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Species delineation and global population structure of Critically Endangered sawfishes (Pristidae)

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Sawfishes are among the most endangered of all elasmobranch species, a factor fostering considerable worldwide interest in the conservation of these animals. However, conservation efforts have been hampered by the confusing taxonomy of the group and the poor state of knowledge about the family's geographical population structure. Based on historical taxonomy, external morphology, and mitochondrial DNA sequences (*NADH-2*), we show here that, globally, the sawfish comprise five species in two genera: *Pristis pristis* (circumtropical), *Pristis clavata* (east Indo-West Pacific), *Pristis pectinata* (Atlantic), *Pristis zijsron* (Indo-West Pacific), and *Anoxypristis cuspidata* (Indo-West Pacific, except for East Africa and the Red Sea). This improved understanding will have implications for the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), International Union for Conservation of Nature (IUCN) Red List assessments, and endangered species laws and regulations in several countries. Furthermore, based on both or either of *NADH-2* and the number of rostral teeth per side, we show that populations of *P. pristis*, *P. pectinata*, *P. zijsron*, and *A. cuspidata* exhibit significant geographic structuring across their respective ranges, meaning that regional-level conservation will be required. Finally, the *NADH-2* gene may serve as a marker for the identification of rostra and fins involved in illegal trade.

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ADDITIONAL KEYWORDS: Chondrichthyes – IUCN Red List – old DNA – *Pristis pristis* – taxonomic confusion.

INTRODUCTION

It is now widely accepted that many sharks and rays are becoming endangered primarily as a result of fishing pressure (from the shark-fin industry and as bycatch), and secondarily as a result of habitat destruction (Dulvy *et al.*, 2008). One of the most readily identified and charismatic of all elasmobranch groups that has become endangered is the sawfish (family Pristidae) (Simpfendorfer, 2000). Sawfishes are emblematic both of the uniqueness of elasmo-

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branchs as a lineage and of endangered animals in general. Sawfishes first appear as fossils during the Eocene, 56 million years ago (Cappetta, 1987; Kriwet, 2004). They are shark-like batoids, characterized by a distinctive long snout with rostral teeth on each side, and can attain gigantic sizes, up to at least 7 m in length. Sawfishes have been listed as endangered since 1996, and Critically Endangered since 2006 by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species, and are controlled in international trade by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), Appendices I (six species) and II (one species).

Current conservation actions and management activities for sawfishes reflect the fact that there are currently seven valid species recognized worldwide (Compagno, 1999, 2005). These are *Anoxypristis cuspidata* (Latham, 1794) and two groups of species within *Pristis*: the *Pristis pristis* group (commonly referred to as the largetooth group), comprising *Pristis microdon* Latham 1794, *Pristis perotteti* Müller & Henle, 1841, and *Pristis pristis* (Linnaeus, 1758); and the *Pristis pectinata* group (commonly referred to as the smalltooth group), comprising *Pristis clavata* Garman, 1906, *Pristis pectinata* Latham, 1794, and *Pristis zijsron* Bleeker, 1851 (Compagno & Cook, 1995; Compagno, 1999, 2005). However, the taxonomy, delineation, and identification of these species have proven problematic for those working in the field, in conservation, and in management (Oijen, Faria & McDavitt, 2007; Wiley *et al*., 2008; Wueringer, Squire & Collin, 2009).

This taxonomic uncertainty is the consequence of several factors, namely: (1) many original species descriptions were extremely abbreviated, in some cases based only on isolated anatomical parts, or used characters that were not diagnostic at the species level; (2) only two holotypes for valid species are currently available for examination; (3) reference material is not available for comparison in museum collections; (4) most museum material consists of dried rostra or young specimens that are easier to transport and store; and (5) the scarcity of these animals in their natural habitat, which makes it difficult to obtain fresh material. Latham (1794) was the first to attempt to identify and describe all the sawfishes of the world. Garman (1913) was the last to treat the Pristidae in its entirety, almost a hundred years ago.

The major questions regarding sawfish taxonomy concern the *P. pristis* group. For instance, in past years, *P. pristis* has been considered to be: (1) a West African/Mediterranean Critically Endangered species, as described in Compagno & Cook (1995) and Wueringer *et al*. (2009); (2) the senior synonym to Atlantic *P. perotteti*, as described in Hoese & Moore (1988) and Carvalho & McEachran (2003); or (3) the senior synonym to a circumtropical largetooth species, as described in McEachran & Fechhelm (1998) and Carvalho, Séret & Schelly (2007). In addition, no morphological attributes were found by prior researchers to distinguish *P. perotteti* (Atlantic or Atlantic–East Pacific) and *P. microdon* (Indo-West Pacific or Indo-Pacific), species that nonetheless have been considered valid (Compagno, 1999, 2005).

In addition to taxonomic uncertainty, data on the possible geographical structuring of sawfish populations are also lacking, because species variation has been examined solely in geographically constrained areas. Understanding if populations of any sawfish species are geographically structured is relevant for management, as it may indicate the scale of conservation efforts required (international, national, regional, etc.). Therefore, although three studies have recently explored genetic variation in northern Australia (Danastas, 2010; Phillips *et al*., 2011) and southern USA (Chapman *et al*., 2011), there remains a pressing need for a comprehensive understanding of species boundaries and population structure of sawfishes at the global level (Feldheim *et al*., 2010).

Given the urgent need for appropriate conservation measures to be deployed to save these animals from global extinction, we undertook a comprehensive survey of geographic variation in both morphology and mitochondrial DNA sequence using both fresh and museum material. Our specific goals were to (a) explore and delineate species boundaries and (b) identify population structure at broad scales where it exists.

MATERIAL AND METHODS

Morphological and DNA sequence variation was examined for all nominal extant species of sawfishes within the family Pristidae (Chondrichthyes), a group distributed, until very recently, across tropical and subtropical marine, estuarine, and freshwater regions of the world. Data were obtained from both field-collected animals and museum specimens. Sampling was conducted to ensure that representatives from all parts of the species' ranges were included where possible. A comprehensive literature survey was carried out, and we adopted the 'taxonomic concept' approach (Franz, Peet & Weakley, 2008) in order to explore the evolution of taxonomic perspectives on the *P. pristis* group.

As most local sawfish populations are considered to be already functionally or actually extinct (Robillard & Séret, 2006; Simpfendorfer, Wiley & Yeiser, 2010), it would be very difficult to obtain specimens in nature for examination. The morphological component of the study therefore relied primarily on specimens deposited in major museums. In total, 634 specimens were examined from the following ichthyological collections (institutional abbreviations follow those of Fricke & Eschmeyer, 2010): AMNH, ANSP, BMNH, FMNH, INPA, MCZ, MNHN, MNRJ, MRAC, RMNH, TCWC, UF, USNM, YPM, and ZMB. Additional material examined included 140 isolated rostra from private collections; x-rays or photographs of 34 specimens from public or private collections and a published source; and number of rostral teeth per side data for 63 specimens from public collections and research articles. Morphological characters and rostral tooth counts described for sawfish in Garman (1913) and Last & Stevens (1994) were examined for specimen identification. In addition, morphometric characters (horizontal distances) were also taken (Fig. 1) for species discrimination with canonical variate analysis (CVA) in JMP (SAS Institute). Finally, to investigate population distinction, each of the most widespread species (all but *P. clavata*) was tested for within-ocean basin differences in the number of rostral teeth per side with analyses of variance (ANOVA) in JMP.

Fresh tissue samples were obtained from: (1) fin clips of live *P. pectinata* during field research along the coast of Florida, USA (Wiley & Simpfendorfer, 2007); (2) fragments of largetooth sawfish rostra, bought at a fish market in northern Brazil (Belém, PA); (3) liver, muscle, and blood samples of specimens from Australia, the Bahamas, South Africa, and the USA, provided by colleagues. These samples were augmented with dry tissue samples taken from museum specimens. In total, genetic information based on sequence variation at the mitochondrial DNA gene *NADH-2* was examined for 213 specimens in this study. Quantitative analyses of the raw data set were precluded due to gaps. Thus, a 480 bp ($N = 130$) was built on the basis of maximizing geographical coverage and avoiding gaps (Table 1). This data set was subjected to both parsimony and distance (uncorrected p) analyses using PAUP* 4.02b (Swofford, 2000) to explore phylogenetic relationships and species delineation. The data set was further subjected to analysis of molecular variance (AMOVA; Excoffier, Smouse & Quattro, 1992) to assess *P. pristis* group population structure between Atlantic, Indo-West Pacific, and East Pacific, using ARLEQUIN 2.0 (Schneider, Roessli & Excoffier, 2000). (This analysis generates Φ_{st} values on a scale that ranges from 0 to 1, in which $\Phi_{st} = 0$ means frequent interbreeding and $\Phi_{st} = 1$ means complete difference between haplotypes.) A smaller data set composed of 144 bp of 13 *A. cuspidata* specimens was also subjected to AMOVA to assess population structure between the Indian Ocean and the West Pacific. A fully aligned *NADH-2* data set including all 213 sequences (containing missing data) was qualitatively examined for haplotype polymorphism related to its geographical origin. This examination was the only source of DNA information regarding the geographical structuring of *P. pectinata* and *P. zijsron*, as neither the 480- nor 144-bp data sets assembled for the quantitative analyses were variable for these species. Finally, low sample size and lack of variation precluded any geographical comparison of *P. clavata* specimens.

RESULTS

Species delineation

No morphological distinction was found among museum specimens of the *Pristis pristis* group (*P. pristis*, *P. perotteti*, and *P. microdon*) sampled globally. All specimens examined had a comparatively broad-based tapering rostrum, origin of first dorsal fin anterior to origin of pelvic fins, and presence of a small but distinct caudal fin lower lobe. A quantitative CVA analysis of the morphometric data failed to show any geographic differentiation among specimens from the Atlantic, Indo-West Pacific, and Eastern Pacific (Fig. 2). The genetic distances among specimens from the different ocean basins were also low relative to the values obtained for the other species in the genus (see below). Genetic distances (uncorrected p) between any two individuals for each ocean basin comparison were: (1) Atlantic and Indo-West Pacific, 0.015 to 0.021; (2) Atlantic and East Pacific, 0.019 to 0.023; and (3) Indo-West Pacific and Eastern Pacific, 0.019 to 0.023. However, phylogenetic analyses of the 480-bp fragment from the *NADH-2* gene ($N = 63$ largetooth sawfish specimens) showed considerable geographical structure. Maximum parsimony analyses assigned the largetooth sawfish into three lineages, each composed of haplotypes from Atlantic, Indo-West Pacific, and East Pacific, with bootstrap values of 87, 94, and 100, respectively. Moreover, a within-ocean basin geographical structure was also observed: West–East Atlantic and Indian Ocean–Australia (Fig. 3).

In the *P. pectinata* group, all three species were morphologically distinct from each other. *Pristis clavata* was distinguished from its congener *P. pectinata* by differences in the placement of the origin of the first dorsal fin, an often incomplete groove at the posterior margin of the rostral teeth, and relative length of the rostrum. The distinction between these two species was corroborated by CVA analyses, which revealed no overlap between *P. clavata* and *P. pectinata* projections (Fig. 2). The morphological distinction between these species was also reflected in their overall genetic differentiation, which was approximately five to ten times greater than that observed among largetooth sawfish from the different ocean basins. Genetic distances (uncorrected p) between *P. clavata* and *P. pectinata* ranged from 0.115 to 0.117. Phylogenetic analyses of the 480-bp fragment of the

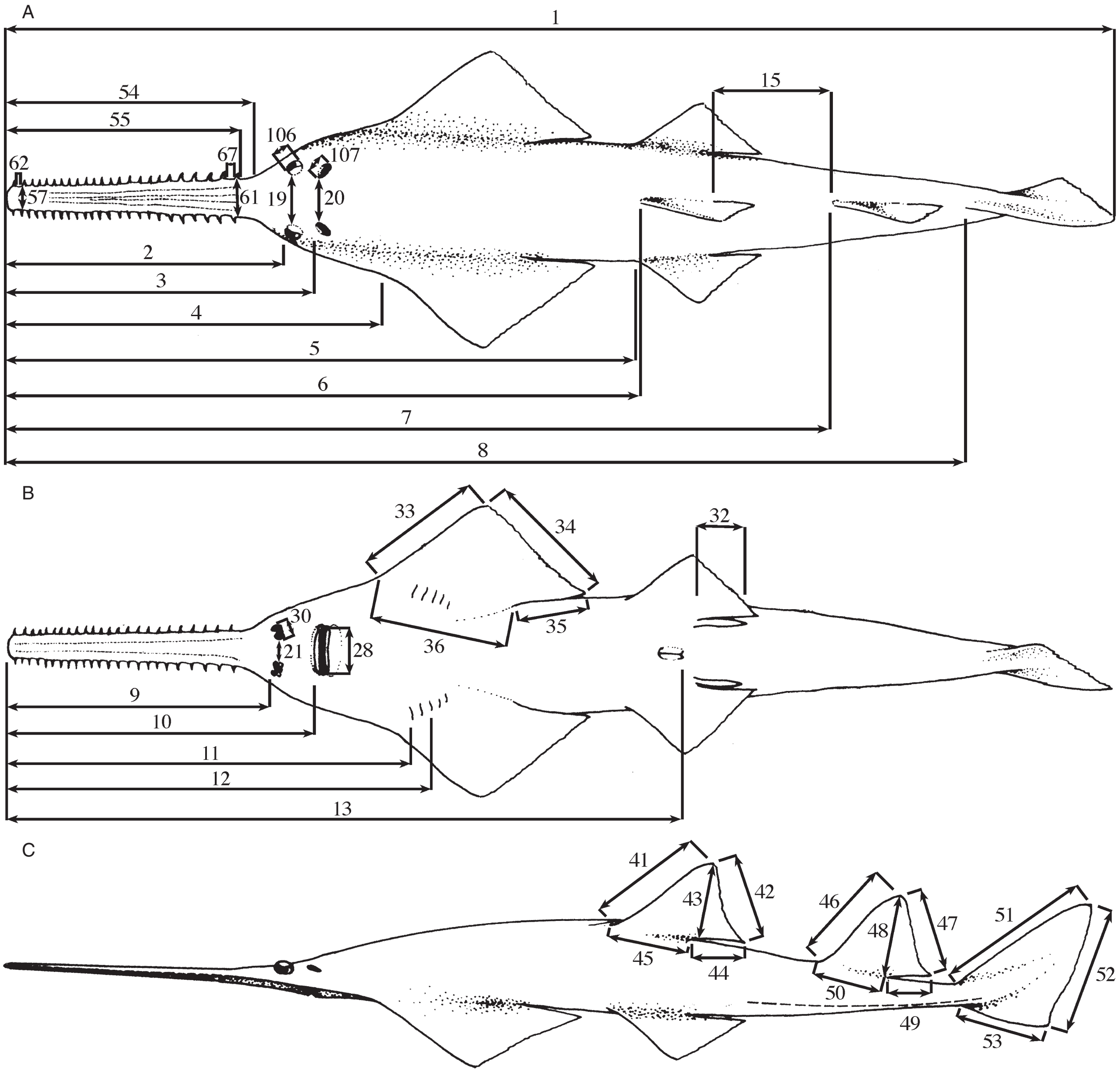

Figure 1. Measurements adopted for Pristidae. A, dorsal view: (1) total length; distance from rostrum tip to (2) eye, (3) spiracle, (4) pectoral fin insertion, (5) pelvic fin insertion, (6) first dorsal fin origin, (7) second dorsal fin origin, and (8) upper caudal fin origin; distance between bases, (15) interdorsal; distance between inner corners, (19) eyes, (20) spiracles, (106) eye length, and (107) spiracle length; rostrum measurements, (54) total length, (55) standard length, (57) rostrum width anterior, (61) rostrum width posterior, (62) interlateral rostral tooth anterior, and (67) interlateral rostral tooth posterior. B, ventral view, distance from rostrum tip to: (9) outer nostril, (10) mouth, (11) first gill, (12) third gill, and (13) posterior cloaca; distance between inner corners, (21) nostrils; pectoral fin lengths, (33) anterior margin, (34) posterior margin, (35) inner margin, and (36) base; other measurements, (28) mouth width, (30) nostril length, (32) clasper outer length. C, lateral view, first dorsal fin lengths: (41) anterior margin, (42) posterior margin, (43) height, (44) inner margin, and (45) base; second dorsal fin lengths: (46) anterior margin, (47) posterior margin, (48) height, (49) inner margin, and (50) base; caudal fin lengths, (51) upper lobe, (52) posterior margin, and (53) lower lobe. Drawings from Food and Agricultural Organization of the United Nations (FAO) Species Catalogues.

