A summary of the available data on shark fishing activities in Papua New Guinea

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Summary and key results

This paper has been produced under the ACIAR funded project titled '*Sustainable Management of the Shark Resources in PNG: Socio-economic and Biological Characteristics*'. It summarises existing time series data held by the National Fisheries Authority (NFA) that are relevant to shark fishing activities in Papua New Guinea (PNG). The data presented are relevant to both the socio-economic and biological components of the project. The key findings of the paper are summarised as follows:

- Available data that is relevant to small-scale and/or large scale shark fishing activities in PNG include shark fin purchase data, international trade (export and import) data and fishery catch and effort data.

- **The NFA shark fin purchase data** shows that fin purchases were reported in a total of 14 provinces for the 2004 to 2012 period and the average annual total purchases for the period was 13,253 kilograms. Purchases peaked at just under 26,000 kilograms in 2012 but preliminary data suggests a large decline in total fin purchases to 7,500 kilograms in 2013.

- Potential issues with the NFA shark fin purchase data that require further investigation include double counting of purchases and possible data collection gaps due to exporting by vertically integrated businesses (that catch and export fin) and purchases by non-registered buyers. The usefulness of the data could be improved with more detailed information on the ward from which fin have been purchase from and also the entity type (e.g. fisher, buyer, company). Despite these issues, the collection of fin purchase data provides a cost-effective means to monitoring shark fin activities (particularly if it represents small-scale activities) and should be maintained.

- Analysis of NFA shark fin purchase data by province and local level government area (LLG) provides an indication of where shark fin production is occurring. High quantity provinces identified include the National Capital District (NCD), Milne Bay, Manus, New Ireland and Morobe. High quantity LLGs within these and other provinces are also identified. Data collection targeted at high quantity LLGs may represent value for money for the project given the high amount of shark fishing that is likely to be occurring in these areas.

- **The NFA export data for shark longline and tuna longline companies** report an average annual export quantity of 169,300 kilograms. This includes a peak of 548,000 kilograms in 2011 which is likely to be dominated by exports from the Tuna Longline Fishery. Export quantities in 2013 declined to their lowest

quantity for the period of 64,000 kilograms. Export prices for shark fin appear to be significantly underreported in the data.

- Quantities in the NFA export data are far higher than quantities reported in the NFA shark fin purchase data. This indicates that the NFA shark fin purchase data are more representative of small-scale shark fin production activities which is to be expected given that small-scale fishers and middlemen have direct access to domestic shark fin purchasers. It also suggests that PNG's shark fin production has historically been dominated by large-scale rather than small-scale production activities.

- Quantities in the NFA export data are far higher than quantities reported in both FAO export statistics and Hong Kong import statistics. If the NFA data sourced from companies are accurate, then FAO estimates of PNG's shark fin exports are underreported by an order of magnitude of up to 46 times. Low quantities in the Hong Kong data relative to the NFA export data suggest that companies are exporting to somewhere other than Hong Kong (discussions with the shark longline industry have indicated that Taiwan is the main destination).

- **Shark Longline Fishery data** shows that the fishery's catch was largely dominated by blue shark between 2002 and 2005 but became dominated by silky shark catches post 2006. The catch of silky shark peaked in 2011 at 1.23 million kilograms, when total catch was 1.42 million kilograms. In the two years since 2011, reported catches in the fishery declined significantly and total catch in 2013 was 0.71 million kilograms. The fishery has now ceased its operations with a ban on the retention of silky shark introduced in 2014.

1. Introduction

Over the last three decades, the international harvest of shark species has increased considerably. This has been driven by an escalation in the prices paid for shark fin, propelled by rising demand for fin in China (Bonfil 1994; Clarke 2004; Mejuto & Garcia-Cortes 1996; Rose 1996). The sustainability of these trends has become a major concern for fishery management organisations as most shark species are highly susceptible to overexploitation due to their slow growth rates and low productivity (Hoenig and Gruber 1996; Stevens et al. 2000).

For the Pacific Island nation of Papua New Guinea (PNG), domestic catches of shark have followed these international trends (Kumoru 2003; Opu 2007). There is evidence of increased catches by the country's small-scale inshore fishers (Foale 2005; Sabetian & Foale 2006) for whom shark fin represents an easy opportunity to access cash. For larger-scale offshore fishers, there has also been evidence of increased targeting and retention of shark, with a separately managed shark fishery being established in 2002 (Kumoru 2003). Given these developments, there is a need for greater information about PNG's shark catches. The ACIAR funded project titled '*Sustainable Management of the Shark Resources in PNG: Socio-economic and Biological Characteristics*' aims to address this need.

The current paper has been produced under the latter project. Its main aim is to provide an improved understanding of existing time series data that relate to shark fishing activities in PNG. To do this, relevant data that are collected by the National Fisheries Authority (NFA) (the agency responsible for fisheries management in PNG) are summarised and evaluated. Observations that may guide research under the current ACIAR project are also identified.

In doing all of the above, this paper provides insights that are relevant to multiple components of the project including those focused on artisanal biological sampling, socio-economic data collection and stock assessment. Furthermore, by providing recommendations on ways to potentially improve the data that is available on shark fishing, this paper contributes to the project's overall objectives of facilitating more informed management of PNG's shark fisheries.

2. Available data

The data available on shark fishing in PNG varies according to the type of fishing activity. Two categories are referred to here: small-scale fishing and large-scale fishing.

Small-scale fishing refers to activities by fishers that are restricted to shallow, inshore waters. Such fishers use small, low-technology vessels (e.g. canoes, traditional sailing craft and dinghies) or shore based fishing methods (e.g. collecting and spearing). In PNG, small-scale fishing for shark occurs throughout the islands and coastal areas. Such fishing can be subsistence based, providing food for consumption or trade; culturally or spiritually based, as is the case for the '*shark calling*' practices of fishers in New Ireland (Groves 1936; Köhnke 1974; Ruben & Rosman 1981); or commercially based as is the case for fishing for shark fin where fins are sold for cash.

Large-scale fishing is undertaken by larger, more technologically advanced vessels in offshore waters. By travelling greater distances, staying at sea longer and using larger, more efficient fishing gear, these fishers take larger catches (on a per vessel basis). Such fishing activities are typically commercial. In recent years in PNG, large-scale shark fishing has mainly occurred in a single target fishery – the Shark Longline Fishery (Kumoru 2003). A number of large-scale fisheries also take shark as bycatch. These include the Tuna Longline Fishery and the Prawn Trawl Fishery (ref).

Time series data on small-scale fishing activities are typically limited. This reflects the difficulties associated with monitoring such activities given the large number of fishers involved and the isolated and dispersed nature of such fishing. The only data that does exist often comes from one off studies. In the case of PNG, such one off studies include Kaly and Preston (2006), Kaly (2005) and Kaly (2006). In the case of large-scale fisheries, time series catch and effort data are ordinarily collected by fishery management organisations. This is the case in PNG. The more commercial nature of large-scale fishing also means that fishery product export data can often be a valuable source of information.

For shark fishing in PNG specifically, three sources of time series data are available:

- ***Shark fin purchase data:*** this data is collected by NFA from registered shark fin buyers . These data are likely to capture the production of shark fin by small-scale fishers and, to less of a degree, large-scale fishers. If dominated by small-scale purchases, this data could provide an indication of trends in small-scale shark fishing.

- ***Shark product export data:*** the data provided by NFA has been collected from companies associated with the large-scale Shark Longline and Tuna Longline fisheries. The data are collected as NFA must approve all exports of fisheries products. These data provide an indication of the quantity of shark fin production within these two fisheries and the kina value that this production generates.

- ***Fishery catch and effort data:*** NFA collects such data for individual large-scale fisheries. For the Shark Longline Fishery, catch and effort data has been collected for the fishery since it started in 2001. Such data are also available for large-scale shark bycatch fisheries but are not presented here.

In what follows, each of the above data sets are presented, analysed and discussed.

3. NFA Shark Fin Purchase Data

The NFA Shark Fin Purchase Data is provided by shore-based operators who are licensed to purchase, process and trade a range of fishery products including shark. The requirement to be licensed allows NFA to monitor and approve trade in these marine products. The data presented here reflect purchases of shark fin by licensed operators from fishers and other small-scale, village based buyers and middle-men.

Shark fin purchase quantities are collected on a monthly basis. The data includes the following fields which have been accessed by the authors for the current report:

- Province – this is the province of the seller from which the shark was bought;
- Local level government (LLG) area – this is the LLG of the seller from which the shark fin was bought;
- Species – the species group with which the purchased shark fin is associated with.

The data also includes details of the company making the purchase, the month and year of summarised purchases and product type (including whether it is wet or dry product), whether the product is a high or low value species/product and details of the supplier/seller. However, this data has not yet been accessed and investigated.

The Shark Fin Purchase Data is first presented in aggregate by province, then by LLG for key provinces and then species group. Data are presented for the 2004 to 2012 period. Preliminary 2013 data are only presented in aggregate in the next section of the report as at the time of writing it could not be confirmed how complete 2013 data were.

It should be noted that the Shark Fin Purchase Data may not capture all fin production in PNG. First, anecdotal evidence of buyers not registered with NFA being approved to make intra-provincial and/or transfers of shark fin (author's own field observations) represents one potential gap in this data. Secondly, shark fin that reach the export market through vertically integrated business structures (structures that include the entire supply chain - harvesting, processing and exporting) would not be picked up as such fin are not subject to a purchase transaction within PNG.

Aggregate and provincial fin purchases

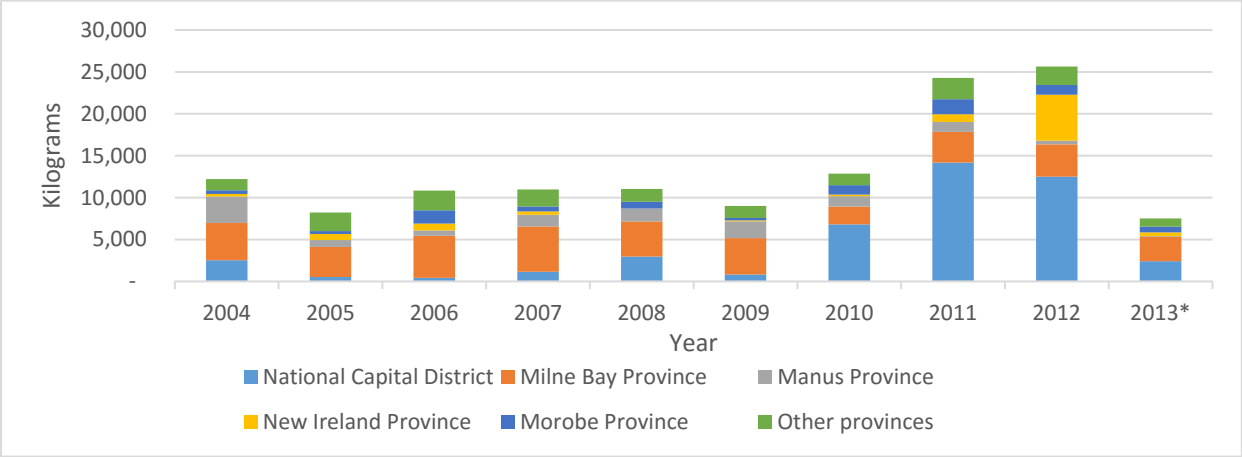
Purchases of shark fin remained relatively stable between 2004 and 2010 at between approximately 8,000 kilograms and 13,000 kilograms (Figure 1, Table 1). In the years that immediately followed, purchases increased considerably. In 2011, purchases increased by 89% relative to 2010 to just over 24,276 kilograms. Purchases increased further to 25,631 kilograms in 2012. Preliminary 2013 data suggests a dramatic turnaround, with a 71 per cent decline in the total quantity of fin purchases to 7,508 kilograms in 2013.

The increases between 2009 and 2012 coincide with the ban on Bech-de-mer fishing introduced throughout PNG in 2009 (Pomat 2012). This could suggest a shift in targeted fishing effort from Bech-de-mer to shark, the next highest value marine resource readily available to many fishers.

The preliminary estimate for 2013 is the lowest quantity recorded for the entire 2004 to 2013 period and falls were reported across all but one province in 2013 (Table 1). There has been recent evidence of an overall fall in fin purchasing activity within PNG as a result of reduced demand and prices on international markets (William White, personal communication, October 2014; and author's own observations). The scale of these falls in purchase volumes deserves some attention to confirm what is driving them.

Fin purchases were reported against a total of 14 provinces and one '*retained*' category. Reported purchases were dominated by purchases from sellers in the National Capital District (NCD) and Milne Bay Province (MBP). An additional three provinces reported distinctly high quantities: Manus Province, New Ireland Province and Morobe Province. The remainder of this section focuses on the reported purchases from these five high quantity provinces.

Figure 1 – Shark fin purchase origin reported by large-scale buyers by province, kilograms, 2004 – 2013*



Note: *2013 data is preliminary.

Table 1 – shark fin purchase origin reported by large-scale buyers by province, kilograms, 2004 – 2013*

Province	2004	2005	2006	2007	2008	2009	2010	2011	2012	*2013**	*Total*
National Capital District	2,538	531	439	1,160	2,970	823	6,802	14,173	12,508	*2,425*	***44,370***
Milne Bay Province	4,442	3,581	5,021	5,407	4,182	4,340	2,130	3,669	3,855	*2,867*	***39,494***
Manus Province	3,153	827	627	1,386	1,547	2,007	1,246	1,189	436	*112*	***12,530***
New Ireland Province	311	720	811	402	-	116	181	909	5,478	*443*	***9,371***
Morobe Province	435	341	1,583	585	805	282	1,138	1,806	1,177	*703*	***8,853***
East Sepik Province	0	858	528	484	329	723	3	404	544	*40*	***3,912***
Central Province	523	476	536	446	312	408	32	355	223	*126*	***3,437***
A.R. of Bougainville	188	227	543	506	277	20	550	305	719	*46*	***3,381***
Western Province	-	331	424	169	163	60	74	658	522	*700*	***3,100***
Madang Province	350	15	1	42	31	36	472	689	123	-	***1,759***
Oro Province	146	218	207	144	179	46	66	76	48	*26*	***1,157***
West New Britain Province	27	54	81	69	18	115	167	40	-	*20*	***591***
Retained	-	0	-	146	34	26	-	-	0	-	***205***
Gulf Province	2	1	2	-	183	-	-	2	-	-	***188***
East New Britain Province	95	32	30	22	-	-	-	1	0	-	***180***
Annual Total	**12,212**	**8,213**	**10,833**	**10,967**	**11,030**	**9,000**	**12,860**	**24,276**	**25,631**	**7,508**	***132,529***

Note: *2013 and Total data is preliminary.

National Capital District

Fin purchase data for the NCD is only reported down to the provincial level. NCD purchase quantities between 2004 and 2009 were relatively low, getting as low as 439 kilograms in 2006 (Table 1). Large quantities have only been

reported since 2010 with 6,802 kilograms reported in 2010, 14,173 kilograms in 2011 and 12,508 kilograms in 2012. The preliminary 2013 data suggests a substantial 81 per cent drop in NCD purchases to 2,425 kilograms.

The high quantity of purchases being reported as purchased from NCD based sellers (fishers and/or middlemen) is indicative of a high amount of shark fin being landed in Port Moresby. With Port Moresby being a major export hub for PNG, there may be a risk that some NCD shark fin purchases are being double counted. For example, buyers in NCD may purchase fin from other provinces and then on-sell to other NCD buyers. However, buyers are typically restricted to purchasing from sellers within their local province. The high purchase quantities reported for NCD and the degree to which double counting might be occurring there requires further exploration.

Milne Bay Province

Purchases from sellers based in MBP between 2004 and 2010 have exceeded 3,500 kilograms in all but one year, that year being 2010 (Figure 2, Table 2). MBP purchases peaked at 5,407 kilograms in 2007 and then fell to just above 4000 kilograms in 2008 and was maintained at a similar level in 2009. Purchases then fell in 2010 to their lowest level at 2,130 kilograms and it is unclear what caused this decline. Purchases recovered in 2011 to 3,669 kilograms and 3,855 kilograms in 2012. The preliminary 2013 data (Table 1) suggests a 26 per cent decline in MBP fin purchases to 2,867 kilograms. This fall, however, is small relative to the falls observed in other provinces in 2013.

Total purchases from MBP over the period 2004 to 2012 were dominated by purchases from four LLGs – Bwanabwana, Yaleyemba, Louisiade and Kiriwina. Together, reported purchases in these four LLGs accounted for 59 per cent of total reported volumes for MBP over the full period.

Bwanabwana and Yaleyemba were associated with the highest quantity of shark fin purchases, both with a total of 6,112 kilograms and an average annual quantity of 679 kilograms for the 2004 to 2012 period. Purchases from Bwanabwana for the 2004 to 2012 period were relatively consistent ranging between 384 kilograms (in 2010) and 2011 kilograms (2006). Shark fin purchases from Yaleyemba have been relatively more variable, with peaks of 1320 kilograms and 1467 kilograms reported in 2009 and 2011 respectively and a low of 143 kilograms reported in 2010.

Shark fin purchase volumes from Louisiade and Kiriwina were far higher in years prior to 2010. For Louisiade, the average purchase quantity between 2004 and 2009 was 771 kilograms. From 2010 to 2012 it was far lower at 210 kilograms. Similarly for Kiriwina, the average purchase volume between 2004 and 2009 was 616 kilograms compared to 168 kilograms for the years between 2010 and 2012. It's possible that shark was taken opportunistically while fishing for bech-de-mer in these LLGs and that shark fin production has now declined with the bech-de-mer fishery's closure. Another possible factor may have been greater market access while the bech-de-mer fishery was open. Firstly, buying companies used to send out boats to buy bech-de-mer when the fishery was in operation. This would have also allowed fishers to easily sell their shark fins from the islands in these LLGs. Similarly, the higher returns from bech-de-mer relative to shark fin would have made travel to market to sell shark fins together with bech-de-mer more viable.

Figure 2 –shark fin purchases from Milne Bay Province, 2004 to 2012

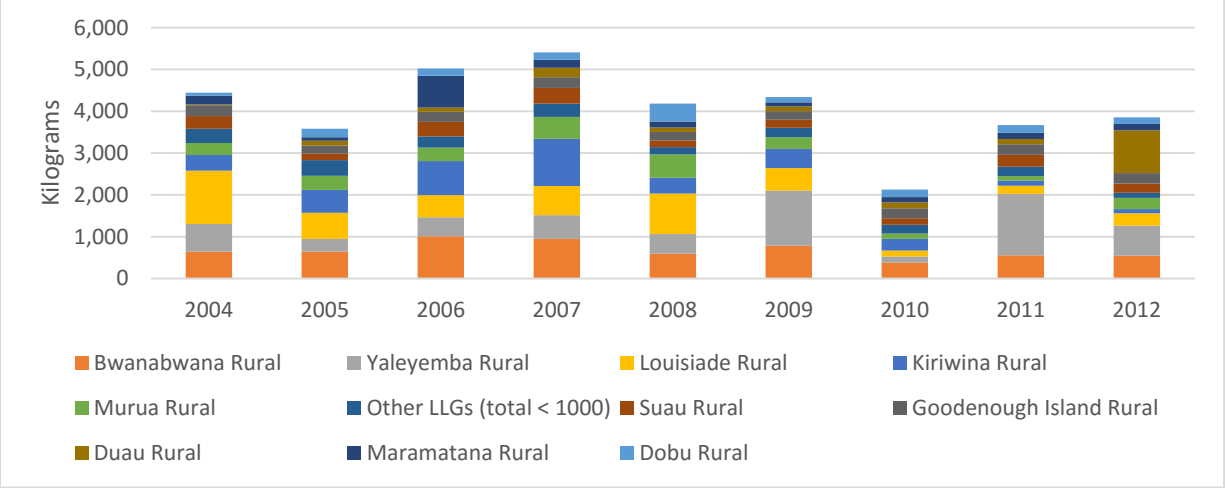


Table 2 – shark fin purchases by LLG for Milne Bay Province, kilograms, 2004 - 2012

LLG	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Bwanabwana Rural	643	644	1,011	947	593	786	384	556	546	**6,112**
Yaleyemba Rural	661	306	456	568	470	1,320	143	1,467	722	**6,112**
Louisiade Rural	1,274	625	528	697	967	535	141	195	294	**5,256**
Kiriwina Rural	376	544	813	1,128	380	457	282	120	101	**4,199**
Murua Rural	290	337	323	526	561	279	126	110	267	**2,819**
Suau Rural	302	157	348	374	160	192	156	283	225	**2,197**
Goodenough Isl. Rur.	260	193	241	259	205	204	238	253	247	**2,099**
Duau Rural	18	114	97	223	108	112	138	128	1,021	**1,960**
Maramatana Rural	209	84	761	193	141	99	130	147	155	**1,918**
Dobu Rural	71	202	174	177	427	128	180	184	157	**1,699**
West Ferguson Rural	255	252	80	94	62	68	52	53	27	**943**
Makamaka Rural	17	76	59	113	35	60	82	36	32	**509**
Huhu Rural	20	32	63	73	51	62	59	85	37	**483**
Weraura Rural	6	9	57	36	21	19	19	48	24	**238**
Alotau Urban	43	7	4	1		20				**74**
Daga Rural			5					4		**9**
Grand Total	**4,442**	**3,581**	**5,021**	**5,407**	**4,182**	**4,340**	**2,130**	**3,669**	**3,855**	**36,627**

Manus Province

A total of 12,418 kilograms of fin were purchased from sellers based in Manus Province between 2004 and 2012 making Manus the third largest fin producing province for the period (Table 3). The peak quantity occurred in 2004 at 3,153 kilograms (Figure 3). Quantities then declined in 2005 and 2006 before increasing in 2007. Purchase quantities, averaged 1,475 kilograms per year between 2007 and 2011. Purchase quantities then fell significantly in 2012 to 436 kilograms, their lowest level for the 2004 to 2012 period. Preliminary 2013 purchase data (Table 1) suggests quantities purchased from Manus Province may have fallen even further to 112 kilograms.

Nigoherm is by far the most dominant Manus LLG in terms of reported purchases. Purchases from this LLG totalled 3,300 kilograms between 2004 and 2012, although the majority of these purchases have been reported since 2007. The data for remaining Manus LLGs are quite patchy. Pobuma, Rapatona, Bisikani/Soparibeu and Pomutu/Kurti/Andra all have greater than 1000 kilograms of reported purchases for the 2004 to 2012 period, but of these only Rapatona had a sizable quantity reported in 2012 of 110 kilograms with the remaining LLGs reporting 19 kilograms or less. Rapatona, is probably one of the most consistent Manus Province LLGs with reported purchases greater than 100 kilograms in all but one of the nine years between 2004 and 2012. Balopa LLG has exhibited volumes greater than 100 kilograms in three of the five most recent years between 2008 and 2012. However, the remaining two years are associated with very low recordings of 6 kilograms in 2009 and 11 kilograms in 2012.

Figure 3 – shark fin purchases from Manus Province, 2004 to 2012

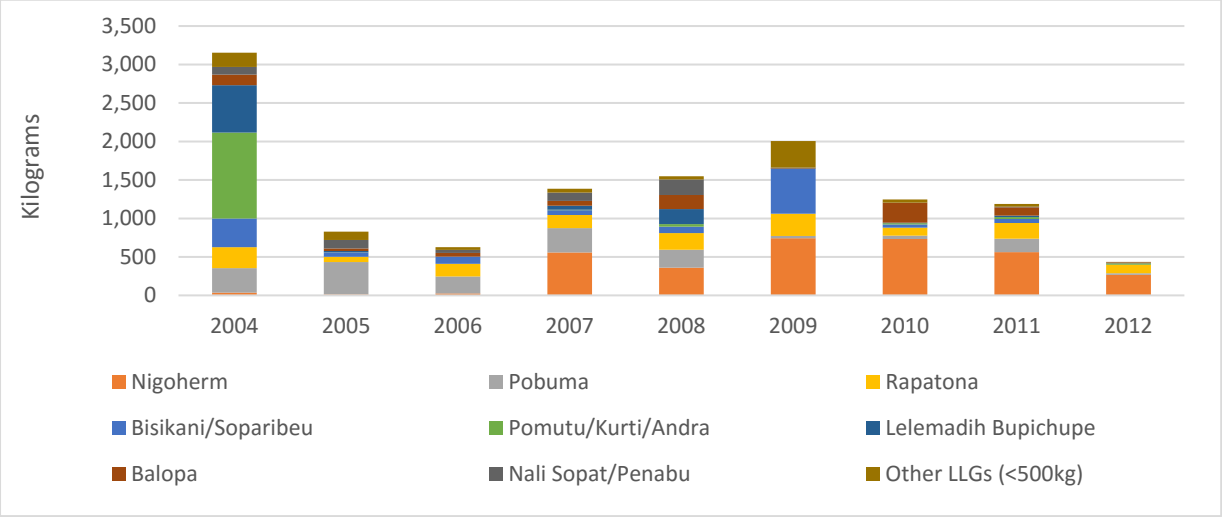


Table 3 – shark fin purchases by LLG for Manus Province, kilograms, 2004 - 2012

LLG	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Nigoherm	36	12	26	559	361	743	734	562	268	**3,300**
Pobuma	319	422	221	314	232	30	44	175	19	**1,776**
Rapatona	271	68	163	170	217	289	102	204	110	**1,596**
Bisikani/Soparibeu	373	58	94	63	83	586	42	51		**1,350**
Pomutu/Kurti/Andra	1,118	3		6	34	0	16	25	19	**1,220**
Lelemadih Bupichupe	615	14		52	196	1	6	20	3	**907**
Balopa	137	34	48	63	181	6	259	108	11	**847**
Nali Sopat/Penabu	99	110	41	108	203	5	2	8	2	**578**
Lorengau Urban	102	72		18	3	261		1	4	**462**
Los Negros	55	24	25	16	36	5	13	34		**208**
Aua Wuvulu	28	11	10	7		81	28			**164**
Tetedu				8	1	0		1		**10**
Grand Total	**3,153**	**827**	**627**	**1,386**	**1,547**	**2,007**	**1,246**	**1,189**	**436**	**12,418**

New Ireland Province

Historically, relatively low quantities of shark fin were reported as being purchased from sellers in New Ireland Province. Quantities had never got above 1000 kilograms prior to 2012 and were as low as 116 kilograms as recently as 2009 (Figure 4, Table 4). Additionally, in 2008, nil purchases were reported. However, between 2011 and 2012, purchases increased more than five-fold from 909 kilograms to 5,478 kilograms. The cause of the increase in 2012 is unclear and preliminary data (Table 1) indicate a fall to a historically more normal level of 443 kilograms in 2013. Without the high purchase quantity in 2012, total purchases from New Ireland for the 2004 to 2012 would be relatively low.

Tikana and Lovongai LLGs have accounted for the majority of fin purchases from New Ireland. For both LLGs, quantities reported prior to 2012 never got much above 200 kilograms. In 2012, reported purchases for Tikana increased more than 14 times from 101 kilograms in 2011 to 1324 kilograms in 2012. For Lovongai, purchases increased by a multiple of just over 9 times, from 142 kilograms in 2011 to 1,324 kilograms in 2012. Murat LLG had the third highest purchase quantity for the 2004 to 2012 period, a high proportion of which was recorded prior to 2008. Purchases from Murat increased between 2011 and 2012 from 68 kilograms to 359 kilograms, a small amount in absolute terms relative to other New Ireland LLGs. Other LLGs which reported high quantities in 2012 included Namatanai (with 884 kilograms), Kavieng (706 kilograms) and Central Niu Ailan (579 kilograms).

Figure 4 – shark fin purchases from New Ireland Province, 2004 - 2012

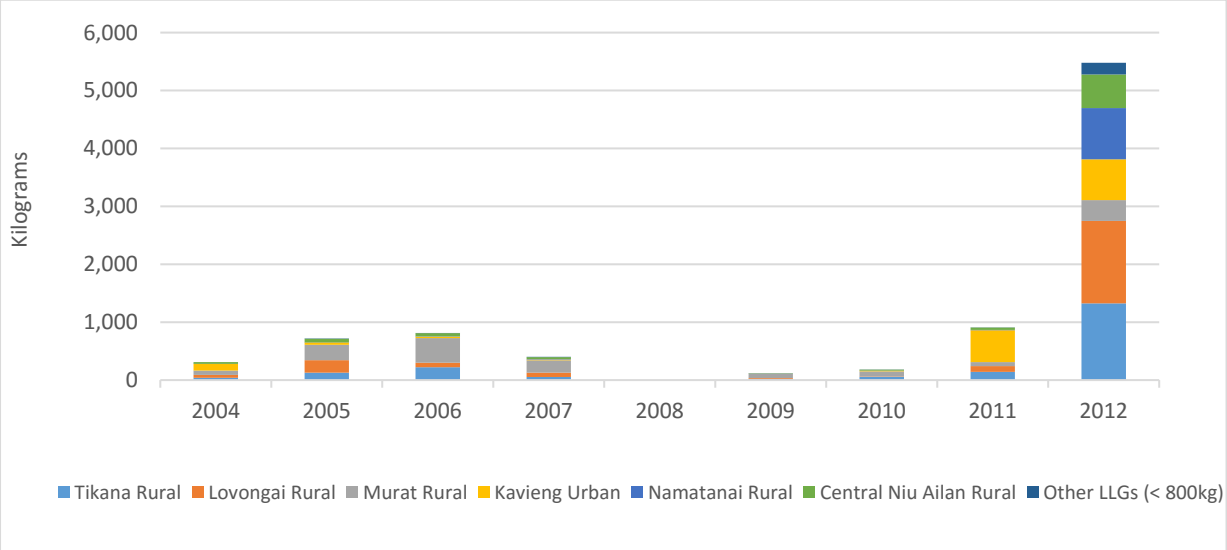


Table 4 – shark fin purchases by LLG for New Ireland Province, kilograms, 2004 - 2012

LLG	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Tikana Rural	41	128	222	53		20	54	142	1,324	**1,983**
Lovongai Rural	49	216	79	76		14	8	101	1,424	**1,966**
Murat Rural	74	266	426	213		72	90	68	359	**1,567**
Kavieng Urban	115	41	24	15		2	12	550	706	**1,463**
Namatanai Rural	0	0	5	8		0	1	6	884	**905**
Central Niu Ailan Rural	32	64	55	32		6	15	43	579	**825**
Nimamar Rural		6	0						132	**138**
Konoagil Rural				5		3	1	1	64	**73**
Tanir Rural			0	1					6	**7**
Grand Total	**311**	**720**	**811**	**402**		**116**	**181**	**909**	**5,478**	**8,928**

Morobe Province

Three of the four highest reported purchase quantities for Morobe Province occurred in the three years between 2010 and 2012 (Figure 5, Table 5). This coincides with the ban on Bech-de-mer and could reflect a shift in fishing effort in the province towards shark to replace lost income. Further investigation would be required to confirm this. Preliminary data (Table 1) suggests that purchase volumes in Morobe Province did decline in 2013 by 44 per cent to 703 kilograms although this is not far below the Province's average quantity for the 2004 to 2012 period of 906 kilograms.

Purchases are highly concentrated in two LLGs – Siassi Rural and Morobe Rural. Combined, the two LLGs accounted for 76 per cent of total purchase volumes between 2004 and 2012. Purchases from Morobe Rural have increased in every year since 2009 and peaked in 2012 at 724 kilograms. For Siassi Rural, purchases increased substantially in 2010 and 2011 but then declined, from 841 kilograms in 2011 to 265 kilograms in 2012.

Figure 5 –shark fin purchases from Morobe Province, 2004 - 2012

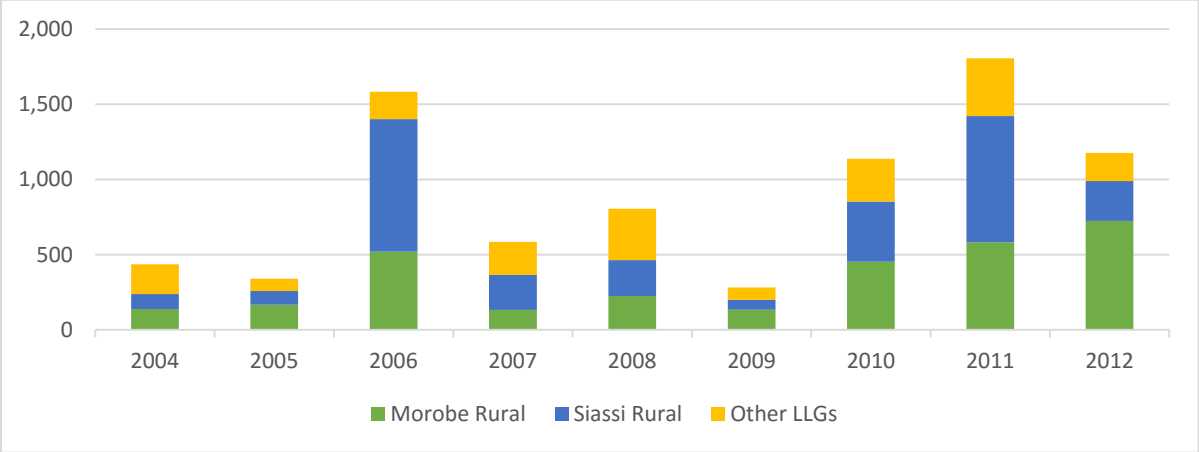


Table 5 – shark fin purchases by LLG for Morobe Province, kilograms, 2004 - 2012

LLG	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Siassi Rural	98	91	881	233	239	66	401	841	265	**3,114**
Morobe Rural	139	167	520	132	225	133	453	582	724	**3,075**
Hube Rural	150	18	19	125	100		31	15	27	**485**
Yabim Mape Rural	43	50	144	52	89	13	9	34		**434**
Wasu Rural		8	6	9	22	11	159	98	34	**346**
Labuta Rural					0	58	83	60	69	**270**
Lae Urban	4	6	13	13				176		**211**
Salamaua Rural				21	127	1			11	**160**
Sialum Rural					3		3		36	**43**
Kotte Rural									10	**10**
Onga/Waffa Rural			2							**2**
Nabak Rural								1		**1**
Grand Total	**435**	**341**	**1,583**	**585**	**805**	**282**	**1,138**	**1,806**	**1,177**	**8,150**

Other high volume LLGs

Shark fin purchases were reported against a total of 124 LLGs over the period 2004 to 2012. Beyond LLGs in the five high volume provinces, there are only six other LLGs that report greater than 1000 kilograms of purchases for the 2004 to 2012 period (Table 6). Of these, Wewak Islands Rural LLG, in the East Sepik Province, is by far the highest volume LLG with total purchases of 2,359 recorded for the 2004 to 2012 period, followed by Buka LLG in the North Solomons Province with 1,801 kilograms. The remaining four include Madang Urban (Madang Province), Kiwai Rural (Western [Fly]), Amazon Bay Rural (Central) and Daru Urban (Western [Fly]).

Table 6 – shark fin purchases from high volume LLGs in low volume provinces, kilograms, 2004–2012

LLG	Province	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Wewak Islands Rural	East Sepik	0	281	229	276	151	555		323	544	**2,359**
Buka	North Solomons (Bougainville)	107	87	289	222	156	7	331	141	461	**1,801**
Madang Urban	Madang	6		1	3	28	30	472	689	123	**1,351**
Kiwai Rural	Western (Fly)				81	158	59	74	518	455	**1,345**
Amazon Bay Rural	Central	78	39	194	138	61	37	32	351	205	**1,134**
Daru Urban	Western (Fly)		331	424	88	5			140	65	**1,053**

Fin purchases by species group

While fin purchases are reported against are range shark species groups for the 2004 to 2012, the information may not be very reliable given that typically fins have already been removed from the shark when purchased, making identification difficult. Furthermore, the majority of purchased fins are reported as "unspecified" (between 37% and 50% for any year in the period 2004 to 2012) (Table 7). As a result, the species level data is not discussed any further but is presented for information.

Table 7 – shark fin purchase quantities by species group, kilograms, 2004 – 2012

Species group	2004	2005	2006	2007	2008	2009	2010	2011	2012	TOTAL
Blue Shark	160			23	54	2	84	440	173	**936**
Brown Shark	1,373		3	17	1,428	238	761	4,770	3,166	**11,757**
Hammerhead					7					**7**
Mako (fin)				6	28		2	196	51	**284**
Saw Shark	438					55	187			**679**
Unspecified	10,241	8,213	10,830	10,921	9,411	8,706	11,802	18,096	21,706	**109,925**
White Shark					91		24	773	535	**1,423**
White Tip					10					**10**
Grand Total	**12,212**	**8,213**	**10,833**	**10,967**	**11,030**	**9,000**	**12,860**	**24,276**	**25,631**	**125,021**

4. NFA Shark Export Data

The catching of shark in PNG is largely driven by the high prices received for shark fin on export markets. As a result, the majority of fin produced in PNG is exported. Therefore, export data can provide a good alternative indicator of shark harvest levels in PNG.

The shark product export data presented here are titled '*Shark product exports by shark and tuna longline companies*'. As the name suggests, these data do not necessarily capture all shark product exports from PNG as they exclude other fishery sectors. The data provided includes annual export quantities and value (in kina) for the 1999 to 2013 period under the following three categories:

- *Shark (frozen);*
- *Shark (trunk frozen); and,*
- *Shark fin*.

Collection of this data is via licensed exporting companies filling out export documentation which is submitted whenever they export. The dataset reports export amounts on a monthly basis.

Two other relevant data sources are also presented to allow validation and comparison. First, export data from the Food and Agriculture Organisation (FAO) (sourced via FAO's Fish Stat J download) are used to validate the NFA company export data. The FAO compiles annual trade statistics for fisheries products for all countries including PNG. In terms of shark products, FAO export data includes PNG quantities and values up to 2011 under three categories:

- *Shark fins, dried, salted, etc.;*
- *Sharks nei [not elsewhere included], fresh or chilled; and,*
- *Sharks nei, frozen*.

Finally, Hong Kong import data sourced from the Hong Kong Census and Trade Department are also used to validate the NFA company export data. Hong Kong has historically been the main destination for internationally traded shark fin (Clarke 2004, Vannuccini 1999). As a result, data on Hong Kong's imports of shark fin from PNG could provide a good indicator of total shark fin exports from PNG, or at the very least, a minimum amount. The Hong Kong import data reported are available by month for the period January 1997 to November 2014 (at the time of writing).

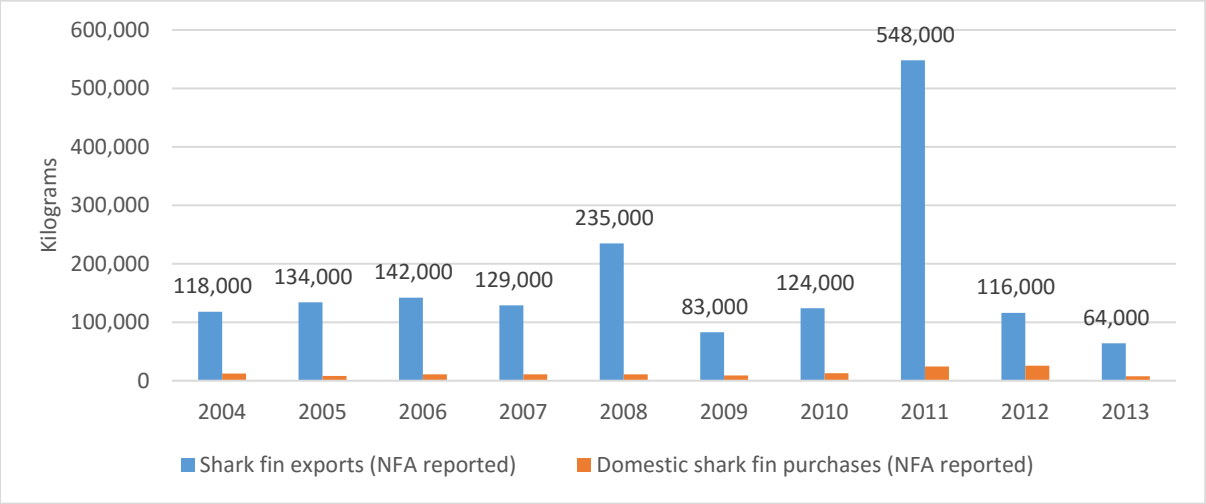
In what follows, statistics on shark fin export quantities, shark fin export values and exports of other shark products are presented. A number of adjustments to the value data were required. All kina values and prices have been converted to real terms, meaning that they have been adjusted for the impact of inflation using a PNG consumer price index series (sourced from the Bank of PNG, www.bankpng.gov.pg) and are reported in 2013 kina terms. Finally, FAO export values are reported in US dollar terms and so were converted to PNG kina using historical exchange rates series (sourced from the Bank of PNG, www.bankpng.gov.pg).

Shark fin export quantities

Between 2004 and 2013, annual shark fin exports from shark and tuna longline companies are estimated to have varied between 64,000 (in 2013) and 548,000 kilograms (in 2011) with the latter quantity being a high outlier (Figure 6). The average export quantity for the period was 169,000 kilograms. It is unclear whether these quantities relate to dried weights or wet (frozen) weights, although it is most likely dried.

Despite this, these export quantities are substantially higher than the NFA estimates of fin purchases discussed previously – the highest fin purchase quantity was 25,631 kilograms in 2012 (Figure 6). This large difference indicates that the shark fin exported by shark and tuna longline companies are not captured within NFA's shark fin purchase data. It is likely that the majority of these companies operate as vertically integrated companies that harvest, process and export shark products themselves. If this is the case and these shark products don't change hands between businesses within-PNG, then these shark products won't be captured in the NFA purchase data. This is not a problem with the NFA purchase data, but merely something to be aware of when interpreting these data sets.

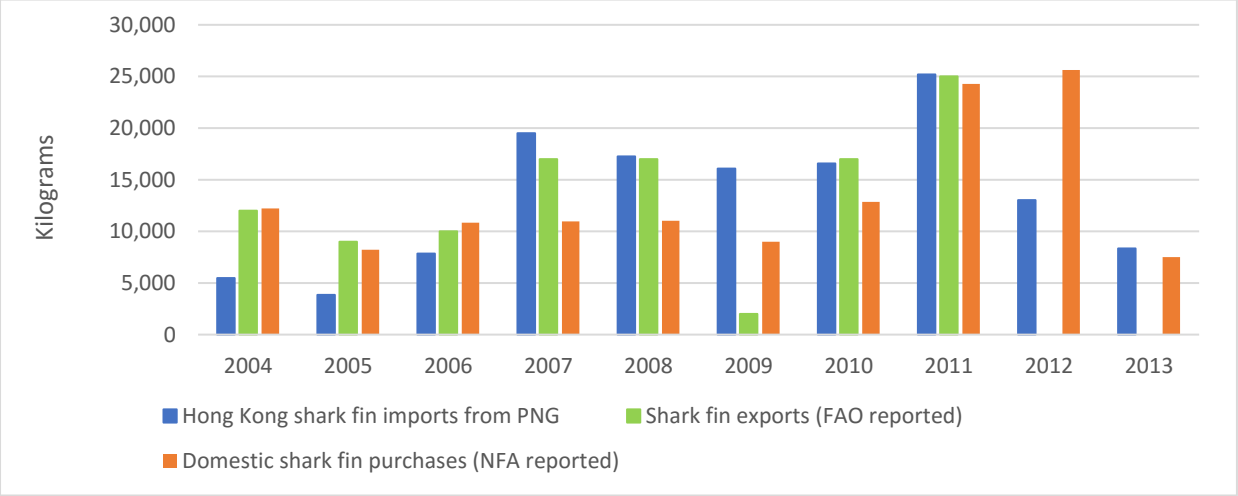
Figure 6 – company exports of shark fin and NFA reported shark fin purchases, 2004 - 2013*



Analysis of reported shark fin quantities in the FAO export data and Hong Kong import data reveals that both series are in fact far more similar to the NFA shark fin purchase data than they are to the NFA export data (Figure 7). Both trade series suggest that exports of shark fin from PNG increased post 2006 and were maintained at levels between around 16,000 kilograms and 20,000 kilograms between 2007 and 2010 (although the FAO estimate suggests a very low quantity in 2009 which is likely to be an error[1]). Then in 2011 exports peaked at around 25,000 kilograms. Hong Kong import figures suggest a decline since 2011 to 13,023 kilograms in 2012 and then 8,338 kilograms in 2013.

[1] In some years, FAO Export Data for PNG are marked as '*FAO estimate from available sources of information*'. This implies that the data available for a given year was unreliable or not available and required an estimate to be constructed based on other available information. Hence, errors in the FAO data are likely.

Figure 7 – quantity of Hong Kong shark fin imports from PNG (2004 - 2013), FAO shark fin exports from PNG (2004 - 2011) and NFA domestic shark fin purchases (2004 - 2013)



Notes: Hong Kong shark fin import data is sourced from Hong Kong Trade Statistics, Census and Trade Department and are based on an extract of HS codes 03055920, 03055950, 03055960, 03056920 03056930 03056940 03057111 03057112 03057121 03057122 03057190 16042011 and 16042091. FAO shark fin export data were sourced via Fish Stat J and are the "Exports - Shark fins, dried, salted, etc." category.

These observations have a number of implications. First the data reveals that the majority of PNG's shark fin exports are likely to be associated with the shark and tuna longline fisheries. Furthermore, these exports go somewhere other than Hong Kong. Discussions with industry have indicated Taiwan as the main destination for the shark longline fishery.

The majority of shark and tuna longline shark fin is not being captured in the NFA purchase data (most likely due to vertical integration within the fishery). The implication of this is that the NFA shark fin purchase data may be far more representative of small-scale shark fin activities. This could be further explored if data on the seller of shark fin was available. The consistency between quantities reported in the NFA purchase data and the Hong Kong import data also suggests that product from this part of the PNG supply chain may historically have gone to Hong Kong.

The most important implication is that the inconsistency between the FAO export data and the NFA company export data suggests that FAO estimates are severely underestimated. Assuming that the NFA company export data and the NFA purchase data represent separate parts of the PNG shark fin supply chain, combining the two separate data series would likely provide an improved (but not completely accurate) estimate of PNG's shark fin exports (Table 8). These numbers would suggest that FAO estimates are underreported by an order of magnitude of up to 46 times (in 2009). Estimates of shark fin exports from other large-scale PNG fisheries and an improved understanding of the PNG shark fin supply chain would allow these estimates to be improved. This will be further explored under the current project.

Table 8 – estimation of PNG's total shark fin exports using NFA company export data and NFA purchase data

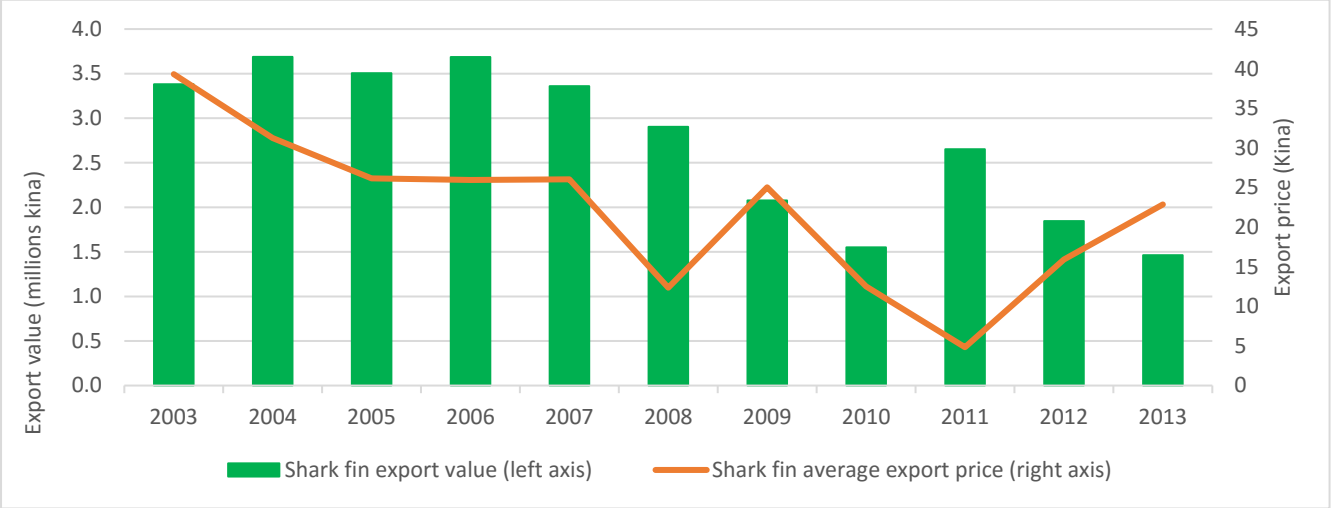
	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Assumed large-scale fin exports (NFA Shark and Tuna Longline Exports)	118,000	134,000	142,000	129,000	235,000	83,000	124,000	548,000	116,000	64,000
Assumed small-scale fin exports (NFA Shark Fin Purchases)	12,000	8,000	11,000	11,000	11,000	9,000	13,000	24,000	26,000	8,000
Estimated total exports	**130,000**	**142,000**	**153,000**	**140,000**	**246,000**	**92,000**	**137,000**	**572,000**	**142,000**	**72,000**
FAO estimates of shark fin exports	12,000	9,000	10,000	17,000	17,000	2,000	17,000	25,000	na	na

Shark fin export value

The value of shark fin exported by shark and tuna longline companies is reported to have varied between K1.5 million and K3.7 million in real terms between 2004 and 2013 (Figure 8). Average export prices for fin initially followed a declining trend, falling from K31.3 per kilogram in 2004 to as low as K4.8 per kilogram in 2011. Prices are estimated to

have recovered in the two years that followed to K22.9 in 2013. Relative to fin prices reported elsewhere (Fowler & Seret 2010; Fong & Anderson 1998; Hopkins 2011), these prices appear low and inaccurate.

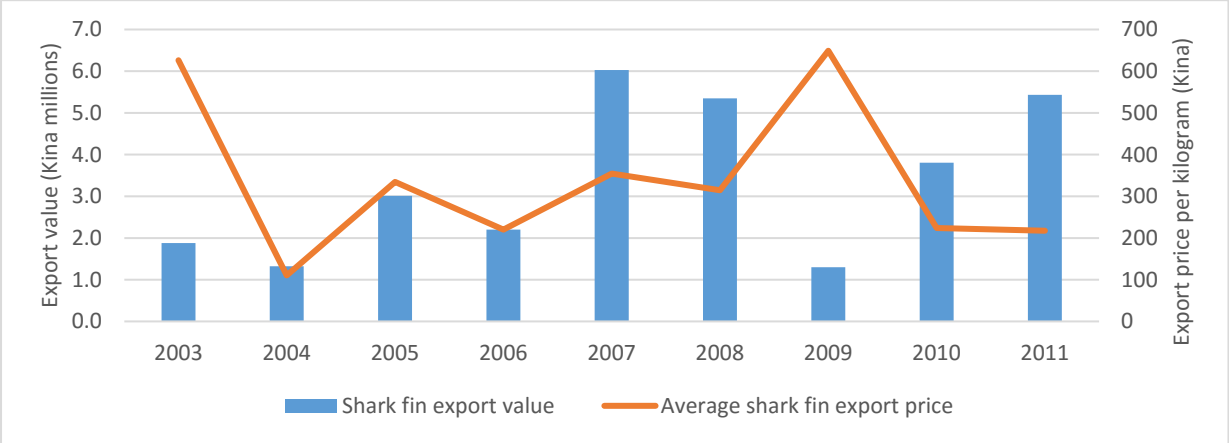
Figure 8 – real value (left axis) and unit prices (right axis) of company fin exports, NFA estimates, 2004 - 2013



Note: value and price data are in nominal terms and have not been adjusted for inflation.

Comparison of the NFA export values to FAO estimates also suggests some inaccuracies in the NFA data. FAO export prices for PNG are substantially higher, averaging K339 per kilogram between 2003 and 2011 in real terms, and get as high as K649 per kilogram in 2009 (this appears excessively high and may reflect issues with the FAO 2009 estimates mentioned previously) (Figure 9). The fin export values in each data series don't differ as significantly, with the FAO values varying between K1.3 million and K6 million. But, given the large differences in reported quantities between the two data series, the observed similarity is coincidental. While data on the value of Hong Kong shark fin imports could provide interesting insights, these have not been accessed for this report.

Figure 9 – real value (left axis) and unit prices (right axis) for PNG shark fin exports, FAO estimates, 2004 to 2013



Note: data for 2005 2006 2007, 2008, 2010 and 2011 are marked as '*FAO estimate from available sources of information*'.

