Zoological Journal of the Linnean Society, 2019, **186**, 116–189. With 40 figures.

Reading between the lines: revealing cryptic species diversity and colour patterns in *Hypselodoris* nudibranchs (Mollusca: Heterobranchia: Chromodorididae)

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Received 16 December 2017; revised 16 May 2018; accepted for publication 27 May 2018

A molecular phylogeny is presented for 48 species of the genus *Hypselodoris* (Family: Chromodorididae), which incorporated 64 newly sequenced specimens. *Hypselodoris* is monophyletic and divided into clades that exhibit varying support. Novel diversity was found, with the distinctness of 17 new species of *Hypselodoris* supported by the molecular phylogeny, subsequent species delimitation analysis and morphological data. The following species are described here: ***Hypselodoris alburtuqali*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris brycei*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris cerisae*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris confetti*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris iba*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris juniperae*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris katherinae*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris lacuna*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris melanesica*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris paradisa*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris perii*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris roo*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris rositoi*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris skyleri*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris variobranchia*** Gosliner & Johnson **sp. nov.**, ***Hypselodoris violacea*** Gosliner & Johnson **sp. nov.** and ***Hypselodoris yarae*** Gosliner & Johnson **sp. nov**. Further examination of colour patterns supports previous suggestions that inheritance of colour patterns from common ancestors occurs, as do convergences, driven by Müllerian mimicry.

ADDITIONAL KEYWORDS: biogeography – coral reefs – Coral Triangle – cryptic species – mimicry – molecular phylogeny – morphology – new species – species richness.

INTRODUCTION

The Indo-Pacific genus *Hypselodoris* Stimpson, 1855 is one of the most diverse lineages within the megadiverse nudibranch family Chromodorididae (Gosliner *et al.*, 2015). The World Register of Marine Species (WoRMS; WoRMS Editorial Board, 2017) lists 59 species as accepted members of this genus. The most recent review of this group, by Gosliner & Johnson (1999), added 12 new species to the genus and taxonomically reviewed most of the described species. Since then, publication of a molecular phylogeny of the Chromodorididae (Johnson & Gosliner, 2012) demonstrated the need for revision of the systematics

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[Version of Record, published online 14 September 2018; http://zoobank.org/urn:lsid:zoobank.org:pub:F0065FD2-417C-4334-A985-EFF297428340]

of *Hypselodoris* and other genera. Former Atlantic and eastern Pacific species included in *Hypselodoris* were transferred to *Felimare* Marcus & Marcus, 1967, and species of *Risbecia* Odhner, 1934 were included in *Hypselodoris*. Additionally, since the review by Gosliner & Johnson (1999), several other species of *Hypselodoris* have been described: *Hypselodoris alaini* Ortea, Espinosa & Buske, 2013, *Hypselodoris apolegma* Yonow, 2001, *Hypselodoris babai* Gosliner & Behrens, 2000, *Hypselodoris fortunensis* Ortea, Espinosa & Buske, 2013, *Hypselodoris jacksoni* Wilson & Willan, 2007, *Hypselodoris katherythros* Yonow, 2001, *Hypselodoris lalique* Ortea & Caballer, 2013 in Ortea *et al.* (2013) and *Hypselodoris samueli* Caballer & Ortea, 2012.

The aim of the present study was further to elucidate the evolutionary history of the clade *Hypselodoris* by generating a more detailed phylogeny to test relationships at the species level and to examine colour evolution and the use of mimicry within this genus. Extensive fieldwork in many portions of the Indo-Pacific tropics has brought many apparently new species to light. This new material provides the opportunity to test the presence of cryptic species within these taxa and to determine whether geographically isolated individuals represent distinct species, as was determined for species of the genera *Glossodoris* and *Doriprismatica* (Matsuda & Gosliner, 2017). Of particular interest is the issue of species composition within the *Hypselodoris bullockii* complex. Rudman (1999a) has considered a wide range of colour variants as conspecific, whereas others (e.g. Gosliner *et al.*, 2015) consider this group to represent a series of cryptic species. The determination of these attributes has a bearing on evolutionary features of many aspects of the comparative biology of these species, including biogeography and evolution of colour patterns.

Members of *Hypselodoris* are brightly coloured species that inhabit the coral reefs of the Indo-Pacific tropics and adjacent temperate regions. Coral reefs are home to some of the most remarkable colours and patterns in nature. These colours and patterns allow for conspecific and interspecific signalling, camouflage, crypsis and protection from predation (Edmunds, 1987). Some of the most striking colour and pattern variations are found in the opisthobranchs, often having bright and contrasting coloration. Owing to their abundance of chemical defenses that can be produced *de novo* or acquired from their diet (Cimino & Ghiselin, 1989, 1999, 2009), this colouration is thought to be attributed to aposematism (Gosliner & Behrens, 1989; Gosliner, 2001). Aposematic organisms are those that use colour as a warning advertisement, indicating that a species is either chemically or otherwise defended (Gosliner & Behrens, 1989). The conspicuousness of nudibranch coloration has been found to be correlated positively with toxicity (Cortesi & Cheney, 2010) and, in an early review by Gosliner & Behrens (1989), it was found that 50% of opisthobranch species exhibit aposematism, whereas the remainder use other colour-related defense strategies, such as crypsis or camouflage. Gosliner (2001) offered further experimental proof of unpalatability in chromodorid nudibranchs. These findings provide evidence for the evolution of colour (and aposematism) as a defensive trait in nudibranchs.

Colour is often relied upon as an identification tool for opisthobranchs, recognized as such in taxonomic descriptions (Rudman, 1984; Gosliner, 2011) and in field guides (Gosliner *et al.*, 2008, 2015). This reliance is dependent on the idea that individuals of the same species share the same or very similar colour patterns. However, colour variation within a species has been recognized previously, and although many consider it an exception to the rule (Edmunds, 1987), more recent molecular studies have elucidated considerable variation within species (e.g. Pola *et al.*, 2006; Ornelas-Gatdula *et al.*, 2012; Valdés *et al.*, 2013; Padula *et al.*, 2016; Almada *et al.*, 2016; Layton *et al.*, 2018), challenging this perception.

Rudman (1991) suggested that the colour patterns of chromodorid nudibranchs, within species, are stable. However, where colour variations are evident, they can be distinct and are thought to occur allopatrically. Across the family, particular colour patterns can be used to characterize larger groups of unrelated species, which led Rudman to describe a series of distinct colour groups, into which most chromodorid species can be placed. For these colour groups, Rudman made the following five observations: (1) similarities in colour pattern occur most often between unrelated species; (2) unrelated species within a colour group are often sympatric and occur in a particular geographical region; (3) any closely related species within a colour group tend to be allopatric and exhibit a more widespread geographical range; (4) sympatric colour groups are highly developed in isolated geographical regions outside the tropics; and (5) those species that make up sympatric colour groups are likely to be abundant locally (Rudman, 1991). It has been suggested previously that Müllerian mimicry is likely to be at play among similar-coloured chromodorid nudibranchs (Gosliner & Behrens, 1989; Gosliner, 2001), which is reliant on some species being aposematic in order to explain the extensive amount of mimicry that is found within this family (Haber *et al.*, 2010). This type of mimicry is particularly evident in the chromodorid genus *Hypselodoris*, although the extent of aposematism and mimicry in this group is still unclear given the uncertainty of the systematics of the group, especially within the *H. bullockii* complex. In the present study, the phylogeny of the genus *Hypselodoris* was revisited, and descriptions of 17 previously undescribed species are included. With these taxonomic

revisions and expanded phylogeny, issues of evolution of colour patterns and biogeography in *Hypselodoris* were also re-examined in light of this new evidence.

MATERIAL AND METHODS

MOLECULAR WORK

Taxon sampling

The specimens used for sequencing in this study were collected primarily for molecular work and were preserved in 95% ethanol. A total of 105 specimens, 64 newly sequenced and 41 with one or more genes already published and available on GenBank, were used for phylogenetic reconstruction. Two hundred and twenty-seven new sequences from 95 of these specimens are available on GenBank with accession numbers MG645394–MG645621. Vouchers and types were deposited at the California Academy of Sciences (CASIZ), the Western Australian Museum (WAM) and the National Museum Philippines (NMP). Specimens sampled are listed in the Supporting Information (Table S1), along with their corresponding voucher numbers, GenBank accession numbers and collection sites.

DNA extraction

The Qiagen DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA, USA) spin column extraction method was used for extracting genomic DNA from specimens. Final DNA extractions were suspended in 50–200 µL AE buffer depending on the size of the tissue sample.

Gene selection and PCR amplification

Amplification of double-stranded products from the cytochrome *c* oxidase I (*COI*) and *16S* mitochondrial genes and the histone 3 (*H3*) nuclear gene was achieved through polymerase chain reaction (PCR) using gene-specific primers (Table 1). The PCR was carried out using a 25 µL reaction volume. Each reaction consisted of the following: 2.5 µL 10× PCR buffer, 0.5 µL dNTPs (10 mM stock), 0.085–0.1 µL $MgCl_2$ (50 mM stock), 0.25 µL of each primer (25 µM stock), 5 µL betaine, 1 µL bovine serum albumin, 0.5 µL Hot-Start Taq (25 units/µL stock), 12.00–12.15 µL of Millipore-H_2O, and 2 µL of DNA template. All reactions were run on a BioRad C1000 Thermal Cycler (Bio-Rad Laboratories) following gene-specific protocols (Table 2).

The PCR products were then examined using gel electrophoresis on 1% Tris-Borate-EDTA-agarose gel stained with ethidium bromide. Successful products were cleaned using ExoSAP-IT (USB Scientific). Samples showing strong bands in gel electrophoresis were cleaned using 2 µL of ExoSAP-IT to 5 µL of PCR product and those showing weak bands were cleaned using 1 µL of ExoSAP-IT to 7 µL of PCR product. The standard protocol for ExoSAP-IT was followed and run on a BioRad C1000 Thermal Cycler (Bio-Rad Laboratories).

Sequencing

Clean PCR products were copied and fluorescently labelled with dye-terminators (Big Dye 3.1 ABI). Each 10 µL reaction contained the following: 1.63 µL of 5× reaction buffer, 0.5 µL of primer (10 µM stock), 0.75 µL

Table 1. Primers used for DNA amplification for the genetic markers *COI*, 16S and *H3*

Primer	Reference	Sequence	Substitution model for Bayesian inference
COI			
CO1490L	Folmer *et al.* (1994)	5′-GGTCAACAAATCATAAAGATATTGG-3′	Codon position 1: SYM+G
CO2198H	Folmer *et al.* (1994)	5′-TAAACTTCAGGGAGACCAAAAAATCA-3′	Codon position 2: GTR+I+G
			Codon position 3: HKY+I+G
jgLCO1490*	Geller *et al.* (2013)	5′-TITCIACIAAYCAYAARGAYATTGG-3′	
jgHCO2198*	Geller *et al.* (2013)	5′-TAIACYTCIGGRTGICCRAARAAYCA-3′	
16S			
16Sar	Palumbi *et al.* (1991)	5′-CGCCTGTTTATCAAAAACAT-3′	GTR+I+G
16Sbr	Palumbi *et al.* (1991)	5′-CCGGTCTGAACTCAGATCACGT-3′	
H3			
H3F	Colgan *et al.* (1998)	5′-ATGGCTCGTACCAAGCAGACVGC-3′	Codon position 1: JC+G
H3R	Colgan *et al.* (1998)	5′-ATATCCTTRGGCATRATRGTGAC-3′	Codon position 2: GTR+I
			Codon position 3: GTR+G

Substitution models estimated by PartitionFinder and used in Bayesian inference are also included for each gene and codon position. *The 'jg' primer set was used for *COI* samples that failed to amplify using the primers from Folmer *et al.* (1994). The 'jg' primers were developed from the Folmer *et al.* (1994) primers CO1490L and CO2198H by Geller *et al.* (2013). Nucleotide positions with fourfold degeneracy were replaced with inosine nucleotides (dITP), which form binding pairs with any nucleotide present. Positions with twofold degeneracy were synthesized with mixed nucleotides to create a primer pool that can accommodate all nucleotide variants. These replacements are labelled 'I', 'R' and 'Y' in the sequence (Geller *et al.*, 2013).

Table 2. PCR protocols for genetic markers *COI*, 16S and *H3* by primer set

Genetic marker	*COI*				16S		*H3*	
Primer set	CO1490L, CO2198H		jgLCO1490, jgHCO2198		16Sar, 16Sbr		H3F, H3R	
PCR phase	Temperature (°C)	Time (s)	Temperature (°C)	Time (s)	Temperature (°C)	Time (s)	Temperature (°C)	Time (s)
Initial denaturation	94	180	95	600	94	180	94	180
Cycles	×39 of the following		×35 of the following		×39 of the following		×35 of the following	
Denaturation	94	30	95	30	94	30	94	30
Annealing	50	30	48	30	50	30	54	30
Extension	72	60	72	45	72	60	72	60
Followed by								
Final extension	72	300	72	600	72 25	300 300	72	600

of Big Dye, 5.12 µL of Millipore-H_2O and 2 µL of cleaned PCR product. These reactions were run on either a BioRad C1000 Thermal Cycler (Bio-Rad Laboratories) or a BioRad MyCycler Thermocycler (Bio-Rad Laboratories) using the STeP fast cycling protocol (Platt *et al.*, 2007) for cycle sequencing. Precipitation of the labelled, single-stranded DNA was carried out by adding 2.5 µL of EDTA followed by sequential washing and centrifugation using 100 and 70% ethanol to form DNA pellets. Samples were placed in a 60 °C incubator for 8 min to evaporate all remaining ethanol. Ten microlitres of HiDi formamide (Applied BioSystems) was added to each DNA pellet, and the DNA was then denatured in formamide at 94 °C for 2 min and immediately cooled on ice for 5 min. These denatured and fluorescently labelled DNA fragments were then sequenced in both directions on the ABI 3130 Genetic Analyzer in the Center for Comparative Genomics at the California Academy of Sciences.

Sequence alignment and analyses

The forward and reverse strands for each gene fragment that was sequenced were assembled, trimmed at the primer sites and edited using Geneious v. 7.1 and v. 9.0 (Biomatters). Alignment of *COI*, 16S and *H3* sequences was initially done using MAFFT alignment (Katoh *et al.*, 2009), and additional editing was done by hand. Alignments of all genetic markers were then concatenated for further use in phylogenetic reconstruction. Saturation was checked by plotting the uncorrected p-distances for transitions and transversions against the uncorrected p-distances for all substitutions for each codon position in *COI* and *H3* using PAUP* v. 4.0a147 (Swofford, 2002). Saturation in 16S was checked by plotting the uncorrected p-distances for transitions and transversions against the total number of character differences. Evolutionary relationships were estimated for the concatenated genetic markers using Bayesian inference (BI) and maximum likelihood (ML) analyses. Best-fit evolution models for BI and partition definitions for ML were determined using PartitionFinder (Lanfear *et al.*, 2012). The dataset was partitioned by genetic marker and codon position. Bayesian inference was performed in MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003), and the dataset was run for 5×10^7 generations, with Markov chains sampled every 1000 generations, and the standard 25% burn-in calculated. Convergence was checked using TRACER v. 1.6.0 (Rambaut *et al.*, 2014). A 50% majority rule consensus tree of calculated posterior probabilities (pp) was created using the remaining tree estimates. Tree branches were considered strongly supported if posterior probabilities were ≥ 0.95. Those with posterior probability values of ≤ 0.94 were considered to have low support. Randomized accelerated maximum likelihood (RAxML) v. 7.2.6 (Stamatakis, 2006) was used to estimate non-parametric bootstrap values with the evolution model GTR-GAMMA and was set for 5×10^4 fast bootstrap runs. Branches with bootstrap values of ≥ 70 were considered strongly supported, whereas those with values < 70 were considered weakly supported.

Species delimitation

In-group cryptic diversity and species delimitations were characterized using the automatic barcode gap discovery (ABGD) method outlined by Puillandre *et al.* (2012). The ABGD method identifies what are referred to as 'barcode gaps', or breaks between intra- and interspecific variation, by using genetic pairwise distances. This was achieved by using the Jukes–Cantor model to estimate a *COI* genetic distance matrix in *MEGA* v. 6.06 and subsequently uploaded to the ABGD

Web-based interface (http://wwwabi.snv.jussieu.fr/public/abgd/). Settings were kept at default, apart from the relative gap width (*X*), which was set to one.

Evolution of colour pattern and gill morphology

Three hypotheses were examined regarding colour pattern evolution in the *Hypselodoris* genus. Each hypothesis varied in classification and designation of *Hypselodoris* species into different colour groups. The first two datasets were gleaned from the literature (Rudman, 1991; Gosliner *et al.*, 2015), and a current hypothesis was developed during this study. The current hypothesis also included traits of elevated and vibrating gill morphology. A vibrating gill has been noted in many chromodorid species (Rudman, 1984) as being important taxonomically. This is a gill that vibrates back and forth in the living animal.

The genetic data used to create the BI and ML phylogenetic estimates for ancestral character state reconstruction analyses were from a subset of the full phylogenetic dataset described above that included only one representative of each *Hypselodoris* species. This was done to avoid potential confounding noise from undescribed species owing to uncertainty concerning their morphological character states. From this dataset, 1000 trees were randomly sampled from a subset of 25 000 postburn-in trees from our BI estimate and pruned of outgroups using the package Ape v. 5.1 (Paradis *et al.*, 2004) in R v. 3.4.2 (R Core Team, 2017). Ancestral character state reconstructions were then conducted to examine the evolution of colour and gill morphology using a Bayesian framework implemented in BayesTraits v. 3 (Pagel *et al.*, 2004) under the multistate model of evolution using reverse jump with a hyperexponential prior. A Markov chain Monte Carlo (MCMC) was run for 2×10^7 iterations and sampled every 1000 generations with a burn-in of 5×10^5.

Ancestral area reconstruction

Ancestral geographical ranges were estimated using the Bayesian binary MCMC (BBM; Ronquist & Huelsenbeck, 2003) approach implemented in the software RASP (reconstruct ancestral state in phylogenies) v. 4.0 (Yu *et al.*, 2015). To limit uncertainty from the BBM analysis, outgroups and redundant *Hypselodoris* species were pruned from the BI consensus estimate. The geographical ranges of remaining taxa were defined based on the current knowledge of *Hypselodoris* distributions (Gosliner & Johnson, 1999; Gosliner *et al.*, 2008), which consisted of eight regions: northeastern Indian Ocean (A), temperate South Africa (B), Coral Triangle (C), Western Pacific (D), Western Australia (E), Hawaii (F), Red Sea (G) and temperate Australia (H). For the BBM analysis, ten MCMCs were run, each for 1×10^7 cycles with a sampling frequency of 1000, and discarded the first 2500 runs as burn-in. The remaining parameters were set to default (temperature, 0.1; model, JC; and among-site rate variation, equal).

Morphological methods

Morphological techniques were used to examine all previously undescribed species investigated here. Species were dissected by ventral incision using a Nikon SMZ-U dissection microscope. The reproductive system was removed by dissection and the morphology depicted by using a camera lucida drawing attachment. The buccal mass was removed and examined. The mass was placed in 10% sodium hydroxide (NaOH), allowed to soak for 4–24 h and then rinsed in double-distilled or deionized water. Once all connective tissue was removed, the radula and jaws were dried and mounted on stubs for examination by scanning electron microscope (SEM). Structures were then coated with gold/palladium using a Cressington 108 Auto vacuum sputter coater. Scanning electron micrographs were produced using a Hitachi SU3500 SEM. Specimens and dissected structures were deposited at the California Academy of Sciences in the Invertebrate Zoology Department collection (CASIZ).

RESULTS

SYSTEMATICS

Phylogenetic reconstruction and species delimitation

Our larger dataset and our subset dataset used in the ancestral character analyses gave fairly congruent estimates (Fig. 35; Supporting Information, Figs S1, S2). The larger phylogeny presented here (Fig. 35), based on concatenated *COI*, 16S and *H3* sequences using both BI and ML analyses, reinforces the monophyly of *Hypselodoris* with strong support (pp = 1.00). The sister relationship of *Hypselodoris* to *Thorunna* is only weakly supported in this study (pp = 0.9). Within the *Hypselodoris*, there are a number of supported clades with high posterior probabilities and bootstrap values. A well-supported clade (pp = 1.00) containing *H. bullockii* and six other species that are sister to the rest of *Hypselodoris* includes: *Hypselodoris rositoi* Gosliner & Johnson sp. nov., *Hypselodoris violacea* Gosliner & Johnson sp. nov., *Hypselodoris variobranchia* Gosliner & Johnson sp. nov., *H. apolegma* Yonow, 2001, *Hypselodoris brycei* Gosliner & Johnson sp. nov., *H. melanesica* Gosliner & Johnson sp. nov. and *H. bullockii* Collingwood, 1881.

A second, large clade of 11 species, including *Hypselodoris nigrostriata* Eliot, 1904, *Hypselodoris*

confetti Gosliner & Johnson sp. nov., *Hypselodoris zephyra* Gosliner & Johnson, 1999, *Hypselodoris roo* Gosliner & Johnson sp. nov., *Hypselodoris lacuna* Gosliner & Johnson sp. nov., *Hypselodoris regina* Marcus & Marcus, 1970, *Hypselodoris krakatoa* Gosliner & Johnson, 1999, *Hypselodoris cerisae* Gosliner & Johnson sp. nov., *H. jacksoni* Wilson & Willan, 2007, *Hypselodoris reidi* Gosliner & Johnson, 1999 and *Hypselodoris iba* Gosliner & Johnson sp. nov., is also well supported (pp = 1.00). This clade is subdivided into two subclades, one of which is well supported (pp = 1.00) and includes the first four species listed above. The second subclade is only weakly supported for *H. lacuna* (pp = 0.89) but is strongly supported for the remaining six species (pp = 1.00).

The sister group to the two clades discussed above consists of a poorly supported clade (pp = 0.92) forming two subclades, both of which have strong support. The first of these subclades includes 16 species (pp = 1.00), further separated into a weakly supported subclade including almost no support for *Hypselodoris perii* Gosliner & Johnson sp. nov., as sister to the still weakly supported (pp = 0.88) following species: *Hypselodoris paulinae* Gosliner & Johnson, 1999, *Hypselodoris kaname* Baba, 1994, *Hypselodoris obscura* (Stimpson, 1855), *Hypselodoris infucata* (Rüppell & Leuckart, 1828), *Hypselodoris capensis* (Barnard, 1927), *Hypselodoris carnea* (Bergh, 1889), *Hypselodoris nigrolineata* (Eliot, 1904), *Hypselodoris ghardaqana* (Gohar & Aboul-Ela, 1957) and *Hypselodoris bollandi* Gosliner & Johnson, 1999, and a strongly supported further subclade (pp = 1.00) including *Hypselodoris skyleri* Gosliner & Johnson sp. nov., *Hypselodoris paradisa* Gosliner & Johnson sp. nov., *Hypselodoris katherinae* Gosliner & Johnson sp. nov., *Hypselodoris rudmani* (Gosliner & Johnson, 1999), *Hypselodoris bertschi* (Bergh, 1880) and *Hypselodoris maritima* (Baba, 1949). The second subclade of this sister group includes 11 species and is also strongly supported (pp = 1.00). This subclade includes *Hypselodoris yarae* Gosliner & Johnson sp. nov., *Hypselodoris imperialis* (Pease, 1860), *Hypselodoris tryoni* (Garrett, 1873), *Hypselodoris pulchella* (Rüppell & Leuckart, 1830), *Hypselodoris emma* Rudman, 1977, *Hypselodoris whitei* (Adams & Reeve, 1850), *Hypselodoris purpureomaculosa* Hamatani, 1995, *Hypselodoris alburtuqali* Gosliner & Johnson sp. nov., *Hypselodoris decorata* (Risbec, 1928), *Hypselodoris juniperae* Gosliner & Johnson sp. nov. and *Hypselodoris maculosa* (Pease, 1871). *Hypselodoris yarae* is sister to the remaining members of this clade, and the remaining members form two subclades that are well supported (pp = 1.00 for both). The first of these subclades includes the three members of what used to be the distinct genus *Risbecia* Odhner, 1934. The second subclade includes the seven species considered to form the *H. maculosa* clade.

Automatic barcode gap discovery analysis of the *COI* dataset resulted in delimitation of 41 distinct *Hypselodoris* species. All newly described species fell into separate groups and provide further support for the results of the phylogenetic reconstruction analyses. Uncorrected p-distances for *COI* were also used to examine the divergence of newly described species (Supporting Information, Table S2) to determine the range of variation within and between species.

Colour variation and patterns

The majority of species treated here have discreet colour patterns that do not vary a great deal among individuals of the same species. There are two major exceptions found in this study. *Hypselodoris iba* was found to have two distinct colour morphs (Fig. 14). Not only do these morphs exhibit no significant genetic difference, but they have also been observed mating with each other. *Hypselodoris variobranchia* varies in its gill colour, where the gill can be either purple or orange (Fig. 25C–F).

The three sets of species groups, Rudman (1991), Gosliner *et al.* (2015) and a current hypothesis, were compared by analysing colour characters to examine which species groups represent monophyletic groups in our subsequent phylogenetic analysis and which exhibit one or more instances of convergence (Fig. 36). The relevant colour groups were chosen from study by Rudman (1991), which included at least one representative of *Hypselodoris*. This resulted in nine different colour groups (Fig. 36A). Only two species have no other representatives of their colour group within *Hypselodoris*. In the case of *H. lacuna*, only members of the *Chromodoris aspersa* colour group have a similar colour pattern. Likewise, *H. regina* has a similar colour pattern to members of the *Chromodoris quadricolor* colour group that includes only species of *Chromodoris*. All other colour groups exhibit at least one instance of convergence between different lineages of *Hypselodoris*. Of the eight colour groups used by Gosliner *et al.* (2015) to group species of *Hypselodoris* (Fig. 36B), three small groups have no cases of convergence between clades (the purple-lined group, the red–brown-lined group and the species with red–purple rings or spots). The remaining five groups exhibit at least one case of convergence of colour patterns within *Hypselodoris*. In the six groups included in the current hypothesis (Fig. 36C), only *H. regina* does not have any other member of *Hypselodoris* with the same colour pattern, and it was convergent with species of the *C. quadricolor* group. The remaining five groups have at least one instance of convergence with other species of *Hypselodoris* from different clades. Two instances of convergence were particularly noteworthy in the current hypothesis.

The pink–purple colour group includes all species within the *H. bullockii* clade and also includes *H. iba*, which sits in the large clade including *H. nigrostriata* (Fig. 37). The yellow spots and purple group also shows convergence, where *H. imperialis* and *H. pulchella* share their colour pattern with *H. bollandi* and *H. ghardaqana* (Fig. 38).

Gill morphology characters were also analysed to examine convergence among species groups (Fig. 39). Gill morphologies included elevated, vibrating and regular. *Hypselodoris ghardaqana* shares the vibrating gill morphology with *H. imperialis*, *H. pulchella* and *H. tryoni,* showing convergence. Elevated gills are present in only six species, namely *H. krakatoa*, *H. regina*, *H. cerisae*, *H. jacksoni*, *H. iba* and *H. reidi*, and do not include any cases of convergence with any other lineages of *Hypselodoris*. The remaining species are all defined by regular gills, which are present across all *Hypselodoris* lineages.

Biogeography

The ancestral area reconstruction analysis (Fig. 40) suggested that the ancestor for *Hypselodoris* most probably originated from the Coral Triangle, which resulted in dispersal events west (Indian Ocean) and east (western Pacific). The BBM estimate recovered a high number of instances of dispersal events across the *Hypselodoris* phylogeny, and multiple colonizations of the Red Sea from the Indian Ocean and Hawaii from the western Pacific. Interestingly, despite the likelihood of dispersal in *Hypselodoris*, there were only two instances of colonization into temperate regions. Most dispersal events took place in more tropical regions, mainly between the Indian Ocean, the Coral Triangle and the western Pacific.

Species descriptions

Family Chromodorididae Bergh, 1981

Genus *Hypselodoris Stimpson, 1855*

Hypselodoris alburtuqali Gosliner & Johnson **sp. nov.**

(Figs 1A, 2A, 3, 4A)

LSID: urn:lsid:zoobank.org:act:5597044A-A9B3-4A7F-8FBF-25A512DB71CF

Hypselodoris sp. 2 Gosliner *et al.*, 2015: 254, bottom left photograph.

Type material

Holotype: CASIZ 192295, subsampled for molecular study, dissected, Abulad Island, Farasan Islands, Red Sea, Saudi Arabia, 8 m depth, 10 March 2013, T. M. Gosliner.

Type locality

Abulad Island, Farasan Islands, Saudi Arabia, Red Sea.

Geographical distribution

Saudi Arabian Red Sea.

Etymology

Hypselodoris alburtuqali is named for the Arabic word for ‘the orange one’, al burtuqali, owing to the orange coloration of this species.

Description

External morphology: Living animals (Fig. 1A) moderately large, reaching 30 mm in length. Body translucent pink, with about eight continuous or interrupted longitudinal lines on dorsal surface of notum. Anterior and posterior ends of the animal more opaque white than pink. Additional opaque white lines located on sides of animal and on posterior portion of foot. Longitudinal rows of dark brown spots situated between opaque white lines of notum and foot. Wide red–orange marginal band present along entire mantle and foot margins. Eight unipinnate gill branches having a translucent white base and bright red–orange pigment on apical surfaces and outer margin. Bulb of perfoliate rhinophores opaque white with two red–orange transverse bands and bearing about ten densely arranged lamellae. Base of rhinophores translucent white.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2A). Glands situated anteriorly and posteriorly, with no glands present in the central lateral regions of body margin. Nine to ten glands on either side of anterior end of the body, with arc of nine glands situated posteriorly.

Buccal armature: Muscular portion of buccal mass about twice length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass (Fig. 3A) bearing numerous jaw rodlets (Fig. 3B). Rodlets narrowly ovoid, with single, acutely pointed apex. Radular formula of holotype 44 × 26.0.26 (Fig. 3C). Rachidian row of teeth absent (Fig. 3D). Innermost lateral teeth having one or two large, triangular denticles on inner side of bifid primary cusp, with another one to two outer denticles. Next several laterals lacking inner triangular denticle but possessing two or three denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 3E) all lacking inner denticles but having three or four sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and shorter tooth shape, with three or four rounded outer denticles (Fig. 3F), often larger than bifid cusps.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 4A). Ampulla thick, tubular, narrowing

Figure 1. Living animals. A, ***Hypselodoris alburtuqali*** Gosliner & Johnson **sp. nov.**, CASIZ 192295, holotype, Saudi Arabia. B, ***Hypselodoris brycei*** Gosliner & Johnson **sp. nov.**, WAM S96082, holotype, Montebello Islands, Western Australia, photograph by Nerida Wilson. C, ***Hypselodoris cerisae*** Gosliner & Johnson **sp. nov.**, specimen from Hachijo Island, Japan, Nishina Masayoshi. D, ***Hypselodoris confetti*** Gosliner & Johnson **sp. nov.**, CASIZ 191070, Papua New Guinea, photograph by J. Goodheart. E, *Hypseldoris ghardaqana* (Gohar & Abu-Ela, 1957), CASIZ 192282, Saudi Arabia. F, ***Hypselodoris juniperae*** Gosliner & Johnson **sp. nov.**, CASIZ 177550, Radama Islands, Madagascar. G, ***Hypselodoris katherinae*** Gosliner & Johnson **sp. nov.**, CASIZ 176773, eastern Peninsular Malaysia. H, ***H. katherinae*** Gosliner & Johnson **sp. nov.**, CASIZ 177532, Batangas, Luzon, Philippines. I, ***H. katherinae*** Gosliner & Johnson **sp. nov.**, CASIZ 181300, Batangas, Luzon, Philippines. All photographs by T. Gosliner unless otherwise indicated.

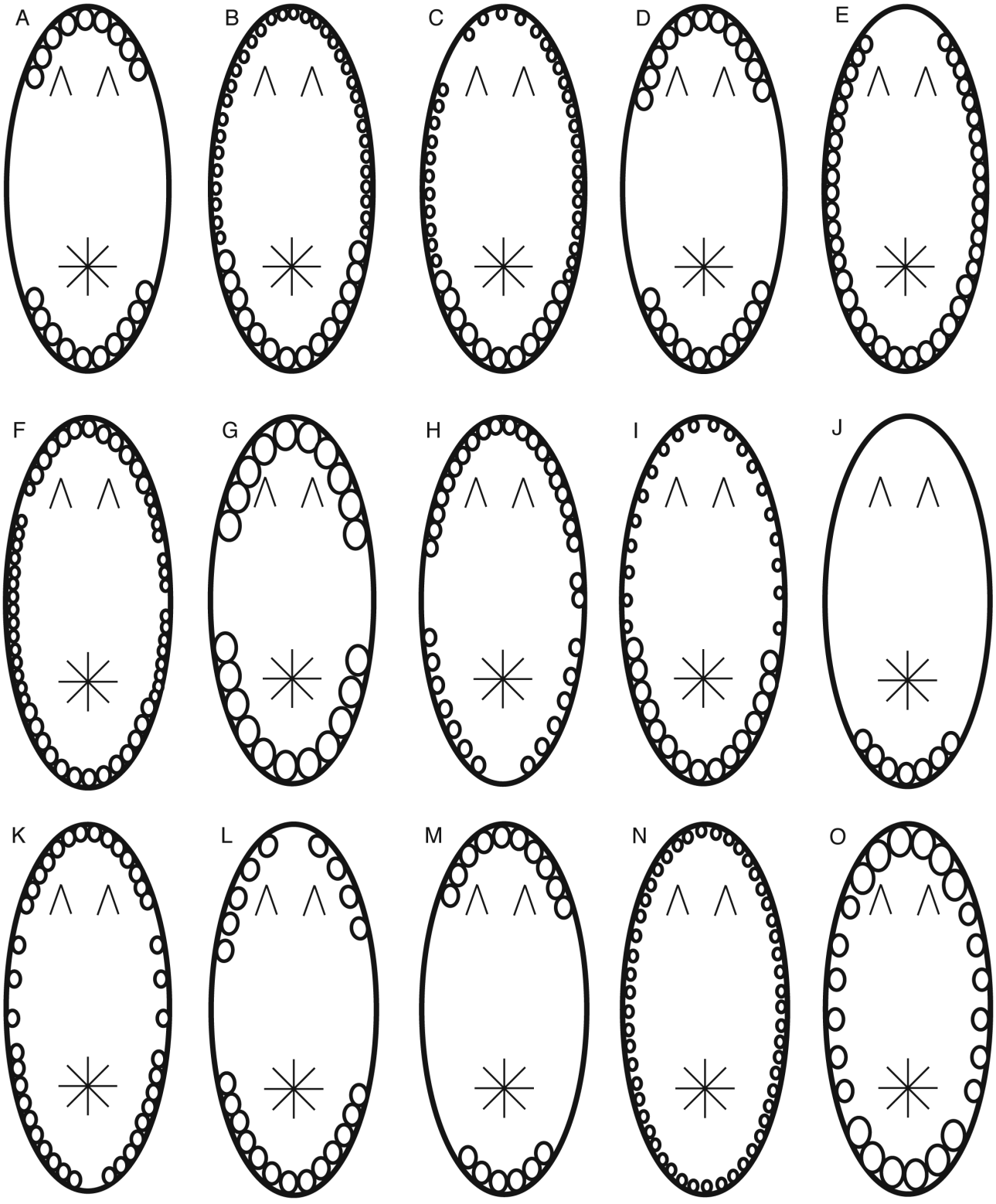

Figure 2. Mantle glands. A, ***Hypselodoris alburtuqali*** Gosliner & Johnson **sp. nov.**, CASIZ 192295, holotype. B, ***Hypselodoris cerisae*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 178350. C, ***Hypselodoris confetti*** Gosliner & Johnson **sp. nov.**, CASIZ 191070. D, *Hypselodoris decorata* (Risbec, 1928), CASIZ 184316. E, *Hypselodoris ghardaqana* (Gohar & Abu-Ela, 1957), CASIZ 192282. F, ***Hypselodoris iba*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041279.

G, ***Hypselodoris juniperae*** Gosliner & Johnson **sp. nov.**, CASIZ 177550. H, ***Hypselodoris katherinae*** Gosliner & Johnson **sp. nov.**, CASIZ 177532. I, ***Hypselodoris krakatoa*** Gosliner & Johnson, 1999, CASIZ 206801. J, ***Hypselodoris lacuna*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 208652. K, ***Hypselodoris paradisa*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 191464. L, ***Hypselodoris perii*** Gosliner & Johnson **sp. nov.**, NMP 041281. M, ***Hypselodoris roo*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 204801. N, ***Hypselodoris rositoi*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041283. O, ***Hypselodoris skyleri*** Gosliner & Johnson **sp. nov.**, composite of five specimens (CASIZ 200649, CASIZ 177305, NMP 041284, CASIZ 200552 and CASIZ 217424).

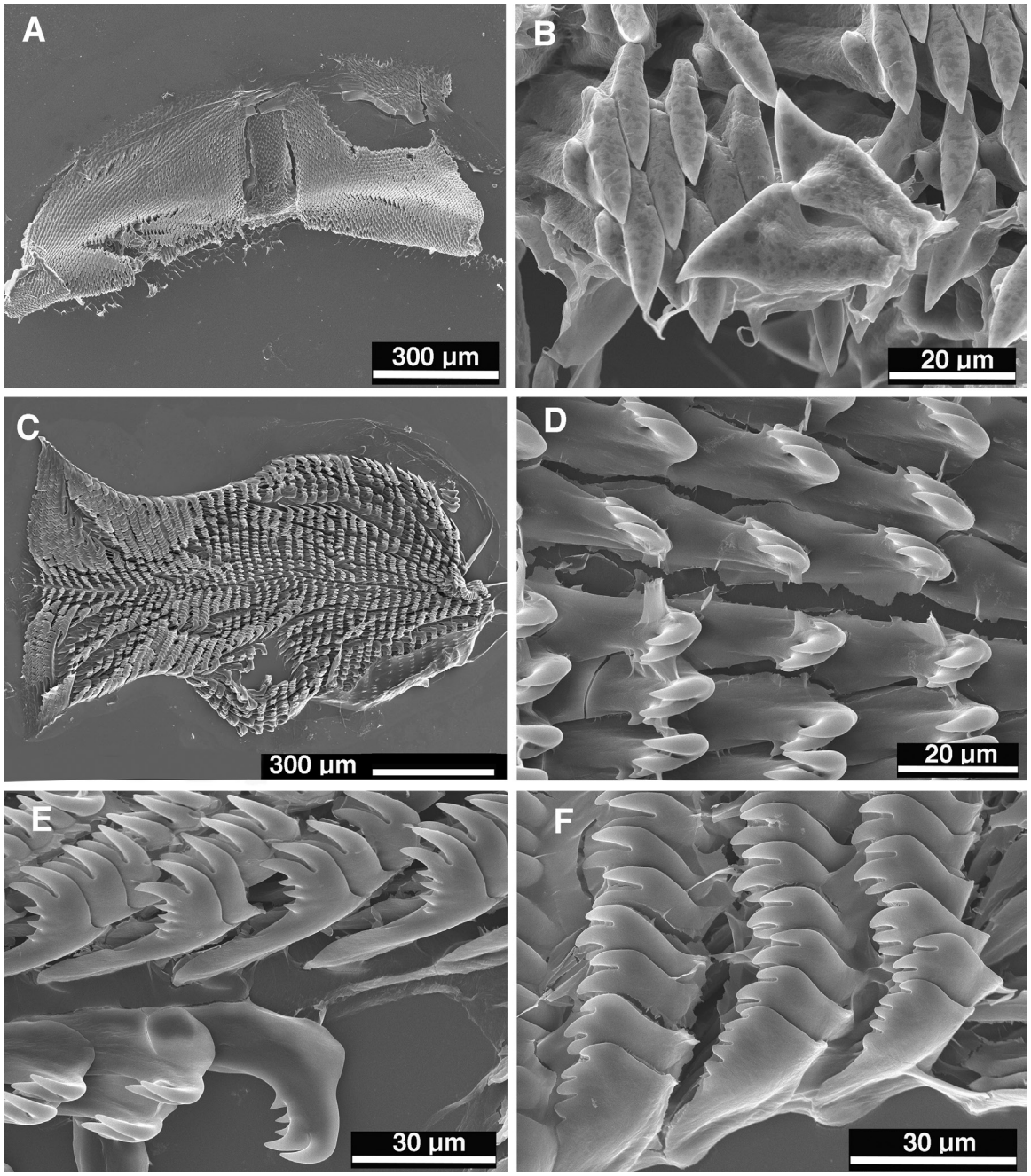

Figure 3. ***Hypselodoris alburtuqali*** Gosliner & Johnson **sp. nov.**, CASIZ 192295, holotype, buccal armature. A, portion of jaw. B, jaw rodlets. C, entire radula. D, innermost teeth. E, middle lateral teeth. F, outermost teeth.

