one-third of total blade length); blades of falcigers partially serrated, with serrations capilliform, curved, looking upwards, present in about one-third to two-fifths of total blade length (Figure 9I); vertex markedly prominent, sub-conical. Shaft of falcigers camerated, with cavity divided sub-distally into three longitudinal partitions (Figure 9I).

DNA sequence data

Locality: Several localities in Korea and another possibly from China (NIBRIV0000810291, NIBRIV0000810299; Table 1). GenBank accession numbers: MT511711–MT511715 (COI), MT540476–MT540480 (16S rDNA) (Table 1). Aligned length of sequences: 622 bp fragment from COI obtained with primer pair polyLCO/polyHCO (Carr *et al.*, 2011; Table 2), 479 bp fragment from 16S rDNA obtained with primer pair 16SarL/16SbrH (Palumbi, 1996). Intraspecific genetic distances did not exceed 1% for both genes (Table 3).

Remarks

Perinereis linea (Treadwell, 1936) belongs to the *P. aibuhitensis* species group featured by having short dorsal cirri throughout the body and heterogomph falcigers' blades straight with incurved terminal tooth markedly elongated forming a distinct tendon. *Perinereis linea* resembles *P. babuzai* comb. nov. and *P. singaporiensis* because they share the areas VI–V–VI ridge pattern λ -shaped (Figures 5D, 6E, 8A, 9A), contrary to the π -shaped pattern present in the remaining species of the group (Figure 4F), including *P. aibuhitensis* (Figure 3A, B). Nonetheless, in *P. linea*, area VI has broad-petite bars (Figures 5D, 6E, 8A, 9A), whereas *P. singaporiensis* has long smooth-bars in area VI. In *P. linea*, the distal dorsal ligules are conical in anterior parapodia (Figures 5G, 6D, 9E), whereas in *P. singaporiensis* they are bluntly rounded in the same parapodia. In *P. linea*, the distal dorsal ligule is subequal to the median ligule in posterior parapodia (Figures 5I, J, 9G, H), whereas in *P. singaporiensis* they project beyond median ligule in the same parapodia. In *P. linea*, the area III lacks laterally isolated paragnaths (Figures 5D, 8B, 9B), present in *P. singaporiensis*. Finally, in *P. linea* the area V has usually

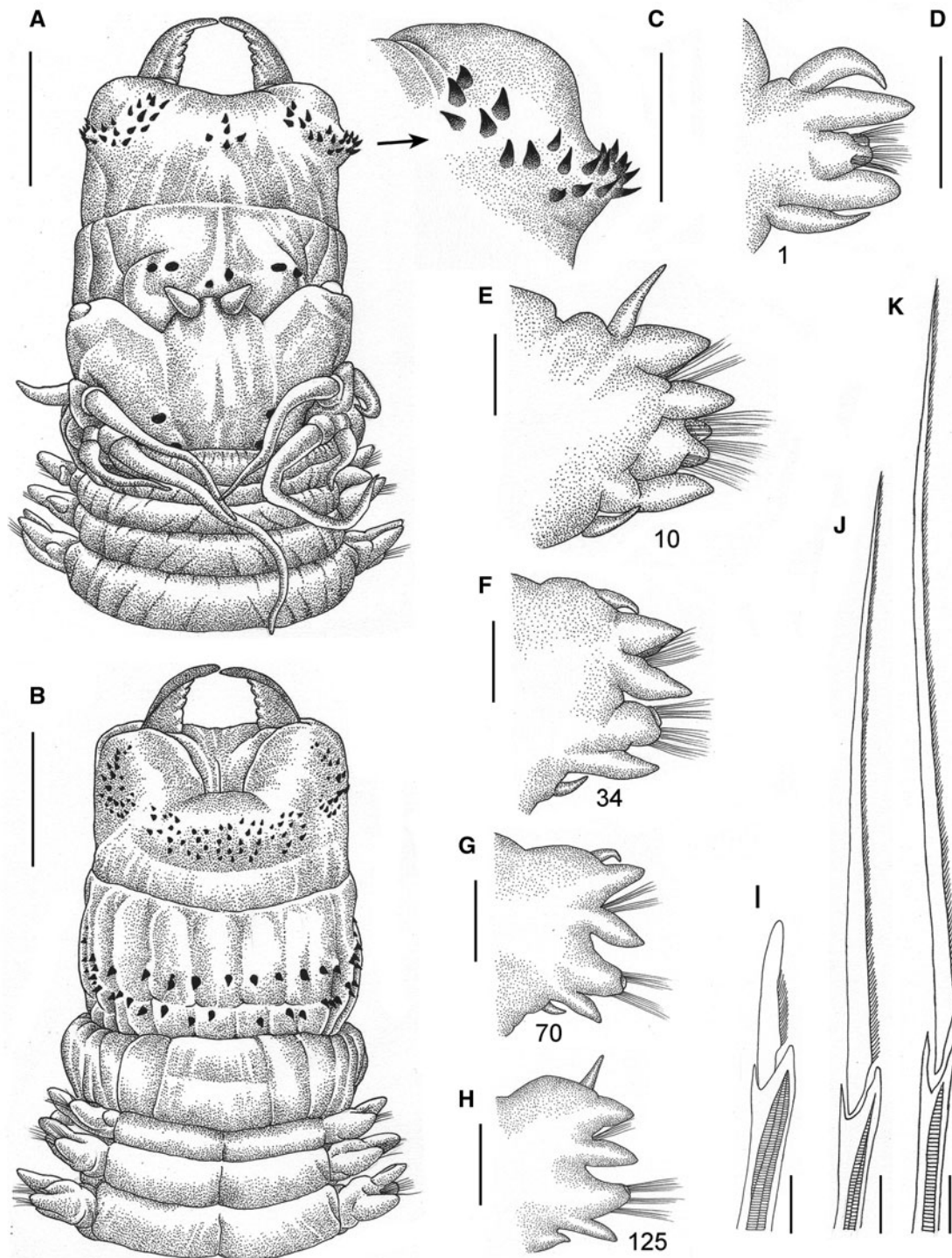


Fig. 9. *Perinereis lineae* (Treadwell, 1936). Non-types from Ganghwo Island, Korea: (A–C) NIBRIV0000783811; (D–K) NIBRIV0000783812. (A) Anterior region in dorsal view; (B) anterior region in ventral view; (C) right flank of maxillary ring (note curved paragnaths on area II); (D–H) parapodia, numbers refer to the chaetiger; (I) heterogomph falciger from neuropodial supracicular fascicle (chaetiger 34); (J) heterogomph spiniger from neuropodial subacicular fascicle (chaetiger 70); (K) homogomph spiniger from notochoetae (chaetiger 34). Scale bars: A, B, 2 mm; C–H, 1 mm; I–K, 20 μ m.

three (seldom 4–5) paragnaths, whereas *P. singaporiensis* usually has one paragnath (rarely none) in the same area. On the contrary, *P. lineae* is readily distinguished from *P. babuzai* comb. nov. by the distal dorsal ligule of medium size and projecting markedly beyond the notoacicular (short, barely projected in *P. babuzai*).

Treadwell (1936) described *Nereis* (*Neanthes*) *lineae* and *N. (Neanthes) orientalis* as new species from Amoy, China, based upon single atoke and epitoke specimens, respectively. Hartman (1938) re-examined the type materials and regarded

both species as identical to *P. aibuhitensis* (Grube, 1878) from Palau, no further details on the synonymies were given although both species were treated as synonyms of *P. aibuhitensis* in further studies (Hartman, 1956, 1959). Later, Wu (1967) reviewed some nereidid species from Taiwan, including *N. (Neanthes) lineae* which was considered valid in *Perinereis*; however, it was distinguished from *P. aibuhitensis* by having area I with four paragnaths in a quadrate arrangement (area I with 1–2 in *P. aibuhitensis*) and postero-dorsal tentacular cirri extending to chaetiger 6 (chaetigers 2–5 in *P. aibuhitensis*). It is noteworthy that Olga Hartman read

the first draft of Wu's study (Wu, 1967: 74) and likely recognized the treatment of *P. linea* as a species different from *P. aibuhitensis*, although any argumentations were given by Wu (1967).

Imajima (1972) described *P. vancaurica tetradentata* from Tokyo (Japan) based upon a single specimen and distinguished from the stem species by having area I with four cones in a cross (two in *P. vancaurica*) and from *P. linea* by presenting area V with cones in a triangle (longitudinal row in *P. linea*); likewise, the single record of *P. linea* from Taiwan (Wu, 1967) was included in the subspecies. Subsequently, Paik (1975, 1977, 1989), following Imajima's (1972) study, repeatedly recorded *P. vancaurica tetradentata* from several localities in the south and west of Korea.

Wu *et al.* (1985) synonymized Treadwell's species *N. (Neanthes) linea* and *N. (Neanthes) orientalis* with *P. aibuhitensis* based upon the original descriptions and atoke and epitoke individuals from China, although no argumentations on the proposal of synonymies were provided. They recorded the species from the Yellow Sea's subtropical waters until Xiamen and Taiwan, but it was also recorded in Hainan's tropical island. On the other hand, *P. vancaurica tetradentata* and its records from Korea (e.g. Paik, 1975, 1977, 1989), and *P. linea* from Taiwan (Wu, 1967), were not included in the monography. Hutchings *et al.* (1991) reviewed *Perinereis* species recorded from Australia, including the type material of *P. aibuhitensis*. They maintained *N. (Neanthes) linea* and *N. (Neanthes) orientalis* as junior synonyms of *P. aibuhitensis* based upon the literature; however, after examining the type material of *P. vancaurica* and compared with the original description of *P. vancaurica tetradentata*, they considered the latter as a synonym of the stem species.

Lee *et al.* (1992) studied *P. aibuhitensis* from Korea's western coast, using both atoke and epitoke specimens. They stated that the variation on the number, arrangement and shape of paragnaths has led to confusion of *P. aibuhitensis* with other species such as *N. (Neanthes) linea*, *N. (Neanthes) orientalis*, *P. vancaurica tetradentata*, and even *Neanthes virens* Sars, 1835 (= *Alitta sensu* Bakken & Wilson, 2005). They also maintained both Treadwell's species as *P. aibuhitensis*, but proposed *P. vancaurica tetradentata* as a junior synonym of *P. aibuhitensis*. Later, Imajima (1996) recognized the synonymy of his subspecies. Khebovich (1996) and Sun & Yang (2004) examined specimens of *P. aibuhitensis* from Korea and China. They continued considering *N. (Neanthes) linea* and *N. (Neanthes) orientalis* synonyms mostly based upon Wu *et al.* (1985), although *P. vancaurica tetradentata* was not mentioned either.

More recently, Arias *et al.* (2013) reinstated and featured *P. linea* by combining specimens from Spain, Korea, and China. They presented it as a redescription even though the type material was not examined. Their available specimens of *P. linea* were compared to and distinguished from Australian specimens of *P. aibuhitensis* by having area III without lateral groups of paragnaths (present in *P. aibuhitensis*), area II with crescentic rows of paragnaths (short and straight rows in *P. aibuhitensis*), and epitokes with 28–29 pre-natatory chaetigers (21–23 chaetigers in *P. aibuhitensis*). Likewise, they deemed *P. linea* as an alien species in the Mar Menor lagoon, Spain (Western Mediterranean), after determining fish bait importation as the possible vector of introduction and studying some reproductive and ecological traits from the population. Moreover, they suggested that *P. linea* may be similar to *P. vancaurica tetradentata*, and this was later supported by Sato (2017) after examining the subspecies type specimen.

