Three new species of bacterivorous Chrysopetalidae and Microphthalmidae (Annelida) inhabiting a whale fall off eastern Australia

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Abstract. A natural whale fall was opportunistically trawled at ~1000 m depth during the 2017 research vessel '*Investigator*' voyage whilst sampling bathyal and abyssal communities along the eastern Australian margin. Colonising the whale bones were a diverse assemblage of annelids including three new species of free-living Phyllodocida (*Boudemos paulinae* sp. nov., *Pleijelius keni* sp. nov. and *Microphthalmus hvalr* sp. nov.). *Boudemos paulinae* sp. nov. (Chrysopetalidae, Calamyzinae) is a smaller sized species (< 2 mm) compared to its congeners (35-40 mm) and exhibits stylet jaw and notochaetal morphology observed in juveniles of the sister species *Boudemos flokati* (Dahlgren, Glover, Baco & Smith, 2004) from whale falls in the NE Pacific. Notochaetal serration patterns distinguish *Pleijelius keni* sp. nov. from its only congener *P. longae* Salazar-Vallejo & Orensanz, 2006 described in the family Hesionidae from wood falls in NW Atlantic. DNA sequence analysis using the COI, 16S and 18S gene fragments revealed that *Pleijelius keni* sp. nov. fell within the Microphthalmidae clade, this relationship was also supported by morphological observations. These results necessitated a formal transfer of the genus *Pleijelius* to the family Microphthalmidae. *Microphthalmus hvalr* sp. nov. is the first *Microphthalmus* species described from bathyal depths and is distinguished from its numerous congeners inhabiting shallow-water interstitial sediments by the absence of notochaetae.

Introduction

When whales die and sink, their carcasses (whale falls) provide a food source for a wide variety of organisms. Decomposition of a whale carcass passes through a series of successional stages of deep-sea communities. These stages are roughly subdivided into the mobile scavenger stage, comprised of mostly fish and crustaceans, the enrichment-opportunistic stage, comprised of mostly polychaetes and crustaceans, and the sulfophilic stage, dominated by microbial mats (Smith & Baco, 2003).

Annelids frequently comprise the most abundant and diverse component of whale-fall communities (Dahlgren *et al.*, 2004; Fujiwara *et al.*, 2007; Smith *et al.*, 2015). Annelids commonly found include the notable 'zombie worms' *Osedax* (Siboglinidae) and those of the

families Ampharetidae, Dorvilleidae, Hesionidae, and Chrysopetalidae, particularly subfamily Calamyzinae (Dahlgren *et al.*, 2004; Watson *et al.*, 2016; Shimabukuro *et al.*, 2020).

A skeleton of a pilot whale (possibly *Globicephala macrorhynchus*, Delphinidae, Odontoceti, Cetacea (see O'Hara *et al.*, 2020)) was opportunistically trawled off Byron Bay, New South Wales, Australia in 2017 (O'Hara, 2017). Associated with the bones was a diverse community of annelids (Gunton *et al.*, 2021), with nine new species from five families (Dorvilleidae: *Ophryotrocha dahlgreni*, *O. hanneloreae*, *O. ravarae*; Hesionidae: *Vrijenhoekia timoharai*; Nereididae: *Neanthes adriangloveri*, *N. visicete*; Orbiniidae: *Orbiniella jamesi*; Siboglinidae: *Osedax waadjum* and *O. byronbayensis*) being described by Georgieva *et al*. (2023). Among the remaining undescribed taxa from this whale fall were species of *Boudemos*, *Pleijelius,* and *Microphthalmus* initially attributed to the families Chrysopetalidae, Hesionidae, and Microphthalmidae respectively by Gunton *et al*. (2021) and Georgieva *et al*. (2023).

Chrysopetalidae Ehlers, 1864 is characterised by notochaetal paleae and/or notochaetal spines in fans covering the dorsum. The family is currently subdivided into the subfamilies Chrysopetalinae Ehlers, 1864 (paleate), Dysponetinae Aguado, Nygren & Rouse, 2013 (spinous), and Calamyzinae Hartmann-Schröder, 1971 (spinous free-living taxa, symbiont taxa lacking spinous notochaetae but with notoaciculae). The family contains 29 genera and ~ 110 species; the majority of genera are found in the deep sea (Watson, 2022). Phylogenetic studies of the relationships within Chrysopetalidae using DNA sequence data with a phyllodocid outgroup recovered Dysponetinae and Calamyzinae as sister groups, and Chrysopetalinae and Calamyzinae as sister groups when using a syllid outgroup (Watson *et al.*, 2016, fig. 2A–B). Watson *et al*. (2019) found Chrysopetalinae as the sister to Calamyzinae using a hesionid outgroup as did Cepj *et al*. (2022).

Calamyzinae is a clade of both free-living and ectoparasitic chrysopetalids. Free-living taxa have been successful in exploiting deep-sea chemosynthetic environments such as anoxic basins, hydrocarbon seeps, sunken wood and whale falls (Watson *et al.*, 2016) and often achieving very high biomass (Zaika *et al.*, 1999; Dahlgren *et al.*, 2004). Currently known free-living calamyzins comprise three genera that include meiofaunal to very small-sized species of *Vigtorniella* Kiseleva, 1992; *Micospina* Watson *et al.*, 2016; and *Boudemos* Watson *et al.*, 2016. The taxa are so morphologically similar that cryptic species (Wiklund *et al.*, 2009) and even cryptic genera (Watson *et al.*, 2016) have been suggested. Thus, molecular data are crucial in separating free-living calamyzin genera and species (Watson *et al.*, 2016).

Within Hesionidae, Hartmann-Schröder (1971) erected the subfamily Microphthalminae with interstitial genera *Hesionides* Friedrich, 1937 and *Microphthalmus* Mecznikow, 1865. The placement of *Microphthalmus* in Hesionidae was questioned based on morphology (Westheide, 1982, 2013; Westheide & Purschke, 1992; Pleijel & Dahlgren, 1998; Dahlgren *et al*., 2000). Recently the Microphthalminae was elevated to the family rank (Salazar-Vallejo *et al*., 2019) based on a morphological phylogeny and contains the

genera *Fridericiella* Hartmann-Schröder, 1959; *Hesionella* Hartman, 1939; *Hesionides* Friedrich, 1937; *Microphthalmus* Mecznikow, 1865; *Struwela* Hartmann-Schröder, 1959; *Uncopodarke* Uchida in Uchida, Lopéz & Sato, 2019; and *Westheideius* Salazar-Vallejo, de León-González & Carrera-Parra, 2019.

The relationships among families Chrysopetalidae, Hesionidae, and Microphthalmidae remain unresolved. Earlier morphology-based cladistic analyses recovered the sister group relationship between Chrysopetalidae and Hesionidae (Glasby, 1993; Pleijel & Dahlgren, 1998), but results of some subsequent molecular studies contradicted this (Aguado *et al.,* 2013; Huč *et al.*, 2024). The close relationships between Chrysopetalidae and Hesionidae was corroborated by recent phylogenomic analyses in Tilic *et al.* (2022) who proposed the clade Hesionoidea that includes Microphthalmidae represented by *Struwela*. The aim of this study was to formally describe three new species from the genera *Boudemos*, *Pleijelius,* and *Microphthalmus* collected from a natural whale fall off Byron Bay, New South Wales, Australia and given in open nomenclature in Gunton *et al*. (2021) and Georgieva *et al*. (2023).

Materials and methods

Sample collection

All material used in this study was collected during the 2017 "Sampling the abyss" voyage (IN2017_V03) of the Australian Research Vessel (RV) '*Investigator*'. Operation 100 of the voyage comprised a beam trawl conducted on 9 June 2017 in the Byron Bay area (28.05°S 154.08°E – 28.10°S 154.08°E) at 999–1013 m, which recovered a complete skull and several vertebrae of a pilot whale (Georgieva *et al.*, 2023, figs 1–2). Annelids were picked off the bones and preserved in 95% ethanol. The specimens were roughly sorted onboard to the family level, and were then shipped to the Australian Museum, Sydney (AM) and the Museum and Art Gallery of the Northern Territory, Darwin (MAGNT).

Specimens were examined using stereo and compound microscopes at AM and MAGNT. Specimens of *Microphthalmus* were placed on temporary glycerol slides and photographed using a digital camera under a compound microscope at AM. *Boudemos* and *Pleijelius* specimens used for scanning electron microscopy (SEM) were dehydrated in ethanol, critical-point dried, gold coated, and imaged with a JEOL JSM-6480LA scanning electron microscope at Macquarie University, Sydney.

Morphological terminology follows Watson (2022) and descriptions include types and positions of notochaetae and neurochaetae; measurements of entire body length width from tips of neurochaetae across mid-body. Reported segment number includes indication of whether a specimen was entire (E) or not entire (NE) (e.g., 15NE, 15 segments not entire). Roman numerals in figures of the anterior ends indicate anterior segments I–V. Type and non-type specimens of the three new species were deposited at AM and MAGNT.

DNA extraction, PCR amplification and sequencing

Three gene (COI, 16S and 18S) fragments for the three species described here were sequenced earlier (Georgieva *et al.*, 2023) (Table 1). However, the 18S gene fragment for *Boudemos paulinae* sp. nov. (NHM_240E) was not successfully amplified (Georgieva *et al.*, 2023).

To add information to the analysis, tissue samples were obtained from another Chrysopetalidae, *Dysponetus* sp. IN039, also collected during the 2017 "Sampling the abyss" voyage (Freycinet Marine Park, Tasmania, 41.72°S, 149.12°E, 2794 m). DNA extraction was performed using a Bioline Isolate II genomic DNA kit following the manufacture's protocols. Amplifications of the COI, 16S and 18S genes was conducted using six sets of primers. COI: polyLCO (forward) GAYTATWTTCAACAAATCATAAAGATATTGG, polyHCO (reverse) TAMACTTCWGGGTGACCAAARA ATCA (Carr *et al.*, 2011). 16S: Ann16SF (forward) GCGGTATCCTGACCGTRCWAAGGTA (Sjölin *et al.*, 2005), 16SbrH (reverse) CCGGTCTGAACTCAGATCACGT (Palumbi, 1991). 18S: TimA (forward) AMCTGGTTGATC CTGCCAG (Noren & Jondelius, 1999), 1100R2modified (reverse) CGGTATCTGATCGTCTTCGA (Kupriyanova *et al.*, 2006).

Polymerase chain reaction (PCR) mixtures consisted of 0.4 µl of each primer (forward and reverse), 1 µl of template. DNA, 2 µl Coral Load Qiagen PCR buffer, 1.5 µl MgCl$_2$, 1.5 µl dNTPs, 0.1 MyTaq DNA Polymerase Bioline and 13.1 µl water, making a total mixture of 20 µl. PCRs were conducted in a Thermal Cycler with the following conditions; COI: 94°C/1 min, 5 cycles 94°/40 s, 45°/40 s, 72°/60 s, followed by 35 cycles 94°/40 s, 51°/40 s, 72°/60 s, and finally 72°/5 min 16S: 94°/3 min, 35 cycles of 94°/30 s, 50°/30 s, 72°/90 s, and finally 72°/7 min 18S: 94°/3 min, 40 cycles of 94°/30 s, 52°/30 s, 72°/30 s and finally 72°/5 min. Successful PCR products were sent to Macrogen South Korea where they were purified, and standard Sanger sequencing was performed. DNA vouchers (DNA extractions) were stored in the Frozen Tissue Collection in the Australian Centre for Wildlife Genomics (AM).

