



# Nereididae (Annelida) phylogeny based on molecular data

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## Abstract

Nereididae is one of Annelida's most diverse and well-studied families; despite this, only recently have molecular approaches been used to access phylogenetic hypotheses within the family. At least two nereidid groups can be identified based on mitochondrial gene order; however, this type of molecular information is not available for most taxa, and relationships of subfamilies are still poorly understood. In the present study, we used nuclear and mitochondrial markers to evaluate relationships within Nereididae and verified hypotheses on subfamilies delineation and relationship. Our results suggest the paraphyletic status of Gymnonereidinae and Nereidinae, as well as some genera within these subfamilies. Despite this, a revision of these subfamilies delineation and diagnoses was presented to match current phylogenetic understanding of the group. We suggest reverting to the original definition of Gymnonereidinae to include only the genera originally proposed by Banse in 1977. Our results also support monophyly of a large group that can be defined by mitochondrial gene order. This group includes most taxa identified as Nereidinae, and therefore, we suggest that this feature should be used as diagnostic of the subfamily.

**Keywords** Errantia · Gene order · Gymnonereidinae · Molecular systematics · Namanereidinae · Nereidinae · Phyllodocida · Pleistoannelida · Polychaeta

## Introduction

Nereididae Blainville, 1818 is a group of polychaetes annelids that comprises 43 recognized genera and 770 species that occur in a variety of environments, from continental freshwaters to deep sea. They are one of the most speciose

and well-studied families of marine annelids. and representatives of Nereididae are important for ecological research, as invasive and bioindicator taxa, as economically valuable fishing bait, and as food supply (Bakken et al., 2022). Nereididae also includes the model organism *Platynereis dumerilii* (Audouin & Milne Edwards, 1833) used for genetics and developmental studies (e.g., Reish & Gerlinger, 1997; Olive, 1999; Fischer & Dorresteijn, 2004, Özpolat et al., 2021).

The current taxonomy and understanding of nereidid phylogeny are confusing. Studies focusing on the group as a whole have been limited, and researchers have applied different sets of morphological characters in phylogenetic analyses (Bakken & Wilson, 2005; Fitzhugh, 1987; Glasby, 1991; Santos et al., 2005), producing different hypotheses of evolutionary relationship within the group. Table 1 summarizes classification schemes that have been used to identify hypothesized subfamilies within Nereididae. Nereidinae Blainville, 1818, which includes the type species of the family, *Nereis pelagica* Linnaeus, 1758, was erected to include all species with paragnaths and/or papillae on the pharynx and biramous parapodia; Namanereidinae Hartman, 1959, first described as Lycastinae Corrêa, 1948, but subsequently redescribed and renamed by Hartman (1959), was recognized to include all species of Nereididae

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**Table 1** Phylogenetic proposals for genera and subfamilies within Nereididae. (-) Not placed in any subfamily. Only genera included in previous phylogenetic studies are shown. For a complete list of genera within Nereididae, see Bakken et al. (2022)

Genera	Before 1987 <sup>a</sup>	Fitzhugh (1987) <sup>b</sup>	Santos et al. (2005) <sup>c</sup>
<i>Ceratocephale</i> Malmgren, 1867	Gymnonereidinae	Gymnonereidinae	Gymnonereidinae
<i>Gymnonereis</i> Horst, 1919			
<i>Micronereides</i> Day, 1963			
<i>Tambalagama</i> Pillai, 1961			
<i>Dendronereis</i> Peters, 1854	Dendronereidinae		Dendronereidinae
<i>Dendronereides</i> Southern, 1921			Clade A
<i>Australonereis</i> Hartman, 1954	Nereidinae		
<i>Laeonereis</i> Hartman, 1945			
<i>Olganereis</i> Hartmann-Schröder, 1977			
<i>Leptonereis</i> Kinberg, 1865			Clade B
<i>Sinonereis</i> Wu & Sun, 1979			
<i>Tylonereis</i> Fauvel, 1911			
<i>Tylorrhynchus</i> Grube, 1866			
<i>Ganganereis</i> Misra, 1999			-
<i>Kinberginereis</i> Pettibone, 1971			-
<i>Nicon</i> Kinberg, 1865			-
<i>Rullierinereis</i> Pettibone, 1971			-
<i>Stenoninereis</i> Wesenberg-Lund, 1958			-
<i>Websterinereis</i> Pettibone, 1971			Clade C
<i>Ceratonereis</i> Kinberg, 1865		Nereidinae	
<i>Cheilonereis</i> Benham, 1916			
<i>Solomononereis</i> Gibbs, 1971			
<i>Unanereis</i> Day, 1962			
<i>Eunereis</i> Malmgren, 1865			Nereidinae
<i>Hediste</i> Malmgren, 1867			
<i>Nereis</i> Linnaeus, 1758			
<i>Platynereis</i> Kinberg, 1865			
<i>Alitta</i> Kinberg, 1865			-
<i>Compositia</i> Hartmann-Schröder, 1985			-
<i>Imajmainereis</i> de León-González & Solís-Weiss, 2000			-
<i>Leonnates</i> Kinberg, 1865			-
<i>Neanthes</i> Kinberg, 1865			-
<i>Nectoneanthes</i> Imajima, 1972			-
<i>Paraleonnates</i> Chlebovitch & Wu, 1962			-
<i>Perinereis</i> Kinberg, 1865			-
<i>Pseudonereis</i> Kinberg, 1865			-
<i>Simplisetia</i> Hartmann-Schröder, 1985			-
<i>Wuinereis</i> Khlebovich, 1996			-
<i>Micronereis</i> Claparède, 1863	Notophycinae		Notophycinae
<i>Namalycastis</i> Hartman, 1959	Namanereidinae	Namanereidinae	Namanereidinae
<i>Namanereis</i> Chamberlin, 1919			