In the present study, we confirm *P. linea* as a senior synonym of *P. vancaurica tetradentata* and propose the former species as a senior synonym of *N. (Neanthes) orientalis* based on the examination and redescription of type materials and comparison with one type specimen and topotypes of *P. aibuhitensis*.

The redescription of the type material of *N. (Neanthes) linea* matches consistently with the original description except that the paragnaths on area V are arranged in a triangle instead of the longitudinal row reported by Treadwell (1936). The morphological characters of atoke holotype of *N. (Neanthes) linea* and the non-modified features of epitoke type specimen of *N. (Neanthes) orientalis* are identical to each other, such as the areas VI–V–VI ridge pattern, the shape, and arrangement of paragnaths, the type of falcigers, among others. These two nominal species were described in the same publication as new species (Treadwell, 1936). However, since *N. (Neanthes) linea* is valid nowadays in *Perinereis* and the type specimen of *N. (Neanthes) orientalis* is in a reproductive stage, we consider *P. linea* has priority over *N. (Neanthes) orientalis* (ICZN, 1999, Arts 24.2.1, 24.2.2.).

The atoke morphology of *P. linea*'s specimens and that of the holotype of *P. vancaurica tetradentata* is similar. Some slight differences between both species can be found, such as the slightly narrower, shorter and paler paragnaths in *P. vancaurica tetradentata*; however, the single Japanese specimen revised renders difficult its recognition as a distinct species based solely in such slight differences. Additional Japanese material was not available in this study. No further taxonomic records of *P. linea*, either as *P. vancaurica tetradentata* or *P. aibuhitensis*, have been reported in Japan since the original description. The populations have likely been extirpated by habitat loss due to anthropological developments in estuarine mudflats (Sato, 2017). The species has been reported in Japan (as *P. vancaurica tetradentata*) in biochemical studies, but these are doubtful since the means of identification are unknown (e.g. Ina & Matsui, 1980; Kobayashi *et al.*, 1984; Yuasa & Takagi, 2001).

The atoke differences between *P. linea* and *P. aibuhitensis* stated by Arias *et al.* (2013) regarding the presence of lateral groups of paragnaths on area III and the arrangement of paragnaths on area II are here confirmed as useful to distinguish the species. Also, we found that two other diagnostic features on the pharynx can readily distinguish both species. In *P. linea*, the areas VI–V–VI ridge pattern is λ -shaped (Figures 5D, 6E, 8A, 9A), whereas in *P. aibuhitensis* it is π -shaped (Figure 3A, B). Likewise, in *P. linea* the anterior band of areas VII–VIII has two rows with single paragnath on both furrows and ridges (Figures 5D, 8B, 9B), whereas in *P. aibuhitensis* the anterior band has one row with single paragnath only on furrows (Figure 3C, D). This distinction is also supported by the DNA sequence comparison for both COI and 16S rDNA between *P. linea* from North-east Asia and *P. aibuhitensis* from Palau (type locality) (Figure 2). Pairwise distance between *P. linea* and *P. aibuhitensis* was ~25% for COI and 10% for 16S rDNA (Table 3).

Furthermore, the single epitoke male of *P. linea* (type of *N. (Neanthes) orientalis*) from Xiamen, China (type locality) was here examined and described. Epitoke specimens of *P. aibuhitensis* were not available in this study. A description of the species' reproductive morphology using individuals from Palau (type locality) has not been performed yet. Nonetheless, Horst (1924) reported the species using epitokes from West Java (Indonesia), and Arias *et al.* (2013) mentioned a few epitoke details of the species based on Australian material. No other differences between both species were detected following Horst (1924) and Arias *et al.* (2013) other than the starting of the natatory parapodia. In *P. linea* from China, the natatory parapodia start from chaetiger 20 (Figures 6F, 7A; Monro, 1934), whereas in the Indonesian and Australian populations of *P. aibuhitensis* they start from chaetiger 21 and 23, respectively.

Habitat

Euryhaline species distributed in estuarine areas. It dwells in intertidal mudflats and common cordgrass (*Spartina anglica*)

areas (Wu *et al.*, 1985; Sun & Yang, 2004), and dominates in the uppermost part of the littoral zone with gravels or mud mixed with stones in Changkou, Qingdao (China), among communities of the brachyuran crabs *Helice* sp. and *Scopimera* sp. in high densities (100 inds m⁻²) (Wu *et al.*, 1985). On the western coast of Korea, the species also reaches high densities (130 inds m⁻²) at the upper littoral zone, which plays an essential role in recycling intertidal mudflat sediment (Choi & Lee, 1997).

Reproduction

Breeding season in Xiamen (Fujian, China) is from February to May with reproductive peaks from late March to early April, at water temperatures above 17 °C; the ratio of males to females is 1:1.7; the diameter of zygotes is 186–214 µm (Chen *et al.*, 1992; Sun & Yang, 2004). In Mayidao Island, Zhoushan (Zhejiang, China), the swarming is from May to June with water temperatures around 20 °C (Zheng & Fan, 1986); whereas in the western coast of Korea, it occurs continuously from early spring to autumn (Choi & Lee, 1997).

Type locality

Amoy (Xiamen), Fujian, China.

Distribution

East China Sea, Yellow Sea, Sumida-gawa River (Tokyo, Japan). The records in the Mediterranean Sea (Arias *et al.*, 2013) are questionable (see Discussion).

Perinereis shigungensis (Hsueh, 2019) comb. nov.

Neanthes shigungensis Hsueh, 2019: 190–191, figs 15, 16, table 2.

Diagnosis (based upon Hsueh, 2019)

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with broad-petite bars on area VI; areas VI–V–VI ridge pattern π -shaped; area III with laterally isolated paragnaths; areas VII–VIII with anterior band consisting of two rows; distal dorsal ligule anteriorly conical, subequal in size throughout; neuroacicular ligule posteriorly shorter than median ligule; falcigers with camerated shaft divided into two partitions; postero-dorsal tentacular cirri extending to chaetiger 3.

Remarks

Neanthes shigungensis Hsueh, 2019 is here transferred to *Perinereis* based on having bar-shaped paragnaths on area VI. The species resembles *P. rookeri* by having broad-petite bars on area VI, distal dorsal ligule subequal to median ligule, areas VI–V–VI ridge pattern π -shaped, areas VII–VIII with the anterior band having two rows, and area III with distinct laterally isolated paragnaths. Nonetheless, both species can be distinguished by the number of paragnaths on several pharyngeal areas, the tendon's length formed by the incurved terminal tooth of falcigers' blade, and the extension of postero-dorsal tentacular cirri. In *P. shigungensis* comb. nov., the number of paragnaths on some areas is much higher (area I: 7–8; area III: 48–65; area VII–VIII: 57–58) than that in *P. rookeri* (area I: 1–3; area III: 18; area VII–VIII: 33). In *P. shigungensis* comb. nov., the tendon of falcigers' blade equals half of the total blade length, whereas in *P. rookeri* it equals one-third to two-fifths of the blade length. Finally, in *P. shigungensis* comb. nov. the postero-dorsal tentacular cirri extend posteriorly to chaetiger 3, whereas in *P. rookeri* they extend posteriorly to chaetiger 1.

Habitat

Intertidal mud bottom.

Reproduction

Unknown.

Type locality

Shigung, Changhua County, Taiwan.

Distribution

The species is known only from the type locality, Shigung (Taiwan).

Perinereis vitabunda (Pflugfelder, 1933) comb. nov.
(Figures 1D–F, 10)

Nereis vitabunda Pflugfelder, 1933: 71–72, fig. 12A–D; Harms, 1934: 29–30 (habitat); Wesenberg-Lund, 1958: 29 (species list); Salazar-Vallejo *et al.*, 2014: 23 (species list).

Neanthes vitabunda: Hartman, 1959: 251 (source of synonymy); Fauchald, 1972: 409 (species list); Wilson, 1984: 226 (species list); Glasby *et al.*, 2009: 14 (species list).

Type material

Lectotype (designated here): PMJ Ann-167, Belawan, Sumatra, Indonesia, coll. J.W. Harms, 1927 or 1929.

Diagnosis

Species of subgroup 2A belonging to '*P. aibuhitensis*' species group. Specimens with transversally arranged broad-petite bars on area VI; areas VI–V–VI ridge pattern π -shaped; area III with laterally isolated paragnaths; areas VII–VIII with anterior band consisting of one row; distal dorsal ligule distinctly short throughout; neuroacicular ligule markedly projected; falcigers with camerated shaft divided into three partitions; postero-dorsal tentacular cirri extending to chaetiger 1.

Description

Lectotype atoke, incomplete, in good condition except already cut off into two parts at fourth and fifth chaetigers, 63 mm LT, 13 mm L15, 3.8 mm W15, with 83 chaetigers. Body colour brownish (Figure 10A), with three darkish longitudinal lines of tegument on dorsum of segments: one mid-dorsal line (maybe due to dark dorsal vessel) and two dorsolateral lines present throughout; body intensively covered by salt granules in dorsum.

Prostomium campanulate, as long as wide; anterior end broad, distally complete; anterolateral gap aside palpophore broad, twice as wide as basal diameter of antennae (Figure 10A). Nuchal organs deeply embedded, small, as wide as one-third of diameter of posterior pair of eyes.

Palpophores sub-conical, thick, as long as wide, as long as half of entire prostomium; sub-distal transverse groove distinct, deeply embedded (Figures 10A, B). Palpostyles oval, half as wide as diameter of palpophore.

Antennae tapered, thick, short; extending forwards to three-fifths of palpophore and posteriorly to distal quarter of length of prostomium; antennae separated with gap 1.6 times as wide as basal diameter of antennae (Figure 10A).

Paired eyes blackish, arranged in trapezoid form; gap between both pairs twice as wide as diameter of posterior pair of eyes (Figure 10A); anterior pair of eyes sub-oval, twice as wide as basal diameter of antennae, gap between both eyes as wide as 3 times diameter of eyes, with lens distinct, whitish, covering 80% of eye; posterior pair of eyes sub-rounded, 1.5 times as wide as basal diameter of antennae, with lens distinct, whitish, placed in middle of eye and covering 70% of it.

Apodous anterior segment 2.5 times wider than long, 1.5 times as long as chaetiger 1 (Figure 10A, B), with even anterior margin, dorsum without marked transverse wrinkles.

