

Reevaluation and New Species of *Kainonereis* Chamberlin, 1919 (Annelida: Polychaeta: Nereididae)

Víctor Manuel Conde-Vela^{1,*}, Xuwen Wu², and Sergio Ignacio Salazar-Vallejo¹

¹El Colegio de la Frontera Sur, Departamento de Ecología Acuática, Chetumal, Quintana Roo 77010, Mexico

²Department of Marine Organism Taxonomy and Phylogeny, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China

(Received 21 November 2017; Accepted 19 January 2018; Published 13 February 2018; Communicated by Benny K.K. Chan)

Citation: Conde-Vela VM, Wu X, Salazar-Vallejo SI. 2018. Reevaluation and new species of *Kainonereis* Chamberlin, 1919 (Annelida: Polychaeta: Nereididae). Zool Stud 57:6. doi:10.6620/ZS.2018.57-06.

Víctor Manuel Conde-Vela, Xuwen Wu, and Sergio Ignacio Salazar-Vallejo (2018) *Kainonereis* Chamberlin, 1919 was proposed to include only one species, *K. alata*, based on epitokes provided with elytriform structures in chaetigers 5-7. The species was thoroughly described and illustrated, but its unique features were enigmatic and the genus is currently regarded as *taxon inquirendum*. In order to have a better understanding of its diagnostic features and determine how this genus differs from similar ones, type material of *K. alata* and two other species bearing elytriform structures—*Nicon polaris* Hartman, 1967 and *Rullierinereis elytracirra* Sun and Wu, 1979, including additional material from Gulf of California and Caribbean Sea—were examined. Because the *K. alata* type material is in good condition and the presence of elytriform structures in chaetigers 5-7 is confirmed, this paper regards it as a valid genus. Given that the elytriform structures, or dorsal discs, together with a set of diagnostic features, are consistent in structure and position in all epitokes examined, they are regarded as homologous structures delineating *Kainonereis*. Consequently, *K. alata* is redescribed, the new combinations *K. polaris* comb. n. and *K. elytracirra* comb. n. are proposed and redescribed, and two new species are described: *K. chamberlini* sp. n. from the Caribbean Sea, and *K. peltifera* sp. n. from the Gulf of California. Also, the discovery of an atoke on *K. polaris* comb. n. allowed us to better distinguish *Kainonereis* from the similar genera *Nicon* Kinberg, 1865 and *Rullierinereis* Pettibone, 1971. A key to identifying all known *Kainonereis* species is also included.

Key words: Epitoky, Sexual dimorphism, Modified dorsal cirri, Dorsal discs, Polychaetes.

BACKGROUND

Epitoky is the most common reproductive method among nereidids and involves the transformation of benthic forms, or atokes, into pelagic forms, or epitokes (or heteronereis), for reproduction in the water column (Schroeder and Hermans 1975; Fischer 1999). The almost homogeneous body of atokes becomes regionally modified during epitoky into two or three regional patterns along the body: the non-natatory, natatory

and posterior regions (Read 2007). The body wall becomes very thin, and most inner organs are transformed into gonads, and some organs undergo hypertrophy. Among other changes, the eyes become expanded, the anterior cirri enlarged, dorsal cirri and ventral basally enlarged in first chaetigers, dorsal cirri usually become crenulated in natatory chaetigers of males, some parapodial lobes leaf-shaped, typical sipingers and falcigers are replaced by larger paddle-like chaetae in the natatory region, and the pygidium with papillae

*Correspondence: E-mail: victorconde2323@gmail.com

surrounding the anus, often arranged in rosette (Herpin 1925; Reish 1957; Fauvel 1959; Clark 1961; Schroeder and Hermans 1975; Fischer 1999).

The first observations of nereidid epitokes drove early authors to establish different genera for them, such as *Heteronereis* Ørsted, 1843, *Naumachius* Kinberg, 1865, *Nicomedes* Kinberg, 1865, *Eunereis* Malmgren, 1865, *Iphinereis* Malmgren, 1865, and *Hedyle* Malmgren, 1867 (Ørsted 1843; Kinberg 1865; Malmgren 1865, 1867). Detailed observations by Ehlers (1867) and Malmgren (1867, 1869) showed that these modified worms were actually reproductive forms of other already known genera. Among these, species in the genera *Heteronereis*, *Iphinereis*, *Naumachius*, and *Nicomedes* were regarded as reproductive forms of *Nereis* or *Nereilepas* species by Ehlers (1867), Chamberlin (1919:193) thought that species of *Hedyle* and *Naumachius* belonged to *Pseudonereis*, and Hartman (1948) regarded *Nicomedes* as indeterminable. Only *Eunereis* is currently recognized as valid (Bakken and Wilson 2005).

The use of nereidid epitokes as a source of diagnostic features has been limited, even to distinguish similar species (Smith 1958). Although some genera might show some similarities, other attributes besides pharyngeal armature and chaetae can be useful for generic identification, such as concretely parapodial features in epitokes. Further, it has been shown that parapodial transformation and other features such as anal papillation are sex-specific and reliable (Boilly-Marer 1972 1976). For example, most used features in *Platynereis* Kinberg, 1865 species include pigmentation patterns, length of anterior cirri, number of pre-natatory segments, shape of anal papillae in males, presence of unmodified posterior parapodia, and even oocyte color (Read 2007). Pamungkas and Glasby (2015) showed that the following are useful for epitoke identification: body patterns shared among epitokes of different genera, the number of body regions and if parapodia are modified or not in such regions, if both dorsal and ventral cirri are modified in non-natatory region, and if dorsal cirri are crenulated or smooth in the natatory region. In summary, pharyngeal and parapodial features are used to identify species and genera from epitokes by comparing their morphology with already known atokes.

It is now uncommon to use epitokes to establish genera and describe new species (e.g.

Chamberlin 1919; Horst 1924, Treadwell 1942; Read 2007). An interesting issue is if features regarded as diagnostic allow the reliable inclusion of epitokes in particular species or genera. Problems arise when atoke forms are unknown, or such atokal pharyngeal and parapodial features are no longer available after epitokal transformation because typically-used features for atoke-based genera and species are found in such structures (Gravier 1934; Fauchald 1977; Hartmann-Schröder 1977).

Kainonereis Chamberlin, 1919 provides a way to effectively define a genus using epitokes. Chamberlin (1919:196) examined unusual (greek: καινόος), pelagic nereidids from Kiribati in the Western Tropical Pacific. The most distinctive features he noted were highly modified bifid antennae and elytriform dorsal cirri in chaetigers 5-7, which are sufficient to propose a new genus for the species. Recently, the type species, *K. alata* Chamberlin, 1919, was regarded as *taxon inquirendum* (de León-González and Trovant 2013:73; Read 2018). This conclusion is problematic because the original description is long, detailed, and accompanied by good illustrations, its type material is in good condition, and its features are unique and distinctive. Besides, there are two species with elytriform cirri in chaetigers 5-7, *Nicon polaris* Hartman, 1967 and *Rullierinereis elytracirra* Wu and Sun, 1979, both species lacking paragnaths or papillae in their pharynx, and therefore closely related to *K. alata*. Additionally, two specimens with elytriform dorsal cirri in chaetigers 5-7 were discovered from the Caribbean Sea and four from the Gulf of California; we decide to compare these with the type material of *K. alata*.

In order to clarify its taxonomic status, we redescribe *K. alata* and emend *Kainonereis* based on parapodial features of both atokes and epitokes. To determine if *N. polaris* and *R. elytracirra* resemble the morphology of *K. alata*, type materials of these species are examined and redescribed. Two new *Kainonereis* species are also described. A key to all *Kainonereis* species is provided.

MATERIALS AND METHODS

Because *Kainonereis* is a monotypic genus, material from other species currently included in other genera were also studied if it included modified elytriform dorsal cirri along some

anterior chaetigers. All available specimens were examined, and only descriptions of type material were included.

Specimens belong to collections from the following institutions: LACM-AHF - Los Angeles County Museum of Natural History, Los Angeles; MBMCAS - Marine Biological Museum, Institute of Oceanology, Chinese Academy of Sciences; UMML - Marine Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Sciences, University of Miami; USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C.

All available specimens were examined under a stereomicroscope. When possible, specimens were whole-mounted and examined under a compound microscope to detect parapodial and chaetal changes along the body. Some specimens were stained with methyl-green to improve the visibility of structures. To observe parapodial features and chaetae under microscope, some parapodia were removed and mounted in semi-permanent slides with ethanol-glycerol. At first, four parapodia were examined and sometimes dissected to observe variations in the number of ligules developed on each chaetiger, one or two parapodia from chaetigers 5-7, another one from 8-12, and one or two from the natatory region; this scheme was followed in the species' descriptions.

All drawings and photographs are of epitokes, unless otherwise indicated. The photographs were taken with a digital camera with an adaptor for both microscopes. In some cases, a set of photographs were made and combined manually to improve composition in Adobe Photoshop®. Plates were prepared by assembling separate photos with Adobe Photoshop®. Because parapodial tissue is delicate in most specimens, drawings of parapodia from non-natatory and natatory regions were made to prevent repositioning and rupture of structures often overlapped or not easily recognizable. The drawings of parapodia were made in Illustrator®, and structures were slightly moved from their original positions to facilitate recognition without altering their real proportions. Also, in the photographs, natatory chaetae were digitally overexposed to improve recognition of finer parapodial structures.

Bakken and Wilson's (2005) terminology was followed to describe parapodia, and terms 'achaetous ring' and 'anterior cirri' were used instead of 'peristomium' and 'tentacular cirri', respectively, as suggested by Santos et al. (2005).

RESULTS

SYSTEMATICS

Order Phyllodocida Dales, 1962 Family Nereididae de Blainville, 1818

Genus *Kainonereis* Chamberlin, 1919

Kainonereis Chamberlin 1919:194 (key), 196 (etymol.).

Type species: Kainonereis alata Chamberlin, 1919, by original designation.

Diagnosis: (emended, new features highlighted in boldface). Two antennae, **separate (not fused)** or sometimes basally fused in male epitokes, **articulated** in some species. Four pairs of articulated anterior cirri. **Pharynx bare. Chaetigers 1 and 2 with neuroacicula only. Notopodial prechaetal lobes present, subconical to digitate in atokes, rounded in epitokes.** Body of epitokes divided into two regions (one pre-natatory and one natatory). Chaetigers 5-7 with dorsal cirri modified into elytriform structures or dorsal discs in epitokes. **Males with notopodial homogomph falcigers and spinigers in chaetigers 1-7. Females with notopodial homogomph spinigers in chaetigers 1-7. Notopodial dorsal ligule present from chaetiger 4 in males, chaetiger 3 in females.**

Distribution: Species of the genus are found in tropical, temperate and polar regions, from surface down to 935 m depth; habitat unknown.

Remarks: Species belonging to *Kainonereis* are easily identified by having elytriform dorsal cirri in chaetigers 5-7 only in epitokes. Chamberlin (1919) noted that their specimens were similar to other already described heteronereis; however, he considered two main attributes as sufficient to erect a new genus: the bifurcate appendages on the prostomium, and the elytriform structures on chaetigers 5-7. Even in the key, Chamberlin (1919:194) used the basally fused antennae as the main feature to separate it from all other genera. Also, he thought that *Kainonereis* was closely related to *Nereis* (Chamberlin 1919:197), perhaps after the epitokal condition of the specimens, and because he did not observe the everted pharynx.

K. alata has only been recorded once since its original description from the Eastern Tropical Pacific (Hernández-Alcántara and Solís-Weiss 1991:254). Two additional records of *Kainonereis* species have been made but in other genera: one from the Yellow Sea as a new species of

Rullierinereis Pettibone, 1971, *R. elyrocirra* by Wu and Sun (1979); and another from Antarctica as a new species of *Nicon* Kinberg, 1865, *N. polaris* by Hartman (1967).

It must be emphasized that atoke morphology of *Kainonereis* was unknown until now. An atoke specimen was found as part of *N. polaris*' type material, but it was not described even though it was available at the time of its first description (Hartman 1967:68). This specimen has bare pharynx, articulated anterior cirri, notopodial prechaetal lobes and only homogomph spinigers in notopodia, all these are diagnostic features of *Nicon* (de León-González and Trovant 2013:69). However, although roughly similar, there are sufficient features to separate *Kainonereis* atokes from *Nicon* ones (see below, under *K. polaris* (Hartman, 1967) comb. n.).

