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# Are maldanids from deep-sea reduced habitats closely related? Implications of a new wood-fall species of *Nicomache* from the South China Sea

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A new wood-fall-associated maldanid discovered at a depth of 2,321 m in the South China Sea is here morphologically and molecularly described as *Nicomache tigilli* sp. nov. The new species is characterized as having 21 chaetigers, a prostomium rounded anterior, an arched cephalic keel, anterior ends of nuchal grooves curved outwards, 3–6 acicular spines on chaetigers 1–3, notopodia with simply long and narrow capillary chaetae, and an anal funnel with triangular, unequal-sized anal cirri. Our molecular analyses of the genus *Nicomache*, encompassing *COI*, *16S*, *18S*, and *28S* genes support establishing the new species, which appear phylogenetically closely related to the other species of the genus from reduced habitats.

## KEYWORDS

new species, South China Sea, deep-sea, polychaetes, Maldanidae

## 1 Introduction

Maldanidae, a sedentary tube-building polychaete family known as bamboo worms, are widely distributed from the intertidal to the deep sea and from sandy beaches to muddy sediments, including chemosynthetic environments (Paterson et al., 2009; De Assis et al., 2012; Kobayashi et al., 2018; He et al., 2023). Maldanidae comprise more than 270 species and 45 genera (Pamungkas et al., 2019) grouped into six subfamilies (Rhodininae Arwidsson, 1906, Lumbriclymeninae Arwidsson, 1906, Notoproctinae Detinova, 1985, Maldaninae Malmgren, 1867, Nicomachinae Arwidsson, 1906, and Euclymeninae Arwidsson, 1906). Euclymeninae are reported as paraphyletic, with members of

Nicomachinae nested within them (Kobayashi et al., 2018). Nicomachinae differ from Euclymeninae in having a strongly arched head not forming a cephalic plate, versus an obliquely truncated head forming a cephalic plate with a thin rim around its margin. In turn, the pygidium is key to distinguishing the genera in Nicomachinae, so that incomplete specimens cannot be accurately identified. Within Nicomachinae, *Nicomache* currently includes 17 species (De Assis et al., 2007; Kongsrud and Rapp, 2012), which are characterized by a lack of cephalic plate and having a long cephalic keel on the prostomium, short and curved nuchal grooves, acicular spines on the first three neuropodia, rostrate neurochaetae arranged in one row on following chaetigers, and well-developed funnel-shaped pygidium. *Petaloproctus* resembles *Nicomache*, but has an anal plate with a reduced dorsal border (De Assis et al., 2010). Four species of Nicomachinae have been recorded to date in Chinese coastal waters, namely, *Nicomache inornata* (Moore, 1903), *N. lumbricalis* (Fabricius, 1780), *N. personata* Johnson 1901, and *Petaloproctus terricolus* Quatrefages 1866 (Yang and Sun, 1988; Liu, 2008). However, with the exception of *N. lumbricalis*, all other reports cannot be confirmed due to a lack of voucher specimens. The other four species of *Nicomache* have been described from reducing environments: *N. arwidsoni* (Blake, 1985) and *N. venticola* (Blake and Hilbig, 1990) from the Pacific Ocean, *N. lokii* (Kongsrud & Rapp, 2012) from an Arctic vent, and *N. ohtai* (Miura and Hashimoto, 1991) from Japanese cold seeps. All of them belong to the subgenus *Loxochona* and are characterized by having anal funnels distally oblique in lateral view. In this paper, we describe a new species of *Nicomache* from China, found inhabiting a peculiar chemosynthetic environment, deep-sea wood falls. Despite malidanids being frequently found in this particular habitat (Wolff, 1979; Pailleret et al., 2007), there are no previous records from Chinese waters. Deep-sea wood falls are known to serve as stepping stones for the dispersal of species inhabiting other reduced environments, such as hydrothermal vents and cold seeps (Bienhold et al., 2013; Chen and Linse, 2020), while providing a specialized habitat and energy source that contributes to trigger species evolution in the overall oligotrophic deep ocean. Therefore, we are also exploring the possible relationships of our new species with other malidanids inhabiting reducing environments.

## 2 Materials and methods

### 2.1 Specimen collection and morphological observations

Wood falls were collected from Zhongnan Seamount in the South China Sea on 23 December 2021 during the Cruise TS2-10-2 using the submersible Shenhai Yongshi (Deep Sea Warrior). Malidanids were extracted from wood (Figures 1A, B), preserved in 75% ethanol, and deposited in the Sample Repository of the Second Institute of Oceanography (RISO, Ministry of Natural Resources, Hangzhou, China) after being studied. Morphological and morphometric observations were done under a Zeiss

Stereomicroscope Discovery V20 (Germany) and a Zeiss compound microscope Axio Imager A2 (Germany). Detailed observations of key morphological traits were done under a scanning electron microscopy (SEM; HITACHI TM-1000, Japan). Morphological terminology follows De Assis et al (2010).