Tentacular cirri slender, smooth (Figures 10A, B); postero-dorsal cirri extending posteriorly to chaetiger 1, 1.5 times as long as antero-dorsal cirri; antero-dorsal cirri extending posteriorly to half of apodous segment; postero-ventral cirri extended

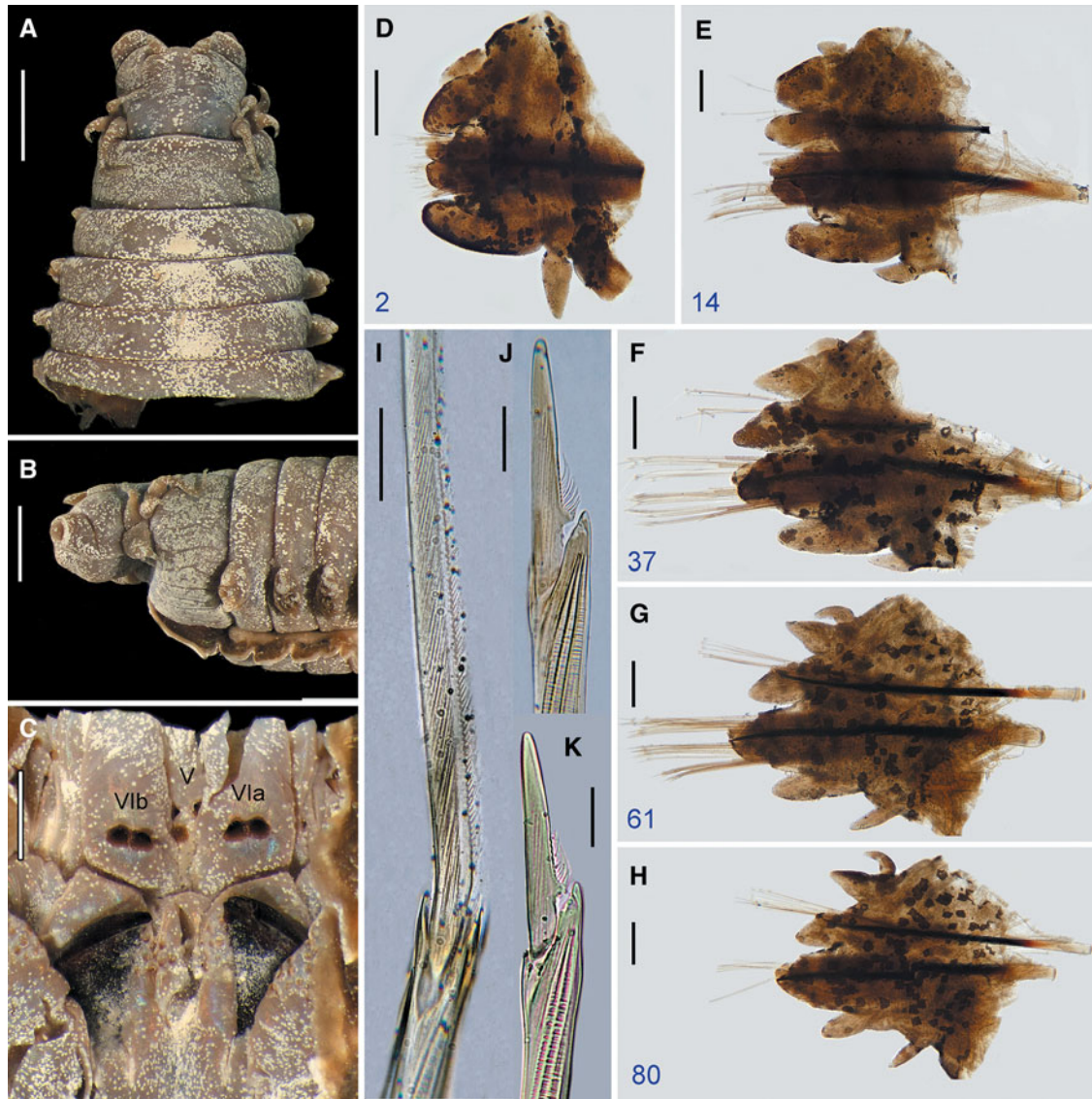


Fig. 10. *Perinereis vitabunda* (Pflugfelder, 1933) comb. nov. Holotype (PMJ Ann-167), Belawan, Sumatra, atoke: (A) anterior region in dorsal view; (B) anterior region in lateral view; (C) non-everted pharynx in ventral view (roman numerals referring to areas); (D–H) parapodia, numbers refer to the chaetiger; (I) homogomph spiner from neuropodial supracicular fascicle (chaetiger 98); (J) heterogomph falciger from neuropodial supracicular fascicle (chaetiger 98); (K) heterogomph falciger from neuropodial subacicular fascicle (chaetiger 37). Scale bars: A, B, 2 mm; C, 0.5 mm; D–H, 0.2 mm; I–K, 20 μ m.

over first quarter of prostomium; antero-ventral cirri as long as postero-ventral cirri and extending to half of palpophore; cirrophores cylindrical, postero-dorsal cirrophores as long as antero-dorsal cirrophores, antero-ventral cirrophores broadest, postero-ventral cirrophores narrowest.

Pharynx not everted, previously dissected with pharyngeal bulb and its surrounding muscle removed from body, separated in vial. Jaws with eight slightly developed and blunt denticles; pulp cavity as long as one-half of jaw, with two thick canals. Pharynx with paragnaths brownish on maxillary ring and reddish paragnaths on oral ring (Figure 10C), consisting of uniform-base cones, except broad-petite bars on area VI; merged paragnaths and plate-like basements absent. Area I: 6, cones of similar size in pentagon-shaped patch, one central cone; areas IIa: 12 and IIb: 11, three irregular rows of uneven cones in slightly curved, conical patch, distal cones smaller; area III: 36, four slightly regular rows of cones with similar size in sub-rounded patch, with distinct lateral isolated groups; areas IVa: 31 and IVb: 31, four regular transverse rows of uneven cones in slightly curved, sub-oval patch, distal-most cones shorter; area V: 3, triangular patch

of coarse cones of similar size, two proximal cones in transverse row and single distal cone on same level as distal-most paragnath on area VI; areas VIa: 2, VIb: 2, one transverse row of even, coarse broad-petite bars with rounded tip and slightly melted base (Figures 1D–F, 10C), coalesced; areas VII–VIII: 39, cones only, coarse, even; paragnaths disposed of in two well-separated bands of coarse and similar-sized cones, with anterior band consisting of one furrow row (one stout paragnath on each region), and posterior band with two transverse rows displaced from each other (furrow row proximal with one cone on each region, ridge row distal with 2–3 cones on each region). Areas VI–V–VI ridge pattern, π -shaped. Gap between area VI and areas VII–VIII broad, as wide as palpophore.

Paired oesophageal caeca present.

Parapodia with blackish, glandular, notopodial patches, more distinct in posterior chaetigers.

Notopodia consisting of dorsal cirrus, dorsal ligule (distal and proximal), and median ligule in biramous parapodia; notopodial prechaetal lobe or notoacicular process not developed throughout.

Dorsal cirri conical, thick, short (Figure 10D–H), extending up to two-thirds of distal dorsal ligule throughout; dorsal cirri subequal to proximal ligule throughout (Figure 10D–H), inserted medially to dorsal ligules in all parapodia.

Proximal dorsal ligule even towards posterior end; 1.3 times as long as distal dorsal ligule throughout; one small, sub-oval glandular patch throughout.

Distal dorsal ligule becoming gradually shorter towards posterior end (Figure 10E–H), extending beyond end of notoaciculæ in anterior parapodia (Figure 10E), subequal in medial parapodia (Figure 10F, G), shorter in posterior parapodia (Figure 10H); bluntly conical in anterior parapodia (Figure 10E), conical in following ones (Figure 10F–H); markedly shorter than median ligule throughout; one small, sub-oval glandular patch, smaller than that in proximal dorsal ligule throughout.

Median ligule bluntly rounded in anteriormost and anterior parapodia (Figure 10D, E), bluntly conical and becoming slightly shorter and narrower in following parapodia (Figure 10F–H).

Neuropodia consisting of neuroacicular ligule with superior and inferior lobes, ventral ligule, and ventral cirrus; neuropodial postchaetal lobe reduced throughout.

Neuroacicular ligule subequal to ventral ligule in anteriormost parapodia (Figure 10G), slightly longer in anterior parapodia, distinctly longer in following parapodia (Figure 10I–K); neuroacicular ligule 1.7 times as wide as ventral ligule in anteriormost and anterior parapodia, 2.3 times as wide as ventral ligule in medial and posterior parapodia.

Superior lobe rounded, subequal to inferior lobe and neuroacicular ligule throughout (Figure 10D–F).

Inferior lobe rounded, slightly longer than neuroacicular ligule in first 27 parapodia (Figure 10D, E), becoming narrower in following parapodia.

Ventral ligule digitiform, thick and subequal to median ligule in anteriormost parapodia (Figure 10D), becoming narrower and shorter in following parapodia (Figure 10E–H).

Ventral cirri conical, thick and markedly short in anteriormost and anterior parapodia (Figure 10D–F), becoming slightly longer and narrower in following parapodia; ventral cirri as long as one-half of ventral ligule in anteriormost parapodia, one-quarter in anterior parapodia, extending to base of ventral ligule in following parapodia.

Pygidium missing.

Aciculæ black, with basal end uncoloured. Notoaciculæ absent in chaetigers 1 and 2 (Figure 10D). Neuroaciculæ markedly extending beyond distal end of notoaciculæ throughout and from distal end of median ligule in medial and posterior parapodia (Figure 10G, H).

Notochaetae all homogomph spinigers; 5–7 spinigers present in anterior parapodia, 8–9 spinigers in medial parapodia, 10–12 spinigers in posterior parapodia.

Supracicular neurochaetae consisting of homogomph spinigers and heterogomph falcigers, both present throughout; 4–7 spinigers present in anteriormost and anterior parapodia, 3–4 spinigers in medial parapodia, 5–6 spinigers in posterior parapodia; 12–14 falcigers in anteriormost parapodia, 6–8 falcigers in anterior parapodia, 5–6 falcigers in medial parapodia, 3–4 falcigers in posterior parapodia.

Subacicular neurochaetae consisting of heterogomph spinigers and heterogomph falcigers, both present throughout; two spinigers present in anteriormost and anterior parapodia, 1–2 spinigers in medial and posterior parapodia; 16–20 falcigers in anteriormost and anterior parapodia, 14–15 falcigers in medial parapodia, 8–10 falcigers in posterior parapodia.

Blades of both homogomph (Figure 10I) and heterogomph spinigers finely serrated towards toothed edge, evenly spaced,

long with high *b/a* ratio (10–14.5). Blades of heterogomph falcigers long with low *b/a* ratio (*b/a*: 2–2.3), slender, straight, distal end digitiform with incurved terminal tooth very long forming distinct tendon (equalling about two-fifths of total blade length: 0.39–0.43); blades of falcigers partially serrated, with serrations capilliform, curved, looking upwards, present in about three-fifths (0.6–0.61) of total blade length (Figure 10J, K); vertex between distal and basal end on serrated edge markedly prominent, sub-conical. Shaft of falcigers cambered, with cavity divided sub-distally into three longitudinal partitions (Figure 10J).

