

Clarification of *Aetobatus ocellatus* (Kuhl, 1823) as a valid species, and a comparison with *Aetobatus narinari* (Euphrasen, 1790) (Rajiformes: Myliobatidae)

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ABSTRACT.— *Aetobatus narinari* is generally considered to have a circumglobal distribution but some have suggested that it consists of more than one cryptic species. Recent molecular studies have provided evidence of a species complex, with an Indo–West/Central Pacific clade and a Western Atlantic clade. This paper investigates the nomenclature of the Indo–West Pacific species and provides a redescription of *Aetobatus ocellatus* (Kuhl, 1823). *Aetobatus ocellatus* is very similar morphologically to *Aetobatus narinari* but differs in having a slightly longer tail and a different dorsal coloration. A major taxonomic revision of the *A. narinari* complex is required to determine the number of species present, their distributional ranges and effective field characters. The conservation status of members of this complex needs to be evaluated.

Key words: *Aetobatus ocellatus* – *Aetobatus narinari* – Indo–West Pacific – redescription – eagle rays

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INTRODUCTION

The family Myliobatidae, eagle rays (Chondrichthyes: Rajiformes), a group of medium to large rays with wing-like pectoral fins, is comprised of four genera. The genus *Myliobatis* has the largest number of valid nominal species (12) compared with *Aetobatus* (at least 3), *Aetomylaeus* (4) and *Pteromylaeus* (2). Members of the genus *Aetobatus* differ from the other genera in having a deeply notched nasal curtain, the upper and lower teeth in a single row at all growth stages, and the lower jaw with chevron-shaped teeth (Capapé & Quignard, 1975; Compagno & Last, 1999). The supraspecific taxon *Aetobatus* was designated by Blainville (1816) as a subgenus for *Raja aquila*; the type species for the genus *Aetobatus* was subsequently designated to be *Raja narinari* by Müller & Henle (1841).

Two nominal species, *A. narinari* and *A. flagellum* (Bloch & Schneider, 1801), within this genus are generally considered valid, with *A. guttata* (Shaw, 1804) and *A. ocellatus* (Kuhl, 1823) listed as questionable species by some authors. *Aetobatus narinari* was described by Euphrasen (1790), as *Raja narinari*, and in his description he clearly refers to the ‘Narinari brasiliensibus’ of

Willughby (1686) based on a specimen from Brazil, as well as a specimen he collected from St Barthelemy in the West Indies. Thus, both of these Western Atlantic locations are considered type localities for this species (Eschmeyer, 2009). Although some authors placed *A. flagellum* in the synonymy of *A. narinari* (e.g. Fowler, 1941; Dor, 1984), this species is a smaller, valid member of the genus *Aetobatus* (Compagno & Last, 1999; White *et al.*, 2006).

Aetobatus narinari has historically been considered to have a circumtropical distribution, but some studies have suggested that it may consist of a species complex (e.g. Jensen & Caira, 1998; Compagno & Last, 1999; Compagno *et al.*, 2005; Marie & Justine, 2005; Last & Stevens, 2009). A recent molecular study by Richards *et al.* (2009) assessed the validity of *A. narinari* as a single, widespread species using mitochondrial and nuclear sequence data from specimens collected in the Western, Central and Eastern Pacific and the Western Atlantic Oceans. Their findings provided strong evidence that this species is indeed a complex of at least 2 or 3 species, with the Western/Central Pacific lineage clearly distinct from the Western Atlantic and Eastern Pacific. This then raises the issue of what species name is available for the Indo–

West/Central Pacific species, and how it differs from the other species in this complex.

In the Indo–West/Central Pacific region, the *A. narinari* complex has a complicated nomenclatural history that needs to be critically examined. Two species names were proposed by Forsskål (1775) for *A. narinari*-like species from the Red Sea. The first of these, *Raja mula*, is considered available (Fricke, 2008), but since it hasn't been used as a valid name since 1899, it should be considered *nomen oblitum*. The second, *Raja tajara hörraeka*, is unavailable as it is not binominal because alternative Arabic vernacular names were used (Eschmeyer, 2009). Russell (1803) provided a short, but adequate, description and figure of an *Aetobatus* from Coromandel in India, but as with the other species in his substantial publication, he assigned only a vernacular name (Eel tenkee) which is non-binominal and cannot be considered an available name (ICZN Art. 11.4). In 1804, Shaw described the Guttated Ray *Raja guttata*, in a composite description based on records from India (based on Russell, 1803), Madagascar (based on records from Commerson) and Brazil (Marcgrave, 1648). However, since no types were designated and it is now known to consist of multiple species, use of this species name does not support nomenclatural stability. Furthermore, the name *Raja guttata* Shaw, 1804 is objectively invalid as it is a primary homonym of *Raja guttata* Bloch & Schneider, 1801 and thus must not be used (R. Fricke, pers. comm.).

In 1823, Kuhl provided a brief description of a new eagle ray, *Myliobatus ocellatus*, from Java (Indonesia) and reported that it agrees with Russell's (1803) illustration of 'Eel tenkee' from India, but no types were designated. *Aetobatus ocellatus* has been referred to as a valid taxon by a number of authors (Garman, 1913; Fowler, 1941; Talwar & Kacker, 1984; Talwar & Jhingran, 1992; Goren & Dor, 1994; Mould, 1994; Froese *et al.*, 1996; Kapoor *et al.*, 2002; Sujatha, 2002; Bonfil & Abdallah, 2004; Eschmeyer, 2009; Richards *et al.*, 2009). Thus, *Aetobatus ocellatus* (Kuhl, 1823) is the first available suitable name for the Indo–West/Central Pacific member of the *A. narinari* complex, with Java as the type locality. A number of species have been described since Kuhl's description of *A. ocellatus* from the Indo–West/Central Pacific that are considered conspecific with *A. narinari*. These include *Raia quinqueaculeata* Quoy & Gaimard, 1824, *Myliobatis eeltenkee* Rüppell, 1837, *M. macroptera* McLelland, 1841, *Raja edentula* Forster in Lichtenstein, 1844, *Goniobatis meleagris* Agassiz, 1858, and *Myliobatis punctatus* Miklukho-Maclay & Macleay, 1886. These should be considered junior synonyms of *Aetobatus ocellatus*.

In other regions of the world, the nomenclatural history of the *A. narinari* group is far more stable. In the Eastern Pacific, Gill (1865) described *Aetobatis laticeps* from off California, and in the Eastern Atlantic, Duméril (1861)

described *Aetobatis latirostris* from off Gabon, West Africa. Both of these species have since been considered junior synonyms of *Aetobatus narinari*. There are no junior synonyms of *A. narinari* in the Western Atlantic.

The present study provides a redescription of *Aetobatus ocellatus* as a valid species and designates a neotype for the species. Comparisons are made with *Aetobatus narinari* from the Western Atlantic.

Since the turn of the 20th Century (e.g. Shipley, 1900), the metazoan parasites of "*Aetobatus narinari*" have been the focus of numerous studies. Although in many cases, the notion that the "spotted eagle ray" may actually consist of a complex of species has gone largely unnoticed by parasitologists (e.g. Shipley & Hornell, 1906; Linton, 1916; Brooks & Mayes, 1980; Marques *et al.*, 1997), this has not always been the case. For example, Jensen & Cairn (1998) reported differences in the tapeworm faunas of host specimens identified as "*Aetobatus narinari*" collected from the Gulf of California, Gulf of Thailand and Timor Sea in Australia that might be indicative of the lack of conspecificity of spotted eagle rays among these localities. More recently, Marie & Justine (2005) reported that, of the 7 species of monocotylid monogeneans reported from spotted eagle rays, 5 species were known only from spotted eagle rays taken from localities in the Indo–Pacific, and not from those taken from the Atlantic Ocean. Marie & Justine (2006) explored this notion more formally, focusing specifically on a species of the monocotylid monogenean genus *Thaumatocotyle* that appears to parasitise spotted eagle rays in the Atlantic and Pacific Oceans. In fact, cognizant of the potential existence of a complex of host species, Marie & Justine (2005, 2006) referred to the host of their worms as *Aetobatus cf. narinari*.

The primary objective of the parasitic treatments provided in this paper is to place the previous records of metazoan parasites of spotted eagle rays (*A. narinari* complex) into the context of the taxonomic determinations for this ray complex proposed here. Thus, the names attributed to host individuals for the parasite records presented here have been modified, based on the localities from which the stingray hosts were collected, to reflect the eagle ray taxonomy proposed here. Clearly these treatments would benefit greatly from further investigation.

METHODS

Morphometric characters were established for eagle rays and are defined in Table 1. A total of 65 measurements, expressed as proportional measurements of disc width (DW), were taken for the neotype (MZB 18225) of *Aetobatus ocellatus* and 11 other specimens (CSIRO H 2490–01, CSIRO H 4426–19, CSIRO H 6131–02, IPMB 38.01.08, IPPS BO296, IPPS HBO2, RMNH 33021, RMNH unregistered, SMEC 75, SMEC 76 and SMEC

Table 1. Definition of the morphometric characters taken for myliobatid rays.