### 2.2 DNA extraction and PCR amplification

DNA was extracted from the body wall tissue using a DNeasy Tissue Kit (Qiagen) following the manufacturer's protocol. Amplifications of specific partial fragments of the *COI*, *16S*, and *28S* genes were carried out using distinct primer pairs: LCO1490/HCO2198 for *COI* (Folmer et al., 1994), 16Sar/16Sbr for *16S* (Palumbi, 1996), and Po28R4/28F5 for *28S* (Struck et al., 2006; Passamaneck et al., 2004). The polymerase chain reaction (PCR) mixtures contained 0.5 U of polymerase (Phanta Super-Fidelity DNA Polymerase, Vazyme, China), 2.5  $\mu$ L of 10  $\times$  buffer solution (supplied by the polymerase manufacturer), 0.5  $\mu$ L of dNTP solution (2.5 mM), 1  $\mu$ L of each primer (10  $\mu$ M), 1  $\mu$ L of template DNA, and ddH<sub>2</sub>O (to bring the final volume to 25  $\mu$ L). The PCR amplification conditions were as follows: *COI*: 95°C/4 min, 35 cycles of (95°C/30 s, 45°C/45 s, and 72°C/1 min), and 72°C/7 min; *16S*: 95°C/4 min, 35 cycles of (95°C/30 s, 50°C/30 s, and 72°C/1 min), and 72°C/7 min; *18S*: 95°C/4 min, 35 cycles of (95°C/30 s, 50°C/1 min, and 72°C/2 min), and 72°C/10 min; *28S*: 95°C/4 min, 7 cycles of (95°C/30 s, 55°C/30 s, and 72°C/2 min); and 35 cycles of (95°C/30 s, 52°C/30 s, and 72°C/2 min), and 72°C/10 min. The PCR products were purified using the QIAquick PCR purification kit (Qiagen, CA, USA) and then sequenced using the bi-directional Sanger sequencing method, which was conducted by Sangon (Shanghai, China).

### 2.3 Phylogenetic analyses

We constructed a molecular phylogenetic tree based on the four selected genes using sequences of nine species of Nicomachinae and one of *Metasychis* cf. *gotoi* (Maldaninae) from GenBank (Table 1).

The homologous sequences were normally aligned with MAFFT (Kato and Standley, 2013), using the “—auto” strategy and concatenated using PhyloSuite v1.2.2 (Zhang et al., 2020) to select the best partitioning scheme and evolutionary models for the predefined partitions using PartitionFinder 2 (Lanfear et al., 2017), with the greedy algorithm and Corrected Akaike Information Criterion.

The phylogenies were inferred from the concatenated dataset using maximum likelihood (ML) and Bayesian inference (BI). The ML phylogenies were inferred using IQ-TREE (Nguyen et al., 2015) under the Edge-linked partition model for 5,000 standard bootstraps, and the Shimodaira–Hasegawa-like approximate likelihood-ratio test (Guindon et al., 2010). The BI phylogenies were inferred using MrBayes 3.2.6 (Ronquist et al., 2012) under a partition model (two parallel runs, 2,000,000 generations), discarding the initial 25% of the sampled data as burn-in.

