



## Article

# New Species of *Macellicephala* McIntosh, 1885 (Annelida, Polynoidae), Associated with the Reef Stage of a Whale Fall †

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## Abstract

Decomposing whale carcasses on the seabed (whale falls) are known to support distinct communities, with many taxa new to science. This paper describes a new polynoid species, *Macellicephala irisae* sp. nov., from a natural whale fall at 1240 m depth in Santa Catalina Basin off California, USA. The new species was associated with a cladorhizid sponge growing on a bone, transitioning from the sulphophilic to reef stage. We also highlight the biodiversity of exclusively deep-sea Macellicephalinae subfamily and its most species-rich genus *Macellicephala*. Morphological and molecular data support the description of the new species, which is also placed within a phylogenetic context using COI, 16S and 18S markers. The new species possesses distinctive filamentous notochaetae not previously reported in *Macellicephala*, and with the future increase in taxon coverage, an erection of new genus may be warranted.

**Keywords:** taxonomic novelty; host association; molecular phylogeny; COI; 16S; 18S; whale fall succession

## 1. Introduction

In generally food-constrained deep-sea ecosystems, large organic falls, including whale falls, act as food oases for organisms adapted to exploit these sporadic influxes of organic material [1–4]. Whale falls, in particular, provide discrete resource-rich patches which vary in both time and space and can pass through a series of successional stages, including a mobile-scavenger stage, enrichment-opportunist stage, a sulphophilic stage, and a reef stage [2]. Thus, whale falls and other food-rich patches at the seafloor enhance habitat complexity and promote biodiversity within deep-sea ecosystems [2,5–8]. Decomposing whale carcasses on the seafloor have been shown to support distinctive communities of deep-sea macrofauna [1,2,7], including annelid worms. Annelids commonly found include the remarkable ‘zombie worms’ *Osedax* Rouse, Goffredi & Vrijenhoek, 2004 [9] and members of families Ampharetidae, Dorvilleidae, Hesionidae and Chrysopetalidae [10–14].

In this paper we describe a new species from the scale-bearing annelid family Polynoidae Kinberg, 1856 [15] (Figure 1A,B). This species was collected from a cladorhizid



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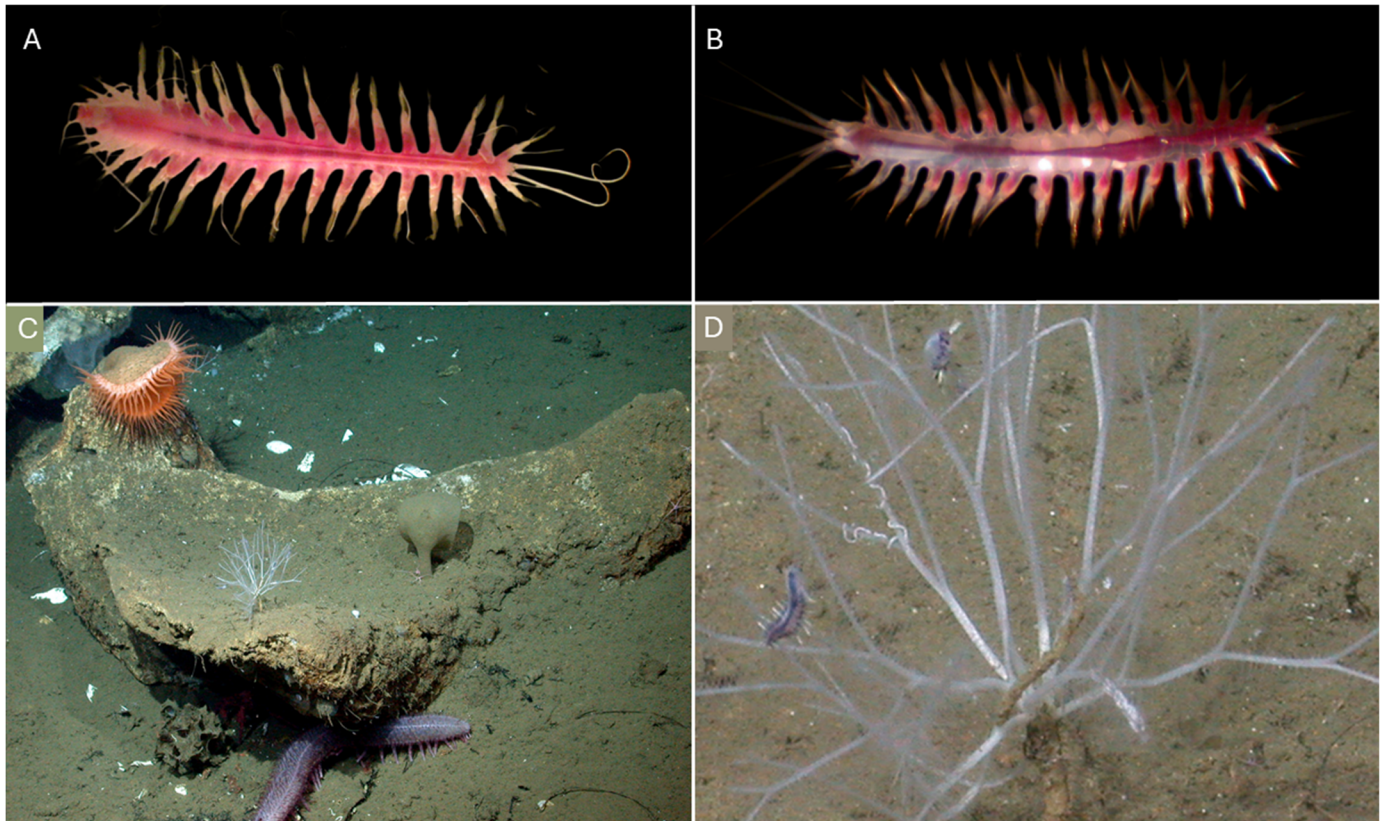
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sponge (Figure 1C,D) attached to a whale scapula (Figure 1C) from the Santa Catalina whale fall [1]. The whale fall is the remains of a 21 m long balaenopterid discovered in 1987 and located at ~1240 m depth, ~33°12' N, ~118°30' W [1]. The discovery of this particular whale confirmed the first records of a chemoautotrophic community containing vesicomyid clams, bathymodiolin mussels and bacterial mats living on a whale carcass [1,16], creating the hypothesis that whale-falls could act as 'stepping-stones' for the dispersal of fauna on ecological and evolutionary timescales.



