Zootaxa 4652 (2): 265–295
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4652.2.3
http://zoobank.org/urn:lsid:zoobank.org:pub:C90037B7-82AA-4C80-8860-3D75D90A2F98

Description of a new *Moridilla* species from North Sulawesi, Indonesia (Mollusca: Nudibranchia: Aeolidioidea)—based on MicroCT, histological and molecular analyses

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Abstract

We describe a new species, *Moridilla jobeli* **sp. nov.**, belonging to the marine heterobranch group Aeolidioidea. Up to now, it is only recorded from Bunaken National Park, North Sulawesi, Indonesia. A combination of histological, computer tomographic and scanning electron microscopic methods was applied in order to describe and illustrate the anatomy of *Moridilla jobeli* **sp. nov.** in detail. Furthermore, we conducted molecular analyses which include available partial COI and 16S rRNA sequences, as well as the nuclear gene Histone 3 (H3) of Facelinidae and Aeolidiidae. NeighborNet analyses, species delimitation tests and phylogenetic reconstruction methods show the distinctiveness of the new species from the type species *Moridilla brockii* Bergh, 1888 and the two recently described species *Moridilla fifo* Carmona & Wilson, 2018 and *Moridilla hermanita* Carmona & Wilson, 2018, as well as the monophyly of the genus. A phylogenetic analysis of the Facelinidae and Aeolidiidae does not result in a resolved tree, therefore relationship of former assumed closely related genera, *Noumeaella* Risbec, 1937 and *Palisa* Edmunds, 1964, cannot be discussed in detail.

Abstrak

Kami mendeskripsikan spesies baru, *Moridilla jobeli* **sp. nov.**, dari taxon Aeolidioidea, dikumpulkan di Sulawesi Utara, Indonesia, dengan menerapkan metode histologis, tomografi komputer dan metode scanning electron microscopic, untuk menganalisis anatominya secara rinci. Selanjutnya analisis molekuler dilakukan dengan memasukkan sekuens yang tersedia dari COI parsial, 16S rRNA, parsial dan Histone 3 (H3) dari Facelinidae dan Aeolidiidae. Analisis NeighborNet, tes delimitasi spesies dan metode rekonstruksi filogenetik menunjukkan kekhasan spesies baru dari jenis spesies *Moridilla brockii* Bergh, 1888 dan dua spesies *Moridilla fifo* Carmona & Wilson, 2018 dan *Moridilla hermanita* Carmona & Wilson, 2018, yang baru-baru ini dijelaskan, serta monophyly dari genus. Analisis filogenetik dari Facelinidae dan Aeolidiidae tidak menghasilkan pohon yang terselesaikan, oleh karena itu hubungan keduanya yang diasumsikan terkait erat dengan genera *Noumeaella* Risbec, 1937 dan *Palisa* Edmunds, 1964, tidak dapat dibahas secara rinci.

Key words: Facelinidae, Aeolidiidae, *Noumeaella*, *Palisa,* systematics, species delimitation, integrative taxonomy

Accepted by V. Padula: 24 Jun. 2019; published: 8 Aug. 2019

Introduction

During various species diversity studies in Bunaken National Park, North Sulawesi, Indonesia (Eisenbarth *et al.* 2018; Kaligis *et al.* 2018), four undescribed species of *Noumeaella* Risbec, 1937 were recorded. Edmunds (1970) postulated a close relationship between *Noumeaella*, *Palisa* Edmunds, 1964 and *Moridilla* Bergh, 1888, based on similarities of rhinophores, foot tentacles, cerata shape and radula morphology. Thus, assignment of new detected species to one of these genera is difficult without a thorough morphological analysis applying all state of the art techniques like histological studies or micro-computed tomography. Additionally, the relationship of these three genera within the Facelinidae was not thoroughly analysed by any morphological or molecular phylogenetic studies. Latest molecular studies render Facelinidae paraphyletic (Carmona *et al.* 2013; Mahguib & Valdés 2015; Goodheart *et al.* 2015; Goodheart 2017; Goodheart *et al.* 2018; Martynov *et al.* 2019) and even contradict a close relationship of these genera. *Palisa* groups with some facelinid taxa, whereas *Noumeaella* groups with other facelinids as sister taxon to Aeolidiidae. *Moridilla brockii* (included only in one study on Aeolidiidae) clusters with facelinid species but not with *Noumeaella* (Carmona *et al.* 2013). In the available genomic studies (Goodheart 2017; Goodheart *et al.* 2017, 2018; Martynov *et al.* 2019) *Moridilla* was not included; however, *Palisa* groups with genera that also show a closer relationship to *Moridilla* (see Carmona *et al.* 2013) than to *Noumeaella*. The description of the monotypic genus *Moridilla* with *Moridilla brockii* was based on a single individual from Pulau Dapur, Java, Indonesia (Bergh 1888). Various records throughout the Indo-Pacific seem to confirm a wide spread distribution of this species. Recent morphological descriptions of two further species from Papua New Guinea and Northern Australia (Carmona & Wilson 2018) increase information on this genus, however data given for some characters are insufficient.

A barcoding approach of the Bunaken material from the studies of Eisenbarth *et al.* (2018) and Kaligis *et al.* (2018) revealed that two of the therein mentioned *Noumeaella* species actually group with the genus *Moridilla.* This corroborates the difficulty in assigning specimens correctly to the genera mentioned. Here we want to clarify and support the affiliation of one of these new species, *Moridilla jobeli* **sp. nov.**, to other described *Moridilla* species and demarcate this new species from other similar looking *Moridilla* and *Noumeaella* species. We also address the phylogenetic relationship of these two genera within the Facelinidae by a first molecular phylogenetic approach of this taxon and discuss the current systematic situation.

Material and methods

Taxon sampling. Specimens were collected in Bunaken National Park (BNP), North Sulawesi, Indonesia during 2015-2016 by scuba diving (Figure 1, Table 1). For details see Eisenbarth *et al.* (2018). One further specimen from Bangka Island, North Sulawesi, Indonesia, collected in 2017, was also included in the analysis, as it looks similar to the new species. All individuals were sampled between 4 to 12 m water depths from various substrates such as *Caulerpa racemosa*, coral rubble and sponges. No association to any specific hydrozoan substrate was observed. Specimens were photographed alive and subsequently transferred to 96% ethanol or preserved in formaldehyde/seawater (1:5), after removing a small piece for barcoding. Detailed information on specimens with our internal identifiers and museum numbers will be available in Diversity Workbench (Triebel *et al.* 2018) within the module Diversity Collection. Type material is stored in the Museum Zoologicum Bogoriense in Bogor, Java, Indonesia (MZB.Gst.21.592; MZB.Gst.21.593) and Sam Ratulangi University, Manado, North Sulawesi, Indonesia (SRU20190001). All further material is stored at Sam Ratulangi University collection. For specific numbers see Table 1.

Morphological investigation. One specimen (SRU20190001, 15 mm) was embedded in hydroxyethyl methacrylate for serial sectioning (2.5 µm) (Kulzer ®7100). Sections were stained with toluidine blue and investigated under an Olympus microscope (CX41). Regions of special interest were photographed with an Olympus DP22 and analysed with the accompanying software cellSensV1.15, or a ZEISS AXIO, Imager.Z2M with ZEISS AxioCam HRc and the software AxioVision, Release 4.8.1 (11-2009). For MicroCT analyses, one paratype (MZB.Gst.21.593) was stained with a 1% iodo-potassium iodide solution (lugolian solution), then critically point dried with the automated critical-point-dryer Leica EM CPD300 and scanned with a SkyScan1272 -CT scanner with the following parameters: source voltage: 26kV, source current: 197 µA, exposure time: 900 ms, rotation steps: 0.1 over 360, frame averaging: 8, random movement: 15, 3 horizontal scans combined, image pixel size: 2,999 µm. Reconstructed images were imported into Thermofisher Amira 6.5.0 to segment individual structures. The arithmetic function was used to separate the individual materials and subsequently exported as .tif stacks. Volume rendering was performed with Volume Graphics VGStudio Max 3.2.

Following the CT-scan, this specimen (MZB.Gst.21.593) was rehydrated, radula and jaws removed and used for scanning electron microscopy with a ZEISS SIGMA 300 VP and SmartSEM vers. 5.09. Jaws were also investigated under the light microscope.

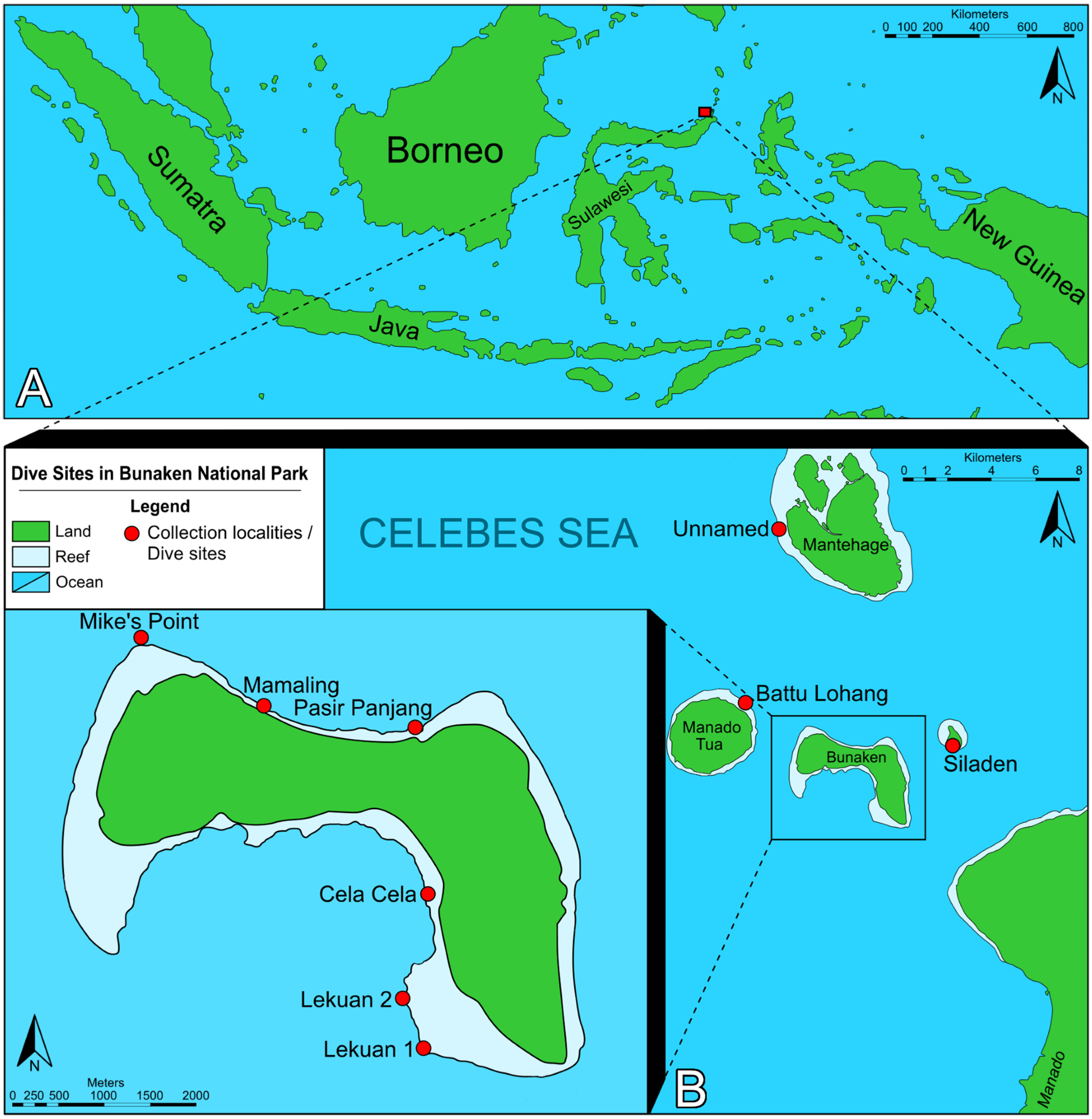

FIGURE 1. Location of study area: (A) Indonesia and Sulawesi with dashed lines indicating close-up area in B. (B) Localities (red dots) in Bunaken National Park (BNP).

Molecular analyses. Mitochondrial cytochrome c oxidase subunit I (COI) and 16S rRNA were sequenced for 12 *Moridilla* specimens and seven specimens belonging to Facelinidae (Table 1). Based on the results of Korshunova *et al.* (2017) and Goodheart *et al.* (2018) with regard to paraphyly of Facelinidae and outgroup results, we retrieved all available sequences of Facelinidae and Aeolidiidae from GenBank. According to the published phylogenetic analyses we chose available sequences of *Unidentia* and some Flabellinoidea as outgroup. Accession numbers of all used sequences are listed in Table 2. Additionally we run an analysis including more cladobranch members. Details are provided in Supplementary Table 1.

DNA-Isolation has been carried out by means of QIAGEN® DNeasy Blood and Tissue-Kit, following manufacturer's instructions. Partial sequences of mitochondrial COI (ca. 680bp) and ribosomal 16S (ca. 450bp) were amplified by polymerase chain reaction (PCR) using the primers LCO1490-JJ (5' –CHACWAAYCATAAAGATATYGG-3') and HCO2198-JJ (5'-AWACTTCVGGRTGVCCAAARAATCA-3') (Astrin & Stüben 2008) for COI; 16Sar-L (5′ -CGCCTGTTTATCAAAAACAT-3') and 16Sbr-H (5′- CCGGTCTGAACTCAGATCACGT-3') (Palumbi *et al.* 2002) for 16S. The amplification of COI was carried out by denaturation for 15 min at 95 °C, followed by 15 touchdown cycles [94 °C for 35 s, 55 °C (-1 per cycle) for 90 s, 72 °C for 90 s] along with 25 standard cycles (94 °C for 35 s, 40 °C for 90 s, and 72 °C for 90 s), with a final extension of 10 min at 72 °C. Amplification of partial 16S was performed by denaturation for 15 min at 95 °C, followed by nine touchdown cycles [94 °C for 45 s, 56 °C (−1 °C per cycle) for 45 s, 72 °C for 90 s] along with 25 standard cycles (94 °C for 90 s, 48 °C for 90 s, and 72 °C for 90 s), with a final extension of 10 min at 72 °C. PCR products were sequenced by Macrogen Europe (Netherlands).

Alignments were obtained using the web server of MAFFT (Kuraku *et al.* 2013) in default settings with the progressive method G-INS-1. Two alignments were used for this study: 1) The full data set, based on nuclear gene H3 and mitochondrial genes 16S and COI, comprises sequences of 151 specimen including all available Facelinidae and Aeolidiidae sequences from NCBI and new sequences, with a length of the concatenated alignment of 1480 positions (H3 positions 1-327, 16S rRNA positions 328-822, COI positions 823-1480); 2) The reduced data set comprises sequences of 35 specimens, and includes only sequences of *Moridilla*, *Noumeaella* and *Palisa,* and the outgroups mentioned above, in a concatenated data set of COI and 16S (COI positions 1– 658, 16S rRNA positions 659–1118). Maximum Likelihood (ML) analyses of all analyses were performed using RAxML v0.6.0 BlackBox (Kozlov *et al.* 2018) with default settings and automatic bootstopping.

