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Stochastic demographic analyses of the silvertip shark (*Carcharhinus albimarginatus*) and the common blacktip shark (*Carcharhinus limbatus*) from the Indo-Pacific

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ABSTRACT

Information on how shark populations respond to fishing mortality (*F*) is critical to developing successful management and conservation strategies. However, data on catch, fishing effort and species abundance are often lacking for shark populations – preventing stock assessments from being conducted. Static demographic models circumvent this issue as they only require life history parameters. Age-structured Leslie Matrix models were developed and applied for silvertip shark *Carcharhinus albimarginatus* and common blacktip shark *Carcharhinus limbatus* sampled from heavily fished populations in the Indo-Pacific. Stochasticity was introduced to these models by varying vital rates though Monte Carlo simulations. Varying levels of *F* were introduced to the analyses to determine how both species respond to fishing pressure. Management scenarios were further developed to determine strategies that could facilitate sustainable harvesting. The demographic estimates demonstrated that without fishing both species would have increasing populations ($\lambda = 1.06\,\text{yr}^{-1}$ for *C. albimarginatus* and $1.05\,\text{yr}^{-1}$ for *C. limbatus*) until density dependent effects occur. However, both populations would decline when low levels of *F* ($>0.1\,\text{yr}^{-1}$) were applied to all age-classes. The matrix elasticities revealed that changes to fertility elements had little effect on λ, while changes in juvenile survival led to the largest changes. However, age-at-first-capture analysis suggests protecting the juvenile life stage of both species would be an ineffective management strategy as both species mature at old ages. An age-at-last-capture analysis suggests these species could be harvested while maintaining increasing populations through a gauntlet fishery. This required *F* to be restrained to individuals <100 cm TL while protecting the older age-classes to preserve the breeding stock. This strategy would allow up to 16% and 13% of this size class to be harvested for *C. limbatus* and *C. albimarginatus*, respectively, until density dependent effects begin to manifest. However, this strategy depends on the ability to successfully protect all other age-classes from fishing – a strategy that may not be pragmatic in developing nations where little regulation occurs.

1. Introduction

The world's highest shark catches occur in the Western Central Pacific, in particular Indonesia. Indonesia has the world's largest shark fishery with reported catches of an average 110,000 t per year – more than any other nation (Lack and Sant, 2008). Both Indonesia and Papua New Guinea (PNG) lie within the Coral Triangle, a region of specific conservation concern due to high biological diversity including some of the world's richest chondrichthyan faunas (Last and White, 2011; White and Kyne, 2010). However, both nation's shark fisheries remain poorly understood as they are largely unregulated and catches are mostly unreported (White and Kyne, 2010). As of yet, no stock assessments have been conducted on Papua New Guinean shark fisheries (White and Kyne, 2010), although some data from PNG have been included in assessments for the greater western central Pacific (Rice and Harley, 2012, 2013). Stock assess-

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ments have been attempted in Indonesia although the lack of long term species-specific catch and effort data has so far precluded dynamic stock analyses from being undertaken (Blaber et al., 2009). However, static demographic models do not require such data and may be used to provide management-relevant information using only life history parameters (Cortés, 1998; Simpfendorfer, 2004a). Information on species-specific biology are available from Indonesia (Drew et al., 2015; Hall et al., 2012; White, 2007; White et al., 2008) and PNG (D'Alberto et al., 2016; Smart et al., 2016, 2017). Therefore, demographic models provide an opportunity to better understand these populations even though limited fisheries data are available (Simpfendorfer, 2004a).

Static demographic models became popular for shark stocks in the 1990's (Au and Smith, 1997; Cailliet et al., 1992; Cortés, 1999; Simpfendorfer, 1999a,b) and now include a range of analyses that can incorporate stochasticity (Cortés, 2002; Cortés et al., 2012; McAuley et al., 2007). Demographic estimates provide a variety of statistics that summarise a population's growth rate, generation length, reproductive outputs and stable-age distribution. Each of these demographic outputs can be produced from either life tables or matrix models (Caswell et al., 1998). While similar estimates are produced by both methods (Mollet and Cailliet, 2002), matrix models can be structured to examine either stage or age-classes – allowing them to be tailored to the information available (Simpfendorfer, 2004a). Additionally, the elasticities of individual matrix elements can provide useful information on the ages or life stages that will respond best to management (Heppell et al., 2000, 1999). Therefore, the trend in fisheries and ecological literature is moving towards matrix model approaches because of the ability of these methods to assess the potential effects of management and conservation strategies (Simpfendorfer, 2004a).

The silvertip shark, *Carcharhinus albimarginatus* and the common blacktip shark *Carcharhinus limbatus* are species that require demographic assessment in the Indo-Pacific region due to human pressures and conservation concern. *C. albimarginatus* is a reef associated species with a patchy distribution in the Indo-Pacific (Ebert et al., 2013). It's reef association means that it is encountered infrequently by commercial tuna fisheries (Kumoru, 2003; Smart et al., 2017), although there is evidence that they are caught in subsistence and artisanal fisheries (White, 2007). Information on its life history, space use and habitat preferences are now available (Bond et al., 2015; Espinoza et al., 2015; Smart et al., 2017). However, as its catches are largely unreported, no population assessments have ever been conducted on this species. Therefore, its ability to withstand the effects of fishing is unknown and little information on its population status is available to inform conservation or management.

C. *limbatus* has a circumglobal distribution and is fished throughout much of its range (Ebert et al., 2013). Stock assessments and demographic analyses conducted on US populations have demonstrated that this species can be fished sustainably (Cortés, 1998; Cortés et al., 2002; SEDAR, 2012). Unfortunately, information from these assessments cannot be used to manage the Indo-Pacific population as demographic models are strongly dependent on the vital rates used to construct them. As the Indo-Pacific *C. limbatus* population grows larger and matures later than US conspecifics (Smart et al., 2015; Wintner and Cliff, 1996), these demographic estimates would be unsuitable. Therefore, demographic analyses that are based on local life history parameters are required to effectively inform conservation and fisheries management in the region.

The data-poor nature of Indonesian and PNG shark fisheries has been an impediment to conducting full stock assessments. However, static demographic models can accommodate data paucity and thus, act as an important assessment tool until sufficient fisheries data become available for data-rich conventional stock assessments, or until results of other data-poor approaches become available (Simpfendorfer, 2004a). Therefore, the aim of this study was to use static demographic models to produce demographic information on *C. albimarginatus* and *C. limbatus* populations from the Indo-Pacific region. This was achieved by applying age-structured Leslie matrix models for both populations using locally obtained life history parameters. These parameters were sourced from the region of the Indo-Pacific that surrounds PNG and Indonesia. Specifically, the life history parameters for *C. albimarginatus* were sourced from studies published from PNG fisheries (Smart et al., 2017), while the parameters for *C. limbatus* were sourced from studies published from Indonesian fisheries (Smart et al., 2015; White, 2007). Inferences about population growth rates, susceptibility to fishing pressure and potential management scenarios were determined from these demographic estimates.

2. Methods

2.1. Life history parameters

Life history parameters were taken from the literature to form the foundation of vital rates to use in demographic analyses (Table 1). Vital rates were defined as lower level components of the demographic estimates that underlie the Leslie Matrix elements (Brault and Caswell, 1993). Reproductive vital rates were used to estimate the age-specific fecundity (number of female pups per year, m_t). As both species have 1:1 embryo sex ratios and biennial reproductive cycles (White, 2007; White et al., 2006), this was performed by multiplying the respective litter sizes of each species by 0.5 then dividing this value by 2. Age-at-maturity (t_{mat}) was determined using the age where 50% of individuals were mature from logistic maturity ogives (Smart et al., 2017; White, 2007). Age-at-first-reproduction (t_{repro}) was calculated as t_{mat} + the gestation period (Mollet and Cailliet, 2002).

2.1.1. Mortality estimation

Natural mortality (M) was estimated for both species using indirect methods. These included the age-independent equations proposed by Pauly (1980), Chen and Yuan (2006), Jensen's (1996) k invariant method and Jensen's (1996) maturity method as modified for use with sharks by Hisano et al. (2011). Two age-dependent methods were also applied following Chen and Watanabe (1989) and Peterson and Wroblewski (1984).

Pauly's (1980) method used the equation:

$$\ln(M) = -0.0066 - 0.279 * \ln(L_\infty) + 0.6743 * \ln(k) + 0.4634 * \ln(T)$$

where L_∞ and k are parameters from the von Bertalanffy growth function (VBGF) and T is temperature in °C.

Chen and Yuan's (2006) method was calculated as:

$$\ln(M) = 1.46 - 1.01 * \ln(t_{\max})$$

where t_0 and k were parameters from the VBGF and $t_{\max}$ was the longevity calculated as:

$$t_{\max} = \left(t_0 - \frac{\ln(0.05)}{k}\right)$$

However, this equation overestimated longevity for *C. albimarginatus* with a particularly implausible estimate of 142 years. Therefore, this estimator was removed for this species.

Jensen's (1996) k invariant method was calculated as:

$$M = 1.6 * k$$

Jensen's maturity method (1996) as modified for use with sharks by Hisano et al. (2011) was calculated as:

$$M = \frac{1.65}{t_{mat} - t_0}$$

Table 1
Life history parameters for *C. albimarginatus* from PNG and *C.limbatus* from Indonesia, the statistical distributions and lower/upper bounds used in Monte Carlo Simulations. All parameters are specific to females only. Standard errors are given in parentheses. Ranges of $t_{\max}$ values are given as this parameter is dependent on k.

Type	Parameter	Estimate	References
Carcharhinus albimarginatus			
Growth	L_∞ (cm)	497.9 (±101.2)	Smart et al. (2017)
	k (yr^{-1})	0.02 (±0.007)	Smart et al. (2017)
	t_0 (years)	−7.67 (±1.23)	Smart et al. (2017)
	$t_{\max}$ (years)	30–32	Smart et al. (2017)
	Max age from vertebral analysis (years)	18	Smart et al. (2017)
	Residual standard error of VBGF	10.26	Smart et al. (2017)
Fecundity	t_{mat} (years)	14.8 (±1.3)	Smart et al. (2017), Stevens (1984)
	Litter size	6 (±1.8)	Bass et al. (1973), Wheeler (1962)
	Gestation Period (months)	12	Bass et al. (1973), Wheeler (1962)
	Reproductive cycle (years)	2	White et al. (2006)
Carcharhinus limbatus			
Growth	L_∞ (cm)	264 (±76.5)	Smart et al. (2015)
	k (yr^{-1})	0.11 (±0.007)	Smart et al. (2015)
	t_0 (years)	−2.44 (±0.19)	Smart et al. (2015)
	$t_{\max}$ (years)	20–21	Smart et al. (2015)
	Max age from vertebral analysis (years)	17	Smart et al. (2015)
	Residual standard error of VBGF	8.01	Smart et al. (2015)
Fecundity	t_{mat} (years)	7 (±1.5)	Smart et al. (2015)
	Litter size	6 (±1.8)	White (2007)
	Gestation Period (months)	12	White (2007)
	Reproductive cycle (years)	2	White (2007)

Two methods were applied to produce age-dependent mortality estimates (M_t). Chen and Watanabe (1989) hypothesised that M should be highest at the youngest and oldest age-classes producing a "bathtub" shape. They therefore, derived two equations: one which described declining mortality during the early years of life and a second that described increasing mortality towards the end of life (Simpfendorfer, 2004b). These equations are also derived using parameters from the VBGF:

$$M_t = \begin{cases} \dfrac{k}{1-e^{-k(t-t_0)}}, & t < t_m \\ \dfrac{k}{a_0 + a_1(t-t_m) + a_2(t-t_m)^2}, & t \geq t_m \end{cases}$$

where

$$\begin{cases} a_0 = 1 - e^{-k(t_m - t_0)} \\ a_1 = k e^{-k(t_m - t_0)} \\ a_2 = -\dfrac{1}{2} k^2 e^{-k(t_m - t_0)} \end{cases}$$

and

$$t_m = -\frac{1}{k}\ln(1 - e^{kt_0}) + t_0$$

where M_t is the natural mortality at age t, k and t_0 are parameters from the VBGF.

Peterson and Wroblewski's (1984) method estimates M by using dry weight as scaling factor:

$$M_{wt} = 1.92wt^{-0.25}$$

where wt is the weight-at-age t. This is then converted to M_t using a length-weight relationship and length-at-age data (Simpfendorfer, 2004b). Such an approach yields wet weight and thus a conversion factor of one fifth is used for sharks to give dry weight (Cortés, 2002). Length-at-weight was calculated for *C. limbatus* using the relationship given by Dudley and Cliff (1993) for the South African population which has a similar growth profile to the Indonesian population (Smart et al., 2015). However, this method could not be used to estimate M_t for *C. albimarginatus*, as no length-weight relationship is available for this species from any region.

Estimates of M_t were transformed into annual probabilities of age-specific survival (S_t) (to form Leslie Matrix elements) as:

$$S_t = e^{-M_t}$$

The proportion of the population surviving to the beginning of each class (l_t) was also calculated from M as:

$$l_t = l_{t-1}e^{-M_t}$$

2.2. Demographic model

Demographic analyses were conducted using a static age-structured Leslie Matrix model with a post-breeding census (Aires-da-Silva and Gallucci, 2007; Caswell, 1989; Mollet and Cailliet, 2002). These demographic analyses were single sex models carried out exclusively for females – as is typical for demographic analyses on elasmobranchs (Simpfendorfer, 2004a). Leslie matrices use matrix algebra to estimate the finite rate of population growth (λ) as the dominant eigenvalue from fertility (f) and survival (S) data (Caswell, 1989). The finite rate of population growth can be related to the intrinsic rate of population growth (r) produced by life tables via the relationship (Simpfendorfer, 2004a):

$$\lambda = e^r$$

Population growth is stable when $\lambda = 1$, decreasing when $\lambda = <1$ and increasing when $\lambda = >1$. Additionally, the stable age distribution (w) and reproductive values (v) were estimated as the right and left eigenvectors, respectively.

To construct the Leslie Matrices, m_t was estimated using knife-edge maturity – where age-classes older than or equal to t_{repro} produced an equal number of female pups per year, while all age-classes younger than the t_{repro} produced none. While it is common in many shark species for larger individuals to produce larger mean litter sizes, such data were not available for either population. Therefore, knife-edge m_t was assumed. Following Caswell (1989), fecundity is defined here as the maximum reproductive output (vital rates) while fertility is defined as the actual reproductive performance (matrix elements). Age-specific fertility (f_t) was calculated as:

$$f_t = \begin{cases} 0, & t < t_{repro} \\ S_{t-1} * m_t, & t \geq t_{repro} \end{cases}$$

The basis for the Leslie Matrices was:

$$N_{t+1} = AN_t$$

where N is a vector describing the population's age composition at time t and A is the transition matrix (Caswell, 1989):

$$A = \begin{bmatrix} f_0 & f_1 & f_2 & \ldots & f_t \\ S_0 & 0 & 0 & \ldots & 0 \\ 0 & S_1 & 0 & \ldots & 0 \\ \vdots & \ddots & \ddots & \ldots & \vdots \\ 0 & 0 & 0 & S_t & 0 \end{bmatrix}$$

Mean generation time (G) and net reproductive rate (R_0) were calculated from the Leslie Matrices (Simpfendorfer, 2004a). G is the mean period between birth of a parent and the birth of their offspring:

$$G = \sum_{t=t_{repro}}^{t_{max}} te^{-\ln(\lambda)t} l_t m_t$$

R_0 is the total number of female offspring produced per individual in their lifetime according to rates of m_t and l_t:

$$R_0 = \sum_{t=t_{repro}}^{t_{max}} l_t m_t$$

2.3. Monte Carlo simulations

Estimates of vital rates for marine species can often be difficult to obtain and are subject to high uncertainty (Caswell et al., 1998). Therefore, it was important to consider the effect of that uncertainty by incorporating stochasticity into demographic analyses (Cortés, 2002). Monte Carlo simulations were used to stochastically vary specific vital rates to incorporate uncertainty into matrix projections and demographic parameters (Cortés, 1999, 2002). This involved randomly selecting vital rates from assumed statistical distributions, performing demographic analyses for 10,000 simulations and summarising the results with mean and quantile values. The statistical distributions of λ, G and R_0 were analysed to ensure that each distribution was well captured during the simulations. The vital rates varied in the Monte Carlo simulations were longevity, L_∞, k, t_0, t_{mat}, litter size and M_t.

Parameter estimates from the VBGF (L_∞, k and t_0) were sampled from normal distributions created from mean and standard errors (Table 1). t_{mat} was also drawn from a normal distribution using the mean and standard error of the age where 50% of the population was mature (Table 1). A normal distribution was also used for litter size. However, standard errors were unavailable for both species which is common for elasmobranchs (Cortés, 2002). Therefore, it was assumed that the standard error was one third of the mean litter size based on observations from studies that provided this statistic (Cortés, 2002). These values were then used in further calculations of $t_{\max}$ and M in each simulation.

Longevity was included as a varied vital rate in the simulations as it can be difficult to estimate for large bodied sharks (Francis et al., 2007). Longevity was used to determine the number of age-classes required for A and was drawn from a uniform distribution. This was created using the maximum age from vertebral analyses as the lower bound and theoretical longevity calculated from VBGF parameters (t_{max}) (Mollet et al., 2002) as the upper bound (Table 1):

$$t_{max} = 7 * \ln\left(\frac{2}{k}\right)$$

M or M_t were also varied by randomly selecting one of the estimators (Table 2) in each Monte Carlo simulation. Each of these estimates were calculated within each simulation using the drawn estimates of L_∞, k, t_0 and t_{mat}. A growth curve derived from drawn estimates of L_∞, k and t_0 for each simulation was used in the calculations for the Peterson and Wroblewski (1984) estimator for *C. limbatus*.

Summaries of the stable-age distributions and the reproductive values (w and v) were produced for unfished populations from the Monte Carlo simulations. However, these summaries required a constant longevity and therefore this vital rate was not varied. In this study, an unfished population was not considered a virgin stock as all of the vital rates used in the demographic analyses were estimated from fished populations. Therefore, the term "unfished population" was defined here as a scenario where the instantaneous fishing mortality (F) was reduced to zero.

2.4. Matrix elasticities

Elasticity analysis measures the proportional changes of individual matrix elements on λ while holding other elements constant (de Kroon et al., 1986). As elasticities identify the ages where changes to S or f will most affect λ, they provide valuable information for conservation and management (Simpfendorfer, 2004a). Elasticities of matrix elements (e_{ij}) were calculated as (Caswell, 1989):

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\lambda w, v'}$$

where a_{ij} is the matrix element corresponding to row i and column j, v_i is the value of row i in the reproductive value vector v, w_j is the value of column j in the stable age distribution vector w and $\langle w, v \rangle$ is the scalar product of vectors w and v. The sum of all matrix element elasticities equals 1.

As elasticity values are highly dependent on the vital rates used, deterministic methods cannot be calculated from a mean matrix produced from Monte Carlo Simulations (Wisdom et al., 2000). Therefore, to provide a sensitivity analysis following the implementation of Monte Carlo simulations, elasticity values were summed over the age-classes of three life history phases: fertility, juvenile survival and adult survival (Heppell et al., 2000). Here, juvenile is defined as any age-class younger than t_{mat}. This was performed after each simulation so that variations to $t_{\max}$ and t_{repro} were accounted for. To identify the effects of management on compensation between survival and fertility; elasticity ratios were calculated between fertility and both juvenile and adult survival phases following Cortés (2002). A compensation ratio of 4.0 indicates that a 10% decrease in the respective survival phase would require a 40% increase in fertility to maintain the original λ (Cortés, 2002; Heppell et al., 1999).

2.5. Management scenarios

The length-selective nature of shark fisheries means that F is rarely constant across age-classes. Therefore, the effects of varying F across age-classes (F_t) was examined and compared to scenarios where F was age-independent. Two age-selective harvest strategies were applied for both species: age-at-first-capture (AAFC) (Cortés, 1998; Simpfendorfer, 1999b) and age-at-last-capture (AALC). AAFC represents management strategies where juveniles are excluded from the fishery (such as protecting nursery areas). Conversely, AALC represents management strategies that implement gauntlet

Table 2
Age-specific natural mortality (M_t) estimates (yr^{-1}) for *C. albimarginatus* and *C. limbatus.*

Age (yrs)	Pauly	Jensen[1]	Jensen[2]	Chen and Watanabe	Pauly	Jensen[1]	Jensen[2]	Chen and Yuan	Chen and Watanabe	Peterson and Wroblewski
	C. albimarginatus				*C. limbatus*					
0	0.05 -0.06	0.03	0.07 – 0.08	0.12 - 0.16	0.21-0.20	0.16-0.17	0.12 – 0.31	0.15 -0.23	0.45 - 0.49	0.34 – 0.40
1				0.11 - 0.14					0.34 - 0.36	0.27 – 0.32
2				0.10 - 0.13					0.28 - 0.29	0.23 – 0.27
3	Same value for all ages			0.09 – 0.12	Same value for all ages				0.24 - 0.25	0.20 – 0.24
4				0.09 - 0.11					0.21 - 0.22	0.18 - 0.22
5				0.08 - 0.10					0.19 - 0.20	0.17 – 0.20
6				0.08 - 0.09					0.18 - 0.18	0.16 – 0.19
7				0.07 - 0.09					0.17 - 0.17	0.16 – 0.18
8				0.07 - 0.08					0.16 - 0.16	0.15 – 0.17
9				0.07 - 0.08					0.15 - 0.15	0.14 – 0.17
10				0.06 - 0.08					0.15 - 0.15	0.14 - 0.17
11				0.06 - 0.07					0.14 - 0.14	0.13 – 0.16
12				0.06 - 0.07					0.14 - 0.14	0.13 - 0.16
13				0.06 - 0.07					0.13 - 0.13	0.13 - 0.15
14				0.06 - 0.06					0.13 - 0.13	0.12 – 0.15
15				0.06 - 0.06					0.13 - 0.13	0.12 – 0.15
16				0.05 - 0.06					0.13 - 0.13	0.11 – 0.14
17				0.05 - 0.06					0.13 - 0.13	0.11 – 0.14
18				0.05 - 0.05					0.13 - 0.13	0.11 – 0.14
19				0.05 - 0.05					0.12 - 0.12	0.11 – 0.14
20				0.05 - 0.05					0.12 - 0.12	0.11 – 0.14
21				0.05 - 0.05					-	-
22				0.05 - 0.05					-	-
23				0.04 - 0.05					-	-
24				0.04 - 0.05					-	-
25				0.04 - 0.05					-	-
26				0.04 - 0.04					-	-
27				0.04 - 0.04					-	-
28				0.04 - 0.04					-	-
29				0.04 - 0.04					-	-
30				0.04 - 0.04					-	-
31				0.04 - 0.04					-	-
32				0.04 - 0.04					-	-

Jensen[1]: k invariant method.
Jensen[2]: age-at-maturity method.

fisheries – where the juveniles are harvested while the breeding stock is protected (Prince, 2005). Each of these scenarios represent commonly implemented management measures designed to protect different population demographics (Aires-da-Silva and Gallucci, 2007; McAuley et al., 2007; Walker, 1998).

To conduct these scenarios, F_t was incorporated into the survivorship elements of the Leslie Matrices such that the total mortality was the sum of F_t and M_t:

$$S_t = e^{-(M_t + F_t)}$$

Scenarios that examined the effects of an age-independent F were determined by calculating the limiting level of F that produces a stable population ($F_{CRITICAL}$). This was estimated by systematically increasing F equally across all age-classes until $\lambda = 1$ (Brewster-Geisz and Miller, 2000; Simpfendorfer, 1999b). The harvest rate that produces a stable population ($U_{CRITICAL}$) was estimated by transforming $F_{CRITICAL}$ from an instantaneous to an annual mortality rate as:

$$U_{CRITICAL} = 1 - e^{-F_{CRITICAL}}$$

$U_{CRITICAL}$ is the maximum proportion of the population that could be harvested each year before population declines occur.

AAFC analyses were performed by applying an equal level of F across all the age-classes caught by the fishery while assuming that $F = 0\ \text{yr}^{-1}$ for age-classes that have not yet entered the fishery. λ was estimated as the AAFC and F are systematically increased (Simpfendorfer, 1999b). AALC analysis was conducted by applying F equally across all the age-classes caught by the fishery while assuming that $F = 0\ \text{yr}^{-1}$ for ages that have left the fishery. λ was also estimated as the AALC and F were systematically increased. These analyses also incorporated Monte Carlo error to incorporate stochasticity into estimates of λ. Estimates of $F_{CRITICAL}$ and $U_{CRITICAL}$ were calculated for the age-classes exposed to the fishery.

Potentially sustainable harvest strategies that were identified by the AAFC and AALC analyses were explored further. Where analyses identified that a minimum or maximum size limit could be used as sustainable harvest strategies, a selectivity-at-age model was estimated using knife-edge selectivity for a given size limit. These selectivity-at-age models were computed using the variation around length-at-age estimates from the literature (Smart et al., 2017, 2015) using a generalised linear model with a binomial error structure and a logit-link function in the ‘R’ programme environment (R Core Team, 2013).

All of the matrix models, elasticity analyses and population projections were conducted in the ‘R’ programing environment (R Core Team, 2013) using the ‘popbio’ package (Stubben and Milligan, 2007).

3. Results

3.1. Natural mortality estimates

The age-dependent estimates produced by Chen and Watanabe's (1989) approach produced the highest mortality estimates for both species (Table 2). However, the full "U shape" of these curves did not occur as there was no increase in M_t for the final age-classes (Table 2). It is likely that the increase in M_t occurs at ages older than $t_{\max}$ due to the low k parameters of both species (Table 1). The M_t for the first age-class ranged from 0.12–0.16 yr^{-1} and 0.45–0.49 yr^{-1} which decreased to 0.04 yr^{-1} and 0.12 yr^{-1} for *C. albimarginatus* and *C. limbatus*, respectively. Variation between estimates was low for *C. albimarginatus* and ranged 0.03 yr^{-1} for the Jensen (1996) k invariant method to 0.16 yr^{-1} as upper estimate of Chen and Watanabe's (1989) method (Table 2). However, Jensen's (1996) k invariant method provided a very low estimate of M due to a low k value. This estimate was deemed to be unrealistically low for an age-independent value and was removed from the analysis.

M estimates were also similar for *C. limbatus*, with age-independent estimates ranging from 0.12 to 0.31 yr^{-1}, with both of these estimates based on the lower and upper estimates of the Jensen (1996) maturity method (Table 2). Age-dependent methods provided more variation although by age 3 both methods estimate M_t within the same range as the age-independent methods (Table 2).

3.2. Matrix elasticities

Matrix elasticities did not differ between the unfished population nor varying levels of F (Table 3). Juvenile survival had the highest elasticity phase for both species, followed by adult survival and then fertility. Juvenile survival elasticities were higher for *C. albimarginatus* than for *C. limbatus* at 0.77 and 0.62, respectively (Table 3). This identifies that the population growth of *C. albimarginatus* is more sensitive to changes in juvenile survival than *C. limbatus*. The fertility elasticities were very low for both species (Table 3). Accordingly, the elasticity ratios showed that increases in fertility cannot compensate for adult nor juvenile survival for either species without being biologically implausible. For example, for *C. albimarginatus* to compensate for an F of 0.1 on juveniles, the average number of pups (of both sexes) per year would need to increase to an average of 14.78, which is beyond the capacity of the species.

3.3. Stable-age distribution (w) and reproductive values (v)

The unfished stable-age distributions of both species showed that the proportion of the population in each age-class declined exponentially with age (Fig. 1a and b). *C. limbatus* had higher proportions of individuals in its early age-classes in comparison to *C. albimarginatus*. However, this is likely to be an artefact of the older $t_{\max}$ of *C. albimarginatus* which means that individuals were spread across more age-classes. The 95% quantiles of the Monte Carlo simulations showed a narrowing at age 4 for *C. limbatus* and age 7 for *C. albimarginatus*. This occurred as low values of w for younger ages classes produce higher values of w in older age-classes and vice versa. Therefore, there is a point on the curve where the same approximation of w occurs regards of the shape of the distribution.

The reproductive values of both species peaked where t_{repro} occurred (Fig. 1c and d). For *C. limbatus*, the reproductive values were similar between ages 8–12 before decreasing to age 20 ($t_{\max}$) (Fig. 1d). The peak in reproductive values was more pronounced for *C. albimarginatus* and occurred between ages 14–20 (Fig. 1c).

Greater variation occurred during the Monte Carlo simulations for reproductive values than the stable-age distributions for both species (Fig. 1c and d). This occurred as reproductive values were dependent on values of t_{mat}, M_t and litter size whereas the stable-age distributions were only dependent on values of M_t. At their peak, v values had a coefficient of variation of 24.20 for *C. albimarginatus* and 27.91 for *C. limbatus*

3.4. Population growth under different management scenarios

Increasing population growth occurred for both *C. albimarginatus* and *C. limbatus* in the absence of fishing mortality (Table 3). *C. albimarginatus* and *C. limbatus* had similar growth rates of $\lambda = 1.06$ and $\lambda = 1.05$, respectively (Table 3). However, *C. albimarginatus* had a larger G and R_0 (Table 3). Similar decreases in λ occurred for both species as F increased (Fig. 2), although R_0 decreased more rapidly for *C. albimarginatus* than for *C. limbatus* (Table 3). G did not change for either species as F increased (Table 3). The distributions of key demographic parameters (λ, G and R_0) from the Monte Carlo simulations demonstrate that the full variability of each parameter was captured during the 10,000 simulations (see supplementary material). However, G had a bimodal distribution for both species which identifies that some uncertainty remained around this parameter. Post-hoc analysis revealed that this distribution occurred as age-dependent M methods (Chen and Watanabe, 1989; Peterson and Wroblewski, 1984) produced larger G estimates than age-independent methods. Therefore, the upper quantile for G of both species was very large.

Both populations declined (4% per year for *C. albimarginatus* and 6% per year for *C. limbatus*) when $F = 0.1$ yr^{-1} (Table 3). When F was increased to 0.3 yr^{-1}, *C. albimarginatus* and *C. limbatus* populations declined 22% and 23% per year, respectively (Table 3; Fig. 2). When F was age-independent, the $F_{CRITICAL}$ was 0.07 yr^{-1} and 0.05 yr^{-1} for *C. albimarginatus* and *C. limbatus*, respectively (Fig. 2). These results

Table 3
Demography estimates for *C. albimarginatus* and *C. limbatus* under different age-independent fishing mortalities. Values in parentheses are 95% quantiles of the Monte Carlo simulations.

F	λ	G	R_0	Elasticities			Elasticity ratios	
				Fertility	Juvenile survival	Adult survival	Juvenile survival	Adult survival
C. albimarginatus								
0	1.06 (0.99–1.12)	21.94 (12.06–39.75)	4.35 (0.66–10.32)	0.05 (0.04–0.06)	0.77 (0.69–0.90)	0.17 (0.05–0.27)	14.78	3.38
0.1	0.96 (0.90–1.01)	22.124 (12.16–40.16)	0.62 (0.12–1.43)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.80	3.39
0.2	0.87 (0.81–0.91)	21.93 (12.11–39.84)	0.10 (0.054–0.24)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.81	3.36
0.3	0.78 (0.73–0.83)	22.06 (12.07–40.08)	0.02 (0.01–0.05)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.78	3.38
C. limbatus								
0	1.05 (0.95–1.16)	16.00 (7.64–36.7)	2.26 (0.63–4.85)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.00	3.11
0.1	0.94 (0.86–1.06)	16.10 (7.55–36.97)	0.78 (0.19–1.87)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.00	3.11
0.2	0.86 (0.78–0.95)	15.94 (7.45–36.78)	0.29 (0.05–0.81)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	6.98	311
0.3	0.77 (0.70–0.86)	16.18 (7.61–37.07)	0.12 (0.02–0.38)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.03	3.12

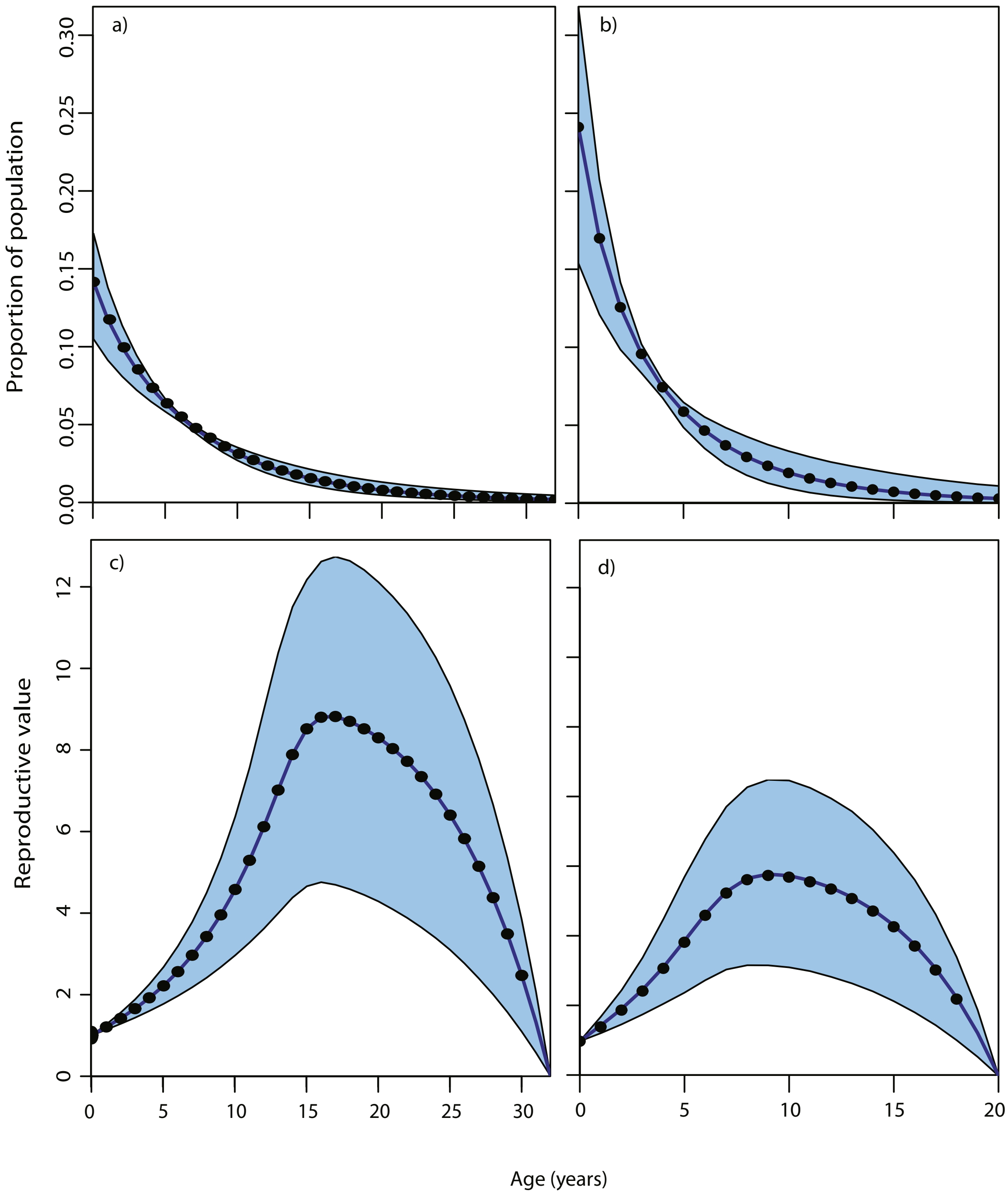

Fig. 1. The stable age distributions (a–b) and reproductive values (c–d) for unfished populations of *C. albimarginatus* (a, c) and *C. limbatus* (b, d). The blue shaded areas represent the 95% quantiles of the Monte Carlo simulations. These distributions were determined using Monte Carlo simulations with $t_{\max}$ set at 32 years for *C. albimarginatus* and 20 years for *C. limbatus*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicate that neither species can tolerate moderate levels of fishing pressure when all age-classes are exposed to fishing.

The AAFC analysis for both species revealed that all juvenile age-classes (age-classes younger than the age-at-maturity) would need to be excluded from the fishery before F could increase beyond its initial $F_{CRITICAL}$ level (Fig. 3). For *C. albimarginatus*, this scenario meant that ages 0–15 all required exclusion from fishing (Fig. 3). For *C. limbatus*, F could not be increased beyond the $F_{CRITICAL}$ level unless ages 0–7 were excluded from fishing (Fig. 3). Each of these values is approximately equivalent to t_{mat}, which identifies that to sustainably harvest the adult age-classes, all of the juvenile age-classes must be protected.

The gauntlet fishery scenario revealed that exclusively harvesting the young-of-the-year (YOY) of both species could maintain increasing population growth while supporting reasonable harvest levels (Table 4; Fig. 4). Up to 48% ($F = 0.65\,\text{yr}^{-1}$) of YOY *C. albimarginatus* could be harvested each year while maintaining a stable population. This corresponds to a maximum size limit of ~80 cm TL (Table 4). If several early age-classes (ages 0–5 years) were exposed to the fishery, 13% of those age-classes could be fished ($F = 0.14\,\text{yr}^{-1}$). This corresponds to a maximum size limit of ~100 cm TL (Table 4).

The gauntlet fishery scenario showed that this strategy would also work for *C. limbatus*, although it could not sustain the same

Table 3
Demography estimates for *C. albimarginatus* and *C. limbatus* under different age-independent fishing mortalities. Values in parentheses are 95% quantiles of the Monte Carlo simulations.

F	λ	*G*	R_0	Elasticities			Elasticity ratios	
				Fertility	Juvenile survival	Adult survival	Juvenile survival	Adult survival
C. albimarginatus								
0	1.06 (0.99–1.12)	21.94 (12.06–39.75)	4.35 (0.66–10.32)	0.05 (0.04–0.06)	0.77 (0.69–0.90)	0.17 (0.05–0.27)	14.78	3.38
0.1	0.96 (0.90–1.01)	22.124 (12.16–40.16)	0.62 (0.12–1.43)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.80	3.39
0.2	0.87 (0.81–0.91)	21.93 (12.11–39.84)	0.10 (0.054–0.24)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.81	3.36
0.3	0.78 (0.73–0.83)	22.06 (12.07–40.08)	0.02 (0.01–0.05)	0.05 (0.04–0.06)	0.77 (0.68–0.89)	0.17 (0.05–0.27)	14.78	3.38
C. limbatus								
0	1.05 (0.95–1.16)	16.00 (7.64–36.7)	2.26 (0.63–4.85)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.00	3.11
0.1	0.94 (0.86–1.06)	16.10 (7.55–36.97)	0.78 (0.19–1.87)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.00	3.11
0.2	0.86 (0.78–0.95)	15.94 (7.45–36.78)	0.29 (0.05–0.81)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	6.98	311
0.3	0.77 (0.70–0.86)	16.18 (7.61–37.07)	0.12 (0.02–0.38)	0.09 (0.07–0.13)	0.62 (0.50–0.73)	0.28 (0.20–0.39)	7.03	3.12

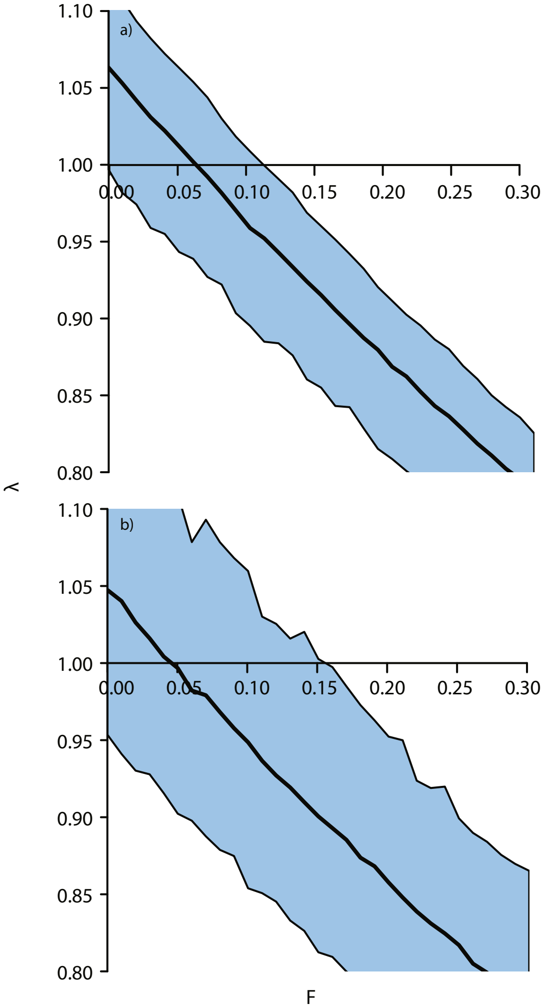

Fig. 2. The relationship between the finite rate of population increase (λ) and instantaneous fishing mortality (*F*) for (a) *C. albimarginatus* and (b) *C. limbatus*. $F_{CRITICAL}$ occurs when λ = 1. The blue shaded areas represent 95% quantiles of the Monte Carlo simulations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

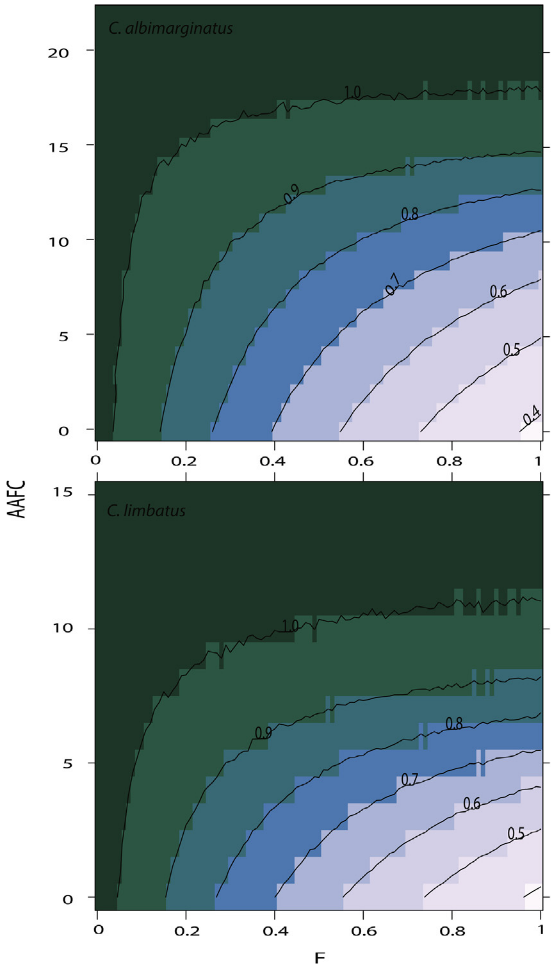

Fig. 3. Contour plot of finite rate of population increase (λ) as a function of fishing mortality (*F*) and age-at-first-capture (AAFC) for *C. albimarginatus* and *C. limbatus.* Estimates of λ were estimated using Monte Carlo Simulations to incorporate stochasticity. An increasing population occurs when λ > 1 (Dark green area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

levels of fishing pressure as *C. albimarginatus* (Table 4; Fig. 4). Up to 38% ($F = 0.48\ \text{yr}^{-1}$) of the first age-class and up to 16% ($F = 0.17\ \text{yr}^{-1}$) of the first three age-classes could be harvested while maintaining a stable population. This also corresponds to maximum size limits of ~ 80 cm TL and ~100 cm TL, respectively (Table 4).

A selectivity-at-age model identified that a 100 cm TL size limit could be applied for both species (Fig. 5). An assumption of this model was that knife-edge selectivity occurs where individuals larger than 100 cm TL are excluded from fishing. This selectivity captured age-classes up to an age of 5 for *C. albimarginatus* and up to an age of 3 for *C. limbatus* (Fig. 5). Therefore, the $F_{CRITICAL}$ for this size limit was $0.14\ \text{yr}^{-1}$ for *C. albimarginatus* and $0.17\ \text{yr}^{-1}$ for *C. limbatus* (Table 4). This selectivity-at-age was possible as less variation in length-at-age occurred at younger ages for both species (Smart et al., 2017, 2015). However, due to the substantial vari-

Table 4
The effect of age-at-last-capture (AALC) on $F_{CRITICAL}$ and $U_{CRITICAL}$ for *C. albimarginatus* and *C. limbatus*. The length-at-age estimates are sourced from the literature (Smart et al., 2017, 2015) and include standard error (S.E) calculated from the variation in the growth curves.

AALC (years)	$F_{critical}$	$U_{critical}$	Length-at-age ± S.E (cm)
C. albimarginatus			
1	0.65	0.48	79.3 (±3.6)
2	0.35	0.30	87.6 (±5.5)
3	0.21	0.19	95.7 (±7.4)
4	0.17	0.16	103.6 (±9.3)
5	0.14	0.13	111.4 (±11.1)
6	0.11	0.10	119.1 (±12.9)
7	0.10	0.10	126.6 (±14.6)
8	0.09	0.09	134.0 (±16.3)
9	0.08	0.08	141.2 (±18.0)
10	0.07	0.07	148.2 (±19.7)
C. limbatus			
1	0.48	0.38	83.2 (±16.6)
2	0.27	0.24	102.0 (±22.8)
3	0.17	0.16	118.9 (±28.4)
4	0.13	0.12	134.0 (±33.4)
5	0.11	0.10	147.6 (±37.9)

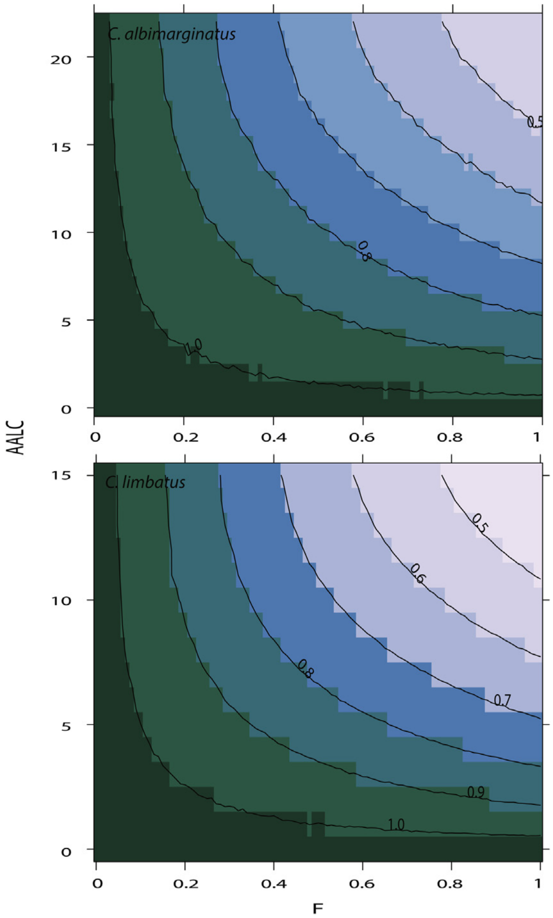

Fig. 4. Contour plot of finite rate of population increase (λ) as a function of fishing mortality (*F*) and age-at-last-capture (AALC) for *C. albimarginatus* and *C. limbatus*. Estimates of λ were estimated using Monte Carlo Simulations to incorporate stochasticity. An increasing population occurs when λ > 1 (Dark green area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

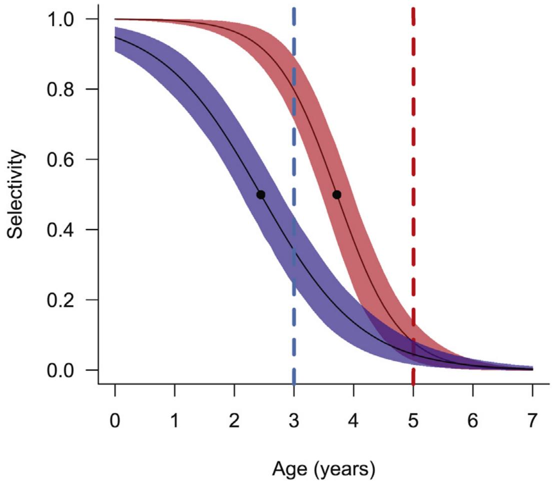

Fig. 5. Selectivity-at-age for both species at a maximum size limit of 100 cm TL. *C. limbatus* is represented by the blue curve with bootstrapped 95% confidence intervals represented by the shaded area. The dashed blue line represents the age-class where an *F* of 0.17 yr^{-1} was sustainable according the AALC analysis. *C. albimarginatus* is represented by the red curve with bootstrapped 95% confidence intervals represented by the shaded area. The dashed red line represents the age-class where an *F* of 0.14 yr^{-1} was sustainable according the AALC analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ation in length-at-age for older ages, no minimum size limit was able to restrict *F* to specific older ages classes based on the AAFC analysis.

3.5. Comparison with other *Carcharhinus* species

C. albimarginatus and *C. limbatus* have demographic parameters that are similar to other large *Carcharhinus* species (Table 5). A typical trait of larger *Carcharhinus* species was a low rate of λ and a large *G* which was evident for *C. brachyurus*, *C. obscurus*, *C. plumbeus* and *C. leucas* whose *G* ranged from 19.8–26.2 years (Table 5). *C. albimarginatus* had a similar *G* (22.24 years) which is unsurprising as all of these species are slow growing and have a large maximum length (>300 cm TL). *C. limbatus* from Indonesia had different demographic parameters to conspecifics from the eastern Gulf of Mexico as they had a higher λ and *G* (Table 5). This suggests that regional differences in their life history lead to different demographic characteristics. Only 2 of the 14 *Carcharhinus* species analyses by (Cortés, 2002) had a higher adult survival elasticity in comparison to their juvenile elasticity (Table 5). These two species were *C. tilstoni* and *C. sorrah*, both of which are smaller bodied and faster growing than most other *Carcharhinus* species (Harry et al., 2013).

4. Discussion

The present study provides an improved understanding of the population biology and demography of two shark species harvested in the Indo-Pacific and importantly, predicts how their populations may respond to different management approaches. The demographic estimates show that both *C. albimarginatus* and *C. limbatus* lack the propensity to be harvested sustainably unless fishing is limited to specific age-classes. If the entire age ranges of either species are exposed to fisheries, then overfishing (population declines that do not equilibrate) will occur at very low levels of *F* (>0.1 yr^{-1}). Of the different management scenarios examined, the exclusive harvest of YOY individuals was the most sustainable fishing strategy for both species. *C. albimarginatus* is one of the least studied reef associated shark species and prior to this study little was known about

Table 5
Demographic estimates for 14 *Carcharhinus* species produced using Monte Carlo simulations by Cortés (2002). Values in parentheses are the upper and lower 95% quantiles of the Monte Carlo simulations.

Species	λ	G	Elasticities		
			Fertility	Juv. Survival	Adult Survival
C. tilstoni	1.15 (1.05–1.23)	6.0 (4.3–7.8)	0.15 (0.11–0.19)	0.42 (0.33–0.50)	0.44 (0.37–0.51)
C. longimanus	1.12 (1.04–1.22)	7.0 (5.5–8.6)	0.13 (0.10–0.15)	0.50 (0.42–0.57)	0.38 (0.32–0.44)
C. falciformis	1.11 (1.08–1.14)	10.6 (9.9–11.5)	0.09 (0.08–0.09)	0.64 (0.61–0.68)	0.27 (0.24–0.31)
C. sorrah	1.09 (0.93–1.36)	4.3 (2.8–5.6)	0.19 (0.15–0.26)	0.37 (0.22–0.49)	0.44 (0.34–0.55)
C. porosus	1.09 (1.03–1.15)	8.4 (7.5–9.6)	0.11 (0.1–0.12)	0.58 (0.54–0.63)	0.31 (0.27–0.35)
C. galapagensis	1.09 (1.05–1.14)	10.8 (9.2–12.2)	0.09 (0.08–0.10)	0.61 (0.57–0.65)	0.30 (0.26–0.34)
C. brachyurus	1.04 (1.03–1.06)	23.3 (21.9–25.0)	0.04 (0.04–0.04)	0.77 (0.75–0.79)	0.19 (0.17–0.21)
C. brevipinna	1.04 (1.01–1.07)	10.4 (9.7–10.8)	0.09 (0.08–0.09)	0.61 (0.59–0.65)	0.30 (0.25–0.32)
C. obscurus	1.03 (1.02–1.04)	26.2 (24.2–28.2)	0.04 (0.03–0.04)	0.68 (0.65–0.71)	0.29 (0.26–0.31)
C. plumbeus	1.02 (1.01–1.04)	19.8 (16.7–22.7)	0.05 (0.04–0.06)	0.69 (0.66–0.72)	0.26 (0.23–0.29)
C. leucas	1.00 (0.99–1.01)	21.6 (20.5–23.1)	0.04 (0.04–0.05)	0.77 (0.75–0.80)	0.18 (0.16–0.21)
C. limbatus[a]	0.97 (0.93–1.07)	10.0 (8.2–14.8)	0.09 (0.06–0.11)	0.60 (0.42–0.66)	0.31 (0.23–0.50)
C. amblyrhynchos	0.94 (0.90–0.98)	9.6 (8.7–10.8)	0.09 (0.09–0.10)	0.61 (0.57–0.65)	0.30 (0.26–0.33)
C. acronotus	0.85 (0.71–0.97)	4.2 (3.7–5.0)	0.19 (0.17–0.21)	0.47 (0.40–0.56)	0.34 (0.26–0.40)

[a] Population from the Eastern Gulf of Mexico, USA.

its demography or the impacts of fishing on its population. While demographic analyses have been conducted on *C. limbatus* populations (Chen and Yuan, 2006; Cortés, 1998, 2002; Liu et al., 2015), these analyses were lacking for the Indo-Pacific population which grows larger and matures later than its Atlantic Ocean conspecifics (Smart et al., 2015).

Estimates of λ are highly variable for elasmobranchs and can be as high as 1.6 yr^{-1} and 1.4 yr^{-1} for species such as the scalloped hammerhead (*Sphyrna lewinii*) and blue shark (*Prionace glauca*), respectively (Cortés, 2002). However, many slow growing and long lived shark species have much lower λ as they are less productive (Cortés, 2002; Liu et al., 2015). *C. albimarginatus* and *C. limbatus* are two such species as they had slow population growth rates ($\lambda = 1.06\ \text{yr}^{-1}$and $\lambda = 1.05\ \text{yr}^{-1}$, respectively) when their populations were unfished. The population growth rates of both species declined markedly as low levels of *F* were introduced to the demographic analyses. When $F = 0.1\ \text{yr}^{-1}$, both populations declined by 4–6% and when *F* was increased to 0.3 yr^{-1} they declined by more than 20% per year. These demographic results demonstrate that neither species was able to tolerate moderate levels of harvest when their entire age ranges were exposed to fishing.

Failure to account for any uncertainty or variation in vital rates could potentially jeopardise the accuracy of λ – the most important demographic parameter (Caswell et al., 1998). This study accounted for this uncertainty and variation by using Monte Carlo simulations to provide summary statistics around demographic parameters (Beerkircher et al., 2003; Coelho et al., 2015; Cortés, 2002). While the means of λ, *G*, and R_0 fell within expected ranges, the Monte Carlo simulations showed broad variation around each parameter. Particularly, large variation occurred around *G* for both species which had bimodal distributions. This distribution was caused by a using combination of age-dependent and age-independent *M* estimators in the Monte Carlo simulations. As age-dependent estimators produce lower values of M_t for older age classes (Chen and Watanabe, 1989; Peterson and Wroblewski, 1984), this resulted in older *G* estimates and thus greater uncertainty around this parameter. Additionally, the elasticity analyses identified that the majority of the variation around λ resulted from changes to survivorship elements (particularly for juveniles) during the Monte Carlo simulations. Elasticity analyses identify which matrix elements have the greatest proportional effect on λ (de Kroon et al., 1986). For both species, matrix elasticities were low for fertility and highest for juvenile and adult survivorship. By producing matrix elasticities in the Monte Carlo simulations, variation and uncertainty were also factored into these analyses (Cortés, 2002). These simulations demonstrated that some variation occurred around juvenile and adult survivorship elasticities but very little around fertility. This indicates that varying vital rates that affected fertility produced few changes to λ while altering *M* and *F* had the greatest influence. Therefore, survivorship elements had the greatest influence over both λ and *G*, demonstrating that care must be taken when estimating *M* to ensure appropriate estimates are used.

As vital rates are used to construct matrix elements they must be carefully scrutinised so that overconfidence in the resulting demographic estimates do not mislead management. The life history parameters of both species were drawn from multiple life history studies (Bass et al., 1973; Smart et al., 2017, 2015; Wheeler, 1962; White, 2007) and many of these parameters (e.g., 12-month gestation period and biennial reproductive cycle) are typical of the genus *Carcharhinus* (Last and Stevens, 2009). While the litter sizes were variable for both species, these were empirical values recorded in the field (Bass et al., 1973; Wheeler, 1962; White, 2007) and thus confidence can be placed around their means and ranges. The greatest uncertainty in these life history parameters was around t_{max} and t_{mat} as these parameters were drawn from life history studies with limited samples (Smart et al., 2017, 2015). However, the elasticities for both species determined that fertility elements had little influence on λ in comparison to survivorship. Therefore, small deviations from true population values of reproductive and longevity parameters would have little effect in comparison to inaccurate *M* estimates. This is problematic as *M* is one of the most difficult parameters to estimate for marine taxa (Kenchington, 2014). The estimates of *M* produced for both species varied between approaches and therefore this vital rate had the most uncertainty. While this study has accounted for this uncertainty by incorporating Monte Carlo simulations, its results should still be interpreted with caution until more definitive estimates of *M* are available for both species.

The demographic estimates produced for both species are within expected ranges as they are comparable to those of similar whaler shark species (family: Carcharhinidae). When Leslie Matrices with Monte Carlo simulations were applied to a range of shark species; large whaler sharks (maximum size > 2.5 m TL) typically had mean λ of 1.02–1.06 yr^{-1} when the populations were unfished (Cortés, 2002). The unfished populations of *C. albimarginatus* and *C. limbatus* corresponded to this as they had a mean λ of 1.06 yr^{-1} and 1.05 yr^{-1}, respectively. Previous demographic studies on large whaler sharks that also included *F* found similar results to the present study. Life table analyses performed on silky sharks (*C. falciformis*) estimated that $r = 0.05\ \text{yr}^{-1}$ ($\lambda = 1.05\ \text{yr}^{-1}$) when the population was unfished. However, the population declined as *F* approached 0.05 yr^{-1} (Beerkircher et al., 2003). Similarly, sandbar shark (*C. plumbeus*) populations in the US were determined to increase at a rate of 1.3% per year when unfished but declined when low levels of *F* were applied across all age-classes (Cortés, 1999). When a range of fishing strategies were examined, it was determined and that large juveniles (100–150 cm TL) were the most vulnerable life stage (Cortés, 1999). However, if harvest was limited to only YOY *C. plumbeus* then this age-class could be fished sustainably at low levels (Cortés, 1999).

The exclusive harvest of juveniles through gauntlet fisheries has been demonstrated as one of the most sustainable management strategies for shark fisheries (Prince, 2005). It relies on the principle that when *M* is high for juvenile age-classes, it can be replaced by *F* without affecting the population growth (Cortés et al., 2012). As long as only the juveniles are harvested, the breeding stock is protected and can replace the young sharks taken by the fishery. The most successful example of this strategy is the dusky shark (*C. obscurus*) gillnet fishery in Western Australia (WA) (McAuley et al., 2007; Simpfendorfer, 1999a). *C. obscurus* had a low *r* of 0.04 yr^{-1} ($\lambda = 1.04\,yr^{-1}$) and an $F_{CRITICAL}$ of 0.04 yr^{-1} when all age-classes were exposed to fishing (Simpfendorfer, 1999a). However, when fishing was limited to YOY, up to 64% ($F_{CRITICAL} = 1.04\,yr^{-1}$) could be harvested before the population would decline (Simpfendorfer, 1999a). The present study determined that a similar strategy could be applied for *C. albimarginatus* and *C. limbatus* as up to 48% ($F_{CRITICAL} = 0.65\,yr^{-1}$) and 38% ($F_{CRITICAL} = 0.48\,yr^{-1}$) of YOY, respectively can be harvested without population declines until density-dependent effects begin to manifest. However, with this management strategy it is imperative that fishing be limited to these age-classes (McAuley et al., 2007; Simpfendorfer, 1999a). If the juveniles and adults were also caught by the fishery (even at low levels) then a gauntlet strategy would fail and the population would decline.

In addition to examining a gauntlet fishery scenario, this study examined the efficacy of protecting the juvenile age-classes to maintain sustainable harvest levels. This management strategy can be particularly effective for small and productive shark species (Simpfendorfer, 1999b) but less effective for large less productive shark species (Cortés, 1998). The AAFC analysis in this study demonstrated that a stable population would not occur for either species unless all immature age-classes were protected from fishing. Given that *C. albimarginatus* and *C. limbatus* mature at 14.8 and 7.6 years respectively (Smart et al., 2017, 2015), a large portion of the population would need to be protected for this management strategy to succeed. However, catches of *C. limbatus* from Indonesia show that the majority of landed individuals were juveniles (White, 2007). Similarly, the age-classes included in Smart et al. (2017) show that mostly immature *C. albimarginatus* were caught by PNG longline fisheries. Delaying harvest until these species mature to achieve sustainable *F* levels would potentially maximise conflict with fishers and would also risk recruitment overfishing (Cortés, 1998). Therefore, management strategies that focus on protecting immature age-classes would likely be ineffective and difficult to regulate for both populations.

While both species had similar life history and demographic estimates, subtle differences in management are required to maintain sustainable harvest levels. *C. albimarginatus* could sustain higher levels of YOY and juvenile harvest than *C. limbatus*. This is due to *C. albimarginatus* having higher reproductive values (left eigenvector; v) across age-classes. Reproductive values define the relative contribution to future population growth that an individual in a particular age-class is expected to make (Morris and Doak, 2002). Therefore, as YOY and younger juvenile age-classes contribute little to future population growth, these individuals can sustain moderate harvest through gauntlet fishing without detriment to the population. As *C. albimarginatus* has higher v across its adult age-classes, it is able to replace harvested age-classes at a greater rate than *C. limbatus* – sustaining higher levels of *F*. Therefore, when only the YOY are fished, *C. albimarginatus* can sustain an *F* of 0.65 yr^{-1} ($U = 0.48\,yr^{-1}$) while *C. limbatus* can sustain an *F* of 0.48 yr^{-1} ($U = 0.38\,yr^{-1}$), until density dependent effects occur. While both species have different growth profiles (Smart et al., 2017, 2015), a maximum size limit of 100 cm TL would restrict fishing to age-classes that can sustain higher levels of *F* for both species. This size limit would encapsulate individuals up to an age of 3 for *C. limbatus* and 5 for *C. albimarginatus*, thus allowing for an increased $F_{CRITICAL}$ of 0.17 yr^{-1} and 0.14 yr^{-1}, respectively.

5. Conclusions

The harvest strategies presented in this study demonstrate that both *C. albimarginatus* and *C. limbatus* can be fished without their populations declining given appropriate management. Critically though, only limited information is available on either species stock status, posing a serious challenge for stock assessments (Brooks et al., 2010). A current *F* is required to determine whether a stock has been overfished, and an estimate of biomass or a time series of relative abundance is needed to evaluate overfishing criteria (Cortés et al., 2012). Furthermore, a lack of catch information from artisanal and subsistence fisheries will provide challenges in estimating these analytical reference points and provide difficultly in scaling sustainable harvest levels (Brooks et al., 2010). For a gauntlet fishery to be sustainable, the older age-classes must be protected from fishing (Prince, 2005; Simpfendorfer, 1999a). Total protection of older age-classes can be a difficult task even in well managed fisheries (McAuley et al., 2007). Subsequently, restricting fishing effort to the necessary length-classes may prove difficult in developing nations where subsistence and artisanal fisheries are complex, dispersed and difficult to monitor and manage. With this in mind, the most conservative approach to sustaining both populations would be to the limit *F* on the young adults and first breeders by implementing a maximum size limit of 100 cm TL. This precautionary measure is warranted as mature individuals require the greatest protection (Cortés et al., 2012). The target level of *F* for these age-classes should also be set at a conservative level which is lower than the maxima provided by this study as some uncertainty still exists around these demographic parameters. Further studies that attempt to directly estimate *M* would be beneficial as this vital rate was the most uncertain for these species and had the most influence over the matrix analyses. Therefore, a better understanding of *M* can lead to more robust assessments being undertaken. Once more detailed data on catch, fishing effort and species abundance on the fisheries are available, the results of this study can be combined with other derived analytical reference points. This will then determine if these populations have been overfished and establish the best approach to ensure they are harvested sustainably into the future.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.03.002.

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SUSTAINABLE SHARK AND RAY FISHERIES IN PAPUA NEW GUINEA

Sector snapshot:

- The rising value of shark products on international markets over recent years has seen an increasing contribution of shark and ray resources to the revenues of PNG's fisheries sector and the livelihoods of PNG's coastal communities
- Very limited fisheries and ecological data exists for sharks and rays in PNG waters, with the exception of catch data from the targeted commercial longline fishery and data on the domestic trade of dried shark fin
- PNG's NFA and the Australian Centre for International Agricultural Research (ACIAR) funded a programme that has provided detailed information on the current exploitation of shark and ray resources in PNG and generated a number of management options
- A total of 130 shark and ray species are known to occur in PNG waters, with about half of these currently harvested by one or more fisheries
- Sharks and rays are caught in a number of fisheries, both commercial and artisanal, as both target and incidental catch
- A target longline fishery, operating out of Rabaul, accounted for the largest catches of sharks in PNG with an average annual shark catch of ~2,500 t (based on 2007-2013 catch data); this fishery closed in July 2014
- The tuna longline fishery has a bycatch of sharks with an average annual shark catch of 175 t (based on 2006-2015 catch data); this tuna fishery is in decline and is now restricted to the southern EEZ
- The tuna purse seine fishery has an average annual bycatch of sharks and rays of 809 t (based on 2006-2015 catch data); it is the largest commercial fishery in PNG
- The Gulf of Papua prawn trawl fishery has a diverse bycatch of sharks and rays with an estimated average annual shark and ray catch of 140 t (based on 2006-2011 data)
- The small-scale coastal fisheries throughout PNG comprise a variety of gear types and fishing methods as well as habitat types; based on dried shark fin data, average annual shark catches in the coastal fisheries were estimated to be 440 t (based on 2010-2013

shark fin data) while no data exists to estimate ray catches although harvesting does occur

- In some areas, e.g. Western, East Sepik and Bougainville provinces, shark products are not entering the current data collection system with anecdotal accounts of trade across international borders occurring

Summary:

Sharks and rays have previously been shown to be an important export commodity for PNG's fisheries. However, there was no detailed information on the sustainability of the fisheries which interact with PNG's shark and ray resources and catches were generally poorly understood. A Shark Management Plan was established for the target shark longline fishery in 2002. However, there were little data on the catch composition of sharks and rays in the prawn trawl fishery and the various coastal fisheries in PNG. Development of evidence-based options for managing PNGs shark and ray resources is required. This policy brief describes how sharks and rays in PNG's fisheries can be more sustainably managed into the future.

Introduction:

Papua New Guinea's marine environment supports a variety of industries, including fishing, tourism, oil and gas exploration and production, mining, and shipping. Commercial fisheries which either target or have significant bycatch of sharks and rays are the shark and tuna longline, purse seine and the prawn trawl fisheries. Sharks and rays are also taken in various coastal fisheries through gillnetting, hook and line fishing, trapping, seine netting, etc. Although these small-scale fisheries usually have much lower catches of sharks and rays, their management can be complicated by the fact that shark fishing can sometimes be closely linked to community livelihoods and wellbeing. Managing sharks and rays sustainably into the future requires reliable and robust reference data to produce evidence-based management options. This requires an understanding of the species being used, their biological attributes, their connectivity with adjacent regions, as well as the social and economic characteristics of the fisheries involved.

Policy considerations:

This research programme provided new data about shark and ray catches in PNG fisheries, and insights into eleven key issues affecting the long-term sustainable use of these resources and how PNG manages them.

1. Meeting international obligations

The project has found that a number of species caught in the various fisheries in PNG are currently listed on either Appendix I or II of CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora). Appendix I species (i.e. four species of sawfish) are considered threatened with extinction and CITES prohibits international trade for commercial purposes. Appendix II species (i.e. oceanic whitetip shark, scalloped hammerhead, great hammerhead, smooth hammerhead, silky shark, thresher sharks, whale sharks, manta and devilrays) are not necessarily threatened with extinction but may become so, unless trade is regulated; these species require the development of a Non-Detriment Finding (NDF) before international trade can be allowed. A significant proportion of the dried shark fins exported from PNG include CITES Appendix I or II species. Given PNG is a party to CITES, non-compliance could impact trade in other sectors through a Review of Significant Trade.

This relates to all fisheries and is a current issue for PNG.

2. Improving understanding of coastal fisheries and livelihood linkages

Small-scale coastal fisheries are a national priority for the PNG National Fisheries Authority. This project has found that some small scale fishers have a high dependence on shark products in coastal areas such as Milne Bay Province where communities on the outer islands of the province rely on income from dried marine products such as shark fin due to their lack of alternative incomes options and distance from markets. Improving the sustainable use of PNG's sharks and rays will provide long-term benefits to many coastal fishers by ensuring a future resource. There is still a paucity of information (e.g. species compositions, biological attributes, environmental preferences, connectivity) on sharks and rays caught in the coastal fisheries, and links to livelihoods and community aspirations. Better information is required to improve our understanding of how sharks and rays are utilised, community dependence on these resources, and the potential to improve management and explore alternative livelihoods to ensure that sharks and rays are sustainably used, and where necessary protected.

This relates to the coastal fisheries sector and is a current issue for PNG.

3. Maintenance of the national fisheries observer program

This project documents the value of, and the need to maintain and support the excellent NFA fisheries observer program. The high-quality, trained observers available in PNG allow for collection of extremely valuable and accurate catch data from the commercial fisheries. Where observer coverage is high, e.g. purse seine fishery, data collection is accurate and reliable. Where there is lower observer coverage, e.g. tuna longline and prawn trawl fisheries, data is less reliable and increasing coverage would drastically improve the data robustness. PNG should ensure this observer program is retained and ideally increased to ensure accurate data is collected to allow for better management decisions to be developed.

This relates to the longline, purse seine and prawn trawl fisheries and is a current challenge.

4. Compliance and enforcement of current management measures

Non-compliance with existing management measures has been demonstrated in several fisheries. This undermines the sustainable management initiatives put in place by NFA. Different compliance programs and enforcement mechanisms should be investigated to determine the most cost effective method, e.g. increasing observer coverage, electronic/video monitoring, etc.

This relates to any fishery with regulations in place and is a current issue.

5. Data collection and management

Data collection and management is a fundamental ongoing requirement for fishery management. The mechanisms through which data are managed needs to be improved to ensure data is suitable for various uses and archived effectively for longitudinal uptake. For example, data from the shark and tuna longline fisheries was pooled for a number of years which makes it impossible to identify catches in the different fisheries. Additionally, double counting is possibly an issue with the shark fin trade data reported by domestic buyers of fin, particularly when the product moves through more than one buyer within PNG.

This relates to all fisheries and is a current issue.

6. Improving understanding of market chains

There is a need to improve the understanding of the market chains for shark products and the factors that drive their trade. Market chains within PNG include small-scale fishers, large-scale fishers, small-scale processors and buyers as well as large-scale buyers and exporters. The socio-economic benefits generated at each stage of the market chain for shark products varies and is an important consideration for management. Understanding the drivers of trade can also better inform management. For example, shark catches are correlated with the sea cucumber and fish maw fisheries as they use the same market chains. Thus, when sea cucumber fishing occurs, a higher value for shark fin can be obtained so catches increase.

This relates to all fisheries and is a current issue.

7. Monitoring of new, expanding or trial fisheries

Any new, expanding or trial fisheries which do, or are likely to, catch (either by target or bycatch) sharks and rays need to be monitored as they will potentially impact on the sustainable use of these resources in PNG. Trial fisheries can operate for many years and during this time data collection needs to be maintained and considered in relation to the other fisheries in PNG. Good observer coverage is critical for these fisheries when they begin or expand.

This relates to all fisheries and is a current issue.

8. Develop a National Plan of Action (NPOA) for Sharks

The development of a detailed NPOA for sharks for PNG is urgently required and will help PNG develop a more holistic view of shark management. To date, most decisions are based only on individual commercial fisheries, with the coastal fisheries sector not adequately considered. Demographic analyses of key shark species undertaken during this project, as well as other recent ones conducted in the WCPFC (oceanic whitetip and silky shark), indicate that population declines are highly likely without adequate fisheries management. These results need to be addressed in the NPOA with management options on how to best mitigate population declines.

This relates to all fisheries and should be considered in the near future.

9. Safe handling and release guides with associated training

In some fisheries, the safe return of sharks or rays to the water may be needed. This includes: whale sharks and devil rays in the purse seine fishery, sharks in the tuna longline fishery, sawfish in trawl and coastal fisheries, etc. In these instances, safe handling and release guides are required to improve the survivability of the specimens. Safe handling practices are also required to ensure the safety of the fishers themselves as large sharks and rays can be dangerous if handled incorrectly. Improving the survival of released sharks and rays will improve the sustainable management practices being adopted.

This relates to all fisheries and should be considered in the near future.

10. Use of the shark and ray project (FIS/2012/102) data to improve shark management

The large quantity of validated fisheries data collected during the ACIAR project FIS/2012/102 provides an important baseline for future fisheries management. If used correctly, these data will underpin future management of sharks and rays in PNG.

11. Community stewardship

In the coastal fisheries sector, improved resource stewardship, conservation incentives, collaborative management arrangements and compliance and monitoring need to be explored to find ways to more effectively manage shark and ray resources in a way that also balances livelihoods and food security. This would be supported by engagement with and education of PNG's coastal communities to build an improved understanding amongst community members of the vulnerability of shark and ray species to overfishing.

This effects the coastal fisheries sector and is a future action requiring increased information on the characteristics of these fisheries and the socio-economic characteristics of the communities that depend on them.

Key messages:

- ACIAR-funded research has provided rigorous and comprehensive baseline data which can be used to develop evidence-based management actions for sharks and rays in PNG
- The national fisheries observer program needs to be maintained as it provides the crucial fisheries dependent data which is fundamental to fisheries assessments
- Demographic analyses of key species (e.g. silky shark, grey reef shark, silvertip shark) indicate that population declines are highly likely if the fisheries catching them are not adequately managed
- Although sharks are caught by a suite of fisheries in PNG, there is a strong overlap in species composition between the fisheries; thus assessment of the sustainability of sharks and rays in a particular fishery needs to take into account all other fisheries interacting with the same species
- There is a need to meet certain international obligations, particularly for CITES listed species; Australia researchers have the necessary skills and experience to guide PNG agencies through this complicated process to ensure compliance with international trade obligations
- In some sectors, a large number of livelihoods are dependent on shark products; ensuring long term sustainability of these resources is critical to supporting these livelihoods in the future

Conclusion:

Ensuring the sustainability of shark and ray fisheries is challenging given the very low productivity of most shark and ray species. Balancing this with the importance of shark products to many livelihoods is critical and social and economic information is crucial in addressing this issue. The comprehensive data produced by the ACIAR-funded research provides evidence-based policy considerations to assist with managing PNG's shark and ray resources sustainability. This will ensure long-term access to these resources and support the livelihoods dependent on them.

Acknowledgements

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Taxonomy and Genetic Workshop

Training and protocol guide

ACIAR Project FIS/2012/102:

Sustainable management of the shark resources of Papua New Guinea: socioeconomic and biological characteristics of the fishery

William White
Sharon Appleyard
Leontine Baje

Taxonomy component

8-12th and 22-25th September 2014

The main aim of the taxonomy component of the workshop was to provide detailed information on basic taxonomic techniques. This was achieved through an introduction and induction (for safety purposes) to the Australian National Fish Collection, overview of the importance of taxonomy, introducing nomenclature and types, using unique identifiers, introducing how to identify sharks and rays, introducing the methods for laying out and photographing specimens, introducing methods of fixing and preserving specimens, etc. The majority of the training was achived by in the laboratory using shark and ray samples collected in the Gulf of Papua.

The second week of the workshop was primarily focused on application of the skills learnt throughout the first two weeks of the workshop. This was achieved by working through a known taxonomic problem - a new species of eagle ray - and exploring the techniques required for such a taxonomic study, i.e. taking morphometric measurements, capturing meristic data from radiographs, seclection of and photographing type specimens. This work will be published in an international journal and thus this component is not included in this protocol guide.

Why are biological collections important?

Biological collections represent the biodiversity of a region. They are dynamic resources that must be managed as biological libraries which help to define the structure and distribution of the region's fauna. They are also an extremely cost-effective method of representing the fauna of a region. The cost of a research cruise or survey trip is far greater than the cost of maintaining a biological collection.

Biological collections have many uses such as:

1) Provide a historical baseline for biodiversity, e.g. confirm presence of species in an area where they no longer occur (e.g. due to overfishing) and understanding changes in biodiversity due to climate change;
2) Provide validated geographical point data for species for use in biogeographic studies;
3) Construction of reference guides by providing the basis for which species descriptions can be prepared;
4) Solving cryptic speciation with closely-related sibling species and to resolve taxonomic problems of rare or difficult to obtain specimens;
5) Training of fisheres researchers;
6) Genomics - specimens in collections are becoming increasingly important sources for genetic samples for a variety of studies, e.g. molecular phylogenies, population genetics. Collections are important libraries of information for genomic research.

Dried specimen collection at the National Natuurhistorisch Museum (Naturalis) in Leiden, Netherlands

Nomenclature

Nomenclature is the system of principles, rules and terms relating to naming and is one of the most crucial components of taxonomy. It is more specifically the application of scientific names to taxa, following the recognized classification scheme and the agreed rules and conventions. In the case of animals, this is the the International Commission of Zoological Nomenclature (ICZN, 2000). Although it is a crucial component of taxonomy, it is still often misused and poorly understood.

Before a new species can be named, a thorough investigation of the nomenclature for that particular genus and species is required. Do any older binominal scientific names exist? In the case of fishes, the best tool to use to determine what names are available for a species is The Catalog of Fishes (http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp). This site allows for searching of all species a particular genus, or for a specific species, and provides a list of all of the other scientific names which have been attributed to that species in the past. Also a very good tool for checking spelling and authority(ies) of a species.

Synonyms

In general, the oldest name that is available for a species is the name that should be attributed to that species. When multiple names are available for a species, the oldest valid name is considered the senior synonym and the more recent names are considered junior synonyms of that species name.

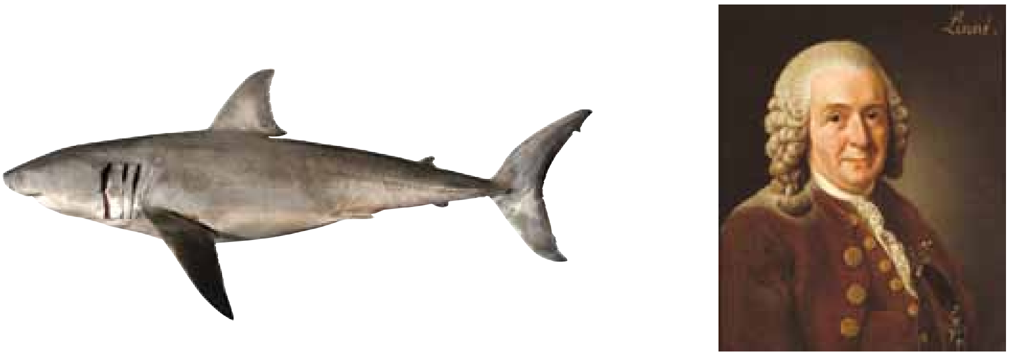
Authorities

The author(s) who first described/formally named a species originally are termed the authority. A scientific name is often written as:

Aetomylaeus nichofii (Bloch & Schneider, 1801)

In this case Bloch & Schneider first named this species in 1801 so will be always known as the authority for this species. The authority will either be written within brackets, or without brackets. If the genus name has changed since the species was first described, then brackets must be used; if the genus name has remained unchanged, no brackets are used.

In the above example, Bloch & Schneider first described this species in the genus *Raja*, therefore it was subsequently moved into another genus, thus the authority is placed within brackets. In contrast, for *Isurus oxyrinchus* Rafinesque, 1810, the genus name has remained the same since it was first described, thus no brackets are used.



The authority for the White Shark is Carl Linnaeus (right) who first described it as *Squalus carcharias*. Since the genus has changed it is written as - *Carcharodon carcharias* (Linnaeus, 1758)

Types

When describing a new species, a type specimen(s) will be nominated for that taxon for which that organism is formally attached. It is imperative that type specimens are well maintained in fish collections.

Different kinds of types exist, depending on how they were originally designated:

Holotype – a single specimen that was clearly designated by the authorities to represent the species;

Paratype – additional/secondary specimens that were listed in the type series in addition to the holotype;

Syntype – when more than one type was used to name a species, but no single specimen was designated as the holotype; not used in modern times but older names often have syntypes representing the species;

Lectotype – a specimen later selected to be the primary type for a species originally described from a set of syntypes. Important to have a single, name-bearing type as a type series can sometimes be found to contain more than one species;

Paralectotype – all remaining specimens in a syntype series which were not designated as the lectotype;

Neotype– a specimen that is later selected to serve as the primary type for a species for which the holotype was lost or destroyed, or where the original author never cited a specimen. Preferably to have from the same location cited by the original author if known.

Paratype of the Sailback Houndshark *Gogolia filewoodi* Compagno 1973 from off Madang, Papua New Guinea - in the University of PNG fish collection

Dried lectotype (skin) of the Ganges Shark *Glyphis gangeticus* (Müller & Henle, 1839)

Operational taxonomic units (OTU's)

OTU's are often used to distinguish between species when their identity is not fully known. For example, '*Carcharhinus* sp. A (bar tail)' could be used as an OTU for a shark which you are observing in the field which you cannot identify other than to genus level.

The use of OTU's enables accurate data to still be collected in the field or in laboratory even though the species name is not known. Also can be useful for variants of a known species. For example, if some *Carcharhinus sorrah* were observed during surveys which had a distinct white stripe on the sides, this variant could be referred to as '*Carcharhinus sorrah* (white stripe)' until it is investigated further.

The advantages of using OTU's is that it highlights where potential identification problems may exist and also provides standardisation of names allowing easier interpretation of the data.

Unique numbers or codes

The use of unique numbers or species codes to distinguish taxa is an ideal way to avoid changing scientific names by providing a consistent, never changing code. It can also be a simpler way to record data, particularly for observers.

FAO codes are unique three-digit codes, e.g. FAL will always refer to Silky Shark *Carcharhinus falciformis* even if the genus or species name changed in the future (which can and does happen at times).

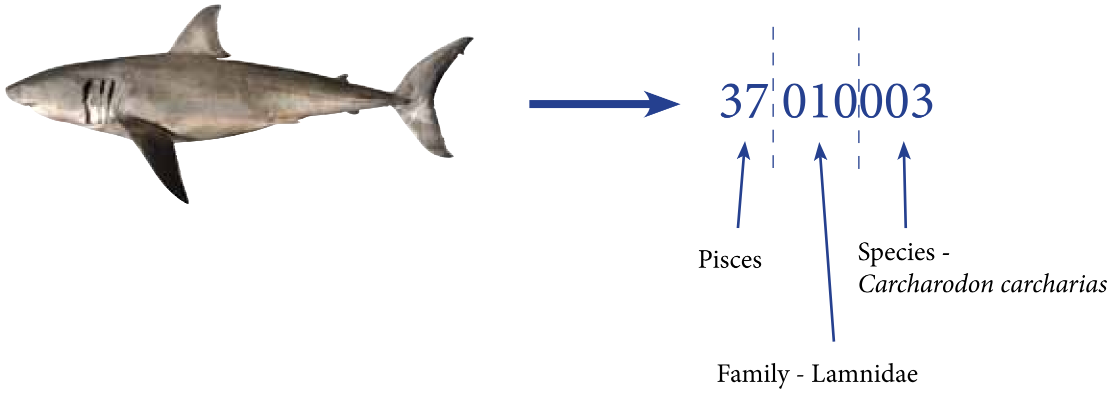
The Codes for Australia's Aquatic Biota (CAAB; marine.csiro.au/caab) allocates an 8-digit number to all marine species in Australia, including fishes. This was developed CSIRO in Hobart.

First 2-digits refer to major group – '37' used for Pisces – all fishes

Next 3-digits refer to family – '017' refers to Triakidae (gummy sharks)

Next 3-digits refer to species – e.g. 37 017001 refers to the Gummy Shark *Mustelus antarcticus*

The CAAB code for a species remains the same even if the species or genus name changes.



Linking specimens to other data sources

Specimens retained for a collection are referred to as a 'voucher specimen'. A retained specimen , or voucher, must have a direct link to the data associated with it (e.g. depth, capture location, date caught, collector, etc) as well as any images, genetic samples, vertebral samples, etc, also retained.

Museums have registration numbers, e.g. CSIRO H 7453-01, which are unique and this number is linked to all samples or parts and images which have come from that specimen.

Field codes are often used as temporary unique identifiers of specimens which allow the same linkage to data and images; these will be given museum registration numbers once deposited into a museum collection.

For the PNG shark and ray project, the label numbers developed for the project are a unique identifier (e.g. 070001) and will be used as a field code prior to museum registration number being allocated for any voucher specimens. This number will never be repeated during this project. The same number is used for any vertebral or tissue samples retained and thus will ensure data linkage for a particular specimen. Images will also be linked to that number.

A Zebra Shark *Stegostoma fasciatum* collected by an observer on a trawl trip in the Gulf of Papua which has been given and unique identifier - label number 100038 which will act as the field code for that specimen.

Identification of sharks and rays

It is critical to use appropriate regional species guides for identifying sharks and rays from a particular area. In the case of PNG, due to the strong overlap with Australia, *Sharks and Rays of Australia* is currently the most appropriate guide for identifying PNG species, but not all.

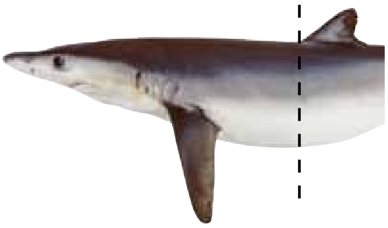
Each group has a different suite of diagnostic characters and it is important to learn what characters are important for what groups. Examples include:

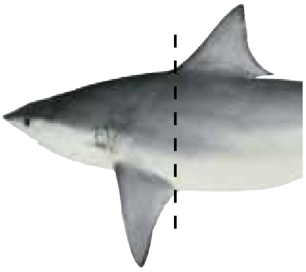
Hammerhead sharks (Sphyrnidae):

- shape and width of head

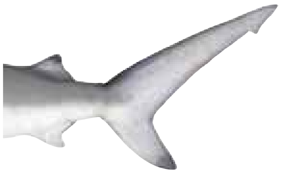
Whaler sharks (Carcharhinidae):

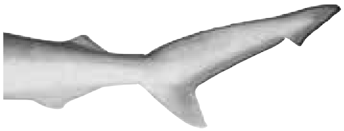
- position of 1st dorsal fin (e.g. origin in relation to pectoral fin)





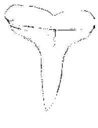
- position of 2nd dorsal fin in relation to 1st dorsal fin, and size of anal fin compared to 2nd dorsal fin





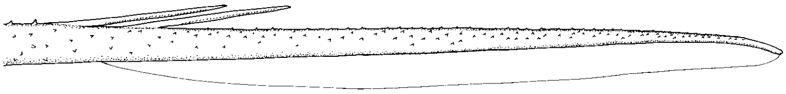
- shape of snout (in dorsoventral view)

- shape of teeth, especially upper teeth

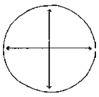


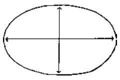
Stingrays (Dasyatidae):

- presence of skin folds on underside of tail

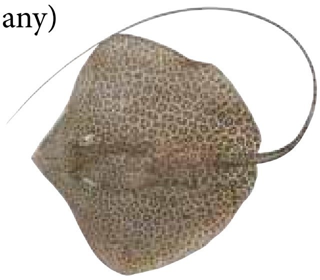


- shape of tail base in cross-section (round or depressed/oval)

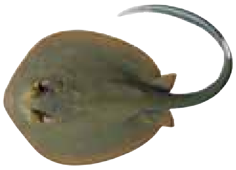




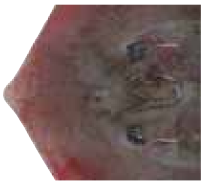
- colour pattern (if any)



- shape of disc (quadrangular, circular, oval)



- eye size (relative to snout length)



Dichotomous keys are extremely useful for identifications and most regional guides should include such keys or similar tools to assist with identification of specimens.

Identifying shark specimens during Taxonomy Training Workshop

Photographing specimens

It is important to obtain good quality images of specimens being retained, prior to being fixed. Once specimens have been fixed, the body and fins cannot be easily moved and the natural coloration has been lost.

The most important step in obtaining good quality images of sharks and rays (and fish in general) is in positioning of the specimen prior to photographing.

In general, the primary image taken for sharks is a lateral image of the left side. For rays and some sharks (e.g. angelsharks), the primary image taken is a dorsal image of the whole body and tail.

Sharks

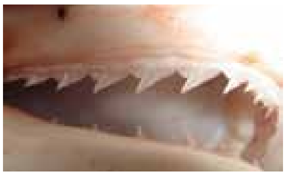
The first step in positioning a shark for a photo is to get the body and tail in a straight horizontal position. From there, the body can be propped up so that it is lying in a completely lateral position (see below).

Once the body is positioned, it is important to get the fins into a natural, horizontal position. Care should be taken to make sure all parts of the fin (particularly the free rear tip) will be visible in the photo and that the fin is not bent upwards or drooping down. Spending a few extra minutes to get a shark specimen in a good position for a photo will save time in the long run.

A shark specimen set up for a lateral photograph in the field in Indonesia. In this case, small rocks and damp paper towel were used to prop up the body and fins.

Secondary images are also important which will highlight other important aspects of the shark being photographed. These vary slightly in different groups but some of the most common secondary images which are useful include:

ventral head



teeth

fin close-ups

lateral head

Shark-like rays

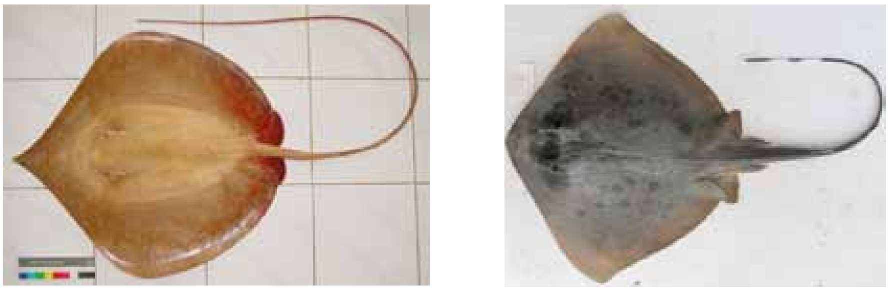
The shark-like rays (such as shovelnose rays, guitarfish, shark rays, sawfish) should be positioned in a manner similar to that for sharks, but in a dorsal position.

Firstly, align the specimen straight in the horizontal axis, ensuring pectoral and pelvic fins are laying flat and not wrinkled, bent upwards or hidden under the body. Position the dorsal fins and caudal fin in a horizontal plane. Ensure the fins are all pointing in the one direction, i.e. the dorsal fins and upper caudal lobe pointing upwards. Pins can be useful for positioning the fins.

A guitarfish (or wedgefish) specimen set up for a dorsal photograph in the field in Indonesia. In this case, pins were used to help position the dorsal and caudal fins.

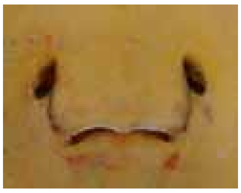
Stingrays

Stingrays are also photographed in a dorsal view, with care being taken to ensure the edge of the disc is straight and flat, as well as being symmetrical. The long tail should be curved up alongside the animal. The tail should be kept straight for a short distance and then curved evenly so that the tip ends up alongside the disc or in front of it depending on its relative length.

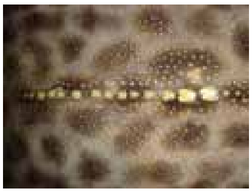


Stingrays set up for a dorsal photograph. The disc is set up evenly and flat and the tail is straight initially and then curved around and towards or past edge of disc.

Secondary images are also important and as with sharks, they vary between groups. Common secondary images include:



oronasal region



enlarged denticles on midline

lateral tail of a maskray - pins used to expose venmtral skin fold; also highlights banding on tail

Taking tissue samples

Muscle or fin-clip samples are important to obtain from specimens prior to fixing. Formalin denatures DNA so once a specimen has been fixed in formalin it is very difficult to obtain usable DNA.

For sharks and rays, a small fin clip is all that is required or a muscle sample can be taken. If the specimen is being fixed, the muscle sample should be taken from the right side (since left side usually used for photographs so should remain untouched) of a shark, and from the ventral surface of a ray. Fin-clips should be taken from the right pectoral or pelvic fins.

Tissue samples or fin clips can be either frozen or placed in 2ml cryovials with a suitable preservative, e.g. 100% ethanol or DMSO solution. The sample should be labelled with the same unique identifier used as the field code for that specimen to ensure it can be linked to that specimen in the future.

Taking a muscle sample from a shark specimen during the Taxonomy Training Workshop

Fixing and preserving specimens

Fish specimens for museum collections are typically first fixed in 10% formalin before being preserved in 70% ethanol.

Formalin fixes the tissue and the specimens become hard. Formaldehyde is normally around 40% strength, but this is treated as 100% formalin and thus watered down to 10% formalin for fixing whole specimens.

It is ideal to retain a specimen whole rather than cut into the gut cavity or to gut the animal. Since the gut contains bacteria and acids, the body cavity needs to be injected with formalin so that it reaches these areas faster and prevents deterioration of the internal organs. For this purpose, full strength formalin is used.

Injecting full strength formalin into the gut cavity of a shark specimen prior to placing in formalin for fixing during the Taxonomy Training Workshop

Safety: Formalin is carcinogenic and care must be taken when handling.

- adequate ventilation is required and, especially in enclose spaces, gas masks with suitable filters are required when using
- safety glasses and gloves should always be used
- store in a well sealed container

Formalin will act as a decalcifier so long term storage in formalin will result in the calcified components of the body to breakdown. Specimens in museums are often preserved long term in 70% ethanol. After 4-8 weeks, specimens in formalin can be transferred, or 'stepped-up' into 70% ethanol.

Stepping-up process:

1) Remove specimens from formalin and place in a container with flowing water;
2) Rinse specimens in water for several hours, changing water several times;
3) Place specimens into a container of 30% ethanol overnight;
4) Remove from 30% container and place into a container of 50% ethanol for at least one night;
5) Remove from 50% container and store in adequate 70% ethanol container

Stepping up into ethanol allows for much safer examination of specimens without the need of gas mask or fume cupboard (although good ventilation still recommended).

Selection of specimens for fixing and preserving

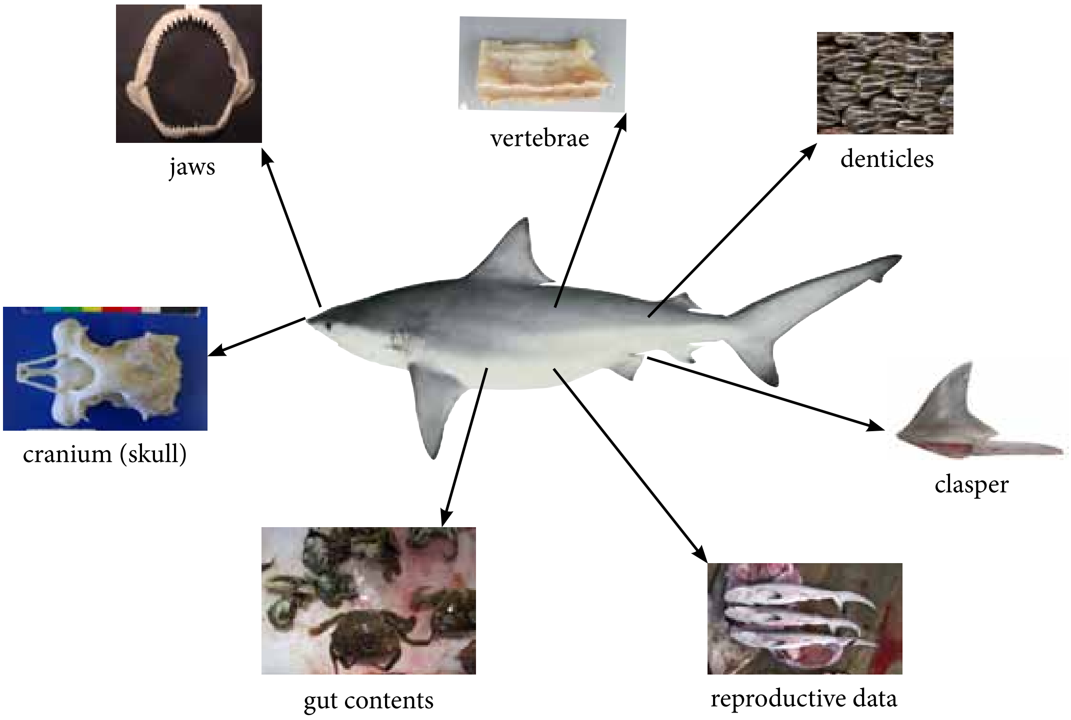
The number of specimens to retain is dependent on a number of factors, such as size of the animal, rarity of species, taxonomic issues (e.g. in a species complex?), number already retained from the same locality, etc.

Ideally, 5 specimens of each species is often adequate for a particular region, but it is also ideal to obtain a variety of sizes as well as both males and females. If poorly represented in collections or rare then it may be important to retain any specimens that are obtained. If there are taxonomic issues then more specimens should be retained as more than one species could be involved.

When an adequate number of whole specimens have been retained, any surplus specimens (e.g. from trawl bycatch studies) can be used for other purposes to reduce wastage:

1) Biological data collection – reproductive, age and growth (vertebrae) and diets (guts);
2) Skeletal collection – retain heads or other body parts frozen or fixed;
    - for sharks, jaws and crania can be valuable for taxonomic studies;
    - for rays, the buccal area (mouth) can be valuable for taxonomic studies;
    - claspers of adult males are also vaulable for taxonomic studies.

Some of the many uses for a surplus shark specimen:



Storing fixed specimens

It is important to use suitable sized and shaped containers for storing fixed specimens. If a shark specimen placed into a smaller container and is curled or twisted, then it will fix into this position and will be extremely difficult to straighten. Bent and twisted specimens are not as useful for taxonomic purposes since accurate measurements cannot be taken.

Ideally, specimens should be fixed as straight and flat as possible. Circular containers and drums can be very good for stingrays, but not as good for medium to large sharks. Rectangular containers are ideal for sharks so they can be kept straight. Small sharks can be fixed in rectangular plastic containers for a short time (at least 2 days) and then placed into smaller drums as by this stage they will be fixed enough to ensure they wont become bent or twisted.

Another important consideration for storage containers is the seal on the lid. A loose fitting lid (like on many rectangular clear boxes) will lead to more evaporation and fumes from formalin allowed to escape. This is particularly important for when specimens are stepped-up into ethanol which will evaporate much quicker.

The types of containers used depends largely on what is available in a particular area and some can be very expensive. Glass jars with good seals are very useful for fish, but only a limited number of sharks and rays are small enough for long term storage in jars. Examples of various containers include:

Plastic boxes such as this are good for short-term fixing of specimens - the plastic can become brittle and the lids usually don’t have good seals, thus not good for long term storage

30L and 60L plastic drums are made of good quality plastic and have screw leads with rubber seals. Ideal for longer term storage. Some issues with sharks become bent and twisted.

Large tanks such as this 1000L plastic tank with a wheel base are good for long-term storage and can be easily moved around.

Large rectangular fish boxes are good for storing sharks and rays but will require seals to be added (e.g. car door rubber)

These blue plastic drums are available in many locations and can be cheap. The lids should have a rubber seal and the metal strap can produce a nice seal for longer-term storage.

Packing specimens for freight

Once specimens have been fixed, they can be packaged for freight following the steps below:

In formalin:

1) Remove specimens from the formalin and place in a large container of water.
2) Flow water through the container for several hours, fully replacing the water several times.
3) After several hours in water, empty the container
4) Wrap each specimen in muslin (cheesecloth), or other light and non-dyed fabric, which has been dampened with water. Ensure the entire specimen is covered.
5) Place specimen into a plastic bag
6) Let as much air out of bag as possible and tie or tape up.
7) Place several bagged specimens into a larger plastic bag and tie up (2 or 3 layers of bags required to prevent leakage).
8) Place specimens into containers for freight (blue drums above ideal).

In ethanol:
As above skip steps 1-3, and in step 4 moisten muslin with 20-50% ethanol rather than water.

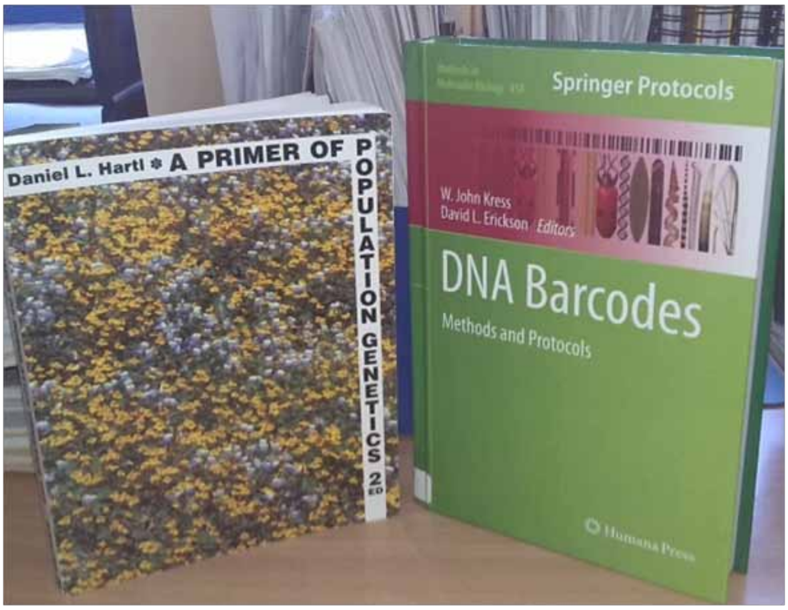
If specimens have tail or fin spines, wrap the spines with strips of muslin before wrapping the specimen in muslin to ensure the spines dont puncture the plastic bags.

When freighting specimens, always ensure all necessary paperwork is included on <u>each</u> package, i.e. Customs declaration, Import permit, CITES declaration, loan paperwork, etc.

Genetic component

15-19th September 2014

The main aim of the Genetics and DNA barcoding component of the workshop was to give an introduction to practical genetics for sharks and rays and an overview of the DNA barcoding process. This was achieved through the introduction and induction (for safety purposes) to the genetics labs, overview and use of key genetic equipment (such as centrifuges, multi-channel pipettes, electrophoresis units), introduction to sample acquisition and preservation of shark and ray tissues for genetic samples, introduction to DNA, molecular genetics and barcoding of the cytochrome oxidase I (COI) gene of the mitochondrial DNA. The wider application of mtDNA and DNA for connectivity studies, parentage, gene flow analyses and species identifications was also discussed.



Schedule

Day 1

Induction to genetics lab; meet genetics researchers, brief overview of research undertaken in CSIRO lab (i.e. Collections, Population Genetics for fisheries and biodiversity, Environmental Genomics, Aquaculture)

- introduction to genetic/molecular biology techniques overview (centrifugation, pipetting, micro measurements, ultra low freezers, autoclaves, standard laboratory equipment)
- Sample acquisition (sample and voucher specimens, importance of sterile sub-sampling techniques) and preparation (storage buffers, freezing, ethanol, DMSO) – cross over and integration with fish taxonomy
- Commence DNA extractions for 96 samples (need small amount of tissue – 25mg per specimen, samples from first trawl Observer (BAN14-01) and Observer 1 (JCM14-02) and Observer 5 (NOL14-01) from June 2014 long line trips; following samples from the previous week and the morphological analyses in the fish taxonomy labs). Overnight digestion of tissues

Day 2

Complete genomic DNA extractions, undertake FTA Whatmann card extraction on 5 samples

- Nanodrop quantification of resulting DNA
- Polymerase Chain Reaction (PCR) for CO1 amplification on the 96 DNA samples (PCR amplification takes approx 3 hrs)
- Introduction to PCR, barcoding (i.e. what is barcoding, uses of barcoding for species and sample identification)
- Background and history of the Barcode of Life Database (BOLD) (theory); DNA barcoding in fish, sharks and rays

Day 3

- Agarose electrophoresis to inspect CO1 amplicon success
- CO1 amplicon cleanup/purification of successful samples, Nanodrop quantification of cleaned amplicons
- DNA Big Dye Terminator (BDT) cycle sequencing reactions on the successful CO1 amplicons (cycle sequencing reactions take approx 2.5hr)
- Introduction to cycle sequencing, uses, applications

Day 4

- CO1 BDT sequencing product purification
- Sequencing sample preparation for loading onto the sequencer (done in house, bi-directional sequencing on CSIRO's 3130XL DNA Autosequencer)
- Discussion on using commercial suppliers for DNA sequencing

Day 5

- Analysis of CO1 sequences using sequencing software (e.g. Genious, BioEdit)
- Sequence alignments and barcode preparation, quality controls, data processing and archiving
- Introduction to the BOLD database and GenBank (http://www.barcodinglife.com/; http://www.ncbi.nlm.nih.gov/) – BLAST of sequences from sequencing run
- Followup on protocols/workflows undertaken prior

Sample acquisition

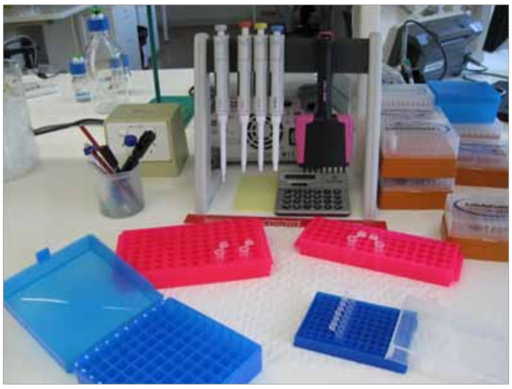
Sample and voucher specimens, importance of sterile sub-sampling techniques) and preparation (storage buffers, freezing, ethanol, DMSO).

