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A review of walking shark (Hemiscylliidae: *Hemiscyllium*) distributions in Papua New Guinea and description of a new species

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Abstract

Walking sharks (*Hemiscyllium*) comprise 9 morphologically similar species whose identification relies on distinctive color patterns, genetic markers, and geographically restricted distributions. The genus is endemic to Australia and the island of New Guinea, a region that coincides with the global hotspot for carpet shark diversity (Orectolobiformes) that has been shaped by complex tectonic and sea-level histories. Although knowledge of walking shark distributions has been updated over the past two decades, the species endemic to eastern Papua New Guinea remain poorly known. This study addresses these gaps by investigating the distributions of walking sharks in eastern Papua New Guinea. We used a series of in-situ surveys to review the ranges of walking shark species and to document their species-specific color patterns, complemented by an assessment of genetic markers to confirm the updated geographical distributions across species and explore phylogeographic patterns in the region. We present updated distributions for two species (*H. michaeli* and *H. hallstromi*), as well as a theory for the development of a mosaic of disjunct, non-overlapping distributions previously unreported for the genus. Additionally, we describe a tenth member of the genus, *Hemiscyllium dudgeonae*, n. sp., which is likely to be highly threatened. We present possible mechanisms that may have produced this mosaic of distributions and influenced speciation in the region. Finally, we discuss the conservation implications of these findings.

Keywords: taxonomy; ichthyology; biogeography; cryptic species; SNPs; ND4; genetics; carpet, epaulette sharks

Introduction

The Coral Triangle, encompassing Papua New Guinea (PNG), the Philippines, Timor-Leste, the Solomon Islands and parts of Indonesia and Malaysia, represents one of the major centers of marine biodiversity globally (Briggs 2005, Allen 2008). The region has been influenced by a complex history of tectonic plate movements and sea level fluctuations, both creating and removing barriers for species dispersal, isolation, and recolonization across different time scales (Barber 2009, Pellissier et al. 2018). Among the high diversity of corals and fish, the region is a notable center for tropical elasmobranchs (sharks and rays), particularly for carpet sharks (Orectolobiformes) (Weigmann 2016). The highest species richness of carpet sharks occurs where the western Pacific and eastern Indian Oceans converge, coinciding with the Coral Triangle and northern Australia (Compagno 2001, Weigmann 2016, Boyd & Seitz 2021). The area has strongly influenced the evolution and speciation of carpet sharks, particularly for wobbegongs (Orectolobidae) and the 9 species of walking sharks, also commonly known as epaulette sharks (Corrigan & Beheregaray 2009, Allen et al. 2016, Dudgeon et al. 2020, Boyd & Seitz 2021).

Walking sharks of *Hemiscyllium* Müller & Henle, 1838 are endemic to northern Australia, the island of New Guinea, and several of its satellite islands (Allen et al. 2016, Dudgeon et al. 2020). These small, predominantly nocturnal, benthic sharks typically reach total lengths of 70–80 cm, with the largest reported at 107 cm (Allen et al. 2016, Weigmann 2016). They are commonly found in shallow coastal habitats, including coral reefs, seagrass beds, and mangroves, usually at depths less than 10 m, but have been recorded as deep as 50 m (Weigmann 2016). Walking sharks exhibit extremely restricted home ranges of only a few hundred square meters to a few square kilometers due to their limited mobility and benthic lifestyle (Erdmann & Dudgeon 2024). Additionally, these sharks are oviparous, depositing small oval-shaped egg cases on the sea floor, which further restricts their dispersal abilities.

Our understanding of walking shark species distributions has changed dramatically over the past 20 years. The genus was reviewed by Dingerkus & Defino (1983) and Compagno (2001), who recognized 5 species, including *Hemiscyllium freycineti* (Quoy & Gaimard, 1824); *Hemiscyllium hallstromi* Whitley, 1967; *Hemiscyllium ocellatum* (Bonnaterre, 1788); *Hemiscyllium strahani* Whitley, 1967; and *Hemiscyllium trispeculare* Richardson, 1843. At that time, these 5 species were believed to exhibit broad overlapping ranges across northern Australia, New Guinea, extending to Sumatra, Malaysia, and the Solomon Islands. However, subsequent investigations revealed that the extralimital records were erroneous and there is no contemporary evidence of *Hemiscyllium* from areas outside of New Guinea and Australia (Allen et al. 2016). Extensive fieldwork and genetic analyses in the early 2000s resulted in the description of 4 additional species: *Hemiscyllium galei* Allen & Erdmann, 2008;

Hemiscyllium henryi Allen & Erdmann, 2008; *Hemiscyllium michaeli* Allen & Dudgeon, 2010; and *Hemiscyllium halmahera* Allen et al., 2013. These findings significantly advanced our knowledge of walking shark distributions, indicating that each species has geographically restricted, non-overlapping ranges. All 9 species of walking shark are morphologically similar and their identification relies heavily on color-pattern differences, genetics and knowledge of their geographic ranges (Allen et al. 2016, Erdmann & Dudgeon 2024).

Habitat disjunctions such as deep water (>200 m) and turbid, soft-bottomed environments created by large freshwater outflows have been hypothesized to cause biogeographic breaks between walking shark species distributions (Allen et al. 2016, Dudgeon et al. 2020). Typically, distributions are associated with reefs, shoals, and satellite islands connected by shallow waters (<50–100 m). However, *Hemiscyllium* are likely absent from some of the large islands in the New Guinea region (e.g., New Britain, New Ireland and Manus) due to deep-water barriers, despite being within 50–150 km of known populations (Allen et al. 2016). The disjunct, non-overlapping distributions of walking sharks have been attributed to their limited dispersal abilities during all stages of the life cycle (Allen et al. 2016). Further, these factors influence the ability of walking sharks to adapt to localized disturbances, such as coastal developments, environmental degradation, marine pollution, and limited harvest for subsistence fisheries and the marine ornamental trade (VanderWright et al. 2022). 5 of the 9 species are currently listed as threatened with extinction on the IUCN Red List under criterion B (which relates to their restricted geographic range) – a criterion that only applies to approximately 3% of all sharks (Dulvy et al. 2021, VanderWright et al. 2022). Although recent research has improved our understanding of distribution patterns, large areas of the coastline of New Guinea remain unexplored with respect to *Hemiscyllium*. The paucity of data available, particularly regarding geographic distributions and population genetics for these site-associated species, limits the ability to formulate conservation strategies.

Recent phylogenetic and biogeographic analyses have provided further insights into the historical dispersal and diversification of walking sharks, linking their evolutionary history to tectonic activity and sea-level changes (Dudgeon et al. 2020). The most basal taxon, *H. strahani*, was likely present on the northern coastline of New Guinea approximately 9 million years ago (Ma) and subsequently diversified into western and eastern groups. It has been suggested that ancestors of the western group may have "hitched a ride" on island arc fragments that moved westward to form what is now known as Halmahera, giving rise to *H. halmahera* (Allen et al. 2013, Dudgeon et al. 2020). Subsequently, the region around the Bird's Head Peninsula was colonized giving rise to *H. henryi*, *H. galei*, and *H. freycineti* between 4 and 2 Ma. Conversely, the eastern group was more likely a result of gradual eastward and southward movement between 6 and 3 Ma, giving rise to the PNG endemics *H. michaeli* and *H. hallstromi*, as well as *H. ocellatum* (Queensland) and *H. trispeculare* (Western Australia and Aru) (Dudgeon et al. 2020).

Although, there are relatively few studies of individual species, most research to date has involved *H. ocellatum* in Queensland (Goto et al. 1994, Wheeler et al. 2021, Shackleton et al. 2022) and *H. galei*, *H. freycineti*, and *H. halmahera* in eastern Indonesia (Insani et al. 2022, Tapilatu et al. 2022, Akbar et al. 2023, Ichsan et al. 2023, Fahmi et al. 2025). The present study is the first to investigate the species endemic to eastern PNG, with a primary focus on *H. michaeli*. This region requires further investigation to determine the full distribution limits of *H. hallstromi* and *H. michaeli*, the potential for hybridization zones or the possibility for undescribed species (Allen et al. 2016, Erdmann & Dudgeon 2024). Moreover, PNG presents an important area of interest due to its recent and ongoing tectonic activity (Taylor et al. 1999 Hill & Hall 2003, Brandl et al. 2024), which has contributed to high levels of endemism in other taxa including reptiles (Kraus 2021, Oliver et al. 2024), amphibians (Hill et al. 2022, 2023), and fishes (Allen & Werner 2002).

The current study was designed to fill knowledge gaps relating to the distributions of endemic walking shark species in eastern PNG, using genetic markers to explore phylogeographic patterns in the region. Herein we present updated distribution limits for *H. michaeli* and *H. hallstromi*¸ as well as a theory of a mosaic of disjunct, non-overlapping distributions in Milne Bay and Oro provinces of eastern PNG previously unreported for this genus. Additionally, we describe a tenth member of the genus, including detailed photos, comprehensive morphometrics and an updated species key based on diagnostic markings. We use the mitochondrial ND4 gene complemented by single nucleotide polymorphisms (SNPs) to confirm the updated geographical distributions across species and distinguished the new species from others within the genus.

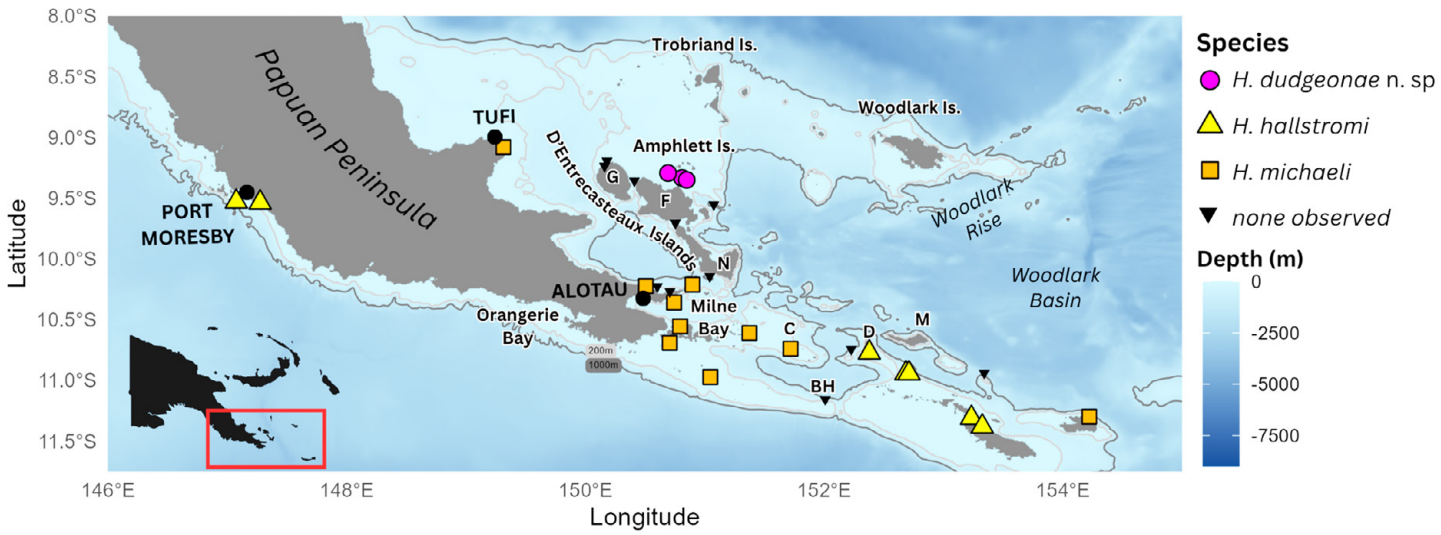

Figure 1. Bathymetric map of the study area in Papua New Guinea and *Hemiscyllium* species observations (BH =Bramble Haven; C =Conflict Islands; D =Deboyne Group; G =Goodenough Island; F =Fergusson Island; M =Misima Island; N =Normanby Island).

Materials and Methods

Data collection. In-situ surveys were conducted between November 2023 and March 2025 within Milne Bay, Oro, and Central provinces of PNG (Fig 1). Surveys were conducted using a combination of diving, snorkelling, and reef walking to catch walking sharks by hand. Surveys targeted coral reefs, seagrass beds, and mangrove habitats, from the waterline down to 3 m, reaching maximum depths of up to 25 m. Sampling occurred during both daytime and night-time hours to account for potential diel activity patterns. A total of 70 dedicated surveys were completed, with an average duration of 84 min (range 25–270 min), with one sample from Wreck Bay in Far North Queensland (FNQ), Australia collected during an opportunistic survey by author MVE. Walking sharks were sampled from 15 locations spanning 35 sites (Supp. Table 1).

Upon capture, walking sharks were transferred into a tub containing sea water. Morphometrics (total length and girth in cm), weight (g), photos, blood (~1 ml) and tissue samples (~1x1 cm) from the caudal fin were collected from each individual prior to release. Tissue samples were stored in 80–100% ethanol for downstream molecular analyses. Blood samples were stored on Whatman Dried Blood Spot Cards and left to dry for 24–48 hrs, prior to storage in individual ziplock bags with a silica desiccant. Species were identified in the field based on their species-specific color patterns and the GPS coordinates, location name and depth of the capture were recorded.

Technical terms and measurements follow Compagno (2001). Subcaudal length was measured along the ventral margin of the caudal fin from the posteriormost base of the anal fin to the tip of the caudal fin. Total length and head length are abbreviated as TL and HL respectively. Head length was measured from the snout tip to the dorsal terminus of the fifth gill slit. Vertebral counts were obtained from radiographs of the holotype and female paratype. Specimens examined in this study are deposited in the fish collections of the Queensland Museum, Brisbane (QM), University of Papua New Guinea, Port Moresby (UPNG), and the Western Australian Museum, Perth (WAM). A juvenile specimen of the new taxon, 257 mm TL, previously misidentified and designated as a paratype of *H. michaeli* by Allen & Dudgeon (2010), is deposited at the United States National Museum of Natural History, Washington, DC (USNM).

Mitochondrial sequencing

DNA was extracted for sequencing from fin tissues or blood samples from 44 individuals representing a spread of the locations sampled for each species. DNA was extracted from <25 mg of fin tissue or 10–20 µl blood preserved on Whatman Dried Blood Cards using Qiagen DNeasy Blood & Tissue Extraction Kits according to the manufacturers' instructions. The mitochondrial NADH dehydrogenase subunit 4 gene (ND4) was amplified through polymerase

chain reaction (PCR) using the primers: ND4-F: 5' -CACCTATGACTACCAAAAGCTCATGTAGAAGC - 3' (Arevalo et al. 1994) and H12293- Leu-R: 5'–TTGCACCAAGAGTTTTTGGTTCCTAAGACC - 3' (Inoue et al. 2001). The ND4 gene was selected as previous studies have demonstrated its effectiveness for distinguishing between *Hemiscyllium* species (Allen & Erdmann 2008, Allen & Dudgeon 2010, Dudgeon et al. 2020).

Reactions were conducted in 20 µl total amounts and consisted of: 2 µl each primer (10nM), 10 µl 2 x MyTaqTM Mix, 2 µl MilliQ water and 2 µl DNA template. PCRs were conducted on Eppendorf Mastercycler Nexus thermocyclers and consisted of an initial denaturation step at 95 °C for 5 min, followed by 30 cycles of 95 °C for 15 sec, 56 °C for 30 sec and 72 °C for 1 min, and a final extension at 72 °C for 7 min. PCR products were cleaned using ExoSAP-IT PCR Product Cleanup Reagent (Applied Biosystems) following the manufacturers protocols. Genomic DNA was quantified using a Qubit 4.0 Fluorometer (Life Technologies, Carlsbad, CA, USA). Final PCR products were sequenced in both forward and reverse directions by Macrogen Korea using Applied Biosystems BigDye Terminator v3.1 reagents and the Applied Biosystems 3730 DNA analyser. All new sequences were deposited in GenBank. The sequences for each dataset were aligned across all taxa plus one representative of *Chiloscyllium punctatum* as an outgroup using Geneious Prime 2025.1.3 (https://www.geneious.com). Existing *Hemiscyllium* sequences (n =52) from Dudgeon (2020) were also used so as to include all species from within the genus. A Neighbor-Joining Kimura 2-parameter phylogenetic tree was constructed with statistical support for branch nodes evaluated across 1,000 bootstrapped replicates in MEGA12 (Kumar et al. 2024). Pairwise differences were calculated between sequences and mean distances within and between species calculated based on 1,000 bootstrap replicates. Additionally, the maximum variation within groups and minimum distance between groups were determined. Rossel Island, Calvados Chain, and FNQ were identified as areas of interest due to their locality, color patterns, and position in the phylogenetic tree, and therefore they were included as separate groups for further testing of pairwise differences. The consensus tree was then visualized using the Interactive Tree of Life (iTOL) software (Letunic & Bork 2021).

Single nucleotide polymorphism (SNPs)

SNPs were generated using the DArTSeq approach from Diversity Arrays Technologies (DArT, Canberra, Australia). Samples were processed with the proprietary DArT Pty Ltd analytical pipeline, which includes technical replicates from a subset of samples to assess genotyping reproducibility (Georges et al. 2018).

Fin clips and blood samples from the current surveys (n =217) and from historical collections (n =35) were sent to DArT for sequencing and SNP genotyping. DNA was extracted from fin clips by DArT, however DNA was extracted from blood samples prior to transport using Qiagen DNeasy Blood & Tissue Extraction Kits according to the manufacturers' instructions. Additionally, an existing SNPs library of *H. ocellatum* samples (n =119) (Shackleton et al. 2022) was co-analysed. By combining data sets we were able to include representatives from all described *Hemiscyllium* species (Supp. Table 1).

SNPs quality control and filtering. The dartRverse (Gruber et al. 2018, Mijangos et al. 2022) package was used for quality control and filtering of the SNP data within version 4.5.1 (R Core Team 2025) through the RStudio interface (Posit Team 2025). The SNP data were stringently filtered on RDepth (lower =2, upper =25), call rate of loci and individuals (0.99 and 0.9 respectively), and reproducibility (0.99). Further filtering included taglength (lower =50, upper =69), secondaries, and a final filter on the call rate of loci (1). Finally technical duplicates were removed from the dataset (Supp. Table 2).

To reduce potential biases in outputs from skewed sample sizes, a second dataset with fewer individuals (n =74) was generated by removing some of the samples of the most represented species: *H. ocellatum*, *H. michaeli*, and *H. hallstromi*. Where available, individuals that had been used for both the ND4 sequencing and the SNPs were retained, and efforts were made to include individuals across multiple locations throughout the distribution of each species (Supp. Table 1). Dataset A is the complete dataset and Dataset B is the subsampled dataset.