Morphometric character	Methodology
Disc width	Direct distance between pectoral-fin apices
Total length	Direct distance from snout tip to tip of tail (when undamaged)
Pre-dorsal length	Direct distance from snout tip to origin of dorsal fin
Disc length	Direct distance from snout tip to pectoral-fin free rear tip
Snout to pectoral-fin insertion	Direct distance from snout tip to insertion of pectoral fin (taken in dorsal position)
Disc thickness	Greatest thickness of body (usually under scapular region)
Snout to pectoral-fin origin	Direct distance from snout tip to origin of pectoral fin (use thumb to feel location of origin)
Posterior orbit to pectoral-fin insertion	Direct distance from the posterior edge of orbit (not eye) to insertion of pectoral fin
Snout to maximum width (horiz.)	Horizontal distance from snout tip to level of greatest width of body (run a line between pectoral-fin apices and place a pin at this level on the dorsal midline, then measure from snout tip to pin)
Pectoral-fin anterior margin	Distance from origin of pectoral fin to its apex
Pectoral-fin posterior margin	Distance from apex of pectoral fin to its free rear tip (if rounded use point of greatest angle)
Pectoral-fin base length	Distance from origin of pectoral fin to its insertion (taken in dorsal position)
Pectoral-fin inner margin	Distance from insertion of pectoral fin (taken in dorsal position) to its free rear tip (if rounded use point of greatest angle)
Head length (ventral)	Direct distance from inner edge of fifth gill slit to snout tip
Preorbital length	Direct distance from anterior edge of orbit to snout tip
Preorbital length (horiz.)	Horizontal distance from anterior edges of orbits to snout tip
Head width at pectoral-fin origins	Width of head at pectoral-fin origins (use thumb to feel location of origin)
Head height at pectoral-fin origins	Vertical height of head at pectoral-fin origins (use thumb to feel location of origin)
Head width at mid-eye	Width of head at level of mid-eye
Head height at mid-eye	Vertical height of head at level of mid-eye
Interorbital width	Distance between inner-most soft margins of each orbit (press calipers in against cranium on either side at mid-orbits)
Interspiracular width	Distance between inner-most margins of each spiracle
Spiracle length (longest)	Greatest diameter of the spiracle
Spiracle width (narrowest)	Diameter of the spiracle perpendicular to above measurement
Orbit diameter	Greatest diameter of the orbit (not exposed eye)
Eye diameter	Greatest diameter of the eye (not including outer orbit structure)
Orbit and spiracle length	Distance from anterior margin of orbit to posteriormost edge of the spiracle aperture
Preoral length	Direct distance from snout tip to soft anterior edge of lower jaw (not to tooth plates if extended anteriorly)
Prenasal length	Direct distance from snout tip to anterior margin of left nostril
Prenasal length (horiz.)	Horizontal distance from snout tip to anterior margins of nostrils
Rostral lobe width	Width of rostral lobe (taken below mideye)
Rostral lobe length	Direct distance from snout tip to posterior edge of rostral lobe (if exact location of posterior edge not clear use point of greatest angle)
Mouth width	Width of exposed part of mouth
Internarial width (external)	Shortest distance between incurrent nasal apertures
Nasal curtain length	Horizontal measurement from anteriormost margin of nostril to posterior margin of nasal curtain
Nasal curtain width	Greatest width of nasal curtain

Table 1. cont'd.

Morphometric character	Methodology
Nostril length (internal)	Greatest diameter of nostril (taken by elevating left side of nasal flap to reveal nostril)
Width of first gill slit	Greatest width of first gill slit
Width of third gill slit	Greatest width of third gill slit
Width of fifth gill slit	Greatest width of fifth gill slit
Distance between first gill slits	Shortest distance between first gill openings
Distance between fifth gill slits	Shortest distance between fifth gill openings
Tail at axil of pelvic fins (width)	Width of tail at pelvic-fin insertion
Tail at axil of pelvic fins (height)	Height of tail at pelvic-fin insertion
Tail at origin of stinging spine(s) (width)	Width of tail at origin of stinging spine (when >1 stings present base on origin of first sting)
Tail at origin of stinging spine(s) (height)	Height of tail at origin of stinging spine (when >1 stings present base on origin of first sting)
Pectoral-fin insertion to spine origin (horiz.)	Horizontal distance from pectoral-fin insertions to origin of stinging spine
Length of first stinging spine	Length of stinging spine from its exposed origin to its tip (taken in dorsal view)
Length of second stinging spine	Length of second stinging spine, when present, from its exposed origin to its tip (origin usually located beneath first sting)
Pectoral-fin insertion to dorsal-fin origin (horiz.)	Horizontal distance from pectoral-fin insertions to origin of dorsal fin
Dorsal-fin length	Direct distance from origin of dorsal fin to its free rear tip
Dorsal-fin anterior margin	Direct distance from origin of dorsal fin to its apex
Dorsal-fin height	Vertical height of fin from its base to its apex
Dorsal-fin posterior margin	Direct distance from apex of dorsal fin to its free rear tip
Dorsal-fin inner margin	Direct distance from insertion of dorsal fin to its free rear tip
Snout to anterior cloaca	Direct distance from snout tip to the anteriormost edge of the cloaca
Cloaca anterior to tail tip	Direct distance from the anteriormost edge of the cloaca to the tail tip (when undamaged)
Cloaca anterior to stinging spine	Horizontal distance from the anteriormost edge of the cloaca to origin of the stinging spine(s)
Width across pelvic fin bases	Direct distance between pelvic-fin origins (based on visible origins and not embedded, cartilaginous structures)
Greatest span of pelvic fins	Greatest span of pelvic fins when placed in natural position (not stretched)
Pelvic-fin length	Distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to posteriormost point of fin
Pelvic-fin anterior margin	Direct distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to its apex (use point of greatest angle when broadly rounded)
Pelvic-fin base	Direct distance from pelvic-fin origin (based on visible origins and not embedded, cartilaginous structures) to its insertion
Pelvic-fin posterior margin	Direct distance from apex of pelvic fin to its free rear tip (use point of greatest angle when broadly rounded)
Pelvic-fin inner margin	Direct distance from insertion of pelvic fin to its origin (based on visible origins and not embedded, cartilaginous structures)

244). For comparison, 5 specimens of *A. narinari* from the Western Atlantic were measured in full. Meristics were obtained from radiographs of the neotype (MZB 18225) and 3 other specimens of *Aetobatus ocellatus* (CSIRO H 2490–01, CSIRO H 4426–19, CSIRO H 6131–02). Counts generally follow Last & White (2008) for dasyatids, with some minor modifications: the first enlarged anterior element of the pelvic fin (with at least 4 and up to 6 distal segments fused at their bases) is counted as one; first synarcual centra are included in vertebral counts as there are no denticles to obscure centra; pre-dorsal diplospondylous counts are used rather than pre-sting counts; intermediate pectoral-fin radial elements were assigned to a pterygial unit based on the relative level of overlap with each of the adjacent units; and distal propterygial and metapterygial elements were considered to form part of the main skeleton and were not incorporated into counts; the notochord of the tail was excluded from counts. Only juvenile specimens were radiographed and some parts were poorly calcified. Pectoral and pelvic radial counts indicated by an asterisk (*) are minimum counts as additional radials not evident on radiograph may be present. A question mark indicates that the count was not possible due to poor calcification or inadequate exposure.

Muscle tissue samples were taken from specimens collected in the field and stored in either 95% alcohol or DMSO until processed in the laboratory. Total DNA was extracted from the tissue samples using High Pure PCR Template Preparation Kit (Roche Diagnostics). Extracted total DNA was stored at -20°C . Sub-sets of the extracted template were diluted to 1/10 of original strength and stored for subsequent use in PCR reactions. Samples were PCR amplified using Hot Start Taq (Promega) using primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (Naylor *et al.*, 2005). These primers are designed to bind to the ASN and ILE tRNA regions flanking the NADH2 gene in the mitochondrial genome of elasmobranchs. PCR reactions were generally carried out in 25 μl tubes by adding 1–2 μl of DNA template containing 1 unit of Taq, PCR buffer, 2.5 mM, MgCl_2 , 1.0 mM of dNTPs, and 1.0 mM of each primer. The reaction cocktail was denatured at 94°C for 3 minutes, after which it was subjected to 35 cycles of $94^{\circ}\text{C}/30\text{s}$, $48^{\circ}\text{C}/30\text{s}$ and $72^{\circ}\text{C}/90\text{s}$ followed by an indefinite hold in the thermal cycler at 4°C .

A sample of the completed PCR reaction was run on 1% agarose gels, stained, visualised and photographed under UV light to assess the success of PCR amplification. Samples with successful amplification products were purified using purification plates (Millipore, MA) attached to a vacuum manifold. The purified PCR products were quantified and diluted to between 30–100 $\text{ng}/\mu\text{L}$ and subsequently sent to SeqWright (Houston, TX) for sequencing. The software packages Phred and Phrap were used to read sequence traces, assign quality values, make base calls and produce output files for subsequent

alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences to yield a nucleotide alignment.

The aligned nucleotide sequences were subjected to Phylogenetic analysis using PAUP* (v4.0b106). The data were subjected to Neighbour joining based on K2P Distance, Parsimony and Maximum Likelihood analysis using parameter optimised models that best fit the data. The topologies across all methods were consistent with each other.

Specimens are referred to by the following prefixes for their registration numbers: BMNH, British Museum of Natural History, London; CSIRO, Australian National Fish Collection, Hobart; IPMB, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia; IPPS, Institut Penyelidikan Perikanan Sarawak, Kuching, Sarawak; MNHN, Muséum national d'Histoire naturelle, Paris; MZB, Museum Zoologicum Bogoriense, Jakarta; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; SMEC, Zoology Department of the Sabah State Museum, Kota Kinabalu, Malaysia. In the molecular trees, field codes (prefixed by AU, BJ, BO, BOD, CM, FY, HBO, JDD, NT or KA) are provided for samples collected by three of us (JC, KJ, GN), and data and images for these specimens are available at <http://tapeworms.uconn.edu>.

SYSTEMATIC ACCOUNT

Genus *Aetobatus* Blainville, 1816: 122 (Type species: *Raja narinari* Euphrasen)

Leiobatus Klein, 1775: 316 (not valid: does not conform to binominal nomenclature)

Leiobatis Walbaum (ex Klein), 1792: 581 (not available: work rejected for nomenclatural purposes)

Aetobatis Blainville, 1825: 38 (incorrect spelling of *Aetobatus*)
Aetobates Richardson, 1846: 198 (incorrect spelling of *Aetobatus*)

Stoasodon Cantor, 1849: 1416 (Type species: *Raja narinari* Euphrasen, monotypic)

Goniobatis Agassiz, 1858: 385 (Type species: *Raja flagellum* Bloch & Schneider, monotypic)

SPECIES.— *Aetobatus* includes at least 3 nominal species, *A. flagellum* (Bloch & Schneider), *A. narinari* (Euphrasen, 1790), and *A. ocellatus* (Kuhl, 1823). *Aetobatus laticeps* (Gill, 1865) from the Eastern Pacific is probably also valid but no specimens were examined during this study. *Aetobatus latirostris* (Duméril, 1861) from the Eastern Atlantic, also currently considered a synonym of *A. narinari*, is questionable and requires further investigation. At least one apparently undescribed species also occurs in the North-west Pacific.

