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The Namanereidinae (Polychaeta: Nereididae). Part 1, Taxonomy and Phylogeny

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ABSTRACT. A cladistic analysis and taxonomic revision of the Namanereidinae (Nereididae: Polychaeta) is presented. The cladistic analysis utilising 39 morphological characters (76 apomorphic states) yielded 10,000 minimal-length trees and a highly unresolved Strict Consensus tree. However, monophyly of the Namanereidinae is supported and two clades are identified: *Namalycastis* containing 18 species and *Namanereis* containing 15 species. The monospecific genus *Lycastoides*, represented by *L. alticola* Johnson, is too poorly known to be included in the analysis. Classification of the subfamily is modified to reflect the phylogeny. Thus, *Namalycastis* includes large-bodied species having four pairs of tentacular cirri; autapomorphies include the presence of short, subconical antennae and enlarged, flattened and leaf-like posterior cirrophores. *Namanereis* includes smaller-bodied species having three or four pairs of tentacular cirri; autapomorphies include the absence of dorsal cirrophores, absence of notosetae and a tripartite pygidium. *Cryptonereis* Gibbs, *Lycastella* Feuerborn, *Lycastilla* Solís-Weiss & Espinasa and *Lycastopsis* Augener become junior synonyms of *Namanereis*.

Thirty-six species are described, including seven new species of *Namalycastis* (*N. arista* n.sp., *N. borealis* n.sp., *N. elobeyensis* n.sp., *N. intermedia* n.sp., *N. macroplatis* n.sp., *N. multiseta* n.sp., *N. nicoleae* n.sp.), four new species of *Namanereis* (*N. minuta* n.sp., *N. serratis* n.sp., *N. stocki* n.sp., *N. sublittoralis* n.sp.), and three widespread species groups (*Namalycastis abiuma*, *Namanereis littoralis*, *N. quadraticeps*). Fourteen species are newly placed into synonymy, *Lycastis maxillo-falciformis* Harms, *L. maxillo-ovata* Harms, *L. maxillo-robusta* Harms, *Lycastis meraukensis* Horst, *L. nipae* Pflugfelder, *L. ouanaryensis* Gravier, *L. ranauensis* Feuerborn, *L. vivax* Pflugfelder, *Lycastopsis augeneri* Okuda, *L. tecolutlensis* Rioja, *Namalycastis rigida* Pillai, *N. tachinensis* Rosenfeldt, *N. vuwaensis* Ryan, and *Namanereis littoralis* Hutchings & Turvey. A neotype is designated for *Namalycastis hawaiiensis* (Johnson), and lectotypes are designated for *Namalycastis geayi* (Gravier), *N. senegalensis* (Saint-Joseph), *N. terrestris* (Pflugfelder), *Namanereis amboinensis* (Pflugfelder) and *N. littoralis* (Grube). Keys to genera and species are given.

Namanereidinae are generally confined to the tropics and subtropics. Maximum species-diversity occurs in the Caribbean and Indo-Pacific, in particular in coastal areas subjected to recent uplifting, where both littoral-zone and freshwater (riparian and subterranean) forms occur. Phylogenetic results indicate that in both *Namalycastis* and *Namanereis* there is a preference for freshwater habitats among species with apomorphic traits (corollary being that marine habitats are favoured by the plesiomorphic members). This suggests that the ancestor of the Namanereidinae was a euryhaline coastal species.

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Introduction

The Namanereidinae are one of the most successful groups of polychaetes in fresh and brackish waters (Wesenberg-Lund, 1958). Many species show a particular preference for littoral and supralittoral areas in association with decaying vegetation including mangroves, the strand zone on beaches and inland waters such as riverbanks and sinkholes (subterranean waters). Some species can tolerate highly polluted waters. For example, high densities of several *Namalycastis* species have been found in the organically-rich riverine and estuarine sediments throughout the Indo-Pacific (Kalaiselvi & Ayyakkannu, 1986; Jaweir, 1987), and *N. littoralis* occurs in the intertidal areas of the Ria de Bilbao, Spain, which are subject to considerable industrial pollution (Gibbs & Saiz Salinas, 1996). Further, namanereidine species have been the subject of toxicity studies involving hydrocarbons and bioaccumulation of heavy metals (Jaweir & Habash, 1987; Varshney & Abidi, 1988; Athalye & Gokhale, 1991).

The ability to inhabit low salinity and/or semi-terrestrial environments, not normally tolerated by other polychaetes, has meant that the Namanereidinae have had to acquire a range of specialised physiological, morphological and reproductive adaptations. These include modifications to the eye, integument and epidermis to prevent desiccation (Sadasivan Tampi, 1949; Storch & Welsch, 1972a,b), modification to the nephridia to get rid of excess water (Krishnan, 1952; Florence Mary, 1966), the production of large yolky eggs and an apparent tendency towards hermaphroditism (or parthenogenesis), which has been reported in four species (Johnson, 1908; Feuerborn, 1931a; Gopala Aiyar, 1935; Runganadhan, 1943; Glasby *et al*., 1990). In some species the presence of segmental gill hearts and a rich supply of capillaries in posterior segments, especially in the leaf-like dorsal cirri, presumably enables a more efficient uptake of oxygen in low oxygen tension environments (Feuerborn, 1931a). Further, by waving the posterior end in the water current some species may further enhance oxygen uptake (Rasmussen, 1994). Unfortunately knowledge of these adaptive features is available only for a few species and taxonomically useful characters cannot be easily derived at present.

Despite being reasonably well known from a biological point of view, the Namanereidinae are poorly known in terms of their taxonomy, phylogeny and biogeography (the latter is addressed more fully in Part 2 of this issue). Apart from a brief review of the group by Hartman (1959a), the Namanereidinae have never been the subject of a rigorous taxonomic revision, despite being recognised as a distinct subgroup of the Nereididae for over 150 years. Hartman re-diagnosed the subfamily on the basis of the lack of pharyngeal papillae and paragnaths, lack of notopodial lobes, reduced numbers of notosetae, and the presence of three or four pairs of tentacular cirri. More recently the monophyly of the group was established, delineated either by the absence of “dorsal cirri ceratophores” (cirrophores, more correctly), or by the “reduced notopodia” (Fitzhugh, 1987). Glasby (1991) proposed two additional synapomorphies of the group, the presence of spherical palpostyles and the ventral position of the notoacicula (= dorsal acicula) within the parapodia. Characterisation of the parapodia in this way is preferred since “reduced notopodia” also occur in other nereidoid families, such as Hesionidae. Both cladistic studies place the Namanereidinae as one of the oldest lineages of the nereid clade (i.e. derived from a phyllodociform ancestor), supporting the views of Saint-Joseph (1900) and Gravier (1902b). By contrast, a number of authors held the view that Namanereidinae evolved from a nereid ancestor, presumably by a series of reductions and losses (Southern, 1921; Banse, 1977b; Feuerborn, 1931a; Corrêa, 1948).

As a result of the revision by Hartman (1959a), the Namanereidinae were considered to consist of two species-rich genera, *Namalycastis* Hartman, 1959a and *Namanereis* Chamberlin, 1919, the poorly-known genus *Lycastoides* Johnson, 1903 and a doubtful genus (not named) represented by “*Lycastis*” *geayi*. All species in *Lycastopsis* Augener, 1922 were transferred to *Namanereis*. Since then an additional two genera have been described, both monospecific: *Cryptonereis* Gibbs, 1971 and *Lycastilla* Solís-Weiss & Luis Espinasa, 1991. All of the above genera were established for species which, at the time, it appears were “decidedly different” from others (e.g., Chamberlin, 1919; Gibbs, 1971). Characters traditionally used to distinguish the genera included: body size, the number of pairs of tentacular cirri (3 or 4), and the relative size of the dorsal cirri along the body (increasing in size posteriorly or equal in size throughout). In addition, *Lycastoides* was diagnosed on the basis of an anteriorly bilobed prostomium in which the lobes were produced to form antennae, *Lycastilla* on the basis of “articulate” antennae and cirri and a distally recurved notoacicula, and *Cryptonereis* lack prostomial antennae and have capillary setae at maturity. These genera were thus described without consideration of whether the diagnostic features were plesiomorphic (in which case they are inappropriate to delineate the genus) or apomorphic. From the phylogenetic point of view, which is adopted here, only apomorphic characters delineate monophyletic groups and the taxonomy of the group should reflect phylogeny.

Historical review

The name “Namanereinae” [sic] was first proposed by Hartman (1959a) for the group of nereids lacking pharyngeal armature and having reduced parapodial lobes. The improperly formed subfamily name continued to be used by Hartman (1965), Winterbourn (1969) and Gibbs (1971). The correctly formed name, Namanereidinae, appears to have been first used by Banse (1977a: 117) and subsequently by B.-L. Wu *et al*. (1985) and Fitzhugh (1987) in their subfamily diagnoses, probably in recognition of Pettibone’s (1971) emendation of the family name from Nereidae to Nereididae. The subfamily name is formed by adding the latinised suffix “-inae” to the stem of the type genus *Namanereis*, in this case, “Namanereid-”. The stem, for the purposes of the Code, is found by deleting the case ending “-is” of the genitive singular, Namanereidis.

Prior to Hartman (1959a) this group of polychaetes was referred to variously as Lycastidae (e.g., Schmidt, 1935), Lycastinae Corrêa, 1948, and informally as lycastiden or lycastids (e.g., Feuerborn, 1931a) based on the genus *Lycastis* Savigny, 1822. The generic name *Lycastis* was well entrenched in the systematic literature up until 1959, although the earliest references to *Lycastis* species were not Namanereidinae. These included several species described by Chiaje (1828, 1841) and illustrated by him in 1822. The species described in the 1841 account (pp. 96–97) included *L. blainvillei*, *L. otto*, *L. ockenii*, *N. ranzani* and *N. edwardsii*. The last two species were placed in *Nereis* rather than *Lycastis*, but in grouping the species together Chiaje probably regarded them as members of *Lycastis*. Each species was described in four to five lines and the figures included a dorsal view of the whole animal and a transverse section showing the parapodia and dorsal cirri. As was customary at the time, no type material was preserved.

According to Hartman (1959b), *L. otto, L. ockenii* and *L. ranzani* are indeterminable, *L. edwardsii* belongs possibly in the Nephtyidae, and *L. blainvillei* is possibly a *Namanereis*. However, based on Chiaje's illustration, *L. blainvillei* is unlikely to be a *Namanereis sensu* Hartman or even belong to the Namanereidinae as it lacks dorsal cirri (or at least has very indistinct ones) on the first five setigerous segments, and has very prominent (leaf-like) dorsal cirri on the remaining parapodia, which are unlike those of *Namalycastis* species. The same species is also described by Audouin & Edwards (1833) as *Nereis blainvillii* [sic].

Other species described by Chiaje (1841) under *Lycastis* were *N. caudata*, *N. coccinea*, *N. quadricorna*, *N. tethycola*, *N. flexuosa*, *N. sextentaculata*, *N. delineata* and *N. ventilabrum*. None of these species appears to be referable Namanereidinae. *Nereis caudata* is a species belonging to the *Neanthes arenaceodentata* group, *N. coccinea* is a junior primary homonym of *Nereis coccinea* Renier (now *Lumbrinereis*), *N. tethycola* is indeterminable, *N. flexuosa* belongs to the hesionid genus *Ophiodromus*, *N. sextentaculata* questionably belongs to the Syllidae or Cirratulidae (Hartman, 1959b). Chiaje's species *N. quadricorna* and *N. delineata* and *N. ventilabrum* are not listed under Nereididae in the Hartman (1959b) catalogue.

Blainville (1828) also incorrectly listed two species under *Lycastis*: *Nereis armillaris* Müller (a Syllidae) and *N. incisa* Fabricius (a Nephtyidae). Castelnau (1840) described *armillaris* under *Lycastis*.

The first true namanereidine species discovered, *Lycastis brevicornis* was described by Audouin & Edwards (1833) based on a specimen collected on the Atlantic coast of France (Table 1). It has not been collected since—the record of Amoureux & Calvário (1981) from the Tagus estuary, Portugal, is most probably *Namanereis littoralis*. Since *L. brevicornis* was described, namanereidine species have been described sporadically, with an average of just under 2.5 species every ten years. Two periods in particular saw an upsurge in the number of species described (Table 1). The first period, which corresponded to French Expeditions to French Guiana (see Geay, 1901) and Senegal between 1900 and 1903, resulted in the description of three new species, *Lycastis geayi* Gravier, 1901, *L. senegalensis* Saint-Joseph, 1900 and *L. ouanaryensis* Gravier, 1901. Also during this period, Johnson (1903) described a new genus, *Lycastoides* and two new species, *Lycastoides alticola* and *Lycastis hawaiiensis*. The second period of discovery corresponded to the German Sunda Expeditions to Indonesia (1929–1934) and resulted in the description of a new genus, *Lycastopsis*, and six new species, *Lycastopsis amboinensis* Pflugfelder, 1933, *L. catarractarum* Feuerborn, 1931a, *Lycastis nipae* Pflugfelder, 1933, *Lycastis ranauensis* Feuerborn, 1931a, *Lycastis terrestris* Pflugfelder, 1933 and *Lycastis vivax* Pflugfelder, 1933. Also during this period *Lycastopsis hummelincki* Augener, 1933b and *Lycastis longicirris* Takahasi, 1933 were described.

Important early studies of the taxonomy of Namanereidinae included Gravier's (1902b) "Sur le genre *Lycastis*", in which the morphology and habitat of all species known at the time were described. Gravier indicated in a phylogenetic tree that *Lycastis* represented the ancestral nereid. Southern's (1921) description of *Lycastis indica* was remarkable for the detail in which he described the structure and distribution of the setae. His method of identifying and illustrating individual clusters of setae in the nereid parapodium was a significant advance in the technique used to distinguish nereid species. The only available description of a namanereidine larva is that of Feuerborn (1931a) who described a 3-setiger stage of *L. ranauensis*. It closely resembles the larvae of other nereids, particularly in having biramous parapodia.

Hartman (1959a) redescribed and renamed the subfamily as the nominal genus (*Lycastis*) was shown to be preoccupied (see Remarks under description of *Namalycastis*). Also, she described a new genus *Namalycastis* and synonymised *Lycastopsis* Augener, a genus containing mainly tropical species, with *Namanereis* Chamberlin, a monospecific genus largely restricted to the subantarctic. Some authors, for example Hartmann-Schröder (1973, 1977, 1980) and Hartmann-Schröder & Marinov (1977) followed this synonymy, whilst others like Pettibone (1963), Imajima (1972) and Orensanz (1982) maintained the traditional view and continued to recognise *Lycastopsis*. At the species level, Hartman (1959a) promoted the view that there was very little distinction between members of either genus, suggesting (in the extreme case) that all previously described species could be assigned either to the type species of *Namanereis* (*N. quadraticeps*), or to a single species resembling the type of *Namalycastis* (*Lycastis abiuma*). Only *Lycastopsis hummelincki* was regarded as sufficiently distinct to warrant a brief diagnosis and recognition as a second species of *Namanereis*. By contrast, earlier workers like Pflugfelder (1933) and Harms (1948) adopted a typological approach and described new species often on the basis of very small morphological differences. Harms (1948) for example put considerable emphasis on minute differences in the shape of the jaws to distinguish three species of *Lycastis* (now *Namalycastis*): *L. maxillo-falciformis*, *L. maxillo-ovata* and *L. maxillo-robusta*, all of which are considered herein to be junior synonyms of *Namalycastis terrestris* Pflugfelder, 1933.

In the present study, species represent the smallest taxonomic unit in the systematic hierarchy (subspecies are not recognised) that can be delineated by a unique character or combination of characters. Populations not able to be characterised by any unique attributes are not given

Table 1. Nominal namanereidine taxa, including new species described here, arranged chronologically by year of description. Availability and whereabouts of the type specimens is indicated for each species. See text under “Terminologies, definitions and abbreviations” for explanation of institutional abbreviations; spp.gp. = species group.

year	nominal species and subspecies	binomial used here/senior synonym	types, availability and repositories
1833	*Lycastis brevicornis* Audouin & Edwards	*Namalycastis brevicornis*	holotype? (MNHN)
1849	*Lycastis quadraticeps* Blanchard in Gay	*Namanereis quadraticeps* spp.gp.	neotype (AM)
1872	*Lycastis pontica* Bobretzky	*Namanereis pontica*	perhaps lost
1872	*Lycastis littoralis* Grube	*Namanereis littoralis* spp.gp.	lectotype (ZMB), paralectotypes (ZMB, MPW)
1872	*Lycastis abiuma* Grube	*Namalycastis abiuma* spp.gp.	holotype (ZMB)
1900	*Lycastis senegalensis* St-Joseph	*Namalycastis senegalensis*	lectotypes & paralectotypes (MNHN)
1901	*Lycastis geayi* Gravier	*Namalycastis geayi*	lectotypes & paralectotype (MNHN)
1901	*Lycastis ouanaryensis* Gravier	syn. *Namalycastis senegalensis*	paratypes (MNHN)
1903	*Lycastoides alticola* Johnson	*Lycastoides alticola*	lost
1903	*Lycastis hawaiiensis* Johnson	*Namalycastis hawaiiensis*	neotype (AM)
1918	*Lycastis meraukensis* Horst	syn. *Namalycastis abiuma* spp.gp.	syntypes (RNHL)
1921	*Lycastis indica* Southern	*Namalycastis indica*	possibly lost
1922	*Lycastopsis beumeri* Augener	syn. *Namanereis littoralis* spp.gp.	syntypes (HZM)
1926	*Namanereis kartaboensis* Treadwell	*Namalycastis kartaboensis*	holotype (AMNH, dried)
1931	*Lycastopsis catarractarum* Feuerborn	*Namanereis catarractarum*	neotype (HZM)
1931	*Lycastis ranauensis* Feuerborn	syn. *Namalycastis hawaiiensis*	lost
1933	*Lycastis longicirris* Takahashi	*Namalycastis longicirris*	perhaps lost
1933	*Lycastis nipae* Pflugfelder	syn. *Namalycastis abiuma* spp.gp.	holotype & paratypes (PMJ)
1933	*Lycastis terrestris* Pflugfelder	*Namalycastis terrestris*	lectotype (PMJ)
1933	*Lycastis vivax* Pflugfelder	syn. *Namalycastis abiuma* spp.gp.	syntypes (PMJ)
1933	*Lycastopsis amboinensis* Pflugfelder	*Namanereis amboinensis*	lectotype & paralectotypes (PMJ)
1933b	*Lycastopsis hummelincki* Augener	*Namanereis hummelincki*	syntypes (HZM)
1937	*Lycastopsis augeneri* Okuda	syn. *Namanereis littoralis* spp.gp.	lost
1946	*Lycastopsis tecolutlensis* Rioja	syn. *Namanereis amboinensis*	lost
1948	*Lycastis ?maxillo-falciformis* Harms	syn. *Namalycastis terrestris*	possibly lost
1948	*Lycastis ?maxillo-ovata* Harms	syn. *Namalycastis terrestris*	possibly lost
1948	*Lycastis ?maxillo-robusta* Harms	syn. *Namalycastis terrestris*	possibly lost
1948	*Lycastis siolii* Corrêa	*Namalycastis siolii*	ZIB? (not seen)
1950	*Lycastoides pontica neapolitana* la Greca	syn. *Namanereis pontica*	possible types (SZN) (not seen)
1961	*Namalycastis meraukensis zeylanica* de Silva	syn. *Namalycastis abiuma* spp.gp.	syntypes (NMC)
1965	*Namalycastis profundis* Hartman	syn. *Profundilycastis profundus* (see Hartmann-Schröder, 1977b)	holotype (AHF)
1965	*Namalycastis rigida* Pillai	syn. *Namalycastis abiuma* spp.gp.	holotype (UPSL), paratypes (BMNH, UPSL)
1969	*Namalycastis tiriteae* Winterbourn	*Namanereis tiriteae*	holotype (NMNZ)
1971	*Cryptonereis malaitae* Gibbs	*Namanereis malaitae*	holotype & paratypes (BMNH)
1977	*Namanereis beroni* Hartmann-Schröder & Marinov	*Namanereis beroni*	holotype & paratypes (BAS) paratypes (HZM)
1980	*Namalycastis vuwaensis* Ryan	syn. *Namanereis tiriteae*	holotype? (AM)
1981	*Namalycastis fauveli* Nageswara Rao	no change	holotype & paratypes (ZSI) (not seen)
1982	*Namanereis littoralis* Hutchings & Turvey	syn. *Namanereis quadraticeps* spp.gp.	holotype & paratypes (AM)
1984	*Namalycastis tachinensis* Rosenfeldt	syn. *Namalycastis fauveli*	holotype & paratypes (HZM)
1990	*Lycastopsis riojai* Bastida-Zavala	*Namanereis riojai*	holotype & paratypes (USNM), paratypes (UABCS)
1991	*Lycastilla cavernicola* Solís-Weiss & Espinasa	*Namanereis cavernicola*	holotype (ICML) & paratypes (USNM, BMNH, AM, HZM)
present	*Namalycastis arista* n.sp.	no change	holotype & paratypes (BMNH)
present	*Namalycastis borealis* n.sp.	no change	holotype (USNM), paratypes (AHF, USNM, ZMUC)
present	*Namalycastis elobeyensis* n.sp.	no change	holotype & paratypes (HZM)
present	*Namalycastis intermedia* n.sp.	no change	holotype & paratypes (USNM)
present	*Namalycastis macroplatis* n.sp.	no change	holotype (HZM), paratypes (BMNH, HZM)
present	*Namalycastis multiseta* n.sp.	no change	holotype & paratypes (BMNH)
present	*Namalycastis nicoleae* n.sp.	no change	holotype (QM)
present	*Namanereis serratis* n.sp.	no change	holotype & paratypes (ZMA)
present	*Namanereis minuta* n.sp.	no change	holotype & paratypes (ZMA)
present	*Namanereis stocki* n.sp.	no change	holotype & paratypes (ZMA)
present	*Namanereis sublittoralis* n.sp.	no change	holotype & paratypes (ZMA)

binomial names; rather they are considered "metaspecies" (*sensu* Donoghue, 1985) and, under this concept, are potentially paraphyletic. In this study, related "metaspecies" are contained within species groups. The "species group" designation is an informal taxon recommended by Wiley (1981: 199). Thus species groups designate problem taxa in need of further study by, for example, genetic methods or studies of reproductive biology.

Materials and methods

Forty-one nominal species and subspecies of Namanereidinae were evaluated on the basis of preserved specimens and descriptions in the literature. The type specimens of 27 of the 41 nominal species were examined, although some doubt exists about the type status of the specimens of *Namalycastis brevicornis* (Audouin & Edwards) (see under Remarks for the species). The types of *Lycastis siolii* Corrêa, 1948 and *Namalycastis fauveli* Nageswara Rao, 1981, although probably in existence, were not available to loan; the types of the remaining species are most probably lost or destroyed (Table 1).

"Material examined" contains specimens for which character data were compiled using a comprehensive and standardised character list (Appendix). "Other material examined" contains specimens generally in poor condition, which could not be studied in the same detail. Descriptions are based primarily on adult specimens and the size range of material examined is given for each species. "Adult" females are defined as individuals possessing microscopically visible coelomic gametes; for most species adult females had more than 30 setigers. "Juvenile" specimens (those lacking coelomic gametes) are listed in the material examined, but were generally excluded from the descriptions; worms with fewer than about 20 setigers were rare.

Sexual maturity of each specimen was determined by making a small dorsolateral incision in the body wall to open the coelom. A sample of coelomic fluid was extracted and examined for gametes using a depression slide. The maximum diameters of ten oocytes was measured to determine the mean and standard deviation. Mature oocytes were identified by the presence of a thin outer envelope (see Schroeder & Hermans, 1975) and/or by their large size and small standard deviation (Olive, 1983). Presence of sperm was determined by examining coelomic fluid under the compound microscope (400 or 1,000 × magnification).

Descriptions are based on morphological, mainly external, characters. The Namanereidinae lack many of the traditionally-used taxonomic features found in other Nereididae (e.g., notopodial lobes and pharyngeal paragnaths), and in order to distinguish species it was necessary to use meristic and numerical characters. Hardened structures such as jaws and setae, which tend to be very durable even in poorly preserved specimens, provided a suite of useful characters. Routine systematic procedures involved the dissection of the pharynx, following the method of Fauchald (1977: 7) to reveal the jaws. Small jaws and those illustrated, were removed and examined in greater detail using a compound microscope then returned to the pharyngeal cavity after description. A parapodium from the left side (L.S.) or right side (R.S.) (based on a dorsal view of the worm) of setigers 3, 10, 60, 120, 180, 240 was removed and mounted for setal counts and measurements. Setal fascicles/rows were identified and the relative positions of setal clusters in relation to the acicular ligule recorded under the dissecting microscope by viewing the parapodium both on its side (anterior or posterior view; Fig. 1a) and distally (Fig. 1b,c). The origin of each setal cluster (fascicle or row) within the parapodium could be seen in slide preparations. Semi-permanent slides of parapodia for each species were made using Polyvinyl Lactophenol, and a nailpolish sealant; the slides form part of the author's personal collection, which will be deposited in the NIWA collection.

Measurements of head length and width, setae and oocytes were made using an ocular graticule. The articulation of compound setae was studied under transmitted light of a compound microscope, making transparent the socket at the distal end of the shaft. Elongation of the boss, or high-point of the socket, was estimated by the ratio L_b/L_c, where L_b is the length of the boss from the distal tip to the base of the hinge, and L_c is the length of the collar from the tip to the base of the hinge (Fig. 2).

Full synonymies are given for each species, including references to a species in checklists (indicated as "list only") and in the general biological literature. Synonymies at the generic level included only those references where a description of the genus was given. Habitat descriptions were compiled from the literature and from personal collecting records. Distributions were based on material examined and those published records for which I was reasonably sure of the species identity. Geographic co-ordinates were given for type material; for non-type material the place name as stated on the label was given. Geographic names and co-ordinates were checked against *The Times* "Atlas of the World" (1985, comprehensive edition, 7th edition, Times Books, London) and the GEOnet database (http://www.nima.mil). The etymology of specific and generic names was based primarily on Brown (1956).

Diagnoses, descriptions and keys (excluding the keys to the genera) were constructed using the DELTA system, Descriptive Language for Taxonomy, a standardised format for coding taxonomic descriptions (Dallwitz, 1980; Dallwitz & Paine, 1986; Partridge *et al.*, 1988; DELTA website http://www.biodiversity.uno.edu.delta). Generic descriptions were given in as much detail as possible so that characters states common to a group of species were not repeated at the lower (species) level. Apomorphic characters at the generic level appear in bold.

In the species descriptions, quantitative character state data for primary types (holotype, neotype, syntype, or lectotype) were presented first, followed by the state(s) for the other types and non-types. When primary types were unavailable, the state(s) for paratypes was given first, followed by those of non-type material. State values may be qualified by a comment on the relative frequency of occurrence of each state within a species, with "rare" indicating a frequency of between about 10–20%, and "very rare" for frequencies of less than about 10%.

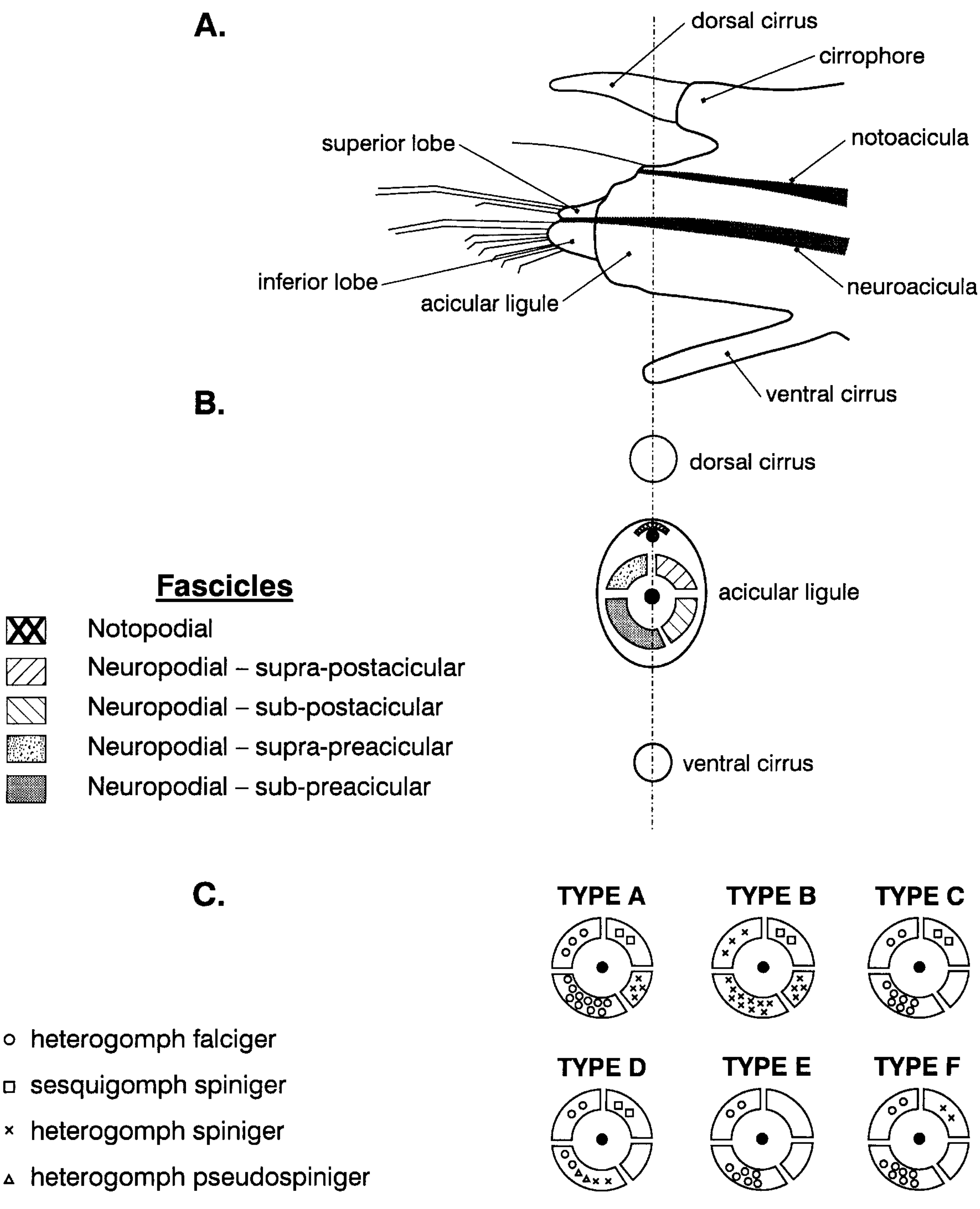

Figure 1. Namanereidine parapodium from an anterior segment showing parapodial and setal terminology used in the present study. (*A*) posterior view showing generalised form of parapodium and major features; (*B*) distal view showing position of each fascicle; (*C*) schematic representation of the neuropodium, viewed distally to show the six basic types setal arrangement. Types A–F referred to in each species diagnosis and in the character list (Appendix, characters 26–31).

Species keys are artificial and do not have any phylogenetic implications. They were constructed to minimise the number of decision-making steps. Trichotomies were permitted as they make the keys shorter (i.e. less decision-making steps). In order to facilitate identification, reliable characters, or those having state values that could be easily and accurately assigned to any specimen, generally appear early in the keys even if they do not always produce the best split of the taxa. Explanation of the mechanics of key construction is given in Dallwitz & Paine (1986).

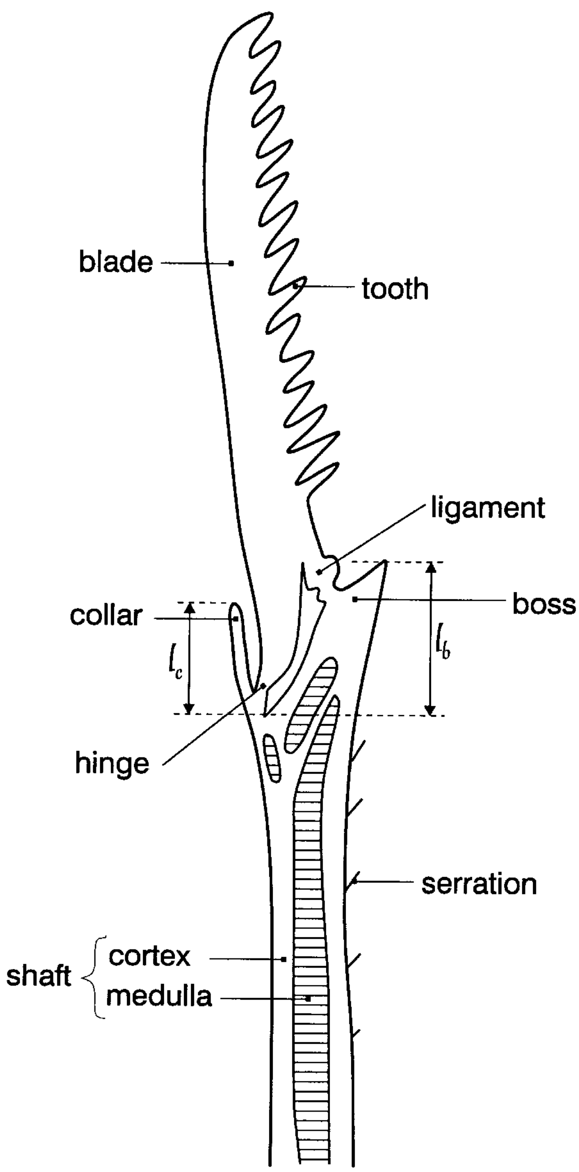

Figure 2. Heterogomph falciger showing terminology and measurements used in the present study. The length of the boss (l_b) and collar (l_c) for both heterogomph and sesquigomph setae is expressed as a ratio for each species (after Gustus & Cloney, 1973).

Terminology, definitions and abbreviations

Terms used are generally those in standard use in nereid and polychaete systematics (e.g., Day, 1967; Fauchald, 1977; Hutchings & Reid, 1990) (Fig. 1a). Setal ultrastructure terminology follows Gustus & Cloney (1973) (Fig. 2). The term sesquigomph *sensu* Perkins (rather than hemigomph *sensu* Fauchald) is used to describe the type of compound setae intermediate between homogomph and heterogomph types. Sesquigomph setae (Fig. 11g) are characteristic setae of the notopodial fascicle and the supra-postacicular fascicle of the neuropodia in the Namanereidinae (Fig. 1b,c). They have an asymmetrical articulation of the shaft, like heterogomph setae (Fig. 11e), however, it is far less pronounced; homogomph setae by contrast are more or less symmetrical. In transmitted light the articulation of the sesquigomph setae will appear as two tines, the longer about 1½ × the length of the shorter, hence the preference for the term "sesquigomph". Sesquigomph setae may be easily confused with homogomph types in transmitted light if care is not taken to view the setae laterally (i.e. with blade serrations visible).

Setae are arranged in single rows or bundles ("fascicles") and following Southern (1921) setal arrangement is considered to be of considerable taxonomic importance at both the species and generic level. When viewed from the tip, four distinct clusters of setae may be recognised in the neuropodia: a supra-postacicular fascicle, a supra-preacicular fascicle, a sub-postacicular fascicle and a sub-preacicular fascicle (Fig. 1b). The notosetae of the Namanereidinae, when present, emerge from the superior position relative to the dorsal acicula and are therefore considered homologous with setae in the supra-acicular fascicle of the notopodia in other Nereididae.

The terminologies used for parapodial lobes generally follow those of Hylleberg *et al*. (1986) and Hutchings & Reid (1990), except that the superior notopodial lobe (present in members of the outgroup) is referred to here as the presetal notopodial lobe. Superior and inferior lobes extend distally from the "acicular ligule" (Fig. 1a), a term not defined by the above authors. As the namanereidine parapodium has elements of both the notopodia (dorsal cirrus, notoacicula and sometimes notosetae) and neuropodia (ventral cirrus, acicular ligule, neuroacicula, neurosetae), it is referred to in the descriptions simply as a podium (pl., podia).

The head-end cirri of nereids have both peristomial and segmental origins (Gilpin-Brown, 1958, and references therein), with the anterior pairs arising from the peristomium and the posterior pairs of segmental origin. A recent neurological study appears not to contradict this view (Orrhage, 1993). However, both types of cirri are here referred to as "tentacular cirri" in order to simplify the descriptions, although separate terms may be more appropriate given the putative separate origins (Glasby, 1993). Similarly, although the collar-like segment between the prostomium and the first setigerous segment in the adult is apparently the result of the fusion of the peristomium (the area around the mouth), with the first larval segment during ontogeny, for reasons of simplicity and historical continuity, it is referred to here as the peristomium. Latest opinion suggests that the peristomium of nereids—and many other polychaetes—may in fact be limited to the buccal lips (Fauchald & Rouse, 1997; Rouse & Fauchald, 1997), and therefore that the collar-like achaetous region visible in adult nereids is entirely of segmental origin; however, this needs to be verified, at least for the nereids.

The following institutional abbreviations are used in Table 1 and throughout the text:

AHF Allan Hancock Foundation, Los Angeles (now under the auspices of the Natural History Museum of Los Angeles County)
AM Australian Museum, Sydney
AMNH American Museum of Natural History, New York
ASL Academy of Sciences, Leningrad
BAS National Museum of Natural History, Bulgarian Academy of Sciences, Sofia
BMNH British Museum (Natural History), London
CAS California Academy of Sciences, San Francisco
HZM Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg
ICML Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico
MCBM Centro de Biologia Marinha, Universidade Federal do Paraná, Paranaguá, Brazil
MNHN Muséum national d'Histoire naturelle, Paris
MPW Muzeum Przyrodnicze Wrocław, Uniwersytet Wrocławski, Wrocław, Poland
MU Massey University, Palmerston North, New Zealand
NIWA National Institute for Water and Atmospheric Research, Wellington (formerly New Zealand Oceanographic Institute)
NMC National Museum, Colombo
NMNZ Museum of New Zealand, Te Papa Tongarewa (formerly National Museum of New Zealand), Wellington
NMV Museum of Victoria (formerly National Museum of Victoria), Melbourne
NTM Northern Territory Museum of Arts and Sciences, Darwin, Australia
OM Otago Museum, Dunedin, New Zealand
PMBC Phuket Marine Biological Center, Phuket, Thailand
PMJ Phyletisches Museum Jena, Friedrich-Schiller-Universität, Jena, Germany
QM Queensland Museum, Brisbane
RNHL Rijksmuseum van Natuurlijke Histoire, Leiden
SAM South African Museum, Cape Town
SSM Naturhistoriska Riksmuseet, Stockholm
SZN Museum of the Stazione Zoologica, Naples
UABCS Universidad Autónoma de Baja California Sur, La Paz, Mexico
UH University of Hawaii at Manoa, Honolulu
UPSL University of Peradeniya, Peradeniya, Sri Lanka
USNM National Museum of Natural History, Washington D.C.
UUZM Uppsala Universitets Zoologiska Museum, Uppsala
ZIB Departmento de Zoologia Instituto de Biociências, Universidade de São Paulo
ZMA Zoölogisch Museum, Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam, Amsterdam
ZMB Museum für Naturkunde, Institut für Systematische Zoologie (formerly Zoologisches Museum, Universität Humboldt), Berlin
ZMUC Zoologisk Museum, Kobenhavn Universitet, Copenhagen
ZSI Zoological Survey of India, Calcutta

Taxonomic and phylogenetic characters

Characters and character states for the taxonomic study of the Namanereidinae and their nearest relatives (outgroups) are discussed below. Those used also in the phylogenetic analysis are indicated alpha-numerically, listed in the Appendix and scored in Table 2.

Number of setigerous segments. The maximum number of setigers of individuals of all species fall readily into one of two groups: those with fewer than 150 setigers (1a) and species having greater than 150 setigers (1b). The range in maximum number of setigers in taxa allocated state a was 36–131, and for state b, 166–386. Species in the first group attain sexual maturity at some point less than 150 setigers, but there are insufficient observations to determine accurately the number of setigers at maturity in members of the second group (indeed some individuals may attain maturity with less than 150 setigers).

Among the outgroup taxa, the Hesionidae and Nereididae (excluding *Tylorrhynchus heterochaetus*) appear to have the fewer number of setigers, although the same attention to intraspecific variation was not paid to the outgroup. The Chrysopetalidae are equivocal with species of *Chrysopetalum* falling into the smaller category and species of *Bhawania* into the larger.

Body shape. Viewed dorsally, most Namanereidinae and all outgroup taxa are uniform in width anteriorly and taper gradually posteriorly (2a). A few namanereidine species are decidedly wider mid-anteriorly and taper gradually anteriorly and posteriorly from this widest point (2b). The bulge coinciding with the maximum width appears to correspond to an increased thickness of the longitudinal muscle of the body wall, although this needs to be confirmed histologically.

Epidermal pigment. The presence of epidermal brown pigment on the dorsal surface of the body especially anteriorly and posteriorly (3a) is very prominent in some species. Although the brown pigment fades with time in preserved specimens, enough colour is usually present to enable this character to be scored even in specimens stored tens of years in alcohol. Other species, notably members of *Namanereis*, which include many subterranean species, lack epidermal pigment (3b). The outgroup is equivocal.

Prostomium. Prostomia are broad and appear foreshortened anteriorly. The ratio of the basal width relative to the mid-dorsal length (w/l) is relatively constant within the subfamily, ranging from 1.3 to 2.6 (4a). Other nereids and hesionids belonging to the outgroup also show a similarly-shaped prostomium. In contrast, nereids belonging to *Australonereis* and *Olganereis* and both chrysopetalid species examined have relatively elongate prostomia with a w/l ratio of less than 1.3 (4b).

The presence of a mid-anterior cleft and a mid-dorsal groove on the prostomium is a prominent feature of some species, especially in *Namalycastis* (e.g., Figs. 12a, 20a). However, the depth (or prominence) of the cleft and dorsal groove is variable in preserved specimens, depending on the position of the pharynx when fixed. An everted proboscis generally results in a widening of the prostomium relative to its length and, consequently, the anterior cleft (if present) and dorsal groove become less prominent. A retracted proboscis results in a more prominent cleft and dorsal groove. However, allowing for these "fixation" effects, species either exhibit a cleft anterior edge and longitudinal groove extending posteriorly to the mid-posterior prostomium (5b) or a cleft/

groove was absent (5a). In the latter case the dorsal surface of the prostomium was either flat or very slightly concave. The outgroup is equivocal.

Antennae. Most Namanereidinae possess well-developed lateral antennae, the exceptions being *Cryptonereis malaitae* Gibbs, in which they are absent and *Namalycastis fauveli* Nageswara Rao in which they are minute. Antennae are either subconical (6a) as in *Namalycastis* species (e.g., Figs. 21a, 23a) or cirriform (6b) as in all *Namanereis* species (e.g., 31a, 33a), except in *Namanereis quadraticeps* (Blanchard in Gay), where they are distally rounded (subspherical) (6c). The antennae most often extend beyond the tip of the prostomium, but range in length from minute protrusions to extending beyond the palpostyles. The relative length of the antennae may prove to be a good cladistic character, but given the present difficulties in scoring overlapping quantitative characters and that for many species there were too few specimens to properly estimate intra-specific variation, this character was not used in the present analysis.

At the junction with the prostomium the antennae normally pinch in at the base, appearing distinct from the prostomium; however in *Lycastoides alticola* Johnson the antennae are described by Johnson (1903) as being "produced insensibly" from prostomial frontal lobes: this may be a possible autapomorphy of the species.

A median antenna is lacking (7b) in the Namanereidinae, like other Nereididae, but in some outgroup taxa a median antennae may be present (7a).

Eyes. Several species, often those associated with subterranean waters, lack eyes (8d), or at least the pigment associated with them. The absence of eyes may be the result of selection; however, this is not a sufficient reason for *a priori* exclusion of the character from the phylogenetic analysis. It is conceivable that all Namanereidinae lacking eyes form a clade whose ancestor also lacked eyes. Like other nereids, most Namanereidinae have two pairs of eyes, with anterior and posterior pairs approximately equal in size or the anterior pair of eyes slightly larger than the posterior pairs (8a). In a few species the posterior pair may be markedly smaller the anterior pair (8b) or the anterior pair may be slightly smaller than the posterior pair (8c). The outgroups all have state 8a.

As concerns the lens, two distinct states are recognised in the subfamily. The most common is for the lens to be absent, or at least indistinct from the vitreous body (9a). In the other condition, a well-developed lens is clearly distinguished from the surrounding vitreous body (9b) (Figs. 21a, 40a). The latter is present in a few species only and is not the result of sexual modification (epitoky). The outgroup apparently have both states, although the degree to which this character may be polymorphic in outgroup species is unknown. Species lacking eyes were scored as unknown for this character.

Palps. While there are difficulties with the interpretation of palp morphology within nereidoids, especially in regard to homology, the unique occurrence of spherical palpostyles (distal region of the palp) (10a) in all ingroup species is strong evidence of monophyly (Glasby, 1993). The shape of the palpostyles of other nereids is subconical (10b). Palps of the Hesionidae and Chrysopetalidae outgroups show various degrees of articulation, but their overall shape may be described as approximately cylindrical (10c). However, whether the "pseudoarticulated" palp of these groups is homologous with the palpophore (basal region) or with the palpostyle of the Nereididae is not known. Palp shape and the following two characters were included in the cladistic analysis in order to retest monophyly of the Namanereidinae and Nereididae, and outgroup relationships.

Nuchal organs. Nuchal organs may be either externally exposed (11a) as in the Hesionidae and Chrysopetalidae or not externally exposed (11b) as in the Nereididae. As noted previously (Glasby, 1993) this remains a tentative (and simplistic) interpretation of the character. However, at present there are too few comparative studies of nuchal organs at and below the family level for a more detailed characterisation of the structural modifications of these organs (see Purschke, 1997 for a review).

Peristomium. Glasby (1993) considered that the peristomium of nereidoids may either be absent, or at least not visible in adult individuals (12a) as in the Hesionidae and Chrysopetalidae. Fauchald & Rouse (1997) and Rouse & Fauchald (1997) suggest that the adult peristomium is "limited to the [buccal] lips". In the Nereididae however, the peristomium is apparently fused with the first segment (12b), as evidenced by the separate origin of the head-end cirri during ontogeny—anterior pairs derived from the peristomium and posterior pairs from cephalisation of the first segment (Gilpin-Brown, 1958). There appears to be no recent neurological studies on nereid larvae to refute this view; indeed Orrhage's (1993) neurological study of adult nereids would seem to lend support to the hypothesis of Gilpin-Brown.

Peristomium length, a character used in a previous cladistic analysis of the Nereididae (Glasby, 1991), is not informative at this level: *Olganereis* is the only taxon having an elongate peristomium (greater than length of setiger 1), all other Gymnonereidinae considered here and the Namanereidinae have the shorter type (equal to or less then length of setiger 1). The length of the peristomium may be correlated with pharyngeal length, which in turn may be related to a species' feeding capabilities, but this would require further study.

Tentacular cirri. The number of pairs of tentacular cirri is one of the few characters that has been used by previous authors to support the division of the Namanereidinae into two major lineages: *Lycastopsis* (= *Namanereis sensu lato* Hartman, 1959a) and *Namalycastis* (e.g., Hartman, 1959a; Feuerborn, 1931a; Pflugfelder, 1933; Rioja, 1946; Winterbourn, 1969). Namanereidinae can have four pairs of tentacular cirri (13b) like other nereids, or the posteroventral pair may be lacking (13a). As mentioned previously, tentacular cirri here includes both the two anterior pairs derived from the peristomium as well as the one, or two, pairs of posterior cirri derived from the cephalisation of the first larval setiger. Species having four pairs of tentacular cirri, have a full complement of tentacular cirri as early as the 10-setiger stage (see Remarks for *Namanereis stocki* n.sp.), similar to that in other nereids, which range from 4–9 setigers (Dales, 1950; Smith, 1950; Gilpin-Brown, 1959). Species having three pairs of tentacular cirri have the full complement by at least by the 13-setiger stage (Hartmann-Schröder, 1980). Whether species having only three pairs have lost the posteroventral pair during ontogeny as suggested by Hartmann-Schröder (1977) for *Namanereis hummelincki* (here referred to as *N. cavernicola*) needs to be confirmed.

Amongst the outgroup taxa, the nereids have four pairs (two pairs peristomial plus two pairs segmental), the Chrysopetalidae either have three or four pairs (all segmental) (13c) and the Hesionidae may have six pairs (13d) or eight pairs (13d), all of which are segmentally derived.

The cirrostyles of the tentacular cirri may be faintly jointed (14b) as in some Namanereidinae (Figs. 16a, 35a) or smooth (14a) as in other species and in the outgroups. However, this observation is based on light microscopy and remains tentative, pending a separate more thorough study using SEM. Cirrophores of ingroup taxa are generally poorly developed compared to other Nereididae. Larger species tend to have better-developed cirrophores than smaller ones, indicating that the character may be size dependent; it was therefore not included in the cladistic analysis. The unusually elongated cirrophores of *Lycastoides alticola* may be an autapomorphy of the species, but the species is so poorly known in other respects that it was not included in the analysis.

The posterodorsal pair of tentacular cirri of Namanereidinae shows considerable variation in length, extending posteriorly from setiger 1 to 9, depending on the species. The length of the posterodorsal pair appears to be positively correlated with the length of other tentacular cirri. Although the character is useful for distinguishing between namanereidine species in combination with other characters, the difficulty in assigning discrete states precluded its use in the analysis.

Pharynx. The ornamentation of the pharynx is a rich source of cladistic characters for some nereids (see for example, Fitzhugh, 1987; Glasby, 1991) and nereidoids (Glasby, 1993), but not for the Namanereidinae. The subfamily has been diagnosed in the past as lacking pharyngeal paragnaths and papillae (15a) and paragnaths; however, in the course of the present study it was found that juveniles of both *Lycastopsis amboinensis* Pflugfelder and *L. hummelincki* Augener have pharynges adorned with a single row of minute papillae (Fig. 3). The papillae appear to correspond in position to those on the oral ring of other nereids, but their alignment in a single row around the entire oral ring is peculiar and casts some doubt on whether or not this feature is actually homologous with the oral papillae of other nereids. Pharyngeal papillae are absent in the adults.

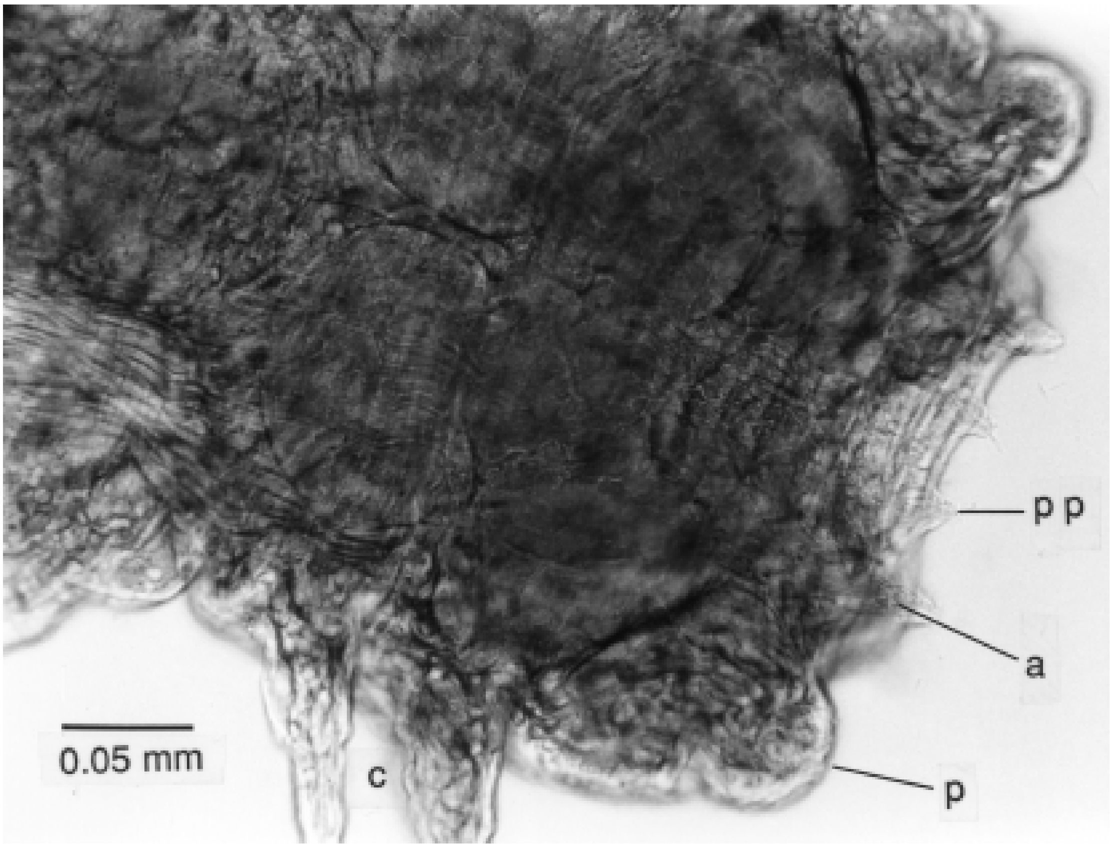

Figure 3. *Namanereis amboinensis*. A 13-setiger specimen (ZMA V.Pol. 2893) with partially everted pharynx showing pharyngeal papillae (*pp*), antennae (*a*), palps (*p*) and tentacular cirri (*c*).

Regionalisation of the pharynx is well defined in the Namanereidinae with regions I–VIII recognisable, as in other nereids. In general, there is no variation in the size and shape of these regions between species, although the structure of Area V in *Namanereis quadraticeps* is unique (an autapomorphy) in being pad-like, apparently as a result of the fusion of Areas V–VI. Other Namanereidinae have Area V unfused and represented by a narrow medial groove.

Most of the nereid species in the outgroup have a papillated pharynx (15b) whilst the hesionid and chrysopetalid outgroups lack papillae; however, other hesionid species may have papillae and strictly speaking, the family is polymorphic for this character.

Jaws. The homology of jaws and jaw-like structures among nereidoids is particularly difficult and has been discussed previously (Glasby, 1993). In this previous study the jaws of Chrysopetalidae were described as "sickle-shaped" (like those of Nereididae), even though chrysopetalid workers refer to the jaws of this group as "stylets". Chrysopetalid "stylets" whilst much more delicate than nereid jaws, and possibly having a slightly different orientation within the pharynx, nevertheless appear to be morphologically very similar to nereid jaws. In particular, the jaws of both groups have a single robust terminal tooth followed by a series of smaller teeth along the cutting edge (16a; Watson Russell, 1991: fig. 4Y2). In the present analysis sickle-shaped jaws are scored as present in the chrysopetalid and nereid outgroups and most of the ingroup. A few namanereidine species have a peculiar arrangement whereby the distal-most of the series of proximal teeth was enlarged to the size of the terminal tooth, giving the jaw a bifid appearance, together with few (or no) true proximal teeth (16b) (Figs. 37b, 47b). The Hesionidae are polymorphic for this character.

Parapodia. The structure of the parapodia is a rich source of characters for members of Nereidinae and Gymnonereidinae; however, their reduction in complexity in the Namanereidinae has resulted in fewer potential taxonomic characters. Only the shape of the retractile tip of the acicular ligule and the size and shape of the dorsal cirri show useful interspecific variation (Fig. 1a).

Feuerborn (1931a: fig. 10) indicates that 3-setiger individuals of *Lycastis ranauensis* Feuerborn (= *N. hawaiiensis* herein) have biramous parapodia suggesting that the notopodia may be lost during ontogeny. This view, and the opinion of Southern (1921) may have led Banse (1977b: 612) to the view that the reduced notopodial condition in the Nereididae is derived, as discussed earlier. The observation of Feuerborn could not be verified in the present study.

The degree to which the first pairs of parapodia are supported by internal aciculae varies in the taxa under study. The Namanereidinae, *Stenoninereis* and some Hesionidae have both noto- and neuroaciculae in the parapodia of the first 2 setigers (and subsequent ones) (17a). In other taxa the parapodia of setiger 1 only lack notoaciculae (17b) as in species of *Chrysopetalum*, or parapodia of both setigers 1 & 2 lack notoaciculae (17c) as in the remaining Nereididae.

Notopodial lobes and ligules. Notopodial lobes are absent in all Namanereidinae and in the Hesionidae, *Hesione* and *Ophiodromus* (18a), but a range of notopodial forms occur in the other outgroup taxa. Two states are here identified: presence of a single pre-setal lobe (18b), and presence of distinct, flattened notopodial lobes, including a well-developed median ligule and usually also a dorsal ligule (18c). Homologies are difficult to establish, but based on general similarity and position, the single notopodial lobe of the chrysopetalids is here considered homologous with those of the hesionid, *Leocrates*.

Neuropodial lobes and ligules. The Namanereidinae and most of the outgroups have a single acicular neuropodial ligule (19a) (Fig. 1a). Three other states are present in other outgroup taxa: presence of an acicular neuropodial ligule and a ventral ligule (19b); presence of an acicular neuropodial ligule and post-setal lobe (19c); and the combination of an acicular neuropodial ligule, ventral ligule and post-setal lobe (19d).

The retractile tip of the acicular neuropodial ligule of Namanereidinae is generally small and difficult to see (especially in small specimens), and most easily observed in the larger, anterior parapodia. It is generally well developed and bilobed (20b), comprising a superior and an inferior lobe in *Namalycastis* species (Figs. 10c, 20c), and poorly developed and subconical (20a) in *Namanereis* species (Figs. 33c, 37c). The ligule tip of *Namanereis quadraticeps* was also scored as "subconical" in the analysis, although it is slightly more globular than in most other species of *Namanereis*. Both states occurred in the outgroup taxa. The shape of the retractile tip may vary in shape along the body depending on the position of the neuroacicula, which protrudes into the ligule. When the neuroacicula is fully retracted, the neuropodial ligule is barely visible.

Dorsal cirri. Amongst the ingroup the dorsal cirri of parapodia of the mid-posterior region may be either approximately conical (21a) as in *Namanereis* species (Figs. 43d, 45d), or the basal region may be flattened, leaf-like (21b) as in many *Namalycastis* species (Figs. 10d, 12d). Within *Namalycastis*, the larger species tend to have more leaf-like dorsal cirri, but the feature is not entirely correlated with body size, nor restricted to Namanereidinae. For example, the small-bodied gymnonereidine *Stenoninereis martini* also has flattened dorsal cirri. Rasmussen (1994) describes a counter-current circulatory system in the dorsal cirri of *Namalycastis abiuma* (= *N. borealis* n.sp. herein). It is possible that such a circulatory system is a general feature of the subfamily since all namanereidine species examined in this study have well-vascularised dorsal cirri (particularly those of posterior parapodia).

The dorsal cirri of anterior parapodia of some ingroup taxa have a slightly enlarged, well-defined basal article or cirrophore (22b) (Figs. 23c, 26c), although by comparison with other Nereididae, Hesionidae and Chrysopetalidae, it may be considered poorly developed. Other species lack such a cirrophore (22a). Whether the flattened basal region of the dorsal cirri in namanereidine species is homologous with the cirrophore is unclear. Retractability of the cirrostyles into the cirrophores, as occurs in some chrysopetalid genera (Perkins, 1985), probably does not occur in the Namanereidinae and therefore casts some doubt over the homology of features associated with the basal region of the dorsal cirri.

Aciculae. The number and form of the internal setae (aciculae) that support the parapodia does not show any taxonomically-informative variation within the Namanereidinae. The distally recurved dorsal aciculae (notoaciculae) of *Lycastilla cavernicola* (herein referred to under *Namanereis*), which was thought to be a generic feature by Solís-Weiss & Espinasa (1991), is probably an artifact of fixation or preservation (see Remarks for this species).

At the subfamily level, the ventral position of the notoacicula is an important character—the notoacicula having shifted ventrally where it supports the neuropodium together with the neuroacicula (23b); this condition was shown to be derived in an earlier more-general analysis (Glasby, 1991). In other nereids and the other outgroup taxa, the notoacicula supports a true notopodial lobe, or if a notopodial lobe is absent, then it supports the dorsal cirrus (23a). Further, Glasby (1991) found that the absence of true notopodial lobes and ligules in the Namanereidinae was a symplesiomorphy with the Hesionidae, which therefore confounded the broader question of whether the parapodia of Namanereidinae could be referred to as derived or plesiomorphic. In the present study, some namanereidine individuals appeared to have a minute lobe associated with the notoacicula (e.g., Fig. 10d), suggesting that it may be more correct to score Namanereidinae as having extremely reduced notopodial lobes (rather than absent, as scored for the present analysis). In either case, the reduced notopodial condition of Namanereidinae is a unique feature among nereidoids, presumably resulting from the notopodia having been “grafted” on top of the neuropodia. The important point, however, is that there is at least one parapodial character (ventral position of notoacicula or “reduced notopodia”) that unequivocally supports namanereidine monophyly; the issue of whether the namanereidine parapodia are referred to as biramous, sub-biramous or uniramous, is mainly of semantic interest and discussed further under the subfamily Remarks.

Glandular patches. Glandular patches are present on the dorsal edge of the parapodia of some nereids (24b). The Namanereidinae lack such glandular patches (24a).

Setal types and distribution. Within nereidoids, setae arise from the parapodia either in fascicles (i.e. bundles; often in some kind of pattern such as multiple short, curved rows), or in simple rows (Glasby, 1993). Like other nereids, all of the Namanereidinae have fascicles in the subacicular position and rows in the supra-acicular position, therefore the character is uninformative at this level of analysis and the distinction between rows and fascicles would unnecessarily complicate the descriptions. Therefore, from this point on groups of setae are referred to by the more traditional term, “fascicle”. Four distinct fascicles are recognised in the ingroup: above the acicula there are the preacicular and postacicular fascicles and below the acicula there are the preacicular and postacicular fascicles (Fig. 1b).

Members of the Nereididae often have only one type of seta per fascicle, though there are many exceptions. Further, the setae of a particular fascicle appear to arise from the same position at the base of the parapodium and emerge at a similar angle in relation to the aciculae. Therefore, based on morphological criteria (specifically the similarity of position), I make the preliminary assumption that the setae occurring within a particular fascicle between species are homologous. This assumption may be later tested in the cladogram (criterion of phylogenetic position).

In an earlier cladistic analysis of the Nereididae, setal type was coded as two separate characters: the type of shaft, specifically the symmetry of the articulation and the type of blade (Glasby, 1991). This was done as the type of shaft and blade were not highly correlated in the taxa examined. In the present analysis however, the range of setal types in both the ingroup and outgroup taxa is far less and each setal type is considered a single character state, characterised by combining shaft and blade type, for example “heterogomph falciger” or “sesquigomph spiniger”. However, variation in shaft articulation and blade type within a fascicle did occur *along the body* of some namanereidine species and both proved to be useful specific characters within the ingroup. For example, in some species heterogomph spinigers replace heterogomph falcigers in the parapodia of posterior setigers (28, 31). Variation in the form of the setal blade included an increase in the size and length of the serrations on the blades of heterogomph setae in parapodia of posterior setigers (34).

Notosetae of Namanereidinae are either represented by sesquigomph spinigers, which may or may not be present in every parapodium (25a), or they may be absent (25b). In addition, the outgroups may have homogomph spinigers (25c), capillaries (25d) and paleae/spines (25e) in this position.

Neurosetal patterns in the ingroup are more diverse, and the following discussion of the characters refers to the fascicle positions illustrated in Fig. 1b. Supra-acicular neurosetae in the postacicular fascicle are typically sesquigomph spinigers (26a) (Figs. 11g, 31e), except for *Namanereis pontica*, which exhibits an autapomorphic loss of setae in this position (26b) and *Namanereis quadraticeps*, which has heterogomph spinigers in this position (26c) (Fig. 44e). The outgroup also have heterogomph falcigers (26d).

In anterior parapodia, supra-acicular neurosetae in the preacicular fascicle are usually heterogomph falcigers (27a) (Fig. 10f), but heterogomph spinigers (27b) (Fig. 18f) are present in *Namalycastis geayi*. The outgroup may also have sesquigomph falcigers (27c) or lack setae in this position (27d). In posterior parapodia some namanereidine species have heterogomph spinigers (28b) in this position, but heterogomph falcigers are more common (28a). That is, given that segments are added posteriorly in annelids, heterogomph spinigers in this position represent a feature acquired later in ontogeny, and in a sense may be regarded as “replacing” the heterogomph falcigers. The outgroup taxa have heterogomph falcigers, sesquigomph spinigers (28c), or no setae (28d) in posterior parapodia.

Subacicular neurosetae in the postacicular fascicle may be either heterogomph spinigers (29a) (Fig. 10g), or absent (29b) in the Namanereidinae. Absence of spinigers occurs in species traditionally grouped under *Lycastopsis* as well as in *Lycastilla cavernicola* Solís-Weiss & Espinasa, 1991, and two new species described here. However, these last three species and *L. hummelincki* differ from other *Lycastopsis* in possessing subacicular "pseudospinigers" (Fig. 37g) that cannot be easily classed as postacicular or preacicular. If postacicular, then they would be homologues of true heterogomph spinigers. However, a preliminary cladistic analysis with these taxa coded for pseudospinigers in the postacicular fascicle was less parsimonious than the one presented here in which the pseudospinigers are regarded as preacicular (character 30). In the outgroup taxa, other setal types in this position included heterogomph falcigers (29c) and sesquigomph spinigers (29d).

Subacicular neurosetae in the preacicular fascicle in the Namanereidinae may be heterogomph falcigers (30a), heterogomph spinigers (30b) or several types of heterogomph setae grading from falcigers to spinigers, including pseudospinigers (30c) (Fig. 37g). The outgroup has sesquigomph falcigers (30d) and heterogomph falcigers and sesquigomph spinigers (30e). The type of setae in this fascicle in posterior setigers is generally similar throughout the Namanereidinae, except in a few species where there was replacement of the anterior heterogomph falcigers with heterogomph spinigers. In the outgroup, setae in this position were sesquigomph falcigers (31d).

Setal form. In the Namanereidinae the heterogomph falcigers in the sub-neuroacicular fascicle in setiger 10 exhibit various blade shapes and degrees of serration. Blade shapes range from weakly falcate, broad and short (32a) as in *Namanereis* species (Figs. 34f, 38f) to weakly falcate, narrow and elongate (32b) as in many *Namalycastis* species (Figs. 11f, 16f). In addition, *Namalycastis geayi* and some of the outgroup taxa have spinigerous setae (32c) in this position. Outgroups additionally have heterogomph falcigers that are strongly falcate and elongate (32d) and strongly falcate and short (32e).

The distal region, or blade, of the heterogomph falciger is typically evenly serrated along its length (33a), although the coarseness of the serrations ranges from relatively fine to coarse; in some species and in the two chrysopetalid outgroups heterogomph falcigers in the parapodia of posterior setigers have blades in which the serrations increase in coarseness proximally (toward the shaft) (33b). Serrations are absent (33c) in *Namalycastis brevicornis* and *N. kartaboensis* as well as in some outgroup taxa. Although the setae in this position exhibit further qualitative differences in the nature of the blade serrations (degree of coarseness, length of teeth/hairs), which are described in the species accounts, the differences could not be translated into meaningful cladistic characters. However, further investigation using standard morphometric techniques, or geometric morphometrics, may be rewarding.

The degree of elongation of the boss at the distal end of the setal shaft was not a very useful cladistic character. The boss of sesquigomph spinigers was greatly elongate (ratio >2.3) in *Namanereis beroni* (an autapomorphy for the species), but among all other species the ratio varied more or less continuously between 1.2–2.2. Similarly, the degree of elongation of the boss of heterogomph falcigers in the preacicular fascicle of the neuropodia varied little between most species being typically heterogomph, although it was very elongate in *Namalycastis fauveli* (an autapomorphy).

When present in posterior parapodia, the heterogomph spinigers in the postacicular fascicle below the acicula vary in form, having proximally finely-serrated blades (34a) in some species, with minor variation in the serration length, to having blades in which the proximal serrations are markedly coarser (34b) (Figs. 20i, 21g). The outgroup have the former state.

Like other nereids, the blades of both spinigerous and falcigerous setae in the Namanereidinae are joined to the shaft by a ligament extending proximally from the serrated region of the blade and a hinge extending from the base of the blade (Fig. 2); the ligament and hinge may be difficult to see in the finer spinigerous setae and poorly preserved specimens. In *Cryptonereis malaitae* Gibbs however, the blades and shafts of falcigerous setae are fused or partially fused, an autapomorphy for the species.

Micro-surface structure of nereid setae is generally poorly known. When viewed under SEM the setal shafts of most Namanereidinae appear to have a fine microstructure. In at least two species, *Namanereis quadraticeps* and *C. malaitae*, the surface serrations are very prominent (Fig. 4c), even when viewed under a light microscope (400 × total magnification). Other Namanereidinae and outgroup taxa lack such prominent serrations on the setal shafts (Fig. 4a,b). Therefore, two states are recognised: smooth or nearly so (35a), and serrated (35b).

Pygidium, shape. Two pygidial states are tentatively recognised in the Namanereidinae: a multi-incised rim (36a) characteristic of *Namalycastis* species (Fig. 8b), and a tripartite rim with two large lateral lobes and smaller pointed dorsal lobe (36b), a feature of most *Namanereis* species (Fig. 8d). The outgroup may also have a button-shaped, smooth rim (36c) and a wing-like pygidium with lateral lobes (36d).

Uncertainty over the distinction between states 36a and 36b is due the possibility that the character is size-dependent. The tripartite condition is typical of smaller namanereidine species (i.e. the "*Lycastopsis*" group), whereas the larger *Namalycastis* species are typically multi-incised (Fig. 8b). The intermediate-sized species, *N. quadraticeps*, typically has a tripartite pygidium (36b), but the larger dorsal lobe is faintly incised (Fig. 8d). Further, the character also shows intraspecific variability, although there is apparently no obvious correlation between pygidium form and individual size. *Lycastilla cavernicola* and a new species of *Namanereis* are polymorphic having both states (36a and b).

Anal cirri. The shape of the anal cirri in the Namanereidinae shows only slight variation. Most species have approximately conical-shaped anal cirri, approaching cirriform in species with longer ones (37a). However, in *C. malaitae* and *N. quadraticeps*, anal cirri are shorter and stouter than normal, appearing as an extension of the pygidium (37b). In *Namalycastis senegalensis*, they are flattened (37c) and resemble the posterior dorsal cirri (autapomorphy); this type of anal cirri also occurs rarely in *N. abiuma* and *N. indica*. The position of the anal cirri on the pygidium shows little interspecific variation, ranging from lateral to ventrolateral in all species, and may be affected by factors associated with preservation.

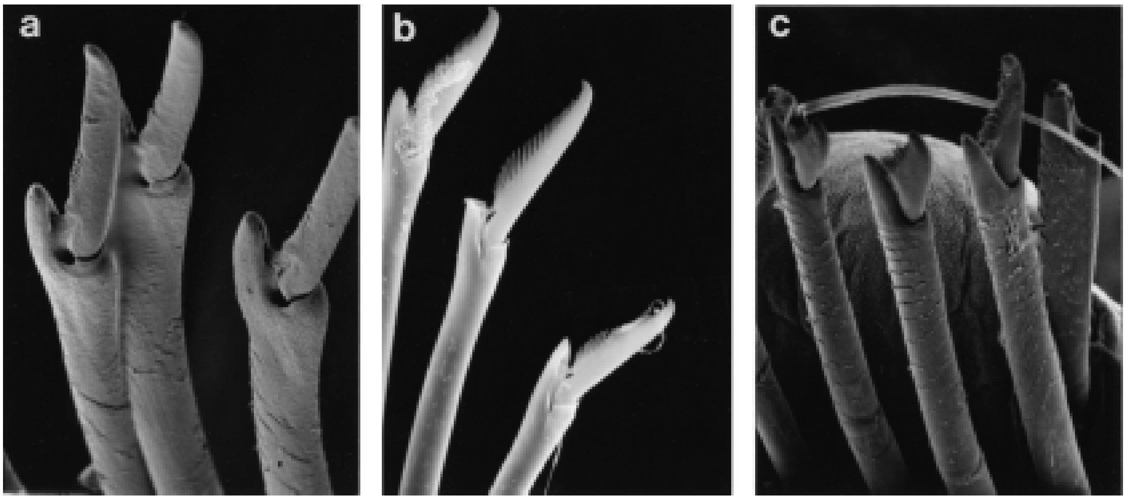

Figure 4. Scanning electron micrographs of subacicular heterogomph falcigers showing different degrees of surface microstructure on shafts: (*a*) faintly textured shafts of *Namalycastis hawaiiensis* (AM W20257), falcigers from parapodium 2, (*b*) smooth shafts of *Namanereis catarractarum* (AM W202965), falcigers from parapodium 16, (*c*) heavily serrated shafts of *Namanereis quadraticeps* species group (ZMUC POL-941), falcigers from parapodium 2.

Oocytes. Oocytes of the Namanereidinae may either be spherical (38a), or ellipsoidal (38b). Ellipsoidal eggs tended to be large and yolky (with few in each ovigerous segment) whereas the spherical eggs tended to be smaller and far more numerous in each ovigerous segment. The eggs of *N. quadraticeps* were exceptional in being very large and spherical. Unfortunately this character is very incompletely known for many namanereidine and outgroup species.

Epitokal setae. Up until now epitokal setae have only been reported for a single namanereidine species, *Cryptonereis malaitae* Gibbs. The present study indicates that their presence is more widespread within the group than originally thought. Unlike the broad, flattened "paddle-like" blades of truly epitokal nereids, the epitokal setae of Namanereidinae are either slender compound spinigers (39a; Fig. 17h), or long, slender capillaries (39b) as in *C. malaitae* (Fig. 40g). Epitokal setae were scored as absent (39c) if they could not be seen in sexually mature individuals, but for species not being represented by mature individuals, the character could not be scored. The outgroup may have paddle-bladed compound spinigers (39d).

Sexual strategy. Unfortunately, there are few data available on the type of sexual strategy employed by namanereidine species. Like other nereids (and indeed most polychaetes), most species appear to have separate sexes, but whether they are direct developers or have free or brooded larvae is unknown. Species for which hermaphroditism has been reported include *Lycastopsis catarractarum* (see Feuerborn, 1931a), *Namanereis quadraticeps* (see Johnson, 1908), *Namalycastis ranauensis* (herein a junior synonym of *N. hawaiiensis*) (see Feuerborn, 1931a) and *Namalycastis indica* (see Gopala Aiyar, 1935). Further, *N. indica* apparently has direct development of the egg and larvae in cocoons (Runganadhan, 1943). Unfortunately, we cannot be certain of the species identification in the studies by Gopala Aiyar (1935) and Runganadhan (1943), since the present study has revealed that there are two similar *Namalycastis* species occurring on the coast of India. Direct development, either externally in cocoons or in the adult tube or internally (viviparity), has been reported in several species of Nereididae (Wilson, 1991), and will probably be found to be common in the Namanereidinae as a means of providing maximum protection for developing young. The character is too poorly known at this stage to be informative in a cladistic analysis.