- Degradation of tissues occurs as soon as an organism dies. Cell membranes start to break down and enzymes and chemicals from the cells start to break down organic molecules in the cells including DNA and RNA
    - DNA = deoxyribonucleic acid is a molecule that encodes the genetic instructions or makeup of all living organisms and viruses; is a nucleic acid and is essential for life. Is a double helix molecule containing nucleotides of guanine, adenine, thymine or cytosine as well as a sugar called deoxyribose and a phosphate group
    - RNA = ribonucleic acid is a molecule that is important in coding, decoding, regulation and expression of genes. Together with DNA, RNA is a nucleic acid essential for life
- DNA is more robust than RNA and the DNA molecules are relatively strong – however their length makes them weak and enzymes can degrade the DNA molecules by cutting them up into smaller sections
- The important consideration when preserving tissues for DNA use is to reduce the number of damaging factors – keep them cold and dry
- Above 65°C, the DNA double stranded helix loses its bond and becomes single stranded (denaturation) – for preserving DNA, the colder the better (but avoid multiple cycles of freezing and thawing as ice crystals can damage the molecule). Long term storage of tissues for DNA should be at -20°C, -80°C or in liquid nitrogen
- Water is also damaging to DNA as it helps with the transport of enzymes and chemicals, and is a good environment for bacteria. Therefore, dehydrating or removing water from tissues will also help to preserve DNA – can extract DNA from dried scales, from tissue around otoliths, fin clips, FTA (membrane developed by Whatmann in the 1980's) samples

- Liquid nitrogen is best preservative for DNA but is expensive and not practical for field use
- Ethanol (EtOH) is a good preservative as it drives out water from tissues and cells and dehydrates the tissues. Higher percentage of ethanol the better (recommend using absolute or 95%). Do not use methylated ethanol or denatured ethanol
- The ratio of ethanol to tissue is important – only need small amount of tissue (up to 100mg) and then flood the tube with ethanol. Screw cap tubes are the most secure for storing and preserving tissues and samples for DNA
- Silica gel is also used by botanists for dry and preserving plant specimens
- DMSO – is a salt solution, often used in environments where ethanol cannot be obtained. Can be used as an alternative
- FTA will secure DNA and if stored in dry conditions (can preserve DNA for up to 30 years?) Cards are useful when ethanol cannot be used or where samples need to be shipped by post
- Minimise cross contamination (from humans and other samples). Risk of contamination is largest when working with DNA rich and DNA poor tissues or specimens – all sampling tools should be cleaned at the start and in between sampling steps (use 70% ethanol)
- Accurate labelling is essential – labels/identifiers need to be used in the processing line and in the molecular lab so that individual samples can always be tracked – if using ethanol to preserve tissues, use waterproof paper and pencil to write the labels and insert into the tube
- On arrival into the lab, samples must be processed (including identification – shark and ray alpha taxonomy), excess tissue stored for future use, voucher specimens retained. Voucher and record information recorded into database and hard copy files
- Samples for DNA extraction taken to molecular lab for further processing

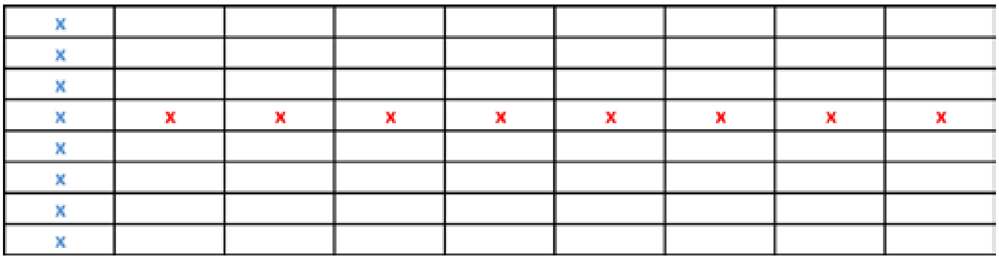
Plate orientation

The samples that we receive are usually in screw cap tubes in 100 well boxes (10 rows × 10 columns, n = 100 samples) however the equipment (PCR cyclers, eight channel pipettors, sequencer) and molecular setups in the laboratory are all based on 96 well plate formats (8 rows × 12 columns, n = 95 samples + 1 –ve control).



It is essential that the sample spreadsheets from the 100 well boxes are used to develop up the DNA extraction and PCR sampling spreadsheets and liquid handling via vertical lifts, and it is important to note the orientation will be different.

Vertical lifts refer to sampling in columns (x); while horizontal lifts refer to sampling in rows (x).



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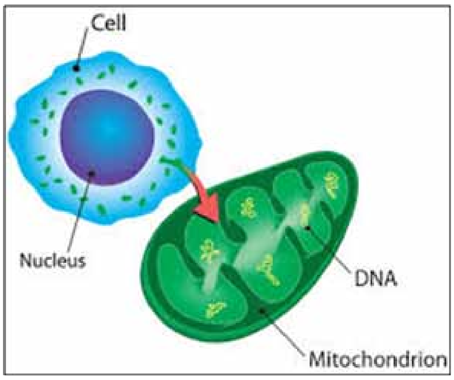
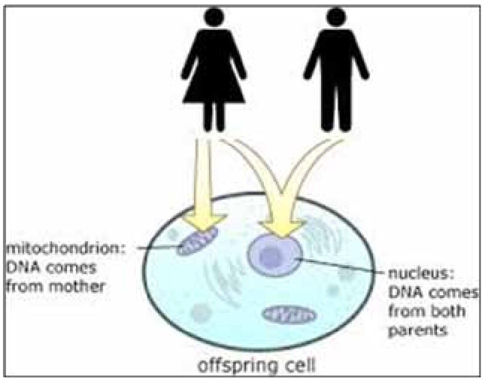
It is important that sampling sheets for DNA extractions, PCR and downstream sequencing accompany the samples. The labels that are given to each sample from the beginning (when the observer takes the vertebrae sample) should be used throughout the genetic processing chain.

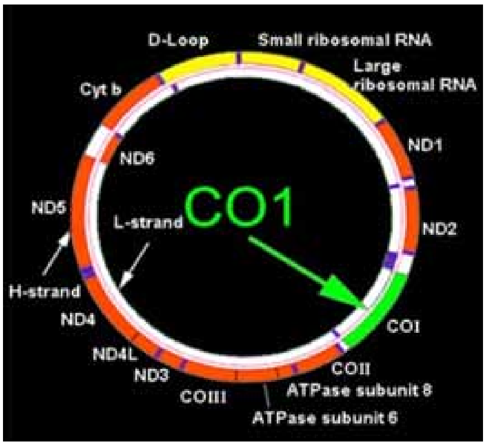
Genetic markers

We extract DNA from tissues so that the DNA can be used in downstream processes such as PCR and sequencing which enable individuals to be identified from a species perspective, and for use in population genetics and connectivity assessments.

- The DNA that we extract from the shark tissues is total genomic DNA and this consists of nuclear DNA (nDNA) and mitochondrial DNA (mtDNA)
- From extracted DNA, we screen for genetic markers in the genome. These can be nuclear DNA markers or mitochondrial DNA markers.
- nDNA is contained within the nucleus of eukaryotic organisms. The nDNA encodes more of the genome than the mitochondrial DNA and is bi-parentally inherited from parents to offspring
- mtDNA is the DNA located in the organelles called mitochondria. mtDNA and nDNA are thought to have separate evolutionary origin with mtDNA being derived from circular genomes of the bacteria that were engulfed by the early ancestors of eukaryotic cells. In most organisms, the mtDNA is inherited along the maternal line and unlike nDNA, there is usually not rearrangement in mtDNA from mother to offspring. The mutation rate of mtDNA is higher than that of nDNA and can be measured; hence mtDNA is used for evolutionary studies and species tracking







- Genetic/molecular markers such as microsatellites, single nucleotide polymorphisms and sequencing of mitochondrial DNA and nuclear DNA genes are utilised for the assessment of genetic connectivity among individuals, populations and species; additionally, sequencing specific areas of the mtDNA genome (e.g. CO1) enables researchers to accurately assign specimens to species
- Genetic markers (both types) are inherited from parents; generally show high levels of variation (although nDNA markers are usually more hypervariable); can be analysed at any life cycle stage; are permanent and can not be lost; are unchangeable; are generally not impacted by the environment; can be assessed using non-destructive techniques
- However, genetic markers, unlike morphological traits or characters are invisible until specialised genetic analyses are undertaken

Genomic DNA extraction

The Promega Wizard SV 96 well extraction protocol (https://au.promega.com/products/dna-and-rna-purification/genomic-dna-purification-kits/wizard-sv-96-genomic-dna-purification-system/; https://au.promega.com/resources/protocols/technical-bulletins/101/wizard-sv-96-genomic-dna-purification-system-protocol/) is one of many commercial DNA extractions kits for use with fish/shark/ray tissues.

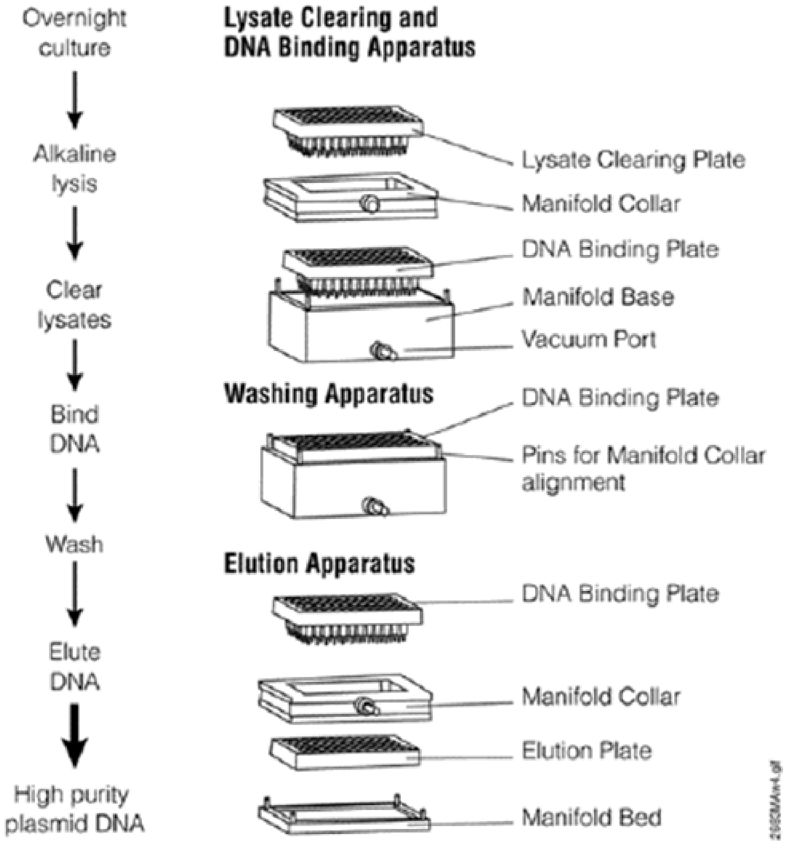
The extraction protocol that researchers use often depends on the type of tissue being used, personal preference, cost effectiveness, availability and resultant genomic DNA quantity and quality. Kits might be based on spin columns, magnetic beads or phenol/chloroform. The Wizard SV extraction protocol (our routine extraction method) is based on a spin column format – the spin column contains a silica resin that selectively binds DNA depending on the salt conditions.

The Wizard protocol provides high throughput 96 well format for fast, simple preparation of intact, purified genomic DNA from different sample types. The resultant DNA can be used for agarose gel analyses, restriction enzyme digestions and polymerase chain reactions (PCRs). The components of the commercial kit are stored at room temperature, except for Proteinase K which is stored at -20C.

Here the tissues are being extracted for total genomic DNA, not RNA and will be used downstream for various molecular applications including PCR, mitochondrial DNA (mtDNA) COI barcoding and nuclear population genetic analyses.

Prepare:

1. Wizard SV 96 Genomic DNA Purification plate; 96 well vacuum manifold; vacuum trap
2. Between each tissue sampling, spray dissection tools with 70% ethanol to minimise cross-contamination; need small amount of tissue – approximately 25mg per samples
3. Sample digestion is at least overnight for fish/shark muscle samples
4. If run out of time the next morning after sample digestion you can add 250ul lysis buffer and freeze at -70°C. The samples must be pre-warmed back to 55°C for 1 hour before processing
5. Lab gloves are worn at all times to prevent cross contamination (both sample and human) and minimize exposure to chemicals such chaotrophic salts
6. See below for overview of extraction protocol



Wizard Extraction Protocol

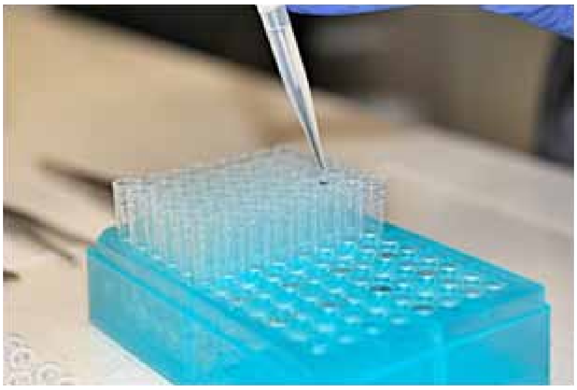
Tissue Lysis

The lysis step (the nuclei lysis buffer contains a high concentration of chaotropic salt – guanidine thiocyanate). Chaotropes destabilise the hydrogen bonds and hydrophobic interactions in the cells. Proteins are destabilised, including nucleases and the nucleic acids are disrupted, setting up the conditions for the transfer to silica columns. The lysis buffer also contains detergents and enzymes such as Proteinase K to help with protein solubilisation and lysis.

- Dissect out tissue sample of ~25mg tissue and place into microtube tubes racked in blue box – if tissues have been frozen, use directly. If have been in EtOH, dry off EtOH then rinse in H2O first
- Aim to use the given amount of tissue as excess tissue mass can clog the columns

- Add the following Wizard SV solutions to each tube using a multi-channel pipette stepper:

Digestion Solution	1×
Nuclei Lysis Solution	200ul
0.5M EDTA (pH8.0)	50ul
ProteinaseK (20mg/ml)	25ul
Total	275ul per tube



- Seal with doomed strip caps, vortex briefly

- Leave samples in oven overnight at 55°C or on a heat block (at least 16-18hrs, some tissues may need digestion for up to 36 hours)

Binding the DNA to the column and Washing the DNA

The chaotropic salts help to bind the DNA from the cells to the silica column. Additionally ethanol is added to help with the binding. The lysates are now centrifuged or vacuumed through the silica membrane and the DNA is bound to the column (the impurities, protein and polysaccharides are washed through). The silica membrane is then washed several times with the last wash step also containing ethanol to remove any salts, which is crucial to obtaining high yields and good quality DNA. After the final ethanol wash, the columns are vacuumed to further dry the column to remove the ethanol and produce a clean eluant.

- Next morning, if continuing with protocol, add 250ul Lysis buffer to sample tube (NB: samples must be processed while warm). Mix contents by pipette and then transfer each sample (using 12 channel 300ul pipette) to binding plate which has been situated already on vacuum manifold (or load into column assemblies)

- Apply vacuum until lysates have passed through
- Add 1ml of SV Wash Solution (with EtOH added) to each well and apply vacuum. Repeat for a total of 3 washes

- Apply vacuum for an additional 7 minutes to dry the membranes
- Transfer vacuum manifold to the elution setup, use deep well plate for elution collection

DNA elution

We use water as the eluant and when it is added to the membrane for elution, the nucleic acids become hydrated, and are released from the membrane. Low DNA yields can result from incomplete lysis (see first step), not using good quality ethanol for diluting buffers or binding to the membrane

- elute using 200ul water (or if smaller amounts of tissue are used, this volume can be reduced accordingly) - add 100ul of ddH2O to each well and let sit for 20 minutes before applying the vacuum; add a further 100ul of ddH2O to each well and let sit for 15 minutes before applying the vacuum
- Pipette the DNA solutions into Eppendorf Twin Tec plates and seal with 12 cap strips. Store plate in 4°C fridge, until ready to quantify each sample on the Nanodrop
- Any notes from the DNA extraction step (e.g. samples that did not pass through the columns, samples that were mixed up or cross contaminated, samples that did not digest well) should be included in the lab book/protocol updates

Whatman FTA Elute DNA extraction (Alternate tissue storage and DNA extraction method)

FTA Elute cards use patented Whatman FTA technology (http://www.sigmaaldrich.com/catalog/product/aldrich/z747580?lang=en&region=AU) for simple and fast processing of nucleic acids. The FTA Elute matrix is chemically treated with proprietary reagents (cellulose paper base impregnated with a surfactant, chelating agent, buffer and free radical trap) that lyse cells on contact and release nucleic acids. DNA is recovered from the FTA card through a simple elution process of water and heat. Inhibitory components are retained in the card matrix. Samples can be collected and shipped at room temperature, no need for ethanol preservation. Gloves should be worn during this protocol to prevent cross contamination.

- Muscle and liver samples were placed onto the FTA card on 9 September and left to air dry for at least 3 hours
- The cards were then closed and placed into foil and stored dry at room temperature until 16 September when extractions were undertaken
- Using the card punch and mat, 4×3mm punches are taken from each sample card and transferred into a 1.7ml microfuge tube. Between each sample, take a cleaning punch (from card), eject the punch and then start on the new sample

- 500ul of sterile water is added to the tube; the tube is pulse vortexed 5 times
- Excess water is squeezed out of the punches and the remaining water is removed with a pipette.
- A further 100ul of sterile water is added to the tube containing the punches and vortexed for 5 seconds
- The tube is then heated at 95°C for 1 hour
- After 1 hour, the tube is removed from the heat block, pulse vortexed 60 times and then briefly centrifuged (13 000rpm for 2 minutes) with the remaining liquid transferred to a new microfuge tube
- The eluant in the tube contains the DNA and should now be quantified on the Nanodrop

NanoDrop 8000 (UV-Vis Spectrophotometer)

The Nanodrop unit is used to assess the concentration and purity of nucleic acids (using small 1-2ul volumes). The sample ID information is entered into the Nanodrop 8000 and samples are loaded onto the staging plate. The samples are simultaneously captured between an array of upper and lower optical surfaces. When the sample arm is closed, the arm slightly compresses the droplet and a column of liquid is formed.

A spectral measurement of each sample is made based on the path length. When the samples has been analysed, the staging plate is wiped with a Kim wipe and the next sample applied.

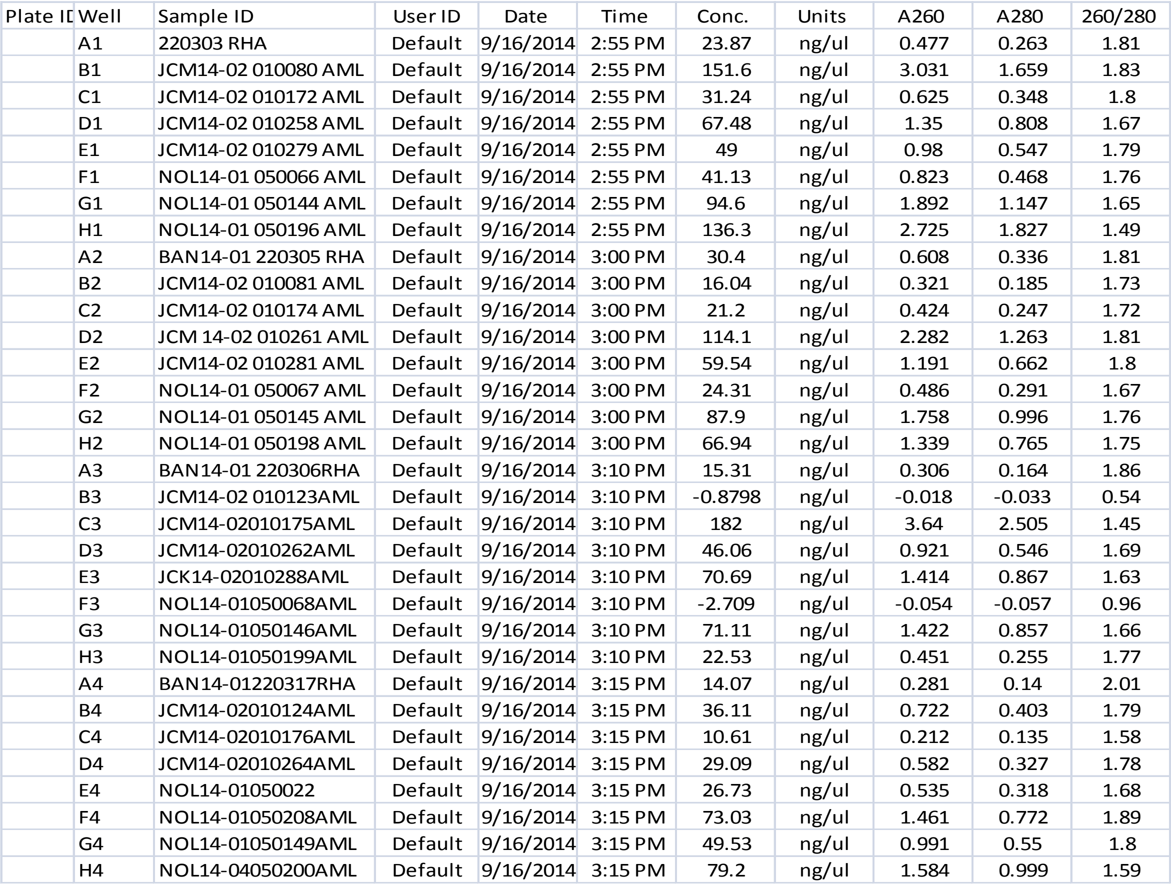


Plate ID	Well	Sample ID	User ID	Date	Time	Conc.	Units	A260	A280	260/280
	A1	220303 RHA	Default	9/16/2014	2:55 PM	23.87	ng/ul	0.477	0.263	1.81
	B1	JCM14-02 010080 AML	Default	9/16/2014	2:55 PM	151.6	ng/ul	3.031	1.659	1.83
	C1	JCM14-02 010172 AML	Default	9/16/2014	2:55 PM	31.24	ng/ul	0.625	0.348	1.8
	D1	JCM14-02 010258 AML	Default	9/16/2014	2:55 PM	67.48	ng/ul	1.35	0.808	1.67
	E1	JCM14-02 010279 AML	Default	9/16/2014	2:55 PM	49	ng/ul	0.98	0.547	1.79
	F1	NOL14-01 050066 AML	Default	9/16/2014	2:55 PM	41.13	ng/ul	0.823	0.468	1.76
	G1	NOL14-01 050144 AML	Default	9/16/2014	2:55 PM	94.6	ng/ul	1.892	1.147	1.65
	H1	NOL14-01 050196 AML	Default	9/16/2014	2:55 PM	136.3	ng/ul	2.725	1.827	1.49
	A2	BAN14-01 220305 RHA	Default	9/16/2014	3:00 PM	30.4	ng/ul	0.608	0.336	1.81
	B2	JCM14-02 010081 AML	Default	9/16/2014	3:00 PM	16.04	ng/ul	0.321	0.185	1.73
	C2	JCM14-02 010174 AML	Default	9/16/2014	3:00 PM	21.2	ng/ul	0.424	0.247	1.72
	D2	JCM 14-02 010261 AML	Default	9/16/2014	3:00 PM	114.1	ng/ul	2.282	1.263	1.81
	E2	JCM14-02 010281 AML	Default	9/16/2014	3:00 PM	59.54	ng/ul	1.191	0.662	1.8
	F2	NOL14-01 050067 AML	Default	9/16/2014	3:00 PM	24.31	ng/ul	0.486	0.291	1.67
	G2	NOL14-01 050145 AML	Default	9/16/2014	3:00 PM	87.9	ng/ul	1.758	0.996	1.76
	H2	NOL14-01 050198 AML	Default	9/16/2014	3:00 PM	66.94	ng/ul	1.339	0.765	1.75
	A3	BAN14-01 220306RHA	Default	9/16/2014	3:10 PM	15.31	ng/ul	0.306	0.164	1.86
	B3	JCM14-02 010123AML	Default	9/16/2014	3:10 PM	-0.8798	ng/ul	-0.018	-0.033	0.54
	C3	JCM14-02010175AML	Default	9/16/2014	3:10 PM	182	ng/ul	3.64	2.505	1.45
	D3	JCM14-02010262AML	Default	9/16/2014	3:10 PM	46.06	ng/ul	0.921	0.546	1.69
	E3	JCK14-02010288AML	Default	9/16/2014	3:10 PM	70.69	ng/ul	1.414	0.867	1.63
	F3	NOL14-01050068AML	Default	9/16/2014	3:10 PM	-2.709	ng/ul	-0.054	-0.057	0.96
	G3	NOL14-01050146AML	Default	9/16/2014	3:10 PM	71.11	ng/ul	1.422	0.857	1.66
	H3	NOL14-01050199AML	Default	9/16/2014	3:10 PM	22.53	ng/ul	0.451	0.255	1.77
	A4	BAN14-01220317RHA	Default	9/16/2014	3:15 PM	14.07	ng/ul	0.281	0.14	2.01
	B4	JCM14-02010124AML	Default	9/16/2014	3:15 PM	36.11	ng/ul	0.722	0.403	1.79
	C4	JCM14-02010176AML	Default	9/16/2014	3:15 PM	10.61	ng/ul	0.212	0.135	1.58
	D4	JCM14-02010264AML	Default	9/16/2014	3:15 PM	29.09	ng/ul	0.582	0.327	1.78
	E4	NOL14-01050022	Default	9/16/2014	3:15 PM	26.73	ng/ul	0.535	0.318	1.68
	F4	NOL14-01050208AML	Default	9/16/2014	3:15 PM	73.03	ng/ul	1.461	0.772	1.89
	G4	NOL14-01050149AML	Default	9/16/2014	3:15 PM	49.53	ng/ul	0.991	0.55	1.8
	H4	NOL14-04050200AML	Default	9/16/2014	3:15 PM	79.2	ng/ul	1.584	0.999	1.59

DNA Storage

- Check quantity and quality of extracted DNA on Nanodrop
- Solution with A260/A280 ratio around 1.6-1.9 is good
- Following quantification, making working stock/plate of 10-15ng/ul for each sample
- Remainder of DNA to be stored in 96 well plates in -80°C freezer.

Polymerase Chain Reaction (PCR)

PCR is a molecular biology technique based on DNA replication and is used to amplify a single copy of a piece of DNA. PCR generates thousands to millions of copies of the particular sequence. PCR was developed in 1983 by Kary Mullis and is now the baseline/core technique used in most molecular investigations. PCR cycles are performed in PCR cyclers – there are a multitude of different branded cyclers on the market – however they all perform the same function (amplification of nucleic acids, i.e. DNA or RNA).

PCR is based on thermal cycling – cycles of repeated heating and cooling of DNA for melting and replication of DNA. The reaction occurs when a DNA sample (template), primers (short DNA fragments) which are complimentary to the DNA region of interest along with nucleotides, a DNA polymerase and other reagents are added into a sample tube. These reagents are necessary to produce a successful PCR reaction.

The PCR process can be thought of as 'making a muffin'. Here, the analogy between PCR and muffin baking is outlined.

When we make muffins, we:

- Select the right ingredients e.g., butter, cocoa/vanilla, sugar, water/milk, self raising flour and weigh them out in the appropriate portions and place them into a bowl
    - In PCR, we select the buffers, primers, additives, water, good quality and quantity DNA and using a pipette, we add the components into a single microfuge tube
- Mix the muffin ingredients by stirring or whisking in a single bowl and then

place heaped spoonfuls into a multi-well muffin tin

  - In PCR, we briefly vortex and spin down the components, then using a pipette we sub-aliquot the ‘master mix’ components into small PCR strip tubes

- Set the oven at the required temperature , place the muffin tin into the oven and turn on the timer for the appropriate cooking period
  - In PCR, we place the microfuge tubes into the PCR cycler (basically an ‘oven’), set up the required cycling parameters (i.e. temperature and time) and start the PCR cycling program

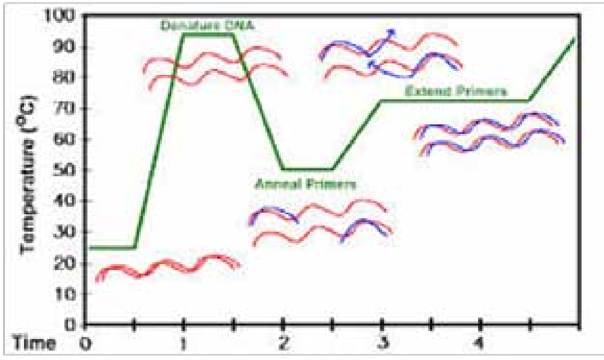
- After baking for the required time, pull the muffin tin out of the oven, leave the muffins to cool and then eat. The muffin taste will largely depend on whether cocoa or vanilla was used
  - Once the PCR program has finished, run the PCR samples out on a gel. If the appropriate primers were used, a PCR product will be visible

There are three main steps in each PCR cycle and each cycle approximately doubles the amount of target DNA through exponential cycling. The target DNA is generated in 30-40 PCR cycles. The three steps are:

1. Denaturing – the tube containing the template DNA is heated to over 90°C (typically, 94°C or 95°C) which separates the double stranded DNA helix into two separate strands. The high temperature breaks the bonds between the nucleotides that form the DNA strand

2. Annealing – PCR copies specific sequences of the genome through targeting of areas. The primers added to the PCR reaction mix, direct the ‘targeting’. PCR will only copy the specific DNA sequences that are complimentary to the primer (man-made oligonucleotide) sequences. During this step, the primers anneal or bind to the target DNA region at the beginning of the sequences to be copied. The annealing temperature used in a PCR reaction depends on the primer sequences and is usually between 50-60°C

3. Extension – during this step, the reaction is heated to 72°C and at the regions marked by the primers, the added nucleotides in the tube are added to the annealed primers by the DNA polymerase to produce a new strand of DNA complimentary to each of the single template strands. After the extension, two identical copies of the original DNA sequence are produced. After this step, the PCR cycle begins again



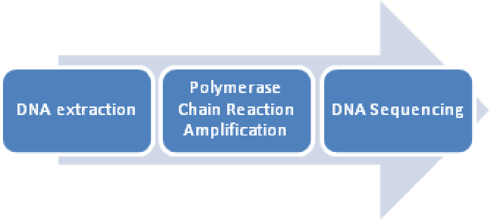
Fish and Shark DNA Barcoding

Barcoding is used for the quick identification of species based on extracting an individual's DNA from tissue. DNA barcoding contributes to the taxonomic identification of species by expanding the number of tools that can be utilised to differentiate species and taxa. As a biodiversity discovery tool, DNA barcoding helps to highlight species that are potentially new to science. In fish and shark & ray barcoding, identification of species is based on extracting a DNA sequence from the COI (cytochrome c oxidase I) gene region of mtDNA. Barcoding consists of:

1. Building the barcode library of known reference species
2. Matching or assigning an unknown sample to the reference database

DNA barcoding has:

- enabled researchers to accurately assign specimens (eggs to adults, tissue fragments, prey, stomach contents etc) to species. Research has predominantly been undertaken on fish to date, with some work on decapods and echinoderms with requests to determine species identification for fillets (e.g. in a forensics context), confirm/refute species identification in processed/canned products, for fisheries prosecutions, as part of contributions to the international BarCode of Life (BOLD) initiative (http://www.fishbol.org/index.php), FISH-BOL http://www.fishbol.org/index.php, and more recently as part of a new BioPlatforms Australia (BPA) DNA barcoding initiative
- contributed to categorisation of Australian species (and Census of Marine Life), greater understanding of genetic connectivity of species from international water (e.g. sharks from Papua New Guinea) and help to identify threatened species (e.g. sharks, black cod, bluefin tuna) in domestic and international waters



DNA barcodes consist of a standardised short sequence of DNA between 400-800 base pairs. By using advancements in molecular genetics, high throughput sequencing, bioinformatics and international databases, barcoding enables researchers to quickly and accurately recognise species. Molecular barcodes should be associated with voucher specimens.

FISH-BOL is a global effort to assemble a standardised reference sequence of all fish species. Was initiated in 2005 and is based on the sequencing of the standard 655 base pair fragment of cytochrome c oxidase I (for further explanation, see Ward, 2012, FISH-BOL, A Case Study for DNA Barcodes).

Barcoding PCR

The template DNA is added to specific COI primers and a PCR reaction is undertaken.

- COI mtDNA fragments are amplified in each sample; PCR reactions are set up in a DNA free area (the laminar flow hood) and DNA is then added at the bench
- The PCR ingredients are thawed, and the working primer solutions are made up at 10uM concentration. All PCR ingredients (GoTaq, primers, BSA) are kept at -20°C when not in use. Working stocks of diluted DNA (e.g. 10ng/uL) are kept at 4°C when not in use
- The PCR reagents are mixed together and vortexed briefly, then spun down and aliquoted into each PCR tube – a negative control (without DNA) is also run as a PCR control
- If starting with lyophilized primers (dried primers), spin the primer tube down, and resuspend to 100uM in molecular grade water before making working stock primers at 10uM
- Primers used are: 10uM FishF1(fwd) TCA ACC AAC CAC AAA GAC ATT GGC AC, Ward *et al.*, 2005) and FishR2 (rev) ACT TCA GGG TGA CCG AAG AAT CAG AA Ward *et al.*, 2005)
- PCR reactions undertaken in a Perkin Elmer GeneAmp® System 9700 thermal cycler in a total volume of 25µl, with standard PCR cycling conditions
- The GoTaq master mix contains the DNA polymerase, nucleotides and PCR reagents such as buffer and magnesium chloride

PCR Reaction (for a single samples, the PCR ingredients volumes are upscaled depending on the number of samples being investigated, a PCR Master Mix is used)

PCR reagents

	1X	40X
GoTaq Master Mix	12.5ul	500.0ul
Water	7.5ul	300.0ul
Bovine Serum Albumin	1.0ul	40.0ul
10uM F1 primer	1.0ul	40.0ul
10uM R2 primer	1.0ul	40.0ul
DNA template	2.0ul	

Mix all the reagent volumes listed in the PCR recipe above in a 2ml microfuge tube (by pipetting up and down or flick mixing the tube). Before opening the cap, briefly spin the tube down for 5 seconds. Aliquot 23ul of the Master Mix into each PCR tube (we used strip cap tubes) in the laminar flow hood- the PCR tubes are then take to the lab bench where the 2ul of template DNA is added. The PCR tubes are briefly pulsed down and then placed into the PCR cycler and the PCR cycle below is undertaken.

PCR Cycle

94°C X 3 min

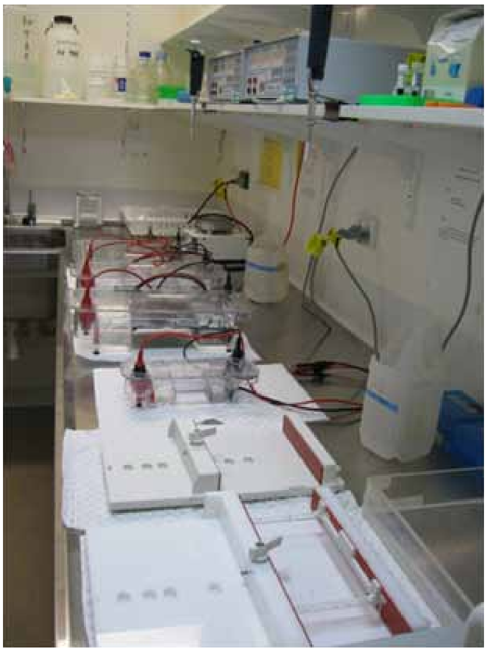
94°C X 1 min, 52°C X 1 min 30 sec, 72°C X 1 min - for 35-40 cycles

72°C X 10 min

15°C hold (until PCR tubes are taken off the cycler)

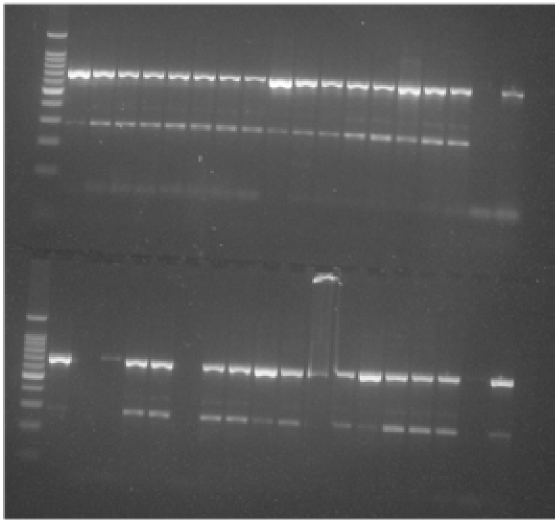
- After the PCR reaction is complete, the samples are run out on an agarose gel (using electrophoresis) for visual inspection of PCR success. The PCR samples can be placed in the 4°C fridge until electrophoresis
- We use 2.5% 1× TAE (Tris, Acetic acid, EDTA) gels. Measure out the agarose, add the dry ingredient to 100mL of TAE buffer, boil in the microwave

- Allow the agarose to cool slightly before adding 10uL SYBR SAFE (a chemical which enables the visual inspection of the PCR fragments when the gel is placed on a blue light box). Pour the cooled agarose into a gel casting tray with combs

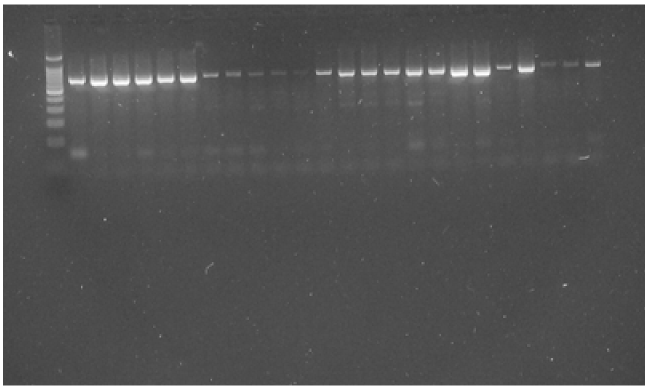


- When the gel is firm, remove the combs and place the gel into an electrophoresis rig filled with 1× TAE buffer
- 8ul of the PCR reaction is loaded onto the gel (if using GoTaq, the PCR samples can be added directly to the gel as the loading dye is already present in the sample), alongside a DNA ladder (with fragments of known sizes) and electrophoresed for 45 minutes at 120 volts
- At the end of the run, place the gel onto the blue light box (or onto a gel imaging system) and using the digital camera, take a photo of the agarose gel – positive samples (single banded PCR products) are then cleaned using magnetic beads in preparation for Big Dye Terminator Cycle Sequencing

Often PCR conditions (ingredients, ratios, DNA amount and cycling parameters) may need optimising before a successful single banded PCR product is obtained. Typically, the parameters that are optimised are the annealing temperature of the PCR cycle (i.e. the higher the annealing temperature, the more stringent the amplification process (increasing the annealing temperature by 2°C can reduce sub-banding/multiple bands); the amount of template DNA added to the PCR reaction (i.e. there is a compromise between adding too much DNA and not enough DNA) and adding PCR additives such as BSA to improve the efficiency of the PCR.



52°C



54°C and diluted DNA

AMPure, BDT, CleanSeq and Sequencing of fragments

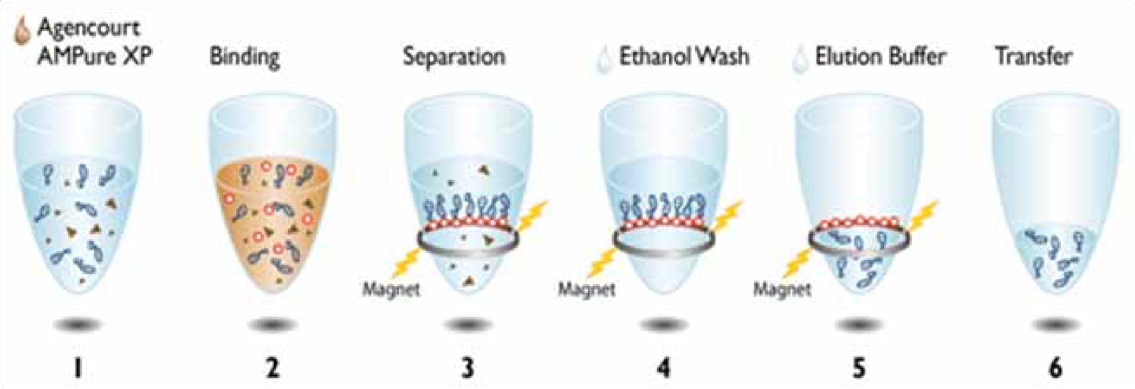
Following agarose checks of PCR products (here we are looking for bands approximately 650 base pairs) positive PCR products (generally single bands) are purified (i.e. cleaned) using AMPure™ magnetic beads according to the manufacturer's instruction and used in downstream applications such as Big Dye Terminator Cycle Sequencing.

AMPure

From the Beckmancoulter website:
https://www.beckmancoulter.com/wsrportal/wsrportal.portal?_nfpb=true&_windowLabel=UCM_RENDERER&_urlType=render&wlpUCM_RENDERER_path=%2Fwsr%2Fresearch-and-discovery%2Fproducts-and-services%2Fnucleic-acid-sample-preparation%2Fagencourt-ampure-xp-pcr-purification%2Findex.htm#2/10//0/25/1/0/asc/2/A63880///0/1//0/

Agencourt AMPure XP system is a highly efficient, easily automated PCR purification system that delivers superior quality DNA with no salt carryover. Requiring no centrifugation or filtration, Agencourt AMPure XP can be easily used in manual and automated 96- or 384-well formats

Process overview



1. PCR reaction
2. Binding of PCR amplicons to magnetic beads
3. Separation of PCR amplicons bound to magnetic beads from contaminants
4. Washing of PCR amplicons with Ethanol
5. Elution of PCR amplicons from the magnetic particles
6. Transfer away from the beads into a new plate

Protocol

- Prior to use, let the AMPure beads come to room temperature and then flick mix or vortex to make sure the beads are well dispersed in the liquid (the liquid should appear brown)
- Beads are added to the PCR mix at a ratio of 1:1.8. So, if you have 17ul of PCR product left after the agarose gel, you would need to add 31ul of bead solution to each PCR sample
- Mix the PCR product and beads solution by pipetting up and down 10 times
- Let the mixed samples incubate at room temperature for about 10-15 minutes
- Then place the mixed samples onto the magnetic SPIRI plate for at least 5 minutes
- Then aspirate the solution; when aspirating it is important to keep the sample tubes on the magnetic plate and do not disturb the ring of magnetic beads. Aspirate (using a pipette and tip) carefully and take off the liquid in the tube

- Two wash steps (using freshly prepared 80% ethanol) are now undertaken – add 200ul of 80% ethanol to the tubes, leave 5-10 minutes and aspirate the ethanol. Repeat for another wash
- Remove the tubes from the magnetic plate and let air dry at room temperature (15-20 minutes although longer time maybe required) (the residual ethanol needs to be evaporated off, as carry over ethanol impacts on the performance of downstream applications)
- Once the beads are dry, add 40ul of water, mix gently by pipetting (10 ×) and place back onto the SPIRI plate to separate the beads
- Transfer 35ul of the cleared solution to new tubes – your cleaned PCR product is now ready for Nanodrop quantification (can proceed directly to quantification, or can store the cleaned PCR product at -20°C). Depending on the PCR product type, the cleaned PCR product is used for direct Sanger Sequencing or fragment analysis on the 3130XL autosequencer

Nanodrop after AMPure

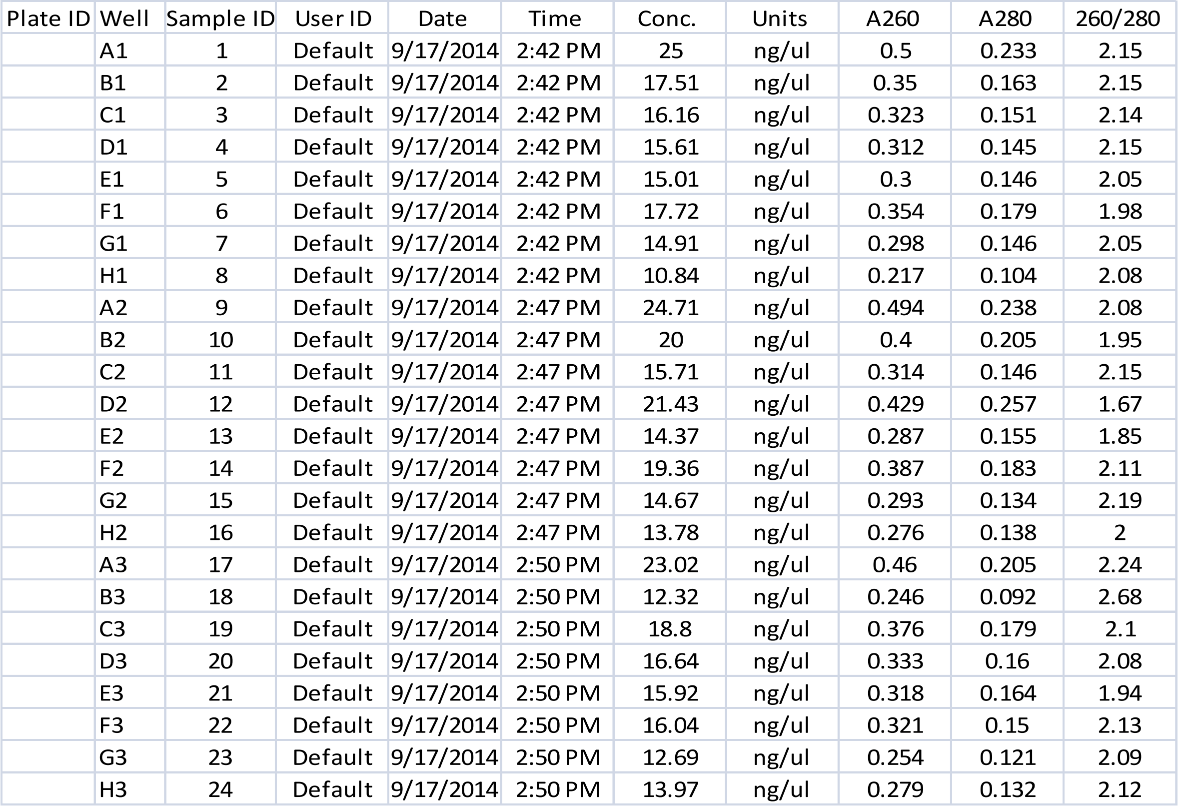


Plate ID	Well	Sample ID	User ID	Date	Time	Conc.	Units	A260	A280	260/280
	A1	1	Default	9/17/2014	2:42 PM	25	ng/ul	0.5	0.233	2.15
	B1	2	Default	9/17/2014	2:42 PM	17.51	ng/ul	0.35	0.163	2.15
	C1	3	Default	9/17/2014	2:42 PM	16.16	ng/ul	0.323	0.151	2.14
	D1	4	Default	9/17/2014	2:42 PM	15.61	ng/ul	0.312	0.145	2.15
	E1	5	Default	9/17/2014	2:42 PM	15.01	ng/ul	0.3	0.146	2.05
	F1	6	Default	9/17/2014	2:42 PM	17.72	ng/ul	0.354	0.179	1.98
	G1	7	Default	9/17/2014	2:42 PM	14.91	ng/ul	0.298	0.146	2.05
	H1	8	Default	9/17/2014	2:42 PM	10.84	ng/ul	0.217	0.104	2.08
	A2	9	Default	9/17/2014	2:47 PM	24.71	ng/ul	0.494	0.238	2.08
	B2	10	Default	9/17/2014	2:47 PM	20	ng/ul	0.4	0.205	1.95
	C2	11	Default	9/17/2014	2:47 PM	15.71	ng/ul	0.314	0.146	2.15
	D2	12	Default	9/17/2014	2:47 PM	21.43	ng/ul	0.429	0.257	1.67
	E2	13	Default	9/17/2014	2:47 PM	14.37	ng/ul	0.287	0.155	1.85
	F2	14	Default	9/17/2014	2:47 PM	19.36	ng/ul	0.387	0.183	2.11
	G2	15	Default	9/17/2014	2:47 PM	14.67	ng/ul	0.293	0.134	2.19
	H2	16	Default	9/17/2014	2:47 PM	13.78	ng/ul	0.276	0.138	2
	A3	17	Default	9/17/2014	2:50 PM	23.02	ng/ul	0.46	0.205	2.24
	B3	18	Default	9/17/2014	2:50 PM	12.32	ng/ul	0.246	0.092	2.68
	C3	19	Default	9/17/2014	2:50 PM	18.8	ng/ul	0.376	0.179	2.1
	D3	20	Default	9/17/2014	2:50 PM	16.64	ng/ul	0.333	0.16	2.08
	E3	21	Default	9/17/2014	2:50 PM	15.92	ng/ul	0.318	0.164	1.94
	F3	22	Default	9/17/2014	2:50 PM	16.04	ng/ul	0.321	0.15	2.13
	G3	23	Default	9/17/2014	2:50 PM	12.69	ng/ul	0.254	0.121	2.09
	H3	24	Default	9/17/2014	2:50 PM	13.97	ng/ul	0.279	0.132	2.12

Concentrations between 10-25ng/ul.

COI BDT sequencing

- Following successful PCR, AMPure bead cleanup and template quantification, the samples are used in a BDT sequencing reaction
- BDTs should be sub-aliquoted into smaller volumes and stored at -20°C (in the dark as the chemical is both light and temperature sensitive). The BDT buffer should be stored at 4°C

BDT sequencing

From the Life Technologies website:

Big Dye terminator chemistry - http://www.appliedbiosystems.com/absite/us/en/home/applications-technologies/dna-sequencing-fragment-analysis/overview-of-dna-sequencing/sequencing-chemistries.html

Process Overview

Cycle sequencing is a simple method in which successive rounds of denaturation, annealing, and extension in a thermal cycler result in linear amplification of extension products. The products are then injected into a capillary. All current Applied Biosystems DNA sequencing kits use cycle sequencing protocols. Fluorescent DNA sequencing can also be performed using a chemistry in which the dyes are attached to the ddNTPs, thereby requiring only one reaction tube per sample, instead of four. Since only one reaction tube is required for the dye terminator reaction, this chemistry is simpler to use than dye primer chemistry. DNA template, unlabeled primer, buffer, the four dNTPs, the four fluorescently labeled ddNTPs, and AmpliTaq® DNA Polymerase are added to the reaction tube. Fluorescent fragments are generated by incorporation of dye-labeled ddNTPs. Each different ddNTP (ddATP, ddCTP, ddGTP, or ddTTP) will carry a different color of dye. All terminated fragments (those ending with a ddNTP), therefore, contain a dye at their 3' end.

Protocol

- Based on the size of your fragment of interest (for COI this is approximately 650bp) and the cleaned PCR fragment quantity, the following is a guide to the amount of template PCR required

PCR Product:

100-200bp	1-3ng
200-500bp	3-10ng
500-1000bp	5-20ng
1000-2000bp	10-40ng
>2000bp	20-50ng

- For COI, between 5-20ng of cleaned PCR product is required for a sequencing reaction per sample
- Unlike in standard PCR where the primers are used at 10uM concentration – for BDT sequencing, make primer aliquots of 3.2pM concentration (i.e. 10ul of the 10uM primer + 15ul of water = 3.2pM, made fresh each time you prepare sequencing reactions) are used
- For sequencing, prepare a master mix for each forward and reverse primer (i.e. for bi-directional sequencing, need 2 master mixes) (for each PCR sample, you will have two cycle sequencing reactions)
- Total sequencing reaction volume is 20.0ul

Cycle sequencing reagents (for either Forward primer reactions or Reverse primer reactions)

Forward Master Mix

	1X	30X	
Big Dye Terminators	1.0ul	30.0ul	
BDT buffer	3.5ul	105.0ul	18.5ul of Master Mix to PCR tube
3.2pM FishF1 Primer	1.0ul	30.0ul	+ 1.5ul of template per sample
Water	13.0ul	390.0ul	
Cleaned PCR template	1.5ul		
Total Volume	**20.0ul**		

Reverse Master Mix

	1X	30X	
Big Dye Terminators	1.0ul	30.0ul	
BDT buffer	3.5ul	105.0ul	18.5ul of Master Mix to PCR tube
3.2pM FishR2 Primer	1.0ul	30.0ul	+ 1.5ul of template per sample
Water	13.0ul	390.0ul	
Cleaned PCR template	1.5ul		
Total Volume	**20.0ul**		

Mix all the reagent volumes listed in the cycle sequencing PCR recipe above in a 2ml microfuge tube (by pipetting up and down or flick mixing the tube). Before opening the cap, briefly spin the tube down for 5 seconds. Aliquot 18.5ul of the Master Mix into each PCR tube (we used strip cap tubes) in the laminar flow hood- the PCR tubes are then take to the lab bench where the 1.5ul of cleaned PCR product is added. The PCR tubes are briefly pulsed down and then placed into the PCR cycler and the PCR cycle below is undertaken.

Cycling conditions

- 96°C × 1 min
- 96°C C × 10 sec
- 52°C × 5 sec x 25cycles
- 60°C C × 4 min
- Hold at 15°C

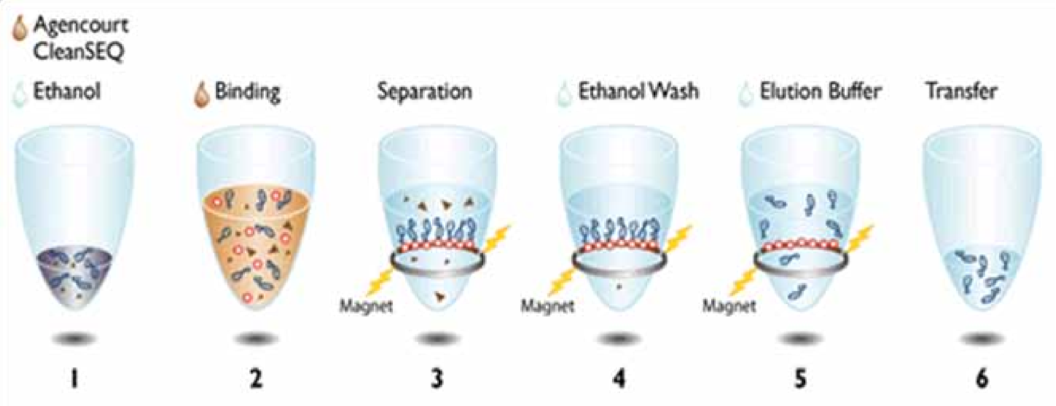
- Once cycle sequencing finished, can store products at -20°C (covered) or continue with CleanSeq cleanups. If cycle sequencing products are stored, ensure they come to room temperature prior to cleaning with CleanSeq.

CleanSeq

From the Beckmancoulter website:

The Agencourt CleanSEQ system is a rapid, high performance dye-terminator removal process based on Solid Phase Reversible Immobilization (SPRI) technology. The paramagnetic bead format requires no centrifugation or filtration and is easily performed manually or fully automated for high throughput dye-terminator removal. The Agencourt CleanSEQ system produces sequences with longer Phred 20 read lengths and higher signal intensities than any other purification technology.

Process Overview



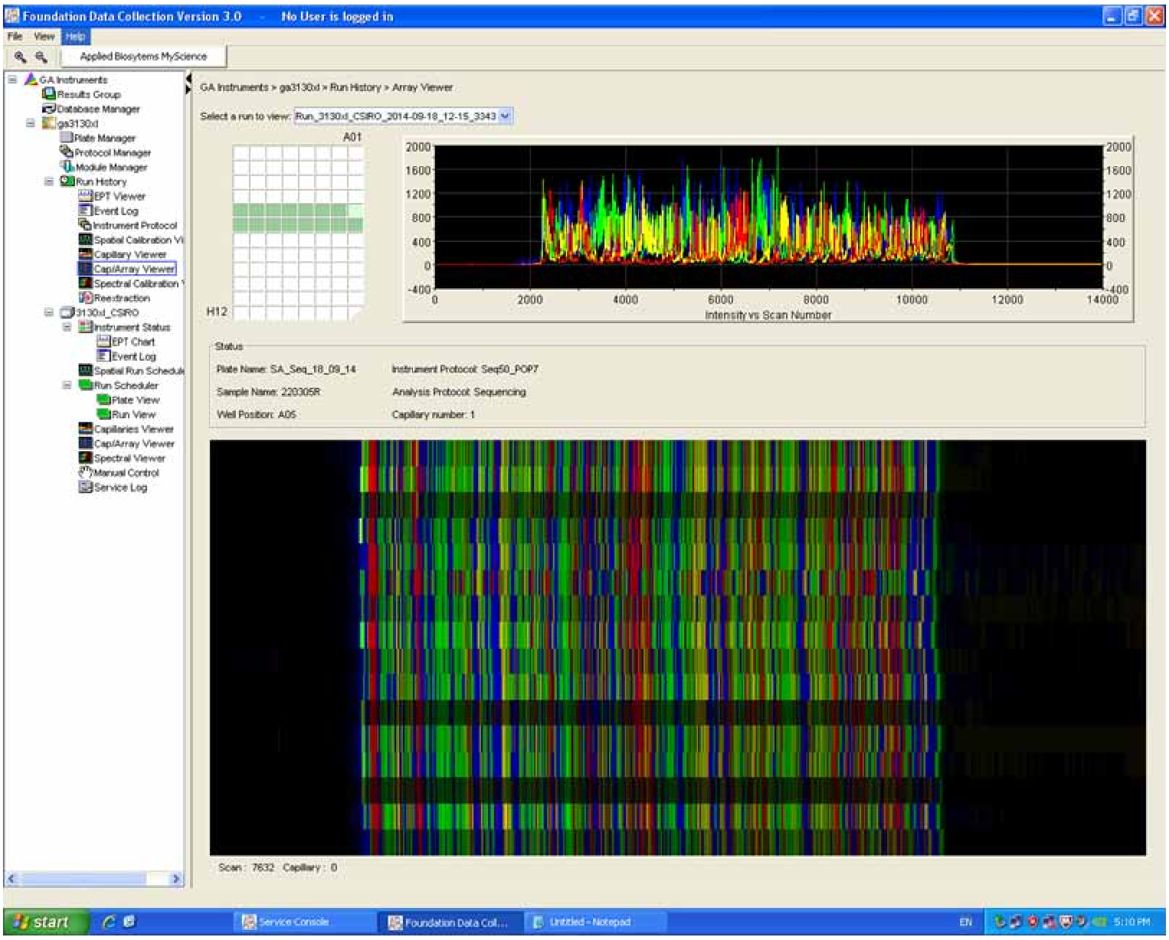
1. Add Agencourt CleanSEQ reagent and ethanol to sequencing reaction
2. Bind sequencing products to magnetic beads
3. Separate sequencing products from contaminants with magnetic field
4. Wash with ethanol
5. Elute from magnetic particles
6. Transfer away from magnetic beads

Protocol

- Prior to use, let the CleanSeq beads come to room temperature and then flick mix or vortex to make sure the beads are well dispersed in the liquid (the liquid should appear brown)
- Add 10ul of the bead solution to your 20ul sequencing reaction
- Add 62ul of 85% ethanol (freshly prepared on the day) to each sample. Mix by pipetting 10× and place the tubes onto the SPIRI plate

- Leave the tubes on the magnetic plate for 10 minutes. Then aspirate the liquid. When aspirating it is important to keep the sample tubes on the magnetic plate and do not disturb the ring of magnetic beads. Aspirate (using a pipette and tip) carefully and take off the liquid in the tube
- With the tubes still on the SPIRI plate, wash the beads with 100ul of 85% ethanol. Leave for 10 minutes, then aspirate off the ethanol
- Remove the tubes from the magnetic plate and let air dry at room temperature (15-20 minutes although longer time maybe required) (the residual ethanol needs to be evaporated off, as carry over ethanol impacts on the performance of downstream applications)
- Once the beads are dry, add 40ul of water, mix gently by pipetting (10 ×) and place back onto the SPIRI plate to separate the beads
- Take off 25ul of the cleaned sequencing reaction and pipette into new tubes
- Your cleaned sequencing product is now ready for direct Sanger Sequencing. If sequencing is going to be undertaken at a later date, cover the sequencing reactions with aluminium foil and freeze until use

- Purified fragments are sequenced on an Applied Biosystems 3130XL DNA autoanalyser. forward and reverse sequences are analysed in Geneious vers 5.6.5
- Production of the final DNA barcode sequence from the raw sequencer output (the sequence traces) involves several steps and producing a consensus sequence from the F and R traces
- The R sequence trace is reversed complimented; it is then aligned with the F sequence trace
- Traces are trimmed with the primer sequences removed from the 5' end



Select a run to view: Run_3130xl_CSIRO_2014-09-18_12-15_3343

Status

Plate Name: SA_Seq_18_09_14

Instrument Protocol: Seq50_POP7

Sample Name: 220305R

Analysis Protocol: Sequencing

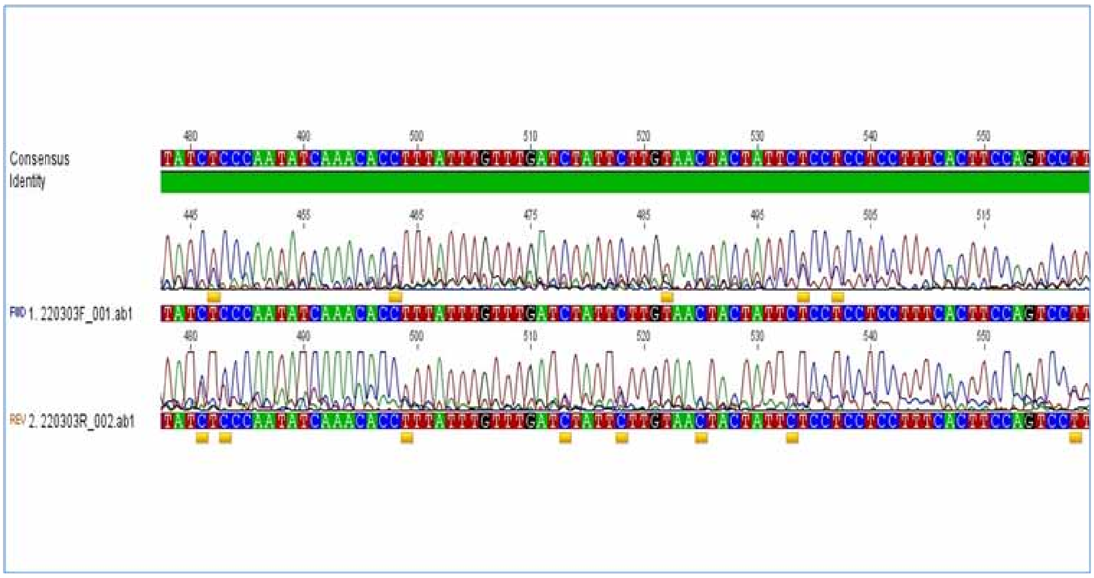
Well Position: A05

Capillary number: 1

Scan : 7632 Capillary : 0

and 3' end. A single sequence alignment or consensus sequence is then produced per sample

- Visually inspect the sequences, manually undertake base calls if required
- The consensus sequence (of approximately 650 base pairs) is used as the 'barcode'. Each successfully sequenced sample has a corresponding COI barcode (e.g. Shark 220303 below)



- via the Geneious portal or other 3rd party sequencing programs, consensus sequences were directly compared with GenBank database (http://www.ncbi.nlm.nih.gov/, all GenBank+EMBL+DDBJ+PDB sequences) using the basic local alignment search tool (BLASTn) and http://www.barcodinglife.com/
- database comparisons enable a molecular identification of each sample (e.g. 220303 = *Rhizopriondon taylori*)
- the molecular identification is used alongside morphological data, photos, age and growth data to verify or refute species identification and observer validation
- a database and or spreadsheets of the sequencing results should be maintained; COI barcodes are also uploaded to the BOLD database, along with various compulsory metadata information

Equipment and consumables for Barcoding

In addition to the equipment that is outlined above, the laboratory setup for DNA barcoding (tissue sampling, DNA extraction, PCRs, agarose electrophoresis, amplicon fragment cleaning) should also contain

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FULL PAPER

Aetomylaeus caeruleofasciatus, a new species of eagle ray (Myliobatiformes: Myliobatidae) from northern Australia and New Guinea

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Received: 25 February 2015 / Revised: 26 May 2015 / Accepted: 26 June 2015

Abstract A new species of eagle ray, *Aetomylaeus caeruleofasciatus* sp. nov., is described based on specimens collected in northern Australia and southern Papua New Guinea. The new species is very closely related to *Aetomylaeus nichofii* and was previously considered to be conspecific with this species. The new species and *A. nichofii* differ from their congeners in having a dorsal pattern of seven or eight transverse pale blue bands. As with other eagle ray species, morphological characteristics which distinguish the closely related species were largely obscured by intraspecific variation. The clearest morphological differences were apparent when comparing adult males to adult males and adult females to adult females, e.g. disc longer in adult female *A. caeruleofasciatus* compared to adult female *A. nichofii*. The two species also differ in the number of pelvic radials in both females and males and show subtle colour differences. A neotype is also allocated for *A. nichofii*.

Keywords *Aetomylaeus* · New species · Australia · Papua New Guinea · Morphology

Introduction

Members of the genus *Aetomylaeus* Garman 1908 (Myliobatiformes: Myliobatidae) differ from the other valid eagle ray genera, i.e. *Aetobatus* and *Myliobatis*, in having the pectoral fins joining the head just below the level of the eye and the dorsal fin lacking a free rear tip (White 2014). Six species occur in this genus, two of which, *Aetomylaeus asperrimus* (Waite 1909) and *Aetomylaeus bovinus* (Geoffroy St. Hilaire 1817), were until recently placed in the genus *Pteromylaeus* Garman 1913 (White 2014). Four species are known to occur in the Indo-West Pacific, of which only one, *Aetomylaeus nichofii* (Bloch and Schneider 1801), has a colour pattern consisting of faint blue bands on the dorsal surface without spotting or reticulations.

Aetomylaeus nichofii was first described by Bloch and Schneider (1801) as *Raja nichofii*, without any type material allocated. In the corrigenda of that publication, they corrected the name to *niehofii*, but since Bloch and Schneider consistently use *nichofii*, the original spelling can be continued under the 2000 code (Eschmeyer 2014). Bloch and Schneider's description is based on the illustration of "Aquila marinæ species" in Willughby (1686; Appendicis, tab. 10, fig. 3) which depicts a narrow-banded eagle ray (Fig. 1). The type locality was given as "*mare Indicum*" (Indian sea), but Willughby's record was most likely based on a specimen observed by the Dutch physician Jacobus Bontius during his time in the East Indies (=Indonesia). Thus, the type locality is probably Indonesian seas.

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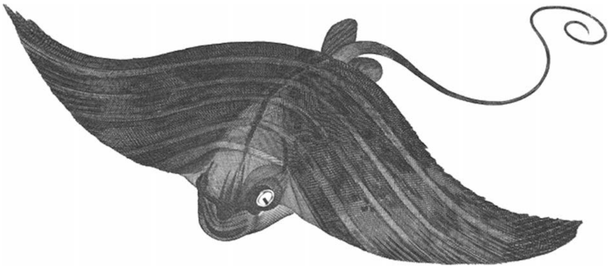

Fig. 1 The original illustration of "Aquila marinæ species" in Willughby (1686) which formed the basis for Bloch and Schneider's (1801) description of *Raja nichofii*

Aetomylaeus nichofii was thought to have a broad distribution in the Indo-West Pacific from the Arabian Gulf eastwards to northern Australia and New Guinea, extending northwards in the NW Pacific to Taiwan and southern Japan. Recent molecular studies (e.g. Naylor et al. 2012) suggested that this species may represent a species complex, with populations from northern Australia highly divergent from Indonesian and Malaysian populations. In this study, northern Australian and New Guinean populations are formally named and described as a new species and compared with the true *A. nichofii*. In the absence of type material, a neotype is also designated for *A. nichofii*.

Materials and methods

A total of 60 measurements were taken from the measured specimens by the senior author, following the methodology proposed for eagle rays by White et al. (2010). The holotype (CSIRO H 6629-01) and 11 paratypes (CSIRO C 4470, CSIRO CA 1250, CSIRO CA 1254, CSIRO T 684, CSIRO H 958-01, CSIRO H 3919-01, QM I 12534, QM I 27894, QM I 27930, QM I 33854 and QM I 34830) of the new species were measured in full (Table 1). In addition, a subset of key morphological characters was taken in the field from two adult male paratypes from Papua New Guinea (KFRS unreg. [field code 210386], KFRS unreg. [field code 210356]). The largest female specimen (CSIRO H 958-01) has a damaged right pectoral fin tip, so an estimated disc width was obtained by measuring the intact left side and doubling this measurement. For comparison, the neotype (CSIRO H 4426-13) and 24 specimens (BMNH 1867.11.28.165, BMNH 1909.7.12.35 and 36, CSIRO H 4426-12, CSIRO H 6131-03, CSIRO H 6209-01, CSIRO H 6209-02, CSIRO H 6235-01, CSIRO H 7394-07, CSIRO H 7394-08, HUMZ 33108, HUMZ 109131, HUMZ 109482, MNHN 1979-0213, NMMBP 6290, NMMBP 15673, NMMBP 15674, NMMBP 15675, NMMBP unreg. (field#077), NMMBP unreg. (field#078), NMMBP unreg. (field#079), NMMBP unreg. (field#152), ZMH 26027 and ZMH 103106) of *Aetomylaeus nichofii* were also measured in full (Table 1). Total length and disc width are abbreviated as TL and DW, respectively.

Meristics were obtained from digital radiographs of the holotype and six paratypes of the new species (CSIRO C 4470, CSIRO CA 1250, CSIRO CA 1254, CSIRO T 684, CSIRO H 958-01 and CSIRO H 3919-01) and from the neotype and nine other specimens of *A. nichofii* (CSIRO H 4426-12, CSIRO H 6131-03, CSIRO H 6209-01, CSIRO H 6209-02, CSIRO H 6235-01, CSIRO H 7394-07, CSIRO H 7394-08, HUMZ 33108 and HUMZ 109131). Four additional specimens of the new species (CSIRO H 958-02, -03, -04, -05) and two of *A. nichofii* were also radiographed, but were not adequately calcified due to their small size and thus counts could not be taken. Meristic methodology generally follow Last and White (2008) for dasyatids, with some minor modifications: the first enlarged anterior element of the pelvic fin (with at least four and up to six distal segments fused at their bases) is counted as one; first synarcual centra are included in vertebral counts as there are no calcified denticles or bucklers to obscure centra (counts also provided without synarcual centra); predorsal diplospondylous counts are used rather than pre-sting counts; intermediate pectoral-fin radial elements were assigned to a pterygial element based on the relative level of overlap with each of the adjacent element; and distal propterygial and metapterygial elements were considered to form part of the main skeleton and were not incorporated into counts; the notochord of the tail was excluded from counts. The rostral pectoral radials were difficult to accurately count in the majority of specimens due to the thick muscle and level of overlap where they are located.

The material was examined from the: BMNH, British Museum of Natural History, London, UK; CSIRO, Australian National Fish Collection, Hobart, Australia; HUMZ, Hokkaido University Museum, Hakodate, Japan; KFRS, Kanudi Fisheries Research Station (now housed at the University of Papua New Guinea), Port Moresby; MNHN, Muséum national d'Histoire naturelle, Paris, France; MZB, Museum Zoologicum Bogoriense, Jakarta, Indonesia; NMMBP, National Museum of Marine Biology and Aquarium, Taiwan; NTM, Museum and Art Gallery of the Northern Territory, Darwin, Australia; QM, Queensland Museum, Brisbane, Australia. For the new species, a complete synonymy is provided, whereas only an incomplete partial synonymy (first use of each combination) is provided for *A. nichofii*.

Molecular analysis of *Aetomylaeus* samples were conducted at the College of Charleston (USA) by Gavin Naylor and colleagues. The methodology used in this work is outlined in Naylor et al. (2012) and White et al. (2015). In addition to the sequences obtained in Naylor et al. (2012), three of the paratypes from Papua New Guinea were also incorporated into this analysis.

Table 1 Proportional dimensions as percentages of disc width for the holotype (CSIRO H 6629-01) and the 13 measured paratypes of *Aetomylaeus caeruleofasciatus*, and the neotype (CSIRO H 4426-13) and 24 other specimens of *Aetomylaeus nichofii*

	A. caeruleofasciatus				*A. nichofii*			
	Holotype	Paratypes (*n* = 13)			Neotype	Other material (*n* = 24)		
		Min.	Max.	Mean		Min.	Max.	Mean
Disc width (mm)	436	221	591	360	320	233	602	368
Total length	226.6	204.3	235.7	214.8	213.1	193.3	226.5	207.1
Predorsal length	56.5	50.4	58.6	53.4	51.5	50.7	58.2	53.4
Disc, length	60.7	55.4	67.3	60.0	57.1	55.2	62.2	58.8
Snout to pectoral-fin insertion	53.4	48.0	59.3	52.3	50.2	48.3	55.1	51.1
Disc thickness	11.8	9.7	10.9	10.6	9.7	9.1	11.1	9.9
Snout to pectoral-fin origin	13.6	11.0	14.8	13.0	13.8	11.9	14.2	13.0
Posterior orbit to pectoral-fin insertion	4.0	2.1	3.2	2.6	2.6	1.8	3.7	2.9
Snout to maximum width (horiz.)	41.5	33.7	46.8	39.0	36.4	33.2	41.6	37.8
Pectoral-fin anterior margin	51.4	48.9	56.7	51.7	49.8	48.4	52.8	50.6
Pectoral-fin posterior margin	49.9	47.0	51.9	49.4	51.3	43.4	51.9	47.9
Pectoral-fin base length	42.8	39.7	47.5	42.9	41.7	38.0	45.3	41.3
Pectoral-fin inner margin	8.3	6.5	8.7	7.4	8.5	7.3	10.0	8.2
Head length (ventral)	25.4	23.0	27.0	25.3	24.3	23.3	25.4	24.4
Preorbital length	7.4	7.3	9.1	8.3	8.5	6.7	9.8	8.1
Preorbital length (horiz.)	5.5	4.2	6.3	5.3	5.9	3.7	6.2	5.0
Head width at pectoral-fin origins	15.0	14.3	16.8	15.4	16.1	13.8	17.1	15.4
Head height at pectoral-fin origins	10.3	9.3	10.5	9.3	8.4	7.5	10.3	8.7
Head width at mid-eye	12.8	12.6	15.6	13.7	13.8	11.8	16.5	14.1
Head height at mid-eye	9.5	7.5	9.1	8.2	7.5	7.0	9.1	8.1
Interorbital width	7.8	7.7	9.4	8.5	7.8	7.8	9.1	8.3
Interspiracular width	11.0	10.7	12.8	11.9	11.6	10.1	12.8	11.6
Spiracle length (longest)	7.3	6.0	7.7	6.9	6.5	6.2	8.9	7.2
Spiracle width (narrowest)	1.8	1.1	2.3	1.4	1.0	0.8	2.0	1.2
Eyeball diameter	4.8	4.3	5.6	4.9	5.5	3.7	6.3	5.0
Eye diameter	2.6	2.2	2.7	2.6	2.9	2.1	3.6	2.6
Eyeball and spiracle length	11.9	11.5	13.8	12.7	12.5	11.5	13.8	12.5
Preoral length	10.4	10.0	11.9	10.8	10.1	9.7	11.8	10.5
Prenasal length	6.9	6.7	7.8	7.2	6.3	6.0	7.9	7.0
Prenasal length (horiz.)	5.8	6.0	7.2	6.5	5.6	5.0	7.0	6.2
Rostral lobe width	11.0	9.8	12.9	11.0	11.2	9.6	12.8	10.9
Rostral lobe length	3.5	2.8	4.0	3.4	3.8	1.9	4.7	3.5
Mouth width	7.5	6.6	8.5	7.4	7.1	6.6	8.7	7.4
Width of upper tooth plate	4.5	4.4	5.7	4.9	4.5	3.9	4.9	4.4
Width of lower tooth plate	4.2	3.8	4.8	4.3	4.1	3.3	4.4	3.8
Internarial width (external)	6.0	5.2	6.6	6.0	5.6	5.0	6.3	5.6
Nasal curtain length	5.6	4.3	5.7	5.0	4.8	4.0	5.5	4.7
Nasal curtain width	8.6	7.2	8.8	8.1	8.2	7.3	8.5	7.8
Nostril length (internal)	4.2	3.1	4.3	3.8	4.1	2.9	4.5	3.7
Width of first gill slit	1.6	1.6	2.1	1.8	2.0	1.6	2.1	1.8
Width of third gill slit	1.9	1.6	2.0	1.9	2.0	1.6	2.4	1.9
Width of fifth gill slit	1.2	1.1	1.6	1.2	1.1	0.9	1.5	1.2
Distance between first gill slits	13.0	11.1	13.7	12.4	13.4	11.3	14.7	12.7
Distance between fifth gill slits	6.8	6.3	7.5	6.8	7.4	7.1	8.5	7.6
Tail at axil of pelvic fins (width)	3.4	2.5	3.6	2.9	2.8	2.4	3.6	3.0

Table 1 continued

	A. caeruleofasciatus				*A. nichofii*			
	Holotype	Paratypes (n = 13)			Neotype	Other material (n = 24)		
		Min.	Max.	Mean		Min.	Max.	Mean
Tail at axil of pelvic fins (height)	3.4	3.2	3.8	3.5	3.4	2.7	4.0	3.5
Pectoral-fin ins. to dorsal-fin origin (horiz.)	3.4	1.6	2.7	2.1	2.1	1.3	3.7	2.6
Dorsal-fin length	9.3	7.8	10.3	9.1	10.3	8.3	11.6	9.4
Dorsal-fin anterior margin	7.0	5.5	8.2	6.9	8.0	6.0	8.0	7.0
Dorsal-fin height	4.2	3.6	5.6	4.3	4.4	3.4	4.7	4.2
Dorsal-fin posterior margin	5.8	4.7	6.6	5.5	6.1	4.4	7.0	5.4
Snout to anterior cloaca	51.0	45.7	57.3	50.2	47.3	46.1	54.6	49.1
Cloaca anterior to tail tip	175.6	152.2	180.9	163.1	165.9	144.7	180.4	157.5
Width across pelvic fin bases	10.3	9.6	12.6	10.5	12.0	9.7	12.6	10.7
Greatest span of pelvic fins	17.0	13.8	17.7	16.2	17.9	16.1	20.3	18.5
Pelvic-fin length	13.5	11.6	15.4	13.5	13.7	10.9	14.4	12.8
Pelvic-fin anterior margin	13.0	10.5	14.3	12.5	13.0	11.1	14.3	12.4
Pelvic-fin base	7.5	5.6	9.0	7.0	6.6	5.6	8.5	6.9
Pelvic-fin posterior margin	4.9	4.7	6.8	5.9	6.0	4.8	7.9	6.4
Pelvic-fin inner margin	7.9	6.8	9.2	8.3	8.4	6.8	8.6	7.6
Clasper outer length	5.3	5.0	5.0	5.0	–	2.1	5.2	3.7

Aetomylaeus caeruleofasciatus sp. nov.

(New English name: Blue-banded Eagle Ray) (Figs 2–5a, 6, 7, 11, 12; Tables 1, 2).

Aetomylaeus nichofii: Gloerfelt-Tarp and Kailola 1984: 44 (in part – Area C record); Sainsbury et al. 1985: 54, fig. (northwestern Australia); Kailola 1987: 33 (Gulf of Papua and Orangerie Bay, Papua New Guinea); Last and Stevens 1994: 450, pl. 79, figs (in part); Compagno and Last 1999 (in part): 1514, 1517, fig. (northern Australia and New Guinea); Hutchins 2001: 16 (Western Australia); Stobutzki et al. 2002: 809 (northern Australia); Kyne et al. 2005: 321, 325, fig. 1D (Queensland, Australia); Last and Stevens 2009: 468, pl. 85 (fig. 52.2), figs (in part); Larson et al. 2013: 22.

Myliobatis australis: Blaber et al. 1985: 259 (misidentification; Dampier).

Aetomyleus nichofii: Allen and Swainston 1988, 28, pl. 5.70 (northwestern Australia); Russell and Houston 1989: 79 (Arafura Sea); Blaber et al. 1994: 391 (Gulf of Carpentaria); Allen 1997, 48, pl. 5.10 (northeastern Australia); Stobutzki et al. 2002: 806 (northern Australia).

Aetomylaeus cf. *nichofii* 2: Naylor et al. 2012: 83, fig. 62 (Arafura Sea).

Holotype. CSIRO H 6629-01 (GenBank accession KP851149), adult male 436 mm DW (988 mm TL), bay south of Eagle Point anchorage, Western Australia, 16°14.73’ S, 124°23.71’ E, 10–15 m depth, 15 Aug. 2006.

Paratypes (*n* = 21). CSIRO C 4470, subadult male 351 mm DW (717 mm TL), 27 miles northwest of Fairway Buoy, Gulf of Carpentaria, Queensland, Australia, 13.5 m depth, 30 Oct. 1972; CSIRO CA 1149, male embryo 140 mm DW (323 mm TL), west of Admiralty Gulf, Western Australia, 14°03’ S, 124°05’ E, 116–117 m depth, 24 Jun. 1980; CSIRO CA 1250, female 322 mm DW (690 mm TL), north of Joseph Bonaparte Gulf, Western Australia, 12°23’ S, 129°21’ E, 70–72 m depth, 2 Jul. 1980; CSIRO CA 1254, juvenile male 230 mm DW (500 mm TL), north of Joseph Bonaparte Gulf, Western Australia, 13°20’ S, 128°20’ E, 84–88 m depth, 28 Jun. 1980; CSIRO T 684, female 350 mm DW (825 mm TL), north of Wessel Islands, Northern Territory, Australia, 9°47’ S, 136°20’ E, 50 m depth, 22 Feb. 1982; CSIRO H 958-01, pregnant female ~592 mm DW, probably off Wessel Islands or north of Darwin, Northern Territory, Australia, 21 Mar. 1987; CSIRO H 958-02, female embryo 173 mm DW (401 mm TL), CSIRO H 958-03, male embryo 188 mm DW (431 mm TL), CSIRO H 958-04, male embryo 171 mm DW (414 mm TL), CSIRO H 958-05, male embryo 172 mm DW (402 mm TL), all pups of CSIRO H 958-01; CSIRO H 3919-01, female 221 mm DW (474 mm TL), west of Weipa, Gulf of Carpentaria, Queensland, Australia, 12°29.1’ S, 141°29.2’ E, 24 m depth, 3 Mar. 1995; KFRS unregist. (field code 220559; genetic accession GN15806), female 232 mm DW (505 mm TL), Freshwater Bay, Gulf of Papua, Papua New Guinea, 8°6’57.6” S, 145°52’1.2” E, 14–17 m depth, 8 Jun. 2014; KFRS unregist. (field code 220600; genetic accession GN15815), female 225 mm DW (458 mm TL),

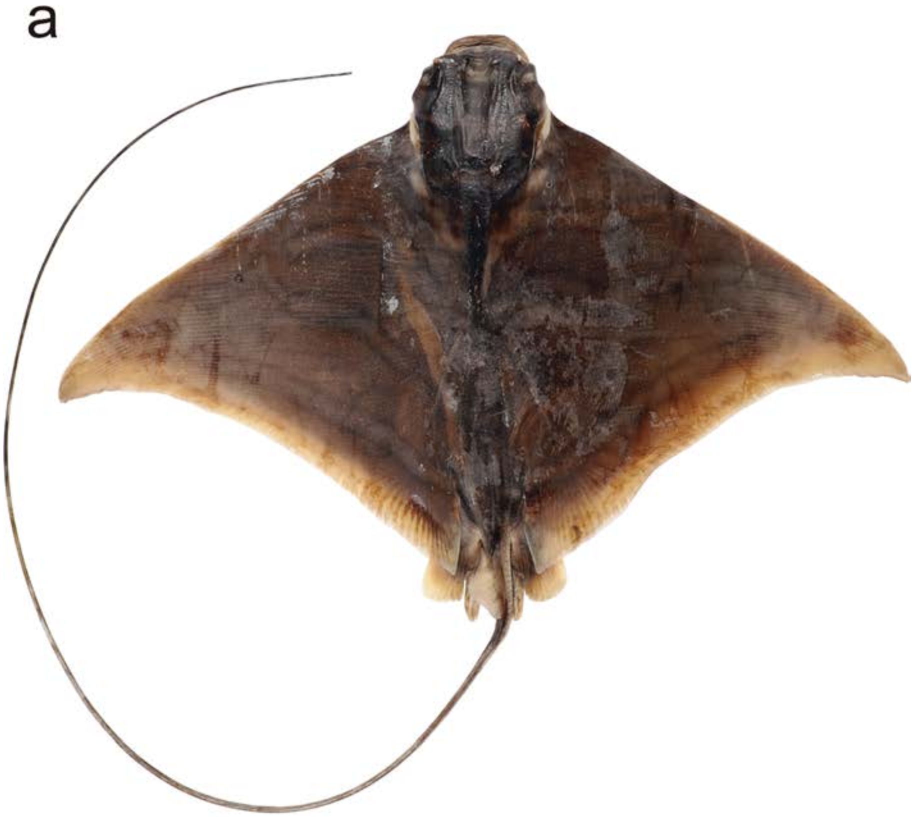

Fig. 2 Holotype of *Aetomylaeus caeruleofasciatus* n. sp. (CSIRO H 6629-01, adult male 436 mm DW, preserved): **a** dorsal view; **b** ventral view (excluding tail)

Freshwater Bay, Gulf of Papua, Papua New Guinea, 8°4’22.2” S, 145°46’5.4” E, 18–20 m depth, 12 Jun. 2014; KFRS unregist. (field code 220447; genetic accession GN15839), female 223 mm DW (494 mm TL), Freshwater Bay, Gulf of Papua, Papua New Guinea, 8°6’39.6” S, 145°53’57” E, 15–19 m depth, 19 Jun. 2014; KFRS unregist. (field code 210386), adult male 432 mm DW (933 mm TL), Gulf of Papua, Papua New Guinea, 8°6’24” S, 145°40’6” E, 20 m depth, 24 Nov. 2014; KFRS unregist. (field code 210356), adult male 447 mm DW, Gulf of Papua, Papua New Guinea, 8°5’19” S, 145°36’27” E, 18–27 m depth, 24 Nov. 2014; QM I 12534, juvenile male 249 mm DW (517 mm TL), off Brampton Island, Queensland, Australia, 20°49’ S, 149°12’ E, 22 m depth, 13 Aug. 1957; QM I 27894, adult male 434 mm DW (899 mm TL), Gulf of Carpentaria, Queensland, Australia,

Fig. 3 Dorsal view of a juvenile *Aetomylaeus caeruleofasciatus* n. sp. (paratype CSIRO CA 1254, male 230 mm DW, fresh)

Fig. 4 Ventral head of the holotype of *Aetomylaeus caeruleofasciatus* n. sp. (CSIRO H 6629-01, adult male 436 mm DW, preserved)

11°59.9’ S, 138°42’ E, 51 m depth, 9 Dec. 1990; QM I 27930, juvenile male 241 mm DW (522 mm TL), Gulf of Carpentaria, Queensland, Australia, 11°59.9’ S, 138°42’ E, 51 m depth, 9 Dec. 1990; QM I 33854, female 335 mm DW, Hervey Bay, Queensland, Australia, 25°13’ S, 152°43’ E, 8 m depth, 11 Jun. 2002; QM I 34830, adult male 480 mm DW, Arafura Sea, Northern Territory, Australia, 10°06.8’ S, 137°42.5’ E, 46 m depth, 21 Nov. 1991.

Other specimens (*n* = 6). AMS I 34389-027, juvenile male 350 mm DW (690 mm TL), off Shoalwater Bay, Queensland, Australia, 22°21’ S, 150°45’ E, 43 m depth, 25 Oct. 1993; NTM S 11786 (two male specimens), 488 and 468 mm DW, north of Goulburn Islands, Arafura Sea, Australia, 10°49.02’ S, 133°50’ E, 59 m depth, 7 Dec. 1985; NTM S 12952, female 544 mm DW, Arafura Sea, Australia, 10°34.02’ S, 134°28.98’ E, 60 m depth, 24 Oct. 1990; NTM S 12956, male 437 mm DW, Arafura Sea, Australia, 10°57’ S, 135°04.02’ E, 52 m depth, 25 Nov. 1990.

Diagnosis. A small *Aetomylaeus* (attaining about 590 mm DW) with the following combination of characters: dorsal surface greenish to yellowish brown with a series of seven transverse pale bluish bands (sometimes faint), without dark spots or blotches; ventral surface whitish, pectoral fins usually not dusky distally; tail rather long (1.5–1.8 times DW); no stinging spine; head short and narrow; rostral lobe fleshy, relatively broad, short, with a rounded apex; teeth in seven rows in each jaw, with a broad median row flanked by three smaller rows on each side; dorsal-fin origin level with pelvic-fin insertions; pectoral-fin radials 84–88 (excluding concealed propterygial radials anterior of eyes); total vertebral centra (including synarcual) 80–86; males with 14 or 15 pelvic radials (excluding clasper); females with 20 or 21 pelvic radials; males mature by 434 mm DW.

Description. *External morphology.* Disc diamond shaped, broad, moderately long, width about 1.65 (1.49–1.80) times disc length; anterior projection of head 4.47 (4.05–5.09) in disc length; axis of greatest width of disc just posterior to scapular region, over anterior abdominal cavity, its horizontal distance from snout tip 1.29 (1.23–1.54) times in distance from tip of snout to pectoral-fin insertion; moderately deep, greatest thickness above scapular region and posterior head, thickness 8.44 (9.14–10.28) in disc width; without denticles or thorns; a short, bony ridge on midline above scapular region. Pectoral fins very large, wing-like, triangular, weakly to moderately falcate; anterior margin weakly convex to nearly straight, becoming more convex distally; apex narrowly rounded to abruptly angular, pectoral angle 60 (56–64)°; posterior margin shallowly concave (moderately concave in larger specimens); free rear tip angular; inner margin moderately convex; length of anterior margin 51.4 (48.9–56.7)% DW, 1.20 (1.12–1.30) times its base length, inner margin 5.13 (4.94–6.56) in its base; fin origin below and just behind posterior margin of eye; apex located behind pectoral mid-base; insertion posterior to pelvic-fin origin by about half eye diameter, just anterior to dorsal-fin origin; free rear tip overlapping about half to nearly entire pelvic-fin anterior margin.

Head pronounced, relatively low, short and relatively narrow; projecting well anterior to pectoral-fin origins; subquadrangular in cross section at pectoral-fin origin; cranial region of head truncate to slightly convex in dorsoventral view; snout abruptly convex anterior of eyes, becoming deeply concave in lateral view at origin of rostral lobe; weakly convex ventrally; ventral head length 25.4 (23.0–27)% DW, 1.72 (1.54–1.80) times width at pectoral-fin origins, 4.71 (3.92–5.90) times preorbital length (horizontal), 3.29 (2.74–3.35) times interorbital width; preoral snout length 1.38 (1.39–1.63) times mouth width, 1.74 (1.65–1.98) times internarial width, 0.80 (0.84–0.96) times distance between first gill slits; head width at pectoral-fin origin 15.0 (14.3–16.8)% DW, 1.46 (1.42–1.85) times its height. Rostral lobe fleshy, relatively broad, short, not noticeably longer in adult males; broadly rounded in dorsoventral view with a rounded apex; narrowly rounded in lateral view; its length 3.5 (2.8–4.0)% DW, 7.33 (6.17–9.30) in head length, its width 1.37 (1.26–1.53) in head width at pectoral-fin origin.

Interorbital space moderately broad, very slightly concave, with a broad medial depression over cranial fontanelle, without ridges, denticles or thorns; interorbital width 7.8 (7.7–9.4)% DW, 1.64 (1.56–2.01) times eyeball length, 0.61 (0.58–0.66) times head width at mid-eye; margins of cranial fontanelle narrowest posteriorly, gradually widening anteriorly. Eyes relatively large, circular, lateral on head (eyes not visible in dorsal view), angling inwards anteriorly, diameter 2.79 (2.32–3.01) in spiracle length, 5.75 (5.50–6.41) in head width at pectoral-fin origin; eyeballs usually not visible above upper margin of head (visible above upper margin of head in adult males); a small but distinct, pointed bony protuberance (tubercle) present on anterior orbit just anterior to upper eyeball in adult males. Spiracles moderately large, diagonally elliptical to almost slit-like, situated almost entirely laterally on head (opening not visible in dorsal view, but lower margin sometimes visible), just posterior to concealed edge of eyeball and above pectoral-fin origin, length 7.3 (6.0–7.7)% DW, 4.15 (3.12–6.92) times width; upper margin with a fleshy fold which is slightly convex to nearly straight and angled inwards near posterior margin of spiracle.

Nostrils narrowly oval with a narrow, fleshy oronasal groove; anterior nasal fold thin, membranous, internal; posterior nasal fold larger, fleshy, extending more than half of nostril width from its lateral margin; internarial space 0.96 (0.91–1.23) in prenasal length, 1.41 (1.36–1.75) times nostril length. Nasal curtain large, broad, elongate, width 1.55 (1.44–1.73) times length; lateral margin weakly concave; posterior margin weakly bilobed, with a shallow median notch, bordered by a long, curtain-like fringe following contour of lower jaw; apices broadly rounded; apex and posterolateral margin recessible within oronasal groove; a small, low fleshy protuberance present on mid ventrolateral margin.

Mouth moderately large, broad, transverse, located ventrally, width 7.5 (6.6–8.5)% DW, 0.72 (0.62–0.72) times preoral length, 1.98 (1.79–2.38) in head width at pectoral-fin origin; margin of lower jaw nearly straight to slightly convex (with shallow median concavity in adult female paratype CSIRO H 958-01), not indented at symphysis; not strongly protrusible; no anterior teeth of lower jaw visible when mouth closed; skin on chin and at margin of lower jaw fleshy, papillate.

Gill openings small, elongate S-shaped, forming a weakly fringed lobe laterally; length of first gill slit 1.42 (1.26–1.73) times length of fifth gill slit, 4.58 (3.46–5.04) in mouth width; distance between first gill slits 2.16 (1.88–2.36) times internarial space, 0.50 (0.45–0.53) times ventral head length; distance between fifth gill slits 1.13 (1.03–1.29) times internarial distance, 0.26 (0.24–0.29) times ventral head length.

Pelvic fins relatively small, narrow; narrowly quadrangular, anterior margin nearly straight, apex broadly rounded, posterior margin moderately convex with scalloped edge, free rear tip very broadly rounded, inner margin slightly convex; extending well beyond pectoral-fin free tips; pelvic-fin length 13.5 (11.6–15.4)% DW, 1.31 (1.19–1.38) times width across fin bases, inner margin 7.9 (6.8–9.2)% DW. Claspers of adult males ($n = 2$) relatively short, moderately broad, tapering very slightly to tip, apex bluntly pointed, outer length 5.3 (5.0)% DW.

Dorsal fin small, triangular, raked back, its origin level with pelvic-fin insertions; anterior margin nearly straight; apex broadly rounded; posterior margin nearly straight, joining midline of tail without a free rear tip; predorsal length 1.77 (1.71–1.98) in disc width, fin length 9.3 (7.8–10.3)% DW, height 0.45 (0.39–0.57) times its length.

Tail very long, slender, whip-like, its length (from cloaca origin) 1.76 (1.52–1.81) times disc width; tapering gradually to a distance of about dorsal-fin length from dorsal fin, then becoming whip-like; base compressed, oval in cross section at pelvic-fin insertion, tail width at pelvic insertion 0.99 (0.70–1.03) times height; oval to elongate quadrangular or hexangular in cross section immediately behind dorsal fin; a weak, ridge-like dorsal skin fold present anteriorly; a weak, very low ventral skin fold usually present, evident as a fleshy keel near base; a very weak, ridge-like lateral skin fold present on either side anteriorly. No stinging spines.

Dentition. Teeth in seven rows in each jaw, coalesced to form plates; middle series of teeth in both jaws broad and hexagonal, flanked by three rows of much smaller, similarly sized, diamond-shaped teeth on each side arranged in a pavement-like fashion; median tooth row transverse in upper jaw, slightly curved in lower jaw; median tooth row 6–8 times width of lateral tooth rows; lower jaw tooth plate width 4.2 (3.8–4.8)% DW, upper jaw tooth plate width 4.5 (4.4–5.7)% DW.

Fig. 5 Lateral view of the head of: **a** holotype of *Aetomylaeus caeruleofasciatus* n. sp. (CSIRO H 6629-01, adult male 436 mm DW, preserved). Orbital thorn visible just anterior to mid-eye; **b** neotype of *Aetomylaeus nichofii* (CSIRO H 4426-13, subadult male 320 mm DW, preserved)

Meristics. Vertebral centra total (including synarcual) 84 (80–86, $n = 6$ paratypes); total (excluding synarcual) 80 (75–82; $n = 6$); monospondylous (including synarcual) 38 (31–42; $n = 6$); monospondylous (excluding synarcual) 34 (27–38; $n = 6$); predorsal diplospondylous 7 (8–14; $n = 2$); post-dorsal diplospondylous 39 (34–36; $n = 2$); total diplospondylous 46 (44–55; $n = 6$). Total pectoral-fin radials (excluding propterygial radials anterior of eyes) 86 (84–88; $n = 6$); propterygium (anterior of eyes) 8 ($\sim$8 or $\sim$9; $n = 6$); propterygium (posterior of eyes) 15 (14–16; $n = 6$), mesopterygium 28 (25–28; $n = 6$), metapterygium 43 (42–45; $n = 6$). Pelvic-fin radials: 1 (2 or 3 fused elements) + 14 (14 or 15; $n = 2$ males); 1 (2 fused elements) + 18 ($n = 2$ females).

Colour. In preservative (based on holotype): Dorsal surfaces medium brown with a series of faint transverse bands on disc; transverse bands on body very faint, appearing as a pale broad band flanked either side by a narrow, darker brown band; bands barely evident anteriorly or on middle of disc; disc with a narrow whitish anterior margin and broader pale posterior margin. Ventral surfaces pale yellowish; pectoral-fin tips dusky at extremity; a dark area present on head from first gills forward to over nasal area is probably an artefact of preservation of this specimen. Tail mostly brown; anterior ventral surfaces whitish.

When fresh: In juvenile male paratype CSIRO CA 1254, dorsal surface greenish to yellowish brown with a series of seven transverse pale blue bands (Fig. 3); first and anteriormost band across interorbit; second band across anterior spiracles; third band extending from edge of disc across posterior margin of spiracles; fourth posterior to spiracles (bifurcated near disc margin on left side); fifth and sixth bands across mid-disc (joining together on left side, fifth band almost joining fourth on right side and only extending half way to disc edge), seventh running across pectoral-fin insertions centrally and following contour of posterior disc margin for about two-thirds their length (not visible at fin apices); transverse bars more posteriorly located medially and, in bands 4–7, curving anteriorly towards pectoral-fin apices.

In adult female (CSIRO H 958-01), dorsal colouration similar to juvenile, but with bluish bands slightly less distinct; interorbital band very faint (Fig. 7). Late-term embryos from this female (CSIRO H 958-02, -03, -04, -05) with a paler brown background colouration and blue transverse bars more distinct.

Transverse bars 5 and 6 united on pectoral fins in some specimens, but sometimes completely separate (can vary from left and right sides on any one specimen).

Ventral surfaces whitish, usually without dusky pectoral-fin tips or posterior margins.

Size. Type specimens ranged in size from 140 to $\sim$592 mm DW. Four males between 230 and 350 mm DW

Fig. 6 Dorsal fin and anterior tail of the holotype of *Aetomylaeus caeruleofasciatus* n. sp. (CSIRO H 6629-01, adult male 436 mm DW, preserved). Note slight damage at the joint of the posterior margin with the tail; no free rear tip present when undamaged

were juvenile, a 351 mm DW male was adolescent, and five males of 432–480 mm DW were adult, based on the level of calcification of their claspers. Eight free-swimming females ranged in size from 221 to ~592 mm DW. The longest specimen recorded was 988 mm TL for the 436 mm DW holotype. Four late-term embryos from a ~592 mm DW female (CSIRO H 958-01) ranged in size from 171 to 188 mm DW (401 to 431 mm TL). Another pup (CSIRO CA 1149) had a disc width of 140 mm and total length of 323 mm.

Distribution. Restricted to northern Australia and New Guinea (Fig. 11). In Australia, occurs from the Dampier Archipelago in Western Australia to Hervey Bay in Queensland. In New Guinea, validated from records from Freshwater Bay in the Gulf of Papua and Orangerie Bay. Found on soft bottoms at depths of 8–117 m.

Etymology. Derived from the combination of the Latin *caeruleus* (blue) and *fasciatus* (band) in allusion to the distinctive transverse blue bands present on the dorsal surface of the disc.

Aetomylaeus nichofii (Bloch and Schneider 1801)

(English name: Banded Eagle Ray) (Figs 1, 5b, 8–12; Tables 1 and 2).

Aquila marinæ species Willughby 1686: Append. Tab. 10, fig. 3 (probably East Indies).

Raja nichofii Bloch and Schneider 1801: 364 (type locality: Indian sea = East Indies; based on Willughby).

Raja niehofii Bloch and Schneider 1801: 579.

Mookarrha-Tenkee Russell 1803: vol. I, pl. 7 (India; not a valid binomial name).

Raja fasciata Shaw 1804: 286 (based on Willughby and Russell).

Aetobatus nichofii: Blainville 1816: 112.

Raja nieuhowii: Cuvier 1816: 138.

Myliobatus nieuhofii: Müller and Henle 1841: 177 (in part – Indian records).

Myliobates nieuhofii: Richardson 1846: 198 (in part – Chinese Seas).

Myliobatis nieuhofi: Bleeker 1861: 30 (Singapore).

Myliobates nieuhofi var. *cornifera* Annandale 1909: 52, pl. 2 (fig. 4) (type locality: Bay of Bengal, Balasore, Orissa Coast, India).

Aetomylaeus nichofii: Garman 1913: 436 (India, Indonesia and Japan).

Aetomyleus nichofii: Chevey 1932 (Indo-China).

Myliobatis nichofii: Fowler 1938: 19 (Malaya).

Fig. 7 Fresh colouration of adult (CSIRO H 958-01, pregnant female ~592 mm DW) and late-term embryos (CSIRO H 958-02, -03, -04 and -05, 171–188 mm DW) of *Aetomylaeus caeruleofasciatus* n. sp.