Subfamily placement: The subfamily affinities of *Kainonereis* have not been addressed previously. Even though *Kainonereis* was well described and illustrated, it was not included in previous phylogenetic analyses (Fitzhugh 1987; Santos et al. 2005), likely because the incompatibility of adding epitoke features are not compatible with an atoke-based matrix, avoiding unnecessary problems.

Based on the supposed relationship with *Nicon* and *Rullierinereis*, *Kainonereis* could be placed in Gymnonereidinae *sensu* Fitzhugh (1987), or in any subfamily in the Santos et al. (2005) phylogeny; it did not show close affinity with related genera *Nicon* and *Rullierinereis*, or with any other remaining genera, and therefore they could not be placed in a specific subfamily (Santos et al. 2005). Given that *Kainonereis* is not compliant with any subfamily as currently defined, it is regarded here as subfamily *incertae sedis*. This situation must not affect its recognition as a valid genus, since it can be separated from other genera without paragnaths or papillae.

Epitokal morphology

Kainonereis species share some distinctive epitokal features that diverge from typical nereidid morphology. To help recognize them, relevant features of the genus are summarized and illustrated in figure 1.

Parapodia

Based on the transformation of parapodia, epitokes have two body regions: a non-natatory

region comprising chaetiger 1 to 14, and a natatory region comprising chaetigers 15 to the end of the body. In turn, the non-natatory region is sub-divided into three regions, based on the modifications in parapodial cirri: a) chaetigers 1-4 with both dorsal and ventral cirri basally to medially swollen; b) chaetigers 5-7 with dorsal cirri elytriform and ventral cirri cirriform; c) chaetigers 8-14 with both dorsal and ventral cirri cirriform. Other relevant features are: the late appearing of notopodial dorsal ligule up to chaetiger 4 in males (Fig. 6E), while in females it appears from chaetiger 3 (Fig. 1D); the notopodial prechaetal lobes increase in size and become rounded, separating notably the dorsal and ventral notopodial ligules (Figs. 1D-E); and the absence of crenulated dorsal cirri in parapodia from natatory region of males.

The parapodia of the natatory region have a set of lamellae. Dorsal and ventral cirri develop two basal lamellae, one above or upper, and one below or lower of each cirrus (Fig. 1E); generally, the upper lamella is larger than the lower one in both cirri. Also, a larger, dorsal lamella is present, not always well defined and separated from the upper lamella of dorsal cirri (Fig. 1E). Moreover, neuropodial postchaetal lobes become modified into a large lamella, typically distally multilobate (Fig. 1E).

Dorsal discs

Chaetigers 5-7 are distinct by having modified elytriform structures (Figs. 1A-C). There were some doubts concerning how dorsal cirri are modified into elytra-like features, or if they are separate structures. In *K. elyrocirra* comb. n. (Wu and Sun 1979, Fig. 8d) and in *K. polaris* comb. n. (Hartman 1967, Pl. 19, Fig. B), the cirrostyle was illustrated as arising from the stalk, whereas in *K. alata*, it was illustrated as inserted to the elytriform structure (Chamberlin 1919, Pl. 28, Fig. 9). The examination of the type material of *K. elyrocirra* comb. n. and *K. polaris* comb. n. confirms that cirrostyles are not basal nor projected from the stalk, but rather arise from the elytriform structure.

Although there is no clear discontinuity, stalk and disc are distinguished in the cirrophores of *Kainonereis*: the stalk is the narrow, basal section, while the disc is the plate-like, distal one; it must be added that the disc surface has no ornamentation (Figs. 1A-C). The stalk is inserted in the lower disc surface, *i.e.*, a peltate insertion, as it is clear in *K. peltifera* sp. n. (Fig. 6B), but not so obvious in the other species. This is because their discs are not

rounded, and are arranged vertically in relation to the parapodium. The discs can be modified into thick structures, as in some specimens of *K. alata* and *K. chamberlini* sp. n. (Figs. 3F and 4E, respectively), likely resulting from the fixation process. Finally, the cirrostyles are the short, distal portion, generally attached to the lower surface of the discs (Figs. 1A-C), not always completely discernible.

Chaetae

Chaetae only include notopodial homogomph falcigers along chaetigers 3-7 in male epitokes. At first instance, the presence of notopodial homogomph falcigers in *K. alata* was regarded as a specific trait (Chamberlin 1919). However, females of *K. chamberlini* sp. n., *K. peltifera* sp. n. and *K. polaris* comb. n. do not have notopodial homogomph falcigers, only notopodial spinigers along chaetigers 3-14. This fact indicated sex-

related chaetal dimorphism in *Kainonereis* species. It is well known that epitoke males and females are dimorphic in parapodial morphology, but chaetal dimorphism is really rare in nereidids; one example is the presence of simple, ribbed chaetae in posterior chaetigers of males of *Platynereis pulchella* Gravier, 1899 and *P. polyscalma* Chamberlin, 1919 (Gravier 1899; Chamberlin 1919; Holly 1935).

Sex

Males were identified by the presence of whitish sperm bundles in coelom of *K. peltifera* sp. n., or free sperm in *K. alata* and *K. elytracirra* comb. n. Certainly, the morphology of sperm could not be observed directly under a compound microscope, but the whitish color, shape and position in body and parapodia of both bundles and free-floating tiny spheres are indicative of male gametes. A female specimen of *K. peltifera* sp. n.

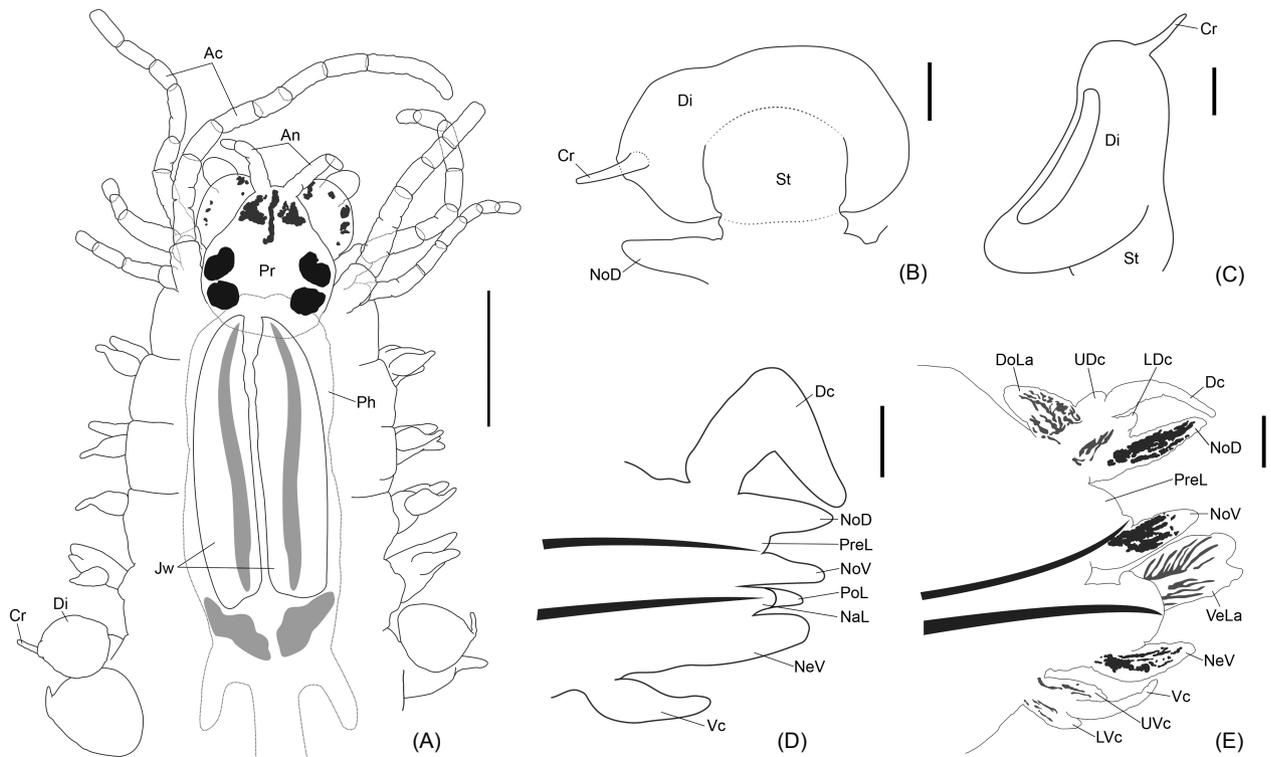


Fig. 1. Morphology of *Kainonereis* Chamberlin, 1919 species. *K. chamberlini* sp. n. A-C, E (USNM 1422199); *K. polaris* comb. n. D (USNM 55514). (A) anterior end, dorsal view (transparency, 10x); (B) elytriform dorsal cirrus from mounted parapodium 6, anterior view; (C) same, non-mounted, lateral view; (D) parapodium 3, anterior view; (E) parapodium 40, anterior view. Abbreviations: Ac, anterior cirri; An, antennae; Cr, cirrostyle; DoLa, dorsal lamella of dorsal cirri; Di, disc; Jw, jaws; LDc, lower lamella of dorsal cirrus; LVc, lower lamella of ventral cirrus; NaL, neuroacicular ligule; NeV, neuropodial ventral ligule; NoD, notopodial dorsal ligule; NoV, notopodial ventral ligule; Ph, pharynx; PoL, neuropodial postchaetal lobe; Pr, prostomium; PreL, notopodial prechaetal lobe; St, stalk; UDc, upper lamella of dorsal cirrus; UVc, upper lamella of ventral cirrus; Vc, ventral cirrus; VeLa, ventral neuropodial lamella. Scale bars: A = 0.3 mm; B-E = 50 µm. All chaetae omitted.

was the only one with few oocytes in coelom and parapodia. Epitoke specimens of *K. chamberlini* sp. n. and *K. polaris* comb. n. were identified as females after comparison with *K. peltifera* sp. n.

Key to species of *Kainonereis* Chamberlin, 1919 (epitokes)

1. Antennae basally fused, separated distally; palps directed ventrally *K. alata* Chamberlin, 1919 (Abaiang, Kiribati)
- Antennae free from each other, separated; palps directed forwards 2
2. Elytriform structures with discs large, almost covering the whole segment *K. polaris* (Hartman, 1967) comb. n. (Bransfield Strait, Antarctica)
- Elytriform structures with discs small, not covering whole segment 3
3. Chaetiger 10 with notopodial ligules digitate with blunt tips; neuropodial postchaetal lobes longer than neuroacicular ligules *K. elytracirra* (Wu and Sun, 1979) comb. n. (Yellow Sea, China)
- Chaetiger 10 with notopodial ligules conical with pointed tips; neuropodial postchaetal lobes shorter than neuroacicular ligules 4
4. Elytriform structures with discs thick, cup-like, perpendicular to body axis *K. chamberlini* sp. n. (La Guajira Peninsula, Colombia)
- Elytriform structures with discs thin, plate-like, parallel to body axis *K. peltifera* sp. n. (Gulf of California, Mexico)

Kainonereis alata Chamberlin, 1919 (Figs. 2A-B; 3A-K)

Kainonereis alata Chamberlin 1919:197-202, Pl. 28, Figs. 6-8, Pl. 29, Figs. 1-8.

Type material: Pacific Ocean, Kiribati. Holotype USNM 19388 and paratypes USNM 19386 (5), all males, R/V Albatross, Sta. H3964 (25°49'43"N, 171°43'37"W), off Apaiang, Gilbert Islands, Kiribati, 3 January 1900, Coll. United States Fish Commission.

Type locality: Off Abaiang (Apaiang), Kiribati, at surface.

Description: Holotype (USNM 19388) complete, male epitoke, 8.5 mm long, 0.8 mm wide at chaetiger 10, 50 chaetigers; delicate, bent backwards, several parapodia previously removed. Paratypes (USNM 19386) complete, male epitokes, 6-8 mm long, 1 mm wide at chaetiger 10, 50-54 chaetigers (Fig. 3A), presence of sperm in coelom. Body yellowish, tapering posteriorly (Fig. 3A), no staining pattern observed with green-methyl.