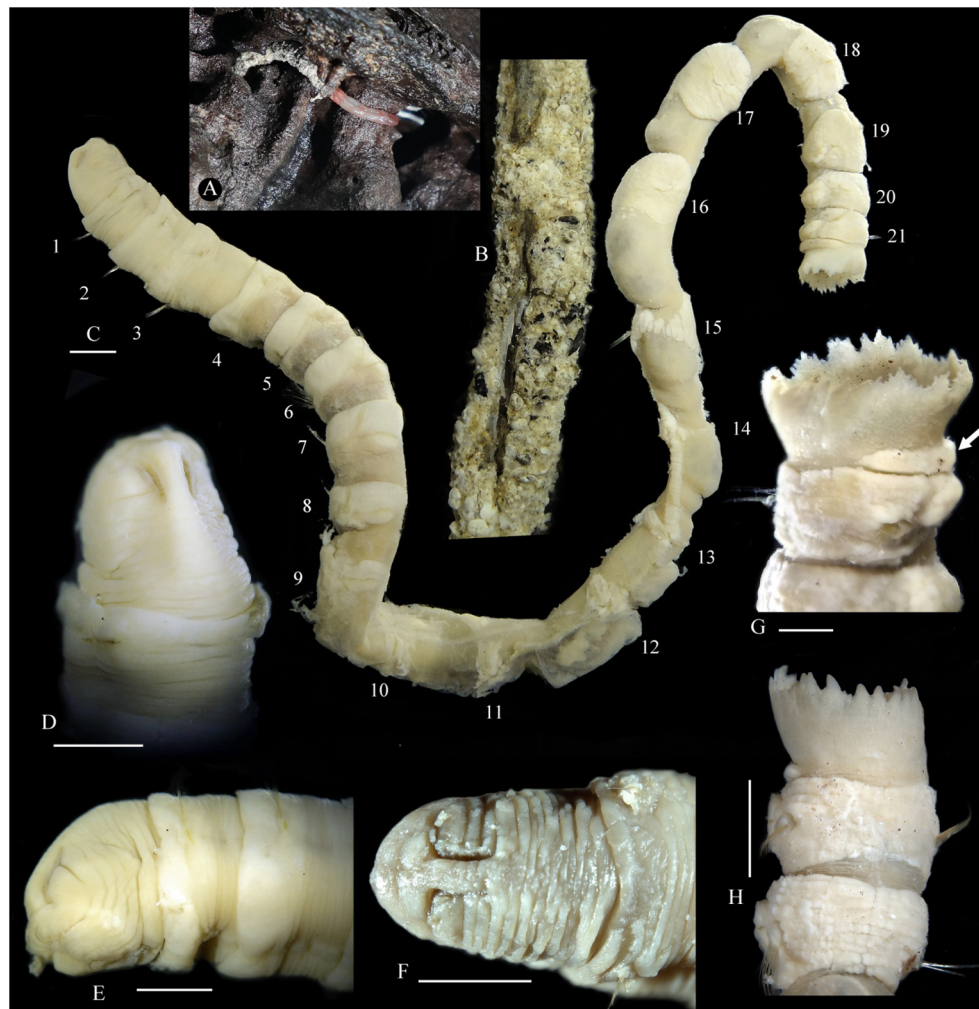


FIGURE 1

*Nicomache tigilli* sp. nov. (A) Living specimen attached to a wood fall. (B) Tube. Preserved specimens: (C) body; (D) anterior end in dorsal view; (E) anterior end in lateral view; (F) anterior end in dorsal view; (G) 21th chaetiger and anal funnel, The arrow shows the glandular pad. (H) Pygidium in dorsal view. (B-E, G) Holotype; and (F, H) paratype. Scale bar: 0.25 cm.

## 3 Results

### 3.1 Systematics

Family: Maldanidae (Malmgren, 1865)

Subfamily: Nicomachinae (Arwidsson, 1907)

Genus: *Nicomache* (Malmgren, 1865)

Type of species: *Sabella lumbricalis* (Fabricius, 1780)

*Nicomache (Loxochona) tigilli* sp. nov.

Figures 1–3

urn:lsid:zoobank.org:act:3B3930B9-D534-4105-B58D-A9FAF52CD579

#### 3.1.1 Material examined

Holotype: B6317400001, complete specimen, ca. 110-mm long, ca. 5.0-mm wide, coll. Biao Chen, Zhongnan Seamount, South China Sea, 14.01943°N, 115.5016°E, 2,321-m depth.

Paratypes: B6317400002, one complete specimen, ca. 98.2-mm long, ca. 4.2-mm wide, same collection data as holotype.

B6317400003: One complete specimen, ca. 113-mm long, ca. 4.5-mm wide, the same collection data as the holotype, partly used for DNA sequencing and SEM.

#### 3.1.2 Diagnosis

The body has 21 chaetigers, without a chaetous pre-pygidial segment. The distal margin of the anal funnel is slightly oblique in lateral view, with the ventral part longer than the dorsal part. The prostomium is rounded anteriorly. The anterior ends of the nuchal grooves curve outwards. The neuropodia of chaetigers 1–3 with 3–6 have strongly pointed acicular spines.

#### 3.1.3 Etymology

The specific name *tigilli* is the genitive form of the Latin *tigillum* (meaning small piece of wood), referring to the habitat of the new species.

TABLE 1 Sample and sequence information for each taxa that were used in our analyses.

taxon	18S	28S	16S	COI	locality	habitat depth(m)	Refs.
<i>Nicomache cf. lumbricalis</i>	LC366967	LC366003	LC365954	LC342667	Off Otsuchi, Iwate, Japan	478–484	<a href="#">Kobayashi et al., 2018</a>
<i>Nicomache ohtai</i>	LC366943	LC365983	LC365938	LC342643	Off Hatsushima, Sagami Bay, Kanagawa, Japan; <b>cold seep area</b>	858	<a href="#">Kobayashi et al., 2018</a>
<i>Nicomache</i> sp.	LC366934	LC366021	LC365930	LC342634	North knoll of Iheya Ridge, Okinawa; <b>hydrothermal vent field</b>	1420	<a href="#">Kobayashi et al., 2018</a>
<i>Nicomache lumbricalis</i>	MG975479	–	MG975463	MG975595	Svalbard, Arctic	235	<a href="#">Eilertsen et al., 2018</a>
<i>Nicomache quadrispinata</i>	MG975475	MG975581	MG975460	MG975590	off Jan Mayen, Norway	616	<a href="#">Eilertsen et al., 2018</a>
<i>Nicomache minor</i>	MG975473	MG975580	MG975458	MG975588	Hvite Sea, Russia	Unknown	<a href="#">Eilertsen et al., 2018</a>
<i>Nicomache lokii</i>	MG975465	MG975576	MG975455	MG975584	Antarctic; <b>hydrothermal vent field</b>	2608	<a href="#">Eilertsen et al., 2018</a>
<i>Nicomache personata</i>	LC006051	LC208085	–	LC006052	Oshoro Bay, Hokkaido, Japan	shallow water; seagrass bed	1. <a href="#">Kajihara et al., 2015</a> for COI and 18S rDNA 2. <a href="#">Shinri et al., 2018</a> for 28S rDNA
<i>Nicomache tigilli</i> sp. nov.	–	OQ842972	OQ842971	OQ832608	Zhongnan Seamount, South China Sea; <b>Wood falls</b>	2321	this study
<i>Petaloproctus dentatus</i>	LC366941	LC365981	LC365936	LC342641	Off Kasumi, Hyogo, Japan;	1820–1870	<a href="#">Kobayashi et al., 2018</a>
<i>Metasychis cf. gotoi</i>	LC366955	LC366022	LC365966	LC342655	Off Otsuchi, Iwate, Japan	118–119	<a href="#">Kobayashi et al., 2018</a>

The bold data denote chemosynthetic environments.

