Revision of *Sinonereis* Wu & Sun, 1979 (Annelida: Nereididae)

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**ABSTRACT**

The genus *Sinonereis* Wu & Sun, 1979 and the species *Sinonereis heteropoda* Wu & Sun, 1979 were described from Chinese waters, based on only epitokous specimens with modified dorsal cirri in chaetigers 5-7 and bare pharynx. In the same publication, another species based on only atokes was described, *Nicon sinica* Wu & Sun, 1979. We show that *N. sinica* is a junior synonym of *S. heteropoda* based on their affinities in chaetal and parapodial features. We redefine *Sinonereis* and formally synonymize *N. sinica* and *S. heteropoda*. *Sinonereis* closely resembles *Nicon* Kinberg, 1865 and *Kainonereis* Chamberlin, 1919, but *Sinonereis* differs from them by having napiform dorsal cirri in chaetigers 5-7, and by lacking notopodial dorsal ligules in chaetiger 3 in both atokes and epitokes.

**KEY WORDS**
Nereididae, modified dorsal cirri, epitoky, sexual dimorphism, polychaetes, new synonym.

**MOTS CLÉS**
Nereididae, cirres dorsaux modifiés, épitoquie, dimorphisme sexuel, polychètes, synonyme nouveau.
INTRODUCTION

Epitoky in nereidids consists in several morphological and physiological changes for a short pelagic life for reproduction, where the modified adults or epitokes swim and release their gametes in the water column; the unmodified individuals prior the sexual maturity are called atokes (Clark 1961; Schroeder & Hermans 1975). The morphological modification often involves changes in parapodial, chaetal and sometimes pharyngeal ornamentation morphology. The linking of the atokes or non-reproductive stage with their respective epitokes of the same species is often difficult. Some genera have been established based on epitokes only because the epitokal modifications are very distinctive, but since the atoke morphology is not known, it is possible that some atoke-based species in different genera are actually the non-reproductive stage of another epitoke-based species; hence the importance of studying both epitoke and atoke morphology of known species (Conde-Vela et al. 2018).

The finding of some nereidid epitokes showing a unique combination of morphological features prompted Wu & Sun (1979: 95, 96) to propose a new genus, Sinonereis to include a new species, S. heteropoda. The morphological features were that the pharynx had no papillae nor paragnaths, and that dorsal cirri of chaetigers 5-7 were modified as a “bulbous base and styliform terminal end”. In the same publication, Wu & Sun (1979) also recorded Nicon Kinberg, 1865 in China seas, and described another new species N. sinica based on several atokous specimens. Both species are very similar because they share the same characters of pharynx and chaetae as well as the same distribution range, and the main difference lies in the modified dorsal cirri in chaetigers 5-7 which are absent in N. sinica.

Subsequently, Miura (1990) recorded Nicon sinica in Japanese waters and found the species exhibit well-defined sexual dimorphism based on a number of specimens selected from a single sample. Males had dorsal cirri modified and neuropodial postchaetal lobes, matching the description of S. heteropoda, whereas females and immatures, showing no heteronereid transformations, were readily recognized as N. sinica. Miura (1990) concluded that the two species might belong to different stages of a single species, but he preferred to retain both species as valid instead of elucidating the synonymous status due to the unavailability of the type material. Sinonereis closely resembles Kainonereis Chamberlin, 1919 because they both have a bare pharynx as well as modified dorsal cirri along chaetigers 5-7, but their affinities have not been assessed, mainly because the latter had not been revised until quite recently (Conde-Vela et al. 2018). In this contribution, we redescribe S. heteropoda based on the type material. Also, the synonymy of N. sinica with S. heteropoda is addressed, and the relationship between Sinonereis and Kainonereis, and also other similar genera, is discussed.

MATERIAL AND METHODS

Type materials of Sinonereis heteropoda and Nicon sinica are deposited in the collections of the Marine Biological Museum, Chinese Academy of Sciences (MBMCAS). Specimens were examined using a Zeiss Stemi SV 11 Apo stereomicroscope; to observe parapodial features and chaetae, some parapodia were removed and mounted in semi-permanent slides with ethanol-glycerol to be observed under a Zeiss Axiostar plus compound microscope. All parapodia are in anterior view. Photographs were taken with an AxioCam MRc5 digital camera with an adaptor.