**Figure 1.** (A) *Macellicephalo irisae* sp. nov., live image of holotype NHMUK.ANEA 2019.8146. (B) *Macellicephalo irisae* sp. nov., live image of paratype NHMUK.ANEA 2026.701, with eggs visible through segment 8–14. (C) Right scapula of the whale in Santa Catalina Basin with associated sessile fauna, including the predatory tunicate *Megalodicopia* sp., the Venus flytrap anemone *Actinoscyphia* sp. and cladorhizid sponge; surrounding sediment contains vesicomyid clams and holothurian. (D) Detail of cladorhizid sponge showing two specimens of *Macellicephalo irisae* sp. nov. crawling over the sponge.

The Santa Catalina skeleton, estimated to have arrived at the sea floor in ~1948 [17], was crucial for studying whale fall successional stages, including a decades-long, sulfophilic stage [18]. At the time of sampling reported in this publication (2005), the whale fall was thus >50 years old. The bones showed differences in bacterial mat cover and presence of species dependent on chemosynthesis, with individual bones likely in the different successional stages, ranging from the late sulphophilic to the early reef stage. The scapula, from which the worms were collected, is suggested to be transitioning into the reef stage based on limited evidence of microbial mats and chemosynthetic fauna, as well the presence of the sessile, suspension-feeding megafauna attached to the bone (Figure 1C).

This whale fall has been previously shown to support a diverse and novel polynoid fauna by Pettibone [19], who reported two previously known polynoid species—*Bathykurila guaymasensis* Pettibone, 1989 [20], originally described from the Guaymas Basin hydrothermal mounds, and *Subadyte mexicana* Fauchald, 1972 [21], from deep waters off Mexico. The

report of *B. guaymasensis* suggested a link between whale falls and hydrothermal vents, both chemosynthetic habitats. Two newly described species at that time—*Peinaleopolynoe santacatalina* Pettibone, 1993, and *Harmothoe craigsmithi* Pettibone, 1993—provided further evidence for whale falls as reservoirs of novel biodiversity. Later, Glover et al. [22] reported on *B. guaymasensis* from the same whale fall (and from the nearby Santa Cruz whale fall), showing it exhibits sexual dimorphism and molecular diversity suggesting that the nominal species *B. guaymasensis* may potentially consist of two sympatric species.

Unlike Pettibone's specimens, which were reported as "collected on or within 0.5 m of the bones" during the sulphophilic stage [19], the novel polynoid species reported here was found in association with a cladorhizid sponge attached to the whale scapula (Figure 1C,D), and it was not reported by Pettibone [19]. Given the ~15-year sampling gap, this may suggest that the novel polynoid species is associated with a different successional whale fall stage—the reef stage [2,18]. Furthermore, the oil content of individual whale bones varies, with scapulae showing a moderate lipid content, with values of ~15–30% [23], making them likely to enter the reef stage faster than other more lipid-rich bones, such as the caudal vertebrae.

The new species described here belongs to the subfamily Macellicephalinae Hartmann-Schröder, 1971 [24], which is known to be restricted to deep-sea habitats (e.g., [25,26]) or analogous environments, such as anchialine caves [27] and polar shelves [28–30]. Within Macellicephalinae, the genus *Macellicephala* McIntosh, 1885 [31], is the most species rich, currently with 23 valid species [32]. Here, a description of a new species in this genus, *Macellicephala irisae* sp. nov., is provided with the support from morphological and molecular data.

## 2. Materials and Methods

### 2.1. Sample Collection

The Santa Catalina whale fall was sampled at 1240 m depth, 33°11.72 N, 118°29.46 W using the ROV *Tiburón* from Monterey Bay Aquarium Research Institute during a research cruise in February 2005. This cruise formed part of an ongoing research program on numerous whale fall habitats in this region led by C.R. Smith. Specimens were collected using the suction sampler and rotating basket of the ROV *Tiburón* and preserved for DNA analyses and standard morphology. Specimens for DNA sequencing were preserved in 95% ethanol and stored in 4 °C, and specimens for standard morphology were fixed in 10% formalin in seawater and subsequently transferred to 70% ethanol.

### 2.2. Morphological Analysis

Specimens were examined and imaged using light and scanning electron microscopy (SEM). Photomicrographs of both live and fixed specimens were taken using Nikon 4500 Coolpix (Nikon, Tokyo, Japan) and Optem microscope eyepiece adapter (Optem, New York, NY, USA). Specimens were measured at widest part of the body, including parapodia but excluding chaetae. Specimens for scanning electron microscopy (SEM) were dehydrated in ethanol, critical point dried, gold-coated and imaged using a Hitachi S2500 (Hitachi, Tokyo, Japan) and Phillips XL-30 SEM (Phillips, Amsterdam, The Netherlands) in the Imaging and Analysis Facility at the Natural History Museum. The type material and voucher specimens for sequences were deposited at the Natural History Museum in London, UK.

### 2.3. Molecular Analysis

Extraction of DNA was done with DNeasy Tissue Kit (Qiagen, Hilden, Germany) following the protocol supplied by the manufacturer. Approximately 1800 bp of 18S were amplified using the primers 18SA 5'-AYCTGGTTGATCCTGCCAGT-3' [33] and 18SB 5'-

ACCTTGTTACGACTTTTACTTCCTC-3' (Nygren & Sundberg 2003) [34]. Around 450 bp of 16S were amplified with the primers ann16Sf 5'-GCGGTATCCTGACCGTRCWAAGGTA-3' [35] and 16SbrH 5'-CCGGTCTGAACTCAGATCACGT-3' [36], and around 650 bp of cytochrome c oxidase were amplified using LCO1490 5'-GGTCAACAAATCATAAAGATATTGG-3' [37] and COI-E 5'-TATACTTCTGGGTGCCGAAGAATCA-3' [38]. PCR mixtures contained ddH<sub>2</sub>O, 1 µL of each primer (10 µM), 2 µL of template DNA and puReTaq Ready-To-Go PCR Beads (GE Healthcare, Chicago, IL, USA) in a mixture of a total of 25 µL. The temperature profile was as follows: 96 °C/240 s – (94 °C/30 s – 50 °C/30 s – 72 °C/60 s) × 45 cycles – 72 °C/480 s. PCR products were purified using Millipore Multiscreen 96-well PCR Purification System, and sequencing was performed on an ABI 3730XL DNA Analyser (Applied Biosystems, Waltham, MA, USA) at The Natural History Museum Sequencing Facility, using the same primers as in the PCR reactions plus two internal primers for 18S, 620F 5'-TAAAGYTGTYGCAGTTAAA-3' [34] and 1324R 5'-CGGCCATGCACCACC-3' [39].