### 3.1.4 Description

The body is long, cylindrical with 21 chaetigers and a pygidial funnel, without an achaetous pre-pygidial segment. Segments are shorter on the anterior and posterior body, and longer on the middle body (Figure 1C). Glands as well-developed circular bands in the anterior part of chaetigers 1–8, then present mainly on parapodial rami in the following chaetigers, and a prominent semicircular pad on the anteroventral side of the pygidial funnel (Figure 1G).

The head is well-defined, with an arched cephalic keel (Figures 1D, E). The prostomium is rounded anteriorly, with a wide prostomial palpode (anterior part). Paired nuchal grooves are long, deep, inverted J-shaped, and curved outwards in the anterior part (Figures 1E, F). Ocelli are not seen. The mouth is large, oval, and with a thick lower lip. Anterior six chaetigers are short, with its length being half of its width, the length of chaetiger 7 is approximately 1.0–1.3 times its width; chaetiger 8 is the shortest, chaetigers 9–19 are about twice as long as wide or longer; the last two chaetigers are shorter than wide. The pygidial funnel is short, with a straight distal margin in lateral view and an irregularly serrated border, with many small digitate papillae or triangular lobes (Figures 1G, H).

All chaetigers are biramous, with noto- and neuropodial chaetae. Neuropodia of chaetigers 1–3, with 3–6 straight acicular neuropodial spines with slender tips (Figure 3A), are replaced by a single row of rostrate uncini in the following neuropodia. There are 12–15 uncini in chaetiger 4, up to 56 in mid-body chaetigers, and 22–35 in posterior chaetigers. The capitium of uncinus has 2–4 teeth in a row, many small accessory teeth on two sides, and a tuft of subrostral bristles under the main fang (Figures 3B–H). From chaetiger 4, notochaetae are arranged in double rows (Figures 3H, K), as simple capillaries lack wings, the same in the anterior and posterior chaetigers (Figures 3I–N), but gradually changing from parallel to the neurochaetae at first few chaetigers to vertical to neurochaetae in the middle and posterior segments.

Oocytes are in anterior and middle segments, up to 108 µm in diameter (Figure 3O). Tubes are irregularly curved, covered with coarse sand and foraminifers, adhered to wood falls.

Distribution and feeding: known only from type locality; associated to wood falls (Figures 1A, B); and dissected gut containing many small wood chips (Figure 3P).

Remarks: *Nicomache tigilli* sp. nov. resembles *N. ohtai* in the shape of head, acicular spines, and rostrate uncini, but differs in having 21



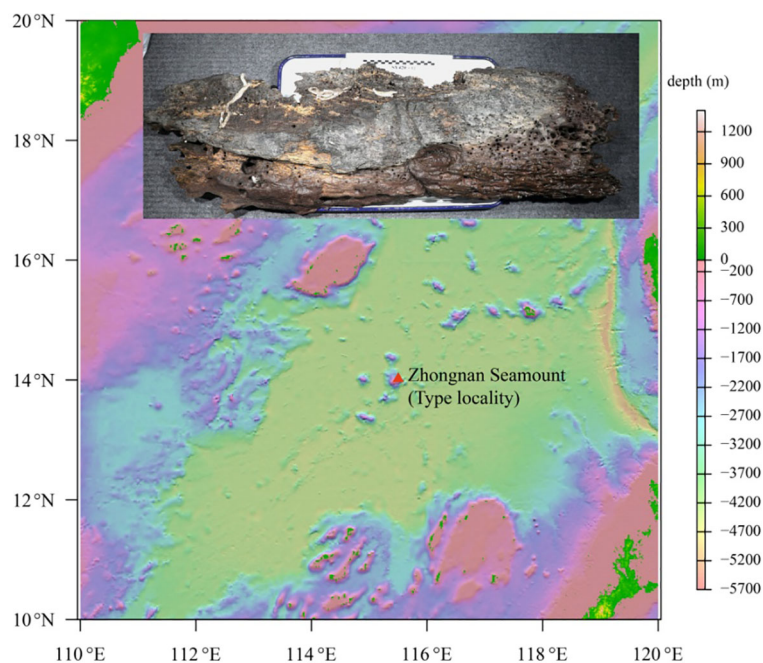


FIGURE 2  
Geographic location of Zhongnan Seamount.

chaetigers (32 in *N. ohtai*), short thin spinulose capillaries absent (present on all notopodia in *N. ohtai*). Spinulose notochaetae are present on most species of *Nicomache*, while simple capillary notochaetae are only present in *N. arwidsoni*, *N. canadensis*, *N. lokii* and *N. tigilli* sp. nov., which can be distinguished from these three species by having more (3–6 vs. 1–2) acicular spines on chaetigers 1–3. Remarkably, a distinct semicircular pad is present on anteroventral side of pygidial funnel of *N. tigilli* sp. nov., which is readily stained with methyl green as the glands on the parapodia rami. Moreover, it is easily removed and the tissues beneath it are identical to those of the adjacent body wall, indicating that it is not an achaetous pre-pygidial segment.