Table 2 Ranges of proportional dimensions as percentages of disc width for adult males and adult females of *Aetomylaeus caeruleofasciatus* n. sp. and *Aetomylaeus nichofii*

	A. caeruleofasciatus			*A. nichofii*			
	Males ($n = 4$)		Female	Males ($n = 4$)		Females ($n = 2$)	
	Min.	Max.		Min.	Max.	Min.	Max.
Disc width (mm)	432	447	592	362	438	465	602
Total length	207.1	226.6	–	186.1	199.3	183.4	213.3
Predorsal length	53.6	56.5	–	52.2	54.8	54.1	58.2
Disc, length	58.9	61.3	67.3	58.0	59.9	59.9	62.2
Snout to pectoral-fin insertion	51.9	53.4	59.3	50.1	52.0	52.5	55.1
Disc thickness	10.2	11.8	10.9	9.2	9.9	9.7	10.8
Snout to pectoral-fin origin	12.1	13.6	13.6	11.9	13.6	12.0	13.7
Posterior orbit to pectoral-fin insertion	42.0	43.9	47.8	40.8	41.8	42.9	45.7
Snout to maximum width (horiz.)	33.7	41.5	43.3	33.6	40.1	37.9	40.8
Pectoral-fin anterior margin	48.9	51.4	52.6	48.4	50.8	50.5	52.0
Pectoral-fin posterior margin	49.1	49.9	51.9	47.4	51.9	46.9	49.5
Pectoral-fin base length	41.7	43.3	46.9	40.8	42.3	43.5	45.3
Pectoral-fin inner margin	6.5	8.3	8.7	7.4	10.0	7.6	8.6
Head length (ventral)	24.8	25.8	26.8	23.4	25.1	24.2	25.3
Preorbital length	7.4	8.6	8.7	7.2	8.7	6.7	9.8
Preorbital length (horiz.)	5.2	5.5	5.7	4.4	5.6	3.7	6.2
Head width at pectoral-fin origins	14.9	15.2	15.2	14.8	16.1	14.6	15.1
Head height at pectoral-fin origins	8.3	10.5	9.3	7.5	8.7	8.5	9.0
Head width at mid-eye	12.6	14.1	13.1	13.1	13.9	12.8	13.9
Head height at mid-eye	8.1	9.5	8.3	7.3	8.5	7.8	8.4
Interorbital width	7.7	8.0	8.5	7.8	8.3	8.0	8.7
Interspiracular width	11.0	12.0	11.8	11.2	11.8	10.8	11.7
Spiracle length (longest)	6.7	7.3	7.0	6.2	7.3	6.8	8.1
Spiracle width (narrowest)	0.9	2.3	1.2	0.9	1.2	0.9	1.9
Orbit diameter	4.4	5.0	4.3	4.4	5.4	3.7	5.1
Eye diameter	2.3	2.6	2.6	2.1	2.9	2.1	2.2
Orbit and spiracle length	11.7	12.8	13.3	11.6	12.8	11.7	12.6
Preoral length	10.4	10.7	11.9	9.8	11.2	9.7	11.2
Prenasal length	6.9	7.5	7.8	6.6	7.7	6.7	7.2
Prenasal length (horiz.)	5.8	6.8	7.2	5.8	6.7	5.8	6.5
Rostral lobe width	11.0	11.9	10.0	10.4	11.6	9.6	10.6
Rostral lobe length	2.8	3.7	3.9	3.0	4.1	3.3	4.7
Mouth width	7.2	7.5	8.5	7.2	8.5	6.9	7.6
Width of upper tooth plate	4.5	4.5	5.7	4.4	4.9	4.6	4.9
Width of lower tooth plate	4.2	4.2	4.8	4.0	4.4	4.0	4.1
Internarial width (external)	5.9	6.0	6.2	5.3	6.2	5.2	5.7
Nasal curtain length	4.6	5.6	5.2	4.0	5.1	4.8	5.0
Nasal curtain width	8.1	8.6	8.8	7.4	8.3	7.4	7.9
Nostril length (internal)	3.4	4.2	3.7	3.3	4.4	3.1	3.8
Width of first gill slit	1.6	2.1	1.8	1.6	2.0	1.9	2.1
Width of third gill slit	1.9	2.0	1.8	1.8	2.0	1.9	2.0
Width of fifth gill slit	1.2	1.4	1.1	1.0	1.4	0.9	1.4
Distance between first gill slits	12.1	13.0	13.7	11.8	12.7	12.1	13.3
Distance between fifth gill slits	6.3	6.8	7.0	7.1	7.8	7.2	7.8
Tail at axil of pelvic fins (width)	2.5	3.4	3.5	2.5	3.2	2.4	3.5

Table 2 continued

	A. caeruleofasciatus			*A. nichofii*			
	Males ($n = 4$)		Female	Males ($n = 4$)		Females ($n = 2$)	
	Min.	Max.		Min.	Max.	Min.	Max.
Tail at axil of pelvic fins (height)	3.4	3.6	3.5	3.0	4.0	3.8	4.0
Pectoral-fin ins. to dorsal-fin origin (horiz.)	1.3	3.3	–	1.7	3.4	2.1	3.7
Dorsal-fin length	8.6	9.7	–	9.2	10.9	9.1	11.6
Dorsal-fin anterior margin	6.5	7.1	–	7.0	8.0	6.4	7.5
Dorsal-fin height	4.2	5.6	–	4.1	4.7	4.0	4.7
Dorsal-fin posterior margin	5.0	5.8	–	4.8	6.2	4.7	7.0
Snout to anterior cloaca	49.4	51.0	57.3	47.9	50.7	50.3	54.6
Cloaca anterior to tail tip	156.0	175.6	–	137.8	149.1	128.8	161.4
Width across pelvic fin bases	10.2	10.6	12.6	9.7	11.3	10.5	12.6
Greatest span of pelvic fins	14.7	17.7	–	17.5	19.8	17.9	20.3
Pelvic-fin length	13.2	13.9	15.0	12.8	13.3	13.2	15.5
Pelvic-fin anterior margin	11.5	13.0	14.3	11.1	13.8	12.2	14.3
Pelvic-fin base	6.3	7.5	9.0	6.2	7.0	7.5	8.5
Pelvic-fin posterior margin	4.9	5.4	6.6	5.7	7.1	7.0	7.5
Pelvic-fin inner margin	7.9	9.1	8.7	7.2	8.6	6.8	7.7
Clasper outer length	5.0	5.3	–	4.8	5.8	–	–

Aetomylus nichofii: Fowler 1941: 467 (in part – exc. Australian records = probably *M. tenuicaudatus*).

Neotype. CSIRO H 4426-13, subadult male 320 mm DW (682 mm TL), Muara Angke fish market, Jakarta, Indonesia, 17 Oct. 1995.

Other material. BMNH 1867.11.28.165, adult male 415 mm DW, probably Indonesia; BMNH 1909.7.12.35-36 (two adult males), 438 mm DW (815 mm TL) and 405 mm DW (805 mm TL), off Odisha coast, India, Bay of Bengal (syntypes of *Myliobates nieuhofi* var. *cornifera*); CSIRO H 4426-12, juvenile male 247 mm DW (526 mm TL), collected with holotype; CSIRO H 6130-02, female 200 mm DW, Muara Angke fish market, Jakarta, Indonesia, 4 Apr. 2001; CSIRO H 6131-03, juvenile male 246 mm DW (500 mm TL), Muara Angke fish market, Jakarta, Indonesia, 6 Apr. 2001; CSIRO H 6209-01, juvenile male 252 mm DW (487 mm TL), CSIRO H 6209-02, juvenile male 234 mm DW (530 mm TL), Mukah fish market, Sarawak, Malaysia, 13 Jun. 2002; CSIRO H 6235-01, Kota Kinabalu fish market, Sabah, Malaysia, 8 Apr. 1999; CSIRO H 7394-07, subadult male 410 mm DW (849 mm TL), CSIRO H 7394-08, female 602 mm DW (1284 mm TL), Da-xi [Tashi] fish market, Yilan, Taiwan, 13 Mar. 2012; HUMZ 33108, adult male 419 mm DW, Taiwan or southern Japan; HUMZ 109131, pregnant female 465 mm DW (853 mm TL), Taiwan or southern Japan; HUMZ 109482, pregnant female 588 mm DW, near Kaohsiung, Taiwan, 16 Apr. 1986; MNHN 1979-0213, subadult male 393 mm DW (801 mm TL), Pakistan, 1977; MZB 15030, juvenile male ~255 mm DW, Muara Angke fish market, Jakarta, Indonesia, 4 Apr. 2001; MZB 15169 (GenBank accession EU398509), juvenile male 196 mm DW, Muara Angke fish market, Jakarta, Indonesia, 20 May 2005; NMMBP 6290, female 341 mm DW, Kaohsiung, Taiwan; NMMBP 15673, subadult male 436 mm DW (870 mm TL), NMMBP 15674, subadult male 430 mm DW (877 mm TL), NMMBP 15675, female 308 mm DW, Taiwan, 23 Jan. 2011; NMMBP unreg. (field#077), female 251 mm DW (521 mm TL), Taiwan; NMMBP unreg. (field#078), male 317 mm DW (656 mm TL), Taiwan; NMMBP unreg. (field#079), female 234 mm DW, Taiwan; NMMBP unreg. (field#152), juvenile male 322 mm DW (575 mm TL), Taiwan; NTM S 13157-026, juvenile male 240 mm DW (542 mm TL), Negombo landing place, Sri Lanka, 25 Sep. 1991; ZMH 25701, juvenile 315 mm DW, near Katang, East Andaman Sea, Thailand, 8 Dec. 1993; ZMH 26027, female 473 mm DW (947 mm TL), off West Java, Indonesia, 06°25’ S, 105°34’ E, 30 Apr. 1983; ZMH 103106 (ex ISH 171-1965), juvenile male 232.5 mm DW (489 mm TL), Mumbai, India, 18°49.8’ N, 72°33.5’ E, 26 Feb. 1965.

Diagnosis. A small *Aetomylaeus* (attaining about 720 mm DW) with the following combination of characters: dorsal surface greyish brown with a series of usually eight (sometimes seven) transverse pale bluish bands (sometimes faint), without dark spots or blotches; ventral

Fig. 8 Dorsal view of the neotype of *Aetomylaeus nichofii* (CSIRO H 4426-13, subadult male 320 mm DW, fresh)

surface whitish, pectoral fins dusky distally; tail rather long (1.4–1.8 times DW); no stinging spine; head short and narrow; rostral lobe fleshy, relatively broad, short, with a rounded apex; teeth mostly in seven rows in each jaw, with a broad median row flanked by three smaller rows on each side; dorsal-fin origin level with pelvic-fin insertions; pectoral-fin radials 84–88 (excluding concealed propterygial radials anterior of eyes); total vertebral centra (including synarcual) 83–93; males with 16–19 pelvic radials (excluding clasper); females with 20 or 21 pelvic radials; males mature at 400–420 mm DW.

Size. Attains at least 720 mm DW; males mature at 390–420 cm DW; size at birth probably around 17 cm DW.

Distribution. Occurs in the Indo-West Pacific from the Persian/Arabian Gulf westwards to Indonesia, and north to Taiwan, China and southern Japan. Mostly found inshore over soft substrates to depths of at least 115 m.

Discussion

Recent taxonomic studies on eagle rays (e.g. White et al. 2010, 2013) have shown that it can be very difficult to find good diagnostic characters to separate species which generally exhibit low levels of interspecific variability, but are also extremely intraspecifically variable. It is thus important to compare similar-sized specimens when trying to find useful characters to distinguish similar species. The new species described in this paper, *Aetomylaeus caeruleofasciatus*, is a prime example of this. Until now, it was considered to be conspecific with *A. nichofii* which has

Fig. 9 Dorsal view of an adult female *Aetomylaeus nichofii* from Malaysian Borneo (not retained, 500 mm DW, fresh)

Fig. 10 Ventral view of a female *Aetomylaeus nichofii* from Malaysian Borneo (not retained, 350 mm DW, fresh)

a wide range in the Indo-West Pacific. A similar example was provided by White et al. (2013) in which a new large eagle ray, which was previously considered to be conspecific with *Aetobatus flagellum* (Bloch and Schneider 1801), was found to be endemic to the Northwest Pacific, i.e. *Aetobatus narutobiei* White et al. 2013. In this case, the ray was well known as it is part of the predator eradication program in Ariake Bay in southern Japan, but the taxonomy had not been thoroughly investigated.

Comparison of morphometric data for *A. caeruleofasciatus* and *A. nichofii* revealed that both were intraspecifically variable, and thus interspecific differences were

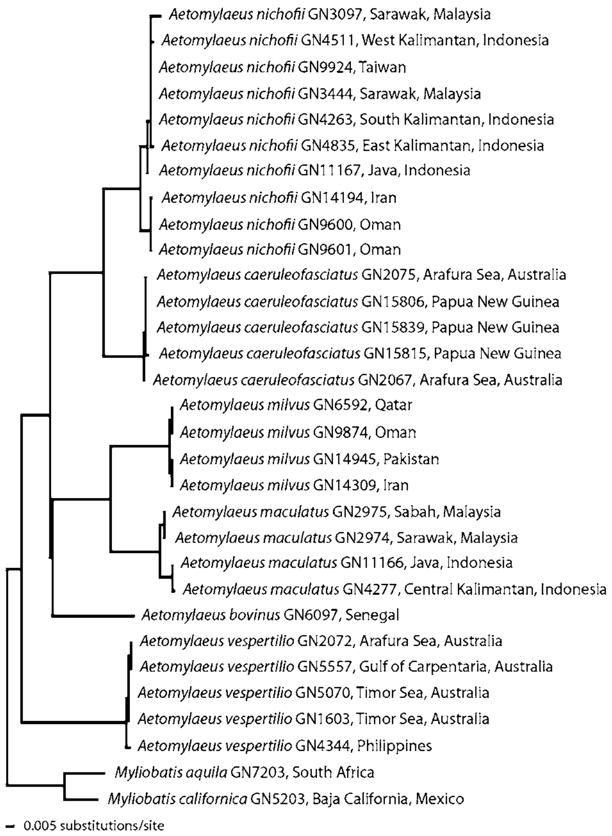

Fig. 11 Neighbour-joining tree for *Aetomylaeus* species based on *P* distance with two species of *Myliobatis* as outgroups, using NADH2 sequences

difficult to ascertain. However, when comparing similar-sized specimens of each sex, a number of interspecific differences could be found. Comparison of the morphometric data for adult females showed that *A. caeruleofasciatus* ($n = 1$) differs from *A. nichofii* ($n = 2$) in the following characteristics: longer disc (its length 67.3 vs. 59.9–62.2 % DW, snout to pectoral-fin insertion 59.3 vs. 52.5–55.1 % DW; snout to cloaca 57.3 vs. 50.4–54.6 % DW); and longer head (its length 27.5 vs. 24.3–25.5 % DW). Comparison of adult males showed that *A. caeruleofasciatus* ($n = 4$) differs from *A. nichofii* ($n = 4$) in having a longer tail (total length 207.1–226.6 vs. 186.1–199.3 % DW; tail length 156.0–175.6 vs. 137.8–149.1 % DW). A comparison of morphometric data for juveniles <300 mm DW of *A. caeruleofasciatus* ($n = 4$) and *A. nichofii* ($n = 6$) did not reveal any, non-overlapping differences between the two species. Thus, morphometric data obtained in this study indicates that adult females and adult males of the two species can be distinguished, but it failed to separate juvenile specimens.

Aetomylaeus caeruleofasciatus differs from *A. nichofii* in the number of pelvic radials in males (14 or 15 vs. 16–19, excluding clasper and first enlarged element) and females (18 or 19 vs. 20 or 21, excluding first enlarged element). The two species have a similar colour pattern, but *A. nichofii* often has an eighth bluish band present on the dorsal surface, with the seventh band being slightly more anteriorly positioned and the eighth band present as a narrower, less distinct band. The blue bands also appear to be less distinct in adults of *A. nichofii* than in *A. caeruleofasciatus*, but more freshly caught individuals need to be examined to determine if this is a useful character.

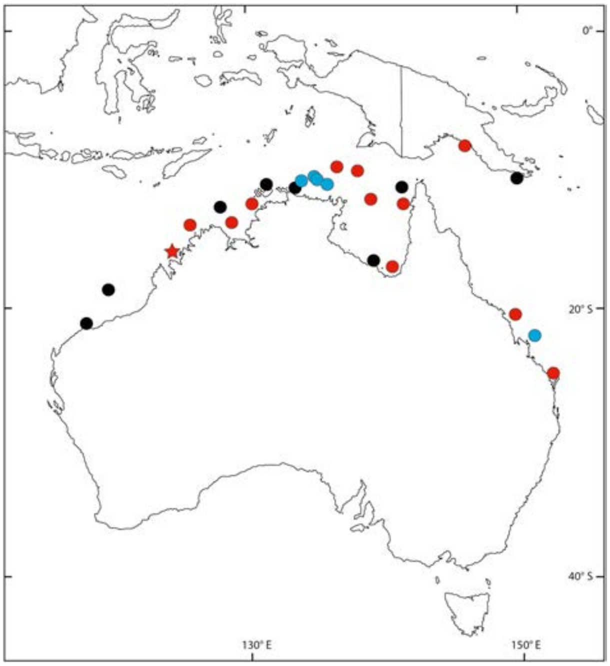

Fig. 12 Map showing the distribution of *Aetomylaeus caeruleofasciatus* n. sp.: the *red star* denotes capture locality of the holotype, *red circles* denote paratypes, *blue circles* denote non-type specimens, and *black circles* denote other records

The two species are also divergent from each other based on sequences of the CO1 and NADH2 genes. Sequences of the NADH2 gene from two Australian and three Papua New Guinean specimens of *A. caeruleofasciatus* grouped separately from the other species of *Aetomylaeus* and were closest to, but well separated from, *A. nichofii* (Fig. 12). The new species sequences had an average pairwise difference of 77 (7.3 %) from Borneo samples and 74 (7.0 %) from Persian Gulf samples for the NADH2 sequences. In contrast, the average pairwise difference amongst the 15 Borneo samples was only 3.3 (3.1 %) (see Naylor et al. 2012). Similarly, COI sequences of the new species have an average genetic divergence of 4.96 % from *A. nichofii*. These molecular and morphological results provide very strong support for recognising these forms as separate species.

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An annotated checklist of the chondrichthyans of Papua New Guinea

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Abstract

An annotated checklist of the chondrichthyan fishes (sharks, rays, and chimaeras) of Papua New Guinean waters is herein presented. The checklist is the result of a large biodiversity study on the chondrichthyan fauna of Papua New Guinea between 2013 and 2017. The chondrichthyan fauna of Papua New Guinea has historically been very poorly known due to a lack of baseline information and limited deepwater exploration. A total of 131 species, comprising 36 families and 68 genera, were recorded. The most speciose families are the Carcharhinidae with 29 species and the Dasyatidae with 23 species. Verified voucher material from various biological collections around the world are provided, with a total of 687 lots recorded comprising 574 whole specimens, 128 sets of jaws and 21 sawfish rostra. This represents the first detailed, verified checklist of chondrichthyans from Papua New Guinean waters.

Key words: Sharks, rays, chimaeras, Papua New Guinea, biodiversity, collections

Introduction

Chondrichthyans are a diverse group of cartilaginous fishes which inhabit a diverse range of habitats globally from well upstream in freshwater rivers to >3000 m deep in oceanic trenches. Chondrichthyan biodiversity is continually being updated and refined. To understand global biodiversity, it is important to understand regional biodiversity and nowhere in the world is this greater than in the Coral Triangle.

Papua New Guinea (PNG) lies within the highly diverse Coral Triangle and is one of the most diverse places in the world, not only in terms of its biota, but also its cultures, geomorphology, history and languages (Gressitt, 1982). The island of New Guinea, named by Spanish explorer Yñigo Ortiz de Retez in 1545, has had a complex history. In 1884, the northern half of PNG was colonised by Germany as German New Guinea while the southern half was colonised by the United Kingdom as British New Guinea. The United Kingdom transferred British New Guinea to the Commonwealth of Australia and after the Great War, German New Guinea became a Mandate Territory of Australia. In September 1975, PNG established independence from Australia and became part of the Commonwealth.

The first collection of shark and ray material from PNG waters was onboard the French vessel *La Coquille* (renamed *Astrolabe* in 1826) under the command of the explorer Louis Isidore Duperrey (1786–1865). This circumnavigation of the earth between 1822 and 1825 included visit and subsequent collecting from Port Praslin in New Ireland in 1824 by René Primevère Lesson (1794–1849) and Propser Garnot (1794–1838) (see Lesson, 1829–1831) (Cretella, 2010). The first species described from PNG, based on this material, were *Trygon halgani* Lesson, 1829 (=*T. lessoni*) and *Scyllium ferrugineum* Lesson, 1831 (=*Nebrius ferrugineus*).

Between 1874 and 1876, Georg Gustav F. von Schleinitz captained the *S.M.S. Gazelle* to a number of southwest Pacific locations, including New Guinea where material was collected and five species of sharks and rays were recorded from Bougainville and New Ireland (Peters, 1877). The first Australian to work on fishes in PNG was Sir William John Macleay (1820–1891) who collected in southern PNG in 1875 on-board the *Chervert*. Although no sharks or rays were recorded, he subsequently described collections of numerous species obtained by Andrew Goldie (Macleay 1883a, 1883b, 1884). Andrew Goldie (1840–1891) was a naturalist and merchant who made numerous ethnological and biological collections in southeastern PNG from 1876 until his death in 1891, mainly between Port Moresby and KapaKapa (Gibbney, 1972), as well as east to the D-Entrecasteaux Islands. Goldie saw his collections as a commercial venture and was thus unpopular with other scientists. Many of his discoveries were allegedly made by the German naturalist Carl von Hunstein (Gibbney, 1972). Among the shark and ray specimens collected by Goldie, now deposited at Museum Victoria (NMV) and Australian Museum (AMS) collections, were the holotypes of *Pastinachus ater* (AMS I.9762) and *Urogymnus granulatus* (AMS I.9763) described by Macleay. In 1886, Macleay and de Miklouho-Maclay noted two rays from the Admiralty (Manus) and Hermit Islands. Lamberto Loria (1855–1913), an Italian explorer and naturalist, explored southeastern PNG in 1889–1890 and 1892–1897, but published very little about his work in PNG (Ceci, 2006). Two sharks collected by Loria from southeastern PNG in 1890 are deposited in the Museo Civico di Storia Naturale di Genova 'Giacomo Doria' in Genova, Italy, but were not examined in this study.

Several German expeditions by naturalists also resulted in shark and rays being collected during the late 1800s and early 1900s while northern PNG was colonised as German New Guinea. Otto Finsch (1839–1917), a colonial explorer and naturalist, visited PNG between 1879 and 1885 and was the first European to explore the Sepik River. The botanist Carl Adolf Georg Lauterbach (1864–1937) made several expeditions to German New Guinea, including to the Ramu River in both 1896 and 1899 (van Steenis Kruseman, 1959), likely when the *Pristis pristis* rostrum (ZMB 14507) was collected. Richard Thurnwald (1869–1954), an Austrian anthropologist, undertook ethno-sociological studies in New Guinea between 1906 and 1912, including southern Bougainville and the Sepik River (Lowie, 1954). He collected a *Pristis pristis* rostrum, ZMB 32538 in November 1909, which is labelled from Bismarck Archipelago. Theodore Josef Bürgers (1881–1954) was a German zoologist who participated in the German Sepik Expedition (Kaiserin-August-Fluss Expedition) in 1912–1913 (Schindlbeck, 2015), which included a collection of a *Pristis pristis* rostrum (ZMB 33545).

The first American expedition into PNG which recorded sharks or rays was the Crane Expedition between November 1928 and October 1929, which included in May 1929 a trip through the upper Sepik River to duplicate on a smaller scale the German expedition of 1912–1913 (Webb, 1995). Albert William Herre (1868–1962), an American ichthyologist and lichenologist, was part of this expedition and although he wrote "Very little opportunity was afforded to collect while on the Sepik" he did record *Pristis perotteti* (=*Pristis pristis*) and purchased two rostra from Korogo villagers (Herre, 1936; CAS SU 41013 and 41014) and a *Pristis zijsron* rostrum. He also collected a *Dasybatus uarnak* (=*Himantura australis*; CAS SU 28205) specimen from Rabaul in East New Britain in April 1929, prior to the expedition moving to the Sepik.

In 1943, Ian S.R. Munro (Commonwealth Scientific and Industrial Research Organisation, CSIRO) established a collection of fishes which formed the foundation of the Australian National Fish Collection in Hobart. Munro was the first to work extensively on the fishes of the New Guinea region and his fishes of New Guinea checklist (Munro, 1958), additions to the fish fauna of New Guinea (Munro, 1964), and book (Munro, 1967) are still some of the most detailed studies of the region to date. With the aim to assist with development of fisheries for local communities, the Australian Commonwealth Department of Territories and the Australian Administration in PNG undertook a series of surveys onboard the MV *Fairwind* between August 1948 and March 1950 (Munro, 1958). Sections of this cruise were undertaken by Ian S.R. Munro and Gilbert Whitley (1903–1975) and a total of 492 species were collected by the *Fairwind*, with 185 new records (Munro, 1958, 1967). Tragically, the vessel and all crew was lost at sea off New South Wales on its return from Port Moresby during a cyclone.

In PNG itself, the Department of Agriculture and Livestock established a Fisheries Division in 1954 and the Research and Surveys Branch in 1968 which was located at Kanudi Fisheries Research Station, Konedobu, Port Moresby. Between the 1960s and 1980s, Lionel W.C. Filewood (b. 1936) worked for the Department of Agriculture, Stock and Fisheries at Kanudi (Watkins & Beolens, 2015). Filewood is known for his work on the sharks and rays of PNG (Filewood, 1973) and he made substantial collections of sharks and rays (>500 specimens) which were deposited in the KFRS fish collection established in the mid-1950s. The fish collection was at its peak in the 1970s and 1980s but slowly fell into disrepair and was neglected, and following the closure of the Kanudi Fisheries Research Station in the 1990s, it was essentially abandoned. The University of PNG showed interest in the KFRS collections and negotiated with NFA for its relocation to its Waigani campus where it was planned to become part of the Natural Science Resource Centre collections, and where it can be utilized for teaching and research purposes. In 2000, Patricia Kailola led the rehabilitation of the KFRS collection including moving it to the Department of Biological Sciences at the University of PNG (Fig. 1). Unfortunately, more than 80% of the shark and ray specimens present in the collection were destroyed prior to this rehabilitation and the quality of many of the remaining specimens was severely reduced. This rehabilitation was supported by the National Fisheries Authority (est. 1998), the University of PNG and the Australian Centre for International Agricultural Research (ACIAR). Without these efforts, it is possible that no specimens in the KFRS collection would be accessible today.

In 2010, a collaborative project organised by the Muséum National d'Histoire Naturelle (MNHN), Pro Natura International (PNI), Institut de Recherche pour le Développement (IRD) and University of Papua New Guinea (UPNG), set out to take an inventory of the deep water (between 100–1500m depth) benthic biodiversity in the PNG Bismarck and Solomon Seas area. This 2010 BIOPAPUA expedition was followed up by the Papua Niugini Biodiversity Expedition which focused on deepwater areas in the Bismarck Sea in 2012 (Samadi *et al.*, 2014). A third survey in 2014, the MADEEP and Kavieng expedition, surveyed deepwater off Madang and New Ireland. The fishes collected from these expeditions were deposited in the National Taiwan University Museum (NTUM). The sharks and rays collected off the Madang Province are listed in Fricke *et al.* (2014) and a checklist of the fishes of New Ireland is currently in preparation. In 2015, the first author examined all the shark and ray material collected on these expeditions which has resulted in description of a number of new species (White *et al.*, 2016a, b; 2017c, d, e). These expeditions were crucial for improving our understanding of the deepwater shark and ray fauna of PNG which was largely unknown previous to 2010.

In 2014, the Australian Centre for International Agricultural Research (ACIAR) funded a 4-year project led by the National Fisheries Authority and CSIRO entitled "Sustainable management of the shark resources of Papua New Guinea: socioeconomic and biological characteristics of the fishery" (FIS/2012/102) led by the senior author. A component of this project was to collect biodiversity information on sharks and rays in PNG and attempt to improve the fish collection by expanding the current holdings of sharks and rays. More than 400 specimens were obtained during this project, which are deposited in either the KFRS collection at UPNG or the Australian National Fish Collection at CSIRO, Hobart.

An exhaustive literature search and extensive examination of shark and ray material collected from PNG in various museum collections was undertaken to produce this checklist and it is expected this will form an important foundation for future biodiversity work in PNG.

FIGURE 1. The current location of the KFRS collection in the biological sciences area of the University of PNG.

Methods

The checklist includes the authorship, type designation for genera and species, the status and deposition of type material, and the type locality if available. Following the scientific name of a species are the common name in English and the local synonymy for all known PNG taxa, including authors. Each species account has a subsection on PNG voucher specimens and includes institutional acronyms following Fricke & Eschmeyer (2017) [note, in addition, PMH is used as an acronym for the Private shark and ray jaw collection of Mark Harris], institutional accession numbers and additional deposition information including specimen size (TL = total length, DW = disc width, PCL = precaudal length), sex, location, depth of capture, and date of capture, if known. A remarks subsection follows with any specific information relating to that species, including taxonomic history, such as nomenclature and systematics, if applicable. Every attempt was made to confirm the occurrence of all species reported from PNG waters. If not fully verified, a comment will be made in the remarks section.

Literature searches were confined to published articles and books, with the exception of several key reports and unpublished references which were considered important contributions to the knowledge of the chondrichthyan fauna of PNG. These articles are Filewood (1973) and Kailola (1987) as the records provided in these papers related to KFRS specimens that do or once did exist. In general, broader global references were not included in the synonymy unless they clearly state the New Guinea range, e.g. Ebert *et al.* (2013); Compagno, 1984, 2001; Last & Stevens (2009). Such references were not included in the local synonymy if only related to the distribution map they provide since these are often highly generalised.

As mentioned in the Introduction, more than 80% of the 500 plus shark and ray specimens originally deposited in the KFRS collection were lost or destroyed. Although these records no longer exist and identification cannot be verified, they do still hold some useful distribution information and may be relevant to future studies. As a result, a list of all KFRS specimens that no longer exist are provided, with collection data, in Appendix I.

Results

A total of 131 species, comprising 36 families and 68 genera, were recorded. The most speciose families are the Carcharhinidae with 29 species and the Dasyatidae with 23 species. Verified voucher material from various biological collections around the world are provided, with a total of 687 lots recorded comprising 574 whole specimens, 128 sets of jaws and 21 sawfish rostra.

Figure 2 shows the number of specimen lots (all museum holdings combined) collected in 5-yearly increments from 1820–24 through to 2015–20. This clearly highlights the two major collection periods for sharks and rays in PNG waters, firstly the Filewood collections in the 1960s and early 1970s, and secondly the collections of the current project (plus the deepwater BIOPAPUA collections) from 2010 to 2016. The significance of the number of lost or destroyed specimens (red bars) is clearly visible in this figure.

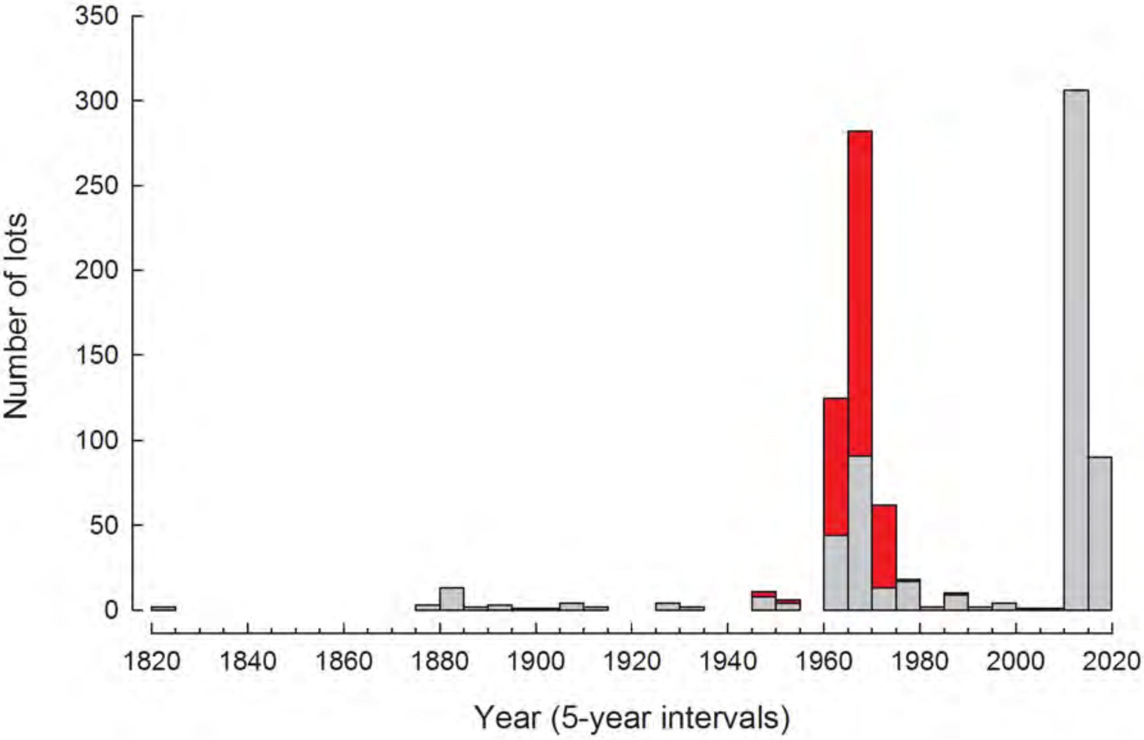

FIGURE 2. Number of museum specimen lots from PNG waters per 5-yearly intervals between 1820 and the present. All museum collections combined; grey bars dnote existing lots; red bars denote lost or destroyed lots.

Order Hexanchiformes

Family Hexanchidae Gray, 1851
Cow Sharks

Genus *Hexanchus* Rafinesque, 1810a
Sixgill Sharks

Hexanchus Rafinesque, 1810a: 14. Type species: "*Squalus griseus* Lacépède", by original designation, a junior synonym of *Squalus griseus* Bonnaterre, 1788.

Hexanchus griseus (Bonnaterre, 1788)
Bluntnose Sixgill Shark

Squalus griseus Bonnaterre, 1788: 9. Types unknown according to Boeseman *in* Hureau & Monod (1973). Type locality: "La Méditerranée [= Mediterranean Sea]".

Local synonymy: *Hexanchus griseus*—Kailola, 1987: 2 (Rabaul, New Britain); White *et al.*, 2018: 34, figs (PNG).
PNG voucher material: None; a specimen (KFRS E.361, Rabaul, New Britain) was destroyed.

Remarks: Images of a large individual hooked by recreational sports fishers off Walindi in Kimbe Bay (West New Britain) on a small seamount in about 90 m depth just before being released confirm this species from PNG. Only two records of this species in PNG highlight the limited deepwater fishing in PNG waters rather than rarity of the species.

Order Squaliformes

Family Squalidae Blainville, 1816
Dogfishes

Genus *Squalus* Linnaeus, 1758
Dogfishes

Squalus Linnaeus, 1758: 233. Type species: *Squalus acanthias* Linnaeus, 1758, by subsequent designation of Gill, 1862: 39.

Species indeterminable: *Squalus blainvillei*?—Kailola, 1987: 23 (Rabaul; based on KFRS E.346, two juveniles, 10 Nov. 1968 which were destroyed; label identification *Squalus fernandinus*). *Squalus megalops*—Kailola, 1987: 22 (Gulf of Papua). Without specimens or images, neither of these names can be attributed to species known to occur in PNG waters (see below).

Squalus crassispinus Last, Edmunds & Yearsley, 2007
Fatspine Spurdog

Squalus crassispinus Last, Edmunds & Yearsley, 2007: 11, Figs 1–4. Holotype: CSIRO H 2547-06. Type locality: North West Cape, Western Australia.

Local synonymy: *Squalus* sp.—Fricke *et al.*, 2014: 14 (Madang Province); White *et al.*, 2018: 36, figs (PNG).

PNG voucher material: (3 spec.) CAS 66115, female 655 mm TL, south of Pig Island, Madang, 5°10.41’ S, 145°50.46’ E, 300 m depth, 17 May 1987; NTUM 10301, female 671 mm TL, Bismarck Sea, 13 Dec. 2012; QM I 21399, adult male 483 mm TL, off Lae, Huon Gulf, Nov. 1984.

Remarks: First record of this species in PNG and deepest record for this species. Previously considered an Australian endemic, known from off the North West Shelf in Western Australia at depths of 187–262 m (Last &

Stevens, 2009). These specimens represent the largest specimens known for this species; previously 580 mm TL. CO1 sequences of the NTUM specimen confirm the identification of this species (Wei-Jen Chen, unpubl. data).

Squalus* cf. *edmundsi
Papuan Spurdog

Local synonymy: White *et al.*, 2018: 38, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11497, female 243 mm TL, west of New Hanover, New Ireland, 2°21' S, 149°56' E, 340–465 m depth, 6 Sep. 2014.

Remarks: Very close to *Squalus edmundsi* White, Last & Stevens, 2007 from Indonesia and Australia but slight differences in the NADH2 sequences were found (G. Naylor, unpubl. data). More specimens needed of this species, including adults, to allow for confirmation of its exact identity.

***Squalus montalbani* Whitley, 1931**
Philippine Spurdog

Squalus montalbani Whitley, 1931: 310. Holotype: USNM 70256. Type locality: Sombrero Island, Luzon, Philippines.

Local synonymy: White *et al.*, 2018: 40, figs (PNG).

PNG voucher material: (1 spec.) CSIRO H 8002-01, female 1060 mm TL, north of Kavieng town, New Ireland, 2°31.42' S, 150°38.78' E, 680 m depth, 29 Sep. 2015.

Remarks: First record of this species from PNG and also the deepest and largest specimen recorded. Previously known from Australia, Indonesia and Philippines in depths of 295–670 m and a maximum size of 910 mm TL (Last & Stevens, 2009).

Family Centrophoridae Bleeker, 1859
Gulper Sharks

Genus *Centrophorus* Müller & Henle, 1837a
Gulper Sharks

Centrophorus Müller & Henle, 1837a: 115. Type species: *Squalus granulosus* Bloch & Schneider, 1801, by monotypy.

Local synonymy: *Centrophorus armatus*—Filewood, 1973: 1 (off Lae). *Centrophorus moluccensis*—Kailola, 1987: 22 (Lae; Madang). Without specimens to confirm identification, these records could be any of the four species of *Centrophorus* listed below.

***Centrophorus atromarginatus* Garman, 1913**
Dwarf Gulper Shark

Centrophorus atromarginatus Garman, 1913: 200, pl. 13, figs 1–4. Holotype: MCZ 1117-S, Suruga Gulf, Japan; type was erroneously re-catalogued as MCZ 1455-S (Hartel & Dingerkus, 1997).

Local synonymy: White *et al.*, 2018: 42, figs (PNG).

PNG voucher material: (5 spec.) CAS 64520 (2 spec.), female 433 mm TL, adult male 564 mm TL, southwest of Bil Bil Island, north of Gogol River, Bismarck Sea, 5°18' S, 145°46' E, 10 May 1987; CSIRO H 8101-01, female 710 mm TL, off Lae, Huon Gulf, 6°44.22' S, 147°7.55' E, 430 m depth, 3 Nov. 2016; QM I 21400, female 574 mm TL, off Lae, Huon Gulf, 300 m depth, Nov. 1984; USNM 295139, adolescent male 640 mm TL, southwest of Bil Bil Island, north of Gogol River, Bismarck Sea, 5°18' S, 145°46' E, 183 m depth, 10 May 1987.

Remarks: Compagno & Niem (1998a) first documented this species from off northern PNG. Found to be a common catch in deepwater off Lae during recent fish surveys using rod and line (F. Neira, MARSCCO, pers. comm.) in November 2016. Has previously been referred to as *Centrophorus armatus* elsewhere (e.g. Chen & Cheng, 1982) so earlier records of *C. armatus* in PNG (Filewood, 1973) may refer to this species.

Centrophorus granulosus (Bloch & Schneider, 1801)

Gulper Shark

Squalus granulosus Bloch & Schneider, 1801: 135. Holotype: ZMB, whereabouts unknown; no locality. Neotype: AMNH 78263, Canary Islands, Spain; neotype designation by White *et al*. (2013).

Local synonymy: White *et al.*, 2018: 44, figs (PNG).

PNG voucher material: (1 spec.) ASIZ P0080731, juvenile male 562 mm TL, off Madang, 5°01.11' S, 145°51.45' E, 640–675 m depth, 2 Oct. 2010.

Remarks: A large pregnant female (1600 mm TL, 30 kg) was recently caught off Lae and images of the specimen were verified by the author. A circumglobally distributed species.

Centrophorus longipinnis White, Ebert & Naylor, 2017

Longfin Gulper Shark

Centrophorus longipinnis White, Ebert & Naylor, 2017: 86, figs 11–15. Holotype: NMMB-P 15756. Type locality: Chenggong, Taiwan.

Local synonymy: White *et al.*, 2018: 46, figs (PNG).

PNG voucher material: CSIRO H 8103-01 (paratype), pregnant female 890 mm TL, Huon Gulf, off Lae, 6°45.147' S, 147°2.783' E, 460 m depth, 4 May 2017; CSIRO H 8103-02 (paratype), late-term embryo 350 mm TL, taken from CSIRO H 8103-01.

Remarks: Two specimens recently caught in the Huon Gulf off Lae which became types in the recent species description. Also known from Taiwan and Indonesia.

Centrophorus moluccensis Bleeker, 1860

Smallfin Gulper Shark

Centrophorus moluccensis Bleeker, 1860: 3. Holotype: RMNH 7415. Type locality: Ambon, Indonesia.

Local synonymy: White *et al.*, 2018: 48, figs (PNG). Although listed in Kailola (1987), no verification of the species can be made to determine as to whether it refers to this species or one of the other three species in this genus.

PNG voucher material: (4 spec.) CSIRO H 8001-01, female 870 mm TL, north of Kavieng town, New Ireland, 2°30.63' S, 150°47.62' E, 409 m depth, 29 Sep. 2015; CSIRO H 8002-02, female 980 mm TL, north of Kavieng town, New Ireland, 2°31.42' S, 150°38.78' E, 680 m depth, 29 Sep. 2015; KFRS E628, female 960 mm TL, north of Kavieng town, New Ireland, 2°31.42' S, 150°38.78' E, 680 m depth, 29 Sep. 2015; NTUM 11496, juvenile male 333 mm TL, northwest of Kavieng, New Ireland, 2°23' S, 150°35' E, 534–650 m depth, 31 Aug. 2014.

Remarks: The most common species caught in deeper water off New Ireland during a short survey of sharks and rays below 400 m depth in September 2015.

Genus *Deania* Jordon & Snyder, 1902
Birdbeak Dogfishes

Deania Jordan & Snyder, 1902: 80. Type species: *Deania eglantina* Jordan & Snyder, 1902, by monotypy, a junior synonym of *Acanthidium calceum* Lowe, 1839.

Deania quadrispinosa (McCulloch, 1915)
Longsnout Dogfish

Acanthidium quadrispinosum McCulloch, 1915: 100, pl. 14 (figs 5–8). Holotype: AMS E.5452 [or E.5453] missing. Type locality: between Gabo Island and Cape Everard in Victoria, Australia.

Local synonymy: White *et al.*, 2018: 50, figs (PNG).

PNG voucher material: (1 spec.) NTUM 10310, female 310 mm TL, Hanisch Harbour, Huon Gulf, 6°45' S, 147°38' E, 480–680 m depth, 10 Dec. 2012.

Remarks: The status of the various nominal species of *Deania* is currently under investigation by Sho Tanaka (pers. comm.).

Family Etmopteridae Fowler, 1934
Lanternsharks

Genus *Etmopterus* Rafinesque, 1810a
Lanternsharks

Etmopterus Rafinesque, 1810a: 14. Type species: *Etmopterus aculeatus* Rafinesque, 1810a, by monotypy.

Etmopterus evansi Last, Burgess & Séret, 2002
Blackmouth Lanternshark

Etmopterus evansi Last, Burgess & Séret 2002: 214, Figs 2c, 4c, 6c, 8c. Holotype: CSIRO H 3141-16. Type locality: off Rowley Shoals, Western Australia.

Local synonymy: *Etmopterus evansi*—White *et al.*, 2017c: 339, Figs 11b, 12 (Madang and Manus Provinces); White *et al.*, 2018: 52, figs (PNG).

PNG voucher material: (4 spec.) ASIZ P. P0080732, adult male 343 mm TL, west of Manus Island, 679–685 m depth, 29 Sep. 2010; ASIZ P. P0080733, female 177 mm TL, Astrolabe Bay, Madang, 608–610 m depth, 5 Oct. 2010; NTUM 10312, juvenile male 172 mm TL, Astrolabe Bay, Madang, 520–575m depth, 14 Dec. 2012; NTUM 10317, male 299 mm TL, east of Cape Croisiles, Madang, 680–689 m depth, 16 Dec. 2012;.

Remarks: First recorded from PNG by White *et al.* (2017c) based on four specimens collected from deepwater. Previously known from northwestern Australia and eastern Indonesia at depths of 430–555 m, thus represent the deepest records for this species (to 689 m depth).

Etmopterus fusus Last, Burgess & Séret, 2002
Pygmy Lanternshark

Etmopterus fusus Last, Burgess & Séret 2002: 217, Figs 1b, 3b, 5b, 7b. Holotype: CSIRO H 3149-06. Type locality: off Dampier Archipelago, Western Australia.

Local synonymy: *Etmopterus fusus*—White *et al.* (2017c): 339, Figs 11c, 13 (PNG); White *et al.*, 2018: 54, figs (PNG).

PNG voucher material: (1 spec.) NTUM 10318, female 256 mm TL, north of Taviltae, Madang, 500–510 m depth, 17 Dec. 2012.

Remarks: First recorded from PNG by White *et al.* (2017c) based on a specimen collected from deepwater. Previously known from only 7 specimens from northwestern Australia in depths of 430–550 m; possibly also off Java in Indonesia at depths of 120–200 m.

Etmopterus samadiae White, Ebert, Mana & Corrigan, 2017c
Papuan Lanternshark

Etmopterus samadiae White, Ebert, Mana & Corrigan, 2017c: 340, figs 1–6, 7d, 8. Holotype: NTUM 10078. Type locality: Madang, Papua New Guinea.

Local synonymy: *Etmopterus* sp.—Fricke *et al.*, 2014: 14 (Madang Province). *Etmopterus samadiae*—White *et al.* (2017c): 340, figs 1–6, 7d, 8 (northern PNG); White *et al.*, 2018: 56, figs (PNG).

PNG voucher material: (17 spec.) ASIZ P.73777 (paratype), adult male 230 mm TL, ASIZ P.73778 (paratype), female 188 mm TL, ASIZ P.73765 (paratype), pregnant female 277 mm TL, off Lae, Huon Gulf, Morobe Province, 06°51.841' S, 147°04.672' E, 395–406 m depth, 22 Aug. 2010; ASIZ P0080739 (6 specimens), 235–275 mm TL, off Madang, 5°00.43' S, 145°49.74' E, 460–466 m depth, 2 Oct. 2010; ASIZ P0080734, female 224 mm TL, off Madang, 5°01.27' S, 145°49.74' E, 502–529 m depth, 2 Oct. 2010; NTUM 10078 (holotype), adult male 265 mm TL, east of Malmal Passage, Madang, 05°07' S, 145°50' E, 527–539 m depth, 30 Nov. 2012; NTUM 10313 (paratype), female 269 mm TL, northern Cape King William, Morobe Province, 06°00' S, 147°38' E, 785 m depth, 10 Dec. 2012; NTUM 10314 (paratype), female 258 mm TL, Astrolabe Bay, Madang, 05°22' S, 145°48' E, 420–490 m depth, 14 Dec 2012; NTUM 10315 (paratype), female 154 mm TL, Astrolabe Bay, Madang, 05°22' S, 145°48' E, 340–385 m depth, 14 Dec. 2012; NTUM 10316 (3 specimens; paratypes), female 177 mm TL, subadult male 201 mm TL, female 228 mm TL, west of Kairiru Island, East Sepik, 03°19' S, 143°27' E, 422–425 m depth, 19 Dec. 2012.

Remarks: First recorded in PNG by Fricke *et al.* (2014) as *Etmopterus* sp.; recently described as a new species by White *et al.* (2017c), endemic to PNG. Most similar to *Etmopterus brachyurus* (Smith & Radcliffe *in* Smith, 1912) from the Northwest Pacific. Endemic to PNG.

Family Dalatiidae Gray, 1851
Kitefin Sharks

Genus *Isistius* Gill, 1865
Cookiecutter Sharks

Isistius Gill 1865: 264. Type species: *Scymnus brasiliensis* Quoy & Gaimard, 1824, type by monotypy.

Isistius brasiliensis (Quoy & Gaimard, 1824)
Cookiecutter Shark

Scymnus brasiliensis Cuvier, in Quoy & Gaimard, 1824: 198. Holotype: MNHN A-7787, 140 mm TL female, off Brazil.

Local synonymy: *Isistius brasiliensis*—Duncker & Mohr, 1926: 84 (northern PNG); Parin, 1966: 163, fig. 2 (northern PNG); Parin *et al.*, 1977 (northern PNG); Kailola, 1987: 22 (northern PNG); White *et al.*, 2018: 58, figs (PNG).

PNG voucher material: (2 spec.) UF 79884, adult male ~385 mm TL, north of Ninigo Islands, 0°2’ S, 144°55’ E, 20 m depth, 10 Nov. 1969; ZMH 10215, female 208 mm TL, north of Manus Island, 0°0’ N, 146°5’ E, 24 Jul. 1908.

Remarks: First recorded by Duncker & Mohr (1926) from northern PNG, based on ZMH 10215. Not recorded during recent surveys but images taken by fishery observers of bite marks on scombrids and billfish landed on longline vessels are from this species. Further specimens required to determine whether the rarer *Isistius plutodus* Garrcik & Springer, 1964 also occurs in PNG waters.

Order Orectolobiformes

Family Orectolobidae Gill, 1896

Wobbegongs

Genus *Eucrossorhinus* Regan, 1908

Tasselled Wobbegongs

Eucrossorhinus Regan, 1908: 357. Type species: *Crossorhinus dasypogon* Bleeker, 1867, by monotypy.

Eucrossorhinus dasypogon (Bleeker 1867)

Tasselled Wobbegongs

Crossorhinus dasypogon Bleeker, 1867: 400, pl. 21 (fig. 1). Syntypes: ?BMNH 1867.11.28.209, RMNH 7411, RMNH 5118. Type locality: Waigio and Aru Islands, Indonesia.

Local synonymy: *Orectolobus dasypogon*—Ogilby & McCulloch (1908): 272 (Samarai Island); Fowler, 1934: 385 (Samarai Island); Filewood, 1973: 9 (PNG). *Orectolobus ogilbyi*—Regan, 1909: 529 (Samarai Island); Fowler, 1941: 97 (New Guinea). *Eucrossorhinus dasypogon*—Whitley, 1940: 83 (Samarai and Kwato islands); Munro, 1967: 5, pl. 1, fig. 2 (New Guinea); Compagno, 1984: 180 (PNG); Compagno, 2001: 151 (PNG); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93, fig. (Bootless Bay); Last & Stevens, 2009: 135 (PNG); Drew *et al.*, 2012: 5 (Bootless Bay); White *et al.*, 2018: 60, figs (PNG).

PNG voucher material: (4 spec.) AMS I.5405 (syntype of *Orectolobus ogilbyi*), adult male 1160 mm TL, Samarai Island, Milne Bay Province, 10°37' S, 150°40' E, 1902; AMS IB.4783 [section of jaw registered as AMS I.40874-001; selection of teeth as AMS I.41134-001], adult male 1144 mm TL, Morobe Province, 6°25' S, 147°12' E, 1960; KFRS E.037B (dried jaws only), female ~1440 mm TL, Basilisk Passage, Central Province, ~9°32'09" S, 147°07'51" E, Aug. 1964; PMH 308-1 (dried jaws only), public fish camp at Kairuku, 5 m depth, 26 Nov. 1996.

Remarks: First recorded from off Samarai Island based on specimen AMS I.5405 which was included in Ogilby & McCulloch's (1908) revision of the Orectolobidae as *Orectolobus dasypogon*. Regan (1909) considered this specimen and Torres Strait material as a distinct species *Orectolobus ogilbyi*. Seen by divers at various locations throughout PNG.

Genus *Orectolobus* Bonaparte, 1834

Wobbegongs

Orectolobus Bonaparte, 1834: 39 (as subgenus of *Scyllium*). Type species: *Squalus barbatus* Gmelin, 1789, by subsequent designation.

Orectolobus ornatus (De Vis, 1883)

Ornate Wobbegong

Crossorhinus ornatus De Vis, 1883: 289. Holotype: QM I.164 (dry mount). Type locality: Moreton Bay, Queensland.

Local synonymy: *Crossorhinus barbatus*—Macleay, 1883a: 597 (Port Moresby); Ogilby, 1890: 181 (Port Moresby). *Orectolobus ornatus*—Fowler, 1934: 385 (Port Moresby); Munro, 1958: 111 (Port Moresby); Filewood, 1973: 9 (PNG); Compagno, 1984: 180 (PNG); Compagno, 2001: 158 (PNG); White *et al.*, 2018: 62, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.037A (dried jaws only), Basilisk Passage, Central Province, ~9°32’09” S, 147°07’51” E, Aug. 1964.

Remarks: First recorded from off Port Moresby by Macleay (1883a). A photograph of a specimen from L.W. Filewood’s collection is most likely the individual that the KFRS jaw was taken from; KFRS E.037A was a speared specimen and the photograph clearly shows a spear wound on the dorsal head. Whole specimens and associated genetic samples needed to confirm this species record. A destroyed specimen (KFRS E.320, adult male 649 mm TL, east of Negro Head, Milne Bay) was also identified as *O. ornatus*.

Orectolobus wardi **Whitley, 1939a**

Northern Wobbegong

Orectolobus wardi Whitley, 1939a: 264. Holotype: AMS IA.7784. Type locality: Cape Keith, Melville Island, North Territory, Australia.

Local synonymy: *Orectolobus ogilbyi*—Filewood, 1973: 9 (PNG). *Orectolobus wardi*—Kailola, 1987: 6 (Bristow Island reef, Western Province); Last & Stevens, 2009: 144 (southeastern PNG); White *et al.*, 2018: 64, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973) as *Orectolobus ogilbyi*; information provided in Filewood’s key (i.e. nasal tentacle simple, skin flaps very few and simple) confirm as this species. Subsequently recorded by Kailola (1987) from Bristow Island reef in Western Province (based on KFRS E.455, adult female, 28 Mar. 1973, which has been destroyed); possibly restricted to the very eastern portion of PNG in the Western Province. Specimens and associated genetic samples required to confirm it is conspecific with the northern Australian and Aru Island material.

Orectolobus **sp. 1 (cf.** ***leptolineatus*****)**

Papuan Wobbegong

Local synonymy: *Orectolobus* sp.—Fricke *et al.*, 2014: 13 (Madang). *Orectolobus* sp. 1—White *et al.*, 2018: 66, figs (PNG).

PNG voucher material: (1 spec.) NTUM 10302, adult male ~800 mm TL, Madang Bay, Madang, Dec. 2012.

Remarks: First recorded from Madang by Fricke *et al.* (2014). Morphologically appears most similar to *Orectolobus leptolineatus* Last, Pogonoski & White 2010; molecular data (NADH2 and CO1 sequences) place it closest to this species but with some divergence; more specimens needed to determine whether this is a distinct species.

Family Hemiscylliidae Gill, 1862

Bamboo Sharks

Genus ***Chiloscyllium*** Müller & Henle, 1837a

Bamboosharks

Chiloscyllium Müller & Henle, 1837a: 112. Type species: *Scyllium plagiosum* (Anonymous [Bennett], 1830, by subsequent monotypy.

Chiloscyllium plagiosum **(Anonymous [Bennett], 1830)**

Whitespotted Bamboo Shark

Scyllium plagiosum Anonymous [Bennett], 1830: 694. Holotype probably lost. Neotype: CAS 36046; neotype designation by Dingerkus & DeFino (1983). Type locality: Java Sea, Indonesia.

Local synonymy: *Chiloscyllium plaviosus*—Filewood, 1973: 8 (north side of PNG). *Chiloscyllium plagiosum*—Kailola, 1987: 7 (eastern Papua and New Guinea coast); Fricke *et al.*, 2014: 12 (Madang); White *et al.*, 2018: 68, figs (PNG).

PNG voucher material: none.

Remarks: Recorded by Filewood (1973) as *Chiloscyllium plaviosus* from north side of PNG and subsequently as *C. plagiosum* by Kailola (1987). A number of destroyed specimens identified as *C. plagiosum* were deposited in the KFRS collection were taken from the northern coastline (Gogol River area, Tamara Island, Ramu River area, and Darapap area). No specimens currently exist for this species in PNG but a photograph of a specimen from Filewood's collection confirms its presence in PNG.

Listed during recent fish surveys off Madang (Fricke *et al.*, 2014) based on an underwater image but it only shows part of the tail of an individual and the spotting pattern matches *H. strahani* rather than *C. plagiosum.*

Chiloscyllium punctatum Müller & Henle, 1838b

Brownbanded Bambooshark

Chiloscyllium punctatum Müller & Henle, 1838b: 18 [pl. 3]. Neotype: AMNH 38153; neotype designation by Dingerkus & De Fino, 1983. Type locality: Jakarta, Java, Indonesia.

Local synonymy: *Chiloscyllium punctatum*—Filewood, 1973: 8 (PNG); Kailola, 1987: 7 (Daru, Yule Island, Orokolo Bay, Gulf of Papua and New Guinea coast); Allen, 1998: 67 (Milne Bay); Compagno, 2001: 176 (PNG); Allen *et al.*, 2003: 112 (Milne Bay); Last & Stevens, 2009: 147 (New Guinea); Fricke *et al.*, 2014: 13 (Madang); White *et al.*, 2018: 70, figs (PNG).

PNG voucher material: (42 spec.) CSIRO H 7614-01, juvenile male 300 mm TL, south of Kerema, Gulf of Papua, 8°3'1.2" S, 145°45'7.2" E, 16–17 m depth, 20 Jun. 2014; CSIRO H 7803-01, juvenile male 200 mm TL, south of Kerema, Gulf of Papua, 8°4'22.2" S, 145°46'5.4" E, 18–20 m depth, 12 Jun. 2014; CSIRO H 7811-01, female 350 mm TL, south of Kerema, Gulf of Papua, 8°3'16.2" S, 145°44'57.6" E, 15–17 m depth, 22 Jun. 2014; CSIRO H 7827-01, juvenile male 420 mm TL, south of Deception Bay, Gulf of Papua, 8°2'34" S, 144°38'31" E, 22–25 m depth, 7 Dec. 2014; CSIRO H 7830-01, female 730 mm TL, south of Deception Bay, Gulf of Papua, 8°8'22" S, 144°28'47" E, 20–21 m depth, 9 Dec. 2014; CSIRO H 8009-01, juvenile male 380 mm TL, CSIRO H 8009-02, female 270 mm TL, Freshwater Bay, Gulf of Papua, 8°9'48.66" S, 145°57'58.2" E, 16–20 m depth, 25 Aug. 2015; CSIRO H 8010-01, juvenile male 300 mm TL, CSIRO H 8010-02, juvenile male 210 mm TL, west of Avirara, Gulf of Papua, 8°19'20.88" S, 146°11'55.98" E, 8–10 m depth, 26 Aug. 2015; CSIRO H 8011-01, female 710 mm TL, CSIRO H 8011-02, female 200 mm TL, west of Avirara, Gulf of Papua, 8°19'3.24" S, 146°11'50.1" E, 12 m depth, 27 Aug. 2015; CSIRO H 8012-01, juvenile male 270 mm TL, southwest of Avirara, Gulf of Papua, 8°20'38.46" S, 146°12'46.38" E, 12–14 m depth, 27 Aug. 2015; CSIRO H 8013-01, female 360 mm TL, Freshwater Bay, Gulf of Papua, 8°13'42.18" S, 146°5'15.18" E, 16–18 m depth, 29 Aug. 2015; CSIRO H 8014-01, female 180 mm TL, southwest of Lalapipi, Gulf of Papua, 8°15'19.5" S, 146°7'4.56" E, 14–16 m depth, 29 Aug. 2015; CSIRO H 8016-01, female 260 mm TL, CSIRO H 8016-02, juvenile male 230 mm TL, south Kerema, Gulf of Papua, 8°3'58.14" S, 145°46'38.64" E, 15–16 m depth, 30 Aug. 2015; CSIRO H 8026-01, female 290 mm TL, Freshwater Bay, Gulf of Papua, 8°8'23" S, 146°3'40" E, 8–15 m depth, 10 Apr. 2015; CSIRO H 8152-01 (dried jaw), female 810 mm TL, south of Deception Bay, Gulf of Papua, 8°9' S, 144°28' E, 19–23 m depth, 9 Dec. 2014; KFRS E.601, female 290 mm TL, Freshwater Bay, Gulf of Papua, 8°9'31.62" S, 146°1'38.04" E, 16 m depth, 24 Aug. 2015; KFRS E.604, juvenile male 260 mm TL, west of Avirara, Gulf of Papua, 8°17'54.3" S, 146°12'18.9" E, 9–10 m depth, 26 Aug. 2015; KFRS E.607, juvenile male 300 mm TL, Freshwater Bay, Gulf of Papua, 8°9'9.78" S, 145°59'2.22" E, 15–18 m depth, 30 Aug. 2015; KFRS E.609, female 310 mm TL, southeast of Kerema, Gulf of Papua, 8°4'4.14" S, 145°47'30.3" E, 17–18 m depth, 31 Aug. 2015; KFRS E.618, female 840 mm TL, south of Kerema, Gulf of Papua, 8°1'21" S, 145°43'35.4" E, 17–18 m depth, 22 Jun. 2014; KFRS E.621, female 810 mm TL, west of Avirara, Gulf of Papua, 8°19'38" S, 146°11'41" E, 16–17 m depth, 28 Aug. 2015; KFRS E.630, female 260 mm TL, Freshwater Bay, Gulf of Papua, 8°8'6.66" S, 145°59'23.58" E, 14–19 m depth, 24 Aug. 2015; KFRS E.633, female 280 mm TL, Freshwater Bay, Gulf of Papua, 8°9'48.66" S, 145°57'58.2" E, 16–20 m depth, 25 Aug. 2015; KFRS E.634, juvenile male 280 mm TL, west of Avirara, Gulf of Papua, 8°19'3.24" S, 146°11'50.1" E, 12 m depth, 27 Aug. 2015; KFRS E.639, juvenile male 320 mm TL, southwest of Avirara, Gulf of Papua, 8°20'38.46" S, 146°12’46.38” E, 12–14 m depth, 27 Aug. 2015; KFRS E.640, female 260 mm TL, KFRS E.641, juvenile male 300 mm TL, southwest of Lalapipi, Gulf of Papua, 8°14’39.24” S, 146°6’12.96” E, 17–19 m depth, 29 Aug. 2015; KFRS E.671, female 180 mm TL, Freshwater Bay, Gulf of Papua, 8°8’19.2” S, 145°57’4.2” E, 14–18 m depth, 14 Jun. 2014; KFRS E.712, juvenile male 280 mm TL, south of Kerema, Gulf of Papua, 8°2’40.2” S, 145°46’1.8” E, 15–16 m depth, 7 Jun. 2014; KFRS E.719, juvenile male 320 mm TL, KFRS E.720, juvenile male 390 mm TL, south of Kerema, Gulf of Papua, 8°3’16.2” S, 145°44’57.6” E, 15–17 m depth, 22 Jun. 2014; KFRS E.753, female 200 mm TL, south of Deception Bay, Gulf of Papua, 8°2’16” S, 144°38’26” E, 22–23 m depth, 15 Dec. 2014; KFRS E.760, female 420 mm TL, south of Deception Bay, Gulf of Papua, 8°1’21” S, 144°39’16” E, 21–24 m depth, 16 Dec. 2014; KFRS E.765, female 850 mm TL, Gulf of Papua, 8°10’48” S, 144°26’47” E, 24 m depth, 8 Dec. 2014; KFRS E.772 (4 spec.), 3 males, 1 female, 222–307 mm TL, no collection data; KFRS E.773, juvenile male 292 mm TL, Freshwater Bay, Gulf of Papua, Aug./Sep. 1976.

Remarks: First recorded from PNG by Filewood (1973), but listed as not common. Abundant in the prawn trawl grounds of the Gulf of Papua. Recently photographed during fish surveys off Madang (Fricke *et al.*, 2014) and in coastal fisheries catches off Wewak (trap fishery).

Hemiscyllium hallstromi Whitley, 1967

Papuan Epaulette Shark

Hemiscyllium hallstromi Whitley, 1967: 178. Holotype designated by Whitley, along with other types, were alive at Taronga Zoo aquarium but was subsequently impossible to determine which specimen was the holotype. Lectotype: AMS I.15717-001; lectotype designated by Dingerkus & DeFino (1983). Type locality: Port Moresby.

Local synonymy: *Chiloscyllium ocellatum*—Macleay, 1883a: 597 (New Guinea); Ogilby, 1888: 8 (Port Moresby); Ogilby, 1890: 181 (Port Moresby); Munro, 1958: 111 (Port Moresby); Filewood, 1973: 8 (PNG). *Hemiscyllium ocellatum*—Fowler, 1928: 17 (Port Moresby); Fowler, 1934: 386 (Port Moresby); Whitley, 1940: 73 (Port Moresby); Fowler, 1941: 81 (Port Moresby); Munro, 1967: 5, pl. 1, fig. 4 (New Guinea). *Chiloscyllium freycineti*—Tortonese, 1964: 20 (Port Moresby). *Hemiscyllium hallstromi* Whitley, 1967: 178 (Port Moresby)—Dingerkus & DeFino, 1983 (in part): 40, figs 28, 29 (Port Moresby); Compagno, 1984: 197 (PNG); Kailola, 1987: 8 (Port Moresby); Compagno, 2001: 180, fig. (southeastern PNG); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93, fig. (Bootless Bay); Allen & Erdmann, 2008: 107 (southeastern PNG); Allen & Dudgeon, 2010: 29 (southeastern PNG); Drew *et al.*, 2012: 5 (Bootless Bay); Ebert *et al.*, 2013: 256, pl. 34, fig. (PNG); Allen *et al.*, 2013: 134 (southeastern PNG); Allen *et al.*, 2016: 70, figs (southeastern PNG); White *et al.*, 2018: 72, figs (PNG).

PNG voucher material: (35 spec.) AMS IB.7939, juvenile male 175 mm TL, received in 1967 from Taronga Zoo Aquarium; AMS IB.7910 (egg case only), 68 mm long, laid in Taronga Zoo Aquarium, 23 May 1967; AMS I.13450, 721 mm TL, Port Moresby, Sep. 1914; AMS I. 15584–001 (paralectotype), male 756 mm TL, Port Moresby area, received in 1970 from Taronga Zoo Aquarium; AMS I. 15717–001 (lectotype), male 720 mm TL, Port Moresby area, received in 1970 from Taronga Zoo Aquarium; AMS I.17103–001, female 383 mm TL, Taukura Point, southeast of Port Moresby, 9°32’ S, 147°09’58” E, 1 m depth, 20 Jun. 1970; KFRS E.033A and KFRS E.033B (dried jaws only), Kanudi Bay, Port Moresby, 2 Dec. 1964; KFRS E.042A–C (3 dried jaws only), Yule Island, Jun. 1964; KFRS E.068 (4 spec.), juvenile male 262 mm TL, 3 females 323–326 mm TL, Taurama Beach, Port Moresby, 26 Jul. 1965; KFRS E.377 (2 spec.), females 364–395 mm TL, Kanudi, Port Moresby; KFRS E.386 (3 spec.), females 250–437 mm TL, Taurama Beach, Port Moresby, 24 Sep. 1969; KFRS E.396, female 336 mm TL, Taurama Beach, Port Moresby, 24 Sep. 1969; KFRS E.510, adult male 712 mm TL, Taurama Beach, Port Moresby; MCZ S-971, male 390 mm TL, Port Moresby, received June 1890; *MSNG 38000 (not verified in this study), juvenile male, Port Moresby, 1890; NMV A 18751 (3 spec.), 2 females 320mm TL, 1 male 452 mm TL, between Port Moresby and Kapa, Gulf of Papua, May 1881; NMV A 19097, adult male 720 mm TL, Hood Bay, 10°4’58” S, 147°46’58” E, ~1882; USNM 30567, female 342 mm TL, Port Moresby, 7 May 1882; USNM 40018, female 395 mm TL, USNM 40024, adult male 726 mm TL, Port Moresby, 7 Feb 1889; ZMB 12710 (3 spec.), 2 females 320–638 mm TL, adult male ~710 mm TL, New Guinea, [1880–1884]; ZMB 13322, male 834 mm TL, New Britain, [1880–1884].

Remarks: First reported from PNG in the late 1800’s with a number of specimens collected in the 1880’s. The locality of the New Britain record (ZMB 13322) is likely an error since no members of this group are known to occur on this island and the limited dispersal of this group makes it unlikely (Allen *et al.*, 2016). The other specimen from ZMB (ZMB 12710) has only New Guinea as the locality but the collector was Finsch who only collected from PNG and not West Papua, thus can be confidently assigned to PNG. Commonly seen by divers in Bootless Bay near Port Moresby. Endemic to PNG.

Hemiscyllium michaeli **Allen & Dudgeon, 2010**

Michael's Epaluette Shark

Hemiscyllium michaeli—Allen & Dudgeon, 2010: 19, figs 2–4. Holotype: USNM 218602. Type locality: Harvey Bay, Milne Bay Province.

Local synonymy: *Hemiscyllium freycineti*—Whitley, 1940: 75 (Samarai Island); Dingerkus & DeFino, 1983 (in part): 38, fig. 25 (Harvey Bay, Trobriand Island, Samarai, Milne Bay); Compagno, 1984 (in part): 196 (PNG); Compagno, 2001 (in part): 179, fig. (PNG). *Chiloscyllium freycineti*—Munro, 1958: 111 (Collingwood Bay); Compagno, 1984: 197 (PNG). *Hemiscyllium trispeculare*—Allen *et al.*, 2003: 112 (Milne Bay). *Hemiscyllium* species—Allen & Erdmann, 2008: 107 (Milne Bay Province); Allen *et al.*, 2013: 134, fig. 8 (eastern Papua New Guinea). *Hemiscyllium michaeli* Allen & Dudgeon, 2010: 19, figs 2–4 (Milne Bay Province)—Ebert *et al.*, 2013: 256, pl. 34, fig. (PNG); Allen *et al.*, 2016: 81, figs (Milne Bay Province); White *et al.*, 2018: 74, figs (PNG).

PNG voucher material: (8 spec.) AMS IA.5741 (paratype), 285 mm TL, AMS IA.5742 (paratype), 365 mm TL, vicinity of Samarai, 10°36.633' S, 150°39.690' E, Feb. 1933; AMS IB.5429, female 755 mm TL, Morobe, received 1962 from Taronga Park Zoo; CU 24992 (paratype), 695 mm TL, Milne Bay; QM I 12038, female 719 mm TL, Samarai Island, 10°37' S, 150°40' E, 22 Oct. 1953; USNM 218602 (holotype), female 610 mm TL, coral reef at Harvey Bay, Oro Province, 08°54.440' S, 148°30.306' E, less than 10 m depth, 6/7 Aug. 1975; USNM 221705 (paratype), 257 mm TL, Kuia Island, 08°35.350'S, 150°51.332'E, Trobriand Islands, 1 m depth, 11 Jun. 1970; WAM P. 32840-001 (paratype), female 544 mm TL, under wharf at Samarai Island, 10°36.633' S, 150°39.690' E, 6 m depth, 10 Apr. 2003.

Remarks: First recorded from PNG by Whitley (1940), based on specimens collected in 1933 from Samarai Island, as *Hemiscyllium freycineti*. Described as a distinct species in 2010, restricted to Milne Bay and Oro Provinces in southeastern PNG. Endemic to PNG. Two destroyed specimens from the KFRS collection (E.321, Tuma Island, Trobriands, 25 Jul. 1967, male 625 mm TL and female 664 mm TL) which were identified as *Hemiscyllium* sp. (*freycineti*) would most likely refer to this species.

Hemiscyllium strahani **Whitley, 1967**

Hooded Epaulette Shark

Hemiscyllium strahani Whitley, 1967: 176, fig. 1. Holotype: AMS IB.7938. Type locality: Incorrectly assumed to be from Port Moresby area by Dingerkus & DeFino, 1983.

Local synonymy: *Hemiscyllium strahani* Whitley, 1967: 176, fig. 1 (PNG)—Dingerkus & DeFino, 1983: 46, fig. 34 (Massas Island, Madang); Compagno, 1984: 198 (PNG); Kailola, 1987: 8 (Massas Island, Madang); Compagno, 2001: 182, fig. (eastern PNG); Allen & Erdmann, 2008: 107 (eastern PNG); Allen & Dudgeon, 2010: 29 (eastern PNG); Ebert *et al.*, 2013: 256, pl. 34 (eastern PNG); Allen *et al.*, 2013: 134 (eastern PNG); Fricke *et al.*, 2014: 13, fig. 2 (Madang); Allen *et al.*, 2016: 89, figs (Madang, Wewak); White *et al.*, 2018: 76, figs (PNG).

PNG voucher material: (5 spec.) AMS IB. 7938 (holotype), female 735 mm TL, New Guinea via Taronga Park Zoo Aquarium, received Oct. 1967; IRSNB 18574, adult male, Laing Island, Madang, 4°13.73' S, 144°56.57' E, Jan. to Jun. 1976; NTUM 10173, adult male 638 mm TL, south of Urembo Island, 5°15.9' S, 145°47.1' E, 18–27 m depth, 6 Dec. 2012; SMNS 4836, female 668 mm TL, New Guinea; USNM 221701, adult male 594 mm TL, southern tip of Massas Island, Madang, 5°10' S, 145°50' E, 6 Nov. 1978.

Remarks: First described based on a New Guinea specimen sent to Taronga Zoo by Whitley (1967). Dingerkus & De Fino (1983) incorrectly assumed the type locality was Port Moresby area but Allen *et al.* (2016) confirmed this species only occurs in northern New Guinea from Jayapura in West Papua to Madang in PNG.

Recent molecular data (ND2 data) suggest that the West Papua and PNG specimens may represent different species and some coloration differences are evident between specimens from these locations. One specimen, SMNS 4836, has only the location 'New Guinea' on the label, but given it was collected by a German collector (Schode) and deposited in a German collection, it is presumed this came from northern PNG when it German New Guinea.

Family Stegostomatidae Gill, 1862
Zebra Sharks

Genus *Stegostoma* Müller & Henle, 1837a
Zebra Sharks

Stegostoma Müller & Henle, 1837a: 112. Type species: *Squalus fasciatus* Bloch & Schneider, 1801, by original designation, equals *Squalus fasciatus* Hermann, 1783.

Stegostoma fasciatum (Hermann, 1783)
Zebra Shark

Squalus fasciatum Hermann, 1783: 302. Based on *Squalus varius* Seba, 1759. A senior homonym of *Squalus fasciatus* Bonnaterre, 1788 = *Poroderma africanum* (Gmelin, 1789). No types known.

Local synonymy: *Stegostoma fasciatum*—Filewood, 1973: 8 (PNG); Compagno, 2001: 186 (PNG); Baine & Harasti, 2007: 93 (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Last & Stevens, 2009: 153 (PNG); Drew *et al.*, 2012: 5 (Bootless Bay); White *et al.*, 2018: 80, figs (PNG). *Stegostoma varium*—Kailola, 1987: 9 (Sepik and Ramu River mouths; Orangerie Bay, Darapap, Hall Sound, Kerema).

PNG voucher material: (8 spec.) CSIRO H 7611-01, female 620 mm TL, south of Kerema, Gulf of Papua, 8°5'9" S, 145°40'22.2" E, 16–23 m depth, 15 Jun. 2014; CSIRO H 7613-01, female 390 mm TL, Freshwater Bay, Gulf of Papua, 8°8'15" S, 145°59'29.4" E, 14–15 m depth, 13 Jun. 2014; CSIRO H 8107-01 (dried jaw), juvenile male 690 mm TL, Freshwater Bay, Gulf of Papua, 8°6'52" S, 145°58'29" E, 13–17 m depth, 11 Sep. 2015; KFRS E.610, juvenile male 720 mm TL, south of Kerema, Gulf of Papua, 8°5'11.64" S, 145°47'59.58" E, 16–20 m depth, 14 Sep. 2015; KFRS E.665, juvenile male 790 mm TL, Freshwater Bay, Gulf of Papua, 8°5'56" S, 145°56'17" E, 23–25 m depth, 27 Nov. 2014; KFRS E.721, juvenile male 600 mm TL, south of Kerema, Gulf of Papua, 8°2'9.6" S, 145°42'29.4" E, 14–15 m depth, 17 Jun. 2014; ZMB 10175, juvenile male 313 mm TL, New Britain; ZMB 12709, juvenile male ~330 mm TL, New Britain, [1880–1884].

Remarks: First recorded from PNG by Filewood (1973) but specimens deposited in Berlin (ZMB) was collected by Otto Finsch and Eduard Hernsheim, German naturalists who operate in PNG in the 1870s and 1880s. Kottelat (2013) placed *Squalus fasciatus* into the synonymy of *Stegostoma tigrinum* (Forster, 1781), however consideration for protecting nomenclatural stability should be taken into account.

Family Ginglymostomatidae Gill, 1862
Nurse Sharks

Genus *Nebrius* Rüppell, 1837
Nurse Sharks

Nebrius Rüppell, 1837: 62. Type species: *Nebrius concolor* Rüppell, 1837, by monotypy.

Nebrius ferrugineus **(Lesson, 1831)**
Tawny Shark

Scyllium ferrugineum Lesson, 1831: 95. Syntypes whereabouts unknown. Type locality: Port Praslin [=Lambom], New Ireland; Offack Bay, Waigeo, Indonesia.

Local synonymy: *Scyllium ferrugineum* Lesson, 1831: 95 (Port Praslin, New Ireland). *Ginglymostoma concolor*—Macleay, 1883a: 597 (New Guinea). *Ginglymostoma mulleri*—Günther, 1910: 487 (Port Praslin, New Ireland). *Ginglymostoma ferrugineum*—Fowler, 1934: 385 (Port Moresby); Munro, 1967: 5, pl. 1, fig. 3 (New Guinea). *Nebrius ferrugineum*—Munro, 1958: 111 (Milne Bay; Otua Island, Bougainville; Tami Island, Morobe Province); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago). *Nebrius ferrugineus*—Filewood, 1973: 9 (Papua New Guinea); Compagno, 1984: 208 (PNG); Compagno, 2001: 196 (PNG); Allen *et al.*, 2003: 112 (Milne Bay); Last & Stevens, 2009: 151 (PNG); White *et al.*, 2018: 78, figs (PNG).

PNG voucher material: (5 spec.) CSIRO C 1125, juvenile male 478 mm TL, CSIRO C 1126, juvenile male 440 mm TL, Cannac Island, Laughlan Island Group, Milne Bay, 9°18' S, 153°35' E, 15 Feb. 1950; KFRS E.001 (dried jaws), 2515 mm TL, Mission Point, Yule Island, 13 Nov. 1963; USNM 221733, female 670 mm TL, Kuia Island, Trobriand Islands, Milne Bay Province, Jun. 1970; NMV A 18927, juvenile male 690 mm TL, between Port Moresby and Kapa Kapa, Central Province, May 1881.

Remarks: First recorded in PNG by Lesson (1831) off Port Praslin [=Lambom] in New Ireland; this record and one from off Waigeo were used for the original description of this species. No specimens caught during recent surveys but images of a large specimen from the Gulf of Papua was taken by fisheries observers; also an underwater photograph from Kavieng, New Ireland by Dean Tully.

Family Rhincodontidae Müller & Henle, 1839
Whale Shark

Genus *Rhincodon* Smith, 1829
Whale Shark

Rhincodon Smith, 1829: 443. Type species: *Rhiniodon typus* Smith, 1828, by monotypy, as interpreted by the ICZN, 1984 (Opinion 1278).

Rhincodon typus **(Smith, 1828)**
Whale Shark

Rhiniodon typus Smith, 1828: 2. Holotype: MNHN 9855 (stuffed and mounted). Type locality: Table Bay, South Africa.

Local synonymy: *Selache maxima*—Thomas, 1887: 380 (Redscar Bay). *Rhincodon typus*—Munro, 1958: 112 (Redscar Bay); Munro, 1967: 6, pl. 1, fig. 6 (New Guinea). *Rhincodon typus*—Filewood, 1973: 3 (PNG); Compagno, 2001: 202 (PNG); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); White *et al.*, 2018: 82, figs (PNG). *Rhiniodon typus*—Compagno, 1984: 210 (PNG).

PNG voucher material: None.

Remarks: First recorded by Thomas (1887), as *Selache maxime*, based on observations of a number of individuals moving close to the vessel he was onboard; colour pattern description and size clearly relate to this species. Observer by divers at various locations around PNG; caught (and released) by purse seiners operating in northern pelagic PNG waters.

Order Lamniformes

Family Pseudocarchariidae Compagno, 1973
Crocodile Sharks

Genus *Pseudocarcharias* Cadenat, 1963
Crocodile Sharks

Pseudocarcharias Cadenat, 1963: 526 (proposed as a subgenus of *Carcharias* Rafinesque, 1810a, but used throughout in generic form). Type species: *Pseudocarcharias pelagicus* Cadenat, 1963, by original designation, a junior synonym of *Carcharias kamoharai* Matsubara, 1936a.

Pseudocarcharias kamoharai (Matsubara, 1936)
Crocodile shark

Pseudocarcharias kamoharai Matsubara, 1936: 380. Holotype: FAKU 1823; apparently lost according to Compagno (2001). Type locality: Koti, Japan.

Local synonymy: White *et al.*, 2018: 94, figs (PNG).

PNG voucher material: None.

Remarks: Recorded by fisheries observers' on-board tuna longline and purse seine vessels.

Family Alopiidae Bonaparte, 1838
Thresher Sharks

Genus *Alopias* Rafinesque, 1810a
Thresher Sharks

Alopias Rafinesque, 1810a: 13. Type species: *Alopias macrourus* Rafinesque, 1810a, by monotypy, a junior synonym of *Squalus vulpinus* Bonnaterre, 1788: 9.

Alopias pelagicus Nakamura, 1935
Pelagic Thresher

Alopias pelagicus Nakamura, 1935: 2, 3, pl. 1, fig. 2. Syntypes: whereabouts unknown. Type locality: Su-Ao fish market, Taiwan.

Local synonymy: White *et al.*, 2018: 84, figs (PNG).

PNG voucher material: None.

Remarks: Caught as bycatch in the pelagic longline fisheries in PNG; verified by photographs, with accompanying muscle and vertebral samples, from fisheries observers. Records of *Alopias vulpinus* (Bonnaterre, 1788) from PNG waters are most likely misidentifications of this species.

Alopias superciliosus Lowe, 1841
Bigeye Thresher

Alopecias superciliosus Lowe, 1841: 39. Also Lowe, 1849: 18 (sometimes dated 1839). Holotype: whereabouts unknown. Type locality: Madeira, Eastern Atlantic.

Local synonymy: White *et al.*, 2018: 86, figs (PNG).

PNG voucher material: None.

Remarks: Caught as bycatch in the pelagic longline fisheries in PNG; verified by photographs, with accompanying muscle and vertebral samples, from fisheries observers.

Family Lamnidae Müller & Henle, 1838a
Mackerel Sharks

Genus *Isurus* Rafinesque, 1810a
Mako Sharks

Isurus Rafinesque, 1810a: 12, pl. 13, fig. 1. Type species: *Isurus oxyrinchus* Rafinesque, 1810a, by monotypy.

Isurus oxyrinchus Rafinesque, 1810a
Shortfin Mako

Isurus oxyrinchus Rafinesque, 1810a: 12, pl. 13, fig. 1. Also Rafinesque, 1810b: 45. Holotype unknown. Type locality: Sicily, Mediterranean Sea.

Local synonymy: *Isurus oxyrinchus*—Kailola, 1987: 3 (Kavieng); White *et al.*, 2018: 88, figs (PNG).

PNG voucher material: None.

Remarks: Caught as bycatch in the pelagic longline fisheries in PNG; verified by photographs, with accompanying muscle and vertebral samples, from fisheries observers. A dried jaw previously identified as *I. oxyrinchus* (AKPM 4) was re-identified as *Carcharhinus falciformis*.

Isurus paucus Guitart, 1966
Longfin Mako Shark

Isurus paucus Guitart, 1966: 3, figs. 1, 2A, 3A, 3C. Syntypes: possibly in the Instituto de Biologia or Instituto de Oceanologia, Cuba; no type known according to Compagno (2001). Type locality: Collected in the Caribbean near Cuba.

Local synonymy: White *et al.*, 2018: 90, figs (PNG).

PNG voucher material: None.

Remarks: Caught as bycatch in the pelagic longline fisheries in PNG; verified by photographs from fisheries observers.

Family Odontaspididae Müller & Henle, 1839
Sandtiger Sharks

Genus *Carcharias* Rafinesque, 1810a
Sandtiger Sharks

Carcharias Rafinesque, 1810a: 10. Type species: *Carcharias taurus* Rafinesque, 1810a, by monotypy.

Carcharias taurus Rafinesque, 1810a
Grey Nurse Shark

Carcharias taurus Rafinesque, 1810a: 10, pl. 14, fig. 1. Holotype unknown. Type locality: Sicily, Mediterranean Sea.

Local synonymy: White *et al.*, 2018: 92, figs (PNG).

PNG voucher material: None.

Remarks: Confirmed from PNG based on an underwater photograph taken by Bob Halstead in 60 m off Milne Bay (White *et al.*, 2018).

Order Carcharhiniformes

Family Scyliorhinidae Gill, 1862
Catsharks

Genus *Atelomycterus* Garman, 1913
Marbled Catsharks

Atelomycterus Garman, 1913: 100. Type species *Scyllium marmoratum* Anonymous [Bennett], 1830; type by monotypy.

Atelomycterus marmoratus (Anonymous [Bennett], 1830)
Coral Catshark

Scyllium marmoratum Anonymous [Bennett], 1830: 693. Holotype: BMNH 1953.5.10.5 (skin). Type locality: Sumatra, Indonesia.

Local synonymy: *Atelomyoterus marmoratus*—Filewood, 1973: 7 (probably in PNG); *Atelomycterus marmoratus*—Compagno, 1984: 294 (northern PNG); Kailola, 1987: 12 (Western Papua; PNG north coast); White *et al.*, 2018: 96, figs (PNG).

PNG voucher material: None.

Remarks: No specimens available for this species in PNG. Specimens required to confirm that they are conspecific with *A. marmoratus*; appears to be restricted to the northern coastline.

Atelomycterus marnkalha Jacobsen & Bennett, 2007
Eastern Banded Catshark

Atelomycterus marnkalha Jacobsen & Bennett, 2007: 24, Figs 1–7. Holotype: CSIRO H 6144-01. Type locality: Torres Strait, Queensland, Australia.

Local synonymy: *Atelomycterus marnkalha* Jacobsen & Bennett, 2007: 19 (southern reaches of PNG)—Last & Stevens, 2009: 206 (PNG); Ebert *et al.*, 2013: 312 (southern PNG); White *et al.*, 2018: 98, figs (PNG).

PNG voucher material: None.

Remarks: Restricted to Northern Territory and Queensland in Australia, but also recorded from the southern reaches of PNG in the Torres Strait by Jacobsen & Bennett (2007).

Genus *Cephaloscyllium* Gill, 1862
Swellsharks

Cephaloscyllium Gill, 1862: 408, 412. Type species: *Scyllium laticeps* Duméril, 1853 by original designation.

Cephaloscyllium stevensi Clark & Randall, 2011
Steven’s Swellshark

Cephaloscyllium stevensi Clark & Randall, 2011: 25, Figs 2–7. Holotype: USNM 359091. Type locality: east coast of PNG.

Local synonymy: *Cephaloscyllium stevensi* Clark & Randall, 2011: 25, Figs 2–7; Ebert *et al.*, 2013: 330, pl. 44 (Milne Bay and New Ireland); White *et al.*, 2018: 100, figs (PNG).

PNG voucher material: (7 spec.) CSIRO H 6820-01, female 445 mm TL, New Ireland, 2°41' S, 150°31' E, 240–274 m depth, between October 1988 and April 1995; NTUM 10323, female 206 mm TL, north of Taviltae, Madang, 4°31' S, 145°31' E, 380–382 m depth, 17 Dec. 2012; NTUM 11495, female 603 mm TL, east of Lat, East New Britain, 4°35' S, 152°25' E, 575–616 m depth, 26 Apr. 2014; USNM 329583, adult male 524 mm TL, USNM 358812, adult male 543 mm TL, New Ireland, 2°41' S, 150°31' E, 240–274 m depth, between October 1988 and April 1995; USNM 358814 (head only), female 660 mm TL, Milne Bay, 10°15' S, 151°03' E, 17 Mar. 1993; USNM 359091, adult female 586 mm TL, Milne Bay, 10°15' S, 150°46.48' E, 244 m depth, 15 Dec. 1993.

Remarks: Very similar to *Cephaloscyllium signourum* Last, Séret & White, 2008 from Queensland, Australia but differ slightly in some morphological characters and also at a molecular level (NADH2 sequences, G. Naylor, unpubl. data). Endemic to PNG.

Family Pentanchidae Smith, 1912
Deepwater Catsharks

Genus *Apristurus* Garman, 1913
Ghost Catsharks

Apristurus Garman, 1913: 96. Type species: *Scylliorhinus indicus* Brauer, 1906, by original designation.

Apristurus macrostomus Zhu, Meng & Li *in* Meng *et al.*, 1985
Broadmouth Catshark

Apristurus macrostomus Zhu, Meng & Li *in* Meng *et al.*, 1985: 45 (English p. 49), Fig. 2. Holotype: SCSFRI D 00807. Type locality: off Zhujiang, South China Sea.

Local synonymy: White *et al.*, 2017e: 26, Figs 11A, 12A (Madang, Manus and Morobe Provinces); White *et al.*, 2018: 102, figs (PNG).

PNG voucher material: (7 spec.) ASIZ P. P0080735, adult male 422 mm TL, ASIZ P0080737, adult male 449 mm TL, Vitiaz Strait, Morobe, 05°57.190' S, 147°37.440' E, 860–880 m, 7 Oct. 2010; ASIZ P. P0080736, adult male 485 mm TL, Astrolabe Bay, Madang, 05°24' S, 145°50.550' E, 760–875 m, 6 Oct. 2010; NTUM 10319, adult male 377 mm TL, Broken Water Bay, Madang, 03°52' S, 144°41' E, 600–800 m, 18 Dec. 2012; NTUM 10320, female 257 mm TL, Wab Bay, Madang, 05°34' S, 146°23' E, 802–875 m, 8 Dec. 2012; NTUM 11489, adolescent male 400 mm TL, southeast of Manus Island, 03°31' S, 148°03' E, 780–855 m, 22 Apr. 2014; NTUM 11490, female 325 mm TL, southeast of Madang, 05°28' S, 146°09' E, 760 m, 8 May 2014.

Remarks: First recorded from PNG by White *et al.* (2017e) based on above material. Previously only known from the South China Sea. Identification confirmed with molecular data (see Fig. 8 in White *et al.*, 2017e).

Apristurus nakayai Iglésias, 2013
Milk-eye Catshark

Apristurus nakayai Iglésias, 2013: 516, Figs 2–5. Holotype: MNHN 2003-1983. Type locality: Coriolis Bank, New Caledonia.

Local synonymy: White *et al.*, 2017e: 26, Figs 11B, 12B, 13 (New Ireland); White *et al.*, 2018: 104, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11488, adult male 559 mm TL, south of Manne Island, New Ireland, 02°48' S, 150°42' E, 672–1150 m depth, 4 Sep. 2014.

Remarks: First recorded from PNG by White *et al.* (2017e); previously known only from New Caledonia. Represents only the second specimen known of this species. Identification confirmed with molecular data (see Fig. 8 in White *et al.*, 2017e). A second PNG adult male was also caught, but not retained, off Lae (stations CP 3639, 7°22.582' S, 147°31.797' E, 900–932 m depth, 23 Aug. 2010).

Apristurus yangi White, Mana & Naylor, 2017e
Yang's Longnose Catshark

Apristurus yangi White, Mana & Naylor, 2017e: 25, Figs 1–6. Holotype: ASIZ P0080718. Type locality: Vitiaz Strait, Morobe Province, PNG

Local synonymy: White *et al.*, 2017e: 25, Figs 1–6 (New Ireland and Vitiaz Strait); White *et al.*, 2018: 106, figs (PNG).

PNG voucher material: (2 spec.) ASIZ P0080718 (holotype), adult female 437 mm TL, Vitiaz Strait, Morobe Province, 06°02.030' S, 147°37.490' E, 700–701 m depth, 7 Oct. 2010; NTUM 11491, female 205 mm TL, northwest of Kavieng, New Ireland, 02°20' S, 150°38' E, 630–786 m depth, 29 Aug. 2014.

Remarks: First recorded from PNG by White *et al.* (2017e); belongs to the *longicephalus*-group of the genus *Apristurus*. Endemic to PNG.

Apristurus sp. 1
Papuan Shortsnout Catshark

Local synonymy: White *et al.*, 2017e: 37, Figs 11C, 12C (Astrolabe Bay); White *et al.*, 2018: 108, figs (PNG).

PNG voucher material: (1 spec.) ASIZ P0080719, juvenile male 250 mm TL, Astrolabe Bay, Madang, 05°22.530' S, 145°55.550' E, 851–865 m depth, 6 Oct 2010.

Remarks: First recorded from PNG by White *et al.* (2017e); belongs to the *brunneus*-group of the genus *Apristurus*; only known from a single juvenile specimen without supporting genetic samples making species identification very difficult. More specimens needed to determine the identity of this species.

Genus *Galeus* Rafinesque, 1810a
Sawtail Catsharks

Galeus Rafinesque, 1810a:13. Type species: *Galeus melastomus* Rafinesque, 1810a, by subsequent designation of Fowler (1908: 53).

Galeus corriganae White, Mana & Naylor, 2016a
Corrigan's Catshark

Galeus corriganae White, Mana & Naylor, 2016a: 256, Figs 1–4. Holotype: NTUM 10171. Type locality: Madang, PNG.

Local synonymy: *Galeus gracilis*—Fricke *et al.*, 2014: 12 (Madang Province). *Galeus corriganae* White *et al.*, 2016a: 256, Figs 1–4 (Madang and West New Britain, PNG); White *et al.*, 2018: 110, figs (PNG).

PNG voucher material: (7 spec.) ASIZ P0080738 (paratype), 2 specimens, female 278 mm TL and juvenile male 247 mm TL, off Madang, 05°01.270' S, 145°50.210' E, 502–529 m depth, 2 Oct. 2010; NTUM 10171 (holotype), adolescent male 306 mm TL, west of Sek Island, Madang, 05°04'S, 145°51' E, 582–587 m depth, 28 Nov. 2012; NTUM 10321 (paratype), adolescent male 282 mm TL, north of Taviltae, Madang Province, 04°30' S, 145°34' E, 600–660 m depth, 17 Dec. 2012; NTUM 10322 (paratype), juvenile male 203 mm TL, north of Taviltae, Madang Province, 04°29' S, 145°31' E, 500–510 m depth, 17 Dec. 2012; NTUM 11492 (paratype), adolescent male 372 mm TL, southeast of Murien, West New Britain, 06°10' S, 149°18' E, 510–743 m depth, 7 May 2014; NTUM 11493 (paratype), juvenile male 271 mm TL, south of Murien, West New Britain, 06°08' S, 149°10' E, 430–620 m depth, 6 May 2014.

Remarks: First recorded from PNG by Fricke *et al.* (2014) as *Galeus gracilis* Compagno & Stevens, 1993 based on NTUM 10171; described as a new species by White *et al.* (2016a). Morphologically similar to *Galeus priapus* Séret & Last, 2008 from New Caledonia but differs in several characters and at a molecular level (see Fig. 4 in White *et al.*, 2016a). Endemic to PNG.

Genus *Parmaturus* Garman, 1906
Filetail Catsharks

Parmaturus Garman, 1906: 203. Type species: *Parmaturus pilosus* Garman, 1906. Type by subsequent designation. Type designated by Jordan, 1920: 518.

Parmaturus lanatus Séret & Last, 2007
Whitetip Catshark

Parmaturus lanatus Séret & Last, 2007: 35, Figs 8, 9. Holotype: MNHN 2007-1499. Type locality: Tanimbar Island, Indonesia.

Local synonymy: *Parmaturus lanatus*—Fricke *et al.*, 2014: 12 (Madang Province); White *et al.*, 2018: 112, figs (PNG).

PNG voucher material: (2 spec.) NTUM 10202, both female 209 mm TL, east of Sek Island, Madang, 05°06' S, 145°53' E, 980–985 m depth, 1 Dec. 2012.

Remarks: First recorded from PNG by Fricke *et al.* (2014). Previously only known from the holotype from eastern Indonesia. Additional specimens, including adults, required to confirm that the PNG specimen is conspecific with the Indonesian holotype.

Parmaturus sp. 1
Whitefin Catshark

Local synonymy: White *et al.*, 2018: 114, figs (PNG).

PNG voucher material: (1 spec.) ASIZ P0080722 (holotype), juvenile male 250 mm TL, west of Manus Island, 02°14.13' S, 147°25.05' E, 679–685 m depth, 2 Oct. 2010.

Remarks: Similar to *P. albimarginatus* from New Caledonia but differs in a number of key characters. Adult specimens required.

Family Triakidae Gray, 1851
Houndsharks

Genus *Gogolia* Compagno, 1973
Sailback Houndsharks

Gogolia Compagno, 1973: 383. Type species *Gogolia filewoodi* Compagno, 1973, by original designation.

Gogolia filewoodi Compagno, 1973
Sailback Houndshark

Gogolia filewoodi Compagno, 1973: 394, figs 1–7. Holotype: AMS I. 16858-001. Type locality: Astrolabe Bay, Papua New Guinea.

Local synonymy: *Gogolia filewoodi* Compagno, 1973: 383, Figs 1–7 (Astrolabe Bay)—Compagno, 1984: 389 (Astrolabe Bay); Kailola, 1987: 13 (Astrolabe Bay); Compagno & Niem, 1998b: 1302; Ebert *et al.*, 2013: 394, pl. 54 (PNG); Fricke *et al.*, 2014: 13 (Madang Province); White *et al.*, 2018: 116, figs (PNG).

PNG voucher material: (2 spec.) AMS I 16858-001 (holotype), pregnant female 722 mm TL, 1 mile north of Gogol River mouth, Astrolabe Bay, Madang Province, 5°18' S, 145°50' E, 73 m depth, 18 Jul. 1970; CAS 27588 (paratype), late-term embryo 224 mm TL; KFRS E.414 (paratype), late-term embryo, 224 mm TL, taken from holotype.

Remarks: First recorded from PNG by Compagno 1973 based on a pregnant female (and two late-term embryos) collected in 1970 by L.W. Filewood; no further specimens have been encountered since this date. The CAS paratype, one of the two late-term embryos, is listed as 'not found' by Eschmeyer *et al.* (2017). Endemic to PNG.

Genus *Hemitriakis* Herre, 1923
Houndsharks

Hemitriakis Herre, 1923: 70. Type species: *Hemitriakis leucoperiptera* Herre, 1923, by original designation.

Hemitriakis sp. 1
Papuan Houndshark

Local synonymy: White *et al.*, 2018: 118, figs (PNG).

PNG voucher material: None.

Remarks: First record for this genus in PNG waters; verified from photograph taken from a specimen caught and released off northern New Ireland in 2015. Possibly conspecific with an undescribed species from off Ghizo Island in the northern Solomon Islands. Although a genetic sample was retained from the two Solomon Islands specimens (Global Cestode Database www.tapewormdb.uconn.edu; G. Naylor, unpubl. data), no specimens were retained. Specimens required to confirm if the Solomon Islands and PNG individuals are conspecific and to describe the species.

Genus *Iago* Compagno & Springer, 1971
Bigeye Houndsharks

Iago Compagno & Springer, 1971: 616. Type species: *Eugaleus omanensis* Norman, 1939. Type by original designation.

Iago garricki Fourmanoir & Rivaton, 1979
Longnose Houndshark

Iago garricki Fourmanoir & Rivaton, 1979: 434, Fig. 2. Holotype: MNHN 1978-0694. Type locality: northwest of Efate, Vanuatu.

Local synonymy: White *et al.*, 2018: 120, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11494, juvenile female 223 mm TL, northwest of Kavieng, New Ireland, 2°28'S, 150°44' E, 333–420 m depth, 24 Apr. 2014.

Remarks: First record of this genus and species from PNG. Previously known from Vanuatu, northern Australia, Indonesia and the Philippines.

Family Hemigaleidae Hasse, 1879
Weasel Sharks

Genus *Hemigaleus* Bleeker, 1852
Weasel Sharks

Hemigaleus Bleeker, 1852: 45. Type species: *Hemigaleus macrostoma* Bleeker, 1852, by subsequent designation.

Hemigaleus australiensis White, Last & Compagno, 2005
Sicklefin Weasel Shark

Hemigaleus australiensis White, Last & Compagno, 2005: 40, Fig. 1. Holotype: CSIRO H 5949-01. Type locality: northwest of Geraldton, Western Australia.

Local synonymy: *Negogaleus microstoma* - Filewood, 1973: 3 (PNG). *Hemigaleus microstoma*—Kailola, 1987: 20 (western Papua; Gulf of Papua; Orangerie Bay; New Britain?); White *et al.*, 2018: 122, figs (PNG).

PNG voucher material: (26 spec.) CSIRO H 7810-03, female 310 mm TL, south of Kerema, Gulf of Papua, 8°2'55.8" S, 145°44'57" E, 14–16 m depth, 19 Jun. 2014; CSIRO H 7819-01, female 420 mm TL, south of Kerema, Gulf of Papua, 8°03' S, 145°46' E, 18–22 m depth, 30 Nov. 2014; CSIRO H 7832-01, female 480 mm TL, south of Deception Bay, Gulf of Papua, 8°8'20" S, 144°24'53" E, 17–20 m depth, 11 Dec. 2014; CSIRO H 7834-02, female 500 mm TL, south of Deception Bay, Gulf of Papua, 8°1'54" S, 144°39'13" E, 22–25 m depth, 15 Dec. 2014; CSIRO H 8003-01, female 380 mm TL, Freshwater Bay, Gulf of Papua, 8°9'15.54" S, 146°02'49.1" E, 12–14 m depth, 24 Aug. 2015; CSIRO H 8017-01, female 290 mm TL, Freshwater Bay, Gulf of Papua, 8°6'1.56" S, 145°50'16.02" E, 13–16 m depth, 30 Aug. 2015; CSIRO H 8019-01, female 310 mm TL, south of Kerema, Gulf of Papua, 8°2'49.5" S, 145°43'41.34" E, 17–19 m depth, 31 Aug. 2015; CSIRO H 8165-01 (dried jaws), female 500 mm TL, south of Deception Bay, Gulf of Papua, 8°2'8" S, 144°38'33" E, 22 m depth, 14 Dec. 2014; CSIRO H 8168-01 (dried jaws and chondrocranium), adult male 720 mm TL, south of Deception Bay, Gulf of Papua, 8°0' S, 144°27' E, 19–21 m depth, 9 Dec. 2014; CSIRO H 8158-01 (dried jaws), juvenile female 580 mm TL, south of Kerema, Gulf of Papua, 8°5'50" S, 145°39'11" E, 16–17 m depth, 22 Nov. 2014; CSIRO H 8162-01 (dried jaws), adult male 650 mm TL, south of Kerema, Gulf of Papua, 8°4'26" S, 145°40'55" E, 17–20 m depth, 7 Sep. 2015; KFRS E.041 (dried jaws), Kairuku, Central Province, late Oct. 1964; KFRS E.223A and E.223B (dried jaws), Gulf of Papua, Feb. 1966; KFRS E.304 (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.600, juvenile male 270 mm TL, Freshwater Bay, Gulf of Papua, 8°9'31.62" S, 146°1'38.04" E, 16 m depth, 24 Aug. 2015; KFRS E.626, female 360 mm TL, KFRS E.627, female 310 mm TL, Freshwater Bay, Gulf of Papua, 8°6'1.56" S, 145°50'16.02" E, 13–16 m depth, 30 Aug. 2015; KFRS E.631, female 470 mm TL, Freshwater Bay, Gulf of Papua, 8°8'6.66" S, 145°59'23.58" E, 14–19 m depth, 24 Aug. 2015; KFRS E.667, female 460 mm TL, Freshwater Bay, Gulf of Papua, 8°8' S, 146°1' E, 14–15 m depth, 29 Nov. 2014; KFRS E.672, male 560 mm TL, Freshwater Bay, Gulf of Papua, 8°8'19.2" S, 145°57'4.2" E, 14–18 m depth, 14 Jun. 2014; KFRS E.674, male 560 mm TL, south of Deception Bay, Gulf of Papua, 8°9'5" S, 144°26'53" E, 22–24 m depth, 9 Dec. 2014; KFRS E.743, adult male 740 mm TL, south of Deception Bay, Gulf of Papua, 8°8' S, 144°27' E, 17–18 m depth, 9 Dec. 2014; KFRS E.755, female 300 mm TL, south of Deception Bay, Gulf of Papua, 8°2'16" S, 144°38'26" E, 22–23 m depth, 15 Dec. 2014; KFRS E.756, female 290 mm TL, south of Deception Bay, Gulf of Papua, 8°4'23" S, 144°38'55" E, 22–31 m depth, 14 Dec. 2014; KFRS E.767, male 520 mm TL, south of Deception Bay, Gulf of Papua, 8°8'14" S, 144°29'13" E, 21–22 m depth, 14 Dec. 2014.

Remarks: Once considered to be conspecific with *Hemigaleus microstoma* Bleeker, 1852 which occurs in the Western Central Pacific. White *et al.* (2005) noted that its presence in PNG needs validating. Restricted to northern Australia and PNG; possibly restricted to the southern coast from Western Province through to Orangerie Bay.

Genus *Hemipristis* Agassiz, 1843
Snaggletooth Shark

Hemipristis Agassiz, 1843: 237, 302. Type species: *Hemipristis serra* Agassiz, 1843, by subsequent designation; based on a fossil type species.

Hemipristis elongata (Klunzinger, 1871)
Snaggletooth Shark

Dirrhizodon elongatus Klunzinger, 1871: 665. Holotype: SMNS 1640 (dry); probably lost. Type locality: Al-Qusair, Egypt, Red Sea.