Phylogenetic analysis

Overview of methods. Relationships within the Namanereidinae were analysed using cladistic methods. Taxa were grouped on the basis of shared, derived characters (synapomorphies) into a series of nested, hierarchical units, or monophyletic groups. PAUP version 3.1 (Swofford, 1993) and HENNIG86 (Farris, 1988) were used to infer phylogenies, and the parsimony options used (Fitch and Wagner) permitted free character state reversibility. Multistate characters were *a priori* considered unordered since in no cases was there good evidence to support a particular character order. Further, for most of the multistate characters generally only two states occurred in the ingroup (additional states applicable to outgroup taxa). Therefore ordering these particular characters would add little additional phylogenetic information on ingroup relationships. Characters that exhibited polymorphism for a particular taxon, or those that were inapplicable or unknown/uncertain, were coded in the data matrix with a question mark (Table 2); in both programs this has the effect of assigning to the taxon the state which is most parsimonious, given the position of the taxon on the tree. Thus for absent data, the optimised values can be tested

Table 2. Characters and character states for the cladistic analysis of the Namanereidinae (ingroup) and outgroup. A question mark (?) indicates polymorphism or inapplicable/unknown/uncertain states (see text for explanation). Characters and character states are listed in the Appendix.

taxa	characters and states
	1 2 3
INGROUP	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9
malaitae	a a b a a d b a b a b b a a a a a a a a a a a b a b a a a b a a a a ? b b b b
amboinensis	a a b a a b b b b a b b a ? a a a a a a a a b a b a a a b a a a a ? a b a b b
beroni	a a b a a b b d ? a b b a b a a a a a a a a b a b a a a b a a a a ? a b a b c
catarractarum	a a b a a b b b a a b b a a a a a a a a a a b a b a a a b a a a a ? a b a b c
hummelincki	a a b a a b b d ? a b b a b a b a a a a a a b a b a a a b c c a a a a b a b c
littoralis	a a b a a b b a a a b b a ? a a a a a a a a b a b a a a b a a a a ? a b a b c
pontica	a a b a a b b a a a b b a a a a a a a a a a b a b b a a b a a a a ? a b a ? ?
riojai	a a b a a b b a a a b b a a a a a a a a a a b a b a a a b a a a a ? a b a ? ?
tiriteae	a a b a a b b d ? a b b a a a a a a a a a a b a b a a a a a a a a a ? a ? ?
serratis n.sp.	a a b a a b b d a a b b a ? a b a a a a a a b a b a a a b a a a a ? a b a b c
cavernicola	a a b a ? b b d ? a b b a b a b a a a a a a b a b a a a b c c b a a a ? a b c
sublittoralis n.sp.	a a b a a b b a a a b b a a a a a a a a a a b a b a a a b a a a a ? a b a ? ?
abiuma	b a a a b a b a a a b b b a a a a a a b b b b a a a a a a a a a b a b a a ? a ?
brevicornis	b a ? a b a b a a a b b b a a a a a a b b b b a a a a a a a a a c b a a a a ?
elobeyensis n.sp.	a a b a b a b a a a b b b b a a a a a a b b b a b a a a a a a a b a b a b a a ?
fauveli	b b b a b a b ? b a b b b a a a a a a a b b b a a a a a a a a a a b a a a a a a a
geayi	b b b a b a b a a a b b b a a a a a a b b b b a a a b b a b b c a a a a a ? c
hawaiiensis	b a b a b a b a a a b b b a a a a a a b b b b a ? a a a a a a b b b a a a a c
indica	b b b a b a b a b a b b b b a a a a a a b b b a a a a a a a a a b b b a b ? a a
kartaboensis	b a b a b a b a a a b b b b a a a a a b b b b a a a a a a a a a b c b a a a ? ?
longicirris	b ? b a b a b a a a b b b a a a a a a a ? b b b a a a a a a a a a b ? b ? ? a ? c
senegalensis	b b b a b a b a a a b b b a a a a a a b b b b a a a a b a a b b a b a a c a a
siolii	b ? b a b a b c ? a b b b a a a a a a a a b b b a a a a b a a b b ? ? ? ? ? ? ?
terrestris	b a a a b a b a a a b b b a a a a a a b b b b a a a a a a a a a b a a a ? a ? ?
borealis n.sp.	b a a a b a b a a a b b b a a a a a a b b b b a a a a a a a a a b a a a a a a c
stocki n.sp.	a a b a ? a b d ? a b b b b a b a a a a a a b a b a a a b c c a a a a ? a ? c
intermedia n.sp.	a a b a b a b a a a b b b ? a a a a a a b b b a b a a b a a b b a a a b a a c
nicoleae n.sp.	a a b a b a b a a a b b b a a a a a a a b ? b b a a a a a a a a a b a a a b a ? c
multiseta n.sp.	b a a a b a b a b a b b b a a a a a a b b b b a a a a a a a a a b a b a a a ? c
macroplatis n.sp.	b b a a b a b a a a b b b a a a a a a b b b b a a a a b a a b b a b a a a ? ?
arista n.sp.	b b b a b a b a a a b b b a a a a a a b b b b a a a a b a a b b a b a a a ? ?
minuta n.sp.	a a b a ? b b d ? a b b b b a b a a a a ? a b a b a a a b c c b a a a b a ? ?
quadraticeps	a a b a a c b a b a b b b a a a a a a a a a a b a a c a a b a a a a ? b b b a c
	1 2 3
OUTGROUP	1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9
Stenoninereis	a a b a b b b a a b b b b a a a a c a a a b a a a a b d a a a c a a a d a ? ?
Dendronereides	a a a a b b b a a b b b b a b a c c c b a b a a a a c c d d d a c a a a a ? a
Tylorrhynchus	b a a a b a b a a b b b b a b a c c a b a b a a a a a a a a a b ? a a ? a ? d
Australonereis	a a a b b a b a a b b b b a b a c c d b a a a b c c a a d e a e a a a a a ? c
Olganereis	a a b b a b b a b b b b b a b a c c b b a a a b c c a a a a a a a a a ? a ? ?
Hesione	a a ? a a b b a ? c a a e a a ? c a a b a b a a b b d d c a a d c ? a a a ? ?
Ophiodromus	a a a a ? b a a b c a a d a a ? a a a a a b a b d d a a c a a d a ? a ? a ? ?
Leocrates	a a ? a a b a a ? c a a e a a ? a b a a a b a a d b d d a a a d c a a c a ? ?
Chrysopetalum	a a ? b a b a a b c a a b a a a b b a a a b a ? e b d d c a a d b ? a ? a ? ?
Bhawania	b a ? b a b a a b c a a c a a a a b a a a b a ? e b d d c a a d b ? a ? a ? ?

subsequently, when more complete data become available. This strategy is considered justifiable since most of the absences in the present dataset are due to unknown or uncertain character state assignment (c. 59% among ingroup taxa); by contrast, inapplicable data and polymorphisms accounted for only about 23% and 18% of cases, respectively.

The use of absence/presence coding (Pleijel, 1995) could potentially eliminate the problem of inapplicable characters, which can lead to "lies" in the dataset by introducing impossible character state reconstructions. However, absence/presence coding can introduce other problems into the analysis, specifically the weighting of features that can be broken into many discrete characters

(= character linkage); although Pleijel suggests that the weighting problem can be solved by *a priori* downweighting of linked characters, the benefit derived from using this technique for the relatively few cases of inapplicable characters in the dataset does not appear to outweigh the additional analytical complexity (specifically, an additional assumption).

Character polarity and outgroups. Polarity was determined using the method of outgroup comparison (Watrous & Wheeler, 1981). The poor fossilisation potential of nereid jaws (Szaniawski, 1974; Colbath, 1986), and of polychaetes in general, precluded the use of palaeontological evidence to polarise characters. Further, data on the ontogeny of species of Namanereidinae are mostly lacking (Reish, 1957). A 3-setiger individual of *Lycastis ranauensis* Feuerborn (= *Namalycastis hawaiiensis* Johnson) was shown to have biramous parapodia (Feuerborn, 1931a) suggesting that the notopodia may be lost during ontogeny, but the generality (*sensu* Nelson, 1978) of this observation needs to be confirmed before it can be used to polarise characters. Interestingly, two characters (28, 31) in the present analysis could be polarised using ontological evidence: the occurrence of heterogomph spinigers in the parapodia of posterior (ontogenetically more recent) parapodia in a few species is evidence for their derived nature; the alternative state, the occurrence of heterogomph falcigers is the more general condition (this suggested polarity agrees with that derived using the outgroups).

Appropriate outgroups for the Namanereidinae can be found among the subfamilies Gymnonereidinae and Nereidinae (Fitzhugh, 1987; Glasby, 1991, 1993). Within both of these nereid groups, a previous analysis using the two-step method of W.P. Maddison *et al*. (1984) showed that most of the character states of the more derived nereids (*Neanthes*, *Perinereis*, *Tylonereis*, *Nicon*, *Profundilycastis*) had no effect on the determination of the plesiomorphic state of the namanereidine ancestor (= outgroup node) (Glasby, 1990). Therefore, these taxa were excluded from the present analysis. More distant outgroups, belonging to Hesionidae and Chrysopetalidae, were also included in the analysis in order to get a better estimation of plesiomorphic states, given the observed degree of character state variation within the nereid outgroups. Both families were found to form an exclusive sister group relationship with the Nereididae (Glasby, 1993; Pleijel & Dahlgren, 1998).

The outgroup taxa used in the present analysis included five species of Gymnonereidinae: *Stenoninereis martini* Wesenberg-Lund, *Dendronereides heteropoda* Southern, *Tylorrhynchus heterochaetus* (Quatrefages), *Australonereis ehlersi* (Augener) and *Olganereis edmondsi* (Hartman); three species of Hesionidae: *Ophiodromus didymocerus* (Schmarda), *Leocrates chinensis* (Kinberg), *Hesione splendida* Savigny; and two Chrysopetalidae representing *Bhawania* and *Chrysopetalum*. Character states for the outgroups were obtained mostly directly from specimens and supplemented by descriptions from the literature, especially Perkins (1985) and Watson Russell (1991) for the Chrysopetalidae.

In order to minimise assumptions about monophyly of both the ingroup and outgroup, most parsimonious cladograms for both groups were estimated in one step using a simultaneous (unconstrained) analysis (C. Clark & Curran, 1986; Nixon & Carpenter, 1993). That is, both outgroups and ingroups were treated as terminal taxa.

Monophyly of the Namanereidinae. Fitzhugh (1987) identified the Namanereidinae as the only monophyletic subfamily in the Nereididae. He proposed a revised classification of the Nereididae, expanding the definition of the Gymnonereidinae and changing the definition of the Nereidinae to include the monogeneric subfamily, Notophycinae. The preferred cladogram of Fitzhugh's (1987: fig. 1), identified the Gymnonereidinae and the Nereidinae together as the sister group (the phylogenetically most closely related group) of the Namanereidinae.

Two additional synapomorphies, the possession of spherical palpostyles and the ventral position of the notoacicula (= dorsal acicula), provide further evidence of the monophyly of the Namanereidinae (Glasby, 1991). Other apparently unique features of the Namanereidinae that warrant further investigation are the thick layer of cuticle and epidermis that covers the eyes (Sadasivan Tampi, 1949), the peculiar enzyme content of the integument (Storch & Welsch, 1972b) and the presence of segmental "gill hearts" at the ventral base of the dorsal cirri, which has been reported in at least two species of *Namalycastis* (Feuerborn, 1931a; Rasmussen, 1994). These features may represent adaptations to semi-terrestrial life, including periodic exposure and low oxygen tensions; the possible occurrence of these features in other unrelated "semi-terrestrial" polychaetes would be interesting and would lend support to an adaptation hypothesis.

Characters. Thirty-nine, mainly morphological, characters were employed in the analysis, as described in the previous section and listed in the Appendix. Autapomorphies of terminal taxa were not included in the analysis (except when part of a multistate character); however, they appear in the descriptions, diagnoses and keys in the Taxonomy section. Characters were mainly qualitative or quantitative with discrete states. Two exceptions were the maximum number of setigers (1) and the prostomial shape as expressed as a ratio of prostomium width vs length (4). These characters were admitted into the cladistic analysis as there was no overlap in the states identified, at least among the ingroup. Some cladists would argue that admission of any quantitative characters into a cladistic analysis, whether they be overlapping or exhibit mutually exclusive states, is problematical (e.g., Pimental & Riggins, 1987), but as shown by Thiele (1993), the inclusion of such data in a cladistic analysis can result in the improved resolution of a phylogenetic hypothesis. For character 1, two mutually exclusive (non-overlapping) character states were identified amongst the Namanereidinae: maximum number setigers less than 150, and maximum number of setigers greater than 150 (see previous discussion under Taxonomic and Phylogenetic Characters). The ratio of prostomium width vs length (4) was relatively uniform in the Namanereidinae and a single state (4a) was assigned to all species. However, for both quantitative characters the outgroup was polymorphic, making the polarity assignment equivocal.

Data analysis. The large number of taxa in the present data set (Table 2) meant that heuristic search options, which do not guarantee to find all optimal trees, had to be used.

PAUP *analysis*: A two-step heuristic search involved firstly the calculation of an initial set of trees by random stepwise addition and branch swapping (tree bisection-reconnection, TBR), followed by a second round of branch swapping (TBR) on the initial trees. Trees resulting from random addition sequence provide a range of different length (near minimal) trees from which to begin branch swapping, as recommended by Swofford (1993). The second round of branch swapping increases the chance of finding all the trees of an island (Swofford, 1993). The default starting "seed" of random numbers was used initiate the random search. For the initial search, ten thousand replicates were performed with no more than one tree saved for each random replicate in branch swapping (i.e. NCHUCK = 1; CHUCKLEN = 1) before the next replicate began. This type of search strategy may be thought of as a "long, thin search".

PAUP options were set as follows: MULPARS on and COLLAPSE off, the latter as recommended by Swofford (1993) when employing random addition searches.

The second round of branch swapping used the same options as for the first round except that "chuckling" limits were not imposed. Maximum number of trees was set to 10,000. Resultant trees were then compared to those from the first round search by adding them to those resulting from the second search, without duplication—using the GETTREES (MODE = 7) command in PAUP. If none of the first round trees are added (i.e. they were found in the second round search) then only one island (*sensu* Swofford, 1993) of trees exists. That is, branch swapping on any of the trees resulting from the first round search will guarantee to find all of the minimal-length trees.

Minimal-length trees resulting from the first and second round searches were filtered using an outgroup topology constraint, in an attempt to reduce the number of minimal-length trees (many of the resulting most parsimonious trees differed only in the arrangement of the ten outgroup taxa). The outgroup constraint—((*Bhawania*, *Chrysopetalum*, *Hesione*, *Leocrates*, *Ophiodromus*), (*Stenoninereis*, ((*Dendronereides*, *Tylorrhynchus*), (*Australonereis*, *Olganereis*))))—was consistent with the topology derived in a previous study (Glasby, 1991).

The hierarchical information contained in multiple cladograms was summarised using three types of consensus trees (an Adams consensus tree could not be calculated for lack of sufficient computer memory). A Strict Consensus tree contains groups that are consistent with all minimal-length trees and is therefore useful for identifying clades that are unequivocally supported by the data; a 50% Majority-rule tree contains all groups that are found in over half of the minimal-length trees and thus may be thought of as a median tree; and the Nelson consensus tree (*sensu* Nelson, 1979) is the largest clique of most frequently replicated clusters in all minimal-length trees. It will often show an intermediate degree of resolution between the Strict and Majority-rule trees. The Strict and 50% Majority-rule consensus trees were calculated using PAUP, and the Nelson tree calculated using COMPONENT 2.0 (Page, 1993). Following the arguments of Anderberg & Tehler (1990) a revised classification is based on the results of the Strict Consensus tree (cf Miyamoto, 1985 for a contrasting view).

HENNIG86 *analysis*: Cladograms were generated using the HENNIG86 heuristic algorithms "mhennig*" and "bb*". An initial set of cladograms was obtained by a single pass through the data with sequential addition of terminal taxa and limited branch swapping (no more than one topology retained for each tree resulting from sequential addition of terminals). Extended branch swapping (bb*) was applied to each of these topologies and all shortest cladograms retained, or as many as can fit in the available memory. This combination of commands is recommended by Fitzhugh (1989) and Platnick (1989) for large data sets. The "exact" algorithms in HENNIG86, which find all minimum length trees, were too time consuming for this set of data and the computer hardware.

Phylogenetic results and discussion. The first round search in PAUP yielded 394 trees with length 137, consistency index of 0.555 and a retention index of 0.813 (Table 3). Filtering these trees using the constrained outgroup topology described above reduced the number of trees to 16. A second round of branch swapping on the first of these trees (no. 4) yielded 10,000 minimum length trees with the same length, ci and ri. The tree buffer overflowed suggesting that the effectiveness of the search was reduced. Addition (without duplication) of the 16 trees from the first round search to the 10,000 resulting from the second round resulted in no additional trees. Therefore all 16 trees were included in the set of 10,000. This means that only one island exists and swapping on any one of the 16 minimal-length trees would find all possible minimal-length trees given sufficient computing resources.

The existence of only one island in the present data is significant. Since trees within an island are generally more similar than between islands (D.R. Maddison, 1991) then we can be reasonably sure that, even though we have only a subset of minimal-length trees, those that are missing will not be too different from those that we have (i.e. differing only by a single rearrangement of branches). The result is not surprising since D.R. Maddison (1991) found that in a study of 37 data matrices, only those with retention indices less than 0.67 exhibited multiple islands.

The analysis using HENNIG86 yielded 2,178 minimal-length trees, which also had length = 137, ci = 0.55 and ri = 0.81 (Table 3), and apparently represented a subset of the trees produced by PAUP 3.1. Successive weighting (an *a posteriori* method of weighting available in both PAUP and HENNIG86) was not applied to the present data set (in order to reduce the number of trees) because both heuristic searches resulted in more minimal-length trees than could fit in the available computer memory (10,000 and 2,178 respectively), and the effect of using this method on a

Table 3. Summary statistics for minimal-length cladograms resulting from the cladistic analyses of the Namanereidinae, using PAUP 3.1 and HENNIG86. See text for explanation of cladistic search options. *ci* = consistency index; *ri* = retention index.

analysis	search options	number trees	minimal-length tree	*ci*	*ri*
PAUP	first round search (random/TBR)	394	137	0.555	0.813
	filter	16	137	0.555	0.813
	second round search (TBR on tree #15)	10,000 (overflow)	137	0.555	0.813
HENNIG86	mhennig, bb	2,178 (overflow)	137	0.55	0.81

subset of the most parsimonious trees has not, to my knowledge, been investigated. Further, a number of authors caution against using this form of *a posteriori* weighting for data coded in ways other than additive binary (Farris, 1969; Sankoff & Rousseau, 1975; Carpenter, 1988).

The high number of minimal-length trees (and consequent low resolution of consensus trees, see below) is the result of both too few characters for the number of taxa, and the high level of homoplasy exhibited by many of the characters. Homoplasies are one of the major sources of incongruence in a cladogram. However, not all incompatible occurrences of apomorphies may be attributed to parallel or convergent evolution. Some may be the result of misinterpreted characters in need of re-evaluation. This may apply to several characters used in the analysis, especially the initial assumptions made on the homology of setae of different fascicles. Unfortunately, a character analysis of the large number of minimal-length trees, although technically possible given sufficient time and computer resources, could not be undertaken. A more effective approach would undoubtedly be to introduce further characters into the analysis, for example from a comparative study of DNA. Likewise, any attempt at assessing the confidence that one can place on the cladograms, for example using bootstrap analysis or other randomisation tests such as PTP or tPTP (see Trueman, 1993 for an outline of these methods), would be premature given the existence of multiple cladogenic hypotheses.

Considering the large number of minimal-length trees it was considered inappropriate to select one as a "best" hypothesis of relationships. Rather, it seems more pertinent to ask "what is the shared information content of these minimal-length trees?" This is summarised in the consensus trees (Figs. 5–7). The high number of collapsed nodes in the Strict Consensus tree indicates that there is low consistency between the minimal-length trees, and therefore that the information content in the data is low (Fig. 5). Closer inspection of the collapsed nodes shows that most (64%) are associated with terminal branches or those one step deeper. The first branch at the base of the namanereidine clade is dichotomous, meaning that every one of the 10,000 minimal-length trees supports the division of the Namanereidinae into two, roughly equal clades. On the basis of this result the generic classification of the Namanereidinae is revised. The two clades are described below as genera. The larger, containing 18 species, takes the name *Namalycastis*, and the smaller with 15 species takes the oldest available generic name of its constituent species, namely *Namanereis*. The revised classification is presented below.

Like the Strict Consensus tree, the Majority-rule and Nelson Consensus trees (Figs. 6,7) are not the most parsimonious solutions, so in a sense they do not represent the best explanation of the data. However, in the absence of an objective way to choose between the 10,000 competing minimal-length trees, I consider that they represent the best available hypotheses on the phylogeny of the group. The Majority-rule tree in particular, being the most highly resolved of the consensus trees, is the most informative hypothesis, and therefore also the easiest to refute (Fig. 7). Nevertheless, it appears to make good biogeographical sense, as discussed below, and as demonstrated in a more rigorous cladistic biogeographical study (Glasby, this volume).

Monophyly of the Namanereidinae is indicated in the present simultaneous (unconstrained) analysis, thus supporting earlier studies (Fitzhugh, 1987; Glasby, 1991). Autapomorphies of the group are the possession of spherical palpostyles (10a) and the ventral position of the notoacicula (23b). The presence in anterior parapodia of both noto- and neuroacicula (17a) is present in the Namanereidinae, *Stenoninereis*, the hesionids *Ophiodromus*, *Leocrates* and the chrysopetalid *Bhawania*. Whether it is an apomorphic or a plesiomorphic feature cannot be determined on the consensus trees; however in 6% of all minimal-length trees *Stenoninereis* is placed outside the clade containing other Gymnonereidinae, as a unique sister species to the Namanereidinae (Fig. 7). One possibility is that the occurrence of both noto- and neuroacicula in anterior parapodia in *Stenoninereis* (and some hesionids and chrysopetalids) is homoplastic and has evolved independently several times in the nereidoids, and may be dependent in some way on the cephalisation process involving the transformation of anterior parapodia into tentacular cirri.

Well-supported clades in the Majority-rule tree (Fig. 7), or those being present in 95% or more of the minimal-length trees, are:

Within *Namalycastis*, there is a group of mainly South American species (*N. geayi* (*N. arista* n.sp., *N. macroplatis* n.sp., *N. senegalensis*, *N. siolii*)) delineated by the presence of heterogomph spinigers in the preacicular fascicle of parapodia of posterior setigers (31b). This group is the sister group of two Indo-Pacific forms, *N. fauveli* and *N.*

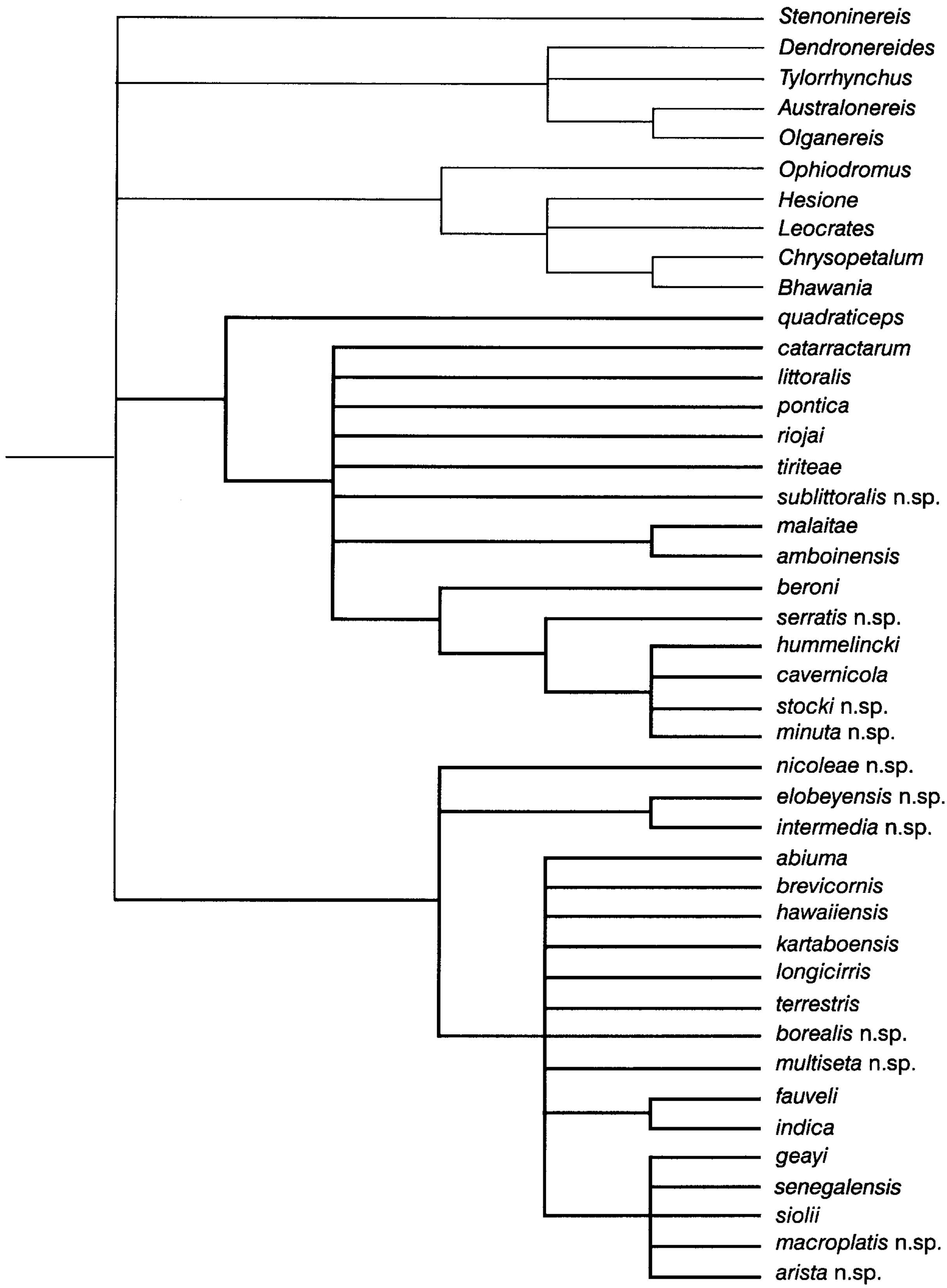

Figure 5. Strict Consensus tree summarising the cladistic relationships of 10,000 minimal-length trees (l = 137; ci = 0.55; ri = 0.81) resulting from the analysis of the Namanereidinae and 10 outgroups. Namanereidinae clades designated by heavy line.

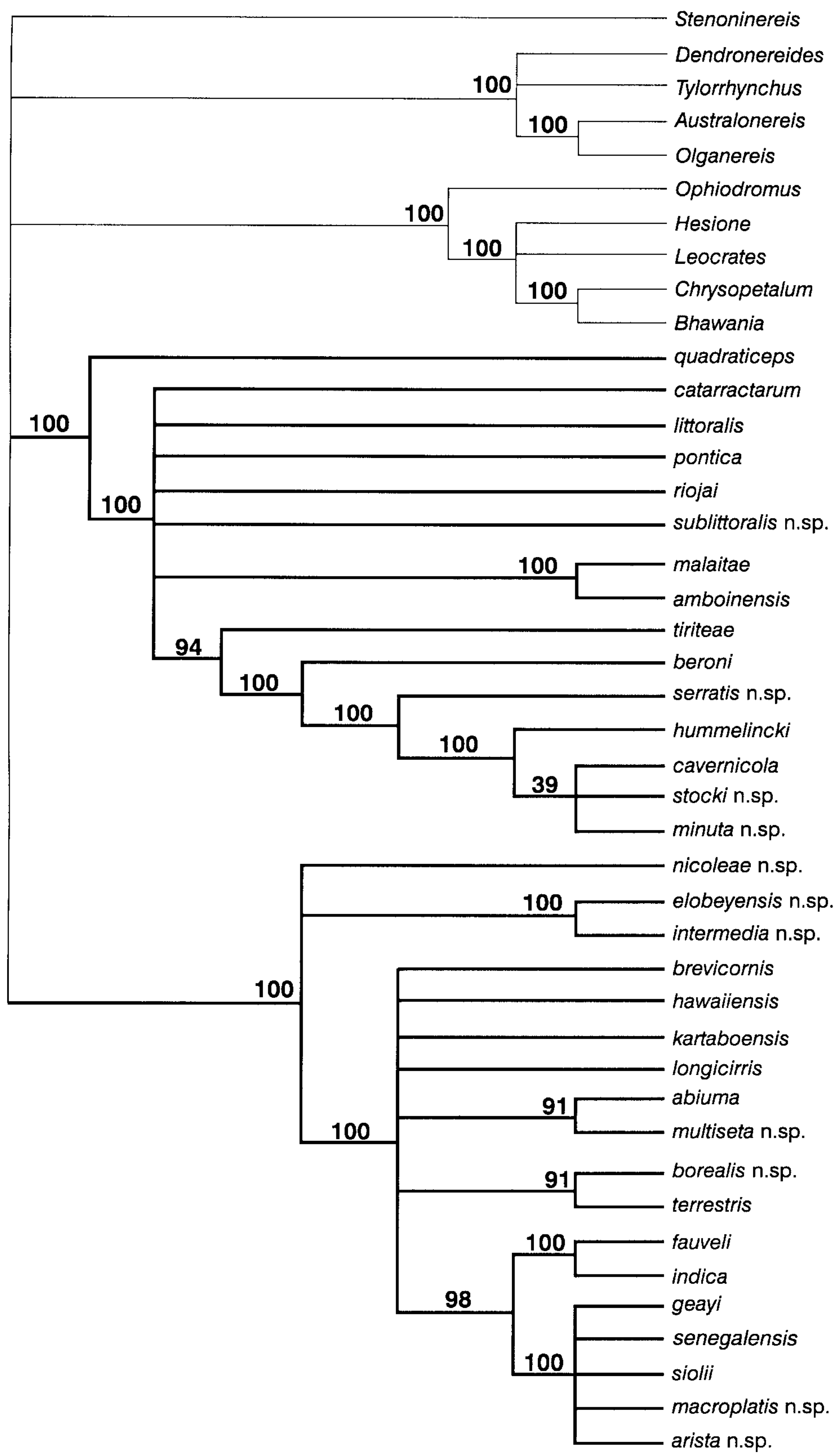

Figure 6. Nelson Consensus tree summarising the cladistic relationships of 10,000 minimal-length trees (l = 137; ci = 0.55; ri = 0.81) resulting from the analysis of the Namanereidinae and 10 outgroups. Namanereidinae clades designated by heavy line. Percentages of minimal-length trees supporting each clade are indicated.

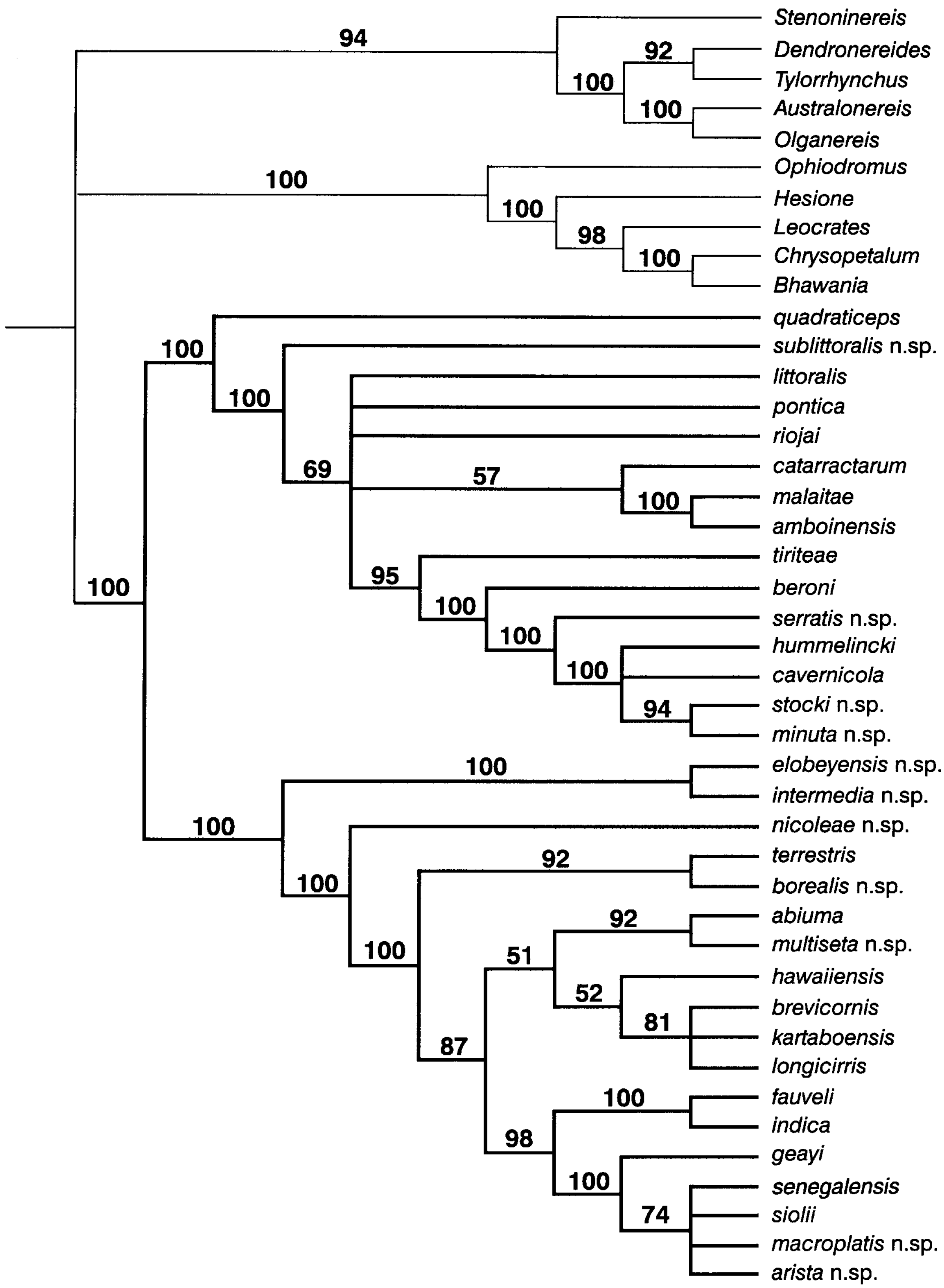

Figure 7. 50% Majority-rule Consensus tree summarising the cladistic relationships of 10,000 minimal-length trees (l = 137; ci = 0.55; ri = 0.81) resulting from the analysis of the Namanereidinae and 10 outgroups. Namanereidinae clade designated with heavy line. Percentages of minimal-length trees supporting each clade are indicated.

indica, recognised by the presence of a well-developed lens (9b; homoplastic feature that also occurs in *N. multiseta* and some species of *Namanereis*). The clade containing these two groups, found in 98% of all minimal-length trees, is characterised by two synapomorphies, a distinct body shape in which the greatest width is mid-anteriorly (2b; rather than anteriorly), and by the presence of slender, compound spinigerous epitokal setae (39a), although the latter character is poorly known. Another well-supported clade within *Namalycastis* is (*N. elobeyensis* n.sp., *N. intermedia* n.sp.), amphi-Atlantic species, recognised by the presence of faintly jointed cirrostyles of the tentacular cirri (14b) and the absence of notosetae (25b), both homoplastic features, the latter one also delineating the genus *Namanereis*. The grouping of all *Namalycastis* species, excluding *N. elobeyensis* n.sp. and *N. intermedia* n.sp., is supported by the presence of a bilobed acicular neuropodial ligule (20b), although this necessitates a reversal to the subconical-shaped ligule in *N. indica* and *N. siolii*. Within this last clade, *N. nicoleae* n.sp., which is apparently the only Gondwanan member of the group (excluding the widespread species group *N. abiuma*), is the sister species of a larger group, including both Indo-Pacific and American species, delineated by having greater than 150 setigers (1b) and a pygidium with a multi-incised rim (36a); this large group probably corresponds most closely to the original concept that Hartman (1959a) had for the genus.

Within *Namanereis* there is a group of groundwater species having a mainly Caribbean distribution—(*N. serratis* n.sp. (*N. cavernicola, N. hummelincki* (*N. minuta* n.sp., *N. stocki* n.sp.)))—supported by the synapomorphy of terminally bifid jaws (16b). The sister species to this group is the cave-dwelling *N. beroni*, known today only from New Guinea. The sister species to the larger group including *N. beroni* is the riverine species, *N. tiriteae* which has been found in New Zealand and Fiji. Together, all species form a clade, found in 95% of all minimal-length trees, comprising cryptic freshwater species and delineated by the autapomorphic loss of eyes (8d).

In a second clade within *Namanereis, N. amboinensis* and *N. malaitae* are sister species united by the synapomorphic presence of epitokal capillary setae (39b) and the presence of a well-developed lens (9b), although the occurrence of this latter feature in *N. quadraticeps* and *Namalycastis* is a homoplasy. The clade containing three Indo-Pacific species—*N. catarractarum* as sister species to *N. amboinensis* and *N. malaitae*—is tenuous, supported by the presence of very small posterior eyes (8b; relative to the anterior pair) in both *N. catarractarum* and *N. amboinensis* but this requires a reversal to the plesiomorphic condition (8a; anterior and posterior eyes equal in size) in *N. malaitae*. Finally, the position of the Gondwanan species group, *N. quadraticeps*, at the base of the *Namanereis* clade is indicated in all minimal-length trees. The ancestors of this taxon gave rise to all other *Namanereis* species by the reduction in the number of tentacular cirri from four (13b) to three pairs (13a), the loss of notosetae (25b), and the change in shape of the oocytes from spherical (38a) to ellipsoidal (38b). Clearly these are an impressive series of ancestor-descendent changes, and they suggest that there may have been a series of intermediate forms that may have become extinct, or await discovery.

Further discussion of the phylogeny within the Namanereidinae is presented in the Remarks of each species in the Taxonomy section.

Classification. The following is a revised classification of the Namanereidinae based on the results of the cladistic analysis. The poorly-known species *Lycastoides alticola* was excluded from the cladistic analysis and as such its position within the subfamily remains unknown. Species are arranged as indicated in the Strict Consensus tree. Changes to the generic status of a species first proposed here are indicated with "n.comb." after the species name. Autapomorphies in the generic and subfamily diagnoses are indicated in italics.

Subfamily Namanereidinae Hartman, 1959a

Genus *Lycastoides* Johnson, 1903, questionable/incertae sedis

- *L. alticola* Johnson, 1903

Genus *Namalycastis* Hartman, 1959a

- *N. nicoleae* n.sp.
- *N. elobeyensis* n.sp.
- *N. intermedia* n.sp.
- *N. abiuma* (Grube, 1872) species group
- *N. brevicornis* (Audouin & Edwards, 1833) n.comb.
- *N. hawaiiensis* (Johnson, 1903)
- *N. kartaboensis* (Treadwell, 1926) n.comb.
- *N. longicirris* (Takahasi, 1933)
- *N. terrestris* (Pflugfelder, 1933)
- *N. borealis* n.sp.
- *N. multiseta* n.sp.
- *N. fauveli* Nageswara Rao, 1981
- *N. indica* (Southern, 1921)
- *N. geayi* (Gravier, 1901) n.comb.
- *N. senegalensis* (Saint-Joseph, 1900)
- *N. siolii* (Corrêa, 1948)
- *N. macroplatis* n.sp.
- *N. arista* n.sp.

Genus *Namanereis* Chamberlin, 1919

- *N. quadraticeps* (Blanchard in Gay, 1849) species group
- *N. catarractarum* (Feuerborn, 1931a)
- *N. littoralis* (Grube, 1872) species group
- *N. pontica* (Bobretzky, 1872) n.comb.
- *N. riojai* (Bastida-Zavala, 1990) n.comb.
- *N. tiriteae* (Winterbourn, 1969) n.comb.
- *N. sublittoralis* n.sp.
- *N. malaitae* (Gibbs, 1971) n.comb.
- *N. amboinensis* (Pflugfelder, 1933)
- *N. beroni* Hartmann-Schröder & Marinov, 1977
- *N. serratis* n.sp.
- *N. hummelincki* (Augener, 1933b)
- *N. cavernicola* (Solís-Weiss & Espinasa, 1991) n.comb.
- *N. stocki* n.sp.
- *N. minuta* n.sp.

Taxonomic account

NAMANEREIDINAE Hartman

Lycastinae Corrêa, 1948: 245.

Namanereinae Hartman, 1959a: 160.

Namanereidinae.–B.-L. Wu, Sun & Yang, 1981: 42; 1985: 44.–Fitzhugh, 1987: 174–175.

Description. Prostomium with paired lateral antennae (rarely absent). Palps biarticulate, palpophores compact, unarticulated; *palpostyles spherical*. Peristomium length equal to or less than length of setiger 1. Tentacular cirri, three or four pairs (two pairs peristomial; one or two pairs segmentally derived). Pharynx divided into oral and maxillary rings; without paragnaths or papillae (but see below); Area V (oral ring) a narrow longitudinal groove or pad. Parapodia reduced, lacking true notopodial lobes or ligules but dorsal cirri present; notoacicula and neuroacicula in all setigers (including first two); *notoacicula in ventral position*; neuropodia with single acicular ligule. Notosetae, when present, are sesquigomph spinigers. Neurosetal types and arrangement variable, include sesquigomph spinigers, heterogomph falcigers and heterogomph spinigers in supra-acicular fascicles; heterogomph spinigers heterogomph pseudospinigers and heterogomph falcigers in subacicular fascicles. Sexual (epitokal) modifications include enlargement of eyes and presence of capillary and slender compound setae.

Type genus. *Namanereis* Chamberlin, 1919.

Remarks. The autapomorphic features of the subfamily are the spherical palpostyles and ventral position of the notoacicula (Glasby, 1991). The subfamily description also includes several features that have not been recognised previously, such as the compact and unarticulated palpophores, the length of the peristomium equal to or less than the length of setiger 1, the presence of a narrow longitudinal groove or pad on Area V of the oral ring, and parapodia of the first two setigers carrying both noto- and neuroacicula. These latter features are, however, either plesiomorphic or homoplastic.

A relatively short peristomium also occurs in some Gymnonereidinae (Glasby, 1991). The relative length of the peristomium appears to be correlated in some way with the position of the tentacular cirri. Nereids having short peristomia also have their "tentacular" cirri arising from the peristomium, whereas nereids having relatively long peristomia (greater than length of setiger 1) appear to have the tentacular cirri arising from between the peristomium and the prostomium. Given that the anterior two pairs of tentacular cirri are thought to be derived from the peristomium and that two pairs (or one pair in the case of some Namanereidinae) are segmentally derived (Gilpin-Brown, 1958 and references therein; see previous discussion), it seems that the ontogenetic development of the peristomium differs markedly in the two groups. This observation could be verified by a comparative study of the innervation of larvae and newly metamorphosed juveniles. For the present cladistic analysis however, the character is phylogenetically uninformative since *Olganereis edmondsi* is the only nereid in the analysis having the elongate type of peristomium.

Both paragnaths and papillae were thought to be absent from the pharynx of Namanereidinae (Hartman, 1959a; Fitzhugh, 1987). However, pharyngeal papillae were found to be present in juveniles (less than c. 15 setigers) of *Namanereis amboinensis* and *N. hummelincki*. They appear to be arranged in a single row around the oral ring since they are visible in a partially everted pharynx (Fig. 3). The papillae are apparently lost in the adults of these species.

The presence of both the notoacicula and neuroacicula in the parapodia of the first two setigers is unusual among the Nereididae and was found to be a symplesiomorphy in an earlier more general analysis (Glasby, 1991). *Stenoninereis* and some hesionids share the symplesiomorphy with the Namanereidinae. In contrast, most nereids lack the notoacicula in the most anterior two pairs (Chamberlin, 1919; Southern, 1921), which is a synapomorphy for a large group, including members of Nereidinae and Gymnonereidinae.

Historically, there has been little agreement on an appropriate descriptive term for the parapodia of Namanereidinae—biramous, sub-biramous and uniramous have all been suggested. Taking "ramous" to mean a branch or prong, such as the notopodia (consisting of notoacicula, notosetae and ligules) or neuropodia (consisting of neuroacicula, neurosetae and ligules), then clearly the parapodia in Namanereidinae are neither bi- or uniramous. Sub-biramous perhaps best describes the reduced notopodial condition of the namanereidine parapodia. However, the problem with this term is that it has also been used to described the parapodial condition of other polychaetes such as dorvilleids, eunicids, certain hesionids, in which the notopodia is less-well developed than the neuropodia but for which there is a distinct interramal space. By contrast, an interramal space is not present in the Namanereidinae because the notopodia has "grafted" onto the neuropodia so completely as to have obliterated it (Fig. 1a). Therefore, it is probably not useful, or necessary, to use this or any of the other simplified terms above to describe the namanereidine parapodia. The issue of whether the reduced parapodia of the Namanereidinae is derived or plesiomorphic is discussed elsewhere (see discussion under Taxonomic and Phylogenetic Characters).

Two genera are recognised, *Namalycastis* with 18 species, and *Namanereis* with 15 species. The generic status of *Lycastoides* is uncertain.

Etymology. See etymology for the genus, *Namanereis*.

Key to the genera of Namanereidinae (excluding *Lycastoides*)

1 Antennae short, subconical (Fig. 12a); dorsal cirri anteriorly with cylindrical cirrophores, posteriorly cirrophores are flattened (leaf-like) (Fig. 8a); notosetae usually present; pygidium usually button-shaped, multi-incised (Fig. 8b); mature individuals with numerous, spherical oocytes in each segment .... *Namalycastis*

—— Antennae relatively long in relation to prostomium size, usually cirriform (Fig. 35a), rarely subconical (Fig. 38a), absent in *N. malaitae* (Fig. 40a), subspherical in *N. quadraticeps* (Fig. 44a); dorsal cirri lacking cirrophores, short and similar in length throughout (Fig. 8c); notosetae absent, except in *N. quadraticeps* (Fig. 44e); pygidium with two large lateral regions and dorsally a smaller pointed one (Fig. 8d); mature individuals with few, ovoid oocytes in each segment (spherical in *N. quadraticeps*) .... *Namanereis*

The presence of notosetae is an easy character to interpret and should be used as a first step in identifying the genus: its presence in the specimen being identified indicating a *Namalycastis* species or the subantarctic species *Namanereis quadraticeps*. Lack of notosetae means that the species may be one of the remaining *Namalycastis* species or a *Namanereis* species. The next step is to use the only unequivocal character separating the two genera, shape of the dorsal cirri, with the warning that this character may be misinterpreted in one narrowly-distributed species, *Namalycastis nicoleae*, which has only weakly developed leaf-like dorsal cirri in posterior setigers. The other characters in the key should be used to confirm identification, although the shape of the pygidium is potentially a difficult character to recognise for the non-expert.

Lycastoides Johnson, indeterminable/*incertae sedis*

Lycastoides Johnson, 1903: 213.–Fauchald, 1977: 89

Type species. *Lycastoides alticola* by monotypy.

Remarks. *Lycastoides*, erected for a single species *L. alticola*, is poorly known, and therefore not included in the cladistic analysis. There is no doubt that the genus belongs to the Namanereidinae having reduced notopodia, lacking pharyngeal papillae and paragnaths and apparently having spherical palpostyles, but there is considerable uncertainty over whether it deserves its generic status. The only features setting it apart from *Namanereis* are (i) having the antennae produced from prostomial lobes; and (ii) having the cirrophore of the posterodorsal pair of tentacular cirri greatly elongated. The first attribute is particularly difficult to interpret, especially in small species (such as *L. alticola*). Some *Namanereis* (e.g., *N. cavernicola*) have antennae that appear to merge basally with the prostomium, although not to the extent of that illustrated for *L. alticola* (see Johnson, 1903: pl. XVII, fig. 24). Further, the form of the antennae and prostomium may be affected by preservation methods and its usefulness needs to be further investigated. The second feature, the elongated form of the cirrophore, is also difficult to interpret. Cirrophores of varying degrees of development are found in *Namanereis* but none that are “greatly elongate”. As the feature is subject to different interpretations, it would be desirable to examine the cirrophores of *L. alticola* first hand to establish whether the character state distinctions are justifiable. Unfortunately no material of this species exists (see Remarks below).

Lycastoides alticola Johnson

Fig. 9

Lycastoides alticola Johnson, 1903: 212–214, pl. XVI, figs. 14–16, pl. XVII, figs. 24–27.

Material examined. None.

Diagnosis. Eyes absent. Jaws with single robust terminal tooth. Notosetae absent. Neurosetal types not known in detail. Sub-neuroacicular setae: heterogomph spinigers in postacicular fascicle. Sub-neuroacicular spinigers in mid-posterior region with blades having long, fine serrations proximally.

Description. Following account based on description and illustrations of Johnson (1903). Holotype segmentally complete. 54 setigers, 15 mm long, 1 mm wide (position along body not specified). At setiger 10 length of parapodia about 0.33 × body width.

Prostomium. Deeply cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium 1.6 × wider than long. Antennae cirriform, smooth, extending beyond tip of palpostyle; aligned over inner edge of palps. Eyes absent.

Peristomium. Tentacular cirri with cirrophores distinct—posterodorsal pair with “greatly elongated common basal joint” (= ceratophore); cirrostyles faintly jointed (anterodorsal and posterodorsal pairs with 5 joints). Anterodorsal tentacular cirri 1.4 × length anteroventral. Anterodorsal tentacular cirri 0.5 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 5. Jaws with single robust terminal tooth, 3–4 subterminal teeth (probably includes teeth ensheathed), moderately sclerotised.

Parapodia. Acicular neuropodial ligule subconical. Dorsal cirri 2.0 × length of podium at setiger 3, 2.5 × length of podium in mid-body.

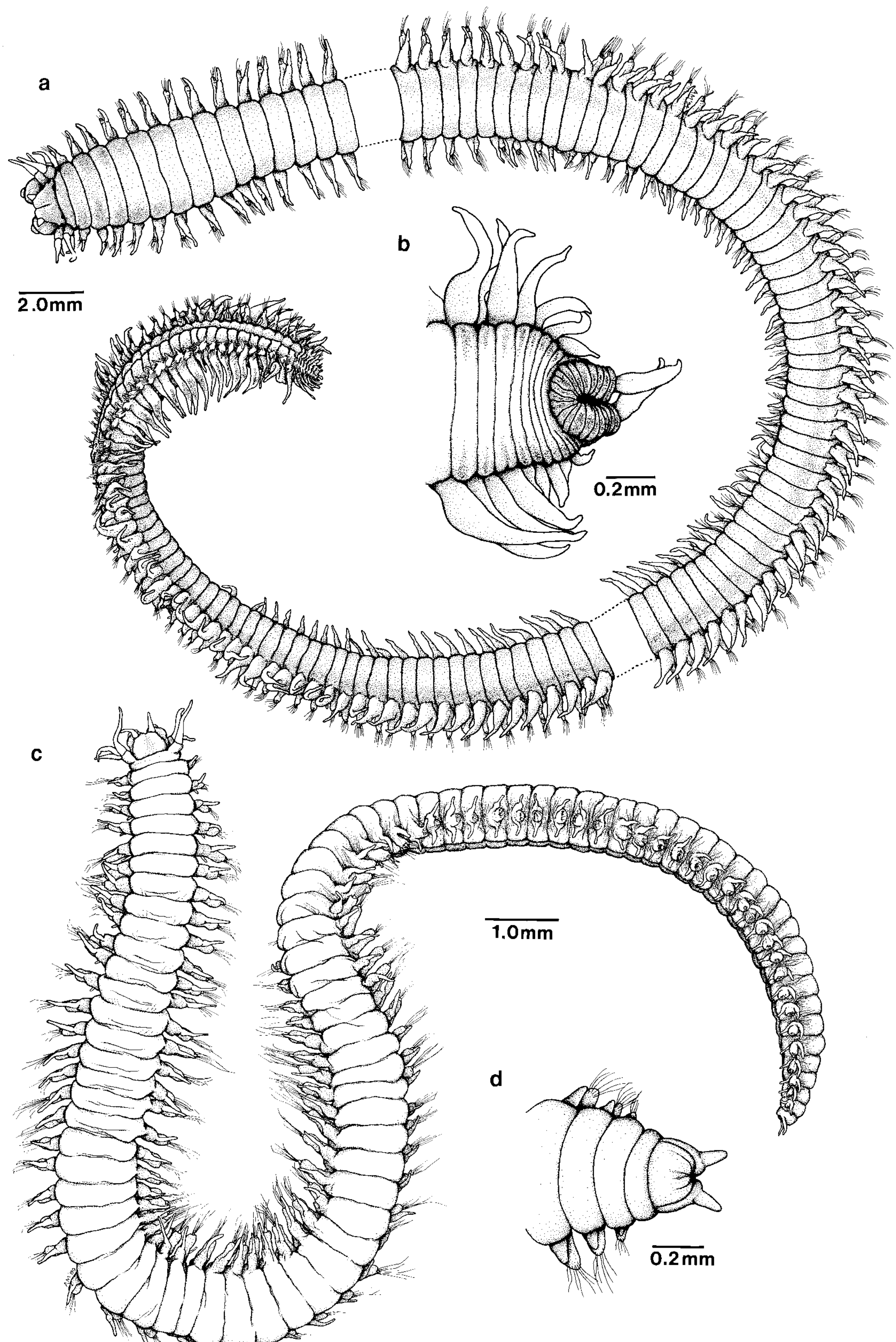

Figure 8. Typical forms of *Namalycastis* (above) and *Namanereis* (below). (*a*) body plan of a typical *Namalycastis* (*Namalycastis abiuma* species group non-type [AM W20239]), (*b*) pygidium of a typical *Namalycastis* (*Namalycastis abiuma* species group non-type [AM W20240]), dorsal view; (*c*) body plan of typical *Namanereis* (*Namanereis cavernicola* non-type [AHF POLY 1228]); (*d*) pygidium of a typical *Namanereis* (*Namanereis littoralis* non-type [AM W20280]), dorsal view.

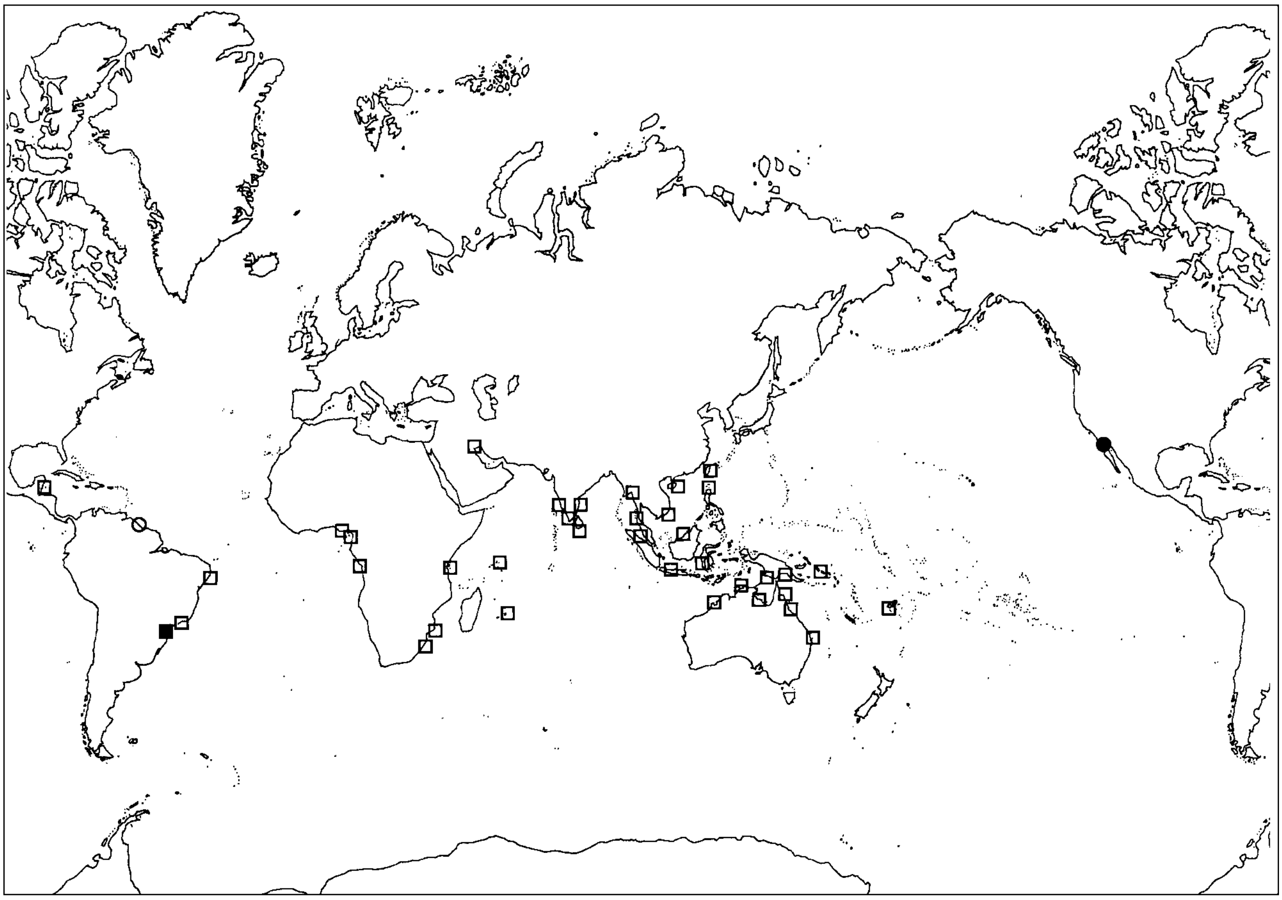

Figure 9. Distribution of *Lycastoides alticola* ●, *Namalycastis abiuma* species group □ and *N. arista* n.sp. ○, based on material examined and authenticated literature records. Also indicated is the type locality of *Namalycastis abiuma* ■.

Setae. Supra-neuroacicular setae: sesquigomph spinigers (most probably) in postacicular fascicle, 2 in podium 30; setal type unknown in preacicular fascicle. Sub-neuroacicular setae: heterogomph spinigers, 1 in podium 30; heterogomph falcigers in preacicular fascicle, 3 in podium 30 (unsure whether setae in post- or preacicular fascicle).

Heterogomph setae with boss not prolonged. Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 9.1 × longer than width of shaft head, large number of teeth; ventral-most 4.9 × longer than width of shaft head, 21 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having long, fine serrations proximally.

Remarks. Data for the present description are taken entirely from Johnson's (1903) description, as no specimens are known to exist. Measurements are taken from Johnson's illustrations (pl. XVI, figs. 14–16; pl. XVII, figs. 24–29) and are approximations. Some characters, including the type of setae in the supra-neuroacicular (preacicular) fascicle (if present), and all those relating to the pygidium and sex of the species, were not described by Johnson and therefore are absent in the present description.

The type material of H. P. Johnson is notoriously difficult to locate and much of it may be lost (M. Pettibone, pers. comm., 1986). The most likely repositories, the AHF and the Museum of Comparative Zoology, Harvard University, Cambridge, were checked without success (the former Institution was checked personally, the latter one by correspondence with the curator). However, the description of Johnson (1903) is sufficiently detailed to indicate that the species is probably valid, even though some doubt exists over the generic status. Distinguishing features include the absence of eyes, antennae produced "insensibly" from the prostomial lobes, presence of four pairs of tentacular cirri, the relatively long, slender dorsal cirri in anterior and mid parapodia, the long antennae, and the articulated posterodorsal tentacular cirri which extend back to about setiger 5. However, the observation that this species has four pairs of tentacular cirri should be viewed cautiously. As noted by Hartman (1959a) it seems to have been assumed by earlier workers that nereids typically have four pairs of tentacular cirri and that the fourth pair, when lacking, was the result of accidental loss (in my experience the tentacular cirri of nereids are rarely lost as a result of collection/preservation processes). Indeed Johnson (1908) apparently overlooked two pairs of tentacular cirri in a description of *Namanereis quadraticeps* (Johnson, 1908: fig. 1).

The species is probably most similar to *N. cavernicola*, which was described from high altitude in Mexico, but also occurs in the Caribbean. As remarked upon by Solís-

Weiss & Espinasa (1991), both species have a cleft prostomium, articulated and well-developed antennae, tentacular and anal cirri, lack eyes, have jaws with few teeth and a small body size. Also setal types and distribution appear similar. The only apparent differences between the two species are that *L. alticola* has four pairs of tentacular cirri (*vs* three pairs in *N. cavernicola*) and an elongated cirrophore of the dorsal-most tentacular cirri. If, as remarked above, there was a misinterpretation of the number (and form) of the tentacular cirri, then the two species may be conspecific.

Habitat. The type habitat is about 2150 m above sea level in freshwater.

Distribution. Type locality Sierra de Laguna, Baja, Mexico.

Etymology. Johnson presumably named the species after the L. *altus*, meaning high, and the L. *colo*, meaning abide or inhabit.

Namalycastis Hartman

Lycastis.–Audouin & Edwards, 1833: 221.–Castelnau, 1840: 16 (in part).–Quatrefages, 1865: 498–499 (in part).–Ehlers, 1868: 449 (in part).–Grube, 1872: 47–48 (in part).–Gravier, 1902b: 373 (in part).–Johnson, 1903: 214–215 (in part).–Horst, 1909: 4–5 (in part).–Fauvel, 1923b: 331; 1932: 89; 1953: 166.–Uschakov, 1955: 204 (in Russian); 1965: 185 (in English). *Non* Savigny, 1822.

Namalycastis Hartman, 1959a: 163–164.–Day, 1967: 301.–Winterbourn, 1969: 282–284 (in part).–Fauchald, 1977: 89.

Description. Body with many setigerous segments (generally, adults with greater than 150). Prostomium anteriorly cleft (usually); *antennae short, subconical*. Eyes, two pairs. Tentacular cirri, 4 pairs; cirrophores present but may be indistinct. Pharynx with Area V as narrow medial groove. Jaws with a single robust terminal tooth. Dorsal cirri usually increasing in length in length posteriorly; cirrophores cylindrical anteriorly, *flattened (leaf-like) posteriorly*. Notosetae present, sesquigomph spinigers (rarely absent). Neurosetae present, type A or B (Fig. 1c). Supra-neuroacicular setae: sesquigomph spinigers in postacicular fascicle; heterogomph falcigers or heterogomph spinigers (rarely) in preacicular fascicle. Subneuroacicular setae: heterogomph spinigers in postacicular fascicle; heterogomph falcigers or heterogomph spinigers (rarely) in preacicular fascicle. Falcigers with blade attached to setal shaft by a ligament and hinge (Fig. 2). Setal shafts distally smooth. Pygidium with multi-incised rim. Dioecious. Oocytes small, 116 ± 17 µm (max. diameter); spherical.

Type species. *Lycastis abiuma* Grube, 1872, by subsequent designation (Hartman, 1959a).

Remarks. According to Hartman (1959a), *Lycastis* was erected for two species, *Nereis armillaris* Müller (now known to be a syllid of the genus *Typosyllis*) and *Nereis versicolor* Müller (a nereid of the subfamily Nereidinae). *Lycastis* is therefore a junior synonym of both *Nereis* and *Typosyllis* and a new generic name was needed. That *Lycastis* was representative of two or more unrelated taxa was recognised early on by Quatrefages (1865), Ehlers (1868), Grube (1872), Gravier (1902b), Johnson (1903) and Leiper (1908). The situation was partially remedied when Chamberlin (1919) erected the genus *Namanereis* to contain all 10 previously described namanereidine species (described under the name *Lycastis*) excluding *Lycastoides alticola*, which was kept in a separate genus. When Hartman (1959a) revised the Namanereidinae she proposed the new name *Namalycastis* to include all species having four pairs of tentacular cirri. Species having three pairs of tentacular cirri were retained in *Namanereis* (note that Hartman apparently regarded *N. quadraticeps* as having three pairs of tentacular cirri). Ten years after Hartman's revision of the subfamily the definition of *Namalycastis* was broadened slightly when Winterbourn (1969) shoe-horned his new species, *N. tiriteae* into the genus, a species having only three pairs of tentacular cirri. However, in other important respects this species does not fit into *Namalycastis* and it is herein transferred to the genus *Namanereis* (see Remarks for *N. tiriteae*), hence the "in part" in the synonymies.

There is some confusion over whether the genus *Paranereis* is a junior synonym of *Namalycastis* (as suggested by Hartman, 1959a), and further, who was the authority of its type species, *Lycastis abiuma*. As far as I can ascertain, Fritz Müller collected, and donated to Grube, specimens of both *Lycastis abiuma* and *L. littoralis*. Grube (1872) paraphrased Müller who considered that the former species was referable to *Paranereis*, a genus described earlier by Kinberg (1866). However, later in the description, Grube states that he (Grube) did not find enough characters to refer the species to *Paranereis*, and in the remainder of the paper refers to the species under *Lycastis*. Therefore, since the opinion of Müller does not constitute a publication (under the ICZN guidelines), the species can not be regarded as having been published under the name *Paranereis*. As to the authority of the species, the charitable view would be to refer to "Müller in Grube" since it appears as though Grube may have paraphrased a letter by Müller describing the new species (K. Fauchald, pers. comm., 1997). However, since Grube provided an important degree of interpretation as to what genus the species belonged, it seems more prudent to take Grube as the sole authority. The year of publication, variously cited as 1871 and 1872, is clearly 1872; 1871 was the date that Grube orally presented the paper.

The present generic description differs, most notably, from recent descriptions (Day, 1967; Fauchald, 1977) in that setae may be entirely spinigerous and therefore allows for the inclusion of the aberrant species, *Namalycastis geayi* (Gravier). In addition the presence of a deep median cleft in the prostomium, flattened dorsal cirri (cirrophores) of parapodia of posterior setigers and a pygidium with a multi-incised rim are features that have not been included in previous generic diagnoses. Autapomorphies of the genus, as determined in the cladistic analysis, are the presence of short, subconical antennae and the flattened cirrophores of posterior dorsal cirri.

Etymology. From the Greek *Nama*, meaning spring or stream, and *lycastis*, referring to the freshwater habitat common to many species.

Key to the species of *Namalycastis*

1 Heterogomph falcigers present in sub- and supra-preacicular fascicle in all parapodia 2

—— Heterogomph falcigers in anterior parapodia, replaced by heterogomph spinigers posteriorly in sub- and supra-preacicular fascicle 13

—— Only heterogomph spinigers present in sub- and supra-preacicular fascicle in all parapodia .... *N. geayi*

2 Notosetae absent or present (*N. nicoleae* only); pygidium tripartite, with two small lateral lobes and a smaller pointed dorsal lobe; small species with mature individuals up to 90 setigers 3

—— Notosetae always present; pygidium usually with multi-incised rim; large species with mature individuals over 100 setigers 4

3 Antennae extending short of tip of palpophore; notosetae are sesquigomph spinigers; sub-neuroacicular falcigers in setiger 10, dorsally, with blades having many teeth (50 teeth or more) .... *N. nicoleae* n.sp.

—— Antennae extending beyond tip of palpophore; notosetae absent; sub-neuroacicular falcigers in setiger 10, dorsally, with blades having 22 to 35 teeth .... *N. elobeyensis* n.sp.

4 Sub-neuroacicular spinigers in mid-posterior parapodia with blades having short, fine serrations proximally (Fig. 12g) 5

—— Sub-neuroacicular spinigers in mid-posterior parapodia with blades having coarse serrations proximally (Fig. 20i) 7

5 Antennae minute (Fig. 17a); heterogomph setae with boss extremely prolonged .... *N. fauveli*

—— Antennae distinct, but extending short of tip of palpophore; heterogomph setae with boss not prolonged 6

6 Prostomium anteriorly deeply cleft (Fig. 30a); dorsal cirri usually less than 2 × length of parapodium of setiger 3; more than 5 (up to 15) supra-neuroacicular heterogomph falcigers in each parapodium .... *N. terrestris*

—— Prostomium anteriorly shallowly cleft (Fig. 12a); dorsal cirri usually greater than 2 × length of parapodium of setiger 3; less than 5 supra-neuroacicular heterogomph falcigers in each parapodium .... *N. borealis* n.sp.

7 Supra-neuroacicular falcigers in parapodia of setiger 10 with smooth blades 8

—— Supra-neuroacicular falcigers in parapodia of setiger 10 with serrated blades 9

8 Tentacular cirri with smooth cirrostyles; supra-neuroacicular falcigers in parapodia of setiger 10 with blades less than 4 × longer than width of shaft head .... *N. brevicornis*

—— Tentacular cirri with cirrostyles faintly jointed; supra-neuroacicular falcigers in parapodia of setiger 10 with blades 6–7 × longer than width of shaft head .... *N. kartaboensis*

9 Prostomium 1.3 to 2.3 × wider than long; usually less than 10 sesquigomph spinigers in neuropodial supra-acicular fascicle in midbody 10

—— Prostomium 2.4 × wider than long or more; 10–30 sesquigomph spinigers in neuropodial supra-acicular fascicle in midbody .... *N. multiseta* n.sp.

10 Sub-neuroacicular spinigers with proximally coarsely serrated blades present from parapodia of setiger 3 to 17; approximately equal numbers of falcigers and spinigers in neuropodial subacicular fascicle 11

—— Sub-neuroacicular spinigers with proximally coarsely serrated blades present from parapodia of setiger 30 to 150; many more falcigers than spinigers in neuropodial subacicular fascicle 12

11 Tentacular cirri with cirrophores distinct; dorsal cirri increasing slightly in length posteriorly .... *N. indica*

—— Tentacular cirri with cirrophores indistinct; dorsal cirri increasing greatly in length posteriorly .... *N. longicirris*

12 Brown epidermal pigment dorsally and on pygidium; sub-neuroacicular falcigers in parapodia of setiger 10, dorsally, with blades about 4–7 × longer than width of shaft head and having up to 18 teeth .... *N. abiuma* sp. group

—— Epidermal pigment absent; sub-neuroacicular falcigers in parapodia of setiger 10, dorsally, with blades about 8–11 (rarely less) × longer than width of shaft head and having 35 to 70 (rarely fewer) teeth .... *N. hawaiiensis*

13 Notosetae absent; small species with mature individuals up to 90 setigers .... *N. intermedia* n.sp.

—— Notosetae present, as sesquigomph spinigers; large species with mature individuals usually exceeding 100 setigers 14

14 Acicular neuropodial ligule simple, subconical; supra-neuroacicular falcigers in parapodia of setiger 10 with blades smooth or only serrated basally, about 8 × longer than width of shaft head .... *N. siolii*

—— Acicular neuropodial ligule bilobed; supra-neuroacicular falcigers in parapodia of setiger 10 with blades serrated over most of their length, 3.3 to 7.5 × longer than width of shaft head 15

15 Dorsal cirri usually greater than twice (up to five times) length of parapodium at setiger 3; dorsal-most sub-neuroacicular falcigers in parapodia of setiger 10 with blades having 5 to 12 teeth 16

—— Dorsal cirri less than twice length of parapodium at setiger 3; dorsal-most sub-neuroacicular falcigers in parapodia of setiger 10 with blades having 16 to 30 teeth .... *N. macroplatis* n.sp.

16 Prostomium less than 1.4 × wider than long; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss less than 1.3 × length of collar; fine hair-like projection from tip of falciger blades .... *N. arista* n.sp.

—— Prostomium usually 1.4–1.7 × wider than long; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss 1.4 × length of collar or more; falciger blades distally smooth .... *N. senegalensis*

Namalycastis abiuma (Grube)

Figs. 1c, 9, 10a–h; Table 4

Lycastis abiuma Grube, 1872: 47–49.

Material examined. HOLOTYPE: Brazil, Desterro [= Santa Catarina Island] (27°35'S 48°31'W), coll. & leg. Fr. Müller (ZMB Q3436).

Diagnosis. Prostomium shallowly cleft anteriorly, antennae extending to tip of palpophore. Notosetae present, though very few and not in every setiger. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 5.4 × longer than width of shaft head, moderately serrated, 11 teeth, teeth about uniform in length. Sub-neuroacicular falcigers in setiger 10 dorsally with blades 6.2 × longer than width of shaft head, 13 teeth. Sub-neuroacicular spinigers in posterior region with blades having coarse serrations proximally.

Description. Holotype well preserved, segmentally complete, no gametes in coelom. 141 setigers, 45 mm long, 2.2 mm wide at setiger 10; at setiger 10 length of parapodia 0.34 × body width.

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter flat. Colour in alcohol brown. Epidermal pigment absent, probably faded.

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape approximately trapezoidal, laterally slightly indented; 2.1 × wider than long. Antennae smooth, extending to tip of palpophore; aligned over inner edge of palps. Eyes absent, probably faded (Fig. 10a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.5 × length anteroventral. Anterodorsal tentacular cirri 0.7 × length posterodorsal. Posterodorsal tentacular cirri 1.4 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 5 (Fig. 10a). Jaws with single robust terminal tooth, 4 subterminal teeth, 4 teeth ensheathed proximally, brown (Fig. 10b).

Parapodia. Acicular neuropodial ligule bilobed (Fig. 10c). Superior lobe papilliform. Inferior lobe globular. Dorsal cirri increasing in length posteriorly; 1.1 × length of podium at setiger 3 (Fig. 10c), 1.1 × length of podium in mid-body, 2.6 × length of podium posteriorly; 3.1 × longer than wide posteriorly (Fig. 10d). Ventral cirri 0.5 length of podium at setiger 3, 0.4 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 12, few, though absent in podia selected for mounting (3, 10, 30, 60, 120) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (Fig. 10e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.4 × longer than width of shaft head, moderately serrated, 11 teeth, 0.40 × total blade length, teeth about uniform in length (Fig. 10f). Sub-neuroacicular falcigers in setiger 10 with blades moderately serrated; dorsal-most 6.2 × longer than width of shaft head, 13 teeth; ventral-most 4.8 × longer than width of shaft head, 7 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades moderately serrated. Sub-neuroacicular spinigers in anterior region with blades finely serrated (Fig. 10g); posteriorly, from setiger 120, blades having coarse serrations proximally (Fig. 10h). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium with multi-incised rim. Anus dorsoterminal.

Remarks. Since *Lycastis abiuma* is the type species of the genus, the preceding description of the holotype is necessary in order to unambiguously characterise the species, and hence the genus. Unfortunately, the exact limits (morphological and geographical) of this species could not be determined with the present data, and many other specimens have been tentatively identified under the informal taxon name, *Namalycastis abiuma* species group (description following). This informal taxon includes specimens from Brazil (although not near the type locality), that nevertheless differ sufficiently from the holotype as to raise doubts about conspecificity.

Habitat. The type habitat is unknown but specimens collected about 840 km to the north at Guanabara were from intertidal muddy sand under *Avicennia schaueriana* and *Laguncularia racenosa* (Rabelo, 1988). Penedo River specimens in north-eastern Brazil found under the bark of decaying *Rhizophora* branches (Lana, 1984).

Distribution. Known only from the type locality, Santa Catarina Island, Brazil (Fig. 9), though members of the species group (below) are widely distributed.

Etymology. Unknown.

Namalycastis abiuma (Grube) **species group**

Figs. 1c, 8a,b, 9; Table 4

Lycastis meraukensis Horst, 1918: 246–247.–Fauvel, 1932: 82; 1953: 166–167, fig. 85b.
Lycastis indica. Horst, 1924: 148.–Fauvel, 1932: 82–83, pl. II, figs. 1–2 (in part); 1940: 257 (in part).–Aziz, 1938: 27, pl. V, fig. 14, pl. VI, fig. 25, pl. VIII, figs. 96–97.–Ghosh, 1963: 240. *Non* Southern.
Lycastis nipae Pflugfelder, 1933: 68–69, figs. 4–6.
Lycastis vivax Pflugfelder, 1933: 69, figs. 7–8.
Lycastis senegalensis.–Monro, 1939: 217. *Non* Saint-Joseph.
Lycastris [sic] *indica*.–Day, 1951: 27. *Non* Southern.
Namalycastis meraukensis zeylanica Silva, 1961: 172–173, fig 5A–E.

