

HOKKAIDO UNIVERSITY

Title	Molecular Phylogeny of the Family Capitellidae (Annelida)
Author(s)	Tomioka, Shinri; Kakui, Keiichi; Kajihara, Hiroshi
Citation	Zoological Science, 35(5), 436-445 https://doi.org/10.2108/zs180009
Issue Date	2018-10
Doc URL	https://hdl.handle.net/2115/75605
Type	journal article
File Information	Zoological Science35-5_436-445(2018).pdf



Hokkaido University Collection of Scholarly and Academic Papers : HUSCAP

ZOOLOGICAL SCIENCE **35**: 436–445 (2018)
© 2018 Zoological Society of Japan

Molecular Phylogeny of the Family Capitellidae (Annelida)

Shinri Tomioka[1]*, Keiichi Kakui[2], and Hiroshi Kajihara[2]

[1]*Rishiri Town Museum, Senhoshi, Rishiri Is., Hokkaido 097-0311, Japan*
[2]*Department of Biological Sciences, Faculty of Science, Hokkaido University, N10 W8, Sapporo, Hokkaido 060-0810, Japan*

Capitellids have emerged as monophyletic in most but not all recent molecular phylogenies, indicating that more extensive taxon sampling is necessary. In addition, monophyly of most or all capitellid genera was questionable, as some diagnostic characters vary ontogenetically within individuals. We tested the monophyly of Capitellidae and eight capitellid genera using phylogenetic analyses of combined 18S, 28S, H3, and COI gene sequences from 36 putative capitellid species. In our trees, Capitellidae formed a monophyletic sister group to Echiura, and *Capitella* was also monophyletic, separated by a long branch from other capitellids. Well-supported clades each containing representatives of different genera, or containing a subset of species within a genus, indicated that *Barantolla*, *Heteromastus*, and *Notomastus* are likely not monophyletic. We mapped three morphological characters traditionally used to define capitellid genera (head width relative to width of first segment, number of thoracic segments, and number of segments with capillary chaetae) onto our tree. While *Capitella* showed unique character states, states in the other genera were decidedly not phylogenetically informative. Morphology-based capitellid taxonomy will require a fine-scale reevaluation of character states and detection of new characters.

Key words: Capitellida, capitellids, Scolecida, Sedentaria, systematics

INTRODUCTION

The family Capitellidae Grube, 1862 consists of free-living, benthic, earthworm-like annelids and contains about 190 species (Rouse and Pleijel, 2001; Read, 2010). It includes *Capitella teleta* Blake, Grassle & Eckelbarger, 2009, formerly known as "*Capitella* sp. I" (Grassle and Grassle, 1976), which is now used as a model annelid in the field of evolutionary developmental biology, and for which the complete genome has been sequenced (e.g., Ferrier, 2012; Seaver et al., 2012; Lauri et al., 2014; Seaver, 2016). Furthermore, some other species in the genus *Capitella* have been used as bioremediators of organically enriched sediments (e.g., Tsutsumi et al., 2005; Kinoshita et al., 2008) or environmental bioindicators of disturbed habitats (e.g., Reish, 1955; Grassle and Grassle, 1976; reviewed in Dean, 2008). While all capitellids are similar in external morphology, they have successfully colonized diverse environments. Although most species inhabit bottom substrata such as polluted sediments (e.g., Tsutsumi, 1987; Ahn et al., 1995; Méndez et al., 2001; Dean, 2008; Croquer et al., 2016), sandy beaches (e.g., Delgado et al., 2003; Incera et al., 2006; Papageorgiou et al., 2006; García-Garza and De León-González, 2011; Tomioka et al., 2012), and seagrass beds (e.g., Nakaoka et al., 2002; Omena and Creed, 2004; Eklöf et al., 2005; Tanner, 2005; Tomioka et al., 2013), some dwell among squid egg masses (e.g., Hartman, 1947), or burrow into molluscan shells (Blake, 1969) or whale bones (e.g., Fujiwara et al., 2007; Amon et al., 2013; Silva et al., 2016; Sumida et al., 2016). Capitellidae is one of the few metazoan groups where some species exhibit poecilogony (e.g., Chia et al., 1996; Tsutsumi, 2005), or polymorphism in larval development, which has been reported only in some other polychaete groups (e.g., cirratulids, Petersen, 1999; spionids, David et al., 2014) and gastropod molluscs (e.g., Vedetti et al., 2012; McDonald et al., 2014). While capitellids are thus evolutionarily interesting, their phylogenetic relationships have scarcely been studied.

Since Eisig's (1887) extensive monograph on Capitellidae, this family has remained a taxonomically well-defined group (e.g., Hartman, 1947; Fauchald, 1977; Hutchings, 2000). In both morphology-based cladistic analyses (Rouse and Fauchald, 1997) and subsequent molecular analyses of annelid phylogeny (Bleidorn et al., 2003; Struck and Purschke, 2005; Rousset et al., 2007; Struck et al., 2007; Goto et al., 2013), Capitellidae has nearly always emerged as a monophyletic group (Fig. 1A–E). On the other hand, some 19th century naturalists (Carus, 1863; Malmgren, 1865; Haeckel, 1866; Quatrefages, 1866) did not regard Capitellidae as a group, and in Goto's (2016) multi-locus analysis of Echiura, the putative sister taxon to Capitellidae (Weigert et al., 2014), the four capitellid species included as outgroup taxa did not comprise a monophyletic group (Fig. 1F), although the author himself suggested that this might have been the result of poor taxon sampling of capitellids. The monophyly of capitellids thus requires further testing with increased taxon sampling.

Capitellidae presently includes 44 genera (Fauchald, 1977; Piltz, 1977; McCammon and Stull, 1978; Rullier and