### 3.1.5 Molecular analysis

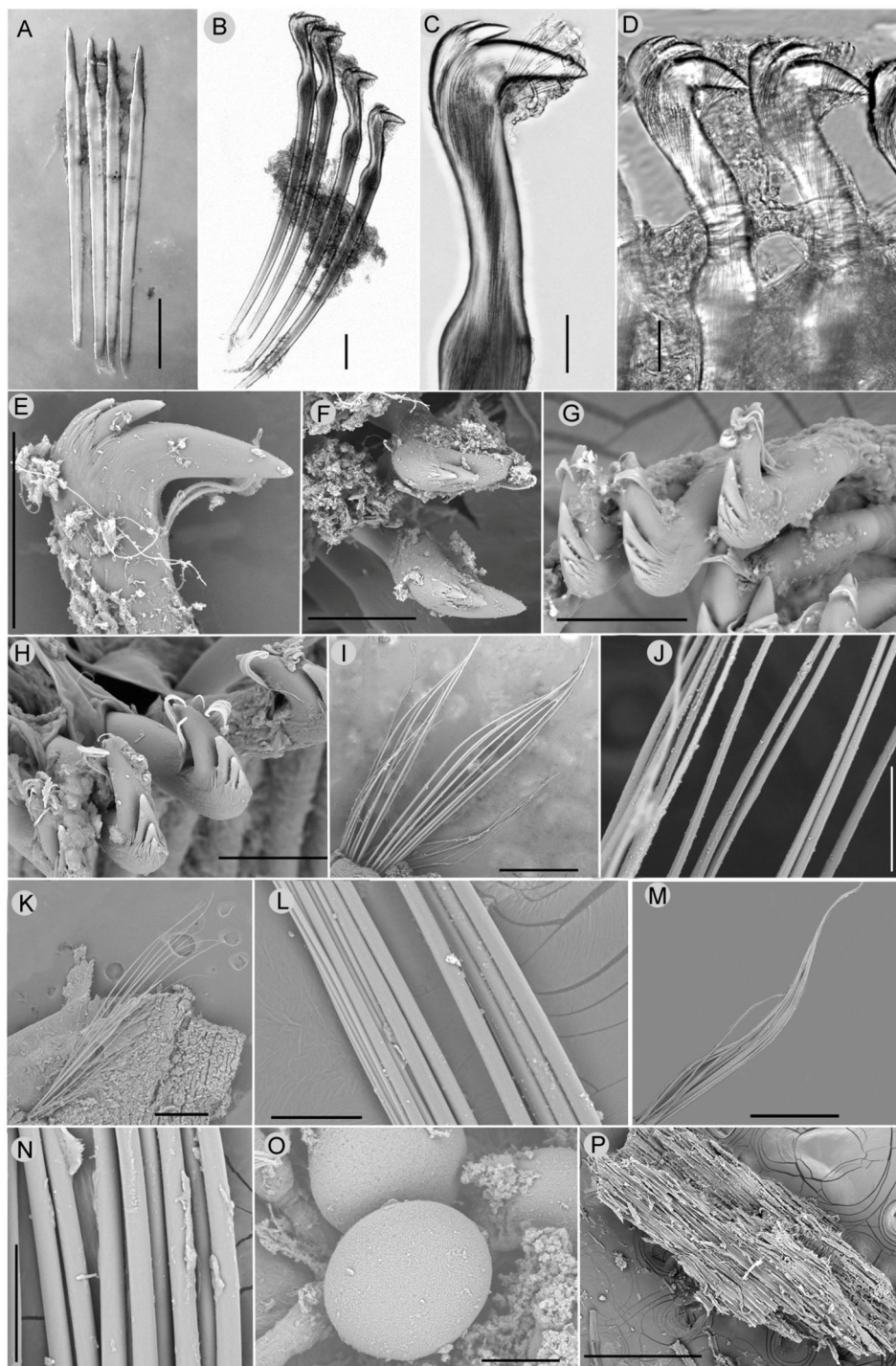
The dataset of the 28S rDNA, 16S rDNA, and *COI* partial sequences of *N. tigilli* sp. nov. (B6317400003) contained 563 bp, 480 bp, and 611 bp (Accession number OQ842972, OQ842971, and OQ832608), respectively. Interspecific pairwise genetic distances between *N. tigilli* sp. nov. and its close relatives ranged from 9.46% to 21.41% (Table 2), with the smallest distances (9.29%–14.14%) occurring between the species from chemosynthetic environments (*N. lokii*, *N. ohtai*, and *Nicomache* sp. with GenBank accession number LC342634) and *N. tigilli* sp. nov., while those between other species of *Nicomache* ranged from 12.75% to 25.5%. The ML and BI combined phylogenetic trees were totally congruent and generally well supported (Figure 4). The species from *Nicomache* clustered into a clade with PP > 0.95, with those from chemosynthetic environments and our new species forming a monophyletic group with maximum support. *Nicomache minor* Arwidsson,

1906 and *N. personata* cluster together with high support, being a sister group to *N. lumbricalis*.

## 4 Discussion

*Nicomache tigilli* sp. nov. can be clearly distinguished morphologically and molecularly from the 17 species of *Nicomache* accepted to date (De Assis et al., 2007; Kongsrud and Rapp, 2012), and is the first species of the genus inhabiting deep-sea wood falls. Moreover, the wood chips found in the gut strongly suggest feeding on wood-associated bacteria, in addition to organic matter from surrounding sediments, as suggested for *N. lokii* (Kongsrud and Rapp, 2012).