Aetobatus ocellatus (Kuhl, 1823)

Figs 1–6, Table 2

- Raja mula* Forsskål, 1775: ix (Jeddah, Red Sea).
Raja tajara Forsskål, 1775: ix (Jeddah, Red Sea).
Raja narinari (non Euphrasen): Bloch & Schneider, 1801: 361 (Tahiti).
Eel tenkee Russell, 1803: 5, pl. 8 (Coromandel, India). Binominal system of naming not used thus not valid.
Raja guttata (non Bloch & Schneider): Shaw, 1804 (type locality: Madagascar, Coromandel, Brazil). Objectively invalid.
Myliobatus ocellatus Kuhl, 1823 (type locality: Java, Indonesia).
Raia quinqueaculeata Quoy & Gaimard, 1824: 200, pl. 43 (type locality: Guam).
Myliobatis narinari (non Euphrasen): [Bennett, 1830]: 694 (Sumatra).
Myliobatis eltenkee Rüppell, 1837: 70, pl. 19, fig. 3 (type locality: Jeddah in Saudi Arabia; Massawa in Red Sea).
Aetobatis indica: Swainson, 1839: 321 (based on Russell, 1803: Coromandel, India).
Myliobatis macroptera McLelland, 1841: 60, pl. 2, fig. 1 (type locality: Bengal).
Aetobatis narinari (non Euphrasen): Müller & Henle, 1841: 179 (India, Red Sea).
Raja edentula Forster in Lichtenstein, 1844: 227, 256 (type locality: Tanna, Vanuatu).
Stoasodon narinari (non Euphrasen): Cantor, 1849: 1416 (Penang, Malay Peninsula, Singapore).
Goniobatis meleagris Agassiz, 1858: 385 (type locality: Hawaiian Islands). Description poor and no types allocated; likely refers to this species as is only myliobatid found off Hawaii.
Myliobatis punctatus Miklukho-Maclay & Macleay, 1886: 675, pl. 4, figs 1–6 (type locality: Admiralty and Lub Islands, Australia).
Miliobatis punctatus: Miklukho-Maclay & Macleay, 1886: pl. 46 (Australia). Misspelling in original description.
Aetobates narinari (non Euphrasen): Sauvage, 1891: 519 (Madagascar).
Aetobatus narinari (non Euphrasen): Brigham, 1902: 20 (Honolulu).
Aetobatis guttata (non Bloch & Schneider): Annandale, 1909: 56 (Bay of Bengal).
Aetobatis punctatus: Günther, 1910: 497 ('south Sea').
Pteromylaeus punctatus: Garman, 1913: 439 (Admiralty Islands).
Aetobatus punctatus: Whitley, 1940: 224, figs 251, 257 (Australia).
Aetobatus flagellum (non Bloch & Schneider): Misra, 1959: 108, fig. 30 (India).
Stoasodon ocellatus: Whitley, 1964: 34 (Australia).
?Aetobatus guttatus (non Bloch & Schneider): Compagno, 1999: 497.
Aetomylaeus ocellatus: Sujatha, 2002: 157 (India).
Aetobatus cf. *narinari*: Compagno *et al.*, 2005: 77 (Philippines).
?Aetobatus cf. *guttatus*: Compagno *et al.*, 2005: 78 (Philippines).

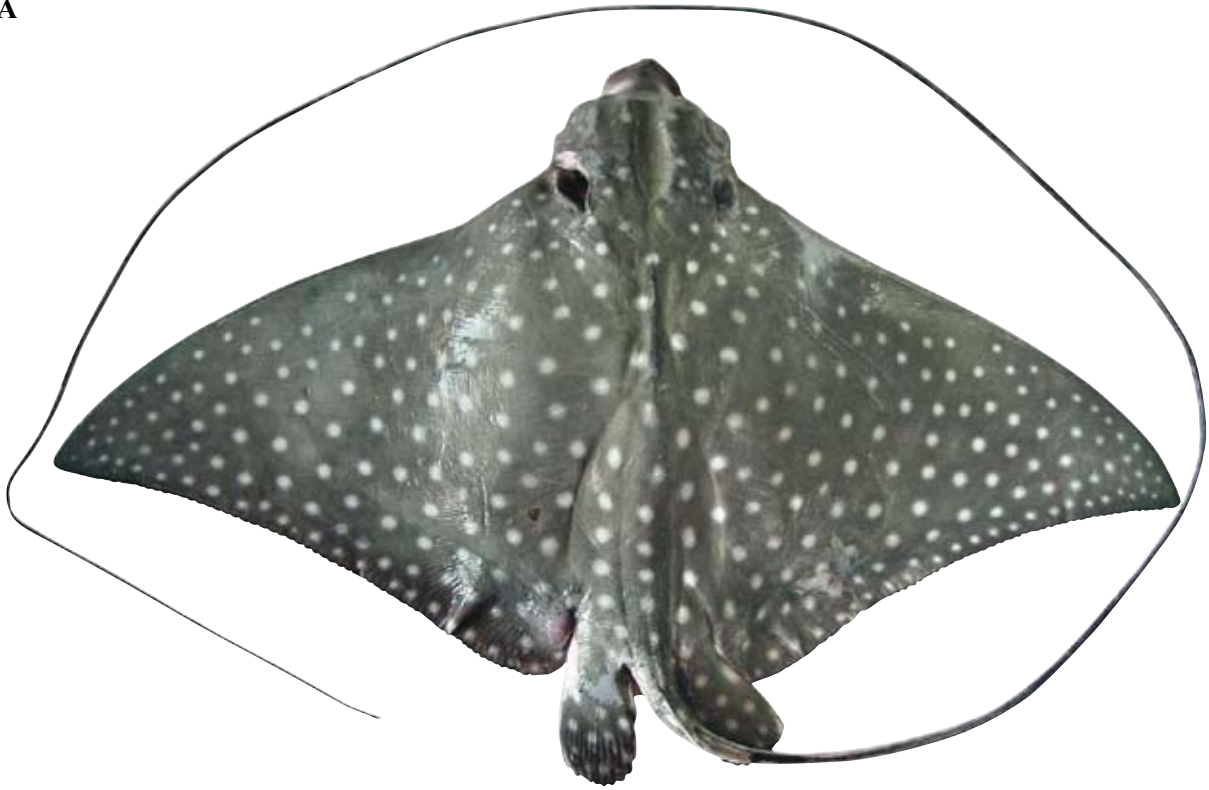
Neotype. MZB 18225, juvenile male 477 mm DW (1422 mm TL), Muara Angke fish landing site, Jakarta, Indonesia, 20 May 2002.

Other material. 13 specimens: CSIRO H 2490–01, juvenile male 456 mm DW (1330 mm TL), east of Brunswick Heads, New South Wales, Australia, 29°24' S, 153°23' E, 25–28 m, 08 Jun. 1990; CSIRO H 4426–19, female 498 mm DW (tail removed beyond dorsal fin), Muara Angke fish landing site, Jakarta, Indonesia, 17 Oct. 1995; CSIRO H 6131–02, juvenile male 577 mm DW (1528 mm TL), Muara Angke fish landing site, Jakarta, Indonesia, 06 Apr. 2001; IPMB 38.01.07 (head only), Kota Kinabalu fish market, Sabah, Malaysia, 04 May 2004; IPMB 38.01.08, juvenile male 704 mm DW, Kota Kinabalu fish market, Sabah, Malaysia, 30 May 2003; IPPS BO296, juvenile male 447 mm DW (1309 mm TL), Mukah, Sarawak, Malaysia, 02°53.52' N, 112°05.44' E, 22 May 2003; IPPS HBO2, female 740 mm DW (tail damaged), Sarawak, Malaysia, 2002; MNHN A8905 (holotype of *Raja quinqueaculeata*, dried dorsal fin and stinging spines only), Guam, ~13°30' N, ~145° E, ca. 1817–1820; RMNH 33021, juvenile male 417 mm DW, Tami River, Papua New Guinea, 24 Jun. 1955; RMNH unregistered, female 482 mm DW (1322 mm TL), Halmahera Sea, Indonesia; SMEC 75, female 371 mm DW (tail missing), SMEC 76, juvenile male 352 mm DW (tail missing), Kota Kinabalu fish landing site, Sabah, Malaysia, Oct. 1996; SMEC 244, female 481 mm DW (1362 mm TL), Kota Kinabalu fish landing site, Sabah, Malaysia, 1997.

DIAGNOSIS.— A large *Aetobatus* (reaching at least 300 cm DW) with the following combination of characters: dorsal surfaces with a dark greenish grey base coloration, variably white spotted (rarely ocellated); different NADH2 gene structure; relatively long tail (mean total length 281% DW, mean anterior cloaca to tail tip 230.2% DW); stinging spines relatively long (mean length of first spine 9.7% DW); teeth plates in a single row, those in lower jaw chevron-shaped; pectoral-fin radials about 102–116 (excluding proterygial radials anterior of eyes); total vertebral centra (including synarcual) 99–101.

