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Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae)

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Abstract

The taxonomic history of the genus *Manta* has been questionable and convoluted, with *Manta* having one of the most extensive generic and species synonymies of any living genus of cartilaginous fish. Having previously been considered a monotypic genus with a single recognized species, *Manta birostris* (Walbaum 1792), new evidence, in the form of morphological and meristic data, confirm that two visually distinct species occur, both with wide ranging distributions through many of the world's oceans. *Manta birostris* stands as the most widely distributed member of the genus, while *Manta alfredi* (Krefft 1868), resurrected herein, represents a smaller, more tropical species. Separation of the two species is based on morphometric measurements and external characters including colouration, dentition, denticle and spine morphology, as well as size at maturity and maximum disc width. The two species of *Manta* are sympatric in some locations and allopatric in other regions. A visual key was constructed which highlights the conspicuous, diagnostic features of the two species using data collected throughout their respective geographical ranges. A third, putative species, referred to here as *Manta sp. cf. birostris*, in the Atlantic may be distinct from *M. birostris*, but further examination of specimens is necessary to clarify the taxonomic status of this variant manta ray. The results of this study will aid in the differentiation of members of this genus both in the field and in preserved specimens. The splitting of this long-standing monospecific genus will help to highlight the specific threats facing the different species of *Manta* (e.g. targeted fishing, bycatch fisheries, boat strikes and habitat degradation) and will ultimately assist in the correct assessment of their respective worldwide conservation status.

Key words: Taxonomy, elasmobranch, diagnostic features, morphology, manta ray, colouration, *Manta birostris*

Introduction

The devil rays (Family Mobulidae, Suborder Myliobatoidei, Order Rajiformes), are currently divided into two distinctive genera, *Mobula* Rafinesque, 1810 and *Manta* Bancroft, 1828. The taxonomic history of the genus *Manta* has been convoluted, with *Manta* having one of the most extensive generic and species synonymies of any living genus of cartilaginous fish. In all there have been 10 generic and 25 specific synonyms with the latter mostly without type specimens (Lamont 1824; Lesueur 1824; Mitchill 1824; Whitley 1936; Beebe and Tee-Van 1941; Fowler 1941; Bigelow and Schroeder 1953). Currently this genus is considered to be monotypic (Eschmeyer *et al.* 1983; Homma *et al.* 1999; Compagno 1999; Clark 2002b; McEachran and Aschliman 2004). *Manta birostris* (Walbaum 1792) is reported to occur circumglobally as far north as Rhode Island and southern California on the United States east and west coasts, Japan, Egypt, and the Azores in the northern hemisphere and as far south as Peru, Uruguay, South Africa and New Zealand in the southern hemisphere.

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Opportunistic dissections and incidental catches of manta rays throughout their distribution have only contributed to the confusion with variable reports of maximum disc widths, size at maturity, external colouration patterns, tooth counts and the presence and absence of a tail spine (Lamont 1824; Lesueur 1824; Mitchill 1824; Coles 1916; Gudger 1922; Whitley 1936; Beebe and Tee-Van 1941; Barton 1948; Bigelow and Schroeder 1953; Nishida 1990; Last and Stevens 1994; Homma *et al.* 1999; Ebert 2003; White *et al.* 2006; Marshall *et al.* 2008). Several of these inconsistencies have led to speculation over the validity of the monospecific status of *Manta* (Notarbartolo-di-Sciara and Hillyer 1989, Compagno 1999) and have highlighted the need for further clarification.

Historical accounts and morphometric measurements of *M. birostris* have been incomplete or have used non-standardised methods, which have resulted in unclear descriptions that are difficult to interpret or compare to other data (e.g. Lamont 1824; Lesueur 1824; Müller and Henle 1841; Coles 1916). Moreover, like all mobulid rays, specimens of *M. birostris* are poorly represented in ichthyological collections, as individuals are extremely large and specimens are difficult to keep intact, preserve or store in archives (Notarbartolo-di-Sciara 1987). Most museum specimens have either been misplaced, lost, or replaced with body casts that fail to depict important colouration patterns or lack diagnostic characters such as denticles or teeth. The most detailed morphological descriptions of *Manta* come from individuals caught in the Galapagos Islands in 1928 (Beebe and Tee-Van 1941), two specimens examined from Bimini, Bahamas, single specimens from the west coast of Florida and New Jersey in the United States (Bigelow and Schroeder 1953), and a single individual caught in the Whitsunday Islands in Australia (Whitley 1936). However, even these more thorough accounts fail to provide sufficient detail for a conclusive or comprehensive worldwide treatment, with most authors recommending further, more critical comparative studies and morphological examinations that go beyond superficial comparisons of colouration (Beebe and Tee-Van 1941; Bigelow and Schroeder 1953).

The rarity of adequate specimens in collections continues to thwart efforts to clarify taxonomic issues within this genus. The advent of sophisticated genetic analyses have to some degree modified the criteria necessary for taxonomic classification (Frankham *et al.* 2002, Weins 2007). However, as members of the genus *Manta* are typically observed as carcasses at fish markets and landing sites or by divers in the wild, it is important that putative species of *Manta* can be differentiated visually in the field or from photographs using reliable 'field-marks' (as in bird-watching) or alternatively from samples or measurements obtained during examinations or dissections.

The hypothesis that the genus *Manta* was not monotypic was initially investigated in southern Mozambique and South Africa using morphological measurements, external characters, size at maturity data, maximum disc width data, natural colouration patterns and behavioural observations. Observations of consistent size, colouration and behavioural differences between two recognisable 'variants' prompted a wider-scale examination of differences between populations at established aggregation sites worldwide or at locations where dead specimens from fisheries were available.

Methods

Observations of manta rays in the wild off southern Mozambique, the island of Yap, the Revillagigedo Archipelago, Mexico and the Maldives in addition to the examination of specimens from small-scale fisheries in Inhambane (Mozambique), Lombok (Indonesia) and bather-protection nets in Durban (South Africa) and the added examination of specimens in museum collections at the Australian Museum (Sydney), Iziko-South African Museum in Cape Town, and the Museum of Comparative Zoology at Harvard University in Cambridge, USA allowed for broad geographical comparisons of morphology and colouration.

Morphometric measurements used in this study to describe proportional dimensions followed standards used in Notarbartolo-di-Sciara (1987), Compagno (2001) and Manjaji-Matsumoto and Last (2006), with additional characters added specifically for the genus *Manta* (Marshall *et al.* 2008). Measurements were often taken to the nearest centimetre (cm) for larger measurements, which were later converted to millimetres to

facilitate comparisons, and to the nearest millimetre (mm) for smaller measurements. All morphological measurements were expressed as percentage disc length (DL) as sometimes the pectoral fins of the rays had been severed for transport or for processing reasons by fishermen before individuals could be examined. Furthermore, proportional dimensions using DL rather than disc width (DW) allow for comparison to preserved specimens in museums or ichthyological archives that have been stored with the pectoral fins removed or that have been fixed with the pectoral fins curled dorsally (Notobartolo-di-Sciara 1987; Francis 2006).

Meristic counts, such as tooth counts, were also taken. Lower jaws were removed and tooth counts made at a later time under favourable lighting conditions, with rows counted across the entire length of the tooth band and files (lingual to labial aligned teeth) counted at the midline. Skin samples were taken from the dorsal and ventral surfaces of the pectoral fin just lateral to the body cavity in the middle of the pectoral fin. When possible total body mass in kilograms (kg) was determined using heavy-duty scales. In the field, only quick internal examinations to determine maturity status were possible following standards in Walker (2005). When possible the number of turns in the spiral valve were also counted and the mass of the liver was determined. Tissue samples were collected and stored in 90% ethanol for subsequent genetic analysis.

When possible, teeth and denticles were examined using a JEOL 6460 LA scanning electron microscope (SEM) at The University of Queensland. Samples were initially rinsed and cleaned before they were dehydrated using a graded series of ethanol baths and then dried flat in a desiccation cupboard. Approximately 2 mm sections of tooth bands were taken from either side of the midline of each lower jaw examined. Tooth and denticle samples were platinum sputter coated (~15 nm) using an EIKP IB-5 Sputter Coater set at 6mA for five minutes. All SEM images were made using an acceleration voltage of 10 kV. A sagittal plane computed tomography (CT) image of the calcified mass and embedded spine (located at the base of the tail of some specimens) was made at The University of Queensland.

Photographs of manta rays from the six field sites (Inhambane, Mozambique; Durban, South Africa; Lombok, Indonesia, the Revillagigedo Archipelago, Mexico, the Maldives and the island of Yap) were compared along with additional images from other locations, including the Yaeyama Islands and Ogasawara Island (Bonin Islands) (Japan), Stradbroke Island and Exmouth (Australia), Palau (Micronesia), Florida (USA), Holbox (Mexico), the Hawaiian Islands (USA) and the Bahamas.

A map depicting the regional distribution of *Manta* was generated using data points collected from approximately 100 known aggregation sites or sighting records worldwide. Images (n = 2231) from the first author's photographic library plus the libraries of professional photographers were used in addition to the private libraries of other researchers, scuba diving centres, tourists, manta ray catalogues/databases, magazines/books, museum specimens, and publications. Only clear, good quality images in which individual rays could be identified using the visual key generated for this genus were used for this study.

Although extensive synonymies exist for the genus *Manta*, synonymies were only selected for each of the described species of *Manta* if the characteristics, drawings, or photographs in the original descriptions were detailed enough to allow for their identification as one of the three putative species.

Results

During the course of the study, two distinct species of *Manta* were identified from the examined field sites and specimens. Below these two species are distinguished. A third form, termed *Manta sp. cf. birostris*, was differentiated from specimens examined and photographed from the Atlantic Ocean and the Caribbean but further evidence is needed to elucidate its taxonomic status. Notes on this third putative species are provided and contrasted with the two species described below.

Genus *Manta* Bancroft, 1829

Definition of the genus and generic synonymy follows Bigelow and Schroeder (1953).

***Manta birostris* (Walbaum, 1792).**

Selected synonymy. *Brachioptilon hamiltoni* Newman, 1849 (see Beebe and Tee-van 1941, as *Manta hamiltoni*); *Ceratoptera ehrenbergii* Müller and Henle, 1841.

Common names. Giant manta ray, Pacific manta ray, devilfish, chevron manta, pelagic manta, oceanic manta.

Diagnosis. Disc approximately 2.2–2.3 times as broad as it is long. Maximum disc width over 7000 mm. Slender whip-like tail. Reduced caudal spine predominantly encased in a calcified mass present on the dorsum of tail immediately posterior to the dorsal fin. Dermal denticles situated on long, sagittally oriented, raised ridges in the dermis that extend down the length of both the dorsal and ventral surfaces. Dental ligament embedded with small cusped teeth on the lower jaw measuring roughly 25% of total disc length with approximately 12–16 rows, 220–250 files across entire width of the band. Total tooth counts of 3000–4000 for entire tooth band. Upper jaw contains at least two rows of enlarged denticles that span the same width of the upper jaw as the tooth band on the lower jaw.

Morphometrics. See Table 1 for complete measurements of *Manta birostris*. A total of ten non-overlapping proportional measurements were identified that could be used to separate *Manta birostris* from *Manta alfredi* (highlighted in Table 2).

Colouration. Dorsal surface black, with large, conspicuous, white shoulder patches in the supra-branchial region, with or without black spots within them (Fig. 1a, 2a–h). Shoulder patches, which occur on either side of a dark midline, are distinct and approximately triangular in shape with hook shaped lateral extensions (Fig. 2a–h). Anterior edge of shoulder patches runs medially from spiracle in an approximately straight line parallel to the edge of the upper jaw, a diagnostic character of this species (Fig. 2a–h). Pale to white chevron shaped patch, of variable size, extends anteriorly from the anterior insertion point of the dorsal fin (Fig. 1a). Small blazes of white colour are also often visible on the dorsal tips of the pectoral fins (Fig. 1a).

Mouth black to charcoal grey in colouration (Fig. 1b). Dark colouration around mouth often extends posteriorly on the ventral surface from the base of the cephalic fins to the anterior edge of the first gill slits (Fig. 1b, 3a–h). Ventral surface largely cream to white with dark grey to black spots and patches most commonly occurring on the abdominal region between gill slit openings and anterior to the opening of the cloaca (Fig. 1b). Spots do not occur medially between the five gill slits or on the pectoral fins lateral to the body cavity (Fig. 3a–h). Medium to large black semi-circular spots posterior to the fifth gill slits are present (Fig. 1b). Posterior third of disc charcoal-coloured forming a V-shaped margin along the posterior edges of the pectoral fins (Fig. 1b, 3a–h), a diagnostic feature for *M. birostris*.

A melanistic form occurs that is entirely black on the dorsal surface and predominately black on the ventral surface except for a variably-sized white blaze along the ventral mid-line. Typical spot patterns are often visible along the white portion of the midline, which are centralised on the abdominal region and absent medially between the gill slits (Fig. 4a,b). A whitish, or leucistic, colour morph has also been documented which exhibits increased white colouration on the dorsal surface, a near white or completely white face and mouth and light ventral colouration, including an interrupted charcoal-coloured pectoral fin margin (Fig. 4a,b). This leucistic colour form appears to be rare, with less than a dozen observed specimens documented worldwide. All other morphological and meristic characters were the same as other examined individuals of *M. birostris*.

TABLE 1. Morphometric measurements of *Manta alfredi* from South Africa and *Manta birostris* from Lombok, Indonesia.