Like the FAO estimates of PNG's fin export quantities, it is likely that FAO export values are also underreported. The potential magnitude of underreporting is demonstrated here. Taking the export quantity estimated in Table 8 for 2011 of 572,000 kilograms and applying the 2011 FAO export unit price of K217 per kilogram generates a value of K124.1 million. This compares to a much lower FAO estimate of K5.4 million for the same year. Given that the quantity reported in 2011 is an outlier, it may be more reasonable to do the same calculation for 2010. Combining the estimated export quantity of 137,000 kilograms with FAO export price of K223 per kilogram gives an export value of K30.5 million. This compares to the FAO estimate for 2010 of K3.8 million which is approximately 90 per cent lower.

Exports of other shark products

Two non-fin categories exist on the NFA database for shark product exports from Shark and Tuna Longline companies: 'shark (frozen trunk)' and 'shark (frozen)'. Quantities of 'shark (frozen)' are only reported in 2012 and 2013 and only in relatively small amounts (3% or less of non-fin exported quantities). Quantities of 'shark (frozen trunk)' exports have varied between 1.3 million kilograms (2004) and 1.9 million kilograms (2009) between 2004 and 2013 with higher quantities being reported post 2005.

The value of 'shark (trunk frozen)' exports varied between K2.2 million (2004) and K4.2 million (2009) and averaged K2.9 million over the 2004 to 2013 period. In 2013, K2.6 million worth of 'shark (trunk frozen)' exports are reported. This is far greater than the K1.5 million worth of shark fin exports reported by companies in the same year. This again highlights that shark fin export prices reported in the NFA company export data are likely to be underreported.

FAO data on PNG exports of other shark products are patchy with quantities reported in only six years between 1999 and 2011. Just over 180,000 kilograms were reported in 2004 and less than 40,000 kilograms were reported in the remaining five years (2001, 2003, 2005, 2010 and 2011). This data appears to not be very reliable. Hong Kong import data for other shark products has not been accessed as it would probably not be informative given that the Hong Kong market is largely focused on shark fin as opposed to other shark products.

5. The Shark Longline Fishery

Until recently, the Shark Longline Fishery was the only large-scale fishery in PNG that targeted shark. Its formation came about with increased targeting of shark in the nineties by a number of PNG tuna longline vessels. NFA introduced a management plan in 2002 (Kumoru 2003) in response in order to manage targeted shark longline fishing under a separate fishery. As a managed large-scale fishery, NFA has collected and maintained fishery catch and effort information (via logbook data) for the fishery. However, a ban on the retention of silky shark (a key species for the fishery) was introduced in mid-2014 in line with recommendations by the Western Central Pacific Fisheries Commission's (WCPFC). As a result the fishery has stopped operating. Reported here are catch data for the period between 2002 and 2013 together with effort and vessel characteristic data for the 2012 and 2013 data. Catch data for the 2014 year are not yet available. A comparison of the Shark Longline Fishery catch data for shark fin to the NFA company fin export data is also provided.

Shark Longline Fishery catch data

The composition of the fishery's catch has changed substantially since 2002, from a catch dominated by blue shark to a catch dominated by silky shark (Figure 10, Table 9). After a relatively small catch in 2002, total catch increased to 1.36 million kilograms in 2003. In that year and the two years that followed, blue shark accounted for approximately two thirds of total catch while silky shark only accounted for between 11 and 15 per cent of total catch. However, post 2005, the share of catch made up by silky shark gradually increased and has been approximately 80 per cent or higher since 2008. Blue shark has only accounted for between 1 and 2 per cent of total catch since 2009.

The catch of silky shark peaked in 2011 at 1.23 million kilograms, when total catch was 1.42 million kilograms. Reported silky shark catch has since declined by 31 per cent to 0.85 million kilograms in 2012 before declining by a further 29 per cent to 0.61 million kilograms in 2013. Total catch in 2013 was 0.71 million kilograms, half what it was in 2011.

Other species groups reported in the fishery's catch have included hammerhead shark, grey reef shark, blacktipped shark and blacktip shark. Although not shown here, non-shark catches were 431,100 kilograms or 30 per cent of the fishery's total catch in 2012 and 247,500 kilograms or 25 per cent of total catch in 2013.

Figure 10 – catch by key species group (excluding non-shark) for the Shark Longline Fishery, 2002 to 2013

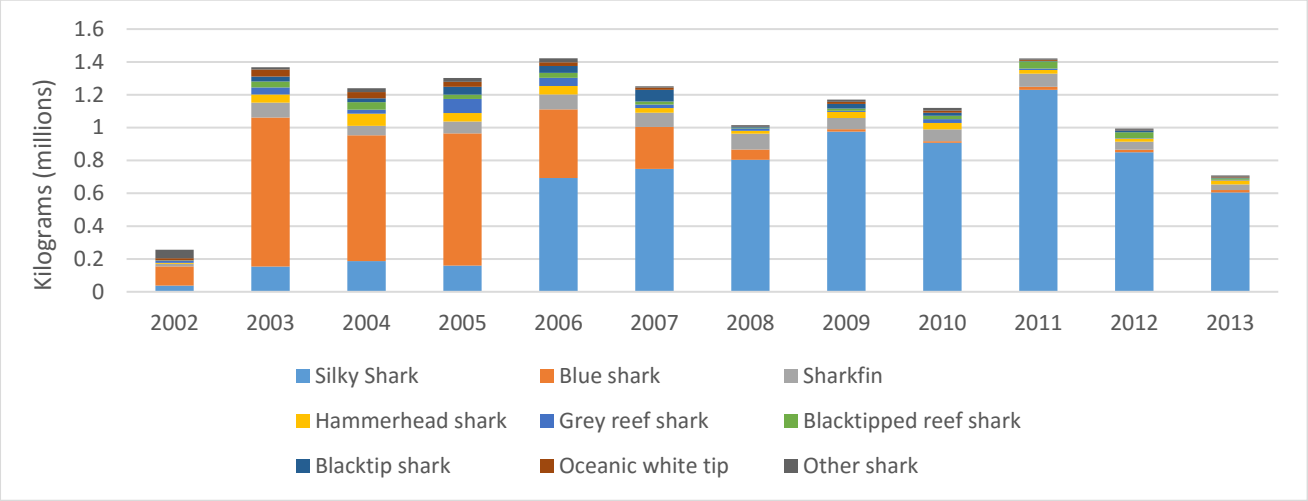


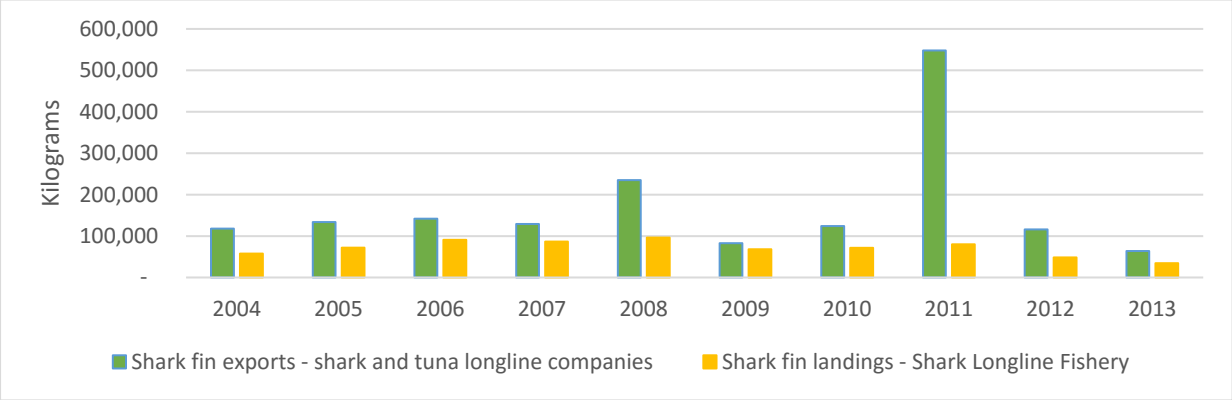
Table 9 - catch by species group (excluding non-shark) for the PNG Shark Longline Fishery, kilograms, 2002 - 2013

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	TOTAL
Silky Shark	37.7	154.3	187.4	159.6	692.6	748.5	804.5	976.1	907.3	1229.7	849.8	605.3	**7352.8**
Blue shark	117.1	907.2	765.6	805.5	418.6	255.7	61.7	14.5	10.2	18.9	15.9	14.1	**3405**
Sharkfin	15.5	90.9	57.7	72	90.9	86.8	96.5	68.2	71.7	80.2	48.4	34.5	**813.3**
Hammerhead shark	6.5	49.8	74.2	51.6	51.4	28.4	17.7	36.6	39.1	22.3	18.6	24.3	**420.5**
Grey reef shark	12	42.4	24	86.2	49.5	20.6	15	7.3	23.9	8.4	2.6	4.1	**296**
Blacktipped reef shark	2.4	36.7	46.1	26.4	30.9	19.2	5	13.6	19.8	44	36.5	9.1	**289.7**
Blacktip shark	0.9	29.5	23.2	46.9	41.9	70.7	7.4	28.4	18.9	2.8	11.3	4.3	**286.2**
Oceanic white tip	12.1	42.7	38.1	30.7	22.1	13.9	3.1	12.3	12.9	7.2	3.6	5.5	**204.2**
Shark unidentified	50.4	1.9	10.9	8.5	1	0	0.1	0.1	0.1	4.6	6.1	2.2	**85.9**
Tiger shark	0.1	2.3	4.2	11.1	13.2	2.6	3.5	9.1	8.8	2.2	1.2	1.7	**60**
Silvertip shark	1.7	8.7	6.6	3.1	8	3.5	1.2	2.9	6.4	0.4	0.4	0.4	**43.3**
Galapagos shark	0.2	1.4	2	0.7	1.6	1.2	0.2	1.2	1	0.3	0.1	2.9	**12.8**
Total annual catch	**256.6**	**1367.8**	**1240**	**1302.3**	**1421.7**	**1251.1**	**1015.9**	**1170.3**	**1120.1**	**1421**	**994.5**	**708.4**	**13270**

Shark fin has also been a relatively large component of reported catch. The average quantity of shark fin reported for the 2002 to 2013 period was 67,800 kilograms with the peak quantity of 96,500 kilograms occurring in 2008. Like total catches, shark fin quantities have declined since 2011 from 80,200 kilograms to 48,400 kilograms in 2012 and 34,500 kilograms in 2013. It is unclear whether these fin weights are dry weight or wet weight. It is also unclear whether the shark fin category represents fins removed from sharks reported in other catch categories, or, if it relates to fins removed from finned and discarded sharks, and may be a mixture of both.

Comparison of this shark fin landing data to the NFA shark and tuna longline company export data show that, with the exception of 2011, shark fin landings by the Shark Longline Fishery were equivalent to greater than 40 per cent of shark fin exports reported by shark and tuna longline companies and get as high as 82 per cent (in 2009) (Figure 11). In the high export year of 2011, shark fin production in the Shark Longline Fishery was equivalent to only 15 per cent of company exports. This would suggest that the increase in exports in 2011 is likely to have largely come from shark fin landings in the Tuna Longline Fishery. To confirm this, catch data for the latter fishery would need to be analysed.

Figure 11 – shark fin exports by shark and tuna longline companies and shark fin landings in the Shark Longline Fishery, 2004 to 2013



Shark Longline Fishery vessel and effort data

Effort and vessel data have only been accessed for the fishery for 2012 and 2013. Ten vessels operated in the fishery in 2012. This declined to eight vessels in 2013. The decline in fishery catch between 2012 and 2013 therefore equated to a decline in average catch per vessel from 142.6 tonnes per vessel in 2012 to 124.1 tonnes per vessel in 2013.

The average vessel size in the 2012 to 2013 period was 24.5 metres with the smallest vessel being 17.8 metres and the largest being 30.2 metres. Effort levels appear to have declined between the two years, from 2.0 million hooks in 2012, or 198,464 hooks per vessel, to 0.94 million hooks in 2013. However, this latter figure is likely to be lower than the true figure as one vessel was missing data on hook numbers. The average number of hooks per vessel for those vessels that did report hook data in 2012 was 134,703 hooks per vessel.

6. Discussion and conclusion

The importance of NFA's shark fin purchase data

It has been difficult to evaluate the accuracy of the shark fin purchase data. One key issue that should be further explored is the degree to which there might be double counting of shark fin purchased between provinces. This could potentially be explored by simply looking at data that reports who the seller of the fin is. Another issue relates to the amount of shark fin that are not captured in the purchase data either due to vertically integrated businesses and/or non-registered businesses dealing in shark fin. If these issues prove meaningful, attempts to correct for them in historical data as well as in future data collection efforts could prove valuable, particularly if the information is to be used to assess the status of PNG's shark stocks and/or monitor of future shark catches.

The usefulness of the fin purchase data could also be improved with more detailed information. In particular, the entity type that is purchased from (e.g. 'fisher', 'small buyer', 'company buyer') and the seller's ward (or island) could be informative. While the latter might add additional administrative burden for buyers, during recent field work one of the authors observed that NFA registered buyers maintained information on the seller's ward and/or island. Such information would improve monitoring and management capabilities.

Despite the above issues, the shark fin purchase data provides a good source of information regarding shark fin production in PNG. If the data largely represents small-scale activities (as has been hypothesised here), the data may provide a cost-effective means to monitoring small-scale shark fin activities at the national, provincial and LLG level. For these reasons, maintaining the shark fin purchase data collection process and its integrity should be a high priority.

Key focus areas for the project

Analysis of the purchase data showed that the NCD appears to be a hub for shark fin trading. Engaging with purchasers there could provide access to a large number of entities involved in the supply chain for fins. Consistently high purchase quantities from Milne Bay Province should make it a key focus for the project particularly Bwanabwana, Yaleyemba, Louisiade and Duau LLGs. Recent declines in fin purchases from Manus Province may indicate reduced shark fishing

activity, but these changes may still be of interest to the socio-economic component of the project. The large increases in purchases from New Ireland need to be substantiated and the implications of such large changes understood. Key LLGs to focus on in New Ireland would include Tikana, Lovongai, Kavieng and Namatanai. The Siassi and Morobe Urban LLGs of Morobe Province have also reported high purchases of fin and are likely to be of interest. Other LLGs with high fin purchase quantities include Wewak Islands, Buka, Madang Urban, Kiwai and Amazon Bay.

Improving information on exports of shark products

The NFA export data presented only related to exports by shark longline and tuna longline companies. But these estimates were far larger than quantities in the NFA shark fin purchase data, and gave an indication of the potential scale of difference between large-scale and small-scale shark fin production. A key issue with this data is the likely underreporting of shark fin prices. Efforts to better understand and/or improve this information could prove valuable.

An improved understanding of PNG's shark fin exports could be possible if additional data sources for shark fin trade data could be accessed. As a start accessing export data for other non-target fisheries such as the Prawn Trawl Fishery could assist. However, having one aggregated data series that captures all of PNG's exports of shark products would be most useful. Potential sources of such information might include PNG customs and/or quarantine bodies. Having one source of data shark product trade would avoid interpretation errors that can arise as the characteristics of trade change. For example, observations in the field (William White, personal communication, October 2014) suggest that falling demand in China is seeing more PNG shark fin being exported to non-traditional markets including Indonesia and United Arab Emirates. This would mean that data sources such as the Hong Kong import statistics which may have previously provided a reliable indication of a component of PNG's shark fin exports may now not be so reliable.

A key finding regarding PNG's exports of shark fin was that the FAO estimates are likely to be significantly underreported with fin exports by shark and tuna longline companies not being captured in official FAO records. This could be due to the way company fins are exported (e.g. if they are transhipped at sea, although transhipment for vessels greater than 600 tonnes is prohibited). It may also be caused by companies exporting their fin to destinations other than Hong Kong (in the case of shark longline companies, Taiwan), with FAO statistics being similar to Hong Kong import statistics and potentially being based on them. Such underreporting is consistent with observations by Clarke et al. (2006) although not to the degree suggested here.

A potential improvement to total shark fin export estimates for PNG has been provided here in Table 8. But this requires further work to confirm the inaccuracy of FAO statistics and to improve the accuracy of the new estimates. This should be a focus of the project. The size of these changes to official FAO estimates, if confirmed, are not insignificant and could alter current knowledge on the importance of PNG as an international supplier of shark fin. This could be an important output of the current project.

Historical fishery data could prove valuable for the project

The data on the Shark Longline Fishery provides a good picture of the history of the fishery in terms of its catch and how the fishery has change from a fishery dominated by catches of blue shark to one dominated by silky shark. Obtaining historical effort data will likely be a priority for the stock assessment component of the current project. Further work collating and analysing historical catch data for other non-target fisheries would also be useful.

Concluding remarks

A key objective of the current project is to improve the information that is available on shark fishing in PNG. The current paper represents a first step towards doing this. The information that has been presented here has shown that the quantities of shark fin being produced in PNG were following an increasing trajectory leading up to 2012. But since then the trend has reversed and shark fin production quantities are at historically low levels. The cause of this is a fall in fin demand and prices, with the Chinese government ban on luxury food banquets and changes in consumer attitudes being cited as contributing factors (Whitcraft et al. 2014). For PNG, the ceasing of activity in the Shark Longline Fishery in 2014 will further contribute an overall decline in shark harvest levels and the production of shark fin. Despite these changes, the need to improve information and management of sharks in PNG remains a high priority,

given that markets and incentives can change quickly and that also that shark stocks in some parts of PNG may already be overexploited.

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TRAINING REPORT

To be completed by awardee, with mentor's comments from #8

Awardees comments	**Crawford ID number:** TAS-752-2016 Sharks
2	**Name, position and contact details** Dr Ralph Mana, Senior lecturer, School of Natural Science University of Papua New Guinea, Port Moresby, PNG **Address**: PO Box 320, University 134, Waigani, National Capital District, Papua New Guinea **Ph:** + 675 326 7387 **Email**: rmana@upng.ac.pg
3	**Title of training project, dates and venue of training** Age and growth determination in fishes and curatorial training for museum collections CSIRO Australian National Fish Collection, Hobart 22-24th February 2017 James Cook University, Townsville 27th February to 3rd March 2017
4	**Training activities (please provide a brief account (max 1000 words) of your activities)** The 3 days my student William Tamarua and myself spent at CSIRO Fish Collection was educational and enlightening. The scale of collection of chondrichthyan fish was amazing. Procedures involved in preserving those large specimens was fairly straight forward however in order to keep those specimens in good condition a large volume of ethanol is needed not to mention the space allocated for storage. Dr. White's explanation of the properties/phenomenon that make up the coloration in some specimens was interesting-indicating layers of skin mucus that produce different colors when seen at different conditions. PNG caught specimens were there too making the collection a regional one. The procedure of operating an x-ray machine was explained by a specialist. This technology is providing a new way of viewing internal structures especially the hard parts such as bones and cartilage. The technique gives a new dimension in taxonomic procedures enabling scientists to appreciate the hard parts such as teeth, jaws, skull and vertebrae of the fish which define taxon groups. In addition the studio for

photography was equally interesting. Good quality pictures of specimens makes taxonomic work more convincing. The person who was showing us around the x-ray and photographic set-up was helpful. For the first time we witnessed the product of 3-dimension printing and the 3-dimension printer (not operational though). It was fascinating indeed to hold a 3-dimension printed fish skull. The technology will contribute to science and teaching in a big way.

At the molecular laboratory Sharon was taking us throughout the set-up and eloquently explained how the procedures are applied from the beginning where a tissue is prepared up until the genes sequences are elucidated. The different types of equipment and their functions are clearly explained that make up the various stages in determining the barcoding of biological tissue of any given species. Another interesting aspect of the molecular laboratory is the presence of different types of equipment that can be used for teaching and basic research in PNG universities. Small centrifuge machine and spectrophotometer are few examples of the equipment that can be used in UPNG Biological Sciences division. Finally and but the least, Sharon stressed the importance of keeping the DNA samples under -80^{o}C in deep freezers at all times. This is to avoid loss of samples because it usually takes tremendous amount work to collect samples out in the field.

I was fortunate enough to have met with the representative of Crawford Fund Mr. Neville Mendham. I also met with tuna biologists Drs Campbell Davies and Jessica Farley.

At JCU Townsville, Dr. Andrew Chin and his students were of great assistance. Andrew himself taught us everything from constructing a fishing gear to catch shark to processing shark for aging study. At the laboratory his students showed us how to prepare vertebrae for observation under the dissecting microscope. Determination of number of rings on the vertebrae was challenging at first but eventually we tend to get it right after several attempts to count rings. I was also amazed to learn of the several projects that the postgraduate students are involved in such as sharks behavioral and species composition studies in different Asian countries including Okinawa in Japan.

We were given a tour around the campus and interestingly we witnessed various building construction going on. The new facilities including lecture rooms, practical laboratories and many more not to mention students' luxury space.

We also met with a scientist (Marcus) who is working with PNG counterparts to promote Niugini black bass sports fishing among other projects at PNG. His concern about promoting such economic ventures at local level was really appreciated. I might meet with him in the near future.

Finally, we visited the Great Barrier Reef Aquarium. The tour was thoroughly done by a staff and it was impressive to see the largest coral ecosystem under one roof. Establishment of turtle hospital at the aquarium gives a meaningful purpose to the aquarium. I gained a good insight into the operational facilities that sustain the overall function of the aquarium such as the water filtration system, coral growth section and

	others. All in all, what I was exposed to was more than I expected. The several days I spent at Hobart and Townsville was truly educational and enlightening particularly in sharks research and conservation work. It provides a new stepping stone for me to continue the cooperation I have established with William and Andrew.
5	**Has the training met your expectations and how have the expected outcomes (see application) been achieved?** The training at Hobart and JCU were professionally conducted by the experts in sharks taxonomy, molecular and genetics research and aging studies. I can say that the outcome was more than expected. The training has consolidated the collaborative work that I am involved with William and Andrew since 2014.
6	**What are the expected benefits to agricultural R&D and food production in your country** The immediate benefit I can think of right away is sustainable fisheries for our shark resource at PNG. Sharks bring in hard cash for our local economy as well as the industrial fisheries operation. If we can harvest the resource on a sustainable manner by protecting breeding stock and harvest only certain size of fish, shark resource can support our local people for a long time to come. In order to achieve sustainable shark fisheries, identification of species, sharks population in our waters and growth rate and age of sharks at maturity researches are paramount. In the future more research work is recommended to reveal the true situation of the sharks resource in PNG and the surrounding waters.
7	**What arrangements have been made to maintain contact on your return home?** I have been working with Dr. White for 3 years now and I sense that future collaboration will continue as he has applied for various funds to support what we are doing and beyond. A shark researcher at Simon Fraser University Canada is a colleague of William and she will be in PNG next month April to conduct a survey on sawfish. Dr. Andrew Chin's collaboration will continue and currently a PNG student Ms. Leontine Baje is working under him for her Master's degree. In the future I would like to see more PNG students go train at JCU not only in science but other field as well. Personally I am looking forward to tag life sharks with Andrew in the near future.
Mentors comments	
8	**Please provide an account of the training (250-300 words) suitable for the basis of an item to be included in The Crawford Fund newsletter "Highlights" or as a press release. If available please attach a (high res) photograph.** The training activities undertaken by Dr Ralph Mana and prospective student William

Tamarua highlighted the importance of holding these in-country workshops. Being able to show people how to collect biological data, curate specimens, age fish, etc., in a world-class laboratory with equipment not accessible in many countries has many benefits. It also highlights the importance of a network of collaborators from various institutions. In this case, CSIRO provided the taxonomic and genetic training while JCU provided the ecological and biological training.

At CSIRO, Ralph and William were first shown through the Australian National Fish Collection which includes the largest shark and ray collection in the southern Hemisphere. The importance of properly maintaining a fish collection and the future benefits in having good quality specimens was particularly important to show given the National Fish Collection in PNG is located at the University of PNG where Ralph is located but is in very poor shape with little to no curation. In order to highlight the importance of a good collection, William White showed them the various projects the ANFC has undertaken such as marine bioregionalisation used for marine bioregional planning, the Atlas of Living Australia, and the Tree of Life of Chondrichthyan Fishes projects. Dr Sharon Appleyard showed Ralph and William through the genetics laboratory and explained to them the various information that can be gleaned from a small piece of tissue.

Figure: Dr William White showing Dr Ralph Mana a large stingray holotype specimen inside the Australian National Fish Collection.

Figure: William Tamarua in the genetics laboratory at CSIRO Marine Laboratories in Hobart.

At JCU, Dr Andrew Chin showed Ralph and William through the fisheries research laboratories and showcased the methods for obtaining details biological data. Students Leontine Baje (from National Fisheries Authority in PNG) and Michael Grant showed Ralph and William how age and growth on sharks is undertaken using the shark's vertebrae. This information will assist with setting up joint student studies such as Honours projects with UPNG in the future.

	 Figure: Dr Ralph Mana, William Tamarua and Michael Grant at Reef Headquarters in Townsville.  Figure: Michael Grant demonstrating to Dr Ralph Mana and William Tamarua the saws used for sectioning dried shark vertebrae.
9	**Do you have any ideas on future training needs?** More specific student focused training would be very beneficial in the future. The first step will be to see whether the current training leads to some joint Honours projects and then if so, focus on some more detailed training for a student in Australia.
10	**Do you have any general comments you would like to share with the Crawford Fund?** This sort of training activity is seen by some to be a trivial exercise but the benefits to

	researchers in other countries can be great. Crawford Fund projects can put the icing on the cake for other existing projects by helping to undertake important training not identified at the start of a 3 or 4 year project.

Please email the report to Crawford@crawfordfund.org

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Rhinobatos manai sp. nov., a new species of guitarfish (Rhinopristiformes: Rhinobatidae) from New Ireland, Papua New Guinea

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Abstract

A new species of guitarfish (*Rhinobatos*) is described based on a single specimen collected in 2014 from off New Ireland in Papua New Guinea. This specimen represents the first record of the family Rhinobatidae in Papua New Guinean waters. Based on molecular data, the new species appears to be most similar to *Rhinobatos whitei* (Philippines) and *Rhinobatos sainsburyi* (northern Australia), but is distinguished based on its coloration, morphology and certain meristic characters.

Key words. *Rhinobatos*, New Ireland, new species, Oceania, Rhinobatidae

Introduction

The recently established Order Rhinopristiformes consists of four families of rays, i.e. Glaucostegidae, Pristidae, Rhinobatidae and Trygonorrhinidae (Last *et al.*, 2016), each of which have representatives in Australasia. In Papua New Guinean waters, this order is represented by four species of sawfish (Pristidae) and one species of giant guitarfish (Glaucostegidae). No species from the families Trygonorrhinidae or Rhinobatidae are known to occur in the region following this new familial arrangement. During recent deepwater trawl surveys of Papua New Guinea by the French research vessel *Alis*, a single adult specimen of an unidentified *Rhinobatos* was collected from off New Ireland. This specimen represents the first record of this genus and of the family Rhinobatidae in Papua New Guinean waters.

The genus *Rhinobatos* is represented globally by 15 valid nominal species, 12 of which are distributed in the Indo-West Pacific and the remaining three in the eastern Atlantic (Last *et al.*, 2016). In the Oceania region, only a single species is known to occur, *Rhinobatos sainsburyi* Last, 2004. This species occurs off northern Western Australia and off the Northern Territory of Australia at depths of 70–200 m. The new *Rhinobatos* species, which is formally described and named in this paper, represents the first record of this family from the South-West Pacific. This new species is compared to other members of the genus *Rhinobatos*.

Materials and methods

The holotype was collected during deepwater surveys around New Ireland in 2014 onboard the French research vessel *Alis* of the Institut de Recherche pour le Développement (IRD, Nouméa). This specimen was subsequently sent, with other fish specimens collected, to the National Taiwan University Museum (NTUM) in Taipei. Morphometric methodology follows Last *et al.* (2004) which is considered the standard for this group and morphometric data are presented as a percentage of total length (Table 1). Meristics were taken from radiographs of the holotype. Tooth rows and nasal lamellae counts were taken directly from the holotype. In the recently published

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description of a new guitarfish *Rhinobatos borneensis* (Last *et al.*, 2016), Table 1 (containing the morphometric values for the types) was inadvertently omitted from the published version. This table is included herein in Appendix 1.

The holotype of the new species was sampled for muscle tissue on-board the *RV Alis* immediately postcapture. The sample was temporarily stored in 95% alcohol in the field. DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc Norcross, GA). Extracted total DNA was stored at -20 °C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via the Polymerase Chain Reaction (PCR). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µl volume comprising 0.3 µM primers, 2.5 mM MgCl2, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA), and 50–100 ng template DNA. The reaction mixture was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio), and bi-directionally sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego USA).

DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd Auckland, New Zealand. Available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within the Geneious Package (Biomatters Ltd Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. A Neighbour-Joining (NJ) tree was constructed from the aligned NADH2 sequences (1044 bp) using Tamura Nei Distance. The tree was generated using the software package PAUP*4.0 version a148 and is presented in Fig. 7.

Comparative material for this study includes specimens examined in other recent local treatments of the genus (Last *et al*., 2004a, 2004b, 2006, 2014).

***Rhinobatos manai* sp. nov.**
Papuan Guitarfish
(Figs. 1–6; Table 1)

Holotype. NTUM 11500, adult male 731 mm TL, northwest of Kavieng, New Ireland, Papua New Guinea, 02°30’S, 150°44’E, 191–290 m depth, 7 Sep 2014.

Diagnosis. A *Rhinobatos* distinguished by the following combination of characters: disc wedge-shaped, its dorsal surface covered in minute dermal denticles but without thorns; snout long, snout length 3.6 times interspiracular distance; orbit moderately large, diameter 1.7 times spiracle length; nostrils oblique, length 1.6 times internarial distance; anterior nasal flaps inserted into internarial space well away from nostril margin; posterior nasal flaps broad; ridges of rostral cartilage well-separated dorsally and almost parallel; prebranchial sensory-pore patch narrow, extending to first gill slit; distance between first gill slits 1.5 times distance between fifth gill slits; distance between fifth gill slits 3.4 times in ventral head length; postscapular sensory canal long, not grooved, extending more than three-quarters distance to pectoral-fin insertions; dorsal fins moderately tall; pelvic-fin inner margin shorter than its base; interdorsal distance more than 3.1 times first dorsal-fin base; outer spiracular fold distinctly larger than inner fold; dorsal margin of caudal fin ~2 times preventral margin; 171 post-synarcual (free) vertebral centra; 188 total vertebral centra; 52 nasal lamellae; and dorsal disc brownish, covered with well-defined rusty brown spots and blotches and poorly defined white spots with greyish edges.

Description. Disc wedge shaped, bluntly angular anteriorly, angle anterior to eyes about 56°; outer margins broadly rounded, more narrowly rounded distally; length 1.37 times width. Pelvic fins elongate, short-based, base length about 0.78 of inner margin; length 1.73 times their base length, 2.75 times width; anterior margin convex, apex broadly rounded, posterior margin weakly convex. Tail elongate, slender, tapering gradually; in cross-section nearly flat ventrally, rounded dorsally; length from anterior cloaca to tail tip 1.39 times precloacal length, 1.34

times disc length, 6.32 times body width at pelvic-fin insertions; tail width 1.99 times depth at pelvic-fin insertions, 2.41 times at first dorsal-fin origin, 1.68 times at second dorsal-fin origin. Dermal fold ventrolateral on tail, originating slightly anterior to free rear tip of pelvic fin, reaching just behind ventral caudal fin origin; fold well developed, maximum width in interdorsal space about a quarter width of spiracle.

TABLE 1. Morphometric data for the holotype of *Rhinobatos manai* **sp. nov.** (NTUM 11500) Measurements expressed as percentages of total length.

	R. manai	*R. whitei*	
		Adult males	
	Holotype	Min.	Max.
Total length	731	556	641
Disc width—maximum	31.6	30.9	32.6
Disc length	43.4	41.3	42.7
Head length—dorsal	23.3	21.7	23.2
Head length—ventral	28.6	27.7	29.2
Snout length (presocket)	17.6	15.4	17.0
Orbit diameter	3.5	4.0	4.2
Spiracle length	2.1	2.5	2.5
Orbit and spiracle length	4.6	4.8	5.1
Interorbital width	3.5	3.5	3.7
Interspiracular width	4.9	5.1	5.2
Preoral length	20.6	18.2	19.8
Mouth width	5.8	5.7	6.4
Prenarial distance	16.4	14.4	16.1
Nostril length	4.5	3.8	4.0
Anterior aperture—width	1.4	1.2	1.3
Anterior nasal flap—base length	2.7	2.7	2.9
Anterior nasal flap—width	1.4	1.3	1.4
Posterolateral nasal flap—total length	3.6	3.3	3.4
Posterolateral nasal flap—width	1.1	0.5	0.6
Posterior nasal flap— base length	3.0	2.8	2.9
Posterior nasal flap—width	1.2	1.0	1.2
Distance across anterior nasal apertures	10.6	8.9	9.4
Internarial distance (minimum)	2.8	2.4	2.7
Distance between anterior nasal flaps	2.9	2.3	2.6
Distance from nostril to disc margin	3.1	3.1	3.3
Third gill opening—width	1.5	1.3	1.5
Distance between first gill openings	12.3	12.5	13.1
Distance between fifth gill openings	8.4	8.5	9.1
Pelvic fin—length	14.1	13.4	13.8
Pelvic fin—anterior margin length	8.1	7.7	8.1
Pelvic fin—width	5.1	5.6	5.8
Pelvic fin—base length	8.1	6.6	7.0
Pelvic fin—inner margin length	6.3	7.6	7.8
First dorsal fin—length	6.5	6.7	7.1

.....continued on the next page

TABLE 1. (Continued)

	R. manai	*R. whitei*	
		Adult males	
First dorsal fin—anterior margin length	9.7	10.1	11.5
First dorsal fin—height	7.9	7.5	7.8
First dorsal fin—base length	4.3	4.3	4.4
First dorsal fin—inner margin length	2.2	2.4	2.8
Second dorsal fin—length	6.3	6.8	7.2
Second dorsal fin—anterior margin length	9.3	9.3	10.5
Second dorsal fin—height	7.5	6.2	7.0
Second dorsal fin—base length	4.6	4.8	5.0
Second dorsal fin—inner margin length	1.8	2.0	2.5
Caudal fin—dorsal margin	14.3	14.6	15.0
Caudal fin—preventral margin	7.2	6.5	6.9
Caudal fin—lower postventral margin	8.2	0.0	0.0
Snout to first dorsal-fin origin	56.2	56.1	56.7
Snout to second dorsal-fin origin	73.9	72.9	73.7
Snout to upper caudal-fin origin	85.5	85.0	85.4
Snout to lower caudal-fin origin	86.3	86.5	87.2
Snout to pelvic-fin origin	39.2	38.1	39.5
Snout to anterior vent	41.9	40.6	42.0
Pelvic-fin insertion to dorsal-fin origin	9.8	10.3	11.2
Interdorsal distance	13.3	12.2	12.5
Caudal peduncle length (dorsal)	6.8	7.0	7.2
Body width—pelvic insertion (tail)	9.2	9.5	10.0
Disc width—anterior orbit	18.3	17.4	17.7
Body width—first dorsal-fin origin	9.2	8.9	9.2
Body width—second dorsal-fin origin	4.3	4.6	5.0
Body depth—maximum (scap)	3.8	5.0	6.5
Body depth—pelvic-fin insertion	4.6	4.4	4.6
Body depth—first dorsal-fin origin	3.8	3.7	3.7
Body depth—second dorsal-fin origin	2.5	2.3	2.4
Clasper—outer length	8.4	–	–
Clasper—inner length	13.1	–	–
Clasper—base length	1.2	–	–

Head elongate, ventral length 28.6% TL; snout moderately long and bluntly pointed; preoral snout length 3.58 times mouth width, 7.32 times internarial distance, 1.44 times dorsal caudal fin margin, 6.69 times distance from nostril to margin of disc; snout length (direct) 3.58 times interspiracular length, 4.99 times orbit diameter, 5.10 times interorbital width; interorbital space weakly concave, relatively broad; eye dorsolateral, not elevated or protruding; orbit relatively small, diameter 1.65 times spiracle length, 1.02 times interorbital width. Spiracle narrowly bean-shaped, moderately large; two weakly compressed spiracular folds on posterior margin, innermost fold half or less length of outer fold, distance between bases of folds subequal to length of inner fold. Nostril moderately large, oblique, nasal flaps well developed; anterior aperture suboval, width slightly exceeding length; nostril length 3.32 times anterior aperture width, 1.69 times anterior nasal-flap base length, 1.45 times distance from nostril to edge of disc, 1.59 times internarial width. Anterior nasal flap relatively well developed with long, slender process anteriorly; flap base 1.84 times its width at process, 1.97 times anterior aperture width; insertion in

internarial space well mesial to nostril margin, its distance from nostril about equal to half width of anterior nasal aperture; distance between their insertions 3.67 in distance between lateral margins of anterior apertures, 0.97 in internarial width; process of flap about twice as long as wide at its base, overlapping posteromesial edge of posterolateral nasal flap and determining inner margin of anterior aperture. Posterolateral nasal flap lobe-like, broadest medially, length 3.36 times width; originating at lateral extremity of anterior nasal aperture, extending postero-medially as a free fold almost to medial margin of posterior flap. Posterior nasal flap broadly lobe-like, base length 2.58 times its width, not reaching innermost end of nostril, inserted well forward of posterior tip; width subequal to anterior aperture width, 1.09 times posterolateral nasal-flap width. Nasal lamellae 52.

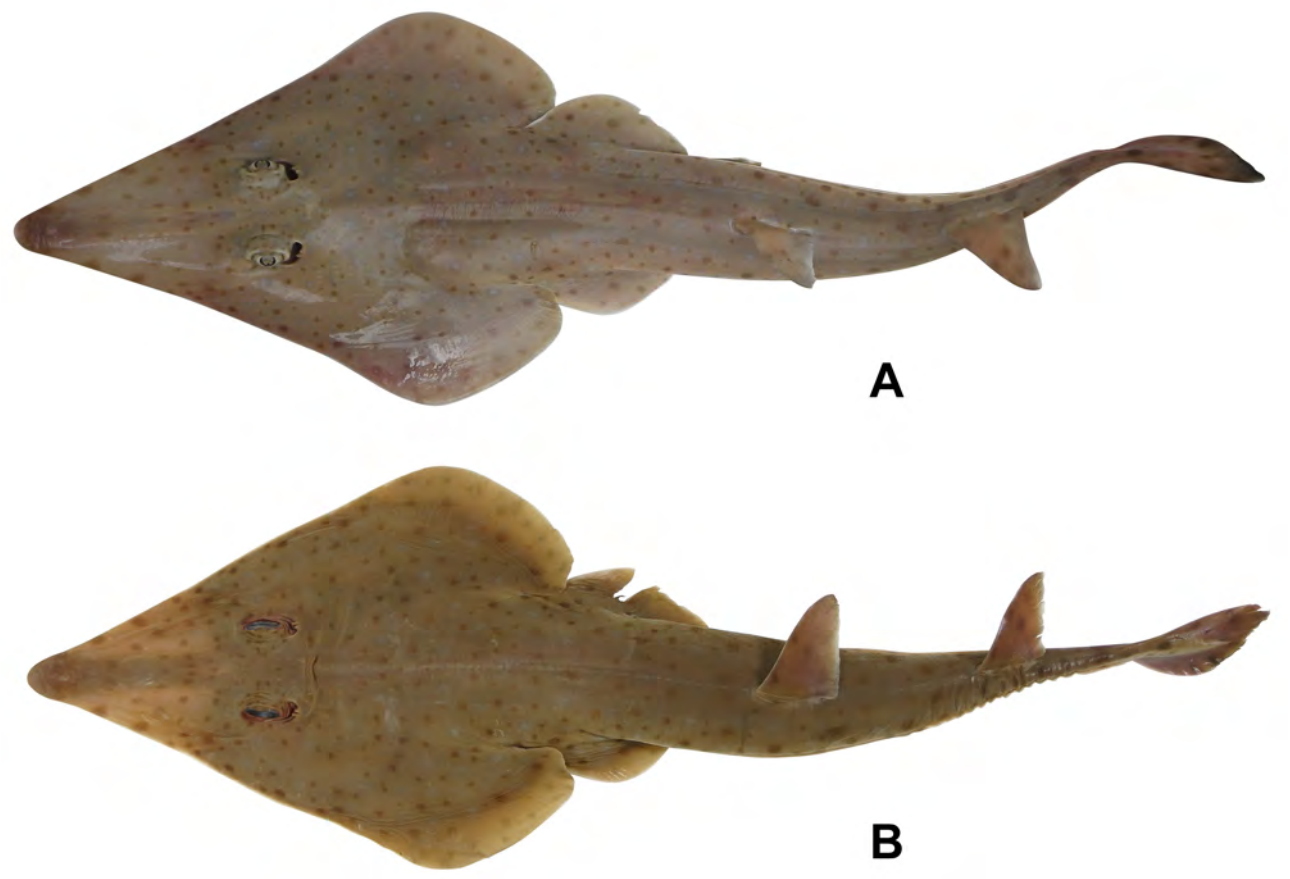

FIGURE 1. Dorsal view of *Rhinobatos manai* **sp. nov.**, adult male holotype, 731 mm TL (NTUM 11500): A. freshly caught; B) preserved.

Mouth moderately wide, width 1.29 times nostril length, 7.26 in precloacal length; positioned about level with hind margin of orbit; jaws not greatly thickened. Upper jaw weakly convex, upper lip arched slightly, no preoral groove; lower lip pronounced, not separated from post-oral groove by ridges of strongly corrugated skin; short lateral grooves around corners of mouth. Teeth small, blunt, crowns rhomboidal; teeth quincuncial, ~92 rows in upper jaw and ~86 rows in lower jaw; upper and lower jaw teeth similar in shape and size. Gill openings weakly s-shaped, fifth less so; length of third gill slit 2.94 in nostril length, 5.53 in distance between fifth gill slits; distance between first gill slits 1.47 times distance between fifth gill slits; distance between fifth gill slits 2.98 times internarial distance, 1.46 times mouth width, 3.40 in ventral head length.

Dorsal fins of moderate size, upright, relatively narrow, not falcate, apices narrowly rounded to almost angular; anterior margins convex distally, posterior margins nearly straight; free rear tips forming right angle, not produced; first dorsal-fin slightly taller than second, length of first dorsal fin 0.82 times its height, base length 1.99 times inner margin length; second dorsal-fin length 0.85 times its height, base length 2.58 times inner margin length. First dorsal-fin origin well behind pelvic-fin rear tip, interspace 0.73 times interdorsal distance; interdorsal space relatively short, 1.78 times second dorsal-fin height, 3.08 times base length of first dorsal-fin, 1.95 times interspace

between second dorsal-fin insertion and upper origin of caudal fin. Caudal fin small, dorsal caudal margin 1.98 times preventral margin length. Mature clasper slender, relatively short, inner length 13.1% TL; tip acute, glans weakly expanded.

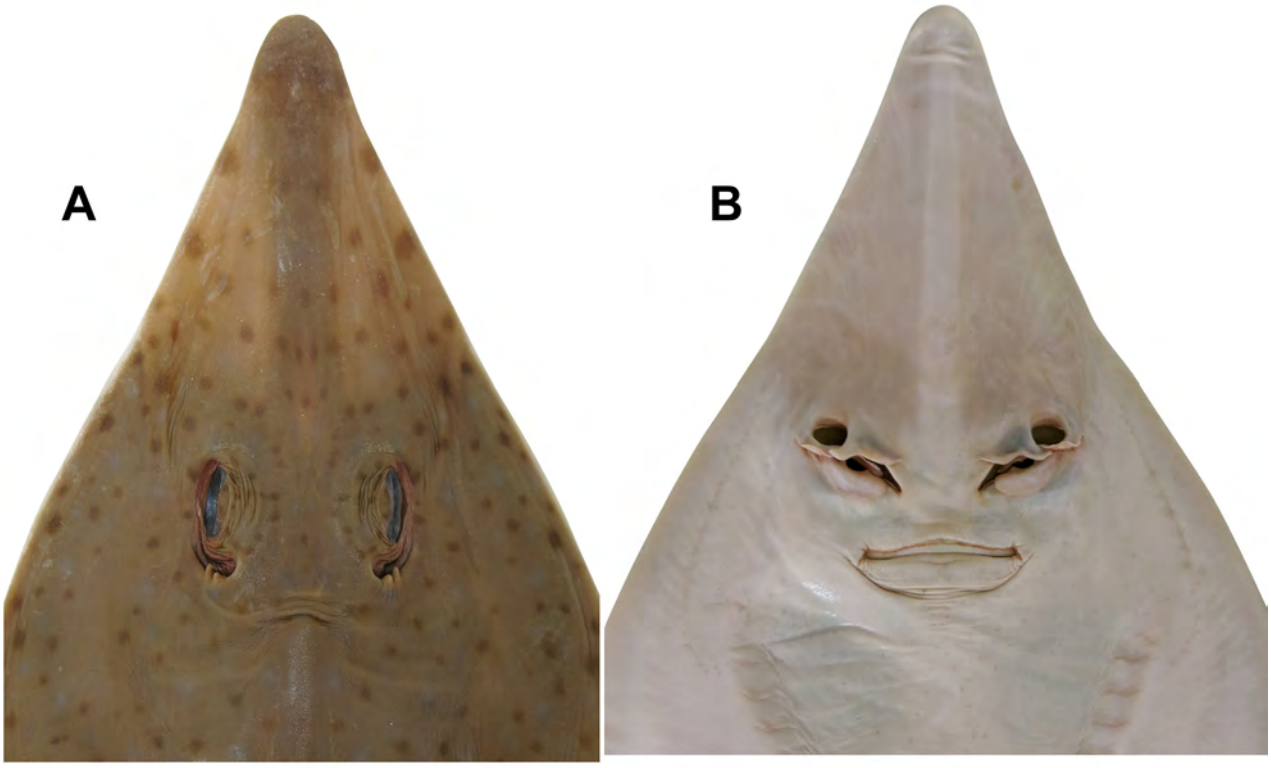

FIGURE 2. Head of preserved adult male holotype, 731 mm TL (NTUM 11500): A. dorsal view; B. ventral view.

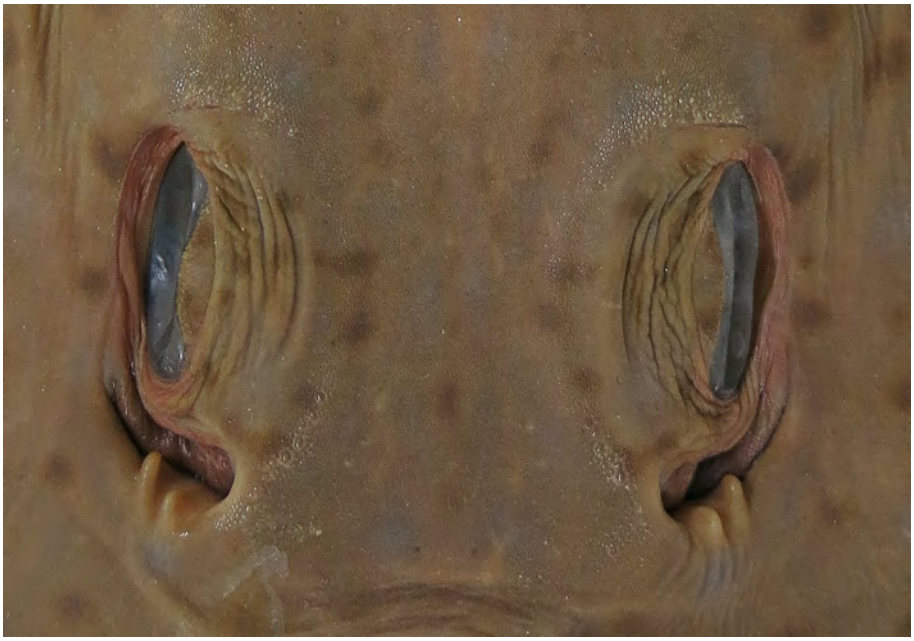

FIGURE 3. Orbital region of *Rhinobatos manai* **sp. nov.**, preserved adult male holotype, 731 mm TL (NTUM 11500).

Dermal denticles minute, close-set, covering entire body and fins; thorns and tubercles absent; dorsal surface with narrow series of slightly enlarged, seed-like denticles around orbit, along midline, and on scapular region; around orbit, enlarged denticles most pronounced anteriorly at preorbit and posteriorly, with posterior patch

extending over upper spiracle margin; along midline, enlarged denticles most pronounced above abdomen; weakly represented between dorsal fins and barely evident on caudal peduncle; enlarged denticles irregular in size and shape, largest with crenulate anterior margins; dorsal surface of claspers naked at tip and near pelvic-fin insertion. Ventral surface uniformly covered with minute denticles, including upper lip edges, near insertion of anterior nasal flap, below posterolateral and posterior nasal flaps, and on tail beneath pelvic fins, and most of claspers; a dense covering of small denticles over nasal lamellae.

Prebranchial sensory pore patch relatively narrow, extending posteriorly to level of first gill slit. Postscapular sensory canal long, notched near fifth gill slits, terminating about an orbit diameter from pectoral-fin insertions; canal deeply embedded, not forming shallow groove.

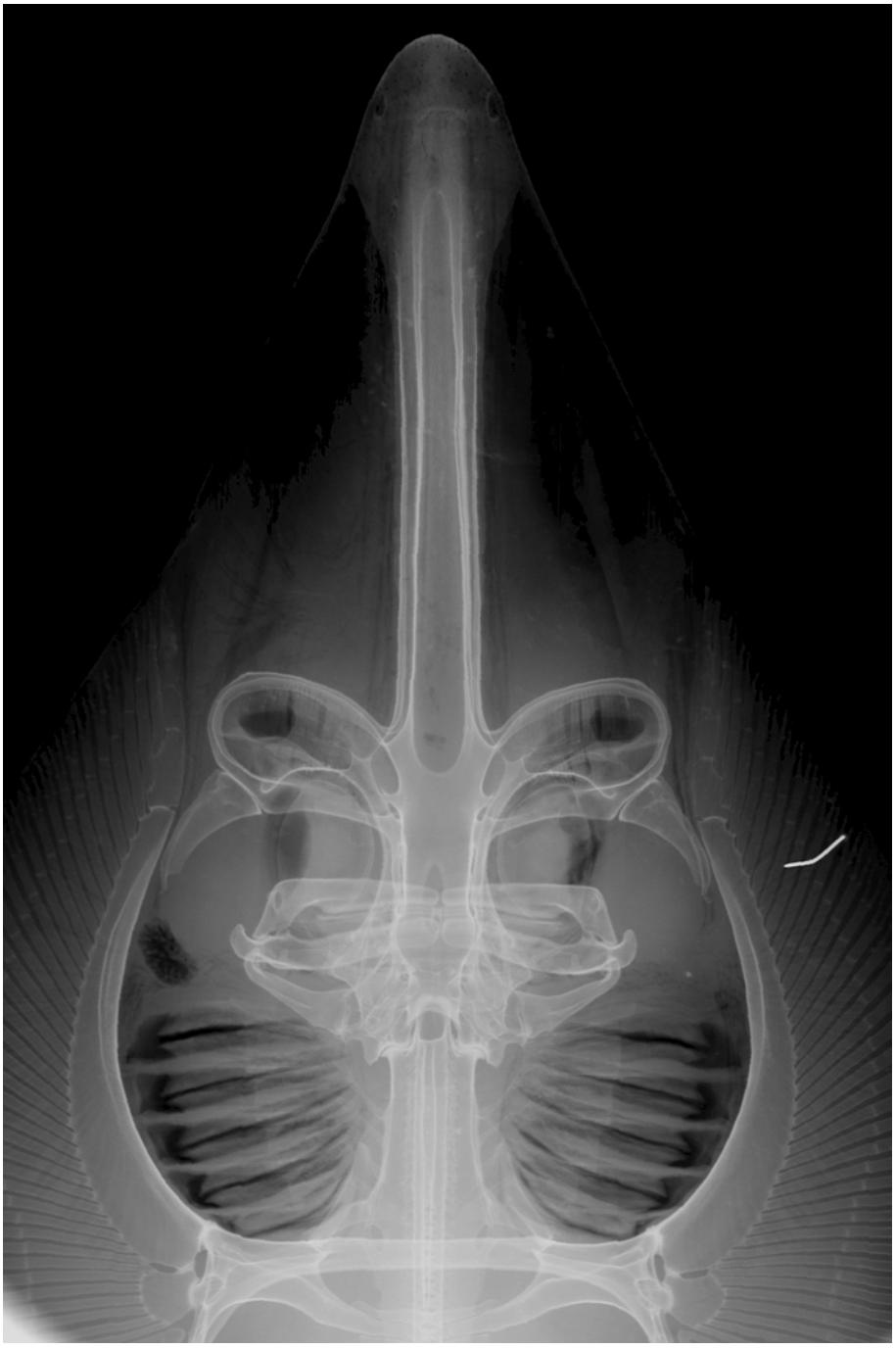

FIGURE 4. Radiograph of the chondrocranium of *Rhinobatos manai* **sp. nov.**, preserved adult male holotype, 731 mm TL (NTUM 11500).