The reduced data set, which includes only the three genera, was used for detailed delimitation analyses to evaluate distinctiveness of the three genera and *Moridilla* species: Distance analysis was performed in BioEdit Vers. 7.2.5 (Hall 1999), NeighborNet analysis were carried out by using SplitsTree 4.14.3 (Huson & Bryant 2006). Species delimitation tests were conducted in the graphic ABGD web version (Puillandre *et al.* 2012) for COI, and the bPTP web server (Zhang *et al.* 2013) for COI and16S. Species delimitation tests were performed in default settings.

Results

Systematics

Nudibranchia Cuvier, 1817

Cladobranchia Willan & Morton, 1984

Family Facelinidae Bergh, 1889

Genus *Moridilla* Bergh, 1888

Type species. *Moridilla brockii* Bergh, 1888

Diagnosis. The genus *Moridilla* is characterized by the following features: Body elongate, slender, tapering at posterior end of foot. Foot narrow; foot corners tentacular elongated. Rhinophores side by side, papillate. Tentacles elongate. Anterior cerata in slanted rows with innermost dorsal cerata unique in shape, significantly elongated, in coiled position, differently coloured; get fully extended in length and waved about forcefully when animal feels threatened. Jaw medium sized, masticatory border strong, slightly curved with single row of denticles. Radula uniseriate. Penis unarmed. Semi-serial receptaculum seminis (Bergh 1888; Edmunds 1970).

Moridilla jobeli **sp. nov. Schillo & Wägele**
(Figures 2–10)

Type material. Holotype: Museum Zoologicum Bogoriense, Bogor, Java, Indonesia: MZB.Gst.21.592; collected 20th October 2016 by Jobel Dialao; Cela cela, Bunaken, BNP, North Sulawesi, Indonesia, 1°36'42.4''N, 124°46'04.7''E; depth 9.2m; length 20 mm; tail used for barcoding (GenBank No. MK514311, MK478682).

Paratypes: Museum Zoologicum Bogoriense, Bogor, Java, Indonesia: MZB.Gst.21.593; collected 20th October 2016 by Jobel Dialao; Cela cela, Bunaken, BNP, North Sulawesi, Indonesia, 1°36'42.4''N, 124°46'04.7''E; depth 9.2m; one specimen, length 35 mm; tail used for barcoding (GenBank No. MK514312). Collection of Sam Ratulangi University, Manado, North Sulawesi, Indonesia: SRU20190001; collected 19th August 2015 by Jobel Dialao; Cela cela, Bunaken, BNP, North Sulawesi, Indonesia, 1°36'42.4''N, 124°46'04.7''E; depth 7m; one specimen, length 15 mm, used for serial sectioning.

Additional material, see Table 1. All further material is deposited in the collection of Sam Ratulangi University, Manado, Indonesia.

Type locality and live observation. Only recorded from several localities in Bunaken National Park, North Sulawesi, Indonesia (Figure 1, Table 1). When disturbed, animals started to swim with lateral movements to avoid disturbance and inner cerata are forcefully extended, as typical for the genus.

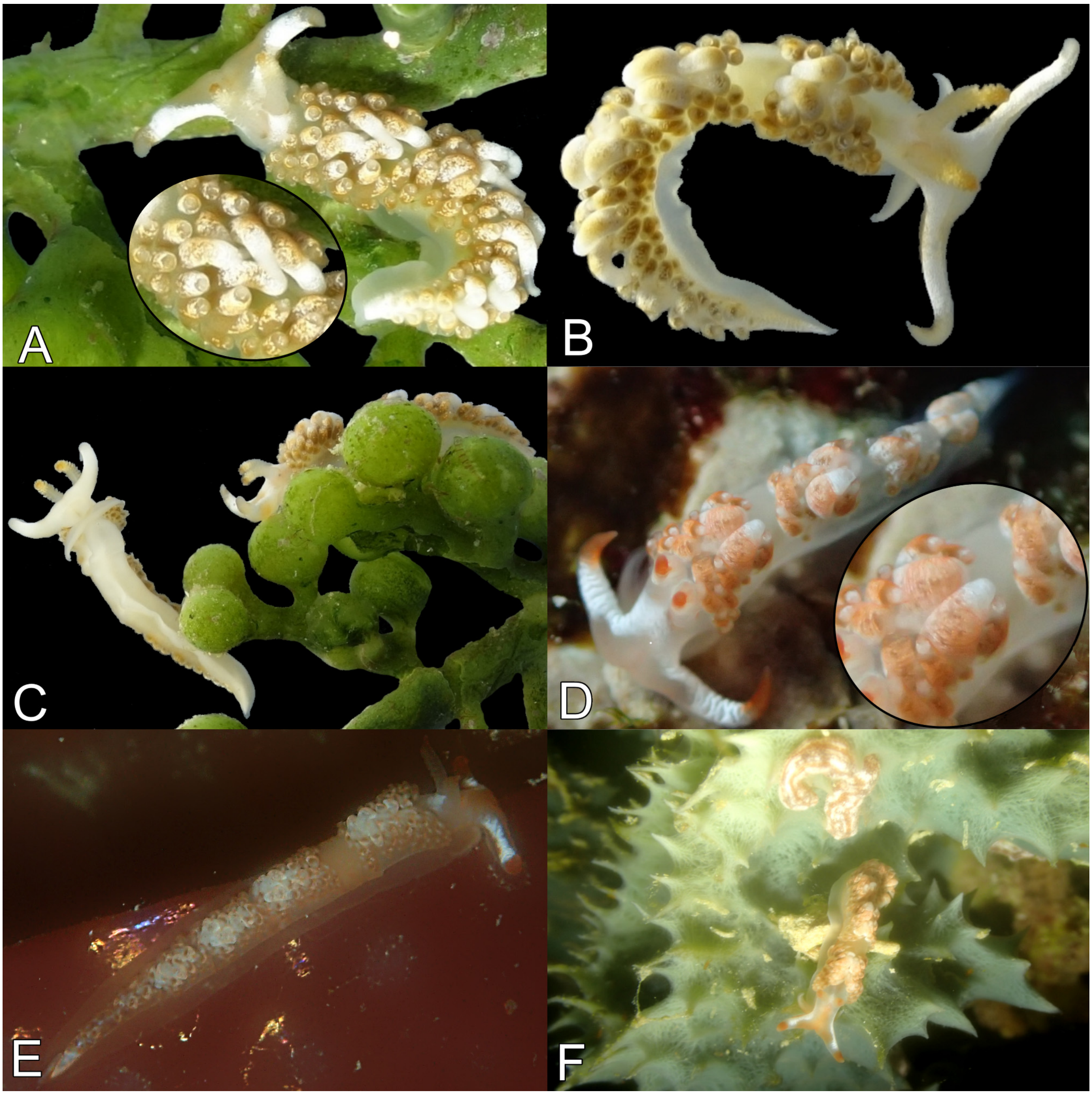

FIGURE 2. *Moridilla jobeli* **sp. nov**.: Living animals. (A) SRU2015/01/Nosp2-15Bu-2 on *Caulerpa racemosa*, with close-up of cerata. (B) Paratype SRU20190001. (C) Paratype SRU20190001ventral view, SRU2015/01/Nosp2-15Bu-2 lateral view on original substrate *Caulerpa racemosa*. (D) SRU2016/02/Nosp2-16Bu-1 in situ, with close-up of cerata. (E) SRU2016/02/Nosp2-16Bu-5 crawling on sponge. (F) Holotype MZB.Gst.21.592 in situ on sponge.

TABLE 1. Specimens collected in North Sulawesi, Indonesia used for this study. Species names, locality, date of collection, size of specimen, fixation, type of investigation, voucher numbers and GenBank accession numbers are presented (FSW: formaldehyde/seawater; EtOH: ethanol).

Species	Locality	**Date of collection**	**Size of living animal**	**Fixation**	**Type of investigation**	**Voucher No.**	**GenBank COI**	GenBank 16S
Moridilla jobeli **sp. nov. Holotype**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	20.Oct.2016	20 mm	FSW and EtOH	barcodes	**MZB.Gst.21.592**	MK514311	MK478682
Moridilla jobeli **sp. nov. First paratype**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	20.Oct.2016	35 mm	FSW and EtOH	μ-CT, preparation of radula and jaw, barcodes,	**MZB.Gst.21.593**	MK514312	-
Moridilla jobeli **sp. nov. Second paratype**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	19.Aug.2015	15 mm	FSW	histology (serial section-ing)	**SRU20190001**	-	-
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	19.Aug.2015	15 mm	EtOH	barcodes	SRU2015/01/ Nosp2-15Bu-2	MK514313	MK478683
Moridilla jobeli **sp. nov.**	Bunaken, Mamaling, 1°37'50.6''N, 124°45'48.0''E	21.Aug.2015	12 mm	EtOH	barcodes	SRU2015/01/ Nosp2-15Bu-3	MK514314	MK478684
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	25. Aug.2015	60 mm	FSW	barcodes	SRU2015/01/ Nosp2-15Bu-4	MK514315	MK478685
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	25. Aug.2015	25 mm	EtOH	barcodes	SRU2015/01/ Nosp2-15Bu-5	MK514316	MK478686
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	25. Aug.2015	30 mm	EtOH	barcodes	SRU2015/01/ Nosp2-15Bu-6	MK514317	MK478687
Moridilla jobeli **sp. nov.**	Bunaken, Mikes Point, 1°38'12.6''N, 124°44'23.0''E	28. Aug.2015	18 mm	EtOH	barcodes	SRU2015/01/ Nosp2-15Bu-7	MK514318	MK478688
Moridilla jobeli **sp. nov.**	Bunaken, Lekuan 2, 1°36'04.4''N, 124°45'54.4''E	20.Oct.2016	14 mm	EtOH	barcodes	SRU2016/02/ Nosp2-16Bu-1	MK514319	MK478689
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	22. Oct.2016	40 mm	EtOH	barcodes	SRU2016/02/ Nosp2-16Bu-5	MK514320	MK478690
Moridilla jobeli **sp. nov.**	Bunaken, Cela cela, 1°36'42.4''N, 124°46'04.7''E	23. Oct.2016	12 mm	FSW and EtOH	μ-CT, barcodes	SRU2016/02/ Nosp2-16Bu-6	MK514321	MK478691
Moridilla sp.	Bangka, Tanjung Husi, 1°44'07.7''N, 125°09'05.6''E	25.Sep.2017	12 mm	EtOH	barcodes	SRU2017/01/ Nosp1-17Ba-1	MK514322	MK478692
Caloria indica (Bergh, 1896)	Siladen, 1°37'35.7''N, 124°48'03.6''E	18. Aug.2015		EtOH	barcodes	SRU2015/01/ Cain-15Bu-5	MK514323	MK478693
Caloria sp.	Bunaken, Pasir Panjang, 1°37'41.7''N, 124°45'57.0''E	16. Aug.2015		EtOH	barcodes	SRU2015/01/ Casp-15Bu-1	MK514324	MK478694
Cratena sp.	Mantehage, Unnamed, 1°43'11.7''N, 124°43'33.7''E	24. Oct.2016		EtOH	barcodes	SRU2016/02/ Crsp5-16Bu-1	MK514325	MK478695

......*continued on the next page*

TABLE 1. (Continued)

Species	Locality	**Date of collection**	**Size of living animal**	**Fixation**	**Type of investigation**	**Voucher No.**	**GenBank COI**	GenBank 16S
Facelina sp.	Mantehage, Unnamed, 1°43'11.7''N, 124°43'33.7''E	24. Oct.2016		EtOH	barcodes	SRU2016/02/ Fasp3-16Bu-4	MK514326	MK478696
Facelina sp.	Bunaken, Mikes Point, 1°38'12.6''N, 124°44'23.0''E	23. Oct.2016		EtOH	barcodes	SRU2016/02/ Fasp8-16Bu-1	MK514327	MK478697
Favorinus sp.	Manado Tua, Battu lohang, 1°38'46.1''N, 124°42'48.0''E	24.Aug.2015		EtOH	barcodes	SRU2015/01/ Fasp-15Bu-1	MK514328	MK478698
Favorinus sp.	Bunaken, Lekuan 1, 1°35'46.4''N, 124°46'03.4''E	06.Sep.2017		EtOH	barcodes	SRU2017/02/ Fasp-17Bu-1	MK514329	-

Etymology. This species is dedicated to Jobel Dialao, Bunaken Island, whose outstanding skills and dedication in finding and collecting marine heterobranchs are honoured here.

External morphology and colour (Figures 2A–F**)**. Length of living specimens up to 60 mm; body elongate and slender, tail pointed. Rhinophores smooth anteriorly, with dense papillae only in posterior part. Oral tentacles twice the length of rhinophores (Figure 2B); propodial tentacles of similar length as rhinophores, with tips recurved and pointed (Figure 2C). Cerata arranged in indistinct 4–6 clusters, with the first right and left cluster separated from the hind groups by the elevated pericardial area (Figures 2B, D). Cluster in the hind part distinguishable mainly by the large inner cerata leaving a bare mid-dorsal zone, whereas small outer cerata arranged in one to two irregular lines (Figure 2B). Cerata curved inwardly. No distinct notum border present. Foot slightly wider than body when crawling on substrate. Genital openings behind first cerata cluster, followed closely by the nephropore. Anus situated between the second and third cerata cluster.

General colouration of the specimens varying from pale to more intense orange (Figures 2A–F). Notum, foot and foot tentacles translucent-opaque, only in few specimens with a tinge of darker cream or orange colouration at the dorsum; head usually translucent, in few specimens darker in colouration (cream to orange). Tips of rhinophores cream coloured to light brownish or orange, but base never with coloration. White patch behind rhinophores, sometimes continuing anteriorly between rhinophores. First two thirds of oral tentacles with white pigmentation at least in the posterior part; towards tips cream, brownish or orange coloured. Longest inner cerata white with light brownish or orange colouration at the base, tips always translucent; smaller cerata with less white pigmentation than longest cerata. Tail dorsally with white pigment.

Anatomy and histology

(Figures 3–10, Suppl. Videos, Suppl. Fig. 1).

Two specimens, one juvenile (histology; paratype SRU20190001), one adult (μ-CT; paratype MZB.Gst.21.593**)** were investigated (see Table 1). The first supplementary video shows a 3D reconstruction of μ-CT scans of *Moridilla jobeli* **sp. nov. (**paratype MZB.Gst.21.593). Some organs are displayed in diverse colours. The second supplementary video shows a series of μ-CT scans of cross sections through M*oridilla jobeli* **sp. nov. (**paratype MZB.Gst.21.593) from posterior to anterior. The Supplementary Figure 1 gives an overview of the positions of organs in μ-CT scans of longitudinal sections of the animal.

Digestive tract (schematic outline in Figure 3A, μ-CT reconstructions in Figures 4A–D). Mouth opening surrounded by thick specialized vacuolated epithelium (Figure 5A); leading into very short oral tube, surrounded by transversal muscle layer; epithelium consisting of specialized vacuolated cells, strongly ciliated; no mucus cells interspersed. Muscular pharynx medium sized, bulbous (Figure 4B); cuticle lining of smooth labial disc and pharyngeal lumen less cuticularized than jaws and radula (staining rose coloured and not greenish) (Figure 5B). Jaw plates aliform (Figures 4C, 5B); masticatory border with one row of 6–7 prominent denticles (Figures 6A, B). Radula formula 20 x 0.1.0 (Figure 7A). Main denticle of triangular rachidian teeth flanked by two smaller denticles on both sides throughout complete length of radula (Figures 7A–D), except of one tooth with three denticles on one side (Figure 7D).