Local synonymy: *Hemipristis elongatus*—Filewood, 1973: 3 (PNG); Kailola, 1987: 20 (Yule Island); *Hemipristis elongata*—White *et al.*, 2018: 124, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.005 (dried jaws), Hall Sound, Central Province, Oct. 1963.

Remarks: First recorded in PNG by Filewood (1973), presumably based on KFRS E.005. One specimen observed in a prawn trawl vessel freezer in Western Province and two dried fins confirmed as this species photographed from Milne Bay Province during recent surveys.

Family Carcharhinidae Jordan & Evermann, 1896
Requiem Sharks

Genus *Carcharhinus* Blainville, 1816
Whaler Sharks

Carcharhinus (subgenus of *Squalus*) Blainville, 1816: 121. Type species: *Carcharias melanopterus* Quoy & Gaimard, 1824, by subsequent designation of the International Commission on Zoological Nomenclature.

Carcharhinus albimarginatus (Rüppell, 1837)
Silvertip Shark

Carcharias albimarginatus Rüppell, 1837: 164, pl. 18 (fig. 1). Lectotype: SMF 3582 (dry and mounted); lectotype designation by Rosenblatt & Baldwin (1958). Type locality: Ras Muhammad, Sinai, Egypt, Red Sea.

Local synonymy: *Carcharhinus albolimbatus*—Filewood, 1973: 7 (PNG). *Carcharhinus albimarginatus*—Kailola, 1987: 15 (Basilisk Passage, Port Moresby; Orangerie Bay; Goodenough Island); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); White *et al.*, 2018: 126, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.048, Cape Saint George, New Ireland, May 1965.

Remarks: Observed by divers in a number of locations, although becoming scarcer. Caught by coastal fishers and was a common catch of the targeted shark longline fishery.

Carcharhinus altimus (Springer, 1950)
Bignose Shark

Eulamia altima Springer, 1950: 9. Holotype: USNM 133828. Type locality: Cosgrove Reef, Key West, Florida, USA.

Local synonymy: White *et al.*, 2018: 128, figs (PNG).

PNG voucher material: None.

Remarks: First confirmation of this species from PNG waters. One specimen caught by longline in 432 m off Kavieng in late 2015; multiple records from target shark longline catches in the Milne Bay Province in 2014, with supporting genetic samples; identification confirmed with NADH2 sequences (G. Naylor, unpubl. data).

Carcharhinus amblyrhynchoides (Whitley, 1934)
Graceful Shark

Gillisqualus amblyrhynchoides Whitley, 1934: 189, Fig. 4. Holotype: QM I.2003. Type locality: Cape Bowling Green, Queensland, Australia.

Local synonymy: ?*Carcharhinus "pleurotaenia"*—Filewood, 1973: 6 (PNG). *Carcharhinus amblyrhynchoides*—Kailola, 1987: 15 (Western Papua; Astrolabe Bay; Port Moresby; Binaturi River; Yule Island; New Britain); Eley, 1988: 15 (Tureture); White *et al.*, 2018: 130, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.180B (dried jaws), Tatana, Fairfax Harbour, Port Moresby, 7 Oct. 1965.

Remarks: Filewood (1973) referred to a *limbatus* group species as *C. "pleurotaenia"* Broad-nosed Spinner; close to *C. limbatus* but with a shorter and broader snout and less than 85 precaudal vertebrae. These characters and its similarity to *C. limbatus* make it most likely to be *C. amblyrhynchoides*; although this cannot be confirmed, a set of dried jaws (KFRS E.180B) collected in 1965 and part of Filewood's collection confirms he had recorded this species in PNG.

Carcharhinus amblyrhynchos (Bleeker, 1856)

Grey Reef Shark

Carcharias (*Prionodon*) *amblyrhynchos* Bleeker, 1856: 467. Holotype: RMNH 7377 (head and skin). Type locality: near Solombo Island, Java Sea, Indonesia.

Local synonymy: *Galeolamna tufiensis* Whitley, 1949a: 24 (off Tufi Harbour)—Whitley, 1949b: 345 (Papua); Whitley, 1951: 389, fig. 1 (Tufi, Port Moresby). *Carcharhinus tufiensis*—Munro, 1958: 112 (Port Moresby and Tufi); Munro, 1967: 10, pl. 1, fig. 10 (New Guinea). *Carcharhinus tjutjot*—Filewood, 1973: 5 (Papua New Guinea). *Carcharhinus amblyrhynchos*—Garrick, 1982: 106 (Papua; off Tufi Harbour; Port Moresby); Allen, 1998: 67 (Milne Bay); Compagno, 1984: 460 (PNG); Kailola, 1987: 14 (PNG); Gochfeld, 1996: 43 (southern New Ireland); Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Fricke *et al.*, 2014: 14 (Madang); White *et al.*, 2018: 132, figs (PNG).

PNG voucher material: (19 spec.) AMS IB.2334 (holotype of *Galeolamna tufiensis*; teeth only), 1473 mm TL, off Tufi Harbour, 9°05' S, 149°20'E, 1 Oct. 1948; CSIRO C 1677 (paratype of *Galeolamna tufiensis*; jaws), juvenile male 673 mm TL, CSIRO C 1918 (paratype of *Galeolamna tufiensis*; chondrocranium, teeth and shagreen), juvenile male 738 mm TL, off Tufi Harbour, 9°05' S, 149°20'E, 1 Oct. 1948; CSIRO C 41 (head only), off Tufi Harbour, 9°05' S, 149°20'E, 1 Oct. 1948; CSIRO H 7838-01, juvenile male 730 mm TL, Gulf of Papua, 2014; KFRS E.047D (dried jaws), male, Cape Saint George, New Ireland, May 1965; KFRS E.0263 (dried jaws), male 778 mm TL, New Britain, Sep. 1966; KFRS E.316 (dried jaws), Tuma Island, Trobriand Islands, 30 Jul. 1967; KFRS E.324 (dried jaws), Vakuta, Trobriand Islands, 6 Aug. 1967; KFRS E.325B (dried jaws), KFRS E.325C (dried jaws), Nukuana Reef, Milne Bay Province, ~8°31'15" S, 150°13'14" E, 21 Jul. 1967; KFRS E.363, embryo male 245 mm TL, Bougainville, 50 m depth, 2 Aug. 1969; KFRS E.365 (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.370A (dried jaws), KFRS E.370B (dried jaws), Numa Numa, Bougainville, Aug. 1969; KFRS E.464 (dried jaws), Hein Island, Umboi Island, Siassi Group, 5 May 1968; KFRS E.716, juvenile male 710 mm TL, Gulf of Papua, 2014; USNM 39991, juvenile male 610 mm TL, Port Moresby; ZMB D 2461 (dried upper jaw), Bismarck Archipelago, Nov./Dec. 1909.

Remarks: First recorded from PNG by Whitley (1949a) who described it as a new species, *Galeolamna tufiensis*; considered a junior synonym of *Carcharhinus amblyrhynchos* by Garrick (1982). Common throughout PNG and regularly caught in longline and coastal fisheries. Filewood (1973) listed the species *C. tjutjot* (=*"menisorrah*) Reef Whaler which is characterised by having a more pointed snout than *C. leucas*, precaudal vertebrae more than 100, sometimes a fine interdorsal ridge, lower teeth cusps moderately slender; these characters align with *C. amblyrhynchos* and, more importantly, 8 of the dried jaws identified as this species deposited KFRS from Filewood's collection had the identification of *Carcharhinus tjutjot* on the label. *Carcharhinus tjutjot* belongs to the *dussumieri*-*sealei* group and *C. menisorrah* is also a name previously attributed to this group; the only member of this group in PNG is *Carcharhinus coatesi* (see further detail below).

Carcharhinus amboinensis (Müller & Henle, 1839)

Pigeye Shark

Carcharias (*Prionodon*) *amboinensis* Müller & Henle, 1839: 40, pl. 19 (teeth). Holotype: RMNH D2582 (skin). Type locality: Ambon Island, Indonesia.

Local synonymy: *Carcharhinus amboinensis*—Filewood, 1973: 5 (PNG); Kailola, 1987: 16 (Binaturi River; Bougainville; Ramu River mouth; Yule Island; Bootless Bay; Port Moresby); Last & Stevens, 2009: 253 (PNG and Bougainville); White *et al.*, 2018: 134, figs (PNG).

PNG voucher material: (5 spec.) KFRS E.019, Ramu River mouth, 18 Jul. 1965; KFRS E.031, Kairuku, Yule Island, 20 Oct. 1964; KFRS E.179, male, near McDhui wreck, Port Moresby, 26 Apr. 1965; KFRS E.368, Numa

Numa, Bougainville, Aug. 1969; KFRS E.622, female 910 mm TL, Freshwater Bay, Gulf of Papua, 8°5'38" S, 145°50'37" E, 13–14 m depth, 30 Aug. 2015.

Remarks: First recorded by Filewood (1973) with dried jaws from his collection collected in the mid-1960s. Recorded in the coastal and trawl fisheries catches in southern PNG (Daru to Milne Bay).

Carcharhinus brevipinna (Müller & Henle, 1839)
Spinner Shark

Carcharias brevipinna Müller & Henle, 1839: 31, pl. 9. Holotype: RMNH D2525 (mounted skin). Type locality: Java, Indonesia.

Local synonymy: *Carcharhinus brevipenna*—Filewood, 1973: 6 (PNG). *Carcharhinus brevipinna*—Kailola, 1987: 16 (Papuan coast to as far east as Losuia); White *et al.*, 2018: 136, figs (PNG).

PNG voucher material: (4 spec.) CSIRO H 8106-01 (dried jaw), female 930 mm DW, south of Kerema, Gulf of Papua, 8°3'17" S, 145°43'53" E, 17 m depth, 2 Sep. 2015; KFRS E.159A (dried jaws), KFRS E.159B (dried jaws), Fairfax Harbour, Port Moresby, 27 Aug. 1965; KFRS E.625, female 870 mm TL, south of Purari River mouth, Gulf of Papua, 8°0'50" S, 145°2'17" E, 12 m depth, 6 Sep. 2015.

Remarks: First recorded from PNG by Filewood (1973) with two jaws in KFRS collected in mid-1960s. Regular catch of longline, trawl and coastal fisheries during recent surveys.

Carcharhinus cautus (Whitley, 1945)
Nervous Shark

Galeolamna greyi cauta Whitley, 1945: 2, Fig. 2. Holotype AMS IB.1622 (teeth and skin). Type locality: Shark Bay, Western Australia.

Local synonymy: *Carcharhinus melanopterus* (in part)—Filewood, 1973: 5 (PNG); *Carcharhinus cautus*—Kailola, 1987: 16 (Port Romilly; Sigabadu); Last & Stevens, 2009: 257 (PNG); White *et al.*, 2018: 138, figs (PNG).

PNG voucher material: (2 spec.) KFRS E.009A (dried jaws), Hall Sound, Central Province; KFRS E.011, Kairuku area, Yule Island, Aug. 1964.

Remarks: A set of dried jaws deposited in the KFRS collection confirmed as this species was originally identified as *Carcharhinus melanopterus*, suggesting that the two species were confused at this time. Not recorded during recent surveys.

Carcharhinus coatesi (Whitley, 1939b)
Australian Blackspot Shark

Platypodon coatesi Whitley, 1939b: 234, Fig. 7. Holotype: QM I.6226. Type locality: Hinchinbrook Passage, Queensland, Australia.

Local synonymy: *Carcharias menisorrah*—Ogilby, 1888: 2 (Port Moresby); Ogilby, 1889: 1768 (Port Moresby). *Eulamia menisorrah*—Fowler, 1928: 20 (Port Moresby); Fowler 1934: 385 (Port Moresby); Fowler, 1941: 161 (Port Moresby). *Carcharhinus dussumieri*—Munro, 1958: 112 (Ningin Island, New Ireland); Munro, 1967: 10, pl. 1, fig. 12? (New Guinea); Filewood, 1973: 7 (PNG?); Kailola, 1987: 14 (PNG). *Carcharhinus menisorrah*—Munro, 1958: 112 (southern New Guinea); Munro, 1967: 10, pl. 1, fig. 11 (New Guinea); Filewood, 1973: 7 (PNG). *Carcharhinus menisorrah* (=*coatesi*) Filewood, 1973: 7 (PNG). *Carcharhinus sealei*—Compagno, 1984: 498 (PNG); Kailola, 1987: 17 (PNG). *Carcharhinus coeatesi*—White *et al.*, 2018: 140, figs (PNG).

PNG voucher material: (23 spec.) CSIRO C 1039, 465 mm TL, between Normanby and Samarai Islands, Milne Bay Province; CSIRO H 7801-01, male 480 mm TL, Freshwater Bay, Gulf of Papua, 8°5'45" S, 145°52'36" E, 14–16 m depth, 8 Jun. 2014; CSIRO H 7810-01, female 430 mm TL, CSIRO H 7810-02, male 350 mm TL, south of Kerema, Gulf of Papua, 8°2’55.8” S, 145°44’57” E, 14–16 m depth, 19 Jun. 2014; CSIRO H 8163-01 (dried jaws), adult male 760 mm TL, Freshwater Bay, Gulf of Papua, 8°3’45” S, 145°46’49” E, 13–18 m depth, 9 Sep. 2015; CSIRO H 8170-01 (dried jaws), adult male 730 mm TL, Gulf of Papua, 2015; CSIRO H 8159-01 (dried jaws), adult male 740 mm TL, south of Kerema, Gulf of Papua, 8°3’40” S, 145°36’45” E, 18 m depth, 22 Nov. 2014; CSIRO H 8167-01 (dried jaws), adult male 770 mm TL, east of Fly River mouth, Gulf of Papua, 8°40’ S, 144°7’ E, 13–20 m depth, 2 Dec. 2014; KFRS E.008 (dried jaws), female, Hall Sound, Central Province, 13 Nov. 1963; KFRS E.010A (dried jaws), KFRS E.010B (dried jaws), north of Pinupaka Anchorage, Hall Sound, Central Province, 12 Jun. 1964; KFRS E.279C (dried jaws), north of Yule Island, Apr. 1966; KFRS E.311A (dried jaws), KFRS E.311B (dried jaws), KFRS E.311C (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.669, female 580 mm TL, east of Fly River mouth, Gulf of Papua, 8°42’0” S, 144°6’ E, 18–19 m depth, 5 Dec. 2014; KFRS E.692, female 440 mm TL, KFRS E.693, juvenile male 380 mm TL, south of Kerema, Gulf of Papua, 8°2’55.8” S, 145°44’57” E, 14–16 m depth, 19 Jun. 2014; KFRS E.695, female 400 mm TL, KFRS E.696, juvenile male 440 mm TL, south of Kerema, Gulf of Papua, 8°3’15” S, 145°44’21.6” E, 17–19 m depth, 7 Jun. 2014; KFRS E.699, juvenile male 430 mm TL, Freshwater Bay, Gulf of Papua, 8°5’45” S, 145°52’36” E, 14–16 m depth, 8 Jun. 2014; KFRS E.710, juvenile male 420 mm TL, Freshwater Bay, Gulf of Papua, 8°5’24.6” S, 145°51’7.2” E, 13 m depth, 22 Jun. 2014; KFRS E.715, adult male 740 mm TL, Gulf of Papua, 2014.

Remarks: First reported from Port Moresby by Ogilby (1888) as *Carcharias menisorrah.* Previously considered to be a synonym of *Carcharhinus dussumieri* (Valenciennes *in* Müller & Henle, 1839); recently resurrected as a valid species for the Australian and New Guinea members of the *dussumieri*-*sealei* complex. Very common in the Gulf of Papua.

Carcharhinus falciformis **(Bibron, 1839)**

Silky Shark

Carcharias (*Prionodon*) *falciformis* Bibron *in* Müller & Henle, 1839: 47. Holotype: MNHN 0000-1134. Type locality: Cuba, Western Atlantic.

Local synonymy: *Carcharhinus falciformis*—Filewood, 1973: 7 (Papua New Guinea); Kailola, 1987: 14 (PNG); White *et al.*, 2018: 142, figs (PNG).

PNG voucher material: (2 spec.) AKPM 4 (dried jaws), juvenile female ~1300 mm TL, Rabaul, East New Britain; KFRS E.046 (dried jaws), Cape Saint George, New Ireland, May 1965.

Remarks: First recorded from PNG by Filewood (1973). Caught in large numbers by the pelagic longline and purse seine fisheries in PNG. Commonly misidentified as *Carcharhinus brachyurus* (Günther, 1870), which does not occur in PNG, and *C. galapagensis* (Snodgrass & Heller, 1905) which has not been verified from PNG.

Carcharhinus fitzroyensis **(Whitley, 1943)**

Creek Whaler

Galeolamna (*Uranganops*) *fitzroyensis* Whitley, 1943: 117, Fig. 2. Holotype: AMS IB. 1229 (skin and teeth). Type locality: Fitzroy River estuary, Rockhampton, Queensland, Australia.

Local synonymy: White *et al.*, 2018: 144, figs (PNG).

PNG voucher material: (3 spec.) CSIRO H 8023-01, juvenile male 760 mm TL, east of Fly River mouth, Gulf of Papua, 8°17’40” S, 144°15’49” E, 17–24 m depth, 2 Apr. 2015; KFRS E.623, juvenile male 660 mm TL, south of Kerema, Gulf of Papua, 8°3’2” S, 145°43’10” E, 13–16 m depth, 1 Sep. 2015; KFRS E.776 (dried jaws), no label on jaw but likely a previously registered specimen, new registration number allocated April 2017.

Remarks: Previously thought to be an Australian endemic species. Caught in low numbers by coastal and prawn trawl fisheries in the Western Province and Gulf of Papua; probably restricted to these areas.

Carcharhinus leucas (Valenciennes, 1839)
Bull Shark

Carcharias (*Prionodon*) *leucas* Valenciennes *in* Müller & Henle, 1839: 42. Syntypes (4): only 2 stuffed syntypes still in existence; MNHN A-9650, MNHN A-9652. Type locality: Antilles, Western Atlantic.

Local synonymy: *Carcharhinus leucas*—Filewood, 1973: 5 (PNG); Haines, 1979a: 6 (Purari Delta); Haines, 1979b: 94 (Purari Delta); Compagno, 1984: 479 (New Guinea); Kailola, 1987: 16 (Fly River to Yule Island); Taniuchi & Shimizu, 1991: 5 (Sepik River); Kan & Taniuchi, 1991: 3 (near Angoram, Sepik River); White *et al.*, 2018: 146, figs (PNG).

PNG voucher material: (2 spec.) CSIRO C 1800 (teeth only), Port Moresby, 25 Sep. 1948; FUMT-P10850, juvenile male 852 mm TL, Magendo 1, Sepik River, 5 Sep. 1989.

Remarks: First recorded from PNG by Filewood (1973), but first specimen recorded was in 1948 from Port Moresby (CSIRO C 1800).

Carcharhinus limbatus (Valenciennes, 1839)
Common Blacktip Shark

Carcharias (*Prionodon*) *limbatus* Valenciennes *in* Müller & Henle, 1839: 49, pl. 19 (teeth). Syntypes (2): only 1 syntype still in existence; MNHN 0000-3468 (mounted skin). Type locality: Martinique, Lesser Antilles, Western Atlantic.

Local synonymy: *Carcharhinus limbatus*—Filewood, 1973: 6 (PNG); Compagno, 1984: 482 (PNG); Kailola, 1987: 16 (off the Sepik and Ramu River mouths; Bougainville; New Britain; Trobriands; Orangerie Bay; Gulf of Papua and Western Papua); White *et al.*, 2018: 148, figs (PNG).

PNG voucher material: (21 spec.) CSIRO H 8105-01 (jaw), female 760 mm TL, west of Avirara, Gulf of Papua, 8°15'41" S, 146°6'47" E, 16–18 m depth, 29 Aug. 2015; CSIRO H 7828-02 (dried jaw), juvenile male 700 mm TL, south of Deception Bay, Gulf of Papua, 8°2'33" S, 144°39'21" E, 25–31 m depth, 7 Dec. 2014; KFRS E.015A-E (5 sets of dried jaws), Hall Sound, Central Province, 11/12 Nov. 1964; KFRS E.023 (dried jaws), Hall Sound, Central Province, Sep. 1964; KFRS E.155A (dried jaws), near McDhui wreck, Port Moresby, 7 Aug. 1965; KFRS E.177 (dried jaws), Kiriwina lagoon, Losuia, Milne Bay Province, 17 Nov. 1965; KFRS E.180A (dried jaws), Tatana, Fairfax Harbour, Port Moresby, 7 Oct. 1965; KFRS E.273 (dried jaws), New Britain, Sep. 1966; KFRS E.312 (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.366 (dried jaws), KFRS E.369 (dried jaws), Mission Point, Yule Island, 4 Sep. 1968; KFRS E.406 (dried jaws), no data; KFRS E.448 (dried jaws), Tureture, Daru, 13 Dec. 1971; KFRS E.449 (dried jaws), mouth of Binaturi River, Western Province; KFRS E.717, female 760 mm TL, KFRS E.718, juvenile male 690 mm TL, Gulf of Papua, 2014; KFRS E.777 (dried jaws), no label on jaw but likely a previously registered specimen, new registration number allocated April 2017.

Remarks: First recorded from PNG by Filewood (1973). Common catch of coastal fisheries and in prawn trawl bycatch.

Carcharhinus longimanus (Poey, 1861)
Oceanic Whitetip Shark

Squalus longimanus Poey, 1861: 338, pl. 19 (figs 9, 10). No type known. Type locality: Cuba, Western Atlantic.

Local synonymy: *Carcharhinus maou*—Filewood, 1973: 7 (PNG). *Carcharhinus longimanus*—Kailola, 1987: 17 (Kranket Island; Milne Bay); White *et al.*, 2018: 150, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973) as *Carcharhinus maou* (Lesson, 1829), a junior synonym of *C. longimanus*. Records of Kranket Island and Milne Bay by Kailola (1987) based on two destroyed KFRS specimens (E.94, Kranket Island, Madang, Dec. 1962; E.322, 2020 mm TL, Milne Bay district, 2 Aug. 1967).

Carcharhinus macloti (Müller & Henle, 1839)

Hardnose Shark

Carcharias (*Hypoprion*) *macloti* Müller & Henle, 1839: 34, pl. 10. Holotype: RMNH (stuffed). Type locality: New Guinea.

Local synonymy: *Hypoprion macloti*—Munro, 1958: 113 (Milne Bay Province, New Britain). *Carcharhinus macloti*—Munro, 1967: 9, pl. 1, fig. 9 (New Guinea); Filewood, 1973: 6 (PNG); Compagno, 1984: 486 (New Guinea); White *et al.*, 2018: 152, figs (PNG).

PNG voucher material: (13 spec.). CSIRO H 7834-01, juvenile male 410 mm TL, south of Deception Bay, Gulf of Papua, 8°1'54" S, 144°39'13" E, 22–25 m depth, 15 Dec. 2014; CSIRO H 7835-01, juvenile male 410 mm TL, south of Deception Bay, Gulf of Papua, 8°2'16" S, 144°38'26" E, 22–23 m depth, 15 Dec. 2014; CSIRO H 7825-02 (dried jaw), female 840 mm TL, east of Fly River mouth, Gulf of Papua, 8°37' S, 144°11' E, 17–19 m depth, 13 Dec. 2014; CSIRO H 8153-01 (dried jaw), adult male 770 mm TL, east of Fly River mouth, Gulf of Papua, 8°36'48" S, 144°11'19" E, 17–23 m depth, 1 Apr. 2015; CSIRO H 8108-01 (dried jaw and cranium), female 810 mm TL, south of Kerema, Gulf of Papua, 8°1'58.08" S, 145°45'17.52" E, 12–15 m depth, 16 Sep. 2015; CSIRO H 8152-02 (dried jaw and cranium), female 820 mm TL, south of Deception Bay, Gulf of Papua, 8°9' S, 144°28' E, 19–23 m depth, 9 Dec. 2014; KFRS E.303 (5 sets of dried jaws), Orangerie Bay, Jun. 1967; KFRS E.739, female 380 mm TL, south of Deception Bay, Gulf of Papua, 8°0' S, 144°42' E, 18–21 m depth, 8 Dec. 2014; KFRS E.751, juvenile male 390 mm TL, Freshwater Bay, Gulf of Papua, 8°11' S, 146°1' E, 19–20 m depth, 29 Nov. 2014.

Remarks: Holotype collected by Heinrich Christian Macklot in August 1828 during an expedition to New Guinea onboard the *HM corvette Triton*; although a German naturalist, he was employed through the Rijksmuseum in Leiden and the expedition was to Dutch New Guinea (=West Papua), thus not collected from PNG. First recorded from PNG by Munro (1958) from Milne Bay Province and New Britain. Commonly taken as bycatch in the Gulf of Papua prawn trawl fishery and by gillnet fishers at the mouth of the Sepik River.

Carcharhinus melanopterus (Quoy & Gaimard, 1824)

Blacktip Reef Shark

Carcharias melanopterus Quoy & Gaimard, 1824: 194, pl. 43 (figs 1, 2). Lectotype: MNHN 0000-1129; lectotype designation by Eschmeyer (1998). Type locality: Pulau Waigeo, West Papua, Indonesia.

Local synonymy: *Carcharias melanopterus*—Peters, 1877: 853 (New Ireland). *Carcharhinus spallanzani*—Munro, 1958: 112 (Bostrem Bay, Milne Bay Province, New Ireland, New Britain); Munro, 1967: 11, pl. 1, fig. 13 (New Guinea). *Carcharhinus melanopterus*—Filewood, 1973: 5 (PNG); Kailola, 1987: Manus Island; New Britain; Salamaua; Hula Bay; Gulf of Papua; Port Moresby area); Gochfeld, 1996: 43 (southern New Ireland); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93 (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay); White *et al.*, 2018: 154, figs (PNG).

PNG voucher material: (5 spec.) CSIRO C57, male embryo 473 mm TL, Koke village, Port Moresby, 11 Nov. 1948; KFRS E.007 (dried jaws), female, Taurama Beach, Port Moresby, ~9°31'48.05" S, 147°14'48.41" E, 12 Dec. 1963; KFRS E.318 (dried jaws), Tuma Island, Trobriand Islands, 25 Jul. 1967; ZMB 12711, female ~555 mm TL, Port Moresby, [1880–1884]; ZMB unreg. (chondrocranium and vertebral column only), ~650 mm TL, Astrolabe Bay, Madang, 1909 or 1910.

Remarks: First recorded from PNG by Peters (1877) from off New Ireland. Commonly observed over shallow coastal reefs. Common catch of coastal fisheries.

Carcharhinus obscurus (Lesueur, 1818)

Dusky Shark

Squalus obscurus Lesueur, 1818: 223, pl. 9. No types known. Type locality: east coast of USA.

Local synonymy: White *et al.*, 2018: 156, figs (PNG).

PNG voucher material: None.

Remarks: First confirmed record from PNG. Caught occasionally by the longline fisheries, but not recorded from coastal fisheries catches.

Carcharhinus plumbeus (Nardo, 1827)

Sandbar Shark

Squalus plumbeus Nardo, 1827: 26, 35 (no. 24). No types known. Type locality: Adriatic Sea.

Local synonymy: *Carcharhinus plumbeus*—Filewood, 1973: 6 (PNG); White *et al.*, 2018: 158, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973), but with a comment that its occurrence needs confirmation. Caught as bycatch in the pelagic longline fisheries in PNG and occasionally in coastal fisheries; verified by photographs, with accompanying muscle and vertebral samples, from fisheries observers.

Carcharhinus sorrah (Valenciennes, 1839)

Spot-tail Shark

Carcharias (*Prionodon*) *sorrah* Valenciennes *in* Müller & Henle, 1839: 45, pl. 16. Lectotype: RMNH 4294, Type locality: Java, Indonesia.

Local synonymy: *Carcharhinus spallanzani*—Filewood, 1973: 7 (PNG). *Carcharhinus sorrah*—White *et al.*, 2018: 160, figs (PNG).

PNG voucher material: (9 spec.) KFRS E.003A (dried jaws), KFRS E.003B (dried jaws), Hall Sound, Yule Island, Central Province, 11 Nov. 1963; KFRS E.004 (dried jaws), north of Yule Island, Central Province, 11 Jun. 1963; KFRS E.343A-C (3 spec.), two females 293 and 300 mm TL, one juvenile male 300 mm TL, KFRS E.344A-B (2 spec.), females 327 and 340 mm TL, Kairuku, Yule Island, Central Province, 2 Oct. 1968; KFRS E.367 (dried jaws), no collection data.

Remarks: First recorded from PNG by Filewood (1973) as *C. spallanzani* (=*sorrah, isobel*, etc) and listed as "very common". Caught by coastal fisheries.

Carcharhinus tilstoni (Whitley, 1950)

Australian Blacktip Shark

Galeolamna pleurotaenia tilstoni Whitley, 1950: 100, Figs. 1, 2. Holotype: AMS IB.2421 (jaws and skin). Type locality: Joseph Bonaparte Gulf, Australia.

Local synonymy: White *et al.*, 2018: 162, figs (PNG).

PNG voucher material: (2 spec.) CSIRO H 7833-01, juvenile male 540 mm TL, south of Deception Bay, Gulf of Papua, 8°2'19" S, 144°37'12" E, 22–24 m depth, 15 Dec. 2014; CSIRO H 8151-01 (dried jaw), female 800 mm TL, east of Fly River mouth, Gulf of Papua, 8°42' S, 144°3' E, 19–22 m depth, 3 Dec. 2014.

Remarks: Previously thought to be an Australian endemic species. Caught in prawn trawl fisheries and by coastal fisheries in PNG, from Western Province to Milne Bay Province and also recently recorded at mouth of Sepik River in East Sepik Province. Very similar and easily misidentified as *C. limbatus*; confirmed based on specimens and genetic data (S. Appleyard and G. Naylor, unpubl. data).

Genus Glyphis Agassiz, 1843

Speartooth Sharks

Glyphis Agassiz, 1843: 243. Type species: *Carcharias* (*Prionodon*) *glyphis* Müller & Henle, 1839. Type by absolute tautonymy, *C. glyphis* mentioned in text.

Glyphis garricki Compagno, White & Last, 2008
Northern River Shark

Glyphis garricki Compagno, White & Last, 2008: 204, Figs 1–6. Holotype: CSIRO H 5262-01. Type locality: East Alligator River, Northern Territory, Australia

Local synonymy: *Carcharhinus gangeticus* - Filewood, 1973: 5 (PNG); Haines, 1979a: 6 (Purari Delta); Haines, 1979b: 6 (Purari Delta). *Glyphis* species—Kailola, 1987: 18 ("very similar third species" - PNG). *Glyphis garricki* Compagno *et al.*, 2008: 204 (Baimuru; Port Romilly)—Last & Stevens, 2009: 276 (PNG); Compagno *et al.*, 2010: 41 (Baimuru; Port Romilly); Ebert *et al.*, 2013: 480, pl. 69 (PNG); White *et al.*, 2015a: 1, figs 4 and 6 (Daru; Katatai); White *et al.*, 2018: 164, figs (PNG).

PNG voucher material: (3 spec.) KFRS E.217 (dried jaws), adult male ~1500–1700 mm TL, KFRS E.219 (dried jaws), Port Romilly, Gulf Province, 7°33' S, 144°50' E, 12 Mar. 1966; KFRS E.473 (dried jaws), 1020 mm TL, Baimuru, Gulf Province, 7°33' S, 144°51' E, 28 Mar. 1974. In Compagno *et al.* (2008), the dried jaws above were listed as LWF-E217, LWF-E219, LWF-E473; loaned to LJV Compagno, possibly still in South African Museum in Cape Town.

Remarks: Filewood (1973) included the species *C. gangeticus* and *C. glyphis* in his key to PNG sharks and rays which were distinguished from the other *Carcharhinus* species in have feeble precaudal pits and flattened snouts; longitudinal, shallow precaudal pits is a key distinguishing feature between *Glyphis* and *Carcharhinus* species which have a deep crescentic pit. The key characters provided by Filewood (1973) which distinguish his *C. gangeticus* and *C. glyphis* were the number of lower teeth (15 pairs vs. 12–14 pairs) and number of precaudal vertebrae (more than 100 vs. less than 100). The number of lower teeth matches *G. garricki* and *G. glyphis* but the number of vertebrae is opposite. But, in the couplet for *C. glyphis* the 'less' in "precaudal vertebrae less than 100" has been crossed off and replaced with a > by hand, suggesting an error in the printed version; thus it is likely that the precaudal counts were swapped around for the two species. Dried jaws of *G. garricki* from the KFRS collection were originally identified as *C. gangeticus*. Recently recorded by White *et al.* (2015) from coastal fisheries catches in Western Province where it is caught occasionally.

Glyphis glyphis Müller & Henle, 1839
Speartooth Shark

Carcharias (*Prionodon*) *glyphis* Müller & Henle, 1839: 40, Pl. 14. Holotype: ZMB 5265 (stuffed). Type locality: probably Indian Ocean; Roberts (2007) suggested type locality may be the South China Sea.

Local synonymy: *Carcharhinus glyphis*—Filewood, 1973: 5 (PNG); Haines, 1979a: 11 (Purari Delta); Haines, 1979b: 94 (Purari Delta). *Glyphis glyphis*—Compagno, 1984: 509 (New Guinea); Kailola, 1987: 17 (PNG); Compagno *et al.*, 2008: 213 (Port Romilly; Alligator Island, Fly River); Last & Stevens, 2009: 277 (PNG); Compagno *et al.*, 2010: 41 (Port Romilly; Alligator Island, Fly River); Ebert *et al.*, 2013: 482, pl. 69 (PNG); White *et al.*, 2015a: 1, figs 2, 3 and 5 (Katatai); White *et al.*, 2018: 166, figs (PNG). *Glyphis* cf *glyphis*—Roberts, 2007: 282 (New Guinea).

PNG voucher material: (3 spec.) CSIRO H 7670-01 (dried jaws), pregnant female ~2370–2600 mm TL, Katatai, Daru, Western Province, 9°01'15" S, 143°20'31" E, 23 Oct. 2014; KFRS E.218 (dried jaws), juvenile female ~1600–1800 mm TL, Port Romilly, Gulf Province, 7°33' S, 144°50' E, 12 Mar. 1966; KFRS E.405B (dried jaws), ~1600–1800 mm TL, Alligator Island, 200 miles upstream in Fly River, 7°19' S, 141°11' E, Feb. 1970. In Compagno *et al.* (2008), the KFRS dried jaws above were listed as LWF-E218 and LWF-E405B; loaned to LJV Compagno, possibly still in South African Museum in Cape Town.

Remarks: First recorded from PNG by Filewood (1973) as *Carcharhinus glyphis* (see comments in *G. garricki* remarks above). Recently recorded by White *et al.* (2015) from coastal fisheries catches in Western Province where it is caught occasionally.

Genus *Loxodon* Müller & Henle, 1838a
Sliteye Shark

Loxodon Müller & Henle, 1838a: 36. Type species: *Loxodon macrorhinus* Müller & Henle, 1839, by subsequent monotypy; appeared first with no included species.

Loxodon macrorhinus Müller & Henle, 1839
Sliteye Shark

Loxodon macrorhinus Müller & Henle, 1839: 61, pl. 25. Holotype: ZMB 4479. Type locality: unknown (probably Indian Ocean).

Local synonymy: *Loxodon macrorhinus*—Filewood, 1973: 4 (PNG); Kailola, 1987: 18 (Tuma Island; Orangerie Bay; Gulf of Papua); White *et al.*, 2018: 168, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973). Recently observed in low numbers, probably due to their small size, off southern New Ireland and northern East New Britain in the catches of the target shark longline fishery; no specimens retained but vertebrae and genetic samples taken; identification confirmed with molecular data (S. Appleyard, unpubl. data). A photograph of a specimen caught as bycatch by a deepwater snapper fisher off Kavieng district, New Ireland, also verified as this species. Depth of capture not known but >100 m depth.

Genus *Negaprion* Whitley, 1940
Lemon Sharks

Negaprion Whitley, 1940: 111. Type species: *Aprionodon acutidens queenslandicus* Whitley, 1939b, by original designation, a junior synonym of *Negaprion acutidens* (Rüppell, 1837).

Negaprion acutidens (Rüppell, 1837)
Sicklefin Lemon Shark

Carcharias acutidens Rüppell, 1837: 65, pl. 18 (fig. 3). Lectotype: SMF 2825 (stuffed); lectotype designation by Klausewitz (1960). Type locality: Jeddah, Saudi Arabia, Red Sea.

Local synonymy: *Negaprion acutidens*—Filewood, 1973: 3 (PNG); Compagno, 1984: 518 (New Guinea); Kailola, 1987: 18 (Binaturi River mouth to Trobriand Islands); White *et al.*, 2018: 170, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.314, Tuma Island, Trobriand Islands, 25 Jul. 1967.

Remarks: First recorded from PNG by Filewood (1973). Recorded from coastal fisheries catches in Western and Milne Bay Provinces during recent surveys.

Genus *Prionace* Cantor, 1849
Blue Shark

Prionace Cantor, 1849: 1381. Type species: *Squalus glaucus* Linnaeus, 1758, designated by the ICZN (on official list, Opinion 723.3d, 1965, name no. 1660).

Prionace glauca (Linnaeus, 1758)
Blue Shark

Squalus glaucus Linnaeus, 1758: 235. No types known. Type locality: northeastern Atlantic (localities include England and Italy).

Local synonymy: *Prionace glauca*—Filewood, 1973: 3 (PNG); Kailola, 1987: 18 (PNG); White *et al.*, 2018: 172, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973). Common in bycatch of pelagic fisheries in PNG; verified by photographs, with accompanying muscle and vertebral samples, from fisheries observers during recent surveys. Found to be occasionally misidentified as longfin mako *Isurus paucus*.

Genus *Rhizoprionodon* Whitley, 1929

Sharpnose Sharks

Rhizoprionodon Whitley, 1929: 354; a replacement name for *Rhizoprion* Ogilby, 1915, preoccupied by *Rhizoprion* Jourdan, 1861 in mammals. Type species: *Carcharias* (*Scoliodon*) *crenidens* Klunzinger, 1880, by original designation, a junior synonym of *Carcharias acutus* Rüppell, 1837.

Rhizoprionodon acutus (Rüppell, 1837)

Milk Shark

Carcharias acutus Rüppell, 1837: 65, pl. 18 (fig. 4). Lectotype: SMF 2783 (stuffed). Type locality: Jeddah, Saudi Arabia, Red Sea.

Local synonymy: *Rhizoprionodon acutus*—Filewood, 1973: 4 (PNG); Kailola, 1987: 18 (Darapap; Gogol River mouth; Ramu River mouth; Rabual; Orangerie Bay; Port Moresby; Yule Island); Fricke *et al.*, 2014: 12 (Madang); White *et al.*, 2018: 174, figs (PNG).

PNG voucher material: (24 spec.) AMS I 16667-003, female 605 mm TL, AMS I 16667-006, female 757 mm TL, Bostrem Bay, Madang Harbour, 5°4'58" S, 145°48'4" E, 27 Jul. 1969; CSIRO H 7800-01, juvenile male 340 mm TL, Freshwater Bay, Gulf of Papua, 8°6'57.6" S, 145°52'1.2" E, 14–17 m depth, 8 Jun. 2014; CSIRO H 7804-01, female 350 mm TL, Freshwater Bay, Gulf of Papua, 8°6'45.6" S, 145°50'49.8" E, 21–22 m depth, 13 Jun. 2014; CSIRO H 7812-01, female 360 mm TL, Freshwater Bay, Gulf of Papua, 8°5'24.6" S, 145°51'7.2" E, 13 m depth, 22 Jun. 2014; CSIRO H 7824-01, adult male 770 mm TL, east of Fly River mouth, Gulf of Papua, 8°39' S, 144°6' E, 11–15 m depth, 12 Dec. 2014; CSIRO H 7829-01, juvenile male 360 mm TL, south of Deception Bay, Gulf of Papua, 8°1'53" S, 144°38'48" E, 20–22 m depth, 7 Dec. 2014; CSIRO H 7835-02, juvenile male 430 mm TL, south of Deception Bay, Gulf of Papua, 8°2'16" S, 144°38'26" E, 22–23 m depth, 15 Dec. 2014; CSIRO H 8007-01, female 420 mm TL, west of Avirara, Gulf of Papua, 8°17'34.08" S, 146°10'34.92" E, 10–12 m depth, 25 Aug. 2015; CSIRO H 8163-02 (chondrocranium and dried jaws), adult male 790 mm TL, south of Kerema, Gulf of Papua, 8°3'45" S, 145°46'49" E, 13–18 m depth, 9 Sep. 2015; CSIRO H 8162-02 (dried jaws), adult male 790 mm TL, south of Kerema, Gulf of Papua, 8°4'26" S, 145°40'55" E, 17–20 m depth, 7 Sep. 2015; CSIRO H 8169-01 (dried jaws), adult male 770 mm TL, Freshwater Bay, Gulf of Papua, 8°8'35" S, 145°56'26" E, 18–26 m depth, 9 Apr. 2015; CSIRO H 8164-01 (dried jaws), adult male 790 mm TL, south of Deception Bay, Gulf of Papua, 8°3'53" S, 144°41'8" E, 21–31 m depth, 7 Dec. 2014; KFRS E.016A (dried jaws), adult female, KFRS E.016B (dried jaws), adult female, Hall Sound, Central Province, 11/12 Nov. 1964; KFRS E.279B, juvenile male 305 mm TL, north of Yule Island, Central Province, Apr. 1966; KFRS E.668, juvenile male 340 mm TL, Freshwater Bay, Gulf of Papua, 8°8' S, 146°1' E, 14–15 m depth, 29 Nov. 2014; KFRS E.670, adult male 760 mm TL, east of Fly River mouth, Gulf of Papua, 8°40' S, 144°7' E, 13–20 m depth, 2 Dec. 2014; KFRS E.700, juvenile male 360 mm TL, Freshwater Bay, Gulf of Papua, 8°5'45" S, 145°52'36" E, 14–16 m depth, 8 Jun. 2014; KFRS E.714, juvenile male 320 mm TL, Freshwater Bay, Gulf of Papua, 8°5'38.4 S, 145°50'44.4" E, 14–15 m depth, 16 Jun. 2014; KFRS E.723, juvenile male 320 mm TL, Freshwater Bay, Gulf of Papua, 8°6'57.6" S, 145°52'1.2" E, 14–17 m depth, 8 Jun. 2014; KFRS E.730, juvenile male 370 mm TL, KFRS E.731, juvenile male 390 mm TL, Freshwater Bay, Gulf of Papua, 8°6'45.6" S, 145°50'49.8" E, 21–22 m depth, 13 Jun. 2014; KFRS E.766, female 430 mm TL, south of Deception Bay, Gulf of Papua, 8°1'53" S, 144°38'48" E, 20–22 m depth, 7 Dec. 2014.

Remarks: First recorded from PNG by Filewood (1973). Sometimes confused with *Carcharhinus macloti*. Common in the bycatch of the Gulf of Papua prawn trawl fishery and in coastal fisheries in PNG.

Rhizoprionodon oligolinx **Springer, 1964**
Grey Sharpnose Shark

Rhizoprionodon (*Protozygaena*) *oligolinx* Springer, 1964: 621, Figs 12–13, Pl. 2 (fig. c). Holotype: USNM 196799. Type locality: Bangkok market, caught in Gulf of Thailand.

Local synonymy: White *et al.*, 2018: 176, figs (PNG).

PNG voucher material: None.

Remarks: Based on a dried jaw in the KFRS collection which appears to be conspecific with this species. Other specimens required from PNG to further validate. Also known from Australia based on a single specimen caught in the Gulf of Carpentaria (Last & Stevens, 2009).

Rhizoprionodon taylori **(Ogilby, 1915)**
Australian Sharpnose Shark

Physodon taylori Ogilby, 1915: 117. Holotype: QM I.738 [not QM I.4539], apparently lost. Type locality: Townsville, Queensland, Australia.

Local synonymy: *Rhizoprionodon taylori*—Filewood, 1973: 4 (PNG); Kailola, 1987: 18 (Western Papua to Yule Island; Madang?); Last & Stevens, 2009: 284 (PNG); Ebert *et al.*, 2013: 498, pl. 73 (PNG); White *et al.*, 2018: 178, figs (PNG).

PNG voucher material: (23 spec.) CSIRO H 7612-03, female 420 mm TL, south of Kerema, Gulf of Papua, 8°1’12” S, 145°42’2.4” E, 13–14 m depth, 21 Jun. 2014; ; CSIRO H 7814-08, male 360 mm TL, CSIRO H 7814-09, male 360 mm TL, CSIRO H 7814-11, pregnant female 580 mm TL, south of Kerema, Gulf of Papua, 8°3’1.2” S, 145°45’7.2” E, 16–17 m depth, 20 Jun. 2014; KFRS E.260 (12 embryos), 28–90 mm TL, Fairfax Harbour, Port Moresby, 7 Aug. 1965; KFRS E.279A, juvenile male 230 mm TL, north of Yule Island, Central Province, Apr. 1966; KFRS E.653, female 560 mm TL, south of Deception Bay, Gulf of Papua, 8°1’23” S, 144°36’37” E, 21–22 m depth, 29 Nov. 2014; KFRS E.675, female 540 mm TL, east of Fly River mouth, Gulf of Papua, 8°9’5” S, 144°26’53” E, 22–24 m depth, 9 Dec. 2014; KFRS E.698, female 580 mm TL, south of Kerema, Gulf of Papua, 8°2’3.6” S, 145°44’12” E, 16 m depth, 17 Jun. 2014; KFRS E.702, male 560 mm TL, Freshwater Bay, Gulf of Papua, 8°6’39.6” S, 145°53’57” E, 15–19 m depth, 19 Jun. 2014; KFRS E.706, male 450 mm TL, south of Kerema, Gulf of Papua, 8°4’25.3” S, 145°44’36” E, 18–21 m depth, 11 Jun. 2014; KFRS E.711, female 340 mm TL, Freshwater Bay, Gulf of Papua, 8°6’4.2” S, 145°53’12.6” E, 13 m depth, 16 Jun. 2014.

Remarks: First recorded from PNG by Filewood (1973), listed as uncommon. Very abundant in the bycatch of the Gulf of Papua prawn trawl fishery. Small species with most size classes not large enough to get caught in gillnets targeting barramundi.

Genus ***Triaenodon*** **Müller & Henle, 1837a**
Whitetip Reef Shark

Triaenodon Müller & Henle, 1837a: 113. Type species: *Carcharias obesus* Rüppell, 1837, by subsequent monotypy; appeared first without species then added by Bonaparte (1838).

Triaenodon obesus **(Rüppell 1837)**
Whitetip Reef Shark

Carcharias obesus Rüppell, 1837: 64, pl. 18 (fig. 2). Lectotype: SMF 3149 (stuffed); lectotype designation by Klausewitz (1960). Type locality: Jeddah, Saudi Arabia, Red Sea.

Local synonymy: *Triaenodon apicalis*—Munro, 1958: 113 (Milne Bay Province); Munro, 1967: 11, pl. 1, fig. 11 (New Guinea). *Triaenodon obesus*—Filewood, 1973: 3 (PNG); Compagno, 1984: 537 (New Guinea); Allen, 1998: 67 (Milne Bay); Baine & Harasti, 2007: 93, fig. (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck

Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay); Fricke *et al.*, 2014: 14 (Madang); White *et al.*, 2018: 180, figs (PNG).

PNG voucher material: (4 spec.) CSIRO C 271, female embryo 473 mm TL, shoal between Cannac Island & Wabomat Island, Laughlan Island Group, Milne Bay Province, 09°18’ S, 153°40’ E, 17 Oct. 1949; KFRS E.269 (dried jaws), female 1080 mm TL, New Britain area, Sep. 1966; KFRS E.340, Main Reef, Fishermans Island, Port Moresby, 24 Nov. 1968; KFRS E.629, east of Nago Island, Kavieng, New Ireland, 02°35’47.8” S, 150°45’7.42 E, 40 m depth, 30 Sep. 2015.

Remarks: First recorded from PNG by Munro (1958) from the Milne Bay region. Very common reef species throughout PNG, often seen by divers; evidence of local depletion in a number of areas.

Family Galeocerdidae Poey, 1875

Tiger Shark

Genus Galeocerdo Müller & Henle, 1837a

Tiger Shark

Galeocerdo Müller & Henle, 1837a: 115. Type species: *Squalus arcticus* Faber, 1829, by subsequent designation in Bonaparte (1838).

Galeocerdo cuvier (Péron & Lesueur *in* Lesueur, 1822)

Tiger Shark

Squalus cuvier Péron & Lesueur *in* Lesueur, 1822: 351. No types known. Type locality: northwestern Australia.

Local synonymy: *Galeocerdo cuvieri*—Munro, 1958: 113 (Dyke Ackland Bay). *Galeocerda cuvieri*—Munro, 1967: 9, pl. 1, fig. 8 (New Guinea). *Galeocerdo cuvier*—Filewood, 1973: 4 (PNG); Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); White *et al.*, 2018: 182, figs (PNG).

PNG voucher material: (4 spec.) KFRS E.014 (dried jaws), ~1830 mm TL, near Idia Island, 15 mile west of Port Moresby, 3 Dec. 1963; KFRS E.055 (dried jaws), Ramu River mouth, 19 Jul. 1965; KFRS E.379 (dried jaws), ~2430 mm TL, north end of Yule Island, Central Province, 8 Nov. 1969; KFRS E.775 (dried jaws), no label, new registration number allocated Apr. 2017 (possibly = E.480, Tatana, Port Moresby, 12 Sep. 1975, which cannot be located).

Remarks: First recorded from PNG by Munro (1958) from Dyke Ackland Bay in Oro Province. Caught by longline fisheries and coastal fisheries in PNG. Previously placed in the family Carcharhinidae but differs in a number of key characteristics from other members of that family (including very long upper labial furrows reaching to level of eye, strong keels on caudal peduncle, an obvious spiracle, and embryonic connection not via a placental connection) and also differs at a molecular level (Naylor *et al.*, unpubl. data).

Family Sphrynidae Gill, 1872

Hammerhead Sharks

Genus *Eusphyra* Gill, 1862

Winghead Shark

Eusphyra Gill, 1862: 403. Type species: *Zygaena blochii* Cuvier, 1816, by original designation (and by monotypy).

Eusphyra blochii (Cuvier, 1816)

Winghead Shark

Zygaena blochii Cuvier, 1816: 127. Holotype: ZMB 7835 (stuffed). Type locality: unknown; Fowler, 1941 thought type was from India.

Local synonymy: *Eusphyra blochii*—Filewood, 1973: 2 (PNG); Kailola, 1987: 21 (Ramu River mouth; Broken Water Bay; eastern Papua; Port Moresby; Yule Island; Orokolo Bay); White *et al.*, 2018: 184, figs (PNG).

PNG voucher material: (23 spec.) CSIRO H 7612-01, female 410 mm TL, south of Kerema, Gulf of Papua, 8°1'12" S, 145°42'2.4" E, 13–14 m depth, 21 Jun. 2014; CSIRO H 7614-06, female 420 mm TL, CSIRO H 7614-07, female 420 mm TL, south of Kerema, Gulf of Papua, 8°3'1.2" S, 145°45'7.2" E, 16–17 m depth, 20 Jun. 2014; CSIRO H 7615-02, female 410 mm TL, CSIRO H 7615-03, juvenile male 410 mm TL, south of Kerema, Gulf of Papua, 8°2'55.2" S, 145°43'30" E, 17 m depth, 20 Jun. 2014; CSIRO H 8000-01, female embryo 320 mm TL, CSIRO H 8000-02, female embryo 330 mm TL, CSIRO H 8000-03, female embryo 350 mm TL, south of Kerema, Gulf of Papua, 8°3.65' S, 145°42.18' E, 19 m depth, 2 Sep. 2015; CSIRO H 8166-01 (dried jaws and chondrocranium), female 670 mm TL, southwest of Kerema, Gulf of Papua, 8°4' S, 145°38' E, 14–15 m depth, 30 Nov. 2014; KFRS E.054A (dried jaws), KFRS E.054B (dried jaws), Ramu River mouth, Madang Province, 19 Jul. 1965; KFRS E.345A, female 293 mm TL, KFRS E.345B, juvenile male 290 mm TL, Kairuku, Yule Island, Nov. 1968; KFRS E.679, female 940 mm TL, Katatai, Daru, Western Province, 9°1'15.13" S, 143°20'30.59" E, 22 Oct. 2014; KFRS E.690, juvenile male 440 mm TL, south of Kerema, Gulf of Papua, 8°2'55.8" S, 145°44'57" E, 14–16 m depth, 19 Jun. 2014; KFRS E.703, juvenile male 400 mm TL, Freshwater Bay, Gulf of Papua, 8°6'39.6" S, 145°53'57" E, 15–19 m depth, 19 Jun. 2014; KFRS E.707, juvenile male 400 mm TL, south of Kerema, Gulf of Papua, 8°3'25.2" S, 145°43'3.6" E, 17–19 m depth, 19 Jun. 2014; KFRS E.709, juvenile male 410 mm TL, Freshwater Bay, Gulf of Papua, 8°5'24.6" S, 145°51'7.2" E, 13 m depth, 22 Jun. 2014; KFRS E.729, juvenile male 370 mm TL, Freshwater Bay, Gulf of Papua, 8°6'45.6" S, 145°50'49.8" E, 21–22 m depth, 13 Jun. 2014; KFRS E.742, male 650 mm TL, east of Fly River mouth, Gulf of Papua, 8°16' S, 144°20' E, 20–22 m depth, 6 Dec. 2014; KFRS E.795 (3 spec.), embryos 320–350 mm TL, south of Kerema, Gulf of Papua, 8°3.65' S, 145°42.18' E, 19 m depth, 2 Sep. 2015.

Remarks: First recorded from PNG by Filewood (1973) who commented that it was found in inshore muddy waters. Very common bycatch in the Gulf of Papua prawn trawl fishery and in coastal fisheries, particularly in the Western and Gulf Provinces.

Genus *Sphyrna* Rafinesque, 1810a

Hammerhead Sharks

Sphyrna Rafinesque, 1810a: 60. Type species: *Squalus zygaena* Linnaeus, 1758, by subsequent designation (Bonaparte, 1838).

Sphyrna lewini (Griffith & Smith, 1834)

Scalloped Hammerhead

Zygaena lewini Griffith & Smith, 1834: 640, pl. 50. No types known. Type locality: south coast of Australia [New Holland].

Local synonymy: *Sphyrna lewini*—Whitley, 1949b: 345 (Goodenough Bay); Fraser-Brunner, 1950: 217 (Menapi); Munro, 1967: 8, pl. 1, fig. 7 (New Guinea); Filewood, 1973: 2 (PNG); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); White *et al.*, 2018: 186, figs (PNG).

PNG voucher material: (22 spec.) CSIRO H 7612-02, juvenile male 600 mm TL, south of Kerema, Gulf of Papua, 8°1'12" S, 145°42'2.4" E, 13–14 m depth, 21 Jun. 2014; CSIRO H 7613-04, female 530 mm TL, Freshwater Bay, Gulf of Papua, 8°8'15" S, 145°59'29.4" E, 14–15 m depth, 13 Jun. 2014; CSIRO H 7614-02, juvenile male 550 mm TL, CSIRO H 7614-03, juvenile male 490 mm TL, CSIRO H 7614-04, juvenile female 520 mm TL, CSIRO H 7614-05, juvenile male 500 mm TL, south of Kerema, Gulf of Papua, 8°3'1.2" S, 145°45'7.2" E, 16–17 m depth, 20 Jun. 2014; CSIRO H 7615-04 (dried jaws), juvenile male 540 mm TL, south of Kerema, Gulf of Papua, 8°2'55.2" S, 145°43'30" E, 17 m depth, 20 Jun. 2014; CSIRO H 7616-02, juvenile female 530 mm TL, south of Kerema, Gulf of Papua, 8°3'1.2" S, 145°45'7.2" E, 14–15 m depth, 17 Jun. 2014; CSIRO H 7617-03 (dried jaws), juvenile female 540 mm TL, south of Kerema, Gulf of Papua, 8°3'3.6" S, 145°37'52.2" E, 16 m depth, 15 Jun. 2014; CSIRO H 8160-01 (dried jaws and chondrocranium), juvenile male 930 mm TL, west of Avirara, Gulf of Papua, 8°18'39" S, 146°11'27" E, 12–14 m depth, 27 Aug. 2015; KFRS E.006 (dried jaws), Hall Sound, Central Province, 11 Nov. 1963; KFRS E.310 (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.385 (dried jaws), Torokina Bay, Bougainville, 28 Aug. 1969; KFRS E.651, female 980 mm TL, southwest of Kerema, Gulf of Papua, 8°5'37" S, 145°38'6" E, 24–25 m depth, 26 Nov. 2014; KFRS E.694, juvenile male 510 mm TL, south of Kerema, Gulf of Papua, 8°2'46.8" S, 145°43'30.6" E, 14–17 m depth, 18 Jun. 2014; KFRS E.697, juvenile male 500 mm TL, south of Kerema, Gulf of Papua, 8°3'15" S, 145°44'21.6" E, 17–19 m depth, 7 Jun. 2014; KFRS E.704, juvenile female 540 mm TL, KFRS E.705, juvenile male 510 mm TL, south of Kerema, Gulf of Papua, 8°4'25.3" S, 145°44'36" E, 18–21 m depth, 11 Jun. 2014; KFRS E.713, juvenile female 520 mm TL, south of Kerema, Gulf of Papua, 8°4'47.4" S, 145°47'0.6" E, 20–21 m depth, 12 Jun. 2014; USNM 295163, juvenile female 530 mm TL, isolated reef about 200 m south of Wongat Island, Bismarck Sea, Madang Province, 5°13'58" S, 145°45' E, 3 m depth, 23 May 1987; CAS 68163, near Jais Aben boat dock, Madang, 5°9'19" S, 145°47'59" E.

Remarks: First recorded from PNG by Whitley (1949b) from Goodenough Bay. Commonly caught in a variety of fisheries, from inshore prawn trawling in the Gulf of Papua to pelagic longline fisheries.

Sphyrna mokarran **(Rüppell, 1837)**

Great Hammerhead

Zygaena mokarran Rüppell, 1837: 66, pl. 17 (fig. 3). Lectotype: SMF 3590 (stuffed); lectotype designation by Klausewitz (1960). Type locality: Massawa, Eritrea, Red Sea.

Local synonymy: *Sphyrna tudes*—Filewood, 1973: 2 (PNG). *Sphyrna mokarran*—Kailola, 1987: 21 (western Papua; Hall Sound; Port Moresby; Bootless Bay; Salamaua); White *et al.*, 2018: 188, figs (PNG).

PNG voucher material: (2 spec.) KFRS E.176 (dried jaws), Tatana, Fairfax Harbour, Port Moresby, 7 Oct. 1965; KFRS E.259 (dried jaws), Kanudi Bay, Port Moresby, 4 Aug. 1966.

Remarks: First recorded from PNG by Filewood (1973) as *S. tudes* (=*mokarran*). Recorded from prawn trawl fishery bycatch and from coastal fisheries catches during recent surveys, but in low numbers.

Sphyrna zygaena **(Linnaeus, 1758)**

Smooth Hammerhead

Squalus zygaena Linnaeus, 1758: 234. Syntype: NRM LP 88 (see Fernholm & Wheeler, 1983). Type locality: Mediterranean Sea and Atlantic (incl. Spain, France, Italy, Greece, Syria).

Local synonymy: *Sphyrna zygaena*—Filewood, 1973: 2 (may occur in PNG); White *et al.*, 2018: 190, figs (PNG).

PNG voucher material: None.

Remarks: Mainly recorded from temperate regions but also found in some tropical regions. Confirmed from coastal fisheries catches in Milne Bay Province; molecular data supports the identification (S. Appleyard, unpubl. data).

Order Rhinopristiformes

Family Pristidae Bonaparte, 1838

Sawfishes

Genus *Anoxypristis* White & Moy-Thomas, 1941

Knifetooth Sawfish

Anoxypristis White & Moy-Thomas, 1941: 397. Type by being a replacement name for *Oxypristis* Hoffmann, 1912, preoccupied by *Oxypristis* Signoret, 1861 in *Hemiptera*.

Anoxypristis cuspidata (Latham, 1794)
Knifetooth Sawfish

Pristis cuspidatus Latham, 1794: 279, pl. 26 (fig 3). Neotype: MNHN 0000-1250. Type locality: Malabar, India.

Local synonymy: *Platypristis cuspidata*—Filewood, 1973: 10 (PNG). *Platypristis cuspidatus*—Filewood, 1973: 10 (PNG). *Anoxypristis cuspidata*—Kailola, 1987: 24 (Daru; Gulf of Papua; Hall Sound; Yule Island; Bootless Bay; Orangerie Bay; Darapap; south of Ramu River mouth); White *et al*., 2017a: 277 (PNG); White *et al.*, 2018: 192, figs (PNG). *Anoxypristis cuspidatus*—Taniuchi & Shimizu, 1991: 5 (Oriomo River Estuary).

PNG voucher material: (3 spec.) FUMT−P10855, male 1182 mm TL, Oriomo River Estuary, Western Province, 24 Sep. 1989; KFRS E.619, female 1330 mm TL, west of Avirara, Gulf of Papua, 8°18'39" S, 146°11'27" E, 12–14 m depth, 27 Aug. 2015; KFRS E.796, female embryo 570 mm TL, Nigoherm Islands, Bismarck Archipelago, 0°33' S, 144°10' E.

Remarks: First recorded from PNG by Filewood (1973). White *et al.* (2017a) summarises sawfish records from PNG but most survey reports only record 'sawfish' with species verification not possible. Dried fins observed from coastal fisheries during recent surveys in the Gulf and Western Provinces; whole specimens observed in prawn trawl bycatch during recent surveys; commonly caught at the mouth of the Sepik River and off Broken Water Bay in East Sepik Province. An additional 16 specimens (9 registered lots) from the KFRS collection are considered lost or destroyed.

Genus *Pristis* Linck, 1790
Sawfishes

Pristis Linck, 1790: 31. Type species: *Squalus pristis* Linnaeus 1758. Type by monotypy (also by absolute tautonymy).

Pristis clavata Garman, 1906
Dwarf Sawfish

Pristis clavata Garman, 1906: 208. Holotype: MCZ 733-S. Type locality: Queensland, Australia.

Local synonymy: Dulvy *et al*., 2016: 142 (PNG); White *et al.*, 2017a: 277 (PNG); White *et al.*, 2018: 194, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.428 (dried rostrum), rostrum length 178 mm, Daru, Western Province.

Remarks: An additional 8 specimens (6 registered lots) from the KFRS collection are considered lost or destroyed; all collected in the mid 1960's. Dried fins observed from coastal fisheries during recent surveys in the Gulf and Western Provinces. White *et al.* (2017a) lists reports from unpublished survey reports from the 1970s; species identifications not verifiable.

Pristis pristis (Linnaeus, 1758)
Largetooth Sawfish

Squalus pristis Linnaeus, 1758: 235. No types known. Type locality: Mediterranean Sea, Indian Ocean, western Atlantic; localities include Marseille, France; Italy; Lesbos Island, Greece; Syria; Brazil.

Local synonymy: *Pristis perotteti*—Herre, 1936: 434 (Koragu, Sepik River). *Pristis microdon*—Munro, 1958: 115 (Sepik River); Munro, 1964: 145 (southern New Guinea); Filewood, 1973: 10 (PNG); Berra *et al.*, 1975: 319 (Laloki River system); Roberts, 1978: 26 (Middle Fly River); Haines, 1979a: 6 (Purari Delta); Haines, 1979b: 94 (Purari Delta); Coates, 1987: 236 (Sepik River); Allen & Coates, 1990: 33, 51 (Sepik River); Allen, 1991: 36 (Middle Fly River, Middle and Lower Sepik and Ramu rivers); Ishihara *et al.*, 1991: 83 (Sepik River; Lake Murray; Oriomo River); Ogawa, 1991: 91 (Lake Murray; Sepik River); Tanaka, 1991: 71 (Lake Murray; Sepik River);

Taniuchi *et al.*, 1991: 27 (Sepik River; Lake Murray; Oriomo River); Taniuchi & Shimizu, 1991: 5 (Sepik River; Lake Murray; Oriomo River); Mizue & Hara, 1991: 63 (Sepik River); Watabe, 1991: 103 (Lake Murray; Sepik River); Allen *et al.*, 1992: 296 (Bunapas village, Ramu River); Coates, 1993: 361 (Sepik River); Hyslop, 1996: 5 (Angabanga River); Powell & Powell, 1999: 350 (Bougainville); Swales *et al.*, 1999: 404 (Fly River); Hitchcock, 2002: 120 (Bensbach River); Storey *et al.*, 2009: 441 (Middle Fly River); Last & Stevens, 2009: 297 (PNG). *Pristiopsis leichhardti*—Munro, 1964: 145 (northern New Guinea); Munro, 1967: 19, pl. 2, fig. 25 (New Guinea). *Pristiopsis microdon*—Munro, 1967: 20, pl. 2, fig. 26 (New Guinea). *Pristis pristis*—Kailola, 1987: 24 (PNG); Faria *et al.*, 2013: 140 (Ramu River; Bismarck Archipelago; Fly River; Strickland River); White *et al.*, 2017a: 277 (PNG); White *et al.*, 2018: 196, figs (PNG). *Pristis* sp.—?Kan & Taniuchi, 1991: 3 (near Angoram, Sepik River).

PNG voucher material: (25 spec.) AMS IB. 2854 (dried rostrum), 735 mm SL, Laloki River, near Bomana, Central Province, 6 Aug. 1952; CAS 63666 (two dried rostra), near Bunapas Mission, Ramu River, 18 Oct. 1987; CAS SU 41013, (dried rostrum), CAS SU 41014 (dried rostrum), Koragu, 215 miles from sea, Sepik River, 23 May 1929; FUMT-P10851, juvenile male 801 mm TL, Magendo 3, Sepik River, 3 Sep. 1989; FUMT-P10854, female 970 mm TL, Miwa, Lake Murray, 17 Sep. 1989; KFRS E.024 (dried rostrum), rostrum length 1270 mm, Pinupaka, Hall Sound, Central Province, Oct. 1963; KFRS E.026A (dried rostrum), rostrum length 194 mm, KFRS E.026B (dried rostrum), rostrum length 203 mm, Vanapa River, 40 miles upstream, Central Province, 27 Jun. 1964; KFRS E.027A (dried rostrum), rostrum length 225 mm, KFRS E.027B (dried rostrum), rostrum length 242 mm, Laloki River, Central Province, Aug. 1964; KFRS E.032A (dried rostrum), rostrum length 242 mm, KFRS E.032B (dried rostrum), rostrum length 263 mm, Yule Island, Central Province, Jun. 1964; KFRS E.429A (dried rostrum), rostrum length 292 mm, KFRS E.429B (dried rostrum), rostrum length 237 mm, Oriomo River, Western Province; KFRS E.774, Sapuka, Fly River, 8°10’1” S, 141°59’46” E, 21 Oct. 2007; QM I 3686 (dried rostrum), QM I 3687 (dried rostrum), no collection data (only PNG); USNM 217001, female 809 mm TL, Lake Herbert Hoover and Wam River and swampy lagoons along Middle Fly, 509–512 km upriver from Toro Pass, Fly River Basin, 25 Nov. 1975; USNM 217002, juvenile male 916 mm TL, side channel of Strickland 4 km downstream from Massy Bakers Junction, 450 km upriver from Toro pass, Fly River Basin, 6 Dec. 1975; ZMB 14507 (rostrum, jaw, cranium, stomach, scapulocoracoid, gills), Ramu River, 1896 or 1899; ZMB 32538 (dried rostrum), Bismarck Archipelago, 26 Nov. 1909; ZMB 33545, juvenile female ~780 mm TL, “Tschessbandai”, west of Koragu, Sepik River, Aug. 1913; ZMB 33553 (dried rostrum), New Guinea.

Remarks: First recorded from PNG by Herre (1936) from Koragu in the Sepik River based on an expedition there in 1929; a specimen deposited at the ZMB collection in Berlin collected from Ramu River in either 1896 or 1899. White *et al.* (2017a) summarised published and unpublished sawfish records for PNG; most reports refer to just sawfish although many are attributable to this species. An additional 9 specimens (6 registered lots) from the KFRS collection are considered lost or destroyed; all collected in the mid 1960’s. Dried fins observed from coastal fisheries during recent surveys in the Gulf and Western Provinces; whole specimen observed in prawn trawl bycatch in 2014. Considered depleted from some river systems in PNG but more information is urgently required.

Pristis zijsron Bleeker, 1851
Green Sawfish

Pristis zijsron Bleeker, 1851: 442. Holotype: RMNH 7418 (rostrum only). Type locality: Bandjarmasin, Kalimantan, Indonesia.

Local synonymy: *Pristis zijaron*—Filewood, 1973: 10 (PNG). *Pristis zijsron*—Kailola, 1987: 24 (Daru; Balimo; Gulf of Papua; Bootless Bay); White *et al.*, 2017a: 277 (PNG); White *et al.*, 2018: 198, figs (PNG).

PNG voucher material: (3 spec.) CAS SU 40592 (rostrum), ~1515 mm TL, Sepik River, 1 May 1929; KFRS E.378 (dried rostrum), rostrum length 285 mm, Balimo area, May−Jul. 1968; KFRS E.411 (dried rostrum), rostrum length ~880 mm, Bootless Bay, Port Moresby, 8 May 1970.

Remarks: First recorded from PNG by Filewood (1973). Dried fins observed from coastal fisheries during recent surveys in the Gulf and Western Provinces. An additional specimen from the KFRS collection is considered lost or destroyed.

Family Rhinidae Müller & Henle, 1841
Wedgefishes

Local synonymy: *Rhinobates jaram* Montrouzier, 1857: 498 (Woodlark Island). *Rhynchobatus djiddensis*—Munro, 1958: 113 (Mukawa). Neither of above can be verified to a species but refer to a member of this family.

Genus *Rhina* Bloch & Schneider, 1801
Bowmouth Guitarfish

Rhina Bloch & Schneider, 1801: 352. Type designation by indication under ICZN Opinion 6. On official list; *Rhina* Schaeffer, 1760, *Rhina* Walbaum, 1792, and *Rhina* Rafinesque, 1810a placed on Official Index (Opinion 345). Valid as *Rhina* Bloch & Schneider, 1801.

Rhina ancylostoma Bloch & Schneider, 1801
Bowmouth Guitarfish

Rhina ancylostomus Bloch & Schneider, 1801: 352, pl. 72. Lectotype: ZMB (lost), Paralectotype, ZMB 4621 (1, dry, lost). Type locality: Coromandel, India.

Local synonymy: *Rhina anclyostoma*—Filewood, 1973:10 (PNG); Kailola, 1987: 26 (Sepik River mouth); White *et al.*, 2018: 200, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.476 (dried jaws), no collection data.

Remarks: First recorded from PNG by Filewood (1973), presumably based KFRS E.476; KFRS E.476 not present in elasmobranch cards in the collection; the only KFRS specimen of this species was a dried jaw KFRS E.262 (Sepik River mouth, Jul. 1966) which was listed as found in 2000 but was not found in the current study; possibly previously found without a registration number and allocated a new number unnecessarily, but cannot be confirmed. Recorded from coastal fisheries catches and as bycatch from the Gulf of Papua prawn trawl fisher during recent surveys.

Genus *Rhynchobatus* Müller & Henle, 1837a
Wedgefishes

Rhynchobatus Müller & Henle, 1837a:116. Type species: *Rhinobatus laevis* Bloch & Schneider, 1801, by monotypy.

Rhynchobatus australiae Whitley, 1939b
Whitespotted Wedgefish

Rhynchobatus djiddensis australiae Whitley, 1939b: 245, Fig. 14. Holotype: AMS IA.4959. Type locality: off Manning River mouth, New South Wales, Australia.

Local synonymy: *Rhynchobatus djiddensis*—Filewood, 1973 (in part): 10 (PNG). *Rhynchobatus australiae*—White *et al.*, 2018: 202, figs (PNG).

PNG voucher material: None.

Remarks: Filewood (1973) recorded only *Rhynchobatus djiddensis* from PNG; included in synonymy of this species and *R. palpebratus* by default but may not have encountered both species at that time. Recently verified from coastal fisheries catches from the Milne Bay Province and from underwater photographs taken off Kavieng by D. Amon (Lissenung Island).

Rhynchobatus palpebratus Compagno & Last, 2008
Eyebrow Wedgefish

Rhynchobatus palpebratus Compagno & Last, 2008: 230, Figs. 1–3. Holotype: CSIRO H 3384-01. Type locality: northwest of Wessel Islands, Northern Territory.

Local synonymy: *Rhynchobatus djiddensis*—Munro, 1967: 18, pl. 2, fig. 23 (New Guinea); Filewood, 1973 (in part): 10 (PNG). *Rhynchobatus palpebratus*—Last *et al*., 2016g: 74 (PNG); White *et al.*, 2018: 204, figs (PNG).

PNG voucher material: (18 spec.) CSIRO H 7805-01, female 580 mm TL, Freshwater Bay, Gulf of Papua, 8°8'19.2" S, 145°57'4.2" E, 14–18 m depth, 14 Jun. 2014; CSIRO H 7820-02, female 650 mm TL, south of Deception Bay, Gulf of Papua, 8°7' S, 144°29' E, 18 m depth, 1 Dec. 2014; CSIRO H 7823-01, juvenile male 830 mm TL, south of Deception Bay, Gulf of Papua, 8°8' S, 144°27' E, 17–18 m depth, 9 Dec. 2014; CSIRO H 7825-01, female 540 mm TL, east of Fly River mouth, Gulf of Papua, 8°37' S, 144°11' E, 17–19 m depth, 13 Dec. 2014; CSIRO H 7828-01, female 490 mm TL, south of Deception Bay, Gulf of Papua, 8°2'33" S, 144°39'21" E, 25–31 m depth, 7 Dec. 2014; CSIRO H 7836-02, juvenile male 470 mm TL, south of Deception Bay, Gulf of Papua, 8°2'31" S, 144°38'46" E, 21–23 m depth, 16 Dec. 2014; CSIRO H 8109-02 (teeth and chondrocranium), adolescent male 990 mm TL, west of Avirara, Gulf of Papua, 8°16' S, 146°10' E, 24–26 m depth, 28 Nov. 2014; CSIRO H 8161-02 (claspers and dried jaws), adult male 1060 mm TL, west of Avirara, Gulf of Papua, 8°20'8" S, 146°11'49" E, 14–16 m depth, 28 Aug. 2015; KFRS E.035, female embryo 121 mm TL, Yule Island, Central Province, Nov. 1962; KFRS E.658, female 780 mm TL, southeast of Vailala, Gulf of Papua, 8°3'7" S, 145°28'43" E, 20–21 m depth, 23 Nov. 2014; KFRS E.660, female 540 mm TL, southwest of Kerema, Gulf of Papua, 8°5'22" S, 145°34'29" E, 19 m depth, 25 Nov. 2014; KFRS E.737, juvenile male 810 mm TL, east of Fly River mouth, Gulf of Papua, 8°42' S, 144°3' E, 19–22 m depth, 3 Dec. 2014; KFRS E.738, juvenile male 490 mm TL, east of Fly River mouth, Gulf of Papua, 8°43' S, 144°7' E, 18–20 m depth, 3 Dec. 2014; KFRS E.740, juvenile male 640 mm TL, south of Deception Bay, Gulf of Papua, 8°0' S, 144°42' E, 18–21 m depth, 4 Dec. 2014; KFRS E.748, female 430 mm TL, Gulf of Papua, 18–21 m depth, 4 Dec. 2014; KFRS E.757, female 530 mm TL, south of Deception Bay, Gulf of Papua, 8°4'23" S, 144°38'55" E, 22–31 m depth, 14 Dec. 2014; KFRS E.761, female 560 mm TL, south of Deception Bay, Gulf of Papua, 8°3'22" S, 144°40'17" E, 28–29 m depth, 6 Dec. 2014; KFRS E.764, female 500 mm TL, east of Fly River mouth, Gulf of Papua, 8°18'44" S, 144°20'42" E, 27–30 m depth, 13 Dec. 2014.

Remarks: First recorded from PNG by Munro (1967) as *R. djiddensis*. Filewood (1973) also recorded this species from PNG but the information provided could not distinguish whether referring to this species or *R. australiae* (or both). Common in the coastal fisheries catches and in the bycatch of the Gulf of Papua prawn trawl fishery during recent surveys; caught mainly on soft bottoms where *R. australiae* typically found on sandy areas adjacent to or amongst rocky reef habitat.

Family Rhinobatidae Müller & Henle, 1837
Guitarfishes

Genus *Rhinobatos* Linck, 1790

Rhinobatos Linck, 1790: 32. Type species *Raja Rhinobatos* Linnaeus, 1758; type assumed from tautonymy.

Rhinobatos manai White, Last & Naylor, 2016b
Papuan Guitarfish

Rhinobatos manai White, Last & Naylor, 2016b: 589, Figs 1–6. Holotype: NTUM 11500. Type locality: northwest of Kavieng, New Ireland, Papua New Guinea.

Local synonymy: *Rhinobatos manai* White *et al*., 2016b: 589, Figs 1–6 (Kavieng, New Ireland); White *et al.*, 2018: 206, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11500, adult male 731 mm TL, northwest of Kavieng, New Ireland, 02°30'S, 150°44'E, 191–290 m depth, 7 Sep. 2014.

Remarks: Only known from a single specimen caught during deepwater surveys off New Ireland in 2014; recently described as a new species by White *et al.* (2016b). Endemic to PNG.

Rhinobatos cf. *schegelii*
Enigma Guitarfish

Local synonymy: White *et al.*, 2018: 208, figs (PNG).

PNG voucher material: (1 spec.) NMV A 14200, female 700 mm TL, no locality data [presumably southeastern PNG], 1890.

Remarks: Only known from a single specimen labelled as collected by Andrew Goldie in 1890. Andrew Goldie collected in southeastern PNG only, from the Gulf of Papua to Milne Bay Province. Very similar to *Rhinobatos schegelii* from Taiwan and Japan and possibly conspecific. Some doubts exist over the locality of this specimen as PNG given that in the tropical Indo-West Pacific region, members of this genus typically occur in deeper shelf or upper slope waters, at a depth unlikely to have been fished in PNG in the 1890s. Additional specimens are required to confirm the validity of this species in PNG waters.

Family Glaucostegidae Last, Séret & Naylor 2016c
Giant Guitarfishes

Genus *Glaucostegus* Bonaparte, 1846
Giant Guitarfishes

Glaucostegus Bonaparte, 1846: 14. Type species *Rhina cemiculus* Geoffrey St. Hilaire, 1827, by subsequent designation by Jordan & Evermann, 1896: 61 as *Rhina rhinobatos* Shaw = *Rhina cemiculus* Geoffroy.

Glaucostegus typus (Anonymous [Bennett], 1830)
Giant Guitarfish

Rhinobatus typus Anonymous [Bennett], 1830: 694. Syntypes: BMNH 1852.8.30.17 (dry). Type locality: Sumatra, Indonesia (syntype); India.

Local synonymy: *Rhinobatus armatus*—Peters, 1877: 853 (Bougainville). *Rhinobatus granulatus*—Macleay, 1883a: 598 (New Guinea); Ogilby, 1888: 15 (southeastern New Guinea); Fowler, 1941: 315 (Port Moresby). *Rhinobatus thouini*—Macleay, 1883b: 280 (Hood Bay). *Rhinobatos granulatus*—Fowler, 1928: 24 (Port Moresby); Kailola, 1987: 27 (Yule Island). *Rhinobatos thouiniana*—Fowler, 1934: 386 (Fife Bay and Hood Bay). *Rhinobatos batillum*—Whitley, 1940: 168 (Fife Bay and Port Moresby); Munro, 1958: 113 (Kapa Kapa); Munro, 1967: 19, pl. 2, fig. 24 (New Guinea); Haines, 1979a: 6 (Purari Delta). *Rhinobatos armatus*—Filewood, 1973: 10 (PNG); Kailola, 1987: 27 (Port Romilly). *Glaucosteus typus*—White *et al.*, 2018: 210, figs (PNG).

PNG voucher material: (16 spec.) KFRS E.066, female 337 mm TL, Kairuku, Yule Island, Central Province, Jun. 1965; KFRS E.500, juvenile male 397 mm TL, Arehara, Punari River, 20 Apr. 1975; KFRS E.501, juvenile male 407 mm TL, no collection data [possibly = KFRS E.417, one of two males from Western Province]; KFRS E.612, female 410 mm TL, KFRS E.613, juvenile male 410 mm TL, KFRS E.614, juvenile male 380 mm TL, Mullins Harbour, Milne Bay Province, 10°29’2” S, 149°55’40.5” E, <0.2 m depth, 11 Mar. 2016; KFRS E.725, juvenile male 410 mm TL, Freshwater Bay, Gulf of Papua, 8°6’57.6” S, 145°52’1.2” E, 14–17 m depth, 8 Jun. 2014; NMV A 18753 (3 spec.), females 361–375 mm TL, between Port Moresby and KapaKapa, Central Province, May 1881; USNM 40022 (3 spec.), females 280–365 mm TL, Port Moresby; USNM 218541, female 520 mm TL, USNM 218601, juvenile male 340 mm TL, west end of Parama Island, Western Province, 9°1’11” S, 143°21’36” E, 15 Dec. 1975; ZMB 9737, juvenile female 437 mm TL, Bougainville, [probably mid-1875, SMS *Gazelle* survey].

Remarks: First recorded by Peters (1877) as *Rhinobatus armatus* from Bougainville, presumably based on

ZMB 9737, collected during an expedition on the SMS *Gazelle*. Commonly caught by coastal fishers in the Western and Milne Bay Provinces, and probably elsewhere. Dried fins and whole specimens observed during recent surveys.

Order Rajiformes

Family Arhynchobatidae Fowler, 1934
Softnose Skates

Genus *Notoraja* Ishiyama, 1958
Velvet Skates

Notoraja (subgenus of *Breviraja*) Ishiyama, 1958: 322. Type species: *Raja tobitukai* Hiyama, 1940, by original designation (also monotypic).

Notoraja sereti White, Last & Mana, 2017d
Papuan Velvet Skate

Notoraja sereti White, Last & Mana, 2017d: 220, Figs 1–8. Holotype: NTUM 10067. Type locality: southeast of Sek Island, Madang, Papua New Guinea.

Local synonymy: *Insentiraja subtilispinosa*—Fricke *et al.*, 2014: 15 (Madang Province). *Notoraja sereti* White *et al.*, 2017d: 219, Figs 1–8 (Madang Province)—White *et al.*, 2018: 216, figs (PNG).

PNG voucher material: (3 spec.) NTUM 10042 (paratype), female 458 mm TL, east of Sek Island, Madang, 5°06' S, 145°53' E, 960–980 m depth, 30 Nov. 2012; NTUM 10067 (holotype), female 459 mm TL, southeast of Sek Island, Madang, 5°07' S, 145°53' E, 980 m depth, 2 Dec. 2012; NTUM 10330 (paratype), adolescent male 363 mm TL, Astrolabe Bay, Madang, 5°21' S, 145°53' E, 800–820 m depth, 14 Dec. 2012.

Remarks: Only recently discovered based on 3 specimens caught during deepwater surveys off Madang Province in 2012; recently described as a new species by White *et al.* (2017d). Endemic to PNG.

Family Rajidae Blainville, 1816
Hardnose Skates

Genus *Dipturus* Rafinesque, 1810a
Hardnosed Skates

Dipturus Rafinesque, 1810a: 16. Type species: *Raja batis* Linnaeus, 1758, by monotypy.

Dipturus sp. 1
Luanah's Skate

Local synonymy: White *et al.*, 2018: 218, figs (PNG).

PNG voucher material: (5 spec.) ASIZ P0080720, female 249 mm TL, Astrolabe Bay, Madang Province, 5°20.13' S, 145°49.68' E, 608–610 m depth, 5 Oct. 2010; ASIZ P0080721, juvenile male 314 mm TL, off Madang, 5°01.27' S, 145°50.21' E, 502–529 m depth, 2 Oct. 2010; NTUM 10327, juvenile male 342 mm TL, east of Cape Croisiles, Madang Province, 4°52' S, 145°50' E, 610–620 m depth, 16 Dec. 2012; NTUM 10328, female 350 mm TL, north of Taviltae, Madang Province, 4°29' S, 145°31' E, 500–510 m depth, 17 Dec. 2012; NTUM 10329, juvenile male 342 mm TL, Dogreto Bay, West Sepik, 3°18' S, 143°02' E, 440 m depth, 22 Dec. 2012.

Remarks: First record of this family and genus from PNG. A new species currently being described based on this material.

Family Anacanthobatidae von Bonde & Swart, 1923
Legskates

Genus *Sinobatis* Hulley, 1973
Legskates

Sinobatis (subgenus of *Anacanthobatis*) Hulley, 1973: 153. Type species: *Anacanthobatis borneensis*, Chan, 1965, by original designation (also monotypic).

Sinobatis sp. 1
Papuan Legskate

Local synonymy: White *et al.*, 2018: 220, figs (PNG).

PNG voucher material: (1 spec.) NTUM 10326, female 196 mm TL, northwest of Maman Island, Madang Province, 4°0' S, 144°54' E, 800–860 m depth, 24 Dec. 2012.

Remarks: First record of this family and genus from PNG. Morphologically similar to *Sinobatis bulbicauda* Last & Séret, 2008 from northwestern Australia but differs in some characters and in structure of NADH2 gene (G. Naylor, unpubl. data); adult specimens required to confirm identity.

Order Torpediniformes

Family Torpedinidae Bonaparte, 1838
Torpedo rays

Genus *Tetronarce* Gill, 1862
Pelagic torpedoes

Tetronarce Gill, 1862. Type species: *Torpedo occidentalis* Storer, 1843, by monotypy and original designation.

Tetronarce formosa (Haas & Ebert, 2006)
Taiwanese Torpedo

Torpedo formosa Haas & Ebert, 2006: 2, Figs 1–3. Holotype: CAS 223471. Type locality: Ta-Shi Fish Market, northeastern Taiwan.

Local synonymy: White *et al.*, 2018: 214, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11498, juvenile male 258 mm TL, northwest of Kavieng, New Ireland, 2°27' S, 150°40' E, 335–340 m depth, 28 Aug. 2014.

Remarks: First record of this family and genus in PNG; first record of this species outside of Taiwanese waters, possibly suggests a much broader range than previously thought.

Family Narcinidae Gill, 1862
Numbfishes

Genus *Narcinops* Whitley, 1940
Longtail Numbfishes

Narcinops Whitley, 1940: 164. Type species *Narcine tasmaniensis* Richardson, 1841; by original designation.

Narcinops cf. *nelsoni*

Plain Numbfish

Local synonymy: *Narcine nelsoni*—Fricke *et al.*, 2014: 14 (Madang Province); White *et al.*, 2018: 212, figs (PNG).

PNG voucher material: (5 spec.) ASIZ P0073800, 138 mm TL, off Lae, Huon Gulf, 7°28.181' S, 147°31.394' E, 280–302 m depth, 23 Aug. 2010; NTUM 10324 (2 spec.), female 90 mm TL, juvenile male 113 mm TL, west of Kairiru Island, East Sepik Province, 3°20' S, 143°28' E, 325–345 m depth, 19 Dec. 2012;

Remarks: First recorded from PNG by Fricke *et al.* (2014) from Madang Province. Similar to the West Australian Numbfish *Narcinops lasti* (Carvalho & Séret, 2002) but differs in some morphological characters; molecular data supports this species being different from *N. lasti* from northwestern Australia (G. Naylor, unpubl. data), but no eastern Australian *N. nelsoni* are included in the current analyses. The species is close to *N. nelsoni* but seems to differ in having slightly larger eyes.

Order Myliobatiformes

Family Hexatrygonidae Heemstra & Smith, 1980

Sixgill Stingray

Genus *Hexatrygon* Heemstra & Smith, 1980

Sixgill Stingray

Hexatrygon Heemstra & Smith, 1980: 1. Type by original designation (also monotypic).

Hexatrygon bickelli Heemstra & Smith, 1980

Sixgill Stingray

Hexatrygon bickelli Heemstra & Smith, 1980: 6, figs 1–13, 15. Holotype: SAIAB [formerly RUSI] 997. Type locality: washed up on beach at Port Elizabeth, South Africa, southwestern Indian Ocean.

Local synonymy: White *et al.*, 2018: 222, figs (PNG).

PNG voucher specimens: None.

Remarks: Based on a specimen caught, but not retained, off New Hanover during deepwater surveys off New Ireland (stations CP 3651, 2°37.809' S, 150°02.904' E, 840–865 m depth, 27 Aug. 2010).

Family Gymnuridae Fowler, 1934

Butterfly Rays

Genus *Gymnura* van Hasselt, 1823

Butterfly Rays

Gymnura van Hasselt, 1823: 316. Type species: *Raja micrura* Bloch & Schneider, 1801, by monotypy.

Gymnura australis (Ramsay & Ogilby, 1886)

Australian Butterfly Ray

Pteroplatea australis Ramsay & Ogilby, 1886: 575. Holotype: AMS A.9357. Type locality: Cape Hawke, New South Wales, Australia.

Local synonymy: *Gymnura tentaculata*—Filewood, 1973:11 (PNG). *Aetoplatea tentaculata*—Kailola, 1987: 31 (Gulf of Papua; Yule Island). *Gymnura australis*—Last & Stevens, 2009: 464 (New Guinea); Yokota *et al.*, 2016: 513 (New Guinea); White *et al.*, 2018: 224, figs (PNG).

PNG voucher material: (28 spec.) CSIRO H 7617-01, female 230 mm DW, southwest of Kerema, Gulf of Papua, 8°3'3.6" S, 145°37'52.2" E, 16 m depth, 15 Jun. 2014; CSIRO H 7806-01, adult male 430 mm DW, Freshwater Bay, Gulf of Papua, 8°9' S, 145°58'37.8" E, 18 m depth, 15 Jun. 2014; CSIRO H 7815-01, female 580 mm DW, south of Deception Bay, Gulf of Papua, 8°0'58" S, 144°36'7" E, 22 m depth, 29 Nov. 2014; CSIRO H 7816-01, female 260 mm DW, south of Deception Bay, Gulf of Papua, 8°1'54" S, 144°38'58" E, 22–23 m depth, 30 Nov. 2014; CSIRO H 8005-01, juvenile male 280 mm DW, Freshwater Bay, Gulf of Papua, 8°12'37.38" S, 146°3'31.32" E, 15–18 m depth, 24 Aug. 2015; CSIRO H 8008-01, juvenile male 270 mm DW, Freshwater Bay, Gulf of Papua, 8°9'43.44" S, 145°59'30.12" E, 18–19 m depth, 25 Aug. 2015; KFRS E.286 (3 spec.), embryos 92–94 mm DW, Yule Island, Central Province, Mar. 1966; KFRS E.381, adult male 369 mm TL, Yule Island, Central Province, 1 Dec. 1969; KFRS E.532 (4 spec.), 3 females 261–342 mm DW, 1 juvenile male 247 mm DW, no collection data [possibly part of lot KFRS E.110, 5 spec., Yule Island, Jun. 1964]; KFRS E.603, juvenile male 240 mm DW, west of Avirara, Gulf of Papua, 8°19'30.24" S, 146°12'2.16" E, 10–11 m depth, 26 Aug. 2015; KFRS E.632, adult male 360 mm DW, west of Avirara, Gulf of Papua, 8°18'57.54" S, 146°12'4.2" E, 8–10 m depth, 26 Aug. 2015; KFRS E.635, 440 mm DW, west of Avirara, Gulf of Papua, 8°19'44.22" S, 146°13'39.18" E, 10–11 m depth, 25 Aug. 2015; KFRS E.636, female 320 mm DW, west of Avirara, Gulf of Papua, 8°17'34.08" S, 146°10'34.92" E, 10–12 m depth, 25 Aug. 2015; KFRS E.673, juvenile male 260 mm DW, south of Deception Bay, Gulf of Papua, 8°1'54" S, 144°38'58" E, 22–23 m depth, 30 Nov. 2014; KFRS E.691, female 250 mm DW, south of Kerema, Gulf of Papua, 8°2'55.8" S, 145°44'57" E, 14–16 m depth, 19 Jun. 2014; KFRS E.708, juvenile male 280 mm DW, Freshwater Bay, Gulf of Papua, 8°5'24.6" S, 145°51'7.2" E, 13 m depth, 22 Jun. 2014; KFRS E.726, juvenile male 250 mm DW, south of Kerema, Gulf of Papua, 8°5'11.4" S, 145°47'10.8" E, 20 m depth, 11 Jun. 2014; KFRS E.727, male 320 mm DW, south of Kerema, Gulf of Papua, 8°4'33" S, 145°47'18" E, 16–19 m depth, 7 Jun. 2014; KFRS E.735, adult male 460 mm DW, Freshwater Bay, Gulf of Papua, 8°9' S, 145°58'37.8" E, 18 m depth, 15 Jun. 2014; KFRS E.805, KFRS E.806, KFRS E.807, late-term embryos from 720 mm DW female, southwest of Kerema, Gulf of Papua, 8°5'28" S, 145°37'31" E, 18–23 m depth, 7 Apr. 2015; KFRS E.808, female 609 mm DW, Freshwater Bay, Gulf of Papua, 8°9'0" S, 145°58'37.8" E, 18 m depth, 15 Jun. 2014.

Remarks: First recorded from PNG by Filewood (1973) as *Gymnura tentaculata*. Very common in the bycatch of the Gulf of Papua prawn trawl fishery; also observed in catches of the trap fishery at Wewak on the north coast during recent surveys.

Family Dasyatidae Jordan, 1888

Stingrays

Genus *Hemitrygon* Müller & Henle, 1838a

Stingrays

Hemitrygon Müller & Henle, 1838a: 90. Type species *Trygon bennettii* Müller & Henle, 1841, by subsequent monotypy (by Müller & Henle, 1841).

Hemitrygon longicauda (Last & White, 2013)

Merauke Stingray

Dasyatis longicauda Last & White, 2013: 3, Figs 1–6. Holotype: MZB 21462. Type locality: Merauke, West Papua, Indonesia.

Local synonymy: *Dasyatis fluviorum*—Kailola, 1987: 28 (Port Romilly; Yule Island; Bootless Bay; Orangerie Bay; south of Ramu River mouth). *Dasyatis longicauda*—Last *et al.*, 2016a: 557 (southern New Guinea). *Hemitrygon longicauda*—White *et al.*, 2018: 226, figs (PNG).

PNG voucher material: (15 spec.) CSIRO H 7798-01, female 140 mm DW, CSIRO H 7798-02, juvenile male 160 mm DW, CSIRO H 7798-03, juvenile male 140 mm DW, west of Oriomo River, Western Province, 9°4'26.04" S, 143°8'31.9" E, <1 m depth, 25 Oct. 2014; CSIRO H 8020-01, female 250 mm DW, east of Fly River mouth, Gulf of Papua, 8°34'22" S, 144°4'31" E, 9 m depth, 1 Apr. 2015; CSIRO H 8022-01, female 220 mm DW, CSIRO H 8022-02, female 290 mm DW, CSIRO H 8022-03, female 310 mm DW, east of Fly River mouth, Gulf of Papua, 8°13'6" S, 144°7'24" E, 7–10 m depth, 2 Apr. 2015; CSIRO H 8024-01, female 240 mm DW, southwest of Deception Bay, Gulf of Papua, 8°6'39" S, 144°25'45" E, 12–15 m depth, 3 Apr. 2015; KFRS E.645, juvenile male 120 mm DW, east of Fly River mouth, Gulf of Papua, 8°13'6" S, 144°7'24" E, 7–10 m depth, 2 Apr. 2015; KFRS E.685, female 140 mm DW, KFRS E.686, female 140 mm DW, KFRS E.687, female 160 mm DW, KFRS E.688, female 140 mm DW, west of Oriomo River, Western Province, 9°4'26.04" S, 143°8'31.9" E, <1 m depth, 25 Oct. 2014; KFRS E.798, female 258 mm DW, KFRS E.799, juvenile male 137 mm DW, no collection data [no label but probably previously registered specimens collected in the 1960s or 1970s].

Remarks: First recorded in PNG by Kailola (1987), but specimens in the KFRS collection identified as *Dasyatis fluviorum*, now lost, which are most likely this species were collected in the mid-1960s. Common in very shallow waters in the Western, Gulf and Central Provinces. Previously placed in the genus *Dasyatis.*

Genus *Himantura* Müller & Henle, 1837

Whiprays

Himantura Müller & Henle, 1837b: 400. Type species: *Raja sephen uarnak* Forsskål, 1775, by subsequent designation.

Himantura australis Last, White & Naylor, 2016f

Australian Whipray

Himantura australis Last, White & Naylor, 2016f: 378, Figs 1–5. Holotype: CSIRO H 7798-04. Type locality: west of Oriomo River, Western Province.

Local synonymy: *Trygon uarnak*—Peters, 1877: 853 (Carteret Islands). *Himantura uarnak*—Munro, 1958: 114 (Carteret Islands); Munro, 1967: 15 (New Guinea); Filewood, 1973: 12 (PNG); Haines, 1979a: 6 (Purari Delta); Haines, 1979b: 94 (Purari Delta); Taniuchi & Shimizu, 1991: 5 (Oriomo River estuary). *Himantura fava*—Kailola, 1987: 28 (Yule Island). *Himantura australis* Last *et al.*, 2016f: 378, Figs. 1–5 (Western Province); Last *et al.*, 2016a: 561 (New Guinea); White *et al.*, 2018: 228, figs (PNG).

PNG voucher material: (11 spec.) CAS SU 28205, juvenile male 277 mm DW, Rabaul, East New Britain, 28 Apr. 1929; CSIRO H 8100-03, juvenile male 237 mm DW, Motupore Island, Bootless Bay, 9°31'19" S, 147°17'2" E, <1 m depth, 15 Sept. 2016; CSIRO H 7798-04 (holotype), juvenile male 415 mm DW, west of Oriomo River, Western Province, 9°04.43' S, 143°08.53' E, 25 Oct. 2014; CSIRO H 7839-01 (paratype), juvenile male 333 mm DW, Daru fish market, Western Province, 9°03.91' S, 143°12.59' E, 21 Oct. 2014; CSIRO H 7840-01 (paratype), juvenile male 241 mm DW, fishing camp near Daru, Western Province, 9°02.26' S, 143°11.49' E, 24 Oct. 2014; KFRS E.123, female 292 mm DW, Yule Island, Central Province, Aug. 1964; KFRS E.615, juvenile male 240 mm DW, Mullins Harbour, 10°26'50" S, 145°56'27" E, < 1 m depth, 11 Mar. 2016; KFRS E.768 (paratype, field accession 230247), late-term embryo 300 mm DW (from female 1400 mm DW), south of Purari River, Gulf of Papua, 7°55'S, 145°09' E, 16–18 m depth, 1 Dec. 2014; KFRS E.769 (paratype, field accession 220349), juvenile female 350 mm DW, Katatai, Western Province, 9°01.25' S, 143°20.51' E, 23 Oct. 2014; KFRS E.770 (paratype, field accession 220420), juvenile female 286 mm DW, fishing camp near Daru, Western Province, 9°02.26' S, 143°11.49' E, 24 Oct. 2014; USNM 218545, juvenile male 280 mm DW, east side of Daru wharf, Daru, 10 Oct. 1975.

Remarks: First recorded from PNG by Peters (1877) as *Trygon uarnak*. Previously thought to be conspecific with the wider ranging *Himantura uarnak* (Gmelin, 1789) but recently separated as a distinct species found in northern Australia and New Guinea; records from northern PNG and the outer islands, e.g. the Carteret Islands, need to be validated as being this species. Common in bycatch of the Gulf of Papua prawn trawl fishery and coastal seine net fisheries during recent surveys.

Himantura leoparda Manjaji-Matsumoto & Last, 2008
Leopard Whipray

Himantura leoparda Manjaji-Matsumoto & Last, 2008: 294, Figs 1–4. Holotype: CSIRO H 2903-01. Type locality: northwest of Weipa, Gulf of Carpentaria, Queensland, Australia.

Local synonymy: *Himantura leoparda*—Manjaji-Matsumoto & Last, 2008: 293 (PNG); White *et al.*, 2018: 230, figs (PNG).

PNG voucher material: (7 spec.) CSIRO H 7614-12, juvenile male 380 mm DW, south of Kerema, Gulf of Papua, 8°3'1.2" S, 145°45'7.2" E, 16–17 m depth, 20 Jun. 2014; CSIRO H 7807-02, juvenile male 420 mm DW, southwest of Kerema, Gulf of Papua, 8°2'22.2" S, 145°37'13.2" E, 15–16 m depth, 15 Jun. 2014; CSIRO H 7809-01, juvenile male 400 mm DW, south of Kerema, Gulf of Papua, 8°1'53.4" S, 145°43'0.6" E, 16–18 m depth, 18 Jun. 2014; CSIRO H 7820-01, juvenile male 400 mm DW, south of Deception Bay, Gulf of Papua, 8°7' S, 144°29' E, 18 m depth, 1 Dec. 2014; KFRS E.643, juvenile male 450 mm DW, east of Fly River mouth, Gulf of Papua, 8°34'22" S, 144°4'31" E, 9 m depth, 1 Apr. 2015; KFRS E.722, juvenile male 400 mm DW, south of Kerema, Gulf of Papua, 8°2'9.6" S, 145°42'29.4" E, 14–15 m depth, 17 Jun. 2014; KFRS E.747, female 470 mm DW, east of Fly River mouth, Gulf of Papua, 8°36' S, 144°1' E, 11–15 m depth, 11 Dec. 2014.

Remarks: First listed as from PNG in Manjaji-Matsumoto & Last (2008); first confirmed record based on specimens. Common in bycatch of the Gulf of Papua prawn trawl fishery.

Genus *Maculabatis* Last, Naylor & Manjaji-Matsumoto, 2016b
Whiprays

Maculabatis Last, Naylor & Manjaji-Matsumoto, 2016b: 361. Type species *Trygon gerrardi* Gray, 1851, by original designation.

Maculabatis astra (Last, Manjaji-Matsumoto & Pogonoski, 2008)
Blackspotted Whipray

Himantura astra Last, Manjaji-Matsumoto & Pogonoski, 2008: 304, Figs 1–5. Holotype: CSIRO H 3377-01. Type locality: Gulf of Carpentaria, Queensland, Australia.

Local synonymy: *Himantura uarnak*—Munro, 1967: pl. 2, fig. 18 (New Guinea). *Himantura gerrardi*—Kailola, 1987: 28 (Darapap; near New Britain; Port Romilly; Yule Island; Orangerie Bay). *Himantura astra*—Last & Stevens, 2009: 441 (New Guinea). *Maculabatis astra*—Last *et al.*, 2016a: 575 (southern New Guinea); White *et al.*, 2018: 232, figs (PNG).

PNG voucher material: (25 spec.) CSIRO H 7617-02, female 240 mm DW, southwest of Kerema, Gulf of Papua, 8°3'3.6" S, 145°37'52.2" E, 16 m depth, 15 Jun. 2014; CSIRO H 7808-01, juvenile male 170 mm DW, south of Kerema, Gulf of Papua, 8°2'3.6" S, 145°44'12" E, 16 m depth, 17 Jun. 2014; CSIRO H 7814-02, juvenile male 260 mm DW, south of Deception Bay, Gulf of Papua, 7°58'52" S, 144°40'7" E, 22–23 m depth, 28 Nov. 2014; CSIRO H 7822-01, female 330 mm DW, east of Fly River mouth, Gulf of Papua, 8°40' S, 144°6' E, 14–18 m depth, 5 Dec. 2014; CSIRO H 7826-01, juvenile male 440 mm DW, south of Deception Bay, Gulf of Papua, 8°3'22" S, 144°40'17" E, 28–29 m depth, 6 Dec. 2014; KFRS E.528, female 238 mm DW, KFRS E.529, female 205 mm DW, KFRS E.530, female 238 mm DW, KFRS E.531, juvenile male 221 mm DW, no collection data; KFRS E.602, female 220 mm DW, west of Avirara, Gulf of Papua, 8°19'44.22" S, 146°13'39.18" E, 10–11 m depth, 25 Aug. 2015; KFRS E.649, female 260 mm DW, south of Deception Bay, Gulf of Papua, 7°58'52" S, 144°40'7" E, 22–23 m depth, 28 Nov. 2014; KFRS E.650, juvenile male 220 mm DW, south of Deception Bay, Gulf of Papua, 8°1'59" S, 144°35'28" E, 21 m depth, 29 Nov. 2014; KFRS E.661, juvenile male 190 mm DW, KFRS E.662, female 190 mm DW, south of Kerema, Gulf of Papua, 8°5'43" S, 145°40'6" E, 23–24 m depth, 26

Nov. 2014; KFRS E.663, juvenile male 210 mm DW, KFRS E.664, female 150 mm DW, Freshwater Bay, Gulf of Papua, 8°10’18” S, 145°58’37” E, 24–25 m depth, 27 Nov. 2014; KFRS E.666, female 520 mm DW, Freshwater Bay, Gulf of Papua, 8°5’56” S, 145°56’17” E, 23–25 m depth, 27 Nov. 2014; KFRS E.728, 200 mm DW, south of Kerema, Gulf of Papua, 8°4’33” S, 145°47’18” E, 16–19 m depth, 7 Jun. 2014; KFRS E.732, female 220 mm DW, KFRS E.733, female 370 mm DW, Freshwater Bay, Gulf of Papua, 8°6’45.6” S, 145°50’49.8” E, 21–22 m depth, 13 Jun. 2014; KFRS E.744, female 250 mm DW, south of Kerema, Gulf of Papua, 8°4’ S, 145°43’ E, 16–20 m depth, 30 Nov. 2014; KFRS E.746, female 480 mm DW, east of Fly River mouth, Gulf of Papua, 8°41’ S, 144°8’ E, 20 m depth, 2 Dec. 2014; KFRS E.762, juvenile male 190 mm DW, south of Deception Bay, Gulf of Papua, 8°2’31” S, 144°38’46” E, 21–23 m depth, 16 Dec. 2014; KFRS E.782, female 163 mm DW, no collection data; USNM 218546, juvenile male 270 mm DW, east side of Daru wharf, Daru, Western Province, 10 Oct. 1975.

