

Redescription of the Indo-Pacific polychaete *Neanthes pachychaeta* (Fauvel, 1918) n. comb. (Annelida, Phyllodocida, Nereididae) and its synonyms

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ABSTRACT

Type specimens of three Indo-west Pacific nereidid polychaetes are redescribed: *Ceratonereis pachychaeta* Fauvel, 1918, *Nereis* (*Ceratonereis*) *ramosa* Horst, 1919 and *Nereis* (*Lycoris*) *anchylochaeta* Horst, 1924. No significant morphological differences were found between the three species. The latter two names are therefore relegated to junior synonymy with the oldest, *C. pachychaeta*. A lectotype is identified from among the syntypes of *C. pachychaeta* in order to stabilise the name and type locality of the species. Further, *C. pachychaeta* is newly transferred to the genus *Neanthes*, based on a comparison of generic level features, especially the presence of paragnaths on the oral ring. Newly collected specimens of *Neanthes pachychaeta* n. comb. from Indonesia, Philippines, northern Australia, Japan and French Polynesia are described and the living coloration reported for the first time. Apart from its striking red-orange colour, the species may be recognised by having paragnaths atop a plate-like basement and thick, hammer-headed fused falcigers in posterior parapodia. The new material and new synonymies give *N. pachychaeta* n. comb. a widespread Indo-Pacific distribution.

KEY WORDS

Annelida,
Nereididae,
Ceratonereis,
Nereis,
Neanthes,
new combinations.

RÉSUMÉ

Redescription du polychète *Neanthes pachychaeta* (Fauvel, 1918) *n. comb.* (Annelida, Phyllodocida, Nereididae) de l'Indo-Pacifique et ses synonymes.

Les spécimens types de trois polychètes néreididés de l'ouest de l'Indo-Pacifique sont redécrits: *Ceratonereis pachychaeta* Fauvel, 1918, *Nereis* (*Ceratonereis*) *ramosa* Horst, 1919 et *Nereis* (*Lycoris*) *anchylochaeta* Horst, 1924. Aucune différence morphologique significative n'a été trouvée entre les trois espèces. En conséquence, les deux derniers noms sont relégués en tant que synonymes plus récents de *C. pachychaeta*, le nom le plus ancien. Un lectotype est identifié parmi les syntypes de *C. pachychaeta* afin de stabiliser le nom et la localité type de l'espèce. De plus, *C. pachychaeta* est nouvellement transféré dans le genre *Neanthes*, basé sur une comparaison des caractères de niveau générique, particulièrement la présence de paragnathes sur l'anneau oral. Des spécimens de *Neanthes pachychaeta* *n. comb.* nouvellement collectés en Indonésie, aux Philippines, dans le nord de l'Australie, au Japon et en Polynésie française sont décrits et la coloration des individus vivants est rapportée pour la première fois. Indépendamment de sa couleur rouge-orange saisissante, l'espèce peut être identifiée par la présence de paragnathes placés au sommet d'un support en forme d'assiette, et des soies falcigères, épaisses et terminées en marteau, fusionnées sur le parapode postérieur. Le nouveau matériel et les nouvelles synonymies donnent *N. pachychaeta* *n. comb.* et distribution Indo-Pacifique répandue.

MOTS CLÉS

Annelida,
Nereididae,
Ceratonereis,
Nereis,
Neanthes,
nouvelles combinaisons.

INTRODUCTION

In the early 1900s, over a period of less than twenty years, three different names have apparently been applied to Indo-west Pacific nereidid (Annelida, Polychaeta, Nereididae Johnston, 1865) specimens possessing unusually large paragnaths atop a plate-like basement on the pharynx and fused falcigerous neurochaetae in posterior parapodia. Fauvel (1918) described this form as *Ceratonereis pachychaeta* based on specimens collected from Djibouti, Red Sea and Madagascar. Horst (1919, 1924) described it as *Nereis* (*Ceratonereis*) *ramosa*, then *Nereis* (*Lycoris*) *anchylochaeta*, based on sexually modified forms (epitokes) from eastern Indonesia. The possibility of conspecificity was apparently not considered, although Horst (1924: 157) noted similarities firstly between *Nereis* (*Lycoris*) *anchylochaeta* and *Nereis picteti* Malaquin & Dehorne, 1907 and then later (1924: 180) between *Nereis* (*Ceratonereis*) *ramosa* and both *Ceratonereis pachychaeta* and *Nereis thysanota* Ehlers, 1920. In this paper, we redescribe the type material of *Ceratonereis*

pachychaeta, *Nereis* (*Ceratonereis*) *ramosa* and *Nereis* (*Lycoris*) *anchylochaeta*, as well as additional material collected from widespread Indo-Pacific localities, in order to stabilise the species name and its concept. We also compare this material with the closely similar *Nereis picteti* and *Nereis thysanota* both from Ambon, Indonesia. The generic position of all three species is re-assessed based on modern concepts of the genera (e.g., Bakken & Wilson 2005; Santos *et al.* 2005), and all are transferred to the large genus *Neanthes*, whose definition is amended accordingly.

MATERIAL AND METHODS

Most newly collected specimens were fixed in 10% formaldehyde-seawater and preserved in 70% ethanol solution; a few specimens were fixed in 95% ethanol for ongoing genetic studies. Light microscopy observations were made using a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse 80i compound microscope with Nomarsky optics; photographs

were made on both microscopes using a Qimaging Micropublisher 5.0 RTV digital camera.

Body width was measured at chaetiger 10, excluding parapodia. Paragnath numbers in areas II, IV, VI were countered and reported as left-side first, then right-side, under a dissection microscope. The parapodium on which falcigers become fully (or partially) fused was determined using a high-powered dissection microscope (up to 110× total magnification); potentially more accurate methods involving slide preparations of dissected sequential parapodia, or mounting specimens whole under a compound microscope, could not be used because of the loan conditions or because the specimens were too large. Latitude and longitude for the newly collected material was captured using GPS with a WGS 84 datum; those for the type material were obtained through Google Earth and are approximate. The distribution map was created using PanMap software (Dipenbroek *et al.* 2000).

ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris;
MZB	Museum of Zoology, Bogor;
NTM	Museum and Art Gallery of the Northern Territory, Darwin;
QM	Queensland Museum, Brisbane;
RMNH	Natural History Museum, Leiden (formerly Rijksmuseum van Natuurlijke Historie);
VM	Museum of Natural History and Archaeology, Norwegian University of Science and Technology, Trondheim;
ZMA	Zoological Museum, Amsterdam.

SYSTEMATICS

Order PHYLLODOCIDA Dales, 1962
Family NEREIDIDAE Johnston, 1865

Genus *Neanthes* Kinberg, 1865

Neanthes Kinberg, 1865: 171. — Fauchald 1977a: 89. — Wilson 1984: 210; 1988: 5. — Wu *et al.* 1985: 143, 144. — Bakken & Wilson 2005: 527.

Nectoneanthes Wilson, 1988: 5. — Wu *et al.* 1985: 161.

Not *Nectoneanthes* Imajima, 1972.

TYPE SPECIES. — *Neanthes vaalii* Kinberg, 1865 by original designation. Southern Australia.

