

## *Hemiscyllium halmahera*, a new species of Bamboo Shark (Hemiscylliidae) from Indonesia

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### Abstract

*Hemiscyllium halmahera* new species is described from two specimens, 656-681 mm TL, collected at Ternate, Halmahera, Indonesia. The new species is clearly differentiated on the basis of colour pattern. Its features include a general brown colouration with numerous clusters of mainly 2-3 dark polygonal spots, widely scattered white spots in the matrix between dark clusters, relatively few (< 10), large dark spots on the interorbital/snout region, a pair of large dark marks on the ventral surface of the head, and a fragmented post-cephalic mark consisting of a large U-shaped dark spot with a more or less continuous white margin on the lower half, followed by a vertical row of three, smaller clusters of 2-3 polygonal dark marks. The new species is most similar in general appearance to *H. galei* from Cenderawasih Bay, West Papua, which differs in having 7-8 large, horizontally elongate dark spots on the lower side between the abdomen and caudal-fin base, a cluster of solid dark post-cephalic spots, and usually about 25 dark spots on the upper surface of the head.

### Zusammenfassung

Beschrieben wird die neue Art *Hemiscyllium halmahera* auf der Grundlage von zwei Exemplaren mit 656-681 mm TL (Gesamtlänge), die bei Ternate, Halmahera, in Indonesien gefangen wurden. Sie sind durch ihr Farbmuster eindeutig unterscheidbar. Zu den Merkmalen der neuen Art gehören eine allgemein bräunliche Farbgebung mit zahlreichen Gruppen von meist 2-3 dunklen vieleckigen Flecken, weit verteilte weiße Flecken in der Grundfarbe zwischen den schwarzen Fleckengruppen, relativ wenige (< 10) große dunkle Flecken in der Zwischen-Augen- und Schnauzenregion, ein Paar großer dunkler Zeichen an der bauchwärtigen Oberfläche des Kopfes sowie ein zusammengesetztes Zeichen hinter dem Kopf, das aus einem

großen dunklen U-förmigen Fleck mit mehr oder weniger durchgehendem weißen Rand im unteren Teil und einer senkrechten Reihe von drei kleineren Gruppen aus 2-3 dunklen vieleckigen Markierungen besteht. Im allgemeinen Erscheinungsbild ähnelt die neue Art stark *H. galei* von der Cenderawasih-Bucht, West-Papua, deren Vertreter sich aber durch 7-8 große, waagrecht längliche dunkle Flecken an der Unterseite zwischen Abdomen und Basis der Schwanzflosse unterscheiden, sowie durch eine Gruppe einheitlich dunkler Flecken hinter dem Kopf und gewöhnlich 25 dunkle Flecken auf der Kopfoberseite.

### Résumé

*Hemiscyllium halmahera*, une nouvelle espèce, est décrit sur base de deux spécimens, 656-681 mm de LT, collectés à Ternate, Halmahera, Indonésie. La nouvelle espèce se distingue clairement par le patron de coloration. Ses caractéristiques comprennent une coloration d'ensemble brune avec nombre de groupes de généralement 2-3 taches polygonales sombres, des taches blanches largement disséminées sur la matrice parmi des groupes sombres, relativement peu (moins de 10) de grandes taches foncées dans la région interorbitale/rostrale, une paire de grandes marques sombres sur la partie ventrale de la tête et une marque fragmentée post-céphalique qui consiste en une grande tache sombre en forme de U avec une marge blanche plus ou moins continue sur la moitié inférieure, suivie d'une rangée verticale de trois amas plus petits de 2-3 marques polygonales foncées. En apparence générale, la nouvelle espèce évoque le plus *H. galei* de Cenderawasih Bay, West Papua, qui diffère par la présence de 7-8 grandes taches sombres étalées à l'horizontale sur le côté inférieur, entre l'abdomen et la base de la caudale, par un ensemble de taches postcéphaliques foncées et, généralement, d'environ 25 taches sombres sur la partie supérieure de la tête.

## Sommario

*Hemiscyllium halmahera* nuova specie è descritta sulla base di due esemplari, di 656-681 mm TL, raccolti a Ternate, Halmahera, Indonesia. La nuova specie è chiaramente distinguibile sulla base della colorazione. Questa include una tonalità bruna diffusa con numerosi grappoli di 2-3 macchie poligonali scure, macchie bianche sparpagliate nella matrice tra i grappoli scuri, relativamente poche (<10) grandi macchie scure sulla regione interorbitale/muso, un paio di grandi screziature scure sulla superficie ventrale della testa e una in sede post-cefalica, frammentata, composta da una grande macchia scura a forma di U con un margine bianco più o meno continuo nella metà inferiore, seguita da una fila verticale di tre grappoli minori di 2-3 macchie poligonali scure. La nuova specie è molto simile nell'aspetto generale a *H. galei* della Cenderawasih Bay, Papua occidentale, che si distingue per avere 7-8 grandi macchie scure, allungate orizzontalmente sul lato inferiore tra l'addome e la base della pinna caudale, un gruppo di ben definite macchie scure post-cefaliche e di solito per circa 25 macchie scure sulla superficie superiore della testa.