The morphological and molecular phylogenetic relationship within Nicomachinae did not reveal clear interspecific relationships, likely because a few species of *Nicomache* were included (De Assis and Christoffersen, 2011; Eilertsen et al., 2018; Kobayashi et al., 2018). The monophyly of Nicomachinae was suggested based on three species (*N. lumbricalis*, *P. terriculus*, and *Micromaldane ornithochaeta* Mesnil, 1897), with the Euclymeninae as sister clade (De Assis and Christoffersen, 2011) and later confirmed molecularly (Kobayashi et al., 2018). However, the Euclymeninae were paraphyletic because Nicomachinae were nested within. *Nicomache lokii*, a widespread hydrothermal vent species, showed slightly higher inter- than intra-populations when comparing its Arctic and Antarctic populations (Eilertsen et al., 2018). The phylogenetic topology in Eilertsen et al. (2018) was similar to ours, except for the absence of the chemosynthetic clade,



**FIGURE 3**

*Nicomache tigilli* sp. nov. micrographs: (A) Acicular spines from chaetiger 3. (B) Neurochaetae from chaetiger 4. (C) Capitium of uncinus. (D) neurochaetae from chaetiger 17. (E, F) Lateral and top view of the capitium of an uncinus from chaetiger 5. (G, H) Capitium of uncini from chaetiger 15 and 20, respectively. (I, J) Notochaetae from chaetiger 5 and its partial enlargement. (K, L) Notochaetae from chaetiger 15 and partial enlargement. (M, N) Notochaetae from chaetiger 20 and partial enlargement. (O) Oocytes. (P) Small wood chip extracted from gut. Scale bars: (A, B, E-H, L, N, O) = 50µm, (C, D) = 20 µm, (I, K, M, P) = 500 µm, (J) = 100 µm.

TABLE 2 Pairwise average Kimura 2-parameter (K2P) genetic distances for the taxa that were used in this study based on the COI gene sequences.

	1	2	3	4	5	6	7	8	9	10
1. <i>Nicomache tigilli</i> sp. nov.										
2. <i>Metasychis</i> cf. <i>gotoi</i>	0.260									
3. <i>Nicomache</i> cf. <i>lumbricalis</i>	0.214	0.304								
4. <i>Nicomache lokii</i>	0.132	0.298	0.211							
5. <i>Nicomache lumbricalis</i>	0.214	0.299	0.011	0.206						
6. <i>Nicomache minor</i>	0.211	0.300	0.206	0.201	0.204					
7. <i>Nicomache ohtai</i>	0.095	0.281	0.203	0.141	0.205	0.231				
8. <i>Nicomache personata</i>	0.205	0.295	0.214	0.217	0.206	0.127	0.219			
9. <i>Nicomache quadrispinata</i>	0.211	0.300	0.198	0.217	0.192	0.255	0.202	0.223		
10. <i>Nicomache</i> sp.	0.095	0.273	0.201	0.132	0.205	0.231	0.093	0.213	0.198	
11. <i>Petaloproctus dentatus</i>	0.211	0.284	0.203	0.210	0.202	0.181	0.203	0.184	0.211	0.225

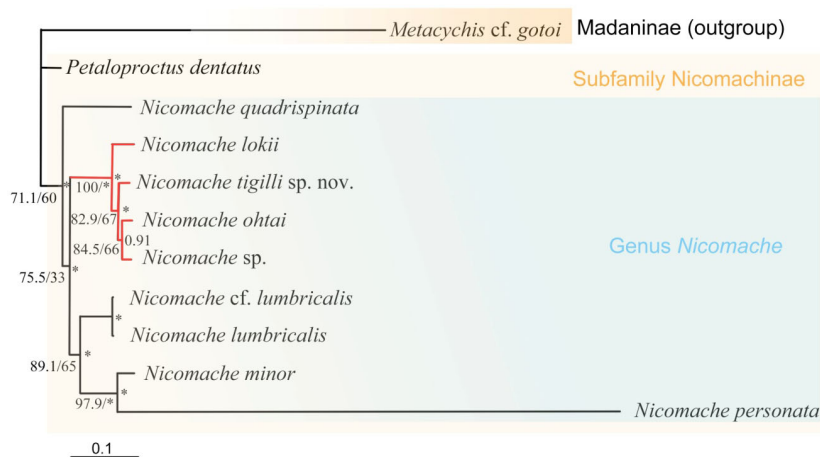


FIGURE 4 Phylogenetic tree obtained by the Bayesian inference based on the concatenated dataset of 16S rDNA, COI gene, 18S rDNA, and 28S rDNA sequences. The branch serves as the SH-aLRT support/standard bootstrap support (BP; left) and Bayesian posterior probabilities (PP, right) are indicated adjacent to each node. \*PP > 0.95 and BP > 95%. The well-supported *Nicomache* clade from reducing habitats highlight with red.

as they included only one species associated to these environments. Conversely, our results (notably the smaller COI distances) strongly support the species of *Nicomache* from chemosynthetic environments to form an evolutionarily separated clade. Deep-sea chemosynthetic environments, such as hydrothermal vents, cold seeps, and organic falls have discontinuous and extremely patchy distributions that may constitute dispersal barriers likely promoting speciation. However, wood falls, like other deep-sea organic-matter-enriched environments, are known to serve as stepping stones, not

only for wood associated species (Romano et al., 2020), but for seep species, such as the gastropod *Cordesia provannoides* Warén and Bouchet, 2009 or the siboglinid tubeworms (Dando et al., 1992). *Nicomache tigilli* sp. nov. is phylogenetically closer to vent/seep species of *Nicomache* than to those from non-reducing environments, independently of depth. Therefore, we hypothesize that sunken wood provides a specialized habitat facilitation dispersal, but also promotes speciation, to the species of *Nicomache* living in a wide range of chemosynthetic environments.



## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repository and accession number(s) can be found in the article/supplementary material.

## Ethics statement

The article presents research on animals that do not require ethical approval for their study.

## Author contributions

YW: Writing – review & editing, Writing – original draft, Methodology, Formal analysis. YZ: Writing – review & editing, Resources, Investigation, Data curation. DZ: Writing – review & editing, Visualization, Methodology, Funding acquisition. CW: Writing – review & editing, Supervision, Resources, Conceptualization.

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## Conflict of interest

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## References

- Arwidsson, I. (1906). Studien über die skandinavischen und arktischen Maldaniden nebst Zusammenstellung der übrigen bisher bekannten Arten dieser Familie. Inaugural-Dissertation zur Erlangung der Doktorwürde. Der Mathematisch-Naturwissenschaftlichen Sektion der Philosophischen Fakultät zu Upsala, Upsala Universität, Upsala. 1–308.
- Arwidsson, I. (1907). Studien über die skandinavischen und Arktischen Maldaniden nebst Zusammenstellung der übrigen bisher bekannten Arten dieser Familie. *Zoologische Jahrbcher. Supplement* 9, 1–308.
- Bienhold, C., Pop Ristova, P., Wenzhöfer, F., Dittmar, T., and Boetius, A. (2013). How deep-sea wood falls sustain chemosynthetic life. *PLoS One* 8, e53590–e53590. doi: 10.1371/journal.pone.0053590
- Blake, J. A. (1985). Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific. I. Euphrosinidae, Phyllocididae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. *Bull. Biol. Soc. Wash* 6, 67–101.
- Blake, J. A., and Hilbig, B. (1990). Polychaeta from the vicinity of deep-sea hydrothermal vents in the Eastern Pacific Ocean and records from the Juan de Fuca and Explorer Ridge systems. *Pac Sci.* 44, 219–253.
- Chen, C., and Linse, K. (2020). From wood to vent: first coccolinid limpet associated with hydrothermal activity discovered in the Weddell Sea. *Antarct Sci.* 32, 354–366. doi: 10.1017/S095410202000022X
- Dando, P. R., Southward, A. F., Southward, E. C., Dixon, D. R., Crawford, A., and Crawford, (1992). Shipwrecked tube worms. *Nature*. 356, 667–667. doi: 10.1038/356667a0
- De Assis, J. E., Alonso, C., and Christoffersen, M. L. (2007). A catalogue and taxonomic keys of the Subfamily Nicomachinae (Polychaeta : Maldanidae) of the world. *Zootaxa*. 1657, 41–55.
- De Assis, J. E., Bleidorn, C., and Christoffersen, M. L. (2012). “Maldanidae malmgre”. in Handbook of Zoology, A natural history of the phyla of the animal kingdom,” in *Annelida*. Ed. A. Schmidt-Rhaesa (De Gruyter, Osnabrück), 1–12.
- De Assis, J. E., and Christoffersen, M. L. (2011). Phylogenetic relationships within Maldanidae (Capitellida, Annelida), based on morphological characters. *Syst. Biodivers* 9, 233–245. doi: 10.1080/14772000.2011.604358
- De Assis, J. E., Christoffersen, M. L., and Lana, P. D. C. (2010). Phylogenetic analysis of *Petaloproctus* (Maldanidae: Polychaeta), with description of a new species from southeastern Brazil. *Sci. Mar* 74, 111–120. doi: 10.3989/scimar.2010.74n1
- Detinova, N. N. (1985). Taxonomy, composition and distribution of polychaetes subfamily lumbriclymeninae (Maldanidae). *Explor. Fauna Seas*. 34 (42), 25–29.
- Eilertsen, M. H., Georgieva, M. N., Kongsrud, J. A., Linse, K., Wiklund, H., Glover, A. G., et al. (2018). Genetic connectivity from the Arctic to the Antarctic: Sclerolinum contortum and Nicomache lokii (Annelida) are both widespread in reducing environments. *Sci. Rep* 8, 4810. doi: 10.1038/s41598-018-23076-0
- Fabricius, O. (1780). *Fauna groenlandica, systematice sistens animalia groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque, synonyma auctorum plurimum, descriptionem, locum, victum, generationem, mores, usum capturamque singuli, pro ut detegendi occasio fuit, maximaque parte secundum proprias observationes* (Ioannis Gottlob Rothe: Hafniae & Lipsiae), 1–452.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3 (5), 294–299.
- Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., and Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. *Syst. Biol.* 59, 307–321. doi: 10.1093/sysbio/syq010
- He, X., Xu, T., Chen, C., Liu, X., Li, Y., Zhong, Z., et al. (2023). Same (sea) bed different dreams: Biological community structure of the Haima seep reveals distinct biogeographic affinities. *Innovation Geoscience*. 1, 100019. doi: 10.59717/j.xinn-geo.2023.100019
- Kajihara, H., Tomioka, S., Kakui, K., and Iseto, T. (2015). Phylogenetic position of the queer, backward-bent entoproct loxosoma axisadversum (Entoprocta: solitaria: loxosomatidae). *Species diversity*. 20, 83–88. doi: 10.12782/sd.20.1.083
- Katoh, K., and Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. doi: 10.1093/molbev/mst010