Table 1. Sawfish specimens successfully sequenced for the mitochondrial gene *NADH-2*

Species ocean basin	Locality	No. of specimens (sequence sizes: 144–1047 bp)	No. of specimens included in quantitative analyses (sequence size: 480 bp)	Sample source
Pristis pristis group				
East Pacific	Panama	1	1	Museum
West Atlantic	Suriname	1		Museum
	Brazil	77	55	Fish market
East Atlantic	Liberia	1		Museum
	Congo	4		Museum
	Angola	2		Museum
	unknown E. Atlantic locality	3	1	Museum
Indian Ocean	South Africa	2		Museum
	Tanzania	2		Museum
	Mozambique, Zambezi River	1	1	Museum
	Madagascar	1	1	Museum
	unknown east Indian Oc. locality	1		Museum
West Pacific	Vietnam	1		Museum
	Indonesia, New Guinea, Lake Jamur	1	1	Museum
	Indonesia, New Guinea, Lake Sentani	4		Museum
	Papua New Guinea, Bismarck Arch.	1		Museum
	Australia	5	3	Field, Aquarium
Pristis clavata				
West Pacific	Malaysia, Borneo	1		Museum
	Australia	4	3	Field
Pristis pectinata				
West Atlantic	Bahamas	3	3	Field
	USA, Florida	55	46	Field, Museum
	Mexico	1		Museum
	Suriname	1		Museum
	Guyana	2		Museum
East Atlantic	Senegal	1		Museum
	Congo	1		Museum
unknown region	unknown locality	2		Museum
Pristis zijsron				
Indian Ocean	South Africa	1	1	Aquarium
	Red Sea	1		Museum
	Persian Gulf	3		Museum
	Iraq	2		Museum
West Pacific	Thailand, Gulf of Thailand	1		Museum
	Indonesia	1		Museum
	Australia	9	7	Field, Museum
	New Zealand, Tasman Sea	1		Museum
unkown region	unknown locality	1		Museum
Anoxypristis cuspidata				
Indian Ocean	Persian Gulf	1		Museum
	India	1		Museum
West Pacific	Indonesia	1		Museum
	Indonesia, southern New Guinea	3		Museum
	Australia	7	7	Field
unkown region	unknown locality	1		Museum
	Total	213	130	

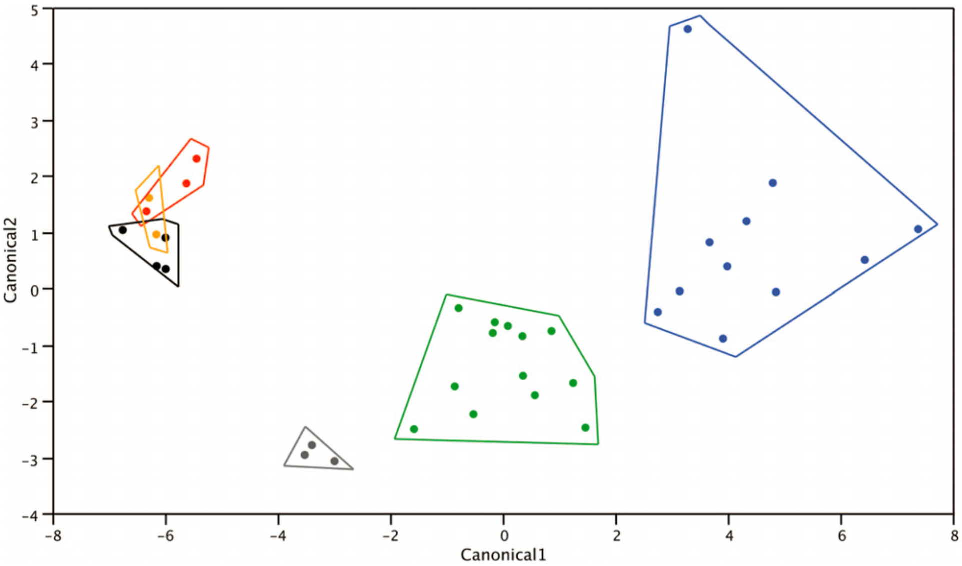

Figure 2. Plot of *Pristis* spp. individuals projected onto the first two canonical factors for visualization of the ordering of the taxa in the multivariate space based on body morphometrics and number of rostral teeth. *Pristis pristis* group dots are coloured by ocean basin: Atlantic in red, Indo-West Pacific in orange, and Eastern Pacific in black; other *Pristis* species are coloured as follows: *Pristis zijsron* in blue, *Pristis pectinata* in green, and *Pristis clavata* in grey.

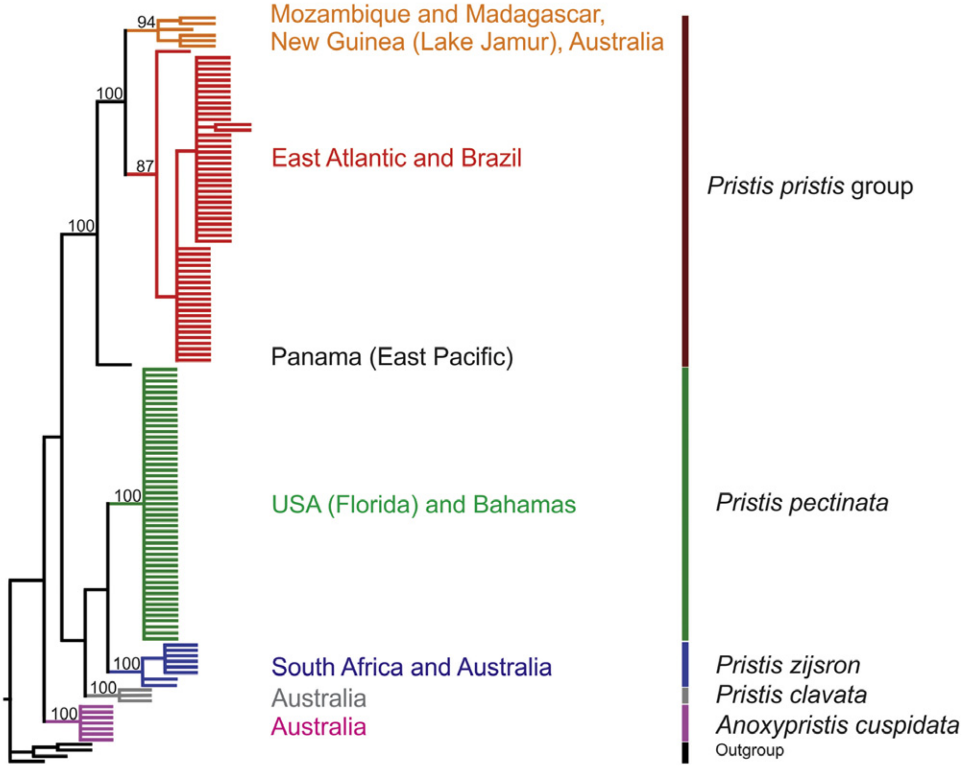

Figure 3. Majority-rule consensus tree of 10 000 bootstrap pseudoreplicates constructed using maximum parsimony based on 480-bp sequences of the mitochondrial DNA gene *NADH-2* of sawfish specimens sampled along the geographical range of the group. Clades with high bootstrap support are coloured with geographical origin noted. Outgroup species included in the analyses were *Aetobatus narinari*, *Raja rhina*, *Dasyatis annotata*, and *Rhizoprionodon porosus* (available from G. Naylor's database).

Table 2. Geographic distribution of *NADH-2* haplotypes from sawfishes that were quantitatively and qualitatively analysed for geographical population structure

	Haplotypes per ocean basin				
Species	West Atlantic	East Atlantic	Indian Ocean	West Pacific	East Pacific
Anoxypristis cuspidata			V	Y, X, W	
Pristis pristis group	H, I, J, K, L, M, N, O, P, Q, Z, α	F, G	R	S, T, U	β
Pristis pectinata	C, D, E	C–E?			
Pristis zijsron			A	A, B	

The haplotype missing data on a segregating locus is identified by the closest known haplotypes, followed by a question mark.

NADH-2 gene, based on three *P. clavata* and 49 *P. pectinata* individuals, corroborated that they form distinct lineages (Fig. 3).

Pristis zijsron could be distinguished from *P. clavata* and *P. pectinata* by several morphological characters. These involved inter-rostral teeth space, length of rostral teeth, rostral tooth counts, squamation pattern, and shape of caudal fin. The distinction of *P. zijsron* from other congeneric species was also shown by CVA analyses that revealed no overlap of *P. zijsron* projections with any other species (Fig. 2). Genetic distances (uncorrected p) to smalltooth congeners were: 0.107 to 0.109, for *P. zijsron* and *P. clavata*; and 0.094 to 0.098, for *P. zijsron* and *P. pectinata*. Values were relatively similar to those between *P. clavata* and *P. pectinata*, also reflecting its morphological differentiation from them. From a phylogenetic perspective, quantitative analyses of the 480-bp *NADH-2* fragment included eight *P. zijsron* individuals. Only two haplotypes were identified. Maximum parsimony analyses assigned these into a single lineage, with maximum bootstrap support (Fig. 3).

Finally, no morphological distinction was found among *A. cuspidata* museum specimens sampled throughout the northern Indian Ocean and the West Pacific. All specimens examined lacked rostral teeth on the basal quarter of the saw, and had other typical characteristics of the species regarding rostral tooth shape, distribution of dermal denticles, nostril shape, relative position of fins, and shape of caudal fin. Phylogenetic analyses of the 480-bp fragment of the *NADH-2* gene based on seven *A. cuspidata* individuals corroborated the hypothesis that this species forms one single lineage (Fig. 3).

POPULATION STRUCTURE

For *A. cuspidata*, population structure analyses based on the 144-bp *NADH-2* sequence data revealed a very low level of gene flow between northern Indian Ocean ($N = 2$) and West Pacific ($N = 11$): $\Phi_{st} = 0.84012$ (AMOVA, $P = 0.011$). In a qualitative analysis, when all available data were pooled across 14 specimens, with fragments varying in length between 144 and 1047 bp, four haplotypes were identified (Table 2). These were distributed as follows: one northern Indian Ocean haplotype ($N = 2$ specimens); one Indonesian haplotype ($N = 1$ specimen); two New Guinean–Australian haplotypes ($N = 10$ specimens); and one specimen that lacked locality information, but had a northern Indian Ocean haplotype. A distinction between Indian Ocean and Western Pacific specimens was also found in the number of rostral teeth per side. Indian Ocean specimens (IO; $N = 21$ counts) mostly had a higher number of rostral teeth per side than the Western Pacific specimens (WP; $N = 28$ counts): IO = 25.6 and WP = 21.2, on average (ANOVA, $P < 0.0001$; Table 3).

Analyses based on the 480-bp *NADH-2* sequence revealed restricted gene flow among *P. pristis* group populations: (1) Atlantic ($N = 56$) and Indo-West Pacific ($N = 6$), $\Phi_{st} = 0.909$ (AMOVA, $P < 0.0001$); (2) Atlantic and Eastern Pacific ($N = 1$), $\Phi st = 0.916$ (AMOVA, $P = 0.015$); and (3) Indo-West Pacific and Eastern Pacific, $\Phi st = 0.894$ (AMOVA, $P < 0.0001$). A qualitative analysis of haplotypes corroborates these findings. When all available data were pooled across 108 specimens, with fragments varying in length between 144 and 1047 bp (full gene), a total of 19 haplotypes were identified. These were distributed geographically as follows: (1) one East Pacific haplotype ($N = 1$ specimen); (2) 12 Western Atlantic haplotypes ($N = 78$ specimens) and two Eastern Atlantic haplotypes ($N = 10$ specimens); (3) one Indian Ocean haplotype ($N = 7$ specimens), one Vietnamese–New Guinean haplotype ($N = 7$ specimens), and two Australian haplotypes ($N = 5$ specimens) (Table 2). This finer-scale substructuring of *P. pristis* group populations was only partly corroborated by the regional variation in the number of rostral teeth. This is

Table 3. Within-ocean basin frequency distribution of the number of rostral teeth per side in the four most widespread sawfish species

Species ocean basin	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Anoxypristis cuspidata																					
Indian Ocean									2	3	5	11	7	8	5	1					
West Pacific				4	5	4	10	12	5	4	5	3	1			1	1				
Pristis pristis group																					
West Atlantic	1		4	23	46	37	56	27	1	1											
East Atlantic	1	2	8	22	13	4															
Indian Ocean			1	3	5	10	8	4													
West Pacific	1	4	6	8	17	35	30	18	10	5											
East Pacific		1	1	3	23	19	15	14	6	1											
Pristis pectinata																					
West Atlantic							1	1		2	3	11	16	10	14	3	1				
East Atlantic							2	4	3	16	14	20	1	1							
Pristis zijsron																					
Indian Ocean														1	4	5	6	6	4	1	1
West Pacific											4	7	5	7	5	2	4		2		

because Western and Eastern Atlantic specimens differed significantly, but Indian Ocean and Western Pacific specimens did not. The Western Atlantic specimens (WA; $N = 98$ counts) had a higher number of rostral teeth per side than the Eastern Atlantic specimens (EA; $N = 25$ counts): WA = 19.0 and EA = 17.1, on average (ANOVA, $P < 0.0001$) (Table 3).

For *P. pectinata*, a qualitative examination of *NADH-2* sequences revealed no geographical structuring of the haplotypes. The only two Eastern Atlantic specimens sequenced produced one haplotype that was also found in the Western Atlantic ($N = 62$ specimens; three haplotypes in total were found) (Table 2). On the other hand, population structure between these two subregions was suggested by the variation of rostral teeth number per side. Western Atlantic specimens ($N = 31$ counts) had a higher number of rostral teeth per side than Eastern Atlantic specimens ($N = 31$ counts): WA = 26.3 and EA = 23.7, on average (ANOVA, $P < 0.0001$) (Table 3).

No geographical structuring of haplotypes was found in *P. zijsron* after a qualitative examination of sequences. This is because the only South African specimen sequenced had the same haplotype as another sampled in Australia (Table 2). (The other seven Australian specimens all had a second haplotype.) However, the geographical variation of the number of rostral teeth per side suggested population structure between these subregions. Indian Ocean specimens ($N = 14$ counts) mostly had a higher number of rostral teeth per side than Western Pacific specimens ($N = 18$ counts): IO = 30.2 and WP = 27.0, on average (ANOVA, $P < 0.0001$) (Table 3).

DISCUSSION

SPECIES DELINEATION

The results of this study demonstrate that the currently accepted taxonomy of the sawfishes (family Pristidae) requires modification: our analysis recognizes a total of five species in two genera. This change is required because the *P. pristis* group that has previously been recognized as containing up to three species, in fact appears to be one species. No changes are required for other species, which were demonstrated to be clearly defined and valid taxa.