## INTRODUCTION

The family Hemiscylliidae, commonly known as bamboo, epaulette, or walking sharks, contains small, slender sharks characterised by nasoral and perioral grooves, short barbels, a small transverse mouth below the eyes, two similar-sized dorsal fins, and a long slender tail. Only two genera are known, both described by Müller & Henle (1837 & 1838), *Chiloscyllium* with seven Indo-Pacific species, and *Hemiscyllium* with nine species, including the new taxon described herein. The family was last reviewed by Compagno (2002), who recognized five *Hemiscyllium*: *H. freycineti* (Quoy & Gaimard, 1824), *H. hallstromi* Whitley, 1967, *H. ocellatum* (Bonnaterre, 1788), *H. strahani* Whitley, 1967, and *H. trispeculare* Richardson, 1843. Two additional species, *H. galei* and *H. henryi* were described by Allen & Erdmann (2008) from the Bird's Head Peninsula of western New Guinea (West Papua Province, Indonesia), and a third addition, *H. michaeli* was described by Allen & Dudgeon (2010) from eastern Papua New Guinea. The members of the genus are morphologically very similar, and unfortunately most species are poorly represented in museum collections, precluding detailed morphological/meristic comparisons. Therefore, colour patterns and genetic differences remain the most valuable "tools" for distinguishing species.

Sharks of the genus *Hemiscyllium* are small (usually under about 80 cm), nocturnally active, bottom-living animals, which exhibit a peculiar "walk-

ing" gait while foraging for benthic invertebrates and fishes. Although biological data is sparse for most species, they are generally oviparous with elliptical egg capsules being deposited on the reef. Hatchlings are rarely encountered, but the few reported specimens were about 15 cm TL (Compagno, 2001).

Due to their reproductive mode, limited swimming ability, and poor dispersal capability most species have restricted distributions. The two Australian species, *H. ocellatum* and *H. trispeculare*, are the most widespread, ranging around most of the northern half of the continent. The remaining species, with the exception of the new species described below, have restricted regional New Guinea distributions (indicated in parentheses; also see Fig. 1): *H. freycineti* (Raja Ampat Islands, and possibly adjacent West Papua mainland), *H. galei* (Cenderawasih Bay, West Papua), *H. hallstromi* (Gulf of Papua to Milne Bay Province, Papua New Guinea), *H. henryi* (Kaimana coastline and Triton Bay, West Papua), *H. michaeli* (Milne Bay and Oro provinces, Papua New Guinea), and *H. strahani* (Madang along north coast of Papua New Guinea to Jayapura, Papua Province, Indonesia). All of these species were illustrated and discussed by Allen & Erdmann (2012).

The current paper describes a new species from Halmahera, the first record for the genus from beyond the Australia-New Guinea region. Two specimens and tissue samples of each were collected by M. Erdmann during a night dive at the island of Ternate in the Halmahera group of islands, Indonesia. Subsequent DNA analysis indicates it is a separate species.

## MATERIALS AND METHODS

Technical terms and measurements mainly follow those explained and illustrated by Compagno (2001). Snout length is the distance from the snout tip to the anterior edge of the mouth. Subcaudal length is the combined measurement of the upper postventral caudal-fin margin and terminal caudal-fin margin. Total length and head length are abbreviated as TL and HL respectively. Vertebral counts were obtained from radiographs. Vertebral counts and measurements for the holotype are given first followed by the range for paratypes (in parentheses) in the description below. Type specimens are deposited at Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB) and the Western Australian Museum, Perth (WAM).

Tissue samples were obtained for both type specimens of the new taxon from Ternate, Indonesia. This was compared with samples of *H. freycineti*, *H. galei*, *H. henryi*, *H. michaeli*, and *H. ocellatum*, which had been previously analysed (Allen and Erdmann 2008; Allen and Dudgeon, 2010). Total genomic DNA was extracted from 25 mg of fin tissue using the DNeasy Tissue Extraction Kit (Qiagen) following the instructions of the supplier. A fragment including partial mitochondrial NADH Dehydrogenase subunit 4 gene (ND4), tRNA-His and tRNA-Ser genes was amplified through polymerase chain reaction (PCR) using the primers: ND4-F: 5' - CACCTATGACTACCAAAGCTCATGTAGAAGC - 3' (Arevalo et al. 1994) and H12293-Leu-R: 5' - TTGCACCAAGAGTTTTTGGTTCCTAAGACC - 3' (Inoue et al. 2001). Reactions were conducted in 30  $\mu$ l total amounts and consisted of: 10  $\mu$ M each primer, 400  $\mu$ M of each dNTP, 3 units *Taq* polymerase, 1 x PCR Buffer (Qiagen) and 30-50 ng extracted DNA. PCRs were conducted on 9700 Perkin Elmer 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. The PCR products were cleaned using Isolate PCR and Gel Kit (Bioline). Sequences were conducted in both forward and reverse directions using Big Dye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) following manufacturer's instructions. Sequencing products (20ul) were precipitated by adding 5  $\mu$ l EDTA (125mM, pH8.0) and 60  $\mu$ l 100% ethanol and centrifuged for 45 min at 3000 rpm (30 cm diameter rotor). The pellet was washed with 60  $\mu$ l 70% ethanol and centrifuged for 15 min at 3000 rpm and then products resolved on a 3730xl Genetic Analyser (Applied Biosystems).

