Journal of the
Ocean Science Foundation

2016, Volume 23

Review of the bamboo shark genus *Hemiscyllium* (Orectolobiformes: Hemiscyllidae)

GERALD R. ALLEN
Department of Aquatic Zoology, Western Australian Museum,
Locked Bag 49, Welshpool DC, Perth, Western Australia 6986, Australia
E-mail: gerry.tropicalreef@gmail.com

MARK V. ERDMANN
Conservation International Indonesia Marine Program,
Jl. Dr. Muwardi No. 17, Renon, Denpasar 80235, Indonesia
California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, USA
Email: mverdmann@gmail.com

WILLIAM T. WHITE
CSIRO Australian National Fish Collection,
GPO Box 1538, Hobart, Tasmania 7000, Australia
Email: william.white@csiro.au

FAHMI
Research Centre for Oceanography, Indonesian Institute of Sciences (P3O LIPI),
Jl. Pasir Putih No. 1, Ancol Timur, Jakarta 14430, Indonesia
Email: fahmi_lipi@yahoo.com

CHRISTINE L. DUDGEON
University of Queensland, School of Biomedical Sciences,
St Lucia, Queensland 4072, Australia
Email: c.dudgeon@uq.edu.au

Abstract

The bamboo sharks, genus *Hemiscyllium*, comprises a group of nine species mainly restricted to New Guinea and northern Australia, including islands, reefs, and shoals separated from mainland areas by shallow seas. The Indonesian island of Halmahera is the only location lying outside the core region that is inhabited by these sharks. The nine species in the genus are reviewed and their approximate distribution documented, as follows: *H. freycineti* (Raja Ampat Islands, West Papua); *H. galei* (Cenderawasih Bay, West Papua); *H. hallstromi* (Torres Strait, Australia and southeastern Papua New Guinea); *H. halmahera* (Halmahera, Indonesia); *H. henryi* (vicinity

of Triton Bay, West Papua); *H. michaeli* (Milne Bay Province, Papua New Guinea); *H. ocellatum* (northeastern Queensland, Australia); *H. strahani* (central coast of northern New Guinea); and *H. trispeculare* (northwestern Australia and Aru Islands, Indonesia). The most reliable means of identification is color pattern, in combination with geographic distribution: morphology is less useful due to considerable morphological variation, mostly reflecting the highly variable condition of preserved specimens, and meristic comparisons are limited by mostly small sample sizes. Therefore, a key to species based on color pattern is presented, as well as comprehensive illustrative coverage for each species.

Key words: taxonomy, systematics, species, elasmobranch, sharks, Australia, New Guinea, Indo-Pacific Ocean, biogeography, marine biodiversity.

Citation: Allen, G.R., Erdmann, M.V., White, W.T., Fahmi & Dudgeon, C.L. (2016) Review of the bamboo shark genus *Hemiscyllium* (Orectolobiformes: Hemiscyllidae). *Journal of the Ocean Science Foundation*, 23, 51–97.

doi: http://dx.doi.org/10.5281/zenodo.164197

Introduction

The genus *Hemiscyllium* Müller & Henle, 1838 contains small, distinctly patterned sharks, inhabiting the Australia-New Guinea region and the nearby eastern Indonesian island of Halmahera. This genus and the seven Indo-Pacific species of *Chiloscyllium* Müller & Henle, 1837 are the only representatives of the family Hemiscyllidae Gill, 1862. Commonly known as bamboo, epaulette, or walking sharks, they are characterized by nasoral and perioral grooves, short nasal barbels, a small transverse mouth below the eyes, two similar-sized dorsal fins, and a long slender tail. The family was last reviewed by Dingerkus & DeFino (1983) and Compagno (2001), and both of these studies recognized five species of *Hemiscyllium*: *H. freycineti* (Quoy & Gaimard, 1824); *H. hallstromi* (Whitley, 1967); *H. ocellatum* (Bonnaterre, 1788); *H. strahani* Whitley, 1967; and *H. trispeculare* Richardson, 1843. Four additional species have been described in recent years, including *H. galei* Allen & Erdmann, 2008; *H. henryi* Allen & Erdmann, 2008; *H. michaeli* Allen & Dudgeon, 2010; and *H. halmahera* Allen, Erdmann & Dudgeon, 2013. The members of the genus are very similar in body shape and general proportions and, aside from the two Australian species, are poorly represented in museum collections, precluding useful morphological and meristic comparisons. Moreover, the soft and pliable bodies of these sharks, which are often badly misshapen after preservation, results in a wide range of potentially inconsistent measurements. Fortunately they possess distinctive color patterns, and the salient markings generally persist in preservative.

Hemiscyllids are small (usually less than about 85 cm TL and frequently less than 70 cm TL), nocturnally active, bottom-living sharks, which exhibit a peculiar "crawling" gait while foraging for benthic invertebrates and fishes. Many, and probably all, members of the family are oviparous, depositing eggs on the bottom in oval egg cases (Compagno 2001). Although this reproductive mode was reported for all but one (with unknown biology) species of *Chiloscyllium*, there is no information for the species of *Hemiscyllium*, other than *H. ocellatum*, which is also oviparous (Compagno 2001). Assuming that all species are oviparous, it would appear that dispersal opportunities are thus very limited, which may explain the relatively restricted distributions for the individual species. In addition, hatchlings (which are rarely encountered) are essentially independent, miniature adults and, like adults, appear to be strongly home-ranging. The actual distribution of individual species is generally far more restricted than previously reported: Dingerkus & DeFino (1983), Last & Stevens (2009), Compagno & Niem (1998), Compagno (2001), and Allen (2009) have all included erroneous distributional ranges for some species, either encompassing the entire northern coastline of Australia or the periphery of New Guinea.

The purpose of the current paper is to review the state of knowledge of this poorly understood genus, with special emphasis on species identification and the accurate delineation of species ranges. Although morphometric data are included, color pattern, combined with geographic range, remains the best means for distinguishing species. Accordingly, numerous photographs are included of each species and a key is provided based on prominent

color-pattern features. The mitochondrial-DNA marker ND4 has also been shown to be useful for distinguishing species within this genus (Allen *et al*. 2013). Consequently, a separate genetic study involving all nine species of this group is currently in preparation by Dudgeon *et al*.

Materials and Methods

Technical terms and measurements mainly follow those explained and illustrated by Compagno (2001). Subcaudal length (as used by Dingerkus & DeFino [1983]) is the combined measurement of the upper postventral caudal-fin margin and terminal caudal-fin margin. Total length (TL) was measured from the snout tip to the posterior tip of the caudal fin. Head length (HL) was measured from the snout tip to the anterior base (origin) of the pectoral fin. Vertebral counts were obtained from radiographs of available material.

Specimens examined in this study are deposited in the fish collections of the following institutions: Australian Museum, Sydney (AMS); Natural History Museum, London (BMNH); Australian National Fish Collection, Hobart (CSIRO); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSNB); Cornell University, Ithaca, New York (CU); Kanudi Fisheries Research Station (KFRS, now housed at University of Papua New Guinea, Port Moresby); Muséum National d'Histoire naturelle, Paris (MNHN); Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (LIPI), Cibinong, Java, Indonesia (MZB); Pusat Penelitian dan Pengembangan Oseanologi, Jakarta, Java, Indonesia (NCIP, now housed at MZB); Museum and Art Gallery of the Northern Territory, Darwin (NTM); Naturalis-Nationaal Natuurhistorisch Museum, Leiden (RMNH); South Australian Museum, Adelaide (SAMA); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Queensland Museum, Brisbane (QM); United States National Museum of Natural History, Washington, D.C. (USNM); Western Australian Museum, Perth (WAM); Universiteit van Amsterdam (ZMA, now housed at RMNH); Museum für Naturkunde, Berlin (ZMB).

Genus *Hemiscyllium* Müller & Henle, 1838

Hemiscyllium Müller & Henle, 1838: 34 (type species, *Squalus ocellatus* Bonnaterre, 1788, by monotypy).

Diagnosis. Hemiscylliid sharks reaching approximately 850 mm TL; snout short and blunt, distance from snout tip to mouth 1.4–3.2% TL; eyes and supraorbital ridges well elevated; nostrils terminally located on snout tip; nasal barbels very short, 0.7–1.8% TL; mouth slightly closer to snout tip than to eyes; lower labial folds not connected across chin by dermal fold; distance from snout tip to first gill slit 9.9–13.4% TL; distance from anal opening to origin of anal fin 39.4–49.4% TL; pectoral and pelvic fins thick and heavily muscular; pectoral-fin skeleton with propterygium fused to mesopterygium; total vertebral centra 176–204; color pattern variable, generally consisting of large and small dark spots on head and body, and distinctive post-cephalic marking (often an ocellus) above pectoral fin.

Morphometric features. Body and tail relatively slender, tapering posteriorly; precaudal length 1.2–1.4 and head length (HL) 6.2–8.3 in TL; head depth (at pectoral-fin origin) 0.9–1.5 in greatest width of head; eye length 2.6–4.9 in snout length; eye height 1.7–4.2 in eye length; fleshy interorbital space 0.9–1.6 and bony interorbital space 1.2–2.3 in snout length; snout blunt and short, snout length 2.0–3.4, snout tip to mouth 4.4–9.9, snout tip to spiracle 1.1–2.6, snout tip to first gill slit 1.0–1.3, all in HL; gill slits on rear part of head, above and slightly anterior to pectoral-fin base; distance between first and fifth gill slit 2.2–3.8 in HL; height of gill slits gradually increasing posteriorly, first 2.3–5.2 and fifth 1.8–3.4 in snout length.

Mouth small and transverse, positioned well forward on ventral surface of head, its width 1.0–1.4 in snout length; short barbel on each side of ventral snout, length 3.3–7.5 in snout length; maximum width of lower labial flap 3.3–6.1, length of postoral fold (upper labial furrow) 2.5–5.1, length of lower labial furrow 2.3–6.9, all in snout length; teeth pavement-like, composed of numerous rows; individual teeth broad-based with single posteriorly-directed cusp, cusps of innermost rows more developed.

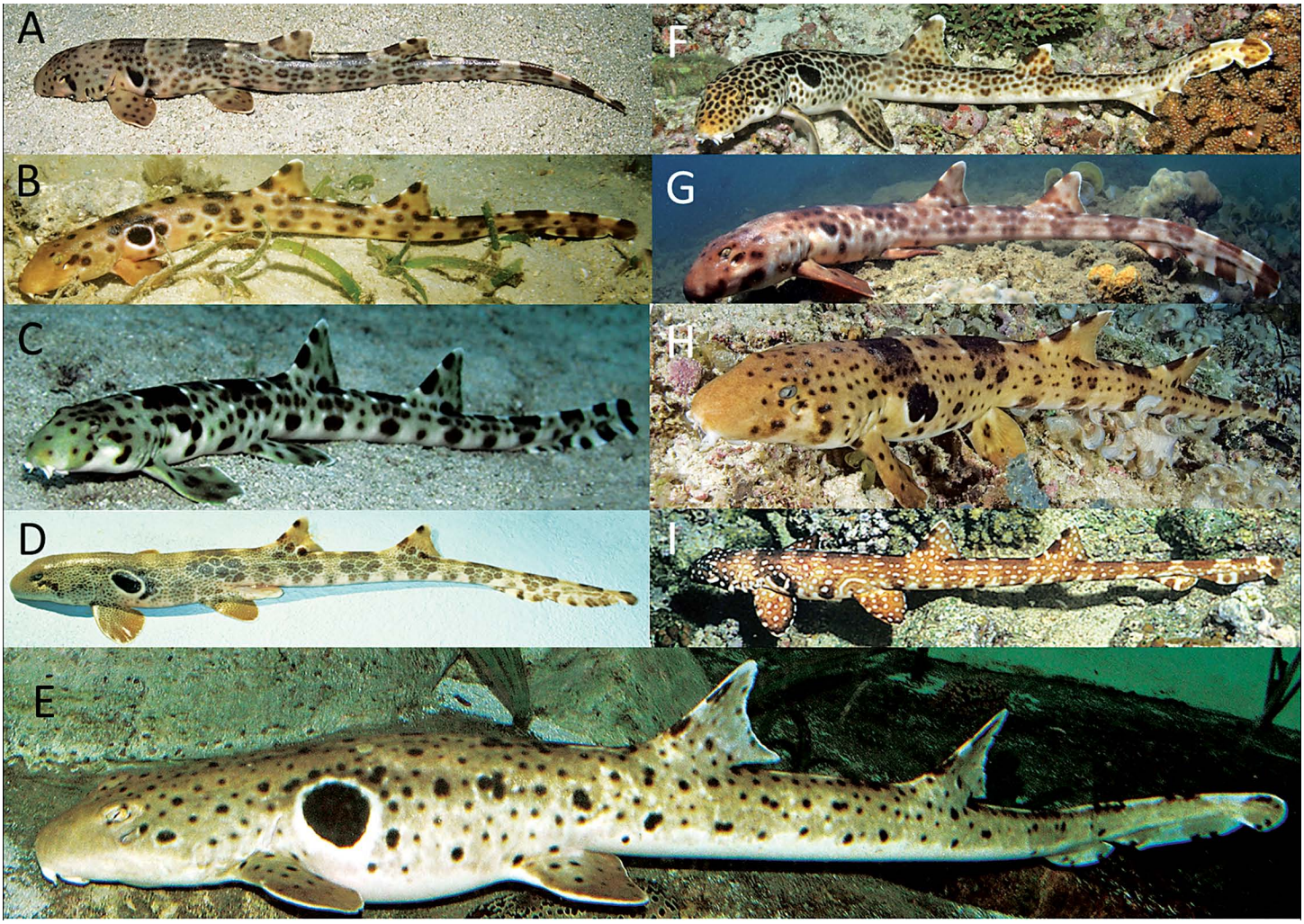

Figure 1. *Hemiscyllium* species A) *H. freycineti*, B) *H. hallstromi*, C) *H. galei*, D) *H. trispeculare*, E) *H. ocellatum*, F) *H. michaeli*, G) *H. halmahera*, H) *H. henryi* & I) *H. strahani* (G.R. Allen, except G by M.V. Erdmann, H by B. Jones, I by S. Michael).

Snout to first dorsal-fin origin 2.4–3.0, snout to pelvic-fin origin 3.1–3.8, snout to cloaca 2.9–3.7, cloaca to anal-fin origin 2.0–2.5, cloaca to caudal-fin tip 1.2–1.5, all in TL. Pectoral fins below gill openings, their length 1.0–1.8 in HL; pelvic fins immediately anterior to vertical line passing through first dorsal-fin origin, their length 1.1–1.8; dorsal fins positioned well back on body, first and second dorsal fins nearly equal in height; first dorsal-fin base 1.3–2.5 in HL, first dorsal-fin height 0.7–1.4 in first dorsal-fin base; free margin of first dorsal fin 1.0–2.8 in first dorsal-fin height; interdorsal space 0.9–1.6 in HL; second dorsal-fin base 1.4–2.4 in HL; second dorsal-fin height 0.8–2.1 in second dorsal-fin base; free margin of second dorsal fin 1.3–3.1 in second dorsal-fin height; long and low anal fin just anterior to caudal fin; anal-fin base 1.0–2.4 in HL, anal-fin height 2.2–5.1 in anal-fin base; free margin of anal fin 0.9–2.3 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 2.0–4.7 in HL; subcaudal length 5.2–8.2 in TL.

Etymology. The genus name is derived from the Latin *hemi*, meaning half and the Latinized *scyllium* (from the Greek *skylion*), meaning dogfish. The gender is considered neuter.

Color. Color-pattern features are highly diagnostic and constitute the best means of separating species. Although differences in the overall patterns of the nine species are obvious (Fig. 1), head and post-cephalic markings are particularly diagnostic (Figs. 2 & 3). Fortunately, these markings usually persist after long periods of preservation. For example, the basic pattern is still clearly discernable on specimens of *H. freycineti* at MNHN, after more than 190 years in preservative (Fig. 4). Although the color pattern of preserved specimens is generally similar to the live coloration, the ground color is usually tan to brownish, with older specimens usually darker. The pattern of dark markings, particularly with respect to the post-cephalic ocellus and general spotting on the head and body is usually apparent.

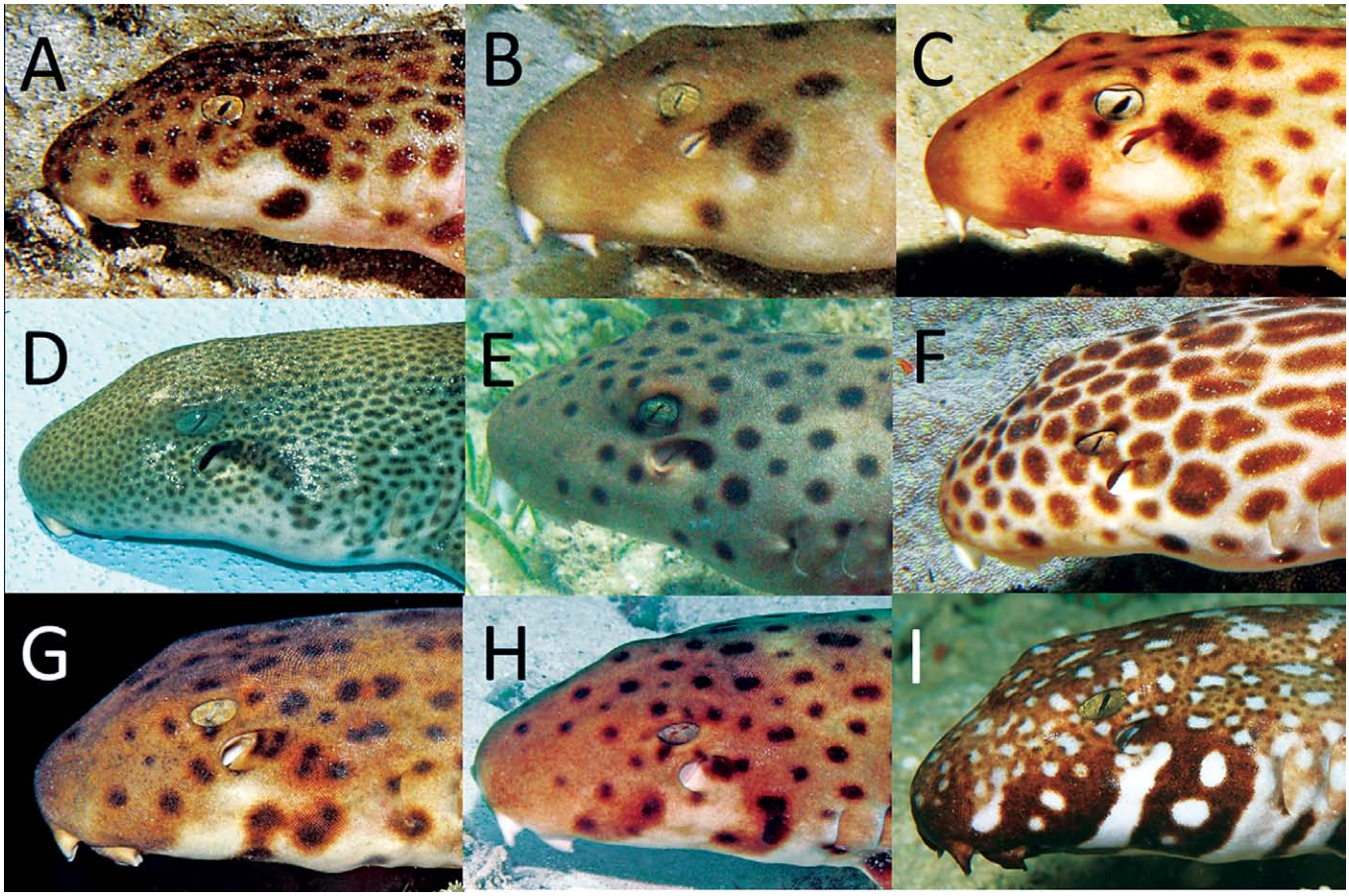

Figure 2. *Hemiscyllium* spp., head markings: A) *H. freycineti*, B) *H. hallstromi*, C) *H. galei*, D) *H. trispeculare*, E) *H. ocellatum*, F) *H. michaeli*, G) *H. halmahera*, H) *H. henryi*, and I) *H. strahani* (G.R. Allen, except E by A. Lewis, G & I by M.V. Erdmann).

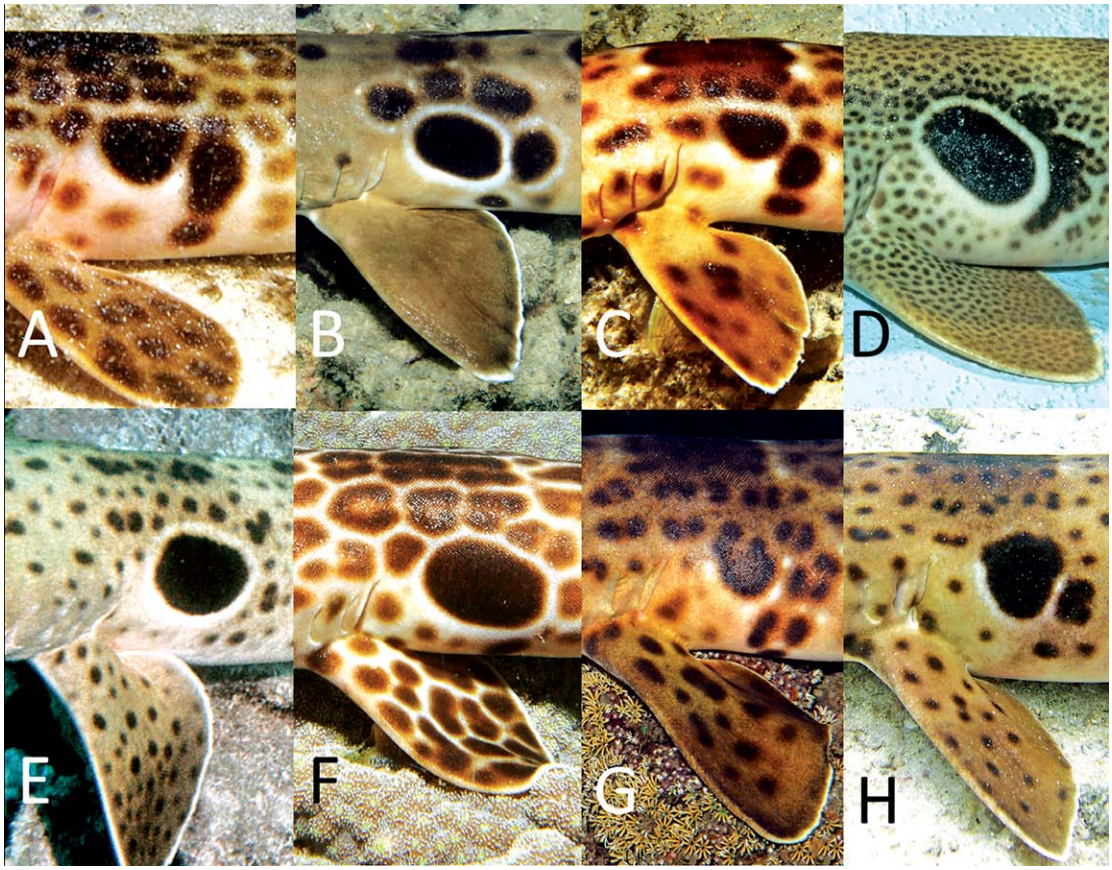

Figure 3. *Hemiscyllium* spp., post-cephalic markings: A) *H. freycineti*, B) *H. hallstromi*, C) *H. galei*, D) *H. trispeculare*, E) *H. ocellatum*, F) *H. michaeli*, G) *H. halmahera*, & H) *H. henryi* (G.R. Allen, except E by R. Steene, G by M.V. Erdmann). Note: *H. strahani*, which has a unique overall pattern, not shown.

Figure 4. *Hemiscyllium freycineti*, preserved female lectotype of *Scyllium malaisianum*, MNHN 7767, 685 mm TL, Waigeo, Raja Ampat Islands, Indonesia (photograph courtesy of MNHN).

A description of the live coloration and comprehensive illustrative coverage is included for each of the species accounts below. We do not include additional description of preserved color patterns, since live color patterns are mostly preserved in museum specimens. Small juveniles differ greatly from larger individuals, but, aside from a few species, remain largely undocumented. We provide photos or drawings of juvenile forms when available.

Distribution. *Hemiscyllium* species are generally confined to the Australia-New Guinea region (Fig. 5) with the exception of a single species (*H. halmahera*) from the Indonesian island of Halmahera, which lies only about 130 km west of the Raja Ampat Group of western New Guinea (West Papua Province, Indonesia). The local distribution encompasses reefs, shoals, and satellite islands connected to the mainland by relatively shallow water (usually not deeper than about 50–100 m), since these sharks are generally unable to cross deep-water barriers, even if the distance is only a few km. Given their benthic reproductive mode and limited swimming ability, poor dispersal capability is the likely explanation for the highly restricted distributions of most of the species.

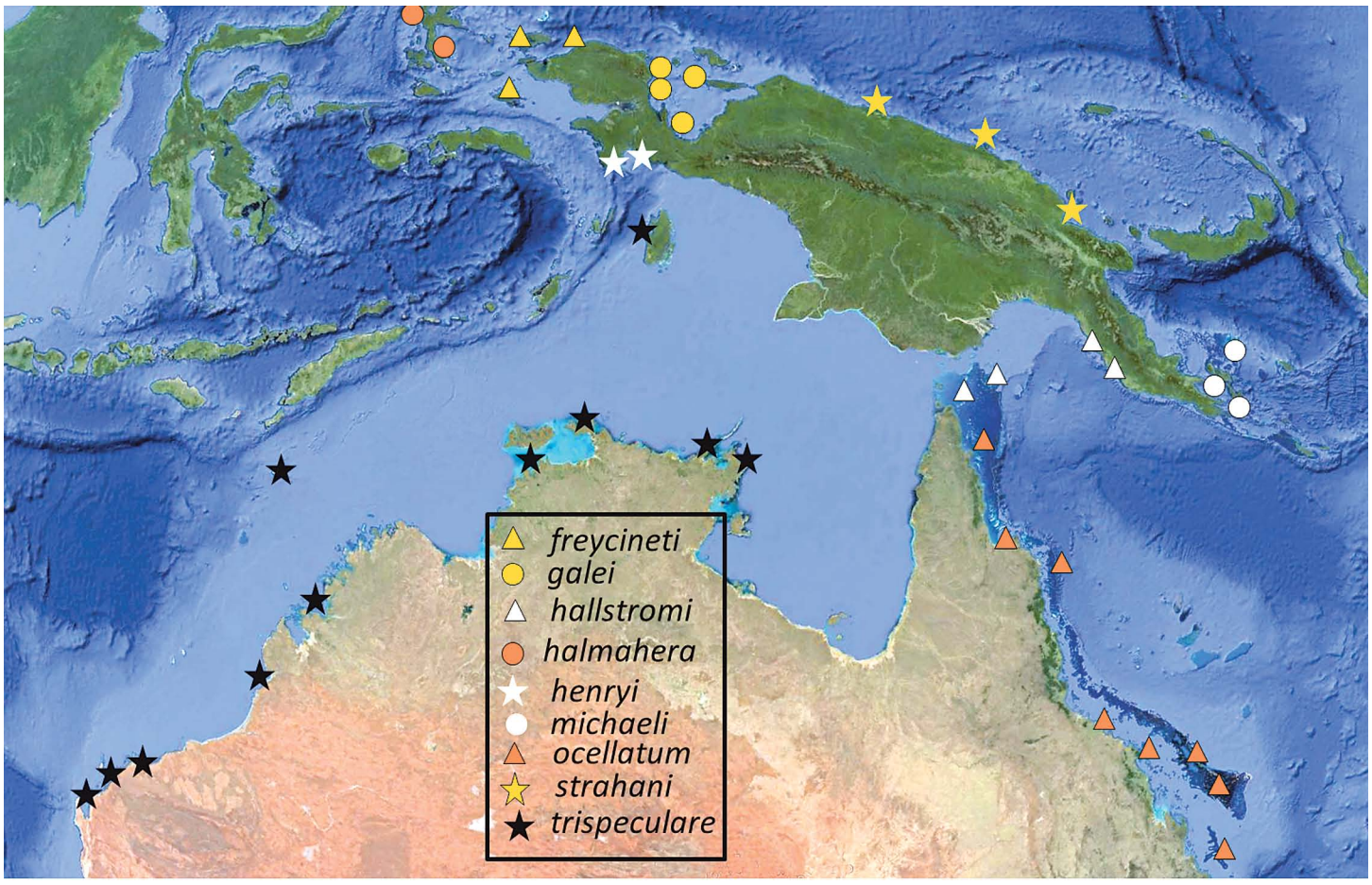

Figure 5. Map of the Australia-New Guinea region showing distributions of species of *Hemiscyllium*.