* Corresponding author. E-mail: shinri.tomioka@gmail.com
doi:10.2108/zs180009

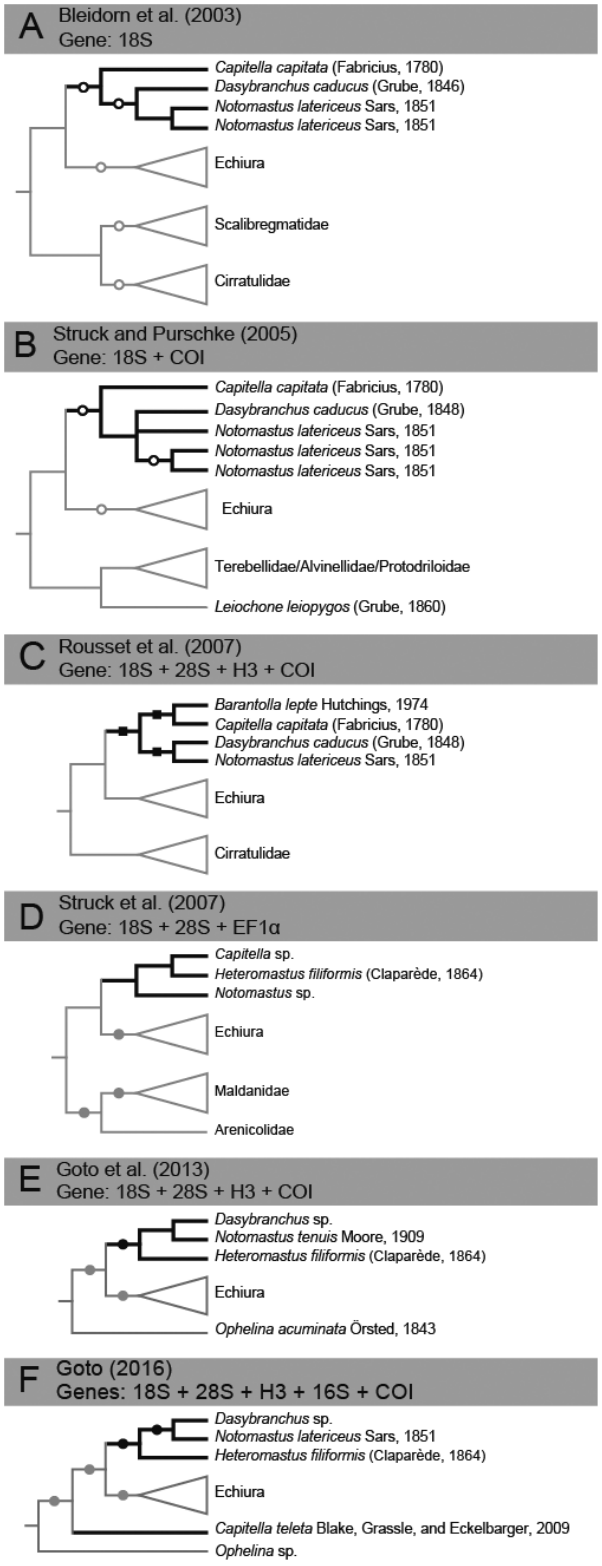


Fig. 1. (A–F) Partial tree topologies from selected, previous molecular studies that included more than two OTUs from Capitellidae. Nodes with open circles are supported with a bootstrap value (BS) greater than 90% in maximum-parsimony analyses and a posterior probability (PP) of 1.00 from Bayesian inference (BI). Nodes with solid circles are supported with a BS greater than 90% in maximum-likelihood analyses and 1.00 PP from BI. Nodes with solid squares are supported by a jackknife value greater than 90%.

Amoureux, 1979; Amaral, 1980; Ewing, 1982; Amoureux, 1983; Kirkegaard, 1983; Brown, 1987; Garwood and Bamber, 1988; Warren, 1991; Capaccioni-Azzati and Martín, 1992; Warren and Parker, 1994; Blake, 2000; Buzhinskaja and Smirnov, 2000; Green, 2002; Magalhães and Bailey-Brock, 2012), most of which are likely not monophyletic, and among which phylogenetic relationships remain uninvestigated. Rouse and Pleijel (2001: p. 44) remarked, “the taxonomy of Capitellidae is in serious need of revision”, because genera were, and still are, defined in a way that does not reflect phylogeny. Genera have been diagnosed based on unique combinations of morphological characters, such as the shape of the head, number of thoracic segments, arrangement/type of chaetae, presence or absence of branchiae, and shape of the pygidium (Fauchald, 1977; Blake et al., 2009). This ‘unique combination’ approach itself is unlikely to lead to monophyletic taxa (Sundberg, 1993; Sundberg and Pleijel, 1994), and one diagnostic character, the arrangement of chaetae, is known to change ontogenetically within individuals (Ewing, 1982; Fredette, 1982; George, 1984).

In this study, we conducted a molecular phylogenetic analysis of capitellid worms from Japanese waters to test the monophyly of Capitellidae and some of its constituent genera. This allowed us to also examine whether some of the generic diagnostic characters mentioned above are concordant with phylogenetic relationships.

MATERIALS AND METHODS

Sampling and identification

About 400 specimens of capitellid polychaetes were collected at 29 localities around Japan from 2012 to 2016. The anterior portions of specimens were fixed in 10% formalin–seawater and later transferred into 70% ethanol for morphological observation; the posterior or middle portions were preserved in 99% ethanol for DNA extraction. DNA was extracted from a few individuals from each locality, and then molecularly barcoded using the genes H3 (nuclear histone H3), 18S (nuclear 18S ribosomal RNA), and COI (mitochondrial cytochrome *c* oxidase subunit I). From 42 specimens from which a sequence was obtained for at least one of these markers, 31 were selected to represent putative species (operational taxonomic units, or OTUs) to be included in analyses (Table 1). As outgroup taxa, one individual each of the maldanid *Nicomache personata* Johnson, 1901 (partially sequenced by Kajihara et al., 2014) and the naidid oligochaete *Tubifex tubifex* (Müller, 1774) (cultured by Professor Takashi Shimizu, Hokkaido University) were sequenced (Table 1). All specimens not destroyed for DNA extraction have been deposited in the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo (Table 1).

Capitellid specimens were identified to the genus level based on combinations of the following five characters: *i*) width of the head relative to the first segment (Type A, head half the width of the first segment; Type B, head same width as first segment) (Fig. 2A, B); *ii*) number of thoracic segments; *iii*) arrangement/type of chaetae; *iv*) presence or absence of branchiae; and *v*) shape of the pygidium. The 31 specimens selected for analysis, each representing a single, putative species, were identified as representing eight genera (Table 2). Because most specimens were missing the posterior portion of the body upon collection, characters *iv*) and *v*) were not included in the character-state analysis. The first character (head type) was consistent irrespective of the state of the proboscis (i.e., whether it was extruded or retracted) or the degree of body contraction (ST pers. obs.).

Table 1. List of specimens used in this study, with species name, sampling locality or source, habitat, DDBJ/ENA/GenBank accession numbers for 18S, 28S, H3, and COI sequences, the museum catalogue number (ICHUM), and references.