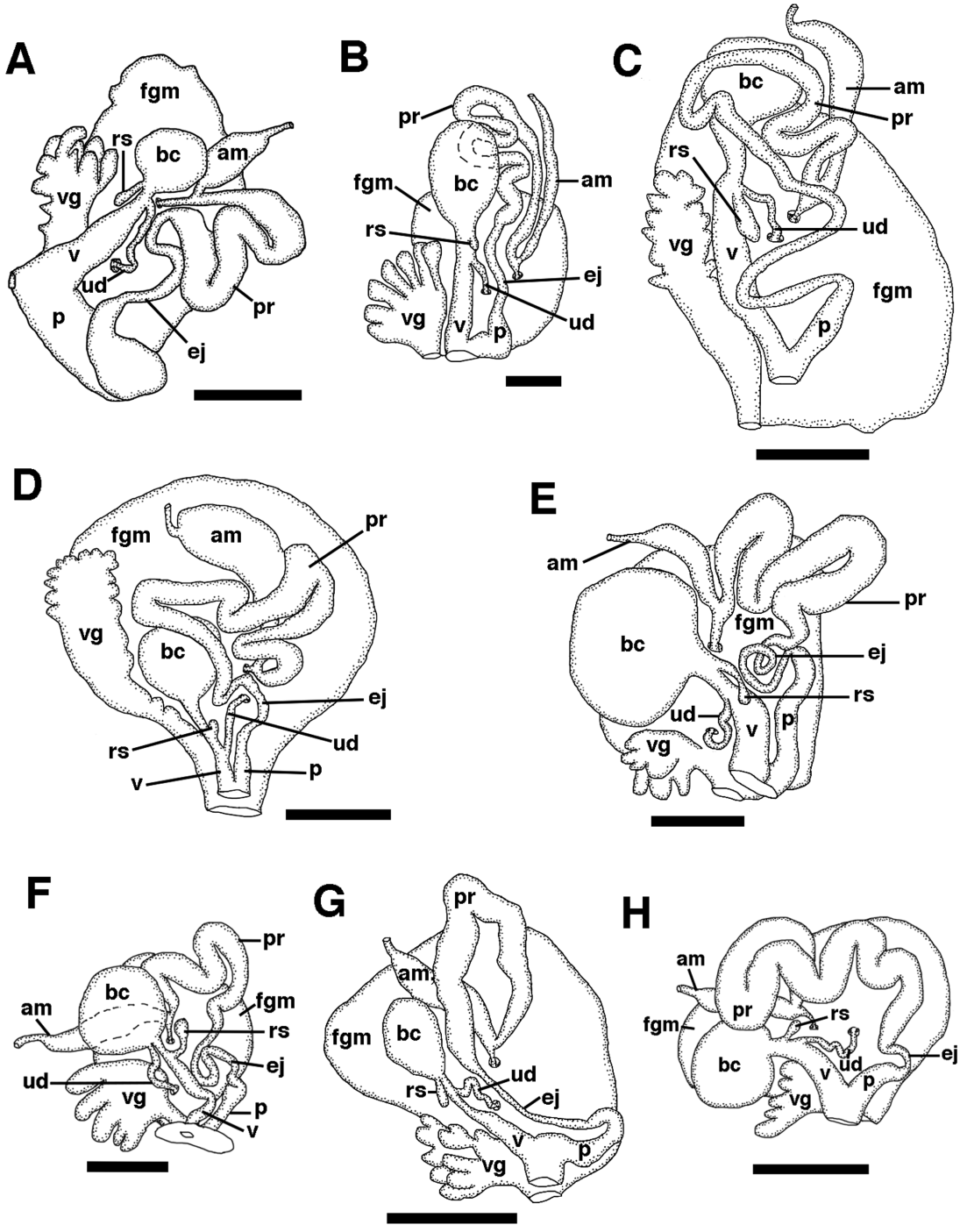

Figure 4. Reproductive systems A, ***Hypselodoris alburtuqali*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ19229, scale bar: 0.5 mm. B, *Hypselodoris maculosa* (Pease, 1871), CASIZ 139595, scale bar: 0.75 mm. C, ***Hypselodoris brycei*** Gosliner & Johnson **sp. nov.**, paratype, WAM S12628, scale bar: 3.0 mm. D, *Hypselodoris apolegma* (Yonow, 2001), CASIZ 083743, scale bar: 2.0 mm. E, ***Hypselodoris cerisae*** Gosliner & Johnson **sp. nov.**, holotype CASIZ 178350, scale bar: 0.85 mm. F, *Hypselodoris krakatoa* Gosliner & Johnson, 1999, CASIZ 206801, Philippines, scale bar: 1.0 mm. G, ***Hypselodoris confetti*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 191070, scale bar: 0.60 mm. H, *Hypselodoris decorata* (Risbec, 1928), CASIZ 184316, scale bar: 0.60 mm. am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of the vas deferens; fgm, female gland mass; p, penis; pr, prostatic portion of vas deferens; rs, receptaculum seminis; ud, uterine duct; v, vagina; vg, vestibular gland.

somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick and narrowing slightly as it transitions into muscular, ejaculatory portion. Ejaculatory portion widening again before entry into wider penial bulb. Penial bulb adjacent to straight, very wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively short vagina leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Moderately long uterine duct emerging from vagina close to base of bursa and female gland mass, near albumen gland.

Remarks

The colour pattern of *H. alburtuqali* most closely resembles that of *Goniobranchus* sp. 29 (Gosliner *et al.*, 2015: 227 upper left photograph), with which it is sympatric. Our molecular phylogeny (Fig. 35) clearly indicates that this species is in the *H. maculosa* clade. It is sister to the clade that includes *H. decorata* (Risbec, 1928), *H. juniperae* sp. nov., *H. maculosa* (Pease, 1871) and *H. yarae* sp. nov. and is shown to represent a distinct species in our ABGD analysis. The colour pattern most closely resembles that of *H. decorata* and *H. yarae*, but *H. alburtuqali* has a narrower red–orange margin, more longitudinal opaque white lines and more, smaller brown spots compared with *H. decorata* and *H. yarae*. Additionally, *H. decorata* has opaque white spots and purple markings on its anterior and posterior margins of the notum that are absent in *H. alburtuqali* and *H. yarae*. All of the members of this clade, including those species that were studied by Gosliner & Johnson (1999) and are not included in the present molecular phylogeny, have distinctive colour patterns on their rhinophores. *Hypselodoris alburtuqali*, *H. maculosa*, *H. peasei*, *Hypselodoris insulana* Gosliner & Johnson, 1999, *Hypselodoris alboterminata* Gosliner & Johnson, 1999 and *H. juniperae* have two reddish rhinophoral rings. In contrast, the rhinophores of *Hypselodoris violabranchia* Gosliner & Johnson, 1999 have a reddish base and a violet apex. The rhinophores of *H. decorata* and *H. yarae* have three red rhinophoral rings, and those of *Hypselodoris maridadilus* Rudman, 1977, *H. whitei* (Adams & Reeve, 1850) and *H. emma* all have uniformly red rhinophores with a white apex. Of those species with two red rhinophoral rings, *H. insulana* and *H. peasei* lack dark brownish spots on the notum and have more numerous opaque white lines on the notum, and *H. juniperae* has purple rather than dark brown spots and opaque white spots rather than lines on the notum.

Hypselodoris alburtuqali has mantle glands that are distributed completely around the anterior and posterior margins of the mantle, with no glands present along most of the lateral notal margins. Of the other members of this clade, only *H. maculosa*, *H. decorata*, *H. juniperae*, *H. alboterminata* and *H. whitei* have this arrangement of mantle glands (Gosliner & Johnson, 1999; present study, Fig. 2). *Hypselodoris peasei*, *H. insulana*, *H. violabranchia* and *H. emma* have a similar arrangement of mantle glands, but lack glands along the anterior edge and have anterior glands only along the anterolateral margins (Gosliner & Johnson, 1999). In *H. maridadilus*, the mantle glands are distributed along the entire margin of the mantle with the exception of the anterior margin, which is devoid of glands, whereas in *H. yarae*, the mantle glands are present all around the mantle margin.

The radulae of most members of this clade are very similar in the shape of their teeth and in the number of denticles on the teeth. *Hypselodoris alburtuqali* has three or four denticles on the middle lateral teeth, as do *H. alboterminata*, *H. decorata*, *H. insulana*, *H. yarae* and *H. juniperae*. In *H. emma* and *H. maculosa* there are four or five denticles, and *H. violacea* has five or six denticles (Gosliner & Johnson, 1999; present study).

The reproductive system of *H. alburtuqali* is unique among members of the *H. maculosa* clade in having a much wider vagina (Fig. 4A). In *H. maculosa* (Fig. 4B) *H. decorata* (Fig. 4H) and *H. yarae* (Fig. 33B), the vagina is much narrower. In *H. alburtuqali*, *H. decorata* and *H. maculosa*, the receptaculum seminis is situated at the base of the bursa copulatrix or immediately below it, whereas in *H. yarae* it is much more distally situated. In *H. alburtuqali*, the uterine duct connects to the vagina immediately below the bursa and receptaculum, whereas in *H. decorata* and *H. maculosa* the uterine duct branches from the vagina well below the base of the bursa and receptaculum. In *H. yarae*, the uterine duct emerges from the base of the vagina, near the genital opening, and has an expanded base adjacent to its juncture with the vagina.

HYPSELODORIS BRYCEI GOSLINER & JOHNSON **SP. NOV.**

(FIGS 1B, 4C, 5)

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Chromodoris bullocki misidentification, not *C. bullockii* Collingwood, 1881, Wells & Bryce, 1993: 8, upper figure.

Hypselodoris bullocki misidentification, not *H. bullockii* (Collingwood, 1881), Debelius, 1997: 233 uppermost photograph.

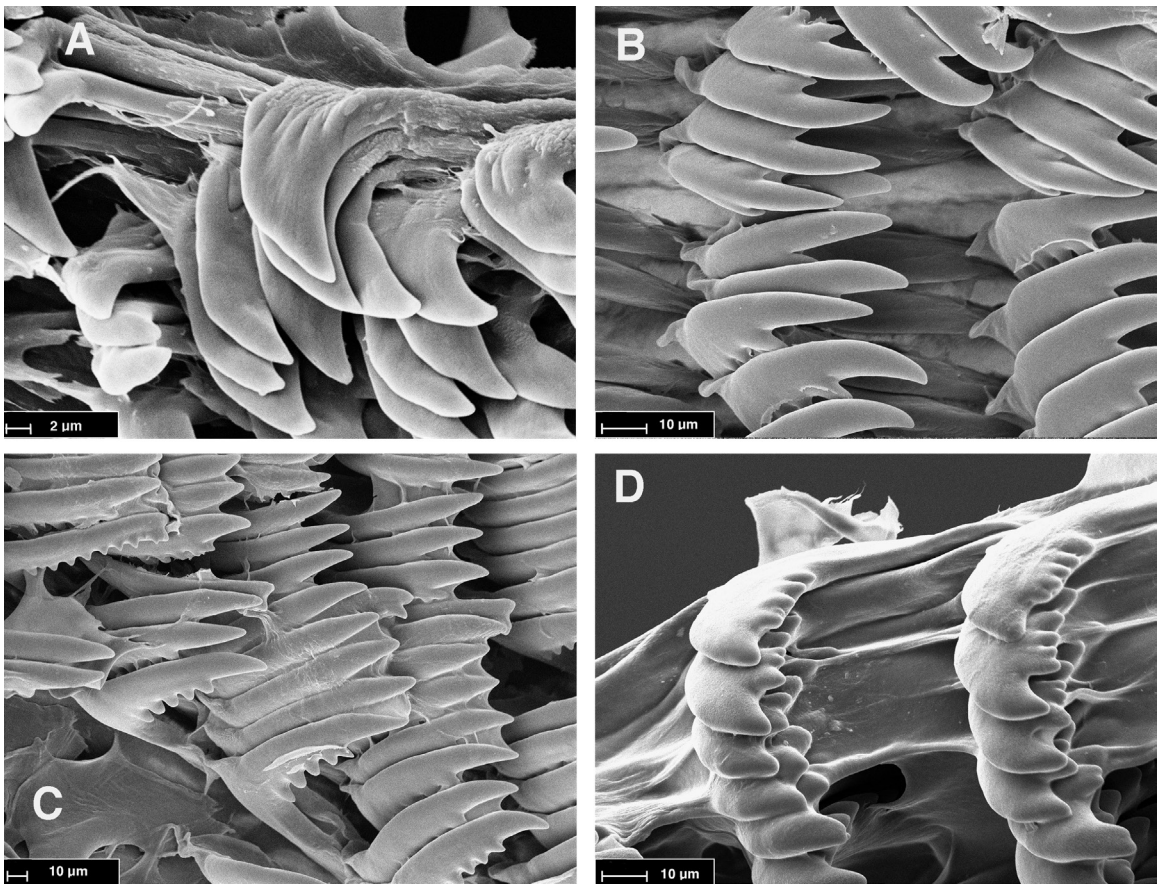

Figure 5. ***Hypselodoris brycei*** Gosliner & Johnson **sp. nov.**, paratype, WAM S12628. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

Hypselodoris cf. *bullocki* 2 Debelius & Kuiter, 2007: 117, upper photographs.
Hypselodoris sp. 9 Gosliner *et al.*, 2008: 268, bottom photograph.
Hypselodoris sp. 18 Gosliner *et al.*, 2015: 263, upper left photograph.

Type material
Holotype: WAM S96082, subsampled for molecular study, Epsilon Island, Montebello Islands, Western Australia, 20.4513°S, 115.5827°E, 7 m depth, 15 April 2015, S. Morrison.

Paratypes: WAM S96083, subsampled for molecular study, Western Australia, 20.4513°S, 115.5827°E, 7 m depth, 15 April 2015, A. Hara and A. Hosie. WAM S96157, subsampled for molecular study, 5.2 km NE of Ah Chong Island, Montebello Islands, Western Australia, 20.4992°S, 115.5899°E, 15 m depth, 16 April 2015, A. Hara. WAM 12628, five specimens, one dissected, St. 16, Dampier Archipelago, NW Legendre Island, Western Australia, 31 July 2000, C. Bryce.

Type locality
Epsilon Island, Montebello Islands.

Geographical distribution
Known only from the Houtman Abrolhos Islands to the Exmouth Region and Dampier Archipelago, Western Australia (Wells & Bryce, 1993; Debelius, 1997).

Etymology
Hypselodoris brycei is named for our colleague, Clay Bryce of the Western Australian Museum, who has collected and photographed very many new species of nudibranchs. He was the first to document this new species and has collected most of the material studied here.

Description
External morphology: Living animals (Fig. 1B) moderately large, reaching 50 mm in length. Body translucent white, with a deep violet marginal band encircling the margin of notum. More purple submarginal pigment found inside marginal band. Nine to 11 thin, unipinnate gill branches on notum. Gill branches with purple base and

red–orange outer two-thirds. Base of gill pocket purple. Bulb and base of rhinophores bright red orange, with ~41 small lamellae. Base of rhinophore sheath deep violet to purple. Edge of foot with purple marginal band.

Mantle glands: Subcutaneous mantle glands entirely absent.

Buccal armature: Muscular portion of buccal mass about twice length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 5A). Rodlets narrow, with short base and evenly curved, with single, acutely pointed apex. Radular formula of one paratype, WAM 12628, ~70 × 92.0.92. Rachidian row of teeth absent (Fig. 5B). Innermost lateral teeth having one rounded denticle on inner side of bifid primary cusp with another three to four outer denticles. Denticles not extending far beyond middle of elongate primary cusp. Next several laterals lacking inner triangular denticle but possessing four to six denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 5C) all lacking inner denticles, but having five to nine rounded, triangular outer denticles and extended primary cusp. Outermost teeth having a narrower base and shorter tooth shape, with five or six rounded outer denticles (Fig. 5D), often larger than bifid cusps.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 4C). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick and narrowing slightly as it transitions into muscular ejaculatory portion. Prostatic portion enveloping bursa copulatrix. Ejaculatory portion convoluted, narrow, entering short, wider penial bulb. Penial bulb adjacent to slightly curved, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum seminis appressed against vagina. Moderately long uterine duct emerging from vagina close to base of bursa and female gland mass, near the albumen gland.

Remarks

The colour pattern of *H. brycei* is distinctive from all other members of the genus. It most closely resembles *Thorunna daniellae* (Kay & Young, 1969) (Gosliner *et al.*, 2015: 250 upper right photograph), but *H. brycei* is a larger species, reaching 50 mm in length, whereas *T. daniellae* rarely exceeds 20 mm in length. Our molecular phylogeny (Fig. 35) clearly indicates that *H. brycei* is in the *H. bullockii* clade, where it is the sister species to *H. apolegma* (Yonow, 2001). Yonow (2001) described *H. apolegma* as a species of *Risbecia*, but Johnson & Gosliner (2012) clearly demonstrated that *Risbecia* is nested within *Hypselodoris* and that *H. apolegma* is not in the same clade as the species formerly included in *Risbecia* but is closely related to *H. bullockii*. Of the members of the *H. bullockii* clade, *H. brycei* is the only species with a white body colour and a violet marginal band. All members of the *H. bullockii* clade lack mantle glands and are unique among *Hypselodoris* species in this regard. The radula of *H. apolegma* appears to contain more teeth than that of *H. brycei* (Yonow, 2001; present study). Yonow (2001) described the radula formula of *H. apolegma* as 96 × 120.0.120, whereas the specimen of *H. brycei* had a formula of 70 × 92.0.92. The denticles of the radular teeth of *H. brycei* do not extend much beyond the middle of the primary cusp, whereas in *H. apolegma* they extend almost to the end of the cusp. The reproductive system of *H. brycei* has a much shorter penial papilla and long ejaculatory duct, whereas *H. apolegma* (Fig. 4D) has a longer, wider penial bulb and a shorter ejaculatory duct.

HYPSELODORIS CERISAE GOSLINER & JOHNSON **SP. NOV.**

(FIGS 1C, 2B, 4E, 6)

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Hypselodoris krakatoa? misidentification, not *H. krakatoa* Gosliner & Johnson, 1999; Garthwaite, 2002; Masayoshi, 2002.

Type material

Holotype: CASIZ 178350, subsampled for molecular study, Long Dong, Taipei County, Taiwan, 10 m depth, 9 August 2008, C. Chen.

Paratypes: CASIZ 219744, Sokoda, Hachijo Island, Japan, 7 m depth, 1 July 2001, Nishina Masayoshi. CASIZ 175726, subsampled for molecular study, Rayner's Rock, off Pulau Aur, Malaysia, 20 m depth, 3 October 2007, T. Gosliner.

Comparative material examined: H. krakatoa Gosliner & Johnson, 1999.

Type locality

Long Dong, Taipei County, Taiwan.

Geographical distribution

Known from Japan, Taiwan and Malaysia.

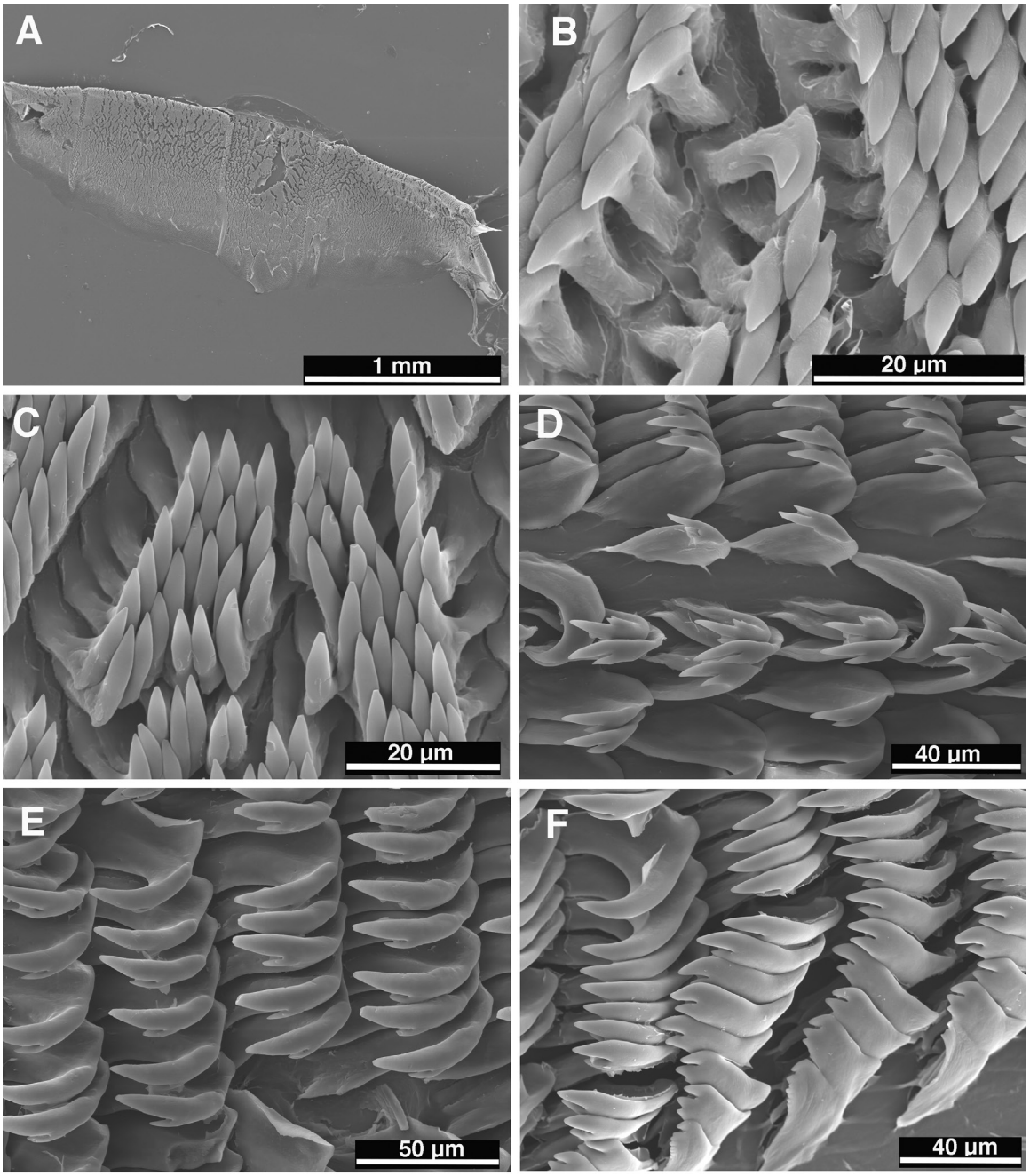

Figure 6. ***Hypselodoris cerisae*** Gosliner & Johnson **sp. nov.** A, entire jaw, holotype, CASIZ 178350. B, jaw rodlets, paratype, CAS 175726. C, jaw rodlets, holotype, CASIZ 178350. D, inner lateral teeth, holotype, CAS 178350. E, middle lateral teeth, holotype, CASIZ, 178350. F, outer lateral teeth, paratype, CAS175726.

Etymology

Hypselodoris cerisae is named for Cerise Chen, who first found this species in Taiwan and collected the holotype specimen. Cerise has a keen interest in octocoral biology but also a more general interest in marine biodiversity.

Description

External morphology: Living animals (Fig. 1C) moderately large, reaching 20–35 mm in length. Colour pattern complex with golden honey ground colour. Notum ornamented with purple on anterior, lateral and posterior margins. Irregular dark brown to black longitudinal

lines present on notum, with few opaque white spots along sides of dark lines. Gill pocket well elevated from notum. Seven to nine narrow, thin, unipinnate gill branches on notum. Gill branches red–orange on upper outer surface, opaque white internally and externally at base. Rhinophores uniformly bright red–orange except at opaque white apex. Rhinophores with ~21 small lamellae, Edge of foot with purple marginal band.

Mantle glands: Subcutaneous mantle glands (Fig. 2B) uniformly distributed along entire margin in the specimens from Taiwan (CASIZ 178350) and Japan (CASIZ 219744), but absent from some portions of the lateral edges in the specimen from Malaysia (CASIZ 175726).

Buccal armature: Muscular portion of buccal mass slightly larger than length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass (Fig. 6A) bearing numerous jaw rodlets (Fig. 6B, C. Rodlets narrow with short base and evenly curved, with single, acutely pointed apex and occasional lateral flange. Radular formula of holotype (CASIZ 178350) 59 × 36.0.36 and paratype (CAS 175726) 52 × 56.0.56. Rachidian row of teeth absent (Fig. 6D). Innermost lateral teeth having one to two triangular denticles on inner side of bifid primary cusp. Denticles absent from outer side of tooth (Fig. 6D). Next several laterals and middle lateral teeth (Fig. 6D, E) with bifid cusp, lacking inner or outer denticles. Outermost one to three teeth having a narrower base and shorter tooth shape, with one to five rounded outer denticles (Fig. 6F), smaller than bifid cusps.

Reproductive system: Reproductive organs of the holotype (Fig. 4E) and one paratype (CASIZ 175726) fully mature and virtually identical anatomically. Ampulla thick, short, tubular and slightly curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens relatively short, convoluted, curved and thick and narrowing slightly as it transitions into muscular, ejaculatory portion. Ejaculatory portion relatively short, convoluted, narrow, entering short, wider penial bulb. Penial bulb adjacent to slightly curved, wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum seminis appressed against vagina, near middle of vagina. Moderately short uterine duct emerging from vagina opposite receptaculum, entering female gland mass, near albumen gland.

Remarks

The colour pattern of *H. cerisae* is similar to that of *H. krakatoa* Gosliner & Johnson, 1999, but differs in several consistent respects. In *H. cerisae*, the body has much more pink to purple pigment, whereas in *H. krakatoa* the notum is suffused with patches of burnt orange. Both species have prominent purple pigment on the anterior margin of the mantle, but in *H. cerisae* the posterior end is also purple, whereas it is burnt orange in *H. krakatoa*. The body appears lower and wider in *H. cerisae* than in *H. krakatoa*, but in *H. krakatoa* the mantle margin is more extensive laterally, overhanging the lateral edges of the body. There are seven to nine gill branches in *H. cerisae* and only six or seven in *H. krakatoa*. The mantle glands are distributed in a similar manner in both species, where they are largely uniformly spaced around the entire mantle margin. In our molecular analysis (Fig. 35), *H. cerisae* is sister to a clade that includes *H. jacksoni* Wilson & Willan, 2007, *H. reidi* Gosliner & Johnson, 1999 and *H. iba* sp. nov. Additionally, *H. krakatoa* and *H. reginae* Marcus & Marcus, 1970 form a trichotomy with the clade that includes *H. cerisae*. All members of this largest clade have a gill peduncle that is well elevated from the notum.

The shape of the jaw rodlets and radular teeth is also similar in *H. cerisae* and *H. krakatoa*, but the number of teeth per radular row differs. In the two specimens of *H. cerisae* (CASIZ 178350 and 175726) the radula formula was 59 × 36.0.36 and 52 × 56.0.56, respectively. In four specimens of *H. krakatoa* the radula formula was 57 × 74.0.74 (CASIZ 206801; Fig. 7), 57 × 72.0.72 (CASIZ 177371), 51 × 66.0.66, 46 × 60.0.60 and 30 × 35.0.35 (last three from Gosliner & Johnson, 1999). Generally, the radula of *H. cerisae* has fewer lateral teeth per row than that of *H. krakatoa*.

The reproductive system of *H. cerisae* has several consistent differences from that of *H. krakatoa* (CASIZ 206801; Fig. 4F). In *H. cerisae*, the vagina is shorter and wider than that of *H. krakatoa*, and the uterine duct and receptaculum seminis are situated more distally than in *H. krakatoa*, where the uterine duct and receptaculum are immediately below the bursa copulatrix.

HYPSELODORIS CONFETTI GOSLINER & JOHNSON SP. NOV.

(FIGS 1D, 2C, 4G, 8)

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Hypselodoris kanga misidentification, not *H. kanga* Rudman, 1977; Rudman, 1999b: lower photograph.
Hypselodoris kanga misidentification, not *H. kanga* Rudman, 1977, Debelius & Kuiter, 2007: 126, top three photographs.

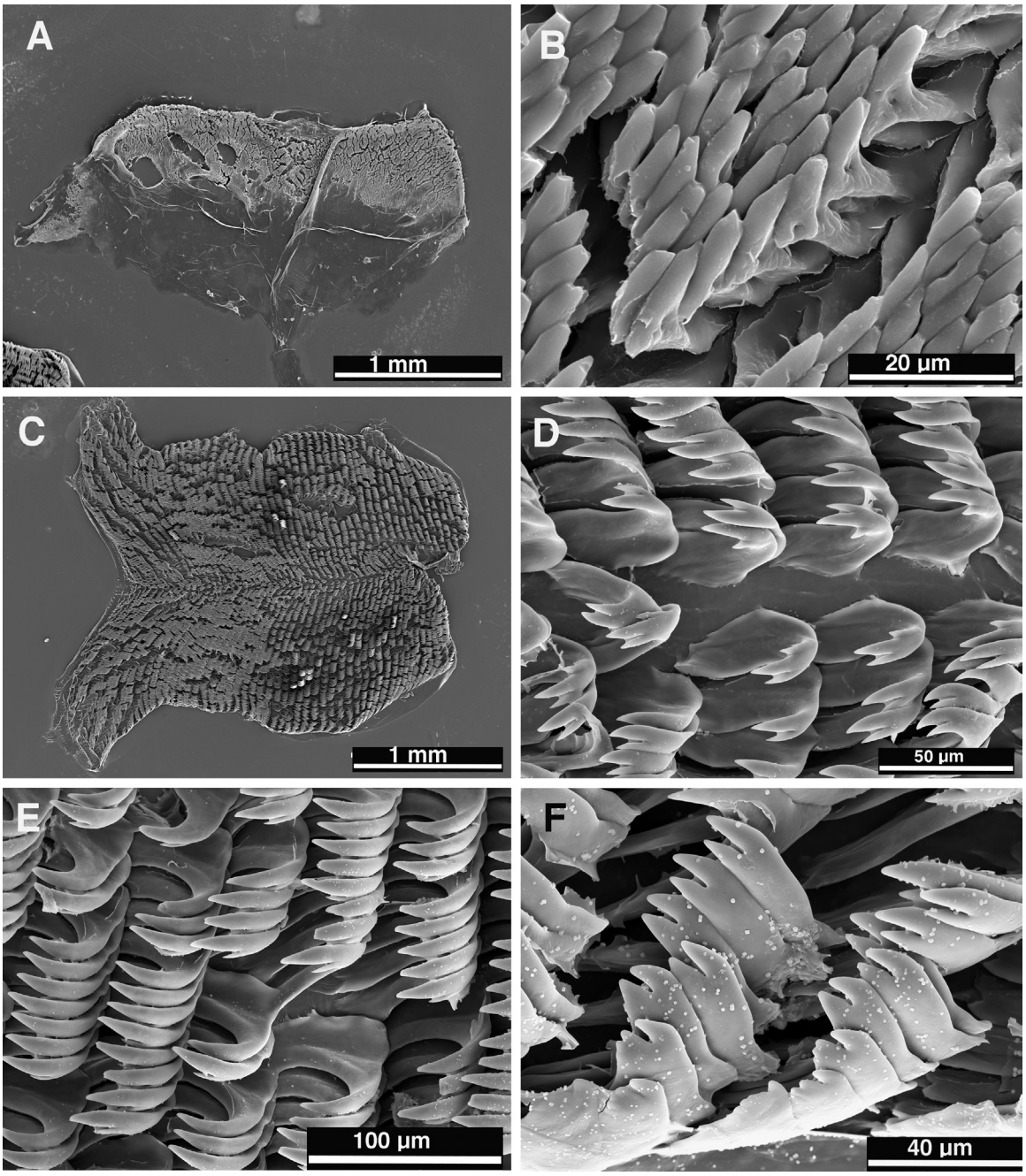

Figure 7. *Hypseldoris krakatoa* Gosliner & Johnson, 1999, CASIZ 206801. A, entire jaw. B, jaw rodlets. C, entire radula. D, inner lateral teeth. E, middle lateral teeth. F, outer lateral teeth.

Hypselodoris sp. 2 Gosliner *et al.*, 2008: 264: bottom photograph.
Hypselodoris sp. 2 Humann & DeLoach, 2010: 339: middle right photograph.

Type material
Holotype: CASIZ 191070, subsampled for molecular study, dissected, Siar Island, 5.183333°S, 145.806667°E, Madang, Papua New Guinea, 10 m depth, 9 November 2012, Heok Hui Tan.

Paratypes: CASIZ 176067, one specimen, Panglao Channel, Tagbilaran, Bohol, Philippines, 28 June 2004, Gosliner, 2004 Panglao Expedition. CASIZ 190503, one specimen, Bali, Indonesia, 1998. CASIZ 190504, one specimen, Bali, Indonesia, 1998.

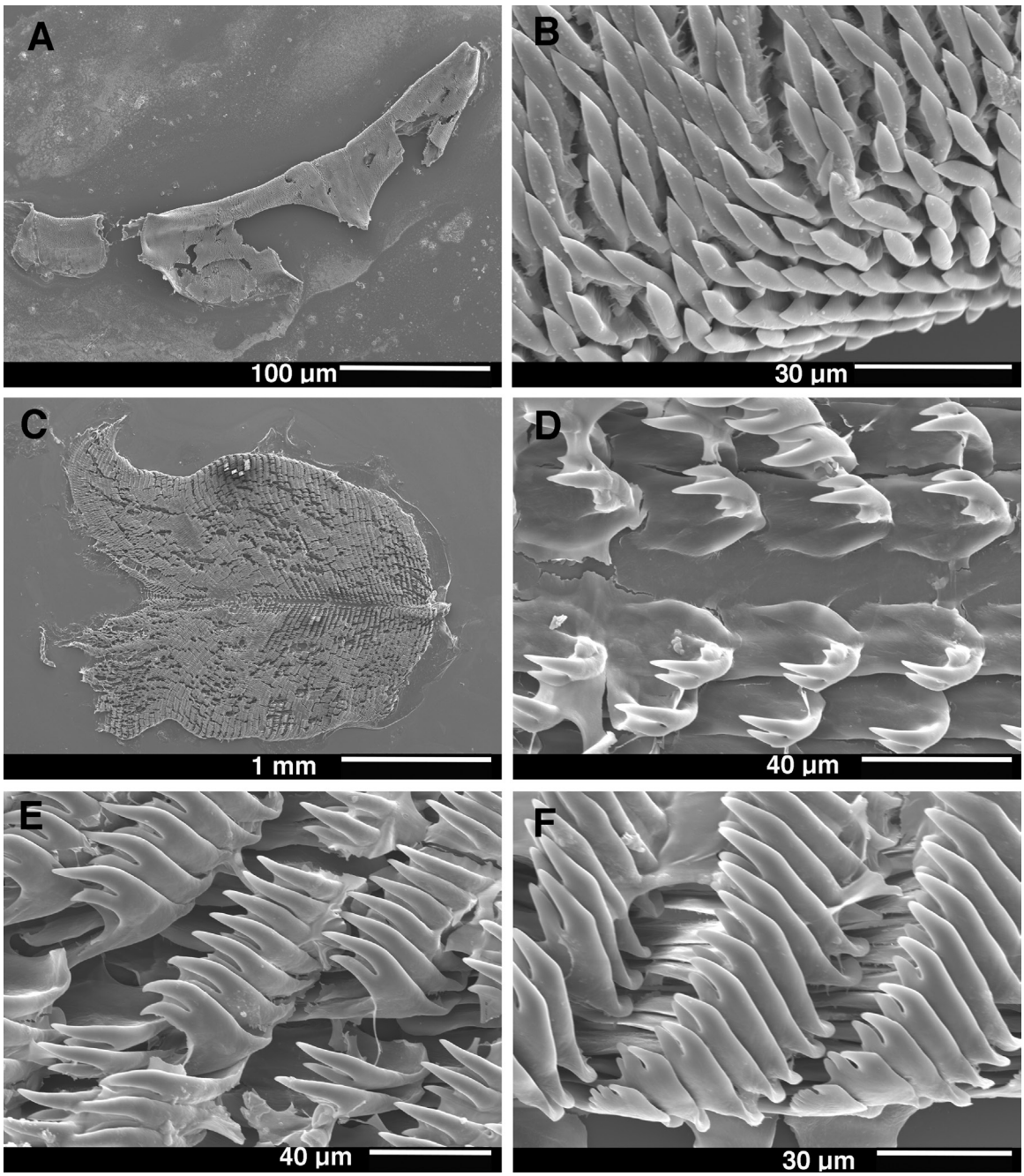

Figure 8. ***Hypselodoris confetti*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 191070. A, entire jaw. B, jaw rodlets. C, entire radula. D, inner lateral teeth. E, middle lateral teeth. F, outer lateral teeth.

Type locality
Siar Island, Madang Papua New Guinea.

Geographical distribution
Known from Papua New Guinea and the Philippines (present study) and probably also Hong Kong and Indonesia (Debelius & Kuiter, 2007).

Etymology
Hypselodoris confetti comes from the Italian word confetti that means sweets, referring to the multicoloured sweets that were thrown to people at Italian carnivals. In the 19th century it was used to refer to brightly coloured pieces of paper tossed out during parades. This species is marked with bright blue, yellow and black spots resembling confetti.

Description

External morphology: Living animals (Fig. 1D) moderately large, reaching 35 mm in length. Body colour whitish to grey–blue. Notum ornamented with large yellow spots and smaller dark blue to black spots scattered over the surface. Large blue areas found near the mantle margin. Additional spots of same colour found on sides of body and foot. Gill pocket slightly elevated from notum. Seven to nine narrow, thin, unipinnate gill branches on notum. Gill branches with purple lines along edges of inner and outer surface. Apex of gill branch red–orange. Central portion of middle of outer face of gill branches with three to five yellow spots. Base of rhinophores deep purple, extending onto basal half of club. Upper half of rhinophore club bright red rhinophores with 19 small lamellae.

Mantle glands: Subcutaneous mantle glands (Fig. 2C) uniformly distributed along entire margin in the specimen from the holotype.

Buccal armature: Muscular portion of buccal mass much larger than length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass (Fig. 8A) bearing numerous jaw rodlets (Fig. 8B). Rodlets narrow with short base and evenly curved, with single, acutely pointed apex. Radula broad, nearly as wide as long (Fig. 8C). Radular formula of holotype (CASIZ 191070) 66 × 75.0.75. Rachidian row of teeth absent (Fig. 8D). Innermost lateral teeth having three triangular denticles on inner side of bifid primary cusp. Denticles absent from outer side of tooth. Next several laterals and middle lateral teeth (Fig. 8E) with bifid cusp, lacking inner or outer denticles. Two outermost teeth having a narrower base and shorter tooth shape, with one to five rounded outer denticles (Fig. 8F), smaller than bifid cusps.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 4G). Ampulla thick, short, tubular and straight, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Proximal prostatic portion of vas deferens relatively long, convoluted, curved and thick and narrowing slightly as it transitions into muscular, ejaculatory portion. Ejaculatory portion relatively long, slightly curved and narrow, entering elongate, wider penial bulb. Penial bulb adjacent to straight, wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Moderately long vagina narrowing and leading to small, straight receptaculum seminis and larger spherical, thin-walled bursa copulatrix. Receptaculum seminis appressed against vagina, at base of bursa. Moderately short uterine duct emerging from vagina immediately below receptaculum, entering female gland mass near albumen gland.

Remarks

Hypselodoris confetti, together with *H. roo*, has often been misidentified as *H. kanga* (Rudman, 1999b; Debelius & Kuiter, 2007). The distinguishing features separating *H. confetti* and *H. roo* are discussed in the remarks after the description of the latter species. *Hypselodoris confetti* and *H. kanga* are geographically separated, with *H. kanga* being found in the Indian Ocean from Tanzania to Thailand (Gosliner *et al.*, 2015) and *H. confetti* being restricted to the western Pacific (present study). Several consistent differences permit the separation of *H. confetti* and *H. kanga*. *Hypselodoris kanga* has bluish purple lines on the notum and sides of body that are absent in *H. confetti*, and *H. confetti* has additional black spots on the notum and marginal blue spots that are absent in *H. kanga*. In our molecular analysis (Fig. 35), *H. confetti* is sister to a clade that includes *H. zephyra* Gosliner & Johnson, 1999 and *H. roo* sp. nov., and *H. nigrolineata* is sister to these three species. Molecular samples of *H. kanga* were not available for study.