SNPs genotyping analyses. Analyses were conducted within the dartRverse package using version 4.5.1 (R Core Team 2025) through the RStudio interface (Posit Team 2025). Principle coordinate analysis (PCoA) was applied to both Dataset A and B to visualize and compare trends between datasets using the gl.pcoa function. Further analyses were only conducted on Dataset B. Pairwise FST values between populations, along with confidence

intervals and p-values, were calculated based on the method by Weir and Cockerham (Weir & Cockerham 1984) using the function gl.fst.pop (Gruber et al. 2018, Mijangos et al. 2022). Fixed differences, percent fixed differences and the significance of the count of fixed differences were calculated to identify operational taxonomic units (OTUs) using the function gl.fixed.diff with 100 replications undertaken in the simulation to estimate probability of false positives (Gruber et al. 2018). As with the mitochondrial analysis, fixed difference analysis was also calculated with Rossel Island, Calvados Chain and FNQ as unique groups in addition to the main species groups.

Maximum likelihood analysis was conducted to assess the phylogenetic relationships amongst the *Hemiscyllium* samples based on SNPs. Firstly, the filtered datasets were converted into .fasta files as a single sequence tag per individual and imported to the Galaxy public server (usegalaxy.org.au/) for further analysis (Abueg et al. 2024). The IQ-TREE tool (Minh et al. 2020) was used to generate maximum likelihood trees and a consensus tree for both datasets. Models of best fit based on AIC scores were determined with ModelFinder (Kalyaanamoorthy et al. 2017). Consensus trees for each dataset were constructed from 1,000 bootstraps (Hoang et al. 2018) and visualized with the Interactive Tree of Life program (Letunic & Bork 2021).

Results

Distributions of PNG endemics. A total of 28 locations were surveyed including 11 locations where no sharks were observed (Fig. 1). At each location surveyed, there was never more than one species present. Surveys expanded the known range of *H. hallstromi* by 475 km to a relatively small area of Milne Bay spanning the Deboyne Group, Calvados Chain, and Sudest Island, with a linear distance of approximately 175 km between sites. Conversely, *H. michaeli* was found to be widespread between Tufi in Oro Province and Rossel Island in Milne Bay, with a linear distance of 600 km between survey sites. Two of the 10 sampling locations (The Conflict Islands and Rossel Island), were outside of the previously reported range for the species, extending the distribution by approximately 350 km eastward. The Calvados Chain and adjacent Sudest Island separate the *H. michaeli* population at Rossel Island from the remainder of its range. Despite surveys conducted at multiple locations at the D'Entrecasteaux Islands (n =6) and nearby Uama Island, no walking sharks were observed during surveys.

During our surveys, a third distinctive color morph (Fig. 2) was observed at the Amphlett Group north of the D'Entrecasteaux Islands, with 12 individuals collected from three sites. Given the uniqueness of the pattern and the consistency of this pattern between individuals collected in the Amphlett Islands, it was hypothesized that it was a new species, leading to a comprehensive morphological and phylogenetic investigation.

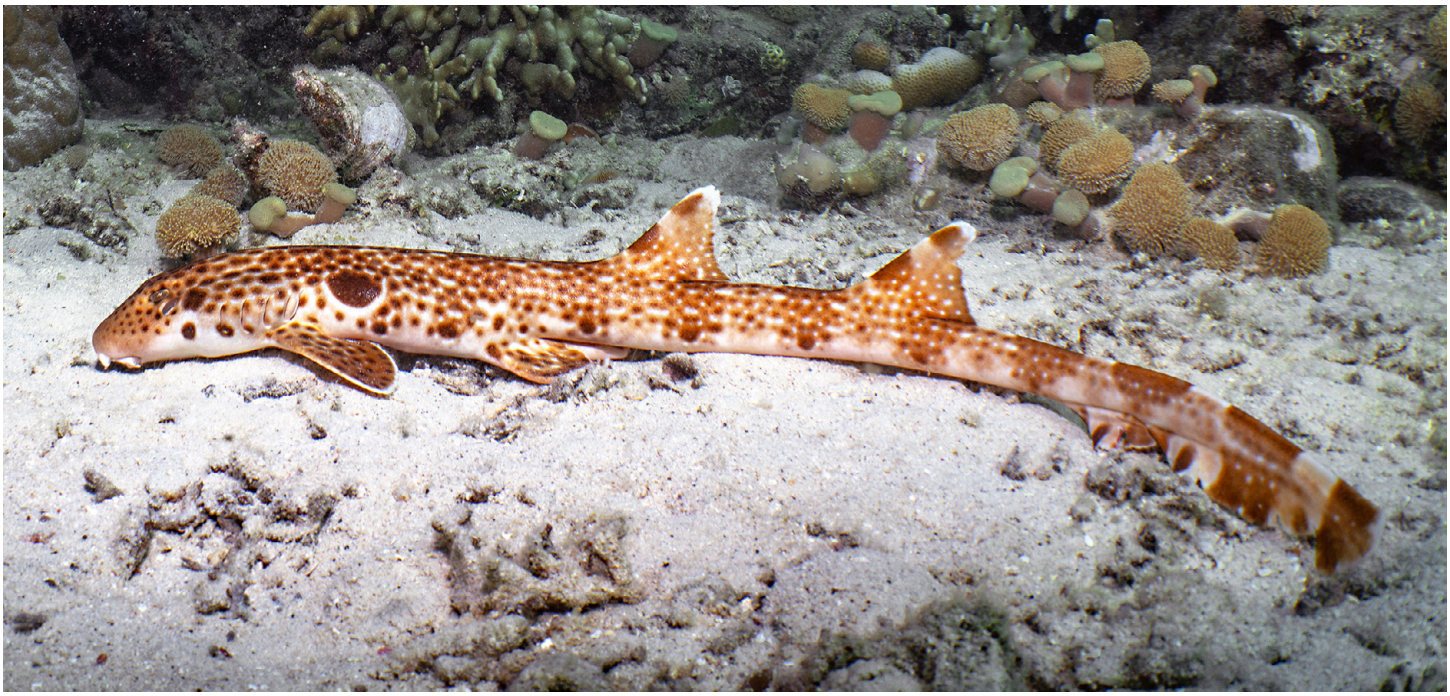

Figure 2. *Hemiscyllium dudgeonae*, n. sp., male holotype, WAM P. 36018–001, 673 mm TL, near Yabwaia Island, Milne Bay Province, Papua New Guinea at 8 m (N. Ichida).

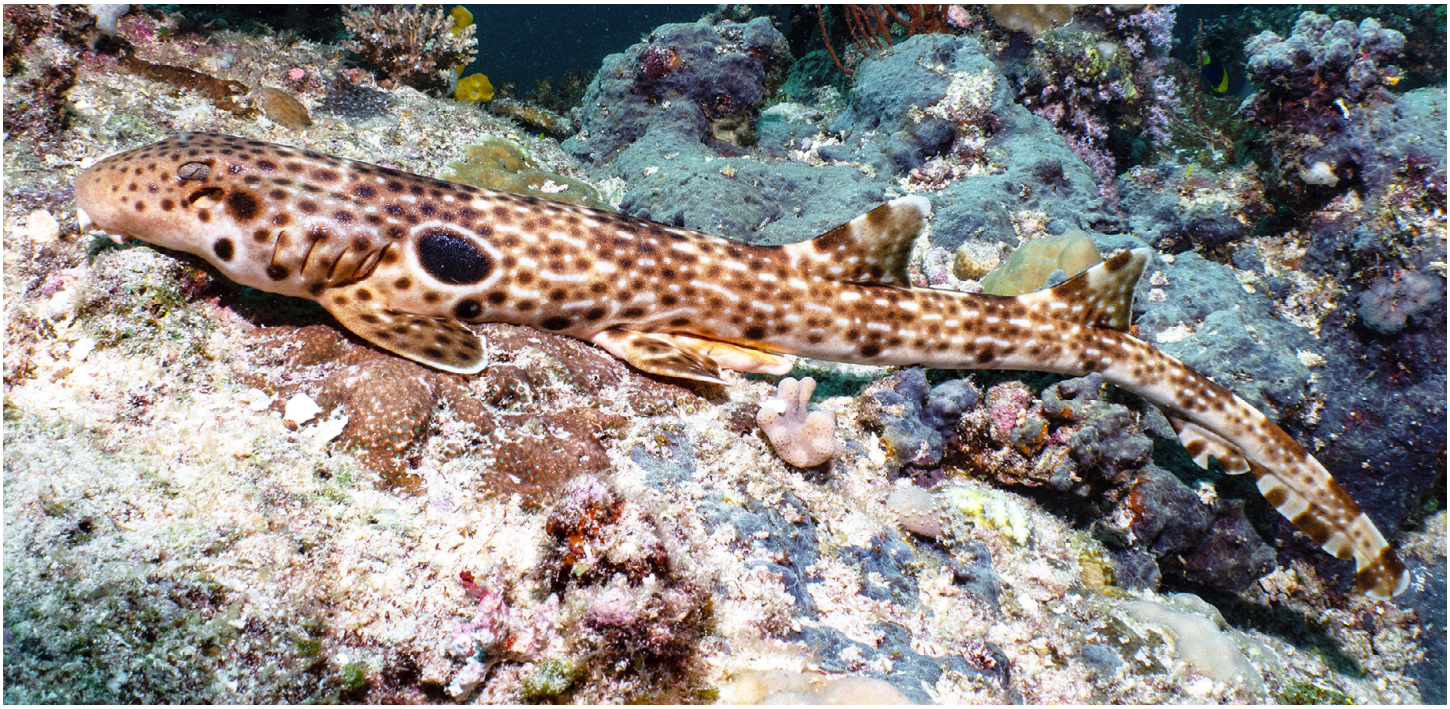

Figure 3. *Hemiscyllium dudgeonae*, n. sp., male paratype, UPNG E0534, 610 mm TL, Nubwageta, Milne Bay Province, Papua New Guinea at 2 m (M.V. Erdmann).

Hemiscyllium dudgeonae, n. sp. Allen, Erdmann & Blakeway

Dudgeon's Epaulette Shark

urn:lsid:zoobank.org:act:6357D7DC-A4CF-4FF4-8696-964B1E947430

Figures 2–6 & 7J,K&L, 8, 9, 11A, 13B & 14D; Table 1

Holotype. WAM P.36018-001, male, 673 mm TL, Papua New Guinea, Milne Bay Province, Amphlett Islands, about 3.8 km SE of Yabwaia Island, -9.3347, 150.8103, outer reef slope in 8 m, M.V. Erdmann, 16 March 2025.

Paratypes. UPNG E0534, male, 610 mm TL, same collecting details as holotype except Watota Island (locally known as Nubwageta), off northwest corner, -9.2941, 150.6935, seagrass beds in 1–2 m, C.L. Dudgeon, 15 March 2025; QM I.41556, female, 620 mm TL, same collecting details as holotype except Watota Island, off northwest corner, -9.2941, 150.6935, mangrove roots in 0.5 m depth, N. Panta, 16 March 2025; USNM 221705, 257 mm TL, PNG, Milne Bay Province, Trobriand Islands, Kuia Island (usually referred to as Munuwata), -8.5891, 150.8555, in 1 m, B.B. Collette, 11 June 1970.

Diagnosis. A species of *Hemiscyllium*, distinguished from all congeners by a combination of brown freckling interspersed with white spots and white dashes on head and most of body, becoming less conspicuous on tail; including about 38–48 brown spots on snout region, 11 or 12 brown spots on interorbital, about 30 brown spots on dorsal surface of each pectoral fin, about 30 brown spots on each pelvic fin, a prominent post-cephalic ocellus, a relatively large pair of intense dark brown spots just behind and below spiracle, and a row of 7 widely spaced spots along lower side. Also distinguished from congeners by some differences in DNA sequences.

Description. Vertebral centra 187 (190 for female paratype); body and tail relatively slender, tapering posteriorly; precaudal-fin length 1.2, HL 6.6 (6.2–6.3), both in TL; maximum head height 2.3 (2.2–2.5) and

maximum head width 1.9 in HL; eye length 3.2 (3.5–3.8) in snout length, eye height 2.4 (2.0) in eye length; fleshy interorbital space 1.4 (1.3–1.4), bony interorbital space 1.9 (1.8–2.0), both in snout length; snout blunt and short, snout tip to eye 2.7 (2.8–3.3), snout tip to mouth 7.3 8.9–9.9), snout tip to spiracle 2.3 (2.3–2.6), snout tip to first gill slit 1.3 (1.4–1.5), all in HL; gill slits on rear part of head, above to slightly anterior of pectoral-fin base; distance between first and fifth gill slit 3.1 (3.2–4.0) in head length; height of gill slits gradually increasing posteriorly, the first 5.4 (3.8–3.9) and fifth 3.2 (2.2–2.3), both in snout length.

Mouth small and transverse, positioned well forward on ventral surface of head, its width 1.3 (1.1–1.2) in snout length; short barbel on each side of ventral snout, its length 4.5 (5.9–6.2) in snout length; maximum width of lower labial flap 6.0 (5.1–6.2), length of postoral fold (upper labial furrow) 3.0 (2.6–3.7), length of lower labial furrow 3.3 (4.7–6.0), all in snout length; teeth pavement-like, composed of numerous rows; individual teeth broad-based with single posteriorly directed cusp , the cusps of innermost rows more developed.

Pre-first dorsal-fin length 2.6 (2.7), prepelvic-fin length 3.5 (3.4–3.6), snout to vent length 3.5 (3.1–3.4), vent to anal fin origin 2.4 (2.4–2.5), vent to caudal-fin tip 1.4 (1.4–1.5), all in TL. Pectoral fins below gill openings, their length 1.4 (1.3–1.5) in HL; pelvic fins immediately anterior to vertical line passing through first dorsal fin origin, their length 1.0 (1.0–1.1) in HL; dorsal fins positioned well back on body, first dorsal fin similar or slightly higher than second; first dorsal-fin base 1.9 (2.0–2.2) in HL, first dorsal-fin height 1.0 (1.0–1.1) in first dorsal-fin base; first dorsal-fin free margin 2.3 (1.8–2.0) in first dorsal-fin height; interdorsal space 1.4 (1.4–1.5) in HL;

TABLE 1

Proportional measurements (as % of TL) for type specimens of *Hemiscyllium dudgeonae*, n.sp.

	Holotype WAM P. 36018	Paratype QM I.41556	Paratype UPNG E0534		Holotype WAM P. 36018	Paratype QM I.41556	Paratype UPNG E0534
Sex	male	female	male		male	female	male
Total length	673	620	610	Barbel length	1.3	1.2	0.8
Precaudal length	81.7	84.7	80.3	Snout to 1st dorsal origin	38.6	37.1	37
Head length	15.2	16	16.1	Snout to pelvic origin	28.7	29	28
Head width	8	8.2	8.4	Snout to anus	28.5	32.7	29.5
Head depth	6.5	7.3	6.6	Anus to anal-fin origin	41.6	40.8	41.1
Preanal body depth	3.6	3.9	3.4	Anus to tail tip	69.8	66.9	69.3
Snout - 1st gill slit	11.6	11.6	10.5	Interdorsal distance	10.5	10.8	11.1
1st to 5th gill slit	4.9	4	5.1	Pectoral-fin length	11.1	11.9	10.7
First gill slit height	1	1.5	1.3	Pelvic-fin length	10.1	10.8	10.2
Fifth gill slit height	1.8	2.6	2.1	1st dorsal-fin base	7.9	7.4	8
Eye diameter (horizontal)	1.8	1.6	1.3	1st dorsal-fin height	7.9	7.1	7
Eye diameter (vertical)	0.7	0.8	0.7	1st dorsal-fin free margin	3.4	3.9	3.6
Fleshy interorbital width	4.2	4	3.8	2nd dorsal-fin base	8.2	8.9	8.2
Bony interorbital width	3	3.1	2.5	2nd dorsal-fin height	7.3	6.5	6.9
Snout to eye	5.6	5.6	4.9	2nd dorsal-fin free margin	2.8	3.7	3.3
Snout to spiracle	6.7	6.9	6.2	Anal-fin base	8.8	10	9.5
Snout to mouth	2.1	1.6	1.8	Anal-fin height	3.1	2.7	3.1
Lower labial furrow length	1.6	1.6	1.3	Anal-fin free margin	1.5	1.5	1.1
Lower labial flap width	1	1.1	0.8	Subcaudal	18	16.1	19.2
Upper labial furrow length	1.9	1.6	1.3	Clasper length (inner)	8.9		9.8
Mouth width	4.3	4.7	4.4	Clasper length (outer)	7.1		6.4

Figure 4. *Hemiscyllium dudgeonae*, n. sp., male paratype, UPNG E0534, 610 mm TL, Nubwageta, Milne Bay Province, Papua New Guinea at 2 m (M.V. Erdmann).

second dorsal-fin base 1.9 (1.8–2.0) in head length; second dorsal-fin height 1.1 (1.2–1.4) in second dorsal-fin base; second dorsal-fin free margin 2.6 (1.7–2.1) in second dorsal-fin height; long and low anal fin just anterior to caudal fin; anal-fin base 1.7 (1.6–1.7) in HL, anal-fin height 2.8 (3.1–3.6) in anal-fin base; anal-fin free margin 2.1 (1.9–2.7) in anal-fin height; elongate and thick precaudal tail (section of body between anus and caudal fin), its depth at level of anal-fin origin 4.3 (4.1–4.7) in HL; subcaudal length 5.6 (5.2–6.2) in TL.

Color in life and when freshly collected. (Figs. 2–6) Overall tannish brown, grading to plain white on ventral surface; a dense freckling of brown and white spots and white dashes on head and most of body, becoming less conspicuous on tail; about 38–48 brown spots on snout region, 11 or 12 brown spots on interorbital, about 30 brown spots on dorsal surface of each pectoral fin, and about 15 spots on each pelvic fin, brown spots on head and body generally increasing in size posteriorly from snout to predorsal and prepelvic regions, then gradually decreasing in size; prominent, intensely dark brown markings include a large (> eye size) post-spiracle spot and a slightly smaller spot below on cheek surrounded by a white area with a well-developed, white-rimmed, post-cephalic ocellus (Figs. 7J–L), and a ventral row of 7 widely spaced dark brown spots, first below post-cephalic ocellus, second a short distance anterior to pelvic-fin insertion, third below anteriormost part of first dorsal fin, fourth below free margin of first dorsal fin, fifth below second dorsal-fin origin, sixth below free margin of second dorsal fin, and seventh slightly anterior to anal-fin origin; a series of 7 brown saddles or bars sometimes apparent, often faint, with intense dark spots forming ventral terminus of each bar or saddle; two or three prominent dark brown saddle-like markings with white intermediate area along anterior edge of both dorsal fins; apex of both dorsal fins white; caudal fin and adjacent anal fin with three brown bars with intervening, broad, whitish areas, each containing a large brown spot along ventral margin.