Salivary glands highly branched, reaching into base of anterior left and right cerata group; composed of many narrow tube like structures uniting into a long single duct leading into pharynx (Figures 3A, 4A, D); glandular tubes of salivary gland composed of violet stained cells surrounding a small central lumen (Figure 5C); tube leading into pharynx and composed of very small cuboidal non-glandular cells with ciliated cells interspersed. Oesophagus very short, still lined with cuticle (Figure 5D). Stomach large (Figures 3A, 4B, D); epithelium of stomach composed of specialized vacuolated cells and ciliated cells (Figures 5E, F). Right and left anterior digestive gland ducts opening next to each other into frontal part of stomach (Figures 4B, 5F); posterior left duct starting in posterior part of stomach and running dorsally towards posterior end of body; composed of small specialized vacuolated cells surrounding a tiny lumen. Digestive gland ducts leading to cerata; composed of thin branches (Figures 4B, D) with small specialized vacuolated cells; digestive gland in cerata highly folded with glandular and enzyme producing cells interspersed by ciliated cells (Figure 8A). Cnidosacs elongate, sometimes as a winding long tube; surrounded by longitudinal and circular muscles (Figure 8B). Epithelium of cnidosacs composed of large cells with huge vacuole usually with one cnidocyst; transitions from digestive gland to cnidosac sometimes long, surrounded by same type of muscle fibres as cnidosac; with ciliated cells (Figure 8B). Transition from stomach into intestine situated in anterior part of stomach, slightly towards left side (Figure 3A). Folded epithelium consisting of cuboidal specialized vacuolated cells with large basal nuclei and long cilia; typhlosole in first third of intestine (Figure 8C). Anus opening in a small papilla on right side of body (Figures 4D, 8D).

Reproductive system (schematic outline in Figure 3B, µ-CT reconstruction in Figures 4A, C). Reproductive system androdiaulic. Specimen prepared for histology in male phase. Gonad lying mainly ventrally, reaching anterior of stomach and digestive gland; composed of many densely lying follicles with spermatogonians (Figure 9A). Adult specimen with large gonad also lying ventrally to digestive gland branch, with large blossom like follicles filled with sperm and peripheral lying oogonia (Figure 9B). Short hermaphroditic duct leading to ampulla, epithelium of the duct consisting of cuboidal cells with long cilia and big nuclei. Tube-like winding ampulla situated above and partly within female glands; surrounded by thick muscular layer and packed inside with irregular arranged autosperms; epithelium with ciliated cuboidal to disc shaped cells (Figure 9C). Proximal vas deferens ciliated with prismatic cells and basal nuclei. Vas deferens continuing in prostatic part (Figure 9D); epithelium comprising of alternating ciliated and glandular cells. Unarmed penis located within muscular and highly ciliated penial sheath; opening in atrium together with nidamental glands (Figures 3B, 4D). Receptaculum seminis opening in proximal oviduct (Figure 3B); epithelium highly folded, with cuboidal, spongy cells and apical cilia; surrounded by muscular layer. Lumen of receptacle in the histologically investigated juvenile animal empty (Figure 9E), but filled with sperms in the specimen investigated by µ-CT. Proximal oviduct composed of cylindrical cells with big nuclei. Nidamental glands of histologically investigated animal in immature condition showing sections with smaller and larger coils (Figure 9F); mucus cells in all sections alternating with ciliated cells. Only very little mucus formation was observed (Figure 9F). Adult specimen with highly folded nidamental glands (Figures 4C, D). Atrium opening laterally on right side, in front of anal opening; epithelium consisting of ciliated, cylindrical cells with large nuclei and few mucus cells with violet granules interspersed.

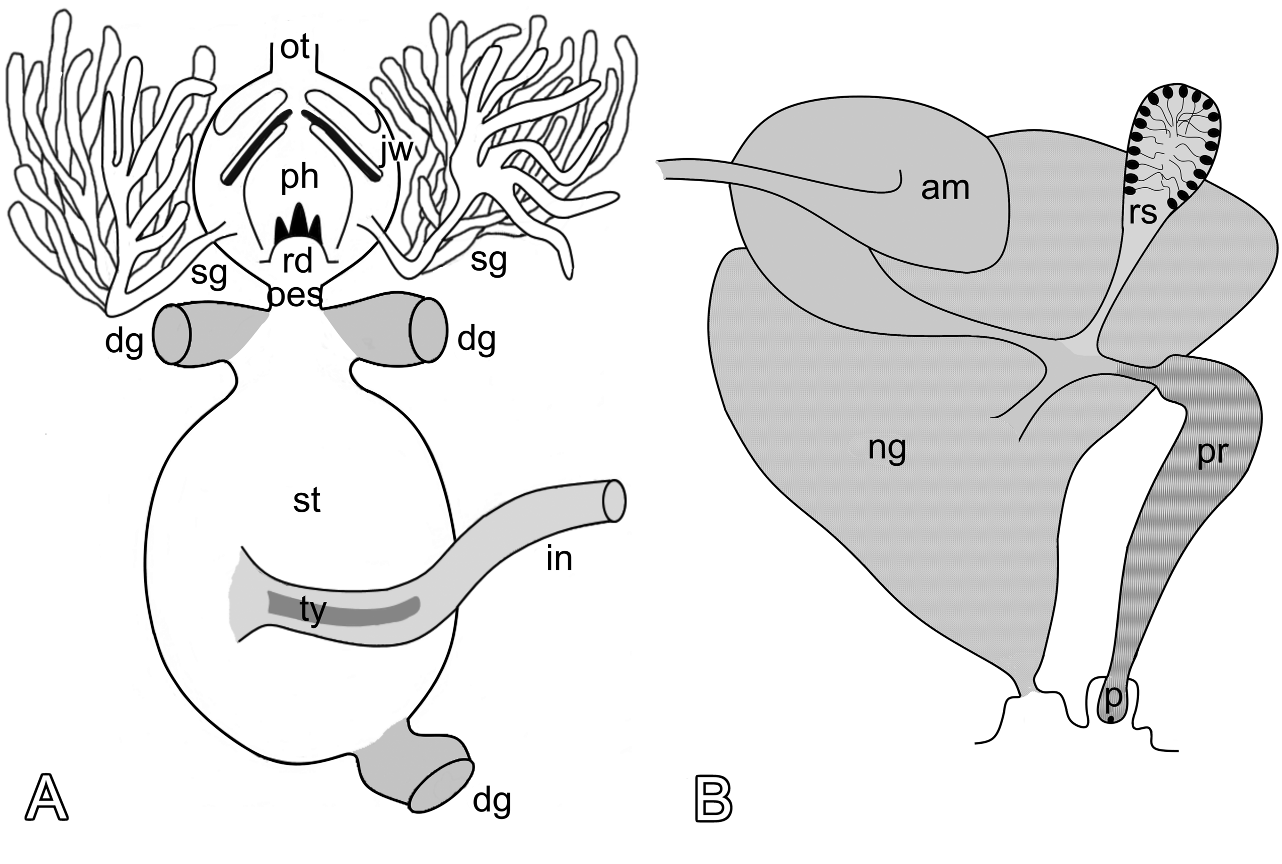

FIGURE 3. *Moridilla jobeli* **sp. nov.**: Schematics based on paratypes MZB.Gst.21.593 and SRU20190001. (A) Digestive system. (B) Genital system. Abbrevations: am, ampulla; dg, digestive gland; oes, oesophagus; in, intestine; jw, jaw; ng, nidamental gland; ot, oral tube; p, penis; ph, pharynx; pr, prostate; rd, radula; rs, receptaculum seminis; sg, salivary gland; st, stomach; ty, typhlosole.

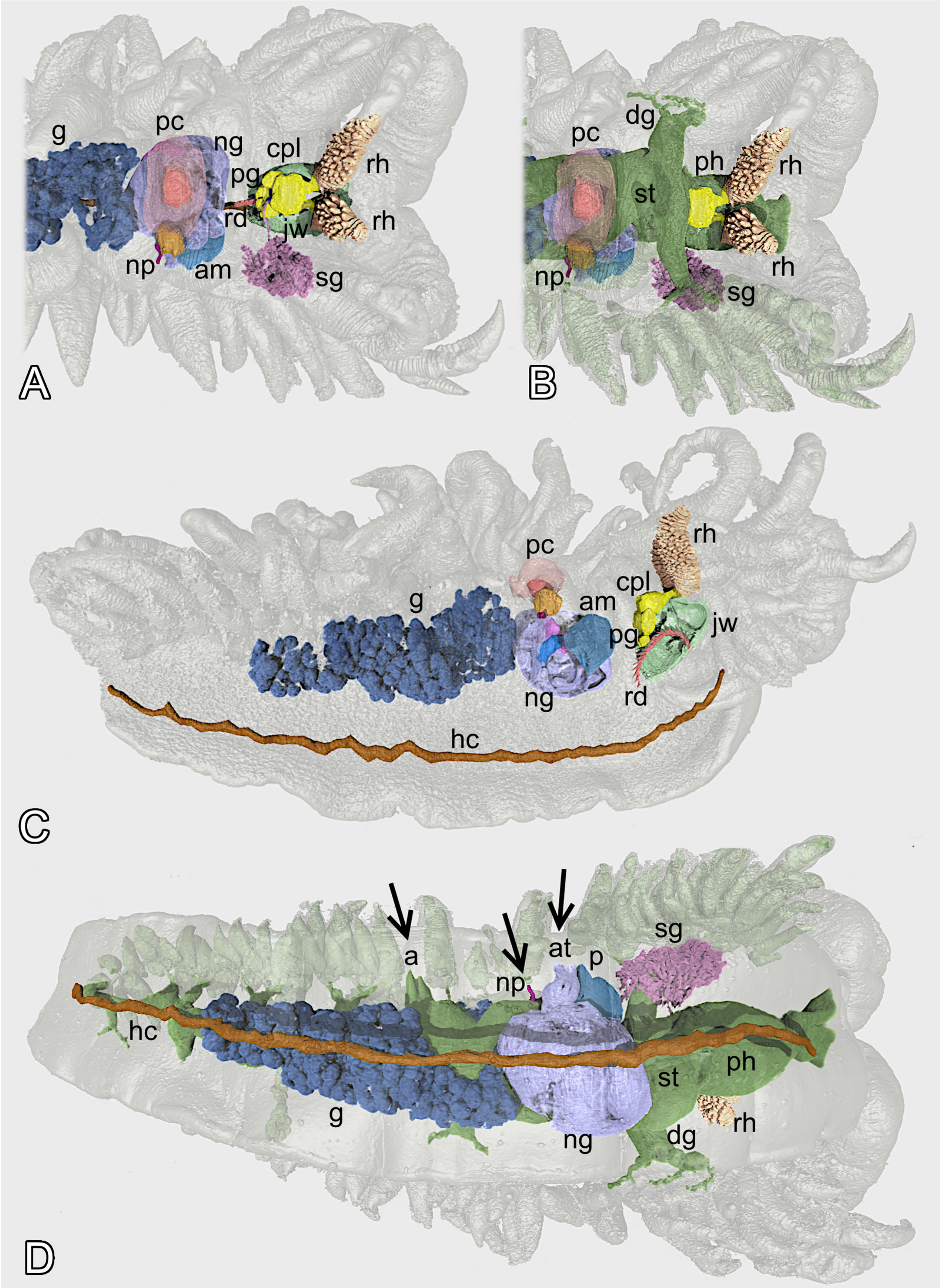

FIGURE 4. *Moridilla jobeli* **sp. nov.**: MicroCT reconstructions of paratype MZB.Gst.21.593. Epidermis rendered transparent, digestive system greenish, reproductive system bluish, nervous system yellow. (A) Dorsal view of anterior body without digestive system, except pharynx. (B) Dorsal view of anterior body with digestive system. (C) Lateral view without digestive system; nidamental gland and jaw sagittal sectioned. (D) Ventral view with digestive system; note openings of penis and nidamental gland, followed by nephropore and further back anus (arrows). Abbrevations: a, anus; am, ampulla; at, atrium; cpl, cerebro-pleural ganglia; dg, digestive gland; hc, haemolymph channel; g, gonad; jw, jaw; ng, nidamental gland; np, nephropore; pc, pericardium (transparent) with ventricle shining through; pg, pedal ganglia; ph, pharynx; rd, radula; rh, rhinophores; sg, salivary gland; st, stomach.

Circulatory and excretory system (Figures 4A–D; 10A, B). Pericardium in anterior part of visceral cavity (Figure 4A); epithelium very delicate with flat cells; ventricle muscular, atrium thin-walled (Figure 10A). A distinct haemolymph channel running ventrally to digestive gland and gonad from anterior to posterior part of foot (Figures 4C, D). Syrinx funnel-shaped; inner lumen densely folded with cilia (Figure 10B).Voluminous kidney situated on top of gonad, mainly to the right side, sometimes intermingling with digestive gland. Epithelium cells highly vacuolated with big basal nuclei.

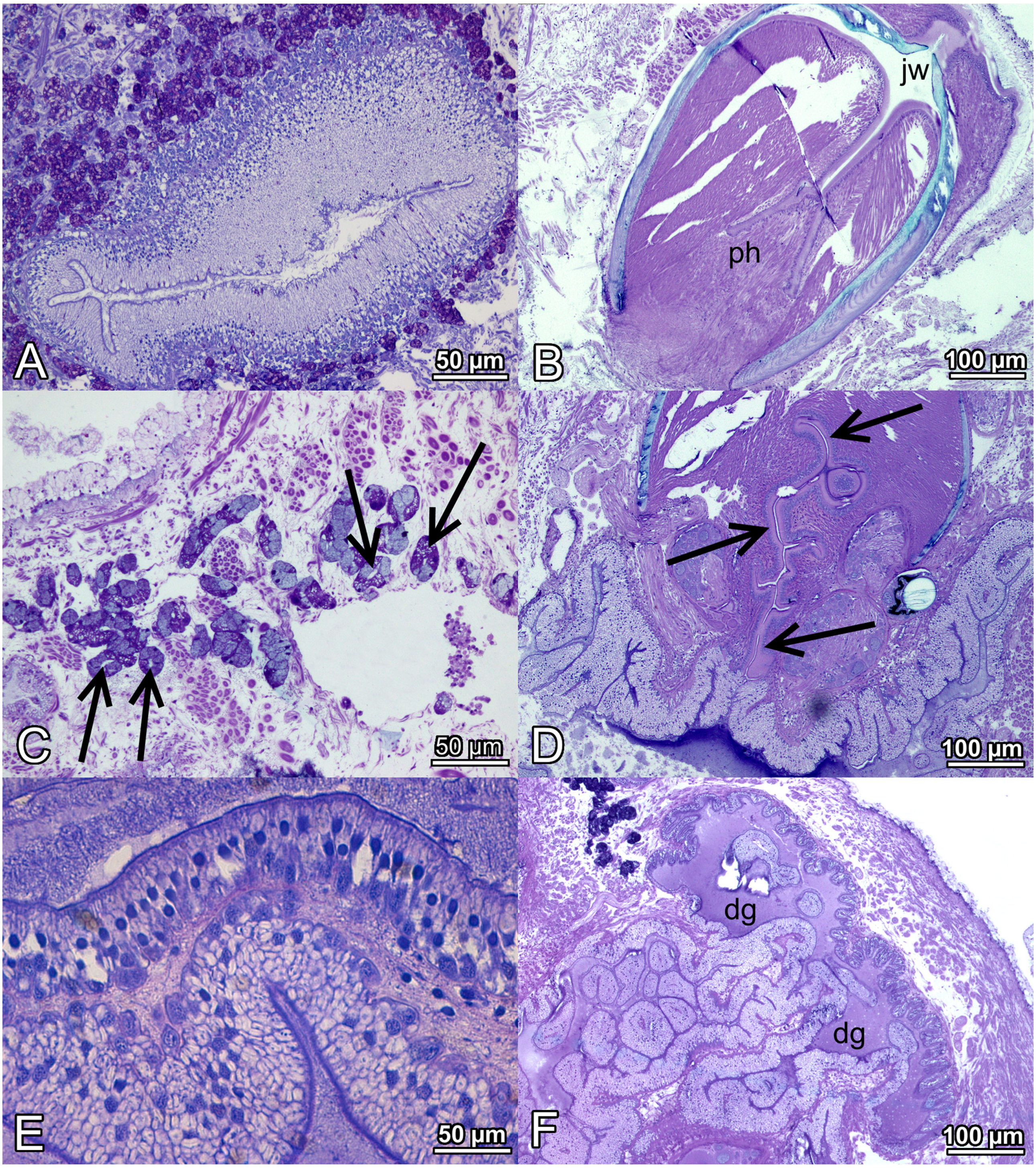

FIGURE 5. *Moridilla jobeli* **sp. nov.**: Digestive system of paratype SRU20190001. (A) Mouth opening; note the specialized vacuolated cells. (B) Pharynx with jaws. (C) Salivary glandular ducts (arrows). (D) Transition pharynx to oesophagus; please note the cuticle in the oesophagus (arrows). (E) Stomach epithelium. (F) Stomach and transition to left and right anterior digestive gland ducts. Abbrevations: dg, digestive gland; jw, jaw; ph, pharynx.