TABLE 1

Range of morphometric values (as percentage of TL) for species of *Hemiscyllium*

	all species	*freycineti*	*galei*	*hallstromi*	*halmahera*	*henryi*	*michaeli*	*ocellatum*	*strahani*	*trispeculare*
sample size	**87**	**4**	**2**	**13**	**2**	**3**	**5**	**27**	**3**	**28**
Total length (mm)	257–815	337–685	543–568	280–756	656–681	564–815	257–695	287–657	476–731	403–720
Precaudal length	73.2–84.1	77.2–78.6	76.8–82.7	74.5–80.5	76.4–78.3	75.5–83.9	77.6–82.5	75.0–80.6	77.3–84.1	73.2–83.1
Preanal-fin length	69.9–78.8	72.0–75.4	70.5–71.8	72.3–75.6	74.2–75.0	73.2–74.3	72.6–77.0	71.4–78.8	73.3–77.1	69.9–77.1
Head width	6.8–10.4	8.2–10.2	7.5–8.8	7.2–9.6	8.3–8.8	8.5–9.8	7.9–10.3	6.8–9.8	8.7–9.5	7.4–10.4
Head depth	4.5–8.5	6.6–8.4	7.8–8.6	4.5–7.5	6.7–7.3	7.3–8.2	7.1–8.3	5.1–8.4	6.5–7.1	6.2–8.5
Preanal body depth	2.9–6.7	5.5–6.7	3.5–3.6	3.4–4.6	5.2–5.3	3.8–3.9	3.5–4.7	2.9–5.6	4.7–6.1	2.9–5.7
Snout - pectoral-fin origin (HL)	10.8–16.1	13.5–13.8	12.7–13.8	13.0–14.6	12.5–13.3	13.4–13.7	13.0–15.2	10.8–16.0	12.0–14.1	12.1–16.1
Snout - 1st gill slit	9.9–13.4	10.8–12.2	11.7–12.1	10.6–13.4	11.5–11.9	10.7–11.4	11.3–12.1	9.9–12.1	10.8–11.9	10.4–13.1
1st to 5th gill slit	3.6–6.6	5.0–5.5	4.3–4.8	3.6–5.8	4.9–5.0	4.8–5.2	4.2–6.6	3.6–5.9	4.6–5.3	3.8–6.6
First gill slit height	1.0–2.5	1.5–1.7	1.2–1.4	1.2–2.0	1.4–1.5	1.5–1.9	1.4–2.1	1.0–2.0	1.4–1.8	1.5–2.5
Fifth gill slit height	1.8–3.2	2.2–3.0	1.8–2.6	1.8–2.9	2.0–2.1	2.2–2.6	2.1–2.9	1.9–2.9	2.3–2.7	1.9–3.2
Eye diameter (horizontal)	1.2–2.2	1.7–1.9	1.7–1.8	1.2–2.0	1.7–1.8	1.5–1.7	1.4–1.9	1.4–1.8	1.5–1.9	1.5–2.2
Eye diameter (vertical)	0.4–1.0	0.5–0.8	0.7–1.0	0.5–0.9	0.7–0.9	0.6–0.7	0.5–0.7	0.4–0.9	0.5–0.8	0.5–1.0
Bony interorbital width	2.4–3.9	2.7–3.1	3.2–3.4	2.7–3.7	3.3–3.5	3.2–3.4	2.8–3.7	2.4–3.8	2.6–3.8	2.8–3.9
Fleshy interorbital width	3.6–5.3	3.7–4.6	4.2–4.8	3.8–5.0	3.9–4.1	4.0–4.7	3.6–4.9	3.8–5.3	4.1–5.1	4.0–5.2
Snout to eye (snout length)	4.3–6.6	5.6–5.9	6.2	5.4–6.4	5.7–5.8	5.0–6.0	4.3–6.4	4.7–6.1	5.3–6.0	5.1–6.6
Snout to spiracle	5.4–7.6	5.9–6.8	6.6–7.1	6.2–7.4	6.6–6.8	6.2–6.9	6.4–7.1	5.4–6.8	6.2–6.7	6.1–7.6
Snout to mouth	1.4–3.2	1.4–2.3	2.5–2.6	1.7–3.0	2.3–2.7	2.0–2.2	1.9–2.4	1.7–2.7	1.6–1.9	1.8–3.2
Lower labial furrow length	0.8–1.9	1.3	0.9	0.8–1.5	1.1–1.3	1.1–1.2	0.9–1.9	0.8–1.7	1.3–1.4	1.0–1.6
Maximum width lower labial flap	0.5–1.8	1.1–1.3	1.3–1.4	0.6–1.8	1.1	1.0–1.5	0.6–1.4	0.9–1.5	0.5–1.2	0.7–1.6
Postoral fold	1.0–2.2	1.4–1.7	1.7–1.8	1.4–2.2	1.7–1.8	1.5–1.8	1.4–1.9	1.2–2.1	1.0–1.7	1.2–2.0
Mouth width	3.9–5.5	4.4–4.8	4.8–5.1	4.1–5.4	4.2–4.9	4.3–5.1	4.3–5.2	3.9–5.1	4.5	4.2–5.5
Barbel length	0.7–1.8	1.0–1.1	1.1–1.4	1.0–1.6	1.1–1.2	1.5–1.7	0.9–1.5	1.0–1.6	0.9–1.0	0.7–1.8
Snout -1st dorsal origin	33.3–41.3	36.6–37.8	37.2–37.4	33.5–37.6	37.9–40.2	36.8–40.4	33.3–41.3	33.3–38.9	36.0–38.2	33.7–39.0
Snout - pelvic origin	25.4–33.2	28.7–29.7	27.8–28.0	26.6–29.6	29.0–31.2	27.5–30.1	26.8–30.3	26.1–30.6	27.4–29.0	25.4–33.2
Snout - anal opening	27.0–34.8	29.8–32.0	29.7–30.2	28.1–31.1	32.2–33.5	30.3–31.6	27.6–31.3	27.6–32.0	29.8–30.5	27.0–34.8
Anal opening – anal-fin origin	39.4–49.4	42.0–43.6	40.5–41.6	42.7–45.5	40.8–42.9	41.7–44.1	43.1–49.4	40.1–47.5	43.9–46.4	39.4–45.1
Anal opening - tail tip	64.8–75.7	68.5–69.5	68.9–69.6	67.7–70.6	67.0–68.8	66.7–69.9	67.9–75.7	67.2–73.4	68.4–69.1	64.8–73.0
Interdorsal distance	8.8–15.0	12.1–12.3	11.2–11.9	10.8–12.6	11.3–11.8	12.9–13.7	10.5–15.0	10.3–14.7	11.2–11.9	8.8–13.9
Pectoral-fin length	8.6–13.1	9.3–11.1	11.0–11.6	9.0–11.7	11.0–11.7	11.0–11.5	8.6–12.3	8.6–11.7	10.6–10.9	10.1–13.1
Pelvic-fin length	8.5–12.9	9.6–10.0	11.2–11.5	8.5–11.3	9.8–10.4	9.9–10.5	8.6–11.0	8.6–11.4	9.6–10.0	9.2–12.9
1st dorsal-fin base	6.2–10.3	7.3–7.9	8.4–9.3	6.6–9.1	7.4–8.5	6.9–7.7	6.4–8.8	7.0–9.2	7.5–8.6	6.2–10.3
1st dorsal-fin height	5.2–10.1	6.0–7.3	6.7–7.2	5.3–8.1	6.4–8.1	8.2–10.1	5.2–8.9	5.7–8.0	6.2–6.7	5.6–8.7
1st dorsal-fin free margin	2.5–5.3	3.3–3.8	3.7–5.2	2.5–3.8	3.9–4.5	4.2–4.9	2.8–5.3	3.0–4.8	3.6–4.2	3.0–5.2
2nd dorsal-fin base	6.4–9.7	7.4–8.4	7.7–8.1	7.1–9.7	7.7–8.1	7.0–8.3	6.4–8.7	6.7–8.6	7.3–8.0	6.4–9.3
2nd dorsal-fin height	4.9–8.2	5.5–6.9	7.2–7.5	5.3–7.3	7.4	7.0–8.0	4.9–8.1	4.9–7.7	6.0–6.4	5.4–8.2
2nd dorsal-fin free margin	2.3–4.6	2.8–3.4	2.4–3.3	2.5–3.4	3.7–4.0	3.5–4.1	2.6–4.1	2.4–3.8	3.0–4.1	2.3–4.6
Anal-fin base	6.4–12.3	8.6–9.8	8.8–9.8	7.6–9.9	7.8–9.2	9.0–9.8	6.4–9.4	7.1–11.0	7.9–9.2	7.5–12.3
Anal-fin height	1.3–4.2	2.2–2.7	2.9	1.3–3.0	2.8–2.9	3.0–3.3	1.6–2.7	1.6–2.9	2.4–2.8	1.9–4.2
Anal-fin free margin	0.9–2.8	1.5	1.5–1.7	1.0–2.8	1.6–1.9	1.5–2.0	1.2–1.8	1.1–2.0	1.0–1.7	0.9–3.9
Subcaudal	11.6–19.2	12.8–18.9	17.3	12.5–18.2	16.2–17.6	16.6–18.1	12.8–19.2	11.6–18.0	12.5–16.9	12.2–18.8

The two Australian species, *H. ocellatum* and *H. trispeculare*, are the most widespread, ranging around the respective northeastern and northwestern portions of the continent. The remaining species, with the exception of *H. halmahera*, have restricted regional New Guinea distributions, i.e. *H. freycineti* (Raja Ampat Islands, and probably the adjacent West Papua mainland), *H. galei* (Cenderawasih Bay, West Papua), *H. hallstromi* (Torres Strait and Gulf of Papua to the eastern extremity of Papua New Guinea), *H. henryi* (Triton Bay to southwestern Bomberai Peninsua, West Papua), *H. michaeli* (Milne Bay and Oro provinces, Papua New Guinea), and *H. strahani* (north coast of New Guinea from the vicinity of Madang, Papua New Guinea at least as far west as the vicinity of Jayapura, Papua Province of Indonesia).

Although our field and museum investigations have yet to uncover a single example of overlapping ranges among the nine described species, the precise limits to the distribution of many of the New Guinea species are not well-known. In general, their distributions seem bounded by either deep water (which they appear to be unable to cross) or habitat disjunctions caused primarily by large-river outlets with associated mangrove/soft-bottom habitat. Nonetheless, there are significant stretches of the New Guinea coastline that remain unknown with respect to *Hemiscyllium* occurrence, including the Gulf of Papua north of Port Moresby, the Casuarina Coast between Merauke and Etna Bay on the south of New Guinea, the Bomberai Peninsula and Bintuni Bay, the northern Bird's Head between Sorong and Manokwari, the Sarmi coastline west of Jayapura, and the Huon Gulf region between Lae and Tufi. Further surveys are planned for each of these regions in order to determine the precise geographic ranges of the New Guinea *Hemiscyllium* species.

Importantly, there are no substantiated records of *Hemiscyllium* from most of the larger islands off the coast of New Guinea including Biak, Manus, New Britain, New Ireland, Bougainville (or even Kai or Seram); while many of these islands are within 50–150 km of known populations of *Hemiscyllium*, they are separated by deep (>200 m, and often >1000 m) channels that appear to prevent dispersal. The only islands off New Guinea that do support *Hemiscyllium* species are either connected to the shallow Papuan continental shelf (i.e. Misool and Salawati in Raja Ampat, as well as Aru, Yapen, & D'Entecasteaux), or are comprised of island-arc fragments that were once close to the New Guinea mainland but have subsequently moved further away by tectonic action (i.e. Halmahera, as well as Batanta and Waigeo in Raja Ampat).

Sexual dimorphism. Male hemiscyllids, like other elasmobranchs, possess distinctive paired claspers used to grasp the female during copulation. This structure varies greatly in size within species. Apparently, immature sharks, even those in excess of 500–600 mm TL, have small undeveloped claspers (Fig. 6, upper) until the onset of maturation, at which time they undergo pronounced enlargement (Fig. 6, lower). Judging from the apparent rarity of intermediate-sized claspers, the transformation from small to large is probably rapid. Although our sample size is relatively small, mature males have the inner clasper length 6.7–11.9% TL and outer clasper length 5.5–9.5% TL (n=17) vs. inner clasper length 2.8–4.5% TL and outer clasper length 0.9–

Figure 6. *Hemiscyllium* spp., comparison of male claspers– *H. henryi*, immature, 564 mm TL (upper); *H. galei*, mature, 568 mm TL (lower)(G.R. Allen).

2.0% TL for immature males (n=13). We lacked a sufficient sample size of males to determine whether or not there is a diagnostic difference in clasper size between species.

Biology. Hemiscyllids are usually found in shallow water, either on coral reefs or mixed sand, rubble, and seagrass flats. They exhibit a distinctive crawling form of locomotion, by utilizing their muscular pectoral and pelvic fins (Goto *et al*. 1999). It is not unusual to encounter these sharks in wading depths or stranded in rock pools at extreme low tides, sometimes only partially submerged. Wise *et al*. (1998) noted that the Australian *H. ocellatum* is able to survive in an environment with cyclic periods of low oxygen concentration, suggesting that it is tolerant to both mild hypoxia and cyclic exposure to extreme hypoxia. Söderström *et al*. (1999) further showed that blood pressure drops by 50% during hypoxia, indicative of a compensatory cerebral vasodilatation that maintains cerebral blood flow. Although these sharks are routinely encountered in less than 2–3 m depth, our deepest records are from approximately 20–30 m.

These sharks are nocturnally active, remaining more-or-less stationary in the shelter of crevices, ledges, or under table coral (*Acropora*) during daylight hours. Principal food items include small bottom fishes, cephalopods, shelled mollusks, and crustaceans (Compagno 2001). Heupel & Bennett (1998) analyzed stomach contents of *H. ocellatum* from Australia's Great Barrier Reef and found worms and crabs to be by far the dominant items, with smaller amounts of shrimps, small fishes, and amphipods.

Videos of *H. freycineti*, *H. halmahera*, and *H. ocellatum* (accessed 29 October 2016 at https://www.youtube.com) show a mating ritual in which the male first grasps the female with its jaw teeth, either by one pectoral fin or higher on the body above the pectoral fin. Once the female is firmly secured, the pair either lie stationary on the bottom, side by side, or swim horizontally for a short period, then rolling over or spinning with the genital areas of each shark in close proximity. The sharks then assume a vertical "head-stand" position while the male inserts one of its claspers. The pair remain locked in this embrace for up to several minutes before suddenly separating and swimming off in different directions. Aquarium observations indicate *Hemiscyllium* species are oviparous, depositing eggs on the bottom in oval-shaped cases, which, for *H. ocellatum*, are about 80–90 mm long and about 40 mm wide. According to information from a video ("Baby Epaulette Sharks at the Tennessee Aquarium" by TennesseeAquarium.org; accessed 10 October 2016 at https://www.youtube.com/watch?v=CXUvB-cj9cA), young *H. ocellatum* emerge from the egg case about 130 days after it is laid, at a size of approximately 150 mm TL. The young reach a size of about 200 mm TL after 4 months, about 300 mm TL after 12–18 months, and about 450–510 mm TL after two years.

Remarks. Proportional measurements were of limited utility in the current study, although we obtained morphometric data for 39 separate measurements (Table 1). The main problem was a lack of sufficient specimens for most species, with the exception of *H. hallstromi*, *H. ocellatum*, and *H. trispeculare*. Although we frequently detected differences between species for various proportional measurements, such as snout length, barbel length, pectoral-fin length, among others, the differences were almost always found between species represented by only a few specimens, which tend to show a narrow range of values. For example, the second dorsal-fin height of *H. freycineti* (5.5–6.9% TL) differed from the collective values (7.0–8.0% TL) for *H. galei*, *H. halmahera*, and *H. henryi*, but these 4 species were represented by a total of only 11 specimens. In contrast, 55 specimens of *H. ocellatum* and *H. trispeculare* revealed a broad range of values (4.9–8.2% TL) for this same measurement, indicating that a similarly wide range could be expected for most species if sufficient material was available. Unfortunately, the prospect for collecting 20–30 specimens of each of the data-deficient species is unlikely due to the increasing difficulty of obtaining collecting permits, and the difficulties involved with preserving and transporting specimens of this size, even though they are small in relation to most sharks. Another consideration is the high conservation value placed on these charismatic, but vulnerable, animals, both by the dive-tourism industry as well as environmental agencies. Fortunately, the critical need for specimens has been ameliorated to a certain degree by the use of tissue samples and concurrent photographic vouchers. In our experience, tissue samples can easily be excised from living sharks by divers, offering an effective alternative to collecting museum specimens. Analysis of the mitochondrial-DNA marker ND4 revealed that sequences distinguish the six species studied by Allen *et al*. (2013) and this approach is currently being applied to all species. Moreover, future studies involving entire genomes will no doubt further clarify the phylogenetic relationships within the genus.

Key to the species of *Hemiscyllium*

1a. Head and body with numerous white spots and dash-like markings; chin and underside of snout with extensive dark brown markings (Fig. 43; northern New Guinea) .....*H. strahani* (p. 89)

1b. Head and body without white markings or, if present, relatively few and concentrated dorsally around dark saddles; underside of snout without extensive dark brown marking, usually plain white, or with a pair of large dark spots (in *H. halmahera*) 2

2a. Post-cephalic marking lacks a distinct ocellus (Figs. 3A, C & G) 3

2b. Post-cephalic marking includes a large, distinct ocellus (Figs. 3B, D, E, F & H) 5

3a. Lower side of body with horizontal row of 7–8 large, round -to-horizontally ovate, dark spots (Cenderawasih Bay, West Papua) .....*H. galei* (p. 66)

3b. Lower side of body without row of large, round-to-horizontally ovate, dark spots 4

4a. Ventral surface of head with a pair of large dark spots (Fig. 24); scattered, small white spots on body; snout region of adult with only a few small dark spots (Fig. 2G) .....*H. halmahera* (p. 74)

4b. Ventral surface of head without a pair of large dark spots; no small white spots on body; snout region of adult with numerous small dark spots (Fig. 2A)(Raja Ampat Islands, West Papua) .....*H. freycineti* (p. 61)

5a. Head, body, and fins covered with polygonal, leopard-like spots (eastern Papua New Guinea) ....*H. michaeli* (p. 81)

5b. Head, body, and fins covered with numerous spots, but more-or-less round and not polygonal or leopard-like 6

6a. Preorbital snout with dense network of small brown spots (Fig. 2D)(northwestern Australia and Aru Islands, Indonesia) .....*H. trispeculare* (p. 92)

6b. Preorbital snout without dark spots or with only a few spots (Fig. 2B, E & H) 7

7a. Post-cephalic ocellus surrounded by large black spots (Fig. 3B); dark spots usually absent on head in front and below eyes (Fig. 2B); many body spots at least twice eye size (southeastern Papua New Guinea) ....*H. hallstromi* (p. 70)

7b. Post-cephalic ocellus surrounded by relatively small spots; at least a few spots usually present on head in front and below eyes; most dark spots less than twice eye size 8

8a. Post-cephalic ocellus usually composed of an irregularly shaped ocellus (typically a merged double-ocellus), surrounded by a poorly defined white halo (Figs. 3H & 31)(Triton Bay region, West Papua) ....*H. henryi* (p. 78)

8b. Post-cephalic ocellus (Fig. 3E) composed of a single large, round spot surrounded by a distinct white halo (Queensland, Australia) .....*H. ocellatum* (p. 84)

Hemiscyllium freycineti (Quoy & Gaimard, 1824)

Freycinet's Epaulette Shark

Figures 1A, 2A, 3A, 4 & 7–13; Table 1.

Scyllium freycineti Quoy & Gaimard, 1824: 192 (type locality: Waigiou=Waigeo, Raja Ampat Islands, West Papua Province, Indonesia).
Scyllium malaisianum Lesson, 1831: 94, Poissons, Pl. 6 (type locality: Waigiou = Waigeo, Raja Ampat Islands, West Papua Province, Indonesia); Günther 1870: 411.
Chiloscyllium malaianum (misspelling) Müller & Henle, 1841 (or 1838): 20.
Chiloscyllium freycineti Regan, 1908: 359 (in part).
Hemiscyllium freycineti Garman, 1913: 46.

Diagnosis. A species of *Hemiscyllium* distinguished by a dense network of relatively large brown spots covering head, body, and fins, those on side of body generally arranged in clusters forming polygons; post-cephalic ocellus generally fragmented, consisting of large, dark-brown, anterodorsal spot and posterior dark-brown bar or vertical row of 2–3 coalesced spots; series of about 9 bars from level of pectoral fins to tail tip, each consisting of a dark-brown saddle on back continued on side of body as a darkening of the polygon-shaped clusters of brown spots; prominent saddle-like markings near base of anterior edge of both dorsal fins, a smaller less conspicuous saddle or large spot on margin above, near apex of fin; snout and dorsum of head profusely covered with brown spots, about 50–60 anterior to spiracle in adults; dorsal surface of pectoral and pelvic fins usually with more than 10 large brown spots and a narrow white posterior margin.

Morphometric features. (based on 4 specimens, 337–685 mm TL) Precaudal length 1.3 in TL, head length 7.3–7.7 in TL; head width 1.3–1.7 in HL; head depth 1.2–1.3 in head width; eye length 3.0–3.6 in snout length,

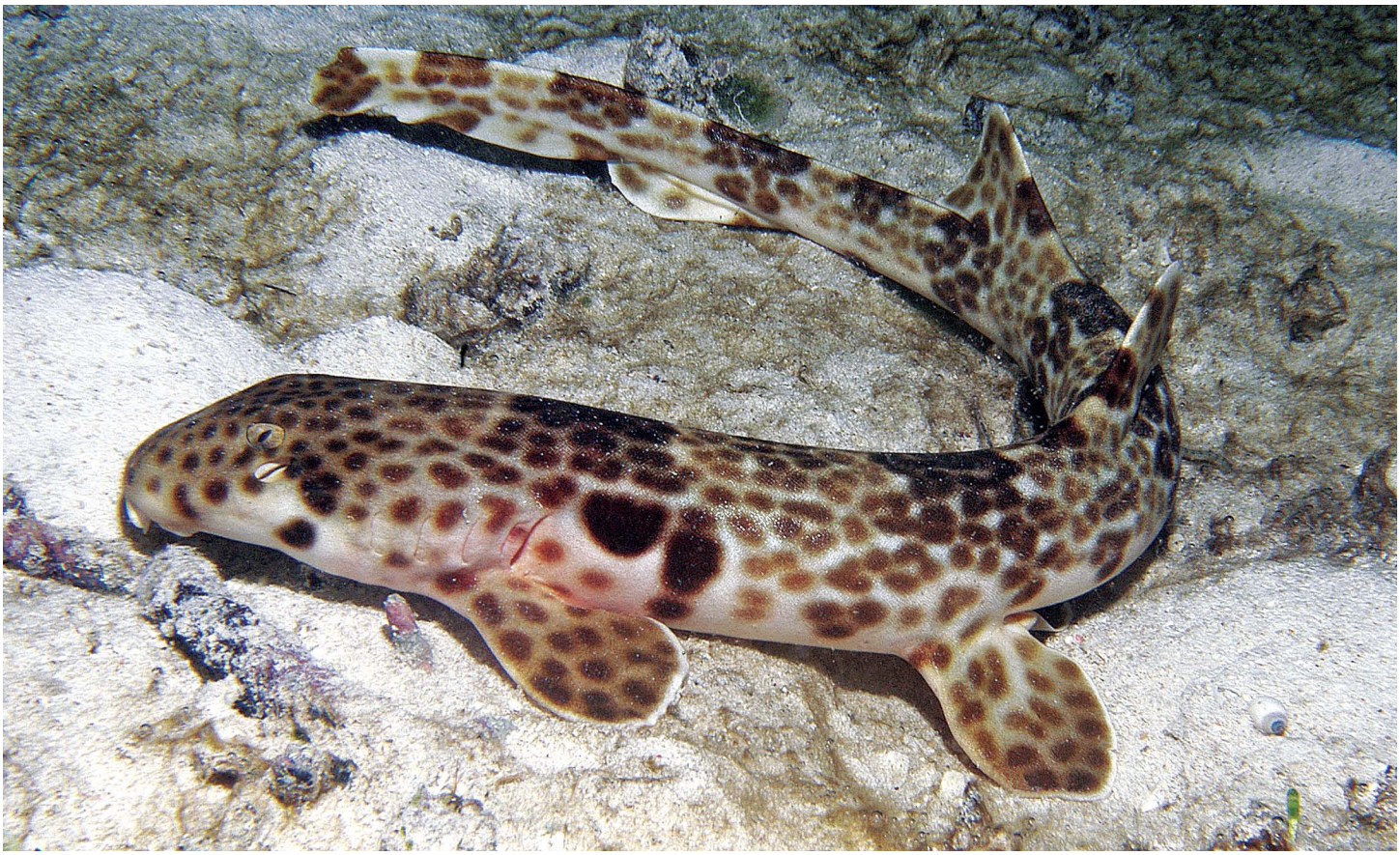

Figure 7. *Hemiscyllium freycineti*, approx. 650 mm TL, Kri Island, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen).

eye height 2.2–3.6 in eye length; fleshy interorbital space 1.3–1.5, bony interorbital space 1.8–2.1, both in snout length; snout length 2.3–2.4, snout tip to mouth 5.8–9.9, snout tip to spiracle 2.0–2.3, snout tip to first gill slit 1.1–1.3, all in HL; distance between first and fifth gill slit 2.5–2.8 in HL; height of first gill slit 3.4–4.4, height of fifth gill slit 1.9–2.8, both in snout length.

Mouth width 1.2–1.3, length of nasal barbel 5.2–7.9, maximum width of lower labial flap 4.2–5.2, length of postoral fold (upper labial furrow) 3.0–4.1, length of lower labial furrow 3.1–4.4, all in snout length.

Snout to first dorsal-fin origin 2.6–2.7, snout to pelvic-fin origin 3.3–3.5, snout to cloaca length 3.1–3.4, cloaca to anal-fin origin 2.2–2.4, cloaca to caudal-fin tip 1.4–1.5, all in TL. Pectoral-fin length 1.2–1.5 in HL; pelvic-fin length 1.4–1.5 in HL; first dorsal-fin base 1.7–1.8 in HL, first dorsal-fin height 1.0–1.4 in first dorsal-fin base; free margin of first dorsal fin 1.8–1.9 in first dorsal-fin height; interdorsal space 1.0–1.1 in HL; second dorsal-fin base 1.6–1.8 in HL; second dorsal-fin height 1.2–1.6 in second dorsal-fin base; free margin of second dorsal fin 1.6–2.4 in second dorsal-fin height; anal-fin base 1.4–1.6 in HL, anal-fin height 3.5–5.5 in anal-fin base; free margin of anal fin 1.4–1.8 in anal-fin height; body depth at level of anal-fin origin 2.0–2.5 in HL; subcaudal length 5.3–7.8 in TL.

Vertebral counts. Total vertebral centra 188–194 (6 specimens from Dingerkus & DeFino [1983])

Color in life. (Figs. 7–12). Overall pale yellowish brown, grading to white on ventral surface with a dense network of relatively large brown spots covering head, body, and fins, those on side of body generally arranged in clusters forming polygons; post-cephalic ocellus (Figs. 3A and 9) generally fragmented, consisting of large dark-brown, anterodorsal spot and posterior dark-brown bar or vertical row of 2–3 coalesced spots; series of about 9 bars from level of pectoral fins to tail tip, each consisting of a dark brown saddle on back continued on side of body as a darkening of the polygon-shaped clusters of brown spots; prominent saddle-like markings near base of anterior edge of both dorsal fins, a smaller less conspicuous saddle or large spot on margin above, near apex of fin; snout and dorsum of head profusely covered with brown spots, about 50–60 anterior to spiracle in adults; 3 large (about twice eye size), dark-brown-to-blackish spots on cheek, below and behind eye, dorsalmost in contact with spiracle; dorsal surface of pectoral and pelvic fins of adults usually with more than 10 large brown spots and a narrow white margin. Two subadults (Figs. 10 and 11), approximately 320–420 mm TL, with same basic pattern, but with fewer brown spots on head and body. Live colors of juveniles unknown, but preserved specimens display prominent dark bars (Fig. 13).

Figure 8. *Hemiscyllium freycineti*, approx. 580 mm TL, Kri Island, Raja Ampat Islands, West Papua, Indonesia (M.V. Erdmann).

Distribution and habitat. This species is common throughout the Raja Ampat Islands including Misool, Salawati, Batanta, and Waigeo, off the extreme western end of the island of New Guinea (Fig. 5). Importantly, it has not been observed (and local villagers are confident it does not exist there) in the Ayau-Asia atoll system off the northeast corner of Waigeo, which, although a mere 40 km offshore, is separated from the mainland by depths of over 1500 m. *Hemiscyllium freycineti* no doubt occurs along the nearby mainland, but records are lacking aside from a juvenile, 148 mm TL, reported from Amsterdam Island (0°22.309' S, 132°9.479' E) as *Hemiscyllium* sp. by Dingerkus & DeFino (1983). Importantly, the easternmost and southernmost limits of distribution of the species along the mainland are currently unknown; future studies will aim to determine the position of the break between *H. freycineti* and *H. galei* along the northern coast of the Bird's Head Peninsula between Sorong and Manokwari, and that between *H. freycineti* and *H. henryi* along the Bintuni Bay and Bomberai Peninsula coastline. The preferred habitat includes shallow seagrass flats and coral reefs to depths of at least 10 m, but usually in less than about 2–3 m. It is usually encountered in the open at night and shelters under rocks and coral ledges during the day. The first author found 9 individuals while wading over a mainly dry section of reef flat at Kri Island (0°33.324' S, 130°41.103' E), measuring approximately 200 x 100 m, during an exceptionally low spring tide in April 2013.