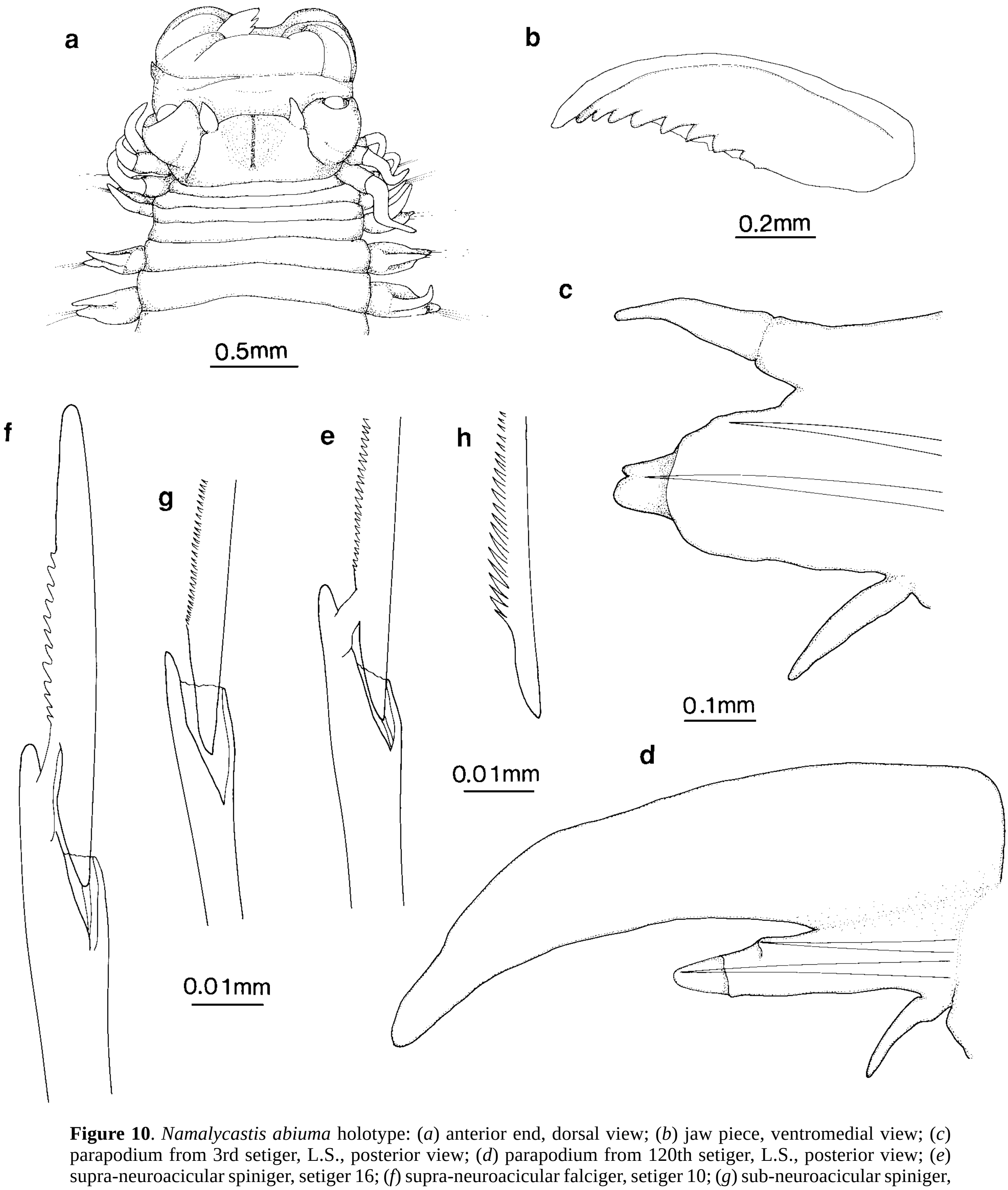

Figure 10. *Namalycastis abiuma* holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., posterior view; (*d*) parapodium from 120th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 16; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 10; (*h*) proximal region of blade of sub-neuroacicular spiniger, setiger 120.

Namalycastis abiuma.–Russell, 1962: 6.–B.-L. Wu & Chen, 1963: 20.–Kirkegaard, 1983: 225–6.–Lana, 1984: 109–111, figs. 105–106 (unpublished); 1987: 1061 (list only).–Rabelo, 1988: 5–9, fig. 1A–F.

Namalycastis rigida Pillai, 1965: 131, 133–136, figs. 8J, 9A–I.

Namalycastis indica.–S.-K. Wu, 1967: 51–52, fig. 2a–c.–Day, 1967: 301, fig. 14.2p–s (?in part).–Gibbs, 1971: 147.–Jaweir, 1987: 229–230. *Non* Southern.

Namanereidinae gen. and spec. indet. Hartmann-Schröder, 1979: 120, figs. 225–6.

Namalycastis cf. *abiuma*.–Hutchings & Glasby, 1985: 104–106, fig. 2a–g (in part).

Material examined. Brazil, Penedo River, Pontal do Sul 2(MCBM BPO-1216). Nigeria, Niger Delta at Koluama 2+10 juv.(AM W24249); Ramos River 1(AM W24250). Cameroun, East of Victoria 1(ZMUC POL-926). Zaire, Banane [= Banana] 2(BMNH ZK 1939.7.17.31–32), 1(BMNH ZK 1939.7.17.33). Mozambique, Morrumbene estuary 1(BMNH ZK 1955.4.1.102). Tanzania, Tanga 2(HZM V6736). Iraq, Basrah, Shatt-al-Arab 10(ZMB 10822), 3(HZM P-13642). Seychelles, Mahé 1(MNHN UE 930). Sri Lanka, Dondra Head 15(AM W20236). India, Vellår River 3(AM W20251), 4(AM W20252), Kerala State, Kayaukulaue Kayal 2(MNHN UE 931), Kerala State, Wypin 5(MNHN AZ 431). Burma, Rangoon 2(BMNH ZK 1931.6.22.70). Thailand, Gulf of Thailand, Bang Sapam Noi [?= Ban Sapam] 2(PMBC 4613), 1(PMBC 4614); Ao Yon 1(PMBC 4615). S. Vietnam, Cochinchine 1(MNHN UE 932). Indonesia, Sulawesi, Ujung Pandang many (ZMA V.Pol. 626); Java, Jepara 4(P. Garwood, pers. coll.). Borneo, Brunei, Kedalayan River (a tributary of the Brunei River) 3(NTM W325), 2(NTM W326). Hainan, 3(ASL 1/11367), 1(ASL 3/11379). Taiwan, Long-Shin 1(USNM 35389). Australia, Western Australia, Derby, 1 headless spec. (HZM P16573); Northern Territory, Port Essington, West Bay 1(NTM W3598), McArthur River, Muggs Mistake 1(NTM W3737), near Black Rocks Landing 1(NTM W3081); Queensland, Lizard Island, Crystal Beach 22(AM W20243), Cairns, Trinity Bay Inlet 1(QM GH3915-in part), Port Douglas 1(QM GH2863-in part), Hinchinbrook Island, Missionary Bay, Coral Creek 2(AM W19480), South Pine River, Bramble Bay 2(AM W20242), Brisbane River, 2 mile reach 1(AM W4951), Serpentine Creek, Cribb Island 4(QM G7495); New South Wales, Yamba 2(AM W7496). Fiji, Viti Levu, Lauwaki 17(AM W20240), Momi Bay 2(AM W20237), 2(AM W20238), Viti Levu Bay, near Marotu 7(AM W20241), Nasivi River at Tavua 1(AM W20239).

Lycastis meraukensis Horst TYPE: New Guinea, Exp. S. W. New Guinea 1904/5, coll. J.W.R. Koch, det. Augener, 1934, from Museum Leiden, parapodia only (HZM V10641).
Lycastis nipae Pflugfelder HOLOTYPE: Sumatra, Strasse von Medan-Belawan, leg. Harms, 17.2.1929 (PMJ Ann. 163). PARATYPES: collection details as for holotype (PMJ Ann. 164).
Namalycastis rigida Pillai PARATYPES: Philippines, Luzon, Malabon 4(UPSL RTS 18), 3(BMNH ZK 1965.33.13–15).
Lycastis vivax Pflugfelder SYNTYPES: Sumatra, Perbaoengen [= Perbaungan] 1(PMJ Ann. 165). 51 specimens measured.

Other material examined. South Africa, St. Lucia estuary, 1(BMNH ZK 1963.1.67), 1(SAM A20334). Mauritius 1(BMNH ZK 1928.1.4.1). India, Madras, Vizagapatam Backwater 1(BMNH ZK 1938.5.7.22). ?Sumatra, Pertjoet collection 4(BMNH 1998.176–179), 15(BMNH 1998.180–189). Sulawesi, Ujung Pandang 1(PMJ Ann. 221) (specimen removed from syntype series of *Namanereis amboinensis* Pflugfelder—Ann. 166). New Guinea, Paili [?= Paile], Marshall Lagoon 1(AM W4946). Nigeria, Odeama Creek, 1(AM W24251). Belize, Anderson Lagoon, 3(USNM 178861).

Lycastis meraukensis Horst SYNTYPES: Irian Jaya, Merauke 9(RNHL 1347).
Namalycastis meraukensis zeylanica Silva SYNTYPES: Sri Lanka, Dondra Head 2(NMC AP2).

Diagnosis. Brown epidermal pigment, brown dorsally and on pygidium. Prostomium usually shallowly cleft anteriorly, antennae usually extending short of tip of palpophore. Notosetae present or absent. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.3–5.7 × longer than width of shaft head (rarely to 4.0), finely to moderately serrated (very rarely lacking serrations), 4–15 teeth (very rarely 0–20), teeth about uniform in length. Sub-neuroacicular falcigers in setiger 10 dorsally with blades 3.7–7.2 × longer than width of shaft head, up to 18 teeth. Sub-neuroacicular spinigers in mid-posterior region with blades having coarse serrations proximally.

Description. Following description based largely on non-type material, but also includes types of *Namalycastis rigida*, *Lycastis meraukensis*, *Lycastis nipae* and *Lycastis vivax*. Specimens range from 93–294 setigers, 23–150 mm long, 2.0–7.0 mm wide at setiger 10 (upper limits for syntypes of *Lycastis meraukensis*). At setiger 10 length of parapodia 0.27–0.50 × body width.

Body. Uniform in width anteriorly, tapering gradually posteriorly (rarely, very slight taper or tapering only in far posterior region) (Fig. 8a). Dorsum convex. Venter flat. Colour in alcohol brown to yellow-white. Epidermal pigment light brown anterodorsally, dark brown postero-dorsally and on pygidium, rarely uniform brown pigmentation on entire dorsum. Living colour reddish-brown dorsally; increasing in intensity posteriorly.

Prostomium. Shallowly cleft anteriorly (rarely deeply), with narrow longitudinal groove extending from tip to mid-posterior prostomium occasionally ending in pit or transverse ridge. Prostomium shape approximately triangular to trapezoidal, laterally slightly indented or notched (rarely); 1.5–2.3 × wider than long. Antennae smooth, usually extending short of tip of palpophore, rarely extending beyond tip of palpophore or short of tip of prostomium; aligned over inner edge of palps to mid-palps. Eyes 2 pairs, black, or purple (very rarely), arranged obliquely or transversely, equal in size, or posterior pair slightly smaller; lenses indistinct.

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.2–1.6 × length anteroventral (rarely 1.0–2.0). Anterodorsal tentacular cirri 0.7–0.9 × length posterodorsal (rarely 0.6–1.0). Posterodorsal tentacular cirri 1.2–1.5 × length posteroventral (rarely 1.1–1.8). Posterodorsal tentacular cirri extending posteriorly to setiger 2–4. Jaws with single robust terminal tooth (wide gap separating terminal and first subterminal tooth occasionally), 4–5 subterminal teeth (rarely 3–6), 3–5 teeth ensheathed proximally, brown or black (very rarely).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular. Dorsal cirri increasing in length posteriorly or, very rarely, similar in length throughout; 0.9–1.8 × length of podium at setiger 3 (very rarely 0.7–2.8), 1.3–3.8 × length of podium in mid-body (rarely 0.6–4.5), 2.1–5.4 × length of podium posteriorly (rarely 1.1–11.2); 1.7–2.7 × longer than wide posteriorly (very rarely 1.1–3.5) (Fig. 10d). Ventral cirri 0.34–0.69 length of podium at setiger 3, 0.25–0.48 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 4–33, though may be entirely absent in some individuals or absent in some parapodia (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4–1.6 × length of collar (rarely 1.3–1.7). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.3–5.7 × longer than width of shaft head (rarely to 4.0), finely to moderately serrated (very rarely lacking serrations), 4–15 teeth (very rarely 0–20), 0.19–0.45 × total blade length (very rarely 0.13–0.55), teeth about uniform in length. Sub-neuroacicular falcigers in setiger 10 with blades finely to moderately serrated; dorsal-most 3.7–5.6 × longer than width of shaft head (rarely to 7.2), 3–10 teeth (very rarely 0–18); ventral-most 3.4–5.6 × longer than width of shaft head, 2–8 teeth (very rarely 0–10). Sub-neuroacicular falcigers in mid-posterior region with blades finely to moderately serrated, or increasingly coarsely serrated proximally (very rarely). Sub-neuroacicular spinigers in anterior region with blades finely serrated; posteriorly from setiger 30–120 (rarely from 10), blades having coarse serrations proximally. Setae pale or dark. Acicula in mid-body brown or black.

Pygidium. Pygidium with multi-incised rim (Fig. 8b). Anus dorsoterminal or terminal. Anal cirri arising ventrally or ventrolaterally, approximately conical (rarely flatenned), smooth, 0.6–1.8 × width pygidium (rarely to 0.2).

Sex. Mature oocytes 103–130 µm (4 specimens measured), straw-coloured, with external membrane (though very thin). Epitokal setae absent (but see below).

Variation. Morrumbene (Mozambique) and Tanga (Tanzania) specimens smaller with 81–120 setigers, 19–33 mm long and 1.6–1.7 mm wide at setiger 10; posterior dorsal cirri more elongate than above, 3.3–5.0 × longer than wide. Basrah (Iraq) specimens with 134–156 setigers, 80–85 mm long, 3.1–4.4 mm wide at setiger 10; sub-neuroacicular falcigers have very few teeth on blades, 2–3 on dorsal-most, 0–1 on ventral-most (few teeth not result of wear); sub-neuroacicular spinigers in mid-posterior region with blades finely serrated proximally. Ao Yon (Thailand) specimen with 140 setigers, 38 mm long, 1.9 mm wide at setiger 10; sub-neuroacicular setae in postacicular fascicle are heterogomph spinigers or heterogomph pseudospinigers (very rarely); anal cirri 2.3 × width of pygidium. Cochinchine (S. Vietnam) specimen is very large at 247 setigers, 335 mm long, 8.5 mm wide at setiger 10; epidermal pigment dark brown dorsally, except dorsal cirri unpigmented; jaws with 8 subterminal teeth; dorsal cirri in mid-body very long, 7.9 × length of podium; numerous subneuropodial heterogomph falcigers (22 in podium 10, 27 in podium 60, 28 in podium 120, 13 in podium 180); sub-neuroacicular spinigers in mid-posterior region with blades finely serrated proximally; sexually mature male with slender compound spinigers (epitokal) in addition to regular complement of setae.

Remarks. Specimens described here closely approximate the description of the holotype of *Lycastis abiuma*; however the variation encompassed is far more than that normally attributed to a species in the Namanereidinae. Therefore the specimens included in the description are given the informal taxon ranking of “species group” as they include forms (described under “Variation”) that can not be distinguished by unique features. However, it may be possible in future to identify good species from among these variant forms using molecular techniques (DNA sequencing) and/or statistical analysis of morphometric data. If using a statistical approach then additional specimens different sizes from each region would have to be examined.

Two general patterns of size-related variation are apparent in the material examined. Small specimens, for example the 10 juveniles (ranging from 44 to about 80 setigers) from Koluama R., Nigeria (AM W24249) and the Belizean specimens (USNM 178861), have falciger blades that are generally more elongate (like pseudo-spinigers) and more heavily serrated—sometimes coarsely serrated proximally—than larger specimens. For this reason, specimens with less than about 80 setigers cannot be easily identified to species; indeed in the form of the setae they can be easily mistaken for *Namalycastis hawaiiensis*. Extremely large individuals such as the single Cochinchine specimen have unusually large numbers of setae (especially subneuropodial heterogomph falcigers) and in this particular case additional slender compound spinigers that most likely are epitokal setae; however, the Cochinchine specimen also has unpigmented dorsal cirri and finely-serrated posterior sub-neuroacicular spinigers, both features that are not normally associated with large size, raising the possibility that it may be a distinct species. Other large specimens, such as one from Penedo R. (MCBM BPO-1216), sometimes have smooth-bladed falcigers in the anterior parapodia and serrated ones posteriorly, raising the possibility that the smooth-bladed types are the result of wear, especially considering that smaller specimens from Penedo R. have finely-serrated falciger blades anteriorly, which is more typical of the species group. Smooth-bladed falcigers were also recorded in specimens from Baía de Guanabara, Rio de Janeiro (Rabelo, 1988).

Considering the species-group status of this taxon, synonymies must remain tentative. However, the following species are likely to be junior synonyms of *Namalycastis abiuma*: *Lycastis meraukensis* Horst, *L. nipae* Pflugfelder, *L. vivax* Pflugfelder, *Namalycastis rigida* Pillai and its subspecies *N. meraukensis zeylanica* Silva. The types of all of these species were examined and included in the present description; those of *L. meraukensis* (RNHL 1347) were briefly examined at the RNHL, but later attempts to borrow the material failed, as according to van der Land (pers. comm., 1987), the type specimens were mislaid, probably as a result of the reorganisation of the spirit collection. During the initial examination it was noted that the small specimens also possessed notosetae, like the larger ones, although there were generally fewer in each parapodium (absent in some). This is contrary to Horst's (1918) observation that the small specimens lacked entirely "notopodial bristles" (notosetae). In other respects the type specimens agreed well with Horst's description, although the pigment had faded somewhat from a dorsum described in 1918 as being "dark flesh-coloured" with a "red-brown ring around the anal segment" to the present condition of yellowish throughout with the anal segment unpigmented. Setal counts and measurements for *L. meraukensis* from the Merauke area are included in the description. The data come from two parapodia (setigers 3, 57) removed from the syntypes and re-registered with the Hamburg collection (HZM V10641). Collection details for HZM V10641 agree with those of the syntypes, however there is no indication on the label that they were actually removed from the syntypes.

The specimens of *L. rigida* examined include three paratypes (BMNH ZK 1965.33.13–15; UPSL RTS 18) and the holotype (UPSL RTS 18). A characteristic feature of *L. rigida*, according to Pillai, is that the longitudinal medullary columns (Fig. 2) within the shafts of the heterogomph spinigers and heterogomph falcigers are broken distally. While this is true for some setae, others of the same type have the medullary columns intact. In addition, setae with broken medullary columns are commonly found in other populations of *N. abiuma* sp. group and indeed, in other *Namalycastis* species. For this reason it is considered a poor character for distinguishing namanereidine species.

The results of the cladistic analysis indicate that *N. abiuma* sp. group is the sister species of the Indo-Pacific species *N. multiseta* n.sp. Such a relationship would indicate that the ancestor of both species probably also had an Indo-Pacific distribution. Further, records of *N. abiuma* sp. group in the Caribbean and on the Atlantic coasts are possibly relatively late arrivals, perhaps the result of dispersal given the species preference for coastal plant material accumulations (below).

Habitat. Commonly found intertidally on mud flats, often in the mangrove zone of estuaries associated with decaying vegetation. For example, in the decaying wood of Sago palm (Horst, 1918); with the fibrous husks of *Nypa* palm nuts (Gibbs, 1971); waste from a date factory (Jaweir, 1987); under decaying mats of *Enteromorpha* (P. Hutchings, pers. comm., 1987); in coconut fibre detritus in Fiji and Sri Lanka (personal observation); in rotting sugar cane debris in Fiji (personal observation). Also found in the *Nypa* zone (Pflugfelder, 1933; R. Hanley, pers. comm., 1989); and in the intertidal zone of an estuary beneath stones (S.-K. Wu, 1967).

Distribution. The species group, including the synonymies suggested above, gives the taxon a circumglobal distribution between 30°N and 30°S (Fig. 9). New records include Nigeria, Zaire, Seychelles, Burma, Thailand, Java, Borneo (Brunei), Sulawesi, China (Hainan), Taiwan, Fiji and Belize.

Namalycastis arista n.sp.

Figs. 1c, 9, 11a–g; Table 4

Material examined. HOLOTYPE: Guyana, Paradise Beach (15°34'N 57°57'W), mud in tidal zone, coll. Dr R. Ramsammy and M. Tamessar, 12.11.1970 (BMNH 1998.190). PARATYPES: Guyana, collection details as for holotype 2(BMNH 1998.191–192). 3 specimens measured.

Diagnosis. Prostomium anteriorly shallowly cleft, shape 1.2 × wider than long (1.3–1.4). Antennae extending short of tip of palpophore. Notosetae present. Neurosetae Type A anteriorly (Fig. 1c). Heterogomph falcigers replaced by heterogomph spinigers in posterior parapodia. Supra-neuroacicular falcigers in setiger 10 with blades 7.7 × longer than width of shaft head (8.2–9.4), finely serrated, 5 teeth (10–12), teeth about uniform in length; fine hair-like projection from tip of falciger blades.

Description. Holotype well preserved, segmentally complete, no gametes in coelom. Paratypes well preserved, segmentally complete. 182 setigers (229), 75 mm long (70), 2.4 mm wide at setiger 10 (3.0). At setiger 10 length of parapodia 0.43 × body width (0.48–0.49).

Body. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Dorsum convex. Venter convex. Colour in alcohol yellow-brown or brown. Epidermal pigment absent.

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, sometimes slightly indented laterally; 1.2 × wider than long (1.3–1.4). Antennae smooth, extending short of tip of palpophore, aligned over inner edge of palps to over mid-palps. Eyes 2 pairs, black, arranged transversely, inner pair slightly smaller; lenses indistinct (Fig. 11a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 2.0 × length anteroventral (2.0–2.5). Anterodorsal tentacular cirri 0.9 × length posterodorsal (0.7–0.9). Posterodorsal tentacular cirri 1.9 × length posteroventral (2.0–2.2). Posterodorsal tentacular cirri extending posteriorly to setiger 4 (Fig. 11a). Jaws with single robust terminal tooth, 4 subterminal teeth (5), 4 teeth ensheathed proximally (3–4), brown (Fig. 11b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform (very short). Inferior lobe subconical (Fig. 11c,d). Dorsal cirri increasing greatly in length posteriorly; 2.2 × length of podium at setiger 3 (1.9–2.1) (Fig. 11c), 3.2 × length of podium in mid-body (3.7–4.7), 5.5 × length of podium posteriorly (5.4); 5.7 × longer than wide posteriorly (5.8) (Fig. 11d). Ventral cirri 0.50 length of podium at setiger 3 (0.52–0.62), 0.71 length of podium posteriorly.

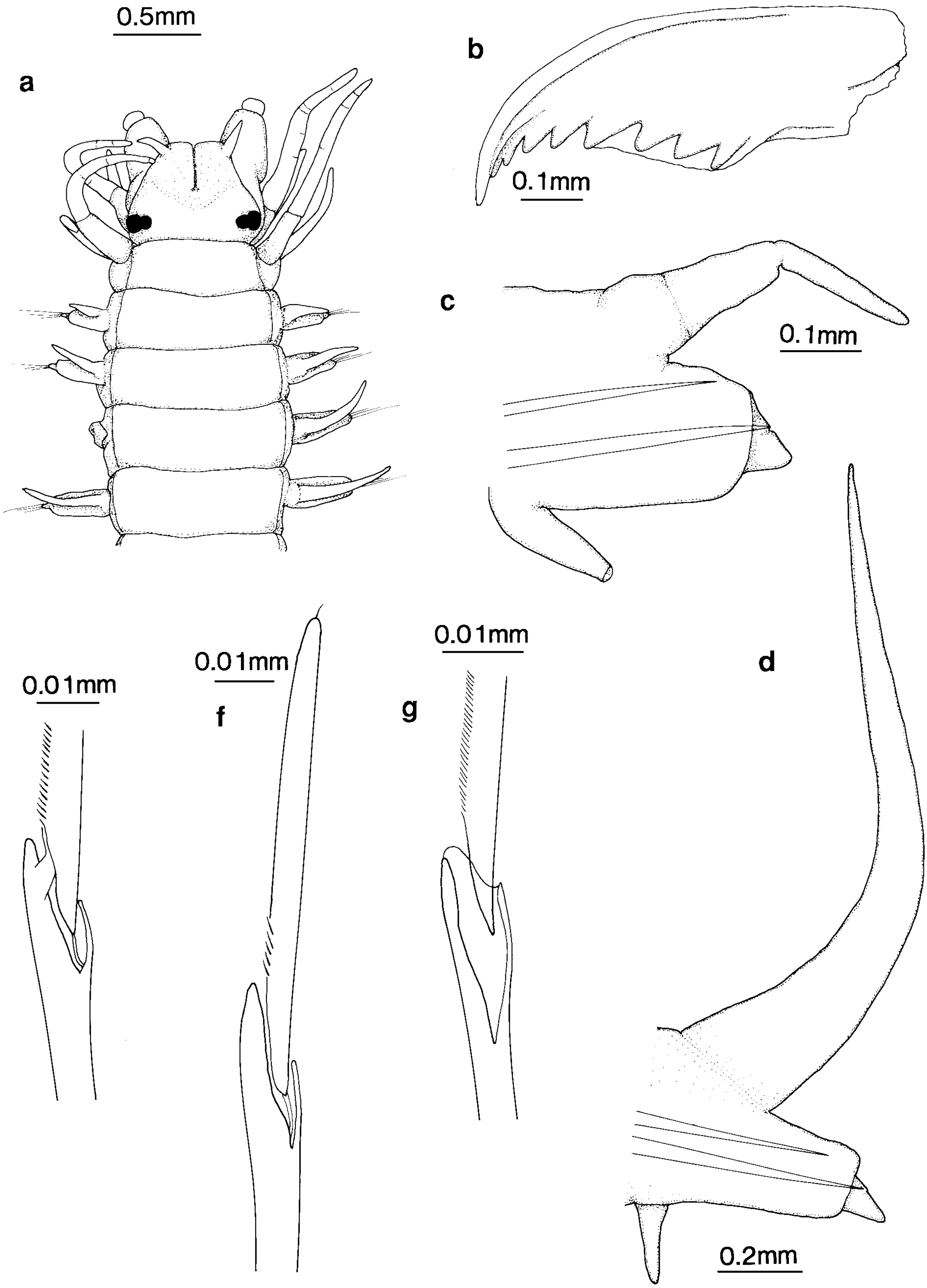

Figure 11. *Namalycastis arista* n.sp. holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view, ventral cirrus truncated; (*d*) parapodium from 120th setiger, L.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger (not fully side on), setiger 10; (*g*) sub-neuroacicular spiniger, setiger 10.

Setae. Notopodial sesquigomph spinigers from setiger 3 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.2 × length of collar (1.2–1.3) (Fig. 11e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 7.7 × longer than width of shaft head (8.2–9.4), finely serrated, 5 teeth (10–12), 0.10 × total blade length (0.21–0.22), teeth about uniform in length (Fig. 11f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 8.2 × longer than width of shaft head (9.3–10.8), 10 teeth (6–7); ventral-most 6.0 × longer than width of shaft head (7.0), 5 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Fine hair-like projection from tip of falciger blades (visible under 1,000 × magnification) (Fig. 11f). Sub-neuroacicular spinigers in anterior region with blades finely serrated (Fig. 11g); posteriorly, from setiger 120 (120–180), blades having coarse serrations proximally. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium with multi-incised rim, though lobes may be may be weakly defined. Anus dorsoterminal, or terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 3.5 × width pygidium (2.0).

Remarks. This species resembles closely *Namalycastis senegalensis* (Saint-Joseph) and *N. macroplatis* n.sp. in having heterogomph falcigers replaced by heterogomph spinigers posteriorly. However, *N. arista* n.sp. differs from these other two species in having a relatively longer prostomium, supra-neuroacicular sesquigomph spinigers with a relatively short boss, and having long-bladed falcigers. In addition, all falcigers have a fine hair-like projection, visible only under high magnification (1,000 × or greater), extending from the tip of the blades.

Phylogenetically, the new species forms a monophyletic group together with *N. senegalensis*, *N. macroplatis* n.sp., *N. siolii*; the clade is tenuous however, since only 74% of the minimal-length trees reflect this grouping (Fig. 7). The addition of *N. geayi* circumscribes a group that is present in all minimal-length trees, one supported by the replacement in preacicular fascicles of heterogomph falcigers anteriorly with heterogomph spinigers posteriorly. All species in the larger clade occur in the north-eastern region of South America.

Habitat. The types are from mud in the tidal zone.

Distribution. Type locality Guyana, Paradise Beach (Fig. 9).

Etymology. From the L. *arista*, meaning beard of grain or awn, referring to the single hair-like distal extension of the falciger blades.

Namalycastis borealis n.sp.

Figs. 1c, 12a–g, 13; Table 4

Namalycastis abiuma.–Hartman, 1959a: 155–156, pl. 3, figs. 1–4.–Heard & Sikora, 1972: 473 (list only).–Gardiner, 1976: 143–144, fig. 13f–i.–Subrahmanyam, Kruczynski & Drake, 1976: 176, 185 (list only).–Subrahmanyam & Coultas, 1980: 802, 813 (list only).–Gardiner & Wilson, 1979: 163 (key only).–Heard, 1982: 6, figs. 2a–d, 5a.–Rasmussen, 1994: 20–23, figs. 4, 5A–D, 6, 7. *Non* Grube.

Namanereis ouanaryensis.–Andrew & Nancy, 1953: 7–9. *Non* Gravier.

Lycastopsis beumeri.–Wesenberg-Lund, 1958: 14–17, figs. 9–11 (in part, Bonaire, Lagoen, stn. 308 only). *Non* Augener.

Material examined. HOLOTYPE: USA, North Carolina, Beaufort (34°43'N 76°44'W), Pivers Island, near fishing pier, intertidal, muddy sand #NC 110, coll. C. Jenner and S.L. Gardiner, 13 April 1973, det. as *Namalycastis abiuma* by S.L. Gardiner, 1976 (USNM 52926). PARATYPES: N. Newport River, headwaters at US highway 17, intertidal mud, salinities 0.5–6‰, coll. 9–25–69 3(ZMUC POL-928); Georgia, Sapelo Island (31°26'N 81°15'W), roadside ditch at Raccoon Bluff Rd, just north of Cabretta Rd jct., under bark on pine tree branch, loc. 1, coll. E. Rasmussen, 20 January 1972, 18(ZMUC POL-927), 10–11 November 1971, 10(ZMUC POL-929), stn. 6A, 10–11 November 1971, 2(ZMUC POL-930) (specimens studied by Rasmussen), ditch NE of measuring point, 30 March 1971, 1(ZMUC POL-931); Florida, St. Andrews Bay (30°01'N 85°08'W), 8–2, St. Andrews Bay, 2(AHF n10411), East Goose Creek, under seaweed drift with earthworms, coll. E.V. Kemarek, 17 April 1966, det. C.D. Long as *Namalycastis abiuma* 2(USNM 58129). NON-TYPES: Mississippi, Ocean Springs 4(USNM 178868); Bahamas, Bimini 1(USNM 24525); Belize, Twin Cays 3(USNM 178862); Sittee River mouth 3(USNM 178865); Grand Cayman, Salt Creek 2(ZMA V.Pol. 2785); Hispaniola, Puerto Plata 1(HZM V2894); Aruba, Spaans Lagoon 1(ZMA V.Pol. 2786). 13 specimens measured.

Other material examined. USA, North Carolina, Beaufort 1(USNM 28172); Florida, Indian River 1(USNM 33235), Tampa Bay 4(USNM 45573), Boca Ciega Bay, Pinellas County many (USNM 33096). Belize, Twin Cays 1(USNM 178863), 1(USNM 178864), Anderson lagoon 8(USNM 178866); Sapodilla lagoon 1(USNM 178867). Bonaire, stn. 308, southern shore of lagoon 3(ZMA V.Pol. 2884).

Diagnosis. Epidermal pigment light brown anterodorsally, darker brown posteriorly and on pygidium. Prostomium anteriorly shallowly cleft. Antennae extending short of tip of palpophore. Dorsal cirri of setiger 3 greater than 2 × length of parapodium (usually). Notosetae present or absent. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 5.0 × longer than width of shaft head (5.1–6.3), moderately or finely serrated, 17 teeth (15–32), teeth about uniform in length. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally.

Description. Holotype well preserved, segmentally complete, sperm rosettes in coelom. Other material generally well preserved (Belizean specimens poorly preserved), including some complete individuals. 129

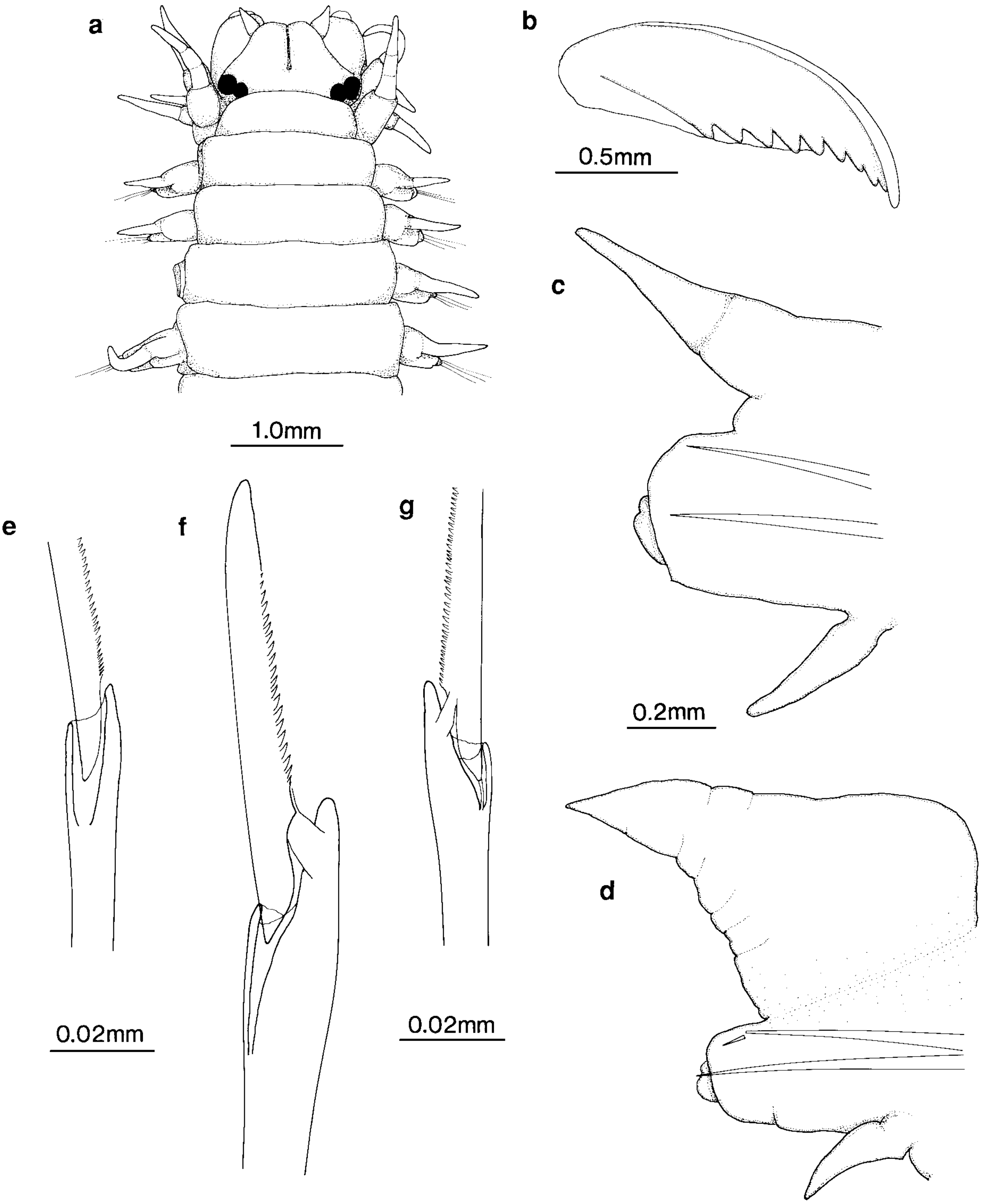

Figure 12. *Namalycastis borealis* n.sp. holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., posterior view; (*d*) parapodium from 120th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 120.

setigers (119–232), 73 mm long (55–110), 3.2 mm wide at setiger 10 (2.2–4.5). At setiger 10 length of parapodia 0.33 × body width (0.26–0.42).

Body. Uniform in width anteriorly, tapering gradually posteriorly (very rarely uniform width over most of body and tapering only over far posterior region). Dorsum convex. Venter flat or convex (very rarely). Colour in alcohol yellow-white to brown. Epidermal pigment light brown anterodorsally, darker brown posteriorly and on pygidium; rarely pigment absent (Mississippi specimen lilac-coloured due to oocytes).

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium (rarely ending in pit). Prostomium shape roughly triangular, laterally slightly indented or notched; 1.6 × wider than long (1.4–2.1). Antennae smooth, extending short of tip of palpophore, aligned over inner edge of palps to mid-palps. Eyes 2 pairs, black, or purple (rarely), arranged obliquely or transversely, posterior pair slightly smaller or equal in size; lenses indistinct (Fig. 12a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.2 × length anteroventral (1.2–1.7). Anterodorsal tentacular cirri 0.9 × length posterodorsal (0.6–1.0). Posterodorsal tentacular cirri 1.3 × length posteroventral (1.1–1.9). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (2–4) (Fig. 12a). Jaws with single robust terminal tooth, 4 subterminal teeth (4–6, rarely to 7), 5 teeth ensheathed proximally (3–5, rarely to 6), brown or black (Fig. 12b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 12c,d). Dorsal cirri increasing slightly in length posteriorly; 2.4 × length of podium at setiger 3 (1.1–3.3) (Fig. 12c), 2.1 × length of podium in mid-body (1.0–4.1), 3.8 × length of podium posteriorly (2.0–6.9); 1.4 × longer than wide posteriorly (1.7–3.2) (Fig. 12d). Ventral cirri 0.56 length of podium at setiger 3 (0.41–0.58), 0.46 length of podium posteriorly (0.26–0.49).

Setae. Notopodial sesquigomph spinigers from setiger 10 (7–27), though absent in some parapodia and entirely in some individuals (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4 × length of collar (1.5–1.6) (Fig. 12e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.0 × longer than width of shaft head (5.1–6.3), moderately to finely serrated, 17 teeth (15–32), 0.48 × total blade length (0.39–0.74), teeth about uniform in length (Fig. 12f). Sub-neuroacicular falcigers in setiger 10 with blades moderately to finely serrated; dorsal-most 4.0 × longer than width of shaft head (4.6–5.8), 18 teeth (12–20, rarely 6–28); ventral-most 3.9 × longer than width of shaft head (3.9–5.0), 6 teeth (6–13, rarely 2–15). Sub-neuroacicular falcigers in mid-posterior region with blades moderately to finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally (Fig. 12g). Setae pale. Acicula in mid-body brown or black (lighter basally).

Pygidium. Pygidium with multi-incised rim. Anus terminal, or dorsoterminal. Anal cirri arising ventrolaterally or ventrally, approximately conical, smooth, 0.3 × width pygidium (0.4–1.2).

Sex. Mature oocytes 105–153 µm (two specimens measured), straw-coloured or lilac, with external membrane. Epitokal setae are absent.

Remarks. *Namalycastis borealis* n.sp. has been commonly referred to in the taxonomic and ecological literature as *N. abiuma* Grube. It differs from members of the widespread *N. abiuma* species group however, in having a greater number of serrations on the falciger blades (and having a greater portion of the blade serrated), and in having sub-neuroacicular spinigers posteriorly with blades finely serrated rather than coarsely serrated as in *N. abiuma* sp. group. Both taxa co-occur in Belize.

Rasmussen (1994) describes living specimens of *N. borealis* n.sp. (as *N. abiuma*) from Sapelo Is., Georgia as unpigmented and translucent and having prominent capillary blood vessels in the dorsal cirri, especially posterior ones. The specimen from Bimini, Bahamas differs slightly in setal morphology from typical *N. borealis*: the supra-neuroacicular falcigers have 32 teeth on the falciger blade, representing 0.74 of the total blade length. In other respects though the specimen is typical of *N. borealis*.

In the cladistic analysis, the new species is grouped together with *Namalycastis terrestris*, a species apparently with a restricted distribution in south-east Asia. This sister group relationship seems to be incongruent with the present day distribution of these two species—widespread dispersal seems unlikely considering the present restricted distribution of both species, although dispersal with subsequent extinction of populations is possible. A vicariant explanation involving an expanding earth hypothesis is offered in a separate paper (Glasby, this volume).

Habitat. The holotype was collected intertidally from muddy sand and shell fragments. *Namalycastis borealis* n.sp. is commonly associated with decaying vegetation in brackish coastal areas of variable salinity. In the northern part of its range the species has been found under the bark of dead pine trees (Heard, 1982; Rasmussen, 1994), under seaweed drift with earthworms, and under a log in the *Spertina* [sic] (?= *Spartina*) zone; in the south of its range (Belize) the species has been found in the mangrove zone associated with rotting mangrove tree branches together with *Namanereis amboinensis* (personal observations).

Distribution. Type locality North Carolina, Beaufort. The synonymy with *N. abiuma non* Grube gives the species a widespread distribution in eastern and southern USA (Fig. 13). The synonymy with *Namanereis ouanaryensis sensu* Andrew & Nancy extends the distribution to the Bahamas, and the synonymy with *Namanereis beumeri sensu* Wesenberg-Lund extends the distribution to Bonaire. New records for Belize and the Caribbean Islands of Grand Cayman and Aruba.

Etymology. From the L. *borealis*, meaning northern, referring to the more northerly distribution of this species in the Americas compared to the similar *N. abiuma* sp. group.

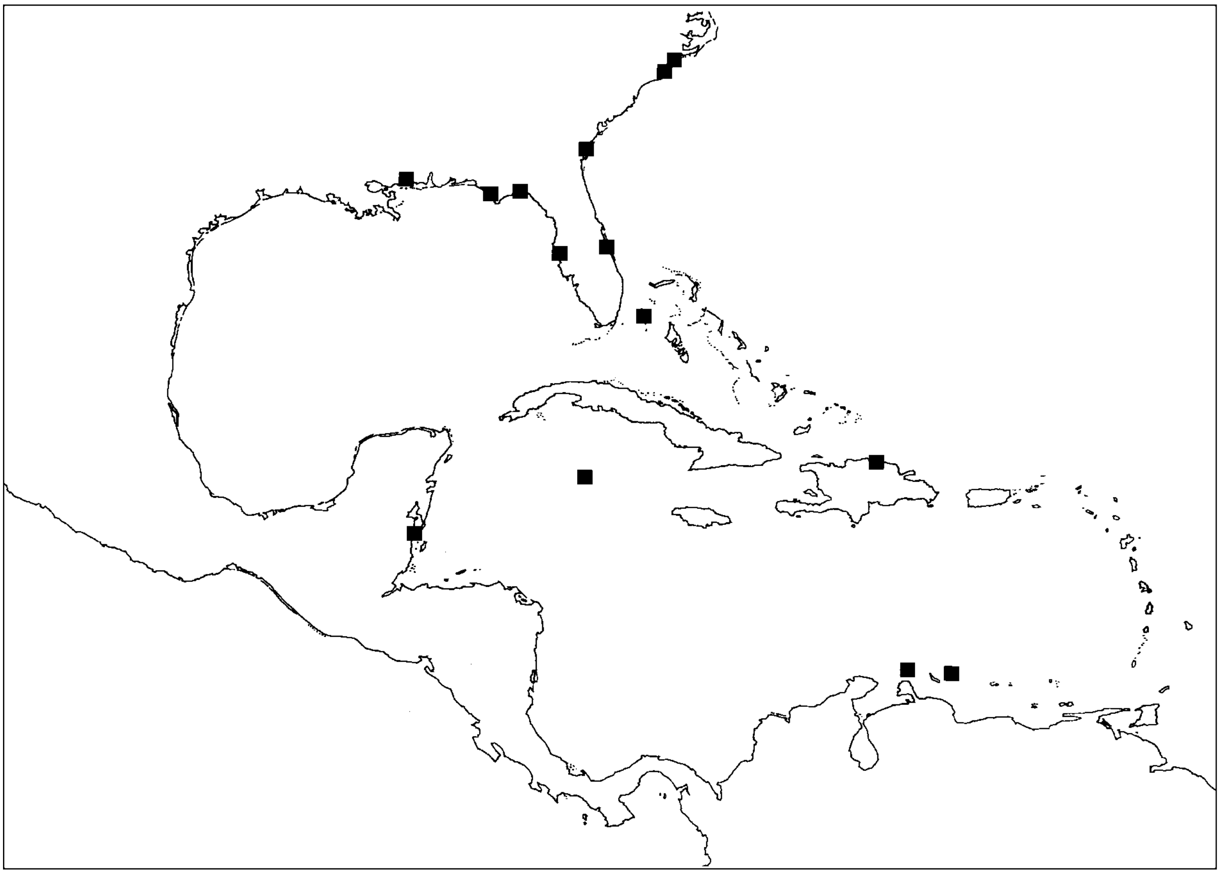

Figure 13. Distribution of *Namalycastis borealis* n.sp., based on material examined.

Namalycastis brevicornis (Audouin & Edwards) n.comb.

Figs. 1c, 14a–e, 15; Table 4

Lycastis brevicornis Audouin & Edwards, 1833: 223–226, pl. XIV, figs. 6–12.–Castelnau, 1840: 16–17.–Grube, 1850: 300; 1870: 312–313.–Quatrefages, 1865: 499–500.–Fauvel, 1923b: 331–332.

Lycastis brevipalpe Audouin & Edwards, 1833: pl. XIV, figs. 6–12 (possible error for *brevicornis* in figure caption).

Lycastis ouanaryensis.–Fauvel, 1923a: 126–127 (in part). *Non* Gravier.

Material examined. POSSIBLE HOLOTYPE: France, La Rochelle (46°10'N 1°10'W), MNHN [A[1](R)–1868-no. 133a]. NON-TYPE: French Guiana, no. 3443 3(MNHN UE 933). Brazil, Ilha de Marajó 1(HZM V9432). 4 specimens measured.

Other material examined. “Iles Sandwich” 1(MNHN UE 914), det. Fauvel, 1942.

Diagnosis. Prostomium anteriorly shallowly cleft. Antennae extending beyond tip of palpophore. Tentacular cirri with smooth cirrostyles. Notosetae present. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades less than 3.6 × longer than width of shaft head, smooth.

Description. Purported holotype poorly preserved, jaws removed, anteroventral tentacular cirri left side missing; last few segments missing. Other material well preserved, including some complete individuals. 130 setigers (133–166); 120 mm long (53–143); 3.5 mm wide at setiger 10 (3.3–5.0). At setiger 10 length of parapodia 0.26–0.34 × body width.

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter flat. Colour in alcohol yellow-white, yellow-brown to red-brown (red-brown colour perhaps due to stain in preservative). Epidermal pigment absent.

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, 1.5–1.6 × wider than long. Antennae smooth, extending beyond tip of palpophore, aligned over mid-palps to inner edge of palps. Eyes 2 pairs, black, arranged obliquely, equal in size or posterior pair slightly smaller; lenses indistinct.

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth (tentacular cirri damaged in holotype). Anterodorsal tentacular cirri 1.2–2.0 × length anteroventral. Anterodorsal tentacular cirri 0.6–0.9 × length posterodorsal. Posterodorsal tentacular cirri 1.2–2.0 ×

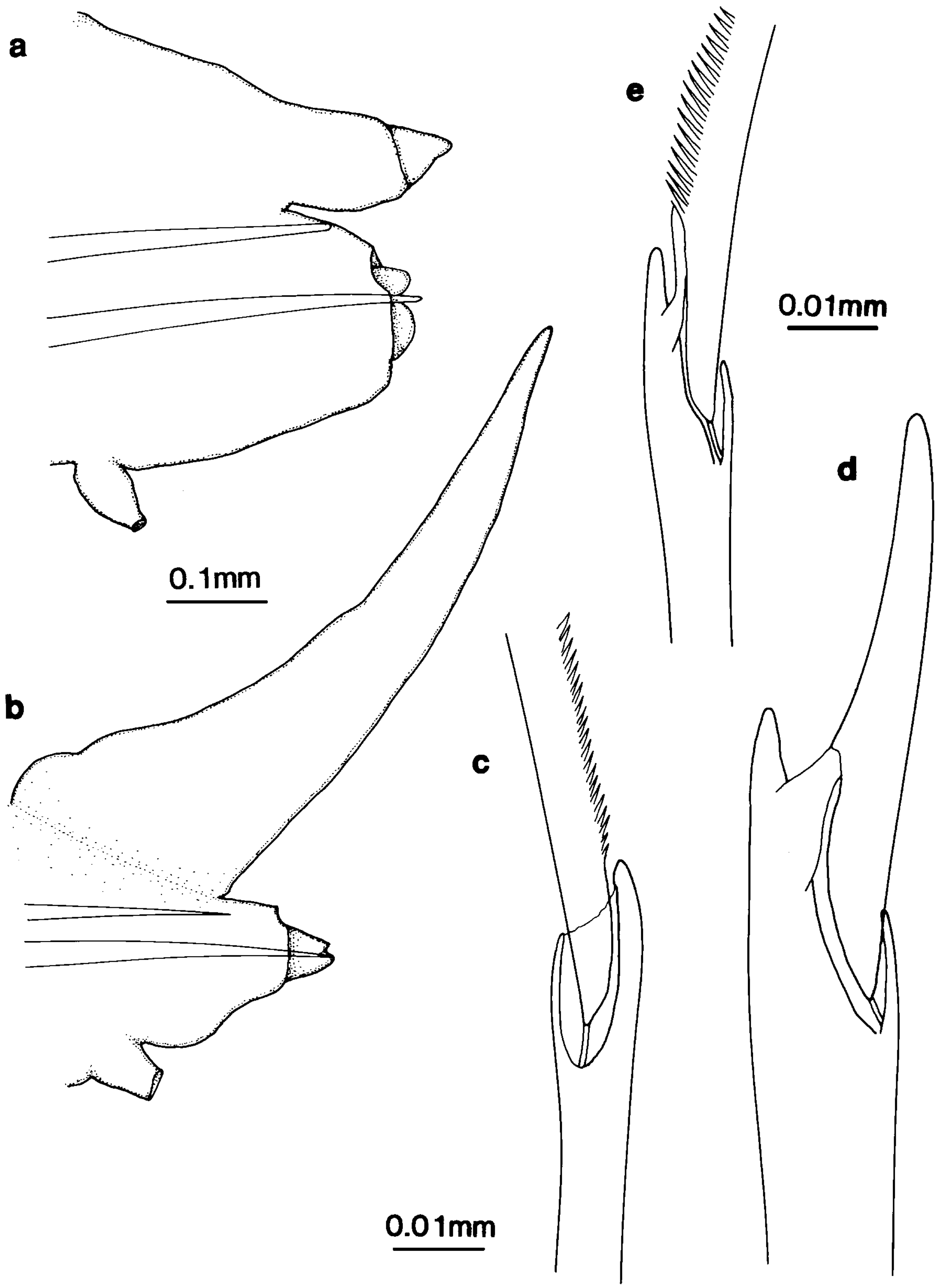

Figure 14. *Namalycastis brevicornis* possible holotype: (*a*) parapodium from 10th setiger, L.S., anterior view, ventral cirrus truncated; (*b*) parapodium from 120th setiger, L.S., anterior view, ventral cirrus truncated. Non-type, French Guiana (MNHN): (*c*) supra-neuroacicular spiniger, setiger 10. (*d*) Holotype, supra-neuroacicular falciger, setiger 10. (*e*) Non-type, French Guiana (MNHN), sub-neuroacicular spiniger, parapodium 150.

length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 1–2. Jaws with single robust terminal tooth (jaws absent in holotype), 4 subterminal teeth, 4–6 teeth ensheathed proximally, brown.

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 14a,b). Dorsal cirri increasing slightly to greatly in length posteriorly; 0.67–1.1 × length of podium at setiger 3 (Fig. 14a), 2.4 × length of podium in mid-body (0.50–1.0), 5.7 × length of podium posteriorly (1.4–6.6); 3.7 × longer than wide posteriorly (3.6–6.4) (Fig. 14b). Ventral cirri 0.42–0.51 length of podium at setiger 3, 0.27 length of podium posteriorly (0.24–0.36).

Setae. Notopodial sesquigomph spinigers from setiger 2–3 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.6 × length of collar (1.5–1.7) (Fig. 14c). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 3.6 × longer than width of shaft head (2.8–3.2), smooth (Fig. 14d). Sub-neuroacicular falcigers in setiger 10 with blades smooth; dorsal-most 3.2 × longer than width of shaft head (2.8–3.0); ventral-most 3.2 × longer than width of shaft head (3.0–3.1). Sub-neuroacicular falcigers in mid-posterior region with blades smooth. Sub-neuroacicular spinigers in anterior region with blades finely serrated; posteriorly, from setiger 120–150, blades having coarse serrations proximally (Fig. 14e). Setae pale. Acicula in mid-body brown (dark).

Pygidium. Pygidium with multi-incised rim (pygidium missing in holotype). Anus terminal or dorsoterminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 0.6–0.7 × width pygidium.

Sex. Mature oocytes straw-coloured.

Remarks. The description is based primarily on the non-type material; however, counts and measurements for some characters pertaining to the presumed holotype are given. The specimen from La Rochelle (MNHN A[1](R)-1868-no. 133a), is putatively the type (J. Renaud-Mornant, pers. comm.), and is indicated as such by the colour of the label. However, some doubt about its type status exists for the following reasons: (i) Audouin & Edwards indicate in the type description that the species was collected from Noirmoutier, a small island on the Atlantic coast, whereas the specimen examined is from La Rochelle a short distance to the south, (ii) Saint-Joseph (1900) indicates that the type from Noirmoutier has no pharynx. Audouin & Edwards indicate that the type, when described in 1833, had the pharynx everted. It is conceivable that in the period between 1833 and when Saint-Joseph examined it, the pharynx could have been detached and lost. In contrast, the specimen from La Rochelle examined here has the pharynx *retracted* and dissected, though the jaws are absent, and (iii) Grube (1870) also described a specimen of *N. brevicornis* from Paris Museum as being without a pharynx, although confusingly it was recorded as being from La Rochelle.

A specimen identified by Amoureux & Calvário (1981) and Calvário (1984) as *Namalycastis brevicornis* from the Tage estuary (Portugal) was apparently misidentified. The specimen, which is now dried out on a slide, has been re-examined and identified as *Namanereis littoralis* (P. Gibbs, pers. comm., 1996).

The results of the cladistic analysis indicate that *N. brevicornis* forms a monophyletic group together with *N. kartaboensis* and *N. longicirris*, with 81% of the minimal-length trees supporting such a relationship (Fig. 7); however, the clade is collapsed in both the Strict and Nelson Consensus trees (Figs. 5,6).

Habitat. The type habitat is given only as the coast at Noirmoutier. Today the island has a variety of coastal habitats including sandy beaches, rocky headlands, salt marshes in the north and east and a vast muddy sand flat at Passage du Gois. A brief survey of these habitats in 1986 failed to find the species. However, descriptions of a bright red, nereid-like polychaete inhabiting salt farm areas of the north-east (L. Billard, pers. comm., 1986) could represent the species.

Specimens from Brazil, Ilha de Marajó were found on a beach in brackish to freshwater.

Distribution. Type locality Noirmoutier, France. New records for French Guiana, Brazil, and possibly Hawaii (Fig. 15). "Iles Sandwich" probably refers to the Hawaiian Islands, though other possibilities exist (see under Distribution of *Namalycastis senegalensis*).

Etymology. Audouin & Edwards probably derived the specific name from the L. *brevis*, meaning short, and probably the L. *cornu* for horn, referring to the very short palps, which however, is characteristic of the subfamily.

Namalycastis elobeyensis n.sp.

Figs. 1c, 15, 16a–g; Table 4

Lycastis senegalensis.–Augener, 1918: 218. *Non* Saint-Joseph.

Material examined. HOLOTYPE: West Africa, Spanish Sahara [now Equatorial Guinea], Eloby Isl. [now Elobey Grande Island] (1°01'N 9°29'E), coll. A. Hupfer, det. Augener, 1918 (HZM V937). PARATYPES: label details as for holotype 4(HZM P-22042). 4 specimens measured.

Diagnosis. Prostomium anteriorly shallowly cleft or cleft absent. Antennae extending beyond tip of paplophore. Notosetae absent. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 5.6 × longer than width of shaft head (5.4–5.7), moderately or finely serrated, 19 teeth (18–25), teeth about uniform in length or increasing in length slightly proximally. Dorsal-most sub-neuroacicular falcigers in setiger 10 with blades having 22–35 teeth.

Description. Holotype moderately well preserved, segmentally complete, mature oocytes in coelom. Paratypes moderately well preserved, including some complete individuals. 76 setigers (87), 16.5 mm long (11.5), 1.0 mm wide at setiger 10 (0.9–1.1). At setiger 10 length of parapodia 0.46 × body width (0.38–0.43).

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-white. Epidermal pigment absent.

Prostomium. Cleft absent or shallow; longitudinal groove absent or extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, 1.4 × wider than long (1.5–1.7). Antennae smooth, extending beyond tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs, black, arranged transversely, equal in size; lenses indistinct (Fig. 16a).

Peristomium. Tentacular cirri with cirrophores indistinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 1.8 × length anteroventral (1.7–2.0). Anterodorsal tentacular cirri 1.0 × length posterodorsal (0.7–1.0). Posterodorsal tentacular cirri 2.0 × length posteroventral (1.6–2.0). Posterodorsal tentacular cirri extending posteriorly to setiger 4 (4–5) (Fig. 16a). Jaws with single robust terminal tooth, 9 subterminal teeth (8–11, includes ensheathed teeth), brown (Fig. 16b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 16c,d). Dorsal cirri increasing slightly in length posteriorly; 1.4 × length of podium at setiger 3 (1.1–1.4) (Fig. 16c), 2.5 × length of podium in mid-body (1.5–1.9), 4.5 × length of podium posteriorly (5.0); 7.2 × longer than wide posteriorly (4.9–7.0) (Fig. 16d). Ventral cirri 0.70 length of podium at setiger 3 (0.87), 0.52 length of podium posteriorly.

Setae. Notosetae absent. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles (some setae emerge subacicularly in mounted podia) and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.3 × length of collar (1.4–1.5) (Fig. 16e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.6 × longer than width of shaft head (5.4–5.7), moderately or finely serrated, 19 teeth (18–25), 0.62 × total blade length (0.61–0.69), teeth about uniform in length or increasing in length slightly proximally (Fig. 16f). Sub-neuroacicular falcigers in setiger 10 with blades moderately or finely serrated; dorsal-most 6.0 × longer than width of shaft head (5.7–7.4), 20 teeth (22–35); ventral-most 5.1 × longer than width of shaft head (5.0–5.7), 15 teeth (17–25). Sub-neuroacicular falcigers in

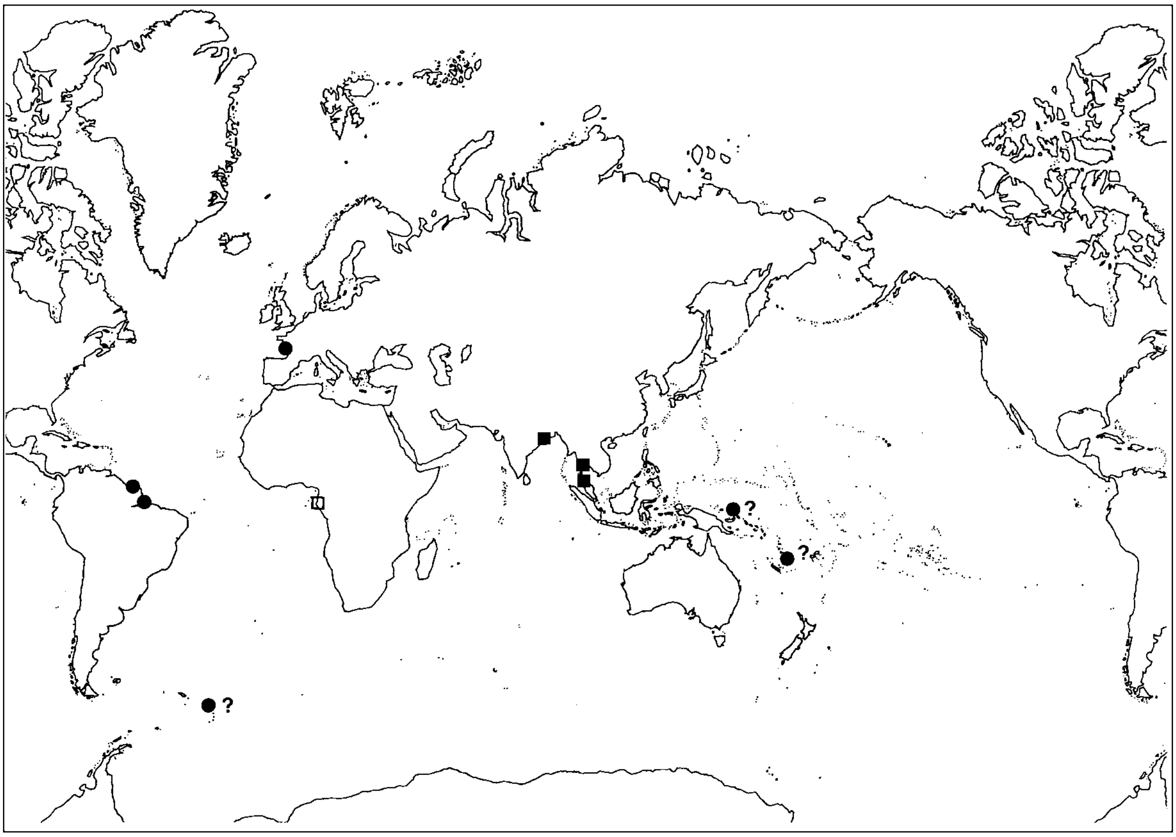

Figure 15. Distribution of *Namalycastis brevicornis* ●, *N. elobeyensis* n.sp. □, and *N. fauveli* ■, based on material examined and authenticated literature records.

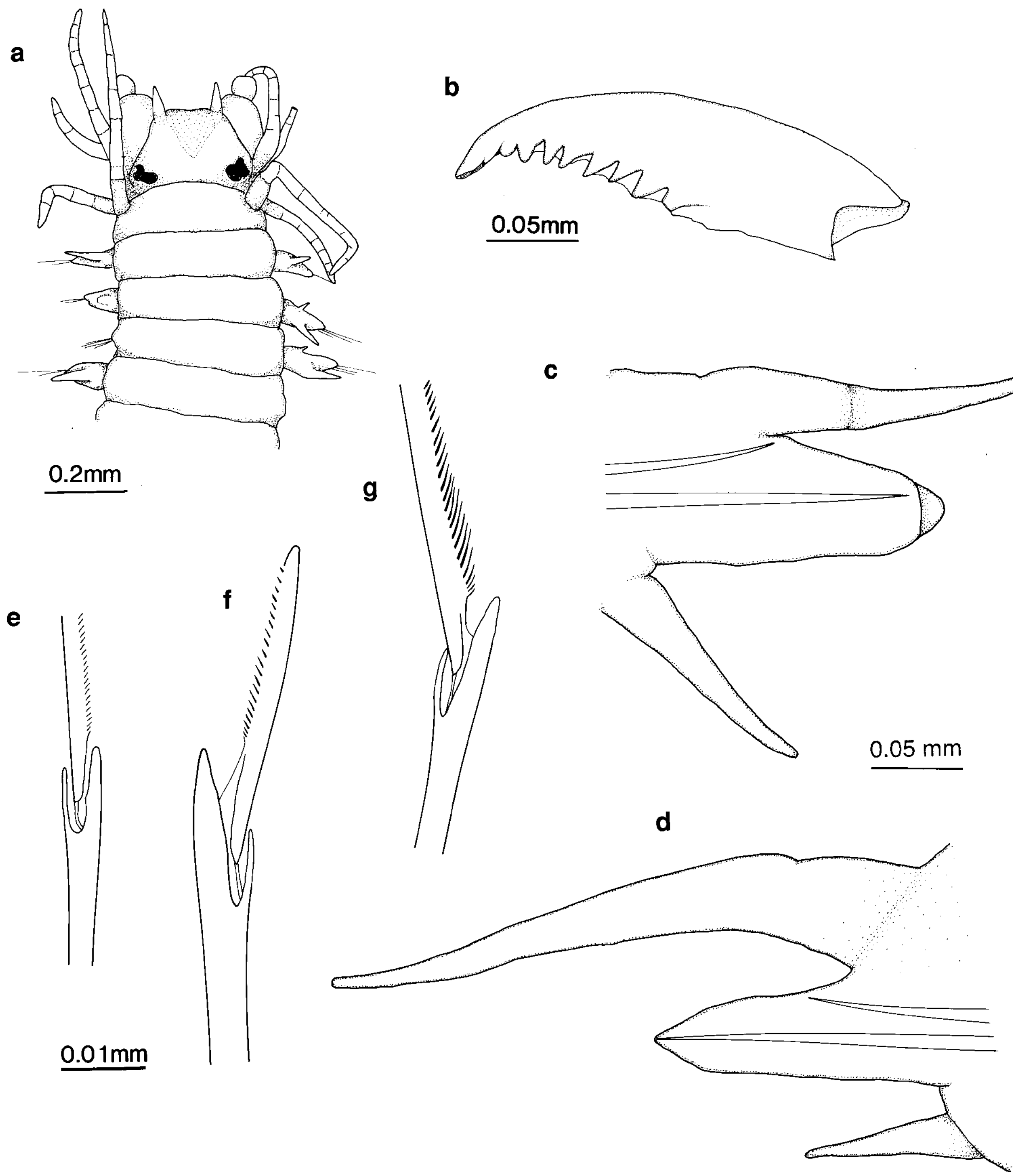

Figure 16. *Namalycastis elobeyensis* n.sp. holotype: (*a*) anterior end, dorsal view, parapodia 2 & 3, L.S., damaged; (*b*) jaw piece, dorsal view; (*c*) parapodium from 4th setiger, R.S., posterior view; (*d*) parapodium from 60th setiger, R.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 10.

mid-posterior region with blades finely or moderately serrated. Sub-neuroacicular spinigers in anterior region with blades finely serrated; posteriorly, from setiger 30 (10–30) with blades having coarse serrations proximally (Fig. 16g). Setae pale. Acicula in mid-body light brown.

Pygidium. Pygidium tripartite with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 4.0 × width pygidium (3.5).

Sex. Mature oocytes 93 µm (107, 2 specimens measured), straw-coloured, without external membrane.

Remarks. *Namalycastis elobeyensis* n.sp. resembles most closely the group of *Namalycastis* species, including *N. abiuma* (Grube) sp. group which have supra- and sub-neuroacicular falcigers continuing posteriorly, i.e. not replaced by spinigers. It differs from *N. abiuma* sp. group in having a small body size at maturity, lacking notosetae, having falciger blades with a greater number of teeth and sub-neuroacicular spinigers with blades coarsely serrated proximally from setiger 10–30. In this last feature, in particular, the species resembles *N. indica* (Southern) and *N. hawaiiensis* (Johnson). However, *N. indica* has notosetae present and *N. hawaiiensis* has fewer teeth on the falciger blades.

The cladistic analysis shows that the species is at the base of the namanereidine clade, together with *N. intermedia* n.sp. and *N. nicoleae* n.sp. All consensus cladograms (Figs. 5–7) indicate a sister group relationship with the Gulf of Mexico species, *N. intermedia*, giving the clade an amphi-Atlantic distribution. Synapomorphies for *N. elobeyensis* n.sp. and *N. intermedia* n.sp. are the absence of notosetae and the possession of faintly jointed cirrostyles, although the latter feature is polymorphic in *N. intermedia* and homoplastic within the Namanereidinae.

Habitat. Unknown

Distribution. Known only from the type locality Equatorial Guinea, Elobey Grand Island [formerly Eloby Is.] (Fig. 15).

Etymology. The species is named after the type locality.

Namalycastis fauveli Nageswara Rao

Figs. 1c, 15, 17a–h; Table 4

Namalycastis fauveli Nageswara Rao, 1981: 215–217, fig. 2A–E.
Namalycastis tachinensis Rosenfeldt, 1984: 73, figs. 12–18.

Material examined. *Namalycastis tachinensis* HOLOTYPE: Thailand, Tachin River mouth, near Bangkok (13°44'N 100°30'E), TP-6, stn. 1-A (HZM P17966). PARATYPE: Thailand, Tachin River mouth 1(HZM P17967). NON-TYPES: Thailand, Songkhla Lake, coll. ?Pairoj, 1982 5(PMBC 7244). India, Chilka lagoon, sample no. 1552 EBS/ZSI/BERHAMPUR (C.A. Nageswara Rao, pers. coll.). 7 specimens measured.

Other material examined. Thailand, Songkhla Lake, bottle labelled *Ceratocephale* NICA 1(PMBC 7245).

Diagnosis. Body widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Prostomium anteriorly shallowly cleft of cleft absent. Antennae minute. Notosetae present. Neurosetae Type A (Fig. 1c). Heterogomph setae with boss extremely prolonged. Supra-neuroacicular falcigers in setiger 10 with blades slightly curved, 8.0–9.5 × longer than width of shaft head, finely serrated, 20–40 teeth (rarely to 12), teeth about uniform in length.

Description. Types of *N. tachinensis* well preserved, other material also in good condition, including some complete individuals. 134–282 setigers, 21–45 mm long, 1.1–1.7 mm wide at setiger 10. At setiger 10 length of parapodia 0.29–0.42 × body width.

Body. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Dorsum convex though more highly arched mid-anteriorly. Venter flat. Colour in alcohol yellow-white to yellow-brown (rarely). Epidermal pigment usually absent, although some irregular orange pigment on head of one specimen.

Prostomium. Anterior cleft absent or shallow (rarely), with narrow, shallow longitudinal groove extending from tip to mid-posterior prostomium (dorsal groove rarely absent). Prostomium shape roughly trapezoidal, laterally notched or slightly indented; 1.5–2.4 × wider than long. Antennae minute, aligned over mid-palps. Eyes 2 pairs, black, arranged transversely; lenses present (Fig. 17a).

Peristomium. Tentacular cirri with cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.5–2.0 × length anteroventral. Anterodorsal tentacular cirri 0.9–1.1 × length posterodorsal. Posterodorsal tentacular cirri 1.1–2.0 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 1 to anterior edge of setiger 2 (Fig. 17a). Jaws with single robust terminal tooth, 2–3 subterminal teeth, 2–4 teeth ensheathed proximally, brown (Fig. 17b).

Parapodia. Acicular neuropodial ligule weakly bilobed (Fig. 17c). Dorsal cirri increasing slightly (or greatly) in length posteriorly; 0.69–1.3 × length of podium at setiger 3 (Fig. 17c), 1.1–2.4 × length of podium in mid-body, 1.8–6.0 × length of podium posteriorly; 1.9–3.6 × longer than wide posteriorly (Fig. 17d). Ventral cirri 0.30–0.63 length of podium at setiger 3, 0.18–0.33 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 3–7 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.2–1.5 × length of collar (Fig. 17e). Heterogomph setae with boss extremely prolonged. Supra-neuroacicular falcigers in setiger 10 with blades slightly curved, 8.0–9.5 × longer than width of shaft head, finely serrated, 20–40 teeth (rarely to 12), 0.57–0.65 × total blade length (rarely to 0.27), teeth about uniform in length (Fig. 17f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 8.2–11.4 × longer than width of shaft head, 40–60 teeth; ventral-most 6.0–7.3 × longer than width of shaft head, 8–25 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally (Fig. 17g). Setae pale. Acicula in mid-body brown.

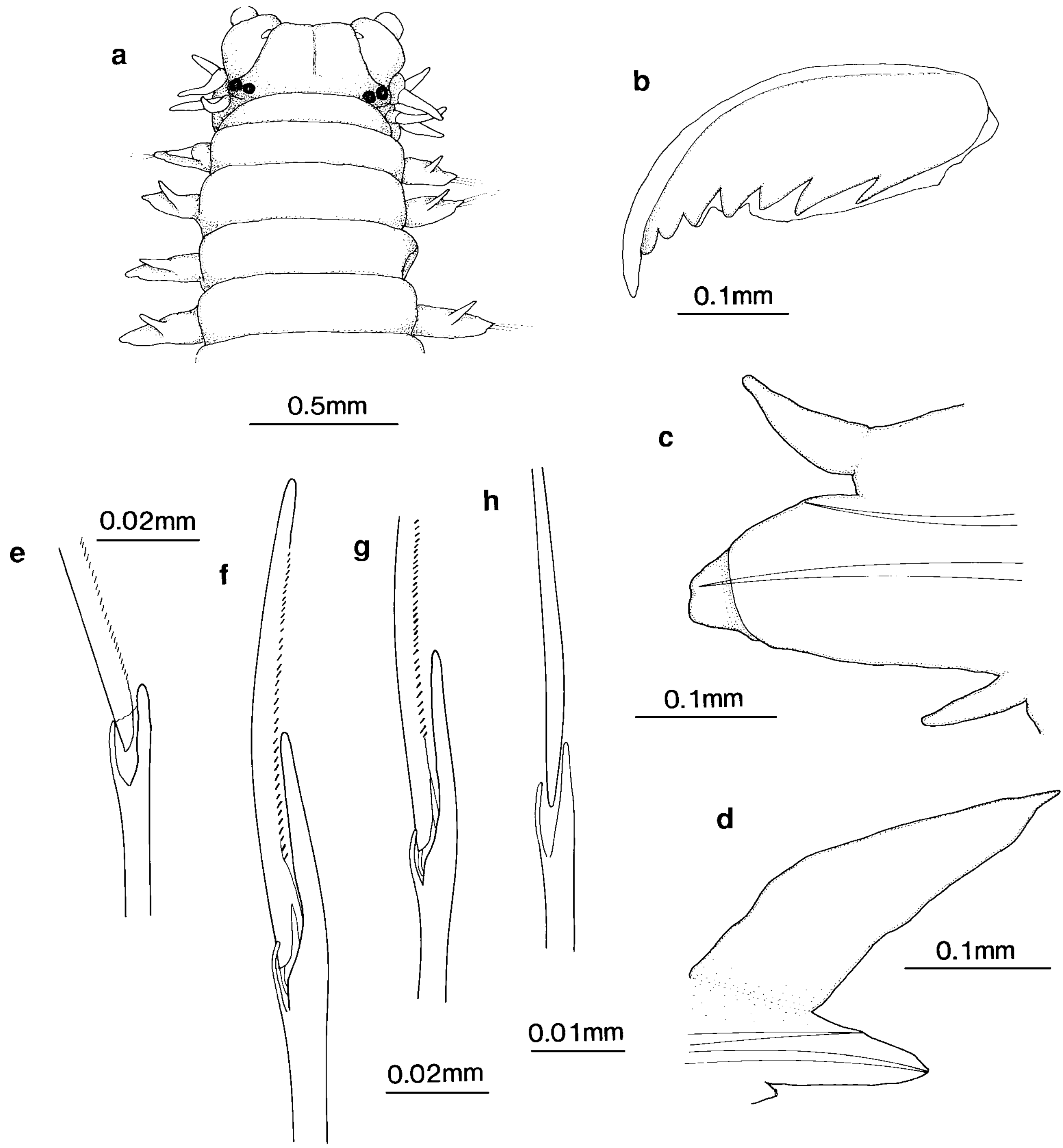

Figure 17. *Namalycastis fauveli* Tachin River (HZM P17966): (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, R.S., anterior view; (*d*) parapodium from 120th setiger, L.S., anterior view, ventral cirrus truncated. Non-type (C.A. Nageswara Rao, pers. coll.): (*e*) supra-neuroacicular spiniger, setiger 30; (*f*) supra-neuroacicular falciger, setiger 30; (*g*) sub-neuroacicular spiniger, setiger 120. (*h*) Non-type (PMBC 4616), epitokal sub-neuroacicular compound spiniger.