- Kobayashi, G., Goto, R., Takano, T., and Kojima, S. (2018). Molecular phylogeny of Maldanidae (Annelida): Multiple losses of tube-capping plates and evolutionary shifts in habitat depth. *Mol. Phylogenet. Evol.* 127332–127344. doi: 10.1016/j.ympev.2018.04.036
- Kongsrud, J. A., and Rapp, H. T. (2012). *Nicomache (Loxochona) lokii* sp. nov. (Annelida: Polychaeta: Maldanidae) from the Loki's Castle vent field: an important structure builder in an Arctic vent system. *Polar Biol.* 35, 161–170. doi: 10.1007/s00300-011-1048-4
- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2017). PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Biol. Evol.* 34, 772–773. doi: 10.1093/molbev/msw260
- Liu, R. (2008). *Checklist of marine biota of China seas (in chinese)* (Beijing: Science Press), 446.
- Malmgren, A. J. (1865). Nordiska hafs-annulater. *Öfversigt af Königlich Vetenskapsakademiens förhandlingar Stockholm.* 22, 181–192.
- Malmgren, A. J. (1867). Annulata polychaeta spetsbergiae, grönlandiae, islandiae et scandinavicae hactenus cognita. *Öfversigt Af Kongliga Vetenskaps-Akademiens Förhandlingar Stockholm.* 24, 127–235.
- Miura, T., and Hashimoto, J. (1991). *Nicomache ohtai*, new species (Polychaeta: Maldanidae) collected from the Hatsushima cold-seep in Sagami Bay. *Proc. Biol. Soc. Wash.* 104, 159–165.
- Moore, J. P. (1903). Polychaeta from the coastal slope of Japan and from Kamchatka and Bering Sea. *Proc. Acad. Nat. Sci. Phila.* 55, 401–490.
- Nguyen, L. T., Schmidt, H. A., von Haeseler, A., and Minh, B. Q. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol. Biol. Evol.* 32, 268–274. doi: 10.1093/molbev/msu300
- Pailleret, M., Haga, T., Petit, P. A., Privé-Gill, C., Saedlou, N., Gaill, F., et al. (2007). Sunken wood from the Vanuatu Islands: identification of wood substrates and preliminary description of associated fauna. *Mar. Ecology.*, 28233–28241. doi: 10.1111/j.1439-0485.2006.00149.x
- Pamungkas, J., Glasby, C. J., Read, G. B., Wilson, S. P., and Costello, M. J. (2019). Progress and perspectives in the discovery of polychaete worms (Annelida) of the world. *Helgol. Mar. Res.* 73. doi: 10.1186/s10152-019-0524-z
- Passamaneck, Y. J., Schander, C., and Halanych, K. M. (2004). Investigation of molluscan phylogeny using large-subunit and small-subunit nuclear rRNA sequences. *Mol. Phylogenet. Evol.* 32 (1), 25–38. doi: 10.1016/j.ympev.2003.12.016
- Paterson, G. L., Glover, A. G., Froján, C. B., Whitaker, A., Budaeva, N., Chimonides, J., et al. (2009). A census of abyssal polychaetes. *Deep Sea Res. 2 Top. Stud. Oceanogr.* 56, 1739–1746. doi: 10.1016/j.dsr2.2009.05.018
- Romano, C., Nunes-Jorge, A., Le Bris, N., Rouse, G. W., Martin, D., and Borowski, C. (2020). Wooden stepping stones: Diversity and biogeography of deep-sea wood boring Xylophagidae (Mollusca: Bivalvia) in the North-East Atlantic Ocean, with the description of a new genus. *Prot. Mar. Sci.* 7, 579959. doi: 10.3389/fmars.2020.579959
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542. doi: 10.1093/sysbio/sys029
- Shinri, T., Keichi, K., and Hiroshi, K. (2018). Molecular phylogeny of the family capitellidae (Annelida). *Zoolog Sci.* 35, 436–445. doi: 10.2108/zs180009
- Struck, T. H., Pursche, G., and Halanych, K. M. (2006). Phylogeny of eunicida (Annelida) and exploring data congruence using a partition addition bootstrap alteration (PABA) approach. *Syst. Biol.* 55 (1), 1–20. doi: 10.1080/10635150500354910
- Warén, A., and Bouchet, P. (2009). New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep Sea Res. 2 Top. Stud. Oceanogr.* 56, 2326–2349. doi: 10.1016/j.dsr2.2009.04.013
- Wolff, T. (1979). Magrofaunal utilization of plant remains in the deep sea. *Sarsia* 64, 117–143. doi: 10.1080/00364827.1979.10411373
- Yang, D., and Sun, R. (1988). *Polychaetous annelids commonly seen from China coastal waters (in chinese)* (Beijing: China Agriculture Press), 64–265.
- Zhang, D., Gao, F., Jakovlić, I., Zou, H., Zhang, J., Li, W. X., et al. (2020). PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. *Mol. Ecol. Resour.* 20, 348–355. doi: 10.1111/1755-0998.13096