Etymology. The species was named in honor of Louis de Freycinet, captain of the French naval vessel *Uranie*, which made an epic three-year voyage (1817–1820) of exploration

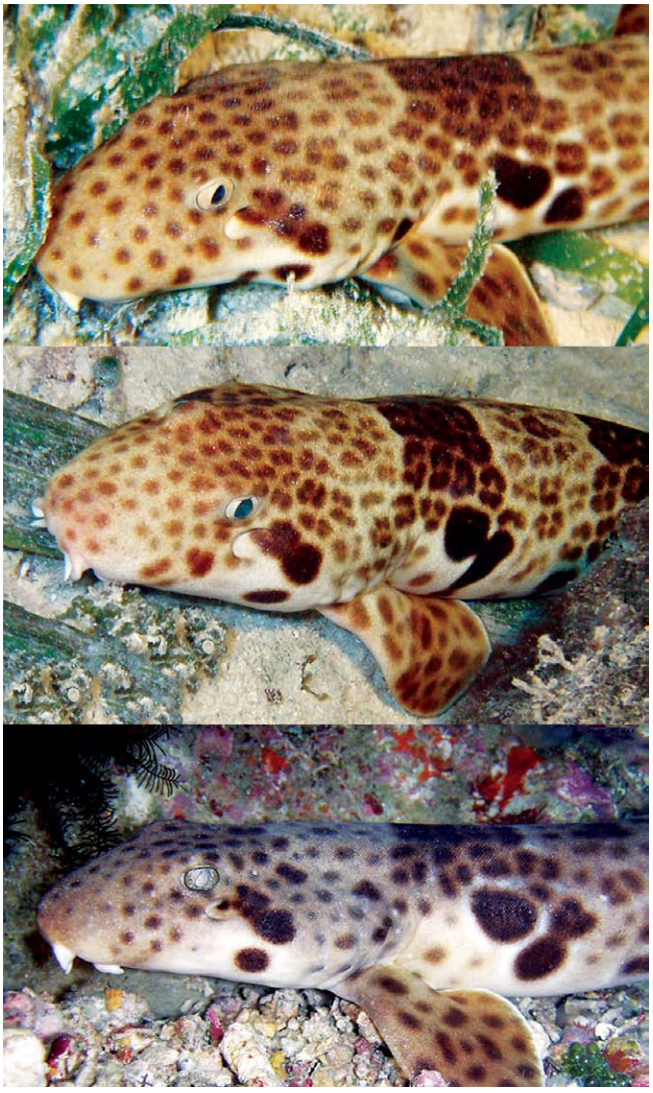

Figure 9. *Hemiscyllium freycineti*, variability of markings on head and post-cephalic area, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen & M.V. Erdmann).

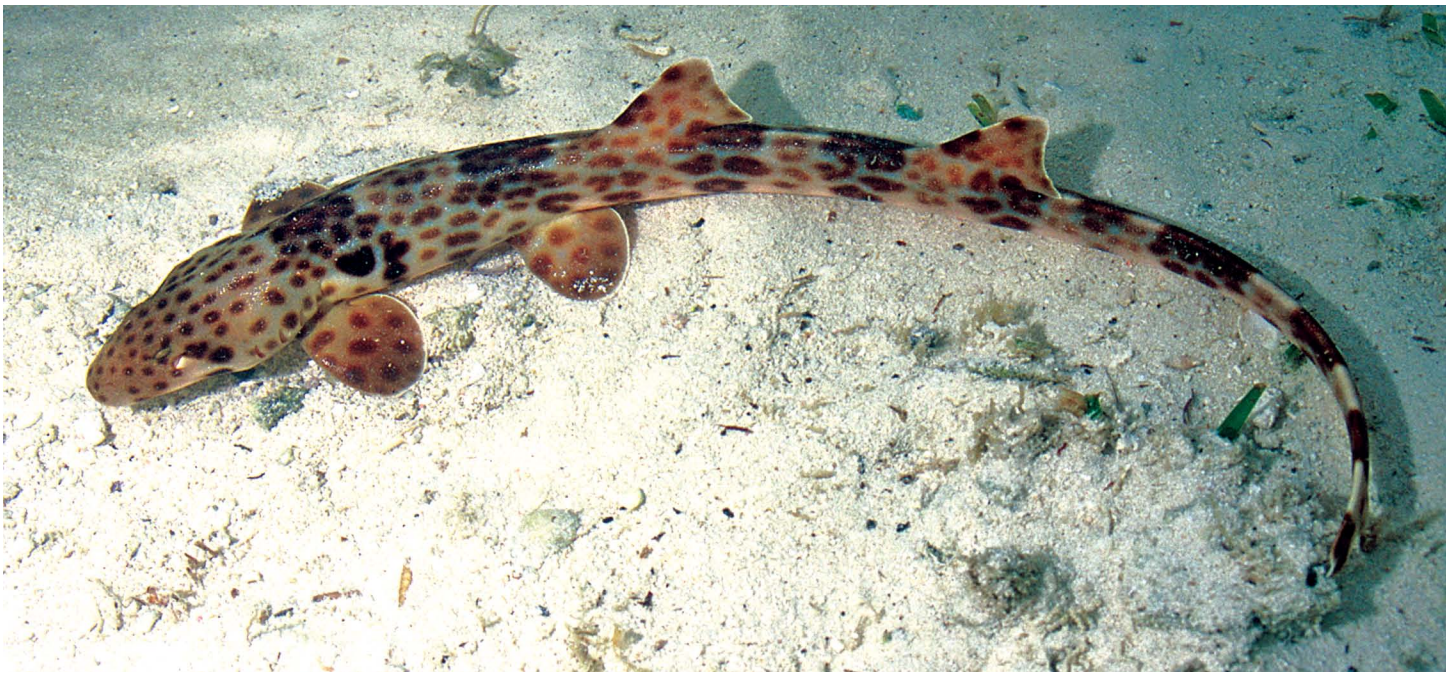

Figure 10. *Hemiscyllium freycineti*, approx. 420 mm TL, Kri Island, Raja Ampat Islands, West Papua, Indonesia (G.R. Allen).

and discovery. Although never punished for a clear breach of naval regulations, Captain Freycinet achieved considerable notoriety by sneaking his wife Rose aboard the ship, who ultimately endured the entire journey. The ship anchored at a small island off the north coast of Waigeo, Raja Ampat Islands in December 1818, spending about three weeks provisioning for the next leg of the journey (to Guam) and collecting natural history specimens, including the shark that now bears Freycinet's name.

Comparisons. This species was confused with *Hemiscyllium michaeli* by past authors (see remarks section below). However, the two species, which have widely separated geographic distributions (at opposite ends of New Guinea), are readily distinguished on the basis of color pattern (compare Figs. 7–12 with Figs. 33–36). Both species have a profuse covering of brown spots with a large post-cephalic ocellus. The leopard-like spots of *H. michaeli* are generally larger and more distinctly polygonal. In contrast the spots of *H. freycineti* are round to transversely elongate and are darkened at regular intervals to form 8–9 dorsal bars or saddle-like markings (including those on tail). Moreover, the markings of *H. freycineti* are more diffuse and less dense compared to those of *H. michaeli*. The difference in spot pattern between the two species is particularly evident on the head (Figs. 2A vs. 2F & 12). The spots of *H. michaeli* remain leopard-like in this region and are more densely arranged compared with the relatively sparse arrangement of spots on *H. freycineti*. In addition, *H. michaeli* possesses a vivid post-cephalic ocellus, whereas that of *H. freycineti* is comparatively poorly defined and usually fragmented. Comparison of similar-sized juveniles of *H. freycineti* (Fig. 13) and *H. michaeli* (Fig. 36) reveals less pronounced bars and a more ornate pattern consisting of a number of large spots between the pectoral and pelvic fins and smaller ocellated spots on the head and body of *H. freycineti*.

The morphometric data (Table 1) suggest that *H. freycineti* differs to a small degree from the other species in some metrics (however, only 4 specimens were examined, and a larger sample will likely erode these differences). Nevertheless, *H. freycineti* has a longer (5.0–5.5% TL) first to fifth gill slit distance, a shorter snout (5.6–5.9% TL), a narrower mouth (4.4–4.8% TL), and a shorter first dorsal-fin base (7.3–7.9% TL) than *H. galei* (vs. 4.3–4.8, 6.2, 4.8–5.1, and 8.4–9.3% TL respectively). It also has a narrower bony interorbital (2.7–3.1% TL) vs.

Figure 11. *Hemiscyllium freycineti*, approx. 320 mm TL, Kri Island, Raja Ampat Islands, West Papua, Indonesia (M.V. Erdmann).

H. galei, *H. halmahera*, and *H. henryi* (collective range of 3.2–3.5% TL); a wider interdorsal space (12.1–12.3% TL) vs. *H. galei*, *H. halmahera*, and *H. strahani* (collective range of 11.2–11.9% TL); a narrower interdorsal space (12.1–12.3% TL) than H. henryi (12.9–13.7% TL); a shorter first dorsal-fin free margin (3.3–3.8% TL) than *H. halmahera* and *H. henryi* (collective range of 3.9–4.9% TL); and a shorter second dorsal fin (length 5.5–6.9% TL) than *H. galei*, *H. halmahera*, and *H. henryi* (collective range of 7.0–8.0% TL).

Remarks. This species was erroneously reported from eastern Papua New Guinea (Milne Bay and Oro provinces) by Dingerkus & DeFino (1983), who confused it with the yet-to-be described *H. michaeli*. Based on this record from the eastern end of the island, Compagno (1984, 2001) incorrectly assumed that its range encompassed the entire coastline of New Guinea. The correct distribution for *H. freycineti* and *H. michaeli*, which respectively occupy the westernmost and easternmost portions of New Guinea, was discussed by Allen & Erdmann (2008) and Allen & Dudgeon (2010).

The species was described by Quoy & Gaimard (1824) on the basis of two specimens from Waigeo. They wrongly attributed authorship to Cuvier, stating that Cuvier had used the name *freycineti* on labels that accompanied the specimens in the exhibition hall of the Paris Museum (MNHN). However, Quoy & Gaimard provided the first published description and are therefore credited

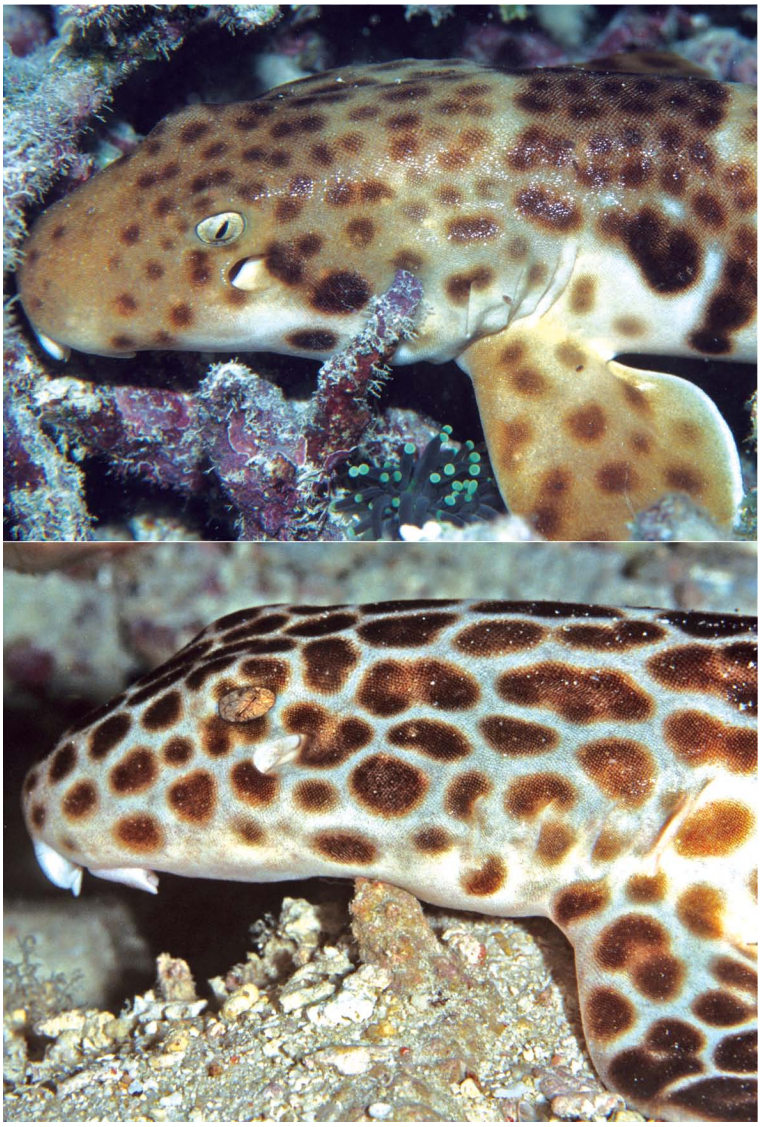

Figure 12. Head markings of *H. freycineti*, approx. 650 mm TL (upper) and *H. michaeli*, approx. 700 mm TL (lower)(G.R. Allen).

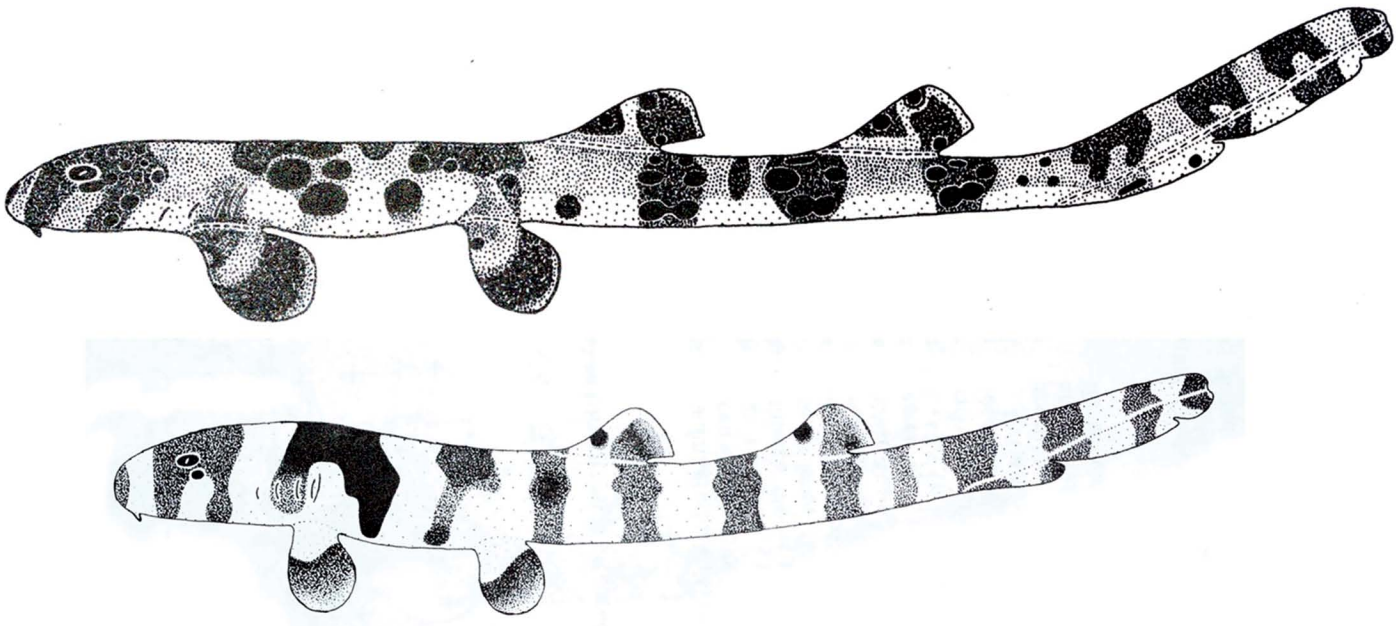

Figure 13. *Hemiscyllium freycineti*, juveniles, 214 mm TL (upper) and 148 mm TL (lower), West Papua, Indonesia, from Dingerkus & DeFino (1983).

with authorship. The larger specimen (MNHN A.7792), a male, 321 mm TL, was designated as the lectotype by Dingerkus & DeFino (1983). Apparently unaware of Quoy & Gaimard's description, the species was described as *Scyllium malaisianum* by Lesson (1831) based on a 685 mm TL specimen, also collected at Waigeo.

Material examined. (all Raja Ampat Islands, West Papua, Indonesia; asterisk indicates detailed morphological data taken, see Table 1) MNHN A. 7767* (lectotype of *Scyllium malaisianum*), female, 685 mm TL, Waigeo Island; MNHN A. 7792* (lectotype; also paralectotype of *S. malaisianum*), juvenile male, 321 mm TL, Waigeo, Island; MNHN B. 2962 (paralectotype; also paralectotype of *S. malaisianum*), juvenile male, 293 mm TL, Waigeo Island; RMNH 20499*, juvenile male, 429 mm TL, Sissi, near Misool Island; USNM 246780, south coast Misool Island; ZMA 112.225*, female, 337 mm TL, between Waigeo and Saonek Islands.

Hemiscyllium galei Allen & Erdmann, 2008

Cenderawasih Bamboo Shark

Figures 1C, 2C, 3C, 6 & 14–17; Table 1.

Hemiscyllium galei Allen & Erdmann, 2008: 96, figs. 2A, 3–6 (type locality: near Rumberpon Village, western Cenderawasih Bay, West Papua Province, Indonesia).

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly a combination of white lines and spots along margins of large dark saddles on back, scattered white spots (mainly on upper side), and a row of 7–8 well-defined, horizontally-ovate, dark spots on lower side between abdomen and caudal-fin base.

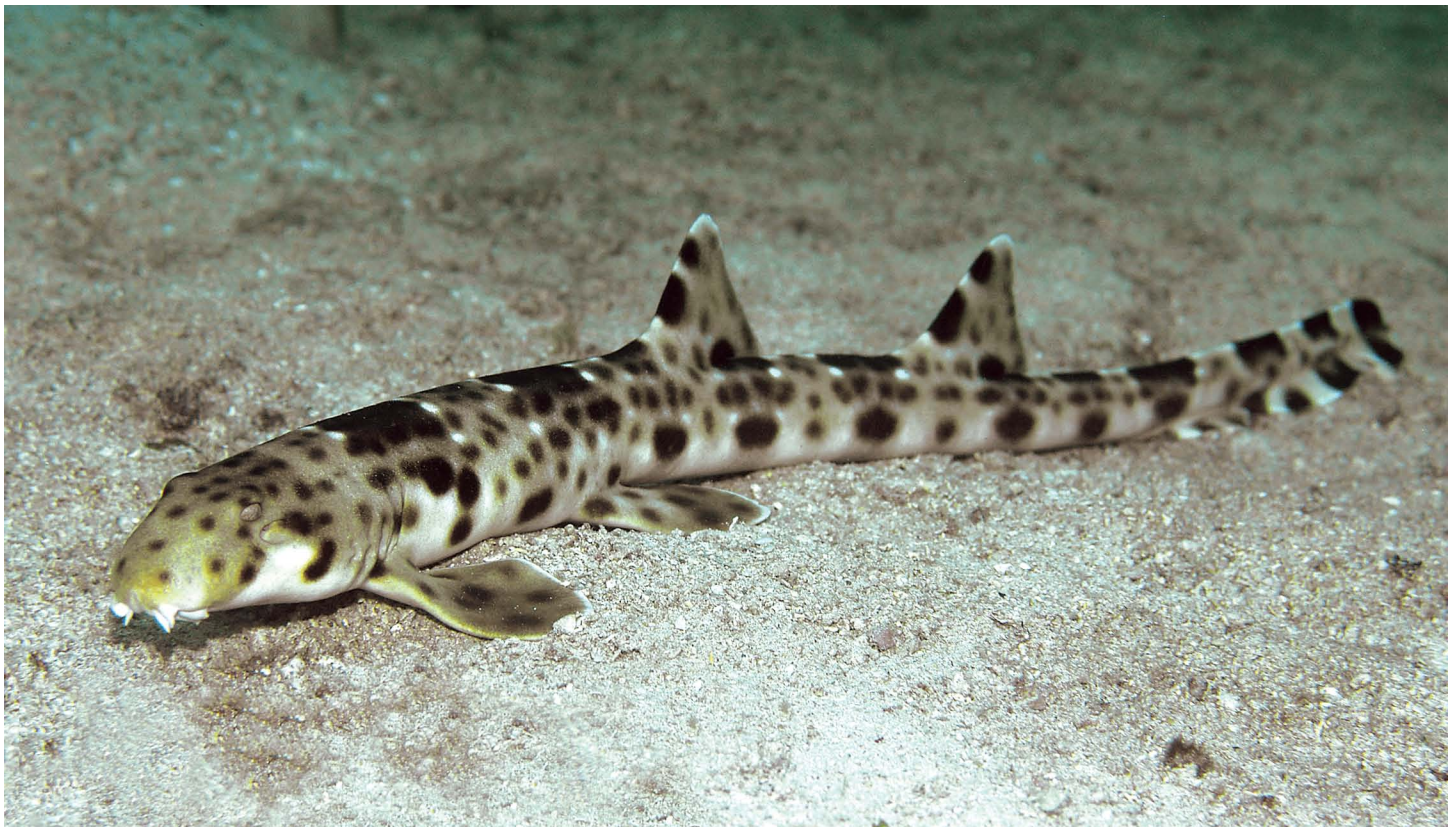

Figure 14. *Hemiscyllium galei*, approx. 650 mm TL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

Morphometric features. (based on 2 specimens, 543 and 568 mm TL) Precaudal length 1.2 in TL, head length 7.2–7.9 in TL; head width 1.4–1.8 in HL; head depth 0.9–1.1 in head width; horizontal eye diameter 3.4–3.6 in snout length, vertical diameter 1.8–2.5 in horizontal diameter; fleshy interorbital width 1.3–1.5, bony interorbital width 1.8–1.9, both in snout length; snout tip to eye 2.0–2.2, snout length 2.4–2.5, snout tip to spiracle 1.9, snout tip to first gill slit 2.9–3.0, all in HL; distance between first and fifth gill slit 2.9–3.0 in HL; height of first gill slit 4.4–5.2 and fifth 2.4–3.5, both in snout length.

Mouth width 1.2–1.3, nasal barbel length 4.5–5.5, maximum width of lower labial flap 4.6–4.8, length of postoral fold (upper labial furrow) 3.4–3.6, length of lower labial furrow 6.6–6.7, all in snout length.

Snout tip to first dorsal-fin origin 2.7, snout tip to pelvic-fin origin 3.6, snout tip to cloaca 3.3–3.4, cloaca to anal-fin origin 2.4–2.5, cloaca to caudal-fin tip 1.4–1.5 in TL; pectoral-fin length 1.2 in TL; pelvic-fin length 1.1–1.2 in TL; dorsal fins positioned well back on body, about equal in height; first dorsal-fin base 1.5 in HL, first dorsal-fin height 1.3 in first dorsal-fin base; free margin of first dorsal fin 1.7–1.9 in first dorsal-fin height; interdorsal distance 1.1–1.2 in HL; second dorsal-fin base 1.6–1.8 in HL; second dorsal-fin height 1.0–1.1 in second dorsal-fin base; free margin of second dorsal fin 2.2–3.1 in second dorsal-fin height; anal-fin base 1.4 in HL, anal-fin height 3.1–3.3 in anal-fin base; free margin of anal fin 1.8–1.9 in anal-fin height; body depth at level of anal-fin origin 3.7–3.9 in HL; subcaudal length 5.8 in TL.

Vertebral counts. Total vertebral centra 195 in holotype (end of caudal fin of paratype missing).

Color in life. (Figs. 14–17) Generally gray to pale reddish-brown (fawn), white on ventral surface, with relatively large, dark-brown, poorly-defined post-cephalic ocellus and, immediately behind, a dark brown bar composed of several merged spots (Fig. 15); 3 progressively smaller, dark brown saddles across back from rear edge of head to dorsal-fin base, a similar saddle between dorsal fins, and 4 additional dark saddles on dorsal edge of tail (total of 4 large saddles on body outlined with large brown spots, darker than surrounding spots; each

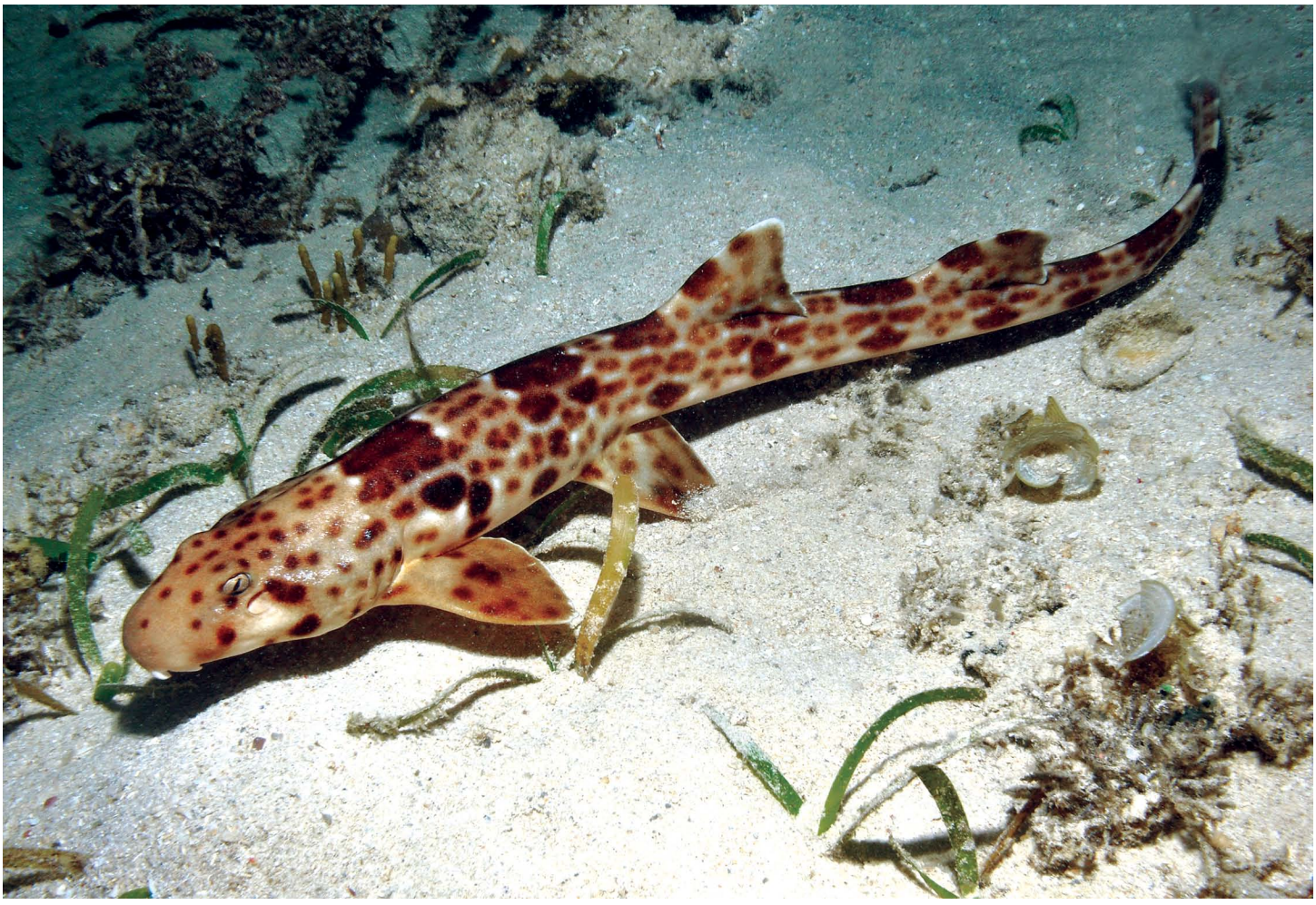

Figure 15. *Hemiscyllium galei*, approx. 650 mm TL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

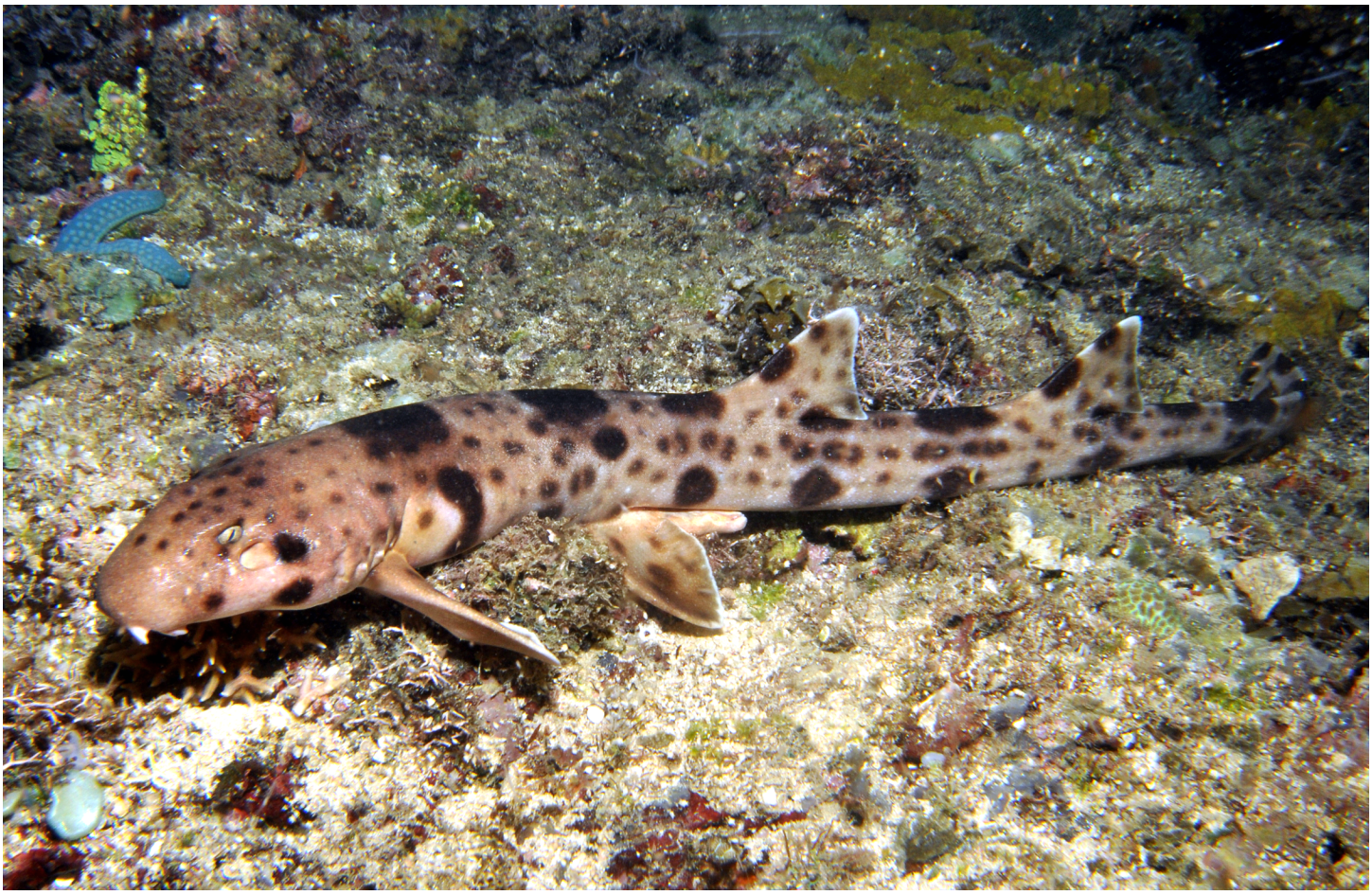

Figure 16. *Hemiscyllium galei*, approx. 550 mm TL, North Yapen, West Papua, Indonesia (G.R. Allen).

saddle with white anterior and posterior margins); head and body covered with relatively dense network of round to polygon-shaped brown spots, those on dorsal surface of head smaller than eye, usually numbering less than 10 (but as many as about 25, see Fig. 17) on snout anterior to eye level; also, an irregular matrix of white spots on side of body; side of head with whitish area below spiracle edged posteriorly with 2–3 large, dark-brown spots, each about eye size or larger, uppermost overlapping posterior edge of spiracle; dorsal fins each with about 4–5 poorly defined brown spots and pair of prominent blackish saddles on anterior edge; pectoral and pelvic fins with 9–13 and 8–11 variably sized brown spots respectively on dorsal surface and a narrow white posterior margin. Freshly collected holotype is illustrated in Fig. 17.