A classic approach to morphology and genetics failed to provide evidence of species-level differentiation within the *P. pristis* group. No morphological characters were found to delimit specimens globally into separate species groups, and specimens from different ocean basins were not found to be distinct by morphometrics. In practice, taxonomists define a group of organisms as a distinct species only if the group consistently differs from other groups (Ridley, 2004). If traditional taxonomic practice is followed, the *P. pristis* group should not be further subdivided. The genetic distance data indicate that ocean basin variation among *P. pristis* group specimens is considerably smaller than the variation among *P. pectinata* group congeners. This also supports the idea that the *P. pristis* group is a single species as, in practice, two populations are considered as belonging to different species if they are as genetically differentiated as two well-recognized species of a related group (Frankham, Ballou & Briscoe, 2004). Therefore, both types of data support the single species hypothesis.

While apparently in contrast with the single species hypothesis, the phylogenetic analysis indicating three ocean basin clades (Atlantic, Indo-West Pacific, and East Pacific, consistent with *P. perotteti*/*P. pristis*, *P. microdon*, and *Pristis zephyreus* Jordan, 1895, respectively) does not suggest that the *P. pristis* group is composed of three isolated units or species. This is because the mitochondrial DNA is inherited maternally, without recombination (Avise, 2004), reflecting only the movement of females (Heist, 2004). Therefore, if *P. pristis* exhibits female philopatry, females return to their natal estuary for reproduction, and gene flow could be male mediated (which would not be detected in the present study because of the nature of the molecular marker used). It is not known if female philopatry occurs in any sawfish (Phillips *et al*., 2011). However, this is a plausible possibility, as it has been demonstrated to occur in several sharks (Heupel & Hueter, 2001; Pardini *et al*., 2001; Pratt & Carrier, 2001; Feldheim, Gruber & Ashley, 2002, 2004; Hueter *et al*., 2004; Keeney *et al*., 2005; Duncan *et al*., 2006; DiBattista *et al*., 2008; Schultz *et al*., 2008; Karl *et al*., 2011b; Daly-Engel *et al*., 2012b), as well as in other marine vertebrates (Allendorf & Waples, 1996; Bowen & Karl, 2007; Dankel, Skagen & Ulltang, 2008). In addition, treating the *P. pristis* group as a single species is in accordance with studies on other large marine vertebrates with a nearly global distribution that exhibit a similar pattern of ocean basin-structured mitochondrial DNA lineages, such as the green turtle *Chelonia mydas* (Bowen *et al*., 1992), bigeye tuna *Thunnus obesus* (Bremer *et al*., 1998), scalloped hammerhead *Sphyrna lewini* (Duncan *et al*., 2006), blacktip shark *Carcharhinus limbatus* (Keeney & Heist, 2006), and great barracuda *Sphyraena barracuda* (Daly-Engel, Randall & Bowen, 2012a).

Although not unanimously accepted, at least over the last six decades, the concept of a single circumtropical sawfish species with the features here defined for the *P. pristis* group (robust rostrum, origin of first dorsal fin anterior to origin of pelvic fins, and presence of a caudal-fin lower lobe) has already been proposed, under different species names, by other authors over a long period of time. These include, at least, Günther (1870), Garman (1913), Fowler (1936), Poll (1951), Dingerkus (1983), Daget (1984), Séret & McEachran (1986), McEachran & Fechhelm (1998), and Carvalho *et al*. (2007).

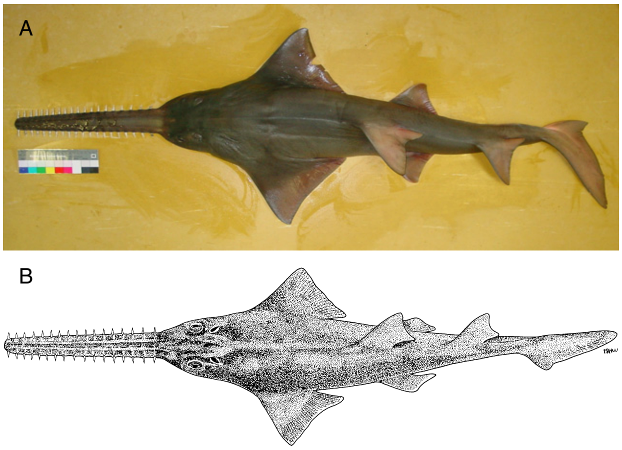

Figure 4. The largetooth sawfish *Pristis pristis*. A, dorsal view of specimen from north-western Australia (photo: W. White); B, line drawing from FAO Species Catalogues.

Several names have been applied to the *P. pristis* group species (most commonly *P. pristis*, *P. microdon*, and *P. perotteti*); we here propose the taxon be identified as *P. pristis* (Fig. 4, see below for its redescription). This is in accordance with Rule 23.1 (Statement of the Principle of Priority) of the International Code of Zoological Nomenclature (ICZN, 1999), which states that 'the valid name of a taxon is the oldest available name applied to it'. In addition, according to Rule 23.9 (Reversal of precedence; ICZN, 1999), no younger name may take precedence over *P. pristis* based on an argument of prevailing usage, because *P. pristis* has been used as a valid name after 1899.

Pristis pristis, as described in Linnaeus (1758), is here interpreted as a composite, and the name has had different meanings over the past century. In relation to other studies, our concept of *P. pristis*: (1) is congruent with that described by Dingerkus (1983), McEachran & Fechhelm (1998), and Carvalho *et al*. (2007); (2) is more inclusive than that described by Robins & Ray (1986) and Hoese & Moore (1988), who considered *P. pristis* as a senior synonym to *P. perotteti*, and is also more inclusive than that of McEachran & Carvalho (2002) and Carvalho & McEachran (2003), who considered *P. pristis* as a senior synonym to *P. perotteti* and *P. zephyreus*; and (3) excludes that of Garman (1913), Miranda-Ribeiro (1923), Fowler (1936), Irvine & Brown (1947), Bigelow & Schroeder (1953), Kreft & Stehmann (1973), Stehmann & Bürkel (1984), Stehmann (1990), Last & Stevens (1994, 2009), Compagno & Cook (1995), Compagno (1999, 2005), and Wueringer *et al*. (2009), in which *P. pristis* referred to a West African/Portuguese/Mediterranean species, bearing the following features – robust rostrum, origin of the first dorsal fin above the origin of pelvic fins, and absence of a caudal fin lower lobe (see *P. pristis* redescription for discussion on possible historical causes for this concept of *P. pristis*).

The other four currently recognized sawfish species are valid. Both morphology and genetics support the current specific status of *P. clavata*, *P. pectinata*, *P. zijsron*, and *A. cuspidata*. We only propose modifications on what is currently known about the distribution range of these species based on data associated with the museum specimens examined. The full ranges for each species are: *P. clavata* has an Eastern Indian-West Pacific range; *P. pectinata* has an Atlantic range; *P. zijsron* has a wide distribution throughout the Indo-West Pacific; and *A. cuspidata* is distributed in the Indo-West Pacific, except for East Africa and the Red Sea (see Material examined). Useful references for descriptions of morphology and diagnostic characters for each of these species are Bigelow & Schroeder (1953), Last & Stevens (1994, 2009), McEachran & Fechhelm (1998), and Compagno & Last (1999), among others. The number of rostral teeth per side is mostly non-diagnostic, but as this is such a conspicuous character in the group, the minimum and maximum number of rostral teeth per side is also provided for each of these species as follows: 18–27 for *P. clavata*; 20–30 for *P. pectinata*; 23–37 for *P. zijsron*; and 16–33 for *A. cuspidata*.

An artificial key to all sawfish species (Pristidae) is provided below. This key describes diagnostic external morphology characters.

1a. Rostral teeth absent from basal quarter of saw; rostral teeth blade-like and barbed on posterior edge with sharp margins in young; rostral teeth falciform with sharp margins in adults; dermal denticles present on rostrum, head, and anterior margin of fins, but only scattered along other parts of body; nostrils relatively narrow, with small nasal flaps, with groove connecting the incurrent aperture to the side of the head; origin of first dorsal fin posterior to the origin of the pelvic fins (above the end of the base of the pelvic fin); pectoral fin bases narrow; caudal fin lunate with distinctive subterminal projection on upper lobe, and lower lobe well developed.......... *Anoxypristis cuspidata*

1b. Rostral teeth present on basal quarter of the saw (along all rostrum); rostral teeth awl-like, with rounded anterior and flattened posterior margins, the posterior margin occasionally grooved in the young; rostral teeth with flattened and grooved posterior margin in adults; dermal denticles present on entire body; nostrils relatively broad, with large nasal flaps, without groove connecting the incurrent aperture of the nares to the side of the head; origin of first dorsal fin varies from anterior, above, to posterior to the origin of pectoral fins (up to above half of the base of the pelvic fin); pectoral fin bases broad; caudal fin posterior margin straight or slightly convex, with upper lobe without distinctive subterminal projection and lower lobe absent or small, but prominent... 2 *Pristis*

2a. First dorsal fin origin anterior to pelvic fin origins.......... *Pristis pristis*

2b. First dorsal fin origin above or posterior to pelvic fin origin.......... 3

3a. Rostrum length 22.9–33.6% of total length; rostral teeth on the anterior region of the rostrum noticeably closer in comparison with those at the posterior region (space between the two anteriormost rostral teeth only 9.6–47.5% of the space between the two posteriormost rostral teeth); rostral teeth at the posterior region of the rostrum widely spaced, 25.8–90.9% of the width of the base of the rostrum; squamation pattern not uniform in juveniles, with larger dermal denticles along the midline on dorsal region; posterior margin of caudal fin convex in juveniles and straight in adults, origin of first dorsal fin posterior to pelvic fin insertion, about half way across the base of pelvic fin.......... *Pristis zijsron*

3b. Rostrum length 20.4–30.3% of total length; rostral teeth on the anterior region of the rostrum not noticeably closer in comparison with those at the posterior region (space between the two anteriormost rostral teeth 18.9–65.5% of the space between the two posteriormost rostral teeth); rostral teeth at the posterior region of the rostrum more narrowly spaced, reaching 15.3–53.7% of the width of the base of the rostrum; squamation pattern uniform in juveniles; posterior margin of caudal fin straight in juveniles and adults, origin of first dorsal fin above or slightly posterior to the origin of pelvic fins.......... 4

4a. Rostrum length 20.9–30.3% of total length; space between the two anteriormost rostral teeth 18.9–63.3% of the space between the two posteriormost rostral teeth; space between the two posteriormost rostral teeth 15.3–53.7% of the width of the base of the rostrum; groove at the posterior margin of the rostral teeth reaches the base of the rostral teeth; origin of first dorsal fin above the origin of pelvic fins.......... *Pristis pectinata*

4b. Rostrum length 20.4–23.1% of total length; space between the two anteriormost rostral teeth 28.6–65.5% of the space between the two posteriormost rostral teeth; space between the two posteriormost rostral teeth 24.8–32.1% of the width of the base of the rostrum; groove at the posterior margin of the rostral teeth often incomplete (not reaching the base of the rostral teeth); origin of first dorsal fin slightly posterior to origin of pelvic fins.......... *Pristis clavata*

TAXONOMIC IMPLICATION

The largetooth sawfish *P. pristis* is now redescribed as follows.

PRISTIS PRISTIS (LINNAEUS, 1758)

FIG. 4; TABLES 4 AND 5

Squalus pristis Linnaeus, 1758: 235 (valid as). Type-locality: 'Europa'.

Pristis antiquorum Latham, 1794: 277, pl. 26 (synonym). Unnecessary replacement name for *Squalus pristis* Linnaeus 1758

Pristis canaliculata Bloch & Schneider, 1801: 351 (synonym). Based on Latham: 277, pl. 26, which is *Pristis antiquorum* (= *Squalus pristis*).

Pristis leichhardti Whitley, 1945: 44 (synonym). Type locality: Lynd River, northern Queensland, Australia.

Pristis microdon Latham, 1794: 280, pl. 26 (synonym). Type-locality: not stated.

Pristis perotteti Müller & Henle 1841: 108, 192 (synonym). Type locality: Senegal. No type material – possible paratype: MNHN A-9699, female 2850 mm total length (TL), stuffed (Séret & McEachran, 1986).

Pristis zephyreus Jordan 1895: 383 (synonym). Type locality: Presidio River, Sinaloa, Mexico (East Pacific). Holotype: CAS-SU 12670; rostrum, head, and skin.

Diagnosis: A sawfish with robust rostrum, noticeably diverging posteriorly (rostrum width between two posteriormost rostral teeth 1.7–2 times the width between the second anteriormost rostral teeth). The number of rostral teeth per side ranges from 14 to 23. Rostral teeth with groove on the posterior margin. First dorsal-fin origin well anterior to pelvic-fin origins. Lower lobe of the caudal fin well defined (lower anterior margin about half as long as the upper anterior margin).

Nomenclatural discussion: The original *P. pristis* description (Linnaeus, 1758) is here interpreted as representing a composite species. The Linnaean *P. pristis* description consisted of an identifying phrase ('shark with a flat bony, sword-shaped snout toothed on both sides', translated from the Latin). The nine references cited within this source described or depicted different sawfish specimens with either largetooth (Clusius, 1605) or smalltooth (Rondelet, 1554) characteristics. Subsequently, Latham (1794) revised the sawfishes. But in an odd nomenclatural decision, Latham (1794) made *P. pristis* a synonym to his newly described *Pristis antiquorum*. Cited references in the *P. antiquorum* description included Linnaeus's original *P. pristis* description and the nine references originally cited by Linnaeus. The only new aspect in Latham's (1794) *P. antiquorum* description was a drawing of a largetooth sawfish rostrum and a listing of body proportions. The rostrum depicted in Latham's paper is clearly that of a largetooth sawfish. However, the body proportions were only poorly described. For example, pelvic fins were loosely described as 'situated almost underneath the first dorsal'. The caudal fin was described as 'occupying the tail both above and beneath, but longer on the upper part'. We hypothesize that the poor description and citations referring to different sawfish species made it confusing for subsequent authors to interpret and identify *P. antiquorum* as a largetooth sawfish. Specifically, we believe Müller & Henle (1841) misidentified one smalltooth sawfish as *P. antiquorum*. Müller & Henle's (1841) morphological traits for *P. antiquorum* are 20–30 rostral teeth per side, gaps between rostral teeth increasing 3–4 times at the base, first dorsal fin origin above the origin of pelvic fins, and no lower caudal lobe. All of these characters describe a generalized smalltooth sawfish (*P. clavata*, *P. pectinata*, or *P. zijsron*). Duméril (1865) subsequently solidified the error in the literature by combining elements of Latham's (1794) description of the *P. antiquorum* (largetooth) rostrum with Müller & Henle's (1841) description of the body proportions for a smalltooth *Pristis*. Finally, Garman (1913) correctly asserted that *P. pristis* had priority over *P. antiquorum*. He defined *P. pristis* as a Mediterranean (European) sawfish with morphological characters as described in Duméril (1865). As this chimaeric 'species' would never be found in nature, Garman (1913) unwittingly established the myth of the extremely rare Mediterranean/West African *P. pristis* in the literature.