The shape of the jaw rodlets and radular teeth is also similar in *H. confetti* and *H. kanga*, but the number of teeth differs markedly. In *H. confetti*, the radular formula is 66 × 75.0.75, whereas in *H. kanga* the radula formula was 107 × 93.0.93 (Rudman, 1977). In *H. confetti*, the innermost lateral tooth has three denticles on the inner side of the two primary cusps, whereas in *H. kanga* there is only a single inner denticle (Rudman, 1977). In *H. kanga*, the remaining teeth except for the outermost two teeth all lack denticles other than the two primary cusps. In *H. kanga*, the second to fifth teeth have three to five denticles on their outer margin. From the sixth to the 82nd tooth there are no denticles, and the two outermost teeth have a single denticle. In the radula of *H. nigrolineata*, the innermost tooth has a single inner denticle and the remaining teeth are all devoid of denticles (Rudman, 1977). In *H. zephyra*, the innermost tooth has a single inner denticle and most of the remaining teeth entirely lack denticles other than the two primary cusps (Gosliner & Johnson, 1999). The outermost teeth have three to six denticles, and the two adjacent teeth have only a single denticle.

The reproductive system of *H. confetti* differs from those of *H. krakatoa*, *H. nigrolineata* and *H. kanga*. In *H. confetti*, the receptaculum seminis is situated immediately adjacent to the bursa copulatrix, whereas in the other three species it is situated more proximally on the vagina (Rudman, 1977; Gosliner & Johnson 1999). In *H. confetti*, the ejaculatory portion of the vas deferens is shorter and less convoluted than in the other three species.

HYPSELODORIS DECORATA (RISBEC, 1928) (FIGS 2D, 4H, 9, 10)

Chromodoris decorata Risbec, 1928: 152–154, fig. 43, pl. VII, fig. 4.
Hypselodoris maculosa misidentification, not *H. maculosa* Pease, 1871; Gosliner *et al.*, 2015: 254, second photograph from top on left.

Material examined
CASIZ 191315, subsampled for molecular study, Mizegwadan Reef, 5.16000°S, 145.82333°E, Madang, Papua New Guinea, 20 m depth, 18 November 2012, V. Knutson. CASIZ 191214, two specimens, one dissected, south point, Pana Tibun islet, 5.196667°S, 145.806667°E, 14 November 2012, Anthony Berberian. CASIZ 190661, one specimen, dissected, Bethlehem, 13.67°N, 120.84°E, Tingloy, Maricaban Island, Batangas, Luzon, Philippines, 17 November 2012, T. Gosliner. CASIZ 184316, one specimen, dissected, Bethlehem, 13.67°N, 120.84°E, Tingloy, Maricaban Island, Batangas, Luzon, Philippines, 2 October 2010, T. Gosliner. CASIZ 208606, one specimen, off Bamboo Beach 13.52°N, 120.96°E, Batangas Channel, Puerto Galera, Mindoro Oriental, Philippines, 11 April 2015, T. Gosliner. CASIZ 176776, two specimens, West Beach, Pulau Tenggol, South China Sea, Malaysia, 29 September 2007, T. Gosliner. CASIZ 197309, one specimen, Calatagan 13.91°N, 120.60°E, Batangas, Luzon, Philippines, 19 May 2014, C. Piotrowski. CASIZ 217267, one specimen, Bonito (Culebra) Island 13.63°N, 120.95°E, Tingloy, Batangas, Luzon, Philippines, 21 April 2016, T. Gosliner. CASIZ 217358, two specimens, Dive and Trek reef, 13.80°N, 120.91°E, Bauan, Batangas, Luzon, Philippines, 17 April 2016, Brenna Green.

Type locality
New Caledonia.

Geographical distribution
Known from the Marshall Islands, Vanuatu, New Caledonia, Indonesia, Papua New Guinea, the Philippines and Malaysia (present study).

Description
External morphology: Living animals (Fig. 9) moderately large, reaching 25 mm in length. Body long, slender, translucent pink, with four thin, continuous opaque white longitudinal lines on dorsal surface of notum. Broad orange band found along lateral margins of notum, often with interior undulations and opaque white spots. Anterior and posterior ends of the animal with purple to orange areas with opaque white spots. Rows of reddish to purple spots found on notum, with more diffuse purple pigment found around periphery situated between opaque white lines. Similar pattern of lines and spots found on lateral margins of the body and foot. Seven to eight unipinnate gill branches having a translucent white base and inner margin and bright red–orange pigment on apical surfaces and outer margin. Bulb of perfoliate rhinophores opaque white with two red transverse bands and bearing ~14–16 densely arranged lamellae. Base of rhinophores translucent white with a third red transverse ring.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2D). Glands situated anteriorly and posteriorly, with no glands present in the central lateral regions of body margin. Eight to ten glands on either side of anterior end of the body, with arc of 15–20 glands situated posteriorly. Their arrangement was based upon four specimens examined.

Buccal armature: Muscular portion of buccal mass slightly longer than oral tube. Chitinous labial cuticle (Fig. 10A) found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 10B). Rodlets sharply angled with single, acutely pointed apex and posterolateral extensions. Radular formula of two specimens 55 × 26.0.26 (CASIZ 190661) and 48 × 26.0.26 (CASIZ 191214) (Fig. 10C). Rachidian row of teeth absent (Fig. 10D). Innermost lateral teeth having one or two large, triangular denticles on inner side of bifid primary cusp, with another one to two outer denticles. Next several laterals lacking inner triangular denticle but possessing two denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 10E) all lacking inner denticles but having three to four sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and shorter tooth shape, with two to four rounded outer denticles (Fig. 10F).

Reproductive system: Reproductive organs (Fig. 4H) fully mature in two specimens examined (CASIZ 1908661, CASIZ 184316). Ampulla thick, tubular, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick and narrowing slightly as it transitions into short, narrow, muscular ejaculatory portion. Ejaculatory portion widening into penial bulb. Penial bulb adjacent to curved, slightly wider vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum situated near base of bursa. Moderately long uterine duct emerging from vagina close to base of bursa and female gland mass, near albumen gland.

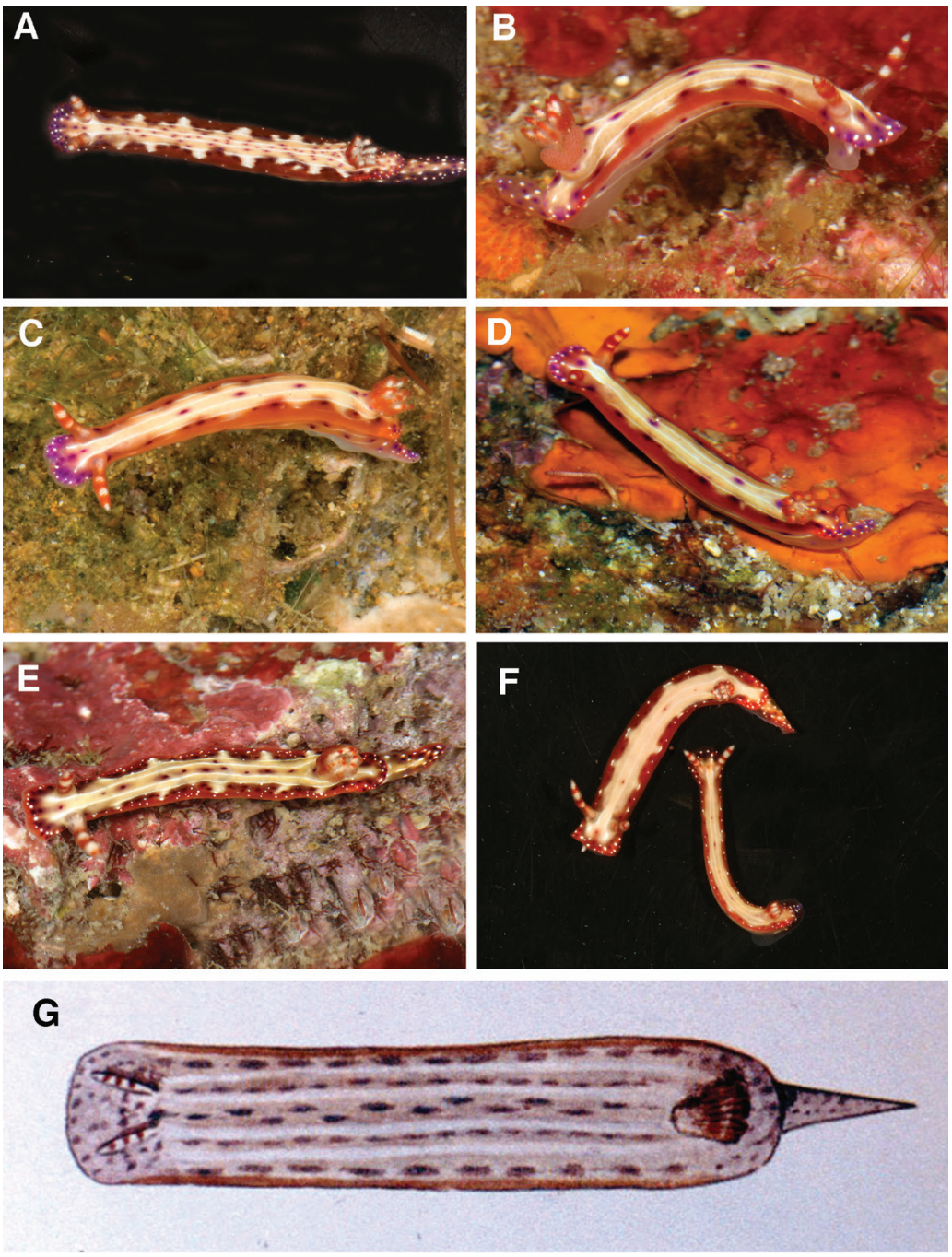

Figure 9. *Hypselodoris decorata* (Risbec, 1928), living animals. A, CASIZ 191315, Madang, Papua New Guinea, photograph by Vanessa Knutson. B, CASIZ 217614, Mabini, Batangas, Philippines. C, CASIZ 184316, Tingloy, Batangas, Philippines. D, CASIZ 190661, Tingloy, Batangas, Philippines. E, CASIZ 217358, Bauan, Batangas, Philippines. F, CASIZ 191214, Madang, Papua New Guinea, photograph by Vanessa Knutson. G, living animal from Risbec (1928), New Caledonia.

Remarks

Hypselodoris decorata is very similar to *H. maculosa* (Pease, 1871) and was regarded as a synonym of this species by Rudman (1986). Johnson (2005) suggested that *H. decorata* has several distinguishing attributes of its colour pattern that separate it from *H. maculosa*, including the presence of three rather than two red rhinophoral rings. Owing to this confusion, we have provided a complete description of *H. decorata* for purposes of comparison with that described for

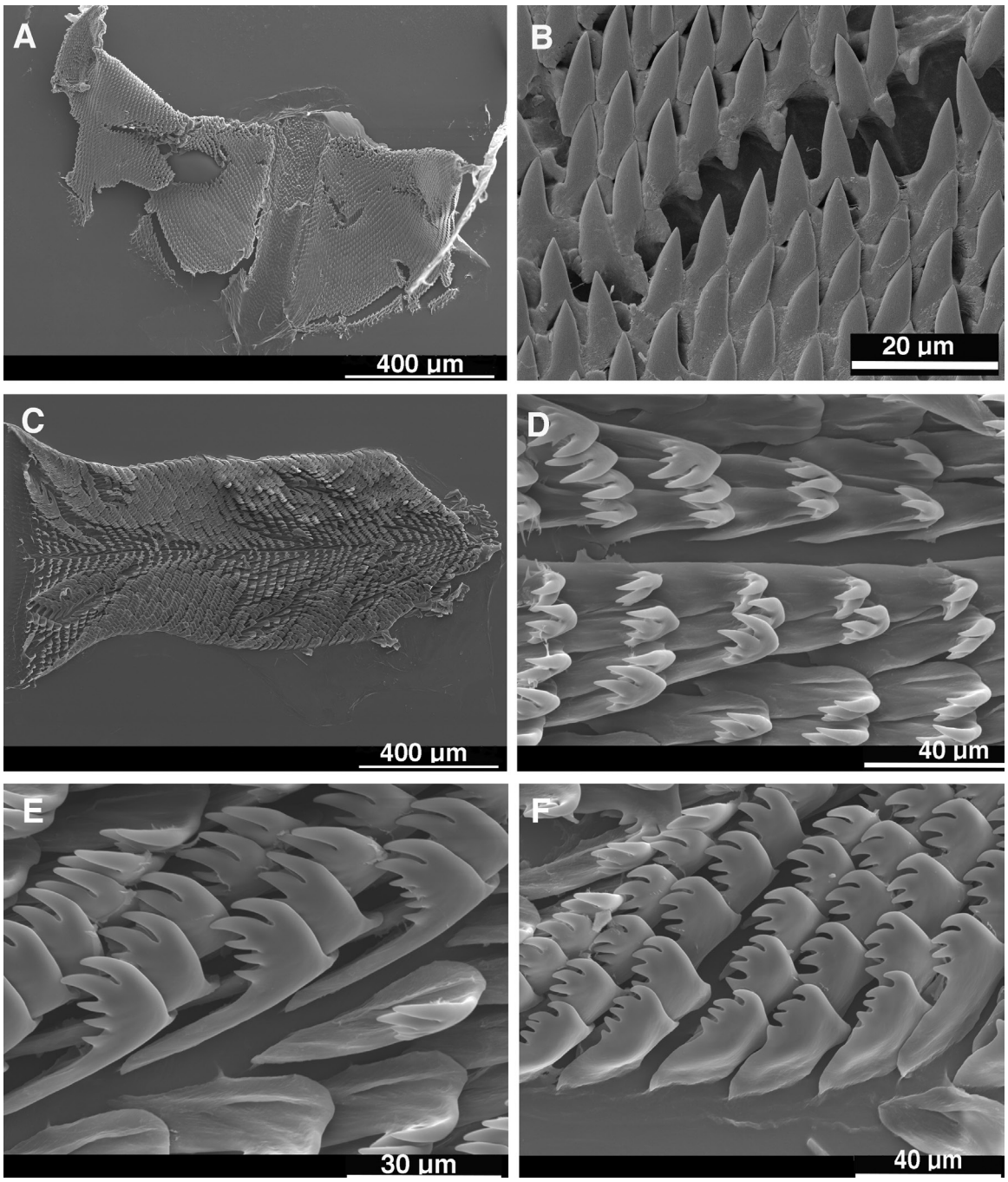

Figure 10. *Hypselodoris decorata* (Risbec, 1928). A, entire jaw, CASIZ 190661. B, jaw rodlets, CASIZ 191214. C, entire radula, CASIZ 190661. D, inner lateral teeth, CASIZ 190661. E, middle lateral teeth, CASIZ 190661. F, outer lateral teeth, CASIZ 190661.

H. maculosa (Rudman, 1986; Gosliner & Johnson, 1999). The fact that specimens identified here as *H. maculosa*, with two rhinophoral rings, cluster together with species separate from *H. decorata* (with three rhinophoral rings) in our molecular phylogeny gives credence to the observation by Johnson (2005) that these represent distinct species. *Hypselodoris decorata* is sister to *H. juniperae* sp. nov., described later in this study, and *H. maculosa*. In addition to the colour differences noted by Johnson (2005), there appear to be distinct anatomical differences between the two species. In *H. decorata*, posterior glands are present, but there are no anterolateral mantle glands, and anterior mantle glands may be present or absent.

In *H. maculosa*, posterior mantle glands are present, as are anterolateral and anterior glands. In *H. decorata*, the middle lateral teeth possess fewer denticles (three or four), whereas those of *H. maculosa* have four or five denticles (Fig. 11). The reproductive system of *H. decorata* has a very short ejaculatory segment of the vas deferens, whereas that of *H. maculosa* has a much more elongate ejaculatory segment (Fig. 4B). Also, the receptaculum seminis of *H. decorata* is situated immediately below the bursa, whereas it is much closer to the uterine duct in *H. maculosa*. Both species appear to be sympatric in the Marshall Islands, Papua New Guinea and the Philippines. Differences between this species and *H. alburtuqali* and other members of *H. maculosa* are detailed in the remarks section of *H. alburtuqali*.

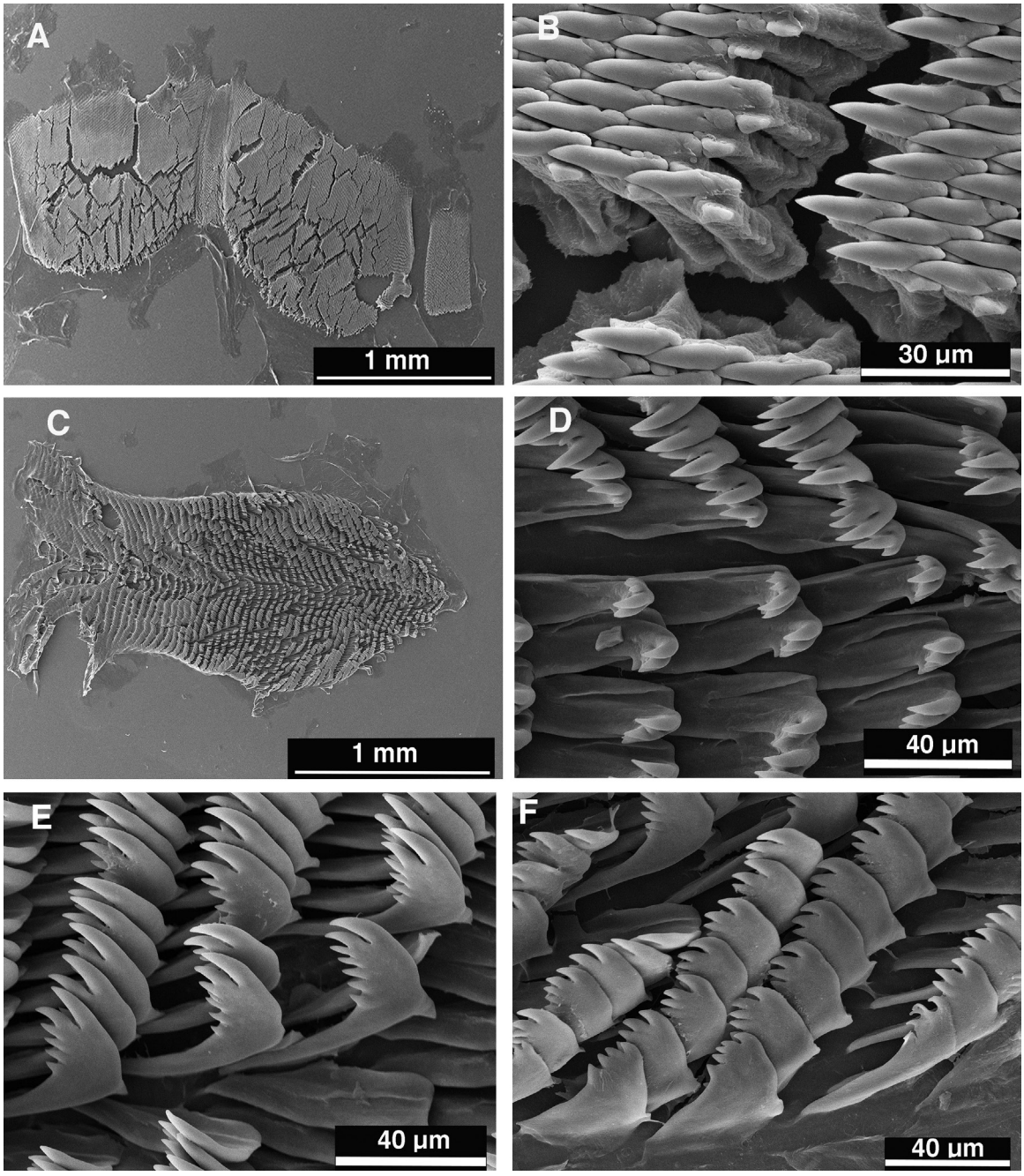

Figure 11. *Hypselodoris maculosa* (Pease, 1871), CASIZ 139545. A, entire jaw. B, jaw rodlets. C, entire radula. D, inner lateral teeth. E, middle lateral teeth. F, outer lateral teeth.

HYPSELODORIS GHARDAQANA (GOHAR & ABOUL-ELA, 1957)

(FIGS 1E, 2E, 12, 13A)

Chromodoris ghardaqana Gohar & Aboul-Ela, 1957: 220–222, pl. 1, fig. 3, pl. 2, figs. 4, 5; *Risbecia ghardaqana* Gohar & Aboul-Ela, 1957; Rudman, 1987: 374, figs 37b, 39b, 40–41.

Material examined

CASIZ 192282, two specimens, one dissected, West Manghar Island, 16.9504333 N°, 041.8108667E°, Red Sea, Saudi Arabia, 8 March 2013, T. Gosliner.

Geographical distribution

Known only from the Red Sea (Rudman, 1987; present study).

Description

External morphology: Living animals (Fig. 1E) large, reaching 75 mm in length. Body translucent white, with irregular large yellowish spots and a continuous dark blue marginal band. Translucent white foot ornamented by dark blue marginal band. Gill white, with dark blue line on interior and outer edge or gill rachis. Thirteen unipinnate gill branches. Perfoliate rhinophores white basally and dark blue apically, bearing ~18 densely arranged lamellae.

Mantle glands: Subcutaneous mantle glands simple rounded in shape (Fig. 2E). Glands dense, found along entire mantle margin except at anterior end.

Buccal armature: Muscular portion of buccal mass approximately equal in length to oral tube. Buccal mass consisting of chitinous labial cuticle at anterior end of muscular portion of buccal mass. Jaws bearing numerous rodlets (Fig. 12A). Rodlets narrowly triangular, with single, acutely pointed apex. Radular formula of holotype 63 × 55.0.55. Rachidian row of teeth absent (Fig. 12B). Innermost lateral teeth have a single small triangular denticle on inner side of bifid primary cusp and lacking outer denticles. Next several laterals lacking inner triangular denticle and also lacking denticles on outer side of primary bifid cusps. Outer lateral cusp much shorter than inner one. Midlateral teeth (Fig. 12C) also lacking inner denticles but

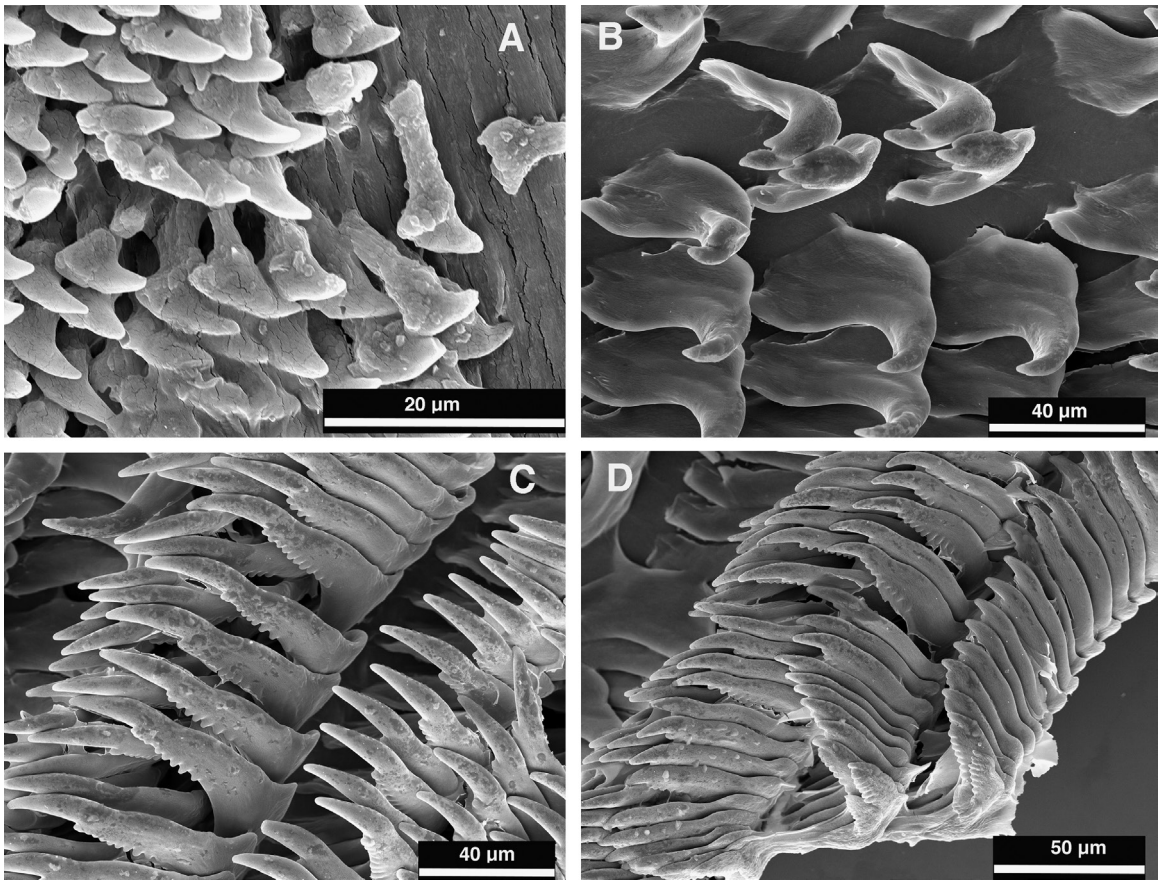

Figure 12. *Hypselodoris ghardaqana* (Gohar & Aboul-Ela, 1957), CASIZ 192282. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

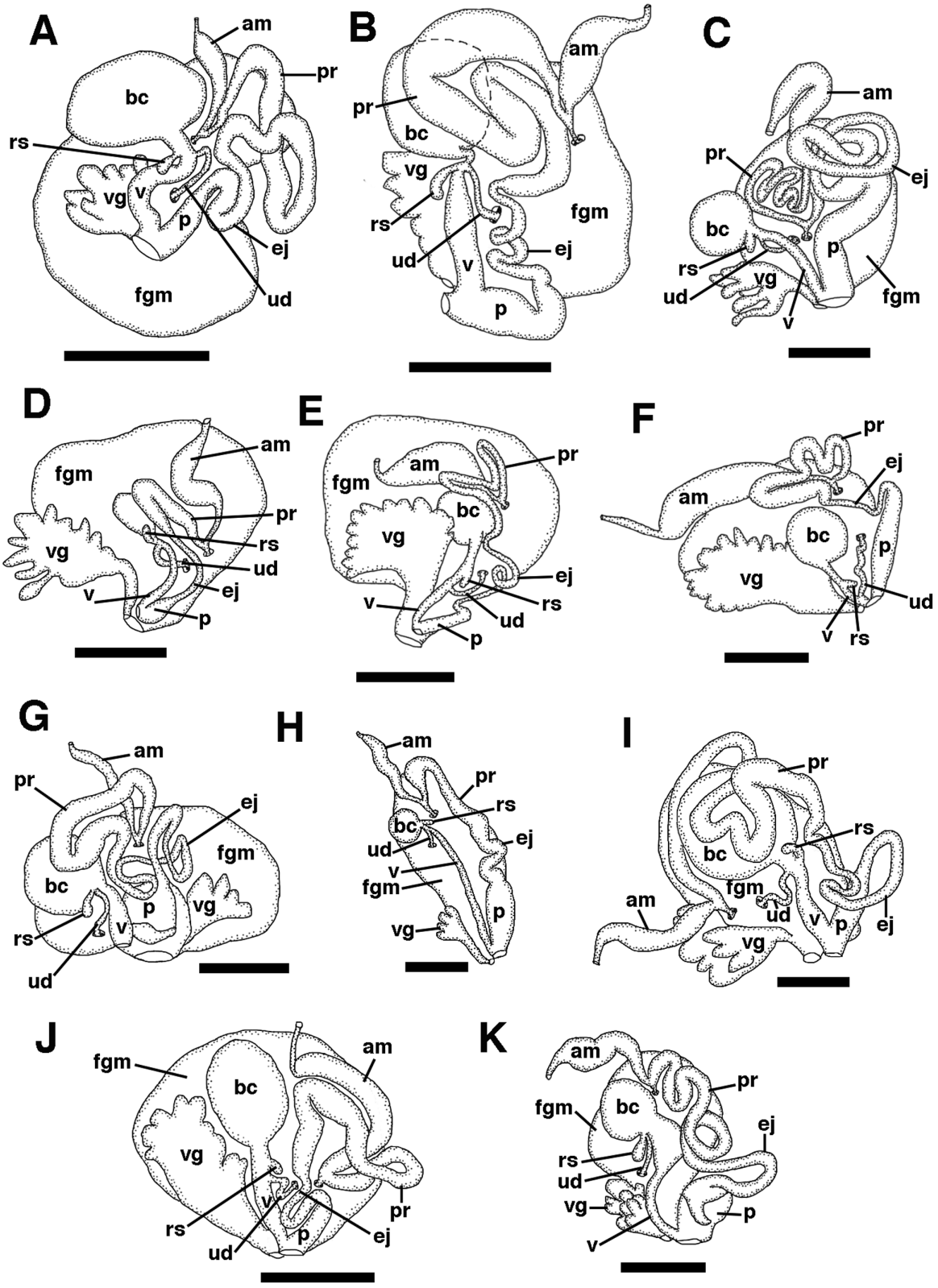

Figure 13. Reproductive systems. A, *Hypselodoris ghardaqana* (Gohar & Aboul-Ela, 1957), CASIZ 192282, scale bar: 3.5 mm. B, ***Hypselodoris iba*** Gosliner & Johnson **sp. nov.**, CASIZ 177777, scale bar: 3.0 mm. C, ***Hypselodoris katherinae*** Gosliner & Johnson **sp. nov.**, CASIZ 181257, scale bar: 1.0 mm. D, ***Hypselodoris lacuna*** Gosliner & Johnson **sp. nov.**,

possessing five to ten triangular outer denticles. Outer cusp of bifid cusp much shorter than inner one. Outer teeth lacking inner denticles and having six to eight triangular outer denticles (Fig. 12D). Outermost teeth with narrower base and more elongate tooth shape.

Reproductive system: Reproductive organs fully mature (Fig. 13A). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into the oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens curved and thick, narrowing slightly while transitioning into muscular, ejaculatory portion. Ejaculatory portion curving into segment entering elongate, slightly widened penial bulb. Penial bulb adjacent to curved, wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Elongate, curved vagina leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Relatively short uterine duct emerging from about half of the length along duct to bursa.

Remarks

This species was originally described as a species of *Chromodoris* distinct from both *C. pulchella* (Rüppell & Leuckart, 1828) and *Chromodoris annulata* Eliot, 1904 (Gohar & Abu-Ela, 1957). Rudman (1987) maintained the distinctness of the three species but transferred *C. pulchella* and *C. ghardaqana* to *Risbecia*. Johnson & Gosliner (2012), based on molecular phylogeny, showed that species of *Risbecia* are nested in *Hypselodoris* and that maintenance of *Risbecia* creates a paraphyletic *Hypselodoris*. They also demonstrated that *C. annulata* should be considered as a species of *Goniobranchus*. *Hypselodoris ghardaqana* was not included in their analysis but was hypothesized to be a member of the *Risbecia* clade of *Hypselodoris*. A surprising result of the present study is that *H. ghardaqana* is not a close relative of the members of the *Risbecia* clade, but rather is sister to *H. bollandi*. *Hypselodoris nigrolineata* is sister to both *H. ghardaqana* and *H. bollandi*. The colour pattern of *H. bollandi* is similar to that of *H. ghardaqana* in that both species have a white body colour with yellow spots. The rhinophores and gill of *H. ghardaqana* are ornamented with dark blue pigment, whereas they are ornamented with red in *H. bollandi*. *Hypselodoris bollandi* also has dark brown pigment on the notum. In all three species, the middle lateral teeth bifid cusps have a characteristic shape, with an elongated inner cusp and a short outer cusp, with numerous denticles below the outer cusp. The colour pattern of *H. ghardaqana* is remarkably convergent with that of its sympatric congener, *H. pulchella*.

HYPSELODORIS IBA GOSLINER & JOHNSON **SP. NOV.**

(FIGS 2F, 13B, 14, 15)

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Hypselodoris bullocki, misidentification, not *Chromodoris bullockii* (Collingwood, 1881); Humann & DeLoach, 2010: 338, middle right and lower left photographs.
Hypselodoris sp. 5 Debelius & Kuiter, 2007: 118.
Hypselodoris sp. 10 Gosliner *et al.*, 2008: 269, top photograph.
Hypselodoris sp. 14 Gosliner *et al.*, 2015: 261, bottom two photographs.

Type material

Holotype: NMP 041279 (formerly CASIZ 177511), subsampled for molecular study, Aphol's Reef, 13.65835°N, 120.90144°E, Tingloy, Maricaban Island, Batangas, Philippines, 35 m depth, 21 March 2008, P. Paleracio.

Paratypes: CASIZ 177777, dissected, subsampled for molecular study, Aphol's Reef, 13.65835°N, 120.90144°E, Tingloy, Maricaban Island, Batangas, Philippines, 35 m depth, 23 April 2008, P. Paleracio. CASIZ 180419, dissected, subsampled for molecular study, Aphol's Reef, 13.65835°N, 120.90144°E, Tingloy, Maricaban Island, Batangas, Philippines, 35 m depth, 17 May 2009, P. Paleracio. CASIZ 186103, two specimens, Malajibomanoc (Chicken Feather) Island, 13.62772°N, 120.96592°E, Tingloy, Batangas, Philippines, 40 m depth, 16 May 2011, P. Paleracio.

CASIZ 208587, scale bar: 0.5 mm. E, ***Hypselodoris melanesica*** Gosliner & Johnson **sp. nov.**, CASIZ 069787, scale bar: 0.7 mm. F, *Hypselodoris bullockii* (Collingwood, 1881), CASIZ 085905, scale bar: 1.0 mm. G, ***Hypselodoris paradisa*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 191464, scale bar: 0.5 mm. H, ***Hypselodoris perii*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041281, scale bar: 0.3 mm. I, ***Hypselodoris roo*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041282, scale bar: 1.0 mm. J, ***Hypselodoris rositoi*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041283, scale bar: 1.2 mm. K, ***Hypselodoris skyleri*** Gosliner & Johnson **sp. nov.**, CASIZ 177305, scale bar: 0.5 mm. am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of the vas deferens; fgm, female gland mass; p, penis; pr, prostatic portion of vas deferens; rs, receptaculum seminis; ud, uterine duct; v, vagina; vg, vestibular gland.

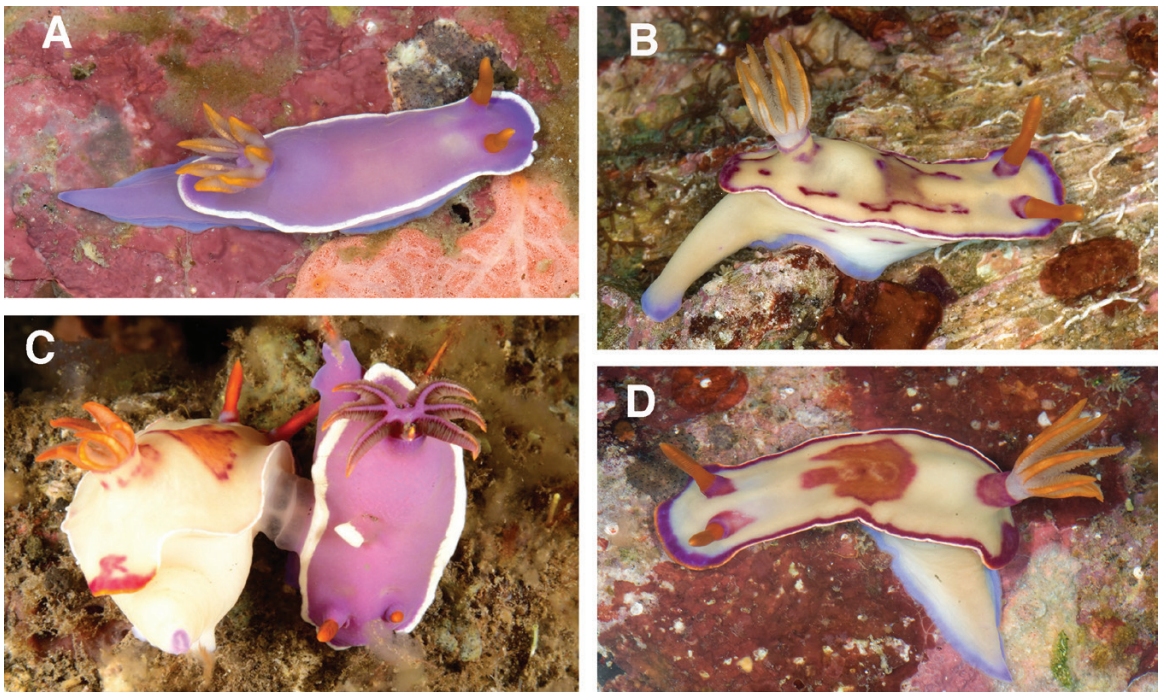

Figure 14. ***Hypselodoris iba*** Gosliner & Johnson **sp. nov.**, living animals. A, paratype, CASIZ 180419, Tingloy, Batangas, Philippines. B, holotype, NMP 041279, Tingloy, Batangas, Philippines. C, two specimens of different colour morphs mating, southwestern Sangeang, Indonesia, David Cowdery. D, paratype, CASIZ 177777, Tingloy, Batangas, Philippines.

CASIZ 217217, MAB 325, Dead Palm dive site, 13.69493372°N, 120.884687°E, Calumpan Peninsula, Mabini, Batangas, Luzon, Philippines, 30 m depth, 16 April 2016, P. Paleracio.

Type locality
Aphol's Reef, Tingloy, Maricaban Island, Batangas, Philippines.

Geographical distribution
Known from Indonesia and the Philippines (Gosliner *et al.*, 2008).

Etymology: Hypselodoris iba is named for the Tagalog word iba, meaning different or distinctive.

Description
External morphology: Living animals (Fig. 14) large, reaching 70 mm in length. Body wide, tapering to narrow, rounded posterior end of notum. Foot wide, elongate posteriorly. Gill with six to eight unipinnate branches. Gill branches with white pigment at base, becoming orange in outer portion. Gill pocket well elevated from notum. Rhinophores with 20–24 lamellae. Colour pattern occurs in two distinct morphs. In first morph, body generally uniformly purple, with uniformly wide opaque white marginal band or occasionally orange band. Rhinophores uniformly orange, with orange or purple pigment on base of rhinophore sheaths. Second morph generally off-white to beige, with thin white marginal band, transitioning to orange anteriorly and posteriorly. Submarginal blood red band may be present, transitioning to purple anteriorly. Blood red blotches present on central region of notum, on base of gill pocket and base of rhinophore sheaths. purple band present near opening of rhinophore sheaths. Blood red blotches may also be present on lateral faces of body. Wide purple band present along lateral margin of foot.

Mantle glands: Subcutaneous mantle glands large and concentrated posteriorly, with 12–16 glands. Smaller, irregularly distributed glands present along lateral and anterior margins (Fig. 2F).

Buccal armature: Muscular portion of buccal mass about the same size as the length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 15A). Rodlets narrow, triangular with short base and evenly curved, with single, acutely pointed apex. Radular formula of two paratypes 63 × 98.0.98 (CASIZ 177777) and 66 × 88.0.88 (CASIZ 180419). Rachidian row of teeth absent (Fig. 15B, C). Innermost lateral teeth lacking inner denticles or having single acutely pointed denticle on inner side of bifid primary cusp.