Prostomium as long as wide, pentagonal, anterior margin absent, medial shallow groove present; palps directed ventrally (Figs. 3B, C); eyes reddish, nearly rounded, anterior and posterior

pairs overlapped, sometimes pigments faded off (Fig. 3B). Antennae basally fused in a faintly annulated stem with two distal smooth articles, half as long as the stem (Figs. 3C, D). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles articulated, longest one reaching chaetiger 4 (Fig. 3B). Pharynx not everted; jaws enlarged, cutting edge with eight to nine teeth, faintly developed.

Body divided into two regions: 1) pre-natatory region include chaetigers 1-14, sub-divided into three regions; 2) natatory region from chaetiger 15 to end of body.

First two chaetigers with neuroacicularae only, remaining chaetigers with noto- and neuroacicularae. In chaetigers 1 and 2 (Fig. 3E), dorsal cirri swollen basally, tip narrow, digitate, distinctly separated from cirrophore. Dorsal ligule as long as neuropodial postchaetal one, digitate. Acicular neuropodial ligule rounded, postchaetal lobe digitate, twice longer than acicular ligule; neuropodial ventral ligule digitate, slightly longer than postchaetal lobe. Ventral cirrus pyriform, cirrostyle barely distinct.

Notopodial dorsal ligules absent in chaetiger 3 (Fig. 3H), present from chaetiger 4, as long as notopodial ventral ligule; remaining structures similar as in first two chaetigers.

In chaetigers 5-7 (Fig. 3F), dorsal disc petal-like, discs progressively larger, third one surpassing following segment; cirrostyle short, indistinctly separated from bases. Notopodial dorsal ligule as long as notopodial ventral one; both ligules tapering and separated by a short, digitate prechaetal lobe. Acicular neuropodial ligule subconical, as long as postchaetal lobe; neuropodial ventral ligule tapering, as long as acicular neuropodial lobe. Ventral cirrus cirriform, shorter than neuropodial ventral ligule.

In chaetigers 8-14 (Figs. 2A; 3G), dorsal cirrus digitate, as long as notopodial dorsal ligule. Both notopodial dorsal and ventral ligules digitate, subequal; both notopodial ligules separated by a large, rounded prechaetal lobe. Acicular neuropodial ligule subconical, slightly shorter than notopodial ventral ligule; postchaetal lobe rounded, half as long as acicular neuropodial ligule; neuropodial ventral ligule digitate, slightly swollen basally, as long as acicular neuropodial ligule. Ventral cirrus digitate, shorter than neuropodial ventral ligule.

Parapodia from 15 to end of body similarly modified throughout (Figs. 2B; 3I). Dorsal cirrus smooth, slender, as long as notopodial dorsal

ligule. Basal portion of dorsal cirrus with two small basal lamellae, upper lamella slightly longer than lower one; and one large, dorsal lamella, division between it and upper lamella conspicuous. Both notopodial dorsal and ventral ligules digitate, subequal; both notopodial ligules separated by a large, rounded prechaetal lobe. Acicular neuropodial ligule enlarged, digitate; postchaetal lobe enlarged into a lamella, longer and wider than acicular neuropodial ligule; neuropodial

ventral ligule digitate, medially inserted to acicular neuropodial ligule, shorter than it. Ventral cirrus cirriform, shorter than acicular neuropodial ligule, with two basal lamellae.

Notochaetae homogomph spinigers; homogomph falcigers in chaetigers 3-7. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

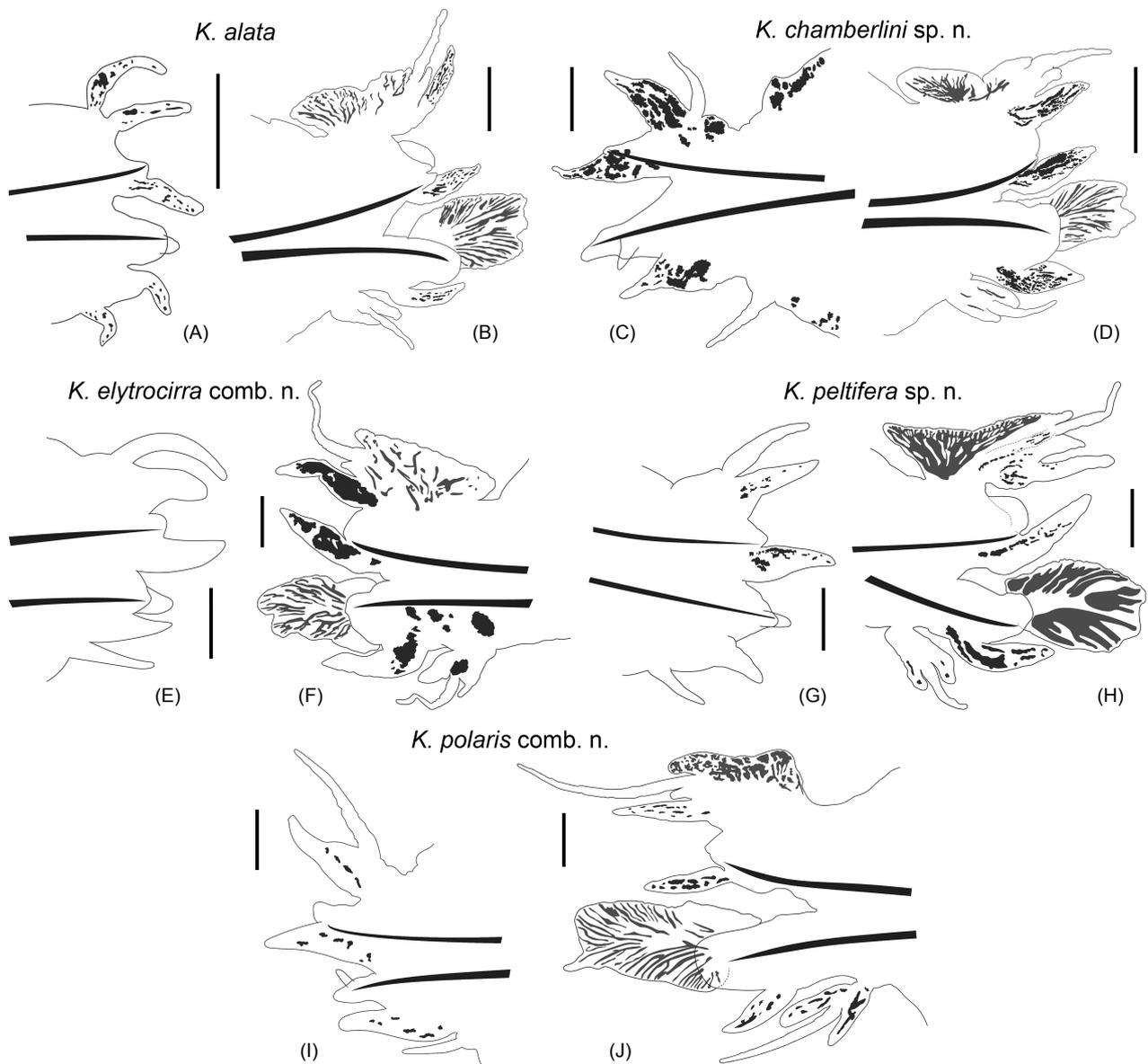


Fig. 2. Drawings from parapodia of *Kainoneis* species. *K. alata* A, B (USNM 19386); *K. chamberlini* sp. n. C (UMML 22.1126), D (USNM 1422199); *K. elyrocirra* comb. n. E, F (MBMCAS A-44); *K. peltifera* sp. n. G, H (LACM-AHF 7400p); *K. polaris* comb. n. I, J (USNM 55514). (A) parapodium 11, anterior view; (B) parapodium 40, anterior view; (C) parapodium 11, anterior view; (D) parapodium 25, anterior view; (E) parapodium 12, anterior view; (F) parapodium 20, anterior view; (G) parapodium 10, anterior view; (H) parapodium 22, anterior view; (I) parapodium 13, posterior view; (J) parapodium 30, posterior view. Scale bars: A, B = 50 μ m; C-H = 0.1 mm; I-J = 0.2 mm. E redrawn from Wu and Sun (1979:109). All chaetae omitted.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tip. Notopodial homogomph falcigers with minute falcate tips,

teeth minute (Fig. 3J). Neuropodial heterogomph spinigers pectinate, teeth fine, decreasing towards tip. Heterogomph falcigers pectinate, teeth minute,



Fig. 3. *Kainoneis alata* Chamberlin, 1919. Paratypes males (USNM 19386). (A) whole specimen, dorsal view; (B) anterior end, dorsal view; (C) anterior end, ventral view; (D) close-up of prostomium, dorsal view (arrow points beginning of ceratostyles); (E) parapodium 3, anterior view; (F) parapodium 5, anterior view; (G) parapodium 11, posterior view; (H) close-up of noto- and neuropodium, chaetiger 3 (dorsal and ventral cirri omitted); (I) parapodium 40, posterior view; (J) notopodial homogomph falciger, parapodium 2; (K) pygidium, dorsal view. Abbreviations: An, antennae; Pa, palps. Scale bars: A = 1 mm; B, C = 0.5 mm; D, K = 0.1 mm; E-I = 50 μ m; J = 10 μ m.

distal tooth stout, incurved, fused to blade; supra- and sub-acicular falcigers similar.

Pygidium not modified, with two lobes (Fig. 3K); anal cirri as long as last four chaetigers, lost in most specimens (Fig. 3K).

Remarks: The original description is long, detailed and accurate, but additional features have been included herein for improvement. There are, however, some differences to the original description: first, two chaetigers are not “biacicular”, but only have neuroaciculae; achaetous ring is dorsally as long as first chaetiger (only longer than it ventrally); the original illustration of the fourth chaetiger (Chamberlin 1919, Pl. 29, Fig. 1) is inverted; the parapodia in chaetigers 8-14 do not resemble those present in most-anterior ones, they differ in the shape of ligules and cirri; the natatory region begins at chaetiger 15, instead of 12; the color of the notopodial homogomph falcigers are not black or dark brown, but lighter as remaining chaetae.

Kainonereis alata is easily separated from remaining species because it has antennae with a ringed stem and bifurcated tips, and palps markedly directed downwards as is the case in some *Platynereis* species (Read 2007). The antennae of *K. alata* are markedly modified by being fused basally, such that the superficially annulated prolongation corresponds with the fused ceratophores, whereas the terminal, diverging appendages correspond to ceratostyles. Because of this, these antennae are herein referred to as basally fused antennae (Figs. 3C, D). This is a unique structure, as Chamberlin (1919:194) highlighted in his key (and we did in ours), but being restricted to a single species, this feature is herein regarded as a specific feature. The basally fused antennae likely are male-specific, but, as females were not found, this cannot be corroborated.

As in all males examined, the notopodial dorsal ligules appear from chaetiger 4 instead of chaetiger 3. This has been previously reported in some species, like *Sinonereis heteropoda* Wu and Sun, 1979 and *Typhlonereis gracilis* Hansen, 1879 (Wu and Sun 1979, Bakken 2003), but without sex distinctions; here, however, it is regarded as a male sexual feature in *Kainonereis*. The notopodial homogomph falcigers in males of *K. alata* are wider and shorter than those present in the males of *K. elyrocirra* comb. n. and *K. peltifera* sp. n. The shape of the dorsal discs of *K. alata* is similar to *K. polaris* comb. n., but they are shorter in *K. alata* than in *K. polaris* comb. n. Further differences

are included under the remarks sections of the remaining species.

***Kainonereis chamberlini* sp. n.**

(Figs. 1A-C, E; 2C-D; 4A-K)

urn:lsid:zoobank.org:act:1CD1B233-2D85-4ADA-B5C8-030C41AD2E53

Type material: Caribbean Sea, Colombia. Holotype USNM 1422199, female, R/V Pillsbury, Cruise 6806, St. 768 (12°33'N, 71°11'W), NE off La Guajira Peninsula, Colombia, 65 m, 28 July 1968. Northwestern Atlantic Ocean, Bahamas. Paratype UMML 22.1126, female, R/V Pillsbury, Cruise 6406, St. 197 (27°59'N, 79°20'W), NW Little Bahama Bank, 576 m, 11 August 1964.

Type locality: Northeastern off La Guajira Peninsula, Colombia, 65 m depth.

Etymology: Named after the late Dr. Ralph Vary Chamberlin, a very prolific taxonomist in several groups, as an homage to his work in polychaete taxonomy and proposing the genus *Kainonereis*.

