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A Revision of the *Perinereis nuntia* Species Group (Polychaeta: Nereididae)

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ABSTRACT. The *Perinereis nuntia* species group is revised on the basis of material from worldwide localities. Twenty available names are reduced to 12 recognised species, including two new species: *Perinereis akuna* (from southern Australia) and *P. namibia* (from southern Africa). Specimens from Indonesia and from Juan Fernandez Islands cannot be identified and may represent two additional undescribed species. *Perinereis broomensis* Hartmann-Schröder, 1979 is synonymised with *P. nuntia* (Savigny, 1818) for the first time. A key to species is provided.

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The *Perinereis nuntia* species group is characterised by an arc of bar-shaped paragnaths on Area VI of the eversible proboscis. These nereidid worms are common in intertidal and shallow marine waters and are widely distributed on the coasts of the southern continents and the tropical Indo-Pacific (Fig.1). Wilson (1993) studied two unidentified species in the *P. nuntia* species group from southeastern Australia and provided guidelines for the interpretation of morphological variability. In this paper we apply the results of Wilson (1993) to a worldwide revision of the *Perinereis nuntia* species group. The remaining species in the genus *Perinereis* have been treated by Hutchings *et al.* (1991).

Perinereis nuntia (Savigny, 1818) was described from the Gulf of Suez. There are few subsequent published records until the radical treatment of Fauvel (1932), who synonymised *P. nuntia* with a number of species previously regarded as distinct. Most recent authors have followed Fauvel, and *P. nuntia* has now been recorded from all southern hemisphere continents except Antarctica, from Japan through South-east Asia to India and the Middle-East. Fauvel's influence has also resulted in the widespread adoption of trinomens in an attempt to account for morphological variability in this supposed species. Fauvel's trinomens apparently were not intended to represent geographical variants or subspecies since each was credited with a wide distribution and several varieties were often recorded from the same locality or region. Fauvel (1932: 109) observed that "Between the varieties of this unsettled species many specimens are intermediate, and so gradual are the transitions that they cannot be assigned definitely to any variety". Trinomens continue to be widely used in the literature for this species group, which includes 20 nominal species and

varieties (Table 1). Wilson (1993) could not recognise subspecific taxa in this group in a study of seven populations in southeastern Australia, but there has been no attempt to revise the taxonomy of the group globally.

Materials and Methods

Collections representing about 50 populations from throughout the range of the *Perinereis nuntia* group were examined (Fig.1). Paragnaths were counted for all Areas and qualitative differences in paragnath type and setal distributions were also recorded (see Wilson, 1993 for a descriptions of morphological methods and terminology). Body length and width, and jaw length measurements were recorded in mm; jaw length was used as a size measure for morphometric purposes (following Wilson, 1993). Width measurements refer to the body width at setiger 10 and (where the condition of the specimen permits) is given as two figures, the first excluding parapodia, the second (in parentheses) including parapodia but excluding setae. Use of the terms anterior and posterior in descriptions of the relative positions of paragnaths apply to the fully everted proboscis, with the maxillae in the anterior-most position (as drawn in Fig.12a,b). Systat version 4.0 (Wilkinson, 1988) running on an MS-DOS personal computer was used for all statistical analyses.

Institutions from which material was borrowed are referred to in the text by the following codes: AM – Australian Museum, Sydney, Australia; HZM – Zoological Institute and Museum, Hamburg University, Hamburg, Germany; MNHN – National Museum of Natural History, Paris, France; NMV – Museum of Victoria, Melbourne, Australia; NMW – National Museum of Wales, Cardiff, Wales; NR – collection of N. Rozbaczylo, Pontificia Universidad Catolica de Chile, Santiago, Chile; NTM – Northern Territory Museum and Art Gallery, Darwin, Australia; PMBC – Phuket Marine Biological Center, Phuket, Thailand; QM – Queensland Museum, Brisbane, Australia; SAMA – South Australian Museum, Adelaide, Australia; SAMC – South African Museum, Cape Town, South Africa; SRP – collection of Sun Ruiping, Institute of Oceanology, Academia Sinica, Qingdao, Peoples Republic of China; USNM – United States National Museum, Washington, USA; WAM – Western Australian Museum, Perth, Australia; WMP – Wroclaw Museum, Wroclaw, Poland; ZMA – Zoological Museum, Amsterdam, The Netherlands; ZMB – Zoological Museum, Berlin, Germany; ZMK – Zoological Museum, Copenhagen, Denmark.

Tables are listed in the Appendix.

Statistical Analysis

In this paper we apply canonical variates analysis (CVA, otherwise known as multiple discriminant analysis) to the problem of species identifications among numerous populations of closely related worms from around the world. The characters used in the CVA were paragnath counts for each area of the proboscis. Canonical variates analysis requires *a priori* groupings of specimens, however these groupings can be at the level of local populations. Subsequent recognition of a smaller number of clusters in the final analysis is an exploratory technique described by Wiley (1981: 361-365). This use of CVA as a clustering technique as an aid to species determinations is an extension of the approach of Wilson (1993), who used CVA to cluster

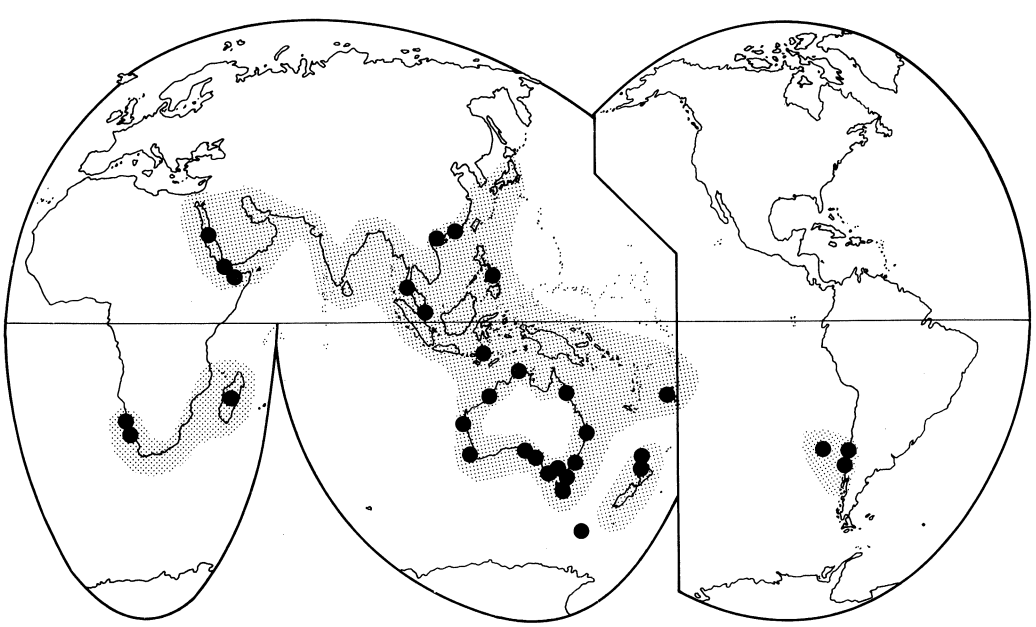

Fig.1. Distribution map of range of *Perinereis nuntia* species group (stippled area), and localities for collections used in this study (filled dots).

populations into two species that had been independently distinguished using electrophoresis.

The validity of canonical variates analysis depends on normality of the data and homogeneity of variances. These assumptions were tested for the two most numerous species: *Perinereis nuntia* and *P. vallata*. Departures from normality were checked by probability plots of cumulative percent-frequencies (as recommended by Reyment *et al.*, 1984), homogeneity of variances was tested by F-tests. Using these methods Area I and V paragnath counts for some samples appeared to be non-normal and/or have heterogeneous variances. However, omitting these variables had little effect on the results of preliminary analyses. Reyment *et al.* (1984) note that multivariate methods such as CVA appear to be reasonably robust to departures from normality and analyses were performed with all variables included.

It is also necessary to exclude (or allow for) the possibility that differences between populations might be size-related. Wilson (1993) concluded that size-dependent variation in paragnath counts was not significant. This result was confirmed in this study; calculation of coefficients of determination (r) shows that variation in size accounts for only 7.5% of the total variation in paragnath counts in *P. nuntia* and 9.0% in *P. vallata*. We also needed to be confident that each local population sample comprised only one species. Within samples there were no qualitative differences and frequency distributions of paragnath counts for each area of the proboscis appeared to be unimodal. We therefore conclude that each sample contains a single species.

Fifty local population samples were available for analysis. Qualitative differences were immediately apparent among the specimens and were used to distinguish smaller data sets for CVA. Two taxa were distinguished by additional bands of numerous, minute paragnaths on Areas VII-VIII. Frequency distributions of paragnath counts in each Area appeared to be unimodal and these species are identified in the systematic account as *Perinereis akuna* n.sp. (= *Perinereis* sp. A of Wilson, 1993) and *P. rhombodonta* Wu, Sun & Yang, 1981. A third series of samples was distinguished by an indented prostomium, the absence of paragnaths from Areas I and II, novel arrangements of paragnaths on Areas V and VI, and bar-shaped paragnaths on Area VI arranged stepwise (rather than in an even line or arc as in all other species described here). This material was also excluded from the statistical analysis and is identified below as *P. caeruleis* (Hoagland, 1920).

The remaining material, representing the bulk of the collection, was divided into two groups distinguished by the presence or absence of smooth, parallel bar-shaped paragnaths on Area IV of the proboscis (Wilson, 1993: fig.7). This new character seemed to be taxonomically useful for two reasons: (i) presence/absence of bars on Area IV showed almost no variation within samples (the only minor exception being three specimens of *Perinereis namibia* n.sp.; see below); (ii) among related genera, many species also have bars on Area IV (*Neanthes*, *Ceratonereis sensu lato*; Wilson, 1984, unpublished data). Other genera contain no known

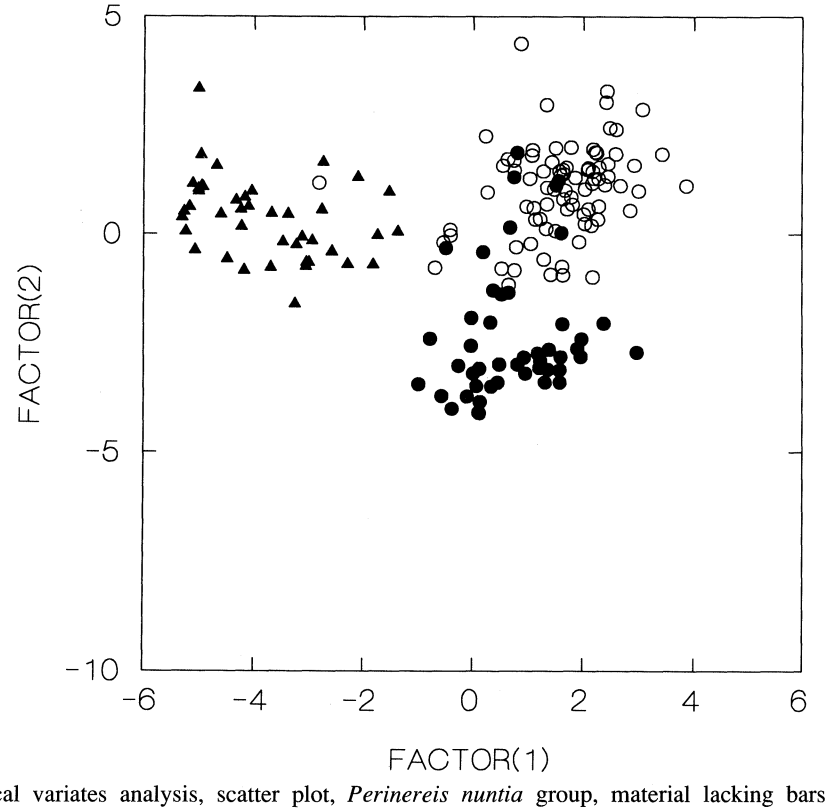

Fig.2. Canonical variates analysis, scatter plot, *Perinereis nuntia* group, material lacking bars on Area IV, factor(2) versus factor(1). Filled circles = *P. nuntia* (Red Sea); open circles = *P. nuntia* (Indo-Pacific); filled triangles = *P. namibia*.

species with bars on Area IV (*Nereis*, *Platynereis*; Wilson, 1985). Thus, presence or absence of bars on Area IV may be useful at a higher taxonomic level.

Species lacking bars on Area IV. Worms lacking parallel bars on Area IV came from samples from the Red Sea, South Africa, South-east Asia, northern Australia, China, Hong Kong and Fiji. Canonical variates analysis clustered the 14 samples into two clusters. Examination of locality data showed that the clusters represent geographically separate populations and are recognised in the descriptions below as *Perinereis namibia* n.sp. and *P. nuntia* (Savigny, 1818). The results of the CVA are presented as a plot of factor scores for each canonical variate. Canonical loadings for Factor 1 indicate that paragnath counts for Area VII-VIII best discriminate the two species (Table 2). There is some separation of populations of *P. nuntia* from the Red Sea from populations from the Indo-Pacific by Factor 2 scores, however the level of separation is comparable to that seen between conspecific populations of *Perinereis* sp. B by Wilson (1993). There are no discernable differences in parapodia or other taxonomic characters among these specimens, all of which we refer to a single species. Factor 3 scores do not provide any additional separation of taxa and are not plotted here. Factors 1 to 3 cumulatively account for 92% of the total variation; Factors 1 and 2 account for 86%. Frequency distributions of paragnath counts that showed the highest loadings for Factors 1 and 2 are provided in Figure 3.

Since CVA maximises the separation between groups compared with the variation within groups, this technique is inappropriate for attempting to discriminate samples comprised of few specimens. Three populations were represented by samples of only one or two specimens: *Perinereis ponuiensis* Augener, 1927, *P. rumphii* Horst, 1919 and *Perinereis* sp. 1 (from Juan Fernandez Islands). These samples were retained in the CVA in the hope that their affinities would be indicated by the canonical variates analysis. *Perinereis ponuiensis* is provisionally retained as a distinct species, *P. rumphii* is synonymised with *P. nuntia*, and *Perinereis* sp. 1 remains unidentified and may represent an undescribed species. These decisions are justified in the Remarks section under each species.

Species with bars on Area IV. Parallel bars on Area IV were present in samples from Madagascar, southern Australia, New Zealand, Macquarie Island and Chile.