DIAGNOSIS (MODIFIED FROM BAKKEN & WILSON 2005). — Prostomium with entire anterior margin and four pairs of tentacular cirri. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx with conical paragnaths and occasionally smooth bar-like paragnaths, oral ring with conical paragnaths; paragnaths may emerge from plate-like basement. Each parapodium minimally having four lobes/ligules and two cirri: dorsal and ventral notopodial lobes, dorsal and ventral neuropodial lobes, and single dorsal and ventral cirrus; dorsal cirrus lacking basal cirrophore. Notoaciculae absent from chaetigers 1 and 2. Notochaetae include homogomph spinigers. Neurochaetae minimally include homogomph spinigers and heterogomph falcigers (both dorsally) and heterogomph falcigers (ventrally); heterogomph falcigers of posterior body may show varying degrees of anchyolisation (= fusion of chaetal shaft and blade).

REMARKS

Neanthes as presently conceived is polyphyletic (Bakken & Wilson 2005), and the definition is broader than most – perhaps all – other nereidid genera. It is emended here to allow for the presence of plate-mounted (= melted, *sensu* Bakken *et al.* 2009) paragnaths. Although the newly included species, *N. pachychaeta* n. comb., described below fits the definition of the genus, it does not resemble closely the type species, *Neanthes vaalii*. Therefore, it is highly likely that classifications based on future phylogenetic analyses will result in a restricted concept of *Neanthes* that will not include *N. pachychaeta* n. comb. Nevertheless, this option was considered preferable to others, including leaving the species in *Ceratonereis*, reassignment to another existing genus or creation of a new genus in the absence of a robust phylogeny of Nereididae (see Remarks of species for further discussion).

Neanthes pachychaeta (Fauvel, 1918) n. comb.
(Figs 1-7; 8D)

Ceratonereis pachychaeta Fauvel, 1918: 506-508, fig. 3a-h (Djibouti and Madagascar); 1919 (20 September): 403-407, pl. 15, figs 22-25, text fig. 8; Fauvel 1931: 20, pl. 2, figs 8-12; 1932: 88, 89. — Day 1967: 325, fig. 14.10m, n

(no new material). — Imajima 1972: 72-74, fig. 16a-p, fig. 17. — Rullier 1972: 80. — Soemodihardjo *et al.* 1980: 34.

Nereis (Ceratonereis) pachychaeta – Fauvel 1933: 57; 1953: 196, figs 99a-h.

Nereis pachychaeta – Amoureux *et al.* 1978: 85.

Simplisetia pachychaeta – Hartmann-Schröder 1985: 48 (listing only).

Nereis (Ceratonereis) ramosa Horst, 1919 (4 December): 62-64, fig. 3; 1924: 178-180, pl. 35, figs 1-3 (eastern Indonesia). The 1919 and 1924 accounts are almost identical and concern the same specimens.

Nereis (Lycoris) anchylochaeta Horst, 1924: 155-157, pl. 30, figs 8, 9a-c.

Nereis anchylochaeta – Fauvel 1953: 177, fig. 89a-e (no new material).

Ceratonereis anchylochaeta – Hartman 1956: 280, 281. — Wu *et al.* 1985: 170, 171: fig. 95a-1.

Simplisetia anchylochaeta – Hartmann-Schröder 1985: 48 (listing only).

Ceratonereis longicauda Treadwell, 1943: 1-3, figs 1-7 (synonymy with *Nereis (Lycoris) anchylochaeta* proposed by Hartman 1956: 280, 281).

TYPE MATERIAL EXAMINED. — **Madagascar.** Sarodrano, to the south of Tuléar (= Toliara), 23°31.0'S, 43°43.1'E, *Ceratonereis pachychaeta* former syntype, lectotype here designated (MNHN POLY TYPE 184) (coll. F. Geay). — Same collection data as lectotype, 2 paralectotype specimens (MNHN POLY TYPE 1511 [comprising two anterior fragments but apparently discontinuous, intervening fragment and posterior-most chaetigers missing], MNHN POLY TYPE 182).

Djibouti. Gulf of Aden, Gulf of Tadjoura, îles Musha et entre les récifs du Pingouin et du Météore, 11°40.76'N, 43°10.45'E, dragage, 20 m, 13.III.1904, 1 specimen (MNHN POLY TYPE 690) (coll. Gravier) (note that former syntype [MNHN POLY TYPE 183], Madagascar, Tuléar, à Sarodrano, année prélèvement uniquement, coll. F. Geay, 1906, stn 52, is an unidentified nereidid, not *Ceratonereis pachychaeta*).

Nereis (Lycoris) anchylochaeta: **Indonesia.** Lesser Sunda Islands, Sapeh Strait, *Siboga*, stn 49a, 8°24.49'S, 119°4.40'E, 1 syntype (ZMA Vpol 0731.01) (also in the same vial as syntype are three entire specimens of *Platynereis* sp. and one posterior fragment of ?*Platynereis* sp.). — Irian Jaya, Aru Islands, Pearl Banks, anchorage off Pulu Jedan, *Siboga*, stn 273, 5°24.80'S, 134°40.06'E, 1 syntype (ZMA Vpol 0731.02) (pharynx dissected and removed by an

earlier worker). — Sulawesi, Salebabu Island, anchorage off Lirung, *Siboga*, stn 133, 3°57.29'N, 126°42.41'E, 4 syntypes (RMNH 1325). — Ambon, *Siboga*, stn 231, 1 syntype (RMNH 1326). — Lesser Sunda Islands, Postillon Islands, anchorage off Pulu Sarassa, *Siboga*, stn 43, 7°11.00'S, 118°12.0'E, 3 syntypes (RMNH 1327).

Nereis (Ceratonereis) ramosa: **Philippines.** Sulu Islands, south-east side of Pearl-bank, *Siboga*, stn 96, 5°46.95'N, 119°43.45'E, 27.VI.1899, 1 epitokous ♂ syntype (ZMA Vpol 908).

Indonesia. Timor, S coast, anchorage off Noimini, *Siboga*, stn 296, 10°14.00'S, 124°5.50'E, 24.I.1900, 5 syntypes, largest specimen an epitokous ♀ (ZMA Vpol 909). — South coast of Flores, (est. 9°S, 121°E), coll. G. A. J. van de Sande, 1909, 1 syntype (RMNH1349) [photographed but not measured].

NON-TYPE MATERIAL EXAMINED. — **Japan.** Shirahama Harbour, Chiba, 34° 54.7'N, 139° 55.7'E, 0.5 m, coll. F. Pleijel, 6.XI.2008, 1 specimen (VM 65220).

Philippines. Sulu Islands, anchorage off North Ubian, *Siboga*, stn 99, 6°07.50'N, 120°26.00'E, 16-23 m, 28.VI.1899, lithothamnion bottom (identified as *Nereis* sp.), 1 specimen (RMNH 21121).

Indonesia. North Sulawesi, Manado, 1°28.80'N, 124°16.80'E, MD12/26-6-06/4, 2 specimens (NTM W23176). — MD26/8-7-06/3, 2 specimens (NTM W23178). — MD19/15-6-06/5, 1 specimen (NTM W23177). — Bali, 8°50'S, 115°20'E, 1 specimen (NTM W18253). — Aru Islands, Pulau Babi, RUMPHIUS Expedition III, 5°35.17'S, 134°9.17'E, coll. J. Schochet, 20.X.1977, 1 specimen (MZB unregistered). — Borneo Bank, *Siboga*, stn 80, 2°25.02'S, 117°43.02'E, 40-50 m, 13.VI.1899, coral sand, 1 specimen (RMNH 21120) (identified as *Nereis* sp.). — Lesser Sunda Islands, *Siboga*, stn 310, 8°30.0'S, 119°7.50'E, 73 m, 12.II.1900, sand-coral, 1 specimen (RMNH 21122). — Lesser Sunda Islands, Sumbawa, Saleh Bay, *Siboga*, stn 312, 8°18.96'S, 117°41.00'E, 274 m, 14.II.1900, 1 specimen (RMNH 21119) (originally misidentified in the type series of *Nereis (Lycoris) sumbawensis* Horst).