Phylogenetic analysis

Overlapping fragments were assembled into consensus sequences and edited in Geneious Prime 2019.0.4 (https://www.geneious.com). A BLAST analysis (Altschul *et al.*, 1990) was performed to confirm the correct region had been amplified, to compare with other sequences on GenBank, and to check for contamination. New sequences were submitted to GenBank (Table 1).

Sequences from the family Chrysopetalidae (31 species and 74 sequences), Microphthalmidae (5 species 16 sequences), Hesionidae (5 species, 8 sequences), Pilargidae (1 species, 2 sequences) and Nereididae (1 species, 3 sequences) were downloaded from GenBank (Table 1). The pilargid (*Hermundura*) was added following the molecular analysis of Huč *et al.* (2024), where *Hermundura fauveli* grouped with Microphthalmidae. The specimen SIO:BIC A16381, used in the present analysis, was reported as *H. fauveli* on GenBank but as *H. americana* in Huč *et al.* (2024), here we used the name *H. americana*, no other sequences of *H. fauveli* were publicly available. The nereidid, *Nereis pelagica*, was used as an outgroup following the findings of Georgieva *et al.* (2023).

Sequences were aligned using the Geneious plugins with the default settings: MAFFT (Katoh *et al.*, 2002) for 16S and 18S and MUSCLE (Edgar, 2004) for COI. Concatenated sequences for all three genes were made in Geneious. JModelTest (Darriba *et al.*, 2012) was used to find the best model for each gene fragment using the Akaike information criteria. The model GTR+I+G was selected for COI, GTR+G for 16S, and TIM2+G for 18S. Maximum Likelihood phylogenetic trees were constructed in IQ-TREE 2 (Minh *et al.*, 2020), with 10000 bootstrap alignments. Ultrafast Bootstrap values were computed, only values > 50% UFBoot were displayed. Trees were visualised in FigTree v1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator.

Molecular results

Further sequencing of the 18S gene fragment for *Boudemos paulinae* sp. nov. was unsuccessful. Two gene fragments were successfully sequenced for *Dysponetus* sp. IN039 (16S and 18S, Table 1). The combined dataset had 3,313 aligned positions (COI with 618 positions, 16S rDNA with 557 positions, and 18S rDNA with 2138 positions).

Maximum Likelihood analysis of combined COI, 16S and 18S sequence data revealed five major clades with low support (< 50 % UFBoot). Sequences from Chrysopetalidae did not form a monophyletic group. Instead, sequences from Hesionidae, Microphthalmidae and Pilargidae fell within the Chrysopetalidae sequences (Fig. 1). The Chrysopetalidae was broken down into three smaller clades, Calamyzinae (clade 1), Chrysopetalinae (clade 2) and Dysponetinae (clade 5) (Fig. 1).

Clade 1 contained species belonging to the subfamily Calamyzinae (*Calamyzas-Spathochaeta-Micospina-Craseoschema-Natsushima-Laubierus-Shinkai-Iheyomytilidicola-Vigtorniella-Calamyzinae-Boudemos*). The three sequences attributed to species in the genus *Boudemos* were not recovered as monophyletic, *Boudemos paulinae* sp. nov. was recovered as sister group to *Boudemos ardabilia*, *B. flokati* and all other sequences in the Calamyzinae clade (*Calamyzas-Spathochaeta-Micospina-Craseoschema-Natsushima-Laubierus-Shinkai-Iheyomytilidicola-Vigtorniella-Calamyzinae*) with strong support (SHaLRT: 100%, UFBoot: 100%). Clade 2 comprised a strongly supported (SHaLRT: 99.6%, UFBoot: 88%) monophyletic clade of chrysopetalids (*Hyalopale-Paleanotus-Treptopale-Bhawania-Arichlidon*) of the subfamily Chrysopetalinae and was sister group to clade 1, with low support (SHaLRT: 79.3%, UFBoot: 66%). Clade 3 contained the hesionids included in the analysis (*Leocrates-Hesione-Elisesione-Dysponetus*). Note that *Dysponetus hesionides* Boggemann, 2009 was recovered within the Hesionidae in accordance with examination of type material that confirmed a hesionid morphology (CW unpubl.).

Microphthalmidae (clade 4) was sister to Hesionidae, Calamyzinae and Chrysopetalinae but this relationship had low support (SHaLRT: 41.7%, UFBoot: 66%). This clade comprised *Microphthalmus hvalr* sp. nov., *Pleijelius keni* sp. nov. and the microphthalmids, *Microphthalmus listensis*,

Table 1. Chrysopetalidae, Microphthalmidae, Hesionidae, Nereididae and Pilargidae taxa used in molecular phylogenetic analysis with museum voucher number and GenBank accession numbers. Em-dashes indicate no data available. Bold new sequences from the present study. *no voucher, whole specimen used in analysis.

Species	Voucher	Collection locality	COI	16S	18S
CHRYSOPETALIDAE					
Arichlidon reyssi	SMNH 97306	Banyuls, France	EU555054	EU555045	EU555036
Bhawania cryptocephala	GP0256	Goa, India	KX525479	—	KX290697
Bhawania cryptocephala	GP0257	Goa, India	KX525480	—	KX290698
Bhawania goodei	—	Florida, USA	MK058438	—	—
Bhawania heteroseta	SMNH 97305	Florida, USA	EU555053	EU555044	EU555035
Boudemos ardabilia	SMNH 97313	Sweden and Norway	EU555052	EU555051	EU555042
Boudemos flokati	SMNH 97311	California, USA	EU555065	EU555034	EU555043
Boudemos paulinae sp. nov.	NHM_240E*	off Byron Bay, NSW, Australia	OQ801414	OQ820954	—
Calamyzas amphictenicola	SIO:BIC A3274	Koster Area, Sweden	JX078956	JX093563	JX078939
Calamyzinae sp.	SIO:BIC A3410	Lau Basin, W Pacific	JX078957	JX078951	—
Craseoschema thyasiricola	ANEA NHMUK 2019.7339	Gulf of Cadiz, NE Atlantic	MK988420	MK988419	MZ450127
Dysponetus bulbosus	SMNH 83511	Adelaide, SA, Australia	JQ623501	DQ442570	JX078946
Dysponetus caecus	—	Koster, Sweden	AF221568	EU555047	AY839568
Dysponetus hesionides	ZMHP 24960B	Cape basin SE Atlantic	—	GQ426604	GQ426554
Dysponetus populonectens	—	California, USA	JQ623495	JX078955	JX078947
Dysponetus sp.	IN039*	Freycinet, Tas, Australia	—	**PQ032722**	**PQ032723**
Dysponetus sp. NZ HW-2008	SMNH 97308	New Zealand	EU555055	EU555048	EU555038
Hyalopale zerofskii	SIO:BIC A8082	California, USA	MN258705	MN175301	MN175297
Iheyomytilidicola lauensis	SIO:BIC A2267	Tonga, W Pacific	JF304502	JX078952	JX078942
Laubierus alvini	SIO:BIC A2282	Costa Rica, E Pacific	JF304494	JX078950	JX078940
Micospina auribohnorum	SIO:BIC A1427	Costa Rica, E Pacific	JX093564	JX078949	JX078941
Natsushima bifurcata	MB29-000186	Gulf of Cadiz, NE Atlantic	JF304492	JX078953	JX078943
Natsushima sashai	SIO:BIC A2218	Costa Rica, E Pacific	JF304497	JX078954	JX078944
Paleanotus bellis	BMBM-0845	Speiden Channel, Washington, USA	MH242887	—	—
Paleanotus sp.	SMNH 97310	New Zealand	EU555057	EU555050	EU555041
Paleanotus sp. 3	MAGNT W23461	Heron Island, Qld, Australia	JN588618	—	—
Shinkai fontefridae	SIO:BIC A2204	Costa Rica, E Pacific	JF304499	JX078948	—
Shinkai longipedata	SIO:BIC A2283	Costa Rica, E Pacific	JF304500	—	JX078945
Spathochaeta octopodis	NSMT-Pol H-654	Kumano Sea, Japan, N Pacific	LC381959	LC381961	—
Treptopale homalos	MAGNT W23460	Heron Island, Qld, Australia	JN569295	—	—
Treptopale paromolos	MAGNT W23475	Darwin, NT, Australia	JN588620	—	—
Vigtorniella zaikai	SIO:BIC 5640	Black Sea	—	KU057932	KU057929