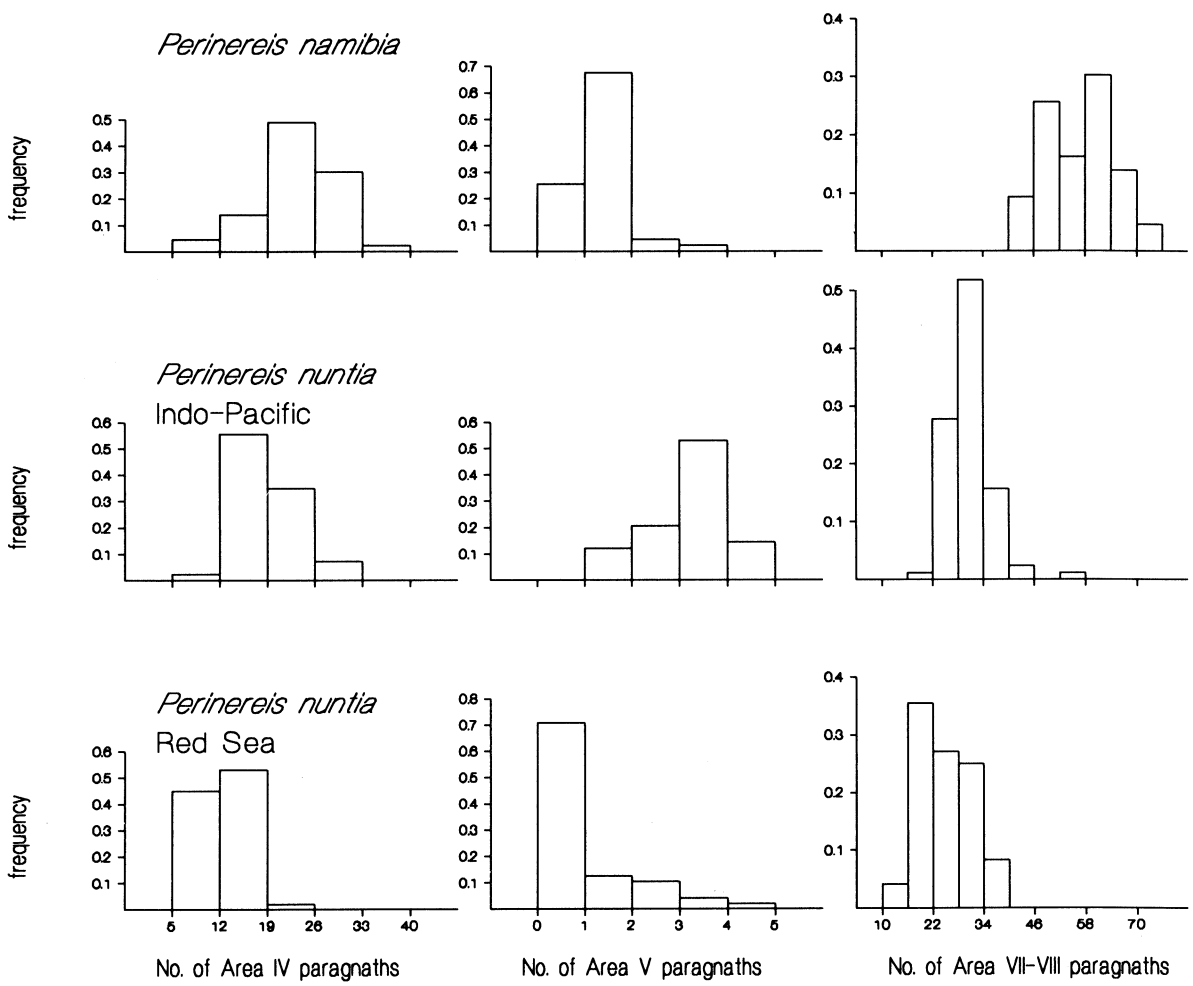

Fig.3. Frequency distributions, species lacking bars on Area IV; Area IV, V and VII-VIII paragnath counts.

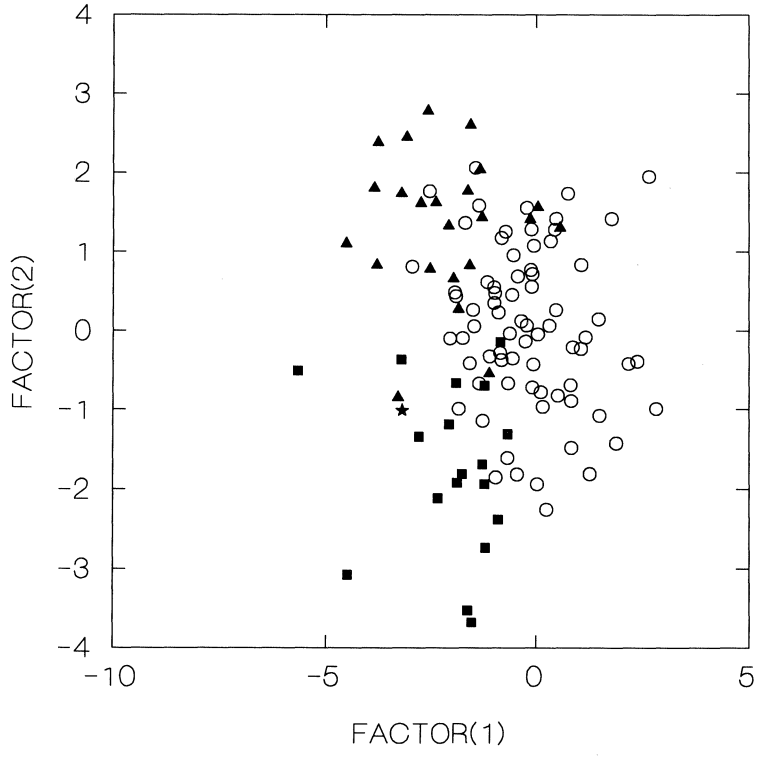

Fig.4. Canonical variates analysis, scatter plot, *Perinereis vallata* samples, factor(2) versus factor(1). Open circles = *P. vallata* (Australia); filled squares = *P. vallata* (Chile); filled triangles = *P. vallata* (New Zealand); star = *Perinereis* sp. (Indonesia).

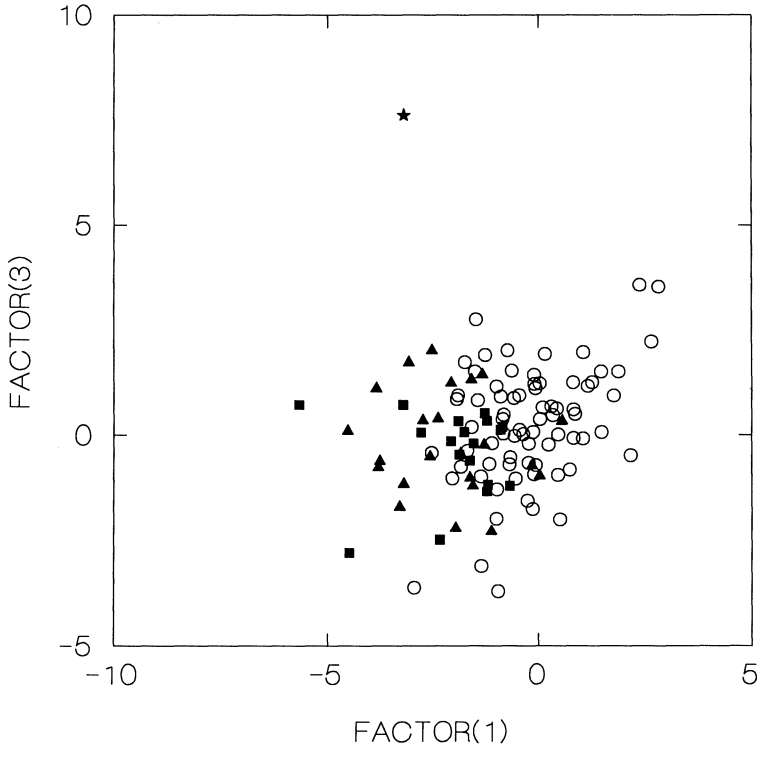

Fig.5. Canonical variates analysis, scatter plot, *Perinereis vallata* samples, factor(3) versus factor(1). Open circles = *P. vallata* (Australia); filled squares = *P. vallata* (Chile); filled triangles = *P. vallata* (New Zealand); star = *Perinereis* sp. (Indonesia).

Among this material, *Perinereis akuna* n.sp. has already been distinguished (as *Perinereis* sp. A) by Wilson (1993). The remaining material showed no qualitative differences and was subjected to CVA, resulting in a single specimen from Madagascar (identified below as *Perinereis majungaensis*) being plotted as distinct from all other material. Outliers compress the scale on which remaining groups may be distinguished. If this outlier is excluded and the data re-analysed no distinct clusters of specimens can be recognised (canonical loadings are presented in Table 3). There is some separation of samples from Australia, New Zealand and Chile on Factors 1 and 2 (Fig.4), but the level of separation of populations and the similarity of percent-frequency histograms of paragnath counts (Fig.6) are comparable to that seen in five conspecific populations of *Perinereis* sp. B (Wilson, 1993). We do not feel justified in recognising more than one species among this material, which is identified below as *Perinereis vallata*. The identity of a single specimen from Indonesia remains equivocal; this specimen is separated by Factor 3 scores (Fig.5) and is discussed below as *Perinereis* sp. 2.

Descriptive statistics for all of these species are provided in Table 4.

Systematic Account

The following is a list of all species described here:

P. akuna n.sp.
P. caeruleis (Hoagland, 1920)
P. gualpensis Jeldes, 1963*
P. maindroni Fauvel, 1943
P. majungaensis Fauvel, 1921
P. matthaii Aziz, 1938*
P. mictodonta (Marenzeller, 1879)*
P. namibia n.sp.
P. nuntia (Savigny, 1818)
P. ponuiensis Augener, 1927
P. rhombodonta Wu, Sun & Yang, 1981
P. vallata (Grube, 1858)
Perinereis sp. 1 [Juan Fernandez]
Perinereis sp. 2 [Indonesia]

(We have not been able to examine material of those species marked with an asterisk.)

The *Perinereis nuntia* group can be diagnosed and described as follows. Species descriptions do not repeat this information.

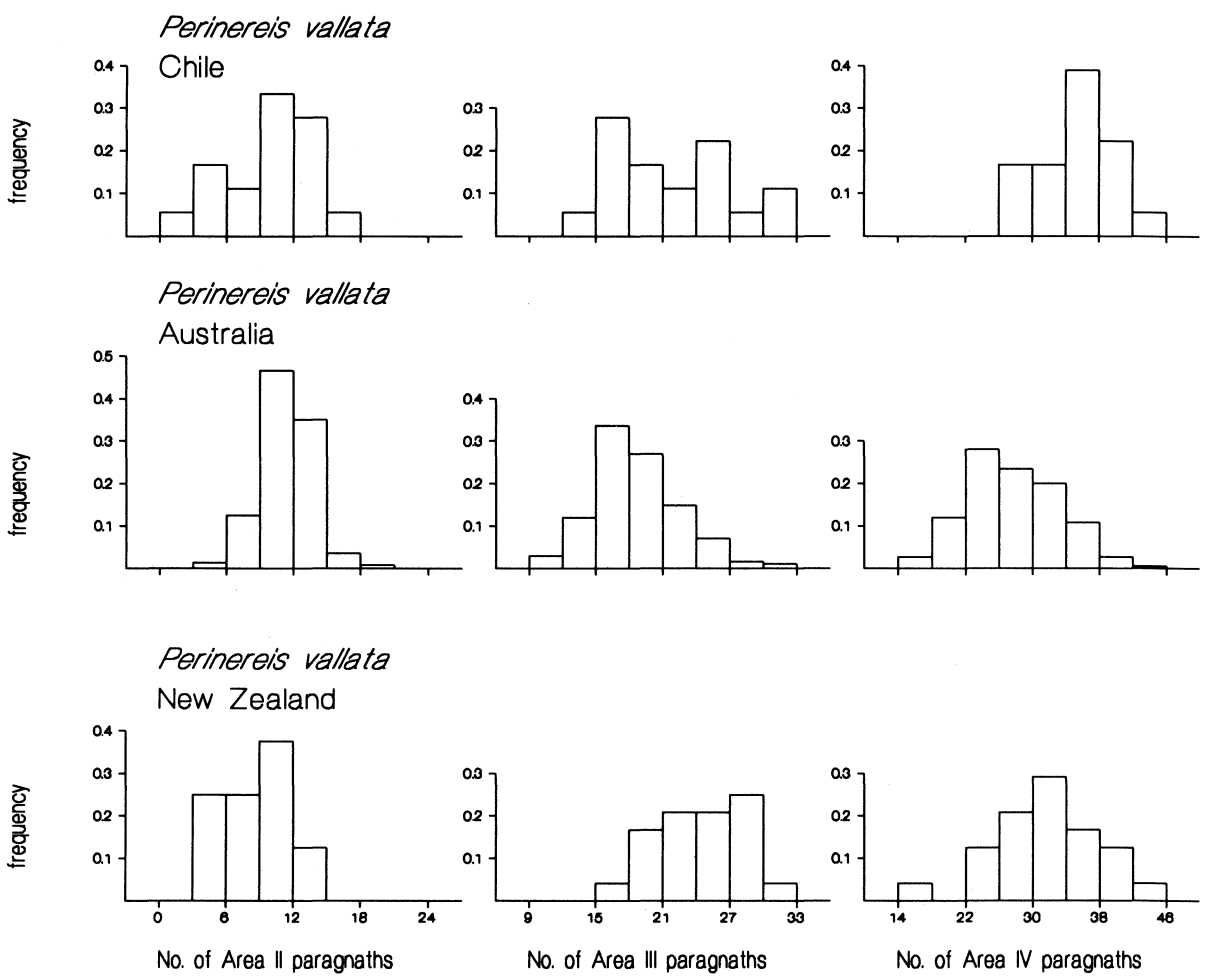

Fig.6. Frequency distributions, *Perinereis vallata* samples, Areas II, III and IV paragnath counts.

Perinereis nuntia Species Group

Diagnosis. Nereidids with eversible pharynx with conical paragnaths on both rings. Area VI with 3-20 bar-shaped paragnaths or a mixture of bars and cones on each side in a single line or arc. Notosetae homogomph spinigers. Superior notopodial lobe similar in length to inferior notopodial lobe throughout (in atokes).