Remarks: First recorded from PNG by Munro (1967) as a misidentification of *Himantura uarnak*. Very similar to *Maculabatis toshi* (see below) but differs in subtle morphological characters and colour pattern (spotted vs. mostly plain); but colour varies greatly across a large number of individuals so it is possible these species are in fact conspecific. Very common in the bycatch of the Gulf of Papua prawn trawl fishery. Previously placed in the genus *Himantura.*

Maculabatis toshi (Whitley, 1939b)

Brown Whipray

Himantura toshi Whitley, 1939b: 258. Holotype: AMS IA.39. Type locality: Clarence River Estuary, New South Wales, Australia.

Local synonymy: *Himantura* (?) *gerrardi*—Filewood, 1973: 12 (PNG). *Maculabatis toshi*—Last *et al.*, 2016a: 581 (southern PNG); White *et al.*, 2018: 234, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.683 (head only), female 820 mm DW, Daru fish market, Daru, Western Province, 23 Oct. 2014.

Remarks: First recorded from PNG by Filewood (1973) as *Himantura* (?) *gerrardi*; the characters provided in Filewood’s key includes “colour pattern of few pale-centred spots far apart, sometimes also irregular white splashes, tail usually strikingly banded” which matches the adult colour pattern of *M. toshi*. Possibly conspecific with *M. astra.* Appears to be more restricted to inshore muddy areas. Previously placed in the genus *Himantura.*

Genus *Megatrygon* Last, Naylor & Manjaji-Matsumoto, 2016b

Smalleye Stingray

Megatrygon Last, Naylor & Manjaji-Matsumoto, 2016b: 356. Type species *Trygon microps* Annandale, 1908, by original designation (also monotypic).

Megatrygon microps (Annandale, 1908)

Smalleye Stingray

Trygon microps Annandale, 1908: 393, pl. 27. Holotype: ZSI F2410/1. Type locality: Bay of Bengal, off Chittagong coast, India.

Local synonymy: White *et al.*, 2018: 236, figs (PNG).

PNG voucher material: None.

Remarks: First confirmed record of this species in PNG. Several large individuals observed in the bycatch of the prawn trawl fishery operating in the Gulf of Papua during recent surveys. Previously placed in the genus *Dasyatis.*

Genus *Neotrygon* Castelnau 1873
Maskrays

Neotrygon Castelnau, 1873: 122. Type species *Raya trigonoides* Castelnau, 1873; type by monotypy.

Neotrygon annotata (Last, 1987)
Plain Maskray

Dasyatis annotatus Last, 1987: 57, Fig. 1. Holotype: CSIRO T 449. Type locality: Northwest Shelf, Western Australia.

Local synonymy: *Neotrygon* (?) *uhlenbergi*—Filewood, 1973: 13 (PNG); *Himantura uylenbergi*—Kailola, 1987: 29 (west of Daru to Orangerie Bay). *Neotrygon annotata*—Last *et al.*, 2016a: 584 (southern New Guinea); White *et al.*, 2018: 238, figs (PNG).

PNG voucher material: (34 spec.) CSIRO H 7817-01, adult male 240 mm DW, south of Deception Bay, Gulf of Papua, 8°0'27" S, 144°35'37" E, 21–22 m depth, 30 Nov. 2014; CSIRO H 7821-01, adult male 260 mm DW, CSIRO H 7821-02, adult male 280 mm DW, Gulf of Papua, 4 Dec. 2014; CSIRO H 7836-01, female 260 mm DW, south of Deception Bay, Gulf of Papua, 8°2'31" S, 144°38'46" E, 21–23 m depth, 16 Dec. 2014; CSIRO H 7837-01, female 190 mm DW, south of Deception Bay, Gulf of Papua, 8°2' S, 144°40'19" E, 24 m depth, 16 Dec. 2014; KFRS E.114, adult male 244 mm DW, Orangerie Bay, Jun. 1964; KFRS E.252A, juvenile male 142 mm DW, Eastern Papua, 1 Mar. 1966; KFRS E.281, juvenile male 103 mm DW, Gulf of Papua, Mar. 1966; KFRS E.347A, juvenile male 101 mm DW, KFRS E.347B, male 128 mm DW, KFRS E.347C, female 150 mm DW, Gulf of Papua, Jan. 1969; KFRS E.466, adult male 201 mm DW, Freshwater Bay, Gulf of Papua, 8°15' S, 146°0' E, 3 Nov. 1973; KFRS E.478A (1 of 3 specimens remaining), adult male 233 mm DW, close to Daru-Bobo passage, Daru, Western Province, 30 Apr. 1974; KFRS E.654, adult male 260 mm DW, KFRS E.655, female 290 mm DW, KFRS E.656, female 200 mm DW, south of Deception Bay, Gulf of Papua, 8°0'27" S, 144°35'37" E, 21–22 m depth, 30 Nov. 2014; KFRS E.676, juvenile male 140 mm DW, southwest of Deception Bay, Gulf of Papua, 8°8'20" S, 144°24'53" E, 17–20 m depth, 11 Dec. 2014; KFRS E.741, adult male 270 mm DW, southwest of Deception Bay, Gulf of Papua, 8°16' S, 144°20' E, 20–22 m depth, 6 Dec. 2014; KFRS E.745, female 250 mm DW, east of Fly River mouth, Gulf of Papua, 8°41' S, 144°8' E, 20 m depth, 2 Dec. 2014; KFRS E.750, female 290 mm DW, south of Deception Bay, Gulf of Papua, 8°7' S, 144°29' E, 18 m depth, 1 Dec. 2014; KFRS E.752, adult male 230 mm DW, south of Deception Bay, Gulf of Papua, 8°2'8" S, 144°38'33" E, 22 m depth, 14 Dec. 2014; KFRS E.754, adult male 200 mm DW, south of Deception Bay, Gulf of Papua, 8°2'16" S, 144°38'26" E, 22–23 m depth, 15 Dec. 2014; KFRS E.758, adult male 250 mm DW, south of Deception Bay, Gulf of Papua, 8°2'19" S, 144°37'12" E, 22–24 m depth, 15 Dec. 2014; KFRS E.763, female 120 mm DW, southwest of Deception Bay, Gulf of Papua, 8°11'55" S, 144°27'41" E, 27–28 m depth, 6 Dec. 2014; KFRS E.784, adult male 210 mm DW, KFRS E.785, female 222 mm DW, KFRS E.786, female 207 mm DW, KFRS E.787, adolescent male 219 mm DW, KFRS E.788, adolescent male 197 mm DW, KFRS E.789, female 178 mm DW, adolescent male 202 mm DW, KFRS E.790, female 235 mm DW, KFRS E.791, adolescent male 191 mm DW, KFRS E.792, juvenile male 170 mm DW, KFRS E.797, all without labels, allocated new registration numbers April 2017, no collection data.

Remarks: First recorded from PNG by Filewood (1973) as *Neotrygon* (?) *uhlenbergi*; the specific names comes from *Dasybatis uylenburgi* Giltay, 1933, recently considered a junior synonym of *Brevitrygon walga* (Müller & Henle, 1841). Common in the bycatch of the Gulf of Papua prawn trawl fishery. Probably restricted to the southernmost regions of Papua, from Orangerie Bay westwards.

Neotrygon australiae Last, White & Serét, 2016h
Australian Bluespotted Maskray

Neotrygon australiae Last, White & Serét, 2016h: 542, Figs 5b, 6b, 7b, 9. Holotype: CSIRO H 7016-01. Type locality: southwest of Weipa, Gulf of Carpentaria, Queensland, Australia.

Local synonymy: *Neotrygon kuhldi*—Filewood, 1973 (in part): 13 (PNG; misspelling of *kuhlii*). *Neotrygon* *australiae* Last *et al.*, 2016h: 542 (Daru, Western Province); Last *et al.*, 2016a: 585 (New Guinea); White *et al.*, 2018: 240, figs (PNG).

PNG voucher material: (2 spec.) KFRS E.680 (field code 220341), adult male 301 mm DW, KFRS E.681 (field code 220342), adult male 301 mm DW, Daru fish market, Western Province, 9°03.91′ S, 143°12.59′ E, 22 Oct. 2014.

Remarks: Previously considered to be conspecific with *Neotrygon kuhlii* (Müller & Henle, 1841) but recently described as a new species from northern Australia (not east coast), Papua New Guinea and eastern Indonesia. Filewood (1973) lists *N. kuhldi* but with variable characters (such as colour) so probably includes multiple species. Possibly restricted to parts of the Western and Gulf provinces with *N.* cf. *trigonoides* replacing it further eastwards; ranges for the species in the *kuhlii* complex in PNG needs investigating.

Neotrygon picta Last & White, 2008

Speckled Maskray

Neotrygon picta Last & White, 2008: 316, Figs 1–4. Holotype: CSIRO H 5771-01. Type locality: east pf Rockhampton, Queensland, Australia.

Local synonymy: *Neotrygon kuhldi*—Filewood, 1973 (in part): 13 (PNG; misspelling of *kuhlii*). *Neotrygon picta*—Last & Stevens, 2009: 455 (possibly southern New Guinea); Last *et al.*, 2016a: 591 (southern PNG); White *et al.*, 2018: 242, figs (PNG).

PNG voucher material: (3 spec.) CSIRO H 7799-01, female 200 mm DW, west of Oriomo River, Western Province, 9°4’26.04” S, 143°8’31.9” E, 26 Oct. 2014; KFRS E.759, juvenile male 140 mm DW, east of Fly River mouth, Gulf of Papua, 8°37’59” S, 144°5′23” E, 8–9 m depth, 13 Dec. 2014; USNM 218544, female 260 mm DW, east side of Daru wharf, Daru, Western Province, 10 Oct. 1975.

Remarks: Filewood (1973) lists *N. kuhldi* from PNG and mentions two forms, i.e. “either pale with speckles and usually few blue spots, or marbled with dark speckles (possibly 2 species)”; the marbled species likely refers to this species.

Neotrygon cf. *trigonoides*

Papuan Maskray

Local synonymy: *Trygon kuhlii*—Peters, 1877: 853 (New Ireland); Ogilby, 1888: 19 (southeastern New Guinea). *Dasyatis kuhlii* –Fowler, 1934: 386 (Port Moresby); Fowler, 1941: 427 (New Guinea); Gochfeld, 1996: 43 (southern New Ireland); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93, fig. (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay). *Amphotistius kuhlii*—Munro, 1958: 114 (New Guinea); Kailola, 1987: 28 (PNG). *Amphotistius kuhli*—Munro, 1967: 15, pl. 2, fig. 20 (New Guinea). *Neotrygon kuhldi*—Filewood, 1973 (in part): 13 (PNG; misspelling of *kuhlii*). *Neotrygon* cf. *trigonoides*—White *et al.*, 2018: 244, figs (PNG).

PNG voucher material: (9 spec.) CSIRO C 850, juvenile male 151 mm DW, Haidana Island, Port Moresby, 24 Jul. 1948; CSIRO H 8100-01, female 275 mm DW, Motupure Island, Bootless Bay, Port Moresby, 9°31’19” S, 147°17’2” E, <1 m depth, 15 Sep. 2016; KFRS E.057, female 137 mm DW, Laing Island, Madang, 16 Jul. 1965; KFRS E.491, juvenile male 149 mm DW, Pot Island, Siassi, Umboi Islands, Morobe Province, 27 Jan. 1968; KFRS E.526 (2 spec.), adolescent male 243 mm DW, adult male 281 mm DW, no collection data; KFRS E.793, female 219 mm DW, KFRS E.794, female 260 mm DW, no labels, new registration number allocated April 2017, no data; ZMB 9721, adolescent male 261 mm DW, Carteret Islands, New Ireland, 1874–1875 [probably mid-1875, SMS *Gazelle* survey].

Remarks: First recorded from PNG by Peters (1877) from Carteret Islands, New Ireland (ZMB 9721). Colour pattern and morphology aligns most closely to *Neotrygon trigonoides* (Castelnau, 1873) but probably not conspecific; specimens from throughout PNG are required to determine whether more than one species is involved.

Neotrygon cf. *westpapuensis*
West Papuan Maskray

Local synonymy: White *et al.*, 2018: 246, figs (PNG). Some of the records listed for *N.* cf. *trigoinoides* above may refer to this species.

PNG voucher material: CSIRO unregistered, adult male 37 cm DW, CSIRO unregistered, female 22 cm DW, Wewak, East Sepik Province, September 2017.

Remarks: Colour and genetic differences distinguish this species from *N. australiae* and *N.* cf. *trigonoides*. Base don coloration and CO1 sequence data, this species is most similar to and possibly conspecific with the recently described *N. westpapuensis* Borsa, Arlyza, Hoareau & Shen, 2017 from Cenderwasih Bay. Unfortunately this description was based almost entirely on DNA with no useful field characters provided which prevented detailed comparisons without examing specimens.

Genus *Pastinachus* Rüppell, 1829
Cowtail Rays

Pastinachus Rüppell, 1829: 51. Type species *Raja sephen* Forsskål 1775, by subsequent designation (Garman 1913: 375).

Pastinachus ater (Macleay, 1883a)
Broad Cowtail Ray

Taeniura atra Macleay, 1883a: 598. Holotype: AMS I.9762. Type locality: Port Moresby district, Papua New Guinea.

Local synonymy: *Trygon sephen*—Peters, 1877: 853 (New Britain); Ogilby, 1888: 20 (southeastern New Guinea); Günther, 1910: 495 (New Britain); Duncker & Mohr, 1934: 84 (Seeadler Harbour, Manus). *Taeniura atra* Macleay, 1883a: 598 (Port Moresby district). *Dasyatis sephen*—Fowler, 1934: 386 (Port Moresby); Munro, 1958: 114 (New Guinea); Munro, 1967: 15, pl. 2, fig. 19 (New Guinea); Haines, 1979a: 6 (Purari Delta); Haines, 1979b: 94 (Purari Delta). *Pastinachus dephen* - Filewood, 1973: 12 (PNG, misspelling of *sephen*). *Pastinachus atrus*—Last & Stevens, 2009: 456 (New Guinea). *Pastinachus sephen*—Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay). *Pastinachus ater*—White *et al.*, 2018: 34, figs (PNG).

PNG voucher material: (4 spec.) AMS I.9762 (holotype), female 404 mm DW, Port Moresby, 9°29' S, 147°05' E, 1883; KFRS E.043 (dried jaws), adult male, Rabaul, East New Britain, 1964; KFRS E.044 (dried jaws), adult male, Kairuku, Yule Island, Central Province, 18 Jan. 1965; USNM 218543, juvenile male 410 mm DW, Parama Island, Western Province, 15 Dec. 1975.

Remarks: First recorded from PNG by Peters (1877) as *Trygon sephen* from New Britain. Macleay (1883a) described as a new species, *Taeniura atra*, based on a specimen collected from off Port Moresby; subsequently included in the synonymy of *Pastinachus sephen* but recently resurrected as a valid species. Caught occasionally by prawn trawlers and probably also by coastal fishers.

Genus *Pateobatis* Last, Naylor & Manjaji-Matsumoto, 2016b
Whiprays

Genus *Pateobatis* Last, Naylor & Manjaji-Matsumoto, 2016b: 362. Type species *Trygon uarnacoides* Bleeker, 1852, by original designation.

Pateobatis fai (Jordan & Seale, 1906)
Pink Whipray

Himantura fai Jordan & Seale, 1906: 184, Fig. 2. Holotype: USNM 51712. Type locality: Apia, Upolu Island, Samoa.

Local synonymy: White *et al.*, 2018: 250, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.689, west of Oriomo River, Western Province, 9°4'26.04" S, 143°8'31.9" E, 26 Oct. 2014.

Remarks: Previously placed in the genus *Himantura.*

Pateobatis hortlei (Last, Manjaji-Matsumoto & Kailola, 2006)

Hortle's Whipray

Himantura hortlei Last, Manjaji-Matsumoto & Kailola, 2006: 22, Figs 1–7. Holotype: CSIRO H 5155-01. Type locality: Minajerwi River estuary, West Papua, Indonesia.

Local synonymy: *Himantura nasuta* - Filewood, 1973: 12 (PNG). *"Himantura nasuta*"—Kailola, 1987: 29 (Pai'ia Inlet, Gulf of Papua). *Himantura hortlei*—Last *et al.*, 2006 (possibly PNG). *Pateobatis hortlei*—Last *et al.*, 2016a: 601 (PNG); White *et al.*, 2018: 252, figs (PNG).

PNG voucher specimens: (17 spec.) CSIRO H 7615-01, female 280 mm DW, south of Kerema, Gulf of Papua, 8°2'55.2" S, 145°43'30" E, 17 m depth, 20 Jun. 2014; CSIRO H 7616-01, juvenile male 220 mm DW, south of Kerema, Gulf of Papua, 8°1'26.4" S, 145°44'1.2" E, 14–15 m depth, 17 Jun. 2014; CSIRO H 7802-01, male 370 mm DW, south of Kerema, Gulf of Papua, 8°5'11.4" S, 145°47'10.8" E, 20 m depth, 11 Jun. 2014; CSIRO H 7814-02, juvenile male 250 mm DW, CSIRO H 7814-03, juvenile male 290 mm DW, south of Deception Bay, Gulf of Papua, 7°58'52" S, 144°40'7" E, 22–23 m depth, 28 Nov. 2014; CSIRO H 8020-02, juvenile male 160 mm DW, east of Fly River mouth, Gulf of Papua, 8°34'22" S, 144°4'31" E, 9 m depth, 1 Apr. 2015; CSIRO H 8021-01, female 410 mm DW, east of Fly River mouth, Gulf of Papua, 8°39'21" S, 144°8'46" E, 11–17 m depth, 1 Apr. 2015; CSIRO H 8025-01, juvenile male 240 mm DW, south of Deception Bay, Gulf of Papua, 8°6'39" S, 144°25'45" E, 12–15 m depth, 5 Apr. 2015; KFRS E.642, female 300 mm DW, east of Fly River mouth, Gulf of Papua, 8°34'22" S, 144°4'31" E, 9 m depth, 1 Apr. 2015; KFRS E.646, juvenile male 290 mm DW, KFRS E.647, juvenile male 290 mm DW, KFRS E.648, juvenile male 250 mm DW, south of Deception Bay, Gulf of Papua, 7°58'52" S, 144°40'7" E, 22–23 m depth, 28 Nov. 2014; KFRS E.657, juvenile male 250 mm DW, south of Deception Bay, Gulf of Papua, 8°0'27" S, 144°35'37" E, 21–22 m depth, 30 Nov. 2014; KFRS E.677, juvenile male 250 mm DW, KFRS E.678, juvenile male 260 mm DW, south of Deception Bay, Gulf of Papua, 8°9'6" S, 144°26'25" E, 20–24 m depth, 5 Dec. 2014; KFRS E.734, juvenile male 230 mm DW, south of Kerema, Gulf of Papua, 8°2'22.2" S, 145°37'13.2" E, 15–16 m depth, 15 Jun. 2014; KFRS E.749, juvenile male 250 mm DW, south of Deception Bay, Gulf of Papua, 8°7'0" S, 144°29' E, 18 m depth, 1 Dec. 2014.

Remarks: First recorded from PNG by Filewood (1973) as *Himantura nasuta*. An unregistered specimen collected from West Papua in 1954–55 examined by the senior author during a visit to the RMNH collection in Leiden, Netherlands, had a handwritten label which read:

Himantura nasuta **nov**
L.W. Filewood det. July 1968
(The second known specimen!)

One of the destroyed KFRS specimens, E.292, collected from Pai'ia Inlet in July 1967 had the comment 'holotype' on the collection card, presumably the first specimen recorded for this species. Thus, Filewood appears to have intended to describe this species as new and call it *Himantura nasuta*, but no formal description was ever published. Common in the bycatch of the Gulf of Papua prawn trawl fishery. One specimen observed in the bycatch of the trap fishery in Wewak on the north coast, suggesting a wider distribution around mainland New Guinea. Previously placed in the genus *Himantura.*

Pateobatis jenkinsii (Annandale, 1909)

Jenkins' Whipray

Trygon jenkinsii Annandale, 1909: 28, Figs 4, 4a. Holotype: ZSI F2473/1 (dried skin and jaws). Type locality: off Ganjam Coast, India.

Local synonymy: *Pateobatis jenkinsii*—Last *et al.*, 2016a: 602 (New Guinea); White *et al.*, 2018: 254, figs (PNG).

PNG voucher material: None.

Remarks: Underwater photograph taken by Bob Halstead the first confirmation of this species in PNG. Previously placed in the genus *Himantura.*

Genus *Pteroplatytrygon* Fowler, 1910

Pelagic Stingray

Pteroplatytrygon Fowler, 1910: 474. *Trygon violacea* Bonaparte 1832, by original designation (also monotypic).

Pteroplatytrygon violacea (Bonaparte, 1832)

Pelagic Stingray

Trygon violacea Bonaparte, 1832: fasc. 1, punt. 6, Pl. 155. Syntypes: ANSP 385, ANSP 386, ?NMW 91239 (dry). Type locality: Italy, western Mediterranean Sea.

Local synonymy: White *et al.*, 2018: 256, figs (PNG).

PNG voucher material: None.

Remarks: Based on data and images collected from observers on tuna longline vessels.

Genus *Taeniura* Müller & Henle, 1837a

Fantail Rays

Taeniura Müller & Henle, 1837a: 117. Type species: *Trygon ornatus* Gray, 1830, by monotypy, synonym of *T. lymma.*

Taeniura lessoni Last, White & Naylor, 2016f

Oceania Fantail Ray

Taeniura lessoni Last, White & Naylor, 2016f: 387, Figs 8–12. Holotype: CSIRO H 7724-01. Type locality: Landoro Passage off Uepi Island, Marovo Lagoon, Solomon Islands.

Local synonymy: *Trygon halgani* Lesson, 1829: 100 (Port Praslin [=Lambom], New Ireland). *Taeniura lymma*—Müller & Henle, 1841: 171 (New Ireland); Günther, 1910 (in part): 495 (New Ireland); Munro, 1958: 114 (New Ireland). *Taeniura lessoni*—Last *et al.*, 2016f: 392 (Kokopo, East New Britain; Kavieng, New Ireland); Last *et al.*, 2016a: 605 (PNG); White *et al.*, 2018: 258, figs (PNG).

PNG voucher material: (2 spec.) MNHN A 7994 (2 spec.), female 147 mm DW, male 148 mm DW, Port Praslin, New Ireland, 1822-1825.

Remarks: First recorded from PNG by Lesson (1829) who described it as a new species, *Trygon halgani*, based on material from Waigeo, Indonesia and Port Praslin [=Lambom], New Ireland. Since the illustration and description in Lesson (1829) highlights the blue stripes on the tail, which *T. lessoni* lacks, *T. halgani* is considered a junior synonym of *T. lymma*. Underwater photographs from Kavieng district (New Ireland) and off Kokopo (East New Britain) confirm this species from PNG.

Taeniura lymma (Forsskål, 1775)

Bluespotted Fantail Ray

Raja lymma Forsskål, 1775: 17. No types known. Type locality: Al-Luhayya, Yemen, Red Sea.

Local synonymy: *Taeniura lymma*—Ogilby, 1888: 20 (southeastern New Guinea); Günther, 1910 (in part): 495 (Manus Island); Fowler, 1928: 25 (Port Moresby); Fowler, 1941: 401 (Port Moresby); Munro, 1958: 114 (New Guinea); Munro, 1967: 14, pl. 2, fig. 16 (New Guinea); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93, fig. (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay); Fricke *et al.*, 2014: 15, fig. 3 (Madang). *Taeniura lymna*—Macleay, 1883a: 598 (New Guinea); Gochfeld, 1996: 43 (southern New Ireland); White *et al.*, 2018: 260, figs (PNG). *Discobatis marginipinnis* Miklouho-Maclay & Macleay, 1886: 676, Figs 7–15 (Manus Island). *Taeniura lymara*—Filewood, 1973: 12 (PNG).

PNG voucher material: (13 spec.) BMNH 1974.5.25.1, female 245 mm DW, north end of Buriwadi Island, Trobriand Islands, 9 May 1970; CSIRO H 8100-02, male 151 mm DW, Motupore Island, Bootless Bay, 9°31'19" S, 147°17'2" E, <1 m depth, 15 Sept. 2016; FMNH 120119, northwest tip of Motupore Island, Bootless Bay, 9°31'19" S, 147°17'4" E, 21 Jan. 2011; FMNH 120120, female ~200 mm DW, fringing reef around Lion Island, Bootless Bay, 9°32'12" S, 147°16'28" E, 21 Jan. 2011; KFRS E.527, juvenile male 148 mm TL, no collection data; KFRS E.611, juvenile male 140 mm DW, Bubuleta, Milne Bay, 10°21'9" S, 150°38'37" E, <1 m, 10 Mar. 2016; KFRS E.617, female 180 mm DW, Bubuleta, Milne Bay, 10°20'30" S, 150°39' E, <1 m, 11 Mar. 2016; NTUM 10296, adult male 233 mm DW, Madang market, 12 Dec. 2012; USNM 39975, juvenile male 210 mm DW, Port Moresby, ; USNM 206313, female 280 mm DW, north coast off Towai Pt, Kiriwina Island (Labai), Trobriand Islands, 8 Jun. 1970; USNM 206314, juvenile male 215 mm DW, Kuia Island, Trobriand Islands, Jun. 1970; USNM 222553, embryo 34 mm DW, USNM 222620, female 130 mm DW, east side of Daru wharf, Daru, Western Province, 10 Oct. 1975.

Remarks: First recorded from PNG by Ogilby (1888) from 'southeastern New Guinea'. Previously thought to be widespread, but recent description of *T. lessoni* (see above) suggests *T. lymma* is replaced by *T. lessoni* in at least New Ireland and New Britain; more research required to determine whether these two species co-occur in any areas.

Genus *Taeniurops* Garman, 1913

Round Fantail Rays

Taeniurops Garman, 1913: 399. Type species: *Taeniura meyeni* Müller & Henle, 1841, by subsequent designation.

Taeniurops meyeni (Müller & Henle, 1841)

Blotched Fantail Ray

Taeniura meyeni Müller & Henle, 1841: 172, pl. 55. Syntypes: MNHN 0000-2428, ZMB 4660. Type locality: Mauritius, Mascarenes, southwestern Indian Ocean.

Local synonymy: *Taeniura melanospilos*—Kailola, 1987: 29 (Bougainville). *Taeniura meyeni*—Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago). *Taeniurops meyeni*—White *et al.*, 2018: 262, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Kailola (1987) as *Taeniura melanospilos* from Bougainville, based on a destroyed specimen, KFRS E.388 (tail only) collected from Bougainville in 1969. Observed underwater, and verified from photographs, recently from Kavieng district of New Ireland.

Genus *Urogymnus* Müller & Henle, 1837b

Giant Whiprays

Urogymnus Müller & Henle, 1837b: 434. Type species *Raja asperrima* Bloch & Schneider, 1801, by being a replacement name.

Urogymnus acanthobothrium Last, White & Kyne, 2016e
Mumburarr Whipray

Urogymnus acanthobothrium Last, White & Kyne, 2016e: 163, Figs 1–7. Holotype: WAM P. 34488-001. Type locality: West Arm of Cambridge Gulf, Western Australia.

Local synonymy: *Urogymnus acanthobothrium*—Last *et al.*, 2016e: 163, Figs 1–7 (Gulf of Papua); Last *et al.*, 2016a: 613 (southern PNG); White *et al.*, 2018: 264, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Last *et al.* (2016e) based on records from observers on prawn trawl vessels in the Gulf of Papua. Holotype and several other specimens were caught in rivers in Northern Australia, and it is thus likely to inhabit the riverine areas in the Gulf and Western Provinces of PNG.

Urogymnus asperrimus (Bloch & Schneider, 1801)
Porcupine Ray

Raja asperrima Bloch & Schneider, 1801: 367. Holotype: ZMB 7836 (dry skin, partial specimen). Type locality: Mumbai, India.

Local synonymy: *Urogymnus africanus*—Filewood, 1973: 12 (PNG). *Urogymnus asperrimus*—Kailola, 1987: 29 (New Britain; Yule Island; Bougainville); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); White *et al.*, 2018: 266, figs (PNG).

PNG voucher material: (2 spec.) KFRS E.265 (dried jaws), adult male, New Britain, Sep. 1966; KFRS E.682, juvenile male 520 mm DW, Katatai, Western Province, 9°1'15.13" S, 143°20'30.6" E, 23 Oct. 2014.

Remarks: First recorded from PNG by Filewood (1973) as *Urogymnus africanus*, a junior synonym of *U. asperrimus*. Destroyed KFRS specimens were collected from Yule Island, Hall Sound and Bougainville.

Urogymnus dalyensis (Last & Manjaji-Matsumoto, 2008)
Freshwater Whipray

Himantura dalyensis Last & Manjaji-Matsumoto 2008: 284, Figs 1, 2a, 3–4. Holotype: CSIRO H 2503-01. Type locality: Pentecost River (Bindola Creek junction), Western Australia.

Local synonymy: *Himantura* sp.—Compagno & Roberts, 1982: 337, fig. 12 (Lake Murray). *Himantura* sp. undet.—Kailola, 1987: 29 (Fly River). *Himantura chaophraya*—Monkolprasit & Roberts, 1990: 207 (Fly River basin; in this species group); Last & Stevens, 1994: 399 (Fly River Basin). *Himantura dalyensis*—Last & Manjaji-Matsumoto, 2008: 289 (possibly Fly River Basin); Last & Stevens, 2009: 442 (possibly Fly River Basin). *Urogymnus dalyensis*—Last *et al.*, 2016a: 615 (Fly River Basin); White *et al.*, 2018: 268, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Compagno & Roberts (1982), as *Himantura* sp., from the Fly River basin. Fly River record (photograph only) was considered as belonging to the *Himantura chaophraya* (=*Urogymnus polylepis* (Bleeker, 1852)) species group. Specimens needed to confirm it is conspecific with this species. Possibly widespread in the extensive river systems of PNG. Previously placed in the genus *Himantura.*

Urogymnus granulatus (Macleay, 1883a)
Mangrove Whipray

Trygon granulata Macleay, 1883a: 598. Holotype: AMS I.9763. Type locality: Port Moresby, Papua New Guinea.

Local synonymy: *Trygon granulata* Macleay, 1883a: 598 (Port Moresby); *Himantura granulata*—Whitley, 1928:

211 (Port Moresby); Munro, 1958: 114 (Port Moresby); Munro, 1967: 15, pl. 1, fig. 17 (New Guinea); Kailola, 1987: 28 (Port Moresby); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Last & Stevens, 2009: 445 (New Guinea). *Dasyatis granulatus*—Fowler, 1934: 386 (Port Moresby). *Himantura granulatus*—Berra *et al.*, 1975: 319 (Laloki River system). *Urogymnus granulatus*—White *et al.*, 2018: 270, figs (PNG).

PNG voucher material: (3 spec.) AMS I.9763, juvenile female ~330 mm DW, Port Moresby, 1883; KFRS E.616, female 310 mm DW, Mullins Harbour, 10°30'48" S, 149°56'8" E, <1 m depth, 11 Mar. 2016, NMV A 14199, juvenile male 310 mm DW, probably southern PNG, 1880.

Remarks: First recorded from PNG by Macleay (1883a) who described the species based on a specimen collected from off Port Moresby. Common in shallow, coastal mangrove areas.

Family Urolophidae Müller & Henle, 1841
Stingarees

Genus *Spinilophus* Yearsley & Last, 2016
New Ireland Stingaree

Spinilophus Yearsley & Last, 2016: 36. Type species *Urolophus armatus* Müller & Henle, 1841, by original designation (also monotypic).

Spinilophus armatus (Valenciennes, 1841)
New Ireland Stingaree

Urolophus armatus Valenciennes *in* Müller & Henle, 1841: 174. Holotype: MNHN 0000-2331. Type locality: New Ireland.

Local synonymy: *Urolophus armatus* Müller & Henle, 1841: 174 (New Ireland)—Garman, 1913: 407 (New Ireland); Fowler, 1941: 443 (New Ireland); Munro, 1958: 114 (New Ireland); Munro, 1967: 13 (New Guinea); Kailola, 1987: 32 (New Ireland). *Droliphus armatus*—Filewood, 1973:11 (New Britain; misspelling). *Spinilophus armatus*—Last *et al.*, 2016i: 678 (New Ireland); White *et al.*, 2018: 272, figs (PNG).

PNG voucher material: (1 spec.) MNHN 0000-2331, juvenile male 170 mm TL, New Ireland, [1820–1830s].

Remarks: Only known from a single specimen taken off New Ireland in the 1800s by Lesson and Garnot. Previously placed in the genus *Urolophus*. Only known from a single specimen collected by Lesson and Garnot off New Ireland prior to 1841. Assuming the collector and New Ireland location for the specimen are correct, it is most likely the specimen was collected from Port Praslin, just north of Tawanlik Cape and south of Lambom; this site was visited by during the *Voyage autour du monde* onboard the *Coquille* on the 12 August 1823. However, this species was never mentioned in the fish descriptions by Lesson following the voyage.

Genus *Urolophus* Müller & Henle, 1837a
Stingarees

Urolophus Müller & Henle, 1837a: 117. Type species: *Raja cruciata* Lacepède, 1804, by original designation.

Urolophus bucculentus Macleay, 1884
Sandyback Stingaree

Urolophus bucculentus Macleay, 1884: 172. Holotype: AMS B.642. Type locality: outside Port Jackson, New South Wales, Australia.

Local synonymy: White *et al.*, 2018: 274, figs (PNG).

PNG voucher material: (1 spec.) NTUM 11499, 210 mm DW (tail missing), west of New Hanover, New Ireland, 2°25' S, 149°54' E, 269–279 m depth, 6 Sep. 2014.

Remarks: First record of this species from PNG and first record outside of Australia; previously considered to be endemic to southeastern Australia. Identification verified with molecular data (G. Naylor, unpubl. data).

Family Aetobatidae Agassiz, 1858

Pelagic Eagle Rays

Genus *Aetobatus* Blainville, 1816

Pelagic Eagle Rays

Aetobatus Blainville, 1816: 112. Type species: usually given as *Raja narinari* Euphrasen, 1790, by subsequent designation by Müller & Henle (1837 or 1838).

Aetobatus ocellatus (Kuhl, 1823)

Spotted Eagle Ray

Myliobatus ocellatus Kuhl *in* van Hasselt, 1823: 316. No original types designated; Neotype: MZB 18225; neotype designation by White *et al*. (2010). Type locality: Java, Indonesia.

Local synonymy: *Myliobatis punctatus* Miklouho-Maclay & Macleay, 1886: 675, pl. 46 (figs 1-6) (Hermit Islands; Admiralty Islands). *Aetobatus punctatus*—Munro, 1958: 114 (Haidana Island; Waterfall Bay, New Britain). *Aetobatus ocellatus*—Munro, 1967: 16, pl. 2, fig. 21 (New Guinea); White *et al.*, 2018: 280, figs (PNG). *Aetobatus narinari*—Filewood, 1973: 14 (PNG); Haines, 1979a: 6 (Purari Delta); Allen *et al.*, 2003: 112 (Milne Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay). *Aetobatis narinari*—Gochfeld, 1996: 43 (southern New Ireland).

PNG voucher material: (3 spec.) FMNH 120552, female ~350 mm DW, boat jetty at Tahira, Bootless Bay, Port Moresby, 9°30'26" S, 147°17'12" E, 18 Jan. 2011; KFRS E.684, male 880 mm DW, Daru fish market, Daru, Western Province, 23 Oct. 2014; NMV A 15817 (stuffed), 545 mm DW, no collection data.

Remarks: First recorded from PNG by Miklouho-Maclay & Macleay (1886) who described it as a new species, *Myliobatis punctatus*, from the Hermit and Admiralty Islands. Previously considered synonymise with *Aetobatus narinari* (Euphrasen, 1790) but the latter species restricted to the Atlantic Ocean. Previously placed in the family Myliobatidae.

Family Myliobatidae Bonaparte, 1838

Eagle Rays

Genus *Aetomylaeus* Garman, 1908

Smoothtail Eagle Rays

Aetomylaeus Garman, 1908: 252. Type species: *Myliobatis maculatus* Gray, 1834, by original designation; misspelled *Aetomyleus* in Zoological Record for 1908.

Aetomylaeus caeruleofasciatus White, Last & Baje, 2015b

Bluebanded Eagle Ray

Aetomylaeus caeruleofasciatus White, Last & Baje, 2015b: 5, Figs 2–5a, 6–7, 11–12. Holotype: CSIRO H 6629-01. Type locality: bay south of Eagle Point anchorage, Western Australia.

Local synonymy: *Aetomylaeus nichofii*—Filewood, 1973: 14 (PNG); Kailola, 1987: 33 (Gulf of Papua; Orangerie Bay). *Aetomylaeus caeruleofasciatus* White *et al.*, 2015b: 94, fig. 12 (Gulf of Papua); White & Last, 2016a: 710 (southern New Guinea); White *et al.*, 2018: 276, figs (PNG).

PNG voucher material: (26 spec.) CSIRO H 7813-01, female 370 mm DW, Freshwater Bay, Gulf of Papua, 8°10'18" S, 145°58'37" E, 24–25 m depth, 27 Nov. 2014; CSIRO H 7818-01, juvenile male 200 mm DW, Freshwater Bay, Gulf of Papua, 8°11' S, 146°1' E, 19–20 m depth, 29 Nov. 2014; CSIRO H 7831-01, juvenile male 200 mm DW, south of Deception Bay, Gulf of Papua, 8°10'56" S, 144°27'8" E, 25–31 m depth, 10 Dec. 2014; CSIRO H 8004-01, juvenile male 250 mm DW, Freshwater Bay, Gulf of Papua, 8°9'31.62" S, 146°1'38.04" E, 16 m depth, 24 Aug. 2015; CSIRO H 8012-03, juvenile male 340 mm DW, west of Avirara, Gulf of Papua, 8°20'38.46" S, 146°12'46.38" E, 12–14 m depth, 27 Aug. 2015; CSIRO H 8015-01, female 240 mm DW, Freshwater Bay, Gulf of Papua, 8°9'9" S, 145°59'50.46" E, 15–16 m depth, 29 Aug. 2015; CSIRO H 8018-01, female 270 mm DW, Freshwater Bay, Gulf of Papua, 8°9'9.78" S, 145°59'2.22" E, 15–18 m depth, 30 Aug. 2015; CSIRO H 8027-01, juvenile male 260 mm DW, Freshwater Bay, Gulf of Papua, 8°13'5" S, 146°5'23" E, 7–15 m depth, 10 Apr. 2015; CSIRO H 8109-01 (dried tooth plates), adult male 480 mm DW, west of Avirara, Gulf of Papua, 8°16' S, 146°10' E, 24–26 m depth, 28 Nov. 2014; CSIRO H 8150-01 (jaws and claspers), adult male 430 mm DW, south of Kerema, Gulf of Papua, 8°4' S, 145°43' E, 16–20 m depth, 30 Nov. 2014; KFRS E.305 (dried jaws), Orangerie Bay, Jun. 1967; KFRS E.533 (2 spec.), juvenile male 224 mm DW, adolescent male 320 mm DW, no collection data; KFRS E.605, female 260 mm DW, west of Avirara, Gulf of Papua, 8°20'14.52" S, 146°12'31.68" E, 12–14 m depth, 27 Aug. 2015; KFRS E.606, female 240 mm DW, west of Avirara, Gulf of Papua, 8°20'19.8" S, 146°12'30.12" E, 9–10 m depth, 28 Aug. 2015; KFRS E.608, female 260 mm DW, southeast of Kerema, Gulf of Papua, 8°3'58.14" S, 145°46'38.64" E, 15–16 m depth, 30 Aug. 2015; KFRS E.624, adolescent male 370 mm DW, Freshwater Bay, Gulf of Papua, 8°7'33" S, 146°0'24" E, 12–13 m depth, 3 Sep. 2015; KFRS E.644, adult male 480 mm DW, south of Deception Bay, Gulf of Papua, 8°1'53" S, 144°38'21" E, 21–24 m depth, 6 Apr. 2015; KFRS E.652 (paratype, field code 210356), adult male 450 mm DW, southwest of Kerema, Gulf of Papua, 8°5'19" S, 145°36'27" E, 18–19 m depth, 24 Nov. 2014; KFRS E.659 (paratype, field code 210386), adult male 430 mm DW, south of Kerema, Gulf of Papua, 8°6'24" S, 145°40'6" E, 20 m depth, 24 Nov. 2014; KFRS E.701 (paratype, field code 220477), female 220 mm DW, south of Kerema, Gulf of Papua, 8°6'39.6" S, 145°53'57" E, 15–19 m depth, 19 Jun. 2014; KFRS E.724 (paratype, field code 220559), female 230 mm DW, south of Kerema, Gulf of Papua, 8°6'57.6" S, 145°52'1.2" E, 14–17 m depth, 8 Jun. 2014; KFRS E.736 (paratype, field code 220600), female 220 mm DW, south of Kerema, Gulf of Papua, 8°4'22.2" S, 145°46'5.4" E, 18–20 m depth, 12 Jun. 2014; KFRS E.778, female 247 mm DW, KFRS E.779, juvenile male 225 mm DW, KFRS E.780, juvenile male 302 mm DW, no label, new registration number allocated April 2017, no collection data.

Remarks: First recorded from PNG by Filewood (1973). Previously considered conspecific with *Aetomylaeus nichofii* (Bloch & Schneider, 1801), but recently separated as a distinct species. Common in the bycatch of the Gulf of Papua prawn trawl fishery.

Aetomylaeus vespertilio (Bleeker, 1852)

Ornate Eagle Ray

Myliobatis vespertilio Bleeker, 1852: 85. Holotype: RMNH 7460. Type locality: Jakarta, Java, Indonesia.

Local synonymy: *Aetomylaeus maculata*—Filewood, 1973: 14 (PNG). *Aetomylaeus maculatus*—Kailola, 1987: 33 (PNG). *Aetomylaeus vespertilio*—White *et al.*, 2018: 278, figs (PNG).

PNG voucher material: None.

Remarks: First recorded from PNG by Filewood (1973) as *Aetomylaeus maculata*. Colour notes by Filewood (1973), i.e. "rear half of disk with pale "eyespots" and black lines", is distinctive of *A. vespertilio* and not the white spotted *Aetomylaeus maculatus* (Gray, 1834). A dried tail recently recorded from a recent catch at the mouth of the Sepik River in East Sepik Province; an old photograph of Filewood's clearly depicts this species, probably from southern PNG.

Family Rhinopteridae Jordan & Evermann, 1896

Cownose Rays

Genus *Rhinoptera* Cuvier, 1829
Cownose Rays

Rhinoptera Cuvier, 1829: 401. Type species *Myliobatis marginata* Geoffroy St. Hilaire, 1817, by subsequent designation; type designated by Bonaparte, 1838: 6 (of separate), also by Hay, 1902: 321. Appeared first as *Rhenoptera* van Hasselt, 1823: 318 and *Rhinoptera* van Hasselt, 1824: 90, regarded as *nomina nuda*. Cuvier's "Les Rhinoptera Kuhl" evidently sufficient to Latinise; two included species.

Rhinoptera neglecta Ogilby, 1912
Australian Cownose Ray

Rhinoptera neglecta Ogilby, 1912: 32. Holotype: whereabouts unknown. Type locality: Moreton Bay, Queensland, Australia.

Local synonymy: *Rhinoptera javanica*—Filewood, 1973: 14 (PNG); Kailola, 1987: 34 (Ramu River mouth; few other Papuan locations); Last *et al.*, 2016d: 738 (PNG). *Rhinoptera neglecta*—White *et al.*, 2018: 282, figs (PNG).

PNG voucher material: (5 spec.) CSIRO H 8006-01, female 430 mm DW, west of Avirara, Gulf of Papua, 8°19’44.2” S, 146°13’39.18” E, 10–11 m depth, 25 Aug. 2015; CSIRO H 8012-01, juvenile male 500 mm DW, west of Avirara, Gulf of Papua, 8°20’38.6” S, 146°12’46.38” E, 12–14 m depth, 27 Aug. 2015; KFRS E.620, juvenile male 510 mm DW, west of Avirara, Gulf of Papua, 8°18’39” S, 146°11’27” E, 12–14 m depth, 27 Aug. 2015; KFRS E.637, female 370 mm DW, KFRS E.638, juvenile male 510 mm DW, west of Avirara, Gulf of Papua, 8°19’44.2” S, 146°13’39.18” E, 10–11 m depth, 25 Aug. 2015.

Remarks: First recorded in PNG by Filewood (1973). Verified specimens collected during recent surveys of the bycatch of the Gulf of Papua prawn trawl fishery. Common in the coastal fisheries catches in some areas, e.g. Wewak; north coast specimens needed to confirm that they are the same species.

Family Mobulidae Gill, 1893
Devilrays

Genus *Mobula* Rafinesque 1810b
Devilrays

Mobula Rafinesque, 1810b: 48, 61. Type species *Mobula auriculata* Rafinesque, 1810b (= *Raia mobular* Bonnaterre, 1788); by monotypy (also by absolute tautonymy).

Mobula alfredi (Krefft, 1868)
Reef Manta

Deratoptera alfredi Krefft, 1868: 3, 9, Fig. Holotype: AMS I.1731 (stuffed and painted). Type locality: Watson’s Bay at entrance to Sydney Harbour, New South Wales, Australia.

Local synonymy: *Manta birostris*—Munro, 1967 (in part): 15, pl. 2, fig. 18 (New Guinea); Filewood, 1973 (in part): 14 (PNG); Allen, 1998: 67 (Milne Bay); Allen *et al.*, 2003: 112 (Milne Bay); Baine & Harasti, 2007: 93 (Bootless Bay); Hamilton *et al.*, 2009: 73 (northern Bismarck Archipelago); Drew *et al.*, 2012: 5 (Bootless Bay). *Mobula alfredi*—White *et al.*, 2018: 284, figs (PNG).

PNG voucher material: None.

Remarks: Previously considered to be a junior synonym of *M. birostris*. Previously placed in the genus *Manta*, recently found to be a junior synonym of *Mobula* (White *et al.*, 2017b). Occasionally observed by divers throughout PNG; one individual recorded from the bycatch of the Gulf of Papua prawn trawl fishery during recent surveys.

Mobula birostris (Walbaum, 1792)

Giant Manta

Raja birostris Walbaum, 1792: 535. No types known. No locality stated in description.

Local synonymy: *Manta birostris*—Munro, 1967 (in part): 15, pl. 2, fig. 18 (New Guinea); Filewood, 1973 (in part): 14 (PNG). *Mobula birostris*—White *et al.*, 2018: 286, figs (PNG).

PNG voucher material: None.

Remarks: Most records of manta rays in coastal reef areas are of *M. alfredi* (see above). Previously placed in the genus *Manta*, recently found to be a junior synonym of *Mobula* (White *et al.*, 2017b). Occasionally recorded from the bycatch of the purse seine fishery.

Mobula kuhlii (Valenciennes, 1841)

Pygmy Devilray

Cephaloptera kuhlii Valenciennes *in* Müller & Henle, 1841: 185, Pl. 59 (left). Lectotype: MNHN 0000-1596. Type locality: India.

Local synonymy: *Mobula diabolus*—Filewood, 1973: 14 (PNG). *Mobula eregoodootenkee*—Fricke *et al.*, 2014: 15 (Madang). *Mobula kuhlii*—White *et al.*, 2018: 288, figs (PNG).

PNG voucher material: (1 spec.) KFRS E.285 (clasper only), adult male, Fairfax Harbour, Port Moresby, 26 Nov. 1965.

Remarks: First recorded from PNG by Filewood (1973) as *Mobula diabolus*, a name which has been attributed to multiple species of devilrays but is a junior synonym of *M. mobular* (Bonnaterre, 1788). Fricke *et al.* (2014) recorded *M. eregoodootenke* from off Madang; now considered a junior synonym of *M. kuhlii* (White *et al.*, 2017b). Occasionally observed by divers off Kavieng in New Ireland.

Mobula mobular (Bonnaterre 1788)

Giant Devilray

Raia mobular Bonnaterre, 1788: 5. No types known. Type locality: Montredon, near Marseille, France, Mediterranean Sea.

Local synonymy: White *et al.*, 2018: 290, figs (PNG).

PNG voucher material: None.

Remarks: No confirmed PNG specimens recorded, but recorded in the bycatch of the purse seine fishery. It is one of the most abundant devilrays in pelagic fisheries in tropical Western Central Pacific waters, thus its presence in PNG is very likely. Previously thought to be restricted to the Mediterranean Sea, White *et al.* (2017b) found that *M. japanica* (Müller & Henle, 1841) was conspecific, thus a circumglobal species.

Mobula tarapacana (Philippi, 1892)

Chilean Devilray

Cephaloptera tarapacana Philippi, 1892: 8, Pl. 3 (fig. 2). Holotype: whereabouts unknown. Type locality: 12 miles west of Iquique, Tarapacà Province, Chile.

Local synonymy: White *et al.*, 2018: 292, figs (PNG).

PNG voucher material: None.

Remarks: No confirmed PNG specimens recorded, but recorded in the bycatch of the purse seine fishery. It is a distinctive and regularly caught devilray in pelagic fisheries in tropical Western Central Pacific waters, thus its presence in PNG is very likely.

Order Chimaeriformes

Family Chimaeridae Rafinesque, 1815

Shortnose Chimaeras

Genus *Chimaera* Linnaeus, 1758

Chimaeras

Chimaera Linnaeus, 1758: 236. Type *Chimaera monstrosa* Linnaeus, 1758, by Linnaean tautonymy.

Chimaera ogilbyi Waite, 1898
Ogilby's Chimaera

Chimaera ogilbyi Waite, 1898: 56, Pl. 11. Syntypes: AMS I.3732, AMS I.3724, AMS I.3736, AMS I.3737. Type locality: off Sydney, New South Wales, Australia.

Local synonymy: *Hydrolagus ogilbyi*—Fricke *et al.*, 2014: 16 (Madang Province). *Chimaera ogilbyi*—Finucci *et al.*, 2018: 191, fig. 5d (East Sepik Province); White *et al.*, 2018: 294, figs (PNG).

PNG voucher material: (2 spec.) NTUM 10332, juvenile male 362 mm TL, 129 mm body length, NTUM 10333, female 287 mm TL, 109 mm body length, west of Kairiru Island, East Sepik Province, 3°20'S, 143°28'E, 378–495 m depth, 19 Dec. 2012.

Remarks: First recorded from PNG by Fricke *et al.* (2014), based on NTUM 10332 and 10333 collected in 2012; note that these were collected from off the East Sepik Province and not Madang and thus was probably confused with the *Hydrolagus* cf. *mitsukurii* specimen (see below) which was taken from off Madang. Despite some molecular differences, these specimens are morphologically identical with Australian *C. ogilbyi* specimens and were considered conspecific by Finucci *et al.* (2018). Previously placed in the genus *Hydrolagus*.

Genus *Hydrolagus* Gill, 1862

Ghostsharks

Hydrolagus Gill, 1862: 331. Type species *Chimaera colliei* Lay & Bennett, 1839, by monotypy.

Hydrolagus* cf. *mitsukurii
Papuan Ghostshark

Local synonymy: White *et al.*, 2018: 296, figs (PNG).

PNG voucher material: (2 spec.) NTUM 10331, female 281 mm PCL, Astrolabe Bay, Madang, 5°21'S, 145°49'E, 520–575 m depth, 14 Dec. 2012.

Remarks: First record of this species and genus from PNG; generic placement tentative. Similar to *Hydrolagus africanus* (Gilchrist, 1922) and *H. mitsukurii* (Jordan & Snyder, 1904); more specimens needed to confirm its identity.

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APPENDIX 1. List of specimens deposited in the KFRS collection which have since been lost or destroyed and were not located during a thorough search in 2016. Note: some specimens were found in the collection without labels and were subsequently allocated new numbers, but they likely belong to one of the species listed in the supplementary file.

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Taxonomic status of maskrays of the *Neotrygon kuhlii* species complex (Myliobatoidei: Dasyatidae) with the description of three new species from the Indo-West Pacific

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Abstract

The bluespotted maskray, *Neotrygon kuhlii* (Müller & Henle, 1841), once thought to be widely distributed in the Indo-West Pacific, consists of a complex of several species and the type series consists of multiple species; its nomenclature is discussed. A lectotype and paralectotype are designated and the species rediagnosed based on the types and a fresh specimen from Honiara (Solomon Islands), near to the collection locality of the lectotype (Vanikoro, Solomon Islands). Molecular and morphological data provide confirmatory evidence that this maskray is distinct from some other regional forms. Three members of the complex from the Western Pacific identified in earlier studies are confirmed to be new species; *Neotrygon australiae* sp. nov. (Australia, New Guinea and eastern Indonesia), *N. caeruleopunctata* sp. nov. (Indian Ocean), and *N. orientale* sp. nov. (North-West Pacific). These species differ from each other and *N. kuhlii* in their adult size, anterior angle of the disc, number and distribution of blue spots on the dorsal disc, and other more subtle morphometric and meristic characters. Another largely plain-coloured *Neotrygon*, also currently misidentified as *N. kuhlii*, is sympatric with *N. orientale* sp. nov. in the South China Sea and off Taiwan. *Neotrygon varidens* (Garman) is resurrected as the valid name for this ray. A key is provided to species of the genus.

Key words: Dasyatidae; *Neotrygon australiae*; *N. caeruleopunctata*; *N. kuhlii*; *N. orientale*; *N. varidens*; bluespotted maskray; new species; species complex; Indo-West Pacific

Introduction

The genus *Neotrygon* Castelnau was resurrected by Last & White (2008) as a valid generic name for the maskrays, a group of stingrays (Dasyatidae), and this decision has been subsequently supported by new molecular and morphological data (Naylor *et al*., 2012; Puckridge *et al*., 2013). The group contains six valid nominal species: the Australian endemics *N. annotata* (Last, 1987), *N. leylandi* (Last, 1987), *N. ningalooensis* Last, White & Puckridge, 2010, and *N. picta* Last & White, 2008; a South-West Pacific species *N. trigonoides* (Castelnau, 1873); and the wide-ranging Indo-West Pacific *N. kuhlii* (Müller & Henle, 1841) thought to belong to a species complex (Last & Stevens, 2009). Recent phylogenetic studies of the genus have confirmed that *N. kuhlii* does in fact belong to a species complex (Puckridge *et al*., 2013). The *kuhlii*-complex is presently under revision by two of us (PL & WW). Although there is now compelling molecular evidence to recognise more than a single species, members of the complex are very similar morphologically. Identification of species-level taxa has been considered problematic as there is clear evidence of population differentiation within the complex. Nevertheless, some putative species which occur sympatrically support recognition of divergent forms as separate species. Puckridge *et al.* (2013) identified 9 variants (or clades) of the *kuhlii* group in the Indo-West Pacific, and this has been subsequently supported by NADH2 data from the Chondrichthyan Tree of Life project (G. Naylor, pers. comm.). The 9 clades represented material from across the broader region, but did not include specimens from the Solomon Islands, the type locality of *N. kuhlii*.

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Nomenclatural resolution of these species issues has been considered a high priority as members of the *kuhlii*-complex are important food fishes throughout the Indo-Pacific. A multi-authored guide to rays of the world is nearing publication and the authors wished to resolve taxonomic issues in the complex for the purpose of this book. To further confuse matters, the identity of the species-level taxon referable to *N. kuhlii* has not been elucidated. Given that some uncertainties still exist at population levels, the authors focused herein on new taxa that are clearly distinguishable based on both morphological and molecular data. A broader revisionary summary of the group requires more data from the Indian Ocean.

Neotrygon kuhlii (Müller & Henle, 1841) was described on the basis of four syntypes: two preserved specimens from Vanikoro, Solomon Islands (MNHN 0000-2440), one from New Guinea (MNHN A-7931), and a dry specimen from 'Indien' (RMNH 2472). Of the preserved material, the two specimens from the Solomon Islands are largest and largely resemble a specimen figured in Müller & Henle (1841) (Fig. 1). The most intact specimen (tail intact) is designated herein as the lectotype and the second Solomon Islands syntype (tail missing) as a paralectotype. Fish markets at Honiara (Solomon Islands) were visited in 2015 in search of new material. A single specimen of the *kuhlii*-complex was collected that is very similar in coloration and shape to Müller & Henle's Solomon Island types. Sequencing of mitochondrial genes, cytochrome c oxidase I (COI) and ubiquinone (NADH2) of this specimen indicated that it is distinct from all other members of the *kuhlii*-complex, and from all other members of the genus. A rediagnosis of the 'true' *N. kuhlii* is provided with a description of three new species occurring in the Western Pacific. A plain-coloured *Neotrygon*, presently thought to be synonymous with *N. kuhlii*, occurs sympatrically in the North-West Pacific with one of our un-named taxa, and is referrable to *Trygon varidens* Garman, 1885. Characteristics of this species are briefly discussed.

Materials and methods

Characteristics of the disc (including squamation, and tooth row and meristic counts) follow standards used in Manjaji (2004) and Manjaji-Matsumoto & Last (2006). Morphometric methods, including tail fold measurements, follow Last & White (2008). However, there are a couple of specific modifications: the distance from the pectoral insertions to the caudal sting was taken horizontal to minimise errors from distortions of the tail. A new suite of characters were used to characterise the spotted colour pattern in members of this complex. A rectangular section of the disc surface, referred to herein as the 'medial belt' is defined as the central part of the disc bordered laterally by lines joining the posterior edge of each spiracle and the insertions of the pectoral fins, anteriorly by a transverse line joining the posterior edges of each spiracle, and posteriorly by a transverse line joining the pectoral-fin insertions. A count of the number of subcircular blue spots (excluding small black speckle-like markings) in the medial belt and the diameter of the three largest of these was recorded for each measured specimen; spots need to be mostly within the belt to be included in this count. Also, the diameters of the largest spots on the disc were also recorded. Diameters of ocelli are taken as the widest measurement.

Meristics were obtained from radiographs of: one specimen of *N. kuhlii* (CSIRO H 7723-01); the holotype (CSIRO H 7016-01) and 4 paratypes of *N. australiae* sp. nov. (CSIRO CA 3247, CSIRO CA 4307, CSIRO T 693 and CSIRO H 3914-01); the holotype (MZB unreg [ex CSIRO H 7852-03]) and 8 paratypes of *N. caeruleopunctata* sp. nov. (CSIRO H 6124-01, CSIRO H 6124-02, CSIRO H 6202-03, CSIRO H 6202-04, CSIRO H 7851-01, CSIRO H 7851-02, CSIRO H 7852-01 and CSIRO H 7852-01); the holotype (MZB unreg [ex CSIRO H 7858-01]) and 5 paratypes of *N. orientale* sp. nov. (CSIRO H 6130-01, CSIRO H 6136-01, CSIRO H 6136-04, CSIRO H 7099-09 and CSIRO H 7848-01).

Overall, 63 characters, expressed as proportional measurements of disc width (DW), were taken from: the lectotype (MNHN A2440, 1 of 2), paralectotype (MNHN A2440, 2 of 2) and one other non-type specimen (CSIRO H 7723-01) of *N. kuhlii*; the holotype (CSIRO H 7016-01) and 5 paratypes of *N. australiae* sp. nov. (CSIRO CA 3247, CSIRO CA 4307, CSIRO T 693, CSIRO H 3914-01 and CSIRO H 7017-01); the holotype (MZB unreg [ex CSIRO H 7852-03]) and 5 paratypes of *N. caeruleopunctata* sp. nov. (CSIRO H 6124-01, CSIRO H 6202-03, CSIRO H 6202-04, CSIRO H 7851-01 and CSIRO H 7852-01); the holotype (MZB unreg [ex CSIRO H 7858-01]) and 5 paratypes of *N. orientale* sp. nov. (CSIRO H 6130-01, CSIRO H 6136-01, CSIRO H 6136-04, CSIRO H 7099-09 and CSIRO H 7848-01).

Types are deposited in the Australian National Fish Collection (CSIRO), at the Commonwealth Scientific and

Industrial Research Organisation's Marine Laboratories in Hobart (Tasmania), Museum Zoologicum Bogoriense (MZB) in Jakarta, and the Muséum National d'Histoire naturelle (MNHN) in Paris. A detailed synonymy is not provided for each species (this will form part of the broader revision of this genus which is in preparation); the Clade to which they are referrable to in Puckridge *et al.* (2013) and in Naylor *et al.* (2012) is provided for each.

Cytochrome c oxidase I (COI) sequences were obtained as part of a previous larger study (Puckridge *et al*., 2013). To complement this, a COI sequence was obtained for a specimen of *N. kuhlii* from the Solomon Islands using the methods outlined in Holmes *et al*. (2009). The number of base substitutions per site averaging over all sequence pairs between groups were analysed using the Jukes-Cantor model. The rate variation among sites was modelled with a gamma distribution (shape parameter = 2). The analysis involved 21 nucleotide sequences. All positions containing gaps and missing data were eliminated with a total of 431 positions in the final dataset. Evolutionary analyses were conducted in MEGA version 6.06 (Tamura *et al*., 2013)

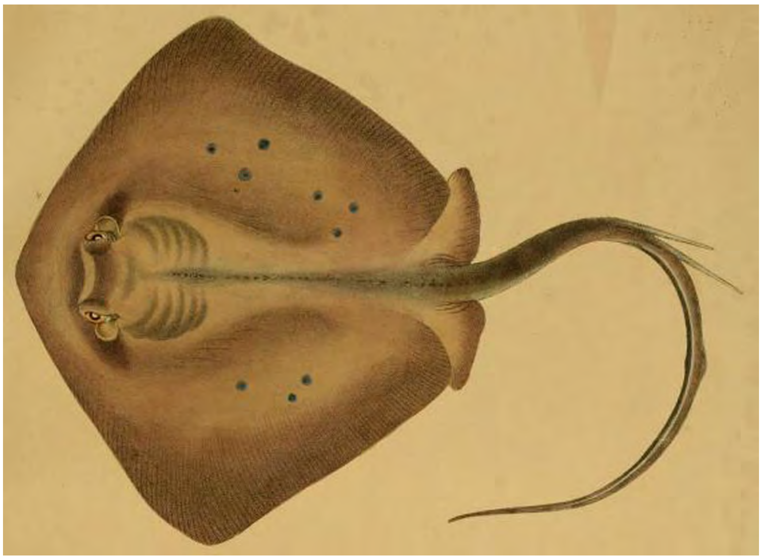

FIGURE 1. Original illustration of *Trygon kuhlii* in Müller & Henle (1841).

Neotrygon kuhlii (Müller & Henle, 1841)
(Figs. 1, 2, 4, 5a, 6a, 7a; Table 1)

Trygon kuhlii Müller & Henle, 1841: p. 164, pl. 50 (Vanikoro, Solomon Islands).

Lectotype. MNHN 2440 (1 of 2 specimens), female 156 mm DW, Vanikoro, Santa Cruz Group, Solomon Islands, 1829 (herein designated).

Paralectotype. MNHN 2440 (2 of 2 specimens; tail missing), female 159 mm DW, Vanikoro, Santa Cruz Group, Solomon Islands, 1829.

Other material. CSIRO H 7723-01, female 295 mm DW, Plaza fish market, Honiara, Solomon Islands, 7 May 2015.

Diagnosis. A medium-sized *Neotrygon* of the *kuhlii*-complex (reaching at least 30 cm DW) with the following combination of characters: disc broader than long, width ~1.2 times length; pectoral apices narrowly rounded; snout rather fleshy, broadly angular, angle ~107°, length 1.7–2.1 times interorbital width; maximum width relatively well back on disc, length from snout tip to pectoral-fin insertion 1.8–1.9 times and disc width 2.5–2.6 times horizontal distance from snout tip to maximum disc width; preoral length 2.4–2.8 times mouth width; internasal distance 1.5–1.8 in prenasal length; interspiracular distance 13–15% DW; nostril length 2.8–4.1% DW; nasal curtain width 8–8.3% DW; small mouth, width 6.4–6.8% DW; horizontal distance from cloaca to caudal sting base ~55% of disc length; thornlets present in nuchal region, absent from tail in all sizes; dermal denticles absent; pectoral-fin radials 113 (based on new specimen); total vertebral centra (including synarcual) 133, trunk centra (including synarcual) 39; blue spots very small and sparse, largest spot on disc 0.3–0.5 times eye width; 0–6 (mean

3.0) blue spots on medial belt, largest ~2.1% DW; mask-like marking pronounced, not covered with dark peppery spots; ventral surface of disc and pelvic fins with broad dark greyish submarginal bands; ventral tail fold and adjacent tail bluish grey when fresh.

Distribution. Tropical South-West Pacific, off the Solomon Islands; Santa Cruz Islands and Guadalcanal. Probably more widespread in Oceania but limits of its distribution need to be defined.

Remarks. The two former syntypes (MNHN 2440, 156 and 159 mm DW) from the eastern Solomon Islands (Vanikoro) are both females, presumably immature. The designated lectotype (156 mm DW) has strongly faded skin, almost pale brown with evidence of very small, white ocelli on both (confined to two spots on right side), with the tail intact; white central core of ocellus 1.2–1.7 mm diameter, surrounded by thin darker ring ~0.5 mm; the tail is mainly pale with two dark saddles confined to the dorsal part after caudal sting; entire tail tip is brownish on both surfaces. The designated paralectotype (159 mm DW) has ~29 similar-sized ocelli (some possibly missing), still evident beside orbits and irregularly dispersed over disc (diameter white core 1–2.6 mm); additional dark speckles are present on the orbital membrane, interorbit and over the central disc (<1.5 mm diameter). In both specimens, the posterior margins of ventral disc are probably darker than centrally; outer edge of ventral fold darker than its base (discussed by Müller & Henle, 1841).

A third much smaller syntype (MNHN A7931) collected from New Guinea by Quoy & Gaimard, is a late-term male embryo (~100 mm DW) with a rudiment of its umbilical cord still evident. The specimen is heavily bleached, being uniformly pale with no indication of colour (Fig. 3a). Morphometrics of these preserved types may be slightly affected by preservation, as the lectotype in particular has very flexible skin that may alter some anterior measurements. The fourth syntype from Leiden is probably RMNH 2472, an adult male (~270 mm DW) which is dried and stuffed (Fig. 3b).

Identification of the primary type specimen used in the Müller & Henle's description and excellent figure to designate a lectotype of the species has proven problematic. The number of blue spots and the presence of two caudal stings in their figure does not coincide with any of the types. Also, the illustration is of a female whereas the probable Leiden syntype is an adult male. Either their illustration is a composite image (most likely) or the dry Leiden adult male is not a syntype. The Leiden type (RMNH 2472) is listed as from Java, collected by Kuhl & van Hasselt. Müller & Henle's description, the type location is listed as 'Indien' which although often presumed to be India, was often used for East India or East Indies, present day Indonesia. Thus, this provides some support for the Javan specimen as the fourth syntype of *T. kuhlii*. But it should be noted that in other species descriptions, Müller & Henle refer to Java in the locations provided so there is still an element of uncertainty over the exact syntype specimen. Müller & Henle's description also refers to a sting (rather than two): 'der Stachel am Ende des vordem Viertels'. Still, a discrepancy remains as to their sizes; the syntype measured appears to be about 139.5 mm DW (largest width '5 Zoll, 4 Linie' based on Müller & Henle) which is much smaller than the first size of maturity of any member of the *kuhlii*-complex. The paucity and very small sizes of blue spots appears typical of maskrays from the Solomon Islands; blue-spotted maskray populations from India (inferentially specified as the location of the fourth syntype by Eschmeyer, 2016) and Indonesia (often referred to as 'Indien' in old museum labels and incorrectly accorded to India) have medium to large blue spots, usually in much higher densities. The size of spots and their distribution in Müller & Henle's figure (Fig. 1) is very similar to that of the two Vanikoro types (Fig. 2). On that basis, the most complete MNHN specimen, a 156 mm DW female in good condition with tail and caudal sting intact, is hereby designated as the lectotype. The second Vanikoro type becomes a paralectotype. This embryonic syntype (MNHN A7931) probably equals *N. australiae* sp. nov., and the dried RMNH syntype probably equals *N. caeruleopunctata* sp. nov. based on its size and capture location.

The meristic details of the *N. kuhlii* types were not obtained so counts are based solely on a newly collected specimen (CSIRO H 7723-01): total pectoral-fin radials 113; propterygium 45, mesopterygium 19, metapterygium 49. Pelvic-fin radials: 1 + 25–26. Vertebral centra total (including synarcual) 133; total (excluding synarcual) 128; monospondylous (including synarcual) 44; monospondylous (excluding synarcual) 39; pre-sting diplospondylous 64; post-sting diplospondylous 25. Count of the pectoral-fin radials (i.e. 113) is high for a *kuhlii*-group member. This specimen resembles the Vanikoro lectotype in shape and colour. Its COI sequence indicates that this species is distinct from all other *kuhlii*-group members (Appendix 1). In a similar analysis for the chondrichthyan Tree of Life project using the NADH2 gene, the specimen was basal and separate from all other forms of the *kuhlii*-group (G. Naylor, pers. comm.).

FIGURE 2. Dorsal view of *Neotrygon kuhlii* types from Vanikoro, Solomon Islands (preserved): (A) lectotype (MNHN A 2440, 1 of 2, female 154 mm DW); (B) paralectotype (MNHN A 2440, 1 of 2, female 162.7 mm DW).

FIGURE 3. Dorsal view of: (A) embryonic syntype of *Neotrygon kuhlii* from West Papua, New Guinea (MNHN A7931, embryo 99.7 mm DW; probably equals *Neotrygon australiae*); (B) dried probable syntype of *Neotrygon kuhlii* from Java, Indonesia (RMNH 2472, adult male ~271 mm DW; probably equals *Neotrygon caeruleopunctata*).

FIGURE 4. Freshly caught specimen of *Neotrygon kuhlii* (CSIRO 7723-01, female 295 mm DW) from Honiara, Solomon Islands: (A) dorsal view; (B) ventral view.

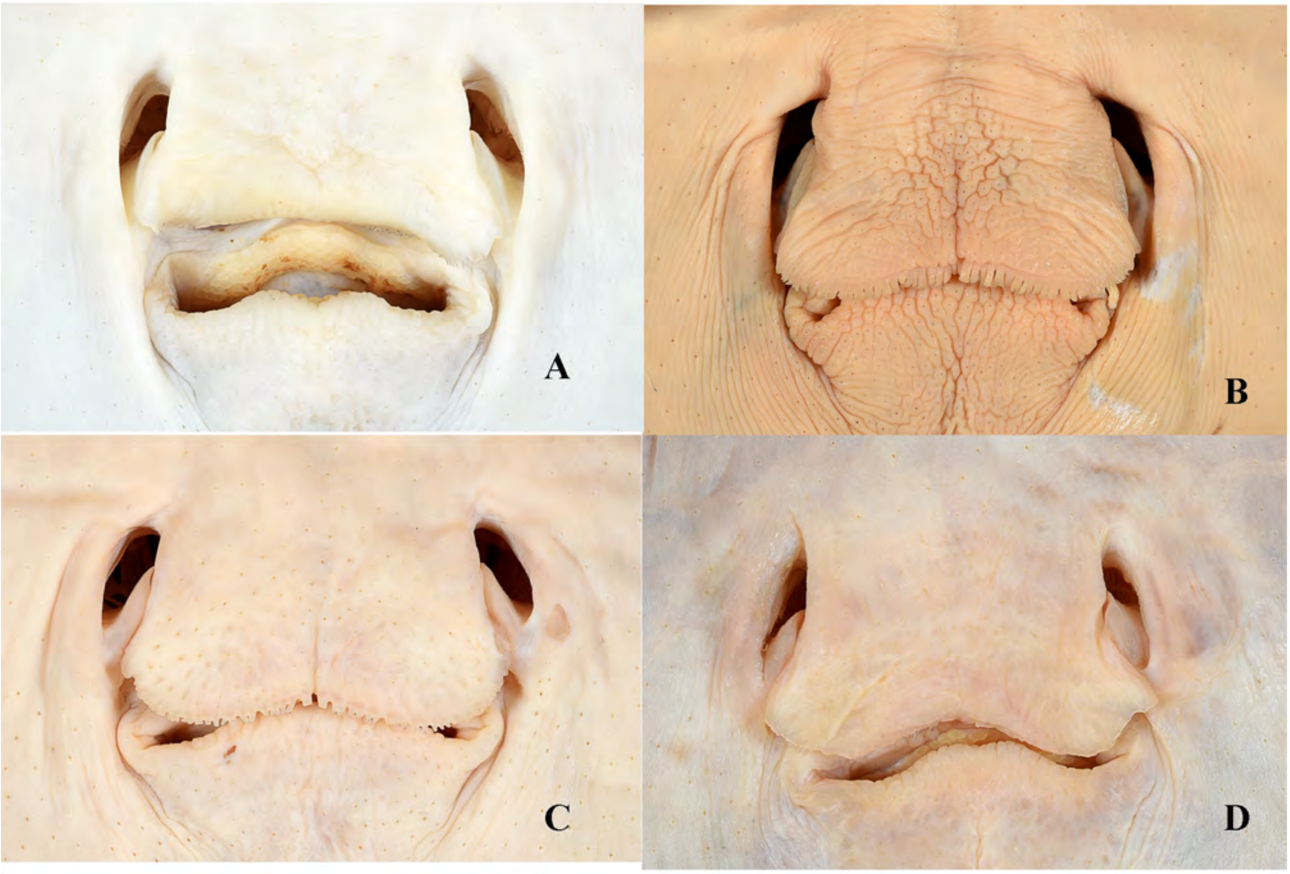

FIGURE 5. Oronasal region of: (A) *Neotrygon kuhlii* (CSIRO 7723-01, female 295 mm DW); (B) *Neotrygon australiae* sp. nov. (CSIRO CA 3247, adult male 379 mm DW); (C) *Neotrygon caeruleopunctata* sp. nov. (CSIRO H 6202-03, adult male 311 mm DW); (D) *Neotrygon orientale* sp. nov. (CSIRO H 6130-01, female 254 mm DW).

TABLE 1. Morphometric data for the lectotype (MNHN 2440, 1 of 2), paralectotype (MNHN 2440, 1 of 2), and one other specimen (CSIRO H 7723-01) of *Neotrygon kuhlii,* and for the holotype of *Neotrygon australiae* sp. nov. (CSIRO H 7016-01), and ranges and means for the measured paratypes. Measurements expressed as a percentage of disc width.

		N. kuhlii		***N. australiae* sp. nov.**			
	Lectotype	Paralect.	Other material	Holotype	Paratypes		
					Min.	Max.	Mean
Disc width (mm)	156	159	295	213	171	343	
Total length	189.2	–	211.2	224.6	159.1	223.5	199.5
Disc length	82.2	81.3	81.7	82.6	79.8	85.1	82.4
Snout to pectoral-fin insertion	71.4	70.0	71.9	72.0	68.1	74.9	71.7
Disc thickness	12.0	12.3	11.1	12.6	11.8	14.3	12.8
Snout (preorbital) length	17.2	16.4	16.1	14.1	13.3	14.6	13.8
Snout (preorbital) horizontal length	14.4	13.6	13.6	12.0	10.5	11.3	11.0
Pelvic-fin (embedded) length	17.3	17.0	19.9	19.3	18.4	22.3	21.0
Width across pelvic-fin base	14.5	13.8	16.4	15.4	15.6	18.4	16.7
Greatest width across pelvic fins	31.7	34.0	39.7	41.2	29.6	40.1	35.1
Cloaca origin to tail tip	120.2	–	141.1	154.1	90.2	153.7	129.9
Tail width at axil of pelvic fins	7.2	7.4	7.6	8.3	7.3	9.0	8.1

......*continued on the next page*

TABLE 1. (Continued)

		N. kuhlii			***N. australiae* sp. nov.**		
	Lectotype	Paralect.	Other material	Holotype		Paratypes	
					Min.	Max.	Mean
Tail height at axil of pelvic fins	4.1	4.7	5.0	6.0	5.0	6.0	5.5
Pectoral-fin insertion to sting origin	34.2	–	44.0	36.9	32.6	40.3	36.7
Cloaca origin to sting	–	–	45.1	36.9	35.0	44.0	40.0
Tail width at base of sting	3.0	–	3.3	2.9	2.9	3.5	3.2
Tail height at base of sting	2.9	–	2.8	3.4	3.0	3.4	3.2
Sting 1 length	21.6	–	–	9.2	14.9	21.5	18.0
Sting 2 length	–	–	–	16.6	0.0	24.7	12.3
Snout preoral (to lower jaw) length	18.0	16.1	16.4	13.3	12.5	16.1	14.1
Mouth width	6.4	6.8	6.4	7.3	6.5	7.3	7.0
Distance between nostrils	7.4	7.9	7.0	7.5	6.3	7.7	7.2
Interorbital width	8.5	9.4	7.5	8.7	6.7	8.3	7.5
Inter-eye width	18.6	17.3	16.1	17.7	15.1	17.5	16.3
Snout to maximum width	39.7	39.7	38.7	40.3	39.4	43.5	41.7
Eye length	5.8	5.4	5.8	6.0	5.3	6.7	5.8
Orbit diameter	9.2	8.6	8.2	7.8	7.9	8.9	8.6
Spiracle length	7.5	7.9	6.9	7.2	6.7	8.0	7.5
Interspiracular width	14.5	15.4	13.4	15.1	14.1	16.0	15.3
Orbit and spiracle length	11.6	12.1	10.9	10.2	10.6	12.6	11.5
Nostril length	3.2	2.8	4.1	4.0	3.4	4.0	3.6
Snout prenasal length	13.6	12.0	12.6	10.2	9.1	11.2	10.1
Nasal curtain length	4.6	3.8	4.1	5.7	5.3	5.8	5.5
Nasal curtain width	8.2	8.0	8.3	8.5	8.4	9.1	8.9
Orbit to pectoral-fin insertion	44.5	45.4	48.7	50.3	46.5	54.1	51.2
Snout to origin of cloaca	69.0	67.1	70.1	70.5	67.8	71.0	69.6
Width 1st gill slit	2.7	2.7	3.1	3.0	3.0	3.7	3.2
Width 3rd gill slit	2.7	3.3	3.1	3.6	3.4	4.0	3.6
Width 5th gill slit	2.1	2.0	2.1	2.8	1.9	2.9	2.4
Head length	41.2	38.5	38.9	37.7	36.8	38.5	37.7
Distance between 1st gill slits	–	17.8	15.7	17.0	15.9	17.6	16.7
Distance between 5th gill slits	–	9.0	8.0	8.8	8.4	9.7	8.9
Cloaca length	4.8	5.0	6.3	4.1	3.9	6.4	5.5
Clasper postcloacal length	–	–	–	11.0	10.9	25.3	19.5
Clasper length from pelvic axil	–	–	–	5.0	4.1	18.0	13.3

Neotrygon australiae sp. nov.

(Figs. 5b, 6b, 7b, 9; Table 1)

Neotrygon kuhlii Clade 5—Puckridge *et al*., 2013: p. 6.
Neotrygon kuhlii 4—Naylor *et al*., 2012: p. 77, fig. 58.

Holotype. CSIRO H 7016-01 (tissue accession BW-A6850), juvenile male 235 mm DW, southwest of Weipa, Gulf of Carpentaria, Queensland, 12°53.96′ S, 141°12.71′ E, 36–38 m depth, 20 Feb 2009.

Paratypes. 8 specimens: CSIRO CA 3236, adult male 280 mm DW, north of Port Hedland, Western Australia, 19°28.2′ S, 118°49′ E, 38–46 m depth, 20 Aug 1982; CSIRO CA 3247, adult male 379 mm DW, north of Port Hedland, Western Australia, 19°36′ S, 118°22′ E, 34–36 m depth, 21 Aug 1982; CSIRO CA 4307, female 306 mm DW, northwest Australia; CSIRO H 3914-01, adult male 287 mm DW, west of Weipa, Gulf of Carpentaria, Queensland, 12°26.9′ S, 141°27.6′ E, 28 m depth, 8 Mar 1995; CSIRO H 6144-19 (tissue accession BW-A9396), female 180 mm DW, northwest of Prince of Wales Island, Torres Strait, Queensland, 10°36.68′ S, 141°36.42′ E, 17 m depth, 16 Jan 2004; CSIRO H 7017-01 (tissue accession BW-A7794), juvenile male 180 mm DW, north of Mornington Island, Gulf of Carpentaria, Queensland, 16°12.92′ S, 138°58.95′ E, 27–28 m depth, 22 Feb 2009; CSIRO H 7018-01 (tissue accession BW-A6849), female 145 mm DW, northwest of Mornington Island, Gulf of Carpentaria, Queensland, 16°19.00′ S, 138°39.53′ E, 23–24 m depth, 23 Feb 2009; CSIRO T 693, juvenile male 245 mm DW, north of Wessel Islands, Northern Territory, 9°47′ S, 136°20′ E, 50 m depth, 22 Feb 1982.

Other material. 12 specimens: CSIRO CA 712, adolescent male 255 mm DW, Mud Cod Bay, Northern Territory, 14°02′ S, 136°24′ E, Jun 1979; CSIRO CA 1241, female 336 mm DW, north of Admiralty Gulf, Western Australia, 12°53′ S, 125°36′ E, 83–91 m depth, 1 Apr 1981; CSIRO CA 3248, adult male 362 mm DW, northwest of Port Hedland, Western Australia, 20°00.2′ S, 117°55′ E, 34–36 m depth, 22 Aug 1982; CSIRO CA 4309, female 190 mm DW, northwest Australia; CSIRO H 959-3, juvenile male 191 mm DW, north of Wessel Islands, Northern Territory, 10° S, 137° E, Mar 1987; CSIRO H 47-1, female 351 mm DW, north of Wessel Islands, Northern Territory, 9°47′ S, 136°20′ E, 50 m depth, 22 Feb 1982; CSIRO H 960-02, female 363 mm DW, probably northern Australia, 22 Mar 1987; CSIRO H 5590-01, male 300 mm DW, north of Groote Eylandt, 13°09.8′ S, 136°45.4′ E, 27 m depth, 24 Sep 1998; CSIRO T 692, juvenile female 157 mm DW, north of Wessel Islands, Northern Territory, 9°47′ S, 136°20′ E, 50 m depth, 22 Feb 1982; CSIRO H 7853-01 (tissue accession BW-A5960), female 255 mm DW, CSIRO H 7853-02 (tissue accession BW-A5961), juvenile male 204 mm DW, Tanjung Luar fish landing site, Lombok, Indonesia, 8°45′ S, 116°35′ E, 25 Oct 2008; CSIRO H 7304-07 (tissue accession BW-A10112), adult male 383 mm DW, CSIRO H 7304-08 (tissue accession BW-A10113), 318 mm DW, CSIRO H 7304-09 (tissue accession BW-A10114), 305 mm DW, Tanjung Luar fish landing site, Lombok, Indonesia, 8°45′ S, 116°35′ E, 4 Aug 2010; CSIRO H 7217-05 (tissue accession BW-A11341), 290 mm DW, CSIRO H 7217-06 (tissue accession BW-A11342), 286 mm DW, Tanjung Luar fish landing site, Lombok, Indonesia, 8°45′ S, 116°35′ E, 24 Jan 2011; KFRS unreg (field code 220341), adult male 301 mm DW, KFRS unreg (field code 220342), adult male 301 mm DW, Daru fish market, Western Province, Papua New Guinea, 9°03.91′ S, 143°12.59′ E, 22 Oct 2014; MNHN A7931 (syntype of *N. kuhlii*), late-term embryo, male 99.7 mm DW, West Papua, New Guinea, 7°30′ S, 132°30′ E, 1827.

Diagnosis. A large *Neotrygon* of the *kuhlii*-complex (reaching at least 45 cm DW; males maturing at ~28 cm DW) with the following combination of characters: disc much broader than long, width 1.2–1.3 times length; pectoral apices narrowly angular; snout fleshy, broadly rounded to weakly angular, angle 101–103°, length 1.6–2.1 times interorbital width; maximum width relatively well back on disc, length from snout tip to pectoral-fin insertion 1.7–1.8 times and disc width 2.3–2.5 times horizontal distance from snout tip to maximum disc width; preoral length 1.8–2.3 times mouth width; internasal distance 1.3–1.6 in prenasal length; interspiracular distance 14–16% DW; nostril length 3.4–4% DW; nasal curtain width 8.4–9.1% DW; small mouth, width 6.5–7.3% DW; horizontal distance from cloaca to caudal sting base 42–52% of disc length; thornlets present in nuchal and lumbar regions in large individuals, absent from tail in all sizes; dermal denticles entirely absent from body; pectoral-fin radials 105–113; total vertebral centra (including synarcual) 129–134, trunk centra (including synarcual) 37–41; blue spots large, largest spot on disc 0.7–1.2 times eye width; 2–17 (mean 9.4) blue spots on medial belt, largest 3.3–5.6% DW; mask-like marking subtle, usually lightly covered with dark peppery spots (dark spots not widespread over central disc); ventral surface of disc with distinct dark greyish brown submarginal bands; ventral tail fold almost entirely dark.

Description. Disc quadrangular, straight to weakly convex anteriorly and not produced; much broader than long, width 1.21 times length in holotype (1.17–1.25 in paratypes); snout angle 103° (101–103°); axis of greatest width of disc relatively well back on disc, almost over scapular region, its distance from snout tip 1.78 (1.67–1.77) times in distance from tip of snout to pectoral-fin insertion; body relatively robust, thickness 7.9 (7.0–8.5) times in disc width, raised slightly above cranium; apex broadly rounded, narrowly or abruptly angular, pectoral angle 87° (84–89°); posterior margin straight to weakly convex; free rear tip narrowly angular. Pelvic fins narrowly subtriangular, anterior margin almost straight, apex narrowly rounded, posterior margin moderately convex, united with inner margin (free rear tip indiscernible); rather small, length 19.3% (18.4–22.3%) DW; 1.25 (1.14–1.34) times width across fin bases. Claspers of adult males large, depressed, tapering, acutely pointed apically; outer length (from axil of pelvic fin) 18.0% DW.

Tail moderately broad-based, tapering rapidly to caudal stings, with dorsal and ventral skin folds; base moderately depressed, broadly oval in cross-section, weakly convex above and below, width 1.40 (1.33–1.63) times depth; subcircular to rhomboidal in cross-section near origin of ventral skin fold, width 1.06 (0.95–1.22) times height at fold origin; tapering evenly in dorsoventral view posterior to caudal stings; moderately compressed at end of caudal stings; damaged distally beyond folds in one large paratype; both dorsal and ventral skin folds prominent; tail very compressed, narrowly suboval in cross-section above mid ventral fold, width 0.55 (0.52–0.66) times depth; at end of fold weakly depressed, width 1.00 (0.52–0.93) times height; dorsal surface of tail posterior to caudal-sting bases with a weak naked groove (partly housing ventral-most sting and extending for about half to its full length); no skin folds present along lateral margin of tail. Dorsal skin fold well developed, short-based, pronounced, length about 10 (7–19) times its height, 1.31 (1.03–1.46) in snout length, 6.34 (4.00–6.61) in length of ventral fold; its height 1.09 (0.74–1.53) in height of mid-ventral fold; origin sometimes coincident with apex of second sting, sometimes with a short low ridge before elevated portion; elevated portion slightly less than or equal to snout length. Ventral skin fold relatively long, 68.2 (50.1–68.3)% DW, relatively narrow, tapering, deepest forward of dorsal skin fold; much longer based and distinctly taller than dorsal skin fold; length 1.47 (1.46–1.99) in disc width; depth at quarter length 0.78 (0.37–0.67), at mid length 0.72 (0.52–0.63), at three quarter 0.86 (0.40–0.85) in adjacent tail height; originating almost below or just forward of first sting origin; horizontal distance from cloaca to sting origin 1.91 (1.61–1.97) in precloacal length.

Snout fleshy (more so in large paratypes), short, broadly rounded; not acute at apex, but without obvious apical lobe; angle 103° (101–103°); narrowly rounded when viewed laterally, becoming slightly more depressed towards apex; preoral snout length 1.82 (1.89–2.31) times mouth width, 1.77 (1.74–2.11) times internarial distance, 0.78 (0.79–0.91) times distance between first gill slits; direct preorbital snout length rather short, 1.63 (1.63–2.09) times interorbital length; snout to maximum disc width 2.48 (2.30–2.54) in DW; interorbital space narrow, weakly concave (almost straight in some paratypes); eyes large, dorsolateral, strongly protruding, ventral margin partly covered by thick skin fold; orbit greatly elevated above disc and interorbital space, diameter 0.92 (0.76–0.93) in spiracle length, eye length 1.19 (1.13–1.41) in spiracle length; inter-eye distance 2.94 (2.59–3.07) times eye length. Spiracles large, crescentic with dorsolateral opening; dorsal margin with a medial protuberance. Nostril narrowly oval to slit-like, directed longitudinally to slightly oblique; lateral margin fleshy; anterior nasal fold internal, very narrow, membranous; broad oronasal groove present; internarial space 1.36 (1.26–1.56) in prenasal length, 1.88 (1.78–2.28) times nostril length. Nasal curtain relatively narrow, skirt-like, short, width 1.50 (1.45–1.72) times length; weakly bilobed, posterior margin of each lobe moderately convex; surface crenulated, papillate, sometimes with weak medial groove and covered with minute pores; apex recessible within lateral margin of oronasal groove; lateral margin almost straight, smooth-edged, usually partly enveloped by narrow posterior fold of nostril; posterior margin strongly fringed, concave medially, vaguely following contour of lower jaw, usually overlapping lower jaw when mouth closed in holotype and most paratypes.

Mouth small, jaws strongly asymmetric; lateral grooves shallow, curved slightly, extending from nostril to slightly below lower jaw, length much shorter than nasal curtain length; not projecting forward when open, not protrusible; skin on chin and margin of lower jaw very fleshy, strongly papillate; teeth uniformly close-set in both jaws, in oblique rows, not arranged in obvious quincunx, in paratype CSIRO T 693 rows in upper jaw ~24, lower jaw ~31. Upper jaw strongly arched, strongly double convex; teeth of anterior part of upper jaw concealed when mouth closed; symphysial part of jaw projecting anteroventrally. Lower jaw strongly convex with a truncate to weakly concave anterior margin, interlocking into upper jaw when mouth closed; teeth not visible when mouth closed. Upper jaw of juvenile male syntype (CSIRO T 693) with a raised row of greatly enlarged teeth with long caniniform cusps (directed lingually) near the middle of each side of jaw; teeth otherwise similar in shape, cusps more or less subequal to their base length; those at symphysis barely larger than those adjacent. Teeth in lower jaw smaller than those of upper jaw, broad based, low, with semi-truncate to slightly concave distal margins, those toward angle of lower jaw with slightly shorter cusps; no rows of enlarged teeth in jaw. Floor of mouth in paratypes with two very long, lobe-like, very closely spaced, medial oral papillae (holotype not dissected); no smaller papillae near angle of each jaw.

Gill openings elongate S-shaped, forming a weakly fringed lobe laterally; length of first gill slit 1.09 (1.14–1.59) times length of fifth gill slit, 2.39 (1.88–2.40) times in mouth width; distance between first gill slits 2.26 (2.12–2.54) times internarial space, 0.45 (0.43–0.46) times ventral head length; distance between fifth gill slits 1.17 (1.14–1.35) times internasal distance, 0.23 (0.22–0.26) times ventral head length.

Total pectoral-fin radials 112–113 (105–111); propterygium 44 (42–45), mesopterygium 17 (14–19), metapterygium 51–52 (46–49). Pelvic-fin radials: 1 (1) + 18–19 (18–19 in male paratypes, 23 in female paratype). Vertebral centra total (including synarcual) 132 (129–134); total (excluding synarcual) 129 (123–130); monospondylous (including synarcual) 37 (39–41); monospondylous (excluding synarcual) 34 (34–36); pre-sting diplospondylous 76 (66–71); post-sting diplospondylous 19 (17–25).

Squamation. Disc and tail of holotype lacking dermal denticles; a single series of variable-length, narrow, spear-shaped to narrow lanceolate thornlets along mid-line of disc on nape; median row continuous on nape, with 11 (8–13) thornlets when developed, anteriormost thornlets smallest; row length slightly shorter than or equal to interspiracular width; two largest thornlets larger than those adjacent, angle at less than 45° to horizontal (appearing saw-shaped in lateral view); no thornlets on lumbar region or tail; lateral scapular thorns absent. In largest paratypes (CSIRO CA 3236, CSIRO CA 3247 and CSIRO CA 4307), row of thornlets on nape almost connected with a well-developed lumbar row; lumbar series weakly developed in CSIRO H 3914-01; nape and lumbar series both absent in smallest paratypes (CSIRO H 7017-01 and CSIRO H 7018-01).

Two caudal stings in holotype (1 or 2 in paratypes), intact, second much longer than first; caudal stings very elongate, slender, narrow based, longest sting exceeding preorbital length; enveloping membrane absent; distance from sting base to pectoral-fin insertion 36.9% (32.6–40.3%) DW, 4.02 (1.78–2.44) times first sting length; distance from cloaca to sting base 0.45 (0.42–0.52) in disc length.

Colour. Live coloration (based on holotype). Dorsal surface pale yellowish brown and blue-spotted, barely graduating to slightly paler yellowish pink along margin of disc and pelvic fins; eye dark, orbital membrane darker than disc. Blue spots large, irregularly spaced, ocellate, with pale bluish white centres and surrounded by thick, diffuse-edged darker grey blue outer rings; distributed widely over disc; well represented on medial belt; thornlets in medial row white and contrasted with skin; mask-like marking on head distinct, medium brown with whitish blotch on posterior edge; dark speckles most concentrated on mask and comparatively sparse elsewhere. Ventral surface uniformly white centrally on disc, submarginal band greyish and distinct. Tail slightly darker than disc dorsally before caudal sting, becoming even darker then with black and white bands toward its tip; sides of tail dusky; dorsal and ventral folds blackish.

In preservative (based on holotype). Dorsal surface pale yellowish, darker greyish on head and across mid-disc and tail; palest around disc submargin (disc edge blackish); mask and orbital membranes dark, with a moderate peppering of small black spots; bluish spots large (in paratypes largest spots 4–6.2% DW), appearing as greyish blue markings with pale centres (somewhat ocellate). Ventral surface of disc and pelvic fins almost uniformly white with narrow black edge; submarginal bands barely detectable, weak and diffuse-edged in smallest paratypes. Tail darker dorsally than ventrally; ventral surface forward of ventral fold pale to faintly dusky (slightly darker in some paratypes, but noticeably paler than dorsal surface); ventral fold dark with a very narrow pale base; dorsal fold uniformly dark; banding on post-fold tail primarily black with three narrow, pale bands (banding on paratypes variable); stings greyish white. Claspers distinctly paler than dorsal tail, similar on dorsal and ventral surfaces.

Size. Type specimens consisted of three adult males of 280–379 mm DW, three juvenile males of 180–245 mm DW, and three females of 145–306 mm DW. Other material examined includes and adult male of 383 mm DW, an adolescent male of 255 mm DW and a female of 351 mm DW. Specimens observed at the Tanjung Luar fishing port in Lombok (from local catches) included females of up to 452 mm DW and adult males up to 410 mm DW.

Distribution. Type specimens were collected from northern Australia, from off Port Hedland, east to northeastern Gulf of Carpentaria (Fig. 8) at depths of 23–50 m. Other specimens taken from off Daru (northern Torres Strait Islands) in Papua New Guinea and Lombok in Indonesia. Found over and adjacent to rocky and coral reefs from shallow water to at least 91 m depth. Specimens recorded off eastern Queensland to northern New South Wales are referrable to *Neotrygon trigonoides* and it is possible *N. australiae* does not overlap but additional research is required. The extent of the range of this species in New Guinea needs more research.

Etymology. Epithet demarcates the Australasian distribution of this member of bluespotted mask ray complex of the genus *Neotrygon*. Vernacular: Australian Bluespotted Maskray.

FIGURE 6. Lateral view of the post-caudal sting tail of: (A) *Neotrygon kuhlii* (CSIRO 7723-01, female 295 mm DW); (B) *Neotrygon australiae* sp. nov. (CSIRO CA 4307, female 306 mm DW); (C) *Neotrygon caeruleopunctata* sp. nov. (CSIRO H 6202-04, female 324 mm DW); (D) *Neotrygon orientale* sp. nov. (CSIRO H 7848-01, female 343 mm DW).

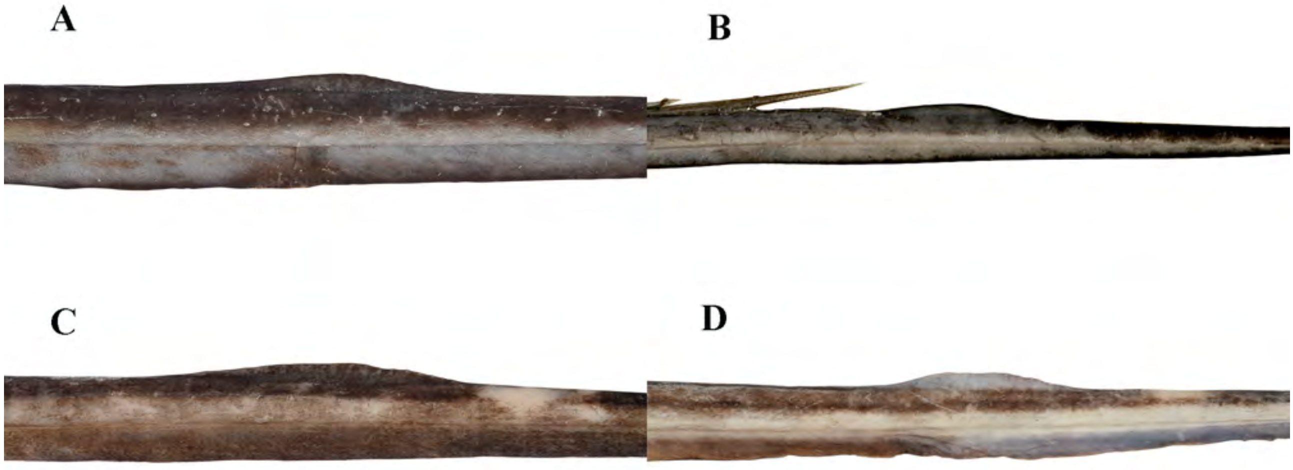

FIGURE 7. Lateral view of the mid-tail showing respective heights of the dorsal and ventral tail folds: (A) *Neotrygon kuhlii* (CSIRO 7723-01, female 295 mm DW); (B) *Neotrygon australiae* sp. nov. (CSIRO CA 4307, female 306 mm DW); (C) *Neotrygon caeruleopunctata* sp. nov. (CSIRO H 6202-04, female 324 mm DW); (D) *Neotrygon orientale* sp. nov. (CSIRO H 7848-01, female 343 mm DW).

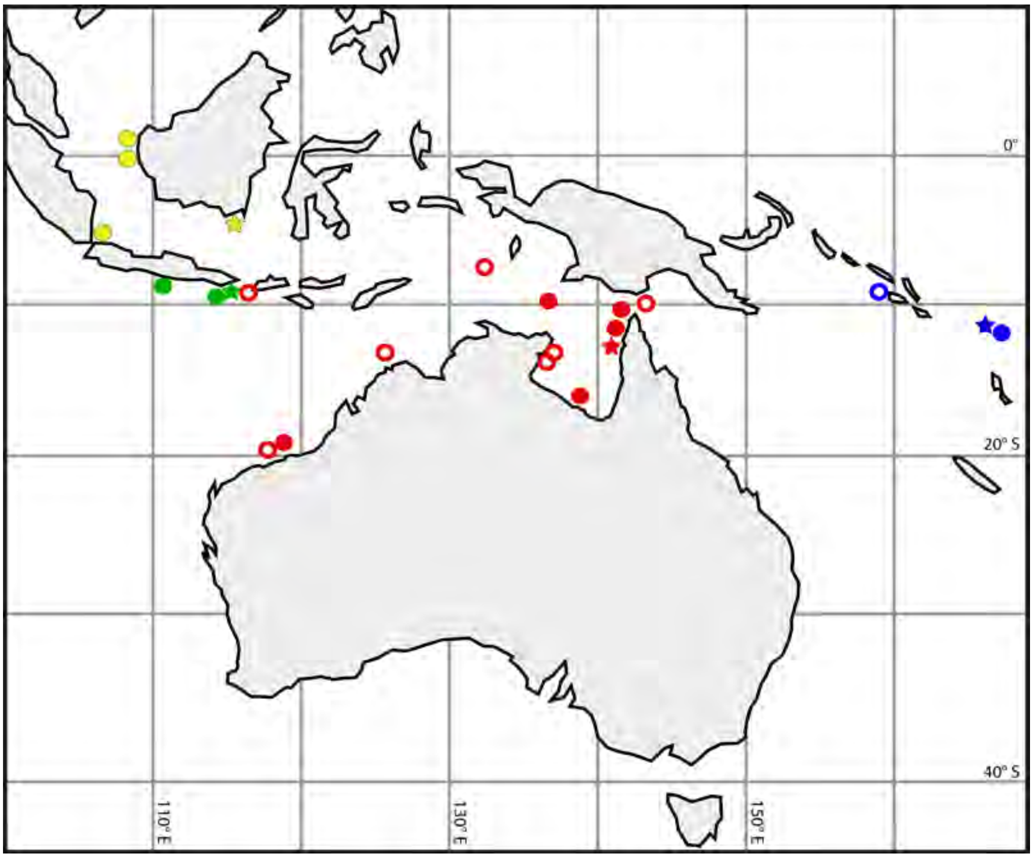

FIGURE 8. Map showing the locations of the type material and other specimens examined of *Neotrygon kuhlii* (blue), *Neotrygon australiae* sp. nov. (red), *Neotrygon caeruleopunctata* sp. nov. (green) and *Neotrygon orientale* sp. nov. (yellow). Stars denote primary types (holotype or lectotype), solid circles denote secondary types, and open circles denote non-type material examined.

Neotrygon caeruleopunctata sp. nov.

(Figs. 5c, 6c, 7c, 10, 11; Table 2)

Neotrygon kuhlii Clade 6—Puckridge *et al*., 2013: p. 6.

Holotype. MZB unreg (ex CSIRO H 7852-03) (tissue accession BW-A2572), adolescent male 227 mm DW, Kedonganan fish market, Bali, Indonesia, 8°45′ S, 115°10′ E, 17 Apr 2004.

Paratypes. 9 specimens: CSIRO H 7851-01, adolescent male 295 mm DW, CSIRO H 7851-02, male 273 mm DW, Kedonganan fish market, Bali, Indonesia, 8°45′ S, 115°10′ E, 16 Apr 2004; CSIRO H 7852-01 (tissue accession BW-A2573), female 247 mm DW, CSIRO H 7852-02, female 280 mm DW, collected with holotype; CSIRO H 6202-03, adult male 311 mm DW, CSIRO H 6202-04, female 324 mm DW, Kedonganan fish market, Bali, Indonesia, 8°45′ S, 115°10′ E, 18 Apr 2004; CSIRO H 7850-01 (tissue accession BW-A5731), female 350 mm DW, Sadeng fishing port, Central Java, Indonesia, 8°11.5′ S, 110°48′ E, 18 Oct 2008; CSIRO H 6124-01 (tissue accession BW-A2580), female 264 mm DW, CSIRO H 6124-02, male 245 mm DW, Kedonganan fish market, Bali, Indonesia, 8°45′ S, 115°10′ E, 24 Aug 2002.

Diagnosis. A large *Neotrygon* of the *kuhlii*-complex (reaching at least 47 cm DW; males maturing at 31 cm DW) with the following combination of characters: disc much broader than long, width 1.2–1.3 times length; pectoral apices abruptly angular; snout fleshy, broadly rounded to obtuse, angle 125–130°, length 1.8–2.4 times interorbital width; maximum width relatively well forward on disc, length from snout tip to pectoral-fin insertion 1.9–2 times and disc width 2.6–2.9 times horizontal distance from snout tip to maximum disc width; preoral length 1.6–2.3 times mouth width; internasal distance 1.4–1.8 in prenasal length; interspiracular distance 13–14% DW; nostril length 2.5–3.5% DW; nasal curtain width 8–9.4% DW; small mouth, width 6.6–7.9% DW; horizontal distance from cloaca to caudal sting base 51–56% of disc length; thornlets present in nuchal and lumbar regions in large individuals, absent from tail in all sizes; dermal denticles entirely absent from body; pectoral-fin radials 105–110; total vertebral centra (including synarcual) 133–142, trunk centra (including synarcual) 38–43; blue spots medium-sized, largest spot on disc 0.5–0.8 times eye width; 0–3 (mean 0.8) blue spots on medial belt, largest 1.7–2.7% DW; mask-like marking dark, not covered with dark peppery spots; ventral surface of disc and pelvic fins with sharply defined dark greyish brown submarginal bands; ventral tail dark before caudal sting; ventral tail fold almost entirely dark in young.