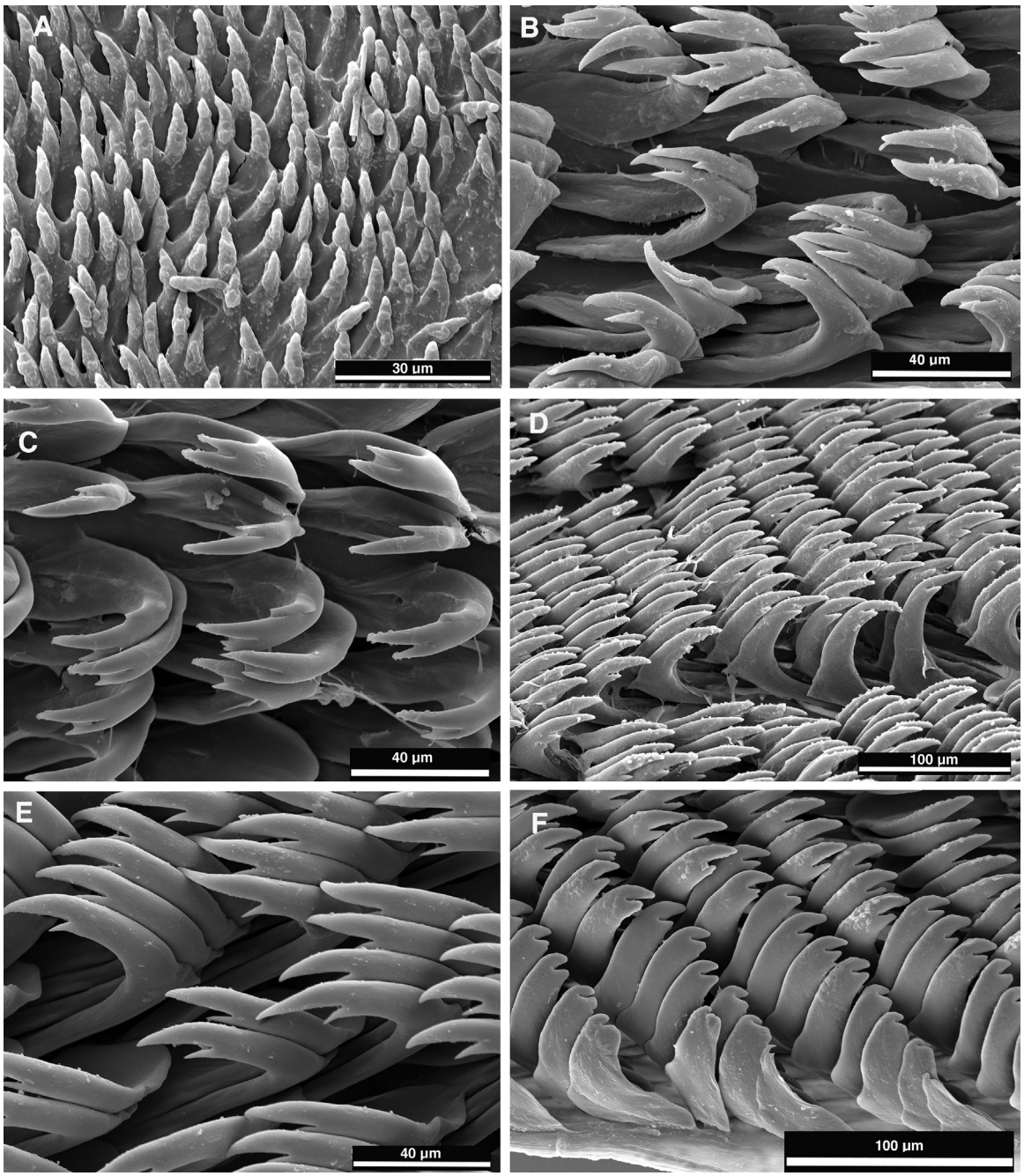

Figure 15. ***Hypselodoris iba*** Gosliner & Johnson **sp. nov.**, buccal armature. A, jaw rodlets, CASIZ 177777. B, inner lateral teeth, CASIZ 177777. C, inner lateral teeth, CASIZ 180419. D, middle lateral teeth, CASIZ 177777. E, middle lateral teeth, CASIZ 180419. F, outer lateral teeth, CASIZ 180419.

Outer surface of inner lateral without outer lateral denticles. Next several laterals (Fig. 15D, E) and all but outermost lateral teeth with only a bifid primary cusp. Outer cusp much shorter than inner cusp. Outermost teeth having a narrower base and shorter tooth shape, with zero to two rounded outer denticles (Fig. 15F) below bifid cusps.

Reproductive system: Reproductive organs (Fig. 13B) of two paratypes fully mature (CASIZ 177777 and CASIZ 180419). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens curved and thick and narrowing

slightly as it transitions into muscular, ejaculatory portion. Prostatic portion enveloping bursa copulatrix. Ejaculatory portion moderately to highly convoluted, narrow, entering short, wider penial bulb. Penial bulb adjacent to slightly curved, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long, wide vagina leading to small, curved receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum seminis appressed against vagina immediately below bursa copulatrix. Moderately long uterine duct emerging from vagina close to base of bursa and female gland mass, near the albumen gland.

Remarks

This species has been considered as a synonym of *H. bullockii* (Humann & DeLoach, 2010) or as an undescribed species (Debelius & Kuiter, 2007; Gosliner *et al*., 2008, 2015). This has been complicated further by the fact that *H. iba* has two distinct colour morphs, and one of them is also similar to *H. variobranchia* sp. nov. described here. For a detailed comparison, see the remarks on *H. variobranchia* sp. nov. The most reliable way to distinguish *H. iba* from members of the *H. bullockii* clade is by the presence of mantle glands in *H. iba*. No members of the *H. bullockii* clade have mantle glands (present study). The two colour morphs have been observed copulating with each other (Fig. 14C; Köhler, 2002). Not only are the two colour morphs observed copulating, but they show very little genetic divergence. The holotype (CASIZ 177511), a light morph specimen, is only 0.3% different in its *COI* gene from a purple morph specimen from the same locality (CASIZ 180419), and a third specimen (CASIZ 177777, also a light morph) from the same locality is 0.6% different from the other two. The subsequent ABGD analysis confirms that these three specimens are conspecific with each other and distinct from all other species.

Hypselodoris iba is also similar in appearance to *Thorunna punicea* (Rudman, 1995). In *T. punicea*, the gills vibrate when the animal is active, the reproductive system has a large receptaculum seminis and the foot has an opaque white line along its margin. In *H. iba*, the gills do not vibrate and the foot is lined with purple, and it has a small receptaculum seminis and denticulate outer lateral teeth rather than simply bifid ones. In our phylogenetic analysis, *T. punicea* clearly nests with other species of *Thorunna* rather than with members of *Hypselodoris*.

Hypselodoris iba is a member of large clade that includes *H. reidi*, *H. jacksoni*, *H. cerisae*, *H. krakatoa*, *H. regina* and *H. lacuna*. None of these species has a colour pattern similar to either colour morph of *H. iba*. All members of this clade, with the exception of *H. lacuna*, have an elevated gill pocket and mantle glands arranged all around the perimeter of the mantle margin (Gosliner & Johnson, 1999; Wilson & Willan, 2007; present study). Members of this clade also have an inner lateral tooth with a single inner denticle and no denticles on the outer side of the bifid cusps. All members of this clade have the majority of teeth with no inner or outer denticles and the outer cusp of the tooth much smaller than the inner cusp.

HYPSELODORIS JUNIPERAE GOSLINER & JOHNSON SP. NOV.

(FIGS 1F, 2G, 16)

LSID: urn:lsid:zoobank.org:act:3E59FD3C-9CDD-4663-A867-EF74877AB7A8

Hypselodoris cf. *maculosa* Rudman, 1999b, in part.

Type material

Holotype: CASIZ 175550, subsampled for molecular study, dissected, wall at south end of reef, 14.157833°S, 47.6485°E, west of Nosy Valiha, Îles Radama, Madagascar, 15 October 2005, T. Gosliner and S. Fahey.

Type locality

West of Nosy Valiha, Îles Radama, Madagascar.

Geographical distribution

Known from Madagascar (present study) and possibly Sri Lanka (Houben, 2007), South Africa (Ogden, 2005) and Reunion Island (Bidgrain, 2005).

Etymology

This small but striking species is named for author Rebecca Johnson's daughter, Juniper Rodgers. Juniper, also one of a kind, loves bright colours and patterns, and when she was only 4 years old said, 'Slugs are just like land nudibranchs'. This nudibranch is for you.

Description

External morphology: Living animals (Fig. 1F) small, reaching 9 mm in length. Body long, slender, translucent pink, with four groups of small white tubercles arranged longitudinally in linear fashion. Two additional rows of submarginal spots. Deep purple spots found between areas of white spots, arranged in longitudinal rows. Centre of spots darker purple than outer portions. Broad orange band along lateral margins of notum, with deeper orange anteriorly and posteriorly in region of mantle glands. Anterior and posterior ends of the animal with purple areas. Similar pattern of lines and spots found on lateral margins of the body and foot. Five to six unipinnate gill branches

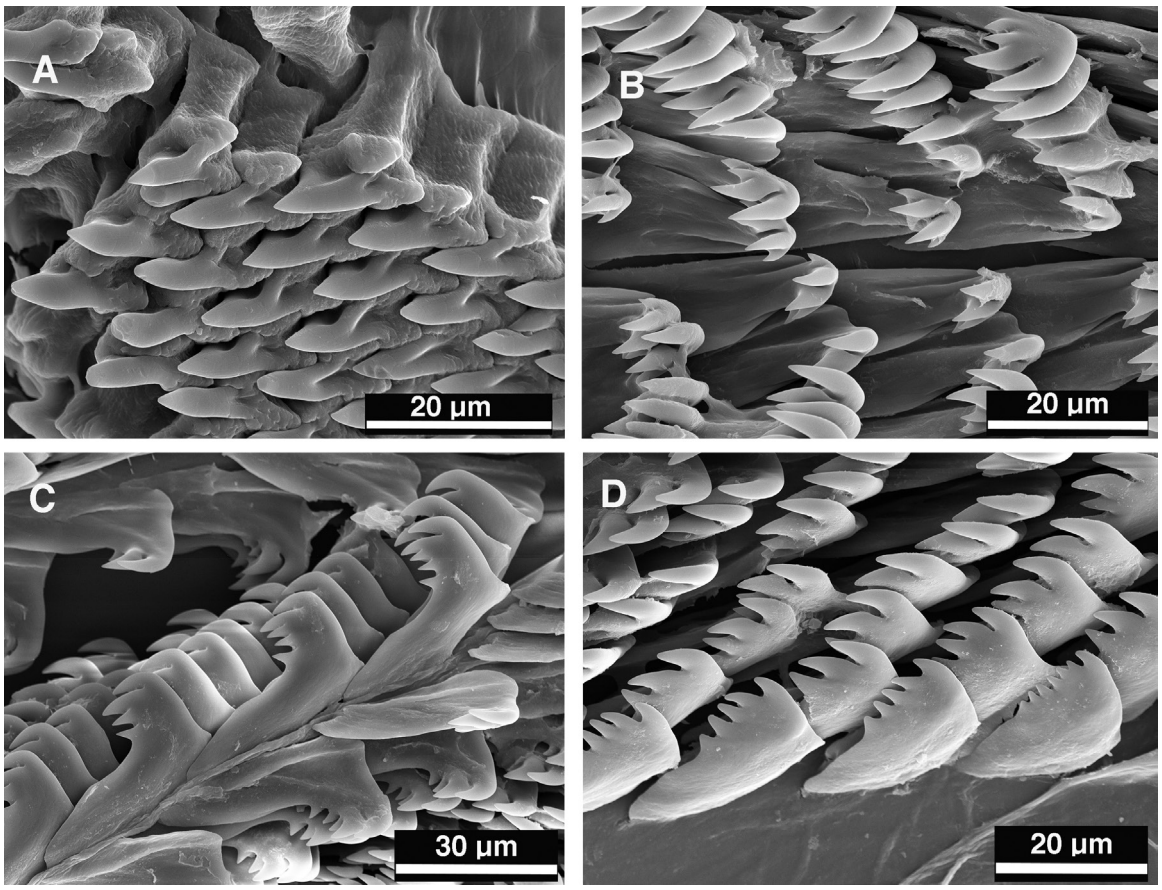

Figure 16. ***Hypselodoris juniperae*** Gosliner & Johnson **sp. nov.**, buccal armature, holotype, CASIZ 175550. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

having a translucent white base and inner margin and bright red–orange pigment on outer surface margin. Bulb of perfoliate rhinophores opaque white, with two red transverse bands and bearing ~11 densely arranged lamellae. Base of rhinophores translucent white.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2G). Glands situated anteriorly and posteriorly, with no glands present in the central lateral regions of body margin. Ten glands on either side of anterior end of the body, with arc of ten glands situated posteriorly.

Buccal armature: Muscular portion of buccal mass longer than oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 16A). Rodlets sharply angled with single, acutely pointed apex and posterolateral extensions. Radular formula of holotype (CASIZ 175550) 33 × 19.0.19. Rachidian row of teeth absent (Fig. 16B). Innermost lateral teeth having one large triangular denticle on inner side of bifid primary cusp, with another two outer denticles. Next several laterals lacking inner triangular denticle but possessing two denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 16C) all lacking inner denticles but having two or three sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and shorter tooth shape, with three to five rounded outer denticles (Fig. 16D).

Reproductive system: Reproductive organs immature.

Remarks

Hypselodoris juniperae is a member of a clade that includes *H. alburtuqali*, *H. decorata* and *H. maculosa* and is sister to *H. maculosa*. The ABGD analysis indicates that *H. juniperae* from the western Indian Ocean is distinct from *H. maculosa* from the western Pacific and they are 6.5–7.2% divergent in their *COI* gene, whereas the two western Pacific *H. maculosa* are 2.7% divergent from each other. The colour pattern of *H. juniperae* is similar to that of *H. maculosa*, but differs in having white spots arranged in lines rather than thin continuous lines (Bidgrain, 2005; Ogden, 2005; Houben, 2007; present study).

There appear to be fewer mantle glands in *H. juniperae* than in *H. maculosa* (Gosliner & Johnson, 1999: fig. 29D; present study). The jaw rodlets of *H. juniperae* have a shorter cusp than do those of *H. maculosa* (Figs 11B, 16A; Rudman, 1986: fig. 16E). The radula of *H. juniperae* is much narrower than that of *H. maculosa*, with only 19 teeth per half row as compared with 28–51 teeth per half row in *H. maculosa* (Rudman, 1986). The inner lateral teeth of *H. maculosa* have two or three denticles on the inner side of the bifid cusps and an additional two denticles on the outer side of the cusps (Fig. 11D; Rudman, 1986: fig. 16A, B), whereas in *H. juniperae* there is only a single inner denticle and one or two outer ones (Fig. 16B). The reproductive systems cannot be compared owing to the immaturity of the single specimen of *H. juniperae*.

HYPSELODORIS KATHERINAE GOSLINER & JOHNSON SP. NOV.

(FIGS 1G–I, 2H, 13C, 17)

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Hypselodoris sp. 3 Gosliner *et al.*, 2008: 265, top photograph.
Hypselodoris sp. 4 Gosliner *et al.*, 2008: 265, second photograph.
Hypselodoris sp. 8 Gosliner *et al.*, 2015: 259, top right photograph.
Hypselodoris sp. 9 Gosliner *et al.*, 2015: 259, middle left photograph.

Type material
Holotype: CASIZ 176771, subsampled for molecular study, dissected, Pulau Chebeh, off NW tip of Tioman Island, eastern Malaysia, 5 October 2007, T. Gosliner.

Paratypes: CASIZ 176772, one specimen, subsampled for molecular study, Batu Sepoi, off SW coast of Tioman Island, eastern Malaysia, 4 October 2007; CASIZ 177532, molecular sample of CASIZ 176772, same locality and date. CASIZ 176773, two specimens, Nichi Asu Maru wreck, off Kuantan, east coast of Malaysia, 6 October 2007, T. Gosliner. CASIZ 176774, one specimen, Tiger Point, Pulau Tioman, eastern Malaysia, 2 October 2007, T. Gosliner. CASIZ 175728, two specimens, Nichi Asu Maru wreck, off Kuantan, east coast of Malaysia, 6 October 2007, T. Gosliner. CASIZ 181300, one specimen, subsampled for molecular study, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 20 May 2009, T. Gosliner. CASIZ 181251, two specimens, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 21 May 2009, T. Gosliner. CASIZ 181227, one specimen, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 21 May 2009, T. Gosliner. CASIZ 177532, one specimen, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 21 March 2008, T. Gosliner.

Type locality
Pulau Chebeh, off NW tip of Tioman Island, eastern Malaysia.

Geographical distribution
Known from the Philippines, eastern Malaysia and Indonesia (Gosliner *et al.*, 2008).

Etymology
This species is named for Katherine Piatek, Senior Program Manager of the Institute of Biodiversity Science and Sustainability at the California Academy of Sciences, who has provided immense support for the research undertaken in the Philippines. Her assistance has been crucial to the successful completion of many research expeditions.

Description
External morphology: Living animals (Fig. 1G–I) moderately large, 20–32 mm in length. Body long, slender, translucent pink to peach. Fine parallel or intersecting red longitudinal lines or interrupted dashes on notum sides of body and foot. Large, scattered opaque white tubercles on notum of larger individuals. Scattered blue–purple spots found around margin of notum and foot, forming continuous line in some specimens. Pigment more dense in centre of spot. Seven to nine unipinnate gill branches having a translucent white base and inner margin and bright red–orange pigment on inner and outer surfaces of rachis and some gill filaments. Bulb of perfoliate rhinophores mostly red–orange, with some translucent white on anterior face. Bulb with eight to 16 congested lamellae. Base of rhinophores red anteriorly, with opaque white on posterior face.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2H). Glands situated around entire margin of anterior and posterior ends in two specimens examined (CASIZ 177532, CASIZ 176771). Few scattered lateral glands also present. Anterior and posterior glands larger than lateral ones.

Buccal armature: Muscular portion of buccal mass about equal in length to oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 17A). Rodlets narrow and acutely pointed anteriorly, with single

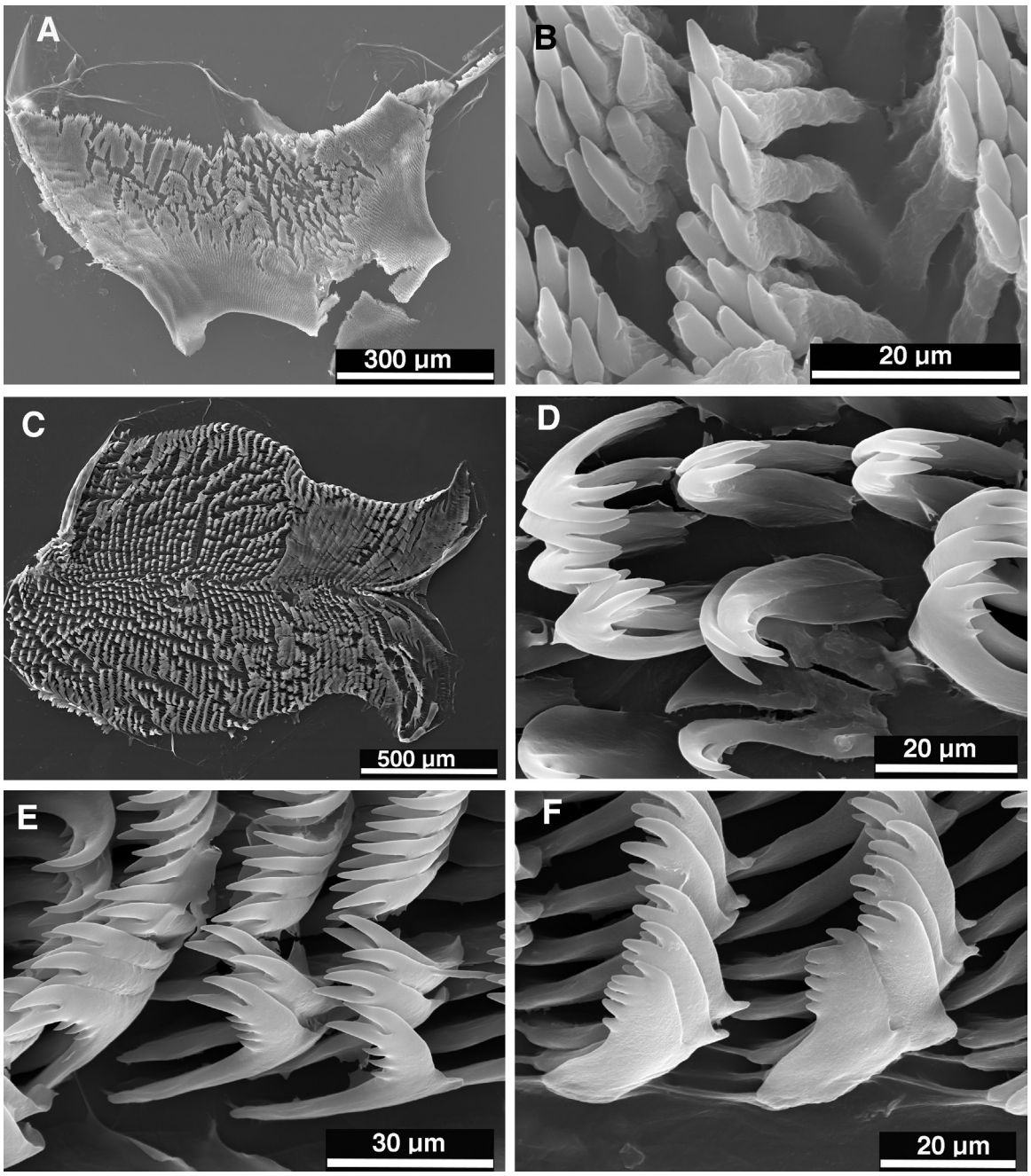

Figure 17. ***Hypselodoris katherinae*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 181251, buccal armature. A, entire jaw. B, jaw rodlets. C, whole radula. D, inner lateral teeth. E, middle lateral teeth. F, outer lateral teeth.

apex (Fig. 17B). Radular formula of holotype (CASIZ 176771) 55 × 53.0.53, and 61 × 67.0.67 in one paratype (CASIZ 181251; Fig. 17C). Rachidian row of teeth absent (Fig. 17D). Innermost lateral teeth having one to three triangular denticles on inner side of bifid primary cusp, with another one or two denticles on the outside. Next several laterals lacking inner triangular denticles but possessing one to three denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 17E) all lacking inner denticles but having three to five sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and somewhat shorter tooth shape, with four to seven rounded to pointed outer denticles (Fig. 17F).

Reproductive system: Reproductive organs fully mature in one specimen examined (CASIZ 176771; Fig. 13C). Ampulla thick, tubular, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct

entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick, covering bursa copulatrix. Vas deferens narrowing slightly as it transitions into long, convoluted, muscular ejaculatory portion. Ejaculatory portion widening into enlarged penial bulb. Penial papilla distinctly curved with broad base, devoid of penial hooks. Penial bulb adjacent to thick, slightly narrower vaginal duct at common gonopore. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Vagina thick, curved, leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum situated near base of bursa. Moderately short, narrow uterine duct emerging from vagina distal to base of bursa and female gland mass, near albumen gland.

Remarks

Hypselodoris katherinae is a member of a large clade that includes *H. skyleri* sp. nov., *H. paradisa* sp. nov., *H. maritima*, *H. rudmani* Gosliner & Johnson, 1999 and *H. bertschi* Gosliner & Johnson, 1999. It is sister to *H. paradisa* and *H. skyleri*. The ABGD analysis indicates that *H. katherinae* is clearly distinct from *H. skyleri* and *H. paradisa*. All three species have longitudinal lines, but they are opaque white in *H. paradisa* and brown in *H. skyleri*. *Hypselodoris katherinae* is unique among described members of *Hypselodoris* in having longitudinal red lines or dashes. In *H. paradisa* and *H. skyleri* there are additional opaque white spots that are absent in *H. katherinae*. *Hypselodoris paradisa* also has minute black spots that are absent in the other two species. The three species also differ in the ornamentation of the rhinophores. All three have red pigment on the rhinophores, but in *H. katherinae* there are no distinct rings, whereas there are two rings in *H. paradisa* and three rings in *H. skyleri*. In *H. katherinae* and *H. paradisa* there are only a few lateral mantle glands, whereas they are largely continuous in the many specimens of *H. skyleri* examined.

The jaw rodlets of *H. katherinae* have only a single cusp, whereas there may be one or two cusps in *H. paradisa* and one to three cusps in *H. skyleri*. The radulae of *H. katherinae*, *H. paradisa* and *H. skyleri* all have a similar formula and teeth of a similar shape.

The reproductive system is similar in all three species. In *H. katherinae*, the vagina is elongate and uniformly wide. In *H. paradisa*, the vagina is short and uniformly wide, and *H. skyleri* has a relatively thin, elongate vagina, where the portion below the bursa copulatrix is much wider. All three species, together with the sister clade including *H. maritima*, *H. bertschi* and *H. rudmani*, have a much wider penial bulb than is found in other species of *Hypselodoris* (Gosliner & Johnson, 1999; present study). In *H. katherinae*, the penial papilla is curved with a broad base, whereas it is blunt and discoidal in *H. paradisa* and conical in *H. skyleri*. The penis of *H. rudmani* is unique in having a ring of muscular plates at the apex of the papilla.

HYPSELODORIS LACUNA GOSLINER & JOHNSON SP. NOV.

(FIGS 2J, 13D, 18A–D, 19)

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Hypselodoris sp. 11 Gosliner *et al.*, 2008: 270, top photograph.
Hypselodoris sp. 20 Gosliner *et al.*, 2015: 2639, bottom right photograph.

Type material

Holotype: NMP 041280 (formerly CASIZ 182758), subsampled for molecular study, Bethlehem 13.67329°N, 120.84093°E, Tingloy, Batangas, Philippines, 17 May 2010, T. Gosliner.

Paratypes: CASIZ 208587, one specimen, dissected, Coral Cove, 13.51664°N, 120.99176°E, Puerto Galera, Mindoro Oriental, Philippines, 31 March 2015, P. J. Aristorenas. CASIZ 208188, one specimen, tissue removed for molecular study, Batangas Channel, 13.5199°N, 120.9604°E, Puerto Galera, Mindoro Oriental, Philippines, 12 April 2015, T. Gosliner. CASIZ 208190, one specimen, tissue removed for molecular study, Manila Channel, 13.5223°N, 120.9485°E, Puerto Galera, Mindoro Oriental, Philippines, 13 April 2015, T. Gosliner. CASIZ 217345, one specimen, Bethlehem 13.67329°N, 120.84093°E, Tingloy, Batangas, Philippines, 18 April 2016, T. Gosliner. CASIZ 177617, one specimen, dissected, Bethlehem 13.67329°N, 120.84093°E, Tingloy, Batangas, Philippines, 17 April 2008, T. Gosliner. CASIZ 208652, one specimen, Boulders, 13.51286°N, 120.98309°E, Puerto Galera, Mindoro Oriental, Philippines, 26 April 2015, T. M. Gosliner. CASIZ 208646, one specimen, La Laguna, 13.52496°N, 120.97114°E, Puerto Galera, Mindoro Oriental, Philippines, 8 April 2015, T. M. Gosliner. CASIZ 069756, north end of Pig (Tab) Island, Madang, Papua New Guinea, 10 m depth, 30 July 1989, T. Gosliner. CASIZ 068776, one specimen, Cement Mixer Reef, Madang, Papua New Guinea, 16 July 1989, T. Gosliner. CASIZ 075842, one specimen, Barracuda Point, Madang, Papua New Guinea, 7 m depth, 23 November 1990, T. Gosliner.

Geographical distribution

Known from the western Indian Ocean of Aldabra Atoll to the western Pacific of Vanuatu, Indonesia, Papua New Guinea, the Philippines and Japan (Gosliner *et al.*, 2008).

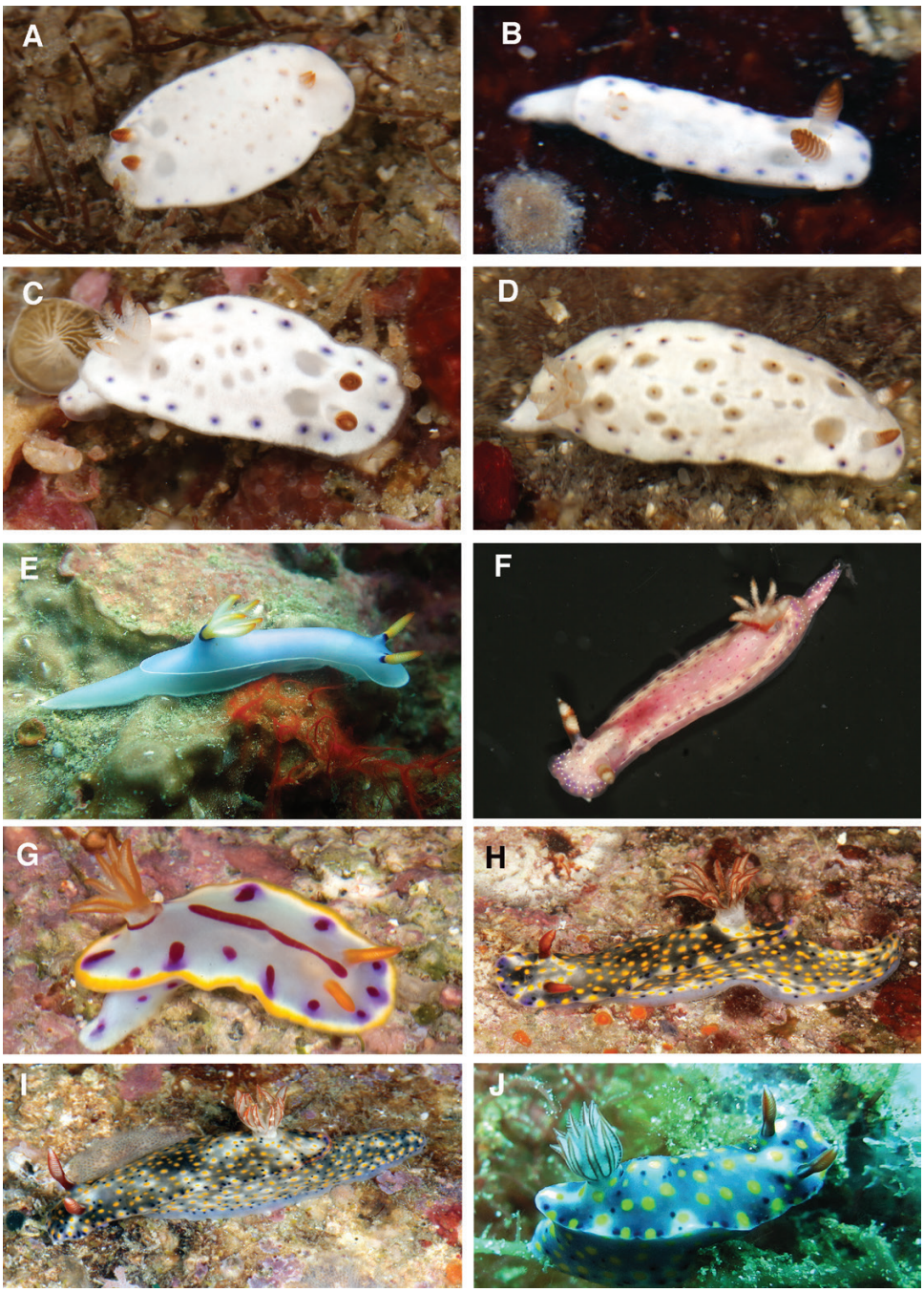

Figure 18. Living animals. A, ***Hypselodoris lacuna*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 177617, Tingloy, Batangas, Philippines. B, ***H. lacuna*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 208188, Puerto Galera, Mindoro Oriental, Philippines. C, ***H. lacuna*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 217345, Tingloy, Batangas, Philippines. D, ***H. lacuna*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 208652, Puerto Galera, Mindoro Oriental, Philippines. E, ***Hypselodoris melanesica*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 190823, Madang, Papua New Guinea. F, ***Hypselodoris paradisa*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ 191464, Madang, Papua New Guinea, photograph by Vanessa Knutson. G, ***Hypselodoris perii*** Gosliner & Johnson **sp. nov.**, NMP 041281, Mabini, Batangas, Philippines. H, ***Hypselodoris roo*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 204801, Puerto Galera, Mindoro Oriental, Philippines. I, ***H. roo*** Gosliner & Johnson **sp. nov.**, CASIZ 208193, paratype, Puerto Galera, Mindoro Oriental, Philippines. J, ***H. roo*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 186098, Mabini, Tingloy, Philippines.

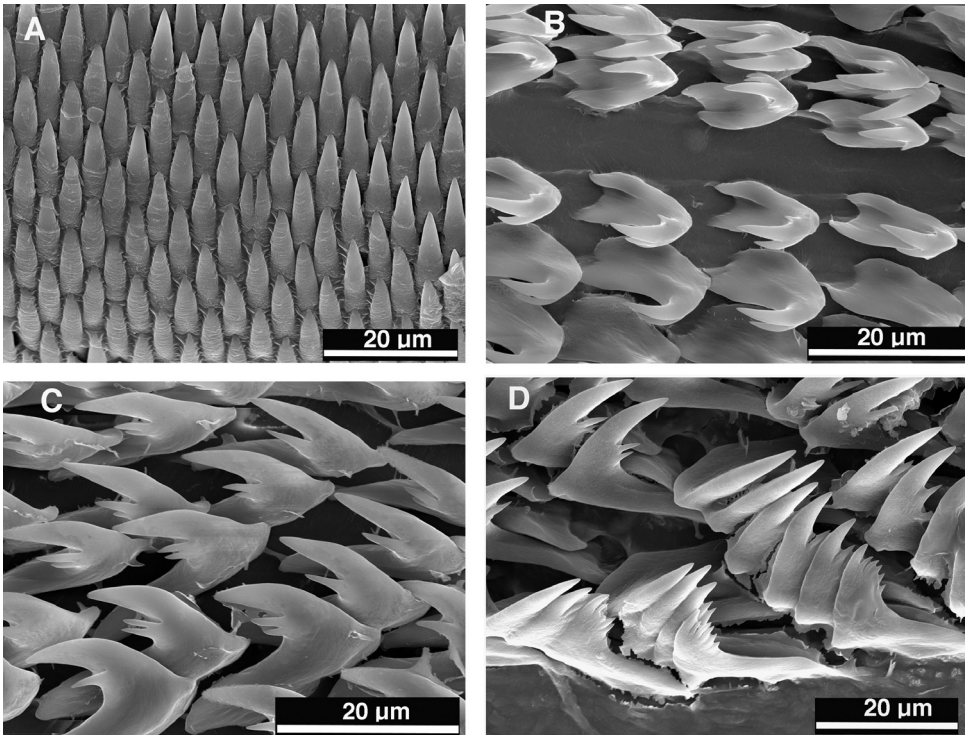

Figure 19. ***Hypselodoris lacuna*** Gosliner & Johnson **sp. nov.**, buccal armature. A, jaw rodlets, paratype, CASIZ 208587. B, inner lateral teeth, paratype, CASIZ 177617. C, middle lateral teeth, paratype, CASIZ 177617. D, outer lateral teeth, paratype, CASIZ 208587.

Etymology

This species is named *Hypselodoris lacuna* based on the translucent areas on the notum that resemble holes in the body wall.

Description

External morphology: Living animals (Fig. 18A–D) small, reaching 12 mm in length. Body opaque white, with round translucent areas on notum that resemble holes in body wall. Two large, translucent circles situated posterior to rhinophores, and smaller circles located over surface of notum. Small black spot located in the centre of most smaller translucent circles. Ring of blue spots present along submarginal area of notum. Centre of spot darker than outer diffuse area. Blue spots also present on posterior end of foot. Gill branches white, with reddish tip. Seven unipinnate gill branches present in all specimens examined. Perfoliate rhinophores white basally and bright red apically, bearing about eight or nine densely arranged lamellae.

Mantle glands: Subcutaneous mantle glands simple, rounded in shape (Fig. 2J). Six to twelve glands present posteriorly in seven specimens examined. Anterior and lateral glands absent.

Buccal armature: Muscular portion of buccal mass much smaller than oral tube. Buccal mass consisting of chitinous labial cuticle at anterior end of muscular portion of buccal mass. Jaws bearing numerous rodlets, narrow and acutely pointed, largely undivided but with an occasional bifid cusp (Fig. 19A). Radular formula of paratype (CASIZ 208587) 46 × 36.0.36. Rachidian row of teeth absent (Fig. 19B). Innermost lateral teeth with one or two small, triangular denticles on inner side of bifid primary cusps and one outer denticle. Inner cusp of bifid cusp much longer than outer one. Next several laterals lacking inner and outer denticles on sides of primary bifid cusps. Midlateral teeth (Fig. 19C) also lacking inner denticles, but with a single triangular outer denticle or entirely lacking denticles. Outer cusp of bifid cusp much shorter than inner one. Outer teeth lacking inner denticles, with up to four triangular outer denticles (Fig. 19D). Outermost teeth with narrower base and more elongate tooth shape.

Reproductive system: Reproductive organs fully mature (Fig. 13D). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into the oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens curved and thick, narrowing gradually

while transitioning into narrow, muscular ejaculatory portion. Ejaculatory portion curving into segment entering short, wider penial bulb. Penial bulb adjacent to curved, narrow vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Elongate, curved vagina leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Relatively short uterine duct emerging from vagina distal to junction of receptaculum and bursa.

Remarks

Hypselodoris lacuna is unique among members of this genus in having translucent circles and a ring of small blue spots along the submarginal area of the notum. Its colour pattern more closely resembles that of *Chromodoris aspersa* (Gould, 1852), but it has red rhinophoral and gill pigment rather than light orange. This species is at the base of a clade that includes *H. iba*, *H. reidi*, *H. regina*, *H. jacksoni*, *H. cerisae* and *H. krakatoa*, although that relationship is weakly supported. All members of this clade, with the exception of *H. lacuna*, have an elevated gill pocket and mantle glands arranged all around the perimeter of the mantle margin (Gosliner & Johnson, 1999; Wilson & Willan, 2007; present study). *Hypselodoris lacuna* has only posterior mantle glands, and the gill pocket is not elevated. One feature that *H. lacuna* shares with other members of this clade is the presence of radular teeth where the inner cusp is much longer than the outer one.

HYPSELODORIS MELANESICA GOSLINER & JOHNSON SP. NOV.

(FIGS 13E, 18E, 20)

LSID: urn:lsid:zoobank.org:act:948DE50E-A684-4E57-8126-658578AF3E06

Hypselodoris bullocki misidentification, not *C. bullockii* Collingwood, 1881; Johnson, 2000; Coleman, 2001: 79, lower right photograph; Gaensslen, 2007; Rudman, 2007; Hanchard, 2009.
Hypselodoris sp. 7 Gosliner *et al.*, 2008: 268, second photograph from top.
Hypselodoris sp. 16 Gosliner *et al.*, 2015: 262, bottom left photograph.

Type material

Holotype: CASIZ 191246, subsampled for molecular study, Southern Sek Island, 5.0985°S, 145.8210°E, 8 m depth, Madang Lagoon, Madang, Papua New Guinea 15 November 2012.

Paratypes: CASIZ 185100, five specimens, one subsampled for molecular study, various locations, Milne Bay, Milne Bay Province, 5–12 m depth, R. Steene. CASIZ 069754, one specimen, Anemone Reef, near Ruo, Island, Madang Lagoon, Madang, Papua New Guinea, 20 July 1989, M. Jebb. CASIZ 069787, one specimen, dissected, Madang Lagoon, Madang, Papua New Guinea, August 1989, M. Gosliner. CASIZ 069785, three specimens, Madang Lagoon, Madang, Papua New Guinea, August 1989, M. Gosliner. CASIZ 065356, one specimen, Hole in the Wall, north of Hussein Village, north of Madang, 20 m depth, 3 February 1988, T. Gosliner. CASIZ 071237, one specimen, patch reef off N side Kranket Island, 24 m depth, 24 January 1988, T. Gosliner. CASIZ 071474, two specimens, Takahate Bay, Big Nggela Island, Florida Group, Solomon Islands, 15–23 m depth, 1 September 1986, R. Van Syoc. CASIZ 191392, one specimen, N. Tadwai Island, 4.985°S, 145.7915°E, Madang Lagoon, Madang, Papua New Guinea, 11 m depth, 22 November, 2012. CASIZ 191160, one specimen, Sek Island, Madang Lagoon, Madang, Papua New Guinea, 12 November 2012. CASIZ 191227, one specimen, Southern Sek Island, 5.0985°S, 145.8210°E, 8 m depth, Madang Lagoon, Madang, Papua New Guinea, 15 November 2012. CASIZ 190823, one specimen, Cement Mixer Reef, 5.15176°S, 145.81832°E, 2–23 m depth, Madang Lagoon, Madang, Papua New Guinea 12 December 2012, T. Gosliner. CASIZ 191326, one specimen, south Rempi 5.0367°S, 145.8066°E, Madang, Papua New Guinea, 19 November 2012, Francois Michonneau. CASIZ 191139, one specimen, Bilbil Island 5.2967°S, 145.7816°E, Madang, Papua New Guinea, 22 m depth, 12 November 2012, Heok Hui Tan. CASIZ 191066, one specimen, N. Siar Island, 5.1967°S, 145.8067°E, Madang, Papua New Guinea 9 November 2012, Heok Hui Tan. CASIZ 190842, one specimen, from orange sponge, Madang Lagoon, November–December 2012, Marco Oliverio.