Table 1. *Continued…*

Table 1. *Continued.*

Species	Voucher	Collection locality	COI	16S	18S
HESIONIDAE					
Elisesione imajimai	NSMT-Pol H-665	Sagami Bay, Japan, N Pacific	LC361354	—	LC361352
Hesione pantherina	—	Vellar estuary, India	MG251654	—	—
Hesione picta	SWU 31305	Gulf of Thailand, Thailand	—	KF006978	—
Hesione reticulata	NSMT-Pol N-620/ NSMT-Pol 113205	Zaimokuza, Kanagawa, Japan	LC169753	—	—
Leocrates chinensis	SMNH 83510	Lifou, New Caledonia	DQ442565	DQ442575	DQ442589
MICROPHTHALMIDAE					
Microphthalmus hvalr sp. nov.	NHMUK ANEA 2022.434	off Byron Bay, NSW, Australia	OQ801419	OQ820955	OQ803222
Microphthalmus hvalr sp. nov.	AM W.54817.001	off Byron Bay, NSW, Australia	OQ801420	OQ820956	—
Microphthalmus listensis	85792	List, Germany	MN855130	MN855210	—
Microphthalmus similis	76290	List, Germany	MN855131	—	—
Pleijelius keni sp. nov.	AM W.54809.001	off Byron Bay, NSW, Australia	OQ801439	OQ820989	—
Pleijelius keni sp. nov.	NHM_240A*	off Byron Bay, NSW, Australia	OQ801438	OQ820988	OQ803239
Struwela camposi	SIO-BIC A13437	Mexico	MZ562518	NC_087882	PP033480
NEREIDIDAE					
Nereis pelagica	BAMPOL0063 (COI)/ SMNH75831 (16S, 18S)	Dixon Island, British Columbia, Canada (CO1)/ Bohuslän, Sweden (16S/18S)	HM473499	AY340470	AY340438
PILARGIDAE					
Hermundura americana	SIO:BIC A16381	Pagan River, Virginia, USA	PP050562	PP034424	—
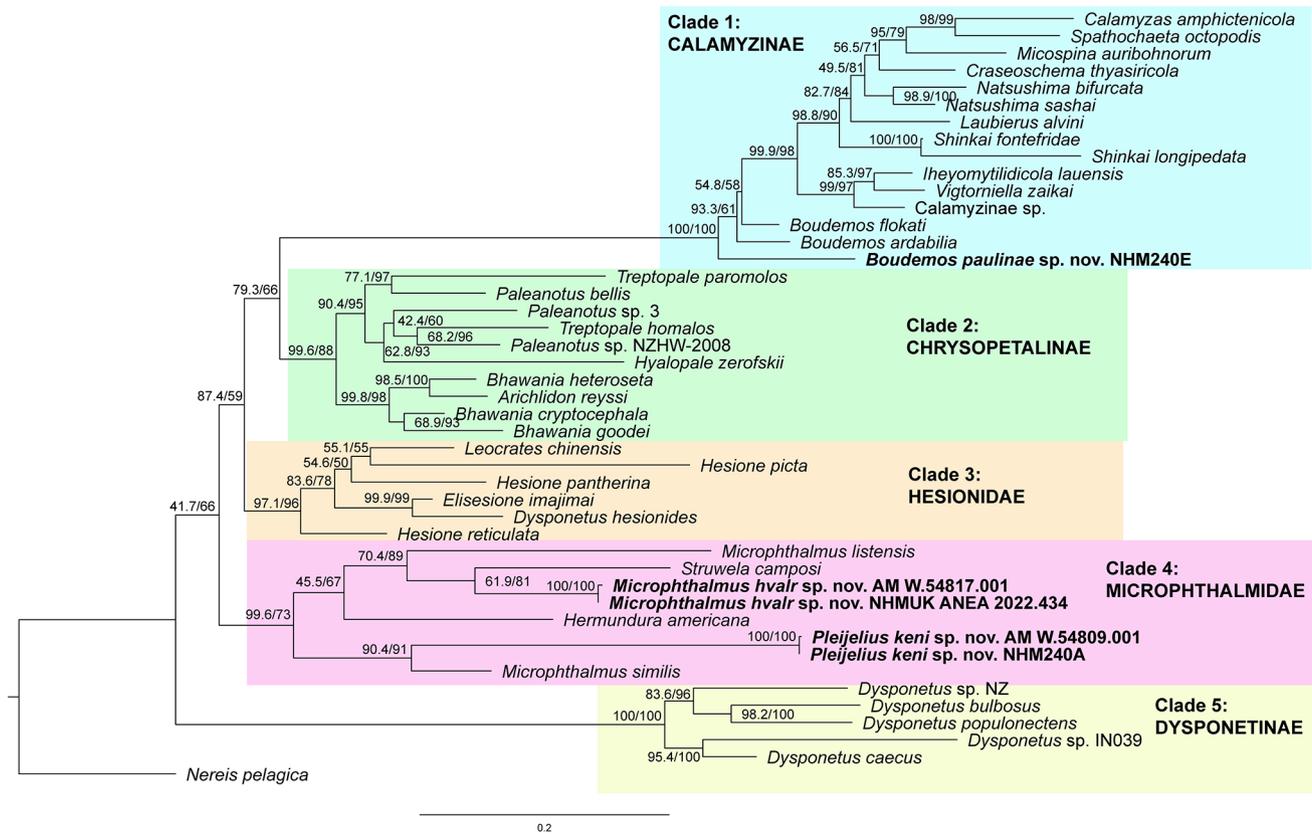
Figure 1. Phylogenetic relationships among representatives of Chrysopetalidae, Microphthalmidae, Hesionidae, Nereididae, and Pilargidae obtained from Maximum Likelihood analysis of combined dataset of COI, 16S and 18S gene fragments in IQTREE. Node labels show SHaLRT support (%) / ultrafast bootstrap (UFBoot) support (%). Values > 50% UFBoot displayed.

M. similis, *Struwela camposi* and the pilargid *Hermundura americana*. Within this clade *Pleijelius keni* sp. nov. was recovered as sister group to *Microphthalmus similis* with strong support (SHaLRT: 90.4%, UFBoot:91%).

Dysponetinae (clade 5) was the basal group to the two other Chrysopetalidae clades (Calamyzinae (clade 1) and Chrysopetalinae (clade 2)), Hesionidae (clade 3) and Microphthalmidae (clade 4). Dysponetinae comprised a strongly supported (SHaLRT: 100%, UFBoot: 100%) monophyletic group of *Dysponetus* species, not including *Dysponetus hesionides*.

SYSTEMATICS

Phylum Annelida Lamarck, 1802

Class Polychaeta Grube, 1850

Order Phyllodocida Dales, 1962

Family Chrysopetalidae Ehlers, 1864

Diagnosis (from Watson, 2022). Body length very short to very long; flattened or arched dorsum, flattened ventrum. Prostomium well developed with median antenna (lacking in Calamyzinae), two **lateral antennae** and differentiated **ventral palps** or simple lobe-shaped prostomium with undifferentiated two lateral antennae and palps; eyes present or absent. Nuchal organs present in all free-living taxa. First

or tentacular segment achaetous, with pair of tentacular cirri in most taxa, variable in symbiotic calamyzins. Midbody chaetal segments with **dorsal and ventral cirri**. **Muscular pharynx with eversible proboscis and pair of grooved stylet jaws**; terminal proboscidial papillae present except in symbiont taxa; mouth appendages present in chrysopetalins and dysponetins. Notochaetae paleate, spinose or absent; neurochaetae compound and/or simple; **chaetal types camerate**. **Pygidial lobe** with or without pair of anal cirri.

Remarks. Bold text indicates characters present in all taxa within the family Chrysopetalidae. Camerate paleal notochaetae was initially proposed as evidence for monophyly of Chrysopetalidae (Westheide & Watson Russell, 1992; Fauchald & Rouse, 1997). Internal cameration of chrysopetalid noto and neurochaetae is seen in all Chrysopetalinae, Dysponetinae and free-living Calamyzinae; lack of neurochaetal compartmentalisation in adults of symbiotic calamyzins is hypothesised as secondary loss (Aguado *et al*., 2013; Watson *et al*., 2016). Watson and Faulwetter (2017) considered the grooved jaw form, present across taxa in all chrysopetalid subfamilies, as a synapomorphy that supports the monophyly of the family Chrysopetalidae.

Sub-family Calamyzinae Hartmann-Schröder, 1971

Diagnosis (from Watson *et al*., 2016). Very small to large-bodied. Prostomium a shallow lobe fused with anterior

segments, two digitiform lateral antennae, palps ventral or ventrolateral; **median antenna absent**, eyes mostly absent. Segment I generally with dorsal cirri, ventral cirri absent in symbiotic genera; chaetae absent or present. Segment II with dorsal cirri and notochaetae; neurochaetae compound with 'whip-like' spinigerous blades or simple hooks, ventral cirri present or absent. Strongly muscularised foregut, large terminal papillae absent or present; jaws present or absent; mouth cover absent. Simple notochaetae present or absent; neurochaetae compound falcigers or simple hooks. Internally camerated chaetae present or absent. Pygidium rounded, with or without anal appendages.

Remarks. Bold text indicates characters present in all taxa within the subfamily Calamyzinae. The subfamily comprises four species in three free-living genera (*Boudemos*, *Micospina*, and *Vigtorniella*) and 25 species in 15 ecto- and endo- symbiont genera (Watson, 2022). All members of the Calamyzinae lack a median antenna, as well as modification of chaetal types and ontogenetic jaw change (Dahlgren *et al*., 2004; Aguado *et al*., 2013; Watson *et al*., 2016).

Genus *Boudemos* Watson *et al*., 2016

Type species. *Vigtorniella flokati* Dahlgren *et al*., 2004.

Diagnosis (from Watson *et al*., 2016 emend.**)** Very small to moderately large-bodied; length of mature individuals ~2 mm for 20 segments to 40 mm for ~ 90 segments, respectively. Eyes present or absent. Pair of stylet jaws present or absent. Notochaetae slender or robust with slight differences in margin serration pattern. **Compound falcigerous neurochaetae with bifid joints**. Prechaetal neuropodial lobe present in larger species, absent in smaller species. Neurochaetae with swollen inner joint and shallow groove on blades in larger-bodied species; absent in individuals of smaller-bodied species.

Remarks. The diagnosis was emended to include the very small-bodied new species with paedomorphic chaetal characters (see Diagnostic Remarks). Bold text indicates characters present in all species of *Boudemos*. The genus *Boudemos* was erected for *Vigtorniella flokati* Dahlgren *et al*., 2004 inhabiting whale falls in the Pacific, and *V. ardabilia* Wiklund *et al*., 2009 from a whale fall in Sweden and fish farms in Norway (Watson *et al.,* 2016). These two larger-bodied species are morphologically almost identical, but molecular evidence support their differentiation. The name *Vigtorniella* was retained for the type species, *Vigtorniella zaikai* (Kiseleva, 1992).

Boudemos paulinae sp. nov.

urn:lsid:zoobank.org:act:0D045480-D246-41C1-B360-711E154ECF7D

Fig. 2A–D

Boudemos sp.—Georgieva *et al.,* 2023, east coast of Australia.

Material examined

Holotype. AM W.55400 (body length 1.8 mm for 20 segments, width 0.7 mm, mature gametes 0.04 mm in diameter present).

Paratypes. AM W.55401 (approximately 100 mostly broken specimens with 6–20 segments; only 2 entire specimens include 7E, L: 0.56 mm, W: 0.35 mm; 12E, L: 0.9 mm, W: 0.55 mm). MAGNT W032913 (1 specimen).

DNA vouchers. NHM_240E.

Type locality. A pilot whale skeleton off Byron Bay, NSW, Australia.

Description. Body very small, elongate, slightly broader anterior end, narrowed posteriorly. Preserved material whitish, covered in white bacteria. Erect 'spiky' notochaetal fans interlocking over dorsum (Fig. 2A–B). Prostomium anterior edge half rounded with prostomial structures only visible in ventral view: two small digitiform lateral antennae inserted towards posterior prostomial margin; two small, glandular, ovoid, fused palps, mid position at posterior base of prostomium; eyes absent (Fig. 2B–C).

Short, barrel-shaped muscular pharynx with coarse internal septa, terminal mouth papillae present. Two stylets composed of dark brown, toothed, terminal platelets facing outwards; each connected posteriorly to individual elongate, hyaline structures with a mid-way flange.

Achaetous segment I with one pair of dorsal and ventral tentacular cirri. Dorsal cirri pair, slightly longer, more robust than ventral pair, characteristically project out wing-like, dorso-laterally from anterior end; ventral cirri pair on small cirrophores immediately adjacent to palps (Fig. 2B–C). Notopodia of segment II with notochaetae and pair of longer dorsal cirri; neuropodia with 'whip-like' spinigerous neurochaetae, ventral cirri absent. Segment III biramous, notopodia with notochaetae, longer dorsal cirri, neuropodia with slender falcigerous neurochaetae and slender ventral cirri (Fig. 2A, C). Segment IV onwards down body similar to segment III, with medium-size dorsal cirri (Fig. 2A) and slender ventral cirri (Fig. 2B).