Species	Sampling locality or source	Habitat	Accession number				Catalogue number	Reference
			18S	28S	H3	COI		
Ingroup								
Barantolla sp. 1	Muroran, Hokkaido (42.3049°N, 140.9885°E)	seagrass bed	LC208025	LC208055	LC208087	LC208116	5397	this study
Barantolla sp. 2	Oura Bay, Okinawa (26.5540°N, 128.0416°E)	tidal mud flat	LC208026	LC208056	LC208088	LC208117	5398	this study
Capitella teleta Blake, Grassle & Eckelbarger, 2009 (1)	Ainan, Ehime (32.9206°N, 132.5189°E)	muddy sediments beneath aquaculture rafts	LC208027	LC208057	LC208089	LC120636	5167	Tomioka et al. (2016), this study
Capitella teleta 2	GenBank	–	JF509728	–	JF509713	–	–	Andrade et al. (2011)
Capitella aff. *teleta*	Gamo, Miyagi (38.2578°N, 141.0144°E)	tidal mud flat	LC208028	LC208058	LC208090	LC120642	5130	Tomioka et al. (2016), this study
Capitella sp. 1	Monbetsu, Hokkaido (44.3645°N, 143.3546°E)	seagrass bed	LC208029	LC208059	LC208091	LC120651	5399	Tomioka et al. (2016), this study
Capitella sp. 2	Akkeshi, Hokkaido (43.0185°N, 144.8346°E)	seagrass bed	–	LC208060	–	LC208118	5400	this study
Capitella sp. 3	Onosato River, Osaka (34.3765°N, 135.2509°E)	tidal mud flat	LC208030	LC208061	LC208092	LC012038	5401	this study
Capitella sp. 4	Manko-Higata, Okinawa (26.1941°N, 127.6836°E)	tidal mud flat	LC208031	LC208062	LC208093	–	5402	this study
Capitella sp. 5	Hatsukaichi, Hiroshima (34.2756°N, 132.2669°E)	tidal mud flat	LC208032	LC208063	LC208094	–	5403	this study
Decamastus sp. 1	Hachi-Higata, Hiroshima (34.3260°N, 132.8979°E)	tidal mud flat	LC208033	LC208064	LC208095	–	5404	this study
Decamastus sp. 2	off Manabe Island (34.3772°N, 133.6162°E)	unknown [a biological dredge from the TR/V Toyoshio-maru (Hiroshima University)]	LC208034	LC208065	LC208096	LC208119	5405	this study
Heteromastus sp. 1	Akkeshi Lake, Hokkaido (43.0515°N, 144.8568°E)	tidal mud flat	LC208035	LC208066	LC208097	LC208120	5406	this study
Heteromastus sp. 2	Hachi-Higata, Hiroshima (34.3260°N, 132.8979°E)	tidal mud flat	LC208036	LC208067	LC208098	LC208121	5407	this study
Heteromastus sp. 3	Nagura-Amparu, Ishigaki Island, Okinawa (24.4007°N, 124.1407°E)	tidal mud flat	LC208037	LC208068	LC208099	LC208122	5408	this study
Heteromastus sp. 4	Sone-Higata, Fukuoka (33.8243°N, 130.9663°E)	tidal mud flat	LC208038	LC208069	LC208100	LC208123	5409	this study
Heteromastus sp. 5	Fushino River, Yamaguchi (34.0215°N, 131.4154°E)	tidal mud flat	LC208039	LC208070	LC208101	LC208124	5410	this study
Heteromastus sp. 6	Edo River, Tokyo (35.7007°N, 139.9252°E)	tidal mud flat	–	LC208071	LC208102	LC208125	5411	this study
Heteromastus sp. 7	Manose River, Kagoshima (31.4487°N, 130.2949°E)	tidal mud flat	LC208040	LC208072	LC208103	LC208126	5412	this study
Heteromastus sp. 8	Koajiro-Higata, Kanagawa (35.1635°N, 139.6296°E)	tidal mud flat	LC208041	LC208073	–	LC208127	5413	this study
Heteromastus filiformis (Claparède, 1864)	GenBank	–	DQ790081	DQ790038	–	–	–	Struck et al. (2007)
Leiohrides sp. 1	Hachi-Higata, Hiroshima (34.3260°N, 132.8979°E)	tidal mud flat	LC208042	LC208074	LC208104	LC208128	5414	this study
Leiohrides sp. 2	Koajiro-Higata, Kanagawa (35.1635°N, 139.6296°E)	tidal mud flat	LC208043	LC208075	LC208105	–	5415	this study

Table 1. Continued.

Species	Sampling locality or source	Habitat	Accession number				Catalogue number	Reference
			18S	28S	H3	COI		
Leiohrides sp. 3	Komi, Iriomote Island, Okinawa (24.3511°N, 123.9381°E)	dead-coral debris sediment on tidal flat	LC208044	LC208076	–	–	5416	this study
Mastobranchus sp. 1	Komi, Iriomote Island, Okinawa (24.3511°N, 123.9381°E)	dead-coral debris sediment on tidal flat	LC208045	–	LC208106	LC208020	5417	this study
Mediomastus opertaculeus Tomioka, Hiruta & Kajihara, 2013	Abashiri, Hokkaido (44.0493°N, 144.2596°E)	seagrass bed	LC208046	LC208077	LC208107	AB794985	4372	Tomioka et al. (2013), this study
Notomastus sp. 1	Tama River, Tokyo (35.5411°N, 139.4401°E)	tidal mud flat	LC208047	LC208078	LC208108	LC208129	5424	this study
Notomastus sp. 2	Yagachi Island, Okinawa (26.6507°N, 128.0091°E)	tidal mud flat	LC208048	LC208079	LC208109	LC208130	5425	this study
Notomastus sp. 3	off Owase (34.1611°N, 136.8436°E)	unknown [a biological dredge from the TR/V Seisui-maru (Mie University)]	LC208049	LC208080	LC208110	–	5426	this study
Notomastus sp. 4	Suou-Nada (33.7475°N, 131.5810°E)	unknown [a biological dredge from the TR/V Toyoshio-maru (Hiroshima University)]	LC208050	LC208081	LC208111	–	5427	this study
Notomastus sp. 5	Torinoe-Higata, Okayama (34.4734°N, 133.5296°E)	tidal mud flat	LC208051	LC208082	LC208112	LC208131	5428	this study
Notomastus sp. 6	Takahashi River, Okayama (34.5427°N, 133.7025°E)	tidal mud flat	LC208052	LC208083	LC208113	LC208132	5429	this study
Notomastus sp. 7	Fukiage Beach, Kagoshima (31.4416°N, 130.2832°E)	open sandy beach	LC208053	LC208084	LC208114	–	5430	this study
Notomastus hemipodus Hartman, 1945	GenBank (Bamfield, Canada)	–	HM746728	–	HM746759	–	–	Paul et al. (2010)
Notomastus latericeus Sars, 1851	GenBank (Bohuslän, Sweden)	–	AY040697	–	DQ779747	–	–	Siddall et al. (2001), Rousett et al. (2007)
Notomastus tenuis Moore, 1909	GenBank	–	DQ790084	DQ790044	–	–	–	Struck et al. (2007)
Outgroup								
Arhynchite hayaoi Tanaka & Nishikawa, 2013	GenBank	–	AB771462	AB771474	AB771487	AB771495	–	Goto et al. (2013)
Bonellia sp.	GenBank	–	AB771463	AB771475	AB771488	AB771496	–	Goto (2016)
Ikedosoma gogoshimense Ikeda, 1904	GenBank	–	AB967989	AB968002	AB968013	AB968026	–	Tanaka et al. (2014)
Listriolobus sorbillans (Lampert, 1883)	GenBank	–	AB967995	AB968006	AB968019	AB968032	–	Tanaka et al. (2014)
Lumbricus polyphemus (Fitzinger, 1833)	GenBank	–	HQ728904	HQ728938	–	–	–	James and Davidson (2012)
Nicomache personata Johnson, 1901	Oshoro Bay, Hokkaido (43.3639°N, 141.4317°E)	seagrass bed	LC006051	LC208085	LC005496	LC006052	–	Kajihara et al. (2014), this study
Ophelina acuminata Örsted, 1843	GenBank	–	DQ790085	DQ790045	HM746761	–	–	Struck et al. (2007)
Tubifex tubifex (Müller, 1774)	Cultured by Professor Takashi Shimizu	soft mud in a vat	LC208054	LC208086	LC208115	LC208133	5431	this study

DNA extraction, PCR amplification, and sequencing

Total DNA was extracted from the middle or posterior portion of worms with a DNeasy Blood & Tissue Kit (Qiagen, Germany). Four regions [18S, 28S (nuclear 28S rRNA), H3, and COI] were sequenced for the 31 capitellid and two outgroup species. Primers used for PCR amplification and sequencing are listed in Table 3. Based on the sequence of *Mediomastus opertaculeus* Tomioka, Hiruta & Kajihara, 2013, a specific primer (Mastus_COI_F) was designed by using Primer3Plus (Rozen and Skaletsky, 2000). PCRs were performed with an iCycler thermal cycler (BioRad, USA) in 10-μl reaction volumes each containing 1 μl of total DNA template, 1 μl of 10× Ex *Taq* buffer (TaKaRa Bio, Japan), 2 mM each dNTP, 1 μM each primer, and 0.25 U of TaKaRa Ex *Taq* DNA polymerase (5 U/μl; TaKaRa Bio) in deionized water. PCR conditions were 95°C for 90 s; 35 cycles of 95°C for 30 s, 50°C for 30 s, and 72°C for 1 min (COI, H3) or 2 min (18S, 28S); and 72°C for 7 min. PCR products were purified following the method of Boom et al. (1990) with some modifications (Kobayashi et al., 2009). Terminator reactions were done with a BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Life Technologies, USA) following the manufacturer's protocol. Sequencing was performed with a 3730 DNA Analyzer (Applied Biosystems, USA). Sequences were checked and assembled by using MEGA ver. 5.2.2 (Tamura et al., 2011). They have been deposited in the DDBJ/ENA/GenBank databases under accession numbers LC012038 and LC208025–LC208133. In addition, our dataset contained 37 sequences downloaded from public databases (Table 1).