Geographical distribution

Known only from the Papua New Guinea and the Solomon Islands (present study).

Etymology

Hypselodoris melanesica is named for Melanesia, the region to which this species is geographically restricted.

Description

External morphology: Living animals (Fig. 18E) of moderately size, reaching 30 mm in length. Body translucent purple, with thin white band encircling the margin of notum and foot. Five unipinnate gill branches on notum. One large specimen (CASIZ 071237) with seven gill branches. Gill branches light orange, with darker orange at their common base. Base of gill pocket

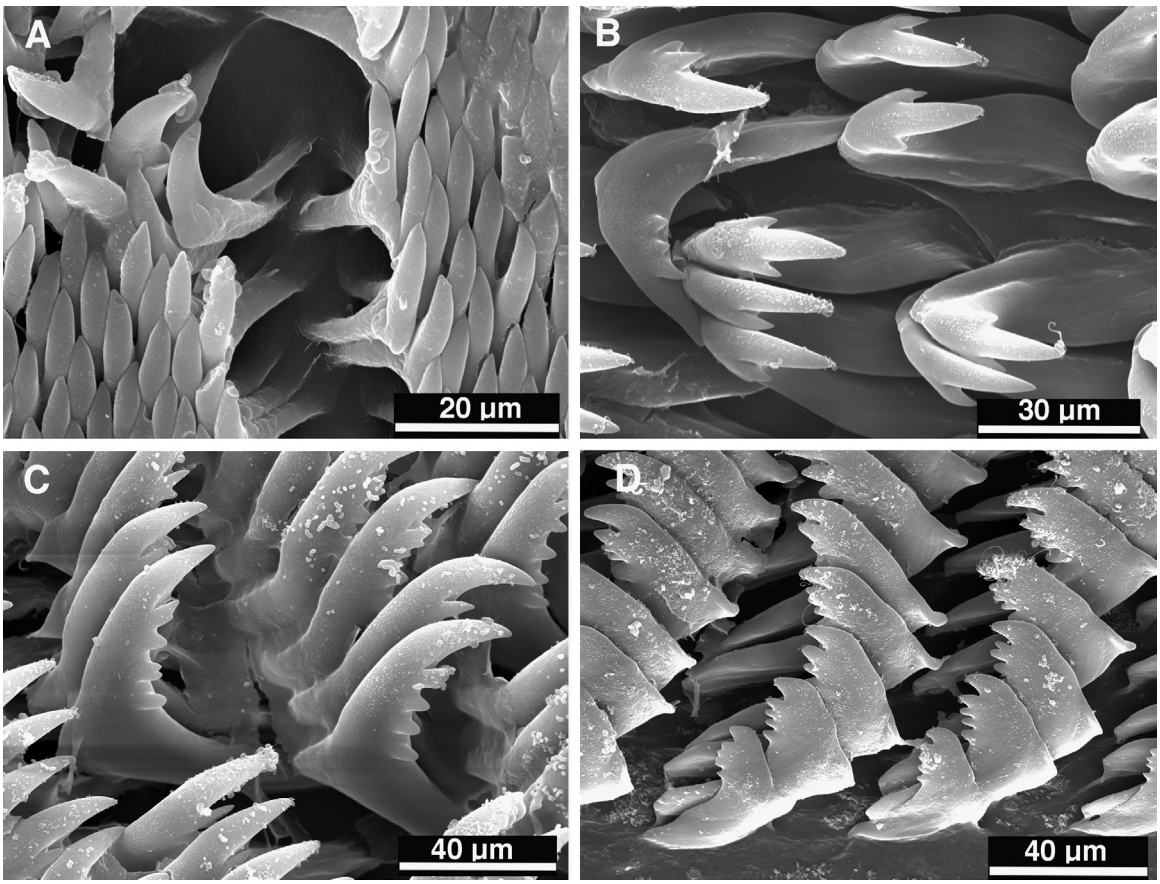

Figure 20. ***Hypselodoris melanesica*** Gosliner & Johnson **sp. nov.**, buccal armature, paratype CASIZ 069787. A, jaw rodlets. B, inner lateral teeth, paratype, CASIZ 177617. C, middle lateral teeth, paratype, CASIZ 177617. D, outer lateral teeth, paratype, CASIZ 208587.

deep violet. Bulb of rhinophores bright orange, with redder apex. Bulb with ~25 densely packed lamellae. Base of rhinophore sheath deep violet to purple.

Mantle glands: Subcutaneous mantle glands entirely absent.

Buccal armature: Muscular portion of buccal mass about twice the length of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 20A). Rodlets narrow with short base and evenly curved, with single, acutely pointed apex. Radular formula of one paratype (CASIZ 069787) 57 × 59.0.59. Rachidian row of teeth absent (Fig. 20B). Innermost lateral teeth having one pointed denticle on inner side of bifid primary cusp, with another one or two outer denticles. Denticles not extending far beyond middle of elongate primary cusp. Next several laterals lacking inner triangular denticle but possessing three or four denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 20C) all lacking inner denticles but having four or five rounded to triangular outer denticles and extended primary cusp. Outermost teeth having a narrower base and shorter tooth shape, with three rounded outer denticles (Fig. 20D), often larger than bifid cusps.

Reproductive system: Reproductive organs of the paratype (CASIZ 069787) fully mature (Fig. 13E). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick, and narrowing slightly as it transitions into muscular ejaculatory portion. Prostatic portion enveloping bursa copulatrix. Ejaculatory portion convoluted, narrow, entering short, wider penial bulb. Penial bulb adjacent to straight, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis

and larger spherical, thin-walled receptaculum seminis. Receptaculum seminis appressed against vagina in distal half of vaginal length. Moderately short uterine duct emerging from vagina close to base of bursa and entering female gland mass near the albumen gland.

Remarks

In our phylogenetic analyses, *H. melanesica* is always sister to *H. bullockii* but forms a distinct clade. In the ABGD analysis, *H. melanesica* is included in the same group as *H. bullockii*, thus suggesting that they should be considered as conspecific. Their uncorrected p-distances for the *COI* gene range between 2.0 and 2.6% different, right near the boundary for consideration of these two as distinct species. Although *H. melanesica* resembles *H. bullockii* in its shape and body colour, there are consistent morphological differences. In *H. bullockii*, the body colour is generally light pink to a deep purple. There may or may not be darker pigment at the base of the gill and the rhinophores. When present, the purple pigment is a wide band that is very diffuse, without distinctly defined edges. In contrast, *H. melanesica* is always light purple in colour and always has well-defined narrow bands of darker pigment at the base of the rhinophores and gill. The bands at the base of the rhinophores of *H. melanesica* always have a break in the band on the posterior side of the rhinophores. Internally, *H. melanesica* (CASIZ 069787) has a radular formula of 65 × 68.0.68 vs. 77 × 97.0.97 in one specimen of *H. bullockii* (CASIZ 083685). Also, the primary cusps of the radular teeth of *H. melanesica* appear shorter than those of *H. bullockii* (Figs 20, 21). The reproductive system of *H. melanesica* has a shorter penial bulb and a longer ejaculatory duct that is more convoluted than that found in *H. bullockii* (Fig. 13F). Also, *H. melanesica* has a longer vaginal duct than that of *H. bullockii*.

Hypselodoris melanesica is known only from Papua New Guinea and the Solomon Islands, whereas *H. bullockii* is known from the western Pacific of Australia, New Caledonia, Malaysia, Indonesia, Japan, Taiwan, Philippines, Marshall Islands (Gosliner *et al.*, 2008) and Palau (present study). *Hypselodoris melanesica* and *H. bullockii* are geographically isolated and have minor but consistent differences in their coloration and internal morphology spanning several

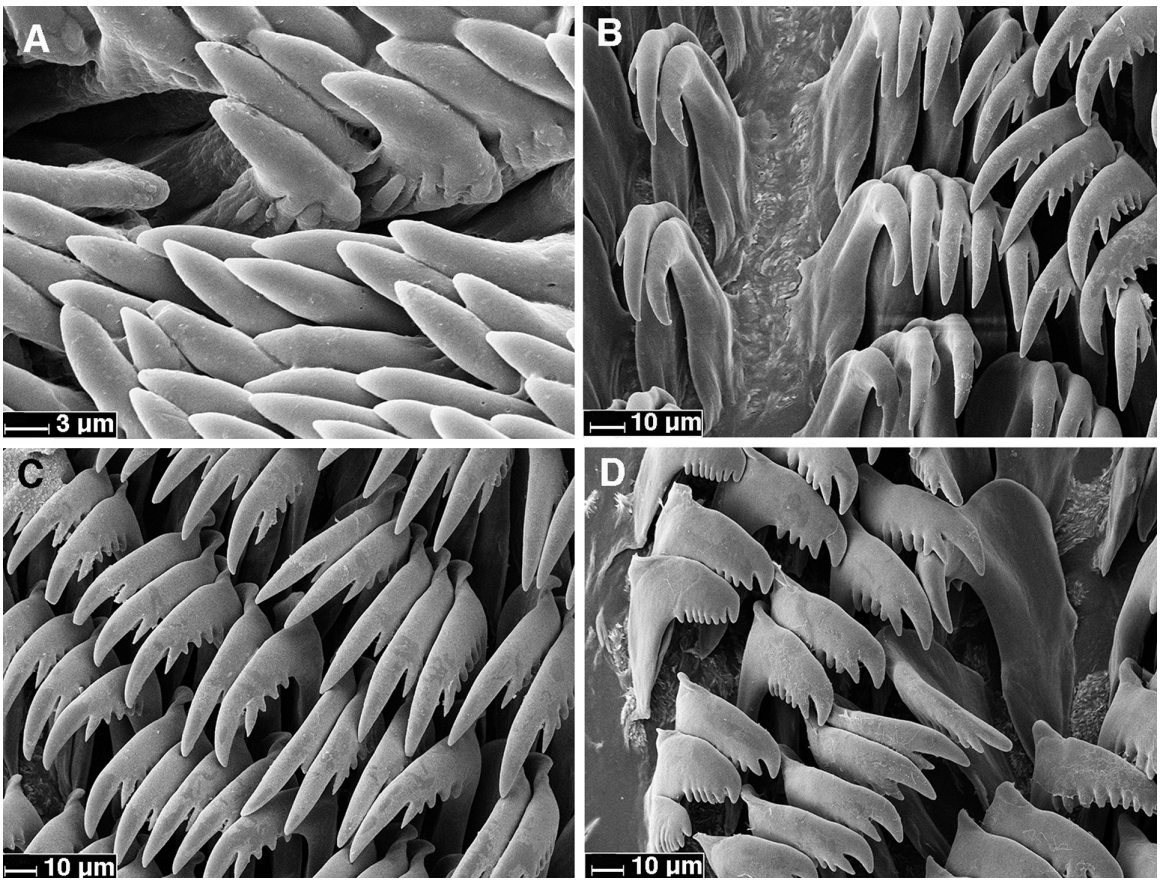

Figure 21. *Hypselodoris bullockii* (Collingwood, 1881), buccal mass. A, jaw rodlets, CASIZ 083685. B, inner lateral teeth, CASIZ 085905. C, middle lateral teeth, CASIZ 085905. D, outer lateral teeth, CASIZ 085905.

organ systems. Based on these consistent differences, we consider *H. melanesica* as a distinct species from *H. bullockii* despite the fact that the ABGD analysis clusters these species as conspecifics.

HYPSELODORIS PARADISA GOSLINER & JOHNSON **SP. NOV.**

(FIGS 2K, 13G, 18F, 22)

LSID: urn:lsid:zoobank.org:act:48A65392-E850-4EC0-BB40-E67E2322D01F

Type material
Holotype: CASIZ 191464, subsampled for molecular study, dissected, reef close, 39 m depth, Pig (Tab Island), 5.1634°S, 145.83833°E, Madang Lagoon, Madang, Papua New Guinea, 28 November, 2012.

Type locality
Outer barrier reef north of Tab Island, Madang Lagoon, Papua New Guinea.

Geographical distribution
Presently known only from northern Papua New Guinea.

Etymology
Hypselodoris paradisa is named for the Greek word for paradise, referring to the tropical habitat of this species.

Description
External morphology: Living animal (Fig. 18F) moderately small, reaching 10 mm in length. Body translucent pink, with series of rows of opaque white spots, dashes and interrupted lines on dorsal surface of notum. V-Shaped reddish mark present posterior to rhinophores. Anterior and posterior ends of notum with purple markings; also present on posterior end of foot. Pink marginal band present along notal rim. Black spots arranged in linear rows between white markings. Six unipinnate gill branches having a translucent white base and bright red–orange pigment on apical surfaces and outer margin. Bulb of perfoliate rhinophores opaque white, with three red–orange

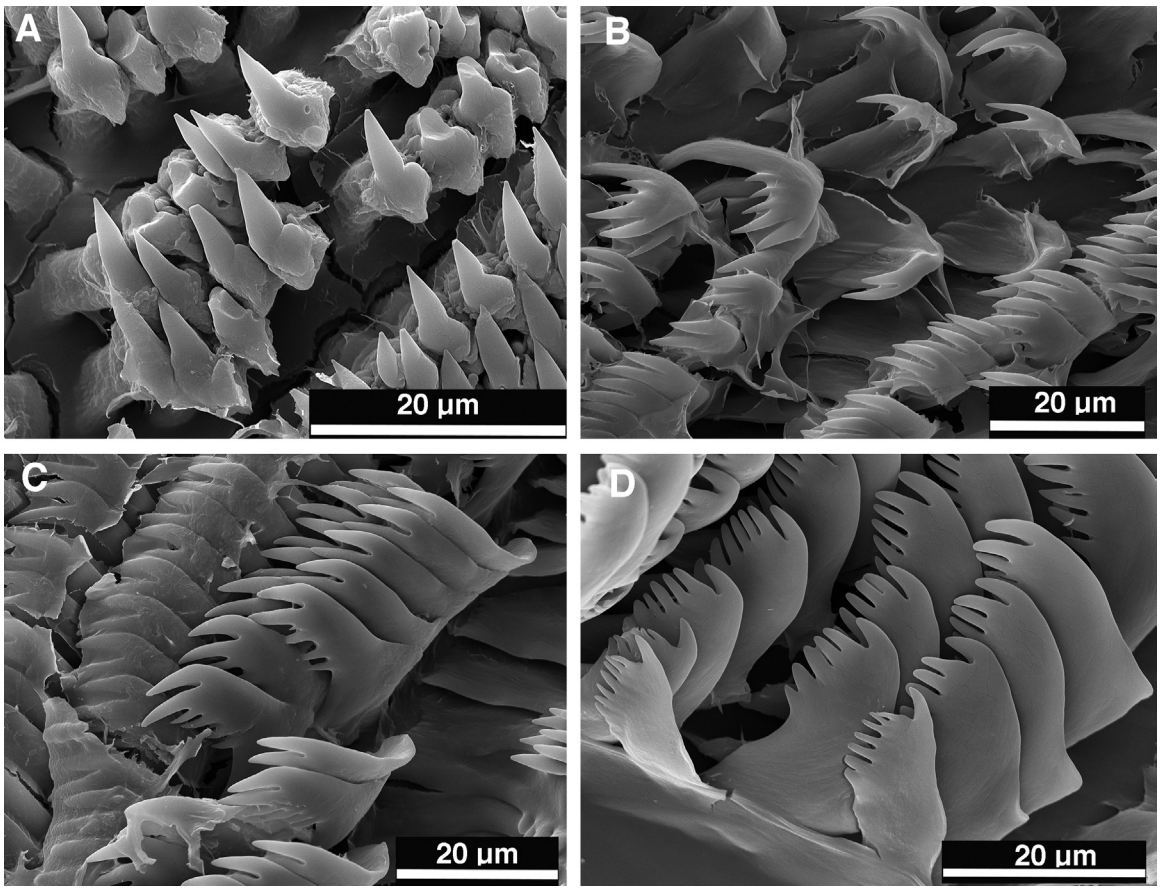

Figure 22. ***Hypselodoris paradisa*** Gosliner & Johnson **sp. nov.**, holotype, CASIZ191464. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

transverse bands; bearing about ten densely arranged lamellae. Base of rhinophores translucent white.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2K). Glands densely situated anteriorly and posteriorly, with few glands present in the central lateral regions of body margin. About 15 glands on either side of anterior end of the body, with arc of ~20 glands situated posteriorly. Three lateral glands present on either side of lateral margin of notum.

Buccal armature: Muscular portion of buccal mass slightly longer than glandular portion of oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 22A). Rodlets narrowly ovoid, with single, acutely pointed apex and wider base. Radular formula of holotype 46 × 55.0.55. Rachidian row of teeth absent (Fig. 22B). Innermost lateral teeth having single triangular denticles on inner side of bifid primary cusp, with another one to two outer denticles. Next several laterals lacking inner triangular denticle but possessing two or three denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 22C) all lacking inner denticles but having four or five sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and shorter tooth shape, with four to six rounded outer denticles (Fig. 22D), often larger than bifid cusps.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 13G). Ampulla thin, tubular, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick, and narrowing slightly as it transitions into muscular ejaculatory portion. Ejaculatory portion highly convoluted and long, widening again before entry into broad penial bulb. Penial bulb adjacent to straight, very wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively short vagina leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum adjacent to bursa at distal end of vagina. Moderately long uterine duct emerging from vagina close to base of bursa and female gland mass, near albumen gland.

Remarks
The phylogenetic relationship of this species to *H. katherinae* and *H. skyleri* is discussed above in the remarks section of *H. katherinae*. This species has similarity in its colour pattern to the sympatric species, *H. maculosa* and *H. decorata*, with the presence of opaque white lines and longitudinally arranged black spots. Despite the similarity of colour pattern, *H. paradisa* is in a distinct clade from both *H. maculosa* and *H. decorata*. Both *H. paradisa* and *H. decorata* have three reddish rhinophoral bands, whereas *H. maculosa* only has two bands. *Hypselodoris paradisa* has a reddish V-shaped patch on the head that is absent in both other species. *Hypselodoris paradisa*, like other members of its clade, has a broader radula than members of the *H. maculosa* clade and has a broad penial papilla, as in other members of its clade.

HYPSELODORIS PERII GOSLINER & JOHNSON **SP. NOV.**

(FIGS 2L, 13H, 18G, 23)

LSID: urn:lsid:zoobank.org:act:0E629152-88A2-4635-B40C-C9B0BEF05659

Noumea sp. Debelius, 1997: 218, middle photograph.
Noumea sp. Coleman, 2001: 84.
Hypselodoris sp. 8. Debelius & Kuiter, 2007: 123, middle photograph.
Hypselodoris sp. 13. Gosliner *et al.*, 2015: 261, upper right photograph.

Type material
Holotype: NMP 041281, (formerly CASIZ 182751), dissected, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 40 m depth, 17 May 2010, Peri Paleracio.

Type locality
Mainit Bubbles, Mabini, Batangas, Luzon Island, Philippines, 13.6880278°N, 120.95809°E.

Geographical distribution
Known only from Bali, Indonesia (Debelius, 1997) and Batangas, Philippines from deep reefs (Gosliner *et al.*, 2008, 2015; present study).

Etymology
Hypselodoris perii is named for good friend and diver guide extraordinaire, Peri Paleracio, who found the first specimen of this species in the Philippines. Peri has discovered many new species of marine life in the Philippines, and it is a pleasure to honor his efforts with this new species.

Description
External morphology: Living animals (Fig. 18G) large, reaching 35 mm in length. Body translucent white, with wine-red medial line and scattered, elongate wine-red oval rings surrounded by diffuse purple pigment. Wide yellow to yellow–orange marginal band present along entire mantle margin. Wine-red ring

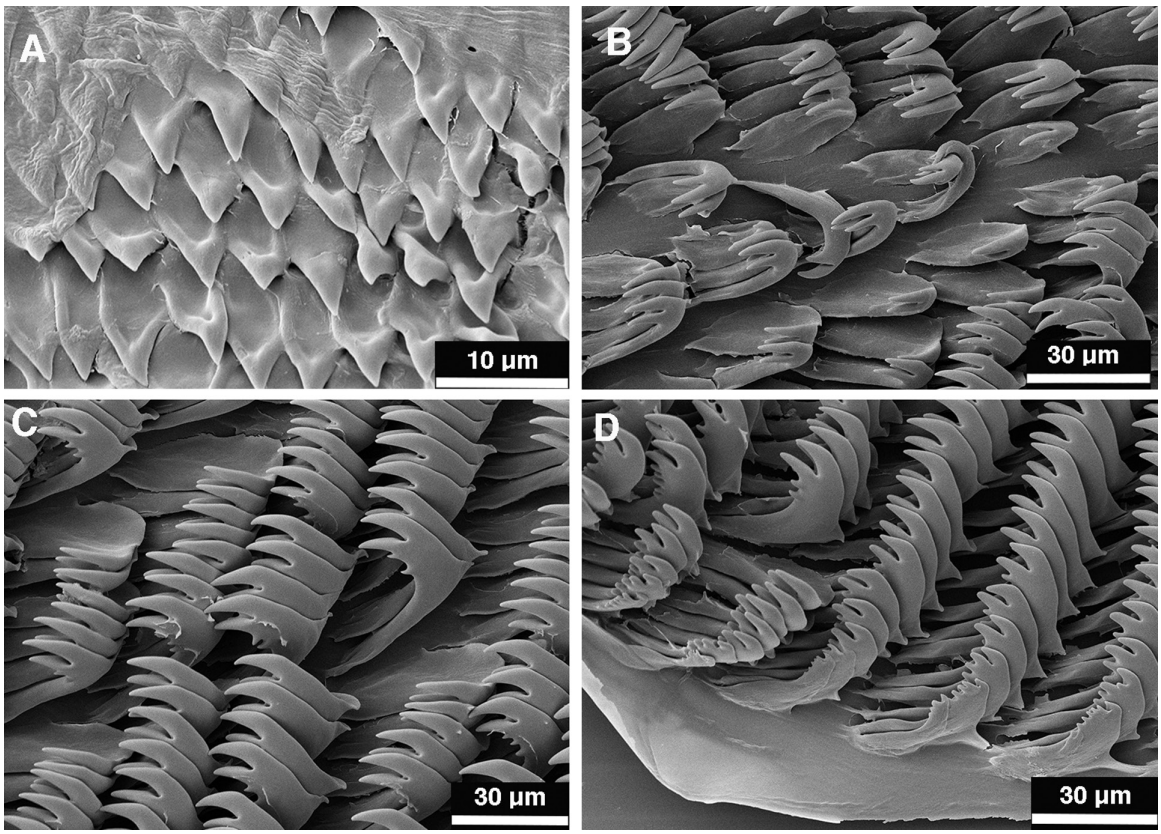

Figure 23. ***Hypselodoris perii*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041281, buccal armature. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

encircling base of gill sheath. Translucent white foot ornamented by wine-red spots having larger areas of purple surrounding them. Eight unipinnate gill branches with translucent white base and bright red–orange pigment on apical surfaces and outer margin. Perfoliate rhinophores uniformly bright red–orange, bearing ~17 densely arranged lamellae.

Mantle glands: Subcutaneous mantle glands simple rounded in shape (Fig. 2L). Glands situated anteriorly and posteriorly, with no glands present along central regions of mantle margin. Four to five glands on either side of anterior end of the body, with an arc of 13 glands situated posteriorly.

Buccal armature: Muscular portion of buccal mass approximately equal in length to oral tube. Buccal mass consisting of chitinous labial cuticle at anterior end of muscular portion of buccal mass. Jaws bearing numerous rodlets (Fig. 23A). Rodlets broadly triangular, with single acutely pointed apex. Radular formula of holotype 42 × 40.0.40. Rachidian row of teeth absent (Fig. 23B). Innermost lateral teeth have a single large, triangular denticle on inner side of bifid primary cusp and lacking outer denticles. Next several laterals lacking inner triangular denticle and lacking denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 23C) also lacking inner denticles but possessing two or three triangular outer denticles. Outer teeth lacking inner denticles and having two to five triangular outer denticles (Fig. 23D). Outermost teeth with narrower base and more elongate tooth shape.

Reproductive system: Reproductive organs of holotype not fully mature, but arrangement of all major organs evident (Fig. 13H). Ampulla thick, tubular and slightly convoluted, narrowing somewhat before bifurcating into the oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens curved and thick, narrowing slightly while transitioning into muscular ejaculatory portion. Ejaculatory portion curving into segment entering short, enlarged penial bulb. Penial bulb adjacent to straight, slender vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Elongate vagina leading to minute receptaculum seminis and larger

spherical, thin-walled receptaculum seminis. Short uterine duct emerging from about half of the length along duct to bursa. Uterine duct relatively short and entering female gland mass near albumen gland.

Remarks

The colour pattern of *H. perii* clearly differentiates it from the all other described species. It is the only species with an elongate medial longitudinal reddish line and reddish oval markings. The most similar species is *Hypselodoris dollfusi* (Pruvot-Fol, 1933), which was re-described by Gosliner & Behrens (2000). Although both species are translucent white, with a yellow marginal band and wine-red and purple markings, there are numerous differences in the external colour pattern of the two species. *Hypselodoris dollfusi* lacks the medial longitudinal line that is present in *H. perii*. In *H. dollfusi*, the wine-red markings are narrow circles, which contain purple pigment. In contrast, *H. perii* has broad reddish ovals surrounded by diffuse purple pigment. In *H. dollfusi*, there are red and purple rings at the base of the rhinophores and the gill pocket, whereas in *H. perii* there is only a red ring at the base of the gill. In *H. dollfusi*, the gill and rhinophores are deep red, whereas they are red–orange in *H. perii*. The red pigment on the gill of *H. dollfusi* is restricted to the axis of each gill branch, whereas in *H. perii* the entire external surface of each gill branch is red–orange. Externally, both *H. dollfusi* and *H. perii* have anterior and posterior mantle glands and lack glands in the centre portion of the body. The glands are more numerous in *H. dollfusi* (12–18 anterior glands per side of the body and 22 posterior glands) vs. three or four anterior glands per side and 13 posterior glands in *H. perii*.

Internally, there are also differences between the two species. The radular formula of *H. dollfusi* contains more rows of teeth (66 vs. 42) and more teeth per row than does the radula (88 vs. 40) of *H. perii*. In the single individual of *H. dollfusi* examined, the left inner lateral teeth had a single inner denticle, whereas the right inner laterals lacked a denticle. In *H. perii*, both the left and the right inner laterals bear a single denticle. In *H. perii*, the middle laterals bear two or three outer denticles, whereas the middle laterals of *H. dollfusi* lack denticles. Only the outer four to ten teeth of *H. dollfusi* bear outer denticles, whereas all of the middle and outer lateral teeth of *H. perii* have denticles. There are minor differences in the reproductive system of the two species, but given that the reproductive system of *H. perii* was not fully mature, it is difficult to make detailed comparisons based on the present material.

The two species are geographically isolated, with *H. dollfusi* being restricted to the Arabian Sea and *H. perii* being known only from Bali and the Philippines. Unfortunately, no material suitable for molecular study is available for *H. dollfusi*. In the present molecular analysis, *H. perii* is sister to a large clade that includes members of the *H. obscura*, *H. capensis* (Barnard, 1927), *H. kaname* and *H. maritima* clades. Gosliner & Behrens (2000), based on morphological similarities, speculated that *H. dollfusi* was likely to be most closely related to the clade that includes *H. paulinae*, *H. fucata* and *H. kaname*. They noted that these four species shared three apomorphies: an erect rather than spreading branchial plume, a short jaw element shaft; and a receptaculum seminis that inserts into the vagina at the base of the bursa copulatrix. *Hypselodoris perii* also shares these characteristics. Our molecular studies place *H. perii* in close proximity to the clade that includes *H. paulinae* and *H. kaname*. Additional molecular studies that include *H. fucata* and *H. dollfusi* need to be conducted to explore these possible relationships further.

HYPSELODORIS ROO GOSLINER & JOHNSON SP. NOV.

(FIGS 2M, 13I, 18H–J, 24)

LSID: urn:lsid:zoobank.org:act:2AEED331-248A-49A9-AC93-C0A38921233E

Hypselodoris kanga misidentification, not *H. kanga* Rudman, 1977; Krampf, 2007.
Hypselodoris kanga misidentification, not *H. kanga* Rudman, 1977; Debelius & Kuiter, 2007: 127, lower left photograph.
Hypselodoris sp. 7 Gosliner *et al.*, 2015: 258, upper right photograph.

Type material

Holotype: NMP 041282 (formerly CASIZ 181272), subsampled for molecular study, dissected, Mainit Bubbles, 13.6880278°N, 120.95809°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 21 May 2009, T. Gosliner.

Paratypes: CASIZ 186098, one specimen, Mainit Bubbles, 13.6880278°N, 120.8971833°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 4 May 2011, T. Gosliner. CASIZ 204801, one specimen, Giant Clam dive site, 13.51356°N, 120.95809°E, Puerto Galera, Mindoro Oriental, Philippines, 19 April 2015, T. Gosliner. CASIZ 208541, one specimen, Giant Clam dive site, 13.51356°N, 120.95809°E, Puerto Galera, Mindoro Oriental, Philippines, 28 March 2015, T. Gosliner. CASIZ 208193, one specimen, Giant Clam dive site, 13.51356°N, 120.95809°E, Puerto Galera, Mindoro Oriental, Philippines, 25 March 2015, T. Gosliner. CASIZ 217236, one specimen, Murals dive site, 13.6993°N, 120.8824°E, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, 22 April 2016, T. Gosliner. CASIZ 217308, Pyramid dive

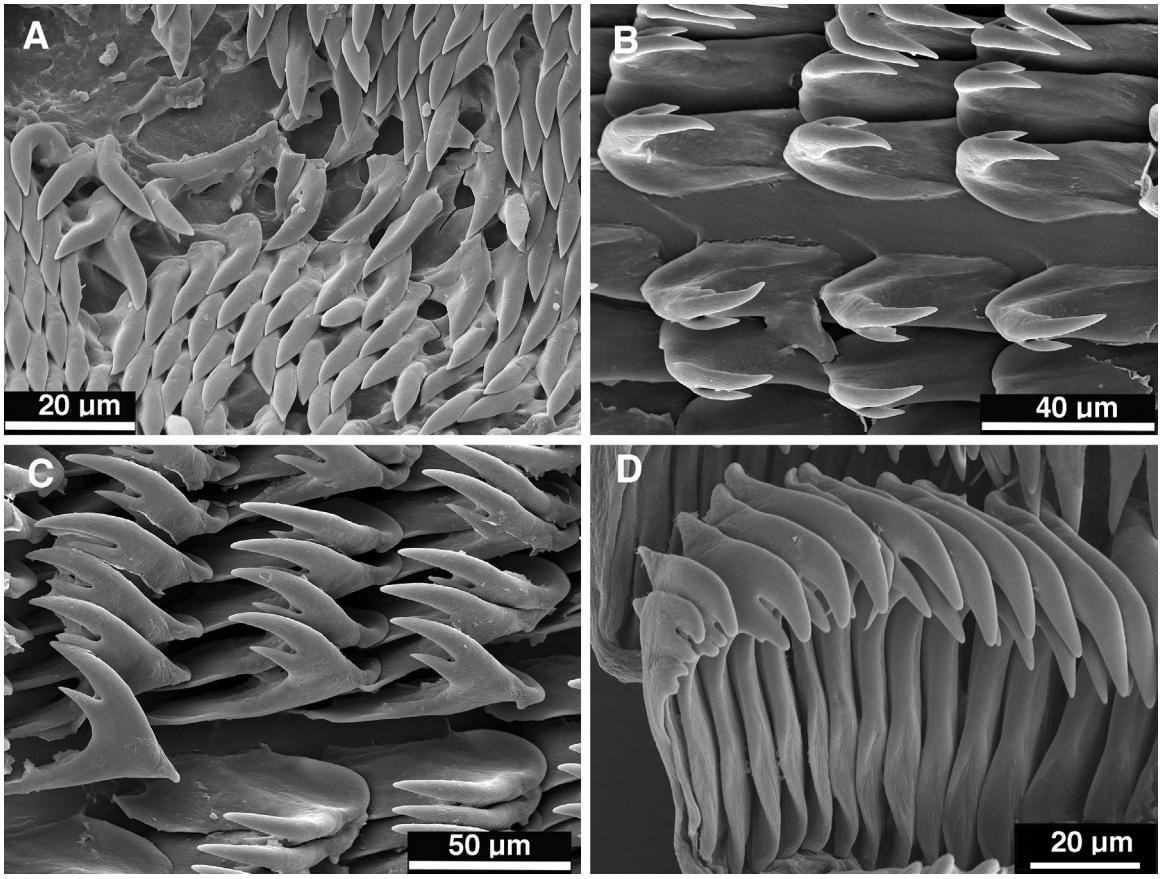

Figure 24. ***Hypselodoris roo*** Gosliner & Johnson **sp. nov.**, buccal armature. A, jaw rodlets, holotype, NMP 041282. B, inner lateral teeth, paratype, CASIZ 189173. C, middle lateral teeth, paratype, CASIZ 189173. D, outer lateral teeth holotype, NMP 041282.

site, 9.1721°N, 123.2519°E Dauin, Negros Oriental, Philippines, 7 April 2016, T. Gosliner.

Type locality
Mainit Bubbles, Mabini, Batangas, Philippines.

Geographical distribution
Known from Indonesia and the Philippines (Debelius & Kuiter, 2007; present study).

Etymology
Hypselodoris roo comes from the A. A. Milne character Roo, the kangaroo whose mother is Kanga. This species is named *H. roo*, because it has often been mistaken for *H. kanga*.

Description
External morphology: Living animals (Fig. 18H–J) moderately large, reaching 45 mm in length. Body colour whitish to grey–blue. Sides of body high, with narrow mantle margin tapering posteriorly into rounded lobe. Notum ornamented with small to large yellow spots and smaller dark blue to black spots scattered over the surface. Areas of blue are present on the notum and sides of body. Additional spots of same colour found on sides of body and foot. Gill pocket slightly elevated from notum. Nine to eleven narrow, thin, unipinnate gill branches held erectly from gill pocket. Gill branches with red lines along edges of inner and outer surface. Apex of gill branch red–orange. Central portion of middle of outer face of gill branches with several opaque white spots. Base of rhinophores red, with opaque white spot on posterior face. Upper half of rhinophore club bright red. Rhinophores with 13–14 small lamellae.

Mantle glands: Subcutaneous mantle glands variable in distribution (Fig. 2M). Posterior glands always present; lateral glands always absent; anterior glands present or absent. This arrangement was based on seven specimens examined, four of which had both anterior and posterior mantle glands and three that lacked anterior glands.

Buccal armature: Muscular portion of buccal mass somewhat larger than length of oral tube. Chitinous

labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 24A). Rodlets narrow with short base and evenly curved, with single, acutely pointed apex. Radula broad, nearly as wide as long. Radular formula of holotype (CASIZ 191070) 71 × 79.0.79. Rachidian row of teeth absent (Fig. 24B). Innermost lateral teeth having irregular triangular denticle on inner side of bifid primary cusp. Denticles absent from outer side of tooth. Next several laterals and middle lateral teeth (Fig. 24C) with bifid cusp, lacking inner or outer denticles. Two outermost teeth having a narrower base and shorter tooth shape, with one or two rounded outer denticles (Fig. 24D), smaller than bifid cusps.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 13I). Ampulla thick, short, tubular and curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Proximal prostatic portion of vas deferens relatively long, convoluted, curved and thick and narrowing slightly as it transitions into muscular ejaculatory portion. Ejaculatory portion relatively long, convoluted and narrow, entering elongate, wider penial bulb. Penial bulb adjacent to straight, wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively moderately long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum seminis curving upwards towards base of bursa. Moderately long uterine duct emerging from vagina immediately below receptaculum, entering female gland mass, near albumen gland.

Remarks

Hypselodoris roo, together with *H. confetti*, has often been misidentified as *H. kanga* (Rudman, 1999b; Debelius & Kuiter, 2007). These two species also have some external similarity to *H. infucata*. A detailed comparison of *H. confetti* and *H. kanga* is found above in the remarks for *H. confetti*. In our phylogenetic analysis, *H. roo* is sister to *H. zephyra* Gosliner & Johnson, 1999 and both are sister to *H. confetti*. In contrast, *H. infucata* is a well-separated clade and is sister to *H. obscura*.

Hypselodoris zephyra has intersecting blue lines on the notum, whereas *H. roo* has bluish pigment, but the blue never forms lines. *Hypselodoris roo* also has yellow spots, compared with the irregular yellow pustules found in *H. zephyra*. *Hypselodoris roo* has black spots, which are absent in *H. zephyra*. *Hypselodoris zephyra* lacks the opaque white spot on the basal portion of the posterior part of the rhinophores that are present in *H. roo*.

There are also clear anatomical differences between *H. roo*, *H. confetti*, *H. kanga* and *H. infucata*. All four species have bluish pigment and yellow spots. In *H. roo* and *H. infucata*, the markings on the gill branches are red, whereas they are deep blue in *H. kanga* and *H. confetti*. In *H. infucata*, the red pigment on the gills is found on the gill rachis and pinnae, whereas in *H. roo* there is red pigment on the inner gill rachis and in two lines on the outer edge, with red and opaque white markings in between the two outer lines. The rhinophores of *H. roo* have an opaque white spot on the inner side of the base that is absent in *H. infucata*. The sides of the body of *H. roo* are higher than in *H. infucata*, and the mantle margin is narrower. Also, *H. infucata* has a broad posterior end of the notum rather than a tapered posterior lobe found in *H. roo*.

There are differences in the arrangement of mantle glands in the species within this clade. In *H. roo and H. zephyra* there are usually anterior and posterior mantle glands, but anterior glands may also be lacking in some specimens of *H. roo. Hypselodoris confetti* and *H. nigrostriata* have mantle glands all around the mantle margin, whereas *H. kanga* has only posterior glands. The shape of the jaw rodlets and radular teeth is also similar in *H. roo*, *H. zephyra*, *H. confetti* and *H. kanga*, but the number of teeth varies slightly.

As noted above, in the reproductive system of *H. confetti* the receptaculum seminis is situated immediately adjacent to the bursa copulatrix, whereas in *H. roo*, *H. zephyra* and *H. nigrostriata*, it is situated more proximally on the vagina (Rudman, 1977; Gosliner & Johnson 1999; present study).

HYPSELODORIS ROSITOI
GOSLINER & JOHNSON **SP. NOV.**
(FIGS 2N, 13J, 25A, B, 26)

LSID: urn:lsid:zoobank.org:act:0FA7479F-032D-403E-8D72-69A1A90623DB

Type material

Holotype: NMP 041283 (formerly CASIZ 186099), subsampled for molecular study, dissected, Malajibomanoc (Chicken Feather Island), 13.628°N, 120.966°E, 30 m depth, Batangas Bay, Batangas Province, Luzon, Philippines, 16 May 2011.

Paratype: CASIZ 220675, one specimen, Cavite Province, Luzon, Philippines, May 2009, specimen provided by Denis Ty of Aquascapes Philippines Company.

Geographical distribution

Known only from the Batangas and Cavite provinces of Luzon, Philippines (present study).