The terminology follows Bakken & Wilson (2005) to describe parapodia for atokes, and Conde-Vela et al. (2018) for epitokes. The terms ‘achaetous ring’ and ‘anterior cirri’ were used instead of ‘peristomium’ and ‘tentacular cirri’, respectively, as suggested by Santos et al. (2005).

SYSTEMATICS

Order PHYLLODOCIDA Dales, 1962
Family NEREIDIDAE de Blainville, 1818

Genus Sinonereis Wu & Sun, 1979

Sinonereis Wu & Sun, 1979: 95.

Type species. — Sinonereis heteropoda Wu & Sun, 1979, by original designation.

Distribution. — The only species, Sinonereis heteropoda, is distributed along Eastern Asian coasts (Yellow Sea to eastern Japan). The genus has been signaled from the Atlantic Ocean but these records deserve confirmation.

Diagnosis (emended, new features highlighted in boldface). — Prostomium with entire anterior margin. Four pairs of anterior cirri. Pharynx surface smooth. Upper notopodial ligule present from chaetiger 4 in atokes and epitokes. Notopodial prechaetal lobe present throughout body. In males, chaetigers 5 to 7 with napiiform dorsal cirri (i.e., cirrophores globose or ovoid, cirrostyles cirriform); parapodia of natatory region with four lamellar processes (dorsal lamella, ventral lamella, upper and lower lamellae of ventral cirri); females without heteronereid transformation. Notochaetae homogomph spinigers; neurochaetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicles, heterogomph spinigers and falcigers in sub-acicular fascicles.

Remarks

The original diagnosis by Wu & Sun (1979) focused in the presence of dorsal cirri with ‘inflated’ cirrophores in anterior chaetigers. Relevant features included in the new diagnosis are the presence of notopodial prechaetal lobes throughout the body, the presence of dorsal lobes in natatory chaetigers, the occurrence of notopodial dorsal ligules from chaetiger 4 in both atokes and epitokes (instead of 3 as usual in most nereidids), and the lack of heteronereid transformation in females. Other key features are the lack of both upper and lower lamellae (usually upper or both lamellae are present) and crenulations in dorsal cirri of natatory chaetigers.

The finding of Sinonereis heteropoda and Nicon sinica in the collections of the Marine Biological Museum, Chinese Academy of Sciences (MBMCAS) is discussed.
Wu et al. (1985) placed *Sinonereis* into the subfamily Nereeidae based on the presence of biramous parapodia, a small number of chaetae in the first chaetigers, and single ventral cirrus in all chaetigers (Wu et al. 1985: 44). Later, Sun & Yang (2004) placed *Sinonereis* in the subfamily Gymnonereidinae sensu Fitzhugh (1987) because of the lack of paragnaths in pharynx, and the presence of biramous parapodia.

In the phylogenetic analysis by Santos et al. (2005), *Sinonereis* has an uncertain subfamily condition, a similar condition for several other genera. In their cladograms, *Sinonereis* appeared in a clade together with *Leptonereis* Kinberg, 1865, *Tyloereis* Fauvel, 1911 and *Tylorrhynchus* Grube, 1866 (Santos et al. 2005: figs 7, 8). This clade was supported by the character of enlarged notopodial dorsal ligules (in posterior chaetigers) (Santos et al. 2005), which match with *Leptonereis*, *Tyloereis*, and *Tylorrhynchus*, but not with *Sinonereis*. *Sinonereis* resembles *Tyloereis* and *Tylorrhynchus* by having neuropodial falcigers but separated from them by having basally expanded dorsal cirri, and uniloated neuropodial postchaetal lobes (Santos et al. 2005); additional differences with these genera are the presence of pharyngeal papillae and compound spinigers only in *Tyloereis*, and lack of both notopodial dorsal ligules and neuropodial ventral ligules in *Tylorrhynchus*, whereas *Sinonereis* species have no papillae in pharynx, have both compound falcigers and spinigers, and both notopodial dorsal ligules and neuropodial ventral ligules.

*Sinonereis heteropoda* Wu & Sun, 1979
(Figs 1-3)

Description of Epitoke

Body

Holotype of *Sinonereis heteropoda* (MBMCAS A-36) male, complete with 60 chaetigers, 12.6 mm long, 1.5 mm wide at chaetiger 10 (including parapodia); paratype (MBMCAS A-37) male, complete with 60 chaetigers, 12.6 mm long, 1.5 mm wide at chaetiger 10. Body yellowish, tapering posteriorly, pigmentations absent (Fig. 2A-C); whitish bundles of sperm in coelom present.