Description: Holotype (USNM 1422199) complete, female epitoke, delicate, 8 mm long, 0.6 mm wide at chaetiger 10, 56 chaetigers (Figs. 4A-C). Paratype (UMML 22.1126) female epitoke complete, delicate, prostomium and posterior end damaged, anal cirri missing, 9 mm long, 0.5 mm wide at chaetiger 10, 58 chaetigers (Figs. 4D-E). Body yellowish, tapering posteriorly, stained with green-methyl to improve contrast, no staining pattern observed.

Prostomium longer than wide, pentagonal, anterior margin entire, medial shallow groove present; one pair of antennae, biarticulated, ceratophore three times longer than ceratostyle; eyes black, anterior eyes reniform, posterior ones ovate, anterior eyes slightly larger than posterior ones (Figs. 1A; 4B-C). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles articulated, longest one reaching chaetiger 6 (Figs. 1A; 4B-C). Pharynx not everted; jaws enlarged, cutting edge smooth (Fig. 1A).

Body divided into two regions: 1) pre-natatory regions include chaetigers 1-14, sub-divided into three regions; 2) natatory region from chaetiger 15 to end of body.

First two chaetigers with neuroaciculae only, remaining with both noto- and neuroaciculae. In chaetigers 5-7 (Figs. 1B-C; 4C, H), dorsal discs calyx-like (i.e. with a concave inner surface), cirrostyle narrow, laterally inserted. Notopodial

dorsal ligule as long as notopodial ventral one; both ligules digitate, separated by an intermediate rounded process. Acicular neuropodial ligule subconical, twice longer than postchaetal lobe; neuropodial ventral ligule digitate, slightly longer than acicular neuropodial lobe. Ventral cirrus cirriform, half as long as acicular neuropodial lobe.

In chaetigers 8-14 (Figs. 2C; 4I), dorsal cirrus cirriform, shorter than notopodial dorsal ligule. Notopodial dorsal ligule half as long as notopodial ventral one; both ligules subconical, tapering, and separated from each other; prechaetal lobe inconspicuous. Acicular neuropodial ligule subconical; postchaetal lobe digitate, half as

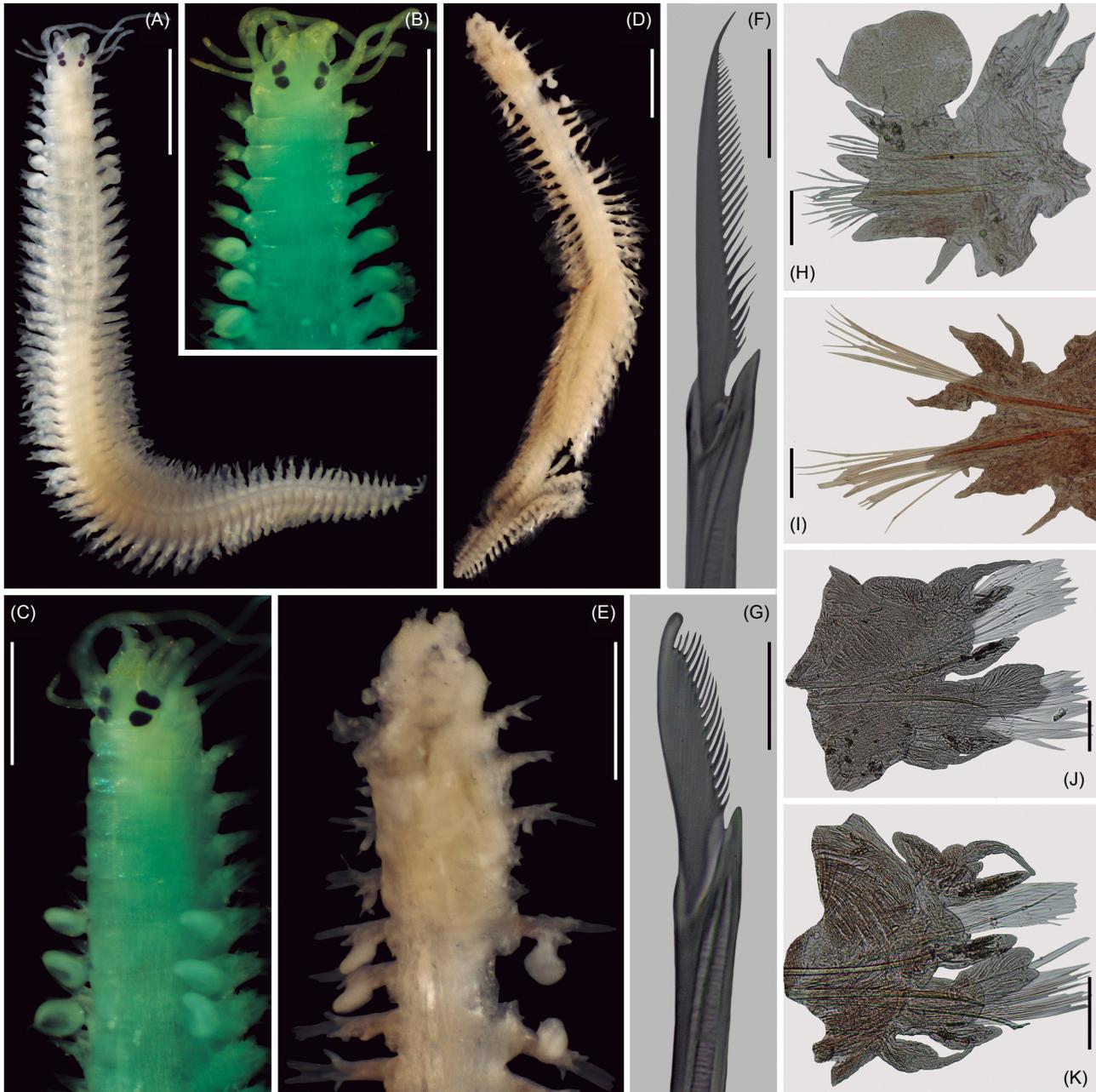


Fig. 4. *Kainonereis chamberlini* sp. n., A-C, F-H, J, K, holotype (USNM 1422199); D, E, I, paratype (UMML 22.1126). (A) whole specimen, dorsal view; (B) anterior end, dorsal view; (C) same, lateral view; (D) whole specimen, dorsal view; (E) same, lateral view; (F) neuropodial sub-acicular heterogomph spiniger, chaetiger 6; (G) neuropodial sub-acicular heterogomph falciger, parapodium 6; (H) parapodium 6, anterior view; (I) parapodium 11, anterior view; (J) parapodium 25, anterior view; (K) parapodium 40, anterior view. Scale bars: A, D = 1 mm; B, C, E = 0.5 mm; F, G = 10 μ m; H-K = 0.1 mm.

long as acicular neuropodial ligule; neuropodial ligule subconical, slightly shorter than acicular neuropodial lobe. Ventral cirrus cirriform, shorter than neuropodial ventral ligule.

Parapodia from 15 to end of body similarly modified throughout (Figs. 1E; 2D; 4J-K). Dorsal cirrus smooth, slender, as long as notopodial dorsal ligule, becoming slightly longer than towards posterior chaetigers, with two small basal lamellae, upper lamella slightly larger than lower one; dorsal lamella twice longer than upper one, distinction between it and upper lamella always conspicuous. Both notopodial dorsal and ventral ligules digitate to lanceolate, subequal; both notopodial ligules separated by a rounded process. Acicular neuropodial ligule digitate; postchaetal lobe becoming into a lamella, as wide as acicular neuropodial ligule, distal end bilobate; neuropodial ventral ligule digitate, medially inserted to acicular neuropodial ligule, slightly longer than it. Ventral cirrus cirriform, as long as acicular neuropodial ligule, with two small basal lamellae.

Notochaetae homogomph spinigers. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tip. Neuropodial heterogomph spinigers pectinate, teeth fine, decreasing towards tip (Fig. 4F); heterogomph falcigers pectinate, teeth fine, distal tooth stout (Fig. 4G), supra- and sub-acicular falcigers similar. Pygidium not modified, with two lobes; anal cirri faintly articulated, as long as last 3 segments.

Remarks: The study of material collected during the University of Miami Deep Sea Expeditions allowed us to find two specimens of this species and encouraged us to revise the genus. The specimens were found in two places and at different depths, with a distance of about 2000 km between them. Though the paratype is anteriorly damaged and diagnostic features such as antennae and anterior cirri are missing, parapodial features are almost identical to those present in the holotype.

The species can be recognized easily by its cup-like discs, shorter than remaining structures in the same parapodium. Paratype has discs compressed (laterally flattened), so the central hollow is inconspicuous, likely as consequence of the fixation process, but their size, shape and position are very similar to those present in the holotype. Other distinctive features are that dorsal

cirri are shorter than notopodial dorsal ligules, and notopodial ventral ligules are as long as acicular neuropodial ligules in chaetigers 8-14; whilst in remaining species, dorsal cirri are subequal to longer than notopodial dorsal ligules, and notopodial ventral ligules are longer than acicular neuropodial ligules. The jaws of *K. chamberlini* sp. n were observed through the partly transparent body wall, having an almost smooth cutting edge, presumably as a consequence of epitoky (Fig. 1A). Natatory parapodia of *K. chamberlini* sp. n resemble those found in *K. alata*, mainly in the clear differentiation between upper dorsal cirri and dorsal lamellae, and proportion of ligules and lamellae, but the two species can be separated by both the shape and proportion of elytriform structures, and shape of ligules along chaetigers 8-14.

***Kainonereis elytracirra* (Wu and Sun, 1979)
reinst., comb. n.
(Figs. 2E-F; 5A-K)**

Rullierinereis elytracirra Wu and Sun 1979:108-111, Figs. 8A-P; Wu et al. 1985:61-63, Fig. 32.

Kainonereis alata Sun and Yang 2004:72-73, Fig. 34 (*non* Chamberlin, 1919).

Type material: Yellow Sea, China. Holotype MBMCAS A-42 and paratype MBMCAS A-44 male, R/V Handan, Collection No. H130B-5, St. 3073 (34°30'N, 121°30'E), SW Yellow Sea, China, 20 m, 28 April 1959.

Type locality: Southwestern Yellow Sea, China, 20-25 m depth.

Description: Holotype (MBMCAS A-42) male epitoke complete, 13 mm long, 1 mm wide at chaetiger 10, 59 chaetigers, pharynx everted, anal cirri missing. Paratype (MBMCAS A-44) male epitoke complete, delicate, anal cirri missing, 12.5 mm long, 1 mm wide at chaetiger 10, 55 chaetigers (Figs. 5A-B), presence of sperm in coelom. One of the paratypes (MBMCAS A-43) missing. Body yellowish, tapering posteriorly, no distinct pigmentation pattern observed.

Prostomium slightly wider than long, pentagonal, anterior margin entire, medial shallow groove present; one pair of antennae, not articulated, tips eroded; eyes black, ovate, anterior eyes slightly larger than posterior ones (Fig. 5A). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles faintly articulated, tips eroded, longest one reaching chaetigers 4-5 (Figs. 5A-B). Pharynx smooth; jaws dentate, cutting edge with six teeth visible.

Body divided into two regions: 1) pre-natatory regions include chaetigers 1-14, sub-divided into three regions; 2) natatory region from chaetiger 15 to end of body.

First two chaetigers with neuroaciculae only, remaining chaetigers with noto- and neuroaciculae. In chaetigers 3-4 (Fig. 5G), cirrophore of dorsal cirrus swollen basally, ovate, tips narrow, digitate,



Fig. 5. *Kainoneis elyrocirra* (Wu and Sun, 1979) comb. n. Paratype male (MBMCAS A-44). (A) anterior end, dorsal view; (B) whole specimen, dorsal view; (C) notopodial homogomph falciger, parapodium 4; (D) neuropodial supra-acicular heterogomph falciger, parapodium 4; (E) neuropodial sub-acicular heterogomph falciger, parapodium 7; (F) neuropodial supra-acicular heterogomph spiniger, parapodium 4; (G) parapodium 4, anterior view; (H) parapodium 6, anterior view; (I) parapodium 7, anterior view; (J) parapodium 19, anterior view; (K) parapodium 44, anterior view. Scale bars: A, B = 1 mm; C-F = 10 μ m; G-K = 0.1 mm.

distinctly separated from bases. Notopodial dorsal ligule as long as notopodial ventral one, notopodial dorsal ligule absent in chaetiger 3; both ligules tapering and separated by a short, rounded prechaetal lobe. Acicular neuropodial ligule subconical, postchaetal lobe longer and narrower than acicular neuropodial ligule; neuropodial ventral ligule tapering, swollen basally and medially, distinctly larger than notopodial ligules. Ventral cirrus pyriform, longer than notopodial and neuropodial lobes.