Location	South Africa	South Africa	South Africa	Lombok	Lombok	Lombok	Lombok
Sex	Female	Male	Female	Female	Female	Female	Male
Disc Width (mm)	2370	2330	2330	3765	3800	3568	3850
	%DL	**%DL**	**%DL**	**%DL**	**%DL**	**%DL**	**%DL**
Disc Length	100.00	100.00	100.00	100.00	100.00	100.00	100.00
Disc Width	237.00	220.79	220.79	228.88	228.23	227.26	215.69
Anterior Projection	40.00	39.60	39.60	36.78	35.74	35.67	34.73
Rostrum to Pelvic Fin	99.00	99.01	99.01	101.52	101.32	100.76	100.28
Pre-dorsal Length	87.00	85.15	85.15	83.89	82.28	79.62	79.55
Pre-cloacal Distance	85.00	84.16	84.16	79.03	82.28	76.11	78.15
Disc Thickness	20.00	24.75	22.77	23.10	28.83	29.30	25.21
Pectoral Length 1	93.00	92.08	89.11	92.16	90.09	90.76	85.71
Pectoral Length 2	122.00	113.86	112.87	112.46	110.51	112.74	102.52
Pectoral Length 3	94.00	96.04	93.07	98.78	97.30	94.27	96.92
1st Gill Slit Length	21.00	22.77	22.77	20.97	22.52	22.29	21.01
2nd Gill Slit Length	24.00	23.86	23.76	24.01	24.02	23.57	22.13
3rd Gill Slit Length	25.00	23.76	23.76	22.98	23.48	22.29	21.29
4th Gill Slit Length	23.50	20.79	21.78	20.36	20.30	19.75	18.82
5th Gill Slit Length	18.00	17.33	17.82	15.50	14.83	14.97	15.52
Distance Between 1st Gill Slits	27.00	23.76	25.74	25.65	24.92	23.25	23.53
Distance Between 5th Gill Slits	14.00	13.86	14.85	12.58	12.61	12.42	11.76
Rostrum to 1st Gill Slit	20.00	19.80	19.80	18.30	19.22	19.75	17.65
Rostrum to 5th Gill Slit	43.50	42.08	42.57	44.07	42.94	42.99	41.46
Cephalic Fin Length	26.00	26.73	22.77	27.36	28.23	28.34	26.89
Cephalic Fin Width	12.00	12.38	11.88	13.37	14.11	11.46	11.76
Diameter of Eye	2.40	2.97	1.98	3.95	4.50	4.20	3.47
Cranial Width	54.00	51.49	52.48	58.36	56.76	58.28	51.82
Head Length	35.00	32.67	31.68	32.83	34.29	32.48	31.09
Mouth Width	37.00	30.69	33.66	38.30	37.54	36.94	34.17
Lower Toothband Length	21.50	23.76	23.76	24.80	24.44	25.73	25.21
Internarial Distance	34.00	30.69	30.69	34.04	31.83	32.48	30.81
Spiracle Length	4.10	2.18	2.28	2.92	2.98	3.69	3.31
Interspiracle Distance	45.00	44.55	44.55	50.46	48.05	47.13	45.10
Dorsal Fin Base	17.00	14.36	15.84	13.37	12.91	13.69	12.89
Dorsal Fin Height	11.00	10.40	9.90	8.81	7.87	8.34	8.40
Dorsal Fin Anterior Margin	10.30	14.85	15.84	14.29	13.21	13.38	12.89
Width Across Pelvic Fin Base	22.00	19.80	20.79	16.72	18.32	17.20	17.09
Pelvic Fin Length	28.00	23.76	21.78	25.41	22.52	24.20	24.93
Pelvic Fin Anterior Margin	17.00	18.81	17.82	13.37	12.31	11.46	10.92
Clasper Inner Length	N/A	15.84	N/A	N/A	N/A	N/A	24.65
Tail Length	113.00	97.03	102.97	89.06	N/A	89.17	N/A
Tail Width	2.10	1.49	1.58	1.58	N/A	1.53	N/A
Tail Height	2.20	2.18	2.08	1.64	N/A	1.66	N/A

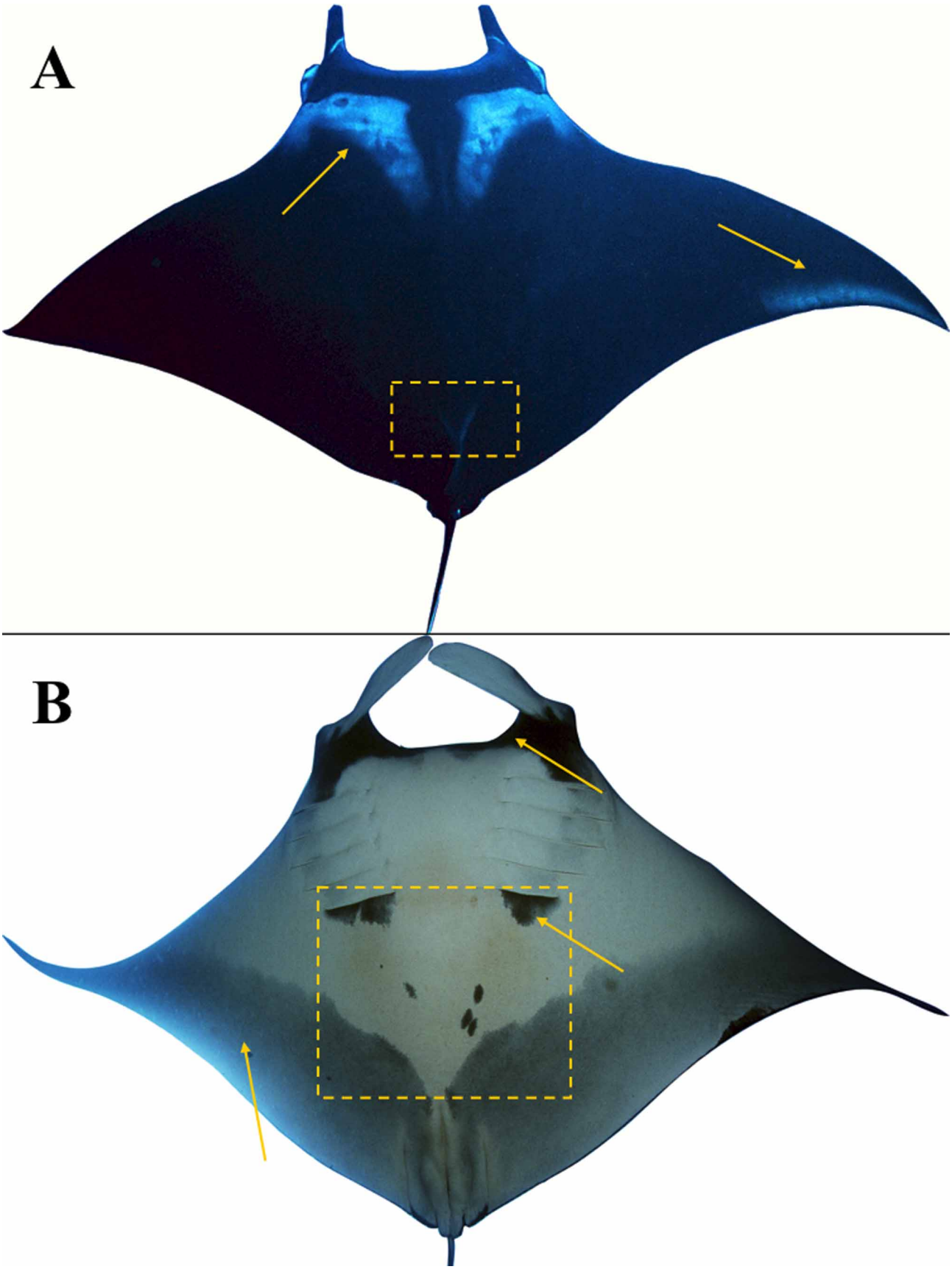

FIGURE 1. Natural colouration patterns in *Manta birostris*: (a) dorsal surface, arrows pointing to the shape and colouration of the shoulder patches and the colouration on the pectoral fins, box showing chevron shaped marking anterior to dorsal fin; (b) ventral surface, box showing region of highest spot density and distribution, arrows showing size of spot anterior to the 5th gill slit, colouration of mouth region, and colouration of the pectoral fin margin.

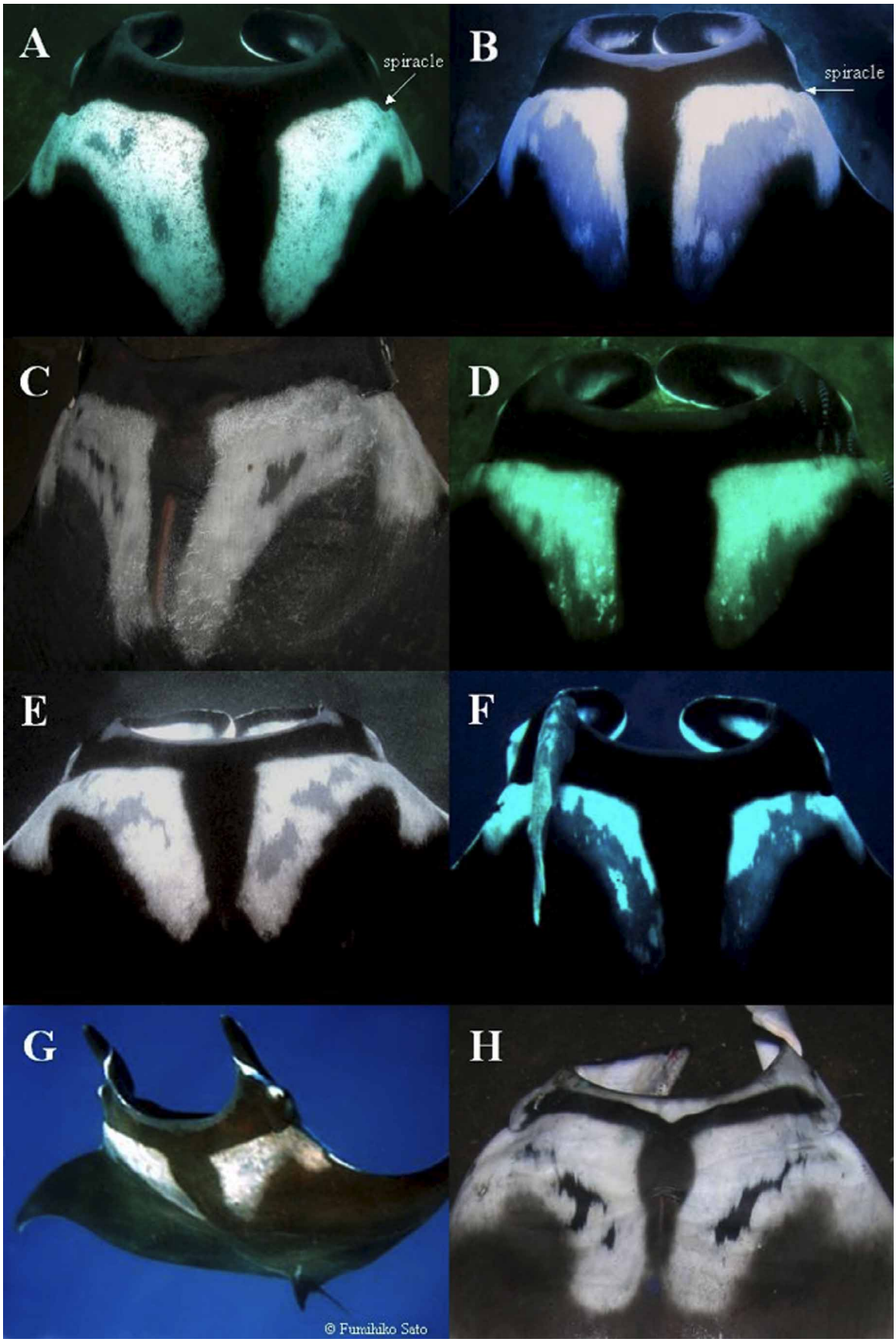

FIGURE 2. Variation in dorsal supra-branchial shoulder patch markings on *Manta birostris* shown on individuals from: (a) Inhambane, Mozambique; (b) Inhambane, Mozambique; (c) Lombok, Indonesia; (d) Inhambane, Mozambique; (e) Brothers Islands, Red Sea; (f) Revillagigedo Archipelago, Mexico; (g) Ogasawara Islands, Japan; (h) Lombok, Indonesia.

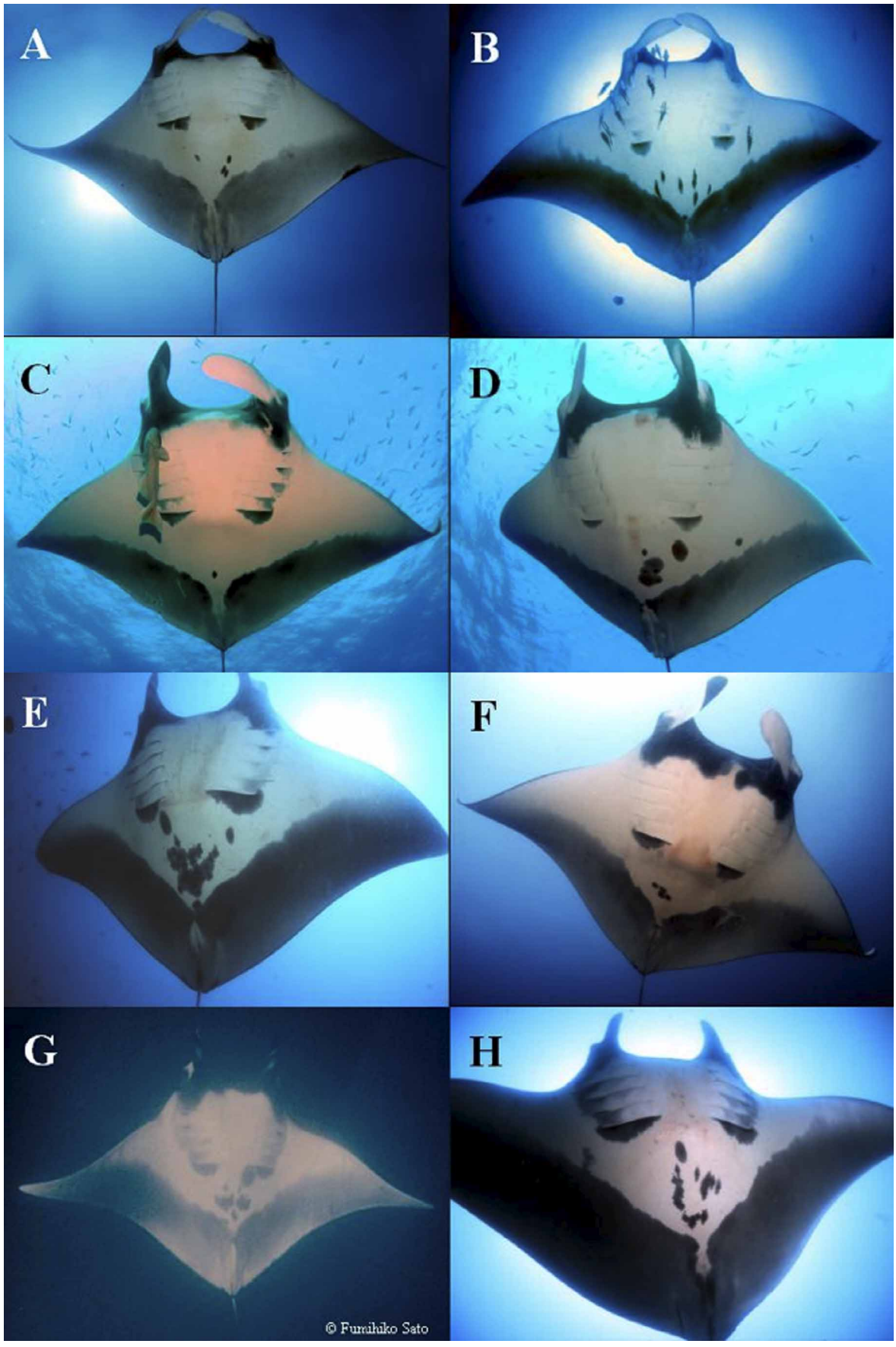

FIGURE 3. Variation in ventral markings on *Manta birostris* from: (a) Inhambane, Mozambique; (b) Inhambane, Mozambique; (c) Revillagigedo Archipelago, Mexico; (d) Revillagigedo Archipelago, Mexico; (e) Inhambane, Mozambique; (f) Inhambane, Mozambique; (g) Ogasawara Islands, Japan; (h) Inhambane, Mozambique.