Relevant aspects of other junior synonyms are as follows: (1) *P. microdon* (Latham, 1794) is a juvenile *P. pristis*, based on the rostrum depicted in the original description of the species; (2) Bloch & Schneider (1801) renamed *P. antiquorum* to *Pristis caniculata* to reflect the grooved posterior margins of the rostral teeth, a trait mentioned by Latham (1794) to define *P. antiquorum*, but one that is actually diagnostic for the genus *Pristis*; (3) Müller & Henle (1841) clearly described a *P. pristis* specimen collected from freshwater in Senegal (West Africa) as their *P. perotteti*; (4) Jordan (1895) described *P. zephyreus* based on differences in morphological proportions from West African *P. perotteti*, also invoking biogeographical differences to justify his designation of the Eastern Pacific population as a separate species. Finally, *Pristis mississippiensis* Rafinesque, 1820 is not a synonym of *P. pristis*, as the specimen on which this species was based has 26/27 rostral teeth per side, counts that are

Table 4. *Pristis pristis* proportional dimensions in percentage of total length

	F, 1595 mm Brazil, Amazon River, near Manaus INPA uncat.	F, 2850 mm Senegal (estuary) MNHN A-9699	M, 833 mm Vietnam, Mekong River estuary MNHN A-3527	F, 842 mm Indonesia, probably Jakarta RMNH 7417	M, 928 mm Indonesia, Borneo Bandjarmasin? RMNH 7419	F, 3032 mm Indonesia, New Guinea, Lake Sentani RMNH 28609	F, 2710 mm Indonesia, New Guinea, Lake Sentani RMNH 28608	F, 940 mm Panama, Tuyra River, Marrigante FMNH 8192	M, 860 mm Panama, Chucunaque River AMNH 44011
02 Rostrum tip to eye	27.1	27.0	29.7	30.9	28.3	23.8	24.7	25.4	29.5
03 Rostrum tip to spiracle	30.2	29.5	33.5	34.4	31.3	26.7	27.3	28.9	32.6
04 Rostrum tip to pectoral fin insertion		37.9	38.9	27.9	37.1	36.8	35.8	36.2	39.8
05 Rostrum tip to pelvic fin insertion		60.7	62.3	64.8	56.5	60.9	61.6	53.7	59.7
06 Rostrum tip to 1st dorsal fin origin	53.6	54.6	55.7	58.2	52.0	54.7	54.4	53.4	54.4
07 Rostrum tip to 2nd dorsal fin origin	73.0	73.7	74.2	77.7	69.3	75.9	74.5	74.4	72.4
08 Rostrum tip to upper caudal fin origin		86.0	85.5	89.5	80.6	88.0	86.3	86.6	84.4
09 Rostrum tip to outer nostril	26.1	27.0	28.9	29.1	27.6	22.3	23.1	23.7	28.0
10 Rostrum tip to mouth	30.5	29.1	33.3	33.4	31.7	26.7	27.5		32.8
11 Rostrum tip to 1st gill	39.2	38.4	41.1	41.2	39.7	36.3	36.5	37.2	
12 Rostrum tip to 3rd gill	42.8	41.1	44.2	44.5	43.4	41.1	40.2	39.9	
13 Rostrum tip to posterior cloaca	67.2		66.0	65.9	62.7	68.4	64.0		61.7
15 Interdorsal	10.4	11.6	10.5	10.8	10.6	12.2	11.3		10.2
19 Distance between eyes		4.5	5.5	5.6	4.9	6.0	6.0	6.0	
20 Distance between spiracles		3.9	4.4	4.5	4.0	4.8	4.8	4.3	
21 Distance between nostrils	2.3	2.6	2.2	2.2	2.2	2.1	2.2	2.5	2.4
28 Mouth width		5.3	5.2	5.6	5.0	6.1	5.8		5.2
30 Nostril length		1.1	2.1	2.0	1.9	2.0	2.0	2.0	1.9
32 Clasper outer length			1.6		1.4				1.6
33 Pectoral fin, anterior margin	11.9	11.8	10.8	10.1	11.0	14.0	14.0	10.3	9.5
34 Pectoral fin, posterior margin	14.2		12.7	12.1	12.3	20.0	17.2	15.8	13.4
35 Pectoral fin inner margin	6.3	4.0	5.1	5.5	5.1	6.6	8.1		5.0
36 Pectoral fin base	11.6	1.2	11.7	9.9	10.2	13.9	11.8	9.7	10.1
41 1st dorsal fin, anterior margin	11.1	9.3	11.4	10.4	9.5			8.4	10.8
42 1st dorsal fin posterior margin	8.3	5.8	5.9	5.8	6.2				10.5
43 1st dorsal fin height		6.7	6.5	6.1	7.0			6.9	6.9
44 1st dorsal fin inner margin	3.3	2.5	3.1	2.9	2.8	3.1	3.9		3.5
45 1st dorsal fin base	6.3	7.5	8.4	7.4	6.6	9.1	8.9	6.4	7.0
46 2nd dorsal fin anterior margin	9.7	8.8	10.4	9.5				9.1	10.0
47 2nd dorsal fin posterior margin	8.2	6.2	5.4	5.7					8.9
48 2nd dorsal fin height		6.8	6.8	5.7				6.4	6.5
49 2nd dorsal fin inner margin		2.4	3.3	3.3	2.6	3.3	3.3		3.1
50 2nd dorsal fin base	6.3	5.4	6.3	7.2	5.5	6.4	6.1	5.4	5.9
51 Caudal fin upper lobe	16.9	13.2	16.4	15.7	15.7		16.1	15.8	15.9
52 Caudal fin posterior margin	13.2	11.2	11.9	12.6	11.9	15.4	16.2		11.5
53 Caudal fin lower lobe	8.2	8.4	8.7	7.3	7.7	8.2	9.2	10.7	8.1
54 Rostrum total length	23.6	22.6	25.8	26.7	25.0	20.1	20.6	20.8	25.0
55 Rostrum standard length	22.7	24.0	24.9	25.2	23.0	19.3	21.2	20.1	24.1
57 Rostrum width anterior		2.2	2.5	2.5	2.3	2.2	2.2	3.1	
61 Rostrum width posterior	4.2	4.3	4.4	4.2	4.1	4.3	4.4	4.7	
62 Interlateral rostral tooth anterior	1.0	0.9	1.0	1.2	0.9	0.9	0.9		
67 Interlateral rostral tooth posterior	1.5	1.4	1.5	1.8	1.4	1.3	1.3		
82 Number of rostral teeth left	17	17	19	18	20	16	17	17	21
83 Number of rostral teeth right	18	17	19	18	20	17	18	18	21
106 Eye length		1.2	1.9	2.0	1.8	1.5	1.5		
107 Spiracle length		1.4	1.7	1.4	1.3	2.0	1.5		

F, female; M, male.

Table 5. Summary of morphometric and meristic measurements for *Pristis pristis* examined in this study

	N	Minimum (mm)	Maximum (mm)	Average	Standard deviation
01 Total length	78	89.5	5790.0	1177.0	1097.1
02 Rostrum tip to eye	28	28.5	1370.0	386.2	287.5
03 Rostrum tip to spiracle	27	119.0	1500.0	442.2	311.2
04 Rostrum tip to pectoral fin insertion	26	143.0	1990.0	554.9	431.9
05 Rostrum tip to pelvic fin insertion	25	219.0	3620.0	924.5	775.8
06 Rostrum tip to 1st dorsal fin origin	26	203.0	3350.0	846.9	696.3
07 Rostrum tip to 2nd dorsal fin origin	26	262.0	4450.0	1137.8	942.3
08 Rostrum tip to caudal fin origin	31	299.0	5010.0	1134.0	1044.1
09 Rostrum tip to outer nostril	29	26.7	1300.0	364.6	267.6
10 Rostrum tip to mouth	26	30.5	1480.0	433.4	315.3
11 Rostrum tip to 1st gill	10	342.0	1150.0	745.8	368.9
12 Rostrum tip to 3rd gill	9	368.0	1260.0	774.2	409.9
13 Rostrum tip to posterior cloaca	13	531.0	2035.0	866.4	514.1
15 Interdorsal	26	36.8	495.0	152.0	118.4
19 Distance between eyes	26	21.1	183.2	71.1	43.1
20 Distance between spiracles	27	19.0	145.0	58.9	36.5
21 Distance between nostrils	32	6.9	145.0	35.4	29.5
28 Mouth width	27	4.7	330.0	79.4	71.4
30 Nostril length	29	8.4	80.0	26.8	17.6
32 Clasper outer length	14	1.6	280.0	28.6	72.5
33 Pectoral fin, anterior margin	22	9.8	820.0	181.7	187.0
34 Pectoral fin, posterior margin	19	101.5	1070.0	271.2	248.3
35 Pectoral fin inner margin	18	34.5	290.0	95.6	75.0
36 Pectoral fin base	20	10.2	800.0	181.4	181.7
41 1st dorsal fin, anterior margin	21	10.7	460.0	141.9	111.3
42 1st dorsal fin posterior margin	15	48.5	400.0	138.9	96.3
43 1st dorsal fin height	16	51.5	350.0	111.1	89.8
44 1st dorsal fin inner margin	18	23.8	135.0	52.8	34.7
45 1st dorsal fin base	19	56.7	400.0	140.9	103.8
46 2nd dorsal fin anterior margin	20	5.8	430.0	127.2	103.6
47 2nd dorsal fin posterior margin	16	5.0	370.0	122.1	92.2
48 2nd dorsal fin height	16	4.9	350.0	106.3	90.5
49 2nd dorsal fin inner margin	18	1.9	165.0	50.6	40.3
50 2nd dorsal fin base	20	4.9	300.0	97.3	72.4
51 Caudal fin upper lobe	22	10.5	840.0	220.3	204.0
52 Caudal fin posterior margin	21	9.5	740.0	203.3	187.0
53 Caudal fin lower lobe	22	6.0	280.0	121.3	90.2
54 Rostrum total length	137	21.7	1530.0	740.9	420.0
55 Rostrum standard length	198	20.8	1475.0	648.0	388.7
57 Rostrum width anterior	187	2.4	248.0	69.8	44.5
61 Rostrum width posterior	283	3.4	320.0	114.3	74.5
62 Interlateral rostral tooth anterior	205	0.9	54.9	19.7	15.5
67 Interlateral rostral tooth posterior	123	1.0	85.4	42.2	22.0
82 Number of rostral teeth left	344	14	22	18.2	1.5
83 Number of rostral teeth right	346	14	23	18.2	1.6
106 Eye length	24	11.7	44.9	21.4	9.4
107 Spiracle length	24	11.1	62.1	21.5	13.3

too high for *P. pristis*. Similarly, *Pristis woermanni* Fischer, 1884 is not a synonym of *P. pristis*, as its holotype also bears a high number of rostral teeth: 25/25.

Remarks: Garman (1913) was the first to link *P. pristis* to a drawing in Clusius (1605), one of the references cited by Linnaeus (1758) in the species description. Zorzi (1995) cited this link based on

Garman (1913), but disagreed with him on the interpretation of the drawing. Garman (1913) considered that the specimen depicted lacked a subcaudal lobe, whereas Zorzi (1995) considered it to have one. We agree with Zorzi's (1995) interpretation of the drawing, but disagree with Garman (1913), and consequently also with Zorzi, that *P. pristis* is based on Clusius (1605). As stated above, we interpret *P. pristis* originally as a composite species.

Description: A large sawfish with a shark-like body, head flattened with a comparatively broad-based, robust, and stout rostrum that tapers posteriorly and bears a series of lateral rostral teeth. The rostrum originates just anterior to the eyes (dorsally) and nostrils (ventrally). The tip of the rostrum is rounded.

Rostral teeth are triangular, slender, and elongated. The rostral teeth have a groove at the posterior margins at all maturation stages (detected as early as in neonates). Rostral teeth are relatively evenly spaced, although slightly closer toward tip of rostrum. The posteriormost rostral teeth are located just anterior to base of rostrum. The number of rostral teeth varies in number between 14 and 23.

Spiracles are located well behind eyes, on top of the head. Nostrils, mouth, and gill slits (five pairs) are located entirely ventrally on the head. Nostrils are short and broad, anterior to and separated from mouth, partially covered by large nasal flaps. Mouth is transverse and nearly straight.

The trunk is elongated and cylindrical dorsally, but strongly flattened below. Pectoral fins are distinct from head, broadly triangular, and not forming a disk as in the more modified batoids. Hind margins are straight, with posterior tip anterior to axil of pelvic fins. Pelvic fins are composed of a single lobe, triangular, and only moderately expanded. The two dorsal fins are large and well separated. They are of similar shape and size, although the first is slightly larger than the second. Both dorsal fins have strongly concave posterior margins and narrowly rounded apices. The first dorsal fin is located well anterior to the origin of the pelvic fin.

There is no clear division between the trunk and tail regions, the latter being stout and shark-like, with low lateral ridges. The caudal fin is well developed, with a concave rear edge and a short but noticeable lower lobe. Dorsal and lateral surfaces are uniformly brownish, with whitish ventral surface.

Size: The largest specimen examined in the present study was a female of 5790 mm TL (BMNH, uncatalogued, unknown locality). Prater (1939) reported a 6096-mm specimen caught off Mumbai. Large specimens recently reported include a 7000-mm specimen from Brazil (Almeida, 1999), and a 6000-mm specimen from Australia (Peverell, 2005). Carvalho & McEachran (2003) cited 7500 mm as the maximum TL for this species.

Life history: Characterized by late maturity, low fecundity, and slow growth, contributing to a low intrinsic rate of population increase. The breeding season in Lake Nicaragua probably extended from May to July, with parturition taking place from early October into December (Thorson, 1976). Also in Lake Nicaragua, size at birth ranged from at least 730–800 mm TL, with litter sizes of 1–13 (mean 7.3), following a gestation period of about 5 months (Thorson, 1976). Thorburn *et al.* (2007) suggest that in Western Australia individuals of between 800 and 900 mm TL were recently born. In Lake Nicaragua, sexual maturity is reached at about 10 years of age and approximately 3000 mm TL, with a reproductive period lasting about 20 years (Thorson, 1982). Maturity is attained at lengths greater than 2400 mm in the Indo-West Pacific population (Compagno & Last, 1999). In Lake Nicaragua, breeding occurs every other year (Thorson, 1976) and individuals spend much, if not all, of their lives in freshwater, with reproduction of the population occurring primarily in the lake (Thorson, 1982). In Queensland, Australia, the species appears to pup in freshwater but can move into estuarine and coastal marine habitats (Peverell, 2005).

Information about age and growth are as follows. In northern Australia and Papua New Guinea, the number of vertebral centra rings varied between 0 and 48, with the first appearing to be formed soon after birth, the second within a few months of birth, and the third over 1 year from birth (Tanaka, 1991). Therefore, specimens with three rings appeared to be 1 year old (Tanaka, 1991). If the second and successive rings were formed annually, the largest specimen with 46 rings would have been 44 years old (Tanaka, 1991). A von Bertalanffy model was fitted to the back-calculated data (BCD) and the observed data (OD), with the following parameters generated: for BCD, $L_\infty = 398$ cm, $K = 0.047$ year^{-1}, and $t_0 = -5.54$ years; for OD, $L_\infty = 363$ cm, $K = 0.066$ year^{-1}, $t_0 = -4.07$ years. The annual growth rate was 180 mm in the first year and 100 mm in the tenth year (Tanaka, 1991). However, this is in contrast with data from the West Pacific, in which young are born at 500 mm, and an individual grew from 600 to 2600 mm in 3 years (Thorburn & Morgan, 2005). Thorburn *et al.* (2007) found the number of annuli, in conjunction with length–frequency data, suggested that in Australia individuals of 1000 mm TL were approximately 1 year old, those between 1400 and 1600 mm TL were approximately 2 years old, those between 1800 and 2200 mm TL were approximately 3 years old, and that the largest ones between 2300 and 2800 mm TL were likely to be at least 4 years old. Preliminary vertebral growth ring analysis estimated a maximum age of 51 years (Peverell, 2006). Thorson (1982) suggested that specimens in Lake Nicaragua grow 350–400 mm in their first year, 120 mm in their tenth year, and 40–50 mm during each of the last 10 years of life, with a lifespan of over 30 years and maximum size of 4300 mm. On the basis of Thorson's (1982) data, von Bertalanffy growth parameters were estimated by Simpfendorfer (2000) as $L_\infty = 456$ cm, $K = 0.089$ year^{-1}, and $t_0 = -1.98$ years. Simpfendorfer (2000) estimated an intrinsic rate of increase of 0.05–0.07 per year and population doubling times of 10.3–13.6 years.