Remarks

Perinereis vitabunda (Pflugfelder, 1933) comb. nov. belongs to the *P. aibuhitensis* species group based on having short dorsal cirri throughout the body, and blade of heterogomph falcigers straight with incurved terminal tooth markedly elongated forming a distinct tendon. *Perinereis vitabunda* comb. nov. resembles *P. aibuhitensis*, *P. kinmenensis* comb. nov., *P. rookeri* and *P. belawanensis* comb. nov. These species share areas VI–V–VI ridge pattern π -shaped, area VI with broad-petite bars, and area III with distinct laterally isolated paragnaths. Nonetheless, *P. vitabunda* comb. nov. is different from *P. rookeri* and *P. belawanensis* comb. nov. by having the anterior band of areas VII–VIII with one transverse row present on furrows (two rows on furrows and ridges of the latter two species). Likewise, *P. vitabunda* comb. nov. can be distinguished from *P. aibuhitensis*, *P. kinmenensis* comb. nov. and *P. rookeri* because the neuroacicular ligule is projecting markedly beyond median ligule in posterior parapodia (Figure 10G, H), and the distal dorsal ligule does not project beyond notoaciculæ in medial and posterior parapodia (Figure 10G, H); whereas in *P. aibuhitensis*, *P. kinmenensis* comb. nov. and *P. rookeri* the neuroacicular ligule is subequal to or slightly shorter than the median ligule, and the distal dorsal ligule is markedly projecting beyond notoaciculæ in medial and posterior parapodia. *Perinereis vitabunda* comb. nov. is more related to *P. belawanensis* comb. nov. in terms of habitat and locality; however, they are different in several aspects (see remarks of the latter species). The combination of both the markedly short tentacular cirri and distal and proximal dorsal ligule regions is unique in *P. vitabunda* comb. nov., rendering it easy to recognize among the *Perinereis* G2.

Perinereis vitabunda comb. nov. is a semi-terrestrial species from Sumatra described in *Nereis* by Pflugfelder (1933). The type material was never redescribed since the original description. The species was transferred to *Neanthes* by Hartman (1959) and recognized in that genus ever since (Fauchald, 1972; Wilson, 1984; Glasby *et al.*, 2009). Nonetheless, after revising the type specimens, the species is here transferred to *Perinereis*. *Perinereis vitabunda* comb. nov. has not been recorded since the original description. The specimens used by Pflugfelder (1933) were collected by Jürgen W. Harms in 1927 or 1929, who provided a detailed description of the habitat of the species (Harms, 1934).

The lot with the syntypes of *P. vitabunda* comb. nov. (PMJ 167) consisted of two specimens. The shape of the prostomium, the paragnaths' arrangement on the pharynx, the longest tentacular cirri, and the shape of the 20th dissected chaetiger of one of the specimens match the description and illustrations by Pflugfelder (1933). Consequently, that specimen has above been redescribed, newly illustrated, and it is here designated as lectotype (ICZN, 1999, Art. 74.7). The second syntype shared the diagnostic features of *P. belawanensis* comb. nov., and it was removed and separated (PMJ Ann-167a).

Habitat

Semi-terrestrial. Living in burrows dug within low-humidity sandy-clay soil covered with grass turf or within the chimney-like

mud mounds constructed by the mud lobster *Thalassina* sp.; inland dispersal limited by the level of highest tide, which is usually only reached once a month during the full moon (Harms, 1934). Living specimens are very agile; they escape at high speed into their burrows, usually found along with its congener *P. belawanensis* comb. nov. (Pflugfelder, 1933).

Reproduction

Unknown.

Type locality

Belawan, Sumatra, Indonesia.

Distribution

The species is known only from the type locality, Belawan, and Perbaongan (= Perbaungan), both in Sumatra (Indonesia).

Discussion

Species groupings in *Perinereis*

Current *Perinereis* species groupings (*sensu* Hutchings *et al.*, 1991) based on the number of paragnaths on area VI are troublesome since some species can overlap in two or even three groups. The number of transverse bars on area VI can vary on some *Perinereis* species typically regarded with one transverse bar (Horst, 1889; de Saint-Joseph, 1898; Fauvel, 1914), although this is more frequent in species having typically two (Wu *et al.*, 1985; Lee *et al.*, 1992; Khlebovich, 1996; Arias *et al.*, 2013; this study) or more transverse bars (Wilson & Glasby, 1993; Glasby & Hsieh, 2006; Park & Kim, 2007; Tosuji *et al.*, 2019; Villalobos-Guerrero, 2019). A more reliable solution could be based primarily on the simultaneous usage of this and other two or three less variable features, such as the enlargement of proximal dorsal ligule throughout the body (suggested secondarily by Hutchings *et al.*, 1991), the relative length of dorsal cirri, the areas VI–V–VI ridge patterns, the type of transverse bars on area VI, the number of anterior bands of paragnaths on areas VII–VIII, or the type of heterogomph falcigers' blade. However, a better understanding of the genus is still needed to select the appropriate characters.

Notwithstanding, the subgroup 2A (hereafter S2A) seems to construct a distinct, independent clade (Bakken & Wilson, 2005) and probably deserves a separate genus. *Perinereis variodentata* was the single species of this subgroup included by Bakken & Wilson (2005) in a phylogenetic analysis of Nereidinae *sensu* Fitzhugh (1987). It was nested in a different clade from the type species *P. amblyodonta* and separated from a sibling clade with two '*P. nuntia*' species and two '*Neanthes*' species. The S2A members' morphology is markedly different from that of the type species based upon Hutchings *et al.* (1991) and our observations of some Australian *P. amblyodonta* specimens (ZMB 5274), but similar to '*P. nuntia*' species group *sensu* Wilson & Glasby, 1993 also belonging to different genera (Glasby & Hsieh, 2006; Villalobos-Guerrero, 2019). The members of these two (S2A and '*P. nuntia*' group) can only be distinguished by the number of bars on area VI following Hutchings *et al.* (1991), but this character used alone is not reliable. We have noticed that S2A is mostly represented by members with short dorsal cirri and blade of heterogomph falcigers straight with markedly elongated terminal tooth forming distinct tendon, and thus here consistently arranged into the '*P. aibuhitensis*' species group. None of the members within the '*P. nuntia*' species group present these characters simultaneously; whereas the remaining species of S2A have elongated dorsal cirri and blade of heterogomph falcigers convex with short terminal tooth and inconspicuous tendon. A more comprehensive revision of the

species within S2A is imperative to delimit their morphology and set the proper foundations to establish or reinstate a genus.

Current species in *Perinereis* G2

According to Hutchings *et al.* (1991), *Perinereis* G2 was represented only by the species of the S2A featured by having area VI with two bar-shaped paragnaths and dorsal ligules (= proximal dorsal ligules, this study) not greatly expanded in posterior parapodia. This group encompassed eight species (type localities in brackets): *Perinereis aibuhitensis* (Grube, 1878) [Palau], *P. brevicirrata* (Treadwell, 1920) [Brazil], *P. camiguinoides* (Augener, 1922) [Juan Fernandez Islands], *P. jascooki* Gibbs, 1972 [Cook Islands], *P. kuwaitensis* Mohammad, 1970 [Kuwait], *P. singaporiensis* (Grube, 1878) [Singapore], *P. vancaurica* (Ehlers, 1868) [Nicobar Islands] and *P. variodentata* (Augener, 1913) [Western Australia]. They considered that the subgroup 2B (hereafter S2B) species were not yet recorded; however, they overlooked *P. mochimaensis* Liñero-Arana, 1983 from Venezuela, which presented two bars on area VI and enlarged proximal dorsal ligules in posterior parapodia. Later, de León-González & Solís-Weiss (1998) described two species with proximal dorsal ligules becoming enlarged towards the posterior end and included into S2B: *Perinereis cariboea* from the Mexican coast of the Caribbean Sea, and *P. osoriotaffali* from the Gulf of California. More recently, de León-González & Goethel (2013) described *P. rookeri* from the northern Gulf of Mexico and incorporated it into the *Perinereis* S2A.

Two additional species need to be included in *Perinereis* S2A due to having this subgroup's characteristic features: *Perinereis horsti* Gravier, 1902 from Djibouti was previously considered a junior synonym of *P. vancaurica*, but it was re-established and treated as a valid species (Yousefi *et al.*, 2011); whereas *P. linea* (Treadwell, 1936) from China was recognized as different to his previous senior synonym *P. aibuhitensis* (Arias *et al.*, 2013) and is confirmed as a valid species in this study. The five species formerly considered in *Neanthes* but here transferred to *Perinereis* also have characteristic features of G2 species: *Perinereis babuzai* comb. nov., *P. belawanensis* comb. nov., *P. kinmenensis* comb. nov., *P. shigungensis* comb. nov. and *P. vitabunda* comb. nov. In this regard, a total of 19 *Perinereis* G2 species are currently valid. Sixteen species belong to S2A (65% are members of '*P. aibuhitensis*' group), and the remaining three species to S2B (Table 4).

Perinereis is well-represented in the Eastern and South-eastern Asian seas, although before this study only four species of G2A there were known: *Perinereis aibuhitensis*, *P. linea*, *P. singaporiensis* and *P. vancaurica*. Another five species are here recognized; thus, nine species of G2 are now recorded from these regions.

Perinereis linea: species complex or alien species?

Perinereis linea is here regarded as a senior synonym of *N. (Neanthes) orientalis* and *P. vancaurica tetrudentata*, with distribution restricted to the East China Sea, Yellow Sea and a single freshwater locality in Tokyo (Japan). However, the status of a population reported from the Mediterranean Sea remains to be resolved.

Arias *et al.* (2013) reported an alien population of *P. linea* in the Mediterranean coast of Spain apparently imported by anglers as live bait for recreational fishing in the Mar Menor lagoon. They studied atoke and epitoke specimens of that population, compared them with specimens from South-western Korea (obtained from a fishing-bait supplier), and assigned all material to a single species. The epitoke males and females were characterized by having 28–29 pre-natatory chaetigers, fertilization occurring internally in the female coelom, zygotes and larvae released through openings in

Table 4. Valid *Perinereis* species currently in species Group 2 *sensu* Hutchings *et al.* (1991)