Pygidium. Pygidium with multi-incised rim. Anus terminal or dorsoterminal. Anal cirri arising ventrally or laterally, approximately conical, smooth, 0.2–2.2 × width pygidium.

Sex. Mature oocytes 84.2 µm (± 8, 1 specimen measured), straw-coloured, without external membrane (may not be fully mature). Epitokal setae are slender compound spinigers (Fig. 17h).

Remarks. The holotype and paratypes of *N. fauveli* are registered with the Zoological Survey of India. Unfortunately, all attempts to borrow this material have failed. Nevertheless, Nageswara Rao's description of *N. fauveli* is sufficiently detailed to support the synonymy with *Namalycastis tachinensis* Rosenfeldt. A feature not previously recognised for this species is the shape of the body, which is widest mid-anteriorly. The maximum width at setigers 9–20 appears to correspond to the maximum thickness of longitudinal muscle. However, as the shape of the body may be affected to some degree by handling and fixation the character should be used with caution.

Other Namanereidinae to share this apparent apomorphic feature are the South American species, *N. geayi, N. indica, N. senegalensis, N. macroplatis* n.sp. and *N. arista* n.sp. The presence of a swollen anterior end could not be verified in *N. siolii*. *Namalycastis fauveli* and *N. indica* together are the sister group of these latin species. Together the clade is supported tenuously by the presence of a well-developed lens, a feature that also occurs in *N. multiseta* and some species of *Namanereis*.

The specimen with epitokal compound spinigers (PMBC 7245) is a sexually mature male, with many sperm rosettes in the coelom. Epitokal setae occur in both the supra- and the subacicular positions of the neuropodia in setiger 29.

Habitat. The types were collected on a beach of the Bytarani River, India. Other specimens were collected in the brackish region of the Tachin River, Thailand near the waters edge in sandy mud sediment (Rosenfeldt, 1984).

Distribution. Type locality India, Bytarani River, Haripur, Chandbali (Orissa). The synonymy with *N. tachinensis* extends the distribution to Thailand, Tachin River (Fig. 15). New records for Thailand, Songkhla Lake and India, Chilka lagoon.

Etymology. Nageswara Rao named this species after the French polychaete worker, P. Fauvel.

Namalycastis geayi (Gravier) **n.comb.**

Figs. 1c, 18a–g, 19; Table 4

Lycastis geayi Gravier, 1901: 399–402; 1902c: 361–366, figs. 11–17 (repeat of 1901 except includes figures).–Perkins & Savage, 1975: 33 (list only).

Material examined. LECTOTYPE: French Guiana, no. 46, coll. M. Geay, 1901 (MNHN UE 922). PARALECTOTYPES: French Guiana, no. 46, coll. M. Geay, 1901 5(MNHN UE 923). NON-TYPE: French Guiana, no. 1551, coll. M. Geay, 1901, det. Fauvel, 1941 1(MNHN UE 924). 4 specimens measured.

Diagnosis. Prostomium anteriorly shallowly cleft or cleft absent. Antennae extending short of tip of palpophore or short of tip of prostomium. Eyes 2 pairs, arranged longitudinally or nearly so. Jaws up to 15 subterminal teeth including ensheathed ones. Dorsal cirri short, similar in length throughout, not exceeding 1–2 × length of parapodia. Notosetae present. Neurosetae Type B (Fig. 1c).

Description. Lectotype well preserved, segmentally complete, no gametes in coelom. Other material well preserved, including some complete individuals. 242 setigers (c. 215), 62 mm long (49–73), 1.4 mm wide at setiger 10 (1.3–1.7). At setiger 10 length of parapodia 0.18 × body width (0.20–0.27).

Body. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Dorsum convex. Venter convex. Colour in alcohol yellow-white. Epidermal pigment absent.

Prostomium. Anterior cleft absent or shallow, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, lateral indentation absent or present; 1.8 × wider than long (1.6–1.9). Antennae smooth, extending short of tip of palpophore or short of tip of prostomium, aligned over mid-palps. Eyes 2 pairs (faded slightly in lectotype), black, arranged longitudinally or nearly so, equal in size; lenses absent (Fig. 18a).

Peristomium. Tentacular cirri with cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.8 × length anteroventral (2.0–2.6). Anterodorsal tentacular cirri 1.1 × length posterodorsal (1.2–1.3). Posterodorsal tentacular cirri 1.3 × length posteroventral (1.5–1.8). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (posterior edge in lectotype) (Fig. 18a). Jaws with single robust terminal tooth, 6 subterminal teeth (5–6), 7 teeth ensheathed proximally (6–10), light brown (Fig. 18b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe very short, papilliform. Inferior lobe globular (Fig. 18c). Dorsal cirri similar in length throughout; 1.4 × length of podium at setiger 3 (1.2–1.4) (Fig. 18c), 1.5 × length of podium in mid-body (0.8–1.1), 2.6 × length of podium posteriorly (1.4–1.8); 1.9 × longer than wide posteriorly (1.7) (Fig. 18d). Ventral cirri 0.61 length of podium at setiger 3 (0.52–0.62), 0.49 length of podium posteriorly (0.46).

Setae. Notopodial sesquigomph spinigers from setiger 3 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph spinigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph spinigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.3 × length of collar (1.3–1.6) (Fig. 18e). Heterogomph setae with boss slightly prolonged (Fig. 18f,g). Sub-neuroacicular spinigers in mid-posterior region with blades having long, fine serrations proximally (Fig. 18g). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium with multi-incised rim. Anus terminal or dorsoterminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 1.2 × width pygidium (1.0).

Sex. Epitokal setae absent.

Remarks. The type material from the MNHN is supposedly the paratypes (M.N. Helléouet, pers. comm., 1986), but they are more likely to be syntypes as (i) no holotype could

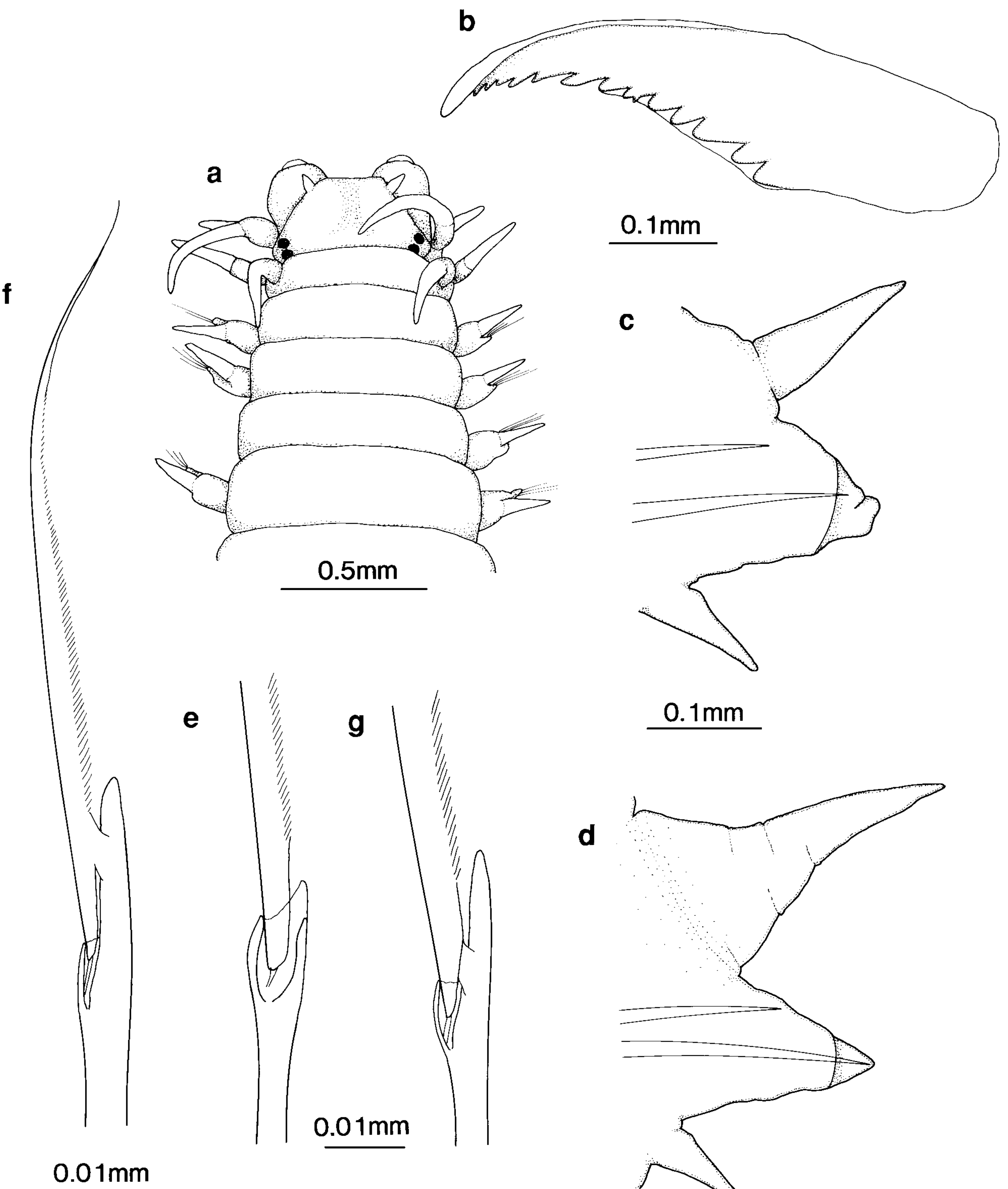

Figure 18. *Namalycastis geayi* lectotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 180th setiger, L.S., anterior view; (*e*) supra-neuroacicular (postacicular) spiniger, setiger 10; (*f*) supra-neuroacicular (preacicular) spiniger, setiger 10; (*g*) sub-neuroacicular (postacicular) spiniger, setiger 10.

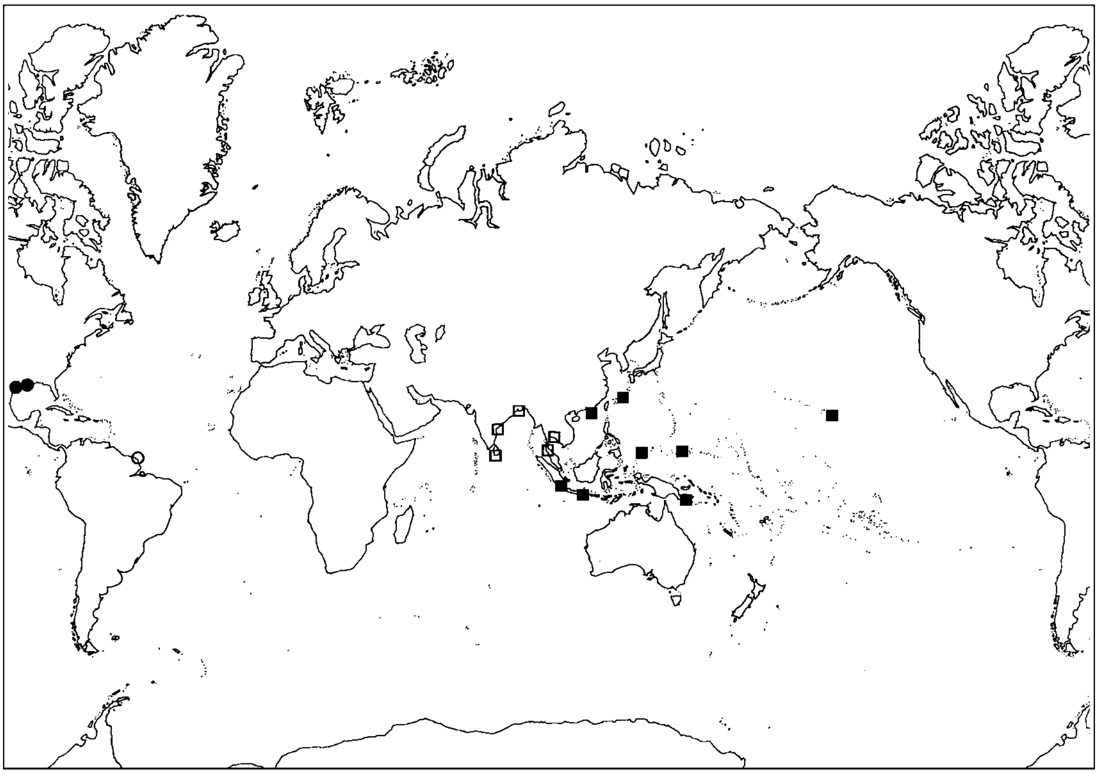

Figure 19. Distribution of *Namalycastis geayi* ○, *N. hawaiiensis* ■, *N. indica* □, and *N. intermedia* n.sp. ●, based on material examined.

be located in the collections of the MNHN, and (ii) no single specimen was expressly indicated as such by Gravier. Therefore, I am following recommendation 73F of the International Zoological Commission in designating a lectotype rather than assume a holotype exists.

Namalycastis geayi is a unique member of the Namanereidinae in lacking falcigerous setae. The species is further distinguished by having jaws with a large number of teeth (up to 15, including ensheathed ones), very short dorsal cirri throughout, many setigerous segments, and eyes arranged longitudinally or nearly so. Phylogenetically it belongs with a clade of four other South American species—*N. senegalensis*, *N. siolii*, *N. macroplatis* n.sp. and *N. arista* n.sp.

Habitat. The types were collected from the muddy banks of freshwater creeks of the Ouanary River. Also from a spring (or sinkhole) in coarse sediment where the water was drinkable (Gravier, 1901).

Distribution. According to Gravier (1901, 1902c) all material collected by Geay was from the Ouanary River area, French Guiana (Fig. 19). No other records exist.

Etymology. Gravier named the species in honour of M.F. Geay who collected this species and other namanereidine species on French Expeditions to French Guiana.

Namalycastis hawaiiensis (Johnson)

Figs. 1c, 4a, 19, 20a–i; Table 4

Lycastis hawaiiensis Johnson, 1903: 210–212, pl.XVI, figs. 11–13, pl. XVII, figs. 17–23.–Horst, 1909: 2–4, fig. 145.
Lycastis ranauensis Feuerborn, 1931a: 639–651, figs. 6–10; 1931b: 240–241; 1935: 256–262 (ecological notes); 1936: 137–139 (physiological notes).–Augener, 1933a: 193–194.–Schmidt, 1935: 3–10, figs. 1–2.
Namalycastis hawaiiensis.–Hartman, 1959a: 163–164.
Namalycastis abiuma.–Hartman, 1966: 203.–Bailey-Brock, 1987: 297–298, fig. 3.II.71a–c. *Non* Grube.
Namalycastis sp.–Maciolek & Brock, 1974: 63 (table only, in part).

Material examined. NEOTYPE: Hawaiian Islands, Oahu, Honolulu (21°19'N 157°50'W), Manoa Stream at Dole Street bridge, mud and detritus; coll. C. Glasby & N. Somers, 2.2.87 (AM W20261). NON-TYPE: Oahu, Manoa Stream 22(AM W20257), 6(AM W20253), 1(AM W20262), 1(UH unreg.); Heeia Stream 10(AM W20255), 2(AM W20256); Kahana Stream 14(AM W20260). Kauai, stream near Niumalu Park 18 (AM W20254). Hawaii, Kiholo Bay no. 1 north pond, 7/8/72, 5(UH unreg.), Kiholo ponds 3&5, 7/8/72, 3(UH unreg.), Kiholo pond E17, 6(AM W20263), Kiholo pond E14, 9(AM W20259); Lower Kiholo Bay 13(AM W20258). New Guinea, Milne Bay, Garnadodo 1(USNM 178869). Palau Islands, Arakataoch Stream, about 1.5 km SE of Ngarekeai village 2(USNM 33261). Hong Kong, Lam Tsuen River 1(AM W20269), New Territories, Ho Chung River 1(AM W20270). Java, west Java 1(ZMA V.Pol. 625),

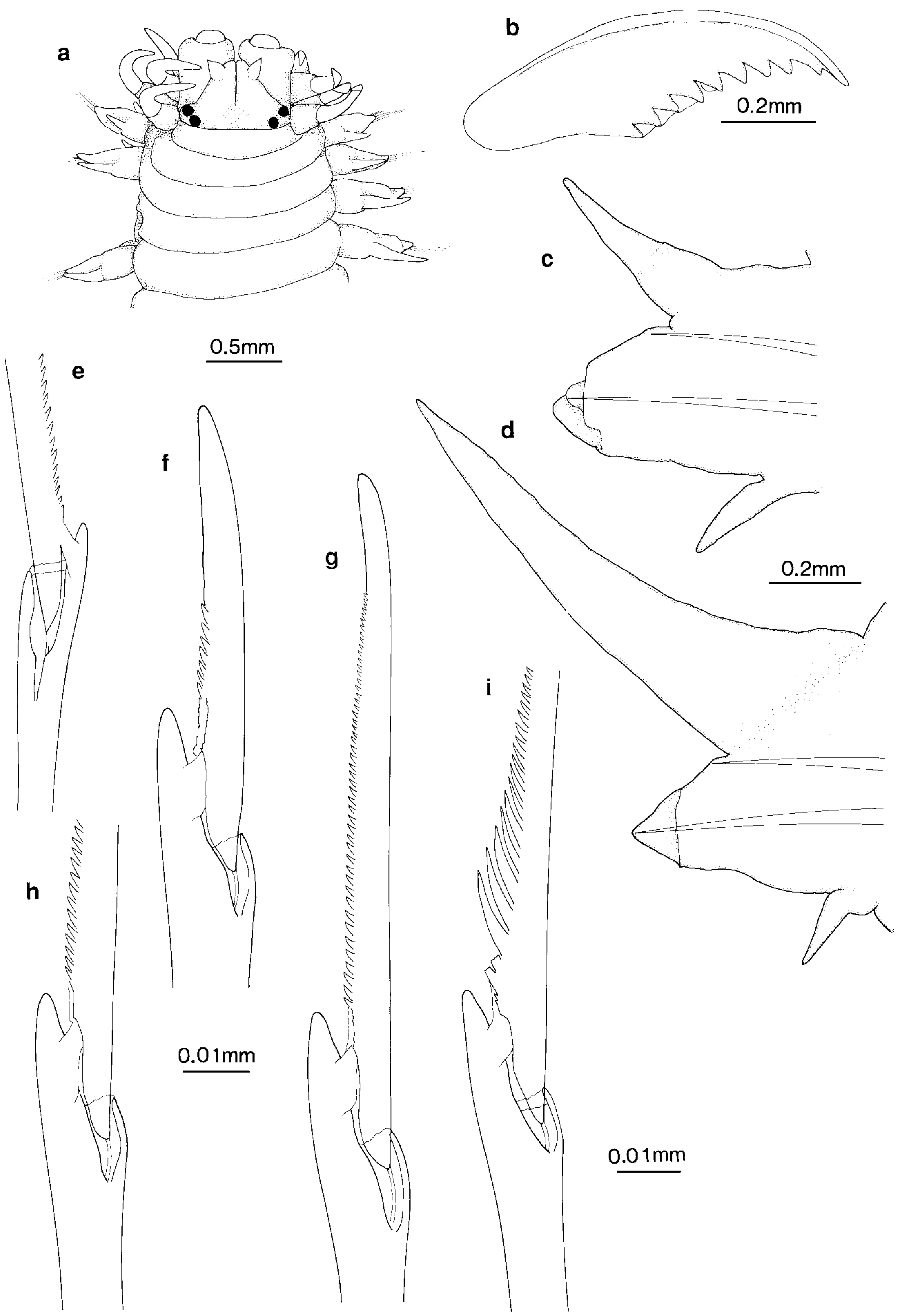

Figure 20. *Namalycastis hawaiiensis* neotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S. posterior view; (*d*) parapodium from 120th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 9; (*g*) sub-neuroacicular falciger (dorsal-most), setiger 9; (*h*) sub-neuroacicular spiniger, setiger 9; (*i*) sub-neuroacicular spiniger, setiger 120.

2(ZMA V.Pol. 2779); Buitenzorg 4(MNHN UE 915). 14 specimens measured.

Other material examined. Java, Buitenzorg, 4(RNHL 1344), 2(HZM V12107); Sumatra, Ranauab River, 5(HZM V11934); Hawaii, Oahu, Ewa 1(HZM P14369); Truk, Moen 1(UH unreg.); Japan, Ryukyu Is., Amani-Oshima 14(AM W20271).

Diagnosis. Epidermal pigment absent. Prostomium anteriorly shallowly cleft (usually). Antennae extending short of tip of palpophore. Notosetae usually absent. Neurosetae Type A (Fig. 1c). Supra-neuroacicular setae: heterogomph falcigers in preacicular fascicle. Sub-neuroacicular setae: heterogomph spinigers in postacicular fascicle. Supra-neuroacicular falcigers in setiger 10 with blades 5.6 × longer than width of shaft head (4.6–6.8), finely serrated, 6 teeth (4–16), teeth about uniform in length. Sub-neuroacicular falcigers in setiger 10 dorsally with blades 8.4–11.3 (rarely less) times longer than width of shaft head, 35–70 teeth (rarely fewer).

Description. Neotype well preserved, segmentally complete, immature oocytes in coelom. Other material well preserved, segmentally complete. 157 setigers (46–199), 66 mm long (11–81), 2.6 mm wide at setiger 10 (1.2–2.7). At setiger 10 length of parapodia 0.43 × body width (0.34–0.47).

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter convex or flat, usually with shallow medial groove. Colour in alcohol yellow-white to yellow-brown. Epidermal pigment absent. Living colour pale pink throughout.

Prostomium. Shallow anterior cleft present or absent (rarely), with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly triangular or trapezoidal (rarely), laterally notched or slightly indented; 1.6 × wider than long (1.3–2.3). Antennae smooth, extending short of tip of palpophore, aligned over mid-palps to inner edge of palps. Eyes 2 pairs, black (rarely purple or red), arranged obliquely, equal in size or posterior pair slightly smaller; lenses absent (Fig. 20a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 2.0 × length anteroventral (1.1–2.2). Anterodorsal tentacular cirri 0.9 × length posterodorsal (0.6–0.9). Posterodorsal tentacular cirri 1.8 × length posteroventral (1.1–1.7). Posterodorsal tentacular cirri extending posteriorly to setiger 3–4 (Fig. 20a). Jaws with single robust terminal tooth, 4 subterminal teeth (4–7), 5 teeth ensheathed proximally (3–5), brown or yellow (rarely) (Fig. 20b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 20c). Dorsal cirri increasing slightly in length posteriorly; 2.1 × length of podium at setiger 3 (1.5–2.7) (Fig. 20c), 1.8 × length of podium in mid-body (1.3–3.0), 7.6 × length of podium posteriorly (3.0–8.0); 3.5 × longer than wide posteriorly (2.0–3.7) (Fig. 20d). Ventral cirri 0.40 length of podium at setiger 3 (0.35–0.57), 0.40 length of podium posteriorly (0.24–0.60).

Setae. Notosetae absent (very rarely present) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (1.5–1.6) (Fig. 20e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.6 × longer than width of shaft head (4.6–6.8), finely serrated, 6 teeth (4–16), 0.31 × total blade length (0.23–0.50), teeth about uniform in length (Fig. 20f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated (Fig. 4a); dorsal-most 8.4 × longer than width of shaft head (8.4–11.3, rarely less), 35 teeth (35–70, rarely fewer) (Fig. 20g); ventral-most 4.6 × longer than width of shaft head (3.6–6.4), 2 teeth (3–8). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated and/or increasingly coarsely serrated proximally; falcigers with proximally coarsely serrated blades from setiger 120 (setiger 30 in smaller specimens). Sub-neuroacicular spinigers in anterior region with blades finely serrated (Fig. 20h); posteriorly, from setiger 120 (setiger 30 in smaller specimens) blades having coarse serrations proximally (Fig. 20i). Setae dark (rarely pale). Acicula in mid-body black (rarely brown).

Pygidium. Pygidium with multi-incised rim (rarely weakly incised or smooth). Anus terminal. Anal cirri arising ventrolaterally (rarely laterally), approximately conical, smooth, 1.0 × width pygidium (0.70–2.5).

Sex. Mature oocytes 140–155 µm, straw-coloured, with thin external membrane. Epitokal setae absent. Hermaphrodite, according to Feuerborn (1931a).

Remarks. The designation of a neotype for *Namalycastis hawaiiensis* is desirable as the type specimens are probably lost. Further, the species has a wide distribution in the central and west Pacific and has been confused with *Lycastis ranauensis* Feuerborn.

The type description of *N. hawaiiensis* is based on three syntypes, two were collected in a "spring near Honolulu", and the other in the Hawaiian Islands (exact locality unknown). Johnson does not mention where the syntypes were deposited, if at all, and they may reasonably be assumed to be unavailable (see remarks for *N. alticola*). The specimen selected as neotype from Manoa Stream, near Dole Street Bridge, Honolulu, was collected in freshwater as were Johnson's specimens. The exact locality of the "spring near Honolulu" mentioned by Johnson (1903) is unknown.

The designated neotype fits Johnson's type description very well, considering the range of variation in this species. In particular, Johnson records both the long-bladed and the typical falcate setae as "having a few coarse serrations … while their tips are smooth". These are the so-called sub-neuroacicular falcigers as described here, but only the setae of posterior parapodia have coarsely serrated blades. This type of seta is very characteristic of *N. hawaiiensis*. In addition, Johnson (1903) records the only pigmentation to be on the "tips of the dorsal posterior pair (of tentacular cirri)", which are yellow, and that the living colouration is "flesh-colored". This finding also agrees with the material at hand.

The specimens examined from the Kona coast, Hawaii (Kiholo Bay region) were those identified as Polychaeta sp. and *Namalycastis* sp. by Maciolek & Brock (1974). Their material also probably included *Namanereis littoralis* sp. group. Specimens described by Horst (1909) as *Lycastis hawaiiensis* generally fit the description given here except that they have the occasional notosetal sesquigomph spiniger. The specimen from Truk differs slightly from the other material in having brown pigment on the prostomium and dorsally on the first few segments and posterior segments, including a brown pygidium.

The synonymy with *Lycastis ranauensis* Feuerborn is based on comparison with specimens from the Ranauab River, Sumatra (HZM V11934). Although not designated as types, it seems likely that these were the specimens collected on the Sunda Expedition of 1928–9 and reported by Feuerborn (1931a). Feuerborn (1931a: 642) reports that 12 specimens were originally collected in the Wadi Kuala, an outflow of Lake Ranau, but only five specimens are now present in the collection of the HZM. It appears that some individuals may have been used for physiological and reproductive studies (see Feuerborn, 1935, 1936).

The phylogenetic position of *Namalycastis hawaiiensis* is uncertain. There is weak support for a sister group relationship with *N. brevicornis*, *N. kartaboensis* and *N. longicirris* as indicated by the presence of this clade in only 52% of the minimal-length trees; the clade is collapsed in both the Strict and Nelson consensus trees (Figs. 5,6).

Habitat. The neotype habitat is the muddy banks of Manoa Stream (freshwater). Other Hawaiian material was collected from streams, swamps, aquaculture ponds and coastal, often slightly saline, anchialine ponds (*sensu* Holthuis, 1973). Salinity of the various localities ranged from fresh to very slightly brackish. Sediment ranged from mud to muddy sand. The species is found in the top few centimetres of sediment or on the surface of sediment under leaf litter, stones, coconut shells or other debris near the edge of the water. The species is most abundant in areas of heavy nutrient load and is often found in association with the oligochaete *Branchiura sowerbyi* Beddard and talitrid amphipods.

Hawaiian specimens all found in short, swiftly flowing streams up to a few kilometres from the sea, extending downstream to within a few hundred metres from the sea, where the water is slightly brackish. Palau Island material and the specimens of *Lycastis ranauensis* Feuerborn from South Sumatra were also found in a freshwater stream, although the latter was collected about 400–450 km from the sea. Like some of the Hawaiian specimens, the ones from Sumatra were also collected under the loose bark of a floating tree (Feuerborn, 1931a). The species survives well in freshwater aquaria (Feuerborn, 1931a; J. Bailey-Brock, pers. comm., 1985) and has even been found in cisterns.

Distribution. Neotype from Hawaiian Islands, Oahu. The synonymy with *N. ranauensis* extends the distribution to Sumatra and Java. New records for Hawaiian Islands of Hawaii and Kauai; New Guinea; Palau Islands; Hong Kong; Japan (Ryukyu Is.); Truk (Fig. 19). Feuerborn (1935) reports an attempted introduction of the species into Skutari Lake, Yugoslavia.

Etymology. The species is named after the island group where it was discovered.

Namalycastis indica (Southern)

Figs. 1c, 19, 21a–i; Table 4

Lycastis indica Southern, 1921: 578–582, pl. XIX, fig. 2A–J, text-fig. 2a–d.–Fauvel, 1930: 19; 1932, 82–83, pl. III, figs. 1–2 (in part); 1940: 257 (in part); 1953: 167–168, figs. 84a,b, 85a.
Namalycastis indica.–Hartman, 1959a: 163–164.–Silva, 1965: 207–209; 1965: 543.
Namalycastis longicirris.–Rosenfeldt, 1984: 72–73, figs. 6–11. *Non* Takahasi.

Material examined. NON-TYPE: India, Salt Lake near Calcutta, 5(ZSI unreg.); Ganges River 2(AM W20268). Thailand, Gulf of Thailand 1 (PMBC 4617); Gulf of Thailand, Chao Phya River 1(PMBC 4618); Songkhla Lake 8(PMBC 4616), 2(PMBC 4619). 12 specimens measured.

Other material examined. India, Chilka lagoon 2(ZSI 1458), 1(ZSI unreg.); Tachin River 2 (HZM P17972)—det. Rosenfeldt, 1984.

Diagnosis. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Prostomium anteriorly shallowly cleft. Antennae extending beyond tip of palpophore to short of tip of palpophore. Dorsal cirri increasing in length slightly posteriorly. Notosetae present. Neurosetae Type A arrangement (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 5.7–8.9 × longer than width of shaft head, finely serrated, 11–22 teeth, teeth about uniform in length. Coarsely serrated sub-neuroacicular spinigers from setiger 3–10. Epitokal setae are slender compound spinigers.

Description. Non-type material generally well preserved (setae poorly preserved in Salt Lake specimens), including some complete individuals. 100–260 setigers, 13–61 mm long, 1.1–2.3 mm wide at setiger 10. At setiger 10 length of parapodia 0.34–0.64 × body width (occasionally to 0.86).

Body. Widest mid-anteriorly (corresponding to increased muscularisation between setigers 9–20), tapering gradually anteriorly and posteriorly. Dorsum convex. Venter flat with deep medial groove, or convex in one specimen turgid with oocytes. Colour in alcohol yellow-white to yellow-brown. Epidermal pigment absent. Living colour pale pink with subcutaneous green pigment posterodorsally.

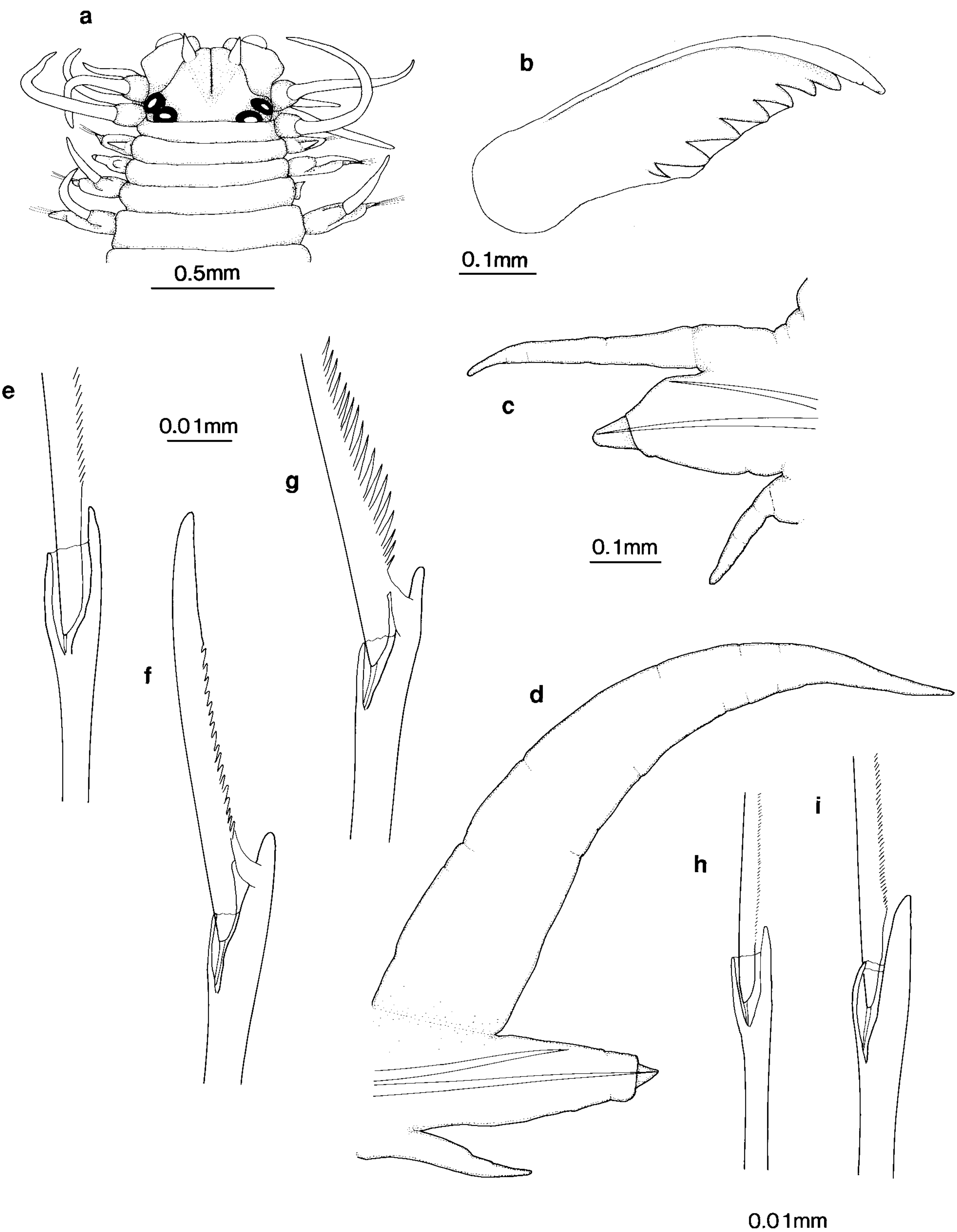

Figure 21. *Namalycastis indica* (ZSI unreg.): (*a*) anterior end, dorsal view, dorsal cirrus on parapodium 2, L.S., missing; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 4th setiger, L.S., posterior view; (*d*) parapodium from 160th setiger, R.S., posterior view. Non-type (AM W20268): (*e*) supra-neuroacicular spiniger, setiger 7; (*f*) supra-neuroacicular falciger, setiger 7; (*g*) sub-neuroacicular spiniger, setiger 7. (*h, i*) Non-type (PMBC 4618), two types of sub-neuroacicular epitokal compound spinigers.

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium (often ending in pit or shallow depression). Prostomium shape roughly triangular or trapezoidal (rarely), laterally notched or slightly indented, rarely not notched or indented; 1.5–2.0 × wider than long. Antennae smooth, extending beyond tip of palpophore or short of tip of palpophore, aligned over inner edge of palps to over mid-palps. Eyes 2 pairs, black or red, arranged longitudinally or obliquely, equal in size or posterior pair slightly smaller (eyes absent in some specimens—probably faded); lenses present (Fig. 21a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles faintly jointed or rarely smooth. Anterodorsal tentacular cirri 1.8–2.5 × length anteroventral. Anterodorsal tentacular cirri 0.6–0.9 × length posterodorsal. Posterodorsal tentacular cirri 1.7–2.5 × length posteroventral (occasionally to 1.2). Posterodorsal tentacular cirri extending posteriorly to setiger 5–6 (to setiger 3 in small specimens) (Fig. 21a). Jaws with single robust terminal tooth, 2–5 subterminal teeth, 3–5 teeth ensheathed proximally, brown (Fig. 21b).

Parapodia. Acicular neuropodial ligule subconical or rarely, slightly bilobed (Fig. 21c). Dorsal cirri increasing slightly in length posteriorly; 0.88–1.9 × length of podium at setiger 3 (Fig. 21c), 2.0–4.0 × length of podium in mid-body (occasionally 1.2–5.0), 3.2–6.7 × length of podium posteriorly; 4.1–6.0 × longer than wide posteriorly (Fig. 21d). Ventral cirri 0.33–0.72 length of podium at setiger 3, 0.50–0.71 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 1–4 (occasionally from setiger 7) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4–1.6 × length of collar (Fig. 21e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.7–8.9 × longer than width of shaft head, finely serrated, 11–22 teeth, 0.35–0.58 × total blade length, teeth about uniform in length (Fig. 21f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 6.0–11.3 × longer than width of shaft head, 15–30 teeth; ventral-most 5.0–7.5 × longer than width of shaft head, 8–15 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated and/or increasingly coarsely serrated proximally; falcigers with proximally coarsely serrated blades from setiger 10–30. Sub-neuroacicular spinigers in anterior region with blades finely serrated; posteriorly, from setiger 3–10, with blades having coarse serrations proximally (Fig. 21g). Setae pale. Acicula in mid-body black or brown.

Pygidium. Pygidium tripartite with 2 large lateral lobes and smaller pointed dorsal lobe (difficult to see dorsal lobe). Rarely pygidium drawn out into funnel shape. Anus terminal. Anal cirri arising ventrolaterally or laterally, approximately conical or flattened (rarely), smooth, 3.0–8.0 × width pygidium (occasionally to 1.5).

Sex. Mature oocytes 105 µm (± 5, 1 specimen measured), straw-coloured, with thin external membrane. Epitokal setae in females are slender compound spinigers (unknown in males) (Fig. 21h,i).

Remarks. The type material described by Southern (1921) was collected from three localities: the Beliaghatta Canal, Calcutta region (5 specimens); Garia, also in the Calcutta region (1 specimen); and about 2,000 km distant, the Cochin Backwater, near Ernakulam (southwest India) (1 specimen). Southern's description is devoted, in the main part, to the 5 specimens from the Beliaghatta Canal with 7, possibly 8, of the 9 illustrations pertaining to those specimens.

Southern (1921: 580) states that the specimen from Cochin Backwater differs from the Calcutta specimens in two aspects: (i) the Cochin specimen has, in podium 10–60, a single sesquigomph spiniger (hemigomph of Southern) in the notopodia, whereas in the Calcutta specimens this seta is absent, and (ii) the Cochin specimen has shorter antennae (tentacles of Southern) and tentacular cirri than the Calcutta specimens. These differences, especially the shorter tentacular cirri, are possibly specific with the specimen from Cochin Backwater likely to belong to another species, *N. abiuma* sp. group. However, some doubt will exist until the type material is examined. As there is doubt about the specific identity of the Cochin Backwater specimen, the type locality should be restricted to the Calcutta region.

Type material of *N. indica*, if still in existence, should be housed with the Indian Museum, Zoological Survey of India (Calcutta). Attempts to borrow the type material have failed, however, some specimens from Salt Lake, near Calcutta were borrowed and examined. These specimens were probably described by Fauvel (1940) as *Lycastis indica*. However, both Fauvel's 1932 and 1940 accounts of *N. indica* include *N. abiuma* sp. group. In the 1932 account, specimens from the Vizagapatam Backwater are identified here as *N. abiuma* sp. group, and in the 1940 account specimens from Vypin and Kayankulam Kayal are also referred to *N. abiuma* sp. group (see Material examined section of *N. abiuma* sp. group).

Namalycastis indica and *N. abiuma* sp. group are similar in external appearance, and unless setal types and distributions are examined carefully, the two species are very difficult to separate. As most descriptions of *N. indica* in the taxonomic literature, with the exceptions of Southern (1921) and Silva (1965), fail to give an adequate account of setal types and distributions, it is quite possible that the two species have been widely confused. Doubtful taxonomic references to *N. indica* include those of Ghosh (1963), Day (1967), and Sunder Raj & Sanjeera Raj (1987).

References to *N. indica* in the broader biological literature include those of Gopala Aiyar (1935), Chakravorty (1937), Runganadhan (1943), Sadasivan Tampi (1949), Krishnan (1952), Florence Mary (1966), Srinivasa Rao & Rama Sarma (1981), and Ramesh Babu *et al*. (1983). Considering the presence of at least two similar species in the coastal regions of India, the identity of specimens referred to in these papers will remain uncertain until the namanereidine fauna of the subcontinent is better known. This would be very interesting in the case of Gopala Aiyar's (1935) material from Madras, which he concludes are protandrous hermaphrodites. Also, Runganadhan presented a paper at the Thirtieth Indian Science Congress in 1943 describing the life history of *Lycastis indica* and its adaptations to low salinities, including modifications to the integument, and reproductive adaptations including development of the egg in a cocoon and the absence of a free-swimming trochophore stage.

Namalycastis indica is the sister species of *N. fauveli*, which is also found in India and Thailand. The clade is delineated by the presence of a well-developed lens, a homoplastic feature that also occurs in *N. multiseta* and some species of *Namanereis.*

Habitat. *Namalycastis indica* inhabits fresh to slightly brackish water of cisterns, pools and lagoons. May also occur in estuaries. Often encountered among debris and in mud at the waters edge (Southern, 1921). At one type locality site the species was found in mud; at another in rotting cocoa nut shell floating in the water together with the freshwater oligochaete *Branchiura sowerbyi* Beddard (Southern, 1921).

In the Ganges River the species occurs in organically polluted waters (BOD_5 6–60+) with the larger animals able to tolerate higher levels of pollution (R.K. Sharan, pers. comm., 1986). Sharan also remarked that the benthos almost disappeared during the monsoon season (July–September) due to strong currents, erosion and heavy deposition of silt.

Distribution. Type locality India, Calcutta region. Other records from India (east coast), Calcutta region, Bangladesh (Ganges delta); Sri Lanka (Negombo Lagoon, Angulana estuary). The synonymy with *N. longicirris sensu* Rosenfeldt extends the distribution to the Gulf of Thailand. New records for the Upper Ganges River and Songkhla Lake (Thailand) (Fig. 19).

Etymology. The species was named after the subcontinent where it was discovered.

Namalycastis intermedia n.sp.

Figs. 1c, 19, 22a–i; Table 4

Material examined. HOLOTYPE: USA, Louisiana, Cameron Parish (29°47'N 93°19'W), North of Rockefeller Wildlife Refuge, freshwater; coll. Whitehead, April 1963, don. Walter J. Harman (USNM 178870). PARATYPES: Louisiana, locality details as for holotype 20(USNM 31011). NON-TYPE: Texas, Jefferson County, Fence Lake, coll. B. Callahan, 19 September 1975 2(USNM 54905). 8 specimens measured.

Diagnosis. Prostomium anteriorly deeply to shallowly cleft. Antennae extending beyond tip of palpophore. Notosetae absent. Neurosetae Type A arrangement (Fig. 1c). Heterogomph falcigers replaced by heterogomph spinigers in posterior parapodia. Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.8–7.6), finely or moderately serrated (rarely), 26 teeth (19–31), teeth increasing in length very slightly proximally or teeth about uniform in length.

Description. Holotype moderately well preserved, some setal and body wall damage, segmentally incomplete, immature oocytes in coelom. Paratypes moderately well preserved, including some complete individuals. 86 setigers, 14.2 mm long, 1.1 mm wide at setiger 10 (0.8–1.3). At setiger 10 length of parapodia 0.42 × body width (0.32–0.52).

Body. Uniform in width anteriorly, tapering gradually posteriorly sometimes not until far posterior region. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-white. Epidermal pigment absent.

Prostomium. Anterior cleft deep or shallow, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly triangular or trapezoidal; 1.6 × wider than long (1.3–1.8). Antennae smooth, extending beyond tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs (though pigment dispersed slightly), black, arranged obliquely or transversely, equal in size; lenses absent (Fig. 22a).

Peristomium. Tentacular cirri with cirrophores indistinct; cirrostyles smooth or very faintly jointed. Anterodorsal tentacular cirri 1.3 × length anteroventral (1.3–2.0). Anterodorsal tentacular cirri 0.6 × length posterodorsal (0.6–0.9). Posterodorsal tentacular cirri 1.7 × length posteroventral (1.4–2.0). Posterodorsal tentacular cirri extending posteriorly to setiger 5 (3–5) (Fig. 22a). Jaws with single robust terminal tooth, 3 subterminal teeth (2–4), 5 teeth ensheathed proximally (4–6), brown (Fig. 22b).

Parapodia. Acicular neuropodial ligule subconical (22c,d). Dorsal cirri increasing slightly in length posteriorly or similar in length throughout; 1.3 × length of podium at setiger 3 (1.0–3.2) (Fig. 22c), 1.4 × length of podium in mid-body (0.70–3.1), 2.5 × length of podium posteriorly (0.70–3.5); 2.7 × longer than wide posteriorly (3.1–3.6) (Fig. 22d). Ventral cirri 0.30 length of podium at setiger 3 (0.38–0.54), 0.53 length of podium posteriorly (0.21).

Setae. Notosetae absent. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4).

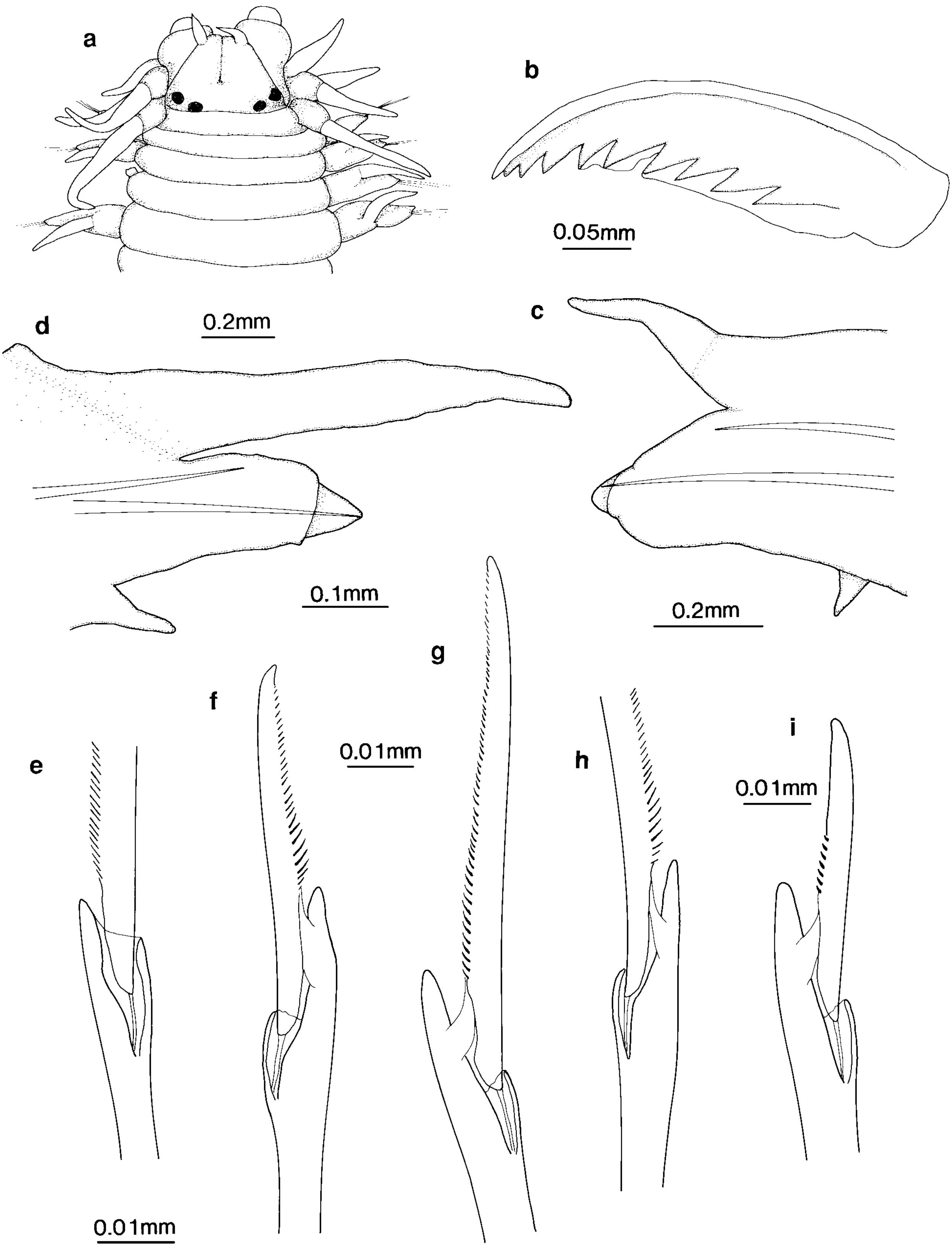

Figure 22. *Namalycastis intermedia* holotype: (*a*) anterior end, dorsal view. (*b*) Paratype (USNM 31011), jaw piece, ventromedial view. (*c*) Holotype, parapodium from 3rd setiger, L.S., posterior view. (*d*) Paratype (USNM 31011), parapodium from 90th setiger, R.S., posterior view. Holotype: (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular falciger (dorsal position), setiger 14; (*h*) sub-neuroacicular spiniger, setiger 60; (*i*) sub-neuroacicular falciger (ventral-most), setiger 14.

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4 × length of collar (1.5–1.8) (Fig. 22e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.8–7.6), finely or moderately serrated (rarely), 26 teeth (19–31), 0.65 × total blade length (0.44–0.66), teeth increasing in length slightly proximally or teeth about uniform in length (Fig. 22f). Sub-neuroacicular falcigers in setiger 10 with blades finely or moderately serrated (rarely); dorsal-most 8.0 × longer than width of shaft head (7.2–10.6), large number of teeth (30+) (Fig. 22g); ventral-most 4.4 × longer than width of shaft head (4.2–6.8), 25 teeth (6–30). Sub-neuroacicular falcigers in mid-posterior region with blades finely or moderately serrated (rarely). Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally (Fig. 22h). Setae pale or dark (rarely). Acicula in mid-body brown.

Pygidium. Pygidium drawn out into funnel shape, tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising laterally, approximately conical, smooth, 2.0 × width pygidium.

Sex. Mature oocytes 291–301 µm (2 specimens), straw-coloured, with external membrane. Epitokal setae absent.

Remarks. *Namalycastis intermedia* n.sp. resembles closely another north American species, *N. borealis* n.sp., but may be distinguished from *N. borealis* by having the supra-neuroacicular falcigers replaced by heterogomph spinigers in far posterior parapodia, partial replacement of sub-neuroacicular falcigers by heterogomph spinigers in parapodia of far posterior setigers, and in having long-bladed falcigers in the dorsal position of the subacicular fascicle. The partial replacement of falcigers with spinigers in the parapodia of posterior setigers gives the new species a superficial resemblance to the group of species having the falcigers fully replaced by spinigers posteriorly (this group includes *Namalycastis senegalensis*, *N. arista* n.sp. and *N. macroplatis* n.sp.). However, the results of the cladistic analysis reveal a sister group relationship with *N. elobeyensis* n.sp., indicating that the partial replacement of falcigers with spinigers in the parapodia of posterior setigers may be a homoplasy. Alternatively, the partial replacement condition may be an autapomorphy of the species, and therefore it may be appropriate to rescore this character in future cladistic analyses of the group.

Habitat. Holotype and paratypes from Louisiana collected in freshwater.

Distribution. Type locality USA, Louisiana, Cameron Parish. Other records from USA, Texas, Jefferson County (Fig. 19).

Etymology. From the L. *intermedia*, meaning that is between, indicating the intermediate nature of this species in having falcigers only partially replaced by spinigers posteriorly.

Namalycastis kartaboensis (Treadwell) n.comb.

Figs. 1c, 23a–h, 24; Table 4

Namonereis [sic] *kartaboensis* Treadwell, 1926: 101–103, fig. 33A–C.

Material examined. NON-TYPE: Surinam, Surinam River at Paramaribo, wreck of Goslar 1(ZMA V.Pol. 2896). French Guiana, no. 46, coll. M. Geay, 1901, 2(MNHN UE 916). Three specimens measured.

Other material examined. HOLOTYPE: Guyana, Kartabo [= Kartabu Point] (6°23'N 58°41'W) (AMNH 3542).

Diagnosis. Prostomium anteriorly shallowly cleft. Antennae extending beyond tip of palpophore to short of tip of palpophore. Tentacular cirri with cirrostyles faintly jointed. Notosetae present. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with smooth blades, 5.8–7.0 × longer than width of shaft head.

Description. Non-type material well preserved, including some complete individuals. 122–178 setigers, 1.4–2.9 mm wide at setiger 10. At setiger 10 length of parapodia 0.49–0.69 × body width.

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-brown. Epidermal pigment absent.

Prostomium. Anterior cleft absent, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal; 1.4–1.6 × wider than long. Antennae smooth, extending beyond tip of palpophore or short of tip of palpophore, aligned over mid-palps to over inner edge of palps. Eyes 2 pairs, black, arranged obliquely or transversely, equal in size or posterior pair (i.e. inner pair) slightly smaller; lenses absent (Fig. 23a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 1.6–2.0 × length anteroventral. Anterodorsal tentacular cirri 0.6–0.7 × length posterodorsal. Posterodorsal tentacular cirri 1.7–3.0 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 5–7 (Fig. 23a). Jaws with single robust terminal tooth, 4–8 subterminal teeth, 3–4 teeth ensheathed proximally, brown, moderately sclerotised (Fig. 23b).

Parapodia. Acicular neuropodial ligule faintly bilobed (Fig. 23c,d). Dorsal cirri increasing slightly in length posteriorly or increasing greatly in length posteriorly; 1.4–1.6 × length of podium at setiger 3 (Fig. 23c), 1.4–2.7 × length of podium in mid-body, 2.5–4.7 × length of podium posteriorly; 4.5–4.6 × longer than wide posteriorly (Fig. 23d). Ventral cirri 0.44–0.57 length of podium at setiger 3, 0.32–0.42 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 4–5, though absent in some parapodia (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in

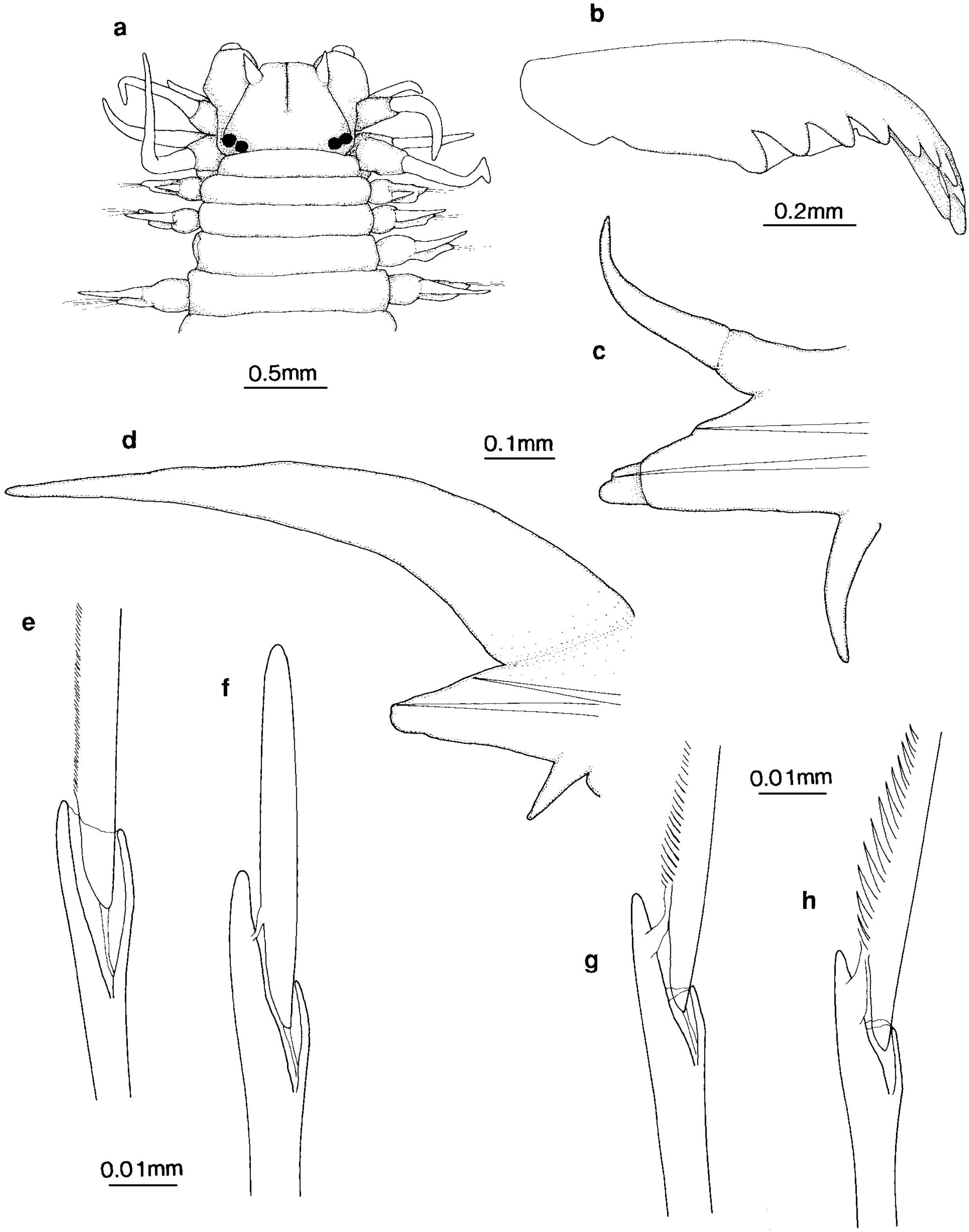

Figure 23. *Namalycastis kartaboensis* French Guiana (MNHN UE 916): (*a*) anterior end, dorsal view; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, L.S., posterior view; (*d*) parapodium from 180th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 10; (*h*) sub-neuroacicular spiniger, setiger 120.

postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.3–1.4 × length of collar (Fig. 23e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with smooth blades, 5.8–7.0 × longer than width of shaft head (Fig. 23f). Sub-neuroacicular falcigers in setiger 10 with blades smooth and/or finely serrated (dorsal-most ones only); dorsal-most 5.2–8.0 × longer than width of shaft head, 0–11 teeth; ventral-most 5.2–5.3 × longer than width of shaft head. Sub-neuroacicular falcigers in mid-posterior region with smooth blades. Sub-neuroacicular spinigers in anterior region with finely serrated blades (Fig. 23g); posteriorly, from setiger 30–60, with blades having coarse serrations proximally (Fig. 23h). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium with multi-incised rim. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 6–8 × width pygidium.

Remarks. The holotype is not included in the description above as it is in very poor condition as a result of dehydration and is incomplete posteriorly, consisting of 2 fragments, about 75 segments in all. The specimen fits the dimensions given by Treadwell (1926) and is very coiled, which Treadwell also mentioned.

Two specimens taken from the paratype series of *N. ouanaryensis* (Gravier) (MNHN UE 926), are reidentified here as *N. kartaboensis* and removed from the type series. The two specimens were not apparently included in the type description or illustrations of Gravier (1901), and furthermore, do not fit the description of *N. ouanaryensis*, here considered a junior synonym of *N. senegalensis* (Saint-Joseph).

Namalycastis kartaboensis appears to be similar to *N. brevicornis* Audouin & Edwards and *N. abiuma* sp. group in having falcigerous setae continuing to the pygidium. It may be distinguished from both these species however in having long, straight falciger blades that are usually smooth, although the dorsal-most sub-neuroacicular falcigers may be serrated. *Namalycastis kartaboensis* forms a monophyletic group with *N. brevicornis* and *N. longicirris*, although the grouping is present in only 81% of all minimal-length trees and the relationship is collapsed in both the Strict and the Nelson Consensus trees (Figs. 5,6).

Habitat. The type habitat is unknown. The Paramaribo specimen was collected in 0–2 m in mud.

Distribution. Type locality Guyana, Kartabu Point. New records for Surinam and French Guiana (Fig. 24).

Etymology. Treadwell named the species after the old name (Kartabo) for the type locality.

Namalycastis longicirris (Takahasi)

Figs. 1c, 24; Table 4

Lycastis longicirris Takahasi, 1933: 42–46, figs. 1–6.–Okuda, 1935: 244 (list only).
Namalycastis longicirris.–Hartman, 1959a: 163–164.

Material examined. None.

Diagnosis. Prostomium anteriorly shallowly cleft. Antennae extending short of tip of palpophore. Dorsal cirri increasing greatly in length posteriorly. Notosetae present. Neurosetae Type A arrangement (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 8.4–11.4 × longer than width of shaft head, finely serrated, 36–60 teeth, teeth about uniform in length. Sub-neuroacicular spinigers with proximally coarsely serrated blades, present from at least setiger 17.

Description. Following description compiled from Takahasi (1933). Syntypes segmentally complete, various stages of sexual maturity. 100–180 setigers, 80–120 mm long, 2–4 mm wide at setiger 10. At setiger 10 length of parapodia 0.34 × body width.

Body. Dorsum highly arched. Venter usually flat, but highly arched in sexually mature specimens. Epidermal pigment absent. Living colour pale pink throughout (yellowish-green posteriorly in the male, milky white in mature specimens).

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium (ending in shallow transverse groove). Prostomium shape roughly trapezoidal; 2.0 × wider than long. Antennae smooth, extending short of tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs (rarely an additional eye on one side), black, arranged obliquely or transversely (rarely), equal in size; lenses absent.

Peristomium. Tentacular cirri with cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri about 1.9 × length anteroventral. Anterodorsal tentacular cirri about 0.65 × length posterodorsal. Posterodorsal tentacular cirri about 2.0 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 5–8. Jaws with single robust terminal tooth, 7–8 subterminal teeth (uncertain whether ensheathed teeth included).

Parapodia. Dorsal cirri increasing greatly in length posteriorly; about 1.6 × length of podium at setiger 3, about 6.0 × length of podium posteriorly; about 7.5 × longer than wide posteriorly. Ventral cirri about 0.35 length of podium at setiger 3, about 0.38 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers present (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss about 1.4 × length of collar. Heterogomph setae with boss not prolonged. Neuropodial falcigers in setiger 10 with blades 8.4–11.4 × longer than width of

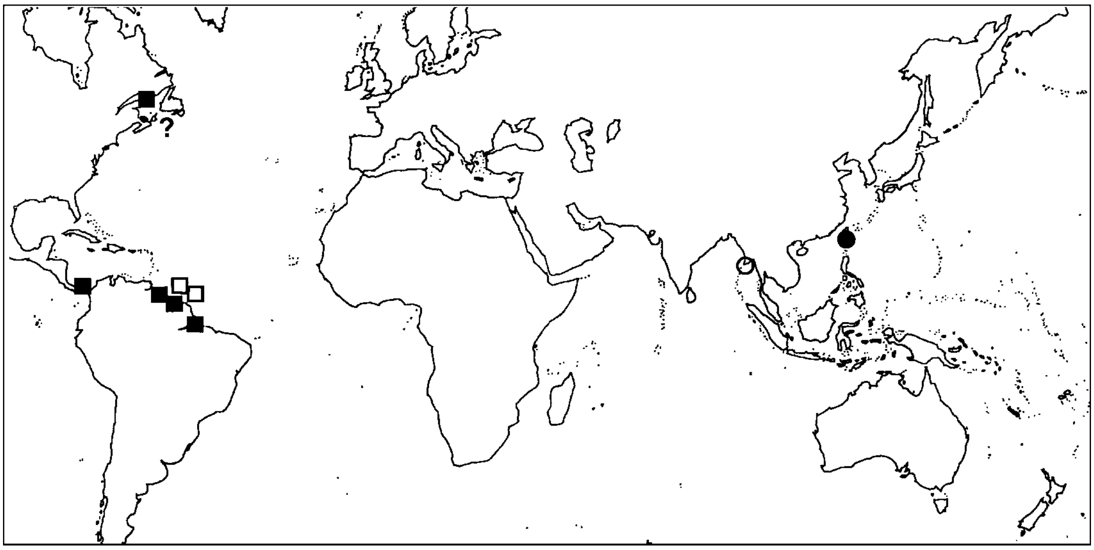

Figure 24. Distribution of *Namalycastis kartaboensis* □, *N. longicirris* ●, *N. macroplatis* n.sp. ■, and *N. multiseta* n.sp. ○; based on material examined and authenticated literature records.

shaft head, finely serrated, 36–60 teeth, 0.46–0.84 × total blade length, teeth about uniform in length. Subneuroacicular spinigers in mid-posterior region with blades having coarse serrations proximally; present from setiger 17 (perhaps earlier). Setae dark, or pale (rarely). Acicula in mid-body black.

Pygidium. Structure of pygidium unknown. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, about 1.2 × width pygidium.

Sex. Epitokal setae absent.

Remarks. According to Takahasi (1933), the types of *N. longicirris* were deposited at the Taihoku Imperial University (now National Taiwan University). Unfortunately, I have been unable to ascertain whether the types are still in Taiwan, nor could they be located by M. Imajima in the collection of the Hokkaido University or other polychaete repositories in Japan (M. Sato, pers. comm., 1987). The types may therefore be lost.

The above description is compiled from Takahasi (1933), which is the only description of this species. The *Namalycastis longicirris* of Rosenfeldt (1984) is reidentified here as *N. indica* (Southern). All measurements and some counts in the description are taken from Takahasi's figures and are therefore approximations. Some differences regarding setal terminology between Takahasi (1933) and the present description should be noted. Takahasi refers to the notopodial and supra-neuroacicular spinigers as "homogomph spinigers without comb" (fig. 5a), whereas they are referred to here as sesquigomph spinigers. Further, it is likely that the absence of a comb (serrations) may be an impression gained by the angle that the spinigers were viewed. A more typical sesquigomph spiniger (fig. 5c) is referred to by Takahasi as a heterogomph spiniger. Therefore the two setae illustrated in Takahasi's figs. 5a and 5c are both sesquigomph spinigers.

The setae illustrated by Takahasi (figs. 5a–e) are from an anterior parapodium, perhaps parapodium 18 (which is illustrated in fig. 3A). Setal measurements given in the present description are taken from these figures, but should still be comparative with setae of setiger 10 in other species descriptions since the morphology of setae varies little between anterior parapodia. In contrast, falciger blade morphology may vary slightly between fascicles within a parapodium. It is not known whether the falciger illustrated by Takahasi is from the supra- or the subacicular position.

Namalycastis longicirris resembles *N. indica* (Southern) and to a lesser extent, *N. hawaiiensis* (Johnson) in general appearance, setal types and freshwater habitat. It differs from both species in having falciger blades with a greater number of serrations. Additionally, it differs from *N. hawaiiensis* in having notosetae. The species is one of several that cannot be placed with any certainty within the phylogeny of the Namanereidinae. In 81% of all minimal-length trees it forms a clade with *N. kartaboensis* and *N. brevicornis*, which like *N. longicirris* are relatively poorly-known species; there is the possibility that they grouped together on the basis of shared unknown features (indicated by a "?" in the data matrix—Table 2). More material of *N. longicirris* needs to be examined in order to better characterise the species.

Habitat. The type habitat is the upper regions (?freshwater) of the Tamsui River; also in canals, ditches, and rice- or lotus-fields. Found in muddy or fine sand often under stones or wood.

Distribution. Type locality Taiwan, Tamsui River region (Fig. 24).

Etymology. The specific name refers to the "enormous length of the dorsal cirri" according to Takahasi.

Namalycastis macroplatis n.sp.

Figs. 1c, 24, 25a–g; Table 4

Lycastis ouanaryensis Gravier, 1901: 397–399 (in part); 1902c: 354–361, figs. 1–10 (in part).

Material examined. HOLOTYPE: Brazil, Marajos Island [= Ilha de Marajó] (1°0'S 49°0'W), beach, brackish to freshwater, coll. W. Ehrhardt, det. Augener, 1923 (HZM P-22040). PARATYPES: Brazil, collection details as for holotype 3(BMNH ZK 1923.9.25.11–13). Surinam, Surinam River (5°50'N 55°50'W), coll. van Heurn, det. Augener, 1927 3(HZM P-22041). NON-TYPE: Anticosti [?= Ile d'Anticosti, Gulf of St. Lawrence, Quebec] no. ?92, coll. M. Schmidt, 1903 1(MNHN UE 917). 8 specimens measured.

Other material examined. Panama, Pedro Miguel Locks, C.Z., coll. S.F.H., 20 February 1937, 2 headless fragments (USNM 178871).

Diagnosis. Prostomium cleft anteriorly. Antennae extending short of or beyond tip of palpophore. Dorsal cirri less then 1.9 × length of podium at setiger 3. Notosetae present. Neurosetae Type A (Fig. 1c). Heterogomph falcigers replaced by heterogomph spinigers in posterior parapodia. Supra-neuroacicular falcigers in setiger 10 with blades 6.4 × longer than width of shaft head (6.2–7.9), finely serrated, 22 teeth (16–21), teeth about uniform in length. Dorsal-most sub-neuroacicular falcigers in setiger 10 with blades having 16–30 teeth.

Description. Holotype well preserved, segmentally complete, immature oocytes in coelom. Other material well preserved, including some complete individuals. 256 setigers (159–220), 128 mm long (60–67), 4.2 mm wide at setiger 10 (2.9–5.0). At setiger 10 length of parapodia 0.35 × body width (0.36–0.53).

Body. Uniform in width anteriorly, tapering gradually posteriorly (rarely) or widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Dorsum convex. Venter flat or convex. Colour in alcohol yellow-white to brown. Epidermal pigment absent or brown pigment on pygidium only (perhaps faded).

Prostomium. Cleft anteriorly (sometimes deeply), with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, laterally notched (rarely) or slightly indented (rarely no notch or indentation); 1.7 × wider than long (1.4–1.9). Antennae smooth, extending beyond tip of palpophore to short of tip of palpophore, aligned over inner edge of palps to mid-palps. Eyes 2 pairs, black, arranged transversely, posterior pair slightly smaller, or equal in size; lenses absent or indistinct (thick cuticle covering eyes of holotype and some paratypes) (Fig. 25a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 2.4 × length anteroventral (1.6–2.5). Anterodorsal tentacular cirri 0.9 × length posterodorsal (0.7–1.0). Posterodorsal tentacular cirri 2.2 × length posteroventral (1.5–2.0). Posterodorsal tentacular cirri extending posteriorly to setiger 3 (3–4) (Fig. 25a). Jaws with single robust terminal tooth, 3 subterminal teeth (3–5), 2 teeth ensheathed proximally (2–3); ensheathed teeth difficult to see in some specimens, including holotype, due to heavily chitinised guard; brown (Fig. 25b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe subconical, usually curved anteriorly (Fig. 25c,d). Dorsal cirri increasing greatly or only slightly in length posteriorly; 1.1 × length of podium at setiger 3 (1.2–1.9) (Fig. 25c), 3.9 × length of podium in mid-body (2.1–3.2), 7.3 × length of podium posteriorly (2.3–4.1); 5.6 × longer than wide posteriorly (5.1–7.1) (Fig. 25d). Ventral cirri 0.56 length of podium at setiger 3 (0.47–0.65), 0.35 length of podium posteriorly (0.33–0.59).

Setae. Notopodial sesquigomph spinigers from setiger 3 (2–7) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles in anterior podia and heterogomph spinigers in preacicular fascicles in posterior podia (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (1.5–1.8) (Fig. 25e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 6.4 × longer than width of shaft head (6.2–7.9), finely serrated, 22 teeth (16–21), 0.37 × total blade length (0.26–0.36), teeth about uniform in length (Fig. 25f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 6.3 × longer than width of shaft head (5.7–7.6), 16 teeth (16–30); ventral-most 6.1 × longer than width of shaft head (5.1–6.5), 20 teeth (8–24). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in anterior region with finely serrated blades; posteriorly, from setiger 30–60, blades having coarse serrations proximally (Fig. 25g) (absent in holotype). Setae pale, or dark. Acicula in mid-body mid to dark brown.

Pygidium. Pygidium with multi-incised rim. Anus terminal or dorsoterminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 1–6 × width pygidium (damaged in holotype).

Remarks. This species closely resembles *Namalycastis senegalensis* (Saint-Joseph), differing in having a greater number of supra-neuroacicular sesquigomph spinigers (Table 4) and in having falciger blades that are longer and have a greater number of teeth. *Namalycastis macroplatis* n.sp. also differs in being dorsally pigmented, although in specimens examined here the pigment appeared to be faded.

Some specimens of *Lycastis ouanaryensis* described by Gravier (1901, 1902c) are conspecific with *N. macroplatis* n.sp. while others are conspecific with *N. senegalensis* (Saint-Joseph), as remarked upon in more

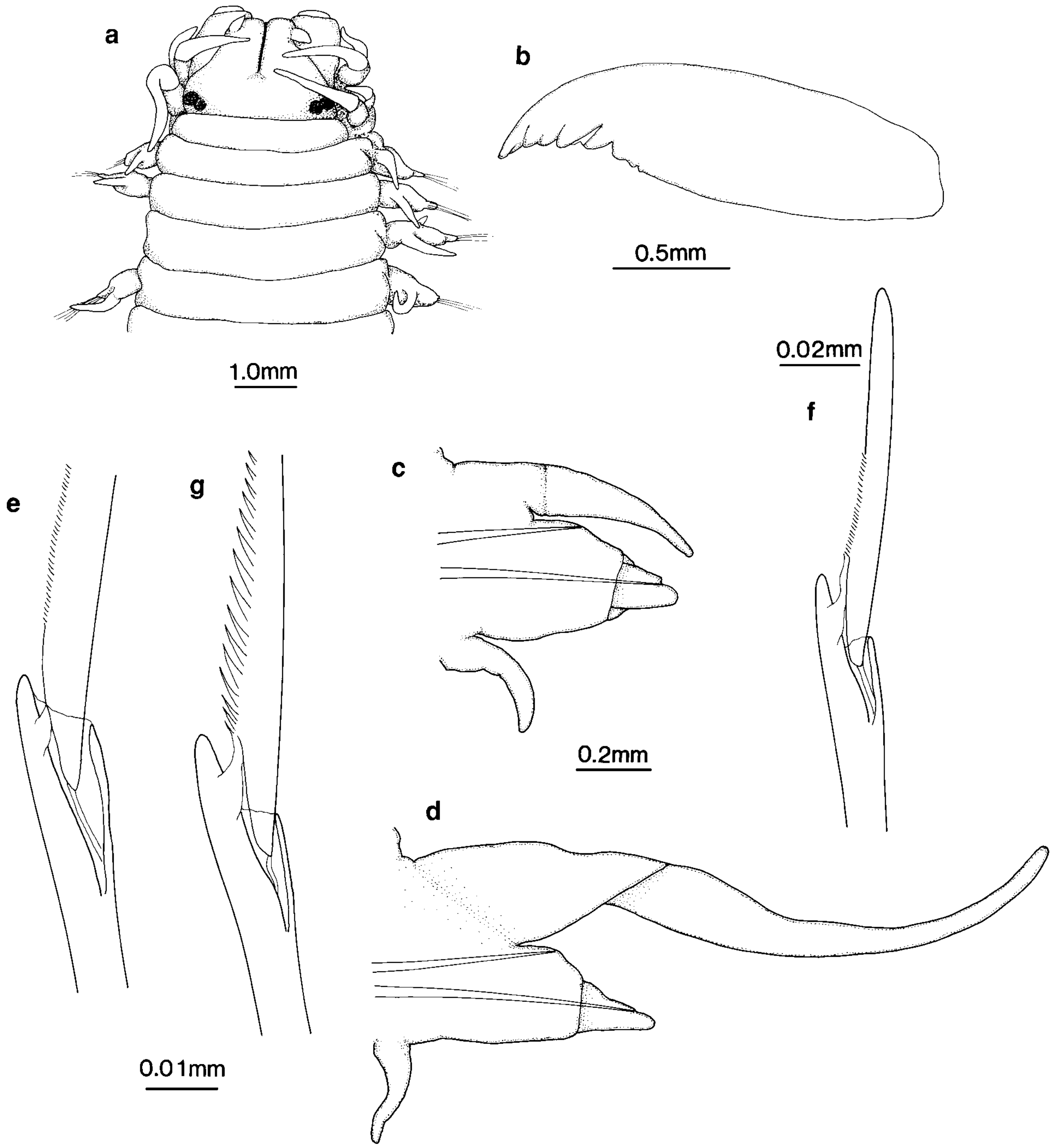

Figure 25. *Namalycastis macroplatis* n.sp. holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 120th setiger, L.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10. (*g*) Non-type, Anticosti (MNHN UE 917), sub-neuroacicular spiniger, setiger 60.

detail for the latter species. *Namalycastis macroplatis* n.sp. belongs to a clade of species with highly-derived features together with *N. senegalensis, N. siolii, N. arista* n.sp. (Fig. 7). Addition of the sister species (*N. geayi*) of this clade circumscribes a group that is characterised by the replacement in preacicular fascicles of heterogomph falcigers anteriorly with heterogomph spinigers posteriorly.