Color variation. The post-cephalic ocellus of the holotype differs from that of the paratypes and the 9 released genetic specimens in having this distinctive marking dorsally truncated, with the upper margin lacking the typical white halo (Figs. 2 & 7J). Another variation was evident in two of the released specimens, both males, 540–549 mm TL, in which the large post-cephalic ocellus was fused with the intense dark brown spot immediately below (Fig. 7L). All of the above anomalies were evident on both right and left sides of the same specimens.

Figure 5. *Hemiscyllium dudgeonae*, n. sp., female paratype, QM I.41556, 620 mm TL, Nubwageta, Milne Bay Province, Papua New Guinea at 2 m (G.R. Allen).

Figure 6. *Hemiscyllium dudgeonae*, n. sp., dorsal view of anterior male holotype, WAM P. 36018–001, 673 mm TL, near Yabwaia Island, Milne Bay Province, Papua New Guinea at 8 m (G.R. Allen).

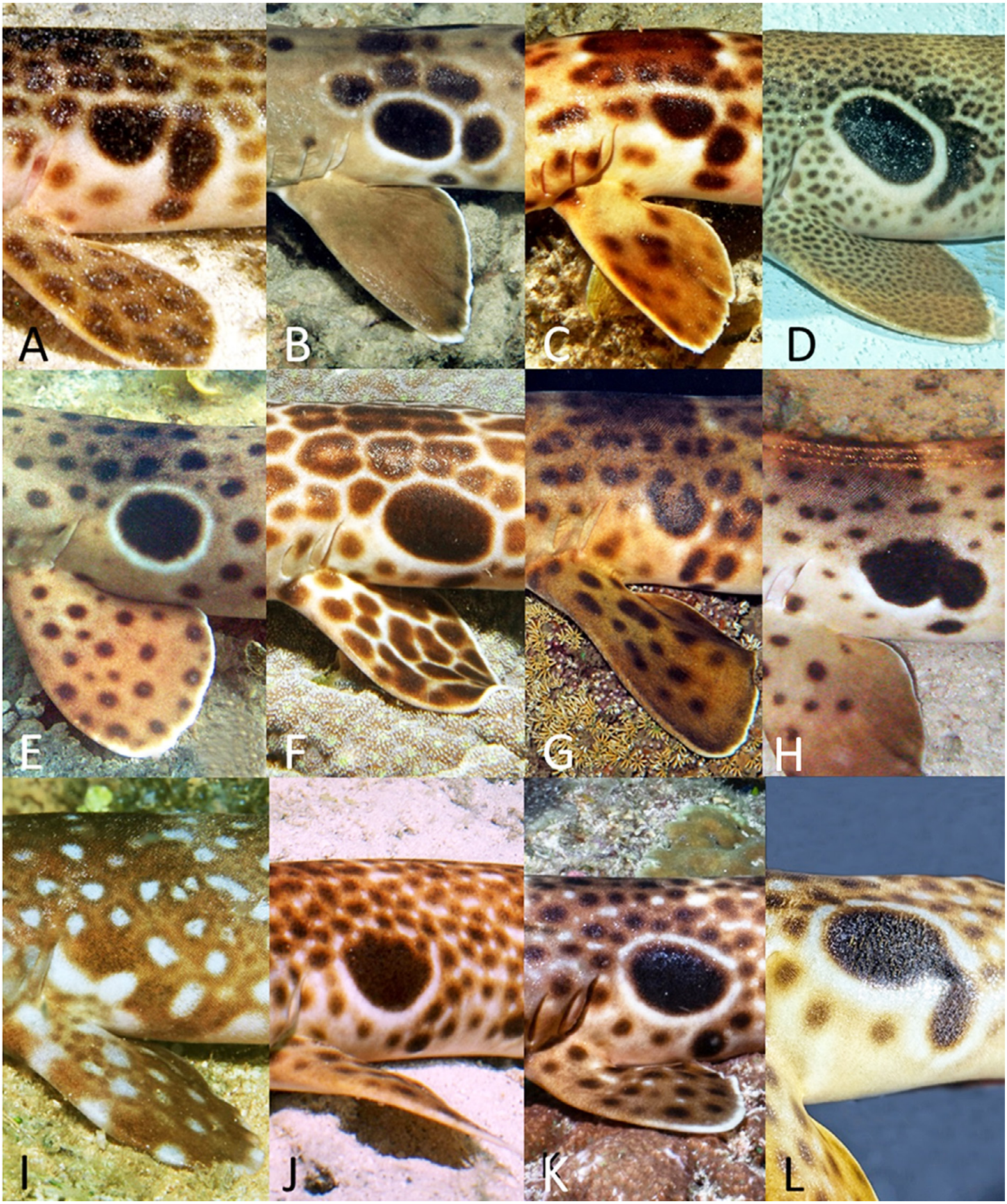

Figure 7. *Hemiscyllium* spp. post-cephalic markings: A) *H. freycineti,* B) *H. hallstromi*, C) *H. galei*, D) *H. trispeculare*, E) *H. ocellatum*, F) *H. michaeli*, G) *H. halmahera*, H) *H. henryi*, I) *H. strahani*, and J, K & L) *H. dudgeonae* (G.R. Allen, except E by R. Steene; G, I, and J by M.V. Erdmann; K by N. Ichida; & L by J. Blakeway).

Color in alcohol. (Fig. 8) Similar to live coloration, although pattern is less intense and whitish areas are pale brown to tannish. A juvenile paratype (USNM 221705, Fig. 8), 257.2 mm TL, has a greatly reduced spot pattern, primarily consisting of about 9 light brown bars on the side and tail, those on the side with a large dark brown mid-lateral spot; a pair of large dark brown spots on cheek region and large brown spot (precursor of characteristic post-cephalic ocellus of adult) behind head.

Distribution and habitat. The new species is currently known only from Milne Bay Province, eastern PNG (Fig. 1) between the Amphlett Islands (off northern Fergusson Island, D'Entrecasteaux Islands) and the Trobriand Islands, though we predict it will likely be found throughout the D'Entrecasteaux and Trobriand Islands, and possibly as far offshore as Woodlark (Muyua) Island; more survey work is urgently needed to confirm the full range of this species. It is typically encountered in shallow depths (< 5 m) among seagrass and scattered coral outcrops on coastal fringing reefs and outer reef slopes while diving both at night and during the day, sheltering under rocky outcrops or tabular corals. The known depth range is approximately 0.5–12 m. Individuals were typically in very shallow water at night and in greater depths during daylight hours.

Etymology. It is a pleasure to name this strikingly patterned species *H. dudgeonae* in honor of Christine L. Dudgeon, a renowned elasmobranch geneticist and ecologist who has researched *Hemiscyllium* phylogenetics and speciation for the past two decades and who first collected this undescribed species. The local common name at the type locality is kadedekedewa, which loosely translates to dog shark or lazy shark with reference to its slow, four-limbed gait. It is known as botabota at the Trobriand Islands.

Remarks. A total of 12 individuals, 392–781 mm TL (avg. 623 mm), were collected, including two females and 10 males. All except the three type specimens were released alive, after blood and tissue samples were collected. Although our sample size is limited, there appears to be a sudden increase in the size of the male claspers

Figure 8. *Hemiscyllium dudgeonae*, n. sp., lateral and dorsal views of preserved juvenile paratype, USNM 221705, 257 mm TL, Munuwata, Trobriand Islands, Milne Bay Province, Papua New Guinea (courtesy USNM).

between about 550–600 mm TL. Larger mature males (Fig. 9) had an average inner-clasper length of 10.3% TL (n =5) vs. 5.8% TL for three individuals 392–560 mm TL. A notable exception to this trend was an apparent underdeveloped individual, 602 mm TL with an inner-clasper length of only 5.5% TL.

The juvenile paratype (USNM 221705, Fig. 8), 257 mm TL was previously designated as a paratype of *H. michaeli* by Allen & Dudgeon (2010), but we find the specimen to be *H. dudgeonae*. It had been collected from from Munuwata, Trobriand Islands, approx. 80 km north of the type locality for *H. dudgeonae*. In addition, two more adults were captured by fishermen at Tuma Island (-8.357, 150.863) in the northwestern portion of the archipelago (pers. comm., photograph by F. Paul).

Comparisons. The members of the genus are very similar with regards to body shape and general proportions, and aside from two Australian species, are poorly represented in museum collections, which precludes meaningful morphological/meristic comparisons. Moreover, the soft pliable bodies of these sharks, which are often badly misshapen after preservation, result in a wide range of potentially inconsistent measurements. Fortunately, they possess distinctive, highly diagnostic color patterns, of which the salient markings generally persist in preservative, and, combined with geographic distribution, offer effective tools for species identification. With the exception of *H. dudgeonae*, *H. hallstromi*, and *H. michaeli*, which occur in relatively close proximity within the confines of Milne Bay Province (the largest marine province in PNG with a sea area of 252,990 km^2), most species exhibit well-separated, allopatric geographic distributions (Fig. 10).

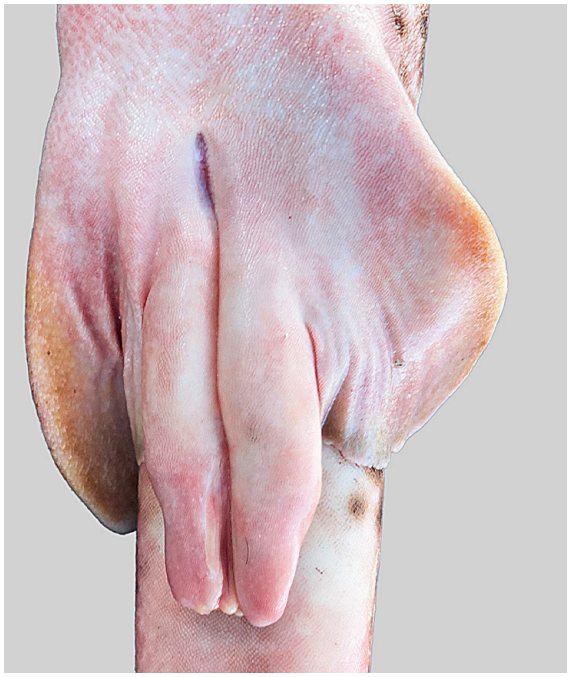

Figure 9. *Hemiscyllium dudgeonae* claspers of holotype,WAM P. 36018–001, PNG (G.R. Allen).

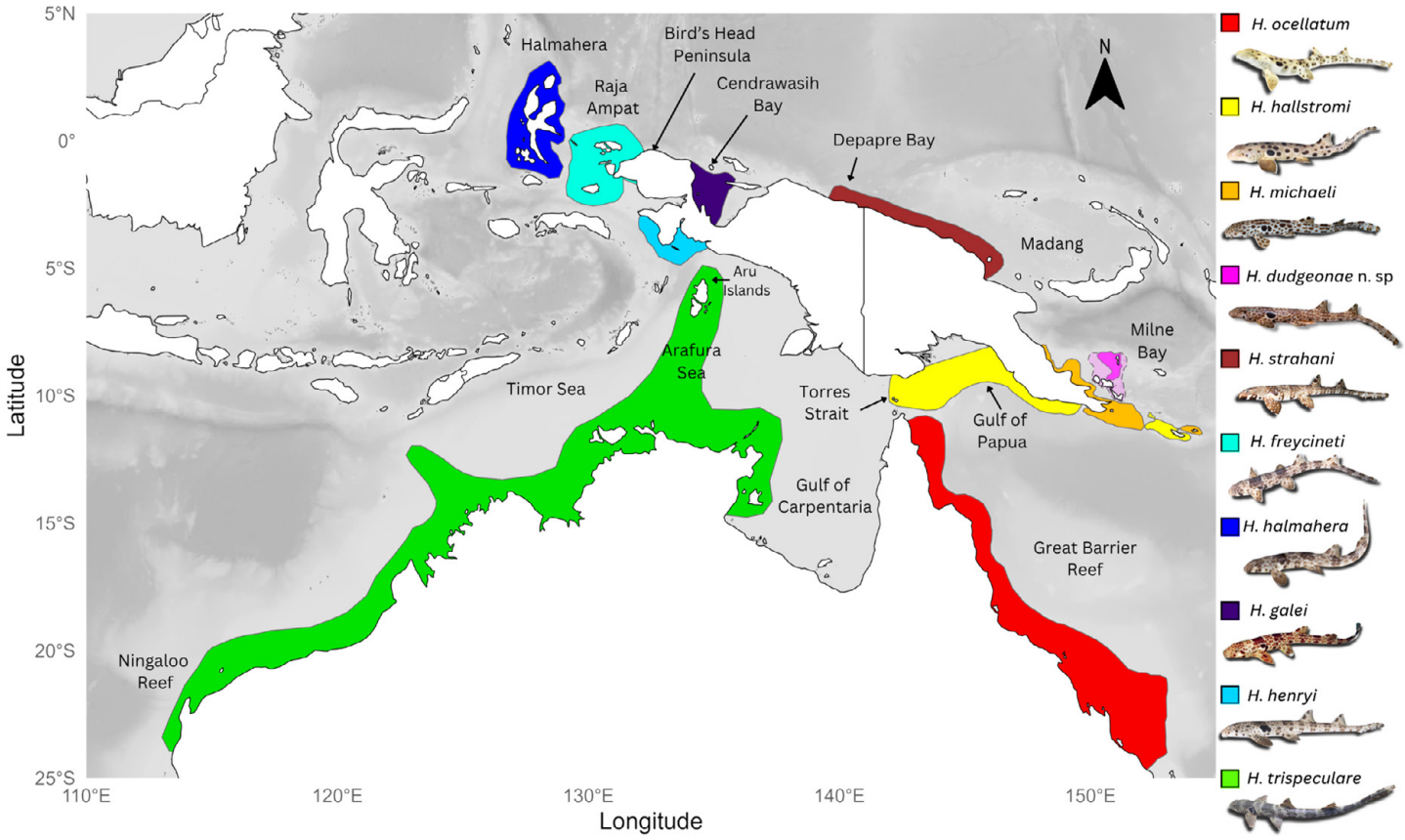

Figure 10. Distribution map for 10 species of *Hemiscyllium*; the distribution of H. *dudgeonae*, n. sp. is included as the known range in solid magenta and the extrapolated distribution as light magenta within dashed line.

Hemiscyllids generally possess a pattern composed of variable-sized brown spots, a series of relatively inconspicuous dark saddles/bars on the back and sides of the body, frequently a prominent post-cephalic ocellus (Fig. 7), and a pair of dark-brown to blackish saddles on the anterior edge of both dorsal fins. Useful diagnostic features include the number, shape, and density of brown spots on the head and body as well as the presence of intervening white spots and dashes, the shape of the post-cephalic ocellus, the presence of proximal dark markings, and any unusual dark markings on the ventral surface of the head. Well-demarcated intervening white spots and dashes on the side of the body (Fig. 11A) are diagnostic for *H. dudgeonae*. Only three other species show white markings, but two, *H. galei* and *H. halmahera*, have relatively few, widely separated white spots (Fig. 11C & D), and *H. strahani* has much wider dash-like markings (Fig. 11B). Moreover, *H. strahani* differs in having distinctive head markings (Fig. 12) and lacks a post-cephalic ocellus (Fig. 7I).

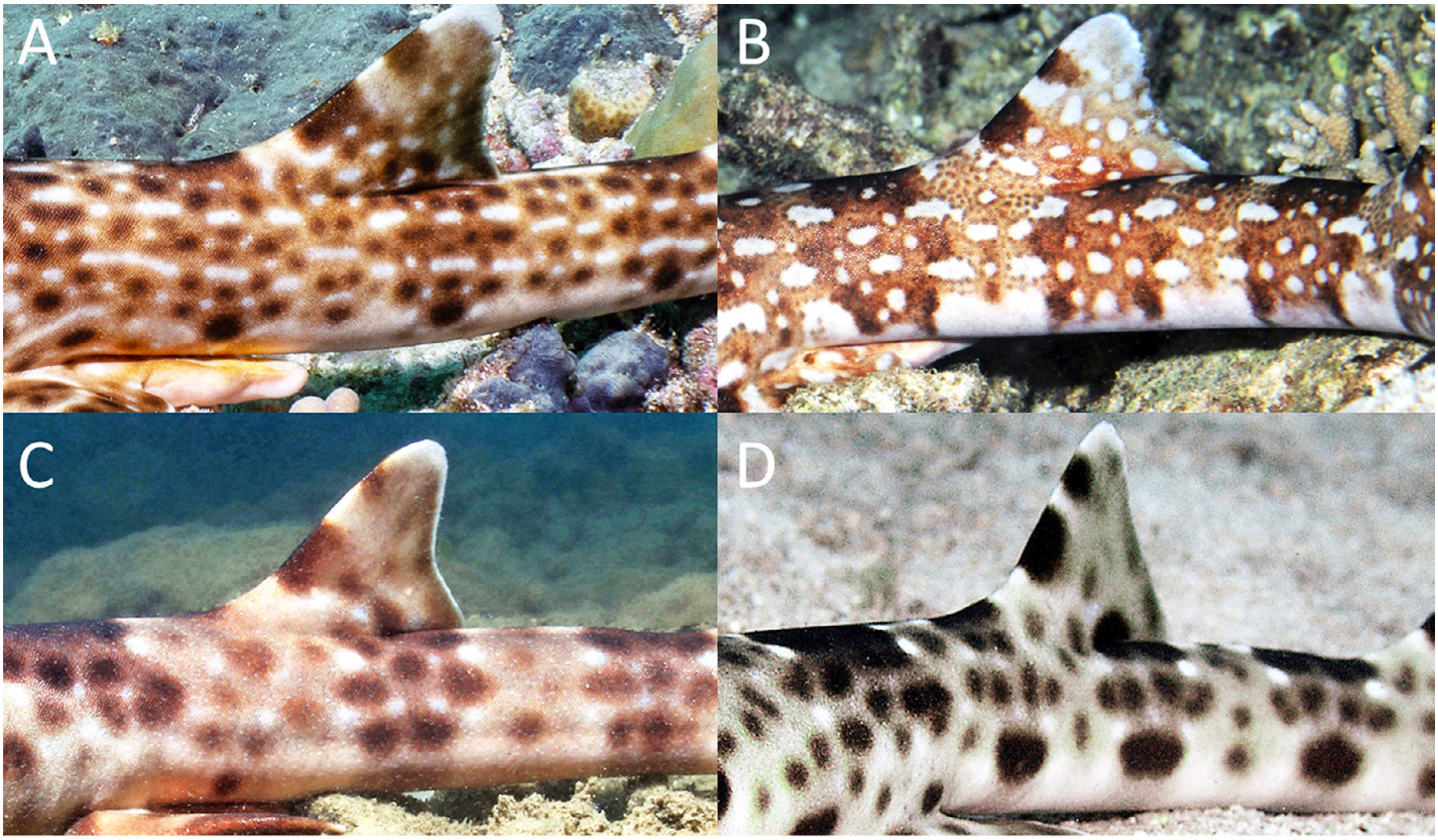

Figure 11. *Hemiscyllium* spp. mid-body markings: A) *H. dudgeonae,* B) *H. strahani*, C) *H. halmahera*, D) *H. galei* (M.V. Erdmann, except D by G.R. Allen).