DESCRIPTION.— Disc diamond-shaped, very broad but relatively short, width about 1.85 (1.63–1.80) times disc length; anterior projection 4.06 (3.54–4.27) in disc length; axis of greatest width of disc well posterior to scapular region, over abdominal cavity, its horizontal distance from snout tip 1.28 (1.16–1.43) times in distance from tip of snout to pectoral-fin insertion; deep, greatest thickness above scapular region and posterior head, thickness 7.92 (7.86–8.86) in disc width; without denticles, ridges or thorns. Pectoral fins very large, wing-like, narrowly triangular, weakly falcate; anterior margin concave basally, nearly straight for first two thirds, moderately to strongly convex distally; apex narrowly rounded to subangular, pectoral angle 56 (52–64)°; posterior margin moderately concave anteriorly, almost straight posteriorly; free rear tip broadly rounded; inner margin convex distally, becoming nearly straight anteriorly; length of anterior margin 49.8 (47.8–51.4)% DW, 1.33 (1.23–1.35) times its base length, inner margin

A



B



Figure 1. Neotype of *Aetobatus ocellatus* (MZB 18225, juvenile male 477 mm DW): A. dorsal view (fresh); B. ventral view (preserved).

Table 2. Morphometric data for the neotype of *Aetobatus ocellatus* (MZB 18225) and ranges and means of 11 other specimens, with ranges and means provided for 5 specimens of *Aetobatus narinari* from the Western Atlantic. Measurements expressed as a percentage of disc width.

	<i>Aetobatus ocellatus</i>			<i>Aetobatus narinari</i>			
	Neotype	Other specimens (n=11)			n=5		
		Min.	Max.	Mean	Min.	Max.	Mean
Disc width (mm)	456	352	740	502.3	420	652	532.8
Total length	298.1	264.8	292.8	281.4	229.4	277.1	263.1
Pre-dorsal length	53.8	53.5	58.6	56.5	56.2	60.2	57.8
Disc, length	54.1	55.7	61.4	58.1	56.9	62.7	59.7
Snout to pectoral-fin insertion	47.3	48.1	54.1	51.3	50.6	53.7	51.7
Disc thickness	12.6	11.3	12.7	12.2	8.6	13.3	11.3
Snout to pectoral-fin origin	13.3	13.2	16.9	15.3	14.2	17.8	16.2
Posterior orbit to pectoral-fin insertion	39.2	37.1	42.3	40.7	39.6	42.8	41.3
Snout to maximum width (horiz.)	36.9	33.7	45.5	39.3	34.8	42.3	39.2
Pectoral-fin anterior margin	49.8	47.8	51.4	49.5	48.7	50.2	49.6
Pectoral-fin posterior margin	47.3	44.4	49.3	47.7	44.8	51.2	48.0
Pectoral-fin base length	37.4	35.7	40.2	38.8	38.1	40.9	39.4
Pectoral-fin inner margin	6.1	6.0	7.3	6.8	6.2	7.7	7.1
Head length (ventral)	24.7	25.3	29.9	27.3	26.5	28.4	27.6
Preorbital length	8.0	8.3	10.3	9.3	9.1	9.9	9.5
Preorbital length (horiz.)	4.6	5.0	7.0	6.1	6.1	7.2	6.7
Head width at pectoral-fin origins	16.1	15.2	17.5	16.5	13.7	18.1	16.3
Head height at pectoral-fin origins	9.5	10.2	12.1	11.1	8.9	11.9	10.5
Head width at mid-eye	14.4	12.9	16.3	14.6	11.9	14.7	13.7
Head height at mid-eye	8.6	8.7	10.7	9.8	8.2	10.0	9.2
Interorbital width	9.2	8.4	10.4	9.5	9.4	10.6	9.9
Interspiracular width	10.5	9.2	11.1	10.3	9.3	11.1	10.2
Spiracle length (longest)	5.0	4.4	6.2	5.1	4.7	5.4	5.0
Spiracle width (narrowest)	2.0	1.7	2.8	2.3	1.6	2.3	2.0
Orbit diameter	4.7	4.0	5.6	4.8	4.1	5.5	4.6
Eye diameter	2.2	1.7	2.3	2.0	1.7	2.6	2.0
Orbit and spiracle length	11.4	9.9	12.3	10.9	9.5	11.7	10.7
Preoral length	8.6	9.6	12.3	10.5	10.7	11.3	10.9
Prenasal length	6.4	6.4	8.1	7.3	7.1	8.3	7.7
Prenasal length (horiz.)	6.1	5.7	7.6	6.6	6.7	7.6	7.2
Rostral lobe width	8.1	8.5	10.0	9.3	8.3	9.9	9.3
Rostral lobe length	3.2	2.9	5.3	4.5	4.7	6.0	5.2
Mouth width	7.8	6.8	8.1	7.4	6.4	7.7	7.2
Internarial width (external)	4.5	3.9	5.0	4.3	3.9	5.1	4.5
Nasal curtain length	4.4	4.2	5.4	4.7	3.8	5.0	4.4
Nasal curtain width	7.4	6.6	8.2	7.2	6.7	8.0	7.5
Nostril length (internal)	3.3	2.6	3.6	3.3	2.3	3.4	2.8
Width of first gill slit	1.8	1.6	2.2	1.8	1.7	2.2	1.9
Width of third gill slit	2.1	1.6	2.1	1.9	1.8	2.5	2.1
Width of fifth gill slit	1.5	1.2	1.8	1.5	1.2	1.7	1.4
Distance between first gill slits	15.7	15.4	17.8	16.1	14.5	16.6	15.7
Distance between fifth gill slits	9.6	9.6	11.4	10.2	9.3	9.8	9.5
Tail at axil of pelvic fins (width)	3.3	2.6	3.7	3.2	2.9	3.5	3.2

Table 2. cont'd.

	<i>Aetobatus ocellatus</i>			<i>Aetobatus narinari</i>			
	Neotype	Other specimens (n=11)			n=5		
		Min.	Max.	Mean	Min.	Max.	Mean
Tail at axil of pelvic fins (height)	3.3	2.8	4.0	3.3	3.0	3.5	3.2
Tail at origin of stinging spine(s) (width)	1.7	1.2	1.9	1.5	1.4	1.8	1.6
Tail at origin of stinging spine(s) (height)	1.9	1.3	2.1	1.9	1.5	2.5	2.1
Pectoral-fin insertion to spine origin (horiz.)	13.6	10.8	13.3	12.2	11.7	12.4	12.1
Length of first stinging spine	–	9.2	10.6	9.7	8.3	9.6	8.9
Length of second stinging spine	–	–	–	–	9.3	9.3	9.3
Pectoral-fin insertion to dorsal-fin origin (horiz.)	7.0	5.0	6.5	5.8	6.0	7.2	6.4
Dorsal-fin length	4.8	4.7	5.8	5.2	4.8	6.1	5.4
Dorsal-fin anterior margin	4.8	4.7	5.7	5.2	4.8	6.2	5.2
Dorsal-fin height	2.7	2.7	3.2	2.9	2.7	3.7	3.1
Dorsal-fin posterior margin	2.4	2.2	2.8	2.5	2.3	2.8	2.5
Dorsal-fin inner margin	1.1	0.9	1.4	1.1	0.8	1.1	1.0
Snout to anterior cloaca	47.4	48.9	55.3	51.1	50.2	53.1	51.9
Cloaca anterior to tail tip	246.8	213.7	241.1	230.2	177.1	226.9	208.3
Cloaca anterior to stinging spine	13.1	11.5	13.5	12.5	11.7	14.6	13.1
Width across pelvic fin bases	10.5	9.5	11.4	10.6	10.2	12.3	11.0
Greatest span of pelvic fins	0.0	16.3	22.5	19.8	18.9	24.2	21.9
Pelvic-fin length	12.9	13.9	16.7	15.5	14.8	17.6	15.7
Pelvic-fin anterior margin	11.8	12.2	14.2	13.4	13.1	15.1	13.8
Pelvic-fin base	6.1	6.2	8.1	7.4	5.5	7.4	6.9
Pelvic-fin posterior margin	7.1	6.3	8.7	7.5	6.3	8.9	7.6
Pelvic-fin inner margin	11.8	9.0	10.4	9.7	7.1	12.2	10.2

6.17 (4.96–6.65) in its base; origin over anterior edge of spiracles; apex located posteriorly to pectoral mid-base; insertion just posterior to pelvic-fin origin; free rear tip partly overlapping pelvic-fin anterior margin.

Head pronounced, deep, short and broad; projecting well anteriorly from pectoral-fin origins; subhexagonal in cross-section at pectoral-fin origin; cranial region of head broadly rounded in dorsoventral view; chondrocranium pronounced above eyes and spiracles; snout abruptly convex before eyes, becoming deeply concave at origin of rostral lobe; nearly straight to slightly convex ventrally; ventral head length 24.7 (25.3–29.9)% DW, 1.53 (1.57–1.76) times width at pectoral-fin origins, 5.33 (3.95–5.09) times preorbital length (horizontal), 2.69 (2.72–3.08) times interorbital width; preoral snout length 1.10 (1.20–1.76) times mouth width, 1.89 (2.03–2.93) times internarial width, 0.55 (0.59–0.73) times distance between first gill slits; head width at pectoral-fin origin 16.1 (15.2–17.5)% DW, 1.69 (1.34–1.59) times its height. Rostral lobe fleshy, moderately long (shortest in juveniles); narrowly parabolic in dorsoventral view with a narrowly rounded apex; bluntly pointed in lateral view; its length 3.2 (2.9–5.3)% DW, 7.78 (5.14–9.22) in

head length, its width 1.98 (1.68–1.93) in head width at pectoral-fin origin.

Interorbital space relatively broad, convex but with a broad medial depression, without ridges, denticles or thorns; interorbital width 9.2 (8.4–10.4)% DW, 1.94 (1.80–2.35) times orbit length, 0.64 (0.58–0.71) times head width at mid-eye. Eyes moderately small, subcircular, lateral to very slightly ventrolateral on head; orbit only slightly elevated above head, diameter 2.25 (2.09–3.03) in spiracle length, 7.30 (7.18–9.36) in head width at pectoral-fin origin. Spiracles large, suboval, situated dorsolaterally posterior to orbit and above pectoral-fin origin, more visible dorsally than laterally; margins without any protuberances or folds; length 5.0 (4.4–6.2)% DW, 2.48 (1.85–2.86) times width.