Description. One pair of biarticulate palps, 1 pair of antennae. Two pairs of eyes, anterior pair more widely spaced than posterior pair. Four pairs of tentacular cirri. Eversible pharynx with 1 pair of jaws. Paragnaths on Area VI bars only or bars and cones. Paragnaths on Area IV cones only or bars and cones. All other Areas with conical paragnaths only. Range of paragnaths observed for each Area: I = 0-9; II = 0-64; III = 2-185 (1 or several almost invariably located in distinct lateral patches); IV = 0-131 cones and 0-13 bars; V = 0-5; VI = 3-20 bars; VII-VIII = 10-250, sometimes including numerous minute cones in a distinct band (posterior when pharynx everted). One pair of ventrally attached anal cirri. Parapodia 1 and 2 lack notosetae, thereafter all parapodia biramous. Notopodia bilobed from setiger 3, superior lobe not expanded or significantly longer than inferior lobe on posterior setigers (in atokes). Dorsal cirrus basally attached to notopodia. Neuropodia bilobed throughout, with ventral cirrus. Notosetae homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers in the dorsal fascicle, heterogomph spinigers and heterogomph falcigers in the ventral fascicle (heterogomph spinigers sometimes absent).

Perinereis akuna n.sp.

Fig.7a-m

Perinereis sp. A Wilson, 1993: 248, fig.7A.

Type material examined. HOLOTYPE: Australia: New South Wales: Coal & Candle Creek, Hawkesbury River, near Akuna Bay, 33°37'S 151°14'E, intertidal under stones in sandy mud, coll. P.A. Hutchings & R.S. Wilson, 19 Oct. 1986, NMV F53985. PARATYPES: same data as holotype, NMV F53986, F53987, 2 paratypes, AM W21385-W21386, 2 paratypes; New South Wales: Batemans Bay, Clyde River, north shore under Princess Highway bridge, intertidal, under stones in muddy shell, coll. R.S. Wilson, 17 July 1987, NMV F53988-53994, 7 paratypes.

Additional material examined. WESTERN AUSTRALIA: Trigg, reef platform, coll. F. Wells, 21 Jan. 1987, AM W202973. SOUTH AUSTRALIA: Sellicks Beach, 14 Mar. 1985, sandy algal turf on limestone platform, intertidal, G.C.B. Poore & H.M Lew Ton (NMV station SA 4), NMV F53996, 1 specimen. NEW SOUTH WALES: Fisheries Creek, Twofold Bay, among oysters, coll. S. Keable & E. Bamber, 12 Dec. 1984, AM W202969, 13 specimens; Fisheries Creek, Twofold Bay, intertidal mud, coll. S. Keable, AM W202976, 7 specimens; Nullica River estuary, Twofold Bay, mud & *Zostera* sievings, coll. S. Keable & P. Hutchings, 18 Sept. 1986, AM W203008, 1 specimen; Nullica River estuary, Twofold Bay, intertidal rock fauna, coll. S. Keable & P. Hutchings, AM W203009, 2 specimens; Merimbula, 150 m from mouth of Back Lake, soft sandstone reef, coll. J.H. Day *et al.*, 23 July 1975, AM W15769, 3 specimens; Batemans Bay, from oysters, 31 Dec. 1969, NMV F53995, 1 specimen; Port Hacking, upper south-west arm, coll. V. Wadley, WAM 15-85, 8 male epitokes; Port Hacking, 6 month settlement plate, 1-2 m, coll. R. Fisher, CSIRO, 21 Dec. 1974, AM W202975, 3 specimens; Woollahra Point, AM W202920, 1 specimen; Botany Bay, 1910, AM W181, 2 specimens; Rushcutters Bay, AM W4786, 1 female epitoke; Spit Bridge marina, Middle Harbour, Sydney, on pilings among barnacles, coll. N. Tait, 29 June 1972, AM W203010, 1 specimen; Port Jackson, AM W4843, 2 specimens; Broken Bay, AM W4841, 1 specimen; Lake Macquarie, 17 July 1953, AM W4838, 1 specimen; north of Coffs Harbour, in sand, 23 Mar. 1972, coll. P. Hutchings, AM W202923, 1 specimen; Point Hastings, east of Murwillumbah, LWM, on sheltered rocks & oysters, coll. I. Loch, 26 Oct. 1976, AM W203011, 2 specimens; Wooli, among oysters on rocks, coll. P. Hutchings, 25 Feb. 1971, AM W203012, 1 specimen. QUEENSLAND: Picnic Cove, Noosa Heads, on loose rocks, semi-sheltered, coll. I. Loch, 21 Oct. 1976, AM W202970, 1 specimen; Middle Banks, Moreton Bay, Nov. 1983-Nov. 1984, P. Saenger & S. Cook, QM GH4028, 1 specimen; Calliope River, Gladstone, coll. P. Saenger, 1974-1983, AM W199377, 1 specimen; Barnes Creek, Mackay, 3 km upstream from mouth, coll. Turner *et al.*, 24 Sept. 1970, AM W203092, 1 specimen.

Description. Type series comprises 12 specimens, size range 18 setigers (anterior fragment), length 5 mm, width 1(1.5) mm, jaw length 0.9 mm to 30 setigers (anterior fragment), length 20 mm, width 2.5(4.5) mm, jaw length 2.5 mm. Median longitudinal band present, width half that of body, of slightly darker brown pigmentation on dorsum of anteriormost 10-15 setigers; entire prostomium and dorsal peristomium also darker. Eyes dark blue/black, subdermal. Length of prostomium equal to width. Antennae one-third as long as prostomium. Tentacular cirri extend back 7-8 setigers. Jaws thin, transparent brown in small specimens, heavier and opaque in larger specimens, always with 5-7 distinct teeth. Paragnaths: I = 2-4; II = 14-26; III = 14-26 (distinct lateral groups present); IV = 15-37 cones, and 2-4 bars; V = 1-4; VI = 6-11 bars; VII-VIII = 42-55 large cones in 2 rows, and 54-141 small cones in a distinct band posterior to the larger paragnaths. Anal cirri as long as posteriormost 7-8 setigers.

Notopodia with 2 similar conical lobes from setiger 2, and basally inserted dorsal cirri of equal length. Small but distinct digitiform presetal lobe present at base of inferior notopodial lobe on setigers 5-30, largest on setigers 10-20. Neuropodia with 2 lobes, dorsal lobe more rounded and shorter throughout, ventral lobe more acute and similar in shape and length to notopodial lobes. Ventral cirri about three-quarters length of ventral neuropodial lobe and basally inserted. All parapodial lobes more slender on posterior setigers but proportions otherwise similar throughout. Neuropodial heterogomph spinigers present throughout.

Remarks. *Perinereis akuna* can be distinguished from all other species in the *Perinereis nuntia* species group by the additional band of minute paragnaths in the posteriormost part of VII-VIII. *Perinereis akuna* occurs in similar habitats and within the range of *P. vallata* in southern Australia; these species can also be separated by paragnath counts for Areas II and VI (Table 4). Wilson (1993) showed that *P. akuna* and *P. vallata* are also distinguished by fixed allelic differences at four enzyme loci.

Etymology. The specific name *akuna* is derived from an Australian aboriginal word now used as a place name near the type locality. It is to be treated as indeclinable.

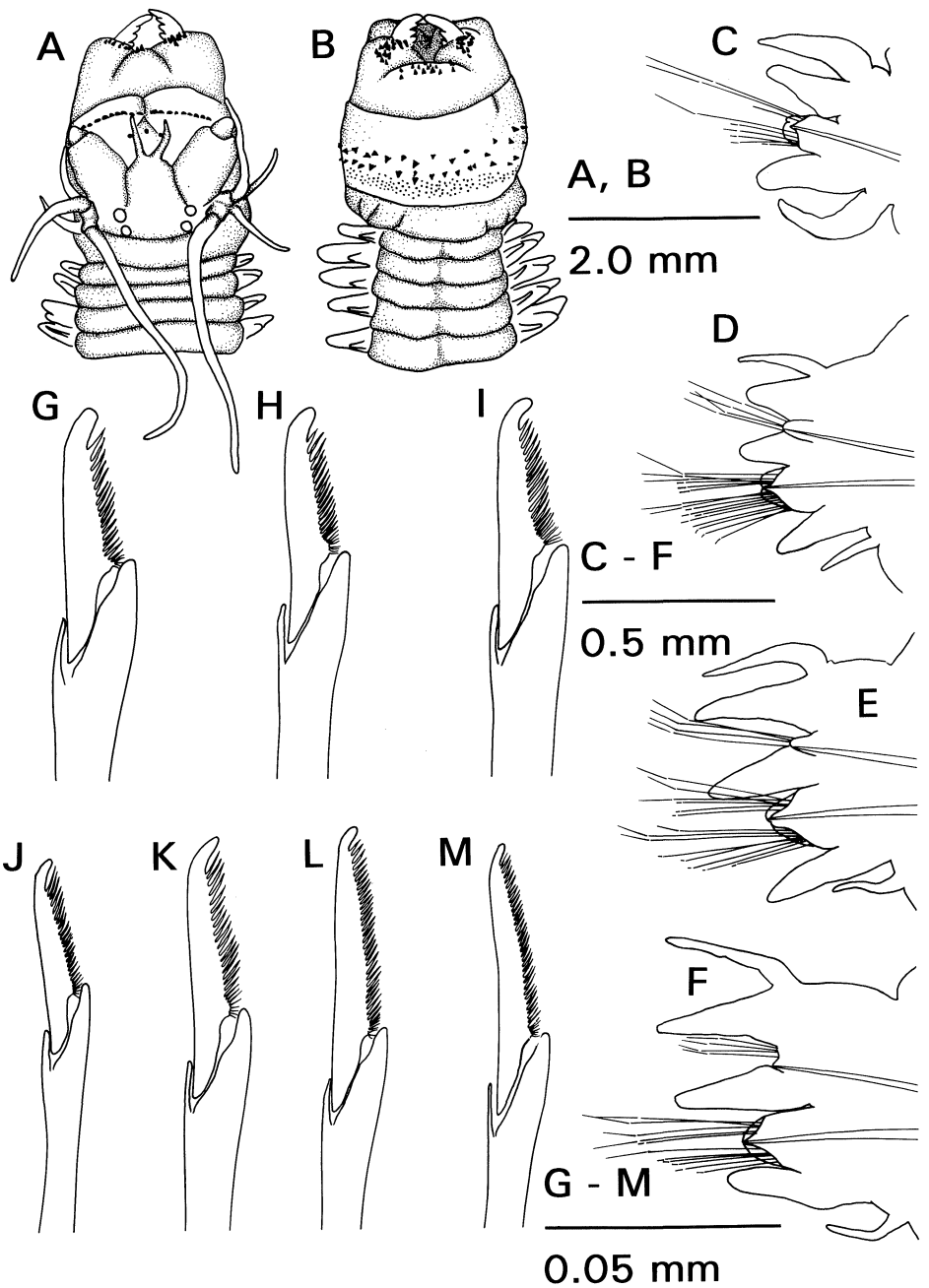

Fig.7. *Perinereis akuna* n.sp. New South Wales: Coal & Candle Creek, Hawkesbury River, 19 Oct. 1986, NMV F53985, holotype: A – extended proboscis, dorsal view; B – extended proboscis, ventral view. New South Wales: Batemans Bay, Clyde River, 17 July 1987, NMV F53988, C – setiger 1 parapodium, anterior view; D – setiger 10 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 87 parapodium, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 57; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 87; J – heterogomph falciger, ventral neuropodial fascicle, setiger 1; K – heterogomph falciger, ventral neuropodial fascicle, setiger 10; L – heterogomph falciger, ventral neuropodial fascicle, setiger 50; M – heterogomph falciger, ventral neuropodial fascicle, setiger 87.

Distribution. Widespread in south-eastern Australia from Gladstone in the north to Twofold Bay in the south. Two isolated records from South Australia and south-western Western Australia. Collected on a variety of hard substrates, including cobble, but apparently restricted to the intertidal zone and can occur in areas of reduced salinity.

Perinereis caeruleis (Hoagland, 1920)

Fig.8a-n

Nereis (Heteronereis) caeruleis Hoagland, 1920: 608-610, pl.47 figs 13-16, pl.48 figs 1-4.