Australia. North-west Shelf, Cartier Reef, stn RH92/8, 12°31.57'S, 123°33.11'E, 1 specimen (NTM W9769). — stn CA/16, 1 specimen (NTM W9781). — Western Australia, Adele Island, stn 1, 15°31.406'S, 123°12.032'E, fore-reef slope, 13.X.2009, 1 specimen (NTM W23695). — Northern Territory, Darwin Harbour, Old Man Rock, 12°18'S, 130°53'E, 1 specimen (NTM W23172). — Fort Hill Wharf, 12°28.29'S, 130°50.80'E, 15.VIII.1998, 1 specimen (NTM W23170). — East Arm Port, 12°29.50'S, 130°52.98'E, 18.VIII.1998, 1 specimen (NTM W23354). — Gove Harbour, 12°13.2'S, 136°41.4'E, pylon 3 m, 7.VI.2001, 1 specimen (NTM W23171). — Queensland, Lizard Island, North Point, 14°38.73'S, 145°27.2'E, 2 m,

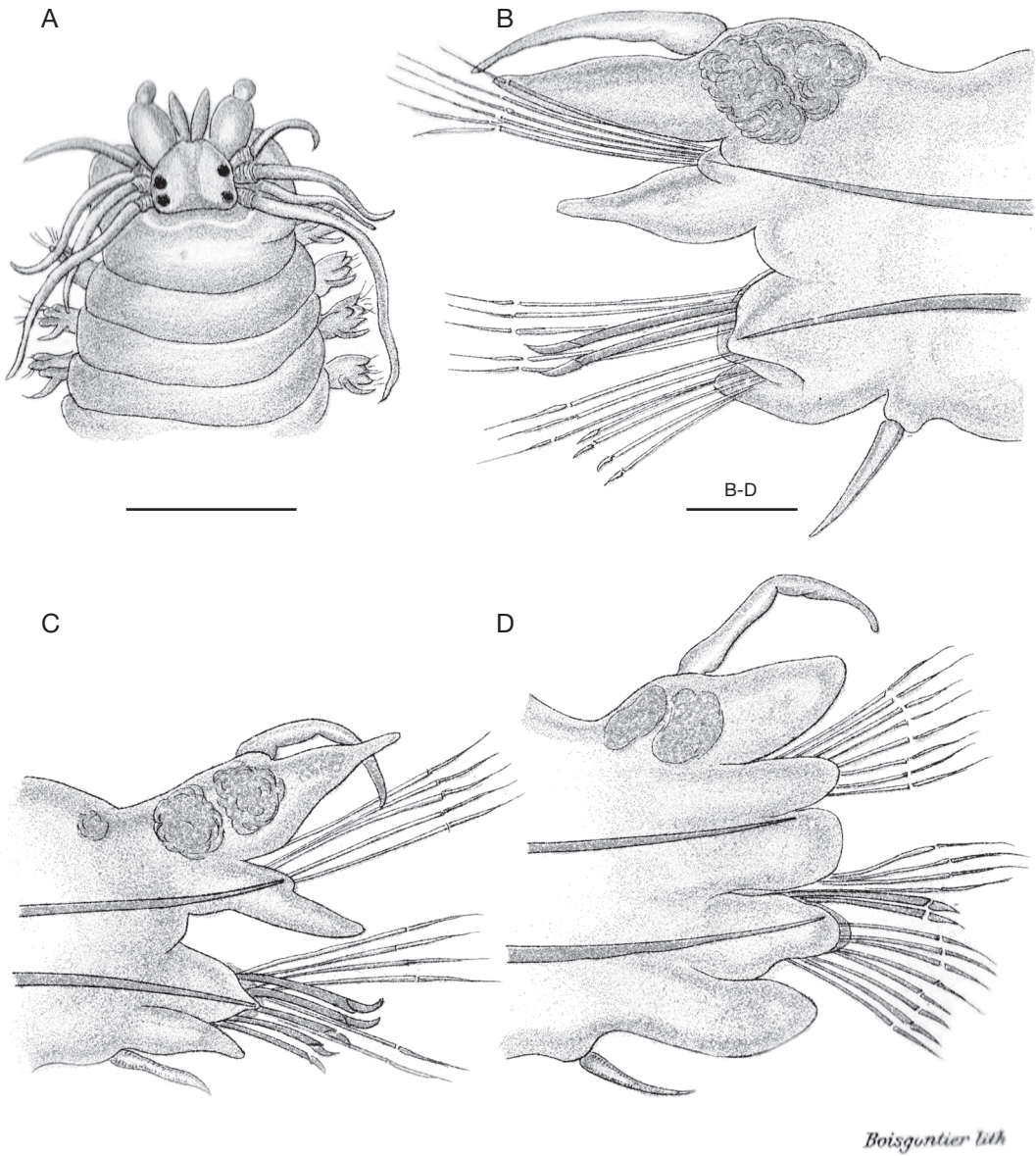


FIG. 1. — *Neanthes pachychaeta* (Fauvel, 1918) n. comb., lectotype MNHN POLY TYPE 184: **A**, head end, dorsal view; **B**, mid body parapodium; **C**, posterior parapodium; **D**, anterior parapodium. After woodcut lithography of Fauvel (1919: pl.15). Scale bars: A, 1 mm; B-D, 0.1 mm.

coll. C. Watson, N. Bruce & P. Bock, 12.IV.2008, mid-shelf fore reef, coral rubble, 2 specimens (NTM W22578). — Day Reef, Outer Great Barrier Reef, 14°28.99'S, 145°32.78'E, 4-10 m, reef slope, *Halimeda*

and rubble, coll. M. Błazewicz-Paskowycz, 19.II.2009, 1 specimen (NTM W22800). — Broomfield Reef, Capricorn Group, 23°15.47'S, 151°57.18'E, 13 m, coral rubble, fore reef (outer), coll. G. Dally, 30.VIII.2008,