Anterior end

Prostomium ovate, wider than long; two independent antennae, half as long as prostomium; palps biarticulated, as long as antennae; eyes black, ovate to reniform, subequal (Figs 1A; 2A, B). Achaetous ring twice longer than first chaetiger; anterior cirri smooth, posterodorsal one reaching chaetiger 14...
**Chaetigers**

Body divided into non-natatory and natatory regions. Non-natatory region subdivided in three subregions: a) chaetigers 1-4 with dorsal cirri fusiform and ventral cirri cirriform; b) chaetigers 5-7 with dorsal cirri napiform and ventral cirri fusiform; and c) chaetigers 8-21 with both dorsal and ventral cirri cirriform. Natatory region from chaetiger 22 to end of body.

First two chaetigers with neuroaciculae only, following chaetigers with both noto- and neuroaciculae. In chaetiger 1, dorsal cirrus cirriform, 1.5 times longer than dorsal ligule. Dorsal ligule digitiform, twice as long as neuroaciculigule. Neuroaciculigule subconical; postchaetal lobe digitate, 1.5 times longer than neuroaciculigule; neuropodial ventral ligule digitate, as long as dorsal ligule. Ventral cirrus cirriform, half as long as neuropodial ventral ligule.

In chaetiger 3 (Fig. 1B), dorsal cirrus fusiform (i.e., cirrophore slightly swollen, cirrostyle distinct), two times as long as notopodial ventral ligule. Notopodial dorsal ligule absent; prechaetal lobe inconspicuous; notopodial ventral ligule digitate, as long as neuropodial postchaetal lobe. Neuroaciculigule subconical, half as long as postchaetal lobe; postchaetal lobe digitate; neuropodial ventral ligule digitate, as long as postchaetal lobe. Ventral cirrus cirriform, half as long as neuropodial ventral ligule.

In chaetigers 5-7 (Fig. 2H, I), dorsal cirrus cirriform with cirrophore globose or ovoid, cirrostyle cirriform. Notopodial dorsal ligule digitate, half as long as dorsal cirrus, as long as notopodial ventral ligule; prechaetal lobe rounded, very small; notopodial ventral ligule digitate, twice longer than neuroaciculigule. Neuroaciculigule subconical; postchaetal lobe digitate; neuropodial ventral ligule digitate, as long as postchaetal lobe. Ventral cirrus cirriform, 0.8 times as long as neuropodial ventral ligule.

In chaetigers 8-21, dorsal and ventral cirri slender, cirriform. Notopodial and neuropodial ligules similar as in chaetigers 5-7.

Chaetigers from 22 to end of body modified (Fig. 2J-K). Dorsal cirrus with cirrophore slightly swollen, cirrostyle cirriform, 1.3 times length of notopodial dorsal ligule, becoming as the same length toward posterior chaetigers; dorsal lamella twice larger than cirrophore of dorsal cirrus. Notopodial dorsal ligules subconical, as long as notopodial ventral ligule; prechaetal lobe rounded, small; notopodial ventral ligule subconical or digitate, twice as long as neuroaciculigule. Neuroaciculigule subconical; postchaetal lobe expanded, lamellar, as long as and as wide as neuroaciculigule, becoming shorter toward posterior chaetigers, tip with a small apex; neuropodial ventral ligule digitate, twice as long as neuroaciculigule. Ventral cirrus cirriform, 0.8 times as long as neuropodial ventral ligule, with two small basal lamellae, becoming inconspicuous toward posterior chaetigers.

**Chaetae**

Notopodial ligules subconical; prechaetal lobe digitate, 0.8 times as long as neuropodial postchaetal lobe; neuropodial ventral ligule digitate, as long as postchaetal lobe. Ventral cirrus cirriform, 0.8 times as long as neuropodial ventral ligule.

**Posterior end**

Pygidium tripartite; anal cirri cirriform, as long as last eight chaetigers (Fig. 2A, insert).

**Description atoke**

**Body**

Holotype of *Nicon sinica* (A-39) atoke specimen with 51 chaetigers, 11.5 mm long, 1.2 mm wide at chaetiger 10; paratype (A-41) immature with 48 chaetigers, 12 mm long, 1.4 mm wide at chaetiger 10. Body yellowish, tapering posteriorly; brown pigment spots in prostomium and palps, brown spots in anterior margin of anterior chaetigers aligned in a band, fading in most-posterior chaetigers. Glandular masses brown at the base of dorsal cirri, both notopodial dorsal and ventral ligules, and neuropodial ventral ligules, in first third of body, enhancing toward posterior chaetigers; glandular masses in neuropodial ventral ligules disappearing toward posterior chaetigers.