Phylogenetic tree construction

To reconstruct phylogeny, we analyzed a combined dataset (18S, 28S, H3, and COI) using maximum likelihood (ML) and Bayesian inference (BI). The outgroup, augmented with additional taxa chosen by reference to recent annelid phylogenomic studies (Struck et al., 2011, 2015; Weigert et al., 2014), contained eight species representing Sedentaria. Sequences were aligned by using MAFFT ver. 7 (Katoh and Standley, 2013) under the options *E-INS-i* for 18S and 28S, and *Auto* for H3 and COI. trimAl ver. 1.2 (Capella-Gutiérrez et al., 2009) was used to remove poorly aligned regions (18S, 693 bases including indels; 28S, 441 bases including indels; COI, six bases including indels; H3, five bases) with the *strict* option. The aligned dataset of 44 species (36 ingroup capitellids and 8 outgroup taxa) comprised 18S (1250 bases including indels), 28S (576 bases including indels), H3 (317 bases without indels), and COI (529 bases including indels).

For the ML analysis, the partition method implemented in RAxML ver. 8.0 (Stamatakis, 2014) was used with the GTR + G substitution model; nodal support values were obtained through ML analyses of 1000 bootstrap pseudoreplicates (Felsenstein, 1985; Tavaré, 1986). For the BI analysis, MrBayes ver. 3.1.2 (Ronquist and Huelsenbeck, 2003) was used with the following substitution models selected by PartitionFinder ver. 1.1.1 (Lanfear et al., 2012) for the partitions: K80 + I + G for 18S and H3 (first and third codon positions); GTR + G for 28S; HKY + I + G for H3 (second codon position) and COI (first and second codon positions); and GTR + I + G for COI (third codon position). A Markov chain Monte Carlo analysis (MCMC) was simulated for 10 million generations and sampled every 100 generations. The first 25% of the trees were discarded as burn-in. The trace files generated by the MCMC runs were inspected in Tracer ver. 1.6.0 (Rambaut

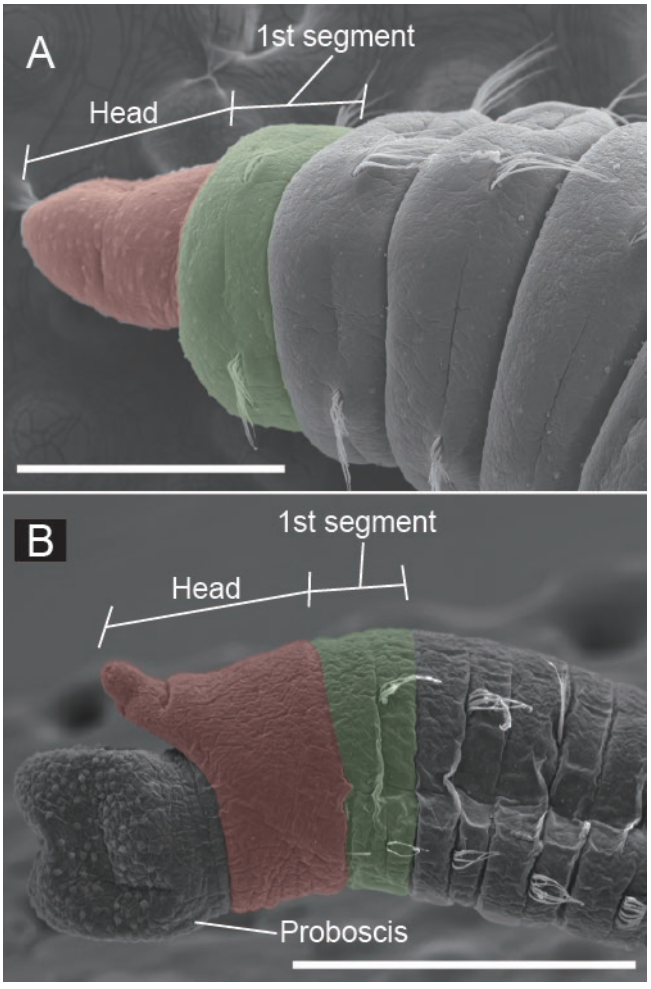


Fig. 2. SEM images showing the two types of head in Capitellidae, with the boundary between the head and first segment labeled. **(A)** *Capitella teleta* (Type A). **(B)** *Mediomastus opertaculeus* (Type B); the width ratio between the head and first segment is constant even when the proboscis is retracted. Scale bars: 1 mm.

Table 2. List of selected morphological character states of capitellid genera in this study. For shape of the head: A, head half the width of first segment; B, head same width as first segment. Asterisk (*) indicates abdominal segments with some pairs of fascicles including both capillary chaetae and hooded hooks on dorsal side.

Genus	Number of thoracic segments	Number of segments with capillary chaetae	Presence or absence of branchiae	Shape of the pygidium	Shape of the head
Barantolla	11	6	unknown	unknown	B
Capitella	9	7 or 9	absent or unknown	without appendages or unknown	A
Decamastus	10	10	unknown	unknown	B
Heteromastus	11	5	unknown	unknown	B
Leiochrides	12	12	present	unknown	B
Mastobranchus	11	11*	unknown	unknown	B
Mediomastus	10	4	absent	with a caudal cirrus	B
Notomastus	11	11	unknown	unknown	B

Table 3. List of PCR and cycle sequencing primers used in this study with genes, primer names, sequences, and references.