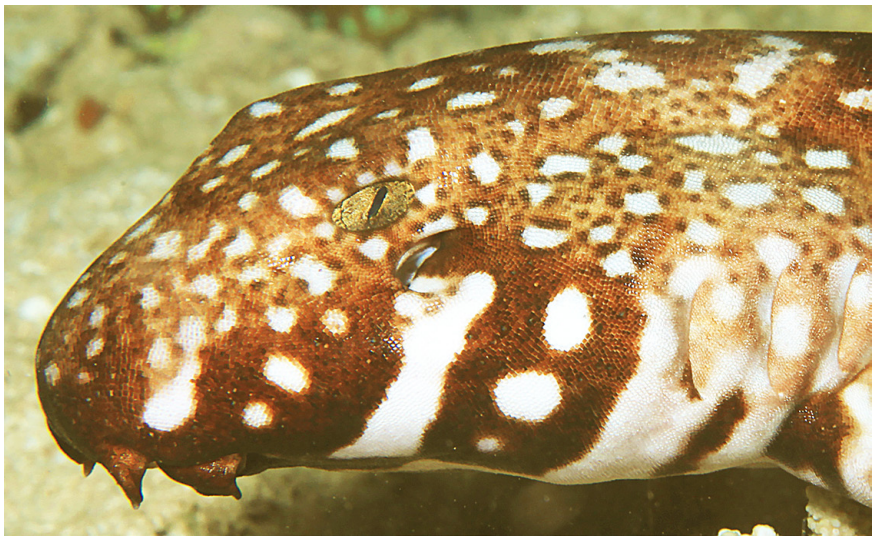

Figure 12. *Hemiscyllium strahani*, adult, Jayapura, papua Province, Indonesia (M.V. Erdmann).

The overall pattern of the new species is most similar to that of *H. michaeli*, particularly the density of brown spots combined with the size and shape of the post-cephalic ocellus (compare Fig. 7F & Fig. 7J–L). However, *H. michaeli* differs in having clusters of brown spots that form a dense covering of leopard-like markings (Fig. 13A) and lacks intervening white spots and dashes. It also differs in lacking the more-or-less isolated pair of large dark spots, one just behind the spiracle, and the other directly below that is surrounded by a broad white area, characteristic of *H. dudgeonae*.

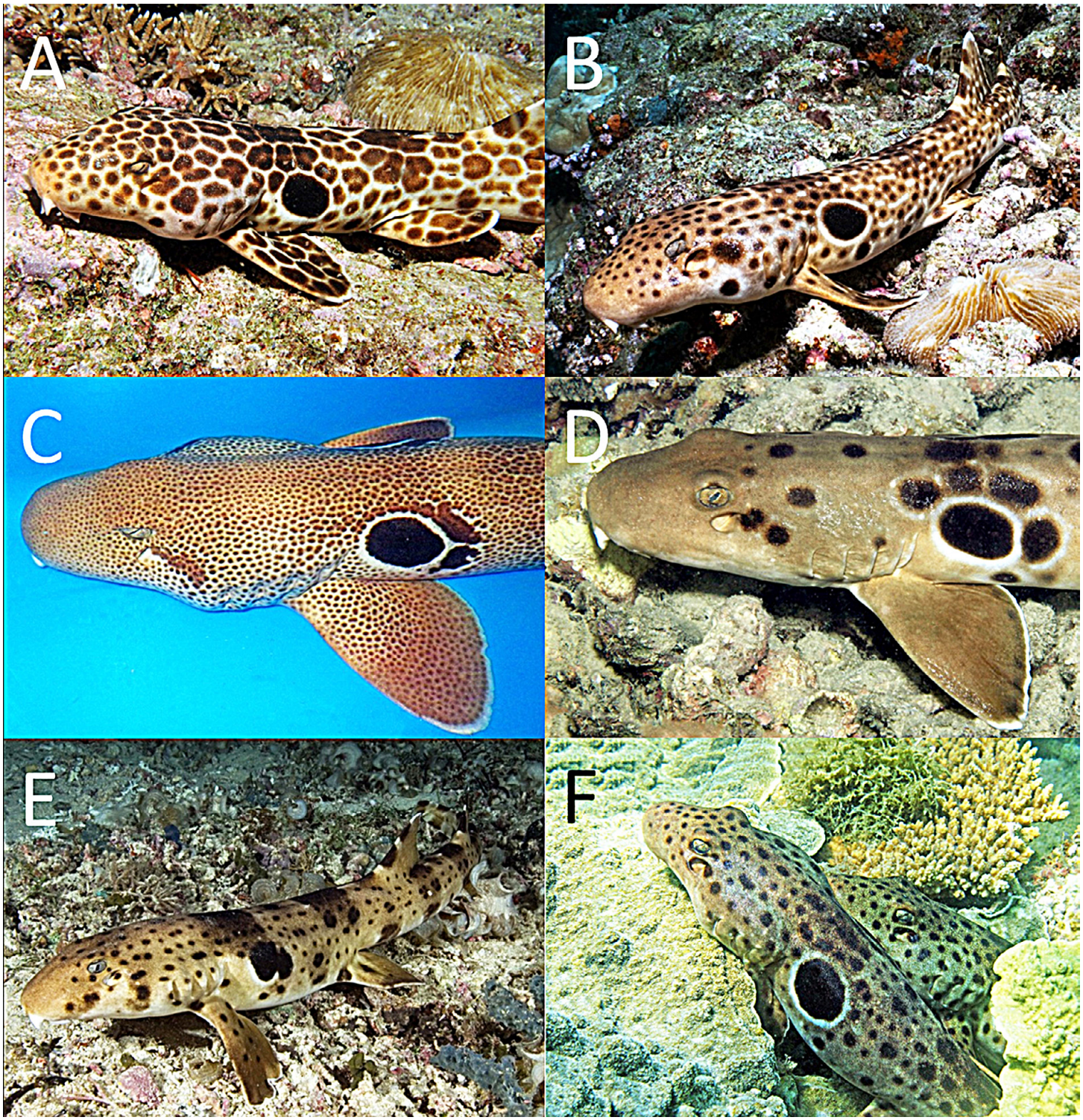

Figure 13. *Hemiscyllium* spp., features in Key: A) *H. michaeli,* B) *H. dudgeonae*, C) *H. trispeculare*, D) *H. hallstromi*, E) *H. henryi* & F) *H. ocellatum* (G.R. Allen, except B by M.V. Erdmann & F by A. Lewis).

Key to the species of *Hemiscyllium*

1a. Ventral surface of head with extensive dark brown markings (Fig. 14A; northern New Guinea) ... ***H. strahani***

1b. Ventral surface of head without extensive dark brown markings, mainly plain white or with a pair of large dark spots 2

2a. Post-cephalic marking lacks distinct ocellus (Fig. 14C) 3

2b. Post-cephalic marking includes a large distinct ocellus (Fig. 14D) 5

3a. Lower side with a horizontal row of 7 or 8 large, round to horizontally ovate, dark spots (14C; Cenderawasih Bay, West Papua, Indonesia) ……..... ***H. galei***

3b. Lower side without a row of large dark spots 4

4a. Ventral surface of head with a pair of large dark spots (Fig. 14B); scattered, small white spots on body; snout region of adult with only a few small dark spots (Fig. 14E; Halmahera Island, Indonesia) ..... ***H. halmahera***

4b. Ventral surface of head without a pair of large dark spots (Fig. 14B); no small white spots on body; snout region of adult with numerous small dark spots (Fig. 14F; Raja Ampat Islands, South West Papua, Indonesia) ..... ***H. freycineti***

5a. Head, body, and fins covered with polygonal, leopard-like spots (Fig. 13A; eastern Papua New Guinea, Tufi to Milne Bay) ..... ***H. michaeli***

5b. Head, body, and fins covered with numerous, round, dark spots, not polygonal and leopard-like) 6

6a. Head and most of body with brown spots interspersed with white spots and dashes (Figs. 11A & 13B: D'Entrecasteaux and Trobriand Islands, Papua New Guinea) .....……..... ***H. dudgeonae*, n. sp.**

6b. Head and most of body with brown spots without interspersed white spots and dashes 7

7a. Preorbital snout with a dense network of small brown spots (Fig. 13C; northern Australia and Aru Islands, Indonesia) ..... ***H. trispeculare***

7b. Preorbital snout with none or few dark spots (Figs. 13D & E) 8

8a. Post-cephalic ocellus surrounded by large black spots; dark spots usually absent on head in front of and below eyes; many body spots at least twice eye-size (Fig. 13D; southeastern Papua New Guinea) ….....……..... ***H. hallstromi***

8b. Post-cephalic ocellus surrounded by relatively small spots; at least a few spots usually present on head in front of and below eyes; most body spots less than twice eye-size 9

9a. Post-cephalic ocellus usually composed of double, merged ocelli surrounded by a poorly defined white halo (Figs. 7L & 13E; Fakfak and Kaimana, South West Papua, Indonesia) ……..... ***H. henryi***

9b. Post-cephalic ocellus composed of a single large round spot surrounded by a distinct white halo (Figs. 7E & 13F; Queensland, Australia) .....……..... ***H. ocellatum***

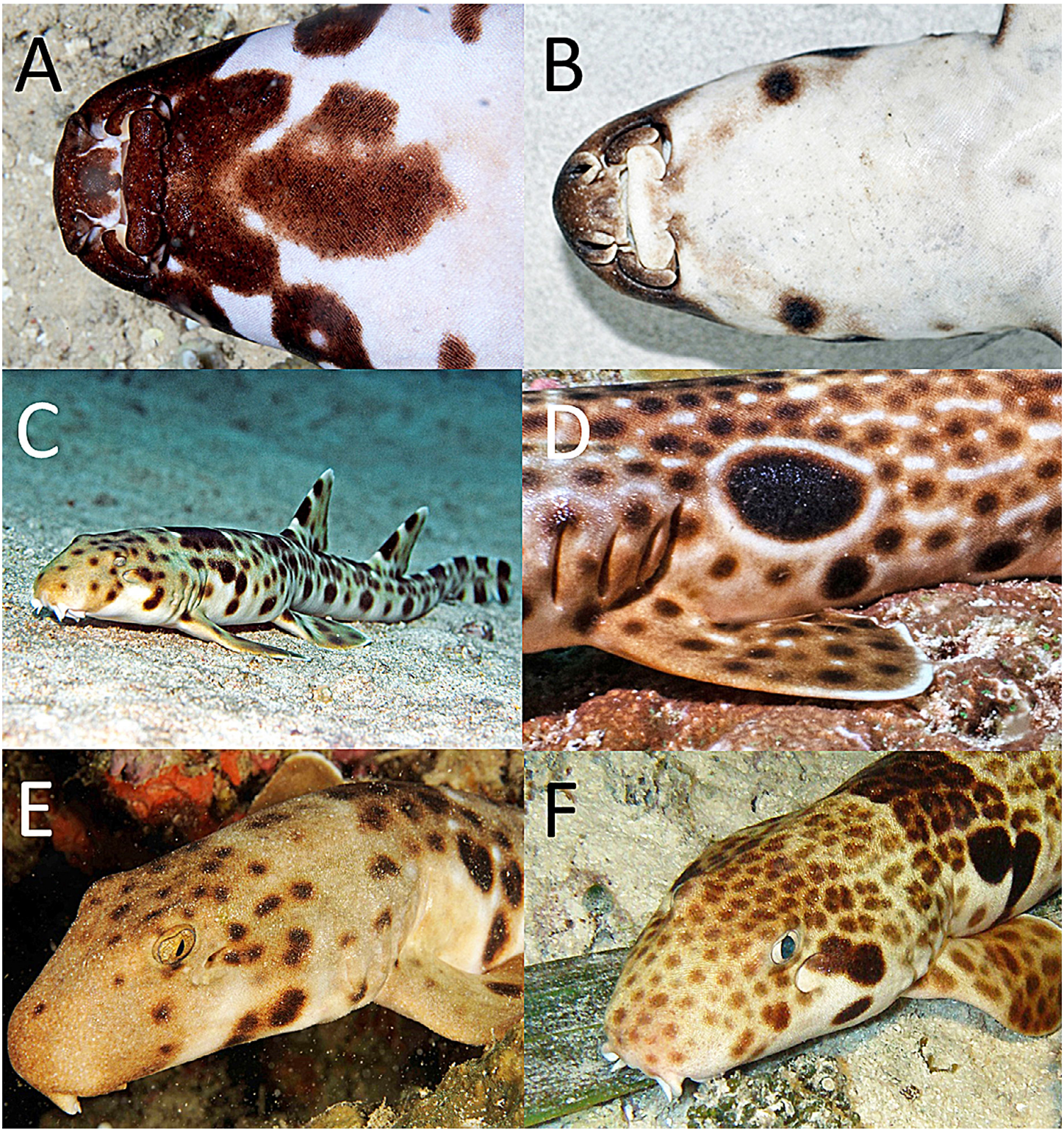

Figure 14. *Hemiscyllium* spp., features in Key: A) *H. strahani,* B) *H. galei*, C) *H. galei*, D) *H. dudgeoni*, E) *H. halmahera* & F) *H. freycineti* (M.V. Erdmann, except B & C by G.R. Allen & E by J. Yonover).

Phylogenetic results for the new species. Genetic analyses were conducted using both the mitochondrial ND4 gene and genome wide SNPs. It was found that *H. dudgeonae* differed significantly from all other described hemiscylliid species with the exception of *H. michaeli* when assessing the ND4 gene. Moreover, *H. dudgeonae* formed a shallow clade with 64% bootstrap support within the *H. michaeli* clade (Fig. 15). The 12 *H. dudgeonae* individuals sampled had identical haplotypes, indicating no structure detected among the three locations sampled. The minimum mean between-group pairwise distances comparing *H. dudgeonae* and the remainder of the genus ranged from 0.15%–4.93%, with the smallest distance to *H. michaeli* and the largest from *H. strahani* (Table 2).

While the ND4 gene indicates a shallow, perhaps recent split from *H. michaeli*, further investigation using SNPs strongly supports the separation of *H. dudgeonae* from other members of the genus (Fig. 16). All 12 individuals were once again compared to samples from each of the remaining 9 *Hemiscyllium* species. The PCoA showed a tight and separate clustering of *H. dudgeonae* individuals (Fig. 16), which is further supported by pairwise FST values ranging from 0.741 to 0.918 when compared to other species within the genus (Table 3). Fixed allele differences ranged from 12% (*H. strahani* and *H. michaeli*) to 22% (*H. henryi* and *H. trispeculare*) when *H. dudgeonae* was compared to other species (Table 4).

ND4 phylogeny of hemiscyllids. A total of 96 *Hemiscyllium* individuals and one *C. punctatum* were sequenced using the ND4 marker across 20 locations, with a trimmed sequence length of 678 bp. The consensus tree followed that of Dudgeon et al. (2020), with *H. strahani* as the most basal followed by *H. ocellatum*, with the remaining species clustering into two main clades: the Indonesian endemics (*H. halmahera*, *H. galei*, *H. henryi*, and *H. freycineti*), and *H. hallstromi*, *H. trispeculare*, and *H. michaeli*. All *H. dudgeonae* samples clustered as a shallow clade within *H. michaeli*. However, a single sample of *H. michaeli* (HM01) from Sideia Island, which is geographically separated from the known range of *H. dudgeonae* by approximately 130 km and multiple large habitat disjunctions, was also present within this shallow clade (Fig. 15). Checks were run including re-extracting and re-sequencing the sample, however the results were consistent.