**Anterior end**

Prostomium subpyriform, as long as wide; two independent antennae, half as long as prostomium; palps biarticulated, as long as antennae; eyes black, rounded, subequal (Fig. 3A, B). Achaetous ring twice longer than first chaetiger; anterior cirri smooth, posterodorsal one reaching chaetiger 14 (Fig. 3A-C). Jaws dentate, each with 6-7 teeth; pharynx bare (Fig. 3E).

**Chaetigers**

First two chaetigers with neuroacicula only, following ones with both noto- and neuroaciculae. In chaetiger 3 (Fig. 3H), dorsal cirri cirriform, 1.5 times longer than dorsal ligule. Notopodial dorsal ligule absent; prechaetal lobe inconspicuous; notopodial ventral ligule digitate, 1.5 times longer than neuroaciculigule. Neuroaciculigule digitate, twice longer than postchaetal lobe; postchaetal lobe subconical, half as long as notopodial ventral ligule; neuropodial ventral ligule digitate. Ventral cirrus cirriform, 0.6 times as long as neuropodial ventral ligule.
In chaetiger 7 (Fig. 3I), dorsal cirrus cirriform, 0.8 times as long as notopodial dorsal ligule. Notopodial dorsal ligule subconical, as long as notopodial ventral ligule; prechaetal lobe rounded, small; notopodial ventral ligule subconical, 1.5 times length of neuroacicular ligule. Neuroacicular ligule subconical, as long as neuropodial ventral ligule; postchaetal lobe digitate, as long as neuroacicular ligule; neuropodial ventral ligule subconical. Ventral cirrus cirriform, 0.6 times as long as neuropodial ventral ligule.

In chaetigers 19 and 39 (Fig. 3J-K), dorsal cirrus cirriform, 0.8 times as long as notopodial dorsal ligule. Notopodial dorsal ligule subconical, 0.8 times as long as notopodial ventral ligule; prechaetal lobe rounded, small; notopodial ventral ligule subconical, twice as long as neuroacicular ligule. Neuroacicular ligule subconical, 0.8 as long as neuropodial ventral ligule; postchaetal lobe digitate, as long as neuroacicular ligule; neuropodial ventral ligule subconical. Ventral cirrus cirriform, half as long as neuropodial ventral ligule.
Fig. 3. — *Nicon sinica* Wu & Sun, 1979: A, D-K, holotype (MBMCAS A-39); B, C, paratype (MBMCAS A-41): A, anterior end, dorsal view; B, whole specimen, dorsal view; C, anterior end, lateral view; D, whole specimen, lateral view; E, sub-acicular heterogomph spiniger, chaetiger 19; F, sub-acicular heterogomph falciger, chaetiger 19; G, chaetiger 3, left parapodium (ventral cirrus missing); H, chaetiger 7, left parapodium; I, chaetiger 19, left parapodium; J, chaetiger 19, left parapodium; K, chaetiger 39, left parapodium. Scale bars: A, B, E, 0.5 mm; C, D, 1 mm; F, G, 10 μm; H-K, 0.1 mm.
**Sinonereis**

Depth in bioclastic sand, sponges and gravel, but they did sp. in the vicinity of Hyères Seamount at 480-705 m.

**Posterior end**
Pygidium tripartite; anal cirri cirriform (one missing in holotype), as long as last four chaetigers (Fig. 3D).

**Remarks**

The examination of the type material revealed a high resemblance between *Sinonereis heteropoda* and *Nicon sinica*, mainly in the long anterior cirri, lack of pharyngeal ornamentation, and quite similar parapodial and chaetal morphology, such as the unusual start of the notopodial dorsal ligules from chaetiger 4, as well as the progressive change of the blade shape in neuropodial falcigers. Wu & Sun (1979) likely overlooked these high similarities because they focused on the modification of dorsal cirri in chaetigers 5-7 in *S. heteropoda*, which were absent in the epitokes of *Nicon* species described in their study, *N. maculata* and *N. moniloceras* (Wu & Sun 1979). The examined material differs slightly from those of Miura (1990) mainly in the size of the cirrophores of dorsal cirri in chaetigers 5-7, and the size of the lamellae in natatory chaetigers, particularly in those joined to the ventral cirri. This difference might reflect changes during the process of transformation.