Distribution and habitat. This species is currently known only from Cenderawasih Bay, West Papua Province, Indonesia (Fig. 5). While it is mostly known from mainland reefs stretching from Manokwari to Nabire, it also has been observed on the western tip of Yapen Island. It has not been observed at any of the islands or patch reefs in the middle of the bay, each of which are surrounded by deep water, typically more than 1000 m. Moreover, its western limit of distribution (and whether there is any overlap with *H. freycineti* along the northern Bird's Head coastline) is still unknown and will be explored in future expeditions to the region. It is assumed that the extensive mangrove and soft-bottom habitats that stretch along the Waropen coastline through to the Mamberamo River outflow, at the northeast corner of Cenderawasih Bay, most likely serves as the eastern barrier to its distribution and effectively separates it from *H. strahani* further to the east. The preferred habitat typically consists of shoreline reefs or shallow patch reefs. All individuals observed or collected to date were encountered at night at depths of 2–25 m.

Etymology. The species was named in honor of Jeffrey Gale. He successfully bid to support the conservation of this species at the Blue Auction at Monaco in September 2007 and has generously supported Conservation International's Bird's Head Seascape marine conservation initiative.

Comparisons. *Hemiscyllium galei* is most similar in color pattern to *H. halmahera* (see Figs. 22–27), from the island of Halmahera, Maluku Province, Indonesia. 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, *H. galei* differs in having a row of 7–8 large, round-to-horizontally-ovate, dark spots on the lower side between the abdomen and caudal-fin base and lacking the pair of large dark spots on the ventral surface of the head typical of *H. halmahera* (see Fig. 24). Although the general configuration of the post-cephalic spot is similar, that of *H. galei* is composed of large solid spots (e.g. Fig. 14) vs. clusters of fragmented spots (with a U-shaped main spot) in *H. halmahera* (see Fig. 23).

Hemiscyllium galei is also similar to *H. freycineti* in that both species possess similar brown spotting on the head and body, as well as distinctive dark saddles on the back. The configuration of the post-cephalic ocellus and associated dark bar is also remarkably similar and both species have three, vertically-oriented, large dark spots immediately posterior to the spiracle. The best means of separation is the presence of brilliant white spots on the margins of the dorsal saddles as well as scattered white spots in *H. galei* (absent in *H. freycineti*; compare Figs. 8 and 14). In addition, *H. galei* is characterized by a row of 7–8 large, round-to-horizontally-ovate, dark spots on the lower side between the abdomen and caudal-fin base vs. pairs of leopard-like spots in approximately the same positions in *H. freycineti*, which are not well differentiated from surrounding spots and usually have paler brown centers (see Figs. 7 and 8).

The morphometric data (Table 1), based on very limited sample sizes, suggest a longer pelvic-fin length (11.2–11.5% TL) compared with *H. freycineti*, *H. halmahera*, *H. henryi*, and *H. strahani* (collective range of 9.6–10.5% TL).

Remarks. The morphometric data for this species were inadvertently transposed in Table 1 of the original description (Allen & Erdmann 2008): the data under the heading "*H. henryi*" belonged to *H. galei*.

Material examined. NCIP 6324 (holotype), male, 568 mm TL, reef near Rumberpon Village, 03°53.757' S, 134°06.638' E, Cenderawasih Bay, West Papua Province, Indonesia; WAM P.32888–001 (paratype), male, 543 mm TL, collected with holotype.

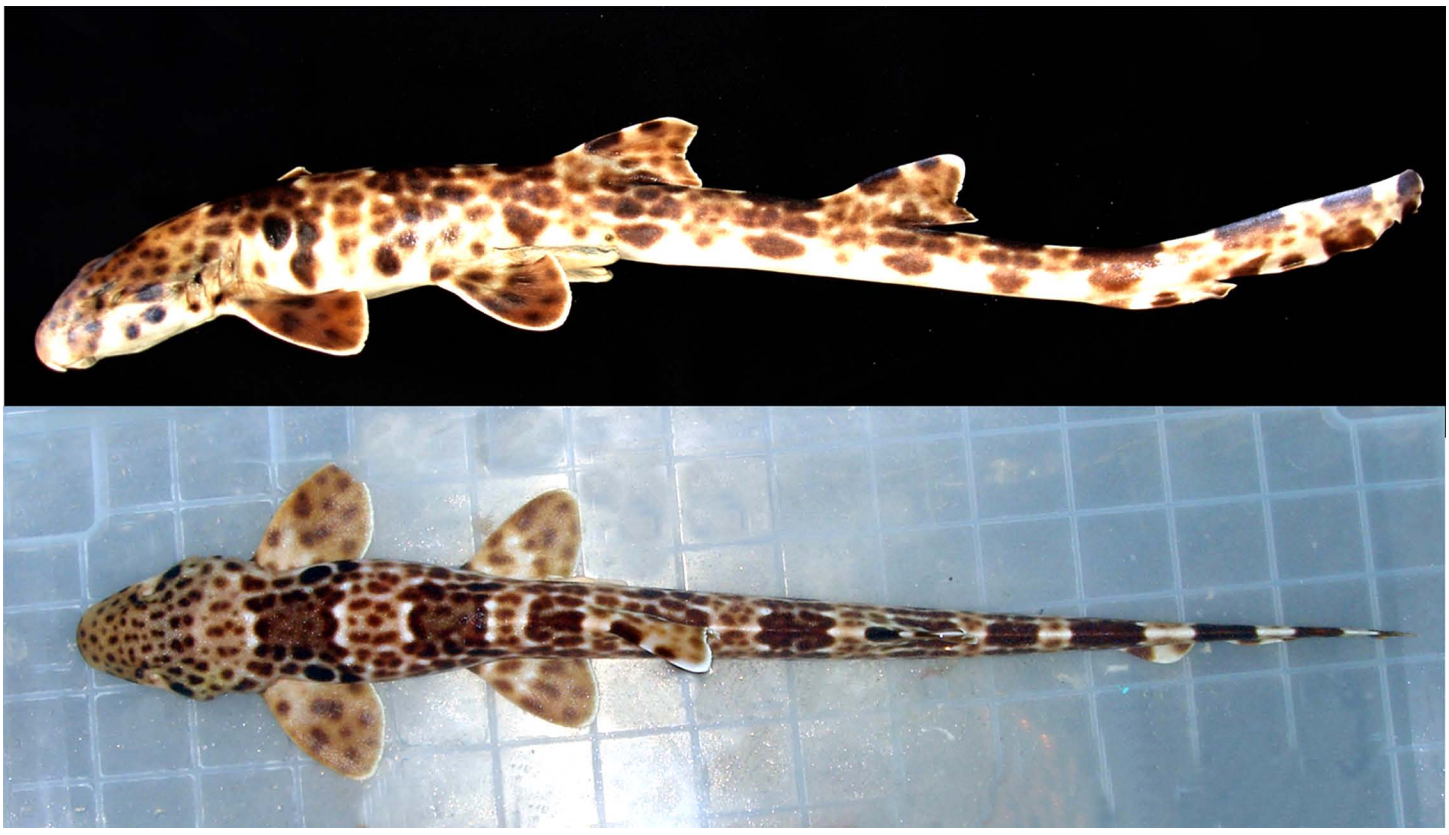

Figure 17. *Hemiscyllium galei*, lateral and dorsal views of freshly collected holotype (NCIP 6324), 568 mm TL, Cenderawasih Bay, West Papua, Indonesia (G.R. Allen).

Hemiscyllium hallstromi Whitley, 1967

Papuan Epaulette Shark

Figures 1B, 2B, 3B & 18–22; Table 1.

Hemiscyllium hallstromi Whitley, 1967: 178 (type locality: Papua New Guinea, assumed to be restricted to the vicinity of Port Moresby).

Diagnosis. A species of *Hemiscyllium* distinguished by large (about 2–5 times eye size) dark-brown spots on head and body, those on anterior half of body frequently with white halo; prominent post-cephalic ocellus with well-defined halo, usually rimmed with about 3–6 large, dark brown spots (sometimes partially coalesced) on dorsal, posterior, and ventral edges; snout uniform yellowish brown without dark spots; cheek usually with pair of large dark-brown spots just below and behind eye (upper spot partially in spiracle opening) and smaller dark-brown spot on lower cheek; interorbital region and rear portion of head (including nape and area just above gill slits) with about 7–8 large, dark-brown spots; pectoral, pelvic, and dorsal fins relatively immaculate except pair of prominent dark-brown saddles on anterior edge of both dorsal fins and a few pale brown spots on dorsal surface of pectoral and pelvic fins. Individuals from the Torres Straits differ noticeably in having fewer and smaller dark spots on the body, and usually fewer dark spots immediately adjacent to the primary post-cephalic ocellus.

Morphometric features. (based on 13 specimens, 280–756 mm TL) Precaudal fin length 1.2–1.3 in TL, head length 6.8–7.7 in TL; head width 1.4–1.9 in HL; head depth 1.0–1.7 in head width; eye length 3.0–4.9 in snout length, eye height 1.9–3.4 in eye length; fleshy interorbital space 1.2–1.4, bony interorbital space 1.7–2.2, both in snout length; snout length 2.2–2.5, snout tip to mouth 4.8–8.1, snout tip to spiracle 1.9–2.2, snout tip to first gill slit 1.0–1.3, all in HL; distance between first and fifth gill slit 2.5–3.6 in HL; height of first gill slit 3.0–4.7 and fifth 2.1–3.3, both in snout length.

Mouth width 1.1–1.4, nasal barbel length 3.9–5.7, maximum width of lower labial flap 3.3–5.3, length of postoral fold (upper labial furrow) 2.6–4.4, length of lower labial furrow 3.9–7.9, all in snout length.

Snout tip to first dorsal-fin origin 2.7–3.0, snout tip to pelvic-fin origin 3.4–3.8, snout to cloaca length 3.2–3.6, cloaca to anal-fin origin 2.2–2.3, cloaca to caudal-fin tip 1.4–1.5, all in TL; pectoral-fin length 1.2–1.6 in HL; pelvic-fin length 1.2–1.6 in HL; first dorsal-fin base 1.5–2.1 in HL; first dorsal-fin height 0.9–1.4 in first dorsal-fin base; free margin of first dorsal fin 1.8–2.5 in first dorsal-fin height; interdorsal space 1.0–1.3 in HL;

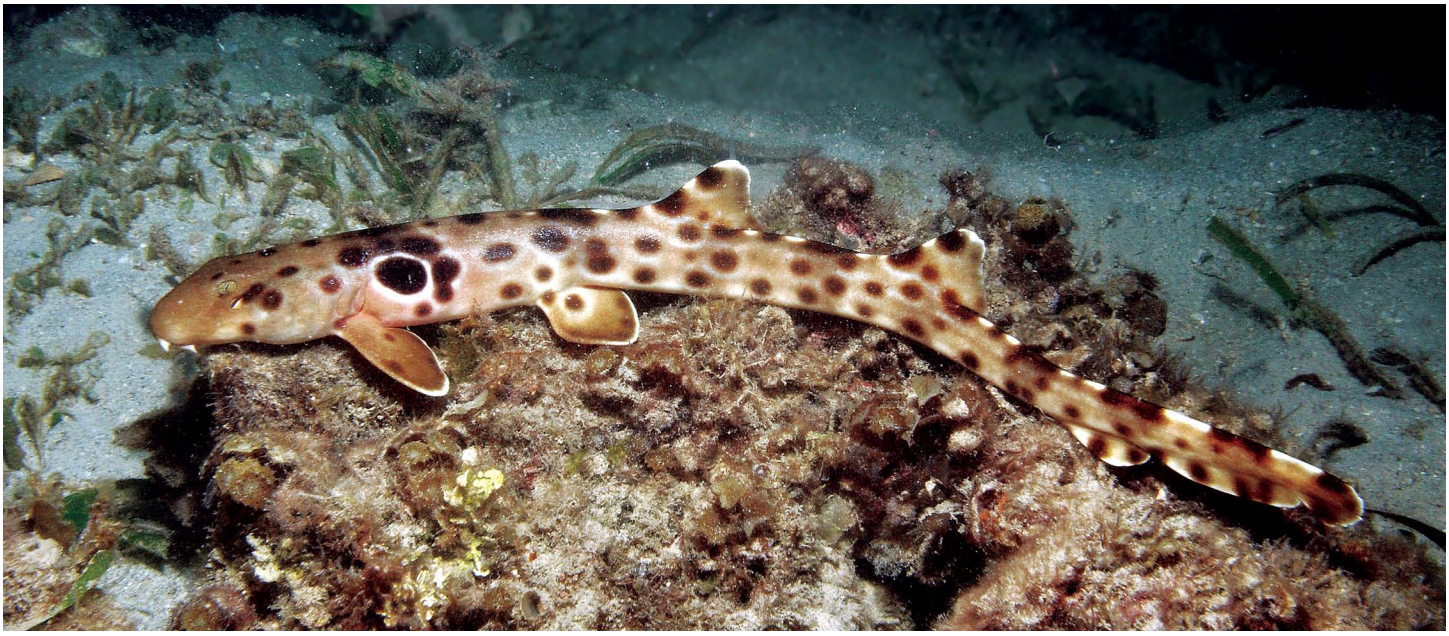

Figure 18. *Hemiscyllium hallstromi*, approx. 550 mm TL, Loloata Island, Bootless Bay, near Port Moresby, Papua New Guinea (G.R. Allen).

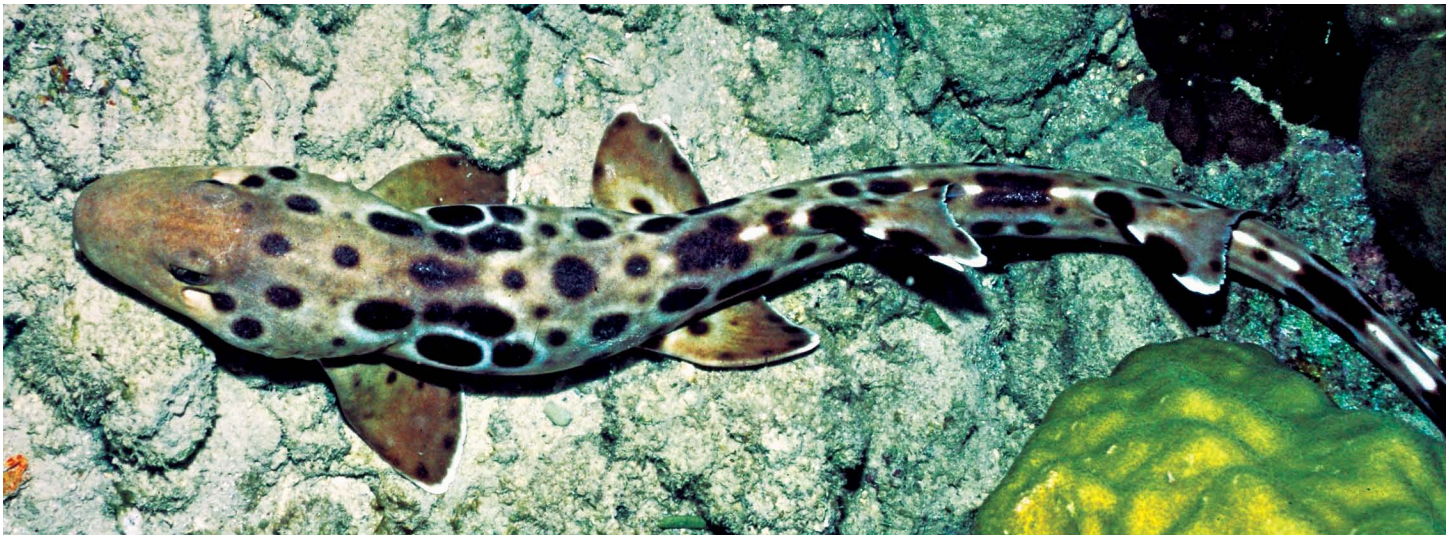

Figure 19. *Hemiscyllium hallstromi*, Bootless Bay, near Port Moresby, Papua New Guinea (B. Halstead).

second dorsal-fin base 1.4–1.9 in HL; second dorsal-fin height 1.2–1.6 in second dorsal-fin base; free margin of second dorsal fin 1.9–2.6 in second dorsal-fin height; anal-fin base 1.3–1.8 in HL; anal-fin height 2.9–6.2 in anal-fin base; free margin of anal fin 1.4–2.2 in anal-fin height; body depth at level of anal-fin origin 3.1–4.0 in HL; subcaudal length 5.5–8.0 in TL.

Vertebral counts. Total vertebral centra 183–194 (9 specimens, including 6 from Dingerkus & DeFino [1983]); precaudal vertebral centra 139–143 (3 specimens).

Color in life. (Figs. 18–20) Individuals from coastal mainland of Papua New Guinea generally golden brown, slightly darker on head, grading to white on ventral surface; prominent post-cephalic marking (Fig. 20) consists of primary large ocellus with well-defined halo, surrounded dorsally and posteriorly by about 3–6 smaller dark-brown spots, sometimes partially coalesced; remainder of body covered with numerous, widely spaced dark-brown spots, nearly all larger than about twice eye size, extending anteriorly to about level of eyes; snout plain without spotting; pectoral, pelvic, and dorsal fins relatively immaculate except pair of prominent dark-brown saddles on anterior edge of both dorsal fins and a few pale brown spots on dorsal surface of pectoral and pelvic fins (spot at base of pelvic fin sometimes forming ocellus); posterior margin of pectoral and pelvic fins narrowly white. Individuals from Torres Straits differ in having fewer and smaller dark spots on the body, and usually fewer dark spots immediately adjacent to primary post-cephalic ocellus (Fig. 21). Live colors of juveniles

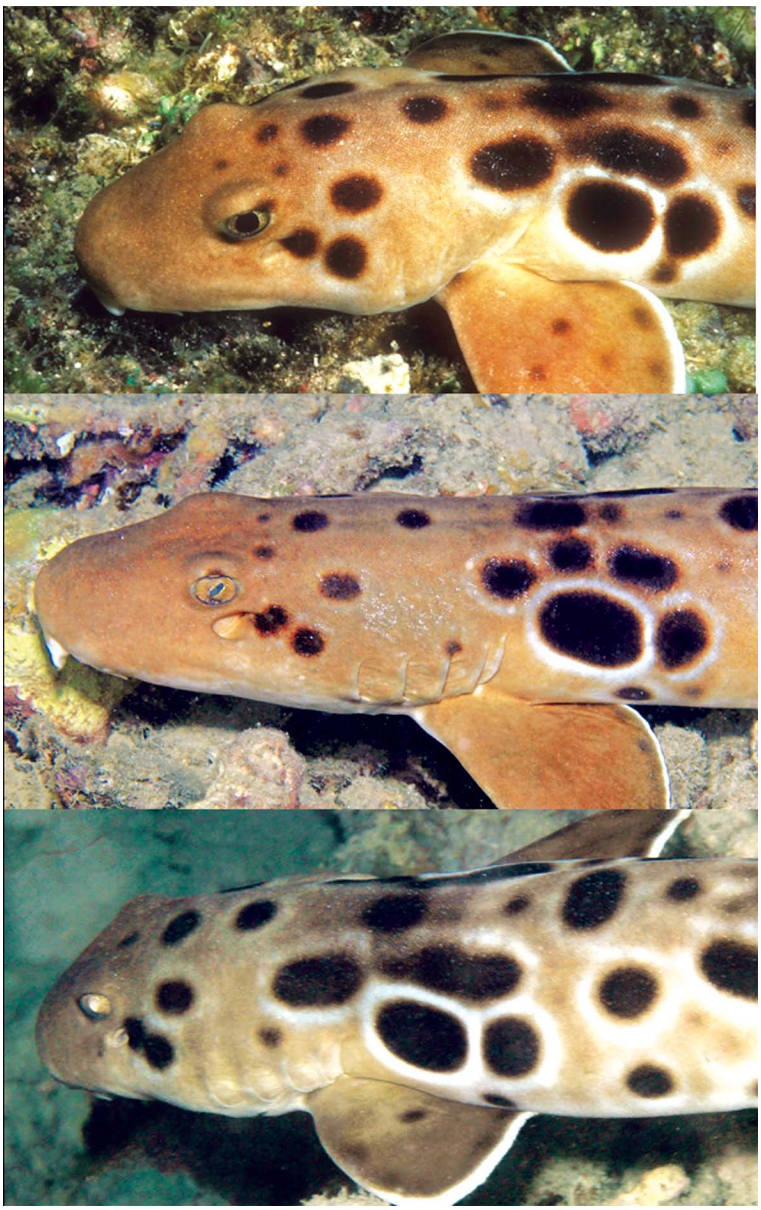

Figure 20. *Hemiscyllium hallstromi*, variability of markings on head and post-cephalic area, Bootless Bay, Papua New Guinea (top by B. Halstead, middle and bottom by M.V. Erdmann).

Figure 21. *Hemiscyllium hallstromi*, preserved specimens, AMS I.1185, 350 mm TL (upper) and AMS I.11859, 280 mm TL (lower), Murray Island, Torres Strait, Australia (G.R. Allen).

unknown, but a preserved specimen (AMS IB.7939), 188 mm TL, is shown in Fig. 22.

Distribution and habitat. This species is known mainly from the vicinity of Port Moresby, Papua New Guinea and the Torres Strait region between the tip of Cape York Peninsula, Queensland, Australia and Papua New Guinea (Fig. 5). Records from the Torres Strait are primarily from Murray Island (9°55.156' S, 144°04.037' E), which lies about 125 km southeast of the Papua New Guinea mainland. The only other record from the strait is from Jervis Reef (10°01' S, 142°13' E) near Badu Island, or approximately 90 km north of the tip of Cape York Peninsula. No doubt the range extends eastward from Port Moresby along the mainland coast for a considerable distance due to suitable habitat availability, but the eastern limit of distribution remains unknown. The eastern extremity of the mainland lies about 400 km southeast of Port Moresby, but marks the limit of distribution for *H. michaeli*. Thus far, there are no records that indicate the co-occurrence of these two species. *Hemiscyllium hallstromi* is presumed to not extend much northwest of Port Moresby into the Gulf of Papua, due to the lack of suitable reef habitat as a result of large river outflows such as the Fly and Kikori Rivers. Similarly, it likely does not extend from the Torres Strait region northwest of Merauke along the "Casuarina Coastline", as the extensive mangrove and soft-bottom habitats found there appear to form a barrier to distribution. The preferrred habitat of *H. hallstromi* includes shallow seagrass flats and coral reefs to depths of at least 20 m. It is usually encountered in the open at night and shelters under rocks and coral ledges during the day.

Etymology. The species was named in honor of Edward Hallstrom, who was a former Director of the Taronga Zoological Park in Sydney, Australia.

Comparisons. This species is most similar to *H. ocellatum* of eastern Australia. Generally, at least for adults, it can be distinguished by the configuration of the post-cephalic marking (Fig. 20), which usually has about 3–6 large, pale-rimmed, dark spots around the dorsal and posterior periphery of the main ocellus. In contrast, *H. ocellatum* lacks the large spots around the periphery of the main ocellus, although there may be a few nearby, dark, non-ocellated spots (see Fig. 38). In addition, the dark body spots of *H. hallstromi* are generally larger, with most at least 2–3 times eye size (variable in *H. ocellatum*, but the majority are eye size or smaller) and possessing

Figure 22. *Hemiscyllium hallstromi*, juvenile, AMS IB.7939, 188 mm TL, Taronga Park Aquarium, Sydney, Australia (G.R. Allen).

a faint whitish halo around them (vs. no halo around spots of *H. ocellatum*). Additionally, the general ground color is pale yellowish brown in *H. hallstromi* vs. pale gray in *H. ocellatum*. A final difference, particularly apparent in underwater photographs (Fig. 19), is the presence of a large ocellus on the base of the pelvic fin in *H. hallstromi* vs. none in *H. ocellatum* (Fig. 38). However, specimens of *H. hallstromi* from the Torres Strait and those of *H. ocellatum* from the northernmost portion of its range (north of about 17°S latitude) are not as clearly demarcated (compare Figs. 21 and 39–40). In fact, specimens from the Torres Strait are frequently confused with *H. ocellatum* and, in some respects, are intermediate in color pattern between the two species. Although we currently identify the Torres Strait specimens as *H. hallstromi*, additional specimens (including tissue samples for genetic study), from scattered locations in this area are needed to fully assess the status of this population.

The morphometric data (Table 1) suggest that *H. hallstromi* has a greater cloaca to anal-fin-origin distance (42.7–45.5 % TL) vs. *H. galei* (40.5–41.6 % TL), although the latter species was represented by only two specimens.