The sample from Far North Queensland grouped within a monophyletic clade with *H. hallstromi* specimens from the Calvados Chain and Port Moresby, and not with the *H. ocellatum* samples. Additionally, the three samples from Rossel Island formed a separate, basal clade from the rest of *H. michaeli* (and the *H. dudgeonae*) with 96% bootstrap support (Fig.15). The minimum pairwise distances between groups, not inclusive of the

TABLE 2

Pairwise distance summary of 97 *Hemiscyllium* specimens relative to the outgroup *Chiloscyllium punctatum* calculated with Neighbor-Joining Kimura 2-parameter analysis and 1,000 Bootstraps of the NADH dehydrogenase subunit 4 (ND4) region (678 sites)

n=number of samples per group, Var.=maximum variation within groups (%), and matrix of minimum distance between groups (%; grey)

Group	Species	Location	n.	Var.	2	3	4	5	6	7	8	9	10	11
1	*H. dudgeonae* n. sp.	Amphlett Islands PNG	12	0	0.15	1.64	3.34	1.65	2.41	2.41	2.72	1.95	4.93	14.33
2	*H. michaeli*	Milne Bay & Oro, PNG	27	1.35	-	1.65	3.18	1.65	2.41	2.41	2.72	1.95	4.61	13.96
3	*H. hallstromi*	Port Moresby & Milne Bay, PNG	18	1.39		-	3.34	1.50	2.41	2.11	2.41	1.80	4.61	13.05
4	*H. ocellatum*	GBR, AUS	6	0.74			-	3.66	3.66	3.66	4.30	3.18	4.29	13.03
5	*H. trispeculare*	NT & Aru	6	1.04				-	2.88	2.57	3.20	2.41	5.27	13.41
6	*H. henryi*	Triton Bay	4	0					-	1.19	2.11	2.11	5.26	13.21
7	*H. freycineti*	Raja Ampat	6	0.29						-	1.19	2.11	4.94	13.22
8	*H. galei*	Cenderawasih Bay	7	0							-	2.73	5.60	13.60
9	*H. halmahera*	Halmahera	4	0.59								-	4.77	13.39
10	*H. strahani*	Depapre Bay	6	0									-	12.07
11	*C. punctatum*		1	n/a										-

TABLE 3

SNPs raw fixed differences (lower) and the percent of fixed differences (upper) calculated for Dataset B

Non-significant p values calculated (alpha=0.05) for the observed fixed differences with 100 replications to undertake in the simulation to estimate probability of false positives are denoted with a *

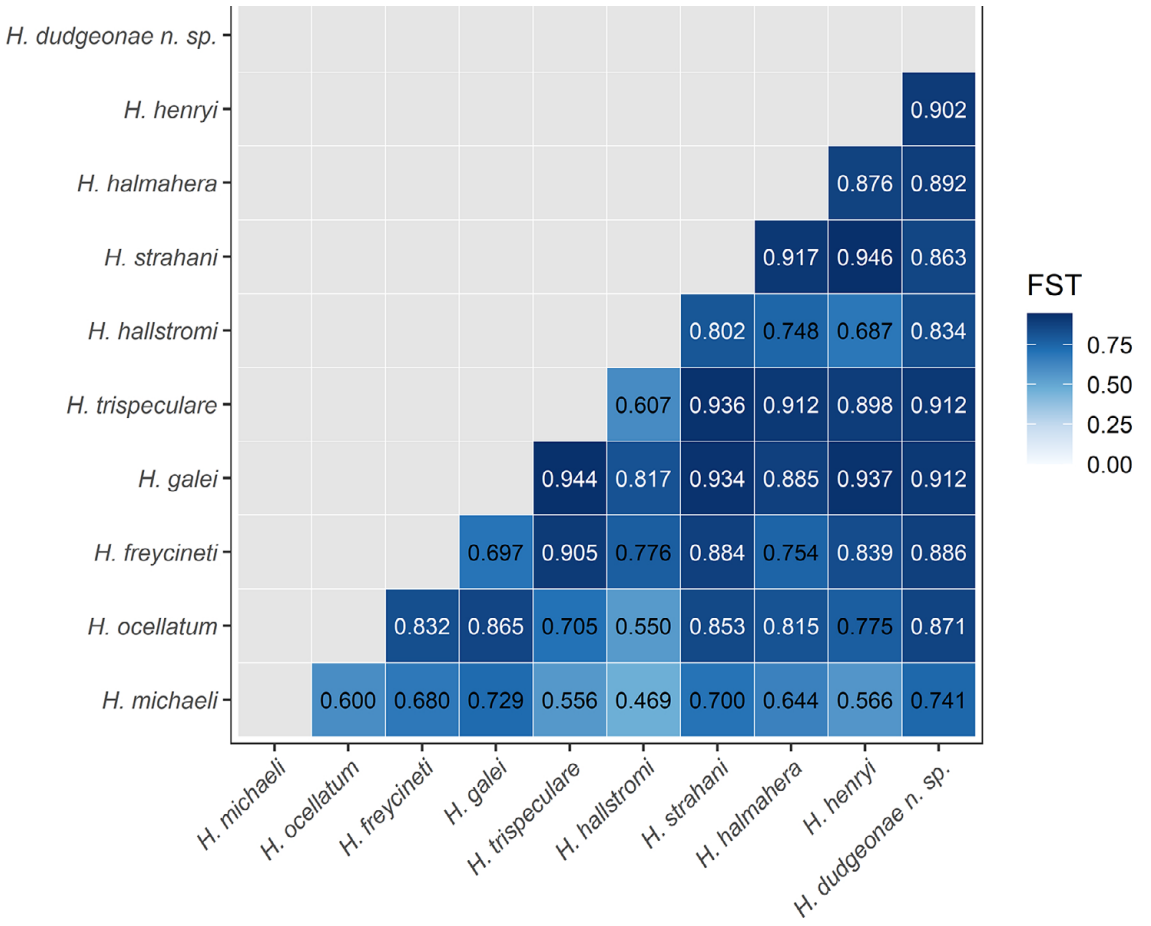

TABLE 4

SNPs raw fixed differences (lower) and the percent of fixed differences (upper) calculated for Dataset B

Non-significant p values calculated (alpha=0.05) for the observed fixed differences with 100 replications to undertake in the simulation to estimate probability of false positives are denoted with a *

Group	Species	1	2	3	4	5	6	7	8	9	10
1	*H. dudgeonae* n. sp.	0	17	19	17	18	22	12	21	12	22
2	*H. freycineti*	1039	0	2	15	6	13	12	19	13	20
3	*H. galei*	1143	141	0	17	8	15	14	21	15	22
4	*H. hallstromi*	1028	922	1038	0	15	13	0*	0*	18	4
5	*H. halmahera*	1117	379	508	920	0	12	12	19	15	20
6	*H. henryi*	1327	764	909	795	727	0	11	16	20	18
7	*H. michaeli*	709	730	845	6*	731	644	0	3	14	4
8	*H. ocellatum*	1253	1142	1271	23*	1132	994	157	0	21	7
9	*H. strahani*	739	790	899	1080	886	1222	825	1307	0	23
10	*H. trispeculare*	1340	1240	1371	244	1222	1069	228	410	1387	0

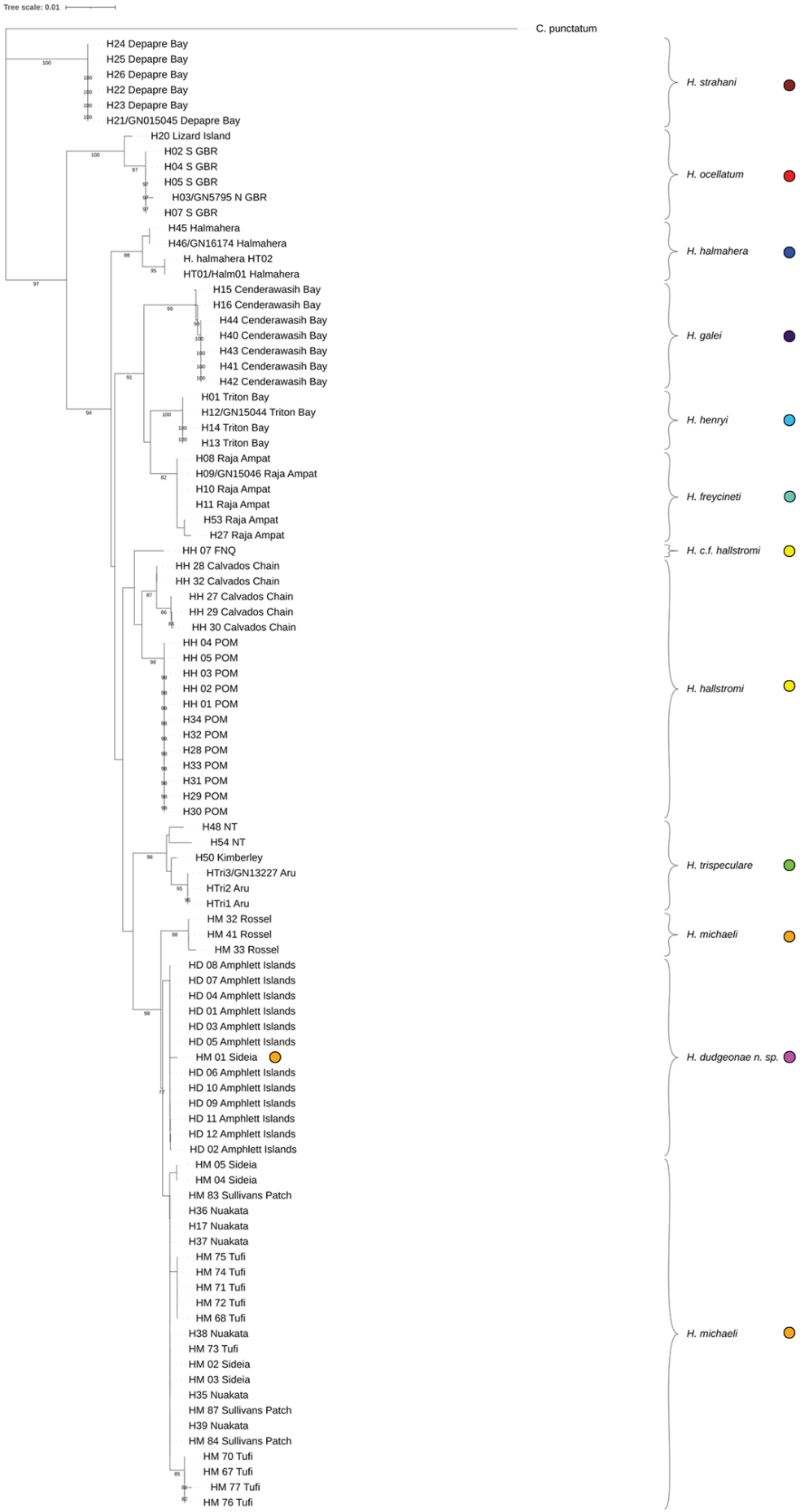

Figure 15. Neighbor-Joining phylogenetic tree for *Hemiscyllium* spp., 1,000 bootstraps of the mt DNA NADH dehydrogenase subunit 4 (ND4) sequence (678 sites), values on branches are bootstrapping percentages (shown only for over 70%)

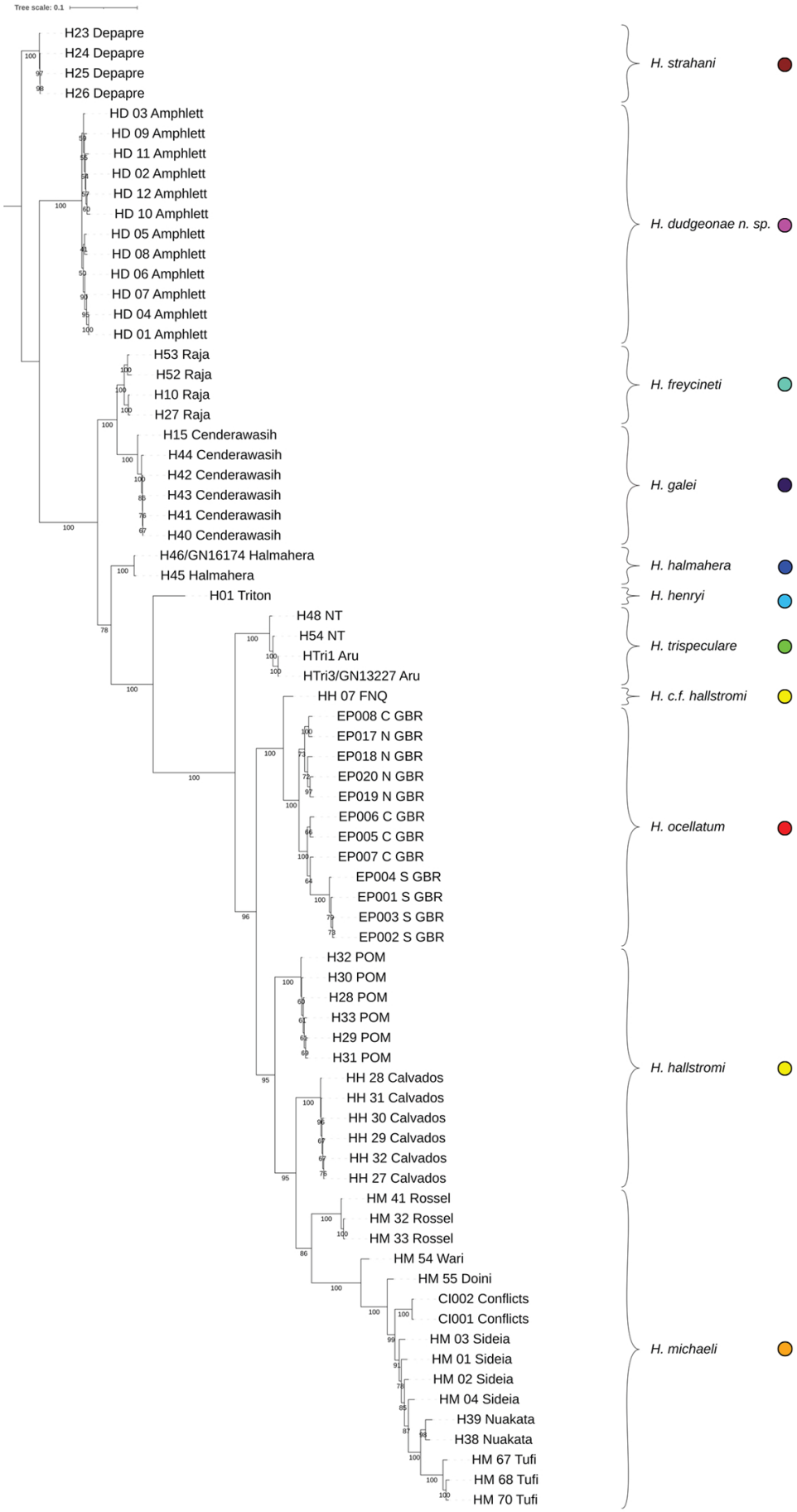

Figure 16. IQTree (Consensus tree) of *Hemiscyllium* spp. based on 6096 loci and 74 individuals in the SNPs Dataset B; the tree is rooted at *H. strahani*. Calculated based on the model of best-fit GTR+F+G4 according to AIC scores (supp. Table 3) and 1,000 ultrafast bootstraps, values on branches are bootstrapping percentages (shown only for over 70%).

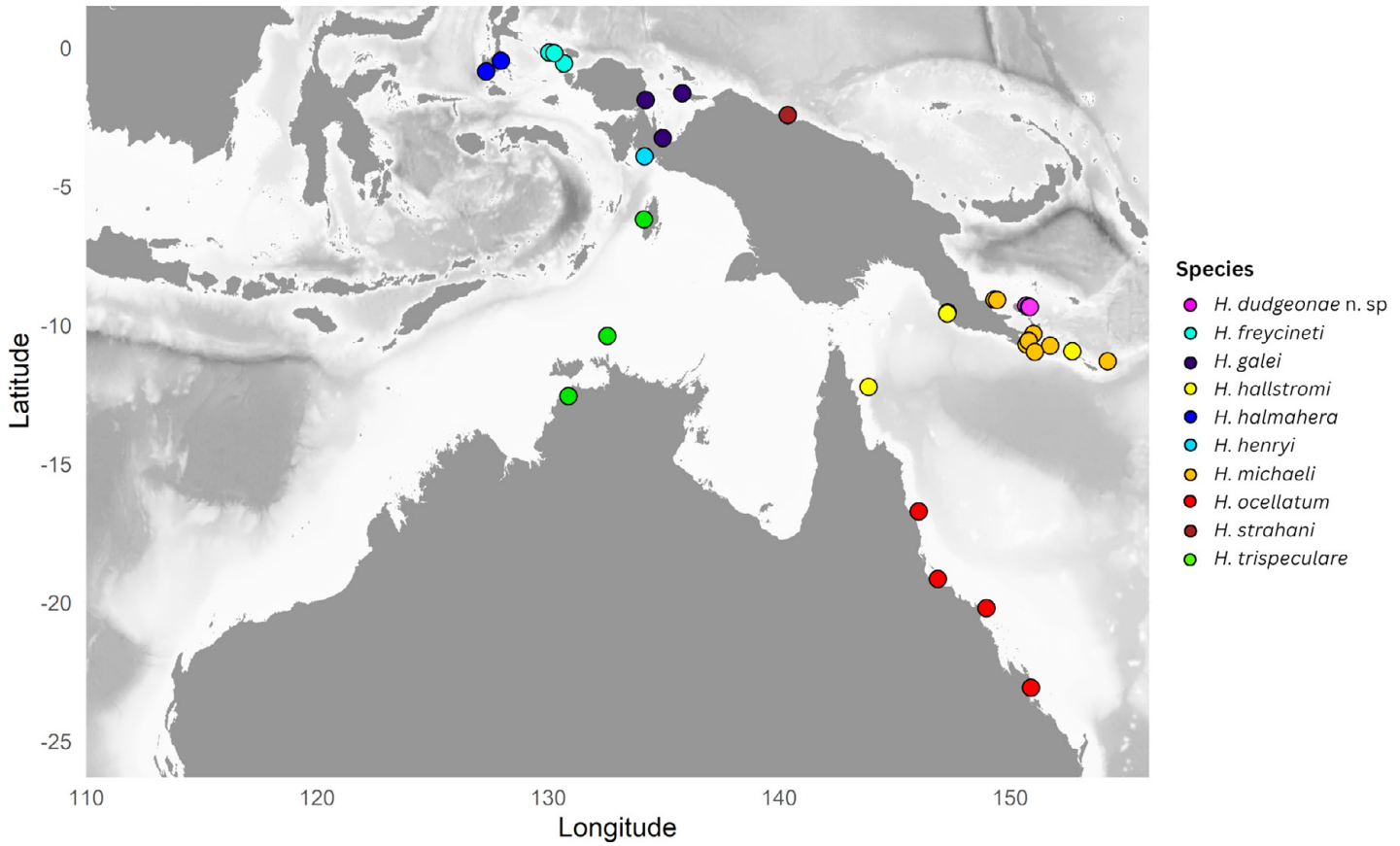

Figure 17. Map showing distribution of sampling locations for *Hemiscyllium* species used for SNPs analysis for dataset B.

outgroup, ranged from 0.15% (*H. michaeli* vs. *H. dudgeonae*) to 5.6% (*H. galei* vs. *H. strahani*). Species that were closer geographically typically displayed smaller pairwise distances between groups (Table 2, Fig 17). Intraspecific variation was observed in 7 of the 10 species and the maximum within-group variation ranged from zero to 1.39%. For the species collected from smaller geographic distances or without habitat disjunctions present, no pairwise divergence was observed: i.e., in *H. dudgeonae*, *H. henryi*, *H. galei*, and *H. strahani*. Within-group variation was present in *H. hallstromi* (1.39%) and *H. michaeli* (1.35%) followed by *H. trispeculare* (1.04%) and *H. ocellatum* (0.74%; Table 2). This within-group variation was explored in more detail for *H. hallstromi* and *H. michaeli*. Within *H. michaeli*, the Rossel Island samples had 0.74% variation, and similar variation was present across major geographic groupings in *H. hallstromi*: 0.74% (Port Moresby vs. Calvados Chain), 1.19% (FNQ vs. Port Moresby), and 1.04% (FNQ vs. Calvados) (Table 5).

SNP genotyping analysis of hemiscyllids. A total of 125,845 SNP loci were detected from 370 individuals, including 14 replicates from 26 locations. Filtering criteria resulted in a total of 6623 loci and 353 individuals in Dataset A. The subset Dataset B comprised 74 individuals from 21 locations with 6106 loci that were used for phylogenetic analysis (Supp. Table 1).

The PCoA for dataset B showed 34.6% of the variation on axis 1 and 16.7% on axis 2. The variation on both axes was driven by species groupings (Fig. 18 A & B). All species were tightly grouped based on the species, including *H. dudgeonae*, with the exception of *H. hallstromi* and *H. michaeli*. These species displayed within-species variation which seem to be driven by the FNQ sample for *H. hallstromi*, and Rossel Island samples for *H. michaeli* (Table 6). These trends remained when comparing axis 1 to axis 3 (12.8%), although *H. dudgeonae* grouped closer to *H. strahani*.