Description. Disc rhombic, straight to weakly convex anteriorly and not produced; much broader than long, width 1.24 times length in holotype (1.20–1.25 in paratypes); axis of greatest width of disc relatively well forward on disc, slightly forward of scapular region, its distance from snout tip 2.02 (1.86–2.02) times in distance from tip of snout to pectoral-fin insertion; body relatively robust, thickness 9.0 (7.7–9.1) times in disc width, raised slightly above cranium; apex broadly rounded to obtuse, pectoral angle 83° (81–87°); posterior margin straight to weakly undulate; free rear tip narrowly angular. Pelvic fins narrowly subtriangular, anterior margin almost straight, apex narrowly rounded, posterior margin convex, united with inner margin (free rear tip indiscernible); rather small, length 20.9% (20.6–21.9%) DW; 1.21 (1.08–1.28) times width across fin bases. Claspers of adult males relatively small, depressed, tapering, acutely pointed apically; outer length (from axil of pelvic fin) 12.5% DW.

Tail moderately broad-based, tapering rapidly to caudal sting (damaged in all types), with dorsal and ventral skin folds; base moderately depressed, broadly oval in cross-section, weakly convex above and below, width 1.48 (1.25–1.72) times depth; subcircular to rhomboidal in cross-section near origin of ventral skin fold, width 1.20 (1.00–1.21) times height at fold origin; tapering evenly in dorsoventral view posterior to caudal sting(s); moderately compressed beneath broken sections of caudal sting(s); damaged distally beyond folds in largest paratypes; both dorsal and ventral skin folds prominent; tail compressed, narrowly suboval in cross-section above mid ventral fold, width 0.70 (0.57–0.91) times depth; at end of fold subcircular, width 0.86 (0.84–1.12) times height; dorsal surface of tail posterior to caudal-sting bases with a weak naked groove (partly housing ventral-most sting); no skin folds present along lateral margin of tail. Dorsal skin fold well developed, short-based, pronounced, length about 12 (9–12) times its height, 1.35 (1.30–1.66) in snout length, 5.39 (5.20–6.09) in length of ventral fold; its height 1.34 (1.17–1.40) in height of mid-ventral fold; origin usually with a short low ridge before elevated portion; elevated portion much shorter than snout length. Ventral skin fold relatively long, 60.0 (49.9–60.3)% DW, relatively narrow, tapering, deepest forward of dorsal skin fold; much longer based and distinctly taller than dorsal skin fold; length 1.67 (1.66–2.00) in disc width; depth at quarter length 0.67 (0.55–0.75), at mid length 0.65 (0.52–0.82), at three quarter 1.06 (0.75–0.97) in adjacent tail height; originating almost below or just forward of first sting origin; horizontal distance from cloaca to sting origin 1.59 (1.51–1.60) in precloacal length.

Snout fleshy (more so in large paratypes), short, obtuse; not acute at apex, but without obvious apical lobe; angle 128° (125–130°); narrowly rounded when viewed laterally, becoming slightly more depressed towards apex; preoral snout length 2.01 (1.63–2.34) times mouth width, 2.19 (1.75–2.28) times internarial distance, 0.83 (0.75–0.95) times distance between first gill slits; direct preorbital snout rather short, length 1.78 (1.91–2.40) times interorbital length; snout to maximum disc width 2.94 (2.64–2.87) in DW; interorbital space narrow, weakly concave; eyes large, dorsolateral, strongly protruding, ventral margin partly covered by thick skin fold; orbit greatly elevated above disc and interorbital space, diameter 0.83 (0.88–1.02) in spiracle length, eye length 1.17 (1.27–1.45) in spiracle length; inter-eye distance 2.93 (3.03–3.37) times eye length. Spiracles large, crescentic with dorsolateral opening; dorsal margin with a medial protuberance. Nostril narrowly oval to slit-like, directed longitudinally to slightly oblique; lateral margin fleshy; anterior nasal fold internal, very narrow, membranous; broad oronasal groove present; internarial space 1.78 (1.43–1.82) in prenasal length, 2.04 (1.92–2.78) times nostril length. Nasal curtain relatively narrow, skirt-like, short, width 1.54 (1.43–1.86) times length; weakly bilobed, posterior margin of each lobe moderately convex; surface crenulated, weakly papillate, sometimes with weak medial groove and covered with minute pores; apex recessible within lateral margin of oronasal groove; lateral margin almost straight, smooth-edged, usually partly enveloped by narrow posterior fold of nostril; posterior margin strongly fringed, concave medially, vaguely following contour of lower jaw, usually overlapping lower jaw when mouth closed.

Mouth small, jaws strongly asymmetric; lateral grooves shallow, curved slightly, extending from nostril to slightly below lower jaw, length much shorter than nasal curtain length; not projecting forward when open, not protrusible; skin on chin and margin of lower jaw very fleshy, strongly papillate; teeth uniformly close-set in both jaws, in oblique rows, not arranged in obvious quincunx, in paratype CSIRO H 6202-03 rows in upper jaw ~26, lower jaw ~33. Upper jaw strongly arched, strongly double convex; teeth of anterior part of upper jaw concealed when mouth closed; symphysial part of jaw projecting anteroventrally. Lower jaw strongly convex with a truncate to weakly concave anterior margin, interlocking into upper jaw when mouth closed; teeth not visible when mouth closed. Upper jaw of adult male paratype (CSIRO H 6202-03) with a raised row of greatly enlarged teeth with long caniniform cusps (directed lingually) near the middle of each side of jaw; teeth otherwise small, length of cusps more or less subequal to their base length; teeth at symphysis barely larger than those adjacent, directed lingually, with long acute to bluntly pointed cusps, slightly less oblique than those posterolaterally. Teeth in lower jaw smaller than those of upper jaw, broad based, cusps rather long, those toward angle of lower jaw with slightly shorter cusps. Floor of mouth in paratypes with two very long, lobe-like, very closely spaced, medial oral papillae (holotype not dissected); no smaller papillae near angle of each jaw.

Gill openings elongate S-shaped, forming a weakly fringed lobe laterally; length of first gill slit 1.44 (1.18–1.32) times length of fifth gill slit, 2.32 (2.14–2.55) times in mouth width; distance between first gill slits 2.62 (2.30–2.44) times internarial space, 0.48 (0.43–0.47) times ventral head length; distance between fifth gill slits 1.45 (1.20–1.41) times internasal distance, 0.26 (0.23–0.25) times ventral head length.

Total pectoral-fin radials 109 (105–110); propterygium 43–44 (43–46), mesopterygium 17–18 (14–19), metapterygium 47–49 (45–49). Pelvic-fin radials: 1 (1) + 21–22 (19–21 in male paratypes, 24–26 in female paratypes). Vertebral centra total (including synarcual) 142 (133–140); total (excluding synarcual) 136 (128–134); monospondylous (including synarcual) 43 (38–41); monospondylous (excluding synarcual) 37 (33–36); pre-sting diplospondylous 74 (64–74); post-sting diplospondylous 25 (18–33).

Squamation. Disc and tail of holotype lacking dermal denticles; a single series of very small, developing thornlets along mid-line of disc on nape in holotype. In larger paratypes (CSIRO H 6202-04 and CSIRO H 7850-01) median row on nape well developed and continuous, up to 10 thornlets, last 3 much larger than those preceding; median disc beyond shoulder with a continuous or broken row of smaller seed-shaped thornlets extending to above cloaca; no thornlets on lumbar region or tail; median row on nape much shorter in length than interspiracular width; angle at less than 45° to horizontal (appearing saw-shaped in lateral view); lateral scapular thorns absent.

Evidence of a single caudal sting in all types except one paratype (CSIRO H 6202-04); stings broken in all cases at their base or removed completely by fishers post capture; distance from cloaca to sting base 0.52 (0.51–0.56) in disc length.

Colour. Live coloration (based on paratype CSIRO 7850-01). Dorsal surface pale greenish brown centrally and blue-spotted, graduating to more intense reddish brown along margin of disc and pelvic fins; eye whitish, orbital membrane similar to disc. Blue spots small to medium-sized, irregularly spaced, ocellate, with pale blue centres and surrounded by darker blue, diffuse-edged outer rings; distributed mainly over central parts of pectoral fins; largely absent through medial belt; thornlets in medial row white and contrasted with skin; dark speckles distributed randomly on disc; mask-like marking on head rather poorly defined, without dense peppering of speckles. Ventral surface colour based on incomplete image, uniformly white on head. Tail similar to disc colour dorsally before caudal sting, becoming paler greyish white then with black and white bands toward its tip; sides of tail white; dorsal fold similar to dorsal tail; ventral fold dusky with narrow black edge.

In preservative (based on holotype). Dorsal surface dark greyish brown, darker greyish on head and slightly darker across mid-disc and tail; slightly paler around disc submargin (disc edge narrowly blackish; less distinct in paratypes); mask relatively indistinct, with weak peppering of small black spots (similar in paratypes); bluish spots small to medium-sized (in paratypes largest spots 2.7–3.9% DW) appearing as almost entirely greyish markings (not or weakly ocellate); larger spots more variable in paratypes (uniformly coloured to ocellate, in paratype CSIRO H 6124-01 spots distinctly ocellate with pale centres); no blue spots in medial belt (mostly also absent but up to 3 spots in paratypes), when present diameter up to 2.7% DW. Ventral surface of disc and pelvic fins largely white with sharply defined dark greyish brown submarginal bands (less defined in largest paratypes) and narrow black edges; submarginal band broad, at pectoral apex exceeding prenarial length; anterior half of ventral disc with a well-defined, black margin (width ~2–3 mm wide). Tail slightly darker dorsally than ventrally; ventral surface forward of ventral fold dark brownish and blotchy; ventral fold uniformly dark (in largest paratypes somewhat darker distally than basally); dorsal fold uniformly dark; banding on post-fold tail primarily black with 4 pale bands (widths and positions of bands variable in paratypes); sting bases greyish white. Clasper dorsal surface slightly paler than dorsal tail; ventral surfaces paler.

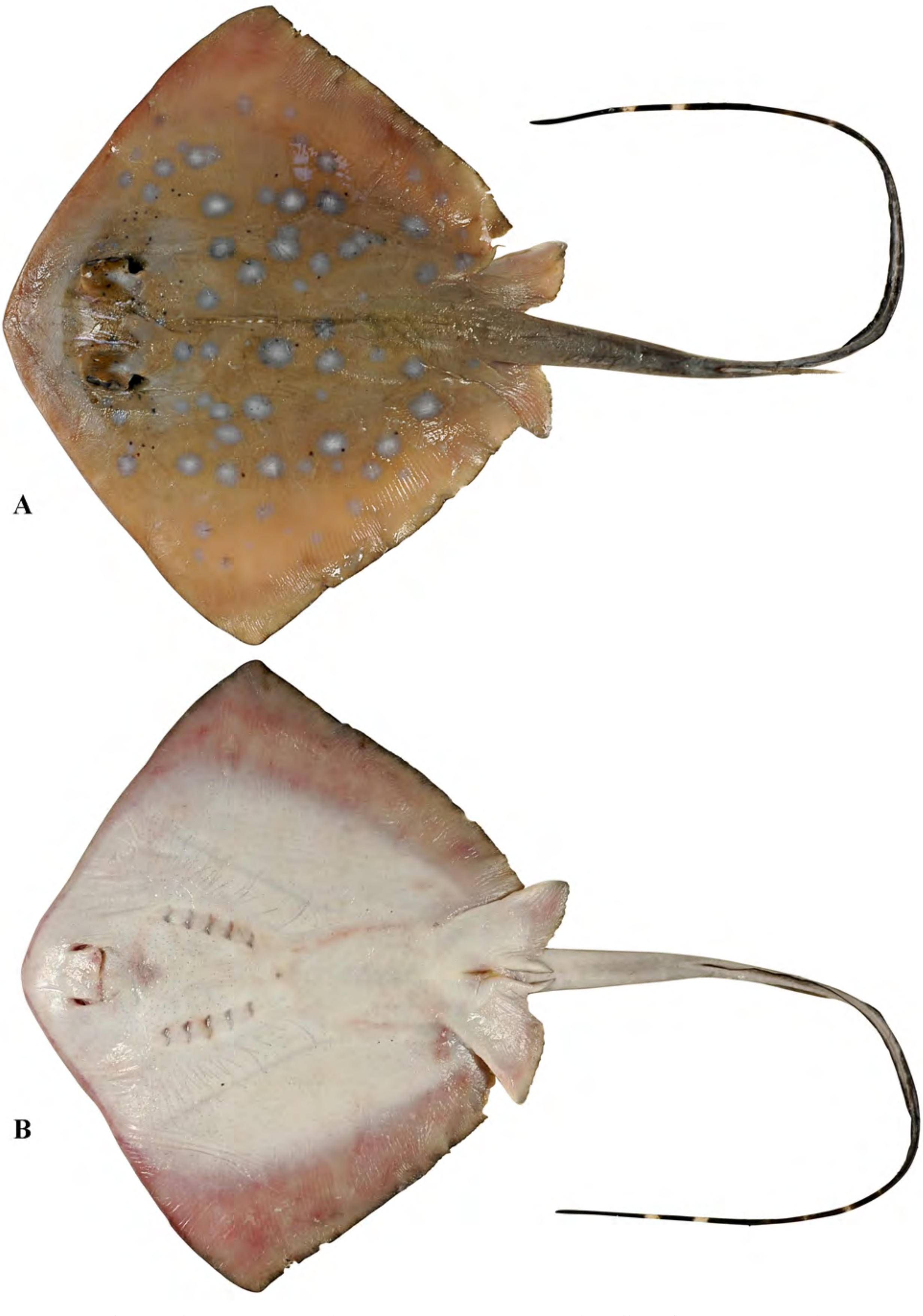

FIGURE 9. Holotype of *Neotrygon australiae* sp. nov. (CSIRO 7016-01, juvenile male 235 mm DW) from Queensland, Australia (fresh): (A) dorsal view; (B) ventral view.

FIGURE 10. Holotype of *Neotrygon caeruleopunctata* sp. nov. (MZB unreg [ex CSIRO H 7852-03]), adolescent male, 225 mm DW) from Bali, Indonesia (preserved): (A) dorsal view; (B) ventral view.

FIGURE 11. Dorsal view (fresh) of an adult female *Neotrygon caeruleopunctata* sp. nov. (CSIRO H 7850-01, 350 mm DW) from Central Java, Indonesia.

Size. Type specimens consist of an adult male of 311 mm DW, two adolescent males of 227 and 295 mm DW, and five females of 247–350 mm DW. White & Dharmadi (2007, as *Dasyatis* cf. *kuhlii* Bali form) reported a size at 50% maturity in males of 312 mm DW and a maximum size of females and males of 471 and 450 mm DW, respectively. They also reported that pregnant females contained two pups with a size at birth of 170 mm DW.

Distribution. Type specimens collected from fish landing sites in Bali and southern Central Java in Indonesia (Fig. 8). Fishers catching this species from these landing sites operate in adjacent waters close to port and are not translocated from other areas. Probably not found east of the Wallace Line based on the presence of *N. australiae* from Lombok, the next island east from Bali, between which the Wallace Line runs. Populations further west in the Indian Ocean are unresolved but are close to this form.

Etymology. Derived from the Latin *caeruleus* (sky blue) and *punctum* (dot or spot) with reference to its bluespotted coloration and having a wider distribution than other blue-spotted forms. Vernacular: Bluespotted Maskray.

TABLE 2. Morphometric data for the holotype of *Neotrygon caeruleopunctata* sp. nov. (MZB unreg [ex CSIRO H 7852-03]),), with ranges and means provided for measured paratypes, and for the holotype of *Neotrygon orientale* sp. nov. (MZB unreg [ex CSIRO H 7858-01]), and ranges and means for the measured paratypes. Measurements expressed as a percentage of disc width.

	N. caeruleopunctata sp. nov.				***N. orientale*** **sp. nov.**			
	Holotype	Paratypes			Holotype	Paratypes		
		Min.	Max.	Mean		Min.	Max.	Mean
Disc width (mm)	227	247	350		213	171	343	
Total length	200.9	178.3	218.2	195.2	181.2	178.0	212.9	200.7
Disc length	80.9	80.0	83.0	82.0	79.3	80.0	83.6	81.0
Snout to pectoral-fin insertion	68.8	69.8	71.5	70.4	67.5	66.8	72.9	69.6
Disc thickness	11.2	11.0	13.1	11.9	12.5	12.3	13.2	12.8
Snout (preorbital) length	15.0	13.9	16.3	15.4	14.2	14.3	14.7	14.5
Snout (preorbital) horizontal length	13.6	11.7	14.5	13.6	12.8	12.3	13.0	12.6
Pelvic-fin (embedded) length	20.9	20.6	21.9	21.3	21.4	21.0	22.4	22.0
Width across pelvic-fin base	17.3	17.1	19.1	18.2	17.5	19.1	20.2	19.7
Greatest width across pelvic fins	29.7	32.6	39.5	37.0	32.4	27.1	42.6	34.5
Cloaca origin to tail tip	133.9	110.6	147.5	126.7	117.3	111.4	146.3	132.9
Tail width at axil of pelvic fins	8.3	8.0	8.9	8.3	7.2	7.6	8.7	8.1
Tail height at axil of pelvic fins	5.6	5.1	6.4	5.4	4.7	4.2	5.8	5.3
Pectoral-fin insertion to sting origin	40.9	38.1	44.5	42.1	34.7	35.7	44.0	40.0
Cloaca origin to sting	42.0	42.4	45.8	44.3	38.4	38.8	44.9	42.2
Tail width at base of sting	3.7	3.4	3.8	3.6	2.7	3.1	3.6	3.3
Tail height at base of sting	3.2	2.7	3.2	3.0	3.0	2.6	3.3	3.0
Sting 1 length	–	–	–	–	–	–	–	–
Sting 2 length	–	–	–	–	–	–	–	–
Snout preoral (to lower jaw) length	14.8	12.9	15.4	14.7	13.9	12.5	15.0	14.2
Mouth width	7.3	6.6	7.9	7.1	7.0	7.0	7.5	7.2
Distance between nostrils	6.8	6.8	7.4	7.0	7.7	7.1	8.0	7.4
Interorbital width	8.4	6.8	8.1	7.3	5.8	6.0	7.6	6.9
Inter-eye width	17.8	15.8	17.2	16.5	16.3	15.6	19.2	17.3
Snout to maximum width	34.0	34.9	37.8	36.5	35.4	35.1	37.5	36.6
Eye length	6.1	4.8	5.5	5.2	6.2	5.1	6.8	5.9
Orbit diameter	8.6	6.9	7.9	7.2	8.4	6.7	9.4	8.3
Spiracle length	7.1	6.9	7.4	7.1	7.0	6.7	7.9	7.4
Interspiracular width	14.4	12.9	13.8	13.4	14.1	13.3	15.5	14.5
Orbit and spiracle length	10.7	9.3	11.0	10.2	11.0	10.2	13.0	11.5
Nostril length	3.3	2.5	3.5	3.0	3.8	3.1	3.8	3.4
Snout prenasal length	12.0	10.5	12.6	11.7	11.2	9.8	11.4	10.6
Nasal curtain length	5.7	4.5	5.6	5.2	5.7	5.0	5.6	5.4
Nasal curtain width	8.7	8.0	9.4	8.6	9.7	8.9	10.0	9.3
Orbit to pectoral-fin insertion	47.2	48.7	52.2	50.3	47.9	46.4	52.9	49.2
Snout to origin of cloaca	67.0	67.4	70.7	68.6	63.9	66.5	71.6	68.0

......continued on the next page

TABLE 2. (Continued)

	N. caeruleopunctata sp. nov.				*N. orientale* sp. nov.			
	Holotype	Paratypes			Holotype	Paratypes		
		Min.	Max.	Mean		Min.	Max.	Mean
Width 1st gill slit	3.2	2.8	3.2	3.0	3.0	2.9	3.5	3.2
Width 3rd gill slit	3.4	3.4	3.9	3.5	3.4	3.2	3.6	3.3
Width 5th gill slit	2.2	2.1	2.7	2.4	2.6	2.0	2.3	2.2
Head length	37.2	36.6	38.5	37.4	34.8	35.0	37.4	36.1
Distance between 1st gill slits	17.7	16.1	17.3	16.7	15.4	15.8	17.0	16.2
Distance between 5th gill slits	9.8	8.4	9.7	9.0	8.7	8.4	9.2	8.9
Cloaca length	5.9	6.3	7.1	6.6	6.6	6.9	7.8	7.3
Clasper postcloacal length	8.7	24.3	24.3	24.3	17.4	20.3	20.3	20.3
Clasper length from pelvic axil	4.5	12.5	12.5	12.5	10.9	13.9	13.9	13.9

Neotrygon orientale sp. nov.

(Figs. 5d, 6d, 7d, 12; Table 2)

Neotrygon kuhlii Clade 2—Puckridge *et al*., 2013: p. 6.
Neotrygon kuhlii 1—Naylor *et al*., 2012: p. 76, fig. 58.

Holotype. MZB unreg (ex CSIRO H 7858-01) (tissue accession GN4267), late-adolescent male 213 mm DW, Muara Kintap, South Kalimantan, Indonesia, 3°54.26′ S, 115°15.53′ E, 30 Nov 2006.

Paratypes. 5 specimens: CSIRO H 6130-01, female 254 mm DW, Muara Angke fish market, Jakarta, Indonesia, 6°06′ S, 106°48′ E, 4 Apr 2001; CSIRO 6136-01, female 240 mm DW, CSIRO 6136-04, adult male 220 mm DW, Muara Angke fish market, Jakarta, Indonesia, 6°06′ S, 106°48′ E, 31 Jan 2003; CSIRO H 7099-09 (tissue accession GN4754), female 171 mm DW, Flamboyan Market, Pontianak, West Kalimantan, Indonesia, 0°2.34′ N, 108°59′ E, 12 Jul 2008; CSIRO H 7848-01 (tissue accession GN4619), female 343 mm DW, Singkawang fish market, West Kalimantan, Indonesia, 0°55.11′ N, 108°59′ E, 28 Jul 2007.

Other material. 6 specimens: CSIRO 6136-02, adult male 238 mm DW, CSIRO 6136-03, female 223 mm DW, CSIRO 6136-05, adult male 215 mm DW, Muara Angke fish market, Jakarta, Indonesia, 6°06′ S, 106°48′ E, 31 Jan 2003; CSIRO H 7099-10 (tissue accession GN4755), female 145 mm DW, CSIRO H 7099-11 (tissue accession GN4756), female 145 mm DW, Flamboyan Market, Pontianak, West Kalimantan, Indonesia, 0°2.34′ N, 108°59′ E, 12 Jul 2008; CSIRO H 7849-01 (tissue accession BW-A7737), female 290 mm DW, Muara Angke fish market, Jakarta, Indonesia, 6°06′ S, 106°48′ E, 8 Oct 2009.

Diagnosis. A small *Neotrygon* of the *kuhlii*-complex (reaching at least 38 cm DW; males maturing at 22 cm DW) with the following combination of characters: disc much broader than long, width 1.2–1.3 times length; pectoral apices abruptly angular; snout fleshy, broadly rounded to weakly angular, angle 124–129°, length 1.9–2.5 times interorbital width; maximum width relatively well forward on disc, length from snout tip to pectoral-fin insertion 1.8–2 times and disc width 2.7–2.9 times horizontal distance from snout tip to maximum disc width; preoral length 1.8–2.2 times mouth width; internasal distance 1.3–1.6 in prenasal length; interspiracular distance 13–16% DW; nostril length 3.1–3.8% DW; nasal curtain width 8.9–10% DW; small mouth, width 7–7.5% DW; horizontal distance from cloaca to caudal sting base 48–56% of disc length; thornlets present in nuchal region and weakly developed in the lumbar regions in adults, absent from tail in all sizes; minute, widely-spaced dermal denticles present on mid-disc of large adults; pectoral-fin radials 105–110; total vertebral centra (including synarcual) 125–141, trunk centra (including synarcual) 36–42; blue spots on disc moderately large, largest 0.5–0.9 in eye width; few blue spots on medial belt, 0–6 (mean 0.4), largest 2.8–3.3% DW; mask-like marking rather pronounced, covered with dark peppery spots; ventral surface of disc with diffuse greyish submarginal bands; ventral tail fold dusky with darker edge.

Description. Disc rhombic, straight to convex anteriorly and not produced; much broader than long, width 1.26 times length in holotype (1.20–1.25 in paratypes); axis of greatest width of disc relatively well forward on disc, slightly forward of scapular region, its distance from snout tip 1.91 (1.82–2.03) times in distance from tip of snout to pectoral-fin insertion; body relatively robust, thickness 8.0 (7.6–8.1) times in disc width, raised slightly above cranium; apex broadly rounded, narrowly or abruptly angular, pectoral angle 88° (85–90°); posterior margin straight to undulate; free rear tip narrowly angular. Pelvic fins narrowly subtriangular, anterior margin almost straight, apex narrowly rounded, posterior margin moderately convex, united with inner margin (free rear tip indiscernible); rather small, length 21.4% (21.0–22.4%) DW; 1.22 (1.06–1.15) times width across fin bases. Claspers of adult males relatively small, narrow, depressed, tapering, acutely pointed apically; outer length (from axil of pelvic fin) 13.9% DW.

Tail moderately broad-based, tapering rapidly to caudal sting(s), with dorsal and ventral skin folds; base moderately depressed, broadly oval in cross-section, weakly convex above and below, width 1.51 (1.35–1.80) times depth; subcircular to rhomboidal in cross-section near origin of ventral skin fold, width 0.98 (0.99–1.17) times height at fold origin; tapering evenly in dorsoventral view posterior to caudal stings; moderately compressed below broken tips of caudal stings; sometimes damaged distally beyond folds; both dorsal and ventral skin folds prominent; tail very compressed, narrowly suboval in cross-section above mid ventral fold, width 0.62 (0.66–0.87) times depth; at end of fold weakly depressed, width 0.95 (0.82–0.98) times height; dorsal surface of tail posterior to caudal-sting bases with a weak naked groove; no skin folds present along lateral margin of tail. Dorsal skin fold well developed, short-based, pronounced, length about 9 (9–12) times its height, 1.91 (1.57–2.08) in snout length, 6.68 (6.58–7.50) in length of ventral fold; its height 1.06 (1.45–2.01) in height of mid-ventral fold; origin usually with a short low ridge before elevated portion; elevated portion much shorter than snout length. Ventral skin fold relatively long, 49.9 (47.1–60.1)% DW, very narrow, tapering, deepest forward of dorsal skin fold; much longer based and slightly taller than dorsal skin fold; length 2.01 (1.66–2.12) in disc width; depth at quarter length 0.34 (0.52–0.82), at mid length 0.54 (0.76–0.87), at three quarter 0.42 (0.70–1.01) in adjacent tail height; originating almost below or just forward of first sting origin; horizontal distance from cloaca to sting origin 1.66 (1.48–1.72) in precloacal length.

Snout fleshy (more so in large paratypes), short, broadly rounded; not acute at apex, but without obvious apical lobe; angle 126° (124–129°); narrowly rounded when viewed laterally, becoming marginally more depressed towards apex; preoral snout length 1.99 (1.75–2.15) times mouth width, 1.81 (1.70–2.13) times internarial distance, 0.91 (0.74–0.95) times distance between first gill slits; preorbital snout short, direct length 2.45 (1.90–2.42) times interorbital length; snout to maximum disc width 2.83 (2.67–2.85) in DW; interorbital space almost flat, narrow; eyes large, dorsolateral, strongly protruding (less obvious in some paratypes), ventral margin partly covered by thick skin fold; orbit greatly elevated above disc and interorbital space, diameter 0.84 (0.80–1.06) in spiracle length, eye length 1.14 (1.10–1.40) in spiracle length; inter-eye distance 2.63 (2.54–3.77) times eye length. Spiracles large, crescentic with dorsolateral opening; dorsal margin with a medial protuberance. Nostril slit-like, directed longitudinally to slightly oblique; lateral margin fleshy; anterior nasal fold internal, very narrow, membranous; broad oronasal groove present; internarial space 1.46 (1.33–1.61) in prenasal length, 2.03 (2.08–2.38) times nostril length. Nasal curtain relatively narrow, skirt-like, short, width 1.69 (1.59–1.99) times length; weakly bilobed, posterior margin of each lobe moderately convex; surface crenulated, weakly papillate, medial groove not obvious, sparsely covered with minute pores; apices recessible within lateral margin of oronasal groove; lateral margin almost straight, smooth-edged, usually partly enveloped by narrow posterior fold of nostril; posterior margin lightly fringed, concave medially, vaguely following contour of lower jaw, usually overlapping lower jaw when mouth closed.

Mouth small, jaws strongly asymmetric; lateral grooves shallow, sometimes almost indistinct, curved slightly, extending from nostril to slightly below lower jaw, length much shorter than nasal curtain length; not projecting forward when open, not protrusible; skin on chin and margin of lower jaw not particularly fleshy, papillate; teeth of paratype CSIRO H 7848–01 uniformly close-set in both jaws, in oblique rows, not arranged in obvious quincunx, rows in upper jaw ~31, lower jaw ~35. Upper jaw strongly arched, strongly double convex; teeth of anterior part of upper jaw concealed when mouth closed; symphysial part of jaw projecting anteroventrally. Lower jaw strongly convex with a truncate to weakly concave anterior margin, interlocking into upper jaw when mouth closed; teeth not visible when mouth closed. Upper jaw of adult female paratype (CSIRO H 7848–01) with a raised row of enlarged teeth with elongate blunt cusps (directed lingually) near the middle of each side of jaw; teeth otherwise similar in shape, cusps shorter than their base length; teeth at symphysis barely larger than those laterally, cups small and directed lingually. Teeth in lower jaw broad based, low, with short knob-like cusps and convex anterior margins; those toward angle of lower jaw with slightly shorter cusps. Floor of mouth in paratypes with two very long, lobe-like, very closely spaced, medial oral papillae (holotype not dissected); no smaller papillae near angle of each jaw.

Gill openings elongate S-shaped, fringe not discernible; length of first gill slit 1.14 (1.28–1.59) times length of fifth gill slit, 2.36 (2.05–2.43) times in mouth width; distance between first gill slits 2.00 (2.03–2.30) times internarial space, 0.44 (0.43–0.46) times ventral head length; distance between fifth gill slits 1.13 (1.13–1.26) times internasal distance, 0.25 (0.24–0.25) times ventral head length.

Total pectoral-fin radials 109 (105–110); propterygium 42–43 (42–44), mesopterygium 17–19 (16–18), metapterygium 48–49 (45–49). Pelvic-fin radials: 1 (1) + 19–20 (19 in a male paratype, 23–26 in female paratypes). Vertebral centra total (including synarcual) 140 (125–141); total (excluding synarcual) 135 (122–141); monospondylous (including synarcual) 41 (36–42); monospondylous (excluding synarcual) 36 (33–35); pre-sting diplospondylous 65 (61–70); post-sting diplospondylous 34 (25–29).

Squamation. Disc and tail of holotype lacking dermal denticles; a single median row of 4–8 variable-length, spear-shaped to narrow lanceolate thornlets on nape, anteriormost thornlets slightly smaller than those at end of row; no thornlets on lumbar region or tail; row length 8–11% DW when present, less than ¾ of interspiracular width; angle much less than 45° to horizontal (appearing vaguely saw-shaped in lateral view); lateral scapular thorns absent. In largest paratype (CSIRO H 7848-01), row of thornlets on nape disjunct from short anterior lumbar row (no thornlets on posterior disc or tail); wide band of minute, upright, widely-spaced dermal denticles extending from interorbit to tail base (evident to the eye as minute specks and barely detectable to touch).

One caudal sting on holotype (two broken stings in largest paratype), not intact; enveloping membrane absent; distance from cloaca to sting base 0.48 (0.48–0.56) in disc length.

Colour. Live coloration (based on holotype). Dorsal surface pale yellowish brown centrally and blue-spotted, graduating to translucent margin of disc and pelvic fins; eye whitish, orbital membrane similar to disc. Blue spots medium-sized, irregularly spaced, weakly ocellate, with faint blue centres and surrounded by only slightly darker blue, diffuse-edged outer rings; distributed mainly over central parts of pectoral fins; present on through medial belt; thornlets in medial row white and contrasted with adjacent skin; dark speckles mostly concentrated around mask; mask-like marking on head rather pronounced, with dense peppering of dark speckles on and around orbits. Ventral surface largely white, marginal band around disc greyish and diffuse edged. Tail similar to disc colour dorsally before caudal sting, darker with black and white or yellowish bands toward its tip; dorsal fold pale, similar to dorsal tail; ventral fold dusky with darker edge.

In preservative (based on holotype). Dorsal surface pale greyish brown; mask well-developed and contrasting with anterior disc, distributed over orbital membranes and in bands between orbits, forward of orbits and blotches besides orbits (two large pale blotches on interorbital space), peppering of small black spots well-developed on mask (less obvious in paratypes); dark blotch but no extended marking on nape; bluish spots medium-sized (in paratypes largest spots 2.5–5% DW), appearing as greyish blue markings with no or indistinct pale centres (rarely ocellate). Ventral surface of disc and pelvic fins predominantly white with narrow dusky edges; submarginal bands barely detectable, weak and diffuse-edged in smallest types (absent in largest paratype). Tail much darker dorsally than ventrally; ventral surface forward of ventral fold largely pale (occasionally with some dusky patches); ventral fold dark distally, sometimes with a very narrow pale base, strongly contrasted with ventral surface of tail anteriorly; dorsal fold uniformly dusky; banding on post-fold tail primarily blackish with 4 pale dusky bands (banding on paratypes variable); sting bases greyish white. Claspers only marginally paler than dorsal tail; ventral surface slightly paler than dorsal surface.

Size. Type specimens consisted of an adult male of 220 mm DW, a late-adolescent male of 213 mm DW, and four females of 171–343 mm DW. White & Dharmadi (2007, as *Dasyatis* cf. *kuhlii* Java form) reported a size at 50% maturity for males of 237 mm DW and a maximum size for females and males of 379 and 324 mm DW, respectively. They also reported that pregnant females contained only a single pup with a size at birth of ~120 mm DW.

Distribution. Type specimens taken from fisheries bycatch and fish landing sites in Kalimantan and West Java (Jakarta) in Indonesia (Fig. 8). Additional specimens also taken from Malaysian Borneo and the Philippines (Naylor *et al.*, 2012). Specimens taken from the Muara Angke landing site in Jakarta were predominantly caught by trap fisheries operating off Sumatra thus its presence in Java is not confirmed. Accurate depth information not available but probably found mostly inshore in depths of less than 100 m.

Etymology. Epithet demarcates the South-East Asian distribution of this member of the bluespotted maskray complex within the genus *Neotrygon*. Vernacular: Oriental Bluespotted Maskray.

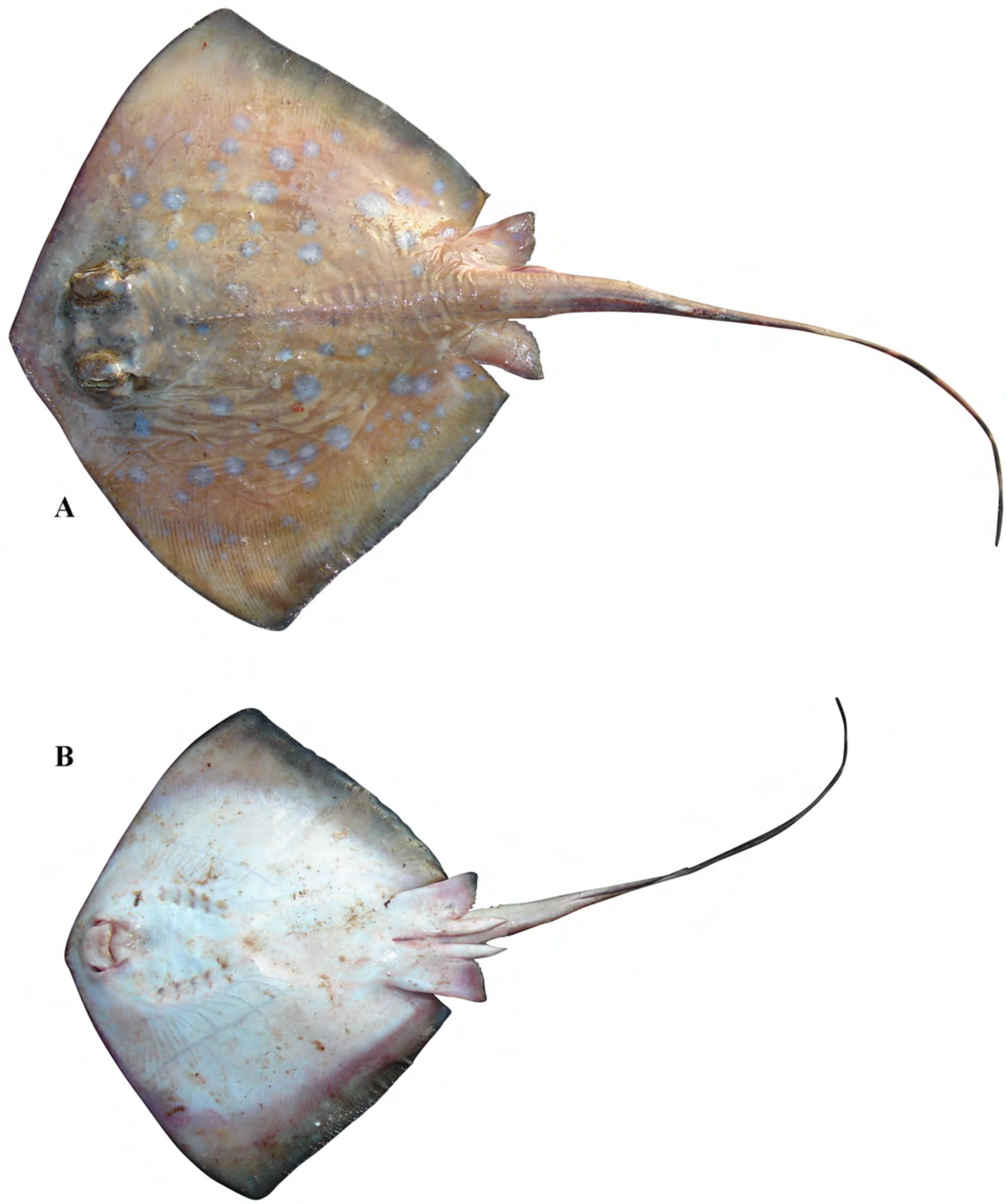

FIGURE 12. Holotype of *Neotrygon orientale* sp. nov. (MZB unreg [ex CSIRO H 7858-01]), late-adolescent male 213 mm DW) from South Kalimantan, Indonesia (fresh): (A) dorsal view; (B) ventral view.

Comparisons

Neotrygon kuhlii is distinguishable from other species treated here in colouration; the three new species all have a more complex pattern of bluish spots or ocelli on the dorsal disc and theses spots are much larger in size. In comparison, the blue-spotted pattern in *N. kuhlii* is very sparse. Of the three species, *N. kuhlii* has a more similar disc shape to *N. australiae* (snout angle <110°) whereas the widest part of the disc is well forward in both *N. caeruleopunctata* and *N. orientale* (snout angle 124–130°). The angularity of the disc is also reflected in the measurement of the horizontal distance from the snout to maximum disc width: exceeding 38.5% DW in *N. kuhlii* and *N. australiae*, less than 38.5% DW in *N. caeruleopunctata* and *N. orientale. Neotrygon kuhlii* also appears to have a narrower tail than *N. caeruleopunctata* (base width 7.2–7.6% vs. 8.0–8.9% DW; base depth 4.1–5.0% vs. 5.1–6.4% DW; width at caudal sting base 3.0–3.3% vs. 3.4–3.8% DW), and longer snout than *N. australiae* and *N. orientale* (direct preorbital length 16.1–17.2% vs. 13.3–14.6% and 14.2–14.7% DW, respectively; horizontal preorbital length 13.6–14.4% vs. 10.5–12.0% and 12.3–13.0% DW, respectively). It also appears to be slightly less thick through the trunk (body depth 11.1–12.3% vs. 12.3–13.2% DW) and have wider interorbit (7.5–9.4% vs. 5.8–7.6% DW) than *N. orientale*.

Two other forms of the *kuhlii*-complex identified by Puckridge *et al*. (2013), Clades 1 and 9 relate to *N. varidens* Garman and *N. trigonoides* Castelnau, respectively. Both of these species were listed in the synonymy of *N. kuhlii* in Garman's (1913) *Plagiostomia*; *N. varidens* questionably. Earlier, Garman (1885), in a paper detailing shark and ray holdings of the Smithsonian Institution (US National Museum), treated *N. kuhlii* and *N. varidens* together as separate species, stating of '*Dasybatus' varidens* 'The species resembles *D. kuhlii* but has a broader disc and no spots'. Recent research has given support for *varidens* as a valid species of *Neotrygon* and the species is currently being redescribed based on material from the Gulf of Thailand, Borneo and Taiwan. The absence or paucity of spots and plain dorsal disc coloration (mauve or dark brown), as well as morphometric details, support the molecular findings.

Neotrygon trigonoides (Clade 9 of Puckridge *et al.*, 2013) is a valid species which occurs along the eastern Australian seaboard, the Great Barrier Reef islands, and off New Caledonia. Last & White (2008) discussed species-level substructure within *N. kuhlii*, suggesting that the taxon was likely to be a species complex and confirmed that, based on morphology, the holotype of Castelnau's *Raya trigonoides* is conspecific with eastern Australian forms of *N. kuhlii*. This finding was supported by Puckridge *et al*. (2013) using molecular data. Borsa *et al*. (2013) also came to a similar conclusion using molecular data and resurrected *N. trigonoides*, but failed to comprehend the need to characterise the type of *N. kuhlii* before making this decision. While some information on spotting was provided, they failed to understand the need to follow standard taxonomic practices used for the family group (stingrays), and provided no other descriptive information on the species. A more robust study of the taxonomy of this species is in progress.

As discussed above, *N. australiae* is distinguishable from the other two new species by its more angular disc. It also has many more and larger bluish spots on the body (mean diameter of largest spot 5.3% vs. 3.3% and 4.1% DW respectively for *N. caeruleopunctata* and *N. orientale*). The medial belt usually has several blue spots (mean number of spots ~9.4) whereas the other species have few or none within the belt (mean number of spots ~0.8 and ~0.4 respectively for *N. caeruleopunctata* and *N. orientale*); these spots on the medial belt when present are substantially larger in *N. australiae* (mean diameter of largest spot 4.6% vs. 0.8% and 1.1% DW respectively for *N. caeruleopunctata* and *N. orientale*).

Neotrygon caeruleopunctata and *N. orientale* are similar in body shape but typically differ in the relative lengths of the tail folds; ventral fold base length 5.2–6.1 times dorsal fold base length in *N. caeruleopunctata* vs. 6.6–7.5 times in *N. orientale*; preorbital length 1.3–1.7 times dorsal fold length vs. 1.6–2.1 times in *N. orientale.* Males of *N. orientale* mature earlier (~22 cm vs. ~31 cm DW) and the species appears to be smaller (attains ~38 cm vs. ~47 cm DW). The ventral tail preceding the caudal sting and the submarginal band on the ventral disc are both typically darker in *N. caeruleopunctata.*

Additional forms close to *N. caeruleopunctata* in the Indian Ocean may represent additional species. More material is needed to resolve their taxonomy.

DNA barcoding can be a useful tool for distinguishing taxa at the species level and has been instrumental in highlighting species complexes such as the *Neotrygon kuhlii*-complex. It should be noted that barcoding results should not be used in isolation, but alongside in-depth morphometric analyses thereby potentially highlighting where cryptic speciation may be present. In this study, the COI barcoding results clearly separated the three new species from their closest congeners, *N. kuhlii*, *N. varidens* and *N. trigonoides.* Representative COI sequences for these 6 species are presented in Appendix 1. *Neotrygon australiae* was least divergent from *N. caeruleopunctata*, while *N. orientale* was least divergent from *N. varidens* (Table 3). *Neotrygon trigonoides* and *N. kuhlii* differed markedly from each other and the three new species and *N. varidens* (Table 3).

TABLE 3. Estimate of evolutionary divergence over sequence pairs between groups. Standard error estimates are shown in italics and were obtained by a bootstrap procedure (1000 replicates).

	1	2	3	4	5	6
1 - *N. kuhlii*	-----	*0.010*	*0.010*	*0.009*	*0.010*	*0.010*
2 - *N. trigonoides*	0.040	-----	*0.010*	*0.009*	*0.009*	*0.008*
3 - *N. australiae*	0.042	0.048	-----	*0.008*	*0.009*	*0.009*
4 - *N. caeruleopunctata*	0.039	0.040	0.030	-----	*0.009*	*0.007*
5 - *N. varidens*	0.044	0.041	0.037	0.034	-----	*0.006*
6 - *N. orientale*	0.043	0.035	0.036	0.028	0.018	-----

Key to the genus *Neotrygon*

1a. Dorsal surface largely plain, without any prominent spots or blotches or reticulations (apart from mask-like pattern on head) 2
1b. Dorsal surface with more or less complex pattern of spots and blotches or reticulations 3
2a. Dorsal surface plain dull greyish green with faint dark transverse bar on eyes; a row of a few thornlets on tail preceding sting in adults; prominent dorsal and ventral tail folds; northern Australia, Gulf of Papua & eastern Indonesia . . . . . . *N. annotata*
2b. Dorsal surface plain, light reddish brown or olivaceous; disc and tail usually without thornlets; dorsal tail fold short but prominent, ventral tail fold low; North-West Pacific . . . . . . *N. varidens*
3a. Dorsal surface with blue/bluish spots (sometimes small) 4
3b. Dorsal surface without blue/bluish spots, but with complex pattern (black-speckled, reticulate or very ornate) 8
4a. Dorsal surface with relatively small and sparse blue spots; dark mask on eyes pronounced; thornlets on nuchal region in large specimens; South-West Pacific 5
4b. Dorsal surface with larger blue spots; dark mask subtle or pronounced; dark spots peppered on disc; thornlets on nuchal and lumbar regions in large specimens 6
5a. No dark peppery spots on upper disc (or very sparse) . . . . . . *N. kuhlii*
5b. Dark peppery spots on disc (concentrated around mask and over central disc) . . . . . . *N. trigonoides*
6a. Large blue ocellate spots, dark mask usually subtle; snout less obtuse, angle < 110°; Australia, New Guinea, eastern Indonesia . . . . . . *N. australiae*
6b. Medium-sized blue spots, dark mask more or less pronounced; snout more obtuse, angle 124-130° 7
7a. Blue spots mainly ocellate; ventral tail before caudal sting and fold dark; thornlets on nuchal and lumbar regions of adults; Indian Ocean . . . . . . *N. caeruleopunctata*
7b. Blue spots weakly ocellate; ventral tail before caudal sting whitish; tail fold dusky and dark edged; thornlets on nuchal region, sometimes with weak denticles on lumbar region; North-West Pacific . . . . . . *N. orientale*
8a. Dorsal surface with dense scattering of small orange spots and larger bluish blotches, mask not pronounced; a row of 4-5 nuchal thornlets; prominent dorsal and ventral tail folds; Western Australia . . . . . . *N. ningalooensis*
8b. Dorsal surface without small orange spots, instead black speckled or with reticulations 9
9a. Dorsal surface with complex honeycomb pattern (sometimes weakly speckled); a few thornlets on mid-dorsal row of disc and tail; prominent dorsal and ventral tail folds; northwestern Australia . . . . . . *N. leylandi*
9b. Dorsal surface with dense black speckling, often on a reticulate background; mid-dorsal row of thornlets only on disc; low dorsal and ventral tail folds; northeastern Australia . . . . . . *N. picta*

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Appendix 1

Cytochrome oxidase subunit 1 (CO1) sequence:

Neotrygon kuhlii (CSIRO H 7723–01; GT8223):
GTAGGCACTGGCCTCAGTTTACTTATCCGAACAGAACTAAGCCAACCAGGCGCTTTACTGGGTGATGATCA
GATTTATAATGTAATCGTTACTGCCCACGCCTTCGTAATAATCTTCTTTATAGTAATACCAATTATAATCGGTGG
GTTTGGTAACTGACTAGTGCCCCTGATGATTGGAGCTCCGGACATAGCCTTTCCACGAATAAACAACATAAG
TTTCTGACTTCTGCCTCCCTCCTTCCTATTACTGCTAGCCTCAGCAGGAGTAGAAGCCGGAGCCGGAACAG
GTTGAACAGTTTATCCTCCATTAGCTGGTAATCTAGCACATGCTGGAGCTTCTGTGGACCTTACAATCTTCTC
TCTTCACCTAGCAGGTGTTTCCTCTATTCTGGCATCCATCAACTTTATCACAACAATTATTAATATAAAACCGC
CTGCAATCTCCCAATATCAAACCCCATTATTCGTCTGATCCATCCTTGTTACAACTGTGCTTCTCCTGCTATCC
CTACCAGTCCTAGCAGCTGGCATTACTATACTCCTCACAGACCGAAATCTTAATACAACTTTCTTTGATCCAG
CTGGAGGAGGAGATCCTATTCTTTAC

Neotrygon australiae (holotype CSIRO H 7016-01, BW-A6850; GenBank acc. KC250635):
CTTATCCGAACAGAATTAAGCCAACCAGGTGCTTTACTGGGTGATGATCAAATTTATAATGTTATCGTTACTG
CCCACGCCTTCGTAATAATCTTCTTTATAGTAATGCCAATTATAATTGGTGGGTTTGGTAACTGACTAGTGCCC
CTGATAATTGGGGCTCCGGACATAGCCTTTCCACGAATAAACAACATAAGTTTTTGACTTCTGCCCCCCTCA
TTCCTATTACTGCTAGCCTCAGCAGGAGTAGAAGCCGGAGCTGGAACAGGTTGAACAGTTTATCCCCCATTA
GCCGGTAATCTAGCACATGCCGGAGCTTCTGTAGATCTTACAATCTTCTCTCTTCACCTAGCAGGTGTTTCCT
CTATTCTGGCATCCATCAACTTTATCACAACAATTATTAATATAAAACCACCTGCAATCTCCCAGTATCAAAC
CCCATTATTCGTCTGATCTATTCTTGTTACAACTGTACTTCTCCTGCTATCCCTACCAGTCCTAGCAGCTGGCA
TTACTATACTCCTCACAGATCGAAATCTTAATACAACTTTCTTCGACCCAGCTGGAGGAGGGGATCCCATTCT
TTACCAA

Neotrygon caeruleopunctata (holotype MZB unreg [ex CSIRO H 7852-03], BW-A2572; GenBank acc. EU398744):
CCTTTACTTAGTCTTTGGTGCATGAGCAGGGATAGTAGGCACTGGCCTCAGTTTACTTATCCGAACAGAACT
AAGCCAACCAGGCGCTTTACTGGGTGATGATCAAATTTATAATGTAATCGTCACTGCCCACGCCTTCGTAAT
AATCTTCTTTATAGTAATGCCAATTATAATTGGTGGGTTCGGTAACTGACTAGTGCCCCTGATAATTGGGGCC
CCGGACATAGCCTTTCCACGAATGAACAACATAAGTTTTTGACTTCTACCTCCCTCATTCCTATTACTGCTAG
CCTCAGCAGGAGTAGAAGCCGGAGCCGGAACAGGTTGAACAGTTTATCCCCCATTAGCTGGTAATCTAGCA
CATGCCGGAGCTTCTGTAGACCTTACAATCTTCTCTCTTCACTTAGCAGGTGTTTCCTCTATTCTGGCATCCA
TCAACTTTATCACAACAATTATTAATATAAAACCACCTGCAATCTCCCAGTATCAAACCCCATTATTCGTCTG
ATCTATCCTTGTTACAACTGTACTTCTCCTGCTATCCCTACCAGTCCTAGCAGCTGGCATTACTATACTCCTCA
CAGACCGAAATCTTAATACAACTTTCTTTGACCCAGCTGGGGGAGGAGATCCCATTCTTTACCAACACCTCT
TC

Neotrygon orientale (paratype CSIRO H 7849-01; BW-A7737; GenBank acc. GU673709):

CCTTTACTTAGTCTTTGGTGCATGAGCAGGGATAGTAGGCACTGGCCTCAGTTTACTTATCCGAACAGAAC
TAAGCCAACCCGGCGCTTTACTGGGTGATGATCAAATTTATAATGTAATCGTCACTGCCCACGCCTTCGTA
ATAATCTTCTTTATAGTAATGCCAATTATAATCGGTGGGTTTGGTAACTGACTAGTGCCCCTGATAATTGG
GGCTCCGGACATAGCCTTTCCACGAATAAATAACATAAGTTTTTGACTTCTACCTCCCTCATTCTTATTACT
GCTAGCCTCAGCAGGAGTAGAAGCCGGAGCTGGAACAGGTTGAACAGTTTATCCCCCATTAGCTGGTAAT
CTAGCACATGCCGGAGCTTCTGTAGACCTTACAATCTTCTCTCTTCACCTAGCAGGTGTTTCCTCTATTCTG
GCATCCATTAACTTTATCACAACAATTATTAATATAAAACCACCCGCAATCTCCCAATATCAAACCCCATT
ATTCGTCTGATCTATTCTTGTTACAACTGTACTTCTCCTGTTATCCCTACCAGTCCTAGCAGCTGGCATTAC
TATACTCCTCACAGACCGAAATCTTAATACAACTTTCTTCGACCCAGCTGGGGGAGGAGATCCCATTCTTT
ACCAACACCTC

Neotrygon varidens (not retained; BW-A2585; GenBank acc. EU398734)
CCTTTACTTAGTCTTTGGTGCATGAGCAGGGATAGTAGGCACTGGCCTCAGTTTACTTATCCGAACAGAACT
AAGCCAACCAGGCGCTTTACTGGGTGATGATCAAATTTATAATGTAATCGTTACTGCCCACGCCTTTGTAATA
ATCTTCTTTATAGTAATGCCAATTATAATCGGTGGGTTTGGTAACTGACTAGTGCCCCTGATAATTGGGGCTC
CGGACATAGCCTTTCCACGAATAAATAACATAAGTTTTTGACTTCTACCTCCCTCATTCTTATTACTGCTAGCC
TCAGCAGGAGTAGAAGCCGGAGCTGGAACAGGTTGAACAGTTTATCCCCCATTAGCTGGCAATCTAGCACA
TGCCGGAGCTTCTGTAGACCTTACAATCTTCTCTCTTCATCTAGCAGGTGTTTCCTCTATTCTGGCATCCATTA
ACTTTATCACAACAATCATTAATATAAAACCACCTGCAATCTCCCAGTATCAAACCCCATTATTCGTCTGATCT

ATTCTTGTTACAACTGTACTTCTCCTGTTATCCCTACCAGTCCTAGCAGCTGGCATTACTATACTCCTCACAG
ACCGTAATCTTAATACAACTTTCTTCGACCCAGCTGGTGGGGGAGATCCCATTCTTTACCAACACCTCTTC

Neotrygon trigonoides (not retained; BW-A6217; GenBank acc. GU673434)
CCTTTACTTAGTCTTTGGTGCATGAGCAGGGATAGTAGGCACTGGCCTTAGTTTACTTATCCGAACAGAACT
AAGCCAACCAGGCGCTTTACTGGGTGATGATCAAATTTATAATGTAATCGTCACTGCCCACGCCTTCGTAAT
AATCTTCTTTATGGTAATGCCAATTATAATCGGTGGGTTTGGTAACTGACTAGTACCCCTGATGATTGGAGCT
CCGGACATAGCCTTTCCACGTATAAACAACATAAGTTTTTGACTTCTACCTCCCTCCTTCCTACTCCTGCTAG
CCTCAGCAGGAGTAGAAGCTGGAGCTGGAACAGGTTGAACAGTTTATCCCCCATTAGCTGGTAATCTAGCA
CATGCCGGAGCTTCTGTAGACCTTACAATCTTCTCTCTTCACCTAGCAGGTGTCTCCTCTATTCTGGCATCCA
TCAACTTTATCACAACAATTATTAATATAAAACCACCTGCAATCTCCCAGTATCAAACCCCATTATTCGTCTG
ATCCATTCTTGTTACAACTGTACTTCTCCTGCTATCCCTACCAGTCCTAGCAGCTGGCATTACCATACTCCTTA
CAGACCGAAATCTTAACACAACTTTCTTTGACCCAGCTGGAGGAGGAGATCCCATTCTTTACCAACATCTC

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Urogymnus acanthobothrium sp. nov., a new euryhaline whipray (Myliobatiformes: Dasyatidae) from Australia and Papua New Guinea

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Abstract

The Mumburarr Whipray, *Urogymnus acanthobothrium* **sp. nov.** is described from a single specimen taken from the Cambridge Gulf, Western Australia, and from images of 10 other specimens from northern Australia and Papua New Guinea (all observed but not collected). It is a very large ray that attains at least 161 cm disc width, making it amongst the largest of the whiprays. The ventral tail below the caudal sting has a low, short-based fold. A ventral tail fold (or a dorsal fold) has not been recorded for any other himanturin stingray in the Indo-West Pacific. Molecular data suggest it is most closely related to a similar but more widely distributed cognate, *U. granulatus*. Both of these species share a suboval disc shape, similar squamation patterns, and the tail posterior to the sting is entirely white (at least in small individuals). *U. acanthobothrium* **sp. nov.** differs from *U. granulatus* in having a longer and more angular snout, longer tail, more posteriorly inserted caudal sting, lacks white flecks on the dorsal surface, and the ventral disc is uniformly white (rather than white with a broad black margin). It co-occurs with two other morphologically distinct *Urogymnus* in the region (*U. asperrimus* and *U. dalyensis*). Like *U. dalyensis* it occurs in both brackish and marine waters. A key is proved to the members of the genus *Urogymnus*.

Key words: *Urogymnus acanthobothrium*, Dasyatidae, giant whipray, new species, Australia, Papua New Guinea

Introduction

The first specimens of this large whipray, a pregnant female and her young, were caught in the Arafura Sea during a field survey of the parasite fauna of northern Australian chondrichthyan fishes. The survey was initiated in 1999 by Janine Caira and Kirsten Jensen as part of a wider study of cestode parasites funded by the American National Science Foundation (NSF; http://tapewormdb.uconn.edu/). For logistical reasons, presumably due to the large size of the female, only tissue and parasite samples were retained. One of us (PL) was approached by the collectors to provide an identification of this ray based on separate images of the female and her offspring. No presently recognised stingray occurring in the Indo-Pacific was known to attain such a large size, elongate oval disc with finely blotched yellowish grey dorsal coloration as an adult and a greyish brown pup. Subsequently, as part of another NSF funded project, a DNA sequence was obtained for the pregnant female specimen which also found it to be distinct from all other regional species (Naylor *et al.*, 2012).

A search to obtain material of this unidentified species was subsequently initiated to enable a formal description of this species. A large research project on northern Australia euryhaline elasmobranchs under the National Environmental Research Program (NERP) resulted in the capture of three unidentified stingrays in tidal rivers within Kakadu National Park in the Northern Territory. Due to permit restrictions, only tissue samples were retained. Molecular sequencing of one of these revealed that it matched the Arafura Sea specimen. Subsequently, an effort was made to collect a whole specimen of this species, and during sampling for euryhaline elasmobranchs under the National Environmental Science Program (NESP) in Cambridge Gulf in the Kimberley region of Western Australia, two specimens were caught with one of these retained.

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In another project running concurrently, observers from the National Fisheries Authority in Papua New Guinea obtained bycatch data and chondrichthyan samples from the Gulf of Papua prawn trawl fishery as part of a joint Australia/Papua New Guinea project. Three additional specimens of this large ray were observed in the shallow marine waters of the Gulf, but due to their size, only images (of two specimens) and tissue samples (from all three specimens) were obtained.

Morphological and molecular analyses of existing specimens indicate the new ray belongs to the recently redefined genus *Urogymnus* (*sensu* Last *et al.*, 2016). This group now consists of the new species, herein formally described and named, and five other valid nominal taxa: *Urogymnus asperrimus* (Bloch & Schneider, 1801), *U. dalyensis* (Last & Manjaji-Matsumoto, 2008), *U. granulatus* (Macleay, 1883), *U. lobistomus* (Manjaji-Matsumoto & Last, 2006) and *U. polylepis* (Bleeker, 1852). A key is provided to this group.

Materials and methods

Morphological methodology follows standards developed for whiprays (Himanturinae) by Manjaji (2004), which are based on modifications from Compagno & Heemstra (1984) and Last & Stevens (1994), as outlined by Last *et al.* (2006), and include some new descriptive features (i.e. morphology of the disc and its attributes, and squamation). Measurements were taken in millimetres (mm) as direct lengths (shortest point-to-point distance). Tooth rows for both upper and lower jaws were counted as diagonal rows across the tooth band beginning at one corner of the mouth (Fischer & Hureau, 1987). A corner of the mouth had to be slit so the tooth rows were fully visible for counting. Meristic data for the unique type (WAM) were obtained from radiographs. Counts follow Compagno & Roberts (1982), with some modifications: an intermediate radial (i.e. those that lie between the propterygium and mesopterygium, or between the mesopterygium and metapterygium) is assigned to the pterygium with the greatest level of overlap of its base to each of the pterygia concerned; the first distal propterygial and metapterygial elements were considered to form part of the main skeleton and were not incorporated into counts; the first enlarged anterior element of the pelvic fin (with 3–4 distal segments fused at their bases) were counted as one. Synarcual centra are not included in vertebral counts as they are obscured by mid-dorsal denticles on radiographs; the notochord of the tail was excluded from vertebral counts. Morphometric data, based on the holotype are presented in Table 1 and expressed as proportions of disc width (DW). Comparative morphometrics and meristics are based largely on Manjaji (2004) who focused more generally on taxonomy of the genus *Himantura* (now formerly including several species of *Urogymnus*; *sensu* Last *et al.*, 2016). Whiprays have developmental stages of the dorsal denticles that are extremely useful for distinguishing species (Manjaji, 2004; Last *et al.*, 2006). The sequence of development usually varies between species, and not all species display all possible stages of development. However, only one specimen of the new species was available for study, so while we were able to obtain some details from photographs of released specimens, our knowledge of denticle development in this species remains poor. The holotype was deposited at the Western Australian Museum, Perth (WAM) as a condition of the collection permit.

***Urogymnus acanthobothrium* sp. nov.**

Mumburarr Whipray
(Figs 1–7 Table 1)

Himantura sp.: Fyler *et al.*, 2009: 107, figs. 58 and 59
Himantura sp. 1: Naylor *et al*., 2012, tissue GN 2103 (specimen NT-96, not retained).
Himantura sp. 5: Last *et al*., 2016, tissues GN 2103, GN 13667, GN 16659, GN 16661, GN 16993, GN 17253, GN 17254 (Fig. 3).
Urogymnus sp. 5: Last *et al*., 2016, tissues GN 13667, GN 17253 (Fig. 5).

Holotype. WAM P. 34488-001, juvenile male 672 mm DW, West Arm of Cambridge Gulf, Western Australia, Australia, 15°33′ S, 127°59′ E, depth 2.2 m, collected by P. Kyne & G. Johnson, 11 Nov 2015.

Other Material. 9 specimens (none retained). Global Cestode Database NT-96 (photographs; tissue accession GN 2103), adult female 1610 mm DW with embryo ~265 mm DW (size estimated from image), east of Wessel

Islands, Northern Territory, Australia, 11°18′ S, 137°00′ E, ~60 m depth, collected by J. Caira & K. Jensen, 17 Nov 1999; PNG field accession 130034 (photograph; tissue accession GN 16659), female 1140 mm DW, east of Aibinio Island, Gulf of Papua, Papua New Guinea, 8°42′ S, 144°07′ E, 18–20 m depth, 2 Dec 2014, collected by S. Tova; PNG field accession 230260 (tissue accession GN 16661), male 1000 mm DW, east of Aibinio Island, Gulf of Papua, Papua New Guinea, 8°36′ S, 144°01′ E, 11–15 m depth, 11 Dec 2014, collected by S. Tova; PNG field accession 180028 (photograph; tissue accession GN 16993), late adolescent male 1030 mm DW, south of Deception Bay, Gulf of Papua, Papua New Guinea, 7°58′10″ S, 144°38′50″ E, 10–14 m depth, 6 Apr 2015, collected by S. Ohuesaho; PNG (no field accession number), photograph, adult male 1100 mm DW, Gulf of Papua, Papua New Guinea, 8°01′4″ S, 144°40′2″ E, 17–23 m depth, 2 Nov 2015, collected by National Fisheries Authority; photograph, female 520 mm DW and juvenile male 580 mm DW (released alive), Wildman River, Northern Territory, Australia, 12°21′30″ S, 132°08′30″ E, depth 7.8 m, collected by P. Kyne & P. Feutry, 29 Aug 2013; photograph, juvenile male 390 mm DW (released alive; tissue accession GN 13667), West Alligator River, Northern Territory, Australia, 12°22′48″ S, 132°15′33″ E, depth 4.2 m, collected by P. Kyne & M. Grubert, 22 Oct 2013; photograph, juvenile male 600 mm DW (released alive), Ord River, Western Australia, Australia, 15°16′42″ S, 128°16′41″ E, depth 8.7 m, collected by P. Kyne & G. Johnson, 7 Nov 2015.

Diagnosis. A species of *Urogymnus* distinguished by a combination of the following characters: disc elongate suboval, snout tip to axis of maximum width 53% DW; anterior disc margin not truncated, almost straight, lateral apices broadly rounded; preorbital snout broadly angular, angle 114°, with a very small apical lobe; preorbit long, length 26% TL, 2.1 times interorbital length; orbits small, protruded slightly; spiracle very large, 8.6% DW, 1.9 in orbit diameter; internasal distance 2.0 in prenasal length, 2.8 times nostril length; preoral snout length 2.6 times mouth width, 2.5 times internarial distance; caudal sting very large, length more than a 30% DW; mid-scapular denticles very small and inconspicuous; secondary denticles very small, rather widely spaced, band delimited but margin not sharply defined, band truncate forward of eye; minute upright tertiary denticles present, barely visible; low and short-based ventral tail fold present; dorsal disc colour variable, plain dark greyish brown to yellowish brown in juveniles, very finely and faintly mottled greyish white to yellowish brown in adults; ventral surface largely white, posterior disc without regular dark margins; tail beyond sting white in young, unknown but possibly paler than anterior tail in adults; propterygial radials 66, 3 times the number of mesopterygial radials; total vertebral segments (excluding synarcual) 151.

Description. Disc elongate suboval, width 94% of its length in holotype; robust, distinctly raised above mid-scapulocoracoid, maximum thickness 0.12 in disc width (DW); snout broadly angular, with a small but pronounced apical lobe, angle 114°; anterior margins almost straight, oblique to longitudinal axis of disc; lateral apices broadly rounded; posterior margin weakly convex, free rear tip narrowly rounded. Pelvic fins rather short, 21.2% DW; width across base 13.0% DW. Mature male unavailable for examination of adult clasper. Tail rather slender, whip-like, tapering evenly toward sting then becoming subcircular, length 2.18 times DW; base rather narrow, moderately depressed in cross-section, width 1.26 times height; caudal sting greatly enlarged, 30.3% DW, broad and strongly depressed. Ventral tail fold short (see Fig. 6), base length 7.8% DW, 0.14 in length from cloaca to sting, 23.7 times maximum height, preceded and followed by short, low fleshy ridge; maximum fold height 21% tail height at same point.

Snout relatively long, strongly depressed; preoral snout length 2.61 times mouth width, 2.46 times internarial distance, 25.3% DW; direct preorbital snout length 2.06 times interorbital length; snout to maximum disc width 53.0% DW; interorbital space almost flat with slight medial depression; orbits small, slightly protruded, diameter 1.89 in spiracle length; eye length 4.06 in spiracle length, intereye distance 7.68 times eye length. Spiracles very large, subrectangular to suboval; situated dorsolaterally; anterior margin oblique and almost straight, its origin beneath mid-orbit; posterior margin straight and strongly curved. Nostrils rather small, laterally expanded slightly, outer margin almost straight, internasal distance 1.97 in prenasal length, 2.83 times nostril length. Nasal curtain skirt shaped, broad and rather short, width 2.07 times length; lateral margin weakly concave, smooth edged; posterolateral apex nested within broad groove; posterior margin very weakly fringed (fringes indistinct and margin forming an angular ridge), weakly double concave; fully overlapping upper jaw and almost touching lower jaw. Mouth arched slightly (Fig. 3); oronasal groove shallow, extending posteriorly from posterolateral edge of mouth to chin, posterior extremities slightly exceeding mouth width apart; skin on ventral surface of lower jaw strongly papillate, in a broad strip around lips. Mouth floor with 2 large, fleshy medial papillae, their height ~4 mm, separated by about ~6 mm; a much smaller ridge-like lateral papilla near each corner of mouth, widely separated from inner pair, height ~2.5 mm; medial papilla simple, subtriangular, rounded distally with irregular margin, longitudinally flattened, subequal in size; largest known individual (Global Cestode Database NT-96, 1610 mm DW) reported to have 5 central and 2 lateral oral papillae. Upper jaw mildly double concave with a bulbous synthesis, lower jaw triple concave; lower jaw interlocking with upper jaw internally (upper jaw deeply recessed in head). Teeth small, broadly subtriangular to rhomboidal, in quincunx; similar in size in upper and lower jaws; surfaces of crowns strongly crenulate. Tooth rows in upper jaw ~40, in lower jaw >40, difficult to count without further dissection.

Gill opening margins narrowly S-shaped, smooth edged; length of first gill slit 1.40 times length of fifth, 2.41 in mouth width; distance between first gill slits 2.33 times internasal distance, 0.44 of ventral head length; distance between fifth gill slits 1.71 times internasal distance, 0.32 in ventral head length.

Squamation. In holotype: Denticle band prominent, lateral disc appearing smooth but densely and evenly covered with minute upright subconical denticles (barely visible with naked eye or detectable by touch except margin of secondary band). Suprascapular denticles 3, very small (length of largest 2.6 mm), similar in size, barely larger than adjacent denticles of secondary band; surfaces irregular; upper surface of crown not obviously flattened. Secondary and tertiary denticles easily distinguishable from each other. Secondary denticles very small, rather widely spaced (interspaces almost half denticle width), heart-shaped, similar in size, usually directed posteriorly, not larger across scapular region than elsewhere in band. Secondary denticle band well developed on disc, extending from just forward of orbit across mid disc then tapering gradually and extending onto tail; margin of band somewhat irregular (not sharply demarcated as an edge); truncate forward of eye, continuous over entire interorbital space, narrowest on mid disc beside spiracles, broadest over scapular region; similar band of denticles extending onto entire dorsal and upper lateral surfaces of tail before caudal sting; similar denticles on lateral edge of tail beneath caudal sting; small prickly upright and rather widely spaced denticles present on tail posterior to sting (some similar denticles near sting base on dorsal base). Tertiary denticles minute, barely detectable, partially embedded, possibly increasing in size with ontogeny (needing confirmation). Ventral surface of disc naked.

Meristics. Total pectoral-fin radials 150; propterygium 66, mesopterygium 22, metapterygium 62. Pelvic-fin radials 1 (includes 3–4 distal elements fused at base) + 22. Vertebral centra (excluding synarcual) 151; monospondylous 57; pre-sting diplospondylous 94; post-sting diplospondylous 0.

Colour. Holotype (when fresh): Disc uniformly yellowish brown dorsally (denticle band similar to rest of disc but denticle crowns slightly paler than adjacent skin); skin also with a few small, irregularly spaced, darker speckles; disc margin with narrow white strip around pectoral fin anteriorly, becoming dusky posteriorly; pupil of eye black, spiracle whitish; anterior tail paler yellow, gradually becoming whitish forward of caudal sting base; sting and tail beyond sting uniformly white (strongly contrasted with yellowish disc); no information available for ventral surface.

Holotype (in preservative): Upper surface uniformly pale brownish with denticle band distinct and paler than surrounding disc; denticle crowns appearing as white specks; spiracle dark greyish interiorly, posterior margin white. Ventral surface of disc largely white, irregular light and dark grey patches centrally and on posterior parts of pelvic fins. Tail largely white above, more yellowish and typically darker ventrally; ventral base greyish with some greyish-brown patches before caudal sting; posterior quarter of ventral tail with a dark brown medial stripe; ventral fold pale brownish and white.

Non types (not retained and descriptions based on images): Late embryo (Global Cestode Database NT-96, Fig. 2A) similar to juvenile above, uniformly dark greyish brown dorsally, tail similarly greyish brown to caudal sting base; sting and tail beyond sting pale greyish. Juvenile male (tissue accession GN 13667, Fig. 2B) darker than adults, uniformly dark greyish brown dorsally, eye and spiracle darker; tail similarly greyish brown to caudal sting base; sting and tail beyond sting white. Female (PNG field accession 130034, Fig. 2C mottled greyish yellow on outer dorsal disc with denticle band paler yellowish and distinct from rest of disc; spiracles bluish white and prominent; tail white near and beyond caudal sting; ventral surface uniformly white (outer pectoral fins pinkish due to skin damage). Adult male (PNG, no field accession number, Fig. 2D) medium brown on dorsal surface and very finely mottled; clasper pinkish white. Adult female (NT-96, Fig. 2E) very finely and very faintly mottled greyish white on outer dorsal disc with denticle band paler yellowish and distinguishable from rest of disc; spiracles bluish grey and prominent; tail base similar to disc before caudal sting; tail missing beyond sting but possibly paler than anterior tail.

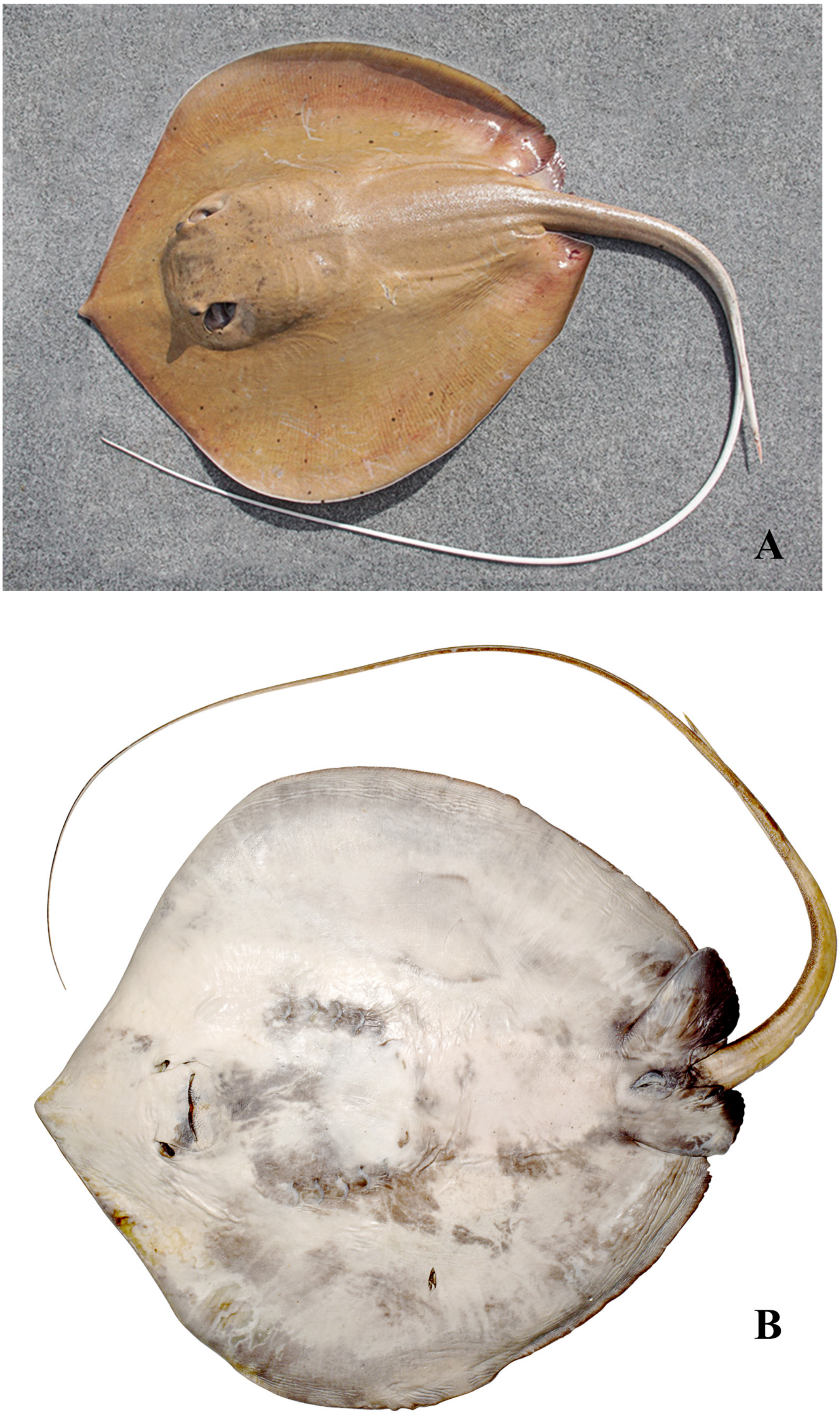

FIGURE 1. *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW): A, dorsal surface, fresh; B, ventral surface, preserved.

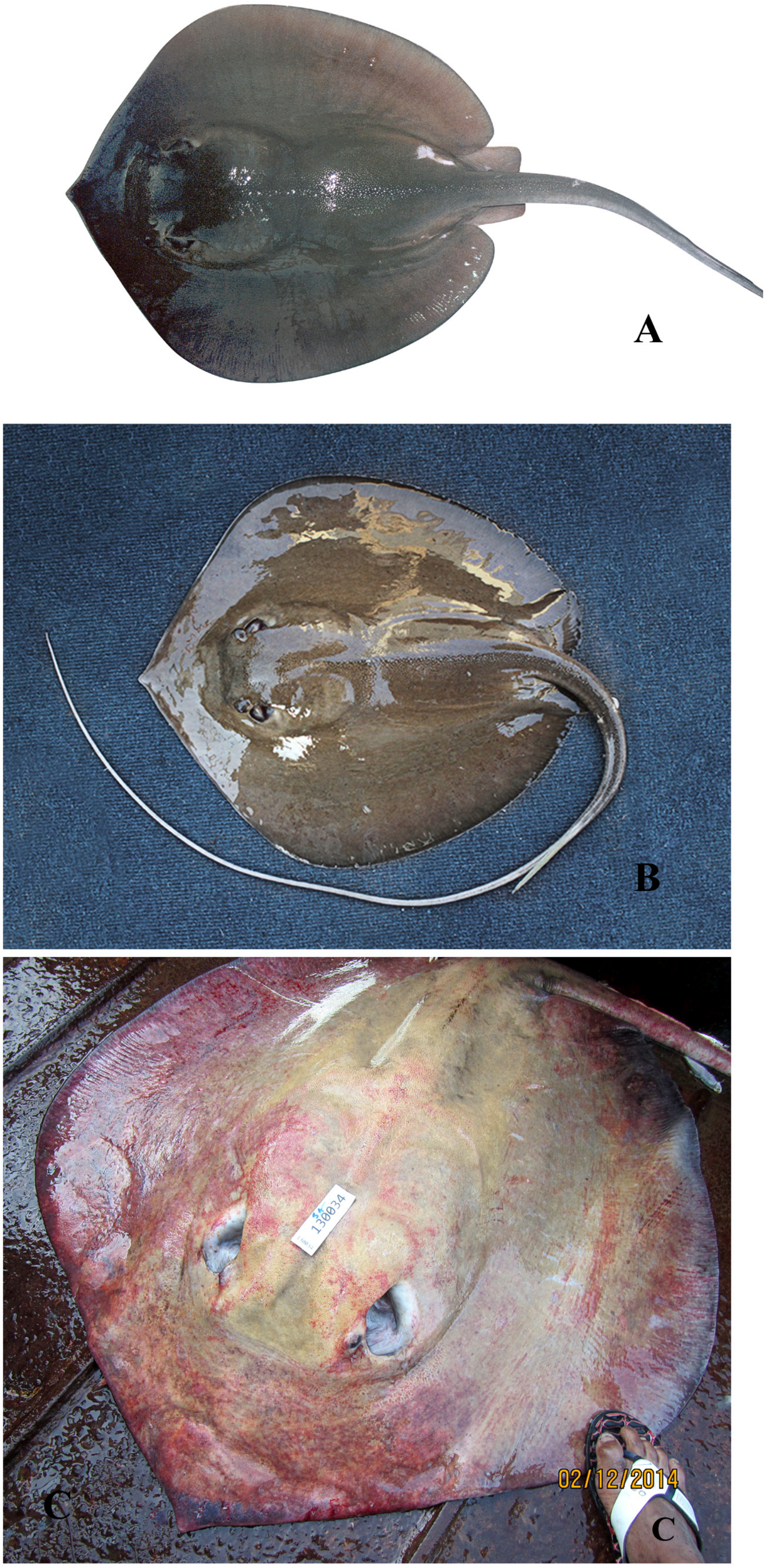

FIGURE 2. Dorsal surfaces of fresh non-types of *Urogymnus acanthobothrium* **sp. nov.**: A, embryo ~265 mm DW, east of Wessel Islands, Northern Territory, Australia (photo: K. Jensen); B, juvenile male 390 mm DW, West Alligator River, Northern Territory, Australia (photo: P. Kyne); C, female 1140 mm DW, Gulf of Papua, Papua New Guinea (photo: S. Tova); D, adult male 1100 mm DW, Gulf of Papua, Papua New Guinea (photo: National Fisheries Authority); E, adult female 1610 mm DW, east of Wessel Islands, Northern Territory, Australia (Photo: K. Jensen).

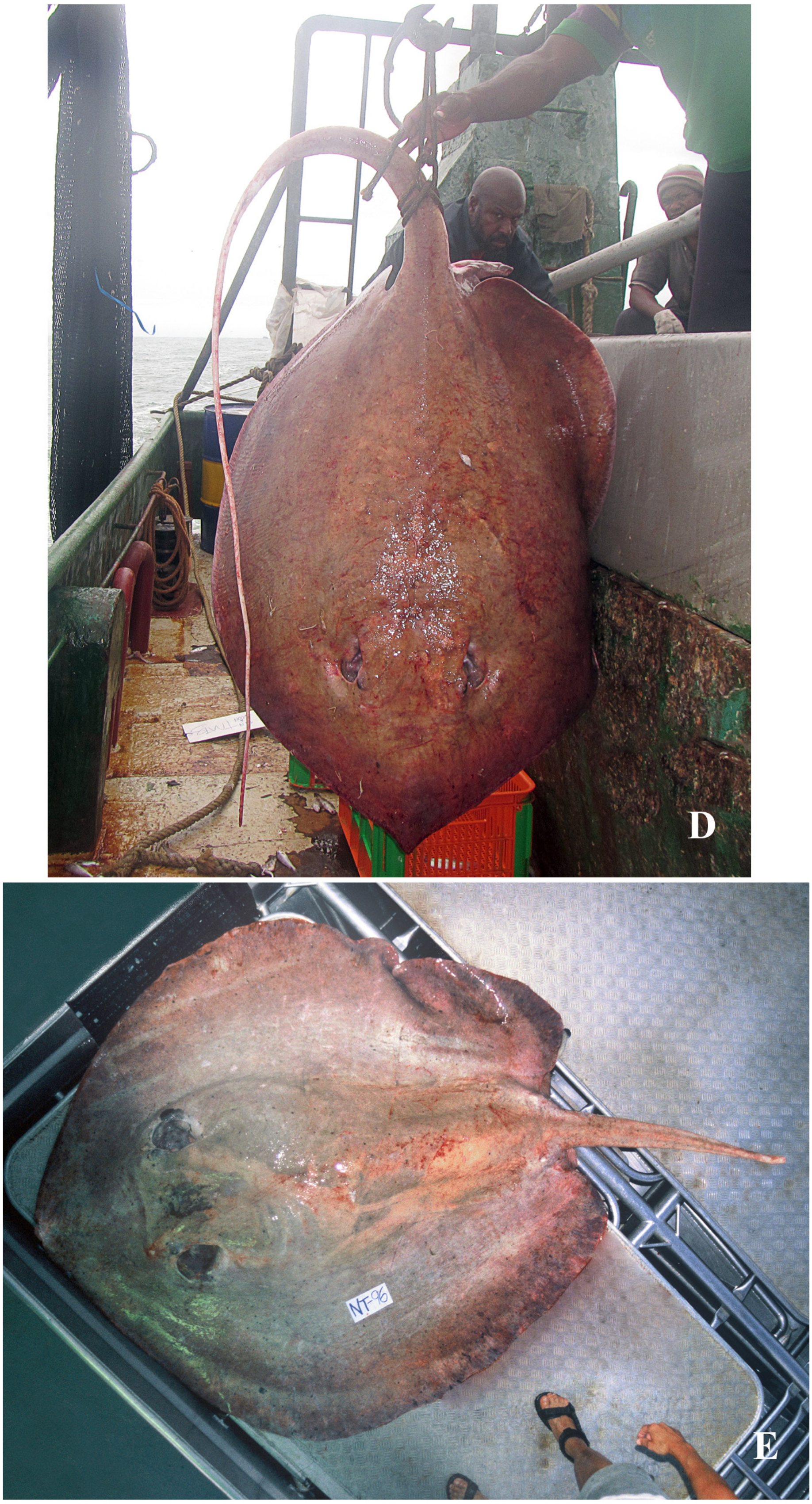

FIGURE 2. (Continued)

FIGURE 3. Oronasal region of *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW, preserved).

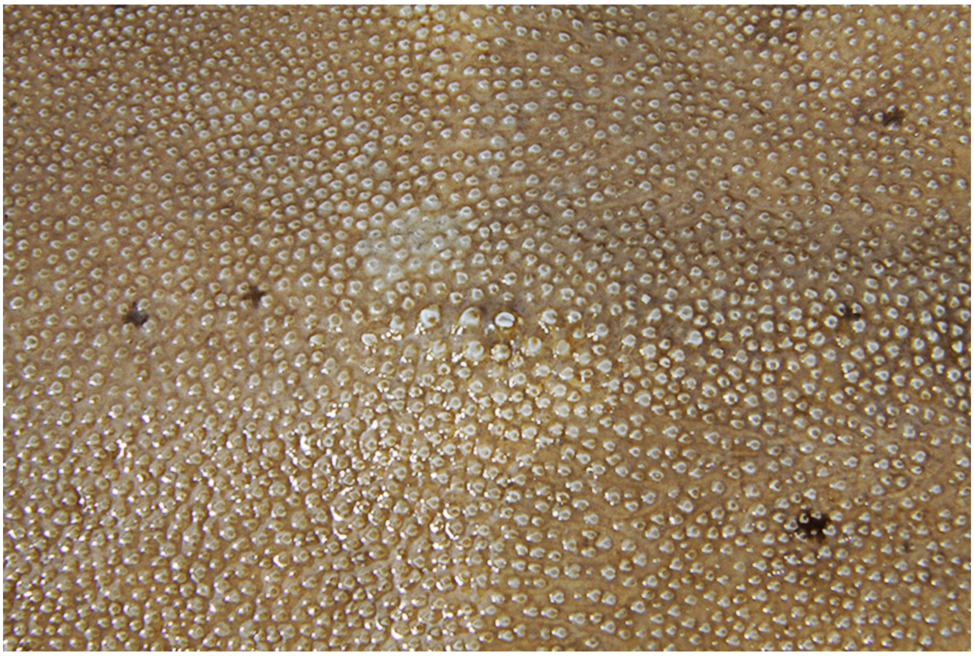

FIGURE 4. Scapular denticles of *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW, fresh).

FIGURE 5. Denticle band at the tail base of *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW, preserved).

FIGURE 6. Tail below caudal sting of *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW, fresh): A, lateral view; B, ventral view. Note the low ventral skin fold below the caudal sting.

Size. Among the largest of all stingrays; adult female (1610 mm DW, 1740 mm disc length) aborted a late embryo (estimated to be ~265 mm DW) on capture. Juveniles (n=5) measured 390–672 mm DW, 430–720 mm DL. A late adolescent male (1030 mm DW) was captured off Papua New Guinea but not retained.

Distribution. Gulf of Papua, Papua New Guinea, and northern Australia (Fig. 8), in brackish reaches of tidal rivers and estuaries, and marine waters. Juveniles have been recorded from lower reaches of the Wildman and West Alligator Rivers, Northern Territory (NT), and the lower Ord River and West Arm of Cambridge Gulf, Western Australia. Juvenile capture depths were 2.2–8.7 m; salinity 14.6–33.1; turbidity 367–>1000 NTU. An adult female was recorded in marine waters at a depth of 60 m east of the Wessel Islands, NT. Subadult specimens caught in the Gulf of Papua were from depths of 10–20 m. Probably more widespread in remote and under-surveyed areas of northern Australia and Papua New Guinea, particularly within the complex river systems and associated coastal zones.

Etymology. A large female collected during a survey of cestode parasites of northern Australian chondrichthyan fishes yielded 4 species of cestodes of the genus *Acanthobothrium* (*A. oceanharvestae*, *A. popi*, *A. rodmani* and *A. zimmeri*) that are found only in this species (Fyler *et al.*, 2009). Hence, the epithet '*acanthobothrium'* is used as a noun in apposition to recognise the historical significance of the parasite project in the discovery of this whipray. The vernacular name 'Mumburarr Whipray' is used to acknowledge the assistance of Traditional Owners in locating this species, in particular the people of the Alligator Rivers region in the Northern Territory. Mumburarr is a local Limilngan language name used by the Minitja people of the West Alligator River region meaning stingray. Coastal, estuarine and riverine stingrays were traditionally hunted for food and the caudal sting was used as a traditional knife.

TABLE 1. Morphometric data for the holotype of *Urogymnus acanthobothrium* **sp. nov.** (WAM P.34488-001), with values (expressed in mm) and ratios expressed as percentages of disc width.

	mm	%
Disc width	672.0	
Total length	2077.0	309.1
Disc length	718.0	106.8
Snout to pectoral-fin insertion	635.0	94.5
Orbit to pectoral-fin insertion	441.0	65.6
Snout to maximum disc width	356.0	53.0
Snout to origin of cloaca	611.0	90.9
Cloaca origin to tail tip	1466.0	218.2
Cloaca origin to caudal sting	386.0	57.4
Pectoral-fin insertion to caudal sting (horiz)	363.0	54.0
Disc thickness	82.0	12.2
Snout (preorbital) length	178.7	26.6
Snout (preorbital horiz.) length	166.6	24.8
Orbit diameter	30.3	4.5
Eye diameter	14.2	2.1
Spiracle length	57.5	8.6
Orbit and spiracle length	72.1	10.7
Interorbital width	86.6	12.9
Inter-eye width	108.7	16.2
Distance between spiracles	111.2	16.6
Head length	366.0	54.5
Preoral length (to lower jaw)	170.3	25.3
Prenasal length	136.1	20.2
Nostril length	24.5	3.6
Nasal curtain length	42.6	6.3
Nasal curtain width	88.1	13.1
Distance between nostrils	69.2	10.3
Mouth width	65.1	9.7
Distance between 1st gill slits	161.0	24.0
Distance between 5th gill slits	118.4	17.6
Width 1st gill slit	27.0	4.0
Width 3rd gill slit	29.0	4.3
Width 5th gill slit	19.3	2.9
Tail width, base of caudal sting	16.5	2.5
Tail width, axil of pelvic fins	53.7	8.0

......*continued on the next page*

TABLE 1. (Continued)

	mm	%
Tail height, base of caudal sting	16.4	2.4
Tail height, axil of pelvic fins	42.8	6.4
Caudal sting 1 length	203.6	30.3
Caudal sting 2 length		
Cloaca length	34.8	5.2
Length pelvic fin (embedded)	142.5	21.2
Width across pelvic-fin base	87.4	13.0
Greatest width across pelvic fins	235.1	35.0
Clasper, postcloaca length	72.1	10.7
Clasper, length from pelvic axil	25.0	3.7

FIGURE 7. Posterior tail of *Urogymnus acanthobothrium* **sp. nov.**, juvenile male holotype (WAM P.34488-001, 672 mm DW, fresh): A, dorsal view; B, lateral view; C, ventral view.

Conservation considerations. While at present there is insufficient data available to assess the extinction risk status of *Urogymnus acanthobothrium* **sp. nov.**, it should be noted that euryhaline elasmobranchs are generally of conservation concern (Lucifora *et al*., 2015). The limited number of existing records suggests that the new species may be naturally rare, and it is likely to possess life history characteristics of large elasmobranchs (i.e. late age at maturity, low fecundity, long lifespan, and low natural mortality) which result in low productivity and a limited ability to recover from population depletion (Musick, 1999).

Juvenile *U. acanthobothrium* in northern Australia receive some refuge in Kakadu National Park where there is no commercial fishing. Juveniles have been recorded in the Wildman and West Alligator Rivers within the Park; access to the latter is completely closed (i.e. no boat access is permitted) providing a unique conservation zone. In the Kimberley region of Western Australia, commercial fishing activities are limited where juveniles have been recorded. The deployment of turtle exclusion devices (TEDs) most likely minimizes their capture in the Australian Northern Prawn Fishery as large rays can be effectively excluded from trawl nets (Brewer *et al*., 2006). This fishery operates across northern Australia, including in the area where the first (adult) specimen was caught. Nevertheless, this species is caught as bycatch of trawling in the Gulf of Papua; that fishery is currently investigating the use of TEDs which would limit future catches of at least the largest specimens.

The sporadic records of *U. acanthobothrium* across northern Australia and the Gulf of Papua suggest a wider distribution than presently known, and an effort should be made to collect more comprehensive data on this species, particularly on its distribution, ecology and interactions with fisheries, to accurately assess its extinction risk status.

Comparisons. *Urogymnus acanthobothrium* **sp. nov.**, which attains at least 161 cm DW, is amongst the largest whiprays. No other himanturin ray in the Indo-West Pacific has a ventral tail fold (present but very narrow in *U. acanthobothrium*); a well-developed fold is present in the Atlantic whipray genus, *Fontitrygon*. Of species of *Urogymnus*, *U. granulatus* is also unusual in that it has a uniformly white tail, and appears to be closest to this species based on NADH2 data (see Figs 3 & 5; Last *et al.*, 2016). Based on the holotype and data provided by Manjaji (2004) for *U. granulatus*, *U. acanthobothrium* has a longer (length ~2.5 vs 1.5–2.1 times combined orbit and spiracle length) and more angular snout (angle 114° vs 122–123°), longer tail (length 2.3–2.4 vs 1.3–2.1 times DW), more posteriorly positioned caudal sting (horizontal length from disc insertion to sting origin ~3.3 vs ~2 times interspiraclar width), more oval tail base (otherwise subcircular), lacks white flecks on the dorsal surface, and the ventral disc is uniformly white (rather than white with a broad black margin). Other members of the genus have a much more angular snout (*U. lobistomus*) or the snout is much more obtuse (almost truncate) anteriorly (*U. dalyensis* and *U. polylepis*). The type of the genus, *U. asperrimus*, also known as the Porcupine Ray, which has an extremely thorny dorsal surface unique within whiprays and lacks a caudal sting, is probably highly derived.

Initially, an enormous ray photographed by Mark Erdmann while diving near Raja Ampat (Papua) was thought to be conspecific with this species, but after subsequent examination of his photographs, it is more likely a very large *Urogymnus polylepis* (Bleeker, 1852). *Urogymnus polylepis* also reaches a huge size and specimens from the Chao Phraya River (Thailand) measured 192 cm DW and at least 242 kg. A close relative from tropical Australia and probably New Guinea, *Urogymnus dalyensis*, is a much smaller ray (reported at 124 cm DW) that co-occurs with *U. acanthobothrium* in parts of this region. It remains a mystery how such a large coastal animal can escape detection for so long. However, the superficial similarity of these *Urogymnus* species in the region, and the paucity of comparative specimens in ichthyological collections because of their large size, are likely reasons.

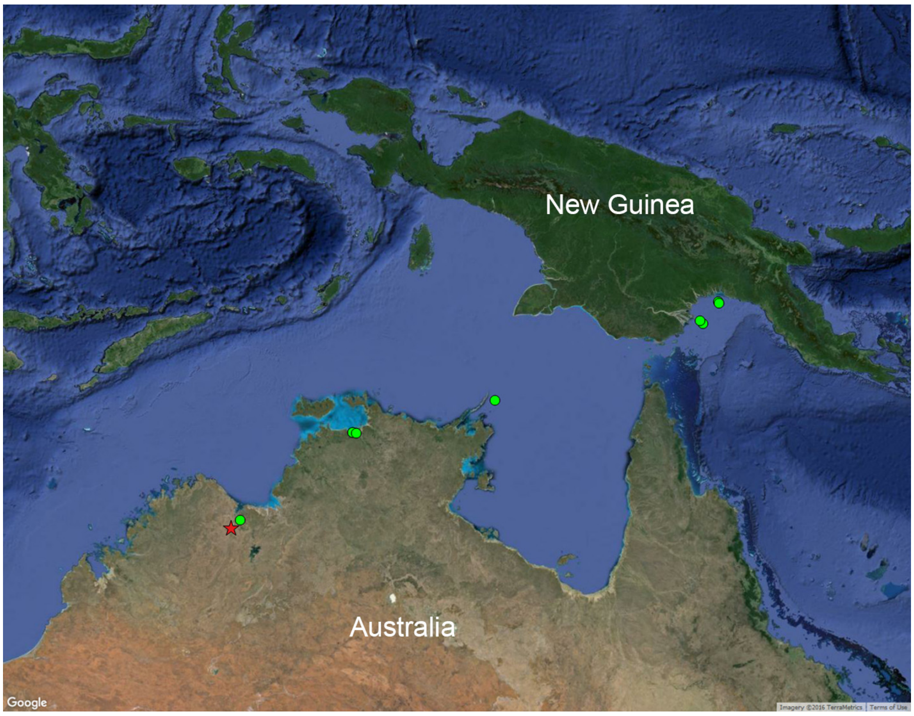

FIGURE 8. Distributional range of *Urogymnus acanthobothrium* **sp. nov.**

Key to species of the genus *Urogymnus*

1. Upper disc very prickly, sparsely covered in long spiny thorns; no caudal sting . . . . *Urogymnus asperrimus* (Indo–West Pacific, and possibly eastern Atlantic)

\- Upper disc rather smooth or covered with small denticles; caudal sting present (if damaged, groove housing sting usually evident). 2

2. Snout very elongate and narrowly pointed; denticle band extending almost to snout tip in adults . . . . *Urogymnus lobistomus* (Indo–Malay Archipelago)
- Snout not elongate, broadly pointed or obtuse with small apical lobe; denticle band not or just extending past snout tip 3
3. Disc broadly pointed, apical lobe small or indistinct; length of snout <2.6 times combined orbit and spiracle length; tail white beyond caudal sting. 4
- Disc obtuse anteriorly with prominent apical lobe; length of snout >2.6 times combined orbit and spiracle length; tail dark beyond caudal sting. 5
4. Short ventral fold on tail; tail very elongate, length 2.3–2.4 times DW; dorsal surface plain coloured, ventral surface of disc lacking prominent dark posterior margin . . . . *Urogymnus acanthobothrium* (northern Australia & Papua New Guinea)
- No ventral fold on tail; tail elongate, length 1.3–2.1 times DW; dorsal surface covered with white flecks (often obscured by dark mucous), ventral surface of disc with prominent dark margin . . . . *Urogymnus granulatus* (Indo–West Pacific)
5. Preoral snout length 3.8–4.3 times mouth width, 2.8–3.2 times internarial distance; preorbital snout length 2.3–2.9 times interorbital length, orbit diameter 49–61% of spiracle length . . . . *Urogymnus polylepis* (Indo–West Pacific)
- Preoral snout length 3.3–3.4 times mouth width, 2.4–2.6 times internarial distance; preorbital snout length 2.1–2.2 times interorbital length, orbit diameter 62–75% of spiracle length . . . .*Urogymnus dalyensis* (northern Australia & probably New Guinea)

Comparative material

Urogymnus dalyensis: 9 specimens. CSIRO H 2503–01 (holotype), juvenile male 620 mm DW, Pentecost River (Bindoola Creek junction), Western Australia, 15°42′ S, 127°51′ E, Sep 1990; CSIRO H 2524–01 (paratype), female 450 mm DW, Gilbert River (crossing of the Burke Development Road), Queensland, Australia, 17°11′ S, 141°45′ E, 0.3 m depth, Aug 1989; CSIRO H 6657–01 (paratype), juvenile male 517 mm DW, Fitzroy River (Telegraph Pool), Western Australia, 17°38′ S, 123°34′ E, 1.1 m depth, 13 Oct 2002; FUMT–P10863 (paratype), female 474 mm DW, Daly River, Northern Territory, Australia, 18 Aug 1989; NTM S 14745–001 (paratype), adolescent male 880 mm DW, Daly River (upstream from crossing), Northern Territory, Australia, 13°46′ S, 130°43′ E, 18 Nov 1998; NTM S 15183–001 (paratype), juvenile male 380 mm DW, Daly River crossing, Northern Territory, Australia, 13°46′ S, 130°42′ E, Jul 1999; NTM S 15184–001 (paratype), juvenile male 415 mm DW, Daly River crossing, Northern Territory, Australia, 13°46′ S, 130°42′ E, Aug 1999; NTM S 16248–001 (paratype), juvenile male 415 mm DW, Daly River (below Oolloo crossing), Northern Territory, Australia, 14°00′ S, 131°14′ E, 9 Jul 2006; WAM P 32955–001 (paratype), juvenile male 464 mm DW, Ord River, Western Australia, 15°34′ S, 128°37′ E, 3.5 m depth, 19 Nov 2002.

Urogymnus granulatus: 5 specimens: CSIRO H 2751–01, juvenile male (475 mm total length), Groote Eylandt, Northern Territory, Australia, 13°49′ S, 136°30′ E, 1 m depth, 2 Sep 1990; CSIRO H 4426–32, adult male (claspers only), Muara Angke fish market, Jakarta, Indonesia, 17 Oct 1995; CSIRO CA 1255, juvenile male, north of Anson Bay, Western Australia, 12°05′ S, 130°00′ E, 54 m depth, 3 Jul 1980; CSIRO H 3864–01, juvenile male 235 mm DW, North Channel, east of Cape York Peninsula, Queensland, Australia, 11°43′ S, 143°28′ E, 20 m depth, 9 Apr 1994; CSIRO H 4417–01, juvenile 330 mm DW, northeast of Shelburne Bay, Queensland, Australia, 11°31.8′ S, 143°28.5′ E, 19 m depth, 3 Dec 1995.

Urogymnus lobistomus: 7 specimens: SMEC 369 (holotype), mature male 492 mm DW, Bintulu, Sarawak, Malaysia, 3°10′ N, 113°01′ E, 15 Jun 2002; SMEC 370 (paratype), juvenile male 280 mm DW, Mukah, Sarawak, Malaysia, 2°54′ N, 112°06′ E, 13 Jun 2002; SMEC 371 (paratype), female 327 mm DW, Mukah, Sarawak, Malaysia, 2°54′ N, 112°06′ E, 2 Jun 2002; IPMB 38.32.02 (paratype) mature male 600 mm DW, Mukah, Sarawak, Malaysia, 2°54′ N, 112°06′ E, 2 Jun 2002; CSIRO H 5472-01, female 343 mm DW, Kuching fish market, Sarawak, Malaysia, 1°25′ N, 110°20′ E, 29 Jan 1999; CSIRO H 5485-01, female 516 mm DW, Kuching fish market, Sarawak, Malaysia, 1°25′ N, 110°20′ E, 2 May 1999; CSIRO H 6214-03, prenatal male pup 184 mm DW, Mukah, Sarawak, Malaysia, 2°54′ N, 112°06′E, 29 Apr 2004.

Urogymnus polylepis: 14 specimens: RMNH T 7452, juvenile male (holotype) 301 mm DW, Java, Indonesia; CSIRO H 5283–01 juvenile male 372 mm DW, SMEC KTG2–23397, juvenile male 524 mm DW, SMEC KTG3–20497, female 545 mm DW, SMEC KTG7–21096, neonatal male 363 mm DW, IPMB MMKG1, juvenile male 515 mm DW, Kinabatangan River, Sabah, Malaysia; MTUF 30233, female 494 mm DW, Rajmehar, India; MTUF 30203, juvenile male 450 mm DW, Bhagalpur, India; MTUF 30204, juvenile male 460 mm DW, MTUF 30205 and MTUF 30206, female 466 mm DW and juvenile male 480 mm DW, Chao Phraya River, Thailand; RMNH 3365 (photo only), unspecified locality; SMEC BFT1–697, female 605 mm TL, Padas River, Sabah, Malaysia; SMEC SKN10–15697, adolescent male 1210 mm DW, Sandakan, Sabah, Malaysia.