Sequences were aligned using Sequencher version 4.6 (Gene Codes). All molecular statistical analyses were conducted using Mega version 5 (Tamura et al. 2011). Maximum likelihood analysis was used to assess the model of best fit for the nucleotide substitution. Both Bayesian Information Criterion (BIC) and Akaike's Information Criterion corrected for small sample sizes (AICc) ranked the Tamura-Nei substitution model (Tamura & Nei 1993) with a discrete Gamma distribution (TN93+G; G=0.38) as having the best fit to the data. The Tamura-Nei (Tamura & Nei 1993) substitution model accounts for variable base frequen-



**Fig. 1.** Map of New Guinea and Halmahera showing collection/observation locations of resident species of *Hemiscyllium*: *H. freycineti* (yellow circles), *H. galei* (white star), *H. henryi* (yellow star), *H. hallstromi* (white squares), *H. halmahera* (green circles), *H. strahani* (red squares), and *H. michaeli* (red circles).

cies, transition rates and rate variation among sites. The TN93+G model was used to construct phylogenetic trees with maximum likelihood analysis. Maximum parsimony trees were also constructed with a specimen of *Chiloscyllium punctatum* as the outgroup taxon. Confidence in tree topology was evaluated by bootstrapping across 1000 bootstrap replicates (Felsenstein 1985). Pairwise distances within and between putative taxa were calculated using the TN93+G model with 1000 bootstrap replicates.

***Hemiscyllium halmahera* n. sp.**

Halmahera Epaulette Shark  
(Figs 2-7; Tables I-II)

**Holotype:** MZB 21248, male, 681 mm TL, north-western Ternate, 00°50.958'N, 127°18.717'E, Halmahera, Indonesia, 10 m, captured by hand, M. Erdmann, 1 May 2012.

**Paratype:** WAM P. 33784-001, female, 656 mm TL, collected with holotype.

**Diagnosis:** A species of bamboo shark belonging to the genus *Hemiscyllium*, distinguished from all

congeners by a unique colour pattern, particularly a light brown background colour with numerous clusters of mainly 2-3 dark polygonal spots, widely scattered white spots in the matrix between dark clusters, relatively few (< 10), large dark spots on the interorbital/snout region, pair of large dark marks on ventral surface of head, and fragmented post-cephalic mark consisting of a large U-shaped dark spot with more or less continuous white margin on lower half, followed posteriorly by vertical row of three, smaller clusters of 2-3 polygonal dark marks. It lacks diagnostic colour pattern features that typify the other known species in the genus, including a black hood or face-mask marking on the head (*H. strahani*), large intensely black ovate spots on body (*H. hallstromi*), ocellated shoulder spot and numerous small black spots on body (*H. ocellatum*), ocellated shoulder spot with two curved black marks on posterior edge and numerous diffuse dark spots on head body and fins (*H. trispeculare*), row of 7-8 large, horizontally ovate dark spots on lower side between abdomen and caudal-fin base (*H. galei*), "double-ocellus" shoulder marking (*H. henryi*), diffuse shoulder marking, numerous dark spots on dorsal surface of head, and pair of