Habitat. The holotype and paratypes (BMNH material) were collected from a beach in brackish to freshwater.

Distribution. Type locality Brazil, Ilha de Marajó. Other records from Surinam (Surinam River) and Panama (Pedro Miguel Locks). The partial synonymy with *L. ouanaryensis* Gravier extends the distribution to French Guiana, although the exact localities are unknown. Possibly introduced to Ile d'Anticosti, Gulf of St. Lawrence, Quebec, though this and other examples of namanereidine species having disjunct distributions will form the basis of a future study (Fig. 24).

Etymology. From the Gk *makros*, meaning long and the Gk *plate* f., meaning the blade of an oar, referring to the long-bladed falcigers characteristic of the species.

Namalycastis multiseta n.sp.

Figs. 1c, 24, 26a–g; Table 4

Material examined. HOLOTYPE: Burma, Rangoon River (16°40'N 96°20'E), 40 m from mouth, pres. Prof. Y.J. Meggett (BMNH ZK 1931.6.22.67). PARATYPES: label details as for holotype 2(BMNH ZK 1931.6.22.68–69). 3 specimens measured.

Diagnosis. Epidermal pigment brown on prostomium, first few segments and pygidium. Prostomium anteriorly shallowly cleft, shape 2.4–2.5 × wider than long. Antennae extending short of tip of palpophore. Notosetae present. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.2 × longer than width of shaft head (4.0–4.3), moderately serrated, 4 teeth (6–9), teeth about uniform in length.

Description. Holotype well preserved, segmentally complete, male gametes in coelom. Paratypes well preserved, segmentally complete. 220 setigers (190–230), 142 mm long (85–110), 5.0 mm wide at setiger 10 (3.8–4.5). At setiger 10 length of parapodia 0.27 × body width (0.24–0.26).

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter flat. Colour in alcohol yellow-white. Epidermal pigment brown on prostomium, first few segments and pygidium.

Prostomium. Shallowly cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal or triangular, laterally slightly indented or notched; 2.4 × wider than long (2.4–2.5). Antennae smooth, extending short of tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs, purple or red, arranged transversely or obliquely, equal in size or posterior pair slightly smaller; lenses present (Fig. 26a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.2 × length anteroventral. Anterodorsal tentacular cirri 0.8 × length posterodorsal (0.9–1.0). Posterodorsal tentacular cirri 1.1 × length posteroventral (1.1–1.2). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (Fig. 26a). Jaws with single robust terminal tooth, 5 subterminal teeth (5–6), 3 teeth ensheathed proximally (4–5), brown (Fig. 26b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 26c,d). Dorsal cirri increasing slightly to greatly in length posteriorly; 2.8 × length of podium at setiger 3 (1.8–2.0) (Fig. 26c), 2.2 × length of podium in mid-body (2.2–2.7), 7.6 × length of podium posteriorly (2.0–3.3); 2.2 × longer than wide posteriorly (2.0–2.5) (Fig. 26d). Ventral cirri 0.60 length of podium at setiger 3 (0.55), 0.45 length of podium posteriorly (0.33–0.42).

Setae. Notopodial sesquigomph spinigers from setiger 9 (9–12) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (1.6) (Fig. 26e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.2 × longer than width of shaft head (4.0–4.3), moderately serrated, 4 teeth (6–9), 0.14 × total blade length (0.29–0.30), teeth about uniform in length (Fig. 26f). Sub-neuroacicular falcigers in setiger 10 with blades moderately serrated; dorsal-most 4.1 × longer than width of shaft head (3.4–4.0), 4 teeth (5–8); ventral-most 3.9 × longer than width of shaft head (3.2–3.6), 3 teeth (1–2). Sub-neuroacicular falcigers in mid-posterior region with blades moderately to finely serrated. Sub-neuroacicular spinigers in anterior region with finely serrated blades; posteriorly, from setiger 60 (30–60), blades having coarse serrations proximally (initially 1 spiniger, increasing to 3 spinigers per fascicle) (Fig. 26g). Setae pale. Acicula in mid-body black, with light-coloured bases.

Pygidium. Pygidium with multi-incised rim. Anus dorsoterminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 1.5 × width pygidium.

Sex. Epitokal setae absent.

Remarks. The type specimens of *Namalycastis multiseta* n.sp. were separated from a lot that also contained two specimens herein identified as *Namalycastis abiuma* sp. group (now BMNH ZK 1931.6.22.70). *Namalycastis multiseta* n.sp. differs from *N. abiuma* sp. group in having coarsely serrated spinigers from setigers 30–60 and in having a greater number (up to 30) of sesquigomph spinigers in the neuropodia of the mid-body (Table 4). The number of sesquigomph spinigers may increase with sexual maturity as the immature paratypes possess fewer setae than the mature holotype. The two species form a clade in both the Majority- rule and Nelson Consensus trees, although the relationship is collapsed in the Strict Consensus tree (Fig. 5). The clade is delineated by the presence of brown epidermal pigment on the dorsum of the body. This feature is however homoplastic, occurring also in *N. terrestris, N. borealis* and *N. macroplatis*.

Habitat. Unknown

Distribution. Type locality Burma, Rangoon River (Fig. 26).

Etymology. From the L. *multus*, meaning much, and *seta*, f., meaning bristle, referring to the large number of sesquigomph spinigers (a type of seta), which is characteristic of this species.

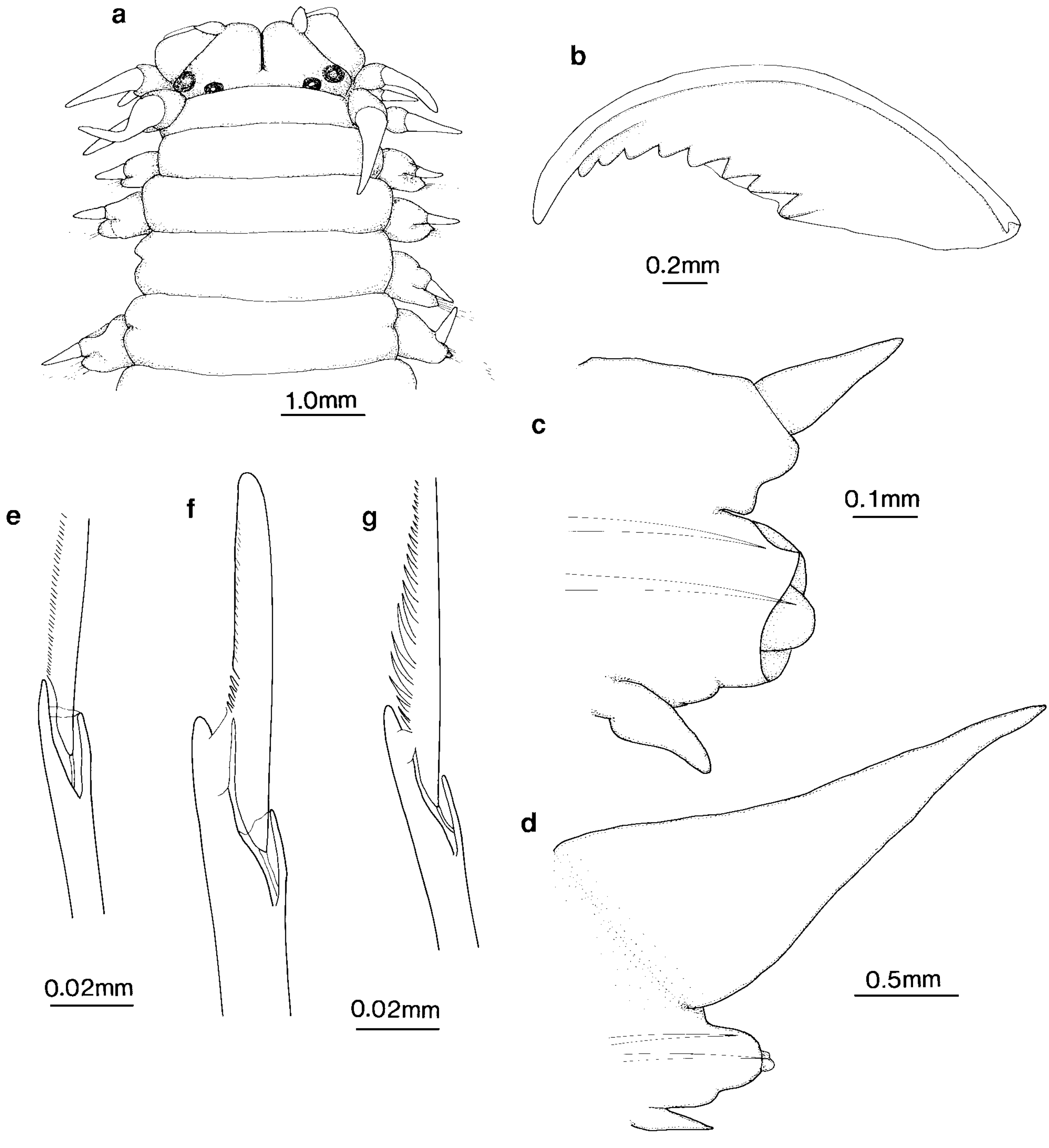

Figure 26. *Namalycastis multiseta* n.sp. holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view, tip of acicular ligule partially retracted; (*d*) parapodium from 180th setiger, L.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 120.

Namalycastis nicoleae n.sp.

Figs. 1c, 27a–h, 28; Table 4

Namalycastis cf. *abiuma*.–Hutchings & Glasby, 1985: 104–106, fig. 2a–g (in part). *Non* Grube.

Material examined. HOLOTYPE: Australia, S.E. Queensland, Brisbane (27°30'S 153°00'E), Airport drain, coll. C. Wallace, 22/viii/1972, (QM G10705). 1 specimen measured.

Diagnosis. Prostomium cleft anteriorly. Antennae extending short of tip of palpophore. Notosetae present. Neurosetae Type A (Fig. 1c), though heterogomph pseudospinigers occasionally present with heterogomph spinigers in sub-postacicular fascicle. Supra-neuroacicular falcigers in setiger 10 with blades 5.8 × longer than width of shaft head, finely serrated, 35–45 teeth, teeth about uniform in length. Dorsal-most sub-neuroacicular falcigers in setiger 10 with blades having 50 or more teeth. Sub-neuroacicular spinigers in mid-posterior region with blades having long, fine serrations proximally.

Description. Holotype well preserved, segmentally complete, no gametes in coelom. 68 setigers, 15 mm long, 1.4 mm wide at setiger 10.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol yellow-white. Epidermal pigment absent. At setiger 10 length of parapodia 0.39 × body width.

Prostomium. Cleft anteriorly, with very shallow dorsal hollow. Prostomium shape roughly triangular; 1.8 × wider than long. Antennae smooth, extending short of tip of palpophore, aligned over mid-palps. Eyes 2 pairs, purple, arranged obliquely, equal in size; lenses absent (Fig. 27a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.8 × length anteroventral. Anterodorsal tentacular cirri 0.9 × length posterodorsal. Posterodorsal tentacular cirri 1.2 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to anterior edge of setiger 3 (Fig. 27a). Jaws with single robust terminal tooth, 2 subterminal teeth, 3 teeth ensheathed proximally, yellow (Fig. 27b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 27c). Dorsal cirri increasing slightly in length posteriorly; 0.61 × length of podium at setiger 3 (Fig. 27c), 0.83 × length of podium in mid-body, 2.4 × length of podium posteriorly; 2.58 × longer than wide posteriorly (Fig. 27d). Ventral cirri 0.35 length of podium at setiger 3, 0.39 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 3 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers and occasionally heterogomph pseudospinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.2–1.4 × length of collar (Fig. 27e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.8 × longer than width of shaft head, finely serrated, 35–45 teeth, 0.74–0.78 × total blade length (serrations extend to tip), teeth about uniform in length (Fig. 27f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated, although proximal serrations may be elongate; dorsal-most 10.2 × longer than width of shaft head, large number of teeth (Fig. 27g); ventral-most 4.1 × longer than width of shaft head, 22 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated, although proximal serrations may be elongate. Sub-neuroacicular spinigers in mid-posterior region with blades having long, fine serrations proximally (Fig. 27h). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 1.3 × width pygidium.

Sex. Mature oocytes very large (greater than 300 µm), though in poor condition. Epitokal setae absent.

Remarks. Hutchings & Glasby (1985) include this species in their description of *N.* cf. *abiuma*, hence the “in part” in the synonymies. The remaining material identified by these authors belongs to the *N. abiuma* species group. *Namalycastis nicoleae* n.sp. may be distinguished from the *N. abiuma* species group by having heterogomph pseudospinigers, falcigers with a greater portion of the blade serrated (and a greater number of teeth) and by having sub-neuroacicular spinigers of parapodia in posterior setigers with long, finely serrated blades.

Phylogenetically, the new species does not group together with any other *Namalycastis* species and, as indicated in the consensus trees (Figs. 5,6), is one of the earliest lineages of the *Namalycastis* clade. It is the only *Namalycastis* species having an exclusive Gondwanan distribution.

Habitat. Holotype from a drain in coastal lowlands (reclaimed mangroves), salinity unknown.

Distribution. Type locality Brisbane, east coast of Australia (Fig. 28).

Etymology. Named in honour of Ms Nicole Somers for her valued assistance with fieldwork during 1986.

Namalycastis senegalensis (Saint-Joseph)

Figs. 1a, 28, 29a–j; Table 4

Lycastis senegalensis Saint-Joseph, 1900: 217–224, pl. 1, figs. 1–7.
Lycastis ouanaryensis Gravier, 1901: 397–399 (in part); 1902c: 354–361, fig. 10 (in part).–Fauvel, 1919: 475; 1923a: 126–127 (in part).–Perkins & Savage, 1975: 33 (list only).
Lycastis quadraticeps.–Fauvel & Rullier, 1959: 515–516. *Non* Blanchard in Gay.
Namalycastis senegalensis.–Hartman, 1959a: 163–164.

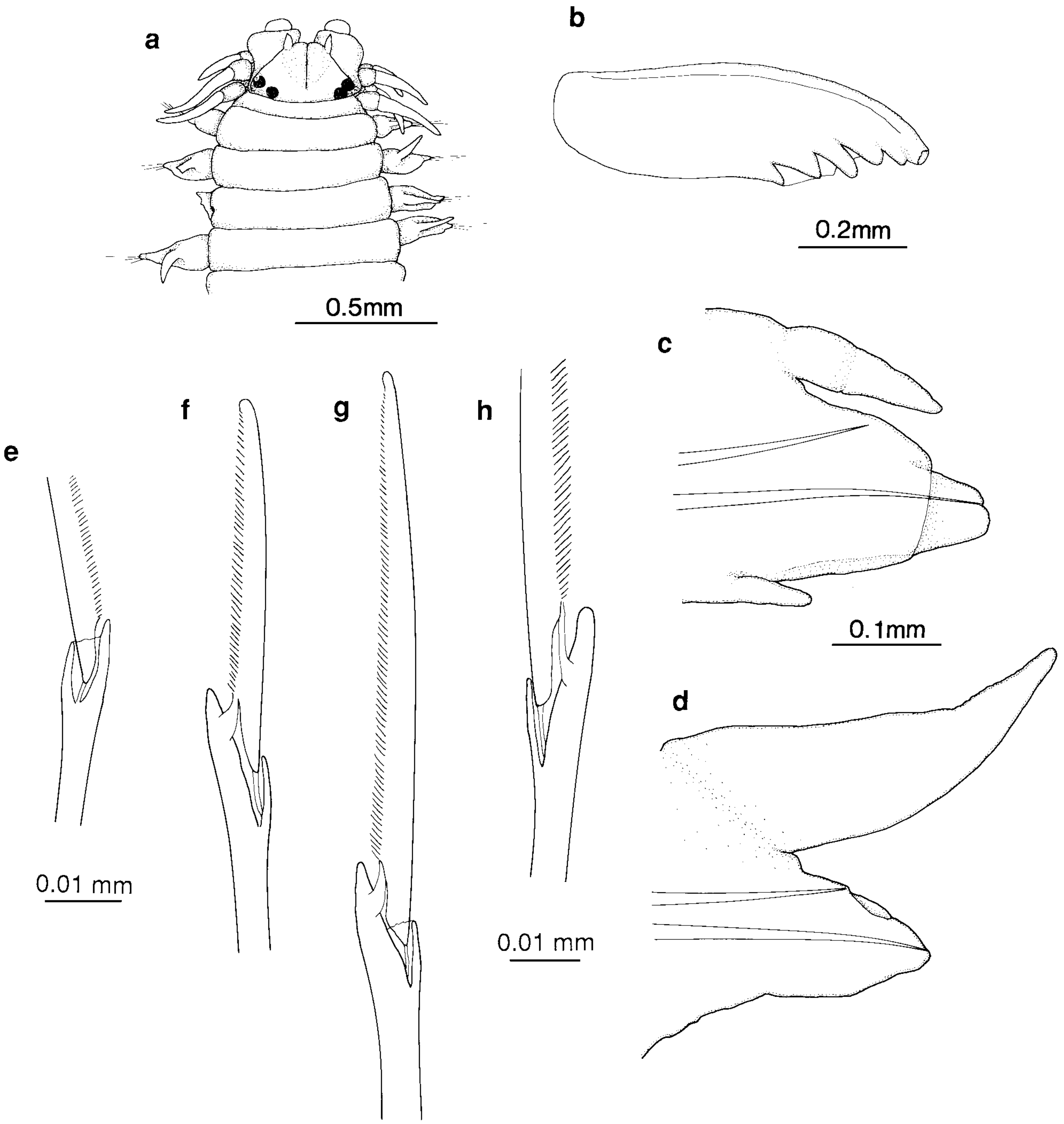

Figure 27. *Namalycastis nicoleae* n.sp. holotype: (*a*) anterior end, dorsal view, posteroventral tentacular cirrus, L.S., missing; (*b*) jaw piece, dorsal view, terminal tooth broken; (*c*) parapodium from 4th setiger, L.S., anterior view; (*d*) parapodium from 60th setiger, L.S., anterior view, ventral cirrus missing; (*e*) supra-neuroacicular spiniger, setiger from mid-body; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular falciger (dorsal position), setiger 30; (*h*) sub-neuroacicular spiniger, setiger 10.

Material examined. LECTOTYPES: Senegal, 133, no. 20, rapporté par Mr Cligny (MNHN UE 918). PARALECTOTYPES: Senegal, collection details as for lectotype 2(MNHN UE 919). NON-TYPE: Anticosti [?= Ile d'Anticosti, Gulf of St. Lawrence, Quebec], no. 92, M. Schmidt, 1903 3(MNHN UE 920). Senegal, Gorée 5(HZM V1008). Nigeria, Odube Creek 7(AM W20282). Cameroun 3(HZM V1006). Zaire, Mouth of Congo River at San Antonio do Zaire 2(HZM V1167). Surinam, Surinam River 2(HZM V10351); Surinam River at Paramaribo, wreck of the Goslar 2(ZMA V.Pol. 2857). Brazil, Marajos Island [= Ilha de Marajó] (mouth of the Amazon River) 2(BMNH ZK 1923.9.25.14–16), 1(HZM V9433); delta of the Amazon River 1(HZM PE405). "Isles Sandwich", det. Fauvel as *Lycastis indica* but not published as such 2(MNHN UE 921).

Namalycastis ouanaryensis PARATYPES: French Guiana, no. 46, coll. M. Geay, 1901 1(MNHN UE 925), 30(MNHN UE 926) (a selection of paratypes). 20 specimens measured.

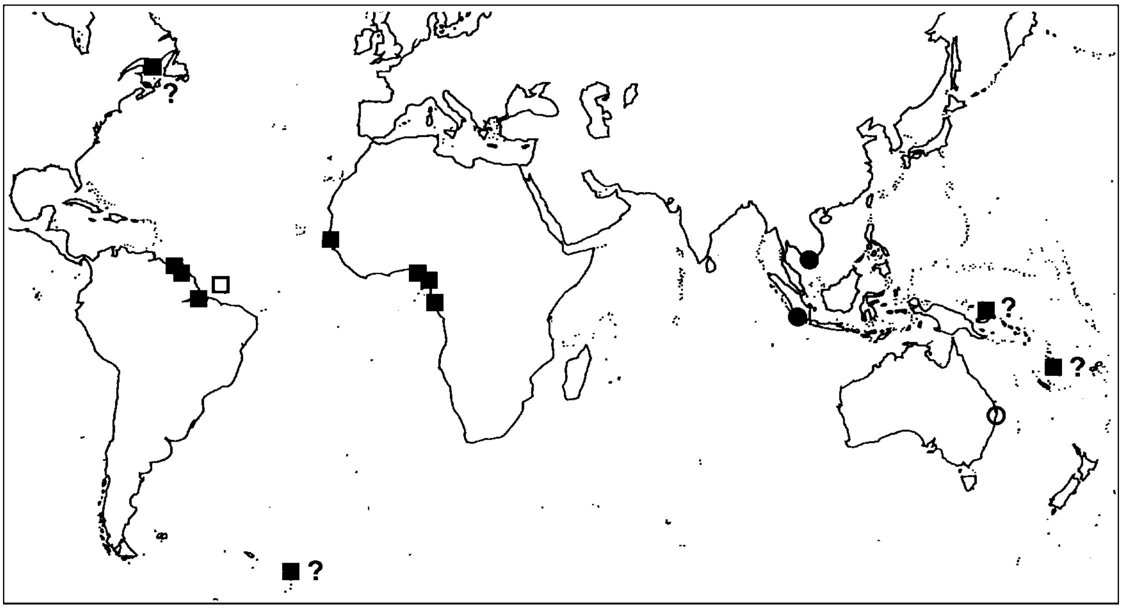

Figure 28. Distribution of *Namalycastis nicoleae* n.sp. ○, *N. senegalensis* ■, *N. siolii* □, and *N. terrestris* ●; based on material examined and authenticated literature records.

Other material examined. NON-TYPE specimens identified by Fauvel (1923a) as *Lycastis ouanaryensis*: French Guiana, Ilet-la-Mère, no. 3733 1(MNHN UE 927); Rivière de Montsinéry, no. 2906 2 juveniles(MNHN UE 928); Mahury, no. 3443 13(MNHN UE 929).

Diagnosis. Prostomium anteriorly shallowly cleft (usually). Antennae extending short of, to beyond, tip of palpophore. Notosetae present. Neurosetae Type A (Fig. 1c). Heterogomph falcigers replaced by heterogomph spinigers in posterior parapodia. Supra-neuroacicular falcigers in setiger 10 with blades 4.8 × longer than width of shaft head (4.1–5.4), finely serrated, 13 teeth (6–20), teeth about uniform in length. Anal cirri flattened.

Description. Lectotype well preserved, segmentally complete, no gametes in coelom. Other material including paratypes of *N. ouanaryensis* generally well preserved, includes some complete individuals. 144 setigers (83–239), 50 mm long (28–175), 4.0 mm wide at setiger 10 (1.2–6.3). At setiger 10 parapodia with length 0.47 × body width (0.20–0.50).

Body. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly. Dorsum convex. Venter flat, very rarely convex or concave. Colour in alcohol brown (very rarely) to yellow-white. Epidermal pigment absent or brown on pygidium (very rarely).

Prostomium. Anteriorly shallowly cleft or cleft absent (rarely), with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal, with or without lateral indentation; 1.7 × wider than long (1.4–1.7, rarely 1.3–1.8). Antennae smooth, extending short of, to beyond, tip of palpophore, aligned over mid-palps to inner edge of palps. Eyes 2 pairs, black or red (probably faded), arranged transversely or obliquely (very rarely), equal in size (rarely) or posterior pair slightly smaller; lenses absent or indistinct (rarely); thick cuticle covering eyes of most specimens (Fig. 29a).

Peristomium. Tentacular cirri with cirrophores distinct, though indistinct in small specimens; cirrostyles smooth. Anterodorsal tentacular cirri 1.8 × length anteroventral (1.3–2.5, rarely to about 3). Anterodorsal tentacular cirri 0.6 × length posterodorsal (0.6–1.0). Posterodorsal tentacular cirri 1.8 × length posteroventral (1.4–2.5). Posterodorsal tentacular cirri extending posteriorly to setiger 4 (3–4, rarely to 6) (Fig. 29a). Jaws with single robust terminal tooth, 2 subterminal teeth (2–4, rarely absent, probably due to wear in Iles Sandwich specimens), 2 teeth ensheathed proximally (2–4, difficult to see in some specimens due to heavily chitinised guard), brown or black (very rarely) (Fig. 29b).

Parapodia. Acicular neuropodial ligule faintly bilobed. Superior lobe papilliform, very short. Inferior lobe subconical, sometimes curved anteriorly, or globular (very rarely) (Fig. 29c,d). Dorsal cirri increasing slightly in length posteriorly or increasing greatly in length posteriorly; 2.5 × length of podium at setiger 3 (1.6–4.8) (Fig. 29c), 2.6 × length of podium in mid-body (2.0–5.7), 2.3 × length of podium posteriorly (2.9–9.7); 2.4 × longer than wide posteriorly (3.7–8.4) (Fig. 29d). Ventral cirri 0.52 length of podium at setiger 3 (0.40–0.95), 0.57 length of podium posteriorly (0.33–0.68).

Setae. Notopodial sesquigomph spinigers from setiger 3 (2–8) (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicle of anterior podia and heterogomph spinigers in preacicular fascicles of

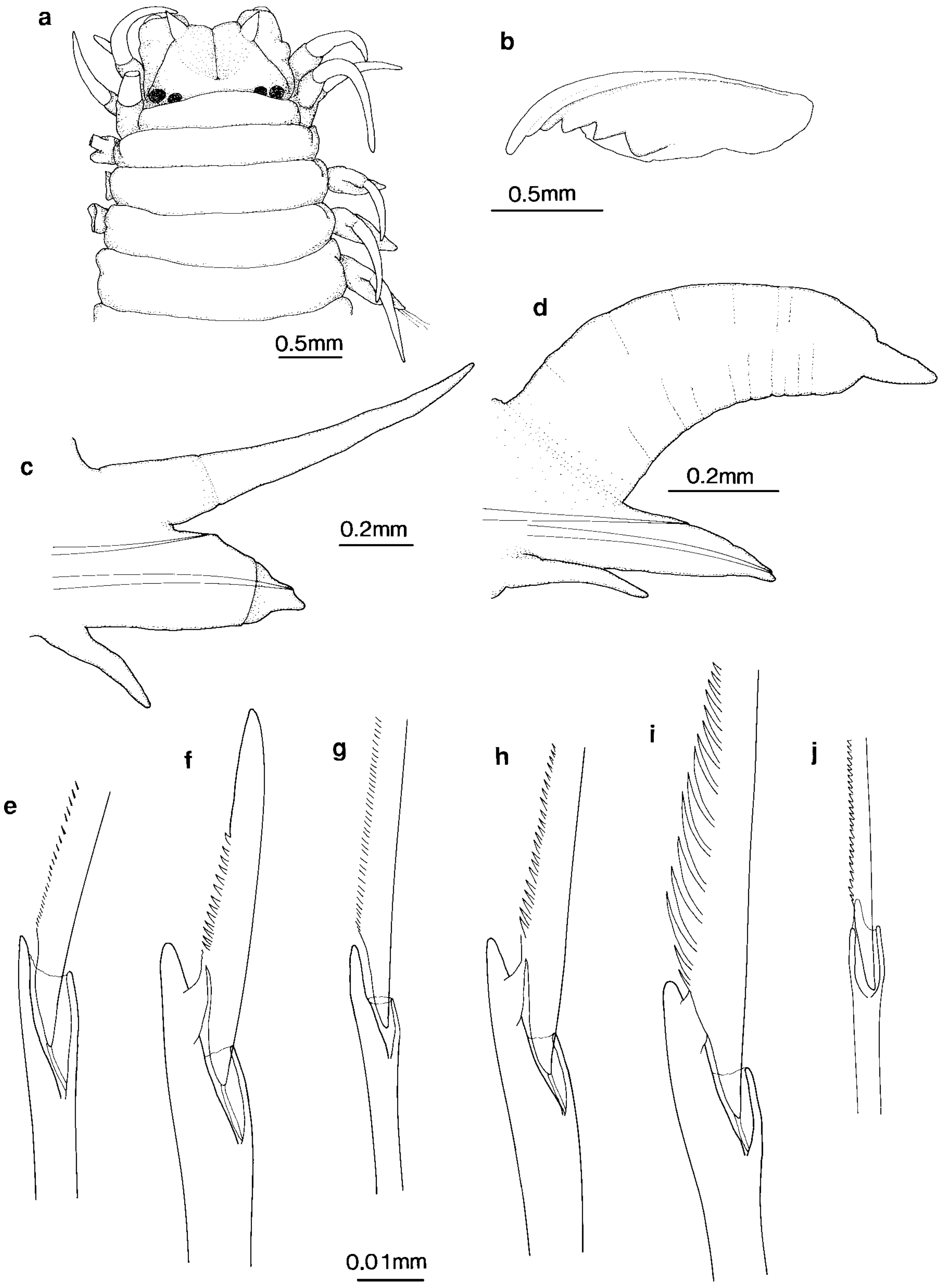

Figure 29. *Namalycastis senegalensis* lectotype: (*a*) anterior end, dorsal view, posterodorsal tentacular cirrus, L.S., broken; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 120th setiger, R.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 30; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) supra-neuroacicular spiniger (preacicular), setiger 120; (*h*) sub-neuroacicular spiniger, setiger 10; (*i*) sub-neuroacicular spiniger, setiger 115. (*j*) Non-type (AM W20282), epitokal compound spiniger, setiger 30.

posterior podia (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (1.4–1.8) (Fig. 29e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.8 × longer than width of shaft head (4.1–5.4), finely serrated, 13 teeth (6–20), 0.34 × total blade length (0.19–0.27), teeth about uniform in length (Fig. 29f); posteriorly falcigers replaced by heterogomph spinigers (Fig. 29g). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 4.0 × longer than width of shaft head (3.7–5.2), 6 teeth (5–12); ventral-most 4.2 × longer than width of shaft head (3.3–4.5), 6 teeth (3–7). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in anterior region with finely serrated blades (Fig. 29h); posteriorly, from setiger 30 (10–120; later in larger animals), blades having coarse serrations proximally (Fig. 29i). Setae pale or dark (rarely). Acicula in mid-body brown or black (rarely).

Pygidium. Pygidium with multi-incised rim; drawn out slightly into funnel-shape. Anus dorsoterminal or terminal (rarely). Anal cirri arising ventrolaterally, flattened, smooth, 4.0 × width pygidium (2.5–5.0).

Sex. Mature oocytes 108 µm (± 4 µm, 1 specimen measured), straw-coloured, with external membrane. Epitokal setae are slender compound spinigers in one sexually mature female from Nigeria (Fig. 29j).

Remarks. According to M.N. Helléouet (pers. comm., 1986) the material of *N. senegalensis* from the MNHN includes the paratypes; however, for the same reasons given in the Remarks for *N. geayi*, I believe the specimens represent syntypes, and accordingly designate one specimen to be a lectotype, and the remaining two as paralectotypes.

The reasons for the synonymy (in part) with *N. ouanaryensis* are as follows: according to Gravier (1901, 1902c), *N. senegalensis* could be distinguished from *N. ouanaryensis* by several characters, most notably by having longer and more slender tentacular cirri, less well-developed posterior dorsal cirri and by the setae. The first two characters are subject to considerable variation depending on fixation and preservation methods and the differences, if real, probably reflect only intraspecific variation.

Gravier does not elucidate the specific setal differences between the two species, but I suspect he is referring to two in particular. Firstly, there is the presence of straight, long-bladed falcigers in some *N. ouanaryensis sensu* Gravier, which are not present in *N. senegalensis*. As discussed below, these long-bladed falcigers belong to a second species, *N. macroplatis* n.sp. The short-bladed falcigers of *N. ouanaryensis* (Gravier, 1902c: fig. 4) correspond closely to those of *N. senegalensis* (Saint-Joseph, 1900, pl. 1, fig. 6). Secondly, the simple "forked setae" of *N. senegalensis* are presumably the shafts of the sesquigomph spinigers with the blades detached. This type of seta is common to both *N. ouanaryensis* and *N. senegalensis* and not diagnostic.

Gravier's (1901, 1902c) descriptions of *Namalycastis ouanaryensis* included two distinct species, although he considered them as sexual forms. Sexually mature females had, according to Gravier, elongate falciger blades (see Gravier, 1902c: fig. 10) and highly vascularised dorsal cirri. Immature individuals (those with no coelomic gametes) had shorter falciger blades (see Gravier, 1902c: fig. 4) and less vascularised dorsal cirri than sexually mature individuals. The discovery of a short-bladed, near-sexually mature female (HZM PE405) and a long-bladed sexually mature male (BMNH ZK 1923.9.25.14–15) refutes Gravier's hypothesis. The extent of vascularisation of the dorsal cirri was variable for both the short and long-bladed types. Therefore, the species with long falciger blades is herein described as a new species, *N. macroplatis* and the species with short falciger blades is *N. senegalensis*.

Fauvel's (1923a) description of *N. ouanaryensis* also includes another species, *Namalycastis brevicornis* Audouin & Edwards, hence the partial synonymy with *N. senegalensis* (see comments for *N. brevicornis*).

At least three species of *Namalycastis* occur sympatrically in the north-east of South America. *Namalycastis senegalensis* was found together with *N. macroplatis* n.sp. in samples from Ilha de Marajó, Brazil (HZM and BMNH) and the Surinam River, Surinam (HZM). *Namalycastis senegalensis* co-occurs with *N. kartaboensis* in the Surinam River at Paramaribo (ZMA V.Pol. 2896) and with *N. brevicornis* at Muhury, French Guiana (MNHN UE 933). Further, both *N. senegalensis* and *N. macroplatis* n.sp. may have been introduced to Gulf of St. Lawrence, Quebec, as both species were found in lots from Anticosti. Whether these species are truly sympatric or occupy different niches within the same general area is not known; further study of namanereidine species of this region would be rewarding and should include specimens held at the MNHN and labelled as *Lycastis ouanaryensis* from Guyane française (= French Guiana) (unregistered in jar labelled A78), which were not examined in this study.

Namalycastis senegalensis forms a monophyletic group with the three other South American species: *N. siolii*, *N. macroplatis* n.sp. and *N. arista* n.sp., as discussed previously under the Remarks of these species. *Namalycastis senegalensis* has the widest distribution of the four species, occurring on either side of the Atlantic. The amphi-Atlantic distribution of this species suggests either that the species is very old, predating the rifting of the Atlantic, or that the species has dispersed from its place of origin. The direction of dispersal is most likely eastward across the Atlantic given the presence of its nearest living relatives in South America. The aberrant records from Gulf of St. Lawrence (Anticosti) and the Pacific (Sandwich Islands) suggests that human-assisted dispersal may also be a possibility.

Habitat. The types were collected from the cracks of pilings in Songrougou Stream, about 100 km from the sea in brackish water. Gravier's (1901, 1902c) material was collected from the roots of *Teredo*-infested mangroves; Gravier (1901, 1902a,c) also found the species under rocks on the coast and in the creeks and marshes of the upper (fluvial) reaches of the Ouanary River. As Gravier's material is a mixture of two species, the habitat information should be viewed cautiously. The Amazon material was from a fresh-brackish water beach. The Odube Creek material was from rotten wood.

Distribution. Type locality Marsassoum on Songrougou Stream, a tributary of the Casamance River, Senegal. The synonymy with *N. ouanaryensis* extends the distribution to French Guiana (Ouanary River, Cayenne [possibly], Ilet-la-Mère, Mahury, Rivière de Montsinéry). The synonymy with *N. quadraticeps non* Blanchard in Gay extends the distribution to Senegal (Dakar). New records, Senegal (Gorée), Nigeria (Odube Ck), Cameroun, Zaire (San Antonio do Zaire), Surinam (Parimaribo) and Brazil (Ilha de Marajó).

Possibly introduced to Ile d'Anticosti, Gulf of St. Lawrence, Quebec and to the Pacific Ocean ("Iles Sandwich"). The name "Sandwich Islands" has been used to refer to the Hawaiian Islands and to the West Pacific islands of Dyaul (Bismarck Archipelago, near New Ireland) and Éfaté Island (Vanuatu) (Motteler, 1986). As Fauvel referred to "Iles" (plural), then the Hawaiian Islands seems most probable. Another possibility, that "Iles Sandwich" refers to the South Sandwich Islands, Scotia Arc off the Antarctic Peninsula, is considered highly improbable given the habitat preference of the species.

Etymology. Saint-Joseph named the species after the country of the type locality.

Namalycastis siolii (Corrêa)

Figs. 1c, 28; Table 4

Lycastis siolii Corrêa, 1948: 245–250, figs. 1–8.
Namalycastis siolii.–Hartman, 1959a: 163–164.

Material examined. None.

Diagnosis. Prostomium cleft anteriorly. Antennae extending short of tip of prostomium. Jaws with 14 subterminal teeth (includes teeth ensheathed). Acicular neuropodial ligule subconical. Dorsal cirri increasing slightly in length posteriorly, from less than length of parapodia anteriorly to slightly more than 2 × its length posteriorly. Notosetae present. Neurosetae Type A (Fig. 1c). Heterogomph falcigers replaced by heterogomph spinigers in posterior parapodia. Supra-neuroacicular falcigers in setiger 10 with blades approx. 8.0 × longer than width of shaft head, smooth or serrated basally.

Description. Following description compiled from Corrêa (1948), hence counts and measurements are approximations. Syntypes segmentally complete or incomplete. 250 setigers (minimum approx.), 100 mm long (minimum approx.), 2 mm wide at setiger 10 (maximum approx.).

Body. Colour in alcohol white. Epidermal pigment absent.

Prostomium. Cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium (with transverse furrow at mid prostomium). Prostomium shape roughly triangular, laterally slightly indented; 2 × wider than long. Antennae smooth, extending short of tip of prostomium, aligned over mid-palps. Eyes 2 pairs, arranged obliquely, anterior pair slightly smaller.

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.9 × length anteroventral. Anterodorsal tentacular cirri 1.5 × length posterodorsal. Posterodorsal tentacular cirri 1 × length posteroventral. Posterodorsal tentacular cirri extending posteriorly to setiger 2. Jaws with single robust terminal tooth, 14 subterminal teeth (may include teeth ensheathed).

Parapodia. Acicular neuropodial ligule subconical. Dorsal cirri increasing slightly in length posteriorly; 0.77 × length of podium at setiger 3, 1.4 × length of podium in mid-body, 1.6 × length of podium posteriorly; 2.4 × longer than wide posteriorly. Ventral cirri 0.47 length of podium at setiger 3, 0.40 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers present (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles, heterogomph falcigers in preacicular fascicles of anterior podia and heterogomph spinigers in preacicular fascicles of posterior podia (Table 4).

Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers with blades 8 × longer than width of shaft head, smooth or serrated basally. Setae pale. Acicula in mid-body dark brown.

Pygidium. Structure of pygidium unknown. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 2.8 × width pygidium.

Remarks. No type specimens or other material of this species could be located. The types of *N. siolii* are most likely in the Departmento de Zoologia Instituto de Biociências, Universidade de São Paulo (P. Lana, pers. comm., 1987), but requests to borrow this material were unsuccessful. The above description was compiled from the description of Corrêa (1948), which is the only account of this species. Measurements and counts derived from Corrêa's description and figures are approximations. For example, the parapodia figured by Corrêa (figs. 6–8) from the anterior, middle and posterior regions were taken to represent setigers 10, 120 and 240 respectively in the present description. Setal morphometrics are based on the falciger in his figure 5, although the setiger from which the seta is taken is not known.

Corrêa's terminology for the setae differs from that used here in several ways. The notopodial setae referred to by Corrêa as "fine heterogomph aristae" are here called sesquigomph spinigers. The spinigers in the neuropodia, referred to by Corrêa as "heterogomph aristae", are here referred to as supra-neuroacicular spinigers (either sesquigomph or heterogomph) and subneuropodial spinigers (heterogomph). This is the most likely interpretation of Corrêa's setal notation based on the accompanying figures and on setal arrangement in other *Namalycastis* species.

The description of *N. siolii* given by Corrêa (1948) is sufficiently detailed to be sure that it is a good species. It closely resembles *N. macroplatis* n.sp. and *N. arista* n.sp. in having falcigers replaced by spinigers posteriorly and in the falcigers having relatively long blades. It differs from both species, however, in the number of teeth on the jaws, in the eyes which are arranged obliquely, and in the length of the dorsal cirri which are much shorter throughout the body in *N. siolii*. The overall similarity of the three species accords with the preferred cladogram (Fig. 7) in which all three species and *N. senegalensis* belong to a monophyletic group, the most-derived group among *Namalycastis* species.

Habitat. The type habitat is a freshwater river in 10–28 m.

Distribution. Type locality Brazil, Amazon region, Tapajóz River (Fig. 28).

Etymology. Unknown.

Namalycastis terrestris (Pflugfelder)

Figs. 1c, 28, 30a–g; Table 4

Lycastis terrestris Pflugfelder, 1933: 66–67, figs. 1–3.
? *Lycastis maxillo-falciformis* Harms, 1948: 337–338, fig. 2a,b.
? *Lycastis maxillo-ovata* Harms, 1948: 338–339, fig. 3a,b.
? *Lycastis maxillo-robusta* Harms, 1948: 335–337, fig. 1a,b.
Lycastis meraukensis.–Rullier, 1957: 158–159. *Non* Horst.
Namalycastis terrestris.–Hartman, 1959a: 163–164.

Material examined. LECTOTYPE: Sumatra, Belawan (3°46'N 98°44'E), leg. Harms, 1927 (PMJ Ann. 162). NON-TYPE: *Lycastis meraukensis*. S. Vietnam, Cholon 2 (MNHN AZ 437), det. Rullier, 1957. 3 specimens measured.

Diagnosis. Prostomium anteriorly deeply cleft. Antennae extending short of tip of palpophore. Notosetae present. Neurosetae Type A (Fig. 1c), up to 15 heterogomph falcigers in supra-preacicular fascicle. Supra-neuroacicular falcigers in setiger 10 with blades 5.9 × longer than width of shaft head (6.6–7.9), finely serrated, 14 teeth (6–10), teeth about uniform in length.

Description. Lectotype well preserved although with white precipitate on epidermis anteriorly, segmentally incomplete (anterior section in two parts), immature oocytes in coelom. Other material in poor condition as a result of dehydration; includes some complete individuals. 200–386 setigers, 100 mm long, 4.3 mm wide at setiger 10 (4.1–6.0). At setiger 10 length of parapodia 0.29 × body width (0.14–0.22).

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter flat. Colour in alcohol brown. Epidermal pigment absent or dark brown dorsally (some green pigment on Cholon specimens). Living colour reddish-brown dorsally increasing in intensity posteriorly.

Prostomium. Deeply cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly triangular, laterally slightly indented or lacking indentation, 2.0 × wider than long (1.9–2.3). Antennae smooth, extending short of tip of palpophore, aligned over mid-palps to inner edge of palps. Eyes 2 pairs (faded in lectotype), purple, arranged transversely or obliquely, posterior pair slightly smaller; lenses absent (Fig. 30a).

Peristomium. Tentacular cirri with cirrophores distinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.8 × length anteroventral (1.6). Anterodorsal tentacular cirri 0.8 × length posterodorsal (1.2). Posterodorsal tentacular cirri 1.8 × length posteroventral (1.9). Posterodorsal tentacular cirri extending posteriorly to setiger 3 (2) (Fig. 30a). Jaws with single robust terminal tooth, 5 subterminal teeth (3–4), 4 teeth ensheathed proximally (3), brown or black (Fig. 30b).

Parapodia. Acicular neuropodial ligule bilobed. Superior lobe papilliform. Inferior lobe globular (Fig. 30c,d). Dorsal cirri increasing slightly in length posteriorly, or similar in length throughout; 1.1 × length of podium at setiger 3 (1.6–2.3) (Fig. 30c), 1.3 × length of podium in mid-body (0.69–0.86), 0.84–1.0 × length of podium posteriorly; 1.3–1.7 × longer than wide posteriorly (Fig. 30d). Ventral cirri 0.45 length of podium at setiger 3 (0.56), 0.18 length of podium posteriorly.

Setae. Notopodial sesquigomph spinigers from setiger 3 (Table 4). Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 4).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.6 × length of collar (1.3–1.4) (Fig. 30e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.9 × longer than width of shaft head (6.6–7.9), finely serrated, 14 teeth (6–10), 0.32 × total blade length (0.14–0.18), teeth about uniform in length (Fig. 30f). Sub-neuroacicular falcigers in setiger 10 with blades smooth or finely serrated; dorsal-most 5.9 × longer than width of shaft head (7.8–8.6), 11 teeth (12–20); ventral-most 5.5 × longer than width of shaft head (4.5–5.1), 10 teeth (0–1). Sub-neuroacicular falcigers in mid-posterior region with blades finely to very finely serrated or smooth. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally (Fig. 30g). Setae pale or dark. Acicula in mid-body brown or black, with lighter bases.

Pygidium. Structure of pygidium obscure. Anal cirri approximately conical.

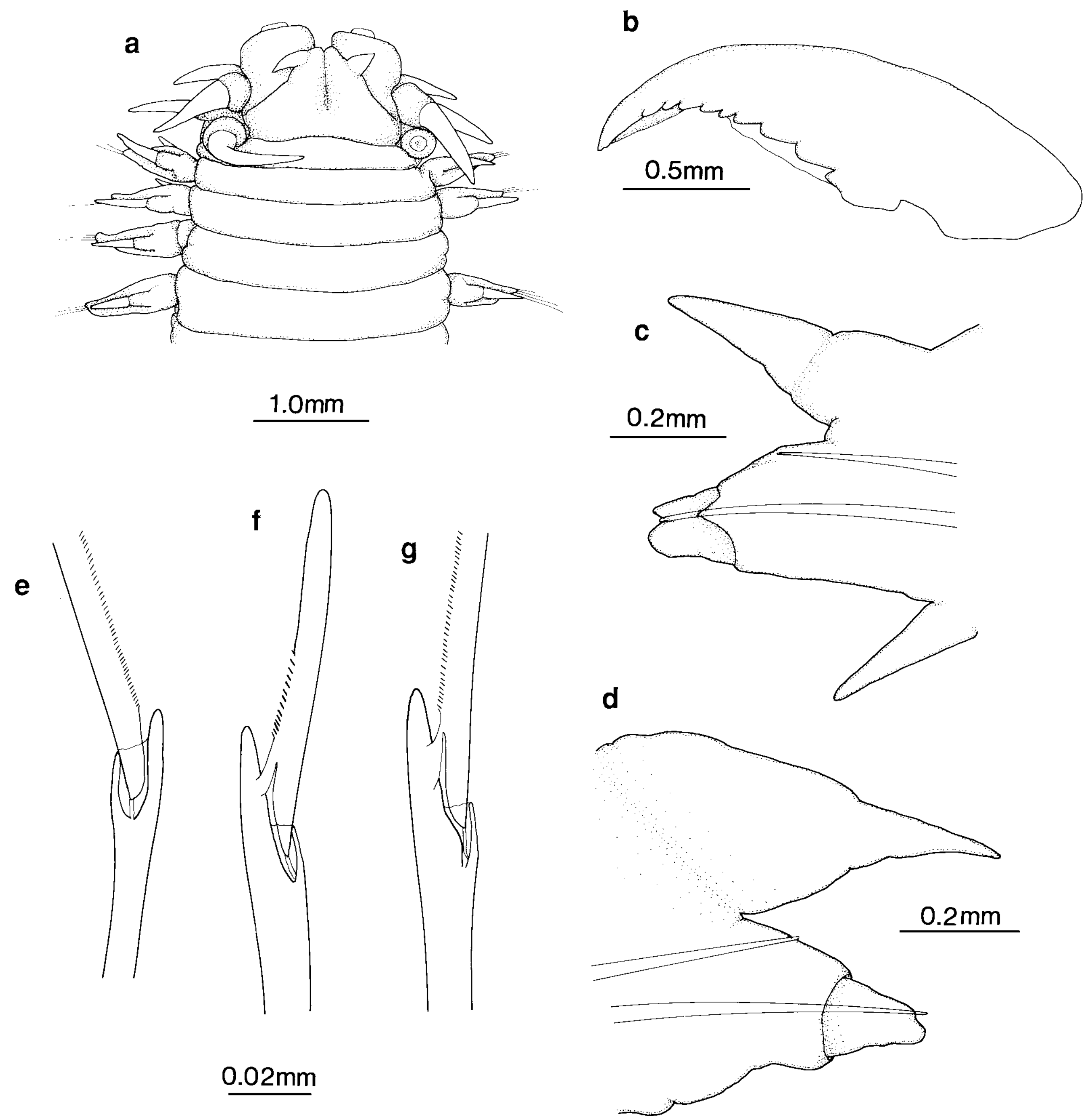

Figure 30. *Namalycastis terrestris* lectotype: (*a*) anterior end, dorsal view, posterodorsal tentacular cirrus, R.S., missing, eyes faded; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, R.S., anterior view; (*d*) parapodium from 120th setiger, L.S., anterior view, ventral cirrus missing; (*e*) supra-neuroacicular spiniger, setiger 3; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 120.

Remarks. A single specimen of the syntype series of *N. terrestris* Pflugfelder was made available to loan. Whether the other syntypes are also in the PMJ is unknown. The syntype examined here lacks parapodium 20 and is therefore probably the same specimen illustrated by Pflugfelder (1933, fig. 2). Also Pflugfelder's illustrations of the head (fig. 1) and setae (fig. 3a,b) resemble those of the specimen at hand. Therefore, this specimen is designated as a lectotype and, if the other specimens in the syntype series exist, they should be designated as paralectotypes.

The white precipitate on the epithelium of anterior segments and the prostomium of the lectotype is probably the result of fixation in Susa (mercuric chloride), which was apparently used by Harms on the expedition. As a result of this precipitate, and also perhaps due to leaching of pigment, the eyes of the lectotype are not visible. Characters states for the eyes were scored using information from Pflugfelder (1933). Also some parapodial characters of posterior segments were scored using the type description.

Namalycastis terrestris resembles members of the *N. abiuma* sp. group, differing in having the blades of the falcigers relatively longer and the ventral-most sub-neuroacicular falcigers with fewer teeth. Also the falcigers are relatively slender for the size of the species. In the cladistic analysis, 92% of minimal-length trees show *N. terrestris* grouped together with the North American species *N. borealis* n.sp. (Fig. 7), however the relationship is collapsed in the Strict Consensus tree (Fig. 5).

The species is probably synonymous with three species described by Harms (1948): *Lycastis maxillo-falciformis*, *L. maxillo-ovata* and *L. maxillo-robusta*, all from Sumatra and Java (specific localities are not given). The most diagnostic characteristic of these species, the blade length and type of serrations of the heterogomph falcigers, both fit that of *N. terrestris*. Harms put considerable importance on the shape of the jaw pieces to differentiate the species—the differences are reflected in the species names—however, I have not found the small variation in overall jaw shape to be useful in distinguishing this or any other namanereidine species.

Storch (1972) used specimens of *N. terrestris* from the type locality to investigate the epithelial sensory receptors of the antennae and palps. He found no significant differences in the arrangement of sensory receptors between this species, several other nereidine species and a hesionid.

Habitat. The lectotype is from the upper littoral zone, reached only by the highest tides; in fine grey-brown clay-sand to a depth of 20–30 cm. Pflugfelder (1933) also noted that the species was "living like earthworms" at Belawan. The Cholon specimens were found in the soil of paddy fields, not far from the sea. Found only during the rainy season when the rice fields were inundated by a mixture of freshwater and brackish water.

Distribution. Type locality Indonesia, Sumatra, Belawan. Other records from S. Vietnam (Phuoc Dienha). The questionable synonymies of Harms' species extends the distribution to Java (Fig. 28).

Etymology. Pflugfelder named the species after its terrestrial habitat.

Namanereis Chamberlin

Lycastis.–Schmarda, 1861: 100.–Quatrefages, 1865: 498–499 (in part).–Ehlers, 1868: 449 (in part).–Grube, 1872: 47–48 (in part).–Gravier, 1902b: 373 (in part).–Johnson, 1903: 214–215 (in part).–Horst, 1909: 4–5 (in part). *Non* Savigny, 1822.

Namanereis Chamberlin, 1919: 196.–Day, 1967: 299.–Fauchald, 1977: 89.–Hartman, 1959a: 160–163.–Hartmann-Schröder, 1973: 95–97; 1977: 58–60.

Lycastopsis Augener, 1922: 42.–Feuerborn, 1931a: 638.–Pettibone, 1963: 150.–Uschakov, 1955: 204 (in Russian); 1965: 183 (in English).–Imajima, 1972: 39.–Fauchald, 1977: 89.–Gibbs & Saiz Salinas, 1996: 618.

Lycastoides.–Jakubova, 1930: 869. *Non* Johnson.

Lycastella Feuerborn, 1931a: 638.

Cryptonereis Gibbs, 1971: 144.–Fauchald, 1977: 88.

Lycastilla Solís-Weiss & Espinasa, 1991: 632.

Description. Body small, few setigerous segments (<150). Prostomial cleft generally absent; antennae generally cirriform (rarely subspherical or absent). Tentacular cirri, 3 pairs (rarely 4 pairs); cirrophores usually indistinct. Area V of pharynx as narrow medial groove or pad (rarely). Dorsal cirri short and similar in length throughout; cirrophores absent. *Notosetae usually absent*. Neurosetae present, though type and arrangement variable. Supra-neuroacicular setae: sesquigomph spinigers (rarely heterogomph spinigers or absent) in postacicular fascicle; heterogomph falcigers in preacicular fascicle. Sub-neuroacicular setae: usually absent in postacicular fascicle, rarely heterogomph spinigers (*N. tiriteae*); heterogomph falcigers (or heterogomph falcigers, pseudospinigers and spinigers in a graded series) in preacicular fascicle. Falcigers with blade attached to setal shaft by a ligament and hinge (Fig. 2) or fused to setal shaft (rarely). Setal shafts distally smooth or with series of small serrations (rarely). *Pygidium tripartite (usually), with 2 large lateral lobes and a smaller pointed dorsal one*. Monoecious or dioecious. Oocytes large (417 ± 112 µm), *ovoid* (rarely spherical).

Type species. *Lycastis quadraticeps* by original designation.

Remarks. As noted earlier, the generic name *Lycastis* is a junior synonym of both *Typosyllis* and *Nereis* and therefore the name is unavailable. The next available name, *Namanereis*, was first used by Chamberlin (1919) for nereids having a proboscis that lacked paragnaths, a prostomium not anteriorly incised, tentacular cirri without long basal articles (= cirrophores) and rudimentary parapodia. Chamberlin specifically excluded *Lycastoides alticola* from his new genus, but presumably regarded all ten other species of *Lycastis* described up until 1919 (Table 1) as belonging to his new genus (the fact that some of these species actually have an incised prostomium was probably not known at the time). He designated *L. quadraticeps* Blanchard in Gay as the type species of the genus. Five species were later transferred to a new genus, *Namalycastis* (Hartman, 1959a) on the basis of (among other things) having four pairs of tentacular cirri. The genus *Namanereis* was therefore left with five species: *Lycastis quadraticeps, L. pontica, L. littoralis, L. brevicornis* and *L. geayi*. The latter two species are herein transferred to *Namalycastis*. Hartman (1959a) redescribed the genus as having members with a small body size, 3 pairs of tentacular cirri, dorsal parapodial lobes (including dorsal cirri) small and inconspicuous throughout the length of the body, notosetae represented by one or a few slender spinigers, ova few and large in size and mature adults being hermaphrodites. She apparently mistakenly considered *Lycastis quadraticeps* to have 3 pairs (rather than 4) of tentacular cirri.

The genus name *Lycastis* as used by Quatrefages (1865), Ehlers (1868), Grube (1872), Gravier (1902b), Johnson (1903) and Horst (1909) included species that now may be ascribed to both *Namanereis* Chamberlin and *Namalycastis* Hartman, that is species having both 3 and 4 pairs of tentacular cirri. Augener (1922) was the first to recognise the existence of a distinct group of Namanereidinae having only 3 pairs of tentacular cirri. He erected the genus *Lycastopsis* for this group and designated *Lycastopsis beumeri* as the type species by monotypy. Membership of the genus expanded to include other small-bodied forms with 3 pairs of tentacular cirri described by Feuerborn (1931a), Pettibone (1963), Uschakov (1965) and Imajima (1972); the last three authors apparently disregarding Hartman's (1959a) suggestion that *Lycastopsis* be relegated to a junior synonym of *Namanereis*. Hartmann-Schröder (1973, 1977, 1986) however, followed Hartman (1959a) in using the name *Namanereis* for species small-bodied Namanereidinae with 3 pairs of tentacular cirri.

The genus *Lycastella*, erected by Feuerborn (1931a) to contain *Lycastis quadraticeps* also becomes a junior synonym of *Namanereis*. The monospecific genus *Cryptonereis*, erected by Gibbs (1971) for *C. malaitae* is newly synonymised with *Namanereis* on the basis of the results of the cladistic analysis (Figs. 5–7). Gibb's species is the sister group of *N. amboinensis* and the clade is positioned well within the *Namanereis* group. The unique feature of *C. malaitae*, the absence of frontal antennae, is therefore an autapomorphy of the species.

Features used by Solís-Weiss & Espinasa (1991) to diagnose the genus *Lycastilla*—articulated and well-developed antennae tentacular cirri and anal cirri, a cleft prostomium, 3 pairs of tentacular cirri, and few teeth on the jaws—agree with the concept of *Namanereis* as re-diagnosed here, although the cleft prostomium is unusual for members of the genus (more typical of *Namalycastis* species). The other character used by these authors to diagnose their genus—the distally recurved notoaciculae—is thought to be an artifact, perhaps caused by poor fixation or preservation, as discussed in the Remarks for *Namanereis cavernicola*.

The present cladistic study identifies a monophyletic group of species having small bodies and 3 or 4 pairs of tentacular cirri, which is delineated by the absence of dorsal cirrophores and notosetae and having a tripartite pygidium. The clade includes all species originally described under *Lycastopsis* and also *Namanereis quadraticeps*. The clade takes the name *Namanereis*, which has date priority over *Lycastopsis*; further the original concept of *Namanereis* included species with 3 or 4 pairs of tentacular cirri. As a result of the present study the genus contains 13 species and two species groups, *N. littoralis* and *N. quadraticeps*.

Etymology. *Nama*, Gr. for spring or stream, and *Nereis*, referring to the freshwater habitat of *Namanereis quadraticeps*.

Key to the species of *Namanereis*

1	4 pairs of tentacular cirri	2
——	3 pairs of tentacular cirri	4
2	Heterogomph spinigers (Fig. 44f) and heterogomph falcigers in supra-neuroacicular fascicle	*N. quadraticeps* sp. group
——	Sesquigomph spinigers (Fig. 34e) and heterogomph falcigers in supra-neuroacicular fascicle	3
3	Antennae cirriform; supra-neuroacicular falcigers in parapodia of setiger 10 with blades 7.6–9.6 × longer than width of shaft head and having many teeth (>50)	*N. minuta* n.sp.
——	Antennae subconical; supra-neuroacicular falcigers in parapodia of setiger 10 with blades 4.0–4.7 × longer than width of shaft head and having few teeth (9–14)	*N. stocki* n.sp.
4	Prostomial antennae absent; falciger blades partially or entirely fused to shaft	*N. malaitae*
——	Prostomial antennae present, 2 pairs; falciger blades not fused to shaft (attached by ligament and hinge)	5
5	Eyes, 2 pairs	6
——	Eyes, absent	11
6	Sesquigomph spinigers present in supra-acicular fascicle	7
——	Sesquigomph spinigers absent	*N. pontica*

7 Jaws with few subterminal teeth (4–8, including ensheathed ones); supra-neuroacicular falcigers in parapodia of setiger 10 with blades having up to 15 teeth 8

—— Jaws with many subterminal teeth (8–12, including ensheathed ones); supra-neuroacicular falcigers in parapodia of setiger 10 with blades having 15 to 25 teeth .... *N. catarractarum*

8 Supra-neuroacicular falcigers in parapodia of setiger 10 with serrations on basal part of blade only; teeth increasing in length slightly proximally (Fig. 31f) 9

—— Supra-neuroacicular falcigers in parapodia of setiger 10 with serrated region covering most of blade; teeth increasing in length greatly proximally (Fig. 38f) 10

9 Venter concave; posterior pair of eyes only slightly smaller than the anterior pair; falciger blades short .... *N. riojai*

—— Venter approximately flat; posterior pair of eyes markedly smaller than anterior pair; falciger blades not foreshortened .... *N. amboinensis*

10 Sub-neuroacicular falcigers (dorsal-most) in parapodia of setiger 10 with blades having 13–16 teeth; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss generally greater than 1.7 × length of collar .... *N. sublittoralis* n.sp.

—— Sub-neuroacicular falcigers (dorsal-most) in parapodia of setiger 10 with blades having 7–13 teeth; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss generally less than 1.6 × length of collar .... *N. littoralis* sp. group

11 Setae in sub-neuroacicular fascicle are heterogomph spinigers (postacicular fascicle) and heterogomph falcigers (preacicular fascicle) .... *N. tiriteae*

—— Setae in sub-neuroacicular fascicle consist of a graded series of heterogomph falcigers, spinigers and pseudospinigers 12

—— Setae in sub-neuroacicular fascicle are heterogomph falcigers only 13

12 Supra-neuroacicular falcigers in parapodia of setiger 10 with blades 4.4–5.4 × longer than width of shaft head, having 15 to 20 teeth; teeth increasing in length greatly proximally; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss 1.7 to 2.2 × length of collar .... *N. hummelincki*

—— Supra-neuroacicular falcigers in parapodia of setiger 10 with blades 5.5–7.9 × longer than width of shaft head, having 35–80 teeth; teeth increasing in length slightly proximally; supra-neuroacicular sesquigomph spinigers in parapodia of setiger 10 with boss up to 1.6 × length of collar .... *N. cavernicola*

13 Jaws with single robust terminal tooth and many subterminal teeth (3–7, including ensheathed ones); dorsal cirri of setiger 3 up to 1.9 × length of parapodium; sub-neuroacicular falcigers in parapodia of setiger 10 with finely serrated blades .... *N. beroni*

—— Jaws with bifid terminal teeth and no subterminal teeth; dorsal cirri of setiger 3 greater than 1.9 × length of parapodium; sub-neuroacicular falcigers in parapodia of setiger 10 with coarsely serrated blades .... *N. serratis* n.sp.

Namanereis amboinensis (Pflugfelder)

Figs. 1c, 3, 31a–g, 32; Table 5

Lycastopsis amboinensis Pflugfelder, 1933: 69–71, figs. 9–11.
Lycastopsis catarractarum.–Lieber, 1931: 255–265, figs. 1–4. *Non* Feuerborn.
Lycastopsis tecolutlensis Rioja, 1946: 211–212, pl. 1, figs. 7–12.–Hartman, 1951: 44; 1954: 415.–Perkins & Savage, 1975: 33 (list only).
Namanereis amboinensis.–Hartman, 1959a: 162–163.
Lycastopsis pontica.–Lana, 1984: 111–113, figs. 107–108; 1987: 1061 (list only). *Non* Bobretzky.

Material examined. LECTOTYPE: Indonesia, Moluccas [= Maluku], Amboina [= Ambon] (3°41'S 128°10'E); under dead basal parts of leaves of Coco palm trees, coll. Harms, 1929/30 (PMJ Ann. 220). PARALECTOTYPES: collection details as for lectotype 32(PMJ Ann. 166). NON-TYPE: Indonesia, Maluku, Ambon 2(HZM V11935). Australia, Great Barrier Reef, Lizard Island 5(P. Gibbs, pers. coll.); West Pethebridge Island 18(P. Gibbs, pers. coll.); Hinchinbrook Island, Missionary Bay 2(AM W19479). Hawaiian Islands, Oahu, Heeia Stream 13(AM W20249), 4(AM W20247), 12(AM W20250), 2(AM W20248). Belize, Sittee River 3(USNM 178872), 38(USNM 178873), 21(USNM 178874), 1(USNM 178875), 10(AM W20265), Sapodilla Lagoon 1(USNM 178876), Twin Cays 4(USNM 178877). Grenada, mineral springs near River Sallee, many (ZMA V.Pol. 2851). Aruba, Rooi Bringamosa 1(ZMA V.Pol. 2852), Fontein many(ZMA V.Pol. 2853), Rooi Awa Marga (ZMA V.Pol. 2880), "Yaragaray" property 1(ZMA V.Pol. 2881), Daimari 7(ZMA V.Pol. 2882), 8(ZMA V.Pol. 2892), 2+3 juveniles(ZMA V.Pol. 2893). Brazil, Paranaguá 4(MCBM BPO-1217). 36 specimens measured.

Diagnosis. Antennae cirriform, smooth. Eyes 2 pairs, posterior pair markedly smaller. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth, although approaching bifid in some Caribbean specimens. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 3.8 × longer than width of shaft head (3.4–5.0), finely or moderately serrated, 8 teeth (7–13), teeth increasing in length slightly proximally. Epitokal setae in males are long, slender capillaries (unknown in females).

Description. Lectotype well preserved although antero-ventral pair of tentacular cirri missing, segmentally complete, mature oocytes in coelom. Other material in variable condition (specimens from HZM V11935 with damage to body wall and setae), including some complete individuals. 65 setigers (24–88), 12 mm long (4.7–20), 0.95 mm wide at setiger 10 (0.7–1.4).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol yellow-brown to white, rarely brown. Epidermal pigment absent. Living colour pale pink throughout, or pale pink with subcutaneous green pigment posterodorsally (in some Belizean and Hawaiian material). At setiger 10 length of parapodia 0.25 × body width (0.23–0.48).

Prostomium. Anterior cleft absent or shallow (very rarely), with shallow dorsal hollow (elongate in Great Barrier Reef material) or with no hollow. Prostomium shape hexagonal to half-circular or roughly trapezoidal (rarely) or roughly triangular (very rarely); 2.2 × wider than long (1.6–2.5). Antennae cirriform, smooth, extending beyond tip of palpophore or beyond tip of palpostyle or short of tip of palpophore (rarely), aligned over inner edge of palps to over mid-palps (rarely). Eyes 2 pairs, black, arrangement variable, posterior pair markedly smaller; lenses present (Fig. 31a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth or faintly jointed. Anterodorsal tentacular cirri 1.0–1.8 × length anteroventral. Anterodorsal tentacular cirri 0.8–1.3 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 2 (1–2) (Fig. 31a). Pharynx with minute papillae around oral ring in juveniles only (Fig. 3). Jaws with single robust terminal tooth, appearing bifid in some Caribbean specimens, 3 subterminal teeth (2–4, rarely 0–5), 3 teeth ensheathed proximally (2–5, rarely 6–7), brown (Fig. 31b).

Parapodia. Acicular neuropodial ligule very small, subconical (Fig. 31d). Dorsal cirri 2.2 × length of podium at setiger 3 (0.58–1.5, rarely to 2.4) (Fig. 31c), 0.51 × length of podium in mid-body (0.49–1.6, rarely to 2.0), 1.2 × length of podium posteriorly (0.44–1.8); 2.0 × longer than wide posteriorly (1.5–3.0) (Fig. 31d). Ventral cirri 0.75 length of podium at setiger 3 (0.19–0.53), 0.2–0.51 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.7 × length of collar (1.6–2.1) (Fig. 31e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 3.8 × longer than width of shaft head (3.4–5.0), finely to moderately serrated, 8 teeth (7–13), 0.24 × total blade length (0.23–0.52), teeth increasing in length slightly proximally (Fig. 31f). Sub-neuroacicular falcigers in setiger 10 with blades finely to moderately serrated; dorsal-most 3.7 × longer than width of shaft head (3.4–4.8), 6 teeth (7–13); ventral-most 3.3 × longer than width of shaft head (3.1–4.4, rarely to 4.7), 2 teeth (5–10). Sub-neuroacicular falcigers in mid-posterior region with blades finely or moderately serrated. Setae pale or dark. Acicula in mid-body brown or black.

Pygidium. Pygidium tripartite with 2 large lateral lobes and smaller pointed dorsal lobe (pygidium sometimes inflated or elongated into funnel shape). Anus terminal or dorsoterminal (rarely). Anal cirri arising ventrolaterally or laterally, approximately conical, smooth or articulated (very rarely), 0.4 × width pygidium (0.2–1).

Sex. Dioecious. Mature oocytes 390–421 µm (five specimens measured), brown or straw-coloured, with external membrane. Epitokal setae in males are long, slender capillaries (Fig. 31g); present from setiger 8 to within few segments of pygidium; 6–10 in notopodia, 5–10 in neuropodia (unknown in females).

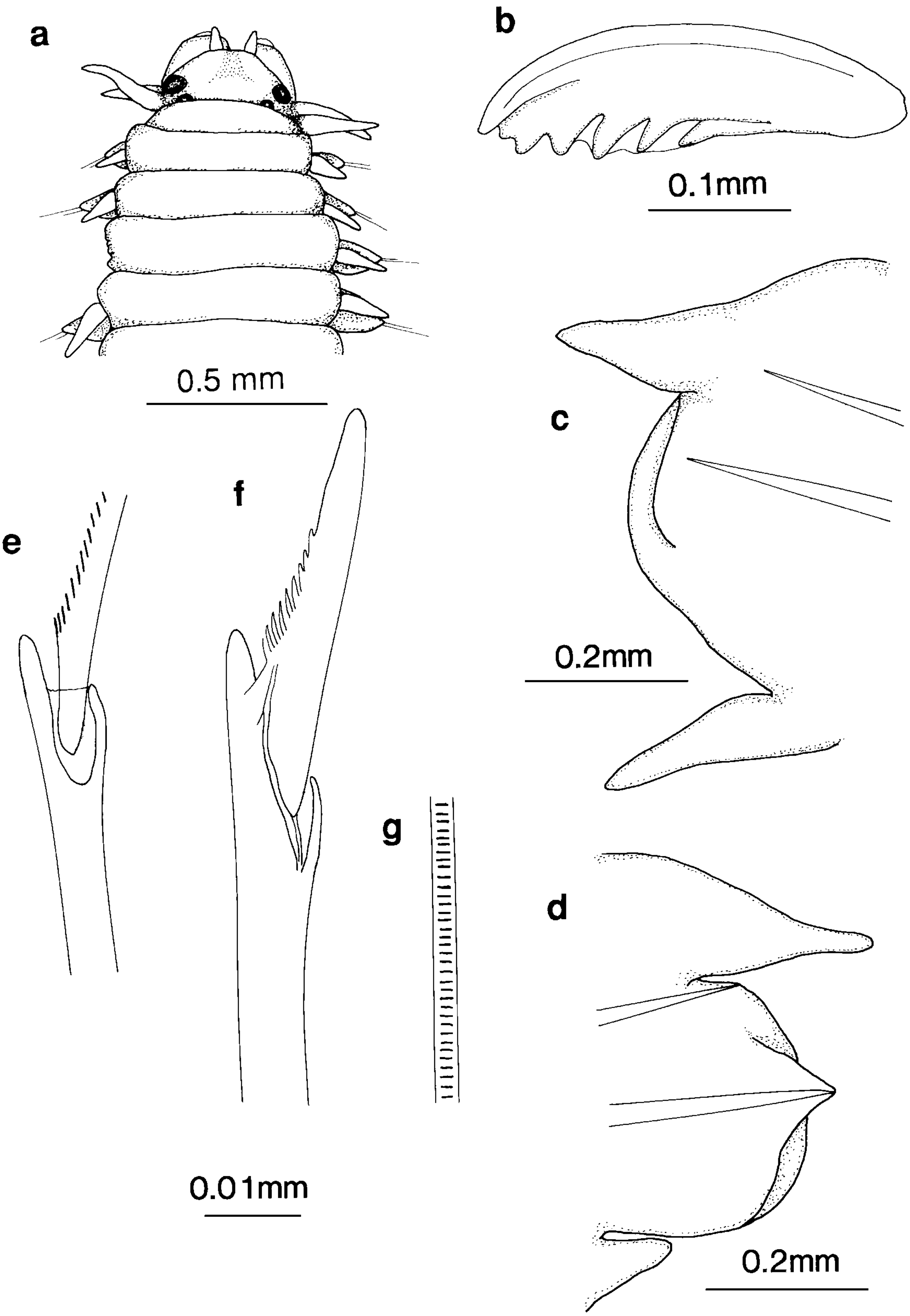

Figure 31. *Namanereis amboinensis* lectotype: (*a*) anterior end, dorsal view, anteroventral pair of tentacular cirri missing; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., posterior view (tip of acicular ligule retracted); (*d*) parapodium from 50th setiger, R.S., posterior view. (*e*) Paralectotype (PMJ Ann. 166), supra-neuroacicular spiniger, setiger 10. (*f*) Lectotype, supra-neuroacicular falciger, setiger 10. (*g*) Non-type (USNM 178874), supra-neuroacicular epitokal capillary seta (mid-section), setiger 30.

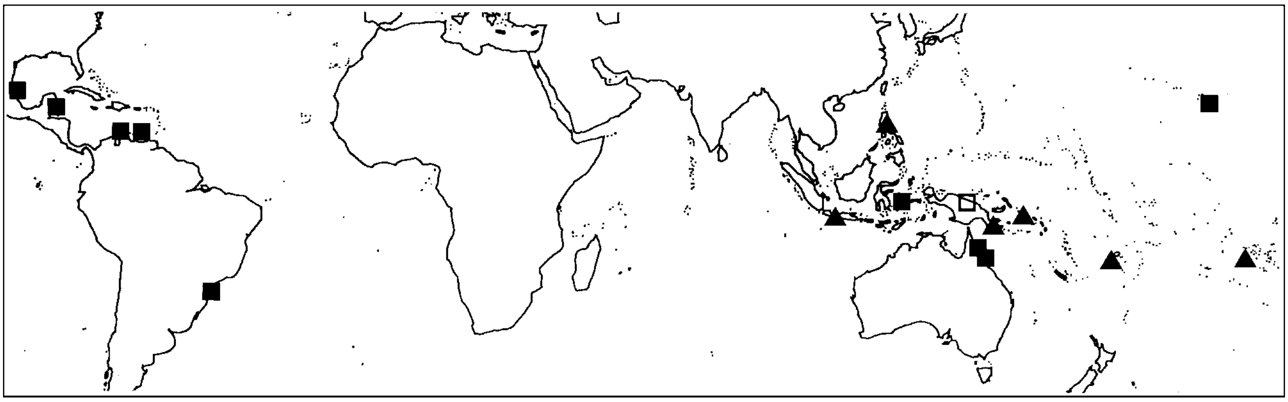

Figure 32. Distribution of *Namanereis amboinensis* ■, *N. beroni* □, and *N. catarractarum* ▲; based on material examined and authenticated literature records.