In chaetigers 5-7 (Figs. 5H-I), dorsal discs elytriform, cirrostyle short, indistinctly separated. Notopodial dorsal ligule as long as notopodial ventral one; both ligules tapering and separated by a short, rounded prechaetal lobe. Acicular neuropodial ligule subconical, half as long as postchaetal lobe; neuropodial ventral ligule tapering, slightly longer than acicular neuropodial lobe. Ventral cirrus cirriform, subequal to neuropodial ventral ligule.

In chaetigers 8-14 (Fig. 2E), dorsal and ventral cirri slender, cirriform; dorsal cirrus slightly longer than notopodial dorsal ligule, ventral cirrus shorter than neuropodial ventral ligule. Notopodial and neuropodial lobes resembling to those present in chaetigers 5-7.

Parapodia from 15 to end of body modified (Figs. 2F; 5J-K). Dorsal cirrus smooth, slender, as long as notopodial dorsal ligule, with two small lateral, basal lamellae, and one large, dorsal lamella. Both notopodial dorsal and ventral ligules digitate to tapering, subequal; both notopodial ligules separated by a large, rounded prechaetal lobe. Acicular neuropodial ligule enlarged, subconical; postchaetal lobe becoming into a lamella, shorter and as wide as acicular neuropodial ligule, tip bilobate; neuropodial ventral ligule digitate to tapering, medially inserted to acicular neuropodial ligule, as long as it. Ventral cirrus cirriform, as long as acicular neuropodial ligule, with two basal, lateral lamellae.

Notochaetae homogomph spinigers; homogomph falcigers in chaetigers 3-7. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tip. Notopodial homogomph falcigers with blunt tips, teeth minute (Fig. 5C).

Neuropodial heterogomph spinigers pectinate, large teeth, decreasing towards tip (Fig.

5F); heterogomph falcigers pectinate, teeth coarse, distal tooth stout (Figs. 5D-E), supra- and sub-acicular falcigers similar.

Pygidium not modified, with two lobes; anal cirri missing.

Remarks: Wu and Sun (1979) made a study about *Nicon* Kinberg, 1865 and *Rullierinereis* Pettibone, 1971 species from China, including the proposal for a new genus, *Sinonereis*. In the key to genera, the unique feature used to distinguish *Nicon* and *Sinonereis* from *Rullierinereis* was the presence of notopodial falcigers in the latter, so it is not surprising they placed their new species in *Rullierinereis* because they had these chaetae. As a consequence, the diagnosis of *Rullierinereis* was extended to include species with elytriform dorsal cirri in anterior chaetigers, and one or two notopodial ligules in posterior chaetigers. Later, Wu et al. (1985) made an improved description of *R. elytracirra* and detailed that the described largest specimen (the holotype) was a female based on the absence of papillae (p. 63), but they did not explain which papillae they referred to. These papillae presumably are those found commonly in dorsal cirri of natatory parapodia of males, as they described for *Leonnates descipiens* Fauvel, 1919: "basalia of dorsal and ventral cirri of transformed parapodia inflated, dorsal cirri with 9-10 papillae" (Wu et al. 1985:71). However, males of *K. alata* and *K. peltifera* sp. n. do not develop such papillae, so such feature is not adequate to distinguish between sexes in this genus. Because the holotype and paratype of *K. elytracirra* comb. n. have other sex-related features as presence of notopodial homogomph falcigers in chaetigers 3-7 and the appearing of notopodial dorsal ligules since chaetiger 4, as well as the presence of sperm in the body, these type specimens were regarded as males.

Sun and Yang (2004) noted the resemblance between the modified dorsal cirri in *R. elytracirra* and *K. alata*, and consequently synonymized them. However, we disagree with these authors on this synonymy. The males of the latter species have basally fused antennae, articulate anterior cirri, palps are directed ventrally, notopodial ligules are as long as acicular neuropodial ones in chaetigers 5-7, and notopodial homogomph falcigers with long teeth (half as long as blade width); whilst in males of *K. elytracirra* comb. n., antennae are separated, palps are directed forwards, notopodial ligules are twice longer than acicular neuropodial ones in chaetigers 5-7, and notopodial homogomph falcigers have minute teeth; *K. elytracirra* comb. n.

resembles *K. chamberlini* sp. n. and *K. peltifera* sp. n., but the former can be recognized by the shape of notopodial dorsal ligules and large neuropodial postchaetal lobes at chaetiger 10, and also by the shape of discs in chaetigers 5-7.

***Kainonereis peltifera* sp. n.**

(Figs. 2G-H; 6A-N)

urn:lsid:zoobank.org:act:AC77BBDB-F6B4-4F3A-886E-FC130054D350

Type material: Pacific Ocean, Mexico. Holotype LACM-AHF 7400h male, paratypes LACM-AHF 7400p male (1) and LACM-AHF 7400p (2) females, R/V Velero III, Sta. 748-37 (21°52'20"N, 105°51'30"W), Isla Isabel, Nayarit, Gulf of California, anchorage, 2 April 1937, collecting gear electric light, Coll. Allan Hancock Foundation.

Type locality: Isla Isabel, Gulf of California, Mexico.

Etymology: Named after the Latin word *peltifer*, -a, -um, meaning 'carrying a pelta', referring to the chaetigers 5-7 bearing flat, rounded discs. Also, *pelta* (Gr. πέλιτη, a thin, rounded shield) is the stem of the Latin word *peltatus* (peltate), used to refer to a type of insertion of the petiole in the lamina of some leaves (e.g. in species of *Nelumbo* Adanson, 1763 or *Umbilicus* de Candolle, 1801); the central insertion of the stalk at the lower surface of the disc matches this kind of insertion.

Description: Holotype (LACM-AHF 7400h) complete, male epitoke, anal cirri missing, 10 mm long, 0.6 wide, 55 chaetigers. Paratypes (LACM-AHF 7400p) complete, male and females epitokes, anal cirri missing. Dissected paratype female, complete, 8 mm long, 0.5 mm wide at chaetiger 10, 50 chaetigers, few oocytes in coelom; dissected paratype male 10 mm long, 0.6 mm wide, 54 chaetigers, few whitish bundles of sperm in coelom. One paratype female with pharynx everted (Fig. 6C). Body off-white in males, yellowish in females, tapering posteriorly, no pigmentation pattern observed.

Prostomium wider than long, pentagonal, anterior margin entire, medial shallow groove present; one pair of antennae, not articulated; eyes black, ovate to reniform, anterior eyes slightly larger than posterior ones (Figs. 6A, C). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles articulated, longest one reaching chaetigers 3-4 (Fig. 6A). Pharynx smooth (Fig. 6C); jaws dentate, cutting edge with nine teeth visible (Fig. 6C).

Body divided into two regions: 1) pre-natatory regions include chaetigers 1-14, sub-divided into three regions; 2) natatory region from chaetiger 15 to end of body.

First two chaetigers with neuroaciculae only, remaining with noto- and neuroaciculae. In chaetigers 1 and 2 (Fig. 6D), cirrophore of dorsal cirrus swollen basally, ovate, cirrostyle narrow, digitate, distinctly separated from base. Dorsal ligule as long as neuropodial postchaetal one, digitate. Acicular neuropodial ligule subconical, postchaetal lobe digitate, twice longer than acicular ligule; neuropodial ventral ligule digitate slightly longer than postchaetal lobe. Ventral cirrus pyriform, cirrostyle slightly distinct.

Notopodial dorsal ligules present from chaetiger 3 in females, from chaetiger 4 in males (Fig. 6E), as long as notopodial ventral ones; remaining structures similar as in first two chaetigers in both sexes.

In chaetigers 5-7 (Fig. 6F), dorsal discs elytriform, cirrostyle short, distinctly separated. Notopodial dorsal ligule as long as notopodial ventral one; both ligules tapering and separated by a short, rounded prechaetal lobe. Acicular neuropodial ligule subconical, as long as postchaetal lobe; neuropodial ventral ligule tapering, slightly longer than acicular neuropodial lobe. Ventral cirrus cirriform, shorter than neuropodial ventral ligule.

In chaetigers 8-14 (Figs. 2G; 6G), dorsal and ventral cirri slender, cirriform; dorsal cirrus as long as notopodial dorsal ligule, ventral cirrus half as long as neuropodial ventral ligule. Notopodial and neuropodial lobes similar to those present in chaetigers 5-7.

Parapodia from 15 to end of body similarly modified throughout (Figs. 2H; 6H, I). Dorsal cirrus smooth, slender, as long as notopodial dorsal ligule. Cirrophores of dorsal cirrus with two small basal, lateral lamellae, upper lamella longer than lower one; and one large, dorsal lamella, division between it and upper lamella sometimes inconspicuous. Both notopodial dorsal and ventral ligules digitate, subequal; both notopodial ligules separated by a large, rounded prechaetal lobe. Acicular neuropodial ligule enlarged, digitate; postchaetal lobe becoming into a lamella, longer than, to subequal as, and as wide as acicular neuropodial ligule; neuropodial ventral ligule digitate, medially inserted to acicular neuropodial ligule, shorter than it. Ventral cirrus cirriform, as long as acicular neuropodial ligule, with two basal, lateral lamellae.

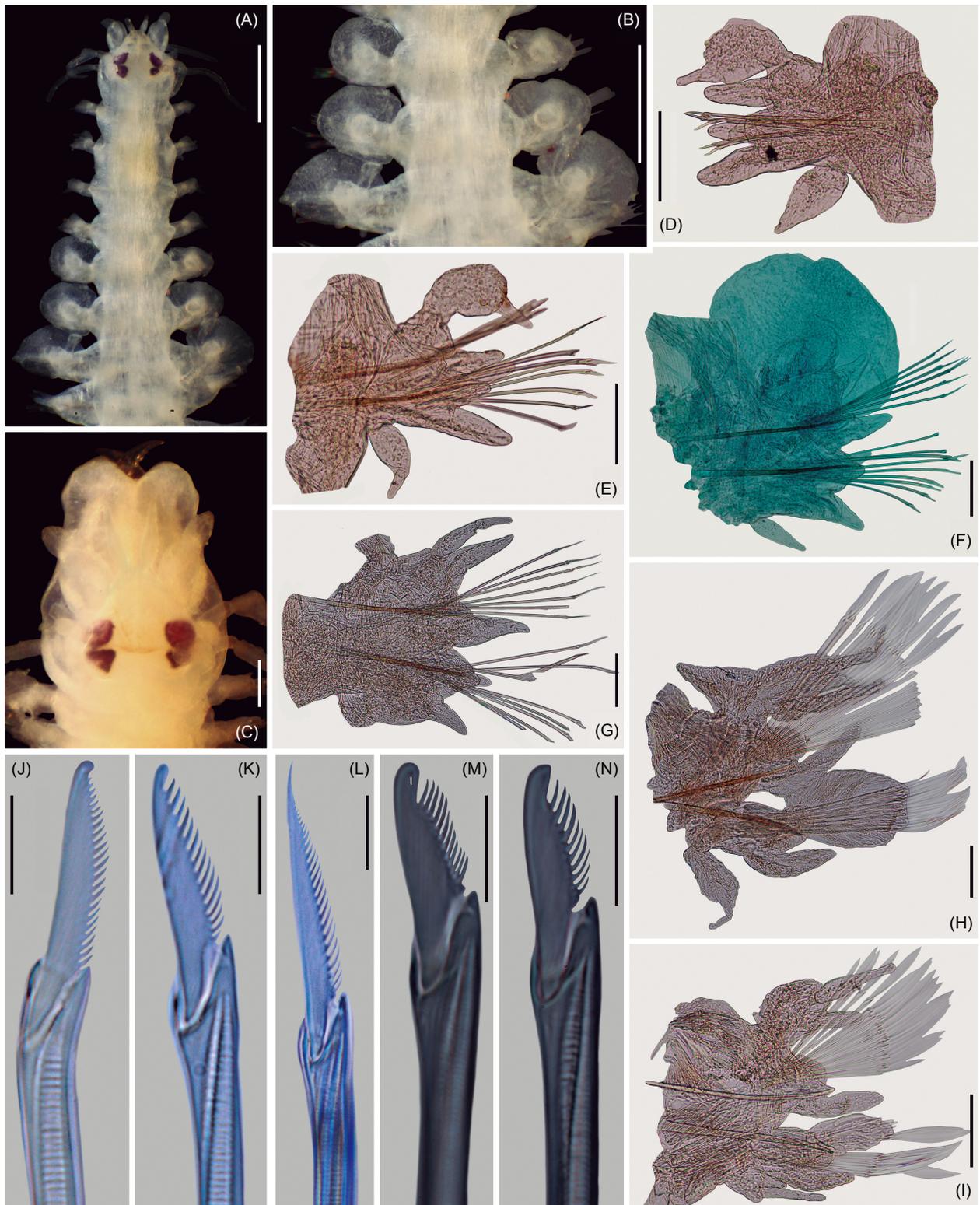


Fig. 6. *Kainonereis peltifera* sp. n. A, B, holotype male (POLY-AHF 7400h); E, J-L, paratype male (POLY-AHF 7400p); C, D, F-I, M, N, paratype females (POLY-AHF 7400p). (A) anterior end, dorsal view; (B) close-up of chaetigers 5-7, dorsal view; (C) close-up of anterior end, dorsal view; (D) parapodium 1, anterior view; (E) parapodium 3, anterior view; (F) parapodium 6, anterior view; (G) parapodium 10, anterior view; (H) parapodium 22, anterior view; (I) parapodium 45, anterior view; (J) notopodial homogomph falciger, parapodium 3; (K) neuropodial sub-acicular falciger, parapodium 3; (L) neuropodial sub-acicular spiniger, parapodium 3; (M) neuropodial supra-acicular falciger, parapodium 10; (N) neuropodial sub-acicular falciger, parapodium 10. Scale bars: A, B, = 0.5 mm; C-I = 0.1 mm; J-N = 10 μ m.