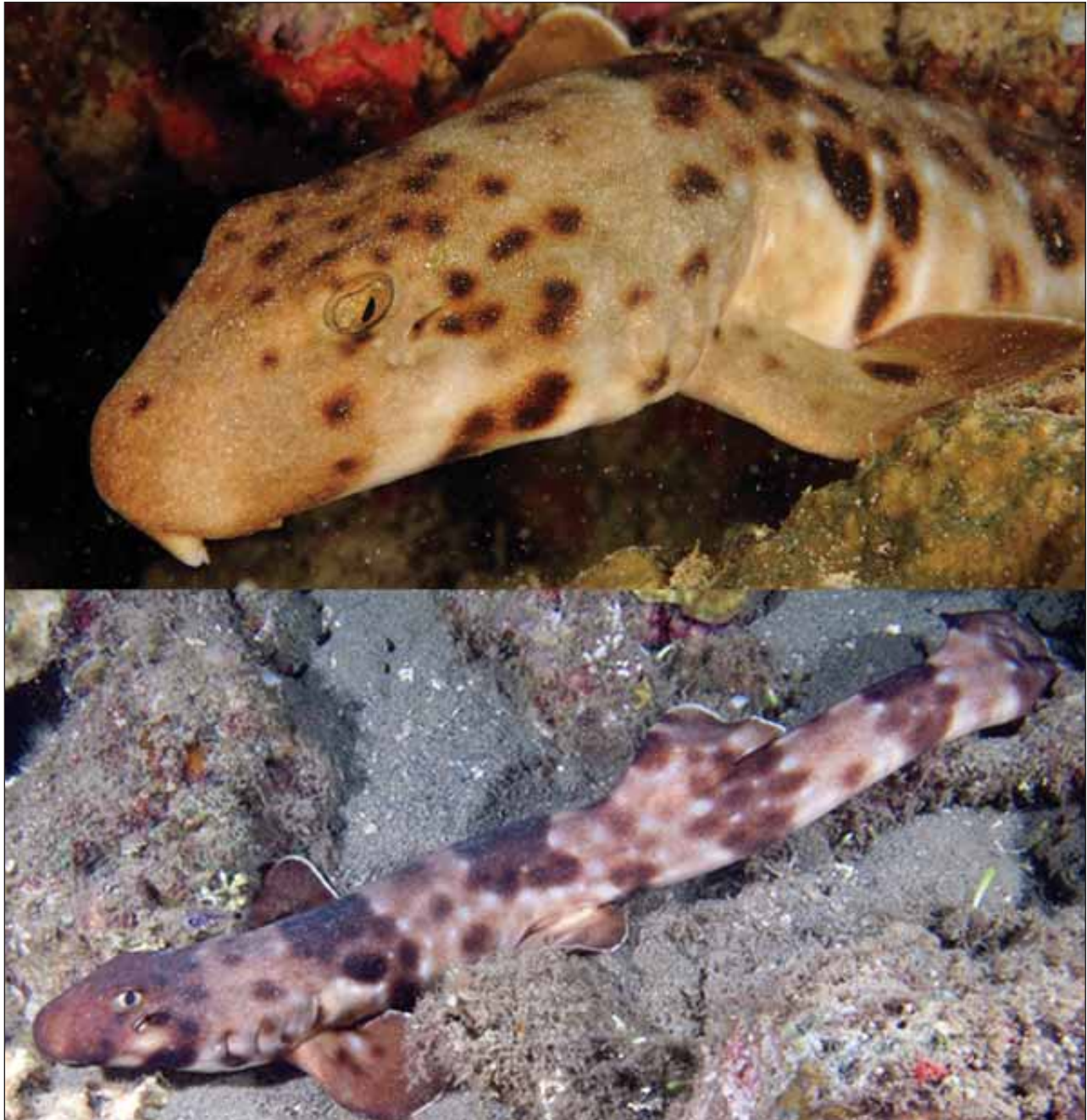


**Fig. 2.** Underwater photograph of *Hemiscyllium halmahera*, male holotype, Ternate Island, Halmahera, Indonesia at depth of 10 m. Photo by M. V. Erdmann.

closely spaced dark post-cephalic ocelli surrounded by white halo (*H. freycineti*), and dense pattern of leopard-like dark spots (*H. michaeli*).

**Description:** Total vertebral centra 195 (includes 39-40 monospondylous centra, 101-102 diplospondylous precaudal centra, and 54 caudal centra); body and tail relatively slender, tapering posteri-

orly; precaudal length 1.3 and HL 6.7 (7.5-8.0) in TL; head height (at pectoral-fin origin) 1.2 in greatest width of head; eye length 3.4 (3.2) in snout length, eye height 1.9 (2.7) in eye length; fleshy interorbital space 1.4 and bony interorbital space 1.7 in snout length; snout blunt and short, snout tip to eye 2.2 (2.4), snout tip to mouth 4.6



**Fig. 3.** Underwater photographs of *Hemiscyllium halmahera*: upper – approximately 650 mm TL, Bacan Island, Halmahera, Indonesia at depth of 10 m. Photo by J. Yonover. Lower – approximately 700 mm TL, Weda Bay, Halmahera, at depth of 5 m. Photo by T. Mulder.

**Table I.** Proportional measurements (as percentage of total length) for type specimens of *Hemiscyllium halmahera*.

Measurement	Holotype MZB 21248	Paratype WAM P. 33784
Sex	male	female
Total length (mm)	681	656
Precaudal length	78.4	76.5
Head width	8.8	8.3
Head depth	7.3	6.7
Preanal body depth	5.3	5.2
Snout - pectoral-fin origin (HL)	12.5	13.4
Snout - 1 <sup>st</sup> gill slit	11.5	11.9
1 <sup>st</sup> to 5 <sup>th</sup> gill slit	5.0	4.9
First gill slit height	1.5	1.4
Fifth gill slit height	2.1	2.0
Eye diameter (horizontal)	1.7	1.8
Eye diameter (vertical)	0.9	0.7
Bony interorbital width	3.5	3.3
Fleshy interorbital width	4.1	3.9
Snout to eye (snout length)	5.8	5.7
Snout to spiracle	6.8	6.6
Snout to mouth	2.7	2.3
Lower labial furrow length	1.3	1.1
Maximum width lower labial flap	1.1	1.1
Postoral fold	1.7	1.8
Mouth width	4.9	4.2
Barbel length	1.1	1.2
Snout - 1 <sup>st</sup> dorsal origin	37.9	40.2
Snout - pelvic origin	29.0	31.2
Snout - anal opening	32.2	33.6
Anal opening - anal-fin origin	42.9	40.8
Anal opening - tail tip	68.8	67.1
Interdorsal distance	11.3	11.8
Pectoral-fin length	11.7	11.0
Pelvic-fin length	10.4	9.9
1 <sup>st</sup> dorsal fin base	8.5	7.4
1 <sup>st</sup> dorsal-fin height	8.1	6.5
1 <sup>st</sup> dorsal-fin free margin	4.9	4.5
2 <sup>nd</sup> dorsal-fin base	8.1	7.7
2 <sup>nd</sup> dorsal-fin height	7.4	7.4
2 <sup>nd</sup> dorsal-fin free margin	3.7	4.0
Anal-fin base	9.2	7.8
Anal-fin height	2.8	2.9
Anal-fin free margin	1.9	1.6
Subcaudal	16.2	17.6
Clasper length (inner)	8.9	-
Clasper length (outer)	6.3	-

(5.8), snout tip to spiracle 1.8 (2.0), snout tip to first gill slit 1.1, 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 2.5 (2.7) in HL; height of gill slits gradually increasing posteri-

orly, the first 3.9 and fifth 2.7 (2.8) in snout length.