Overlapping sequence fragments were merged into consensus sequences using Geneious Prime 2025.0.3 (<https://www.geneious.com>, accessed on 30 April 2026). Sequences in the study were combined with sequences downloaded from NCBI GenBank (Table 1). The three genes were aligned separately using MAFFT [40] with default settings, provided as plug-in in Geneious. The alignment consists of 49 Polynoidae sequences mainly from the subfamily Macellicephalinae, with *Admetella* sp. (Admetellinae) as root and two Eulagiscinae taxa as outgroups, following Murray et al. [41], where those taxa fell closest to the subfamily Macellicephalinae. Maximum Likelihood (ML) analysis was performed using IQTree 2 [42], where ModelFinder [43] selected the optimal models TIM+F+I+G4 for 18S, TIM2+F+I+R4 for 16S and GTR+F+I+G4 for COI. The ML analysis was run with 1000 ultrafast bootstrap replicates. Bayesian phylogenetic analyses (BA) were conducted with MrBayes v.3.2.6 [44]. In the combined Bayesian analysis, the data were partitioned into the three parts (18S, 16S, and COI), the evolutionary model GTR+I+G was applied to each partition, and the parameters used for the partitions were unlinked. The Bayesian analyses were run independently three times for 10,000,000 generations. Of these, 2,500,000 generations were discarded as burn-in. The tree files were interpreted with FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>, accessed on 30 April 2026) and edited using Affinity Publisher (<https://affinity.serif.com>, accessed on 30 April 2026). All sequences obtained in this study have been deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank>).

**Table 1.** The list of taxa and their associated sequences downloaded from NCBI GenBank and included in the phylogenetic analysis in this study.

Taxon Name	18S	16S	COI
<i>Abyssarya acus</i>	MH233230.1	MH233182.1	MH233279.1
<i>Admetella</i> sp.	PX048979.1	PQ368171.1	PQ360816.1
<i>Bathyedithia retierei</i>	MH233215.1	MH233157.1	—
<i>Bathyeliasona mariaae</i>	MH233204.1	MH233149.1	MH233260.1
<i>Bathyeliasona nigra</i>	PX048982.1	PQ368174.1	PQ360818.1
<i>Bathyfauvelia glacigena</i>	MH233236.1	MH233162.1	MH233272.1
<i>Bathyfauvelia ignigena</i>	MH233246.1	MH233188.1	MH233289.1
<i>Bathykurila guaymasensis</i>	DQ074765.1	MG905034.1	MH233265.1
<i>Bathymoorea lucasi</i>	MH233224.1	MH233165.1	MH233284.1
<i>Bathypolaria kondrashovi</i>	MK660181.1	MK559898.1	—
<i>Bathypolaria magnicirrata</i>	JX863895.1	JX863896.1	—
<i>Branchinotogluma elytopapillata</i>	MG799378.1	MG799377.1	MG799389.1

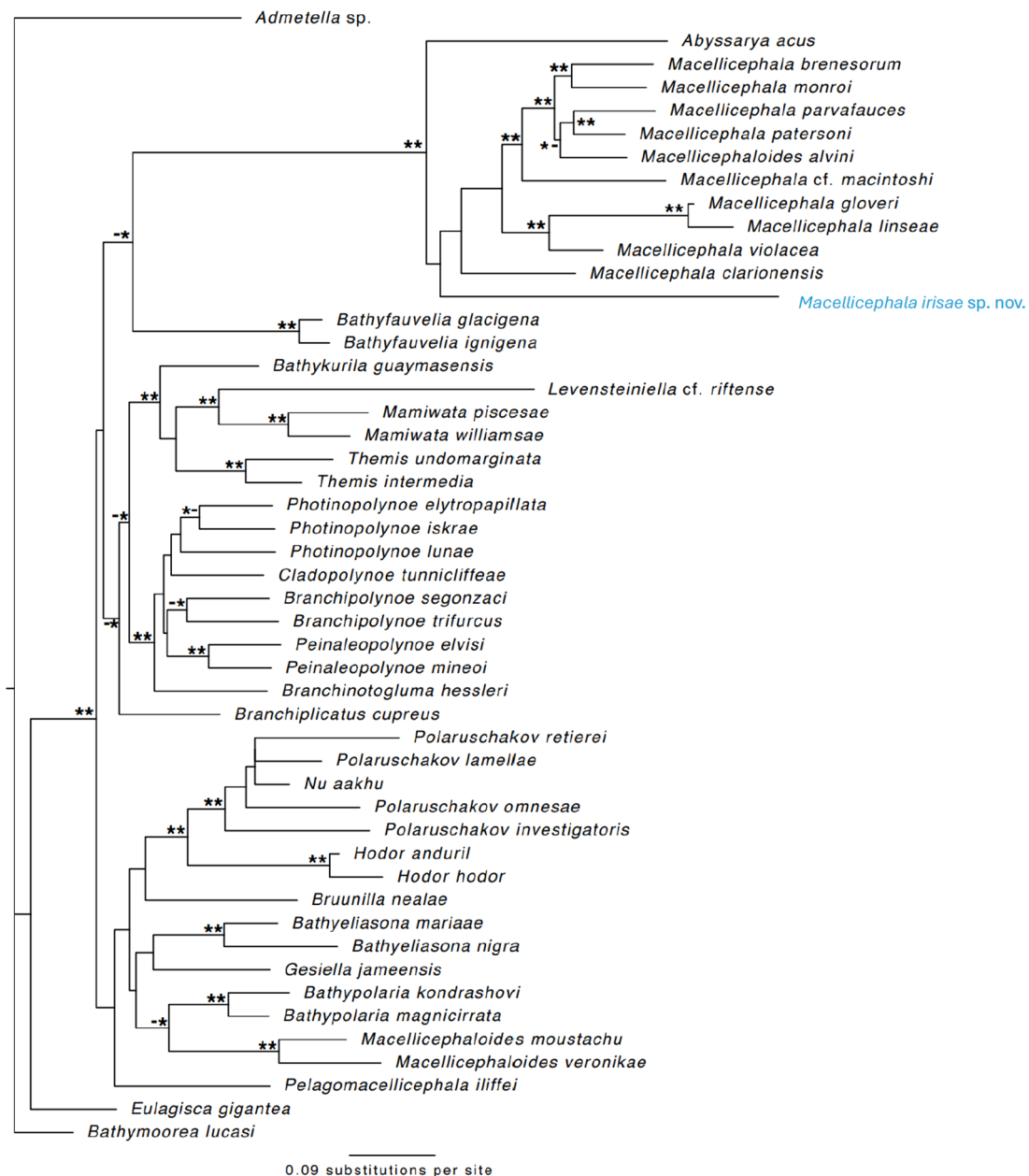
Table 1. Cont.