Gene	Primer name	Sequence (5′ to 3′)	Reference
18S	F1	TACCTGGTTGATCCTGCCAG	Yamaguchi and Endo (2003)
	F2	CCTGAGAAACGGCTRCCACAT	Yamaguchi and Endo (2003)
	F4	GGTCTGTGATGCCCTYAGATGT	Yamaguchi and Endo (2003)
	R6	TYTCTCRKGCTBCCTCTCC	Yamaguchi and Endo (2003)
	R8	ACATCTRAGGGCATCACAGACC	Yamaguchi and Endo (2003)
	R9	GATCCTTCCGCAGGTTCACCTAC	Yamaguchi and Endo (2003)
28S	LSU5	ACCCGCTGAAYTTAAGCA	Littlewood (1994)
	LSU3	TCCTGAGGGAAACTTCGG	Littlewood (1994)
	D2f	CTTTGAAGAGAGAGTTC	Littlewood (1994)
	28Z	CTTGGTCCGTGTTTCAAGAC	Hillis and Dixon (1991)
H3	aF	ATGGCTCGTACCAAGCAGAC	Colgan et al. (1998)
	aR	ATATCCTTRGGCATRATRGTGAC	Colgan et al. (1998)
COI	LCO 1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO 2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. (1994)
	polyLCO	GAYTATWTTCAACAAATCATAAAGATATTGG	Carr et al. (2011)
	polyHCO	TAMACTTCWGGGTGACCAAARAATCA	Carr et al. (2011)
	Cap_COI_F	GGAATTTGAGGTGGGCTTGT	Tomioka et al. (2016)
	Cap_COI_R	CACCACCACCAGTATTATCA	Tomioka et al. (2016)
	Mastus_COI_R	AAGTACGGGGTCTCCWCCWC	this study

et al., 2014) to check whether the number of sampling generations and effective sample sizes (ESS) were large enough for reliable parameter estimates.

RESULTS

Phylogenetic analyses

The ML and BI trees were identical, with some differences at poorly supported terminal nodes; only the ML tree is shown here (Fig. 3). In the trees, Capitellidae is monophyletic, with nodal support of 98/1.00 (BS/PP), and forms the sister group to echiurans (93/1.00) (Fig. 3). Within Capitellidae, four clades appeared in both trees and had relatively high nodal support (greater than 95% BS and 1.00 PP). Clade 1 (100/1.00) includes all OTUs identified as *Capitella* and is separated from the sister clade by a long

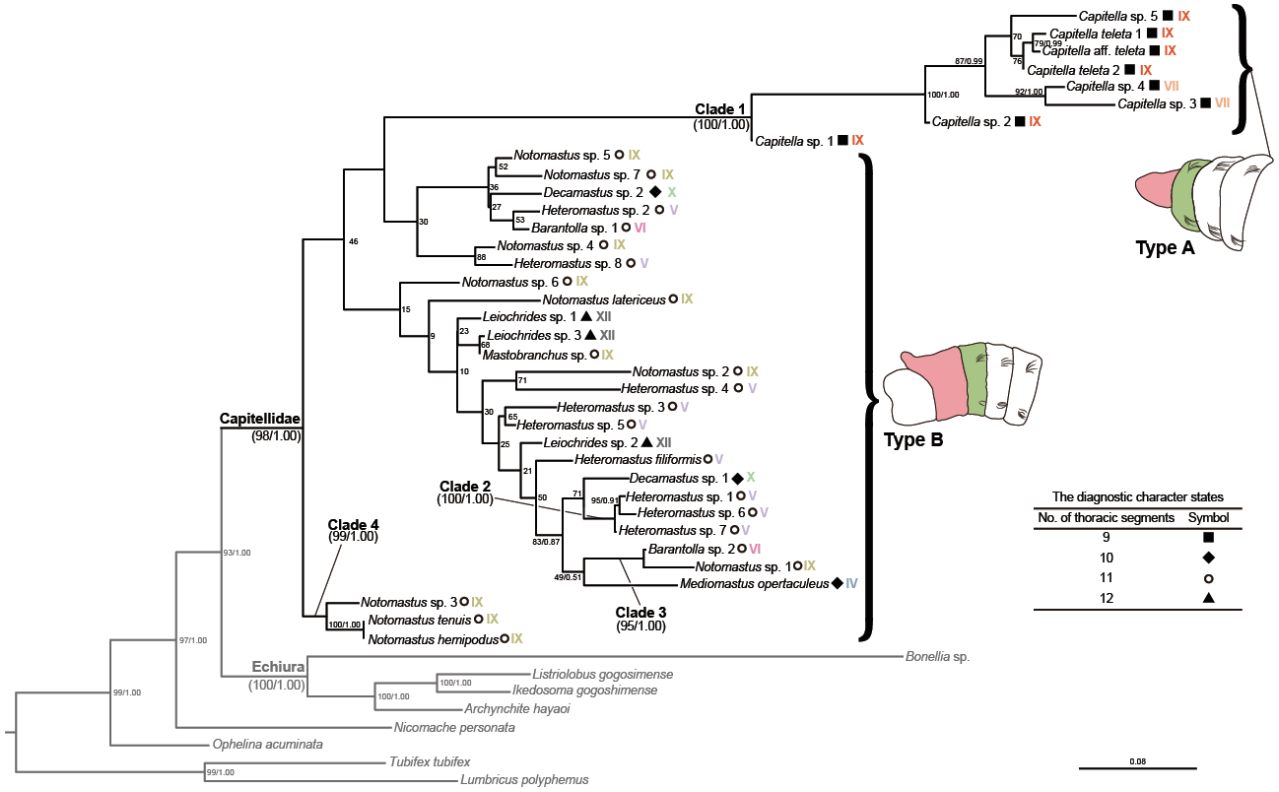


Fig. 3. Maximum-likelihood tree based on a combined dataset of 18S, 28S, H3, and COI gene sequences. Numbers near nodes indicate the maximum-likelihood bootstrap support value in percent and posterior probability from Bayesian inference. Clades with both values shown at the basal node were congruent between the ML and BI trees. Clades with only the bootstrap value were not congruent between the two analyses. The number of thoracic segments is indicated by symbols (see the key at right), and the number of segments with capillary chaetae is indicated by roman numerals.

branch; Clade 2 (100/1.00) contains *Heteromastus* spp. 1, 6, and 7; Clade 3 (95/1.00) consists of *Barantolla* sp. 2 and *Notomastus* sp. 1; and Clade 4 (99/1.00) contains *Notomastus tenuis* Moore, 1909, *Notomastus hemipodus* Hartman, 1945, and *Notomastus* sp. 3. Other nodes in Capitellidae were poorly supported, with values lower than 90% BP and 0.99 PP (Fig. 3).

Distribution of diagnostic characters

Figure 3 shows the distribution on the ML tree of the states of three key characters that have been used to diagnose capitellid genera: *i*) head shape, *ii*) number of thoracic segments; and *iii*) arrangement/type of chaetae. Clade 1 (exclusively comprising *Capitella*) is clearly distinct in that all the constituent members uniquely have the Type-A head and nine thoracic segments; the number of segments with capillary chaetae is either seven or nine, states not found in other capitellid OTUs included in the analysis.

No character states were found to be unique to or specific for the rest of the clades, all of which, however, have the Type-B head. The OTUs in Clades 2 and 4 share the same states for the three characters, but, again, these are not clade-specific. *Barantolla* sp. 2 and *Notomastus* sp. 1 in Clade 3 both have 11 thoracic segments, but this character state also occurs in many other OTUs included in the analysis.

DISCUSSION

The expanded taxon sampling in our study supports the monophyly of Capitellidae, in agreement with several previous phylogenetic studies (e.g., Bleidorn et al., 2003; Struck and Purschke, 2005). The non-monophyly of Capitellidae in Goto (2016) may be attributable to inadequate taxon sampling (e.g., Hillis, 1998; Zwickl and Hillis, 2002) of Capitellidae or by different gene markers having been used in the analyses.

Most nodes except Clade 1 in our trees were weakly supported, and a better-supported tree might show a higher degree of OTUs forming clades by genus. However, a well-supported clade (Clade 3, Fig. 3) contained OTUs representing different genera, indicating that at least the genera *Barantolla* and *Notomastus* (and possibly also *Heteromastus*) are not monophyletic as currently diagnosed. Except for *Capitella*, three of the morphological characters traditionally used in defining capitellid genera (head type; number of thoracic segments; number of segments with capillary chaetae) are not informative for the purpose of delineating genera as natural groups.