Mouth small and transverse, positioned well forward on ventral surface of head, its width 1.2 (1.3) in snout length; short barbel on each side of ventral snout, its length 5.2 (4.6) in snout length; maximum width of lower labial flap 5.0 (5.3), length of postoral fold (upper labial furrow) 3.4 (3.1), length of lower labial furrow 4.5 (5.3), 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 length 2.6 (2.5), prepelvic length 3.4 (3.2), snout to vent length 3.1 (3.0), vent to anal-fin origin 2.3 (2.4), vent to caudal-fin length 1.3, all in TL. Pectoral fins below gill openings, their length 1.1 (1.2) in HL; pelvic fins immediately anterior to vertical line passing through first dorsal-fin origin, their length 1.2 (1.4) in HL; dorsal fins positioned well back on body, first and second dorsal fins nearly equal in height; first dorsal-fin base 1.5 (1.8) in HL, first dorsal-fin height 1.1 in first dorsal-fin base; free margin of first dorsal fin 2.1 (1.4) in first dorsal-fin height; interdorsal space 1.1 in HL; second dorsal-fin base 1.6 (1.7) in HL; second dorsal-fin height 1.0 (1.1) in second dorsal-fin base; free margin of second dorsal fin 2.0 (1.9) in second dorsal-fin height; long and low anal fin just anterior to caudal fin; anal-fin base 1.4 (1.7) in HL, anal-fin height 3.3 (2.7) in anal-fin base; free margin of anal fin 1.5 (1.8) 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 2.2 (2.6) in head length; subcaudal length 6.2 (5.7) in TL.

Clasper of adult male holotype (Fig. 4A) relatively stout and elongate, its length greater than first dorsal-fin height.

Colour in life (Figs. 2-3): generally brown on snout, dorsally on head and body, grading to golden brown on lower side of body, and white on ventral surface; numerous clusters of mainly 2-3 dark polygonal spots (largest about equal to eye) and widely scattered, much smaller, white spots in brownish matrix between dark clusters; two (paratype) or three (holotype), progressively smaller dark grey brown saddles across back from rear edge of head to dorsal-fin base, a similar saddle between dorsal fins, and 4-5 additional dark saddles on dorsal edge of tail; four large saddles on body with narrow white or pale grey anterior and

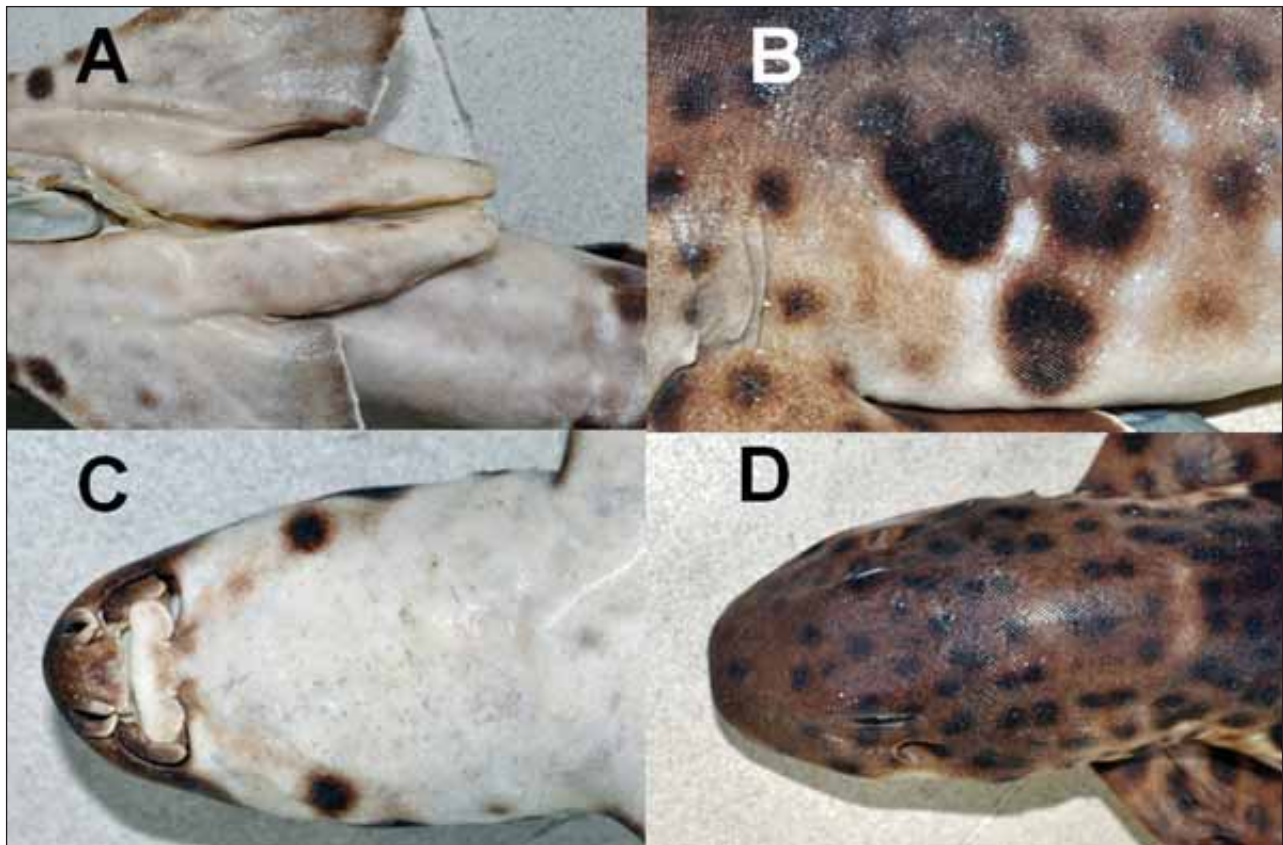
**Table II.** Inter-specific pairwise distance matrix (below diagonal) calculated from the TN93+G model with corresponding matrix (above diagonal) of SE estimates (bootstrap method, 1000 replicates).