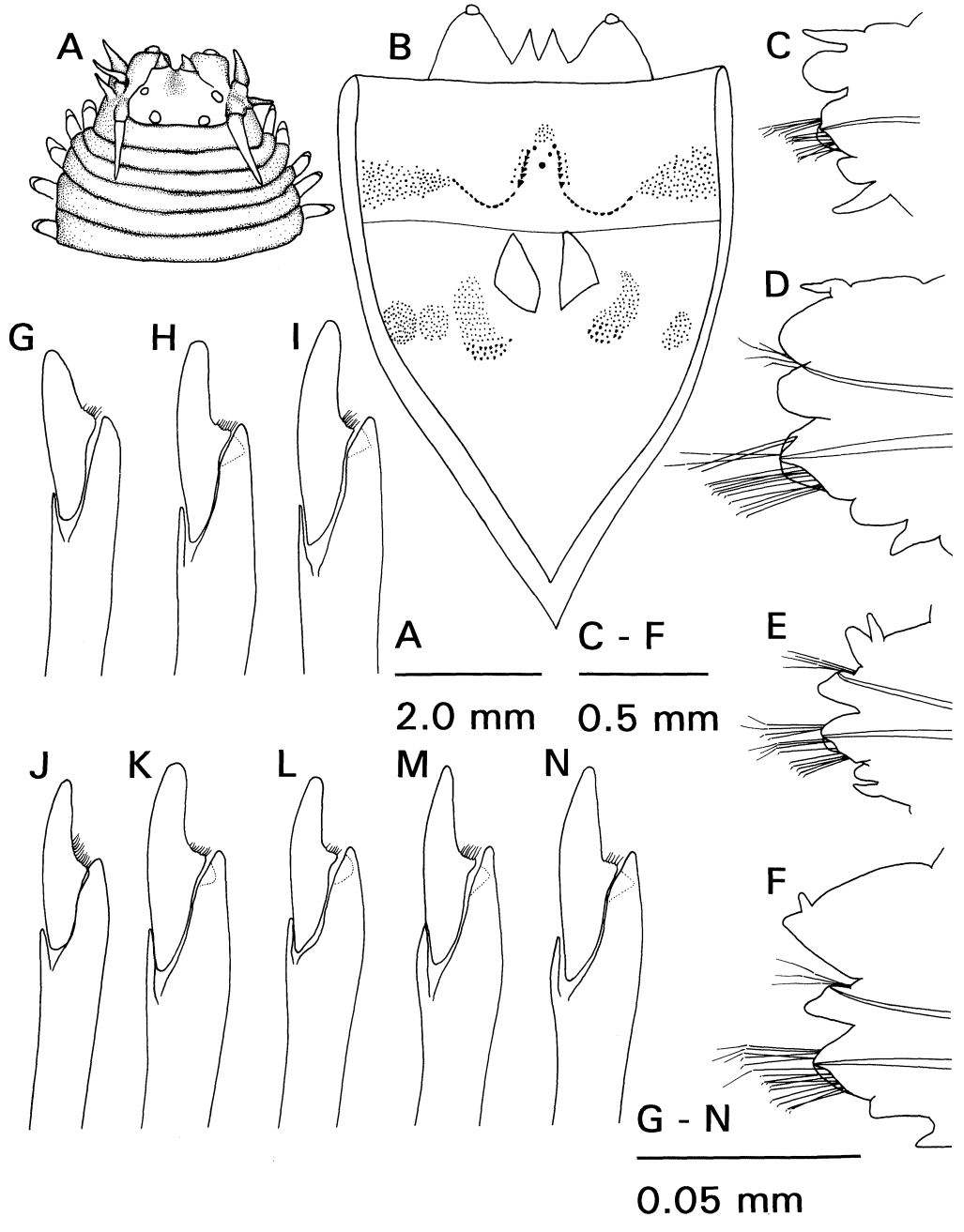

Fig.8. *Perinereis caeruleis* (Hoagland, 1920). Northern Territory: Annersley Point, 16 June 1984, NTM W1806: A – dorsal view of head; B – schematic ventral view of dissected proboscis (not to scale); C – setiger 1 parapodium, anterior view; D – setiger 10 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 237 parapodium, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 50; J – heterogomph falciger, ventral neuropodial fascicle, setiger 1; K – heterogomph falciger, ventral neuropodial fascicle, setiger 10; L – heterogomph falciger, ventral neuropodial fascicle, setiger 50; M – heterogomph falciger, ventral neuropodial fascicle, setiger 120; N – heterogomph falciger, ventral neuropodial fascicle, setiger 237.

Material examined. AUSTRALIA: Northern Territory: Annersley Point, mangrove at base of cliff, Malay Bay Road, intertidal, coll. R. Hanley *et al.*, 19 June 1984, NTM W1772, 5 specimens. Annersley Point, Stn AP1, rock shelf along sandy beach, intertidal, coll. R. Hanley *et al.*, 16 June 1984, NTM W1806, W1811, 4 specimens.

PHILIPPINES: Limbe Strait, coll. "Albatross", 9 Nov. 1909, USNM 18948, holotype.

NEW HEBRIDES: coll. Kawalcasky, MNHN, 1 male epitoke (specimen from P. Fauvel collection, labelled *P. neocaledonica*).

Description. Based on 9 Australian specimens, size range 69 setigers (anterior fragment), length 18 mm, width 1.4(3.4) mm, jaw length 1.4 mm to 313 setigers (entire specimen), length 90 mm, width 2.2(4.5) mm, jaw length 2.1 mm. Pigmentation dark brown on prostomium and anterior dorsum, with prominent darker median longitudinal stripe. Pigmentation posteriorly lighter, limited to mid-dorsal longitudinal stripe. Eyes black. Length of prostomium three-quarters times width. Anterior margin of prostomium indented to a distance equal to half the length of the antennae in some specimens, others with little or no indentation. A prominent circular depression present in anterior prostomium between antennae. Antennae one-third as long as prostomium. Tentacular cirri extend back 2-4 setigers. Jaws heavy, dark brown, with no teeth. Paragnaths: I = 0-2; II = 0; III = 60-90 in a central group, plus 2 distinct lateral groups each of 30-40; IV = 80-100 cones, bars absent; V = 1-4 large cones plus 20-40 small cones posterior to the larger cones; VI = 8-17 bars plus 7-20 cones in distinct patches close to Area V; VII-VIII = about 200-250 very small cones, plus 3-4 large cones on each side close to Area VI. Anal cirri as long as posteriormost 4 setigers.

Parapodia of setigers 1 and 2 directed anteriorly. Anterior notopodia with 2 equal lobes and basally attached dorsal cirrus of equal length. Dorsal notopodial lobe becoming expanded from median setigers, up to twice as long as ventral lobe and with distally attached dorsal cirrus. Anterior neuropodia with 2 unequal lobes, ventral lobe about half as long as dorsal lobe. Median and posterior neuropodia with ventral lobe reduced to a small protuberance on ventral margin of superior neuropodial lobe. Ventral cirri one-quarter as long as superior neuropodial lobe throughout. Neuropodial falcigers with distal portion of blade shorter than proximal (articulated) region (Fig.8g-n). Neuropodial heterogomph spinigers absent from anteriormost 24-35 setigers.

Remarks. The holotype is an epitoke and closely fits the original description of Hoagland (1920). The proboscis and head are in poor condition, nevertheless, there are no significant differences between the holotype and the Australian material.

Perinereis caeruleis differs from all other species described in this paper by having a variably indented prostomium; paragnaths absent from II (and usually from I also); additional groups of paragnaths present on V and VI; and distinctive short-bladed falcigers.

Perinereis neocaledonica Pruvot, 1930 is closely related to *P. caeruleis* and may be a junior synonym. Fauvel (1932) noted that *P. caeruleis* differs from *P. neocaledonica* in having a "normal" Area I (ie, paragnaths present), however the material examined here is variable in this respect. A male epitoke labelled *P. neocaledonica* from Fauvel's collection and collected in the New Hebrides differs in having more numerous small paragnaths on VI (patches of about 40 on each side) and VII-VIII (approximately 380) than the type material of *P. caeruleis* and the material of *P. caeruleis* from northern Australia. Examination of the type material and additional collections from the region of New Caledonia will be required to determine if the South Pacific contains an additional species that should be called *P. neocaledonica.*

Distribution. *Perinereis caeruleis* was previously known only from the Philippines. The material from Annersley Point, near Darwin, represents the first record of *P. caeruleis* from Australia. *Perinereis neocaledonica* is recorded from the Arabian Sea (Fauvel, 1932), Taiwan (Wu, 1967), southern Japan (Imajima *et al.*, 1985), as well as from New Caledonia (Pruvot, 1930; Rullier, 1972) and the New Hebrides (material examined above).

Perinereis gualpensis Jeldes, 1963

Perinereis gualpensis Jeldes, 1963: 3-10.–Rozbaczylo & Castilla, 1973: 220.–Bertrán, 1980: 82-83, fig.1.–Jaramillo *et al.*, 1984: 124,127.

Description (taken from Bertrán, 1980). Paragnaths: I = 0-7; II = 6-17; III = 24-48; IV = 18-39 cones; V = 1-2; VI = 6-11 bars; VII-VIII = 30-47 large cones. Notopodia with 2 equal conical lobes, and digitiform presetal lobe on anterior setigers back to at least setiger 28. Dorsal notopodial lobe not expanded on posterior setigers, dorsal cirrus about as long as dorsal notopodial lobe and basally inserted throughout. Neuropodia with similar lobes throughout, and ventral cirrus about three-quarters as long as neuropodial lobes. Neuropodial heterogomph spinigers are present.

Remarks. We have not been able to examine type material, which is in poor condition (Rozbaczylo & Castilla, 1973). Bertrán (1980) has shown that *P. gualpensis* is similar to Chilean populations of *P. vallata* but differs in having longer antennae, lacking lateral groups on Area III, and having fewer paragnaths on VI than the latter species. The morphometric relationship between number of segments and body length also separates the two species. *Perinereis gualpensis* occurs in estuarine regions subject to more freshwater influence and salinity fluctuations than *P. vallata* (Bertrán, 1980).

Distribution. *Perinereis gualpensis* is known only

from three estuaries in Chile, from fresh and brackish water.

Perinereis maindroni Fauvel, 1943

Fig.9a-g

Perinereis maindroni Fauvel, 1943: 201-202, fig.1e-i.–Fauvel, 1953: 203-204, fig.104e-i.

Material examined. India: Pondicherry, coll. M. Maindron, 1901, MNHN, 1 SYNTYPE.

Description. Size: 50 setigers (entire), length 17 mm, width 1.0(1.6) mm, jaw length not recorded. Peristomium orange-brown, slightly darker than prostomium and setigerous segments, otherwise no pigmentation. Eyes dark red. Prostomium as long as wide, antennae half as long as prostomium. Tentacular cirri extend back 0 (shortest) to 3+ setigers (longest tentacular cirri are broken). Jaws translucent brown, with about 5 teeth. Paragnaths minute translucent orange: I = 0; II = 8, 6; III = 8 (distinct lateral groups not visible); IV = 8, 8 cones, bars absent; V = 1 cone exactly at the apex of VI left & right; VI = 6, 6 evenly spaced bars; VII-VIII 35 in about 2 rows, no additional separate bands of small cones. Anal cirri ventrally inserted, as long as posteriormost 10 setigers.

Notopodia of setigers 1 and 2 with 2 equal triangular lobes, setigers 3-20 with 3 equal triangular lobes, and basally inserted dorsal cirri of similar length. Digitiform presetal lobe absent. Anterior neuropodia with rounded dorsal lobe and acute ventral lobe from setiger 3. Neuropodial lobes equal in length on anterior setigers but dorsal lobe reduced to about half length of ventral lobe by about setiger 20-25. Digitiform postsetal neuropodial lobe present from about setiger 15, initially about half as long as ventral lobe, becoming equal in length to ventral lobe (but narrower) by setigers 20-25. Ventral cirri about as long as ventral neuropodial lobe throughout and basally inserted. Notopodia from setiger 21 with narrow elongate superior lobe becoming 2-3 times as long as ventral lobe on about setigers 25-35. Median notopodial lobe reduced to small presetal lobe

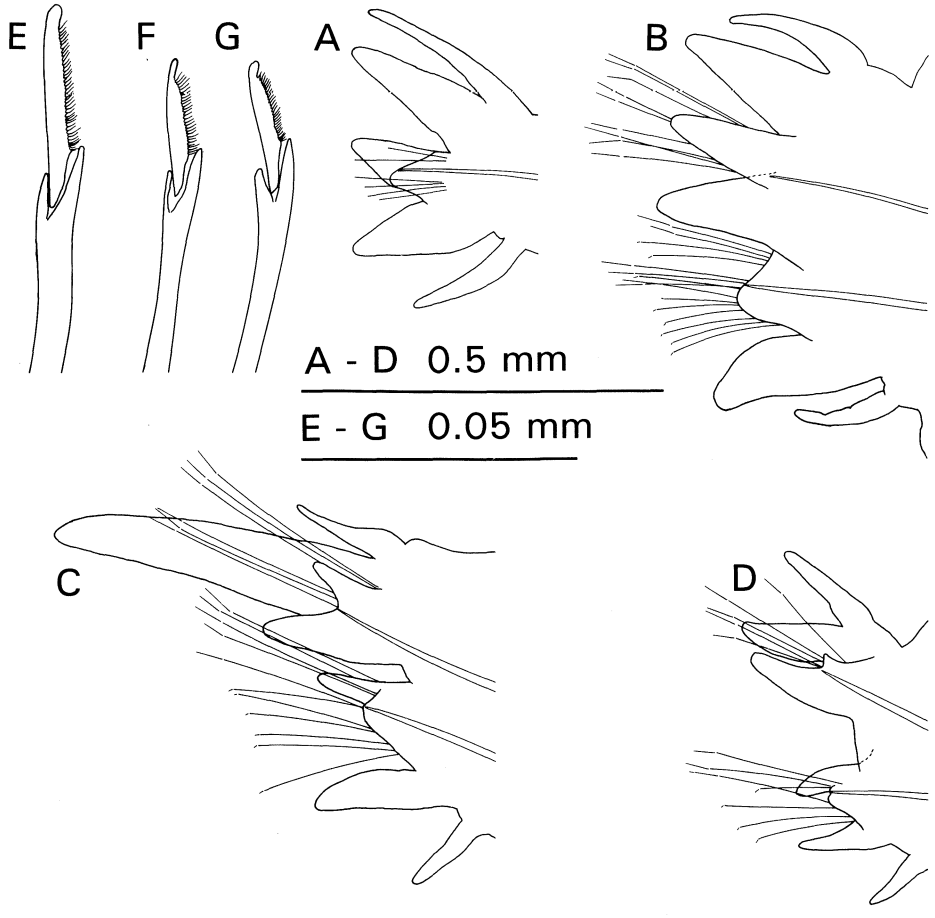

Fig.9. *Perinereis maindroni* Fauvel, 1943. India: Pondichéry, coll. M. Maindron, MNHN syntype: A – setiger 2 parapodium, anterior view; B – setiger 10 parapodium, anterior view; C – setiger 25 parapodium, anterior view; D – setiger 40 parapodium, anterior view; E – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; F – heterogomph falciger, ventral neuropodial fascicle, setiger 10; G – heterogomph falciger, ventral neuropodial fascicle, setiger 45.

by setiger 21, reducing further to less than half length of ventral lobe on about setigers 25-35 and absent on posteriormost setigers. No indication of developing epitoky.

Notosetae present from setiger 3, all homogomph spinigers. Neurosetae homogomph spinigers and heterogomph falcigers in dorsal fascicle, heterogomph spinigers and heterogomph falcigers in ventral fascicle. Neuropodial heterogomph spinigers apparently present throughout (many anterior setae broken).

Remarks. The locality and collector of the specimen examined agrees with that in the original description and it appears certain that this is one of the five specimens examined by Fauvel (1943); we treat it as a syntype. The specimen agrees well with the original description of Fauvel (1943).

The arrangement of paragnaths on *Perinereis maindroni* is unremarkable for the genus, though they are minute and difficult to discern. However, the shape of the notopodia, with three equal lobes anteriorly and a narrow, elongate dorsal lobe in the middle region, is unique among species of *Perinereis*. The division of the body into three marked regions suggests that the specimens may be all epitokes or subepitokes (contrary to Fauvel [1953: 204] who considered some to be atokous).

Distribution. Known only from Pondicherry, 11°57'N 79°48'E, south-eastern India.

Perinereis majungaensis Fauvel, 1921

Perinereis nuntia var. *majungaensis* Fauvel, 1921: 11-13.