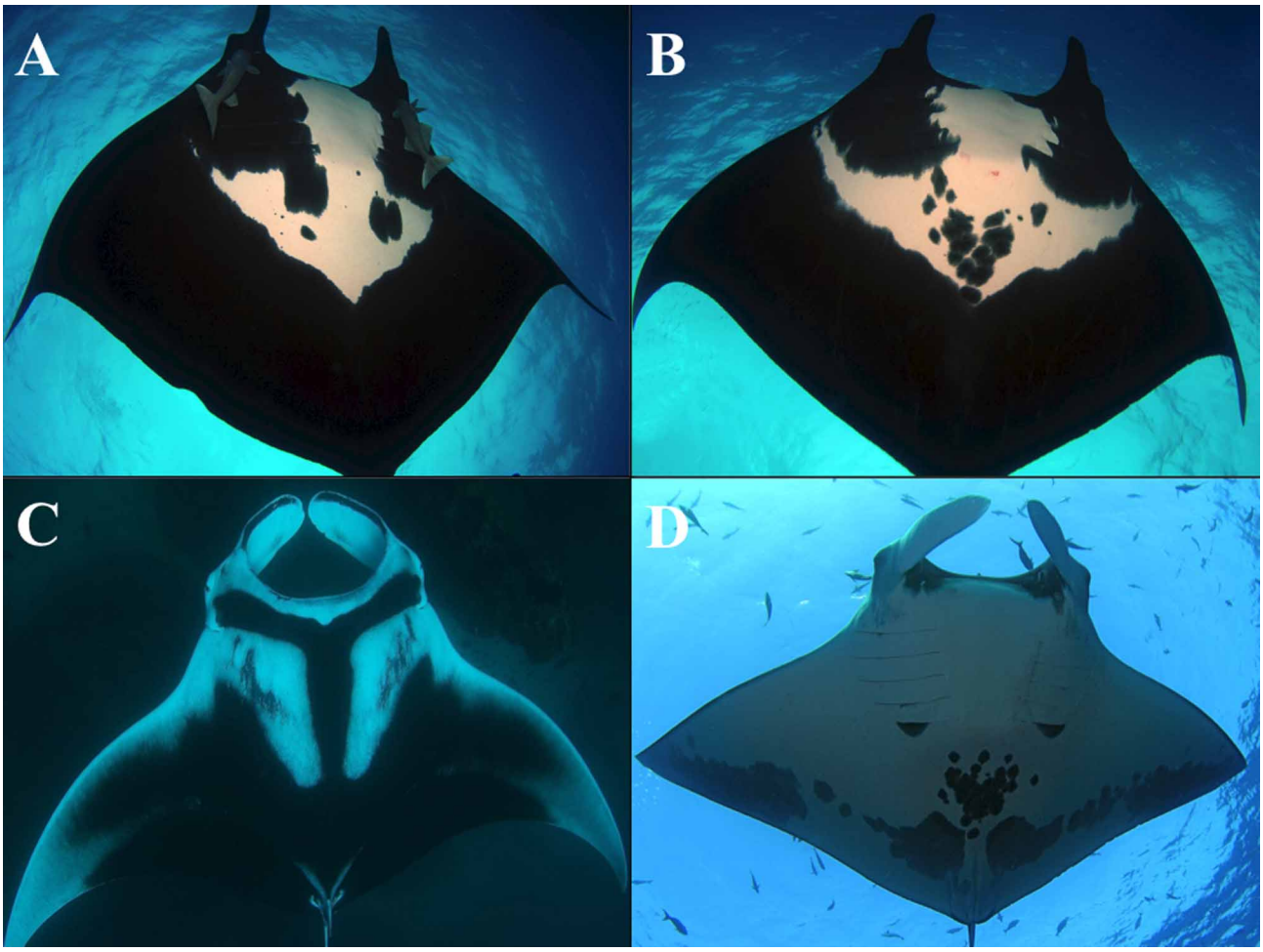

FIGURE 4. (a-b) Examples of the melanisic form of *Manta birostris* from the Revillagigedo Archipelago, Mexico and (c-d) examples of the white, or leucistic, colour morph of *Manta birostris* from southern Mozambique and the Revillagigedo Archipelago, Mexico.

Dentition. Tooth band on lower jaw comprising 64.76–69.65% of total jaw width (Fig. 5a). Tooth band containing 12–16 rows of small cusped teeth (approximately 1.5 mm in length) and 220–250 files across entire width of the band (Fig. 5b). Total tooth counts range from 3000–4000 for entire tooth band. Morphology of individual teeth variable and may be dimorphic between sexes. Each tooth has a bulbous root, which is embedded in the dental ligament and freestanding stalk that ends in a curved cusp that forms the occlusal surface and is oriented to face the lingual side of the jaw (Fig. 5 b-d). Teeth in the tooth band slightly overlap (Fig. 5c). Tooth band absent in upper jaw but two irregular bands of enlarged denticles extend along the upper jaw for a distance equivalent to the length of the lower tooth band (Marshall 2009).

Denticles. Prominent dermal denticles present on both the dorsal and ventral surfaces are randomly distributed along sagittally oriented ridges in the skin (Fig. 6a,b), a diagnostic feature of *M. birostris*. Denticles on the dorsal and ventral surfaces are similar in appearance and distribution, with slightly larger denticles on the ventral surface (Fig. 6a,b). Denticles have pronounced bifid cusps (Fig. 6c) that give the skin a much rougher texture than that of *M. alfredi*. The morphology of the most common denticle form on both the dorsal and ventral surfaces is shown in Fig. 6c,d.

Caudal spine. A calcified mass with an embedded spine is located on the dorsum of tail immediately posterior to dorsal fin (Fig. 7a). The calcified mass rests just under a thin layer of dermis, lacks attachment via collagenous connective tissue to tail and detaches easily if skin is removed (Fig. 7b). Spine with serrated lateral edges is embedded in a large mass of highly mineralised cartilage, similar to that described for *Mobula*

japonica (Notobartolo-di.Sciara 1987) (Fig. 7c). Spine appears to have an enameloid exterior and is slender in shape, approximately 3.5% of the width of the calcified cartilage mass. Tip of spine projects approximately 3 mm out from the surrounding mass (Fig. 7c). A sagittal plane CT scan clearly shows the spine embedded one third of the way into the calcified mass (Fig. 7d). Visual examinations in the field suggest that the size of the calcified mass is positively correlated with disc width. The calcified masses extracted from the two rays examined (male 3850 mm DW/1785 mm DL and female 3765 mm DW/1645 mm DL), were similar in overall shape and were 5.98% and 6.69% of the total DL of the rays respectively.

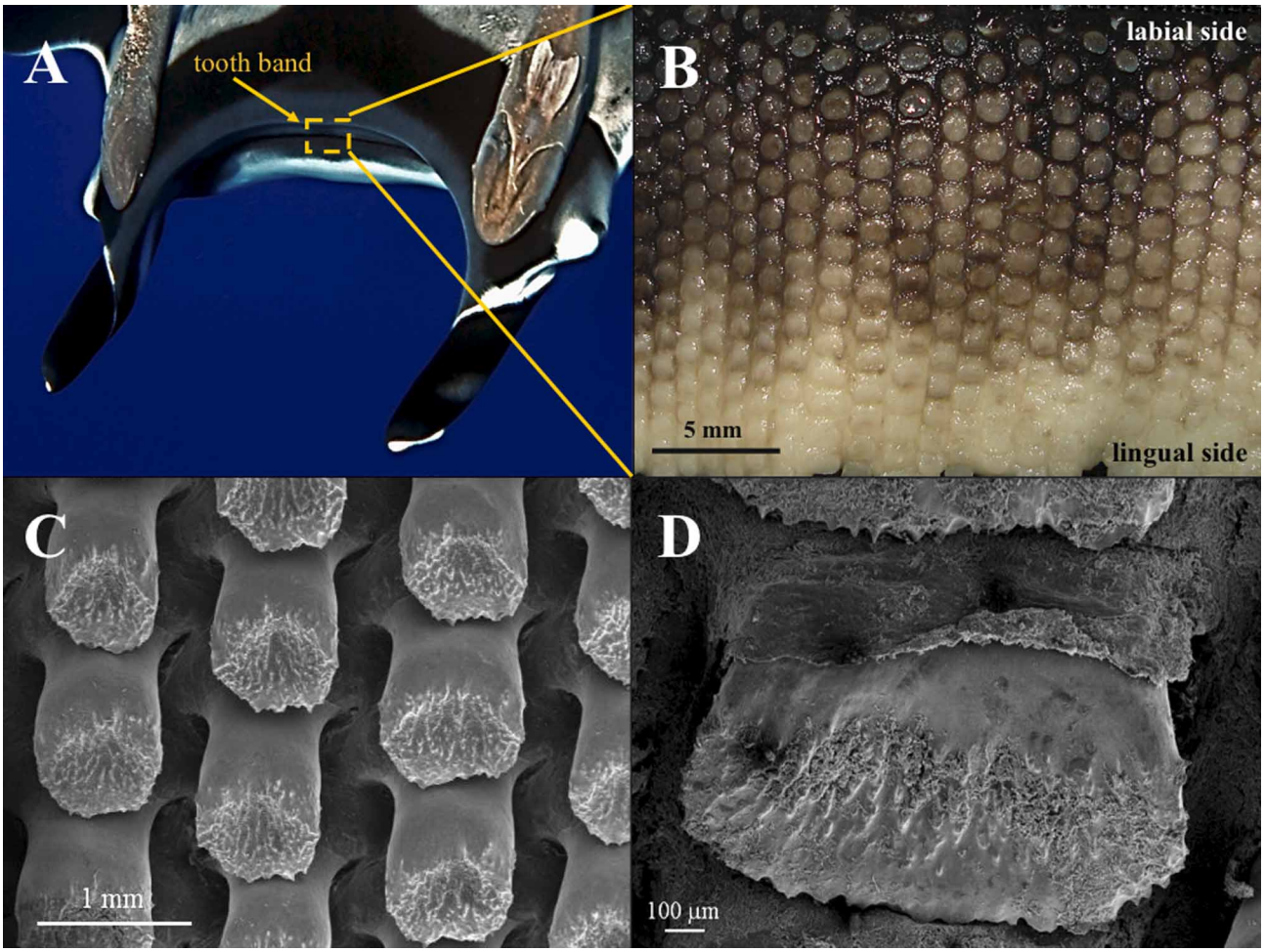

FIGURE 5. Dentition and tooth morphology in *Manta birostris*: (a) lower jaw with elongated tooth band; (b) section of teeth mid-band; (c) embedded teeth of male ray; (d) view of single embedded female tooth.

Size. Dissected specimens of *M. birostris* measured up to 4695 mm DW but estimates of the largest individuals sighted in the field (southern Mozambique and Mexico) were slightly over 6000 mm DW. *Manta birostris* reaches disc widths of at least 7000 mm, with anecdotal reports up to 9100 mm (Compagno 1999). Size at maturity for *M. birostris* may vary slightly throughout its range, but males in southern Mozambique mature at approximately 4000 mm DW (Marshall 2009). In Indonesia, the only mature male examined was 3850 mm DW. Additional fisheries data from Lombok, Indonesia suggest male *M. birostris* mature at 3750 mm (White *et al.* 2006). The only mature females observed or examined (n = 3) in southern Mozambique were in excess of 4695 mm DW. In Indonesia, female *M. birostris* up to 3800 mm DW were immature. Additional fisheries data from Lombok, Indonesia suggest females mature by approximately 4130 mm DW (White *et al.* 2006).

Habitat and distribution. *Manta birostris* occurs in tropical, sub-tropical and temperate waters around the globe (Fig. 8). Commonly sighted along productive coastlines with regular upwelling, oceanic island groups and particularly offshore pinnacles and seamounts (Compagno 1999; Rubin 2002). *Manta birostris* has

been documented to occur as far north as southern California and Rhode Island on the United States west and east coasts, Mutsu Bay, Aomori, Japan, the Sinai Peninsula, Egypt and the Azores Islands in the Northern Hemisphere and as far south as Peru, Uruguay, South Africa and New Zealand in the Southern Hemisphere. In some locations, including Mozambique *M. birostris* is sympatric with *M. alfredi* (Fig. 8). When they do occur together *M. alfredi* and *M. birostris* typically exhibit different habitat use and movement patterns (Marshall 2009).