Núñez et al. (2000) reported *Nicon sinica* from Cape Breton Canyon, Cantabrian Sea, at 917-954 m depth and compared their specimens with those described from Japan, and later Núñez (2004) identified the specimens as *Sinonereis heteropoda*. Núñez et al. (2000) highlighted the lack of pigmentation and higher amount of notopodial homogomph spinigers (23-52) in chaetiger 10, whereas the Japanese specimens have pigmentation and a lower amount of such spinigers (9-15) (Núñez et al. 2000: 32). There are additional differences: in Chinese specimens the posterodorsal pair of anterior cirri reach chaetiger 14, in chaetiger 10 both notopodial dorsal and ventral ligules are subequal and the ventral cirrus is half as long as neuropodial ventral cirule; whereas in the specimens from Cape Breton Canyon the posterodorsal pair of anterior cirri reach chaetiger 6, in chaetiger 10 notopodial dorsal ligule is shorter than notopodial ventral one and the ventral cirrus is longer than neuropodial ventral cirule. On the other hand, Gillet & Dauvin (2000) reported *Sinonereis* sp. in the vicinity of Hyères Seamount at 480-705 m depth in bioclastic sand, sponges and gravel, but they did not include any description or justification. Whether the above two records belong to *Sinonereis* requires a further study to elucidate their status.

**Chetae**

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

Notopodial and neuropodial homogomph spinigers pectinate, teeth decreasing in size toward distal end; neuropodial heterogomph spiniger pectinate, teeth decreasing in size toward distal end, blade shorter than homogomph ones (Fig. 3F). Neuropodial heterogomph falcigers pectinate, teeth minute, distal tooth stout, incurved, with a distal tendin, increasing in size toward posterior chaetigers (Fig. 3G); both supra- and sub-acicular falcigers similar.

**DISCUSSION**

In this contribution, we confirm the proposal of Miura (1990) that the two species belong to different stages of a single species, i.e., *S. heteropoda* and *N. sinica* are described based on epitokes and atokes, respectively. The well-defined sexual dimorphism is also emphasized that not only atokes but also females have no heteronereid transformation.

Further, this revision of the type material supports the synonymy of *Sinonereis heteropoda* and *Nicon sinica*, but we consider *Sinonereis* as a separate genus, because epipodal modification is definitely different between *Nicon* and *Sinonereis*. The main differences are that epitokes of *Nicon* species have no napiform dorsal cirri in chaetigers 5-7, and notopodial dorsal ligules start from chaetiger 3. The genera can also be separated by some other characters as shown in Table 1. For instance, heteronereis of *N. aestuarensis* Knox, 1951 has both upper and lower lamellae of dorsal cirri and a lamella below the notopodial dorsal ligule (Knox 1951), which are all absent in *S. heteropoda*. Parapodia of natatory region have only a ventral lamellar process in *N. maculata* Kinberg, 1865 but four modified processes are present in *S. heteropoda*. Natatory chaetae are present in *N. moniloceras* (Hartman, 1940) but absent in *S. heteropoda* (Hartman 1940; Wu & Sun 1979).

Wu & Sun (1979: 96) compared *Sinonereis* with *Leptonereis* Kimberg, 1865 because the expanded 'shape of the dorsal cirri' and bare pharynx (Kinberg 1865), but they regarded both genera as independent because in *Leptonereis* such structures are in the posterior chaetigers, whereas in *Sinonereis* they are in the anterior chaetigers. Wu et al. (1985) noted that the expanded dorsal cirri in *Leptonereis* species are actually the notopodial dorsal ligules (Hartman 1945) and added the lack of neuropodial postchaetal lobes in *Leptonereis* and present in *Sinonereis*, likely they referred to ventral lamellae present in natatory chaetigers of *Sinonereis* epitokes but absent in the holotype of *L. laevis* after it consists of an atoke specimen (Hartman 1948). Nevertheless, the expanded notopodial ligules in posterior chaetigers are also absent in the atokes of *S. heteropoda*, ensuring its separation from *L. laevis*.