Taxon Name	18S	16S	COI
<i>Branchinotogluma hessleri</i>	MH124626.1	MH127414.1	KY684713.1
<i>Branchiplicatus cupreus</i>	OM007993.1	MH127418.1	KY684706.1
<i>Branchipolynoe segonzaci</i>	MW654526.1	MW654557.1	MW646934.1
<i>Branchipolynoe trifurcus</i>	MW654529.1	MW654558.1	MW646933.1
<i>Bruunilla nealae</i>	MH233216.1	MH233158.1	—
<i>Cladopolynoe tunnicliffeae</i>	MW654530.1	MW654560.1	MW646935.1
<i>Eulagisca gigantea</i>	MG905040.1	KJ676608.1	KJ676633.1
<i>Gesiella jameensis</i>	OP476759.1	KY454413.1	KY454429.1
<i>Hodor anduril</i>	MH233239.1	MH233191.1	MH233258.1
<i>Hodor hodor</i>	MH233238.1	MH233189.1	MH233257.1
<i>Levensteiniella</i> cf. <i>riftense</i>	MW654531.1	MW654564.1	MW646932.1
<i>Levensteiniella undomarginata</i>	MG799376.1	MG799379.1	MG799385.1
<i>Macellicephala brenesorum</i>	MG905041.1	MG905035.1	MG905047.1
<i>Macellicephala</i> cf. <i>macintoshi</i>	PX049008.1	PQ368214.1	PQ360851.1
<i>Macellicephala clarionensis</i>	MH233235.1	MW471322.1	—
<i>Macellicephala gloveri</i>	MG905042.1	KX867371.1	KX867447.1
<i>Macellicephala linseae</i>	MG905043.1	KX867378.1	KX867448.1
<i>Macellicephala monroi</i>	MG905044.1	MG905036.1	—
<i>Macellicephala parvafauces</i>	MH233225.1	MH233153.1	—
<i>Macellicephala patersoni</i>	MG905045.1	MG905037.1	—
<i>Macellicephala violacea</i>	OP476757.1	OP477034.1	JX119016.1
<i>Macellicephaloides alvini</i>	OP651045.1	OP648307	OP648307.1
<i>Macellicephaloides moustachu</i>	MH233212.1	—	—
<i>Macellicephaloides veronikae</i>	PV911684	PV911683	—
<i>Mamiwata piscesae</i>	MW654532.1	MW654563.1	MW646939.1
<i>Mamiwata williamsae</i>	OM007996.1	MW654562.1	MW646938.1
<i>Nu aakhu</i>	MH233209.1	—	—
<i>Peinaleopolynoe elvisi</i>	MH124629.1	MH127422.1	PQ449258.1
<i>Peinaleopolynoe mineoi</i>	MN428337.1	MN428331.1	MN431776.1
<i>Pelagomacellicephala iliffei</i>	OP476758.1	OP477035.1	KY454443.1
<i>Photinopolynoe iskrae</i>	MW654527.1	MW654559.1	MW646936.1
<i>Photinopolynoe lunae</i>	MW654528.1	MW654561.1	MW646940.1
<i>Polaruschakov investigatoris</i>	—	PQ368216.1	PQ360853.1
<i>Polaruschakov lamellae</i>	MH233226.1	MH233194.1	MH233250.1
<i>Polaruschakov omnesae</i>	MH233213.1	MH233164.1	MH233254.1
<i>Themis intermedia</i>	MW654533.1	MW654565.1	MW646937.1
<b><i>Macellicephala irisae</i> sp. nov.</b>	<b>this study</b>	<b>this study</b>	<b>this study</b>

### 3. Results

#### 3.1. Phylogenetic Analyses

DNA was obtained from holotype NHMUK.ANEA 2019.8146 and paratype NHMUK.ANEA 2019.8147, and the sequences from the holotype were used in the molecular analyses. In both analyses, the new species falls within a well-supported clade containing all sequenced *Macellicephala* species, together with *Abyssarya acus* Bonifácio & Menot, 2018, and sequences labelled *Macellicephaloides alvini* (Figure 2). The position of *Macellicephaloides alvini* within *Macellicephala* might be due to DNA contamination or misidentification. *Abyssarya acus* falls basal to *Macellicephala*, and the position of the new species within the *Macellicephala*–*Abyssarya* clade is not well resolved (Figure 2).



**Figure 2.** Majority rule consensus tree from the Bayesian analyses (BA) using 18S, 16S and COI, with 49 taxa from Polynoidae, using taxa from subfamilies Admetellinae Uschakov, 1977, and Eulagiscinae Pettibone, 1997, as outgroups. The bootstrap support values from the Maximum Likelihood (ML) analyses are added in to the Bayesian tree as BA/ML on the nodes. Support values at or above 0.95 for the BA and 95 for ML are shown in the tree as asterisks. Support values from both analyses are shown as \*\*, while if support is low from one of the analyses it is shown as \*- (ML low) or -\* (BA low). No symbols on nodes show that there was low support in both analyses.

### 3.2. Systematics

Polynoidae Kinberg, 1856

Macellicephalinae, Hartmann-Schröder, 1971

*Macellicephalo* McIntosh, 1885

Type-species: *Macellicephalo mirabilis* (McIntosh, 1885)

***Macellicephalo irisae* sp. nov.**

urn:lsid:zoobank.org:pub:9EA4AAC7-07F8-4ADD-AD54-09A37BD17F2A

Figure 1A,B and Figures 3–6

**Materials examined.** Holotype NHMUK.ANEA 2019.8146 (ETOH), GenBank accession numbers PZ310488, PZ314305 and PZ318984; paratype NHMUK.ANEA 2026.701, live, SEM, (Formalin); paratype NHMUK.ANEA 2019.8145 (Formalin); paratype NHMUK.ANEA 2019.8147 (ETOH), GenBank accession numbers PZ310489 and PZ318985. All specimens collected on cladorhizid sponge associated with 21 m, 60 t blue or fin whale carcass, Santa Catalina Basin, southern California, eastern Pacific Ocean, 33°11.72 N, 118°29.46 W, 1244 m, February 2005, Tiburon Dive No. 825, slurp chamber 9.

**Measurements.** Holotype NHMUK.ANEA 2019.8146: 13.1 mm, width 3.9 mm without chaetae, 18 segments; paratype NHMUK.ANEA 2026.701: length 11.2 mm, 4.25 mm wide without chaetae, 18 segments; paratype NHMUK.ANEA 2019.8145: length 20.15 mm, width 6.9 mm without chaetae, 18 segments; paratype NHMUK.ANEA 2019.8147: length 13.4 mm, width 4.75 mm without chaetae, 18 segments.

**Diagnosis.** Body with 18 segments (including the tentacular segment = segment 1). Nine pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17. Prostomium very small, bilobed, no obvious notch between prostomial lobes. Large achaetous tentaculophores of segment 1 lateral to prostomium. Parapodia biramous. Notopodia short and near rectangular with acicular lobe. Notochaetae very fine and filamentous, forming “tufts”, distally with rounded tips. Distal ends of neurochaetae flattened, tapering to blunt tips with two semi-lunar pockets close to shoulder of chaetae. Prominent nephridial papillae on segments 10–12, large and rounded in females, elongated in males.