<sup>a</sup>Based on original diagnoses for each subfamily

<sup>b</sup>Expanded from author's diagnoses

<sup>c</sup>Contributions by Glasby (1991) and Bakken and Wilson (2005) were focused in one single subfamily within Nereididae

that possessed a bare pharynx and reduced notopodial structures and Gymnonereidinae Banse, 1977 which was first diagnosed to include nereidids with bifid ventral cirri and numerous bundles of chaetae in anterior region.

Another two subfamilies have been previously recognized: Species possessing parapodial branchiae were grouped into Dendronereidinae Pillai, 1961, and species which lack antennae on prostomium, lack ligulae on

parapodia, and do not possess a fully eversible pharynx were placed in Notophycinae Knox and Cameron, 1970 (a family-ranked clade originally erected for the very distinct *Micronereis* Claparède 1863). However, when Fitzhugh (1987) performed the first phylogenetic analysis for the family, using a parsimony approach with morphological characters, Dendronereidinae and Notophycinae were considered invalid subfamilies. He expanded Gymnonereidinae to include all species without paragnaths and having biramous parapodia and Nereidinae to include all species with paragnaths. He did not change the diagnosis of Namanereidinae. Further observations emphasized that branchiae, described as a synapomorphy of Dendronereidinae, varied in structure across different genera calling in their hypothesized homology into question (Banse, 1977; Santos et al., 2005).

Subsequent morphological parsimony analyses (Bakken & Wilson, 2005; Glasby, 1991; Santos et al., 2005) failed to recover Gymnonereidinae and Nereidinae as proposed by Fitzhugh. These studies supported monophyly of Namanereidinae and placed this group as the sister taxon to all other Nereididae. Santos et al. (2005) recovered Gymnonereidinae as proposed by Banse (1977) restricting the clade to only four genera: *Gymnonereis* Horst, 1919; *Ceratocephale* Malmgren, 1867; *Tambalagamia* Pillai, 1961; and *Micronereides* Day, 1963. Some authors have suggested that these genera should be synonymized based on the morphological resemblance of these taxa (Böggemann, 2009; Gallardo, 1968; Hylleberg & Nateewathana, 1988; Pettibone, 1970). To date, these genera are still valid taxa, and the synonymy proposed has not been formalized. Bakken and Wilson (2005), on the other side, focused their discussion in Nereidinae, proposing that several genera (e.g., *Neanthes* and *Nereis*) may not represent monophyletic taxa.

Molecular phylogenetic studies of nereidids are scarce and do not examine the group as a whole. Common markers (e.g., COI, 16S, 18S) have not been used to broadly sample across Nereididae, but there are several examples of phylogenetic studies using molecular markers that included some Nereididae taxa (see Hall et al., 2004; Ruta et al., 2007; Magesh et al., 2012; Liu et al., 2012; Drennan et al., 2021). In contrast, Park et al. (2016) used mitochondrial gene order and recognized two distinct groups of Nereididae. This finding was supported by Alves et al. (2020) who showed that a large subset of Nereidinae share a derived mitochondrial gene order. In addition, Alves et al. (2020) found that Namanereidinae was not the sister taxon to all other Nereididae. Though their study was based on complete mitochondrial genomes, the number of taxa included was limited, and, again, improvements to classification were not proposed.

To more thoroughly explore Nereididae phylogeny and evolution, the present study performed a broad phylogenetic analysis using three molecular markers (COI, 16S and 18S) to evaluate the following phylogenetic hypotheses:

(1) Namanereidinae as sister taxa to all other Nereididae; (2) Gymnonereidinae sensu Banse (1977), as supported by Santos et al. (2005); and (3) the Group 1 mtDNA synapomorphy (Alves et al., 2020; Park et al., 2016) is consistent with other molecular data.