Notopodia in mid-body segments with notochaetal fascicle spread out in erect fan-like arrangement (Fig. 2A). Long, slender, simple notochaetae narrow distally, ending in rounded, almost truncate distal tip; with two rows of serrations. Fascicle comprises longer notochaetae appearing slightly flattened mid-chaetae and marginal serrations spaced far apart; shorter notochaetae more rounded in section with finer serrations (Fig. 2D). Notochaetae number 25–30. Dorsal cirri robust, similar length to longer than fascicle with low cirrophores. Dense ciliary patches present inter-ramally and dorsally (Fig. 2D). Notochaetae chambered internally with horizontal striae.

Mid-body neuropodia plus neurochaetae longer than notopodia, ventral cirri insert sub-distally mid-neuropodia, posteriorly directed, fusiform, cirrophores barely observable (Fig. 2B). Acicular lobe pronounced, pointed with small pre-chaetal lobe, with long, robust, single neuroaciculae; neurochaetae insert below aciculae. Neurochaetae compound unidentate falcigers, articles slender with small, curved distal tips, dense, fine serration starting immediately below tip; bifid heterogomph shafts, chambered internally with horizontal striae. Neurochaetae inserted in two loosely defined groups, upper 3-4 with longer blades, lower blades gradually shorter and wider; no neurochaetal shaft joint swelling or neurochaetal blade groove observed. Neurochaetae number 15–20.
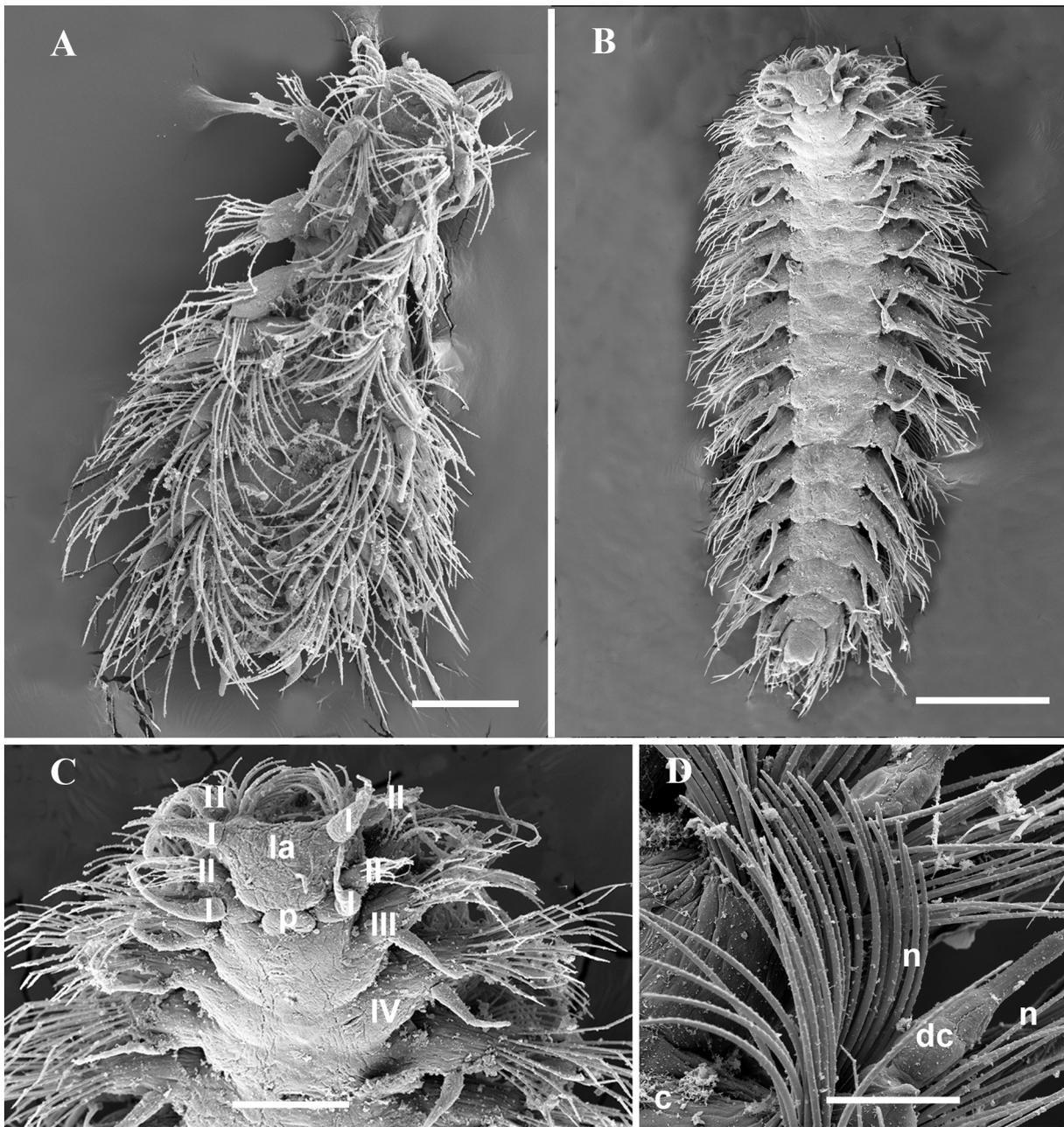
Figure 2. *Boudemos paulinae* sp. nov. A, entire body, dorsal view; B, entire body, ventral view; C, detail of anterior end, ventral view, segment I, achaetous, segment II with cirrose notopodia and accirose neuropodia; III and IV with normal complement of cirri and chaetae; D, detail of notopodium mid-body. Abbreviations: la - lateral antennae; p - palps; n - notochaetae; dc - dorsal cirrus.

Entire pygidium rounded with two anal cirri. Pygidia missing on most specimens with evidence common of part regeneration of posterior segments.

Etymology. *Boudemos paulinae* sp. nov. is named in honour of the first author's mother, Pauline Cleary, who imbued in her from an early age a love of the sea and a sense of critical regard. Pauline's ashes are spread at sea offshore from Byron Bay in the vicinity of the whale fall and the abundant life cycle it sustains.

Diagnosis. Smaller sized species (< 2 mm) compared to its congeners (35–40 mm) and exhibits stylet jaw and notochaetal morphology observed in juveniles of the species *Boudemos flokati*.

Diagnostic remarks. Previously described free-living species *Boudemos flokati* and *B. ardabilia* are large-bodied, *B. flokati* measures 40 mm for 91 segments and the size of *B. ardabalia* ranges from 5 to 35 mm and the number of segments from 28 to 82. In contrast, ovigerous females of *B. paulinae* sp. nov. reach a length of 1.8 mm. The two previously described species also possess distinct swelling at the neurochaetal joint and neurochaetal blades with a groove. Adult notochaetae are thick and robust with frayed spinule ornamentation (Dahlgren *et al*., 2004; Watson *et al*., 2016). Adults of *B. paulinae* sp. nov. lack these chaetal characters.

There are no new morphological characters in *B. paulinae* sp. nov., but their adults (gamete-bearing specimens) possess characters documented for juveniles of *B. flokati*. These

include very slender simple spinous-like notochaetae with two rows of spinelets, with the shorter chaetae being more rounded in cross-section (Dahlgren *et al.*, 2004, fig. 6c, cf. Fig. 2D). A pair of stylet jaws in adults of *B. paulinae* sp. nov. are separated and face outwards with serrated, dark brown terminal platelets and posterior, elongate, hyaline structures bearing a mid-way flange. The same jaw morphology has been described in benthic post-larvae of *B. flokati*, while jaws are lost in adults (Dahlgren *et al.*, 2004; Watson *et al.*, 2016, fig. 8A–C). A similar stylet jaw structure is observed in post-larvae of *Vigtorniella zakai* (Kiseleva, 1992), with the stylet bearing typical sclerotised serrate tips (Watson & Faulwetter, 2017, fig. 21A–B). Entire jaws in *V. zakai* are present in larvae known for extended feeding in the plankton, while only the terminal platelet jaw is retained in meiofaunal adults that settle in high densities on microbial mats in flocculent sediments (Watson *et al.*, 2016).

Family Microphthalmidae
Hartmann-Schröder, 1971

Type species. *Microphthalmus sczelkowii* Mecznikow, 1865.

Diagnosis (from Salazar-Vallejo *et al.,* 2019). Body small, delicate, rarely longer than five mm. Prostomium with 0–2 eyes. **Antennae filiform**. Median antenna position variable. **Palps filiform**, sometimes missing. Tentacular cirri usually on 2–3 distinct segments. **Dorsal cirri thin, smooth, thread-shaped or cirriform**. Parapodia biramous or sub-biramous, lateral, rarely directed ventrally or dorsally. **Pygidium comprising a pair of dorso-lateral anal cirri and ventral anal structures, either anal membrane or a ventral cirrus and a pair of anal cirri**. **No jaws**. Free-living, rarely symbiotic with sand dollars (sea urchins), polychaetes, or sipunculans.

Remarks. Bold text indicates known characters present in taxa within the family Microphthalmidae. The family currently comprises seven genera and 53 accepted species (Read & Fauchald, 2024a). The diagnosis above is emended to include *Pleijelius* because the results of phylogenetic analysis here necessitated transfer of *Pleijelius* to Microphthalmidae, which is also justified by morphology. Shared morphology is observed in the new species of *Pleijelius* and *Microphthalmus*. The main character shared by species of *Pleijelius* and *Microphthalmus* is the position of the median antenna. When present in adults, it is positioned mid-dorsum at the posterior edge of the prostomium at the level of segment I, as described for *Microphthalmus bifurcatus* Hartmann-Schröder, 1974 (fig. 10) and observed in *M. hvalr* sp. nov. (Fig. 3B) and *Pleijelius keni* sp. nov. (Fig. 4B).

According to Salazar-Vallejo *et al.* (2019), the monophyly of the Microphthalmidae is supported by the pygidium transformed into an anal membrane, clearly seen in various *Microphthalmus* spp. The importance of this character needs re-assessment as the pygidium of *Pleijelius* does not possess a ventral anal membrane but instead bears a ventral cirrus and a pair of anal cirri. Similar numbers of body segments, three achaetous anterior segments with six pairs of tentacular cirri, simple notochaetae and falcigerous neurochaetae further support close relationship of *Pleijelius* and most *Microphthalmus* species.

Majority of *Microphthalmus* species are interstitial in sandy and muddy sediments in shallow waters. The deep-sea free-living taxa *Microphthalmus* and *Pleijelius* are found in bathyal to abyssal chemosynthetic habitats in bacterial mats associated with whale and wood fall communities in the Atlantic and Pacific Oceans.

Microphthalmus Mecznikow, 1865

Type species. *Microphthalmus sczelkowii* Mecznikow, 1865.

Diagnosis. Very small bodied. Prostomium with finger-like median antenna positioned mid-dorsum at prostomial posterior edge at level of segment I; pair of lateral antennae and palps positioned antero- ventrally. Achaetous segments I–III each with two pairs of dorsal and ventral tentacular cirri, total six pairs of cirri. Distinctly shorter ventral cirri of segment III compared to five tentacular cirri of three anterior achaetous segments. Sub-biramous parapodia. Notochaetal fascicle absent to less developed; simple notochaetae with one or two rows of subdistal serrations. Neuropodia sometimes with hooked acicula spines; compound falcigerous fascicle sometimes with simple neurochaetae. Pygidium with filamentous dorso-lateral anal cirri and ventral anal lamella lobe with or without fimbriate papillae, with or without medial notch.