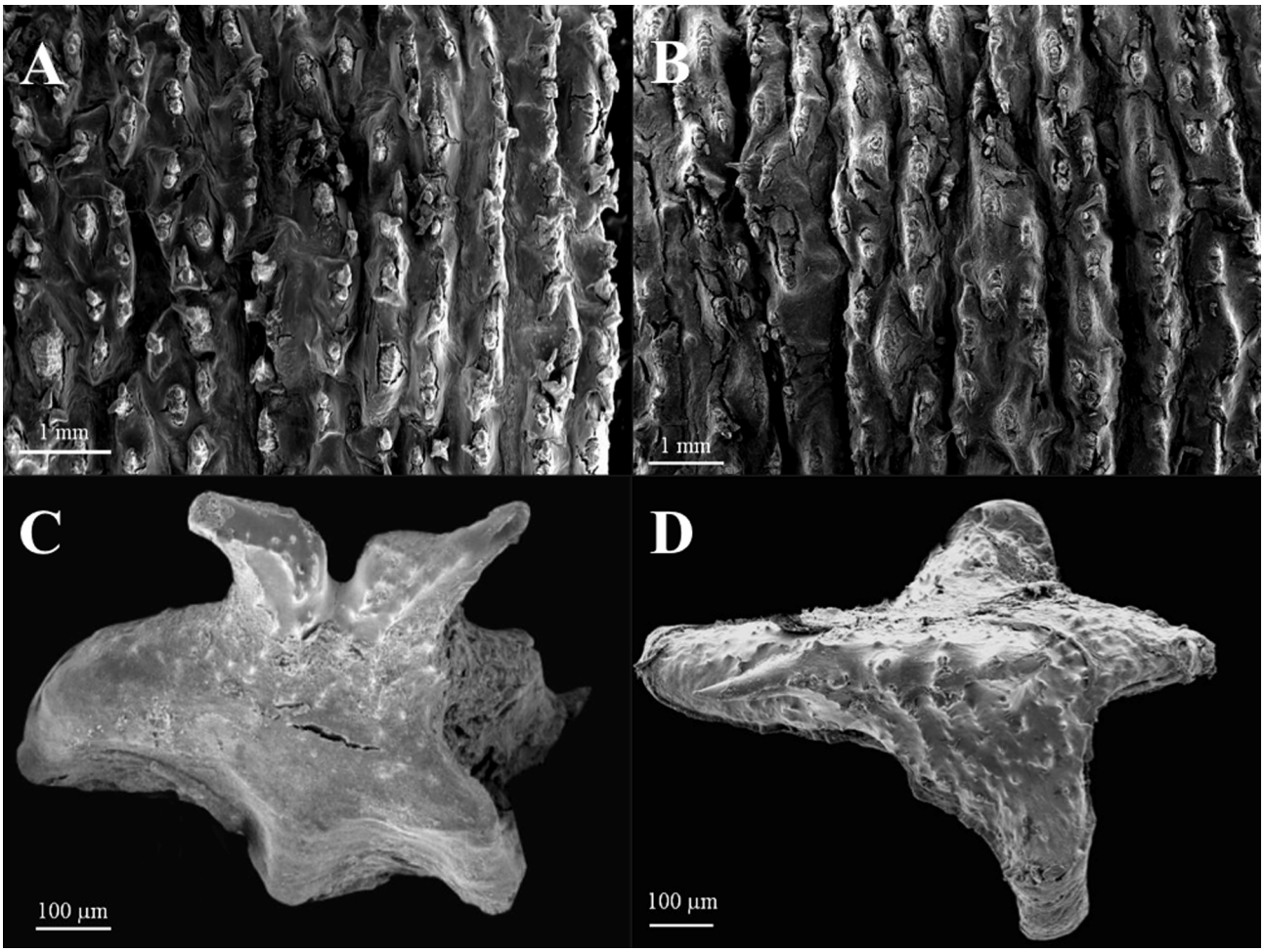

FIGURE 6. Skin and denticle morphology in *Manta birostris*: (a) superior view of dorsal skin in male ray; (b) superior view of ventral skin in female ray; (c) lateral view of single denticle; (d) superior view of single denticle.

Material examined (n = 11). Mature male caught in gill net on 13 May 2007 in the Alas Strait south of TanJung Luar, Lombok (3850 mm DW). Juvenile female caught in gill net on 13 May 2007 in the Alas Strait south of TanJung Luar, Lombok (3765 mm DW). Juvenile female caught in gill net on 13 May 2007 in the Alas Strait south of TanJung Luar, Lombok (3800 mm DW). Juvenile female caught in gill net on 13 May 2007 in the Alas Strait south of TanJung Luar, Lombok (3568 mm DW). Mature female caught in gill net on 13 May 2007 in the Alas Strait south of TanJung Luar, Lombok (4695 mm DW). Mature female killed in June 1949 in Bimini, Bahamas (approx. 4500 mm DW) examined at the Harvard Museum of Comparative Zoology (MCZ 37006). Mature female sampled on 26 September 2007 off the coast of Inhambane, Mozambique (skin sample only). Mature male sampled on 23 December 2006 off the coast of Inhambane, Mozambique (skin sample only). Mature female sampled on 12 October 2007 off the coast of Inhambane, Mozambique (skin sample only). Mature female (melanistic morph) sampled on 24 November 2007 off San Benedicto Island, Mexico (skin sample). Mature female sampled on 24 November 2007 off San Benedicto Island, Mexico (skin sample).

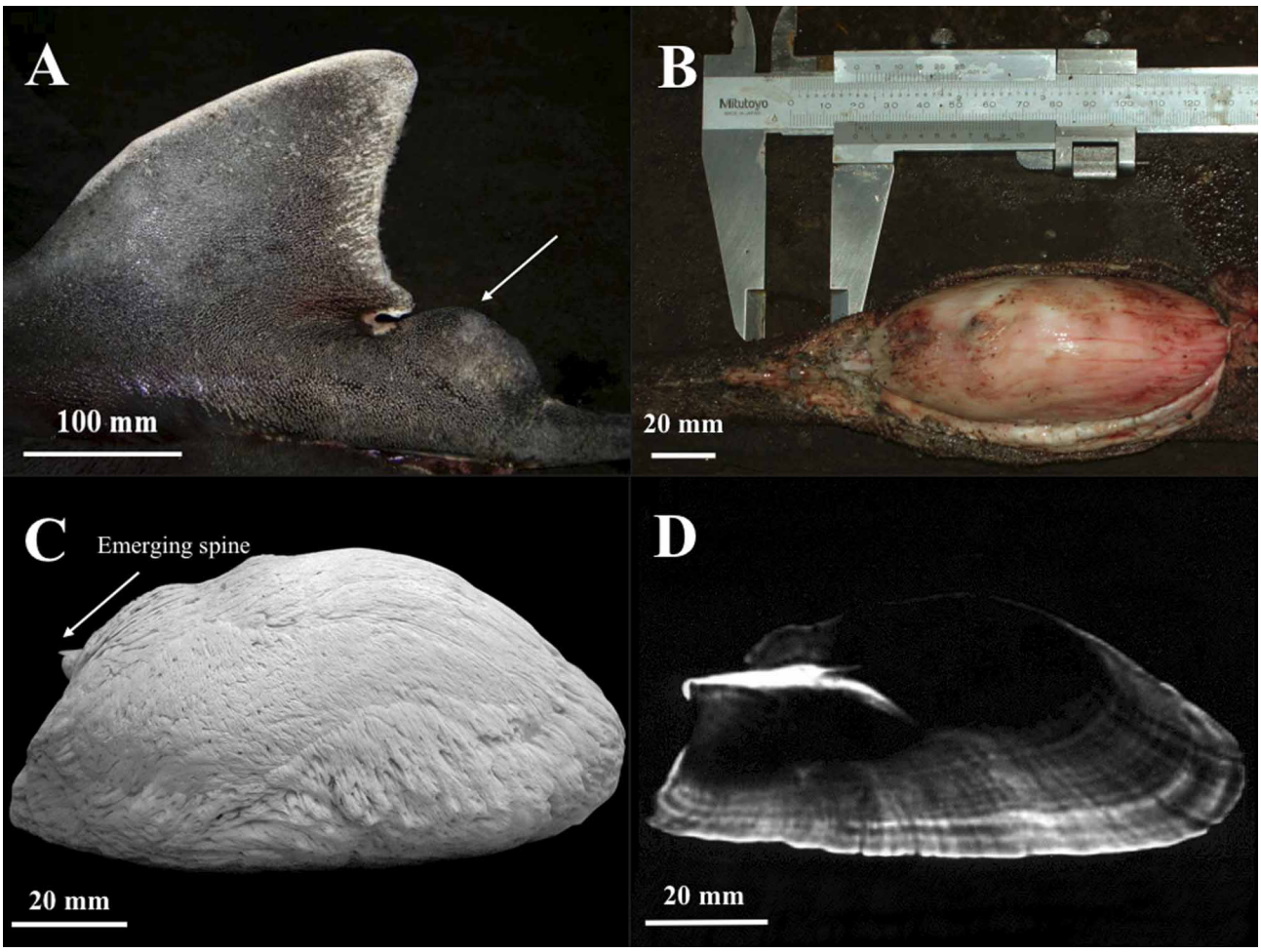

FIGURE 7. Views of calcified mass with embedded spine from *Manta birostris* (entire structure was 106.7 mm total length, 42 mm wide, and 46.7 mm in height and has a mass of 112.5 grams and a density of 1.324 g/cm^3): (a) lateral view of the dorsal fin and calcified mass with embedded spine; (b) superior view after the skin was peeled back to expose the calcified mass; (c) lateral view; (d) sagittal plane CT scan showing the embedded spine.

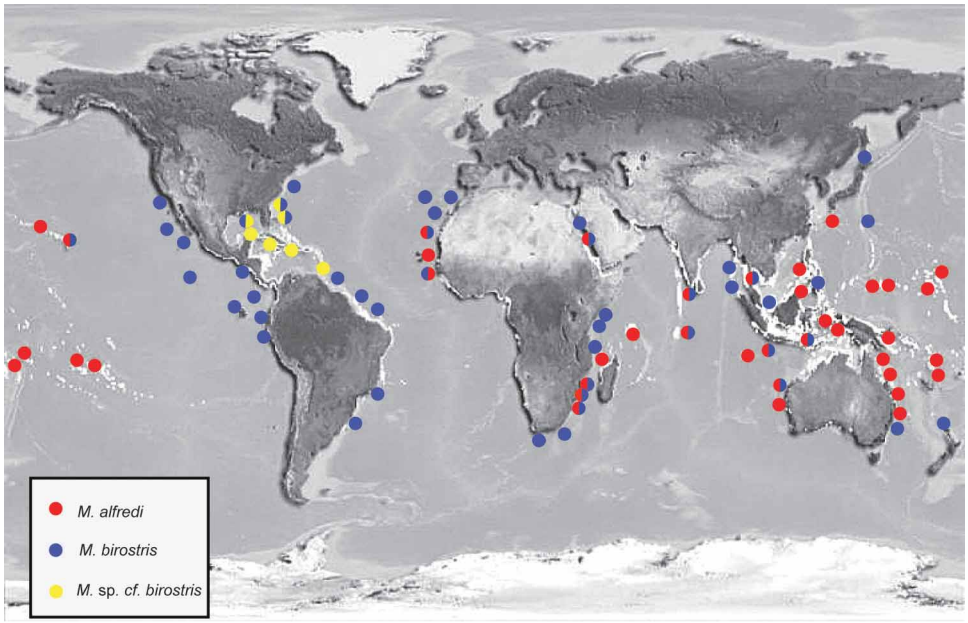

FIGURE 8. Worldwide distribution of *Manta* from preliminary analysis (n= 2231 images from over 100 aggregation sites and sighting records).

***Manta alfredi* (Krefft, 1868).**

Selected synonymy. *Manta fowleri* Whitley, 1936 (see Fowler 1927); *Manta pakota* Whitley, 1936.

Common names. Manta ray, inshore manta ray, Alfred manta, Prince Alfred's ray.

Diagnosis: Disc approximately 2.2–2.4 times as broad as it is long. Maximum disc width size approximately 5500 mm. Slender whip-like tail approximately 123% of disc length if intact. No distinct caudal spine or cartilaginous mass present at base of tail. Some specimens have small hump at the base of the tail on the dorsal surface, while other specimens have a slight depression and groove on the dorsum of the tail immediately posterior to the posterior margin of the dorsal fin. Small, knob-like dermal denticles evenly distributed on both the dorsal and ventral surfaces, with ventral surface having slightly larger denticles. Dental ligament with small cusped teeth on the lower jaw measuring roughly 22% of total disc length with approximately 6–8 rows, 142–182 files across entire width of the tooth band. Total tooth counts of 900–1500 for entire tooth band. Top jaw lacks rows of enlarged denticles.

Morphometrics. See Table 1 for complete measurements of *M. alfredi*. See Table 2 for morphometric comparison of *M. alfredi* to *M. birostris*.

Colouration. Dorsal surface black in colouration (Fig. 9a). Pale to white coloured shoulder patches, with or without dark spots within them, present on the dorsal supra-branchial region (Fig. 9a, 10a–h). Anterior margin of shoulder patch initially emanates posteriorly from spiracle before curving medially, a diagnostic feature of *M. alfredi* colouration (Fig. 10a–h). Towards the midline, colouration again begins to radiate out posteriorly continuing down over the supra-branchial region in variably sized shoulder patches (Fig. 10a–h). Anterior distal side of the shoulder patch may present as an anterior facing hook. Pale colouration may be present along the distal margin of the pectoral fin tips (Fig. 9a). Pale chevron shaped patch typically stretches anteriorly from the insertion point of the dorsal fin.

Ventral surface predominantly cream to white in colouration with variable dark markings (Fig. 9b). Mouth white to light grey in colouration (Fig. 9b, 11a–h). Blue-grey to black spots of variable size can occur across most of the ventral surface (Fig. 9b, 11a–h). The most diverse spot patterns typically occur medially to the five pair of gill slits, centrally on the abdomen and across the posterior half of the pectoral fins (Fig. 9b, 11a–h). A small black semi-circular spot is typically located immediately posterior to the fifth gill slit on each side of the body (Fig. 9b). Pale to dark charcoal-coloured bands are present on the posterior edge of each pectoral fin, typically stretching mid-way down the length of the fins from the pectoral fin tip (Fig. 9b).