	<i>H. halmahera</i>	<i>H. michaeli</i>	<i>H. freycineti</i>	<i>H. galei</i>	<i>H. henryi</i>	<i>H. ocellatum</i>	<i>C. punctatum</i>
<i>H. halmahera</i>	-	0.0052	0.0058	0.0066	0.0059	0.0065	0.0219
<i>H. michaeli</i>	0.0201	-	0.0056	0.0060	0.0057	0.0068	0.0237
<i>H. freycineti</i>	0.0229	0.0226	-	0.0043	0.0036	0.0072	0.0202
<i>H. galei</i>	0.0286	0.0254	0.0130	-	0.0047	0.0077	0.0209
<i>H. henryi</i>	0.0229	0.0227	0.0103	0.0184	-	0.0073	0.0203
<i>H. ocellatum</i>	0.0314	0.0329	0.0372	0.0401	0.0371	-	0.0215
<i>C. punctatum</i>	0.1627	0.1747	0.1545	0.1588	0.1547	0.1572	-

posterior margins; fragmented post-cephalic mark (Fig. 4B), consisting of a large U-shaped dark spot with more or less continuous white margin on lower half, followed by vertical row of three, smaller clusters of 2-3 polygonal dark marks; pair of large round to oval dark marks (Fig. 4C) on ventral surface of head at about level of spiracle; lower side of head, below and slightly posterior to spiracle with 2-3 large, irregular dark spots; relatively

few (< 10) large (smaller than eye, Fig. 4D), dark spots on interorbital/snout region; each dorsal fin with few poorly defined brown spots and pair of prominent blackish saddles on anterior edge, the lowermost ocellus-like with white margin around lower edge; pectoral and pelvic fins with 8-10 and 6-11 variable-sized brown spots respectively on dorsal surface and narrow white posterior margin.

Colour in alcohol (Figs 5-7) similar to the



**Fig. 4A-D.** Diagnostic features of *Hemiscyllium halmahera*: A. claspers of male holotype; B. post-cephalic marking of holotype; C. ventral surface of head of female paratype; D. dorsal surface of head of male holotype. Photos by G. R. Allen.



**Fig. 5.** *Hemiscyllium halmahera*, preserved male holotype, 681 mm TL, Ternate, Halmahera, Indonesia. Photo by G. R. Allen.



**Fig. 6.** *Hemiscyllium halmahera*, dorsal view of preserved holotype, 681 mm TL, Ternate, Halmahera, Indonesia. Photo by G. R. Allen.



**Fig. 7.** *Hemiscyllium halmahera*, preserved female paratype, 656 mm TL, Ternate, Halmahera, Indonesia. Photo by G. R. Allen.





**Fig. 8.** Underwater photograph of *Hemiscyllium michaeli*, approximately 600 mm TL, Milne Bay Province, Papua New Guinea. Photo by B. Halstead.



**Fig. 9.** Underwater photograph of *Hemiscyllium freycineti*, approximately 600 mm TL, Kri Island, Raja Ampat Islands, West Papua Province, Indonesia. Photo by G. R. Allen.

live colour provided above, except the ground colour is tan to reddish brown and the dark spotting on the head, body, and fins is less intense.

**DNA Analysis:** In total, we analysed a 792 base pair (bp) alignment of the mitochondrial ND4 gene from 18 *Hemiscyllium* individuals and one *Chiloscyllium punctatum* individual. There were two new samples for *H. halmahera* that were compared with the 16 sequences included in the previous genetic analyses from Allen and Erdmann (2008) (*H. henryi* = 4; *H. ocellatum* = 5; *H. freycineti* = 4; *H. galei* = 2) and Allen and Dudgeon (2010) (*H. michaeli* = 1). The two *H. halmahera* samples had identical sequences. A total of 6 haplotypes were detected for all *Hemiscyllium* species with all species having one haplotype, except for *H. ocellatum* with two haplotypes. In the total *Hemiscyllium* alignment there were 50 variable sites and 43 parsimony-informative characters. Nucleotide frequencies of *H. halmahera* were similar to the other species and average frequencies for the combined *Hemiscyllium* samples were as follows: A = 32, C = 24, G = 0.11, T = 32. Pairwise distances (*d*) between the *Hemiscyllium* species ranged from 0.0103-0.0401. The *H. halmahera* samples clearly differed from all the other *Hemiscyllium* species with pairwise distances ranging from 0.0201-0.0314 which fall within the range of inter-species

differences for the other members of the genus. Pairwise distances between the *Hemiscyllium* species and the outgroup *Chiloscyllium punctatum* ( $d_{ave} = 0.1559$ ) were over an order of magnitude higher than some of the intra-genus distances. Only *H. ocellatum* showed intra-species distance ( $d = 0.0013$ ) which was an order of magnitude lower than the intra genus distances.

The maximum likelihood (ML) and maximum parsimony (MP) trees both clearly separated out *H. halmahera* from the morphologically similar *H. galei*. *H. halmahera* was positioned in a basal position of the *Hemiscyllium* samples with *H. michaeli*. The phylogenetic analyses produced identical trees for most of taxa, but could not resolve the relative positioning of *H. halmahera* and *H. michaeli* with ML analyses placing *H. michaeli* in the most basal position (with low bootstrap support = 49%) and MP analyses reversing this relationship (bootstrap support = 62%; Fig. 11).