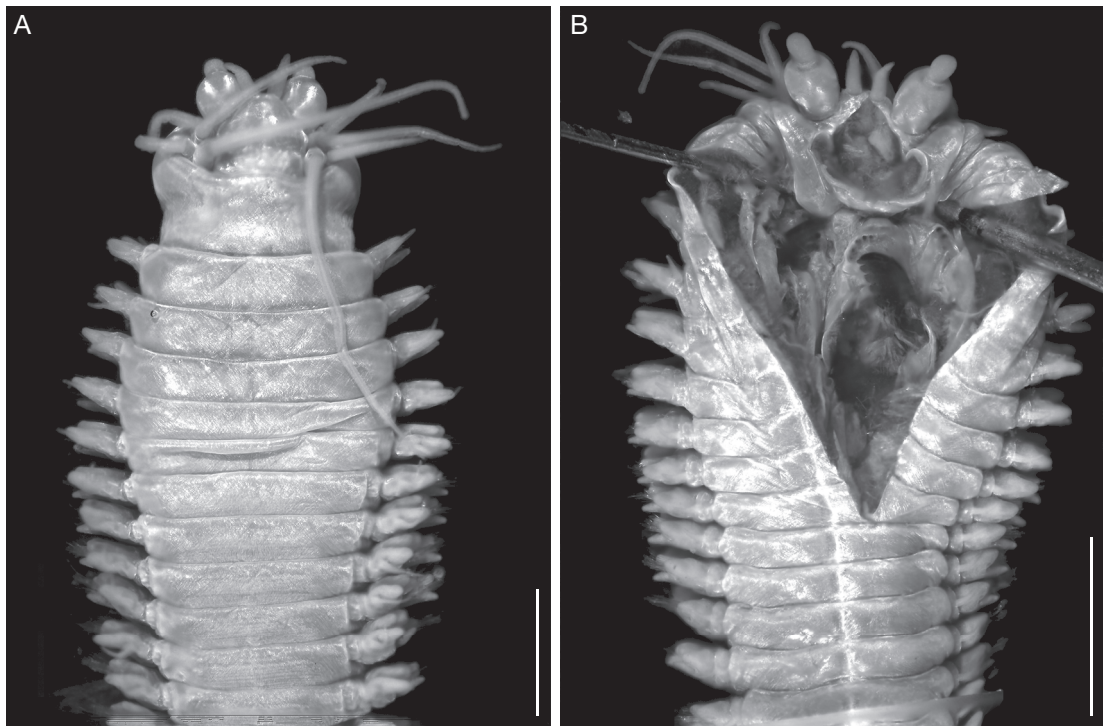


FIG. 2. — *Neanthes pachychaeta* (Fauvel, 1918) n. comb., lectotype MNHN POLY TYPE 184: **A**, head end, dorsal view; **B**, head end, ventral view showing dissected pharynx (tissue of dorsal oral ring damaged). Scale bars: 1 mm.

2 specimens (NTM W22769). — Broomfield Reef, Capricorn Group, 23°15.47'S, 151°57.18'E, 13 m, coral rubble, fore reef, coll. G. Dally, 30.VIII.2008, 1 specimen (NTM W22721). — North West Island, Capricorn Group, 23°16.92'S, 151°42.42'E, 12 m, coral rubble, fore reef, coll. G. Dally, 31.VIII.2008, 1 specimen (NTM W22732). — North Wistari Reef, Heron Island, 23°27.12'S, 151°52.03'E, 12.5 m, 11.XI.2009, 1 specimen (NTM W23173). — Wistari Reef, 23°27.43'S, 151°51.93'E, 28 m, coral rubble, fore reef, coll. G. Dally, 7.IX.2008, 1 specimen (NTM W22709). — North West Island, 23°19.08'S, 151°43.02'E, coll. 18.XI.2009, 1 specimen (NTM W23174). — South East Lamont Reef, 23°35.67'S, 151°03.03'E, 19.XI.2009, 1 specimen (NTM W23175).

French Polynesia. Moorea, south side of island, BIZ-681, 17°36.408'S, 149°48.27'E, 20 m, dead coral on reef flat, coll. J. Moore & M. Bemis, 2.XII.2010, 1 specimen (NTM W23694). — Moorea, off Hilton Hotel, BIZ-523, 17°28.525'S, 149°50.52'E, 35 m, fore reef rubble, coll. C. Meyer & J. Thomas, 9.XI.2010, 1 specimen (NTM W23695).

DESCRIPTION

Lectotype of Ceratonereis pachychaeta (Figs 1-2; values for paralectotypes [$n = 3$] in parentheses) Complete, 90 (65-71) chaetigers, 41 (20-30) mm long, 1.4 (1.4-2.5) mm wide. Longest tentacular cirri (posterodorsal) reaching chaetiger 4 (3-6); antennae 0.7 (0.6-0.8) times prostomial length; clear patch on posterior half of prostomium narrowly produced towards anterior margin (patch discoloured in some specimens). Brown pigment on either anterior side of prostomium and peristomium. Peristomium about 1.4 (1.4-2.0) length of chaetiger 1 and following chaetigers. Paragnaths large, conical, melted type, arise from plate-like basement (except area 1; Fig. 2B). Paragnath counts as follows: area I: 2 (1-2) in longitudinal row; area II: 8 (4-12), 10(4-13) in a single curved row, tending toward 2 rows in lectotype; area III: 3(2-4) in longitudinal line (no lateral ones); area

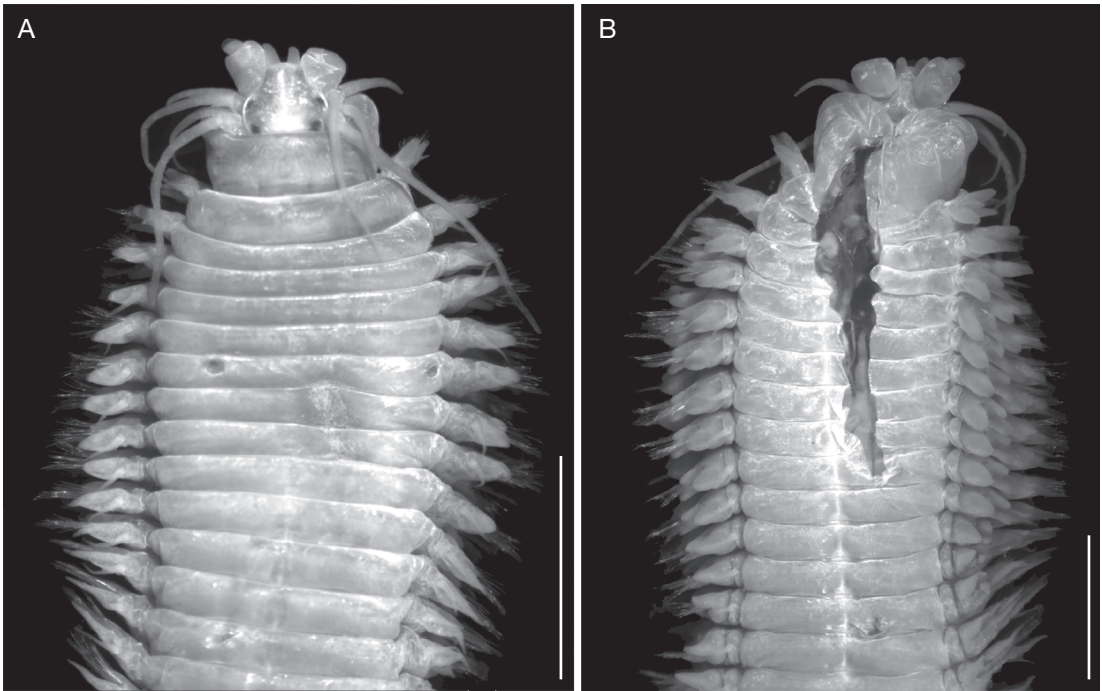


FIG. 3. — *Nereis (Lycoris) anchylochaeta* Horst, 1924, syntype, ZMA VP01 731.02: **A**, head end, dorsal view; **B**, head end, ventral view. Scale bars: 2 mm.