TABLE 2. Species names, voucher numbers and GenBank accession numbers of Facelinidae, Aeolidiidae and outgroup taxa analysed in this study. Underlying grey colour indicates specimens used for the reduced data set in molecular analyses.

Species	Voucher No.	GenBank COI	GenBank 16S	GenBank H3
Austraeolis ornata (Angas, 1864)	-	GQ403774	GQ403752	-
Austraeolis stearnsi (Cockerell, 1901)	-	JQ699571	JQ699483	JQ699395
Burnaia helicochorda (M. C. Miller, 1988)	NMVF155816	KT200148	KT200147	KT200149
Caloria elegans (Alder & Hancock, 1845)	MNCN15.05/53689; MNCN15.05/53690	HQ616751	HQ616738	HQ616780
Caloria indica (Bergh, 1896)	-	KY263168	DQ417273	JQ699389
Cratena minor Padula, Araújo, Matthews-Cascon & Schrödl, 2014	MZSP:116702	KJ940479	-	KM079345
Cratena peregrina (Gmelin, 1791)	MNCN15.05/53691	HQ616752	HQ616715	HQ616781
Cratena pilata (Gould, 1870)	DNAS-4F-32900; CAS184187	KC785096	KY128709	KY128502
Dicata odhneri Schmekel, 1967	BAU2674	LT596560	LT596549	LT596569
Dondice banyulensis Portmann & Sandmeier, 1960	-, MNCN15.05/53693	GQ403773	GQ403751	HQ616804
Dondice occidentalis Engel, 1925	-	JQ699570	JQ699482	JQ699394
Dondice parguerensis Brandon & Cutress, 1985	SRR3726707	KX889730	KC526520	KC526520
Facelina annulicornis (Chamisso & Eysenhardt, 1821)	CASIZ186793	JQ997076	JQ996881	JQ996986
Facelina auriculata (Müller, 1776)	ZMMU:Op-669UK	MK320904	MK320915	-
Facelina bostoniensis (Couthouy, 1838)	CAS184184	KY129046	KY128837	KY128632
Facelina punctata (Alder & Hancock 1845)	-	AF249816	-	-
Facelina quatrefagesi (Vayssière, 1888)	BAU2697	LT596552	LT596545	LT596563
Facelina rubrovittata (Costa A., 1866)	BAU2675	LT596561	LT596550	-
Facelina vicina (Bergh, 1882)	GNMGastropoda9310	KY513634	KY513630	-
Favorinus auritulus Er. Marcus, 1955	CASIZ181203	JX220473	JX220505	JX220441
Favorinus blianus Lemche & Thompson, 1974	CASIZ118892	JX220472	JX220504	JX220440
Favorinus branchialis (Rathke, 1806)	MNCN15.05/53695	HQ616761	HQ616724	HQ616790
Favorinus elenalexiarum García and Troncoso, 2001	CASIZ178875	HM162755	HM162679	HM162588
Favorinus japonicus Baba, 1949	CASIZ182291	JX220468	JX220500	JX220436
Favorinus mirabilis Baba, 1955	CASIZ182194A	JX220464	JX220496	JX220432
Favorinus tsuruganus Baba & Abe, 1964	CASIZ186044	JX220450	JX220482	JX220418
Godiva quadricolor (Barnard, 1927)	CASIZ176385	HM162756	HM162680	HM162589

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TABLE 2. (Continued)

Species	Voucher No.	GenBank COI	GenBank 16S	GenBank H3
Hermissenda crassicornis (Eschscholtz, 1831)	-	JQ699630	JQ699554	KU950212
Hermissenda emurai (Baba, 1937)	-	KU950185	KU950122	KU950214
Hermissenda opalescens (J. G. Cooper, 1863)	-	KU950191	KU950126	KU950220
Hermosita hakunamatata (Ortea, Caballer & Espinosa, 2003)	-	JQ699631	JQ699555	JQ699467
Learchis evelinae Edmunds & Just, 1983	SRR3726693	KX889738	MK100976	-
Learchis poica Ev. Marcus & Er. Marcus, 1960	-	JQ699632	JQ699556	JQ699468
Moridilla brockii Bergh, 1888 (Philippines)	CASIZ186245	JQ997083	JQ996888	JQ996994
Moridilla fifo Carmona & Wilson 2018 (Montebello Islands, West Australia)	WAMS96061	MH673283	-	-
Moridilla hermosita Carmona & Wilson 2018 (Madang, Papua New Guinea)	CASIZ190756[A]	MH673282	-	-
Nanuca sebastiani Er. Marcus, 1957	-	JQ699633	JQ699557	JQ699469
Noumeaella isa Ev. Marcus & Er. Marcus, 1970 (Philippines)	CASIZ 186249	JQ997084	JQ996889	JQ996995
Noumeaella rehderi Er. Marcus, 1965 (Indonesia)	ZSMMol20033794	-	JQ996861	JQ996961
Noumeaella rubrofasciata Gosliner, 1991 (California, USA)	SRR3726700	KX889742	MK100981	-
Noumeaella sp. (Moorea, French Polynesia)	PW-2014	KJ522461	-	-
Noumeaella sp. 1 (Philippines)	CASIZ 186246.1	JQ997090	JQ996895	JQ997002
Noumeaella sp. 2 (Philippines)	CASIZ 186246.2	JQ997091	JQ996896	JQ997003
Noumeaella sp. 3 (Philippines)	CASIZ 186247.1	JQ997085	JQ996890	JQ996996
Noumeaella sp. 4 (Philippines)	CASIZ 186247.2	JQ997086	JQ996891	JQ996997
Noumeaella sp. 5 (Philippines)	CASIZ 186248	JQ997089	JQ996894	JQ997000
Noumeaella sp. 6 (Malaysia)	CASIZ 176743	JQ997053	JQ996849	JQ996950
Noumeaella sp. 7 (Philippines)	CASIZ 186006.2	JQ997088	JQ996893	JQ996999
Noumeaella sp. 8 (Philippines)	CASIZ 186006.1	JQ997087	JQ996892	JQ996998
Noumeaella sp. 9 (Morocco)	MNCN/ADN 51996	JX087548	JX087479	JX087616
Palisa papillata Edmunds, 1964	SRR1950952	KX889743	-	-
Phidiana hiltoni (O'Donoghue, 1927)	-	-	JQ699558	JQ699470
Phidiana lascrucensis Bertsch & Ferreira, 1974	-	KU950197	KU950131	KU950226
Phidiana lynceus Bergh, 1867	MNCN/ADN51994	JX087563	JX087498	JX087634
Phidiana militaris (Alder & Hancock, 1864)	CASIZ186009	-	JQ996875	JQ996979
Phyllodesmium briareum (Bergh, 1896)	CASIZ177239	HQ010492	HQ010528	HQ010460

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TABLE 2. (Continued)

Species	Voucher No.	GenBank COI	GenBank 16S	GenBank H3
Phyllodesmium colemani Rudman, 1991	CASIZ177647	HQ010534	HQ010498	HQ010466
	CASIZ177647			
Phyllodesmium crypticum Rudman, 1981	CASIZ177687	HQ010502	HQ010536	HQ010470
Phyllodesmium horridum (Macnae, 1954)	CASIZ176127	HM162757	HM162681	HM162590
Phyllodesmium hyalinum Ehrenberg, 1831	-	GQ403778	GQ403756	-
Phyllodesmium jakobsenae Burghardt & Wägele, 2004	CASIZ177576	HQ010489	HQ010524	HQ010456
Phyllodesmium kabiranum Baba, 1991	CASIZ173492	-	HQ010512	HQ010444
Phyllodesmium karenae Moore & Gosliner, 2009	CASIZ177313	HQ010483	HQ010517	HQ010448
Phyllodesmium koehleri Burghardt, Schrödl & Wägele, 2008	CASIZ177693	HQ010494	HQ010530	HQ010462
Phyllodesmium lembehensis Burghardt, Schrödl & Wägele, 2008	-	GQ403780	GQ403758	-
Phyllodesmium lizardensis Burghardt, Schrödl & Wägele, 2008	CASIZ177766	HQ010496	HQ010532	HQ010464
Phyllodesmium longicirrum (Bergh, 1905)	-	JQ699634	GQ403761	JQ699471
Phyllodesmium macphersonae (Burn, 1962)	CASIZ176721	HQ010479	HQ010509	HQ010441
Phyllodesmium magnum Rudman, 1991	CASIZ176724	HQ010481	HQ010511	HQ010443
Phyllodesmium opalescens Rudman, 1991	CASIZ177311	HQ010484	HQ010518	HQ010449
Phyllodesmium parangatum Oritz & Gosliner, 2009	CASIZ177769	HQ010501	HQ010535	HQ010469
Phyllodesmium pinnatum Moore & Gosliner, 2003	CASIZ110371	-	HQ010526	HQ010458
Phyllodesmium poindimiei (Risbec, 1928)	CASIZ177570	HQ010486	HQ010521	HQ010452
Phyllodesmium rudmani Burghardt & Gosliner, 2006	CASIZ177622	HQ010493	HQ010529	HQ010461
Phyllodesmium tuberculatum Moore & Gosliner, 2009	CASIZ177520	HQ010490	HQ010525	HQ010457
Pruvotfolia longicirrha (Eliot, 1906)	MNCN15.05/53703	HQ616760	HQ616723	HQ616789
Pruvotfolia pselliotes (Labbé, 1923)	MNCN15.05/53705	HQ616762	HQ616725	HQ616791
Sakuraeolis enosimensis (Baba, 1930)	CASIZ178876	HM162758	HM162682	HM162591
Sakuraeolis japonica (Baba, 1937)	-	KX610997	KX610997	-
Aeolidiidae				
Aeolidia papillosa (Linnaeus, 1761)	ZSM20020700	KF317849	KF317837	KF317859
Aeolidiella alderi (Cocks, 1852)	ZSMMol20020982	HQ616765	HQ616728	HQ616794
Aeolidiella glauca (Alder & Hancock, 1845)	ZMMU:OP-560	KX758255	KX758254	KX758259
Aeolidiella sanguinea (Norman, 1877)	MNCN/ADN51932	JX087538	JX087466	JX087600
Anteaeolidiella cacaotica (Stimpson, 1855)	CASIZ174212	JQ997030	JQ996825	JQ996926

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TABLE 2. (Continued)

Species	Voucher No.	GenBank COI	GenBank 16S	GenBank H3
Anteaeolidiella chromosoma (Cockerell & Eliot, 1905)	CASIZ173060	JQ997018	JQ996812	JQ996911
Anteaeolidiella fijensis Carmona, Bhave, Salunkhe, Pola, Gosliner & Cervera, 2014	-	KX276653	KX276652	KX276655
Anteaeolidiella lurana (Ev. Marcus & Er. Marcus, 1967)	CASIZ186820	JQ997031	JQ996826	JQ996927
Anteaeolidiella oliviae (MacFarland, 1966)	CASIZ181315	JQ997034	JQ996829	JQ996930
Anteaeolidiella saldanhensis (Barnard, 1927)	CASIZ176313	JQ997032	JQ996827	JQ996928
Anteaeolidiella takanosimensis (Baba, 1930)	MNCN/ADN51925	JX087530	JX087458	JX087592
Baeolidia japonica Baba, 1933	CASIZ186795	JQ997059	JQ996856	JQ996957
Baeolidia moebii Bergh, 1888	CASIZ186211	JQ997061	JQ996858	JQ996959
Baeolidia slaamica (Rudman, 1982)	CASIZ177599	JQ997062	JQ996860	JQ996960
Berghia coerulescens (Laurillard, 1832)	ZSMMol20041584	JQ997049	JQ996845	JQ996946
Berghia columbina (Garcia-Gomez & T. E. Thompson, 1990)	MNCN/ADN51938	JX087542	JX087472	JX087606
Berghia creutzbergi Er. Marcus & Ev. Marcus, 1970	MNCN/ADN51945	JX087546	JX087477	JX087614
Berghia marcusi Dominguez, Troncoso & Garcia, 2008	MZUSP103225	KF273244	KF273243	KF273246
Berghia rissodominguezi Muniain & Ortea, 1999	MNCN/ADN51951	JX087552	JX087484	JX087621
Berghia stephanieae (Valdès, 2005)	CASIZ185770	JQ997044	JQ996839	JQ996940
Berghia verrucicornis (A. Costa, 1867)	MNCN15.05/53687	HQ616750	HQ616713	HQ616779
Bulbaeolidia alba (Risbec, 1928)	SRR3726702	KX889719	-	JQ699386
Bulbaeolidia oasis Caballer & Ortea, 2015	CNMO3036	KY563098	-	KY563112
Bulbaeolidia sulphurea Caballer & Ortea, 2015	MHNSM90-0427	KY563097	KY563104	KY563111
Cerberilla affinis Bergh, 1888	CASIZ180421.1	MK091263	JQ996863	JQ996964
Cerberilla annulata (Quoy & Gaimard, 1832)	CASIZ182227	-	JQ996866	JQ996967
Cerberilla bernadettae Tardy, 1965	MNCN/ADN51957	JX087555	JX087489	JX087625
Limenandra confusa Carmona, Pola, Gosliner & Cervera, 2014	SRR3726703	KX889739	-	-
Limenandra fusiformis (Baba, 1949)	CASIZ184526.2	JQ997078	JQ996884	JQ996998
Limenandra nodosa Haefelfinger & Stamm, 1958	CASIZ186792	JQ997081	JQ996886	JQ996992
Spurilla braziliana MacFarland, 1909	MNCN15.05/64110	KF273278	KF273255	KF273304
Spurilla dupontae Carmona, Lei, Pola, Gosliner, Valdès & Cervera, 2014	LACM3254	KF273271	KF273250	KF273297
Spurilla neapolitana (Delle Chiaje, 1841)	CASIZ192390	KF273287	KF273267	KF273319
Spurilla sargassicola Bergh, 1871	CPIC00816	KF273274	KF273252	KF273300
Zeusia hyperborea Korshunova, Zimina & Martynov, 2017	ZNMU:Op-557	KX758256	KX758251	KX758260

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TABLE 2. (Continued)

