

New Species and New Records of the *Perinereis nuntia* Species Group (Nereididae: Polychaeta) from Taiwan and Other Indo-West Pacific Shores

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Christopher J. Glasby and Hwey-Lian Hsieh (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(4): 553-577. This study was undertaken in order to describe new and poorly known species of the *Perinereis nuntia* species group (Nereididae: Polychaeta), which are concurrently being investigated genetically. Six species are described from intertidal waters of Taiwan and adjacent areas, including southern Japan, east-central and southeastern China, Singapore, Malaysia, and Indonesia (Java). These include *P. mictodonta* (Marenzeller, 1879), *P. nuntia* (Savigny, 1818), *P. rhombodonta* (Wu, Sun and Yang, 1981), and 3 new species, *P. shikueii* sp. nov., *P. viridis* sp. nov., and *P. wilsoni* sp. nov. Literature records of *P. nuntia* brevicirris from the region are referred to as *P. mictodonta*; those of *P. nuntia vallata* are referred to as *P. wilsoni* sp. nov. All species can be distinguished by a combination of pharyngeal paragnath numbers and the arrangement, and length ratios of the dorsal cirrus to dorsal notopodial ligule of the anterior and posterior parapodia. A key to tropical and subtropical Indo-West Pacific species of the *P. nuntia* species group is provided. All species inhabit intertidal sandy substrata under rocks or boulders, except *P. viridis* sp. nov., which occurs on reef shores in rock crevices. *Perinereis wilsoni* sp. nov. is found on rocky or reef limestone coasts, whereas the other 4 species occur mainly on sedimentary intertidal flats. The high diversity of the *P. nuntia* species group in Taiwan is attributed to a combination of factors including intrinsic reproductive features and Taiwan's position straddling 2 major biogeographic regions: the tropical Indo-West Pacific and the temperate Japan-East China Sea. The present results reveal a degree of sympatry not previously reported for the genus. <http://zoolstud.sinica.edu.tw/Journals/45.4/553.pdf>

Key words: Taxonomy, Morphology, Multivariate statistics, Sympatry.

A genetic study of marine polychaete worms belonging to the genus *Perinereis* Kinberg (Nereididae: Polychaeta) indicated the existence of 2 unnamed species – identified as *Perinereis* sp. 1 and *Perinereis* sp. 2 – living sympatrically along the coast and in the estuaries of Taiwan (Chen et al. 2002). Both species belong to a group known informally as the *Perinereis nuntia* species group (Wilson and Glasby 1993), and using the present taxonomic literature, both would be referred to as *P. nuntia* (Savigny, 1818). The

P. nuntia species group presently comprises 12 species (Table 1), and 2 more that have not been formally named (Wilson and Glasby 1993). The 7 varieties and subspecies of *P. nuntia* created by Fauvel (1919 1921 1932) and Augener (1913) have either been elevated back to their original species status (e.g., *P. nuntia* var. *vallata* sensu Fauvel, 1932 is now *P. vallata* (Grube, 1858)), or synonymized with other species (Wilson and Glasby 1993). Prior to the revision of Wilson and Glasby, two of these varieties – *P. nuntia* var. *bre-*

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vicirris and *P. nuntia* var. *vallata* – had been widely reported from Taiwan and adjacent seas (Fauvel 1936, Okuda 1938 1939 1940, Okuda and Yamada 1954, Khlebovich and Wu 1962, Imajima 1972, Paik 1972), and another 2, *P. nuntia* var. *typica* and *P. nuntia* var. *majungaensis*, were reported from the Chinese mainland (Khlebovitch 1963). Wu et al. (1985) recognized the 4 varieties occurring in China as “ecological” subspecies because of their small but consistent morphological differences and also because they occupy different ecological zones on the shore. Previous authors also noted the small but consistent differences between the varieties, but found no ecological separation, only that 1 form is usually dominant in any location (Imajima 1972, Paik 1972). In a later paper, Paik (1975) found no significant morphometric differences between *P. nuntia* var. *brevicirris* and *P. nuntia* var. *vallata* and referred both to *P. nuntia*. Wilson and Glasby (1993) were unable to evaluate the status of the *P. nuntia* varieties in East Asia because their study included comparatively few specimens from this area; by contrast, material in the present study is sourced primarily from East Asia (China, Taiwan, and Japan) and Southeast Asia (Indonesia, Malaysia, and Singapore) collected as part of the Phylogeography of the Indo-West Pacific project (Theme project of Academia Sinica, Taiwan to HLH) (Fig. 1). The present study therefore aims to clear up some of these issues: How many different forms occur in Taiwan and adjacent seas?; Can they be separated morphologically?; Does each form have a preferred habitat?; and To what extent do the different forms overlap in distribution?

Despite the fact that the *P. nuntia* species group as currently defined may be non-monophyletic (Bakken and Wilson 2005), the majority of members seem to form a morphologically cohesive group, for which a preliminary genetic analysis indicated monophyly (Kuo 2004). The study of Bakken and Wilson of all nereidids with paragnaths, which included 4 members of the *P. nuntia* species group, showed a sister group relationship between *P. nuntia* and *P. vallata*, with *P. akuna* Wilson and Glasby, 1993 and *P. caeruleis* (Hoagland, 1920) being placed in a distant clade along with members of *Neanthes* Kinberg, *Pseudonereis* Kinberg, and other *Perinereis*. *Perinereis akuna* and *P. caeruleis* were not found in this study, although a similar species, *P. rhombodonta* (Wu, Sun and Yang, 1981), is described. We have identified morphological features of the paragnaths common to all 3 species (but not found in other members of the group) that further support the findings of Bakken and Wilson, and we provide an interim emendation of the diagnosis of the *P. nuntia* species group.

Members of the genus *Perinereis* are common in intertidal areas of the temperate and tropical Indo-Pacific; they are an important part of the invertebrate community of intertidal mud flats, providing a source of food for wading birds and fish (Yoshida 1985). At least 6 *Perinereis* species are harvested commercially for use as live bait for anglers, and as food in mariculture (Gambi et al. 1994, Scaps 2003), including 2 members of the *P. nuntia* group, “*P. brevicirris*” in Taiwan (Chen 1990) and *P. quatrefages* Grube, 1878 [= *P. nuntia*] in Thailand (Hylleberg et al. 1986). Further,

Table 1. Valid species of the *Perinereis nuntia* group according to Wilson and Glasby (1993) showing the original name combination and author, and type locality. *Perinereis akuna*, *P. caeruleis*, and *P. rhombodonta* possibly do not belong to the group (see text)

Species	Original combination	Type locality
<i>P. akuna</i>	<i>Perinereis akuna</i> Wilson and Glasby, 1993	Coal and Candle Creek, Sydney, NSW, Australia
<i>P. caeruleis</i>	<i>Heteronereis caeruleis</i> Hoagland, 1920	Limbe Strait, the Philippines
<i>P. gualpensis</i>	<i>Perinereis gualpensis</i> Jeldes, 1963	Fundo Gualpen, Chile
<i>P. maindroni</i>	<i>Perinereis maindroni</i> Fauvel, 1943	Pondichéry, southeastern India
<i>P. majungaensis</i>	<i>Perinereis nuntia majungaensis</i> Fauvel, 1921	Majunga, Madagascar
<i>P. matthaii</i>	<i>Perinereis matthaii</i> Aziz, 1938	Karachi, Pakistan
<i>P. mictodonta</i>	<i>Nereis mictodonta</i> Marenzeller, 1879	Japan
<i>P. namibia</i>	<i>Perinereis namibia</i> Wilson and Glasby, 1993	Lüderitz, Namibia
<i>P. nuntia</i>	<i>Lycoris nuntia</i> Savigny, 1818	Red Sea
<i>P. ponuiensis</i>	<i>Nereis (Perinereis) ponuiensis</i> Augener, 1924	Auckland, New Zealand
<i>P. rhombodonta</i>	<i>Perinereis rhombodonta</i> Wu, Sun and Yang, 1985	Guangdong, China, South China Sea
<i>P. vallata</i>	<i>Nereis vallata</i> Grube, 1858	Valparaiso, Chile

Australia and the Queensland Museum, Brisbane, Australia. Newly collected worms were made to evert their proboscides by being anesthetized with menthol, and if this alone did not cause eversion then slight pressure was applied to their pharyngeal region. Worms were then fixed in 5% formalin and subsequently preserved in 70% ethanol.

Statistical analysis

Morphological traits of 4 species, *P. mictodonta* (Marenzeller, 1879), *P. nuntia* (Savigny, 1818), *P. shikueii* sp. nov., and *P. wilsoni* sp. nov. were examined statistically. Morphological traits examined included body size, paragnath counts for each area in the pharynx, and the length ratios of the dorsal cirrus to dorsal notopodial ligule (DC:DNL); DC length was measured along the inside length from its tip to the ventral attachment point on the DNL, while DNL length was measured along a line joining the ventral attachment point of the DC to the tip of the DNL. This ratio is a more easily repeatable and sensitive measure of DC length compared to the ratios suggested by Ben-Eliahu (1987). Body size was measured as body width (mm) at chaetiger 10 including the parapodia but not the chaetae. Numbers of paragnaths were counted for 8 areas, namely areas I, II, III (central and lateral positions), IV, V, VI, and VII-VIII. One of 2 length ratios was measured at chaetigers 10 to 20, reported as DC:DNL10 herein, and the other at a posterior chaetiger approximately between 75 to 90, reported as DC:DNL75-90 herein (the posterior parapodia referred to in the taxonomic illustrations were also taken from this region). The chaetal range enabled undamaged parapodia to be selected for study. Thus, 10 morphological traits from 127 specimens were examined. Missing values for the ratio traits were due to incomplete individuals.

Taxonomy

In the descriptions, the character data for the primary type (holotype and lectotype) are given first, followed by values for secondary types (paratypes and paralectotypes). Type and non-type materials and comparative materials are housed in the Australian Museum, Sydney, Australia (AM), Research Museum, Research Center for Biodiversity, Academia Sinica, Taipei, Taiwan (ASIZW), Museum and Art Gallery of the Northern Territory, Darwin, Australia (NTM), Naturhistorisches Museum, Wien, Austria

(NHMW), Queensland Museum, Brisbane, Australia (QM), and the Raffles Museum of Biological Research, Singapore (RMBR). Terminology follows Wilson et al. (2003) except for the term "acicular ligule" which is herein used to refer to the previously un-named neuropodial ligule carrying the superior and inferior prechaetal lobes and the postchaetal lobe.

STATISTICAL ANALYSIS

Linear regression analysis was performed in order to determine the contribution of size to variability in paragnath counts of all areas of the pharynx, and in the ratios of DC:DNL10 and DC:DNL75-90 for the 4 most similar species, *P. mictodonta*, *P. nuntia*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov. Discriminant analysis was conducted to distinguish species. Canonical discriminant analysis was also performed to determine which traits are the principle characters for differentiating species. All statistical analyses were performed using a PC version of the SAS software (SAS Institute 2001).

The results of the linear regression analyses showed that body size did not affect the length ratios of the dorsal cirri to dorsal notopodial ligules at chaetigers 10-20 or those of the posterior chaetigers 75-90 ($p = 0.07$ to 0.44), nor the paragnath counts in most of the areas except in areas I, V, and VII-VIII. Although the counts in these 3 areas correlated with body sizes, their regression coefficients were very low (for counts of areas I, V, and VII-VIII versus sizes, $r = 0.22$, 0.28 , and 0.24 , respectively). These data indicate that the DC:DNL ratios and the paragnath counts are mostly body-size independent.

The results from the multivariate analysis of variance (MANOVA) on all traits examined showed that in *P. mictodonta*, there were no morphological differences between populations in Taiwan and those in Japan, the type locality for the species (Wilks' lambda, $p = 0.06$); similarly, in *P. nuntia*, no differences occurred among the populations distributed in Chechun, Pingtung County, Taiwan, Pari I. of Jakarta, and the southern coast of Singapore (Wilks' lambda, $p = 0.08$ for Pari vs. Singapore populations; $p = 0.05$ for Pari and Singapore pooled vs. Chechun populations). Discriminant analysis revealed that the 4 *Perinereis* species were identified correctly, as no misidentification was detected for any species implying that the 4 species are morphologically distinguishable from

one another.

In the canonical discrimination analysis, *P. nuntia* was well separated from *P. mictodonta*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov.; however, the latter 3 species showed overlapping boundaries (Wilks' lambda, $p < 0.0001$; the 1st 2 canonical variables, Can1 and Can2, combined explained 91.4% of the variation of morphological traits among species, and both canonical correlations were significant, $r_1 = 0.94$, $p < 0.0001$; $r_2 = 0.84$, $p < 0.0001$) (Fig. 2A). On Can1, the most important characters for differentiating species were the DC:DNL10 and DC:DNL75-90 ratios and area VI counts (Fig. 2B). As compared with the other 3 species, *P. nuntia* exhibited smaller DC:DNL10 and DC:DNL75-90 ratios (respectively 0.84 vs. 1.03-1.30 and 0.89 vs. 1.26-2.12) and more parag-

naths on area VI (7.9 vs. 5.3-7.1). On Can2, those characters were again DC:DNL ratios and paragnath counts on area I (Fig. 2B). *Perinereis shikueii* sp. nov. had more paragnaths on area I (4.6 vs. 1.9-3.4), whereas *P. wilsoni* sp. nov. possessed greater ratios on DC:DNL10 and DC:DNL75-90 (1.30 vs. 0.84-1.09 and 2.12 vs. 0.89-1.29, respectively).