The genus *Rullierinereis* Pettibone, 1971 is also closely similar to *Sinonereis* after the bare pharynx and smooth tentacular cirri but a set of both atokous and epipodal features ensure their separation. Atokes of *Rullierinereis* species have notopodial homogomph falcigers and the notopodial dorsal ligules decrease in size and even disappear toward posterior chaetigers, features absent in atokes of *Sinonereis* species; further, atokes of *Sinonereis* have prechaetal notopodial lobes which are absent in *Rullierinereis* species (Pettibone 1971). Moreover, epitokes of *Rullierinereis* species have lower lamellae in dorsal cirri, natatory chaetae, and the females transform into heteronereis, whereas all these features are absent in epitokes of *Sinonereis* species; also, *Sinonereis* male epitokes have napiform dorsal cirri in chaetigers 5-7, feature absent in *Rullierinereis* male epitokes (Table 1) (Pettibone 1971). *Sinonereis* closely re-
sembles *Kainonereis* Chamberlin, 1919 because they have a similar modification of dorsal cirri in chaetigers 5–7 (Chamberlin 1919). However, in *Kainonereis* the dorsal cirrophores are clearly modified into elytriform structures, namely dorsal discs (Conde-Vela et al. 2018), whilst in *Sinonereis* corresponding cirrophores are globose or ovoid. Moreover, males of *Kainonereis* have anterior cirri truly articulated, upper and lower lamellae of dorsal cirri, notopodial homogomph falcigers in first seven chaetigers and well-developed natatory chaetae, all of which are absent in males of *Sinonereis* (Table 1). In addition, females have similar heteronereid modifications as males in *Kainonereis* (only lacking the notopodial homogomph falcigers in first seven chaetigers), whereas in *Sinonereis* females display no heteronereid transformation. The start of notopodial dorsal ligules from chaetiger 4 in males and chaetiger 3 in females is also remarkable in *Kainonereis* epitokes, whereas in *Sinonereis* they start from chaetiger 4 in both males and females.

As an additional confirmation of how problematic it is matching atokes and epitokes, we must recall that the atokes of *Sinonereis*, and atoke and epitokes of some *Kainonereis* species, were regarded as different species in *Nicon* because of the simple definitions of these genera. However, the differences among the epitoke specimens belonging to the genera *Kainonereis*, *Nicon* and *Sinonereis* mentioned above allow us to recognize *Sinonereis* as a distinct, valid genus.

The lack of heteronereid transformations in females has been reported for other nereidid species. Males of *Alitta virens* (Sars, 1835) undergo epitoky and the heteronereis spawn in front of the galleries of the unmodified females, which trap the sperm by moving the water inside, and after release the oocytes and the eggs and the benthic larvae which are retained inside (Bass & Brafield 1972). Also, there are metabolic differences between males and females because of the energetic requirements for swimming (Chatelain et al. 2008). Similarly, females of *Sinonereis heteropoda* could remain inside their galleries in the mud and the fecundation could occur inside, and therefore a restricted distribution is expected. Future studies about the ecology, physiology and reproduction of this species are encouraged to elucidate such issues.

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### Table 1

| Character | Kainonereis | Nicon | Rullierinereis | Sinonereis |
|-----------|-------------|-------|---------------|------------|
| **Body features** | | | | |
| Tentacular cirri | true articulated throughout | smooth throughout or distally articulated | smooth throughout | smooth throughout |
| Number of body regions | 2 in both sexes | 2 or 3 | 2 in males, 3 in females | 2 in both sexes |
| Subregions in non-natatory region | 3 | 2 | 2 | 3 |
| Heteronereid transformation in females | present | present or absent | present | absent |
| **Non-natatory region features** | | | | |
| Start of notopodial dorsal ligules | chaetiger 3 in atokes and females; chaetiger 4 in males | chaetiger 3 in both atokes and epitokes | chaetiger 3 in both atokes and epitokes | chaetiger 4 in both atokes and epitokes |
| Shape of dorsal cirri in chaetigers 5–7 | elytriform | fusiform | fusiform | napiform |
| Notopodial falcigers in chaetigers 5–7 | present in males only | absent | absent | absent |
| **Natatory region features** | | | | |
| Dorsal lamella | present | absent | absent | present |
| Lower lamella of dorsal cirrus | present | present | present | absent |
| Upper lamella of dorsal cirrus | present | present | present | absent |
| Granulations in dorsal cirri of males | absent | absent | present | absent |
| Lamella below notopodial ventral ligule | present | present | absent | absent |
| Natatory chaetae | present or absent | present | present | absent |
| Pygidium with anal papillae | absent | present | present | absent |
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