IV: 4(2-9), ?(4-11); area V: 0; area VI: 0, 0; area VII-VIII: 0-1. Jaws having 4(4-5) teeth. Transition from thick, terminally rounded parapodial lobes to narrower, more elongate and pointed parapodial lobes occurs after chaetiger 10 (11-12). Dorsal cirri noticeably longer 1.5 (1.2-1.6) times than notoacicular lobe on anterior chaetigers and about 1.4 (1.3-1.8) times in mid and posterior body. Prechaetal notopodial lobe present from chaetiger 3 through 27 (16-18). Neuropodial postchaetal lobe present from chaetiger 1 to 29 (18-28). Ventral cirrus inserted basally, about 0.6 (0.5-0.7) times longer than ventral neuropodial lobe anteriorly, about 0.7 (0.6-0.9) times posteriorly. Partially or fully-fused simple neuropodial falcigers numbering 2-3 in dorsal fascicle and 2-4 in ventral fascicle; present from chaetiger 22 (15-28) in dorsal fascicle and chaetiger 55 (45) in ventral fascicle. Anal cirri present (lost in some specimens), ventrally attached, extending forwards about 15 chaetigers.

Syntypes of Nereis (Lycoris) anchylochaeta (Fig. 3) Syntypes ($n = 6$) posteriorly incomplete, range from 1.4-4.0 mm wide, two specimens with pharynx dissected out and now missing. Longest tentacular cirri (posterodorsal) reaching chaetiger 3-7; antennae about 0.7 time prostomial length; clear patch on posterior half of prostomium narrowly produced towards anterior margin. Peristomium and palps slightly darker than remainder of head. Dark stain on left hand side of dorsum on chaetigers 2 and 3 (chemical stain – iodine?). Peristomium about 1.5-1.8 times length of chaetiger 1, which in turn is about 2.0 length of following chaetigers. Paragnaths large, conical, all on plate-like basement. Paragnath counts as follows: area I: 1-3 in a longitudinal line; area II: 7-11, 7-10 in a single row in a curved longitudinal line; area III: 2-6 (0-1 isolated lateral paragnaths); area IV: 4-11, 4-9 (approx. as some paragnaths ill-defined within triangular patch); area V: 0; area VI: 0-5, 0-5 (compact, irregular patch); area VII-VIII: 1-4 widely

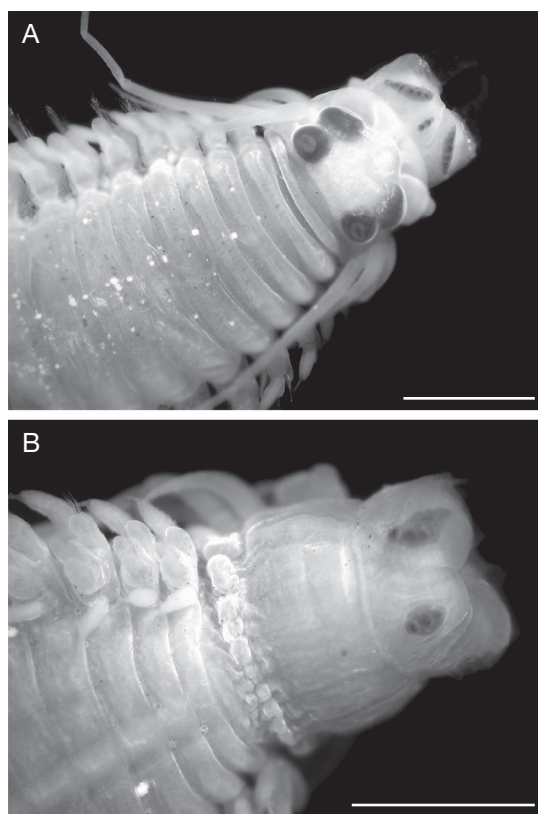


FIG. 4. — *Nereis (Ceratonereis) ramosa* Horst, 1919, syntype, ZMA VPoI 909, epitokous (sex not recorded), with pharynx everted: **A**, head end, dorsal view; **B**, head end, ventral view. Scale bars: 2 mm.

spaced, in single row. Jaws with 4-6 teeth (worn). Distinct transition from thick, terminally rounded parapodial lobes to narrower, more elongate and pointed parapodial lobes occurs after chaetiger 10 or 11. Dorsal cirri noticeably longer (1.0-1.2 times) than notoacicular lobe on anterior chaetigers. Prechaetal notopodial lobe present from chaetiger 3 through 19-45. Neuropodial postchaetal lobe present from chaetiger 1 to 17-48. Ventral cirrus inserted basally, about 0.5-0.8 times length of ventral neuropodial lobe anteriorly, about 0.6-0.8 times in mid body. Partially or fully-fused simple neuropodial falcigers numbering 2-4 in dorsal fascicle and 2-3 in ventral fascicle; present from chaetiger 13-21 in dorsal fascicle and chaetiger 30-36 in ventral fascicle.

Syntypes of Nereis (Ceratonereis) ramosa (Fig. 4). Complete specimens ($n = 3$) 111-151 chaetigers, 32-55 mm long, 2.5-4.0 mm wide. Longest tentacular cirri (posterodorsal) reaching chaetiger 8; antennae 0.5-0.6 times prostomial length; prostomium and peristomium proportions distorted because of epitokal modification including enlarged eyes. Paragnaths large, conical, all on plate-like basement. Paragnath counts as follows: area I: 3 in a longitudinal line; area II: 7-8, 8-9 in a single row in a curved longitudinal line; area III: 3-8 (lateral patches present in specimen with 8); area IV: 4-8, 5-7 (in two slightly offset rows); area V: 0; area VI: 0; area VII-VIII: 0-3, when present ventrally situated. Jaws with 6 teeth. Distinct transition between thick, terminally rounded parapodial lobes to narrower, more elongate and pointed parapodial lobes occurs about chaetiger 11. Dorsal and ventral cirri on first 7 chaetigers showing epitokal modification, swollen with abruptly tapering tip. Prechaetal notopodial lobe present from chaetiger 3. Neuropodial postchaetal lobe present from chaetiger 1. Partially or fully-fused simple neuropodial falcigers in dorsal fascicle numbering 2-3 present at least from chaetiger 8.

Female epitokes (about 70 mm long according to Horst 1919, 1924), about twice the length and breadth of epitokous males. Pygidium of males modified, carrying 20-30 cirri which arise from rim in two distinct tiers; outer rim of the pygidium bearing shorter cirri, medial rim bearing fewer, longer cirri. Pygidium of epitokous females not recorded.

Non-type material

Specimens ($n = 16$, including one epitokous male) range from 36-105 chaetigers, 7.0-46 mm long, 0.9-3.3 mm wide. Body robust, widest about chaetigers 8-10, tapering posteriorly thereafter. Live specimens range from orange to red in colour (Fig. 5), in ethanol red-brown to colourless (pigment fades with time) extending dorsally to anterior half of worm. Prominent paired notopodial spiral glands present in all chaetigers except anterior-most. Longest tentacular cirri (posterodorsal) reaching chaetiger 3-7; antennae 0.4-0.9 times prostomial length; prostomium not indented; 2 pairs of black eyes; brown pigmentation on anterior and lateral prostomium, pearly white patch on mid-posterior prostomium extending to eyes, sometimes narrowly produced towards anterior margin.



FIG. 5. — *Neanthes pachychaeta* (Fauvel, 1918) n. comb.: **A**, specimen from Shirahama, Japan (VM 65220), relaxed; **B**, specimen from Day Reef, northern Great Barrier Reef, Australia (NTM W22800), unrelaxed. Photos: A, Fred Pleijel; B, Arthur Anker. See online version for live colour variation. Scale bars: 5 mm.