A melanistic form of *M. alfredi* occurs that is entirely black on the dorsal surface and predominately black on the ventral surface except for a variably sized white blaze along the mid-line (Fig. 12a,b). *Manta alfredi*'s distinctive ventral spot patterning is often visible on the abdominal region and between the gill slits (Fig. 12a,b). A rare white, or leucistic, colour morph also exists in this species, in which the normally very darkly coloured dorsal surface appears almost entirely white (Fig. 12c,d). The ventral surface may also appear lighter in overall colouration. This leucistic colour morph appears to be rare, with less than twenty observed specimens documented worldwide.

Dentition. Tooth band on lower jaw comprising 54.2–77.4% of total jaw width (Fig. 13a). Tooth band containing 6–8 rows of small cusped teeth (approximately 1–2 mm in length) and 142–182 files across entire width of the tooth band (Fig. 13b,c). Total tooth counts range from 918–1456 for entire tooth band. Morphology of individual teeth are variable and may be dimorphic between sexes. General tooth morphology is shown in figure 13(d). Each tooth has a bulbous root that is embedded in the dental ligament, a freestanding stalk that ends in a curved cusp that forms the occlusal surface and is oriented to face the lingual side of the jaw (Fig. 13b). Teeth in the tooth band do not overlap (Fig. 17c). Upper jaw edentate with no enlarged denticle bands present.

Denticles. Denticles are small, non-overlapping and uniformly distributed along the dorsal and ventral surfaces (Fig. 14a,b). Each denticle comprises a stellate base (which is embedded in the skin, Fig. 14c,d) with a dorso-laterally elongated emergent knob (Fig. 14c,d). Denticles on the ventral surface are larger than those on the dorsal surface, but all are of similar overall morphology (Fig. 14).

TABLE 2. Comparison of morphometric measurements of two species of *Manta* from South Africa and Lombok, Indonesia presented as proportion of total disc length (%DL), with values in bold indicating higher values and non-overlapping minimum and maximum proportional measurements between *Manta alfredi* and *Manta birostris*.

	Manta alfredi				***Manta birostris***			
	Min	**Max**	**Mean**	**N**	**Min**	**Max**	**Mean**	**N**
Disc Width	214.79	237.00	224.87	7	215.69	230.15	226.04	5
Anterior Projection	**39.60**	**54.08**	**43.93**	**5**	34.73	36.78	35.73	4
Rostrum to Pelvic Fin	99.00	101.02	99.79	5	100.28	101.52	100.87	5
Pre-dorsal Length	80.99	101.02	88.85	7	79.55	83.89	81.34	4
Pre-cloacal Distance	76.52	85.00	82.02	7	76.11	82.28	78.89	4
Disc Thickness	20.00	24.75	22.51	3	23.10	29.30	26.61	4
Pectoral Length 1	89.11	93.00	91.40	3	85.71	92.16	89.68	4
Pectoral Length 2	**112.87**	**122.00**	**116.24**	**3**	102.52	112.74	109.56	4
Pectoral Length 3	93.07	96.04	94.37	3	94.27	98.78	96.82	4
1st Gill Slit Length	20.00	22.77	21.39	5	20.97	22.29	21.70	4
2nd Gill Slit Length	21.82	24.00	23.08	5	22.13	24.02	23.43	4
3rd Gill Slit Length	20.91	25.00	22.97	5	21.29	23.48	22.51	4
4th Gill Slit Length	18.37	23.50	20.71	5	18.82	20.36	19.81	4
5th Gill Slit Length	14.28	18.00	16.40	5	14.83	15.52	15.21	4
Distance Between 1st Gill Slits	21.43	27.00	23.95	5	23.25	25.65	24.34	4
Distance Between 5th Gill Slits	10.71	14.85	12.86	5	11.76	12.61	12.35	4
Rostrum to 1st Gill Slit	15.31	20.00	18.25	5	17.65	19.75	18.73	4
Rostrum to 5th Gill Slit	40.00	43.50	41.79	5	41.46	44.07	42.87	4
Cephalic Fin Length	22.77	26.73	25.11	5	**26.89**	**28.34**	**27.70**	**4**
Cephalic Fin Width	8.67	12.38	10.99	5	11.46	14.11	12.68	4
Diameter of Eye	1.98	4.08	3.01	5	3.38	4.50	3.90	5
Cranial Width	50.00	54.00	51.78	5	51.82	58.36	56.30	4
Head Length	30.61	35.00	32.17	5	31.09	34.29	32.67	4
Mouth Width	30.69	37.00	34.53	5	34.17	38.30	36.74	4
Lower Toothband Length	19.90	23.76	21.96	5	**24.44**	**25.73**	**25.05**	**4**
Internarial Distance	30.61	34.00	31.38	5	30.81	34.04	32.29	4
Spiracle Length	2.18	4.10	2.85	3	2.92	3.69	3.22	4
Interspiracle Distance	44.55	45.00	44.70	3	**45.10**	**50.46**	**47.68**	**4**
Dorsal Fin Base	**13.91**	**17.00**	**14.82**	**7**	12.89	13.69	13.17	5
Dorsal Fin Height	**9.09**	**11.44**	**10.08**	**7**	7.60	8.81	8.20	5
Dorsal Fin Anterior Margin	10.30	15.84	13.66	3	13.21	14.29	13.44	4
Width Across Pelvic Fin Base	**19.80**	**22.00**	**20.86**	**3**	16.72	18.32	17.33	4
Pelvic Fin Length	21.78	28.00	24.51	3	22.52	25.41	24.27	4
Pelvic Fin Anterior Margin	**17.00**	**18.81**	**17.88**	**3**	10.92	13.37	12.02	4
Tail Width	1.49	2.10	1.72	3	1.53	1.58	1.56	2
Tail Height	**2.08**	**2.20**	**2.15**	**3**	1.64	1.66	1.65	1

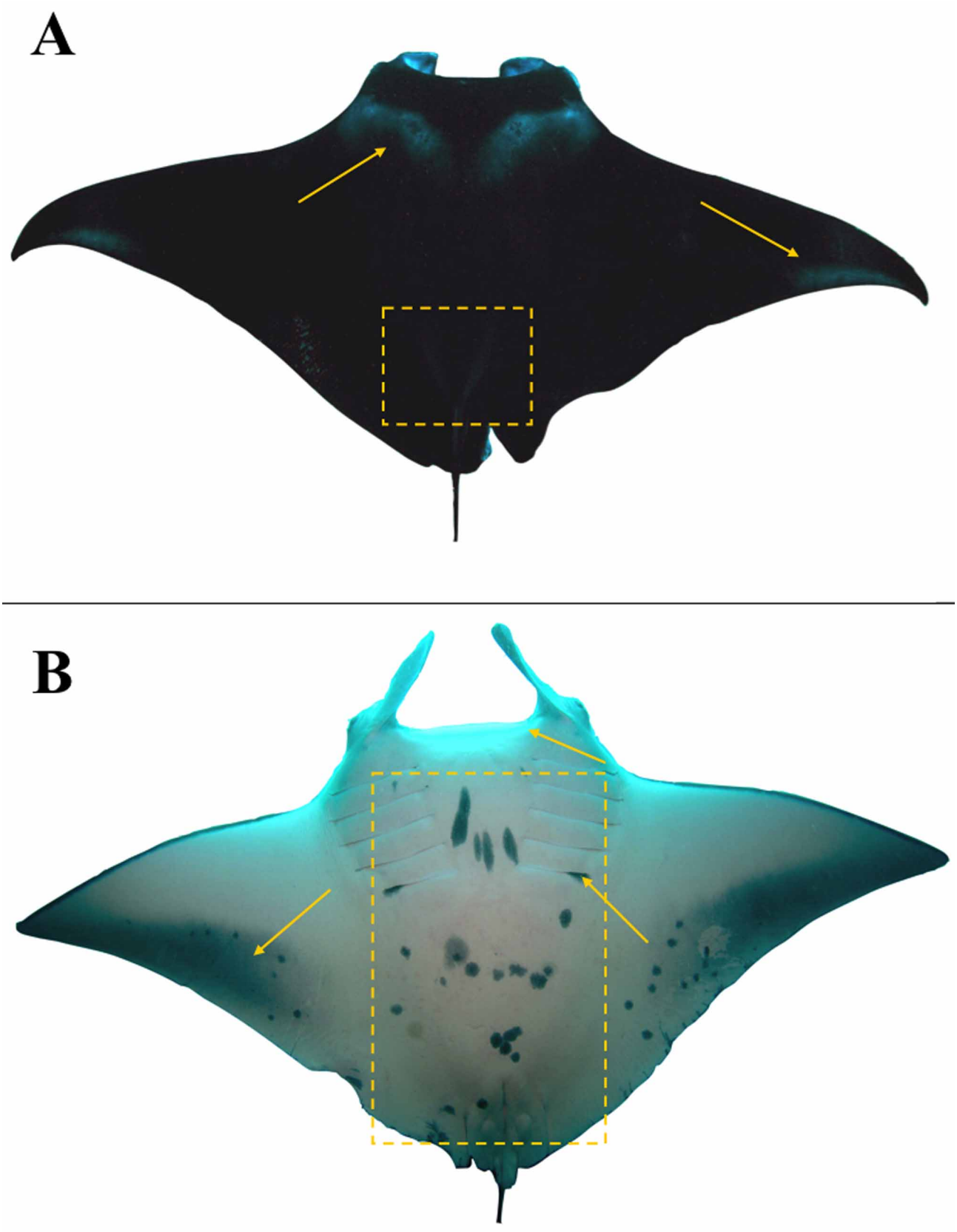

FIGURE 9. General characteristics and natural colouration patterns in *Manta alfredi*: (a) dorsal surface, arrows pointing to the shape and colouration of the shoulder patches and the colouration on the pectoral fins, box showing chevron shaped marking anterior to dorsal fin; (b) ventral surface, box showing region of highest spot density and distribution, arrows showing size of spot anterior to the 5th gill slit, colouration of mouth region, and colouration of the pectoral fin margin.

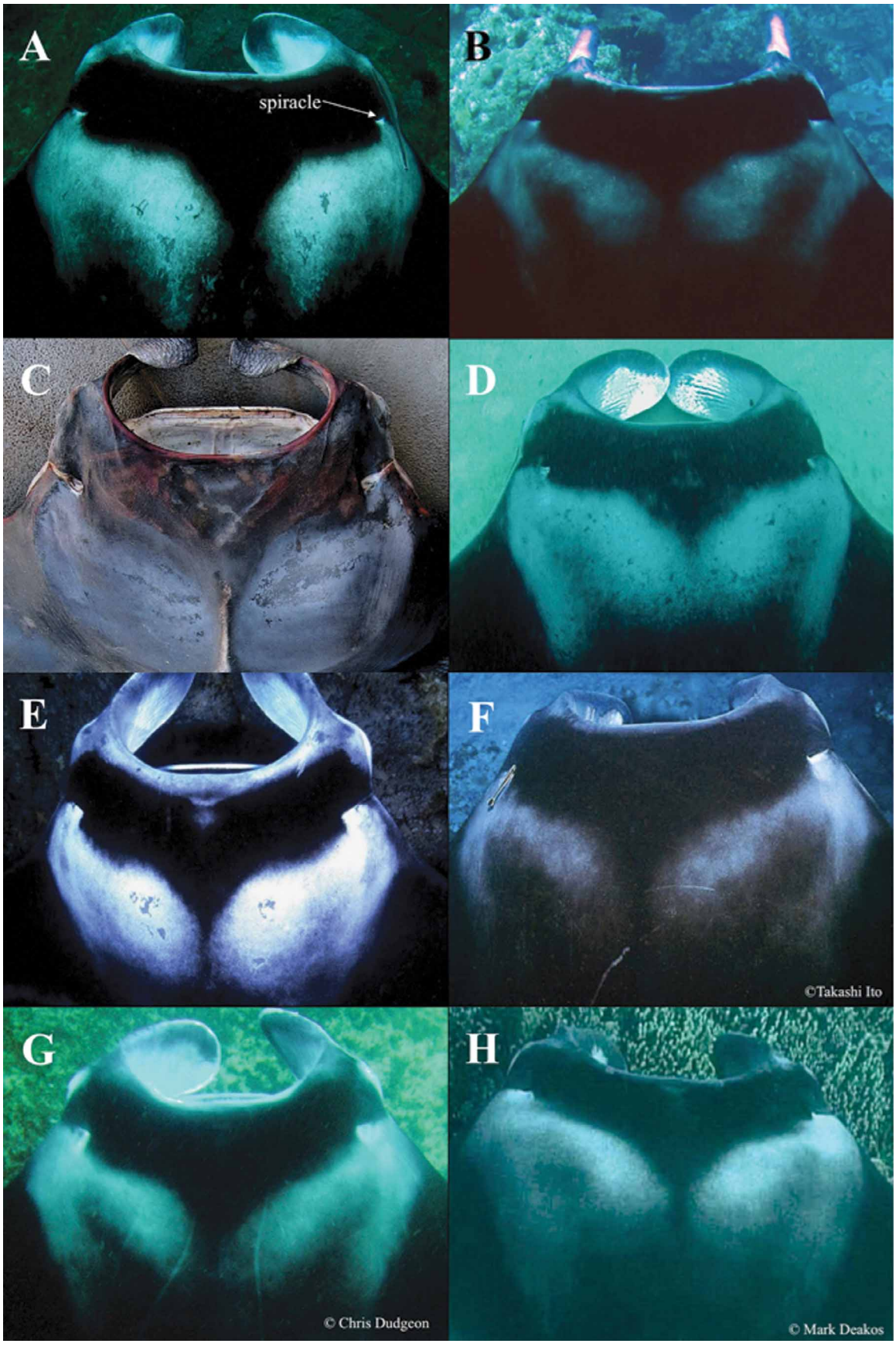

FIGURE 10. Variation in dorsal supra-branchial shoulder patch markings on *Manta alfredi* shown on individuals from: (a) Inhambane, Mozambique; (b) Yap, Micronesia; (c) Durban, South Africa; (d) the Maldives; (e) Inhambane, Mozambique; (f) Yaeyama Islands, Japan; (g) Stradbroke Island, Australia; (h) Hawaii, USA