Remarks. No precise type locality was indicated in Whitley's (1967) original description. However, according to Dingerkus & DeFino (1983), the origin of the type specimens was Port Moresby, based on information received from Eric Friese, a former curator of the Taronga Park Zoo Aquarium. According to Friese, the aquarium received all of its New Guinea fish specimens during the 1960s from the Port Moresby area. Our own field and museum investigations corroborate the restricted distribution of this species. However, four specimens of *H. hallstromi* obtained by Otto Finsch in the 1880s and examined at ZMB present an enigma: three of the specimens (ZMB 12710) are labeled as from New Guinea and the fourth (ZMB 13322) as from the island of New Britain. Although it is assumed that Finsch's collecting activities were confined to German New Guinea (now northern Papua New Guinea and the Bismarck Archipelago, including New Britain), both of these areas lie well outside the documented range of *H. hallstromi*. The supposed New Britain specimen is even more puzzling because, as mentioned in the introduction, the members of this genus appear incapable of crossing deep-water barriers and there are no other records of *Hemiscyllium* sharks from this island. It seems likely that the specimens were mislabeled, and actually originated from the Port Moresby area, but how they were obtained by Finsch remains an unanswered question.

Material examined. (all Papua New Guinea unless stated otherwise; asterisk indicates detailed morphological data taken for Table 1) AMS I. 15717–001* (lectotype), male, 720 mm TL, Port Moresby area, received in 1970 from Taronga Zoo Aquarium; AMS I. 15584–001* (paralectotype), male, 756 mm TL, Port Moresby area, received in 1970 from Taronga Zoo Aquarium; AMS IB.7939, 185 mm TL, received in 1967 from Taronga Zoo Aquarium; AMS I.11851–11860*, 10 specimens, 280–721 mm TL, Murray Island, Torres Strait, Australia (9°55.156' S, 144°04.037' E); AMS I.17103–001, 383 mm TL, Taukura Point, southeast of Port Moresby (9°32' S, 147°09'58" E); AMS I.13450, 723 mm TL, Port Moresby, Papua New Guinea; QM I.22171*, male, 610 mm TL, Jervis Reef, Torres Strait, Australia (10°01' S, 142°13' E); KFRS E.068, male, 262 mm TL, and 3 females, 323–326 mm TL, Yule Island, Port Moresby; KFRS E.377, 2 females, 364–395 mm TL, Kanudi, Port Moresby; KFRS E.386, 3 females, 250–437 mm TL, Taurama Beach, Port Moresby; KFRS E.396, female 336 mm TL, Taurama Beach, Port Moresby; USNM 30567, female, 342 mm TL, Port Moresby; USNM 40018, female, 395 mm TL, Port Moresby; USNM 40024, male, 726 mm TL, Port Moresby; ZMB 12710, 2 females, 320–638 mm TL, and male, about 710 mm TL, New Guinea; ZMB 13322, male 834 mm TL, New Britain, Papua New Guinea.

Hemiscyllium halmahera Allen, Erdmann & Dudgeon, 2013

Halmahera Epaulette Shark

Figures 1G, 2G, 3G & 23–27; Table 1.

Hemiscyllium malayanum [*non* Lesson] (misspelling) Bleeker 1855: 376 (Batjan = Bacan Island).
Hemiscyllium malaisianum [*non* Lesson] Bleeker 1857: 386 (Batjan = Bacan Island).
Hemiscyllium halmahera Allen, Erdmann & Dudgeon, 2013: 123 (type locality: northwestern Ternate, Halmahera, Indonesia).

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly a light brown background color with numerous clusters of mainly 2–3 dark polygonal spots, widely scattered white spots in 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 a fragmented post-cephalic mark consisting of a large U-shaped dark spot with a more-or-less continuous white margin on lower half, followed posteriorly by a vertical row of three smaller clusters of 2–3 polygonal dark marks; pattern generally similar to *H. galei*, but lacking row of 7–8 large, horizontally ovate dark spots on lower side between abdomen and caudal-fin base; pattern also similar to *H. freycineti*, but lacking diffuse shoulder marking, numerous dark spots on dorsal surface of head, and pair of closely spaced dark post-cephalic ocelli surrounded by white halo.

Morphometric features. (based on 2 specimens, 656 and 681 mm TL) Precaudal length 1.3 in TL, head length 6.7–8.0 in TL; head width 1.4–1.6 in HL; head depth 1.2 in head width; eye length 3.2–3.4 in snout length, eye height 2.7–3.4 in eye length; fleshy interorbital space 1.4 and bony interorbital space 1.7 in snout length; snout length 2.2–2.4, snout tip to mouth 4.6–5.8, snout tip to spiracle 1.8–2.0, snout tip to first gill slit 1.1, all in HL; distance between first and fifth gill slit 2.5–2.7 in HL; height of first gill slit 3.9 and fifth 2.7–2.8 in snout length.

Mouth width 1.2–1.3, nasal barbel length 4.6–5.2, maximum width of lower labial flap 5.0–5.3, length of postoral fold (upper labial furrow) 3.1–3.4, length of lower labial furrow 4.5–5.3, all in snout length.

Snout tip to first dorsal-fin origin 2.5–2.6, snout tip to pelvic-fin origin 3.2–3.4, snout to cloaca length 3.0–3.1, cloaca to anal-fin origin 2.3–2.4, cloaca to caudal-fin tip 1.3, all in TL; pectoral-fin length 1.1–1.2 in HL;

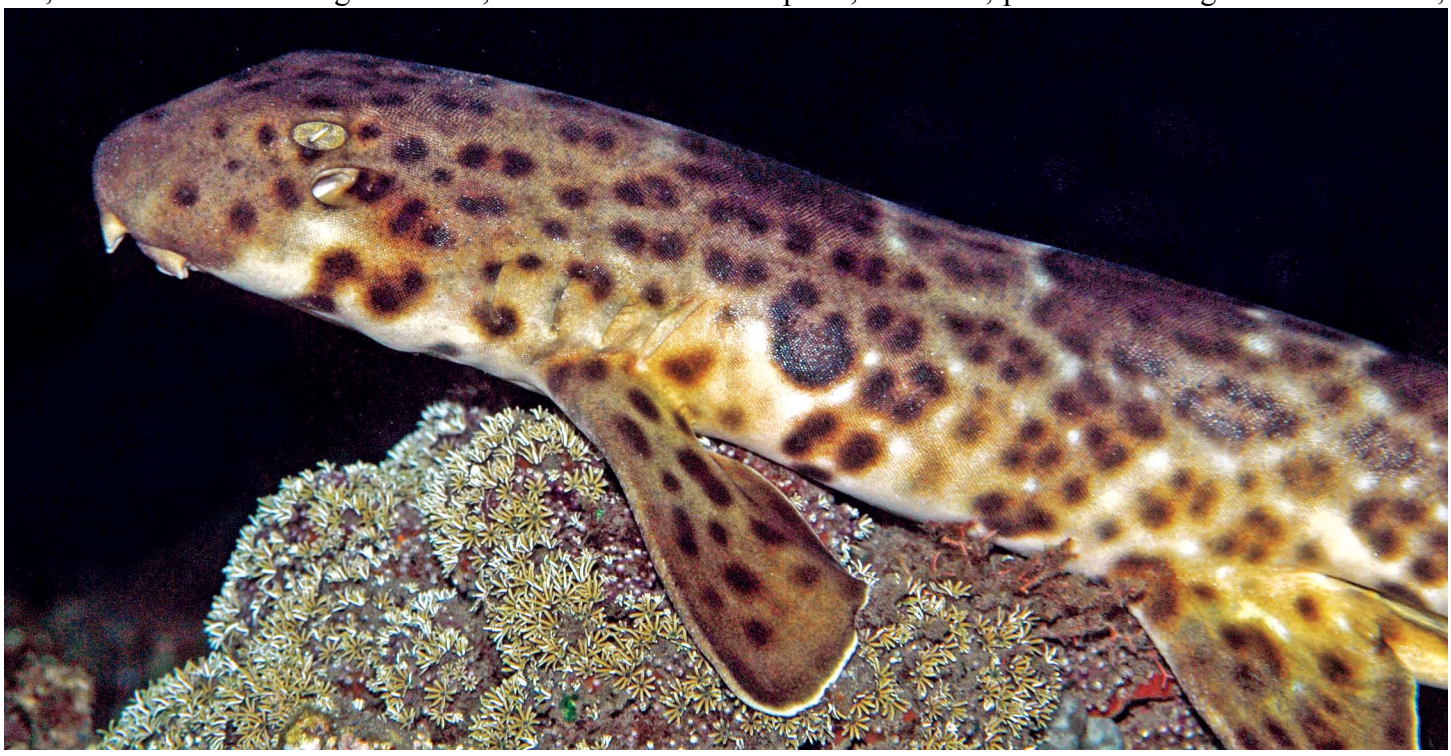

Figure 23. *Hemiscyllium halmahera*, live holotype, male, 681 mm TL, Ternate Island, Halmahera, Indonesia (M.V. Erdmann).

pelvic-fin length 1.2–1.4 in HL; 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 1.4–2.1 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 1.9–2.0 in second dorsal-fin height; anal-fin base 1.4–1.7 in HL, anal-fin height 2.7–3.3 in anal-fin base; free margin of anal fin 1.5–1.8 in anal-fin height; body depth at level of anal-fin origin 2.2–2.6 in HL; subcaudal length 5.7–6.2 in TL.

Vertebral counts. Total vertebral centra 195 (2 specimens).

Color in life. (Figs. 23–27) 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; 2–3 progressively smaller dark-gray-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; 4 large saddles on body with narrow white or pale-gray anterior and posterior margins; fragmented post-cephalic mark (Figs. 3G and 23), consisting of a large U-shaped dark spot with more-or-less continuous white margin on lower half, followed by a vertical row of three smaller clusters of 2–3 polygonal dark marks; pair of large, round-to-oval dark marks (Fig. 24) 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), dark spots (smaller than eye) on interorbital/snout region; each dorsal fin with few, poorly defined, brown spots and a 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 variably sized brown spots, respectively, on dorsal surface and a narrow white posterior margin. Freshly preserved holotype (Fig. 25) generally darker with more pronounced pale-edged dorsal saddles. Juveniles and

Figure 24. *Hemiscyllium halmahera*, ventral head, female paratype, WAM P.33784–001, 656 mm TL, Ternate Island, Halmahera, Indonesia (G.R. Allen).

Figure 25. *Hemiscyllium halmahera*, lateral and dorsal view of holotype, MZB 21248, male, 681 mm TL, Ternate Island, Halmahera, Indonesia (M.V. Erdmann).

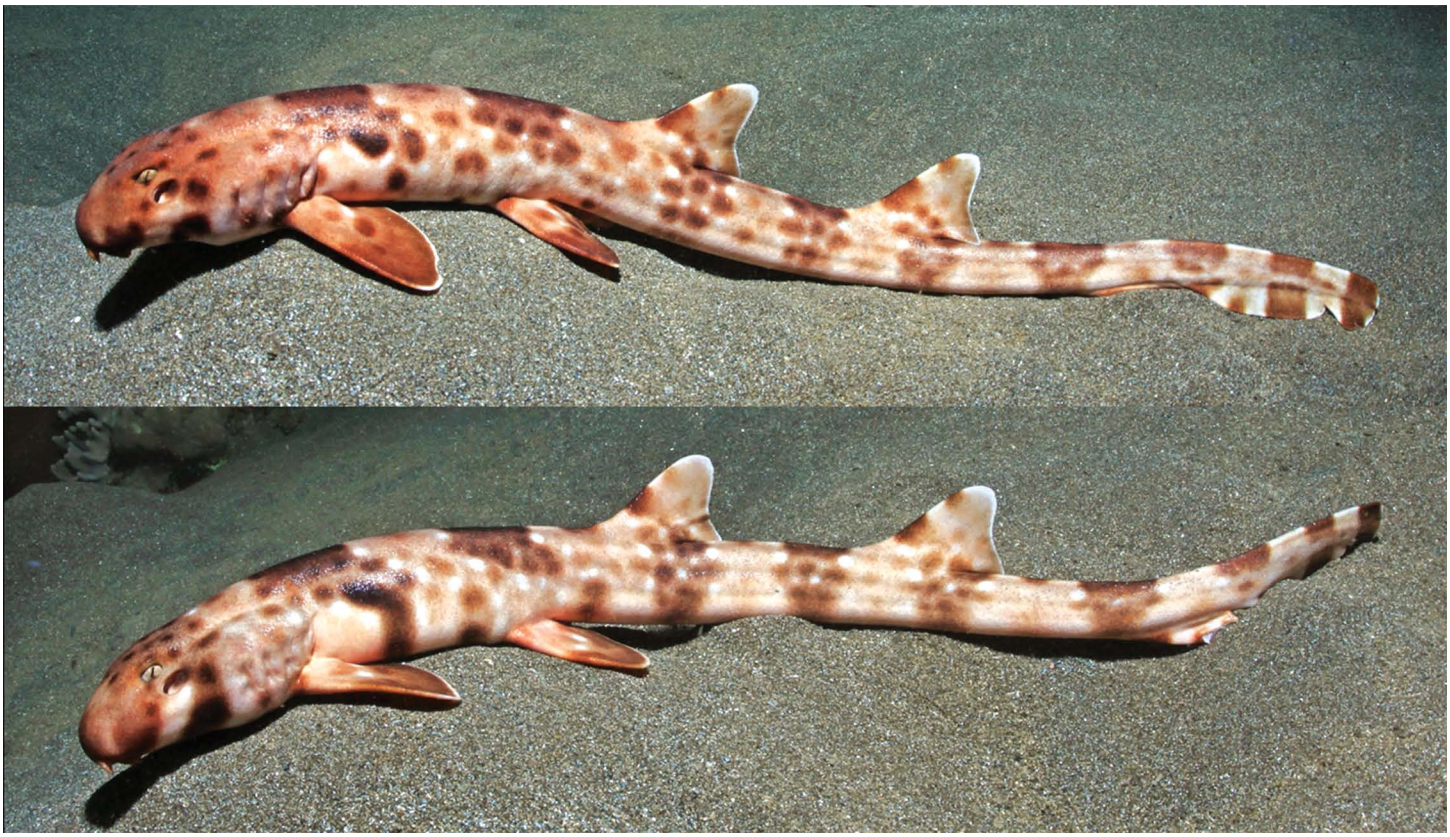

Figure 26. *Hemiscyllium halmahera*, approx. 450 mm TL (upper) and 400 mm TL (lower), Weda Bay, Halmahera, Indonesia (M.V. Erdmann).

subadults (Figs. 26 and 27) with few or no spots on pectoral and pelvic fins, and also showing pronounced dark saddles, extending onto sides as bars, most pronounced in smaller individuals.

Distribution and habitat. This species is known with certainty from satellite islands off the west coast of Halmahera, Indonesia and at Weda Bay in South Halmahera (Fig. 5). 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. This species has also been photographed off southwestern Halmahera at Proco Island (00°25.264' S, 127°44.264' E) 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). It is not currently known if the distribution extends northward along the western Halmahera coastline towards Morotai, nor if it extends eastward towards Buli Bay on the eastern coast of Halmahera.

Etymology. The species was named for the type locality.

Comparisons. This species is most similar in color pattern to *H. galei* (Figs 14–17) from Cenderawasih Bay, West Papua.The differences between the two species are discussed under *H. galei* (p. 68).

The morphometric data (Table 1), based however on very small sample sizes (only 2 specimens for *H. halmahera*), reveal some barely different metrics: *H. halmahera* has a greater preanal body depth (5.2–5.3% TL) vs. *H. galei*, *H. hallstromi*, *H. henryi*, and *H. michaeli* (collective range of 3.4–4.7% TL); a smaller preanal body depth vs. *H. freycineti* (5.5–6.7% TL); a greater snout to cloaca distance (32.2–33.5% TL) vs. *H. freycineti*, *H. galei*, *H. hallstromi*, *H. henryi*, *H. michaeli*, *H. ocellatum*, and *H. strahani* (collective range of 27.6–32.0% TL); a longer free margin on the second dorsal fin (3.7–4.0% TL) vs. *H. freycineti*, *H. galei*, and *H. hallstromi* (collective range of 2.4–3.4% TL); a longer snout to first dorsal distance (37.9–40.2% TL) vs. *H. freycineti* and *H. galei* (collective range of 36.6–37.8% TL); and a longer snout to pelvic fin distance (29.0–31.2% TL) vs. *H. galei* and *H. strahani* (collective range of 27.4–29.0 % TL).

Remarks. This species is the only member of the genus occurring outside the Australia/New Guinea region (Fig. 5), although Halmahera lies only 120 km west of the known range of *H. freycineti* at the Raja Ampat Islands. Allen *et al*. (2013) suggested that the ancestral population of *H. halmahera* was rafted to its current

Figure 27. *Hemiscyllium halmahera*, approx. 350 mm TL, Weda Bay, Halmahera, Indonesia (T. Mulder).

location on an island-arc fragment. This hypothesis is corroborated by paleogeographic reconstructions (Fig. 28), presented by Hall (2002), that show westward-migrating fragments coalescing to form major components of the present Halmahera land mass. Similar scenarios involving dispersal of New Guinea freshwater Heteroptera (water striders) via island-arc fragments were discussed by Polhemus & Polhemus (1998).

Material examined. MZB 21248 (holotype), male, 681 mm TL, northwestern Ternate, 00°50.958' N, 127°18.717' E, Halmahera, Indonesia; WAM P. 33784–001 (paratype), female, 656 mm TL, collected with holotype.

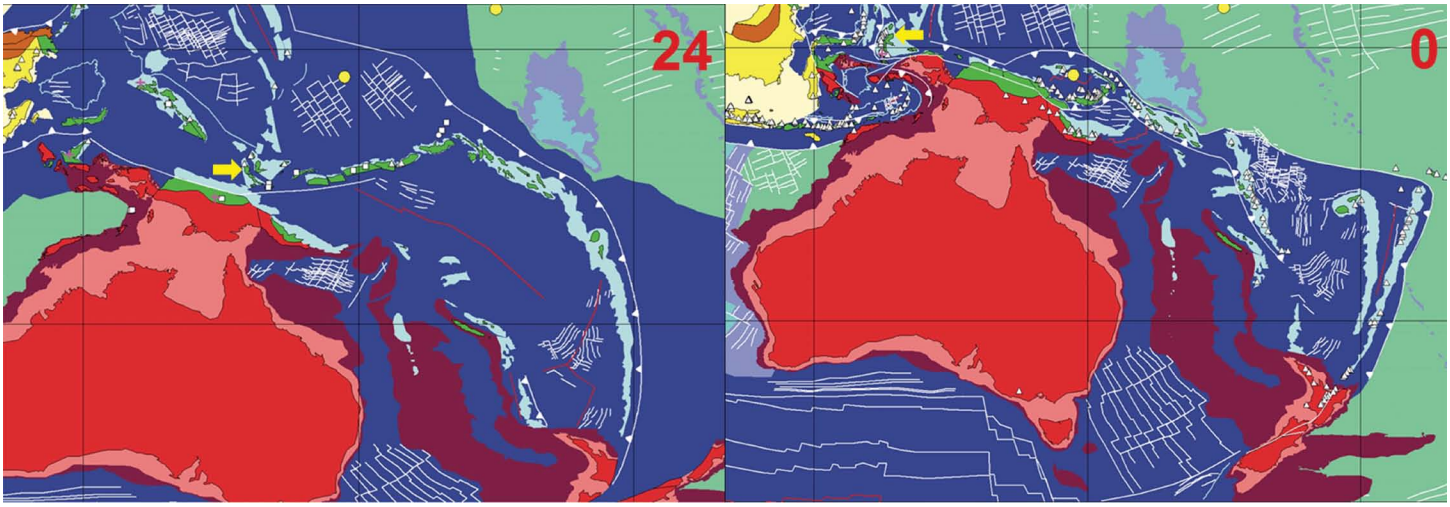

Figure 28. Paleogeographic reconstruction of the southwestern Pacific, adapted from Hall (2002), showing proximity of pre-Halmahera island-arc fragments 24 Mya (yellow arrow at left) and present day position (yellow arrow at right).

Hemiscyllium henryi Allen & Erdmann, 2008

Triton Bamboo Shark

Figures 1H, 2H, 3H, 6 & 29–32; Table 1.

Hemiscyllium henryi Allen & Erdmann, 2008: 102 (type locality: Triton Bay, West Papua, Indonesia).

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly the combination of small scattered spots on the head, body, and fins, including 13–18 spots on interorbital/dorsal snout region and 6–18 spots on dorsal surface of pectoral fins; dark spots at anterior origin of pectoral and pelvic fins; and a distinctive post-cephalic marking consisting of a merged double-ocellus, with a poorly defined white halo; similar to *H. ocellatum* but lacking a post-cephalic ocellus composed of a single round spot surrounded by a distinct white halo, and lacking numerous small dark spots on dorsal fins.

Morphometric features. (based on 3 specimens, 564–815 mm TL) Precaudal length 1.2–1.3 in TL, head length 7.3–7.5 in TL; head width 1.4–1.6 in HL; head depth 1.2 in head width; eye length 3.0–3.8 in snout length, eye height 2.3–2.8 in eye length; fleshy interorbital width 1.1–1.5, bony interorbital width 1.5–1.9, both in snout length; snout length 2.3–2.7, snout tip to mouth 2.2–3.1, snout tip to spiracle 2.0–2.2, snout tip to first gill slit 1.2–1.3, all in HL; distance between first and fifth gill slit 2.7–2.9 in HL; height of first slit 3.2–3.6 and fifth 2.3–2.5, both in snout length.

Mouth width 1.4, nasal barbel length 3.0–4.1, maximum width of lower labial flap 3.3–6.1, length of postoral fold (upper labial furrow) 2.8–4.1, length of lower labial furrow 4.3–5.1, all in snout length.

Snout tip to first dorsal-fin origin 2.5–2.7, snout tip to pelvic-fin origin 3.3–3.6, snout tip to cloaca 3.2–3.3, cloaca to anal-fin origin 2.3–2.4, cloaca to caudal-fin tip 1.4–1.5, all in TL. Pectoral fin length 1.3–1.4 in TL; pelvic fin length 1.3–1.4 in TL; first dorsal-fin base 1.8–2.0 in HL, first dorsal-fin height 0.7–0.8 in first dorsal-fin base; free margin of first dorsal fin 1.7–2.4 in first dorsal-fin height; interdorsal distance 1.0–1.1 in HL; second

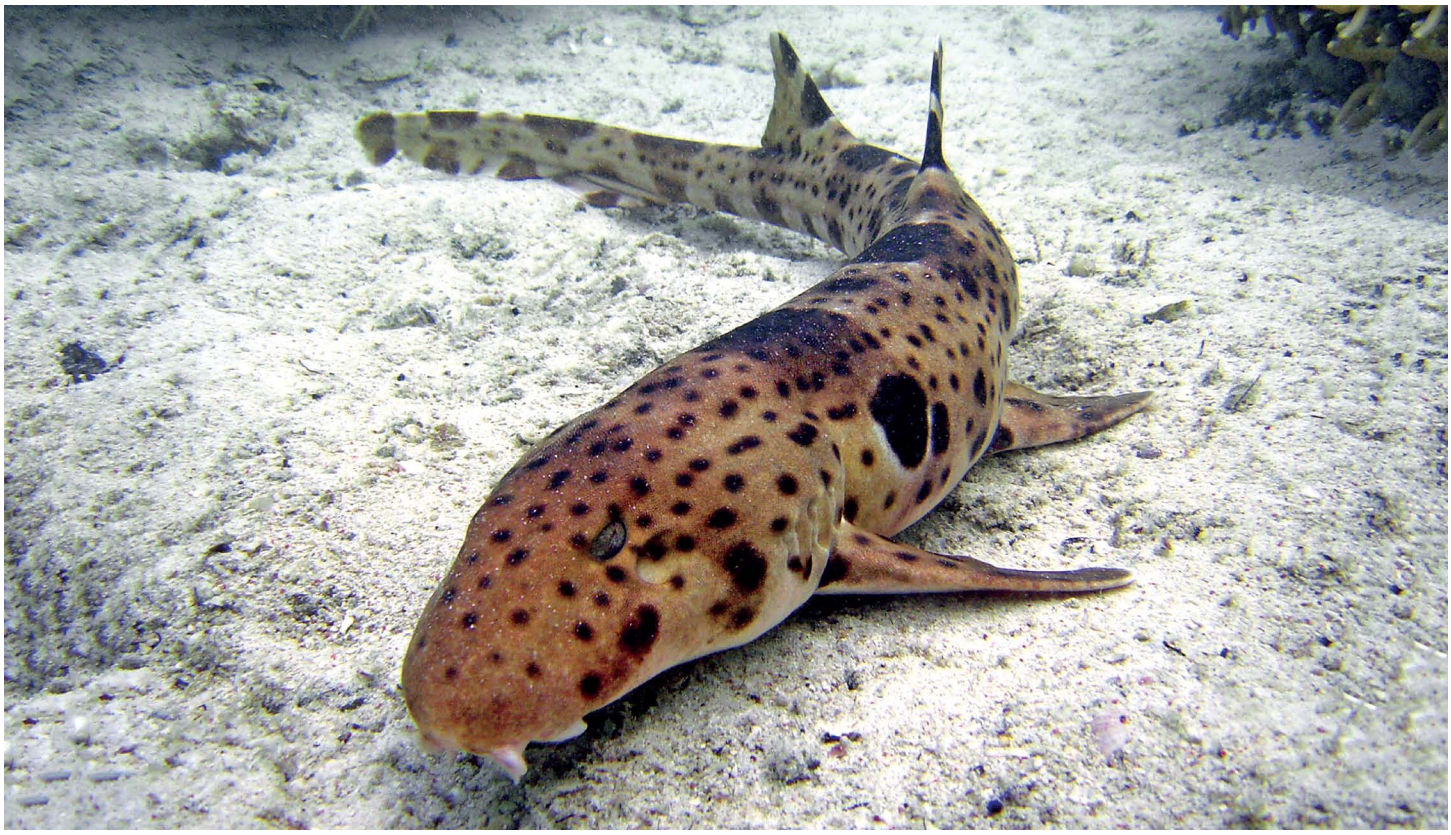

Figure 29. *Hemiscyllium henryi,* live holotype, NCIP 6323, 783 mm TL, Triton Bay, West Papua, Indonesia (G.R. Allen).

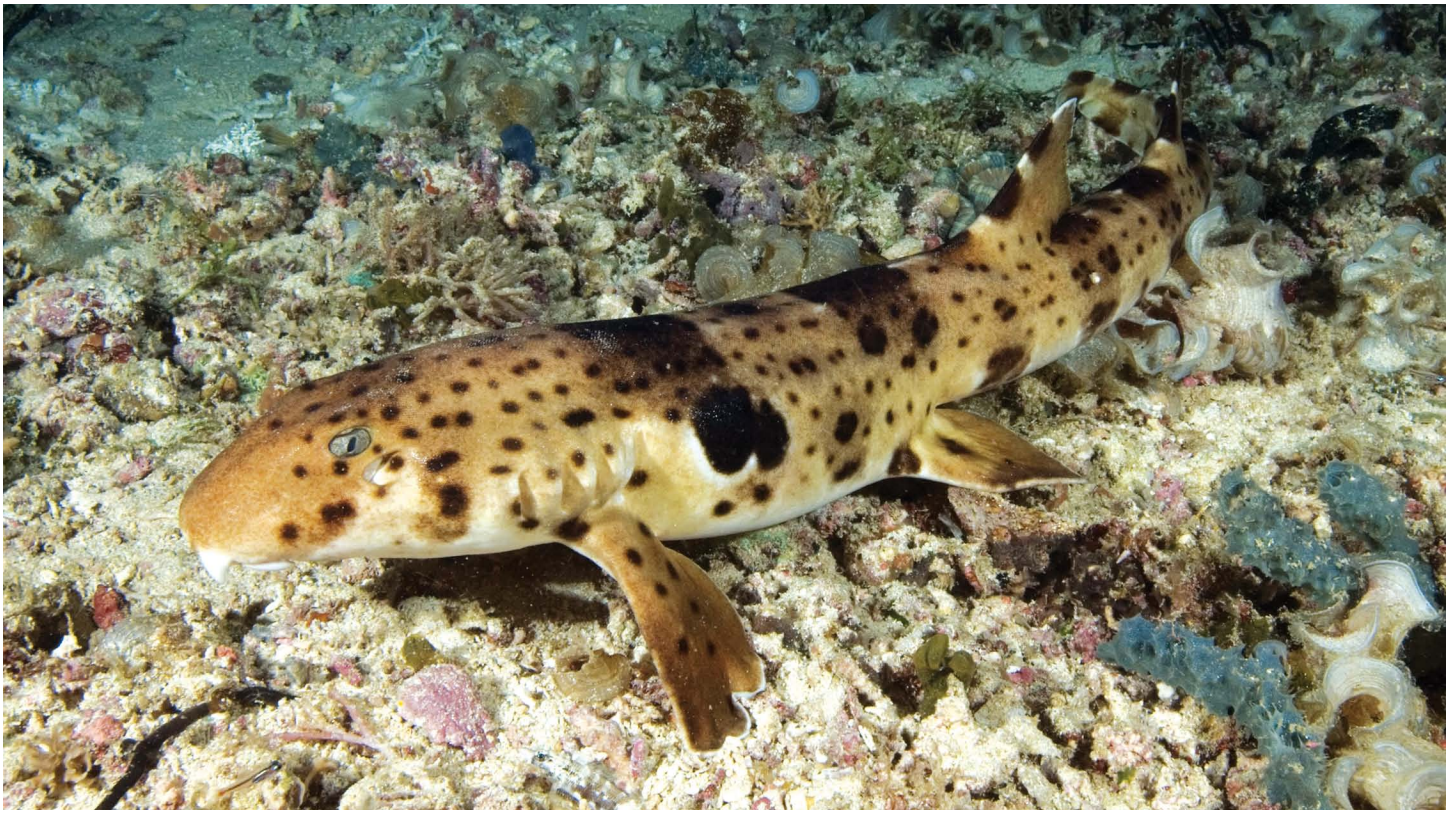

Figure 30. *Hemiscyllium henryi,* approx. 700 mm TL, Triton Bay, West Papua, Indonesia (B. Jones & M. Shimlock, Secret Sea Visions).

dorsal-fin base 1.6–2.0 in HL; second dorsal-fin height 1.0–1.1 in second dorsal-fin base; free margin of second dorsal fin 1.8–2.3 in second dorsal-fin height; anal-fin base 1.4–1.5 in HL, anal-fin height 2.0–3.0 in anal-fin base; free margin of anal fin 1.6–2.3 in anal-fin height; body depth at level of anal-fin origin 3.5–3.6 in HL; subcaudal length 5.5–6.0 in TL.