**Description.** Medium-sized species up to 20.15 mm in length and 6.9 mm width, represented by four specimens. All specimens dorsally complete with 18 segments (Figure 1A,B, Figures 3A and 4A,B). Body long and tapering posteriorly. Nine pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17, elytra mostly missing. Live specimen deep pink in colour (Figure 1A,B), preserved specimens pale yellow (Figures 3A and 4A,B). Integument dorsally covered with small tufts of papillae, best observed under SEM (Figure 5A). Prominent nephridial papillae on segments 10–12: large and rounded in females (Figures 3G and 4C) but elongated in males (Figure 4D).

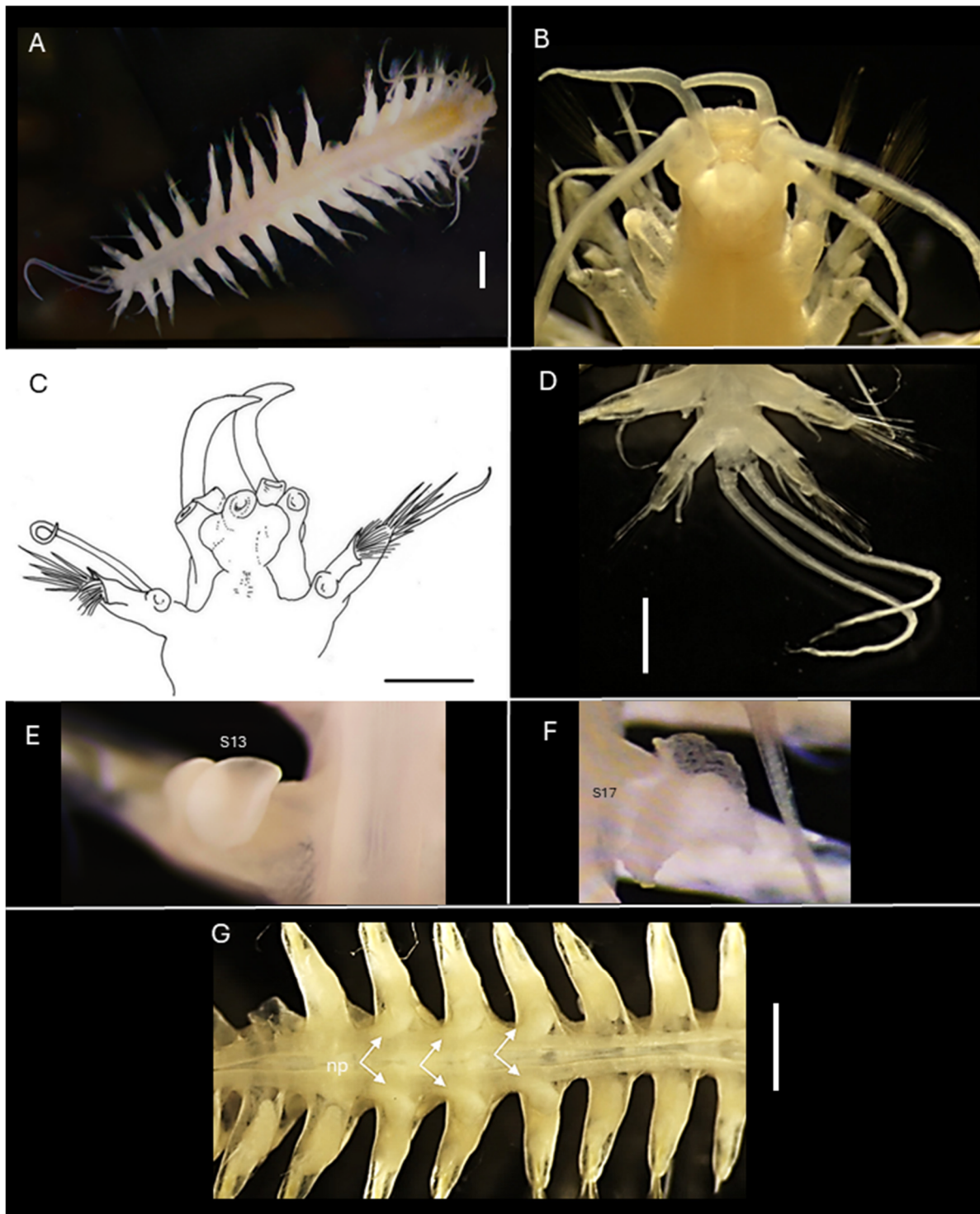
Prostomium very small, bilobed with no obvious notch present between prostomial lobes (Figure 3B,C and Figure 5A). Massive median antennophore positioned anteriorly on prostomium (Figure 3A,B and Figure 5A) with smooth style about four times the length of prostomium (Figure 5A). Large achaetous tentaculophores of segment 1 about a quarter the width of the prostomium, lateral to prostomium (Figures 3C and 5A). Tentacular cirri smooth, dorsal pair about equal to length of median antenna, ventral pair about 2/3 length of median antenna. Palps thick and smooth, tapering to fine points, about twice the length of prostomium. Lateral antennae absent. Frontal filaments absent. Eyes absent.

Bulbous elythrochlores close to proximal end of notopodia. Elytra mostly missing, when observed extremely small (Figure 3E), translucent and almost spherical, without papillae on borders, elytral surface with granular appearance (Figure 6A); irregular and textured elytra also observed even on the same specimen—segment 13 versus segment 17 (Figure 3E,F).