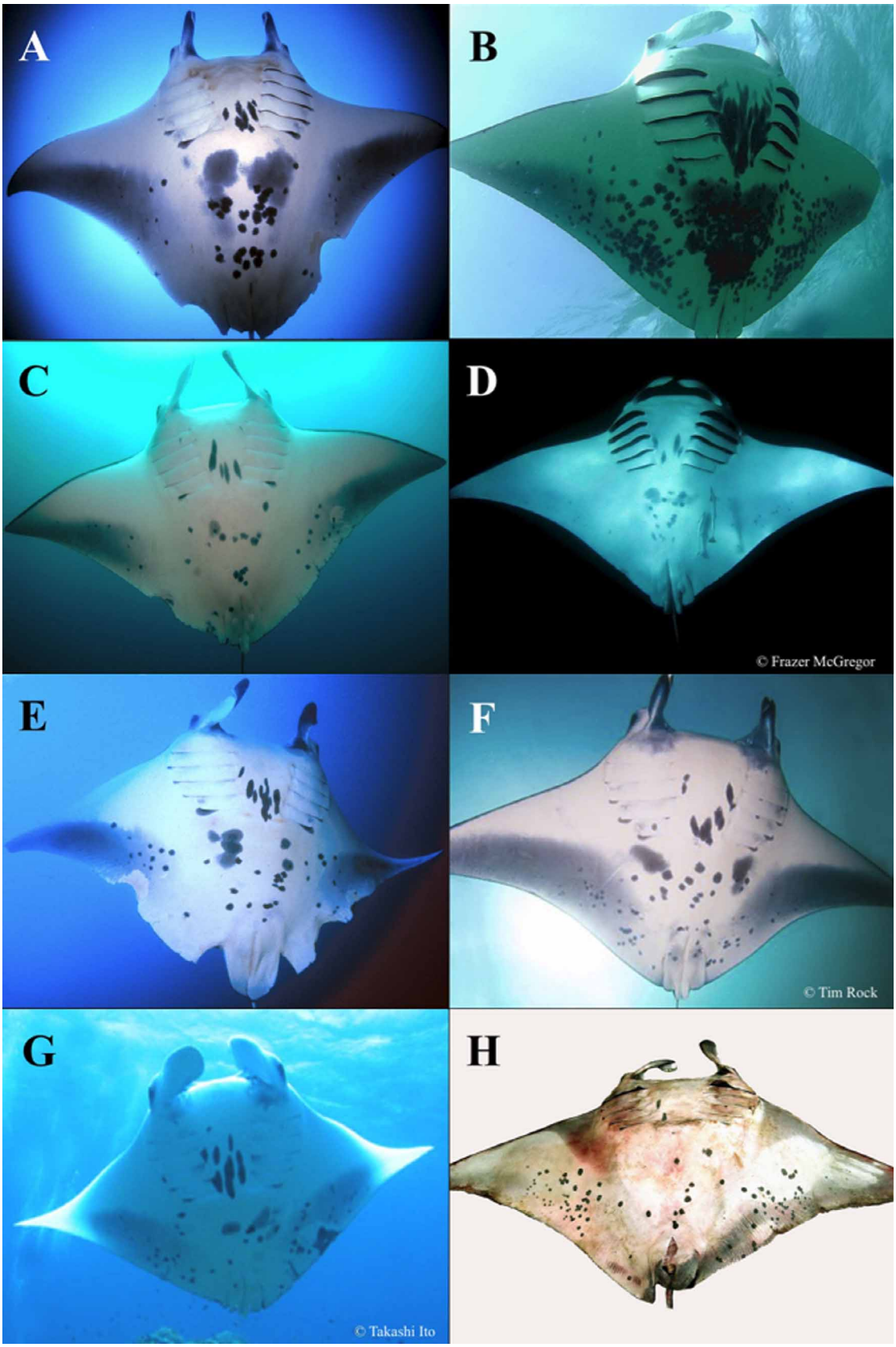

FIGURE 11. Variation in ventral markings on *Manta alfredi* from: (a) Inhambane, Mozambique; (b) the Maldives; (c) Inhambane, Mozambique; (d) Exmouth, Australia; (e) Inhambane, Mozambique; (f) Yap, Micronesia; (g) Yaeyama Islands, Japan; (h) Durban, South Africa.

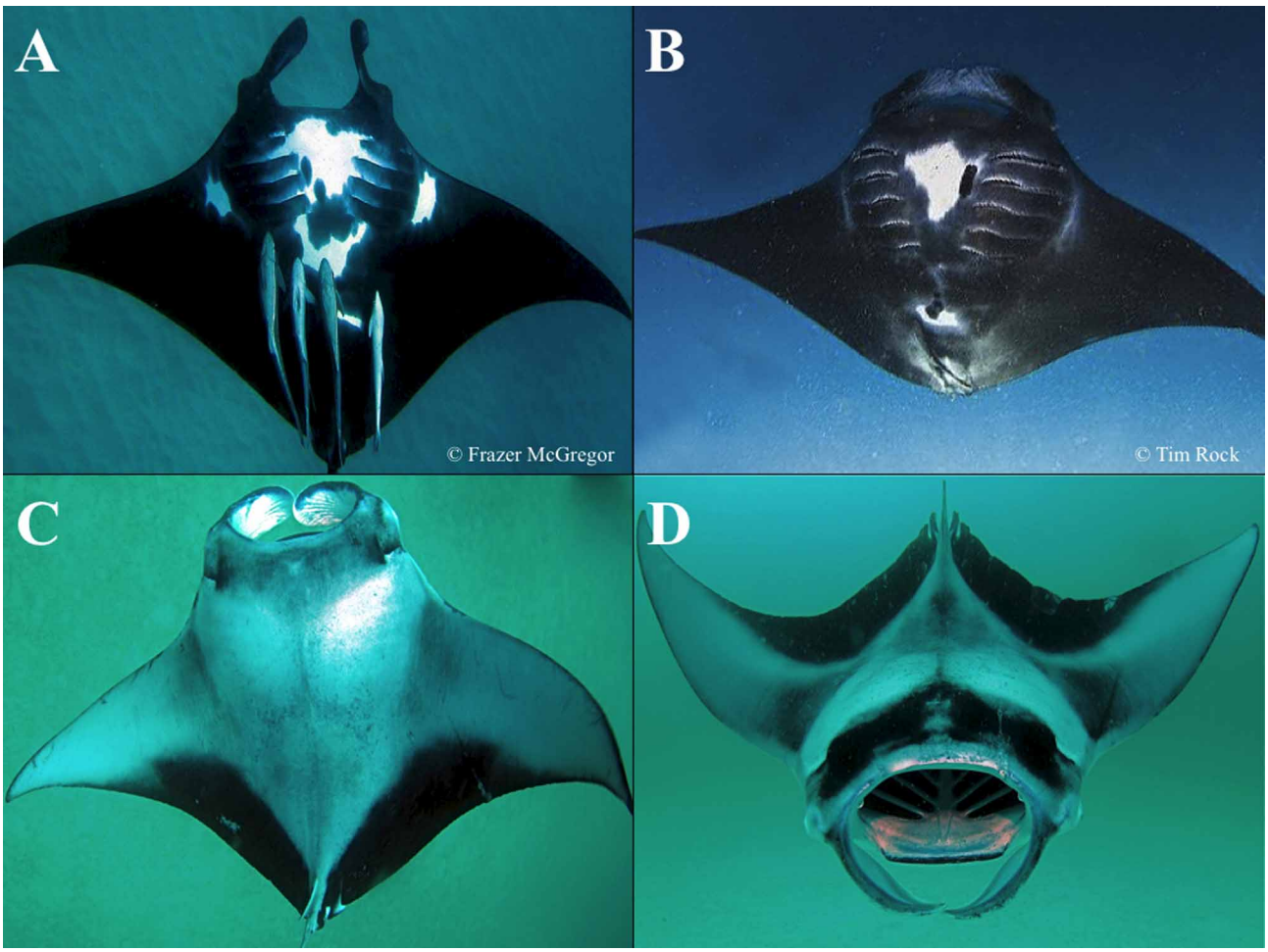

FIGURE 12. (a-b) Examples of the melanisic form of *Manta alfredi* from western Australia and Micronesia and (c-d) examples of the white, or leucistic, colour morph of *Manta alfredi* from the Maldives.

Size. The smallest individuals observed in the wild were approximately 1500 mm DW and a single examined near-term foetus was 1300 mm DW (Marshall *et al.* 2008). Dissected specimens of *M. alfredi* measured up to 3420 mm DW but estimates of the largest individuals sighted in southern Mozambique were slightly over 5000 mm DW. Size at maturity may vary slightly throughout its range, but males in southern Mozambique mature at approximately 3000 mm DW (Marshall, 2009), while females in southern Africa mature at approximately 3900 mm DW (Marshall, 2009).

Habitat and distribution. Commonly sighted inshore, within a few kilometres of land. Found around coral and rocky reefs as well as along productive coastlines with consistent upwelling, tropical island groups, atolls and bays. This species is widespread in the Indian Ocean, with images and sightings of *M. alfredi* from the Red Sea in the north to Durban, South Africa in the south, and from mainland Thailand in the north to waters off Perth, Australia in the south. In the eastern and south Pacific, *M. alfredi* occurs from the Yaeyama islands, Japan in the north to the Solitary Islands, Australia in the south and is sighted as far east as French Polynesia south of the equator and the Hawaiian islands north of the equator. Two reports and photographs of *M. alfredi* from the north Atlantic off the Canary Islands and the Cape Verde Islands and historical reports and photos of *M. alfredi* off the coast of Senegal in north west Africa (Cadenat 1958) are the only evidence of populations of *M. alfredi* in Atlantic waters (Fig. 8).

Material examined (n = 11). Juvenile male caught in bather protection nets on 11 April 2006 off Margate beach, Durban, South Africa (2230 mm DW, mass 71 kg). Juvenile female caught in bather protection nets on 17 July 2006 off Karridene beach, Durban, South Africa (2370 mm DW mass, 75 kg). Juvenile female caught in bather protection nets on 28 April 2006 off Sunwich Port beach, Durban, South Africa (2330 mm DW, mass

71 kg). Mature male caught in Mozambique on 15 January 2004 off Paindaine Beach, Inhambane, Mozambique (3420 mm DW). Juvenile male caught in bather protection nets on 14 June 2004 in Umhlanga Beach, Durban, South Africa (2520 mm DW, mass 107 kg). Juvenile female caught in bather protection nets on 21 June 2004 off South Port, Durban, South Africa (2440 mm DW, mass 101 kg). Juvenile male caught in bather protection nets on 10 August 2004 off Durban, South Africa (2320 mm DW, mass 85 kg). Juvenile male caught in bather protection nets on 15 September 2004 in South Broom, Durban, South Africa (2470 mm DW, mass 105 kg). Near-term male foetus caught in Mozambique on 15 October 2004 in Paindane Beach, Durban, South Africa (1328 mm DW, mass 15 kg). Mature male sampled on 20 March 2006 off the coast of Inhambane, Mozambique (skin sample only). Mature female sampled on 15 September 2007 off the coast of Inhambane, Mozambique (skin sample only).

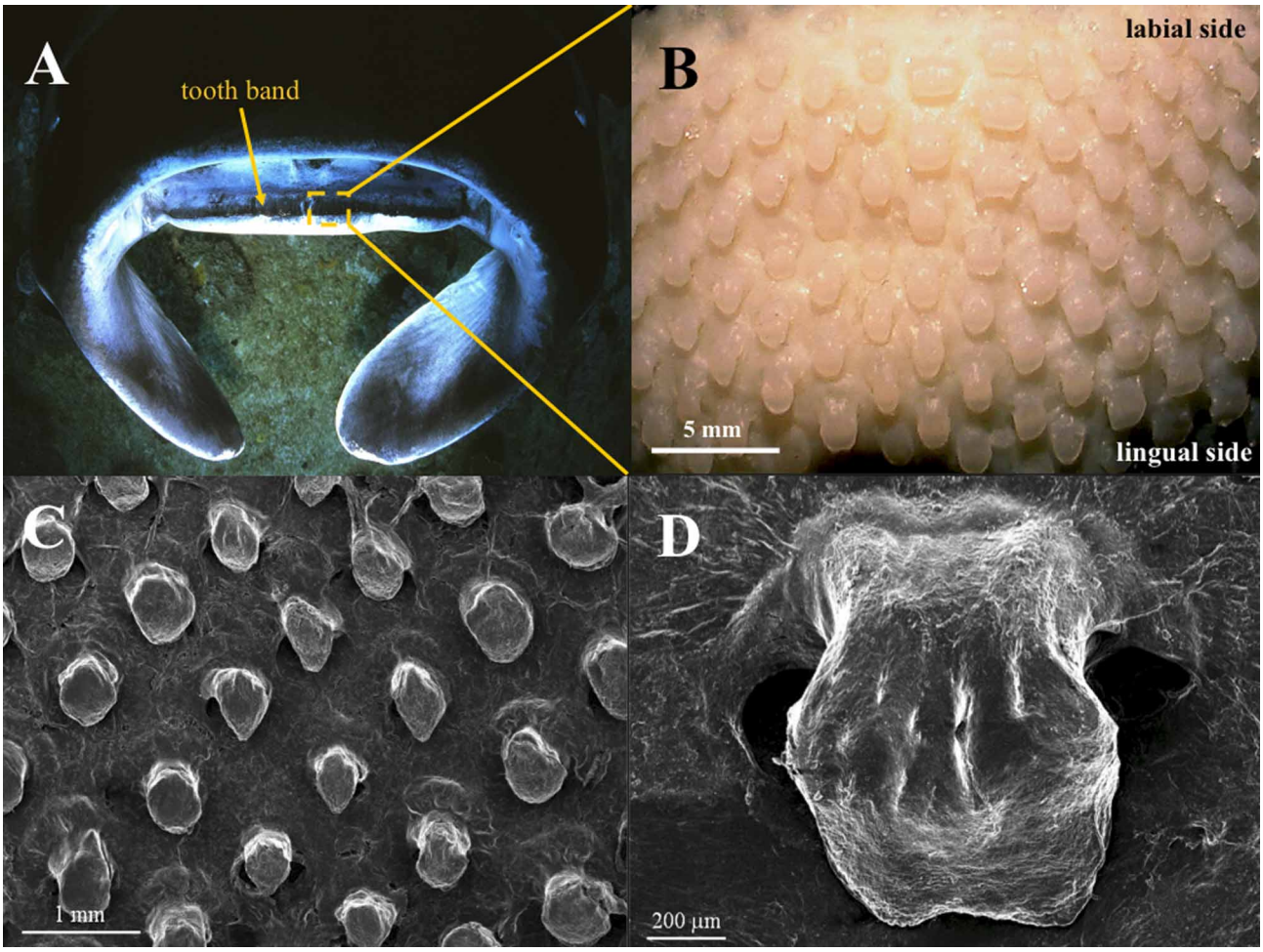

FIGURE 13. Dentition and tooth morphology in *Manta alfredi*: (a) lower jaw with elongated tooth band; (b) section of teeth mid-band; (c) embedded teeth of male ray; (d) view of single embedded female tooth.