Species	Original combination	GR	SG	Type locality
<i>Perinereis aibuhitensis</i> (Grube, 1878)	<i>Nereis</i> (<i>Perinereis</i>) <i>aibuhitensis</i>	2A	Pa	Babeldaob, Palau, Western Caroline Islands
<i>P. babuzai</i> (Hsueh, 2019) comb. nov.	<i>Neanthes babuzai</i>	2A	Pa	Xianxi, Changhua, Taiwan
<i>P. belawanensis</i> (Pflugfelder, 1933) comb. nov.	<i>Nereis belawanensis</i>	2A	Pa	Belawen, Sumatra
<i>P. brevicirrata</i> (Treadwell, 1920)	<i>Nereis brevicirrata</i>	2A	Pa	Santos, Brazil
<i>P. camiguinoides</i> (Augener, 1922)	<i>Nereis</i> (<i>Perinereis</i>) <i>camiguinoides</i>	2A	–	Masatierra, Juan Fernández Islands
<i>P. cariboea</i> de León-González & Solís-Weiss, 1998	<i>Perinereis cariboea</i>	2B	–	Quintana Roo, Mexico, Caribbean Sea
<i>P. horsti</i> Gravier, 1899	<i>Perinereis horsti</i>	2A	–	Djibouti
<i>P. jascooki</i> Gibbs, 1972	<i>Perinereis jascooki</i>	2A	–	Rarotonga, Cook Islands
<i>P. kinmenensis</i> (Hsueh, 2019) comb. nov.	<i>Neanthes kinmenensis</i>	2A	Pa	Kinmen, Fujian, China
<i>P. kuwaitensis</i> Mohammad, 1970	<i>Perinereis kuwaitensis</i>	2A	–	Kuwait City, Kuwait
<i>P. linea</i> (Treadwell, 1936)	<i>Nereis</i> (<i>Neanthes</i>) <i>linea</i>	2A	Pa	Xiamen, Fujian, China
<i>P. mochimaensis</i> Liñero-Arana, 1983	<i>Perinereis mochimaensis</i>	2B	–	Mochima Bay, Venezuela, Caribbean Sea
<i>P. osoriotaffali</i> de León-González & Solís-Weiss, 1998	<i>Perinereis osoriotaffali</i>	2B	–	Sinaloa, Mexico, Gulf of California
<i>P. rookeri</i> de León-González & Goethel, 2013	<i>Perinereis rookeri</i>	2A	Pa	Rookery Bay, Naples, Florida, USA
<i>P. shigungensis</i> (Hsueh, 2019) comb. nov.	<i>Neanthes shigungensis</i>	2A	Pa	Shigung, Changhua, Taiwan
<i>P. singaporiensis</i> (Grube, 1878)	<i>Nereis</i> (<i>Perinereis</i>) <i>singaporiensis</i>	2A	Pa	Singapore
<i>P. vancaurica</i> (Ehlers, 1868)	<i>Nereis vancaurica</i>	2A	Pa	Nancowry, Andaman and Nicobar Islands
<i>P. variodontata</i> (Augener, 1913)	<i>Nereis</i> (<i>Perinereis</i>) <i>variodontata</i>	2A	–	Albany, Western Australia
<i>P. vitabunda</i> (Pflugfelder, 1933) comb. nov.	<i>Nereis vitabunda</i>	2A	Pa	Belawen, Sumatra

GR, *Perinereis* G2 species groupings *sensu* Hutchings *et al.* (1991); SG, *Perinereis* subgroups within Group 2A established in this study; Pa, species belonging to the '*Perinereis aibuhitensis*' species group.

the body wall and incubated in gelatinous masses attached to the female parapodia. Additionally, Mediterranean Sea males have mature sperm with a long and cylindrical head, being of the ent-aquasperm type *sensu* Jamieson & Rouse (1989). However, the epitoke morphology, the reproductive mode, and the sperm anatomy from those populations are different from specimens of *P. linea* from the type locality (Xiamen, China). According to Chen *et al.* (1992), in populations from Xiamen fertilization occurs in the water column where both males and females swarm to discharge gametes and larval development occurs. Also, the epitoke male holotype of *N. (Neanthes) orientalis* (= *P. linea*, this study) from Xiamen has 19 pre-natatory chaetigers, and mature sperms have a shorter and spherical head (Figure 6G), being of the ect-aquasperm type *sensu* Jamieson & Rouse (1989).

Setting apart epitokal modifications, differences in the reproductive modes and gamete morphology also reveal nereidid sibling species (Smith, 1958; Clark, 1961, 1977; Sato, 1999; Sato & Nakashima, 2003). Several groups with similar morphology have diverged into distinct species based on differences in breeding biology: *Platynereis dumerilii/massiliensis* (Hauenschild, 1951; Clark, 1961, 1977; Pfannenstiel *et al.*, 1987), *Hediste diversicolor/japonica/limnicola* (Smith, 1958; Clark, 1977), *H. japonica/atoka/diadora* (Sato, 1999; Sato & Nakashima, 2003), *Alitta virens/grandis* (Khlebovich *et al.*, 1980; Khlebovich, 1996), among others. Several species have shown different reproductive patterns, and tentatively suggested as belonging to separate species: *Perinereis cultrifera* (Grube, 1840) (Durchon, 1955, 1957, 1965) and *Composetia costae* (Grube, 1840) (Durchon, 1956, 1957, 1965). In this regard, the Xiamen population of *P. linea* is different from that studied by Arias *et al.* (2013) from the Mediterranean and (an uncertain locality from) South-western Korea by the different epitoke morphology, the reproductive mechanisms, and the shape of spermatozoa.

Arias *et al.* (2013) indicated that the species imported to Europe is commercially referred to as the 'Korean ragworm' (also 'Korean blue ragworm' or 'Korean jumbo'). However, the precise origin of the Mediterranean population was not addressed. The 'Korean ragworm' were collected in South Korea and exported by wholesalers to France, Italy and Spain from the 1980s to 2000s; however, after the government prohibition of indiscriminate collection of baitworms in the early 2000s, South Korea imports the baitworms from China, North Korea and other Asian regions (T. Park personal observation). Arias *et al.* (2013) also obtained some 'Korean ragworms' apparently from South Korea through a fishing-bait supplier. Thus, the precise origin of their population is uncertain. They may come somewhere from the East China Sea or the Yellow Sea, as occurs in the Japanese trade (Saito *et al.*, 2014). In this study, we analysed western Korean specimens of *P. linea* collected in nature and purchased at Korean and Japanese fishing-bait shops. We demonstrated that all specimens corresponded to the species based upon the epitoke morphology and the molecular data (Figure 2) even though no epitoke material was available for a detailed study of reproductive features. As shown in this study, another species closely related to *P. linea* from the East China Sea is *P. babuzai* comb. nov. We have not examined specimens of that species, but it is readily distinguished from *P. linea* by the development of distal dorsal ligule in posterior parapodia. The parapodia of the specimens reviewed by Arias *et al.* (2013) seems otherwise more similar to *P. linea*; thereby, we cannot disregard the possibility that additional distinct species also occur in the Yellow Sea.

The exotic status of *P. linea* in the Mediterranean Sea is questioned until further detailed studies on epitokal morphology and molecular analyses using material from both the Yellow and Mediterranean Seas are carried out to clarify its taxonomy.

Key to species of Perinereis Kinberg, 1865 belonging to group 2. This key includes all species now regarded as *Perinereis* G2 *sensu* Hutchings *et al.* (1991). However, some excluded species deserve discussion.

Perinereis brevicirrata (Treadwell, 1920) from Santos (Brazil) apparently belongs to the '*P. aibuhitensis*' species group but it is excluded from the key because its morphology is incompletely known, the description is brief and poorly illustrated, and there have been no further redescriptions of the species. de León-González & Goethel (2013) pointed out that *P. brevicirrata* and *P. rookeri* differed in the presence of notopodial prechaetal lobes, the number of transverse rows on areas VII–VIII, and the number of paragnaths on area V. However, we noticed based on the original descriptions that both species lack notopodial prechaetal lobes and the number of rows on areas VII–VIII is unclear in *P. brevicirrata*.

Neanthes multidentata Fassari & Móllica, 2000 from Sicily (Italy) may also belong to the '*P. aibuhitensis*' species group, and seems more closely allied to *P. linea*; however, it differs from *P. linea* by having only conical paragnaths on area VI and spinigers all homogomph in neurochaetae. The bars on area VI of *Perinereis* G2 species are typically regarded as cones due to its small size and pointed shape, and the same misperception could have occurred in *N. multidentata*; also, the spinigers all homogomph in neuropodia is an uncommon condition in *Perinereis*. *Neanthes multidentata* may belong to the '*P. aibuhitensis*' species group although a re-examination of the type material needs to be performed to re-assess those two features.

Finally, *N. jihueiensis* Hsueh, 2019 and *N. sanguensis* Hsueh, 2019 may belong to *Perinereis* G2. They were originally described with conical paragnaths on area VI, which are seemingly bar-shaped, but the pictures in ventral view lack sufficient detail (Hsueh, 2019: 180, 188, Figs 5C, 13C). An examination of the type materials is needed before judging these species in *Perinereis*.

1. Proximal dorsal ligule barely or not enlarged in posterior parapodia Subgroup 2A...2
Proximal dorsal ligule markedly enlarged in posterior parapodia Subgroup 2B 16
2. Dorsal cirri short, not projecting beyond distal dorsal ligule in medial parapodia; blades of heterogomph falcigers straight with markedly elongated incurved terminal tooth '*Perinereis aibuhitensis*' species group 3
Dorsal cirri long, projecting distinctly beyond distal dorsal ligule in medial parapodia; blades of heterogomph falcigers distinctly convex with short incurved terminal tooth 12
3. Ridges of area VI distally and sub-medially coalesced (areas VI–V–VI ridge pattern λ -shaped) 4
Ridges of area VI distally separated from each other (areas VI–V–VI ridge pattern π -shaped) 6
4. Distal dorsal ligule distinctly short in posterior parapodia, projecting barely beyond notoaciculæ
..... *P. babuzai* (Hsueh, 2019) comb. nov. (Taiwan)
Distal dorsal ligule of medium length in posterior parapodia, projecting distinctly beyond notoaciculæ 5
5. Area VI with long bars (smooth-bars); distal dorsal ligule bluntly rounded in anterior parapodia; distal dorsal ligule projecting beyond median ligule in posterior parapodia; area II with paragnaths arranged in oval patch; area III with laterally isolated paragnaths; area V with usually one paragnath (rarely none) *P. singaporiensis* (Grube, 1878) (Singapore)
Area VI with short bars (broad-petite bars); distal dorsal ligule conical in anterior parapodia; distal dorsal ligule subequal to median ligule in posterior parapodia; area II with paragnaths arranged in distinct crescentic rows; area III without laterally isolated paragnaths; area V with usually three paragnaths (seldom 4–5)
..... *P. linea* (Treadwell, 1936) (Xiamen, China)
6. Area VI with long bars (smooth-bars); area III without laterally isolated paragnaths; areas VII–VIII with anterior band having a medial patch of many tiny paragnaths *P. vancaurica* (Ehlers, 1868) (Nicobar Islands, Andaman Sea)
Area VI with short bars (broad-petite bars); area III with distinct laterally isolated paragnaths; areas VII–VIII with anterior band lacking medial patch of tiny paragnaths 7
7. Areas VII–VIII with anterior band having only one furrow row 8
Areas VII–VIII with anterior band having two rows (one on furrows and one on ridges) 10
8. Distal dorsal ligule not projecting beyond notoaciculæ in medial and posterior parapodia; neuroacicular ligule extending markedly beyond median ligule in posterior parapodia; area III with 36 paragnaths
..... *P. vitabunda* (Pflugfelder, 1933) (Sumatra, Indonesia)
Distal dorsal ligule markedly extending beyond end of notoaciculæ throughout; neuroacicular ligule subequal to or slightly shorter than median ligule in posterior parapodia; area III with up to 31 paragnaths 9
9. Ligules in anterior parapodia slender, acuminate; postero-dorsal tentacular cirri reaching chaetiger 2
..... *P. kinmenensis* (Hsueh, 2019) comb. nov. (Kinmen, China)
Ligules in anterior parapodia thickened with blunt tip; postero-dorsal tentacular cirri reaching chaetiger 4–5
..... *P. aibuhitensis* (Grube, 1878) (Palau)
10. Neuroacicular ligule projecting markedly beyond ventral ligule in posterior parapodia; distal dorsal ligule shorter than median ligule throughout body; proximal dorsal ligule longer than distal dorsal ligule
..... *P. belawanensis* (Pflugfelder, 1933) (Sumatra, Indonesia)