## Materials and methods

A total of 39 specimens of Nereididae were included in analyses, representing 20 valid genera. We also included 2 outgroup taxa from Hesionidae and Chrysopetalidae, based in the currently understanding of Phyllodocida and Nereidiformia phylogeny (Dahlgren et al., 2000; Glasby, 1993; Pleijel & Dahlgren, 1998). The present study includes data retrieved from GenBank and BOLD databases, as well as new unpublished sequences obtained from samples collected in southeast Brazilian coast (see Table 2 for complete species list and accession numbers). The criteria for inclusion of previously published data were as follows: (1) We favored taxa from which at least two of the markers were available and these sequences were published in the same study, representing the same specimen or specimens from the same population; (2) we used sequences from specimens for which morphological identification could be traced to experts in Nereididae and Annelida taxonomy; (3) we avoided oversampling of some genera, so available sequences, for some *Nereis* and *Perinereis* species for example, that passed the previous criteria were not included; (4) based on preliminary data curing and analyses, we excluded some sequences available (e.g., sequences for *Alitta virens* (M. Sars, 1835) 18S were available in Genbank; however sequences were too short compared to other 18S sequences or were not properly aligning with used data set). A few sequences included do not conform to the first criteria (e.g., *Tambalagamia* and *Namanereis*, which only COI sequences were available). However, we decided to use these sequences because these represent relevant taxa for the hypotheses tested here. The other three criteria were also checked for these taxa.

The criteria presented above do not completely exclude the possibility of misidentifications, as any possible methodology would not avoid. Despite that, these represent the most appropriate approach to take advantage of the available Nereididae sequences in public databases. To make sure no informative data were excluded, an analysis including all available Nereididae sequences for the three markers was performed using the same methods described herein. We used this large data set analysis to verify if the inclusion of sequences could significantly change the results and conclusions presented here. Since both data set support the same conclusions and considering that the large data set is strongly biased to COI sequences and oversampled genera, we decided to focus our description on the restricted data set

**Table 2** Taxa included in phylogenetic analyses and databases accession numbers for each marker. Most accession numbers are from Genbank, underlined are sequence IDs from BOLD

Taxa	COI	16S	18S	Location	Ref.
<b>Nereididae</b>					
<i>Alitta succinea</i> (Leuckart, 1847)	MW825350	MW826068	MW826081	Brazil	Present study
<i>Ceratocephale abyssorum</i> (Hartman & Fauchald, 1971)	GQ426683	GQ426618	GQ426585	Guinea Basin	(Böggemann, 2009)
<i>Ceratocephale loveni</i> Malmgren, 1867		DQ442614	DQ442616	Sweden	(Ruta et al., 2007)
<i>Ceratonereis longiceratophora</i> Hartmann-Schröder, 1985	AY583701		AB106251	Australia	(Colgan et al., 2006)
<i>Ceratonereis</i> sp.	<u>LIPOL031-08</u>			Australia	BOLD direct submission
<i>Cheilonereis cyclurus</i> (Harrington, 1897)	MF538532	MF538532		South Korea	(Park et al., 2017)
<i>Gymnonereis crosslandi</i> (Monro, 1933)	<u>DISA414-18</u>			USA	BOLD direct submission
<i>Gymnonereis</i> sp.	KY805815	KY704332		India	(Vijapure et al., 2019)
<i>Hediste atoka</i> Sato & Nakashima, 2003	LC323006	LC323043	LC323072	Japan	(Tosuji et al., 2019)
<i>Hediste diadroma</i> Sato & Nakashima, 2003	KX499500	KX499500		South Korea	(Kim et al., 2016)
<i>Laeonereis culveri</i> (Webster, 1879)	MW825351	MW826069	MW826082	Brazil	Present study
<i>Namalycastis abiuma</i> (Grube, 1872)	KU351089	KU351089		China	(Lin et al., 2016)
<i>Namalycastis indica</i> (Southern, 1921)	MG759522	MG759523		Myanmar	(Bolotov et al., 2018)
<i>Namalycastis jaya</i> Magesh et al., 2012	HQ456363	HM138706	JX483867	India	(Magesh et al., 2012)
<i>Namanereis hummelincki</i> (Augener, 1933)	KT235957			Montserrat/ UK	(Shoobs et al., 2016)
<i>Neanthes ceciliae</i> Steiner & Santos, 2004	MW825352	MW826070	MW826083	Brazil	Present study
<i>Neanthes glandicincta</i> (Southern, 1921)	KY094478	KY094478		China	(Lin et al., 2017)
<i>Neanthes meggitti</i> (Monro, 1931)	MF958994	MF959006		Montserrat/UK	(Bolotov et al., 2018)
<i>Nectoneanthes oxypoda</i> (Marenzeller, 1879)	<u>HZPLY588-13</u>			China	BOLD direct submission
<i>Nereis pelagica</i> Linnaeus, 1758		AY340470	AY340438	Sweden	(Rousset et al., 2007)
<i>Nereis</i> sp.	MF960765	MF960765		South Korea	(Kim et al., 2017)
<i>N. icon maculata</i> Kinberg, 1865	MW825353	MW826071		Antarctic sea	Present study
<i>Paraleonnates uschakovi</i> Chlebovitsch & Wu, 1962	KX462988	KX462988		South Korea	(Park et al., 2016)
<i>Perinereis aibuhitensis</i> (Grube, 1878)	KF611806	KF611806		South Korea	(Kim et al., 2015)
<i>Perinereis anderssoni</i> Kinberg, 1866	MW825354	MW826072	MW826084	Brazil	Present study
<i>Perinereis cultrifera</i> (Grube, 1840)	MN812983	MN812983	OQ732688	France	(Alves et al., 2020)
<i>Perinereis nuntia</i> (Lamarck, 1818)	JX644015	JX644015		South Korea	(Won et al., 2013)
<i>Perinereis</i> sp.	MN823962	MN823971	OQ732689	Panama	(Alves et al., 2020)
<i>Platynereis australis</i> (Schmarda, 1861)	MN830367	MN830367	OQ732690	Chile	(Alves et al., 2020)
<i>Platynereis bicanaliculata</i> (Baird, 1863)	MN812984	MN812984	OQ732691	USA	(Alves et al., 2020)
<i>Platynereis dumerilii</i> (Audouin & Milne Edwards, 1833)	AF178678	AF178678		Unknown	(Boore & Brown, 2000)
<i>Platynereis massiliensis</i> (Moquin-Tandon, 1869)	MN812985	MN812985	OQ732692	Wales	(Alves et al., 2020)
<i>Platynereis</i> sp1	MN830365	MN830365	OQ732693	Brazil	(Alves et al., 2020)
<i>Platynereis</i> sp2	MW825355	MW826073	MW826085	Brazil	Present study
<i>Pseudonereis palpata</i> (Treadwell, 1923)	MW825356	MW826074	MW826086	Brazil	Present study
<i>Pseudonereis variegata</i> (Grube, 1857)	MN855134	MN855213	OQ732694	South Africa	(Alves et al., 2020)
<i>Simplisetia</i> cf. <i>erythraensis</i> (Fauvel, 1918)	EU835670			Australia	(Metcalfe & Glasby, 2008)