Remarks. The genus currently includes 35 species (Read & Fauchald, 2024b), the majority of which are very small-bodied (~ 2 mm) interstitial organisms living in subtidal habitats (Westheide, 2013; Salazar-Villejo *et al.*, 2019). Deep-sea dwelling species include *M. bifurcatus* Hartmann-Schröder, 1974 from 310–500 m in the Skagerrak Strait and *Microphthalmus* sp. from sediment and whale bones at 4,200 m in the SW Atlantic (Sumida *et al.*, 2016).

Microphthalmus hvalr sp. nov.

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Fig. 3A–C

Microphthalmus sp.—Gunton *et al.*, 2021: 48, fig. 12 A–C; Georgieva *et al.*, 2023: 177, fig.11 A–F.

Material examined.

Holotype. AM W.55402; 25NE, L: 2.00 mm, W: 0.45 mm, large oocytes (0.12 mm in diameter) present from segments VI–XX. Body comprises anterior end of eight segments, mid- and posterior segments number XVII, including regenerated posterior-most end of five segments with intact pygidium; an additional regenerated posterior end of four segments also with intact pygidium comes off the body at an angle at segment XII.

Paratypes. AM W.54569, NHMUK ANEA 2022.412-420; NHMUK ANEA 2022.434 (about 20 fragmented specimens, including 1E, 23 segments, L: 2.0 mm, W: 0.4 mm; 1 NE 15 segments, comprising anterior end of seven segments plus two mid-body sections, four segments each, with oocytes from segment 6).

DNA vouchers. NHMUK ANEA 2022.434, AM W.54817.001.
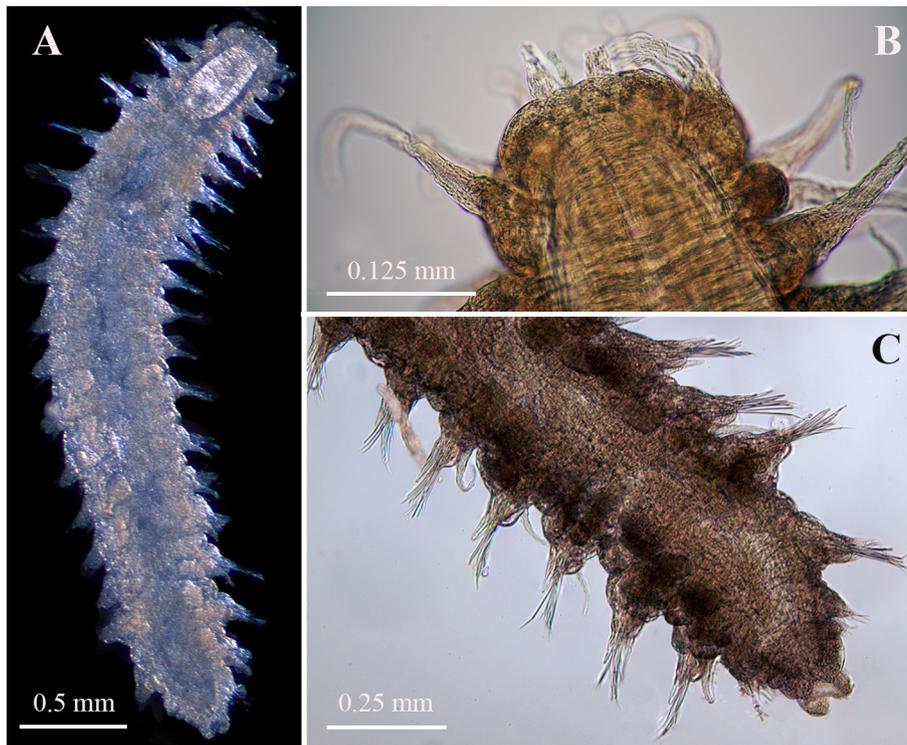
Figure 3. *Microphthalmus hvalr* sp. nov. A, entire body, dorsal view; B, detail of anterior end, dorsal view, showing anterior achaetous segments I-III and prostomium; C, mid and posterior body, dorsal view, showing lack of notochaetae and pygidium.

Type locality. A pilot whale skeleton off Byron Bay, New South Wales, Australia. This is the first bathyal record for a *Microphthalmus* sp. in the SW Pacific.

Description. Body width similar throughout, colour whitish to pale buff with distinct pharynx (Fig. 3A). Muscular pharynx extending to segments V-VI, with 10 broad, cone-shaped pharyngeal papillae visible in paratype; jaws absent.

Prostomium semi-circular, anteriorly slightly cleft, broader than long. Prostomial appendages and body cirri faintly pseudo-articulated, cirriform to often filiform. One pair of relatively short, cirriform lateral antennae and one pair of shorter palps terminally located; slender, finger-like median antenna inserted mid-prostomium, near to posterior prostomial edge, length extends beyond prostomial edge (Fig. 3B). Eyes absent.

Achaetous segments I–III bearing six pairs of long, cirriform tentacular cirri; tentacular ventral cirri of segment III comparatively shorter (Fig. 3B). Dorsal and ventral cirri present from chaetigerous segment IV; dorsal cirri of segment IV shorter than those of segment V and onwards. Parapodia down body sub-biramous; notopodia with dorsal cirri, chaetae absent (Fig. 3C). Neuropodia with pointed pre-chaetal lobe bearing slender acicula, blunt postchaetal lobe with larger, thicker acicula. Compound falcigerous neurochaetae of different lengths, number 11–15 in mid-body; slender blades with serrated edge, heterogomph shafts non-camerate.

Pygidium with one pair dorso-lateral anal cirri, length variable in paratypes, from shorter than, to as long as, to just extending past posterior edge of anal membrane; bi-lobed ventral anal lamella with a shallow medial notch and smooth margins lacking papillae (Fig. 3A, C).

Reproductive morphology. Oocytes and sperm were observed in the same individuals. Paratypes include one individual, 15 NE, with large oocytes 0.12 mm in diameter from segment VI, parapodial seminal receptacles and dark brown, tiny, rounded 'blackberry' shaped structures, putatively sperm, observed in longitudinal patches from segment VII.

Etymology. The name, *hvalr,* is from the Old Norse which incorporates a number of terms pertaining to a whale, including whalebone, the substrate from which the new species was collected.

Diagnosis. All notochaetae absent.

Diagnostic remarks. Morphological characters used to distinguish species in *Microphthalmus* are primarily chaetal and pygidial structures (Westheide, 1967, 1977, 1982, 2013; Westheide & Purschke, 1992). *Microphthalmus* spp. are simultaneous hermaphrodites with unique male copulatory organs (Westheide, 1973, 2013), which have also been suggested as morpho-anatomical characters for species discrimination (Westheide, 2013). However, this character has not been used here as histological work was not possible.

In Australia, *Microphthalmus paraberrans* Hartmann-Schröder, 1982 and *M. westheidei* Hartmann-Schröder, 1982 have been described from subtidal habitats off Western Australia. Both possess sickle-shaped serrate notochaetae as well as pygidia with long anal cirri and anal plates composed of short, broad ventral lamella with smooth margins. *M. hvalr* sp. nov. has relatively short anal cirri and its ventral anal plate is composed of a rounded, smooth lamellate lobe. Thus, the anal plate of *M. hvalr* sp. nov. is similar to those of the Australian species except the plate is much rounder

and the anal cirri are relatively shorter.

Most *Microphthalmus* species possess 2–12 small simple and/or pectinate notochaetae per notopodium while a subtidal commensal *M. hamosus* Westheide, 1982 is one of very few that possesses a single notochaeta per notopodium. The comparison of 38 *Microphthalmus* spp. by Westheide (2013) and 21 *Microphthalmus* species by Salazar-Villejo *et al*. (2019) shows that *Microphthalmus hvalr* sp. nov. lacks diagnostic characters other than the absence of all notochaetae.

Pleijelius Salazar-Vallejo & Orensanz, 2006

Type species. *Pleijelius longae* Salazar-Vallejo & Orensanz, 2006.

Diagnosis. Very small bodied. Prostomium with finger-like median antenna positioned mid-dorsum at posterior edge of prostomium at the level of segment I; pair of lateral antennae and palps positioned antero- ventrally. Achaetous segments I-III each with two pairs of dorsal and ventral tentacular cirri, total 6 cirri. Notochaetal fascicle moderately to abundantly developed: simple notochaetae with one or two rows of subdistal serrations. Neurochaetae may include hooked acicula spines; compound falcigerous fascicle may include simple neurochaetae. Pygidium with well-developed pair of dorso-lateral anal cirri and a ventral medial anal cirrus.

Remarks. *Pleijelius longae*, until now the only species in the genus, has been found on experimental wood panels in the abyss off Massachusetts (Salazar-Villejo & Orensanz, 2006), but these animals appear to be common in wood-fall and whale-fall communities. For example, *Pleijelius* cf. *longae* was reported forming a part of the xalophagid bivalve wood-fall community at 1,500–3,300 m in the SW Atlantic (Saeedi *et al.*, 2019; Shimabukuro *et al*., 2020). Undescribed species of *Pleijelius* have been reported from whale-fall communities in the SW Atlantic (Sumida *et al*., 2016).

Pleijelius keni sp. nov.

Fig. 4A–E

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Pleijelius cf. *longae.*—Gunton *et al*., 2021, SW Pacific, east coast of Australia
Pleijelius.—Georgieva *et al.,* 2023, SW Pacific, east coast of Australia

Material examined

Holotype. AM W.51570, body nearly entire, 20 segments missing posterior-most segments, L: 2.3 mm, W: 0.7 mm.

Paratypes. AM W.55403; MAGNT W032914 (16 specimens of *Pleijelius keni* sp. nov. identified among a lot of *Boudemos paulinae* sp. nov. NHM. 240A. Most specimens fragmented, few entire specimens fell into a similar size range of 25 segments with the greatest length 3 mm. Ovigerous females: 17NE, L: 1.6 mm, W: 0.5 mm, oocytes visible from segment 7, mature eggs 0.08 mm in diameter from segments 13–17; 23E, L: 1.8 mm, W: 0.6 mm; 23E, L: 2.9 mm, W: 1.1 mm; 25E, L: 3.0 mm, W: 0.8 mm. SEM specimen, 19E, L: 1.6 mm, W: 0.5 mm).

DNA vouchers. AM W.54809.001 and NHM_240A.

Type locality. A pilot whale skeleton off Byron Bay, NSW, Australia. This is the first record for a *Pleijelius* species in the SW Pacific Ocean.