Species	Voucher No.	GenBank COI	GenBank 16S	GenBank H3
Outgroup				
Aeolidioidea Gray, 1827				
Unidentiidae Millen & Hermosillo, 2012				
Pacifia amica Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZNMU:Op-614	MG452633	-	MG452602
Pacifia goddardi (Gosliner,2010)	CAS182590	KY129063	KY128854	KY128648
Unidentia angelvaldesi Millen & Hermosillo, 2012	SRR3726696	KX889750	MK100996	-
Unidentia nihonrossija Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZNMU:Op-517	MF523385	MF523464	MF523310
Unidentia nihonrossija Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZNMU:Op-517	-	MG452681	-
Unidentia sandramillenae Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017	ZNMU:Op-617	MG452632	MG452683	MG452601
Flabellinoidea Bergh, 1889				
Coryphellidae Bergh, 1889				
Orienthella trilineata (O'Donoghue, 1921)	CAS179466	KY129064	KY128855	KY128649
Himatina trophina (Bergh, 1890)	ZNMU:Op-531	MF523388	MF523440	MF523313
Flabellinidae Bergh, 1889				
Calmella gaditana (Cervera, Garcìa-Gomez & Garcìa, 1987)	MNCN/ADN51999	JX087556	JX087490	JX087626
Coryphellina rubrolineata(O'Donoghue, 1921)	ZNMU:Op-132	MF523381	MF523437	MF523306
Edmundsella albomaculata (Pola, Carmona, Calado & Cervera, 2014)	MNCN:15.05/69896	KJ721522	KJ721520	KJ721524
Edmundsella pedata (Montagu, 1816)	NTNU-VM:68819	MG452607	MG452657	MG452582
Flabellina affinis (Gmelin, 1791)	MNCN15.05/53696	HQ616753	HQ616716	HQ616782
Paraflabellina ischitana (Hirano & Thompson, 1990)	MNCN15.05/53697	HQ616757	HQ616720	HQ616786
Flabellinopsidae Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017				
Baenopsis baetica (Garcia-Gomez, 1984)	MNCN15.05/53699	HQ616755	HQ616718	HQ616784
Notaeolidiidae Eliot, 1910				
Notaeolidia depressa Eliot, 1905	-	GQ292057	MK100980	-
Samlidae Korshunova, Martynov, Bakken, Evertsen, Fletcher, Mudianta, Saito, Lundin, Schrödl & Picton, 2017				
Luisella babai (Schmekel, 1972)	MNCN15.05/53698	HQ616754	HQ616717	HQ616783
Samla bicolor (Kelaart, 1858)	ZMMU:Op-68	MF523383	MF523436	MF523308

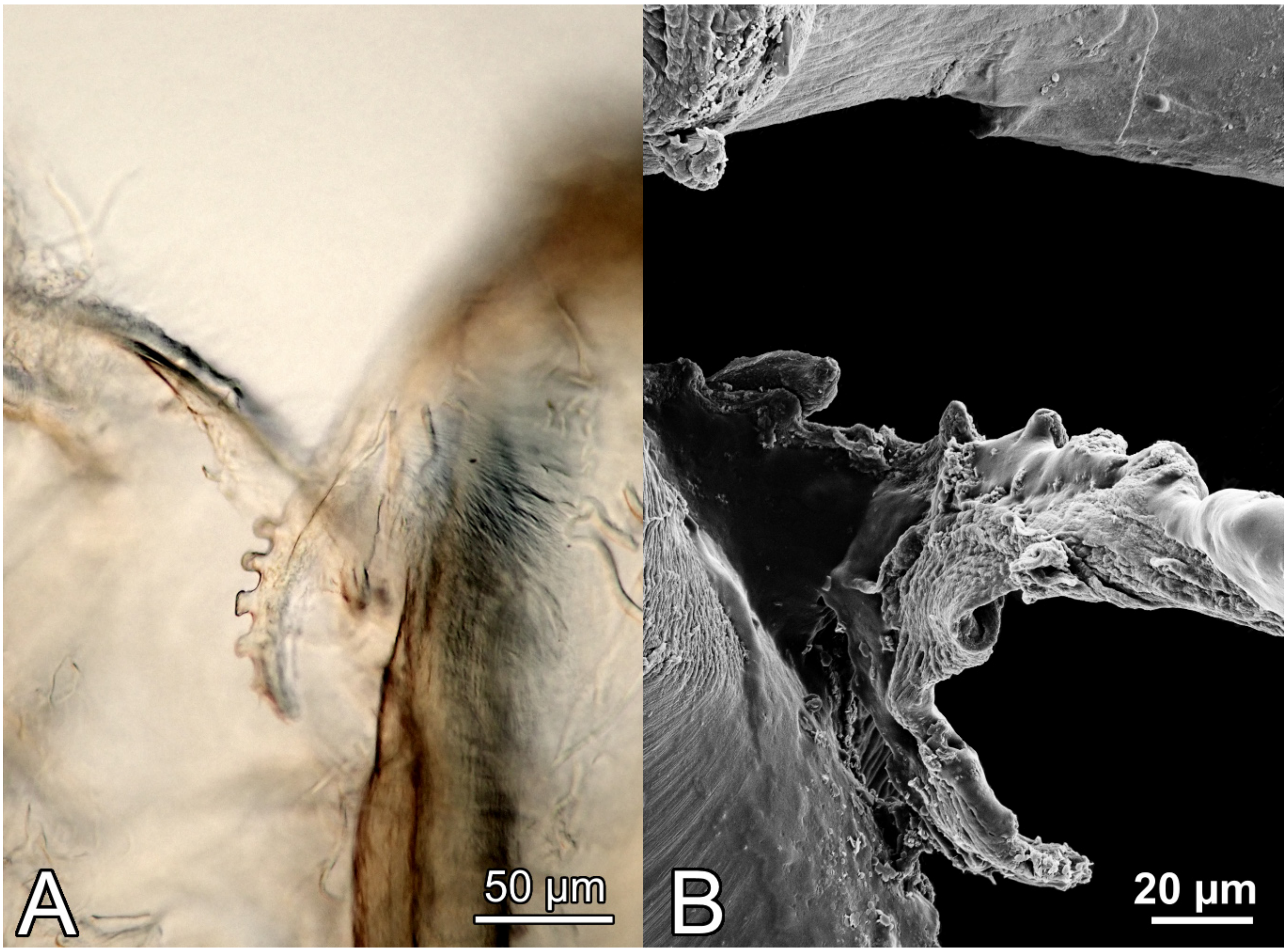

FIGURE 6. *Moridilla jobeli* **sp. nov.**: Pharyngeal structures of paratype MZB.Gst.21.593. (A) Masticatory border of jaw with denticles (light-microscopy). (B) Details of masticatory border of jaw with denticles (SEM).

Nervous system and sensory organs (Figures 4A, C; 10C, D). Ganglia forming a closed ring, surrounding the short oesophagus (Figure 4A). Cerebral and pleural ganglia fused. Eyes situated close to posterior base of rhinophores and connected dorsally to cerebral ganglia with short optical nerve; orientation of pigment cup more to the lateral than dorsal side (Figure 10C). Statocysts between cerebro-pleural and pedal ganglia; with several small otoconia (Figure 10D).

Epithelia and glandular structures. Epidermis of body, cerata and rhinophores composed of specialized vacuolated epithelium (Figure 8B); cells elongate, cylindrical with basal nucleus and numerous vacuoles. Apically, cells covered with microvilli fringe, occasionally short bunched cilia present. Few mucus cells with violet granula interspersed with higher concentration along cerata epithelium. Foot epithelium with specialized vacuolated epithelium composed of elongated cells higher than in dorsal epidermis; intensely ciliated with randomly distributed subepidermal glandular cells stained reddish to violet; higher concentration of subepithelial gland cells towards foot rim. No glandular stripe present in juvenile.

Species delimitation and phylogeny

(Figures 11–13)

Distances of partial COI gene range from 14 to 21 % between *Moridilla jobeli* **sp. nov.** and all available sequences of other *Moridilla* species (Table 3). The NeighborNet analysis of this gene shows the clear clustering of the eleven specimens of *Moridilla jobeli* **sp. nov.** and their close relationship to the sequences of the three other *Moridilla* species (*Moridilla brockii*, *Moridilla fifo* and *Moridilla hermanita*) (Figure 11). Additionally, one specimen from Bangka Island, which was also preliminarily assigned to *Noumeaella*, clearly groups within this *Moridilla* clade.

The twelve *Noumeaella* specimens (including *N. rubrofasciata, N. isa* and N. sp.1–N. sp. 5) and *Palisa papillata* group separately from the *Moridilla* cluster, however the distance is not prominent.

TABLE 3. COI gene pairwise uncorrected *p*-distances amongst all *Moridilla* species.

	Moridilla jobeli	***Moridilla* cf. *brockii***	***Moridilla* sp.**	*Moridilla fifo*	***Moridilla hermanita***
Moridilla jobeli	0.9–1.9	14.2–15.1	14.8–15.7	15.5–16.2	20.4–21.2
Moridilla* cf. *brockii	14.2–15.1	0.0	10.2	13.0	16.8
***Moridilla* sp.**	14.8–15.7	10.2	0.0	12.8	17.1
Moridilla fifo	15.5–16.2	13.0	12.8	0.0	14.2
Moridilla hermanita	20.4–21.2	16.8	17.1	14.2	0.0

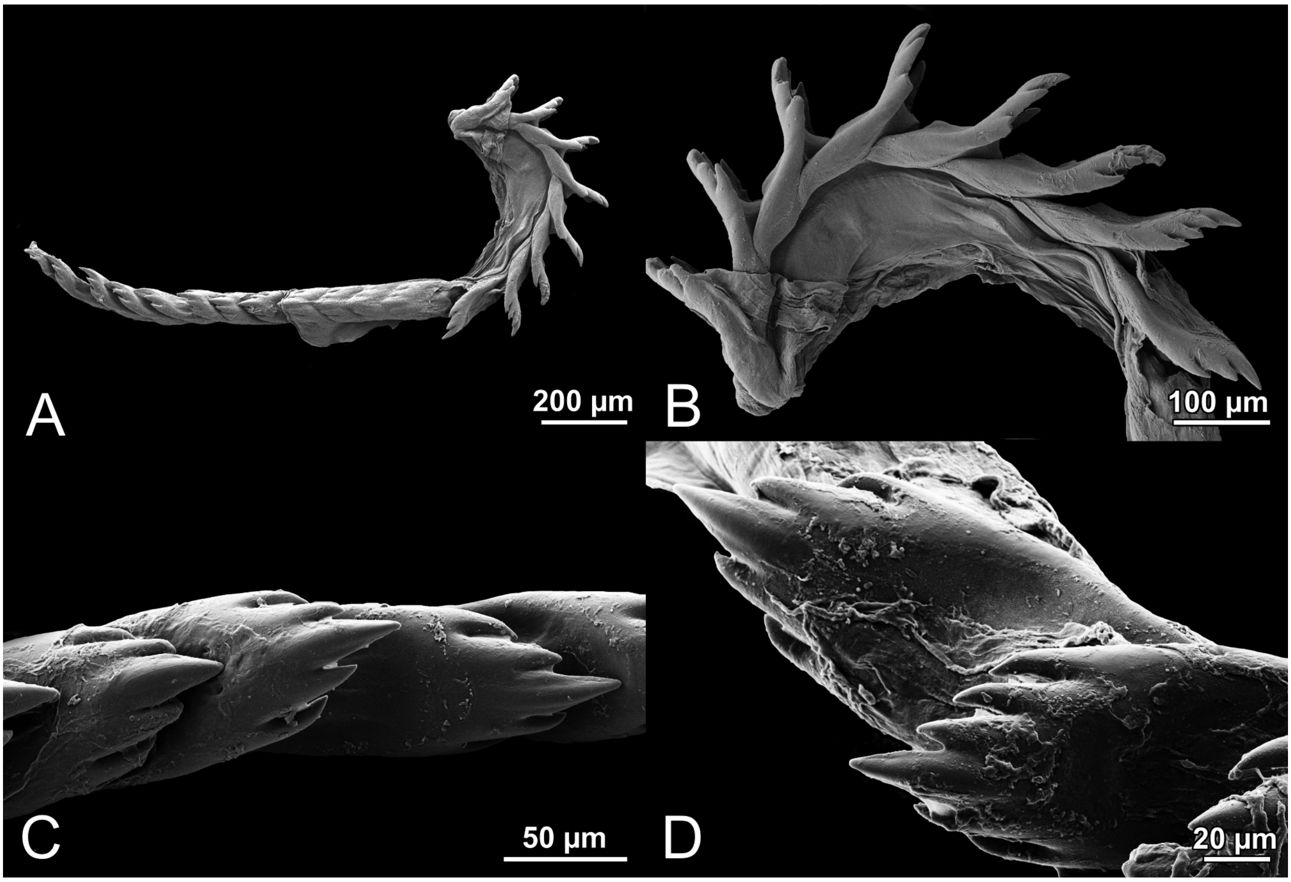

FIGURE 7. *Moridilla jobeli* **sp. nov.**: Scanning electron micrographs (SEM) of radula of paratype MZB.Gst.21.593. (A) Overview of radula. (B) Details of oldest rachidian teeth; lateral denticles partly worn off. (C) Details of rachidian teeth from hind part. (D) Rachidian tooth with an abnormal number (3 instead of 2) of denticles on one side.

Results from the various species delimitation tests are mapped against the Maximum Likelihood tree based on the reduced data set, using available sequences of Unidentiidae as outgroup (Figure 12). All species delimitation tests applied for each gene are consistent in their results and reveal the distinctiveness of *Moridilla jobeli* **sp. nov.** from all other *Moridilla* species. The single specimen from Bangka Island, *Moridilla* sp. (SRU2017/01/Nosp1-17Ba-1) shows distinct divergence to *Moridilla jobeli* **sp. nov.**. Species distinction is also shown for *M. fifo* and *M. hermanita*. Within the *Noumeaella* clade, *Noumeaella* sp. 1 to *Noumeaella* sp. 5 are considered as a single species in all species delimitation tests.

The Maximum Likelihood tree of the reduced data set (16S and COI, including all available *Moridilla*, *Palisa* and *Noumeaella* sequences, Figure 12) reveals monophyly of *Moridilla*. Specimens of *Moridilla jobeli* **sp. nov.** form a sister clade to *Moridilla* sp., and these together a sister clade to *M.* cf. *brockii*. *M. fifo* and *M. hermanita* are sister taxa and stand as a sister clade to all other *Moridilla* species. *Palisa papillata* results in a closer relationship to *Moridilla* than to *Noumeaella*. The genus *Noumeaella* is paraphyletic, with *Noumeaella rubrofasciata* closely related to *Palisa* and *Moridilla,* however with low bootstrap support (43). *Noumeaella isa*, *N. rehderi* and four undescribed species, represented by nine specimens (except for *Noumeaella* sp. 9) are grouped in a clade.

The Maximum Likelihood analysis of the concatenated full data set (H3, 16S and COI) including all available sequences of the families Facelinidae and Aeolidiidae, and some members of the Flabellinoidea and Unidentiidae (Figure 13, 50% majority rule tree), confirm the monophyly of *Moridilla* and *Moridilla jobeli* **sp. nov.** herein with highest bootstrap support (100). *Noumeaella* again is not monophyletic but represented by six different clades with an unresolved relationship. Aeolidiidae are a monophyletic group with very low bootstrap support (51). *Palisa papillata* forms the sister group to *Hermissenda*. Relationships with regard to other facelinid taxa are not resolved. Similar results, but with even lower bootstrap support were also obtained in the data set comprising more and alternative cladobranch outgroups (Supplementary Figure 2). Here, besides the sequence of *Noumeaella rubrofasciata*, all other *Noumeaella* sequences form a monophyletic clade, however bootstrap value is low.