The distinctiveness among *P. mictodonta*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov. was obvious when *P. nuntia* was excluded from the analysis (Wilks' lambda, $p < 0.0001$) (Fig. 3A). As compared with the other 2 species, on Can1, *P. shikueii* sp. nov. was characterized by having more paragnaths on area I, whereas *P. wilsoni* sp. nov. had greater ratios of DC:DNL10. On Can2, *P. mictodonta* had more paragnaths on area V (3.3

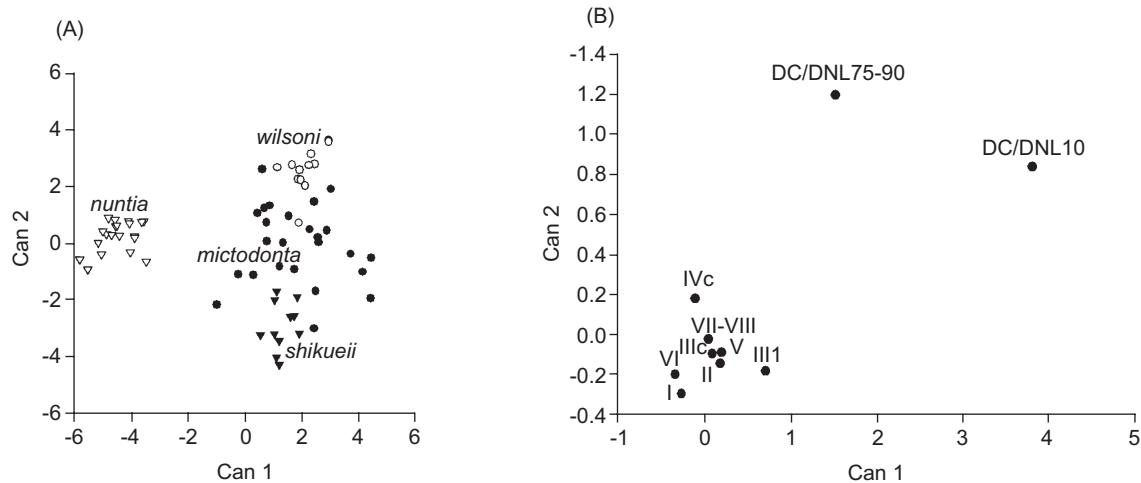


Fig. 2. (A) Canonical discrimination analysis showing the grouping of the 4 *Perinereis* species, *P. mictodonta*, *P. nuntia*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov.; (B) Ordinations of 10 morphological traits on the 1st 2 canonical variable axes, Can1 and Can2.

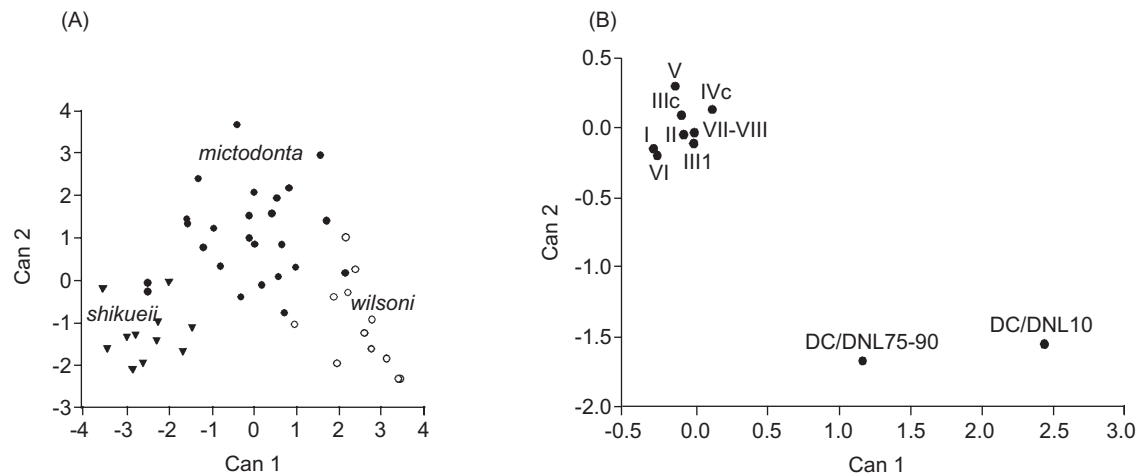


Fig. 3. (A) Canonical discrimination analysis showing the grouping of the 3 *Perinereis* species, *P. mictodonta*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov.; (B) Ordinations of 10 morphological traits on the 1st 2 canonical variable axes, Can1 and Can2.

vs. 2.0-3.1) and area IV (35.2 vs. 25.3-29.8), whereas *P. wilsoni* sp. nov. had greater ratios of DC:DNL75-90 (Fig. 3B).

TAXONOMIC ACCOUNT

Family Nereididae

Perinereis nuntia species group, emended

Perinereis nuntia species group Wilson and Glasby 1993: 259.
Perinereis group 3 Hutchings, Reid and Wilson 1991: 271.

Description (non-reproductive forms): Prostomium with entire anterior margin, 1 pair of biarticulate palps, with faint transverse groove on palpophore and subconical palpostyle; 1 pair of antennae; 2 pairs of eyes, anterior pair more widely spaced than posterior pair. Four pairs of tentacular cirri, each with distinct cirrophores. Eversible pharynx with 1 pair of jaws and conical paragnaths on both rings; area VI with 3-20 bar-shaped or pyramidal-shaped paragnaths on each side in a single line or arc (occasionally 1 or 2 cones present). One apodous anterior segment, greater than length of chaetiger 1. Parapodia 1 and 2 lacking notochaetae and notoacaculae, thereafter parapodia with notochaetae and notoacaculae. Notopodia bilobed from chaetiger 3, dorsal cirrus basally attached. Notopodial prechaetal lobe absent, notoacacula ending in a ridge-shaped acicular process (sensu Bakken 2002) at base of ventral notopodial ligule. Dorsal notopodial ligule similar in size and shape to ventral notopodial ligule throughout (dorsalmost notopodial ligules rarely elongated). Notochaetae homogomph spinigers. Neuropodia bilobed throughout with ventral cirrus. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph spinigers and heterogomph falcigers in subacicular fascicle (heterogomph spinigers sometimes absent).

Remarks: The *P. nuntia* species group was characterized by having an arc of bar-shaped paragnaths (3-20), or a mixture of bars and cones, in area VI of the pharynx (Wilson and Glasby 1993). Cones in area VI are rare in the *P. nuntia* group having been reported in *P. nuntia*, *P. mictodonta* (herein), and *P. viridis* sp. nov. (herein), and when present, there is only 1 or 2 among the bars. In all 3 species, the presence/absence of cones is variable among individuals. Although the dominant paragnaths in area VI of all *Perinereis*

have been referred to as bars (Hutchings et al. 1991, Wilson and Glasby 1993), present observations of *P. rhombodonta* show that the "bars" differ from typical bars in the genus in being much shorter and having a pointed apex rather than being flat-topped (Fig. 7A). In this case, they are more appropriately described as pyramidal-shaped paragnaths. They differ from conical paragnaths, which also have a pointed apex, in that their bases are quadrangular rather than circular. *Perinereis akuna* also has pyramidal paragnaths in area VI (CJG, pers. observ. on topotype material). Other *Perinereis* species suspected of having area VI pyramidal paragnaths are *P. caeruleis* and *P. seridentata* (Hartmann-Schroder, 1959), the latter a species from the Pacific coasts of Central America only recently assigned to *Perinereis* (Hartmann-Schröder 1959, Dean 2001). In addition, all 4 species have a band of small cones in addition to the 1 to 2 (rarely 3) rows of larger cones in areas VII and VIII, a feature not present in other members of the group. These observations, and the finding of Bakken and Wilson (2005) that *P. akuna* and *P. caeruleis* are not closely related to *P. nuntia* and *P. vallata* point to the existence of an unnamed clade of nereidids distinct from the *P. nuntia* species group.

Perinereis mictodonta (Marenzeller, 1879)

Figs. 4, 5A-F.

- Nereis mictodonta* Marenzeller 1879: 118-119, pl. 2, fig. 2; Izuka 1912: 148-151, pl. 16, fig. 1-6.
Perinereis mictodonta: Wilson and Glasby 1993: 264.
Perinereis brevicirris: Imajima and Hartman 1964: 151-152; Wu 1967: 71-72, fig. 11a-d (in part). Not *Nereilepas brevicirris* Grube, 1867.
Perinereis nuntia var. *brevicirris*: Fauvel 1936: 63-64; Okuda 1938: 92, 1939: 231, 1940: 12-13; Okuda and Yamada 1954: 184, fig. 3e; Khlebovich and Wu 1962: 51-52, pl. 3, fig. 3; Imajima 1972: 94-96, fig. 26l, m; Paik 1972: 131-132, fig. 2i, j. Not *Nereilepas brevicirris* Grube, 1867.
Perinereis nuntia brevicirris: Wu et al. 1985: 208-210, fig. 120a, b. Not *Nereilepas brevicirris* Grube, 1867.
Perinereis sp. 1 Chen et al. 2002: 19.

Type materials: Lectotype: *Nereis mictodonta* Marenzeller, 1879 1 (NHMW ZooEv 19919), Japan, coll. Roretz, 1886. Paralectotypes: *Nereis mictodonta* Marenzeller, 1879 4 (NHMW 776), collection details as for lectotype.

Non-type materials: Taiwan: Wazuwei, Tanshui Estuary, Taipei County, 25° 10'N, 121° 24'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19305 (1), NTM W19301 (1), NTM W19303 (1), NTM W19300 (1), NTM W19306 (1), NTM W19302 (1),

NTM W19299 (1); Mitsang, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19315 (1), NTM W19308 (1), NTM W19319 (1), NTM W19312 (1), NTM W19318 (1), NTM W19310 (1), NTM W19311 (1), NTM W19317 (1), NTM W19314 (1), NTM W19307 (1), NTM W19309 (1), NTM W19313 (1), NTM W19316 (1), coll. H.L. Hsieh, 18 Nov. 2000, NTM W19339 (1), NTM W19298 (1); Tonghsiao, Miaoli Co., 24°29'N, 120°39'E, coll. H.L. Hsieh, 4 Nov. 1999, NTM W19320 (1), NTM W19321 (1); Chuwei, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19297 (1), NTM W19296 (1); Beigang R., Yuanlin Co., 23°31'1.8"N, 120°8'35"E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW647 (2); Tsu-Wei, Tanshui Estuary, Taipei Co., 25°8'N, 121°16'E, coll. S.K. Wu, 4 Mar. 1966, ASIZW192 (1); Hai-Po, Lukang, Changhua Co., coll. S.K. Wu, 15 May 1965, ASIZW198 (1); Wai-Mo-Shan, Keelung City, coll. S.K. Wu, 21 Feb. 1965, ASIZW199 (9), She-Zu, Keelung R., Taipei

Co., coll. S.K. Wu, 8 Sept. 1964, ASIZW191 (8); Shangshan, Hsinchu City, 24°46'42.7"N, 120°54'51.4"E, coll. M.J. Kuo, 16 Nov. 2002, ASIZW646 (6), coll. M.J. Kuo, 26 Jan. 2003, ASIZW655 (30), coll. H.L. Hsieh, 22 Mar. 2003, NTM W19419 (1 female epitoke), NTM W19323 (1 female epitoke), NTM W19324 (1 male epitoke); Huwei R., Yuanlin Co., 23°43'17.7"N, 120°10'18.8"E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW648 (49); Beigang R., Yuanlin Co., 23°31'1.8"N, 120°08'35"E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW647 (33); Koamei, Dajia R., Taichung Co., 24°18'43.5"N, 120°33'2.9"E, coll. M.J. Kuo, 26 Jan. 2003, ASIZW652 (1); Budai R., Chiayi Co., 23°22'N, 120°8'E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW650 (1); Touchian R., Hsinchu City, 24°51'2.4"N, 120°56'26.9"E, coll. M.J. Kuo, 26 Jan. 2003, ASIZW651 (1); Bali, Tanshui R., Taipei Co., 25°9'48.3"N, 121°25'17.27"E, coll. M.J. Kuo, 8 Mar. 2003, ASIZW656 (8); Daan R., Taichung Co., 24°24'N, 120°35'E, coll. M.J. Kuo, 26 Jan. 2003, ASIZW653 (39); Houlun R., Miaoli Co., 24°37'23.4"N, 120°45'22.8"E, coll. M.J. Kuo, 26 Jan. 2003, ASIZW654 (24); Juoshui R., Changhua Co., 23°53'6.5"N, 120°17'30.1"E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW649 (58); Tapeng Lagoon, St. 9, Pingtung Co., 22°26.73'N, 120°29' E, coll. H.L. Hsieh, 29 Oct. 2000, NTM W19326 (1), NTM W19329 (1), NTM W19328 (1), NTM W19325 (1 mature female), NTM W19327 (1 mature female); Kaoping R., between Kaohsiung Co. and Pingtung Co., 22°28'N, 120°24'E, coll. J.C. Wu and P.H. Lin, 23 Jan. 1996, NTM W19330 (10). China: Zhejiang Prov., coll. S.L. Zhang, 13 Apr. 1984, AM W199644 (1). Japan: Minamata R., Minamata, Kumamoto, coll. I. Hayashi, 22 Apr. 2000, identified as *P. nuntia brevicirris* 10 (NTM W19420).

Description of lectotype and paralectotypes:

Lectotype posteriorly incomplete, 3.3 mm wide at chaetiger 10 (excluding parapodia); 4.8 mm wide at chaetiger 10 (including parapodia). Paralectotypes with 93-99 chaetigers, 35-37 mm long and 1.6-2.3 mm wide at chaetiger 10 (excluding parapodia); 2.5-3.4 mm wide at chaetiger 10 (including parapodia).