Notochaetae homogomph spinigers; homogomph falcigers in chaetigers 3-7 in males, absent in females. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tips. Notopodial homogomph falcigers with falcate tips, teeth minute (Fig. 6J). Neuropodial heterogomph spinigers pectinate, teeth fine, decreasing towards tips (Fig. 6L). Neuropodial heterogomph falcigers pectinate, teeth minute, distal tooth stout, incurved and fused to blade (Figs. 6K, M-N), sometimes inconspicuous; supra- and sub-acicular falcigers similar, both decreasing in size slightly towards posterior chaetigers.

Pygidium not modified (males or females), with two lobes; anal cirri lost.

Remarks: Hernández-Alcántara and Solís-Weiss (1991:254) likely recorded this as *K. alata* in the Gulf of California, because one of us (SISV) confirmed its generic affinities in the early 1980s; but their material is lost, preventing its confirmation (Solís-Weiss pers. comm.). The type material for this new species was originally identified as 'Nereid' by Olga Hartman, and later as *Nicon moniloceras* by Kristian Fauchald (Leslie H. Harris pers. comm.), likely after the bare pharynx and number of ligules.

This is the only species for which both sexes are known, allowing for direct comparison of their morphology. Chamberlin (1919:197) thought that dorsal discs were only present in males because his specimens were all males; however, elytriform structures are also present in females of *K. peltifera* sp. n. Other typical sex-related differences are missing as the dissimilar number of chaetigers in non-natatory region, or presence of crenulated dorsal cirri and anal papillae in males. The main differences between sexes is that males have notopodial homogomph falcigers in chaetigers 3-7, and lack notopodial dorsal ligules in chaetiger 3, whereas in females there are no homogomph falcigers, but they have notopodial dorsal ligules in chaetiger 3. The species *Typhlonereis gracilis* Hansen, 1879 is similar to *Kainonereis* species in that it lacks notopodial dorsal ligules in first chaetigers, but in *T. gracilis* notopodial dorsal ligules and notochoetae are absent in first four chaetigers and if it is a sex-specific feature could not be determined (Bakken 2003).

Specimens belonging to this species are quickly recognizable by the flat, rounded, delicate

discs in chaetigers 5-7 in both sexes. Males of this species differ from those of *K. alata* and *K. elyrocirra* comb. n.: *K. peltifera* sp. n. has a distinct, falcate distal tooth in notopodial falcigers, and their postchaetal lamellae are longer than acicular neuropodial ligules; whilst in *K. alata* and *K. elyrocirra* comb. n., notopodial falcigers have almost blunt distal ends, and postchaetal lobes are shorter to subequal than acicular neuropodial ligules. Moreover, *K. peltifera* sp. n. has an enlarged anterior end, resembling *K. alata* and *K. chamberlini* sp. n., but *K. peltifera* sp. n. differs clearly from *K. alata* in having separate antennae and from the *K. chamberlini* sp. n. in the shape of dorsal discs.

***Kainonereis polaris* (Hartman, 1967) comb. n.**
(Figs. 1D; 2I-J; 7A-I; 8A-K)

Nicon polaris Hartman 1967:68-69, Pl. 19, Figs. 19A-E.

Type material: Antarctic Ocean, Antarctica. Holotype USNM 55514, female epitoke, and paratype USNM 55515, atoke, R/V Eltanin, Sta. 432 (62°53'31.2"S, 59°21'W), South Shetland Islands, Nelson Island, Coll. University of Southern California, 884-935 m, 7 January 1963.

Type locality: Bransfield Strait, 884-935 m depth.

Epitoke description: Holotype (USNM 55514) complete, female epitoke, 22 mm long, 1 mm wide at chaetiger 10, 66 chaetigers. Specimen in good condition, body yellowish, tapering posteriorly, parapodia previously dissected, no staining pattern observed.

Prostomium wider than long, pentagonal, anterior margin entire, medial shallow groove present; one pair of antennae, not articulated; eyes faded, reddish, rounded, subequal, posterior eyes on lappets extended over achaetous ring (Fig. 7A). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles articulated, longest reaching chaetiger 5 (Fig. 7A). Pharynx bare; jaws dentate, cutting edge with 5-6 teeth visible, eroded teeth (Fig. 7C).

Body divided into two regions: 1) pre-natatory region include chaetigers 1-14, sub-divided into three regions; 2) natatory region from chaetiger 15 to end of body.

First two chaetigers with neuroaciculae only, remaining with both noto- and neuroaciculae. In chaetigers 3-4 (Fig. 1D), dorsal cirrus swollen basally, cirrostyle narrow, digitate, distinctly separated from cirrophore. Both notopodial dorsal

and ventral ligules digitate, subequal. Acicular neuropodial ligule subconical, half as long as postchaetal lobe; postchaetal lobe digitate; neuropodial ventral ligule digitate, slightly longer than postchaetal lobe. Ventral cirrus pyriform, cirrostyle slightly distinct.

In chaetigers 5-7 (Fig. 7D), dorsal discs petal-like, disc with thin, folded margin; cirrostyle narrow,

laterally inserted. Notopodial dorsal ligule as long as notopodial ventral one; both ligules subconical, separated by a short, rounded prechaetal lobe. Acicular neuropodial ligule subconical, as long as postchaetal lobe; neuropodial ventral ligule subconical, slightly longer than acicular neuropodial lobe. Ventral cirrus cirriform, half as long as acicular neuropodial lobe.



Fig. 7. *Kainonereis polaris* (Hartman, 1967) comb. n. Holotype female (USNM 55514). (A) anterior end, dorsal view (arrows point lappets); (B) posterior end, dorsal view; (C) anterior end, pharynx, ventral view; (D) parapodium 7, anterior view; (E) parapodium 13, anterior view; (F) parapodium 19, anterior view; (G) parapodium 30, anterior view; (H) neuropodial supra-acicular heterogomph falciger, parapodium 13; (I) neuropodial sub-acicular heterogomph falciger, parapodium 13. Scale bars: A = 1 mm; B, C = 0.5 mm; D-G = 0.2 mm; H, I = 10 μ m.

In chaetigers 8-14 (Figs. 2I; 7E), dorsal cirrus cirriform, as long as notopodial dorsal ligule. Both notopodial dorsal and ventral ligules subequal,

subconical, tapering, separated by a short, digitate prechaetal lobe. Acicular neuropodial ligule subconical; postchaetal lobe digitate, half as long



Fig. 8. *Kainonereis polaris* (Hartman, 1967) comb. n. Paratype atoke (USNM 55515). (A) anterior end, dorsal view; (B) close-up of prostomium; (C) anterior end, pharynx, ventral view; (D) tube; (E) notopodial homogomph spiniger, parapodium 13 (insert: close-up of teeth); (F) neuropodial sub-acicular heterogomph falciger, parapodium 13; (G) neuropodial sub-acicular heterogomph spiniger, parapodium 1; (H) parapodium 1, anterior view; (I) parapodium 3, anterior view; (J) parapodium 13, anterior view; (K) parapodium 37, anterior view. Scale bars: A-D = 0.5 mm; E = 20 μ m; F, G = 10 μ m; H-K = 0.2 mm.

as acicular neuropodial ligule; neuropodial ligule subconical, as long as acicular neuropodial lobe. Ventral cirrus cirriform, half as long as acicular neuropodial lobe.

Parapodia from 15 to end of body similarly modified throughout (Figs. 2J; 7F-G). Dorsal cirrus smooth, twice longer than notopodial dorsal ligule, with two small basal, lateral lamellae, upper lamella larger than lower one; dorsal lamella twice longer than upper one, division between it and upper lamella slightly conspicuous. Both notopodial dorsal and ventral ligules digitate, subequal; both notopodial ligules separated by a large, rounded prechaetal lobe. Acicular neuropodial ligule digitate; postchaetal lobe becoming into a lamella, as wide as and longer than acicular neuropodial ligule, tip with a rounded lobe and a small apex; neuropodial ventral ligule digitate, medially inserted to and half as long as acicular neuropodial ligule. Ventral cirrus cirriform, as long as acicular neuropodial ligule, with two large basal lamellae.

Notochaetae homogomph spinigers. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tip. Neuropodial heterogomph spinigers pectinate, teeth fine, decreasing towards tip. Neuropodial heterogomph falcigers pectinate, teeth minute, distal tooth stout, incurved, fused to blade (Figs. 7H-I); supra- and sub-acicular falcigers similar, both decreasing in size slightly towards posterior chaetigers.

Pygidium with two lobes (Fig. 7B); anal cirri as long as last seven chaetigers (Fig. 7B).

Atoke description: Paratype (USNM 55515) incomplete, 16 mm long, 1 mm wide at chaetiger 10, 40 chaetigers. Specimen in good condition, body yellowish, tapering posteriorly, no pigmentation pattern observed. Tube flexible, incorporating fine sediment particles, with algal stipe-like structures and shell fragments attached (Fig. 8D).

Prostomium wider than long, pentagonal, anterior margin entire, medial shallow groove present; one pair of antennae, not articulated; eyes faded, subequal, posterior eyes lappets absent (Figs. 8A, B). Achaetous ring as long as first chaetiger; anterior cirri with distinct cirrophores, cirrostyles articulated, longest anterior cirri reaching chaetigers 9-10 (Fig. 8A). Pharynx bare; jaws dentate, cutting edge with 6-7 visible teeth (Fig. 8C).

Parapodial cirri pattern. Dorsal cirri cirriform, longer than notopodial dorsal ligules throughout body; basally inserted on anterior region, displaced medially toward posterior body. Ventral cirri cirriform, basally inserted throughout body, subequal to neuropodial ventral ligules in anterior region, progressively diminishing in size, becoming half as long as ventral ligules towards posterior end.

First two chaetigers with neuroaciculae only, remaining with both noto- and neuroaciculae. In chaetigers 1-2 (Fig. 8H), dorsal cirrus cirriform, 1.5 times longer than dorsal ligule. Dorsal ligule as long as postchaetal lobe and neuropodial ventral ligule; acicular neuropodial ligule subconical, half as long as postchaetal lobe.

Ventral cirrus cirriform, as long as neuropodial ventral ligule.

In chaetigers 3-4 (Fig. 8I), notopodial dorsal ligule present, as long as notopodial ventral one; remaining structures as in first two chaetigers.

In anterior and middle chaetigers (Fig. 8J), dorsal cirrus cirriform, slender, 1.2 times longer than notopodial dorsal ligules. Both notopodial dorsal and ventral ligules subequal, conical, tapering, twice longer than prechaetal lobe; prechaetal lobe digitate. Acicular neuropodial ligule subconical, twice longer than postchaetal lobe; postchaetal lobe digitate; neuropodial ventral ligule subconical, tapering, as long as acicular neuropodial ligule. Ventral cirrus cirriform, half as long as neuropodial ventral ligule.