Peristomium about twice length of first chaetiger; antennae 0.6–0.9 times prostomial length (rarely as short as 0.4) (Fig. 6A); maxillary ring paragnaths large, conical, arise from plate-like basement, which is pale and partly translucent and extends around base of each group of paragnaths (plate occasionally absent on area I) (Fig. 6B); oral ring paragnaths small, conical, present or absent. Paragnath counts as follows: area I: 1–4 (rarely absent) in a longitudinal line; area II: 7–13, 7–13 in a single row in a curved longitudinal line (sometimes with shorter offset second row); area III: 1–8 (arranged in central patch with 1–2 on either side in individuals with higher numbers of paragnaths); area IV: 2–11, 2–9

in a short arc or approx. triangle; area V: 0; area VI: 0–4, 0–5; area VII–VIII: 0–8, in single ventral row. Jaws with 4–6 teeth.

Chaetigers 1–2 with notoaciculum absent and notopodium reduced; neuropodium and cirri similar to subsequent chaetigers. Distinct transition from thick, terminally rounded parapodial lobes to narrower, more elongate and pointed parapodial lobes occurs at chaetiger 8–13. Dorsal cirri noticeably longer (1.2–1.8 times) than notoacicular lobe on anterior chaetigers, about 0.9–1.2 times length notoacicular lobe on mid body chaetigers, and 1.0–2.0 length notoacicular lobe posteriorly; basally attached throughout. Dorsal notopodial ligule same

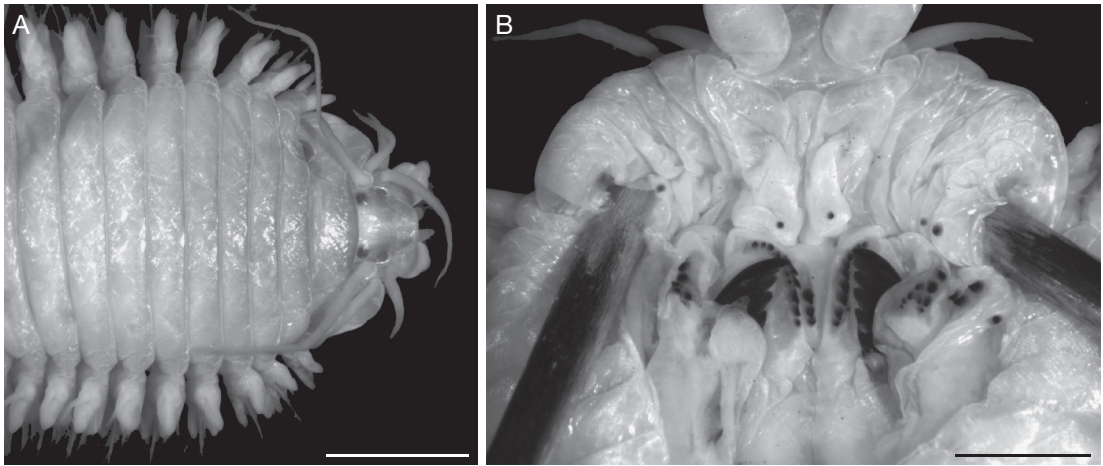


FIG. 6. — *Neanthes pachychaeta* (Fauvel, 1918) n. comb., anterior end of atokous specimen (NTM W23172): **A**, dorsal view; **B**, ventral view showing dissected pharynx and exposed jaws and paragnaths. Scale bars: A, 2.0 mm; B, 1.0 mm.

relative size throughout, although becoming slightly narrower and more pointed posteriorly. Prechaetal notopodial lobe present from chaetiger 3 through 16-39; small and papilla like in mid body. Noto-podial acicular process present. Ventral notopodial ligule entire, slightly shorter than dorsal ligule. Neuropodial prechaetal lobe absent. Neuropodial postchaetal lobe present from chaetiger 1 to 13-52; initially digitiform, thereafter tapered, pointed and triangular; reduced to a small papilliform process by mid body. Ventral neuropodial lobe similar in size throughout. Ventral cirrus inserted basally, about 0.7-0.8 times length of ventral neuropodial lobe anteriorly, about 0.5-0.6 times posteriorly.

Notochaetae homogomph spinigers throughout. Neurochaetae, dorsal fascicle, comprise homogomph spinigers and heterogomph falcigers throughout. Neurochaetae, ventral fascicle, comprise heterogomph spinigers and heterogomph falcigers throughout. Heterogomph falcigers of posterior chaetigers with articulation about as long as blade. Partially or fully-fused simple neuropodial falcigers numbering 1-3 in dorsal fascicle from chaetiger 15-55, and 2-3 in ventral fascicle from chaetiger 27-70. First appearance of fused falcigers appears to be size-dependent, with smallest individual examined lacking them altogether.

One pair of anal cirri present, ventrally attached, extending forwards about 18-20 chaetigers; pygidium a simple oval.

Male epitoke (NTM W23695), 105 chaetigers, 2.6 mm wide and 32 mm long, agrees in all respects with Horst's (1919, 1924) account of male epitokes (particularly the highly characteristic branched appendages on the modified parapodia), except that the dorsal cirrus in the modified region is smooth (not rugose at the ventral base) and the ventral accessory lamellae lack the ramous surface tissue shown by Horst (1919: fig. 3), although the latter do appear internally ramified. These differences may be attributed to tissue damage leading to misinterpretation, especially considering that the lobes and lamellae of modified parapodia are very delicate and overlap each other considerably. Like Horst's epitokous specimens, the present epitoke was colourless apart from the black pigment spots along the lateral body and a transverse band on the dorsal peristomium. It would seem therefore that members of this species, like other swarming nereidids, rapidly lose their pigmentation as they transform into epitokes.

SYNOPTIC DIAGNOSIS

Stout, short-bodied, red to orange coloured *Neanthes* species with pearly white patch on posterior

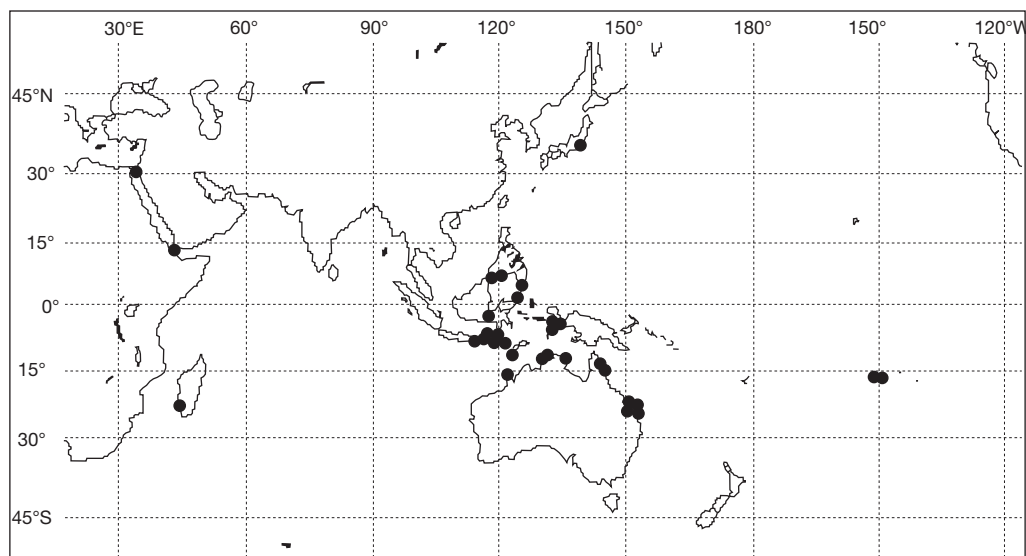


FIG. 7. — Tropical to subtropical Indo-Pacific distribution of *Neanthes pachychaeta* (Fauvel, 1918) n. comb. based on substantiated records.