Prostomium slightly wider than long; antennae 1/3 prostomium length; posterodorsal tentacular cirri extending back to chaetiger 7 (7-13). Jaws brown, dentate cutting edge with 9 (5-8) teeth, proximal few ensheathed. Paragnaths brown, cones on oral ring much larger than those on maxillary ring. Area I with 5 (1-3) conical paragnaths; area II with 16 (20-25) conical paragnaths in an elongate patch; area III with 27 (20-22) conical



Fig. 4. *Perinereis mictodonta* (Marenzeller, 1879), live specimen.

paragnaths in a rectangular patch and an isolated group of 4 (3-5) paragnaths on either side; area IV with 35 (34-39) conical paragnaths in a crescentic patch, bars absent; area V with 3 (1-3) conical paragnaths in a transverse row (or triangle); area VI with 8 (5-9) bars of uneven length, end ones longer; area VII-VIII with 33 (25-34) conical paragnaths arranged in a single band of 2 rows (proximal row on everted pharynx zigzagged).

Dorsal notopodial ligule on posterior

chaetigers not markedly larger than ventral notopodial ligule. Dorsal cirrus length 1.07 (1.00-1.35) times length of dorsal notopodial ligule length anteriorly (chaetiger 10-20); posteriorly dorsal cirrus length 1.04 (1.14-1.88) times length of dorsal notopodial ligule length (chaetiger 75-90). Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule similar in length to acicular neuropodial ligule length in all chaetigers. Neuro-

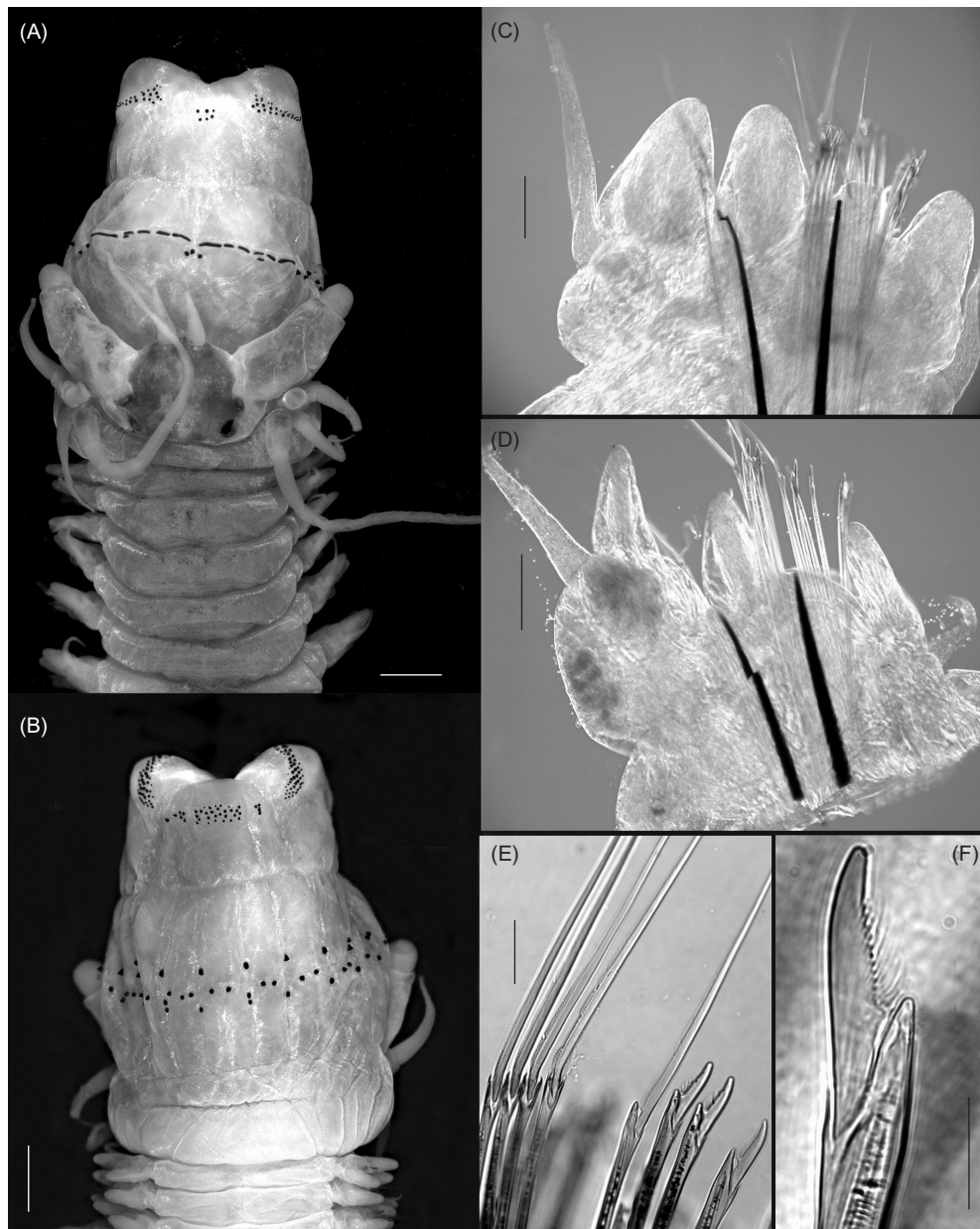


Fig. 5. *Perinereis mictodonta* (Marenzeller, 1879). (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 12, posterior view; (D) posterior parapodium, posterior view; (E) supra-acicular (leftmost) and subacicular (rightmost) neurochaetae from parapodium 9; (F) subacicular neuropodial heterogomph falciger from parapodium 9. A-D: NTM W19339; E, F: NTM W19305. Scale bars: A, B = 1.0 mm; C, D = 0.2 mm; E = 0.05 mm; F = 0.02 mm.

podial dorsal fascicle heterogomph falcigers with serrated blades; serrated region 0.36 (0.40) total blade length. Neuropodial heterogomph spinigers present throughout.

Epidermal pigmentation absent, probably faded. Glandular patches at base of dorsal notopodial ligule on posterior chaetigers; 2 per ligule, proximal one largest.

Variation: Tapeng specimens unusually large, with 119-142 chaetigers for 60-115 mm long and 3.63-5.39 mm wide at chaetiger 10 (excluding parapodia); 5.94-7.70 mm wide at chaetiger 10 (including parapodia). Non-type material with dusky-olive pigmentation on head and dorsum (Fig. 4). Posterodorsal tentacular cirri extending to chaetigers 3-13. Variation in paragnath counts: I: 2-6; II: 11-34; III, central: 13-35; III, lateral: 2-7; IV: 20-52 (conical paragnaths only); V: 1-5 (when 3 present, usually arranged in a triangle); VI: 4-10 (occasionally with 1 or 2 additional cones outside line of arc of bars); VII-VIII: 28-62 (Fig. 5A, B; Table 2). Dorsal cirrus length 0.68-1.29 times length of dorsal notopodial ligule anteriorly (chaetiger 10-20) (Fig. 5C); posteriorly dorsal cirrus length 0.78-1.77 times length of dorsal notopodial ligule (chaetiger 75-90) (Fig. 5D). Larger specimens with distally rounded (rather than subacute) anterior parapodial ligules (Fig. 5C). Neuropodial dorsal fascicle heterogomph falcigers with serrated region 0.24-0.39 total blade length (Fig. 5E, F).

Reproductive forms: Five specimens with epitokal modifications (NTM W19323-19325, 19327, 19419). Pre-epitokal region with slightly modified dorsal cirri on 1st 6 or 7 chaetigers; modified ventral cirri on 1st 5 or 6 chaetigers (variation not apparently sex-related). Epitokal modifications including additional auricular lobes of various sizes at bases of all parapodial ligules and cirri, beginning on chaetiger 19-22 in females (probably depending on degree of development, beginning earlier in more sexually mature individuals), and chaetiger 17 in males; most prominent being lobes on dorsal base of dorsal cirrus and ventral base of ventral cirrus, and a large postchaetal neuropodial lobe. Auricular lobes continuing to within 10-25 chaetigers of pygidium. Also, epitokes appearing to have a greater amount of dusky pigmentation on head and dorsum, and eyes enlarged. Female epitokes with a pair of dorsolateral brown patches and paired brown spots (eyespot?) which occur dorsolaterally on both pre-epitokal and epitokal chaetigers; also a pigment spot present between parapodia, which is most prominent in mid- and

posterior body. No chaetal changes apparent in some epitokes, but others (Tapeng Lagoon specimens) with normal chaetae replaced by serrated, broad-bladed sesquigomph natatory chaetae in modified parapodia. Pygidium of females not modified with papillae. Further information on reproduction in this species available under the name *P. nuntia* var. *brevicirris* (or *brevicirrus*) in Hardege et al. (1994), Hardege and Bartels-Hardege (1995), and Yoshida (1984).

Remarks: Fauvel (1932) relegated *Nereilepas brevicirris* Grube, 1867 to a variety of *P. nuntia*, *P. nuntia* var. *brevicirris*, based on material held in the Indian Museum, Calcutta, collected from India and adjacent areas, giving this taxon a wide southern and northern hemispheric distribution. Consequently, *P. nuntia* var. *brevicirris* has the same name-bearing type as *N. brevicirris* (ICZN 1999: Art. 46.2). Wilson and Glasby (1993) reexamined the type of *N. brevicirris* and concluded that it was the same as *Nereis vallata* Grube, 1858, and that this taxon, now referred to as *P. vallata*, occurs only on southern hemisphere shores. Therefore all reports of *P. nuntia* var. *brevicirris* or *P. brevicirris* from the northern hemisphere, including tropical shores, are likely to be misidentifications. Those from Japan, Korea, and China are herein all referred to as *P. mictodonta*. Wu's (1967) material of *P. brevicirris* from Taiwan consists of a mixture of *P. mictodonta*, *P. wilsoni* sp. nov., and *P. shikueii* sp. nov. Material identified as *P. nuntia brevicirris* from the Indian subcontinent (Fauvel 1932 1953) has not been examined, but is unlikely to be *P. mictodonta*, as this species was not found in suitable habitats in Indonesia, Malaysia, or Singapore. The largest, best-preserved specimen was chosen from among the syntype specimens and designated a lectotype in order to fix a single name bearing type for *P. mictodonta*. The remaining members of the syntype series are designated paralectotypes.

Perinereis mictodonta is most similar to *P. wilsoni* sp. nov., but may be distinguished from this species by the arrangement of paragnaths in area V (3 paragnaths in a triangle in *P. mictodonta*; a single paragnath or 2 or 3 in a longitudinal line in *P. wilsoni* sp. nov.) and by the dorsal cirrus, which is relatively longer in *P. wilsoni* sp. nov. (Table 3). These 2 species cannot be distinguished from each other by paragnath counts (also a conclusion of Paik 1975 and Yoshida 1984), and there appear to be no differences in the morphology of the male and female epitokes between the 2 species (although there are minor differences between

Table 2. Comparison of paragnath counts of the *Perinereis nuntia* species group. Mean, standard deviation and ranges are given. Data for *P. akuna*, *P. caeruleis*, *P. gualpensis*, *P. maindroni*, *P. majungaensis*, *P. matthaii*, *P. namibia*, *P. nuntia*, *P. ponuiensis*, *P. rhombodonta*, and *P. vallata* are taken from Wilson and Glasby (1993). Counts for *P. caeruleis* are approximate because their paragnaths are very small, numerous, and closely spaced. c, cones; b, bars; r, rows; g, groups

	I	II	III (total)	III (lateral)	IV (c)
<i>P. akuna</i> (n = 27)	2.4 ± 0.8 1 - 4	14.8 ± 3.6 6 - 21	18.4 ± 3.7 13 - 27	Present	24.9 ± 6.4 11 - 41
<i>P. caeruleis</i> (n = 3)	0.7 0 - 2	0 0	150 110 - 185	Present	100 85 - 110
<i>P. gualpensis</i>	0 - 7	6 - 17	24 - 48		18 - 39
<i>P. maindroni</i> (n = 1)	0	8,6	8	Absent	8
<i>P. majungaensis</i>	7 - 13	19 - 30	40 - 50	?absent	21 - 23
<i>P. matthaii</i>	0	4 - 7	?	?	?
<i>P. mictodonta</i> (types) (n = 5)	2.6 ± 1.5 1 - 5	21.2 ± 3.4 16 - 25	25.2 ± 3.3 23 - 31	Present	35.8 ± 1.9 34 - 39
<i>P. mictodonta</i> (Taiwan) (n = 36)	3.6 ± 1.4 2 - 6	22.3 ± 5.2 11 - 34	26.4 ± 6.0 16 - 39	Present	35.2 ± 7.3 20 - 52
<i>P. namibia</i> (n = 43)	1.7 ± 0.7 0 - 4	5.5 ± 3.0 0 - 20	16.6 ± 4.0 10 - 26	Present	22.7 ± 5.4 5 - 39
<i>P. nuntia</i> (Red Sea) (n = 9)	1 - 3	5 - 9	9 - 17	Present	9 - 18
<i>P. nuntia</i> (all) (n = 132)	1.8 ± 0.8 0 - 5	6.8 ± 3.0 0 - 23	11.5 ± 4.2 1 - 30	Present	16.5 ± 4.6 5 - 35
<i>P. ponuiensis</i> (n = 2)	1.5 ± 0.7 1 - 2	7.5 ± 2.8 5 - 10	8.5 ± 0.7 8 - 9	Present	18.3 ± 7.4 12 - 25
<i>P. rhombodonta</i> (n = 14)	4.3 ± 1.3 2 - 6	44.9 ± 10.0 29 - 64	93.6 ± 31.4 40 - 142	Absent (3 or 4 g)	84.2 ± 23.8 45 - 131
<i>P. vallata</i> (n = 427)	1.6 ± 0.7 0 - 9	11.0 ± 2.5 1 - 23	18.7 ± 4.4 9 - 35	Present	28.1 ± 5.7 0 - 47
<i>P. shikueii</i> n. sp. (n = 32)	4.6 ± 1.3 2 - 7	21.7 ± 3.4 17 - 27	23.3 ± 2.7 18 - 29	Present	25.3 ± 5.1 21 - 35
<i>P. viridis</i> n. sp. (n = 3)	2	8 - 12	20 - 23	Present	27 - 29
<i>P. wilsoni</i> n. sp. (n = 33)	1.9 ± 0.6 1 - 3	15.2 ± 3.0 9 - 21	19.1 ± 3.3 13 - 26	Present	29.8 ± 3.6 24 - 39