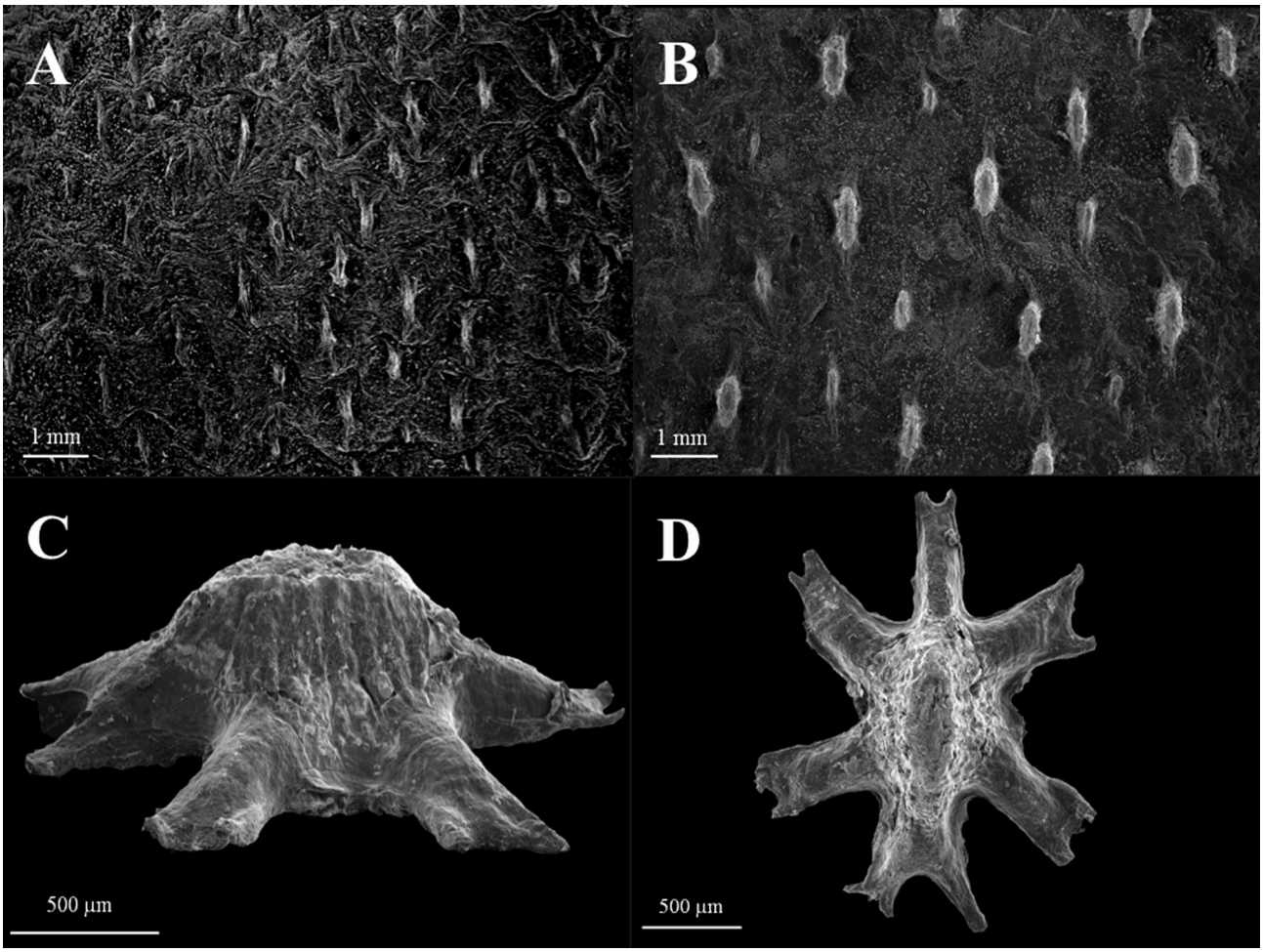

FIGURE 14. Skin and denticle morphology in *Manta alfredi*: (a) superior view of dorsal skin in male ray; (b) superior view of ventral skin in female ray; (c) lateral view; (d) superior view.

Character key for *Manta* (Fig. 15)

(1) Pale to white-coloured shoulder patches present on dorsal supra-branchial region on each side of a dark midline

Shoulder patches are very distinct and approximately triangular in shape with a posterior facing hook on the anterior distal side. Anterior edge of shoulder patches runs medially from spiracle in an approximately straight line parallel to the edge of the upper jaw ..... ***Manta birostris***

Anterior margin of shoulder patch initially emanating posteriorly from spiracle before curving medially. Towards the midline, colouration again begins to radiate out posteriorly continuing down over the supra-branchial region in variably sized and shaped shoulder patches. Anterior distal side of the shoulder patch may present as an anterior facing hook..... ***Manta alfredi***

(2) Ventral colouration and natural markings

Distinctive dark spots located on the ventral surface of disc over abdominal region, with no spots present medially between the five adjacent gill slits. Prominent semi-circular spot extends posteriorly from both of the most posterior gill slits. Charcoal-coloured margin typically present on posterior edges of pectoral fins that extend the entire length of each pectoral fin..... ***Manta birostris***

Distinctive dark spots on the ventral surface of disc can be present across the posterior half of the body and medially between the five adjacent gill slits. Small semi-circular spot extends posteriorly from of both of the most posterior gill slits..... ***Manta alfredi***

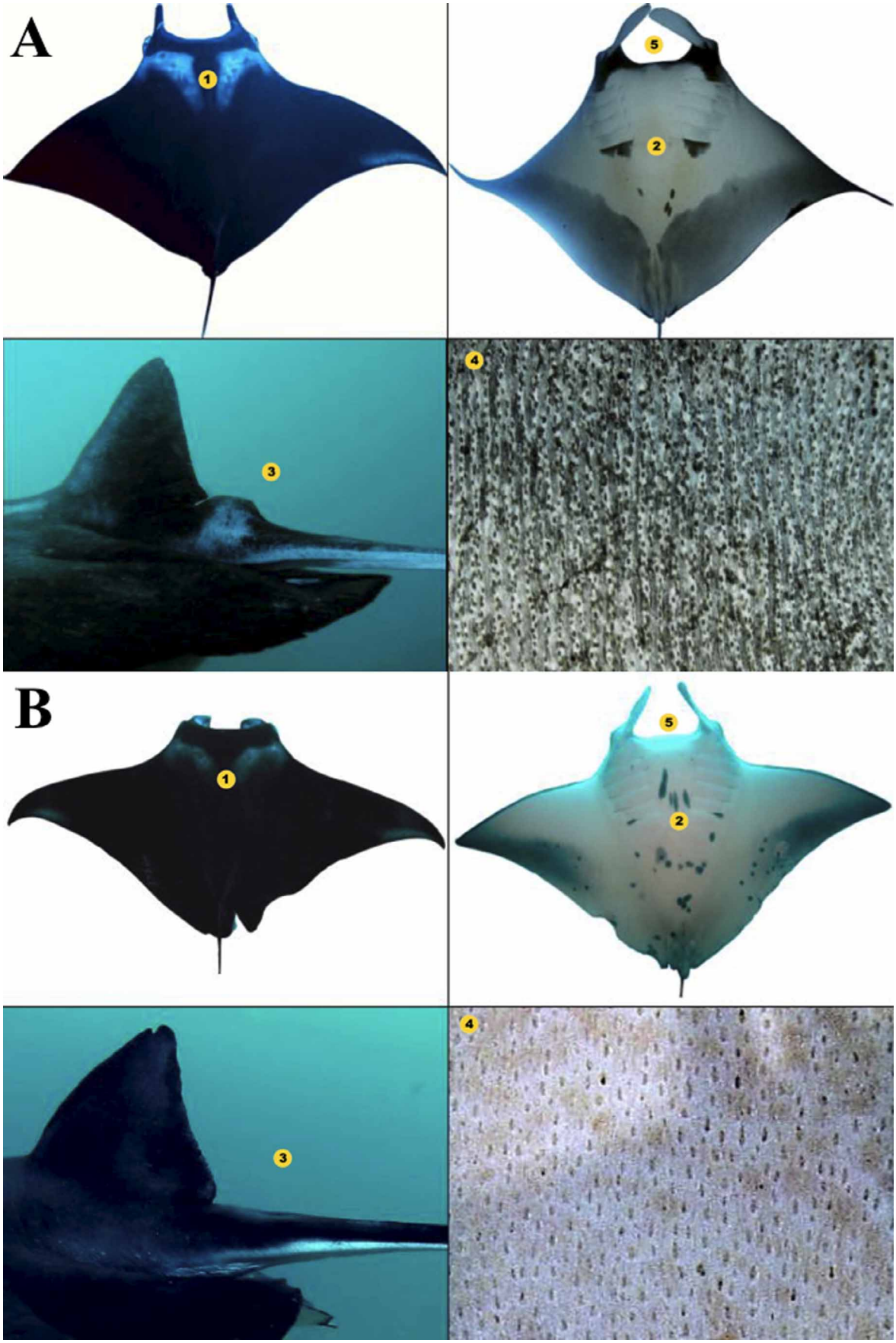

FIGURE 15. Key features used to differentiate *Manta birostris* and *Manta alfredi* in the field: (1) presence, colour and shape of supra-branchial shoulder patches (2) ventral spot distribution and colouration (3) presence or absence of caudal spine (4) appearance of skin and denticle morphology (5) colour of mouth and dentition.

(3) Caudal spine

Caudal spine mostly encased in a calcified mass present on the dorsum of the tail immediately posterior to the dorsal fin ..... ***Manta birostris***
No distinct, removable caudal spine or calcified mass present on tail..... ***Manta alfredi***

(4) Skin and dermal denticles

Skin, which forms distinct, sagittally oriented, ridges and furrows along the entire length of the dorsal and ventral surfaces, is densely embedded with overlapping, multicuspid denticles..... ***Manta birostris***
Skin on both dorsal and ventral surfaces embedded with small non-overlapping, evenly spaced denticles with stellate bases and laterally elongated knob-like (lacking cusps) structures projecting from skin..... ***Manta alfredi***

(5) Mouth colouration and dentition

Mouth black to charcoal grey in colouration. Dark colouration around mouth often extends posteriorly on the ventral surface from the base of the cephalic fins to the anterior edge of the first gill slits. Dental ligament embedded with small cusped teeth on the lower jaw measuring roughly 25% of total disc length with approximately 12–16 rows, 220–250 files across entire width of the band. Total tooth counts of 3000–4000 for entire tooth band. Upper jaw contains at least two rows of enlarged denticles that span the same width of the upper jaw as the tooth band on the lower jaw.... ..... ***Manta birostris***
Mouth is white to light grey in colouration. Dental ligament with small cusped teeth on the lower jaw measuring roughly 22% of total disc length with approximately 6–8 rows, 142–182 files across entire width of the tooth band. Total tooth counts of 900–1500 for entire tooth band. Upper jaw lacks rows of enlarged denticles..... ***Manta alfredi***

Manta sp. cf. *birostris*

Selected synonymy. *Cephalopterus giorna* Lesueur, 1824.

Common names. Atlantic manta ray, Caribbean manta ray

Diagnosis. Overall body shape and size similar to *M. birostris*, although differences in colouration, denticles and dentition occur. Maximum disc width over 6000 mm. Slender whip-like tail with reduced caudal spine predominantly encased in a calcified mass present on the dorsum of tail immediately posterior to the dorsal fin. Small, knob-like dermal denticles occur on both the dorsal and ventral surfaces, which are non-overlapping but densely and non-uniformly distributed. Ventral surface has slightly larger denticles. Terminal mouth with tooth band on lower jaw comprising 77% of total jaw width and containing 9–11 rows of small cusped teeth.

Morphometrics. See Bigelow and Schroeder (1953) for limited morphological measurements.

Colouration. Dorsal surface black in colouration, although sometimes noted to be reddish to brown in colour (Lesueur 1824, Mitchill 1824, Bancroft 1829, Coles 1916, Bigelow and Schroeder 1953, Notarbartolo-di-Sciara and Hillyer 1989), with or without distinct shoulder patches (Fig. 16a,b). When present, white dorsal shoulder patches occur on each side of a darker midline. When present, shape of the shoulder patches are approximately triangular in shape with posterior facing hook on the anterior distal side (Fig. 16a). Anterior edge of shoulder patches runs medially from spiracle in an approximately straight line parallel to the edge of the upper jaw.

Ventral surface cream to white in colouration, including mouth (Fig. 16c,d). Dark grey to black spots and patches are present only on the posterior section of the pectoral fins (posterior to the fifth gill slit) and often centralized on the abdominal region (Fig. 16c,d). Spots do not occur medially between the five gill slits (Fig. 16). Small black semi-circular spots posterior to the fifth gill slits present (Fig. 16c,d). Light to dark charcoal-coloured margin present along the posterior edges of the pectoral fins. Charcoal-coloured margins sometimes terminate mid-fin or sometimes stretch almost the entire length of each pectoral fin but are not always in a distinct “V” shape as in *M. birostris* (Fig. 16d).