Description. Body elongate, segments with poorly defined segmental lines dorsally (Fig. 4A–B); pale buff colour with no obvious pigmentation in preserved specimens. Dense, relatively short length*,* spinous, whitish coloured, notochaetal fascicles, originating dorso-laterally, leaving mid-dorsum bare. Prostomium rectangular to sub-trapezoidal shape, broader than long, with rounded corners. Prostomium not defined dorsally or ventrally by external segmental lines; first ventral segmental line includes segment I (Fig. 4C). Digitiform median antenna arising at posterior-most margin of prostomium at mid-dorsal position on prostomium (Fig. 4A–B); pair of cirriform lateral antennae inserted on anterior prostomial margin (Fig. 4C). Palps inserted just behind former at level of ventral tentacular cirri of segment I; palps same size to slightly shorter than lateral antennae and positioned adjacent level to ventral tentacular cirri of segment I (Fig. 4C). No discreet palphore in most specimens, sometimes faint 'fold' present. Eyes absent. Nuchal organs not discerned.

Large robust muscular pharynx extends to around segment VII. Mouth papillae cirrus-like with rounded bases, cirriform distally; some may be a more cushion-like shape. Mouth papillae number 10, visible when mouth everted. No jaws.

Segments I–III lacking podia and chaetae, each segment with two pairs tentacular cirri; total six pairs. Dorsal cirri on segments I-III long, slender, faintly segmented with sub-conical base not defined cirrophores; ventral cirri shorter than dorsal, particularly on segments I and III (Fig. 4C). Biramous podia with notochaetae and neurochaetae start segment IV (Fig. 4B–C) and continue down body.

Mid-body notopodia shallow mounds with fascicle of spinous notochaetae spread out in fan-like arrangement with shorter spines on inner side of whorl and longer spines in central part (Fig. 4B). Notochaetae number 20–30, spines slightly curved, relatively short in length, shaft may have minute scattered tubercules but distal half to third with the outer margin denticulate composed of two densely close rows of rectangular-shaped teeth extending to distinctive, slightly expanded, truncate, perhaps slightly excavate**,** distal tip (Fig. 4F).

Robust, medium-length dorsal cirri from segment IV, with broad bases, narrowing to cirriform tip, not extending in length beyond notochaetal fascicle. Dorsal cirri smooth not articulated, not alternating in size or position down body (Fig. 4A–B).

Neuropodia composed of anterior elongate lobe and posterior more truncate lobe; large, rounded glands posterior to latter neuropodial lobe (Fig. 4D). Two neuroaciculae present: very slender, pale, superior acicula present at the end of anterior pointed lobe; longer, brown, robust acicula ending mid-way in posterior neuropodial lobe. In one neuropodium of one specimen a single, simple, hooked-shaped, slender acicular spine, parallel to but separate from a robust lower acicula, present and very hard to discern. Ventral cirri composed of broad rounded base and shorter, less broad distal part; almost globular–like in anterior segments becoming more elongate in posterior segments. Ventral cirri mid-body about half to two-thirds length of neuropodial lobe. Ventral cirri inserted on lower edge of ventral ramus immediately posterior to neurochaetal fascicle (Fig. 4C– D).
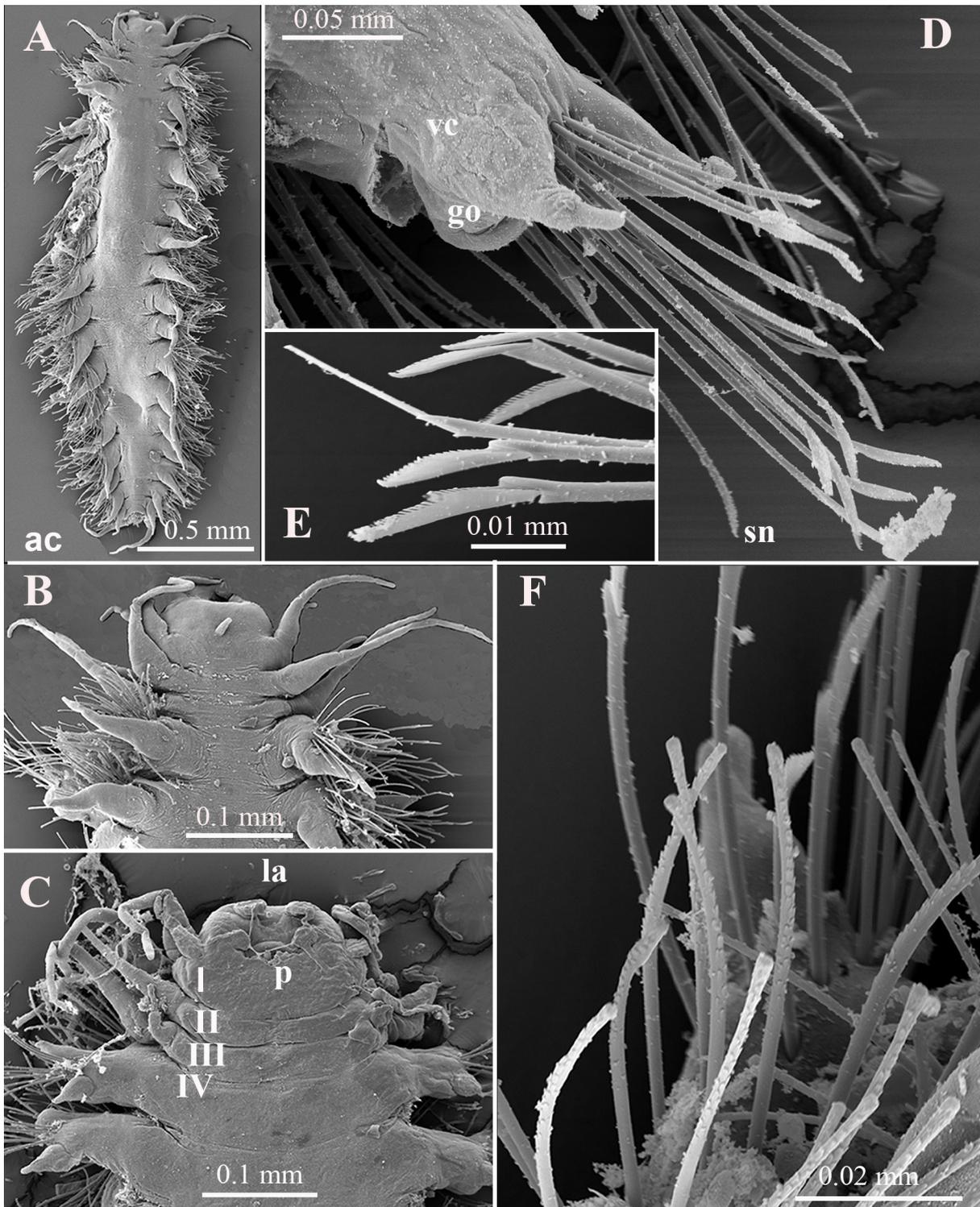
Figure 4. *Pleijelius keni* sp. nov. A, entire body, dorsal view; B, detail of anterior end, dorsal view; C, detail of anterior end, ventral view; D, neuropodium mid-body, ventral view; E, detail of falcigerous neurochaetae; F, detail of flattened and slenderer notochaetae. Abbreviations: ac anal cirri; la lateral antennae; p palps; achaetous segments I-III (note shorter ventral tentacular cirri on segment III), chaetigerous segment IV, ventral view; go - genital organ; sn - simple neurochaeta; vc - ventral cirrus.

Neurochaetal fascicle composed of superior long shafted falcigers with longer blades more directed upwards, number <5; mid and posterior group of unidentate falcigers with medium to shorter length serrate blades, number 12–15 (Fig. 4D– E). Superior-most neurochaetae with 1–2 simple neurochaetae positioned above the superior slender acicula, slightly curved with blade-like distal tip bearing tiny spinelets on concave edge (Fig. 4D); simple neurochaetae may present in other fascicle positions. Neurochaetae with bidentate shafts. Internal cameration absent in notochaetae and neurochaetae.

Nearly all specimens missing posterior-most segments.

Entire pygidium comprising two robust, long, dorso-lateral anal cirri and a single anal cirrus originating ventrally, about quarter the length of lateral anal cirri (Fig. 4A).

Reproductive morphology. Gametes were observed in a nearly entire individual of 17 segments, only missing the posterior end. Large, rounded swollen ventral pads are evident from segment IV. Smaller rounded, swollen structures interpreted as external genital organs are positioned ventrally; they bulge out in between the inferior edge of the neuropodia and ventral cirri and are just visible from segment VII and very clearly present from segments IX, X (Fig. 4D). These appear glandular in function and contain multiple, very small, rounded, dark 'blackberry' shapes indicative of sperm. Smaller oocytes were visible through the ventral body wall with larger oocytes (0.04 mm in diameter) present from segment XII to segment XVII. No external penes or copulatory stylets observed.

Etymology. *Pleijelius keni* sp. nov. is named in honour of the first author's father, Kenneth Watson, who imbued his daughter with a love of nature and scientific curiosity. His ashes are spread at sea offshore from Byron Bay in the vicinity of the whale fall and the abundant life cycle it sustains.

Diagnosis. Notochaetae with two rows of densely serrate margins positioned close together; serrations are rectangular in shape.

Diagnostic remarks. The morphology of *Pleijelius keni* sp. nov. and *P. longae* is similar, including length and number of segments: *P. keni* sp. nov. ~3 mm length, 25E *versus P. longae* length 3.6 mm, 26E. *Pleijelius keni* sp. nov. has a rectangular, narrower body and less dense notochaetal fascicles in comparison with *P. longae* which has chaetigers 4–9 broader than preceding ones (Salazar-Villejo & Orensanz, 2006, fig. 3A; Shimabukuro *et al.*, 2020, fig. 5.3C, colour photo of a live specimen). *Pleijelius keni* sp. nov. and *P. longae* both have 10 pharyngeal papillae; however, their shape is more cirriform in the former and broad, rounded, and mound-like in the latter.

The obvious morphological difference between the two species is notochaetal shape and ornamentation. Notochaetae of *Pleijelius keni* sp. nov. have the distal half to third with two rows of serrate margins densely close together; serrations are of a distinctive rectangular shape. The notochaetal distal tip is slightly expanded, truncate, with a slight concave depression (Fig. 4F). *Pleijelius longae* possesses smooth notochaetal capillaries with a row of 2–4 tiny distal denticles, extending to blunt rounded tip (Salazar-Villejo & Orensanz, 2006, fig. 3D).

Two neuroaciculae, one slender and one robust, are found in examined *Pleijelius keni* sp. nov. and in published figures of *Pleijelius longae*. Rarely a hooked acicula spine is present additionally to the two neuroaciculae in *Pleijelius keni* sp. nov.; a robust single neuroacicula, which in some podia 'doubles over' forming a hook, is illustrated for *P. longae* (Salazar-Villejo & Orensanz, 2006, fig. 5B).

An entire pygidium of *Pleijelius keni* sp. nov. has two long, robust dorso-lateral anal cirri and a single anal cirrus originating ventrally; the latter is poorly visible as most specimens have missing or damaged pygidia. Salazar-Villejo and Orensanz (2006, fig. 2A, 3 A–B) describe the pygidia of *Pleijelius longae* with two pairs of long, robust anal cirri

and no ventral anal structure. Their figures show a damaged posterior end, but a single pair of dorso-lateral anal cirri is visible along with typically compressed posterior-most cirrose segments.