FIGURE 5. Oronasal region of *Rhinobatos manai* **sp. nov.**, preserved adult male holotype, 731 mm TL (NTUM 11500).

Rostral cartilage in holotype long and broad, its shaft not increasing in width in a posterior direction; rostral node broadly expanded and elongate, rounded apically, not angular, axis at widest part of node 9.4% of length of rostral cartilage from snout tip; precerebral cavity broad and uniformly convex posteriorly, narrowly rounded anteriorly at rostral node; rostral cartilage length ~67% of length of neurocranium, ventral edges of rostral cartilage united; nasal capsules large, their transverse axes anterolaterally directed; maximum width across capsules 1.52 times nasobasal length of cranium (base of rostrum to occipital condyles); nasal capsules slightly wider than long; basal plate narrow, its minimum width 5.04 times in nasobasal length; cranial roof with small, narrowly oval fenestra, located well behind precerebral cavity (separated by ~1.4 times its length).

Pectoral skeleton with 30 propterygial, 7 mesopterygial, 2 neopterygial, 27 metapterygial, 66 total radials; anterior radials of propterygium extending forward of nasal capsules by about 10.6% of rostral length. Total pelvic radials 1+24+1; first greatly enlarged, on puboischiadic bar; 24 basipterygial radials; clasper calcified. Vertebral column with 188 total centra (synarcual and free), 171 post-synarcual centra; 17 synarcual centra; 25 monospondylous centra, all centra with ribs; 108 diplospondylous precaudal centra, about 38 diplospondylous caudal centra.

Colour. *In preservative*: Body pale yellowish brown dorsally covered with a complex pattern of small, rusty brown spots and blotches, and small whitish spots with greyish edges; rusty brown spots diffuse-edged and somewhat irregular in size, mostly circular, larger near disc edges and on lateral trunk; whitish spots sparser and more diffuse, poorly defined anteriorly and posteriorly on body; paler near hind margin of pectoral and pelvic fins; paler yellowish brown on translucent areas of snout, lateral cutaneous fold of tail, and between ridges of rostral cartilage; dorsal and caudal fins also with several brownish spots. Ventral surface uniformly white; no dark tip on snout apex.

Size. Only known from the holotype, a 731 mm TL adult male.

Distribution. Holotype collected northwest of Kavieng (02°30'S, 150°44'E), New Ireland, in the Bismarck Archipelago of Papua New Guinea at depths of 191–290 m.

Etymology. Epithet in recognition of Dr Ralph Mana of the University of Papua New Guinea whose invaluable work on the BioPapua projects throughout Papua New Guinea has led to a considerable increase in our knowledge of the deepwater fish fauna of this region.

Molecular analysis. The analysis of the NADH2 data suggests that *Rhinobatos manai* represents a lineage that is distinct from, but closely related to, *R. sainsburyi* and that these two species, in turn, are sister to a clade containing two recently described species from Borneo and the Philippines, *R. borneensis* Last, Séret & Manjaji-Matsumoto, 2016 and *R. whitei* Last, Corrigan & Naylor, 2014, respectively. We caution however that this

inference is based on a single mitochondrial marker. Inclusion of multiple nuclear markers could affect the presented inference.

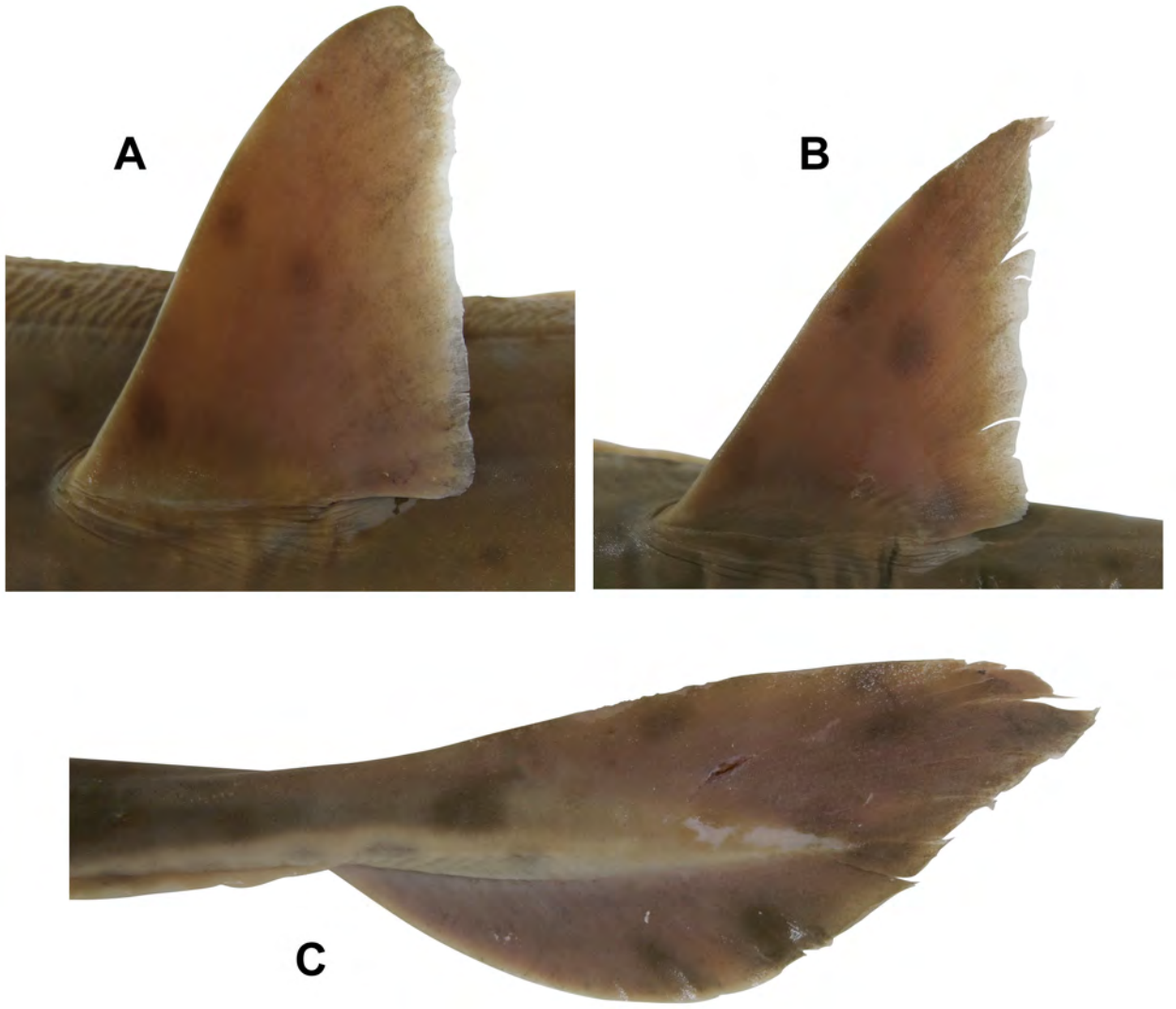

FIGURE 6. Lateral view of the unpaired fins of *Rhinobatos manai* **sp. nov.**, preserved adult male holotype, 731 mm TL (NTUM 11500): A. first dorsal; B. second dorsal; and C. caudal.

Comparisons. The distinctive dorsal colour pattern of small, rusty brown spots and whitish spots with greyish edges distinguishes this species from all other species of *Rhinobatos*. In comparison, *R. borneensis*, *R. holcorhynchus* Norman, 1922, *R. jimbaranensis* Last, White & Fahmi, 2006, *R. lionotus* Norman, 1926, *R. nudidorsalis* Last, Compagno & Nakaya, 2004, *R. sainsburyi*, and *R. schlegelii* Müller & Henle, 1841, all lack such prominent spotting (dorsal coloration uniform or with larger irregular blotches). *Rhinobatos albomaculatus* Norman, 1930, *R. annandalei* Norman, 1926, *R. penggali* Last, White & Fahmi, 2006, and *R. punctifer* Compagno & Randall, 1987 have a colour pattern consisting primarily of white spots, but none of these have a combination of whitish and brownish spots. *Rhinobatos hynnicephalus* Richardson, 1846 has a variable pattern of small dark spots on the dorsal surface, either aggregated in small to large clusters or free. The dorsal surface of *R. irvinei* Norman, 1931 has a distinctive colour pattern of pale orange blotches with dark margins and black spots. *Rhinobatos rhinobatos* Linnaeus, 1758 lacks spots and often has faint bluish grey stripes and blotches on the dorsal body. *Rhinobatos whitei* has the most similar dorsal coloration to *R. manai* **sp. nov.**, consisting of poorly defined white spots and large diffuse dusky and orange blotches. However, *R. manai* differs in having much better defined rusty brown spots and faint white spots with a greyish edge.

Based on its NADH2 sequence, *Rhinobatos manai* belongs to a subgroup of Eastern Indian and Western Central Pacific species, i.e. *R. borneensis*, *R. jimbaranensis*, *R.* cf. *lionotus*, *R. sainsburyi* and *R. whitei* (Fig. 7).

This subgroup of species typically have weak colour patterns with variably developed rusty brown spots or blotches (sometimes plain), with only *R. manai* and *R. whitei* also possessing whitish spots. Although closest to *R. sainsburyi* based on the NADH2 sequence data, *R. manai* is clearly distinct from this species in having: a much longer snout (preorbital length 17.6 *vs*. 13.1–14.7% TL; preoral length 20.6 *vs*. 15.5–17.9% TL; prenarial distance 16.4 *vs.* 12.0–13.6% TL), larger distance between anterior nasal flap insertions (2.9 *vs.* 2.0–2.3% TL), more total free vertebrae (188 *vs.* 175–185), slightly more pectoral radials (66 *vs.* 59–65), and in coloration (large rusty brown blotches and no white spots *vs.* smaller, more regular and better defined rusty brown spots and whitish spots present).

Morphologically, *R. manai* is closest to the recently described *R. whitei* from the Philippines and seems to differ only in the following subtle morphological characteristics: distance across anterior nasal apertures (10.6 *vs.* 8.5–9.7% TL); slightly larger nostrils (nostril length 4.5 *vs.* 3.4–4.1% TL); dorsal fins slightly more separated (interdorsal distance 13.2 *vs.* 11.3–12.9% TL); and a slightly taller second dorsal fin (7.2 *vs.* 5.5–7.0% TL). These two species are most readily distinguished based on their coloration as mentioned previously.

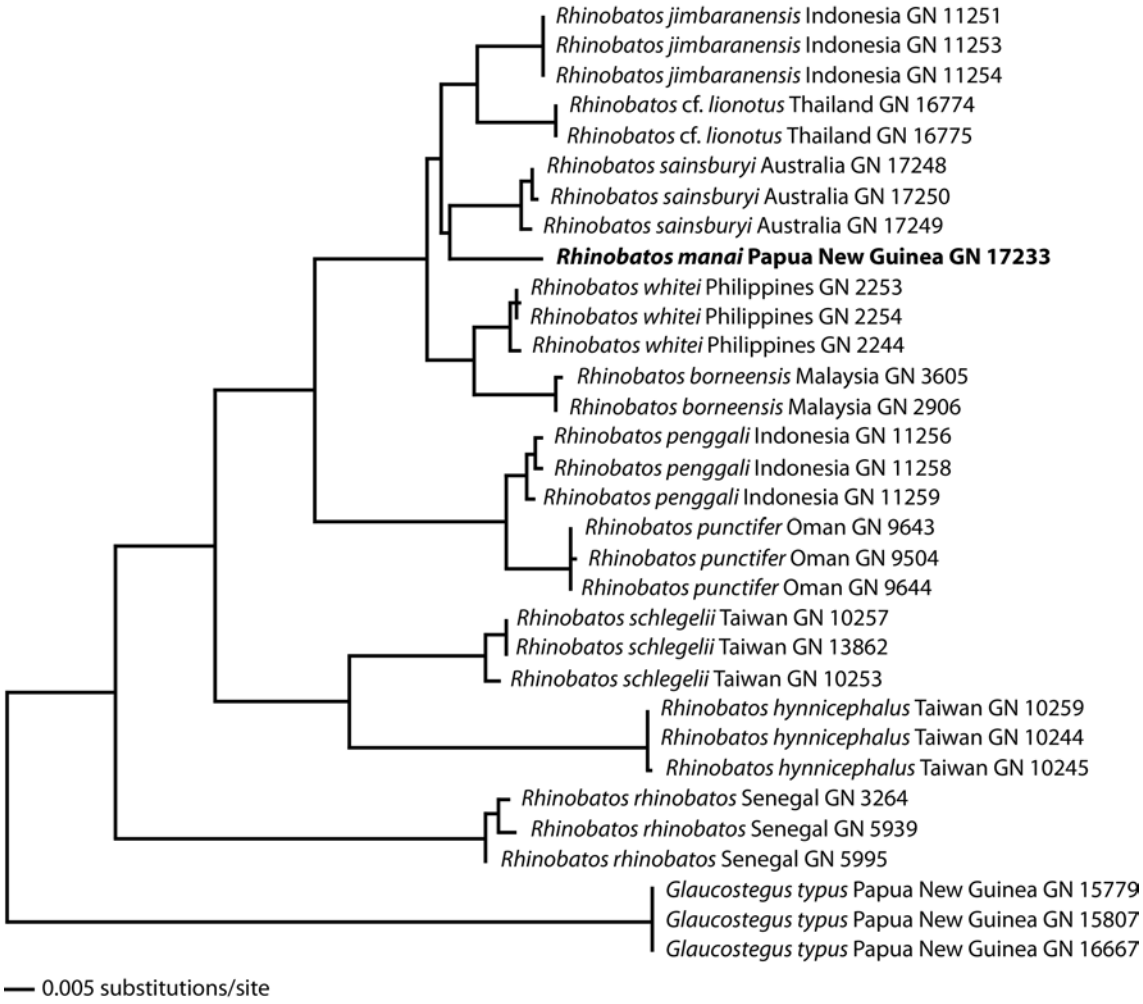

FIGURE 7. Neighbour-joining tree based on p-distances derived from an alignment of mitochondrial NADH2 sequences (1044 sites).

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The holotype was collected during the KAVIENG 2014 expedition (Principal Investigators: Philippe Bouchet, Jeff Kinch and Claude Payri; http://expeditions.mnhn.fr/campaign/kavieng2014) which was part of the *Our Planet Reviewed* expeditions organised jointly by the Muséum National d'Histoire Naturelle (MNHN), Pro-Natura International (PNI) and Institut de Recherche pour le Développement (IRD), with support from Papua New Guinea's National Fisheries Authority. The organisers of this expedition also had supporting funding from the Total Foundation, the Laboratoire d'Excellence Diversités Biologiques et Culturelles (LabEx BCDiv, ANR-10-LABX-0003-BCDiv), the Programme Investissement d'Avenir (ANR-11-IDEX-0004-02), the Fonds Pacifique, and CNRS Institut Ecologie et Environnement (INEE). The expedition was endorsed by the New Ireland Provincial Administration. It operated under a Memorandum of Understanding with University of Papua New Guinea (UPNG), with a permit delivered by the Papua New Guinea Department of Environment and Conservation (DEC). The authors would also like to thank: Dr Wei-Jen Chen (NTUM) for hosting the senior author during a visit to Taipei in January 2016 and providing access to and data for the type material; Jhen-Nien Chen (NTUM) for assistance with accessing the holotype and for obtaining fresh images of the holotype onboard the *RV Alis*; Bernard Séret (MNHN) for providing preliminary images of the preserved holotype; and Shannon Corrigan, Lei Yang and Elisabeth Rochel (College of Charleston) for assisting with obtaining a DNA sequence for the holotype.

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APPENDIX 1. Morphometric data for the holotype of *Rhinobatos borneensis* **sp. nov.** (SMEC 373) with ranges provided separately for two adult male paratypes and three adult-size female paratypes. Measurements expressed as percentages of total length.

	Holotype	Adult males		Large females	
		Min.	Max.	Min.	Max.
Total length (mm)	633	651	686	643	900
Disc width—maximum	29.8	28.9	29.1	28.8	31.0
Disc length	40.9	40.0	41.0	40.3	42.3
Head length—dorsal	21.0	20.2	21.3	18.2	21.8
Head length—ventral	27.4	26.6	27.8	24.4	28.0
Snout length (presocket)	15.7	15.2	15.9	12.6	16.3
Orbit diameter	4.1	3.8	3.9	3.5	4.1
Spiracle length	2.3	2.2	2.5	1.9	2.5
Orbit and spiracle length	4.6	4.3	4.6	4.3	4.6
Interorbital width	2.8	3.0	3.3	3.1	3.3
Interspiracular width	5.1	4.8	4.8	4.9	5.0
Preoral length	18.9	17.7	18.2	16.7	18.9
Mouth width	5.4	5.6	5.7	5.4	5.6
Prenarial distance	14.8	14.3	14.9	13.4	15.3
Nostril length	3.7	3.6	3.8	3.3	3.6
Anterior aperture—width	1.1	1.1	1.3	1.1	1.2
Anterior nasal flap—base length	2.3	2.4	2.5	2.1	2.4
Anterior nasal flap—width	1.5	1.6	1.6	1.3	1.5
Posterolateral nasal flap—total length	3.0	3.0	3.4	2.9	3.4
Posterolateral nasal flap—width	0.6	0.6	0.6	0.6	0.7
Posterior nasal flap— base length	2.3	2.0	2.5	2.4	2.4
Posterior nasal flap—width	1.0	1.1	1.1	0.8	1.1
Distance across anterior nasal apertures	8.8	8.4	9.0	8.2	8.7
Internarial distance (minimum)	2.5	2.3	2.6	2.1	2.4
Distance between anterior nasal flaps	2.7	2.5	2.6	2.3	2.5
Distance from nostril to disc margin	3.3	2.9	3.0	3.2	3.4
Third gill opening—width	1.4	1.3	1.4	1.3	1.5
Distance between first gill openings	12.1	11.7	11.9	11.9	12.2
Distance between fifth gill openings	8.5	8.3	8.3	8.5	9.1
Pelvic fin—length	14.6	14.0	14.3	14.6	14.7
Pelvic fin—anterior margin length	8.5	7.9	8.4	8.3	9.3
Pelvic fin—width	5.6	5.3	5.6	5.7	6.0
Pelvic fin—base length	7.0	7.3	7.5	8.2	8.8
Pelvic fin—inner margin length	7.6	7.3	7.5	6.1	7.0
First dorsal fin—length	6.6	6.6	6.7	6.5	6.8
First dorsal fin—anterior margin length	10.0	8.7	9.2	9.4	10.1
First dorsal fin—height	7.1	7.1	7.3	7.0	7.4
First dorsal fin—base length	4.5	4.3	4.4	4.2	4.7
First dorsal fin—inner margin length	2.1	2.3	2.6	2.0	2.6

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APPENDIX 1. (Continued)

	Holotype	Adult males		Large females	
		Min.	Max.	Min.	Max.
Second dorsal fin—length	6.7	6.4	6.6	6.6	6.7
Second dorsal fin—anterior margin length	9.3	8.8	8.9	9.0	9.2
Second dorsal fin—height	5.7	5.9	6.0	6.3	6.8
Second dorsal fin—base length	4.9	4.4	4.6	4.4	4.9
Second dorsal fin—inner margin length	1.9	1.9	2.1	1.8	2.2
Caudal fin—dorsal margin	13.5	13.5	13.6	13.3	13.5
Caudal fin—preventral margin	6.0	6.2	6.6	6.2	7.0
Caudal fin—lower postventral margin	7.2	6.9	7.0	7.1	7.7
Snout to first dorsal-fin origin	57.0	56.3	57.1	57.4	58.1
Snout to second dorsal-fin origin	74.2	73.7	74.2	74.1	74.5
Snout to upper caudal-fin origin	86.6	86.0	86.6	86.2	87.1
Snout to lower caudal-fin origin	88.0	88.3	88.5	88.0	88.3
Snout to pelvic-fin origin	37.7	37.1	38.1	37.6	39.0
Snout to anterior vent	40.7	39.8	41.1	41.0	41.8
Pelvic-fin insertion to dorsal-fin origin	11.4	11.0	11.1	10.9	11.3
Interdorsal distance	12.7	13.6	13.8	11.7	12.6
Caudal peduncle length (dorsal)	7.6	7.1	8.0	7.2	8.0
Body width—pelvic insertion (tail)	10.3	9.7	10.0	10.2	10.8
Disc width—anterior orbit	16.6	16.1	16.5	16.2	17.3
Body width—first dorsal-fin origin	9.4	9.3	9.4	8.8	9.6
Body width—second dorsal-fin origin	4.7	4.9	5.2	4.5	5.1
Body depth—maximum (scap)	5.1	4.1	4.9	5.1	6.9
Body depth—pelvic-fin insertion	4.5	3.8	4.2	4.4	4.8
Body depth—first dorsal-fin origin	3.7	3.5	3.9	3.2	3.9
Body depth—second dorsal-fin origin	2.3	2.3	2.4	1.8	2.4

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Galeus corriganae sp. nov., a new species of deepwater catshark (Carcharhiniformes: Pentanchidae) from Papua New Guinea

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Abstract

A new species of catshark, provisionally placed in the genus *Galeus*, is described from Papua New Guinea based on 7 specimens collected during recent deepwater surveys of the region. The new species, *Galeus corriganae*, is closest to *G. priapus* from New Caledonia and *G. gracilis* from northwestern Australia but differs in several morphological characters. A reclassification of the catshark groups is required to revise the familial and generic arrangement of the group.

Key words. *Galeus*, catshark, new species, Papua New Guinea, Pentanchidae

Introduction

Deepwater trawl surveys of the waters of Papua New Guinea between 2010 and 2014 using the RV *Alis* have provided the first detailed insights into the sharks and rays occurring on the continental slope of this area. These surveys consist of the BIOPAPUA cruise in 2010 (Pante *et al.*, 2012) and the PAPUA NIUGINI Expedition in 2012 (Samadi *et al.*, 2014), and more recently the MADEEP deep-sea cruise and Kavieng expedition, both in 2014. The catches from these surveys include a number of sharks and rays which were retained and are deposited in fish collections in Taiwan. Included in these samples were several catshark species which had not been documented from Papua New Guinea. In fact, prior to these surveys, only 2 catshark species had been confirmed from Papua New Guinea, *Atelomycterus marnkalha* and *Cephaloscyllium stevensi* and which have only been described within the last 10 years (Jacobsen & Bennett, 2007; Clarke & Randall, 2011).

Catsharks of the order Carcharhiniformes have previously been placed in a single family, the Scyliorhinidae. Iglésias *et al.* (2005) identified a number of paraphylies within the Carcharhiniformes and as a result they resurrected the family Pentanchidae for the catshark species which lack a supraorbital crest on the chondrocranium. This family has been poorly followed in the literature adding to taxonomic confusion amongst the catsharks. Despite the somewhat limited usage of Pentanchidae as a valid family, the molecular and morphological evidence provided by Iglésias *et al.* (2005) strongly support this family and more recent molecular studies further support this familial arrangement (L. Yang, unpublished data).

Prior to the recent deepwater surveys of Papua New Guinea, no members of the Pentanchidae had been recorded from its waters. Fricke *et al.* (2014) reported two pentanchid species, including *Galeus gracilis*. Subsequent examination of the 6 available specimens, taken in the deep water trawl surveys, of this catshark species revealed it to be an undescribed species. This species is herein formally named and described. It should be noted that the generic arrangement of the Pentanchidae is currently under review, thus the placement of this species into the genus *Galeus* Rafinesque, 1810 is only provisional. One Australian catshark species, *Figaro boardmani* (Whitley 1928), was previously placed in the genus *Galeus* before the genus *Figaro* Whitley, 1928 was resurrected

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by Gledhill *et al.* (2008). The new Papua New Guinea species described herein does not have the pelvic fins united over the claspers (forming an 'apron') and has a much shorter caudal peduncle and abdomen. These characters separate it from the genus *Figaro* and placer it most closely with *Galeus.*

Materials and methods

The types were collected during deepwater surveys near Madang in 2010 and 2012 and near West New Britain in 2014 on-board the French research vessel *Alis* of the Institut de Recherche pour le Développement (IRD, Noumea). The specimens were subsequently sent, with other fish specimens collected, to either the National Taiwan University Museum (NTUM) or Academia Sinica (ASIZ) in Taipei. A total of 77 morphometric characters were measured on the holotype (NTUM 10171) and 4 paratypes (NTUM 10321, NTUM 10322, NTUM 11492 and NTUM 11493) following the methodology proposed by Nakaya *et al.* (2008) for the deepwater catshark genus *Apristurus*. The following two measurements from Nakaya *et al.* (2008), caudal height and anal-fin base length (ceratotrichia), were not measured as are more relevant to the genus *Apristurus*. The morphometric data is presented in Table 1 as a percentage of total length. Meristics were taken from radiographs of the 5 NTUM type specimens. Tooth rows counts were taken directly from several types. Male maturity was assigned based on the level of calcification of the claspers: not calcified (juvenile), partially calcified (adolescent). No adult males with fully calcified claspers were observed.

The types of the new species were sampled for muscle tissue on-board the *RV Alis* immediately post capture. The samples were temporarily stored in 95% alcohol in the field. DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc Norcross, GA). Extracted total DNA was stored at -20 °C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via the Polymerase Chain Reaction (PCR). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µl volume comprising 0.3 µM primers, 2.5 mM $MgCl_2$, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA), and 50–100 ng template DNA. The reaction mixture was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio), and bi-directionally sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego USA).

DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd Auckland, New Zealand. Available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within the Geneious Package (Biomatters Ltd Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. Maximum Likelihood Tree was estimated from the data set using the GTR+I+G model. A bootstrap analysis was run separately under the same model conditions to estimate support for each of the nodes in the ML tree. All phylogenetic analyses were carried out using the software package PAUP*4.0 version a148.

The distribution map was generated in QGIS (QGIS Development Team, 2016) using Google Earth base layers.

Galeus corriganae sp. nov.

Corrigan's Catshark
(Figs 1–4, Table 1)

Galeus gracilis—Fricke *et al.*, 2014: 12 (Madang, based on NTUM 10171)

Holotype. NTUM 10171 (tissue accession GN 17185), adolescent male 306 mm TL, west of Sek Island, Madang, Papua New Guinea, 05°04' S, 145°51' E, 582–587 m depth, 28 Nov 2012.

FIGURE 1. Lateral view of the holotype of *Galeus corriganae* **sp. nov.**, NTUM 10171, adolescent male 306 mm TL: (A) fresh; (B) preserved.

FIGURE 2. Ventral view of the head of the holotype of *Galeus corriganae* **sp. nov.**, NTUM 10171, adolescent male 306 mm TL (fresh).

Paratypes. 6 specimens: NTUM 10321 (tissue accession GN 17204), adolescent male 282 mm TL, north of Taviltae, Madang Province, Papua New Guinea, 04°30' S, 145°34' E, 600–660 m depth, 17 Dec 2012; NTUM 10322 (tissue accession GN 17207), juvenile male 203 mm TL, north of Taviltae, Madang Province, Papua New Guinea, 04°29' S, 145°31' E, 500–510 m depth, 17 Dec 2012; NTUM 11492 (tissue accession GN 17225), adolescent male 372 mm TL, southeast of Murien, West New Britain, Papua New Guinea, 06°10' S, 149°18' E, 510–743 m depth, 7 May 2014; NTUM 11493 (tissue accession GN 17224), juvenile male 271 mm TL, south of Murien, West New Britain, Papua New Guinea, 06°08' S, 149°10' E, 430–620 m depth, 6 May 2014; ASIZ unregistered (field code CP 3708-5), 2 specimens, female 278 mm TL and juvenile male 247 mm TL, off Madang, Papua New Guinea, 05°01.270' S, 145°50.210' E, 502–529 m depth, 2 Oct 2010.

Diagnosis. A small, slender *Galeus* with the following combination of characters: relatively broad head, interorbital space 7.2–7.8% TL; pelvic–anal space 12.2–13.0% TL; anal fin relatively small, base length 7.8–8.6% TL; anal-fin posterior margin 5.2–6.3% TL; prepectoral length relatively short, about 18.4–21.5% TL; labial furrows moderately long, not confined to mouth corners, uppers 2.2–2.9% TL; enlarged denticle crest of upper caudal fin originating anterior to origin of ventral caudal lobe; denticles on elevated portion of supracaudal crest forming 2–4 central rows of denticles between much larger obliquely positioned lateral rows; no subcaudal crest; anterior margin of pectoral fins black; anterior half of dorsal fins almost entirely dark or dusky; precaudal centra 83–86.

Description. Body very slender, head height 8.0 in holotype (6.2–6.8 in paratypes)% TL; abdomen long, pectoral–pelvic space 14.2 (12.9–14.3)% TL, 1.43 (1.42–1.76) in head length; pelvic–anal space long, 1.51 (1.42–1.60) times anal-fin base; caudal peduncle elongate, anal–caudal space 0.74 (0.76–0.79) times anal-fin base; peduncle moderately compressed. Snout moderately long, parabolic, tip narrowly rounded; preoral length 7.3 (7.1–8.5)% TL, 0.90 (0.78–0.95) times mouth width; prenarial snout 1.28 (1.18–1.37) times eye length. Eyes small, length 4.3 (4.0–4.6)% TL, 4.74 (4.36–5.03) in head length; eyes slightly dorsolateral on head, with well-developed subocular ridges and nictitating lower eyelids. Spiracles small and subcircular, close to but well separated from eyes; dorsolateral on head. Gill slits moderately long, upper ends about level with lower edges of eyes, fifth gill slit shortest and above pectoral-fin origins; gill filaments not visible externally.

Mouth large, moderately long, arched, width 8.2 (7.7–9.1)% TL, 2.18 (2.31–3.18) times its length; labial furrows well developed, lower furrows only slightly shorter than mouth length, uppers not extending forward to symphysis (Fig. 2). Teeth with mainly 5 cusps (rarely 3); cusps adjacent central cusp well developed, almost half length of central cusp; in 60 (63–69) rows in upper jaw; 60 (54–64) rows in lower jaw.

Denticles on sides of trunk below first dorsal fin tricuspidate, semi-erect, slightly imbricated; crown broadly parabolic with a long, broad-based central cusp and short but distinct lateral cusps; pronounced longitudinal ridge along midline of crown including central cusp. Supracaudal crest well developed, about equal in length to interdorsal space; origin of crest posterior to second dorsal-fin free rear tip, anteriorly pre-crest denticles progressively increasing in size and becoming more oblique on crest; crest becoming elevated anterior to level of origin of lower lobe, elevated portion demarcated by strip of naked skin; denticles in mainly 3 or 4 central rows (2 or 3 in smallest type), rows bordered by larger, more posterolaterally directed lateral denticles (about 2 or 3 times size of central denticles); subcaudal crest absent.

Claspers of adults not available; outer length of partially calcified clasper in largest adolescent male 8.4% TL, inner length 10.7% TL.

Dorsal fins low, strongly raked, anterior margins slightly to moderately convex, apex moderately round, posterior margins almost straight, free rear tips angular, first slightly larger than second, first dorsal-fin height 1.15 (1.10–1.44) times second dorsal-fin height; first dorsal-fin origin over pelvic-fin insertions; second dorsal-fin origin above midbase of anal fin, its insertion well behind insertion of anal fin. Pectoral fins moderately large, broad, anterior margin 10.8 (10.1–11.7)% TL. Pelvic fins small, low, angular, length 10.6 (10.3–11.5)% TL. Anal fin relatively short, base 8.4 (7.8–8.6)% TL, 1.31 (1.36–1.50) in interdorsal space; origin slightly posterior to mid-interdorsal space; anal-fin height 2.48 (1.97–2.29) in base length. Caudal fin slender, moderately long, asymmetrical; dorsal caudal margin biconvex, mesially weakly concave to level with subterminal notch; postventral margin weakly concave, ventral lobe barely evident; subterminal margin straight; terminal caudal margin convex.

Monospondylous centra 39 (38–39); precaudal centra 86 (83–85); caudal 55 (50–54); total 141 (135–138).

Colour. Dark to medium grey above; paler ventrally; four distinct (less distinct once preserved), darker dorsal saddles situated beneath each dorsal fin and on tail (Fig. 1); saddle below first dorsal fin commencing near fin origin, its width slightly narrower than fin base, extending ventrally almost to lateral midline; saddle below second dorsal fin similar, subequal in width to fin base; saddle above apex of lower lobe of caudal fin also of similar size and extends just below lateral midline of fin; broad saddle before terminal lobe of caudal fin, width subequal to length of second dorsal fin, extending across entire width of fin. Dorsal fins with extensions of dark body saddles above base, narrow whitish posterior margins, remaining fin pale grey. Anal fin mostly grey with a narrow (sometimes indistinct) blackish anterior margin, posterior margin whitish. Pectoral fins with a strikingly distinct, narrow black anterior margin (Fig. 2) and a narrow whitish posterior margin; fins darker dorsally than ventrally. Pelvic fins and claspers pale grey, naked skin along dorsal surface of clasper and near cloaca pale. Head distinctly

paler ventrally than dorsally, cheek mostly pale; roof of mouth and tongue dark grey to blackish, floor beneath tongue and jaws whitish.

Size. Only known from the type specimens, 203–372 mm TL. Three are juveniles, 203–271 mm TL, four are adolescent males, 282–372 mm TL, and a single female 278 mm TL.

Distribution. Known only from the type specimens collected off the Madang Province and southwestern West New Britain Province of Papua New Guinea in depths of 500 to 742 m (Fig. 3).

TABLE 1. Morphometrical measurements of the holotype (NTUM 10171) of *Galeus corriganae* **sp. nov.** and ranges for the 4 measured paratypes, expressed as a percentage of total length.

	Holotype	Paratypes	
		Min.	Max.
Total length (mm)	306	203	372
Pre-first dorsal length	44.77	40.39	43.82
Snout to first dorsal-fin insertion	50.00	46.31	50.18
Pre-second dorsal length	62.09	58.13	61.83
Snout to second dorsal-fin insertion	67.32	64.53	67.20
Head length	20.26	19.59	22.75
Prebranchial length	16.29	15.93	18.35
Prespiracular length (horizontal)	12.11	11.27	13.19
Preorbital length (horizontal)	7.05	7.25	7.91
Prenarial length (horizontal to outer margin)	4.56	3.47	4.27
Prenarial length (horizontal to inner margin)	5.48	5.27	5.97
Preoral length	7.31	7.09	8.46
Prepectoral length	18.71	18.36	21.52
Prepelvic length	37.58	35.96	39.25
Snout-vent length	40.85	38.42	41.94
Preanal length	56.86	53.69	59.14
Precaudal length (dorsal)	70.59	70.43	71.22
Head height	8.01	6.17	6.78
Head width at mouth corners	10.14	10.53	11.97
Head width	10.39	10.93	13.23
Mouth width	8.17	7.71	9.09
Mouth length	3.75	2.26	3.40
Internarial width	3.05	2.65	2.74
Upper labial furrow length	2.22	2.18	2.94
Lower labial furrow length	2.24	2.58	2.72
Orbit length	4.27	4.01	4.64
Orbit height	0.89	0.87	1.10
Nostril width	2.42	2.45	2.95
Nostril to mouth distance	2.04	1.82	2.33
Interorbital width	7.32	7.15	7.78
First gill slit height	2.01	2.15	2.66
Third gill slit height	1.64	1.80	2.89
Fifth gill slit height	1.23	1.13	1.95
Intergill width	3.97	3.38	5.19

.....continued on the next page

TABLE 1. (Continued)

	Holotype	Paratypes	
		Min.	Max.
Interdorsal space	11.01	11.69	12.74
First dorsal origin to second dorsal origin	16.69	16.64	18.59
First dorsal insertion to second dorsal insertion	16.84	16.98	18.18
Pectoral-pelvic space	14.18	12.88	14.29
Pectoral free rear tip to pelvic origin	6.69	5.91	8.36
Pectoral origin to pelvic origin	17.11	15.98	17.42
Pectoral insertion to pelvic insertion	20.50	17.57	20.18
Pelvic-anal space	12.66	12.16	13.01
Pelvic origin to anal-fin origin	19.75	18.70	19.88
Anal-caudal space	6.26	5.90	6.71
First dorsal length	8.44	8.62	9.16
First dorsal base length	6.07	5.56	6.62
First dorsal height	3.83	3.57	4.71
First dorsal inner margin length	2.31	2.36	3.11
Second dorsal length	8.21	7.37	8.99
Second dorsal base length	5.93	4.80	6.67
Second dorsal height	3.32	3.22	3.49
Second dorsal inner margin length	2.47	2.27	2.58
Pectoral base length	5.67	4.78	5.87
Pectoral anterior margin	10.78	10.13	11.72
Pectoral posterior margin	6.75	6.96	9.55
Pectoral inner margin	5.34	5.19	5.93
Pelvic anterior margin	5.33	5.17	5.37
Pelvic length	10.58	10.34	11.48
Pelvic base length	7.38	6.32	7.23
Pelvic posterior margin	7.30	7.25	7.82
Pelvic inner margin	4.54	4.17	4.65
Anal base length	8.41	7.81	8.58
Anal anterior margin	7.27	6.07	7.42
Anal posterior margin	4.59	5.15	6.25
Anal height	3.39	3.62	3.96
Anal inner margin	2.11	1.96	2.48
Caudal peduncle height	3.34	3.34	4.02
Caudal-fin length	29.06	27.37	30.07
Caudal-fin height	0.00	0.00	0.00
Caudal-fin preventral margin	9.21	8.13	9.16
Caudal-fin postventral margin	14.96	14.06	16.66
Caudal-fin terminal lobe width	3.17	0.00	3.56
Caudal-fin terminal lobe length	6.30	6.62	6.72
Caudal-fin terminal margin	4.74	4.07	4.93
Clasper outer length	8.43	8.43	8.43
Clasper inner length	10.67	10.67	10.67
Clasper width	2.14	2.14	2.14

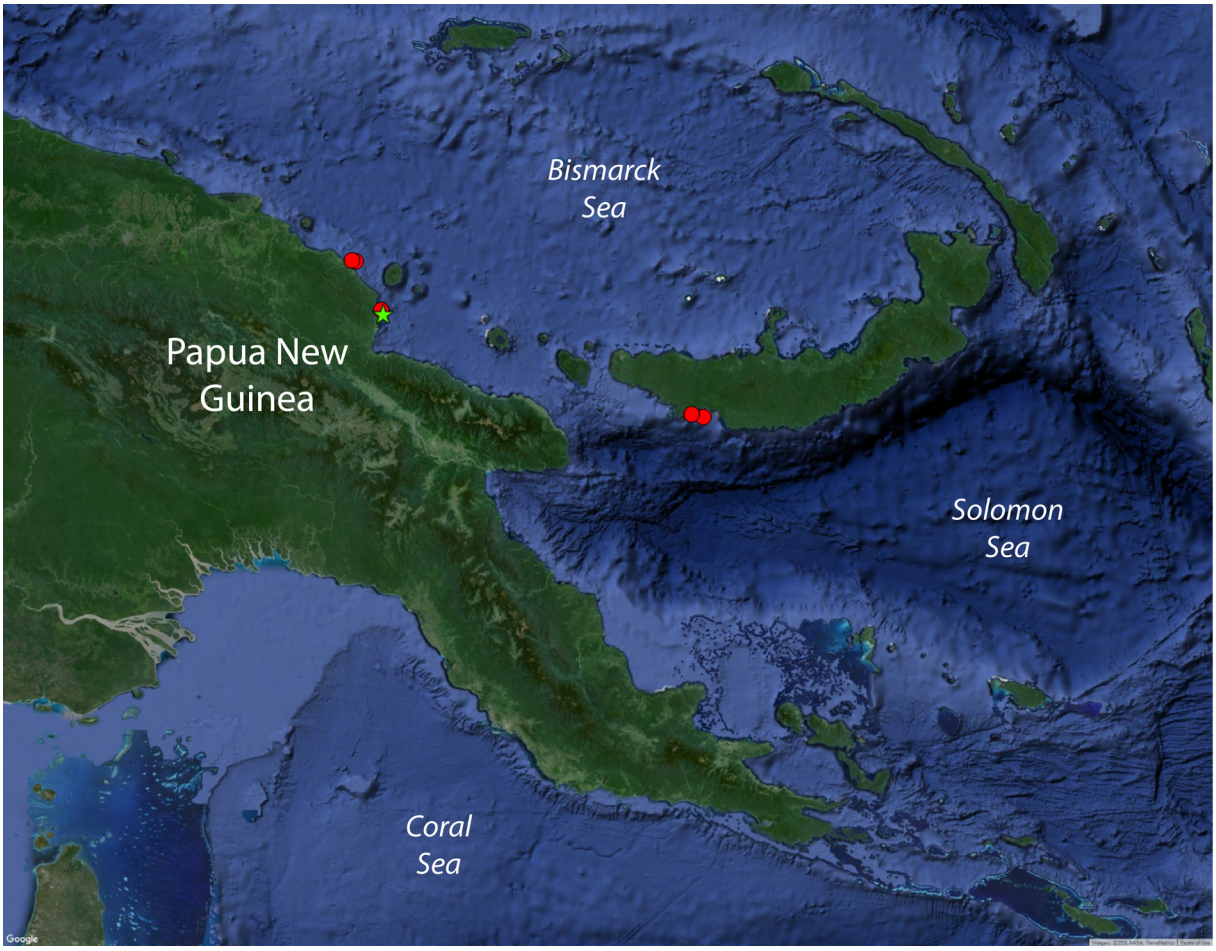

FIGURE 3. Map showing the capture locations of the type specimens of *Galeus corriganae* **sp. nov.** in Papua New Guinea. Green star denotes the holotype and red circles denote the paratypes (Image © NASA, TerraMetrics, Google Earth).

Etymology. Named for Dr Shannon Corrigan whose extensive molecular population and phylogenetic work on sharks has contributed toward an improved understanding of their alpha taxonomy and phylogenetic relationships.

Molecular analysis. The analysis of the NADH2 data (Fig. 4) suggest that *Galeus corriganae* represents a monophyletic lineage that is distinct from, but most closely related to *Galeus priapus* Séret & Last, 2008 from New Caledonia. These two species are, in turn, sister to *G. nipponensis* Nakaya, 1975, *G. longirostris* Tachikawa & Taniuchi, 1987 and *G. eastmani* (Jordan & Snyder, 1904) from the Northwest Pacific (Fig. 4). No tissue samples are available for *Galeus gracilis* Compagno & Stevens, 1993 from northwestern Australia, but this species likely belongs within this complex due to its morphological similarities to *G. priapus* and the new species. It should be noted that this inference is based on a single mitochondrial marker. Inclusion of multiple nuclear markers could affect the presented inference.

Comparisons. Comparisons of the new species with its congeners is restricted to the two most similar species, *G. priapus* and *G. gracilis*, which are also the two closest congeners from a geographical sense. *Galeus corriganae* **sp. nov.** is almost identical in appearance to *Galeus priapus* from New Caledonia but differs from this species in the following characters: broader head (head width 10.4–13.2 vs. 8.3–9.9% TL in *G. priapus*; interorbital width 7.2–7.8 vs. 6.0–7.0% TL), larger eyes (orbit length 4.0–4.6 vs. 2.6–3.5% TL), longer upper labial furrows (2.2–2.9 vs. 1.4–2.1% TL), slightly larger nostrils (nostril width 25–3.0 vs. 2.2–2.3% TL), pelvic and anal fins further apart (pelvic–anal space 12.2–13.0 vs. 10.0–11.7% TL), shorter pelvic-fin base (base length 6.3–7.2 vs. 7.6–9.3% TL) and longer pelvic-fin inner margin (4.2–4.7 vs. 2.8–4.2% TL), shorter anal-fin inner margin (2.0–2.5 vs. 1.3–1.9% TL)

Galeus corriganae **sp. nov.** is also similar to *Galeus gracilis* from northwestern Australia but differs in the following characters: more vertebrae (monospondylous centra 38–39 vs. 33–36 in *G. gracilis*; precaudal centra 83–86 vs. 74–78; total centra 130–134 vs. 135–141), smaller anal fin (posterior margin length 5.2–6.3 vs. 6.4–7.3%

TL), pelvic–anal space much longer (12.2–13.0 vs. 8.0–10.3% TL), claspers of adults likely to be much longer (outer length of adolescent male 8.4 vs. 5.2–7.3% TL in adult males of *G. gracilis*).

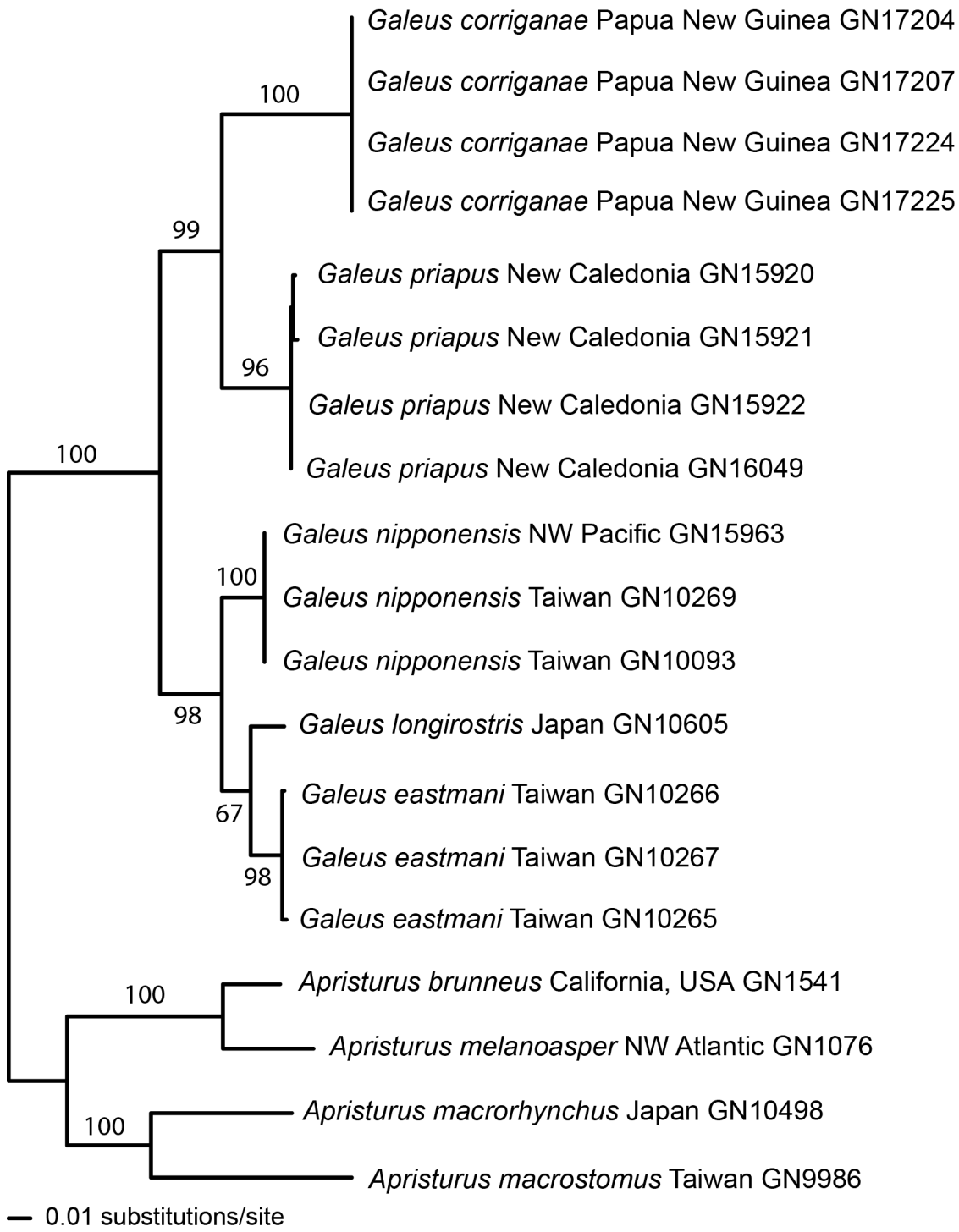

FIGURE 4. Maximum Likelihood tree estimated under the General Time Reversible model (GTR) with model terms to accommodate both Invariant site (I) and Gamma Distributed rates (G). Bootstrap support values are shown from a separate ML bootstrap analysis. Sequences used in this tree are part of the Chondrichthyan Tree of Life project (http://sharksrays.org/).

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The BIOPAPUA deep sea cruise (PIs: Sarah Samadi, Laure Corbari) took place between 22 August and 18 October 2010 on board R.V. *Alis* deployed by Institut de Recherche pour le Développement (IRD) in collaboration with University of Papua New Guinea (UPNG). The PIs acknowledge funding from the CNRS Institut Ecologie et Environnement (INEE) (http://expeditions.mnhn.fr/campaign/biopapua).

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A new species of velvet skate, *Notoraja sereti* n.sp. (Rajiformes: Arhynchobatidae) from Papua New Guinea

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Abstract

A new arhynchobatin skate, *Notoraja sereti* **n. sp.**, is described based on three specimens collected from off Madang (Papua New Guinea) at depths of 800–980 m. This medium-size *Notoraja* skate shares with other velcro skates from the Western Pacific, *N. alisae, N. fijiensis*, *N. inusitata* and *N. longiventralis*, a ventral surface covering of fine denticles giving the skin a velvety feel. *Notoraja sereti* differs from all of these species in having a shorter snout (preorbital length 10.1–11.1 *vs*. 11.5–14.5% TL, prenasal length 8.2–8.9 *vs*, 9.8–12.1% TL), shorter head (dorsal head length 15.2–16.2 *vs*. 17.1–19.3% TL, ventral head length 21.6–22.9 *vs*. 22.9–25.9% TL), fewer pectoral-fin radials (total radials 58–60 *vs*. 61–74), and fewer vertebrae (predorsal diplospondylous centra 66–71 *vs*. 72–82, predorsal centra 90–95 *vs*. 98–107, total centra 126–131 *vs*. 135–152).

Key words: *Notoraja,* new species, velcro skate, Papua New Guinea

Introduction

The deepwater ichthyofauna of Papua New Guinea is very poorly understood. A prime example of this is the paucity of skates (Rajiformes) recorded from the area (Last *et al.*, 2016b). Skates are the most speciose elasmobranch group globally with close to 300 species known, ranging from the tropics to the polar regions. The first major deepwater surveys of Papua New Guinea were conducted between 2010 and 2014 which resulted in the collection of important shark and ray material. Included in this material were a number of skates specimens, three individuals belonging to the family Arhynchobatidae (softnose skates), three to the family Rajidae (hardnose skates), and one to the family Anacanthobatidae (legskates). These represent the first skate species recorded from the northern extremity of the Australasian Plate, in the seas off Papua New Guinea. The softnose skate specimens, collected during the 2012 expedition off Madang, were reported in Fricke *et al.* (2014)'s checklist of fishes of Madang as *Insentiraja subtilispinosa*. However, recent examination of these specimens revealed that they actually represent an undescribed species of *Notoraja*, belonging to a subgroup known as the 'velcro skates' (covered dorsally and ventrally with fine spinular denticles). This species is formally named and described herein and represents the only species of softnose skate currently known to occur in Papua New Guinea (Last *et al*., 2016a).

Materials and methods

The morphological methodology follows Last *et al.* (2008) and Séret & Last (2009). Morphometric measurements were taken from each of the type specimens. Counts of the number of vertebrae, pectoral-fin and pelvic-fin radials, and tooth rows were taken from digital radiographs of the type specimens. In the species description, morphometric

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proportions and meristic values are given first for the holotype, followed by ranges for the two paratypes in parentheses. Type specimens are deposited in the biological collection of the National Taiwan University Museum (NTUM) in Taipei.