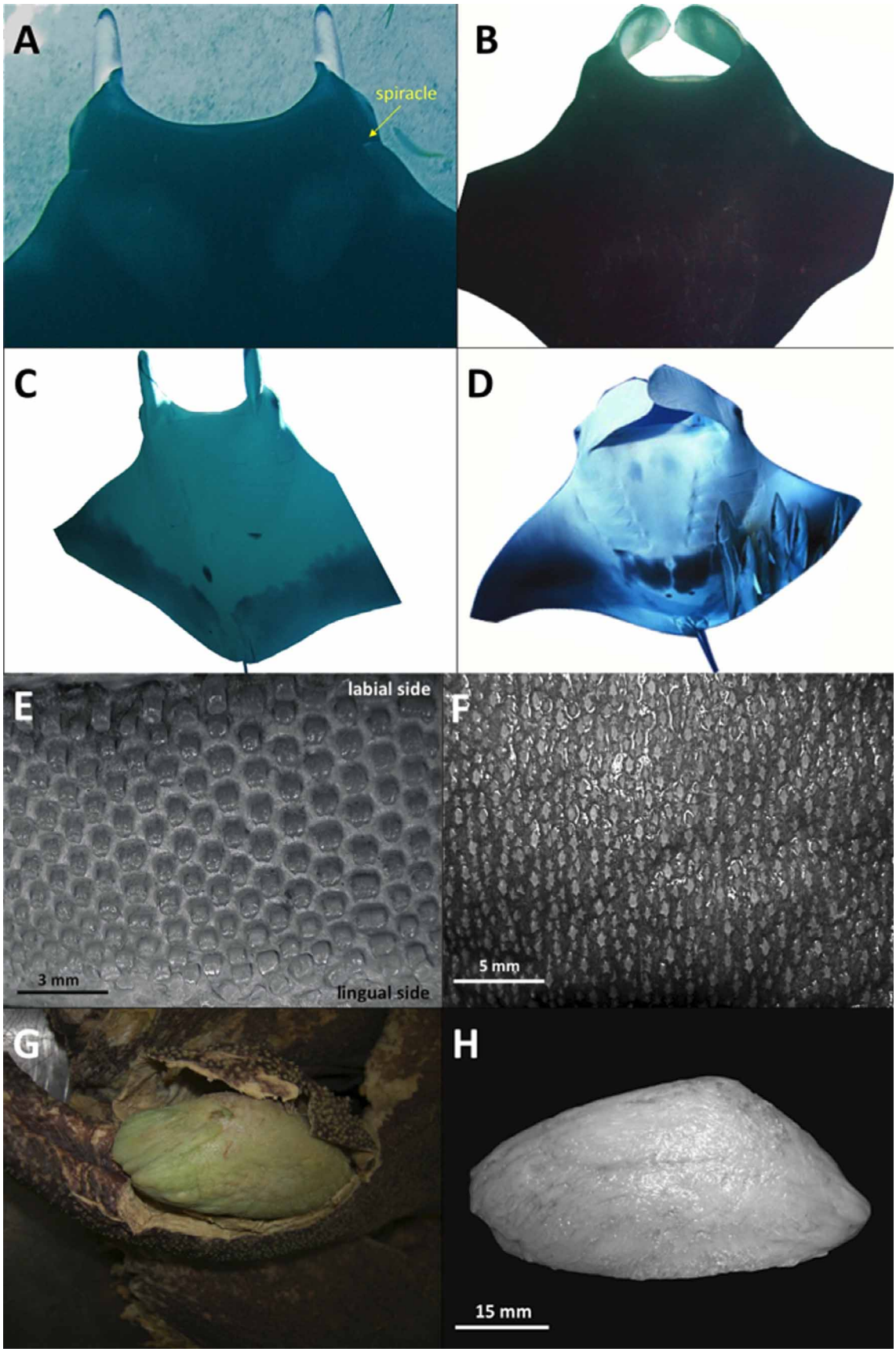

FIGURE 16. Characteristics and differences in *Manta sp. cf. birostris*: Variation in dorsal supra-branchial shoulder patch markings on individuals from: (a) Bahamas (b) Holbox, Mexico; and variation in the ventral markings (c) Bahamas (d) Florida, USA, (e) dentition mid-band, (f) skin and denticle morphology (g-h) cartilaginous mass on tail with embedded spine (entire structure was 70 mm total length, 29 mm wide, and 28 mm in height and has a mass of 41.5 grams).

Dentition. Tooth band on lower jaw comprising 77% of total jaw width (Fig. 16e). Tooth band containing 9–11 rows of small cusped teeth (approximately 1.2 mm in length) Each tooth has a bulbous root, which is embedded in the dental ligament and freestanding stalk that ends in a curved cusp that forms the occlusal surface and is oriented to face the lingual side of the jaw. Teeth in the tooth band do not overlap (Fig. 16e). Tooth band absent in upper jaw but sparsely distributed small denticles are present in upper jaw, similar to those in *M. birostris*.

Denticles. Prominent dermal denticles present on both the dorsal and ventral surfaces are non-overlapping but densly and non-uniformly packed (Fig. 16f). Unlike *M. birostris*, the denticles of *Manta* sp. *cf. birostris* are not distributed along sagittally oriented ridges in the skin. Denticles on the dorsal and ventral surfaces are oriented in an antero-posterior direction and are similar in appearance and distribution, with slightly larger denticles on the ventral surface. Like *M. alfredi*, each denticle comprises a stellate base (which is embedded in the skin) with a dorso-laterally elongated emergent knob.

Caudal spine. Spine with serrated lateral edges embedded in a large mass of highly mineralised cartilage, similar to that described for *Mobula japonica* (Notobartolo-di.Sciara 1987) and *M. birostris*. Calcified mass with embedded spine located on the dorsum of tail immediately posterior to dorsal fin and is encased by a thin layer of dermis (Fig. 16g). Calcified mass (Fig. 16h) lacks attachment via collagenous connective tissue to tail and easily detaches if skin is removed (Fig. 16g). Spine appears to have an enameloid exterior and is slender in shape, approximately 6.9% of the width of the calcified cartilage mass. Tip of spine projects only approximately 2.5 mm out from the surrounding mass. The calcified mass extracted from the specimen examined (male 3480 mm DW) was 4.5% of the total DL of the ray.

Size. Dissected specimens measured up to 4695 mm DW but estimates of the largest individuals sighted in the field were over 6000 mm DW (Coles 1916). It is not known at what size *Manta* sp. *cf. birostris* reaches maturity however males up to at least 3480 mm DW were found to be immature.

Habitat and distribution. *Manta* sp. *cf. birostris* appears to be endemic to the Atlantic Ocean and Caribbean (Fig. 8). Commonly sighted along productive coastlines with regular upwelling and island groups (Lesueur 1824, Mitchill 1824, Bancroft 1829, Coles 1916, Bigelow and Schroeder 1953, Notarbartolo-di-Sciara and Hillyer 1989, Compagno 1999, Marshall 2009). *Manta* sp. *cf. birostris* occurs as far north as North Carolina (Coles 1916) and as far south as Venezuela (Notarbartolo-di-Sciara and Hillyer 1989). In some locations, including within many parts of the Caribbean, *Manta* sp. *cf. birostris* appears to occur in sympatry with *M. birostris*.

Material examined (n = 1). Immature male killed in June 1949 in Bimini, Bahamas (3480 mm DW) examined at the Harvard Museum of Comparative Zoology (MCZ 37005).

Discussion

This study highlighted differences in two species of *Manta* that are sympatric in some locations and allopatric in other regions. A visual key was constructed which highlights the conspicuous, diagnostic features of the two species using data collected throughout their respective geographical ranges. Based on morphometric measurements and external characters including colouration, dentition, denticle and spine morphology, as well as size at maturity and maximum disc width, the genus *Manta* consists of at least two wide-ranging species, *M. birostris* and *M. alfredi*. A worldwide genetic survey has provided support for the current taxonomic findings (Kashawagi *et al.* in review) but additional information from *Manta sp. cf. birostris* in the Atlantic is needed.

Manta birostris is the more widely distributed member of the genus and is present in the Atlantic, Indian and Pacific oceans. *Manta alfredi*, which has been resurrected herein (based also on Whitley's [1936] redescription of the species), is also widespread, occurring in the three tropical oceans, although sighting records from the Atlantic are restricted off Portugal and north-western Africa. A global investigation of major aggregation sites revealed that *M. birostris* may be a more oceanic and migratory species than *M. alfredi*, with

individuals regularly sighted at offshore islands, oceanic seamounts and submarine ridge systems (Yano *et al.* 1999, Rubin 2002). Furthermore, rare or seasonal sightings of *M. birostris* at locations such as New Zealand (Duffy and Abbott 2003), southern Brasil (Luiz *et al.* 2008) and Uruguay (Milessi and Oddone 2003), the Azores Islands and the eastern coast of the United States (Bigelow and Schroeder 1953), may suggest that this species undergoes significant seasonal migrations. In contrast, long-term sighting records of *M. alfredi* at established aggregation sites suggest that this species is more resident to tropical waters and may exhibit smaller home ranges, philopatric movement patterns, or shorter seasonal migrations (Homma *et al.* 1999, Dewar 2008, Kitchen-Wheeler 2008, Marshall 2009).

A third, putative species, *Manta* sp. *cf. birostris*, in the Atlantic may be distinct from *M. birostris*. This putative species shares some characteristics with *M. birostris*, such as a large maximum disc width and the presence of a distinct, reduced caudal spine. However, from the limited specimens and photographs examined, clear differences exist between *Manta* sp. *cf. birostris* and *M. birostris* including dissimilar denticle morphology and distribution, intermediary dentition and, most noticeably, differences in dorsal and ventral colouration. While *Manta* sp. *cf. birostris* occurs in sympatry with *M. birostris* in parts of the Atlantic and Caribbean, there is some evidence that differences in fine-scale habitat selection and seasonal habitat use may occur in some locations (Bigelow and Schroeder 1953, Notarbartolo-di-Sciara and Hillyer 1989). Bigelow and Schroeder's (1953) description of *M. birostris* from the Western Atlantic is one of the most comprehensive descriptions compiled, but includes material from both the wide-ranging *M. birostris* and the localized *Manta* sp. *cf. birostris*. To help clarify the situation, photographs, notations on colouration and descriptions of denticle and tooth morphology of both *M. birostris* and *Manta* sp. *cf. birostris* have been provided to supplement this description. At present there is not enough empirical evidence to warrant the separation of a third species of *Manta.* At minimum, additional examination of dead specimens of *Manta* sp. *cf. birostris* are necessary to clarify the taxonomic status of this variant manta ray. Further examinations of the distribution of *Manta* sp. *cf. birostris*, as well as, studies of its ecology and behaviour within the Atlantic and Caribbean are also recommended. If distinct, we propose that a third species of *Manta*, *Manta giorna*, be resurrected from Lesueur's (1824) description from North America.

Previous examinations of the natural colouration patterns of manta rays in the Pacific and Atlantic oceans concluded that ventral colouration and shoulder patches shape had no recognizable patterns that allowed for geographical separation (Notarbartolo-di-Sciara and Hillyer 1989, Clark 2002b). Furthermore, results of photographic surveys suggested that colouration presented little systematic or taxonomic relevance as a character in this species (Clark 2002b). Results from the current study indicate that earlier conclusions are not valid because *Manta* species are wide ranging and have sympatric distributions in many areas, thus examination by geographical region is not sufficient. While colouration appears to be a good visual character for discriminating between species of *Manta* in the field, on a global basis natural colouration patterns can be highly variable within species. Additionally, while particular characteristics (e.g. shoulder patches, ventral spot patterning, mouth colour) seem to be consistent within species, there were on rare occasion individuals that slightly deviated from conventional colour patterns. While slight variation in colouration is to be expected within species (Weins and Servedio 2000), colouration should still be used cautiously when it is the only discriminating character used to identify a species of manta ray. Beyond the typical variations in natural colouration patterns, black and white colour morphs occur (in varying degrees) in both species of *Manta* (Ishihara *et al.* 2001, Rubin 2002). While not appearing to affect any other characteristics of the species other than their colouration, these extreme variant colour morphs often contributed an added degree of confusion when attempting to discriminate between species of *Manta* in the field or in photographs, especially when close examination was not possible. It should be noted that these colour morphs could be a possible source of error, resulting in mis-identifications in future studies or surveys (Visser *et al.* 2004).

Noteworthy was the existence of both melanistic (black) and leucistic (white) colour morphs in both species of *Manta*, suggesting that these genetic mutations occurred in an ancestral form. *Manta* is the only known genus of elasmobranchs that exhibits an almost entirely black, melanistic, colour morph. Unlike the melanistic form, several species of elasmobranchs have been reported to exhibit albinism or leucism (see

review in Clark 2002a). The white colour morph observed in both species of *Manta* is not albinism (as reported by Ishihara *et al.* 2001), as true albinos are devoid of any dark pigment including in their eyes (Clark 2002a). The condition should rather be termed leucism, which describes specimens with reduced or diminished pigment (Clark 2002a). It is not known why these colour morphs have persisted or why they are more common in some regions than others (Barton 1948; Homma *et al.* 1999; Ishihara *et al.* 2001, Rubin 2002, Marshall 2009) but wide variations in the distribution of pigmented or non-pigmented forms have been reported for other marine animals such as cetaceans (Visser *et al.* 2004).

The current study provides sufficient empirical evidence to warrant the separation of *Manta birostris* and *Manta alfredi*. The results of this study will aid in the differentiation of members of this genus in the field, in preserved museum specimens, in photographs and in historical records. Data on the life history and ecology of both species of *Manta* remain scarce, despite members of the genus being circumglobally distributed and a popular attraction for marine tourism. In recent years, manta rays have become victims of by-catch in fisheries and netting programs, and in select locations their meat, cartilage and branchial filaments have been targeted for consumption, trade and international distribution (Notarbartolo-di-Sciara 1988, Alava *et al.* 2002, Marshall *et al.*, 2006; White *et al.*, 2006). These types of fisheries have severely reduced several regional manta ray populations and as a result the species is listed as Near Threatened/regionally Vulnerable on the IUCN Red List of Threatened Species (Marshall *et al.* 2006). The present reclassification of the genus has major implications for the conservation assessment of the two species. Each species faces different and specific threats in various regions of the world, and the worldwide IUCN status of the genus requires urgent revaluation in light of this revision.

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