Distribution (mostly preterite) and habitat (see also Material examined): Eastern Pacific: Mexico, Guatemala, Nicaragua, Panama, Ecuador, and Peru. Western Atlantic: USA, Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Caribbean Sea, Colombia, Venezuela, Guyana, Suriname, French Guiana, and Brazil. Eastern Atlantic: Mediterranean, Senegal, Republic of Guinea, Guinea Bissau, Gambia, Sierra Leone, Liberia, Ivory Coast, Congo, Democratic Republic of Congo, Angola. Indo-West Pacific: South Africa, Zambia (Zambezi River), Mozambique (Zambezi River), Tanzania, Kenya, Madagascar, Pakistan, Gulf of Aden, India, Thailand, Vietnam, Cambodia, Singapore, Indonesia, Borneo, Philippines, Papua New Guinea, and Australia. Found in coastal, estuarine, and riverine habitats.

The type locality of *P. pristis* cited by Linnaeus (1758) as 'Europe' possibly refers to the Mediterranean Sea. However, no reliable museum specimen nor photographic evidence associated with a definite Mediterranean locality was found by the authors of this study. In fact, to this day, the occurrence of any sawfish species in the Mediterranean remains controversial. Stehmann & Bürkel (1984) argued that sawfish records in the area are questionable. These authors stated that largetooth sawfish records cited in Costa (1850) and Tortonese (1956) were based on museum specimens that had no associated locality data or were mislabelled. Nevertheless, Capapé *et al.* (2006) cited historical records for southern France. Furthermore, Psomadakis, Maio & Vacchi (2009) reported to have located a largetooth museum specimen stated to be from Italy. Sawfishes have been recorded well out of their year-round ranges, as indicated by the reports of *P. pectinata* in New Jersey/New York in the USA and Bermuda (Bigelow & Schroeder, 1953), and of *P. pristis* in Cape Naturaliste, further south than any other sawfish in Australia (Chidlow, 2007). This would argue in favour of their possible presence in the region. Nevertheless, evidence suggests that sawfishes have not formed resident, breeding, or core populations in the Mediterranean. Cultural and archaeological data from the Mediterranean are consistent with a long-standing lack of familiarity with sawfishes: no archaeological studies in the region have yielded sawfish remains (Reese, 1984), there are no depictions of a sawfish in any cultural artifacts (Boehmer, 2002), and where sawfishes are mentioned by the ancient Greeks and Romans, they are never described anatomically, nor are any details given about their behaviour, habits, or range (Thompson, 1947: 219). This is in stark contrast with empirical knowledge of elasmobranchs in the ancient Mediterranean. Classical natural historians wrote at length about the behaviour and morphology of smaller and economically important elasmobranch species, such as dogfishes, skates, and torpedo rays [e.g. Aristotle's *Historia Animalium* and *Generation of Animals* [*c.* 2362 years before present (BP)], Pliny the Elder's *Natural History* (*c.* 1935 BP), and Oppian's *Halieutica* (*c.* 1841 BP)]. If sawfish ever did occur in Mediterranean waters, they would have occurred in low numbers at the periphery of their East Atlantic distribution, which may account for the occasional suggestion of their presence in the region.

Alternatively, the 'Europa' locality in the *P. pristis* original description could refer to sawfish accounts in other parts of the continent's coast arising from a mistaken view that sawfishes had a circumglobal marine distribution, including temperate and even arctic waters. The examples are several: (1) Linnaeus (1746) once included sawfishes as part of the Swedish fauna; (2) in *The History of Fish*, the sawfish is said to inhabit the northern seas of Iceland, Greenland, and Spitsbergen (Anon., 1818?); (3) according to an encyclopedia, '[*sawfish*] inhabit all seas, from the polar ice to the equatorial regions' (Lieber, 1851); Fox (1868: 684) asserted that 'The saw-fish is amongst the most widely distributed of fishes, belonging to the arctic, antarctic, and tropical seas'; (4) a newspaper article called narwhals captured in Norway 'sawfish' (Anon, 1902). This view of sawfishes as cosmopolitan animals may have its root in language. The etymology of the word *pristis* could derive from the Greek word for 'saw', or alternatively, to 'blowing' or 'spouting'. Some classical texts group the fish the Greeks called *pristis* or *pristes*, and the Romans called *serra*, among the elasmobranchs, but just as often, these fishes are grouped with the whales. Furthermore, through the Renaissance period (1450–1600), sawfishes, orcas, swordfishes, and narwhals were popularly referred to as 'sword-fish' in various European languages. Consequently, sawfishes were erroneously assumed to: (1) inhabit Arctic seas, like narwhals (e.g. references cited above); (2) spout like whales (see the drawing in Rondelet 1554); (3) hunt like orcas and swordfishes, based on reports of 'sawfish' rostra (likely from swordfish) being taken from the flesh of whales (Révoil, 1865).

POPULATION STRUCTURE

Population structuring among and within ocean basins was evident for all four sawfish species studied, based on either or both *NADH-2* and the number of rostral teeth per side. Overall, these species exhibit a typical pattern of tropical coastal elasmobranchs, in which the dispersal of females, at least, might occur along coastlines, whereas great oceanic expanses and cold waters work as effective barriers (Duncan *et al*., 2006). Two recent genetic studies using mitochondrial markers on *A. cuspidata* and *P. pristis* corroborate the hypothesis of structured populations. Across northern Australia both species were structured on a much smaller geographical scale (Danastas, 2010; Phillips *et al*., 2011; respectively), suggesting that structuring occurs along coastlines.

Results suggesting a very low level of gene flow between the Indian Ocean and Western Pacific populations of *A. cuspidata* seem consistent. This pattern was obtained by both qualitative (exclusive haplotypes) and quantitative *NADH-2* analyses (Φ_{st}), and the regional variation of the number of rostral teeth per side. In sharks, exclusive Indian Ocean and Western Pacific haplotypes were found for: the blacktip shark, *Carcharhinus limbatus* (Keeney & Heist, 2006); the scalloped hammerhead, *Sphyrna lewini* (Duncan *et al*., 2006); and the zebra shark, *Stegostoma fasciatum* (Dudgeon, Broderick & Ovenden, 2009). Historical and contemporary barriers may be involved in these patterns. The region has a complex geological history, and several biogeographical regions have been identified for marine fishes (Blum, 1989). Periods of lowered sea levels in the last 3 Myr almost closed the sea connection between the Indian and Pacific oceans by a land connection between South-East Asia, New Guinea, and Australia, temporarily isolating marine organisms (Benzie, 1998).

Furthermore, the exclusive haplotypes suggestive of the further substructuring of *A. cuspidata* into Indonesian and New Guinean–Australian groups are consistent with a major marine faunal break in the region. The chondrichthyan fauna of South-East Asia and the South-West Pacific differ considerably, based primarily on demersal species (Last & Séret, 1999). This break has also been effective at the sister species and population levels for several marine organisms, including sharks (see discussion in Dudgeon *et al*. 2009). Three shark species have been shown to be genetically structured between Indonesia and Australia: the zebra shark, *Stegostoma fasciatum* (Dudgeon *et al*., 2009); the spottail shark, *Carcharhinus sorrah*; and the dusky shark *Carcharhinus obscurus* (Ovenden *et al*., 2009). Strong currents and deep trenches may restrict gene flow or isolate species or populations from these regions. Furthermore, the lack of differentiation of haplotypes between Australia and New Guinea suggests that the shallow waters that separate them may serve as a dispersal corridor, as hypothesized for *Stegostoma fasciatum* (Dudgeon *et al*., 2009).

In *P. pristis*, the fixation index (Φ_{st}) values obtained for major ocean basin comparisons revealed a significant restriction of gene flow between Atlantic, Indo-West Pacific, and Eastern Pacific populations. Three biogeographical barriers may be responsible for this: (1) the Isthmus of Panama (IOP), isolating the Eastern Pacific and Atlantic (Coates & Obando, 1996); (2) the cold waters of the Benguela upwelling system, isolating tropical organisms of the Atlantic and Indian oceans (Shannon, 1985); and (3) the immense expanse and deep waters of the Pacific Ocean, making dispersal between the western and eastern portions of this ocean difficult and unlikely for sawfishes, which have a mostly continental shelf distribution (Robertson, Grove & McCosker, 2004; Wiley & Simpfendorfer, 2010). Other shark populations are also structured in similar patterns, along each of these barriers as follows: (1) IOP for the lemon shark, *Negaprion brevirostris* (Schultz *et al*., 2008), and the nurse shark, *Ginglymostoma cirratum* (Karl, Castro & Garla, 2011a); (2) the Benguela current for the scalloped hammerhead shark, *Sphyrna lewini* (Duncan *et al*., 2006); (3) the Eastern Pacific barrier for *Sphyrna lewini* (Duncan *et al*., 2006), the blacktip shark, *Carcharhinus limbatus* (Keeney & Heist, 2006), and lemon sharks *Negaprion acutidens* (Schultz *et al*., 2008).

Moreover, a finer scale level of structuring of *P. pristis* populations within the Atlantic was suggested by quantitative (phylogenetic) and qualitative (exclusive haplotypes) *NADH-2* analyses, and regional variation of the number of rostral teeth per side. Corroborating this, other shark species also show some level of isolation between the Western and Eastern Atlantic: the blacktip shark, *Carcharhinus limbatus* (Keeney & Heist, 2006); the lemon shark, *N. brevirostris* (Schultz *et al*., 2008); and the nurse shark, *G. cirratum* (Karl *et al*., 2011a). These populations might be completely or at least partially isolated because of the mid-Atlantic Ocean's deep and cold waters.

Results for the structuring of *P. pristis* in the Indo-West Pacific were inconclusive. First, the markers were not congruent for gene flow within this ocean basin: the restriction of gene flow between the Indian Ocean and the Western Pacific was suggested by quantitative (phylogenetic) and qualitative (exclusive haplotypes) *NADH-2* analyses, but no geographical variation was found for the number of rostral teeth per side. Interpreting this pattern is difficult, as the variability of non-genetic traits is usually of unknown nature, being the product of complex environmental and genetic influences (Grant, Garcia-Martin & Utter, 1999). Second, the geographical distribution of haplotypes in the Western Pacific did not follow the pattern shown for *A. cuspidata* and other coastal sharks in the region (present study and references cited above).

Lastly, the lack of geographical variability of *NADH-2* sequences for *P. pectinata* and *P. zijsron* may not be interpreted as gene flow between populations of each of these species. This is because a lack of geographical structure suggested by any given molecular marker may result from several reasons, including at least: (1) sufficient gene flow to maintain panmixia; (2) sporadic recruitment from distant areas; (3) recent divergence of the compared populations; and (4) inadequate marker or sample size (Carvalho & Hauser, 1995). Furthermore, Grant *et al*. (1999) suggested that evidence of geographical structuring based on non-genetic traits, such as meristic data, may indicate separate stocks, even when not apparent based on molecular data. Therefore, if we follow their concept, the significant difference in number of rostral teeth observed may indeed be sufficient information to indicate that each species is composed of separated populations: (1) Western/Eastern Atlantic populations for *P. pectinata* and (2) Indian Ocean/Western Pacific populations for *P. zijsron*.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The present delineation of the Pristidae will provide a more stable basis for the progression of conservation efforts for this iconic group of species. The delineation, however, will have a number of significant immediate implications for the conservation of sawfishes. First, existing conservation instruments such as national endangered species laws and regulations and CITES appendices will need to reflect this improved understanding. The CITES Secretariat will also need to consider how to resolve the situation where species that are currently listed in Appendix I (*P. perotteti* and *P. pristis*) and Appendix II (*P. microdon*) have been shown to be the same species (*P. pristis*), albeit in different units or populations. Secondly, assessments on the status of sawfish species that have historically belonged to the largetooth group will need to be updated to reflect the revised taxonomy. This will include the IUCN Red List assessments (http://www.iucnredlist.org) on global extinction risk, which may also benefit from the development of regional assessments for each of the units or populations.

Conservation actions for *P. pristis* must now recognize the circumtropical distribution of this species and develop a coordinated global approach. Such an approach will be vital for the successful outcome of conservation efforts. However, the structuring of the population evident from the mitochondrial DNA results also means that regional-level conservation will be required. In fact, fine-scale genetic analysis (Phillips *et al*., 2011) has shown that even within these broad regions there is a high degree of structuring that will require conservation action at the national and even local level to conserve the genetic diversity of this species. Nevertheless, additional information about sawfish population structure is needed to assist in specific management. For example, mitochondrial DNA has shown strong population structure for *S. lewini* between ocean basins (Duncan *et al*., 2006), but a recent study using nuclear markers (microsatellites) revealed higher connectivity, indicating that there is a previously undetected male-gene flow, and reinforcing the need for studies incorporating mixed-marker analysis to direct management efforts (Daly-Engel *et al*., 2012b). This result indicates that genetic studies of sawfish using nuclear markers will be required to have a full understanding of the connectivity of populations.

The results of this work also demonstrate that it may be useful to help monitor the global trade in sawfish fins and rostra using genetic markers such as the *NADH-2* gene. Similar approaches have been used in the monitoring of other species in the fin trade (Clarke *et al*., 2006), and have proven useful in better understanding trade issues in relation to conservation efforts. Feldheim *et al*. (2010) have also described microsatellite markers that may be useful in monitoring trade, and the combination of these different types of markers should provide a suite of tools to assist in this effort.