- Neuroacicular ligule subequal to or slightly shorter than ventral ligule in posterior parapodia; distal dorsal ligule subequal to or barely shorter than median ligule throughout body; proximal dorsal ligule subequal or shorter than distal dorsal ligule
 11
11. Area I: 7–8; area III: 48–65; area VII–VIII: 57–58; blade of heterogomph falcigers with incurved terminal tooth equaling half of total blade length; postero-dorsal tentacular cirri reaching chaetiger 3 *P. shigungensis* (Hsueh, 2019) comb. nov. (Shigung, Taiwan)
 Area I: 1–3; area III: 18; area VII–VIII: 33; blade of heterogomph falcigers with incurved terminal tooth equaling one-third to two-fifths of total blade length; postero-dorsal tentacular cirri reaching chaetiger 1
 *P. rookeri* de León-González & Goethel, 2013 (Florida, northern Gulf of Mexico)²
12. Area III with up to six paragnaths 13
 Area III with more than 10 paragnaths 14
13. Ridges of area VI distally separated from each other (areas VI–V–VI ridge pattern π -shaped); area VI with 2–4 cones in addition to bars; area I with 4–15 paragnaths *P. variodentata* (Augener, 1913) (Western Australia)
 Ridges of area VI distally and sub-medially coalesced (areas VI–V–VI ridge pattern λ -shaped); area VI without additional cones; area I with single paragnath
 *P. camiguinoides* (Augener, 1922) (Juan Fernández Islands, South Pacific Ocean)
14. Area III with laterally isolated paragnaths; areas VII–VIII with anterior band having only one furrow row; area I with 1–2 paragnaths; areas VII–VIII with 22–30 paragnaths *P. horsti* Gravier, 1899 (Djibouti)
 Area III without laterally isolated paragnaths; areas VII–VIII with anterior band having two rows (one on furrows and one ridges); area I with four or more paragnaths; areas VII–VIII with 33–49 paragnaths 15
15. Distal dorsal ligules bluntly rounded in anterior parapodia; area V with single paragnath; area VI with one lateral cone in addition to bars; postero-dorsal tentacular cirri reaching chaetiger 7
 *P. kuwaitensis* Mohammad, 1970 (Kuwait, Persian Gulf)
 Distal dorsal ligules bluntly conical in anterior parapodia; area V with three paragnaths; area VI without additional cones; postero-dorsal tentacular cirri reaching chaetiger 15 *P. jascooki* Gibbs, 1972 (Cook Islands, South Pacific Ocean)
16. Areas VII–VIII with more than 30; area I with 11 paragnaths *P. mochimaensis* Liñero-Arana, 1983 (Venezuela)
 Areas VII–VIII with fewer than 15 paragnaths; area I with fewer than 5 paragnaths 17
17. Proximal dorsal ligule as long as median ligule in posterior parapodia; distal dorsal ligule bluntly conical in anterior parapodia; distal dorsal ligule; area III with 7 paragnaths
 *P. cariboea* de León-González & Solís-Weiss, 1998 (Quintana Roo, Mexican Caribbean Sea)
 Proximal dorsal ligule extending markedly beyond median ligule in posterior parapodia; distal dorsal ligule bluntly rounded; area III with 17 paragnaths *P. osoriotaffali* de León-González & Solís-Weiss, 1998 (Sinaloa, Gulf of California)

Acknowledgements. The kind support of many curators and collection managers was hugely significant for this study. We are grateful to Karen Osborn, Kathryn Ahlfeld, Geoff Keel, Linda Ward and the late Kristian Fauchald (USNM) for receiving TFGV and TP in their research laboratories. TFGV is also immensely grateful to Birger Neuhaus (ZMB), Tarik Meziane (MNHN) and Luis F. Carrera-Parra (ECOSUR) for providing many facilities in their laboratories to examine the annelid collections in charge, other gathered materials, or both. We much appreciate the kindness of Birger Neuhaus (ZMB), Rolf Beutel (PMJ), Ko Tomikawa (Hiroshima University) and Hironori Komatsu (NSMT), who kindly sent specimens for revision. TP is indebted to Hyun Soo Rho (KIOST) for developing early works of *P. linea*. TP would like to also thank Yun Kyoung Kim for her valuable assistance with the line drawing. We acknowledge Xuwen Wu (Chinese Academy of Sciences), Jun-Hui Lin (Third Institute of Oceanography China), Shi-Chun Sun (Ocean University of China), and Takeru Sakaguchi (Kagoshima City Aquarium) for providing valuable references of difficult access. We also appreciate the support of Isabel C. Molina-Acevedo (UMT) for assisting throughout the vectorial drawing and Alexandra Pardo (Universidad de Antioquia) for running the identification key. Finally, the careful reading by Anja Schulze, Torkild Bakken and two anonymous reviewers greatly improved the final version of the manuscript.

Financial support. This work was supported by the DAAD Short-Term Grants (TFVG, grant number 91673478); CONACYT (TFVG, grant numbers 291062, 291212); National Institute of Biological Resources, Korea (NIBR) research grant (TP, grant numbers NIBR2013-01-030, NIBR202006101); and ECOSUR (TFVG).

References

- Arias A, Richter A, Anadón N and Glasby CJ (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.
- Audouin JV and Milne-Edwards H (1832) Classification des annélides, et description de celles qui habitent les côtes de la France. *Annales des Sciences Naturelles* **27**, 337–447.
- Augener H (1913) Polychaeta I. Errantia. In Michaelsen W and Hartmeyer R (ed), *Die Fauna Südwest-Australiens. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905*. Jena: Gustav Fischer, 4, pp. 65–304.
- Augener H (1922) Litorale Polychaeten von Juan Fernandez. In Skottsberg C (ed), *The Natural History of Juan Fernandez and Easter Island. Vol. 3. Zoology. Part II*. Uppsala: Almqvist & Wiksells, pp. 161–218.
- Bakken T and Wilson RS (2005) Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta* **34**, 507–547.
- Bakken T, Glasby CJ and Wilson RS (2009) A review of paragnath morphology in Nereididae (Polychaeta). *Zoosymposia* **2**, 305–316.
- Bonyadi-Naeini A, Rastegar-Pouyani N, Rastegar-Pouyani E, Glasby CJ and Rahimian H (2017) Nereididae (Annelida: Phyllococida) of the Persian Gulf and Gulf of Oman, including description of two new species and 11 new records. *Zootaxa* **4244**, 91–117.
- Carr CM, Hardy SM, Brown TM, Macdonald TA and Hebert PDN (2011) Tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLoS ONE* **6**, e22232.