**Table 2** (continued)

Taxa	COI	16S	18S	Location	Ref.
<i>Tambalagama fauveli</i> Pillai, 1961	HZPLY601-13			China	BOLD direct submission
<i>Tylorrhynchus heterochaetus</i> (Quatrefages, 1866)	KM111507	KM111507		China	(Chen et al., 2016)
<b>Outgroup</b>					
<i>Arichlidon gathofi</i> Watson Rusell, 2000	MN855127		OQ732695	Panama	(Alves et al., 2020)
<i>Oxydromus pugettensis</i> (Johnson, 1901)	MN855132	MN855211	OQ732696	USA	(Alves et al., 2020)

as it represents a more robust and straightforward approach. Details on species and sequences included in the large data set, as well as all the results using this data, are provided in supplementary material (Table S1 and Figs. S1–S2).

Specimens sequenced here were morphologically identified by PRA and CSGS and vouchers are available at Museu Nacional do Rio de Janeiro (accession numbers MNRJP002863-002867).

Samples were fixed in 100% ethanol and DNA was extracted using Qiagen DNeasy Blood & Tissue extraction kit following manufacturer's spin-column protocol. Selected markers (COI, 16S, and 18S) were amplified by polymerase chain reaction (PCR) using primers and cycling protocols shown in Supplementary Material Table S2. All PCR products were purified using Qiagen QIAquick PCR Purification kit, and purified PCR products were bidirectionally Sanger sequenced by *Genewiz* (New Jersey, EUA).

Each marker was individually aligned using *MAFFT* (Katoh & Standley, 2013) with *L-INS-I* strategy. Aligned sequences were analyzed as individual loci and concatenated into a partitioned supermatrix using *FASconCAT* (Kück & Meusemann, 2010). Phylogenetic trees were reconstructed using Maximum Likelihood (ML) and Bayesian tree Inference (BI) for both concatenated matrix and individual genes. ML trees were obtained using *IQtree 2* (Minh et al., 2020) with *ModelFinder* (Kalyaanamoorthy et al., 2017) to search for appropriate substitution models and *ultrafast bootstrap* (Hoang et al., 2007), with 10,000 replicates, to calculate support. BI analyses were performed in *MrBayes* (Ronquist et al., 2012) with 20 million generations and consensus tree was obtained after a 25% of burn-in (based on convergence of log Ln scores).

Phylogenetic topology tests were performed in *IQtree 2* (Minh et al., 2020) using approximately unbiased (AU) method (Shimodaira, 2002). Three sets of tests were performed (Fig. 1): Test 1 to verify Nereidinae delineations, as (a) Nereidinae is identified by morphological traits (i.e., presence of paragnaths and biramous parapodia) and (b) Nereidinae as all descendants of the common ancestor of all Nereididae with Group 1 mtDNA gene order; Test 2 to verify Gymnonereidinae delineation, (c) as all Nereididae without paragnaths but with biramous parapodia or (d) only species