Vertebral counts. Total vertebral centra 191–194 (3 specimens).

Color in life. (Figs. 29–32) Overall pale gray-brown, white on ventral surface, with large, post-cephalic marking consisting of a merged double-ocellus with a poorly defined white halo (Fig. 31), numerous brown spots covering head and body (becoming more numerous with increased size); pectoral- and pelvic-fin anterior origins with a large spot; pectoral and pelvic fins with 6–18 and 6–10 variably sized brown spots, respectively, on dorsal surface and a narrow white posterior margin; dorsal fins largely devoid of spots (except along base) with a pair of prominent blackish saddles on anterior edge. Freshly preserved coloration of holotype illustrated in Fig. 32.

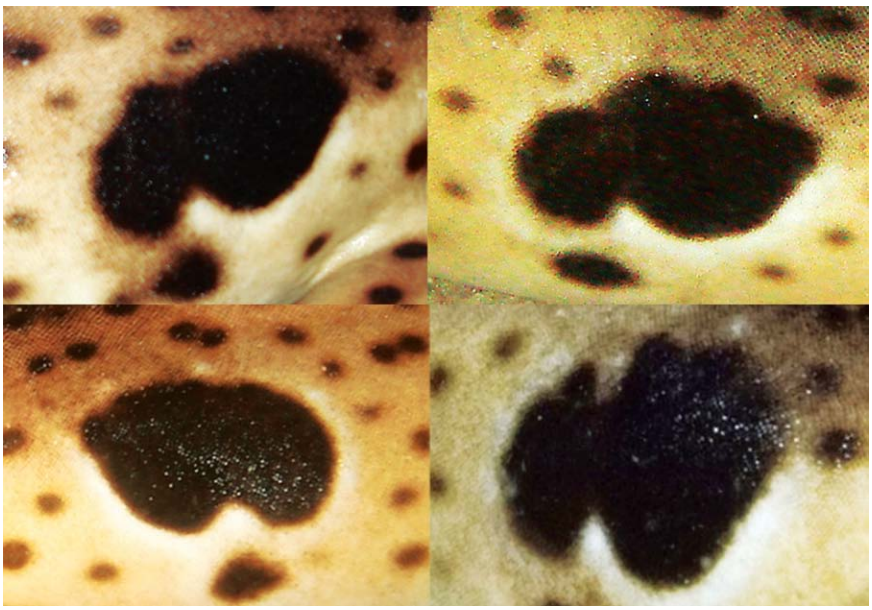

Figure 31. *Hemiscyllium henryi,* post-cephalic markings in 4 adults, Triton Bay, West Papua, Indonesia (G.R. Allen).

Distribution & habitat. This species is known only from western New Guinea (West Papua Province, Indonesia), occurring in the southern Bird's Head region (Fig. 5). It has been observed and collected at Triton Bay and at Selat Iris, a narrow channel between the mainland and Aiduma Island, immediately outside the bay. It was also observed near the Mommon waterfall on the southwestern tip of the Bomberai Peninsula, about 135 km west of Triton Bay. It is unknown if the

distribution extends much farther northwest along the Bomberai; while there is extensive, presumably suitable, coral-reef habitat along this coastline, our surveys to date have failed to record any epaulette sharks. To the southeast of Triton Bay, there is little reef development beyond Etna Bay due to the presence of large river outflows and extensive mangrove swamp that presumably is not suitable for this species. The preferred habitat typically consists of shoreline reefs or shallow patch reefs. Most reports are from depths of about 3–20 m, but one individual was captured by hook and line in about 30 m by the crew of a live-aboard dive boat. Most reported sightings occur at night when the shark is in the open. It is usually seen resting on the bottom, but occasionally is sighted while slowly swimming or "walking" over the bottom with the pectoral and pelvic fins. During the day, it is generally sedentary, sheltering under rocky outcrops or under tabular corals.

Etymology. The species was named in honor of Wolcott Henry of Washington D.C. for his generous support of marine conservation and, in particular, our ichthyological explorations of the Bird's Head region.

Comparisons. *Hemiscyllium henryi* is most similar to *H. ocellatum* of eastern Australia. Both species possess a general pattern of brown spotting and a pair of black saddle-like markings along the anterior edge of each dorsal fin. However, they differ markedly in the shape of the post-cephalic ocellus immediately behind the head. In *H. henryi*, the marking usually consists of a pair of merged ocelli (Fig. 31; except those on the left side of the holotype, which are separated, as in Fig. 29), while in *H. ocellatum* this marking is generally round, intensely black, and very large (more than one-third body depth)(see Fig. 38). Moreover, the surrounding white halo of *H. henryi* is poorly defined in comparison with that of *H. ocellatum*. Another difference is the presence of a large dark spot at the anterior origin of the pectoral and pelvic fins of *H. henryi*, not prominent on *H. ocellatum* (see Fig. 37). In addition, the dark-brown saddle-like markings and bars characteristic of *H. henryi* are less developed (either absent or diffuse) in *H. ocellatum*, and the dorsal fins are mostly spotless in *H. henryi* vs. with numerous small brown spots in *H. ocellatum* (at least in populations south of Townsville, Queensland).

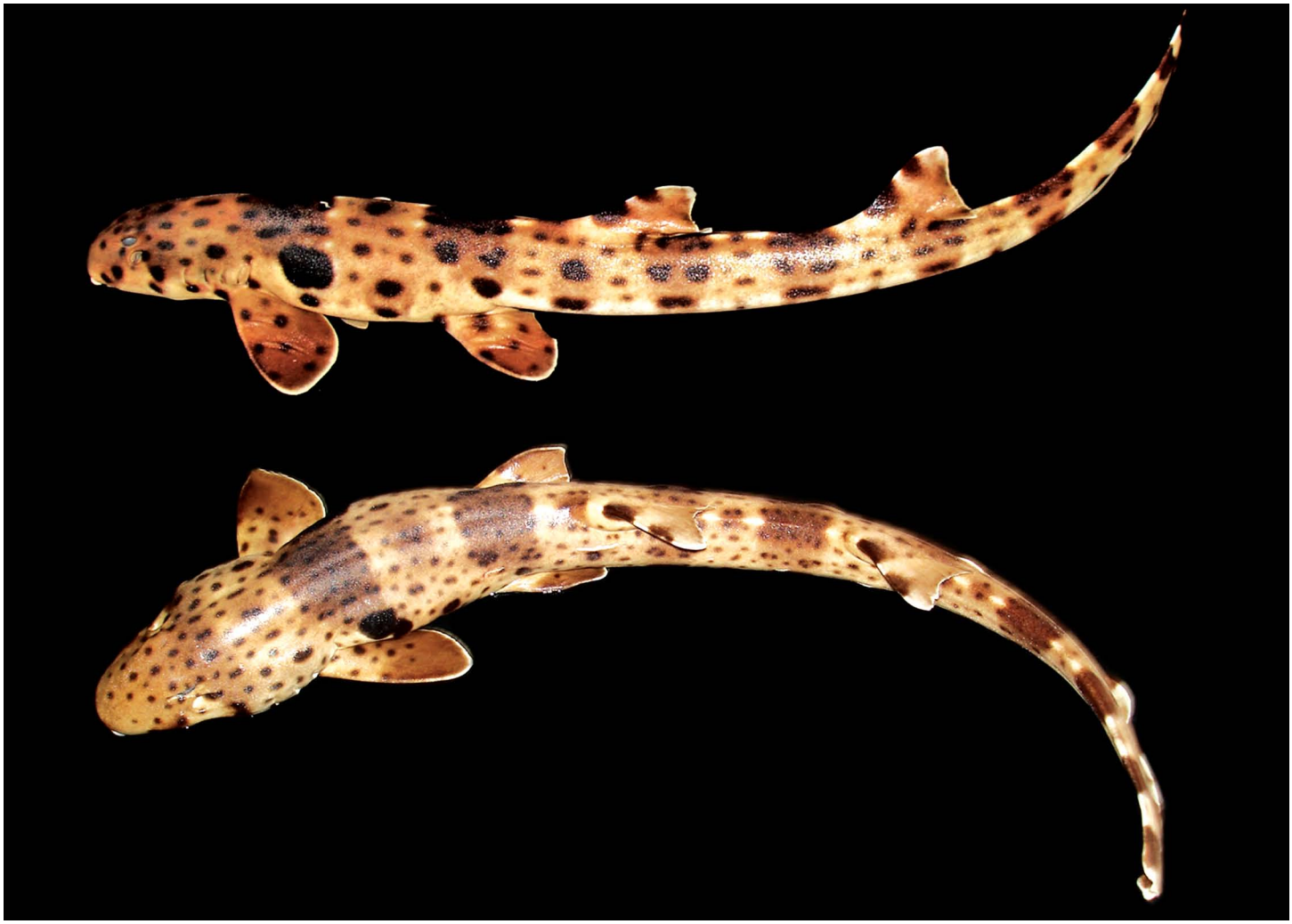

Figure 32. *Hemiscyllium henryi,* lateral and dorsal view of freshly preserved holotype, NCIP 6323, 783 mm TL, Triton Bay, West Papua, Indonesia (G.R. Allen).

The morphometric data (Table 1) based, however, on only 3 specimens of *H. henryi*, suggest the species has a taller first dorsal fin (8.2–10.1% TL) vs. *H. freycineti*, *H. galei*, *H. hallstromi*, *H. halmahera*, and *H. ocellatum* (collective range of 5.3–8.1% TL); a taller anal fin (3.0–3.3% TL) than *H. freycineti*, *H. galei*, *H. hallstromi*, *H. halmahera*, *H. michaeli*, *H. ocellatum*, and *H. strahani* (collective range of 1.3–3.0% TL); longer barbels (1.5–1.7% TL) vs. *H. galei* and *H. michaeli* (collective range of 0.9–1.5% TL); and a different snout to mouth distance (2.0–2.2% TL) vs. *H. galei* and *H. halmahera* (collective range of 2.3–2.7% TL) and *H. strahani* (1.6–1.9% TL).

Remarks. A female specimen (USNM 390771), 815 mm TL, contained eight full-sized ova ranging in diameter from about 25–30 mm. The morphometric data for this species were inadvertently transposed in Table 1 of the original description (Allen & Erdmann 2008): the data under the heading "*H. galei*" belonged to *H. henryi*.

Although known from only three museum specimens, we have examined numerous underwater photographs of this species from the area around Triton Bay, near the type locality.

Material examined. (all from the vicinity of Triton Bay, West Papua, Indonesia) NCIP 6323 (holotype), male, 783 mm TL, small bay in northwestern portion of Selat Iris, 03°54.544' S, 134°09.679' E; USNM 390771 (paratype), female, 815 mm TL, patch reef near center of Triton Bay, 03°50'01.89" S, 134°05'47.94" E; WAM P.32889-001 (paratype), 564 mm SL, collected with USNM paratype.

Hemiscyllium michaeli Allen & Dudgeon, 2010

Michael's Epaulette Shark

Figures 1F, 2F, 3F & 33–36; Table 1.

Hemiscyllium freycineti [*non* Quoy & Gaimard] Dingerkus & DeFino 1983: 38 (in part).
Hemiscyllium michaeli Allen & Dudgeon, 2010: 19 (type locality: Harvey Bay, Oro Province, Papua New Guinea).

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly the combination of dense leopard-like spotting on the body and a conspicuous post-cephalic marking consisting of a large black ocellated spot on the middle of the side, just behind the head; similar in appearance to *H. freycineti* but differs by having denser and more leopard-like dark spots, a larger and better developed post-cephalic ocellus, and more numerous spots on dorsal surface of snout.

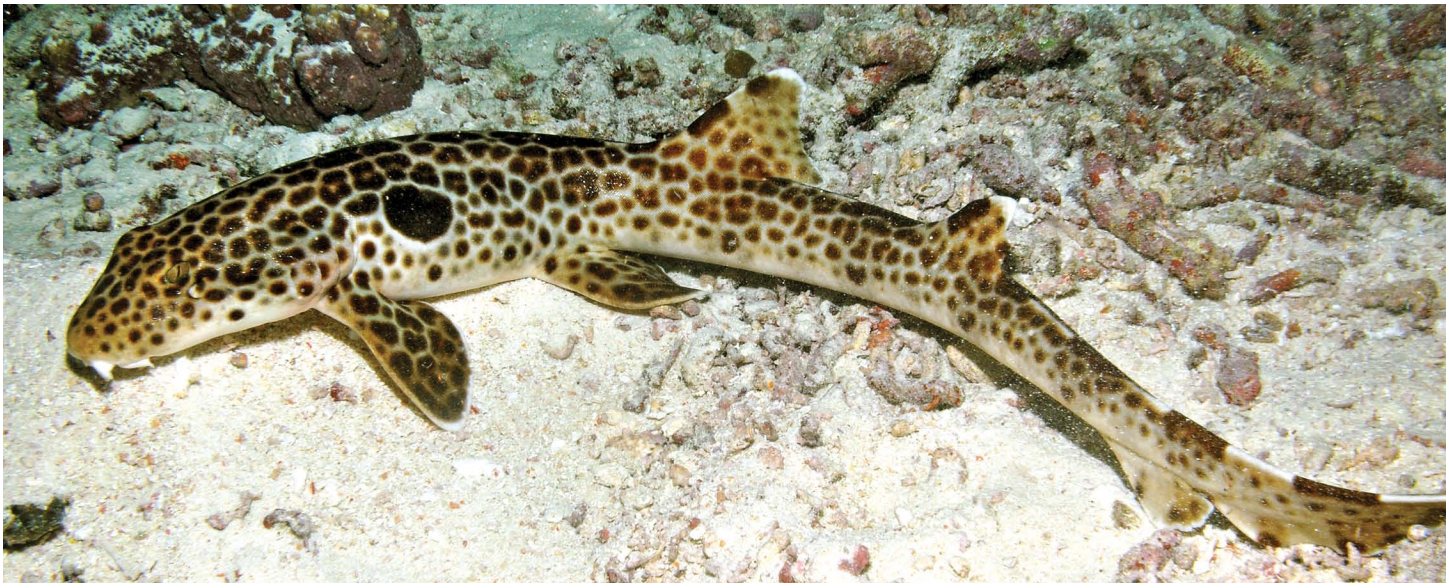

Figure 33. *Hemiscyllium michaeli*, approx. 700 mm TL, Milne Bay Province, Papua New Guinea (G.R. Allen).

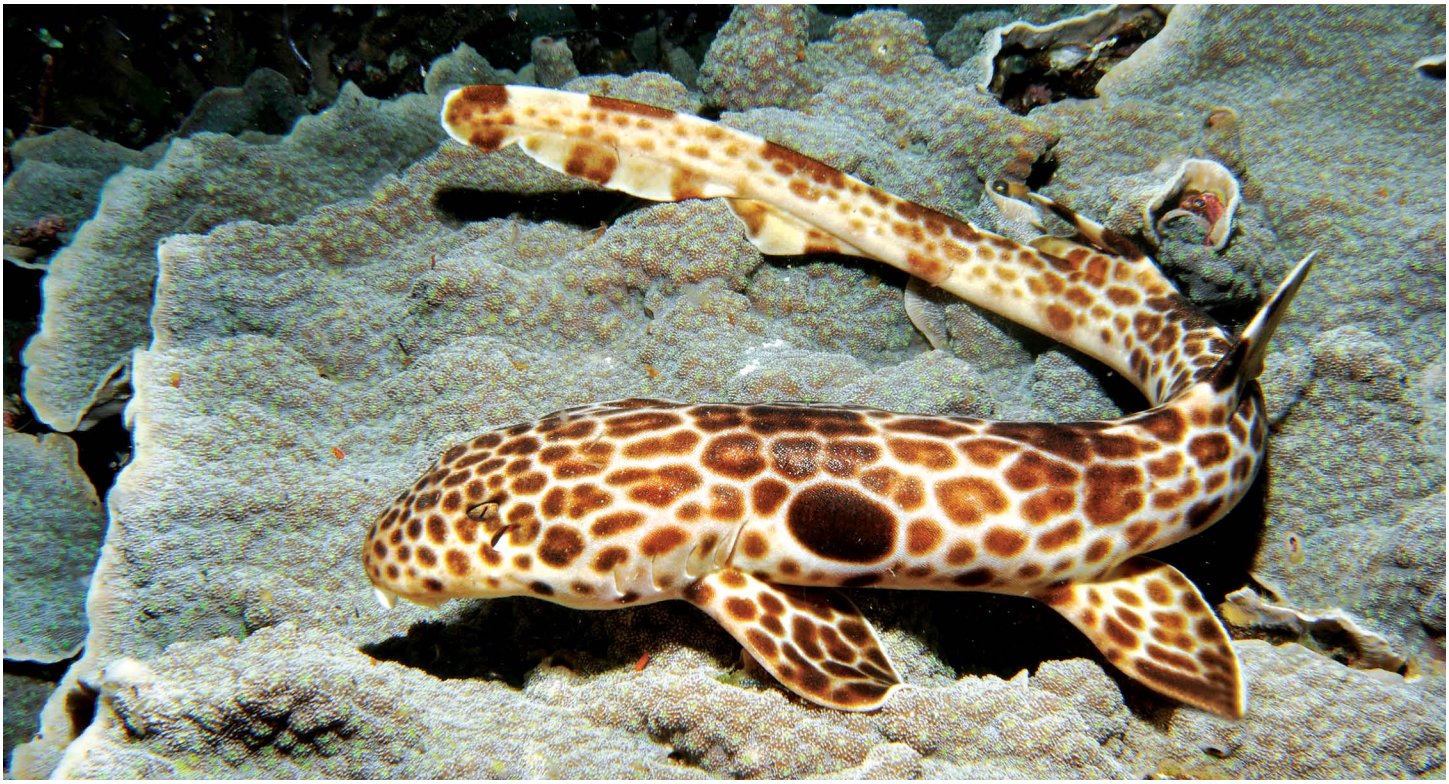

Figure 34. *Hemiscyllium michaeli*, approx. 600 mm TL, Milne Bay Province, Papua New Guinea (G.R. Allen).

Morphometric features. (based on 5 specimens, 257–695 mm TL) Precaudal length 1.2–1.3 in TL, head length 6.7–7.5 in TL; head width 1.4–1.9 in HL; head depth 1.0–1.4 in head width; eye length 3.0–4.1 in snout length, eye height 2.4–3.4 in eye length; fleshy interorbital space 1.2–2.3, bony interorbital space 1.7–2.5, both in snout length; snout length 2.2–3.4, snout tip to mouth 5.1–7.2, snout tip to spiracle 1.9–2.3, snout tip to first gill slit 1.1-1.3, all in HL; height of first gill slit 3.2–5.8 and fifth 2.5–3.9, both in snout length.

Mouth width 1.0–1.4, nasal barbel length 4.1–5.8, maximum width of lower labial flap 3.6–5.6, length of postoral fold (upper labial furrow) 2.8–3.7, length of lower labial furrow 3.5–5.3, all in snout length.

Snout tip to dorsal-fin origin 2.4–2.9, snout tip to pelvic-fin origin 3.3–3.7, snout to cloaca length 3.2–3.6, snout to anal-fin origin 2.0–2.4, cloaca to caudal-fin tip 1.3–1.5, all in TL; pectoral-fin length 1.2–1.7 in HL; pelvic-fin length 1.3–1.7 in HL; first dorsal-fin base 1.9–2.3 in HL; first dorsal-fin height 0.8–1.2 in first dorsal-fin base; free margin of first dorsal fin 1.6–2.0 in first dorsal-fin height; interdorsal space 0.9–1.4 in HL; second dorsal-fin base 1.7–2.2 in HL; second dorsal-fin height 0.8–1.4 in second dorsal-fin base; free margin of second dorsal fin 1.5–2.2 in second dorsal-fin height; anal-fin base 1.5–2.4 in HL; anal-fin height 2.6–4.5 in anal-fin base; free margin of anal fin 1.2–1.8 in anal-fin height; body depth at level of anal-fin origin 3.6–4.5 in HL; subcaudal length 5.2–5.7 in TL.

Color in life. (Figs. 33–36) Overall whitish to pale gray brown with dense network of leopard-like brown spots covering head, body, and fins; large white-rimmed, dark-brown post-cephalic mark (Figs. 33 & 34), its anterior edge about level with posterior edge of pectoral fin; series of about 9–10 bars sometimes apparent, faint on sides, but more conspicuous on tail; 2–3 prominent dark-brown, saddle-like markings along dorsal edge of both dorsal fins. Small subadults (Fig. 35) generally lack leopard-like spots, instead have solid spots on head, body, and fins. A small juvenile (estimated size of 200 mm TL), photographed by R. Halstead (Fig. 36), is mainly white with 10 dark brown bars including one on head and 3 on caudal fin; a few small brown spots on head and anterior body within pale interspaces; characteristic large ocellus is evident, although partially merged with second dark bar.

Vertebral counts. Total vertebral centra 197–204 (5 specimens); precaudal vertebrae 152 (1 specimen).

Distribution and habitat. Known only from eastern Papua New Guinea (Fig. 5), with most observations and collecting records from Milne Bay Province at Samarai Island, vicinity of Alotau, East Cape, Nuakata, Sullivan Patches, and the Trobriand Islands. It has also been collected at Oro Province (formerly Northern Province) in the vicinity of Harvey Bay. As discussed under *H. hallstromi*, it is unclear if the distribution of *H. michaeli* extends

Figure 35. *Hemiscyllium michaeli*, approx. 300 mm TL, Milne Bay Province, Papua New Guinea (R.C. Steene).

along the PNG mainland northwest towards Bootless Bay, nor where its distribution abuts that of *H. hallstromi*. Moreover, the presence of *Hemiscyllium* in the Huon Gulf region between Tufi and Madang on the southeastern PNG mainland is unknown; presumably the large estuarine area around Lae may provide sufficient habitat disjunction to separate *H. michaeli* and *H. strahani*, but this requires documentation. This species is typically encountered on coastal fringing reefs and patch reefs while diving at night, although it is sometimes seen during the day, sheltering under rocky outcrops or tabular corals. The known depth range is approximately 2–20 m.

Etymology. The species was named in honor of Scott W. Michael, an avid shark enthusiast, author, and underwater photographer, who was the first person to notice the difference between this species and *H. freycineti*.

Comparisons. This species is similar in appearance to *H. freycineti* from the Raja Ampat Islands, West Papua Province (far western New Guinea), Indonesia. The differences between these species are discussed under *H. freycineti*.

Remarks. Due to the similarity of color pattern and a misunderstanding of the geographic range, this species was confused with *H. freycineti* by previous authors (Dingerkus & DeFino 1983, Compagno 1984, 2001, Michael 1993, Compagno & Niem 1998).

Material examined. (all from Milne Bay Province, Papua New Guinea unless stated otherwise) USNM 218602 (holotype), female, 610 mm TL, coral reef at Harvey Bay, 08°54.440’ S, 148°30.306’ E, Oro Province, Papua New Guinea; AMS IA.5741-2 (paratypes), 2 specimens, 282-262 mm TL, vicinity of Samari, 10°36.633’ S, 150°39.690’ E; CU 24992 (paratype), 695 mm TL, Milne Bay; USNM 221705 (paratype), 257 mm TL, Kuia Island, 08°35.350’S, 150°51.332’E, Trobriand Islands; WAM P. 32840-001 (paratype), female, 544 mm TL, under wharf at Samarai Island, 10°36.633’ S, 150°39.690’ E.

Figure 36. *Hemiscyllium michaeli*, approx. 200 mm TL, Milne Bay Province, Papua New Guinea (B. Halstead).

Hemiscyllium ocellatum (Bonnaterre, 1788)

Queensland Epaulette Shark

Figures 1E, 2E, 3E & 37–41; Table 1.

Squalus ocellatus Bonnaterre, 1788: 8 (type locality: vicinity of Cooktown, Queensland, Australia).
Scyliorhinus ocellatus Blainville, 1816: 121.
Squalus oculatus (misspelling) Banks & Solander in Gray, 1827: 436.
Hemiscyllium ocellatum Müller & Henle, 1841: 16.
Scyllium ocellatum Blyth, 1847: 726, pl. 25.
Hemiscyllium oculatum (misspelling) Duméril, 1853: 119.
Chiloscyllium ocellatum Günther, 1870: 410.

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly variably sized dark-brown spots covering head and body, denser on dorsal surface, most spots smaller than twice eye size; post-cephalic ocellus well defined and unfragmented, with surrounding halo well differentiated from ground color of body; specimens from southern portion of range (south of about Cairns, Queensland) generally with more prominent spotting on body and fins, including on dorsal portion of head, dorsal surface of pectoral and pelvic fins, and on both dorsal fins; snout region (anterior to eyes) generally without spots or with only a few widely scattered spots; specimens from northern portion of range (from Cairns northwards) generally with fewer and larger dark spots, including none or only a few on pectoral, pelvic, and dorsal fins.

Morphometric features. (based on 27 specimens, 287–657 mm TL) Precaudal length 1.3 in TL, HL 6.3–8.2 in TL; head width 1.4–2.0 in HL; head depth 0.9–1.5 in head width; eye length 2.7–4.1 in snout length, eye height 1.7–4.1 in eye length; fleshy interorbital space 1.0–1.4, bony interorbital space 1.4–2.3, both in snout length; snout length 2.0–2.8, snout tip to mouth 4.7–7.9, snout tip to spiracle 1.8–2.6, snout tip to first gill slit 1.1–1.3, all in HL; distance between first and fifth gill slit 2.2–3.6 in HL; height of first gill slit 3.0–5.0 and fifth 2.0–3.0, both in snout length.

Mouth width 1.0–1.4, nasal barbel length 3.3–5.4, maximum width of lower labial flap 3.9–5.6, length of postoral fold (upper labial furrow) 2.7–4.5, length of lower labial furrow 3.5–5.5, all in snout length.

Snout tip to dorsal-fin origin 2.6–3.0, snout tip to pelvic-fin origin 3.4–3.8, snout to cloaca length 3.1–3.6, cloaca to anal-fin origin 2.1–2.5, cloaca to caudal-fin tip 1.2–1.5, all in TL; pectoral-fin length 1.0–1.6 in HL; pelvic-fin length 1.2–1.7 in HL; first dorsal-fin base 1.5–1.9 in HL; first dorsal-fin height 0.9–1.4 in first dorsal-fin base; free margin of first dorsal fin 1.6–2.2 in first dorsal-fin height; interdorsal space 0.9–1.2 in HL; second dorsal-fin base 1.4–2.1 in HL; second dorsal-fin height 0.9–1.3 in second dorsal-fin base; free margin of second dorsal fin 1.8–2.3 in second dorsal-fin height; anal-fin base 1.1–1.8 in HL; anal-fin height 3.2–4.9 in anal-fin base; free margin of anal fin 1.2–2.2 in anal-fin height; body depth at level of anal-fin origin 2.2–4.7 in HL; subcaudal length 5.6–6.7 in TL.

Figure 37. *Hemiscyllium ocellatum*, approx. 600 mm TL, captive specimen, S.E.A. Aquarium, Singapore (G.R. Allen).

Vertebral counts. Total vertebral centra 183–197 (8 specimens, including 7 from Dingerkus & DeFino [1983]); precaudal centra 144 (1 specimen).

Color in life. (Figs. 37–39) Generally pale gray to light brown grading to white ventrally with variably sized dark-brown spots covering head and body, denser on dorsal surface, most spots smaller than eye size; post-cephalic ocellus relatively well-defined and unfragmented with surrounding halo well differentiated from ground color of body (Fig. 38); specimens from southern portion of range (south of about Cairns) generally with more prominent spotting on body and fins (Figs. 37 & 38), including dorsal portion of head, dorsal surface of pectoral and pelvic fins, and both dorsal fins; snout region (anterior to eyes) either without spots or with relatively wide scattered ones smaller than eye; specimens from northern portion of range (from about Cairns or approximately 17° northwards) generally with fewer and larger dark spots (Figs. 39 & 40); pectoral and pelvic fins grayish brown with narrow white posterior margins, often without spots in small (less than about 350 mm TL) specimens, but with at least a few dark spots in most larger specimens (except far northern Great Barrier Reef off eastern Cape York Peninsula, Figs. 39 & 40); 2–3 dark brown saddles along dorsal margins of both dorsal fins in both southern and northern populations. Some individuals with 8–9 faint dark bars or saddles across back between level of post-cephalic ocellus and tail tip.