MATERIAL EXAMINED

PRISTIS PRISTIS (LINNAEUS, 1758)

FMNH 8182, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8183, unsexed (895 mm TL), 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8184, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8186, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8187, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8188, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8190, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8191, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8193, unsexed (978 mm TL), 3/18–19/1911, Culebra River, Panama (E. Pacific); FMNH 8192, female (940 mm TL), 3/8–9/

1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8194, female, 3/18–19/1911, Culebra River, Panama (E. Pacific); FMNH 8185, 3/8–9/1912, Darién, Tuyra River, Marrigante, Panama (E. Pacific); FMNH 8189, Darién, Tuyra River, Marrigante, Panama (E. Pacific); AMNH 44011 (first of four), female (951 mm TL), 1924, Chucunaque River, Panama (E. Pacific); AMNH 44011 (second of four), female (849 mm TL), 1924, Chucunaque River, Panama (E. Pacific); AMNH 44011 (third of four), male (860 mm TL), 1924, Chucunaque River, Panama (E. Pacific); AMNH 44011 (fourth of four), female (877 mm TL), 1924, Chucunaque River, Panama (E. Pacific); BMNH 1864.1.26.288, female (867 mm TL), Guatemala (E. Pacific); BMNH 1864.1.26.287, female (906 mm TL), Guatemala (E. Pacific); BMNH 1924.8.29.1–10 (first of 11), female (403 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (second of 11), female (397 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (third of 11), female (396 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (fourth of 11), female (381 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (fifth of 11), male, Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (sixth of 11), male (380 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (seventh of 11), unsexed (385 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (eighth of 11), male (406 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (ninth of 11), male (390 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (tenth of 11), male (402 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); BMNH 1924.8.29.1–10 (11th of 11), unsexed (390 mm TL), Gulf of Panama, Saboga, Panama (E. Pacific); UF 210978, isolated rostrum, 9/1961, off the city of Esmeraldas, Esmeraldas State, Ecuador; USNM 00222034, female (870 mm TL), 3/3/1967, Balsas River (above Tucuti), Panama (E. Pacific); USNM 00081072, female (944 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00079308, male (845 mm TL), Chorrera River, Panama (E. Pacific); USNM 00086070, male (1139 mm TL), Balboa, Panama (E. Pacific); USNM 00081067, female (926 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081069, male (780 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081068, female (866 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081071, male (894 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081073, female (1000 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081070, female (950 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00086069, male (821 mm TL), El Capitan, Panama (E. Pacific); USNM 00081074, female (950 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00081066, male (810 mm TL), Tuyra River, Marrigante, Panama (E. Pacific); USNM 00021789, isolated rostrum, Peru or Ecuador; USNM 00111427, isolated rostrum, 5/28–29/1947, Tilapa River estuary, just east of Ocos (~2 miles from the mouth), Guatemala; USNM 00232697, isolated rostrum, Guayaquil, Ecuador; USNM 00232698, isolated rostrum, Gulf of California? (Baja, Mexico)? (stated as 'California' 'USA'); USNM 00232965, isolated rostrum, Panama Bay, Panama (E. Pacific); USNM 00111390, isolated rostrum, 12/24/1912, Darién, Boca de Cupe, Panama (E. Pacific); FMNH 83732, isolated rostrum, Gulf of Mexico; FMNH 83732, isolated rostrum, Gulf of Mexico; MCZ –668, female (784 mm TL), 1873, Amazon River estuary, Marajó Island, Pará State, Brazil; MCZ –302 (first of two) male (985 mm TL), 1865, Belém and environs, Pará State, Brazil; MCZ –302 (second of two), male (874 mm TL), 1865, Belém and environs, Pará State, Brazil; MCZ –667, dry female (2131 mm TL), 1865, Doce River, Espírito Santo State, Brazil; AMNH 55624, male (181 mm TL), 7/1969, Lake Nicaragua, San Carlos, Nicaragua; AMNH 11, isolated rostrum, 'probably 1910', 'probably southern Florida', USA; AMNH 49528, isolated rostrum, 1929, Brazil; ANSP 17388, isolated rostrum, before 1878, Gulf of Mexico; ANSP 17390, isolated rostrum, before 1878, Suriname; MNHN 2003-2612, isolated rostrum, 1958, Pointe-Noire, Congo; MNHN 2003-2611, isolated rostrum, 1958, Pointe-Noire, Congo; MNHN 2003-2613, isolated rostrum, 1958, Pointe-Noire, Congo; MNHN 1902-255, dry female (5100 mm TL), 1902, Sassandra, Ivory Coast; RMNH D3075, isolated rostrum (of a 5000 mm TL specimen), 12/18/1881, Sugary River, Grand Cape Mount, Liberia; RMNH D3078, isolated rostrum, before 1927, Liberia; RMNH D3079, isolated rostrum, before 1962, Suriname; RMNH D2674, dry juvenile, Suriname; MRAC 74723, isolated rostrum, 1951, Luanda, Angola; MRAC 66639, isolated rostrum, 1951, Congo Basin; MRAC 68038, isolated rostrum, 1951, Banana, DR Congo; MRAC 68039, isolated rostrum, 1951, Banana, DR Congo; MRAC A4-45-P-12, isolated rostrum, 11/20/1959 Banana, DR Congo; MRAC A4-45-P-2, isolated rostrum, Banana, DR Congo; MRAC A4-45-P-18, isolated rostrum, 1951, unknown locality (probably W. Africa); ZMB 16109, isolated rostrum, Luanda, Angola; ZMB 32533, isolated rostrum, Aracaju, Sergipe State, Brazil; BMNH 1923.11.13.1, juvenile female (412 mm TL), Caribbean Sea (W. Indies); BMNH 1982.9.13.4, isolated rostrum, 'Mediterranean' (locality information written on the rostrum); BMNH 1843.2.1.8, dry female (200 mm TL), Caribbean Sea (W. Indies); BMNH 2004.11.27.51, isolated rostrum, Sulima, Sierra Leone; USNM 146543 (first of two), female (777 mm TL), 4/27/1947, Lake Izabal, Guatemala; USNM 146543 (second of two), isolated rostrum and wet torso of a female, 4/27/1947, Lake Izabal, Guatemala; USNM 00110174, isolated rostrum, 8/1878, Amazon River, Óbidos, Pará, Brazil; USNM 00111169, isolated rostrum, *c.* 1830, Marowijne (Maroni) River, French Guiana; USNM 00111367, isolated rostrum, 10/1943, Lake Nicaragua, Nicaragua; USNM 00111369, isolated rostrum, 10/1943, Lake Nicaragua, Los Cocos, Nicaragua; USNM 00111423 (first of two), isolated rostrum, 4/10/1946, Lake Izabal (Dulce River, Caribbean), San Felipe, Guatemala; USNM 00111423 (second of two), isolated rostrum, 4/10/1946, Lake Izabal (Dulce River, Caribbean), San Felipe, Guatemala; USNM 00111443, isolated rostrum, 1947, Lake Izabal (Dulce River, Caribbean), San Felipe, Guatemala; USNM 00232688, isolated rostrum, *c.* 1903, Maracaibo?, Venezuela; USNM 00232689, isolated rostrum, *c.* 1903, Maracaibo?, Venezuela; USNM 00232690, isolated rostrum, *c.* 1903, Maracaibo?, Venezuela; uncat. INPA, isolated rostrum, 2002 or earlier, (Ver-O-Peso market, Belém, Pará) Brazil; uncat. INPA, isolated rostrum, 2002 or earlier (Ver-O-Peso market, Belém, Pará) Brazil; uncat. INPA, female (1595 mm TL), Amazon River, near Manaus, Amazonas State, Brazil; MCZ –1259, isolated rostrum, 1906, Cenderawasih Bay, Japen (Yapen) Island, New Guinea, Indonesia; AMNH 49527, isolated rostrum, 1921, Gulf of Thailand, Thailand; MNHN 1938-16, isolated rostrum, Singapore; MNHN A-3527, male (833 mm TL), Mekong River estuary, Vietnam; MNHN A-9699, dry female (2850 mm TL), Senegal; RMNH 7417, female (842 mm TL), before 1879 (auction date), 'probably Batavia' (= Jakarta), Indonesia; RMNH 7419, male (928 mm TL), before 1879 (auction date), 'Banjarmasin?' (Borneo), Indonesia; RMNH 28608, female (2710 mm TL), Lake Sentani, Papua, New Guinea, Indonesia; RMNH 28609, female (3032 mm TL), Lake Sentani, Papua, New Guinea, Indonesia; RMNH D3051, isolated rostrum, 12/12/1953, Lake Sentani, Joka, Papua, New Guinea, Indonesia; RMNH D3103, isolated rostrum, 1960, Coast of Bagamoyo, Tanzania; RMNH D3080, isolated rostrum, 7/5/1864, Ambato, NW Coast of Madagascar; RMNH 4235, female (930 mm TL), 1846, Borneo; RMNH D3057, isolated rostrum, 1954–1955, Digul River, Merah, near Tanah Merah Bay, southern New Guinea, Indonesia; RMNH D3058, isolated rostrum, Digul River, Merah, near Tanah Merah Bay, southern New Guinea, Indonesia; RMNH D3055, isolated rostrum, 1954, Lake Jamur, New Guinea, Indonesia; RMNH D3052, isolated rostrum, 1935 or earlier, Lake Sentani, Papua, New Guinea, Indonesia; RMNH D3054, isolated rostrum, 8/1957, River Moif, Genyem, New Beran, northern New Guinea, Indonesia; RMNH D3056, isolated rostrum, 1954–1955, Digul River, near Tanah Merah Bay, southern New Guinea, Indonesia; RMNH D2026, isolated rostrum, 2/1954, Lake Sentani, Papua, New Guinea, Indonesia; RMNH D2654, dry, unsexed, Borneo; ZMB 4527, male (978 mm TL), Zambezi River, Sena, Mozambique; ZMB 8304, male (980 mm TL), Laguna de Bay (freshwater environment), Luzon Island, Philippines; ZMB 8305, female (1152 mm TL), Laguna de Bay, Luzon Island, Philippines; ZMB 33545, female (762 mm TL), 1913, New Guinea; ZMB 33547, male (840 mm TL), Japan; ZMB 14507, isolated rostrum plus other anatomical pieces, Ramu River, northern Papua New Guinea; ZMB 14882, isolated rostrum, Zanzibar, Tanzania; ZMB 33551, isolated rostrum, Indian Ocean ('East Africa or India or Sri Lanka'); ZMB 33552, isolated rostrum, Indian Ocean ('East Africa or India or Sri Lanka'); ZMB 33553, isolated rostrum, Bismarck Archipelago, Papua New Guinea; ZMB 32538, isolated rostrum, 11/26/1909, Bismarck Archipelago, Papua New Guinea; ZMB 8695, dry male (1027 mm TL), Laguna de Bay, Luzon Island, Philippines; ZMB 8696, dry female (998 mm TL), Laguna de Bay, Luzon Island, Philippines; ZMB 7851, dry male (1235 mm TL), Zambezi River; BMNH 1867.11.28.185, male (880 mm TL), 1867, Indonesia; BMNH 1872.10.18.142, male (1030 mm TL), Laguna de Bay, Luzon Island, Philippines; BMNH 1937.2.17.1, isolated rostrum, Lake Sentani, Papua, New Guinea, Indonesia; BMNH 1982.9.13.3, isolated rostrum, Arabian Sea, 'Vakyan Vakr' near Sonmiani, Pakistan; BMNH 1982.9.13.7, isolated rostrum, 1854, Zambezi River, Terre, Zambia; BMNH 1864.6.28.21, isolated rostrum, Zambezi River, ('Zambezi Expedition'), Mozambique; BMNH 1845.7.3.174, dry female (1170 mm TL), India; BMNH 1872.10.18.141, dry female (1180 mm TL), rivers near Laguna de Bay, Luzon Island, Philippines; UF 147760, female (955 mm TL), 2000, Australia; USNM 00217001, female (809 mm TL), 11/27/1975, Lake Herbert Hoover and Warm River (Fly River basin), Papua New Guinea; USNM 00217002, juvenile male (881 mm TL), 12/7/1975, Strickland River, 4 km downstream of Massey Bakers Junction, Papua New Guinea.

Additional material

Isolated rostra from private collections: 1991, Lake Nicaragua, off Isla Nancita, near Granada, Nicaragua ($N = 1$); 4/1/1998, Lake Nicaragua, 2 km off Isla Zanate, Nicaragua ($N = 1$); 7/1998 or earlier, Lake Nicaragua, Nicaragua ($N = 1$); 7/1998 or earlier, Lake Nicaragua, off Granada, Nicaragua ($N = 2$); 1960, Caribbean Sea, Tortuguero, Costa Rica ($N = 1$); 7/1999–11/2000, northern Brazil (bought at Ver-O-

Peso market, Belém, Pará State) ($N = 88$); after 11/2000, northern Brazil (bought at Ver-O-Peso market, Belém, Pará State) ($N = 13$); Amazon River, northern Brazil ($N = 1$); Amazon River, Santarém, Pará, Brazil ($N = 4$); Amazon River estuary, Macapá, Amapá, Brazil ($N = 2$); Gulf of Thailand, Cambodia ($N = 1$); 9/1999 or earlier, Indonesia (freshwater environment) ($N = 1$); 3/1998 or earlier, Gulf of Papua, Papua New Guinea ($N = 1$); early 1998, Indonesia ($N = 1$); 12/1999, Sepik River, Papua New Guinea ($N = 3$).

Images of rostra from public collections: CAS-SU 12670 (holotype of *P. zephyreus*), X-ray of head and skin (1200 mm TL), 12/24/1894–1/25/1895, Presidio River, Sinaloa, Mexico (E. Pacific); LACM 42018.001, photograph of isolated rostrum, Mazatlán, Mexico (E. Pacific); LACM 42019.001, photograph of isolated rostrum, Baja California, Mexico (E. Pacific); IFAN R977, photograph of isolated rostrum, Joal, Senegal ($N = 1$).

Photographs of isolated rostra from private collections: 1995, Panama Bay, Panama (E. Pacific) ($N = 1$); unknown locality (probably W. Atlantic) ($N = 1$); *c*. 1960, Gulf of Mexico, Tampa, Florida, USA ($N = 1$); late 1960, Lake Nicaragua, Nicaragua ($N = 1$); off northern coast of west Australia ($N = 1$); mid-1960 or earlier, Milingimbi Island, NE Arnhem Land, Australia ($N = 1$).

Photograph of complete specimen from private collection: Female, Espírito Santo State, Brazil ($N = 1$).

Number of rostral teeth per side data from specimens deposited in public collections: SIO 49-110, isolated rostrum, Nicaragua (E. Pacific); SU 11892, male (888 mm TL), 1/10/1896–2/24/1896, Panama (E. Pacific); SU 34467, isolated rostrum, 1940 or earlier, Presidio River, at its mouth (Mazatlán), Sinaloa State, Mexico (E. Pacific); SU 34468, isolated rostrum, Natal, Rio Grande do Norte, Brazil; uncat. CAS, isolated rostrum, Lake Sentani, Papua, New Guinea, Indonesia; SAM 22785(?), isolated rostrum (specimen was originally 4064 mm TL), Wilderness, South Africa; SU 26822, skeleton of a male (305 mm TL), 5/1/1931–5/31/1931, Luzon Island, Philippines; SU 26822, female, Luzon Island, Philippines.

Number of rostral teeth per side and/or morphometric data from published articles: Uncat., isolated rostrum, *c*. 1965, Soro, Republic of Guinea (Robillard & Séret, 2006); uncat. Centre National des Sciences Halieutiques de Boussoura – CNSHB, isolated rostrum, Bongolon, Republic of Guinea (Robillard & Séret, 2006); uncat. IUCN-Bubaque, isolated rostrum, Bijagós, Guinea-Bissau (Robillard & Séret, 2006); uncat., isolated rostrum, 2004, Bolama, Guinea-Bissau (Robillard & Séret, 2006); uncat., isolated rostrum, 2003, Bolama, Guinea-Bissau (Robillard & Séret, 2006); uncat., isolated rostrum, 1983, Guinea-Bissau (Robillard & Séret, 2006); MTUF 30202, male (789 mm TL), Betsiboka River Basin, Madagascar (Taniuchi *et al*., 2003); uncat., female (792 mm TL), Betsiboka River Basin, Madagascar (Taniuchi *et al*., 2003); uncat., male (793 mm TL), Betsiboka River Basin, Madagascar (Taniuchi *et al*., 2003); uncat., male (1450 mm TL), Betsiboka River Basin, Madagascar (Taniuchi *et al*., 2003).

PRISTIS CLAVATA GARMAN, 1906

MCZ –733 (holotype), male (615 mm TL), Queensland, Australia; MCZ 36648, female (654 mm TL), 07/1946, Queensland, mouth of Norman River, Gulf of Carpentaria, Australia; RMNH 4233, female (728 mm TL), New Guinea, 6–8/1828; MNHN 0000-2607, female (790 mm TL), head and skin on wet preserved, Reunion Island; ZMB 7820, dry female (865 mm TL), West Pacific; ZMB 4526, dry female (1250 mm TL), Indian Ocean; ZMB 7821, dry female, West Pacific; ZMB 13850, dry male (772 mm TL), 4/1894, Baram mouth, Borneo, Malaysia; BMNH 1846.10.13.40, dry male (920 mm TL), Bay of Bengal, Calcutta, India; AMNH 49529, isolated rostrum, 1916, 'off New South Wales?', 'Australia?'; RMNH D2664?, dry, unknown locality; ZMB 32534, isolated rostrum, 4/16/1909–7/18/1910, Darvel Bay, northern Borneo, Malaysia; ZMB 32535, isolated rostrum, 4/16/1909–7/18/1910, Darvel Bay, north Borneo, Malaysia; USNM 00232696 (first of three), isolated rostrum, Banyuwangi, East Java, Indonesia; USNM 00232696 (second of three), isolated rostrum, Banyuwangi, East Java, Indonesia; USNM 00232696 (third of three), isolated rostrum, Banyuwangi, East Java, Indonesia.