Nostril narrowly suboval (often distorted after capture), immediately preceded by a broad, shallow, fleshy depression bordering anterolateral margin of the nasal curtain; anterior nasal fold thin, membranous, internal (often barely visible); very deep oronasal groove present; internarial space 1.42 (1.48–1.93) in prenasal length, 1.39 (1.16–1.49) times nostril length. Nasal curtain

large, elongate, lobate, width 1.68 (1.33–1.73) times length; lateral margin straight to concave, smooth edged; posterior margin divided by deep medial notch, bordered by a long, curtain-like fringe, not following contour of lower jaw; posterior margin of each lobe convex with apices narrowly rounded; most of surface finely papillate, covered with minute pores; apex and posterolateral margin recessible within oronasal groove.

Mouth moderately large, transverse, located ventrally, width 7.8 (6.8–8.1)% DW, 0.91 (0.57–0.83) times preoral length, 2.07 (2.05–2.50) in head width at pectoral-fin origin; not protrusible, anterior teeth of lower jaw visible when mouth closed; buccal region intricately papillate; skin on chin and at margin of lower jaw fleshy, strongly furrowed, papillate, indented slightly at symphysis. Teeth in a single row in each jaw, coalesced to form plates;



Figure 2. *Aetobatus ocellatus* (CSIRO H 6131-02, juvenile male 577 mm DW, preserved): A. ventral head view; B. lateral head view.

about 9 narrow, lingually recurved teeth in upper jaw (Fig. 5a), tooth plate well inside palate, its length about half its width; about 18 narrow, chevron-shaped teeth in lower jaw (Fig. 5b), tooth plate protruding distally, its length more than twice its width; roof of mouth with 2 rows of oral papillae, 4 in outer row, 7 in inner row, those in outer row slightly larger than those of inner row; floor of mouth near lingual margin of lower tooth plate with lunate fringe of about 7 variably shaped (usually pointed), less regular oral papillae.

Gill openings small, elongated S-shaped, forming a weakly fringed lobe laterally; length of first gill slit 1.20 (1.10–1.41) times length of fifth gill slit, 4.3 (3.18–5.06) in mouth width; distance between first gill slits 3.45 (3.20–4.23) times internarial space, 0.64 (0.55–0.61) times ventral head length; distance between fifth gill slits 2.12 (2.01–2.70) times internarial distance, 0.39 (0.35–0.41) times ventral head length.

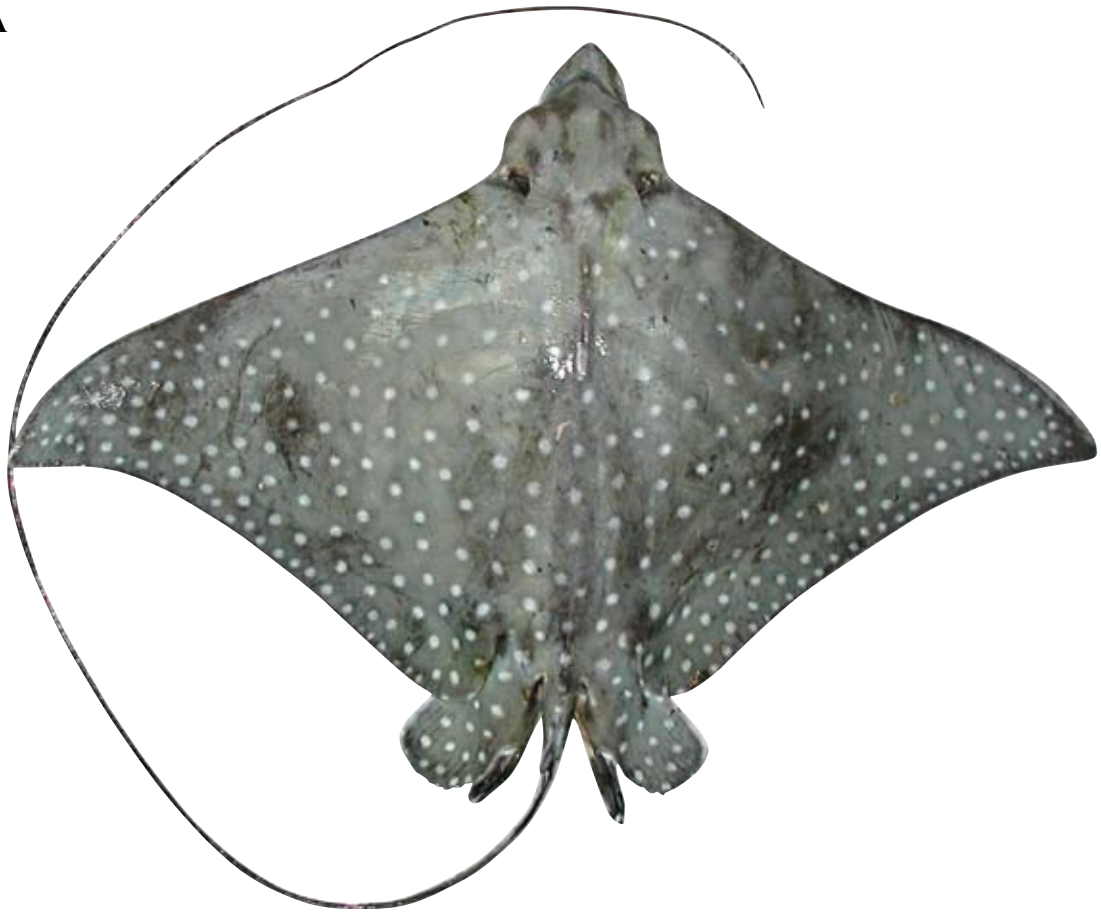
Pelvic fins relatively large, slender, subquadrangular, anterior margin concave, apex broadly angular, posterior margin strongly convex, free rear tip broadly rounded, inner margin weakly convex; extending well beyond pectoral-fin free tips; pelvic-fin length 12.9 (13.9–16.7)% DW, 1.24 (1.33–1.61) times width across fin bases, inner margin 11.8 (9.0–10.4)% DW. Claspers of adult males not examined in detail.

Dorsal fin small, strongly raked, its origin posterior to pelvic-fin insertions by about half of its fin base; anterior margin weakly convex; apex broadly rounded, over insertion of fin; posterior margin slightly convex to straight; free rear tip angular, inner margin very short, nearly straight; predorsal length 1.86 (1.71–1.87) in disc width, fin length 4.8 (4.7–5.8)% DW, height 0.57 (0.51–0.64) times its length, inner margin 4.33 (3.57–5.83) in fin length.

Tail very long, slender, whip-like, its length (from cloaca origin) 2.47 (2.14–2.41) times disc width; tapering gradually at base to stinging spine, and gradually becoming more whip-like beyond sting; base moderately compressed, suboval in cross section at pelvic-fin insertion, tail width at pelvic insertion 1.00 (0.89–1.09) times height; rhomboidal in cross section near origin of stinging spine, width 0.89 (0.62–0.95) times height at first spine origin; no skin folds present; a weak naked groove on dorsal surface of tail immediately posterior to base of stinging-spine(s), almost fully housing spines. Stinging spines 0–5, second longest (when more than one present), very elongate, slender, moderately broad-based, strongly tapered, almost fully serrated laterally; distance from sting base to pectoral-fin insertion 13.6 (10.8–13.3)% DW; longest stinging spine (9.2–10.6)% DW, (1.58–2.15) times dorsal-fin length.

Vertebral centra total (including synarcual) 101 (99–100, n=3); total (excluding synarcual) 97 (94–96);

A



B



Figure 3. Dorsal view of *Aetobatus ocellatus*: A. not retained (field number BOD52, Sandakan, Sabah), adult male 1260 mm DW (fresh); B. IPPS BO296, juvenile male 465 mm DW (fresh).



Figure 4. Lateral tail of *Aetobatus ocellatus*: A. CSIRO H 2490-01, juvenile male 456 mm DW; B. MNHN A8905 (holotype of *Raja quinqueaculeata*, dried dorsal fin and stinging spines only).

monospondylous (including synarcual) 45 (41–45); monospondylous (excluding synarcual) 41 (36–41); pre-dorsal diplospondylous 26 (25–31); post-sting diplospondylous 30 (27–33). Total pectoral-fin radials (excluding propterygial radials anterior of eyes) 102*–107 (109*–116); propterygium (anterior of eyes) ? (11*–16*), propterygium (posterior of eyes) 11* (12*–14), mesopterygium 36–37 (32–37), metapterygium 55*–59* (62*–66). Pelvic-fin radials: 1, 4* (1, 4*–6) + 15* (14*–16).

COLOUR.— When fresh, based on neotype: Dorsal surface greenish grey, slightly darker along posterior margins of pectoral and pelvic fins; all of disc and pelvic fin, and parts of raised portion of head, covered with large, diffuse-edged white spots; spots reasonably similar in size (slightly smaller near disc margin) and evenly spaced; eye bluish black; dark (dorsal) and pale (ventral) surfaces well demarcated (waterline) at anterior edge of disc and its junction with head; waterline extending anteriorly to mid eye and onto forehead; dark dorsal surface on rostral lobe similar, contrasted with its paler ventral surface and posteriorly with pale mid-snout; tail uniform greyish green. Ventral surface yellowish white; edge of rostral lobe dark in some material; outer anterior margin of disc black. Other material: Base colour of dorsal disc variable, greenish, greyish or reddish brown; coverage of white spots variable, usually densest posteriorly, but sometimes confined to posterior edge of disc or absent; dorsal fin and clasper of adult male plain coloured, similar to pelvic fin.