prostomium. Body highly tapered after anterior few chaetigers and with very long anal cirri. Pharynx bearing large, conical paragnaths arising from plate-like basement in maxillary ring and sometimes also in oral ring, arranged as follows: area I: 1-4 in longitudinal row (rarely absent); area II: 4-13 in single curved row; area III: 1-8 in central patch, 0-2 on either side; area IV: 2-11 in two offset rows; area V: 0; area VI: 0-8 in patch; area VII-VIII: 0-8 in single row, widely spaced (i.e. paragnaths may be absent on oral ring). Anterior parapodia with thick, distally rounded lobes; dorsal notopodial ligules not expanded on posterior chaetigers, bearing prominent paired spiral glands basally; both prechaetal notopodial lobes and neuropodial postchaetal lobes present on anterior and mid body chaetigers; dorsal cirrus basally attached to dorsal notopodial ligule on posterior chaetigers; mid body and posterior neuropodial heterogomph falciigers (in dorsal and ventral fascicles) thick, blades hammer-headed, fused or partially fused with shaft (highly variable starting position). Epitokes with ramous parapodial lobes and lamellae; males show parapodial transformation from chaetiger 14-16; females from chaetiger 25.

DISTRIBUTION AND HABITAT

Widespread in the Indo-Pacific from the Red Sea and western Indian Ocean to French Polynesia in the Pacific; latitudinally, the species ranges from southern Japan to Heron Island, Great Barrier Reef, Australia. Reliable locality reports include Japan, South China Sea, Philippines, Indonesia, Malaysia, northern Australia, Madagascar, Red Sea and Gulf of Aqaba (Fig. 7). The records from Marshall Islands by Hartman (1954) and Reish (1968) require confirmation. The species appears to be restricted to coral rubble and encrusting fauna of tropical and sub-tropical coralline environments, particularly reef flats and fore reefs but may occur down to 274 m.

REMARKS

Generic placement

When Fauvel (1918) described *Neanthes pachychaeta* n. comb. (as *Ceratonereis pachychaeta*), he did not observe paragnaths in the oral ring (present observations of Fauvel's syntypes show that a single paragnath is present on one specimen; the range for all material is 0-16). The presence or absence of paragnaths on the oral ring fits much better the

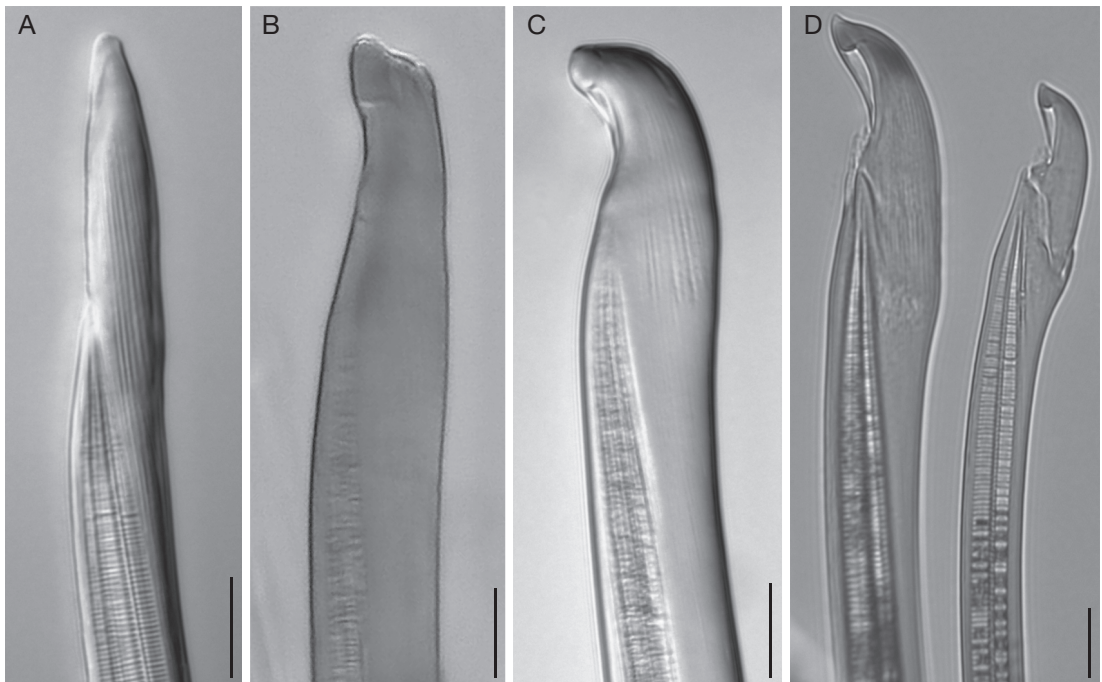


FIG. 8. — Comparison of fused neuropodial falcigers of posterior chaetigers between: **A**, *Hediste japonica* (Izuka, 1908), NTM W19089; **B**, *Simplisetia aequisetis* (Augener, 1913), QM GH3958; **C**, *Neanthes uncinula* Russell, 1962, neotype QM G3957; and **D**, *Neanthes pachychaeta* (Fauvel, 1918) n. comb. (NTM W23172). Scale bars: 0.01 mm.

concept of *Neanthes* than *Ceratonereis* Kinberg, 1865, which is now considered to comprise three unrelated genera – *Ceratonereis*, *Composetia* Hartmann-Schröder, 1985 and *Simplisetia* Hartmann-Schröder, 1985 (Hartmann-Schröder 1985; Khlebovich 1996; Bakken & Wilson 2005) – none of which has oral ring paragnaths. Further, *N. pachychaeta* n. comb. has prechaetal notopodial lobes which are also not present in any of the three genera, but may be present in *Neanthes*. Finally, although *N. pachychaeta* n. comb. has fused neuropodial falcigers like *Simplisetia*, morphological differences in the fused falcigers between the two taxa indicate that they are not homologous; those of *N. pachychaeta* n. comb. have a distal tendon, and are formed by fusion of hammer-headed heterogomph falcigers (Fig. 8D), as indicated by the presence of transitional, partially fused forms, whereas those of *Simplisetia* lack a distal tendon and are formed by fusion of normal-bladed heterogomph falcigers

(Fig. 8B). Similarly, the smooth fused falcigers of *N. pachychaeta* n. comb. bear little resemblance to those of *Hediste* Malmgren, 1867 species. The presence of transitional forms suggests that they too have developed from falciger fusion, but a falciger of a different type (Fig. 8A). Inclusion of *N. pachychaeta* n. comb. in *Hediste* would necessitate an unacceptable broadening of the genus concept because *N. pachychaeta* n. comb. may have fused falcigers in both the dorsal and ventral fascicles in posterior parapodia, and may have oral ring paragnaths present or absent. Also the paragnaths arise from a plate-like basement unlike all *Hediste* species.