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Three new stingrays (Myliobatiformes: Dasyatidae) from the Indo–West Pacific

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Abstract

Three undescribed stingrays were discovered as part of a broader revision of the family Dasyatidae that formed part of the Chondrichthyan Tree of Life project. This research forms part of a sequence of papers on rays aimed at describing unnamed species for inclusion in a multi-authored guide to rays of the world. The first part of this series focused on a redefinition of genera of the family Dasyatidae. The new Indo–West Pacific taxa are represented by separate genera from three dasyatid subfamilies: *Himantura australis* **sp. nov.** (northern Australia and Papua New Guinea), *Taeniura lessoni* **sp. nov.** (Melanesia) and *Telatrygon biasa* **sp. nov.** (Indo–Malay Archipelago). *Himantura australis* **sp. nov.**, which belongs to a complex of four closely related reticulate whiprays, differs subtly from its congeners in coloration, morphometrics and distribution. *Taeniura lessoni* **sp. nov.** is the second species in a genus containing the widely-distributed *T. lymma*, which is possibly the most abundant stingray in shallow coral-reef habitats of the Indo–Pacific, with the new species apparently restricted to Melanesia. *Taeniura lessoni* **sp. nov.** is distinguishable by the absence of a distinctive pair of vivid blue longitudinal stripes on the dorsolateral edges of the tail which is one of the most distinctive features of *T. lymma*. *Telatrygon biasa* **sp. nov.** belongs to a small, recently designated genus of stingrays represented by four species in the tropical Indo-West Pacific. *Telatrygon biasa* **sp. nov.** differs from these species in morphometrics. The new species differs markedly from *T. zugei* in its NADH2 sequence. *Telatrygon crozieri* is resurrected as a valid northern Indian Ocean representative of the *T. zugei* complex.

Key words: Dasyatidae, *Himantura australis*, *Taeniura lessoni*, *Telatrygon biasa*, *Telatrygon crozieri*, new species, Indo–West Pacific

Introduction

The Chondrichthyan Tree of Life project (CToL; https://sharksrays.org) is a 5 year, multi-agency investigation of the biodiversity of sharks, rays and chimaeras due for completion in August 2016. Part of the focus of this project has been to produce an inventory of the world's chondrichthyan fauna and an investigation of the classification of these fishes. One major output of this work has been to assemble a guide to the world's rays with the input of other batoid taxonomic experts (Last *et al.*, in press). Data underpinning this book has been greatly enhanced by insights gained from recent molecular research, unearthing hitherto undiscovered cryptic species and confirming earlier work where the existence of cognates was suspected. It was important to include these taxa in the ray guide as several species are important for ecological reasons and/or where conservation implications exist. Completing revisionary studies of these taxa extended beyond the timelines for producing the guide so a sequence of descriptive papers has been submitted to address this issue.

The stingrays discussed in this paper have all been identified as being un-named in earlier investigations, but their distinctiveness has been confirmed by recent molecular analyses, including sequences of their related taxa (e.g. Naylor *et al*., 2012; 2016). The extreme complexity of a subgroup of whiprays, the *Himantura uarnak* complex, was first identified by Manjaji (2004), then through the Barcode of Life project (http://www.boldsystems.org) and by the CToL data (see Last *et al*., 2016; Fig. 3). The new *Taeniura* by was flagged as problematic by one of us (PL) as part of revision of Indo–Pacific rays, but its distinctiveness from *T. lymma* (Forsskål, 1775) was later confirmed from

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material collected from the Solomon Islands by J. Caira and K. Jensen and subsequent molecular analysis using the NADH2 gene (see Last *et al*., 2016; Fig. 2). The new *Telatrygon* differs from its closest relative *T. zugei* (Müller & Henle, 1841) based on morphometrics (PL, WW) and later confirmed by CToL molecular data (see Last *et al*., 2016; Fig. 1). The aim of this work is to describe and name these taxa.

Materials and methods

Characteristics of the disc (including squamation, and tooth row and meristic counts) follow standards used in Manjaji (2004) and Manjaji-Matsumoto & Last (2006). Morphometric methods, including tail fold measurements where applicable, follow Last & White (2008). There are two noteworthy modifications: (1) the distance from the pectoral insertions to the caudal sting was taken horizontally to minimise errors from distortions of the tail; (2) a sequence of images of individuals of different sizes was needed to characterise colour pattern changes in the genus *Himantura* due to ontogenetic variability. Also, distinction needs to be drawn between 'snout angle' (anterior angle of disc produced at snout tip by a transverse line drawn through anterior margins of orbits) and 'anterior disc angle' (anterior angle of disc produced at snout tip by a transverse line drawn through the disc at its widest point).

Overall, 44 standard characters, expressed as proportional measurements of disc width (DW), were taken from: the holotype (CSIRO H 7798-04) and 5 paratypes (CSIRO H 1134-1, CSIRO H 4016-01, CSIRO H 7840-01, NTM S 11507-006 and KFRS unregistered [220349]) of *Himantura australis* **sp. nov.**; the holotype (CSIRO H 7724-01) and 4 paratypes (CSIRO H 7724-02, QM I 39329, USNM 380822 and USNM 350580) of Taeniura lessoni **sp. nov.**; and the holotype (MZB KA-93) and 5 paratypes (CSIRO H 4426-06, CSIRO H 4426-07, CSIRO H 4426-09, CSIRO H 4426-10 and CSIRO H 5474-21) of *Telatrygon biasa* **sp. nov.** Additional measurements were also taken for the above specimens of *Taeniura lessoni* **sp. nov.** and *Telatrygon biasa* **sp. nov.** to represent details of the tail folds which are present in these species (see Last & White, 2008). For comparison, 4 specimens of *Taeniura lymma* (QM I 6666, QM I 8328, QM I 17668 and QM I 31356), and the lectotype (MNHN 2447), one paralectotype (MNHN 1987-152) and 3 other specimens (ASIZP 67338, ASIZP 72247 and FRIP 3504) of *Telatrygon zugei* were also measured. Additional information on coloration was extracted from images on the elasmobranch parasite database website, http://tapewormdb.uconn.edu/ (coded with CMO3 prefixes).

Meristics were obtained from radiographs of the holotype (CSIRO H 7724-01) and only paratype (CSIRO H 7724-02) of *T. lessoni* **sp. nov.**; and five paratypes of *T. biasa* **sp. nov.** (CSIRO H 4426-05, -06, -07, -09, -10). Vertebrae in the central disc were difficult to count on *H. australis* **sp. nov.** as they were obscured by the secondary denticle band; hence, data for this species is very limited and includes selective counts from four, small non-types (CSIRO H 7629-02, H 7807-02, PNG-232047, PNG-230349).

Types are deposited in the Australian National Fish Collection (CSIRO), at the Commonwealth Scientific and Industrial Research Organisation's Marine Laboratories in Hobart (Tasmania), Museum Zoologicum Bogoriense (MZB) in Jakarta, Northern Territory Museum (NTM), Smithsonian Institution National Museum of Natural History (USNM), and the Kanudi Fisheries Research Station collection (KFRS; housed at University of Papua New Guinea). Comparative material for this study includes specimens examined in other recent treatments of the family, as well as other relevant type material. A detailed synonymy is not provided for each species as this will form part of more detailed revisions of each genus in progress.

Himantura australis sp. nov.

(Figs. 1–7; Table 1)

Himantura toshi (not Whitley): Whitley, 1940: 212 (in part), brief description (misidentification).
Himantura uarnak (not Gmelin): Paxton *et al*., 1989: 42 (listed); Last & Stevens, 1994: 406-07, description, illustration; Last & Stevens, 2009: 449-50, description, illustration (misidentifications).
Himantura uarnak 2: Naylor *et al*., 2012: 70, 255 (molecular data).
Himantura sp. 4: Last *et al*., 2016: figs. 3, 5 (molecular data).

Holotype. CSIRO H 7798-04 (tissue accession GN15798), juvenile male 415 mm DW, west of Oriomo River, Daru, Western Province, Papua New Guinea, 9°04.43'S, 143°08.53'E, 25 Oct 2014.

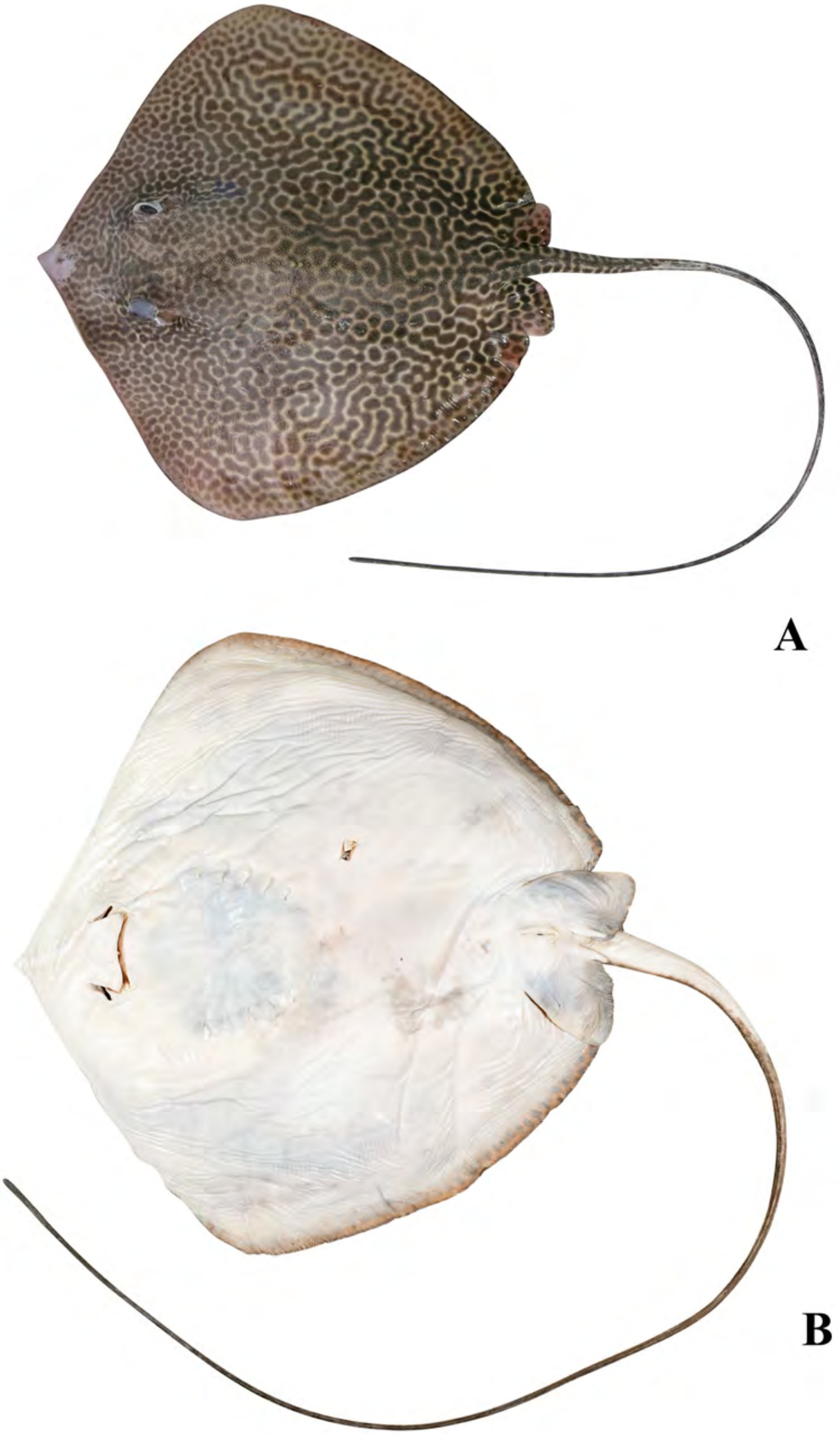

FIGURE 1. Holotype of *Himantura australis* **sp. nov.**, juvenile male 420 mm DW (CSIRO H 7798-04), from Papua New Guinea: (A) Dorsal view (fresh); (B) Ventral view (preserved).

FIGURE 2. Oronasal region of the holotype of *Himantura australis* **sp. nov.**, juvenile male 420 mm DW (CSIRO H 7798-04), from Papua New Guinea (preserved).

FIGURE 3. Denticles of the mid-disc of the holotype of *Himantura australis* **sp. nov.**, juvenile male 420 mm DW (CSIRO H 7798-04), from Papua New Guinea (preserved).

FIGURE 4. Post-caudal sting tail of the holotype of *Himantura australis* **sp. nov.**, juvenile male 420 mm DW (CSIRO H 7798-04), from Papua New Guinea (preserved). A. Dorsal view; B. Lateral view; C. Ventral view.

Paratypes. 13 specimens: CSIRO H 1134-1, late embryo male 292 mm DW, north of Port Hedland, Western Australia, 19°35.6'S, 118°42.8'E, 32–34 m depth, 21 Sep 1987; CSIRO H 1463-3, juvenile male 283 mm DW, north of Cape Lambert, Western Australia, 20°06.1'S, 117°21.4' E, 41 m depth, 20 Sep 1988; CSIRO H 1920-01 (tail only), mother of CSIRO H 1463-3, North-West Shelf, Western Australia, 20 Sep 1988; CSIRO H 4016-01, neonatal female 309 mm DW, north of Cape Preston, Western Australia, 20°21.1'S, 116°07.3'E, 41–42 m depth, 25 Aug 1995; CSIRO H 4422-01, juvenile male 314 mm DW, near Proserpine, Repulse Bay, Queensland, Australia, 20°38'S, 148°41.75'E, 11 Nov 1993; CSIRO H 4542-06, juvenile male 310 mm DW, Kamora River estuary, West Papua, Indonesia, 4°49.36'S, 136°38.17'E, 5–10 m depth, 30 May 1996; CSIRO H 7839-01 (tissue accession GN15784), juvenile male 333 mm DW, Daru fish market, Western Province, Papua New Guinea, 9°03.91'S, 143°12.59'E, 21 Oct 2014; CSIRO H 7840-01 (tissue accession GN15789), juvenile male 241 mm DW, fishing camp near Daru, 9°02.26'S, 143°11.49' E, 24 Oct 2014; NTM S 11144-001, juvenile male 285 mm DW, King Creek, Shoal Bay, Darwin Harbour, Northern Territory, Australia, 12°21.48'S, 131°1.02'E, 15 Jan 1983; NTM S 11507-006, juvenile male 343 mm DW, Ludmilla Creek, Darwin Harbour, Northern Territory, Australia, 12°24.78'S, 130°50.22'E, 19 Dec 1984; KFRS unregistered (field accession 220349; tissue accession GN15785), juvenile female 350 mm DW, Katatai, Western Province, Papua New Guinea, 9°01.25'S, 143°20.51'E, 23 Oct 2014; KFRS unregistered (field accession 220420; tissue accession GN15790), juvenile female 286 mm DW, fishing camp near Daru, Western Province, Papua New Guinea, 9°02.26'S, 143°11.49' E, 24 Oct 2014; KFRS unregistered (field accession 230247; tissue accession GN16607), late-term embryo 300 mm DW (from female 1400 mm DW), Gulf of Papua, Papua New Guinea, 7°55'S, 145°00' E, 1 Dec 2014.

Other material. 15 specimens: CSIRO H 1134-2, juvenile female 297 mm DW, north of Port Hedland, Western Australia, 19°35.6'S, 118°42.8'E, 32–34 m depth, 21 Sep 1987; CSIRO H 1479-03, juvenile female 259 mm DW, CSIRO H 1479-04, juvenile male 255 mm DW, CSIRO H 1479-05, juvenile male 262 mm DW, CSIRO H 1479-06, juvenile female 273 mm DW, north of Dampier Archipelago, Western Australia, 20°09.5'S, 116°47.7'E, 43 m depth, 24 Sep 1988; CSIRO H 2371-02, juvenile female 290 mm DW, CSIRO H 2371-03, juvenile female 278 mm DW, CSIRO H 2371-04, juvenile male 283 mm DW, CSIRO H 2371-05, juvenile male 293 mm DW, north of Cape Lambert, Western Australia, 20°06.1'S, 117°21.4'E, 41 m depth, 20 Sep 1988; CSIRO H 4786-01 (tissue accession GN5082), juvenile male 310 mm DW, CSIRO H 4786-02 (tissue accession GN1596), juvenile male 322 mm DW, near mouth of Buffalo Creek, Lee Point, Northern Territory, Australia, 12°20.25'S, 130°54.48'E, 7 Aug 1997; CSIRO H 7629-02; CSIRO H 7807-02; PNG-232047; PNG-230349.

Diagnosis. A species of *Himantura* distinguished by a combination of the following features: disc weakly rhomboidal; preorbital snout moderately short (length 19–22% DW), rather broad, angle 117–127°, with a distinct apical lobe; lateral apices narrowly rounded; orbits moderately large, often strongly protruding (particularly in young); 1–2, mostly heart-shaped suprascapular denticles (not preceded before and after by a row of smaller primary denticles); secondary denticle band developed before birth; dorsal surface of juveniles (smaller than 370 mm DW) dark spotted or with spots and weak reticulations, subadults and adults (exceeding 390 mm DW) more strongly reticulated; dorsal tail of juveniles with 3 rows of spots before caudal sting, faint dark saddles beyond sting (tail lacking alternating black and white bands); tail uniformly dark ventrally; pectoral-fin radials 146–152; vertebral centra (excluding synarcual) 123; including synarcual 124.

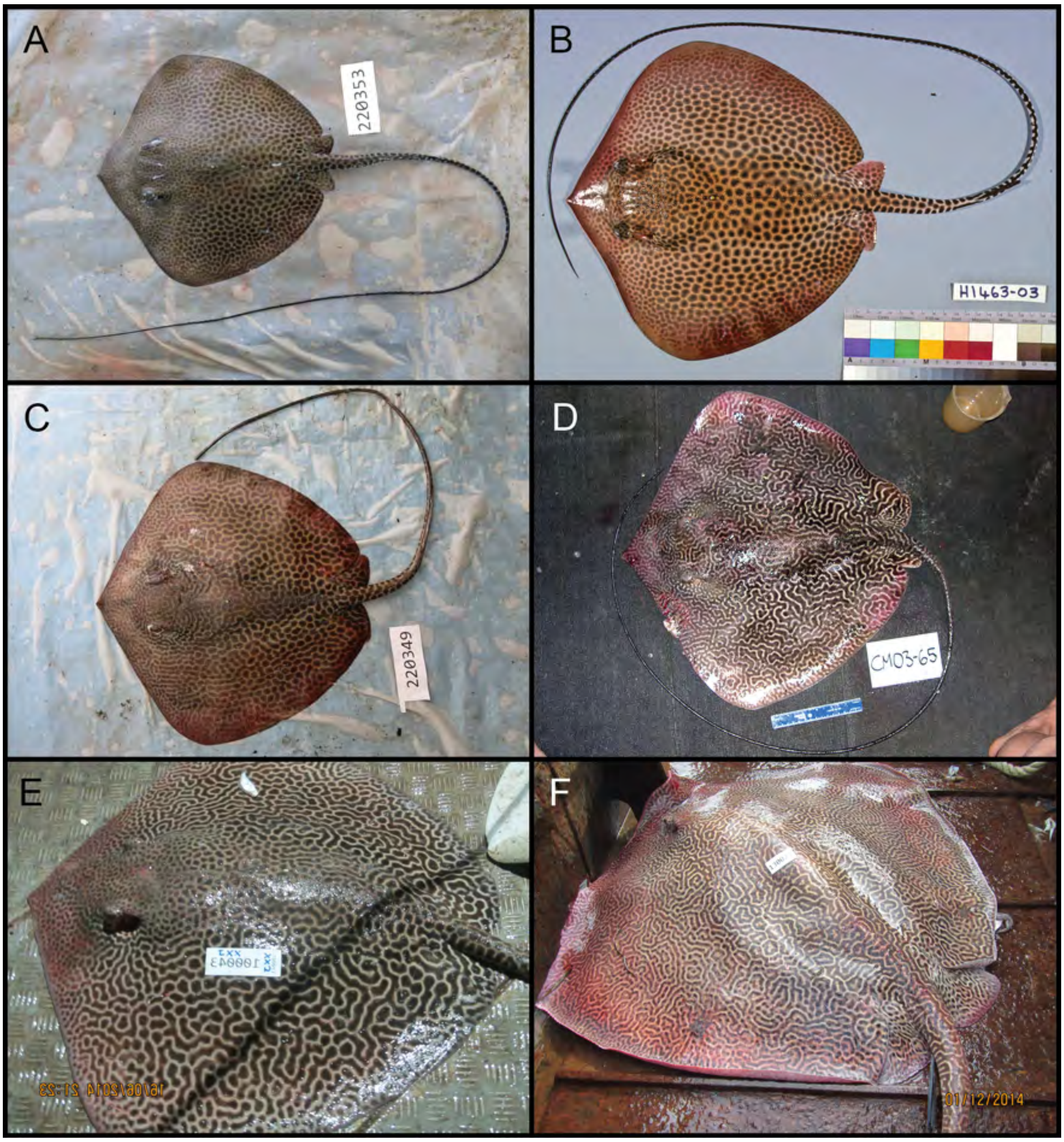

FIGURE 5. Comparison of dorsal colour pattern changes with growth in *Himantura australis* **sp. nov.** (fresh): A. 241 mm DW; B. 283 mm DW; C. 350 mm DW; D. 560 mm DW; E. 830 mm DW; and F. 1400 mm DW.

Description. Disc rhomboidal, width 1.05 in holotype (1.01–1.06 in paratypes, all early juveniles and neonates <350 mm DW) times length; anterior angle 110° (103–118°), pectoral angle 96° (92–94°); most robust on cranial region of head, raised slightly on mid-scapular region, maximum thickness 7.55 (6.37–9.09)% disc width (DW). Snout with a distinct apical lobe, angle 117° (117–127°); anterior margin of disc almost straight (not noticeably double convex), lateral apices narrowly rounded; posterior margin broadly convex, free rear tip narrowly rounded. Pelvic fins rather small, length 18.9 (18.3–19.5)% DW; width across base 13.9 (12.2–15.4)% DW; not protruding far beyond disc. Claspers of adult male unavailable for examination. Tail very long and slender, tapering gently from base toward caudal sting then becoming whip-like; total length 3.8–4.2 times DW when undamaged (3.0 in holotype but tip missing), tail length 3.5–4.0 times precloacal length when intact; base narrow, slightly depressed and oval, width 1.58 (1.26–1.56) times height. No obvious skin folds on dorsal or ventral surfaces of tail, but mid-ventral surface of tail in neonates with a long and narrow, longitudinal fleshy ridge (presumably a rudimentary fold) extending posteriorly from about level of caudal sting for a distance equivalent to tail length before sting; no evidence of ventral ridge in large individuals.

Snout rather short, angular, strongly depressed; preoral snout length 2.04 (2.42–2.55) times mouth width, 2.26 (2.34–2.73) times internarial distance, 20.6 (21.2–21.8)% DW; direct preorbital snout length 1.46 (1.34–1.66) times interorbital length; snout to maximum disc width 40.3 (38.9–43.3)% DW, interorbital space almost flat; eye moderately large, length 2.08 (1.80–2.64) in spiracle length; orbits protruding well beyond disc in young, exceedingly so in neonates and less so in large individuals; diameter 1.21 (1.08–1.58) in spiracle length, interorbital distance 2.54 (2.04–2.56) times orbit. Spiracles large, subrectangular, situated laterally or dorsolaterally.

Nostrils moderately large, narrowly elongate, oblique, posterior half recurved in posterolateral direction; lateral margin with weak double concavity, length 1.94 (1.85–2.28) in internasal distance; internasal distance 1.75 (1.78–2.03) of prenasal length. Nasal curtain subrectangular, skirt-shaped, relatively broad, width 1.85 (1.77–2.11) times length; lateral margin almost straight, smooth edged; posterolateral apex depressible into shallow groove; posterior margin weakly fringed, weakly concave.

Mouth moderately arched; prominent knob at symphysis of upper jaw, retractable mesially into deep notch at symphysis of lower jaw; oronasal groove shallow, extending posteriorly from posterolateral edge of mouth to chin; skin on ventral surface of lower jaw moderately papillose, not confined to narrow strip around lips; no circumoral grooves. Jaws of types not dissected to reveal details of mouth, but images of oral region of discarded material indicate a mouth floor with mainly 4 well-developed papillae (medial pair occasionally separated by a smaller papilla); medial pair simple, broad, flattened, rounded distally, subequal in size (slightly larger than outer pair), located near to each other; single outer papilla located near each corner of mouth, well separated from inner pair. Teeth in a juvenile paratype (CSIRO H 4542-06) small, subequal in size in upper and lower jaws; narrowly rhombic with 1–2 low, transverse ridges on crown, ridges separated by prominent groove; ~59 vertical rows in upper jaw.

Gill openings S-shaped, strongly arched posteriorly, margins smooth; length of first gill slit 1.64 (1.11–1.50) times length of fifth, 2.78 (2.59–3.37) in mouth width; distance between first gill slits 2.39 (2.18–2.54) times internasal distance, 0.48 (0.44–0.48) of ventral head length; distance between fifth gill slits 1.46 (1.45–1.66) times internasal distance, 0.29 (0.29) in ventral head length.

Squamation. Ontogenetic stages 2 and 4 present in available material; stages 0, 1, 3, 5 and 6 not applicable (data on large individuals inadequate). Denticle development relatively rapid; late-term embryos display well-developed suprascapular denticles and a loose band of primary denticles along median disc.

Stage 2: Suprascapular and narrow secondary denticle band present in late embryos. Secondary denticles extending from interorbital region, along median disc, almost to pectoral-fin insertions at birth (240–350 mm DW); 1–2 (usually 2), well-developed, heart-shaped (occasionally pearl-shaped) suprascapular denticles; first suprascapular denticle largest, with convex crown (length 7.2–9.5 mm in morphometric types); second with flatter crown than first; secondary denticles heart-shaped, similar in size to each other and none enlarged beside suprascapular denticles. Denticles absent on tail of neonates.

Stage 4: Secondary denticle band developing more widely over central disc and on head. In juvenile male holotype (CSIRO H 7798-04, 415 mm DW), band moderately dense, covering entire interorbit, width at scapular region ~24% DW; small flattened denticles scattered over median dorsal surface of pre-sting tail; remaining disc smooth. In CMO3-65 (560 mm DW) denticles minute (not tightly spaced), extending well forward of the eyes. In adult (CSIRO H 1920-01) denticles present over nearly all of tail (absent near ventral base); flattened denticles interspersed with slightly larger and more widely spaced, upright, stellate-based tubercular denticles.

Meristics. Total pectoral-fin radials (non-types) 146–152 (n=3); propterygium 60–64, mesopterygium 17–21, metapterygium 68–70. Pelvic-fin radials difficult to count, possibly 25–27 (n=4). Vertebral centra (excluding synarcual) 123 (n=1), (including synarcual) 124 (n=1); monospondylous (including 2nd synarcual) 50–52 (n=2), pre-sting diplospondylous 66–73 (n=4); and post-sting diplospondylous 0 (n=4).

Colour. *When fresh* (holotype): Dorsal disc entirely covered with dark brown, coarsely reticulate colour pattern; reticulate markings differing in length, formed from clusters of sequentially coalesced spots; width of reticulations about half of pupil diameter; reticulations separated from each other by narrower and paler yellow wavy lines (mostly much narrower than dark reticulations); dark spots not fused around outer disc and pelvic-fin margins; tail before caudal sting with 3 irregular rows of dark spots (medially and dorsolaterally), beyond sting more uniformly greyish (blotched but not with alternating light and dark bands), darkest distally. Ventral surface of disc largely white; narrow outer margin of disc and pelvic fins dusky with some small darker markings (margins of paratypes often densely covered with black spots); tail white forward of caudal sting, dark to black posterior to sting, similar to dorsal surface and not banded.

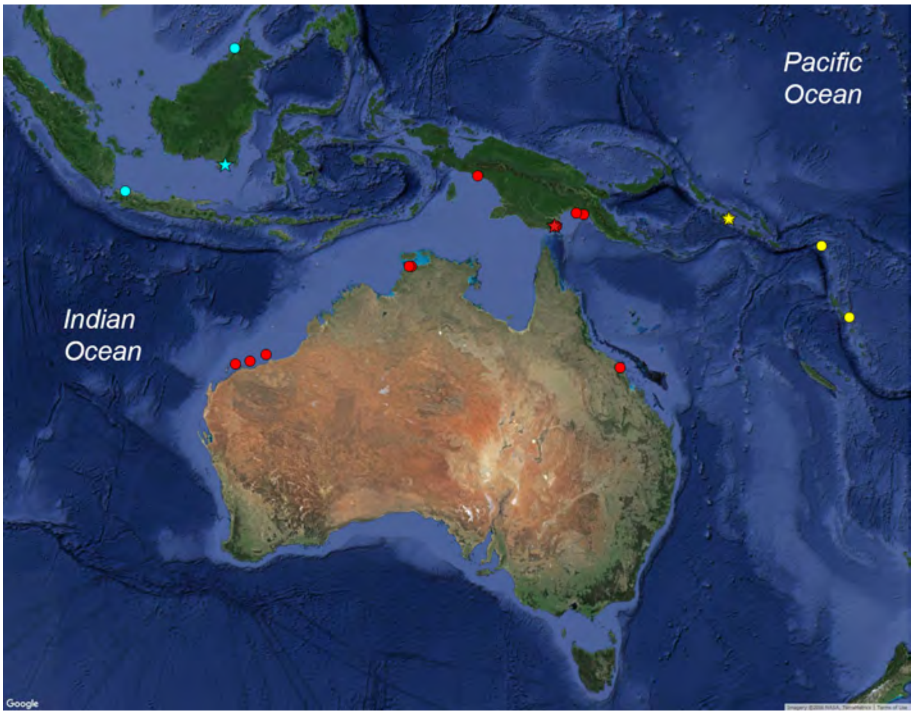

FIGURE 6. Map showing locations of the type material of *Himantura australis* **sp. nov.** (red), *Taeniura lessoni* **sp. nov.** (yellow), and *Telatrygon biasa* **sp. nov.** (blue). Stars denote primary types (holotypes) and solid circles denote secondary types (paratypes). (Map data ©2016 NASA, TerraMetrics, Google Earth).

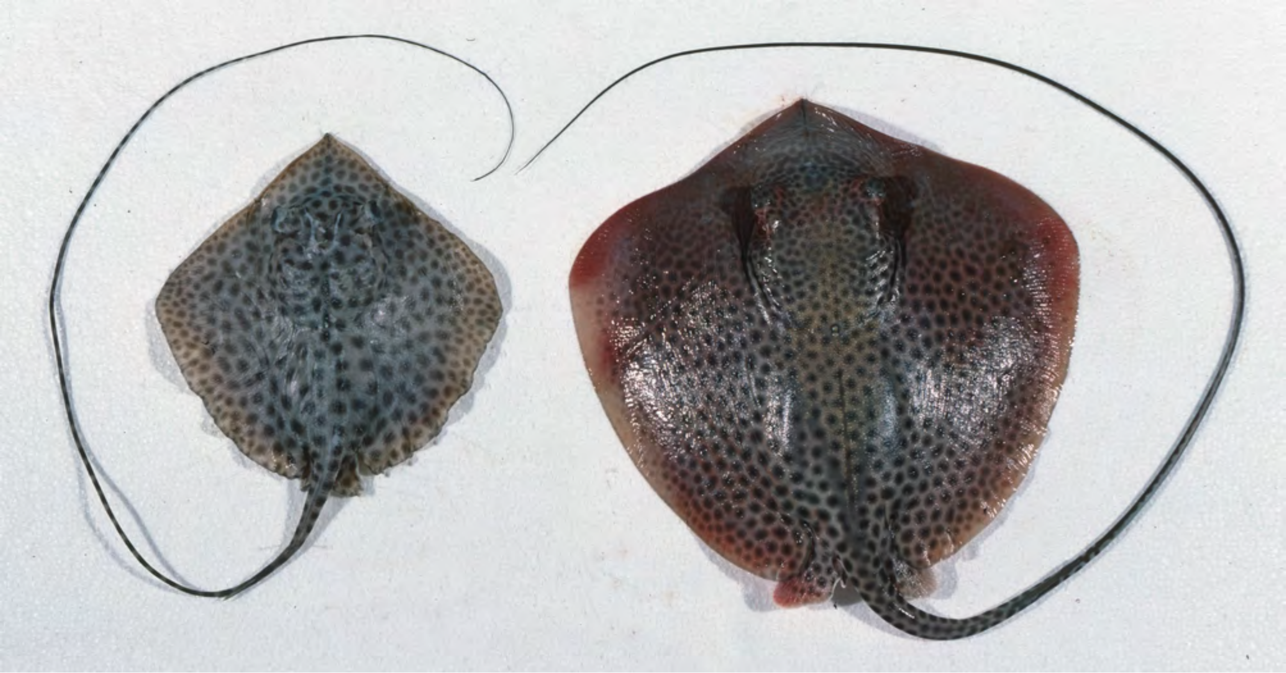

FIGURE 7. Late embryos of *Himantura leoparda* (left, CSIRO H 635-02, 200 mm DW) and *H. australis* (right, CSIRO H 1134-01, 292 mm DW).

Other material: Displays two primary developmental colour morphs (based on all available images, both retained and non-retained material): a dark spotted or spotted/weakly reticulated juvenile form (largest observed 370 mm DW) and subadult and adult forms which are more strongly reticulate (smallest observed 390 mm DW). The smallest individuals (e.g. CSIRO H 7840-01, 241 mm DW, Fig. 5a; CSIRO H 1463-03, 283 mm DW, Fig. 5b) have a honeycomb pattern consisting of irregularly shaped brownish black spots (of more or less similar size and similar to pupil diameter) on central disc separated by narrow yellowish lines; some spots coalesced to form short wavy lines; spots on head and around disc margin typically smaller; dorsal tail before caudal sting with 3 irregular rows of similar dark blotches, not obviously banded beyond sting. Some individuals (e.g. CMO3-57, 290 mm DW) of this morph had the bulk of their markings coalesced to form a distinct reticulate pattern; dark markings only slightly broader than pale lines separating them. Tail of smallest individuals prominently marked; on pre-sting tail upper surface with single median row of dark spots, dorsalateral surfaces with row of similar spots, ventral surface white; lateral spots persist slight beyond caudal sting; anterior tail beyond sting not strongly banded, but with vague light and dark dorsal saddles, sides of tail pale and ventral surface uniformly dark; posterior most part of tail beyond sting entirely black. Smallest fully reticulate form (CMO3-13, 390 mm DW) with very dark, coarse reticulate markings covering entire disc; pale lines separating them much less than half their width; tail markings before caudal sting similar, tail dark greyish or black beyond sting; pattern persisting until about 55 cm DW (CMO3-10, 550 mm DW). Latter stages becoming more finely reticulate (CMO3-65, 560 mm DW, Fig. 5d; PNG not retained 100043, 830 mm DW, Fig. 5e; PNG not retained 130028, 1120 mm DW; PNG not retained 130022, 1400 mm DW, Fig. 5f) or reticulated and partly ocellated (PNG not retained 100096, 1140 mm DW).

TABLE 1. Morphometric data for the holotype (CSIRO H 7798-04) and five paratypes of *Himantura australis* **sp. nov.**, with ratios expressed as percentages of disc width.

	Holotype	Paratypes	
		Range	
Disc width (mm)	415	241	350
Total length	damaged	306.1	419.1
Disc length	95.2	94.0	98.5
Snout to pectoral-fin insertion	84.3	83.6	87.4
Orbit to pectoral-fin insertion	59.9	58.7	61.6
Snout to maximum disc width	40.3	38.9	43.3
Snout to origin of cloaca	79.0	77.2	83.3
Cloaca origin to tail tip	damaged	228.3	335.8
Cloaca origin to caudal sting	39.0	42.0	47.9
Pectoral-fin insertion to caudal sting (horiz)	35.1	34.7	45.6
Disc thickness	13.3	11.0	15.7
Snout (preorbital) length	20.0	19.0	22.4
Snout (preorbital horiz.) length	16.7	16.4	18.9
Orbit diameter	5.4	5.6	6.6
Eye diameter	3.1	3.3	4.0
Spiracle length	6.5	7.1	9.3
Orbit and spiracle length	10.1	9.8	11.3
Interorbital width	13.7	12.0	14.6
Inter-eye width	22.2	21.6	25.2
Distance between spiracles	20.3	19.5	21.6
Head length	45.3	43.5	47.2
Preoral length (to lower jaw)	20.6	21.2	21.8
Prenasal length	16.0	16.0	17.4

......continued on the next page

TABLE 1. (Continued)

	Holotype	Paratypes	
		Range	
Nostril length	4.7	3.9	5.0
Nasal curtain length	6.3	5.1	6.2
Nasal curtain width	11.7	10.1	11.0
Distance between nostrils	9.1	8.0	9.2
Mouth width	10.1	8.6	8.8
Distance between 1st gill slits	21.8	20.0	21.5
Distance between 5th gill slits	13.3	12.5	13.8
Width 1st gill slit	3.6	2.6	3.4
Width 3rd gill slit	3.5	2.9	3.9
Width 5th gill slit	2.2	2.1	2.4
Tail width, axil of pelvic fins	6.8	6.4	8.5
Tail width, base of caudal sting	2.5	2.1	2.6
Tail height, axil of pelvic fins	4.3	4.9	5.8
Tail height, base of caudal sting	2.2	2.0	2.5
Caudal sting 1, length	-	12.8	20.4
Caudal sting 2, length	-	-	-
Cloaca length	6.1	3.9	5.8
Length pelvic fin (embedded)	18.9	18.3	19.5
Width across pelvic-fin base	13.9	12.2	15.4
Greatest width across pelvic fins	34.8	31.8	41.1
Clasper, postcloaca length	8.5	9.1	10.5
Clasper, length from pelvic axil	2.6	2.7	3.1

Size. One paratype (CSIRO H 1463-3), a late-term embryo recovered from an adult female (CSIRO H 1920-01), was 283 mm DW. Two neonates with strong evidence of umbilical scars were 292 and 309 mm DW. A smaller immature male has a healed scar at 241 mm DW. Smallest confirmed adult male 1120 mm DW; largest specimen a 1400 mm DW pregnant female containing 2 embryos 300 mm DW (White, unpublished).

Distribution. Once considered to be conspecific with *Himantura uarnak* (Gmelin, 1789) and widespread in the Indo–West Pacific. Now appears to be confined to the Australasian Plate; known from off Papua New Guinea and northern Australia, from Shark Bay (off Western Australia) to Brisbane (off Queensland); type material displayed in Fig. 6. Depth distribution not well documented, but primarily in shallow-water from near the shore to at least 45 m depth.

Etymology. Noun in apposition referring to the tropical Southern Hemisphere distribution of this *Himantura*. Vernacular name: Australian Whipray.

Comparisons. *Himantura australis* and *H. leoparda* Manjaji-Matsumoto & Last, 2008 are the only members of the genus *Himantura* (*sensu* Last *et al*., 2016) occurring in Australasian seas. The species are similar but differ in coloration: *Himantura australis* has a more reticulated pattern on the dorsal disc in adults (adult *H. australis* have an ocellated pattern, typical of *H. leoparda*, but the ocelli are smaller and remain dominated by reticulations), the suprascapular denticles are few (1–2, rather than being preceded and followed by a row of slightly smaller primary denticles), and the snout is broader (rather than being produced slightly and more angular) in young and mostly in adults. Juveniles differ in the following morphometric details: preoral length 2.04–2.55 times mouth width (vs. 2.79–3.30 in *H. leoparda*), and 20.6–21.8% DW (vs. 23.3–27.6%); distance between first gill slits 2.18–2.54 times internasal distance (vs. 1.98–2.18); distance between fifth gill slits 1.45–1.66 times internasal distance (vs. 1.38–1.40), ~0.29 in ventral head length (vs. 0.25–0.28).

Himantura australis is not sympatric with its other congeners and its relationship to these species is part of a revision of the group in progress. It exhibits strong molecular divergence from the other reticulate *Himantura* species, *H. uarnak* and *H. undulata* (Bleeker, 1852) (see Last *et al*., 2016, Fig. 3). Morphologically it differs from *H. undulata* in having smaller reticulations, a less elongate snout, and lacks a pair of pearl-shaped suprascapular denticles characteristic of *H. undulata*. Its reticulate pattern in adults is typically more pronounced than in *H. uarnak*, but elucidating characters to separate them across all size groups is a work in progress.

Taeniura lessoni **sp. nov.**

(Figs. 8–12; Table 2)

Taeniura sp.: Last *et al*., 2016: figs. 2, 5 (molecular data).

Holotype. CSIRO H 7724-01 (tissue accession GN16865), adult male 209 mm DW, Landoro Passage off Uepi Island, Marovo Lagoon, Solomon Islands, ~8°25.6'S, 157°55.7'E, 2–3 m depth, 13 May 2015.

Paratypes. 4 specimens: CSIRO H 7724-02 (tissue accession GN16866), female 201 mm DW, collected with holotype; QM I 39329 (tissue accession GN16864), female 220 mm DW, collected with holotype; USNM 350580, female 180 mm DW, fringing reef, Lamen Island, 9–18 m depth, Vanuatu, 26 Sep 1998; USNM 380822, immature male 185 mm DW, coral surge channel on northwest coast south of Neo Village, Tomotu Island, Santa Cruz Islands, Solomon Islands, 0–10 m depth, 29 Sep 1998.

Diagnosis. Small, blue-spotted stingray of the genus *Taeniura* lacking of a pair of blue longitudinal stripes along the sides of the tail; a uniformly pale ventral fold; no dorsal fold but upper margin of tail with a firm, blunt ridge; and within the genus possibly a relatively short post-orbital disc (length from rear of orbit to pectoral-fin insertion 63–65% DW), relatively long horizontal snout length (20–21% DW) and prenasal length 14–16% DW, and prenasal length 1.5–1.9 times internasal width.

Description. Disc oval, strongly convex anteriorly; much longer than broad, width 0.87 times length in holotype (0.87–0.88 in paratypes); snout angle 116° (116–122°), anterior disc angle 94° (88–97°); axis of greatest width of disc relatively well forward on disc, anterior to scapular region, its distance from snout tip 1.78 (1.66–1.87) times in distance from tip of snout to pectoral-fin insertion; abdomen robust, thickness 6.3 (5.7–6.5) times in disc width, raised slightly above cranium and central disc; apex very broadly rounded, pectoral angle 107° (104–109°); posterior margin strongly convex; free rear tip abruptly angular. Pelvic fins narrowly subtriangular, anterior margin almost straight to undulate, apex narrowly rounded, posterior margin moderately convex, merged with inner margin (free rear tip indiscernible); large, length 29.7% (28.8–30.8%) DW, 1.53 (1.34–1.69) times width across fin bases. Claspers of adult males large, mildly depressed, tapering, apex bluntly pointed; outer length (from axil of pelvic fin) in adult male holotype 21.2% DW.

Tail robust, firm, tapering gradually to caudal sting(s); ventral skin fold prominent, dorsal skin fold absent; base moderately broad and deep, broadly oval in cross-section, weakly convex to almost flat above and below, width 1.53 (1.47–1.67) times depth; depressed, oval in cross-section near origin of ventral skin fold, width 0.75 (0.36–0.51) times height at fold origin; tapering abruptly evenly in dorsoventral view below caudal sting(s); oval, compressed near tip of caudal sting and above mid-length of ventral fold; tail very compressed, narrowly suboval in cross-section towards its tip, width 0.75 (0.36–0.51) times depth at mid-base of ventral fold; dorsal surface of tail immediately posterior to caudal-sting bases with a weak naked groove (partly housing ventral-most sting and extending for about half to its full length); firm, low fleshy ridge on mid-dorsal tail beyond caudal sting, no skin folds present along lateral margin of tail. Ventral skin fold well-developed over its entire length, long, 66.1% (87.8–95.3)% DW; depth at mid-base 0.94 (0.86–1.38) of tail height at mid-base; originating just forward of first caudal sting origin. Caudal sting positioned posteriorly on tail, horizontal distance from cloaca to sting origin 1.19 (1.14–1.21) in precloacal length.

Snout fleshy (more so in largest paratype), rather short, broadly rounded; not acute at apex and without obvious apical lobe; tip narrowly rounded when viewed laterally; preoral snout length 1.78 (1.77–1.99) times mouth width, 1.98 (2.14–2.32) times internarial distance, 0.88 (0.90–1.01) times distance between first gill slits; direct preorbital snout length 2.78 (2.64–2.88) times interorbital length; snout to maximum disc width 1.79 (1.74–1.93) in DW; interorbital space narrow, flat to weakly convex; eyes large, dorsolateral, protruding, well elevated above disc and interorbital space, diameter 0.84 (0.89–0.98) in spiracle length, eye length 1.18 (1.15–1.34) in spiracle length; inter-eye distance 2.75 (2.62–2.94) times eye length. Spiracles large, subrectangular to crescentic, opening dorsolaterally; dorsal margin a firm ridge. Nostril narrowly oval to slit-like, directed slightly obliquely; lateral margin fleshy; nasal fold on lateral margin partly internal, narrow; oronasal groove present; internarial space 1.46 (1.64–1.94) in prenasal length, 1.87 (1.44–1.78) times nostril length. Nasal curtain small, relatively narrow, skirt-like, short, width 2.16 (1.62–2.21) times length; weakly bilobed, posterior margin of each lobe undulate; curtain surface weakly papillate, usually with weak medial groove and covered with minute pores (often obscure); apex recessible within lateral margin of oronasal groove; lateral margin almost straight, smooth-edged, usually partly enveloped by narrow posterior fold of nostril; posterior margin heavily fringed, slightly concave medially, vaguely following contour and usually overlapping lower jaw when mouth closed (when intact).

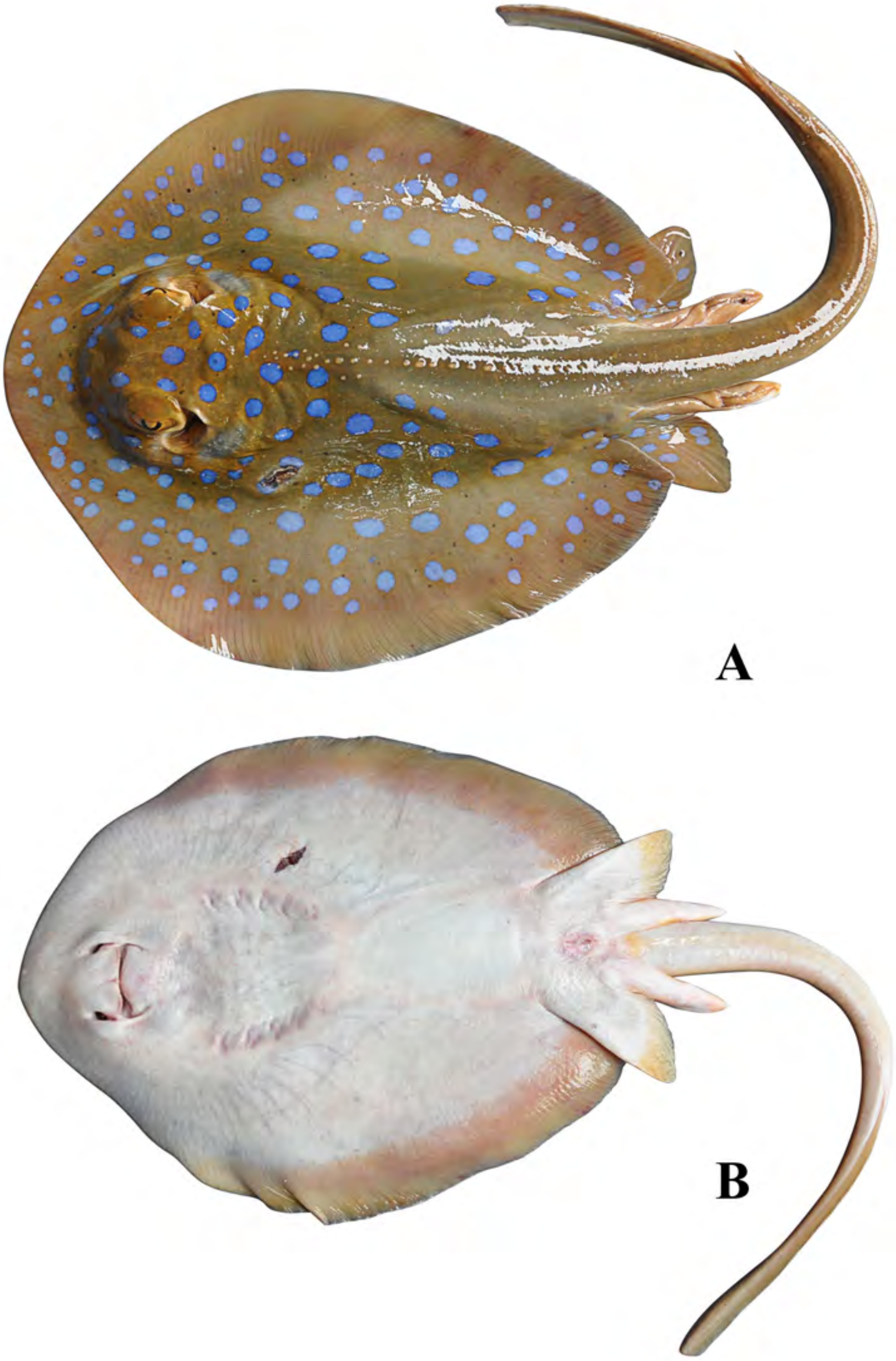

FIGURE 8. Holotype of *Taeniura lessoni* **sp. nov.**, adult male 209 mm DW (CSIRO H 7724-01), from Marovo Lagoon, Solomon Islands (fresh): (A) Dorsal view; (B) Ventral view.

FIGURE 9. Dorsal view of paratype of *Taeniura lessoni* **sp. nov.**, female 220 mm DW (CSIRO QM I 39329), from Marovo Lagoon, Solomon Islands (fresh).

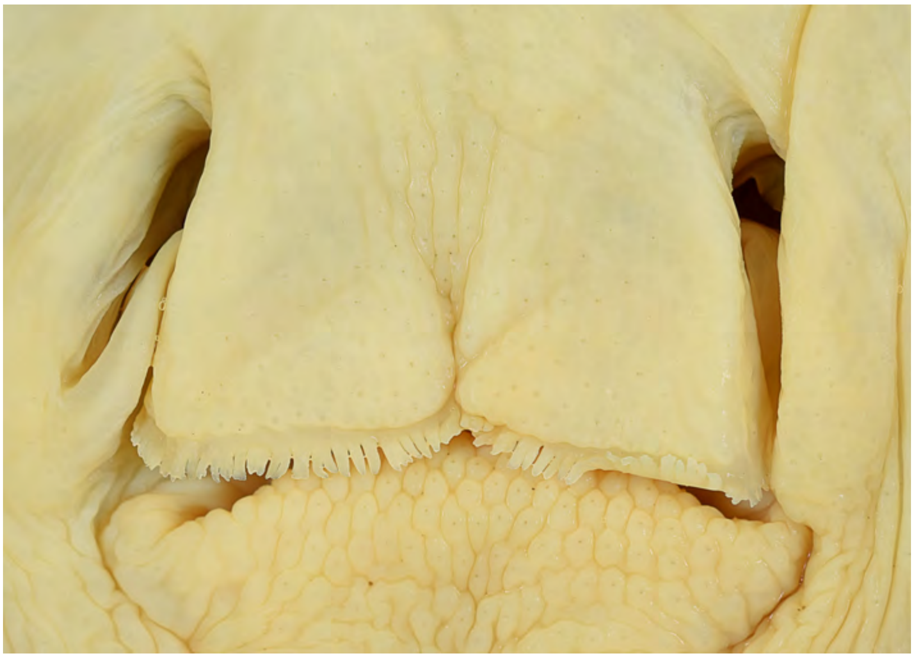

FIGURE 10. Oronasal region the paratype of *Taeniura lessoni* **sp. nov.**, female 180 mm DW (USNM 350580), from Vanuatu (preserved).

FIGURE 11. Denticles of the mid-disc of the holotype of *Taeniura lessoni* **sp. nov.**, adult male 209 mm DW (CSIRO H 7724-01), from Marovo Lagoon, Solomon Islands (preserved).

FIGURE 12. Lateral view of the post-caudal sting tail the holotype of *Taeniura lessoni* **sp. nov.**, adult male 209 mm DW (CSIRO H 7724-01), from Marovo Lagoon, Solomon Islands (preserved); note well-developed ventral skin fold.

Mouth small, jaws strongly asymmetric; lateral grooves short, rather well developed, curved slightly, extending from nostril to below corners of lower jaw; mouth not projecting forward when open, not protrusible; skin on chin and margin of lower jaw very fleshy, strongly papillate; teeth uniformly close-set in both jaws, in few oblique rows, not arranged in obvious quincunx; in paratype (CSIRO H 7724-02) rows in upper jaw ~23, lower jaw ~23. Upper jaw strongly arched, anterior edge strongly double concave; tooth band width similar over its length, only teeth of anteriormost part of upper jaw visible when mouth closed; symphysial part of jaw projecting anteroventrally. Lower jaw strongly convex anteriorly with a rounded anterior margin, lingual edge truncate (tooth band much broader at symphysis than at corner of mouth; partly interlocking into upper jaw when mouth closed; teeth not visible when mouth closed. Upper jaw of female paratype (CSIRO H 7724-02) with 5th tooth rows from each side of jaw having slightly enlarged teeth with longer cusps than those adjacent (directed lingually); teeth otherwise acuspid or with short cusps; those at symphysis barely larger than those adjacent. Teeth in lower jaw smaller than those of upper jaw, broad based, low, with semi-truncate to weakly cuspid distal margins; anteriormost part of crown with cenulate surface; no rows of enlarged teeth in jaw. Floor of mouth in female paratype (CSIRO H 7724-02) with two, slender, lobe-like oral papillae, interspace between them subequal to their distance from corner or mouth (holotype not dissected); no smaller papillae near angle of each jaw.

Gill openings elongate S-shaped, margins entire rather than fringed; length of first gill slit 1.33 (1.29–1.62) times length of fifth gill slit, 2.62 (2.17–2.79) times in mouth width; distance between first gill slits 2.24(2.27–2.54) times internarial space, 0.42 (0.37–0.40) times ventral head length; distance between fifth gill slits 1.38 (1.49–1.54) times internasal distance, 0.26 (0.24–0.26) times ventral head length.

Total pectoral-fin radials 110–112 (110–115); propterygium 48–49 (47–50), mesopterygium 15 (16–18), metapterygium 48 (47–50). Pelvic-fin radials: 1 (1) + 18–19 (19 on right side of male paratype, 23–25 in female paratypes). Vertebral centra total (including synarcual) 175 (181–184 in paratypes); total (excluding synarcual) 175 (180–184); monospondylous (including synarcual) 38 (37–40); monospondylous (excluding synarcual) 38 (37–39); pre-sting diplospondylous 90 (91–101); post-sting diplospondylous 47 (40–55).

Squamation. Dorsal disc and tail of holotype rough to touch, sparsely covered with small to minute dermal denticles; a single row of short, spear-shaped thornlets along mid-line of disc from mid-scapular region to near pectoral-fin insertion; similar thornlets in 2 rows in nuchal region and 2 similar scapular thornlets on each side of and located very close to median row. Much smaller (often microscopic) prickly denticles scattered mainly over central disc and tail; denticles upright with pungent tips. Ventral surface naked. In largest paratypes, thornlet distribution similar to holotype; prickly denticles also well developed in largest female paratype, but largely absent in smaller specimens.

One caudal sting in holotype (1 or 2 in paratypes), intact, very elongate, slender, narrow based, length subequal to periorbital length; enveloping membrane absent; distance from sting base to pectoral-fin insertion 81.1 (71.9–81.4%) DW, 3.98 (2.57–3.96) times first sting length; distance from cloaca to sting base 0.72 (0.67–0.72) in disc length.

TABLE 2. Morphometric data for the holotype (CSIRO H 7724-01) and four paratypes of *Taeniura lessoni* **sp. nov.**, and four non-type specimens of *T. lymma* with ratios expressed as percentages of disc width.

	Taeniura lessoni			*Taeniura lymma*	
	Holotype	Paratypes		Non-types	
		Range		Range	
Disc width (mm)	209	180	220	183	246
Total length	243.1	249.2	262.7	232.5	265.6
Disc length	114.8	110.5	114.6	112.9	120.4
Snout to pectoral-fin insertion	99.1	92.6	96.5	97.6	106.1
Orbit to pectoral-fin insertion	64.6	63.4	65.2	65.6	74.1
Snout to maximum disc width	55.7	51.7	57.4	53.0	57.8
Snout to origin of cloaca	97.8	89.4	94.5	93.5	101.7
Cloaca origin to tail tip	145.3	159.8	168.2	158.8	172.1
Cloaca origin to caudal sting	82.4	75.8	83.1	81.5	89.4
Pectoral-fin insertion to caudal sting (horiz)	81.1	71.9	81.4	78.4	88.3
Disc thickness	15.8	15.4	17.4	14.7	19.0
Snout (preorbital) length	25.4	22.1	25.7	21.5	24.0
Snout (preorbital horiz.) length	20.2	20.0	21.2	17.1	19.4
Orbit diameter	10.1	8.8	9.6	9.4	11.3
Eye diameter	7.2	6.6	7.4	7.3	8.4
Spiracle length	8.5	8.0	9.2	8.5	9.4
Orbit and spiracle length	13.9	11.4	13.0	13.6	15.3
Interorbital width	9.1	8.4	9.1	8.3	9.3
Inter-eye width	19.8	17.7	20.0	17.3	19.4
Distance between spiracles	16.9	15.3	16.9	16.4	17.9
Head length	54.5	49.8	53.8	51.8	57.1
Preoral length (to lower jaw)	20.1	18.6	20.7	17.7	19.2
Prenasal length	14.8	14.3	15.6	12.2	14.7
Nostril length	5.4	4.9	5.9	4.5	5.8
Nasal curtain length	5.7	5.2	6.2	5.6	7.4
Nasal curtain width	12.4	9.1	11.7	10.6	14.2
Distance between nostrils	10.1	8.0	9.1	8.9	9.5
Mouth width	11.3	10.0	10.7	9.2	10.8

......*continued on the next page*

TABLE 2. (Continued)

	Taeniura lessoni			*Taeniura lymma*	
	Holotype	Paratypes		Non-types	
Distance between 1st gill slits	22.7	18.5	21.6	20.9	23.0
Distance between 5th gill slits	14.0	12.0	13.6	13.5	14.7
Width 1st gill slit	4.3	3.8	4.6	3.6	4.1
Width 3rd gill slit	4.8	4.0	4.7	4.2	4.8
Width 5th gill slit	3.2	2.8	3.0	2.8	3.6
Tail width, axil of pelvic fins	12.5	11.7	13.5	11.6	15.0
Tail width, base of caudal sting	6.0	4.2	6.1	5.3	5.8
Tail height, axil of pelvic fins	8.1	7.4	8.8	8.1	9.1
Tail height, base of caudal sting	4.5	4.5	4.9	4.7	5.0
Caudal sting 1, length	20.4	20.6	28.0	20.7	29.1
Caudal sting 2, length	-	20.8	26.8	28.5	30.9
Cloaca length	7.3	6.7	8.3	6.3	8.8
Length pelvic fin (embedded)	29.7	28.8	30.8	32.3	34.3
Width across pelvic-fin base	19.4	17.6	21.4	20.2	24.1
Greatest width across pelvic fins	53.7	41.5	57.3	36.9	50.7
Clasper, postcloaca length	29.0	-	9.4	12.9	35.5
Clasper, length from pelvic axil	21.2	-	4.4	5.8	23.9
Tail width (at broadest part of ventral fold)	1.8	1.2	1.7	1.5	1.9
Tail height (at broadest part of ventral fold)	2.4	2.9	4.4	2.8	3.3
Dorsal skin fold, length				27.8	49.0
Dorsal skin fold, mid-height				0.8	0.9
Ventral skin fold, base length	66.1	87.8	95.3	73.3	91.7
Ventral skin fold, mid-height	2.3	2.5	4.7	2.3	3.8

Colour. Live coloration (based on holotype). Dorsal surface yellowish brown with vivid blue spotting; slightly paler brownish pink along margin of disc and pelvic fins; eye golden, orbital membrane similar to disc. Blue spots small to medium-sized (always smaller than corneal length), not distinctly ocellate irregularly spaced, distributed widely over disc but absent from tail; thornlets on medial disc slightly paler than adjacent skin; no mask-like marking on head distinct or dark speckles; claspers paler than disc. Ventral surface centrally on disc uniformly white; lateral and posterior disc margin, and tips of pelvic fins, with distinct, broad yellowish submarginal bands. Tail similar to disc dorsally, lacking a pair of prominent blue lines extending along its dorsolateral margins; caudal sting pale brownish; pre-sting tail white ventrally, ventral fold pale yellowish to whitish.

Fresh paratypes similar to holotype. Blue markings changed to greyish (with slightly darker spot margins) in preservative in CSIRO and NTM types, however, USNM types retained more blue coloration.

Size. Largest specimen a female paratype 220 mm DW (QM I 39329, 568 mm TL). The holotype is a sexually mature male at 209 mm DW; the other male (paratype USNM 380822) was immature at 185 mm DW. No information is available on birth size.

Distribution. Specimens collected from the Solomon Islands and Vanuatu (Fig. 6), but possibly more widely distributed in Melanesia. Underwater images from off Kavieng (New Ireland), and off Kokopo, East New Britain (Papua New Guinea), were also verified based on colour as being this species. Underwater images viewed on Google Images of *Taeniura* from Fiji also appear to be this species. Probably mainly inshore, types collected from surge channels in fringing coral reefs, to at least 18 m depth.

Etymology. Epithet in recognition of the work of the 19thC French scientist, René Lesson, who once worked on members of this genus in Melanesia. Vernacular: Oceania Fantail Ray.

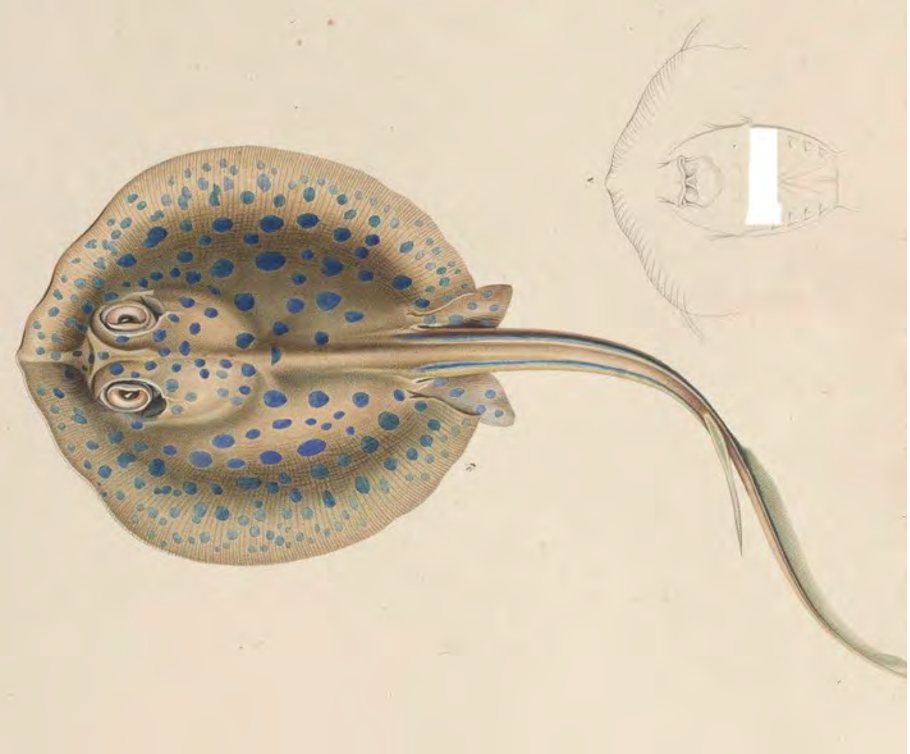

FIGURE 13. Original illustration of *Trygon halgani* from Lesson (1831) clearly showing the paired blue stripes on the tail.

FIGURE 14. Dorsal view of one of the syntypes (MNHN A 7994) of *Trygon halgani* Lesson (preserved).

Comparisons. *Taeniura lessoni* is immediately distinguishable from *T. lymma* in the field by the absence of a pair of blue stripes along the sides of the tail, and the ventral fold is uniformly pale in *T. lessoni* (fold margin darker than its base in *T. lymma* with the tail tip usually white). Closer inspection of the tail of *T. lymma* reveals that its upper post-sting margin in raised slight to form an angular, fleshy ridge that becomes a distinct low fold near the tail tip in juveniles. In the *T. lessoni* types the margin appears as a firm ridge, not forming a fold and its edge is less acute than in *T. lymma*. A comparison of the *T. lessoni* types with 4 similar-sized specimens of *T. lymma* (QM I 17668, QM I 31356, QM I 8328 and QM I 6666) indicated that these species might differ subtly in some morphometrics details: length from rear of orbit to pectoral-fin insertion 63.4–65.2% vs. 65.6–74.1% DW in *T. lymma*; horizontal snout length 20.0–21.2% vs. 17.1–19.4% DW; prenasal length 14.3–15.6% vs. 12.2–14.7% DW, 1.46–1.94 vs. 1.36–1.39 times internasal width; and pelvic-fin length 28.8–30.8% vs. 32.3–34.3% DW. However, no doubt these species are very similar morphologically and more data is needed to determine the extent of interspecific variability. *Taeniura lymma* may also attain a slightly larger size than *T. lessoni* (35 cm rather than 22 cm DW, Last *et al.*, in press).

The distributions of these two similar species do not appear to overlap. Both occur off Papua New Guinea, based on underwater images, but they do not appear to be sympatric. Lesson (1831) described *Trygon halgani* based on material from Waigeo (Indonesia) and Port Praslin (New Ireland). His illustrated syntype (Fig. 13) is clearly referable to *T. lymma* due to the presence of the longitudinal blue stripes on the tail. The two syntypes attributed to this species are listed as being from Port Praslin. Séret & McEachran (1986) compared the two available New Ireland specimens (MNHN A 7994, Fig. 14) to Lesson's drawing, and found some similarities in the pattern of spots between the "larger" specimen and the drawing (mainly on the interorbital space and inner left pectoral fin). However, because of uncertainty as to which of these two specimens Lesson used as the type, they decided to consider both specimens as syntypes and also treated *Trygon halgani* as a junior synonym of *Taeniura lymma*.

Lesson also unequivocally mentioned the existence of ‘two soft blue lines extending along the entire length of the tail’ and these markings are evident in his colour painting of the type (Fig. 13) – a key diagnostic feature of *T. lymma* but absent in *T. lessoni*. However, while the two syntypes of *T. halgani* are in good condition, and the blue spots remain distinctive, the blue stripes on the tail are not clearly evident based on images of these specimens. According to B. Séret (pers. comm.), the blue tail stripes mentioned by Lesson were still visible in the preserved specimens as darker bands (most evident on the "larger" specimen) when examined in the 1980s. The confirmed presence of *T. lessoni* (and possible absence of *T. lymma*) from New Ireland confounds this issue. However, given that Lesson’s illustrated ‘type’ clearly depicts *T. lymma*, *T. halgani* must be considered a synonym of that species. Additional collections of these rays are needed from New Ireland, and the surrounding island groups of Papua New Guinea, to determine the local range of *T. lessoni* in this area and whether the two species co-occur. From information gathered to date, *T. lymma* has been confirmed from Milne Bay (KRFS unregistered specimens), Madang (NTUM 10296), Trobriand Islands (e.g. BMNH 1974.5.25.1, USNM 206313), Port Moresby (FMNH 120119) and Daru (e.g. USNM 222553) in Papua New Guinea. Furthermore, Miklouho-Maclay & Macleay (1886) described *Discobatis marginipinnis* from the Admiralty Islands of PNG. While no type specimens were retained, the illustration and description clearly highlight that the possession of blue lines on the tail diagnostic of *T. lymma*. In comparison, *T. lessoni* has been confirmed from Rabaul (East New Britain) and Kavieng (New Ireland) based on underwater images. Thus, *T. lymma* appears to be common around mainland Papua New Guinea, but *T. lessoni* may be confined to New Ireland and eastern New Britain.

***Telatrygon biasa* sp. nov.**

(Figs. 15–19; Table 3)

Dasyatis zugei (not Müller & Henle): White *et al.*, 2006: 230–31, figs.; Last *et al.*, 2010: 188–89 (figs.) (misidentifications).
Dasyatis cf. *zugei*: Naylor *et al.*, 2012: fig. 56 (molecular data).
Dasyatis sp.: Last *et al.*, 2016: fig. 1 (molecular data).
Telatrygon sp.: Last *et al.*, 2016: fig. 5 (molecular data).

Holotype. MZB, field no. KA-93; tissue accession GN4266), mature male 194 mm DW, Muara Kintap, Kalimantan, Borneo, Indonesia, 03°54.25’S, 115°15.53’E, 30 Nov 2006.

Paratypes. 9 specimens. CSIRO H 4426-05, female 243 mm DW, CSIRO H 4426-06, male 195 mm DW, CSIRO H 4426-07, female 251 mm DW, CSIRO H 4426-09, male 191 mm DW, CSIRO H 4426-10, male 185 mm DW, Muara Angke fish market (probably collected in western Java Sea), Jakarta, Java, Indonesia, 17 Oct 1995; CSIRO H 5474-21 (field no. MMKK68), female 253 mm DW, CSIRO H 5474-22 (field no. MMKK71), male 205 mm DW, CSIRO H 5474-24 (field no. MMKK74), mature male 196 mm DW, Kota Kinabalu fish market, Sabah, Borneo, Malaysia, 15 Feb 1999; CSIRO H 5475-06 (field no. MMKK18), female 254 mm DW, Kota Kinabalu fish market, Sabah, Borneo, Malaysia, 9 Feb 1999.

Diagnosis. A species of *Telatrygon* distinguished by the following combination of characters: snout relatively short, preorbital length 28–29% DW, preoral length 27–28% DW, prenasal length 23–25% DW; disc relatively short, length 97–105% DW; preoral length 1.5–1.6 times width between the first gill openings; eyes small, orbit length 5–7% DW; pectoral-fin radials 107–114; total vertebral centra (excluding 1st synarcual) 85–94.

Description. Disc rhombic, angular anteriorly and apex produced as firm lobe; its width 0.95 times length in holotype (0.97–1.03 in paratypes); axis of greatest width almost over scapular region, its distance from snout tip 1.70 (1.62–1.79) of distance from tip of snout to pectoral-fin insertion; body very depressed, thin, greatest thickness 10.8 (8.99–10.8) times in disc width, barely raised above cranium or above scapular region; anterior margin of disc concave, strongest beside orbits; apex broadly rounded, anterior disc angle 83° (84–91°), pectoral angle 100° (98–101°); posterior margin convex; free rear tip narrowly rounded. Pelvic fins strongly subtriangular; anterior margin almost straight, posterior margin convex or straight; apices narrow and bluntly pointed; free rear tip broadly rounded, inner margin short; very small, length 19.3% (16.2–19.2%) DW; 1.46 (1.15–1.41) times width across fin bases.

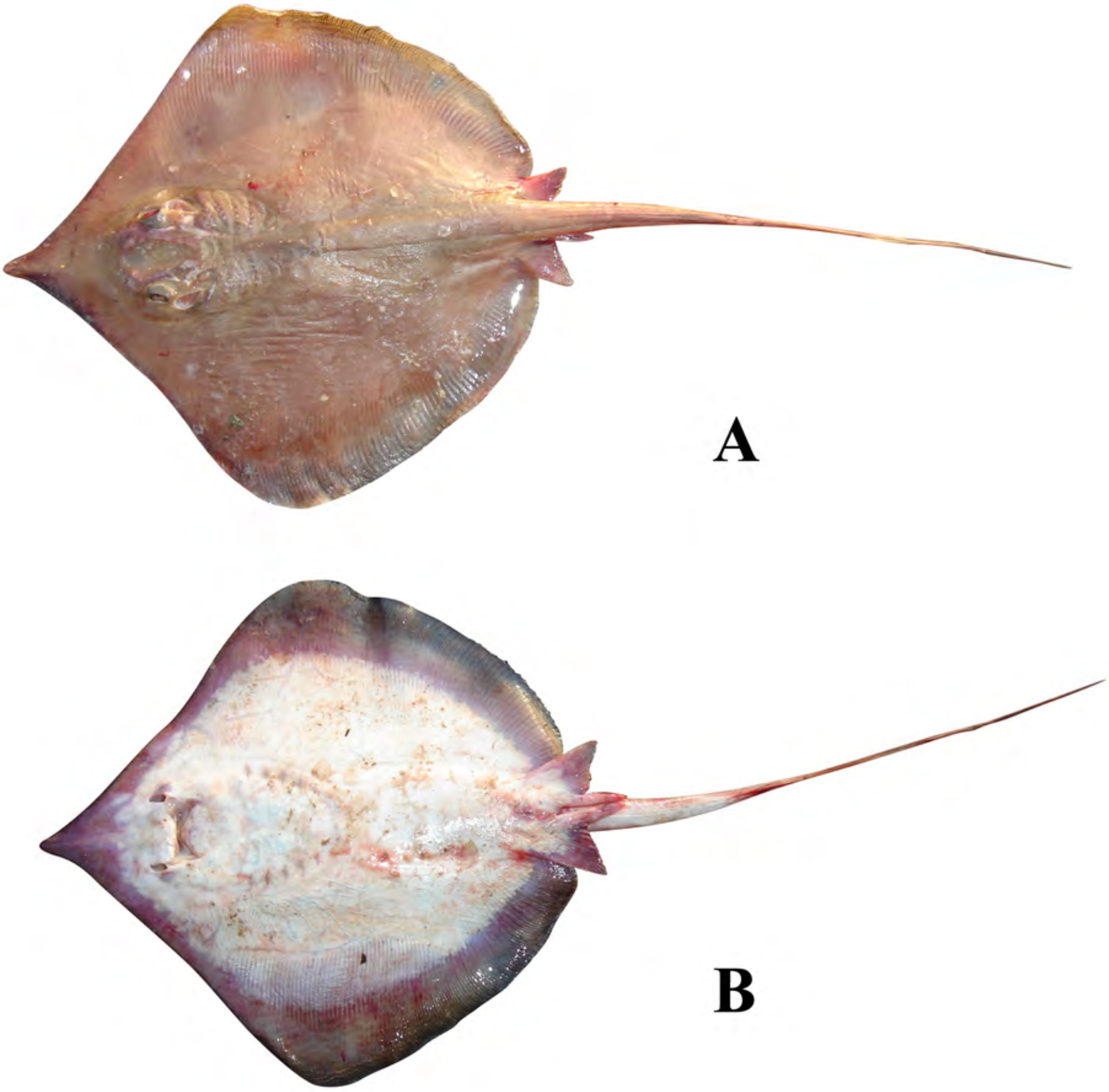

FIGURE 15. Holotype of *Telatrygon biasa* **sp. nov.**, adult male 194 mm DW (MZB KA-93), from Kalimantan, Indonesia (fresh): (A) Dorsal view; (B) Ventral view.

FIGURE 16. Dorsal view of female *Telatrygon biasa* **sp. nov.**, 192 mm DW (KA 477, not retained), from Sarawak, Malaysian Borneo (fresh).

FIGURE 17. Oronasal region the holotype of *Telatrygon biasa* **sp. nov.**, adult male 194 mm DW (MZB KA-93), from Kalimantan, Indonesia (preserved).

FIGURE 18. Denticles of the paratype of *Telatrygon biasa* **sp. nov.**, female 243 mm DW (CSIRO H 4426-05), from Java, Indonesia (preserved). A. Mid-dorsal disc; B. Dorsal tail before sting.

FIGURE 19. Lateral view of the post-caudal sting tail of the paratype of *Telatrygon biasa* **sp. nov.**, female 243 mm DW (CSIRO H 4426-05), from Java, Indonesia (preserved); note low ventral fold and scar on dorsal surface at caudal sting origin (sting missing).

Tail very elongate, slender, postcloacal tail damaged (1.60–2.32) times precloacal length; with a long, low ventral skin fold and usually a much shorter dorsal skin fold; base moderately depressed, suboval in cross-section, weakly convex above and below, width 1.22 (1.35–2.04) times its depth; tapering strongly and evenly to sting base; broadly oval in cross-section near origin of ventral skin fold, width 1.18 (1.24–1.43) times height at fold origin; tapering abruptly below sting insertion; very slender and filamentous beyond sting; variable in cross-section above mid ventral fold, its width 0.57 (0.65–1.20) times depth; at end of ventral fold variably suboval, width 1.03 (0.48–1.32) times height; dorsal surface of tail posterior to sting base with a narrow, tapering, naked groove (presumably housing sting when present); no skin folds or ridges along lateral margin of tail. Dorsal skin fold very low (but always present), merging with a low fleshy ridge anteriorly and posteriorly (fold origin and insertion not well defined); elongate, length about 28 (37–64) times its height, 2.28 (1.03–1.84) in snout length, 4.65 (2.99–3.92) in length of ventral fold; its height 1.39 (0.86–2.05) in height of mid ventral fold. Ventral skin fold very elongate, low, length 1.64 (1.21–1.62) in disc width, damaged in holotype (0.95–1.3 in paratypes) in post cloacal tail; origin 3.5% (3.7–15%) DW after sting origin; depth at quarter length 0.86 (0.61–1.05), at mid length 0.43 (0.41–0.82), at three quarter 0.82 (0.45–0.71) in adjacent tail height; originating posteriorly to sting origin; origin usually distinct but fold usually terminating in low fleshy ridge; distance from cloaca to sting origin 2.37 (2.49–2.94) in precloacal length; length of tail beyond ventral fold damaged (0.95–1.33) in fold length, damaged (2.40–3.12) in tail length. Sensory canals well demarcated on ventral surface.

Snout very elongate, strongly depressed, triangular; apex with a long, narrowly rounded lobe; angle 83.5° (83–92°); preoral snout length 3.06 (2.98–3.47) times mouth width, 2.38 (2.47–2.82) times internarial distance, 1.62 (1.52–1.63) times distance between first gill slits; direct preorbital snout length 2.90 (2.62–2.88) times interorbital length; snout to maximum disc width 1.72 (1.76–1.94) in DW; interorbital space rather broad, slightly concave medially; eye small, dorsolateral, not protruded, its ventral margin partly covered by thin skin fold; orbit not elevated above interorbit, its diameter 1.07 (0.91–1.26) in spiracle length; eye diameter 1.50 (1.37–1.90) in spiracle length; inter-eye distance 3.59 (3.42–3.99) times eye diameter. Spiracle suboval, enlarged, dorsolateral. Nostrils narrow, slit-like, parallel to slightly oblique; anterior margin not elevated; anterior nasal fold internal, narrow, membranous; oronasal groove usually well defined; internasal distance 1.99 (2.04–2.37) in prenasal length, 3.20 (2.69–3.01) times nostril length. Nasal curtain skirt-shaped, elongate, width 1.73 (1.68–1.78) times length; moderately bilobed; its surface flat, smooth, without a longitudinal medial groove and not covered with prominent sensory pores; apex recessible within lateral margin of oronasal groove; lateral margin almost straight, smooth edged; posterior margin finely fringed, weakly concave, following contour of lower jaw, abutting or falling slightly short of symphysis of lower jaw when mouth closed.

Mouth strongly arched in adult males, almost straight in females; jaws asymmetrical; lateral groove weak or absent. Upper jaw strongly arched in holotype, teeth concealed when mouth closed, symphysial part of jaw not projecting ventrally (not visible). Lower jaw very strongly convex, weakly concave at symphysis in all male types, only outer symphysial teeth visible when mouth closed in holotype; not projecting forward when mouth open, mouth not protrusible; skin on chin not fleshy, ridged nor papillate. Floor of mouth in adult male paratype (CSIRO H 4426-09) lacking oral papillae, instead covered with a series of horizontal pleats of skin. Teeth both jaws small, with very long, pointed cups; cusps longer near symphysis than near corners of mouth; close-set in both jaws but not quincuncial; tooth row counts unclear, ~48 rows in upper jaw, ~42 rows in lower jaw.

Gill slits distinctly S-shaped, edges not fringed laterally; length of first gill slit 1.41 (1.26–1.61) times length of fifth gill slit, 2.83 (2.28–3.35) times in mouth width; distance between first gill slits 1.46 (1.62–1.84) times internasal distance, 0.32 (0.33–0.35) times ventral head length; distance between fifth gill slits 0.95(0.98–1.18) times internasal distance, 0.21 (0.20–0.23) times ventral head length.

Squamation. Disc and tail lacking dermal denticles in young or with weak denticles and small thorns confined to median dorsal row in adults. Adult male holotype (MZB KA-93, 162 mm DW) with short row of 6 minute, globular denticles in nuchal region; no thorns on tail; 3 adult male paratypes (CSIRO H 4426-06, 09, 10) with 6–9 globular to weakly lanceolate denticles in nuchal region, 3–6 much larger (but small and varying in size), narrowly lanceolate, thorn-like denticles on midline of tail forward of caudal sting. Female paratypes (CSIRO H 4426-05, H 5475-06, H 5475-21) with 7–13 globular to weakly lanceolate denticles in nuchal region, followed by 0–13 similar post-scapular denticles on posterior disc; 5–9 much larger (but small and varying in size), narrowly lanceolate, thorn-like denticles on midline of tail forward of caudal sting. All type specimens with caudal stings missing at preservation. Distance from caudal sting base to pectoral-fin insertion 36.5% (29.2–32.7%) DW; distance from cloaca to caudal sting base 0.38 (0.32–0.36) in disc length.

Meristics. Total pectoral-fin radials of holotype 107–108 (paratypes 107–114, n=5). Total pelvic-fin radials adult male holotype 16 (paratypes 19–24). Total vertebral segments (excluding first synarcual centra) 85 (88–94); monospondylous centra (excluding first synarcual) 37 (31–36); diplospondylous centra 51 (52–61).

Coloration. When fresh (holotype): Dorsal surface uniformly yellowish greyish, eye golden; dermal denticles white. Ventral surface of disc white centrally; entire margin greyish pink (transparent distally), band broadest beside pectoral apex, sharply demarcated from white part of disc; pelvic fin similar to disc, marginal marking very broad; ventral tail white forward of caudal sting, uniformly yellowish beyond; clasper paler ventrally than dorsally. In preservative (holotype) brownish on dorsal surface; white ventrally with marginal band pale to dusky; dorsal surface of tail and tip brownish black, ventral fold dusky. Images of fresh non-type material similar to holotype or sometimes slightly more brownish in dorsal coloration.

TABLE 3. Morphometric data for the holotype (MZB KA-93) and five paratypes of *Telatrygon biasa* **sp. nov.**, and the postnatal types and three non-types of *T. zugei*. Ratios are expressed as percentages of disc width.

	Telatrygon biasa			*Telatrygon zugei*		*Trygon zugei*	
	Holotype	Paratypes		Non-types		Lectotype	Paralectotype
		Range		Range		NMHN 2447	NMHN 1987-152
Disc width (mm)	194	185	254	186	258	138	105
Total length	damaged	236.0	297.6	189.8	248.8	228.3	257.0
Disc length	105.1	96.9	103.6	105.4	106.6	97.1	92.5
Snout to pectoral-fin insertion	98.5	91.9	96.6	97.8	100.5	88.7	88.1
Orbit to pectoral-fin insertion	64.2	57.9	64.8	61.4	64.9	54.4	56.0
Snout to maximum disc width	58.0	51.5	55.8	55.6	59.3	51.6	48.3
Snout to origin of cloaca	95.4	87.1	94.7	92.6	96.5	84.3	86.4
Cloaca origin to tail tip	0.0	145.4	207.9	0.0	0.0	0.0	0.0
Cloaca origin to caudal sting	40.3	30.8	36.0	0.0	40.9	32.6	31.7
Pectoral-fin insertion to caudal sting (horiz)	36.5	29.2	32.7	0.0	36.4	29.1	36.0
Disc thickness	9.3	8.1	11.1	0.0	0.0	8.9	8.9
Snout (preorbital) length	29.9	28.1	29.0	30.7	32.8	29.3	25.8
Snout (preorbital horiz.) length	28.6	26.9	27.4	30.2	31.0	28.5	24.0
Orbit diameter	5.7	5.0	6.7	5.0	5.9	5.9	6.5
Eye diameter	4.1	3.3	4.4	3.4	3.8	4.0	3.7
Spiracle length	6.1	5.7	6.5	5.1	5.3	5.8	7.3
Orbit and spiracle length	11.6	9.4	10.7	9.4	10.7	9.9	10.7
Interorbital width	10.3	9.2	10.8	10.6	11.1	10.2	8.2
Inter-eye width	14.6	12.9	15.2	14.4	15.4	13.0	14.8
Distance between spiracles	15.1	13.3	15.3	13.5	15.2	14.2	12.9
Head length	56.2	51.3	54.1	54.2	58.2	54.0	52.1
Preoral length (to lower jaw)	29.4	27.4	28.3	31.6	32.2	32.1	27.1
Prenasal length	24.6	22.6	23.8	25.9	27.1	25.4	21.0
Nostril length	3.9	3.3	4.0	3.3	4.0	3.5	3.9
Nasal curtain length	7.5	5.7	6.9	6.4	6.9	5.6	4.6
Nasal curtain width	13.0	10.2	11.6	10.8	12.3	9.8	10.1
Distance between nostrils	12.4	10.0	11.1	10.3	11.8	11.1	9.8
Mouth width	9.6	8.1	9.2	8.7	10.4	10.0	9.3
Distance between 1st gill slits	18.1	17.3	18.4	17.7	18.2	18.5	19.7
Distance between 5th gill slits	11.8	10.8	11.8	11.2	12.0	11.6	11.9
Width 1st gill slit	3.4	2.7	3.0	2.8	3.4	2.1	2.2

……*continued on the next page*

TABLE 3. (Continued)

	Telatrygon biasa			*Telatrygon zugei*		*Trygon zugei*	
	Holotype	Paratypes		Non-types		Lectotype	Paralectotype
		Range		Range		NMHN 2447	NMHN 1987-152
Width 3rd gill slit	3.7	2.7	3.6	2.9	3.5	2.8	3.0
Width 5th gill slit	2.4	1.8	2.2	2.6	2.9	2.1	2.2
Tail width, axil of pelvic fins	7.2	6.3	8.2	7.4	8.4	4.7	6.8
Tail width, base of caudal sting	2.7	2.7	3.9	2.9	7.5	1.9	2.8
Tail height, axil of pelvic fins	5.9	3.4	4.7	3.7	4.8	3.8	5.0
Tail height, base of caudal sting	2.5	2.0	2.7	2.3	3.7	2.2	2.5
Caudal sting 1 length	-	-	-	-	-	17.8	14.3
Caudal sting 2 length	-	-	-	-	-	-	-
Cloaca length	5.0	3.7	5.8	5.3	6.2	3.9	4.3
Length pelvic fin (embedded)	19.3	16.2	19.2	19.6	22.1	16.0	14.9
Width across pelvic-fin base	13.2	12.8	14.0	12.4	13.2	13.2	11.9
Greatest width across pelvic fins	26.4	34.4	40.2	24.7	31.2	29.2	29.1
Clasper, postcloaca length	15.3	0.0	18.0	0.0	17.2	5.9	7.1
Clasper, length from pelvic axil	8.5	0.0	9.5	0.0	10.1	3.7	1.7
Tail width, origin ventral fold	2.6	2.3	3.4	3.0	3.2		
Tail width, at 1/4 of base length ventral fold	1.1	0.9	1.6	1.5	1.7		
Tail width, at 1/2 of base length ventral fold	0.9	0.7	1.8	1.1	1.1		
Tail width, at 3/4 of base length ventral fold	0.7	0.6	0.9	0.7	0.8		
Tail width, insertion ventral fold	0.8	0.5	0.9	0.6	0.6		
Tail height, origin ventral fold	2.2	1.9	2.5	2.1	2.2		
Tail height, at 1/4 of base length ventral fold	1.5	1.2	1.6	1.6	1.7		
Tail height at 1/2 of base length ventral fold	1.5	0.9	1.6	1.1	1.4		
Tail height at 3/4 of base length ventral fold	1.1	0.8	1.0	1.0	1.2		
Tail height, insertion ventral fold	0.8	0.5	1.5	0.9	0.9		
Dorsal tail fold, length	13.1	15.8	27.6	-	75.3		
Dorsal tail fold, height	0.5	0.3	0.5	-	1.0		
Ventral tail fold, length	61.1	61.9	82.4	39.9	75.3		
Ventral fold height, at 1/4 of its base length	1.3	1.0	1.3	0.7	1.4		
Ventral fold height, at 1/2 of its base length	0.7	0.4	0.9	0.8	0.9		
Ventral fold height, at 3/4 of its base length	0.9	0.4	0.6	0.4	0.4		
Tail length beyond ventral fold insertion	15.7	46.6	86.6	-	-		

Size. Largest type 254 mm DW, but reported to reach 287 mm (White & Dharmadi, 2007). Size at maturity for males 168–176 mm DW, and for females 178–193 mm DW. Birth size 70–90 mm DW.

Distribution. Western North Pacific, including Indonesia and Malaysian Borneo. Also reported from the Philippines by Herre (1953), but no specimens have been reported recently. Demersal on continental and insular shelves to ~40 m depth.

Etymology. Noun in apposition of the Indonesian and Malaysian word 'biasa' meaning 'ordinary, common or normal' used herein to reflect the frequent occurrence of this species in local fish markets. In Malaysian Borneo, the ray is known as Pari Biasa or Common Ray. Vernacular: Indonesian Sharpnose Ray.

Comparisons. *Telatrygon* is presently under review (PL) and comparative morphological details for the group have not been fully elucidated. However, the four species of the genus are widely divergent based on their NADH2 sequences (see Last *et al.*, 2016; Fig. 1). The Chinese lectotype (MNHN 2447) and paralectotype (MNHN 1987-152) of the type species of the genus *Telatrygon* (i.e.*T. zugei)*, are juveniles and differ slightly in shape to adults (e.g. ASIZ P67338, ASIZ P72247 and FRIP 3504). The *T. biasa* adults differ from the *T. zugei* adults primarily in dimensions of the head (preorbital snout 28.1–29.0% vs. 30.7–32.8% DW in *T. zugei*; preoral length 27.4–28.3% vs. 31.6–32.2% DW; prenasal length 22.6–24.6% vs. 25.9–27.1% DW), and the disc might be slightly smaller (length 96.9–105.1% vs. 105.4–106.6% DW). The spiracles also appear to be larger in *T. biasa* (length 5.7–6.5% vs. 5.1–5.3% DW), and the ratio of the preoral length to the width of the interspace between the first gill openings is smaller (1.52–1.63 vs. 1.74–1.78). The body shape of *T. acutirostra* (based on FRIP3600) differs significantly from material examined of both *T. biasa* and *T. zugei*: for example, much longer snout (length 39.9% vs. 28.1–32.8% DW), longer prenasal (length 35.1% vs. 22.6–27.1% DW) and smaller eyes (orbit length 3.5% vs. 5.0–6.7% DW).

A stingray of the genus *Telatrygon* from the northern Indian Ocean, originally identified as *Trygon zugei* (e.g. Day, 1878 [pl. cxc, fig. 3]; Day, 1889) has a longer snout (i.e. length 32.5–36.4% DW) and smaller eye (i.e. orbit length 4.3–4.8% DW) than either *T. biasa* or *T. zugei,* and a shorter snout and larger eye than *T. acutirostra*. This northern Indian Ocean species is referrable to *Telatrygon crozieri* (Blyth, 1860).

Nishida & Nakaya (1988) designated a lectotype for *Dasyatis zugei* and provided a detailed explanation for their reasoning. The larger of two preserved specimens, a juvenile male 137 mm DW (reported to be MNHN 1987-152) was selected as the lectotype; the second specimen (MNHN 2447), a smaller male of 106.6 mm DW, was selected as a paralectotype. However, the MNHN collection catalogue (https://science.mnhn.fr/institution/mnhn/search) and specimen label both list the larger of the two as the lectotype, but as MNHN 2447 (rather than MNHN 1987-152). Whether this is a labelling error, or Nishida & Nakaya (1988) accidentally mixed up the numbers in the manuscript, is uncertain. We have followed the MNHN collection database, and current labelling for the more intact, larger specimen (MNHN 2447), as the lectotype.

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Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 2—Description of two new species of *Centrophorus* and clarification of the status of *Centrophorus lusitanicus* Barbosa du Bocage & de Brito Capello, 1864

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Abstract

Centrophorus specimens with a distinctive long-based first dorsal fin (long-finned species) have previously been considered to be *Centrophorus lusitanicus* first described from Portugal. Critical examination of the original description and illustration reveal that *C. lusitanicus* should be considered a junior synonym of *C. granulosus*. However, the specimen considered to be the syntype of *C. lusitanicus* in the Natural History Museum in London is clearly a long-finned species and not conspecific with *C. granulosus*. A more detailed investigation revealed that this specimen should not be considered a syntype and was likely not originally collected off the coast of Portugal. Investigation of long-finned specimens of *Centrophorus* from the Indo-West Pacific and Eastern Atlantic revealed that two undescribed species exist and are herein formally described as *C. lesliei* and *C. longipinnis*. The two species are similar morphologically and belong to the long-snout *Centrophorus* group (e.g. *C. isodon* and *C. harrissoni*) but are clearly separable based on their very long first dorsal fins. The two species differ in relative length of the first dorsal fin and several other characters. They also differ genetically. Nonmetric multidimensional ordination based on morphometric data reveals both species level and ontogenetic differences. A short erratum is also provided for Part 1 of this revision of the *Centrophorus* due to two figure related errors which may cause some confusion.

Key words: *Centrophorus*, new species, Eastern Atlantic, Indo-West Pacific, genetics, taxonomy

Introduction

The complicated nomenclatural history of many *Centrophorus* species has hindered the taxonomic resolution within the genus. The nomenclature of the type species, *Centrophorus granulosus* (Bloch & Schneider, 1801), was detailed by White *et al.* (2013) in their redescription of this species in the first part of this revision of the genus *Centrophorus* Müller & Henle, 1837. This part of the revision deals with an equally complicated species, *Centrophorus lusitanicus* Barbosa du Bocage & de Brito Capello, 1864, a poorly known species described from Portugal. Barbosa du Bocage & de Brito Capello (1864) in their description noted its similarity to *C. granulosus*, but in a subsequent publication (Barbosa du Bocage & de Brito Capello, 1866) they refuted this separation, and included it in the synonymy of *C. granulosus*. *Centrophorus granulosus*, as discussed in detail by White *et al.* (2013), has a complicated nomenclatural history and in the Eastern Atlantic was most commonly used (incorrectly) to refer to a smaller *Centrophorus* species, *C. 'uyato'*. Thus, it should be noted that use of *C. granulosus* may be in reference to either the large, true *C. granulosus*, or the smaller *C. 'uyato'*.

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Günther (1870), in his catalogue of the fishes in the British Museum, resurrected *C. lusitanicus* as valid and noted its close relationship to *C. granulosus*, but pointed out that *C. lusitanicus* has a much longer first dorsal-fin base. Günther (1870) based this on a male specimen 29 inches long presented by Prof. J.V.B. du Bocage. It was subsequently recognised as a valid species by Regan (1908) and Garman (1913), but then again was synonomised with *C. granulosus* by Lozano Rey (1928), and then resurrected again by Nobre (1935). Bigelow & Schroeder (1957) noted the confusion in the literature and concluded that the validity of *C. lusitanicus* was an 'open question' and that more material was needed. The confusion surrounding the validity of this species continued in the literature with Maurin & Bonnet (1970) synonymising *C. lusitanicus* again with *C. granulosus*, while Teng (1958, 1962), Cadenat (1959, 1960), Blache *et al,* (1970), Hureau & Monod (1973), Cadenat & Blache (1981), and Chen & Cheng (1982) considered it as a valid species. To further complicate the matter, Bass *et al.*'s (1976) treatment of *C. lusitanicus* from South Africa agrees with the true *C. granulosus* with specimens recorded to 1.6 m in total length (TL). The treatment for *C. lusitanicus* by Compagno (1981, 1984) and Compagno *et al.* (1989) appears to be a composite of the true *C. granulosus* and *C. lusitanicus*. Munoz-Chapuli & Ramos (1989) provided the first detailed taxonomic information on *C. lusitanicus* and provided comparisons to other Eastern Atlantic species.

The type locality has been another confusing aspect of *C. lusitanicus*. Although described from off Portugal, it has not been confirmed from there since. The original description includes two important pieces of information. Firstly, it is stated that they (Barbosa du Bocage & de Brito Capello) were able to compare specimens in the fresh condition. Secondly, the description states that 'our' fisherman distinguish the two species and have a name for each, "Barroso" for *C. granulosus* [=*uyato*], meaning 'muddy', and "Lixa-de-lei" for *C. lusitanicus*, meaning 'sandpaper'. This strongly suggests that the sharks were caught in local waters off Portugal, and not from Portuguese colonies such as Angola or Mozambique where much of the material that Bocage examined in the Lisbon Museum had come from. Munoz-Chapuli & Ramos (1989) included 11 specimens of *C. lusitanicus* in their revision, coming from Morocco (south of 35° N), Canary Islands, Ghana and Cameroon at depths of 370–610 m, but no specimens from off Portugal. Moura *et al.* (2015) undertook a barcoding study on deepwater chondrichthyans caught during research surveys off mainland Portugal to depths of 750 m, within the documented depth range for *C. lusitanicus.* This study sampled two species of *Centrophorus*, the true *C. granulosus* and *C. 'uyato'*. Interestingly, they also report obtaining CO1 sequences from the BMNH syntype of *C. lusitanicus* which matched 100% to *C. 'uyato'*. Subsequently, these authors again called into to question the validity of *C. lusitanicus* as a valid species.

Surveys of sharks and rays in Madagascar (see http://tapewormdb.uconn.edu) in 1997 and 1999 observed a number of specimens of a long-finned *Centrophorus* of indeterminate species caught in the Mozambique Channel. Naylor *et al.* (2012) included this species in their large NADH2 genetic tree and referred to it as *C.* cf *lusitanicus*. Surveys of the sharks and rays present in the fish markets and landing sites in eastern Indonesia between 2001 and 2006 recorded six species of gulper sharks, *Centrophorus atromarginatus* Garman, 1913; *C. isodon* (Chu, Meng & Li, 1981); *C. moluccensis* Bleeker, 1860; *C. niaukang* Teng, 1959 [=*C. granulosus*]; *C. squamosus* (Bonnaterre, 1788); and *C.* cf *lusitanicus* (White *et al.*, 2006). The latter species possessed the very elongate first dorsal fin, which is considered characteristic of *C. lusitanicus*, and was speculated to be conspecific with the Eastern Atlantic species.

A specimen of *C. lusitanicus* was recorded from Puerto Princesa City in the Philippines during WWF-funded biodiversity surveys in 1999 and 2000 (Compagno *et al.*, 2005). In Taiwan, this species was first recorded by Teng (1958) from Yilan and Kaohsiung as *C. lusitanicus* and by Teng (1962) from Da-xi. Chen & Joung (1993) included a figure of this species but misidentified it as *C. niaukang*. During a biodiversity survey of the sharks and rays of Taiwan in 2012, additional specimens were collected from fish landing sites at Cheng-gong and Da-xi (Ebert *et al.*, 2013). In this paper, it was also referred to as *C.* cf. *lusitanicus* and noted that the species name will likely change following detailed taxonomic investigation. Most recently, several specimens were caught in deepwater in the Huon Gulf in Papua New Guinea in late 2016 and early 2017.

This study clarifies the taxonomic status of *C. lusitanicus* and investigates the taxonomy of the *Centrophorus* species with a characteristic very long-based first dorsal fin.

Methods

The morphometric measurements taken follow those for sharks detailed by Compagno (1984, 2001), but we typically used direct (point-to-point) measurements rather than horizontal measurements. For comparative purposes, we have included both direct and horizontal measurements for some key characters, e.g. predorsal length, head length, preorbital length, prenasal length. Data in the literature are often not suited for direct comparative purposes as the measurement methodologies adopted are frequently not specified. In this paper, morphometrics for all specimens measured were taken by the senior author (WW). Illustrations and descriptions of the measurements taken follow the methodology described by Last *et al.* (2007) for the genus *Squalus* with some additional measurements, i.e. CST—subterminal caudal-fin margin, CTL—terminal caudal-fin lobe, DPI—1st dorsal-fin midpoint to pectoral-fin insertion, D1SL—1st dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), D2SL—2nd dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), DPO—1st dorsal-fin midpoint to pelvic-fin origin, PDI—pelvic-fin midpoint to 1st dorsal fin insertion, and PDO—pelvic-fin midpoint to 2nd dorsal-fin origin, from Compagno (2001). Pectoral-fin free rear tip extension was also measured to highlight the extent to which the free rear tip is produced by measuring the length of the produced free rear tip beyond the posterior margin. Pectoral-fin height was measured from a line between pectoral-fin origin and its insertion and the apex of the fin. In contrast, pelvic-fin height was measured from a perpendicular line from the inner margin to the apex. Dorsal-fin origins are often very difficult to accurately locate externally. This is especially the case for *Centrophorus* species. It is recommended that the back of a finger or thumb is used against the midline to determine the approximate location of the fin origin and that a pin is used to mark the position. This ensures that the same point is used for the other measurements using this anatomical landmark (e.g. predorsal length, fin length, fin anterior margin, fin base length, PDO, and dorsal-fin midbase for DPI and DPO). The holotype (SAMC-F041921) and 6 of the paratypes (BMNH 1867.7.23.2, MNHN 1969-0225, MNHN 1969-0276, SAMC 33320 (2 spec.), SAMC 33321, and ZMB 6455) of *C. lesliei* **n. sp.**, and the holotype (NMMB-P 15756), 13 of the paratypes (CSIRO H 5788-02, CSIRO H 7990-02, CSIRO H 8103-02, CSIRO H 8104-01, CSIRO H 8104-04, CSIRO H 8171-01, FRIP 03628 (1 of 2), NMMB-P 25361, NMMB-P 14051, NMMB-P 15813, NMMB-P 15814, NMMB-P 15859, and BMNH 2017.8.29.1), and one other specimen (CSIRO H 8104-03) of *C. longipinnis* **n. sp.** were measured (Table 1). In the descriptions of the two new species, morphometric values for the holotype are given first, followed in parentheses by the ranges of the measured paratypes (smallest size classes first, followed by larger size classes).

Morphometric measurements for both species, as % TL, were subjected to non-metric multidimensional scaling (MDS) ordination (Primer v5.0 package) (Clarke & Gorley, 2006), to determine the differences between species and the relative level of ontogenetic changes reflected by morphology for both of the new species. One-way Analyses of Similarity (ANOSIM) were employed to test whether morphometric measurements differed significantly between the size classes. Similarity Percentages (SIMPER) were employed when relevant (i.e. when a pairwise ANOSIM result was significant, $P<0.05$), to determine what characters contributed most to the observed differences. Morphometric measurements were analysed without transformation since the preliminary analyses revealed that the stress levels were acceptable for MDS analyses (see Clarke & Gorley, 2006). Several measurements, associated with the clasper, trunk and abdomen heights and widths, and fin spine heights and widths, were not available for measurement for all individuals, so these characters were excluded from the MDS analysis.

Vertebral counts were obtained from radiographs of 3 paratypes of *C. lesliei* **n. sp.** (BMNH 1867.7.23.2, MNHN 1969-0225, and MNHN 1969-0276) and the holotype (NMMB-P 15756) and 10 of the paratypes (CSIRO H 5788-02, CSIRO H 8104-02, CSIRO H 8171-01, FRIP 03628 (2 spec.), NMMB-P 25361, NMMB-P 14051, NMMB-P 15813, NMMB-P 15814, and BMNH 2017.8.29.1) of *C. longipinnis* **n. sp.** It was not possible to obtain x-rays of the holotype or the three SAMC paratypes of *C. lesliei*. Counts were obtained separately for trunk (monospondylous precaudal centra), precaudal (monospondylous precaudal centra + diplospondylous precaudal centra to origin of the caudal-fin upper lobe) and diplospondylous caudal centra (centra of the caudal fin) vertebrae following the methods used by Compagno (1988) for carcharhiniform sharks. Tooth row counts were difficult to determine on large specimens without cutting the jaws and were thus taken *in situ* from a small subset of the types examined. For *C. lesliei*, tooth counts were taken *in situ* from 3 paratypes (MNHN 1969-0225, MNHN 1969-0276, and ZMB 6455) and from the 3 dried jaws (MNHN AB-248, AB-249 and AB-250). For *C. longipinnis*, tooth row counts were taken *in situ* from the holotype (NMMB-P 15756) and four paratypes (CSIRO H 8171-01, NMMB-P 14051, NMMB-P 15813, and BMNH 2017.8.29.1). Skin patches were removed from the right side of a paratype (BMNH 1867.7.23.2) of *C. lesliei* and two paratypes (CSIRO H 8104-01 and NMMB-P 14051) of *C. longipinnis* and used to obtain digital microscope images to highlight denticle morphology. Dermal folds on the ventral surface of the head were counted following Duffy (2007).

The synonymies provided for each of the three species includes specific references, not general references such as Compagno (1984) and other global treatments. Specimen registration numbers are prefixed by the following abbreviations: CSIRO, Australian National Fish Collection, Hobart, Australia; BMNH, British Natural History Museum, London; FRIP (or TFRI), Fisheries Research Institute, Keelung, Taiwan; NMMB-P, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan; SAMC, South African Museum, Cape Town; ZMB, Museum für Naturkunde, Berlin.