A video produced by the Tennessee Aquarium (USA)("Baby Epaulette Sharks at the Tennessee Aquarium" by TennesseeAquarium.org; accessed 10 October 2016 at https://www.youtube.com/watch?v=CXUvB-cj9cA), shows the color pattern of a newly hatched juvenile, approximately 150 mm TL, consisting of a white ground color; a pair of black bars on the head connected to a large, dark-gray dorsal saddle; a prominent black saddle and bar at the level of the pectoral fin that encompasses and is little differentiated from the large post-cephalic ocellus; 8 additional black bars between the level of the pelvic fin and tail tip; and broad black posterior margins on the pectoral and pelvic fins. There are also a few scattered, small dark gray spots, mainly on the anterior half of the body.

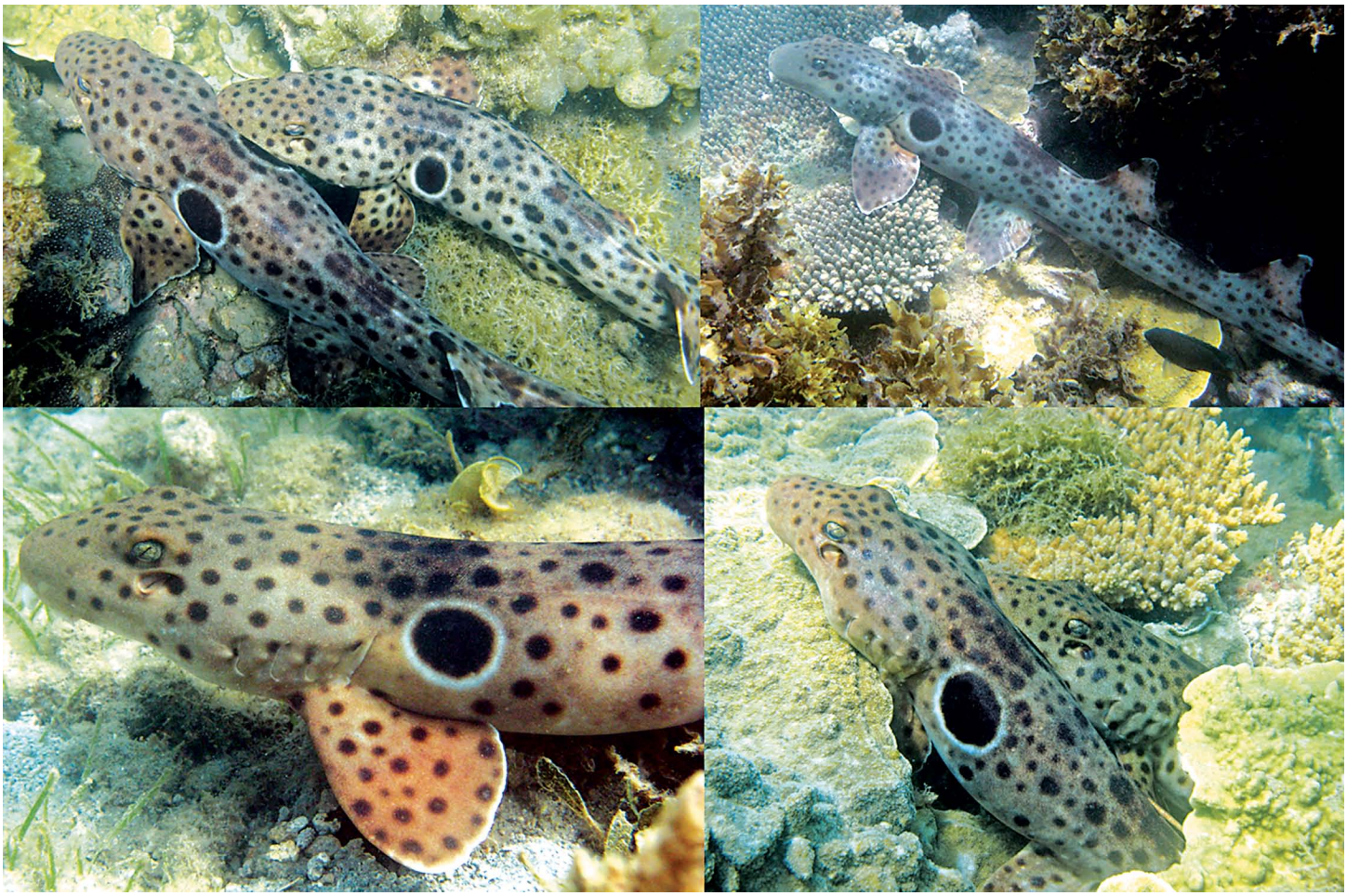

Figure 38. *Hemiscyllium ocellatum*, adults approx. 650–750 mm TL, except lower right approx. 500 mm TL, Magnetic Island, Queensland, Australia (A. Lewis).

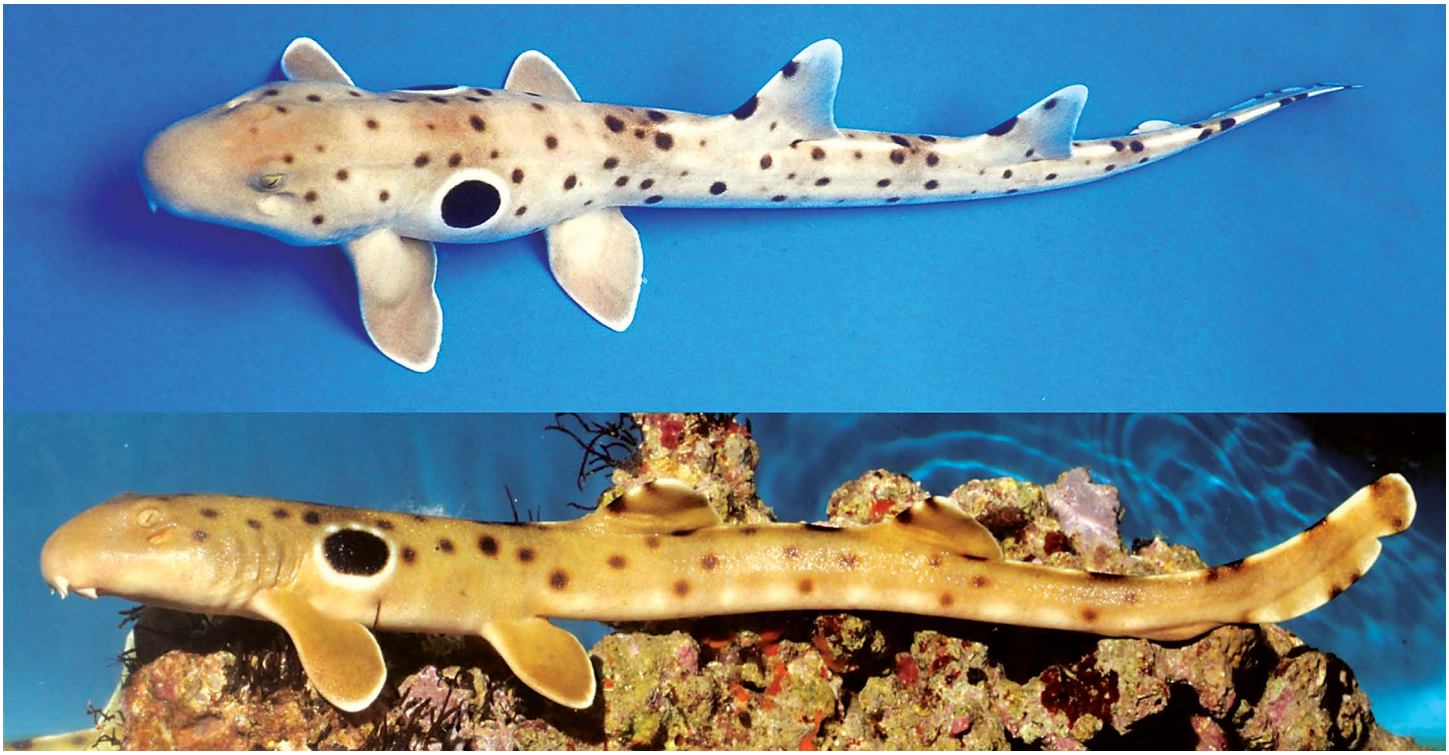

Figure 39. *Hemiscyllium ocellatum*, approx. 700 mm TL (upper) and 500 mm TL (lower), captive specimens from Great Barrier Reef off Cairns, Australia (F. Walsh).

Distribution and habitat. This species is known from Queensland, Australia, ranging from about the northern tip of Cape York Peninsula (approximately 10°44' S) to the southern extremity (approximately 24° S) of the Great Barrier Reef at the Capricorn Group (Fig. 5). The northernmost record (BMNH 1846.9.11.119–120) is from Sunday Island (11°56' S, 143°12' E), a small islet situated less than 3 km from the mainland coast. There are few reliable records from inshore areas of the Queensland coast, although it is not uncommon at Magnetic Island (19°7.340' S, 146°52.708' E; A. Lewis, pers. comm.). It probably occurs around other large islands, such as Great Keppel Island (23°05' S, 150°57' E), the Whitsunday Group (20°15' S, 149°00' E), Great Palm Island (18°05' S, 146°34' E), Hinchinbrook Island (18°18' S, 146°14' E), and Fitzroy Island (16°56' S, 146°00' E). In addition to two BMNH specimens from Sunday Island, we have examined a specimen (SMNS 14850) from Magnetic Island, and the type specimen was captured in the vicinity of Cooktown (15°28' S, 146°15' E). Details of the northernmost limit of distribution are uncertain and more collections are needed from this portion of the distribution, particularly the Torres Straits region, where it appears to be replaced by *H. hallstromi* (see remarks section for *H. hallstromi*). It appears to be most common in sheltered shallow waters of the Great Barrier Reef and is most commonly encountered at night or during low spring tides during daylight, when it is often seen in tide pools or sheltering under rocks.

Etymology. This species was named *ocellatum* (Latin: having small eyes), with reference to the conspicuous eye-like post-cephalic ocellus on each side of the body.

Comparison. This species is most similar to *H. henryi* from West Papua Province, Indonesia and *H. hallstromi* from southeastern Papua New Guinea and the Torres Strait area of far northeastern Australia. Differences are enumerated in Comparison sections for those two species.

Remarks. *Hemiscyllium ocellatum* was first collected in the vicinity of what is now Cooktown, Queensland by Joseph Banks during the voyage of the *Endeavour* under the command of Captain James Cook. The ship was beached at this locality for about seven weeks in June–July 1770 while the hull was being repaired after being damaged by a collision with a coral reef. The shark was eventually described by Pierre Bonnaterre (1788), an ordained priest, who also contributed the volumes on ichthyology to a French encyclopaedia of natural history (Saunders 2012). Bonnaterre's description was based on the earlier treatment of Bank's specimen by Broussonet (1780), who failed to provide a scientific name. Apparently, the type specimen was given to Broussonet by Banks and lodged at the Natural History Museum in Paris, where it presently resides.

Figure 40. *Hemiscyllium ocellatum*, preserved specimen, AMS I.22631–004, 613 mm TL, Escape Reef, northern Great Barrier Reef, Australia (G.R. Allen).

Figure 41. *Hemiscyllium ocellatum*, preserved juvenile specimens, AMS IA.2732, 160 mm TL (upper) and AMS IA.2961 171 mm TL (lower), Great Barrier Reef, Australia (G.R. Allen).

There has been considerable confusion concerning the distributional limits of *H. ocellatum*, with various reports of its range extending across the entire northern coastline of Australia, including northern Western Australia, Northern Territory, and eastern Queensland, as well as New Guinea (Munro 1956, Marshall 1965, Grant 1982, Compagno 1984, 2001, Randall *et al*. 1990, Michael 1993, Last & Stevens 2009, Compagno & Niem 1998, Hoese *et al*. 2006). However, our current investigations have failed to confirm its occurrence beyond Queensland waters. Extensive fish surveys by the Western Australian Museum during the past 40 years have failed to find this species in northwestern Australia and we are confident that it does not occur there.

A specimen of *H. ocellatum* at BMNH (1871.3.29.116) bears the locality of "Solomon Islands" on the label, which is apparently incorrect; most likely it originated from Queensland. Extensive surveys by the first author at the Solomon Islands failed to reveal any hemiscyllid sharks. Moreover, interviews with local fishers and dive guides confirmed that there have been no sightings. Surprisingly, a photo of typical *H. ocellatum* appeared in an illustrated guide to tropical Indian Ocean fishes (Debelius 1993) with text that stated the photograph was taken at the Seychelles. We subsequently contacted the photographer, Norbert Wu (Norbert Wu Productions), who confirmed the photograph was actually taken on the Great Barrier Reef. Compagno (2001) indicated this species possibly occurs in Malaysia and Sumatra, based on records by Stead (1963). These likely represent misidentifications of other small sharks such as *Chiloscyllium*, whose juveniles resemble *Hemiscyllium*. Although naturally absent from the Southeast Asian region, *H. ocellatum* is well-represented at the S.E.A. Aquarium in Singapore, where there is a highly successful captive-breeding program. The aquarium trades and sells live specimens to other public aquaria within and outside of Southeast Asia.

Material examined. (all Queensland, Australia; asterisk indicates detailed morphological data taken for Table 1) MNHN 1003* (holotype of *Squalus ocellatus*), male, 353 mm TL, vicinity of Cooktown; AMS B.8389*, female, 654 mm TL, Port Jackson (=Queensland); AMS E.1950*, female, 650 mm TL, North Reef (15.816° S, 151.833° E); AMS E.1951*, female, 555 mm TL, North Reef; AMS E.2793*, female, 648 mm TL, South Queensland; AMS IA.2063, 170 mm TL, no specific locality; AMS IA.2732, 160 mm TL, Great Barrier Reef off Cairns (approximately 16.7° S, 146.166° E); AMS IA.2961, 171 mm TL, Heron Island (23.433° S, 151.916° E); AMS IA.6087*, male, 651 mm TL, Gladstone (23.85° S, 151.266° E); AMS IB.4538*, male, 287 mm TL, Heron Island; AMS IB.5099*, female, 621 mm TL, Heron Island; AMS IB.5100*, male, 550 mm TL, Heron Island; AMS IB.5101*, female, 430 mm TL, Heron Island; AMS IB.5410*, female, 503 mm TL, Heron Island; AMS IB.6041*, male, 622 mm TL, Swains Reef (approximately 21° S, 152° E); AMS IB.6042*, male, 422 mm TL, Swains Reef; AMS IB.6075*, female, 432 mm TL, Swains Reef; AMS IB.6076*, male, 370 mm TL, Swains Reef; AMS IB.7422*, female, 486 mm TL, Townsville; AMS I.11121*, male, 609 mm TL, off Rockhampton (23.183° S, 145.833° E); AMS I.13985*, female, 380 mm TL, Two Isles (15.016° S, 151.9° E); AMS I.22631–004*, male, 613 mm TL, Escape Reef (15.816° S, 145.833° E); BMNH 1846.9.11.119–120, male, 419 mm TL, and female 426* mm TL, Sunday Island (11.929° S, 143.210° E); BMNH 1855.9.19.1367, male 376 mm TL, BMNH 1867.5.6.3*, female, 538 mm TL, Cape York, Queensland, Australia; BMNH 1870.12.27.1, female, 525 mm TL; BMNH 1911.4.1.40–41*, 2 specimens, 320–482 mm TL; BMNH 1927.2.10.1–2*, 2 specimens, female, 553 mm TL and male, 614 mm TL, Russell Island, Great Barrier Reef (approximately 17°13' S, 145°33' E); BMNH 1933.1.25.1, female, 392 mm TL, Low Isles (approximately 16°23' S, 145°33' E); BMNH 1933.1.25.2*, male, 380 mm TL, North West Islet, Capricorn Group, Queensland, Australia; QM I 236, female, 320 mm TL, North West Island, Capricorn Group, (23°18' S, 151°42' E); QM I 913, female, 274 mm TL, Masthead Island, Capricorn Group (23°32' S, 151°44' E); QM I 5354, male, 406 mm TL, Lindeman Island (20°27' S, 149°02' E); QM I 5443, male, 330 mm TL, Lindeman Island; QM I 7468, male, 664 mm TL; QM I 7469, female, 629 mm TL, Great Barrier Reef; QM I 11935*, female, 657 mm TL, Heron Island, Queensland, Australia (23°27' S, 151°55' E); QM I 31484, male, 740 mm TL, Sarina Inlet (21°24' S, 149°18' E); QM I 31780, female, 341 mm TL, Pompey Group (20°57' S, 151°18' E); SAMA F2110, female, 273 mm TL, north of Cairns (16°15' S, 145°46' E); SMNS 14850, 147.5 mm TL, Fish Cove, Magnetic Island, 21 km northeast of Townsville (18°59'00'' S, 146°55'20'' E); USNM 176692, 2 specimens, 453–535 mm TL, Great Barrier Reef, USNM 176822, 3 specimens, 469–643 mm TL, Great Barrier Reef; USNM 176863, 3 specimens, 421–470 mm TL, Great Barrier Reef; USNM 205380, 2 specimens, 167–269 mm TL, Fairfax Island (approximately 23°51' S, 152°22' E); ZMB 8997, male, 703 mm TL; WAM P.6158–001, male, 339 mm TL, Lady Musgrave Island (23°54.390' S, 152°23.926' E).

Hemiscyllium strahani Whitley, 1967

Hooded Epaulette Shark

Figures 1I, 2I & 42–44; Table 1.

Hemiscyllium strahani Whitley, 1967: 176 (type locality: New Guinea).

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly on head, consisting of numerous small, dark-brown spots on upper half and widely scattered, larger, dark-edged, round-to-rectangular markings, with a pair of broad, dark-brown-to-blackish bands, originating on lower side of snout and cheek and continuing onto ventral surface of head, separated by a much narrower white band and coalescing on throat with expansive dark-brown-to-blackish area that engulfs mouth, chin, and tip of snout; dark cheek bands punctuated by two or more large white spots, and an extensive white area (with irregular brown markings) immediately behind posterior dark band.

Morphometric features. (based on 3 specimens, 476–731 mm TL) Precaudal length 1.2–1.3 in TL, head length 7.1–8.3 in TL; head width 1.3–1.6 in HL; head depth 1.2–1.5 in head width; eye length 2.8–4.1 in snout length, eye height 1.9–4.2 in eye length; fleshy interorbital space 1.2–1.3, bony interorbital space 1.5–2.0, both in snout length; snout length 2.2–2.5, snout tip to mouth 6.7–8.2, snout tip to spiracle 1.9–2.1, snout tip to first gill slit 1.1–1.2, all in HL; distance between first and fifth gill slit 2.5–2.9 in HL; height of first gill slit 2.9–3.8 and fifth 2.1–2.3, both in snout length.

Mouth width 1.2–1.3, nasal barbel length 5.4–6.2, maximum width of lower labial flap 4.8–5.3, length of postoral fold (upper labial furrow) 3.5–5.0, length of lower labial furrow 3.7–4.5, all in snout length.

Snout tip to dorsal-fin origin 2.6–2.8, snout tip to pelvic-fin origin 3.4–3.7, snout to cloaca length 3.3–3.4, cloaca to anal-fin origin 2.2–2.3, cloaca to caudal-fin tip 1.4–1.5, all in TL; pectoral-fin length 1.1–1.3 in HL; pelvic-fin length 1.2–1.4 in HL; first dorsal-fin base 1.6–1.7 in HL, first dorsal-fin height 1.1–1.3 in first dorsal-fin base; free margin of first dorsal fin 1.5–1.9 in first dorsal-fin height; interdorsal space 1.0–1.3 in HL; second dorsal-fin base 1.7–1.8 in HL; second dorsal-fin height 1.1–1.3 in second dorsal-fin base; free margin of second dorsal fin 1.5–2.0 in second dorsal-fin height; anal-fin base 1.3–1.8 in HL, anal-fin height 3.2–3.6 in anal-fin base; free margin of anal fin 1.7–2.3 in anal-fin height; body depth at level of anal-fin origin 2.2–2.8 in HL; subcaudal length 5.9–8.0 in TL.

Figure 42. *Hemiscyllium strahani*, approx. 600 mm TL, near Jayapura, West Papua, Indonesia (M.V. Erdmann).

Vertebral counts. Total vertebral centra 187–194 (3 specimens, including 1 from Dingerkus & DeFino [1983]).

Color in life. (Figs. 42–44) Generally reddish-brown to orange-brown with about 7–8 darker-brown saddles across back and dorsal edge of caudal fin, most saddles extending onto side as broad bars that eventually bifurcate; upper half of body, dorsal fins, and dorsal surface of pectoral and pelvic fins with widely separated, relatively large (average size about equal to eye), dark-margined, round-to-rectangular, white markings; pectoral and pelvic fins also with interrupted white outer margin; head color pattern highly distinctive, consisting of numerous small, dark-brown spots on upper half; widely scattered, larger, dark-edged, round-to-rectangular markings; and a pair of broad, dark-brown-to-blackish bands originating on lower side of snout and cheek, continuing onto ventral surface of head, bands separated by a much narrower white band and coalescing on throat with expansive dark area that engulfs mouth, chin, and tip of snout (Fig. 43); dark cheek bands punctuated by two or more large white spots, and an extensive white area (with irregular brown markings) immediately behind posterior dark band; post-cephalic marking variable (Fig. 44), either weakly developed or relatively well developed, consisting of large, partially ocellated, dark-brown spot; anterior edge of both dorsal fins with a pair of prominent dark-brown markings; subcaudal and anal fin with alternating brown-and-white bars; belly and ventralmost portion of side generally white, except where interrupted by bifurcated brown bars.

Distribution and habitat. This species is restricted to the north coast of New Guinea with the known distribution extending from the vicinity of Madang, Papua New Guinea, westward to at least the Jayapura district of Papua Province, Indonesia (Fig. 5). The only record from an intermediate location consists of an underwater sighting by the first author near Wewak, Papua New Guinea, at Kairiru Island (3°19.066' S, 143°30.502' E). It seems likely that the distribution will extend westward along the north (Sarmi) coast of Papua Province to the vicinity of Cenderawasih Bay, a stretch of coastline that remains unsurveyed. In the absence of further information, we hypothesize the Mamberamo River outlet may provide a habitat disjunction that separates the ranges of *H. strahani* and *H. galei*. The preferred habitat of *H. strahani* consists of both shallow seagrass beds next to shore and coral reefs, to a depth of at least 20 m (based on the Kairiru Island sighting).

Etymology. The species was named in honor of Ronald Strahan, a former Director of the Taronga Zoological Park Aquarium in Sydney, Australia, and donor of the type specimen.

Comparisons. This is the most distinctive species of *Hemiscyllium* and unlikely to be confused with other species. The markings on the head (Fig. 43A) are diagnostic and clearly distinguishable from those of *H. halmahera*, the only other member of the genus with distinctive markings on the ventral surface of the head (Fig. 43B).

The morphometric data (Table 1) based, however, on only 3 specimens of *H. strahani*, suggest the species has a slightly shorter pectoral fin (10.6–10.9% TL) in comparison to *H. galei*, *H. halmahera*, and *H. henryi* (collective range of 11.0–11.7% TL).

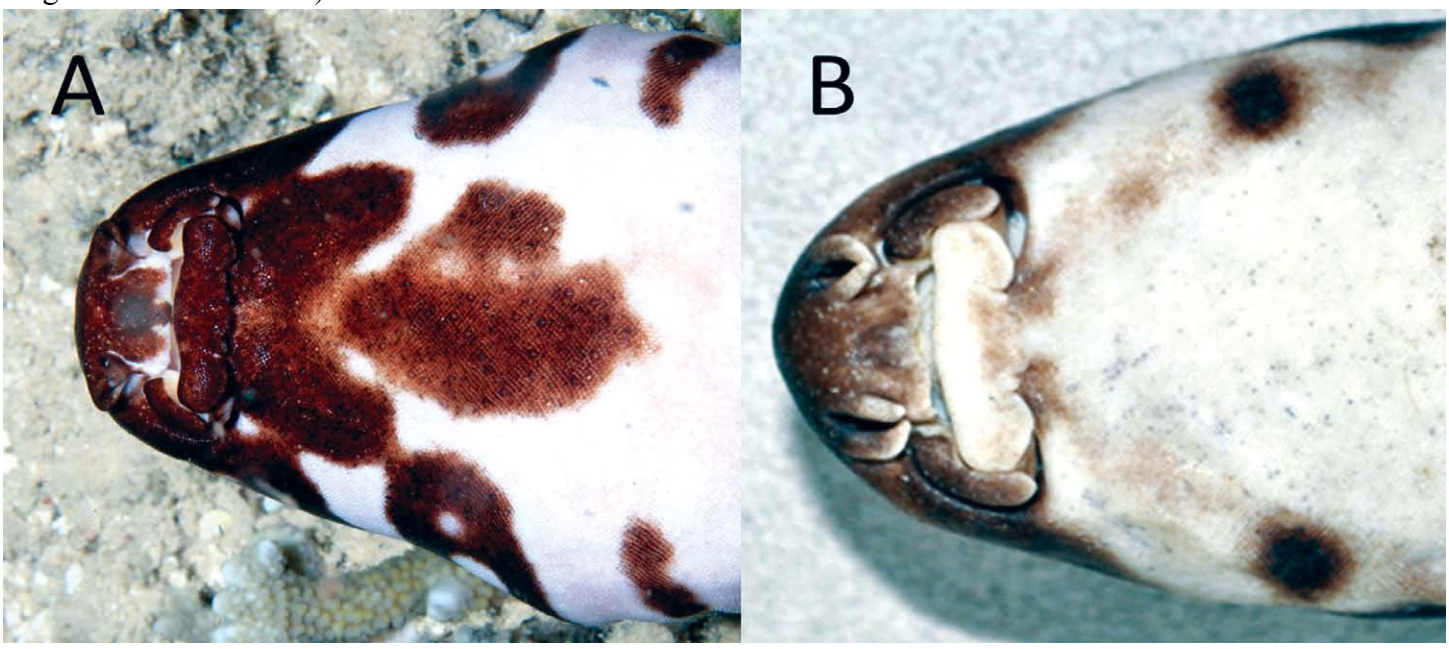

Figure 43. Ventral view of heads: (A) *Hemiscyllium strahani*, approx. 600 mm TL, near Jayapura, West Papua, Indonesia (M.V. Erdmann); (B). *H. halmahera*, WAM P.33784–001, 656 mm TL, Ternate Island, Halmahera, Indonesia (G.R. Allen).

Figure 44. Head views of *Hemiscyllium strahani*, approx. 600 mm TL (upper), near Jayapura, West Papua, Indonesia (M.V. Erdmann; approx. 600 mm TL (lower), Madang, Papua New Guinea (S. Michael).

Remarks. The true distribution of this species has been confused, due to the incorrect assumption by Dingerkus and DeFino (1983) that the type specimen, which was donated to the Australian Museum by the Taronga Zoological Park in Sydney, originated from the Port Moresby area. Based partly on this information, a broad distribution encompassing the entire coastline of New Guinea was reported by Compagno (1984). However, subsequently the distribution was limited to Port Moresby and Madang areas on the southern and northern coasts of Papua New Guinea (respectively) by Compagno (2001), and a similar range (with the addition of Wewak, Papua New Guinea) was reported by Allen & Erdmann (2012). We now conclude that this species is restricted to the northern coast of New Guinea (from Madang to at least Jayapura), based on our museum and field investigations, which failed to uncover any reliable records from the southern coast, including the Port Moresby region. We have observed *H. strahani* at night on shallow coastal reefs and sheltering in caves and crevices during the day, in depths ranging from about 3–18 m.

Material examined. (asterisk indicates detailed morphological data taken for Table 1) AMS IB. 7938* (holotype), female, 735 mm TL, New Guinea via Taronga Park Zoo Aquarium, Sydney, Australia; IRSNB 18574, male, Laing Island, Papua New Guinea (4°13.730' S, 144°56.573' E); MZB 983, 2 females, 551–668 mm TL, and male 504 mm TL, Kajo Bay, Jayapura, Papua Province, Indonesia (2°31' S, 140°43' E); RMNH 33994*, female 476 mm TL, near Jayapura, West Papua; SMNS 4836*, female, 668 mm TL, New Guinea; USNM 221701, male, 594 mm TL, southern tip of Masas Island, Madang, Papua New Guinea (5°10' S, 145°50' E).

Hemiscyllium trispeculare Richardson, 1843

Speckled Epaulette Shark

Figures 1D, 2D, 3D & 45–47; Table 1.