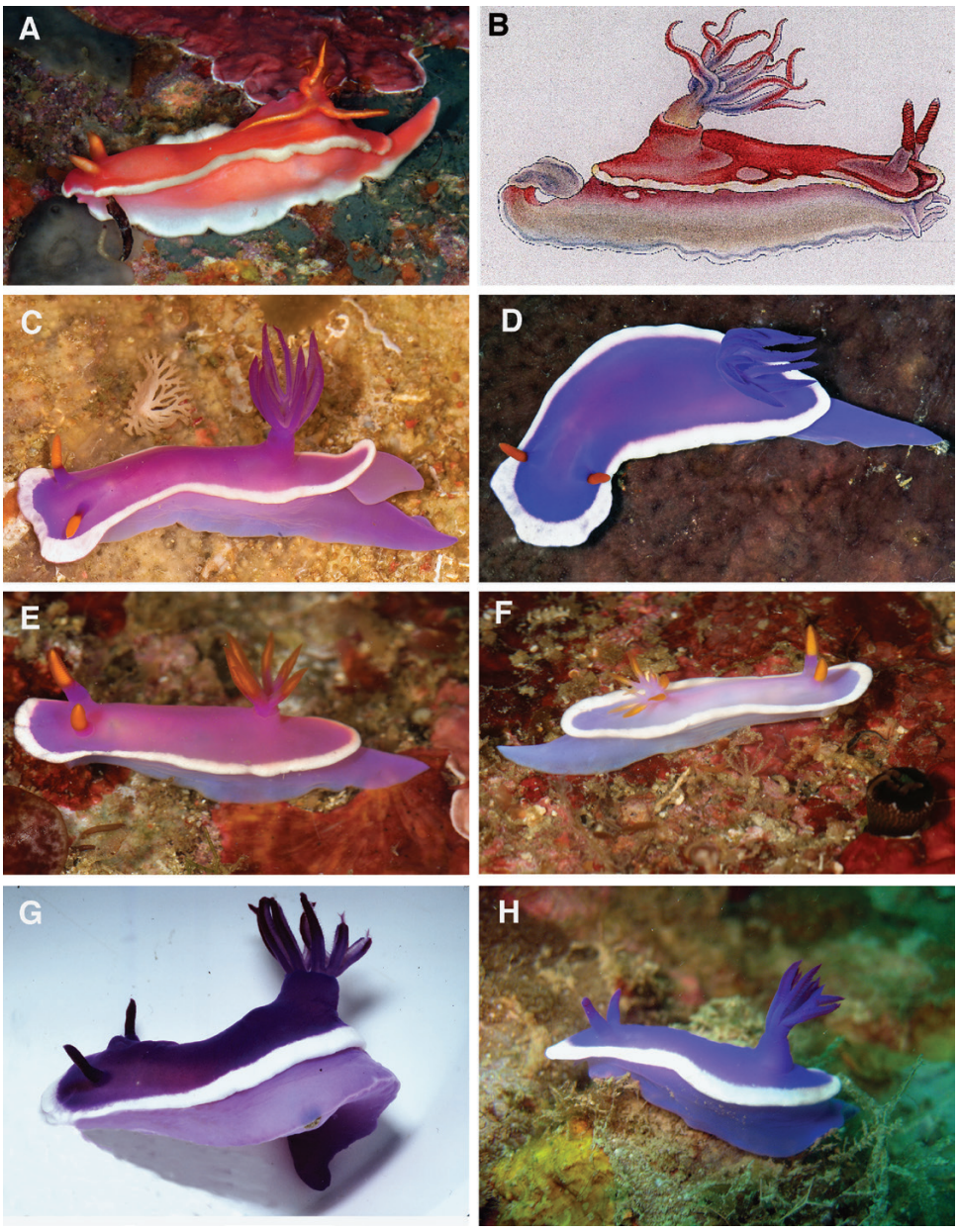

Figure 25. Living animals. A, ***Hypselodoris rositoi*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041283, Tingloy, Batangas, Philippines. B, ***H. rositoi*** Gosliner & Johnson **sp. nov.**, specimen from Albatross Expedition, illustrated by Kumataro Ito. C, ***Hypselodoris variobranchia*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 177618, Tingloy, Batangas, Philippines. D, ***H. variobranchia*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041285, Puerto Galera, Mindoro Oriental, Philippines. E, ***H. variobranchia*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 208189, Puerto Galera, Mindoro Oriental, Philippines. F, ***H. variobranchia*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 212273, Mabini, Batangas, Philippines. G, ***Hypselodoris violacea*** Gosliner & Johnson **sp. nov.**, paratype, CASIZ 071286, Manu Manu Island, Palawan, Batangas, Philippines. H, ***H. violacea*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041286, Busuanga, Palawan, Philippines.

Etymology

The name *rositoi* comes from the Latin for rose, referring to the distinctive rose-pink body colour that is predominant in this species and also honors Kumataro Ito, the artist on the 1908 Albatross Expedition who first illustrated this species (Fig. 25B).

Description

External morphology: Living animals (Fig. 25A) of moderately large size, reaching 50–60 mm in length. Entire dorsal surface deep rose pink, with thick white band encircling the margin of notum. Sides of body lighter pink, fading to white margin of foot. Five

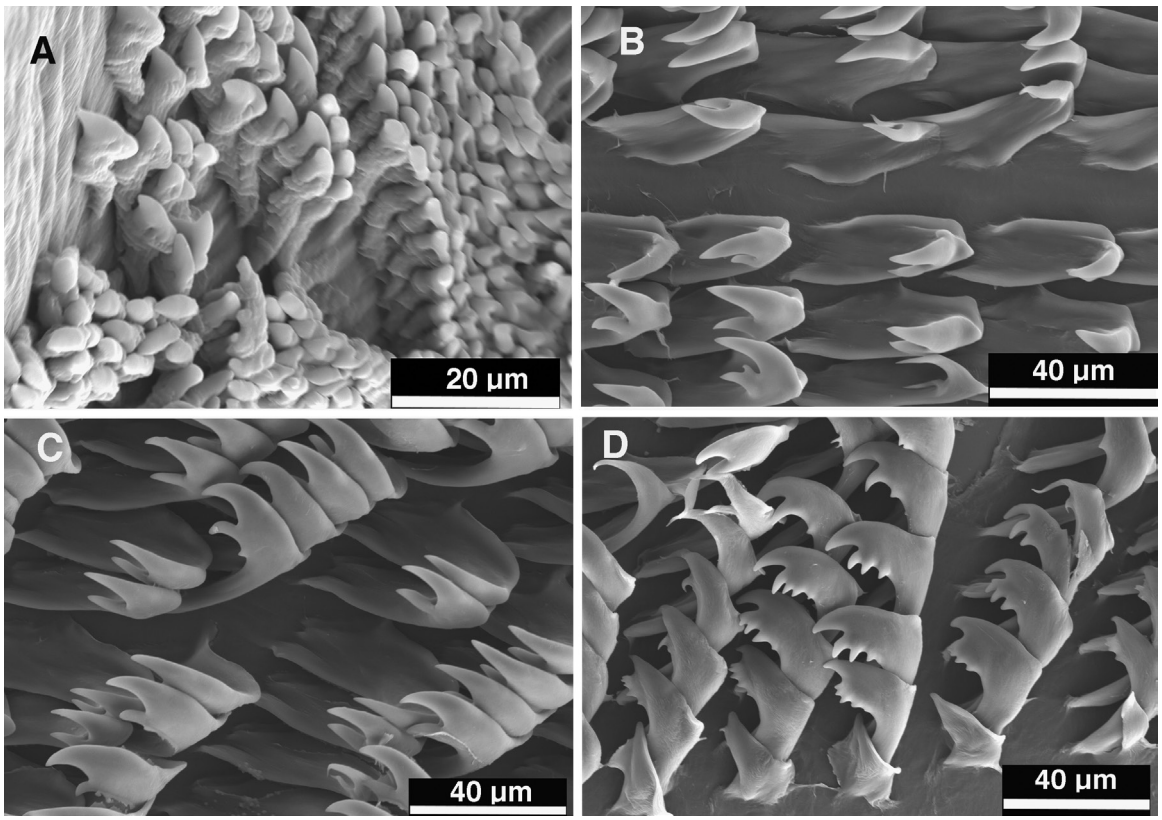

Figure 26. ***Hypselodoris rositoi*** Gosliner & Johnson **sp. nov.**, buccal armature, holotype, NMP 041283. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

unipinnate gill branches on notum. Holotype with four large gill branches and five smaller ones, possibly indicating regrowth from damage. Paratype with nine unipinnate gill branches. Gill pocket well elevated. Gill branches elongate, deep orange, with lighter pigment on inner rachis of each branch. Base of gill pocket deep pink. Bulb of rhinophores bright orange with redder apex. Bulb with ~25–32 densely packed lamellae. Base of rhinophore sheath deep pink.

Mantle glands: Small subcutaneous mantle glands present along entire mantle margin, somewhat enlarged anteriorly and posteriorly (Fig. 2N).

Buccal armature: Muscular portion of buccal mass slightly larger than oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 26A). Rodlets narrow and short with long base and evenly curved, with single, acutely pointed apex. Radular formula of holotype (CASIZ 186099) 66 × 46.0.46. Rachidian row of teeth absent (Fig. 26B). Innermost lateral teeth having one short denticle on inner side of bifid primary cusp, lacking outer denticles. Next several laterals lacking inner and outer denticles, possessing only primary bifid cusps. Midlateral teeth (Fig. 26C) all lacking inner and outer denticles, with exception that single outer denticle may be present on some teeth. Outermost teeth having a narrower base and lacking denticles. Three to four teeth inside outermost teeth, with one to four denticles on outer side of bifid cusp (Fig. 26D).

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 13J). Ampulla thick, tubular and slightly curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick and narrowing abruptly as it transitions into muscular ejaculatory portion. Ejaculatory portion short, curved, narrow, entering short, wider penial bulb. Penial bulb adjacent to straight, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled bursa copulatrix. Receptaculum seminis

appressed against vagina in distal half of vaginal length. Moderately short uterine duct emerging from vagina close to receptaculum and entering female gland mass near the albumen gland.

Remarks

In our phylogenetic analyses, *H. rositoi* is sister to the rest of the *H. bullockii* clade. In the ABGD analysis, *H. rositoi* is indicated to represent a distinct species and is > 13% different in its *COI* gene compared with any other members of the *H. bullockii* clade. *Hypselodoris rositoi* is unique among members of the *H. bullockii* clade in having a bright rose-pink body colour. All other members of the clade are light pink to purple. *Hypselodoris rositoi*, *H. violacea* sp. nov. and *H. variobranchia* sp. nov. are the only members of the *H. bullockii* clade with a broad, solid white marginal band. *Hypselodoris rositoi* is also the only member of the *H. bullockii* clade with obvious mantle glands. Internally, *H. rositoi* has a radula with fewer teeth per half row (46) than found in other members of the *H. bullockii* clade. It is also unique in lacking outer denticles on the vast majority of its middle lateral teeth. All the remaining members of the *H. bullockii* clade have numerous prominent denticles on their middle lateral teeth.

The reproductive system of members of the *H. bullockii* clade has slight variation. In *H. bullockii* (Fig. 13F) and *H. apolegma* (Fig. 4D), the vaginal duct is relatively short, whereas in *H. rositoi*, *H. violacea*, *H. variobranchia*, *H. brycei* and *H. melanesica* the vagina is more elongate. In *H. rositoi*, *H. violacea*, *H. brycei* and *H. melanesica*, the uterine duct branches from the middle of the vagina near the receptaculum seminis, whereas in *H. variobranchia*, the uterine duct branches near the base of the vagina. In *H. rositoi*, the ejaculatory portion of the vas deferens is relatively short, whereas it is much longer in *H. violacea*, *H. variobranchia*, *H. brycei* and *H. melanesica*.

HYPSELODORIS SKYLERI GOSLINER & JOHNSON SP. NOV.

(FIGS 2O, 13K, 27, 28)

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Hypselodoris maculosa? Rudman, 2003.
Hypselodoris sp. 5 Gosliner *et al.*, 2008: 265, third photograph.
Hypselodoris sp. 10 Gosliner *et al.*, 2015: 259, middle right photograph.

Type material

Holotype: NMP 041284 (formerly CASIZ 182780), subsampled for molecular study, dissected, Sea Pen dive site, 13.68736°N, 120.83283°E, Tingloy, Batangas, Luzon, Philippines, 18 May 2010, T. Gosliner.

Paratypes: CASIZ 177305, one specimen, dissected, Sepok Wall, 13.68806°N, 120.82678°E, Tingloy, Batangas, Luzon,

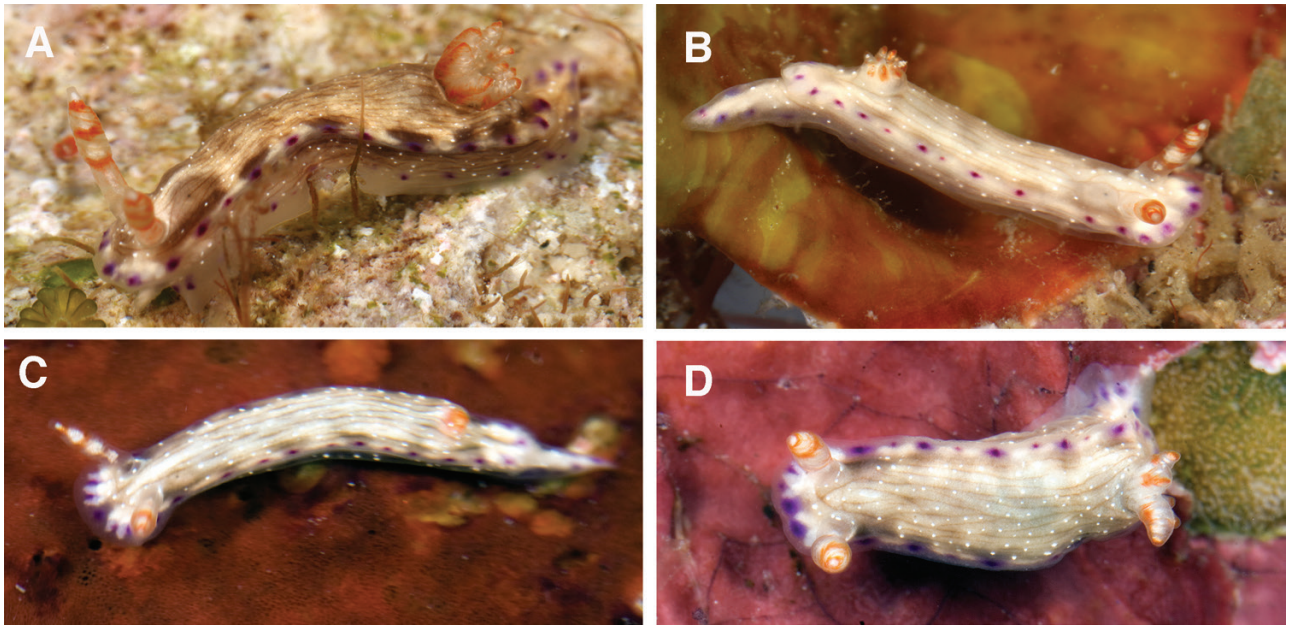

Figure 27. ***Hypselodoris skyleri*** Gosliner & Johnson **sp. nov.**, living animals. A, paratype, CASIZ 217258, Tubod, Siquijor, Philippines. B, paratype, CASIZ 217424, Siaton, Negros Oriental, Philippines. C, holotype, NMP 041284. D, paratype, CASIZ 177305, Tingloy, Batangas, Philippines.

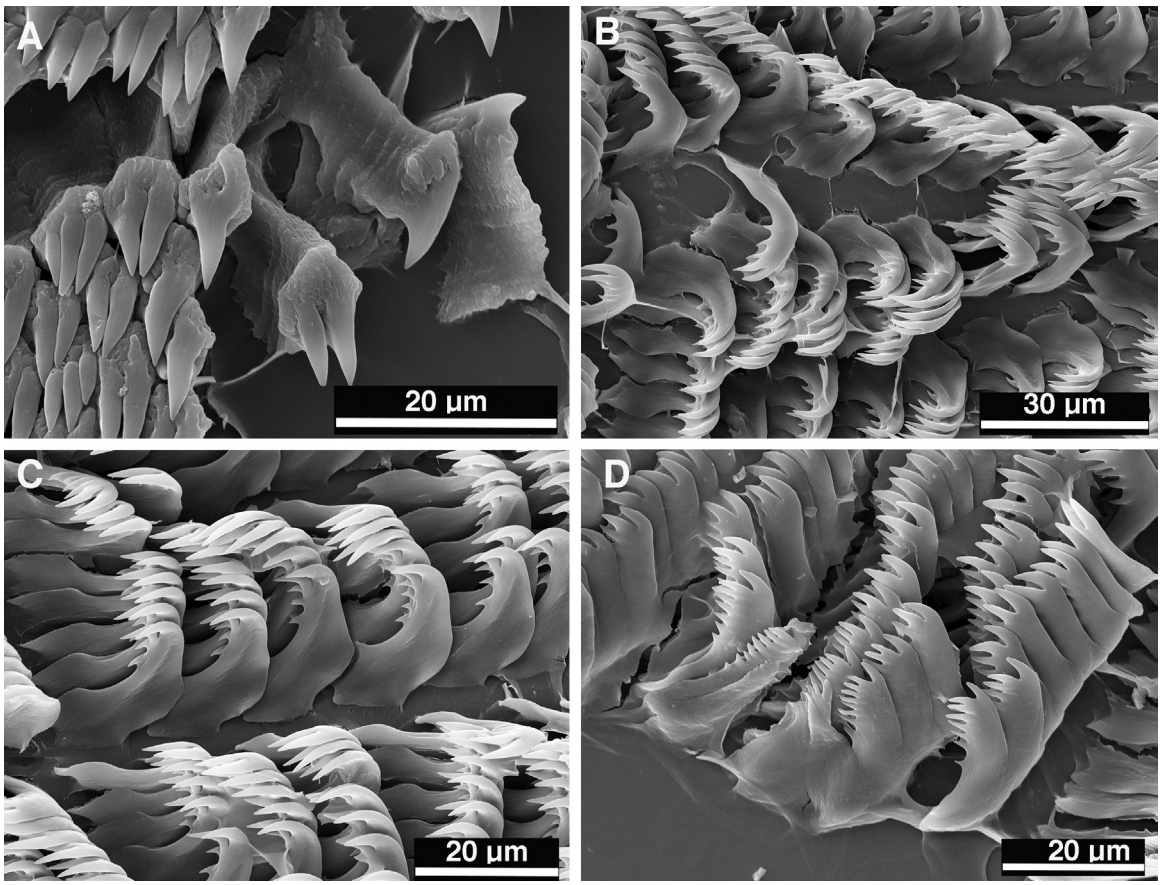

Figure 28. ***Hypselodoris skyleri*** Gosliner & Johnson **sp. nov.**, buccal armature, paratype, CASIZ 177305. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

Philippines, 17 March 2008, T. Gosliner. CASIZ 200649, one specimen, Bonito (Culebra) Island, 13.62978°N, 120.94738°E, Tingloy, Batangas, Luzon, Philippines, 4 May 2014, T. Gosliner. CASIZ 200552, one specimen, off Binacas, 13.77931°N, 120.10959°E, Lubang Island, Mindoro Occidental, Philippines, 29 May 2014, T. Gosliner. CASIZ 217258, one specimen, south side Tubod, 9.0502°N, 123.5144°E, Siquijor Island, Philippines, 10 April 2016, T. Gosliner. CASIZ 217424, one specimen, Tambobo Bay, 9.1374°N, 123.1149°E, Siaton, Negros Oriental, Philippines, 5 April 2016, T. Gosliner. CASIZ 120921, one specimen, Munjor Pinnacle, Enewetak Atoll, Marshall Islands, 21 April 1983, S. Johnson. CASIZ 194004, one specimen, under rock, K9 Pinnacle, Kwajalein Atoll, Marshall Islands, 22 July 2013, S. Johnson.

Type locality

Sea Pen, Tingloy, Maricaban Island, Batangas, Philippines.

Geographical distribution

Known from the Philippines, Indonesia and the Marshall Islands (present study).

Etymology

This species is named for author Rebecca Johnson's son, Skyler (Sky) Rodgers. The beautiful bright white spots on the mantle of this species are reminiscent of bright stars in the sky on a clear night. Sky, thanks for your patience, kindness and thoughtfulness. May you always stay curious about the stars and our place in the universe.

Description

External morphology: Living animals (Fig. 27A–D) small, reaching 15 mm in length. Body long, slender, translucent pink to peach. Fine parallel or intersecting brown longitudinal lines on notum sides of body and foot. Small, scattered opaque white spot situated on small tubercles on notum sides of body and foot. Scattered blue–purple spots found around margin of notum and foot; pigment more dense in centre of spot. Seven to eight unipinnate gill branches having a translucent white base and inner margin and bright red–orange pigment on outer surface of rachis and some gill filaments. Inner surface with opaque white. Bulb of perfoliate rhinophores opaque white with three red transverse bands and bearing about seven

to ten densely arranged lamellae. Base of rhinophores translucent white.

Mantle glands: Subcutaneous mantle glands simple and rounded in shape (Fig. 2O). Glands situated around entire margin of body in six specimens 4–8 mm preserved length. Anterior and posterior glands larger than lateral ones.

Buccal armature: Muscular portion of buccal mass about equal in length to oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 28A). Rodlets sharply angled, acutely pointed with one to three apices and posterior lateral extensions. Radular formula of paratype (CASIZ 177305) 53 × 38.0.38. Rachidian row of teeth absent (Fig. 28B). Innermost lateral teeth having two or three large, triangular denticles on inner side of bifid primary cusp, with another two or three outer denticles. Next several laterals lacking inner triangular denticle but possessing two or three denticles on outer side of primary bifid cusps. Midlateral teeth (Fig. 28C) all lacking inner denticles but having three or four sharply pointed, triangular outer denticles. Outermost teeth having a narrower base and somewhat shorter tooth shape, with five or six rounded to pointed outer denticles (Fig. 28D).

Reproductive system: Reproductive organs fully mature in one specimen examined (CASIZ 177305; Fig. 13K). Ampulla thick, convoluted, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens convoluted, curved and thick and narrowing slightly as it transitions into long, convoluted, muscular ejaculatory portion. Ejaculatory portion widening into much enlarged penial bulb. Penial papilla distinctly curved with broad base, devoid of penial hooks. Penial bulb adjacent to straight, slightly narrow, widening into penial sac. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina widening proximally, leading to minute receptaculum seminis and larger spherical, thin-walled receptaculum seminis. Receptaculum situated near base of bursa. Moderately short, narrow uterine duct emerging from vagina close to base of bursa and female gland mass, near albumen gland.

Remarks

Hypselodoris skyleri is a member of a large clade that includes *H. katherinae* sp. nov., *H. paradisa* sp. nov., *H. maritima*, *H. rudmani* and *H. bertschi*. It is sister to *H. katherinae* and *H. paradisa*. The ABGD analysis indicates that *H. skyleri* is clearly distinct from *H. katherinae* and *H. paradisa*. A detailed comparison of these species is found in the remarks section of *H. katherinae* and *H. paradisa*. The colour pattern of *H. skyleri* is similar to that of *H. maculosa* and *H. decorata* but differs in having brown rather than opaque white lines. In *H. skyleri*, the opaque white spots are scattered over the surface of the body and elevated on small tubercles. In *H. maculosa* and *H. decorata*, the spots are found only on the margins of the body and are flush with the body surface. In both *H. skyleri* and *H. decorata* there are three rhinophoral red rings, whereas there are only two in *H. maculosa*.

Both *H. decorata* (Fig. 2D) and *H. maculosa* (Gosliner & Johnson, 1999: fig. 29D) have mantle glands only at the anterior and posterior ends of the body, whereas *H. skyleri* also has many lateral glands. The jaw rodlets of *H. skyleri* have one to three cusps, whereas *H. decorata* (Fig. 10) and *H. maculosa* (Fig. 11) possess a single cusp. The radulae of *H. skyleri*, *H. maculosa* and *H. decorata* all have a similar formula and teeth of a similar shape. One notable difference is that the cusps and adjacent denticles on the inner and middle lateral teeth are more elongate in *H. skyleri* than in *H. maculosa* and *H. decorata*. In *H. skyleri*, the penis is proportionately wider than in *H. maculosa* and *H. decorata* and possesses a distinct penial papilla.

HYPSELODORIS VARIOBRANCHIA GOSLINER & JOHNSON SP. NOV.

(FIGS 25C–F, 29, 30A)

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Hypselodoris bullocki, misidentification, not *H. bullockii* (Collingwood, 1881); Rudman, 1999a: photograph E; Izumi, 2003; Adams, 2004; Brauchli, 2004; Lau, 2006; Turker, 2006; Debelius & Kuiter, 2007: 116: middle right photograph; Tanke 2008.
Hypselodoris sp. Coleman, 2001: 82, middle photograph, fourth row.
Hypselodoris sp. Coleman, 2001: 82, lower right photograph.
Hypselodoris cf. *bullocki*-1 Debelius & Kuiter, 2007: 116: lower two rows of photographs.
Hypselodoris sp. 6 Gosliner *et al.*, 2008: 268, top photograph.
Hypselodoris sp. 1 Humann & DeLoach, 2010: 339, upper right photograph.
Hypselodoris sp. 15 Gosliner *et al.*, 2015: 262, middle left photograph.

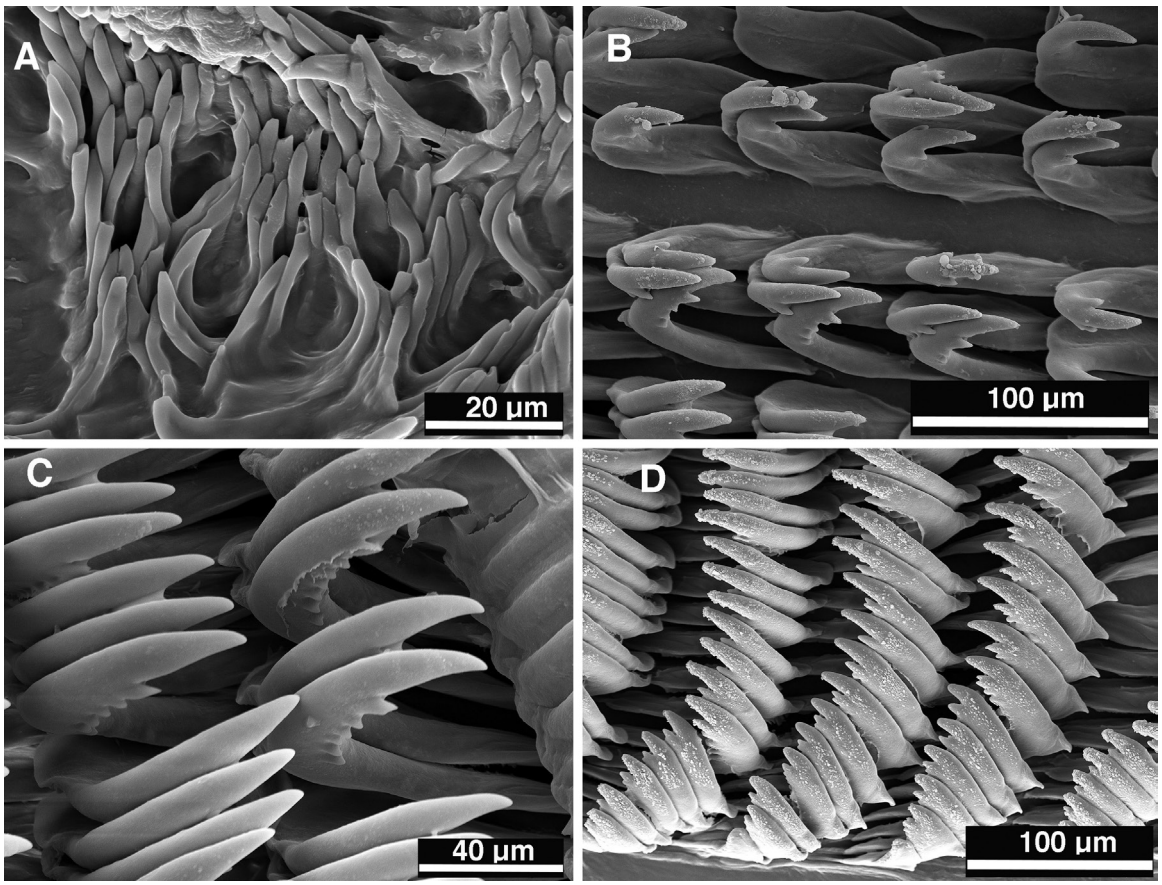

Figure 29. ***Hypselodoris variobranchia*** Gosliner & Johnson **sp. nov.**, buccal armature, holotype, NMP 041285. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

Type material

Holotype: NMP 041285 (formerly CASIZ 177455), subsampled for molecular study, dissected, Aphol's Rock, 13.6586°N, 120.90129°E, 30 m depth, Maricaban Island, Tingloy, Batangas Province, Luzon, Philippines, 17 May 2008, Peri Paleracio.

Paratypes: CASIZ 085901, one specimen, Liuay Rock, Dakak, Zamboanga del Norte, Mindanao, Philippines, 29 March 1993, T. Gosliner. CASIZ 096279, one specimen, Sepok Point, 13.68806°N, 120.82678°E, Maricaban Island, Tingloy, Batangas, Luzon, Philippines, 14 March 1994, Mike Severns. CASIZ 177618, subsampled for molecular study, dissected, Aphol's Rock, 13.6586°N, 120.90129°E, 30 m depth, 17 April 2008, Peri Paleracio. CASIZ 182841, one specimen, Devil's Point, 13.65083°N, 120.84127°E, Tingloy, Maricaban Island, Batangas Province, Luzon, Philippines, 21 May 2010, T. Gosliner. CASIZ 208189, one specimen, subsampled for molecular study, La Laguna, 13.525953°N, 120.970160°E, Puerto Galera, Mindoro Oriental, Philippines, 26 April 2015, T. Gosliner. CASIZ 217246, Bonito Island, 13.6305°N, 120.94763°E, Maricaban Island, Tingloy, Batangas, Luzon, Philippines, 21 April 2016, Brenna Green. CASIZ 217389, Sepok Wall, 13.68806°N, 120.82678°E Maricaban Island, Tingloy, Batangas, Luzon, Philippines, 15 April 2016, Brenna Green. CASIZ 217273, 13.6880278°N, 120.8971833E°, Calumpan Peninsula, Mabini, Batangas, Luzon Island, Philippines, Bubbles, 22 April 2016, T. Gosliner. CASIZ 104704, one specimen, 69 m depth, Horseshoe Cliffs, (26.5000°N, 127.854307°E, 1 km WNW of Onna Village, Okinawa, Japan, R. Bolland.

Geographical distribution

Known from Queensland, Australia (Rudman, 1999a), Malaysia (Lau, 2006), Indonesia, Okinawa, Japan and the Philippines (present study).

Etymology

The name *variobranchia* comes from Latin for variable gills, referring to the gill, which may be either orange or bright purple.

Description

External morphology: Living animals (Fig. 25C–F) of moderately large size, reaching 50 mm in length. Entire

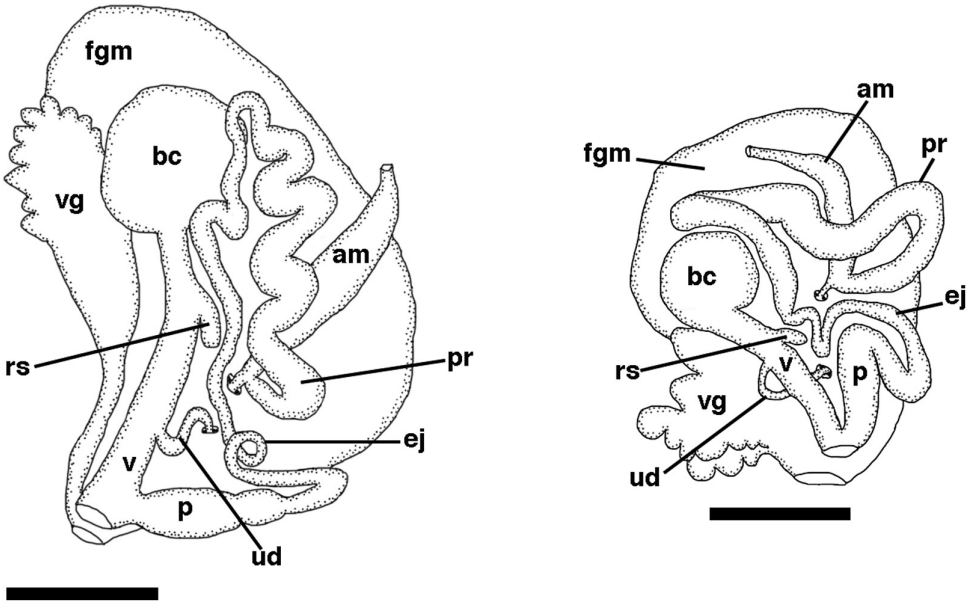

Figure 30. Reproductive systems. A, ***Hypselodoris variobranchia*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041285, scale bar: 1.5 mm. B, ***Hypseldoris violacea*** Gosliner & Johnson **sp. nov.**, holotype, NMP 041286, scale bar: 2.0 mm. am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of the vas deferens; fgm, female gland mass; p, penis; pr, prostatic portion of vas deferens; rs, receptaculum seminis; ud, uterine duct; v, vagina; vg, vestibular gland.

dorsal surface deep purple, with thick, solid opaque white band encircling the margin of notum. Sides of body and margin of foot same colour as notum. Five to nine unipinnate gill branches on notum. Gill branches deep orange or deep purple. In specimens with orange gill branches, common base often with purple. Base of gill pocket well elevated, deep purple. Bulb of rhinophores bright orange throughout. Bulb with 19–23 densely packed lamellae. Base of rhinophore sheath deep purple.

Mantle glands: Mantle glands entirely absent from mantle margin.

Buccal armature: Muscular portion of buccal mass much shorter than oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 29A). Rodlets narrow and short with long base and evenly curved, with single, acutely pointed apex. Radular formula of holotype (CASIZ 177455) 71 × 98.0.98, and 68 × 106.0.106 (CASIZ 177618) in one paratype. Rachidian row of teeth absent (Fig. 29B). Innermost lateral teeth having one short denticle on inner and outer sides of bifid primary cusps. Outer cusp of bifid cusps much shorter than inner one. Next several laterals lacking inner denticles possessing primary bifid cusps and two or three outer denticles. Midlateral teeth (Fig. 29C) all lacking inner denticles, but with five or six prominent outer denticles. Outermost teeth having a narrower base and having three or four outer denticles (Fig. 29D).

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 30A). Ampulla thick, tubular and straight, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens long, convoluted, curved and thick and narrowing abruptly as it transitions into muscular ejaculatory portion. Ejaculatory portion elongate, convoluted, narrow, entering moderately long, wider penial bulb. Penial bulb adjacent to straight, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled bursa copulatrix. Receptaculum seminis appressed against vagina in distal half of vaginal length. Moderately short uterine duct emerging from vagina proximally to receptaculum and entering female gland mass near the albumen gland.

Remarks

In our phylogenetic analyses, *H. variobranchia* is sister to the clade containing *H. bullockii*, *H. melanesica*, *H. brycei* and *H. apolegma*. Externally, it is most similar to *H. rositoi*, *H. violacea* and some colour morphs of *H. iba*, which is a member of a separate clade. All of these species have a wide, solid opaque white

marginal band. Externally, *H. rositoi* has a pink rather than purple body colour, and *H. violacea* has purple rhinophores in contrast to the orange rhinophores of *H. iba* and *H. variobranchia*. Both *H. iba* and *H. rositoi* have mantle glands that are absent in *H. variobranchia* and *H. violacea*. Also, *H. iba* has a higher body profile than that of *H. variobranchia*.

The radula formula of *H. iba*, *H. violacea* and *H. variobranchia* is similar, with almost 100 teeth per half row, whereas *H. rositoi* has only 46 teeth per half row. In *H. iba*, only the innermost radular teeth have denticles other than the two primary cusps, whereas in *H. variobranchia* and *H. violacea* the majority of teeth have numerous outer denticles. In *H. rositoi*, only the outer teeth have prominent outer denticles, with the exception of some of the middle lateral teeth, which may have a single denticles (Fig. 26C). The radula is very similar in *H. variobranchia* and *H. violacea*, but in *H. violacea* the innermost teeth have a longer, more acutely pointed inner cusp of the bifid cusps. This difference in inner cusp length and sharpness is also found in the middle lateral teeth. The reproductive systems of *H. variobranchia* and *H. violacea* differ in a couple of key regards. In *H. variobranchia*, the ejaculatory portion of the vas deferens is far more elongate than in *H. violacea*. In *H. variobranchia*, the uterine duct emerges from the proximal portion of the vagina, whereas in *H. violacea* the uterine duct emerges from the distal third of the vagina. In the ABGD analysis, *H. variobranchia* and *H. violacea* are clearly indicated as distinct species. The three specimens of *H. variobranchia* are only 0.15–0.3% different in their *COI* gene from each other, whereas all three specimens are 8.8–9.0% different from *H. violacea*.

HYPSELODORIS VIOLACEA GOSLINER & JOHNSON SP. NOV.

(FIGS 25G, H, 30B, 31)

LSID: urn:lsid:zoobank.org:act:6D041C56-175A-4A7C-9219-809DB4C8C03D

Hypselodoris bullocki, misidentification, not *H. bullockii* (Collingwood, 1881); Köhler, 2000; Sullivan, 2000; Lau, 2005.

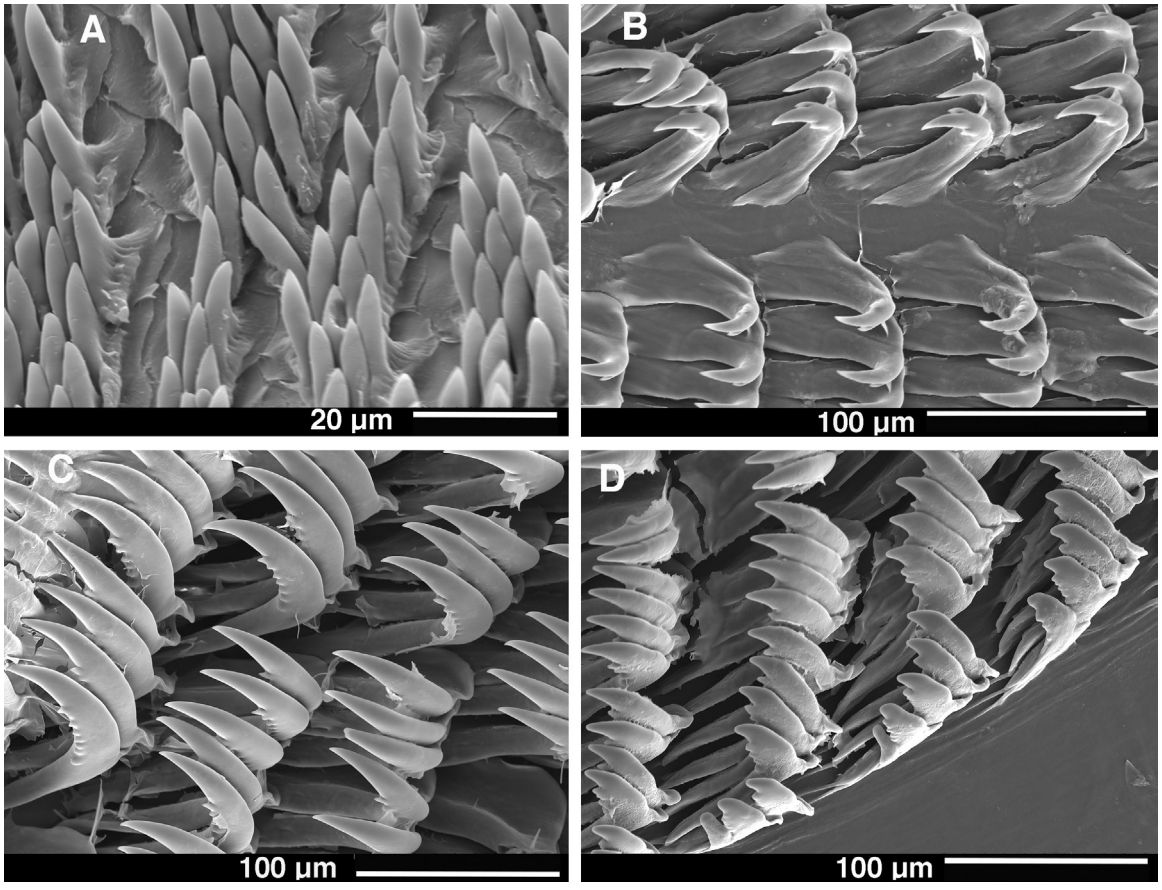

Figure 31. ***Hypselodoris violacea*** Gosliner & Johnson **sp. nov.**, buccal armature, holotype NMP 041286. A, jaw rodlets. B, inner lateral teeth. C, middle lateral teeth. D, outer lateral teeth.

Type material
Holotype: NMP 041286 (formerly CASIZ 182307), subsampled for molecular study, dissected, Magic Reef, 11.99°N, 120.08°E, 10 m depth, Bintuan Barangay, Coron, Busuanga Island, Palawan, Philippines, 24 February 2010, G. Williams.

Paratype: CASIZ 071286, Manu Manu Island, north end of North Verde Island, Palawan, Philippines, 7–17 m depth, 9 June 1988, R. Van Syoc.

Geographical distribution
Known only from Palawan, Philippines and northern Borneo, Malaysia (present study).

Etymology
The name *violacea* is Latin for violet, referring to the intense purple body colour that ornaments the body, gill and rhinophores of this species.