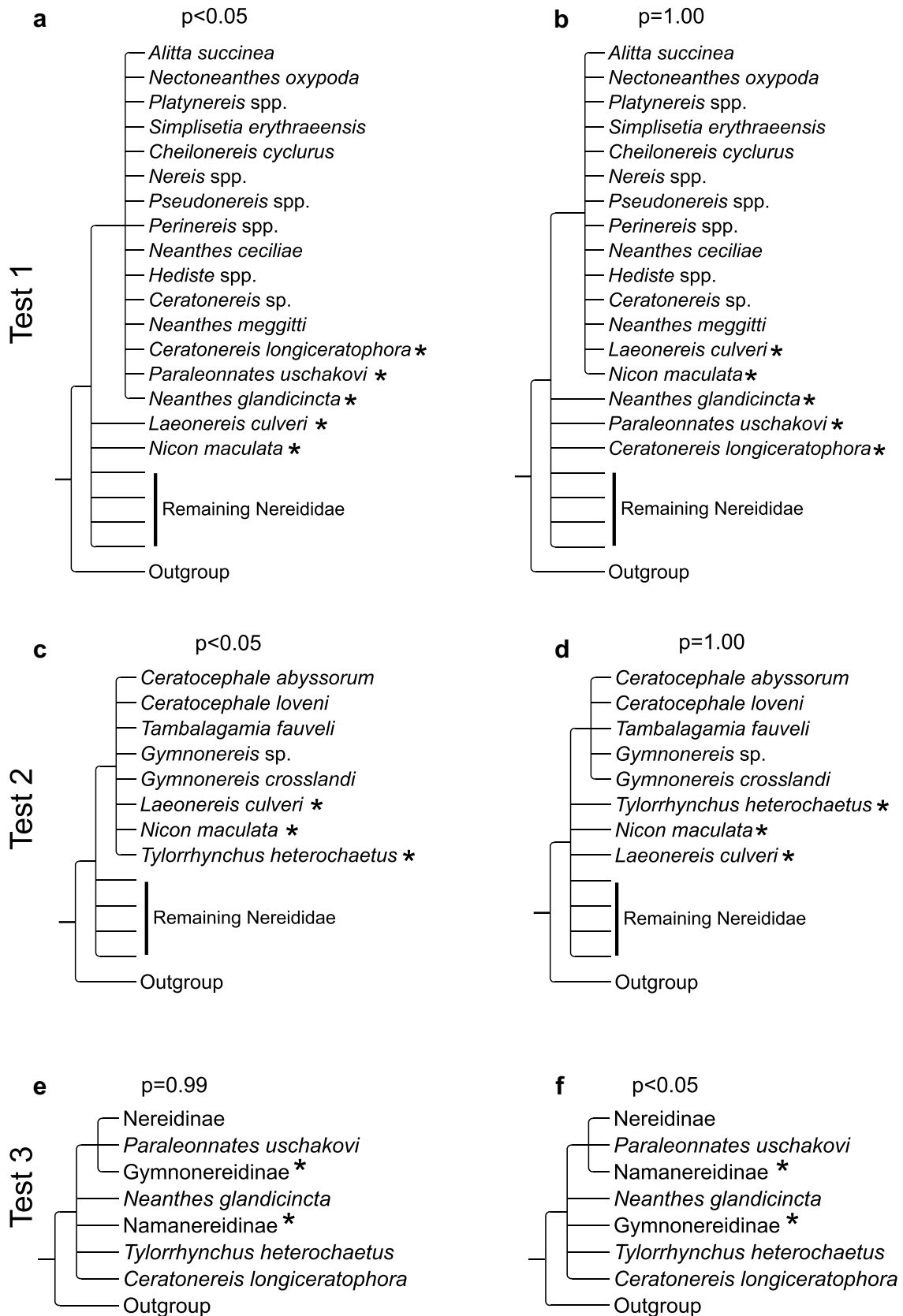
originally included in the subfamily by Banse (1977); and Test 3 that, considering previous test results and subfamilies delineation, we tested the relationship between subfamilies as they are identified in the present study: (e) Gymnonereidinae as sister taxa to the clade Nereidinae + *Paraleonnates uschakovi* or (f) Namanereididae as sister taxa to the same clade. The goal of Test 3 was to verify if both hypotheses had some signal in the data since some support values on the base of reconstructed trees were low to marginal and individual loci analyses for 16S and 18S resulted in a clade with Namanereidinae as sister taxa to Nereidinae species.

## Results

The combined data set included 41 terminal taxa consisting of 7063 aligned positions, from which 3029 sites were variables and 1695 parsimony informative. Bayesian Inference analysis and Maximum Likelihood for the combined data set returned similar topologies (Figs. 2 and 3, respectively). In both cases, Nereididae is monophyletic with high bootstrap support/posterior probability (100/100).

For both analysis, *Ceratonereis longiceratophora* Hartmann-Schröder, 1985, was placed as the sister taxon to all other Nereididae. The next clade to branch in both analyses includes only *Tylorrhynchus heterochaetus*, followed by a clade identified as Namanereidinae. Three other distinct lineages can be identified in both trees: a branch leading to *Neanthes glandicincta*; a second clade including five species identified as Gymnonereidinae; and a large clade with *Paraleonnates uschakovi* + Nereidinae.