Material examined. Madagascar ["Majunga"], MNHN A431, 1 specimen.

Description. A single specimen incomplete posteriorly, size not recorded, gravid female. Paragnaths (given as left, right for paired Areas): I = 8; II = 19, 21; III = about 40 in 3-4 rows; IV = 23, 21 cones, and 13, 12 bars; V = 0? (damaged); VI = 10, 10 bars; VII-VIII = 57 large cones in 2 rows.

Remarks. We do not know if the single specimen we have been able to examine was part of Fauvel's original material of *P. nuntia majungaensis*, which comprised nine specimens. Fauvel's (1921) description provides the following additional information: I = 7-13; II = 20-30; III = 40-50 in four rows; V = 1; VI = 8-10; VII-VIII = three rows of cones. (We have described the specimen examined in this study as having only two rows of cones on Area VII-VIII, but since these cones are irregularly arranged these rows are difficult to describe precisely and little weight can be given to this possible difference.) On the basis of these descriptions, *P. majungaensis* is clearly a distinct species. The high paragnath counts for Areas I, III and the large number of bars on IV distinguish this species from all other species in the *Perinereis nuntia* species-group.

Distribution. Madagascar.

Perinereis matthaii Aziz, 1938

Perinereis matthai Aziz, 1938: 29, pl.3 fig.1, pl.4 figs 29-30, pl.7 figs 56-57.

Description (taken from Aziz, 1938). Prostomium indented anteriorly and with a distinct dorsal groove. Tentacular cirri extend back to setiger 9. Paragnaths: I = 0; II = 4-7; III = cluster of minute, indistinct paragnaths; IV = a cluster; V=0; VI = 6-10 in a transverse row; VII-VIII = absent. Anterior notopodia with 2 unequal lobes. Homogomph spinigers in notopodia, homogomph spinigers and heterogomph falcigers in neuropodia.

Remarks. The absence of paragnaths on VII-VIII distinguishes *P. matthaii* from all other species treated here.

Distribution. Known only from Karachi, Pakistan.

Perinereis mictodonta (Marenzeller, 1879)

Nereis mictodonta Marenzeller, 1879: 118-119, pl.2 fig.2.– Izuka, 1912: 148-151, pl.16 figs 1-6.

Description (taken from Marenzeller, 1879). Tentacular cirri extend back 7-8 setigers. Paragnaths: I = 3; II = oblique tapering group; III = a central group with isolated lateral groups; IV = triangular group; V = 3; VI = a single row of heterogeneous bars; VII-VIII = 3 rows of large cones. Notopodia and neuropodia each with 2 lobes throughout, dorsal notopodial lobe not strongly expanded on posterior setigers.

Remarks. *Nereis mictodonta* was synonymised with *Perinereis nuntia brevicirris* (Grube, 1857) by Imajima (1972), with the following paragnath counts: I = 2-5; II = 22-26; III = about 40; IV = 40-43; V = 3; VI = 4-10 cones and bars; VII-VIII = 34-38 cones in three irregular rows. These counts would exclude this species from *P. nuntia* as diagnosed here (see values in Table 4), however, Imajima also records *P. nuntia vallata* (Grube, 1857) from Japan, with similar but slightly lower paragnath counts. Both taxa described by Imajima (1972) appear very similar to *Perinereis nuntia* (Savigny, 1818) but since we have been unable to examine any material from Japan we defer judgement on the identity of *P. mictodonta*.

Distribution. Japan.

Perinereis namibia n.sp.

Fig.10a-k

Perinereis nuntia vallata.–Day, 1967: 334, fig.14.12.p-s (in part, material from South Africa; not Grube, 1857).

Type material examined. HOLOTYPE: South Africa: Griffiths Bay, Lüderitz, Stn C, coll. S. Penrith & B. Kensley, Mar. 1968, SAMC A20263. PARATYPES: type locality, SAMC A21421, 25 paratypes; type locality, NMV F52582-52584, 3 paratypes; Griffiths Bay, Lüderitz, coll. S. Penrith & B. Kensley, 19 Mar. 1968, SAMC A20078, 4 paratypes.

Additional material examined. South Africa: Lüderitz Bay, coll. L. Schultze, July 1903, ZMB 45109b, 7 specimens. Walvis Bay, Stn WBIF, coll. C. Berrisford, 24 Sept. 1964, SAMC A20030, 2 specimens.

Description (based on type series). Thirty-four

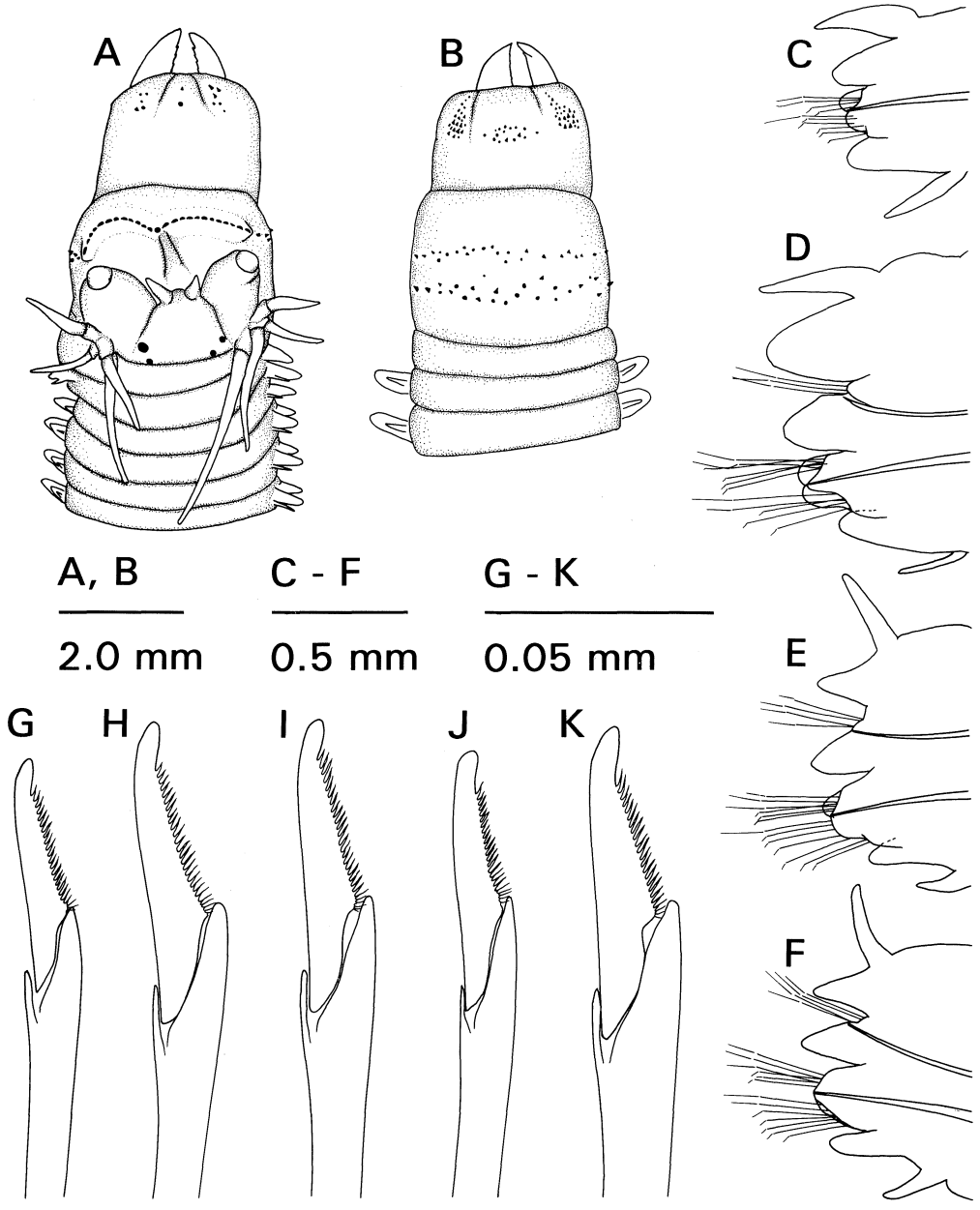

Fig.10. *Perinereis namibia* n.sp. South Africa: Griffiths Bay, Lüderitz, Stn C, coll. S. Penrith & B. Kensley, 19 Mar. 1968, NMV F52582, paratype: A – extended proboscis, dorsal view; B – extended proboscis, ventral view; C – setiger 1 parapodium, anterior view; D – setiger 11 parapodium, anterior view; E – setiger 50 parapodium, anterior view; F – setiger 78 parapodium, anterior view; G – heterogomph falciger, ventral neuropodial fascicle, setiger 1; H – heterogomph falciger, ventral neuropodial fascicle, setiger 11; I – heterogomph falciger, ventral neuropodial fascicle, setiger 78; J – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; K – heterogomph falciger, dorsal neuropodial fascicle, setiger 78.

specimens, 31 setigers (incomplete posteriorly), length 10 mm, width 0.8 mm, jaw length 0.8 mm to 63 setigers (incomplete posteriorly), length 72 mm, width 7 mm, jaw length 3.7 mm. Brown pigmentation on anterior dorsum. Eyes black. Length of prostomium equal to width. Antennae one-third to half as long as prostomium. Tentacular cirri extend back 3-6 setigers. Jaws dark brown, with 4-6 teeth. Paragnaths: I = 1-4; II = 1-20; III = 11-26 (distinct lateral groups present); IV = 5-39 cones, bars absent; V = 0-3; VI = 5-14 bars; VII-VIII = 43-73 large cones in 2-3 rows. Anal cirri as long as posteriormost 5 setigers.

Notopodia with 2 triangular lobes, of similar length and unchanged proportions on posterior setigers. Digitiform presetal notopodial lobe present from setigers 5-25. Dorsal cirri basally inserted, equal in length to notopodial lobes anteriorly, slightly longer than notopodial lobes from about setiger 50. Neuropodia anteriorly with 2 rounded lobes of similar length, dorsal lobe bifid. Ventral neuropodial lobe becoming more acute and shorter than dorsal lobe from about setiger 10. Dorsal neuropodial lobe not noticeably bifid posterior to about setiger 50. Ventral cirri equal in length to neuropodial lobes anteriorly, becoming relatively shorter from about setigers 10-20. Neuropodial heterogomph spinigers present throughout.

Remarks. Descriptive statistics for paragnath counts are provided in Table 4. Two specimens from Walvis Bay (SAMC A20030) possess two to three small bars on Area IV, and appear similar to *Perinereis vallata*. However, these are the only two among 43 specimens with any indication of bar-shaped paragnaths on IV. None of many hundreds of specimens of *Perinereis vallata* examined lacked bar-shaped paragnaths on IV and we prefer to identify these distinctive specimens from southern Africa as a new species: *P. namibia*. *Perinereis vallata* has not been collected in southern Africa.

Etymology. The specific name *namibia* is derived from the African country of the same name and is to be treated as indeclinable.

Distribution. Recorded from Walvis Bay and Griffiths Bay on the coast of Namibia.

Perinereis nuntia (Savigny, 1818)

Fig.11a-g

Lycoris nuntia Savigny, 1818: 313.–Savigny, 1820: 33, pl.4 fig.2.

Neanthes nuntia.–Gravier, 1899: 237 (Savigny, 1818 record repeated).–Fauvel, 1911: 382-383 (Bouchir [=Bushehr], Persian Gulf).

Perinereis nuntia "typique".–Fauvel, 1919: 415 (Djibouti, Gulf of Aden).

Perinereis heterodonta Gravier, 1901: 179, figs 179-181, pl.11 fig.46.–Fauvel, 1911: 394-395.

Perinereis nuntia var. *heterodonta*.–Fauvel, 1919: 419-420 (Djibouti, Gulf of Aden).

Perinereis nuntia var. *djiboutiensis* Fauvel, 1919: 420-421 (Djibouti, Gulf of Aden).

Nereis (Perinereis) heterodonta var. *mictodontoides* Augener, 1913: 177-178.

Nereis (Perinereis) rumphii Horst, 1919: 60.–Horst, 1924: 166-168, pl.33 figs 1-3.

Perinereis broomensis Hartmann-Schröder, 1979: 117-118, figs 211-215.–Hartmann-Schröder, 1980: 60 (new synonymy).

Perinereis weijhouensis Wu *et al.*, 1981: 181-183, figs 114a-k, 115a-d.–Wu *et al.*, 1985: 201-204, figs 114a-k, 115a-d.

Nereis (Lycoris) quatrefagesi Grube, 1878: 79-80.

Perinereis quatrefagesi.–Hylleberg *et al.*, 1986: 5-8, figs 3a-l, 4a-j.

Material examined. RED SEA: coll. de Joussaume, 1894, MNHN jar A108, 9 specimens examined of a total of 15 labelled *Neanthes (Lycoris) nuntia*.

GULF OF ADEN: Djibouti, Illes Musha, à mer basse, dans les fentes des rochers de l'île Maskali, 23 Jan. 1904, MNHN, 8 specimens (material of Fauvel, 1919, but not identified); Djibouti, dans le sable vaseux à l'est de la Résidence, 2 Feb. 1904, MNHN jar A97, 4 syntypes *Perinereis nuntia* var. *djiboutiensis*; Djibouti, Gravier collection, sud du plateau du Serpent, MNHN jar A97, 1 syntype *Perinereis nuntia* var. *djiboutiensis*; Djibouti, Feb. 1933, MNHN jar A97, 9 specimens; Djibouti, 23 Feb. 1904, MNHN jar A97, male epitoke labelled *Perinereis nuntia* var. *heterodonta*; Djibouti, Gravier collection, MNHN jar A526, 4 syntypes *Perinereis heterodonta*; Djibouti, Obock, coll. de Joussaume, 1895, MNHN jar A98 (7 specimens, labelled paratypes; here considered to be syntypes of *Perinereis heterodonta*); Djibouti, Obock, 11 Mar. 1933, MNHN, 6 specimens.

THAILAND: Rawai Beach, Phuket Island, sandy beach, coll. A. Nateewathana, 24 Mar. 1986, PMBC, 5 specimens labelled *P. quatrefagesi*.

PHILIPPINES: Bohol, coll. Semper, WMP 320, 1 syntype *Nereis (Lycoris) quatrefagesi*.

MALAYSIA: Batu Muang, mangrove, coll. Leong Tak Seng, no date, AM W21387, 12 specimens.