SIZE.— The 12 measured specimens examined ranged from 352–740 mm DW (1309–1528 mm TL, n=6) and consisted entirely of immature individuals. Since this species was previously considered as a synonym of *A. narinari*, accurate size information relating to *A. ocellatus* is difficult to separate from data for other species of the *A. narinari* complex. Last & Stevens (2009) report that in Australia, this species (as *A. narinari*) attains up to 3000 mm DW (>8800 mm TL), with males and females maturing at 1000 and 2140 mm DW respectively, and born at 180–260 mm DW. White & Dharmadi (2007) recorded a maximum size of 2144 mm DW for females and 1544 mm DW for males, with 50% male maturity at 998 mm DW. Other specimens recorded during recent surveys of Borneo ranged in size from 510–960 and 640–1320 mm DW for females (3) and males (6) respectively.

DISTRIBUTION.— *Aetobatus ocellatus* is probably widely distributed throughout the tropical and subtropical Indo–West and Central Pacific. Specimens examined in this study were from Australia, Indonesia, Borneo and Guam. The Indo–West and Central Pacific clade in Richards *et al.* (2009) included specimens from Japan, China, Hong Kong, Indonesia and Hawaii. This species is also likely to be present in the Western Indian Ocean, but specimens in collections from this area are generally lacking.

METAZOAN PARASITES.— *Aetobatus laticeps*:

Published records of metazoan parasites likely to have come from individuals of *A. laticeps* are limited. They consist of only 2 species of tapeworms; both are species of the onchobothriid genus *Acanthobothrium* reported from the spiral intestines of their hosts. These are *Acanthobothrium nicoyaense* described by Brooks &

McCorquodale (1995) from the Gulf of Nicoya, western coast of Costa Rica and *Acanthobothrium monksi* described by Marques *et al.* (1997) from the coast of Ecuador.

***Aetobatus narinari sensu stricto*:** A slightly more diverse suite of metazoan parasites has been reported from spotted eagle rays from the Eastern Atlantic; records from the Western Atlantic are lacking altogether. These parasites consist of the leeches *Branchellion torpedinis* reported from spotted eagle rays from Venezuela by Pauls & Provenzano (1999) and *B. ravenelii* from spotted eagle rays, presumably from the northern Gulf of Mexico (Sawyer *et al.*, 1975). Two species of monocotylid monogeneans have also been reported. *Decacotyle floridana* was reported from spotted eagle rays in Beaufort, North Carolina by Pearse (1949) (as *Heterocotyle floridana*), by Hargis (1955a) (as *Heterocotyle aetobatis*), from the Gulf of Mexico off Florida, and from the Yucatán Peninsula in Mexico by Lamothe-Argumedo *et al.* (1997) (also as *H. aetobatis*) and Pulido-Flores & Monks (2005). In addition, *Thaumatocotyle pseudodasybatis* was described by Hargis (1955b) from the ventral surface of spotted eagle rays from the Gulf of Mexico, Florida. In addition, 4 species of tapeworms have been reported from the spiral intestines of spotted eagle rays taken from localities in the Western Atlantic. The lecanicephalidean *Tylocephalum marsupium* and the tetraphyllidean *Acanthobothrium tortum* (as *Onchobothrium tortum*) were described by Linton (1916) from the Dry Tortuga Islands off Florida, and *A. tortum* was later also reported from Venezuela (Mayes & Brooks, 1981). A second species of *Acanthobothrium*, *A. colombianum* was described by Brooks & Mayes (1980) from the Caribbean Sea off Colombia. Furthermore, Mayes & Brooks (1981) reported *Disculiceps* sp. from the spotted eagle ray in Venezuela. Given that this genus normally parasitises carcharhiniform sharks, the latter specimens seem likely to represent *Tylocephalum*, a lecanicephalidean genus which, like *Disculiceps*, possesses a globose scolex, but which, unlike *Disculiceps*, commonly occurs in other myliobatiform rays.

***Aetobatus ocellatus*:** By far the greatest diversity of metazoan parasites of spotted eagle rays have come from those collected in localities throughout the Pacific and Indian Oceans. Records include gnathid isopods (*Gnathia nublina*) described from the gills from spotted eagle rays from Japan (Ota & Hirose, 2009). Four species of nematodes have been reported from the digestive system. These consist of the anisakid *Hysterothylacium aetobatum* described by Lakshmi (2005) from India, and 3 species of gnathostomid nematodes of the genus *Echinocephalus*, specifically *Echinocephalus sinensis* from Australia and New Caledonia (see Beveridge, 1987 and Moravec & Justine, 2006 respectively), and *Echinocephalus spinosissimus* and *E. uncinatus* both from India by Shafee & Natarajan (1976). A total of 7 species of monocotylid monogeneans have been



Figure 5. Tooth plates and oral papillae of *Aetobatus ocellatus* (specimen dissected, not retained, from Sabah, Malaysia): A. upper jaw; B. lower jaw.

reported from the gill and nasal tissue, and dorsal skin of spotted eagle rays. These include the 2 species treated above reported from *A. narinari* sensu stricto from the Atlantic Ocean, specifically *Decacotyle floridana* which has been reported from Hawaii by Yamaguti (1968) [as *Alloheterocotyla (Heterocotyle) aetobatis*] and from Heron Island, Australia by Chisholm & Whittington (1998), and *Thaumatocotyle pseudodasybatis*, reported from New Caledonia and French Polynesia by Marie & Justine (2005, 2006). The following 5 species of monocotylid monogeneans are known only from Indo-Pacific localities (see Marie & Justine, 2006): *Clemacotyle australis*, *Decacotyle elpora*, *Decacotyle octona*, *Dendromonocotyle torosa* and *Empruthotrema kearnii*.

However, tapeworms represent the most diverse elements of the metazoan fauna of Pacific and Indian Ocean spotted eagle rays. Records to date include a total of 28 species representing 4 orders of tapeworms; all species parasitize the digestive system of their hosts, with most occupying the spiral intestine of their hosts. The single diphyllidean, *Echinobothrium boisii*, was reported from Sri Lanka by Southwell (1911). Five species of tetraphyllideans including 3 species of *Acanthobothrium*, have also been reported. These are *A. aetiobatis* reported by Shipley (1900) from Lifu in the Loyalty Islands, *A. dysbios* reported by MacCallum (1921) from Jakarta (as Batavia), Java, Indonesia, and *A. arlenae* described by Campbell & Beveridge (2002) from northern Australia. The remaining 2 tetraphyllideans are the only described species in their respective genera: *Myzocephalus narinari* and *Myzophyllobothrium rubrum*. These were both reported by Shipley & Hornell (1906) from the Gulf of Mannar between India and Sri Lanka. Eight species of trypanorhynchs, each representing a different genus, have also been reported. These include 4 species of the family Eutetrarhynchidae: *Didymorhynchus southwelli* from Sri Lanka (see Beveridge & Campbell, 1988), *Dollfusiella aetobati* from northern Australia (see Beveridge, 1990), *Oncomegas australiensis* also from northern Australia (see Toth *et al.*, 1992) and *Parachristianella baverstocki* from India (see Palm, 2004). In addition, the tentaculid *Kotorella pronosoma* has been reported from Java by MacCallum (1917), the obothriid *Proemotobothrium linstowi* was reported by Palm (2004) from Singapore, the rhinopterid *Shirleyrhynchus aetobatidis* was originally described from Sri Lanka by Shipley & Hornell (1906), and the mixodigmatid *Trygonicola macroporus* was reported from spotted eagle rays from Malaysia by Beveridge & Campbell (1998).

In total, 14 species of lecanicephalidean tapeworms have been reported from spotted eagle rays in the Pacific and Indian oceans. Unfortunately, many of these are known only from their somewhat brief original descriptions which appeared early in the 20th C and are among the earliest reports of parasites from spotted eagle rays ever published. For example, Shipley (1900) described *Adelobothrium aetiobatidis* from Lifu in the

Loyalty Islands. Shortly thereafter, Shipley & Hornell (1905) described *Staurobothrium aetobatidis* and *Tylocephalum aetiobatidis* (originally as *Tetragonocephalum aetiobatidis*) and Shipley & Hornell (1906) described *Cephalobothrium aetobatidis*, *Hornellobothrium cobraformis* and *Kystocephalus translucens*, all 5 of the latter species from eagle rays collected from the Gulf of Mannar between Sri Lanka and India. A few years later, Southwell (1911) described *Calycobothrium typicum* (as *Cyclobothrium typicum*) from Sri Lanka, MacCallum (1917) described *Tenia narinari* presumably from Jakarta (as Batavia), Java, Indonesia and Southwell (1925) described *Tylocephalum yorkei* from India. More recently, new reports have come from Australia. For example, Butler (1987) reported *Hornellobothrium cobraformis* from Moreton Bay, Australia. However, Jensen (2005) considered the 2 specimens deposited by Butler, to represent 2 species distinct from *H. cobraformis* and gave them the letter designations A and B. Jensen (2005) also described *Hornellobothrium extensivum* from northern Australia. Newer reports have come from India, for example, Jadhav & Shinde (1987) described *Tylocephalum aurangabadensis* and most recently, Pramanik & Manna (2007) described *Tylocephalum girindrai*.

However, it is important to note that the unusually large number of species of tapeworms reported from spotted eagle rays in the Pacific and Indian Oceans is cause for some concern. As noted above, the identities of the hosts of these species are based solely on geographic distribution. It would seem prudent to pay particular attention to spotted eagle rays collected from Pacific and Indian Ocean localities for these results lead us to suspect that more than the single species “*Aetobatus ocellatus*” may occur in these regions. We note that, while their results remain to be confirmed, Jensen & Caira (1998) reported differences in the lecanicephalidean tapeworm faunas of eagle rays collected from Thailand and Australia. If it is ultimately determined to be the case that more than a single species of spotted eagle ray occurs in the Indo-Pacific, the host records described above would need further revision.