Our results suggest that *Capitella* is monophyletic (Clade 1, Fig. 3). The implication of the monophyly of *Capitella* is that it should form the basis for research to illustrate evolutionary histories of habitat expansion [e.g., sand interstices (Green, 2002), whale bones (Silva et al., 2016), and squid mass egg (Hartman, 1947)], diversification of larval developmental forms [lecithotrophy, planktotrophy (Blake et al., 2009), and poecilogony (e.g., Chia et al., 1996; Tsutsumi, 2005)], and other interesting features found in this genus.

To better resolve relationships within Capitellidae, broader taxon sampling and additional genetic markers will both be necessary. If there is to be any hope of identifying capitellid genera as natural groups based on morphology, the morphological characters traditionally used in defining genera will require a fine-scale reexamination, and new characters must be sought. In addition, future analyses including species showing specialized features as mentioned above will illustrate character evolution in *Capitella*.

ACKNOWLEDGMENTS

We thank Katsutoshi Ito, Naoto Jimi, Taeko Kimura, Shoichi Kimura, Susumu Ohtsuka, and Takashi Shimizu for providing specimens; Captains Makoto Uchida of TRV *Seisui-maru*, Kazumitsu Nakaguchi of TRV *Toyoshio-maru*, and the crews and researchers on the two vessels for support during cruises; So Ishida, Kiyotaka Hatooka, Takeshi Nakajo, Yusuke Suda, Daisuke Uyeno, and Hiroshi Yamasaki for organizing surveys; Hiromitsu Era, Hisanori Kohtsuka, Tohru Naruse, Shin Nishihira, and Koji Shibazaki for assistance in sampling; the participants in the field trip to Okayama for assistance in sampling; Masahiro Nakaoka, Waka Sato-Okoshi, and the staffs of the Iriomote Station, Akkeshi Marine Station, Takehara Marine Science Station for providing laboratory facilities; Yuanning Li for advice on phylogenetic analysis; Matthew H. Dick for critically revising our manuscript; and the members of the Biodiversity I Laboratory (Department of Natural History Sciences, Hokkaido University) for support in various ways. This work is part of the results from the field workshops “Umisawakai” in Okinawa and “Wakate-polychaetologists” in Misaki.

COMPETING INTERESTS

This work was supported by the Japan Society for the Promotion of Science (JSPS) (Grant Numbers JP16J00388 and JP24240113); the Research Institute of Marine Invertebrates (FY2013); the Tropical Biosphere Research Center, University of the Ryukyus, as Collaborative Research (FY2014); the Fujiwara Natural History Foundation (FY2015); and the Japan Marine Association for Marine Biology (JAMBIO; No. 27–56).

AUTHOR CONTRIBUTIONS

ST designed the study, did morphological observation, performed experiments and analyzed the data. All authors wrote the manuscript. All authors read and approved the final manuscript.

REFERENCES

Ahn IY, Kang YC, Choi JW (1995) The influence of industrial effluents on intertidal benthic communities in Panweol, Kyeonggi Bay (Yellow Sea) on the west coast of Korea. Mar Pollut Bull 30: 200–206

Amaral ACZ (1980) Breve caracterização dos gêneros da família Capitellidae Grube (Annelida, Polychaeta) e descrição de *Nonatus longilineus* gen. sp. nov. Bol Inst Oceanogr 29: 99–106

Amon DJ, Glover AG, Wiklund H, Marsh L, Linse K, Rogers AD, et al. (2013) The discovery of a natural whale fall in the Antarctic deep sea. Deep-Sea Res part II Top Stud Oceanogr 92: 87–96

Amoureux L (1983) Annélides polychètes du golfe d’Aqaba (mer Rouge). Description d’un genre nouveau et de deux espèces nouvelles. Bull Mus Natl Hist Nat Paris Sér 4 5: 723–742

Andrade SCS, Strand M, Schwartz M, Chen H, Kajihara H, Döhren J, et al. (2011) Disentangling ribbon worm relationships: multilocus analysis supports traditional classification of the phylum Nemertea. Cladistics 27: 1–19

Blake JA (1969) Systematics and ecology of shell-boring polychaetes from New England. Am Zool 9: 813–820

Blake JA (2000) Family Capitellidae Grube, 1862. In “Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 7 of 14. The Annelida Part 4. Polychaeta: Flabelligeridae to Sternaspidae” Ed by JA