In posterior chaetigers (Fig. 8K), dorsal cirrus more displaced medially; remaining structures as in anterior and middle chaetigers.

Notochaetae homogomph spinigers. Neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles; heterogomph spinigers and falcigers in sub-acicular fascicles.

Notopodial homogomph spinigers pectinate, teeth decreasing in size towards tip (Fig. 8E). Neuropodial heterogomph spinigers pectinate, teeth fine, decreasing towards tip, shorter than notopodial ones (Fig. 8G). Neuropodial heterogomph falcigers pectinate, teeth minute, distal tooth stout, incurved, fused to blade (Fig. 8F); supra- and sub-acicular falcigers similar, both decreasing in size slightly towards posterior chaetigers.

Pygidium missing.

Remarks: *Kainonereis polaris* comb. n. is easily recognized by having dorsal cirri twice longer than notopodial dorsal ligules and large

postchaetal lamellae with a distal apex in natatory parapodia; whilst remaining species have dorsal cirri subequal and postchaetal lamellae with one or two rounded, distal lobes. This species has a remarkable prostomial modification, which was called 'lappets' by Hartman, clearly illustrated in the original drawing (Hartman 1967, Fig. 19A). The lappets consist of a hypertrophy of the posterior prostomial margin and carry the posterior eyes (Fig. 7A). Like the hypertrophied antennal bases in *K. alata*, these features are regarded as exclusively present in *K. polaris* comb. n. Further, although their presence was not used as a diagnostic feature for this species, they cannot be regarded as a preservation artifact. Furthermore, the petal-like discs resemble those found in *K. alata*, but in *K. polaris* comb. n. they are large, covering the complete dorsal surface of the corresponding chaetiger, whilst in *K. alata* they are short, not covering the chaetigers.

Hartman (1967:68) included two specimens in her description, one was indicated as the type and as an epitoke, but for the atoke she wrote (Hartman 1967:69): "Its atokous stage has not been identified." The comparison of prostomial shape, antennae, eyes, jaws, anterior cirri, the absence of pharyngeal ornamentation, the almost identical shape of parapodial processes and chaetae along chaetigers 8-14, ensure the conspecificity of atoke specimen with the epitoke one. This is the only *Kainonereis* species of which the atokous stage is known. A remarkable feature is the appearing of notopodial dorsal ligule from chaetiger 3 as in epitokal females of other species. Also, the vial with the atoke also contains a tube, as wide as the worm, such that if it belonged to the atoke, at least this species has tubiculous habits. In all *Kainonereis* species, blades of neuropodial falcigers are subequal, finishing in an incurved, fused tooth, giving them a hooked appearance, as usual in other tubiculous genera such as *Platynereis* (e.g. Daly 1973; Read 2007; Cañete et al. 2013; Darbyshire 2014, Merz 2015).

This species was originally regarded as belonging to *Nicon*; however, Hartman recognized the high dissimilarity among conspecifics (Hartman 1967:68). The features she recognized as relevant were the diverging antennae, dentition of jaws, and the prostomial posterior prolongations (lappets) carrying the posterior eyes (Hartman 1967:69), but not the elytriform cirri in chaetigers 5-7. The only *Nicon* species known with fully developed heteronereis is *N. aestuarensis* Knox, 1951, but it differs from epitokes of *Kainonereis* by having

smooth anterior cirri, only one large lamella above dorsal cirri, notopodial ventral ligules develop a lamella, and lack large, rounded prechaetal lobes separating considerably the notopodial ligules (Knox 1951).

Atoke specimens could be easily confused with other *Nicon* species, especially because the contemporary (e.g. Hartman 1958) and current (de León-González and Trovant 2013) generic diagnosis overlap features such as the bare pharynx, notopodial prechaetal lobes and only homogomph spinigers in notopodia. Based on the presence of notopodial prechaetal lobes, *N. polaris* was regarded as resembling *N. aestuarensis*, *N. japonicus* Imajima, 1972, *N. rotunda* Hutchings and Reid, 1990, and *N. sinica* Wu and Sun, 1979 (de León-González and Trovant 2013:70). Although, these species differ notably from *K. polaris* comb. n.: *N. japonicus* lacks articulated anterior cirri, and its neuropodial falcigers are anchylosed; *N. rotunda* has neuropodial homogomph falcigers in anterior chaetigers, and lacks heteronereis phase; and *N. sinica* has distally, faintly annulated (not articulated) anterior cirri (Imajima 1972, Wu and Sun 1979, Hutchings and Reid 1990). Finally, in the short redescription of *Nicon pictus* Kinberg, 1865 (type species of *Nicon*), Hartman (1948) included the presence of neuropodial homogomph falcigers, and large postchaetal lobe in posterior chaetigers; these features are absent in the atoke of *K. polaris* comb. n. It may be noted that *Kainonereis* is a better-defined set of species in comparison to *Nicon* that currently includes different body patterns with distinct features (De León-González and Trovant 2013).

The atoke of *K. polaris* comb. n. also differs from *R. zebra*, the type species of *Rullierinereis* Pettibone, 1971, in both having notopodial dorsal ligules and lacking notopodial homogomph falcigers in posterior chaetigers. In *Rullierinereis*, *R. mexicana* was described based on male and female specimens, being the only species with known epitokes. It can be easily separated from *Kainonereis* species because it has three body regions instead of two, and males lacks notopodial homogomph falcigers and elytriform structures in chaetigers 5-7 (Treadwell 1942, Hartman 1956, Pettibone 1971).

DISCUSSION

Prostomial features

The highly modified prostomial features of *K. alata* and *K. polaris* comb. n. deserve additional comments, especially because the absence of some of these features has been used to separate genera in Nereididae. For example, *Unanereis* Day, 1962 has only one antenna, but it looks like a *Ceratonereis* Kinberg, 1866 in most morphological features. Because it was based on one specimen, the presence of a single antenna might be the result of a complete fusion between the usually separate antennae; this has been documented as a common anomaly in some nereidids (Coutinho and Santos 2014; Sawestri 2013). *Dawbinia* Benham, 1950 is similar to *Unanereis* by having one antenna, but its morphology rather resembles a *Namanereis* Chamberlin, 1919 (likely a third pair of anterior cirri and notopodial aciculum in figure 3E were overlooked or detached), a genus with one species that lacks antennae, *N. malaitae* (Gibbs, 1971). Another case is *Micronereis* Claparède, 1863, unique among nereidids because, among other things, it lacks antennae and has less complex parapodial structures.

In *Kainonereis* species, the antennae of two species have remarkable modifications: in *K. alata*, the ceratophores are basally fused; whilst in *K. chamberlini* sp. n., they have two articles, where the ceratophores are several times longer than ceratostyles (Fig. 1A). We think that the antennae are basally and medially fused, and this might also be a lateral fusion of antennae, but we cannot discard it as an anomaly, even if this feature is present in all type specimens. Additional atoke toptype specimens might help clarify this issue. On the other hand, prostomial lappets in *K. polaris* are so unique that they do not resemble any epitokal modification found in other nereidids.

The anterior cirri of all species, even in atokous stage, have distinct cirrophores and articulated cirrostyles. The cirrostyles of anterior cirri are fragile, dehiscent; probably explained by this same loss of articles, anterior cirri in most specimens are short, reaching chaetigers 4-6 in epitokes. It is likely that other species have articulated antennae, but the ceratostyles were lost during sampling or processing of specimens.

Dorsal discs

By their shape and position, elytriform

structures are similar to those found in polynoids or sigalionids, where elytrae are regarded as modified dorsal cirri (Plyuscheva and Martin 2009), although the presence of both, dorsal cirri and elytrae in the same segment does not support this idea (Darboux 1899; Pleijel 2001). There are, however, some important differences between true elytrae and elytriform structures. In scale worms, elytrae are conformed by an elytron and an elytriphore (or stalk), where the elytron is the plate-like structure composed by epithelium and cuticle (Plyuscheva and Martin 2009), having several modifications with diagnostic importance. In turn, the elytriphore is an external hollow projection including elements of body wall and trunk coelom (Wilkie 2011); further, the elytriphore can have other elements allowing the detachment of elytron, *i.e.*, it is a complex structure (Wilkie 2011).

Conversely, elytriform structures in *Kainonereis* seemingly lack a bipartite organization or internal complexity; they lack any articulation and are instead formed by a continuous tissue. Further, all specimens have a small marginal cirriform projection (cirrostyle) in the expanded part. These elytriform structures are regarded as modified dorsal cirri, such that the cirrophore corresponds with both the peduncle and the depressed, expanded disc, and the cirrostyle correspond with the small, digitate marginal projection at the the lower surface of discs (Figs. 1B-C).

Kainonereis as a distinct genus

All epitokes examined share the presence of dorsal discs in chaetigers 5-7. Because the dorsal discs have similar a form (structural criterion) and are at the same position along the body for all epitokes (positional criterion) (Remane 1952:63-64, Williams and Ebach 2008:140), they are regarded as homologous, and because we assume that these similarities are due to a common ancestor, the dorsal discs are also regarded as homogenous (Fitzhugh 2006:58); this reasoning was also applied for all the remaining structures discussed in this paper. This leads us to conclude that *Kainonereis* is a monophyletic group, diagnosed mainly by the presence of dorsal discs and other remarkable features such as truly articulated anterior cirri, dorsal lamellae of dorsal cirri, and notopodial ligules being clearly separated by a large prechaetal lobe.

The reason the currently defined *Kainonereis* species were regarded as belonging to other,

closely related genera such as *Nicon* or *Rullierinereis* is because generic delineations were not clearly set off. First, finding a bare pharynx in *N. polaris* drove Hartman (1967:68) to include it in that genus. Pettibone (1971:4, 5, 8) considered the generic affinity of *N. polaris* as uncertain but she did not explain why, whereas de León-González and Trovant (2013:73) correctly pointed out the presence of elytriform dorsal cirri as a feature better resembling *Kainonereis* than *Nicon*. Second, in *R. elytracirra* the presence of notopodial homogomph falcigers made Wu and Sun (1979:106) include their species in *Rullierinereis*, but later Sun and Yang (2004) regarded *R. elytracirra* as belonging to *Kainonereis* based on the presence of elytriform dorsal cirri.

It might seem problematic to delineate separate nereidid genera on the basis of epitokes alone because of the complex body transformations involved. For reproductive patterns in Nereididae, after the compilation by Reish (1957, table 1), 9 out of 19 species undergo epitoky, and two others swarm, but their bodies are not modified, and these different reproductive patterns are present within the same genus. Clark (1977) showed that what has been regarded as a single species, turned out to include three different reproductive patterns, probably indicating they are different species as well. All species in *Kainonereis* undergo epitoky, but chances are that some undiscovered species might differ because this reproductive pattern cannot be generalized to the other species in the genus.

Acknowledgments: This work and the new species names have been registered with ZooBank under urn:lsid:zoobank.org:pub:BAF0F24B-5A7E-461D-9FD8-973477FB584A. VMCV thanks Leslie H. Harris and David Ocker for housing facilities, and to LHH by allowing the examination and loan of non-catalogued lots. The authors also thank Nancy Voss for the loan of specimens from the UMML collection, and to Geoff Keel and Karen Osborn for their kind support during a research visit in Washington; also, VMCV acknowledges the support of these colleagues for the deposition of specimens in their respective collections at charge. The authors thank the valuable suggestions by Geoffrey Read and an anonymous reviewer in an early submission in another journal, and two anonymous reviewers for their accurate recommendations in the ZS submission. VMCV has a PhD scholarship from CONACyT (586685).

Author's contributions: VMCM and SISV designed the study and wrote the manuscript. SISV examined *K. alata*, XW examined *K. elytracirra*, and VMCV examined the remaining species. All authors participated in revising the manuscript. All authors read and approved the final manuscript.

Competing interests: VMCV, XW and SISV declare that they have no conflict of interest.

Availability of data and materials: specimens here used are deposited in public collections (LACM-AHF, MBMCAS, UMML, USNM).

Consent for publication: not applicable.

Ethics approval consent to participate: not applicable.