Monophyly of Namanereidinae is supported with high bootstrap support/posterior probability (97/100) and included only two genera, *Namanereis* and *Namalycastis*. Gymnonereidinae sensu Banse (1977) is also supported with high bootstrap/posterior probability values (98/100). Gymnonereidinae included *Gymnonereis*, *Ceratocephale*, and *Tambalagama fauveli* Pillai, 1961, however, both topologies resulted in *Gymnonereis* being paraphyletic. A major clade, herein identified as Nereidinae, was also recovered with high support (100/100). This clade is equivalent to Group 1 defined by mitochondrial gene order found in Alves et al. (2020); for this reason, *Paraleonnates uschakovi*, which has



◀**Fig. 1** Topology tests performed. Test 1, delineation of Nereidinae. Test 2, delineation of Gymnonereidinae. Test 3, relationship between established subfamilies. *p* Values below 0.05 indicate that the topology was not supported by the test. Asterisk (\*) highlights taxa with different placement between tested topologies

Group 2 gene order, is not included in Nereidinae delineation in this study. Many genera (e.g., *Platynereis*, *Nereis* and *Pseudonereis*) were not recovered as monophyletic, but *Hediste* (100/100) and *Perinereis* (99/100) were monophyletic in both results.

Topology Test 1 supported Nereidinae as equivalent to Group 1 hypothesis (Fig. 1b,  $p = 1.00$ ), and Test 2 supported Gymnonereidinae as Banse's (1977) delineation (Fig. 1d,  $p = 1.00$ ). Following these results, Test 3 used these subfamilies delineations. Test 3 supported only the Gymnonereidinae as sister taxa to the clade leading to *Paraleonnates uschakovi* and Nereidinae hypothesis (Fig. 1e,  $p = 0.99$ ), while rejecting the alternative arrangement of subfamilies.

Phylogenetic results for individual genes are provided in supplementary material (Figs. S3 to S8). Overall, gene trees reflect the results described for concatenated data set. Clades supported by combined data were also returned in all three genes individually. Major difference observed was the relative position of Namanereidinae, which was returned as sister group of Nereidinae + Gymnonereidinae in COX1 results, while in 16S and 18S trees, the subfamily were more closely related to Nereidinae (as in Fig. 1f).

## Discussion

Nereididae is comprised of at least three well defined clades including a well-supported Namanereidinae, a Gymnonereidinae clade restricted to Banse (1977) delineation, and a clade which is partially congruent with Nereidinae. For this reason, these clades are herein identified by these established subfamily names. Figure 3 summarizes the main findings of this study.

In the base of the tree, *Ceratonereis longiceratophora* is the sister group to all other Nereididae sampled here, followed by a clade leading to *Tylorrhynchus heterochaetus*. The inclusion of these taxa in any of the supported subfamilies, based on present results, would result in this subfamily being paraphyletic. For this reason, these taxa were left unplaced.

The next lineage to diverge from other nereidids includes a well-supported Namanereidinae. The delineation of Namanereidinae to include only *Namanereis* and *Namalycastis* is well supported by systematics studies (Alves et al., 2018; Glasby, 1999). Previous phylogenetic studies identified two synapomorphies for the subfamily: spherical palpostyles and notoacacula in ventral position (inserted in neuropodia) (Glasby, 1991; Santos et al., 2005). Namanereidinae may also be recognized by

the bare pharynx and the reduced notopodia bearing only dorsal cirri and a notoacacula, which supports neuropodia (sesquiramous parapodia).