Additional material
Isolated rostra from private collections: Unknown date, unknown locality ($N = 1$); unknown date, Borneo, Indonesia ($N = 2$).

Photographs: Unknown date, unsexed (2600 mm TL), N.–NW. Australia (Sainsbury, Kailola & Leyland, 1985: 41) ($N = 1$); unknown date, unsexed (live specimen), Australia ($N = 1$).

PRISTIS PECTINATA LATHAM, 1794

FMNH 9367, isolated rostrum (mounted), Spring 1909, Florida, USA; FMNH 51264, isolated rostrum, Caribbean Sea, Belize; FMNH 51265, isolated rostrum, unknown locality; FMNH 10923, isolated rostrum (and cast), 8/15/1924, Gulf of Mexico, Port Isabel, Laguna Madre, Texas, USA; FMNH 10924, jaws (and cast), 9/11/1924, Gulf of Mexico, Port Isabel, Laguna Madre, Texas, USA; FMNH 51205, jaw, unknown locality; FMNH 36628, dry skin and wet fins of an adult female, before 1930, Caribbean Sea, Key West, Florida, USA; FMNH 51186, skin, 1924, Gulf of Mexico, Port Isabel, Texas, USA; FMNH 1939, juvenile, 1/17/1896, Indian River, Cocoa, Florida, USA; FMNH 76391, female, 6/22/1910, Amazon River, Pará, Brazil; MCZ –1220, isolated rostrum, female, 8/24/1834, Bay of Pascagoula, Mississippi, USA; MCZ –1214, isolated rostrum, 1793?, unknown locality; MCZ 89872, isolated rostrum, 2/1918, Caribbean Sea, Key West, Monroe County, Florida, USA; MCZ 153653, isolated rostrum, unknown locality; MCZ 153664, isolated rostrum, unknown locality; MCZ 153665, isolated rostrum, unknown locality; MCZ 163850, isolated rostrum, unknown locality; MCZ –105, female (664 mm TL), 4/1853, Gulf of Mexico, Mobile, Alabama, USA; MCZ 36960 (first of five), male (1001 mm TL), Gulf of Mexico, Galveston, Texas, USA; MCZ 36960 (second of five), female (1005 mm TL), Gulf of Mexico, Galveston, Texas, USA; MCZ 36960 (third of five), female (988 mm TL), Gulf of Mexico, Galveston, Texas, USA; MCZ 36960 (fourth of five), male (1012 mm TL), Gulf of Mexico, Galveston, Texas, USA; MCZ 36960 (fifth of five), male (1050 mm TL), Gulf of Mexico, Galveston, Texas, USA; MCZ 36659, male (1337 mm TL), 12/1947, Gulf of Mexico, off Galveston, Texas, USA; AMNH 55572 (first of two), male (454 mm TL), 3/1958, (‘R/V Cape St. Mary’) Guyana; AMNH 55572 (second of two), female (419 mm TL), 3/1958, (‘R/V Cape St. Mary’) Guyana; AMNH 225808, female (713 mm TL), 1/1908, USA; AMNH 44010, female (730 mm TL), unknown locality; AMNH 55558, isolated rostrum, 1834, Caribbean Sea, Key West, Florida, USA; ANSP 17343, isolated rostrum, unknown locality; ANSP 92746, isolated rostrum, before 1960, Essequibo River, Demerara, Guyana; ANSP 17401, isolated rostrum, before 1878, S. West Atlantic; ANSP 153754, juvenile male (824 mm TL), 3/25/61, Caribbean Sea, Long Key (Atlantic side), Monroe County, Florida, USA; YPM 1135, isolated head and rostrum, 1926, Pacific Mexico (questionable, probably collected from the Caribbean Sea during the preliminary samplings of the Pawnee II expedition); YPM 14916, female (734 mm TL), 1926, Pacific Mexico (questionable, possibly collected from the Caribbean Sea during the preliminary samplings of the Pawnee II expedition); YPM 14917, juvenile female (715 mm TL), 1926, Pacific Mexico (questionable, possibly collected from the Caribbean Sea during the preliminary samplings of the Pawnee II expedition); YPM 8625, male (829 mm TL), 1886, Indian River, Florida, USA; YPM 11931, isolated rostrum, before 1913, Gulf of Mexico, Louisiana, USA; YPM 11930, isolated rostrum, 1870, South Carolina, Charleston County, USA; YPM 11929, isolated rostrum, before 1916, Louisiana, USA; YPM 3, isolated rostrum (mounted), unknown locality; YPM 15083, isolated rostrum, unknown locality; TCWC 2082.01, female (1440 mm TL), 01/23/1978, Gulf of Mexico, Corpus Christi Bay, Port Aransas, Texas, USA; TCWC 6565.01, isolated rostrum, 04/10/1949, Gulf of Mexico, Mustang Island, Texas, USA; MNHN 1903-427, isolated rostrum, 1900, French Guiana; MNHN 0000-3484, isolated rostrum, Cayenne, French Guiana; MNHN A-9476, stuffed male (733 mm TL), Caribbean Sea, Antilles; MNHN 2003-2614, isolated rostrum, 1958, Pointe-Noire, Congo; MNHN 1986-0397, female (741 mm TL), Port-Etienne (Nouadhibou), Mauritania; MNHN 1990-0002, juvenile male (1035 mm TL), 9/1983, Cacheu, Guinea-Bissau; MNHN 0000-1251 (first of two), male (217 mm TL), Gabon; MNHN 0000-1251 (second of two), female (214 mm TL), Gabon; MNHN 0000-9858, stuffed female (3720 mm TL), 1831, Caribbean Sea, Haiti; MNHN 0000-9859, stuffed female (3760 mm TL), unknown locality; MNHN B-549, full body skin, including head and rostrum of a female (758 mm TL), Senegal?; RMNH D2662, stuffed female (714 mm TL), unknown locality; RMNH D3107, isolated rostrum, before 1944, ‘Paramaribo, Trinidad Island’, Suriname or Trinidad and Tobago?; RMNH D3110, isolated rostrum, unknown locality; RMNH D3105, isolated rostrum, unknown locality; RMNH D3096, isolated rostrum, 9/1963, Tygerbank, Suriname; RMNH D3100, isolated rostrum, 1965, Atlantic; MRAC A4-45-P-9, isolated rostrum, unknown locality; MRAC A4-45-P-17, isolated rostrum, Congo?; MRAC 74240, female (730 mm TL), 1948, Banana Creek, DR Congo; MRAC 1486, female (654 mm TL), 1911, Banana, DR Congo; ZMB 33546, male (370 mm TL), 1/1907, Longji, Cameroon; ZMB 16632, male (342 mm TL), 1/1907, Longji, Cameroon; ZMB 33540, male (351 mm TL), 1/1907, Longji, Cameroon; ZMB 33541, male (331 mm TL), 1/1907, Longji, Cameroon; ZMB 33542, female (339 mm TL), 1/1907, Longji, Cameroon; ZMB 33543, male (335 mm TL), 1/1907, Longji, Cameroon; ZMB 33544, female (348 mm TL), 1/1907, Longji, Cameroon; ZMB 9226, male (641 mm TL), Limbe (‘Victoria’), northern Congo Basin, Cameroon; ZMB 33549, female (349 mm TL), unknown locality; ZMB 33548, female (355 mm TL), unknown locality; ZMB 4524, male (233 mm TL), North Atlantic; ZMB 16106, isolated rostrum, Luanda, Angola; ZMB 16108, isolated rostrum, Luanda, Angola; ZMB 33574, isolated rostrum, unknown locality; ZMB 33587, full-body skeleton, unknown locality; BMNH 1985.6.21.1, male (404 mm total length), 3/1958, (‘R/V Cape St. Mary’) Guyana;

BMNH 1985.6.21.2, female (419 mm total length), 3/1958, ('R/V Cape St. Mary') Guyana; BMNH 1985.6.21.3, female (434 mm total length), 3/1958, ('R/V Cape St. Mary') Guyana; unknown BMNH, female (723 mm TL), unknown locality; BMNH 1906.8.14.47, male (662 mm TL), Florida, USA; BMNH 1982.9.13.6, isolated rostrum, 1886(?), Guyana; BMNH 1982.9.13.5, isolated rostrum, 1886(?), Guyana; BMNH 1842.12.12.33, stuffed male (7602 mm TL), Caribbean Sea; BMNH 1857.6.13.(175?), stuffed male (650 mm TL), unknown locality; BMNH 2004.11.27.47, stuffed male (700 mm TL), unknown locality; BMNH 1908.7.6.30, stuffed female (750 mm TL), Gulf of Mexico, Pánuco River, Near Tampico, Mexico; BMNH 1848.7.28.40, stuffed (715 mm TL), Mexico (W. Atlantic); BMNH 1876.5.24.35, stuffed female (4170 mm TL), 3/1876, Caribbean Sea, San Fernando, Trinidad and Tobago; BMNH 1945.11.12.1, isolated rostrum, Caribbean Sea, West Indies; uncat. UF, isolated rostrum, 1960s, Caribbean Sea, Tortuguero, Costa Rica; UF 48061/Z 5677, isolated rostrum, 1912, Gulf of Mexico, Anna Maria Sound, Anna Maria Island, Manatee County, Florida, USA; unknown UF (? 80992), isolated rostrum, unknown locality; unknown UF (? 16608 or 80991), isolated rostrum, unknown locality; unknown UF (? 90468), isolated rostrum, unknown locality; unknown UF (? 90379), isolated rostrum, unknown locality; unknown UF (? 90378), isolated rostrum, unknown locality; unknown UF (? 83171), isolated rostrum, unknown locality; uncat. UF (Zooarch), isolated rostrum, unknown locality; USNM 00127141, female (801 mm TL), 7/7/1930, Gulf of Mexico, Quatre Bayou Pass, Louisiana, USA; USNM 00121000, female (866 mm TL), Caribbean Sea, Gulf of Venezuela, Venezuela; USNM 00205192, male (1152 mm TL), Cocoa, Florida, USA; USNM 00030678, male (675 mm TL), 1882, Gulf of Mexico, Pensacola, Florida, USA; USNM 00015453, stuffed male (746 mm TL), 5/1875 or earlier, unknown locality; USNM 00029091, isolated rostrum, summer 1870, Gulf of Mexico, Brazos Santiago Harbor, Texas, USA; USNM 00110149, isolated rostrum, Florida, USA; USNM 00110175, isolated rostrum, 'Guanajuato'(?), Mexico; USNM 00110176, isolated rostrum, unknown locality; USNM 00110177, isolated rostrum, unknown locality; USNM 00110248, isolated rostrum, unknown locality; USNM 00110324, isolated rostrum, 7/1939 or earlier, unknown locality; USNM 00111368, isolated rostrum, 10/1943, 'Lake Nicaragua'(?), Nicaragua; USNM 00111392, isolated rostrum, 1/12/1944, unknown locality; USNM 00232685 (first of three), isolated rostrum, Gulf of Mexico, Tarpon Springs, USA; USNM 00232685 (second of three), isolated rostrum, Gulf of Mexico, Tarpon Springs, USA; USNM 00232685 (third of three), isolated rostrum, Gulf of Mexico, Tarpon Springs, Florida, USA; USNM 00232687, isolated rostrum, unknown locality; USNM 00232968, isolated rostrum, Ft. Macon, North Carolina, USA; USNM 00232969, isolated rostrum, unknown locality; USNM 00260348, isolated rostrum, Cape Romain Lighthouse, South Carolina, USA; USNM 00260349, isolated rostrum, Colombia (Atlantic, inferred); USNM 00260350, isolated rostrum, unknown locality.

Additional material

Isolated rostra from private collections: 1993 or earlier, unknown locality ($N = 1$); 1/1997 or earlier, Florida?, USA? ($N = 1$); 1956, Gulf of Mexico, USA ($N = 1$); 6/1999 or earlier, unknown locality ($N = 1$).

Photograph of a complete specimen from a public collection: LACM 42016.001, unsexed (4430 mm TL), 3/8/1882, Indian River Inlet, Florida, USA.

Photographs of rostra from public collections: IFAN R956, female (4600 mm TL), 7/11/1956, Joal, Senegal; IFAN R 1B, unsexed (3150 mm TL), 3/28/1959, Joal, Senegal; IFAN R969, Casamance, Senegal?; IFAN R973, R962, R975, and two uncatalogued IFAN, unknown locality ($N = 5$); LACM 39297.002, .003, .004, .005, 006, .008, and .009, Florida, USA ($N = 7$).

Photographs of isolated rostra from private collections: 1940–1950, Gulf of Mexico, Collier County, Florida, USA ($N = 1$); 2000 or earlier, Florida?, USA? ($N = 1$).

Number of rostral teeth per side data from specimens from public collections: CAS-13512(?), female (723 mm TL), Georgetown, Guyana; LACM 42017.002, Atlantic Ocean; SU 10630, male (690 mm TL), Gulf of Mexico, Florida, USA; SU 14334, male (750 mm TL), 5/1935, Tarpon Bay, Sanibel Island, Lee County, Florida, USA.

Number of rostral teeth per side data from Robillard & Séret (2006): 4/1980 and *c.* 1990, Alcatraz, Republic of Guinea ($N = 2$); Kamsar, Republic of Guinea ($N = 2$); 1988, Kamsar, Republic of Guinea ($N = 1$); Bijagos, Guinea-Bissau ($N = 1$); *c.* 1987, Orango, Guinea Bissau ($N = 1$); Formosa, Guinea-Bissau ($N = 1$); Bolama, Guinea-Bissau ($N = 1$); 1977, Kartong, Gambia ($N = 1$); 1990, Joal, Senegal ($N = 1$); *c.* 1975, Kayar, Senegal ($N = 1$).