**Distribution and habitat:** The new species is known with certainty from satellite islands off the west coast of Halmahera, Indonesia and in Weda Bay in South Halmahera. The type specimens were collected at night in 10 m depth, nestling under coral heads that were sparsely scattered on a steep, black volcanic sand slope off northwestern Ternate Island. It has also been photographed off south-



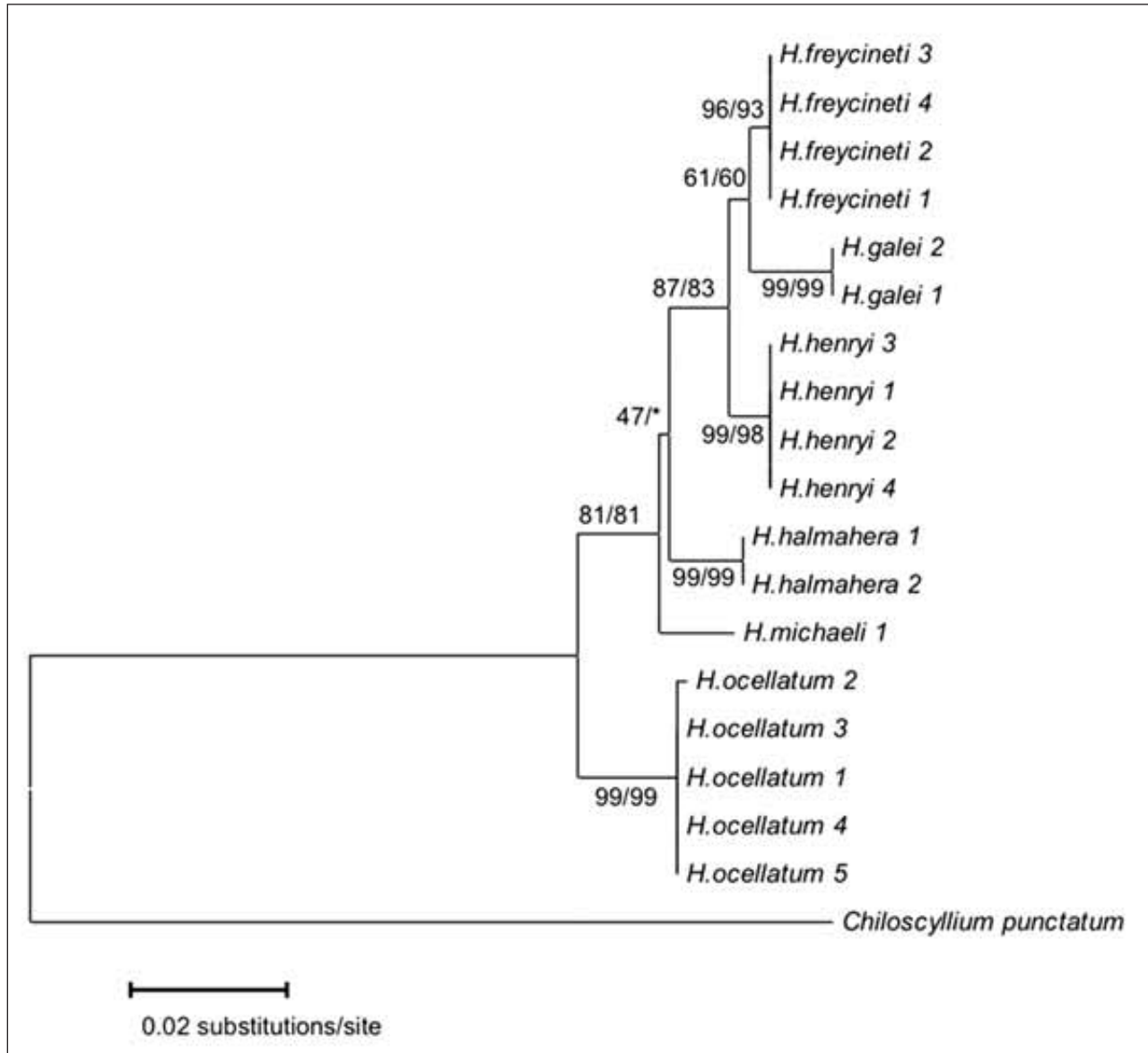
**Fig. 10.** Underwater photograph of *Hemiscyllium galei*, approximately 600 mm TL, Cenderawasih Bay, West Papua Province, Indonesia. Photo by G. R. Allen.

western Halmahera at Proco Island (00°25.264'S, 127°44.264'E), which lies in the Proco Strait between Bacan and mainland Halmahera; at Bacan Island (00°20.371'S, 127°18.153'E); and in Weda Bay in southern Halmahera (00°27.935'N, 127°56.753'E).

**Etymology:** The species is named *H. halmahera* with reference to the type locality. The name is treated as a noun in apposition.

**Remarks:** The new species is the first record for

*Hemiscyllium* beyond the Australia/New Guinea region. Although Halmahera lies in close proximity to New Guinea, the current study extends the known boundary for the genus approximately 300 km further west. As mentioned previously, *Hemiscyllium* species appear to have limited dispersal capabilities, including an apparent inability to cross significant deep-water barriers. For example, the genus is unknown from the island of New Britain, which lies only about 80 km from the



**Fig. 11.** Maximum likelihood (ML) tree (TN93+G) of the ND4 data for six *Hemiscyllium* species. Bootstrap support for 1000 replicates are shown for ML and Maximum Parsimony (MP) trees respectively. ML and MP trees are identical except for the relative positions of *H. halmahera* and *H. michaeli*, which are reversed in the MP phylogeny with bootstrap support of 62% (indicated by \*). The outgroup is *Chiloscyclium punctatum* Müller & Henle, 1838, a member of the other genus in the family Hemiscylliidae.