INDONESIA: off south coast of East Flores, coll. van der Sande, 14 Jan. 1909, ZMA V.Pol 911, 1 syntype *P. rumphii*.

CHINA: Guangxi, Weijhou, intertidal rock, 16 Apr. 1978, material loaned by Sun Ruiping, 4 specimens identified as *P. weijhouensis*; Zhejiang Province, coll. Zhang Song Ling, 13 Apr. 1984, AM W199677, 1 specimen.

HONG KONG: Starfish Bay (south), upper shore under stones, coll. A.S.Y. Mackie, 5 Apr. 1986, NMWZ 1986.079.142-143, 5 specimens; Starfish Bay (south), low tide from rocks & oysters, coll. A.S.Y. Mackie, 3 Apr. 1986, NMWZ 1986.079.144, 1 specimen; east side of Ping Chau, intertidal in gravel, coll. A. Hirayama, 15 Apr. 1986, NMWZ 1986.079.145, 1 specimen; Tsim Bei Tsui, high tide in mud under stones, coll. R. Gibson, 10 Apr. 1986, NMWZ 1986.079.146, 1 specimen; Tso Wo Hang, below mangroves, mud-shell-sand, coll. P.G. Oliver, 6 Apr. 1986, NMWZ 1986.079.147, 2 specimens.

AUSTRALIA: WESTERN AUSTRALIA: Shark Bay, Denham, Stn 65, ZMB 5275, 1 syntype *Perinereis heterodonta* var. *mictodontoides*; Denham, coll. Michaelsen & Hartmeyer, HZM V7922, 2 syntypes *Perinereis heterodonta* var. *mictodontoides*; Broome, Crab Creek, mangroves, coll. G. Hartmann-Schröder, 11 Sept. 1975, HZM P15520, 2 paratypes *Perinereis broomensis*; Broome, main wharf, intertidal under rocks, coll. R. Hanley, 2 Oct. 1984, NTM W2305, 1 specimen;

Enderby Island, mangroves, intertidal, coll. P.A. Hutchings, AM W201967-8, 3 specimens. NORTHERN TERRITORY: Danger Point, Port Bremer, intertidal, under rocks, coll. R. Hanley, 30 May, 1982, NTM W215, 17 specimens. QUEENSLAND: Yorkeys Knob, intertidal, under rocks, coll. R. Hanley, 19-20 Nov. 1984, NTM W2364, W2365, 3 specimens; Proserpine, coll. A. Hansen, Mar. 1973, QM G10508, 1 specimen; Sandgate, coll. R. Hamlyn-Harris, QM G10497, 4 specimens; Dunwich, Stradbroke Island, intertidal mud flats, coll. University of Queensland, 1 Aug. 1956, QM G4014, 1 male epitoke & 2 atokes; Dunwich, Stradbroke Island, sand and mud, coll. H. Krause, 18 Mar. 1961, QM G7125, 1 specimen.

FIJI: Ngoloa Island, beach on south-east shore, coll. C.J. Glasby, 18-19 Feb. 1987, NMV F53984, 16 specimens.

Description (based on 9 specimens from Red Sea, MNHN A108). Nine specimens, 104 setigers (entire worm), length 48 mm, width 1.8(3.0) mm, jaw length 1.7 mm to 78 setigers (incomplete posteriorly), length 67 mm, width 4.5 mm, jaw length 3.0 mm. Pigmentation absent. Eyes red-black with opaque lenses. Prostomium half as long as wide. Antennae three-quarters as long as prostomium. Tentacular cirri extend back 6-14 setigers. Jaws dark brown, with 5-6 teeth. Paragnaths: I = 1-3; II = 5-9; III = 9-17 (distinct lateral groups present); IV = 9-18 cones, bars absent; V = 0-4; VI = 6-9 bars and cones; VII-VIII = 18-38 large cones in 1-2 rows. Anal cirri as long as posteriormost 11 setigers. Neuropodial heterogomph spinigers present throughout.

Syntypes of *Perinereis heterodonta* var. *mictodontoides* comprise 3 specimens, 175 setigers (entire), length 105 mm, width 1.8(2.8) mm, jaw length 1.6 mm to 208 setigers (entire), length 140 mm, width 3.5(4.5) mm, jaw length 2.6 mm. Pigmentation absent. Eyes black. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 3-8 setigers. Jaws dark brown, with 6 teeth. Paragnaths: I = 1-2; II = 1-8; III = 8-14 (distinct lateral groups present); IV = 10-25 cones, bars absent; V = 3-4; VI = 8-13 bars; VII-VIII = 25-31 large cones in 2 rows. Anal cirri as long as posteriormost 6 setigers.

Syntype of *Nereis (Lycoris) quatrefagesi* in very poor condition, comprising 2 anterior fragments for a total of 72 setigers. Body appears almost completely digested, only pale empty skin remaining. Paragnaths in all Areas

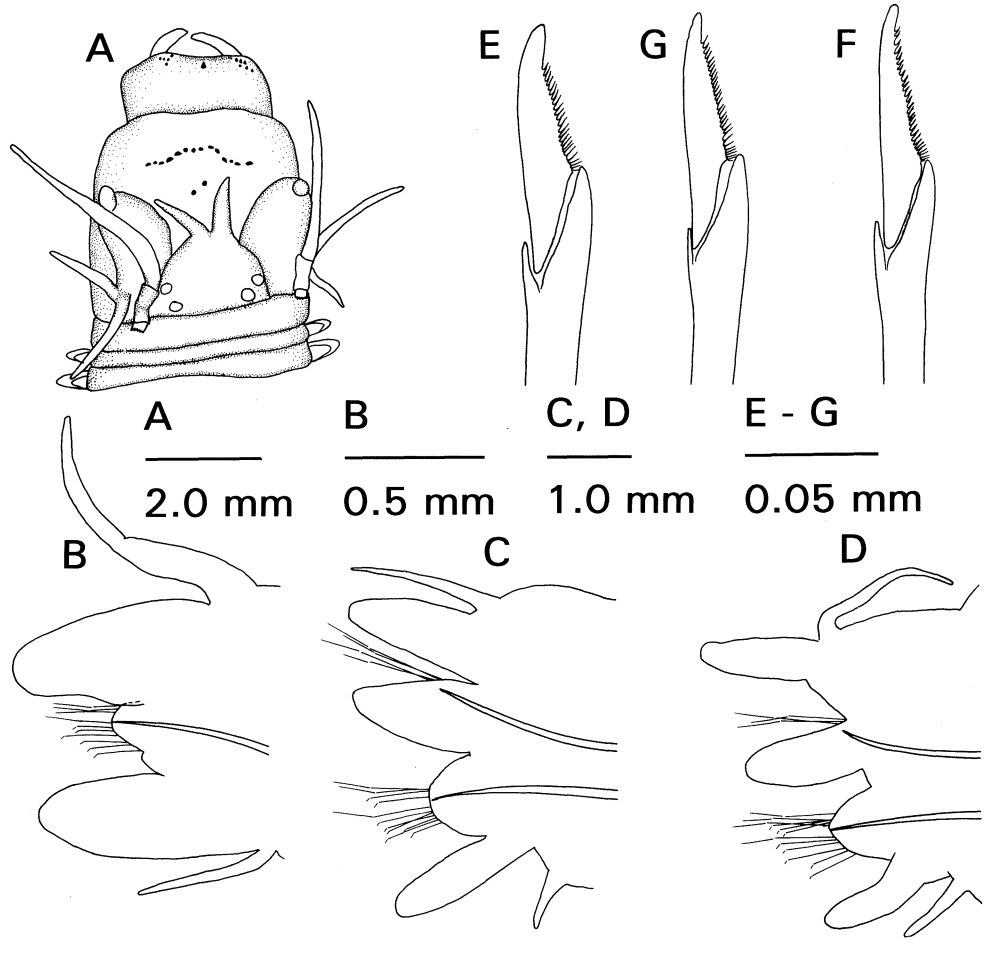

Fig.11. *Perinereis nuntia* (Savigny, 1818). Coll. Jousseaume, 1898, MNHN jar A108: A – extended proboscis, dorsal view; Mer Rouge, coll. Jousseaume, 1894, MNHN jar A108: B – setiger 1 parapodium, anterior view; C – setiger 40 parapodium, anterior view; D – setiger 76 parapodium, anterior view; E – heterogomph falciger, ventral neuropodial fascicle, setiger 3; F – heterogomph falciger, ventral neuropodial fascicle, setiger 40; G – heterogomph falciger, ventral neuropodial fascicle, setiger 76.

have become transparent but can still be counted and general form of soft parts including parapodia are visible. Many setae remain and although all setal types are identifiable, few are intact. Paragnaths: I = 3 (in longitudinal series); II = 7,8; III = 11 (distinct lateral groups present); IV = 16, 18 cones, bars absent; V = 1; VI = 7,8 evenly sized short bars; VII-VIII = 18 in 1-2 uneven rows.

Syntype of *Perinereis rumphii* a mature female epitoke of 159 setigers, jaw length 2.3 mm. Pigmentation absent. Eyes enlarged, red-black. Neuropodial heterogomph spinigers absent. Epitokous parapodia from setiger 30. Dorsal cirri inflated basally setigers 1-6, ventral cirri inflated on setigers 1-4. Dorsal cirri 2 times length of notopodia on setigers 1-6, similar in length to notopodia on median setigers, 3-4 times length of notopodia on posterior 20-30 setigers.

Paragnath count statistics for all material examined are provided in Table 4. Neuropodial heterogomph spinigers absent from anteriormost 3-80 setigers in some specimens.

Remarks. The material listed above is identified as *P. nuntia* (Savigny, 1818) on the basis of the subsequent records of Gravier and Fauvel cited in the synonymy above. Savigny's original material probably no longer exists, however examination of 49 specimens from the vicinity of the type locality indicates that only one species is present in the region and there is little doubt that the name *Perinereis nuntia* is correctly applied to this material.

Perinereis nuntia and several varieties named by Fauvel (1932) have been reported from throughout the southern oceans, South-east Asia, China and Japan. We have referred many of these records to other species of *Perinereis* in this paper; the remaining records will require critical re-appraisal.

Perinereis nuntia appears to exhibit regional variation. Material from the Red Sea has generally lower paragnath values, especially for Areas I, IV, V and VII-VIII, than material from the Indo-Pacific (Fig.3). A possible exception to this pattern is the animals figured by Savigny (1820: pl.4 figs 2.3, 2.4), which have the following paragnath counts: I = 1; II = 9, 7; III = 15; IV = 14, 15; V = 5; VI = 11, 9; VII-VIII = 41. Savigny's figures imply higher paragnath counts than those from any other Red Sea specimens that we have examined, but they may not be accurate. Some separation of populations from these regions in the canonical variates analysis is evident. As discussed in the Statistical Analysis section (above), this separation of the material is not sufficient to justify recognising western and eastern species among the material here referred to *P. nuntia*. The contrary pattern of variation suggested by Savigny's figures also does not support the recognition of two species.

Distribution. Red Sea, Gulf of Aden, and widely distributed throughout the tropical Indo-Pacific, from Thailand, China and Hong Kong, to Australia (north of 27°S), and Fiji.

Perinereis ponuiensis Augener, 1927

Nereis (Perinereis) ponuiensis Augener, 1927: 349-352, figs 5-6.

Material examined. New Zealand: Ponui Island, Auckland, coll. Mortensen, HZM V9725, 1 SYNTYPE; Rangitoto Island, Auckland Harbour, 27 Dec. 1914, ZMK, 1 SYNTYPE.

Description. Two specimens, 50 setigers (incomplete posteriorly), length 48 mm, width 3.5(5.2) mm, jaw length 2.2 mm to 103 setigers (entire), length 85 mm, width 3.0(4.5) mm, jaw length 3.5 mm. Brown pigmentation on anterior dorsum. Eyes black. Length of prostomium half to 1 times width. Antennae half to three-quarters as long as prostomium. Tentacular cirri extend back 5-8 setigers. Jaws dark brown, with 4-5 teeth. Paragnaths: I = 1-2; II = 5-10; III = 8-9 (distinct lateral groups present); IV = 12-25 cones, bars absent; V = 1-2; VI = 4 bars; VII-VIII = 26-27 large cones in 1-2 rows. Anal cirri as long as posteriormost 4 setigers. Superior notopodial lobe 1.5-2 times length of inferior notopodial lobe from about setiger 50. Neuropodial heterogomph spinigers present throughout.

Remarks. Paragnath counts for *Perinereis ponuiensis* are within the range of variation seen in *P. nuntia*. We have retained *P. ponuiensis* as a distinct species on the basis of the apparent constancy of paragnath counts for Area VI: all four specimens described by Augener (1927) possessed only three or four paragnaths on each side in Area VI. The corresponding paragnath counts for *P. nuntia* examined in this study (83 specimens) range from four to 13 with a mean of about seven. The elongation of the superior notopodial lobe on posterior setigers also distinguishes *P. ponuiensis* from *P. nuntia*.

Distribution. Known only from the type material, from Auckland Harbour, North Island, New Zealand.

Perinereis rhombodonta Wu, Sun & Yang, 1981

Perinereis rhombodonta Wu, Sun & Yang, 1981: 179-181, fig.113a-j.–Wu, Sun & Yang, 1985: 199-201, fig.113.

Material examined. CHINA: Guandong, intertidal, sand, coll. Sun Ruiping, 26 May 1976, SRP, 3 specimens; Guangxi, intertidal sand, coll. Sun Ruiping, 20 May 1976, SRP, 3 specimens.

HONG KONG: Starfish Bay (north), mud to high intertidal gravel, coll. C. Erséus, 4 Apr. 1986, NMWZ 1986.079.148, 5 specimens; Starfish Bay (north), shore, coll. R. Gibson, 12 Apr. 1986, NMWZ 1986.079.149, 1 specimen; Starfish Bay (south), high intertidal, sand-mud-clay, coll. A.S.Y. Mackie, 5 Apr. 1986, NMWZ 1986.079.150-151, 11 specimens; Tso Wo Hang, just below mangroves, mud-shell-sand, coll. P.G. Oliver, 6 Apr. 1986, NMWZ 1986.079.152-153, 10 specimens.

THAILAND: Prachuabkirihan Province, Red Shore village, small rocks on beach, coll. Nateewathana & Hylleberg, 10 July 1982, PMBC, 4 specimens.