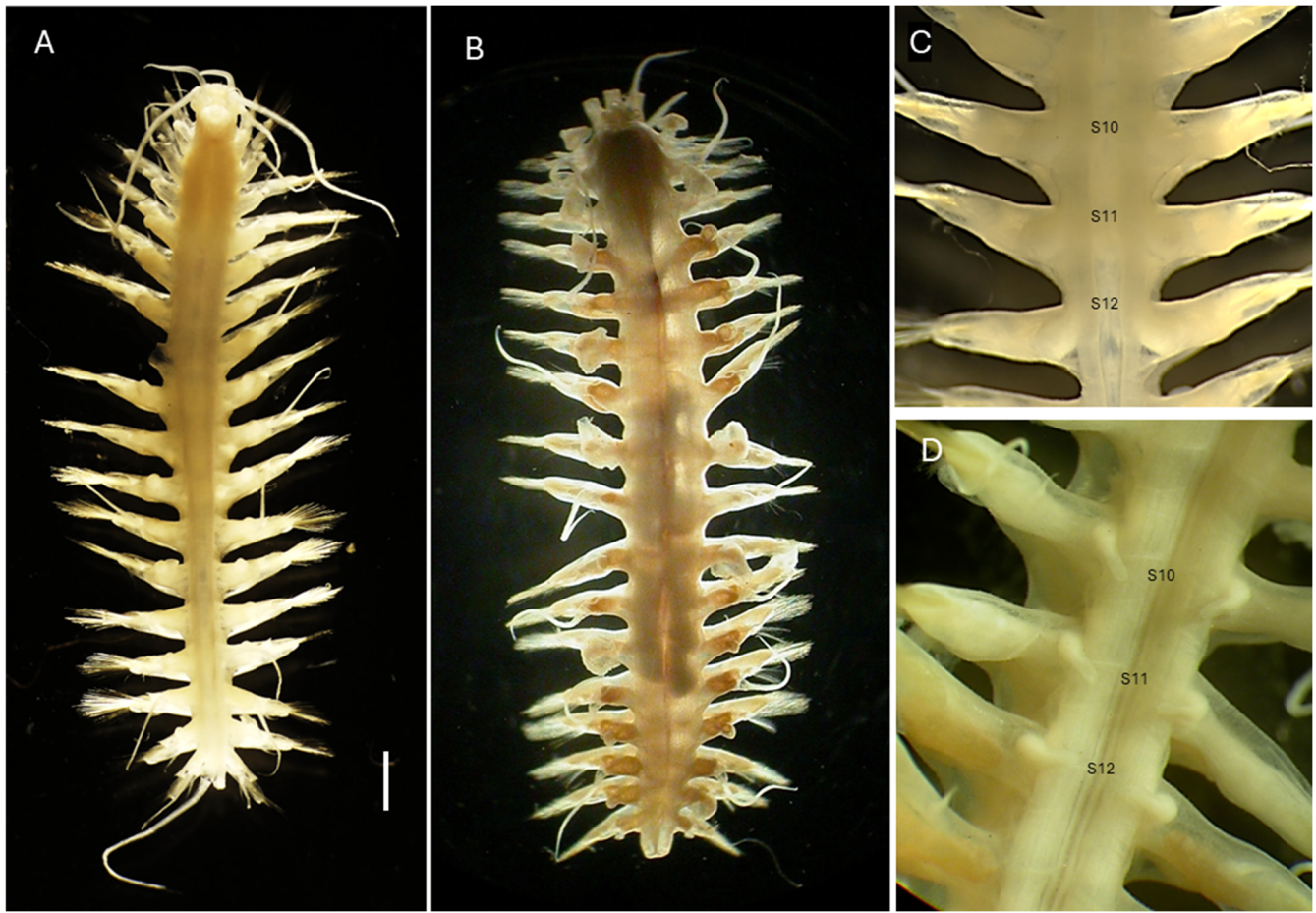
Dorsal cirrophores large, cylindrical (Figure 5B), styles smooth and tapering, extending beyond the end of neurochaetae. Dorsal tubercles not developed. Buccal cirri tapering, about twice as long as following ventral cirri and attached basally on parapodia. Ventral cirri short, tapering, inserted at mid-length of neuropodia.

Parapodia biramous (Figures 5B and 6B). Notopodia reduced, short and near rectangular with prominent prechaetal acicular lobe (Figures 5B and 6B). Notochaetae, very fine and filamentous, forming very fine ‘tufts’ (Figure 6B,D), with distinctly rounded tips (Figure 5E,F and Figure 6D). Notochaetae shorter than neurochaetae. Neuropodia, about equal length to width of body, tapering to triangular prechaetal acicular lobe (Figure 6B). Distal ends of neurochaetae flattened, tapering to blunt tips (Figure 5C,D and Figure 6C),

blades with finely serrated edge (Figure 5C,D), shaft with two semi-lunar pockets close to shoulder of chaetae (Figure 5D).



**Figure 3.** *Macellicephala irisae* sp. nov., preserved holotype NHMUK.ANEA 2019.8146, except for (C). (A) Overview of preserved specimen in dorsal view. (B) Prostomium in anterodorsal view, showing the enlarged ceratophore of median antenna, style missing. (C) Line drawing of paratype NHMUK.ANEA 2019.8147 showing detail of prostomium in dorsal view with palps, styles of median antenna and tentacular cirri missing. (D) Pygidium in ventral view with long anal cirri. (E) Small smooth elytron attached to segment 13 (S13). (F) Small shrivelled and textured elytron attached to segment 17 (S17). (G) Ventrum with enlarged round nephridial papillae on segments 10–12 (marked by arrows), female. All scale bars: 1 mm.