Hemiscyllium trispeculare Richardson, 1843: 5 (type locality: North West Australia).
Chiloscyllium trispeculare Günther, 1870: 41.

Diagnosis. A species of *Hemiscyllium* distinguished by a unique color pattern, particularly a dense covering of close-set, small, brown spots on head and most of body; about 7–8 dark-brown saddles from level of pelvic fins to tail tip, first 4 on body extending across back onto sides and consisting of large polygon-shaped dark marks separated by whitish reticulum; posterior 4 bars more-or-less solid dark-brown dorsally and more diffuse on sides, enclosing numerous small brown spots and a few larger ovate brown markings; ventral portion of side with alternating white-and-brown bars of approximately equal width; post-cephalic ocellus large and well-formed, bordered posteriorly by a dark patch comprising 1 to 3 poorly formed irregular smaller ocelli; both dorsal fins with a pair of dark-brown saddles along anterior margin and pyramid-shaped zone of dark-brown spotting at base; apex and posterior margin of fin narrowly white; pectoral and pelvic fins brown with numerous small brown spots, largest and most conspicuous on basal portion of fin, outer margin narrowly white.

Morphometric features. (based on 28 specimens, 403–720 mm TL) Precaudal length 1.2–1.4 in TL, HL 6.2–8.2 in TL; head width 1.2–1.9 in HL; head depth 1.0–1.5 in head width; eye length 2.6–4.1 in snout length, eye height 1.8–3.9 in eye length; fleshy interorbital space 1.0–1.6, bony interorbital space 1.4–2.0, both in snout length; snout length 2.0–3.2, snout tip to mouth 4.4–7.1, snout tip to spiracle 1.8–2.6, snout tip to first gill slit 1.1–1.3, all in HL; distance between first and fifth gill slit 2.4–3.8 in HL; height of first gill slit 2.3–3.9 and fifth 1.8–2.8, both in snout length.

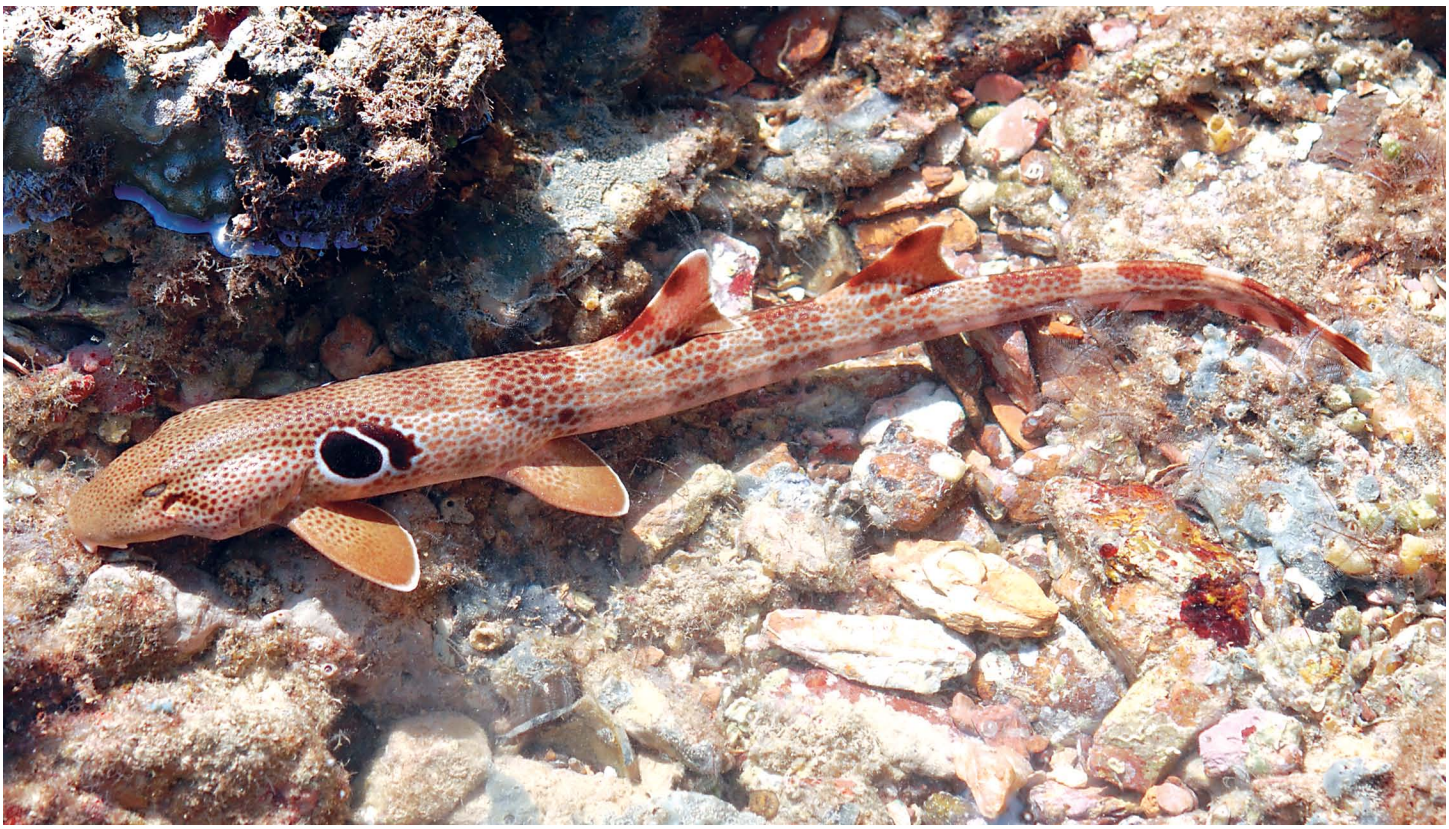

Figure 45. *Hemiscyllium trispeculare*, approx. 650 mm TL, in tidal pool, Darwin, Northern Territory, Australia (M.P. Hammer).

Mouth width 1.0–1.4, nasal barbel length 3.3–7.5, maximum width of lower labial flap 3.6–5.7, length of postoral fold (upper labial furrow) 2.8–5.1, length of lower labial furrow 3.4–5.4, all in snout length.

Snout tip to dorsal-fin origin 2.6–3.0, snout tip to pelvic-fin origin 3.1–3.6, snout to cloaca length 2.9–3.7, cloaca to anal-fin origin 2.0–2.5, cloaca to caudal-fin tip 1.4–1.5, all in TL; pectoral-fin length 1.0–1.5 in HL; pelvic-fin length 1.2–1.6 in HL; first dorsal-fin base 1.3–2.5 in HL; first dorsal-fin height 0.9–1.4 in first dorsal-fin base; free margin of first dorsal fin 1.0–2.8 in first dorsal-fin height; interdorsal space 1.0–1.6 in HL; second dorsal-fin base 1.5–2.4 in HL; second dorsal-fin height 0.9–1.5 in second dorsal-fin base; free margin of second dorsal fin 1.3–2.6 in second dorsal-fin height; anal-fin base 1.0–2.2 in HL; anal-fin height 2.2–4.8 in anal-fin base; free margin of anal fin 1.5–2.2 in anal-fin height; body depth at level of anal-fin origin 2.3–4.3 in HL; subcaudal length 5.5–8.2 in TL.

Vertebral counts. Total vertebral centra 176–191 (9 specimens, including 4 from Dingerkus & DeFino [1983]); precaudal centra 143–150 (5 specimens).

Color in life. (Figs. 45–47) Overall brown to tan, grading to whitish ventrally; dense reticulum of small brown spots, more-or-less round on head (approximately 100-200 spots on portion of head anterior to eyes on adults), and frequently horizontally ovate on body; 9 darker-brown saddles (including aforementioned spots) at level of pectoral fins, pelvic fins, first dorsal fin, midway between dorsal fins, second dorsal fin, anterior to anal fin, and 3 on tail; dorsal portion of saddles frequently composed of clusters of dark-brown polygons extending onto lower half of side; highly conspicuous post-cephalic ocellus with well-developed white halo and bordered posteriorly by a dark patch comprising 1 to 3 poorly formed irregular smaller ocelli (Figs. 46 & 47); dark polygons and dark brown spots extending onto basal portion of dorsal fins; first and second dorsal fins also with pair of dark-brown saddle-like markings on anterior edge and white margin around apex of fin, continued narrowly along posterior margin; caudal fin with 3 similar dark-brown marks (occupying dorsal edge of dark bars); pectoral and pelvic fins brown with numerous dark-brown spots (as many as 100 on pectoral fin), more distinct basally and anteriorly, becoming faint on outer portion, and both fins with narrow, white posterior margin. Last & Stevens (2009) noted

Figure 46. *Hemiscyllium trispeculare*: A) approx. 600 mm TL, Ashmore Reef, Timor Sea, Australia (G.R. Allen); B) approx. 700 mm TL, Aru Islands, Indonesia (G.R. Allen); C) RMNH 7402, 613 mm TL (questionably Kai Islands, Indonesia, see text)(W. White).

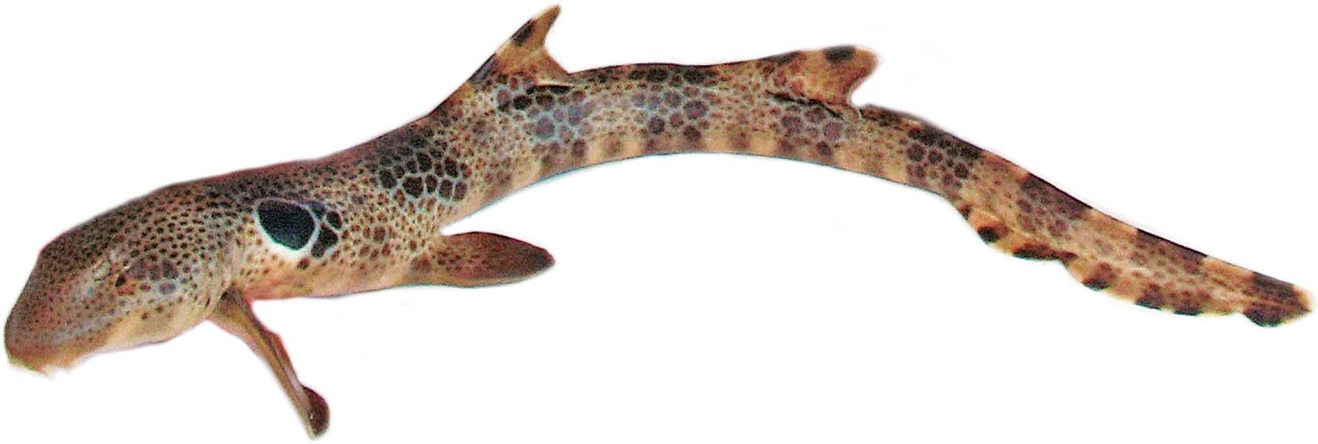

Figure 47. *Hemiscyllium trispeculare*, approx. 500 mm TL, Darwin, Northern Territory, Australia (M.P. Hammer).

that specimens from Northern Territory appear to have much smaller and denser spots than those from Western Australia. Our current investigations confirm this observation and we also note that Indonesian specimens are similar to those from Western Australia in this respect.

Distribution and habitat. This species is known from northwestern Australia, ranging from Exmouth Gulf, Western Australia to Melville Bay and Cape Arnhem, Northern Territory (Fig. 5). It also occurs in Indonesia at the Aru Islands, situated near the edge of the shallow shelf, which periodically formed a land bridge between Australia and New Guinea during the past 2–3 million years (Allen *et al*. 2015). There is also an historic record (Bleeker 1864a) from Kei Besar, Kei Islands, which lie about 120 km east of the Aru Islands, but this needs to be confirmed (see remarks section). The species inhabits trawling grounds such as Exmouth Gulf, Western Australia where depths are generally less than 20 m. It also occurs on reefs and shoals of the northwestern Australian coast, which are exposed to huge daily tidal fluctuations, which can approach 7–10 m in some places. It is regularly encountered in shallow rock pools during low spring tides in the Darwin area (M. Hammer of NTM, pers.comm.).

Etymology. The species name is derived from Latin (*specularis*: to look) and presumably refers to the post-cephalic ocellus bordered posteriorly by additional poorly formed smaller ocelli.

Comparisons. The distinctive color pattern of *H. trispeculare* is unlikely to be confused with any other member of the genus.

Remarks. This species was originally described by Richardson (1843) on the basis of a drawing obtained by Lieutenant Emery, made at Turtle Island, North West Australia. It is uncertain if this refers to the present day North Turtle Island (19°52.898'S, 118°53.999'E), which is about 20 km off the mainland of Western Australia, 57 km northeast of Port Hedland. Richardson eventually obtained a specimen from the *Erebus* and *Terror* voyage, and described it in more detail in a subsequent publication (Richardson 1846). Günther (1870) considered the *Erebus* and *Terror* specimen (BMNH 1953.5.10.1) to be the type. Therefore, Richardson's 1846 specimen is the holotype and not the neotype as designated by Dingerkus & DeFino (1983), and its collection site, given as North West Australia, is the type locality.

The distributional limits for this species in Australian waters is confusing, with many literature reports of its range extending across the entire northern coastline and southward along the east coast of Queensland (Munro 1956, Marshall 1965, Compagno 1984, 2001, Michael 1993, Last & Stevens 2009, Compagno & Niem 1998, Hoese *et al*. 2006). However, our current investigations have failed to confirm its occurrence in eastern Queensland waters, although it may range into the northern (Gulf of Carpentaria) portion of the state. We also question its occurrence at the Kei Islands, as reported by Bleeker (1864a), although we have confirmed the identity of Bleeker's specimen (RMNH 7402, Fig. 46 C). We doubt the possibility of its occurrence in the Kei Islands, given the inability of these sharks to cross deep-water barriers; marine charts indicate depths in excess of 3,000 m between the Aru and Kei Islands. It is likely that the specimen sent to Bleeker originated from the Aru Islands. He received thousands of specimens from his extensive network of contacts throughout the Indonesian Archipelago during his time there from 1842–1860, including numerous specimens from the Aru Islands, which were covered in three publications (Bleeker 1864b, 1868, 1873).

Material examined. (all Australia unless stated otherwise; asterisk indicates detailed morphological data taken for Table 1) BMNH 1953.5.10.1* (neotype), male, 575 mm TL, northwestern Australia; AMS I.5267*, male, 547 mm TL, Darwin, Northern Territory (approximately 12°21' S, 130°51' E); AMS I.5268*, female, 535 mm TL, Darwin; AMS IA.3038*, female, 475 mm TL, Clarence Strait, Northern Territory (approximately 12°01'S, 131°05'E); AMS IA.7534*, 2 specimens, females, 512–630 mm TL, Darwin; AMS IA.7639*, female, 505 mm TL, Darwin; AMS IA.7821*, female, 615 mm TL, Melville Island, Northern Territory (approximately 11°19' S, 130°39' E); AMS IA.24678–038*, female, 496 mm TL, Darwin; AMS IB.400*, male, 618 mm TL, Melville Bay, Northern Territory (approximately 12°15' S, 136°43' E); AMS IB.1070*, female, 639 mm TL, Yirrkala, Northern Territory (approximately 12°15' S, 136°54' E); CSIRO C. 2288*, female, 580 mm TL, CSIRO C 2289*, female, 615 mm TL, Exmouth Gulf, Western Australia (approximately 22° S, 114° E); CSIRO CA.3662*, female, 658 mm TL, Darwin Harbor, Northern Territory (approximately 12°30' S, 130°47' E); NTM S.10004–001, male 625mm TL, Sandy Island, Cobourg Peninsula, Northern Territory (11°07'01" S, 132°16'59" E); NTM S.10603–008, male, 545mm TL, North Oxley Island, Northern Territory (11° S, 132°49'01" E); NTM S.11263–007, female, 298mm TL, Coral Bay, Cobourg Peninsula, Northern Territory (approximately 11°12' S, 132°03' E); NTM S.12329–037, male, 346 mm TL, near West Island, Ashmore Reef, Timor Sea (approximately 12°14' S, 122°57' E); RMNH 35295*, 2 specimens, female, 530 mm TL and male, 531 mm TL, Aru Islands, Banda Sea, Indonesia; RMNH 7402*, male, 613 mm TL, Kai Islands, Maluku Province, Indonesia; SAMA F.9632, male, 790 mm TL, Serrurier Island, Western Australia (21°37'32" S, 114°40'43" E); SMNS 2530*, female, 403 mm TL, Port Darwin, Australia; WAM P.7099*, female, 503 mm TL, Point Sampson, Western Australia (approximately 20°38' S, 117°12' E); WAM P.16287*, 2 specimens, female, 603 mm TL and male, 705 mm TL, Exmouth Gulf, Western Australia (approximately 21°53' S, 114°52' E); WAM P.16288*, female, 710 mm SL, Exmouth Gulf, Western Australia; WAM P. 20143–001*, female 700 mm TL, Rosemary Island, Dampier Archipelago, Western Australia (approximately 20°29' S, 116°32' E); WAM P.20145–001*, male, 720 mm SL, Rosemary Island, Dampier Archipelago, Western Australia; WAM P. 24648*, female, 652 mm TL, Kendrew Island, Dampier Archipelago, Western Australia (approximately 20°29' S, 116°32' E); WAM P.27274–037*, female, 695 mm TL, Broome, Western Australia (17°59.219' S, 122°74.097' E); WAM P.33274–004*, male, 452 mm SL, Adele Island, Western Australia (15°29.474' S, 123°09.798' E); WAM P.33291–039*, male, 513 mm SL, Montgomery Reef, Western Australia (15°53.700' S, 124°20.340' E).

Acknowledgments

We are especially grateful to Conservation International, which provided financial support for field activities and museum visits during the study. We thank the Indonesian Department of Nature Conservation (PHKA) for sponsoring the 2006 expeditions to Cenderawasih and Triton Bays in the Bird's Head region of New Guinea (West Papua Province of Indonesia). We also acknowledge the generous financial support of the Walton Family Foundation and the Paine Family Trust and their continued interest and support of CI's Bird's Head Seascape marine conservation initiative. Moreover, Susan Paine and her children Mercy, Honor, and Samuel accompanied GRA and MVE on a hemiscylliid shark photography expedition to Papua New Guinea during June 2013. We are extremely grateful for the hospitality and generosity of the following dive resort and live-aboard boat owners/managers and their hardworking and efficient staffs: Max Ammer (Papua Diving, Raja Ampat Islands), Craig Howson (*True North* live-aboard), Dick Knight (Loloata Resort, Papua New Guinea), Ken and Josephine Wiedenhoeft (*Putiraja* live-aboard), Alberto Reija and Tony Rhodes (*Damai* live-aboard), Rob Vanderloos (*Chertan* live-aboard). Dive guide Graham Abbott was instrumental in the success of the 2006 expeditions. We are also indebted to Michael Hammer, Burt Jones, Maurine Shimlock, Bob Halstead, Andy Lewis, Scott Michael, Tom Mulder, Roger Steene, Fenton Walsh, and Phil Woodhead for their excellent photographs. Laboratory investigations were generously facilitated by the following museum staff members: Mark McGrouther, Amanda Hay, and Sally Reader (AMS); John Friel (CU); Patrice Pruvost (MNHN); Renny Hadiaty (MZB); Michael Hammer (NTM); Jeff Johnson (QM); Jeff Williams (USNM); Glenn Moore, Mark Allen, and Sue Morrison (WAM); and Alastair Graham and John Pogonoski (CSIRO). David Ebert and Victoria Vasquez provided valuable reviews of the manuscript.

References

Allen, G.R. (2009) *Field guide to marine fishes of tropical Australia and South-east Asia. Fourth Edition.* Western Australian Museum, Perth, Australia, 287 pp.

Allen, G.R. & Dudgeon, C.L. (2010) *Hemiscyllium michaeli*, a new species of bamboo shark (Hemiscyllidae) from Papua New Guinea. *Aqua, International Journal of Ichthyology*, 16(1), 19–30.

Allen, G.R. & Erdmann, M.V. (2008) Two new species of bamboo sharks (Orectolobiformes: Hemiscyllidae) from western New Guinea. *Aqua, International Journal of Ichthyology*, 13(3–4), 93–108.

Allen, G.R. & Erdmann, M.V. (2012) *Reef fishes of the East Indies. Vol. I*. Tropical Reef Research, Perth, Australia, 424 pp.

Allen, G.R., Erdmann, M.V. & Dudgeon, C.L. (2013) *Hemiscyllium halmahera*, a new species of bamboo shark (Hemiscyllidae) from Indonesia. *Aqua, International Journal of Ichthyology*, 19(3), 123–136.

Allen, G.R., Hadiaty, R.K., Unmack, P.J. & Erdmann, M.V. (2015) Rainbowfishes (*Melanotaenia*: Melanotaeniidae) of the Aru Islands, Indonesia with descriptions of five new species and redescription of *M. patoti* Weber and *M. senckenbergianus* Weber. *Aqua, International Journal of Ichthyology*, 21(2), 66–108.

Blainville, H. de (1816) Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin de la Société Philomathique de Paris*, 8, 105–112 [*sic* for 113–120] + 121–124.

Bleeker, P. (1855) Bijdrage tot de kennis der ichthyologische fauna van Batjan. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, 7(3), 359–378.

Bleeker, P. (1857) Verslag van eene nieuwe verzameling visschen van Batjan. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, 13(2), 381–386.

Bleeker, P. (1864a) Notice sur quelques poissons de l'île Grand-Key. *Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afdeling Natuurkunde*, 16(3), 362–363.

Bleeker, P. (1864b) Notice sur la faune ichthyologique des îles Arou. *Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afdeling Natuurkunde*, 16 (3), 366–368.

Bleeker, P. (1868) Deuxième notice sur la faune ichthyologique des îles Arou. *Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afdeeling Natuurkunde (Ser. 2)*, 2, 305–306.

Bleeker, P. (1873) Troisième notice sur la faune ichthyologique des îles Arou. *Verslagen en Mededeelingen der Koninklijke Akademie van Wetenschappen, Afdeeling Natuurkunde (Ser. 2)*, 7, 35–39.

Blyth, E. (1847) Zoological Department. Mr. Blyth's Report. *Journal of the Asiatic Society of Bengal (New Series)*, 16 (7), 725–726.

Bonnaterre, J.P. (1788) *Tableau encyclopédique et methodique des trois règnes de la nature. Ichthyologie*. Chez Panckoucke, Paris, France, 215 pp.

Broussonet, P.M.A. (1780) Mémoire sur les différentes espèces de chiens de mer. *Histoire de l'Académie Royale des Sciences, Paris*, 1780, 641–680.

Compagno, L.J.V. (1984) *FAO species catalogue. Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 1 - Hexanchiformes to Lamniformes*. FAO Fisheries Synopsis 125, i–viii + 1–249.

Compagno, L.J.V. (2001) *Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Volume 2. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes)*. FAO Species Catalogue for Fishery Purposes. No. 1, Vol. 2., FAO, Rome, 269 pp.

Compagno, L.J.V. & Niem, V.H. (1998) Sharks. *In*: Carpenter, K.E. & Niem, V.H. (Eds.) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific, Vol. 2.* FAO, Rome, pp. 1195–1368.

Debelius, H. (1993) *Indian Ocean tropical fish guide*. Aquaprint Verlags GmbH, Neu Isenburg, Germany, 321 pp.

Dingerkus, G. & DeFino, T.C. (1983) A revision of the orectolobiform shark family Hemiscyllidae (Chondrichthys: Selachii). *Bulletin of the American Museum of Natural History*, 176(1), 1–93.

Duméril, A.H. (1853) Monographie de la tribu des Scylliens ou Roussettes (poissons plagiostomes) comprenant deux espèces nouvelles. *Revue et Magasin de Zoologie (Sér. 2)*, 5, 8–25; 73–87; 119–130.

Garman, S. (1913) The Plagiostomia (sharks, skates, and rays). *Memoirs of the Museum of Comparative Zoology*, 36, 1–515.

Gill, T.N. (1862) Analytical synopsis of the order of Squali; and revision of the nomenclature of the genera. *Annals of the Lyceum of Natural History of New York*, 7(art. 32), 367–370.
Goto, T., Nishida, K. & Nakaya, K. (1999) Internal morphology and function of paired fins in the epaulette shark, *Hemiscyllium ocellatum*. *Ichthyological Research*, 46(3), 281–287.
Grant, E.M. (1982) *Guide to fishes. Fifth Edition.* The Department of Harbours and Marine, Brisbane, Queensland, 896 pp.
Gray, J.E. (1827) *List of fish of Australia*. King's Survey of Australia, pp. 435–437.
Günther, A. (1870) *Catalog of fishes in the British Museum. Volume 8*, pp. 410–413.
Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model, and animations. *Journal of Asian Earth Sciences*, 20, 353–434.
Heupel, M.R. & Bennett, M.B. (1998) Observations on the diet and feeding habits of the epaulette shark, *Hemiscyllium ocellatum* (Bonnaterre), on Heron Island Reef, Great Barier Reef, Australia. *Marine and Freshwater Research*, 49(7), 753–756.
Hoese, D. F., Bray, D. J., Paxton, J. R. & Allen, G.R. (2006) Fishes (Part 1) *In*: Beesley, P. L. & Wells, A. (Eds.) *Zoological Catalogue of Australia. Volume 35*. ABRS & CSIRO Publishing, Australia, 670 pp.
Last, P.R. & Stevens, J.D. (2009) *Sharks and rays of Australia. Second edition.* CSIRO, Australia, 656 pp.
Lesson, R.P. (1831) Poissons. Part of Duperrey, L.I. (1826–1830) *Voyage autour du monde, execute par ordre du roi, sur la corvette de La Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825*. Vol. 2(1), Arthus Bertrand, Paris, 471 pp.
Marshall, T.C. (1965) *Fishes of the Great Barrier Reef and coastal waters of Queensland*. Livingston Publishing, Narberth, Pennsylvania, USA, 566 pp.
Michael, S.W. (1993) *Reef sharks and rays of the world.* Sea Challengers, Monterey, California, USA, 107 pp.
Müller, J. & Henle, F.G.J. (1837) Ueber die Gattungen der Plagiostomen. *Archiv für Naturgeschichte*, 3, 394–401, 434.
Müller, J. & Henle, F.G.J. (1838) On the generic characters of cartilaginous fishes, with descriptions of new genera. *Magazine of Natural History (new series)*, 2, 33–37, 88–91.
Müller, J. & Henle, F.G.J. (1838–41) *Systematische Beschreibung der Plagiostomen*. Veit und Comp., Berlin, xxii + 200 pp, 60 pls.
Munro, I.S.R. (1956) Handbook of Australian Fishes. Number 1. *Australian Fisheries Newsletter*, 15(7), 13–20.
Polhemus, D.A. & Polhemus, J.T. (1998) Assembling New Guinea: 40 million years of island arc accretion as indicated by the distributions of aquatic Heteroptera (Insecta). *In*: Hall, R. & Holloway, J.D. (Eds.) *Biogeography and Geological Evolution of SE Asia*. Blackhuys Publishers, Leiden, Netherlands, pp. 327–340.
Quoy, J.R.C. & Gaimard, J.P. (1824) Description des Poissons. Chapter IX. *In*: Freycinet, L. de (Ed.) *Voyage autour du Monde...exécuté sur les corvettes de L. M. "L'Uranie" et "La Physicienne," pendant les années 1817, 1818, 1819 et 1820*. Paris, France, pp. 192–401.
Randall, J.E., Allen, G.R. & Steene, R.C. (1990) *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Publishing, Bathurst, Australia, 557 pp.
Regan, C.T. (1908) A revision of the sharks of the family Orectolobidae. *Proceedings of the Zoological Society of London*, 1908(2), 347–364.
Richardson, J. (1843) *Icones piscium, or plates of rare fishes. Pt I.* Richard & John E. Taylor, London, England, 5 pls.
Richardson, J. (1846) Ichthyology of the voyage of H.M.S. *Erebus & Terror*. *In*: Richardson, J. & Gray, J.E. (Eds.) *The zoology of the voyage of H.H.S. "Erebus & Terror," under the command of Captain Sir J.C. Ross ... during ... 1839–43*. London. Volume 2, viii + 139 pp.
Saunders, B. (2012) *Discovery of Australia's fishes. A history of Australian ichthyology to 1930*. CSIRO Publishing, Collingwood, Victoria, Australia, 520 pp.
Söderström, V., Renshall, G.M.C. & Nilsson, G.E. (1999) Brain blood flow and blood pressure during hypoxia in the epaulette shark *Hemiscyllium ocellatum*, a hypoxia-tolerant elasmobranch. *The Journal of Experimental Biology*, 202, 829–835.
Stead, D.G. (1963) *Sharks and rays of Australian seas*. Angus & Robertson, Sydney, Australia, 211 pp.
Whitley, G.P. (1967) Sharks of the Australasian region. *Australian Zoologist*, 14(2), 173–188.
Wise, G., Mulvey, J.M. & Renshaw, G.M.C. (1998) Hypoxia tolerance in the Epaulette Shark (*Hemiscyllium ocellatum*). *The Journal of Zoology*, 281, 1–5.