In one specimen of *Pleijelius keni* sp. nov., contraction, possibly due to SEM drying, has led to the position of the dorsal cirri being much more dorsally orientated compared to the notochaetal fascicle (Fig. 4A) observed in specimens from the same sample. These other specimens have the notochaetal fascicle visible in dorsal view and partially covering the dorsal cirri, as shown in notopodium of segment IV, on the right side (Fig. 4B).

Discussion

This study described *Boudemos paulinae* sp. nov. (Calamyzinae, Chrysopetalidae), *Pleijelius keni* sp. nov. (Microphthalmidae) and *Microphthalmus hvalr* sp. nov. (Microphthalmidae) based on specimens collected from the first natural whale fall recovered off the eastern coast of Australia. These descriptions, supported by both morphological and molecular data, contributed to our understanding of the composition of annelid communities associated with whale falls.

Based on a phylogenetic analysis including molecular and morphological data, Aguado *et al.* (2013) reorganised the classification of Chrysopetalidae to include subfamilies Chrysopetalinae, Calamyzinae and a newly proposed subfamily Dysponetinae. The results of their analysis recovered a monophyletic Chrysopetalidae with the Calamyzinae and Chrysopetalinae as sister taxa when rooted with *Aphrodita*. However, in Watson *et al.* (2016) Chrysopetalinae was recovered as sister to Dysponetinae, rather than Calamyzinae, when rooted with a syllid. Chrysopetalinae was again the sister to Calamyzinae when a phyllodocid was used for rooting. The latter topology was obtained in Watson *et al.* (2019) when a hesionid was used as outgroup and in Cepj *et al.* (2022) five outgroup terminals (two phyllodocids, a pilargid, a nereidid, and a hesionid) were used.

The results of both this study and those of Georgieva *et al.* (2023) did not support monophyly of Chrysopetalidae. In Georgieva *et al.* (2023) the Dysponetinae-Calamyzinae clade was recovered as the sister to monophyletic Hesionidae, while Chrysopetalidae and Microphthalmidae formed a basal grade. In contrast, in this study, the Chrysopetalinae-Calamyzinae clade was recovered as the sister to Hesionidae, while Microphthalmidae and Dysponetinae formed a basal grade. Here, one sequence of *Dysponetus hesionides* Böggemann, 2009 fell within Hesionidae, however, examination of type material of *D. hesionides* confirmed a hesionid morphology (Watson unpubl.). Both in Georgieva *et al.* (2023) and in the present study analyses were rooted with the same outgroup (*Nereis pelagica*), so the difference in results was due to ingroup selection.

Given such an instability in tree topology depending on both ingroup and outgroup selection, little confidence can be placed in the results suggesting either paraphyly of Chrysopetalidae or phylogenetic position of Microphthalmidae. Thus, we do not propose here any nomenclature change.

Sequences of all *Boudemos* species, including those of

B. paulinae sp. nov., fell within the Calamyzinae clade in both Georgieva *et al.* (2023) and here, which agrees with Watson *et al.* (2016). However, unlike those of Watson *et al.* (2016) and Georgieva *et al.* (2023), our results did not recover a monophyletic *Boudemos*. The monophyly of the genus needs to be accessed in further studies.

The results of this study also have interesting implications for the composition of Microphthalmidae. Salazar-Vallejo *et al.* (2019) elevated Microphthalminae (Hesionidae) to the family rank and redefined the new family to include the type genus *Microphthalmus* and six former hesionid genera based on morphology. A monotypic hesionid genus *Pleijelius* erected for *P. longae* Salazar-Vallejo & Orensanz, 2006 was not included in Microphthalmidae. Georgieva *et al.* (2023) were first to recover *Pleijelius* and *Microphthalmus* as a clade not nested within Hesionidae, but they did not propose a formal transfer to the Microphthalmidae. In this study, *Pleijelius keni* sp. nov., *Microphthalmus hvalr* sp. nov., *Struwela camposi*, *Microphthalmus listensis*, *Microphthalmus similis* and *Hermundura americana* were recovered in a well-supported clade. These molecular results and the morphological synapomorphies of the two former taxa justify the transfer of *Pleijelius* from Hesionidae to Microphthalmidae proposed here. However, a comprehensive molecular analysis of taxa within Microphthalmidae is needed.

In conclusion, the relationships among families Chrysopetalidae, Hesionidae and Microphthalmidae are unlikely to be resolved using sequences of a few gene fragments because the results are affected by the ingroup and outgroup selection. Additional taxon sampling and additional DNA sequence data, preferably such as transcriptomes in Tilic *et al.* (2022), are required to resolve these deeper relationships. Monophyly of Chrysopetalidae and Microphthalmidae as well as composition of Microphthalmidae needs to be addressed in future large-scale analyses. Such analyses will also show whether elevating Microphthalminae to the family status was justified.

Species Numbers 42-44. 42: Annelid, *Boudemos paulinae* sp. nov. 43: Annelid, *Pleijelius keni* sp. nov. 44: Annelid, *Microphthalmus hvalr* sp. nov.

References

Aguado, M. T., A. Nygren, and G. W. Rouse. 2013. Two apparently unrelated groups of symbiotic annelids, Nautiliniellidae and Calamyzidae (Phyllodocida, Annelida), are a clade of derived chrysopetalid polychaetes. *Cladistics* 29: 610–628.
https://doi.org/10.1111/cla.12011

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215(3): 403–410.
https://doi.org/10.1016/S0022-2836(05)80360-2

Böggemann, M. 2009. Polychaetes (Annelida) of the abyssal SE Atlantic. *Organisms, Diversity and Evolution* 9: 251–428.

Carr, C., S. Hardy, T. Brown, T. Macdonald, and P. Hebert. 2011. A TriOceanic perspective: DNA barcoding reveals geographic structure and cryptic diversity in Canadian polychaetes. *PLOS ONE* 6(7): e22232.
https://doi.org/10.1371/journal.pone.0022232

Cepj, B., A. Ravara, and M. T. Aguado. 2022. First mitochondrial genomes of Chrysopetalidae (Annelida) from shallow-water and deep-sea chemosynthetic environments. *Gene* 815: 146159.
https://doi.org/10.1016/j.gene.2021.146159

Dahlgren, T. C., A. G. Glover, A. Baco, and C. R. Smith. 2004. Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysopetalidae) from the deep Pacific Ocean. *Deep-Sea Research* (1) 51: 1873–1887.
https://doi.org/10.1016/j.dsr.2004.07.017

Dahlgren, T. G., J. Lundberg, F. Pleijel, and P. Sundberg. 2000. Morphological and molecular evidence of the phylogeny of Nereidiform polychaetes (Annelida). *Journal Zoological Systematic and Evolutionary Research* 38: 249–253.
https://doi.org/10.1046/j.1439-0469.2000.384150.x

Dales, R. P. 1962. The polychaete stomodeum and the inter-relationships of the families of the Polychaeta. *Proceedings of the Zoological Society, London* 139: 389–428.
https://doi.org/10.1111/j.1469-7998.1962.tb01837.x

Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): 772.
https://doi.org/10.1038/nmeth.2109

Edgar R. C. 2004 MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
https://doi.org/10.1093/nar/gkh340

Ehlers, E. 1864. *Die Borstenwürmer, nach Systematischen und Anatomischen Untersuchungen Gargestellt*. Leipzig: Wilhelm Engelmann.
https://doi.org/10.5962/bhl.title.2081

Fauchald, K. and G. Rouse. 1997. Polychaete systematics: Past and present. *Zoologica Scripta* 26: 71–138.
https://doi.org/10.1111/j.1463-6409.1997.tb00411.x

Friedrich, H. 1937. Polychaetenstudien. I-III. 1. *Hesionides arenaria* n. sp. n. gen., ein neuer Polychaet aus der Otoplanenzone der Nordsee. 2. *Polydora ligni* Webster 1880 in der Ostsee. 3. Über einige Klein Polychaeten von Helgoland. *Kieler Meeresforschungen* 1: 343–351.

Fujiwara, Y., M. Kawato, T. Yamamoto, T. Yamanaka, W. Sato-Okoshi, C. Noda, S. Tsuchida, T. Komai, S. S. Cubelio, T. Sasaki, K. Jacobsen, K. Kubokawa, K. Fujikura, T. Maruyama, Y. Furushima, K. Okoshi, H. Miyake, M. Miyazaki, Y. Nogi, A. Yatabe, and T. Okutani. 2007. Three-year investigations into sperm whale-fall ecosystems in Japan. *Marine Ecology* 28 (1): 219–232.
https://doi.org/10.1111/j.1439-0485.2007.00150.x

Georgieva, M. N., H. Wiklund, D. A. Ramos, L. Neal, C. J. Glasby, and L. M. Gunton. 2023. The annelid community of a natural deep-sea whale fall off Eastern Australia. *Records of the Australian Museum* 75(3): 167–213.
https://doi.org/10.3853/j.2201-4349.75.2023.1800

Glasby, C. J. 1993. Family revision and cladistic analysis of the Nereidoidea (Polychaeta: Phyllodocida). *Invertebrate Taxonomy* 7: 1551–1573.
https://doi.org/10.1071/IT9931551

Gunton, L. M., E. K. Kupriyanova, T. Alvestad, L. Avery, J. A. Blake, O. Biriukova, M. Boggemann, P. Borisova, N. Budaeva, I. Burghardt, M. Capa, M. N. Georgieva, C. J. Glasby, P. W. Hsueh, P. A. Hutchings, N. Jimi, J. A. Kongsrud, J. Langeneck, K. Meißner, A. Murray, M. Nikolic, H. Paxton, D. Ramos, A. Schulze, R. Sobczyk, C. Watson, H. Wiklund, A. Zhadan, and J. Zhang. 2021. Annelids of the eastern Australian abyss collected by the 2017 RV 'Investigator' voyage. *Zookeys* 1021: 1–198.
https://doi.org/10.3897/zookeys.1020.57921.figure18

Grube, A. E. 1850. Die Familien der Anneliden. *Archiv für Naturgeschichte* 16(1): 249–364.

Hartman, O. 1939. New species of polychaetous annelids from Southern California. *Allan Hancock Expeditions* 7: 159–171.

Hartmann-Schröder, G. 1959. Zur Okologie der Polychaeten des Mangrove-Estero-Gabietes von El Salvador. *Beitrage zur Neotropischen Fauna* 1: 69–183.
https://doi.org/10.1080/01650525909380612

Hartmann-Schröder, G. 1971. Annelida, Borstenwurmer, Polychaeta. *Tierwelt Deutschlands* 58: 1–594.

Hartmann-Schröder, G. 1974. Polychaeten von Expeditionen der 'Anton Dohrn' in Nordsee und Skegerrak. *Veröff Institute Meeresforsch Bremerh* 14: 169–274.

Hartmann-Schröder, G. 1982. Die Polychaeten der subtropisch-antiborealen Westküste Australiens (zwischen Cervantes im Norden und Cape Naturaliste im Süden). *Mitteilungen as dem Hamburgischen Zoologischen Museum und Institut* 79: 51–118.