Remarks. The syntype series (PMJ Ann. 166) of *Lycastopsis amboinensis* contained 33 specimens, several headless fragments plus one specimen identified here as *Namalycastis abiuma* Grube species group. Pflugfelder (1933) appeared not to have included the specimen of *N. abiuma* in the type description, therefore the specimen was removed from the type series and re-registered (PMJ Ann. 221). A lectotype (PMJ Ann. 220) is designated from the syntype series. A well-preserved, robust specimen that fitted well the type description was chosen among the 33 types to be the lectotype. The remaining members of the type series, excluding the one specimen of *Namalycastis abiuma*, are designated paralectotypes and retain the original registration number (PMJ Ann. 166).

According to Pflugfelder (1933), *Lycastopsis amboinensis* was referred to as *L. catarractarum* Feuerborn by Lieber (1931), who described the biology of the species. Material examined from Ambon (Amboina), collected by Feuerborn and determined by Augener (HZM V11935), is likely to be this material. It was collected from under leaves of coconut palms, the same habitat as the types. Incidentally, Augener (1933a: 194) in a description of another Namanereidinae, also incorrectly referred to this species as *L. catarractarum*. Harms (1929) refers to a *Lycastopsis* species, perhaps *L. amboinensis* and a *Namalycastis* sp. or possibly spp. as both “Landnereiden” and *Lycastis* species. He describes their physiological adaptations to a semi-terrestrial habitat.

The type description of *L. amboinensis* is reasonably comprehensive, with much emphasis put on body proportions and soft-body characters. Pflugfelder refers to the distinctive shape and teeth of the falcigerous setae of *L. amboinensis* and how they clearly differ from those of *L. catarractarum*. The figure 11 of Pflugfelder (1933) shows a dorsoventral series of setae from one parapodium. The falciger blades have short, even-length teeth with each blade having a relatively short serrated region. Also the number of teeth on the blades is shown to decrease ventrally. These same setal characteristics were found in the present material and represent the most distinctive features of this species. Pflugfelder also describes *L. amboinensis* as being gonochoristic (dioecious), as is the present material, and in this feature it differs from *L. catarractarum*, which is described by Feuerborn (1931a) as being hermaphroditic (monoecious) (but see Remarks for *L. catarractarum*).

Lycastopsis tecolutlensis, a species from the Gulf of Mexico described by Rioja (1946) is here synonymised with *N. amboinensis*. Although it might seem unlikely that two such widely separated species could be conspecific, I could find no features to separate the two forms based on comparison with Rioja’s type description, which is very detailed for the time. Also, material from Belize, near the type locality of *L. tecolutlensis*, was examined and agrees well with the types of *L. amboinensis*. The types of Rioja, long considered lost or destroyed (Salazar-Vallejo, 1989) have recently surfaced. Unfortunately his collection is incomplete and the types of *Lycastopsis tecolutlensis* were not among them (V. Solís-Weiss, pers. comm., 1994).

Material of *N. amboinensis* from Sittee River, Belize (USNM 178873–75), 10(AM W20265) contained a few sexually mature males with epitokal capillary setae. The same type of capillary seta was present a mature male (headless) specimen in the paralectotype series (PMJ Ann. 166). These are the first records of epitokal capillary setae in a *Namanereis* species; the only other namanereidine species having epitokal capillary setae is *Cryptonereis malaitae* Gibbs, which is the sister species of *N. amboinensis* according to the results of the cladistic analysis (Figs. 5–7), and is accordingly transferred to *Namanereis*. The two species also share a well-developed lens, although this feature is homoplastic, being also present in *N. quadraticeps* and some *Namalycastis* species.

The presence of grey-green subcutaneous pigment in a few sexually mature specimens from Belize and Hawaii is another possible epitokous modification. The pigmentation is visible with the naked eye in living specimens and microscopically in preserved specimens, but its nature or function could not be determined. Pharyngeal papillae were observed on a juvenile (13 setiger) specimen from Aruba, Caribbean (ZMA V.Pol. 2893). The specimen has the papillae apparently arranged in a single row, probably on the oral ring (Fig. 3). Papillae are also found in juveniles of *N. hummelincki* (Augener) and further discussed in the Remarks for this species.

Habitat. The types were found under the dead basal parts of the leaves of coco palm trees (Pflugfelder, 1933). Other records indicate the species has a preference for the upper littoral areas of mangroves, especially in calcareous mud, and is often associated with dead and rotting vegetation (e.g., on the leaves and in the hollow centres of rotting mangrove roots; under the bark of rotting branches). At Tecolutla, Mexico, the species occurs on mangrove roots together with species of *Teredo*, *Balanus* and the serpulid *Ficopomatus miamensis* (Treadwell) (Salazar-Vallejo, 1989). In mangrove forests of Belize it co-occurs with *Namalycastis borealis* n.sp. In the Hawaiian Islands, the species co-occurs with a freshwater talitrid amphipod in the upper littoral zone of mangroves, as well as under the bark of logs floating in fresh-brackish water. On the Caribbean island of Aruba the species was collected from a freshwater pond and on Grenada the habitat was a mineral spring fed by ground-water with a chlorinity of 6930 mg Cl/l (salinity = 12.5‰).

Distribution. Circumtropical and circumsubtropical. The type locality is Ambon, Maluku (formerly Amboina, Moluccas), Indonesia. The synonymy with *L. pontica sensu* Lana extends the distribution to Brazil and the synonymy with *L. tecolutlensis* extends the distribution to the Gulf of Mexico. New records for Australia, Hawaiian Islands, Belize, Aruba and Grenada (Fig. 32).

Etymology. Pflugfelder named the species after the type locality, Amboina (now Ambon) in Maluku.

Namanereis beroni Hartmann-Schröder & Marinov

Figs. 1c, 32, 33a–f; Table 5

Namanereis beroni Hartmann-Schröder & Marinov, 1977: 49–51, figs. 1–4.–P. Chapman, 1985: 46 (table).–Hartmann-Schröder, 1986: 224 (list only).
"nereid".–P. Chapman, 1976: 199 (table).

Material examined. PARATYPES: New Guinea, West Sepik Province, cave near Telefomin (5°08'S 141°31'E), about 1700 m above sea level, coll. P. Beron, det. H-S., 1976 5(HZM P13675). 4 specimens measured.

Diagnosis. Antennae cirriform, faintly jointed. Eyes absent. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type C (Fig. 1c). Heterogomph setae with boss slightly prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.6–5.1 × longer than width of shaft head, very finely serrated, 12–17 teeth, teeth increasing in length slightly proximally.

Description. Paratypes well preserved, segmentally complete. 55–69 setigers, 20–26 mm long, 1.2–1.4 mm wide at setiger 10. At setiger 10 length of parapodia 0.38–0.53 × body width.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-white (yellowness due to oocytes). Living colour white according to P. Chapman (1976). Epidermal pigment absent.

Prostomium. Anterior cleft absent, no dorsal groove or hollow. Prostomium shape hexagonal to half-circular; 1.6–2.2 × wider than long. Antennae cirriform, faintly jointed, extending beyond tip of palpostyle to beyond tip of palpophore, aligned over inner edge of palps. Eyes absent (Fig. 33a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 1.3–1.5 × length anteroventral. Anterodorsal tentacular cirri 0.8–1.2 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 2–3 (Fig. 33a). Jaws with single robust terminal tooth, 1–4 subterminal teeth, 3–5 teeth ensheathed proximally, brown (Fig. 33b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 33c,d). Dorsal cirri 1.0–1.4 × length of podium at setiger 3 (Fig. 33c), 0.9–1.7 × length of podium in mid-body, 1.3–2.1 × length of podium posteriorly; 2.6–3.4 × longer than wide posteriorly (Fig. 33d). Ventral cirri 0.38–0.53 length of podium at setiger 3, 0.45–0.60 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers (appearing almost heterogomph) in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 2.3–2.8 × length of collar (Fig. 33e). Heterogomph setae with boss slightly prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.6–5.1 × longer than width of shaft head, very finely serrated, 12–17 teeth, 0.39–0.47 × total blade length, teeth increasing in length slightly proximally (Fig. 33f). Sub-neuroacicular falcigers in setiger 10 with blades very finely serrated; dorsal-most 4.7–5.0 × longer than width of shaft head, 11–14 teeth; ventral-most 4.6–4.8 × longer than width of shaft head, 8–9 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades very finely serrated. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed, shallowly incised, dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally or laterally, approximately conical, smooth, 0.6–1.2 × width pygidium.

Sex. Mature oocytes 550–570 µm (estimate from one specimen, oocytes damaged slightly), straw-coloured, with external membrane. Epitokal setae are absent.

Remarks. *Namanereis beroni* was described from specimens collected near Telefomin during the 1975 British Speleological Expedition to New Guinea (Hartmann-Schröder & Marinov, 1977). The holotype and 20 paratypes are housed in the collection of the National Museum of Natural History of the Bulgarian Academy of Sciences (Sofia), according to Hartmann-Schröder & Marinov (1977). A further five paratypes, housed at the HZM, were borrowed and examined for the present study. According to P. Chapman (1976, 1985), who along with Peter Beron were the biologists on the Expedition, the exact site of the type locality near Telefomin was Bem Tem.

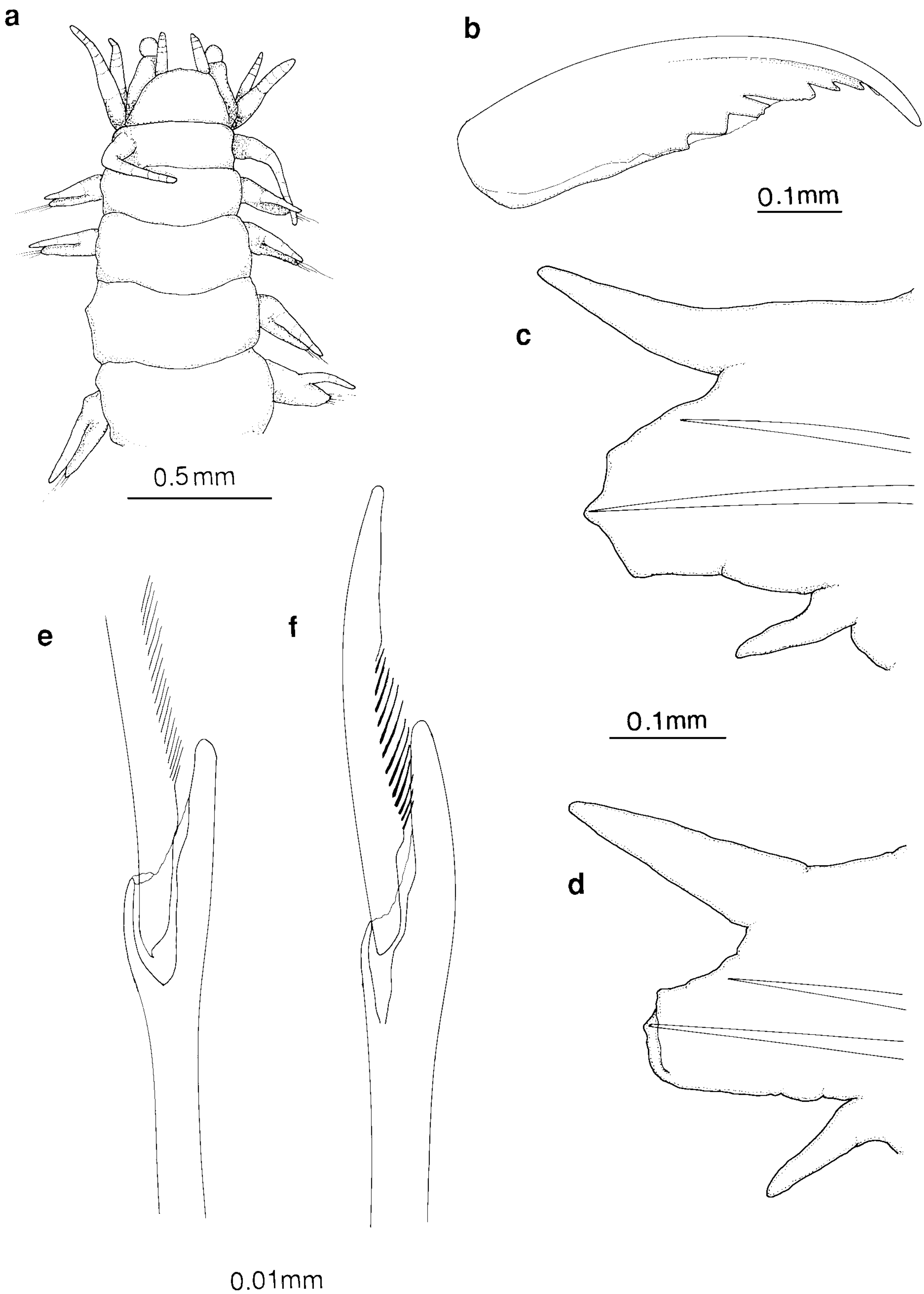

Figure 33. *Namanereis beroni* paratype (HZM P13675): (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., posterior view; (*d*) parapodium from 60th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10.

Namanereis beroni is the sister species to a group of five species, delineated by the presence of terminally bifid jaws, which live predominantly in subterranean waters of the Caribbean. The present day disjunct distribution between these sister groups is difficult to explain without invoking extinction of intermediate forms, undiscovered species, or a biogeographic hypothesis involving a previously vastly reduced Pacific Ocean (Glasby, this volume).

Habitat. The types were found in small puddles of freshwater (water temperature 17–18°C) in a cave about 1700 m above sea level (Hartmann-Schröder & Marinov, 1977). P. Chapman (1976) also indicates that the cave is non-flooding, and the substrate is muddy, containing finely triturated detritus.

Distribution. The type locality is Bem Tem (near Telefomin), West Sepik Province, Papua New Guinea (Fig. 32).

Etymology. The species was named in honour of Dr Peter Beron (Bulgarian National Museum, Sofia), a member of the British Speleological Expedition to New Guinea in 1975.

Namanereis catarractarum (Feuerborn)

Figs. 1c, 4b, 32, 34a–f; Table 5

Lycastopsis catarractarum Feuerborn, 1931a: 651–658, figs. 11–13; 1931b: 240–241.–Berkeley & Berkeley, 1963: 907–908, fig. 1; 1964: 147–148.–Kitching, 1990: 155, 157 (lists).–Glasby, Kitching & Ryan, 1990: 342–347.
Namanereis catarractarum.–Hartman, 1959a: 162–163.

Material examined. NEOTYPE: Java, Bedali [= Malang] (7°59'S 112°45'E), coll. Feuerborn, November 1928, det. Augener (HZM P19668). NON-TYPE: Java, as for neotype 7(HZM V11933); Philippines, Luzon Island, Luna 13(USNM 35670); New Guinea, west of Kowe near Madang 1(AM W202966); Fiji, Wailoku, Savuro Creek near Suva 30(AM W202965). 22 specimens measured.

Other material examined. Solomon Islands, Guadalcanal Island, Mt. Austen 1(BMNH ZB 1970.328). French Polynesia, Society Islands, Tahiti (P. Lehtinen, pers. coll.).

Diagnosis. Antennae cirriform, smooth. Eyes 2 pairs. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth, many subterminal teeth (8–12, including ensheathed ones). Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.8 × longer than width of shaft head (4.2–6.2), finely serrated, 18 teeth (15–25), teeth increasing in length greatly proximally. Monoecious or parthenogenetic.

Description. Neotype moderately well preserved (2 right side tentacular cirri and anal cirri missing), segmentally complete, mature oocytes in coelom. Other material in variable condition (Papua New Guinea material poorly preserved), including some complete individuals. 60 setigers (38–79), 7.9 mm long (4.9–12.5), 0.65 mm wide at setiger 10 (0.70–1.0). At setiger 10 length of parapodia 0.31 × body width (0.30–0.56).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-brown to white. Epidermal pigment absent. Living colour pale pink throughout.

Prostomium. Anterior cleft absent or shallow (rarely), with or without shallow dorsal hollow. Prostomium shape hexagonal to half-circular, or roughly trapezoidal; 2.0 × wider than long (1.8–2.5). Antennae cirriform, smooth, extending beyond, or rarely short of, tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs (rarely 1 pair, perhaps pigment in posterior pair faded); black, or red (Papua New Guinea material and one specimen from Philippines); arranged obliquely or longitudinally (rarely), posterior pair markedly smaller; lenses indistinct (Fig. 34a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.2 × length anteroventral (1.0–1.5). Anterodorsal tentacular cirri 1.0 × length posterodorsal (0.8–1.4). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (1–2) (Fig. 34a). Jaws with single robust terminal tooth, 4 subterminal teeth (3–7), 5 teeth ensheathed proximally (3–7), brown (Fig. 34b).

Parapodia. Acicular neuropodial ligule very small, subconical (Fig. 34c,d). Dorsal cirri 1.1 × length of podium at setiger 3 (0.4–2.4) (Fig. 34c), 1.0 × length of podium in mid-body (0.4–1.8), 1.5 × length of podium posteriorly (0.6–1.4); 2.1 × longer than wide posteriorly (1.1–2.8) (Fig. 34d). Ventral cirri 0.53 length of podium at setiger 3 (0.21–0.44), 0.35 length of podium posteriorly (0.14–0.33).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.5 × length of collar (1.4–1.7, rarely to 1.9) (Fig. 34e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.8 × longer than width of shaft head (4.2–6.2), finely serrated, 18 teeth (15–25), 0.58 × total blade length (0.50–0.64), teeth increasing in length greatly proximally (Fig. 34f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated (Fig. 4b); dorsal-most 4.0 × longer than width of shaft head (4.1–5.5), 16 teeth (13–22); ventral-most 4.0 × longer than width of shaft head (3.1–4.8), 16 teeth (13–20). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe (pygidium rarely elongated into funnel-shape). Anus terminal. Anal cirri arising laterally or ventrolaterally (rarely), approximately conical, smooth, 0.3–1.0 × width pygidium.

Sex. Hermaphrodite (according to Feuerborn, 1931a) or parthenogenetic (see Remarks). Mature oocytes 330 µm (260–320, range of means for 5 specimens), straw-coloured, with external membrane. Epitokal setae absent.

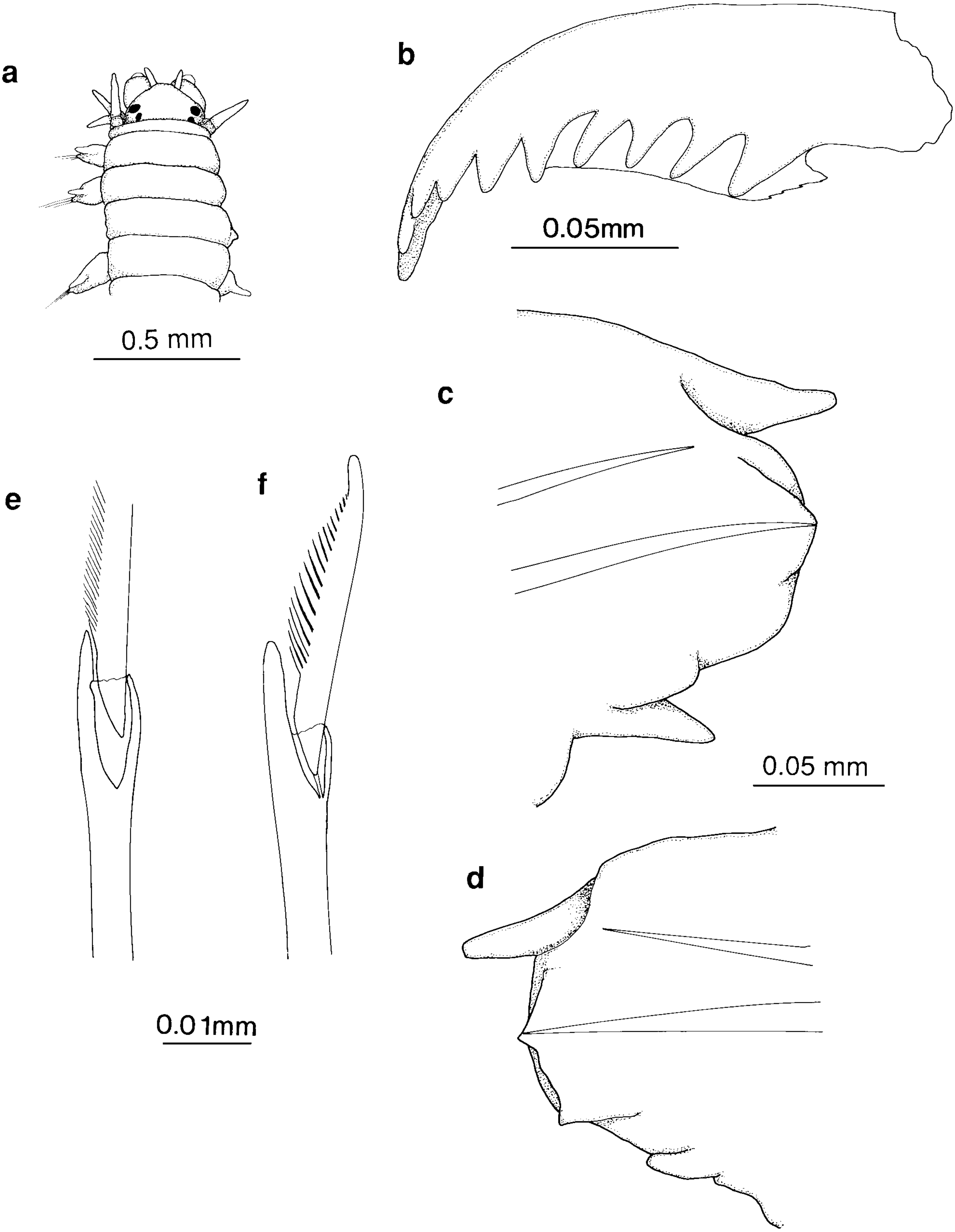

Figure 34. *Namanereis catarractarum* neotype: (*a*) anterior end, dorsal view, R.S. tentacular cirri obscured; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 50th setiger, R.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 31; (*f*) supra-neuroacicular falciger, setiger 31.

Remarks. Feuerborn's types could not be located and a neotype has been designated and described (Glasby *et al*., 1990). Feuerborn (1931a) states that *L. catarractarum* is an hermaphrodite as both male and female gametes were detected in each segment (although mature sperm were not seen). However, no male gametes were detected in the present material, which included sexually mature specimens (27% specimens had very large oocytes ranging in size from 260–320 µm). Therefore *L. catarractarum* may be parthenogenetic (Glasby *et al*., 1990), but this needs to be confirmed.

Material examined here included an unidentified specimen found at about 350 m in moist leaf litter on Guadalcanal Island, Solomon Islands, which was mentioned by Gibbs (1971) following his description of *N. malaitae* (as *Cryptonereis*). This specimen was observed to have a small pair of prostomial antennae (unlike *N. malaitae*, which lacks antennae), and is identified here as *N. catarractarum*. The other unidentified Namanereidinae mentioned by Gibbs (1971) from Kolambangara in the New Georgia Group, Solomon Islands, is in very poor condition and not identifiable.

The specimen from Tahiti, collected at 420 m in wet *Miconia calvescens* forest during a survey of the terrestrial soil fauna of Polynesia (P. Lehtinen, pers. comm., 1990), is also in poor condition and can only be tentatively identified as *N. catarractarum*.

The phylogenetic position of *N. catarractarum* is uncertain. In both the more conservative consensus trees (Strict and Nelson) the species is grouped with six or seven other species of *Namanereis* in an unresolved polychotomy (Figs. 5,6). However, 57% of all minimal-length trees support a sister group relationship with *N. amboinensis* and *N. malaitae* (Fig. 7). The clade containing all three species is not well supported, although the presence of very small posterior eyes (relative to the anterior pair) in both *N. catarractarum* and *N. amboinensis* is autapomorphic, but it requires a reversal to the plesiomorphic condition (anterior and posterior eyes equal in size) in *N. malaitae*.

Habitat. Further details of habitat are given in Glasby *et al*. (1990). The species prefers moist areas adjacent to forest streams and has been found living on the lower (moist) stems and leaves of *Colocasia indica*, the wild banana (*Musa* sp.) and *Pandanas vitiensis*; also in the leaf axils of these species and on vegetation lying on moist ground near streams.

Distribution. Neotype from Java, Bedali (now Malang). Also occurs in Indonesia, Philippines, Papua New Guinea, Solomon Islands, Fiji, and perhaps Tahiti. (Fig. 32).

Etymology. Feuerborn named the species from the Gr. *katarraktes*, latinised *catar(r)acta* f. for waterfall, referring to the type habitat.

Namanereis cavernicola (Solís-Weiss & Espinasa) **n.comb.**

Figs. 1c, 8c, 34, 35a–g; Table 5

Lycastilla cavernicola Solís-Weiss & Espinasa, 1991: 632–635, figs. 1a–e; 2a–f.
Namanereis hummelincki.–Hartmann-Schröder, 1977: 58, figs. 21–24 (in part) *Non* Augener.

Material examined. PARATYPES: Mexico, Guerrero State, Isote Cavern (18°36'40"N 99°33'25"W), 1 650 m above sea level, coll. L. Espinasa, 20 November 1988, 2(USNM 136559). NON-TYPE: St. Vincent (13°15'N 61°12'W), W.I, Golden Grove, SW2; spring pool in *Colocasia* swamp, coll. J.J. Rankin, 31.VII.1972 13(AHF POLY 1227–1229). Cuba, Rio Brazo Seco, 6(HZM P16508). Hispaniola, Mirebalais (18°51'N 72°08'W), 79–622, 8(ZMA V.Pol. 2816). 12 specimens measured.

Diagnosis. Prostomium usually anteriorly cleft, dorsally with shallow hollow. Antennae cirriform, faintly jointed or smooth. Eyes absent. Tentacular cirri, 3 pairs. Jaws with bifid terminal teeth. Notosetae absent. Neurosetae Type D (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 6.2 × longer than width of shaft head (5.5–7.9), very finely to finely serrated, 70–80 teeth (35–60), teeth increasing in length slightly proximally.

Description. Paratypes well preserved, one specimen segmentally complete. Other material well preserved, including some complete individuals, mature oocytes in coelom of some. 73 setigers (60–96), 26 mm long (9.5–34), 2.0 mm wide at setiger 10 (0.60–1.7). At setiger 10 length of parapodia 0.40–0.57 × body width (0.34–0.79).

Body. Widest mid-anteriorly, tapering gradually anteriorly and posteriorly (rarely) or uniform width anteriorly, tapering gradually posteriorly (Fig. 8c). Dorsum convex. Venter flat or convex. Colour in alcohol yellow-white or white with prominent dorsal and ventral blood vessels. Epidermal pigment absent.

Prostomium. Shallowly cleft anteriorly or lacking cleft, with shallow dorsal hollow. Prostomium shape roughly trapezoidal or hexagonal to half-circular (rarely); 1.6–1.9 × wider than long (1.4–2.6). Antennae cirriform, faintly jointed (2–3 joints) or smooth, extending beyond tip of palpostyle, aligned over mid-palps to inner edge of palps. Eyes absent (Fig. 35a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores distinct or indistinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 2.0 × length anteroventral (1.1–2.2). Anterodorsal tentacular cirri 0.5 × length posterodorsal (0.4–0.9). Posterodorsal tentacular cirri extending posteriorly to setiger 6 (3–9) (Fig. 35a). Jaws with bifid terminal teeth, 0 subterminal teeth (1), 0 teeth ensheathed proximally, brown (Fig. 35b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 35d). Dorsal cirri 1.2 × length of podium at setiger 3 (1.6–3.8) (Fig. 35c), 1.1 × length of podium in mid-body (1.3–3.8), 1.3 × length of podium posteriorly (1.6–2.3); 4.3 ×

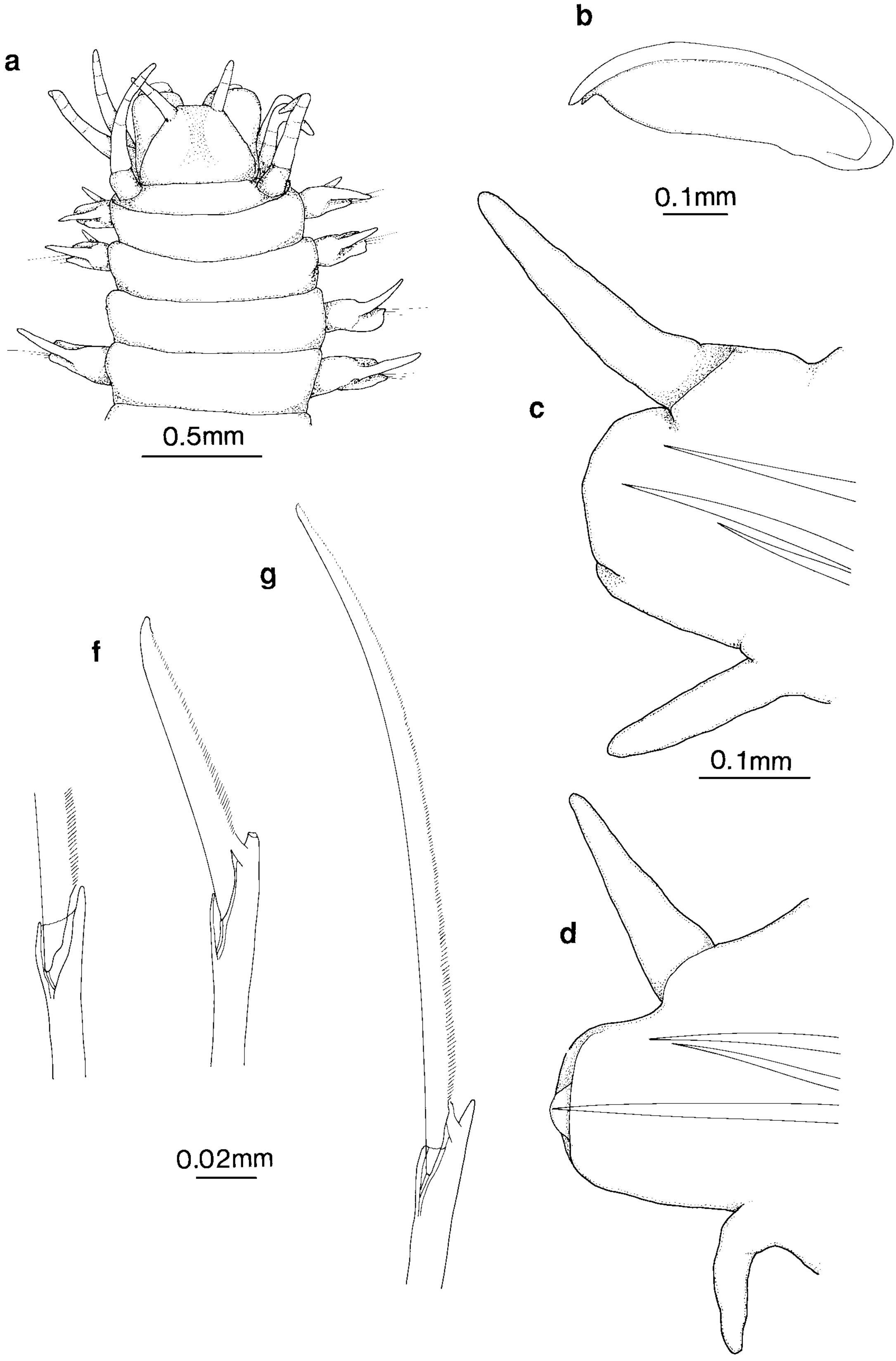

Figure 35. *Namanereis cavernicola* non-type (AHF POLY 1227): (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., posterior view (tip of acicular ligule retracted); (*d*) parapodium from 90th setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 30; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular pseudospiniger, setiger 10.

longer than wide posteriorly (3.5–4.4) (Fig. 35d). Ventral cirri 0.67 length of podium at setiger 3 (0.43–1.2), 0.36 length of podium posteriorly (0.41–0.60).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers, pseudospinigers and/or spinigers in a graded series in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4 × length of collar (1.4–1.6) (Fig. 35e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 6.2 × longer than width of shaft head (5.5–7.9), very finely serrated (i.e. serrations not clearly visible under 40× objective) or finely serrated, 70–80 teeth (35–60), 0.60 × total blade length (0.62–0.73), teeth increasing in length slightly proximally (Fig. 35f). Sub-neuroacicular falcigers in setiger 10 with blades very finely or finely serrated; dorsal-most 16 × longer than width of shaft head (13–20), >100 teeth (Fig. 35g); ventral-most 5.8 × longer than width of shaft head (4.6–7.0), 70 teeth (30–70). Sub-neuroacicular falcigers in mid-posterior region with blades very finely or finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally. Setae pale. Acicula in mid-body dark brown; tips hyaline and recurved, or bent slightly.

Pygidium. Pygidium with multi-incised rim or tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal or dorsoterminal. Anal cirri arising ventrolaterally, cirriform to approximately conical, smooth or faintly articulated, 1.0 × width pygidium (0.5–2.0).

Sex. Mature oocytes 551 µm (one specimen from AHF POLY 1227–1229 measured), straw-coloured (light), with external membrane. Epitokal setae absent.

Remarks. The Caribbean material examined greatly extends the range of this species, previously known only from a cavern 1 650 metres above sea level in Mexico. The Caribbean specimens resemble the Mexican specimens in all respects, except in having slightly longer dorsal cirri. This is not considered sufficient to warrant separate species recognition. The distally recurved notoaciculae, described as a generic attribute by Solís-Weiss & Espinasa (1991), are not as diagnostic as suggested by these authors. Study of several parapodia revealed variation ranging from a very slight curvature to recurved (almost 180°)—indeed only the most distal portion of the aciculae—which appears hyaline and presumably is very weak—show any curvature. Further, some slight curvature was observed also in the neuroaciculae of the same specimens. Distally curved aciculae were not observed in the Caribbean specimens. Therefore this feature is probably an artifact, perhaps resulting from the method of fixation or preservation.

The relationship between *Namanereis cavernicola* and *Lycastoides alticola* appears to be very close as noted by Solís-Weiss & Espinasa (1991). Unfortunately, the latter species is too poorly known to be included in the cladistic analysis. Considering that they are both found in Mexico in high altitude freshwater environments, the possibility that they are synonymous must be considered. Their shared similarities include a cleft prostomium, articulated and well-developed antennae, tentacular and anal cirri, absence of eyes, jaws with few teeth and small body size (Solís-Weiss & Espinasa, 1991). In addition, setal types and distribution are very similar. The antennae, which are produced from the prostomial frontal lobes in *L. alticola*, without the usual constriction at the base, resemble those of *N. cavernicola*—in the latter species the translucent epidermis enhances the appearance as a single structure. Despite these similarities, there are some major differences between the two species—*L. alticola* has 4 pairs of tentacular cirri (instead of 3) and an elongated cirrophore of the dorsal-most tentacular cirri. These differences are more difficult to reconcile and if real would suggest that we are dealing with different species (but see Remarks under *Lycastoides alticola*).

Namanereis cavernicola is also similar in appearance to *Namanereis hummelincki*, though it differs in a number of important setal characters. The sesquigomph spinigers of *N. cavernicola* have a more symmetrical articulation (i.e. relatively shorter boss), and the falcigers generally have blades with a greater number of teeth, which extend along a relatively longer length of the blade and increase in length slightly, proximally. In addition, *Namanereis hummelincki* has shorter posterodorsal tentacular cirri and has fewer pseudospinigers.

In Hispaniola, the species co-occurs with *N. stocki* n.sp., *N. hummelincki* and *N. serratis* n.sp., with the latter species known only from Hispaniola. All three species favour fresh to slightly brackish water (Table 6). A fourth species, *N. littoralis* sp. group also has been recorded from Hispaniola; however, this species is euryhaline, favouring coastal areas, and therefore unlikely to be encountered with the other three species. A similar situation exists in Cuba where all of the above species, except *N. serratis* n.sp., have been found. The Caribbean clearly favours a highly diverse namanereidine fauna.

Hartmann-Schröder's (1977) account of *Namanereis hummelincki* from Cuba includes both *N. cavernicola* and *N. stocki* n.sp., hence the "in part" comment in the synonymies.

Namanereis cavernicola n.sp. forms a clade with *N. hummelincki*, *N. minuta* n.sp. and *N. stocki* n.sp. although the precise relationships of these species to one another in not clear. In the Nelson Consensus tree, *N. cavernicola* is grouped together with *N. stocki* n.sp. and *N. minuta* n.sp., but this relationship is only common to 39% of all trees. More confidence may be placed in its position in the Majority-rule Consensus tree, which sees *N. cavernicola* and *N. hummelincki* as an (unresolved) sister group to *N. minuta* n.sp. and *N. stocki* n.sp. The clade containing all four species is delineated by the presence of a graded series of heterogomph setae (falcigers, pseudospinigers and spinigers) in the subacicular region of the parapodia.

Habitat. Type material from a freshwater pool in a limestone cave at 1 650 metres above sea level, 176 km from Pacific Ocean; cohabiting with copepods and Protozoa. St. Vincent specimens found in a spring pool in a *Colocasia* swamp at c. 415 m. Cuban specimens from a subterranean river in sand and fine gravel.

Distribution. Type locality Mexico, Guerrero State, Isote Cave. New records for Caribbean (St. Vincent, Hispaniola and Cuba) (Fig. 36).

Etymology. From the L. *caverna* meaning cave, grotto or hole, referring to one of the habitats of this species.

Namanereis hummelincki (Augener)

Figs. 1c, 36, 37a–g; Table 5

Lycastopsis hummelincki Augener, 1933b: 352–355, fig. 1a–d.–Wesenberg-Lund, 1958: 12–14, figs. 5–8.–Marcus, 1960: 58–60, figs. 29–32.–Perkins & Savage, 1975: 33 (list only).–Kirkegaard, 1980: 9–11.

Namanereis hummelincki.–Hartman, 1959a: 162–163.–Hartmann-Schröder, 1973: 96–97, figs. 18–20 (in part); 1980: 398–399; 1986: 224 (list only).

Material examined. SYNTYPES: Bonaire (12°15'N 68°27'W), Fontein, 21.V.1930, “In der Zufuhrgosse des Wasserbassins (im Kalkgebeit), 28.3°C, oligohalin = 500 mg Cl pro l” 1(HZM V11930a); 21.IX.1930, “Auf dem Boden des 1. Überdeckten Wasserbassins (im Kalkgebeit)”, temperature and salinity as above, one headless fragment (HZM V 11930b). NON-TYPE: Cuba, Cueva del Solón 1(HZM P-16516). Jamaica, Alluvia River 1(ZMA V.Pol. 2836); Buff Bay River 3(ZMA V.Pol. 2887); Broadgate 3(ZMA V.Pol. 2888); Hispaniola, the spring “Dubreuil II” near Cayes 2(ZMA V.Pol. 2831); the spring “Boislandry” 6(ZMA V.Pol. 2835); Bron Soudaizie 1(ZMA V.Pol. 2879); Grand Ravine du Sud, Cayes 1(ZMA V.Pol. 2886). Curaçao 4(ZMA V.Pol. 2784); Hato 1(ZMA V.Pol. 2715.1), many(ZMA V.Pol. 2787), many(ZMA V.Pol. 2789), many(ZMA V.Pol. 2827), 1(ZMA V.Pol. 2828), 3(ZMA V.Pol. 2870); Rooi Sänchez 4(ZMA V.Pol. 2782), 3(ZMA V.Pol. 2798), 1 (ZMUC POL-932); Bron San Pedro 1(ZMA V.Pol. 2796), 1(ZMA V.Pol. 2819), 2(ZMA V.Pol. 2855), 1(ZMA V.Pol. 2873); Bron Wandongo 1(ZMA V.Pol. 2854), 1(ZMA V.Pol. 2856), 1(ZMA V.Pol. 2867), 2(ZMA V.Pol. 2872); Bron Cajoeda 3(ZMA V.Pol. 2868). Bonaire 1(ZMUC POL-933); Pos Nobo, Plantage Slagbaai many(ZMA V.Pol. 2778), 1(ZMA V.Pol. 2850); Pos Bronswinkel 10(ZMA V.Pol. 2781), 1(USNM 29716), 1(ZMA V.Pol. 2820), 4(ZMA V.Pol. 2869); Fontein 10(ZMA V.Pol. 2783), 9(ZMA V.Pol. 2788), 22(ZMA V.Pol. 2790), 30(ZMA V.Pol. 2794), 9(ZMA V.Pol. 2795), 39(ZMA V.Pol. 2797), 4(ZMA V.Pol. 2801), 2(ZMA V.Pol. 2803), 5(ZMA V.Pol. 2829), many(ZMA V.Pol. 2832), 1(ZMA V.Pol. 2871), 4(ZMA V.Pol. 2878), many(ZMA V.Pol. 2889); Playa Palu many(ZMA V.Pol. 2802); Pos di Tochi 1(ZMA V.Pol. 2830); Plantage Brasil 2(ZMA V.Pol. 2833); near Rincon 1(ZMA V.Pol. 2834); near Transworld Radio 2(ZMA V.Pol. 2837). Barbados, Marley Vale, St. Philip 1(ZMA V.Pol. 2799), 2(ZMA V.Pol. 2800); Bakers Cave 2(ZMUC POL-934), 1(ZMUC POL-935), 1(ZMUC POL-936), 1(ZMUC POL-937). Blanquilla, Playa del Manzanillo 1(ZMA V.Pol. 2877). 13 specimens measured.

Other material examined. Jamaica, Yallahs River 5(BMNH ZB 1988. 1–3), 19(BMNH ZB 1988. 4–8). Curaçao, Boca Spelonk, near Hofje Hato 5(ZMA V.Pol. 2715). Bonaire, Fontein 3(USNM 29715).

Diagnosis. Antennae cirriform, usually smooth. Eyes absent. Tentacular cirri, 3 pairs. Jaws with bifid terminal teeth. Notosetae absent. Neurosetae Type D (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.9 × longer than width of shaft head (4.4–5.4), finely serrated (rarely approaching moderately serrated), 16 teeth (15–20), teeth increasing in length greatly proximally (rarely increasing in length slightly proximally).

Description. Syntype in poor condition, dorsoventrally flattened, segmentally complete, no gametes in coelom. Other material well preserved, segmentally complete. 56 setigers (42–131), 13.5 mm long (9.5–37), 0.9 mm wide at setiger 10 (0.90–2.0). At setiger 10 length of parapodia 0.33 × body width (0.25–0.41).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-brown to yellow-white. Epidermal pigment absent.

Prostomium. Shallow cleft anteriorly (rarely) or cleft absent, shallow dorsal hollow present or absent (very rarely). Prostomium shape hexagonal to half-circular (rarely) or roughly trapezoidal; 2.2 × wider than long (1.7–2.2). Antennae cirriform, smooth or jointed (very rarely); extending beyond tip of palpophore or beyond tip of palpostyle, aligned over inner edge of palps to mid-palps. Eyes absent (Fig. 37a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles faintly jointed or smooth (rarely). Anterodorsal tentacular cirri 1.0 × length anteroventral (0.8–2.2). Anterodorsal tentacular cirri 0.6 × length posterodorsal (0.5–0.9). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (2–4) (Fig. 37a). Pharynx with minute papillae around oral ring (in juveniles only). Jaws with bifid terminal teeth, 0 subterminal teeth (very rarely 1), 0 teeth ensheathed proximally (very rarely 1), brown (Fig. 37b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 37c,d). Dorsal cirri 1.8 × length of podium at setiger 3 (1.0–2.1) (Fig. 37c), 2.3 × length of podium in mid-body (1.0–2.2), 2.2 × length of podium posteriorly (1.2–4.0); 3.7 × longer than wide posteriorly (2.6–3.1) (Fig. 37d). Ventral cirri 0.43–0.67 length of podium at setiger 3, 0.30–0.59 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers, pseudospinigers and/or spinigers in a graded series in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.8 × length of collar (1.6–2.4) (Fig. 37e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.9 × longer than width of shaft head (4.4–5.4), finely serrated (rarely approaching moderately serrated), 16 teeth (15–20), 0.55 × total blade length (0.48–0.58), teeth increasing in length greatly proximally (rarely increasing in length slightly proximally) (Fig. 37f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 10 × longer than width of shaft head (8.7–11.3), large number of teeth (Fig. 37g); ventral-most 4.3 × longer than width of shaft head (4.0–5.0), 18 teeth (16–24). Sub-neuroacicular falcigers in

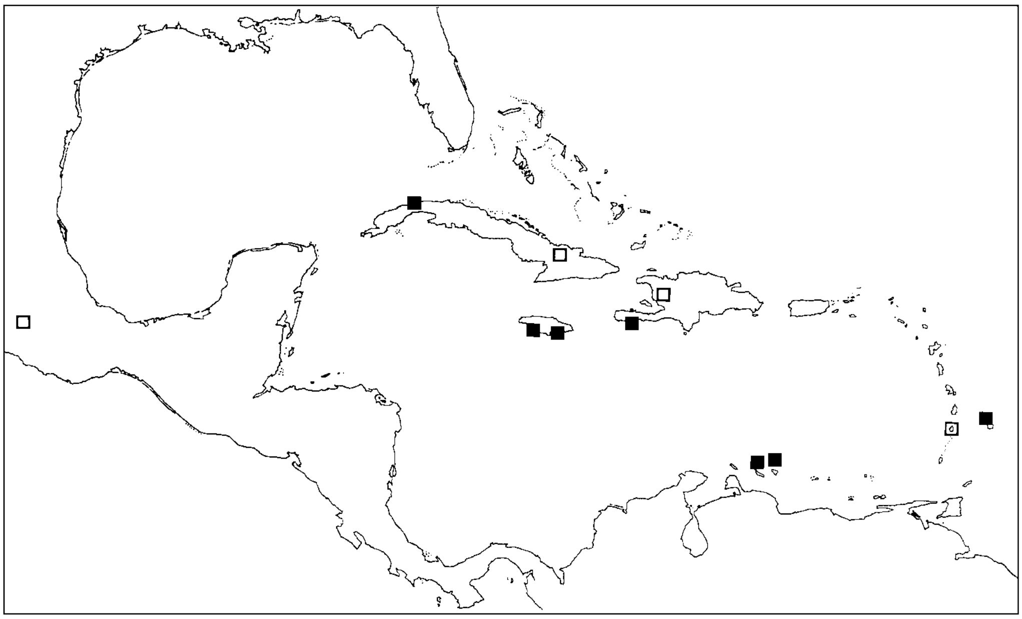

Figure 36. Distribution of *Namanereis cavernicola* □, and *N. hummelincki* ■; based on material examined and authenticated literature records.

mid-posterior region with blades finely serrated. Subneuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal or dorsoterminal (very rarely). Anal cirri arising ventrolaterally or laterally, approximately conical, smooth or faintly articulated, 0.5 × width pygidium (1.0–1.5).

Sex. Dioecious. Mature oocytes 115 µm (according to Marcus, 1960). Epitokal setae absent.

Remarks. The syntype series consists of two specimens, one of which is headless; therefore designation of a lectotype is unnecessary. Both specimens are registered under the number HZM V11930, although the complete specimen has an “a” suffix.

Namanereis hummelincki shares with *N. cavernicola, N. minuta* n.sp. and *N. stocki* n.sp. the presence of heterogomph pseudospinigers (referred to as Pseudo-Grätenborsten by Augener [1933b] and as pseudo-aristate by Marcus [1960]) in the subacicular position of the parapodia. The exact position of the pseudospinigers (pre- or postacicular) is however difficult to determine. The subacicular fascicle has few setae which are evenly spaced along the fascicle, and therefore it is difficult to distinguish between the sub-preacicular and the sub-postacicular positions. For the purposes of establishing initial homologies for the cladistic analysis, the pseudospinigers of this and other *Namanereis* species were presumed to be preacicular (see Appendix, characters 30, 31).

Namanereis hummelincki also shares with these three species bifid jaws that lack subterminal teeth. The presence of both bifid jaws and pseudospinigers in *N. hummelincki, N. cavernicola, N. minuta* n.sp. and *N. stocki* n.sp. indicates a close phylogenetic relationship; however, bifid jaws is apparently homoplastic in *N. serratis* n.sp. (Fig. 7).

Hartmann-Schröder (1973) considered *N. hummelincki* and *N. stocki* n.sp. to be conspecific. Her specimens from Cuba (stn. 11, 32a, 49) are referred to *N. stocki* n.sp., whilst the specimens from stn. 45c are *N. hummelincki* (see also Remarks for *N. stocki* n.sp.). Specimens from the Canary Islands, East Atlantic identified as *N. hummelincki* by Hartmann-Schröder (1988) were not included in this study, and the identification needs to be verified.

The intra-specific variation in the blade length of subacicular falcigers and pseudospinigers is complex. The pseudospinigers first appear in the parapodia of setigers 3 to 10, thereafter they are usually present in every parapodium (usually 1 per fascicle) to the pygidium. Sometimes the pseudospinigers are replaced by true spinigers in the parapodia of setigers 10–60. Further, the blades of the subacicular heterogomph falcigers may be intermediate in length between true falcigers and pseudospinigers. In these cases an even grade of falciger blade lengths was present, ranging from the long dorsal-most pseudospinigers to the short ventral-most true falcigers. The variation in subacicular falcigers and pseudospiniger blade lengths appears not to be related to size or sex. A thorough investigation using multivariate analysis of morphometric characters may be fruitful in quantifying population variability, and therefore species composition.

Two very small specimens from Boca Spelonk, Hato, Curaçao (ZMA V.Pol. 2870 and V.Pol. 2715.1), with 26 and 21 setigers respectively, had a row of very small papillae around the perimeter of the pharynx probably in the oral position. Juvenile pharyngeal papillae are also found in *N. amboinensis* (Pflugfelder), however the extent to which it occurs in the juveniles of other *Namanereis* (and other

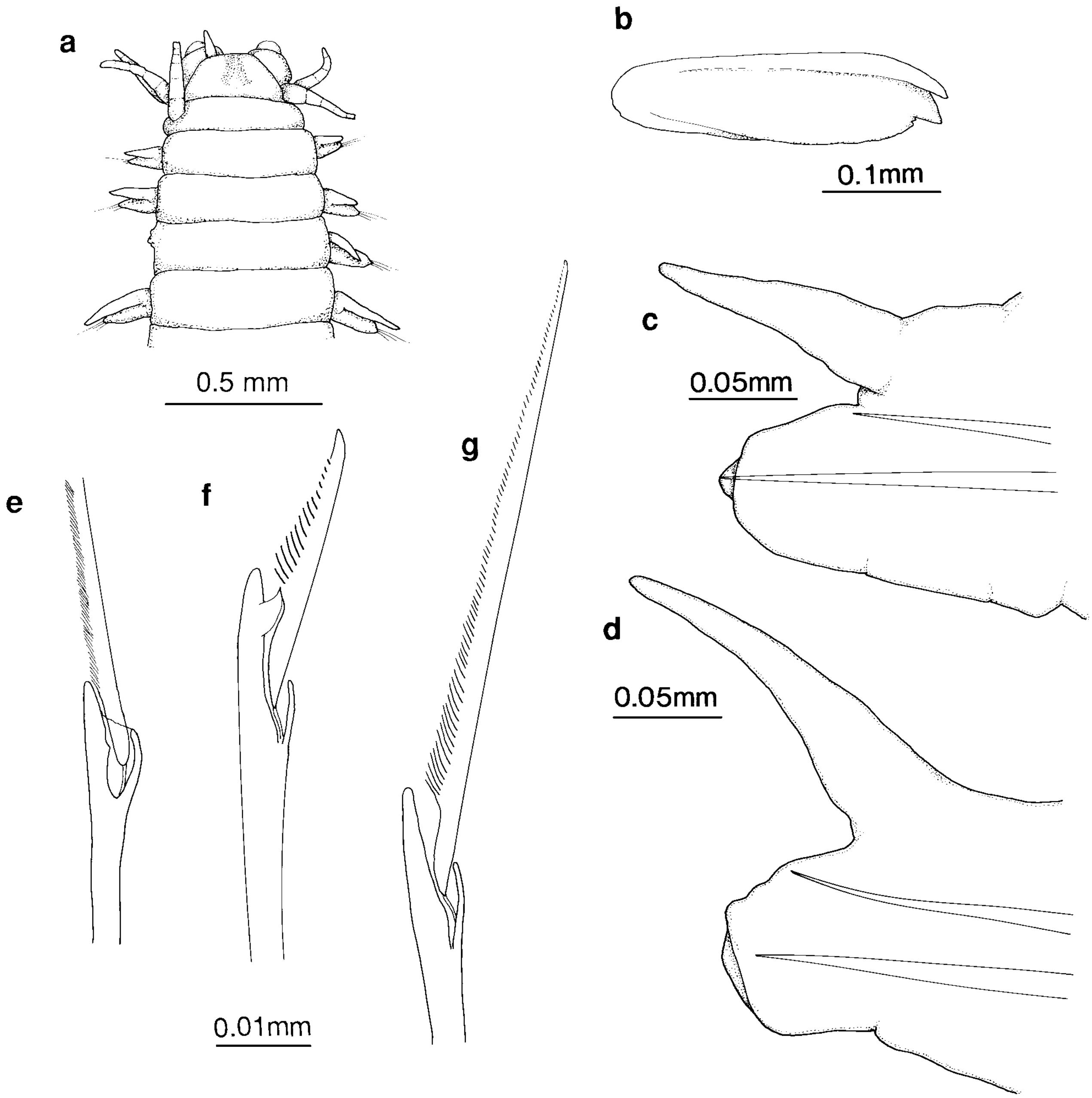

Figure 37. *Namanereis hummelincki* syntype (HZM V11930a): (*a*) anterior end, dorsal view, R.S. antenna and R.S. posterodorsal tentacular cirri missing; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S. posterior view, ventral cirrus missing; (*d*) parapodium from 30th setiger, L.S., posterior view, ventral cirrus missing; (*e*) supra-neuroacicular spiniger (blade not fully side-on), setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular pseudospiniger, setiger 10.

Namanereidinae) is not known. Papillae could only be observed in specimens having the pharynx partially everted so the frequency of their occurrence within the Namanereidinae could be difficult to determine even if small specimens were available. This is the first record of papillae on the pharynx of *Namanereis*.

Habitat. The syntypes were collected from a spring in a karst region with water temperature 28.3°C and chlorinity about 500 mg Cl/l (salinity = 0.9‰) (Augener, 1933b). Specific habitats as recorded by Wesenberg-Lund (1958) include shallow gutters, puddles, and cisterns, often in limestone areas with clayish mud-muddy sand sediment and decaying plant material and detritus with pH 7.2–8.5 and chlorinity 310–2100 mg Cl/l (salinity = 0.6–3.8‰). Hartmann-Schröder (1980) also gives habitat details. The chlorinity range for this material is 30–5500 mg Cl/l (salinity = 0.1–10‰). Specimens from Yallahs River, Jamaica were found about 3 km upstream. According to the collector, D. Lee, the worms were present only between November–February at which time the flow rate was c. 30 cm/sec. Maximum density was about 5 individuals/m^2.

Distribution. Type locality Bonaire, Fontein. Other records include Cuba, Jamaica (newly recorded), Hispaniola, Curaçao, Bonaire, Barbados, Blanquilla (Fig. 36). May be locally abundant, and as suggested by Orensanz (1981) is probably the most frequently reported polychaete species in brackish waters of the islands of the southern Caribbean.

Etymology. Augener named the species in honour of P. Wagenaar Hummelinck, who was leader of the 1930 Dutch Zoological expedition to the Caribbean.

Namanereis littoralis (Grube)

Figs. 1c, 38a–f, 39; Table 5

Lycastis littoralis Grube, 1872: 47–48.
Lycastopsis beumeri Augener, 1922: 42; 1936: 347.–Wesenberg-Lund, 1958: 14–17, figs. 9–11 (in part).–Perkins & Savage, 1975: 33 (list only).
Namanereis littoralis.–Hartman, 1959a: 162–163.

Material examined. LECTOTYPE: *Lycastis littoralis* Grube, Brasilien, Desterro [= Santa Catarina Island] (27°35'S 48°31'W), coll. Grube, leg. Fr. Müller (ZMB Q4006). PARALECTOTYPES: collection details as for lectotype (ZMB 11075) contains 2 vials, one with 7 specimens, the other with 4 specimens.

Other material examined. PARALECTOTYPES: *Lycastis littoralis* Grube collection details as for lectotype (MPW 538), contains 2 vials, one with 7 specimens, the other with 3 specimens. Specimens all in very poor condition. *Lycastopsis beumeri* Augener SYNTYPES: Cuba, Habana, coll. Beumer, det. Augener, 1922 3(HZM V-7061).

Diagnosis. Antennae subconical, smooth. Eyes 2 pairs, posterior pair slightly smaller. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.4 × longer than width of shaft head (4.2–4.8), moderately serrated, 10–12 teeth, teeth increasing in length greatly proximally.

Description. Lectotype in average condition, some setal damage, segmentally complete, mature oocytes in coelom. 97 setigers, 16.5 mm long, 1.0 mm wide at setiger 10; at setiger 10 length of parapodia 0.25 × body width. Paralectotypes examined range from 78–101 setigers, 13–18 mm long, 1.0–1.1 mm wide at setiger 10; at setiger 10 length of parapodia 0.26–0.36 × body width.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol white-brown. Epidermal pigment absent.

Prostomium. Cleft absent anteriorly, shallow dorsal hollow present. Prostomium shape hexagonal to half-circular; 2.0 × wider than long (2.0–2.4). Antennae subconical, smooth, extending to level with tip of palpostyle, aligned over inner edge of palps. Eyes 2 pairs, black, arranged obliquely, posterior pair slightly smaller; lenses indistinct (Fig. 38a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.0 × length anteroventral (1.0–1.6). Anterodorsal tentacular cirri 1.0 × length posterodorsal (0.9–1.0). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (Fig. 38a). Jaws with single robust terminal tooth, 2 subterminal teeth (2–3), 3 teeth ensheathed proximally (3–5), brown (Fig. 38b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 38d). Dorsal cirri 1.8 × length of podium at setiger 3 (0.7–1.0) (Fig. 38c), 1.0 × length of podium in mid-body (0.9–1.0), 1.0 × length of podium posteriorly (1.1–2.5); 2.0 × longer than wide posteriorly (Fig. 38d). Ventral cirri 0.53 length of podium at setiger 3, 0.27 length of podium posteriorly (0.31–0.45).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.4 × length of collar (1.4–1.6) (Fig. 38e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.4 × longer than width of shaft head (4.2–4.8), moderately serrated, 12 teeth (10), 0.50 × total blade length (0.47), teeth increasing in length greatly proximally (Fig. 38f). Sub-neuroacicular falcigers in setiger 10 with blades moderately serrated; dorsal-most 4.2 × longer than width of shaft head (4.4–5.4), 11 teeth (11); ventral-most 4.2 × longer than width of shaft head (3.8–4.9), 10 teeth (9–11). Sub-neuroacicular falcigers in mid-posterior region with blades moderately serrated. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal or dorsoterminal (rarely). Anal cirri arising ventrolaterally or laterally, approximately conical, smooth, 0.6 × width pygidium (0.4–0.5).

Sex. Dioecious. Mature oocytes straw-coloured with external membrane. Epitokal setae absent.

Remarks. The syntype series of *Lycastis littoralis* Grube contained 22 specimens in two lots, 12(ZMB Q4006) and 10(MPW 538). A specimen from ZMB Q4006 was selected as the lectotype and the remaining members of the syntype series are designated paralectotypes. The characterisation of the types of *Lycastis littoralis*, separate from other conspecifics (described in the following account under *Namanereis littoralis* species group), will facilitate any future taxonomic decisions involving this species. For example, if the genus *Lycastopsis* was resurrected then *Lycastis littoralis* becomes the type species of the genus, as originally designated by Uschakov (1955).

A large amount of additional material thought to be conspecific with *Namanereis littoralis* is described in the following account under the informal taxon, species group. Many synonymies are proposed under that taxon, but need to be verified. Only the synonymy with *Lycastopsis beumeri* Augener, for which type material was examined, can be

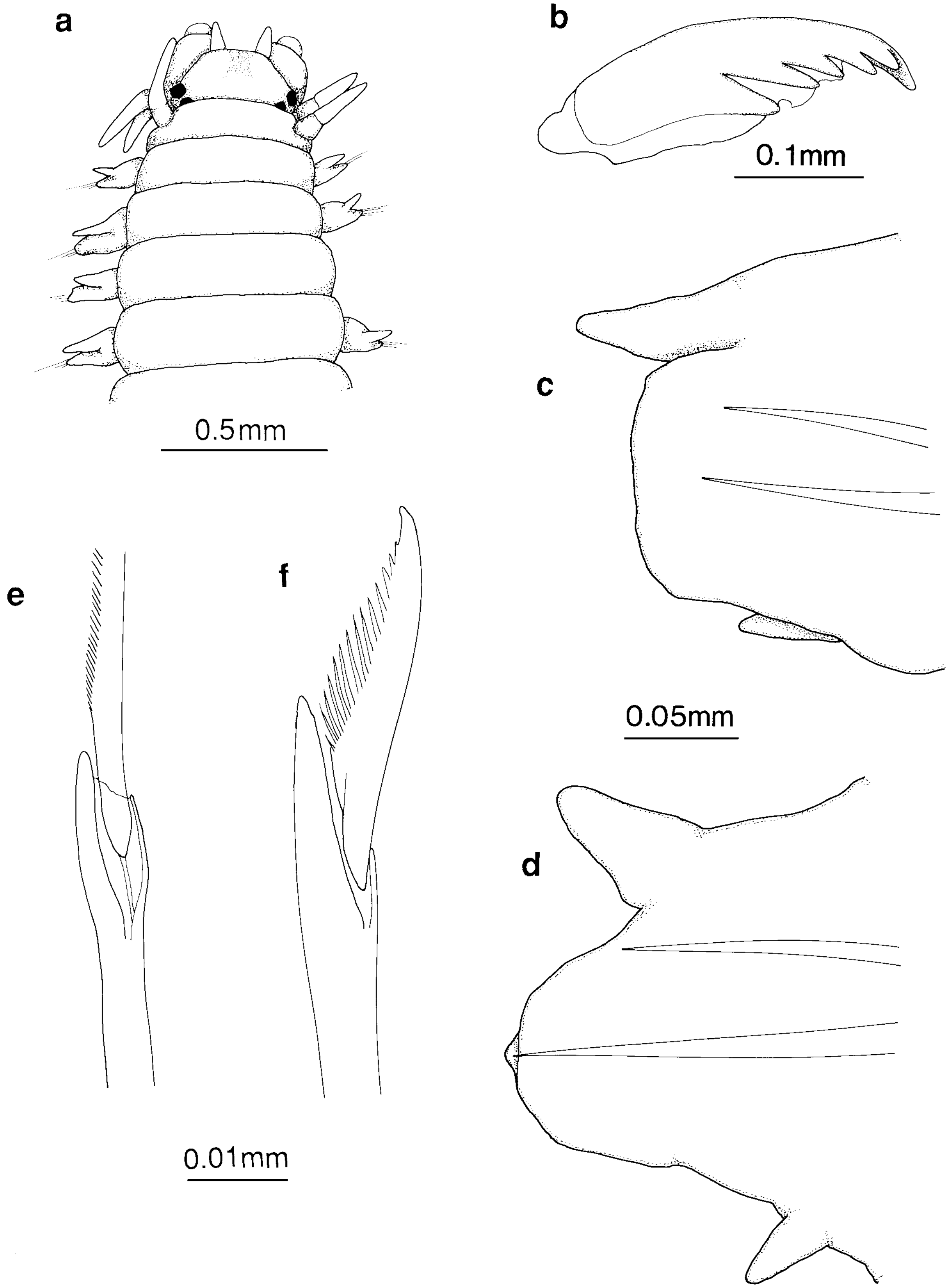

Figure 38. *Namanereis littoralis* lectotype: (*a*) anterior end, dorsal view, R.S. tentacular cirri obscured; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, R.S., anterior view (tip of acicular ligule retracted); (*d*) parapodium of 60th setiger, R.S., anterior view. Paralectotype (ZMB Q4006): (*e*) supra-neuroacicular spiniger, setiger 30; (*f*) supra-neuroacicular falciger, setiger 30.

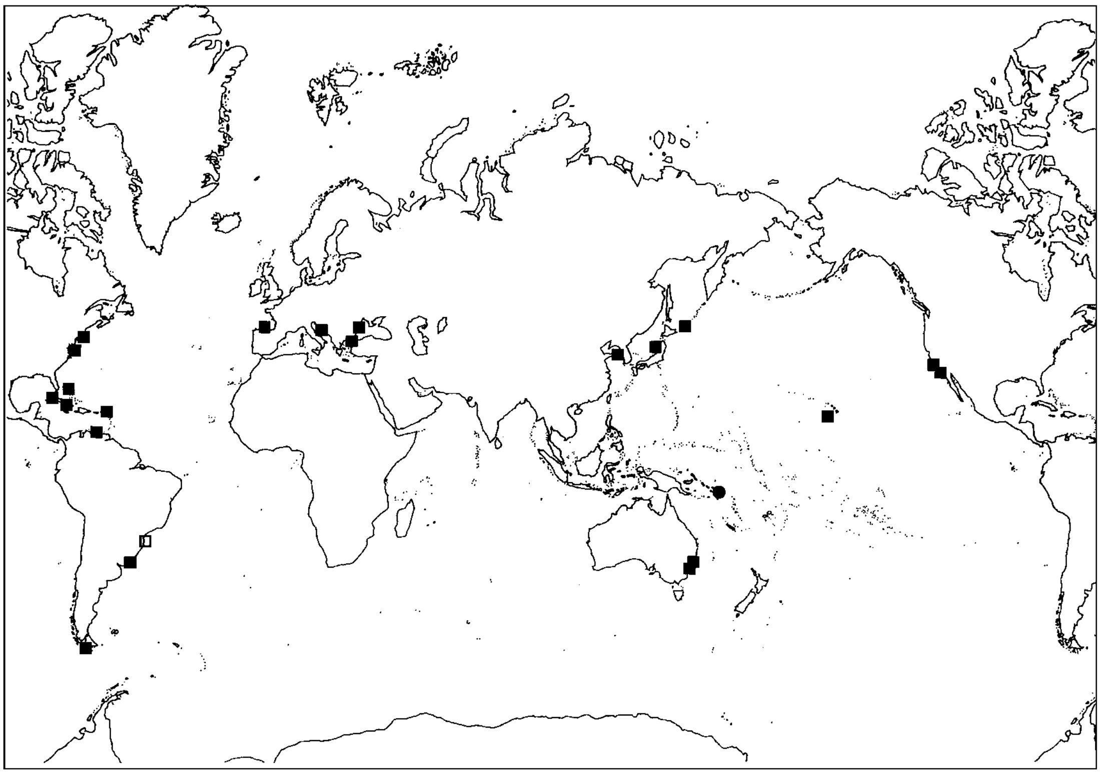

Figure 39. Distribution of *Namanereis littoralis* species group ■, and *N. malaitae* ●; based on material examined and authenticated literature records. Also indicated is the type locality of *N. littoralis* □.

certain at the moment (also the opinion of Feuerborn, 1931a: 651; Marcus, 1960: 61).

Habitat. Grube (1872) does not provide any information on the type habitat at Santa Catarina Island, Brazil.

Distribution. Type locality Brazil, Desterro (now Santa Catarina Island). (Fig. 39).

Namanereis littoralis (Grube) **species group**

Figs. 1c, 8d, 39; Table 5

Lycastis quadraticeps.–Ehlers, 1897: 70 (in part). *Non* Blanchard in Gay.
Lycastopsis beumeri Augener, 1922: 42; 1936: 347.–Wesenberg-Lund, 1958: 14–17, figs. 9–11 (in part).–Perkins & Savage, 1975: 33 (list only).
Lycastis sp.–Zachs, 1933: 128.–Annenkova, 1938: 85.
Lycastopsis augeneri Okuda, 1937: 307–309, figs. 1, 2a–g.–Chlebovitsch, 1961: 177–178.–Chlebovitsch & B.-L. Wu, 1962: 35 (in Chinese), 44 (in Russian), fig. 1A,B.–Uschakov, 1965: 184–185, fig. 62A–E (English translation).–Imajima, 1972: 39–40, figs. 1a–f, 7; 1988: 33 (list only).–Uschakov & B.-L. Wu, 1979: 59–60 (English translation).–Orensanz, 1982: 159 (not described).
Lycastoides pontica.–Greca, 1949: 164–165, figs. 13–18.–Banse, 1959: 302, fig. 5a–c. *Non* Bobretzky.
Namanereis sp.–Ferguson & Jones, 1949: 440.
Lycastopsis pontica.–Pettibone, 1963: 150–152, fig. 41a–e. *Non* Bobretzky.
Namanereis quadraticeps.–Imajima & Hartman, 1964: 142–143.–Marinov, 1966: 72–73, fig. 3a–f.–Hartman, 1968: 519–520.–Katzmann, 1972: 127.–Banse & Hobson, 1974: 69.–Pozar-Domac, 1978: 20 (list only).–Rowe, 1980: 85 (list only). *Non* Blanchard in Gay.
Namanereis pontica.–Hartmann-Schröder, 1973: 95–96, figs. 14–17; 1980: 399, fig. 30; 1986: 224 (in part, list only). *Non* Bobretzky.
Namalycastis sp.–Maciolek & Brock, 1974: 63 (list only, in part).
Lycastopsis pontica neapolitana.–Blake, 1975: 193–194. *Non* Greca.
? *Namalycastis brevicornis*.–Amoureux & Calvário, 1981: 148 (list only).–Calvário, 1984: 201 (list only). *Non* Audouin & Edwards.
Lycastopsis littoralis.–Gibbs & Saiz Salinas, 1996: 618–620, fig. 1a–e, fig. 2a,b.

Material examined. NON-TYPE: Spain, Cantabria, Ria de Bilbao 8(NIWA unreg.). Chile, Tierra del Fuego, Puerto Bridges, coll. Michaelsen, det. Ehlers, 1897 1(HZM V4784). Uruguay, Montevideo, Punta Carteta 2(USNM 24275), 1(USNM 24274). Hispaniola, Golfe de la Gonone many(ZMA V.Pol. 2810). St. Martin, Great Key many(ZMA V.Pol. 2809). St. Barthélemy, Gustavia Harbour 2(ZMUC POL-938), 1(ZMA V.Pol. 2821), 3(ZMA V.Pol. 2823). Tortuga, El Carenero, 1(ZMA V.Pol. 2862). Los Roques, Craskey, 1(ZMA V.Pol. 2894). Bonaire, Goto coast 1(ZMUC POL-939), Playa Palu many(ZMA V.Pol. 2807), 3(ZMA V.Pol. 2865); Playa Funchi 8(ZMA V.Pol. 2811); Salina Bartol many(ZMA V.Pol. 2812); Playa Mangel 2(ZMA V.Pol. 2822); Playa Bengé 1(ZMA V.Pol. 2862); Cay 1(ZMA V.Pol. 2866).

Curaçao, western-most region 4(ZMA V.Pol. 2808), many(ZMA V.Pol. 2864); Bocca Tabla, many(ZMA V.Pol. 2844–46), 3(ZMA V.Pol. 2874), many(ZMA V.Pol. 2895). Aruba, Playa Indieco Cara 1(ZMA V.Pol. 2861). Jamaica, Robins Bay 1(ZMA V.Pol. 2876). Bahamas, Eleuthera, near Marions Bluff, many(ZMA V.Pol. 2875). USA, Massachusetts, Woods Hole region, Gansett 4(USNM 28140), 3(USNM 28142), Eel Pond 2(USNM 28139); Norfolk, Va. 1(AHF n1166); California, Seal Beach Naval Station Wildlife Reserve 1(D. Reish, pers. coll.), Mission Bay 3(AHF n5077), Tomales Bay 3(AHF n5523), Upper Newport Bay 6(AHF n5084); Hawaiian Islands, Hawaii, near Anaehoomalu Bay 1(AM W20267) + 1 specimen gold coated for SEM (author's personal collection); Anaehoomalu S. pond D5, 1/8/72, 10(UH unreg.); Oahu, Heeia stream 2(AM W20266). Japan 10(HZM V12710), 4(MNHN UE 912); Sea of Japan 3(MNHN UE 913), many(ASL 37/45170). Australia, NSW, Yowie Bay (Sydney) 1(AM W20277); Merry Beach, south of Ulladulla 2(AM W202928).

Lycastopsis beumeri Augener SYNTYPES: Cuba, Habana, coll. Beumer, det. Augener, 1922 3(HZM V-7061). 46 specimens measured.

Other material examined. NON-TYPE: Black Sea 2(HZM P13676). USA, Massachusetts, Woods Hole region, Juniper Point 5(USNM 28141), Little Harbour 8(USNM 28138).

Diagnosis. Antennae usually cirriform and smooth. Eyes 2 pairs, posterior pair slightly smaller. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 3.6–5.8 × longer than width of shaft head moderately or coarsely serrated (very rarely finely serrated), 9–15 teeth, teeth increasing in length greatly proximally (very rarely increasing in length slightly proximally).

Description. Material in variable condition (*beumeri* syntypes with body wall partially damaged), including some complete individuals. 35–124 setigers, 4.6–53 mm long, 0.55–1.4 mm wide at setiger 10; at setiger 10 length of parapodia 0.19–0.42 × body width.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat, rarely convex or concave. Colour in alcohol white through brown. Epidermal pigment absent. Living colour pale pink throughout (Hawaiian material).

Prostomium. Cleft absent anteriorly, shallow dorsal hollow present or absent (rarely). Prostomium shape hexagonal to half-circular (very rarely triangular or trapezoidal); 1.7–2.5 × wider than long. Antennae cirriform or subconical (rarely), smooth or jointed (very rarely), extending beyond tip of palpophore, beyond tip of palpostyle or short of tip of palpophore, aligned over inner edge of palps to mid-palps. Eyes 2 pairs (rarely absent, pigment probably faded), black, purple or red, arranged obliquely, longitudinally or transversely, posterior pair slightly smaller; lenses indistinct.

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles faintly jointed or smooth. Anterodorsal tentacular cirri 1.0–1.8 × length anteroventral. Anterodorsal tentacular cirri 0.7–1.1 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 1–3. Jaws with single robust terminal tooth (approaching bifid in some Hawaiian material), 1–4 subterminal teeth, 1–5 teeth ensheathed proximally, brown or yellow (rarely).

Parapodia. Acicular neuropodial ligule subconical. Dorsal cirri 0.43–2.8 × length of podium at setiger 3, 0.49–2.0 × length of podium in mid-body, 0.60–2.7 × length of podium posteriorly; 0.90–2.3 × longer than wide posteriorly. Ventral cirri 0.30–0.75 length of podium at setiger 3, 0.17–0.50 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.2–1.7 × length of collar. Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 3.6–5.8 × longer than width of shaft head, moderately or coarsely serrated (very rarely finely serrated), 9–15 teeth, 0.43–0.60 × total blade length, teeth increasing in length greatly proximally (very rarely increasing in length slightly proximally). Sub-neuroacicular falcigers in setiger 10 with blades moderately or coarsely serrated (very rarely finely serrated); dorsal-most 3.1–5.4 × longer than width of shaft head, 7–13 teeth; ventral-most 3.0–4.8 × longer than width of shaft head, 7–15 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades moderately or coarsely serrated (very rarely finely serrated). Setae pale or dark. Acicula in mid-body brown, black or pale yellow (U.H. material).