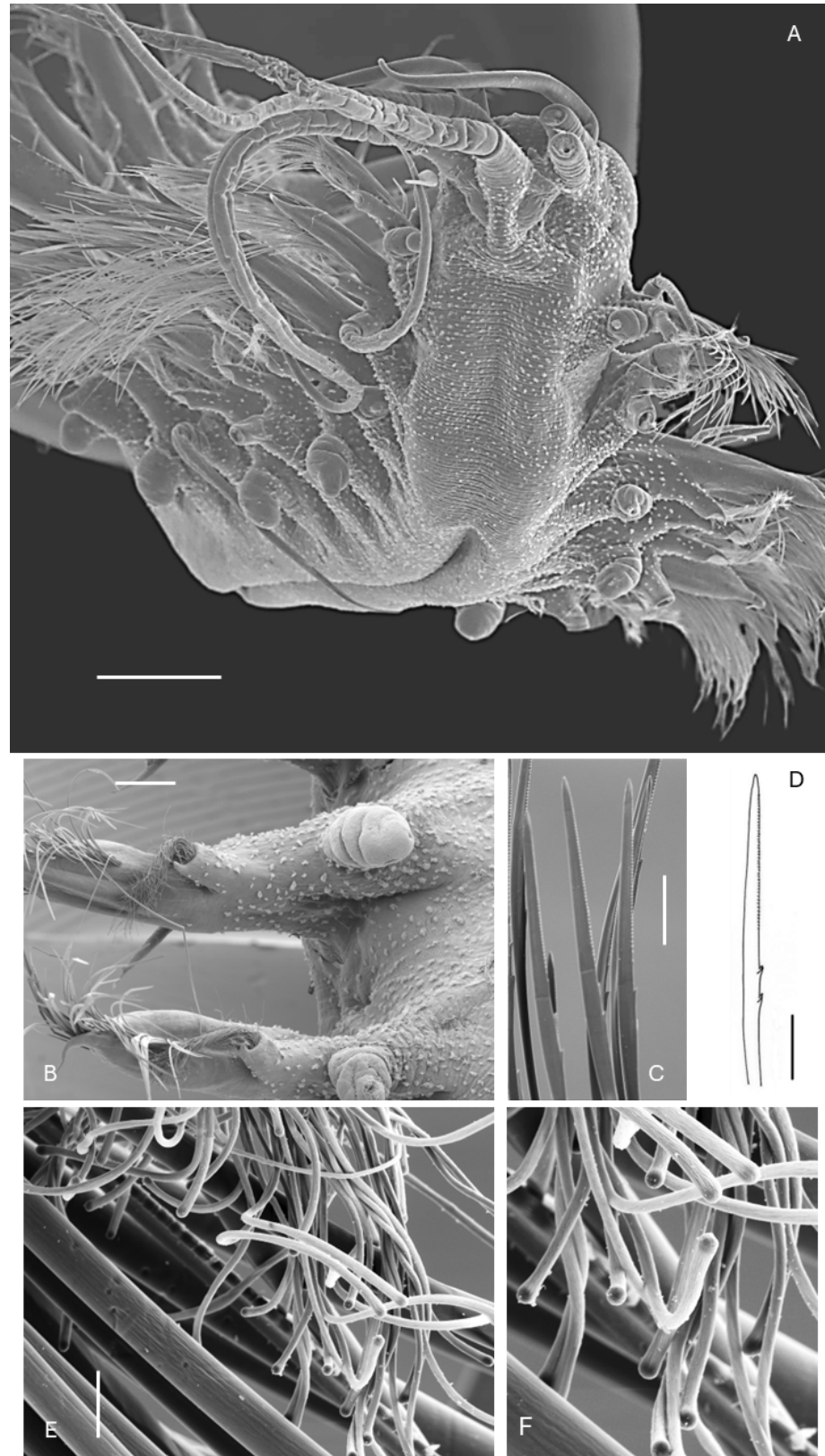
**Figure 4.** *Macellicephala irisae* sp. nov. (A) Paratype NHMUK.ANEA 2019.8147, preserved specimen in dorsal view. (B) Paratype NHMUK.ANEA 2019.8145, preserved specimen in dorsal view. (C) Rounded nephridial papillae on segments 10–12, paratype NHMUK.ANEA 2019.8147, female. (D) Elongated nephridial papillae on segments 10–12, paratype NHMUK.ANEA 2019.8145. Scale bar: 1 mm.

Pygidium distally truncated lobe (Figure 3D), enclosed by posterior segment. Anal cirri smooth, slender and very long (Figure 3A,B and Figure 4A).

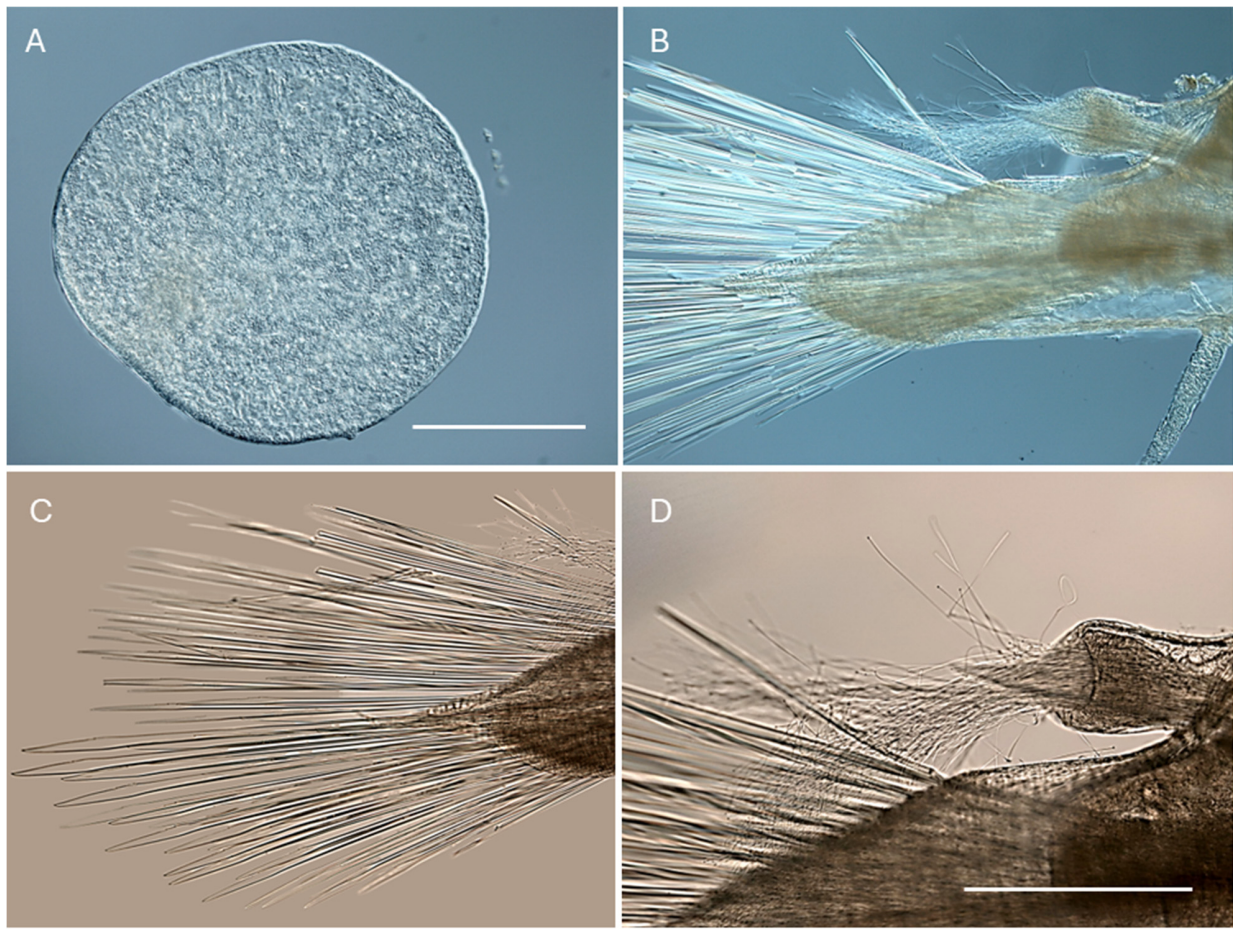
**Etymology.** The species name is dedicated to Iris Altamira to recognise her longstanding contribution to annelid taxonomy.

**Remarks.** A new species agrees well with diagnosis of *Macellicephala* in having the following characters: body with 18 segments, 9 pairs of elytra on segments 2, 4, 5, 7, 9, 11, 13, 15 and 17, prostomium bilobed, with median antenna. Segment 1 without chaetae. Segment 2 with buccal (ventral) cirri longer than following ventral cirri, attached to basal parts of parapodia lateral to mouth. Parapodia biramous, with shorter notopodia and long neuropodia, both rami with elongate acicular processes. Nephridial papillae usually largest on segments 10, 11 and 12. However we cannot comment on the morphology of proboscis, which was not everted in the new species.