Host specificity: Comparison of the parasite records presented above for *Aetobatus laticeps*, *A. narinari* and *A. ocellatus* reveals little overlap among the metazoan parasite faunas of these host species. In fact, only 2 of the 49 taxa treated above have been reported from two of these species of eagle rays. While on the surface, this result might be interpreted to provide compelling support of the contention that these hosts do, in fact, represent distinct species, it is important to note that almost none of these parasite data were collected in a comparative framework with the explicit intent of exploring similarities and differences among the parasite faunas of these host species. In fact, to our knowledge only two studies have been undertaken with that objective in mind and the results of these studies are somewhat inconsistent. While Jensen & Caira (1998) reported differences among the faunas

of spotted eagle rays from the Eastern Pacific, Thailand and Australia, Marie & Justine (2006) found that 2 of the 7 monogenean species investigated parasitised eagle rays from both Atlantic and Pacific Ocean localities. This question would obviously benefit greatly from much more detailed and thorough investigation.

In addition, none of the studies cited above focused on documenting the full complement of metazoan parasites of spotted eagle rays from any of the target regions. Most focused on a particular component of the metazoan parasite fauna, for example monogeneans or nematodes or tapeworms, some concentrated only on subset of the latter faunas (e.g. tetraphyllidean tapeworms, lecanicephalidan tapeworms, trypanorhynch tapeworms, etc.). Investigation of the full complement of metazoan parasites of spotted eagle rays, from any locality, is also clearly in order. The metazoan parasite fauna of *Aetobatus laticeps* appears to be particularly poorly known.

DISCUSSION

As detailed in the introduction of this paper, the nomenclature of the *Aetobatus narinari* complex is very complicated, particularly in the Indo–West Pacific. This paper investigates the nomenclature of the Indo–West Pacific species in this complex and provides a redescription for this species, *Aetobatus ocellatus* (Kuhl, 1823). Since there is no type material for this species, a neotype (MZB 18225) was selected for *A. ocellatus*, which was collected during recent surveys of Indonesian fish landing sites from Java, the type locality for this species. *Aetobatus ocellatus*, which replaces *A. narinari* as the valid name for this species in the Indo–West Pacific, was compared with specimens of *Aetobatus narinari* from the Western Atlantic (see Figs 6, 7 and 8), including the locations given as the type localities for this species, i.e. Saint Barthelemy (West Indies) and Brazil.

Five significant groupings are evident in all three types of analyses (Fig. 6): (i) sequences from the Western North Atlantic form a distinct clade; (ii) sequences from specimens captured in the Gulf of California are distinct; (iii) sequences from the Western North Atlantic and the Eastern Pacific are more closely related to each other than they are to sequences from the Persian Gulf, Mozambique, South East Asia and Australia; (iv) the two specimens from Qatar form a distinct group; (v) sequences from specimens collected in the Philippines, Taiwan, Indonesia, Malaysia, Singapore and northern Australia are similar and do not exhibit compelling geographic substructure.

A major revision of the *Aetobatus narinari* complex is needed to determine its composition and the geographic ranges of its species. Results from molecular work on this complex by Richards *et al.* (2009), and those given in this study, indicate that the Eastern Pacific clade is distinct

from the Western Atlantic and Indo–West/Central Pacific clades. If this clade represents a species-level separation, *Aetobatus laticeps* (Gill, 1865) described from California on the Pacific US coast would become the valid name for this species. Material from the Eastern Pacific needs to be critically compared with other members of this complex from the other ocean basins. Material from the Eastern Atlantic is unusually sparse and thus little information is available for this region currently. Richards *et al.* (2009) proposed an Indo–West Pacific origin for the *A. narinari* species complex with a westerly dispersal into the Atlantic from around the southern tip of Africa and then into the Eastern Pacific. Since a barrier to dispersal has existed for a long period of time for tropical and subtropical species around the southern tip of Africa, it is very unlikely that the Eastern Atlantic species would be conspecific with *A. ocellatus* from the Indo–West Pacific. However, specimens from the Eastern Atlantic need to be critically compared to *A. narinari* from the Western Atlantic to determine whether they are conspecific. If further investigation shows that the Eastern Atlantic form is a separate species, *Aetobatus latirostris* (Duméril, 1861), described from the Gabon coast, would become the valid name for this species.

As mentioned previously, the nomenclature of *A. ocellatus* is quite complicated and a large number of synonyms (at least 29) exist for this species. Fowler (1941) summarised many of these synonyms, but two of these are not conspecific with this species. For example, Fowler (1941) lists *Dicerobatis eregoodoo* (not Cantor) from Saville-Kent (1893) as a synonym of *A. ocellatus*, but the image given in this book (Plate XLVIII) is clearly of a species of *Mobula*. Similarly, he lists *Myliobatis aquila* (not Linnaeus) as a synonym from the same source, but in Saville-Kent (1893) the name used is *Myliobatis australis*. Furthermore, the description by Kent of this species includes ‘Large blue-spotted sting-rays, *Myliobatis australis*, bask lazily in the intervening sandy patches’ indicating it is most likely referring to the Bluespotted Fantail Ray *Taeniura lymma*, which is particularly abundant in this area.

The comparison of *Aetobatus ocellatus* with *A. narinari* from the Western Atlantic revealed that they are very similar morphologically. There are several minor differences in morphometrics between the species, but the ranges for these overlapped: slightly longer tail in *A. ocellatus* than in *A. narinari* (mean total length 281 vs. 263% DW, mean anterior cloaca to tail tip 230.2 vs. 208.3% DW), and a longer stinging spine (mean length 9.7 vs. 8.9% DW). The major difference between these species is the background coloration of the dorsal surfaces. *Aetobatus ocellatus* has a dark greenish, greyish to almost blackish (sometimes with a pinkish tinge) background colour, whereas all Western Atlantic specimens of *A. narinari* have a much paler, medium yellowish brownish (fawn) background colour (Figs 7 and 8).

A



Figure 6. A. Neighbour-Joining tree based on K2P distance; B. Parsimony Bootstrap with 1000 replicates; and C. Maximum Likelihood tree using a GTR+I+Γmodel (General Time Reversible + Invariant sites + gamma distributed rates). Model parameter values were optimized recursively for the Likelihood analysis as the search progressed.

B

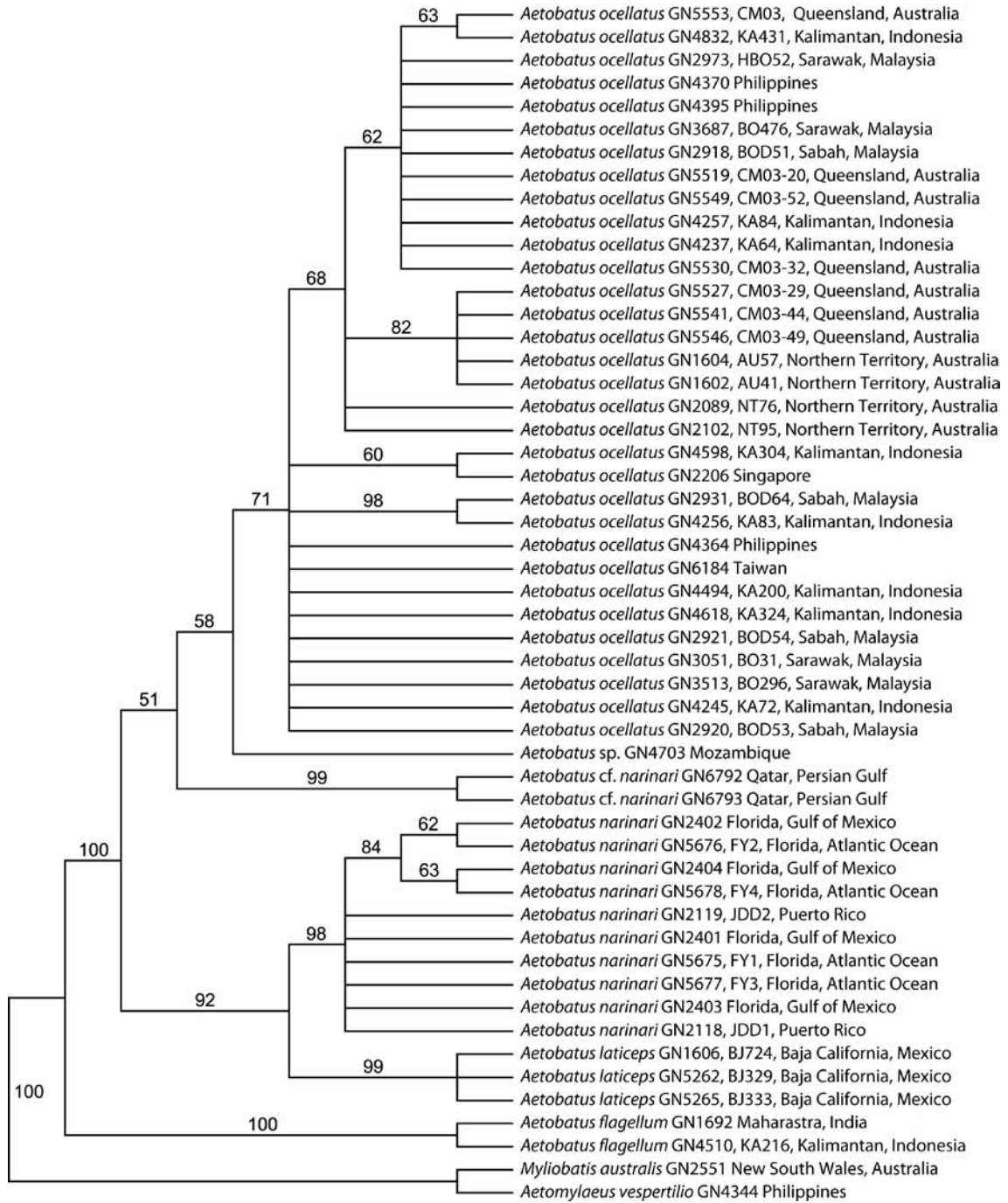


Figure 6. cont'd.

C



Figure 6. cont'd.