- Chen C, Ye Y, Chai Y and Zheng Z** (1992) Study on reproductive ecology of polychaetous annelid, *Perinereis aibuhitensis*. *Journal of Oceanography in Taiwan Strait* **11**, 54–60. [In Chinese].
- Choi JW and Lee JH** (1997) Secondary production of a nereid species, *Perinereis aibuhitensis* in the intertidal mudflat of the west coast of Korea. *Bulletin of Marine Science* **60**, 517–528.
- Clark RB** (1961) The origin and formation of the *Heteronereis*. *Biological Reviews, Cambridge Philosophical Society* **36**, 199–236.
- Clark RB** (1977) Reproduction, speciation and polychaete taxonomy. In Reish DJ and Fauchald K (eds) *Essays on Polychaetous Annelids in Memory of Dr Olga Hartman*. Los Angeles, CA: Allan Hancock Foundation, University Southern California, pp. 477–501.
- Conde-Vela VM** (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.
- Conde-Vela VM and Salazar-Vallejo SI** (2015) Redescriptions of *Nereis oligohalina* (Rioja, 1946) and *N. garwoodi* González-Escalante & Salazar-Vallejo, 2003 and description of *N. confusa* sp. n. (Annelida, Nereididae). *ZooKeys* **518**, 15–49.
- Dales RP** (1962) The polychaete stomodeum and the inter-relationships of the families of Polychaeta. *Proceedings of the Zoological Society, London* **139**, 389–428.
- Darbyshire T** (2014). Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of *Gymnonereis*. *ZooKeys* **427**, 75–108.
- de Blainville H** (1818) Mémoire sur la classe des Sétipodes partie des Vers à sang rouge de M. Cuvier, et des Annélides de M. de Lamarck. *Bulletin des Sciences par la Société Philomathique de Paris* **1818**, 78–85.
- de León-González JA and Goethel CA** (2013) A new species of *Perinereis* (Polychaeta, Nereididae) from Florida, USA, with a key to all *Perinereis* from the American continent. *ZooKeys* **312**, 1–11.
- de León-González JA and Solís-Weiss V** (1998) The genus *Perinereis* (Polychaeta: Nereididae) from Mexican littoral waters, including the description of three new species and the redescriptions of *P. anderssoni* and *P. elenacasoae*. *Proceedings of the Biological Society of Washington* **111**, 674–693.
- de León-González JA, Villalobos-Guerrero TF and Conde-Vela VM** (2020) Nereididae de blainville, 1818. In de León-González JA, Bastida-Zavala JR, Carrera-Parra LF, García-Garza ME, Salazar-Vallejo SI, Solís-Weiss V and Tovar-Hernández MA (eds), *Poliquetos (Annelida: Polychaeta) de México y de América Tropical*, 2nd edition. Monterrey, México: Universidad Autónoma de Nuevo León, pp. 1–39.
- de Saint-Joseph ADA** (1898) Annélides polychètes des côtes de France (Manche et Océan). *Annales des Sciences Naturelles, Zoologie et Paléontologie, Paris* **8**, 209–464.
- Deng J, Ma S, Niu H, Dong S and Su Y** (2007) An experiment of shrimp (*Fenneropenaeus chinensis*) culture by inputting polychaetes (*Perinereis aibuhitensis*). *Transactions of Oceanology and Limnology* **2**, 135–140. [In Chinese].
- Durchon M** (1955) Sur le polymorphisme présenté par quelques Néréidiens (Annélides Polychètes) au moment de la reproduction. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* **46**, 180–194.
- Durchon M** (1956) Mode de reproduction et développement de *Nereis* (*Ceratonereis*) *costae* Grube (Annélide Polychète) à Alger. *Archives de Zoologie Expérimentale et Générale* **93**, 57–69.
- Durchon M** (1957) Biologie comparée des Néréidiens. *Année Biologique* **33**, 31–41.
- Durchon M** (1965) Sur l'évolution phylogénétique et ontogénétique de l'épitoque chez les Néréidiens (Annélides Polychètes). *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* **92**, 1–12.
- Ehlers E** (1868) Die Borstenwürmer (Annelida Chaetopoda) nach Systematischen und Anatomischen Untersuchungen. Leipzig: Verlag von Wilhelm Engelmann, XX+269, pp. 269–748.
- Ehlers E** (1904) Neuseeländische Anneliden. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen Mathematisch-Physikalische Klasse. Neue Folge* **3**, 1–80.
- Fassari G and Mollica E** (2000) *Neanthes multidentata*, a new species of Nereididae (Annelida, Polychaeta) from Sicily. *Marine Life* **7**, 3–6.
- Fauchald K** (1972) Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the Eastern Pacific Ocean. *Allan Hancock Foundation Monographs in Marine Biology* **7**, 1–575.
- Fauchald K** (1977) The polychaete worms, definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County: Los Angeles, CA (USA), Science Series* **28**, 1–188.
- Faulwetter S, Simbora N, Katsiaras N, Chatzigeorgiou G and Arvanitidis C** (2017) Polychaetes of Greece: an updated and annotated checklist. *Biodiversity Data Journal* **5**, e20997.
- Fauvel P** (1914) Annélides polychètes non-pélagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885–1910). *Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert Ier Prince Souverain de Monaco* **46**, 1–432.
- Fauvel P** (1923) Polychètes errantes. *Faune de France* **5**, 1–488.
- Fauvel P** (1932) Annelida Polychaeta of the Indian Museum, Calcutta. *Memoirs of the Indian Museum* **12**, 1–262.
- Fauvel P** (1933) Annélides polychètes du Golfe du Pei Tcheu Ly de la collection du Musée Hoang ho Pai ho. Récoltées par le R.P. Leroy, S.J. et le R.P. Licent S.J. *Publications du Musée Hoang ho Pai ho de Tien Tsin* **15**, 1–67.
- Fauvel P** (1953) *The Fauna of India Including Pakistan, Ceylon, Burma and Malaya: Annelida, Polychaeta*. Allahabad: The Indian Press.
- Fitzhugh K** (1987) Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level. *Bulletin of the Biological Society of Washington* **7**, 174–183.
- Gibbs PE** (1972) Polychaete annelids from the Cook Islands. *Journal of Zoology* **168**, 199–220.
- Glasby CJ and Hsieh HL** (2006) New species and new records of the *Perinereis nuntia* species group (Nereididae: Polychaeta) from Taiwan and other Indo-West Pacific shores. *Zoological Studies* **45**, 553–577.
- Glasby CJ, Timm T, Muir AI and Gil J** (2009) Catalogue of non-marine Polychaeta (Annelida) of the World. *Zootaxa* **2070**, 1–52.
- Glasby CJ, Wei N-WV and Gibb KS** (2013) Cryptic species of Nereididae (Annelida: Polychaeta) on Australian coral reefs. *Invertebrate Systematics* **27**, 245–264.
- Glasby CJ, Wilson RS and 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.
- Gravier C** (1899) Contribution à l'étude des Annélides Polychètes de la Mer Rouge. *Bulletin du Muséum d'Histoire Naturelle, Paris* **5**, 234–244.
- Gravier C** (1902) Contribution à l'étude des annélides polychètes de la Mer Rouge (Suite). *Nouvelles Archives du Muséum d'Histoire Naturelle, Paris, 4e Série* **3**, 147–268.
- Grube AE** (1840) Actinien, Echinodermen und Würmer des Adriatischen- und Mittelmeers, nach eigenen Sammlungen beschrieben. Königsberg: J.H. Bon.
- Grube AE** (1858) Annulata östrediana. Enumeratio Annulorum, quae in itinere per Indiam occidentalem et Americam centalem annis 1845–1848 suscepto legit cl. A. S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinere ad Americam meridionalem collectis, (Fortsættelse [continued]) [2. Familia Euniceae – F. Syllidea]. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening for 1857*, 158–186.
- Grube AE** (1878) Annulata Semperiana. Beiträge zur Kenntniss der Annelidenfauna der Philippinen. *Mémoires de L'Académie Impériale des Sciences de St. Pétersbourg., Ser. 7* **25**, 1–300.
- Gu XY, Jiang XM and Zheng ZM** (2002) Biological characteristics of *Perinereis aibuhitensis* Grube and status of its utilization. *Modern Fisheries Information* **17**, 33–34. [In Chinese].
- Harms JW** (1934) *Wandlungen des Artgefüges unter natürlichen und künstlichen Umweltbedingungen. Beobachtungen an tropischen Verlandungszonen und am verlandenden Federsee*. Leipzig: Tübingen, F. S. Heine.
- Hartman O** (1938) Nomenclatorial changes involving types of polychaetous annelids of the family Nereididae in the United States National Museum. *Journal of the Washington Academy of Sciences* **28**, 13–15.
- Hartman O** (1949) 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** (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.
- Hartman O** (1959) Catalogue of the polychaetous annelids of the world. Part 1. *Occasional Papers of the Allan Hancock Foundation* **23**, 1–353.
- Hartman O** (1974) Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Ocean Expeditions, 1963–1964 and a catalogue and bibliography of the

- species from India. II. *Journal of the Marine Biological Association of India* **16**, 609–644.
- Hauenschild C** (1951) Nachweis der sogenannten atoken Geschlechtsform des Polychaeten *Platynereis Dumerilii* Aud. et M.-Edw. als eigene Art aufgrund von Zuchtversuchen. *Zoologische Jahrbücher. Abteilung für Allgemeine Zoologie und Physiologie der Tiere* **63**, 107–128.
- Horst R** (1889) Contributions towards the knowledge of the Annelida Polychaeta. 34. On species of *Nereis*, belonging to the sub-genus *Perinereis*. *Notes from the Leyden Museum* **11**, 38–45.
- Horst R** (1924) Polychaeta errantia of the Siboga Expedition. Pt. 3. Nereidae and Hesionidae. *Siboga Expeditie Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900* **24**, 145–198.
- Hsueh PW** (2019) *Neanthes* (Annelida: Nereididae) from Taiwanese waters, with description of seven new species and one new species record. *Zootaxa* **4544**, 173–198.
- Hutchings PA, Reid A and Wilson RS** (1991) *Perinereis* (Polychaeta, Nereididae) from Australia, with redescriptions of six additional species. *Records of the Australian Museum* **43**, 241–274.
- Hylleberg J, Nateewathana A and Bussarawit S** (1986) Polychaetes of Thailand, Nereidae (Part 1), *Perinereis* and *Pseudonereis*, with notes on species of commercial value. *Phuket Marine Biological Center Research Bulletin* **43**, 1–22.
- Imajima M** (1972) Review of the annelid worms of the family Nereidae of Japan, with descriptions of five new species or subspecies. *Bulletin of the National Science Museum, Tokyo* **15**, 37–153.
- Imajima M** (1996) Annelida Polychaeta. Biological Research. Tokyo. [In Japanese].
- Ina K and Matsui H** (1980) Survey of feeding stimulants for the sea bream (*Chrysophrys major*) in the marine worm (*Perinereis vancaurica tetradentata*) (Feeding stimulants for fishes Part IV). *Nippon Nōgeikagaku Kaishi* **54**, 7–12.
- International Commission on Zoological Nomenclature (ICZN)** (1999) *International Code of Zoological Nomenclature*, 4th edition. London: International Trust for Zoological Nomenclature (The Natural History Museum).
- Jamieson BGM and Rouse GW** (1989) The spermatozoa of the Polychaeta (Annelida): an ultrastructural review. *Biological Reviews* **64**, 93–157.
- Jansonius J and Craig JH** (1971) Scolecodonts: I. Descriptive terminology and revision of systematic nomenclature; II. Lectotypes, new names for homonyms, index of species. *Bulletin of Canadian Petroleum Geology* **19**, 251–302.
- Khlebovich VV** (1996) Fauna of Russia and neighbouring countries. Polychaetous Annelids, Volume III. Polychaetes of the family Nereididae of the Russian seas and the adjacent waters. *Proceedings of the Zoological Institute of the Russian Academy of Sciences* **140**, 1–221. [In Russian].
- Khlebovich VV and Wu BL** (1962) Polychaetous annelids of the Yellow Sea. III. Family Nereidae (Polychaeta, Errantia). *Studia Marina Sinica* **8**, 33–53. [In Chinese and Russian].
- Khlebovich VV, Komendantov AY and Shklyarevich GA** (1980) Validity of *Nereis virens*, *N. grandis* and *N. brandti* (Annelida, Polychaeta) and variations in the number of their paragnaths. *Zoologicheskii Zhurnal* **59**, 1617–1624. [In Russian].
- Kimura M** (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequence. *Journal of Molecular Evolution* **16**, 111–120.
- Kinberg JGH** (1865) Annulata nova. Nereidum dispositio nova. *Öfversigt af Kongelige VetenskapsAkademiens Förhandlingar* **22**, 167–179.
- Kinberg JGH** (1910) Zoologi. Annulater. Kongliga Svenska Fregatten Eugenies Resa omkring jorden under befäl af C.A. Virgin Anen 1851–1853. *Vetenskapliga iakttagelser på Konung oscar den Förstes befallning utgifna af Kongliga Svenska Vetenskapsakademinien, Zoologi* **3** (Annulaten), 33–78.
- Knox GA** (1951) The polychaetous annelids of Banks Peninsula. Part II. A rock bottom fauna from 80 fathoms. *Records of the Canterbury Museum* **6**, 61–81.
- Kobayashi T, Takasaki Y, Takagi T and Konishi K** (1984) The amino acid sequence of sarcoplasmic calcium-binding protein obtained from sandworm, *Perinereis vancaurica tetradentata*. *European Journal of Biochemistry* **144**, 401–408.
- Lamarck JB** (1802) La nouvelle classes des Annélides. *Bulletin du Muséum d'Histoire Naturelle, Paris, An X*, Disc. d'ouverture, 27 Floréal.
- Lee JH, Je JG and Choi JW** (1992) Taxonomical review of *Perinereis aibuhitensis* Grube, 1878 (Nereidae, Polychaeta) in Korea. *Korean Journal of Systematic Zoology* **8**, 1–10.
- Leuckart RS** (1847) Verzeichnis der zur Fauna Helgoland's gehörenden wirbellosen Seethiere. In Frey H and Leuckart RS (eds), *Beiträge zur Kenntnis Wirbelloser Thiere mit Besonderer Berücksichtigung der Fauna des Norddeutschen Meeres*. Braunschweig: Friedrich Vieweg und Sohn, pp. 136–168.
- Leung J and Chan KYK** (2018) Microplastics reduced posterior segment regeneration rate of the polychaete *Perinereis aibuhitensis*. *Marine Pollution Bulletin* **129**, 782–786.
- Li Y, Li J, Liu T, Wang Y, Zhou Z, Cheng F, Feng C, Cheng X, Liu H and Chen X** (2017) Preparation and antithrombotic activity identification of *Perinereis aibuhitensis* extract: a high temperature and wide pH range stable biological agent. *Food and Function* **8**, 3533–3541.
- Liñero-Arana I** (1983) Dos nuevas especies de Nereidae (Polychaeta: Errantia) de la costa oriental de Venezuela. *Boletín del Instituto Oceanográfico de Venezuela* **22**, 3–6.
- Liu M, Liu H, Wang Q, Guan S and Ge S** (2013) Phylogenetic relationships of twenty-one nereids species inferring two different evolutionary origins? *Aquatic Science and Technology* **1**, 167–180.
- Malmgren AJ** (1865) Nordiska Hafs-Annulater. *Öfversigt af Kongliga Vetenskaps-Akademiens förhandlingar, Stockholm* **22**, 51–110.
- Mohammad MBM** (1970) Description of two new species of Nereidae (Annelida: Polychaeta). *Zoological Journal of the Linnean Society* **49**, 183–186.
- Monro CCA** (1934) On a collection of Polychaeta from the coast of China. *Annals and Magazine of Natural History, Series 10* **13**, 353–380.
- Paik E** (1975) The polychaetous annelids in Korea (III). *Research Bulletin of the Hyosung Women's University (aka Hyosung Women's College)* **17**, 409–438. [In Korean and English].
- Paik E** (1977) Studies of polychaetous annelid worms of the family Nereidae in Korea. *Research Bulletin of the Hyosung Women's University (aka Hyosung Women's College)* **19**, 131–227. [In Korean].
- Paik E** (1982) Taxonomic studies on polychaetous annelids in Korea. *Research Bulletin of the Hyosung Women's University (aka Hyosung Women's College)* **24**, 745–913.
- Paik E** (1989) *Illustrated Encyclopedia of Fauna and Flora of Korea*. Ministry of Education **31**, 1–764. [In Korean].
- Paiva PC, Mutaquilha BF, Coutinho MCL and Santos CSG** (2019) Comparative phylogeography of two coastal species of *Perinereis* Kinberg, 1865 (Annelida, Polychaeta) in the South Atlantic. *Marine Biodiversity* **49**, 1537–1551.
- Palumbi SR** (1996) Nucleic acids II: the polymerase chain reaction. In Hillis DM, Moritz C and Mable BK (eds), *Molecular Systematics*. Sunderland, MA: Sinauer Associates, pp. 205–247.
- Pan W, Liu X, Ge F, Han J and Zheng T** (2004) Perinerin, a novel antimicrobial peptide purified from the clamworm *Perinereis aibuhitensis* Grube and its partial characterization. *Journal of Biochemistry* **135**, 297–304.
- Park T and Kim W** (2007) A taxonomic study on *Perinereis nuntia* species group (Polychaeta: Nereididae) of Korea. *Korean Journal of Systematic Zoology* **23**, 75–85.
- Park T and Kim W** (2017) Description of a new species for Asian populations of the “Cosmopolitan” *Perinereis cultrifera* (Annelida: Nereididae). *Zoological Science* **34**, 252–260.
- Pfannenstiel HD, Grünig C and Lucht J** (1987) Gametogenesis and reproduction in nereidid sibling species (*Platynereis dumerilii* and *P. massiliensis*). *Bulletin of the Biological Society of Washington* **7**, 272–279.
- Pflugfelder O** (1933) Landpolychaeten aus Niederländisch-Indien. Ergebnisse der Sunda-Expedition der Notgemeinschaft der Deutschen Wissenschaft 1929/30. *Zoologischer Anzeiger* **105**, 65–76.
- Read G and Fauchald K** (2018a) World Polychaeta database. *Perinereis* Kinberg, 1865. Available at <https://www.marinespecies.org/polychaeta/aphia.php?p=taxdetails&tid=129380>, accessed 12 November 2019.
- Read G and Fauchald K** (2018b) World Polychaeta database. *Neanthes* Kinberg, 1865. Available at <https://www.marinespecies.org/polychaeta/aphia.php?p=taxdetails&tid=129378>, accessed 14 November 2019.
- Read G and Fauchald K** (2019) World Polychaeta database. *Alitta succinea* (Leuckart, 1847). Available at <https://www.marinespecies.org/polychaeta/aphia.php?p=taxdetails&tid=234850>, accessed 8 March 2020.
- Saito H, Kawai K, Umino T and Imabayashi H** (2014) Fishing bait worm supplies in Japan in relation to their physiological traits. *Memoirs of Museum Victoria* **71**, 279–287.
- Salazar-Vallejo SI, Carrera-Parra LF, Muir AI, de León-González JA, Piotrowski C and Sato M** (2014) Polychaete species (Annelida) described from the Philippine and China Seas. *Zootaxa* **3842**, 1–68.