Description
External morphology: Living animals (Figs 25G, H) of moderately large size, reaching 50 mm in length. Entire dorsal surface deep, dark purple with thick, solid opaque white band encircling the margin of notum. Sides of body and margin of foot same colour as notum. Ten to eleven unipinnate gill branches on notum that may be divided further basally or apically. Gill branches deep purple. Base of gill pocket well elevated, deep purple. Bulb and base of rhinophores deep purple throughout. Bulb with ~31 densely packed lamellae. Base of rhinophore sheath deep purple.

Mantle glands: Mantle glands entirely absent from mantle margin.

Buccal armature: Muscular portion of buccal mass about equal in size with oral tube. Chitinous labial cuticle found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 31A). Rodlets narrow and short with long base and evenly curved, with single, acutely pointed apex. Radular formula of holotype (CASIZ 182307) 66 × 103.0.103. Rachidian row of teeth absent (Fig. 31B). Innermost lateral teeth having one to three short denticles on inner of bifid primary cusp and one denticle on the outer side of the bifid cusp. Outer cusp of bifid cusps much shorter than inner one. Next several laterals lacking inner denticles possessing primary bifid cusps and zero or one outer denticle. Midlateral teeth (Fig. 31C) all lacking inner denticles but with five or six prominent outer denticles. Outermost teeth (Fig. 31D) having a narrower base and having four or five outer denticles.

Reproductive system: Reproductive organs of the holotype fully mature (Fig. 30B). Ampulla thick, tubular and curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens long, convoluted, curved and thick and narrowing abruptly as it transitions into muscular ejaculatory portion. Ejaculatory portion moderately short curved, narrow, entering moderately long, wider penial bulb. Penial bulb adjacent to straight, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, straight receptaculum seminis and larger spherical, thin-walled bursa copulatrix. Receptaculum seminis appressed against vagina in distal half of vaginal length. Moderately short uterine duct emerging from vagina adjacent to receptaculum and entering female gland mass near the albumen gland.

Remarks
The differences between *H. violacea* and other closely related species are discussed above in the remarks section of *H. variobranchia*.

HYPSELODORIS YARAE GOSLINER & JOHNSON SP. NOV.

(FIGS 32–34)

LSID: urn:lsid:zoobank.org:act:5F96599D-CBC6-4073-BF7C-6A059710F8B8

Hypselodoris maculosa not *H. maculosa* (Pease, 1871): misidentification in part, Gosliner & Johnson, 1999: specimen CASIZ 073533; Fraser, 1999; Poddubetskaia, 2003; Lederman, 2005; Houben, 2007.
Hypselodoris sp. 1 Gosliner *et al.*, 2008: 259, middle photograph.
Hypselodoris cf. *maculosa* Johnson & Gosliner, 2012.
Hypselodoris sp. 4 Gosliner *et al.*, 2015: 255, upper left photograph.
Hypselodoris sp. 1 Gosliner *et al.*, 2015: 253, upper right photograph

Type material
Holotype: CASIZ 223316, one specimen, 17 mm, subsampled for molecular study, Doodles dive site (26.8389°S 328917°E), Ponta do Ouro, Mozambique, 16 m depth, 11 May 2014, Yara Tibiriçá.

Paratypes: CASIZ 073533, one specimen, Ifaty, SW Madagascar, 1 km west of Mora Mora Resort, 2 m depth, 27 March 1990, T. Gosliner. CASIZ 223317, one

Figure 32. ***Hypselodoris yarae*** Gosliner & Johnson **sp. nov.**, living animals. A, photograph of specimen from Îles de Radama, October 2005. B, holotype, CASIZ 223316, Ponto de Ouro, Mozambique, photograph by Yara Tibiriçá. C, paratype, CASIZ 223317, Nacala, Mozambique, photograph by Yara Tibiriçá. D, paratype, CASIZ 073533, Ifaty, Madagascar.

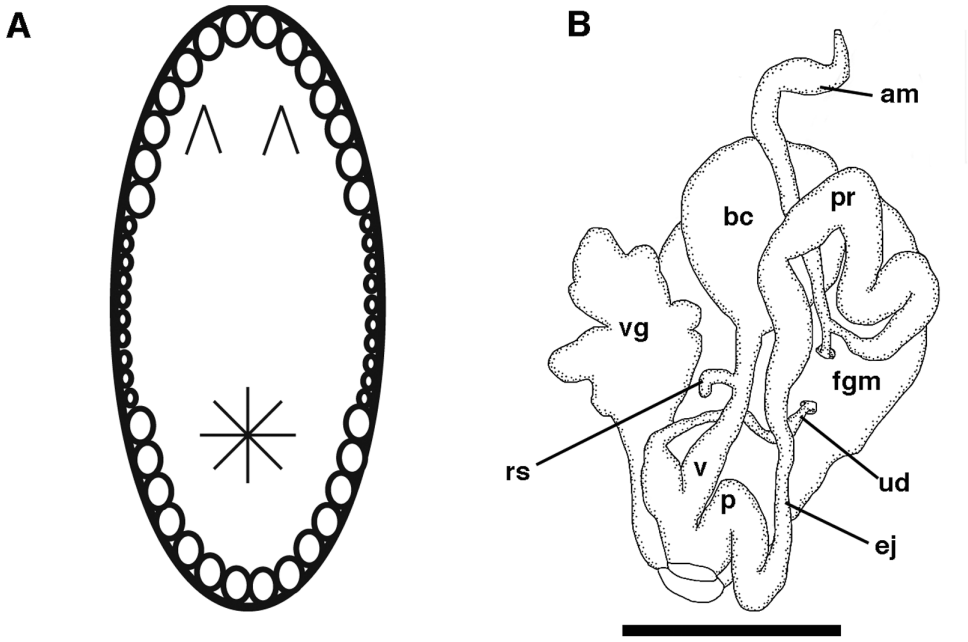

Figure 33. ***Hypselodoris yarae*** Gosliner & Johnson **sp. nov.** A, mantle glands. B, reproductive system, scale bar: 0.5 mm. am, ampulla; bc, bursa copulatrix; ej, ejaculatory portion of the vas deferens; fgm, female gland mass; p, penis; pr, prostatic portion of vas deferens; rs, receptaculum seminis; ud, uterine duct; v, vagina; vg, vestibular gland.

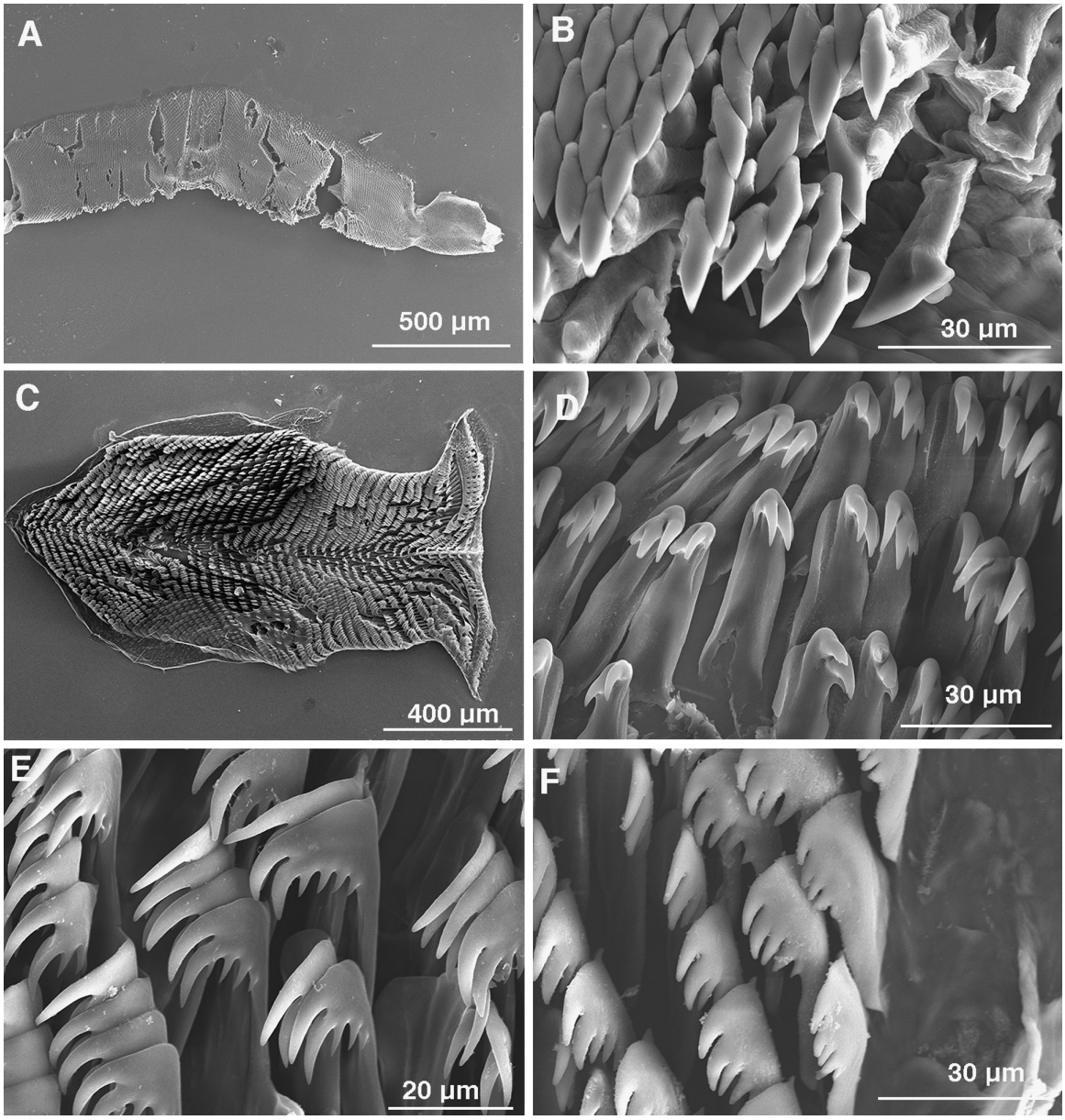

Figure 34. ***Hypselodoris yarae*** Gosliner & Johnson **sp. nov.**, buccal armature, holotype, CASIZ 223316. A, entire jaw. B, jaw rodlets. C, entire radula. D, inner lateral teeth. E, middle lateral teeth. F, outer lateral teeth.

specimen, 26 mm, dissected, subsampled for molecular study, in front of Kwalala Lodge, (14°29′25″S, 40°44′30″E), Nacala, Mozambique, 12 m depth, 9 June 2014, Yara Tibiriçá.

Geographical distribution
Known only from Madagascar and Mozambique and possibly from Kenya (Gosliner *et al.*, 2015: 252, upper right photograph), South Africa (Fraser, 1999), Sri Lanka (Houben, 2007) and the Red Sea (Poddubetskaia, 2003; Lederman, 2005).

Etymology
The name *yarae* honors Yara Tibiriçá, who has advanced our knowledge of western Indian Ocean nudibranchs and collected several specimens of this species.

Description
External morphology: Living animals (Fig. 32) of moderate size, 20–35 mm in length. Entire dorsal surface light pink to tan, with thick orange band encircling the margin of notum. Marginal band often

with undulating margins on inner side. Notum with series of narrow, opaque white longitudinal lines. Large plum to brown spots located between lines. Sides of body and margin of foot same colour as notum. Gill branches orange basally, with opaque white apices. Seven to nine unipinnate, well-elevated gill branches present on notum. Bulb of rhinophores opaque white, with two prominent orange bands and traces of third band basally. Base of rhinophores translucent white. Bulb with ~12–13 densely packed lamellae.

Mantle glands: Mantle glands present along entire mantle margin, larger posteriorly and anteriorly (Fig. 33A).

Buccal armature: Muscular portion of buccal mass smaller in size than oral tube. Chitinous labial cuticle elongate (Fig. 34A), narrow, found at anterior end of muscular portion of the buccal mass bearing numerous jaw rodlets (Fig. 34B). Rodlets straight, narrow and long, with long base. Rodlets evenly curved, with single, acutely pointed apex with lateral lobes. Radular formula of paratype (CASIZ 073533) 45 × 31.0.31 (Fig. 34C). Rachidian row of teeth absent (Fig. 34D). Innermost lateral teeth having zero to two short denticles on inner side of bifid primary cusp and one or two denticles on the outer side of the bifid cusp. Outer cusp of bifid cusps about same size as inner one. Second lateral tooth and next several laterals lacking inner denticles, possessing primary bifid cusps and one ot three outer denticles. Midlateral teeth (Fig. 34E) all lacking inner denticles but with three or four prominent outer denticles. Outermost teeth (Fig. 34F) having a narrower base and three outer denticles.

Reproductive system: Reproductive organs of the paratype (CASIZ 223317) are fully mature (Fig. 33B). Ampulla think, tubular and curved, narrowing somewhat before bifurcating into oviduct and vas deferens. Short oviduct entering female gland mass near albumen gland. Prostatic proximal portion of vas deferens long, convoluted, curved and thick and narrowing abruptly as it transitions into muscular ejaculatory portion. Ejaculatory portion moderately short, straight, narrow, entering moderately short, wider penial bulb. Penial bulb adjacent to straight, moderately wide vaginal duct at common gonopore. Distal end of vas deferens devoid of penial hooks. Female gland mass consisting of large mucous gland and small membrane and albumen glands. Large, lobate vestibular gland situated near exit of mucous gland. Relatively long vagina leading to small, curved receptaculum seminis and larger spherical, thin-walled bursa copulatrix. Receptaculum seminis located in distal half of vaginal length. Long uterine duct, wide at base of vagina, narrowing and entering female gland mass near the albumen gland.

Remarks

This species was initially recognized as genetically distinct from *H. maculosa* by Johnson & Gosliner (2012), as *Hypselodoris* sp. cf. *maculosa*. The present study also indicates a basal position as being sister to the remaining members of its large clade. Its distinctness is also strongly supported by the ABGD analysis. Externally, there are differences between *H. yarae* and other members of the *H. maculosa* clade. This species has a darker body colour than *H. alburtuqali*, *H. decorata* and *H. maculosa*, with fewer, larger brown to plum spots. It also differs from *H. alburtuqali* in having a wide orange margin that usually has undulations along its inner margin. The jaws of *H. yarae* are much narrower and more elongate than are those of *H. alburtuqali* (Fig. 3A), *H. decorata* (Fig. 10A) and *H. maculosa* (Fig. 11A). The most distinctive anatomical features of *H. yarae* from the above three species are the basal insertion of the uterine duct into the vagina that has an expanded base, and the more basal position of the receptaculum seminis.

DISCUSSION

Molecular phylogeny

The first phylogeny of *Hypselodoris*, undertaken by Gosliner & Johnson (1999), was based upon morphological characters. From more recent molecular evidence (e.g. Johnson & Gosliner, 2012; present study), it is now obvious that there were two important flaws in that study. Gosliner and Johnson included species from the Eastern Pacific, Atlantic and Indo-Pacific in the *Hypselodoris* genus, and also considered *Risbecia* as a sister group. The molecular phylogeny of of the Chromodorididae by Johnson & Gosliner (2012) demonstrated that the eastern Pacific and Atlantic clade should be regarded as *Felimare* because it was distinct from an Indo-Pacific clade that included *Thorunna* as the sister group of *Hypselodoris* and with *Risbecia* nested within *Hypselodoris*. Gosliner & Johnson (1999: fig. 60) recognized a series of Indo-Pacific clades that correspond to some of the results obtained here. The '*Risbecia*' species group represents a monophyletic group in both studies, but in the present study it is not basal, but instead sister to another derived clade, the *H. maculosa* clade. The *H. maculosa* clade has very similar composition in both studies, with the exception that in the present study *H. purpureomaculosa* is included in the *H. maculosa* clade. All members of this clade have a narrow, elongate body, a colour pattern with purple or white longitudinal lines, and small, densely

Figure 35. Bayesian inference and maximum likelihood tree of *Hypselodoris*, indicating support values for each node. Bootstrap values are on the left and Bayesian posterior probablilities on the right.

arranged mantle glands that are present anteriorly and posteriorly but absent from the central portion of the mantle. Gosliner & Johnson (1999) identified another clade that included *Hypselodoris bennetti*, *H. regina*, *H. krakatoa*, *H. reidi* and *H. zephyra*. That clade is recovered in the present study, but includes some additional taxa, all of which have an elevated gill and widely scattered mantle glands over the entire mantle margin, with much larger mantle glands found posteriorly. There are no molecular data to test the relationships of *H. bennetti* in the present study. A clade including *H. kaname* and *H. paulinae* was again recovered in both studies and is characterized by species with continuous small mantle glands along the entire surface of the mantle margin, except at the anterior end of the body. The clade of species that includes *H. capensis*, *H. carnea* (Bergh, 1889), *H. infucata*, *H. obscura*, *H. festiva*, *H. placida* (Baba, 1949), *H. sagamiensis* (Baba, 1949) and *H. bollandi* recovered by morphological characters is also largely recovered from molecular data, with slight differences in species largely attributable to lack of molecular data. Species in this clade have a broad body, purple markings with yellow spots, and mantle glands similar to those found in the *H. maculosa* clade. Lastly, a clade that included *H. kanga*, *H. nigrostriata*, *H. bertschi*, *H. maritima*, *H. nigrolineata* and *H. rudmani* in the morphological study is also largely recovered here. Most of these species, including *H. skyleri*, *H. katherinae* and *H. paradisa* described here, have a large bulbous penis and sparse mantle glands that are distributed over most of the mantle margin. The major exception to the congruence between the morphological study and the molecular phylogeny is that *H. nigrostriata* is a member of the same clade as *H. zephyra*. Despite the lack of molecular data for some of the species included in the morphological study (Gosliner & Johnson, 1999) and the present study, there is remarkable congruence in the subclades that are recognized. The major differences are in the relationships between the subclades.

The molecular phylogeny shown here provides strong support for the monophyly of *Hypselodoris*, whereas the sister relationship to *Thorunna* is more weakly supported despite the strong support demonstrated by Johnson & Gosliner (2012) for this relationship. This is likely to be an artefact of taxon sampling, where fewer outgroup taxa were sampled than by Johnson & Gosliner (2012), which was necessitated by the much broader sampling within *Hypeslodoris* in the present study. Despite lower support values for the sister relationship between *Thorunna* and *Hyspelodoris*, a close association between *Throunna, Hyspelodoris*, and *Felimare* was also recovered by Hallas *et al.*, 2017, which included more molecular and dorid taxonomic sampling.

Hypselodoris is strongly supported as a clade, with numerous subclades of varying levels of support. Previously, the phylogeny of the Chromodorididae published by Johnson & Gosliner (2012) included 19 species of *Hypselodoris*. The present phylogeny includes nearly 50 species of *Hypselodoris*, and most of the clades initially suggested by Johnson & Gosliner (2012) are still found in the present study, but their relationship to each other has changed somewhat. For example, Johnson & Gosliner (2012) found a clade that included *H. reidi*, *H. jacksoni* and *H. zephyra* that was sister to the remainder of *Hypselodoris*. That clade persists but is sister to another large clade of species, whereas the *H. bullockii* clade is sister to the remainder of *Hypselodoris*. In both studies, the *H. maculosa* clade is sister to members of the species that were formerly included in *Risbecia* (*H. tryoni*, *H. imperialis* and *H. pulchella*). Previously, within this clade, *H. yarae* (as *H.* sp. cf. *maculosa*) was sister to the '*Risbecia*' clade, whereas in the present study it is sister to both the '*Risbecia*' clade and the rest of the *H. maculosa* clade.

As noted above, many of the subclades recovered using morphological data (Gosliner & Johnson, 1999) are also found here. However, the three major clades of *Hypselodoris* depicted here were not found in the morphological study. Clearly, the morphological study by Gosliner & Johnson (1999) did not provide sufficient resolution of the relationships of the subclades into the larger clades. None of the members of the *H. bullockii* clade were included in the study by Johnson & Gosliner (2012). Their omission is largely attributable to the belief at the time that *H. bullockii* was a species of *Chromodoris* and that *C. bullockii* represented a single variable species. Rudman (1999a) concluded that *H. bullockii* was a single species with a wide range of colour variation. Our study was able to determine that the *H. bullockii* clade is composed of seven distinct species, namely *H. bullockii*, *H. apolegma* and *H. rositoi*, *H. violacea*, *H. variobranchia*, *H. melanesica* and *H. brycei*, which are described in the present study. Additionally, one of the colour forms depicted by Rudman is a member of an entirely different clade (the *H. reidi* clade) and is described here as *H. iba*. Members of the *H. bullockii* clade share key morphological attributes: a pink to purple body colour, large body size, complete lack of mantle glands, radular teeth with a reduced lower cusp and radular teeth with numerous denticles on all teeth across the radula. Members of the other two clades have few, if any, unifying morphological features that characterize the clades. Instead, distinct morphological characteristics are present within their subclades, as noted above.

Rudman (1986) considered *H. decorata* as a synonym of *H. maculosa*. We confirm that *H. maculosa* and

H. decorata represent distinct species as suggested first by S. Johnson (2005) based on both molecular and morphological differences. Gohar & Aboul-Ela (1957) and Rudman (1987) have considered the sympatric species, *H. pulchella* and *H. ghardaqana*, as distinct species but with few morphological differences between them other than slight differences in their colour patterns. A surprising result of this study is that these species are not each other's closest relatives and are members of highly divergent clades. *Hypselodoris pulchella* is a member of the *Risbecia* clade, whereas *H. ghardaqana* is sister to *H. bollandi*.

Another important taxonomic question that arises from this study is whether the three clades should be regarded as separate genera. The same argument could be made in naming all of the subclades discussed here. In fact, any number of divisions of monophyletic clades could be considered as representing distinct genera, and any subdivision is entirely arbitrary. At least 19 described species of *Hypselodoris* have not been investigated by molecular methods owing to the unavailability of appropriately preserved material. Thus, taxon sampling is far from complete. At this time, we strongly believe it is preferable to regard the lineage we call *Hypselodoris* in this study as a single genus. All members of the large clade are recognizable based on their body shape, jaws with elongate denticles and a unifid apex, radular morphology with bifid radular teeth, and a reproductive system with a receptaculum seminis that is much smaller than the bursa copulatrix. Of the three large clades recovered here, only the *H. bullockii* clade has clearly recognizable morphological attributes that distinguish it from other *Hypselodoris*. Therefore, it would not be prudent to name the two other clades that can be recognized only by molecular sequences. Likewise, considering a large number of subclades is also impractical. The subclades share morphological features that unite them, but these features are generally internal and require advanced knowledge of morphology and dissection techniques.

One must ask the philosophical question as to the audience that is served by a particular classification system. Recently, Korshunova *et al.* (2017) modified the classification of aeolid nudibranch taxa into a complex system reliant on dubious, minor morphological features that are not consistent among the species included in these genera. For example, in their table 3, various genera were characterized by differences in the length of the central cusp relative to the adjacent lateral denticles. Williams & Gosliner (1979: fig. 5a) clearly show this range of variation in a single species of Fionidae. Similar variation is present in the denticle morphology of various species of *Tenellia* that were formerly included in the genus *Phestilla*. Not only does this division of taxa into small subunits become cumbersome, but also it does not permit other users of the classification (largely other comparative biologists) to identify taxa readily from living examples. Therefore, we have opted to adopt a broader view, where the larger monophyletic group is considered a genus and where there are external characters that can be used by non-specialist practitioners to be able to recognize taxa.

Morphological patterns

Morphological characters have been used successfully to differentiate taxa within the Chromodorididae (e.g. Rudman 1984; Gosliner & Johnson 1999). These characters span different organ systems and have been used to separate higher taxa and individual species. A review of the variability of these characters, their utility in taxonomy and how they correlate with the molecular results is provided below. In some of the species examined here, it is not possible to explore extensive variability owing to limited numbers of specimens available. The discussions of variability provided are based on examples where a sufficient number of specimens were available to assess variability.

In addition to external coloration and colour pattern, gill morphology is also an important external feature that appears to show species-specific patterns. Whether the gill is held erect or is spreading is a feature observable in living animals that has consistency between individuals of the same species, assuming that the animal has not been stressed and has the gill partly or completely retracted. Likewise, the gill opening, which may be level with the mantle margin or exhibit an elevated conical extension from the mantle through which the gill protrudes, does not appear to vary within species. Our analysis of gill morphology and its evolution (Fig. 39) considered two major characteristics of the gill. The first feature, the presence of an elevated gill pocket, is unique to the clade containing *H. regina*, *H. krakatoa*, *H. cerisae*, *H. reidi*, *H. jacksoni* and *H. iba*, indicating that this feature evolved once from the common ancestor of these taxa and has not been replicated in other lineages. The second feature noted is the presence of a gill that vibrates, as found in the '*Risbecia*' clade described above, but also occurs in *H. ghardaqana* independently. None of the other members of its clade share this characteristic. This shared behaviour is an extension of the colour mimicry found between *H. pulchella* and *H. ghardaqana*, which are sympatric in the Red Sea.

The arrangement of mantle glands (mantle dermal formations) has been used previously to differentiate species of chromodorids. Gosliner & Behrens (1998) used the arrangement of mantle glands to differentiate species of *Chromodoris*, whereas Wilson & Willan (2007) showed greater variability of mantle glands in at least one species of *Chromodoris*. Gosliner & Johnson (1999) demonstrated the utility of mantle

gland arrangement in *Hypselodoris*. Although this study shows some variability within species, mantle glands do provide important characters for separating closely related species, such as between *H. decorata* and *H. maculosa*. In this study, seven specimens of *H. lacuna* exhibited slight variation in the number of mantle glands, but no variation regarding where they were situated along the mantle margin. The value of ascertaining the systematic value of mantle glands is best illustrated in the *H. bullockii* clade, where all members of the clade entirely lack mantle glands.

Morphology of the radular teeth has served as a basis for separating closely related species of chromodorids (Bertsch, 1976, 1978; Rudman, 1984; Gosliner & Johnson, 1999). Bertsch (1978) studied radular variation in *Felimare* (as *Hypselodoris*) and found species-specific differences in radular morphology between closely related species. Hoover *et al.* (2017) found greater variation in some of the characters suggested by Bertsch (1978) and that the presence or absence of a rachidian tooth in *Felimare* was not a distinction between species that molecular studies indicated where the same species. Nonetheless, other features of radular morphology appear to differentiate closely related species, but greater variation needs to be explored more fully within *Hypselodoris*.

The anatomy of the reproductive system has been widely used to separate higher taxa (Rudman, 1984). Its utility is reinforced here, where all members of *Hypselodoris* share the feature of having a receptaculum seminis that is much smaller than the bursa copulatrix, whereas all other chromodorids have the two sperm storage organs that are much more equal in size. In almost all cases where reproductive anatomy was examined in the present study, individuals were shown to be fully mature as evidenced by the complete development of the female nidamental glands. The only exception was in *H. perii*, where the single specimen examined was not fully mature. This fact reduces the issue of ontogenetic variability of reproductive characters. Closely related species where multiple examples were examined for reproductive anatomy, such as *H. decorata* and *H. maculosa*, had consistent differences in the length of the ejaculatory segment; short in *H. decorata* and elongate in *H. maculosa*. Likewise, the relative length and shape of the vaginal duct and point of insertion of the receptaculum seminis into the vagina appear to be reproductive features that are consistently distinct between species.

Colour variation and patterns (Figs 36–38)

Rudman (1991) described a series of colour patterns found in chromodorid nudibranchs and noted that these patterns can reflect convergent evolution between species that are not each other's

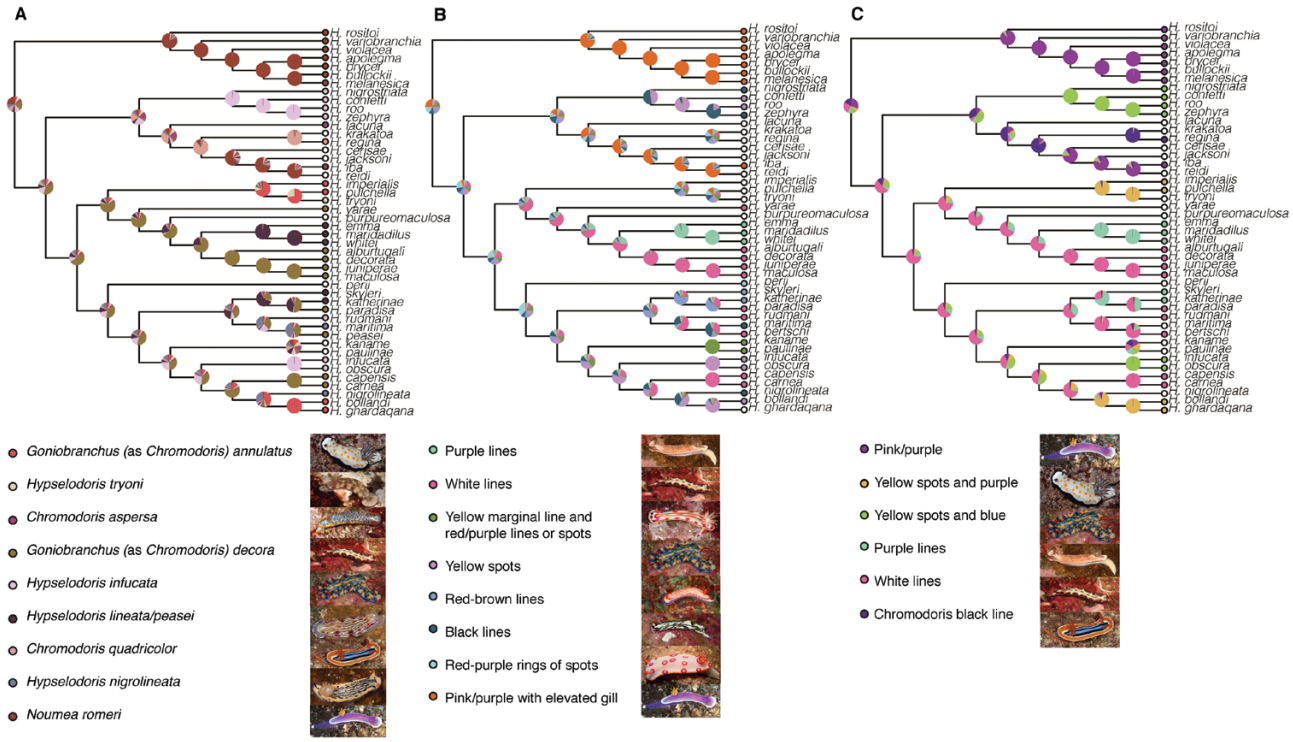

Figure 36. Distribution of *Hypselodoris* species for three colour group models. A, model based on Rudman's colour groups. B, model based on Gosliner *et al.* (2015). C, model based on the present study.

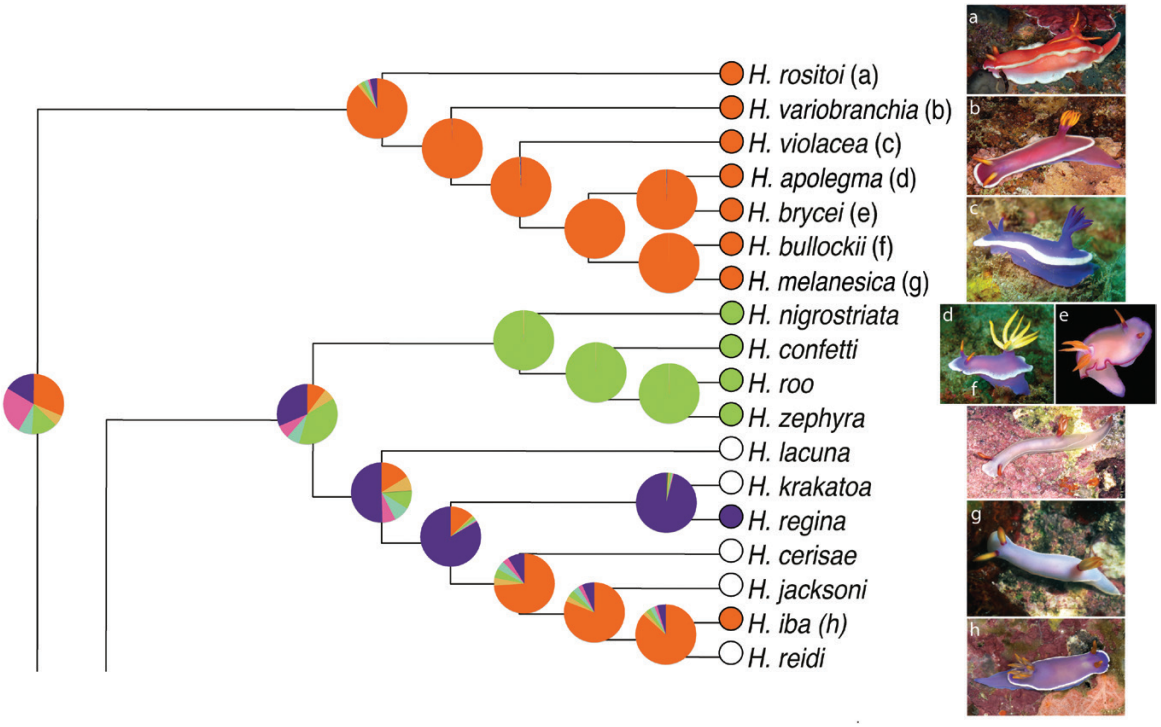

Figure 37. Independent evolution of purple group coloration in *Hypselodoris bullockii* species complex and *Hypselodoris iba*.

closest relatives but provide mimicry complexes of distasteful species (Winters *et al.*, 2018). For example, the *Goniobranchus annulatus* colour group (Rudman, 1987) contains sympatric species of both *Goniobranchus* (as *Chromodoris*) *annulatus* (Eliot, 1904) and *Hypselodoris* (as *Risbecia*). In this study, a series of species groups of *Hypselodoris* outlined by Gosliner *et al.* (2015) and an updated series that reflects our current thinking within this study were examined. A comparison of these three sets of species groups was used to elucidate which species groups represent monophyletic groups and which exhibit instances of convergence. Rudman's colour groups were not meant to identify monophyletic groups but represent taxa across chromodorid genera to identify groups of similar colour. The groups constructed by Gosliner *et al.* (2015) involved only *Hypselodoris* species and grouped species with similar coloration together within a guide used for field identification. The revisions undertaken for our present colour grouping are similar to those of Gosliner *et al.* (2015) but were designed to reduce some of the ambiguity that was evident from their previous groupings. These exercises, originally derived for convenient ways of dealing with groups that had large numbers of species, have provided an opportunity to test the evolution of colour patterns and determine which of these are likely to be attributable to evolution of a colour pattern from a common ancestor and which are attributable to convergence. It also addresses whether convergence in colour patterns has a strong biogeographical component in areas of sympatry.

Gosliner & Johnson (1999) noted that Hawaiian and South African white-lined species of *Hypselodoris* included at least one case of convergent evolution of colour patterns in two distinct geographical regions. Unfortunately, no specimens preserved for genetic studies were available to test these specific hypotheses. However, there were sufficient data to test the phylogenetic relationships of members of several colour groups previously identified.

Of the colour groups identified by Rudman (1991), several are relevant to our study of *Hypselodoris*. The *G. annulatus* (as *C. annulata*) group (Rudman, 1987) contains *G. annulatus*, *H. pulchella*, *H. ghardaqana*, *H. imperialis* and *Hypselodoris godeffroyana*. Three of these species are sympatric in the western Indian Ocean, namely *G. annulatus*, *H. pulchella* and *H. ghardaqana*. It is clear that *G. annulatus* is not closely related to the other two western Indian Ocean species, *H. pulchella* and *H. ghardaqana* (Johnson & Gosliner 2012), but the two *Hypselodoris* species were thought to be closely related to each other (Rudman, 1987). A surprising finding of the present study was that all three of these western Indian Ocean species have acquired this distinctive colour pattern independently. *Hypselodoris pulchella* is most closely related to a possibly undescribed species (*H.* sp. 23) from the western Pacific (that has little

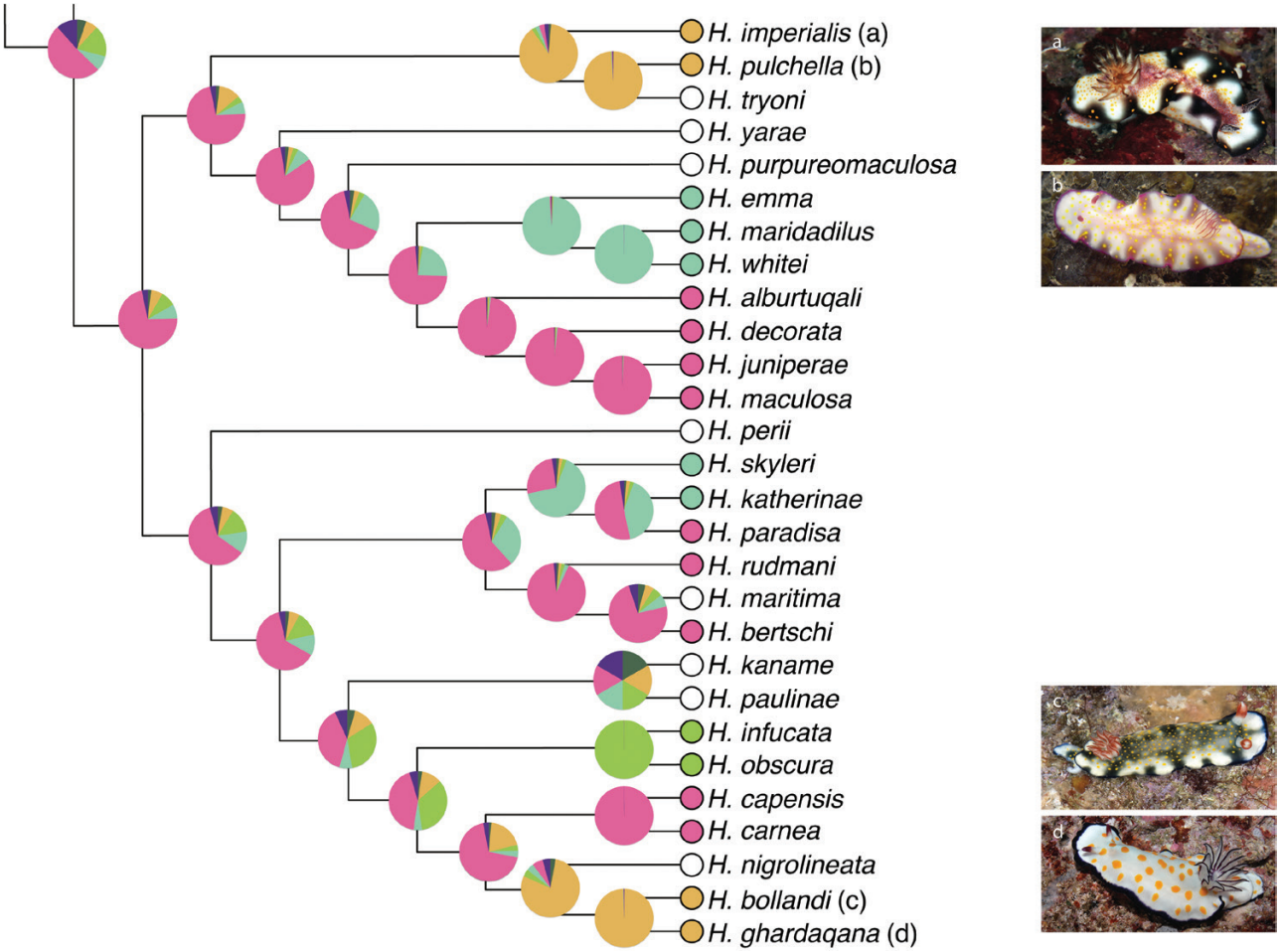

Figure 38. Independent evolution of purple group coloration in *Hypselodoris pulchella* clade and *Hypselodoris bollandi*/*Hypselodoris ghrardaqana* clade based on model developed in the present study.

genetic divergence from *H. pulchella*) and to *H. tryoni*, which has a very different colour pattern and was included in a different colour group by Rudman. In the present study, *H. gharadaqana* is sister to *H. bollandi*, which has a colour pattern that is convergent with the central and western Pacific species, *H. imperialis*, but there is no known instance of sympatry for *H. imperialis* and *H. bollandi*. In our current reconfiguration of colour groups, *H. bollandi* was added to this group.

Rudman (1987) included *H. tryoni*, *Goniobranchus kuniei* (Pruvot-fol, 1930) (as *Chromodoris*), *Goniobranchus leopardus* (Rudman, 1987) and *Goniobranchus geminus* (Rudman, 1987) in a distinct colour group, but no other *Hypselodoris* species share a similar colour pattern. Based on the phylogeny presented by Johnson & Gosliner (2012), this colour pattern arose twice in *Goniobranchus* and once in *Hypselodoris*.