Blake, B Hilbig, PV Scott, Santa Barbara Museum of Natural History, Santa Barbara, pp 47–96
Blake JA, Grassle JP, Eckelbarger KJ (2009) *Capitella teleta* a new species designation for the opportunistic and experimental *Capitella* sp. I, with a review of the literature for confirmed record. Zoosymposia 2: 25–53
Bleidorn C, Vogt L, Bartolomaeus T (2003) New insight into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. Mol Phylogenet Evol 29: 279–288
Boom R, Sol CJA, Salimans MMM, Jansen CL, Wertheim-Van Dillen PME, Van der Noordaa J (1990) Rapid and simple method for purification of nucleic acids. J Clin Microbiol 28: 495–503
Brown B (1987) A new genus and species of Capitellidae (Polychaeta) from the Atlantic coast of the United States. Bull Biol Soc Wash 7: 56–61
Buzhinskaja GN, Smirnov RV (2000) *Abyssocapitella commensalis* gen. et sp. n. associated with the deep-sea pogonophore *Spirobrachia leospira* Gureeva, 1975 (Polychaeta: Capitellidae). Ophelia 52: 171–176
Capaccioni-Azzati R, Martín D (1992) *Pseudomastus deltaicus* gen. et sp. n. (Polychaeta: Capitellidae) from a shallow water bay in the North-Western Mediterranean Sea. Zool Scripta 21: 247–250
Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25: 1972–1973
Carr CM, Hardy SM, Brown TM, Macdonald TA, Hebert DNP (2011) A tri-oceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. PLoS ONE 6: e22232
Carus JV (1863) Vermes. In "Handbuch der Zoologie" Ed by WCH Peters, JV Carus, CEA Gerstaecker, Wilhelm Engelmann, Leipzig, pp 422–484
Chia FS, Gibson G, Qian PY (1996) Poecilogony as a reproductive strategy of marine invertebrates. Oceanol Acta 19: 203–208
Colgan DJ, McLauchlan A, Wilson GDF, Livingston SP, Edgecombe GD, Macaranas J, et al. (1998) Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. Aust J Zool 46: 419–437
Croquer A, Bone D, Bastidas C, Ramos R, García E (2016) Monitoring coastal pollution associated with the largest oil refinery complex of Venezuela. PeerJ 4: e2171
David AA, Matthee CA, Simon CA (2014) Poecilogony in *Polydora hoplura* (Polychaeta: Spionidae) from commercially important molluscs in South Africa. Mar Biol 161: 887–898
Dean HK (2008) The use of polychaetes (Annelida) as indicator species of marine pollution: a review. Rev Biol Trop 56: 11–38
Delgado JD, Núñez J, Riera R, Monterroso Ó (2003) Abundance and diversity patterns of annelids from intertidal sandy beaches in Iceland. Hydrobiologia 496: 311–319
Eisig H (1887) Monographie der Capitelliden des Golfes von Neapel und der angrenzenden Meeres-abschnitte: nebst Untersuchungen zur vergleichenden Anatomie und Physiologie. Fauna Flora Golfes Neapel Angrenzenden Meeres-Abschnitte 16: xxi + 1–906
Eklöf JS, Torre-Castro M de la, Adelsköld L, Jiddawi NS, Kautsky N (2005) Differences in macrofaunal and seagrassblages in seagrass beds with and without seaweed farms. Estuar Coast Shelf Sci 63: 385–396
Ewing RM (1982) A partial revision of the genus *Notomastus* (Polychaeta: Capitellidae) with a description of a new species from the Gulf of Mexico. Proc Biol Soc Wash 95: 232–237
Fauchald K (1977) The polychaete worms. Definitions and keys the orders, families and genera. Nat Hist Mus Los Angeles City Sci Ser 28: 1–188
Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791
Ferrier DEK (2012) Evolutionary crossroads in developmental biology: annelids. Development 139: 2643–2653
Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 3: 294–299
Fredette TJ (1982) Evidence of ontogenetic setal changes in *Heteromastus filiformis* (Polychaeta: Capitellidae). Proc Biol Soc Wash 95: 194–197
Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Noda C, et al. (2007) Three-year investigations into sperm whale-fall ecosystem in Japan. Mar Ecol 28: 219–232
García-Garza ME, De León-González JA (2011) Review of the Capitellidae (Annelida, Polychaeta) from the Eastern Tropical Pacific region, with notes on selected species. ZooKeys 151: 17–52
Garwood PR, Bamber RN (1988) A new genus and species of capitellid polychaete from Northeast England. Ophelia 29: 119–126
George JD (1984) The behavior and life history of a mangrove-dwelling capitellid (Polychaeta). In "Proceedings of the First International Polychaeta Conference, Sydney" Ed by PA Hutchings, The Linnean Society of New South Wales, Sydney, pp 323–337
Goto R (2016) A comprehensive molecular phylogeny of spoon worms (Echiura, Annelida): Implications for morphological evolution, the origin of dwarf males, and habitat shifts. Mol Phylogenet Evol 99: 247–260
Goto R, Okamoto T, Ishikawa H, Hamamura Y, Kato M (2013) Molecular phylogeny of echiuran worms (Phylum: Annelida) reveals evolutionary pattern of feeding mode and sexual dimorphism. PLOS ONE 8: e56809
Grassle JP, Grassle JF (1976) Sibling species in the marine pollution indicator *Capitella* (Polychaeta). Science 192: 567–569
Green K (2002) Capitellidae (Polychaeta) from the Andaman Sea. Phuket Mar Biol Cent Res Bull 24: 249–343
Haeckel E (1866) Allgemeine Entwickelungsgeschichte der Organismen, kritische Grundzüge der mechanischen Wissenschaft von den entstehenden Formen der Organismen, begründet durch die Descendenz-Theorie. Georg Reimer, Berlin
Hartman O (1947) Polychaetous annelids. Part VII. Capitellidae. Allan Hancock Pac Exped 10: 391–480
Hillis DM (1998) Taxonomic sampling, phylogenetic accuracy, and investigator bias. Syst Biol 47: 3–8
Hillis DM, Dixon MT (1991) Ribosomal DNA: molecular evolution and phylogenetic inference. Q Rev Biol 66: 411–453
Hutchings PA (2000) Family Capitellidae. In "Polychaetes & Allies: The Southern Synthesis. Fauna of Australia. Vol. 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula" Ed by PL Beesley, GJB Ross, CJ Glasby, CSIRO Publishing, Melbourne, pp 67–72
Incera M, Lastra M, López J (2006) Effect of swash climate and food availability on sandy beach macrofauna along the NW coast of the Iberian Peninsula. Mar Ecol Prog Ser 314: 25–33
James SW, Davidson SK (2012) Molecular phylogeny of earthworms (Annelida: Crassiclitellata) based on 28S, 18S and 16S gene sequences. Invertebr Syst 26: 213–229
Kajihara H, Tomioka S, Kakui K, Iseto T (2014) Phylogenetic position of the queer, backward-bent entoproct *Loxosoma axisadversum* (Entoprocta: Solitaria: Loxosomatidae). Spec Div 20: 83–88
Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Mol Biol Evol 30: 772–780
Kinoshita K, Tamaki S, Yoshioka M, Srithonguthai S, Kunihiro T, Hama D, et al. (2008) Bioremediation of organically enriched

sediment deposited below fish farms with artificially mass-cultured colonies of a deposit-feeding polychaete *Capitella* sp. I. Fish Sci 74: 77–87

Kirkegaard JB (1983) Bathyal benthic polychaetes from the N.E. Atlantic Ocean, S.W. of the British Isles. J Mar Biol Assoc UK 63: 593–608

Kobayashi N, Ohta Y, Katoh T, Kahono S, Hartini S, Katakura H (2009) Molecular phylogenetic analysis of three groups of Asian epilachnine ladybird beetles recognized by the female internal reproductive organs and modes of sperm transfer. J Nat Hist 43: 1637–1649

Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Biol Evol 29: 1695–1701

Lauri A, Brunet T, Handberg-Thorsager M, Fischer AHL, Simakov O, Steinmetz PRH, et al. (2014) Development of the annelid axochord: insights into notochord evolution. Science 345: 1365–1368

Littlewood DTJ (1994) Molecular phylogenetics of cupped oysters based on partial 28S rRNA gene sequences. Mol Phylogenet Evol 3: 221–229

Magalhães WF, Bailey-Brock JH (2012) Capitellidae Grube, 1862 (Annelida: Polychaeta) from the Hawaiian Islands with description of two new species. Zootaxa 3581: 1–52

Malmgren AC (1865 [1864]) Nordiska hafs-annulater. Öfversigt Kongl Vetenskaps-Akademiens Förhandlingar 21: 51–110

McCammon JA, Stull JK (1978) A new genus and species of Capitellidae (Polychaeta) from California. Bull South Calif Acad Sci 77: 40–43

McDonald KA, Collin R, Lesoway MP (2014) Poecilogony in the caenogastropod *Calyptraea lichen* (Mollusca: Gastropoda). Invertebr Biol 133: 213–220

Méndez N, Linke-Gamenick I, Forbes VE, Baird DJ (2001) Sediment processing in *Capitella* spp. (Polychaeta: Capitellidae): strain-specific differences and effects of the organic toxicant fluoranthene. Mar Biol 138: 311–319

Nakaoka M, Mukai H, Chunhabundit S (2002) Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. Ecol Res 17: 625–638

Omena E, Creed JC (2004). Polychaete fauna of seagrass beds (*Halodule wrightii* Ascherson) along the coast of Rio de Janeiro (southeast Brazil). Mar Ecol 25: 273–288

Papageorgiou N, Arvanitidis C, Eleftheriou A (2006) Multicausal encironental secerity: a flexible framework for microtidal sandy beaches and the role of polychaetes as an indicator taxon. Estuar Coast Shelf Sci 70: 643–653

Paul C, Halanych KM, Tiedemann R, Bleidorn C (2010) Molecules reject an opheliid affinity for *Travisia* (Annelida). Syst Biodivers 8: 507–512