- Sars M** (1835) Beskrivelser og Iagttagelser over nogle moerkelige eller nye i Havet ved den Bergenske Kyst levende Dyr af Polypernes, Acalephernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort Oversigt over de hidtil af Forfatter. Bergen: Trykt paa Thorstein Hallagers Forlag hos Chr. Dahl, R. S. XII.
- Sato M** (1999) Divergence of reproductive and developmental characteristics and speciation in *Hediste species* group. *Hydrobiologia* **402**, 129–143.
- Sato M** (2017) Nereididae (Annelida) in Japan, with special reference to life-history differentiation among estuarine species. In Motokawa M and Kajihara H (eds) *Species Diversity of Animals in Japan: Diversity and Commonality in Animals*. Tokyo: Springer Japan, pp. 477–512.
- Sato M and Nakashima A** (2003) A review of Asian *Hediste* species complex (Nereididae, Polychaeta) with descriptions of two new species and a redescription of *Hediste japonica* (Izuka, 1908). *Zoological Journal of the Linnean Society* **137**, 403–445.
- Schmarda LK** (1861) Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise und die Erdr 1853 bis 1857. Erster Band (zweite halfte) Turbellarian, Rotatorien und Anneliden. Leipzig: Wilhelm Engelmann.
- Semper K** (1873) *Die Palau-Inseln im Stillen Ocean: Reiseerlebnisse*. Leipzig: F. A. Brockhaus.
- Smith RI** (1958) On reproductive pattern as a specific characteristic among nereid polychaetes. *Systematic Zoology* **7**, 60–73.
- Stecher G, Tamura K and Kumar S** (2020) Molecular evolutionary genetics analysis (MEGA) for macOS. *Molecular Biology and Evolution* **37**, 1237–1239.
- Struck TH** (2011) Direction of evolution within Annelida and the definition of Pleistoannelida. *Journal of Zoological Systematics and Evolutionary Research* **49**, 340–345.
- Sun R and Yang D** (2004) Annelida Polychaeta II, Nereidida (Nereididae, Syllidae, Hesionidae, Pilargidae, Nephtyidae). In *Fauna Sinica Invertebrata, Vol. 3*. Beijing: Science Press. [In Chinese].
- Tanaka M** (2016) First record of *Perinereis suluana* (Annelida, Nereididae) from Oura Bay, Okinawa Island, Ryukyu Islands, Japan. *Fauna Ryukyuan* **29**, 5–13.
- Tian Y, Liu H, Wang Q, Zhou J and Tang X** (2014) Acute and chronic toxic effects of Pb²⁺ on polychaete *Perinereis aibuhitensis*: morphological changes and responses of the antioxidant system. *Journal of Environmental Sciences* **26**, 1681–1688.
- Tosuji H and Sato M** (2010) Genetic evidence for parapatric differentiation of two forms of the brackish-water nereidid polychaete *Hediste atoka*. *Plankton & Benthos Research* **5**(Suppl.), 242–249.
- Tosuji H and Sato M** (2012) A simple method to identify *Hediste* sibling species (Polychaeta: Nereididae) using multiplex PCR amplification of the mitochondrial 16S rRNA gene. *Plankton & Benthos Research* **7**, 195–202.
- Tosuji H, Nishinosono K, Hiseh HL, Glasby CJ, Sakaguchi T and Sato M** (2019) Molecular evidence of cryptic species diversity in the *Perinereis nuntia* species group (Annelida: Nereididae) with first records of *P. nuntia* and *P. shikueii* in southern Japan. *Plankton & Benthos Research* **14**, 287–302.
- Treadwell AL** (1920) A new polychaetous annelid of the genus *Nereis* from Brazil. *Proceedings of the United States National Museum* **58**, 467–468.
- Treadwell AL** (1936) Polychaetous annelids from Amoy, China. *Proceedings of the United States National Museum* **83**, 261–279.
- Villalobos-Guerrero TF** (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.
- Villalobos-Guerrero TF and Bakken T** (2018) Revision of the *Alitta virens* species complex (Annelida: Nereididae) from the North Pacific Ocean. *Zootaxa* **4483**, 201–257.
- Villalobos-Guerrero TF and Carrera-Parra LF** (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.
- Villalobos-Guerrero TF and Idris I** (2020) Redescriptions of a neglected species of *Pseudonereis* Kinberg, 1865 (Annelida: Nereididae) and its similar congener from the Eastern Tropical Pacific. *Journal of Natural History* **54**, 1559–1580.
- Villalobos-Guerrero TF and Tovar-Hernández MA** (2014) *Poliquetos errantes* (Polychaeta: Errantia) esclerobiontes del puerto de Mazatlán, Sinaloa (México). *Boletín de Investigaciones Marinas y Costeras* **43**, 43–87.
- Wang J, Zhou Q, Zhang Q and Zhang Y** (2008) Single and joint effects of petroleum hydrocarbons and cadmium on the polychaete *Perinereis aibuhitensis* Grube. *Journal of Environmental Science* **20**, 68–74.
- Wesenberg-Lund E** (1958) Lesser Antillean polychaetes chiefly from brackish waters, with a survey and a bibliography of fresh and brackish water polychaetes. *Studies on the Fauna of Curaçao and other Caribbean Islands* **8**, 1–41.
- Wilson RS** (1984) *Neanthes* (Polychaeta: Nereididae) from Victoria with descriptions of two new species. *Proceedings of the Royal Society of Victoria* **96**, 209–226.
- Wilson RS and Glasby CJ** (1993) A revision of the *Perinereis nuntia* species group (Polychaeta: Nereididae). *Records of the Australian Museum* **45**, 253–277.
- Wu S** (1967) The nereid worms of Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* **6**, 47–76.
- Wu BL, Sun R and Yang DJ** (1985) *The Nereidae (Polychaetous Annelids) of the Chinese Coast*. Beijing: China Ocean Press.
- Yang D, Zhou Y, Zhao H, Zhou X, Sun N, Wang B and Yuan X** (2012) Molecular cloning, sequencing, and expression analysis of cDNA encoding metalloprotein II (MP II) induced by single and combined metals (Cu(II), Cd(II)) in polychaeta *Perinereis aibuhitensis*. *Environmental Toxicology and Pharmacology* **34**, 841–848.
- Yousefi S, Rahimian H, Nabavi MSB and Glasby CJ** (2011) Nereididae (Annelida: Polychaeta) from intertidal habitats in the Gulf of Oman, Iran. *Zootaxa* **3013**, 48–64.
- Yuan X, Chen A, Zhou Y, Liu H and Yang D** (2010) The influence of cadmium on the antioxidant enzyme activities in polychaete *Perinereis aibuhitensis* Grube (Annelida: Polychaeta). *Chinese Journal of Oceanology and Limnology* **28**, 849–855.
- Yuasa HJ and Takagi T** (2001) Genomic structure of the sandworm, *Perinereis vancaurica tetradentata*, troponin C. *Gene* **268**, 17–22.
- Zheng B and Fan G** (1986) Ecological studies on *Perinereis aibuhitensis* Grube in Mayi Island of Zhoushan archipelago. *Journal of Zhejiang Ocean University* **5**, 87–94. [In Chinese].