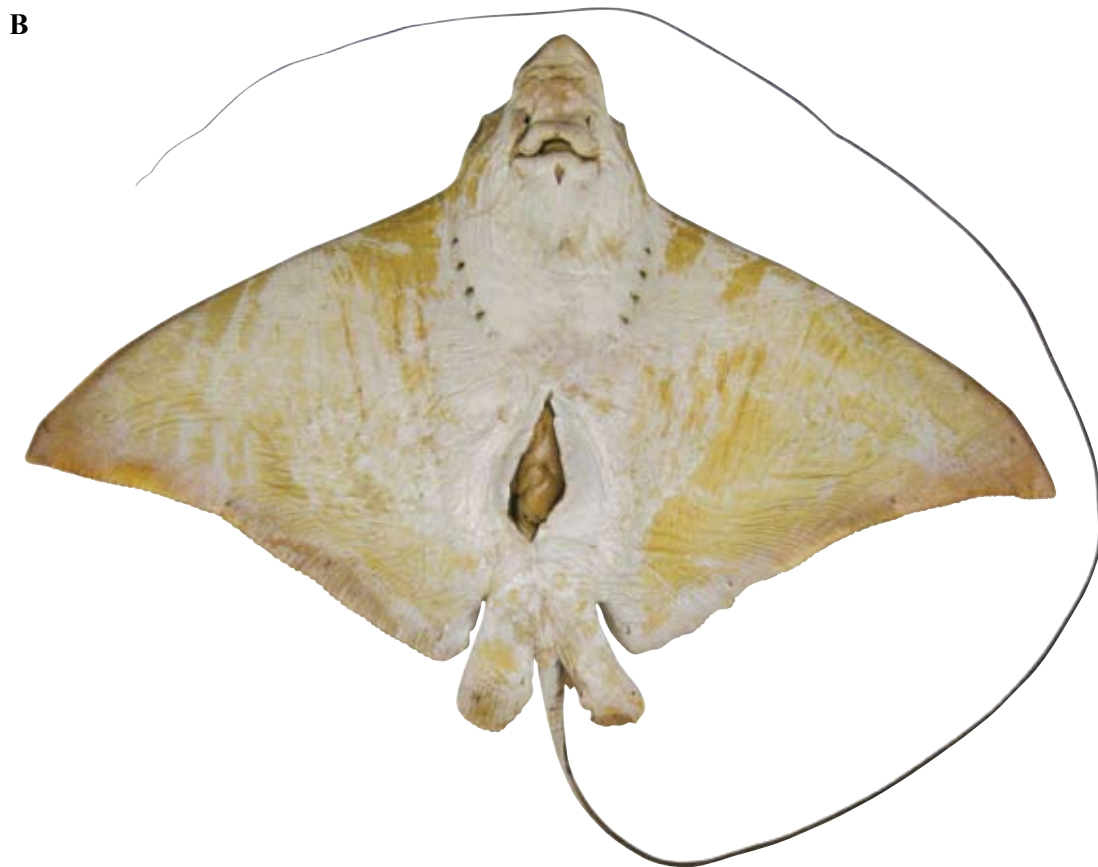
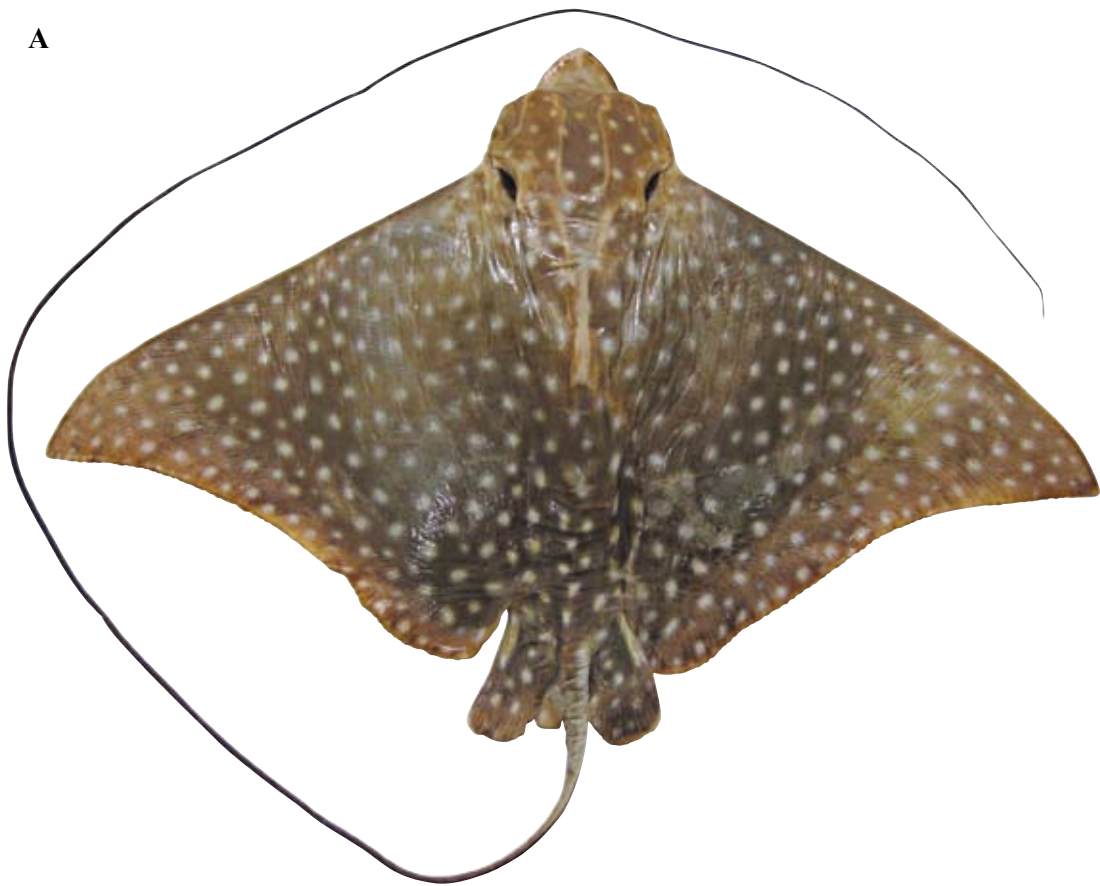


Figure 7. *Aetobatus narinari* (MNHN A7948, female 420 mm DW, preserved): A. dorsal view; B. ventral view.



Figure 8. *Aetobatus narinari* (MNHN A7948, female 420 mm DW, preserved): A. ventral head view; B. lateral head view.

Aetobatus narinari has been assessed as Near Threatened by the IUCN Red List of Threatened Animals (Kyne *et al.*, 2006), but this assessment considers it to be circumglobal; although it states that it is likely to belong to a species complex. Many of the threats listed in this assessment refer to areas in the Indo–West Pacific, thus *A. ocellatus* is probably more threatened than the other members of the complex. Based on the results of this paper and future revisions of the group, the conservation status of the species within this complex needs to be re-assessed.

Comparative material

Aetobatus narinari: 5 specimens. (Western Atlantic) BMNH 74.10.31.11, female 652 mm DW (1496 mm TL), Bermuda, North Atlantic; MNHN A7948, female 420 mm DW (1150 mm TL), Haiti, The Antilles, ca. 19° N, 73° W; MNHN A4053, juvenile male 600 mm DW

(1632 mm TL), eastern Brazil, ~10° N, ~30° W; MNHN A7940 (2 juvenile males), 445 mm DW (1233 mm DW), 547 mm DW (tail tip damaged), Saint Barthelemy, French West Indies, 17°50' N, 62°49' W.

ACKNOWLEDGEMENTS

Recently collected specimens examined for this study were collected during in-depth surveys of fish landing sites throughout Borneo (as part of two National Science Foundation (NSF) funded projects) and Indonesia (as part of two Australian Centre for International Agricultural Research (ACIAR) funded projects). We would like to acknowledge the following awards for support for the collection of some of the elasmobranchs and their tissue samples: NSF PEET Nos. DEB 9521943 and DEB 0118882, NSF BS&I Nos. DEB 0103640, DEB 0542941, and DEB 0542846, and NSF PB&I Nos. 0818696 and 0818823. The ACIAR projects were strongly supported by Barney Smith (ACIAR), Steve Blaber (CSIRO) and Ian Potter (Murdoch University). Thanks also go to Gordon Yearsley (CSIRO), Mabel Manjaji-Matsumoto (Universiti Malaysia Sabah), Annie Lim (Fisheries Biosecurity Centre Sarawak), Fahmi (Indonesian Institute of Sciences), Dharmadi (Research Centre for Capture Fisheries, Jakarta) and John Stevens (CSIRO) for their valuable work in the field. We would also like to acknowledge John Pogonoski (CSIRO) for capturing meristic data and providing editorial comments, Alastair Graham (CSIRO) for providing collection information, Daniel Gledhill (CSIRO) for technical assistance, and Louise Conboy (CSIRO) for image preparation. The senior author would like to thank Bill Eschmeyer and Ronald Fricke for the enlightening and entertaining discussion on the nomenclature of this genus. We would also like to thank the following museum staff for their assistance during this study: Martien van Oijen and Ronald de Ruiter at the Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden; Romain Causse, Bernard Séret, Guy Duhamel, Patrice Pruvost and Zora Gabsi at the Muséum national d’Histoire naturelle (MNHN) in Paris; Patrick Campbell at the British Museum of Natural History (BMNH) in London; Renny Kurnia Hadiaty and Ahmad Jauhar Arief at the Museum Zoologicum Bogoriense (MZB) in Jakarta; Albert Lo and George Jonis at the Sabah Museum Elasmobranch Collection (SMEC) in Kota Kinabalu.

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Suggested citation:

White, W.T., Last, P.R., Naylor, G.J.P., Jensen, K. & Cairns, J.N. (2010) Clarification of *Aetobatus ocellatus* (Kuhl, 1823) as a valid species, and a comparison with *Aetobatus narinari* (Euphrasen, 1790) (Rajiformes: Myliobatidae), pp. 141–164. In: P.R. Last, W.T. White, J.J. Pogonoski (eds) Descriptions of New Sharks and Rays from Borneo. *CSIRO Marine and Atmospheric Research Paper 032*, 165 pp.