Rudman (1983) also considered the *C. aspersa* colour group to include *C. aspersa* (Gould, 1852), *Glossodoris erythraea* Ehrenberg, 1831 and '*Chromodoris lilacina* Gould, 1852' of Kay & Young (1969). *Glossodoris erythraea* has not been identified with any currently recognizable species, and *C. lilacina* of Kay & Young (1969) is regarded as a synonym of *C. aspersa*. *Hypselodoris lacuna* was added to this colour group in our current grouping. It is evident that *C. aspersa* and *H. lacuna* evolved this colour pattern independently.

Rudman (1986) described the *Goniobranchus* (as *Chromodoris*) *decora* colour group as species that have a pink or yellowish pink background colour and some pattern of longitudinal white lines, purple and white spots, often an orange or reddish border and orange bands on white gills and rhinophores. He included *G. decora* (Pease, 1860) (as *Chromodoris*), *Noumea alboannulata* Rudman, 1986, *Thorunna australis* (Risbec, 1928), *Hypselodoris maculosa* (Pease, 1871) and juvenile *Hexabranchus sanguineus* (Rüppell & Leuckart, 1830) as members of this group. To this group, we would

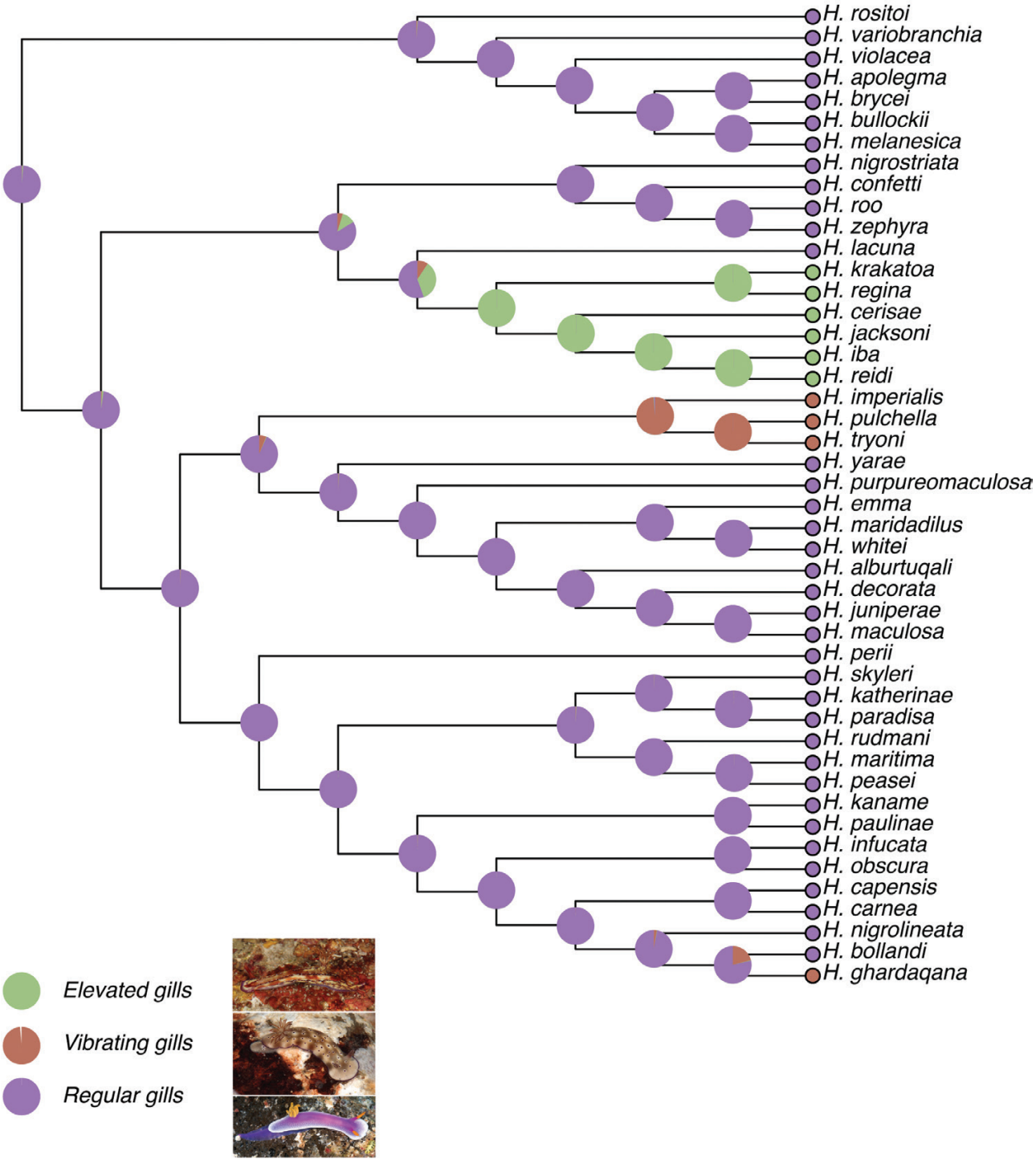

Figure 39. Evolution of elevated and vibrating gills in *Hypselodoris*.

add *Goniobranchus setoensis* (Baba, 1938), *Thournna florens* (Baba, 1949), *H. decorata*, *H. paradisa*, *H. juniperae*, *H. alburtuqali*, *H. alboterminata*, *H. insulana*, *H. violabranchia*, *H. peasei*, *H. bertschi*, *H. carnea*, *H. capensis* and *H. rudmani*.

The *H. infucata* colour group of Rudman (1977) included species with a bluish body colour and yellow markings. He considered seven species to be members of this colour group: *H. infucata*, *H. obscura*, *H. festiva* (Adams, 1861), *H. kanga*, *H. nigrostriata* and two

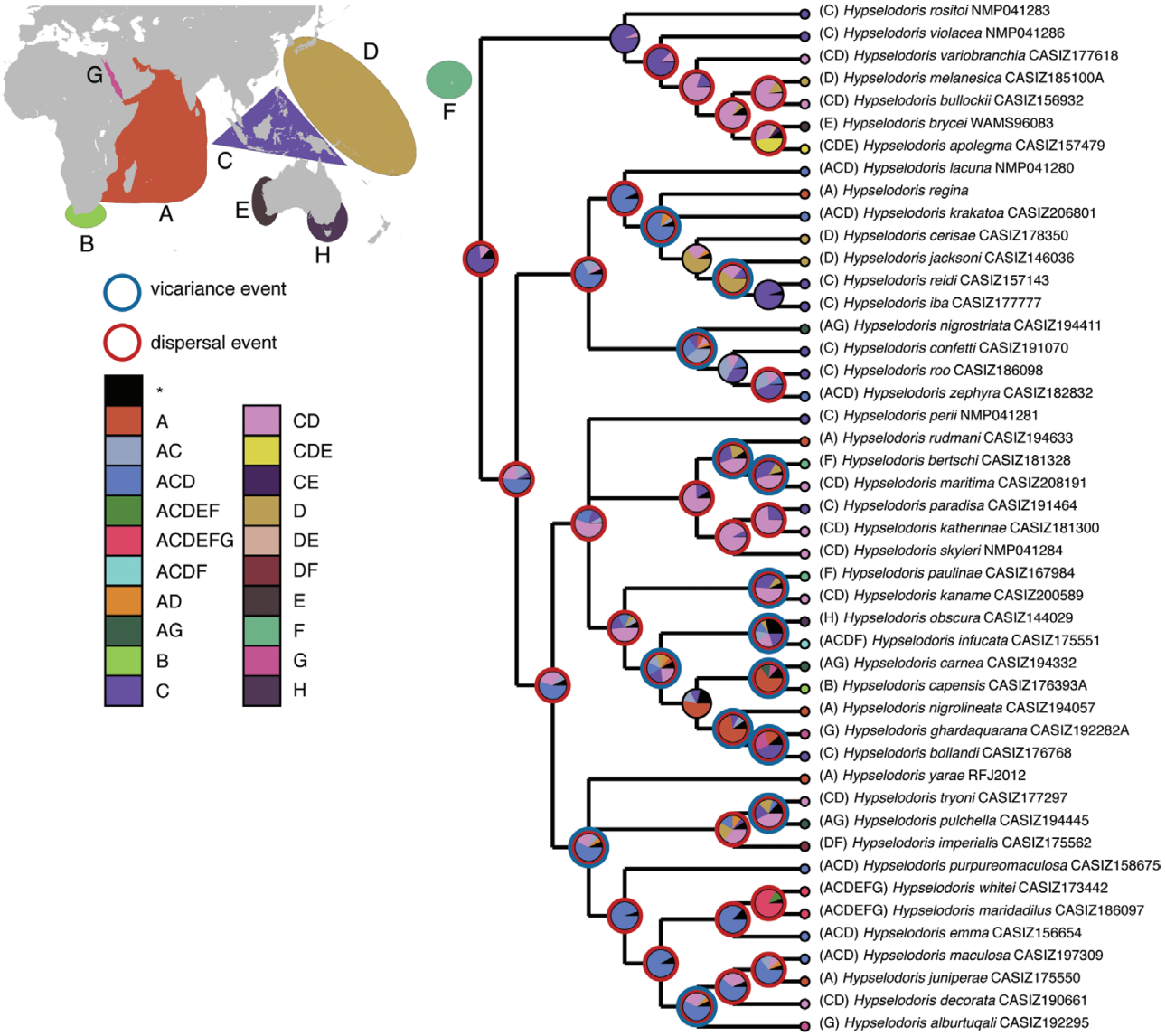

Figure 40. Ancestral area reconstruction estimated in RASP using the Bayesian binary Markov chain Monte Carlo (BBM) approach. Pie charts depict ancestral range probabilities for each node on our pruned Bayesian inference 50% majority-rule consensus tree. Red circles around ancestral range probabilities represent dispersal events, and blue circles represent vicariance events. Tip of each terminal branch represents the species range. Area codes and colours are depicted on the map with geographical divisions labelled. A, Indian Ocean; B, temperate South Africa; C, Coral Triangle; D, Western Pacific; E, Western Australia; F, Hawaii; G, Red Sea; H, temperate Australia.

apparently undescribed species of *Hypselodoris*. We would add the following species to this colour group: *Hypselodoris saintvincentius* (Burn, 1962), *H. confetti*, *H. zephyra*, *H. roo*, *H. rudmani* and *H. sagamiensis*. We would exclude *H. festiva* from this colour group as it has yellow lines rather than spots. Of the remaining ten species, molecular data are available for seven of these. These species are represented in three different clades. *Hypselodoris infucata* and *H. obscura* are sister species in one clade. *Hypselodoris infucata* is widespread, whereas *H. obscura* is limited to subtropical and temperate eastern Australia. Although molecular data are not available for *H. saintvincentius*, it is also likely to be a member of this clade and is restricted to temperate southern and western Australia (Johnson & Valdés, 2001). Another clade of members of this colour group includes *H. nigrostriata*, *H. confetti*, *H. roo* and *H. zephyra*. All but the first of these are sympatric in the western Pacific, and *H. nigrostriata* and *H. zephyra* are sympatric in the western Indian Ocean. The other representative of this group is *H. rudmani*, which is a member of another clade. It is also sympatric with

the latter two species in the western Indian Ocean. It appears that this colour pattern has arisen three separate times within *Hypselodoris* and includes sympatric species from different clades in both the western Pacific and the western Indian Ocean.

Rudman (1977) also discussed the *C. quadricolor* colour group and noted that *H. regina* is the only representative of this group that is not a species of *Chromodoris* and its independent acquisition of a similar colour pattern is clearly convergent with other western Indian Ocean species of *Chromodoris*.

In the same paper, Rudman (1977) also discussed the *H. lineata* colour group that included species with purple or black longitudinal lines: *H. lineata* (Eydoux & Souleyet, 1852), *H. emma*, *Hypselodoris hilaris* (Bergh, 1890), *H. maridadilus* and *H. nigrolineata*. The ambiguity of the identification of the specimens of Eydoux & Souleyet (1852) has been discussed previously (Gosliner & Johnson, 1999). Bergh's description of *Chromodoris hilaris* clearly indicates that its jaws and radula represent a species of *Hypselodoris*, but its identification with other species remains ambiguous (Rudman, 1977). Together with *H. emma*, *H. whitei* and *H. maridadilus*, we include two species, *H. katherinae* and *H. skyleri*, in this colour group. They clearly evolved reddish or purple longitudinal lines twice, independently.

Convergence in colour pattern, generally related to sympatry, is clearly prevalent throughout *Hypselodoris*. This strongly suggests that colour patterns are driven by mimicry complexes related to the unpalatability of all species and the concentration of distasteful substances in the defensive mantle glands.

Variation of colour pattern in nudibranchs, particularly in chromodorids, has received considerable attention recently (Almada *et al.*, 2016; Furfaro *et al.*, 2016; Padula *et al.*, 2016; Layton *et al.*, 2018).Furfaro *et al.* (2016) and Padula *et al.* (2016) found that the species complexes *Felimida* and *Felimare* exhibited colour polymorphism between species that made it extremely difficult to distinguish species on the basis of colour pattern. Almada *et al.* (2016) demonstrated that colour polymorphism was present in the *Felimare picta* complex, but this variation had a strong geographical component, and several of the species in the complex should be regarded as distinct species to preserve the monophyly of the species lineages. Light or dark colour morphs were generally found in different portions of the Atlantic and were generally not found overlapping geographically. Layton *et al.* (2018) found that a few species of *Chromodoris* vary in their colouration, particularly *Chromodoris colemani* Rudman, 1982, which has four distinct colour morphs. The four morphs are geographically isolated and localized in Okinawa, eastern Australia and western Australia. Each morph strongly resembles a different *Chromodoris* species with which it is sympatric. Likewise, they found that *Chromodoris joshi* Gosliner & Behrens, 1998 has two morphs, one with orange colour pigment and the other that strongly resembles *Chromodoris magnifica* (Quoy & Gaimard, 1832) but has subtle differences that allow it to be distinguishable from *C. magnifica*. The two morphs are sympatric in the Philippines. Matsuda & Gosliner (2017) have shown that closely related Indo-Pacific species of *Glossodoris* and *Doriprismatica* have minor but consistent differences in colour pattern, especially in the colours forming the mantle marginal bands. They do not appear to have polymorphic colour morphs.

The present study demonstrates, with few exceptions, that species of *Hypselodoris* do not appear to be polymorphic and that sympatric species may have convergent colour patterns between members of different clades, but that subtle but consistent differences in colour pattern can be used to differentiate species. This is evident in cases such as *H. iba*, which has convergent colour patterns with members of the *H. bullockii* complex, and in the similarities in colour pattern between *H. maculosa*, *H. decora*, *H. juniperae* and *H. paradisa*, and in the convergence between *H. bollandi* and *H. imperialis* and between *H. ghardaqana* and *H. pulchella*. *Hypselodoris maculosa* and *H. decora* represent an interesting case in point where sufficient numbers of individuals allow comparisons of variability. In Fig. 9, *H. decorata* exhibits some degree of morphological variation in dorsal colour pattern, but all individuals consistently have three red–orange rhinophoral bands, whereas all individuals of *H. maculosa* have only two rhinophoral bands. The subtle but consistent colour differences noted here are similar to those found in other recent studies of closely related pseudocryptic species of temperate nudibranchs (Hoover *et al.*, 2015; Lindsay & Valdés, 2016; Uribe *et al.*, 2017). Aposematic colour patterns and mimicry in nudibranchs continue to appear to provide critically important survival strategies. Additionally, subtle but consistent differences between distinct nudibranch taxa have often been overlooked but provide important systematic characters for differentiating distinct lineages. Additional studies are needed to determine how widespread these distinctions are or whether there are other cases where colour pattern does not permit distinction of different lineages determined by molecular methods.

The colour patterns described above have relevance to the phylogeny depicted in Figure 35. Members of the same clade with similar colour patterns are likely to have inherited that pattern from a common ancestor. Alternatively, species within the same clade having representatives in different colour groups are more likely to represent cases of convergence with sympatric

species of other clades. Of the three major clades shown, only the *H. bullockii* clade has species with a unified body colour of pink to purple, with a distinct marginal band of contrasting colour. Members of the *H. krakatoa* subclade do not have similar colour patterns to each other, with the exception of *H. krakatoa* and *H. cerisae*. Some members of this clade have mimetic colour patterns similar to members of other colour groups. For example, *H. regina* has a colour pattern similar to members of the *C. quadricolor* colour group, with which it is sympatric in the western Indian Ocean, whereas *H. iba* has a pattern convergent with members of the *H. bullockii* clade, with which it is sympatric. Members of the *H. maculosa* subclade are are divided into two smaller subclades, one containing *H. emma* and having purple longitudinal lines on the body and the other with white longitudinal lines, suggesting a strong phylogenetic signal for colour pattern in these groups. The remaining subclades do not have strong phylogenetic signals of colour patterns for members.

Biogeographical patterns

The various clades of *Hypselodoris* have a strong biogeographical signal that is representative of their vicariant history. For example, Gosliner & Johnson (1999) documented the radiation of various species of the *H. maculosa* clade in the Hawaiian Islands. Unfortunately, molecular material is not available for most of these Hawaiian endemics to make comparisons with the morphological studies previously undertaken. However, other radiations are clearly evident based on the present study. The *H. bullockii* clade contains seven species that appear to be restricted to portions the Coral Triangle, Western Pacific and western Australia. Although the Philippines has at least five sympatric members of this clade, there are also vicariant patterns evident. *Hypselodoris apolegma* is found throughout the western Pacific from Japan (Okinawa), the Philippines, Indonesia Malaysia (Sabah) and Western Australia (Shark Bay) (as *Chromodoris bullocki*; Wells & Bryce, 1993), whereas its sister species, *H. brycei*, is found only in Western Australia (Houtman Abrolhos Islands to the Exmouth Region and Dampier Archipelago). It is unclear whether these species are sympatric in Western Australia. *Hypselodoris bullockii* is widespread in the western and central Pacific, from Japan, Taiwan, Hong Kong, the Philippines, Indonesia, Malaysia, eastern Australia, the Marshall Islands and New Caledonia, whereas its sister species, *H. melanesica*, is known only from Papua New Guinea and the Solomon Islands (present study), both of which are areas where *H. bullockii* is absent. *Hypselodoris rositoi* is apparently restricted to the northern Philippines, and *H. violacea* is apparently restricted to Sabah, Malaysia and Palawan Island, Philippines. *Hypselodoris variobranchia* is apparently restricted to Japan (Okinawa), Taiwan, the Philippines, Malaysia, Indonesia and Queensland, Australia (present study). In this clade, a widespread Coral Triangle and western Pacific ancestor has radiated into seven species. Two of these (*H. bullockii* and *H. apolegma*) are widespread in these regions. The others have more restricted ranges, as discussed above. It is difficult to ascertain specific vicariant events that isolated populations and resulted in speciation, but the Coral Triangle region is known for high species diversity based on high vicariance owing to sea level change and vulcanism (Gosliner *et al.*, 2008).

Within the second large clade, a widespread Indo-Pacific ancestor is evident. There is no real pattern of distribution within the entire clade, which includes many widespread and apparently endemic species. Within this clade, a subclade containing seven species (*H. lacuna*, *H. regina*, *H. krakatoa*, *H. cerisae*, *H. jacksoni*, *H. reidi* and *H. iba*) has a common ancestor with a widespread Indo-Pacific distribution. Among these species, *H. lacuna* is the most widespread, being found from the western Pacific to Aldabra Atoll in the Seychelles (present study). *Hypselodoris regina* is known only from the western Indian Ocean from Tanzania, Madagascar, Mozambique and South Africa (Gosliner *et al.*, 2008). *Hypselodoris krakatoa* is found in the Coral Triangle and western Pacific from the Philippines, Indonesia and Papua New Guinea (present study). Previous records from Japan, Taiwan, Malaysia and Thailand are of the species described here, *H. cerisae*. *Hypselodoris jacksoni* is restricted to Queensland, Australia. Interestingly, the sister species, *H. reidi* and *H. iba*, are both sympatric in the Philippines and Indonesia, which represents the extent of their known ranges.

Within the second subclade, which contains the four species *H. nigrostriata*, *H. confetti*, *H. roo* and *H. zephyra*, there are oceanic endemics and widespread species. *Hypselodoris nigrostriata* is known from the western Indian Ocean from the Red Sea, United Arab Emirates, Tanzania, Madagascar, Reunion and Mauritius (Gosliner *et al.*, 2008). *Hypselodoris confetti* is known only from Hong Kong, the Philippines, Indonesia and Papua New Guinea. The two sister species, *H. zephyra* and *H. roo*, have overlapping ranges. *Hypselodoris zephyra* is widespread from the Tuamotu Archipelago westwards to Madagascar, whereas *H. roo* is known only from the Coral Triangle of the Philippines and Indonesia.

The third clade is the largest of the three, with 28 species recognized here. Our analysis shows that the common ancestor of this clade was widespread across the Indo-Pacific. Within this clade, the first subclade of note includes ten species: *H. perii*, *H. paulinae*, *H. kaname*, *H. obscura*, *H. infucata*, *H. capensis*, *H. carnea*,

H. nigrolineata, *H. ghardaqana* and *H. bollandi*. *Hypselodoris perii* is sister to the remaining species and is known only from the Philippines and Indonesia (Bali). Morphologically, it is most similar to *H. dollfusi* from Arabian Sea, but no molecular data are available for this latter species that would confirm a sister species relationship. *Hypselodoris paulinae*, known only from the Hawaiian Islands, is sister to *H. kaname*, which is known only from Japan, the Philippines, Indonesia, New Caledonia, Australia and New Zealand. The other species with similar coloration is *H. fucata* from Kenya and South Africa. Unfortunately, no molecular data are available for this species.

Also within this clade, there are two species pairs with tropical and adjacent temperate sister species. In the case of the widespread *H. infucata*, which is found from the Hawaiian Islands to the western Indian Ocean (Gosliner *et al.*, 2015), its sister species, *H. obscura*, is restricted to subtropical and temperate waters of eastern Australia. Another species that appears to be closely related to these two is *H. saintvicentius*, which is endemic to southern and western Australia. Johnson & Valdés (2001) described the anatomy of this species and its distinctions from *H. infucata* and *H. obscura*, but no molecular data are available to compare this species with the other two. The second two sister species are *H. carnea* and *H. capensis*. The first of these species is from the Arabian Sea to tropical South Africa and Mauritius (Gosliner *et al.*, 2008), whereas *H. capensis* is restricted to adjacent subtropical and warm temperate South Africa (Gosliner, 1987). The final three-species subclade comprises *H. nigrolineata*, which is sister to both *H. ghardaqana* and *H. bollandi*. The distribution of *H. nigrolineata* is restricted to the western Indian Ocean of Tanzania, Madagascar and Reunion, whereas *H. ghardaqana* is restricted to the Red Sea, Oman and possibly Thailand, and *H. bollandi* is known only from the Philippines and Japan (Okinawa) and, possibly, Malaysia (Gosliner *et al.*, 2008).

Another related subclade includes *H. skyleri*, *H. paradisa*, *H. katherinae*, *H. rudmani* and *H. maritima*. *Hypselodoris skyleri* is sister to *H. paradisa* and *H. katherinae* and is known only from the Philippines, Indonesia and the Marshall Islands (present study). *Hypselodoris paradisa* is known only from Papua New Guinea, whereas *H. katherinae* is known from eastern Malaysia, the Philippines and Indonesia (Gosliner *et al.*, 2008). Within this group, *H. rudmani*, known only from the western Indian Ocean, is sister to *H. bertschi* and *H. maritima*. *Hypselodoris bertschi* appears to be endemic to the Hawaiian Islands but may also be present in Japan (Gosliner *et al.*, 2008), and *H. maritima* is known from the western Pacific from Japan to Australia and west to Thailand.

The next major clade includes 14 species in two large subclades, with *H. yarae* being sister to the remaining 13 species. *Hypselodoris yarae* is known only from the western Indian Ocean of Madagascar, Mozambique and South Africa. The remaining 12 species are divided into two subclades, the '*Risbecia*' subclade and the *H. maculosa* subclade. The '*Risbecia*' subclade includes three to five species: *H. imperialis*, *H.* sp. 22, *H. tryoni*, *H.* sp. 23 and *H. pulchella*. There is some question as to whether the sister species *H. imperialis* and *H.* sp. 22 represent distinct species, and this study was not able to resolve this issue fully. *Hypselodoris imperialis* appears to be restricted to the Hawaiian Islands and French Polynesia, whereas *H.* sp. 22 is known from Papua New Guinea, Australia, Vanuatu and the Solomon Islands (Gosliner *et al.*, 2008, as *Risbecia* sp. 1). However, they do not appear as distinct species in the ABGD analysis and are 1.8–2.3% different in their *COI* gene. These two taxa require additional, more detailed study. Likewise, *H. pulchella* and *H.* sp. 23 are geographically isolated, with *H. pulchella* being found in the eastern Malaysia and Thailand to the Red Sea and south to South Africa (Gosliner *et al.*, 2008), whereas *H.* sp. 23 is known only from the Philippines and Indonesia. Again, these two taxa require additional study to determine whether they are distinct species.

Within the *H. maculosa* subclade, eight species were studied here: *H. emma*, *H. maridadilus*, *H. whitei*, *H. purpureomaculosa*, *H. alburtuqali*, *H. decorata*, *H. juniperae* and *H. maculosa*. *Hypselodoris emma* is found from the western Pacific to the western Indian Ocean and is sister to *H. maridadilus* and *H. whitei*. *Hypselodoris whitei* is known from the central Pacific Marshall Islands to the western Indian Ocean, but the distribution of *H. maridadilus* is much more convoluted owing to numerous misidentifications and requires additional study. *Hypselodoris purpureomaculosa*, which is sister to *H. alburtuqali*, *H. decorata*, *H. juniperae* and *H. maculosa*, is restricted to the western Pacific from Japan, the Philippines, Indonesia and the Solomon Islands. *Hypselodoris alburtuqali* is endemic to the Red Sea and is sister to *H. decorata*, *H. juniperae* and *H. maculosa*. The precise ranges of *H. maculosa* and *H. decorata* are difficult to ascertain, given the taxonomic confusion that has surrounded these species (see above discussion under remarks for *H. decorata*). Certainly, these two species are sympatric in the western Pacific, but their presence in the Indian Ocean requires confirmation. *Hypselodoris juniperae*, which is sister to *H. maculosa*, is endemic to the western Indian Ocean.

Many of the original patterns of vicariance found in sister species of *Hypselodoris* are masked by overlapping ranges, probably produced by dispersal

subsequent to speciation events. For example, the sister species *H. reidi* and *H. iba* are both restricted to Indonesia and the Philippines and are entirely overlapping in their ranges. In other instances, sister species (e.g. *H. bollandi* and *H. ghardaqana*) are entirely allopatric. Although most clades and subclades discussed above have representatives in the both the western Pacific and western Indian Ocean, all of the members of the *H. bullockii* complex appear to have undergone multiple speciation events in the western Pacific, with the exception of *H. brycei*, which is found on the margins of the Pacific and Indian Oceans. Life history strategies of most species of *Hypselodoris* remain largely unknown and thus shed little light on distribution patterns and possible vicariant events. Most species that have been observed appear to have planktotrophic development and are likely to be capable of long-distance dispersal.

Taxonomic notes

The World Register of Marine Species (WoRMS Editorial Board, 2017) lists 59 currently recognized species of *Hypselodoris*. Several of these taxa appear to be problematic as to whether they should be placed in *Hypselodoris* or whether they should be regarded as valid species with *Hypselodoris*. Each of these problematic species is discussed below.

Hypselodoris alaini *Ortea, Espinosa & Busque, 2013*

This species was described from Guadeloupe in the Lesser Antilles. Turner & Wilson (2008) and Johnson & Gosliner (2012) have demonstrated that all Atlantic and eastern Pacific species formerly included in *Hypselodoris* are members of a different lineage and should be placed in *Felimare*. Additionally, *H. alaini* has a receptaculum seminis that is larger than that found in *Hypselodoris* (Gosliner & Johnson, 1999) and is the same size as that found in species of *Felimare*. We consider this species to be *Felimare alaini* (Ortea *et al.*, 2013) comb. nov.

Hypselodoris andersoni *Bertsch & Gosliner, 1989*

Rudman (2000) clearly articulated how this species is synonymous with *H. peasei*. We concur with this synonymy.

Hypselodoris cuis *Marcus, 1965*

Gosliner & Johnson (1999) suggested that this species should be regarded as a junior synonym of *H. maculosa*. This synonymy has been overlooked in WoRMS.

Hypselodoris fortunensis *Ortea, Espinosa & Busque, 2013*

This species was described from Guadeloupe in the Lesser Antilles. Turner & Wilson (2008) and Johnson & Gosliner (2012) have demonstrated that all Atlantic and eastern Pacific species formerly included in *Hypselodoris* are members of a different lineage and should be placed in *Felimare*. It is far more likely that this species is placed in *Felimare* than in *Hypselodoris*.

Hypselodoris godeffroyana *(Bergh, 1877)*

This species is listed under the accepted name of *Risbecia godeffroyana* in WoRMS Editorial Board (2017) based on specimens first described by Bergh as *Chromodoris godeffroyana* from Tahiti. Johnson & Gosliner (2012) have demonstrated that all members of *Risbecia* are nested within *Hypselodoris*. Pease (1860) described *Doris prismatica* var. *imperialis* from the Hawaiian Islands, and this has been regarded as *H. imperialis* (Johnson & Gosliner, 2012). This species is very similar to *H. godeffroyana*, and there is considerable debate as to whether these two species are distinct. Specimens sequenced here from the Hawaiian Islands and Papua New Guinea exhibit very little genetic divergence, further suggesting they represent a single species, with *H. imperialis* having priority over *H. godeffroyana*.

Hypselodoris katherythros *Yonow, 2001*

Yonow (2001) described this species largely based on the presence of red rather than the purple longitudinal lines of *H. emma* on the notum. Yonow (2001) also noted that *H. katherythros* has a purple line surrounding the gill pocket that she asserted was absent in *H. emma*. In this study, we sequenced two specimens that we identified as *H. emma*, one from the Philippines (CASIZ 156654) with dark red lines on the notum and one from Madagascar with purple lines. Both specimens have a purple line around the gill pocket. Yonow (2001) also suggested that a median ridge is present on the inner lateral tooth of *H. emma* but absent in *H. katherythros*. However, the poor quality of the scanning electron micrographs published in that paper makes any detailed comparison difficult. Also, Rudman's drawing of the inner lateral tooth of *H. emma* (Rudman, 1977: fig. 6A) does not have a prominent ridge. It is likely that this represents individual variation. These two specimens are similar genetically (2.3% different in their *COI* gene) and are considered a single species in our ABGD analysis. Based on these data, we regard *H. katherythros* as a junior synonym of *H. emma*.

Hypselodoris kayae *Young, 1967*

Young (1967) described this species as species of *Hypselodoris*, based on the presence of bifid radular teeth. However, the drawing of the teeth (Young, 1967: fig. 9) does not appear similar to the distinctive bifid

cusp typical of *Hypselodoris*. The jaws (Young, 1967: fig. 10) were depicted as deeply bifid, whereas most *Hypselodoris* species have unifid jaw rodlets. The reproductive system (Young, 1967: fig. 11) also has a large receptaculum seminis, whereas most species of *Hypselodoris* have a greatly reduced receptaculum seminis. The colour pattern, radular formula and reproductive system are all consistent with those of *Verconia simplex* (Pease, 1871), which is also known to occur in the Marshall Islands (Johnson, 2017), the type locality of *H. kayae*. We suggest that *H. kayae* is a synonym of *V. simplex*.

Hypselodoris lalique *Ortea & Caballer, 2013*
This species was described from Guadeloupe in the Lesser Antilles. Turner & Wilson (2008) and Johnson & Gosliner (2012) have demonstrated that all Atlantic and eastern Pacific species formerly included in *Hypselodoris* are members of a different lineage and should be placed in *Felimare*. It is far more likely that this species is placed in *Felimare* than in *Hypselodoris*.

Hypselodoris mouaci *(Risbec, 1930)*
Gosliner & Johnson (1999) considered this species a synonym of *H. whitei*. This synonymy appears to have been overlooked.

Hypselodoris picturata *(Ehrenberg, 1830)*
Rudman (1984: 129) suggested that this species is likely to be a member of the genus *Hypselodoris*, but suggests it is best regarded as a doubtful species because insufficient data are available to distinguish it from other species of *Hypselodoris*.

Hypselodoris pinna *Ortea, 1988*
This species was described from the Cape Verde Islands. Turner & Wilson (2008) and Johnson & Gosliner (2012) have demonstrated that all Atlantic and eastern Pacific species formerly included in *Hypselodoris* are members of a different lineage and should be placed in *Felimare*. It is far more likely that this species is placed in *Felimare* than in *Hypselodoris*.

Hypselodoris samueli *Caballer & Ortea, 2012*
This species was described from Venezuela. Turner & Wilson (2008) and Johnson & Gosliner (2012) have demonstrated that all Atlantic and eastern Pacific species formerly included in *Hypselodoris* are members of a different lineage and are probably placed in *Felimare*. Additionally, *H. samueli* has a receptaculum seminis that is larger than that found in *Hypselodoris* (Gosliner & Johnson, 1999) and is the same size as that found in species of *Felimare*. We consider this species to be *Felimare samueli* (Caballer & Ortea, 2012) comb. nov.

Conclusions

The present study demonstrates the presence of previously undocumented diversity in a genus of chromodorid nudibranchs that has been relatively well studied. The 17 new taxa described here have a relatively uniform distribution across the phylogenetic tree presented, but with additional exploration of the western Pacific and poorly explored portions of the Indian Ocean being responsible for these new discoveries. In this study, key morphological characters across several organ systems provide additional lines of evidence that permit the separation of closely related species recognized on the basis of the molecular phylogeny. Traditional morphological characters, such as colour pattern, distribution of mantle glands, form of the radular teeth and arrangement of the organs of the reproductive system, provide useful characters for recognizing and differentiating species. Despite having some variability, these systems have considerable utility that corresponds to molecular analyses and species delimitation, thereby strengthening the systematic hypotheses presented.

Colour pattern evolution has been shown to have strongly convergent patterns between representatives of different genera (Rudman, 1991; Gosliner, 2001). The present study also indicates that sympatric species of *Hypselodoris* often have convergent colour patterns between representatives of different clades. This is probably attributable to Müllerian mimicry complexes in these strongly chemically defended, distasteful and brightly coloured species. With only a couple of exceptions, most species of *Hypselodoris* studied here display limited polymorphism in colour pattern, and each species has divergent colour patterns with closely related species that provide important species identification tools for differentiating species.

The three major clades of *Hypselodoris* found here all appear to have a widely distributed ancestor in the Indo-Pacific. In the case of the *H. bullockii* clade, the radiation has been restricted largely to the western Pacific and the eastern margin of the Indian Ocean and appears to be absent from the western Indian Ocean. The remaining clades have a widespread Indo-Pacific ancestor and have members with wide distributions in addition to more restricted regional endemics. In many cases, sister species have overlapping ranges and are partly sympatric, indicating probable dispersal after allopatric speciation.

ACKNOWLEDGEMENTS

This work was greatly facilitated by several individuals who helped to ensure that specimens were available for study. We are especially grateful to Anthony Berberian,

Mike Berumen, Philippe Bouchet, Clay Bryce, Cerise Chen, David Cowdery, Shireen Fahey, Jessica Goodheart, Brenna Green, Matthew Jebb, Scott Johnson, Vanessa Knutson, Nishina Masaoshi, Rie Nakano, Peri Paleracio, Chrissy Piotrowski, Alexis Principe, Roger Steene, Yara Tibiriçá, Denis Ty, Mike Severns, Bob Van Syoc, Riley Westgaard, Gary Williams and Nerida Wilson. This research was supported by a grant from the National Science Foundation: DEB 1257630 grant to Terrence Gosliner, Kent Carpenter, Richard Mooi, Luiz Rocha and Gary Williams and REU 1358680 to Richard Mooi, which supported Alessandra Lopez's participation in this project. This collaborative research involved the following partners in the Philippines: former Secretary of Agriculture Proceso J. Alcala; former Philippine Consul General Marciano Paynor and the Consular staff in San Francisco; former Bureau of Fisheries and Aquatic Resources (BFAR) Director Attorney Asis G. Perez; BFAR colleagues, especially Attorney Analiza Vitug, Ludivina Labe; National Fisheries and Research Development Institute (NFRDI) colleagues, especially Director Drusila Bayate and November Romena; US Embassy staff, especially Heath Bailey, Richard Bakewell and Maria Theresa N. Villa; staff of the Department of Foreign Affairs; University of the Philippines (UP) administrators and colleagues including UP President Alfredo Pascual, Vice President Giselle Concepción and Dr Annette Meñez; and the staff of the National Museum of the Philippines, especially Dr Jeremy Barns, Anna Labrador and Marivene Manuel Santos. We also thank Jessie de los Reyes, Marites Pastorfide, Sol Solleza, Boy Venus, Joy Napeñas, Peri Paleracio, Alexis Principe, the staff of Atlantis Dive Resort Puerto Galera (especially Gordon Strahan, Andy Pope, Marco Inocencio, Stephen Lamont and P. J. Aristorenas), the staff of Lago de Oro Beach Club and Protacio Guest House, May Pagsinohin, Susan Po-Rufino, Ipat Luna, Enrique Nuñez, Jen Edrial, Anne Hazel Javier, Jay-o Castillo, Arvel Malubag and Mary Lou Salcedo. Lastly, our sincere thanks are extended to our fellow Academy and Filipino teammates on the expeditions. All the specimens from the Philippines were collected under our Gratuitous Permits (GP-0077-14, GP-0085-15) from the shallow waters of the municipalities of Mabini, Tingloy, Calatagan and Puerto Galera. This is part of the joint Department of Agriculture-NFRDI-California Academy of Sciences Memorandum of Agreement for the ongoing implementation of the National Science Foundation-funded biodiversity expedition in the Verde Island Passage. The specimens were collected in accordance with the terms and conditions of the gratuitous permit and under the supervision of our partners from BFAR Fisheries Regulatory and Quarantine Division and NFRDI. Material for some of several of the species studied here were kindly supported by Dr Philippe Bouchet and supported by the Muséum National d'Histoire Naturelle, Paris. Specifically, The Panglao Marine Biodiversity Project was a joint project of Muséum National d'Histoire Naturelle, Paris (PI: Philippe Bouchet) and University of San Carlos, Cebu City (PI: Danilo Largo), funded by grants from the Total Foundation, the French Ministry of Foreign Affairs, and the Asean Regional Center for Biodiversity Conservation (ARCBC), and operating under a permit from the Philippine Bureau of Fisheries and Aquatic Resources (BFAR). The Madang expedition specimens were obtained during the "Our Planet Reviewed" Papua Niugini expedition organized by Muséum National d'Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le Développement (IRD) and University of Papua New Guinea (UPNG), Principal Investigators Philippe Bouchet, Claude Payri and Sarah Samadi. The organizers acknowledge funding from the Total Foundation, Prince Albert II of Monaco Foundation, Fondation EDF, Stavros Niarchos Foundation and Entrepose Contracting, and in-kind support from the Divine Word University (DWU). The expedition operated under a permit delivered by the Papua New Guinea Department of Environment and Conservation. The Atimo Vatae expedition to South Madagascar (Principal Investigator, Philippe Bouchet) was part of a cluster of Mozambique-Madagascar expeditions funded by the Total Foundation, Prince Albert II of Monaco Foundation, Stavros Niarchos Foundation, and additional support from the Richard Lounsbery Foundation and Triballat, under "Our Planet Reviewed", a joint initiative of Muséum National d'Histoire Naturelle (MNHN) and Pro Natura International (PNI) in partnership with Institut d'Halieutique et des Sciences Marines, University of Toliara (IH.SM) and the Madagascar bureau of Wildlife Conservation Society (WCS). Institut de Recherche pour le Développement (IRD) deployed its research catamaran Antéa. Lastly, we thank the anonymous reviewers of this paper who provided valuable comments for improving the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Specimens used for phylogenetic study organised by family and genus. Those in bold are newly described species in this study.

Table S2. COI P-distances between species studied here.

Figure S1. Bayesian inference estimate of phylogenetic relationships for single species sampling. Bayesian posterior probabilities values are depicted on each node that were <1.00 support.

Figure S2. Maximum likelihood estimate of phylogenetic relationships for single species sampling. Bootstrap values are depicted on each node that were <100 support.