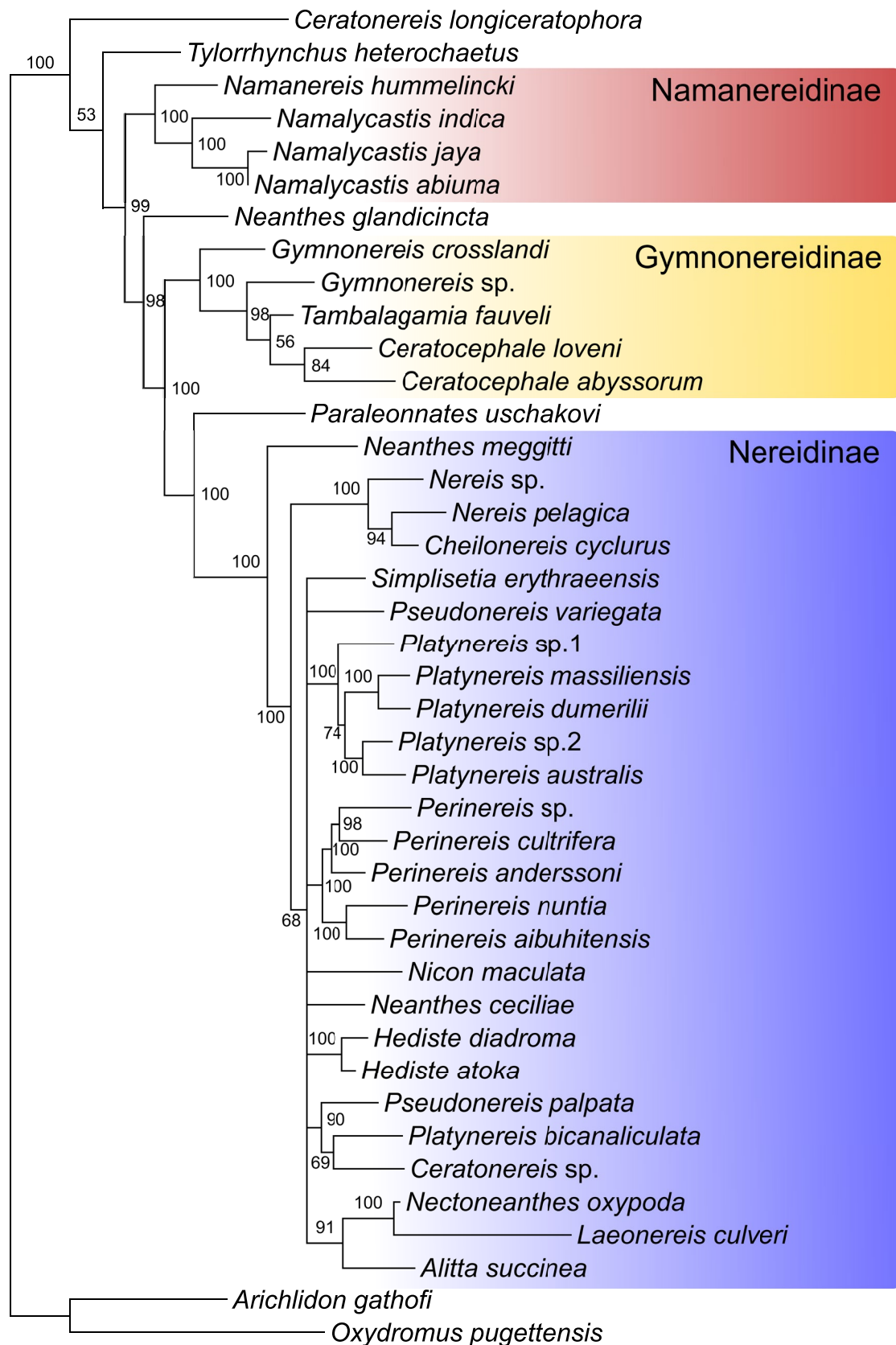
In phylogenies constructed based in morphological features, Namanereidinae species are usually coded with lots of absences in character matrixes, since the group usually lacks structures commonly used in Nereididae systematics such as pharyngeal ornamentation and notopodial projections. The phylogenetic positioning of groups characterized by absences, rather than the presence of a distinct character, is a well-known problem in annelid phylogeny (Purschke et al., 2000; Westheide et al., 1999; Zhong et al., 2011), where these groups are usually wrongly placed as ancestral groups due to its morphological simplicity. Namanereidinae seems to be one of these cases. However, the morphological simplicity of the group may represent secondary reductions (Glasby, 1999), and some of these characters are known as troglomorphic adaptations (Alves et al., 2018; Conde-Vela, 2017), suggesting that Namanereidinae may represent a specialized group within the family.

This hypothesis is, to some extent, supported by the phylogenetic results herein. *Ceratonereis longiceratophora*, which have paragnaths on the pharynx and well developed notopodia, was placed as sister taxa to all other Nereididae, suggesting that these are most likely to be ancestral conditions as they are also found in Nereidinae. Hence, the lack of such characters in Namanereidinae shows that these were secondarily lost.

Indeed, phylogenetic trees presented, and topology test performed (Fig. 1e) support that Namanereidinae evolved independently of the other two subfamilies and that Gymnonereidinae and Nereididae are more closely related groups. Nevertheless, the hypothesis proposed by most phylogenetic studies (Bakken & Wilson, 2005; Glasby, 1991; Santos et al., 2005), in which Namanereidinae is described as sister group of all remaining Nereididae, lacks support in molecular data.

Gymnonereidinae sensu Banse (1977) is also supported by present data. The group was erected to include species of Nereididae with bifid ventral cirri, a very distinct feature within the family (Banse, 1977). The original diagnose also includes dense chaetal bundles in anterior region of the body, and Santos et al. (2005) suggested the presence of subacicular notopodial chaetal bundle to be included as diagnostic for the group. Both phylogenetic results obtained in the present study (Figs. 2 and 3) and topology test performed (Fig. 1c–d) support the reinstatement of Gymnonereidinae sensu Banse (1977), which was already proposed by Santos et al. (2005).

Gymnonereidinae clade in the present study includes *Gymnonereis* spp., *Ceratocephale* spp., and *Tambalagamia fauveli*; all these taxa were included in the original subfamily delineation proposed by Banse (1977). In addition to the taxa listed above, Gymnonereidinae sensu Banse (1977) also



**Fig. 2** Bayesian inference tree. Values on nodes are clade credibility (posterior probabilities). Clades with posterior probability less than 50% were collapsed. Colors identifies subfamilies





the samples are from the same population also used in Alves et al. (2020). However, recent contributions (Conde-Vela, 2021; Sampieri et al., 2021) described that the distribution of *L. culveri* may not reach the southeastern coast of Brazil, where it was collected. Following Sampieri et al. (2021), these populations may represent undescribed species. We kept the name *Laeonereis culveri* for consistency between current results and previous published studies using the same population.