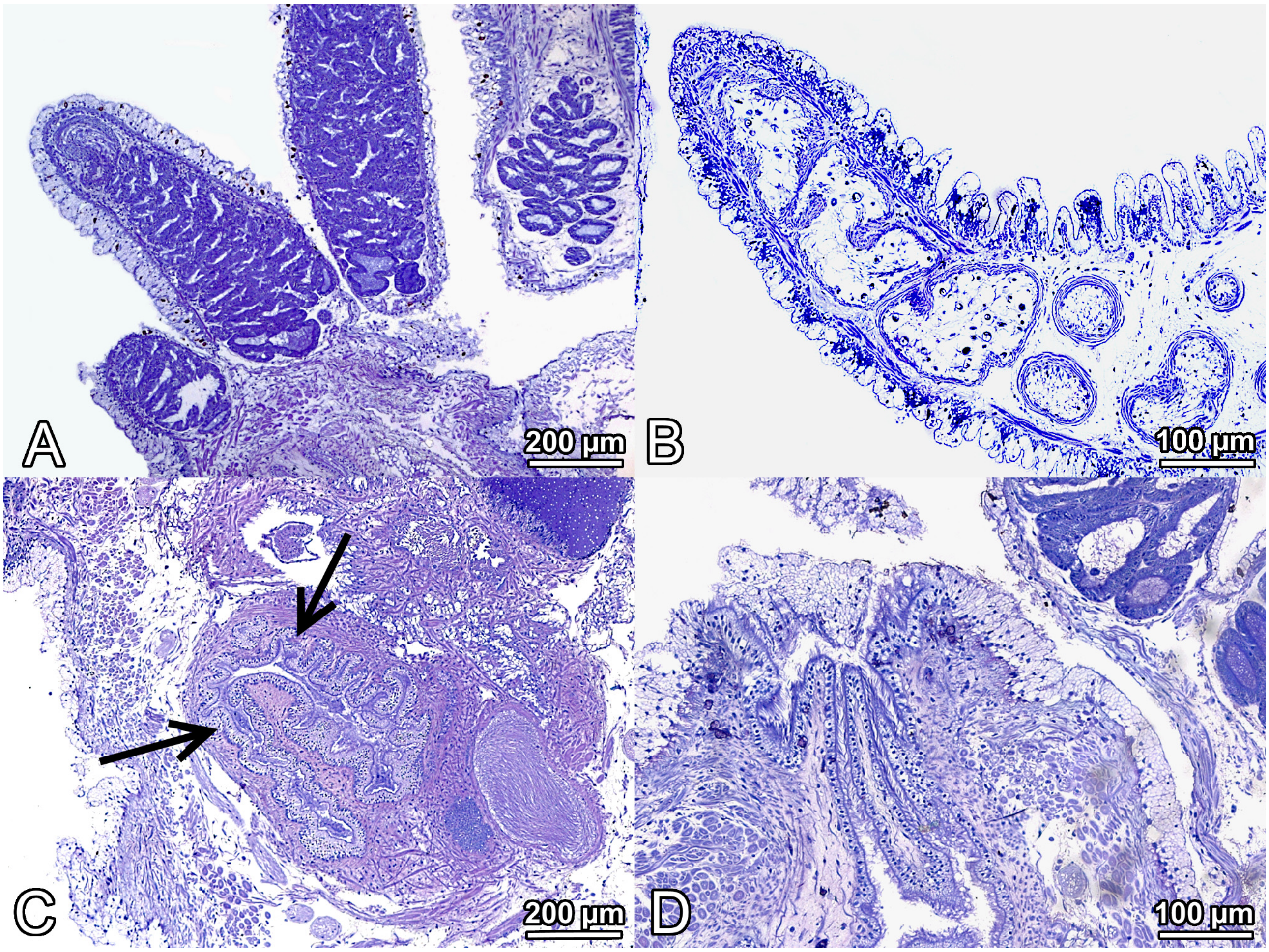

FIGURE 8. *Moridilla jobeli* **sp. nov.**: Digestive system of paratype SRU20190001. (A) Digestive gland in cerata. (B) Cnidosac in one ceras; note the three parts of the sac are one sac winding as a tube in the tip of the ceras. (C) Typhlosole (arrow) in first part of intestine. (D) Anus and anal papilla.

Discussion

For more than 150 years, *Moridilla* was considered as a monotypic genus with only one colourful species, *Moridilla brockii*, widely distributed in the Indo-Pacific. Bergh (1888), when describing the colour of *Moridilla brockii,* referred to the original German description of the collector J. Brock: "…milchweis gewesen, der Rücken mennigroth gesprenkelt, die Rückenpapillen schwärzlichbraun". This translates to "milky white, the dorsum speckled with red (vermilion), the cerata blackish brown". In comparison, our animals are translucent white with distinct white patches. One specimen shows a dorsum with a tinge of orange. Despite the variation in colours observed, none of our animals resembles the original description of *Moridilla brockii*; they neither show the dorsum speckled with reddish nor are the cerata blackish brown. Our animals differ from *M. fifo* and *M. hermanita,* which are both described with bright orange oral tentacles and rhinophores, in missing this colouration at the base of both head tentacles. Additionally, our animals do not show a greyish, bluish or dark colouration of the cerata. *M. fifo* and *M. hermanita* do not have a white pigment patch behind the rhinophores as present in *Moridilla jobeli* **sp. nov.,** although in some of our specimens, this patch is paler than in others.

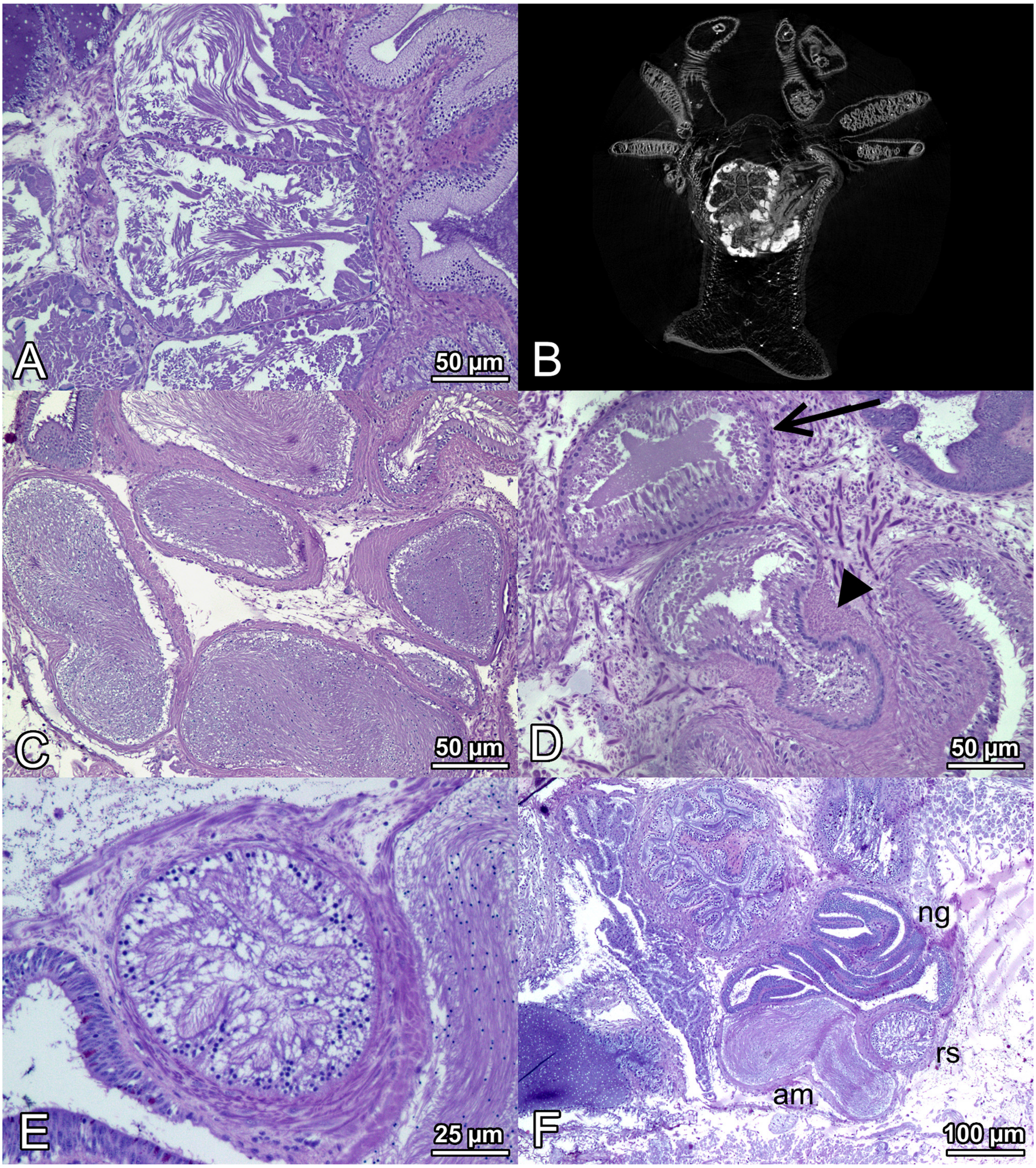

FIGURE 9. *Moridilla jobeli* **sp. nov.**: Genital system; A, C–F based on paratype SRU20190001; B based on paratype MZB. Gst.21.593. (A) Gonad of juvenile specimen with exclusively spermatogonians. (B) Ovotestis of adult animal with oogonians peripheral and spermatogonians centrally (µ-CT). (C) Several cross sections of ampulla. (D) Vas deferens with prostatic part (arrow) and penis in penial sheath (arrowhead). (E) Receptaculum seminis. (F) Cross section of genitalia. Abbrevations: am, ampulla; rs, receptaculum seminis; ng, nidamental gland.

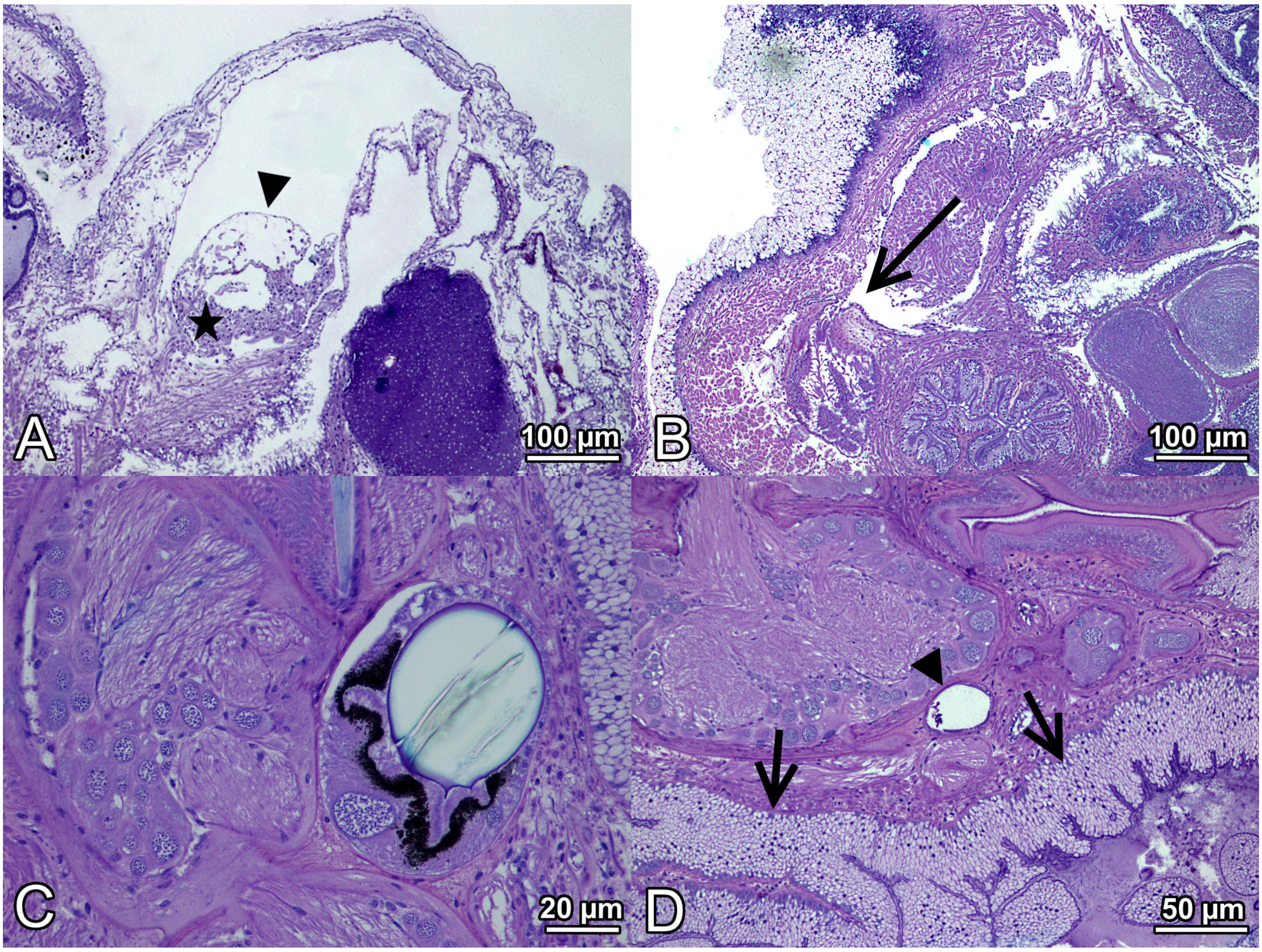

FIGURE 10. *Moridilla jobeli* **sp. nov.**: Anatomy of paratype SRU20190001. (A) Pericard with auricle (arrowhead) and ventricle (star). (B) Syrinx opening in pericard (arrow). (C) Eye on right side. (D) Statocyst on right side with otoconia (arrow head); arrows indicating epithelium of digestive gland when branching from stomach and composed of specialized vacuolated cells.