Huč, S., A. S. Hiley, M. F. McCowin, and G. W. Rouse. 2024. A mitogenome-based phylogeny of Pilargidae (Phyllodocida, Polychaeta, Annelida) and evaluation of the position of *Antonbruunia*. *Diversity* 16(3): 134.
https://doi.org/10.3390/d16030134

Katoh, K., K. Misawa, K. Kuma, and T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.
https://doi.org/10.1093/nar/gkf436

Kiseleva, M. I. 1992. New genus and species of a polychaete of the Chrysopetalidae from the Black Sea. *Zoologicheskii Zhurnal* 72: 128–132. (In Russian)

Kupriyanova, E. K., T. A. Macdonald, and G. W. Rouse. 2006. Phylogenetic relationships within Serpulidae (Annelida: Polychaeta) inferred from molecular and morphological data. *Zoologica Scripta* 35: 421–339.
https://doi.org/10.1111/j.1463-6409.2006.00244.x

Lamarck, J.-B. de. 1802. Discours d'Ouverture, Prononcé le 27 floréal an 10, au Muséum d'Histoire naturelle. Recherches sur l'organisation des corps vivans. *Bulletin Scientifique de la France et de la Belgique* 40: 483–517.

Mecznikow, E. 1865. Beiträge zur Kenntnis der Chaetopoden. *Zeitschrift für Wissenschaften Zoologie* 15: 334–335.

Minh, B. Q., H. A. Schmidt, O. Chernomor, D. Schrempf, M. D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37: 1530-1534.
https://doi.org/10.1093/molbev/msaa015

Norén, M. and U. Jondelius. 1999. Phylogeny of the Prolecithophora (Platyhelminthes) inferred from 18S rDNA sequences. *Cladistics* 15(2): 103–112.
https://doi.org/10.1111/j.1096-0031.1999.tb00252.x

O'Hara T. 2017. IN2017_V03 Voyage Summary.
https://www.cmar.csiro.au/data/trawler/survey_details.cfm?survey=IN2017%5FV03

O'Hara T. D., A. Williams, S.T. Ahyong, P. Alderslade, D. Bray, A. L. Crowther, M. Ekins, M. Eléaume, C. A. Farrelly, J. K. Finn, A. Graham, M. Gomon, K. Gowlett-Holmes, L. Gunton, A. M. Hosie, P. Hutchings, E. Lejeune, F. Koehler, E. Kupriyanova, M. Mackenzie, C. Mah, H. McIntosh, K. L. Merrin, A. Miskelly, M. L. Mitchell, K. Moore, A. Murray, P. M. O'Loughlin, J. Pogonoski, H. Paxton, D. Staples, C. Untiedt, R.S. Wilson, J. Zhang, and N. J. Bax. 2020. The lower bathyal and abyssal fauna of eastern Australia. *Marine Biodiversity Records* 13: 1–27.
https://doi.org/10.1186/s41200-020-00194-1

Palumbi, S. R., A. Martin, S. Romano, and W. O. McMillan. 1991. *The Simple Fool's Guide to PCR*. Honolulu: University of Hawaii.

Pleijel, F. and T. Dahlgren. 1998. Position and delineation of Chrysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). *Cladistics* 14: 129–150.
https://doi.org/10.1111/j.1096-0031.1998.tb00327.x

Rambaut, A. 2018. FigTree v1.4.4 Program distributed by the author (University of Edinburgh, Edinburgh, Scotland).
http://tree.bio.ed.ac.uk/software/figtree/

Read, G. and K. Fauchald. 2024a. World Polychaeta Database. Microphthalmidae Hartmann-Schröder, 1971. Available through the World Register of Marine Species. [accessed 14 October 2024]
https://www.marinespecies.org/aphia.php?p=taxdetails&id=322549

Read, G. and K. Fauchald 2024b. World Polychaeta Database. *Microphthalmus* Mecznikow, 1865. Available through the World Register of Marine Species. [accessed 14 October 2024]
https://www.marinespecies.org/aphia.php?p=taxdetails&id=129313

Saeedi, H., A. F. Bernadino, M. Shimabukuro, G. Falchetto, and P. Y. G. Sumida. 2019. Macrofaunal community structure and biodiversity patterns based on a wood-fall experiment in the deep South-West Atlantic. *Deep Sea Research Part 1, Oceanographic Research Papers* 145: 73–82.
https://doi.org/10.1016/j.dsr.2019.01.008

Salazar-Vallejo, S. I. and J. M. Orensanz. 2006. *Pleijelius longae* n. gen., n. sp., a remarkable deep-water polychaete from the Northwestern Atlantic. *Scientia Marina* 70S3: 157–166.
https://doi.org/10.3989/scimar.2006.70s3157

Salazar-Vallejo, S. I., J. A. León-González, and L. F. Carrera-Parra. 2019. Phylogeny of Microphthalminae Hartmann-Schröder, 1971, and revision of *Hesionella* Hartman, 1939, and *Struwela* Hartmann-Schröder, 1959 (Annelida, Errantia). *PeerJ* 7: e77231-34.
https://doi.org/10.7717/peerj.7723

Shimabukuro, M., J. M. Alfaro-Lucas, A. F. Bernadino, R. B. Ramos, M. M. de Mahiques, and P. Y. G. Sumida. 2020. Chemosynthetic ecosystems on the Brazilian deep-sea margin. In *Brazilian Deep-Sea Marine Biodiversity*, eds. P. Y. G. Sumida, A. F. Bernardino, and F. C. De Léo, pp. 109–132. Switzerland: Springer, Cham.
https://doi.org/10.1007/978-3-030-53222-2_5

Sjölin, E., C. Erséus, and M. Källersjö. 2005. Phylogeny of Tubificidae (Annelida, Clitellata) based on mitochondrial and nuclear sequence data. *Molecular Phylogenetics and Evolution* 35(2): 431–441.
https://doi.org/10.1016/j.ympev.2004.12.018

Smith, C.R and A.R. Baco. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: An Annual Review* 41: 311–354.
https://doi.org/10.1201/9780203180594.ch6

Smith, C. R., A. G. Glover, T. Treude, N. D. Higgs, and D. J. Amon. 2015. Whale-fall ecosystems: recent insights into ecology, paleoecology and evolution. *Annual Review of Marine Science* 7(1): 571–596.
https://doi.org/10.1146/annurev-marine-010213-135144

Sumida, P. Y. G., J. M. Alfaro-Lucas, M. Shimabukuro, H. Kitazato, J. A. A. Perez, A. Soares-Gomes, T. Toyofuku, A. O. S. Lima, K. Ara, and Y. Fujiwara. 2016. Deep-sea whale fall whale fauna from the Atlantic resembles that of the Pacific Ocean. *Scientific Reports* 6(1): 22139.
htpps://doi.org/10.1038/srep22139

Tilic, E., J. Stiller, E. Campos, F. Pleijel, and G. W. Rouse. 2022. Phylogenomics resolves ambiguous relationships within Aciculata (Errantia, Annelida). *Molecular Phylogenetics and Evolution* 166: 107339.
https://doi.org/10.1016/j.ympev.2021.107339

Uchida, H., E. Lopéz, and M. Sato. 2019. New Hesionidae (Annelida) from Japan: Unavailable names introduced by Uchida (2004) revisited with reestablishment of their availability. *Species Diversity* 24: 69–95.
https://doi.org/10.12782/specdiv.24.69

Watson, C. 2022. Chrysopetalidae Ehlers, 1864. In *Handbook of Zoology, a Natural History of the Phyla of the Animal Kingdom. Volume 4: Pleistoannelida, Errantia II*, eds. G. Purschke, M. Böggemann, and W. Westheide, pp. 226–256. Berlin and Boston: De Gruyter GmbH & Co.

Watson, C., I. Carvajal, N. G. Sergeeva, F. Pleijel, and G. W. Rouse. 2016. Free-living calamyzin chrysopetalids (Annelida) from methane seeps, anoxic basins and whale falls. *Zoological Journal of the Linnean Society* 177: 700–719.
https://doi.org/10.1111/zoj.12390

Watson, C. and S. Faulwetter. 2017. Stylet jaws of Chrysopetalidae (Annelida). *Journal of Natural History* 51(47–48): 2863–2924.
https://doi.org/10.1080/00222933.2017.1395919

Watson, C., E. Tilic, and G. W. Rouse. 2019. Revision of *Hyalopale* (Chrysopetalidae: Phyllodocidae; Annelida): an amphi-Atlantic *Hyalopale spinosa* species complex and five new species from reefs of the Caribbean Sea and Indo-Pacific Oceans. *Zootaxa* 4671(3): 339–368.
https://doi.org/10.11646/zootaxa.4671.3.2

Westheide, W. 1967. Monographic der Gattungen *Hesionides* Friederich und *Microphthalmus* Mecznikow (Polychaeta, Hesionidae). *Zeitschrift für Morphologie der Tiere* 61: 1–159.
https://doi.org/10.1007/BF00298775

Westheide, W. 1973. Zwei neue interstitielle *Microphthalmus*-Arten (Polychaeta) von der Bermudas. *Mikrofauna des Meeresbodens* 14: 241–252.

Westheide, W. 1977. Phylogenetic systematics of the genus *Microphthalmus* (Hesionidae) together with description of *M. hartmanae* nov. sp. In *Essays on Polychaetous Annelids in Memory of Dr. Olga Hartman,* eds. D. K. Reish and K. Fauchald, pp. 103–114. Los Angeles: Allan Hancock Foundation, University of Southern California.

Westheide, W. 1982. *Microphthalmus hamosus* sp. n. (Polychaeta, Hesionidae) – an example of evolution leading from the interstitial fauna to a macrofaunal interspecific relationship. *Zoologica Scripta* 11: 189–193.
https://doi.org/10.1111/j.1463-6409.1982.tb00531.x

Westheide, W. 2013. *Microphthalmus mahensis* sp. n. (Annelida, Phyllodocida) together with an annotated key to the genus. *Helgoland Marine Research* 67: 413–422.
https://doi.org/10.1007/s10152-012-0332-1

Westheide, W. and G. Purschke. 1992. *Microphthalmus simplicichaetous* (Annelida, Polychaeta), a new hesionid from the north-western American Pacific coast with exclusively simple chaetae. *Proceedings of the Biological Society of Washington* 105: 132–135.

Westheide, W. and C. Watson Russell. 1992. Ultrastructure of chrysopetalid paleal chaetae (Annelida, Polychaeta). *Acta Zoologie* 73: 197–202.
https://doi.org/10.1111/j.1463-6395.1992.tb01187.x

Wiklund, H., A. G. Glover, P. J. Johanessen, and T. G. Dahlgren. 2009. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. *Zoological Journal of the Linnean Society* 155: 774–785.
https://doi.org/10.1111/j.1096-3642.2008.00469.x

Zaika, V. E., N. G. Sergeeva, and M. I. Kiseleva. 1999. Two polychaete species bordering deep anoxic waters in the Black Sea. *Tavrichesky Medical-Biological Vestnik* 1–2: 56–60.