***Notoraja sereti* n. sp.**
Papuan Velvet Skate
Figs 1–8; Table 1

Insentiraja subtilispinosa—Fricke *et al.*, 2014: 15.

Holotype. NTUM 10067, female 459 mm TL, southeast of Sek Island, Madang, Papua New Guinea, 5°07' S, 145°53' E, Papua Niugini cruise, R/V Alis, station CP3967, 980 m depth, 2 December 2012.

Paratypes. NTUM 10042, female 458 mm TL, east of Sek Island, Madang, Papua New Guinea, 5°06' S, 145°53' E, Papua Niugini cruise, R/V Alis, station CP3963, 960–980 m depth, 30 November 2012; NTUM 10330, adolescent male 363 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 5°21' S, 145°53' E, Papua Niugini cruise, R/V Alis, station CP4027, 800–820 m depth, 14 December 2012.

FIGURE 1 Dorsal view of the holotype of *Notoraja sereti* **n. sp.** (NTUM 10067, female 459 mm TL) immediately post-capture.

Diagnosis. A medium-size species of *Notoraja* with the following combination of characters: disc wider than long, width 47.1–50.3% TL, length 42.0–43.6% TL; short head (dorsal head length 15.2–16.2% TL; ventral head length 21.6–22.9% TL); relatively short snout (preorbital length 10.1–11.1% TL; ventral snout length 11.2–12.1% TL); interspiracular distance 5.3–5.9 TL, internasal distance 6.2–6.8% TL, preorbital length 2.4–3.0 times orbit

length and 2.9–3.6 times interorbital; two dorsal fins, interdorsal space 1.1–1.9% TL; tail width at pelvic-fin axil 0.9-1.6 times its height; single, small preorbital thorn; dorsal and most of ventral surface of disc entirely velvety, covered with fine denticles; median disc and pelvic fins naked in adolescent male; anterior pelvic-fin lobe naked in females (skin naked or with sparse denticles ventrally on mid belly, chin, nasal curtain, and around cloaca); tail long and slender, entirely velvety and without thorn-like denticles; lateral tail folds moderately well developed; nasal lobes expanded, width of nasal curtain 7.9–8.3% TL; anterior pelvic-fin lobe slightly shorter or similar length to posterior lobe; dorsal and ventral surfaces greyish brown to dark bluish grey; total pectoral-fin radials 58–60; monospondylous centra 23–25, total diplospondylous centra 103–106, total centra 126–131.

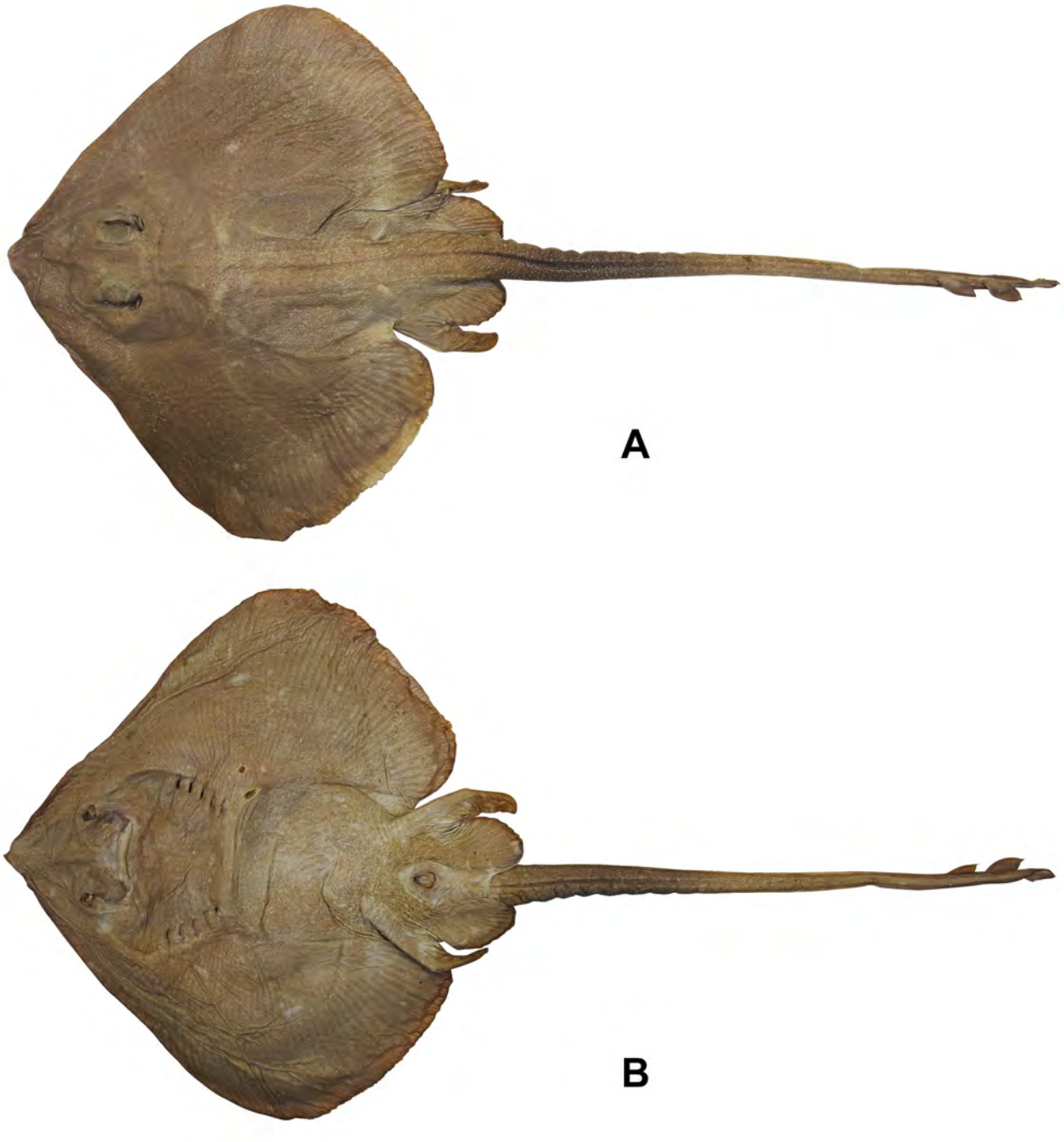

FIGURE 2. Preserved holotype of *Notoraja sereti* **n. sp.** (NTUM 10067, female 459 mm TL): (A) dorsal view; (B) ventral view.

FIGURE 3. Dorsal view of the adolescent male paratype of *Notoraja sereti* **n. sp.** (NTUM 10330, 363 mm TL) immediately post-capture.

FIGURE 4. Dorsal view of the adolescent male paratype of *Notoraja sereti* **n. sp.** (NTUM 10330, 363 mm TL) after preservation.

Description. Disc heart-shaped, 1.17 (1.10–1.12) times as broad as long; maximum angle in front of spiracles 102° (96–100°); anterior margin nearly straight in females, weakly undulate in adolescent male paratype; apices broadly rounded; posterior margin moderately convex. Axis of greatest width 62% (61–64%) of disc length. Preorbital snout length 2.43 (2.98–2.99) times orbit length, 2.93 (3.28-3.58) times interorbital width; preoral snout length 1.76 (1.81–1.91) times internarial distance. Orbit diameter 1.21 (1.10–1.20) times interorbital distance, and 2.04 (1.70–1.78) times length of spiracles. Nasal lobes moderately expanded and rounded, posterior margin weakly fringed.

Mouth wide, its width more than 80 (80–81)% of maximum width of nasal curtain. Upper jaw weakly indented at symphysis; upper and lower jaws slightly convex on either side of symphysis. Teeth with relatively long, pointed cusps arranged in quincunx. Distance between first gill slits 1.82 (1.83) times larger than distance between nostrils; distance between fifth gill slits 1.22 (1.07) times larger than distance between nostrils.

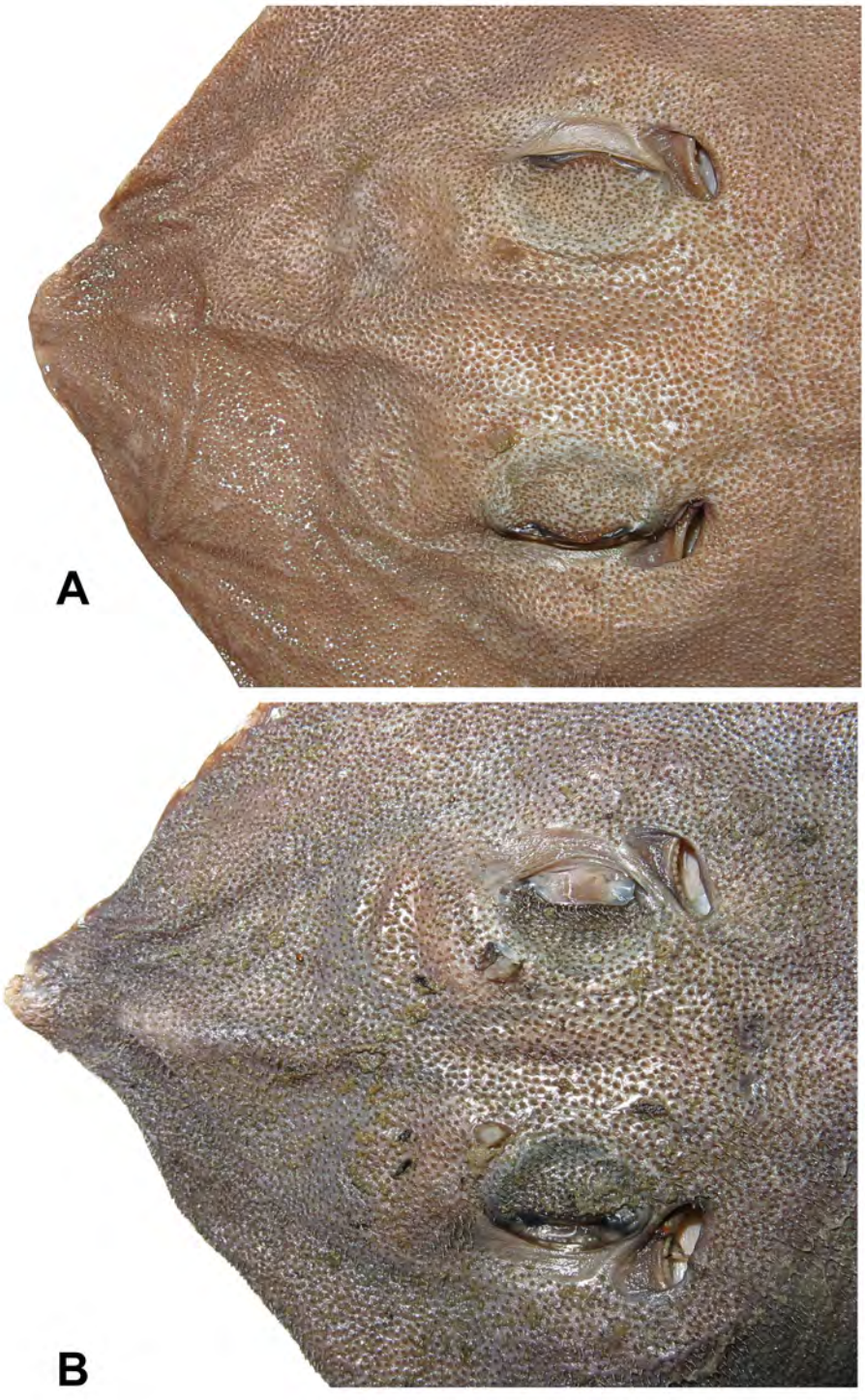

FIGURE 5. Dorsal head of *Notoraja sereti* **n. sp.**: (A) holotype, NTUM 10067, female 459 mm TL; (B) paratype, NTUM 10330, subadult male 363 mm TL.

Pelvic fins deeply incised with lobes connected by radials and membranes, anterior lobe moderately long, reaching to about posterior quarter of posterior lobe in females, finger-like with blunt tip (longer and more acute in adolescent male); posterior lobe with convex lateral margins, its posterior margin crenate due to extension of posterior radials. Tail narrowly oval at base, variably depressed over length; moderately convex dorsally, very weakly convex ventrally; tapering gradually posteriorly; tail width at axils of pelvic fins 1.69 (1.50–2.57) times

width at its midlength, 2.29 (2.48–3.72) times its width at dorsal-fin origin respectively; length from rear of cloaca 1.45 (1.41–1.51) times distance from tip of snout to rear of cloaca; width at first dorsal-fin origin 2.13 (1.30–1.40) times its height; lateral skin folds originating at about anterior third of tail, extending to distal half of epichordal caudal-fin lobe; folds slightly broadening distally, but always narrower than tail width. Dorsal fins strongly raked, of similar shape and size; relatively short and rather low with convex anterior margins, straight or slightly convex posterior margins and broadly rounded rear tips; separated by a short interspace, 50% (36–60%) length of first dorsal-fin base. Epichordal caudal-fin lobe developed, separated by narrow interspace from and distinctly longer than second dorsal-fin base; hypochordal caudal lobe very low, originating near end of lateral fold, confluent with epichordal lobe.

TABLE 1. Morphometric data for the three type specimens of *Notoraja sereti* n.sp. from Papua New Guinea.

	holotype female	paratype subadult male	paratype female
Total length (mm)	459	363	458
Disc width	50.3	47.1	47.8
Disc length (direct)	43.0	42.0	43.6
Snout to maximum width	26.6	25.7	27.9
Snout length (preorbital direct)	10.1	10.6	11.1
Snout to spiracle	15.0	15.0	14.8
Head (dorsal length)	15.2	16.0	16.2
Orbit diameter	4.2	3.6	3.7
Orbit and spiracle length	4.8	4.9	4.6
Spiracle length (main pore)	2.0	2.1	2.1
Distance between orbits	3.5	3.0	3.4
Distance between spiracles	5.8	5.3	5.9
Distance-snout to cloaca	40.9	39.8	41.0
Cloaca to D1	47.3	46.6	47.0
Cloaca to D2	51.7	51.1	50.4
Cloaca to caudal origin	55.4	55.7	53.8
Distance-cloaca to caudal-fin tip	59.4	60.1	58.0
Ventral snout length (pre upper jaw)	11.9	11.2	12.1
Prenasal length	8.7	8.2	8.9
Ventral head length (to fifth gill)	21.6	22.2	22.9
Mouth width	6.7	6.4	6.6
Distance between nostrils	6.8	6.2	6.3
Nasal curtain length	4.3	4.6	4.7
Nasal curtain (total width)	8.3	7.9	8.2
Nasal curtain (min width)	4.4	3.9	4.1
Nasal curtain (lobe width)	2.1	2.0	2.2
Width of first gill opening	1.5	1.3	1.4
Width of fifth gill opening	1.5	0.9	1.0
Distance between first gill openings	12.4	11.4	–
Distance between fifth gill openings	8.3	6.7	–
Clasper (post cloacal length)	–	16.4	–
Length of anterior pelvic lobe	12.7	13.7	13.1
Length of posterior pelvic lobe	13.4	13.7	13.5

.....continued on the next page

TABLE 1. (Continued)

	holotype female	paratype subadult male	paratype female
Pelvic base width	8.4	7.4	7.6
Tail at axil pelvic fins (width)	3.6	3.9	2.7
Tail at axil pelvic fins (height)	2.6	2.4	2.9
Tail at midlength (width)	2.1	1.5	1.8
Tail at midlength (height)	1.3	1.3	1.3
Tail at D1 origin (width)	1.6	1.0	1.1
Tail at 01 origin (height)	0.7	0.7	0.8
D1 base length	3.3	3.2	3.1
D1 height	1.5	1.2	1.5
D1 origin to caudal-fin tip	12.3	13.8	12.0
D2 origin to caudal-fin tip	7.7	8.9	8.2
Caudal-fin length	4.4	4.6	4.0
lnterdorsal distance	1.7	1.9	1.1

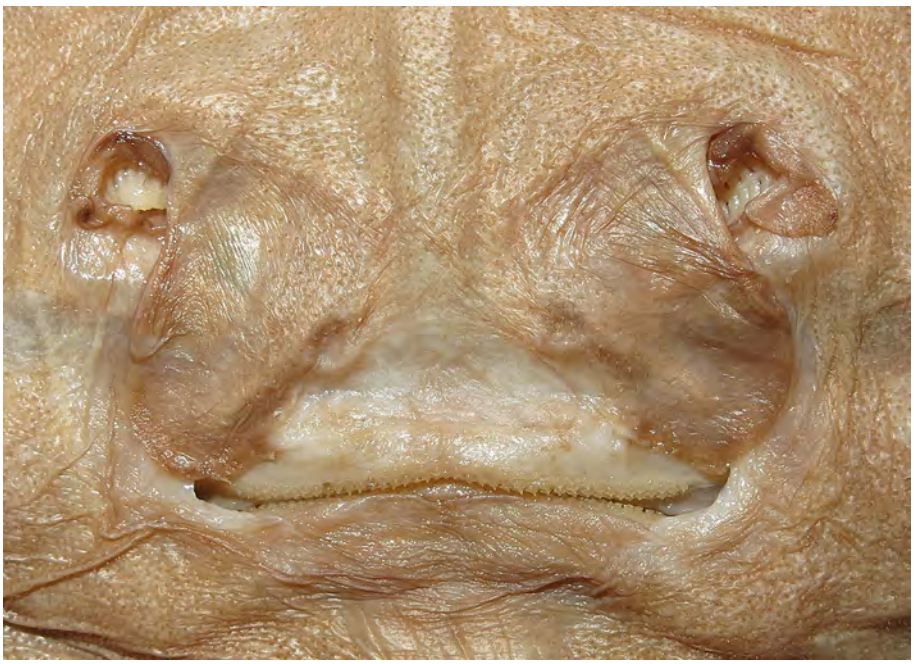

FIGURE 6. Oronasal region of the holotype of *Notoraja sereti* **n. sp.** (NTUM 10067, female 459 mm TL).

FIGURE 7. Dorsal view of the tail tip of the holotype of *Notoraja sereti* **n. sp.** (NTUM 10067, female 459 mm TL).

Dorsal surface of disc velvety, entirely covered with fine, densely spaced, dermal denticles; denticles bristle-like, erect, with almost straight pointed crowns. Ventral surface of disc similarly covered on most surfaces, except median disc (oronasal region, branchial region and belly, Fig. 10b) and entire pelvic fins of adolescent male naked; anterior pelvic-fin lobe naked in females (skin naked or with sparse denticles ventrally on mid belly, chin, nasal

curtain, and around cloaca). A single, small, but conspicuous preorbital thorn present; no other orbital thorns or thorns on disc of types. Tail velvety, densely covered with fine, dermal denticles; no enlarged thorns; a few small, variably spaced thornlets on midline of tail but these very small, barely taller than largest denticles adjacent.

No adult males available; adolescent male paratype with relatively long and very slender clasper, post cloacal length 16.4% TL.

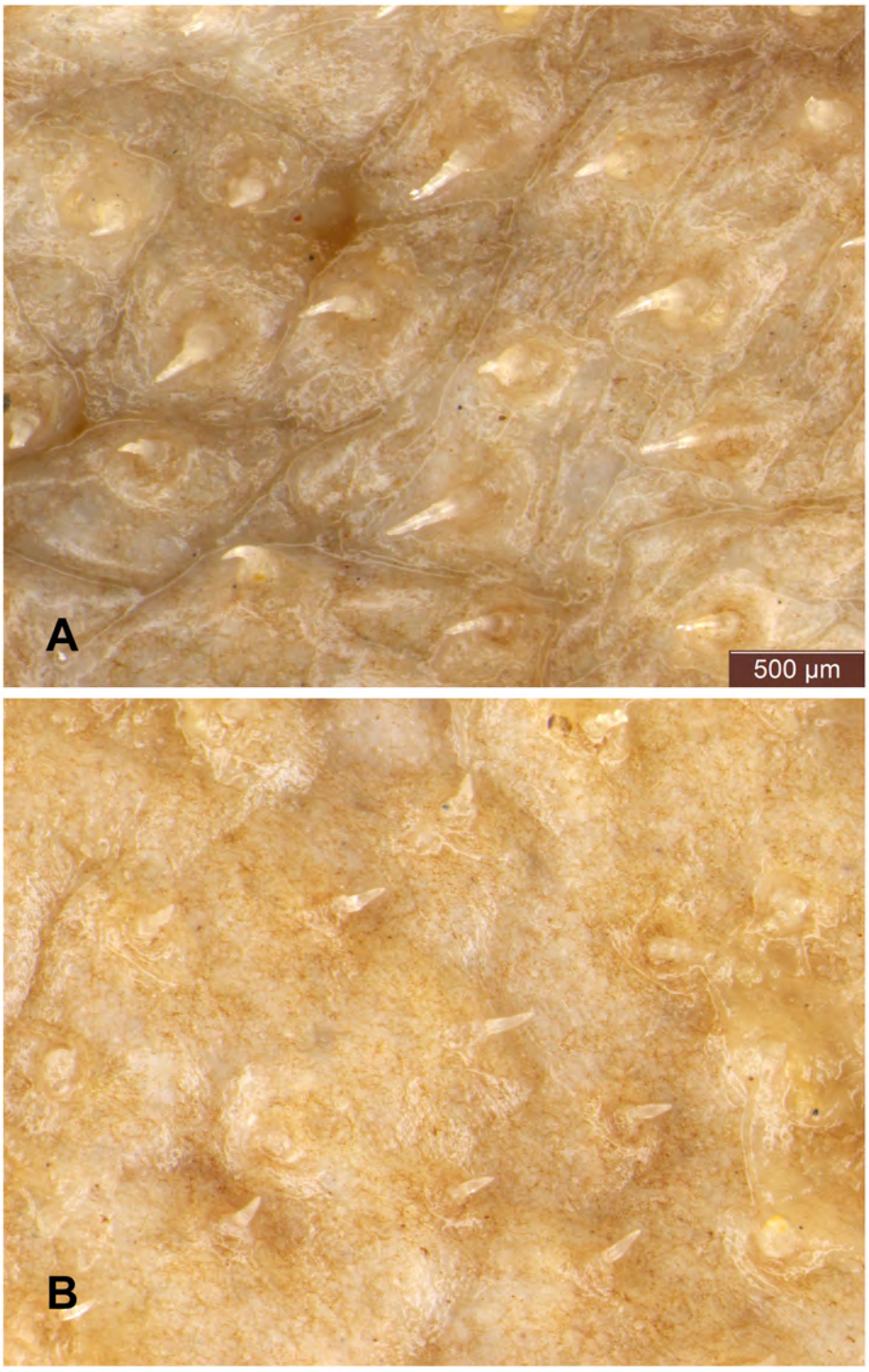

FIGURE 8. Dermal denticles of the holotype of *Notoraja sereti* **n. sp.** (NTUM 10067, female 459 mm TL): (A) dorsal surface; (B) ventral surface).

Tooth rows in upper jaw 43 (39–41); lower jaw 39 (37). Pectoral propterygial radials 27 (26–27); mesopterygial radials 11 (10-11); metapterygial radials 20–21 (22-23); total radials 58–59 (58–60). Monospondylous centra 25 (23–24); diplospondylous predorsal centra 70 (66–71); predorsal centra 95 (90–94);

post-first dorsal-fin origin centra 36 (32–38); total diplospondylous centra 106 (103–104); total centra 131 (126–128).

Colour. Holotype and female paratype (fresh): Dorsal surface uniformly medium brown, slightly paler above orbits and at pectoral insertions; anterior third of tail darker brown with a narrow, darker brownish median stripe originating anterior to dark brown marking (about level with pelvic-fin insertions); dorsal and caudal fins medium brown with darker edges. Ventral surface of disc similar in colour to dorsal disc; anterior third of tail slightly darker brown. When preserved, dorsal coloration slightly paler brown; dark brown dorsal midline obvious on anterior tail, but darker anterior marking on tail more obvious. Adolescent male paratype (fresh): dorsal surface bluish grey with paler anterior pelvic-fin lobes; most of dorsal midline and tail distinctly paler except near tip. When preserved, dorsal coloration dark brown, darkest distally near disc apices; dark midline on anterior tail obvious; dark marking on anterior tail less obvious; ventral surface of disc and tail dark, slightly paler than dorsal surface in adolescent male but similar in females; adolescent male translucent on belly and branchial region, noticeably darker near disc margin.

Size. Known from the three type specimens consisting of two females (459 and 458 mm TL) and an adolescent male (363 mm TL). The clasper of the adolescent male (postcloacal length 16.4% TL) was possibly about three-quarters of full extension (maximum length of adult claspers of *N. sapphira* and *N. azurea* 22.5% and 22.6% TL respectively). Based on the adolescent male size, the females are most likely adults.

Distribution. Off Madang, Papua New Guinea at depths of 800–980 m (Fig. 9).

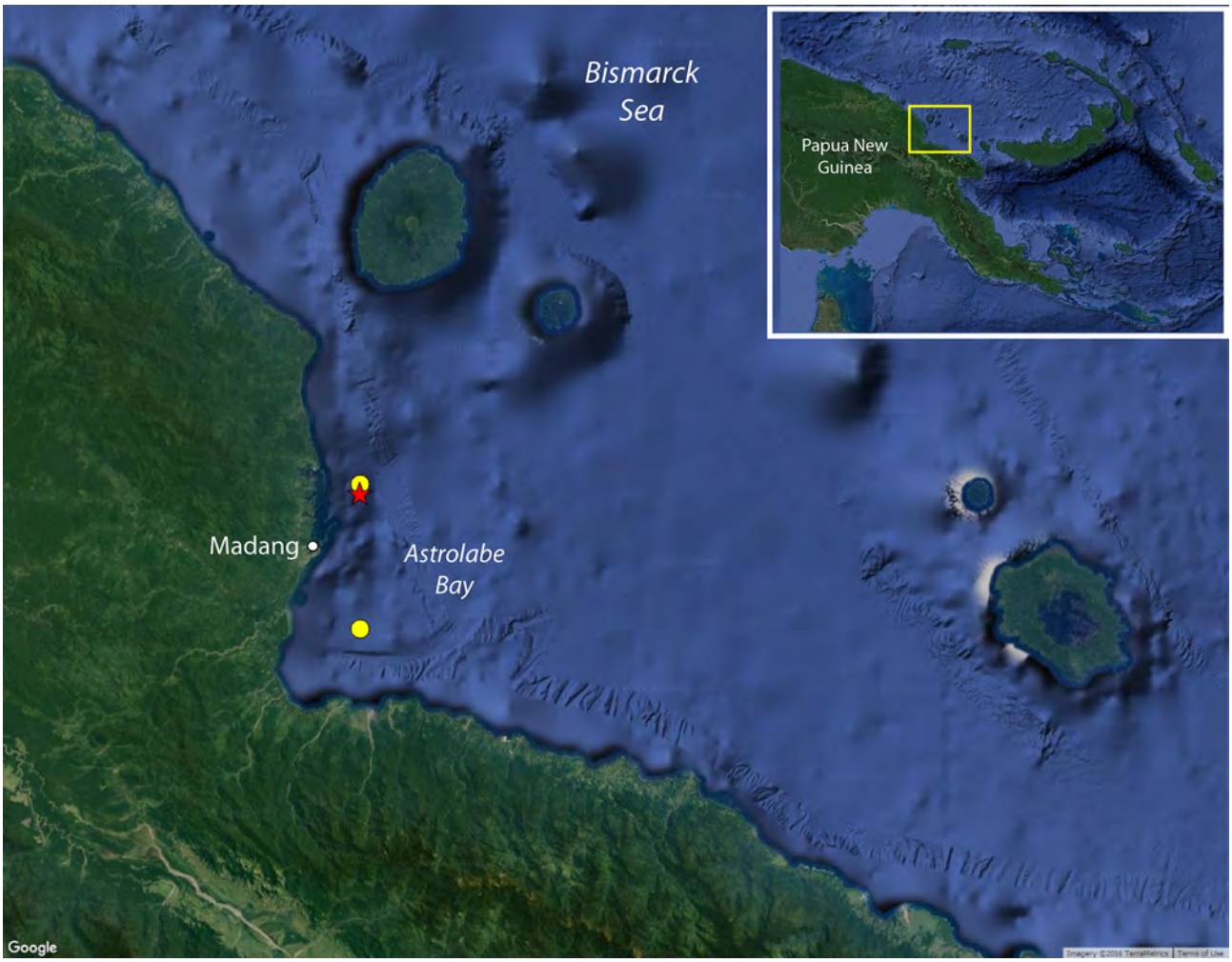

FIGURE 9. Map showing the capture locations of the type specimens of *Notoraja sereti* **n. sp.** (red star denotes holotype, yellow circles paratypes) in Astrolabe Bay, Papua New Guinea. Inset map shows location of main map in context of the whole country (Image © NASA, TerraMetrics, Google Earth).

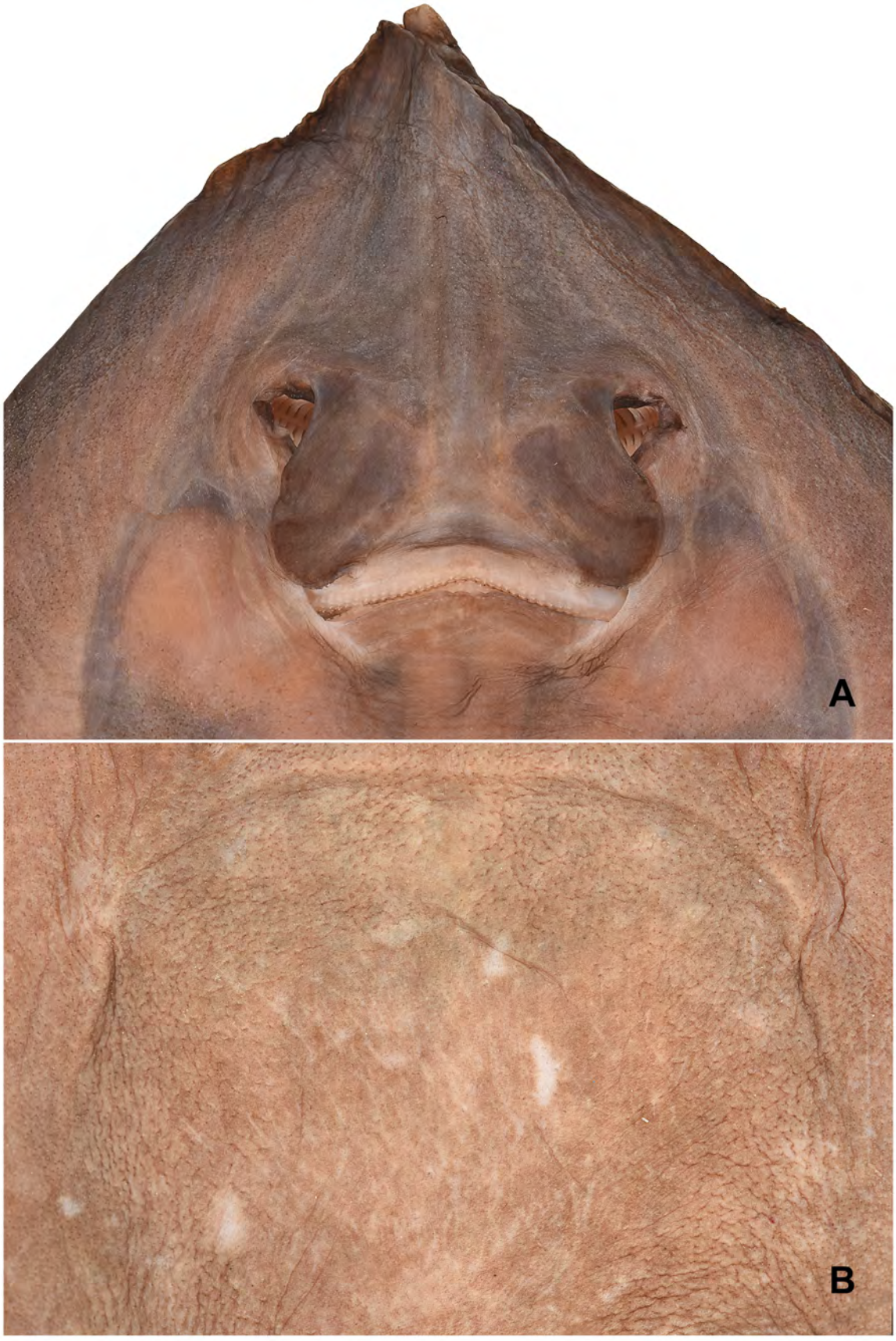

FIGURE 10. Denticle pattern in *Notoraja sereti* **n. sp.** highlighting areas lacking denticles: (A) ventral head of adolescent male paratype (NTUM 10330, 363 mm TL); (B) belly of female paratype (NTUM 10042, 458 mm TL).

Etymology. Named after the highly respected French ichthyologist, Dr. Bernard Séret, who has contributed greatly to the taxonomy of sharks and rays, and in particular to our knowledge of skates of the genus *Notoraja*. English name: Papuan Velvet Skate.

Comparisons. The new species is assigned to the genus *Notoraja* which is particularly diverse in this part of the Indo–Pacific. The dorsal and most of the ventral surfaces of *Notoraja sereti* are entirely covered with fine, densely spaced, dermal denticles which is shared by the velcro skates, *N. alisae* Séret & Last, 2012; *N. fijiensis* Séret & Last, 2012; *N. inusitata* Séret & Last, 2012; and *N. longiventralis* Séret & Last, 2012. In contrast, the remaining species in the genus, i.e. *N. azurea* McEachran & Last, 2008; *N. hirticauda* Last & McEachran, 2006; *N. lira* McEachran & Last, 2008; *N. ochroderma* McEachran & Last, 1994; *N. sapphira* Séret & Last, 2009; *N. sticta* McEachran & Last, 2008; and *N. tobitukai* (Hiyama, 1940), all have a smooth ventral surface entirely devoid of denticles. However, it should be noted that the adolescent male has a poorer coverage of denticles on the ventral surface than the larger females (see e.g. Fig. 10a), and it is likely that denticle coverage on the ventral surface is size related. Juveniles were unavailable for study but they are likely to be less well spinulated (possibly naked) than adults and adolescents.

Notoraja sereti differs from *N. alisae*, *N. fijiensis*, *N. inusitata* and *N. longiventralis* in having a shorter snout (preorbital length 10.1–11.1 *vs*. 11.5–14.5% TL, prenasal length 8.2–8.9 *vs*. 9.8–12.1% TL); a shorter head (dorsal head length 15.2–16.2 *vs*. 17.1–19.3% TL, ventral head length 21.6–22.9 *vs*. 22.9–25.9% TL); fewer pectoral radials (total radials 58–60 *vs*. 61–74) and fewer vertebral centra (predorsal diplospondylous centra 66–71 *vs*. 72–82; predorsal centra 90–95 *vs*. 98–107; total centra 126–131 *vs*. 135–152). It differs from *N. alisae*, *N. inusitata* and *N. longiventralis* in disc length (42.0–43.6 *vs*. 43.8–47.8% TL). It differs from *N. alisae*, *N. fijiensis* and *N. inusitata* in having more widely separated dorsal fins (interdorsal space 1.1–1.9 *vs*. 0.5–0.9% TL).

Notoraja sereti further differs from *N. alisae* in the following characters: disc width 47.1–50.3 *vs*. 50.9–55.5% TL; orbit and spiracle length 4.6–4.9 *vs*. 5.1–5.5% TL; and distance between spiracles 5.3–5.9 *vs*. 6.2–6.7% TL. It further differs from *N. fijiensis* in the following characters: ventral surface dark (*vs*. creamy white); snout to spiracle 14.8–15.0 *vs*. 15.5–16.2% TL; distance from snout to cloaca 39.8–41.0 *vs*. 35.0–38.9% TL; ventral snout length 11.2–12.1 *vs*. 13.2–14.6% TL; and a wider mouth (mouth width 6.4–6.7 *vs*. 5.7–6.2% TL). *Notoraja sereti* further differs from *N. inusitata* in the following characters: snout to spiracle 14.8–15.0 *vs*. 17.3% TL; nasal curtain total width 7.9–8.3 *vs*. 7.2% TL; and fewer radials on the mesopterygium 10–11 *vs*. 16. It further differs from *N. longiventralis* in having a much shorter anterior pelvic-fin lobe (its length 12.7–13.7 *vs*. 14.8–15.0% TL) and shorter distance from the cloaca to the first dorsal fin (46.6–47.3 *vs*. 45.1–45.9% TL).

The new species of arhynchobatid skate is distinguishable from members of the closely related genus *Insentiraja* in having numerous small denticles on the ventral surface (*vs*. ventral surface smooth) and the skin on both dorsal and ventral surfaces not loose and flabby (*vs*. skin noticeably loose and flabby). It also differs from members of another closely-related genus *Brochiraja* in lacking a bifurcate thorn on the snout tip.

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Etmopterus samadiae n. sp., a new lanternshark (Squaliformes: Etmopteridae) from Papua New Guinea

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Abstract

A new species of lanternshark, *Etmopterus samadiae* (Squaliformes: Etmopteridae), is described from off northern Papua New Guinea, in the western Central Pacific Ocean. The new species resembles other members of the "*Etmopterus lucifer*" clade in having linear rows of dermal denticles and most closely resembles *E. brachyurus* from the western North Pacific. The new species occurs along insular slopes between 340 and 785 m depth. The new species can be distinguished from other members of the *E. lucifer* clade by a combination of characteristics, including length of anterior flank branch markings being slightly shorter than its posterior branch, a longer caudal base marking, and irregular and variable number of black, horizontal, dash-like marks on sides of body. Molecular analysis based on the NADH2 marker further supports the distinction of *E. samadiae* from other members of the *E. lucifer* clade.

Key words: Chondrichthyes, *Etmopterus lucifer* clade, new species, Papua New Guinea, molecular analysis

Introduction

The deepwater chondrichthyan fauna around Papua New Guinea has been poorly studied until recent surveys conducted by the RV *Alis* (Pante *et al*., 2012; Samadi *et al*., 2014) provided new records of shark and ray species from this region. Specimens collected during these expeditions were subsequently deposited into fish collections in Taiwan for further examination and identification. Representatives of the squaloid family Etmopteridae, specifically in the genus *Etmopterus*, were among the specimens saved and deposited because the family and genus are a new record for Papua New Guinea. Fricke *et al*. (2014) reported an unidentified *Etmopterus* species collected off Madang and suggested it might be close to *Etmopterus brachyurus* Smith & Radcliffe *in* Smith, 1912, but commented that *E. brachyurus* was restricted to the northwestern Pacific.

Examination of all of the *Etmopterus* material collected during these surveys (n=15, currently housed in Taiwanese fish collections) determined that three species were represented. These included a single specimen of *Etmopterus fusus* Last, Burgess, & Séret, 2002 from off Madang, and four specimens of *Etmopterus evansi* Last, Burgess, & Séret, 2002 from off Madang and Manus Island. The remaining 10 specimens were originally identified as *E. brachyurus*, but upon detailed examination were determined to represent an undescribed species based on several differences in key characteristics. Furthermore, DNA sequence analysis also confirmed that these specimens were closely related to, but distinct from, true *E. brachyurus*. The new species is herein formally described and named.

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Materials and methods

The type specimens were collected during the BIOPAPUA Expedition in 2010 (Pante *et al.*, 2012) and the PAPUA NIUGINI Expedition in 2012 (Samadi *et al.*, 2014) on-board the French research vessel *Alis* of the Institut de Recherche pour le Développement (IRD, Noumea). The specimens were subsequently, along with the other fish specimens, sent to either the National Taiwan University Museum (NTUM) or Academia Sinica (ASIZ) in Taipei.

Morphometric measurements and terminology follow Ebert *et al*. (2011). Meristics include vertebral counts obtained by digital radiographs from the holotype and four paratypes (NTUM 10313, 10314, 10315, 10316 [1 of 3]), and tooth counts taken *in situ* from the holotype and two paratypes (NTUM 10313, 10314).

Comparative material was examined from collections at the Australian Museum, Sydney (AMS), California Academy of Sciences (CAS), CSIRO, iSAM, South African Institute for Aquatic Biodiversity (SAIAB), USNM, and ZMH. Institutional abbreviations follow Sabaj Pérez (2016). Four specimens of *E. brachyurus* were measured in full for comparative purposes: CSIRO H 5611-01 (1, 224 mm TL), CSIRO H 5611-09, CSIRO H 7402-01 and CSIRO H 7401-03.

Tissue samples were taken from the type specimens at sea post-capture, and were temporarily stored in 95% alcohol in the field. Tissue samples were accessioned in the Chondrichthyan Tree of Life project with GN numbers (Gavin Naylor tissue number). DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc Norcross, GA). Extracted total DNA was stored at -20 °C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via the Polymerase Chain Reaction (PCR). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µl volume comprising 0.3 µM primers, 2.5 mM $MgCl_2$, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA), and 50–100 ng template DNA. The reaction mixture was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio), and bi-directionally Sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego USA).

DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd Auckland, New Zealand, available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within Geneious® (Biomatters Ltd Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. The Maximum Likelihood Tree was estimated from the data set using the GTR+I+G model. A bootstrap analysis was run separately under the same model conditions to estimate support for each of the nodes in the ML tree. All phylogenetic analyses were carried out using the software package PAUP*4.0 version a148.

Etmopterus samadiae, new species

Papuan Lanternshark

(Figures 1–10; Table 1)

Etmopterus sp.—Fricke *et al*., 2014: 14 (Madang)

Holotype. NTUM 10078 (tissue accession GN 17184), adult male 265 mm TL, east of Malmal Passage, Madang, Papua New Guinea, 05°07' S, 145°50' E, 527–539 m depth, 30 Nov 2012.

Paratypes. 9 specimens: ASIZ P.73777, adult male 230 mm TL, ASIZ P.73778, female 188 mm TL, ASIZ P.73765, pregnant female 277 mm TL, off Lae, Huon Gulf, Morobe Province, Papua New Guinea, 06°51.841' S, 147°04.672' E, 395–406 m depth, 22 Aug 2010; NTUM 10313 (tissue accession GN 17195), female 269 mm TL, northern Cape King William, Morobe Province, Papua New Guinea, 06°00' S, 147°38' E, 785 m depth, 10 Dec 2012; NTUM 10314 (tissue accession GN 17197), female 258 mm TL, Astrolabe Bay, Madang, Papua New

Guinea, 05°22' S, 145°48' E, 420–490 m depth, 14 Dec 2012; NTUM 10315 (tissue accession GN 17198), female 154 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05°22' S, 145°48' E, 340–385 m depth, 14 Dec 2012; NTUM 10316 (3 specimens; tissue accessions GN 17210–2), female 177 mm TL, subadult male 201 mm TL, female 228 mm TL, west of Kairiru Island, East Sepik, Papua New Guinea, 03°19' S, 143°27' E, 422–425 m depth, 19 Dec 2012.

FIGURE 1. Lateral view of the holotype of *Etmopterus samadiae* n.sp., adult male (NTUM 10078, 265 mm TL), (A) fresh; (B) post-preservation.

FIGURE 2. Dorsal view of paratype of *Etmopterus samadiae* n.sp., female (NTUM 10316, 1 of 3, 177 mm TL), fresh.

Diagnosis. *Etmopterus samadiae* is a relatively small, slender, species of linear–denticled *Etmopterus* that can be separated from its closest congeners within the *E. lucifer* clade by a combination of characteristics including the length of its anterior flank markings being slightly shorter than its posterior branch, long caudal base marking, and irregular and variable number of black, horizontal, dash-like marks on sides of body. The new species is morphologically and genetically (based on the NADH2 marker) closest to *E. brachyurus*, but differs from this species in having a shorter posterior caudal marking (2.8–4.4 vs. 4.2–6.1% TL), a longer caudal base marking (10.6–14.1 vs. 7.0–7.8% TL), and flank marking with a slightly shorter posterior branch (9.1–11.2 vs. 11.4–12.6% TL).

Description. Values expressed as a percentage of total length (TL) for the holotype, followed by the range of values for 9 paratypes (Table 1).

Body fusiform, trunk sub-cylindrical (Fig. 1), width 1.1 (0.7–1.7) in trunk height; head sub-conical, long, 21.3 (20.6–23.7)% TL, slightly depressed, height 0.7 (0.5–0.8) times width. Snout moderately long, conical in lateral view, in dorsal view triangular–shaped becoming rounded at snout–tip (Fig. 3), head width 8.2 (9.8–11.8)% TL. Eyes oval-shape, large, orbit length 3.8 (3.0–3.7) in head and 2.6 (2.0–3.3) times orbit height; orbits with anterior and posterior notches; moderately spaced, inter–orbital space 1.2 (1.2–1.5) in width of head and orbit length 1.2

(1.1–1.4) times in inter–orbital distance. Spiracles small, semi-circular, greatest diameter 0.9 (1.4–2.5)% TL, 6.1 (2.7–4.0) times orbit length, distance to eye 2.9 (1.4–2.6)% TL, eye–spiracle length 0.7 (1.0–1.9) in orbit height. Nostrils large, oblique, length almost equal to internarial width, less than orbit length; anterior nasal flap well developed, triangular, anterior tip extending across nasal opening, length 1.0 (0.5–0.9) times spiracle length. Gill openings small, narrow, slightly oblique, in horizontal series, subequal in height, inter-gill length 4.9 (3.0–4.7)% TL. Mouth broad, length 3.4 (3.3–4.8) times in width, slightly arched, width 0.8 (0.7–0.9) times preoral length.

Teeth dissimilar in upper and lower jaw (Fig. 4); upper teeth multicuspid in three functional series, functional teeth in lower jaw unicuspid in single series; multicuspid upper teeth small, upright, with strong central cusp flanked by 2 or 3 lateral cusplets on each side, decreasing in size distally; teeth in lower jaw fused into single row, blade-like, cusp oblique. Tooth count in first row of upper jaw 33 (27–28) and in first row of lower jaw 35 (28–31).

FIGURE 3 . Ventral head of the holotype of *Etmopterus samadiae* n.sp., adult male (NTUM 10078, 265 mm TL).

FIGURE 4. Upper and lower tooth morphology of the adult male holotype of *Etmopterus samadiae* n.sp. (NTUM 10078, 265 mm TL).

First dorsal fin small, rounded at apex, length of first dorsal fin 8.6 (8.5–9.9)% TL, origin just anterior to pectoral-fin free rear tip; fin base insertion well anterior of pelvic-fin origin; pre–first dorsal fin length 1.3 (1.4–1.8) times inter–dorsal distance; first dorsal–fin spine straight, short, 1.6 (1.3–2.0) times height of first dorsal fin, located over pectoral fin rear margin. Second dorsal fin conspicuously larger, more erect than first dorsal fin, length of first dorsal fin 0.6 (0.6–0.8) times second dorsal fin, height of first dorsal fin 0.4 (0.5–0.7) times second dorsal fin; apex sub–angular, posterior margin concave, free rear tip elongated, length 13.2 (12.2–13.6)% TL, pre–second dorsal length 2.5 (2.6–3.1) times inter–dorsal distance; second dorsal–fin spine large, height slightly taller than fin, curved near tip towards fin apex; origin posterior to insertion of pelvic fins, over pelvic fin free rear tips. Interspace between first and second dorsal fins 1.0 (0.8–1.0) times pre–pectoral length.

Pectoral fins relatively large, length 9.4 (10.1–11.3)% TL, subangular at free rear tips, base 2.0 (1.7–2.1) times in anterior margin, posterior margin nearly straight. Caudal peduncle relatively long, dorsal-caudal space 16.1 (13.6–15.3)% TL, height slightly greater than width, rounded, and tapering posteriorly. Caudal fin elongate, subequal to head length, terminal lobe distinct; length of lower preventral caudal fin margin less than one-half upper caudal fin margin.

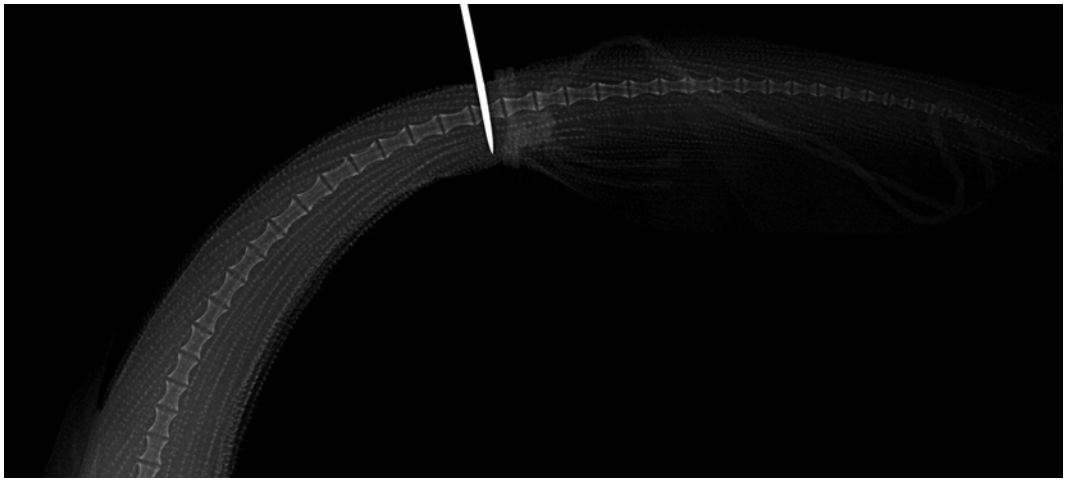

FIGURE 5. Digital radiograph highlighting dermal denticle arrangement of paratype NTUM 10316 [1 of 3]) along caudal peduncle and caudal fin.

FIGURE 6. Dermal denticle morphology and arrangement on lateral side behind second dorsal fin of the adult male holotype of *Etmopterus samadiae* n.sp. (NTUM 10078, 265 mm TL).

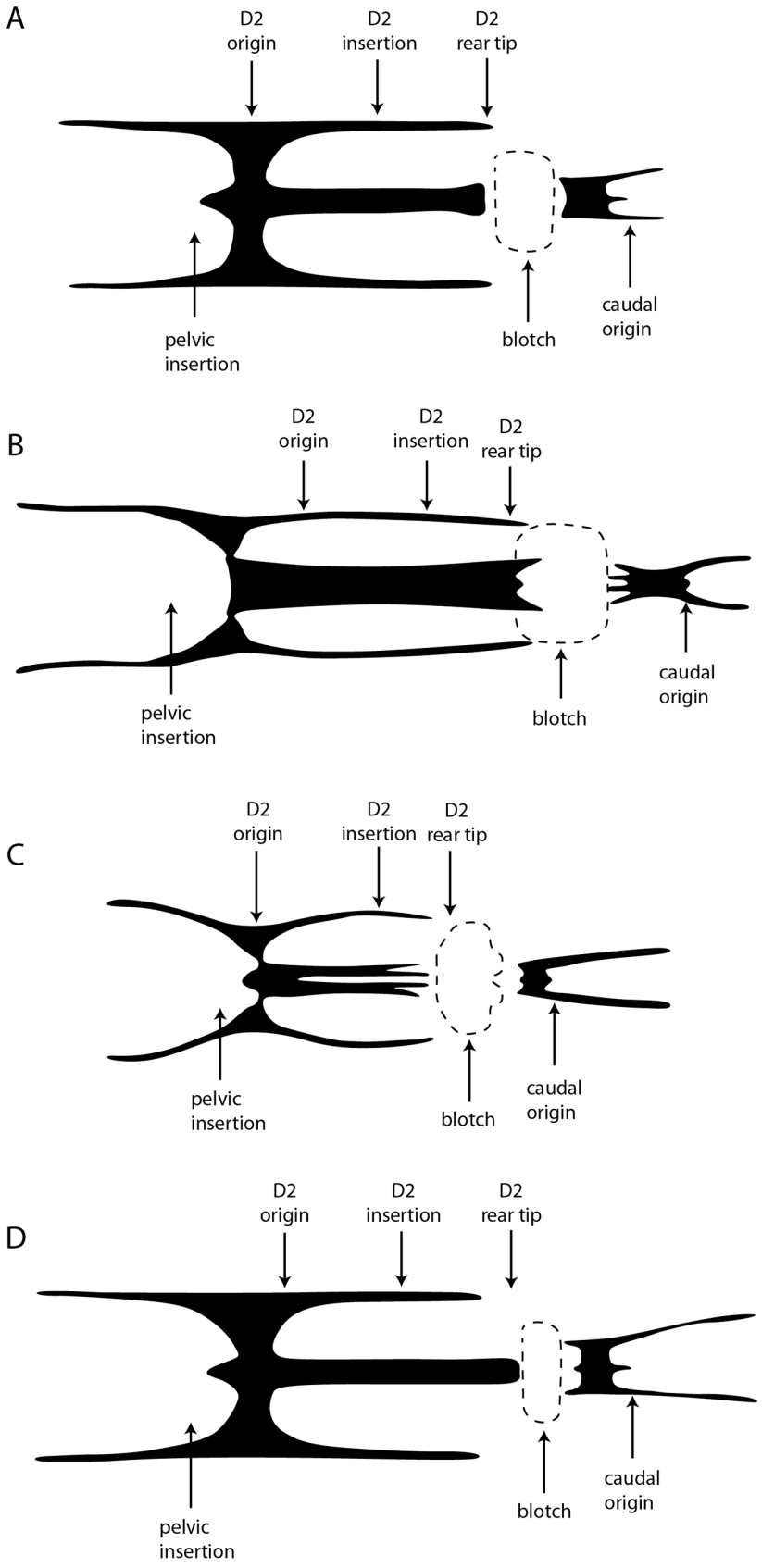

FIGURE 7 . Diagrammatic representation of the flank and caudal base luminescent markings in ventral view of: A) *Etmopterus brachyurus* (CSIRO H 5611-01, largest); B) *Etmopterus dislineatus* (holotype, CSIRO H 1416-01); C) *Etmopterus evansi* (holotype, CSIRO H 3141-16); D) *Etmopterus samadiae* n.sp. (paratype, NTUM 10314).