The results herein mirror Alves et al.'s (2020) study based on mitochondrial genomes. The authors, following the results of Park et al. (2016), suggest that mitochondrial gene order could be used to infer groups in the subfamily level. Alves et al. (2020) indicate that Nereidinae could be expanded to include all species with the mitochondrial gene order referred to as "Group 1," which differs from "Group 2" by the position of three t-RNAs genes encoding for tyrosine, methionine, and aspartic acid. The present analyses returned a clade that includes all species with complete mitochondrial genomes sequenced having Group 1 gene order. We here identify this clade as Nereidinae. The clade containing Group 1 species and related taxa was also supported by topology test performed (Fig. 1a–b).

Although some variation is likely to be found in tRNAs positions within the proposed Nereidinae as new sequences become available, present results, which include a diverse representative of the group, suggest that the ancestral Nereidinae had a Group 1 gene order. And, with this well-marked synapomorphy, this delineation excludes *Paraleonnates uschakovi* of the group, despite its close relationship with the subfamily.

Additional information will be important to confirm or refute the putative synapomorphies proposed in this study. However, following the agreement between the current data with mitochondrial genomes phylogeny, we propose that this new delineation can be more phylogenetically informative for the group.

### Taxonomic implications at the subfamily level

Although some congruence exists between the former classifications and our current phylogenetic results, based on this study and previous analysis (Alves et al., 2020; Bakken & Wilson, 2005; Glasby, 1991; Santos et al., 2005), subfamilies delineation must be revised to match current phylogenetic understanding. Our results do not fully resolve all the relationships among all genera and species; nonetheless, the phylogenies here presented support subfamilies delineation that reflects monophyletic clades. For this reason, we here propose a revised diagnose for Gymnonereidinae and Nereidinae, whereas Namanereidinae is presented but remains unchanged.

**Namanereidinae** (following Glasby, 1999): Palps biarticulate, palpophores compact, unarticulated; palpostyles spherical. Peristomium length equal to or less than length of setiger 1. Tentacular cirri (= anterior cirri), three or four pairs. Pharynx without paragnaths or papillae; Area V (oral ring) a narrow longitudinal groove or pad. Parapodia reduced, lacking true notopodial lobes or ligules but dorsal cirri present; notoacicula and neuroacicula in all chaetigers (including first two); notoacicula in ventral position; neuropodia with single acicular ligule. Notochaetae, when present, are sesquigomph spinigers. Neurochaetal types and arrangement variable include sesquigomph spinigers, heterogomph falcigers, and heterogomph spinigers in supraacicular fascicles and heterogomph spinigers, heterogomph pseudospinigers, and heterogomph falcigers in subacicular fascicles.

**Gymnonereidinae** (following Banse, 1977 and emended based on Santos et al., 2005): Two palps and two antennae. Conical palpostyles. Pharynx without hardened paragnaths; with conical solitary papillae. Prostomium with median cleft. Four pairs of tentacular cirri (= anterior cirri). Peristomium shorter than first chaetiger. Parapodia with dorsal cirri on first two chaetigers; with bifid ventral cirri on most chaetigers; with ligulae. Notopodial subacicular chaetal bundle present. Chaetae homogomph and sesquigomph spinigers (see Conde-Vela, 2021 for discussion and definition of chaetal shaft morphology and nomenclature); very numerous in first 10 to 15 chaetigers, giving the impression of a distinct anterior body region.

**Nereidinae** (emended from Fitzhugh, 1987): Biarticulated palps with elongated palpophores (rarely compact) and spherical or subconical palpostyles. Peristomium with 4 pairs of tentacular cirri (= anterior cirri). Paragnaths present on oral and/or maxillary rings of pharynx, rarely absent in one or both rings. Paragnaths, when present, may be of several forms and arrangement (see Bakken et al., 2009 for a review in paragnaths morphology). Pharyngeal papillae rarely present. Parapodia biramous, with superior and inferior notopodial, and inferior neuropodial ligules. Chaetae compound (rarely simple), most commonly comprising noto- and neuropodial homogomph spinigers, notopodial homogomph falcigers, and neuropodial heterogomph spinigers and falcigers. Mitochondrial gene order of Group 1 type as identified by Park et al. (2016).

### Conclusions

Within Nereididae, molecular data supports existence of at least three clades that can be associated with currently established subfamilies. However, delineations of two

of these subfamilies needed revision and new diagnoses were presented here. The only possible synapomorphy of Nereidinae seems to be the mitochondrial gene order. In addition, relationships within this group seem to be problematic, and a review of some genera is necessary. Delineation of Gymnonereidinae as originally proposed by Banse (1977) appears to be correct, but additional work, and likely revision, of Gymnonereidinae genera is also needed. Finally, Namanereidinae seems to be the only subfamily in which the monophyletic status still shows agreement in all phylogenetic studies so far. The present results support the understanding of this subfamily as a specialized group of Nereididae in which its morphological simplicity represents secondary reductions.

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**Data availability** Data from the sequences used in this study are available on Genbank. Other data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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