	IV (b)	V	VI	VII - VIII
<i>P. akuna</i> (n = 27)	2.9 ± 1.1 1 - 5	2.6 ± 1.1 1 - 4	7.5 ± 1.1 (?b) 5 - 11	116.0 ± 30.4 76 - 191 (2 r)
<i>P. caeruleis</i> (n = 3)	Absent	43 39 - 48	13 (b) 12 - 15	210 200 - 250
<i>P. gualpensis</i>	Absent	1 - 2	6 - 11 (b)	30 - 47
<i>P. maindroni</i> (n = 1)	Absent	1	6 (b)	35 (2 r)
<i>P. majungaensis</i>	12 - 13	1	8 - 10 (b)	57 (2 - 3 r)
<i>P. matthaii</i>	?	0	6 - 10 (b)	0
<i>P. mictodonta</i> (types) (n = 5)	Absent	2.6 ± 0.9 1 - 3	7.2 ± 1.6 (b) 5 - 9	31.6 ± 3.8 25 - 34
<i>P. mictodonta</i> (Taiwan) (n = 36)	Absent	3.3 ± 0.8 1 - 5	5.5 ± 1.3 4 - 10	36.0 ± 7.3 28 - 62
<i>P. namibia</i> (n = 43)	Absent	0.8 ± 0.6 0 - 3	10.4 ± 1.3 (b) 5 - 14	56.4 ± 8.0 (2 - 3 r) 43 - 76
<i>P. nuntia</i> (Red Sea) (n = 9)	Absent	0 - 4	6 - 9 (b+c)	18 - 38 (1 - 2r)
<i>P. nuntia</i> (all) (n = 132)	Absent	1.9 ± 1.4 0 - 5	8.2 ± 2.5 (b+c) 4 - 17	28.0 ± 6.2 10 - 52
<i>P. ponuiensis</i> (n = 2)	Absent	1.5 ± 0.7 1 - 2	3.7 ± 0.4 (b) 3 - 4	26.5 ± 0.7 26 - 27 (1 - 2 r)
<i>P. rhombodonta</i> (n = 14)	Absent	1.1 ± 0.5 1 - 3	11.3 ± 1.5 9 - 14 (b)	113.4 ± 36.0 55 - 165 (1 - 2 r, 5 - 6 g)
<i>P. vallata</i> (n = 427)	2.6 ± 0.6 0 - 5	2.3 ± 1.0 0 - 5	12.5 ± 1.5 5 - 14 (b)	69.0 ± 13.6 42 - 129 (2 - 3 r)
<i>P. shikueii</i> n. sp. (n = 32)	Absent	3.1 ± 0.2 3 - 4	7.1 ± 1.6 4 - 10	38.4 ± 3.5 34 - 52
<i>P. viridis</i> n. sp. (n = 3)	2 - 3	1	2 - 4 (b+c)	38 - 46
<i>P. wilsoni</i> n. sp. (n = 33)	Absent	2.0 ± 0.8 1 - 3	5.3 ± 1.2 4 - 8	29.3 ± 3.2 22 - 34

sexes). Despite the fact that both species are morphologically very similar, they can be distinguished by morphometric analysis of the dorsal cirrus (herein) and by phylogenetic analysis of ITS 1 and 2 sequences (Chen et al. 2002).

Perinereis mictodonta may be distinguished from other members of the *P. nuntia* species group by having a dorsally pigmented body, area V paragnaths arranged in a triangle, area VI with 5.7 (\pm SD1.4) bars, with the outermost bars longest, brown paragnaths with those on the oral ring much larger than those on the maxillary ring, and dorsal cirri equal to, or slightly longer, than notopodial lobe throughout (except for the last few chaetigers) (Table 3). It differs from Red Sea specimens of *P. nuntia* in having a greater number of paragnaths on areas II, III, and IV of the pharynx (Table 2). A specimen from Zhejiang Prov., China (AM W199677) identified as *P. nuntia* by Wilson and Glasby (1993) is redetermined here to be *P. mictodonta* because of the higher paragnath counts on the maxillary ring of the pharynx.

Habitat: Intertidal, in muddy sand to gravely sand substrate, especially under rocks, also associated with oyster beds.

Distribution: Type locality: Japan (no further details; according to Imajima and Hartman (1964) most of Marenzeller's (1879) material was sourced from either Enoshima, near Yokohama, or in the vicinity of the Bay of Miya). Widespread throughout Japan from the Bay of Matsushima in the north

to the Bonin Is. in the south (Izuka 1912). Newly reported from Taiwan and China (Zhejiang Prov.). Accepting the above synonymies, this species is widespread throughout China (Yellow Sea and South China Sea) and also occurs in South Korea (Korea Strait).

Perinereis nuntia (Savigny, 1818)

Fig. 6A-F.

Lycoris nuntia Savigny 1818: 313; 1822: 33, pl. 4, fig. 2.

Perinereis nuntia var. *typica*: Khlebovitch 1963: 58.

Perinereis nuntia typica: Wu et al. 1985: 213, fig. 120c, d. [see Wilson and Glasby 1993 for full synonymy]

Materials: Indonesia: off Jakarta, Pari Is., 5°51.45'S, 106°37.00'E, coll. I. Al-Hakim, 14, 15 Feb. 2003, East Pari I. NTM W19334 (11), NTM W19333 (14); South Pari I. NTM W19332 (14), NTM W19335 (13), NTM W19331 (7). Singapore: St John's I., southern shore, 1°6'N, 103°48'E, coll. C. Glasby and E. Omena, 8 Dec. 2003 NTM W19337 (18), NTM W19042 (1); Labrador Park, south coast Singapore, 1°10'N, 103°47'E, coll. C. Glasby and E. Omena, 9 Dec. 2003, NTM W19336 (3). Taiwan: Haikou, Checheng, Pingtung Co., 22°5'N, 120°42'E, coll. C.A. Chen, 25 Mar. 2003, ASIZW657 (7). Australia: Beagle Reef, Western Australia, 15°21'S, 123°32'E, coll. R. Hanley, 24 Aug. 1991, NTM W6815 (1), NTM W6820 (1), NTM W18998 (1); Queensland, Moon Creek, west side of Fraser I., site MC5, 25.33°S, 152.59°E,

Table 3. Comparison of key features distinguishing *Perinereis mictodonta*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov.

	<i>P. mictodonta</i>	<i>P. shikueii</i> sp. nov.	<i>P. wilsoni</i> n. sp.
Pigmentation	Brown/green pigment on dorsum, although less so than in <i>P. shikueii</i>	Brown/green pigment on dorsum, prostomium; more so than in <i>P. mictodonta</i>	Brown/green pigment on head and pharynx only
Paragnath color	Brown	Black	Brown
Paragnath, relative sizes	Cones on oral ring much larger than those on maxillary ring	Cones on oral ring slightly larger than those on maxillary ring	Cones on oral ring slightly larger than those on maxillary ring
Area IV (cones)	35.3 (\pm 6.8)	25.3 (\pm 5.1)	29.8 (\pm 3.6)
Area V, arrangement	Usually 3 in a triangle	Usually 3 in a transverse line or flat triangle	Singly or 2 or 3 in a longitudinal line
Area VI, number and length of bars	5.7 (\pm 1.4); uneven length (outermost longest)	7.1 (\pm 1.6); short even-length bars	5.3 (\pm 1.2); uneven length (outermost longest)
Dorsal cirri	Equal to or slightly longer than notopodial lobe throughout (except for last few chaetigers), i.e., 1.09 (\pm 0.14) times notopodial lobe anteriorly and 1.29 (\pm 0.30) times posteriorly	Equal to or slightly longer than notopodial lobe throughout, i.e., 1.03 (\pm 0.18) times notopodial lobe anteriorly and 1.26 (\pm 0.27) times posteriorly	1.30 (\pm 0.16) longer than notopodial lobe in anterior and mid body, 2.12 (\pm 0.42) times its length posteriorly

coll. 20 July 1975, QM GH 3921 (1); Moreton Bay, Queensland, sand beach, 27.25°S, 153.2°E, coll. S. Hatfield, 19 Feb. 1997, QM G213807 (1).

Remarks: This species was adequately described by Wilson and Glasby (1993) and by Hylleberg et al. (1986) (as *P. quatrefagesi*). We provide 2 additional observations: 1st, the 1-3 paragnaths in area V are located relatively more proximally to the arc of short bars in area VI on the

everted proboscis compared to other members of the species group (Fig. 6A); and 2nd, in the material we examined, neuropodial heterogomph spinigers were absent from parapodia of the anterior 1/4-1/3 of the body, but present thereafter (Fig. 6C, D). *Perinereis nuntia* may also be distinguished from congeners by the generally low numbers of paragnaths on the maxillary ring (Table 2; Fig. 6A, B), the relatively short length of the tentac-

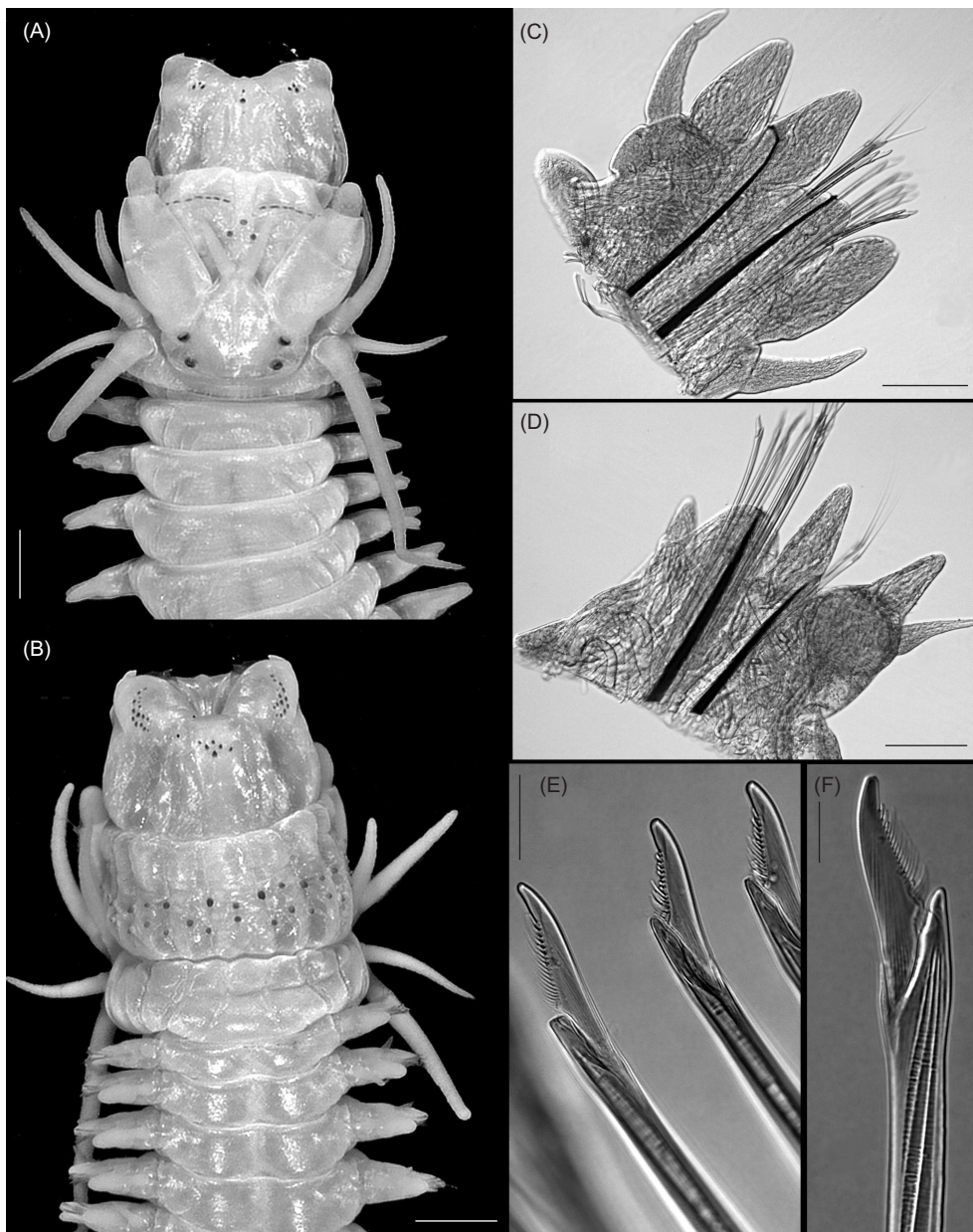


Fig. 6. *Perinereis nuntia* (Savigny, 1818). (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 7, anterior view; (D) posterior parapodium, posterior view; (E) subacicular neurochaetae from parapodium 7; (F) subacicular neuropodial heterogomph falciger from posterior parapodium. A-F: NTM W19042. Scalebars: A, B = 0.5 mm; C, D = 0.2 mm; E, F = 0.02 mm.

ular cirri, with the longest posterodorsal ones extending to chaetigers 6-8 (Fig. 6A, B), and the short dorsal cirri, which extend short of, or level with, the dorsal notopodial ligule throughout except for the last few chaetigers (Fig. 6C, D). Recently dead specimens from Indonesia and Singapore had a pinkish-white iridescent appearance and lacked any substantial pigmentation on the dorsum except for some slightly dusky pigment on the dorsal surface of the head; they had small eyes and a purple median dorsal blood vessel. Hylleberg et al. (1986) noted the same features for Thai specimens.