TABLE 1. Morphometric data and vertebral counts for the holotype and ranges for the 9 measured paratypes of *E. samadiae* **n.sp.** (expressed as a percentage of total length); one PNG specimen of *E. fusus*; ranges for the four PNG specimens of *E. evansi*; and ranges for four Taiwan specimens of *E. brachyurus.*

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Total length (mm)	265	154	277	256	172.0	343.0	224	350
Precaudal length	77.2	76.0	78.4	78.9	76.8	78.4	76.8	79.7
Prenarial length	2.8	2.8	3.8	2.1	3.0	4.4	2.9	3.4
Preoral length	9.3	9.0	11.4	8.2	8.9	11.3	9.4	10.7
Preorbital length	4.8	4.4	6.4	4.5	5.1	5.9	5.3	5.8
Prespiracle length	11.5	10.8	14.2	10.6	10.3	13.6	11.8	13.0
Prebranchial length	16.1	16.2	19.4	16.5	16.2	18.6	17.7	18.3
Head length	21.3	20.6	23.7	21.1	20.2	21.6	21.8	22.8
Prepectoral length	21.0	20.0	23.3	20.6	19.8	22.3	21.1	22.2
Prepelvic length	46.0	46.9	48.7	51.2	47.7	50.1	47.2	50.3
Snout-anterior vent length	50.6	49.2	52.3	54.7	48.8	53.9	50.4	52.3
Pre D1 length	28.7	30.4	32.5	28.1	30.1	34.1	30.8	32.5
Pre D2 length	54.3	54.7	57.0	57.8	55.4	56.9	55.8	56.9
Interdorsal space	21.6	17.9	22.0	25.4	17.2	21.1	18.0	20.3
D2–caudal space	16.1	13.6	15.3	14.2	12.7	22.1	13.6	14.2
Pectoral–pelvic space	19.0	18.8	22.5	26.3	19.3	23.2	21.1	23.3
Pelvic–caudal space	21.3	19.7	22.3	18.4	18.2	21.4	20.7	21.9
Orbit length	5.6	5.6	7.8	5.4	4.5	6.4	5.7	7.1
Orbit height	2.1	2.0	3.2	3.0	2.3	2.8	2.4	3.4
Interorbital space	6.9	7.8	9.1	7.4	8.4	10.3	6.6	7.4
Nostril width	2.8	2.1	3.5	2.6	2.7	3.9	2.3	2.7
Internarial length	3.3	2.9	3.8	2.4	2.9	3.6	2.6	2.8
Anterior nasal flap length	0.9	0.9	1.7	0.8	1.1	1.6	0.8	1.3
Spiracle length	0.9	1.4	2.5	1.8	1.9	3.0	1.2	1.9
Eye–spiracle space	2.9	1.4	2.6	2.8	1.8	2.1	2.3	2.9
Mouth length	2.2	1.7	2.4	2.1	1.5	2.7	1.6	1.9
Mouth width	7.5	7.3	8.9	7.4	7.3	10.5	7.3	7.9
Upper labial furrow length	1.8	1.8	2.8	2.0	1.8	2.0	1.7	1.9
Lower labial furrow length	1.5	1.1	1.6	1.1	1.6	1.6	1.4	1.8
Intergill length	4.9	3.0	4.7	4.9	4.1	4.2	4.2	4.6
1st gill slit height	0.9	1.0	1.4	1.3	1.5	1.5	1.1	1.4
2nd gill slit height	0.9	1.0	1.4	1.6	0.0	1.5	0.9	1.3
3rd gill slit height	1.0	1.0	1.4	1.6	1.4	1.5	0.8	1.2
4th gill slit height	0.9	0.8	1.3	1.5	1.3	1.3	0.5	1.1
5th gill slit height	1.1	1.0	1.3	1.7	1.2	1.4	1.2	1.5
Head height	6.0	5.5	8.3	7.5	7.6	7.8	5.4	7.1
Head width	8.2	9.8	11.8	10.3	10.0	10.8	8.6	9.9
Abdomen width	5.5	5.2	11.8	10.3	6.0	10.5	7.5	8.9
Trunk height	5.3	5.8	9.5	8.5	8.0	8.4	6.7	7.0

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TABLE 1. (Continued)

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Trunk width	5.8	6.3	10.7	8.6	6.2	9.3	5.3	7.7
Tail width	4.1	3.6	4.5	5.1	4.1	4.8	3.6	4.7
Caudal peduncle height	2.2	1.6	2.9	2.7	2.5	3.2	2.4	3.0
Caudal peduncle width	2.0	1.8	2.8	2.6	1.7	2.3	1.9	2.2
Pectoral fin length	9.4	10.1	11.3	9.8	8.6	10.6	9.9	11.0
Pectoral fin anterior margin length	9.2	9.8	11.5	9.9	8.4	8.5	9.8	10.6
Pectoral fin base length	4.6	5.0	6.3	4.6	4.8	6.2	5.0	5.9
Pectoral fin height		6.5	8.4	7.4	0.0	0.0	7.0	7.7
Pectoral fin inner margin length	4.6	4.1	6.1	5.3	0.0	0.0	4.5	5.6
Pectoral fin posterior margin length		5.7	8.1	6.3	0.0	0.0	4.8	5.3
Pelvic fin length	10.8	10.0	11.7	11.9	8.6	9.3	10.1	12.0
Pelvic fin anterior margin length	6.9	5.8	7.8	6.3	4.1	5.7	6.7	7.3
Pelvic fin base length	5.8	5.1	7.1	6.7	6.4	7.1	4.1	6.3
Pelvic fin height	4.4	3.4	4.8	4.2	3.4	4.2	3.0	4.0
Pelvic fin inner margin length	5.4	3.6	5.6	4.1	3.2	3.2	3.5	5.4
Pelvic fin posterior margin length	5.4	5.9	6.8	6.9	6.7	6.7	5.3	6.1
Clasper length outer	2.4	1.1	1.1	–	2.2	2.7	0.0	0.0
Clasper length inner	4.6	6.3	6.3	–	5.1	5.2	0.0	0.0
Clasper base width	1.3	1.6	1.6	–	1.2	1.9	0.0	0.0
D1 length	8.6	8.5	9.9	9.3	8.0	11.0	8.4	9.2
D1 anterior margin length	7.5	7.3	8.8	6.7	9.2	9.2	6.1	8.5
D1 base length	5.5	4.7	6.7	5.3	5.6	6.7	5.0	6.5
D1 height	1.9	2.3	3.3	3.0	3.2	3.6	2.2	3.6
D1 inner margin length	3.8	3.5	5.2	3.9	2.6	4.8	3.3	3.8
D1 posterior margin length	3.6	2.5	3.9	4.5	–	–	2.5	3.5
D2 length	13.2	12.2	13.6	13.3	12.8	13.8	12.3	13.4
D2 anterior margin length	10.3	10.8	12.4	9.7	10.6	11.8	9.8	12.0
D2 base length	7.6	7.1	8.5	8.2	8.3	9.5	6.9	8.7
D2 height	4.3	4.2	5.8	4.9	4.9	5.6	3.8	4.7
D2 inner margin length	5.9	5.0	6.4	5.4	4.7	5.7	5.2	6.0
D2 posterior margin length	5.0	5.5	6.6	6.3	0.0	6.9	4.5	6.3
Caudal dorsal margin	22.8	20.3	24.1	19.1	21.5	23.5	19.6	23.1
Caudal fork width	4.8	4.7	5.4	5.1	5.1	5.1	4.2	5.6
Caudal fork length	11.5	9.4	10.8	10.3	–	–	11.3	12.0
Caudal preventral margin length	10.4	8.6	10.7	10.4	10.3	12.2	10.3	11.8
Caudal lower postventral margin length	3.3	2.0	3.5	4.3	–	–	2.3	2.6
Caudal upper postventral margin length	7.9	8.9	10.4	7.3	–	–	7.1	8.8
Caudal fin subterminal margin length	–	3.4	5.5	3.2	4.7	5.2	4.4	4.7

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TABLE 1. (Continued)

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Caudal fin terminal margin length	–	2.9	4.3	5.1	2.9	5.8	2.7	3.6
Caudal fin terminal lobe length	–	4.6	6.3	5.7	4.9	4.9	6.5	6.7
D1 midpoint–pectoral fin insertion	6.1	6.4	9.6	5.0	8.8	9.2	6.7	8.7
D1 midpoint–pelvic-fin origin	13.5	11.2	14.3	20.5	12.9	13.5	11.9	14.6
Pelvic-fin midpoint–D1 insertion	14.7	12.5	15.4	20.9	13.4	15.1	12.7	15.8
Pelvic-fin midpoint–D2 origin	5.4	4.6	6.3	3.2	2.4	3.8	4.6	6.3
D1 spine length	3.0	3.4	5.4	2.1	2.8	5.0	3.4	3.6
D1 exposed spine length	2.5	2.8	3.9	1.9	2.0	3.9	2.6	2.9
D2 spine length	5.6	7.1	9.8	5.6	5.2	8.5	6.8	7.4
D2 exposed spine length	4.6	5.3	7.6	4.7	3.2	6.3	5.6	6.2
Anterior flank marking length	10.3	8.2	10.4	8.5	7.4	9.6	7.9	9.3
Posterior flank marking length	11.2	9.1	10.8	0.0	8.3	9.7	11.4	12.6
Posterior flank marking width	0.6	0.5	0.8	2.8	0.2	0.6	0.3	0.7
Flank marking base length	4.4	3.5	4.9	9.2	1.5	4.1	2.8	3.4
Caudal base marking length	11.4	10.6	14.1	7.5	10.5	11.6	7.0	7.8
Central caudal marking length	–	–	–	4.7	–	–	–	–
Posterior caudal marking	3.2	2.8	4.4	2.6	2.8	3.6	4.2	6.1
Monospondylous centra	34	36	37	37	38	42	39	45
Diplospondylous trunk centra	21	19	22	19	17	18	19	22
Caudal centra	25	25	27	23	23	25	24	26
Precaudal centra	55	55	59	56	56	59	59	65
Total centra	80	80	86	79	81	82	84	91

Dermal denticles hook-like, posteriorly directed rearwards; organized in distinct rows laterally, characteristic of *E. lucifer* clade members (Fig. 5, 6). Distance between lateral rows mostly consistent along length, decreasing only very slightly towards caudal peduncle. Flank mark area denticles more dense and pointed ventrally.

Luminescent markings distinct, intricate (Fig. 7D); ventral head surface markings blackish, starting from almost at snout tip, extending to level of nostrils and orbits at just below level of anterior notch, then extending straight from just below posterior eye notch towards gill slits, weakly demarcated from belly marking by a weak band of transverse dermal folds across throat extending from below lower edges of first three gill openings on either side. Head dorsal surface photophore pattern as follows: a single midline along back originating at level of first gill slits extending posteriorly to caudal–fin origin; scattered photophores on paler fontanelle area of central head and also on paler area above orbits (as short dashes in some paratypes).

Belly marking originates behind mouth on posterior portion of transverse dermal folds and extends ventrally along pectoral fin bases extending upwards to level with fin origin and upper edges of gill slits, and posteriorly to pelvic fin bases; ventral surface of pectoral fin very dark along lower base and upper base where ceratotrichia originate, bisected by distinct lighter to white band or blotch forming a two–prong fork pattern; margin on lateral trunk (pectoral–pelvic space) very clearly defined, line extending from rear margin of pectoral–fin base nearly to pelvic–fin insertion except for paler area at pelvic-fin origin; dark ventral belly surface continuous onto caudal peduncle to about lower caudal fin origin.

Flank markings well defined (Fig. 7d), consisting of both an anterior and posterior branch; anterior branch relatively short, length 10.3 (8.2–10.5)% TL, slender, nearly straight, extending well anterior to pelvic–fin origin; posterior branch straight, slightly thicker, width at level of base end of second dorsal fin 0.6 (0.5–0.8)% TL, slightly longer than anterior branch (shorter than anterior branch in paratype ASIZ P.73777), length 11.2 (9.1–

10.8)% TL, extending to just anterior to second dorsal-fin free rear tip but well posterior to second dorsal-fin insertion; base of flank marking wide, origin slightly posterior to pelvic-fin insertion. Ventral caudal base marking distinct, short, length about equal to base of flank marking, not extending as a saddle on to caudal peduncle, anterior finger very short, posterior finger long, total length (including base) 11.4 (10.6–14.1)% TL. No central caudal marking. Posterior caudal fin marking very narrow, its length 3.2 (2.8–4.4) % TL.

Vertebral counts: total counts 80 (80–86), total precaudal counts 55 (55–59); monospondylous 34 (36–37); diplospondylous precaudal 21 (19–22); caudal 25 (25–27).

Coloration. In life, greyish to silvery black dorsally and laterally on body, becoming dark black ventrally; transition between lateral and ventral surfaces well demarcated by a paler lateral stripe below the flank markings in most specimens (less distinct in holotype and some paratypes). Dorsal midline with a broad, pale stripe originating just posterior to midpoint of inter-spiracle space, extending to first dorsal fin origin, continuing between dorsal fins, and from second dorsal fin insertion to upper caudal fin origin (Fig. 2); most prominent anterior to first dorsal fin and between dorsal fins, less prominent along upper caudal peduncle; a single row of dark photophores extending along middle of white dorsal stripe. Body with variable number and arrangement of short, horizontal, dash-like black markings (Fig. 8); most numerous in paratype NTUM 10314 (Fig. 8). Pectoral and pelvic fins dark at base and along anterior fin edge, becoming translucent to white on remainder of fins. Dorsal fins dark at base and along anterior edges, becoming translucent to white on remainder of fins. Black lateral flank markings demarcated by surrounding lighter colored lateral flanks (not sharply demarcated in most preserved specimens). Paler colored flank area on lateral surface between pectoral and pelvic fins sharply demarcates lateral and ventral surfaces; ventral surface black. Caudal fin with a distinct, large dark blotch centrally, occupying the area between the posterior finger of the caudal base marking and the upper caudal marking; posterior margin dark. Ventral surface mostly dark black around mouth, belly, and with a dark stripe between pelvic fin insertions and caudal origin; snout not distinctly paler than mouth. After preservation coloration similar but with paler markings often less obvious and coloration becoming a light or dark brown; dorsal median pale stripe and whitish flank area and black lateral flank markings less prominent but still distinct in most cases; dark blotch on central caudal fin obvious and darker pores extending laterally on body still clearly visible under microscope.

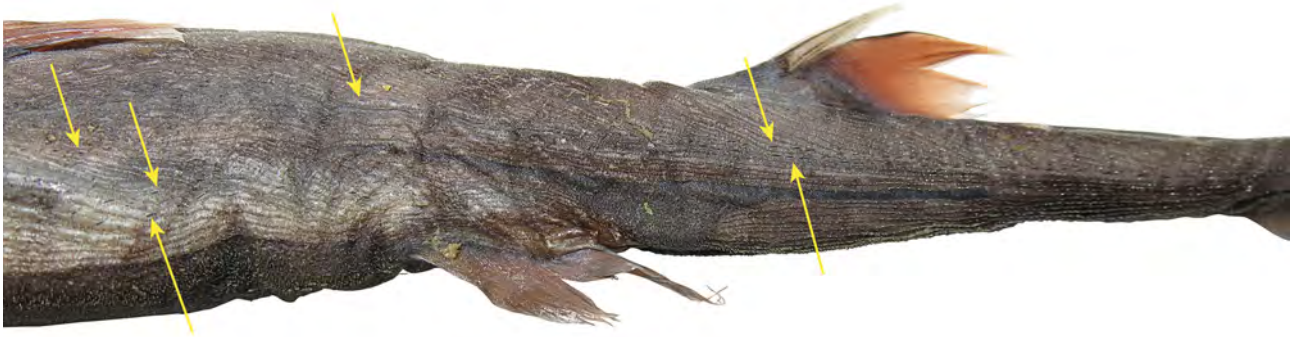

FIGURE 8. Posterior lateral view of *Etmopterus samadiae* n.sp. (paratype, NTUM 10314, female 258 mm TL), highlighting the dash-like markings. Arrows show location of the rows of dash marks.

Molecular analysis. The analysis of the NADH2 data confirms that *Etmopterus samadiae* belongs in the *E. lucifer* clade and represents a monophyletic lineage that is distinct from, but most closely related to *Etmopterus brachyurus* (Fig. 9). It should be noted that this inference is based on a single mitochondrial marker. Inclusion of multiple nuclear markers could affect the presented inference.

Size. Specimens examined ranged in size from 154 to 277 mm TL. A 277 mm TL female (ASIZ P.73765) was found to be pregnant (embryo caudal fin visible in cloaca) and two males 230 (ASIZ P.73777) and 265 mm TL (NTUM 10078) were determined to be mature.

Distribution. The new species is known from off the northern Papua New Guinea mainland, from west of Kairiru Island in East Sepik Province to off Lae in the Huon Gulf (Morobe Province) and at a depth range of 340 to 785 m (Fig. 10).

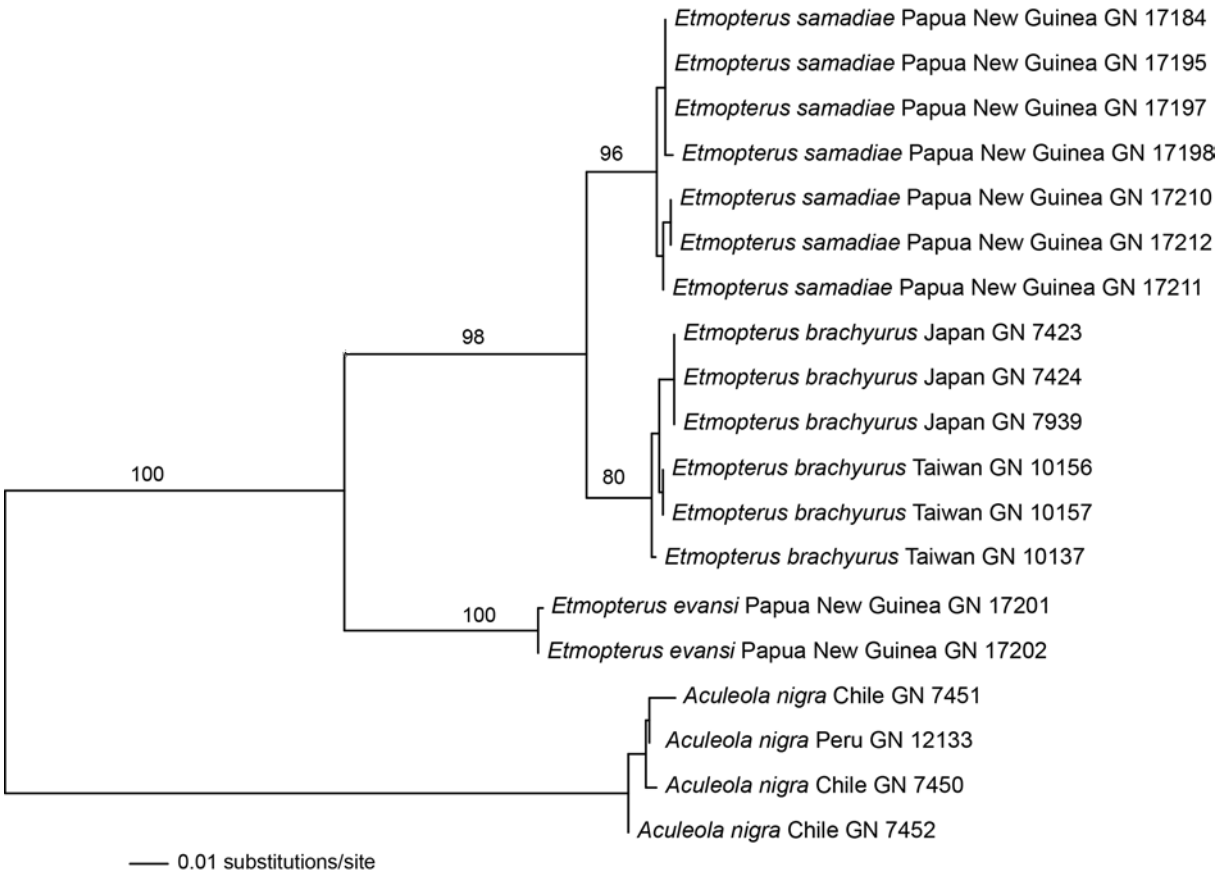

FIGURE 9. Maximum Likelihood tree estimated under the General Time Reversible model (GTR) with model terms to accommodate both Invariant sites (I) and Gamma distributed rates (G). Bootstrap support values are shown from a separate ML bootstrap analysis. Sequences used in this tree are part of the Chondrichthyan Tree of Life project (http://sharksrays.org/).

Etymology. The species is named after Dr Sarah Samadi (MNHN) who was one of the key principal investigators of the 2010 and 2012 MNHN expeditions in Papua New Guinea from which all the type specimens were obtained. The proposed English common name is Papuan Lanternshark.

Discussion

Etmopterus samadiae can be assigned to the "*E. lucifer* clade" as defined by Straube *et al*. (2010) due to its conspicuous flank markings displaying distinct anterior and posterior branches. The members of this clade are also characterized by distinct linear rows of denticles on the dorsal head surface that extend to the flanks, caudal peduncle and caudal-fin base. Diagnostically, the relative lengths of the anterior and posterior flank branches can further subdivide this clade, which currently is comprised of 11 species (Ebert *et al*., 2016).

Etmopterus samadiae has a longer posterior branch on the flank marking (Fig. 7D) and can be separated from five species, *Etmopterus burgessi* Schaff-Da Silva & Ebert, 2006; *Etmopterus evansi* Last, Burgess & Séret, 2002 (Fig. 7C); *Etmopterus lucifer* Jordan & Snyder, 1902; *Etmopterus pycnolepis* Kotlyar, 1990; and *Etmopterus sculptus* Ebert, Compagno, & De Vries, 2011, which have an anterior flank branch that is equal to, or longer than the posterior branch. Of the six species that have longer posterior branches, three species, *Etmopterus alphus* Ebert, Straube, Leslie, & Weigmann, 2016, *Etmopterus molleri* (Whitley, 1939), and *Etmopterus dislineatus* Last, Burgess, & Séret, 2002 (Fig. 7B), have their posterior branch extending past the free-rear tip of the second dorsal fin, while in *E. samadiae* the posterior branch does not extend as far. The Western Atlantic *Etmopterus bullisi* Bigelow & Schroeder, 1957 and the poorly known western Pacific *Etmopterus decacuspidatus* Chan, 1966 both lack a band or spot on the caudal fin; a characteristic found in both the new species and *E. brachyurus*.

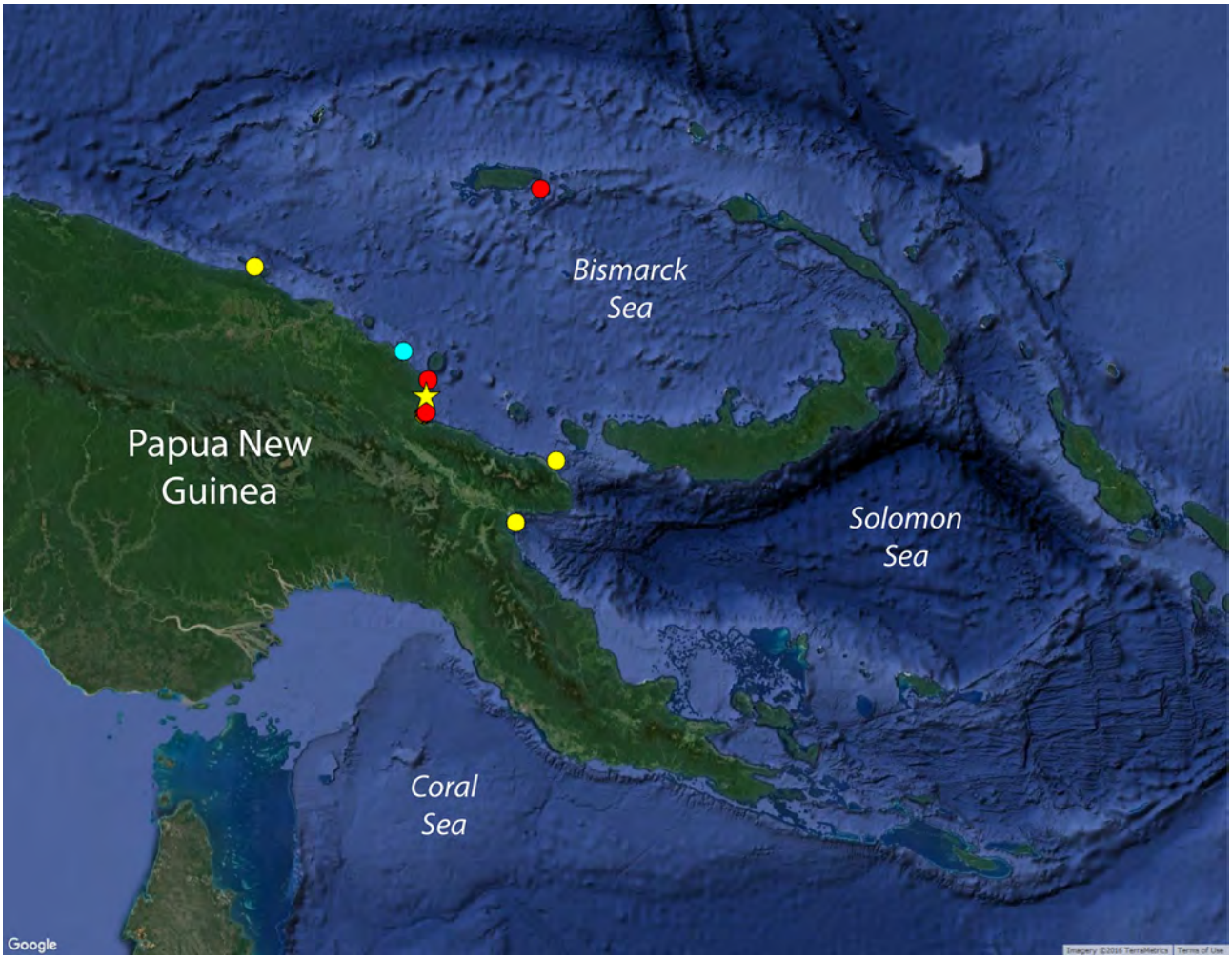

FIGURE 10. Map showing the capture locations of the type specimens of *Etmopterus samadiae* n.sp. (yellow star denotes holotype, yellow circles paratypes), *Etmopterus fusus* (blue circle) and *Etmopterus evansi* (red circles) in Papua New Guinea (Image © NASA, TerraMetrics, Google Earth).

Etmopterus samadiae can be separate from its closest congener, *E. brachyurus* (Fig. 7A, 11a), by a combination of external morphological characteristics including: posterior flank marking 9.1–11.2 vs. 11.4–12.6% TL; flank marking base length 3.5–4.9 vs. 2.8–3.4% TL; length of caudal base marking (from tip of anterior finger to tip of posterior finger) 10.6–14.1 vs. 7.0–7.9% TL; interorbital space 7.8–9.1 vs. 6.6–7.4% TL; monospondylous centra 34–37 vs. 39–45. *Etmopterus brachyurus* has been confirmed from the northwestern Pacific (Philippines, Taiwan and Japan) based on the type locality and molecular analyses (Fig. 9). It has also been recorded from off Western Australia and Queensland (Last & Stevens, 2009).

Four of the *Etmopterus* specimens from Papua New Guinea were tentatively identified as *E. dislineatus* upon first examination due to the presence of black, dash-like markings on the sides (Figs 11b, 12). However, subsequent examination ruled out this species due to a number of morphometric and meristic characters. For example, the total number of vertebral centra of *E. dislineatus* is 88–97 (n=18), whereas the two NTUM specimens had total counts of 81 and 82. Also, the posterior flank marking is far shorter in the PNG specimens than in the type specimens of *E. dislineatus*, i.e. 8.3–9.7 vs. 12.0–14.3% TL. When compared with *E. evansi*, the PNG specimens agreed in general morphology and meristics. Although there were some differences in morphological measurements, most of these differences could have been due to slightly different measurement methodology, and none were significant enough to warrant separating as a distinct species. The PNG specimens all had similar colour pattern with a variable arrangement of black, horizontal, dash-like marks on the lateral body, mostly visible under magnification. Similar markings were also obvious on the type specimens of *E. evansi* and, although less evident, in the specimens of *E. brachyurus* examined. Thus, the four PNG specimens are identified as *E. evansi* and represent a significant eastward range extension from northwestern Australia and the Arafura Sea in Indonesia.

A single specimen (NTUM 10318) was identified as *E. fusus* (Figs 11c, 13) which, similar to above, was previously only known to occur off northwestern Australia and possibly off Java in Indonesia. The capture locations of this specimen and the four *E. evansi* specimens are shown in Fig. 10.

FIGURE 11. Lateral view of (A) *Etmopterus brachyurus* (field code HO-250, female 344 mm TL, Taiwan); (B) *Etmopterus evansi* (ASIZ unreg. field code CP3713, female 177 mm TL, Papua New Guinea); (C) *Etmopterus fusus* (NTUM 10318, female 256 mm TL, Papua New Guinea).

FIGURE 12. Lateral flank marking of *Etmopterus evansi* (NTUM 10312, juvenile male 172 mm TL), highlighting the dark blotch on ventral surface near ventral caudal origin, long posterior finger of caudal base marking, and double line of dashes above flank marking.

FIGURE 13. Posterior luminescent markings (caudal base, central caudal, and posterior markings) on *Etmopterus fusus* (NTUM 10318, female 256 mm TL, Papua New Guinea).

Comparative material examined

Etmopterus alphus—Holotype, iSAM MB-F37564, adult male 325 mm TL, 18°14'S, 37°31'E, 472 m, 17 July 1994. Material information for 28 paratype specimens is listed in Ebert *et al*. (2016).

Etmopterus brachyurus—Holotype, USNM 70257, male 186 mm TL, Jolo Island, Philippines; 17 specimens (8 males, 267–305 mm TL and 9 females, 261–325 mm TL), collected by David A. Ebert, Ta–Chi, Taiwan (24° 53' N, 122° 01' E), April–May 1988; CSIRO H 5611-01 (3 specimens), 128–224 mm TL, CSIRO H 5611-09, female 395 mm TL, Ta-Chi fish market, Taiwan, 1 August 2000; CSIRO H 7401-03, female 246 mm TL, Tongkang fish market, Taiwan, 19 March 2012; CSIRO H 7402-01, female 350 mm TL, Tongkang fish market, Taiwan, 20 March 2012.

Etmopterus burgessi—Holotype, CAS 223476, 355 mm TL, adult male, Ta-Chi, Taiwan, 24° 53' N, 122° 01' E, 11 May 1988; Paratypes (3 specimens), all collected at Ta-Chi, Taiwan, 24° 53' N, 122° 01' E; CAS 223477, adult female, 406 mm TL, 22 May 2005; CAS 223478, juvenile female, 241 mm TL, 23 May 2005; CAS 223479, juvenile female, 239 mm TL, 21 May 2005; CSIRO H 7395-36, adult male 335 mm TL, CSIRO H 7395-37, juvenile male 230 mm TL CSIRO H 7395-38, female 202 mm TL, CSIRO H 7395-39, juvenile male 210 mm TL, CSIRO H 7395-40, female 215 mm TL, Ta-Chi fish market, Taiwan, 14 March 2012.

Etmopterus dislineatus—Holotype, CSIRO H 1416-01, adult male 445 mm TL, Australia; Paratype, CSIRO H 947-2, female, 308 mm TL, Australia.

Etmopterus evansi—Holotype, CSIRO H 3141-06, female 270 mm TL, Rowley Shoals, Western Australia, 29 February 1992; Paratype, CSIRO H 3143-02, adult male 262 mm TL, north of Dampier Archipelago, Western Australia, 10 March 1992; NTUM 10312, juvenile male 172 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 520–575m depth, 14 December 2012; NTUM 10317, male 299 mm TL, east of Cape Croisiles, Madang, Papua New Guinea, 680–689 m depth, 16 December 2012; ASIZ P. unreg (BIOPAPUA field code CP3689-1), adult male 343 mm TL, west of Manus Island, Papua New Guinea, 679–685 m depth, 29 September 2010; ASIZ P. unreg (BIOPAPUA field code CP3713), female 177 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 608–610 m depth, 5 October 2010.

Etmopterus lucifer—Holotype, CAS-SU 6863, adult male, 278 mm in total length (TL), Misaki, Japan; CAS 23662, male, 308 mm TL, off Sandai, Japan.

Etmopterus molleri—Holotype, AMS 5816, female, 295 mm BL, New South Wales, Australia; CAS-SU 23779, female, 347 mm TL, off Sagami Nada; CAS 11225, female, 293 mm TL; CAS 11225, female, 265 mm TL, off Misaki, Japan; CSIRO H 7030-4, female, 374 mm TL, New South Wales, Australia; CSIRO H 7059-2, female, 390 mm TL, New South Wales, Australia.

Etmopterus sculptus—Holotype, SAM 37569, 442 mm TL, mature male, RS *Africana* cruise 060, mesopelagic survey, station A6986 060 01-02B, 33° 22.9´S 17° 29.1´E, 552 m, 04 March 1988. Paratypes, SAM

33011, 498 mm TL, mature female, RS *Africana* cruise 060, mesopelagic survey, station A6987 060 01-03B, 33° 34.6′S 17° 23.6′E, 718 m, 05 March 1988; SAM 37570 (2 specimens), 435 and 501 mm TL, mature male/mature female, RS *Africana* cruise 060, mesopelagic survey, station A6986 060 01–02B, 33° 22.9′S 17° 29.1′E, 552 m, 04 March 1988; SAM 37571 (2 specimens), 474 and 495 mm TL, mature females, RS *Africana* cruise 060, mesopelagic survey, station A6990 060 02-02B, 33° 18.6′S 17° 28.4′E, 480 m, 05 March 1988. ZMH uncatalogued, 10 specimens, R/V *Vityaz*, cruise 17, stations 2637 (3 specimens), 2707 (1), 2735 (1), and 2765 (5).

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Etmopterus samadiae n. sp., a new lanternshark (Squaliformes: Etmopteridae) from Papua New Guinea

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Abstract

A new species of lanternshark, *Etmopterus samadiae* (Squaliformes: Etmopteridae), is described from off northern Papua New Guinea, in the western Central Pacific Ocean. The new species resembles other members of the "*Etmopterus lucifer*" clade in having linear rows of dermal denticles and most closely resembles *E. brachyurus* from the western North Pacific. The new species occurs along insular slopes between 340 and 785 m depth. The new species can be distinguished from other members of the *E. lucifer* clade by a combination of characteristics, including length of anterior flank branch markings being slightly shorter than its posterior branch, a longer caudal base marking, and irregular and variable number of black, horizontal, dash-like marks on sides of body. Molecular analysis based on the NADH2 marker further supports the distinction of *E. samadiae* from other members of the *E. lucifer* clade.

Key words: Chondrichthyes, *Etmopterus lucifer* clade, new species, Papua New Guinea, molecular analysis

Introduction

The deepwater chondrichthyan fauna around Papua New Guinea has been poorly studied until recent surveys conducted by the RV *Alis* (Pante *et al*., 2012; Samadi *et al*., 2014) provided new records of shark and ray species from this region. Specimens collected during these expeditions were subsequently deposited into fish collections in Taiwan for further examination and identification. Representatives of the squaloid family Etmopteridae, specifically in the genus *Etmopterus*, were among the specimens saved and deposited because the family and genus are a new record for Papua New Guinea. Fricke *et al*. (2014) reported an unidentified *Etmopterus* species collected off Madang and suggested it might be close to *Etmopterus brachyurus* Smith & Radcliffe *in* Smith, 1912, but commented that *E. brachyurus* was restricted to the northwestern Pacific.

Examination of all of the *Etmopterus* material collected during these surveys (n=15, currently housed in Taiwanese fish collections) determined that three species were represented. These included a single specimen of *Etmopterus fusus* Last, Burgess, & Séret, 2002 from off Madang, and four specimens of *Etmopterus evansi* Last, Burgess, & Séret, 2002 from off Madang and Manus Island. The remaining 10 specimens were originally identified as *E. brachyurus*, but upon detailed examination were determined to represent an undescribed species based on several differences in key characteristics. Furthermore, DNA sequence analysis also confirmed that these specimens were closely related to, but distinct from, true *E. brachyurus*. The new species is herein formally described and named.

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Materials and methods

The type specimens were collected during the BIOPAPUA Expedition in 2010 (Pante *et al.*, 2012) and the PAPUA NIUGINI Expedition in 2012 (Samadi *et al.*, 2014) on-board the French research vessel *Alis* of the Institut de Recherche pour le Développement (IRD, Noumea). The specimens were subsequently, along with the other fish specimens, sent to either the National Taiwan University Museum (NTUM) or Academia Sinica (ASIZ) in Taipei.

Morphometric measurements and terminology follow Ebert *et al*. (2011). Meristics include vertebral counts obtained by digital radiographs from the holotype and four paratypes (NTUM 10313, 10314, 10315, 10316 [1 of 3]), and tooth counts taken *in situ* from the holotype and two paratypes (NTUM 10313, 10314).

Comparative material was examined from collections at the Australian Museum, Sydney (AMS), California Academy of Sciences (CAS), CSIRO, iSAM, South African Institute for Aquatic Biodiversity (SAIAB), USNM, and ZMH. Institutional abbreviations follow Sabaj Pérez (2016). Four specimens of *E. brachyurus* were measured in full for comparative purposes: CSIRO H 5611-01 (1, 224 mm TL), CSIRO H 5611-09, CSIRO H 7402-01 and CSIRO H 7401-03.

Tissue samples were taken from the type specimens at sea post-capture, and were temporarily stored in 95% alcohol in the field. Tissue samples were accessioned in the Chondrichthyan Tree of Life project with GN numbers (Gavin Naylor tissue number). DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc Norcross, GA). Extracted total DNA was stored at -20 °C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via the Polymerase Chain Reaction (PCR). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µl volume comprising 0.3 µM primers, 2.5 mM $MgCl_2$, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA), and 50–100 ng template DNA. The reaction mixture was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio), and bi-directionally Sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego USA).

DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd Auckland, New Zealand, available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within Geneious® (Biomatters Ltd Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. The Maximum Likelihood Tree was estimated from the data set using the GTR+I+G model. A bootstrap analysis was run separately under the same model conditions to estimate support for each of the nodes in the ML tree. All phylogenetic analyses were carried out using the software package PAUP*4.0 version a148.

Etmopterus samadiae, new species

Papuan Lanternshark

(Figures 1–10; Table 1)

Etmopterus sp.—Fricke *et al*., 2014: 14 (Madang)

Holotype. NTUM 10078 (tissue accession GN 17184), adult male 265 mm TL, east of Malmal Passage, Madang, Papua New Guinea, 05°07' S, 145°50' E, 527–539 m depth, 30 Nov 2012.

Paratypes. 9 specimens: ASIZ P.73777, adult male 230 mm TL, ASIZ P.73778, female 188 mm TL, ASIZ P.73765, pregnant female 277 mm TL, off Lae, Huon Gulf, Morobe Province, Papua New Guinea, 06°51.841' S, 147°04.672' E, 395–406 m depth, 22 Aug 2010; NTUM 10313 (tissue accession GN 17195), female 269 mm TL, northern Cape King William, Morobe Province, Papua New Guinea, 06°00' S, 147°38' E, 785 m depth, 10 Dec 2012; NTUM 10314 (tissue accession GN 17197), female 258 mm TL, Astrolabe Bay, Madang, Papua New

Guinea, 05°22' S, 145°48' E, 420–490 m depth, 14 Dec 2012; NTUM 10315 (tissue accession GN 17198), female 154 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05°22' S, 145°48' E, 340–385 m depth, 14 Dec 2012; NTUM 10316 (3 specimens; tissue accessions GN 17210–2), female 177 mm TL, subadult male 201 mm TL, female 228 mm TL, west of Kairiru Island, East Sepik, Papua New Guinea, 03°19' S, 143°27' E, 422–425 m depth, 19 Dec 2012.

FIGURE 1. Lateral view of the holotype of *Etmopterus samadiae* n.sp., adult male (NTUM 10078, 265 mm TL), (A) fresh; (B) post-preservation.

FIGURE 2. Dorsal view of paratype of *Etmopterus samadiae* n.sp., female (NTUM 10316, 1 of 3, 177 mm TL), fresh.

Diagnosis. *Etmopterus samadiae* is a relatively small, slender, species of linear–denticled *Etmopterus* that can be separated from its closest congeners within the *E. lucifer* clade by a combination of characteristics including the length of its anterior flank markings being slightly shorter than its posterior branch, long caudal base marking, and irregular and variable number of black, horizontal, dash-like marks on sides of body. The new species is morphologically and genetically (based on the NADH2 marker) closest to *E. brachyurus*, but differs from this species in having a shorter posterior caudal marking (2.8–4.4 vs. 4.2–6.1% TL), a longer caudal base marking (10.6–14.1 vs. 7.0–7.8% TL), and flank marking with a slightly shorter posterior branch (9.1–11.2 vs. 11.4–12.6% TL).

Description. Values expressed as a percentage of total length (TL) for the holotype, followed by the range of values for 9 paratypes (Table 1).

Body fusiform, trunk sub-cylindrical (Fig. 1), width 1.1 (0.7–1.7) in trunk height; head sub-conical, long, 21.3 (20.6–23.7)% TL, slightly depressed, height 0.7 (0.5–0.8) times width. Snout moderately long, conical in lateral view, in dorsal view triangular–shaped becoming rounded at snout–tip (Fig. 3), head width 8.2 (9.8–11.8)% TL. Eyes oval-shape, large, orbit length 3.8 (3.0–3.7) in head and 2.6 (2.0–3.3) times orbit height; orbits with anterior and posterior notches; moderately spaced, inter–orbital space 1.2 (1.2–1.5) in width of head and orbit length 1.2

(1.1–1.4) times in inter–orbital distance. Spiracles small, semi-circular, greatest diameter 0.9 (1.4–2.5)% TL, 6.1 (2.7–4.0) times orbit length, distance to eye 2.9 (1.4–2.6)% TL, eye–spiracle length 0.7 (1.0–1.9) in orbit height. Nostrils large, oblique, length almost equal to internarial width, less than orbit length; anterior nasal flap well developed, triangular, anterior tip extending across nasal opening, length 1.0 (0.5–0.9) times spiracle length. Gill openings small, narrow, slightly oblique, in horizontal series, subequal in height, inter-gill length 4.9 (3.0–4.7)% TL. Mouth broad, length 3.4 (3.3–4.8) times in width, slightly arched, width 0.8 (0.7–0.9) times preoral length.

Teeth dissimilar in upper and lower jaw (Fig. 4); upper teeth multicuspid in three functional series, functional teeth in lower jaw unicuspid in single series; multicuspid upper teeth small, upright, with strong central cusp flanked by 2 or 3 lateral cusplets on each side, decreasing in size distally; teeth in lower jaw fused into single row, blade-like, cusp oblique. Tooth count in first row of upper jaw 33 (27–28) and in first row of lower jaw 35 (28–31).

FIGURE 3 . Ventral head of the holotype of *Etmopterus samadiae* n.sp., adult male (NTUM 10078, 265 mm TL).

FIGURE 4. Upper and lower tooth morphology of the adult male holotype of *Etmopterus samadiae* n.sp. (NTUM 10078, 265 mm TL).

First dorsal fin small, rounded at apex, length of first dorsal fin 8.6 (8.5–9.9)% TL, origin just anterior to pectoral-fin free rear tip; fin base insertion well anterior of pelvic-fin origin; pre–first dorsal fin length 1.3 (1.4–1.8) times inter–dorsal distance; first dorsal–fin spine straight, short, 1.6 (1.3–2.0) times height of first dorsal fin, located over pectoral fin rear margin. Second dorsal fin conspicuously larger, more erect than first dorsal fin, length of first dorsal fin 0.6 (0.6–0.8) times second dorsal fin, height of first dorsal fin 0.4 (0.5–0.7) times second dorsal fin; apex sub–angular, posterior margin concave, free rear tip elongated, length 13.2 (12.2–13.6)% TL, pre–second dorsal length 2.5 (2.6–3.1) times inter–dorsal distance; second dorsal–fin spine large, height slightly taller than fin, curved near tip towards fin apex; origin posterior to insertion of pelvic fins, over pelvic fin free rear tips. Interspace between first and second dorsal fins 1.0 (0.8–1.0) times pre–pectoral length.

Pectoral fins relatively large, length 9.4 (10.1–11.3)% TL, subangular at free rear tips, base 2.0 (1.7–2.1) times in anterior margin, posterior margin nearly straight. Caudal peduncle relatively long, dorsal-caudal space 16.1 (13.6–15.3)% TL, height slightly greater than width, rounded, and tapering posteriorly. Caudal fin elongate, subequal to head length, terminal lobe distinct; length of lower preventral caudal fin margin less than one-half upper caudal fin margin.

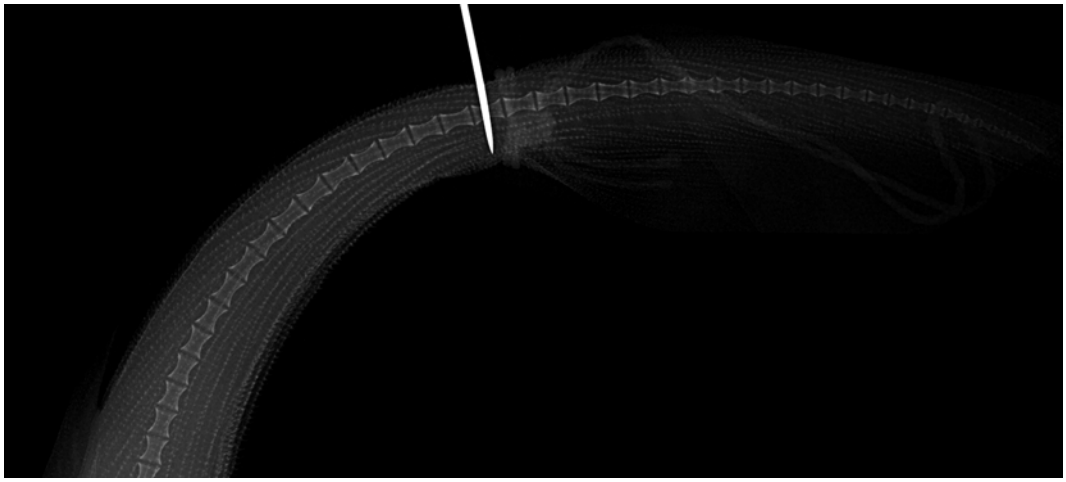

FIGURE 5. Digital radiograph highlighting dermal denticle arrangement of paratype NTUM 10316 [1 of 3]) along caudal peduncle and caudal fin.

FIGURE 6. Dermal denticle morphology and arrangement on lateral side behind second dorsal fin of the adult male holotype of *Etmopterus samadiae* n.sp. (NTUM 10078, 265 mm TL).

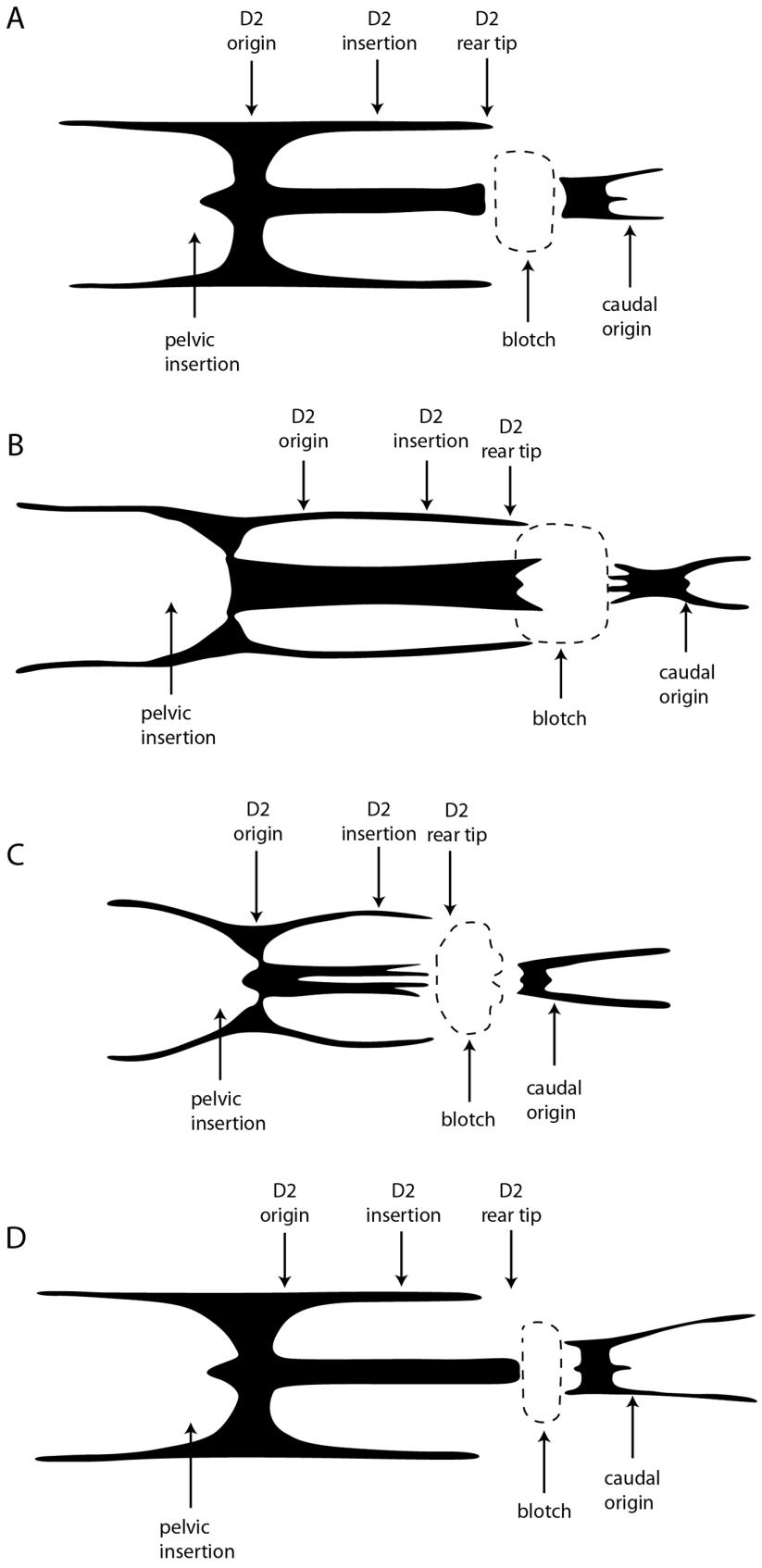

FIGURE 7 . Diagrammatic representation of the flank and caudal base luminescent markings in ventral view of: A) *Etmopterus brachyurus* (CSIRO H 5611-01, largest); B) *Etmopterus dislineatus* (holotype, CSIRO H 1416-01); C) *Etmopterus evansi* (holotype, CSIRO H 3141-16); D) *Etmopterus samadiae* n.sp. (paratype, NTUM 10314).