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe (Fig. 8d). Anus terminal or dorso-terminal (rarely). Anal cirri arising ventrolaterally or laterally, approximately conical, smooth, 0.2–1.3 × width pygidium.

Sex. Dioecious. Mature oocytes 350 µm (250–370, range of means for 5 specimens), straw-coloured (variable shades), with external membrane. Epitokal setae absent.

Variation. Puerto Bridges specimen 53 setigers, 9.0 mm long, 0.90 mm wide at setiger 10; prostomium shallowly cleft anteriorly; posterior pair of eyes much smaller than anterior pair; sub-neuroacicular falcigers in setiger 10: dorsal-most with blades 3.1 × longer than width of shaft head; ventral-most 2.9 × longer than width of shaft head.

Remarks. *Namanereis littoralis* is designated as a species group for the same reasons outlined in the Remarks for *Namalycastis abiuma* sp. group. The specimen from Puerto Bridges, Chile showed even greater deviation from the types of *Lycastis littoralis*, specifically in having the posterior pair of eyes considerably smaller than the anterior pair and in having very short falciger blades. Differences in setal morphology within a species may be the result of abiotic factors like temperature, pH, salinity and ionic concentration (Specht, 1988 and references therein), but equally likely is that the specimen represents an undescribed species, although with only a single specimen it would be unwise to describe it as such at this stage.

At the most southerly extreme of this species range is a specimen collected from Puerto Bridges, Tierra del Fuego, which was misidentified by Ehlers (1897) as *Namanereis quadraticeps* (Blanchard in Gay). According to Ehlers the specimen was found subtidally in 7 fathoms (c. 13 m), which is very unusual for Namanereidinae (most *Namanereis* species are found in the littoral zone and above). The only other subtidal record for a Namanereidinae is that of a confirmed member of the *Namanereis quadraticeps* species group from the Barwon River, southern Australia (in about 4 m of water) and one from the Auckland Islands in 11–14.6 m.

Synonymies presented here under a species group taxon must necessarily remain tentative at this stage, except for that of *Lycastopsis beumeri*. References to *Lycastopsis beumeri* in the taxonomic literature have been checked and all are referred to *N. littoralis*. The material examined by Wesenberg-Lund (1958) contains one lot of *Namalycastis abiuma* species group (3 spec., Lagoen, stn. 308), hence the “in part” in the synonymies.

The type material of *L. augeneri* Okuda, a suspected junior synonym of *Namanereis littoralis*, could not be obtained, although a number of other specimens from Japanese waters were examined. Much of Okuda’s collections are housed at Zoological Institute, Faculty of Science, Hokkaido Imperial University; however, the types of *L. augeneri* are not among them (M. Sato, pers. comm.). The description of *L. augeneri* differs little from the description of *N. littoralis* given here. Okuda records 12–15 teeth for all falciger blades compared to the present counts of 10–12 for the supra-neuroacicular falcigers, 9–11 for the dorsal-most sub-neuroacicular falcigers and 9–11 for the ventral-most sub-neuroacicular falcigers. The falciger illustrated by Imajima (1972: 39, fig. le) closely resembles those of the present material in both the number of teeth and in the great increase in size of teeth toward the proximal part of the blade.

Many binomial names have been used in the systematic literature to refer to this species group, which as circumscribed here has a cosmopolitan distribution. Among them are *Lycastoides pontica* Bobretzky *sensu* Greca, 1949 from the Bosphorus (Turkey) and *Lycastoides pontica* Bobretzky *sensu* Banse, 1959 from Yugoslavia (Adriatic Sea). The descriptions of *Lycastoides pontica* by Greca (1949) and Banse (1959) agree well with the present description except in the case of the relative length of the dorsal cirrus of parapodium 57 illustrated by Banse (1959, fig. 5b). The length, about 2 × the length of the neuropodium, is considerably outside the range for other specimens of *N. littoralis* (0.53–0.77). Such a relatively long dorsal cirrus has however, been observed for some extreme posterior parapodia of some *Namanereis* species, including *N. littoralis*. However, whether parapodium 57 of Banse represents an extreme posterior one is unknown as it was removed from an incomplete specimen. Specimens of *N. littoralis* from the Black Sea (HZM P13676) were originally described by Marinov (1966) as *Namanereis quadraticeps.*

Hartmann-Schröder (1973, 1980, 1986) refers to *N. littoralis* as *Namanereis pontica*. Her material, all from the Caribbean, was not examined, however her descriptions appear more or less the same as that of *N. littoralis*. Hartmann-Schröder (1986) gives a list of localities for *Namanereis pontica sensu* Hartmann-Schröder, only some of which are *N. littoralis*, hence the “in part” given after this reference in the synonymies.

Maciolek & Brock (1974) recorded the species from the Anaehoomalu group of ponds on the Kona coast of Hawaii as *Namalycastis* sp. This material was re-examined and found to represent both *Namanereis littoralis* species group and *Namalycastis hawaiiensis* (Johnson).

References to *Lycastopsis augeneri* from far eastern Russia in the general biology and ecology literature (Buzhinskaja, 1967, 1985; Chlebovitsch *et al*., 1983; Komendantov & Yezhova, 1989a,b; Komendantov *et al*., 1989; Komendantov & Chlebovitsch, 1994) could not be verified, but all are likely to be referable to *N. littoralis* given the locality and habitat.

The phylogenetic position of *N. littoralis* is uncertain (Figs. 5–7). Although more than one species may be expected to be found within this species group with further analysis, the probability is that all will form a monophyletic group. Hence the inclusion of further species in the complex in a future cladistic analysis is not likely to affect significantly the present result.

Habitat. The species prefers the upper littoral zone of coastal areas on a variety of substrata, often associated with decaying vegetable matter (detritus) and freshwater runoff.

In the Caribbean, the species occurs in the upper littoral zone of lagoons, ponds and harbours often found in flotsam (containing decaying plant debris) on muddy sand substrata; in seawater or brackish water seeps from 36 to 130‰ S (Wesenberg-Lund, 1958). Hartmann-Schröder (1980) extends the salinity range to include water that is almost fresh. The present material from the Caribbean was found in water of salinity above 36‰.

The species has recently been recorded from north-eastern Spain. Here it occurs along the tidal banks of the Ria de Bilbao at about mid-tide level under stones lying on mud in areas influenced by freshwater runoff (Gibbs & Saiz Salinas, 1996). In Portugal it occurs intertidally in sand-mud (Amoureux & Calvário, 1981; Calvário, 1984). Banse (1959) records the species as living in coastal ground water in the Adriatic. On the Atlantic coast of the USA Pettibone (1963) reports the species in the upper littoral under large rocks overlying coarse gravelly sand, together with pseudoscorpions, oligochaetes, amphipods.

On the Pacific coast of the USA the species occurs in the upper intertidal zone in areas overgrown by sparse vegetation and affected by freshwater from creeks and streams (Hartman, 1959c). In the Hawaiian Islands, specimens were collected in Heeia stream (Oahu) in muddy sand with surface detritus at the high tide level behind the mangrove (*Rhizophora*) zone. The species was found co-occurring with the numerically dominant *Namanereis amboinensis* (Pflugfelder). The Anaehoomalu (Hawaii) specimens were collected under stones at the waters edge of a near freshwater anchialine pond.

Western Pacific material, including the types of *Lycastopsis augeneri* were collected in the upper littoral zone, under decaying seaweed, associated with the marine oligochaete *Pachydrilus japonicus* Yamaguchi (Okuda, 1937). Other material, described as *L. augeneri*, was recorded in the upper littoral and sublittoral zones, plowed under decomposing algal debris together with talitrid amphipods, myriapods, spiders and insects (larvae and adults) by Chlebovitsch (1961); amongst laminarian holdfasts in the oyster horizon by Chlebovitsch & B.-L. Wu (1962) and Uschakov & B.-L. Wu (1979); and in large numbers (40–100 individuals per square metre) among decomposing *Zostera* and other macrophytes thrown up on the shore (Buzhinskaja, 1967).

Eastern Australian material was collected from the littoral zone at the landward edge of mangroves, under wood (Yowie Bay) and from a gutter in gravel on a coastal rock (basalt) platform at high tide neap (Merry Beach).

Distribution. Type locality Brazil, Santa Catarina Island. The many putative synonymies give this species group a cosmopolitan distribution. New records for Uruguay, Punta Carteta; Jamaica; Tortuga; Los Roques; Bahamas; USA, Virginia, Norfolk; Hawaiian Islands (Oahu); Australia, New South Wales (Yowie Bay and Merry Beach) (Fig. 39).

Namanereis malaitae (Gibbs) **n.comb.**

Figs. 1c, 39, 40a–g; Table 5

Cryptonereis malaitae Gibbs, 1971: 144–147, fig. 6A–F.

Material examined. PARATYPES: Solomon Islands, Malaita Island (9°S 161°E) Alite Harbour, Langa-Langa Lagoon, burrowing in fibres of rotting leaf of coconut palm, MTL, coll. 20.11.1965, R. Soc. Exped. Solomon Islands 7(BMNH ZB 1970.31) (a sample of paratypes housed at the BMNH). 4 specimens measured.

Diagnosis. Epidermal pigment purple-grey dorsally. Antennae absent. Eyes 2 pairs. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 3.7–4.0 × longer than width of shaft head, finely serrated, 7–10 teeth, teeth increasing in length slightly proximally. Blade and shaft of falcigers partially or entirely fused.

Description. Paratypes well preserved; segmentally complete. 53–67 setigers, 11–14 mm long, 1.1–1.2 mm wide at setiger 10. At setiger 10 length of parapodia 0.30–0.34 × body width.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol yellow-white. Epidermal pigment purple-grey dorsally. Living colour purplish according to Gibbs (1971).

Prostomium. Antennae absent. Prostomial cleft absent anteriorly, shallow dorsal hollow. Prostomium shape hexagonal to half-circular; 2.0–2.3 × wider than long. Eyes 2 pairs, black or red, arranged obliquely, posterior pair slightly smaller; lenses present (Fig. 40a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.0–1.3 × length anteroventral. Anterodorsal tentacular cirri 1.0–1.2 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 1 (Fig. 40a). Jaws with single robust terminal tooth, 3 subterminal teeth, 5–6 teeth ensheathed proximally, brown (Fig. 40b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 40c). Dorsal cirri 0.48–0.55 × length of podium at setiger 3 (Fig. 40c), 0.42–0.45 × length of podium in mid-body, 0.82–1.1 × length of podium posteriorly; 0.86–1.1 × longer than wide posteriorly (Fig. 40d). Ventral cirri 0.15–0.17 length of podium at setiger 3, 0.21–0.26 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.6–1.8 × length of collar (Fig. 40e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 3.7–4.0 × longer than width of shaft head, finely serrated, 7–10 teeth, 0.27–0.30 × total blade length, teeth increasing in length slightly proximally (Fig. 40f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 3.2–3.5 × longer than width of shaft head, 8–9 teeth; ventral-most 3.3–3.6 × longer than width of shaft head, 8–9 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Blades and shaft of falcigers partially or entirely fused (Fig. 40f). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe (pygidium sometimes drawn out into funnel-shape). Anus terminal. Anal cirri extending laterally from pygidial lobes, papilliform, smooth, 0.1 × width pygidium.

Sex. Mature oocytes 430 µm (estimate based on the largest oocyte in one mature female), straw-coloured, with external membrane. Epitokal setae are long, slender capillaries (Fig. 40g); present from setiger 8–16, continue to near pygidium; about 20 in notopodium and 8–10 in neuropodium (Gibbs, 1971).

Remarks. The seven paratypes included six specimens that were sexually mature, or nearly mature, and one immature specimen; one specimen had sperm in the coelom. The mature specimens had long, slender capillary setae as described by Gibbs (1971). In addition to the observations of Gibbs (1971) on sexually-acquired characteristics, I found that the eyes of the mature specimens were slightly enlarged, with the anterior ones of each pair almost coalesced with the posterior ones. Eye enlargement is a typical sexually-acquired modification of nereids (R.B. Clark, 1961: 201). This further supports Gibbs' idea that *N. malaitae* has an epitokous phase at maturity. However, both modifications are slight compared to those in truly epitokous nereid species. The slender capillary setae and unmodified parapodia are probably of little value for swimming.

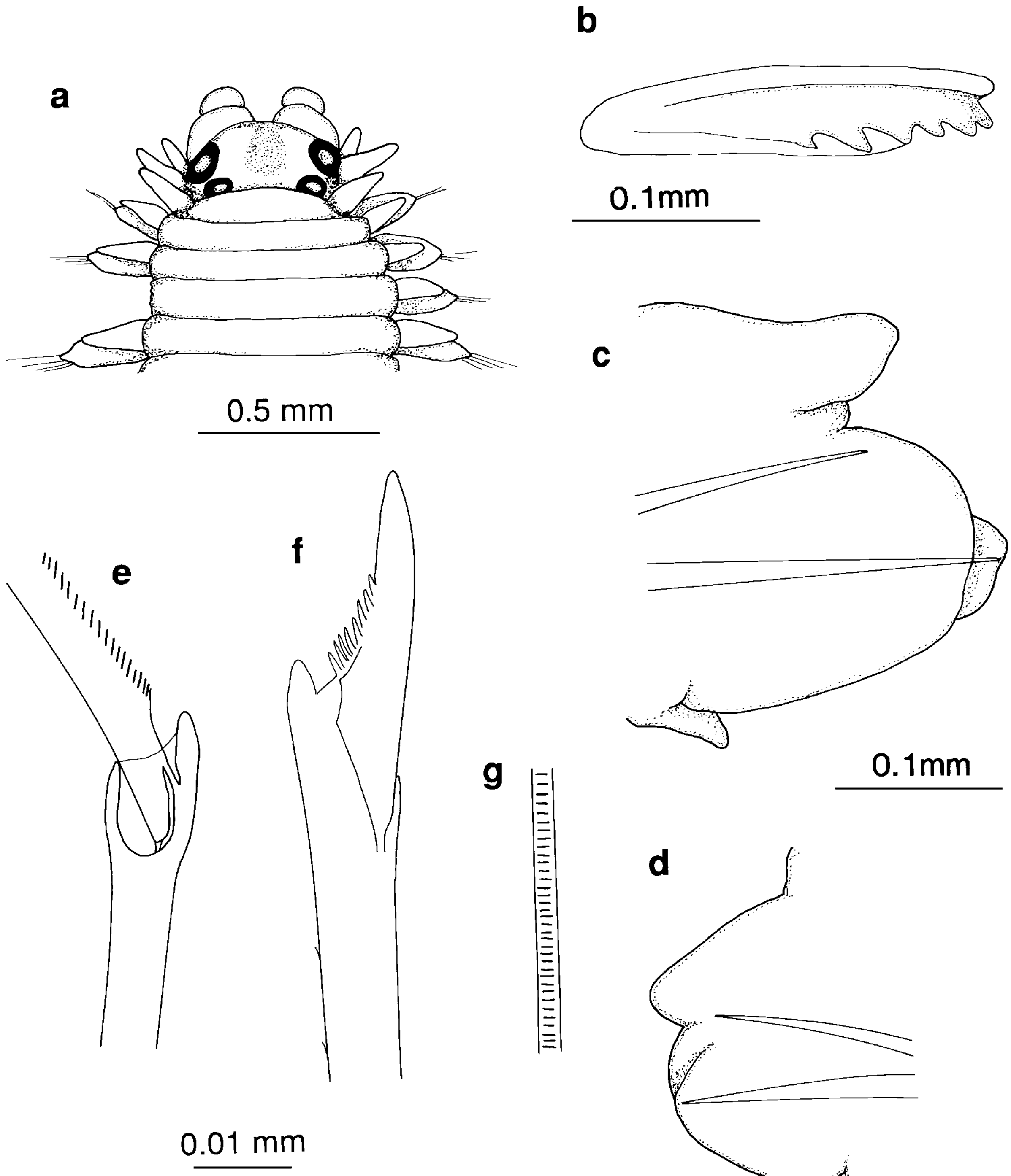

Figure 40. *Namanereis malaitae* paratype (BMNH ZB 1970.31): (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 60th setiger, L.S., posterior view (tip of acicular ligule retracted); (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) epitokal capillary seta (section from mid-seta).

Epitokal capillary setae are also found in *N. amboinensis* (Pflugfelder), a widespread circumtropical and circumsubtropical species. The capillary setae in this species are similar in structure to those of *N. malaitae*, and additionally, there is a similar number and distribution of these setae over the body (see Description of *N. amboinensis*). The two species also have similar reproductive strategies (both dioecious, forming similarly modified epitokes at maturity), similarly articulated sesquigomph spinigers, and similar structure of the blades of heterogomph falcigers. Their sister group relationship in the consensus trees (Figs. 5–7) is therefore not surprising.

Namanereis malaitae also shows some affinity with *N. quadraticeps* Blanchard in Gay in having serrated setal shafts and the papilliform anal cirri. *Namanereis malaitae* may be distinguished from all other members of the subfamily in lacking prostomial antennae and in having falcigers with the blades and shaft partially or entirely fused (Gibbs, 1971).

Habitat. Type material found between the fibres composing a leaf frond of a coconut palm found stranded at about mid-tide level (Gibbs, 1971).

Distribution. Known only from the type locality Solomon Islands, Malaita Island, Alite Harbour (Pacific Ocean) (Fig. 39).

Etymology. Gibbs named the species after Malaita in the Solomon group.

Namanereis minuta n.sp.

Figs. 1c, 41a–f, 42; Table 5

Material examined. HOLOTYPE: Hispaniola, 79–659, Nallee Grande Anse (18°35'55"N 74°10'46"W), coll. Botosaneanu and Notenboom, 5.XII.1979 (ZMA V.Pol. 2792). PARATYPES: Hispaniola, location details as for holotype 1(ZMA V.Pol. 2793); 79–660, Nallee Grande Anse 5(ZMA V.Pol. 2791); 79–651, 3(ZMA V.Pol. 2842); 79–517, Grande Ravine du Sud 2(ZMA V.Pol. 2806); 79–518, Grande Ravine du Sud 1(ZMA V.Pol. 2847); Hispaniola, unknown localities, 79–531 1(ZMA V.Pol. 2843); 79–656 1(ZMA V.Pol. 2841). 5 specimens measured.

Diagnosis. Antennae cirriform, smooth. Tentacular cirri, 4 pairs. Eyes absent. Jaws with bifid terminal teeth (subequal in holotype; equal in paratypes). Notosetae absent. Neurosetae Type D arrangement (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 7.6 × longer than width of shaft head (7.6–9.6), finely serrated, 50 teeth (50+), teeth about uniform in length.

Description. Holotype well preserved, segmentally complete, no gametes in coelom. Paratypes well preserved, segmentally incomplete. 36 setigers, 5.0 mm long, 0.9 mm wide at setiger 10 (0.9–1.4). Parapodia of setiger 10 with length 0.83 × body width (0.67–1.0).

Body. Uniform in width anteriorly, tapering gradually posteriorly (sometimes tapering only in far posterior region). Dorsum convex. Venter convex or flat. Colour in alcohol yellow-brown, yellow-white or brown. Epidermal pigment absent.

Prostomium. Very shallow cleft anteriorly, with narrow longitudinal groove extending from tip to mid-posterior prostomium, or with shallow dorsal hollow (rarely). Prostomium shape hexagonal to half-circular or roughly trapezoidal; 1.8 × wider than long (1.6–1.8). Antennae cirriform, smooth, extending beyond tip of palpostyle or beyond tip of palpophore, aligned over inner edge of palps. Eyes absent (Fig. 41a).

Peristomium. Tentacular cirri, 4 pairs, with cirrophores indistinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 1.9 × length anteroventral (1.3–1.7). Anterodorsal tentacular cirri 0.5 × length posterodorsal (0.3–0.6). Posterodorsal tentacular cirri 2.0 × length posteroventral (1.6–2.5). Posterodorsal tentacular cirri extending posteriorly to setiger 6 (4–8) (Fig. 41a). Jaws with bifid terminal teeth (subequal in holotype; equal in paratypes), 0 subterminal teeth, 0 teeth ensheathed proximally (0–3), brown (Fig. 41b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 41c,d). Dorsal cirrophores anteriorly absent. Cirrophores in mid-posterior segments absent, though cirri often slightly swollen at base. Dorsal cirri similar in length throughout; 1.4 × length of podium at setiger 3 (0.9–1.5) (Fig. 41c), 3.2 × length of podium in mid-body (1.0–2.3), 0.8 × length of podium posteriorly; 6.1 × longer than wide posteriorly (Fig. 41d). Ventral cirri 0.58 length of podium at setiger 3 (0.50–0.73), 0.28 length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers, pseudospinigers and/or spinigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.2 × length of collar (1.2–1.4) (Fig. 41e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 7.6 × longer than width of shaft head (7.6–9.6), finely serrated, 60 teeth (50+), 0.72 × total blade length (0.79–0.81), teeth about uniform in length (Fig. 41f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 9.8 × longer than width of shaft head (16.1–16.6), large number of teeth; ventral-most 5.6 × longer than width of shaft head (5.8–7.6), 28 teeth (30–40). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, faintly articulated, 4.5 × width pygidium.

Remarks. *Namanereis minuta* n.sp. resembles *N. cavernicola* in having jaws with bifid terminal teeth and a graded series of heterogomph falcigers, pseudo-spinigers and/or spinigers in the preacicular fascicle below the neuroacicula. It differs however in having 4 pairs of tentacular cirri rather than 3 pairs. The only other species of *Namanereis* having 4 pairs of tentacular cirri, *N. stocki* n.sp. also has a graded series of heterogomph falcigers, pseudospinigers and spinigers (Type D arrangement), however, this species differs from *N. minuta* n.sp. in having subconical antennae and falciger blades that are both shorter (4.0–4.7 × width of shaft head *vs* 7.6–9.6) and with fewer teeth (9–14 *vs* >50).

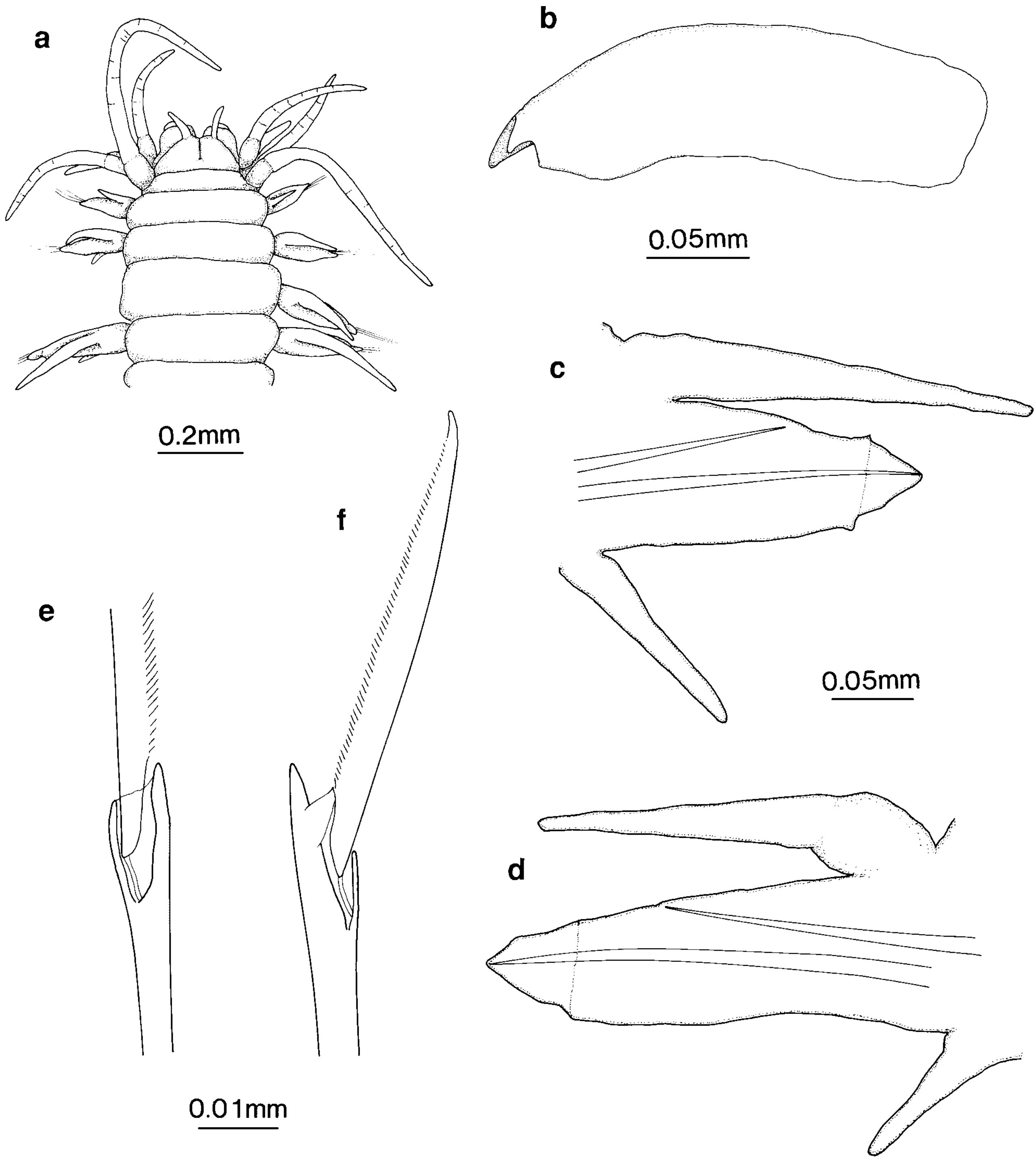

Figure 41. *Namanereis minuta* n.sp. holotype: a. anterior end, dorsal view; b. jaw piece, dorsal view; c. parapodium from 3rd setiger, L.S., anterior view; d. parapodium from 30th setiger, L.S., posterior view; e. supra-neuroacicular spiniger, setiger 30; f. supra-neuroacicular falciger, setiger 30.

The results of the cladistic analysis are equivocal with respect to the phylogenetic position of *N. minuta* n.sp. in relation to *N. stocki* n.sp. and *N. cavernicola*. The three species either form an exclusive clade together as in the Nelson Consensus tree (Fig. 6), or a larger clade together with *N. hummelincki* as in the Strict Consensus tree (Fig. 5), or *N. minuta* n.sp. and *N. stocki* n.sp. form a clade exclusive of *N. cavernicola* and *N. hummelincki* as in the Majority-rule Consensus tree (Fig. 7). Clearly more cladistic data are required to clarify the relationship of these species.

Habitat. Type habitat unknown. Other material from springs and wells with chlorinity 14.2–42.2 mg Cl/l (salinity about 0.1‰).

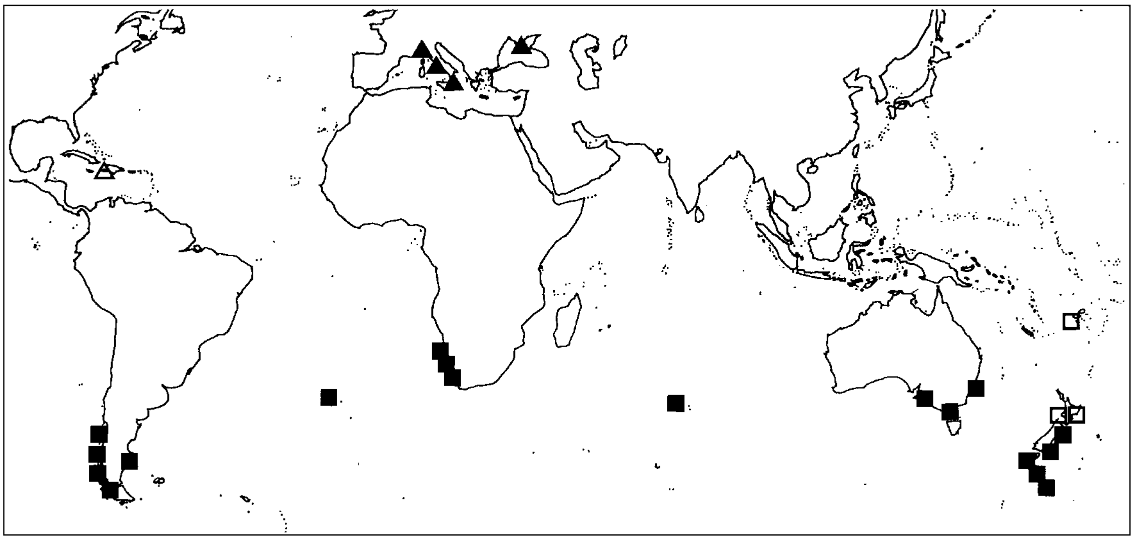

Figure 42. Distribution of *Namanereis minuta* n.sp. △, *N. pontica* ▲, *N. quadraticeps* species group ■, and *N. tiriteae* □; based on material examined and authenticated literature records.

Distribution. Type locality Hispaniola, Nallee Grande Anse. Other material from Grande Ravine du Sud; only known from Hispaniola (Fig. 42).

Etymology. From the L. *minutus*, meaning little or small, referring to the small body size of this species.

Namanereis pontica (Bobretzky) **n.comb.**

Figs. 1c, 42, 43a–e; Table 5

Lycastis pontica Bobretzky, 1872: 1–3, pl. XIV, figs. 1–5.
Lycastoides pontica.–Jakubova, 1930: 869.–Rullier, 1963: 239 (in part, list only).
Lycastoides pontica neapolitana Greca, 1950: 2–3.–Cognetti, 1962: 4.–Hamilton, 1970: 11 (list only).
Lycastopsis pontica neapolitana.–Tenerelli, 1964: 237–239.
Lycastopsis pontica.–Fredj, 1974: 58 (list only).–Perkins & Savage, 1975: 33 (in part, list only).

Material examined. NON-TYPE: Italy, Naples, Santa Lucia 3(ZMA V.Pol. 2897). Black Sea, det. A. Semènov, 1890, 1+1 near-complete headless specimen (ASL 2/21279). Four specimens measured.

Diagnosis. Antennae cirriform to subconical, smooth. Eyes 2 pairs. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type E (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.7–6.2 × longer than width of shaft head, very finely serrated, 15–20 teeth, teeth increasing in length slightly proximally.

Description. Non-type material well to moderately well preserved, including some complete individuals. 72–77 setigers, 9–12 mm long, 0.6–0.8 mm wide at setiger 10. At setiger 10 length of parapodia 0.32 × body width.

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat or concave. Colour in alcohol white or yellow-brown. Epidermal pigment absent.

Prostomium. Cleft absent anteriorly, shallow dorsal hollow. Prostomium shape hexagonal to half-circular; 2.1 × wider than long. Antennae cirriform to subconical, smooth, extending beyond tip of palpophore or short of tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs (faded in Black Sea specimen), black, arranged longitudinally or obliquely, posterior pair slightly smaller; lenses indistinct (Fig. 43a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.4–1.7 × length anteroventral. Anterodorsal tentacular cirri 0.9–1.0 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 2 (Fig. 43a). Jaws with single robust terminal tooth, 2–3 subterminal teeth, 3–4 teeth ensheathed proximally, brown (Fig. 43b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 43c,d). Dorsal cirri 0.83–1.4 × length of podium at setiger 3 (Fig. 43c), 0.64–1.1 × length of podium in mid-body, 0.53–0.77 × length of podium posteriorly; 2.0–2.1 × longer than wide posteriorly (Fig. 43d). Ventral cirri 0.58 length of podium at setiger 3, 0.18–0.25 length of podium posteriorly.

Setae. Supra-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.7–6.2 × longer than width of shaft head, very finely serrated, 15–20 teeth, 0.49–0.50 × total blade length, teeth increasing in length slightly proximally (Fig. 43e). Sub-neuroacicular falcigers in setiger 10 with blades very finely serrated; dorsal-most 4.7–5.8 × longer than width of shaft head, 15–20 teeth; ventral-most 4.2–5.3 × longer than width of shaft head, 12–17 teeth. Sub-neuroacicular falcigers in mid-

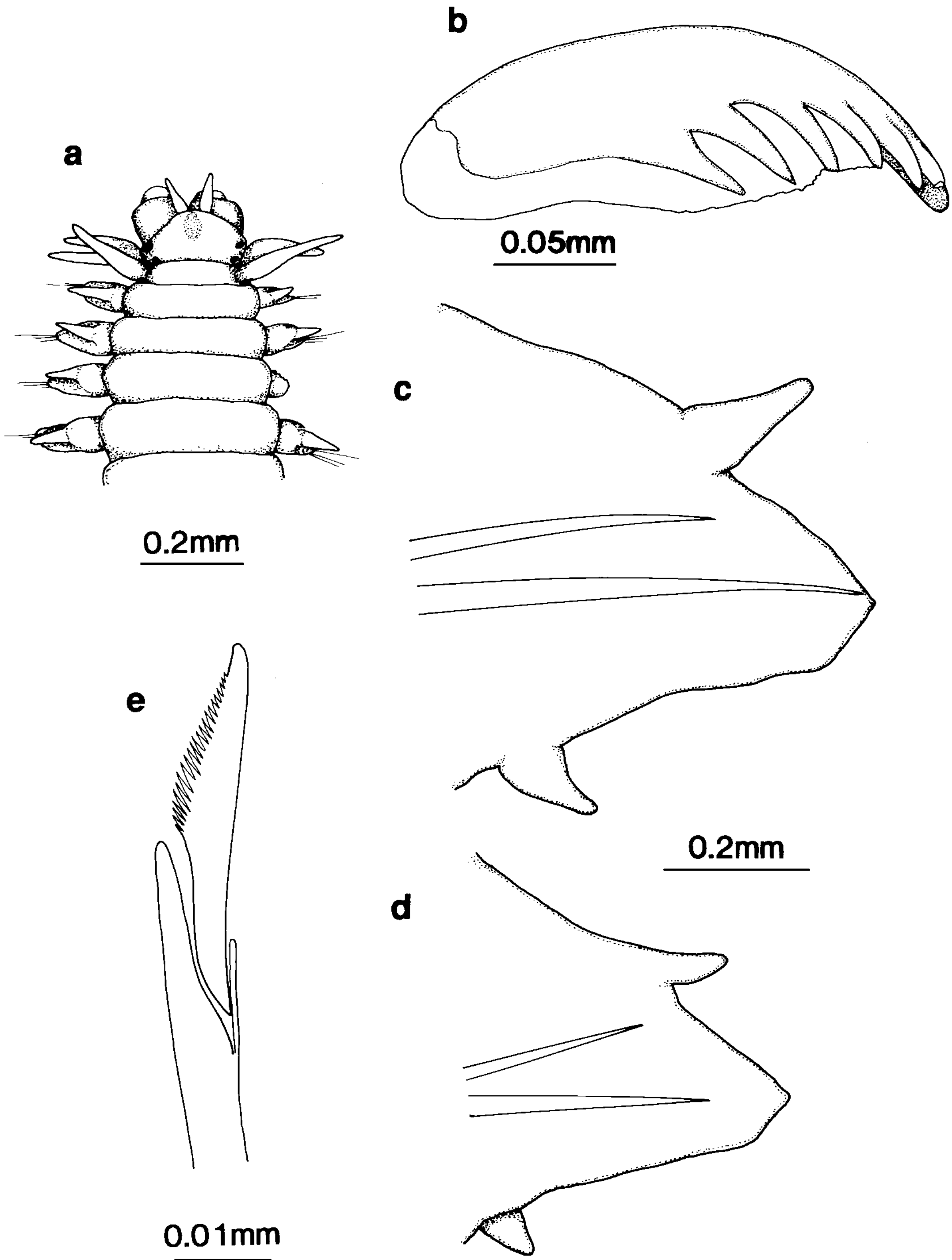

Figure 43. *Namanereis pontica* non-type (ZMA V.Pol. 2897): (*a*) anterior end, dorsal view, R.S. tentacular cirri obscured. Non-type (ASL 2/21279): (*b*) jaw piece, dorsal view; (*c*) parapodium from 11th setiger, L.S., anterior view; (*d*) parapodium from 60th setiger, R.S., posterior view; (*e*) supra-neuroacicular falciger, setiger 6.

posterior region with blades very finely serrated. Setae pale. Acicula in mid-body light brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 0.6–1.0 × width pygidium.

Remarks. The types of *Namanereis pontica* (Bobretzky) were not available for study. Bobretzky's types are not housed at the Zoological Institute, Academy of Sciences, Leningrad according to the Curator of Annelids, Dr Galina Buzhinskaja. As the types may be housed elsewhere in Russia, I am not designating neotypes for this species.

According to Bobretzky (1872), the characteristic features that distinguished *N. pontica* from the known species at that time (*Namalycastis brevicornis* and *Namanereis quadraticeps*), were the presence of 3 pairs of tentacular cirri and the absence of spinigers in the upper setal bundle (presumably notopodia). To this I can add the lack of supra-neuroacicular spinigers, which is unique within the Namanereidinae.

However, there has been some confusion in the literature as to whether or not *N. pontica* has supra-neuroacicular spinigers. Bobretzky's (1872) description is in Russian and probably was not available to some earlier workers. Greca (1950) and Tenerelli (1964) both held the view that the subspecies, *N. pontica neapolitana*, differed from the stem species in lacking supra-neuroacicular spinigers. Both erroneously considered *N. pontica* from the Bay of Sevastopol', Black Sea (also described by Jakubova, 1930) to possess supra-neuroacicular spinigers. *Namanereis pontica neapolitana* Greca therefore shares in common with *N. pontica pontica* the lack of supra-neuroacicular spinigers, and as this appears to be the only character putatively separating the two taxa, they are most likely conspecific. Specimens of *N. pontica neapolitana* identified by Greca (perhaps the types, but no locality or year of collection is indicated, C. Gambi, pers. comm., 1988), are housed in the collection of the Museum of the Stazione Zoologica, Naples. The specimens were unavailable to borrow.

In the species list of Rullier (1963) and the bibliography and checklist of Perkins & Savage (1975) the species is also confused. Rullier (1963) lists other records of *N. pontica* and *Namanereis* sp. from the Mediterranean, Black and Bosporus Seas, but it appears as though some of these may refer to *N. littoralis* sp. group, for example Greca (1949) and Banse (1959). *Namanereis littoralis* sp. group may be distinguished from *N. pontica* by the presence of supra-neuroacicular spinigers in the former and the absence of this type of seta in *N. pontica*. Both species co-occur in the Black and the Mediterranean Seas. The record of *Lycastopsis pontica* from the Azov Sea (Vinogradov, 1960) could not be verified.

The apparent similarity between *N. pontica* and *N. littoralis* sp. group was not borne out in the cladistic analysis. Unfortunately both species fall out in the part of the consensus tree that is highly unresolved (Figs. 5–7).

Habitat. There is no information on the type habitat. The species appears to be rare, occurring amongst dead *Zostera* on the shore in the surf zone (Jakubova, 1930) and in coarse sand of the coast (Greca, 1950). The habitat is therefore similar to that of *N. littoralis* sp. group.

Distribution. Type locality Black Sea, Sevastopol' Bay. Other records from the Mediterranean (Livorno, Gulf of Naples, Gulf of Catania) and the Black Sea, Sevastopol' Bay (Fig. 42). The species may also occur in the Azov Sea (Vinogradov, 1960).

Etymology. Bobretzky named the species after the L. *ponticus* meaning belonging to the Black Sea.

Namanereis quadraticeps (Blanchard in Gay) species group

Figs. 1c, 4c, 42, 44a–g; Table 5

Lycastis quadraticeps Blanchard in Gay, 1849: 24–25, fig. 7.–Quatrefages, 1865: 500.–Ehlers, 1897: 70 (in part); 1900: 214–215; 1901a: 121–122 (in part); 1901b: 260; 1913: 498.–Johnson, 1908: 371–380, figs. 1–5.–Benham, 1909: 242–244, pl. IX, figs. 2–10; 1950: 13.–Augener, 1918: 214–217, pl. 2, fig. 35, pl. 3, fig. 68, text fig. 17; 1924: 39–40.–Day, 1953: 424; 1954: 18; 1959: 523.–Fauvel, 1941: 283.–Wesenberg-Lund, 1962: 89.–Lowry, 1976: 46 (list only).

Lycastella quadraticeps.–Feuerborn, 1931: 638.

Lycastris [sic] *quadraticeps*.–Day, 1934: 38.

Namanereis quadraticeps.–Hartman, 1959a: 162–163; 1964: 97, pl. 31, figs. 10–12.–Hartmann-Schröder, 1962: 393–394; 1974: 147.–Day, 1967: 299, 301, fig. 14.2l–o.–Ringuelet, 1969: 207.–Knox & Cameron, 1970: 79–80.–Rozbaczylo, 1974: 4; 1975: 100–103, figs. 1, 2a–h; 1985: 84.–Orensanz, 1975: 31.–Butler *et al*., 1977: 42 (list only).–Straughan, 1981: 60 (list only).–Knox, Hicks & Bolton, 1985: 116 (list only).

Namanereis littoralis Hutchings & Turvey, 1982: 107–108, fig. 5a–d (specific name becomes a junior secondary homonym of *Namanereis littoralis* Grube, 1872).

Material examined. NEOTYPE: Chile, Straits of Magellan, just north of Bahia San Gregorio (52°34'S 70°10'W), coll. D. Straughan, January 1977 (AM W198509). NON-TYPE: Chile, locality as neotype 10(AM W198510); Puerto Espinal 18(SSM 1619); Sandy Point, Straits of Magellan 11(USNM 178878); Punta Arenas, Straits of Magellan 38(UUZM unreg.). Auckland Island, 7(HZM V9373), Port Ross 6(ZMUC POL-940); 36(ZMUC POL-941), Adams Island 1(ZMUC POL-944). Campbell Islands 5(OM IV163), 6(OM IV162); Perseverance Harbour 18(ZMUC POL-942); 1(ZMUC POL-943); 1(AM W20264). Australia, Victoria, Barwon River, exit of Lake Connewarre 1(NMV F 82869). Namibia, many (HZM V8777). St. Paul 5(ZMB 5839). 18 specimens measured.

Other material examined. South Africa, under Constable Hill on channel side of Langebaan 3(SAM A20335). *Namanereis littoralis* PARATYPES: South Australia, Garden Island near Port Adelaide, coll. Zool. Dept. University of Adelaide, 10.12.1977 2(AM W6774); New South Wales, Towra Point, Botany Bay, mud flat, coll. New South Wales Littoral Society, 27.6.1977 2(AM W12314). 7 specimens measured.

Diagnosis. Antennae subspherical, smooth. Tentacular cirri, 4 pairs. Eyes 2 pairs. Jaws with single robust terminal tooth. Notosetae present, sesquigomph spinigers. Neurosetae Type F (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 3.8 × longer than width of shaft head (3.7–4.9), coarsely serrated, 9 teeth (8–12), teeth increasing in length greatly proximally.

Description. Neotype well preserved, slight body wall damage, segmentally complete, no gametes in coelom. Other material well preserved, segmentally complete. 50 setigers (36–97), 11 mm long (9.2–54), 1.0 mm wide at setiger 10 (0.6–2.1). At setiger 10 length of parapodia 0.24 × body width (0.24–0.41).

Body. Uniform in width anteriorly, tapering in far posterior

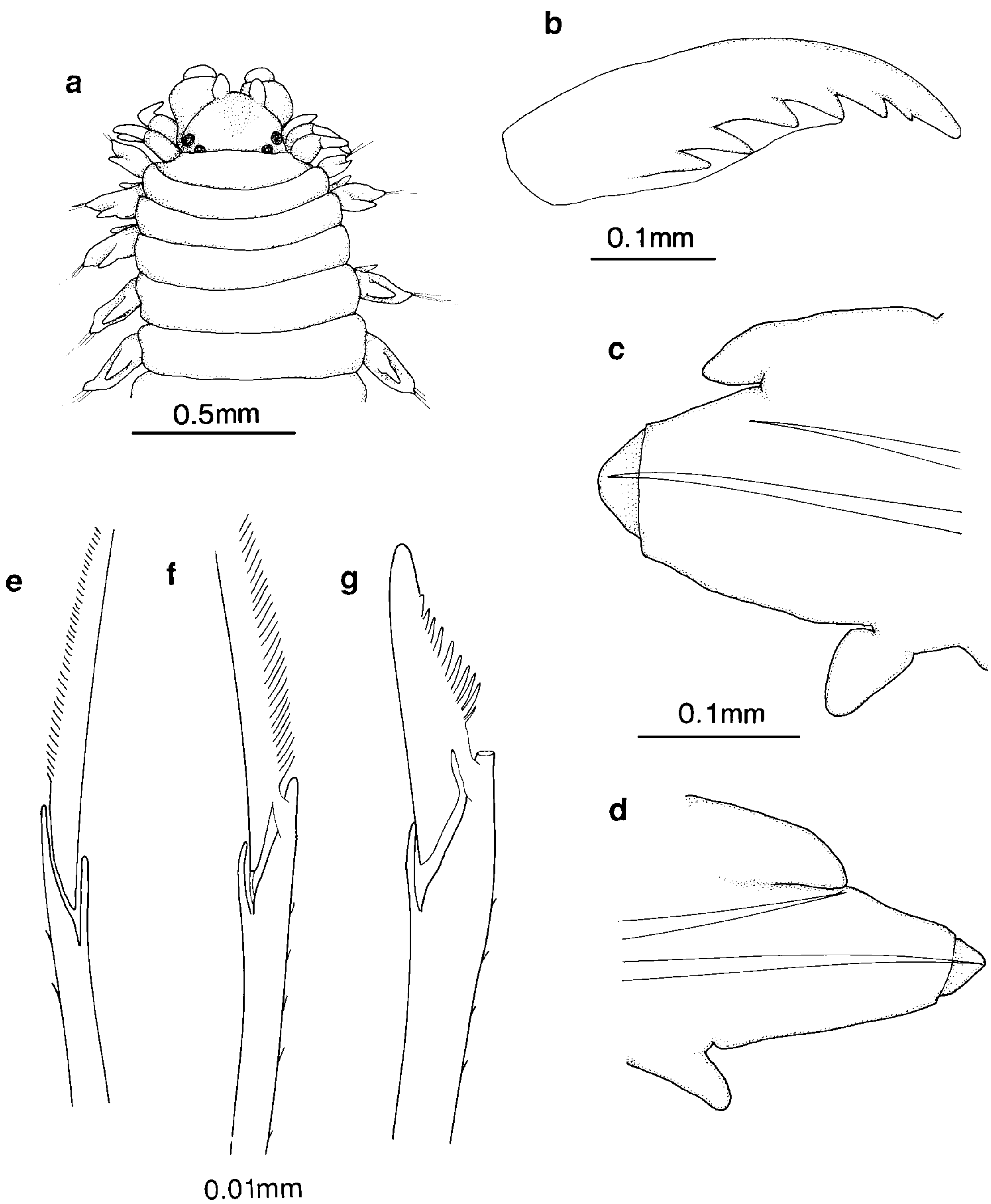

Figure 44. *Namanereis quadraticeps* neotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, R.S., anterior view; (*d*) parapodium from 50th setiger, R.S., posterior view. (*e*) Non-type (UUZM unreg.), notopodial sesquigomph spiniger, mid-body. Neotype: (*f*) supra-neuroacicular spiniger, setiger 10; (*g*) supra-neuroacicular falciger, setiger 10 (tip of boss broken).

region. Dorsum convex with lateral glandular swelling. Venter flat with shallow medial groove in neotype. Colour in alcohol yellow-white or yellow-brown (rarely).

Prostomium. Cleft absent anteriorly, with shallow-deep dorsal hollow. Prostomium shape hexagonal to half-circular; 1.5 × wider than long (1.2–1.8). Antennae subspherical, smooth, extending beyond tip of palpophore or short of tip of palpophore, aligned over inner edge of palps to over mid-palps. Eyes 2 pairs, black, purple or red (depending on intensity of pigment); arranged obliquely or longitudinally (rarely), equal in size; lenses present, though difficult to see in some material (Fig. 44a).

Peristomium. Tentacular cirri, 4 pairs, cirrophores generally well developed, although those of posteroventral pair less so; cirrostyles smooth. Anterodorsal tentacular cirri 1.4 × length anteroventral (0.9–2.1). Anterodorsal tentacular cirri

1.0 × length posterodorsal (0.8–1.1). Posterodorsal tentacular cirri 1.0 × length posteroventral (1.0–2.1). Posterodorsal tentacular cirri extending posteriorly to setiger 1–2 (rarely 2) (Fig. 44a). Jaws with single robust terminal tooth, 2 subterminal teeth (2–6), 4 teeth ensheathed proximally (2–5), brown, often lighter distally (Fig. 44b).

Parapodia. Acicular neuropodial ligule globular (Fig. 44c,d). Dorsal cirri 0.60 × length of podium at setiger 3 (0.53–1.1) (Fig. 44c), 0.73 × length of podium in mid-body (0.38–1.63), 0.69 × length of podium posteriorly (0.28–1.33); 1.67 × longer than wide posteriorly (0.63–2.0) (Fig. 44d). Ventral cirri 0.44 length of podium at setiger 3 (0.28–0.57), 0.26 length of podium posteriorly (0.32–0.40).

Setae. Notopodial sesquigomph spinigers from setiger 8 (4–11) (Table 5). Supra-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles. Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Notopodial sesquigomph spinigers with finely serrated blades (Fig. 44e). Heterogomph setae with boss not prolonged. Supra-neuroacicular heterogomph spinigers with finely serrated blades (Fig. 44f). Supra-neuroacicular falcigers in setiger 10 with blades 3.8 × longer than width of shaft head (3.7–4.9), coarsely serrated, 9 teeth (8–12), 0.44 × total blade length (0.35–0.48), teeth increasing in length greatly proximally (Fig. 44g). Sub-neuroacicular falcigers in setiger 10 with blades coarsely serrated (Fig. 4c); dorsal-most 3.6–4.9 × longer than width of shaft head, 8–12 teeth; ventral-most 3.8 × longer than width of shaft head (3.4–4.4), 8 teeth (8–10). Sub-neuroacicular falcigers in mid-posterior region with blades coarsely serrated. Setae pale or dark (rarely). Acicula in mid-body brown (lighter distally).

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe (pygidium sometimes drawn out slightly into funnel-shape). Anus terminal. Anal cirri arising ventrolaterally or laterally, papilliform (rarely approximately conical), smooth, 0.50 × width pygidium (0.25–0.60).

Sex. Hermaphrodite according to Johnson (1908). Mature oocytes 420–640 µm, straw-coloured, with external membrane. Epitokal setae absent. Nurse cells absent in ovigerous specimens (but see below).

Variation. Specimens from Auckland and Campbell Islands show following additional variation: 60–71 setigers, 15–31 mm long, 1.2–2.4 mm wide at setiger 10; dorsal cirri 0.77–2.2 × length of podium posteriorly; sub-neuroacicular falcigers, 3–7 in podium 30, 3–8 in podium 60; mature oocytes 690 µm; nurse cells in close association with developing oocytes. Specimen from Barwon River, southern Australia (NMV F 82869) is 49 setigers, 12 mm long, 1.1 mm wide at setiger 10; prostomium shape 1.1–1.7 × wider than long; anterior and posterior pairs of eyes arranged obliquely or transversely; supra-neuroacicular falcigers and sub-neuroacicular falcigers in setiger 10 with blades slightly less coarsely serrated than is typical; supra-neuroacicular falciger in setiger with serrated region of blade 0.28–0.44 × total blade length; ventral-most sub-neuroacicular falcigers in setiger 10 with blades having 7 teeth.

Remarks. Comprehensive accounts of this species are given in Rozbaczylo (1975) and Hutchings & Glasby (1985), the latter who designate a neotype from specimens collected by D. Straughan from the Straits of Magellan, Chile. According to both reports, the types of *Namanereis quadraticeps*, from Calbuco, Chile, were not preserved. Also Grube (1870) reports not finding this species in the MNHN, Paris.

The species is here considered as a species group because of the large amount of variation encountered in the present material. At the extreme end of the variation are specimens from New Zealand (Auckland and Campbell Islands) and southern Australia (Barwon River). Specimens from the Campbell Islands collected by G. Marriner, November 1907 (OM IV163) are those described by Benham (1909). The other specimens from there (OM IV162) collected by Benham himself, may represent the remaining material referred to in Benham (1909). However, the original label is in poor condition and difficult to read. Benham states that the eyes lack lenses, however I can discern a small reflective central area within each eyespot that I have interpreted as a lens. In addition, I find the anterior and posterior eyespots approximately the same size whereas Benham describes the anterior pair as being larger. As described under "Variation", these specimens and those of Auckland Island differ from the normal range of variation in the species group, in being much stouter, having a relatively longer dorsal cirri in posterior parapodia, a greater number of sub-neuroacicular heterogomph falcigers in the posterior parapodia, and having very large oocytes with attendant coelomic nurse cells. It is possible that these differences may reflect the advanced state of sexual maturity of these specimens, but they may also represent novel reproductive traits, and if so, the specimens deserve separate species status. Further study is clearly warranted, and until the situation is clarified I prefer the consider them part of a species group. Also the specimen from the Barwon River (Victoria) differs from the typical member of the species group in the fine details of the setae; the other Australian specimens from Port Adelaide (South Australia) and Towra Point (NSW) are however more representative of the species group.

The species has a complex taxonomic history. It was encountered by the many early expeditions to the Subantarctic and described as *Lycastis quadraticeps* (Quatrefages, 1865; Ehlers, 1897, 1900, 1901a,b, 1913; Augener, 1918). Most of the accounts however, apart from that of Quatrefages (1865), were relatively brief reports of its occurrence. The first well-illustrated description of the species was that of Benham (1909). His lateral and ventral views of the head clearly show 4 pairs of tentacular cirri; unfortunately the posteroventral pair of tentacular cirri was not shown in the dorsal view (his fig. 2). Hartman (1954) clearly thought that the species has only 3 pairs of tentacular cirri when she suggested that *N. quadraticeps* may be conspecific with the *Namanereis* species on the west coast of North America, which was known to have only 3 pairs (see also Orensanz, 1982). Hartman's (1964) reproduction of

Benham's (1909) dorsal view of the head probably also contributed to the later confusion about the number of pairs of tentacular cirri.

Hartman (1959a) considered *N. quadraticeps* to be a cosmopolitan species and suggested that nine distinct species were either synonymous with it, or referable to *Namanereis*: *Lycastis littoralis* Grube, 1872, *Lycastopsis beumeri* Augener, 1922; *Lycastoides pontica* Jakubova, 1930, *Lycastopsis catarractarum* Feuerborn, 1932, *L. amboinensis* Pflugfelder, 1933, *L. hummelincki* Augener, 1933b, *L. augeneri* Okuda, 1937, *L. tecolutlensis* Rioja, 1946 and *Namonereis* [sic] *kartaboensis* Treadwell, 1926. Examination of the type material, or material from near the type locality, of all nine species leads to the conclusion that none is synonymous with *N. quadraticeps*. The first eight species belong to the genus *Namanereis* as re-diagnosed here and the last species belongs to *Namalycastis*. Therefore, *N. quadraticeps* is not cosmopolitan as suggested by Hartman (1959a), but restricted to the Subantarctic and temperate shores of the Southern Hemisphere (southern Australia and Namibia, Africa). *Namanereis littoralis* described by Hutchings & Turvey (1982) from southern Australia is then the only junior synonym of *Namanereis quadraticeps*, though given its present species group status this conclusion must remain tentative.

As a result of the confusion over the number of pairs of tentacular cirri and the belief that the species had a cosmopolitan distribution, the species name became widely cited in the taxonomic literature. Incorrect references to *N. quadraticeps* include those of Baker (1929) for specimens from Gaua [now Santa Maria], Vanuatu (= *Namanereis* sp.); Fauvel & Rullier (1959) for specimens from Dakar, Senegal (= *Namalycastis senegalensis*); and Suárez & Fraga (1978) for specimens from Cuba (= *Namanereis* sp.). The following records of *Namanereis quadraticeps* are probably all referable to the *Namanereis littoralis* species group: Marinov (1966) from the Black Sea; Hartman (1968) from California; Katzmann (1972) from Yugoslavia; Banse & Hobson (1974) from British Colombia; Pozar-Domac (1978) from the Adriatic Sea; and Rowe (1980) from California.

It is notable that some polychaete workers (e.g., Day, 1934, 1953, 1954, 1959, 1967; Wesenberg-Lund, 1962; Rozbaczylo, 1974, 1975, 1985; Orensanz, 1975) were not influenced by Hartman's decisions, maintaining the correct view of the species as having 4 pairs of tentacular cirri and a southern temperate to Subantarctic distribution. These were people who, because of the nature of their past studies, would be very familiar with gondwanan polychaete fauna.

Namanereis quadraticeps is the sister species to all other extant species of *Namanereis* (Figs. 5–7). Its ancestor gave rise to all Namanereidinae, including the small-bodied forms that lack dorsal cirrophores and have a tripartite pygidium (*Namanereis* species), and the species having short subconical antennae and flattened leaf-like cirrophores on posterior parapodia (*Namalycastis* species). The many differences that *Namanereis quadraticeps* shows from other members of the genus may be attributed to its derivation from the stem namanereidine species and the consequent retention of many plesiomorphic traits (e.g., 4 pairs of tentacular cirri, presence of notosetae), combined with the autapomorphic features (e.g., peculiar globular antennae, presence of heterogomph spinigers in the supra-acicular fascicle of the neuropodia, and the combination of very large, yolky and spherical-shaped oocytes). Further undescribed species are likely to be found within the species complex. However, any new taxa will probably be found to be part of a monophyletic group together with *N. quadraticeps*.

Habitat. No habitat information was given in the type description (Blanchard in Gay, 1849); however, specimens collected about 30 km north of the type locality (Calbuco), at Islilla de Caullahuapi (near Puerto Montt) were found at the highest high tide level on the edge of a swamp, fed by a small river (Rozbaczylo, 1975). The worms were found under stones, pebbles and between the roots of littoral "gramineas" (wheat, etc.) in association with amphipods, the decapod *Cyclograpsus cinereus* Dana and collembol insects. Other habitat data from South America as follows: at Punta Arenas, littoral, under stones; in algae rhizoids (stranded by a storm); from 2 fathoms (3.7 m), sand bottom (Ehlers, 1897). Ushuaia in a freshwater lagoon; under stones at the mouth of a stream above high tide level (Ehlers, 1897). Puerto Bridges, 7 fathoms (12.9 m) (Ehlers, 1897). Punta Arenas and Puerto Novo, beach at low tide (Ehlers, 1900). Lapataia, under stones on shore (Ehlers, 1901b). Puerto Deseado, S. Argentina, mid-littoral, 1733 individuals per square metre (Ringuelet, 1963 *fide* Arnaud, 1974).

Elsewhere in the Southern Ocean the species has been found on a beach at the low tide level at St. Paul, S. Indian Ocean (Ehlers, 1913); under stones at low tide level at Namibia, Lüderitz Bay (Augener, 1918) and in sand associated with *Laminaria* (Hartmann-Schröder, 1974).

The species is common of the shores of Auckland and Campbell Islands according to Augener (1924) where it occurs on the shore above high water mark, traversed by (presumably) freshwater oozing through the earth; also in sea pools (Benham, 1909). On the Snare Islands the species occurs in the upper eulittoral zone rock crevices and in Otago Harbour and on the Kaikoura Peninsula (New Zealand South Island) it lives in clay banks (Knox & Cameron, 1970; Knox *et al*., 1985). Lowry's (1976) specimens were collected in 11–14.6 metres off Auckland Island.

In Australia, the species is associated with mangroves, often in the supralittoral zone according to Hutchings & Turvey (1982). The Barwon River specimen was found in the channel, about 4 m deep, in muddy substrata with some organic material, salinity 13.7–14.1‰.

Distribution. Neotype locality Chile, Straits of Magellan, just north of Bahia San Gregorio. South-west South America from Puerto Montt, Chile (41°28'S) to Cape Horn (55°59'S); Argentina, Puerto Deseado. South West Africa from Lüderitz Bay, Namibia (26°38'S) to Langebaan Lagoon, South Africa (33°06'S). Also Tristan da Cunha, S. Atlantic Ocean. St. Paul Is., S. Indian Ocean. New Zealand, South Island, Campbell Is., Auckland Is., Snare Is. Australia, NSW, Victoria and South Australia (Fig. 42).

Etymology. Unknown.

Namanereis riojai (Bastida-Zavala) **n.comb.**

Figs. 1c, 45a–g, 46; Table 5

Lycastopsis riojai Bastida-Zavala, 1990: 417–419, fig. 1a–f.

Material examined. PARATYPES: Mexico, BCS, Bahia de La Paz, Pardito Island, 24°52'N 110°38'W, coll. 5 August 1987 2(USNM 128302).

Other material examined. NON-TYPE: Mexico, BCS, Bahia de Los Angeles, Isla Smith 2(CAS 015522); Bahia de La Paz, Playa El Caimancite 2(AM W20279), Muelle Fiscal 2(AM W20280). Six specimens measured.

Diagnosis. Large species, up to 32 mm long for 130 setigers, 1.7 mm wide at setiger 10. Venter concave. Antennae cirriform, smooth. Eyes 2 pairs, posterior pair slightly smaller. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth, which is broad with corrugated ventral surface. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 2.8–3.5 × longer than width of shaft head, moderately serrated, 8 teeth, teeth increasing in length slightly proximally, serrated region of blade 0.32–0.39 × total blade length.

Description. Paratypes in good condition, some setal damage, segmentally complete, no gametes in coelom. 64–78 setigers, 8–12 mm long, 0.7–0.8 mm wide at setiger 10. At setiger 10 length of parapodia 0.21 × body width.

Body. Uniform in width anteriorly, tapering gradually posteriorly. Dorsum convex. Venter concave. Colour in alcohol yellow-white. Epidermal pigment absent.

Prostomium. Cleft absent anteriorly, with no dorsal groove or hollow. Prostomium shape hexagonal to half-circular; 2.0 × wider than long. Antennae cirriform, smooth, extending beyond tip of palpophore or short of tip of palpophore, aligned over inner edge of palps. Eyes 2 pairs, black, arranged longitudinally or obliquely, posterior pair slightly smaller; lenses absent (Fig. 45a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.0–1.2 × length anteroventral. Anterodorsal tentacular cirri 1.0 × length posterodorsal. Posterodorsal tentacular cirri extending posteriorly to setiger 2 (Fig. 45a). Jaws with single robust terminal tooth which is broad with corrugated ventral surface, 1 subterminal teeth, 4 teeth ensheathed proximally, yellow (Fig. 45b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 45c). Dorsal cirri 0.57 × length of podium at setiger 3 (Fig. 45c), 0.43 × length of podium in mid-body, 0.62 × length of podium posteriorly; 1.7 × longer than wide posteriorly (Fig. 45d). Ventral cirri 0.34 × length of podium at setiger 3, 0.25 × length of podium posteriorly.

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.3 × length of collar (Fig. 45e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 3.5 × longer than width of shaft head, moderately serrated, 8 teeth, 0.33 × total blade length, teeth increasing in length slightly proximally (Fig. 45f). Sub-neuroacicular falcigers (dorsal and ventral ones) in setiger 10 with blades moderately serrated; 3.0–3.4 × longer than width of shaft head, 5–8 teeth. Sub-neuroacicular falcigers in mid-posterior region with blades moderately serrated (Fig. 45g). Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 0.2 × width pygidium.

Variation. Specimens from La Paz and Bahia de Los Angeles range in size from 86–130 setigers, 24–32 mm long, 1.3–1.7 mm wide at setiger 10; dorsal cirri 0.83–1.1 × longer than wide posteriorly; supra-neuroacicular falcigers in setiger 10 with blades 2.8–3.4 × longer than width of shaft head, serrated region of blade 0.32–0.39 × total blade length; dorsal-most sub-neuroacicular falcigers in setiger 10 with blades 2.6–2.8 × longer than width of shaft head, ventral-most 2.5–3.1 × longer than width of shaft head.

Remarks. *Namanereis riojai* resembles closely members of the *N. littoralis* species group, however, the two species can be differentiated on setal form. Specifically, the falcigers of *N. riojai* have very short blades in relation to the width of the shaft head and relatively few teeth occurring on the proximal part of the blade. The common occurrence of worn setal tips (Fig. 45g) possibly indicates a long-lived species and/or heavy use of parapodia and setae, perhaps due to crawling on hard or abrasive substrata (the parapodia are oriented ventrolaterally as a result of a deeply concave venter). Setae that were badly distorted through wear were not measured; rather measurements were taken from the pre-emergent setae, which appeared not to differ significantly, dimensionally or in the number or serrations, from emergent ones.

Namanereis riojai is among the more plesiomorphic species of the *Namanereis* clade, but precise sister group relationships could not be established (Figs. 5–7). Nevertheless, a close relationship with *N. littoralis* is expected. This possibility was overlooked by Bastida-Zavala (1990) who did not compare his species with the description or the types of *N. littoralis*. The widespread *N. littoralis* species group is here described as occurring on the Pacific coast of North America from Monterey Bay in the north to San Diego in the south, and perhaps as far south as Ensenada, Mexico (see also Orensanz (1982) who refers to the species as *Lycastopsis augeneri*). *Namanereis littoralis* has not been recorded from the Gulf of California and therefore may not be sympatric with *N. riojai*.

Habitat. Type habitat given only as intertidal (Bastida-Zavala, 1990). Non-type material collected from a "kelp

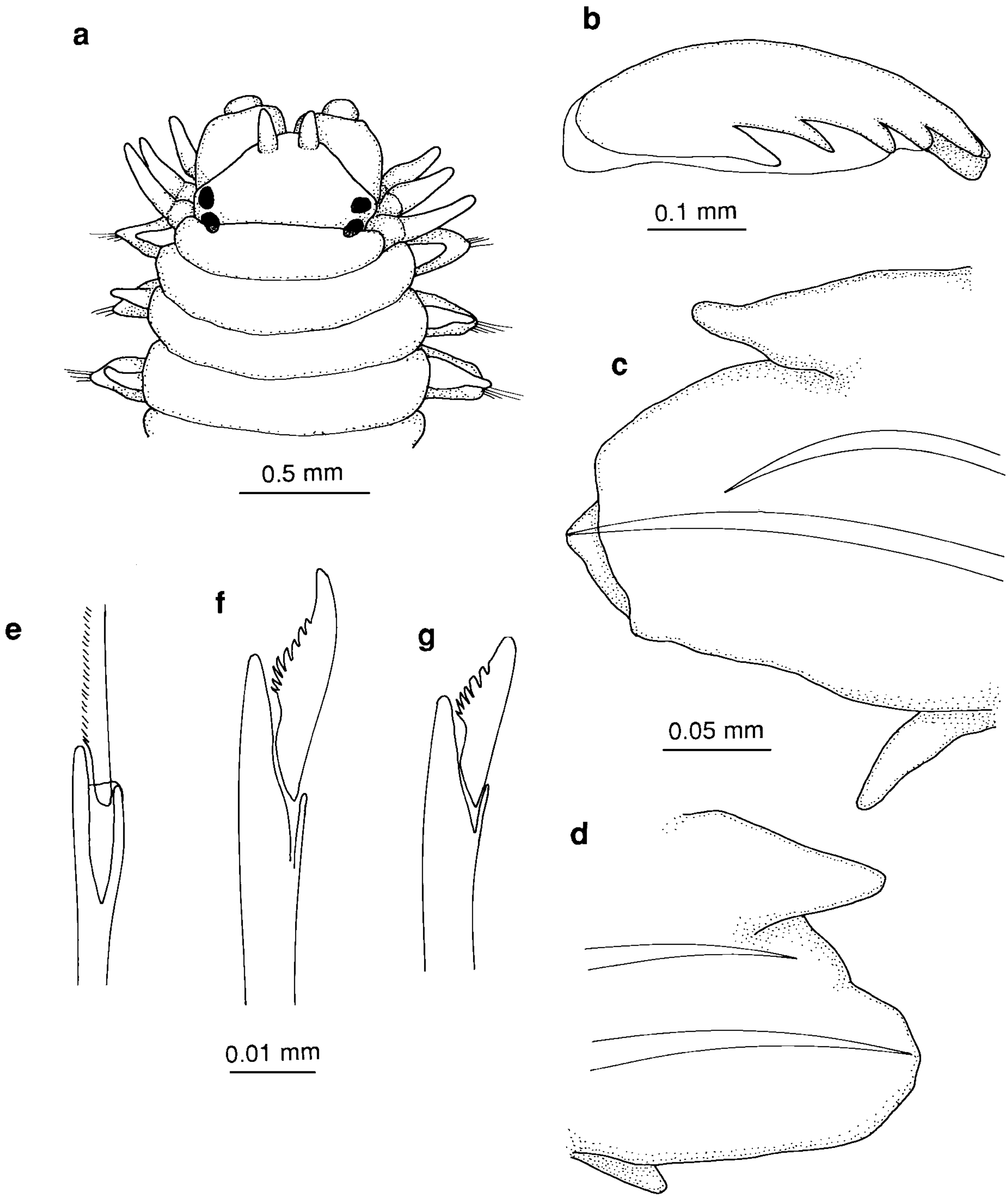

Figure 45. *Namanereis riojai* paratype (USNM 128302): (*a*) anterior end, dorsal view; (*b*) jaw piece, dorsal view; (*c*) parapodium from 9th setiger, L.S., posterior view; (*d*) parapodium from 60th setiger, R.S., posterior view (tip of acicular ligule retracted); (*e*) supra-neuroacicular spiniger, setiger 9 (pre-emergent); (*f*) supra-neuroacicular falciger, setiger 9 (pre-emergent); (*g*) sub-neuroacicular falciger, setiger 60, showing slightly worn blade.

bed". Whether the kelp was growing subtidally or was stranded on the beach is not known.

Distribution. Type locality Bahia de La Paz (El Pardito Island), Mexico. Also known from Bahia de Los Angeles (Fig. 46).

Etymology. Bastida-Zavala named the species in honour of Enrique Rioja, a Spanish biologist who contributed significantly to the knowledge of Mexican polychaetes, including the description of a namanereidine species, *Lycastopsis tecolutlensis*, herein a junior synonym of *Namanereis amboinensis*.

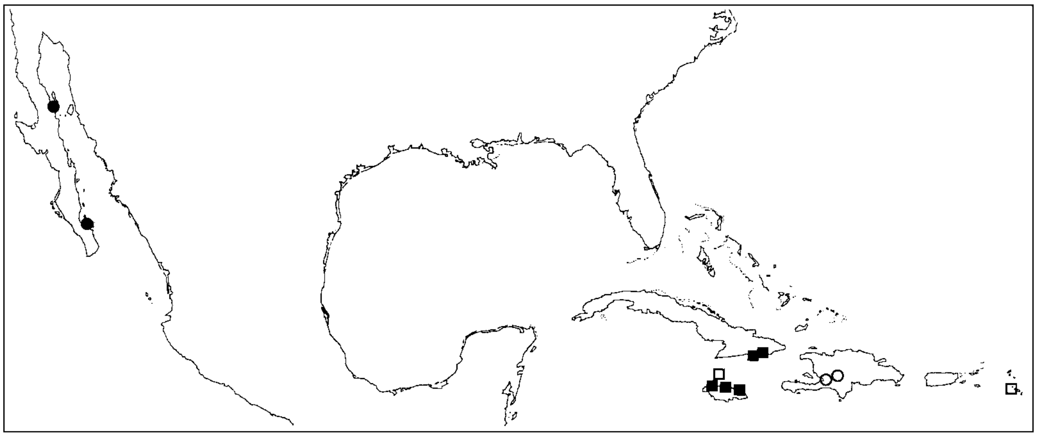

Figure 46. Distribution of *Namanereis riojai* ●, *N. serratis* n.sp. ○, *N. stocki* n.sp. ■, and *N. sublittoralis* n.sp. □; based on material examined and authenticated literature records.

Namanereis serratis n.sp.

Figs. 1c, 46, 47a–f; Table 5

Material examined. HOLOTYPE: Caribbean, Hispaniola, Etang Saumâtre (19°00'N 72°05'W), West Ind. Eil. Exp. (J.H. Stock) 79–527, coll. Botosaneanu and Notenboom, 9.XI.1979 (ZMA V.Pol. 2780). PARATYPES: collected on same expedition as holotype. Hispaniola, Etang Saumâtre, 79–527 many(ZMA V.Pol. 2890); 79–528 many(ZMA V.Pol. 2804); Balisaille Brook, 79–529 1(ZMA V.Pol. 2805); Luc Pierre Well, 79–618, 1(ZMA V.Pol. 2818); Boucancanie River [= Boucan Kani Rivière], 79–623, 1(ZMA V.Pol. 2817). 11 specimens measured.

Diagnosis. Antennae cirriform, usually smooth. Eyes absent. Tentacular cirri, 3 pairs. Jaws with bifid terminal teeth. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.2–4.9, rarely 3.8–5.2), coarsely serrated (moderately serrated in smallest specimen), 8 teeth (6–11), teeth increasing in length greatly proximally.

Description. Holotype well preserved, segmentally complete, mature oocytes in coelom. Other material well preserved, segmentally complete. 77 setigers (32–75), 13.5 mm long (4.4–15.8), 1.0 mm wide at setiger 10 (0.50–1.05). At setiger 10 length of parapodia 0.43 × body width (0.30–0.43, to 0.53 in smallest specimen).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol yellow-brown, yellow-white or dark brown. Epidermal pigment absent (rarely with some brown pigment on dorsum of last few segments).

Prostomium. Cleft absent anteriorly (rarely present), with shallow dorsal hollow. Prostomium shape roughly trapezoidal or hexagonal to half-circular; 2.0 × wider than long (1.8–2.2). Antennae cirriform, smooth or jointed (rarely), extending beyond tip of palpostyle, aligned over inner edge of palps. Eyes absent (Fig. 47a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth or faintly jointed. Anterodorsal tentacular cirri 1.5 × length anteroventral (1.2–2.0). Anterodorsal tentacular cirri 0.7 × length posterodorsal (0.7–1.0). Posterodorsal tentacular cirri extending posteriorly to setiger 4 (3) (Fig. 47a). Jaws with bifid terminal teeth (very short in holotype, longer in some paratypes), 0 subterminal teeth (though 1 or 2 low serrations occasionally present, perhaps due to wear), 0 teeth ensheathed proximally, brown (Fig. 47b).

Parapodia. Acicular neuropodial ligule very small, subconical (Fig. 47c,d). Dorsal cirri 2.1 × length of podium at setiger 3 (1.1–2.4) (Fig. 47c), 0.91 × length of podium in mid-body (0.91–1.2), 1.3 × length of podium posteriorly (1.4–1.8); 3.0 × longer than wide posteriorly (2.6–3.2) (Fig. 47d). Ventral cirri 0.50 length of podium at setiger 3 (0.41–0.64, rarely to 0.78), 0.47 length of podium posteriorly (0.31–0.58).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.8 × length of collar (1.7–2.1) (Fig. 47e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.2–4.9, rarely 3.8–5.2), coarsely serrated (moderately serrated in smallest specimen), 8 teeth (6–11), 0.54 × total blade length (0.45–0.58), teeth increasing in length greatly proximally (Fig. 47f). Sub-neuroacicular falcigers in setiger 10 with blades coarsely serrated (moderately serrated in smallest specimen); dorsal-most 4.2 × longer than width of shaft head (3.8–4.7), 7 teeth (6–10); ventral-most 4.5 × longer than width of shaft head (3.8–4.4), 7 teeth (6–10). Sub-neuroacicular falcigers in mid-posterior region with blades coarsely serrated (uniformly moderately serrated in smallest specimen). Setae pale. Acicula in mid-body dark brown.