Habitat: Singaporean specimens were collected in the upper intertidal region of rocky beaches in sand under boulders and stones. Pari Is. (Indonesia) and Moreton Bay (E. Australia) specimens were from a sand beach. Thai specimens were from the upper intertidal region of sandy beaches, sometimes under rocks (Hylleberg et al. 1986).

Distribution: Type locality: Red Sea. Widespread throughout the tropical Indo-Pacific, including northern Australia; also Gulf of Aden (Wilson and Glasby 1993). New records for Singapore and Taiwan.

***Perinereis rhombodonta* Wu, Sun and Yang, 1981**

Fig. 7A-F.

Perinereis rhombodonta Wu et al. 1981: 179-181, fig. 113a-j; Wu et al. 1985: 199-201, fig. 113; Wilson and Glasby 1993: 268-269.

Materials: Taiwan: Kinmen, Nanshan, 24°28' N, 118°18'E, coll. S.L. Wu, 22 Aug. 2002, ASIZW660 (1); Kinmen, Sharzhou, 24°25'32.8"N, 118°18'28.5"E, coll. S.L. Wu, 20 Aug. 2002, ASIZW659 (1). China: Xuwen Co., Guangdong Prov., coll. C.A. Chen, 18 July 2002, ASIZW658 (8). Hong Kong: Ha Hi Wan, coll. C.A. Chen, 24 July 2002, ASIZW661 (3). Malaysia: Blue Lagoon, near Port Dickson, 3°N, 101°45'E, coll. C. Glasby and E. Omena, 6 Dec. 2003, NTM W19275 (9), NTM W19273 (1), NTM W19274 (1). Singapore: St John's I., southern shore, 1°6'N, 103°48'E, coll. C. Glasby and E. Omena, 8 Dec. 2003, NTM W19272 (1), NTM W19038 (1). Indonesia: Java, Banten Bay, Bojonegara Beach, approx. 6°N, 106°14'E, coll. I. Al-Hakim, 10 May 2003, NTM W19271 (16).

Remarks: This species was adequately described and figured by Wu et al. (1981 1985),

and Wilson and Glasby (1993) provide paragnath counts based on many specimens. It may be distinguished from all other *Perinereis* by having pyramidal paragnaths rather than bars in area VI and by the distinctive rhomboidal arrangement of paragnaths in area VII-VIII (Fig. 7A, B). The pyramidal paragnaths show slight variation from a clearly quadrangular base to a more-rounded, nearly circular base (thus almost being cone shaped). *Perinereis rhombodonta* is most similar to *P. akuna*, which also has an arc of pyramidal paragnaths in area VI, but may be distinguished from this species by the arrangement of paragnaths in area VII-VIII: in *P. akuna* the band of smaller cones is more distant from the jaws than the band of larger cones (in the everted pharynx), whereas in *P. rhombodonta*, the band of smaller cones is closer to the jaws (Fig. 7B).

Habitat: Intertidal, in sand under rocks and boulders.

Distribution: Type locality: Guangdong Prov., China. Widespread throughout the South China Sea including Hong Kong. Also Thailand. First records for Taiwan, Malaysia, Singapore, and Indonesia.

***Perinereis shikueii* sp. nov.**

Fig. 8A-F.

Perinereis brevicirris: Wu 1967: 71-72, fig. 11a-d (in part). Not *Nereilepas brevicirris* Grube, 1867.

Type materials: Holotype: Taiwan: Chuwei, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 4 Feb. 1999, ASIZW663. Paratypes: Chuwei, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 18 Nov. 2000, ASIZW665 (1), RMBR ZRC2005.0092 (1), NTM W19421 (1), RMBR ZRC2005.0093 (1); Chuwei, Tanshui Estuary, Taipei Co., Taiwan, 25°8'N, 121°26'E, coll. H.L. Hsieh, 22 Oct. 1999, ASIZW664 (1), NTM W19422 (1).

Non-type materials: Taiwan: Chuwei, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19290 (1); Chuwei, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 18 Nov. 2000, NTM W19287 (1), NTM W19293 (1); Wazuwei, Tanshui Estuary, Taipei Co., 25°10'N, 121°24'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19292 (1); Mitsang, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L. Hsieh, 22 Oct. 1999, NTM W19295 (1), NTM W19289 (1), NTM W19294 (1); Mitsang, Tanshui Estuary, Taipei Co., 25°8'N, 121°26'E, coll. H.L.

Hsieh, 18 Nov. 2000, NTM W19288 (1), NTM W19291 (1); Bali, Tanshui Estuary, Taipei Co., 25°9'48.3"N, 121°25'17.27"E, coll. M.J. Kuo, 8 Mar. 2003, ASIZW668(2); Tanshui Estuary, Taipei Co., coll. M.J. Kuo, 12 Aug. 2002, ASIZW666 (3); Beigang R., Yuanlin Co., 23°31'1.8"N, 120°8'35"E, coll. M.J. Kuo, 25 Jan. 2003, ASIZW667(9); Koliaw, Tainan, coll. S.K. Wu, 5 Dec. 1964, ASIZW201 (3), ASIZW 194 (1 male epitoke); Tsu-Wei, Keelung, coll. S.K. Wu, 4 Mar. 1966,

ASIZW205 (2); Hsieh-Shang Creek, Tainan, coll. S.K. Wu, 6 Dec. 1964, ASIZW206 (1); Bali, Tanshui R., Taipei Co., 25°9'48.3"N, 121°25'17.27"E, coll. M.J. Kuo, 8 Mar. 2003, ASIZW668 (2).

Description of types: Holotype complete, 111 chaetigers, 70 mm in length, 2.88 mm wide at chaetiger 10 (excluding parapodia); 5.04 mm wide at chaetiger 10 (including parapodia). Paratypes with 100-115 chaetigers for 50-65 mm long and

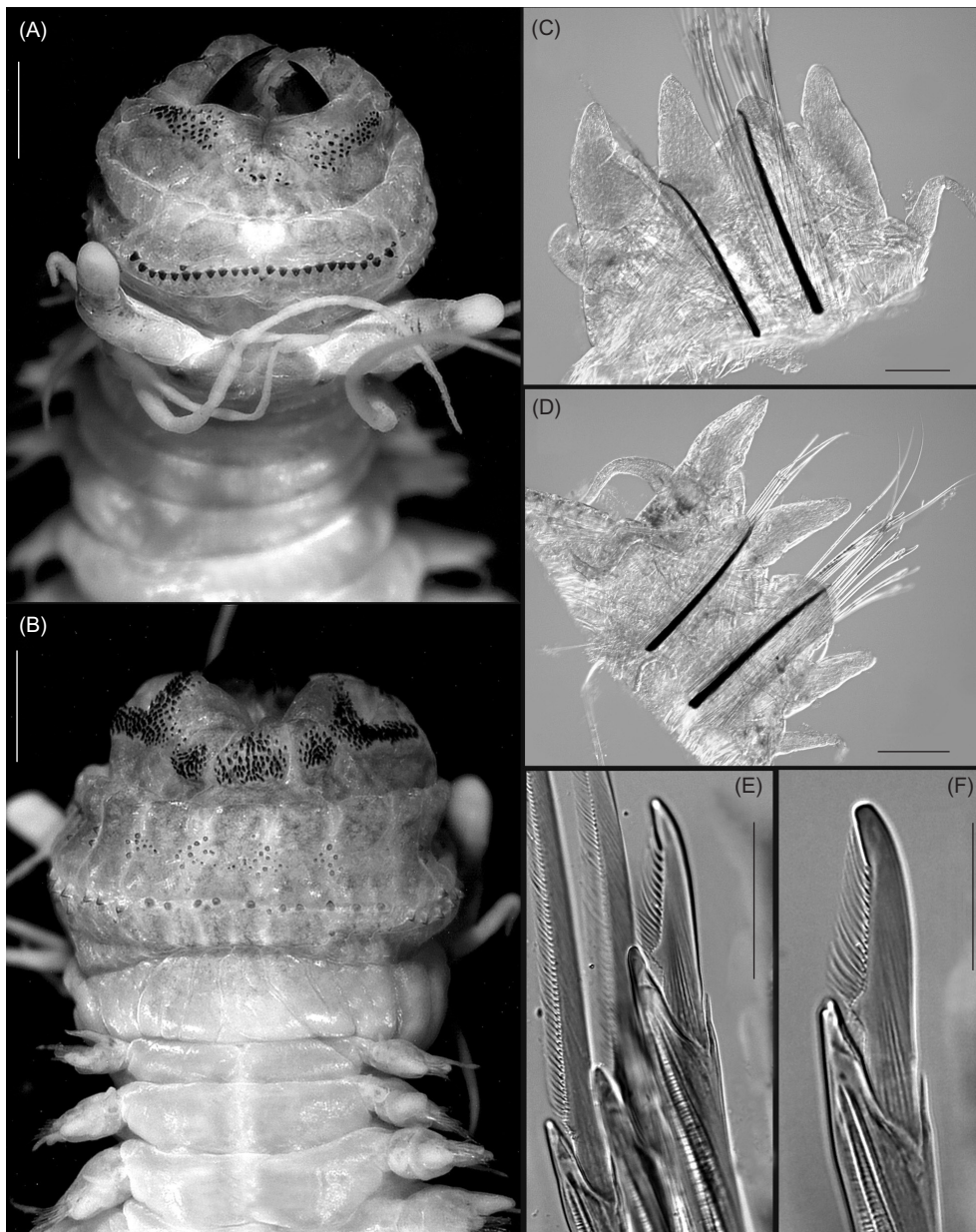


Fig. 7. *Perinereis rhombodonta* Wu, Sun and Yang, 1981. (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 15, anterior view; (D) posterior parapodium, posterior view; (E) subacicular neuropodial heterogomph spinigers and falcigers (dorsal position) from parapodium 15; (F) subacicular neuropodial heterogomph falciger (ventral position) from parapodium 15. A-F: NTM W19038. Scalebars: A, B = 0.5 mm; C, D = 0.2 mm; E, F = 0.02 mm.

1.45-2.64 mm wide at chaetiger 10 (excluding parapodia); 2.40-4.40 mm wide at chaetiger 10 (including parapodia).

Prostomium slightly wider than long, antennae about 1/3 length relative to prostomium length. Posterodorsal tentacular cirri extending back to chaetiger 7 (6-11). Jaws brown, cutting edge dentate with 8 (6-10) teeth (proximalmost ones ensheathed). Paragnaths black, cones on oral ring only slightly larger than those on maxillary

ring. Area I with 7 (2-6) conical paragnaths; area II with 25 (17-26) conical paragnaths in an elongate patch; area III with 20 (14-23) conical paragnaths in central patch, 4 (2-4) laterally on either side; area IV with 32 (21-30) conical paragnaths, bars absent; area V with 3 (3) conical paragnaths in a shallow triangle; area VI with 10 (5-10) bars, outer ones equal in length or only slightly longer than others; area VII-VIII with 38 (36-52) conical paragnaths arranged in a single band of 2 rows (proxi-