TABLE 1. Morphometric data and vertebral counts for the holotype and ranges for the 9 measured paratypes of *E. samadiae* **n.sp.** (expressed as a percentage of total length); one PNG specimen of *E. fusus*; ranges for the four PNG specimens of *E. evansi*; and ranges for four Taiwan specimens of *E. brachyurus.*

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Total length (mm)	265	154	277	256	172.0	343.0	224	350
Precaudal length	77.2	76.0	78.4	78.9	76.8	78.4	76.8	79.7
Prenarial length	2.8	2.8	3.8	2.1	3.0	4.4	2.9	3.4
Preoral length	9.3	9.0	11.4	8.2	8.9	11.3	9.4	10.7
Preorbital length	4.8	4.4	6.4	4.5	5.1	5.9	5.3	5.8
Prespiracle length	11.5	10.8	14.2	10.6	10.3	13.6	11.8	13.0
Prebranchial length	16.1	16.2	19.4	16.5	16.2	18.6	17.7	18.3
Head length	21.3	20.6	23.7	21.1	20.2	21.6	21.8	22.8
Prepectoral length	21.0	20.0	23.3	20.6	19.8	22.3	21.1	22.2
Prepelvic length	46.0	46.9	48.7	51.2	47.7	50.1	47.2	50.3
Snout-anterior vent length	50.6	49.2	52.3	54.7	48.8	53.9	50.4	52.3
Pre D1 length	28.7	30.4	32.5	28.1	30.1	34.1	30.8	32.5
Pre D2 length	54.3	54.7	57.0	57.8	55.4	56.9	55.8	56.9
Interdorsal space	21.6	17.9	22.0	25.4	17.2	21.1	18.0	20.3
D2–caudal space	16.1	13.6	15.3	14.2	12.7	22.1	13.6	14.2
Pectoral–pelvic space	19.0	18.8	22.5	26.3	19.3	23.2	21.1	23.3
Pelvic–caudal space	21.3	19.7	22.3	18.4	18.2	21.4	20.7	21.9
Orbit length	5.6	5.6	7.8	5.4	4.5	6.4	5.7	7.1
Orbit height	2.1	2.0	3.2	3.0	2.3	2.8	2.4	3.4
Interorbital space	6.9	7.8	9.1	7.4	8.4	10.3	6.6	7.4
Nostril width	2.8	2.1	3.5	2.6	2.7	3.9	2.3	2.7
Internarial length	3.3	2.9	3.8	2.4	2.9	3.6	2.6	2.8
Anterior nasal flap length	0.9	0.9	1.7	0.8	1.1	1.6	0.8	1.3
Spiracle length	0.9	1.4	2.5	1.8	1.9	3.0	1.2	1.9
Eye–spiracle space	2.9	1.4	2.6	2.8	1.8	2.1	2.3	2.9
Mouth length	2.2	1.7	2.4	2.1	1.5	2.7	1.6	1.9
Mouth width	7.5	7.3	8.9	7.4	7.3	10.5	7.3	7.9
Upper labial furrow length	1.8	1.8	2.8	2.0	1.8	2.0	1.7	1.9
Lower labial furrow length	1.5	1.1	1.6	1.1	1.6	1.6	1.4	1.8
Intergill length	4.9	3.0	4.7	4.9	4.1	4.2	4.2	4.6
1st gill slit height	0.9	1.0	1.4	1.3	1.5	1.5	1.1	1.4
2nd gill slit height	0.9	1.0	1.4	1.6	0.0	1.5	0.9	1.3
3rd gill slit height	1.0	1.0	1.4	1.6	1.4	1.5	0.8	1.2
4th gill slit height	0.9	0.8	1.3	1.5	1.3	1.3	0.5	1.1
5th gill slit height	1.1	1.0	1.3	1.7	1.2	1.4	1.2	1.5
Head height	6.0	5.5	8.3	7.5	7.6	7.8	5.4	7.1
Head width	8.2	9.8	11.8	10.3	10.0	10.8	8.6	9.9
Abdomen width	5.5	5.2	11.8	10.3	6.0	10.5	7.5	8.9
Trunk height	5.3	5.8	9.5	8.5	8.0	8.4	6.7	7.0

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TABLE 1. (Continued)

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Trunk width	5.8	6.3	10.7	8.6	6.2	9.3	5.3	7.7
Tail width	4.1	3.6	4.5	5.1	4.1	4.8	3.6	4.7
Caudal peduncle height	2.2	1.6	2.9	2.7	2.5	3.2	2.4	3.0
Caudal peduncle width	2.0	1.8	2.8	2.6	1.7	2.3	1.9	2.2
Pectoral fin length	9.4	10.1	11.3	9.8	8.6	10.6	9.9	11.0
Pectoral fin anterior margin length	9.2	9.8	11.5	9.9	8.4	8.5	9.8	10.6
Pectoral fin base length	4.6	5.0	6.3	4.6	4.8	6.2	5.0	5.9
Pectoral fin height		6.5	8.4	7.4	0.0	0.0	7.0	7.7
Pectoral fin inner margin length	4.6	4.1	6.1	5.3	0.0	0.0	4.5	5.6
Pectoral fin posterior margin length		5.7	8.1	6.3	0.0	0.0	4.8	5.3
Pelvic fin length	10.8	10.0	11.7	11.9	8.6	9.3	10.1	12.0
Pelvic fin anterior margin length	6.9	5.8	7.8	6.3	4.1	5.7	6.7	7.3
Pelvic fin base length	5.8	5.1	7.1	6.7	6.4	7.1	4.1	6.3
Pelvic fin height	4.4	3.4	4.8	4.2	3.4	4.2	3.0	4.0
Pelvic fin inner margin length	5.4	3.6	5.6	4.1	3.2	3.2	3.5	5.4
Pelvic fin posterior margin length	5.4	5.9	6.8	6.9	6.7	6.7	5.3	6.1
Clasper length outer	2.4	1.1	1.1	–	2.2	2.7	0.0	0.0
Clasper length inner	4.6	6.3	6.3	–	5.1	5.2	0.0	0.0
Clasper base width	1.3	1.6	1.6	–	1.2	1.9	0.0	0.0
D1 length	8.6	8.5	9.9	9.3	8.0	11.0	8.4	9.2
D1 anterior margin length	7.5	7.3	8.8	6.7	9.2	9.2	6.1	8.5
D1 base length	5.5	4.7	6.7	5.3	5.6	6.7	5.0	6.5
D1 height	1.9	2.3	3.3	3.0	3.2	3.6	2.2	3.6
D1 inner margin length	3.8	3.5	5.2	3.9	2.6	4.8	3.3	3.8
D1 posterior margin length	3.6	2.5	3.9	4.5	–	–	2.5	3.5
D2 length	13.2	12.2	13.6	13.3	12.8	13.8	12.3	13.4
D2 anterior margin length	10.3	10.8	12.4	9.7	10.6	11.8	9.8	12.0
D2 base length	7.6	7.1	8.5	8.2	8.3	9.5	6.9	8.7
D2 height	4.3	4.2	5.8	4.9	4.9	5.6	3.8	4.7
D2 inner margin length	5.9	5.0	6.4	5.4	4.7	5.7	5.2	6.0
D2 posterior margin length	5.0	5.5	6.6	6.3	0.0	6.9	4.5	6.3
Caudal dorsal margin	22.8	20.3	24.1	19.1	21.5	23.5	19.6	23.1
Caudal fork width	4.8	4.7	5.4	5.1	5.1	5.1	4.2	5.6
Caudal fork length	11.5	9.4	10.8	10.3	–	–	11.3	12.0
Caudal preventral margin length	10.4	8.6	10.7	10.4	10.3	12.2	10.3	11.8
Caudal lower postventral margin length	3.3	2.0	3.5	4.3	–	–	2.3	2.6
Caudal upper postventral margin length	7.9	8.9	10.4	7.3	–	–	7.1	8.8
Caudal fin subterminal margin length	–	3.4	5.5	3.2	4.7	5.2	4.4	4.7

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TABLE 1. (Continued)

	E. samadiae n.sp.			*E. fusus*	*E. evansi*		*E. brachyurus*	
	Holotype	Paratypes		NTUM	n = 4		n = 4	
		Min.	Max.	10318	Min.	Max.	Min.	Max.
Caudal fin terminal margin length	–	2.9	4.3	5.1	2.9	5.8	2.7	3.6
Caudal fin terminal lobe length	–	4.6	6.3	5.7	4.9	4.9	6.5	6.7
D1 midpoint–pectoral fin insertion	6.1	6.4	9.6	5.0	8.8	9.2	6.7	8.7
D1 midpoint–pelvic-fin origin	13.5	11.2	14.3	20.5	12.9	13.5	11.9	14.6
Pelvic-fin midpoint–D1 insertion	14.7	12.5	15.4	20.9	13.4	15.1	12.7	15.8
Pelvic-fin midpoint–D2 origin	5.4	4.6	6.3	3.2	2.4	3.8	4.6	6.3
D1 spine length	3.0	3.4	5.4	2.1	2.8	5.0	3.4	3.6
D1 exposed spine length	2.5	2.8	3.9	1.9	2.0	3.9	2.6	2.9
D2 spine length	5.6	7.1	9.8	5.6	5.2	8.5	6.8	7.4
D2 exposed spine length	4.6	5.3	7.6	4.7	3.2	6.3	5.6	6.2
Anterior flank marking length	10.3	8.2	10.4	8.5	7.4	9.6	7.9	9.3
Posterior flank marking length	11.2	9.1	10.8	0.0	8.3	9.7	11.4	12.6
Posterior flank marking width	0.6	0.5	0.8	2.8	0.2	0.6	0.3	0.7
Flank marking base length	4.4	3.5	4.9	9.2	1.5	4.1	2.8	3.4
Caudal base marking length	11.4	10.6	14.1	7.5	10.5	11.6	7.0	7.8
Central caudal marking length	–	–	–	4.7	–	–	–	–
Posterior caudal marking	3.2	2.8	4.4	2.6	2.8	3.6	4.2	6.1
Monospondylous centra	34	36	37	37	38	42	39	45
Diplospondylous trunk centra	21	19	22	19	17	18	19	22
Caudal centra	25	25	27	23	23	25	24	26
Precaudal centra	55	55	59	56	56	59	59	65
Total centra	80	80	86	79	81	82	84	91

Dermal denticles hook-like, posteriorly directed rearwards; organized in distinct rows laterally, characteristic of *E. lucifer* clade members (Fig. 5, 6). Distance between lateral rows mostly consistent along length, decreasing only very slightly towards caudal peduncle. Flank mark area denticles more dense and pointed ventrally.

Luminescent markings distinct, intricate (Fig. 7D); ventral head surface markings blackish, starting from almost at snout tip, extending to level of nostrils and orbits at just below level of anterior notch, then extending straight from just below posterior eye notch towards gill slits, weakly demarcated from belly marking by a weak band of transverse dermal folds across throat extending from below lower edges of first three gill openings on either side. Head dorsal surface photophore pattern as follows: a single midline along back originating at level of first gill slits extending posteriorly to caudal–fin origin; scattered photophores on paler fontanelle area of central head and also on paler area above orbits (as short dashes in some paratypes).

Belly marking originates behind mouth on posterior portion of transverse dermal folds and extends ventrally along pectoral fin bases extending upwards to level with fin origin and upper edges of gill slits, and posteriorly to pelvic fin bases; ventral surface of pectoral fin very dark along lower base and upper base where ceratotrichia originate, bisected by distinct lighter to white band or blotch forming a two–prong fork pattern; margin on lateral trunk (pectoral–pelvic space) very clearly defined, line extending from rear margin of pectoral–fin base nearly to pelvic–fin insertion except for paler area at pelvic-fin origin; dark ventral belly surface continuous onto caudal peduncle to about lower caudal fin origin.

Flank markings well defined (Fig. 7d), consisting of both an anterior and posterior branch; anterior branch relatively short, length 10.3 (8.2–10.5)% TL, slender, nearly straight, extending well anterior to pelvic–fin origin; posterior branch straight, slightly thicker, width at level of base end of second dorsal fin 0.6 (0.5–0.8)% TL, slightly longer than anterior branch (shorter than anterior branch in paratype ASIZ P.73777), length 11.2 (9.1–

10.8)% TL, extending to just anterior to second dorsal-fin free rear tip but well posterior to second dorsal-fin insertion; base of flank marking wide, origin slightly posterior to pelvic-fin insertion. Ventral caudal base marking distinct, short, length about equal to base of flank marking, not extending as a saddle on to caudal peduncle, anterior finger very short, posterior finger long, total length (including base) 11.4 (10.6–14.1)% TL. No central caudal marking. Posterior caudal fin marking very narrow, its length 3.2 (2.8–4.4) % TL.

Vertebral counts: total counts 80 (80–86), total precaudal counts 55 (55–59); monospondylous 34 (36–37); diplospondylous precaudal 21 (19–22); caudal 25 (25–27).

Coloration. In life, greyish to silvery black dorsally and laterally on body, becoming dark black ventrally; transition between lateral and ventral surfaces well demarcated by a paler lateral stripe below the flank markings in most specimens (less distinct in holotype and some paratypes). Dorsal midline with a broad, pale stripe originating just posterior to midpoint of inter-spiracle space, extending to first dorsal fin origin, continuing between dorsal fins, and from second dorsal fin insertion to upper caudal fin origin (Fig. 2); most prominent anterior to first dorsal fin and between dorsal fins, less prominent along upper caudal peduncle; a single row of dark photophores extending along middle of white dorsal stripe. Body with variable number and arrangement of short, horizontal, dash-like black markings (Fig. 8); most numerous in paratype NTUM 10314 (Fig. 8). Pectoral and pelvic fins dark at base and along anterior fin edge, becoming translucent to white on remainder of fins. Dorsal fins dark at base and along anterior edges, becoming translucent to white on remainder of fins. Black lateral flank markings demarcated by surrounding lighter colored lateral flanks (not sharply demarcated in most preserved specimens). Paler colored flank area on lateral surface between pectoral and pelvic fins sharply demarcates lateral and ventral surfaces; ventral surface black. Caudal fin with a distinct, large dark blotch centrally, occupying the area between the posterior finger of the caudal base marking and the upper caudal marking; posterior margin dark. Ventral surface mostly dark black around mouth, belly, and with a dark stripe between pelvic fin insertions and caudal origin; snout not distinctly paler than mouth. After preservation coloration similar but with paler markings often less obvious and coloration becoming a light or dark brown; dorsal median pale stripe and whitish flank area and black lateral flank markings less prominent but still distinct in most cases; dark blotch on central caudal fin obvious and darker pores extending laterally on body still clearly visible under microscope.

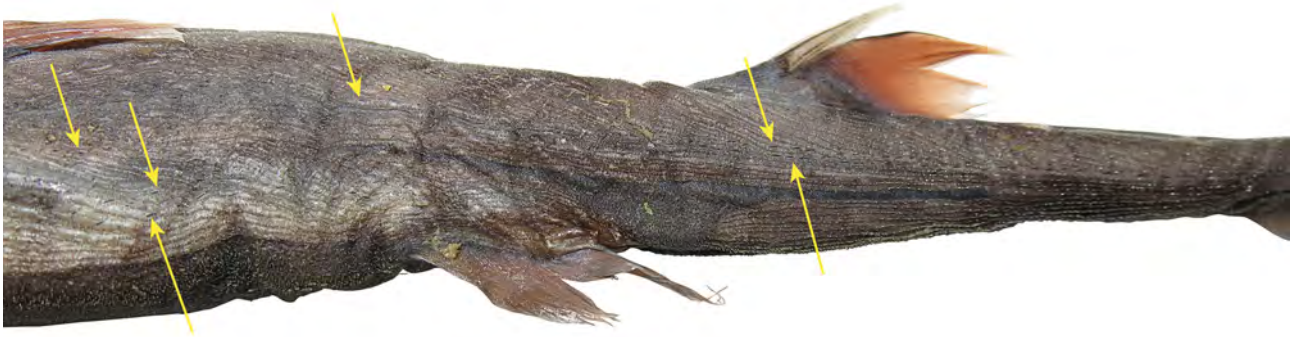

FIGURE 8. Posterior lateral view of *Etmopterus samadiae* n.sp. (paratype, NTUM 10314, female 258 mm TL), highlighting the dash-like markings. Arrows show location of the rows of dash marks.

Molecular analysis. The analysis of the NADH2 data confirms that *Etmopterus samadiae* belongs in the *E. lucifer* clade and represents a monophyletic lineage that is distinct from, but most closely related to *Etmopterus brachyurus* (Fig. 9). It should be noted that this inference is based on a single mitochondrial marker. Inclusion of multiple nuclear markers could affect the presented inference.

Size. Specimens examined ranged in size from 154 to 277 mm TL. A 277 mm TL female (ASIZ P.73765) was found to be pregnant (embryo caudal fin visible in cloaca) and two males 230 (ASIZ P.73777) and 265 mm TL (NTUM 10078) were determined to be mature.

Distribution. The new species is known from off the northern Papua New Guinea mainland, from west of Kairiru Island in East Sepik Province to off Lae in the Huon Gulf (Morobe Province) and at a depth range of 340 to 785 m (Fig. 10).

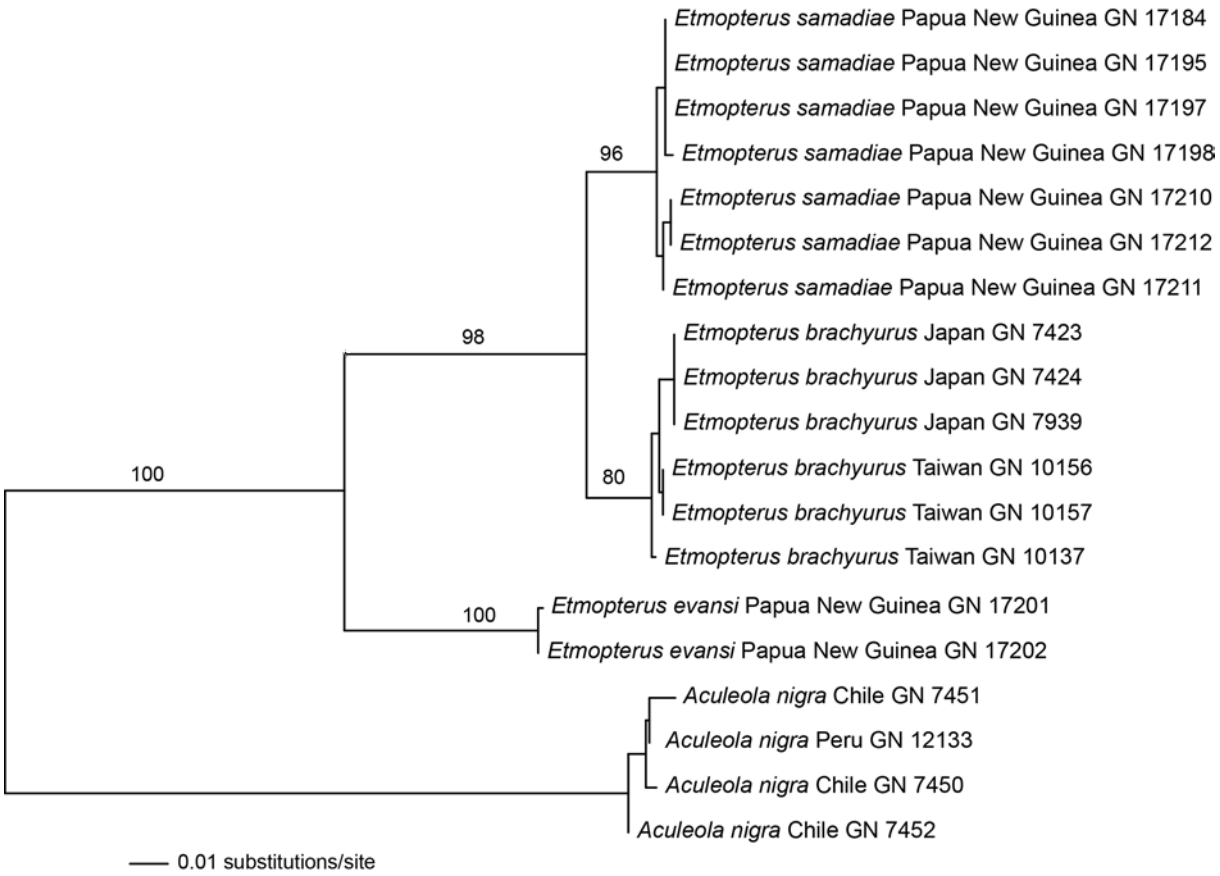

FIGURE 9. Maximum Likelihood tree estimated under the General Time Reversible model (GTR) with model terms to accommodate both Invariant sites (I) and Gamma distributed rates (G). Bootstrap support values are shown from a separate ML bootstrap analysis. Sequences used in this tree are part of the Chondrichthyan Tree of Life project (http://sharksrays.org/).

Etymology. The species is named after Dr Sarah Samadi (MNHN) who was one of the key principal investigators of the 2010 and 2012 MNHN expeditions in Papua New Guinea from which all the type specimens were obtained. The proposed English common name is Papuan Lanternshark.

Discussion

Etmopterus samadiae can be assigned to the "*E. lucifer* clade" as defined by Straube *et al*. (2010) due to its conspicuous flank markings displaying distinct anterior and posterior branches. The members of this clade are also characterized by distinct linear rows of denticles on the dorsal head surface that extend to the flanks, caudal peduncle and caudal-fin base. Diagnostically, the relative lengths of the anterior and posterior flank branches can further subdivide this clade, which currently is comprised of 11 species (Ebert *et al*., 2016).

Etmopterus samadiae has a longer posterior branch on the flank marking (Fig. 7D) and can be separated from five species, *Etmopterus burgessi* Schaff-Da Silva & Ebert, 2006; *Etmopterus evansi* Last, Burgess & Séret, 2002 (Fig. 7C); *Etmopterus lucifer* Jordan & Snyder, 1902; *Etmopterus pycnolepis* Kotlyar, 1990; and *Etmopterus sculptus* Ebert, Compagno, & De Vries, 2011, which have an anterior flank branch that is equal to, or longer than the posterior branch. Of the six species that have longer posterior branches, three species, *Etmopterus alphus* Ebert, Straube, Leslie, & Weigmann, 2016, *Etmopterus molleri* (Whitley, 1939), and *Etmopterus dislineatus* Last, Burgess, & Séret, 2002 (Fig. 7B), have their posterior branch extending past the free-rear tip of the second dorsal fin, while in *E. samadiae* the posterior branch does not extend as far. The Western Atlantic *Etmopterus bullisi* Bigelow & Schroeder, 1957 and the poorly known western Pacific *Etmopterus decacuspidatus* Chan, 1966 both lack a band or spot on the caudal fin; a characteristic found in both the new species and *E. brachyurus*.

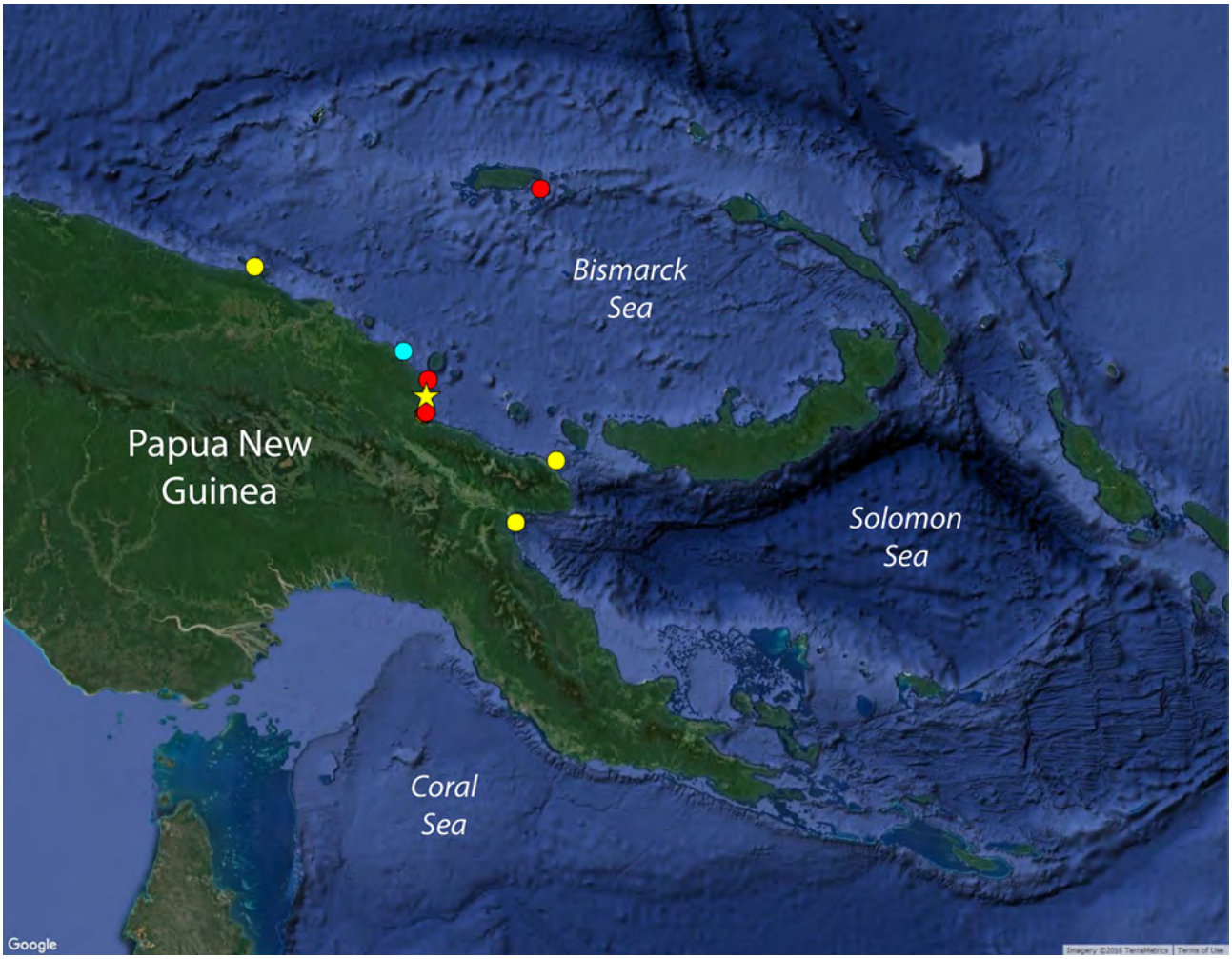

FIGURE 10. Map showing the capture locations of the type specimens of *Etmopterus samadiae* n.sp. (yellow star denotes holotype, yellow circles paratypes), *Etmopterus fusus* (blue circle) and *Etmopterus evansi* (red circles) in Papua New Guinea (Image © NASA, TerraMetrics, Google Earth).

Etmopterus samadiae can be separate from its closest congener, *E. brachyurus* (Fig. 7A, 11a), by a combination of external morphological characteristics including: posterior flank marking 9.1–11.2 vs. 11.4–12.6% TL; flank marking base length 3.5–4.9 vs. 2.8–3.4% TL; length of caudal base marking (from tip of anterior finger to tip of posterior finger) 10.6–14.1 vs. 7.0–7.9% TL; interorbital space 7.8–9.1 vs. 6.6–7.4% TL; monospondylous centra 34–37 vs. 39–45. *Etmopterus brachyurus* has been confirmed from the northwestern Pacific (Philippines, Taiwan and Japan) based on the type locality and molecular analyses (Fig. 9). It has also been recorded from off Western Australia and Queensland (Last & Stevens, 2009).

Four of the *Etmopterus* specimens from Papua New Guinea were tentatively identified as *E. dislineatus* upon first examination due to the presence of black, dash-like markings on the sides (Figs 11b, 12). However, subsequent examination ruled out this species due to a number of morphometric and meristic characters. For example, the total number of vertebral centra of *E. dislineatus* is 88–97 (n=18), whereas the two NTUM specimens had total counts of 81 and 82. Also, the posterior flank marking is far shorter in the PNG specimens than in the type specimens of *E. dislineatus*, i.e. 8.3–9.7 vs. 12.0–14.3% TL. When compared with *E. evansi*, the PNG specimens agreed in general morphology and meristics. Although there were some differences in morphological measurements, most of these differences could have been due to slightly different measurement methodology, and none were significant enough to warrant separating as a distinct species. The PNG specimens all had similar colour pattern with a variable arrangement of black, horizontal, dash-like marks on the lateral body, mostly visible under magnification. Similar markings were also obvious on the type specimens of *E. evansi* and, although less evident, in the specimens of *E. brachyurus* examined. Thus, the four PNG specimens are identified as *E. evansi* and represent a significant eastward range extension from northwestern Australia and the Arafura Sea in Indonesia.

A single specimen (NTUM 10318) was identified as *E. fusus* (Figs 11c, 13) which, similar to above, was previously only known to occur off northwestern Australia and possibly off Java in Indonesia. The capture locations of this specimen and the four *E. evansi* specimens are shown in Fig. 10.

FIGURE 11. Lateral view of (A) *Etmopterus brachyurus* (field code HO-250, female 344 mm TL, Taiwan); (B) *Etmopterus evansi* (ASIZ unreg. field code CP3713, female 177 mm TL, Papua New Guinea); (C) *Etmopterus fusus* (NTUM 10318, female 256 mm TL, Papua New Guinea).

FIGURE 12. Lateral flank marking of *Etmopterus evansi* (NTUM 10312, juvenile male 172 mm TL), highlighting the dark blotch on ventral surface near ventral caudal origin, long posterior finger of caudal base marking, and double line of dashes above flank marking.

FIGURE 13. Posterior luminescent markings (caudal base, central caudal, and posterior markings) on *Etmopterus fusus* (NTUM 10318, female 256 mm TL, Papua New Guinea).

Comparative material examined

Etmopterus alphus—Holotype, iSAM MB-F37564, adult male 325 mm TL, 18°14'S, 37°31'E, 472 m, 17 July 1994. Material information for 28 paratype specimens is listed in Ebert *et al*. (2016).

Etmopterus brachyurus—Holotype, USNM 70257, male 186 mm TL, Jolo Island, Philippines; 17 specimens (8 males, 267–305 mm TL and 9 females, 261–325 mm TL), collected by David A. Ebert, Ta–Chi, Taiwan (24° 53' N, 122° 01' E), April–May 1988; CSIRO H 5611-01 (3 specimens), 128–224 mm TL, CSIRO H 5611-09, female 395 mm TL, Ta-Chi fish market, Taiwan, 1 August 2000; CSIRO H 7401-03, female 246 mm TL, Tongkang fish market, Taiwan, 19 March 2012; CSIRO H 7402-01, female 350 mm TL, Tongkang fish market, Taiwan, 20 March 2012.

Etmopterus burgessi—Holotype, CAS 223476, 355 mm TL, adult male, Ta-Chi, Taiwan, 24° 53' N, 122° 01' E, 11 May 1988; Paratypes (3 specimens), all collected at Ta-Chi, Taiwan, 24° 53' N, 122° 01' E; CAS 223477, adult female, 406 mm TL, 22 May 2005; CAS 223478, juvenile female, 241 mm TL, 23 May 2005; CAS 223479, juvenile female, 239 mm TL, 21 May 2005; CSIRO H 7395-36, adult male 335 mm TL, CSIRO H 7395-37, juvenile male 230 mm TL CSIRO H 7395-38, female 202 mm TL, CSIRO H 7395-39, juvenile male 210 mm TL, CSIRO H 7395-40, female 215 mm TL, Ta-Chi fish market, Taiwan, 14 March 2012.

Etmopterus dislineatus—Holotype, CSIRO H 1416-01, adult male 445 mm TL, Australia; Paratype, CSIRO H 947-2, female, 308 mm TL, Australia.

Etmopterus evansi—Holotype, CSIRO H 3141-06, female 270 mm TL, Rowley Shoals, Western Australia, 29 February 1992; Paratype, CSIRO H 3143-02, adult male 262 mm TL, north of Dampier Archipelago, Western Australia, 10 March 1992; NTUM 10312, juvenile male 172 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 520–575m depth, 14 December 2012; NTUM 10317, male 299 mm TL, east of Cape Croisiles, Madang, Papua New Guinea, 680–689 m depth, 16 December 2012; ASIZ P. unreg (BIOPAPUA field code CP3689-1), adult male 343 mm TL, west of Manus Island, Papua New Guinea, 679–685 m depth, 29 September 2010; ASIZ P. unreg (BIOPAPUA field code CP3713), female 177 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 608–610 m depth, 5 October 2010.

Etmopterus lucifer—Holotype, CAS-SU 6863, adult male, 278 mm in total length (TL), Misaki, Japan; CAS 23662, male, 308 mm TL, off Sandai, Japan.

Etmopterus molleri—Holotype, AMS 5816, female, 295 mm BL, New South Wales, Australia; CAS-SU 23779, female, 347 mm TL, off Sagami Nada; CAS 11225, female, 293 mm TL; CAS 11225, female, 265 mm TL, off Misaki, Japan; CSIRO H 7030-4, female, 374 mm TL, New South Wales, Australia; CSIRO H 7059-2, female, 390 mm TL, New South Wales, Australia.

Etmopterus sculptus—Holotype, SAM 37569, 442 mm TL, mature male, RS *Africana* cruise 060, mesopelagic survey, station A6986 060 01-02B, 33° 22.9´S 17° 29.1´E, 552 m, 04 March 1988. Paratypes, SAM

33011, 498 mm TL, mature female, RS *Africana* cruise 060, mesopelagic survey, station A6987 060 01-03B, 33° 34.6′S 17° 23.6′E, 718 m, 05 March 1988; SAM 37570 (2 specimens), 435 and 501 mm TL, mature male/mature female, RS *Africana* cruise 060, mesopelagic survey, station A6986 060 01–02B, 33° 22.9′S 17° 29.1′E, 552 m, 04 March 1988; SAM 37571 (2 specimens), 474 and 495 mm TL, mature females, RS *Africana* cruise 060, mesopelagic survey, station A6990 060 02-02B, 33° 18.6′S 17° 28.4′E, 480 m, 05 March 1988. ZMH uncatalogued, 10 specimens, R/V *Vityaz*, cruise 17, stations 2637 (3 specimens), 2707 (1), 2735 (1), and 2765 (5).

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The Madang 2012 expedition (Principal Investigators Philippe Bouchet, Claude Payri and Sarah Samadi) was part of the "Our Planet Reviewed" PAPUA NIUGINI project organized by Muséum National d'Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le Développement (IRD) and University of Papua New Guinea (UPNG). The organizers acknowledge funding from the Total Foundation, Prince Albert II of Monaco Foundation, Fondation EDF, Stavros Niarchos Foundation and Entrepose Contracting, in-kind support from the Divine Word University (DWU), and post-expedition support from Agence Nationale de la Recherche (ANR) and the National Science Council of Taiwan (ANR TF-DeepEvo 12 ISV7 005 01) (http://expeditions.mnhn.fr/campaign/papuaniugini).

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Description of a new species of deepwater catshark *Apristurus yangi* n.sp. (Carcharhiniformes: Pentanchidae) from Papua New Guinea

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Abstract

Apristurus yangi, a new species of deepwater catshark, is described from Papua New Guinea based on two specimens collected during recent deepwater surveys. The new species belongs to the *longicephalus*-group which is characterised by its very long snout compared to members of the *brunneus*-group and *spongiceps*-groups. *Apristurus yangi* differs from its closest congeners in a combination of the following characters: 8 intestinal spiral valves; mouth width 7.9–8.6% TL; 32–33 monospondylous centra; 38 precaudal-diplospondylous vertebrae; small in size (female holotype mature at 437 mm TL); egg case small (~5.9 cm long) and with faint longitudinal striations.

Key words: Chondrichthyes, taxonomy, western South Pacific, *Apristurus longicephalus* group, molecular analysis

Introduction

The genus *Apristurus* is the most diverse group of catsharks within the family Pentanchidae with 38 valid nominal taxa (Weigmann, 2016). These catsharks inhabit continental slopes and seamounts at depths of about 24 to 2200 m (mostly >200 m) (Weigmann, 2016). Improved understanding of the deepwater fauna globally, largely due to global development of deepwater commercial fishing and recent deepwater scientific expeditions, revealed many more species than were previously thought to exist. Within *Apristurus*, six of the 38 known species were described in the last decade alone (Weigmann, 2016). In the South West Pacific, 10 species of *Apristurus* are known to occur: *A. ampliceps* Sasahara, Sato & Nakaya, 2008; *A. australis* Sato, Nakaya & Yorozu, 2008; *A. exsanguis* Sato, Nakaya & Stewart, 1999; *A. garricki* Sato, Stewart & Nakaya 2013; *A. longicephalus* Nakaya, 1975; *A. melanoasper* Iglésias, Nakaya & Stehmann, 2004; *A. nakayai* Iglésias, 2012; *A. pinguis* Deng, Xiong & Zhan, 1983; *A. platyrhynchus* (Tanaka, 1909); and *A. sinensis* Chu & Hu, 1981.

Nakaya & Sato (1999) suggested three species groups within *Apristurus* based on morphological characters, i.e. *brunneus*, *longicephalus* and *spongiceps* groups. Subsequently, Sato (2000) and Iglésias *et al.* (2005) found these groupings to be monophyletic based on morphological and molecular information. One of the groups designated by Nakaya & Sato (1999), the *longicephalus* group, is characterised by a long and narrow snout (snout tip to anterior nostrils >6.4% total length). At the time this group was designated, only two species were designated to this group, *A. herklotsi* (Fowler, 1934) and *A. longicephalus.* Since then, two more species have been added, *A. australis* and *A. garricki*.

Deepwater trawl surveys of the waters of Papua New Guinea between 2010 and 2014 using the RV *Alis* have provided the first detailed insights into the sharks and rays occurring on the continental slope of this area. These surveys consist of the BIOPAPUA cruise in 2010 (Pante *et al.*, 2012) and the PAPUA NIUGINI Expedition in 2012 (Samadi *et al.*, 2014), and more recently the MADEEP deep-sea cruise and Kavieng expedition, both in 2014. The

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sharks and rays examined on these surveys were retained and are deposited in fish collections in Taiwan. Several catshark species that had not previously been documented from Papua New Guinea were encountered, one of which was recently described as new, *Galeus corriganae* White, Mana & Naylor, 2016. A number of specimens of *Apristurus* were also collected: seven specimens of *A. macrostomus* Zhu, Meng & Li *in* Meng, Zhu & Li, 1985; one specimen of *A. nakayai*; one specimen of a short snouted species (not yet assigned to species); and two specimens of a long-snouted species. The two long-snouted specimens are herein described as a new species and are compared to other members of the *longicephalus*-group.

Materials and methods

The types were collected during deepwater surveys in Papua New Guinea in 2010 and 2014 on-board the French research vessel *Alis* of the Institut de Recherche pour le Développement (IRD, Noumea). The specimens were subsequently sent, with other fish specimens collected, to either the National Taiwan University Museum (NTUM) or Academia Sinica (ASIZ) in Taipei. A total of 74 morphometric characters were measured on the holotype (ASIZ P0080718) and the paratype (NTUM 11491) following the methodology proposed by Nakaya *et al.* (2008) for the genus *Apristurus*. The morphometric data are presented in Table 1. Measurements are presented as a percentage of total length (TL). Meristics were taken from digital radiographs of the two type specimens. Tooth rows counts were taken directly from the types.

The paratype of the new species was sampled for muscle tissue on-board the RV *Alis* immediately post capture. No tissue samples were taken during the 2010 survey. The sample was temporarily stored in 95% alcohol in the field. DNA was extracted using the E.Z.N.A Tissue DNA Kit (Omega Bio-Tek, Inc Norcross, GA). Extracted total DNA was stored at -20° C until used for amplification of the NADH dehydrogenase subunit 2 (NADH2) region of the mitochondrial DNA via the Polymerase Chain Reaction (PCR). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were used to amplify the target fragment. PCR reactions were generally carried out in 25 µl volume comprising 0.3 µM primers, 2.5 mM $MgCl_2$, 200 µM each dNTP, 10X Ex Taq buffer (20 mM Tris-HCl pH 8.0, 100 mM KCl, 0.1mM EDTA, 1mM DTT, 0.5% Tween 20, 05% Nonidet P-40, 50% Glycerol), 0.25 U TaKaRa Ex Taq (Takara, Mountain View, CA), and 50–100 ng template DNA. The reaction mixture was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio), and bi-directionally Sanger sequenced using BigDye® Terminator chemistry on an ABI 3730xl genetic analyzer (Applied Biosystems®, Life Technologies, Grand Island USA) at Retrogen Inc. Custom DNA Sequencing Facility (San Diego USA).

DNA sequences were edited using Geneious® Pro v. 6.1.7 (Biomatters Ltd Auckland, New Zealand. Available at http://www.geneious.com). The edited sequences were translated to amino acids and aligned with corresponding NADH2 sequences from representatives of closely related species using the MAFFT module within the Geneious Package (Biomatters Ltd Auckland, New Zealand). The aligned amino acid sequences were translated back, but in frame, to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1044 nucleotides long. Maximum Likelihood Tree was estimated from the data set using the GTR+I+G model. A bootstrap analysis was run separately under the same model conditions to estimate support for each of the nodes in the ML tree. All phylogenetic analyses were carried out using the software package PAUP*4.0 version a148. The distribution map was generated in QGIS (QGIS Development Team, 2016) using Google Earth base layers.

Apristurus yangi n.sp.

Yang's Longnose Catshark
Figs 1–9; Table 1

Holotype. ASIZ P0080718, adult female 437 mm TL, Vitiaz Strait, Morobe Province, Papua New Guinea, 06°02.030' S, 147°37.490' E, 700–701 m depth, station number CP3723, 7 Oct 2010.

Paratype. NTUM 11491 (tissue accession GN17228), female 205 mm TL, northwest of Kavieng, New Ireland, Papua New Guinea, 02°20' S, 150°38' E, 630–786 m depth, station number CP4428, 29 Aug 2014.

TABLE 1. Morphometrical measurements of the holotype (ASIZ P0080718) and paratype (NTUM 11491) of *Apristurus yangi* n.sp., and the second known specimen of Apristurus nakayai (NTUM 11488), expressed as a percentage of total length.

	A. yangi		*A. nakayai*
	Holotype	Paratype	n = 1
TL (mm)	437	205	559
PreD2-origin length	60.0	53.4	62.1
PreD2-insertion length	65.4	59.0	68.5
PreD1-origin length	48.7	43.4	47.4
PreD1-insertion length	53.1	48.3	52.6
Head length	23.8	23.5	22.1
Pre-branchial length	20.9	21.5	16.9
Pre-spiracular length	16.4	17.2	11.9
Pre-orbital length	12.6	12.9	7.8
Pre-outer nostril	7.3	7.0	4.5
Pre-inner nostril	9.5	10.1	6.4
Pre-oral length	12.4	12.7	8.1
PreP1 length	23.5	22.3	21.4
PreP2 length	39.7	33.6	37.2
Pre-vent length	44.9	41.0	41.9
Preanal length	52.6	44.9	47.4
Precaudal length	67.7	61.5	69.2
Head height	6.8	5.7	8.9
Head width (mouth corners)	8.6	9.7	9.8
Head width (max)	9.2	10.9	10.1
Mouth width	7.9	8.6	8.3
Mouth length	2.6	2.4	2.6
Internarial width	3.6	4.2	3.4
Upper labial furrow lendth	3.7	3.8	2.9
Lower labial furrow lendth	2.5	3.2	2.1
Orbit length	3.4	3.5	3.3
Orbit height	0.9	1.2	0.9
Nostril width	3.1	3.6	3.2
Nostril-mouth	2.9	2.7	1.7
Interorbital width	5.8	6.7	5.6
1st gill height	1.4	1.5	1.5
3rd gill height	1.9	1.6	1.4
5th gill height	1.4	1.8	1.5
Intergill width	3.4	2.2	4.2
D1-D2 space	6.4	5.2	9.5
D1-D2 origins	11.4	9.8	14.3
D1-D2 insertions	12.3	10.7	15.8
P1-P2 space	9.7	7.2	8.4
P1 tip to P2 origin	2.7	2.4	2.1
P1-P2 origins	16.1	12.8	16.7

.....continued on the next page

TABLE 1. (Continued)

	A. yangi		*A. nakayai*
	Holotype	Paratype	n = 1
P1-P2 insertions	17.6	13.6	16.1
P2-anal space	4.0	3.2	7.9
P2-anal origins	11.3	9.4	15.2
Anal-caudal space	0.7	1.0	0.0
D1 length	8.0	7.8	7.2
D1 base length	4.3	4.4	5.0
D1 height	1.7	1.7	1.6
D1 free lobe length	3.4	2.9	2.5
D2 length	9.3	9.3	9.7
D2 base length	6.6	5.8	6.7
D2 height	2.5	2.2	2.8
D2 free lobe length	4.1	4.4	3.1
P1 base length	8.3	7.1	8.5
P1 anterior margin	12.7	10.5	13.1
P1 posterior margin	9.1	6.3	8.7
P1 inner margin	4.5	5.6	5.8
P2 anterior margin	5.1	4.7	5.0
P2 length	10.0	8.7	10.5
P2 base length	8.6	7.6	8.3
P2 posterior margin	6.4	–	6.5
P2 inner margin	1.7	2.1	3.7
Anal base length (ceratotrichia)	14.9	15.4	16.7
Anal base length (muscle)	16.2	16.8	22.0
Anal anterior margin	5.5	6.0	6.6
Anal posterior margin	11.0	11.0	12.3
Anal height (muscle)	2.7	4.0	4.9
Anal inner margin	0.7	0.8	0.9
Caudal peduncle height	4.4	3.8	4.3
Caudal length	31.1	36.1	31.2
Caudal height	7.5	7.4	8.9
Caudal preventral margin	9.2	11.4	10.1
Caudal postventral margin	19.3	24.3	16.6
Caudal terminal lobe width	2.2	2.6	3.6
Caudal terminal lobe length	5.4	5.9	6.1
Clasper outer length	–	–	4.8
Clasper inner length	–	–	6.3
Clasper width	–	–	2.0

Diagnosis. A long-snouted *Apristurus* with the following combination of characters: long and narrow head, head length 23.5–23.8% TL, interorbital space 5.8–6.7% TL; snout very elongate, preoral length 12.4–12.7% TL, preorbital length 12.6–12.9; mouth wide, its width 7.9–8.6% TL; pelvic–anal space 3.2–4.0% TL; anal fin relatively large, base length 14.9–15.4% TL; anal-fin posterior margin 11.0% TL; prepectoral length relatively long, about 22.3–23.5% TL; labial furrows long, not confined to mouth corners, uppers 3.7–3.8% TL; no enlarged

denticles on upper or lower caudal fin; duodenum of intestine very short, 8 intestinal spiral valves; tip of snout blackish; 32–33 monospondylous centra; 38 precaudal-diplospondylous vertebrae; precaudal centra 70–71; females adult by 437 mm TL; egg case small (~5.9 cm long), with faint longitudinal striations.

FIGURE 1. Lateral view of *Apristurus yangi* **n.sp.**: (A) holotype ASIZ P0080718, adult female 437 mm TL; (B) paratype NTUM 11491, female 205 mm TL.

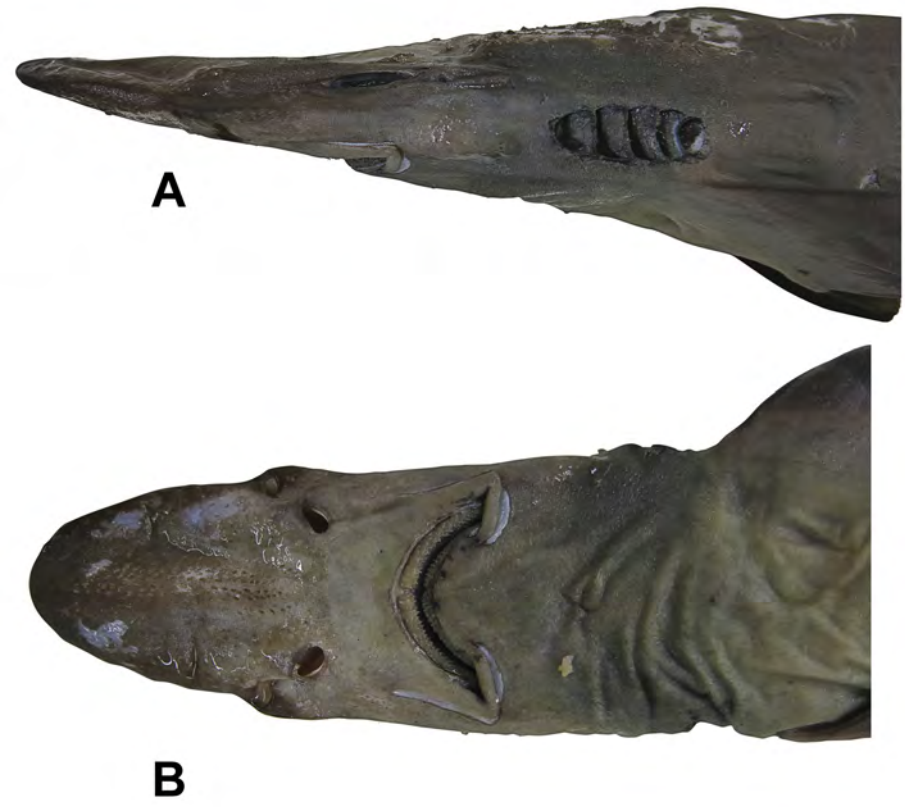

FIGURE 2. Head of *Apristurus yangi* **n.sp.**, holotype (ASIZ P0080718, adult female 437 mm TL); (A) lateral view; (B) ventral view.

FIGURE 3. Dentition of *Apristurus yangi* **n.sp.**, holotype (ASIZ P0080718, adult female 437 mm TL).

FIGURE 4. Dermal denticles of *Apristurus yangi* **n.sp.**, holotype (ASIZ P0080718, adult female 437 mm TL).

Description. Body anterior to pelvic fins slender and cylindrical; height and width of body at the middle point of P1–P2 space almost equal (Fig. 1). Abdomen narrow; P1–P2 space 9.7% TL in holotype (7.2% TL in paratype) much less than preorbital length, i.e. 12.6 (12.9)% TL and anal-fin base 14.9 (15.4)% TL. Posterior part of body compressed laterally; its width about half of its height. Snout extremely long and flattened dorsoventrally (Fig. 2), pre-outer nostril length less than mouth width, i.e. 7.3 (7.0) vs. 7.9 (8.6)% TL), and 2.0 (1.6) times internarial

width. Preoral length 3.4 (3.0) times internarial width, 4.7 (5.3) times mouth length, and 2.1 (1.9) times interorbital width. Preorbital length 2.2 (1.9) times interorbital width, 3.7 (3.7) times orbit length.

Nostril relatively large, expanding obliquely inward from snout edge; nostril width (0.9) 0.8 times internarial width, and subequal to orbit length. Mouth broadly rounded, width 3.0 (3.6) times mouth length; mouth length 0.7 (0.6) times upper labial furrow length. Upper labial furrows long, 1.5 (1.2) times lower furrows. Orbit large, its length subequal to nostril length, 0.6 (0.5) times interorbital width. Subocular fold present, but not conspicuous. Spiracle small, located just behind eye and about level with middle of eye. Five small gill slits; edges of gill septa and gill slits blackish; gill slits about equal in height, 5th situated above pectoral-fin base. Gill septa likely covered with numerous dermal denticles except posteriormost margins (denticles largely worn off in holotype).

FIGURE 5. Egg capsule of *Apristurus yangi* **n.sp.** taken from holotype (ASIZ P0080718, adult female 437 mm TL). Egg capsule length 59 mm.