Uncertainty over the placement of this species in either *Nereis* Linnaeus, 1758 or *Ceratonereis* by original authors appears to be the result of the variability in the presence of paragnaths on the oral ring of the pharynx (presence of paragnaths on the oral ring in *Nereis*, and their absence, in *Ceratonereis*, were

principal characters responsible for generic concepts established by Kinberg [1865]). Further confusion was due to the presence of fused (= anchylosed) falcigerous chaetae in posterior parapodia, which are found in diverse taxa most notably members of *Hediste* (formerly part of *Nereis*; Fig. 8A) and *Simplisetia* (formerly part of *Ceratonereis*; Fig. 8B). Fused falcigers have been reported in several other, seemingly unrelated, species including *Neanthes pleijeli* de León-González & Sallazar-Vallejo, 2003, *Neanthes uncinula* Russell, 1962 (Fig. 8C) and *Websterinereis punctata* (Wesenberg-Lund, 1949). Although those of *N. uncinula* are morphologically most similar to those of *N. pachychaeta* n. comb. (compare Fig. 8C, D), they may not be homologous, as Russell (1962) suggests that they are formed de novo rather than by anchylosis of normal heteromorph falcigers.

Melted paragnaths

No other nereidid appears to have paragnaths mounted on a plate-like basement. These have been referred to as melted paragnaths by Bakken *et al.* (2009), and their homology is uncertain. They were considered as a variation of typical conical paragnaths in this study, especially because similar structures have been found in the epitokes of various species, suggesting that in these cases it may be the result of degeneration of the paragnaths or underlying epithelium. However, this is not the case in *N. pachychaeta* n. comb. as both epitokous (Fig. 4) and atokous (Fig. 6B) forms have the structure equally well developed. A plate-like pharyngeal basement was even noted in the smallest atokous form examined here, a specimen of 36 chaetigers. Literature records of this feature include Fauvel (1919: 405), who emphasised their melted nature, “Les paragnathes sont coniques, très foncés, assez gros, et parfois plus ou moins confluent”; Ehlers (1920: 53), who reported their position on a brown basement, “jede dieser Zahnreihen wird von einer bräunlichen, längsovalen Platte getragen”; Horst (1924: 179) who says “The paragnaths of each group are situated upon a common plate”; Treadwell (1943: 1), “the paragnaths look as if first attached to a plate and this plate then fastened to the pharynx wall”; and finally Amoureux *et al.*

(1978: 85), “et insérés pour chaque groupe sur une bande de couleur brune”. The presence of paragnaths occurring on a (brown) basement plate has been recognized by most of the cited authors as a distinctive character, with the exception of Imajima (1972) and Wu *et al.* (1985), who possibly didn't consider the basement plate to be taxonomically important.

Taxonomy

Neanthes pachychaeta (Fauvel, 1918) n. comb. has date priority over its synonyms, even if one were to take 1919 as the year of publication (Fauvel described the species as new in both 1918 and 1919 [20 September]). *Nereis* (*Ceratonereis*) *ramosa* was described by Horst on 4 December, 1919 and *Nereis* (*Lycoris*) *anchylochaeta* was not described by Horst until 1924. Incidentally, Horst (1924) used two different spellings of the species epithet – *anchylochaeta* and *anchylocheta*. Since the former name contains the proper latin name for hair, *chaeta*, we select *Nereis* (*Lycoris*) *anchylochaeta* as the correct spelling of the taxon, whereupon it becomes fixed under ICZN art. 24.2.3. Fauvel's 1918 and 1919 descriptions are almost identical, but the latter includes a more extensive discussion of characters and congeners and a couple of additional views of the chaetae. The superior woodcut lithographic illustrations of the head and parapodia of syntype MNHN POLY 184 published in 1919 are reproduced here (Fig. 1). According to Solís-Weiss *et al.* (2004), Fauvel's syntype series comprise three lots, MNHN POLY 182, 184, 690, which are all examined here. A fourth lot also labelled as a syntype, MNHN TYPE 183, from Madagascar, Tuléar, is identified here as a different nereidid, not *Neanthes pachychaeta* n. comb. We have designated the complete individual from Madagascar, Tuléar (MNHN TYPE 184) as the lectotype of *Neanthes pachychaeta* n. comb. Although Fauvel actually compiled his description from more than one syntype, it is clear that this specimen was the one he used to illustrate the parapodia and chaetae because it bears the scars of missing parapodia on chaetigers 11, 19, 29, close enough to those that he reported (12, 20, 30) in his description (Fauvel 1919: fig. 8).

Species comparison

Nereis picteti Malaquin & Dehorne, 1907 appears to be very similar to *N. pachychaeta* n. comb. It is likely to be a member of *Neanthes* as currently conceived, as Malaquin & Dehorne (1907) indicate that it has homogomph spinigers only in the mid body (40th segment). Further, the authors do not specifically mention a paragnath base plate or fused falcigers, so synonymy with *N. pachychaeta* n. comb. remains open. Unfortunately we could not locate the type specimens to verify the presence or absence of these features. Both Malaquin and Dehorne worked at the University of Lille when they published their paper in 1907, so the type could still be there, or perhaps the Lille Natural History Museum or the Station Marine de Wimereux, which both belong to the University, but correspondence to those places has failed. Apparently the type was not transferred to the MNHN, as were the types of some other non-Paris based polychaetologists, as they do not appear in the type catalogue of Solís-Weiss *et al.* (2004). Although it would be desirable to determine whether *Neanthes picteti* n. comb. is conspecific with *N. pachychaeta* n. comb. as the former name would become the senior synonym, it will have no bearing on the present lectotype designation.

Nereis thysanota Ehlers, 1920 also possibly belongs to *Neanthes* and is very close to *N. pachychaeta* n. comb. The most striking similarities between the two species are the shared presence of a paragnath base plate (called a “callus” by Ehlers) and the parapodia of the epitokes having ramous lobes and lamellae (in the latter they are identical to the Adele Island epitoke [NTM W23695] described herein). However, one important difference suggests that the two named forms are different: *Neanthes thysanota* n. comb. has 4 or 5 paragnaths in Area V, whereas *N. pachychaeta* n. comb. always lacks paragnaths in this area.

Because of its very broad distribution and considerable morphological variability *Neanthes pachychaeta* n. comb. is probably best thought of as a species group, encompassing *N. thysanota* n. comb. (and possibly also *N. picteti* n. comb.). The species group is defined by the presence of a paragnath base plate and ramous lobes and lamellae on epitokal parapodia, which both appear to be unique features

within Nereididae. The species group appears to be most similar to other *Neanthes* having the combined presence of a prechaetal notopodial lobe, postchaetal neuropodial lobe, dorsal notopodial ligule similar in size on anterior and posterior chaetigers and hammer-headed falcigers. This larger group (a genus?) includes *Neanthes meggitti* (Monro, 1931) and *Neanthes philippinensis* de León-González & Salazar-Vallejo, 2003. Several other incompletely known species may also be a part of this larger group including *Neanthes dawydovi* (Fauvel, 1937), *Neanthes helenae* Kinberg, 1865, *Neanthes manatensis* Pillai, 1965 and *Neanthes irrorata* (Malmgren, 1867). The validity of this proposed species group and the more inclusive group could be assessed using a combined morphological and genetic approach based on types and fresh material collected near the type locality of each species.

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