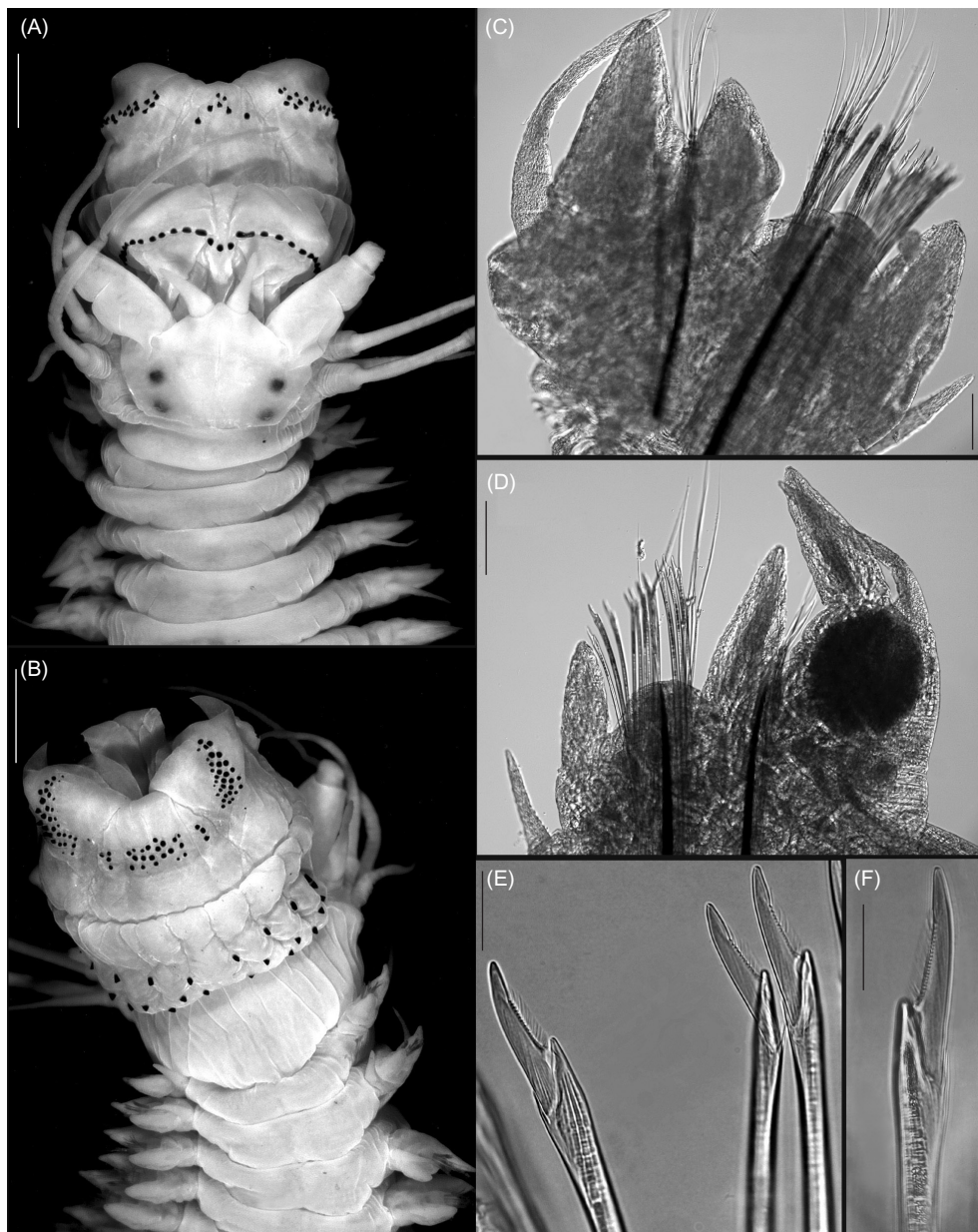


Fig. 8. *Perinereis shikueii* sp. nov. (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 12, anterior view; (D) posterior parapodium, posterior view; (E) subacicular neuropodial heterogomph falciger from posterior parapodium; (F) subacicular neuropodial heterogomph falciger from parapodium 12. A-F: Holotype, ASIZW663. Scale bars: A, B = 1.0 mm; C, D = 0.2 mm; E, F = 0.02 mm.

mal row on everted pharynx zigzagged) (Fig. 8A, B).

Dorsal notopodial ligule on posterior chaetigers not markedly larger than ventral notopodial ligule, although extending further laterally about 2 times length of ventral notopodial ligule due to enlarged basal region. Dorsal cirrus length 1.18 (0.90-1.08) times length of dorsal notopodial ligule length anteriorly (chaetiger 10-20) (Fig. 8C); posteriorly dorsal cirrus length 1.07 (0.69-1.63) times length to dorsal notopodial ligule length (chaetiger 75-90) (Fig. 8D). Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule 1.5-2.0 times (1.0-2.0 times in paratypes) length of acicular neuropodial ligule length. Neuropodial dorsal fascicle heterogomph falcigers with serrated blades; serrated region 0.29 (0.30-0.33) total blade length (Fig. 8E, F). Neuropodial heterogomph spinigers present throughout.

Epidermal pigmentation on prostomium only (and anterior dorsum in some paratypes), faint, dusky brown. Single glandular patch at base of dorsal notopodial ligule on posterior chaetigers (Fig. 8D).

Variation: Non-type materials generally exhibiting no more variation than paratypes, except in paragnath counts (below). In fresher material, some specimens showing more-intense dusky-brownish-green pigment on dorsum, prostomium, and pharynx. Variation in paragnath counts: I: 2-7; II: 17-27; III, central: 14-24; III, lateral: 2-9; IV: 21-35 (cones only, no bars); V: 3 or 4 (when 3 present, usually arranged in a longitudinal row); VI: 4-10; VII-VIII: 34-52 (Table 2). Neuropodial dorsal fascicle heterogomph falcigers with serrated region 0.26-0.33 of total blade length.

A single incomplete male specimen examined (ASIZW 194) with epitokous modification; with enlarged eyes and modified epitokal chaetigers beginning on chaetiger 18. In the pre-epitokal region, parapodia not modified, while 2-6 light-brown spots occurring dorsolaterally on either side of each chaetiger. Two pairs of these spots present on the anterior and posterior margins of each chaetiger slightly larger. In epitokal region, prominent modifications including additional auricular lobes on the dorsal base of the dorsal cirrus and ventral base of the ventral cirrus, and a large postchaetal neuropodial lobe. Dorsal cirri crenulated on 1st 33 epitokal chaetigers.

Remarks: *Perinereis shikueii* sp. nov. is similar to *P. nuntia*, which also has short, even-length bars on area VI. It may be distinguished from *P.*

nuntia in having a greater number of paragnaths in the maxillary ring, viz. areas I (2-7 compared to 0-5), II (17-27 compared to 0-23), III (18-29 compared to 1-30), and IV (21-35 compared to 5-35). As compared with *P. mictodonta* and *P. wilsoni* sp. nov., other characteristic features of this species are the intense dusky-brownish-green pigment on the dorsum prostomium and pharynx, distally elongated and slightly spatulate falciger blades, fewer cones in area IV (25.3 ± 5.1); a large number of even-length bars in area VI (7.1 ± 1.6); area V paragnaths in more or less a straight transverse line; and black paragnaths, those on oral ring subequal to those on maxillary ring (Table 3). It may be distinguished from all other *Perinereis* species primarily on the basis of paragnath numbers (Table 2).

Wu's (1967) material consists of a mixture of *P. mictodonta*, *P. shikueii* sp. nov., and *P. wilsoni* sp. nov. (see below) judging by the range of paragnaths especially those in areas I, V, and VI as well as the DC:DNL ratios.

Etymology: The species is named in honor of Dr. Shi-Kuei Wu who pioneered taxonomic studies of nereidids in Tawian. The species name is pronounced like "shee-gway".

Habitat: Intertidal under rocks in sand and mud.

Distribution: Type locality: Chuwei, Taiwan. Known only from Taiwan.

Perinereis viridis sp. nov.

Fig. 9A-F.

Nereis (Perinereis) singaporiensis: Horst 1924: 169-170, pl. XXXIV, figs, 1, 2. Not Grube 1878.

Perinereis sp. 2 [Indonesia] Wilson and Glasby 1993: 271-272.

Type materials: Holotype: Singapore: Labrador Park, 1°10'N, 103°47'E (approx.), intertidal rocky shore, coll. C. Glasby and E. Omena, 9 Dec. 2003 (NTM W19338). Paratypes: Singapore: St John's I., south shore, 1°6'N, 103°48'E (approx.), rocky shore, coll. C. Glasby and E. Omena, 8 Dec. 2003 ASIZW683 (1), NTM W19424 (1).

Description of types: Holotype complete, 150 chaetigers, comprising anterior 42-chaetiger fragment and posterior 93-chaetiger fragment (mid-section used for DNA study), 2.5 mm wide at chaetiger 10 (excluding parapodia); 4.2 mm wide at chaetiger 10 (including parapodia). Paratypes posteriorly incomplete, 1.5-2.5 mm wide at chaetiger 10 (excluding parapodia); 3.0-4.0 mm

wide at chaetiger 10 (including parapodia).

Prostomium, slightly wider than long, antennae about 1/3 length relative to prostomium length. Posterodorsal tentacular cirri extending back to chaetiger 5 (4). Jaws dark brown, cutting edge dentate, 8 (7-9) teeth (proximalmost ones ensheathed). Paragnaths brown, cones on oral ring slightly larger than those on maxillary ring. Area I with 2 paragnaths (proximal one larger with rectangular base); area II with 11 (8-12) conical

paragnaths in an elongate patch; area III with 20 (18-19) conical paragnaths in central patch, 2 (2-4) laterally on either side; area IV with 42 (27-29) conical paragnaths, 3 (2 or 3) smooth barlike paragnaths near jaws; area V with a single conical paragnath; area VI with 2 or 3 bars, interspersed with 0 or 1 cones; area VII-VIII with 41 (38-46) conical paragnaths arranged in a single band of 2 rows (proximal row on everted pharynx zigzagged) (Fig. 9A, B).

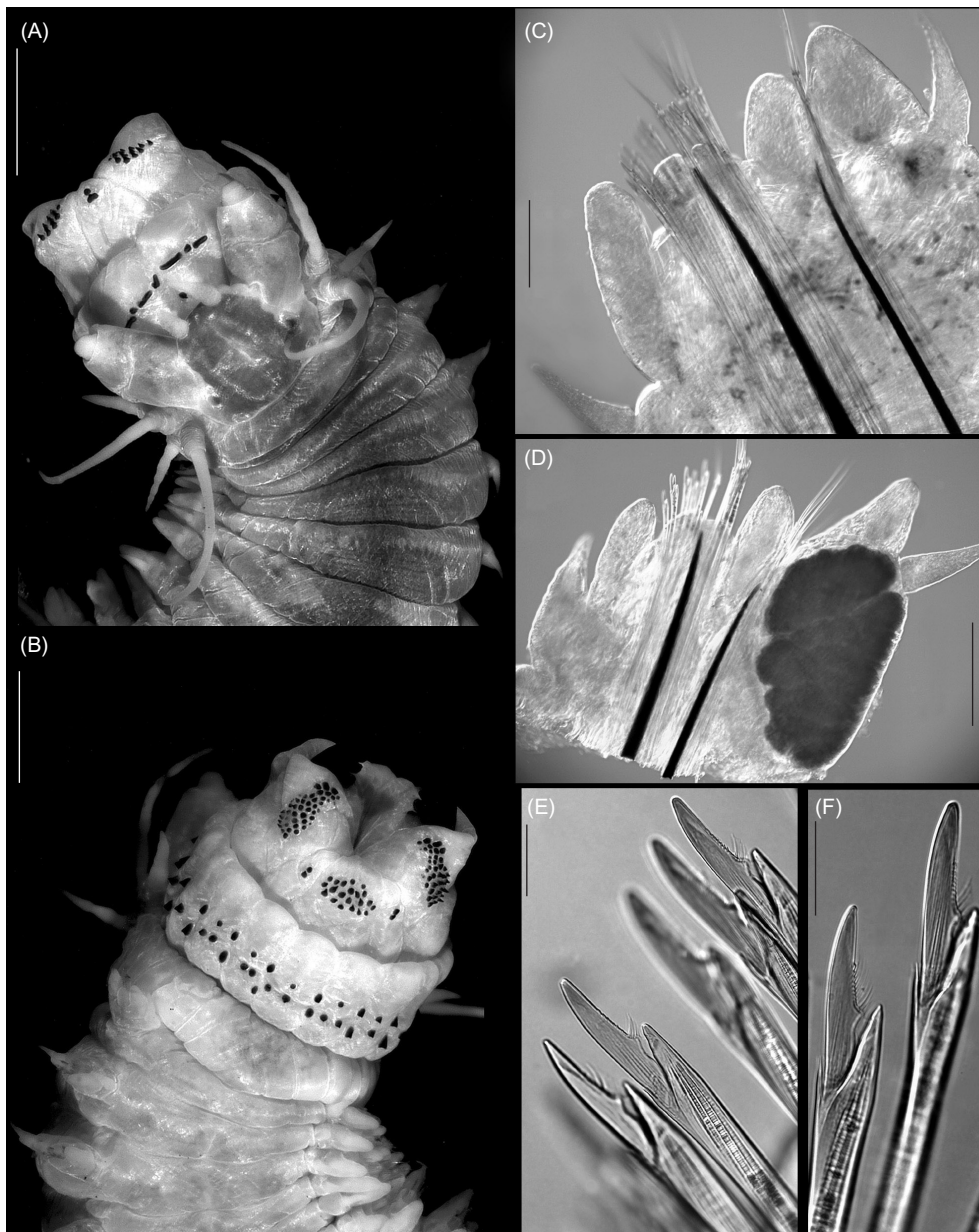


Fig. 9. *Perinereis viridis* sp. nov. (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 11, posterior view; (D) posterior parapodium, posterior view; (E) subacicular neuropodial heterogomph falcigers from parapodium 11; (F) subacicular neuropodial heterogomph falcigers from posterior parapodium. A-F: Holotype, NTM W19338. Scalebars: A, B = 1.0 mm; C, D = 0.2 mm; E, F = 0.02 mm.

Dorsal notopodial ligule on posterior chaetigers not markedly larger than ventral notopodial ligule. Dorsal cirrus length 0.98 (0.80-1.0) times length of dorsal notopodial ligule anteriorly (chaetiger 10-20) (Fig. 9C); posteriorly dorsal cirrus length 1.17 (1.0) times length of dorsal notopodial ligule (chaetiger 75-90) (Fig. 9D). Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule similar in length to acicular neuropodial ligule in all chaetigers. Neuropodial dorsal fascicle heterogomph falcigers with serrated blades; serrated region 0.20 (0.25-0.28) of total blade length (Fig. 9E, F). Neuropodial heterogomph spinigers present throughout.

Epidermal pigmentation on dorsal surface, most intense anteriorly, appearing brown in fixed animal, but green in life (smaller paratype with less-intense pigmentation). Glandular patches at base of dorsal notopodial ligule on posterior chaetigers; 2 or 3 per ligule (Fig. 9D).