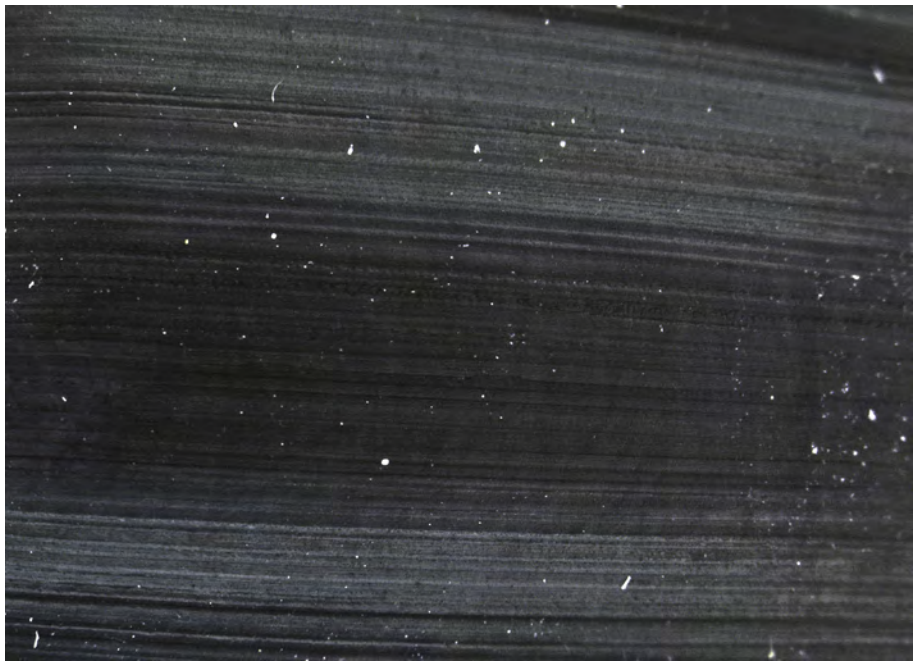

FIGURE 6. Surface of egg capsule of *Apristurus yangi* **n.sp.** extracted from holotype (ASIZ P0080718, adult female 437 mm TL).

Pectoral fin relatively large, broad, expanding laterally; anterior margin 1.3 (1.5) times P1–P2 space; its posterior tip extending to about an orbit length in front of pelvic-fin origin. Pelvic-fin origin located at mid-point between pectoral-fin insertion and anal-fin origin. Pelvic fin small, low, length subequal to P1–P2 space. Anal fin low, its height subequal to nostril length, base length 1.3 (1.6) times pectoral-fin anterior margin, 6.1 (4.2) times its height; its origin about an orbit length behind pelvic-fin insertion.

First dorsal fin located above pelvic–anal interspace; its origin just posterior to pelvic-fin insertion. First dorsal fin small, its height 0.7 (0.8) times second dorsal-fin height. Anterior margins of dorsal fins slightly convex; D1–

D2 space subequal to second dorsal-fin base length. Second dorsal-fin insertion anterior to anal-fin insertion. Caudal fin long, without distinctively enlarged modified denticles on dorsal edge; ventral lobe high and its apex somewhat angular.

Tooth rows on upper jaw 67 (52), on lower jaw 59 (56). Teeth on upper jaw possessing 5 or 7 cusps, either 2–1–2 or 3–1–3 arrangement; 3rd tooth from the symphysis with long central cusp, almost twice length of adjacent cusp; cusps becoming slightly posteriorly projecting from about 10th tooth from symphysis (posteriorly directing in anteriormost teeth also in smaller paratype). Teeth on lower jaw with 5–9 cusps, mostly 7 anteriorly; posteriormost teeth with numerous cusps in maple leaf-like outline (often with 9 cusps), its central cusp not conspicuously elongated. Number of tooth cusps on lower jaw usually more than those on upper jaw when compared at same position.

Denticles from dorsolateral side of body closely spaced, overlapping, leaf-like in shape with 3 cusps, central cusp about half length of crown (Fig. 4); each cusp sharp and pointed with weak ridges on its dorsal surface; outer surface of denticles completely structured by reticulations. No modified or enlarged dermal denticles on the dorsal margin of caudal fin.

Single egg capsule from holotype: 59 mm long and 14 mm wide, narrow, cylindrical, without coiled tendrils on anterior and posterior ends (Fig. 5); anterior margin of the capsule truncated without projection at each corner; weak neckline constriction located anteriorly at about one quarter of length down capsule; lateral edges flanged, fused at posterior end; posterior tip forming narrow tubule tapering toward its end. Surface of egg capsule relatively smooth to touch, but with longitudinal striations clearly visible under magnification (Fig. 6). Colour brownish, eggs taken from oviduct covered with fibrous substance. Respiratory slits at anterior-left and posterior-left side of the capsule; slits covered by thin membrane extended from edge.

Monospondylous centra 32 (33); precaudal diplospondylous centra 38 (38); precaudal centra 70 (71); caudal centra 58 (~61); total centra 128 (~132). Holotype with 8 intestinal spiral valves.

Colour. Colour in alcohol uniformly pale brownish; dorsal side of body a slightly darker than ventral side. Margin of snout tip blackish (more distinct in juvenile paratype). Fins anterior margins darker, most obvious on pectoral fins. Axils of dorsal, pectoral and pelvic fins naked with blackish coloration. Inside of buccal cavity dark blackish brown, without denticles.

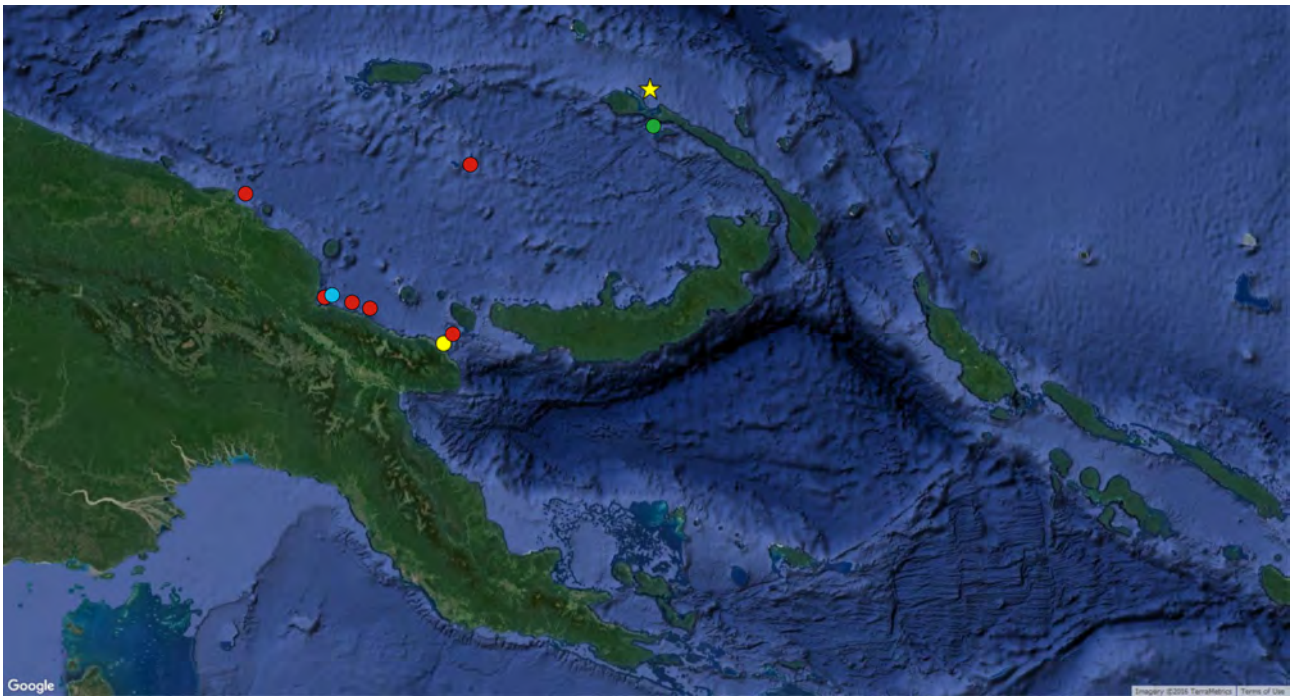

FIGURE 7. Distribution of *Apristurus* species collected in Papua New Guinean waters. Yellow star and circle denotes *A. yangi* holotype and paratype, respectively; red denotes *A. macrostomus* specimens; green *A. nakayai*; and blue the unidentified short snouted species (Image © NASA, TerraMetrics, Google Earth).

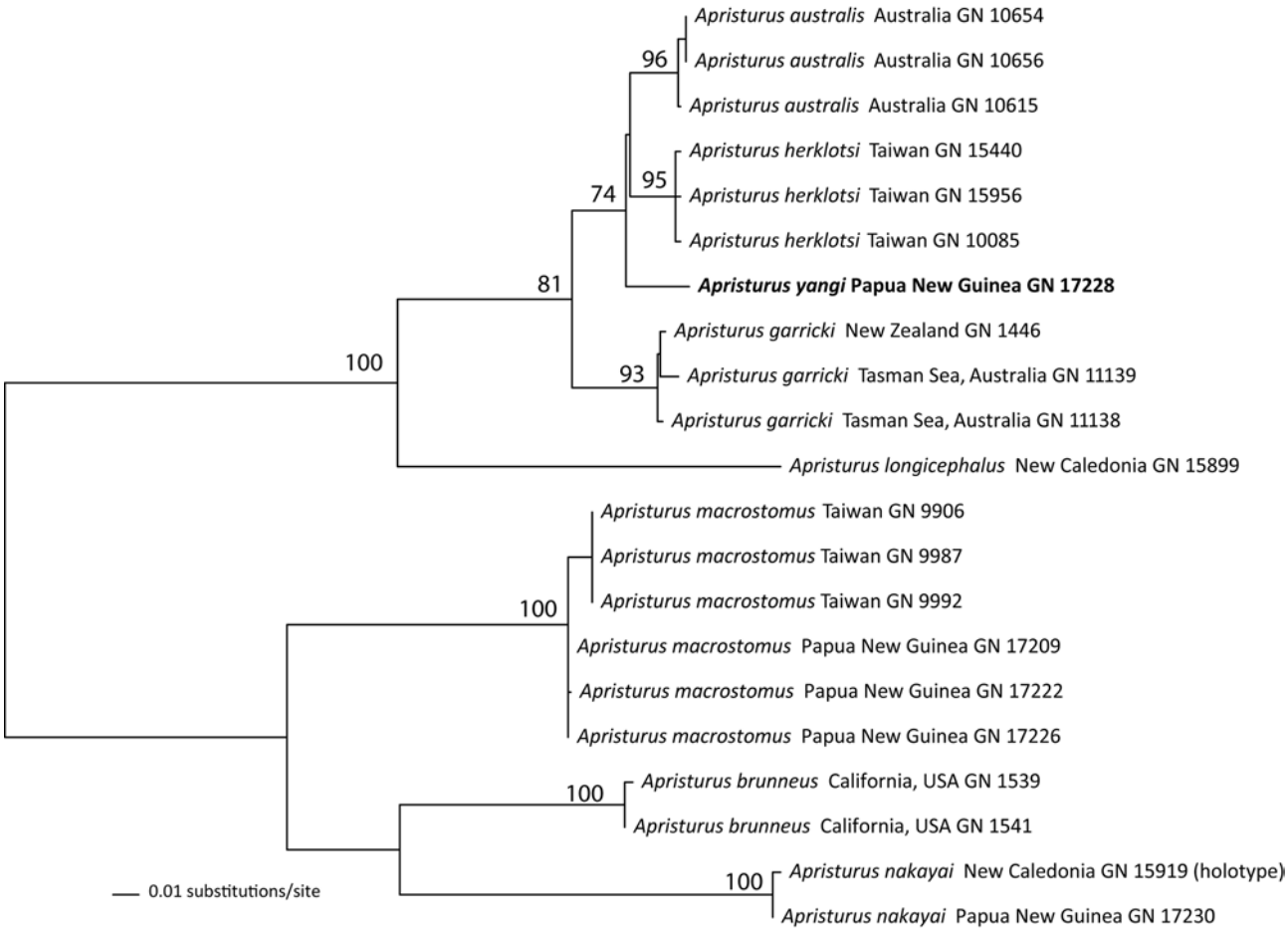

FIGURE 8. Maximum Likelihood Tree under GTR +I +G mode using 1044 aligned sites from the mitochondrial NADH2 gene. Bootstrap support values shown on internal branches when above 50%.

Size and biology. Only known from the two female type specimens, 437 and 205 mm TL. The 437 mm TL holotype was a pregnant female containing a single egg capsule. The holotype contained a single, 73 mm SL lanternfish of the genus *Myctophum*.

Distribution. Type specimens collected from off Kavieng, New Ireland and from the Vitiaz Strait in Morobe Province of Papua New Guinea in depths of 630 to 786 m (Fig. 7).

Etymology. Named for Dr Lei Yang whose extensive molecular phylogenetic work on sharks and rays has contributed toward an improved understanding of their alpha taxonomy and phylogenetic relationships.

Molecular analysis. The analysis of the NADH2 data for the paratype (holotype tissue sample not available) suggests that *Apristurus yangi* represents a monophyletic lineage that is distinct from, but most closely related to *Apristurus herklotsi* from off Taiwan and *Apristurus australis* from off Australia (Fig. 8). These three species are, in turn, sister to *A. garricki* from New Zealand. *Apristurus longicephalus* lies outside this group of four species and together these five species represent the *longicephalus* group within the genus *Apristurus* (Fig. 8). It should be noted that this inference is based on a single mitochondrial marker and inclusion of multiple nuclear markers could affect the presented inference.

Discussion

***Apristurus yangi* comparisons.** The description given herein would be improved greatly with additional material from different sexes and sizes classes. However, obtaining deepwater shark and ray material from Papua New Guinean waters is difficult and opportunities to obtain additional material are extremely limited. Given the dearth of information on the deepwater shark and ray fauna of Papua New Guinea, we considered it important to describe and document this species based solely on the two specimens available.

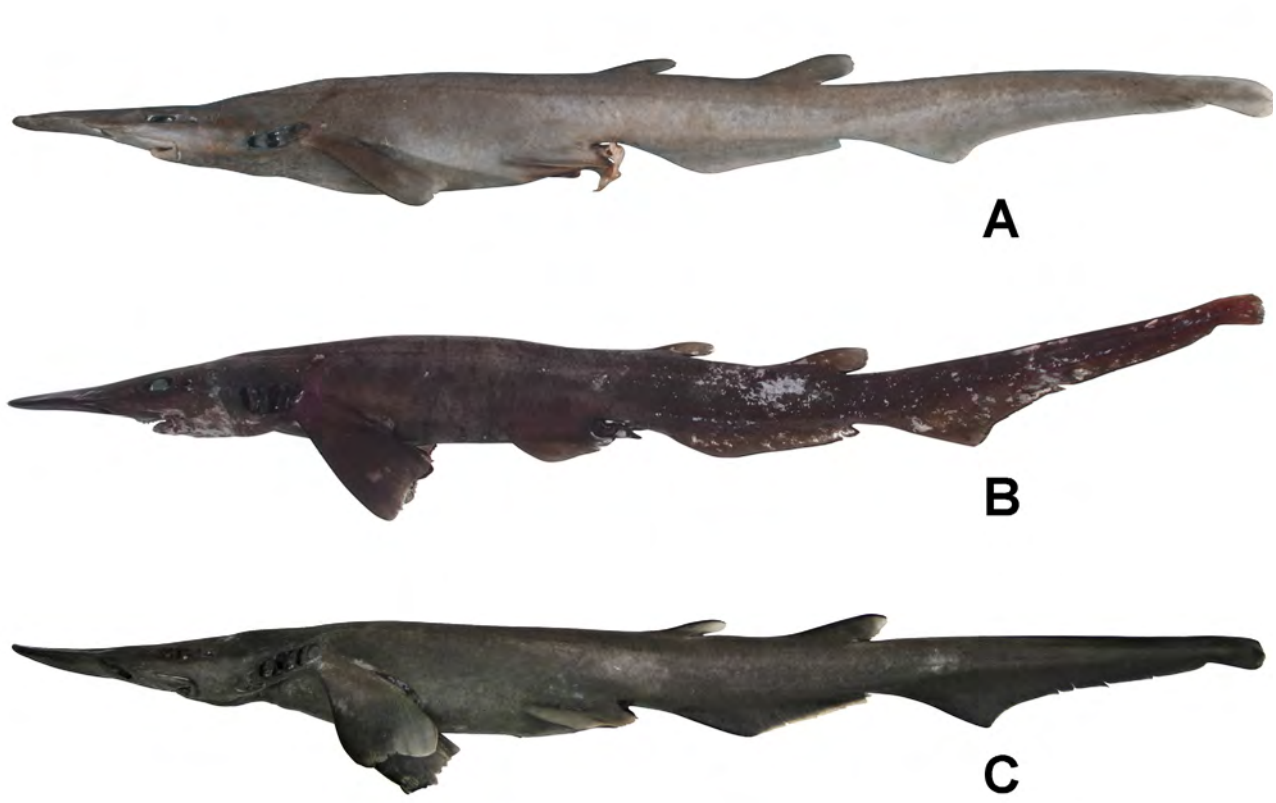

FIGURE 9. Lateral view of: (A) *Apristurus australis* (CSIRO H 2356-01, male 530 mm TL); (B) *Apristurus garricki* (CSIRO H 6067-01, adult male 650 mm TL); (C) *Apristurus herklotsi* (NMMB-P HO-198, female 475 mm TL).

Apristurus yangi **n.sp.** can be easily placed into the *longicephalus*-group of *Apristurus* based on its very long snout with the pre-outer nostril length longer than interorbital width (see Sato *et al*., 2013). *Apristurus longicephalus* differs from *A. yangi*, *A. australis*, *A. garricki* and *A. herklotsi* in having a blackish naked area on ventral side of the abdomen (vs. no blackish naked area); a long duodenum (vs. a very short duodenum); and 13–16 spiral valves (vs. <13 spiral valves) (Sato *et al.*, 2013). This accords with the molecular tree with *A. australis*, *A. garricki*, *A. herklotsi* and *A. yangi* all forming a distinct group well separated from *A. longicephalus* (Fig. 8).

Apristurus yangi differs from *A. garricki* (Figs 9b, 10b) in having a wider mouth (mouth width 7.9–8.6 vs. 6.1–7.5% TL); larger eyes (orbit length 3.4–3.5 vs. 2.2–2.9% TL); wider internarial space (3.6–4.2 vs. 2.8–3.6% TL); fewer monospondylous centra (32–33 vs. 34–37); fewer intestinal spiral valves (8 vs. 11–13); teeth smaller and more numerous (upper jaw with 52–67 vs. 37–50 teeth) and a slightly taller first dorsal fin (height 1.7 vs. 0.7–1.5% TL). The new species is also substantially smaller with the female holotype mature at 437 mm TL, whereas females of *A. garricki* below 504 mm TL are immature, adolescent between 560–574 mm TL and mature over 674 mm TL (Sato *et al.*, 2013).

Apristurus yangi differs from *A. australis* (Figs 9a, 10a) in having a wider mouth (mouth width 7.9–8.6 vs. 5.2–8.0% TL); wider internarial space (3.4–3.5 vs. 2.6–3.4% TL); more precaudal-diplospondylous centra (38 vs. 31–36). It differs from *A. herklotsi* (Figs 9c, 10c) in having more precaudal diplospondylous centra (38 vs. 32–35); a broader prenarial snout (see Figs 9c, 10c); and a paler coloration, particularly ventrally.

The egg capsules provide another useful diagnostic feature for this group. *Apristurus herklotsi* has the smallest egg capsules (44.6 mm long, 12.9 mm wide from a 489 mm TL female) (Sato *et al.*, 2013). Despite its smaller size, the 437 mm TL holotype of *A. yangi* possessed a larger egg capsule (59 mm long, 14 mm wide). Both of these egg capsules are substantially smaller than those recorded from *A. australis* (78.6 mm long, 17.2 mm wide from a 530 mm TL female) and *A. garricki* (74.3 mm long, 19.4 mm wide from a 674 mm TL female) (Sato *et al.*, 2008, 2013). The surfaces of the egg capsules from *A. australis* and *A. garricki* have distinct longitudinal striations whilst those

from *A. herklotsi* are smooth and without striations while those from *A. yangi* are smooth with inconspicuous longitudinal striations (Fig. 6; fig. 9 in Sato *et al.*, 2013).

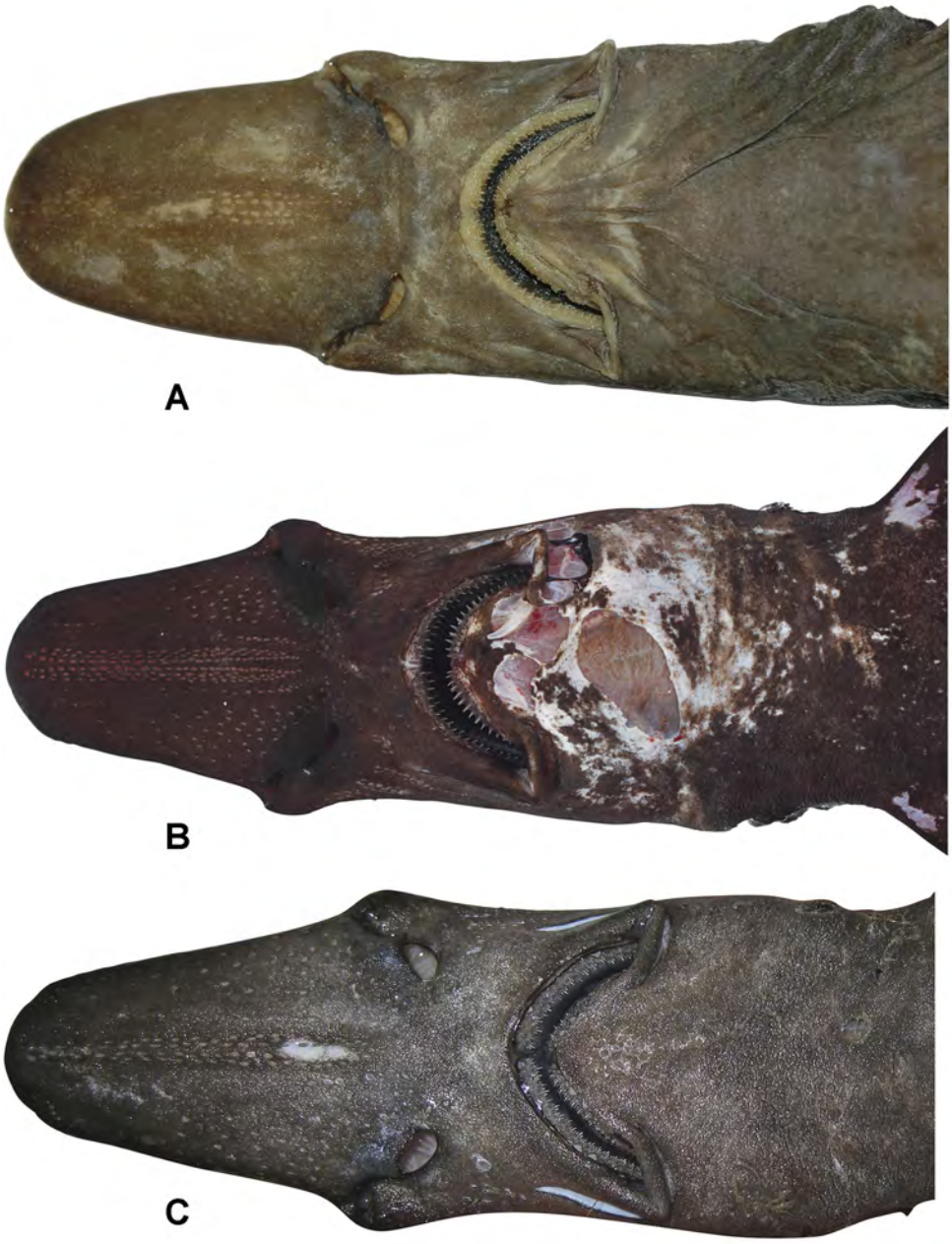

FIGURE 10. Ventral head view of: (A) *Apristurus australis* (CSIRO H 953-07, adult male 616 mm TL); (B) *Apristurus garricki* (CSIRO H 6067-01, adult male 650 mm TL); (C) *Apristurus herklotsi* (NMMB-P HO-198, female 475 mm TL).

Other *Apristurus* species occurring in Papua New Guinea. Prior to the deepwater surveys of Papua New Guinea between 2010 and 2014, no *Apristurus* species were known from the area. This study confirms the presence of four species of *Apristurus* from Papua New Guinean waters.

Most specimens (n = 7) collected were identified as *Apristurus macrostomus* (K. Nakaya, pers. comm.; Figs 11a, 12a) which was also confirmed with molecular data (Fig. 8). This species is known from Japan and Taiwan and south to Sumatra in Indonesia (Nakaya & Kawauchi, 2013). The specimens from Papua New Guinea ranged in size from 257 to 485 mm TL. *Apristurus macrostomus* belongs to the *brunneus*-group and is characterised by the

following combination of characters: first dorsal fin smaller than second dorsal fin; upper labial furrows longer than lowers; first dorsal-fin origin anterior to midpoint of pelvic- and anal-fin bases; pectoral-fin tip extending posterior of midpoint of P1–P2 space; abdomen short; mature at about 40 cm TL; intestinal spiral valves 18–21; monospondylous centra 33–37; precaudal diplospondylous 31–40 (Nakaya & Kawauchi, 2013).

A single specimen of *Apristurus nakayai* was also recorded (NTUM 11488, Figs 11b, 12b), which represents only the second known specimen of this species. Molecular data also confirms the identification of this species with a near identical NADH2 sequence to the holotype of *A. nakayai* from New Caledonia (Fig. 8). This specimen was an adult male of 559 mm TL caught off the Kavieng district of New Ireland in the Bismarck Sea (see Fig. 7). *Apristurus nakayai* belongs to the *brunneus*-group and is characterised by the following combination of characters: shiny white iris (when fresh, Fig. 13); brownish black in colour; first dorsal fin much smaller than second dorsal fin; upper labial furrows longer than lowers; first dorsal-fin origin about opposite midpoint of pelvic- and anal-fin bases; abdomen short; males mature at less than 56 cm TL; intestinal spiral valves 16; monospondylous centra 36; precaudal diplospondylous 37 (Iglésias, 2012).

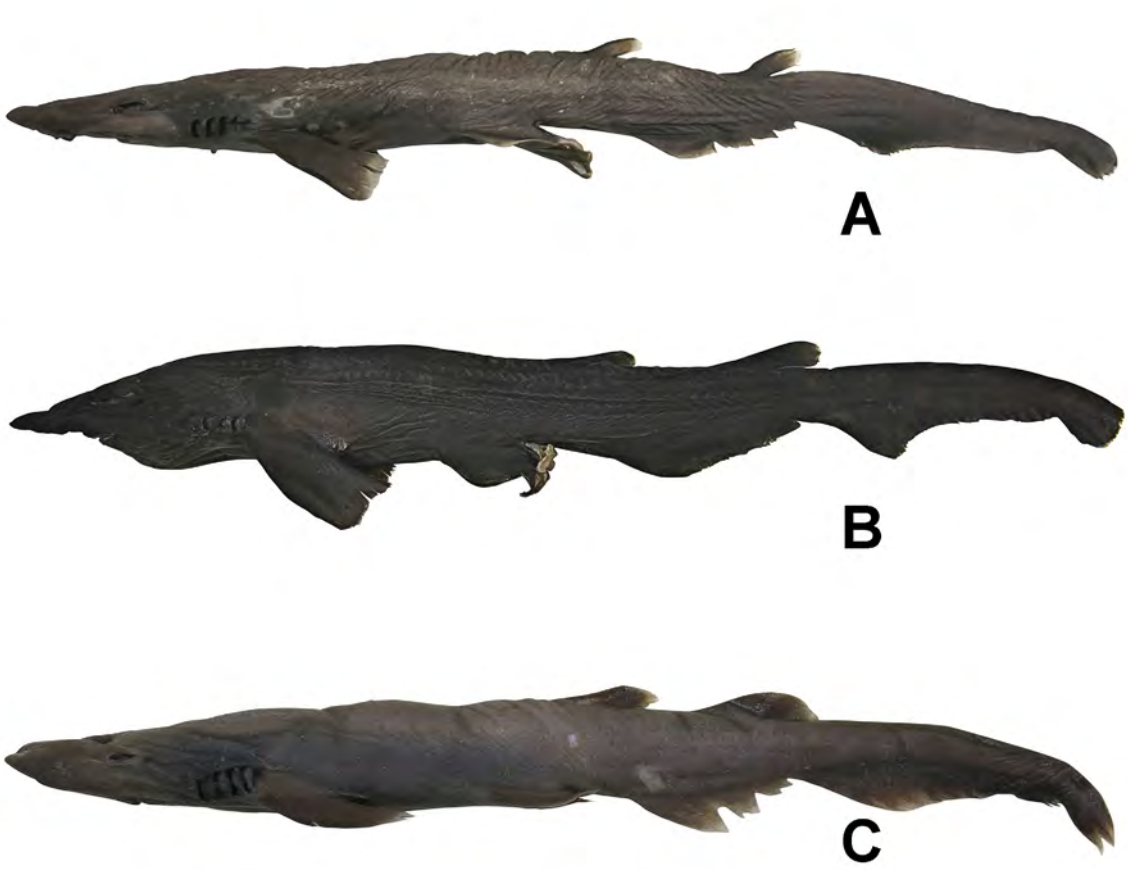

FIGURE 11. Lateral view of: (A) *Apristurus macrostomus* (NTUM 10319, adult male 377 mm TL); (B) *Apristurus nakayai* (NTUM 11488, adult male 559 mm TL); (C) *Apristurus* sp. 1 (PNG short snout) (ASIZ P0080719, juvenile male 250 mm TL).

A single specimen of a short snouted *Apristurus* (ASIZ P0080719) was also recorded from Astrolabe Bay in Madang Province (Figs 11c, 12c) but its specific identity was not determined. Unfortunately no genetic sample was taken from the fresh specimen prior to formalin fixation. Juvenile specimens of *Apristurus* are difficult to identify in the absence of adult characters or DNA sequence data so more specimens of this species are required to determine the species involved. It belongs to the *brunneus*-group based on the following characters: snout wide and short (pre-outer nostril length 3.9% TL); intestinal spiral valves 14 or 15; upper labial furrows longer than lower furrows. This specimen differs from similar-sized *A. macrostomus* in having a shorter prenarial snout (pre-outer nostril length 3.9% TL vs. 6.3% TL in a 257 mm TL *A. macrostomus*) and a more depressed and wider head (interorbital width 8.9 vs. 6.7% TL). It also has less intestinal spiral valves than *A. macrostomus* (14 or 15 vs. 18–

21). Morphologically, it closely resembles *Apristurus gibbosus* Meng, Zhu & Li 1985 from the Northwest Pacific, but differs in having a much shorter P1–P2 space (9.9 vs. 12.9–18.0% TL) and wider internarial space (4.3 vs. 3.0–4.3% TL). Additional specimens, including adults, are required to enable more accurate identification of this species. It appears to be separable from the other three species occurring in Papua New Guinea and is assigned the temporary name *Apristurus* sp. 1 (PNG short snout).

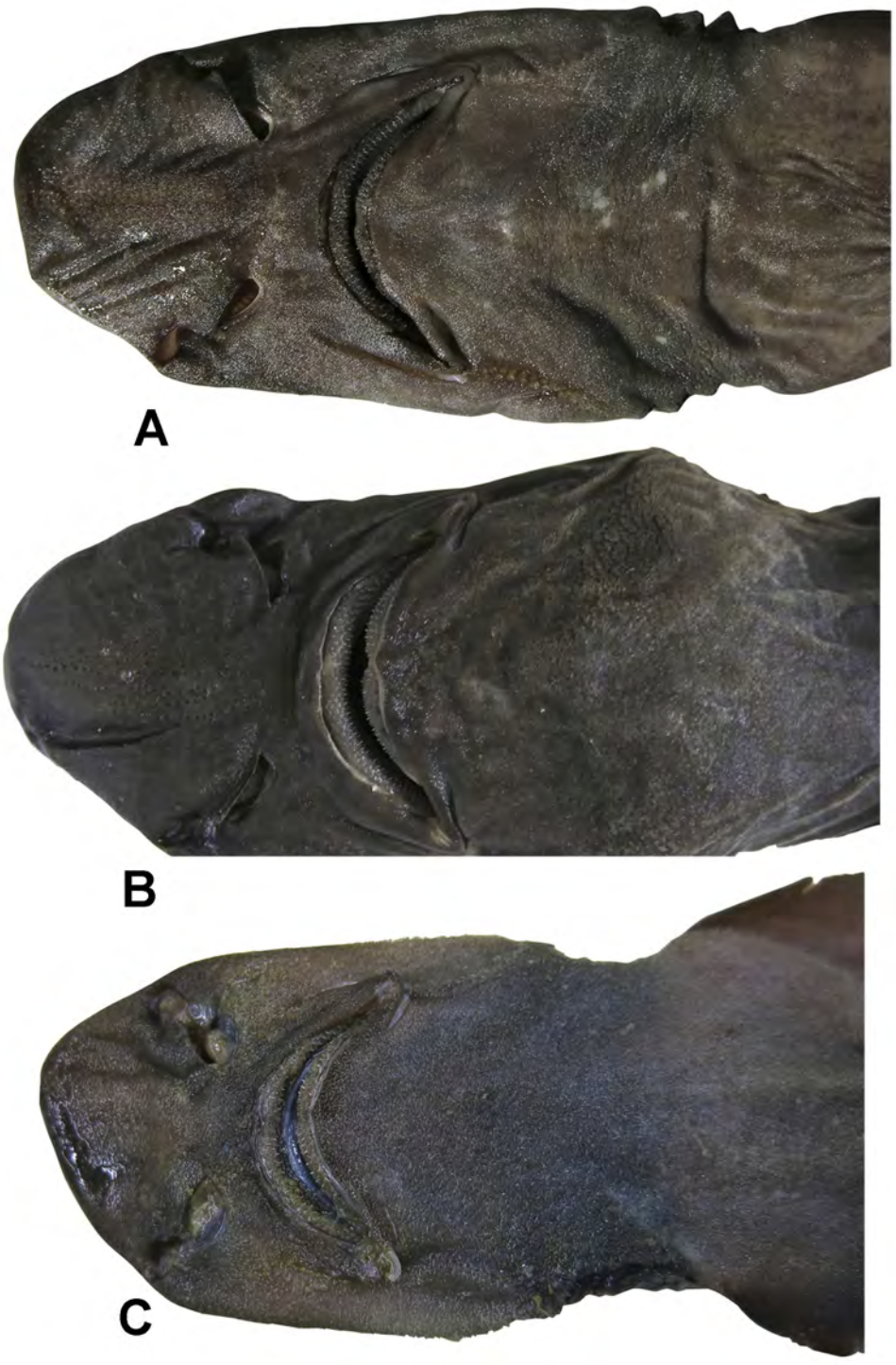

FIGURE 12. Ventral head view of: (A) *Apristurus macrostomus* (NTUM 10319, adult male 377 mm TL); (B) *Apristurus nakayai* (NTUM 11488, adult male 559 mm TL); (C) *Apristurus* sp. 1 (PNG short snout) (ASIZ P0080719, juvenile male 250 mm TL).

FIGURE 13. Lateral head view of *Apristurus nakayai* (NTUM 11488, adult male 559 mm TL) highlighting the distinctive white iris of this species when fresh.

Comparative material

Apristurus australis: CSIRO H 953–07 (holotype), male 616 mm TL, east of Sydney, New South Wales, 33°44–43′ S, 151°53–54′ E, 486–509 m, 18 Dec 1985; CSIRO H 616–01 (paratype), male 535 mm TL, CSIRO H 616–04 (paratype), male 530 mm TL, CSIRO H 616–05, male 558 mm TL, CSIRO H 1287–01 (paratype), male 528 mm TL, CSIRO H 1287–04 (paratype), female 521 mm TL, northeast of Whitsunday Group, Queensland, 19°00′ S, 150°37′ E, 751–752 m, 24 Nov 1985; CSIRO H 860–02 (paratype), female 531 mm TL, east of St. Patrick's Head, Tasmania, 41°36′ S, 148°41′ E, 900–930 m, 06 Aug 1987; CSIRO H 1201–09 (paratype), female 555 mm TL, off Houtman Abrolhos Islands, Western Australia, 29°05′ S, 113°41′ E, 880 m, Feb 1988; CSIRO H 1228–01 (paratype), male 467 mm TL, CSIRO H 1228–02 (paratype), male 543 mm TL, east of St Patricks Head, Tasmania, 41°38′ S, 148°42′ E, 980– 1020 m, 07 Aug 1987; CSIRO H 1229–01 (paratype), female 575 mm TL, CSIRO H 1229–02 (paratype), male 575 mm TL, east of Nowra, New South Wales, 34°53′ S, 151°14′ E, 891–909 m, 11 Apr 1984; CSIRO H 1240–01 (paratype), female 560 mm TL, west of Lihou Reef and Cays, Queensland, 17°03′ S, 150°51′ E, 606–610 m, 06 Dec 1985; CSIRO H 1285–02 (paratype), female 504 mm TL, north of Lihou Reef & Cays, Queensland, 16°54′ S, 151°31′ E, 880 m, 06 Dec 1985; CSIRO H 1286–02 (paratype), male 542 mm TL, Marion Plateau, north-east of Whitsunday group, Queensland, 18°54′ S, 150°25′ E, 1005–1013 m, 25 Nov 1985; CSIRO H 1539–02 (paratype), female 528 mm TL, east of Brush Island, New South Wales, 35°26′ S, 150°54′ E, 900–921 m, 19 May 1988; CSIRO T 459 (paratype), female 562 mm TL, off Bicheno, Tasmania, ca. 42° S, 148° E, 1000 m, 26 Jul 1982; CSIRO H 2356–01, male 530 mm TL, west of Shark Bay, Western Australia, 26°44′ S, 112°19′ E, 735 m, 28 Dec 1989.

Apristurus garricki: CSIRO H 6063–01, female 653 mm TL, Wanganella Bank, Norfolk Ridge, 32°35.67′ S, 167°44.12′ E, 698–719 m, 29 May 2003; CSIRO H 6067–01, adult male 650 mm TL, Wanganella Bank, Norfolk Ridge, 32°35.22′ S, 167°47.66′ E, 1025–1052 m, 30 May 2003; CSIRO H 7389-01, male 729 mm TL, NW Challenger Plateau, Southern Lord Howe Rise, 37°29.50' S, 167°46.40' E, 880–884 m, 26 Jan 1981.

Apristurus herklotsi: CSIRO H 5611-02, female 315 mm TL, Da-xi, 01 Aug 2000; CSIRO H 6292-11, female 458 mm TL, Da-xi, 21 May 2005; CSIRO H 6294-23, female 477 mm TL, , CSIRO H 6294-24, juvenile male 392 mm TL, Da-xi, 23 May 2005; NMMB-P HO-198, female 475 mm TL, Da-xi, 15 Mar 2012.

Apristurus longicephalus: CSIRO H 1204-1, male 385 mm TL, Ashmore Terrace, south of Roti Island, Western Australia, 13°06′ S, 122°18′ E, 900–1000 m, January 1988; CSIRO H 1291-1, adult male 500 mm TL, northeast of Whitsunday Island group, Marian Plateau, Queensland, Australia, 18°59.1′ S, 150°32.6′ E, 879–886 m, 24 Nov 1985; CSIRO H 2549-08, 507 mm TL, west of North West Cape, Western Australia, 21°50.6′ S, 113°46.7′ E, 685–650 m, 24 January 1991.

Apristurus macrostomus: ASIZ P unreg (2 specimens), adult male 422 mm TL, adult male 449 mm TL, Vitiaz

Strait, Morobe, Papua New Guinea, 05°57.190' S, 147°37.440' E, 860–880 m, station number CP3724, 7 Oct 2010; ASIZ P unreg, adult male 485 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05°24' S, 145°50.550' E, 760–875 m, station number CP3716, 6 Oct 2010; NTUM 10319 (tissue accession GN17209), adult male 377 mm TL, Broken Water Bay, Madang, Papua New Guinea, 03°52' S, 144°41' E, 600–800 m, station number CP4043, 18 Dec 2012; NTUM 10320 (tissue accession GN17193), female 257 mm TL, Wab Bay, Madang, Papua New Guinea, 05°34' S, 146°23' E, 802–875 m, station number CP3989, 8 Dec 2012; NTUM 11489 (tissue accession GN17222), adolescent male 400 mm TL, southeast of Manus Island, Papua New Guinea, 03°31' S, 148°03' E, 780–855 m, station number CP4250, 22 Apr 2014; NTUM 11490 (tissue accession GN17226), female 325 mm TL, southeast of Madang, Papua New Guinea, 05°28' S, 146°09' E, 760 m, station number CP4343, 8 May 2014.

Apristurus nakayai: NTUM 11488 (tissue accession GN17230), adult male 559 mm TL, south of Manne Island, New Ireland, Papua New Guinea, 02°48' S, 150°42' E, 672–1150 m depth, station number CP4480, 4 Sep 2014.

Apristurus sp. short snout: ASIZ P0080719, immature male 250 mm TL, Astrolabe Bay, Madang, Papua New Guinea, 05°22.530' S, 145°55.550' E, 851–865 m depth, station number CP3718, 6 Oct 2010.

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Title: Mixed-marker approach reveals varying levels of genetic connectivity in populations of Narrow Sawfish (*Anoxypristis cuspidata*) in Australia and Papua New Guinea.

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Key words: Narrow Sawfish Anoxypristis cuspidata, sawfish, genetics, sex-biased dispersal, Indo-Pacific

ABSTRACT

The Narrow sawfish (*Anoxypristis cuspidata*) belongs to the most endangered family of chondrichthyan fishes, the sawfishes (Pristidae). It has undergone significant declines in range and abundance due to anthropogenic activities including fishing and habitat destruction. Very little is known of adult movements within its entire distribution. In order to better manage and protect this threatened species, understanding habitat usage and behaviour is important. Using a combination of mitochondrial (Control Region (CR) and NADH dehydrogenase 4 (ND4)) and nuclear markers (microsatellites), this study identified the population structure of *A. cuspidata* in Australia and Papua New Guinea (PNG). Significant historic population structuring was found between the east Australian coast, Gulf of Papua and the Gulf of Carpentaria (F_{ST} = 0.082 , P = 0.000) , thought to be an artefact of the biogeographic barrier created by the Torres Strait land bridge. In contrast, no significant overall microsatellite differentiation was apparent (P = 1.000) however, microsatellite results require further investigation due to the low number of suitable markers available for the species. Nonetheless, given the endangered status and lack of knowledge for *A. cuspidata,* this study presents important baseline findings which may be used to facilitate management efforts.

INTRODUCTION

Sawfishes are a unique group of benthic rays consisting of five species separated into two genera; *Pristis* and *Anoxypristis* (Faria et al. 2013). Characterised by a large toothed rostrum, sawfish are commonly distributed in shallow coastal and estuarine environments of tropical and subtropical regions (Last & Stevens, 2009). All sawfish species have undergone significant declines in range and abundance due to anthropogenic pressures including fisheries exploitation, pollution (e.g. mining activity) and habitat loss (Simpfendorfer 2000, Seitz & Poulakis 2006, Dulvy, et al. 2014). As a result, sawfish have been identified as the most endangered family within the class Chondrichthyes (Dulvy et al. 2014). The declining global status of sawfish populations has led to all species being listed as either Endangered or Critically Endangered under the International Union for the Conservation of Nature Red list of Threatened Species (Carlson et al. 2013; D'Anastasi et al. 2013; Kyne et al., 2013a; Kyne et al. 2013b; Simpfendorfer 2013); included on Appendix I of the Convention on Trade in Endangered Species (Vincent et al., 2014) and recently included on Appendix I and II of the Convention on Migratory Species (CMS) (COP11, report Annex VII 2014). Sawfishes are protected nationally in Australia: three *Pristis* species are listed as Vulnerable under the Environmental Protection and Biodiversity Conservation Act (EPBC 1999) and no take restrictions are in place across all northern states. Australia is considered the last stronghold for sawfish (Morgan et al., 2011; Dulvy et al., 2016), with four of the five species found in northern waters (Last and Stevens 2009). Located adjacent to northern Australia, Papua New Guinea (PNG) is also considered to have populations of sawfish (Last & Stevens, 2009), although Dulvy et al. (2016) suggests *P. clavata* is extinct from PNG. Unlike Australia, PNG does not currently have protective measures in place to conserve sawfish and very little is known of their abundance or extent throughout the region.

The narrow sawfish *Anoxypristis cuspidata* is considered the most abundant member of the sawfish family in Australian waters (Peverell 2005) despite undergoing substantial global declines of >30% (Dulvy et al., 2014). Their abundance can be attributed to their life-history characteristics that include higher growth rates, increased fecundity (sexually mature at 2–3 years, breed annually) and shorter life expectancy (9 years) than other sawfish species (Dulvy et al., 2016). Narrow sawfish are usually found inshore, in depths <10m, but also to at least 40 m depth (Peverell 2005; Last and Stevens, 2009). *Anoxypristis cuspidata* use varying ecological niches depending on age, sex and season (Peverell 2005; Tobin et al., 2014) with adults more common in offshore waters at depths of ~40m, while juveniles and pregnant females are found in shallow inshore and estuarine habitats at depths of less than 15 m (Peverell 2005). Commercial net and trawl fishing often pose a risk as the frequency, locality and types of fishing gear used inadvertently target all sawfish size classes (Peverell 2005; Devitt et al., 2015). Moreover, juvenile and pregnant females are disproportionately vulnerable to habitat loss as a result of coastal anthropogenic pressures due to a strong reliance on shallow coastal environments as nurseries (Dulvy et al. 2016; Devitt et al. 2015).

In recent years our understanding of sawfish ecology in northern Australia has advanced considerably (Peverell 2005; Thorburn et al. 2007; D'Anastasi et al. 2010; Morgan et al. 2011; Phillips et al. 2011; Tobin et al. 2014). However, there still remains limited information regarding *A. cuspidata* population structure, sex-biased behaviours and use of nursery grounds. An absence of conventional tagging studies, (due to high post release mortality associated with tagging) (Devitt et al. 2015), highlights the importance of population genetic analyses to delineate population structure

(Simpfendorfer et al. 2016). Available ecological information is primarily for juvenile and sub-adult classes, because they are most commonly captured in fisheries (Peverell 2005; Tobin et al. 2014), however information on movement and connectivity of both juvenile and adult *A. cuspidata* remains unknown. Earlier genetic investigations using the mitochondrial DNA (mtDNA) Control Region gene identified distinct partitioning between an apparently single population in Western Australia and the Gulf of Carpentaria and a second population in eastern Australia (D'Anastasi et al. 2010). Additionally, genetic assessments of Australian populations of *A. cuspidata* found low genetic diversity linked to a recent bottleneck or founder effect, potentially facilitated by Pleistocene sea level fluctuations (D'Anastasi et al. 2010). To-date no ecological or genetic studies have been undertaken for *A. cuspidata* populations inhabiting the PNG region.

Establishing effective management for sharks and rays can be facilitated by understanding aspects of their biology, including behaviours specific to age and sex (Harry et al. 2011). Additionally, the identification of discrete areas where specific life stages may occur (e.g. nursery areas) can also help prioritise management efforts (Heupel et al. 2007). For *A. cuspidata* it is yet to be confirmed if behaviours exhibited by males and females differ. Often strong sex-biased behaviours have been reported in sharks and rays, where females display a level of residency or philopatry and males are more likely to migrate between regions (Chapman et al. 2015; Portnoy et al. 2015). These behaviours can be assessed using genetic tools (mitochondrial and nuclear DNA) when assessing population structure. Mitigating the effects of overexploitation posed by anthropogenic activities is paramount to ensure the survival of sawfish. Recently there have been a number of sawfish recovery and conservation plans announced with both global and Australia-wide focus (Department of Environment 2015; Harrison et al. 2014). Given the endangered status, limited knowledge and call for strategic conservation efforts, this study characterised the genetic connectivity and stock structure of *A. cuspidata* in northern Australia and the Gulf of Papua, PNG.

MATERIALS AND METHODS

Sampling

Fin clips from *A. cuspidata* were sourced from scientific sampling efforts and commercial fisheries between 2000 and 2015 from northern Australia and PNG (Figure 1). Due to the opportunistic nature of collection and the rarity of this species, sample sizes varied between locations.

Laboratory procedures

Genomic DNA (gDNA) was extracted from fin clips using either a modified salting-out method (Sunnucks & Hales 1996) or a Wizard® SV Genomic DNA purification system (Promega, USA). A portion of the mtDNA CR was amplified following D'Anastasi (2010), while the ND4 was amplified using primers ND4-F 5' TGACTACCAAAAGCTCATGTAGAAGC-3' and Leu-Scyliorhinus 5'-CATAACTCTTGCTTGGAGTTGCACCA-3' (Naylor et al., 2005). Polymerase Chain Reaction (PCR) was performed using 5uL 10X Buffer (Promega), 0.125µL Taq polymerase (Promega), 1.0mM $MgCl_2$, 0.5µL of primer (0.5µM), 0.5µM dNTP and 1µL (10-30ng/µL) DNA in 25µL volumes. PCR conditions included an initial denaturation at 94°C for 60 seconds, followed by a touchdown protocol with denaturation at 94°C for 60 seconds, annealing at 54°C for 30 seconds and extension at 72°C for 90

seconds across 5 cycles; the next 5 cycles were performed as stated above with an annealing temperature of 52°C and the final 25 cycles were as above, with an annealing temperature of 50°C. After a total of 35 cycles a final extension step was performed at 72°C for 5 minutes. PCR reactions were completed using either a Bio-Rad C1000 Thermal Cycler (Bio-Rad, Australia) or Applied Biosystem GeneAmp® PCR system 9700 (Life Technologies, Thermo Fisher Scientific). PCR products were sequenced bi-directionally using BigDye® Terminator v3.1 cycle sequencing chemistry (Life Technologies) as per manufacturer's recommendations. Cycle sequenced products were purified using the CleanSEQ kit (Beckman Coulter) and run on an ABI 3130XL AutoDNA sequencer (Life Technologies). Sequences were edited, aligned, and trimmed, with the CR and ND4 sequences concatenated using Geneious vR6.1 (Kearse et al. 2012).

Microsatellite markers were developed following the enrichment protocol of Glenn and Schable (2005). Genomic DNA from one individual was digested with RsaI and XmnI, and SuperSNX24 linkers were ligated onto the ends of the resulting fragments. Five biotinylated tetranucleotide probes [$(ACAT)_6$, $(AGAT)_8$, $(AACT)_8$, $(AAAT)_8$, $(AAGT)_8$] were hybridized to these fragments, and added to streptavidin-coated magnetic beads (Dynabeads®). Further microsatellite primer development can be found in the Supplementary Material.

We developed primers flanking core microsatellite repeats using Primer3 (http://frodo.wi.mit.edu/cgi-bin/primer3/primer3_www.cgi). Characterisation identified seven putative microsatellite markers. Of these, forward primers were synthesised, fluorescently labelled (FAM, NED, PET or VIC) and grouped into two multiplex reactions with four and three markers per multiplex (Table 1). Optimization included PCR in 10µL volumes containing 5µL 2X TYPE-IT master mix (Qiagen), 1µL multiplexed primers (10µM) and 1µL DNA (15-40ng). PCR thermal conditions included initial denaturation of 95°C for 5 minutes, a touchdown protocol with 5 cycles of 95°C for 30 seconds, 57°C for 90 seconds, 72°C for 30 seconds, followed by 5 cycles at 55°C annealing and a final 22 cycles at 53°C annealing. A final extension was performed at 60°C for 30 minutes. All PCR reactions were completed using a Bio-Rad C1000 Thermal Cycler (Bio-Rad). Sequence information for the microsatellite loci has been submitted to GenBank with Accession Numbers x-y??

Data Analysis

For the mtDNA analyses, number of haplotypes (H), haplotype diversities (*h*) and nucleotide diversities (π) were calculated in Arlequin v3.5 (Excoffier and Lischer 2010). A Minimum Spanning Tree (MST) was constructed using output data from Arlequin v3.5. Global tests for differentiation, AMOVA calculations and pairwise F_{ST} including accompanying *P*-values for regional locations were computed using Arlequin v3.5 (Excoffier et al., 2010). For all pairwise analyses, the initial significance level ($P<0.05$) was adjusted for simultaneous pairwise comparisons using a False Discovery Rate described in Narum (2006) to reduce the likelihood of type I errors.