Similar to the ND4 gene, the SNPs consensus ML tree based on the model of best fit (GTR+F+G4) showed strong support for species-level differences (Supp. Table 3; Fig 16). While some trends were consistent between analyses, such as the Rossel Island individuals grouping out separately from the remainder of *H. michaeli*, some interesting differences between methods were noted. The SNP consensus tree clearly separated *H. dudgeonae* from *H. michaeli*, with *H. dudgeonae* as the second most basal species following *H. strahani*. Additionally,

TABLE 5

Pairwise distance summary of 97 *Hemiscyllium* specimens relative to the outgroup *Chiloscyllium punctatum* with *H. michaeli* & *H. hallstromi* broken into sub-groups. Calculated using Neighbor-Joining Kimura 2-parameter analysis and 1,000 Bootstraps of the NADH dehydrogenase subunit 4 (ND4) region of the mitochondrial genome (678 sites).

n=number of samples per group, Var.=maximum variation within groups (%), and matrix of minimum distance between groups (%; grey)

Group	Species	Location	n.	Var.	2a	2b	3a	3b	3c	4	5	6	7	8	9	10	11
1	*H. dudgeonae* n. sp.	Amphlett Islands PNG	12	0	0.15	0.74	1.8	1.64	1.8	3.34	1.65	2.41	2.41	2.72	1.95	4.93	14.33
2a	*H. michaeli*	Milne Bay & Oro, PNG	24	1.35	-	0.74	1.8	1.65	1.8	3.34	1.65	2.41	2.41	2.72	1.95	4.77	13.96
2b	*H. michaeli* ROS	Rossel Island	3	1.48		-	2.26	2.1	2.26	3.18	1.95	2.88	2.88	3.19	2.41	4.61	14.34
3a	*H. hallstromi* POM	Port Moresby	12	1.39			-	0.74	1.19	3.34	1.65	2.41	2.11	2.41	2.26	4.77	13.05
3b	*H. hallstromi* CALV	Calvados Chain, Sudest, Deboyne Group, Milne Bay	5	0.31				-	1.04	3.5	1.5	2.57	2.26	2.57	1.8	4.61	13.24
3c	*H.* cf. *hallstromi* FNQ	FNQ	1	n/a					-	3.03	1.95	2.41	2.11	2.72	1.95	4.45	13.05
4	*H. ocellatum*	GBR, AUS	6	0.74						-	3.66	3.66	3.66	4.3	3.18	4.29	13.03
5	*H. trispeculare*	NT & Aru	6	1.04							-	2.88	2.57	3.2	2.41	5.27	13.41
6	*H. henryi*	Triton Bay	4	0								-	1.19	2.11	2.11	5.26	13.21
7	*H. freycineti*	Raja Ampat	6	0.29									-	1.19	2.11	4.94	13.22
8	*H. galei*	Cenderawasih Bay	7	0										-	2.73	5.6	13.6
9	*H. halmahera*	Halmahera	4	0.59											-	4.77	13.39
10	*H. strahani*	Depapre Bay	6	0												-	12.07
11	*C. punctatum*		1	n/a													-

TABLE 6

SNPs raw fixed differences (lower) and % of fixed differences (upper) calculated for Dataset B with *H. michaeli* & *H. hallstromi* broken into sub-groups. Non-significant p values calculated for the observed fixed differences with 100 replications to undertake in the simulation to estimate probability of false positives are denoted with a ** if p = 1, or * if p = 0.0001

Group	Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*H. dudgeonae* n. sp.	0	17	19	23	23	24	18	22	12	23	21	12	22
2	*H. freycineti*	1039	0	2	22	22	22	6	13	13	22	19	13	20
3	*H. galei*	1143	141	0	24	24	24	8	15	15	24	21	15	22
4	*H. hallstromi* CALV	1423	1359	1486	0	10	5	22	21	3	6	8	25	11
5	*H.* cf.*hallstromi* FNQ	1419	1325	1458	601	0	6	22	19	5	11	1	25	9
6	*H. hallstromi* POM	1441	1343	1472	325	393	0	22	20	2	8	5	25	9
7	*H. halmahera*	1117	379	508	1370	1319	1333	0	12	13	22	19	15	20
8	*H. henryi*	1327	764	909	1253	1178	1198	727	0	12	20	16	20	18
9	*H. michaeli*	757	789	910	172*	288	114**	795	710	0	3	4	14	5
10	*H. michaeli* ROS	1389	1356	1480	349	695	506	1361	1245	192	0	9	25	12
11	*H. ocellatum*	1253	1142	1271	483	47**	311	1132	994	220	569	0	21	7
12	*H. strahani*	739	790	899	1537	1494	1527	886	1222	884	1515	1307	0	23
13	*H. trispeculare*	1340	1240	1371	682	541	569	1222	1069	296	737	410	1387	0

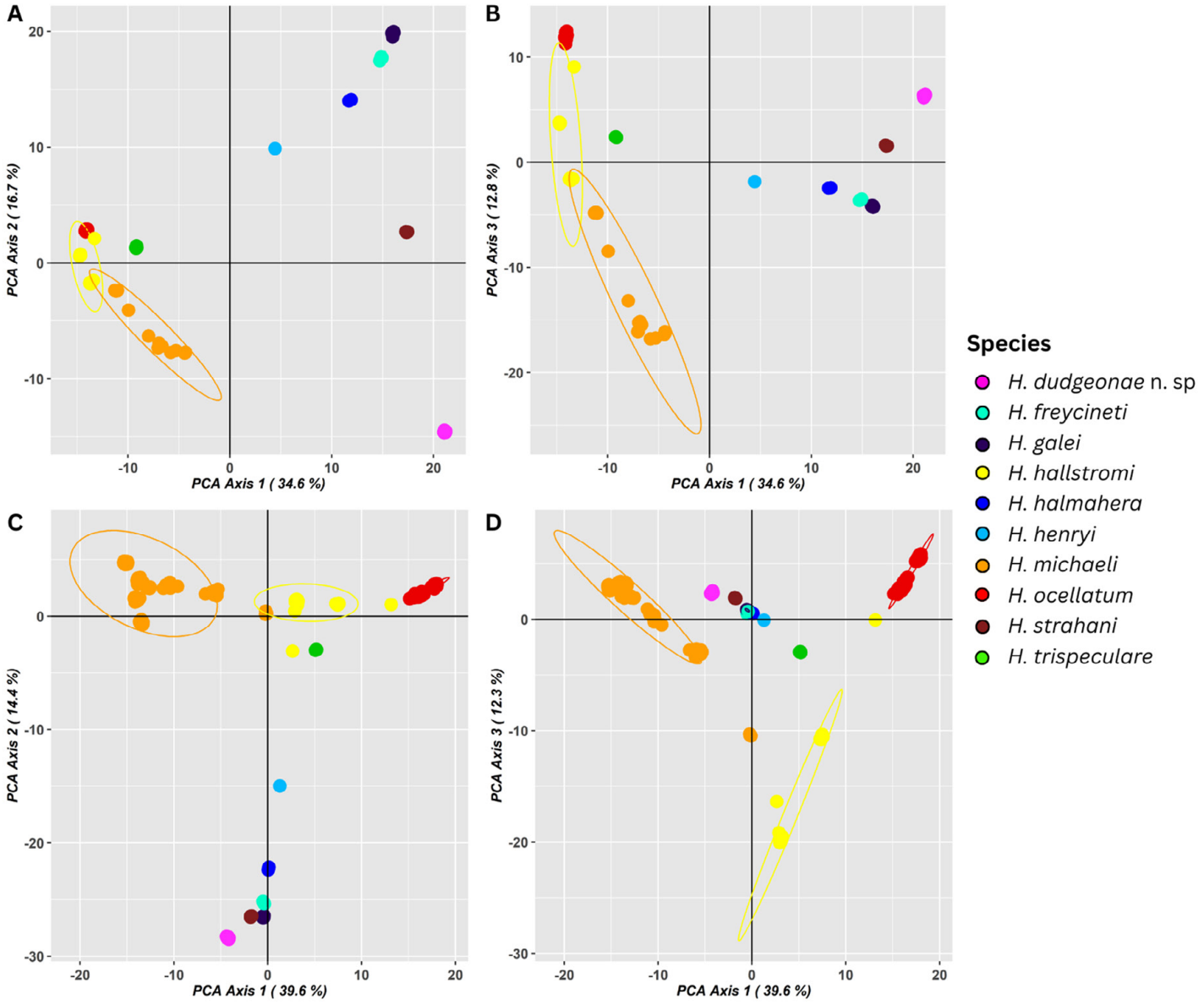

Figure 18. Principal components analysis (PCoA) plotted for *Hemiscyllium* species: A & B) based on the SNPs Dataset B consisting of 74 individuals and 6106 loci from 24 locations a) Axes 1 and 2; b) Axes 1 and 3; C & D) based on the Dataset A consisting of 353 individuals and 26 locations and 6613 loci a) Axis 1 vs. 2; b) Axis 1 vs. 3.

the sample from Sideia Island was clearly in the *H. michaeli* clade, not with *H. dudgeonae.* Additionally, the sample from Far North Queensland instead grouped within the monophyletic tree for *H. ocellatum* rather than *H. hallstromi* as identified by the ND4 gene.

Further, the SNPs clearly identified fine scale intraspecific variation between sampling locations for *H. hallstromi*, *H. michaeli*, *H. ocellatum* and *H. trispeculare* suggesting population structuring at small spatial scales. Intraspecific variation was evident particularly in *H. hallstromi* and *H. michaeli* despite the distribution representing similar, if not smaller, geographic ranges when compared to *H. trispeculare* and *H. ocellatum* (Fig. 18 C & D). Pairwise FST analysis values between species ranged from 0.469–0.946 (Table 3). For *H. dudgeonae*, pairwise FST values ranged from 0.749 (*H. dudgeonae* vs. *H. michaeli*) to 0.912 (*H. dudgeonae* vs. *H. galei* & *H. trispeculare*) supporting *H. dudgeonae* as a new species. Comparatively, the species with the lowest pairwise FST values were *H. michaeli* and *H. hallstromi* (0.469), and *H. hallstromi* and *H. ocellatum* (0.55). The percent of fixed allele differences ranged from none (*H. hallstromi* vs. *H. michaeli* and *H. hallstromi* vs. *H. ocellatum*) to 23% (*H. strahani* vs. *H. trispeculare*). While the raw fixed differences were low for *H. hallstromi* vs. *H. michaeli* (6) and *H. hallstromi* vs. *H. ocellatum* (23), further investigation suggested that these were separate OTUs (Table 4)

Discussion

This study has identified a greater complexity in the distributions of walking shark species endemic to eastern PNG than previously identified. We used a combination of distinct color patterns and genetic methods to describe a new species *H. dudgeonae* from the Amphlett Islands in Milne Bay and update the species distributions of *H. hallstromi* and *H. michaeli*. Additionally, we present evidence of possible cryptic speciation which requires further investigation, discuss potential drivers of speciation, and identify conservation implications.

Describing a new species. The new taxon, *H. dudgeonae* has an apparent restricted distribution that encompasses an approximate area of 7,000 km^2 including the Amphlett Islands (type locality) and Trobriand Islands, lying immediately northward. Currently, *H. dudgeonae* has the smallest known distribution of all walking shark species. Although it is still unconfirmed, despite multiple surveys, it seems likely that this species occurs at the nearby D'Entrecasteaux Islands. The Amphlett Islands, Trobriand Islands and the D'Entrecasteaux Islands are connected by relatively shallow waters (less than 200 m in depth) scattered with shoals, suggesting a lack of habitat disjunctions. Further investigation is required throughout the D'Entrecasteaux Islands and to the east of the Trobriand Islands, across to Woodlark (Muyua) Island to fully establish the distribution of this species.

While *H. dudgeonae* is visually distinct from its congeners, the genetic analysis presented a more complex story. Mitochondrial markers, including the ND4 gene, have proved useful in delineating species differences between geographically separated groups for walking sharks (Dudgeon et al. 2020), however in this study, the ND4 gene alone was insufficient to fully resolve problematic species boundaries prompting the incorporation of genome-wide SNP analysis. The ND4-gene phylogenetic tree showed potential cryptic speciation for *H. dudgeonae*, consistent with a recent divergence. Similar issues have been documented in manta and devil rays, where mitochondrial markers and limited nuclear exons failed to distinguish *Mobula eregoodoo* from *M. kuhlii* (White et al. 2018), yet genome-wide nuclear markers clearly separated the species (Hosegood et al. 2020). These inconsistencies between nuclear and mitochondrial topologies have been attributed to recent and rapid speciation within Mobulidae, increasing the likelihood of incomplete lineage sorting (Hosegood et al. 2020). In the present study, the mitochondrial tree placed *H. dudgeonae* as a shallow clade within *H. michaeli*, including in the lineage one *H. michaeli* individual from Sideia, suggesting introgression or incomplete linage sorting may be occurring. Given the significant geographic barriers including the deep waters of Milne Bay (up to 500 m deep), and the eastern cape, and the D'Entrecasteaux Islands that separate Sideia from the Amphlett Islands, introgression is unlikely. As hemiscyllids have also undergone relatively recent diversification (Dudgeon et al. 2020), incomplete lineage sorting is the more plausible explanation for the observed topological discordance. While the SNPs analysis clearly supports the delineation of *H. dudgeonae* from *H. michaeli*, future studies would benefit from assessing admixture, which was beyond the scope of this study.

A mosaic of distributions. In addition to the description of *H. dudgeonae*, our study reveals a more complex and widespread distribution of walking sharks in eastern PNG than was previously reported by Allen et al. (2016). Our findings suggest *H. michaeli* and *H. hallstromi* both occur in the same general area of Milne Bay Province, but thus far do not appear to exhibit localized sympatric distributions resulting in a non-overlapping mosaic. There are no obvious present-day habitat disjunctions that explain the lack of co-occurrence between these species at the Louisiade Archipelago/Calvados Chain.

Although the precise geographic boundaries between *H. hallstromi* and *H. michaeli* remain uncertain, we are able to provide insights. The geographic break between these species was previously assumed to be Orangerie Bay, which lies on the south coast near the eastern extremity of the mainland (Allen et al. 2016). The bay provides a logical distributional break due to the significant freshwater outflow from the Badila, Sagarai, and Wegulani rivers creating an unsuitable habitat for walking sharks. Nevertheless, the present discovery of *H. hallstromi* east of Orangerie Bay at the Calvados Chain, Deboyne Group and Sudest (Tagula) Island shows an extension of the range for this species.

The range expansion of *H. hallstromi* can be at least partly explained by the presence of nearly continuous, shallow, fringing reef running along the southern edge of the island arc between mainland PNG and Sudest Island, stretching over a linear distance of approximately 350 km. Indeed, the only deep-water breaks over this expanse are the narrow (5–6 km) channels on either side of Bramble Haven Reef (-11.2269°, 152.0098°). While both the mitochondrial and nuclear genetic analysis indicate some level of intraspecific divergence between the Port Moresby and the Milne Bay populations of *H. hallstromi*, it is likely that this reflects genetic structuring due to the large geographic distances separating the populations rather than a case of allopatric speciation. Further investigation spanning the southern reef systems of mainland PNG to Brambles Haven is required to uncover whether the reported break is real or due to limited survey effort. At present, our surveys have not extended west from Orangerie Bay, however we have a photograph of a *H. hallstromi* from Suau (-10.621, 150.017), east of Orangerie Bay (pers. comm., F. Paul). Further areas of interest include Far North Queensland into the Torres Strait, particularly as the only sample collected from Wreck Bay appears to be a potential hybrid of *H. hallstromi* and *H. ocellatum*. Geographically, the Wreck Bay sample is expected to fall within the range of *H. ocellatum* (Allen et al. 2016), yet the ND4 analysis suggests this individual was genetically closer to *H. hallstromi*, but the SNPs suggested it was more closely related to *H. ocellatum* in both the phylogenetic tree and PCoA. More samples across this region are required to fully investigate the potential for backcrossing or cryptic speciation.

Our findings suggest the determinants of the distribution of *H. michaeli* are complex. The species was previously reported from several locations centered around the main water body of Milne Bay (as opposed to Milne Bay Province), ranging northward to the vicinity of Harvey Bay in Oro Province and the Trobriand Islands. However, while we found *H. michaeli* extends into Oro Province, we find the Trobriand Island record is based on a misidentification of *H. dudgeonae* (see paratypes section above). As with *H. hallstromi*¸ both the ND4 gene and SNPs revealed intraspecific variation within *H. michaeli*, with the SNPs indicating some genetic structuring between locations.

The discovery of *H. michaeli* at remote Rossel Island, nearly 400 km from the mainland, is somewhat enigmatic. These individuals appear to be *H. michaeli*, however they are separated from the remainder of that population by *H. hallstromi* in the Deboyne Group, Calvados Chain, and Sudest Island. Indeed, the closest known *H. michaeli* population is at the Conflict Islands, a linear distance of approximately 200 km from Rossel Island. Notably, the Rossel Island population was genetically distinct from the remainder of the *H. michaeli* population using both mitochondrial and nuclear methods. One potential explanation for the genetic distinctiveness of this population is that Rossel Island represents a case of cryptic speciation within *H. michaeli* as both the ND4 gene and SNPs show separation from *H. michaeli* in their respective trees. Cryptic speciation appears to be more frequent among apparently morphologically indistinguishable vertebrates than previously assumed, with mitochondrial and nuclear genetic analyses increasingly uncovering lineages that represent OTUs that are classified as a single species based solely on morphology (Zhang & Wiens 2026). Alternatively, the Rossel Island population may result from an historical hybridization event between *H. hallstromi* and *H. michaeli*. Previous work on *Hemiscyllium* from geographically isolated populations found no genetic overlap between *H. michaeli* and *H. hallstromi*, which show a clear divergence with no haplotype sharing (Dudgeon et al. 2020). However, the increased number and

geographical range of samples used in this study provides greater genetic resolution and improved ability to identify rare variants or undetected structure (Leberg 2002, Nazareno & Jump 2012). The SNP phylogeny places Rossel Island individuals in a monophyletic clade (with 100% bootstrap support) and they cluster between *H. hallstromi* and *H. michaeli* on axes 1 and 2 of the PCoA. While these observations may be due to isolation from the remainder of the population, there is potentially some historical contact related to island movements and the complex geological history in the region (Baldwin et al. 2021, Kraus 2021). Our interpretation remain tentative due to the limited sample size at Rossel Island and the lack of intervening geographic sampling along the southern reef systems: more data are needed to identify ancestral populations and potential hybridization events.