Remarks: There is little doubt that the material described here as *P. viridis* sp. nov. is the same as the specimen described by Wilson and Glasby (1993) as *Perinereis* sp. 2 from Siboga Station 115 (reef on east side of Pajunga I., Kwandang Bay, Sulawesi, Indonesia). The 2 groups of specimens agree well in terms of paragnath counts, especially in regard to the presence of bars in area IV, and the short tentacular cirri. As mentioned by Wilson and Glasby (1993), the specimen from Kwandang Bay was originally identified by Horst as *Nereis vallata*, but Horst did not report that species from the Siboga material. The only *Perinereis* specimen from Station 115 in Horst's account was *P. singaporiensis* Grube, 1878, and it appears that this specimen may indeed have been apart of Horst's original material of *P. singaporiensis*; hence mislabeling has occurred. *Perinereis singaporiensis*, which has been redescribed by both Hylleberg et al. (1986) and Hutchings et al. (1991), appears to differ from *P. viridis* sp. nov. in having only 2 bars in area VI (no cones), and in lacking bars in area IV.

The only other species in the *P. nuntia* species group having bars as well as cones in area IV are *P. akuna*, *P. majungaensis* Fauvel, 1921, and *P. vallata* (Table 2). Like *P. viridis* sp. nov, both *P. akuna* and *P. vallata* have only a few bars (up to 5) in area IV, whereas *P. majungaensis* may have 12 or 13. The new species may be distinguished from *P. akuna* in lacking an additional row of small cones in area VII-VIII and in the form of the heterogomph falciger blades, which are pro-

portionately more serrated in *P. akuna* (Wilson and Glasby 1993: fig. 7G-M). As indicated by Wilson and Glasby (1993) in their key, this new species, which they referred to as *Perinereis* sp. 2, is close to *P. vallata*. However, the additional specimens of *P. viridis* sp. nov. described here indicate that *P. vallata* differs from the present species in having many more paragnaths on the oral ring, VI: 5-14 (mean, 12.5) and area VII-VIII: 42-129 (mean, 69.0) compared to *P. viridis* sp. nov. (area VI: 2-4 and area VII-VIII: 38-51). In addition, *P. vallata* has a greater number of serrations on the heterogomph falciger blades than *P. viridis* sp. nov. (Wilson and Glasby 1993: figs 12G-L, 13D-G).

Etymology: The species is named after the Latin for green, *viridis*, for the live coloration of larger individuals.

Habitat: Intertidal reef and rocky crevices.

Distribution: Type locality: Labrador Park, Singapore. Also from Sulawesi, Indonesia (Horst 1924).

***Perinereis wilsoni* sp. nov.**

Fig. 10A-F.

Perinereis brevicirris: Wu 1967: 71-72, fig. 11a-d (in part). Not *Nereilepas brevicirris* Grube, 1867.

Perinereis nuntia var. *vallata:* Khlebovich and Wu 1962: 51-52, pl. 3; Paik 1972: 131, fig. 2a-h; Imajima 1972: 92-94. Not *Nereis vallata* Grube, 1858.

Perinereis nuntia vallata: Wu et al. 1985: 210-213, fig. 121a-k [note that figures for *P. nuntia vallata* have been transposed with those for *P. cultrifera typica*] Not *Nereis vallata* Grube, 1858.

Perinereis sp. 2 Chen et al. 2002: 19.

Type materials: Holotype: Pitou, Taipei Co., Taiwan, 25°7'N, 121°54'E, coll. H.L. Hsieh, 7 Nov. 2001, ASIZW670. Paratypes: locality data as for holotype, ASIZW671 (1), ASIZW672 (1), NTM W19425 (1), NTM W19426 (1), RMBR ZRC2005.0090 (1), RMBR ZRC2005.0091 (1).

Non-type materials: Taiwan: Lungtung, Taipei Co., Taiwan, 25°6'N, 121°54'E, coll. H.L. Hsieh, 8 Oct. 1998, NTM W19279 (1), NTM W19281 (1), NTM W19284 (1), NTM W19283 (1), NTM W19278 (1), NTM W19280 (1); Shermen, Taipei Co., Taiwan, 25°17'N, 121°33'E, coll. C.A. Chen, 21 Feb. 2003, ASIZW 678 (16); Pa-Chih-Meng, Keelung, coll. S.K. Wu, 21 May 1964, ASIZW193 (3), ASIZW189 (4), ASIZW190(4), ASIZW200 (4); Keng-Liao, Keelung, coll. S.K. Wu, 12 Mar. 1965, ASIZW188 (2); Shih-Meng, Keelung, coll. S.K. Wu, 8 Aug. 1964, ASIZW197 (1), ASIZW195 (2); Wan-Li, Keelung, S.K. Wu, 22 Apr. 1965, ASIZW196

(1); Sharzhou, Kinmen, 24°25'32.8"N, 118°18'28.5"E, coll. S.L. Wu, 20 Aug. 2002, ASIZW675 (10); 22 Aug. 2002, ASIZW676 (1); Watun, Penghu Co., 23°39'29.48"N, 119°34'26.28"E, coll. M.J. Kuo, 19 Mar. 2003, ASIZW682 (1), ASIZW681 (5); Tiehhsien, Penghu Co., 23°32'8.11"N, 119°35'18.95"E, coll. M.J. Kuo, 19 Mar. 2003, NTM W19276 (1), NTM W19277 (3), ASIZW680 (1), ASIZW679 (5); Liukuaitso, Tanshui

Town, Taipei Co., 25°14'N, 121°26'E, coll. H.L. Hsieh, 26 Mar. 2003, NTM W19286 (1 male epitoke), NTM W19285 (1 female epitoke). China: Beihai City, Guangxi Prov., coll. C.A. Chen, 17 July 2002, ASIZW673 (11); Weijihou, Guangxi Prov., coll. C.A. Chen, 8 Sept. 2002, ASIZW677 (1); Hong Kong: Ha Hi Wan, coll. C.A. Chen, 24 July 2002, ASIZW674 (4).

Description of types: Holotype complete, 85

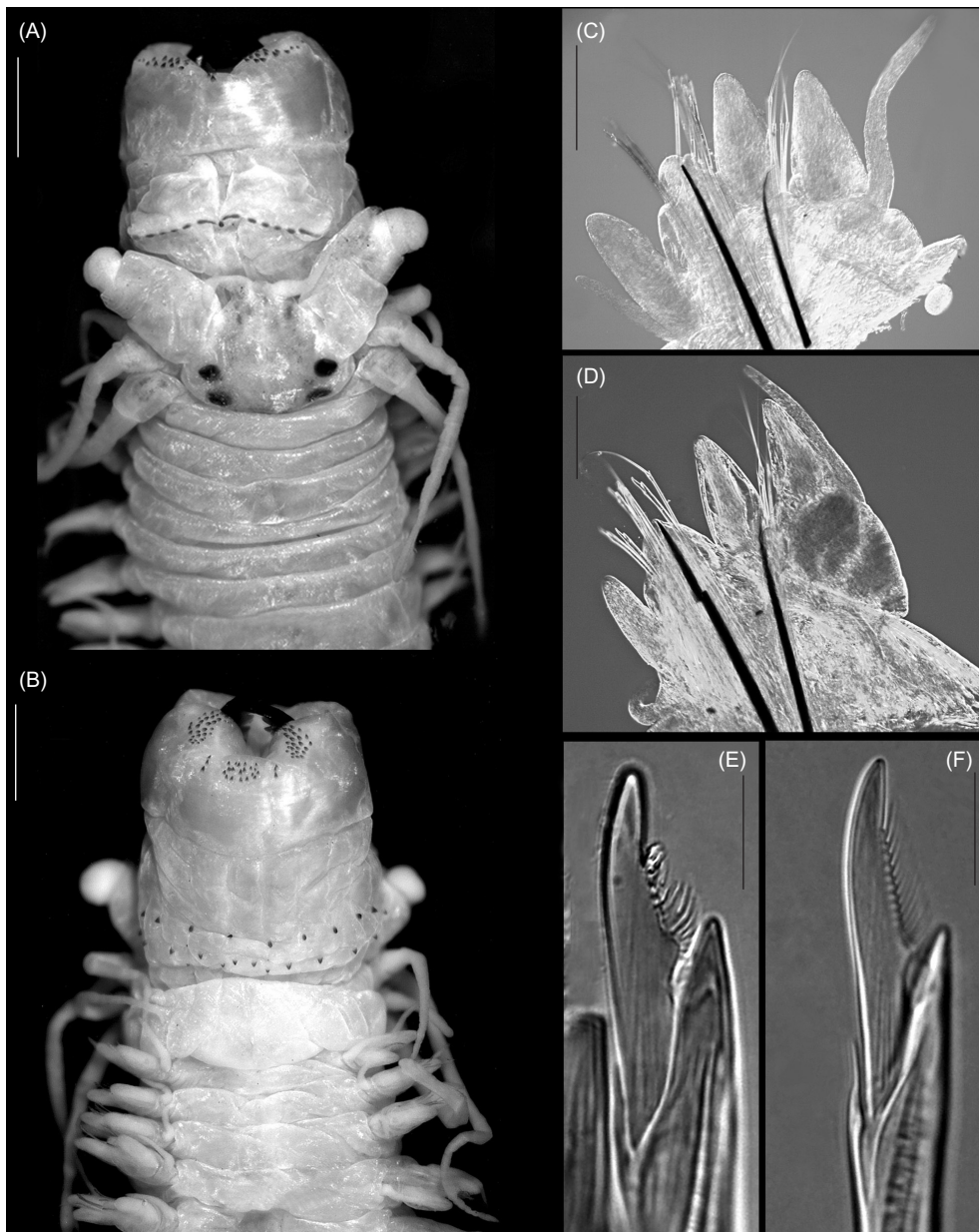


Fig. 10. *Perinereis wilsoni* sp. nov. (A) Anterior end with pharynx everted, dorsal view; (B) anterior end with pharynx everted, ventral view; (C) parapodium 10, posterior view; (D) posterior parapodium, posterior view; (E) supra-acicular neuropodial heterogomph falciger from parapodium 10; (F) supra-acicular neuropodial heterogomph falciger from posterior parapodium. A-F: Paratype, ASIZW672. Scalebars: A, B = 0.5 mm; C, D = 0.2 mm; E, F = 0.01 mm.

chaetigers, 30 mm in length, 1.65 mm wide at chaetiger 10 (excluding parapodia); 2.55 mm wide at chaetiger 10 (including parapodia). Paratypes with 85-110 chaetigers for 31-49 mm long and 1.4-2.3 mm wide at chaetiger 10 (excluding parapodia); 2.3-3.5 mm wide at chaetiger 10 (including parapodia).

Prostomium slightly wider than long, antennae about 1/3 length relative to prostomium length. Posterodorsal tentacular cirri extending back to chaetiger 12 (8-14). Jaws brown, cutting edge dentate with 7 (7-9) teeth (proximalmost ones ensheathed). Paragnaths brown, cones on oral ring slightly larger than those on maxillary ring. Area I with 1 (1-3) conical paragnath; area II with 17 (12-19) conical paragnaths in an elongate patch; area III with 20 (11-19) conical paragnaths in central patch, 2 (2 or 3) laterally on either side; area IV with 32 (26-32) conical paragnaths, bars absent; area V with 2 (1-3) conical paragnaths; area VI with 7 (4-8) bars, the end ones longest; area VII-VIII with 23 (22-30) conical paragnaths arranged in a single band of 2 rows (proximal row on everted pharynx zigzagged) (Fig. 10A, B).

Dorsal notopodial ligule on posterior chaetigers not markedly larger than ventral notopodial ligule. Dorsal cirrus length 1.43 (1.25-1.50) times length of dorsal notopodial ligule anteriorly (chaetiger 10-20) (Fig. 10C); posteriorly dorsal cirrus length 2.35 (1.67-2.88) times length of dorsal notopodial ligule (chaetiger 75-90) (Fig. 10D). Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule similar in length to acicular neuropodial ligule in all chaetigers. Neuropodial dorsal fascicle heterogomph falcigers with serrated blades; serrated region 0.40 (0.32-0.39) of total blade length (Fig. 10E, F). Neuropodial heterogomph spinigers present throughout.

Epidermal pigmentation on prostomium only, faint, dusky-brown. Glandular patches at base of dorsal notopodial ligule on posterior chaetigers; 2 per ligule, more or less equal in size (Fig. 10D).

Variation: Non-type material also only pigmented on head (prostomium and palps) and pharynx, ranging from brown to green. Posterodorsal tentacular cirri extending to chaetigers 8-11. Variation in paragnath counts: I: 1-3; II: 9-21; III, central: 12-23; III, lateral: 2-5; IV: 24-39 (cones only, no bars); V: 1-3 (when 3 present, usually arranged in a longitudinal row); VI: 4-8; VII-VIII: 22-34 (Table 2). Dorsal cirrus length 1.0-1.5 times length of dorsal notopodial ligule anteriorly

(chaetiger 10-20); posteriorly dorsal cirrus length 1.7-2.9 times length of dorsal notopodial ligule (chaetiger 75-90). Neuropodial dorsal fascicle heterogomph falcigers with serrated blades; serrated region 0.26-0.33 of total blade length.

Reproductive forms: Two specimens with epitokal modifications (NTM W19285-6). Epitokes with greatly enlarged eyes, and more heavily pigmented than non-epitokes. In both male and female a pair of dorsolateral brown patches on each pre-epitokal chaetiger; on epitokal chaetigers a single brown spot (eyespot?) occurring dorsolaterally on each chaetiger. Pre-epitokal region with slightly modified dorsal cirri on 1st 6 (female) or 7 (male) chaetigers; modified ventral cirri on 1st 5 (female) or 6 (male) chaetigers. Epitokal modifications including additional auricular lobes of various sizes at bases of all parapodial ligules and cirri, beginning on chaetiger 20 or 21 in females, and chaetiger 17 in males. Parapodial auricular lobes as for *P. mictodonta*, but more prominent (unsure whether this is due to different stage of sexual maturity or is species-specific). In addition dorsal cirri, and to a lesser extent ventral cirri, of modified parapodia crenulated in male. Parapodial modifications continuing to pygidium in male, but ending about 10-12 chaetigers before pygidium in female. In both males and females, normal chaetae replaced by serrated, broad-bladed sesquigomph natatory chaetae in modified parapodia. Pygidium of male modified, in having multiple short papillae in the form of a rosette in addition to normal pair of anal cirri; pygidium of female not modified. Further information on reproduction in this species is available in Yoshida (1984) under the name *P. nuntia* var. *vallata*.