Papua New Guinea mainland. Based on paleogeographic reconstructions presented by Hall (2002) and Hill & Hall (2003) it seems likely that the ancestral population may have colonized Halmahera sometime after 25 MYA when its island-arc fragments precursor came within close proximity of the northern New Guinea mainland. Then according to these reconstructions, the component parts of Halmahera underwent a long, slow westward drift during the Miocene and Pliocene, arriving at their present position over the past few million years. Therefore, it seems highly likely that the ancestral population of *H. halmahera* was rafted from a distant colonization point to its current location. Similar scenarios involving dispersal of New Guinea freshwater Heteroptera (water striders) via island arc fragments were discussed by Polhemus & Polhemus (1998), and may also explain the presence of the bird-of-paradise *Semioptera wallacii* on Halmahera, despite the family Paradisaeidae otherwise being considered endemic to the island of New Guinea and Australia (Irestedt et al., 2009). We moreover note that there are a number of examples of restricted range New Guinea reef fish species whose ranges just penetrate into Halmahera, including *Pseudochromis ammeri* Gill, Allen and Erdmann, 2012, *P. matahari* Gill, Erdmann and Allen, 2009, *P. pylei* Randall and McCosker, 1989, and *Pentapodus numberii* Allen and Erdmann, 2009, as well as a blenny (*Ecsenius randalli* Springer, 1991) considered endemic to Halmahera that is found occasionally in Raja Ampat, West Papua.

The new species is most similar in colour pattern to *H. galei* (Fig. 10) from Cenderawasih Bay, West Papua. Both species have characteristic broad dark saddles with narrow, white anterior and posterior margins on the dorsal surface of the body, as well as similar post-cephalic markings. However, there are significant differences between the two species. *Hemiscyllium galei* differs in having a row of 7-8 large, horizontally ovate spots on the lower side between the abdomen and caudal-fin base and has more spots (usually about 25) on the dorsal surface of the head. In contrast, *H. halmahera* differs in having far fewer head spots (usually less than 10) and possesses a pair of large dark spots on the ventral surface of the head. Although the general configuration of the post-cephalic spot is similar, that of *H. halmahera* consists of clusters of fragmented spots (with a U-shaped main spot) compared to the solid spots of *H. galei*.

At present, the genus is poorly represented in museum collections and therefore morphometric data is of limited value in separating the various species. However, the new species appears to have an unusually thick tail base (preanal body depth) compared to its congeners. For example, the preanal depth for *H. halmahera* is 2.3-2.6 in the head length compared with values of 3.5-4.5 for *H. galei*, *H. henryi*, and *H. michaeli*. However, more specimens are required for most species to fully evaluate these differences.

The species of *Hemiscyllium* are distinguished mainly on the basis of colour pattern. The following key will serve to identify the nine known species.

#### Key to the Species of *Hemiscyllium*

- 1a. Head and snout with an abrupt black hood; body covered with conspicuous large white spots (northern New Guinea) ..... *H. strahani*
- 1b. Head and snout light in colour, without a black hood but with conspicuous black spots above pectoral fins; body with inconspicuous light spots or spots absent ..... 2
- 2a. Dark spot behind gills relatively small, forming a weak ocellus (or semi-ocellate dark spot) and followed posteriorly by dark brown bar (consisting of 2-3 merged spots in vertical row or 2-3 clusters of fragmented spots)..... 3
- 2b. Dark spot behind gills large, forming 1-2 conspicuous white-rimmed ocelli or merged double ocelli without dark brown bar immediately behind ..... 5
- 3a. Lower side with conspicuous horizontal row of row of 7-8 large, horizontally-oval, dark spots (Cenderawasih Bay, West Papua) ..... *H. galei*
- 3b. Lower side without row of large, horizontally-oval, dark spots along lower side ..... 4
- 4a. Ventral surface of head with pair of large dark spots; snout region of adult with only a few small dark spots (Halmahera)..... *H. halmahera*
- 4b. Ventral surface of head without pair of large dark spots; snout region of adult with numerous small dark spots (Raja Ampat Islands, West Papua) ..... *H. freycineti*
- 5a. Head, body, and fins covered with polygonal, leopard-like spots (eastern Papua New Guinea) ..... *H. michaeli*
- 5b. Head body, and fins covered with numerous

- spots, but more or less round in shape and not polygonal and leopard like ..... **6**
- 6a.** Body covered with numerous, densely clustered, dark small and large spots that form a reticular network of light base colour between them; dark cross-bands well defined on ventral surface of tail (northern Australia).....  
..... *H. trispeculare*
- 6b.** Body with fewer large spots that do not form a reticular network of light ground colour between them; dark cross-bands on tail relatively weak or not reaching ventral surface.....  
..... **7**
- 7a.** Lateral ocellus surrounded by large black spots; spots absent on head in front and below eyes (south-eastern Papua New Guinea) .....  
..... *H. hallstromi*
- 7b.** Lateral ocellus surrounded by relatively small spots; spots present on head in front and below eyes ..... **8**
- 8a.** Lateral ocellus composed of single large, round spot surrounded by distinct white halo; dark spot absent at origin of pectoral and pelvic fins; numerous small dark spots usually present on dorsal fins (northern Australia) .....  
..... *H. ocellatum*
- 8b.** Lateral ocellus usually composed of double, merged ocelli surrounded by poorly defined white halo; dark spot present at origin of pectoral and pelvic fins; dorsal fins usually without small dark spots or if present they are restricted to basal portion of fins (Triton Bay region, West Papua) ..... *H. henryi*

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