The very small head, neurochaetae with semi-lunar pockets, body surface with papillae, and filamentous notochaetae differentiate the new species from all known *Macellicephala* species. Tufts of papillae covering the dorsum have not been previously reported in *Macellicephala* but given that these are best observed under SEM (Figure 5A,B), they might have been previously overlooked in other species. Similar papillae have been reported in other Macellicephalinae species, e.g., genus *Macellicephaloides* (e.g., [30]).



**Figure 5.** *Macellicephala irisae* sp. nov., SEM micrograph and line drawing of paratype NHMUK.ANEA 2026.701. (A) Anterior end in anterodorsal view showing prostomium with long median antenna and tentacular cirri (styles missing), dense papillation of the dorsum and parapodia visible. (B) Elytrogerous (top) and cirriferous parapodia. (C) Neurochaetae. (D) Detail of neurochaetae showing two semi-lunar pockets. (E) Filamentous notochaetae. (F) Rounded tips of notochaetae. Scale bars: (A) = 1 mm; (B) = 200  $\mu$ m; (C,D) = 50  $\mu$ m; (E) = 10  $\mu$ m.



**Figure 6.** *Macellicephalo irisae* sp. nov., preserved paratype NHMUK.ANEA 2026.701. (A) Smooth elytron. (B) Parapodium showing reduced notopodium with prominent acicular lobe (ac). (C) Notochaetae. (D) Slender filamentous neurochaetae. Scale bars = (A) = 500  $\mu$ m; (D) = 750  $\mu$ m.

The unique features of the new species, particularly the filamentous notochaetae, may warrant erection of a new genus. However, given the currently limited coverage within the genus *Macellicephalo* and closely related *Abyssarya* (Figure 2), we prefer to remain conservative and include the new species within genus *Macellicephalo*.

In live specimen, paratype NHMUK.ANEA 2026.701, 14 spherical eggs (diameter 340  $\mu$ m) were visible through segments 8 to 13 (Figure 1D). This species exhibits sexual dimorphism in the shape of nephridial papillae present ventrally in segments 10–12 (Figures 3G and 4C,D). As documented in other Polynoidae species (e.g., [22,45]), males show particularly enlarged and elongated nephridial papillae (Figure 4D) in comparison to females (Figure 4C).

**Genetics.** DNA from the holotype (18S, 16S, COI) and paratype (16S, COI) were recovered. Given the current taxon coverage, the new species falls into a well-supported *Macellicephalo-Abyssarya* clade in the phylogenetic analyses (Figure 2). The generic placement of the new species, as well as that of *M. clarionensis* and *Abyssarya* may be re-evaluated in the future with further taxon sampling, especially regarding the fact that DNA from the type species of the genus *Macellicephalo mirabilis* is currently not available.

**Distribution.** Known from the type locality only.

#### 4. Discussion

The scapula of the Santa Catalina whale fall in 2005 showed little evidence of microbial mats, and the associated megafauna consists mainly of suspension feeders (Figure 1C).

However, it should be noted that some cladorhizid sponges, to which the host here belongs, have been previously reported from chemoautotrophic habitats and shown to utilize both methane-oxidizing bacteria and in some cases small crustacean prey as nutrient sources [46]. Thus, this bone appears to be transitioning to the reef stage, with some vestiges of a reducing habitat potentially remaining. The whale fall reef stage is the final, and potentially longest phase of a whale carcass's persistence on the deep seafloor. It follows the mobile scavenger, enrichment, and sulphophilic stages [18], thus occurring after organic nutrients are depleted, leaving the exposed mineral remains of the bones to provide hard, reef-like substrates for sessile megafaunal suspension feeders. Such megafauna can in turn support other species, further enhancing the biodiversity of the whale fall. It is such an association between a cladorhizid sponge and *Macellicephala irisae* sp. nov. that has been observed in this study (Figure 1B). Several new species in the genera *Asbestopluma* Topsent, 1901 [47], and *Cladorhiza* Sars, 1872 [48], have been described from near the type locality reported here (see Lundsten et al. [46] for details). The cladorhizid host imaged (Figure 1C,D) here may belong to one of those species or potentially represent a new species.

Associations between polynoids and various hosts (mainly Echinodermata, Mollusca, Cnidaria, Porifera, Crustacea, and other Annelida) are well-known, with Martin & Britayev [49] reporting on multiple such associations, most of them commensal. Worms likely find shelter and food, while the hosts may benefit from cleaned surfaces or are largely unaffected. For example, the polynoid *Neopolynoe chondrocladiae* (Fauvel, 1943) [50] living inside a cladorhizid sponge has been suggested to act as a “sit-and-wait” predator, using the sponge primarily for shelter [51], whilst the polynoid *Polyeunoa laevis* McIntosh, 1885, was found to feed on soft coral [52]. Some polynoids even show a morphological adaptation to their hosts [53]. However, without any detailed or long-term observations of the polynoid–host interactions, captured only in ROV images in this study (Figure 1C,D)—we cannot provide further insights into this association. Nevertheless, this observation represents the first reported instance of an apparent symbiotic relationship within the genus *Macellicephala*, although symbiosis has been reported in the closely related genus *Abyssarya* [25].

The unusually thin, soft, thread-like notochaetae—a unique feature of *Macellicephala irisae* sp. nov.—are unlikely to aid in locomotion nor do they harbour bacteria associated with the sulphophilic stage. Chaetae that have been previously suggested to aid in host attachment are usually distinctly stout and hooked, as in *Abyssarya acus* (reported in Bonifácio & Menot [25]) or *Uncopolynoe corallicola* (reported in Wehe [54]). On the other hand, the lunar pockets observed here on the shafts on neurochaetae could provide an attachment function (Figure 5C,D). Similar pockets have been previously reported in symbiotic polynoid genera such as *Paradyte*, *Adyte* and *Subadyte* [55,56], although their function remains unknown.

## 5. Conclusions

A new species has been identified within the genus *Macellicephala*, characterized by unique features including filamentous notochaetae, neurochaetae with semi-lunar pockets, a particularly small head, and papillae on the dorsum. These characters may suggest a future re-evaluation of its taxonomic classification, though it is currently retained in *Macellicephala* due to insufficient molecular coverage of related taxa. Ecologically, associations between *Macellicephala* and cladorhizid sponge growing on the whale scapula have been observed at the Santa Catalina whale fall site. This indicates that at least some bones of this whale fall site were transitioning to reef stage after more than 50 years on the seabed, supporting novel biodiversity.

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