Petersen ME (1999) Reproduction and development in Cirratulidae (Annelida: Polychaeta). Hydrobiologia 402: 107–128

Piltz FM (1977) A new genus and species of polychaete (family Capitellidae) from Southern California. Bull Calif Acad Sci 76: 57–60

Quatrefages A de (1866 [1865]) Histoire naturelle des annelés marins et d'eau douce. Annélides et Géphyriens, Tome Second, Deuxième Partie. Librarie Encyclopédique de Roset, Paris

Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) Tracer v1.6 at http://beast.bio.ed.ac.uk/Tracer on 2018-4-26

Read G (2010) Capitellidae Grube, 1862. In "World Polychaeta Database" Ed by G Read, K Fauchald, accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=921 on 2018-1-16

Reish DJ (1955) The relation of polychaetous annelids to harbor pollution. Public Health Rep 70: 1168–1174

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574

Rouse GW, Fauchald K (1997) Cladistics and polychaetes. Zool Scripta 26: 139–204

Rouse GW, Pleijel F (2001) Polychaetes. Oxford University Press, New York

Rousset V, Pleijel F, Rouse GW, Erséus C, Siddall ME (2007) A molecular phylogeny of annelids. Cladistics 23: 41–63

Rozen S, Skaletsky HJ (2000) Primer3 on the WWW for general users and for biologist programmers. In "Bioinformatics Methods and Protocols: Methods in Molecular Biology" Ed by S Krawetz, S Misener, Humana Press, New York, pp 365–386

Rullier F, Amourex L (1979) Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). I. 33. Annélides Polychètes. Ann Inst Oceanogr 55: 145–206

Seaver EC (2016) Annelida models I: *Capitella teleta*. Curr Opin Genet Dev 39: 35–41

Seaver EC, Yamaguchi E, Richards GS, Meyer NP (2012) Expression of the pair-rule gene homologs, *runt*, *Pax3/7*, *even-skipped-1* and *even-skipped-2* during larval and juvenile development of the polychaete annelid *Capitella teleta* does not support a role in segmentation. EvoDevo 3: 8

Siddall ME, Apakupakul K, Burreson EM, Coates KA, Erséus C, Gelder SR, et al. (2001) Validating livanow: molecular data agree that leeches, branchiobdellidans and *Acanthobdella peledina* form a monophyletic group of oligochaetes. Mol Phylogenet Evol 21: 346–351

Silva CF, Shimabukuro M, Alfaro-Lucas JM, Fujiwara Y, Sumida PYG, Amaral ACZ (2016) A new *Capitella* polychaete worm (Annelida: Capitellidae) living inside whale bones in the abyssal South Atlantic. Deep-Sea Res Part I Oceanogr Res Pap 108: 23–31

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313

Struck TH, Purschke G (2005) The sister group relationship of Aeolosomatidae and Potamodrilidae (Annelida: "Polychaeta")—a molecular phylogenetic approach based on 18S rDNA and cytochrome oxidase I. Zool Anz 243: 281–293

Struck TH, Schult N, Kusen T, Hickman E, Bleidorn C, McHugh D, et al. (2007) Annelida phylogeny and the status of Sipuncula and Echiura. BMC Evol Biol 7: 57

Struck TH, Paul C, Hill N, Hartmann S, Hösel C, Kube M, et al. (2011) Phylogenomic analyses unravel annelid evolution. Nature 471: 95–98

Struck TH, Golombek A, Weigert A, Franke FA, Westheide W, Purschke G, et al. (2015) The evolution of annelids reveals two adaptive routes to the interstitial realm. Curr Biol 25: 1993–1999

Sumida PYG, Alfaro-Lucas JM, Shimabukuro M, Kitazato H, Perez JAA, Soares-Gomes A, et al. (2016) Deep-sea whale fall fauna from Atlantic resembles that of the Pacific Ocean. Sci Rep 6: 22139

Sundberg P (1993) Phylogeny, natural groups and nemertean classification. Hydrobiologia 266: 103–113

Sundberg P, Pleijel F (1994) Phylogenetic classification and the definition of taxon names. Zool Scripta 23: 19–25

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumer S (2011) MEGA5: molecular evolutionary genetic analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. Mol Biol Evol 28: 2731–2739

Tanaka M, Kon T, Nishikawa T (2014) Unraveling a 70-year-old taxonomic puzzle: redefining the genus *Ikedosoma* (Annelida: Echiura) on the basis of morphological and molecular analyses. Zool Sci 31: 849–861

Tanner JE (2005) Edge effects on fauna in fragmented seagrass meadows. Austral Ecolo 30: 210–218

Tavaré S (1986) Some probabilistic and statistical problems in the analysis of DNA sequences. Lectures Math Life Sci 17: 57–86

Tomioka S, Suda Y, Kamo T, Ohtomi J, Nishi R, Tanaka R, et al. (2012) Polychaete worms in intertidal zone of an open sandy shore at Fukiagehama, Kagoshima Prefecture, southern Japan. J Natl Fish Univ 61: 65–74 (in Japanese with English abstract)

Tomioka S, Hiruta SF, Kajihara H (2013) Description of *Mediomastus opertaculeus* sp. nov. (Annelida: Capitellidae) from Hokkaido, northern Japan. Spec Div 18: 105–110

Tomioka S, Kondoh T, Sato-Okoshi W, Ito K, Kakui K, Kajihara H (2016) Cosmopolitan or cryptic species? A case study of *Capitella teleta* (Annelida: Capitellidae). Zool Sci 33: 545–554

Tsutsumi H (1987) Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organically polluted cove. Mar Ecol Prog Ser 36: 139–149

Tsutsumi H (2005) Production of planktonic and non-planktonic larvae in a single brood of *Capitella* sp. I and its implications for population persistence in disturbed environment due to organic enrichment of the sediments. Benthos Res 60: 17–24

Tsutsumi H, Kinoshita K, Srithongouthai S, Sato A, Nagata S, Inoue A, et al. (2005) Treatment of the organically enriched sediment below the fish farm with the biological activities of artificially mass-cultured colonies of a small deposit feeding polychaete, *Capitella* sp. I. Benthos Res 60: 25–38

Vedetti JE, Trowbridge CD, Krug PJ (2012) Poecilogony and population genetic structure in *Elysia pusilla* (Heterobranchia: Sacoglossa), and reproductive data for five sacoglossans that express dimorphisms in larval development. Integr Comp Biol 52: 138–150

Warren LM (1991) Problems in capitellid taxonomy. The genera *Capitella*, *Capitomastus* and *Capitellides* (Polychaeta). Ophelia Suppl 5: 275–282

Warren LM, Parker M (1994) *Pseudonotomastus southerni* gen. nov. sp. nov., a new capitellid from the Celtic Sea. Mém Mus Natl Hist Nat Sér. A 162: 299–306

Weigert A, Helm C, Meyer M, Nickel B, Arendt D, Hausdorf B, et al. (2014) Illuminating the base of the annelid tree using transcriptomics. Mol Biol Evol 31: 1391–1401

Yamaguchi S, Endo K (2003) Molecular phylogeny of Ostracoda (Crustacea) inferred from 18S ribosomal DNA sequences: implication for its origin and diversification. Mar Biol 143: 23–38

Zwickl DJ, Hillis DM (2002) Increased taxon sampling greatly reduces phylogenetic error. Syst Biol 51: 588–598

(Received January 17, 2018 / Accepted May 5, 2018)