Potential drivers of distributions and speciation. The finding of distributions of both *H. hallstromi* and *H. michaeli* extending into the eastern part of Milne Bay, without any location where the two species co-occur, raises questions regarding the factors that have driven and maintain this mosaic of distributions. There are multiple possible explanations for the observed pattern of distribution. The most likely is that the biodiversity of this region has been promoted by the variety of habitats formed by tectonic activity along the Indo-Australian and Pacific plate margins (Smith & Milsom 1984, Brandl et al. 2024, Oliver et al. 2024). Eastern PNG, including Milne Bay, is a geologically complex region that has been influenced by a long history of subduction, collision and accretion (Baldwin 2012). The region underwent a major geodynamic reconstruction as it moved from compressional to extensional tectonics, with evidence of volcanism occurring from 10–12 My (Webb et al. 2014, Brandl et al. 2024). From about 8 My onwards, there is also evidence of rifting, which likely drove localized uplift along the Woodlark Rise and Louisiade Archipelago (Webb et al. 2014). The Louisiade Archipelago consisted of approximately 11 large islands prior to the last Glacial Maximum (23–19 My), and since then sea levels have risen by about 134 m, creating over 200 island relicts that make up the present-day archipelago (Shaw et al 2020). These processes resulted in a fragmented seascape of islands, deep-water channels, and shoals that could facilitate allopatric speciation through restricted dispersal and isolation. This complex geological history is considered the driver of insular endemism and the explosion of diversity found among a wide variety of taxa within Milne Bay, including amphibians, reptiles, and fishes (Allen & Werner 2002, Kraus 2021, Oliver et al. 2024). Given the low dispersal ability, strong site-association, and restricted habitat preferences of walking sharks, it is likely that they are similarly subject to insular speciation.

The timing of several key geological events aligns with the estimated periods of divergence and speciation within the eastern clade of walking sharks (Dudgeon et al. 2020). For instance, the estimated time of divergence between *H. hallstromi* and *H. michaeli*, around 4.44 Ma, coincides with the westward propagation of the Woodlark Spreading Center opening and the submergence of the Pocklington Rise (Taylor et al. 1999). These events have likely promoted the intraspecific variation observed between the Rossel Island population and the remaining *H. michaeli* population due to long-term geographic isolation resulting in a lack of gene flow. The trend is also observed when comparing the mainland population of *H. hallstromi* to the population at the Calvados Chain, the Deboyne Group, and Sudest Island. The formation of the D'Entrecasteaux Islands between 7 and 2 Ma (Benyshek & Taylor 2021) may have resulted in a barrier to dispersal, contributing to isolation and the divergence of *H. dudgeonae.* While this study does not include divergence-time estimates, the ND4-gene consensus tree shows a shallow split between *H. michaeli* and *H. dudgeonae*, suggesting a relatively recent split between the two species.

While historical tectonic movements offer a plausible mechanism for producing a split in populations, other possibilities are worth considering. One potential explanation is human-mediated translocation during periods of settlement of the Milne Bay Province. Although some islands in the region were likely colonized to some extent in the late Pleistocene (11.7 kya), many islands were not permanently settled until the late Holocene (~2500–500 years ago). Settlement in the region was typically influenced by climatic fluctuations, with initial settlement dating to ~2500 years ago and a more recent secondary settlement ~500 years ago (Shaw et al. 2017, 2020). During this period, there were several well-established marine trade routes connecting communities across southern and eastern PNG through the regular exchange of goods (Dutton 1982, Skelly et al. 2023, Kneppers et al. 2026). Trade items often included food (fish and pigs), pottery, shells, and ceremonial tools (Skelly et al. 2025, Kneppers et al. 2026). While there is no evidence that walking sharks were transported, it is conceivable they may have been translocated incidentally as a food source, potentially accounting for the distributional patterns observed for *H. michaeli* and *H. hallstromi*.

Another potential mechanism for the dispersal and isolation of walking sharks is predator-mediated dispersal. Waterbirds are increasingly recognized as long-distance vectors for the movement of aquatic organisms, transporting fish eggs, amphibians, and plant material between isolated locations via external attachment (exozoochory) or ingestion (endozoochory) (Hirsch et al. 2018, Silva et al. 2019, Garcia et al. 2023). While there is limited information available for seabirds as vectors, is plausible to suggest that seabirds may promote the dispersal of their prey species along movement corridors. Unlike most fish species that produce numerous small eggs, walking sharks deposit one or two large eggs at a time (80–90 mm in length) that are covered in sticky tendrils which are used to anchor the eggs to coral and other three-dimensional structure (Heupel et al. 1999, Allen et al. 2016). Events such as storms and currents are known to occasionally cause eggs to detach from the substrate and move freely through the water column or to wash up on the shoreline and be picked up by seabirds. Given that egg cases of walking sharks undergo sclerotization, or hardening of the surface, to protect the embryo prior to being deposited on the bottom (Nakaya et al. 2020, Wheeler et al. 2025), it is conceivable that an egg may endure transport by a seabird over a long distance. However, the large size of eggs and relatively low frequency of these unlikely events makes the probability of multiple viable eggs being transported between locations, in numbers sufficient to establish and maintain an isolated population that could lead to speciation, quite unlikely.

Conservation implications. At present, 5 of the 9 species of walking shark are classified as threatened with extinction on the IUCN Red List (Dudgeon et al. 2016, VanderWright et al. 2021a, 2021b, 2021c, 2021d). Primarily this is due to their restricted distributions and limited dispersal abilities at all life stages, making the group particularly susceptible to localized threats. In PNG, habitat degradation caused by coastal development, expansion of palm-oil plantations, and climate-change-induced coral bleaching has collectively degraded an estimated 20% of walking shark habitat in the 10 years prior to 2020 (VanderWright et al. 2022). These pressures are compounded by fishing activities, primarily for subsistence fisheries, with some collection of *H. hallstromi* recorded for the aquarium trade (Militz et al. 2018). Currently, *H. michaeli* and *H. hallstromi* are listed as Vulnerable on the IUCN Red List of Threatened Species under criterion B, which assesses species at risk of extinction due to their restricted geographic range in terms of a small area of occurrence (AOO) and/or extent of occurrence (EOO) (Dudgeon et al. 2016, VanderWrightet al. 2021d). The updated geographical distributions and genetic structuring reported here for both species indicate fragmented populations, which is likely to have direct implications for the conservation status of both species.

At present, it is unclear how the simultaneous eastward range extension and northern range contraction will impact the conservation status of *H. michaeli*. Additionally, it is uncertain what is the full extent of the western limits of *H. michaeli* along northern mainland PNG, and whether the large river outflows on either side of Lae represent a species break with *H. strahani*, as postulated by Allen et al (2016). A previously unreported localized pressure on *H. michaeli* populations in the Oro Province is due to the use of walking shark vertebrae in jewelry solely for sale to tourists (author J.-A. B. observation). For *H. hallstromi*, the eastward range expansion has greatly increased both the AOO and EOO, meaning the species will likely be downgraded to Least Concern under criterion B.

Of the three species found in eastern PNG, the newly described *H. dudgeonae* appears to be of the greatest conservation concern. Currently this species has the smallest distribution of any walking shark and has only been confirmed at three sites in the Amphlett Islands and two sites in the Trobriand Islands. In addition to the small AOO and EOO for this species, there are anecdotal reports from cruise-ship visitors and community members that suggest significant subsistence fishing pressure in these areas, potentially placing this species at greater risk of extinction (author J.-A. B. observation). Additionally, no walking sharks were observed at the D'Entrecasteaux Islands despite surveys undertaken at locations identified as sites at which it had once been easy to find walking sharks by community members. Therefore, it seems plausible that this species has already faced extirpation in some locations. These factors, in addition to the threats that other species in the genus face, are likely to result in *H. dudgeonae* being listed as Endangered when assessed for the IUCN Red List.

Some conservation and management practices for walking sharks can be implemented through the fourth goal of the PNG Constitution which mandates the protection of natural resources and the environment for present and future generations. Similarly, under Section 25 of the Fisheries Management (Amendment) Act 2015, the long-term conservation, management, and sustainable use of marine living resources in the country is a fundamental

objective (Government of Papua New Guinea et al. 2021). Although there are overarching legal frameworks that provide some management capabilities, there are currently no species-specific protections in place for walking sharks in PNG through the National Action for Sharks and Rays (2021–2024) or the Fauna (Protection and Control) Act (Kula & George 1996, Government of Papua New Guinea et al. 2021). Given the threats faced by walking sharks in PNG, we recommend listing all walking shark species found in PNG waters under the Fauna (Protection and Control) Act. Providing these protections would mean all 10 species within the genus would have some form of protection (Erdmann & Dudgeon 2024). Our findings of complex distributions and genetically distinct populations with the potential for cryptic speciation or hybridization should also be considered for future management. This is particularly true for localities with strong fishing pressure to prevent localized extirpation. We emphasize that for localized and national-scale management to be effective, ongoing engagement with traditional land and sea-owners is essential.

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S. TABLE 1. Summary information of *Hemiscyllium* samples used in this study including: Species, Identification number (ID), Location, Latitude and Longitude. Additionally, the type of genetic analysis conducted (genome wide single nucleotide polymorphisms (SNPs) or sequencing of the NADH dehydrogenase subunit 4 (ND4) region of the mitochondrial genome ND4), for samples that were used for SNPs analysis, those denoted with a * were used in Dataset B. Finally, samples that were analysed by Shackleton et al. (2022) and Dudgeon et al. (2020) are denoted by ^ and ** respectively.

Species	ID	Country	Location	Latitude	Longitude	SNPs	ND4	GenBank Accession
H. dudgeonae n. sp.	HD_01	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165919
H. dudgeonae n. sp.	HD_02	Papua New Guinea	Amphlett Islands	-9.3484	150.8106	Y*	Y	PZ165920
H. dudgeonae n. sp.	HD_02R	Papua New Guinea	Amphlett Islands	-9.3484	150.8106	Y	N	
H. dudgeonae n. sp.	HD_03	Papua New Guinea	Amphlett Islands	-9.3484	150.8106	Y*	Y	PZ165921
H. dudgeonae n. sp.	HD_04	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165922
H. dudgeonae n. sp.	HD_05	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165923
H. dudgeonae n. sp.	HD_06	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165924
H. dudgeonae n. sp.	HD_07	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165925
H. dudgeonae n. sp.	HD_08	Papua New Guinea	Amphlett Islands	-9.2941	150.6935	Y*	Y	PZ165926
H. dudgeonae n. sp.	HD_09	Papua New Guinea	Amphlett Islands	-9.3347	150.8103	Y*	Y	PZ165927
H. dudgeonae n. sp.	HD_10	Papua New Guinea	Amphlett Islands	-9.3347	150.8103	Y*	Y	PZ165928
H. dudgeonae n. sp.	HD_11	Papua New Guinea	Amphlett Islands	-9.3506	150.8494	Y*	Y	PZ165929
H. dudgeonae n. sp.	HD_12	Papua New Guinea	Amphlett Islands	-9.3506	150.8494	Y*	Y	PZ165930
H. freycineti	H08	Indonesia	Raja Ampat	-0.5560	130.6780	N	Y**	MF740829.1
H. freycineti	H27	Indonesia	Raja Ampat	-0.5560	130.6780	Y*	Y**	MF740830.1
H. freycineti	H53	Indonesia	Raja Ampat	-0.1890	130.2540	Y*	Y**	MF740831.1
H. freycineti	H52	Indonesia	Raja Ampat	-0.1662	130.0416	Y*	N	
H. freycineti	H09/GN15046	Indonesia	Raja Ampat	-0.5560	130.6780	N	Y**	
H. freycineti	H10	Indonesia	Raja Ampat	-0.5560	130.6780	Y*	Y**	
H. freycineti	H11	Indonesia	Raja Ampat	-0.5560	130.6780	N	Y**	
H. galei	H44	Indonesia	Cenderwasih Bay	-1.6300	135.7930	Y*	Y**	MF740843.1
H. galei	H15	Indonesia	Cenderwasih Bay	-1.8800	134.2090	Y*	Y**	
H. galei	H16	Indonesia	Cenderwasih Bay	-1.8800	134.2090	N	Y**	
H. galei	H40	Indonesia	Cenderwasih Bay	-3.2490	134.9590	Y*	Y**	
H. galei	H41	Indonesia	Cenderwasih Bay	-3.2490	134.9590	Y*	Y**	
H. galei	H42	Indonesia	Cenderwasih Bay	-3.2490	134.9590	Y*	Y**	
H. galei	H43	Indonesia	Cenderwasih Bay	-3.2490	134.9590	Y*	Y**	
H. hallstromi	HH_27	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	Y	PZ165937
H. hallstromi	HH_28	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	Y	PZ165938
H. hallstromi	HH_29	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	Y	PZ165939
H. hallstromi	HH_30	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	Y	PZ165940
H. hallstromi	HH_31	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	N	
H. hallstromi	HH_32	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y*	Y	PZ165941
H. hallstromi	HH_33	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y	N	
H. hallstromi	HH_34	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y	N	
H. hallstromi	HH_34R	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y	N	
H. hallstromi	HH_35	Papua New Guinea	Calvados Chain	-10.9433	152.6858	Y	N	
H. hallstromi	HH_36	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_37	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_38	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_39	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_40	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_41	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_42	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_43	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_44	Papua New Guinea	Calvados Chain	-10.9438	152.7117	Y	N	
H. hallstromi	HH_08	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_09	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_10	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_11	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_12	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_13	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_14	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_15	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_16	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_17	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_18	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_19	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_20	Papua New Guinea	Deboyne Islands	-10.7725	152.3796	Y	N	
H. hallstromi	HH_07	Australia	Far North Queensland (FNQ)	-12.2320	143.8638	Y*	Y	PZ165936
H. hallstromi	HH_07R	Australia	Far North Queensland (FNQ)	-12.2320	143.8638	Y	N	
H. hallstromi	H28	Papua New Guinea	Port Moresby (POM)	-9.5330	147.2910	Y*	Y**	MF740840.1
H. hallstromi	HH_01	Papua New Guinea	Port Moresby (POM)	-9.5301	147.0757	Y	Y	PZ165931
H. hallstromi	HH_02	Papua New Guinea	Port Moresby (POM)	-9.5301	147.0757	Y	Y	PZ165932
H. hallstromi	HH_03	Papua New Guinea	Port Moresby (POM)	-9.5374	147.2764	Y	Y	PZ165933
H. hallstromi	HH_04	Papua New Guinea	Port Moresby (POM)	-9.5376	147.2760	Y	Y	PZ165934
H. hallstromi	HH_05	Papua New Guinea	Port Moresby (POM)	-9.5366	147.2905	Y	Y	PZ165935
H. hallstromi	HH_06	Papua New Guinea	Port Moresby (POM)	-9.5360	147.2908	Y	N	
H. hallstromi	H29	Papua New Guinea	Port Moresby (POM)	-9.5330	147.2910	Y*	Y**	
H. hallstromi	H30	Papua New Guinea	Port Moresby (POM)	-9.5330	147.2910	Y*	Y**	
H. hallstromi	H31	Papua New Guinea	Port Moresby (POM)	-9.5810	147.2780	Y*	Y**	
H. hallstromi	H32	Papua New Guinea	Port Moresby (POM)	-9.5810	147.2780	Y*	Y**	
H. hallstromi	H33	Papua New Guinea	Port Moresby (POM)	-9.5810	147.2780	Y*	Y**	
H. hallstromi	H34	Papua New Guinea	Port Moresby (POM)	-9.5810	147.2780	N	Y**	
H. hallstromi	HH_21	Papua New Guinea	Sudest Island	-11.3100	153.2345	Y	N	