Description (based on material from China). Size range 61 setigers (regenerating anterior fragment), 19 mm long, 1.2(1.6) mm wide, to 107 setigers (entire), 52 mm long, 1.6(2.6) mm long (jaw length not recorded). No distinctive pigmentation. Eyes black. Prostomium half as long as wide. Antennae one-third to one-quarter as long as prostomium. Longest tentacular cirri extend back 10-11 setigers. Jaws translucent brown , with very small teeth. Paragnaths: I = 2-6; II = 29-64; III = 40-150 in 3-4 groups of similar size; IV = 45-131 cones, bars absent; V = 1-3; VI = 9-14 bars; VII-VIII = 40-59 large cones in 1-2 rows, and 81-110 very small cones arranged in 5-6 similar-sized rhomboidal groups anterior to the large cones. Anal cirri as long as posterior-most 8-10 setigers.

Notopodia with 2 similar conical lobes from setiger 2, and basally inserted dorsal cirri of equal length. Digitiform presetal notopodial lobe absent. Neuropodia with 2 lobes, dorsal lobe more rounded and shorter throughout, ventral lobe more acute and similar in shape and length to notopodial lobes. Ventral cirri about three-quarters length of ventral neuropodial lobe and basally inserted. All parapodial lobes more slender on posterior setigers but proportions otherwise similar throughout. Neuropodial heterogomph spinigers present throughout.

Remarks. The arrangement of paragnaths on Area VII-VIII, with distinctive rhomboidal groups anterior to the larger cones, is unique in the genus *Perinereis*. This species has been adequately figured by Wu *et al.* (1981, 1985).

Distribution. Southern China, newly recorded here from Hong Kong and Thailand.

Perinereis vallata (Grube, 1858)

Fig.12a-l,13a-g

Nereis vallata Grube, 1858: 159-160.
Nereilepas brevicirris Grube, 1867: 19, pl.2 fig.2.
Perinereis vallata.–Hartman, 1954: 35
Perinereis nuntia vallata.–Knox & Cameron, 1971: 28.
Perinereis nuntia.–Hutchings & Turvey, 1982: 139-140.–Hartmann-Schröder, 1984: 29.–Hartmann-Schröder, 1985: 76.–Hartmann-Schröder, 1986: 50.–Hartmann-Schröder, 1987: 48-49 (not Savigny, 1818).
Perinereis sp. B Wilson, 1993: 248, fig.7B.

Material examined. AUSTRALIA: WESTERN AUSTRALIA: Quaramup Jetty, Princess Royal Harbour, south of Albany, WAM 41-87, 1 specimen. SOUTH AUSTRALIA: Spencer Gulf: Corny Point, under rocks, coll. W. Zeidler, 12 Oct. 1974, SAMA E1632, 4 specimens; Blythe Island, intertidal in gravel under rocks, coll. S. Parker, 29 Jan. 1986, SAMA E1633, 7 specimens; Reevesby Island, intertidal in gravelly sand under rocks, coll. S. Parker, 23 Jan. 1985, SAMA E1634, 14 specimens. Gulf St Vincent, outer harbour mudflats and mangroves, coll. L. Duncan, 11 Apr. 1975, SAMA E1635, 1 specimen. Onkaparinga estuary, coll. G. Petersen, 1973, SAMA E1636, 7 specimens. Port Willunga Reef, coll. R.L. Jentz, 22 Sept. 1968, NMV F53997, 8 specimens. VICTORIA: Apollo Bay breakwater, intertidal under rocks, coll. R.S. Wilson, 2 Nov. 1984, NMV F53972, 21 specimens; Separation Creek, intertidal under rocks, coll. R.S. Wilson, 28 Oct. 1985, NMV F53983, 20 specimens; Port Phillip Bay, Werribee, Murtcaim main drain, intertidal in coarse shell, coll. R.S. Wilson, 18 Sept. 1985, NMV F53998, 19 specimens; Western Port, Flinders, south end of Kennon Cove, intertidal under rocks in muddy sand, coll. R.S. Wilson, 3 Sept. 1984, 21 specimens (part of material of Wilson, 1993). TASMANIA: Stanley, Godfrey Beach, on rocks, coll. B.J. Smith, 30 Nov. 1968, NMV F53999, 4 specimens; Bicheno, coll. B.J. Smith, 22 Nov. 1968, NMV F54000, 9 specimens; Coles Bay, intertidal cobble, Stn TAS 13, coll. R.S. Wilson, 21 Apr. 1985, NMV F54001, 2 specimens; Flinders Island, Franklin Sound, coll. Essendon Grammar, 25 Nov. 1922, NMV F54002, 6 specimens; Flinders Island, Petrefaction Bay, under rocks in sandy mud, coll. T. Cochrane, 16 May 1986, NMV F54003, 1 specimen. NEW SOUTH WALES: Quarantine Bay, intertidal in sand under rocks, coll. R.S. Wilson, 17 July 1987, NMV F54005, 2 specimens; Botany Bay, 1910, AM W181, 15 specimens.

MACQUARIE ISLAND: NMV F54004, 1 specimen.

NEW ZEALAND: Auckland, 1924/6? [label unclear], MNHN unregistered, 12 specimens in 2 vials; Wellington, coll. M. Filhol, "No. 28", 1875, MNHN A97, 9 specimens.

ST PAUL ISLAND: coll. A.E. Grube, ZMB Q3463, 1 SYNTYPE *Nereilepas brevicirris*.

CHILE: Valparaiso, coll. Krøyer, ZMK unregistered, 5 SYNTYPES *Nereis vallata*. Ancud, coll. C. Rebolledo, Dec. 1984, NR, 11 specimens.

Description (based on 5 syntypes of *Nereis vallata* Grube, 1858). Size range 54 setigers (anterior fragment), 42 mm long, 2.7(4.1) mm wide to 126 setigers (anterior fragment), 115 mm long, 4.0(6.0) mm long (jaw length not recorded). Pigmentation a single transverse dark band dorsally on each segment on the anterior half of the body. Eyes black. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 3-7 setigers. Jaws dark, with no teeth (possibly worn). Paragnaths: I = 2; II = 6-18; III = 18-32 (distinct lateral groups present); IV = 26-40 cones, 0-3 bars (bars absent on one side in one specimen); V = 0-2; VI = 12-16 bars; VII-VIII = 62-89 large cones in 2-3 rows. (Paragnath count statistics for all material examined are provided in Table 4.) Anal cirri as long as posteriormost 4-9 setigers.

Notopodia with 2 triangular lobes, of similar length and unchanged proportions on posterior setigers. Digitiform presetal notopodial lobe present on setigers 5-25. Dorsal cirri basally inserted, equal in length to notopodial lobes anteriorly, slightly longer than notopodial lobes from about setiger 50. Neuropodia anteriorly with 2 rounded lobes of similar length, dorsal lobe bifid. Ventral neuropodial lobe becoming more acute and shorter than dorsal lobe from about setiger 10.

Dorsal neuropodial lobe not noticeably bifid posterior to about setiger 50. Ventral cirri equal in length to neuropodial lobes anteriorly, becoming relatively shorter from about setigers 10-20. Neuropodial heterogomph spinigers present throughout.

Remarks. *Perinereis vallata* is the most common species in the *P. nuntia* species group in southern Australia and Chile, however, similar species also occur in both areas and most published records need to be re-examined. Nevertheless, it is likely that most of the records of *P. nuntia brevicirris* and *P. nuntia vallata* in Day & Hutchings (1979) refer to *Perinereis vallata*. The variability in paragnath counts and parapodial form between *P. vallata* from Australia, New Zealand and Chile is no greater than that observed by Wilson (1993) among populations in south-eastern Australia.

Distribution. Southern Australia from Albany, WA to Botany Bay, NSW, Macquarie Island, New Zealand, St Paul Island and Chile.

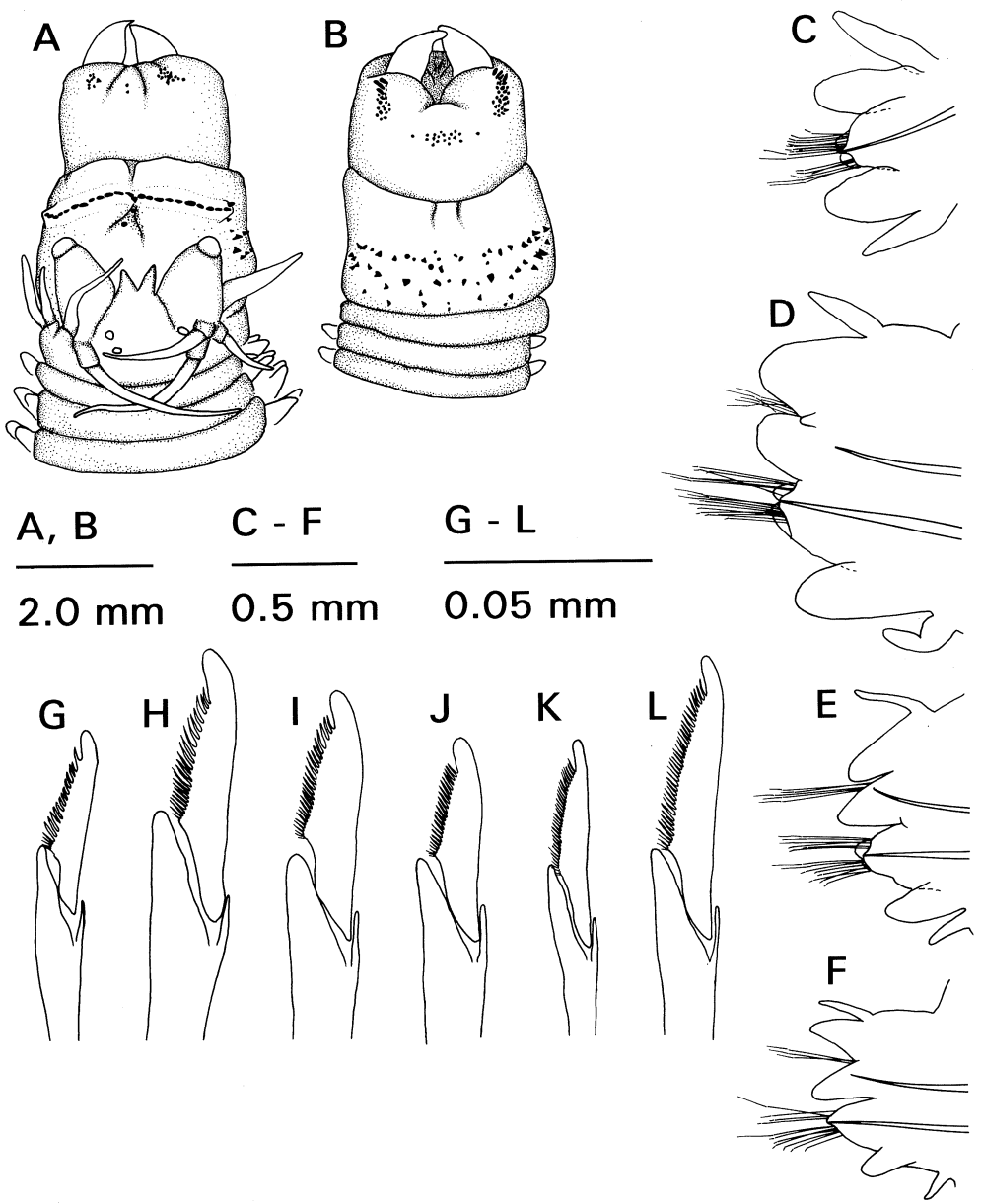

Fig.12. *Perinereis vallata* (Grube, 1857). Victoria, Apollo Bay breakwater, 30 Oct. 1985, NMV F53971: A – extended proboscis, dorsal view; B – extended proboscis, ventral view; C – setiger 1 parapodia, anterior view; D – setiger 10 parapodia, anterior view; E – setiger 50 parapodia, anterior view; F – setiger 110 parapodia, anterior view; G – heterogomph falciger, dorsal neuropodial fascicle, setiger 1; H – heterogomph falciger, dorsal neuropodial fascicle, setiger 10; I – heterogomph falciger, dorsal neuropodial fascicle, setiger 44; J – heterogomph falciger, dorsal neuropodial fascicle, setiger 110; K – heterogomph falciger, ventral neuropodial fascicle, setiger 1; L – heterogomph falciger, ventral neuropodial fascicle, setiger 10.

Perinereis sp. 1 [Juan Fernandez]

Nereis vallata.–Ehlers, 1901: 110-112 (in part, material from Juan Fernandez Islands; not Grube, 1857).

Material examined. Juan Fernandez Islands, coll. Plate, 20 fathoms, ZMB 3728 (material of Ehlers, 1901).

Description. One specimen, 102 setigers (incomplete posteriorly), length not recorded, width 2.6(5.2) mm, jaw length 2.3 mm. Pigmentation absent. Length of prostomium equal to width. Antennae half as long as prostomium. Tentacular cirri extend back 7 setigers. Jaws dark brown, teeth worn. Paragnaths: I = 2; II = 4, 9; III = 24 (distinct lateral groups present); IV = 24, 20 cones, bars absent; V = 2; VI = 11, 14 bars; VII-VIII = 68 large cones in 2-3 rows. Anal cirri lost. Neuropodial heterogomph spinigers present from setiger 3.

Remarks. This specimen is similar to *P. namibia* from South Africa and is within the range of variation for paragnath counts recorded for that species, however we are unwilling to extend the range of *P. namibia* to this disjunct locality on the basis of a single specimen. More material from the Juan Fernandez Islands is required for identification of this species.

Distribution. Juan Fernandez Islands, South Pacific.

Perinereis sp. 2 [Indonesia]

Material examined. INDONESIA: Stn 115, Siboga Expedition, ZMA V.Pol 2352, 1 specimen.

Description. A single specimen in poor condition, 217 setigers (entire), length cannot be determined, width 3.5(5.5) mm, jaw length 3.6 mm. Pigmentation absent. Eyes faded. Length of prostomium equal to width. Antennae one-quarter as long as prostomium. Tentacular cirri extend back 4 setigers. Jaws dark brown, with 6-8 teeth. Paragnaths: I = 2; II = 10, 11; III = 34 (distinct lateral groups present); IV = 32, 33 cones, 3, 2 bars; V = 1; VI = 4, 4 high bars, of uneven length; VII-VIII = 51 large cones in 2 rows. Anal cirri as long as posteriormost 8 setigers. Neuropodial heterogomph spinigers present throughout.