Genetic diversity metrics for the microsatellite markers including, mean number of alleles (N_a), allele richness (A_R), observed and expected heterozygosities (H_o, H_e) and inbreeding coefficients (F_{IS}) calculated in the R- package diveRsity (Keenan et al. 2013). Hardy-Weinberg Equilibrium calculations and Linkage Disequilibrium (LD) was calculated in Genepop 4.0 (Rousset 2008) using the Markov chain algorithm, with a dememorization of 100,000 over 20 batches and 10,000 iterations per batch. The presence of null alleles and effects of allele drop out were evaluated in FreeNA (Chapuis & Estoup

2007). Estimates of global differentiation using F_{ST} and accompanying P-values were calculated in Arlequin v3.5.

RESULTS

A final mitochondrial sequence alignment containing 757bp (269bp fragment of CR and 488bp fragment of ND4, respectively) was analysed. Some samples from the North-West coast failed to amplify using the CR and ND4 mtDNA primers therefore sample size was reduced for mitochondrial results representing that region. Gulf of Papua, East coast and the Gulf of Carpentaria populations all had greater than 40 individuals, while the North-West coast was represented by only 19 individuals (Table 2). There were 11 polymorphic sites, 13 individual haplotypes - four of which were singletons (Figure 2). Haplotype diversity ranged from 0.535 on the East Coast to 0.789 on the North-West Coast with an average haplotype diversity of 0.658 across all sampled locations (Table 2). Global tests for differentiation (P = 0.000) and AMOVA analyses (F_{ST} = 0.082, *P* = 0.000) based on mtDNA haplotype frequencies revealed significant population structuring using mtDNA. Further pairwise comparisons revealed that differentiation exists between all populations excluding the Gulf of Carpentaria and the North-West Coast (F_{ST} = 0.017, *P* = 0.000) (Table 3).

East Coast, Gulf of Carpentaria and North-West Coast locations all had more than 25 individuals for microsatellite analysis (Table 4). Microsatellite results from the Gulf of Papua were unavailable as loci did not amplify reliably. It is unknown if the lack of amplification in these samples was an artefact of degraded primers or if primers were non-specific for the PNG region and require future optimisation. Therefore, microsatellite results presented here are for the three Australian locations exclusively.

Six of the seven microsatellite markers amplified reliably (Ancu152 did not amplify) and were used to genotype 123 *A. cuspidata* individuals from three regions in Australia. Of these six amplified loci, only five were suitable for population genetic analysis after an excess of null alleles was found for one locus (Ancu123) (Table 4). No other significant null allele values were identified and there was no evidence of linkage disequilibrium for the 5 remaining loci (data not shown). For estimates of population differentiation using microsatellites, samples missing alleles at three or more loci were excluded (n = 9), so that each individual had at least three loci and each locus has <5% missing data (total remaining sample size, n = 114). Given the small number of microsatellite loci available, results presented here from the microsatellite analysis should be taken with caution.

The average number of alleles per location (across the 5 loci) were 10.6, 11.2 and 11.6 for the Gulf of Carpentaria, Gulf of Papua and East Coast respectively; average allelic richness ranged from 9.97 to 10.60 on the North-West Coast and Gulf of Carpentaria, respectively (Table 4). Global tests for differentiation revealed no significant population structure (P = 1.000) and AMOVA calculations revealed >98% of variation was within populations, suggesting homogeneity across samples, therefore no further pairwise comparisons were considered.

DISCUSSION

The mixed marker approach undertaken in this study suggests that male and female mediated levels of population structure may differ for *A. cuspidata* in the Australasian region. This study included an additional mtDNA marker (ND4) with a previously analysed mtDNA gene region (CR) (D'Anastasi 2010). By increasing the number of mtDNA regions used for analyses, this has improved the resolution of evolutionary structure identified for *A. cuspidata*. This was also the case for Australian populations of *P. pristis*, whereby the whole mitogenome identified further structuring than was initially reported for the single CR region (Phillips et al. 2011; Feutry et al. 2015). In the current study, results from concatenated mtDNA gene regions indicate strong evolutionary structure was apparent between the Gulf of Papua, the East coast of Australia and the Gulf of Carpentaria.

Significant mtDNA differentiation found for *A. cuspidata* by D'Anastasi et al. (2010), and other sawfish species *P. pristis, P. zijsron* and *P. clavata* (Phillips et al. 2011; Feutry et al. 2015) has been attributed to two potential drivers. Firstly, the presence of the Torres Strait (TS) land bridge and secondly, putative female-mediated philopatry. Throughout the Pleistocene, glacial cycles of low sea levels caused the emergence of biogeographic features and barriers which influence the population structure for a number of marine species (Chenoweth & Hughes, 2003; Blair et al. 2014). In northern Australia, low sea levels exposed the TS land bridge located between Cape York Peninsula and Papua New Guinea (Chappell & Shackleton, 1986). Currently the land bridge is submerged in an average of 12m of water (Chivas et al. 2001), however over the last 2.5 million years only twice have high sea levels inundated the strait (125-115 kya and ~7 kya to present), facilitating an opportunity for marine migration between the east coast of Australia and PNG with locations westward of the Gulf of Carpentaria (Galloway & Kemp, 1981; Torgersen et al. 1985; Chivas et al. 2001; Raymo et al. 2006). The lack of gene flow (as indicated by the mtDNA results of this study) between the East and northern Australian *A. cuspidata* populations could be an artefact of the barrier that the TS land bridge produced. Similar patterns of limited gene flow either side of the land bridge have also been found for a number of other species including olive sea snakes, *Aipysurus laevis* (Lukoschek, et al. 2007); pig-eye sharks, *Carcharhinus amboinensis* (Tillett et al. 2011), spottail sharks, *C. sorrah* (Ovenden, et al. 2009); threadfin salmon, *Polydactylus macrochir* (Horne et al., 2012) and mud crab, *Scylla serrata* (Gopurenko & Hughes, 2002).

Alternatively, the mtDNA structuring identified here could reflect female-mediated philopatry or residency (Chapman et al. 2015). It is well documented that many female shark and rays return to the same region to give birth, and is more specifically referred to as parturition site fidelity or natal philopatry (see Chapman et al. 2015 for definitions). This behaviour is likely the result of selection favouring females that return to give birth in areas where previous generations have been most successful. Commonly, shallow coastal habitats, including the lower reaches of estuaries, are used by pregnant *A. cuspidata* females, providing a refuge for pups and protection for the mother while vulnerable (Peverell, 2005). Evidence from Tobin et al. (2014) found young-of-the-year *A. cuspidata* pups to inhabit and grow in shallow coastal waters, suggesting mothers specifically travel to inshore locations to give birth. The presence of female-mediated philopatry cannot be completely ruled out as microsatellite markers weren't available for the Gulf of Papua populations, therefore contemporary and male mediated gene flow is yet to be assessed between nations.

While mtDNA evidence strongly rejects the null hypothesis of a single panmictic population for *A. cuspidata* across northern Australia and the Gulf of Papua, microsatellite conclusions are less clear and require further validation with additional genetic resources. In this study, microsatellite results suggest no population structure exists across northern Australia. However these results are based on small sample sizes and a reduced number of loci and should be taken with caution. Nonetheless, this is the first mixed marker genetic study using mtDNA and microsatellites for *A. cuspidata* and provides important baseline information.

The inference of a lack of structure based on microsatellites for *A. cuspidata* is in contrast to what is known about other sawfish movements in the region. Phillips et al (2011) found sawfishes of the genus *Pristis* had restricted gene flow across northern Australia, and concluded for all three species (*P. pristis*, *P. zijsron* and *P. clavata*) that movement between the Gulf of Carpentaria and the North-West coast was unlikely. *Anoxypristis cuspidata* is the most unique sawfish in the family Pristidae. The findings of a lack of male-mediated genetic structure across northern Australia may be facilitated by morphological and behavioural differences observed for the species. *A. cuspidata* is described as a bentho-pelagic species (stirlings thesis – sorry I don't have the ref here). The ventral lobe on the caudal fin of *A. cuspidata* is large, especially in comparison with the *Pristis* species which have little to no ventral lobe. In general, fins with a high aspect ratio and distinct ventral lobe, similar to what we see in *A. cuspidata*, are considered to be associated with pelagic swimmers that spend limited time on the benthos (Thomson & Simanek, 1977). Additionally, *A. cuspidata* primarily uses the lower reaches of estuaries, in contrast to *P. pristis* and *P. clavata*, which rely more heavily on the upper reaches (Phillips et al, 2011) . Arguably, the lower reaches of estuaries are less patchy and more available than the upper reaches of estuaries. Reliance on a less patchy environment, may lead to the lower level of genetic structure observed in narrow sawfish compared to other species (see Phillips et al., 2011). Migration of distances greater than 1000 kms is conceivably possible given the shape of *A. cuspidata* caudal fin and the availability of suitable habitat across northern Australia.

Conclusion

Significant partitioning of the East Coast and Gulf of Papua from the other regions, coupled with connectivity between the Gulf of Carpentaria and the North-West Coast based on mtDNA results supports the hypothesis that the Torres Strait land bridge likely shaped the historic genetic architecture of *A. cuspidata* in northern Australia. While inconclusive, results identified using microsatellites has provided some of the first evidence that male-mediated gene flow may be present across large distances in waters off northern Australia. Further work assessing the differences in female and male mediated gene flow is imminently required. Moreover, work assessing the connectivity between Australia and neighbouring countries such as Papua New Guinea and Indonesia should be expanded to better understand how the differences in conservation approaches between countries is affecting the status of this species. Future genetic work should include a greater number of microsatellite markers or nuclear single nucleotide polymorphisms for more robust connectivity assessment.

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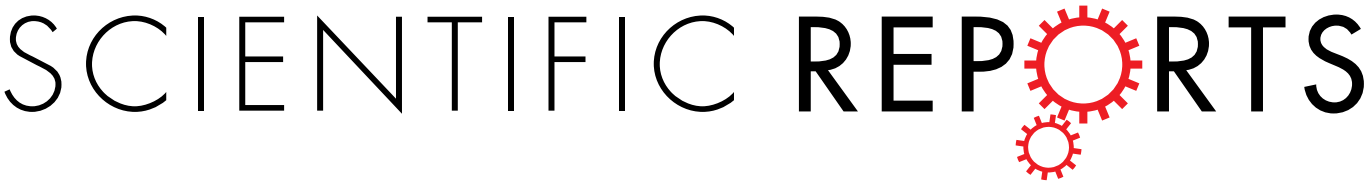

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Variability in multiple paternity rates for grey reef sharks (*Carcharhinus amblyrhynchos*) and scalloped hammerheads (*Sphyrna lewini*)

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This study assessed the presence and prevalence of multiple paternity (MP) in litters of grey reef sharks (*Carcharhinus amblyrhynchos*) and scalloped hammerheads (*Sphyrna lewini*) opportunistically caught in Papua New Guinea (PNG). Litter size between species were significantly different with an average of 3.3 pups for grey reef sharks and 17.2 pups for scalloped hammerhead. Using 14 and 10 microsatellite loci respectively, we identified MP in 66% of grey reef sharks (4 out of 6 litters) and 100% MP in scalloped hammerheads (5 litters). We found high paternal skew (the uneven contribution of sires per litter) and a positive correlation between female adult size and litter size in scalloped hammerheads but not in grey reef sharks. Differences in the frequency of MP between species and the identification of paternal skew may be linked with mating strategies and post-copulatory mechanisms. Multiple paternity is thought to benefit populations by enhancing genetic diversity therefore increasing the population's genetic resilience to extrinsic pressures. The identification of MP in two shark species reported here, further elucidates the complex breeding strategies elasmobranchs undertake.

Increasing resolution of molecular tools allows for a greater understanding of shark and ray (elasmobranch) reproductive systems which are often difficult to observe in the wild[1–3]. Elasmobranchs exhibit a variety of reproductive modes including live-bearing (viviparity), egg laying (oviparity)[4] and parthenogenesis[5] and also display monogamous and polyandrous mating behaviours[6,7]. Elasmobranchs do not often form pairs before and/or after mating and do not provide postnatal care to offspring[8], making their propensity for behavioural monogamy generally low. Instead, it is more likely for females to display polyandrous behaviour, mating with a number of males[8,9], the outcome of which may be a single litter, sired by many males and composed of full and half-siblings (sibs) (i.e. multiple paternity)[10]. Polyandry with multiple paternity has a number of benefits[3,11–13]. Firstly the fitness of the mother is increased as she is more likely to produce offspring; secondly, the adaptive fitness of individuals within litter may be improved as genetic variation is more likely to increase; thirdly, increases in genetic diversity can counteract issues of inbreeding facilitated by close-kin mating (especially for small populations); and finally, multiple paternity can increase the effective population size by providing an opportunity for a greater number of males to mate with an increased number of females[3].

The occurrence and prevalence of multiple paternity within an elasmobranch litter varies between species, populations and even individuals, but reasons for this are poorly understood[3,14]. Previous studies have suggested the likelihood of genetic monogamy or polyandry within a litter is dependent on a number of factors including the mother's size, home range or philopatric tendencies, population size, species-specific behaviours and the presence of post copulatory mechanisms (e.g. sperm storage)[3,12,14–19].

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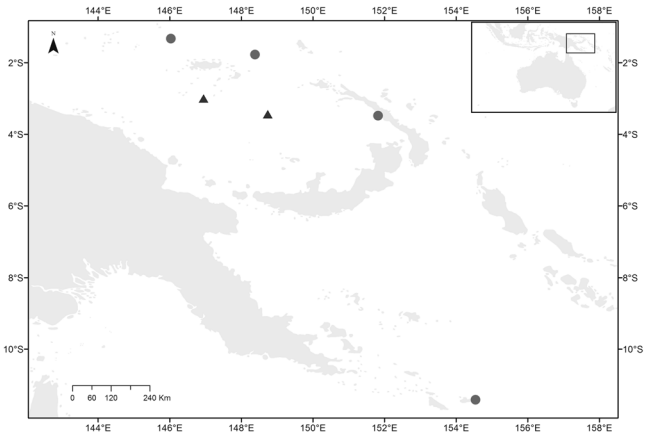

Figure 1. Sample locations for grey reef sharks *C. amblyrhynchos* (circles) and scalloped hammerhead *S. lewini* (triangles) in Papua New Guinea. Map created using ArcMap 10.2.1 (http://desktop.arcgis.com/en/arcmap/).

Sharks have life-history characteristics that make them highly susceptible to population declines, e.g. slow growth, delayed maturation and low fecundity[20,21]. An estimated 25% of all shark and ray species are threatened under the criteria of the International Union for Conservation of Nature (IUCN) Red List, with overfishing considered one of the main causes[21].

In Papua New Guinea (PNG), grey reef sharks (*Carcharhinus amblyrhynchos*) and scalloped hammerheads (*Sphyrna lewini*) are commonly caught by coastal artisanal and commercial fisheries. Regionally, the level of exploitation of both species is undocumented, making it difficult to assess the status of local populations. Globally, overexploitation has led to international conservation measures for scalloped hammerheads (i.e. listed as Endangered on the IUCN Red List[22] and included in Appendix II of the Conservation on International Trade in Endangered Species), while grey reef sharks are recognised as Near Threatened (IUCN Red List), thereby demonstrating the capacity to recover if managed accordingly[23].

Grey reef sharks and scalloped hammerheads differ ecologically; while both species have overlapping distributions, their habitat usage differs. Grey reef sharks have a strong affiliation with reef systems and often smaller individuals will show signs of site attachment to specific reefs[24]. Furthermore, telemetry studies have identified sex-specific movement traits for grey reef sharks, with males more likely to travel to neighbouring reefs than females[25]. Scalloped hammerheads display more complex habitat usage patterns including large ontogenetic differences and broader sex-specific movement traits[26,27]. Generally, juvenile scalloped hammerheads are found in shallower inshore waters, while adults migrate to deeper continental shelf environments[27]. Genetic analyses suggests females are more likely to display philopatric tendencies, adhering to coastal habitats, while males are known to disperse across oceans[19]. Both grey reef sharks and scalloped hammerheads form large female aggregations[27,28] and, once gravid, they are known to move inshore seeking refuge in nursery areas for birthing[19,25]. Additionally, scalloped hammerheads have post-copulatory mechanisms allowing for long-term (months to years)[29] sperm storage.

Obtaining mother and litter information for sharks is challenging given mothers are required to be sacrificed for collection of pups, and the common opportunistic nature of sampling regimes often means sample sizes are limited[3,30]. Recently, MP analyses were undertaken for scalloped hammerheads in southern Africa[30]. Using up to six microsatellite loci, Rossouw *et al.*[30] identified MP in 46% of 13 litters tested. Given maternal population differentiation has been identified between the regions and differences in average litter sizes, South Africa $n = 30$[31] and Indo-Pacific $n = 25$[32], it is of interest if rates of MP also differ between regions. Conversely, there has been no assessment of multiple paternity in grey reef sharks from any location. Here we investigated MP in grey reef sharks and scalloped hammerheads captured in the Indo-Pacific Ocean. Given that all studies which have undertaken paternity tests on shark litters have uncovered MP (see review in Rossouw *et al.*[30]) we predict MP will also be found for both species in this current study. However rates of MP are likely to differ given the variation in behaviour, ecology and physiology between the species. Using suites of microsatellite markers, litters were genetically determined as consisting of full or half sibs with an estimate of the number of fathers and their contribution to the litters in each species also obtained. This is the first study to investigate multiple paternity in grey reef sharks and the first for scalloped hammerheads in the Indo-Pacific Ocean.

Methods

Sampling and Microsatellite Analyses. Sample collection was undertaken on board commercial fishing vessels operating in PNG between 3rd May 2014 and 6th June 2014. Sampling was undertaken by observers deployed as part of an Australian Centre for International Agricultural Research project led by the National Fisheries Authority (NFA) of PNG and CSIRO to assess shark and ray catches throughout the commercial and artisanal fisheries in PNG (experiments approved by ACIAR and CSIRO; project FIS/2012/102). All samples were collected within a single month from the Bismarck and Solomon Seas (Fig. 1). Tissue samples including fin clips, vertebral chord or muscle were collected from pregnant females and all pups. Observers recorded total length of the adult females and measurements from the smallest and largest pups within a litter.

Locus Name	n	N_a	H_o	H_e	PIC
C. amblyrhynchos	26				
C. amb11[1]		14	0.938	0.895	0.878
C. amb3[1]		26	0.844	0.921	0.908
C. amb7[1]		8	0.703	0.759	0.715
C. amb2[1]		13	0.887	0.883	0.863
C. amb27[2]		10	0.797	0.823	0.793
C. amb9[2]		6	0.641	0.601	0.530
C. amb28[2]		12	0.844	0.807	0.779
C. amb4[2]		16	0.828	0.81	0.782
C. amb18[3]		25	0.938	0.952	0.942
C. amb15[3]		15	0.746	0.865	0.842
C. amb5[3]		9	0.813	0.766	0.726
C. amb22[3]		4	0.094	0.134	0.129
C. amb25[4]		10	0.906	0.826	0.797
C. amb20[4]		14	0.828	0.883	0.863
S. lewini	91				
SLE027[1]		9	0.867	0.804	0.773
SLE018[1]		4	0.545	0.516	0.472
SLE089[1]		18	0.966	0.91	0.898
SLE038[2]		7	0.943	0.781	0.744
SLE045[2]		4	0.818	0.721	0.665
SLE054[2]		5	0.685	0.664	0.621
SLE053[3]		12	0.667	0.84	0.817
SLE081[3]		8	0.922	0.787	0.753
SLE071[3]		11	0.582	0.738	0.713
SLE077[3]		13	0.681	0.889	0.873

Table 1. Characterisation of microsatellite loci for grey reef sharks (*C. amblyrhynchos*) and scalloped hammerheads (*S. lewini*). Number of individual mothers and pups (n), number of alleles (N_A), observed heterozygosity (H_o), expected heterozygosity (H_e) and Polymorphic Information Criteria (PIC).

DNA was extracted using the Wizard© SV Genomic DNA Purification system (Promega, Australia); tissue extractions were undertaken using SV minicolumns following modifications to the manufacturer's instructions (i.e. overnight tissue digestion; amount of supernatant used to elute DNA was reduced; DNA elution times increased). DNA was quantified using a Nanodrop 8000 UV-Vis Spectrophotometer (Thermo Scientific, USA) and standardised to 20ng/uL.

Microsatellites from pups in each litter were amplified by Polymerase Chain Reaction (PCR) and compared to genotypes in the corresponding mother. Species-specific microsatellite primers for grey reef sharks and scalloped hammerheads were from Momigliano *et al.*[33] and Nance *et al.*[34] respectively[33,34]. In the current study, microsatellite multiplexes were developed to enable cost effective screening. Forward primers were labelled with 6-FAM, VIC, NED and PET proprietary dyes and multiplexed (Table 1). PCR reactions consisted of GoTaq© Colourless Master Mix (Promega, USA), Bovine Serum Albumin (Promega, USA), 0.2 µM of each individual F and R primer (see Table 1 for multiplexes), and 0.8 ng/µl DNA in a 25 µL reaction. For scalloped hammerheads, thermal cycling consisted of initial denaturation at 94 °C × 3 minutes, 35 cycles of 94 °C × 1 minute, 58 °C × 30 seconds, 72 °C × 1 minute and a final extension of 72 °C × 10 minutes. Thermal cycling for grey reef sharks consisted of a touch-down protocol including initial denaturation at 94 °C × 3 minutes, 35 cycles of 94 °C × 1 minute, 5 cycles of 56 °C × 30 seconds, 5 cycles of 54 °C × 30 seconds, 25 cycles of 52 °C × 30 seconds, 35 cycles of 72 °C × 1 minute and a final extension of 72 °C × 10 minutes. Following PCR amplification, Gene Scan™ LIZ 500® size standard (Thermofisher Scientific, USA) and formamide were added to 3 µL of each PCR reaction and 20 µL sample volumes were run on an ABI 3130XL AutoDNA sequencer (Thermofisher, USA). Genotypes were scored and checked by eye using Geneious© R8.1.4 Microsatellite plug-in program (Biomatters Ltd Auckland, New Zealand).

Statistical Analysis. For each microsatellite locus, numbers of alleles, allele frequencies, and observed (H_o) and expected heterozygosities (H_e) were determined using Genepop web service v4.0.10[35]. Significance of H_o and H_e tests were estimated by the Markov Chain method including 10,000 dememorizations, 500 batches and 10,000 iterations (not reported). Polymorphic information content (PIC) was estimated using Cervus v3.0[36].

Analysis of paternity was initially checked by visual inspection of multi-locus genotypes. Secondly, putative fathers (number of sires) and paternal skew within litters were inferred using two programs: Gerud v2.0[37] which identifies the minimum number of fathers through exclusion calculations, and Colony v2.0.4.5[38] which uses a maximum likelihood approach. Polygamous mating systems were assumed for both sexes to allow for the assignment of full and half-sibs in Colony. Probability of detecting multiple paternity was calculated post-hoc using PrDM software[39] (available at http://publish.uwo.ca/~bneff/software.html). Six different scenarios were tested and

Species	Total Length (cm)	Litter Size	M:F Ratio	Size range of pups (cm)	# Sires (Gerud)	Skew (Gerud)	# Sires (Colony)
C. amblyrhynchos	160	4	3:1	51–54	2	2:2	2
C. amblyrhynchos	160	5	3:2	52–56	2	3:2	3
C. amblyrhynchos	153	3	0:3	40–41	2	2:1	2
C. amblyrhynchos	158	3	1:2	54–56	1	-	1
C. amblyrhynchos	150	2	1:1	45–62	1	-	1
C. amblyrhynchos	177	3	3:0	20–21	2	2:1	2
S. lewini	249	18	8:10	46–50	3	6:10:2	8
S. lewini	292	25	17:8	44–51	3	5:17:3*	7
S. lewini	238	13	NA	5–7	4	3:5:3:2	4
S. lewini	209	13	4:9	38–41	2	10:3*	2
S. lewini	235	17	9:8	42–48	4	8:3:4:2	3

Table 2. Summary of analysed litters, including female total length, litter size, sex ratio of pups (M:F Ratio), size range of pups, number of sires as estimated by Gerud and Colony, skew (paternal) for grey reef sharks (*C. amblyrhynchos*) and scalloped hammerhead (*S. lewini*). NA Indicates pups were too young to identify sex, $*P < 0.05$ chi-square test.

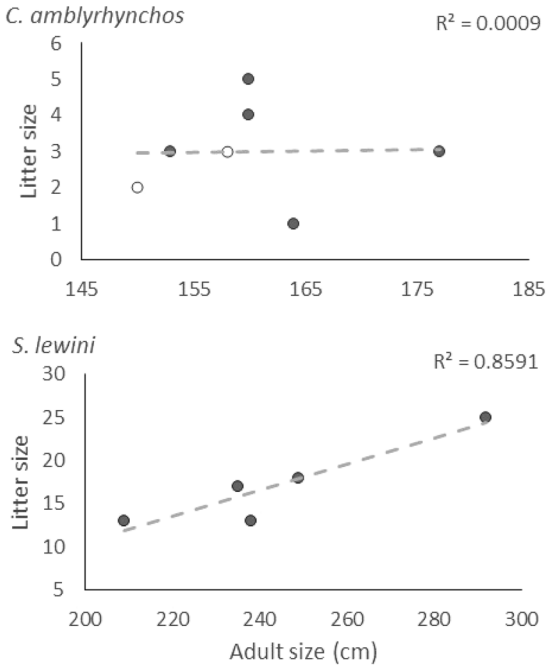

Figure 2. Correlation between adult female length (TL) and litter size for grey reef sharks (*C. amblyrhynchos*) and scalloped hammerhead (*S. lewini*). Shaded points indicate litter with multiple paternity, unshaded represents litters without multiple paternity.

defined according to the number of pups per litter and the minimum number of fathers identified in Gerud v2.0[37]. These scenarios were defined according to the number of pups observed in the present study (for each species) and the degree of paternity tested in other shark PrDM MP analyses[3,13,15].

Results

Six litters of grey reef sharks and five litters of scalloped hammerheads were used to investigate the presence of multiple paternity for sharks captured in PNG waters. Litter size between the species was significantly different ($P = 0.007$, Wilcoxon rank sum test), with grey reef sharks having an average litter of 3.3 pups and scalloped hammerheads an average of 17.2 (Table 2). Sex ratios within litters showed no significant bias towards either sex ($P > 0.05$, chi-square test). Litter size was positively correlated with adult female length for scalloped hammerheads ($P = 0.023$, $R^2 = 0.859$, Pearson's rank correlation) but not for grey reefs ($P = 0.675$, $R^2 = 0.000$) (Fig. 2). We note however, that these analyses are based on small sample sizes (i.e. litter numbers per species) and should be treated with caution.

	Litter Size						
	C. amblyrhynchos			*S. lewini*			
Paternal skew	3	4	5	13	17	18	25
2 males (50:50)	0.74	0.88	0.94	1.00	1.00	1.00	1.00
2 males (66.7:33.3)	0.71	0.84	0.91	1.00	1.00	1.00	1.00
2 males (80:20)	0.47	0.59	0.68	0.94	0.98	0.98	1.00
3 males (33.3:33.3:33.4)	0.88	0.96	0.99	1.00	1.00	1.00	1.00
3 males (57:28.5:14.5)	0.78	0.89	0.94	1.00	1.00	1.00	1.00
4 males (25:25:25:25)	0.93	0.99	1.00	1.00	1.00	1.00	1.00

Table 3. Probability to detect multiple males (PrDM) using different suites of microsatellite markers: 14 loci for *C. amblyrhynchos* and 10 loci for *S. lewini* under a number of paternal skew scenarios.

Alleles were amplified in microsatellite suites of 14 and 10 loci for all mothers and pups across 26 grey reef sharks and 91 scalloped hammerheads, respectively (Table 1). H_o ranged from 0.094–0.938 in grey reef sharks and 0.545–0.966 in scalloped hammerheads. Polymorphic Information Content (PIC) values were generally high, with 86% and 70% of grey reef shark and scalloped hammerhead loci greater than 0.7 respectively. The probability of detecting multiple paternity (PrDM) was highest for scalloped hammerheads (0.94-1), while probabilities were varied and reduced for grey reef sharks (0.47-1; Table 3). Number of loci had less effect than the number of pups within a litter in the detection of multiple paternity. Multiple paternity was identified in 66% of grey reef shark litters (4 out of 6) and in all scalloped hammerhead litters (all five) (Table 2). The number of putative fathers ranged from 1–3 for grey reef sharks and 2–8 for scalloped hammerheads based on Gerud and Colony estimates. In most cases, Colony analysis detected the same or a higher number of sires than Gerud. Paternal skew was identified in two scalloped hammerhead litters indicating an uneven contribution of pups per sire (Table 2).

Discussion

Results from this study provide the first evidence of multiple paternity in grey reef sharks, and the presence of MP in all studied litters of scalloped hammerheads in the Indo-Pacific Ocean. This is the first identification of 100% MP for a species of shark (albeit with a limited number of litters, $n = 5$) and the second within all elasmobranchs studied; 100% multiple paternity ($n = 4$) has previously been identified in the thornback ray *Raja clavata*[40]. Multiple paternity was observed in 66% of grey reef shark litters, but the power to detect multiple paternity decreases with decreasing litter size, as shown in PrDM analyses (Table 3). Given the small litter sizes, it is possible analyses presented here underestimate levels of MP for grey reef sharks. Alternatively, we believe small litter sizes may simply create a limited number of embryos available for fertilization by multiple males.

The percentage of litters reported to have MP for grey reef sharks (66%) is comparable to that of other large live bearing sharks, including the sandbar shark *Carcharhinus plumbeus* (40%)[16]. The benefits of polyandrous behaviour have been previously described and include ensuring successful fertility, increasing genetic diversity and genetic fitness (of mother and pups), and reducing close-kin mating (important, if populations are small or inbred)[41–43]. Our observation that polyandrous mating was detected in the larger of the grey reef shark females may have implications for populations exploited in PNG waters. For example, the gear used in longline fisheries including bait and hook size affect the size selectivity of a harvest[44]. If larger individuals are targeted and these individuals are more likely to undertake MP, their removal could mean reduced effective population size and a potential loss in genetic fitness for the population. It is therefore important future work (including larger sample sizes, than this current study) is undertaken to understand the relationship between MP and female size for grey reef sharks.

The finding of 100% multiple paternity in scalloped hammerhead litters in this study contrasts with another study which identified only 46% multiple paternity across 13 litters in South Africa[30]. Interestingly, however, Rossouw *et al.*[30] reported an average litter size of seven pups, well below the documented litter size for scalloped hammerheads in South Africa ($n = 30$)[31]. Sharks in the Rossouw *et al.*[30] study were captured in bather protection nets, and it is possible the mothers may have aborted the majority of pups prior to landing, potentially limiting the study to a subset of all pups in the litter. This could lead to an underestimate of the level of multiple paternity for scalloped hammerheads in South Africa.

Multiple paternity is thought to be more common in species that display high levels of philopatry and low dispersal rates, as such behaviour is likely to reduce the chance of individuals breeding with a genetically incompatible (related) partner, thereby decreasing the chance of localized inbreeding depression[3,11,43]. For both scalloped hammerhead and grey reef sharks, genetic[19,45] and telemetry studies[25,46] have revealed strong patterns of female mediated site fidelity and male-biased dispersal. Male dispersal has been prevalent enough to facilitate connectivity (gene flow) between reefs spanning 1,200 km for grey reef sharks[45] and across ocean basins for scalloped hammerheads[19]. For both species in PNG, it would seem the presence of MP is unlikely to be driven by the threat of close-kin mating or inbreeding depression, given the significant gene flow facilitated by male dispersal in these species shown elsewhere.

Two of the five scalloped hammerhead litters were identified as having significant paternal skews. The presence of paternal skew, (i.e. the uneven contribution of sires to a litter) is thought to be attributed to a combination

of female choice, the timing/order of males mating, and sperm competition[18,30]. The processes of post-copulatory mechanisms are thought to increase the level of paternal skew within a litter[47–50]. Scalloped hammerheads have complex oviducal glands capable of stimulating bundles of sperm to be released, giving control over sperm utilization and its contribution to paternal skew within a litter[29,51,52]. Additionally, it is thought that polyandrous mating may create an internal environment within a female that promotes sperm competition, leading to increased fertilization and consequently increased fitness of young ('sexy-sperm hypothesis')[53,54]. This hypothesis suggests females mate with different males to create conditions selecting for the most competitive sperm; which results in male offspring possessing the gene for heightened sperm competitiveness and therefore increasing offspring fitness[54]. It is possible males with heightened sperm competitiveness would sire more pups within a litter creating paternal skew. The mechanisms behind paternal skew in scalloped hammerheads could be one or a combination of factors described here and remains unresolved. The observed lack of paternal skew in grey reef sharks may be connected to the smaller litter size of the species; more litters are required to conclusively verify this hypothesis.

The results of this research concur with similar studies and reiterate the prevalence of MP in sharks. Our results highlight the difference in litter size between the grey reef sharks and scalloped hammerheads and demonstrates differences in levels of multiple paternity. Additionally, the discovery of positive correlations between adult size, litter size and MP suggests genetic mating systems in sharks are complex and may be species- and location-specific. Sample sizes presented here are relatively small and further investigation is required to conclusively understand the relationship between adult size and breeding behaviours. However, a number of studies assessing multiple paternity in sharks (and elasmobranchs more widely) have tested five or less litters[1,13,40,42,55,56] and given the opportunistic nature and difficulties associated with sampling gravid elasmobranchs, the findings from this research provide valuable insight for these two species.

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Author Contributions

Conceived and designed the experiment: M.G., S.A., J.O. Provided samples: W.W. Performed the experiment: M.G. Analysed the data: M.G. Prepared figure 1: S.T. All authors reviewed the manuscript.

Additional Information

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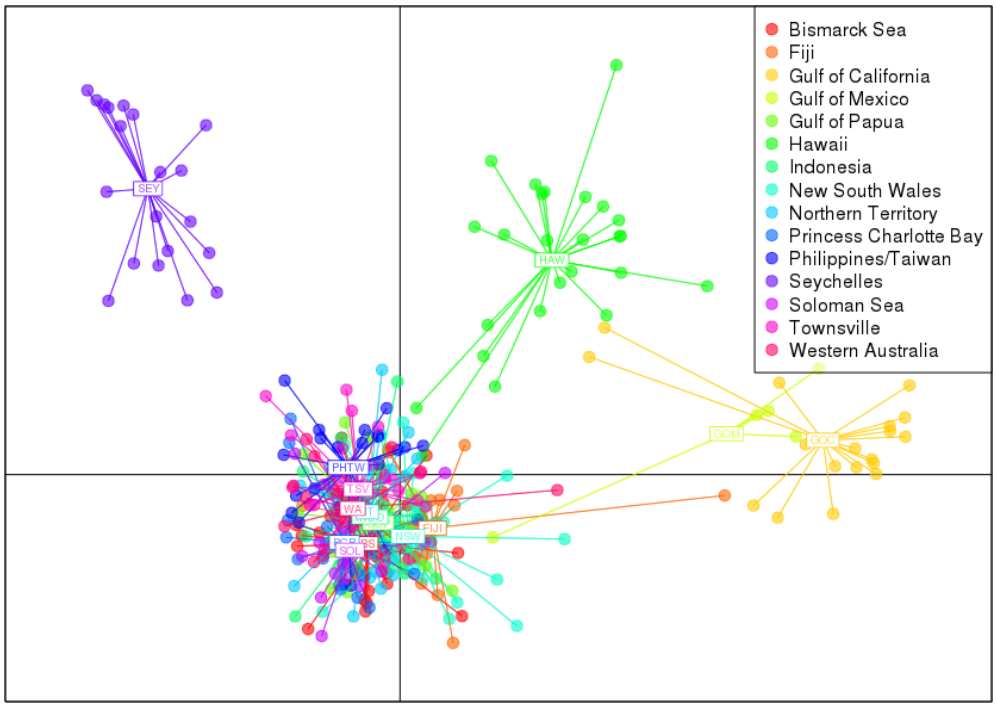
Population Genetics Appendix

The following graphs indicate population structure detected by microsatellite and SNP markers. These are used most commonly to define genetic stock structure for species. Throughout the ACIAR project two markers for genetic stock delineation were used to measure the similarities or dissimilarities between marker types. Our results show there is discordance between marker types which are often used for studies interchangeably. This work is not only important for determining the genetic stock structure for three key species in PNG, but is also providing a robust analytical comparison which is progressing our knowledge in the field of population genetics.

a)



b)

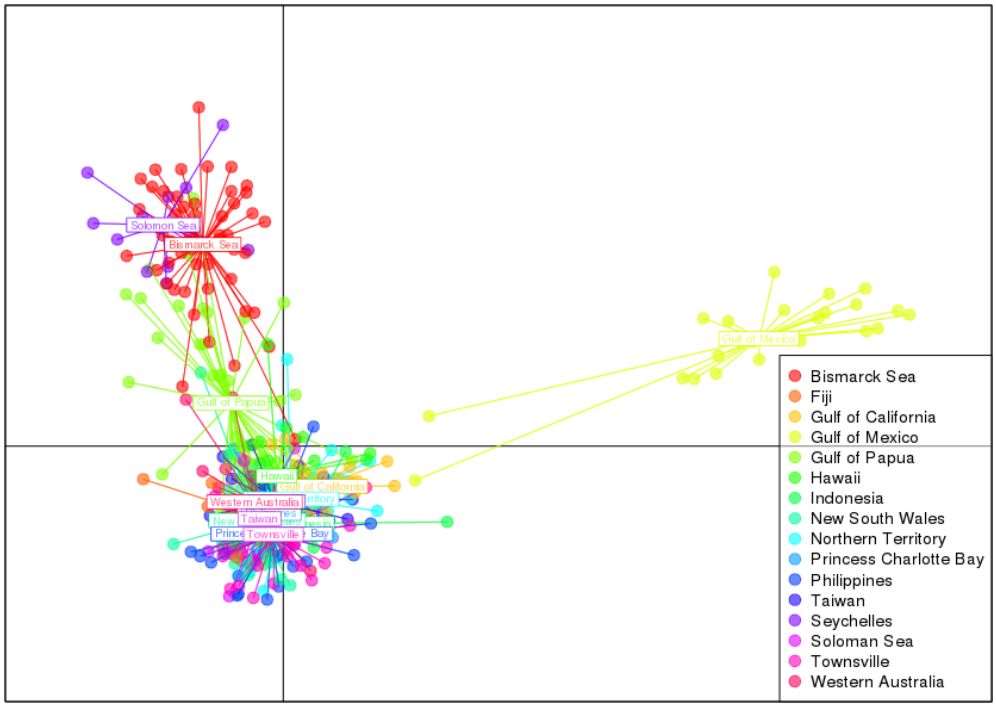
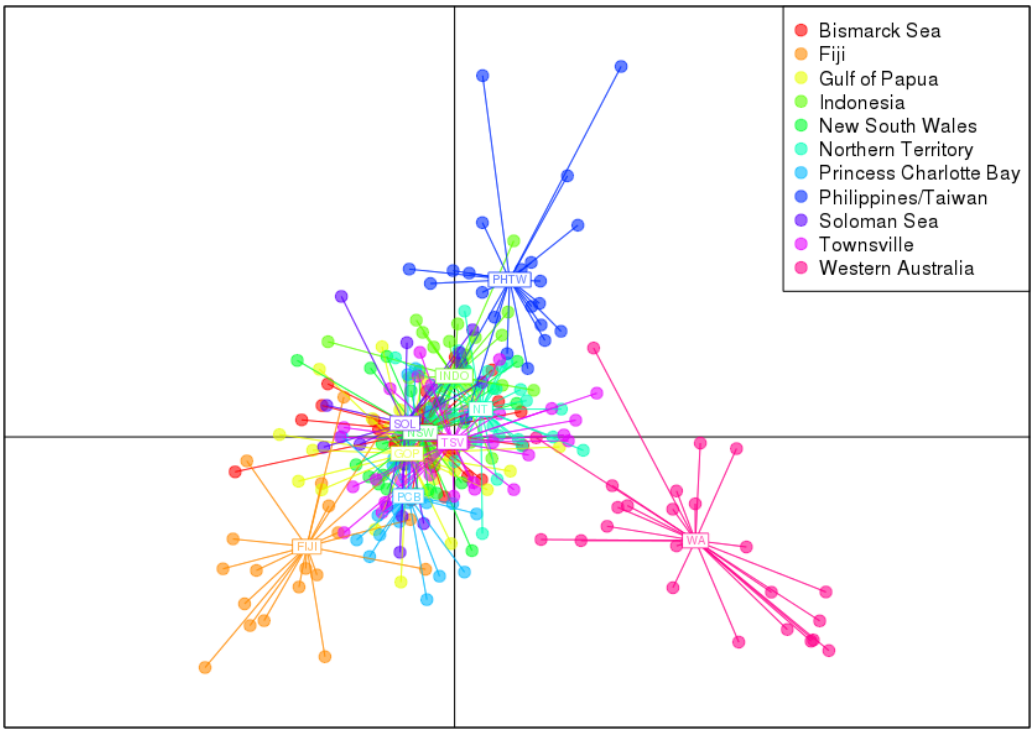


Figure 1.Scalloped hammerhead, S. lewini- Global Population. Plot indicating population structure for (a) SNPs and (b) Microsatellite markers. Each population is indicated by a different colour. Each point represents an individual from the colour population. Distance between points represents the genetic similarity, with individual's closely located together being genetically similar.

a)



b)

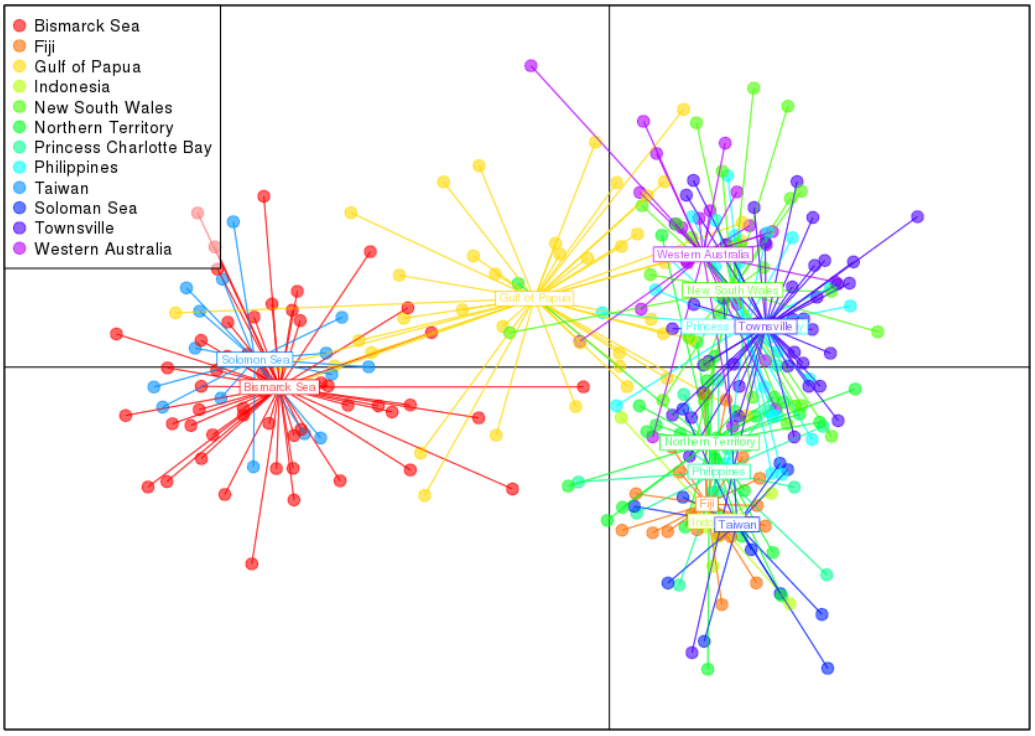
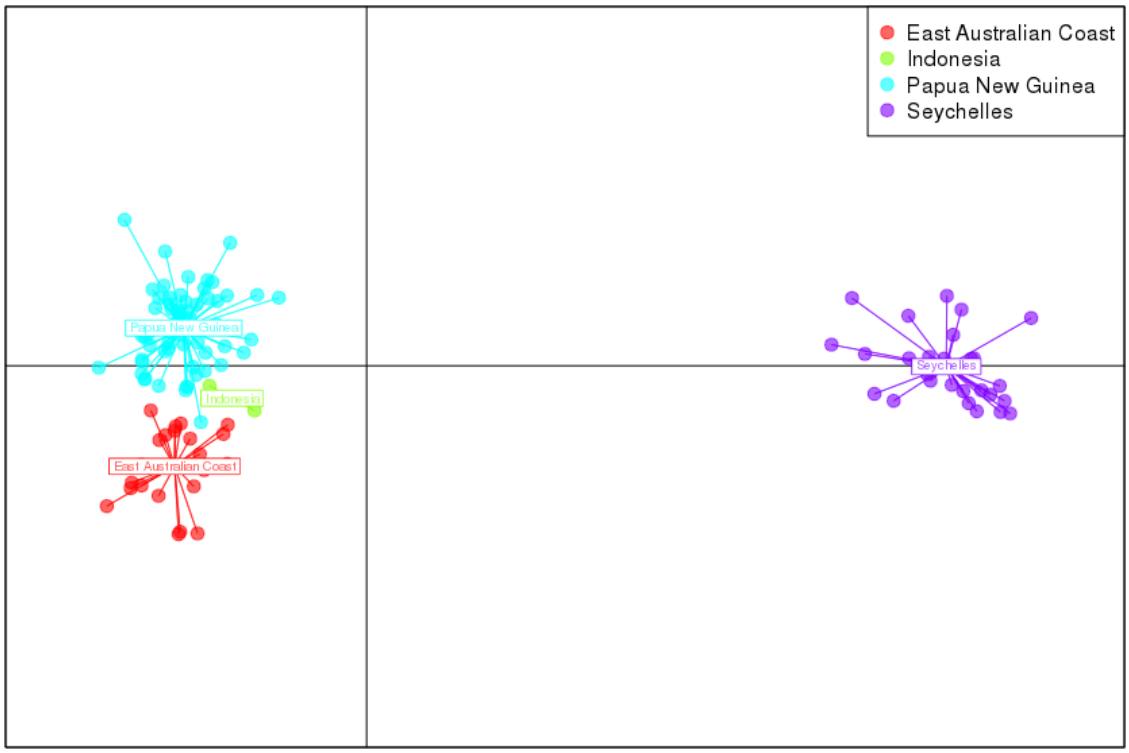


Figure 2. Scalloped Hammerhead, S. lewini- Central Indo-Pacific Ocean. Plot indicating population structure for (a) SNPs and (b) Microsatellite markers. Each population is indicated by a different colour. Each point represents an individual from the colour population. Distance between points represents the genetic similarity, with individual's closely located together being genetically similar.

a)



b)

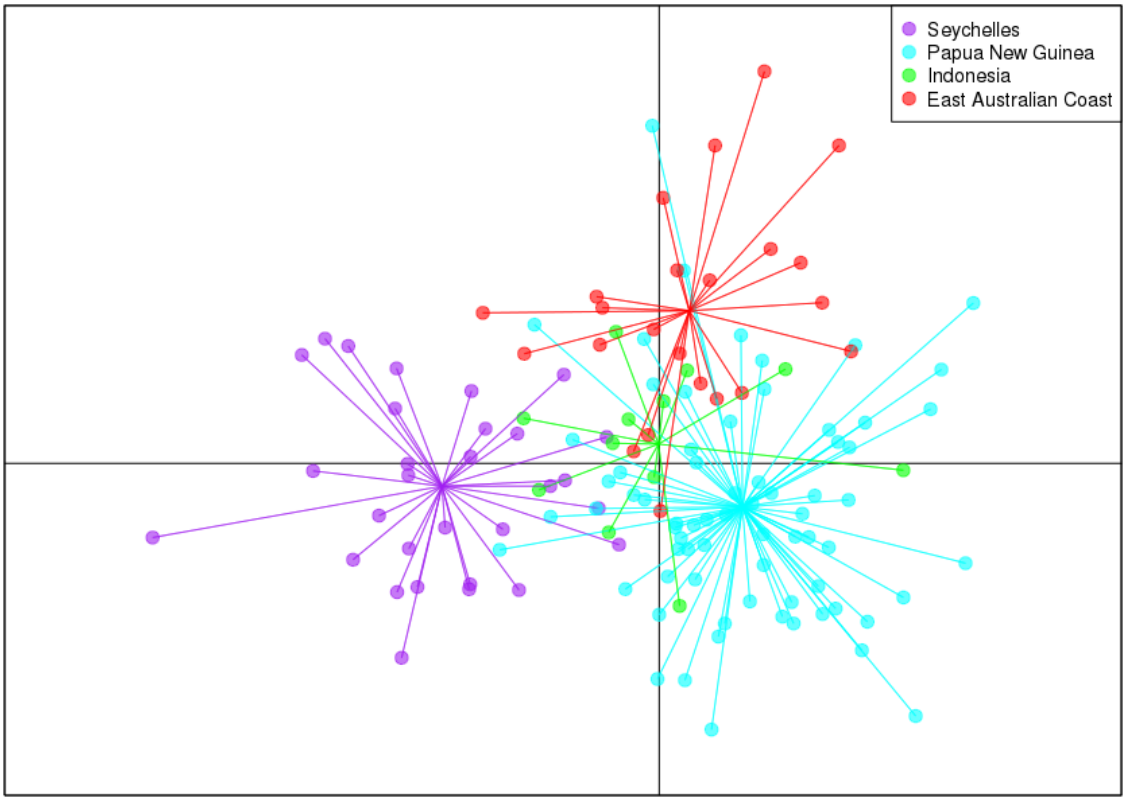


Figure 3. Silvertip shark, C. albimarginatus. Plot indicating population structure for (a) SNPs and (b) Microsatellite markers. Each population is indicated by a different colour. Each point represents an individual from the colour population. Distance between points represents the genetic similarity, with individual's closely located together being genetically similar.

a)

b)

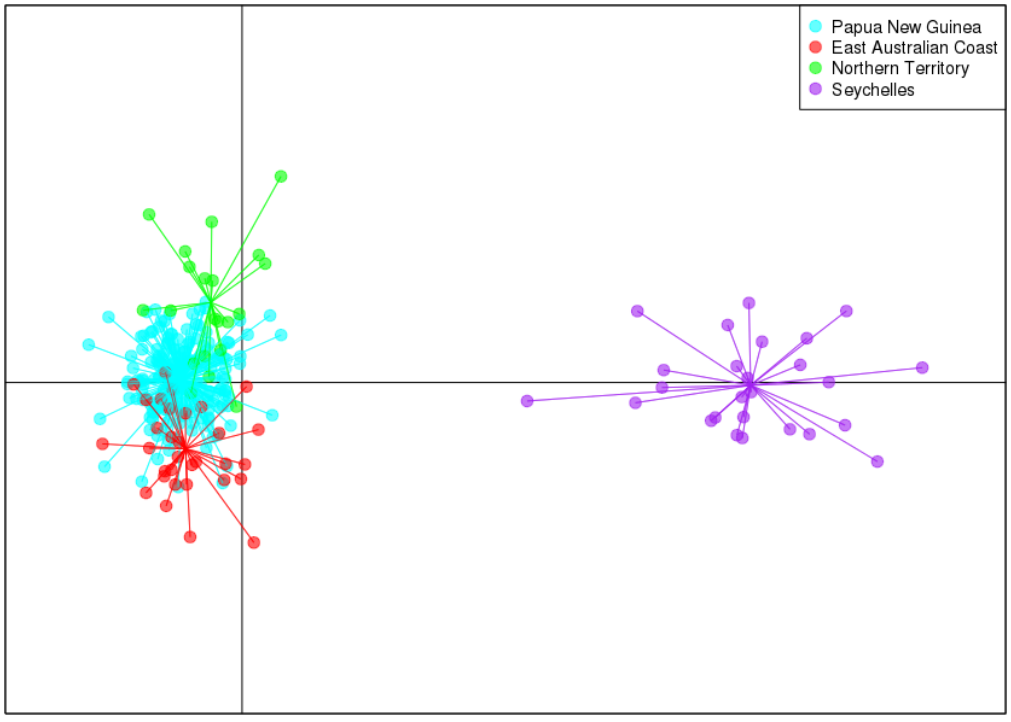


Figure 4. Grey reef shark, C. amblyrhynchos. Plot indicating population structure for (a) SNPs and (b) Microsatellite markers. Each population is indicated by a different colour. Each point represents an individual from the colour population. Distance between points represents the genetic similarity, with individual's closely located together being genetically similar.