H. hallstromi	HH_22	Papua New Guinea	Sudest Island	-11.3100	153.2345	Y	N	
H. hallstromi	HH_23	Papua New Guinea	Sudest Island	-11.3100	153.2345	Y	N	
H. hallstromi	HH_24	Papua New Guinea	Sudest Island	-11.3810	153.3259	Y	N	
H. hallstromi	HH_25	Papua New Guinea	Sudest Island	-11.3810	153.3259	Y	N	
H. hallstromi	HH_26	Papua New Guinea	Sudest Island	-11.3810	153.3259	Y	N	
H. halmahera	H45	Indonesia	Halmahera	-0.4660	127.9460	Y *	Y**	MF740834.1
H. halmahera	H46/GN16174	Indonesia	Halmahera	-0.4660	127.9460	Y *	Y**	MF740833.1
H. halmahera	HT01/Halm01	Indonesia	Halmahera	-0.8490	127.3120	Y *	Y**	MF740832.1
H. halmahera	HT02	Indonesia	Halmahera	-0.8490	127.3120	N	Y**	
H. henryi	H12/GN15044	Indonesia	Triton Bay	-3.8340	134.0970	N	Y**	
H. henryi	H13	Indonesia	Triton Bay	-3.8340	134.0970	N	Y**	
H. henryi	H14	Indonesia	Triton Bay	-3.8340	134.0970	N	Y**	
H. henryi	H01	Indonesia	Triton Bay	-3.9090	134.1610	Y *	Y**	MF740835.1
H. michaeli	HM_22	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_23	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_24	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_25	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_25r	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_26	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_27	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_28	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_29	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_30	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	HM_31	Papua New Guinea	Boia Boia Waga Island	-10.2127	150.8974	Y	N	
H. michaeli	CI001	Papua New Guinea	Conflict Islands	-10.7359	151.7223	Y *	N	
H. michaeli	CI002	Papua New Guinea	Conflict Islands	-10.7358	151.7223	Y *	N	
H. michaeli	CI003	Papua New Guinea	Conflict Islands	-10.7358	151.7223	Y	N	
H. michaeli	CI004	Papua New Guinea	Conflict Islands	-10.7411	151.7282	Y	N	
H. michaeli	CI005	Papua New Guinea	Conflict Islands	-10.7359	151.7230	Y	N	
H. michaeli	CI006	Papua New Guinea	Conflict Islands	-10.7361	151.7234	Y	N	
H. michaeli	CI007	Papua New Guinea	Conflict Islands	-10.7405	151.7213	Y	N	
H. michaeli	CI008	Papua New Guinea	Conflict Islands	-10.7405	151.7213	Y	N	
H. michaeli	CI009	Papua New Guinea	Conflict Islands	-10.7360	151.7231	Y	N	
H. michaeli	CI009r	Papua New Guinea	Conflict Islands	-10.7360	151.7231	Y	N	
H. michaeli	CI010	Papua New Guinea	Conflict Islands	-10.7360	151.7231	Y	N	
H. michaeli	CI011	Papua New Guinea	Conflict Islands	-10.7360	151.7231	Y	N	
H. michaeli	CI012	Papua New Guinea	Conflict Islands	-10.7360	151.7231	Y	N	
H. michaeli	CI013	Papua New Guinea	Conflict Islands	-10.7743	151.7067	Y	N	
H. michaeli	CI014	Papua New Guinea	Conflict Islands	-10.7770	151.7079	Y	N	
H. michaeli	CI015	Papua New Guinea	Conflict Islands	-10.7187	151.7522	Y	N	
H. michaeli	CI016	Papua New Guinea	Conflict Islands	-10.7187	151.7522	Y	N	
H. michaeli	CI017	Papua New Guinea	Conflict Islands	-10.7301	151.7402	Y	N	
H. michaeli	CI018	Papua New Guinea	Conflict Islands	-10.7287	151.7412	Y	N	
H. michaeli	CI019	Papua New Guinea	Conflict Islands	-10.7318	151.7392	Y	N	
H. michaeli	CI020	Papua New Guinea	Conflict Islands	-10.7321	151.7385	Y	N	
H. michaeli	CI021	Papua New Guinea	Conflict Islands	-10.7313	151.7398	Y	N	
H. michaeli	CI022	Papua New Guinea	Conflict Islands	-10.7308	151.7393	Y	N	
H. michaeli	CI023	Papua New Guinea	Conflict Islands	-10.7769	151.7056	Y	N	
H. michaeli	CI024	Papua New Guinea	Conflict Islands	-10.7683	151.7058	Y	N	
H. michaeli	CI025	Papua New Guinea	Conflict Islands	-10.7421	151.7202	Y	N	
H. michaeli	CI026	Papua New Guinea	Conflict Islands	-10.7421	151.7207	Y	N	
H. michaeli	CI027	Papua New Guinea	Conflict Islands	-10.7266	151.7430	Y	N	
H. michaeli	CI028	Papua New Guinea	Conflict Islands	-10.7255	151.7438	Y	N	
H. michaeli	CI029	Papua New Guinea	Conflict Islands	-10.7280	151.7417	Y	N	
H. michaeli	CI030	Papua New Guinea	Conflict Islands	-10.7188	151.7500	Y	N	
H. michaeli	CI031	Papua New Guinea	Conflict Islands	-10.7185	151.7527	Y	N	
H. michaeli	CI032	Papua New Guinea	Conflict Islands	-10.7191	151.7505	Y	N	
H. michaeli	CI033	Papua New Guinea	Conflict Islands	-10.7396	151.7213	Y	N	
H. michaeli	CI034	Papua New Guinea	Conflict Islands	-10.7359	151.7231	Y	N	
H. michaeli	CI035	Papua New Guinea	Conflict Islands	-10.7353	151.7231	Y	N	
H. michaeli	CI041	Papua New Guinea	Conflict Islands	-10.7275	151.7421	Y	N	
H. michaeli	CI049	Papua New Guinea	Conflict Islands	-10.7184	151.7518	Y	N	
H. michaeli	CI056	Papua New Guinea	Conflict Islands	-10.7625	151.7714	Y	N	
H. michaeli	CI057	Papua New Guinea	Conflict Islands	-10.7625	151.7714	Y	N	
H. michaeli	CI058	Papua New Guinea	Conflict Islands	-10.7624	151.7713	Y	N	
H. michaeli	CI063	Papua New Guinea	Conflict Islands	-10.7617	151.7712	Y	N	
H. michaeli	CI067	Papua New Guinea	Conflict Islands	-10.7984	151.8991	Y	N	
H. michaeli	CI068	Papua New Guinea	Conflict Islands	-10.7802	151.8285	Y	N	
H. michaeli	CI069	Papua New Guinea	Conflict Islands	-10.7795	151.8258	Y	N	
H. michaeli	CI089	Papua New Guinea	Conflict Islands	-10.7707	151.6973	Y	N	
H. michaeli	CI090	Papua New Guinea	Conflict Islands	-10.7707	151.6974	Y	N	
H. michaeli	CI091	Papua New Guinea	Conflict Islands	-10.7732	151.7015	Y	N	
H. michaeli	CI092	Papua New Guinea	Conflict Islands	-10.7818	151.8269	Y	N	
H. michaeli	CI131	Papua New Guinea	Conflict Islands	-10.7301	151.7396	Y	N	
H. michaeli	CI133	Papua New Guinea	Conflict Islands	-10.7504	151.7189	Y	N	
H. michaeli	CI135	Papua New Guinea	Conflict Islands	-10.7228	151.7467	Y	N	
H. michaeli	CI136	Papua New Guinea	Conflict Islands	-10.7228	151.7468	Y	N	
H. michaeli	CI139	Papua New Guinea	Conflict Islands	-10.7272	151.7431	Y	N	
H. michaeli	CI164	Papua New Guinea	Conflict Islands	-10.7185	151.7728	Y	N	
H. michaeli	CI204	Papua New Guinea	Conflict Islands	-10.7521	151.8280	Y	N	

H. michaeli	CI205	Papua New Guinea	Conflict Islands	-10.7521	151.8281	Y	N	
H. michaeli	CI208	Papua New Guinea	Conflict Islands	-10.7521	151.8281	Y	N	
H. michaeli	CI254	Papua New Guinea	Conflict Islands	-10.8207	151.8299	Y	N	
H. michaeli	CI256	Papua New Guinea	Conflict Islands	-10.8184	151.8301	Y	N	
H. michaeli	CI257	Papua New Guinea	Conflict Islands	-10.8186	151.8299	Y	N	
H. michaeli	CI258	Papua New Guinea	Conflict Islands	-10.8186	151.8299	Y	N	
H. michaeli	CI259	Papua New Guinea	Conflict Islands	-10.8185	151.8299	Y	N	
H. michaeli	CI260	Papua New Guinea	Conflict Islands	-10.7422	151.7214	Y	N	
H. michaeli	CI261	Papua New Guinea	Conflict Islands	-10.7359	151.7222	Y	N	
H. michaeli	HM_16	Papua New Guinea	Conflict Islands	-10.7290	151.7403	Y	N	
H. michaeli	HM_17	Papua New Guinea	Conflict Islands	-10.7290	151.7403	Y	N	
H. michaeli	HM_18	Papua New Guinea	Conflict Islands	-10.7198	151.7478	Y	N	
H. michaeli	HM_19	Papua New Guinea	Conflict Islands	-10.7198	151.7478	Y	N	
H. michaeli	HM_20	Papua New Guinea	Conflict Islands	-10.7198	151.7478	Y	N	
H. michaeli	HM_21	Papua New Guinea	Conflict Islands	-10.7198	151.7478	Y	N	
H. michaeli	HM_55	Papua New Guinea	Doini Island	-10.6920	150.7069	Y*	N	
H. michaeli	HM_56	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_57	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_58	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_59	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_60	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_61	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_61r	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_62	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_63	Papua New Guinea	Doini Island	-10.6920	150.7069	Y	N	
H. michaeli	HM_06	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_07	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_08	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_09	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_10	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_11	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_12	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_13	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_14	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_14r	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	HM_15	Papua New Guinea	Engineer Group	-10.6104	151.3744	Y	N	
H. michaeli	H17	Papua New Guinea	Nuakata Island	-10.3110	151.0049	N	Y**	
H. michaeli	H35R	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y	N	
H. michaeli	H35	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y	Y**	
H. michaeli	H36	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y	Y**	
H. michaeli	H38	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y*	Y**	
H. michaeli	H39	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y*	Y**	
H. michaeli	H37	Papua New Guinea	Nuakata Island	-10.3110	151.0049	Y	Y**	MF740842.1
H. michaeli	HM_32	Papua New Guinea	Rossel Island	-11.2998	154.2221	Y*	Y	PZ165947
H. michaeli	HM_32R	Papua New Guinea	Rossel Island	-11.2998	154.2221	Y	N	
H. michaeli	HM_33	Papua New Guinea	Rossel Island	-11.2998	154.2221	Y*	Y	PZ165948
H. michaeli	HM_41	Papua New Guinea	Rossel Island	-11.2998	154.2221	Y*	Y	PZ165949
H. michaeli	HM_01	Papua New Guinea	Sideia Island	-10.5559	150.7938	Y*	Y	PZ165942
H. michaeli	HM_02	Papua New Guinea	Sideia Island	-10.5706	150.7974	Y*	Y	PZ165943
H. michaeli	HM_03	Papua New Guinea	Sideia Island	-10.5706	150.7974	Y*	Y	PZ165944
H. michaeli	HM_04	Papua New Guinea	Sideia Island	-10.5706	150.7974	Y*	Y	PZ165945
H. michaeli	HM_05	Papua New Guinea	Sideia Island	-10.5706	150.7974	Y	Y	PZ165946
H. michaeli	HM_78	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_79	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_80	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_81	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_82	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_83	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	Y	PZ165960
H. michaeli	HM_84	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	Y	PZ165961
H. michaeli	HM_85	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_86	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_87	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	Y	PZ165962
H. michaeli	HM_88	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_89	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_90	Papua New Guinea	Sullivans Patch	-10.3586	150.7474	Y	N	
H. michaeli	HM_34	Papua New Guinea	Tufi	-9.0854	149.3160	Y	N	
H. michaeli	HM_35	Papua New Guinea	Tufi	-9.0854	149.3160	Y	N	
H. michaeli	HM_36	Papua New Guinea	Tufi	-9.1007	149.3239	Y	N	
H. michaeli	HM_37	Papua New Guinea	Tufi	-9.1007	149.3239	Y	N	
H. michaeli	HM_38	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_39	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_40	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_64	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_65	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_66	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_67	Papua New Guinea	Tufi	-9.0808	149.3197	Y*	Y	PZ165950
H. michaeli	HM_68	Papua New Guinea	Tufi	-9.0891	149.4271	Y*	Y	PZ165951
H. michaeli	HM_69	Papua New Guinea	Tufi	-9.0808	149.3197	Y	N	
H. michaeli	HM_70	Papua New Guinea	Tufi	-9.0948	149.4251	Y*	Y	PZ165952
H. michaeli	HM_71	Papua New Guinea	Tufi	-9.0948	149.4251	Y	Y	PZ165953
H. michaeli	HM_72	Papua New Guinea	Tufi	-9.0948	149.4251	Y	Y	PZ165954

H. michaeli	HM_73	Papua New Guinea	Tufi	-9.0978	149.4480	Y	Y	PZ165955
H. michaeli	HM_74	Papua New Guinea	Tufi	-9.0978	149.4480	Y	Y	PZ165956
H. michaeli	HM_75	Papua New Guinea	Tufi	-9.0978	149.4480	Y	Y	PZ165957
H. michaeli	HM_76	Papua New Guinea	Tufi	-9.1007	149.3239	Y	Y	PZ165958
H. michaeli	HM_77	Papua New Guinea	Tufi	-9.1007	149.3239	Y	Y	PZ165959
H. michaeli	HM_42	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_43	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_44	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_45	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_46	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_47	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_48	Papua New Guinea	Wari Island	-10.9741	151.0473	Y	N	
H. michaeli	HM_49	Papua New Guinea	Wari Island	-10.9621	151.0628	Y	N	
H. michaeli	HM_50	Papua New Guinea	Wari Island	-10.9621	151.0628	Y	N	
H. michaeli	HM_51	Papua New Guinea	Wari Island	-10.9621	151.0628	Y	N	
H. michaeli	HM_52	Papua New Guinea	Wari Island	-10.9621	151.0628	Y	N	
H. michaeli	HM_53	Papua New Guinea	Wari Island	-10.9621	151.0628	Y	N	
H. michaeli	HM_54	Papua New Guinea	Wari Island	-10.9621	151.0628	Y *	N	
H. ocellatum	EP005	Australia	Central Great Barrier Reef (C_GBR)	-20.2043	148.9767	Y * ^	N	
H. ocellatum	EP006	Australia	Central Great Barrier Reef (C_GBR)	-20.2043	148.9767	Y * ^	N	
H. ocellatum	EP007	Australia	Central Great Barrier Reef (C_GBR)	-20.2043	148.9767	Y * ^	N	
H. ocellatum	EP008	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y * ^	N	
H. ocellatum	EP009	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP010	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP011	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP012	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP013	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP014	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP015	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP016	Australia	Central Great Barrier Reef (C_GBR)	-18.6125	146.4864	Y ^	N	
H. ocellatum	EP016R	Australia	Central Great Barrier Reef (C_GBR)	-18.6125	146.4864	Y ^	N	
H. ocellatum	EP067	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP068	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP069	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP070	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP071	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP072	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP073	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP074	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP075	Australia	Central Great Barrier Reef (C_GBR)	-19.0302	146.4206	Y ^	N	
H. ocellatum	EP076	Australia	Central Great Barrier Reef (C_GBR)	-19.1574	146.8606	Y ^	N	
H. ocellatum	EP118	Australia	Central Great Barrier Reef (C_GBR)	-18.6125	146.4864	Y ^	N	
H. ocellatum	H20	Australia	Lizard Island	-14.6870	145.4530	N	Y**	
H. ocellatum	EP017	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y * ^	N	
H. ocellatum	EP018	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y * ^	N	
H. ocellatum	EP019	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y * ^	N	
H. ocellatum	EP020	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y * ^	N	
H. ocellatum	EP021	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP022	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP023	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP024	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP025	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP026	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP027	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP028	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP029	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP030	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP031	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP033	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP034	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP035	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP036	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP036R	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP037	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP077	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP078	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP079	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP080	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP081	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP082	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP083	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP084	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP085	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP086	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	EP087	Australia	Northern Great Barrier Reef (N_GBR)	-16.7127	146.0340	Y ^	N	
H. ocellatum	H03/GN5795	Australia	Northern Great Barrier Reef (N_GBR)	-16.8670	146.0000	N	Y**	MF740844.1
H. ocellatum	H02	Australia	Southern Great Barrier Reef (S_GBR)	-23.4500	151.9170	N	Y**	
H. ocellatum	H05	Australia	Southern Great Barrier Reef (S_GBR)	-23.4500	151.9170	N	Y**	

H. ocellatum	H07	Australia	Southern Great Barrier Reef (S_GBR)	-23.4500	151.9170	N	Y**	
H. ocellatum	EP001	Australia	Southern Great Barrier Reef (S_GBR)	-23.0792	150.8999	Y * ^	N	
H. ocellatum	EP002	Australia	Southern Great Barrier Reef (S_GBR)	-23.0792	150.8999	Y * ^	N	
H. ocellatum	EP003	Australia	Southern Great Barrier Reef (S_GBR)	-23.0792	150.8999	Y * ^	N	
H. ocellatum	EP004	Australia	Southern Great Barrier Reef (S_GBR)	-23.0792	150.8999	Y * ^	N	
H. ocellatum	EP038	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP039	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP040	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP041	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP042	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP043	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP044	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP045	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP046	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP047	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP048	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP049	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP050	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP051	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP052	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP053	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP054	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP055	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP056	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP057	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP058	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP059	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP060	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP061	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP062	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP063	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP064	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP065	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP066	Australia	Southern Great Barrier Reef (S_GBR)	-24.1106	152.7124	Y ^	N	
H. ocellatum	EP088	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP089	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP090	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP091	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP092	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP093	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP094	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP095	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP096	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP097	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP098	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP099	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP100	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP101	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP102	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP103	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP104	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP105	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP106	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP107	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP108	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP109	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP110	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP111	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP112	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP113	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP114	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP115	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP116	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	EP117	Australia	Southern Great Barrier Reef (S_GBR)	-23.4434	151.9127	Y ^	N	
H. ocellatum	H04	Australia	Southern Great Barrier Reef (S_GBR)	-23.4500	151.9170	N	Y**	MF740845.1
H. strahani	H22	Indonesia	Jayapura	-2.4160	140.3620	N	Y**	
H. strahani	H23	Indonesia	Jayapura	-2.4160	140.3620	Y *	Y**	
H. strahani	H24	Indonesia	Jayapura	-2.4160	140.3620	Y *	Y**	
H. strahani	H25	Indonesia	Jayapura	-2.4160	140.3620	Y *	Y**	
H. strahani	H26	Indonesia	Jayapura	-2.4160	140.3620	Y *	Y**	
H. strahani	H21/GN015045	Indonesia	Jayapura	-2.4160	140.3620	N	Y**	MF740836.1
H. trispeculare	HTri1	Indonesia	Aru	-6.1850	134.1430	Y *	Y**	
H. trispeculare	HTri2	Indonesia	Aru	-6.1850	134.1430	N	Y**	
H. trispeculare	HTri3/GN13227	Indonesia	Aru	-6.1850	134.1430	Y *	Y**	
H. trispeculare	H50	Australia	Kimberley	-15.5170	123.1500	N	Y**	MF740839.1
H. trispeculare	H51	Australia	Kimberley	-13.9500	125.6330	N	N	
H. trispeculare	H48	Australia	Northern Territory (NT)	-12.5560	130.8730	Y *	Y**	MF740837.1
H. trispeculare	H54	Australia	Northern Territory (NT)	-10.3830	132.5506	Y *	Y**	
H. trispeculare	H49	Australia	Northern Territory (NT)	-12.5560	130.8730	N	N	

Supplementary TABLE 2

Filtering summary for SNPs displaying the type of filter, thresholds used, number of loci and number of individuals in order of filtering

Filter	Thresholds	Loci	Individuals
		125845	370
RDepth	lower = 2, upper = 25	112028	370
Callrate - loci	0.99	13415	370
Call rate - ind	0.9	13340	367
Reproducibility	0.99	12043	367
taglength	lower = 50, upper = 69	11259	367
secondaries	Random: Selecting one SNP per sequence tag at random	11018	367
Callrate- loci	1	6618	367
Remove duplicates	0.992	6617	353
Dataset A		6617	353
Dataset B		6100	74

Supplementary TABLE 3

List of top 5 models sorted by AIC scores according to ModelFinder and ultrafast bootstrapping of 1,000 replicates for 1) Dataset A; and 2) Dataset B.
Plus signs denote the 95% confidence sets and minus signs denote significant exclusion

1. SNPs Dataset A

Model	*LogL*	AIC	w-AIC	AICc	w-AICc	BIC	w-BIC
GTR+F+G4	-128117.255	257658.51	0.775	257830.597	0.815	262497.827	0.907
GTR+F+I+G4	-128117.506	257661.013	0.222	257833.612	0.181	262507.126	-0.00868
TVM+F+G4	-128124.045	257670.09	-0.00237	257841.665	-0.00322	262502.61	0.083
TVM+F+I+G4	-128124.193	257672.385	-0.000752	257844.472	-0.000791	262511.702	-0.000881
SYM+G4	-128236.287	257890.574	-3.14E-51	258061.128	-7.11E-51	262709.5	-9.85E-47

2. SNPs Dataset B

Model	*LogL*	AIC	w-AIC	AICc	w-AICc	BIC	w-BIC
GTR+F+G4	-57117.03	114542.06	0.478	114550.096	0.474	115576.23	-0.0448
TVM+F+G4	-57118.524	114543.048	0.292	114550.978	0.305	115570.502	0.786
GTR+F+I+G4	-57117.314	114544.627	0.132	114552.769	0.124	115585.512	-0.000432
TVM+F+I+G4	-57118.616	114545.233	0.0978	114553.268	0.097	115579.402	-0.00918
SYM+G4	-57131.566	114565.132	-4.67E-06	114572.855	-5.41E-06	115579.155	-0.0104