Remarks. This specimen differs from other species of *Perinereis nuntia* in having only four high bars of

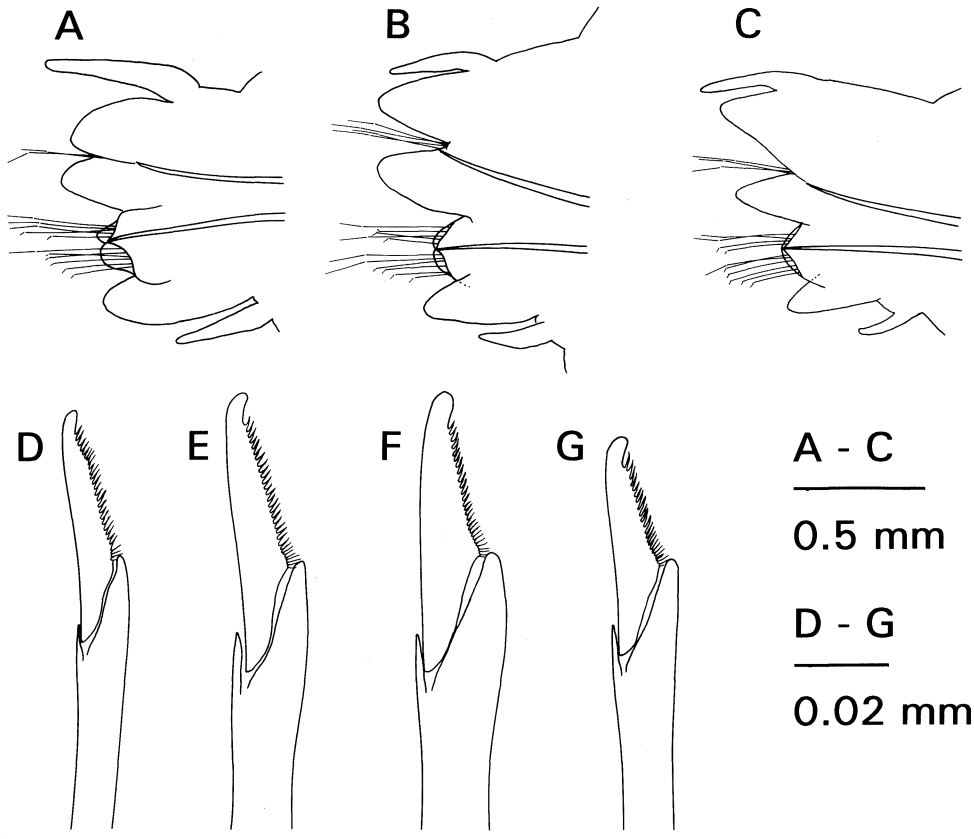

Fig.13. *Perinereis vallata* (Grube, 1857). Chile: Valparaiso, coll. Krøyer, ZMK unregistered, one of five syntypes (142 setiger specimen): A – setiger 3 parapodium, anterior view; B – setiger 40 parapodium, anterior view; C – setiger 130 parapodium, anterior view; D – heterogomph falciger, ventral fascicle, setiger 1; E – heterogomph falciger, ventral fascicle, setiger 40; F – heterogomph falciger, dorsal fascicle, setiger 40; G – heterogomph falciger, ventral fascicle, setiger 130.

uneven length on VI and may represent an undescribed species. However, we prefer not to base a formal description on a single poor specimen. The specimen is labelled *Nereis vallata*, but Horst (1924) did not report that species from the Siboga material. The only *Perinereis* species reported from Stn 115 in Horst's account is *P. singaporiensis*; Horst had four specimens and provided paragnath counts for a single specimen which differ from those for the specimen we have examined. Nevertheless, it is possible that this specimen is part of Horst's original material of *P. singaporiensis*. (*Perinereis singaporiensis* is described in Hutchings *et al.* (1991) and does not belong in the *P. nuntia* complex.)

Distribution. Indonesia.

Discussion

Paragnath shape and number are crucial taxonomic characters in the *Perinereis nuntia* species group. Even poorly preserved or incomplete specimens can usually be identified to species on the basis of paragnath counts, since the retracted proboscis is less likely to be damaged than parapodia and setae. More importantly, intra- and inter-specific variation in paragnath counts is now well understood and most specimens should be identifiable. New qualitative paragnath characters that are taxonomically useful are presence of bars on Area IV, and presence of additional bands of minute paragnaths on Areas VII-VIII.

Previous authors have described taxa partly on the basis of presence of one as against three cones in a triangle in Area V. However, virtually all species may possess one to three paragnaths on Area V, and this arrangement is taxonomically uninformative. The only exception is *Perinereis rhombodonta*, in which Area V always has one paragnath.

Length of the longest pair of tentacular cirri is routinely provided in descriptions but varies considerably within populations. Length of tentacular cirri is usually measured by the number of setigers over which the longest cirrus extends. Since the contraction of the body segments of the worm and of the tentacular cirri are dependent in part on preservation technique, cirrus length is only taxonomically useful where species differ markedly in this characteristic. Among the species described here, most have longest tentacular cirri in the range three to eight setigers long, with only *P. nuntia* (tentacular cirri 6-14 setigers) and *P. rhombodonta* (tentacular cirri 10-11 setigers) being distinct in this respect.

The form of the jaws and their serration are poor taxonomic characters in most species. The jaws are frequently worn to the extent that any serration on the cutting edge is lost. *Perinereis akuna*, *P. maindroni* and *P. rhombodonta*, however, have relatively thin translucent jaws. In all other species the jaws are thick and opaque.

In many genera of nereidids (eg, *Neanthes*) the shape of the parapodia, and the number of parapodial lobes are useful taxonomic characters (Wilson, 1984). Among those species of *Perinereis* treated elsewhere by Hutchings *et al.* (1991) some are readily distinguished by greatly elongated dorsal parapodial lobes of posterior segments. Parapodia in the *Perinereis nuntia* species group, however, are relatively uniform. *Perinereis caeruleis* has expanded (though not elongate) dorsal notopodial lobes on posterior setigers. *Perinereis maindroni* is unique in having three notopodial lobes, with the dorsal lobe narrow and prolonged on median setigers. All other species figured here have very similar parapodia. Ben-Eliahu (1987) suggested an approach to morphometric descriptions of nereidid parapodia. Although a quantitative method for analysis of parapodial form may provide useful data, we lacked facilities to automate Ben-Eliahu's laborious method and relied instead on traditional qualitative comparisons.

Setae, especially falcigers, are usually figured in descriptions of species of *Perinereis*, even though these structures are rarely useful in distinguishing species. Among the species described here, only *Perinereis caeruleis* has distinctive falcigers. The form of the falcigers varies little along the body in *Perinereis nuntia* group species, although falcigers from dorsal fascicles usually have slightly broader blades than those from ventral fascicles.

Artificial Key to Species of the *Perinereis nuntia* Group

This key excludes two species for which we were unable to examine material and which are insufficiently characterised by existing published descriptions: *Perinereis gualpensis* Jeldes, 1963, *P. mictodonta* (Marenzeller, 1879). *Perinereis* sp. 1 [Juan Fernandez] and *Perinereis* sp. 2 [Indonesia], each of which were represented in this study by a single specimen, appear in the key with species from which they cannot presently be differentiated.

1. Anterior 20 notopodia with 3 lobes of similar size ..... *P. maindroni*

—— All notopodia with 2 lobes 2

2. Paragnaths absent from Area II and usually from Area I; an additional arc of cones posterior to the arc of bars on Area VI ..... *P. caeruleis*

—— Paragnaths present on I and II; only a single arc of bars or mixed bars and cones on Area VI 3

3. Paragnaths absent from Area VII-VIII ..... *P. matthaii*

—— Paragnaths present on Area VII-VIII 4

4. Area IV with 3 or more smooth parallel bar-shaped paragnaths in addition to cones 5

—— Area IV with cones only 7

5. Areas VII-VIII with a band of normal conical paragnaths and a distinct posterior band of minute conical paragnaths ..... *P. akuna*

—— Areas VII-VIII without an additional posterior band of minute paragnaths 6

6. Area IV with more than 10 smooth parallel bars; Area III with about 40 cones ..... *P. majungaensis*

—— Area IV with 5 smooth bars at most; Area III with fewer than 35 cones ..... *P. vallata* (& *Perinereis* sp. 2 [Indonesia])

7. Areas VII-VIII with a band of normal conical paragnaths and a distinct anterior band of minute conical paragnaths ..... *P. rhombodonta*

—— Areas VII-VIII without an additional anterior band of minute paragnaths 8

8. Area VI with 3-4 bar-shaped paragnaths ..... *P. ponuiensis*

—— Area VI with 4-17 bar-shaped paragnaths (usually 6 or more) 9

9. Area VII-VIII with 43-76 paragnaths; heterogomph spinigers present in the neuropodia of all setigers ..... *P. namibia* (& *Perinereis* sp. 1 [Juan Fernandez])

—— Area VII-VIII with 10-40 paragnaths (rarely up to 50); heterogomph spinigers frequently absent from a variable number of anterior setigers ..... *P. nuntia*

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APPENDIX

Table 1. Available names, *Perinereis nuntia* species group.

Original combination	Author, year	Type locality
Nereis (Perinereis) binongkae	Horst, 1924	Indonesia
Nereilepas brevicirris	Grube, 1867	St Paul Island
Perinereis broomensis	Hartmann-Schröder, 1979	Western Australia
Heteronereis caeruleis	Hoagland, 1920	Philipines
Perinereis nuntia djiboutiensis	Fauvel, 1919	Gulf of Aden
Perinereis gualpensis	Jeldes, 1963	Chile
Perinereis heterodonta	Gravier, 1899	Red Sea
Perinereis maindroni	Fauvel, 1943	France
Perinereis nuntia majungaensis	Fauvel, 1921	Madagascar
Perinereis matthaii	Aziz, 1938	Karachi, India
Nereis mictodonta	Marenzeller, 1879	Japan
Nereis (Perinereis) heterodonta mictodontoides	Augener, 1913	Western Australia
Perinereis neocaledonica	Pruvot, 1930	New Caledonia
Lycoris nuntia	Savigny, 1818	Gulf of Suez
Nereis (Perinereis) ponuiensis	Augener, 1924	New Zealand
Nereis (Lycoris) quatrefagesi	Grube, 1878	Philipines
Perinereis rhombodonta	Wu Baoling, Sun Ruiping & D.J. Yang, 1985	China
Nereis (Perinereis) rumphii	Horst, 1919	Indonesia
Nereis vallata	Grube, 1857	Chile
Perinereis weijhouensis	Wu Baoling, Sun Ruiping & D.J. Yang, 1985	China

(*Perinereis nuntia bombayensis* Bhatt & Bal, 1966 (described from India) according to the original description, has only conical paragnaths in an arc on Area VI and therefore must be placed in the genus *Neanthes* Kinberg, 1866.)

Table 2. Canonical loadings (correlations between conditional dependent variables and dependent canonical factors), *Perinereis nuntia*-group samples, material lacking bars on Area IV. Factors 1-3 cumulatively account for 92.3% of the total variation.

	Factor(1)	Factor(2)	Factor(3)
I	0.086	0.410	-0.367
IIL	0.119	0.258	0.028
IIR	0.111	0.314	-0.129
III	-0.253	0.234	-0.327
IVLC	-0.247	0.405	-0.350
IVRC	-0.206	0.362	0.085
V	0.352	0.748	0.195
VIL	-0.214	-0.152	-0.198
VIR	-0.214	-0.169	-0.273
VII-VIII	-0.856	0.479	0.074

Table 3. Canonical loadings (correlations between conditional dependent variables and dependent canonical factors), *Perinereis nuntia*-group samples, material with bars on Area IV. Factors 1-3 cumulatively account for 98.2% of the total variation.

	Factor(1)	Factor(2)	Factor(3)
I	-0.007	0.106	0.090
IIL	0.342	-0.102	0.076
IIR	0.386	-0.255	0.124
III	-0.583	0.254	0.285
IVLC	-0.419	-0.231	-0.104
IVLB	0.066	0.029	0.098
IVRC	-0.406	-0.159	-0.088
IVRB	0.172	0.017	-0.028
V	0.177	0.673	-0.021
VIL	-0.190	0.308	-0.726
VIR	-0.243	0.154	-0.753
VII-VIII	-0.031	0.302	-0.139

Table 4. Descriptive statistics, paragnath counts, *Perinereis nuntia*-group.

	I	II	III	IVC	IVB	V	VI	VII-VIII
akuna (n = 27)								
mean±sd	2.4±0.8	14.8±3.6	18.4±3.7	24.9±6.4	2.9±0.9	2.6±1.1	7.5±1.1	116.0±30.4
min-max	1-4	6-21	13-27	11-41	1-5	1-4	5-11	76-191
caeruleis (n = 3)*								
mean	0.7	–	150	100	–	43	13	210
min-max	0-2	–	110-185	85-110	–	39-48	12-15	200-250
namibia (n = 43)								
mean±sd	1.7±0.7	5.5±3.0	16.6±4.0	22.7±5.4	–	0.8±0.6	10.4±1.3	56.4±8.0
min-max	0-4	0-20	10-26	5-39	–	0-3	5-14	43-76
nuntia (n = 132)								
mean±sd	1.8±0.8	6.8±3.0	11.5±4.2	16.5±4.6	–	1.9±1.4	8.2±2.5	28.0±6.2
min-max	0-5	0-23	1-30	5-35	–	0-5	4-17	10-52
ponuiensis (n = 2)								
mean±sd	1.5±0.7	7.5±2.8	8.5±0.7	18.3±7.4	–	1.5±0.7	3.7±0.4	26.5±0.7
min-max	1-2	5-10	8-9	12-25	–	1-2	3-4	26-27
rhombodonta (n = 14)								
mean±sd	4.3±1.3	44.9±10.0	93.6±31.4	84.2±23.8	–	1.1±0.5	11.3±1.5	113.4±36.0
min-max	2-6	29-64	40-142	45-131	–	1-3	9-14	55-165
vallata (n = 427)								
mean±sd	1.6±0.7	11.0±2.5	18.7±4.4	28.1±5.7	2.6±0.6	2.3±1.0	12.5±1.5	69.0±13.6
min-max	0-9	1-23	9-35	0-47	0-5	0-5	5-14	42-129

* Specimens of *P. caeruleis* have paragnaths that are too small, closely spaced and numerous to be counted accurately on dissected specimens.