Remarks: For the same reasons outlined under the "Remarks" for *P. mictodonta*, all reports of *P. nuntia* var. *vallata*, *P. nuntia vallata* and *P. vallata* from the northern hemisphere, including tropical shores, are likely to be misidentifications. Material identified as *P. nuntia* var. *vallata* by Khlebovich and Wu (1962), Paik (1972), Imajima (1972), and as *P. nuntia vallata* by Wu et al. (1985) is the same as the new species described here, but not *Nereis vallata* Grube, 1858. *Perinereis wilsoni* sp. nov. differs from *P. vallata* (Grube), which has bars in addition to cones in area IV (Wilson and Glasby 1993) and is restricted to the southern hemisphere. Records of *P. nuntia vallata* from the Indian subcontinent region (Fauvel 1932 1953) cannot be verified but are unlikely to be *P. wilsoni*. The material identified by Wu (1967) as *P. brevicirris* is a mixture of 3 species, *P.*

mictodonta, *P. wilsoni* sp. nov., and *P. shikueii* sp. nov.

Perinereis wilsoni sp. nov. is very similar to *P. mictodonta*, and had it not been for a significant result of the morphometric analysis of paragnath numbers and parapodial lobe ratios, the 2 taxa could have been treated as variants of a single taxon, or as subspecies. The conclusion to treat them as separate species is supported by the results of an analysis of intertranscribed spacer (ITS) 1 and 2 sequences (Chen et al. 2002). The 2 species may be distinguished in that *P. wilsoni* sp. nov. has fewer cones in area IV (29.8 ± 3.6); area V paragnaths are arranged singly or 2 or 3 in a longitudinal line; and it has relatively longer dorsal cirri, viz. $1.30 (\pm 0.16)$ longer than the notopodial lobe in the anterior and mid-body, $2.12 (\pm 0.42)$ times its length posteriorly (Table 3). *Perinereis wilsoni* sp. nov. differs more substantially from *P. shikueii* sp. nov. in paragnath color and size, the number of cones in area IV, and the relatively longer dorsal cirri. It may be distinguished from all other *Perinereis* species primarily on the basis of paragnath numbers (Table 2).

Etymology: The species is named in honor of our colleague and nereidid specialist, Dr. Robin Wilson, who has contributed much to the systematics of the Nereididae.

Habitat: Intertidal reef flats or rocky shores, under boulders.

Distribution: Type locality: Pitou, Taiwan. Widespread through Taiwan, also the South China Sea (Hong Kong and China). Accepting the above synonymies this species occurs also in Japan (widespread), China (Yellow Sea), and South Korea (Korea Strait).

Key to species of the *Perinereis nuntia* species group of the tropical and subtropical Indo-West Pacific

This key has been adapted and expanded from Wilson and Glasby (1993), to which the reader is referred for identification of species occurring outside the tropical Indo-West Pacific. It includes *P. caeruleis*, which has also been reported from Taiwan under the junior synonym name of *P. neocaledonica* Pruvot, 1930 (Wu 1967). *Perinereis caeruleis* has not been re-collected in recent surveys of the area (A. Chen, pers. comm.).

- 1a. Anterior 20 notopodia with 3 lobes of similar size *P. maindroni*
- 1b. All notopodia with 2 lobes 2
- 2a. Paragnaths absent from area II and usually from area I;

- an additional arc of cones posterior to arc of bars in area VI *P. caeruleis*
- 2b. Paragnaths present in areas I and II; only a single arc of bars or cones in area VI 3
- 3a. Paragnaths absent from areas VII and VIII..... *P. matthaii*
- 3b. Paragnaths present in areas VII and VIII 4
- 4a. Area IV with bars 5
- 4b. Area IV without bars (cones only) 6
- 5a. Area IV with more than 10 bars *P. majungaensis*
- 5b. Area IV with 2 or 3 bars *P. viridis* sp. nov.
- 6a. Area VII-VIII with a band of large cones in 2 rows plus a band of numerous very small cones arranged in 5 or 6 similarly-sized rhomboidal groups *P. rhombodonta*
- 6b. Area VII-VIII with a band of large cones in 2 or 3 rows only 7
- 7a. Neuropodial heterogomph spinigers absent from anterior 1/3-1/4 of body; paragnaths of area V well proximal (compared to other *Perinereis*) to those of area VI *P. nuntia*
- 7b. Neuropodial heterogomph spinigers present throughout; paragnaths of area V only slightly proximal to those of area VI 8
- 8a. Area VI with short even-length bars (outermost only slightly longer if at all) (7.23 ± 1.4 bars) *Perinereis shikueii* sp. nov.
- 8b. Area VI with very uneven-length bars (outermost much longer) (5.4 ± 1.3 bars) 9
- 9a. Dorsal cirri about 1.5 times length of dorsal notopodial lobe anteriorly, increasing to 2-3 times its length posteriorly *Perinereis wilsoni* sp. nov.
- 9b. Dorsal cirri equal to or only slightly longer than dorsal notopodial lobe throughout (except last few chaetigers) *Perinereis mictodonta*

DISCUSSION

Distribution patterns

The *P. nuntia* species group is not uniformly distributed around the island of Taiwan. Generally the group prefers estuarine waters, or seawater with limited freshwater input (e.g., the Penghu Is. in the Taiwan Strait and the western and northern coasts of Taiwan). When suitable habitat is lacking, such as the mountainous east coast of Taiwan, there is a corresponding absence of members of the group (Fig. 1). Only 1 species, *P. shikueii*, was found to be restricted to Taiwanese waters but on the basis of DNA marker data, it may also be found to occur on Kinmen I. and Guangxi Province, China (paper in preparation). *Perinereis mictodonta*, once thought to be restricted to Japan, is now known to be widespread in Korea, Taiwan, and China (Fig. 1). On the west coast of Taiwan, *P. mictodonta* occurs at more localities compared to the more-restricted *P. shikueii* (Fig. 1). In addition, *P. mictodonta* is far more abundant than *P. shikueii* (examples of both species being collected at the same localities and

same dates: 30 vs. 1 individual collected from Wazuwei, Tanshui River estuary on 22 Oct. 1999; 33 vs. 9 individuals from the Beigang River estuary on 25 Jan. 2003; 22 vs. 1 individual from Shangshan intertidal flat at Hsinchu City on 22 Mar. 2003).

Perinereis nuntia has the widest distribution of all the species in this study. It is found in the southern part of Taiwan (Fig. 1) and has also been reported from the Red Sea, tropical Australia, Indo-Pacific countries, southeastern China, the Pacific Philippines, and Fiji (Wilson and Glasby 1993), revealing that it is a widespread Indo-Pacific species. Collection data for *P. rhombodonta* also indicate a wide Indo-Pacific distribution from southern China, Taiwan, and Hong Kong south to Malaysia, Singapore, and Indonesia (Fig. 1); literature records indicate that the species also occurs in Thailand (Wilson and Glasby 1993). *Perinereis wilsoni* occurs from Korea, Japan to the northern coast of Taiwan, through the Penghu Is. and Kinmen I., on down to Hong Kong and Guangxi Province of the southeastern Chinese coast (Fig. 1). It is possibly restricted to the East Asian region. *Perinereis viridis* has a restricted distribution including Singapore and Indonesia (Sulawesi) (Fig. 1), although this may reflect under-sampling of its specialized habitat (rock crevices).

The distribution patterns described above indicate the existence of a biogeographic boundary approximately coinciding with the junction of the South China Sea with the Taiwan Strait and southern Taiwan (Fig. 1). This boundary represents, with a few exceptions, the northernmost limits for widely occurring tropical-subtropical species of *P. nuntia* and *P. rhombodonta*, and the southernmost limits for the temperate-subtropical species of *P. mictodonta* and *P. wilsoni*. While the boundary appears to be quite sharp in Taiwan (at Tapeng Lagoon), on the Chinese coast it is more transitional, with both temperate and tropical species likely to co-occur in a region from about Hong Kong in the north to Xuwen (Hainan I.) in the south. The *Perinereis* species group appears to be absent from latitudes higher than the Yellow Sea and South Korea on the mainland, although the distributions of both *P. mictodonta* and *P. wilsoni* extend through to Hokkaido in the Sea of Japan (Imajima 1972). The Yellow Sea boundary coincides with the results of Wu et al. (1985: 32) who suggested that this sea forms the northern boundary for "subtropical" species, a finding based on a biogeographic analysis of all Chinese

neriidid species.

The present study also confirms the long-held view that some forms in the *P. nuntia* species group occur sympatrically along East Asian shores. Wu et al. (1985) found that the 4 subspecies, *P. n. brevicirris*, *P. n. vallata*, *P. n. typica*, and *P. n. majungaensis*, could all occur in the littoral of the 1 locality and suggested that they were separated ecologically. Paik (1972) reported both *P. n. var. brevicirris* and *P. n. var. vallata* from Korea, but later she considered that there were no significant differences in paragnath patterns between the 2 varieties, and suggested that they both belonged to the form, *P. nuntia* (Paik 1975 1977). In Taiwan, at the local scale, 2 species pairs are sympatrically distributed, namely *P. mictodonta* and *P. shikueii* and *P. rhombodonta* and *P. wilsoni*. The former pair co-habits the same estuaries, for instance, the Tanshui River and Beigang River estuaries, while the latter pair co-occurs at Sharzhou of Kinmen Island. On a regional scale, *P. nuntia*, *P. mictodonta*, *P. shikueii* and *P. wilsoni* are sympatrically distributed on the island of Taiwan. These results show remarkable diversity in Taiwan's *P. nuntia* group. Evolutionary and phylogeographic relationships among these taxa in the region remain unclear. DNA marker analyses are currently being carried out.

Evolutionary processes

With 5 species of the *P. nuntia* group occurring in its coastal waters, Taiwan has one of the highest diversities of this group in the world. An explanation for this high diversity is likely to include both extrinsic (historical) factors related to the position of Taiwan in the Indo-West Pacific, as well as intrinsic (biological) characteristics of each species within the group. The major historical factor responsible for Taiwan's high biodiversity is its position between 2 major biogeographic regions: the tropical Indo-West Pacific and the temperate Japan-East China Sea. Southern Taiwan marks the northernmost point of the coral triangle, an Indo-West Pacific subregion with the highest marine biodiversity in the world (based on data for corals and mollusks) (Veron 1995 2000). As such, southern Taiwan is home to the largely tropical species, *P. nuntia* and *P. rhombodonta*. The remainder of Taiwan, which is under the influence of subtropical-temperate waters, supports an additional 3 species, including *P. mictodonta* and *P. wilsoni* for which Taiwan represent the southernmost limit of these more-temperate species; and *P.*

shikueii, which has a narrow, subtropical distribution in and around Taiwanese waters.

There is limited information on larval development in the *P. nuntia* species group; 1 species, *P. mictodonta*, is known to have benthic larval development (Hardege and Bartel-Hardege 1995). However, there are indications that in nereidids inhabiting tropical coastal waters where ecological conditions are relatively less stable than oceanic waters there is a shortened or absent larval period (Wu et al. 1985, Sato 1999), which in theory would inhibit larval dispersal and promote speciation. Furthermore, Sato (1999: 142) suggested that polychaetes with planktonic development and a diadromus life history are rare in tropical brackish waters. This is related to the limited food supply for planktonic larvae in nutrient-poor tropical oceanic waters (e.g., Nybakken 1997). Such a strategy, if widespread in the group, would tend to restrict dispersal of individuals and promote greater genetic differentiation, which is what has been observed in the *P. nuntia* species group (Kuo 2004).

Microhabitat differences (e.g., salinity gradients, tidal magnitudes, grain sizes, and hydrological regimes) and behavioral differences may also play roles in partitioning sympatric species. Separation of sympatrically distributed species of *Hediste* Malmgren in Japan has been attributed to tidal flat elevation or grain size (Sato and Nakashima 2003). Populations of *Hediste diversicolor* in England show both paragnath number differences and genetic differences between sites within an estuary, and may be responding to differences in diet or a dominant mode of feeding (Hateley et al. 1992). Ecological separation has also been proposed for *P. nuntia brevicirris* [= *P. mictodonta*] and *P. nuntia vallata* [= *P. wilsoni*] as the 2 species co-occur in the same estuary in both China and Japan (Imajima 1972, Wu et al. 1985). Interestingly, although both *P. mictodonta* and *P. wilsoni* co-occur in Taipei County, northern Taiwan, the 2 species were not found in the same estuary or place on the coast in the present study. Both species metamorphose at maturity and spawn freely into the water column at approximately the same time of year in Japan and the Yellow Sea (Yoshida 1984, Wu et al. 1985). Cross-fertilization and hybridization is likely to be avoided however by reproductive-isolating mechanisms involving species-specific spawning behavior mediated by sex pheromones (Yoshida 1984, Hardege et al. 1994, Hardege and Bartels-Hardege 1995). Future investigations on the systematics of the

Perinereis nuntia species group and other coastal nereidids in Taiwan and surrounding waters would benefit therefore by considering both ecological and reproductive factors of the species involved.

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