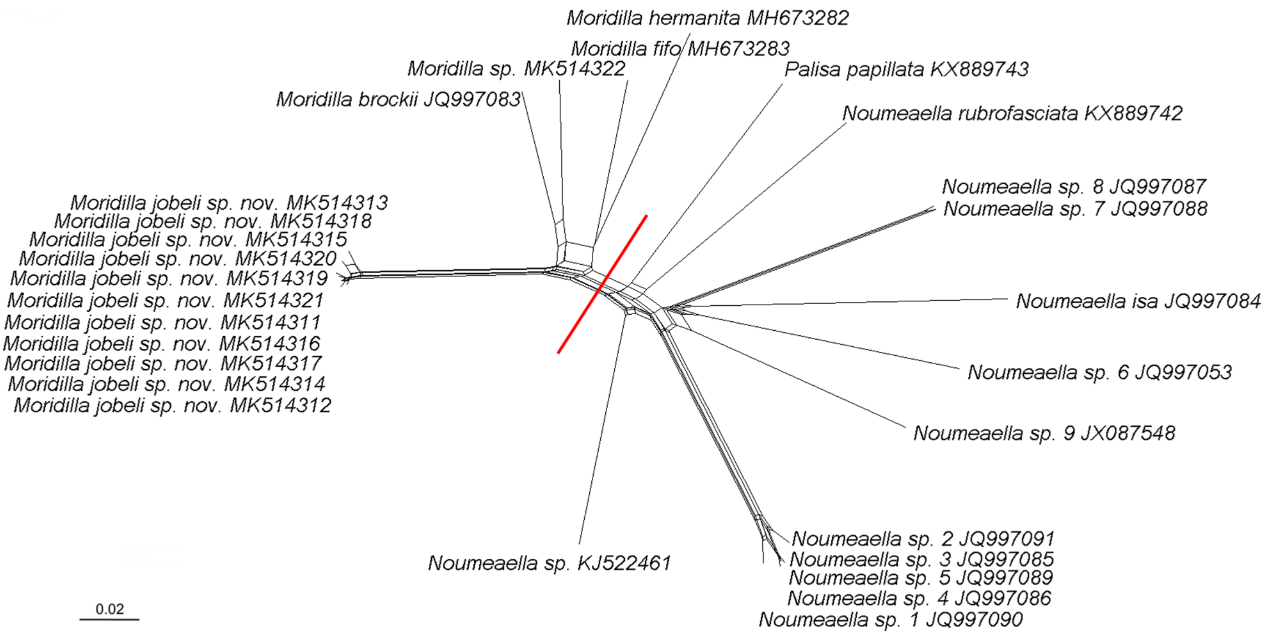

FIGURE 11. COI NeighborNet analysis of reduced data set with *Moridilla*, *Palisa* and *Noumeaella* only. The major split between *Moridilla* and *Palisa/Noumeaella* is visualized by a red line. Please note the low resolution (short edges) between the various species and genera.

With regard to morphology, *Moridilla jobeli* **sp. nov.** has longer foot tentacles than is depicted in the live material of *M. fifo* and *M. hermanita*. Bergh (1888) described the anterior foot with "ausgezogene Fußecken" (p. 682), which indicates shorter tentacles. However, his description is based on a preserved animal. Our preserved material shows long foot tentacles. The shape of the jaws and teeth is very similar in all described *Moridilla* species. The masticatory processes (and only this feature in the pharynx) of *M. brockii* is described as (brownish-) black; in *Moridilla jobeli* **sp. nov.** it is more yellow, similar to *M. hermanita* and *M. fifo*. However, the last two species have 11 to 18 denticles along the border, whereas the new species has only six to seven. The 24 mm *M. brockii* has 23 rows of rachidian teeth, whereas our specimen with an original length of 35 mm shows only 20 teeth. Unfortunately, no length measurements for *M. fifo* and *M. hermanita* are available. *Moridilla fifo* and *Moridilla hermanita* are described with three to four denticles on each side of the main rachidian cusp (although, only two denticles are visible in the depicted figures). Our specimen had only one tooth with three denticles on one side, which therefore seems to be an abnormality. *Moridilla brockii* is similar to our species with only two denticles. Cnidosacs in *M. brockii* are pear-shaped and described as "nicht groß" (not large) (p. 683). In contrast, we observed very elongate and large, even winding cnidosacs in the cerata of *Moridilla jobeli* **sp. nov.**. The position of the anus lies between the second and the third cerata cluster of *Moridilla jobeli* **sp. nov.**, whereas for *M. brockii, M. fifo* and *M. hermanita* it is described to be underneath the third group of cerata. A summary of these distinguishing features is provided in Table 4.

Distance and NeighborNet analysis of COI and the species delimitation tests based on both genes confirm *Moridilla jobeli* **sp. nov.** as a separate species. The short distances in the split-based analysis reflect the low bootstrap values seen in both data sets (full with H3, 16S and COI, reduced with 16S and COI only), as well as the low resolution with regard to relationships between the various species and genera.

One *Moridilla brockii* sequence was included in the first molecular study on Aeolidiidae (Carmona *et al.* 2013). This specimen (CASIZ186245) was not further addressed in the study, and therefore colouration is not mentioned. However, we can only assume its correct identification. Our specimens show a high distance divergence of about 15 % from this single *M.* cf. *brockii* sequence and the distinctness is also shown in the species delimitation tests. One specimen, collected at Bangka Island, clusters with *M.* cf. *brockii* (Figure 11) or *Moridilla jobeli* **sp. nov.** (Figure 12), both branches with low bootstrap support. This animal differs from *Moridilla jobeli* **sp. nov.** mainly in the rhinophores, which are orange in colour from the tip down to the base, as well as in the arrangement of the cerata in distinct clusters. It differs from *M. brockii* in the general coloration. All molecular analyses retrieve the sister group relationship between *M. fifo* and *M. hermanita,* which are recorded from localities lying quite far apart (North Australia versus Papua New Guinea).Together, they form the sister taxa to the other *Moridilla* species in all performed analyses.

The Maximum Likelihood analysis of the families Facelinidae and Aeolidiidae, based on the full data set (H3, 16S and COI) reveals the monophyly of *Moridilla* including *Moridilla jobeli* **sp. nov.**. Aeolidiidae is monophyletic, but the paraphyly of Facelinidae as proposed by Carmona *et al.* (2013), Mahguib & Valdés (2015), Goodheart *et al.* (2015) , Goodheart (2017) and Martynov *et al.* (2019) cannot be confirmed or rejected, since the relationships among the facelinid groups are not resolved. Despite the much larger taxon sampling, including 151 specimens, we thus are also not able to address the relationship of *Palisa* and *Noumeaella* with regard to *Moridilla*. An interesting point is the paraphyly of *Noumeaella*, with regard to an undescribed species from Morocco, that is placed as the sister taxon to all Facelinidae and Aeolidiidae (however, see also Supplementary Figure 2). Paraphyletic *Noumeaella* were also recovered by our reduced data set consisting of *Moridilla*, *Noumeaella* and *Palisa* sequences (Figure 12). Yet, our unresolved tree does not contradict published results based on smaller data sets: 1) *Moridilla* as part of the facelinid clade, which usually now groups with Aeolidiidae (Carmona *et al.* 2013); 2) *Palisa* and *Noumeaella* (except the species from Morocco) as part of the other facelinid clade (Goodheart *et al.* 2017).

We conclude that the genus *Moridilla* comprises five distinct species which can be distinguished based on external morphology, coloration and molecular data. So far, *Moridilla jobeli* **sp. nov.** is only reported from Bunaken National Park, North Sulawesi, Indonesia. The undescribed *Moridilla* species from Bangka Island North Sulawesi and *M. brockii* from Java might comprise two further species from Indonesia. With *M. fifo* from Northern Australia and *M. hermanita* from Papua New Guinea, the distribution of the genus is thus well documented in the Indo-Pacific. However, the many records of "*Moridilla brockii*" specimens from other localities throughout the Pacific are difficult to assess due to the lack of knowledge on colour variation within this species and the vague colour description of the holotype. The rather similar colouration of the newly described *Moridilla* species and the lack of species specific anatomical characters within the genus emphasize the importance of barcoding to avoid misidentification.

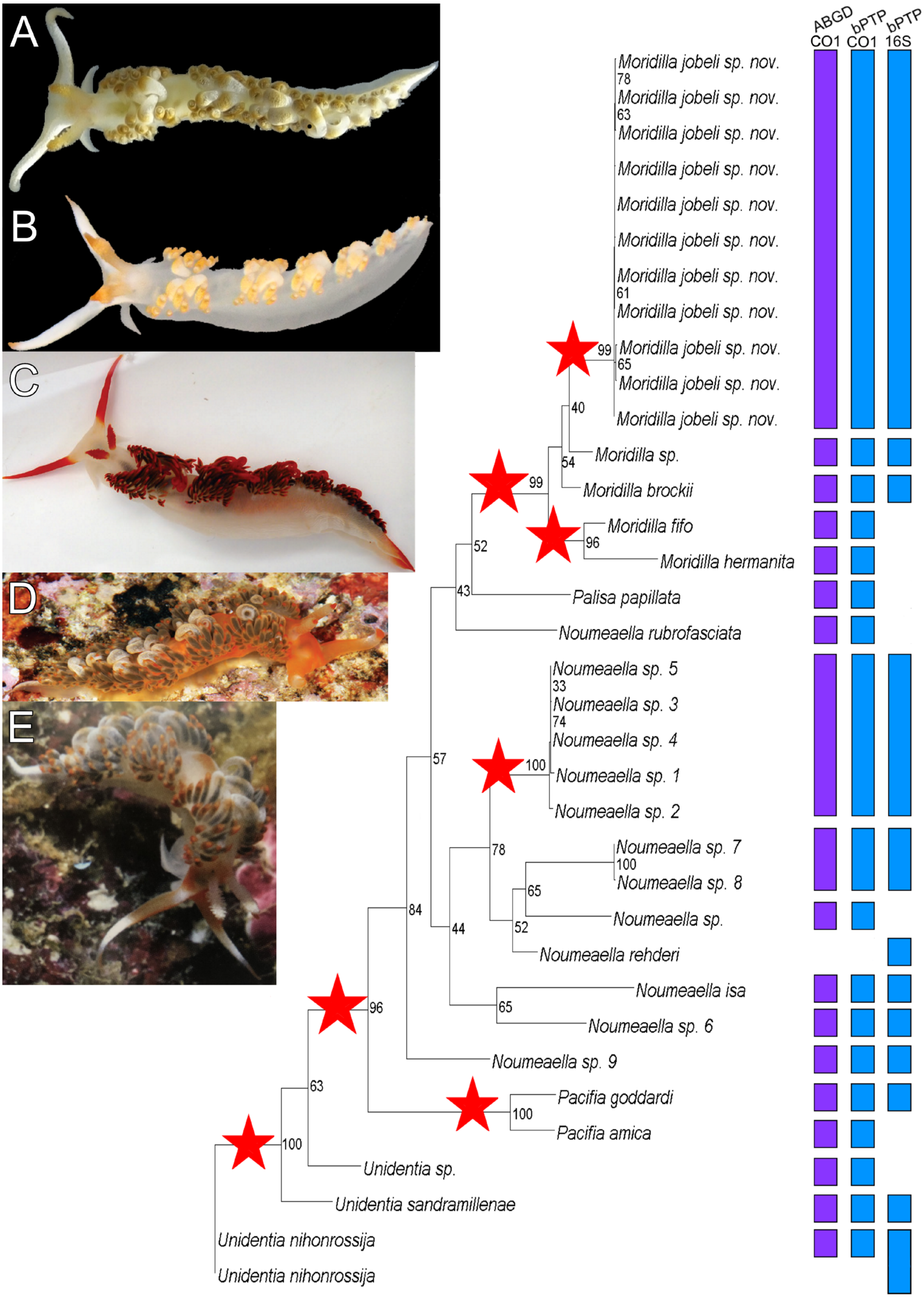

FIGURE 12. Maximum Likelihood tree of reduced data set of concatenated COI and 16S sequence data. Results of species delimitation tests of COI data with ABGD and bPTP tests, as well as 16S data with bPTP test depicted on the right side. Specimen numbers sp. 1 to sp. 9 refer to undescribed species, all listed as *Noumeaella* sp. in GenBank (also see Table 2). Stars indicate bootstrap values higher 90. (A) *Moridilla jobeli* **sp. nov. (**second paratype SRU20190001); (B) *Moridilla sp.* (SRU2017/01/Nosp1-17Ba-1); (C) *Moridilla fifo*; (D) *Moridilla hermanita;* (E) *Moridilla brockii* (C and D after Carmona & Wilson 2018; E after Gosliner *et al.* 2015)

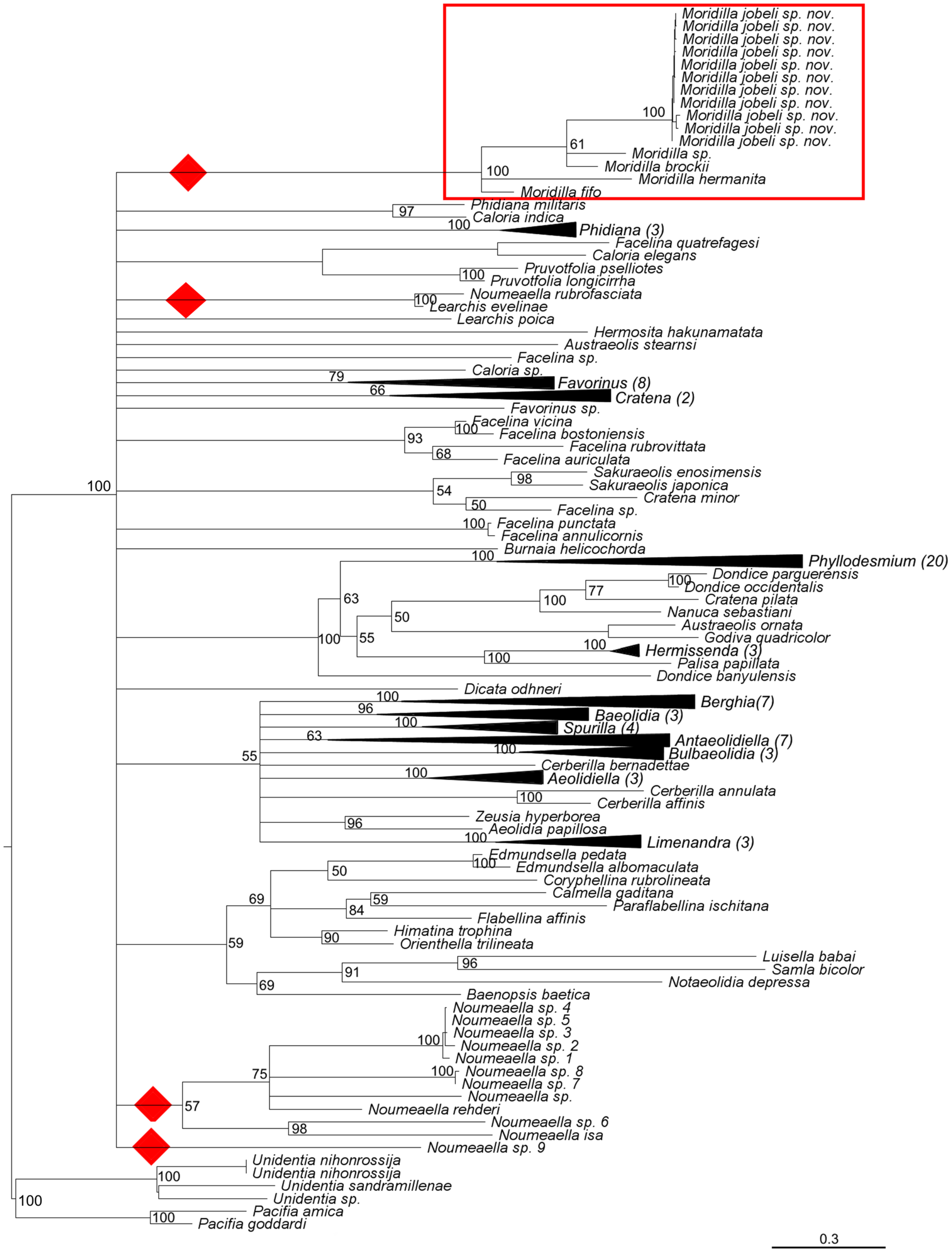

FIGURE 13. Maximum Likelihood tree of the concatenated full data set of H3, 16S and COI sequence data. Some clades are collapsed to condense information. Note the lack of resolution for most facelinid groups. Diamonds help visualize *Moridilla* and *Noumeaella* clades.

TABLE 4. Comparison of the distinguishing characters between the four described *Moridilla* species. Characters in which species are similar are not mentioned. Sources are the original descriptions by Bergh (1888) and Carmona & Wilson (2018) respectively.