REFERENCES

- Adanson. 1763. Familles des Plantes, 2 vols. Vincent, Paris.
- Bakken T. 2003. Redescription and resurrection of *Typhlonereis gracilis* Hansen, 1879 (Polychaeta, Nereididae). *Sarsia* **88**:346-352. doi:10.1080/00364820310002894.
- Bakken T, Wilson RS. 2005. Phylogeny of nereidids (Polychaeta, Nereididae) with paragnathids. *Zool Scr* **34**(5):507-547. doi:10.1111/j.1463-6409.2005.00200.x.
- Benham WB. 1950. Polychaeta and Oligochaeta of the Auckland and Campbell Islands. *Cape Exped Ser Bull* **10**:1-26.
- Boilly-Marer Y. 1972. Sur la signification et le déterminisme des caractères sexuels somatiques chez les Nereidae (Annélides polychètes). *Arch Zool Exp Gen* **113**:369-393.
- Boilly-Marer Y. 1976. Stabilité de la détermination et de la différenciation de caractères sexuels somatiques chez *Nereis pelagica* L. (Annélide Polychète). *J Embryol Exp Morph* **36**(1):183-196.
- Cañete JI, Cárdenas CA, Palacios M, Barria R. 2013. Presencia de agregaciones reproductivas pelágicas del poliqueto *Platynereis australis* (Schmarda, 1861) (Nereididae) en aguas someras subantárticas de Magallanes, Chile. *Lat Am J Aquat Res* **41**(1):170-176.
- Chamberlin RV. 1919. The Annelida Polychaeta of the *Albatross* Tropical Pacific Expedition, 1891-1905. *Mem Mus Comp Zool Harv Coll* **48**:1-514, and plates.
- Claparède R-É. 1863. Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie angestellt. Wilhelm Englemann, Leipzig, pp 120.
- Clark RB. 1961. The origin and formation of the heteronereis. *Biol Rev* **36**(2):199-236. doi:10.1111/j.1469-185X.1961.tb01584.x.
- Clark RB. 1977. Reproduction, speciation and polychaete taxonomy. In: Reish DJ, Fauchald K (eds) *Essays on the Polychaetous Annelids in Memory of Dr Olga Hartman*. Allan Hancock Found, University of Southern California, California, pp. 477-501.
- Coutinho MCL, Santos CSG. 2014. Morphological anomalies

- in polychaetes: *Perinereis* species (Polychaeta: Annelida) examples from the Brazilian coast. *Mem Mus Vic* **71**:45-51.
- Daly JM. 1973. Behavioural and secretory activity during tube construction by *Platynereis dumerilii* Aud & M. Edw. [Polychaeta: Nereidae]. *J Mar Biol Assoc UK* **53**(3):521-529.
- Darboux JG. 1899. Recherches sur les aphroditiens. *Trav Inst Zool Univ Montp St Marit Cette, n sér, Mem* **16**:1-276.
- Darbyshire T. 2014. Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of *Gymnonereis*. *ZooKeys* **427**:75-108. doi:10.3897/zookeys.427.7296.
- Day JH. 1962. Polychaeta from several localities in the Western Indian Ocean. *P Zool Soc Lond* **139**:627-656. doi:10.1111/j.1469-7998.1962.tb01597.x.
- De Candolle AP. 1801. Extrait d'un mémoire sur la famille des Joubarbes. *Bull Sci Soc Philomat Paris* **3**:1-2.
- de León-González JÁ, Trovante B. 2013. A new species of *Nicon* Kinberg, 1866 (Polychaeta, Nereididae) from Ecuador, Eastern Pacific, with a key to all known species of the genus. *ZooKeys* **269**:67-76. doi:10.3897/zookeys.269.4003.
- Ehlers E. 1867. Die Gattungen *Heteronereis* (Oerd) und ihr Verhältniss zu den Gattungen *Nereis* (Gr) und *Nereilepas* (Gr). *Nachr Konigl Ges Wiss Georg-Augusts-Univ Gott* **1867**:209-217.
- Fauchald K. 1977. The polychaete worms: Definitions and keys to the orders, families and genera. *Nat Hist Mus Los Angel Cty Sci Ser* **28**:1-190.
- Fauvel P. 1959. Classe des Annélides Polychètes: Annelida, Polychaeta (Grube, 1851). In: Grassé PP (ed) *Traité de Zoologie Anatomie, Systématique, Biologie*. Paris, pp. 12-196.
- Fischer A. 1999. Reproductive and developmental phenomena in annelids: a source of exemplary research problems. *Hydrobiologia* **402**:1-20. doi:10.1023/A:1003719906378.
- Fitzhugh K. 1987. Phylogenetic relationships within the Nereididae (Polychaeta): implications at the subfamily level. *Bull Biol Soc Wash* **7**:174-183.
- Fitzhugh K. 2006. The abduction of phylogenetic hypotheses. *Zootaxa* **1145**:1-110.
- Gibbs PE. 1971. The polychaete fauna of the Solomon Islands. *Bull Br Mus (Nat Hist)* **21**:101-211.
- Gravier C. 1899. Contribution à l'étude des Annélides Polychètes de la Mer Rouge. *Bull. Mus Natl Hist Nat* **5**:234-244.
- Gravier C. 1934. Remarques sur la morphologie du parapode des Néréidiens. *Ann Sci Nat Zool* **10**(17):347-367.
- Hartman O. 1948. The marine annelids erected by Kinberg with notes on some other types in the Swedish State Museum. *Ark Zool* **42A**:1-137.
- Hartman O. 1956. Polychaetous annelids erected by Treadwell, 1891 to 1948, together with a brief chronology. *B Am Mus Nat Hist* **109**(2):239-310.
- Hartman O. 1958. A new nereid worm from Warm Mineral Springs, Fla., with a review of the genus *Nicon* Kinberg. *J Wash Acad Sci* **48**(8):263-266. <http://www.biodiversitylibrary.org/item/122833#page/301/mode/1up>
- Hartman O. 1967. Polychaetous annelids collected by the USNS *Eltanin* and *Staten Island* Cruises, chiefly from Antarctic seas. *Allan Hancock Monogr Mar Biol* **2**:1-387.
- Hartmann-Schröder G. 1977. The genera *Ceratocephale* Malmgren, *Olganereis* n. gen., and *Profundilycastis* n. gen. (Nereidae, Polychaeta) with a key to the nereid genera without chitinous paragnaths. In: Reish DJ, Fauchald K (eds) *Essays on Polychaetous Annelids in Memory of Dr Olga Hartman*. Los Angeles, California, pp. 141-155.
- Hernández-Alcántara P, Solís-Weiss V. 1991. New records of errantiate polychaetous annelids from the Gulf of California. *B Mar Sci* **48**(2):251-260.
- Herpin R. 1925. Recherches biologiques sur la reproduction & le développement de quelques annélides polychètes. *B Soc Sci Nat Ouest Fr* **5**:1-250.
- Holly M. 1935. Polychaeta from Hawaii. *B Bernice P. Bishop Mus* **129**:1-33.
- Horst R. 1924. Polychaeta Errantia of the Siboga-Expedition. Pt. 3. Nereidae and Hesionidae. *Siboga-Exped Monogr* **99**:145-198.
- Hutchings P, Reid A. 1990. The Nereididae (Polychaeta) from Australia- *Gymnonereidinae* sensu Fitzhugh, 1987: *Australonereis*, *Ceratocephale*, *Dendronereides*, *Gymnonereis*, *Nicon*, *Olganereis* and *Websterinereis*. *Rec Aust Mus* **42**(1):69-100. doi:10.3853/j.0067-1975.42.1990.107.
- Imajima M. 1972. Review of the annelid worms of the family Nereidae from Japan, with descriptions of five new species or subspecies. *B Natl Sci Mus Tokio* **15**(1):37-153.
- Kinberg JGH. 1865. *Annulata Nova* (Nereidum Dispositio Nova. Leonnatidea, Nereidea, Aretidea, Pisenoida, Niconidea). *Ofvers K Vetensk-Akad Forh* **22**(2):167-179.
- Knox GA. 1951. The polychaetous annelids of Banks Peninsula. Part I. Nereidae. *Rec Canterb Mus* **5**(5):213-229.
- Malmgren AJ. 1865. *Nordiska Hafs-Annulater*. *Ofvers K Vetensk-Akad Forh* **22**(2):181-192.
- Malmgren AJ (1867) *Annulata Polychaeta: Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae*. *Hactenus Cognita*. Ex Officina Frenckelliana, Helsingforslæ (Helsinki), pp. 127.
- Malmgren AJ. 1869. Ueber die Gattung *Heteronereis* (Erst.) un ihr Verhältniss zu den Gattungen *Nereis* (Gr.) und *Nereilepas* (Gr.). *Arch Naturgesch* **35**(1):58-61.
- Merz RA. 2015. Textures and traction: how tube-dwelling polychaetes get a leg up. *Invertebr Biol* **134**(1):61-77. doi:10.1111/ivb.12079.
- Ørsted AS. 1843. Grönlands Annulata Dorsibranchiata. *K Dan Vidensk Selsk Naturvidensk Math Afh* **4**:153-216.
- Pamungkas J, Glasby CJ. 2015. Taxonomy of reproductive Nereididae (Annelida) in multispecies swarms at Ambon Island, Indonesia. *ZooKeys* **520**:1-25.
- Pettibone MH. 1971. Revision of some species referred to *Leptonereis*, *Nicon*, and *Laonereis* (Polychaeta: Nereididae). *Smithson Contrib Zool* **104**:1-53.
- Pleijel F. 2001. *Aphroditoidea*. In: Rouse GW, Pleijel F (eds) *Polychaetes*. Oxford University Press, New York, pp. 73-76.
- Plyuscheva M, Martin D. 2009. On the morphology of elytra as luminescent organs in scale-worms (Polychaeta, Polynoidae). *Zoosymposia* **2**:379-389.
- Read GB. 2007. Taxonomy of sympatric New Zealand species of *Platynereis*, with description of three new species additional to *P. australis* (Schmarda). *Zootaxa* **1558**:1-28.
- Read G. 2018. *Kainonereis alata* Chamberlin, 1919. In: Read G, Fauchald K (eds) *World Polychaeta database*.
- Reish DJ. 1957. The life history of the polychaetous annelid *Neanthes caudata* (delle Chiaje), including a summary of

- development in the family Nereidae. *Pac Sci* **11(2)**:216-228.
- Remane A. 1952. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik, Theoretische Morphologie und Systematik I. Akademische Verlagsgesellschaft, Geest and Portig, K.-G., Leipzig, pp. 400.
- Santos CSG, Pleijel F, Lana PDC, Rouse GW. 2005. Phylogenetic relationships within Nereididae (Annelida: Polychaeta). *Invertebr Syst* **19(6)**:557-576. doi:10.1071/IS05001.
- Sawestri S. 2013. The abnormality morphology of *Namalycastis* (Polychaeta: Nereididae) from Jakarta Bay and estuary Way Belau Lampung. *Widyariset* **16**:419-424.
- Schroeder PC, Hermans CO. 1975. Annelida: Polychaeta. In: Giese AC, Pearse JS (eds) *Reproduction of Marine Invertebrates*. Volume III: Annelids and Echiurans. Academic Press, London, pp. 1-213.
- Smith RI. 1958. On reproductive pattern as a specific characteristic among nereid polychaetes. *Syst Zool* **7(2)**:60-73.
- Sun RP, Yang DJ. 2004. *Fauna Sinica, Invertebrata, Vol. 33. Annelida, Polychaeta II. Nereididae, Syllidae, Hesionidae, Pilargidae, Nephtyidae*. Science Press, Beijing, pp. 520.
- Treadwell AL. 1942. Polychaetous annelids from Lower California and the Philippine Islands in the collections of the American Museum of Natural History. *Am Mus Novit* **1172**:1-5.
- Wilkie IC. 2011. Functional morphology and biomechanics of cuticular fracture at the elyrophoral autotomy plane of the scaleworm *Alentia gelatinosa* (Annelida: Polynoidae). *Invertebr Biol* **130(2)**:129-147. doi:10.1111/j.1744-7410.2011.00224.x.
- Williams DM, Ebach MC. 2008. *Foundations of Systematics and Biogeography*. Springer, New York, pp. 309.
- Wu B-L, Sun RP. 1979. Revision of the genera *Nicon* and *Rullierinereis*, with description of a new genus *Sinonereis* (Polychaeta: Nereidae). *Ocean Sel* **2(2)**:95-112.
- Wu B-L, Sun RP, Yang DJ. 1985. Nereidae (Polychaetous annelids) of the Chinese coast. China Ocean Press, Beijing, pp. 234.