PRISTIS ZIJSRON BLEEKER, 1851

RMNH D7418 (holotype), isolated rostrum, Indonesia; FMNH 13266, isolated rostrum, Borneo; MCZ –670, isolated rostrum, mid-1800s, Fiji Islands; AMNH 44048, females (812 and 818 mm TL) and male

(680 mm TL), 1931, Jakarta market, Java, Indonesia (*N* = 3); ANSP 101398, male (723 mm TL), before 1985, unknown locality; YPM 14918, isolated rostrum, unknown locality; MNHN 1888-252, isolated rostrum, 1888, Persian Gulf; MNHN 1986-1077, isolated rostrum, unknown locality; MNHN 1888-253, isolated rostrum, 1888 or earlier, Persian Gulf; MNHN 1895-3, isolated rostrum, 1895, Gulf of Thailand, Thailand?–Cambodia?; MNHN 0000-3485, dry female (819 mm TL), 1830, Red Sea; MNHN 0000-3486, dry female (920 mm TL), Red Sea; MNHN 1967-0949, female (712 mm TL), 1/1929, Tawila Island, Red Sea, Egypt; MNHN 1967-0948, female (723 mm TL), 1929, Red Sea; MNHN 0000-1226, male (890 mm TL), 1856, Ambon, Indonesia; MNHN 1901-492, dry female (1565 mm TL), 1909, Somalia; RMNH 34070, male (393 mm TL), 1872/1877, Java Sea, Ambon, Indonesia; RMNH 34134, caudal fin, Indonesia; RMNH 7418, male (1035 mm TL), before 1879 (auction date), Java Sea, Banjarmasin, Borneo, Indonesia; RMNH 34129, female (761 mm TL), 1864, Banda Sea, Ambon, Indonesia; RMNH 34130, female (766 mm TL), 1864, Banda Sea, Ambon, Indonesia; RMNH 4232, juvenile male (488 mm TL), Sulawesi, Makassar, Indonesia; RMNH D2661, dry female (714 mm TL), Red Sea; RMNH D2663, dry female (860 mm TL), Borneo; RMNH D3102, isolated rostrum, Banda Sea, Ceram Island, Indonesia; RMNH D3109, isolated rostrum, unknown locality; RMNH D3076, isolated rostrum, 1/1915, Surabaya, Java, Indonesia; RMNH D3077, isolated rostrum, before 1939, unknown locality; RMNH D3101, isolated rostrum, 9/18/1962, near Massawa, Red Sea (south), Eritrea; RMNH D3111, isolated rostrum, unknown locality; RMNH D3104, isolated rostrum, unknown locality; RMNH D3113, isolated rostrum, unknown locality; RMNH D3113, isolated rostrum, unknown locality; uncat. RMNH, isolated rostrum, unknown locality; RMNH D3098, isolated rostrum, 9/18/1962, near Massawa, Red Sea (south), Eritrea; RMNH D3097, isolated rostrum, 9/18/1962, Massawa, Red Sea (south), Eritrea; RMNH D3108, isolated rostrum, 1942 or earlier, unknown locality; RMNH D3099, isolated rostrum, before 1860, unknown locality; MRAC A4-045-P-1, isolated rostrum, 'Congo' (probably a mistake); MRAC 98-082-P-0001, isolated rostrum, 1897 or before, Red Sea; MRAC 98-082-P-002, isolated rostrum, unknown locality; ZMB 33554, dry male (2460 mm TL), unknown locality; ZMB 33571, isolated rostrum, unknown locality; ZMB 33572, isolated rostrum, unknown locality; ZMB 33576, isolated rostrum, unknown locality; ZMB 33579, dry, unsexed, unknown locality; BMNH 1925.7.20.59-60 (first of three), isolated head with attached rostrum, Gulf of Aden, Arabian Sea; BMNH 1925.7.20.59-60 (second of three), isolated head with attached rostrum, Gulf of Aden, Arabian Sea; BMNH 1925.7.20.59-60 (third of three), isolated head with attached rostrum, Gulf of Aden, Arabian Sea; BMNH 1867.11.28.184, male (876 mm TL), 1867, W. Pacific; uncat. BMNH, isolated head with attached rostrum, unknown locality; BMNH 1922.1.13.7, wet head and body skin of female (1848 mm TL), Durban Bay, South Africa; BMNH 1925.7.20.53, female (768 mm TL), Gulf of Aden, Arabian Sea; BMNH 1925.7.20.54, female (760 mm TL), Gulf of Aden, Arabian Sea; BMNH 1925.7.20.55, male (782 mm TL), Gulf of Aden, Arabian Sea; BMNH 1925.7.20.56, female (730 mm TL), Gulf of Aden, Arabian Sea; BMNH 1925.7.20.57, female (756 mm TL), Gulf of Aden, Arabian Sea; BMNH 1925.7.20.58, male (790 mm TL), Gulf of Aden, Arabian Sea; BMNH 1880.1.10.2, isolated rostrum, unknown locality; BMNH 1861.5.6.2, isolated rostrum, unknown locality; BMNH 1982.9.13.8, isolated rostrum, before 1960, Persian Gulf, Mesopotamia, Iraq; BMNH 1984.5.29.1, isolated rostrum, Mornington Island, Gulf of Carpentaria, Australia; unknown BMNH, isolated rostrum, Persian Gulf?; BMNH 1982.9.13.10, isolated rostrum, Persian Gulf; BMNH 1982.9.13.9, isolated rostrum, Persian Gulf, Fao (Al-Faw), Iraq; BMNH 1841.12.22.2, isolated rostrum, India; BMNH 1950.10.3.1, isolated rostrum, China Sea; BMNH 2004.11.27.24, isolated rostrum, unknown locality; BMNH 2004.11.27.26, isolated rostrum, unknown locality; BMNH 2004.11.27.28, isolated rostrum, unknown locality; BMNH 2004.11.27.29, isolated rostrum, unknown locality; BMNH 2004.11.27.30, isolated rostrum, unknown locality; BMNH 2004.11.27.31, isolated rostrum, unknown locality; BMNH 2004.11.27.32, isolated rostrum, unknown locality; BMNH 2004.11.27.33, isolated rostrum, unknown locality; BMNH 2004.11.27.34, isolated rostrum, unknown locality; BMNH 2004.11.27.36, isolated rostrum, unknown locality; BMNH 2004.11.27.37, isolated rostrum, unknown locality; BMNH 2004.11.27.38, isolated rostrum, unknown locality; BMNH 2004.11.27.41, incomplete isolated rostrum, unknown locality; BMNH 2004.11.27.42, isolated rostrum, unknown locality; BMNH 1982.9.13.12, isolated rostrum, Persian Gulf, Fao (Al-Faw), Iraq; BMNH 1982.9.13.11, isolated rostrum, Tasman Sea, Rabbit Island, New Zealand; BMNH 2004.11.27.49, dry female (920 mm TL), Sarawak, Borneo, Malaysia; BMNH 2004.11.27.48, dry male (1010 mm TL), unknown locality; BMNH 1858.11.19.8, dry juvenile male (1005 mm TL), Banda Sea, Ambon, Indonesia; BMNH 1996.1.25.4 or 2004.11.27.46, incomplete isolated rostrum, unknown locality; BMNH 1849.1.30.21, dry male (2310 mm TL), Cape of Good Hope, South Africa; BMNH 1982.11.2.1, dry male (2105 mm TL), West Pacific ('East Indies'); USNM 00170489, female (912 mm TL), Sandakan Bay,

Borneo, Malaysia; USNM 00059857, juvenile male (795 mm TL), Clarence River, New South Wales, Australia; USNM 00040003, male (875 mm TL), received on 2/7/1889, Port Jackson, Australia; USNM 00232677, incomplete isolated rostrum, unknown locality; USNM 00263284, incomplete isolated rostrum, unknown locality.

Additional material
Isolated rostra from private collections: 5/1999 or earlier, unknown locality ($N = 1$); 1980, Burketown, Queensland, Australia ($N = 4$).

Photographs of specimens from private collections: Incomplete isolated rostrum, unknown locality ($N = 1$); photo of full-body adult, South Africa (dead specimen from the Sea World Aquarium, Durban, South Africa) ($N = 1$).

Number of rostral teeth per side data from specimens from public collections: CSIRO CA 3357, male (686 mm TL), NW continental shelf, Australia; ORI 951200, Richards Bay?, KwaZulu-Natal, South Africa; SAM 23005, Sri Lanka?; SAM 930519, skeleton of an male (4262 mm TL), Richards Bay, KwaZulu-Natal, South Africa; SU 40592, 5/1/1929–5/31/1929, Sepik River, East Sepik Province, Papua New Guinea; SU 40862, 9/1/1940–9/30/1940, Mindanao Island, Zamboanga State, Philippines.

ANOXYPRISTIS CUSPIDATA (LATHAM, 1794)

MNHN 0000-1250 (neotype), female (799 mm TL), Malabar, India; FMNH 13267, isolated rostrum, Borneo; FMNH 13268, isolated rostrum, Borneo; FMNH 59931, isolated rostrum, unknown locality; FMNH 59933, isolated rostrum, unknown locality; FMNH 91306, female (285 mm TL), 7/27/1976, Trivandrum, Kerala, India; MCZ 669 (first of two), isolated rostrum, unknown locality; MCZ 669 (second of two), isolated rostrum, unknown locality; MCZ 153654, isolated rostrum, unknown locality; AMNH 44009, female (1206 mm TL), 1931, Jakarta, Java Island, Indonesia; ANSP 51299, male (545 mm TL), Bombay, India; YPM 11731, isolated rostrum, China; YPM 11947, isolated rostrum, 1898 or before, unknown locality; MNHN 1986-1076, isolated rostrum, unknown locality; MNHN 1986-1075, isolated rostrum, unknown locality; MNHN 1986-1078, isolated rostrum, Indian Ocean; MNHN 0000-3459, dry female (801 mm TL), Indian Ocean; MNHN 0000-1234 (first of two), male (654 mm TL), Coromandel, Pondicherry, India; MNHN 0000-1234 (second of two), juvenile male (657 mm TL), Coromandel, Pondicherry, India; MNHN 0000-1236, male (646 mm TL), Malabar, India; MNHN A-7909, female (705 mm TL), Malabar, India; RMNH 7420 (first of two), juvenile male (782 mm TL), before 1879, Java Sea, Jakarta or Semarang, Indonesia; RMNH 7420 (second of two), female (716 mm TL), before 1879, Java Sea, Jakarta or Semarang, Indonesia; RMNH 8003, male (717 mm TL), 1852/1854, Indonesia ('O. I. Arch'); RMNH 4846, male (645 mm TL), Indonesia ('Arch. Ind.'); RMNH D2750, dry female (618 mm TL), unknown locality; RMNH D3062, isolated rostrum, Indonesia; RMNH D3064, isolated rostrum, 3/1955, south of Pulau Yos Sudarso ['Frederik (Hendrik) Island'], southern New Guinea, Indonesia; RMNH D3066, isolated rostrum, 3/1955, south of Pulau Yos Sudarso ['Frederik (Hendrik) Island'], southern New Guinea, Indonesia; RMNH D3067, isolated rostrum, Pulau Yos Sudarso ['Frederik (Hendrik) Island'], southern New Guinea, Indonesia; RMNH D3061, isolated rostrum, unknown locality; RMNH D3068, isolated rostrum, 11/15/1966, unknown locality; RMNH D3063, isolated rostrum, before 1938, unknown locality; RMNH D3065, isolated rostrum, unknown locality; ZMB 4523, unsexed (555 mm TL), unknown locality; ZMB 32537, isolated rostrum, Calcutta, India; ZMB 33580, dry, unsexed, unknown locality; ZMB 33581, dry, unsexed, unknown locality; ZMB 33582, dry, unsexed, unknown locality; ZMB 33583, isolated rostrum, unknown locality; ZMB 33584, isolated rostrum, unknown locality; ZMB 32536, isolated rostrum, unknown locality; ZMB 13412, dry, unsexed, unknown locality; ZMB 14688, dry, unsexed, unknown locality; BMNH 1983.1.7.4, male (697 mm TL), 'Christmas Island, Australia or Sumatra, Indonesia'; BMNH 1867.11.28.186, female (686 mm TL), 1867, Indonesia; BMNH 1866.8.14.2, male (655 mm TL), unknown locality; BMNH 1906.10.24.11, female (349 mm TL), Laccadive Sea, Travancore, India; BMNH 1963.9.26.1, male (1215 mm TL), Persian Gulf; BMNH 1867.4.2.197, isolated rostrum, unknown locality; BMNH 1862.7.18.3, isolated rostrum, unknown locality; BMNH 1862.7.18.4, isolated rostrum, unknown locality; BMNH 1862.7.18.5, isolated rostrum, unknown locality; BMNH 1862.7.18.6, isolated rostrum, unknown locality; BMNH 1862.7.18.7, isolated rostrum, unknown locality; BMNH 1862.7.18.8, isolated rostrum, unknown locality; BMNH 1862.7.18.9, isolated rostrum, unknown locality; BMNH 1982.9.13.2, isolated rostrum, unknown locality; BMNH 2004.11.27.44, isolated rostrum, unknown locality; BMNH 2004.11.27.45, isolated rostrum, unknown locality; BMNH 1982.9.13.1, isolated rostrum, Persian Gulf; BMNH 1849.7.27.28, dry female (1185 mm TL), India; BMNH 1858.3.17.8, dry female (1225 mm TL), unknown locality; BMNH 1960.4.1.1, dry male (1040 mm TL), unknown locality; BMNH 1850.11.18.61, dry female (531 mm TL), 'India & Borneo';

BMNH 1850.11.18.50, dry (555 mm TL), unknown locality; BMNH 2004.11.27.50, isolated rostrum and head, Bengal, India; BMNH 1850.11.18.63, dry male (583 mm TL), 'India & Borneo'; BMNH 1860.3.19.1464, dry male (1170 mm TL), E. Indian Ocean; uncat. BMNH, dry female (3280 mm TL), unknown locality; BMNH 1844.3.25.143/2004.11.27.52, isolated rostrum, Tenasserim River, Myanmar (Burma); BMNH 1880.1.3.2, isolated rostrum, 'Atlantic . . .' (probably a mistake); BMNH 1982.11.2.2, dry female (2125 mm TL), W. Pacific ('East Indies'); USNM 00232695, isolated rostrum, Madras, India; USNM 00367980, isolated rostrum, *c.* 1961–1964, Bay of Bengal, Cox's Bazar (town), Bangladesh.

Additional material
Isolated rostra from private collections: 11/1998 or earlier, Australia ($N = 1$); 4/1999 or earlier, Arnhem Land, Australia ($N = 2$); 10/2000 or earlier, Gulf of Papua, Papua New Guinea ($N = 1$); unknown date, Bushehr, Iran ($N = 1$); 1994 or earlier, unknown locality ($N = 3$); 1999 or earlier, unknown locality ($N = 2$).

Photograph of isolated rostrum from a private collection: Early 1980s or earlier, unknown locality ($N = 1$).

Number of rostral teeth per side data from specimens from public collections: AMS I-15557-006, female (557 mm TL), Australia; uncat. CAS (CAS 1975-IX:29), male (528 mm TL), 1975?, Pakistan; uncat. CAS (CAS 1975-IX:29), female (512 mm TL), 1975?, Pakistan; uncat. CAS (CAS 1975-IX:29), skeleton of a male (510 mm TL), 1975?, Pakistan; uncat. CAS (CAS 1975-IX:29), female (518 mm TL), 1975?, Pakistan; uncat. CAS (GVF 2487), male (770 mm TL), Ko Kut, 5–16 miles east, Trat Province, Thailand; uncat. CAS (GVF 2487), female (665 mm TL), Ko Kut, 5–16 miles east, Trat Province, Thailand; uncat. CAS (GVF 2513), male (1660 mm TL), Koh Samui, 1.5–5 miles offshore, Surat Thani Province, Thailand; uncat. CAS (GVF 2513), female (1372 mm TL), Koh Samui, 1.5–5 miles offshore, Surat Thani Province, Thailand; uncat. CAS (GVF 2563), female (1540 mm TL), Koh Samui, 1.5–5 miles offshore, Surat Thani Province, Thailand; uncat. CAS (GVF 2563), female (1556 mm TL), Koh Samui, 1.5–5 miles offshore, Surat Thani Province, Thailand; uncat. CAS (GVF 60–109), female (1404 mm TL), Koh Samui, Surat Thani Province, Thailand; uncat. CAS (GVF 60–134), male (586 mm TL), northern Gulf of Thailand, Thailand; uncat. CAS (GVF 60–134), female (575 mm TL), northern Gulf of Thailand, Thailand; uncat. CAS (GVF 60–134), female (561 mm TL), northern Gulf of Thailand, Thailand; uncat. CAS (GVF 60–134), male (575 mm TL), northern Gulf of Thailand, Thailand; uncat. CAS (GVF 60–210), female (920 mm TL), Trat Province, Thailand; uncat. CAS (GVF 60–397), female (515 mm TL), Ko Chang, Trat Province, Thailand; uncat. CAS (GVF 81), female (1154 mm TL), Thailand; uncat. CAS (GVF 81), male (1008 mm TL), Thailand; uncat. CAS (GVF 81), male (752 mm TL), Thailand; SU 14514, female (610 mm TL), 1/14/1941, Calicut (Kozhikode), Kerala State, India; SU 18036, male (692 mm TL), 2/22/1937, South China Sea, Singapore.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional details of methods and haplotype descriptions.