	Moridilla brockii*	***Moridilla fifo***	***Moridilla hermanita***	***Moridilla jobeli* sp. nov.**
Locality	Edam Island, now Pulau Dapur, small island located north of modern-day Jakarta, Indonesia	Western Australia	Papua New Guinea	Bunaken, North Sulawesi, Indonesia
Size	length of preserved specimen 24 mm	not provided	not provided	largest length of preserved specimen: 25 mm, alive 60 mm
Body	elongate, slender	elongate, moderately broad, narrowing posterior	elongate, moderately broad, narrowing to posterior end of foot	elongate and slender in crawling animals
Color of body	("milchweis gewesen, der Rücken mennigroth gesprenkelt") body milk white, back speckled mennigroth (miniaceous, color of red lead)	translucent white to pale orange	translucent orange; tail tip white on midline	translucent pale to orange, with white patches behind the rhinophores
Color of rhinophores	not described	bright orange, almost red	pale, almost white; tips bright orange	tips cream coloured to light brownish or orange, but base never with coloration
Color of oral tentacles	not described	bright orange, almost red	distal third covered with white pigments, tips bright orange	first two thirds with white pigmentation at least in the back side; towards tips cream, brownish or orange coloured
Color of cerata	("Rückenpapillen schwärzlich braun") blackish brown	some specimens with light blue ceratal surface, with white subapical ring; others with completely white or orange-red pigmented cerata; most specimens have bright orange, almost red, cnidosacs; distal tips of ceratal surface of large, coiled innermost cerata always bright orange-red; cnidosacs not visible in these coiled cerata	olive green digestive gland visible; white subapical ring and bright orange cnidosacs; large, innermost coiled cerata covered with white pigments, cnidosacs not visible in these cerata	longest inner cerata white with light brownish or orange colouration at the base, tips always translucent; smaller cerata with less white pigmentation.
Color of tail	not described	bright orange, almost red on the midline	white on the midline	Transparent, dorsally with white pigment
Oral Tentacles	("Tentakel stark") sturdy	long, 3x length of rhinophores	2x length of rhinophores	2x length of rhinophores
Foot tentacle	probably short	Foot corners tentaculiform, short	Foot corners tentaculiform, short	long
Radula	single row of 7 teeth ("Zahnplatten")	19x0.1.0; 20x0.1.; 25x0.1.0; triangular central cusp, 3-4 smooth denticles on each side	22x0.1.0; triangular central cusp, 3-4 denticles each side	20 x 0.1.0; triangular central cusp, 2 denticles each side

......*continued on the next page*

TABLE 4. (Continued)

	Moridilla brockii[*]	*Moridilla fifo*	*Moridilla hermanita*	*Moridilla jobeli* **sp. nov.**
Jaws	masticatory border strong and curved with one row of denticles, number not given	masticatory boarder up to 18 comb-like denticles	translucent brown, large, broad; masticatory border up to 11 comb-like denticles	masticatory border with 6-7 denticles
Cerata	elongate, in tilted rows, anterior in clusters;	spindle shaped, long abundant; curved inwards, arranged in 5 groups: 1 precardiac, 4 postcardiac; each group has at least 1 long, coiled ceras. Each row 2-10 cerata	spindle-shaped, long abundant, leaving bare zone from behind rhinophores to tail; curved inwards towards dorsal mid line, arranged in up to 5 groups: 1x precardiac, 4x postcardiac; each group 4-8 rows, at least 1 long coiled ceras at upper part of oblique row close midline; Each row 2-8 cerata	Cerata arranged in indistinct 4-6 clusters with the first right and left cluster separated from the hind groups by the elevated pericardial area
Shape of cnidosac	("Nicht groß, birnförmig") not large, pear-shaped	not described	not described	large and winding
Position of anus	beneath 3rd group of cerata	below 3rd group of cerata	beneath 3rd group of cerata	between 2nd and 3rd group of cerata

[*]To prevent translation errors or misunderstandings, for some characteristics the original German description is quoted.

Acknowledgements

We wish to thank the staff of Panorama Dive Resort, Bunaken Island, for their continuous support. Our special thanks goes to Jobel Dialao for the numerous amazing dives. This research was funded by the Federal Ministry of Education and Research (BMBF) in the frame of the "Biodiversity and Health—from Biodiversity to Biomedical Innovation" program to HW (IndoBio project, grant 16GW0118), TFS and GMK (IndoBio project, grant 16GW0117K). NU and AP have grants provided by the German Academic Exchange Service (DAAD). JHE was partly funded by the Alexander Koenig Gesellschaft (AKG). Special thanks to Claudia Etzbauer for her constant support in the laboratory. We also thank Rudolf Meier and Danwei Huang (Singapore) for cooperation. The material was legally collected with permits for the Bunaken National Park to F. Kaligis, R. Bara, H. Wägele, T.F. Schäberle and N. Undap (SI.272/BTNB/PK/2015; SI.399/BTNB/PK/2016). The material is registered in the Reference Collection of the Sam Ratulangi University (Faculty of Fisheries and Marine Science) (SRU2015/01, SRU2016/02, SRU2017/01). The material was loaned to the authors for further investigation. We are very grateful to Markus Lasut and Grevo Gerung (Faculty of Fisheries and Marine Science, Manado) for continuing support and helping in the ABS paper work to follow the Nagoya Protocol. The authors thank the Republic of Indonesia for making this research possible.

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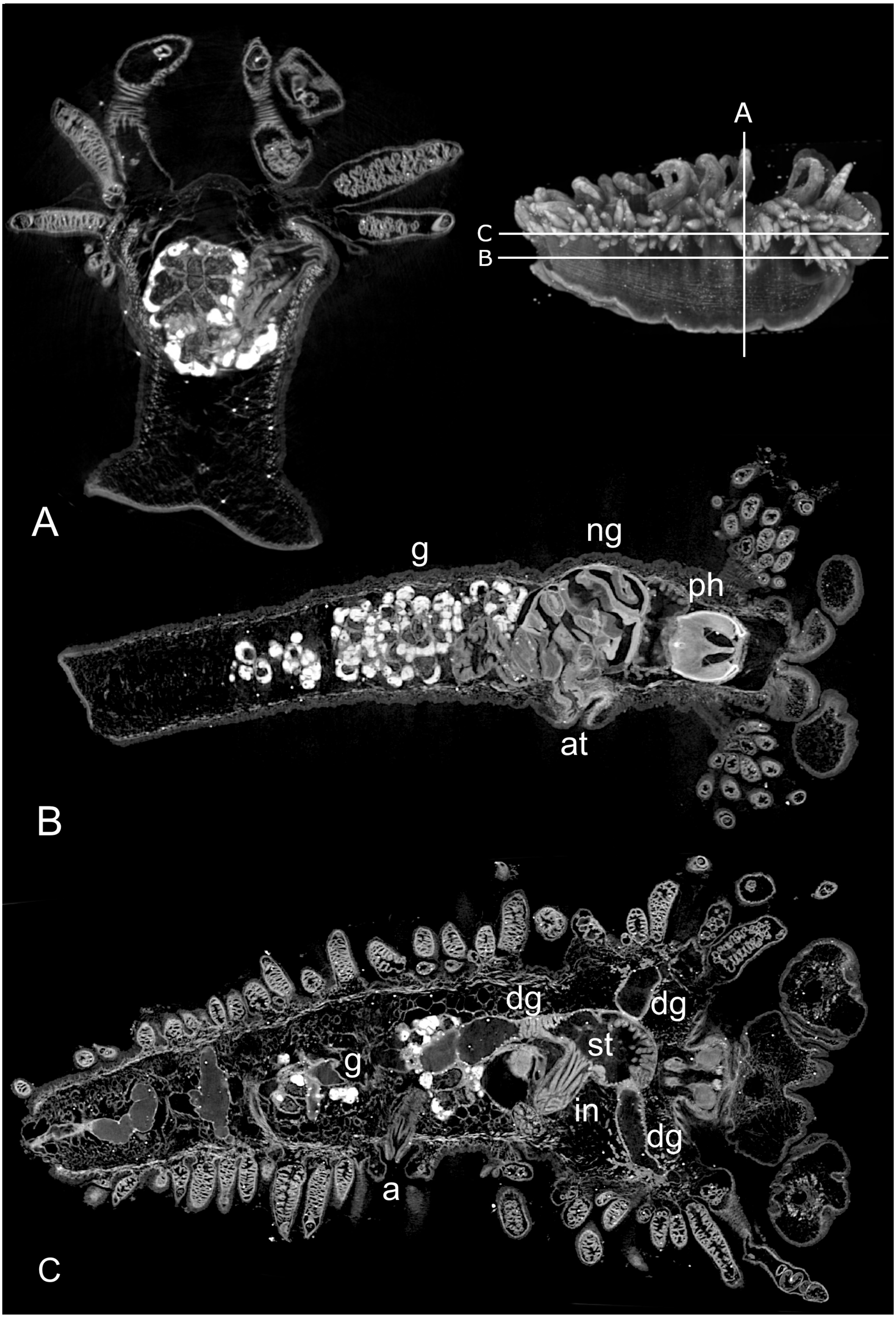
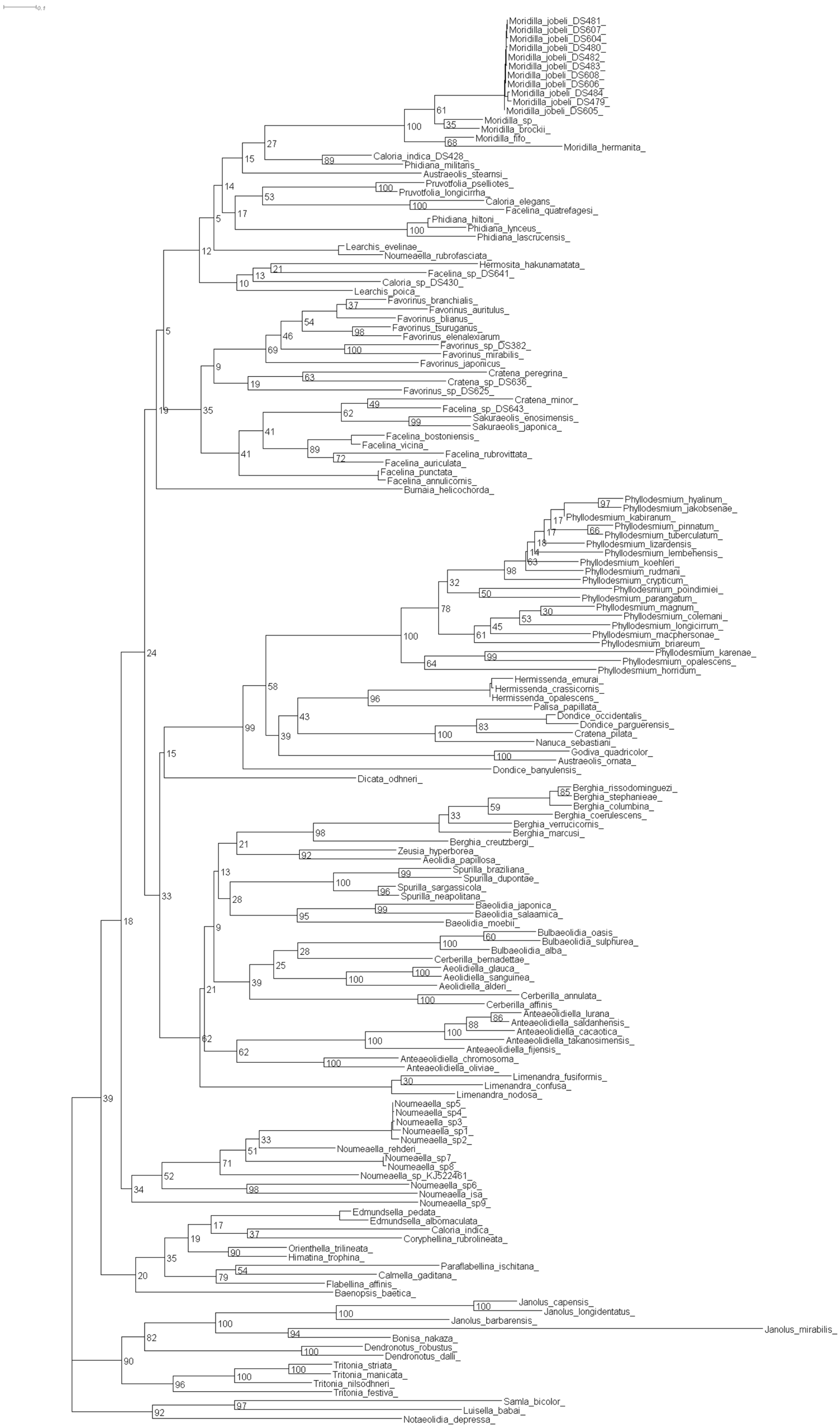


SUPPLEMENTARY FIGURE 1. *Moridilla jobeli* **sp. nov.**: MicroCT scans of paratype MZB.Gst.21.593. (A) Cross section of ovotestis and locations of sections; (B) longitudinal section through pharynx and genital system; (C) longitudinal section through digestive system. Abbrevations: a, anus; at, atrium; dg, digestive gland; g, gonad; jw, jaw; ng, nidamental gland; ph, pharynx; st, stomach.



SUPPLEMENTARY FIGURE 2. Maximum Likelihood tree of the concatenated full data set of H3, 16S and COI sequence data including more and alternative cladobranch taxa as outgroups. Nodes were not collapsed and bootstrap values are indicated.

SUPPLEMENTARY TABLE 1. Additional outgroup taxa used in Maximum Likelihood tree Supplementary Figure 2. Species names, voucher numbers and GenBank accession numbers.

		GenBank Accession No.		
Species	**Voucher No.**	**COI**	**16S**	**H3**
Dendronotoidea Allman, 1845				
Dendronotidae Allman, 1845				
Dendronotus dalli Bergh 1879	ZMMU:Op-295	KM397001	KM397083	KM397094
Dendronotus lacteus (W. Thompson, 1840)	ZMMU:Op-286	KC660034	KC611290	KC660050
Dendronotus robustus A.E. Verrill, 1870	ZMMU:Op-391	KM396970	KM397053	KM397120
Proctonotoidea Gray, 1853				
Proctonotidae Gray, 1853				
Bonisa nakaza Gosliner,1981	CASIZ176146	HM162746	HM162670	HM162579
Janolus barbarensis (J. G. Cooper, 1863)	CASIZ176833	HM162747	HM162671	HM162580
Janolus capensis Bergh, 1907	CAS:IZ:176974	KP940453	KP940448	KP940458
Janolus mirabilis Baba & Abe, 1970	CASIZ179494	HM162750	HM162674	HM162583
Tritonioidea Lamarck, 1809				
Tritoniidae Lamarck, 1809				
Tritonia festiva (Stearns, 1873)	CAS:IZ:184478	KP153291	KP153258	KP153324
Tritonia manicata (Deshayes, 1853)	-	KY629602	KY629592	KY629606
Tritonia striata Haefelfinger, 1963	BAU2696	LT596541	LT596543	LT615408

SUPPLEMENTARY VIDEO 1. *Moridilla jobeli* **sp. nov.:** A 3D reconstruction of MicroCT scans of paratype MZB.Gst.21.593. Organs are visualized in different colours.

SUPPLEMENTARY VIDEO 2. *Moridilla jobeli* **sp. nov.:** Series of MicroCT scans of cross sections through M*oridilla jobeli* **sp. nov.** (paratype MZB.Gst.21.593) from posterior to anterior.