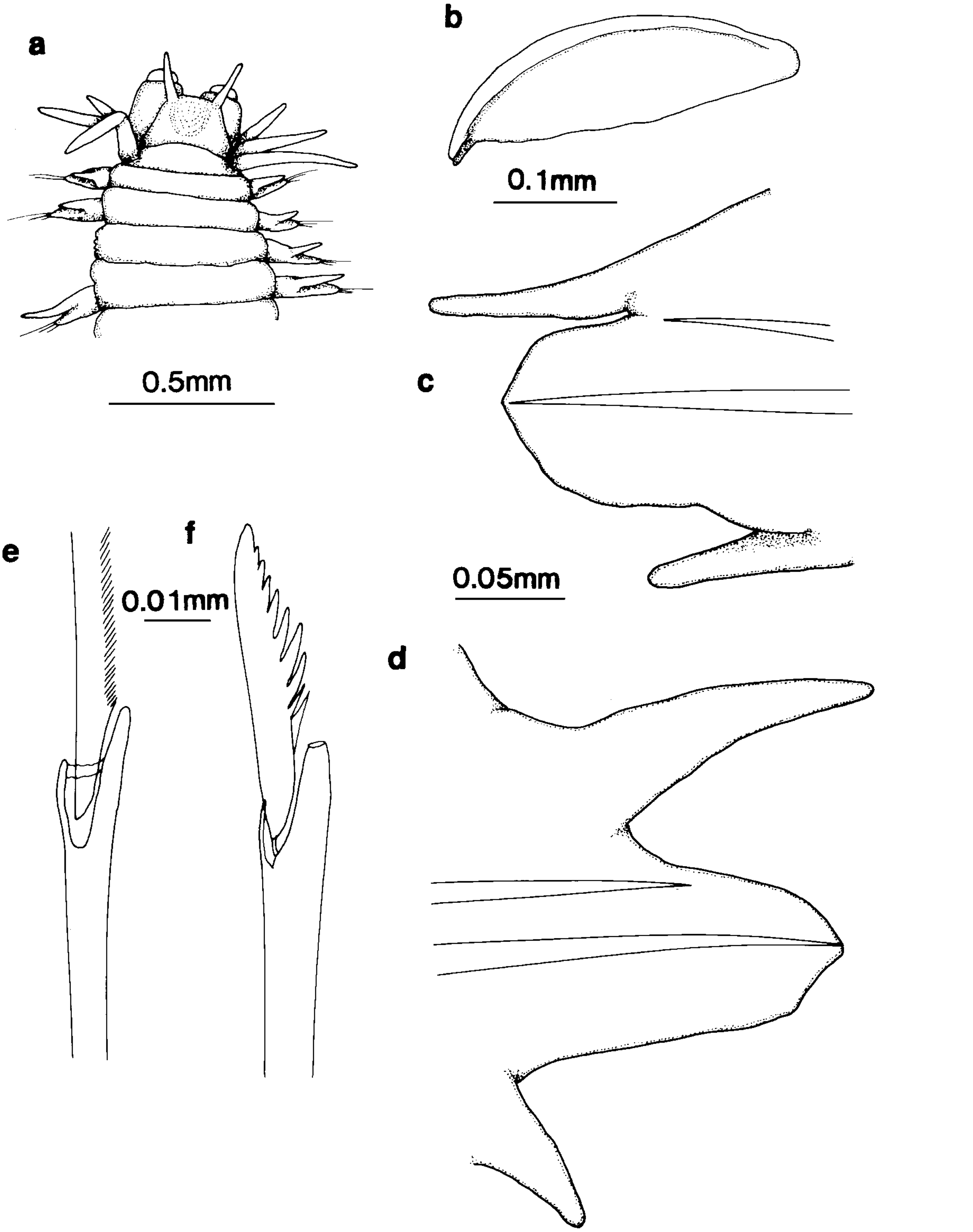

Figure 47. *Namanereis serratis* n.sp. holotype: (*a*) anterior end, dorsal view; (*b*) jaw piece, ventromedial view. Paratype (ZMA V.Pol. 2890): (*c*) parapodium from 3rd setiger, L.S., posterior view. Holotype: (*d*) parapodium from 60th setiger, R.S., anterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10 (tip of boss broken).

Pygidium. Pygidium tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising ventrolaterally or laterally, approximately conical, smooth or articulated (rarely), 1.3 × width pygidium (1.0–2.0).

Sex. Mature oocytes 280 µm (240–344, range of means for 2 specimens), brown, with external membrane. Epitokal setae absent.

Remarks. In terms of overall similarity, *Namanereis serratis* n.sp. closely resembles *N. hummelincki* and *N. cavernicola* and *N. stocki* n.sp. The cladistic analysis bears out this similarity indicating that *N. serratis* n.sp. is the sister species to these other species (Figs. 5–7). All four species have terminally bifid jaws, moderately long tentacular and dorsal cirri, and lack eyes. *Namanereis serratis* n.sp. differs from these species however, in lacking subneuropodial heterogomph spinigers and/or heterogomph pseudospinigers, and in having falcigers with coarsely serrated blades. It also differs from *N. stocki* n.sp. in having 3 rather than 4 pairs of tentacular cirri.

Habitat. The holotype habitat is unknown. The specimen from Luc Pierre well found in freshwater with chlorinity 100.6 mg Cl/l (salinity = 0.2‰).

Distribution. Type locality Caribbean, Hispaniola (Fig. 46).

Etymology. From the L. *serra*, f., meaning saw referring to the coarsely serrated, saw-like nature of the falciger blades.

Namanereis stocki n.sp.

Figs. 1c, 46, 48a–g; Table 5

Namanereis hummelincki.–Hartmann-Schröder, 1973: 96–97, figs. 18–20 (in part); 1977: 58–60, figs. 21–24 (in part). *Non* Augener.

Material examined. HOLOTYPE: Jamaica, St. Ann's Great River (St. Ann's Bay) at bridge (18°25'44"N 77°06'32"W), 82–114, 21.3.1982, (ZMA V.Pol. 2859). PARATYPES: Jamaica, locality details as for holotype 1(ZMA V.Pol. 2891); Montego River by Porto Bello, 82–108 1(ZMA V.Pol. 2825); Broadgate, Wag Water River, 79–51 14(ZMA V.Pol. 2860); Brays River bridge, 79–49 3(ZMA V.Pol. 2826). NON-TYPES: as *Namanereis hummelincki* Cuba, Rio Sabanilla 2(HZM P16518); Arroyo Guabavo 7(HZM P16517); Arroyo Seboruquito [= Arroyo Seboruco] 6(HZM P16519). Hispaniola, 79–581 2(ZMA V.Pol. 2815); 79–582 1(ZMA V.Pol. 2885); 79–580 3(ZMA V.Pol. 2824). 11 specimens measured.

Other material examined. Jamaica, 82–111 1(ZMA V.Pol. 2883); Orange River 1(ZMA V.Pol. 2858). Hispaniola, Cave "Source Diamant" 11(ZMA V.Pol. 2814); Cynodier, Reociene 13(ZMA V.Pol. 2813).

Diagnosis. Antennae subconical, smooth. Eyes absent. Tentacular cirri, 4 pairs. Jaws with bifid terminal teeth. Notosetae absent. Neurosetae Type D (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.0–4.7), moderately or finely serrated, 11 teeth (9–14), teeth increasing in length slightly proximally.

Description. Holotype well preserved, segmentally complete, mature oocytes in coelom. Other material well-moderately well preserved (HZM P16518 dehydrated), including some complete individuals. 80 setigers (55–97), 17 mm long (6.7–22), 0.85 mm wide at setiger 10 (0.70–0.95). At setiger 10 length of parapodia 0.44 × body width (0.44–0.60).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter convex or flat. Colour in alcohol yellow-white or yellow-brown. Epidermal pigment absent.

Prostomium. Very shallow cleft anteriorly, with shallow dorsal hollow or narrow longitudinal groove extending from tip to mid-posterior prostomium. Prostomium shape roughly trapezoidal or roughly triangular (also heart-shaped); rarely slightly indented laterally; 1.6 × wider than long (1.5–2.1). Antennae subconical, smooth, extending beyond tip of palpophore or beyond tip of palpostyle or short of tip of palpophore (rarely), aligned over inner edge of palps. Eyes absent (Fig. 48a).

Peristomium. Tentacular cirri, 4 pairs, cirrophores indistinct; cirrostyles faintly jointed. Anterodorsal tentacular cirri 1.5 × length anteroventral (1.3–2.0). Anterodorsal tentacular cirri 0.5 × length posterodorsal (0.4–0.7). Posterodorsal tentacular cirri 2.0 × length posteroventral (1.5–2.2). Posterodorsal tentacular cirri extending posteriorly to setiger 5 (3–9) (Fig. 48a). Jaws with bifid terminal teeth (subequal in types), 0 subterminal teeth, 4 teeth ensheathed proximally (2–6), brown or yellow (Fig. 48b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 48c,d). Dorsal cirri similar in length throughout; 1.4 × length of podium at setiger 3 (0.9–1.4) (Fig. 48c), 1.3 × length of podium in mid-body (0.7–1.6), 1.3 × length of podium posteriorly (1.2–2.1); 2.8 × longer than wide posteriorly (2.2–3.6) (Fig. 48d). Ventral cirri 0.50 length of podium at setiger 3 (0.34–0.57), 0.32 length of podium posteriorly (0.32–0.42).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers, pseudospinigers and/or spinigers in a graded series in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.8 × length of collar (1.5–1.8) (Fig. 48e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 4.6 × longer than width of shaft head (4.0–4.7), moderately or finely serrated, 11 teeth (9–14), 0.49 × total blade length (0.39–0.54), teeth increasing in length slightly proximally (Fig. 48f). Sub-neuroacicular falcigers in setiger 10 with blades moderately or finely serrated; dorsal-most 7.0 × longer than width of shaft head (6.8–10.7, rarely to 4.7), 32 teeth (12+) (Fig. 48g); ventral-most 4.3 × longer than width of shaft head (3.5–4.8), 2 teeth (3–13). Setae pale or dark (rarely). Acicula in mid-body brown.

Pygidium. Pygidium with multi-incised rim or tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe (pygidium slightly inflated in holotype). Anus terminal. Anal cirri arising ventrolaterally, approximately conical, faintly articulated or smooth, 2.0 × width pygidium (1.5–2.5).

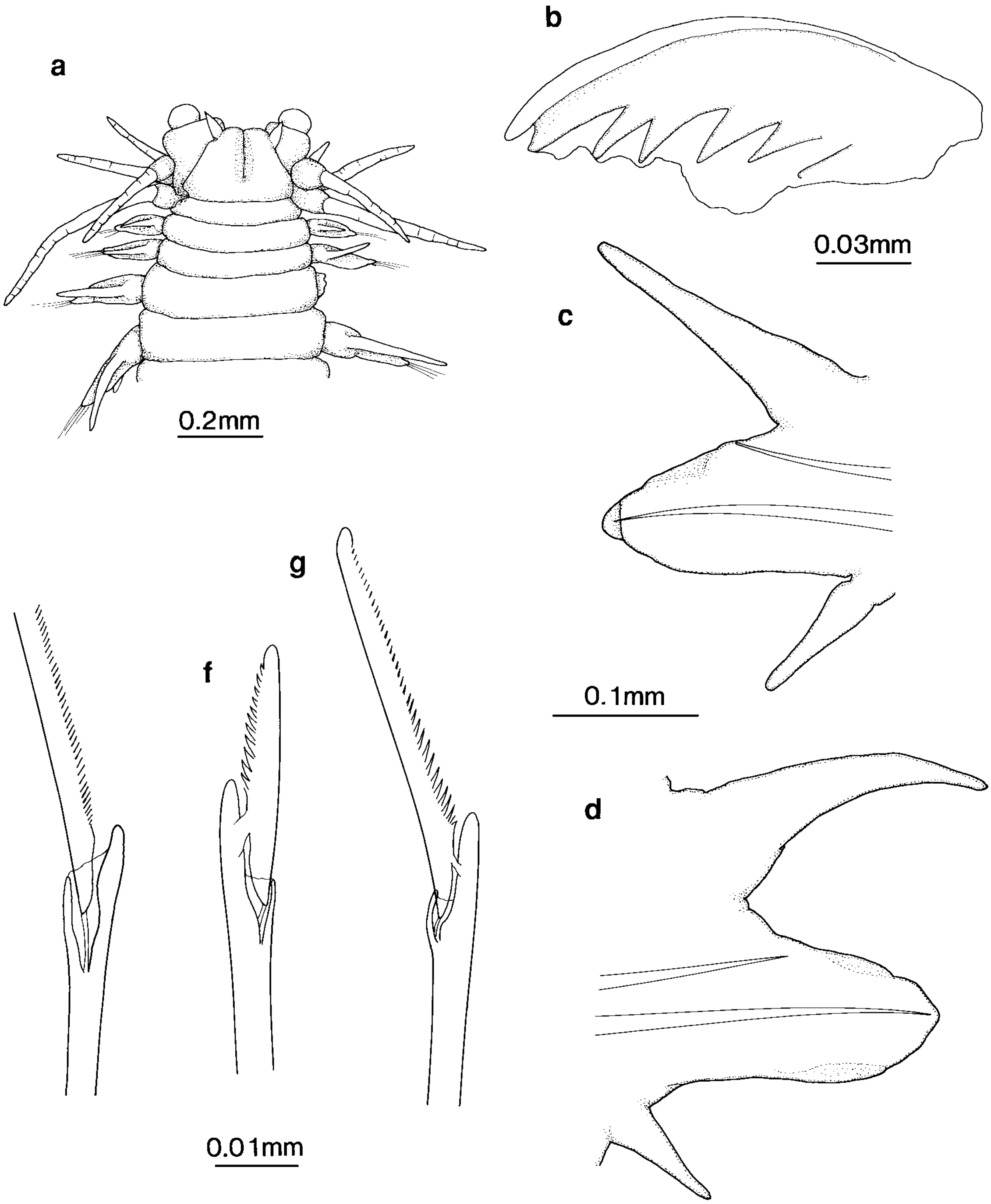

Figure 48. *Namanereis stocki* n.sp. holotype: (*a*) anterior end, dorsal view. (*b*) Paratype (ZMA V.Pol. 2860), jaw piece, ventromedial view. Holotype: (*c*) parapodium from 3rd setiger, R.S., anterior view; (*d*) parapodium from 60th setiger, R.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular falciger (dorsal-most), setiger 10.

Sex. Mature oocytes very large (greater than 300 µm), though in poor condition. Epitokal setae absent.

Remarks. This new species has been confused by Hartmann-Schröder (1973) with *Namanereis hummelincki*, hence the "in part" in the synonymies. Hartmann-Schröder (1973) considered that the forms with 3 pairs of tentacular cirri (*N. hummelincki*) and the forms with 4 pairs (*Namanereis stocki* n.sp.) were conspecific, with the differences reflecting variability between populations. In a later paper on *N. hummelincki* she attributed the variation in the number of pairs of tentacular cirri to size—animals less than 8.5 mm long having 4 pairs, and those greater than 11 mm long having 3 pairs, through reduction of the posterior ventral tentacular cirrus (Hartmann-Schröder, 1977). The specimens referred to in that paper as having 3 pairs of tentacular cirri are here described as a separate species, *N. cavernicola*. Hartmann-Schröder (1980) rejected previous ideas (1973, 1977) regarding variability in the number of pairs of tentacular cirri, after finding a juvenile (13 segments, 1.4 mm long) of *N. hummelincki* with 3 pairs of tentacular cirri.

I conclude that the observed differences in the number of pairs of tentacular cirri are not size-related or related to geographic variation, rather they are species-specific differences associated with at least two closely related species. The material examined here varies in size from 10 setigers (HZM P16519) to 97 setigers (ZMA V.Pol. 2826) and includes a sexually mature male and sexually mature females. I found no evidence of reduction of the posterior ventral tentacular cirri in any of the specimens. *Namanereis stocki* n.sp. has 4 pairs of tentacular cirri from the early juvenile stage (10 setigers, at least) though to adulthood.

Habitat. The details of the holotype habitat are unknown, although all type material appears to be riverine. Cuban material from subterranean freshwater rivers, up to 6 km from the sea, 10–20 m above sea level, in sand and fine gravel (Hartmann-Schröder, 1977). Hispaniolan material from springs and wells, salinity 0.05–5.9‰.

Distribution. Type locality Jamaica. Other records from Cuba and Hispaniola (Fig. 46).

Etymology. Named in honour of the late J. Stock (ZMA) who kindly allowed me to describe the ZMA collection of Caribbean Namanereidinae, which included four new species.

Namanereis sublittoralis n.sp.

Figs. 1c, 46, 49a–f; Table 5

Material examined. HOLOTYPE: Caribbean, Sint Eustatius (17°33'N 63°00'W), Smoke Alley Well, "Plancius Exp." 86–111, 9.III.1986 (ZMA V.Pol. 2848). PARATYPE: Sint Eustatius, locality as for holotype 2(ZMA V.Pol. 2839). NON-TYPE: Jamaica, Rio Secco 10(ZMA V.Pol. 2838), 1(ZMA V.Pol. 2849); Discovery Bay 4(ZMA V.Pol. 2840). 9 specimens measured.

Diagnosis. Antennae cirriform, smooth. Prostomial cleft absent anteriorly. Eyes 2 pairs, very small and closely set (may be coalesced) or absent (holotype). Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth. Notosetae absent. Neurosetae Type C (Fig. 1c). Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.7 × length of collar (1.5–1.9). Supra-neuroacicular falcigers in setiger 10 with blades 6.0 × longer than width of shaft head (4.9–6.0), finely serrated, 15 teeth (11–13), teeth increasing in length greatly proximally.

Description. Holotype well preserved, segmentally complete, no gametes in coelom. Other material well to moderately-well preserved, including some complete individuals. 54 setigers (31–38), 11.5 mm long (4.0–5.0), 0.8 mm wide at setiger 10 (0.55–0.75). At setiger 10 length of parapodia 0.32 × body width (0.30–0.47).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter flat. Colour in alcohol yellow-white or brown. Epidermal pigment absent.

Prostomium. Cleft anteriorly absent, with shallow dorsal hollow present or absent. Prostomium shape hexagonal to half-circular; 1.9 × wider than long (1.9–2.4). Antennae cirriform, smooth, extending beyond tip of palpophore or beyond tip of palpostyle, aligned over inner edge of palps. Eyes 2 pairs (very small and closely set, or coalesced) or absent (holotype), black, arranged longitudinally or transversely, posterior pair slightly smaller; lenses absent (Fig. 49a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth or faintly jointed (rarely). Anterodorsal tentacular cirri 1.3 × length anteroventral (1.1–1.5). Anterodorsal tentacular cirri 0.9 × length posterodorsal (0.7–1.1). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (1–2) (Fig. 49a). Jaws with single robust terminal tooth, 2 subterminal teeth (1–2), 3 teeth ensheathed proximally (2–3), brown (Fig. 49b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 49c,d). Dorsal cirri 1.2 × length of podium at setiger 3 (0.48–1.3) (Fig. 49c), 0.58 × length of podium in mid-body (0.40–1.6), 0.82 × length of podium posteriorly (0.39–0.90); 2.2 × longer than wide posteriorly (1.4–1.9) (Fig. 49d). Ventral cirri 0.23–0.43 length of podium at setiger 3, 0.29 length of podium posteriorly (0.24–0.42).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae absent in postacicular fascicles; heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.7 × length of collar (1.5–1.9) (Fig. 49e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 6.0 × longer than width of shaft head (4.9–6.0), finely serrated, 15 teeth (11–13), 0.53 × total blade length (0.45–0.55), teeth increasing in length greatly proximally (Fig. 49f). Sub-neuroacicular falcigers in setiger 10 with blades very finely serrated (though occasionally dorsal-most falciger with blades finely serrated); dorsal-most 5.7 × longer than width of shaft head (4.0–5.2), 17 teeth (13–16); ventral-most 5.3 × longer than width of shaft head (3.8–5.2), 18 teeth (12–15). Sub-neuroacicular falcigers in mid-posterior region with blades very finely serrated. Setae pale. Acicula in mid-body brown.

Pygidium. Pygidium weakly tripartite, with 2 large lateral lobes and smaller pointed dorsal lobe. Anus terminal. Anal cirri arising laterally or ventrolaterally, approximately conical, smooth, 0.8 × width pygidium (0.5–0.6).

Remarks. The material examined is generally small (less than 54 setigers) and sexually immature. The species closely resembles *Namanereis littoralis* sp. group, but differs in having the falciger blades relatively longer, and in having a

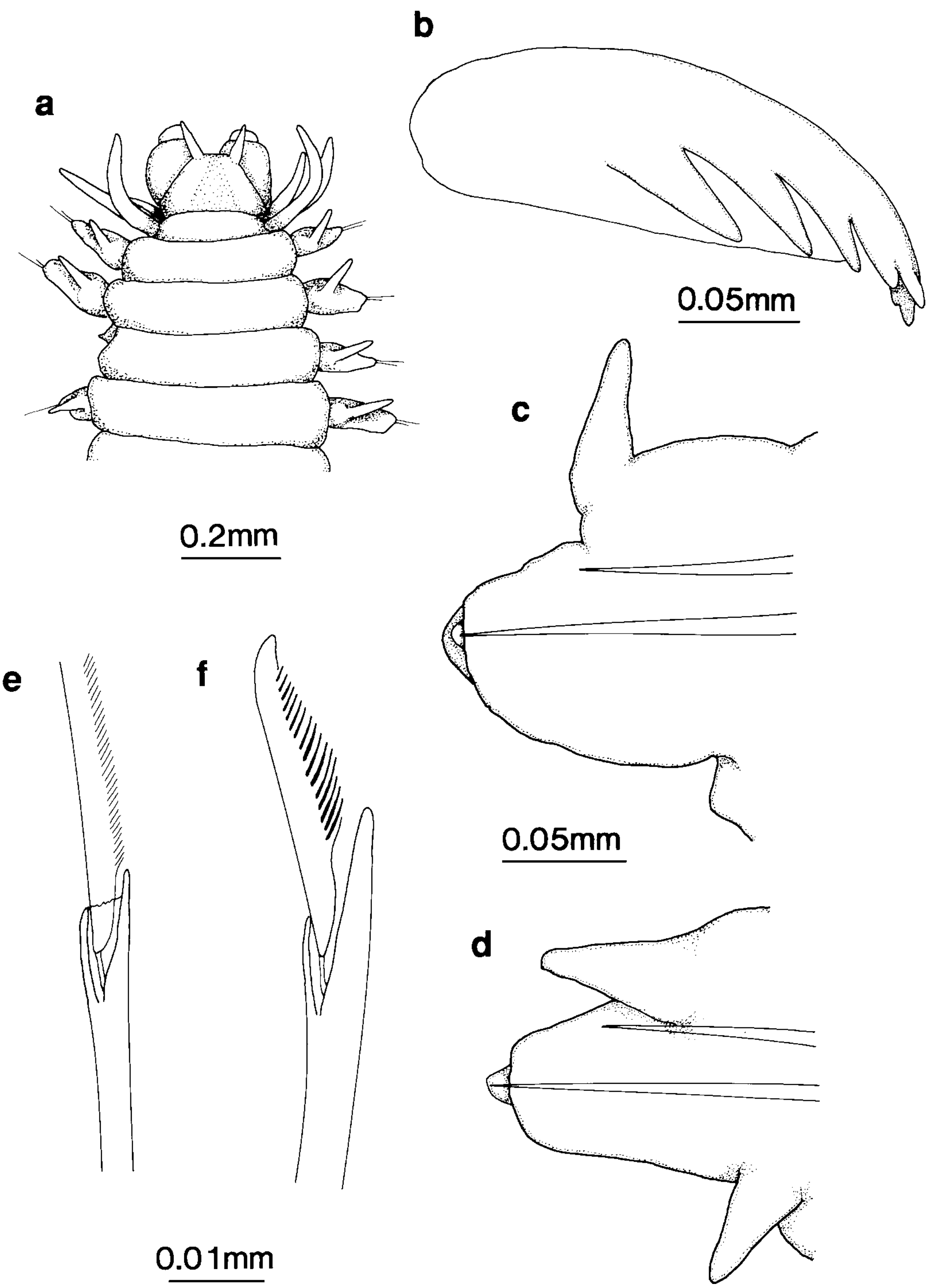

Figure 49. *Namanereis sublittoralis* n.sp. holotype: (*a*) anterior end, dorsal view, L.S. anteroventral pair of tentacular cirri missing; (*b*) jaw piece, dorsal view; (*c*) parapodium from 3rd setiger, L.S., posterior view, ventral cirrus missing; (*d*) parapodium from 43rd setiger, L.S., posterior view; (*e*) supra-neuroacicular spiniger, setiger 10; (*f*) supra-neuroacicular falciger, setiger 10.

greater number of teeth on the blade of the dorsal-most subacicular falciger. In addition, *N. sublittoralis* n.sp. generally has a more prolonged boss on the articulation of the spiniger, although there is some overlap in this character between the two species. Its phylogenetic position within the *Namanereis* clade is equivocal. In both the Strict and the Nelson Consensus trees *N. sublittoralis* n.sp. comes out in the unresolved part of the cladogram together with *N.*

catarractarum, *N. littoralis*, *N. pontica* and *N. riojai* (Figs. 5,6), but in the Majority-rule Consensus tree the species is the sister of all other species of *Namanereis*, except for *N. quadraticeps*: the clade containing the remaining species of *Namanereis* is however only represented in 69% of all minimal-length trees (Fig. 7) and therefore support for this latter phylogeny must be considered weak.

Habitat. Type habitat an open well close to the sea, chlorinity 3 100 mg/l (salinity = 5.6‰). Jamaican paratypes also collected close (2–25 m) to the sea (but periodically cut off from it) in partly dry/crusty sediment with chlorinities ranging from 5 328 to 25 744 mg/l (salinity = 9.6–46.5‰).

Distribution. Type locality Caribbean, Sint Eustatius. Other material from Jamaica (Fig. 46).

Etymology. From the L. prefix *sub-*, meaning under or from, and the L. *littoralis*, meaning of the seashore, referring to the probable close phylogenetic relationship between this species and *N. littoralis*. Also refers to the habitat in shallow subtidal coastal areas, that is, seaward of the supralittoral zone favoured by the *N. littoralis* species group.

Namanereis tiriteae (Winterbourn) **n.comb.**

Figs. 1c, 42, 50a–g; Table 5

Namalycastis tiriteae Winterbourn, 1969: 282–284, figs. 1–7.– Henderson, 1995: 13.
Namalycastis vuwaensis Ryan, 1980: 509–511, figs. 1a–f, 2a–d.

Material examined. *Namalycastis tiriteae* HOLOTYPE: New Zealand, North Island, Tiritea [= Turitea] Stream, coll. M.J.W., 23/03/68, (NMNZ Z.W. 1015). *Namalycastis vuwaensis* Fiji, Viti Levu, Wainisavulevu Creek, above Vuwu Falls, 17°49'55"S 178°02'30"E coll. P. Ryan and N. Penn, 28/07/79 2(AM W20274); Wainisavulevu Creek, coll. P. Ryan 2(AM W20276). 5 specimens measured.

Other material examined. New Zealand, North Island, Mangatainoka River, near confluence with Manawatu River, coll. I. Henderson 1(MU unreg.). *Namalycastis vuwaensis* Fiji, Viti Levu, collection details for "above Vuwu Falls" specimens 4(AM W20275), in very poor condition.

Diagnosis. Antennae cirriform, smooth. Eyes absent. Tentacular cirri, 3 pairs. Jaws with single robust terminal tooth and large gap separating terminal and first tooth. Notosetae absent. Neurosetae Type A (Fig. 1c). Supra-neuroacicular falcigers in setiger 10 with blades 5.0 × longer than width of shaft head (4.4–5.6), finely serrated, 27 teeth (28–34), teeth increasing in length greatly proximally. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally.

Description. Holotype well preserved though body wall of peristomium and setiger 3 slightly damaged, segmentally complete, no gametes in coelom. Other material moderately-well to poorly preserved, including some complete individuals. 76 setigers (112–125), 22 mm long (57–58), 1.5 mm wide at setiger 10 (2.2–2.3). At setiger 10 length of parapodia 0.43 × body width (0.36–0.43).

Body. Uniform in width anteriorly, tapering in far posterior region. Dorsum convex. Venter convex. Colour in alcohol white. Epidermal pigment absent. Living colour pale pink throughout (according to Ryan, 1980).

Prostomium. Shallow cleft anteriorly, with or without shallow dorsal groove or hollow. Prostomium shape roughly trapezoidal; 1.6 × wider than long (1.8–2.1). Antennae cirriform, smooth, extending beyond tip of palpostyle or beyond tip of palpophore, aligned over mid-palps (approaching inner edge). Eyes absent (Fig. 50a).

Peristomium. Tentacular cirri, 3 pairs, cirrophores indistinct; cirrostyles smooth. Anterodorsal tentacular cirri 1.5 × length anteroventral (0.9–1.3). Anterodorsal tentacular cirri 1.1 × length posterodorsal (0.9–1.1). Posterodorsal tentacular cirri extending posteriorly to setiger 2 (2–3) (Fig. 50a). Jaws with single robust terminal tooth, although large gap separates terminal and first tooth, 2 subterminal teeth (2–3), 4 teeth ensheathed proximally (4–5), brown (Fig. 50b).

Parapodia. Acicular neuropodial ligule subconical (Fig. 50c,d). Dorsal cirri 1.9 × length of podium at setiger 3 (1.9–2.9) (Fig. 50c), 1.3 × length of podium in mid-body (1.1–1.7), 1.5 × length of podium posteriorly (1.2–2.0); 4.0 × longer than wide posteriorly (1.9–3.0) (Fig. 50d). Ventral cirri 0.78 length of podium at setiger 3 (0.60–0.71), 0.48 length of podium posteriorly (0.32–0.56).

Setae. Supra-neuroacicular setae include sesquigomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5). Sub-neuroacicular setae include heterogomph spinigers in postacicular fascicles and heterogomph falcigers in preacicular fascicles (Table 5).

Supra-neuroacicular sesquigomph spinigers in setiger 10 with boss 1.6 × length of collar (1.5–1.7) (Fig. 50e). Heterogomph setae with boss not prolonged. Supra-neuroacicular falcigers in setiger 10 with blades 5.0 × longer than width of shaft head (4.4–5.6), finely serrated, 27 teeth (28–34), 0.63 × total blade length (0.62–0.67), teeth increasing in length greatly proximally (Fig. 50f). Sub-neuroacicular falcigers in setiger 10 with blades finely serrated; dorsal-most 5.0 × longer than width of shaft head (4.1–7.5), 28 teeth (27–56); ventral-most 4.3 × longer than width of shaft head (4.2–5.3), 25 teeth (26–32). Sub-neuroacicular falcigers in mid-posterior region with blades finely serrated. Sub-neuroacicular spinigers in mid-posterior region with blades having short, fine serrations proximally (Fig. 50g). Setae pale. Acicula in mid-body brown.

Pygidium. Structure of pygidium unknown. Anus terminal. Anal cirri arising ventrolaterally, approximately conical, smooth, 1.2 × width pygidium (0.8–0.9).

Remarks. The holotype of *Namalycastis tiriteae* Winterbourn, which is kept at the NMNZ (rather than the NIWA as reported by Day & Hutchings, 1979), was compared to probable types of *Namalycastis vuwaensis* Ryan, and the latter species is relegated to a junior synonym of the former. The specimens of *N. vuwaensis* are slightly larger than the

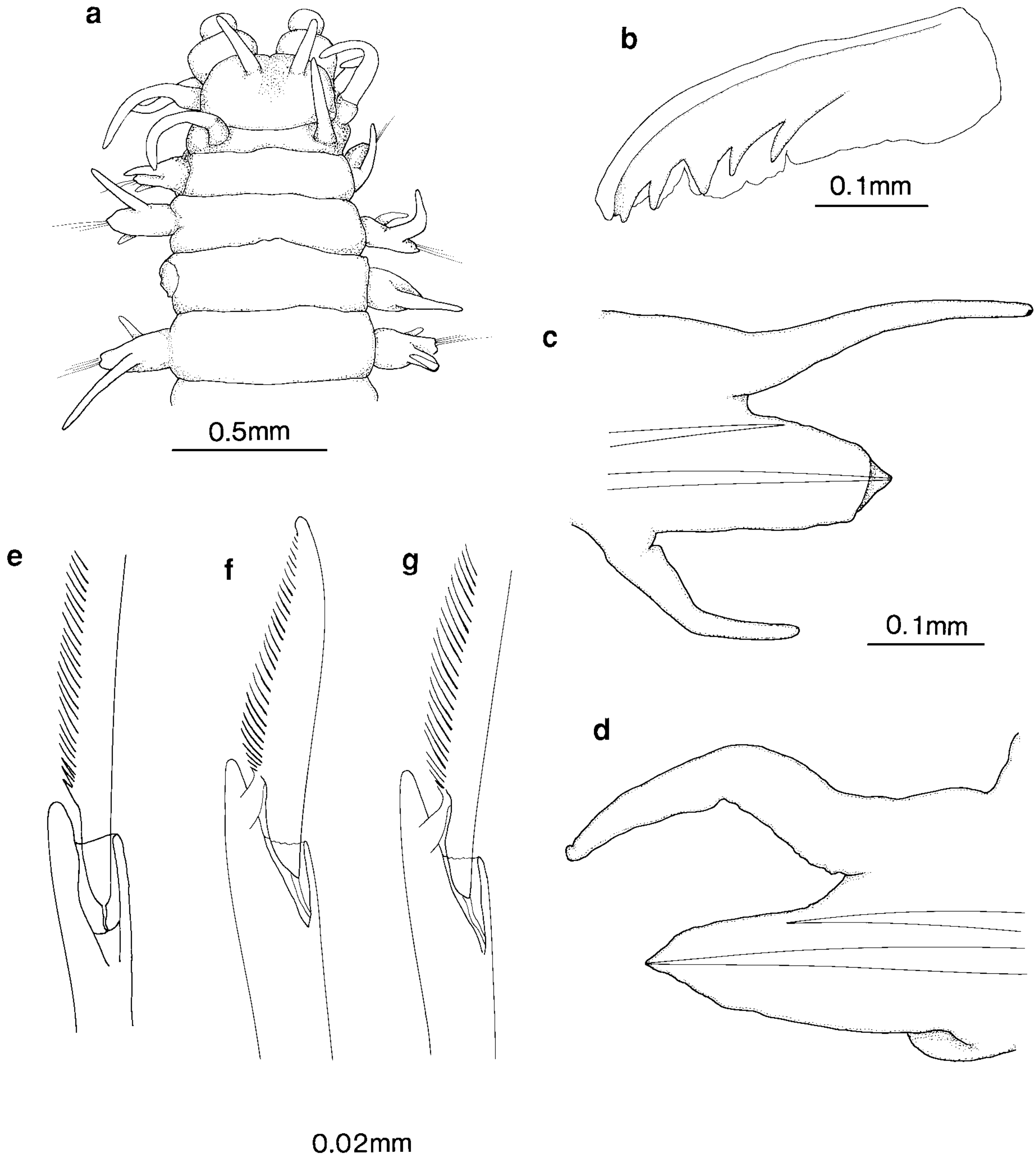

Figure 50. *Namanereis tiriteae* holotype: (*a*) anterior end, dorsal view, damage to dorsum not illustrated; (*b*) jaw piece, ventromedial view; (*c*) parapodium from 3rd setiger, L.S., anterior view; (*d*) parapodium from 60th setiger, L.S., posterior view, ventral cirrus obscured. (*e*) Non-type (AM W20276), supra-neuroacicular spiniger, setiger 10. Holotype: (*f*) supra-neuroacicular falciger, setiger 10; (*g*) sub-neuroacicular spiniger, setiger 10.

holotype of *N. tiriteae* (112–125 setigers *vs* 76 setigers) and show some differences typically associated with size (thickness of dorsal cirri, tentacular cirri and antennae, and greater number of setae); however, in regard to the more diagnostic characters associated with setal morphometrics, the two sets of specimens are essentially indistinguishable.

The holotype of *N. vuwaensis* is according to Ryan (1980) deposited at the NMNZ (Wellington). However, both the alcohol and slide collection of the NMNZ were checked and there is no record of the specimen. Further, Ryan (1980) provides no NMNZ catalogue number for the holotype. It appears likely therefore that the holotype of *N. vuwaensis* was never deposited at the NMNZ, and that material donated to the AM by Ryan and examined here includes the holotype. If this is the case then, it is not possible to distinguish the holotype from among the eight specimens, and they are registered in three separate lots; paratypes were not designated by Ryan.

Namanereis tiriteae was thought to be quite rare in the streams in the south of the North Island of New Zealand. Regular stream surveys in the Manawatu River near the type locality since 1969 failed to find more specimens. However, one specimen was recently collected from the Mangatainoka River, near the confluence with the Manawatu River, and several more have been collected in lowland streams in the Hawkes Bay region, a separate drainage basin to the north-east (I. Henderson, pers. comm., 1996).

The Fijian specimens were all collected in 1979 (Ryan, 1980), prior to the completion of the Wainisavulevu Dam above the collection site. The effect of the dam has been to reduce water flow to sites below. A subsequent trip to the area by P. Ryan and myself in February 1987 failed to find the species. Other evidence also suggests that this dam and others in the area have reduced the diversity of stream invertebrates (Haynes, 1994).

Based on the results of the cladistic analysis *Namalycastis tiriteae* Winterbourn, 1969 is transferred to *Namanereis*. Synapomorphies shared by this and other *Namanereis* species are the absence of dorsal cirrophores and the absence of notosetae. The structure of the pygidium could not be determined from the material studied. Other features typical of *Namanereis* are the cirriform antennae, 3 pairs of tentacular cirri, short-bladed falcigers with blades well serrated and serrations increasing greatly in length proximally. The presence of sub-neuroacicular spinigers in this species is indeed typical of *Namalycastis*, as mentioned by Winterbourn (1969), but the results of the phylogenetic analysis indicate that it is a plesiomorphic trait, and therefore cannot be used to support the placement of this species in *Namalycastis*. Supra-neuroacicular (sesquigomph) spinigers occur in members of both *Namalycastis* and *Namanereis*.

The phylogenetic position of *Namanereis tiriteae* is equivocal. In the Strict Consensus tree the species is grouped with several other *Namanereis* in an unresolved group at the base of the clade (Fig. 5). However, in both the Nelson and the Majority-rule Consensus trees the species is placed as a sister group to other mainly subterranean species, including *N. beroni*, *N. serratis* n.sp., *N. hummelincki*, *N. cavernicola, N. stocki* n.sp., and *N. minuta* n.sp.; the sister group relationship is represented in 95% of all minimal-length tress (Fig. 7). The clade containing *N. tiriteae* and the subterranean species is delineated by the loss of eyes. The loss of eyes in subterranean species is common, and the fact that it has apparently occurred only once (in the ancestor of this clade) in the Namanereidinae is perhaps surprising. *Namanereis tiriteae* may also be found in subterranean habitats in New Zealand and other parts of the South Pacific—its rarity in the freshwater streams of these areas perhaps reflecting an atypical habitat for the species.

Habitat. The type habitat is a freshwater stream 76 m above sea level, about 80 km from the sea following the river (32 km in a direct line overland) in gravelly-mud. Winterbourn (1969) provides the physical and chemical properties of the water. Fijian specimens collected from a freshwater river at least 100 km from the sea and 700 m above sea level, in patches of sand and gravel in still water (see Ryan [1980] for details of the chemical analysis of the stream water).

Distribution. Type locality New Zealand, North Island, Tiritea Stream (near Palmerston North). Also found in the nearby Mangatainoka River and several streams in the Hawkes Bay Region. The synonymy extends the distribution to Fiji, Viti Levu, Wainisavulevu Creek (Fig. 42).

Etymology. Winterbourn named the species after the stream where it was found. Turitea is a Maori word meaning clear or white water.

Discussion and conclusions

Previous studies indicating that the Namanereidinae is a monophyletic group (Fitzhugh, 1987; Glasby, 1991) are supported by the present simultaneous (unconstrained) cladistic analysis. Synapomorphies of the group are the spherical palpostyles and the ventral position of the notoacicula resulting in an indistinct separation between the neuropodia and notopodia. The subfamily contains 33 species (including three species groups) in two similar-sized genera, *Namalycastis* and *Namanereis*. A third genus, *Lycastoides*, containing a single species *Lycastoides alticola*, is possibly a junior synonym of *Namanereis*, but until the type species can be re-examined it is considered as *incertae sedis*.

Namalycastis contains mainly larger-bodied species having four pairs of tentacular cirri and autapomorphies include short, subconical antennae and enlarged, flattened and leaf-like posterior cirrophores. Hartman (1959a) suggested that the aberrant species, *N. geayi*, in which falcigers have been entirely replaced by spinigers, was not assignable to either *Namalycastis* or *Namanereis*. However, based on the results of the present cladistic analysis, *Namalycastis* is paraphyletic without the inclusion of *N. geayi*. The generic definition is emended accordingly. The inclusion of *Namalycastis tiriteae* Winterbourn in *Namalycastis* as suggested by Winterbourn (1969) meant a revision of the generic definition to include species with three pairs of tentacular cirri. Results here suggest that *N. tiriteae* belongs instead to *Namanereis*, and that any similarity with *Namalycastis* species is based on plesiomorphic features. The re-diagnosed genus contains 18 species (7 new), including one species group.

Namanereis contains smaller-bodied species having three or four pairs of tentacular cirri, giant-sized ova, and some species are hermaphroditic. Autapomorphies include the absence of cirrophores on the dorsal cirri, absence of notosetae and a tripartite pygidium. The genus contains 15 species (4 new), including two species groups, *N. littoralis* and *N. quadraticeps*. *Namanereis* includes all species previously described under *Lycastopsis* (for example, Feuerborn (1931a), Pettibone (1963), Uschakov (1965) and Imajima (1972)), as well as the monospecific *Cryptonereis* and *Lycastilla*. The results of the cladistic analysis indicate that *Lycastopsis* is a paraphyletic taxon, without the inclusion of *Cryptonereis* and *Lycastilla* and two new Caribbean species, which have four pairs of tentacular cirri. Given this result the continued recognition of *Cryptonereis* and *Lycastilla* is untenable. The genus *Namanereis* has either been regarded as monospecific taxon, containing only *N.*

quadraticeps (e.g., Day, 1967; Wesenberg-Lund, 1962; Rozbaczylo, 1974, 1975, 1985; Orensanz, 1975), or following Hartman (1959a) to contain all small-bodied Namanereidinae having three pairs of tentacular cirri and giant ova (i.e. synonymous with *Lycastopsis*). Therefore, the concept of *Namanereis* under this second scenario is also paraphyletic.

In revising the classification of this clade of Namanereidinae, two options were available: either restricting the use *Namanereis* to contain only *N. quadraticeps* (i.e. formally recognising a paraphyletic group), or recognising *N. quadraticeps* and its sister group together as a genus. One might argue in favour of the first option on the basis that *N. quadraticeps* is a species group and that its constituent "metaspecies" could turn out to be real species with further analysis; however, the group of species may also turn out to be paraphyletic (although less likely in my opinion), which would necessitate further modification to the generic definition. Therefore, in the interest of stability of nomenclature the second option was chosen; the clade takes the name *Namanereis*, the oldest available generic name among its constituents. Further, Chamberlin's (1919) original concept of *Namanereis* included, I believe, species with three or four pairs of tentacular cirri.

The species groups identified here will probably be found to contain more than one species with further characterisation of the reproductive mode and genetics of the constituent metaspecies; however, using the present morphological character set, they can not be recognised as such. With further study the species groups may be found to contain two or more cryptic species (or sibling species *sensu lato*), that is recently diverged species that have no recognisable phenetic differences, but which may have diverged in other areas such as reproductive biology in response to differences in the environment. Cases of cryptic species are common in both the Nereididae (e.g., Smith, 1958; Fong & Garthwaite, 1994) and marine invertebrates in general (Knowlton, 1993). The Campbell and Auckland Island populations of *Namanereis quadraticeps*, which differ from other members of the *quadraticeps* species group by having coelomic nurse cells nourishing the developing oocytes to an enormous size, constitute a potential cryptic species in this sense, but further study of the reproductive biology of these populations is required in order to understand how this difference could restrict gene flow between the Auckland and Campbell Island population and other allopatric members of the species group.

The other species groups recognised in this study (*Namalycastis abiuma* sp. group and *Namanereis littoralis* sp. group) exhibit a greater amount of morphological variation over their range than is typical for a namanereidine species; however subunits (metaspecies) cannot be distinguished on the basis of unique attributes. A study of genetic variation in all of these species groups would be a fruitful area of investigation and may in turn lead to the finding of small, but significant morphological differences.

Potential paraphyly of the species groups should not affect greatly the outcome of the cladistic analysis (polyphyly would present a more serious problem). The resulting high number of equally most parsimonious trees in the cladistic analysis is partly due to the low ratio of number of informative characters to number of taxa. Nevertheless, all minimal-length trees exhibited the same two clades, *Namalycastis* and *Namanereis*. Habitat preferences and distribution of members of each genus overlap considerably so it is not possible to characterise the genera in these terms. A trend in both genera is for the increased preference for inland freshwater habitats among the more apomorphic species (corollary being that the more euryhaline species are plesiomorphic). This suggests that the phyllodociform ancestor of the Namanereidinae was a euryhaline coastal species.

Most namanereidine species are confined to the tropics and the subtropics, although the *Namanereis quadraticeps* species group, has a southern temperate and Subantarctic distribution and *Namanereis littoralis* species group is widely distributed in temperate areas as well. Excluding the species groups, most species have restricted distributions occupying a single area of endemism: a study of the cladistic biogeography of the group is presented separately (Glasby, this volume). The few cases of disjunct or anomalous distributions among *Namalycastis* especially (e.g., *N. brevicornis*, *N. macroplatis* n.sp., *N. senegalensis*), may be the result of human-assisted introduction: this will be investigated in a later study against criteria for recognising introduced species (J.W. Chapman & Carlton, 1991). Maximum diversity of namanereidine species occurs in the Caribbean and Indo-Pacific. In the latter area in particular tectonic forces due to the convergence of ocean plates and resulting in relatively recent uplifting of coastal areas has probably increased the diversity of available habitats. In these areas one finds a mixture of marine and brackish Namanereidinae occurring together with truly terrestrial forms.

The Namanereidinae are a remarkably successful group of polychaetes. They have radiated into some environments where polychaetes do not usually occur, including the upper littoral zone of beaches and mangrove forests, subterranean waters, freshwater rivers and swamps, even plant-container habitats (Table 6). Indeed, three species—*Namalycastis indica*, *N. hawaiiensis* and *Namanereis hummelincki*—have been found in freshwater cisterns. Namanereidine species occur in a wide range of salinities from fresh (drinkable) water to hypersaline conditions (130‰). Most species are therefore either oligohaline or euryhaline (Table 6).

Success in such environments is dependent on the acquisition of a range of physiological, morphological and reproductive adaptations including the presence of segmental gill hearts and highly vascularised posterior dorsal cirri enabling the more efficient uptake of oxygen (Feuerborn, 1931a; Rasmussen, 1994), modifications to the eye, integument and epidermis to prevent desiccation (Sadasivan Tampi, 1949; Storch & Welsch, 1972a,b), modification to the nephridia to get rid of excess water (Krishnan, 1952; Florence Mary, 1966), and a shift toward hermaphroditism (or parthenogenesis) and viviparity (Johnson, 1908; Feuerborn, 1931a; Gopala

Aiyar, 1935; Runganadhan, 1943; Glasby *et al*., 1990). Further study may reveal some or all of these features to be autapomorphies of the subfamily. The known autapomorphies of the subfamily—spherical palpostyles and modified parapodia supported by both notoacicula and neuroacicula—are also likely to have adaptive significance at some level. One possible advantage of having reduced parapodia may be the ability to inhabit confined spaces, such as under fallen leaves and under the bark of fallen logs, a common niche of several species (e.g., *Namalycastis abiuma* species group, *N. borealis* n.sp., *N. hawaiiensis*, *N. indica*, *Namanereis amboinensis*, *N. catarractarum*, *N. littoralis* species group).

Most species are found in association with decaying wood and leaves (detritus), which may be an important source of food and provide protection from desiccation. At least one species, *Namalycastis borealis* n.sp. is known to eat wood (Rasmussen, 1994), and *Namanereis catarractarum* living in plant container habitats was found to consume oligochaetes, fungal hyphae and spores and other members of its own species—no insect larvae were taken despite their presence in the same vicinity (Glasby *et al*., 1990). These same food items are also available in marine and estuarine environments and leads to the speculation that the ancestor of the Namanereidinae was already well-equipped, in terms of feeding processes, for terrestrial life.

Finally, this work should by no means be considered the last word on the systematics of the Namanereidinae. Indeed, it raises many questions and throughout the paper I make reference to several aspects of the taxonomy and phylogeny of the group that deserve further study. Apart from the obvious one of the clarifying the status of the species groups, I consider two areas as potentially rewarding: further alpha-level taxonomic studies utilising freshly collected material, especially from the Caribbean and north-east of South America where sympatry among Namanereidinae is common, according to the species hypotheses presented here. And secondly, a cladistic analysis to test the present phylogenetic hypothesis, utilising molecular characters derived from a comparative study of DNA sequences. Further, a genetic study could shed light on the origin of sympatric species and, by utilising a molecular clock concept, test whether disjunct or anomalous distributions (among *Namalycastis* species especially) are the result of human-assisted introductions.

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Table 4. Setal numbers and distribution for primary types and other specimens (in parentheses) of *Namalycastis* species. Setal types are sesquigomph spinigers, heterogomph falcigers, heterogomph spinigers. post. = postacicular; pre. = preacicular; * = includes heterogomph pseudospinigers; u = unknown; — = not applicable i.e. setae not present in fascicle.

podia	notosetae	neurosetae (supra-acicular)			neurosetae (subacicular)		
	ses.spin.	post.ses.spin.	pre.het.fal.	pre.het.spin.	post.het.spin.	pre.het.fal.	pre.het.spin.
Namalycastis abiuma							
3	0	2	3	—	2	8	—
10	0	4	3	—	2	6	—
30	0	4	3	—	2	6	—
60	0	4	1	—	1	8	—
120	0	3	1	—	1	3	—
***Namalycastis abiuma* spp.gp.**							
3	0	1–4	1–5	—	1–3 (rarely 0–4)	7–15 (rarely 5–18)	—
10	0–2 (rarely 4)	2–6 (v. rarely 0)	1–6	—	1–3 (rarely 0–5)	5–18	—
30	0–3 (rarely 6)	3–7 (v. rarely 1–10)	0–4	—	1–4 (rarely 0–6)	4–9 (rarely 2–15)	—
60	0–5 (rarely 7)	3–9 (v. rarely 1–14)	1–3 (rarely 0–7)	—	1–4 (rarely 0–7)	4–9 (rarely 2–25)	—
120	0–1	1–6	1–3	—	0–3	3–8	—
180	0	2–6	1–2	—	1–3	3–6	—
***Namalycastis arista* n.sp.**							
3	1	4 (5)	4 (3–4)	0	1 (3)	9 (9–10)	0
10	3	6 (6–10)	5 (3–5)	0	3 (2–3)	11 (11–14)	0
30	1 (1–2)	5 (7–10)	3 (2–3)	0	3 (4)	6 (7–9)	0
60	0 (1–2)	5 (6–7)	3 (2–3)	0	4 (2–3)	5 (6)	0 (0–1)
120	0 (0–1)	5 (6–7)	0 (0–1)	3 (1–3)	4 (1–4)	2 (2–3)	2 (4–5)
180	0	3 (5)	0 (0)	1 (2)	2 (3)	0	4 (4)
***Namalycastis borealis* n.sp.**							
3	0	3 (2–5)	1 (1–4)	—	4 (3–5)	6 (6–15)	—
10	0	2 (3–6, rarely 9)	4 (1–5)	—	1 (3–6)	8 (6–18)	—
30	0 (0–1)	5 (3–8)	3 (1–4)	—	4 (3–7)	5 (3–15)	—
60	0 (0–1)	2 (3–6, rarely 10)	2 (1–4)	—	2 (2–7)	5 (2–9)	—
120	0	2 (2–4, rarely 0–7)	1 (1–3)	—	2 (1–6)	2 (2–8)	—
180	0	3	1	—	3	2	—
Namalycastis brevicornis							
3	1–3	3–4	2–5	—	0–2	13–17	—
10	4 (5–8)	5 (4–10)	4 (3–5)	—	0 (0–1)	17 (15–22)	—
30	6–17	6–14	3–4	—	2	10–15	—
60	7 (5–15)	6 (6–10)	3 (3–4)	—	1 (1–3)	9 (8–14)	—
120	2 (1–4)	3 (3–6)	3 (2–3)	—	1 (0–3)	5 (5–8)	—
180	—	—	—	—	—	—	—
***Namalycastis elobeyensis* n.sp.**							
3	—	3 (1–2)	3 (2–3)	—	3 (1–2)	3 (2–4)	—
10	—	6 (4–5)	1 (2–3)	—	4 (2–4)	3 (2–5)	—
30	—	5 (3–5)	2 (1–2)	—	3 (1–3)	2 (2–3)	—
60	—	2 (2–3)	1 (1–2)	—	2 (1–2)	1 (2–4)	—
Namalycastis fauveli							
3	0–1	1–3	1–3	—	1–4	3–5	—
10	0–2	2–3	3–4	—	3–6	4–6	—
30	0–1	1–4	2–3	—	2–6	2–3	—
60	0–2	1–3	1–3	—	1–6	2–3	—
120	0–2	1–3	1–3	—	1–5	2–5	—
180	0	1–2	0–3	—	1–4	1–5	—
240	0	2	4	—	2	5	—
Namalycastis geayi							
3	5 (6)	6 (5–6)	—	6 (3–5)	4 (3–5)	7 (8–9)	—
10	6 (9–13)	8 (5–7)	—	4 (3–6)	5 (3–5)	8 (5–8)	—
30	6 (5–7)	6 (7–8)	—	3 (3–4)	4 (2–5)	7 (6–7)	—
60	4 (4–6)	6 (4–5)	—	3 (2–3)	3 (3–4)	6 (4–6)	—
120	3 (2–3)	5 (4)	—	2 (2)	3 (2)	5 (4)	—
180	3 (1–2)	3 (2–3)	—	1 (1–2)	2 (1–2)	3 (2)	—
Namalycastis hawaiiensis							
3	—	2 (1–4)	2 (1–4)	—	2 (0–3)	6 (4–10)	—
10	—	4 (2–5)	2 (1–4)	—	1 (0–3)	8 (3–12)	—
30	—	2 (2–5)	2 (1–3)	—	2 (0–2)	5 (2–9)	—
60	—	3 (2–5)	1 (1–2)	—	1 (0–3)	6 (3–6)	—
120	—	2 (1–4)	2 (1–2)	—	1 (0–3)	4 (2–7)	—

Namalycastis indica							
3	0–1	2–4	2–4	—	1–3	3–8	—
10	0–2	4–10	1–4	—	2–7	3–8	—
30	0–2	3–9	1–3	—	2–10	2–7	—
60	0–1	3–11	0–3	—	1–8	2–6	—
120	0	4–6	1–2	—	2–8	1–3	—
180	0	5–7	0–1	—	3–4	0–1	—
***Namalycastis intermedia* n.sp.**							
3	—	1 (1–2)	1	0	1 (0–1)	2 (2–3)	0
10	—	2 (1–2)	1	0	1 (0–2)	3 (2–3)	0
30	—	2 (1–2)	2 (1)	0	1 (1–2)	3 (1–2)	0
60	—	2 (1)	1 (0–1)	0 (0–1)	1 (1–2)	1 (0–2)	0 (1–2)
Namalycastis kartaboensis							
3	0–1	4–5	1–4	—	0–1	4–10	—
10	0–1	2–4	2–3	—	0–2	4–10	—
30	0	1–4	2–3	—	1–2	5–7	—
60	0	3–5	1–2	—	1–2	2–6	—
120	0	3–4	2	—	0–1	4–7	—
180	0	3	1	—	0	4	—
Namalycastis longicirris							
3	u	u	u	—	u	u	—
10	2	≈5	≈3	—	2	6	—
30	u	u	u	—	u	u	—
60	u	u	u	—	u	u	—
120	0	1	1	—	2	2	—
***Namalycastis macroplatis* n.sp.**							
3	0 (0–4)	3 (4–10)	4 (2–5)	0	4 (1–6)	10 (7–15)	0
10	3 (2–7)	13 (5–17)	6 (4–12)	0	6 (2–12)	17 (12–27)	0
30	6 (3–8)	18 (13–40)	5 (4–13)	0 (2–5)	11 (4–26)	8 (7–15)	0 (0–5)
60	6 (1–6)	16 (11–26)	6 (2–4)	0 (0–6)	2 (5–10)	5 (5–11)	8 (2–13)
120	0 (0–1)	0 (6–20)	0	3 (3–6)	2 (3–5)	0	7 (3–10)
180	1 (0)	6 (3)	0	2 (2)	2 (5)	0	6 (3)
240	0	3	0	1	2	0	2
***Namalycastis multiseta* n.sp.**							
3	0	2 (2–3)	5 (2–3)	—	2	17 (13–15)	—
10	3 (0)	10 (5)	5 (3–4)	—	3	20 (14)	—
30	8 (1–7)	30 (10–17)	6 (4)	—	7 (3–7)	15 (8–9)	—
60	4 (2–6)	24 (11–15)	5 (4)	—	10 (4)	14 (7–10)	—
120	0	6 (4)	3 (2)	—	3 (2–3)	9 (4–5)	—
180	0	4 (2)	2	—	3 (2)	4 (5)	—
***Namalycastis nicoleae* n.sp.**							
3	1	2	3	—	4	6	—
10	1	≈5	3	—	4*	3	—
30	1	5	2	—	5*	4	—
60	1	2	1	—	1	3	—
Namalycastis senegalensis							
3	2 (0–2)	6 (3–7, rarely 10)	5 (1–6)	0	4 (1–3, rarely 7)	13 (5–15)	0 (v. rarely 5)
10	2 (0–3)	6 (3–11, rarely 17)	3 (2–12)	0	3 (0–5)	15 (9–26)	0
30	3 (0–4, rarely 7)	14 (4–20, rarely 25)	5 (0–6)	0 (0–1)	2 (2–5, rarely 11)	10 (3–19)	0 (2, v. rarely 32)
60	0 (0–4, rarely 12)	10 (2–16, rarely 30)	1 (0–3)	3 (0–7)	5 (1–7)	8 (1–11, rarely 20)	0 (1–6, v. rarely 30)
120	0 (0–1)	4 (2–15)	0	2 (1–5)	2 (1–7)	2 (0–2)	2 (2–17)
180	0–1	4–12	0	2–5	3–5	0	4–9
240	0	5–7	0	2	3–5	0	3–9
Namalycastis siolii							
3	u	u	u	u	u	u	u
10	3	4	2	0	6	1	0
30	u	u	u	u	u	u	u
60	u	u	u	u	u	u	u
120	1	3–4	0	3–4	6	3	2–3
180	u	u	u	u	u	u	u
240	1	3–4	0	3–4	3–4	0	3–4
Namalycastis terrestris							
3	1 (3–4)	3 (5)	4		2 (3)	7 (6–12)	—
10	2 (10–20)	5 (10–15)	6 (8–10)		8–13	12 (10–20)	—
30	1 (8–25)	4 (7–20)	3 (10)		2 (12–20)	5 (10–15)	—
60	0 (5–22)	2 (5–20)	3 (6–15)		2 (5–20)	8 (8–10)	—
120	0 (3–20)	2 (7–15)	2 (6–12)		2 (8–20)	3 (6–15)	—
180	1–13	4–15	3–10		3–10	5–15	—
240	5	10	12		10	10	—

Table 5. Setal numbers and distribution for primary types and other specimens (in parentheses) of *Namanereis* species. See Table 4 for explanation of abbreviations used. * = heterogomph falcigers with blades grading to pseudospinigers and/or spinigers; ** = heterogomph spinigers in this fascicle occur only in *Namanereis quadraticeps* spp.gp.

	podia	notosetae	neurosetae (supra-acicular)		neurosetae (subacicular)	
		ses.spin.	post.ses.spin. or het.spin.**	pre.het.fal.	post.het.spin.	pre.het.fal.
Namanereis amboinensis						
	3	—	1 (1–3)	1 (0–2)	—	3 (2–4)
	10	—	1 (0–3)	1 (1–2)	—	3 (1–3)
	30	—	1 (0–2)	1 (1–2)	—	4 (2–5)
	60	—	1	1	—	3
Namanereis beroni						
	3	—	1	1	—	2–3
	10	—	1	1	—	2
	30	—	1	1	—	2
	60	—	1	1	—	2–3
Namanereis catarractarum						
	3	—	1 (0–1)	1	—	3 (2–4)
	10	—	1 (rarely 0 or 2)	1 (1–2)	—	3 (rarely 1, 2 or 4)
	30	—	1	2 (1–2)	—	3 (rarely 2 or 4)
	60	—	1	1 (1–2)	—	3 (rarely 2)
Namanereis cavernicola						
	3	—	2 (1–2)	1 (1–2)	—	4 (1–4)*
	10	—	2 (1–2)	1	—	4 (1–6)*
	30	—	3 (0–2)	1	—	3 (1–5)*
	60	—	2 (1)	1 (1–2)	—	3 (1–5)*
Namanereis hummelincki						
	3	—	1 (v. rarely 2)	1	—	2 (1–4)*
	10	—	1	1	—	4 (1–5)*
	30	—	2 (usually 1)	1	—	3 (1–5)*
	60	—	1 (v. rarely 2)	1	—	1–4*
Namanereis littoralis						
	3	—	1 (1–2)	1	—	5 (4)
	10	—	1 (1–2)	1	—	4 (3–5)
	30	—	1	1	—	4 (2–4)
	60	—	1 (1–2)	1	—	3
***Namanereis littoralis* spp.gp.**						
	3	—	0–2	0–2	—	2–7
	10	—	0–3	0–2	—	3–8
	30	—	0–3	1–2	—	2–7
	60	—	0–3	0–2	—	2–7
Namanereis malaitae						
	3	—	1–2	1	—	3
	10	—	1	1	—	3
	30	—	1	1	—	3
	60	—	1	1	—	2–3
***Namanereis minuta* n.sp.**						
	3	—	1 (1–2)	1	—	3 (1–4)*
	10	—	1 (1–2)	1	—	3 (2–4)*
	30	—	1 (1–2)	1 (2)	—	3 (2–4)*
Namanereis pontica						
	3	—	—	1	—	4–5
	10	—	—	1	—	4–5
	30	—	—	1–2	—	4
	60	—	—	1	—	4
***Namanereis quadraticeps* spp.gp.**						
	3	0	1 (1–2)	1 (1–2)	—	4 (4–7)
	10	1 (0–1)	1 (1–2)	1	—	5 (4–8)
	30	1 (1–2)	1 (1–3)	1 (0–2)	—	4 (4–6)
	60	0–2	1–2	1–2	—	2–5

Namanereis riojai						
	3	—	1	1	—	4
	10	—	1	1	—	6
	30	—	1	1	—	4
	60	—	1	1	—	5
***Namanereis serratis* n.sp.**						
	3	—	1	1 (1–2)	—	2 (1–3)
	10	—	1 (0–2)	1 (1–2)	—	2 (1–2)
	30	—	1	1	—	2 (2–3)
	60	—	1	0 (0–2)	—	2 (1–3)
***Namanereis stocki* n.sp.**						
	3	—	1 (1–2)	1 (1–2)	—	3 (1–3)*
	10	—	1	2 (1–2)	—	2 (1–3)*
	30	—	1 (1–2)	1 (1–2)	—	2 (1–3)*
	60	—	1	1	—	3 (1–3)*
***Namanereis sublittoralis* n.sp.**						
	3	—	1 (1–2)	1	—	5 (3–4)
	10	—	1 (0–1)	1 (1–2)	—	4 (2–4)
	30	—	1 (0–1)	1	—	3 (2–4)
	60	—	u	u	—	u
Namanereis tiriteae						
	3	—	0 (1–2)	1	1 (0–1)	2 (3–4)
	10	—	2 (0–2)	1	1 (1–2)	3 (2–3)
	30	—	2 (1–2)	1 (1–2)	1 (1–2)	3 (2–3)
	60	—	2 (1–2)	1 (1–2)	0 (1–2)	1 (0–2)
	120	—	0–2	0–2	0–2	0–1

Table 6. Habitat, distribution and inferred salinity tolerance for namanereidine species.

species	habitat	habitat salinity & inferred tolerance	distribution
Lycastoides alticola	mountain stream	freshwater	Baja California, Mexico
Namalycastis abiuma spp.gp.	upper littoral zone of mudflats; associated with decaying vegetation (e.g., mangroves, *Nypa* palm, *Enteromorpha*, coconuts)	euryhaline	circumglobal between 30°N and 30°S
Namalycastis arista n.sp.	intertidal mud	unknown	Guyana
Namalycastis borealis n.sp.	as *N. abiuma*; also associated with *Spartina*, seaweed strand, pine logs	euryhaline	eastern & southern USA
Namalycastis brevicornis	intertidal sand-mud	euryhaline	possibly amphi-Atlantic
Namalycastis elobeyensis n.sp.	unknown	unknown	Equatorial Guinea
Namalycastis fauveli	estuarine beach, coastal lagoons	euryhaline	India, Thailand
Namalycastis geayi	muddy river banks, springs in coarse sediment	freshwater	French Guiana
Namalycastis hawaiiensis	as *N. indica*; also swamps and coastal anchialine ponds	fresh to slightly brackish water	Hawaiian islands, Indonesia New Guinea, Palau Is, Hong Kong, Ryukyu Is, Truk,
Namalycastis indica	muddy banks of ponds and rivers; often associated with decaying vegetation (e.g., coconuts, leaf litter)	fresh to slightly brackish water	India, Bangladesh, Sri Lanka, Thailand
Namalycastis intermedia n.sp.	unknown	freshwater	southern USA
Namalycastis kartaboensis	mud	unknown	Guyana, Surinam, French Guiana
Namalycastis longicirris	as *N. indica*; also found in rice and lotus fields	?freshwater	Taiwan
Namalycastis macroplatis n.sp.	beach	fresh to brackish water	Brazil, Surinam, French Guiana
Namalycastis multiseta n.sp.	unknown	unknown	Burma
Namalycastis nicoleae n.sp.	coastal lowlands	unknown	eastern Australia
Namalycastis senegalensis	estuaries; in pilings, associated with mangroves	brackish water, perhaps euryhaline	tropical-subtropical, amphi-Atlantic
Namalycastis siolii	rivers	freshwater	Brazil (Amazon region)
Namalycastis terrestris	upper littoral zone; semi-terrestrial in rice fields	fresh to slightly brackish water	southern Vietnam, ?Indonesia
Namanereis amboinensis	upper littoral areas of mangroves associated with decaying vegetation; also freshwater springs	euryhaline	circumtropical and circumsubtropical
Namanereis beroni	cave water	freshwater	New Guinea
Namanereis catarractarum	moist areas near forest streams, often associated with decaying vegetation (e.g., banana & pandanas leaves) or in leaf axils of living pandanas trees	freshwater	Indonesia, Philippines, New Guinea, Solomons, Fiji, ?Tahiti
Namanereis cavernicola	springs, pools, swamps, subterranean waters; in sand and fime gravel	freshwater	Mexico, Caribbean
Namanereis hummelincki	spring water, gutters, puddles and cisterns, fine sediment and decaying plant material & detritus	freshwater	Caribbean
Namanereis littoralis spp.gp.	upper littoral zone, often associated with decaying vegetation and detritus; rarely subtidal	euryhaline	cosmopolitan, except high latitudes
Namanereis malaitae	leaf frond of coconut palm stranded intertidally	unknown	Solomons
Namanereis minuta n.sp.	springs and wells	freshwater	Haiti
Namanereis pontica	littoral, decaying seagrass, coarse sand	unknown	Black Sea, Mediterranean
Namanereis quadraticeps spp.gp.	littoral zone, often in seep zones between coast and freshwater streams, swamps or lagoons; rarely subtidal	euryhaline	southern temperate and subantarctic
Namanereis riojai	unknown	unknown	Baja, Mexico
Namanereis serratis n.sp.	well	freshwater	Haiti
Namanereis stocki n.sp.	subterranean freshwater, springs and wells; in sand and fine gravel	freshwater	Caribbean
Namanereis sublittoralis n.sp.	coastal	euryhaline	Caribbean
Namanereis tiriteae	rivers in gravel, sand and mud sediments	freshwater	New Zealand, Fiji

Appendix

Characters and characters states used in the cladistic analysis of the Namanereidinae and outgroups.

1 Setigers, maximum number: a. <150; b. >150
2 Body shape: a. uniform width anteriorly, tapering gradually posteriorly; b. widest mid-anteriorly, tapering gradually anteriorly and posteriorly
3 Epidermal brown pigment: a. present; b. absent
4 Prostomium shape: a. width:length ratio >1.3; b. width:length ratio <1.3
5 Prostomial cleft: a. absent; b. present
6 Lateral antennae, presence/shape: a. short, subconical; b. elongate, cirriform; c. short, subspherical; d. absent
7 Median antennae, presence: a. present; b. absent
8 Eyes, presence/relative sizes: a. present, equal in size or posterior pair slightly smaller; b. posterior pair markedly smaller; c. anterior pair slightly smaller; d. absent
9 Lenses, degree of development: a, absent or indistinct; b, well-developed
10 Palps, shape: a. biarticulate (i.e. eversible), palpostyles spherical; b. biarticulate, palpostyles subconical (outgroup only); c. pseudoarticulate, approx. cylindrical (outgroup only)
11 Nuchal organs, form a. externally exposed; b. not externally exposed
12 Peristomium, form in adult: a. not visible; b. fused with first segment and bearing two pairs of peristomial cirri
13 Tentacular cirri, number of pairs: a. 3 pairs (i.e. 2 pairs peristomial + 1 pair segmental); b. 4 pairs (i.e. 2 pairs peristomial + 2 pairs segmental); c. 3 pairs (segmentally derived; outgroup only); d. 6 pairs (outgroup only); e. 8 pairs (outgroup only)
14 Cirrostyles of tentacular and peristomial cirri, surface: a. smooth; b. faintly jointed
15 Pharynx, presence of papillae: a. absent; b. present
16 Jaws, number of terminal teeth: a. single robust terminal tooth; b. with bifid terminal teeth
17 Notoaciculae, presence in anterior parapodia: a. anterior parapodia all with notoaciculae; b. parapodia of segment 1 lacking notoaciculae (outgroup only); c. parapodia of segments 1 & 2 lacking notoaciculae (outgroup only)
18 Notopodial lobes, presence/type: a. absent; b. pre-setal lobe only; c. distinct flattened notopodial lobes (includes median ligule and usually dorsal ligule)
19 Neuropodial lobes, type: a. acicular neuropodial ligule only; b. acicular neuropodial ligule and ventral ligule; c. acicular neuropodial ligule and post-setal lobe; d. acicular neuropodial ligule, ventral ligule and post-setal lobe
20 Acicular neuropodial ligule, form: a. subconical; b. bilobed
21 Dorsal cirri of parapodia in mid-posterior segments, shape: a. approximately conical; b. basal region (cirrophore) flattened
22 Cirrophores of anterior dorsal cirri, presence: a. absent; b. present
23 Notoacicula, position in parapodia: a. supporting notopodia proper or dorsal cirrus; b. ventral, just above neuroacicula
24 Glandular patches on dorsal edge of parapodia, presence: a. absent; b. present
25 Notosetae, type/presence: a. sesquigomph spinigers; b. absent; c. homogomph spinigers (outgroup only); d. capillaries (outgroup only); e. paleae/spines
26 Supra-acicular neurosetae in postacicular fascicle in setiger 10, type/presence: a. sesquigomph spinigers (Types A–D); b. absent (Type E); c. heterogomph spinigers (Type F); d. heterogomph falcigers (outgroup only)
27 Supra-acicular neurosetae in preacicular fascicle in setiger 10, type/presence: a. heterogomph falcigers (Types A, C–F); b. heterogomph spinigers (Type B); c. sesquigomph falcigers (outgroup only); d. absent (outgroup only)
28 Supra-acicular neurosetae in preacicular fascicle in posterior setigers, type/presence: a. heterogomph falcigers (Types A, C–F); b. heterogomph spinigers (Type B); c. sesquigomph spinigers (outgroup only); d. absent (outgroup only)
29 Subacicular neurosetae in postacicular fascicle in setiger 10, type/presence: a. heterogomph spinigers (Types A,B); b. absent (Types C–F); c. heterogomph falcigers (outgroup only); d. sesquigomph spinigers (outgroup only)
30 Subacicular neurosetae in preacicular fascicle in setiger 10, type/presence: a. heterogomph falcigers (Types A, C, E, F); b. heterogomph spinigers (Type B); c. heterogomph falcigers, pseudospinigers and spinigers in a series (Type D); d. sesquigomph falcigers (outgroup only); e. heterogomph falcigers & sesquigomph spinigers (outgroup only)
31 Subacicular neurosetae in preacicular fascicle in posterior setigers, type/presence: a. heterogomph falcigers (Types A, C, E, F); b. heterogomph spinigers (Type B); c. heterogomph falcigers, pseudospinigers and spinigers in a graded series (Type D); d. sesquigomph falcigers (outgroup only)
32 Subacicular neurosetae in preacicular fascicle with blades, shape/length: a. weakly falcate, broad & short; b. weakly falcate, narrow & elongate; c. spinigerous; d. strongly falcate, elongate (outgroup only); e. strongly falcate, short
33 Subacicular neurosetae in preacicular fascicle with blades, form serrations: a. evenly serrated along length (fine-coarse), b. includes types that are increasingly coarsely serrated proximally in posterior parapodia; c. serrations absent
34 Subacicular neurosetae in postacicular fascicle in mid-posterior region with blades: a. finely serrations proximally (may be short or long), b. includes types that are coarsely serrated proximally
35 Setal shafts, distal surface markings: a, smooth or nearly so; b. having series of small serrations
36 Pygidium, shape: a. multi-incised rim; b tripartite, with two large lateral lobes and smaller pointed dorsal lobe; c button-shaped, smooth rimmed (outgroup only); d. wing-like lateral lobes (outgroup only)
37 Anal cirri, shape: a. approximately conical to cirriform; b. papilliform (short & stout); c. flattened
38 Oocytes, shape: a. spherical; b. ellipsoidal
39 Epitokal setae, type: a. slender compound spinigers; b. long, slender capillaries; c. absent; d. paddle-bladed compound spinigers (outgroup only)

Note added in press

During the preparation of this paper a new species of *Namanereis*, *N. araps*, has been described from groundwater on the Arabian Peninsula (Glasby, 1997) and there has been a new record (Glasby *et al*., 1998) of the *Namalycastis abiuma* species group from the Hawaiian Islands.

Glasby, C.J., 1997. A new species of *Namanereis* (Polychaeta: Nereididae: Namanereidinae) in groundwater of the Sultanate of Oman, Arabian Peninsula. *Beaufortia* 47(6): 157–162.

Glasby, C.J., M.E. Benbow, A.J. Burky & C.M. Way, 1998. New records of Namanereidinae (Polychaeta: Nereididae) from Hawaii. Records of the Hawaii Biological Survey for 1997. Part 2: Notes. *Bishop Museum Occasional Papers* 56: 67–70.

Full-text PDF of each one of the works in this volume are available at the following links :

Glasby, 1999, *Rec. Aust. Mus., Suppl.* 25: 1–129
http://dx.doi.org/10.3853/j.0812-7387.25.1999.1354

Glasby, 1999, *Rec. Aust. Mus., Suppl.* 25: 131–144
http://dx.doi.org/10.3853/j.0812-7387.25.1999.1355