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

Molecular analysis. Specimens were sampled for liver or muscle tissue by the authors and/or their collaborators, or by fishermen. Samples were temporarily stored in 95% alcohol or in dimethyl sulphoxide solution (DMSO, 20%) in the field. DNA was extracted using the phenol chloroform extraction (Sambrook *et al*., 1989), or using High Pure PCR Template Preparation Kit by Roche Diagnostics (Indianapolis, IN). Extracted total DNA was stored at -20 °C until used for amplification via the Polymerase Chain Reaction (PCR). Samples were amplified using Fermentas Taq with primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (NADH2). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome was used to amplify the target fragment. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of Takara Taq (Clonetech, Mountain View, Ca) PCR buffer, 2.5 mM, MgCL2, 1.0 mM of dNTPs, and 1.0 mM of each primer. The reaction cocktail was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were either purified by centrifugation through size-selective filters (Millipore, Bedford, MA) according to manufacturer's recommendations, or were purified using ExoSAP-IT from USB (Cleveland, Ohio). Purified PCR products were sent off to commercial sequencing centres for sequencing (Seq-Wright, Houston, TX; Beckman-Coulter Genomics, Beverly, MA; Retrogen, San Diego, CA). Sequence trace files were evaluated for quality, translated to amino acids, and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences, to yield a nucleotide alignment that was 1044 nucleotides long.

The alignment was imported into PAUP* (Swofford, 2002) and used to construct a Maximum Likelihood Tree 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 tree. All phylogenetic analyses were carried out using the software package PAUP*4.0 version a152.

Results and discussion

Validity of *Centrophorus lusitanicus*

The complicated nomenclatural history of *C. lusitanicus*, as discussed above, has hindered resolution of this group of gulper sharks. When considering Barbosa du Bocage & de Brito Capello's (1864) description of *C. lusitanicus* in relation to the currently recognised species of *Centrophorus*, several of the characters used to distinguish the new species from *C. granulosus* [=*'uyato'*] relate to the true *C. granulosus*:

- *C. lusitanicus* is much larger
- *C. lusitanicus* has a blackish violet colour
- first dorsal fin base is longer in *C. lusitanicus*
- free rear tip of first dorsal fin more produced in *C. lusitanicus*
- dorsal spines shorter and weaker in *C. lusitanicus*
- *C. lusitanicus* has a shorter snout
- pectoral-fin free tip is less produced in *C. lusitanicus*

These characteristics are perfectly consistent with the key diagnostic characters of true *C. granulosus*. Although the original description does not mention the skin characteristic, it does mention that the name used by 'our fisherman' is 'Lixa-de-lei' which is Portuguese for sandpaper. This also points to *C. granulosus*, which differs from *C. 'uyato'* in having a much rougher skin. This information together with the character information provided in the description and the associated illustration (Fig. 1) strongly suggest that *C. lusitanicus* is a synonym of the true *C. granulosus*. It differs from the smaller (<1 m) *Centrophorus* species with the very long first-dorsal fin base that has been referred to as *C. lusitanicus* in recent literature. Based on our current understanding, three species of *Centrophorus* are known to occur off Portugal, *C. granulosus*, *C. squamosus* and *C. 'uyato'* (e.g. Ebert *et al.*, 2013). Barbosa du Bocage & de Brito Capello's (1864) refers to *C. squamosus*, *C. granulosus* [= *'uyato'*] and their new *C. lusitanicus*. Given the scope of Barbuso du Bocage & de Brito Capello's paper, it seems unlikely that the authors would have missed this common species, thus lending more support to the claim that *C. lusitanicus* is a synonym of the true *C. granulosus*.

FIGURE 1. Lateral view of BMNH 1867.7.23.2 (juvenile male 742 mm TL), previously considered to be a possible syntype of *Centrophorus lusitanicus* (now a paratype of *Centrophorus lesliei* **n.sp.**).

Since the authors refer to the fresh condition, the type locality from off Portugal for *C. lusitanicus* is not in question. However, the surviving apparent 'syntype' of *C. lusitanicus* has long been considered to be BMNH 1867.7.23.2 and is clearly not conspecific with the true *C. granulosus* (Fig. 2) as it has a much longer first dorsal-fin base. This led to an investigation into the type status of *C. lusitanicus* noting that no reference was made in the original description of *C. lusitanicus* to any type specimens. Günther (1870) appears to be the first to link the name *C. lusitanicus* with a specimen of the long-finned species in the British Museum, referring to a male of 29 inches in length. This corresponds to the size and sex of BMNH 1867.7.23.2 (Fig. 2). Günther (1870) does not, however, refer to this specimen as a type, but does include the location as Portugal. In correspondence with the Natural History Museum in London, it was suggested that the type status may have been erroneously given to this specimen (J. Maclaine, pers. comm.). The jar it is placed in contains a yellow lid which was originally used to highlight an important specimen (not type status), thus it is possible someone later mistook this for being a type specimen. The original documentation of this specimen entering the Natural History Museum doesn't mention it being a 'type' specimen. The specimen entered the Natural History Museum by donation from Bocage as *C. granulosus*, and not as *C. lusitanicus*. The final aspect which has led to much confusion is the location of the specimen as Portugal. The original ledger (Fig. 3) includes three specimens donated from Bocage, *Centrophorus crepidalbus*, *C. granulosus* and *Scymnodon ringens*. To the right of the first species, *C. crepidalbus*, is 'In spirit' and 'Portugal'. The two latter specimens have ditto marks underneath 'In spirit', but not underneath 'Portugal'. Indeed no locality data was specified for either of these two specimens when they first arrived in the BMNH collection. Importantly they were never listed as from Portugal.

It could still be argued that the BMNH specimen was most likely collected from Portugal given it was donated from the Lisbon Museum by Bocage unless there was some indication or evidence of alternative collection locations. José Vicente Barbosa du Bocage (1823–1907) became the director of the Zoology of the Natural History Museum of the Polytechnic School in Lisbon in 1858 where his work consisted of acquiring and describing biological collections (Madruga, 2013). Many of these collections were sent to Lisbon by José Alberto de Oliveira Anchieta (1832–1897) who mostly collected in the (then) African Portuguese colonies of Angola and Mozambique (Madruga, 2013). This information, combined with the fact that the long-finned species is well known from this part of Africa, provides reasonable evidence that the BMNH (and ZMB) specimens were likely collected from

Africa and not Portugal. Unfortunately, Anchieta's collections are poorly documented since all the specimens and related correspondences were lost in the 1978 fire which destroyed the entire zoological collection of the Polytechnic School in Lisbon.

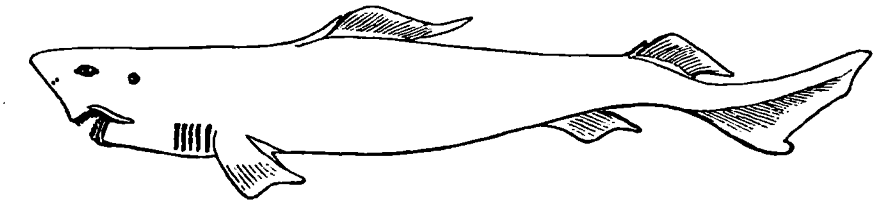
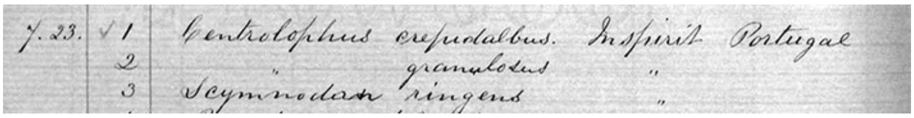


FIGURE 2. Illustration of *Centrophorus lusitanicus* in the original description (Barbosa du Bocage & Brito Capello, 1864).



7.23. ✓1 Centrolophus crepidalbus. In spirit Portugal
2 " granulosus "
3 Scymnodon ringens "

FIGURE 3. Excerpt from the specimen register showing the batch of three sharks, including the possible syntype of *Centrophorus lusitanicus* (as *C granulosus*) BMNH 1867.7.23.2, donated by Bocage. Note the lack of ditto marks beneath Portugal for *Centrophorus granulosus* and no mention of it being a type.

The weight of the available evidence suggests that *C. lusitanicus* refers to the true *C. granulosus* from off Portugal and so must be considered a junior synonym of the latter species. The purported syntype of *C. lusitanicus* (BMNH 1867.7.23.2) is not a type specimen and refers to a separate long-finned species. A second Bocage specimen of the same long-finned species in the Museum für Naturkunde (ZMB 6455, Fig. 4), is likely from the same collection location as the BMNH specimen.

Taxonomic accounts

Centrophorus lesliei n. sp.

African Gulper Shark
(Figs 1, 4–9; Table 1)

Centrophorus lusitanicus—Günther, 1870: 421 (Portugal—erroneously); Regan, 1908: 53 (Portugal—erroneously); Garman, 1913: 199 (Portugal—erroneously); Bigelow & Schroeder, 1957: 84 (in part); Cadenat, 1959: 743, Fig. 1A (West Africa); Cadenat, 1960: 1428, Figs 1–3 (West Africa); Blache *et al.*, 1970: 36, Fig. 73 (Eastern Atlantic); Hureau & Monod, 1973: 39 (Senegal; Portugal—erroneously); Cadenat & Blache; 1981: 56, Figs 33b, 38, 39 (Senegal); Munoz-Chapuli & Ramos, 1989: 65, Figs 1b, 3b, 4d, 5c, 6b, 7b (West Africa).

Centrophorus cf. *lusitanicus*—Naylor *et al.*, 2012: 59, Fig. 43 (Mozambique Channel, Madagascar).

Holotype. SAMC-F041921, pregnant female (embryo removed) 863 mm TL, off Pebane District, Zambezia Province, Mozambique, 17°33'2" S, 38°27'1" E, 433 m depth, 15 Jun. 2015.

Paratypes. (10 specimens) BMNH 1867.7.23.2, juvenile male 742 mm TL, locality unknown [possibly collected from Angola or Mozambique by Anchieta]; MNHN AB-248 (dried jaw, first dorsal fin and skin patch), female 950 mm TL, MNHN AB-249 (dried jaw and dorsal fins), female 930 mm TL, Kayar, Senegal, 14°52'58.8" N, 17°10'1.2" W, 25 Mar. 1958; MNHN AB-250 (dried jaw and skin patch), male 735 mm TL, off Côte d'Ivoire, Feb. 1960; MNHN 1969-0225, juvenile male 408 mm TL, Togo, 5°57' N, 1°34' E, 340 m depth, 2 Oct. 1964; MNHN 1969-0276, female 524 mm TL, west of Bioko Island, Equatorial Guinea, 3°45' N, 8°22' E, 425 m depth, 2 Nov. 1963; SAMC 33320 (1 of 2), late-term embryo 317 mm TL, taken from holotype; SAMC 33320 (2 of 2), female 907 mm TL, collected with holotype; SAMC 33321, female 942 mm TL, off Angoche Island, Nampula Province, Mozambique, 16°19'59" S, 40°7'59" E, 500 m depth, 16 Jun. 2015; ZMB 6455, female 644 mm TL, locality unknown [possibly collected from Angola or Mozambique by Anchieta], donated by Bocage (as *C. granulosus*).

FIGURE 4. Lateral view of ZMB 6455 (female 644 mm TL), a second specimen donated from the Lisbon Museum by Bocage as *Centrophorus granulosus* (now a paratype of *Centrophorus lesliei* **n.sp.**).

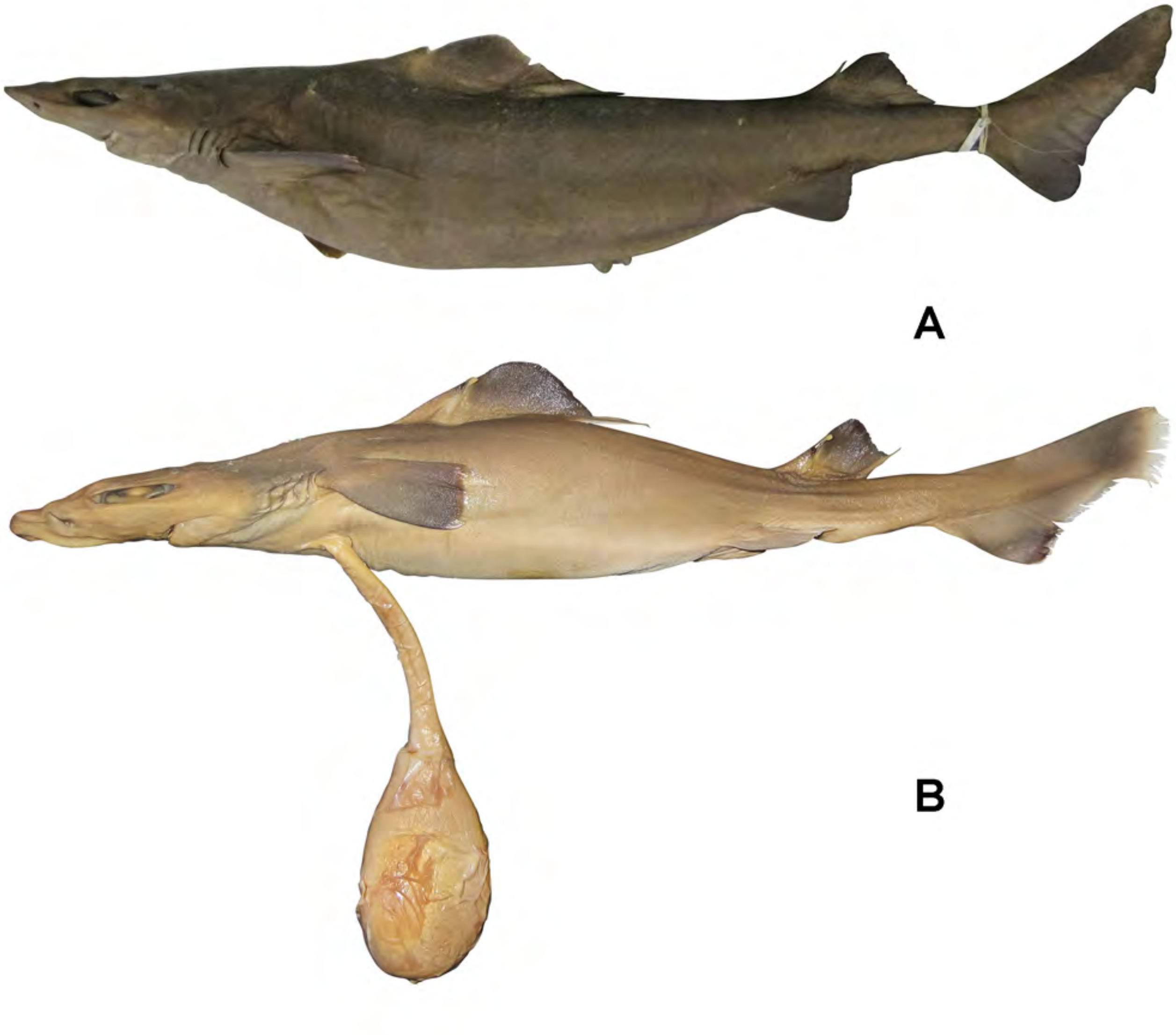


FIGURE 5. Lateral view of *Centrophorus lesliei* **n.sp.**: (A) pregnant female holotype (SAMC-F041921, 863 mm TL); (B) late-term embryo paratype (SAMC 33320, 317 mm TL, taken from holotype).

FIGURE 6. Ventral view of head of the pregnant female holotype of *Centrophorus lesliei* **n.sp.** (SAMC-F041921, 863 mm TL).

FIGURE 7. Ventral view of pectoral fin of *Centrophorus lesliei* **n.sp.**: paratype BMNH 1867.7.23.2, juvenile male 742 mm TL.

FIGURE 8. Teeth of adult female paratype of *Centrophorus lesliei* **n.sp.** (MNHN AB-249, 930 mm TL): (A) upper; (B) lower.

Genetic material (specimens not retained). (5 samples) Field code GA8 (tissue accession GN 2011), female 920 mm TL, St. Augustin, Madagascar, Mozambique Channel, 16 Sep. 1999; Field code GA11 (tissue accession GN 2012), male 750 mm TL, St. Augustin, Madagascar, Mozambique Channel, 16 Sep. 1999; Field code GA12 (tissue accession GN 2013), male 740 mm TL, St. Augustin, Madagascar, Mozambique Channel, 16 Sep. 1999; Field code MG2 (tissue accession GN 1218), male 770 mm TL, south of Toliara, Madagascar, Mozambique Channel, 17 Jan. 1997; Field code MG5 (tissue accession GN 1221), female 900 mm TL, south of Toliara, Madagascar, Mozambique Channel, 17 Jan. 1997.

Diagnosis. A medium sized (<1 m maximum total length) species of *Centrophorus* with the following combination of characters: body relatively slender; head moderately long (21.4–26.4% TL); snout relatively short (horizontal preorbital length 6.5–8.2% TL) and rounded in dorsal view; first dorsal very long based (base length 16.8–19.7% TL, soft fin length 16.0–17.4% TL) and high (height 6.5–7.8% TL), inner margin relatively short (5.7–7.4% TL, 2.3–2.9 in soft fin length); second dorsal fin much smaller in area to first, similar in height to first dorsal fin (height 1.0–1.3 in first dorsal-fin height); pectoral fins large (anterior margin length 11.9–13.4% TL), free rear tip elongate in larger individuals (2.4–4.8% TL); lateral trunk denticles of larger individuals sessile (not raised on pedicels), block-like, not elevated; upper teeth of larger individuals with erect to slightly oblique cusps; lower teeth of all sized specimens much larger than upper teeth, strongly oblique, blade-like; total vertebral centra 119–122; teeth 33–42/29–31.

Description. Body fusiform, relatively slender, nape slightly humped; deepest at mid first dorsal-fin base, trunk height 1.18 (1.06–1.30 in paratypes <525 mm TL; 1.16–1.27 in paratypes >640 mm TL) times width, 0.97 (0.84–0.96; 0.97–1.06) times abdomen height; no lateral ridges; pre-first dorsal length 3.84 (3.45–3.87; 3.59–3.86) in TL; interdorsal space 1.19 (1.24–1.68; 1.11–1.27) in prepectoral length, 1.46 (1.53–1.93; 1.40–1.56) in pre-first dorsal length; pelvic–caudal space 3.19 (2.22–2.42; 2.72–3.19) in pectoral–pelvic space, 1.77 (1.79–2.03; 1.74–1.81) in prepectoral length; dorsal–caudal space 2.35 (1.89–2.00; 2.15–2.57) in interdorsal space. Caudal peduncle moderately short and deep, moderately compressed, its length 12.1 (12.2–12.7; 11.7–12.7)% TL, its height 1.53 (1.67–2.38; 1.49–1.94) times its width; tapering slightly towards caudal fin; no lateral keels; precaudal pits absent.

Head moderately long, moderately broad, width 1.14 (1.17–1.46; 1.18–1.37) times trunk width, 1.16 (1.14–1.79; 1.28–1.85) times abdomen width, length 22.0 (22.7–26.4; 21.4–23.0)% TL, 2.83 (2.21–2.58; 2.68–2.93) in pre-vent length, height 0.89 (0.69–0.93; 0.78–0.90) times width; slightly depressed forward of spiracles, somewhat broadly pear-shaped in cross-section at pectoral-fin origin. Band of transverse dermal folds on ventral surface of head broadly rounded with apex about three quarters of horizontal prenasal length behind symphysis of lower jaw, extending from below lower edges of first four gill slits on either side; up to about 20 folds present.

Snout moderately long, narrowly triangular in lateral view, apex bluntly pointed; lateral prenarial margin rounded; rounded in dorsal view; horizontal length 0.94 (1.02–1.06; 1.05–1.25) times eye length, 0.67 (0.66–0.95; 0.84–0.88) times interorbital space; horizontal prenarial length 1.70 (1.63–2.13; 1.82–2.23) times in preoral length. Nostrils small, slightly oblique; anterior nasal flap with a large, narrowly triangular lobe, with a very small lobe at inner corner of large lobe; internarial space 2.48 (2.59–3.31; 2.48–2.81) in preoral length, 2.37 (1.63–1.74; 1.39–1.50) times nostril length. Eye moderately large, elongate, length 3.84 (3.70–3.84; 3.61–4.36) in head, 3.18 (3.14–3.87; 3.02–3.86) times height; notched anteriorly; strongly notched posteriorly, notch not extending towards spiracle. Spiracle moderately large, semicircular; located dorsolaterally on head, entirely visible in dorsal view; lower margin above level of upper eye, slightly more than its diameter away from eye; no lobe-like fold on posterior margin; greatest diameter 3.48 (2.84–4.28; 2.80–3.81) in eye length. Gill slits directed slightly anteroventrally from top to bottom; relatively equal in size, becoming progressively longer from first to fifth; fifth longest, its height 3.1 (2.5–3.0; 2.6–3.0)% TL.

Mouth almost transverse, upper jaw slightly concave, width 1.15 (1.32–1.50; 1.06–1.21) in preoral length; lower labial furrows slightly shorter than upper furrows; prominent postoral groove, usually more than twice length of upper labial furrows, extending posterolaterally from angle of jaws. Teeth strongly differentiated in upper and lower jaws, with upper teeth much smaller than lower teeth. Upper teeth of adults (based on MNHN AB-248, AB-249 and AB-250) moderately large, with erect cusps, becoming slightly oblique posteriorly towards mouth corners, bases slightly overlapping (Fig. 8a). Lower teeth much larger than uppers, cusps very strongly oblique, blade-like, overlapping, edges with fine serrations (Fig. 8b).

Dermal denticles on flank below first dorsal fin varying greatly in shape between juveniles and adults; absent from insertions of fins. Denticles of a near-term embryo (317 mm TL) small, upright, slender, unicuspid, slightly overlapping. Denticles of larger specimens (based on a 742 mm TL specimen) block-like, sessile (not raised on pedicels), close set but rarely overlapping; anterior edges of crowns shallowly scalloped, posterior edge moderately or bluntly pointed (Fig. 9). Denticles of adult holotype (863 mm TL) similar to 742 mm TL specimen but with less pointed and more rhomboidal crowns.

First dorsal fin very long, relatively high; length 3.81 (3.21–3.76; 3.11–3.86) times its height, 1.69 (1.55–1.65; 1.59–1.74) times second dorsal-fin length; soft-fin length 2.43 (2.13–2.43; 2.24–2.49) times its height; height 1.23 (1.05–1.24; 1.12–1.28) times second dorsal-fin height; anterior margin moderately convex; apex moderately rounded; posterior margin slightly concave, slanting well posteroventrally from top to bottom; free rear tip moderately long, relatively thick basally; inner margin nearly straight, 2.27 (2.49–2.85; 2.37–2.57) in soft-fin length, 1.07 (0.81–0.97; 0.91–0.97) times its height; insertion level with mid pectoral–pelvic space, extremely well forward of pelvic-fin origin, pelvic-fin midpoint to first dorsal-fin insertion 17.0 (13.0–15.2; 15.4–17.6)% TL; base of exposed fin spine level with pectoral-fin free rear tip; spine base moderately broad, exposed anteriorly just above junction of spine and soft portion of fin; exposed fin spine relatively short, robust, strongly tapering distally, anterior margin slightly convex; exposed portion of spine sloping posterodorsally from base (of exposed portion) to apex, shorter in length to exposed portion of second dorsal-fin spine, exposed first dorsal spine length 0.28 (0.24–0.32; 0.28–0.38) times height of fin.

Second dorsal fin moderately large, much smaller in area compared to first dorsal fin, relatively short; second dorsal-fin length 2.76 (2.35–2.84; 2.06–2.84) times its height; anterior margin slightly to moderately convex; apex narrowly rounded; posterior margin weakly concave, sloping strongly posteroventrally from apex; free rear tip moderately long, thick basally, inner margin length 1.96 (1.78–2.02; 2.00–2.84) in soft-fin length, 0.85 (0.67–0.88; 0.64–0.81) times fin height; spine length 0.30 (0.38–0.53; 0.35–0.47) in height of fin; base of exposed fin spine level with anterior part of pelvic-fin inner margin, exposed just above level of junction with spine and soft portion of fin; exposed fin spine relatively long, robust, broad based, strongly tapering distally, recurved.

Pectoral fins large; anterior margin weakly convex, its length 13.0 (12.1–13.1; 11.9–13.4)% TL; base very short, 2.65 (2.24–2.84; 2.44–3.09) in anterior margin length; apex moderately rounded, not falcate; posterior margin almost straight to weakly convex from apex angle of free rear tip then broadly concave; inner margin weakly convex anteriorly and weakly concave posteriorly; free rear tip moderately elongate in adults (less produced in juveniles and embryos), free rear tip 1.13 (0.79–1.24; 1.10–1.23) in inner margin, extending to level of exposed first dorsal-fin spine; origin situated at level of mid-fifth gill slit, partially obscured by gill membrane.

Pelvic fins large, length 11.7 (10.4–10.9; 10.7–12.2)% TL, 1.24 (1.15–1.31; 1.21–1.35) times second dorsal-fin soft length; anterior margin nearly straight; apex moderately rounded; posterior margin weakly concave; free rear tip acutely pointed. Claspers of adult males not available for examination.

Caudal fin relatively long, deep, broad; dorsal margin almost straight to very slightly concave, 1.23 (1.07–1.24; 1.12–1.29) in head length, 1.33 (1.43–1.54; 1.35–1.49) times preventral margin; preventral margin slightly convex, apex moderately rounded to subangular; upper postventral margin nearly straight, lower postventral margin slightly convex, angle between postventral margins moderately concave; terminal lobe moderately large but short, lobe length 2.15 (2.20–2.64; 2.08–2.31) in dorsal caudal margin, terminal margin slightly undulating; apex of upper lobe narrowly rounded.

Meristic data. Total vertebral centra 119–122 (based on 3 paratypes), monospondylous precaudal centra 59–60 (n = 3), diplospondylous precaudal centra 28–29 (n = 2), total precaudal centra 88 (n = 2) and diplospondylous caudal centra ~31–32 (n = 2). Tooth count (n = 6): 17–22 + 16–20 / 14–16 + 14–16; total 33–42/29–31.

TABLE 1. Proportional dimensions as percentages of total length for the holotype of *Centrophorus lesliei* (SAMC-F041921), and ranges for small paratypes (<524 mm TL) and large paratypes (>644 mm TL).

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
Total length (mm)	863	317	524	644	942
Precaudal length	81.9	77.5	80.1	79.5	82.2
Pre-second dorsal length	63.2	59.3	60.7	62.5	63.2
Pre-first dorsal length	27.1	26.1	28.7	26.6	27.6
Pre-first dorsal length (horiz.)	26.0	25.8	29.0	25.9	27.9
Pre-vent length	62.2	57.6	58.6	60.7	62.6
Prepelvic length	60.3	55.4	57.4	59.3	60.9
Prepectoral length	21.3	21.8	25.4	20.5	23.0
Head length	21.3	22.7	25.8	21.1	23.1
Head length (horiz.)	22.0	22.7	26.4	21.4	23.0
Prebranchial length	18.8	18.4	22.6	18.5	20.0
Prespiracular length	12.6	12.6	15.7	12.5	13.4
Preorbital length	5.4	6.2	7.1	6.3	6.8
Preorbital length (horiz.)	6.5	7.1	8.2	7.0	7.5
Snout to inner nostril	4.3	4.3	5.6	4.3	4.8
Prenarial length (horiz.)	3.9	3.9	5.3	3.9	4.3
Preoral length	9.2	10.7	12.0	8.9	9.9
Inner nostril–labial furrow space	5.7	6.4	7.5	5.7	6.2
Mouth width	7.9	8.0	8.5	8.0	8.4
Upper labial furrow length	2.0	2.0	2.3	1.9	2.3
Nostril width	1.6	1.9	2.3	1.6	1.9
Internarial space	3.7	3.6	4.1	3.5	3.7
Interorbital space	8.0	7.5	9.8	7.3	7.7

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TABLE 1. (Continued)

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
Eye length	5.7	5.9	7.0	5.1	6.1
Eye height	1.8	1.8	2.1	1.5	1.8
Spiracle diameter—greatest	1.6	1.6	2.3	1.6	2.0
First gill-slit height	2.4	2.3	2.6	2.0	2.5
Fifth gill-slit height	3.1	2.5	3.0	2.6	3.0
Interdorsal space	17.9	15.1	17.5	17.1	19.2
Dorsal–caudal space	7.6	8.0	8.8	7.1	8.6
Pectoral–pelvic space	38.5	28.1	29.4	34.6	38.2
Pelvic–caudal space	12.1	12.2	12.7	11.7	12.7
First dorsal length	26.4	24.0	24.8	23.1	26.1
First dorsal soft fin length	16.8	16.0	16.3	16.1	17.4
First dorsal anterior margin	14.7	14.2	15.6	13.0	15.0
First dorsal base length	19.0	17.9	18.8	16.8	19.7
First dorsal height	6.9	6.6	7.5	6.5	7.8
First dorsal inner margin	7.4	5.7	6.4	6.2	7.3
First dorsal posterior margin	13.5	12.5	15.5	12.5	15.4
First dorsal exposed spine length	1.9	1.6	2.4	2.2	2.8
First dorsal spine base width	0.7	0.8	0.8	0.9	0.9
Second dorsal length	15.6	14.7	15.7	13.6	15.1
Second dorsal soft fin length	9.4	8.3	9.1	8.6	9.0
Second dorsal anterior margin	11.3	11.5	11.7	9.8	11.6
Second dorsal base length	11.1	10.5	11.1	9.7	11.1
Second dorsal height	5.6	5.3	6.7	5.0	6.6
Second dorsal inner margin	4.8	4.5	4.9	4.1	4.5
Second dorsal posterior margin	6.9	6.3	7.7	7.0	8.5
Second dorsal exposed spine length	1.7	2.0	3.2	2.0	3.1
Second dorsal spine base width	0.6	0.7	0.8	0.6	0.8
Pectoral anterior margin	13.0	12.1	13.1	11.9	13.4
Pectoral inner margin	12.2	9.5	10.4	12.0	13.4
Pectoral base length	4.9	4.3	5.9	4.3	4.9
Pectoral height	10.8	8.3	12.1	10.4	11.8
Pectoral free rear tip length	4.8	2.4	2.8	3.7	4.7
Pectoral posterior margin	10.5	8.1	10.9	10.0	11.0
Pelvic length	11.7	10.4	10.9	10.7	12.2
Pelvic height	6.6	4.9	5.5	6.0	6.8
Pelvic inner margin	6.3	5.3	5.5	6.1	6.8
Dorsal caudal margin	17.8	20.4	22.2	17.2	19.6
Preventral caudal margin	13.4	13.9	14.7	11.8	13.2
Upper postventral caudal margin	7.5	8.0	8.3	6.7	8.0
Lower postventral caudal margin	4.0	4.4	4.5	3.5	5.3

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TABLE 1. (Continued)

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
Caudal fork width	7.1	7.3	8.0	6.6	7.5
Caudal fork length	12.7	14.4	15.1	11.8	13.1
Caudal terminal lobe	8.3	8.1	9.3	7.5	8.5
Caudal subterminal fin margin	2.7	3.4	3.9	2.8	3.4
Head width at anterior of nostrils	6.2	6.1	6.7	6.2	6.7
Head width at mouth	9.6	9.5	10.5	9.6	9.8
Head width	12.0	10.4	12.9	10.7	11.9
Trunk width	10.6	8.2	10.3	7.9	10.1
Abdomen width	10.3	6.7	9.1	5.9	9.3
Tail width	4.9	3.8	5.0	4.1	4.7
Caudal peduncle width	2.5	1.8	2.5	2.0	2.6
Head height	10.6	8.3	9.6	8.6	10.7
Trunk height	12.4	9.9	11.5	9.3	12.2
Abdomen height	12.7	11.4	13.4	9.2	12.2
Tail height	7.2	6.8	8.3	6.9	7.3
Caudal peduncle height	3.8	4.1	4.4	3.7	4.1
Clasper outer length	–	–	–	–	–
Clasper inner length	–	–	–	–	–
Clasper base width	–	–	–	–	–
First dorsal midpoint–pectoral insertion	11.7	7.6	9.4	10.7	11.6
First dorsal midpoint–pelvic origin	23.7	18.8	20.3	22.0	24.7
Pelvic midpoint–first dorsal insertion	17.0	13.0	15.2	15.4	17.6
Pelvic midpoint–second dorsal origin	1.0	0.9	2.3	0.8	1.9

Colour. In preservative: Dorsal and lateral surfaces medium brownish to greyish brown; ventral surfaces slightly paler; waterline between dorsal and ventral colour shades very diffuse on lower sides. Fins without distinct markings in preserved specimens examined (no fresh material observed); dorsal fins and ventral caudal lobe of near-term embryo blackish distally, with upper caudal lobe with a broad whitish margin with a dusky marking anteriorly.

Size. Type specimens ranged in size from 317 to 950 mm TL. The smallest free-swimming individual was 408 mm TL; a late-term embryo of 317 mm TL still possessed a small external yolk sac; Cadenat (1960) recorded an embryo of 395 mm TL from a pregnant female. A female of 863 mm TL was mature and pregnant. Cadenat (1960) reported adult males between 715 and 765 mm TL and adult females between 890 and 990 mm TL.

Distribution. Type specimens were from the Mozambique Channel (Madagascar and Mozambique), and off Senegal, Côte d'Ivoire, Equatorial Guinea, and Togo at depths of 340–500 m. The BMNH and ZMB specimens were most likely collected by Anchieta from Angola or Mozambique in the 1800's. Additional specimens examined by Munoz-Chapuli & Ramos (1989) were recorded as being collected from Morocco, the Canary Islands, and Ghana at depths of 370–610 m.

Etymology. Named after Dr Robin Leslie (Fisheries Branch, Department of Agriculture, Forestry and Fisheries in South Africa) who has contributed greatly to our knowledge of southern African chondrichthyans and provided numerous important specimens and tissue samples for various projects.

FIGURE 9. Lateral trunk denticles (from below first dorsal fin) of *Centrophorus lesliei* **n. sp.**: paratype BMNH 1867.7.23.2, juvenile male 742 mm TL.

FIGURE 10. Map showing the collection locations, where known, of specimens of *Centrophorus lesliei* **n. sp.** (yellow and green) and *Centrophorus longipinnis* **n. sp.** (cyan and pink). Stars denote the holotypes, circles denote paratypes, and triangles denote non-type specimens (Image © NASA, TerraMetrics, Google Earth).

Centrophorus longipinnis n. sp.

Longfin Gulper Shark
(Figs 11–15; Table 2)

Centrophorus lusitanicus—Teng, 1958: 25, fig. 16 (Yilan and Kaohsiung, Taiwan); Teng, 1962: 155, fig. 39 (Tashi); Chen, 1963: 92 (Taiwan); Yang, 1979: 205, Fig. 2 (Taiwan); Chen & Cheng, 1982: 143, Fig. 1 (Taiwan); Chen & Yu, 1986: 112 (Taiwan); Compagno *et al.*, 2005: 52 (Philippines); Hsu & Joung, 2004: 184 (Taiwan); Shen & Wu, 2011: 82, Fig. (Taiwan).

Centrophorus niaukang—Chen & Joung 1993: pl. 2 (fig. 1) (Taiwan).

Centrophorus cf. *lusitanicus*—White *et al.*, 2006: 50, Fig. (Indonesia); White & Dharmadi, 2010: 1364, Fig. 6a, b (Indonesia); Ebert *et al*., 2013: 289 (Taiwan).

Centrophorus sp. 2—Naylor *et al.*, 2012: 59, Fig. 43 (Taiwan).

Centrophorus sp. 3—Naylor *et al.*, 2012: 59, Fig. 43 (Philippines).

Holotype. NMMB-P 15756 (tissue accession GN10189), adult male 720 mm TL, Cheng-gong, Taiwan, 30 Jul. 2011.

Paratypes. (15 specimens) CSIRO H 5788-02 (tissue accession GN11178), female 899 mm TL, Tanjung Luar fish market, Lombok, Indonesia, 11 Apr. 2001; CSIRO H 8104-01 (tissue accession GN11174), female 855 mm TL, CSIRO H 8104-02 (tissue accession GN11175), adult male 679 mm TL, CSIRO H 8104-04 (tissue accession GN11177), female 872 mm TL, Tanjung Luar fish market, Lombok, Indonesia, 19 Aug. 2005; CSIRO H 7990-02, female 825 mm TL, Pelabuhanratu fish market, West Java, Indonesia, 10 Mar. 2009; CSIRO H 8103-01, pregnant female 890 mm TL, Huon Gulf, off Lae, Papua New Guinea, 6°45.147' S, 147°2.783' E, 460 m depth, 4 May 2017; CSIRO H 8103-02, late-term embryo 346 mm TL, taken from CSIRO H 8103-01; CSIRO H 8171-01, adult male 761 mm TL, Da-xi, Taiwan, 14 Apr. 2012; FRIP 03628 (1 of 2), adult male 719 mm TL, FRIP 03628 (2 of 2), juvenile male 637 mm TL, Taiwan, 11 Mar. 1958; NMMB-P 25361, 736 mm TL, adult male, Da-xi, Taiwan, 20 Mar. 2013; NMMB-P 14051, juvenile female 408 mm TL, Cheng-gong, Taiwan, 2 Oct. 2011; NMMB-P 15813, female 905 mm TL, Cheng-gong, Taiwan, 2 Oct. 2011; NMMB-P 15814 (tissue accession GN10190), adult male 745 mm TL, Cheng-gong, Taiwan, 18 Jul. 2011; NMMB-P 15859, adult male 761 mm TL, Cheng-gong, Taiwan, 29 Mar. 2011; BMNH 2017.8.29.1 (to be donated to BMNH), adult male 776 mm TL, Da-xi, Taiwan, 14 Apr. 2012.

Other specimens. (1 specimen) CSIRO H 8104-03 (tissue accession GN11176), adult male 764 mm TL, Tanjung Luar fish market, Lombok, Indonesia, 19 Aug. 2005.

Genetic material (specimens not retained). (3 samples) Tissue accession GN973, Da-xi, Taiwan; Tissue accession GN974, Da-xi, Taiwan; Tissue accession GN1007, Da-xi, Taiwan.

Diagnosis. A medium sized (<1 m maximum total length) species of *Centrophorus* with the following combination of characters: body relatively slender; head moderately long (20.5–25.1% TL); snout relatively short (horizontal preorbital length 6.4–8.4% TL) and rounded in dorsal view; first dorsal extremely long based (base length 20.8–23.3% TL, soft fin length 16.9–20.2% TL) and relatively high (height 5.7–7.2% TL), inner margin relatively short (5.3–6.8% TL, 2.6–3.2 in soft fin length); second dorsal fin much smaller in area to first, similar in height to first dorsal fin (height 1.0–1.3 in first dorsal-fin height); pectoral fins large (anterior margin length 11.0–13.0% TL), free rear tip elongate in larger individuals (2.2–4.0% TL); lateral trunk denticles of larger individuals sessile (not raised on pedicels), block-like, not elevated; upper teeth of larger individuals with erect to slightly oblique cusps; lower teeth of all sized specimens much larger than upper teeth, strongly oblique, blade-like; total vertebral centra 112–122; teeth 38–43/29–31.

Description. Body fusiform, relatively slender, nape only slightly humped; deepest near first dorsal-fin spine, trunk height 1.30 (0.91–1.34 in paratypes >700 mm TL) times width, 0.96 (0.82–1.05 in paratypes >700 mm TL) times abdomen height; no lateral ridges; interdorsal ridge absent; pre-first dorsal length 4.23 (4.12 in 408 mm TL paratype; 3.62–4.26 in paratypes >700 mm TL) in TL; interdorsal space 1.28 (1.61; 1.03–1.38) in prepectoral length, 1.45 (1.69; 1.28–1.62) in pre-first dorsal length; pelvic–caudal space 3.28 (2.60; 2.70–3.50) in pectoral–pelvic space, 1.82 (1.87; 1.62–2.00) in prepectoral length; dorsal–caudal space 2.05 (1.81; 2.09–2.65) in interdorsal space. Caudal peduncle moderately short and deep, moderately compressed, its length 11.5 (12.4; 10.7–12.8)% TL, its height 1.47 (2.11; 1.61–2.15) times its width; tapering slightly towards caudal fin; ventral midline with a groove; dorsal midline with a weak ridge anteriorly becoming a weak groove posteriorly; no lateral keels; precaudal pits absent.

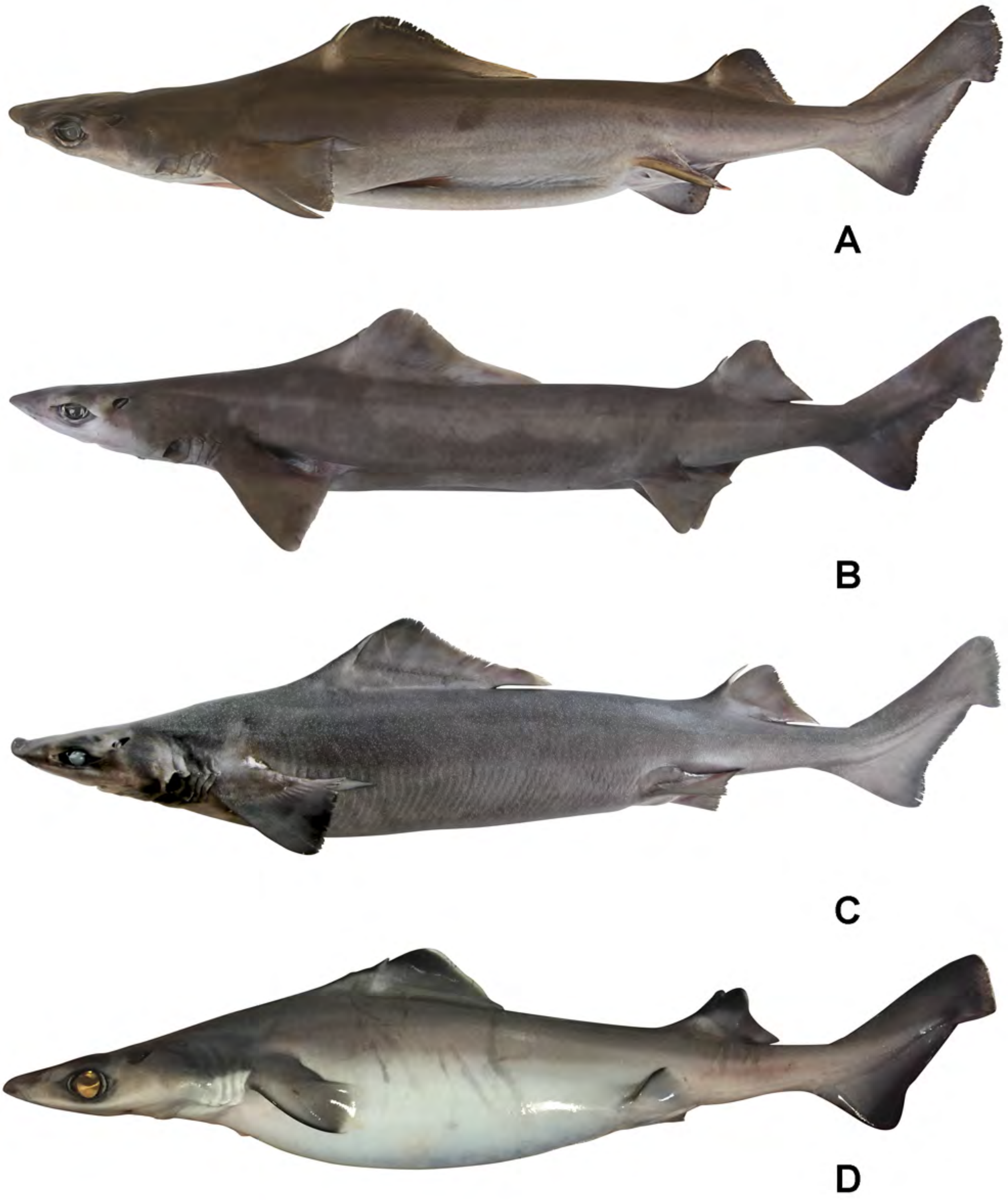

FIGURE 11. Lateral view of *Centrophorus longipinnis* **n.sp.**: (A) adult male holotype (NMMB-P 15756, 720 mm TL); (B) female paratype (CSIRO H 8104-01, 855 mm TL); (C) female paratype (CSIRO H 7990-02, 825 mm TL); (D) late-term embryo paratype (CSIRO H 8103-02, 346 mm TL).

FIGURE 12. Ventral view of head and pectoral fins of *Centrophorus longipinnis* **n.sp.**: female paratype (CSIRO H 7990-02, 825 mm TL).

FIGURE 13. Upper and lower teeth of female paratype of *Centrophorus longipinnis* **n.sp.** (CSIRO H 7990-02, 825 mm TL).

Head moderately long, moderately broad, width 1.72 (1.44; 1.04–1.73) times trunk width, 1.75 (1.85; 1.18–1.81) times abdomen width, length 21.1 (24.3; 20.5–22.4)% TL, 2.96 (2.47; 2.76–3.09) in pre-vent length, height 0.67 (0.75; 0.65–0.96) times width; slightly depressed forward of spiracles, somewhat broadly pear-shaped in cross-section at pectoral-fin origin. Band of transverse dermal folds on ventral surface of head broadly rounded with apex about three quarters of horizontal prenasal length behind symphysis of lower jaw, extending from below lower edges of first four gill slits on either side; up to 19 folds present.

Snout moderately long, narrowly triangular in lateral view, apex bluntly pointed; lateral prenarial margin rounded; rounded in dorsal view; horizontal length 1.24 (1.28; 1.07–1.29) times eye length, 0.78 (0.96; 0.68–0.84) times interorbital space; horizontal prenarial length 1.44 (1.43; 1.40–1.57) times in preoral length. Nostrils small, slightly oblique; anterior nasal flap with a large, narrowly triangular lobe, with a very small, sometimes pale lobe at inner corner of large lobe; internarial space 2.80 (2.67; 2.43–2.95) in preoral length, 1.77 (1.85; 1.53–2.05) times nostril length. Eye moderately large, elongate, length 4.04 (3.98; 3.96–4.66) in head, 2.46 (3.30; 1.94–3.81) times height; notched anteriorly; strongly notched posteriorly, notch not extending towards spiracle. Spiracle moderately large, semicircular; located dorsolaterally on head, entirely visible in dorsal view; lower margin about level with upper eye, slightly less than its diameter away from eye; no lobe-like fold on posterior margin; greatest diameter 3.05 (3.19; 2.57–3.83) in eye length. Gill slits directed anteroventrally from top to bottom, fifth angled more than first; first shortest then becoming progressively longer to fifth; fifth longest, its height 2.6 (3.2; 2.4–3.5)% TL.

Mouth almost transverse, upper jaw slightly concave, width 1.22 (1.29; 1.06–1.22) in preoral length; lower labial furrows slightly longer than upper furrows; prominent postoral groove, more than twice length of upper labial furrows, extending posterolaterally from angle of jaws. Teeth strongly differentiated in upper and lower jaws, with upper teeth much smaller than lower teeth. Upper teeth of adults (based on CSIRO H 7990-02) moderately large, with erect cusps, becoming slightly oblique posteriorly towards mouth corners, bases slightly overlapping (Fig. 13a). Lower teeth much larger than uppers, cusps very strongly oblique, blade-like, overlapping, edges with fine serrations (Fig. 13b).

Dermal denticles on flank below first dorsal fin varying greatly in shape between juveniles and adults; absent from insertions of fins and most of the dorsal surface of claspers. Denticles of a juvenile (408 mm TL) small, upright, slender, unicuspid, closely spaced (slightly overlapping), and posteriorly curved; about 0.4 mm long (Fig. 14a). Denticles of adults (based on a 855 mm TL specimen) block-like, sessile (not raised on pedicels), rhomboidal, close set but not overlapping; anterior edges of crowns shallowly scalloped, posterior edge bluntly pointed (Fig. 14b).

First dorsal fin extremely long, moderately high; length 4.18 (4.18; 3.37–5.03) times its height, 1.76 (1.77; 1.76–1.98) times second dorsal-fin length; soft-fin length 2.86 (2.55; 2.48–3.47) times its height; height 1.14 (1.13; 0.99–1.25) times second dorsal-fin height; anterior margin slightly convex; apex narrowly rounded; posterior margin moderately concave, slanting well posteroventrally from top to bottom; free rear tip moderately long, relatively thick basally; inner margin nearly straight, 2.88 (2.94; 2.60–3.23) in soft-fin length, 1.00 (0.87; 0.82–1.20) times its height; insertion level with mid pectoral–pelvic space, extremely well forward of pelvic-fin origin, pelvic-fin midpoint to first dorsal-fin insertion 15.1 (13.1; 13.2–17.6)% TL; base of exposed fin spine level with pectoral-fin free rear tip; spine base moderately broad, exposed anteriorly just above junction of spine and soft portion of fin; exposed fin spine relatively short, robust, tapering distally, anterior margin slightly convex; exposed portion of spine sloping strongly posterodorsally from base (of exposed portion) to apex, shorter in length to exposed portion of second dorsal-fin spine, exposed first dorsal spine length 0.39 (0.30; 0.23–0.39) times height of fin.

Second dorsal fin moderately large, much smaller in area compared to first dorsal fin, relatively short; second dorsal-fin length 2.69 (2.66; 2.25–2.84) times its height; anterior margin slightly convex; apex narrowly rounded; posterior margin weakly concave, sloping strongly posteroventrally from apex; free rear tip relatively short, thick basally, inner margin length 2.09 (2.05; 1.83–2.40) in soft-fin length, 0.78 (0.81; 0.63–0.83) times fin height; spine length 0.42 (0.32–0.50 in paratypes >700 mm TL) in height of fin; base of exposed fin spine level with mid pelvic-fin inner margin, exposed just above level of junction with spine and soft portion of fin; exposed fin spine relatively long, robust, broad based, tapering distally.

Pectoral fins large; anterior margin weakly convex to nearly straight, its length 12.1 (12.3; 12.0–13.0)% TL; base very short, 2.68 (2.77; 2.26–2.99) in anterior margin length; apex somewhat angular, not falcate; posterior margin nearly straight from apex angle of free rear tip then broadly concave; inner margin slightly concave; free rear tip elongate in adults (less so in juveniles), free rear tip 1.18 (1.04; 1.01–1.14) in inner margin, extending past level of exposed first dorsal-fin spine; origin situated at level of mid-fifth gill slit, partially obscured by gill membrane.

Pelvic fins large, length 11.6 (11.4; 11.0–12.4)% TL, 1.20 (1.14; 1.18–1.44) times second dorsal-fin soft length; anterior margin slightly convex; apex narrowly rounded; posterior margin slightly concave; free rear tip acutely pointed, inner margin very slightly convex. Claspers of adult males relatively short, slender; tapering to a fleshy, narrowly rounded tip (Fig. 15); outer length 2.9 (2.5–3.3)% TL, 3.16 (2.98–3.81) times its base length (n = 8); clasper glans about 0.3 in clasper inner length; apopyle and hypopyle connected by long clasper groove; rhipidion moderately large, laterally expanded, extended from hypopyle to anterior of clasper tip; lateral edge with a slender, straight spine; dermal denticles mostly absent from dorsal surface.

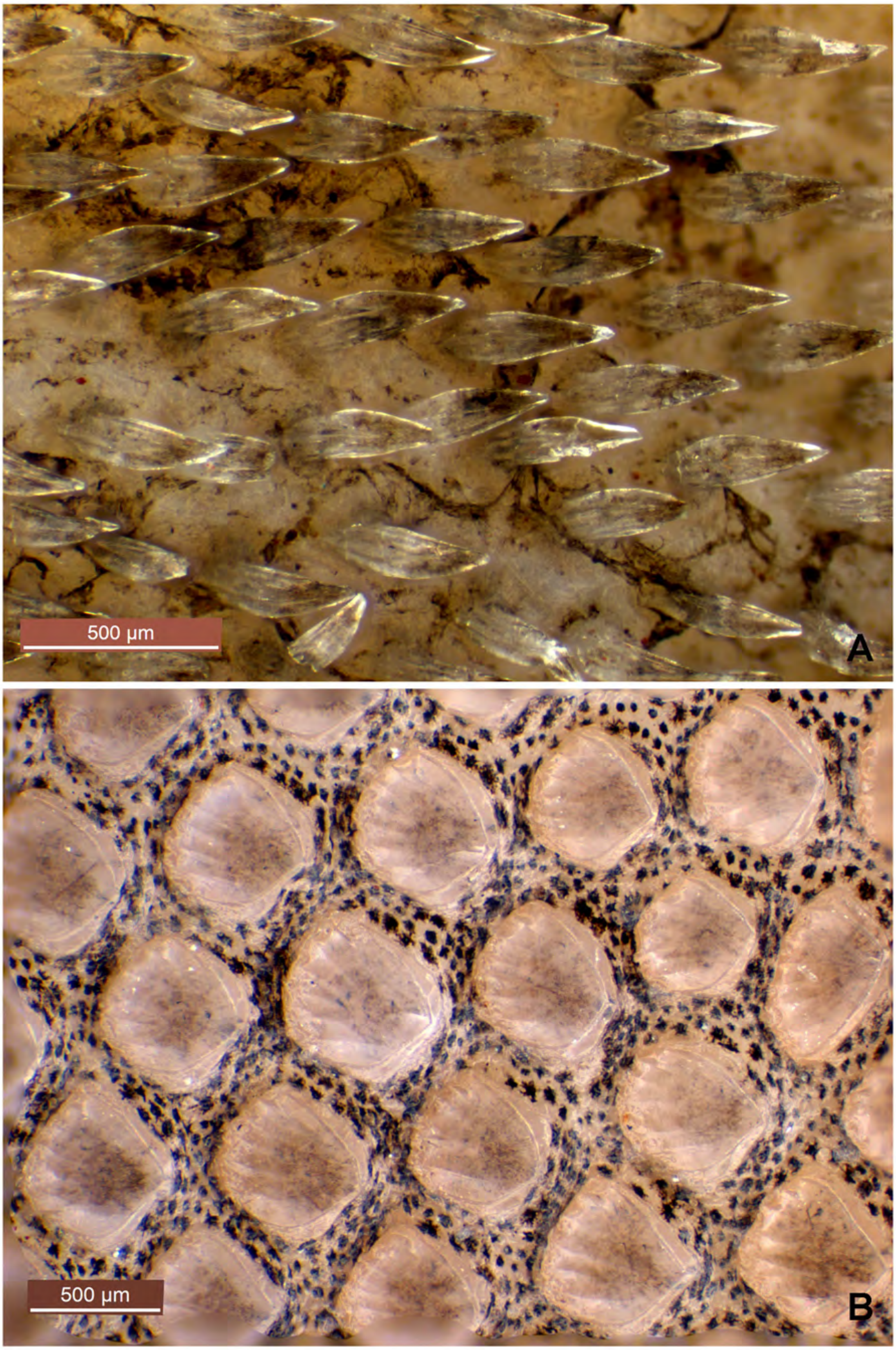

FIGURE 14. Lateral trunk denticles (from below first dorsal fin) of *Centrophorus longipinnis* **n.sp.**: (A) juvenile female paratype, NMMB-P 14051, 408 mm TL; (B) female paratype, CSIRO H 8104-01, 855 mm TL.

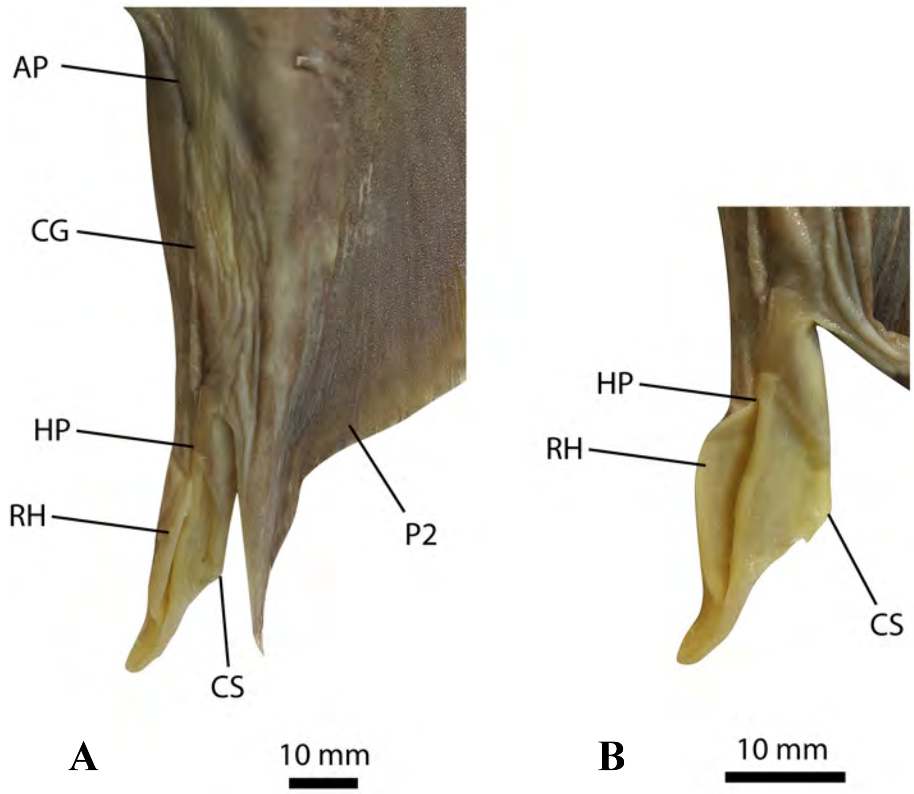

FIGURE 15. Clasper (right) of *Centrophorus longipinnis* (paratype CSIRO H 8104–02, adult male 679 mm TL). A, Glans not dilated; B, Glans spread. Abbreviations: AP, apopyle; CG, clasper groove; CS, clasper spine; HP, hypopyle; P2, pelvic fin; RH, rhipidion.

Caudal fin relatively long, deep, broad; dorsal margin almost straight to slightly concave, 1.17 (1.18; 1.11–1.22) in head length, 1.42 (1.70; 1.32–1.51) times preventral margin; preventral margin slightly convex (more so distally), apex narrowly rounded; upper postventral margin slightly convex, lower postventral margin nearly straight to slightly convex, angle between postventral margins moderately concave; terminal lobe moderately large but short, lobe length 2.31 (2.50; 2.05–2.63) in dorsal caudal margin, terminal margin slightly to moderately convex and slightly undulating; apex of upper lobe narrowly rounded.

Meristic data. Total vertebral centra 118 (112–122), monospondylous precaudal centra 59 (56–62), diplospondylous precaudal centra 28 (25–29), total precaudal centra 87 (83–91) and diplospondylous caudal centra 31 (26–34). Tooth count (n = 5): 20 (19–22) + (21) 19–21 / 15 (15) + 14 (15–16); total 41 (38–43)/29 (30–31).

Colour. When fresh: Dorsal and lateral surfaces brownish, sometimes with a reddish hue (grey in some specimens, particularly smaller specimens); ventral surfaces paler (only slightly paler in paratype CSIRO H 7990-02); waterline between dorsal and ventral colour shades diffuse and poorly defined on body, more distinct on head and caudal peduncle. Fins without markings in larger specimens; tip of free tip of first dorsal fin often paler; near-term embryo with blackish dorsal and caudal fins and black anterior margins to paired fins, with narrow white posterior margin to dorsal and paired fins. Similar colour in preservation; fin markings of embryo less distinct.

Size. Postnatal type specimens ranged from 408 to 905 mm TL; a 637 mm TL male was immature; males adult between 719 and 776 mm TL; an 890 mm TL female was pregnant with a 346 mm TL late-term embryo (both paratypes). White & Dharmadi (2010) recorded: females up to 930 mm TL; an 873 mm TL pregnant female with a single 45 mm TL early-term embryo; males adult between 679 and 775 mm TL, while a 657 mm TL male was immature. Compagno *et al.* (2005) reported on a 737 mm TL immature male.

Distribution. Type material from off Taiwan (Cheng-gong and Da-xi fish landing sites—local fishing grounds), Indonesia (off southwest Java and eastern Lombok), and Papua New Guinea (Huon Gulf) (Fig. 10). Compagno *et al.* (2005) reported this species off Puerto Princesa City in the Philippines (JPAG 226, tissue accession GN4348); differed slightly in ND2 sequence and specimen not examined in this study. Limited depth information available as most specimens collected from fish landing sites; caught from depths of 330–460 m in Papua New Guinea (P. Neira, pers. comm.).

Etymology. Specific name a combination of the Latin *longus* (long) and *pinna* (fin) in allusion to the very distinctive long-based first dorsal fin this species possesses.

TABLE 2. Proportional dimensions as percentages of total length for the holotype of *Centrophorus longipinnis* (NMMB-P 15756), and ranges for small paratypes (<524 mm TL) and large paratypes (>700 mm TL).

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
Total length (mm)	720	346	408	719	905
Precaudal length	81.3	78.9	80.3	79.8	82.4
Pre-second dorsal length	62.5	61.5	62.4	62.1	65.0
Pre-first dorsal length	23.8	24.0	26.3	23.4	27.2
Pre-first dorsal length (horiz.)	23.7	24.3	27.0	23.5	27.7
Pre-vent length	62.6	60.0	61.3	61.1	64.0
Prepelvic length	59.6	58.3	59.2	58.7	60.9
Prepectoral length	20.9	23.2	23.4	19.1	21.4
Head length	20.5	24.7	24.7	20.1	22.1
Head length (horiz.)	21.1	24.3	25.1	20.5	22.3
Prebranchial length	18.5	21.7	22.2	17.3	19.2
Prespiracular length	12.4	14.7	14.8	11.6	12.9
Preorbital length	6.5	7.8	7.9	5.8	6.5
Preorbital length (horiz.)	7.2	8.3	8.4	6.4	7.3
Snout to inner nostril	4.4	5.2	5.9	3.9	4.7
Prenarial length (horiz.)	4.0	5.0	5.2	3.5	4.4
Preoral length	9.4	11.1	12.8	8.6	9.8
Inner nostril–labial furrow space	6.3	7.4	7.6	5.6	6.1
Mouth width	7.7	8.4	8.6	7.2	8.4
Upper labial furrow length	1.9	1.9	2.4	1.5	2.2
Nostril width	1.9	2.3	2.4	1.6	2.0
Internarial space	3.4	4.0	4.2	3.1	3.5
Interorbital space	8.3	8.1	9.0	7.3	8.6
Eye length	5.2	6.1	6.4	4.8	5.4
Eye height	2.1	1.8	2.4	1.4	2.5
Spiracle diameter—greatest	1.7	1.9	2.3	1.3	2.0
First gill-slit height	2.1	2.6	2.9	1.7	2.4
Fifth gill-slit height	2.7	2.9	3.2	2.4	3.5
Interdorsal space	16.4	14.4	15.6	15.0	18.5
Dorsal–caudal space	8.0	6.8	7.9	6.5	7.8
Pectoral–pelvic space	37.7	32.2	33.1	33.7	37.9
Pelvic–caudal space	11.5	11.8	12.4	10.7	12.8
First dorsal length	28.1	26.2	28.4	24.4	29.4
First dorsal soft fin length	19.3	16.9	17.3	17.4	20.2
First dorsal anterior margin	14.5	15.7	17.1	12.1	16.7

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TABLE 2. (Continued)

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
First dorsal base length	22.3	20.8	22.5	20.8	23.3
F irst dorsal height	6.7	6.8	6.9	5.7	7.2
First dorsal inner margin	6.7	5.3	5.9	5.8	6.8
First dorsal posterior margin	16.5	14.1	14.3	15.5	17.8
First dorsal exposed spine length	2.6	2.1	2.2	1.6	2.6
First dorsal spine base width	0.8	0.8	0.8	0.7	0.9
Second dorsal length	15.9	15.1	16.0	14.5	16.4
Second dorsal soft fin length	9.6	8.2	10.0	8.4	9.9
Second dorsal anterior margin	10.8	11.5	12.0	9.9	11.6
Second dorsal base length	11.4	11.2	12.0	10.2	12.1
Second dorsal height	5.9	6.0	6.5	5.5	6.5
Second dorsal inner margin	4.6	4.2	4.9	3.8	4.8
Second dorsal posterior margin	8.8	6.7	7.4	7.2	8.8
Second dorsal exposed spine length	2.5	3.0	3.0	2.1	3.0
Second dorsal spine base width	0.7	0.8	0.8	0.6	0.8
Pectoral anterior margin	12.1	11.0	12.3	12.0	13.0
Pectoral inner margin	12.3	8.8	10.5	10.3	12.1
Pectoral base length	4.5	4.4	4.9	4.1	5.5
Pectoral height	10.4	8.2	10.2	9.9	11.2
Pectoral free rear tip length	3.3	1.5	2.1	2.2	4.0
Pectoral posterior margin	9.0	7.7	9.3	8.2	10.6
Pelvic length	11.6	10.6	11.4	11.0	12.4
Pelvic height	6.0	4.7	5.1	6.0	7.0
Pelvic inner margin	7.0	5.3	6.6	6.0	7.6
Dorsal caudal margin	18.1	19.7	20.6	17.1	19.5
Preventral caudal margin	12.7	12.1	13.0	12.3	13.7
Upper postventral caudal margin	7.8	7.7	8.4	6.9	7.9
Lower postventral caudal margin	4.2	3.8	3.8	3.7	5.6
Caudal fork width	7.6	7.3	7.7	6.9	7.9
Caudal fork length	12.5	14.1	14.3	12.0	14.1
Caudal terminal lobe	7.8	7.9	8.2	7.0	9.1
Caudal subterminal fin margin	2.8	3.3	4.1	2.2	3.0
Head width at anterior of nostrils	6.0	6.3	7.0	5.5	6.6
Head width at mouth	9.4	10.6	11.4	8.4	10.0
Head width	12.2	11.7	11.9	10.1	12.7
Trunk width	7.1	8.0	8.1	6.9	12.2
Abdomen width	6.9	6.3	10.2	6.6	10.7
Tail width	4.9	3.7	4.5	4.5	5.3
Caudal peduncle width	2.8	1.9	2.1	2.1	2.6
Head height	8.1	8.7	9.1	7.7	10.9

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TABLE 2. (Continued)

	Holotype	Paratypes (<524 mm TL)		Paratypes (>644 mm TL)	
		Min.	Max.	Min.	Max.
Trunk height	9.2	11.8	11.8	8.1	12.9
Abdomen height	9.7	7.7	13.9	9.6	12.9
Tail height	7.4	6.8	7.7	6.6	8.4
Caudal peduncle height	4.1	4.1	4.6	3.8	4.4
Clasper outer length	2.9	–	–	2.5	3.3
Clasper inner length	6.8	–	–	6.6	7.2
Clasper base width	0.9	–	–	0.8	1.0
First dorsal midpoint–pectoral insertion	9.6	10.0	10.1	8.6	13.2
First dorsal midpoint–pelvic origin	25.7	19.1	20.3	22.1	25.1
Pelvic midpoint–first dorsal insertion	15.1	13.1	13.7	13.2	17.5
Pelvic midpoint–second dorsal origin	0.3	1.4	2.1	-0.6	1.8

Molecular analyses

The Maximum Likelihood tree generated from the ND2 sequences obtained provide further support for the separation of *C. lesliei* and *C. longipinnis* as valid species (Fig. 16). *Centrophorus lesliei* samples form a distinct group nested within, but separate from, the three long-snout species groups (i.e. *isodon-tesselatus-westraliensis*, *harrissoni*, and *isodon-tesselatus*). The long-snout species group requires further attention and will be dealt with in a subsequent part of this revision series for this genus. It should be noted that none of the sequenced specimens from Madagascar are type species as whole specimens were not retained, however, they were obtained from the Mozambique Channel, close to the locality of the holotype and three paratypes of *C. lesliei*. *Centrophorus longipinnis* forms a distinct group well separated from the long-snout and *C. lesliei* groups. Within the *C. longipinnis* group, two samples (GN 11175 from Indonesia and GN 4348 from the Philippines) show some differences to the main group (Fig. 16). But morphologically, the Indonesian specimen is identical to the other *C. longipinnis* specimens and is considered to be this species.

Moura *et al*. (2015) concluded that the BMNH specimen was *C. uyato* based on DNA sequence comparisons for CO1. This result is inconsistent with the findings we present herein. Morphological data suggest that the BMNH specimen is *C. lesliei* and furthermore, is very distinct from *C. uyato* in possessing a much longer first dorsal-fin base. Munoz-Chapuli & Ramos (1989) recorded vastly different first dorsal-fin ray counts between *C. lusitanicus* (=*C. lesliei*) and *C. granulosus* (=*C. uyato*), i.e. 7–9 vs. 16–19, reflecting the large difference in length of the first dorsal fin. Thus, it is not conceivable that these two species could be considered conspecific, or that the BMNH specimen is a long finned variant of *C. uyato*. Moura *et al.* (2015) state in their acknowledgements that they obtained a tissue sample from the BMNH specimen and also from 'the Aquário Vasco da Gama Museum, and Aldina Inácio…' and state at the end of the sentence state, in parentheses, that 'DNA extraction was unsuccessful'. One possibility is that the BMNH specimen was the one which DNA extraction was not successful on and that a sample from the other source(s) was *C. uyato*. A tissue sample from the BMNH specimen was also collected as part of a broader Chondrichthyan Tree of Life project led by one of us (GN) but despite numerous attempts, no valid DNA sequence could be obtained.

Comparisons between species

The two new species differ from other *Centrophorus* species in the following key characters: first dorsal fin very long-based (base 16.8–23.3 vs. 9.9–17.3% TL in other *Centrophorus* species); pectoral-fin rear tip elongate (vs. not or only slightly produced in *C. squamosus* and *C. granulosus*); denticles of adults flat, pavement-like (vs. raised on pedicels or tear-shaped in *C. squamosus* and *C. granulosus*); second dorsal-fin relatively tall (its height 5.0–6.7 vs. 2.9–3.9% TL in *C. moluccensis*). The best character to easily separate these two species from all other specimens is the extremely long-based first dorsal fin which gives it a very distinctive appearance.

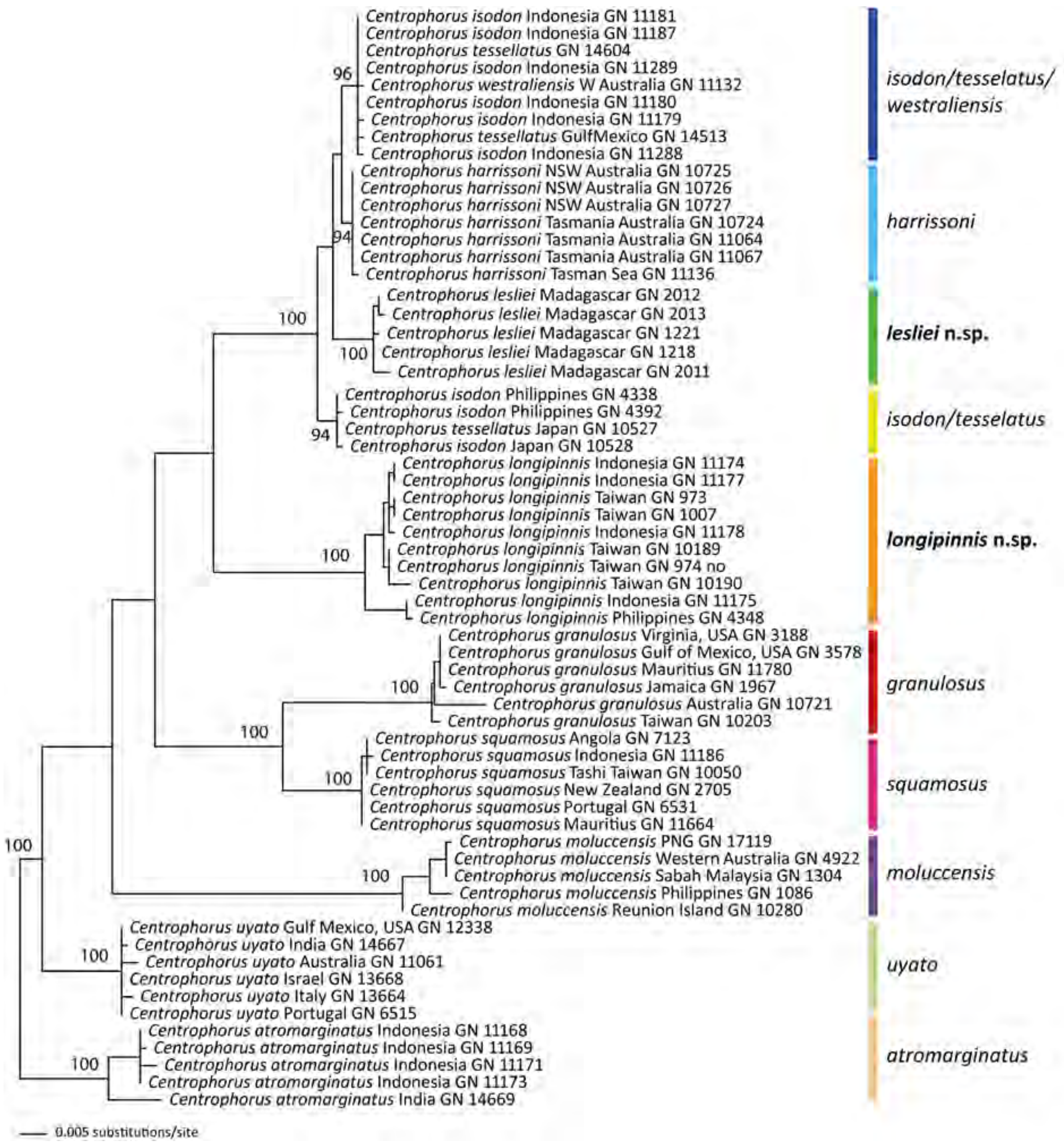

FIGURE 16. Maximum Likelihood tree estimated under the General Time Reversible model (GTR) with model terms to accommodate both Invariant site (I) and Gamma Distributed rates (G). Bootstrap support values are shown from a separate ML bootstrap analysis. Sequences used in this tree are part of the Chondrichthyan Tree of Life project (http://sharksrays.org/).

MDS analysis of the measured types of *Centrophorus lesliei* and *C. longipinnis* showed relatively clear distinction between the two species (Fig. 17). ANOSIM showed the species were significantly different overall ($P<0.05$) but with low support ($R^2 = 0.459$). The measurements shown by SIMPER to be the most responsible for the differences between the two species were (in order of importance): pectoral–pelvic space, first dorsal-fin base length, pre-first dorsal length, and prepelvic length. Given the level of ontogenetic differentiation (see later), the morphometric differences between comparable size classes of the two species provided better resolution.

The measurements shown by SIMPER to be the most responsible for the differences between size class 1 (<524 mm TL) of *C. lesliei* and *C. longipinnis* were (in order of importance): pectoral–pelvic space (28.1–29.4 vs.

32.2–33.1% TL), first dorsal-fin base (17.9–18.8 vs. 20.8–22.5% TL) and prepelvic length (55.4–57.4 vs. 58.3–59.2% TL). Other measurements which differed between size class 1 types of *C. lesliei* and *C. longipinnis* were: pre-second dorsal length (59.3–60.7 vs. 61.5–62.4% TL), preorbital length (horizontal length 6.2–7.1 vs. 7.8–7.9% TL), dorsal–caudal space (8.0–8.8 vs. 6.8–7.9% TL), preventral caudal margin (13.9–14.7 vs. 12.1–13.0% TL), first dorsal-fin soft length (16.0–16.3 vs. 16.9–17.3% TL).

The measurements shown by SIMPER to be the most responsible for the differences between size classes 2 (644–776 mm TL) and 3 (>825 mm TL) of *C. lesliei* and *C. longipinnis* were (in order of importance): first dorsal-fin base length (16.8–19.7 vs. 20.8–23.3% TL), pre-first dorsal length (25.9–27.9 vs. 23.5–27.7% TL), and pectoral–pelvic space (34.6–38.2 vs. 33.7–37.9% TL). Note that the ranges of the latter two measurements show considerable overlap. Other measurements which differed between size classes 2 and 3 types of *C. lesliei* and *C. longipinnis* were: slightly longer pectoral-fin free tip (free tip 3.7–4.7 vs. 2.2–4.0% TL, inner margin 12.0–13.4 vs. 10.3–12.1% TL), shorter first dorsal-fin posterior margin (12.5–15.4 vs. 15.5–17.8% TL), and shorter first dorsal fin (soft fin length 16.1–17.4 vs. 17.4–20.2% TL).

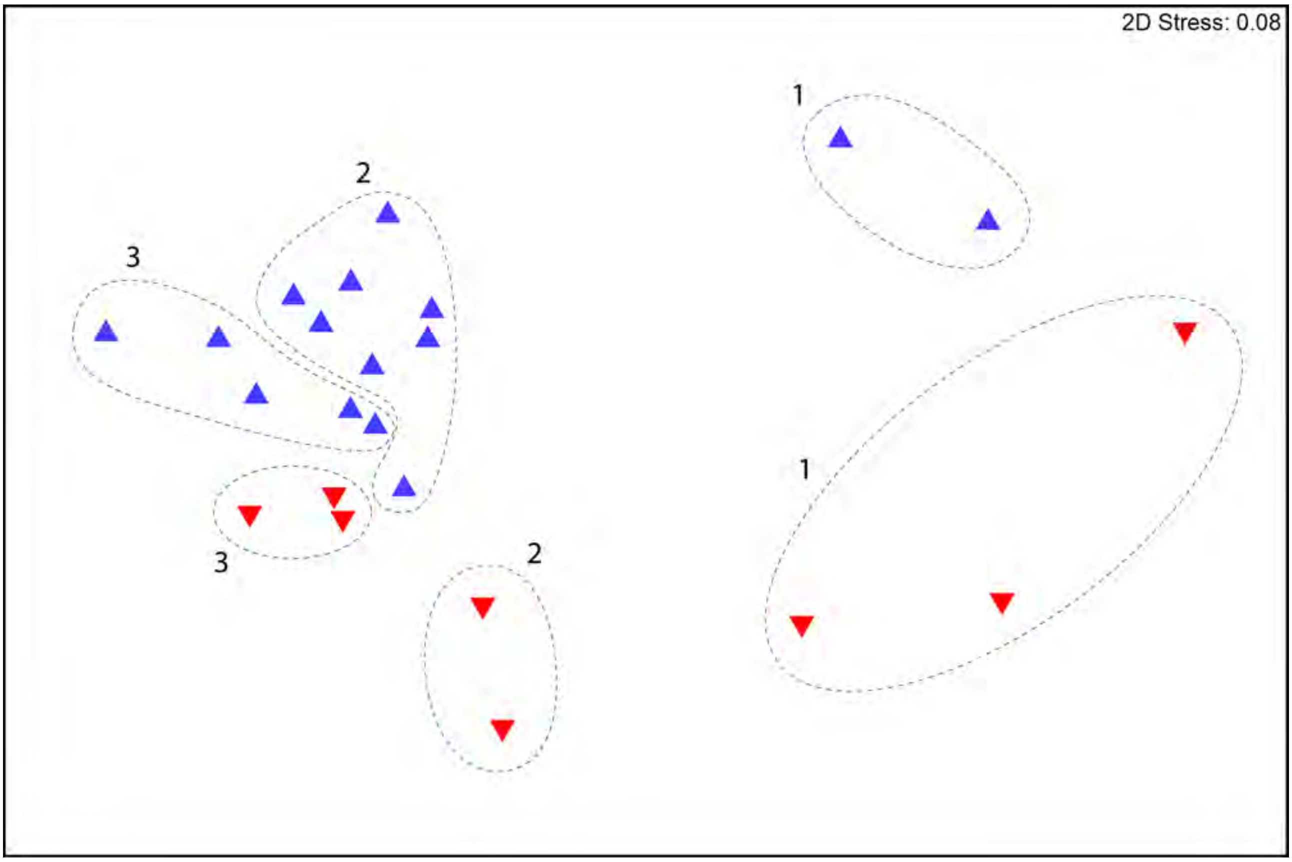

FIGURE 17. Non-metric multidimensional (MDS) ordination of morphometric percentages (%TL) of *Centrophorus lesliei* (red triangles) and *C. longipinnis* (blue triangles). The samples in each of the three size classes used for both species are distinguished by a dashed line—size class 1 (<524 mm TL), size class 2 (644–776 mm TL), and size class 3 (>825 mm TL).

FIGURE 18. Lateral view of the newly designated lectotype of *Centrophorus steindachneri*, NMW 61300 (juvenile male, 426 mm TL); a junior synonym of *Centrophorus granulosus*. Erratum from White *et al.* (2013) where this figure was inadvertently excluded from the final publication.

Intraspecific variation

The MDS plot shows clear ontogenetic differences within each of the two species, with the larger size class (3 = >825 mm TL) grouping to the far left of the plot, the mid-size class (2 = 644–776 mm TL) immediately to the right (but in the left half of the plot), and the smallest size classes (1 = <524 mm TL) to the right of the plot (Fig. 17). ANOSIM showed that within the two species, size classes were significantly different overall ($P<0.01$; 0.729), and in all pairwise tests where sufficient samples were available.

For *C. lesliei*, the measurements shown by SIMPER to be the most responsible for the differences between size classes 1 and 2 were (in order of importance): pectoral–pelvic space (28.1–29.4 vs. 34.6–36.0% TL), prepelvic length (55.4–57.4 vs. 59.3–60.1% TL), pectoral-fin inner margin (9.5–10.4 vs. 13.0–13.4% TL), and pre-second dorsal length (59.3–60.7 vs. 62.5–2.9% TL). Between size classes 1 and 3, SIMPER found the following measurements were most responsible for the differences: pectoral–pelvic space (28.1–29.4 vs. 37.2–38.5% TL), prepelvic length (55.4–57.4 vs. 60.1–60.9% TL), caudal-fin dorsal margin (20.4–22.2 vs. 17.2–17.8% TL), and precaudal length (77.5–80.1 vs. 81.5–82.2% TL). Other measurements which differed between size class 1 and size classes 2 and 3 were: head length (22.7–26.4 vs. 21.4–23.0% TL), snout-vent length (57.6–58.6 vs. 60.7–62.6% TL), preoral length (10.7–12.0 vs. 8.9–9.9% TL), caudal fork length (14.4–15.1 v. 11.8–13.1% TL), and pelvic height (4.9–5.5 vs. 6.0–6.8% TL).

For *C. longipinnis*, the measurements shown by SIMPER to be the most responsible for the differences between size classes 1 and 2 were (in order of importance): head length (24.7 vs. 20.5–22.1% TL), prebranchial length (21.7–22.2 vs. 17.9–19.0% TL), pectoral–pelvic space (32.2–33.1 vs. 31.8–37.9% TL), and preoral length (11.1–12.8 vs. 8.6–9.4% TL). Between size classes 1 and 3, SIMPER found the following measurements were most responsible for the differences: prebranchial length (21.7–22.2 vs. 17.3–19.2% TL), head length (24.7 vs. 20.1–21.4% TL), and pectoral–pelvic space (32.2–33.1 vs. 35.0–37.6% TL). Other measurements which differed between size class 1 and size classes 2 and 3 were: preorbital length (8.3–8.4 vs. 6.3–7.3% TL), prespiracular length (14.7–14.8 vs. 11.6–12.9% TL), prepectoral length (23.2–23.4 vs. 19.1–21.4% TL), snout tip to inner nostrils (5.2–5.9 vs. 3.9–4.7% TL), internarial space (4.0–4.2 vs. 3.1–3.5% TL), mouth width (8.4–8.6 vs. 7.2–8.4% TL), eye length (6.1–6.4 vs. 4.8–5.5% TL), and pelvic height (4.7–5.1 vs. 6.0–7.0% TL).

The denticle morphology of the two new species also differs significantly with size, which was also found in *C. granulosus* (White *et al.*, 2013). Denticles of the smallest juveniles of *C. lesliei* and *C. longipinnis* (Fig. 14a) are unicuspid, upright, slender and backward pointing. In contrast, denticles of specimens >700 mm TL (Figs 9 and 14b) are block-like, sessile (not raised on pedicels), with a blunt cusp becoming less apparent in larger individuals.

Conclusions

The present study represents the second part of a revision of the genus *Centrophorus* and focuses on clarifying the species which have been attributed to *C. lusitanicus* in the literature. Two new species are described and *C. lusitanicus* is considered a junior synonym of *C. granulosus*. The two new species, *C. lesliei* and *C. longipinnis*, belong to the long-snout group of *Centrophorus* which includes: *C. harrissoni*, *C. isodon*, *C. seychellorum*, *C. tesselatus* and *C. westraliensis*. They are clearly separable from these other members in their possession of a very long first dorsal fin. The shorter finned members of this long-snout group require a full revision and will form a subsequent part of this revision series.

This study reinforces the findings of the first part of this series (White *et al.*, 2013) in which understanding intraspecific variation is crucial for adequately describing *Centrophorus* species. The ontogenetic changes between juveniles and adults are often greater than the interspecific differences across all size classes. Future taxonomic studies should, where possible, include adequate samples to allow for better elucidation of intraspecific variation.

Erratum for White *et al.* (2013)

During the publication process of the redescription of *Centrophorus granulosus*, several errors relating to the figures were inadvertently made to the paper which may cause some confusion.

1. ‘Figure 13’—Lateral view of the newly designated lectotype of *Centrophorus steindachneri*, NMW 61300 (juvenile male, 426 mm TL); a junior synonym of *Centrophorus granulosus*.

- This image was excluded from the paper and is included in this paper for future reference (Fig. 18);
- The image shown was of two neonate females of *C. granulosus* which should have been ‘Figure 14’.

2. ‘Figure 14’—Lateral view of neonate females of: A. *Centrophorus granulosus* (CSIRO H 6292–13, 392 mm TL); B. *Centrophorus squamosus* (CSIRO H 6292–14, 407 mm TL).

- The images relating to this figure were used above the ‘Figure 13’ caption by accident. Thus the image used in ‘Figure 13’ in White *et al.* (2013) should be linked with the ‘Figure 14’ caption.
- The image used above this Figure caption relates to ‘Figure 15’ and represents *Centrophorus uyato* and not *C. granulosus.* This image is duplicated in ‘Figure 15’ where it is correctly linked to the caption.

Comparative material

All comparative material examined in this study is listed in White *et al.* (2013) in the material examined section for *C. granulosus* and in the comparative material section.

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Redescription of *Chimaera ogilbyi* (Chimaeriformes; Chimaeridae) from the Indo-Australian region

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Abstract

An integrated taxonomic approach, combining both morphological and molecular data, was adopted to investigate the *Hydrolagus lemures-ogilbyi* group in the Indo-Australian region. Single mitochondrial markers (CO1 and NADH2) provided evidence supporting the separation of four distinct species in this group. However, detailed morphological data collected from specimens from across their range failed to find any consistent differences, and many features previously considered to be diagnostic were found to be variable. Nuclear DNA data also failed to support the differences found with the single mitochondrial markers and, together with the morphological data, supported the hypothesis that only a single species in this group is present in the Indo-Australian region. In addition, the results failed to support the current generic placement of this group in *Hydrolagus*, suggesting they belong to the genus *Chimaera* with doubt over the validity of *Hydrolagus* as a valid genus. The oldest available name for this group is *Chimaera ogilbyi* and a redescription is provided. This species occurs throughout Australia, eastern Indonesia (Java, Bali, and Lombok) and northern Papua New Guinea.

Key words: Chimaeridae, integrated taxonomy, morphology, genetics, discordance, *Chimaera ogilbyi*

Introduction

The family Chimaeridae (shortnose chimaeras) is represented by 38 species across two genera, *Chimaera* Linnaeus, 1758 (16 species) and *Hydrolagus* Gill, 1862 (22 species) (Weigmann, 2016). Gill (1862) proposed the second genus, *Hydrolagus*, based on the absence of an anal fin and the triple division of the claspers in adult males. However, the robustness of the anal fin character has been questioned (Didier *et al*., 2008). Ten species are known from Australian waters of which only two were described prior to 2002: *Chimaera argiloba* Last, White & Pogonoski, 2008, *Chimaera fulva* Didier, Last & White, 2008, *Chimaera macrospina* Didier, Last & White, 2008, *Chimaera obscura* Didier, Last & White, 2008, *Chimaera lignaria* Didier, 2002, *Hydrolagus lemures* (Whitley, 1939), *Hydrolagus homonycteris* Didier, 2008, *Hydrolagus ogilbyi* (Waite, 1898), *Hydrolagus marmoratus* Didier, 2008, and *Hydrolagus trolli* Didier & Séret, 2002.

The species described since 2002 have been described in detail, but the two oldest species, *Hydrolagus lemures* and *Hydrolagus ogilbyi*, have received little attention and separation of these species has been problematic and are regularly confused (Last & Stevens, 2009). Morphologically, there is little difference between the two species. *Hydrolagus ogilbyi* is considered to have a more uniformly brownish to bluish black first dorsal fin (vs. with a black posterior margin in *H. lemures*), a broader dark margin on the second dorsal fin, and their juveniles with dark brown stripes on sides (vs. silvery or white in *H. lemures*) (Last & Stevens, 2009). However, when additional specimens are examined, these characteristics do not hold up and appear to be quite variable. Partitioning of the

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species has often become based more on geographical range, with *H. ogilbyi* currently considered to be constrained to the east coast of Australia, and *H. lemures* more widespread in Australia. Both species are presently considered endemic to Australian waters (Last & Stevens, 2009).

Chimaeroid taxonomy is complex, and confusion with species identification is not unique to these species. Chimaeras are morphologically conservative, and many overlap in distribution and depth range. Species descriptions are often based on only a few specimens, with very little data on intraspecific variation available (Kemper *et al*., 2014). Molecular identification has become an important tool for species delineation in situations where no distinguishing morphological characteristics can be found.

During market surveys of Indonesian fish landing sites between 2001 and 2012, a number of chimaerid specimens were collected. Three species were identified, *Chimaera* cf. sp. E [*sensu* Last & Stevens, 1994], *Hydrolagus* cf *lemures*, and *Hydrolagus* sp. 1 (White *et al.*, 2006). *Chimaera* sp. E of Last & Stevens (1994) was subsequently described as *C. argiloba*, and in that description, the authors state that the Indonesian specimens are probably conspecific with this species. *Hydrolagus* sp. 1 and *Chimaera* cf sp. E were very similar in morphology, but were separated based purely on the absence and presence of an anal fin, respectively. Subsequent DNA barcoding revealed that these two species had identical CO1 sequences, suggesting they were likely conspecific despite the anal fin absence in one specimen. Alternatively, these results could be a reflection of introgression which has not been examined in detail in this group. DNA barcoding of the *H.* cf *lemures* specimens supported them being closest to *H. lemures* from Australia but with possibly significant sequence divergence. Thus, it was considered that this species may represent an undescribed species.

A deepwater trawl survey off Papua New Guinea in 2012 using the RV *Alis* (PAPUA NIUGINI Expedition, Samadi *et al.*, 2014) collected three chimaerid specimens. These represent the first records of the Order Chimaeriformes in Papua New Guinean waters. Two of three specimens possessed the distinctive wavy lateral line of the *lemures-ogilbyi* group and were placed tentatively into this group pending further examination.

In this paper, the *H. lemures-ogilbyi* group is examined in detail using both morphological and molecular data. A lectotype is designated for *H. ogilbyi* (AMS I 3736). Discordance between morphological and molecular data is discussed and a revised account of this group is provided.

Materials and methods

Morphological data. Measurements were taken directly (point to point) using digital calipers or measuring board, following Compagno *et al*. (1990) and Didier (2002). A total of 43 measurements were taken: total length (TL); precaudal length (PCL); body length (BDL); snout-vent length (SVL); trunk length (TRL); pre-second dorsal length (PD2); pre-first dorsal length (PD1); preorbital length (POB); preoral length (POR); prenarial length (PRN); prepectoral length (PP1); prepelvic length (PP2); second dorsal-fin base length (D2B); anterior second dorsal fin, maximum height (D2AH); posterior second dorsal fin, maximum height (D2PH); first dorsal anterior margin (D1A); first dorsal-fin base length (D1B); first dorsal-fin height (D1H); first dorsal-fin spine length (DSA); first dorsal fin, maximum height (D1H); dorsal caudal-fin lobe length (CDM); dorsal caudal-fin lobe height (CDH); total caudal fin length including filament (CTL); ventral caudal-fin lobe length (CVM); ventral caudal-fin lobe height (CVH); head length (HDL); interorbital width (INO); mouth width (MOW); gill slit height (GS1); pectoral-fin anterior margin (P1A); pectoral-fin length (P1L); pelvic-fin anterior margin (P2A); interdorsal space (IDS); dorsal–caudal space (DCS); posterior base of pectoral fin to anterior base of pelvic fin (PPS); anterior edge of first dorsal fin base to anterior edge of pectoral fin base (D1P1); anterior edge of base of first dorsal fin to anterior edge of pelvic base (D1P2); anterior edge of second dorsal fin base to anterior edge of pectoral fin base (D2P1); anterior edge of second dorsal fin base to anterior edge of pelvic fin base (D2P2); eye length (EYL); eye height (EYH); total length of claspers from pelvic fin base to tip (CLT); length of medial branch of clasper from fork to tip (CLM); length of lateral branch of clasper from fork to tip (CLL).

Emphasis was placed on measuring specimens which had accompanying genetic data (CO1 and/or NADH2 sequences) to allow for direct comparison between the datasets. Based on preliminary genetic information, four OTU's (operational taxonomic units) were identified, *H. lemures* (Western Australia only), *H. ogilbyi* (Australia-wide), *H.* cf. *lemures* (Indonesia), and *H.* sp. PNG (Papua New Guinea). The following specimens from each of these OTU's were measured in full: for *H. lemures*, the holotype (AMS E 3591), paratype (AMS E 3592), and 10 other specimens (CSIRO H 2555-14, CSIRO H 2590-13, CSIRO H 4031-03, CSIRO H 6410-04, CSIRO H 6570-01, CSIRO H 6571-01, CSIRO H 6571-13, CSIRO H 6574-19, CSIRO H 6579-13, and CSIRO H 6581-26); for *H. ogilbyi*, the lectotype (AMS I 3736) and 18 other specimens (CSIRO H 2575-24, CSIRO H 2575-25, CSIRO H 2590-14, CSIRO H 4682-05, CSIRO H 5322-02, CSIRO H 5942-01, CSIRO H 5943-01, CSIRO H 7043-07, CSIRO H 7048-02, CSIRO H 7060-05, CSIRO H 7061-08, CSIRO H 7061-09, CSIRO H 7063-01, CSIRO H 7065-03, CSIRO H 7569-01, CSIRO H 7569-02, CSIRO H 8058-01, and CSIRO H 8058-02); for *H.* cf. lemures, 7 specimens (CSIRO H 5691-02, CSIRO H 5860-15, CSIRO H 5860-16, CSIRO H 5889-32, CSIRO H 5889-33, CSIRO H 5889-34, and CSIRO H 7774-02); and for *H.* sp. PNG, two specimens (NTUM 10332 and NTUM 10333). Morphometric data is presented in Table 1 for the four OTU's as well as an overall range for all specimens, with measurements expressed as a proportion of body length. Where differences were found between *H. lemures* and *H. ogilbyi*, measurements were taken from additional specimens to determine whether these differences were reliable.

Specimens examined, including types, are deposited in the Australian Museum, Sydney (AMS); Australian National Fish Collection, Hobart (CSIRO); Museum Zoologicum Bogoriense, Cibinong (MZB); Museum Victoria, Victoria (NMV); and National Taiwan University Museum, Taipei (NTUM).

Molecular analyses. CO1. Specimens of *H. lemures*, *H. ogilbyi* and *H.* cf *lemures* were sequenced for the cytochrome c oxidase I (CO1) DNA barcoding fragment (~650 base pairs) (see Hebert *et al*., 2003; Ward *et al*., 2005; Holmes *et al*., 2009). These sequences were compared with corresponding sequences for the closest species available, *Chimaera argiloba*, with a *Chimaera fulva* sequence used as an outgroup to the *lemures-ogilbyi* group. Note, *Chimaera phantasma* sequences were not available on BOLD for comparison. DNA extractions, PCR reactions, and sequencing followed the protocols in Holmes *et al*. (2009). Kimura two-parameter pairwise genetic distances were estimated for the CO1 datasets and subjected to neighbour-joining (Saitou & Nei, 1987). GenBank accession numbers of all CO1 sequences are provided in the associated figures and are provided in parentheses in the materials examined and comparative material sections.

NADH2. Specimens of *H. lemures*, *H. ogilbyi*, *H.* cf *lemures*, and *H.* sp. PNG were sequenced for the NADH2 marker and compared with the closest species, *C. argiloba* and *C. phantasma*. 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 Kimura two-parameter distance. The tree was generated using the software package PAUP*4.0 version a148 and is presented in Fig. 2.

Results and discussion

Molecular analyses. CO1. The 15 *Hydrolagus lemures* sequences from Western Australian specimens grouped closest to *Hydrolagus* cf. *lemures* from Indonesia (Fig. 1). These two OTU's had an average sequence divergence of

3.2% (minimum inter-OTU divergence of 2.9%) based on these sequences. These two OTU's, in turn, grouped closest to the 24 *Hydrolagus ogilbyi* sequences from across Australia (Western Australia, Victoria, Tasmania, New South Wales, and Queensland). The average (and minimum) sequence divergences between *H. ogilbyi* and *H. lemures* and *H. ogilbyi* and *H.* cf. *lemures* are 6.9 (6.1%) and 6.7% (6.3%). These three OTU's form a discrete grouping which, in turn, is closest to *Chimaera argiloba* (average divergence 9.9%, minimum divergence 9.1%). These CO1 results provide strong evidence for the separation of these three OTU's as distinct taxa.

Interestingly, two specimens that were originally identified as *H. lemures* (CSIRO H 2590-13, Genbank accession EU398878 and CSIRO H 2590-14, Genbank accession EU398880) separated out into the two Australian OTU's, suggesting they are different species. This casted early doubts over the utility of barcoding results since subsequent examination of the two specimens could not find any morphological differences. Also, these specimens were both taken in the same trawl shot off Western Australia.

NADH2. The NJ analysis of the NADH2 locus recovered eight clades (Fig. 2). Specimens of *H. ogilbyi*, *H. lemures*, *H.* cf *lemures*, and *Hydrolagus* sp. were all placed into their own respective clades. Specimens identified as *Chimaera phantasma* fall into two separate lineages, while the two specimens of *C.* cf *phantasma* from the Philippines cluster in their own distinct lineage. *Chimaera argiloba* sequences from Australia and Indonesia also group together. Two specimens originally identified as *H. lemures* in the field (GN10964 and GN15671), fall within the *H. ogilbyi* clade. While neighbour joining analyses should not be taken to reflect accurate phylogenetic relationships, they can be useful in identifying discrete lineages. Thus, the following OTU-level relationships should be interpreted cautiously. The three clades of *C. phantasma* group together, with three *C. phantasma* specimens from Taiwan more closely grouped to *C.* cf *phantasma* from Philippines. The *H. ogilbyi* clade, which contains specimens from different Australian regions, clusters with the *C. phantasma* clades. *Hydrolagus* sp. from PNG is recovered as sister to the *H. ogilbyi*-*C. phantasma* grouping, while *H. lemures* specimens group most closely with *H.* cf *lemures* from Indonesia. *Chimaera argiloba* specimens in this analysis are placed basally with respect to the other clades.

While there is substantial mitochondrial sequence divergence among terminal clades, divergence among deeper splits is minimal. Within clades, there is little sequence divergence. Eight divergent clades might suggest eight distinct species. However, a molecular phylogeny for the Chimaeriformes based on both nuclear and mitochondrial markers (JK in prep), shows strong discordance between the nuclear and mitochondrial signals, and importantly, shows no significant differences between the four OTU's examined in this study at nuclear loci. Detailed analyses of these data will be presented in future publications. Discordance between nuclear and mitochondrial signals have been previously reported for several species. Rabone *et al.* (2015) found that analyses of microsatellite data for triplefins (Tripterygiidae) in New Zealand exhibited far less structure than was seen in the counterpart mtDNA analyses, suggesting extensive gene flow.

The mitochondrial divergence seen among the morphologically similar *lemures*-*ogilbyi* complex might alternatively be a holdover of ancient population structure in the species. In this scenario, the ancestral range of the species could have been more widespread, leading to restricted gene flow and sequence divergence between regions, resulting in the four distinct mitochondrial clades observed. The four clades may subsequently have come back together, as one species. This pattern can be seen in the *H. ogilbyi* clade, which has a more widespread distribution around Australia. Similar patterns have been documented in another chondrichthyan, a deep-sea shark, *Centroselachus crepidater*, that inhabits the Atlantic and Indo-Pacific (Cunha *et al*., 2012). In this study, two divergent mitochondrial clades were recovered but exhibited no geographical structure. The authors concluded that an ancient vicariant event likely lead to the allopatric divergence of the two mitochondrial clades (Cunha *et al*., 2012). It is possible that the four clades of the *lemures*-*ogilbyi* complex are due to similar ancient allopatric divergence.

The focus of this paper is on the *lemures*-*ogilbyi* complex which includes the four OTU's. However, it must be mentioned that the tree topology shows the *C. phantasma* complex as closest to *H. ogilbyi*. The divergences among the *lemures*-*ogilbyi* complex are similar to the divergence between the *C. phantasma* complex and the other clades. This suggests that these three clades may also be part of the *lemures*-*ogilbyi* complex, and may represent another incidence of ancestral isolation followed by contemporary admixture. The same may be said for *C. argiloba*. Future work is needed to determine whether the clades revealed by the mitochondrial markers represent different species or haplotype variants in a single species.

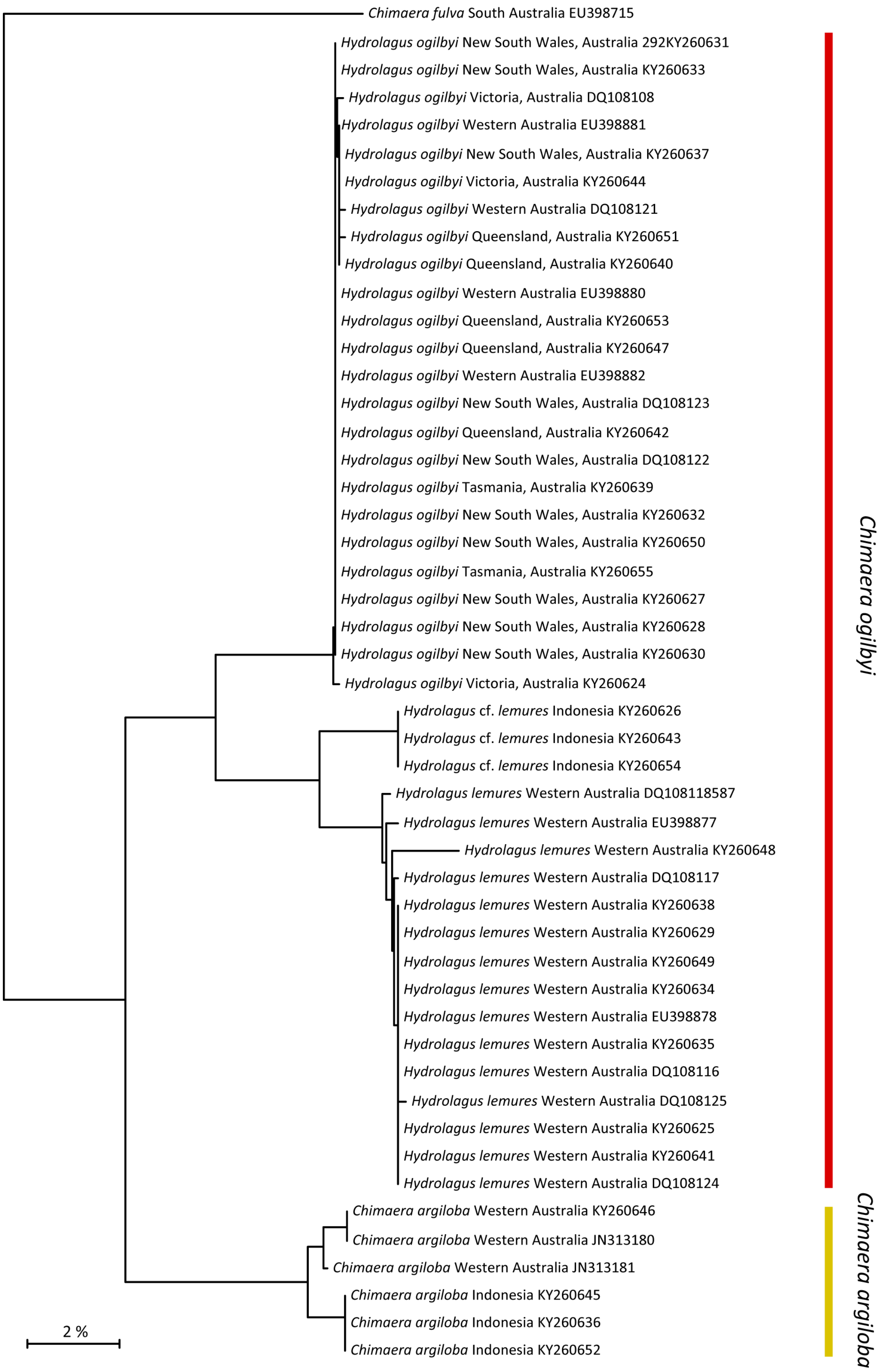

FIGURE 1. Neighbour-joining tree of nucleotide sequence divergence at the barcoding region of the COI using the Kimura two-parameter (K2P) distance generated by BOLD (Barcode of Life Database) for *Chimaera ogilbyi* and its closest congener, *Chimaera argiloba*. Individual sequences labelled with the OTU's used in this paper. Scale bar represents 2% K2P distance. GenBank accession numbers are listed.

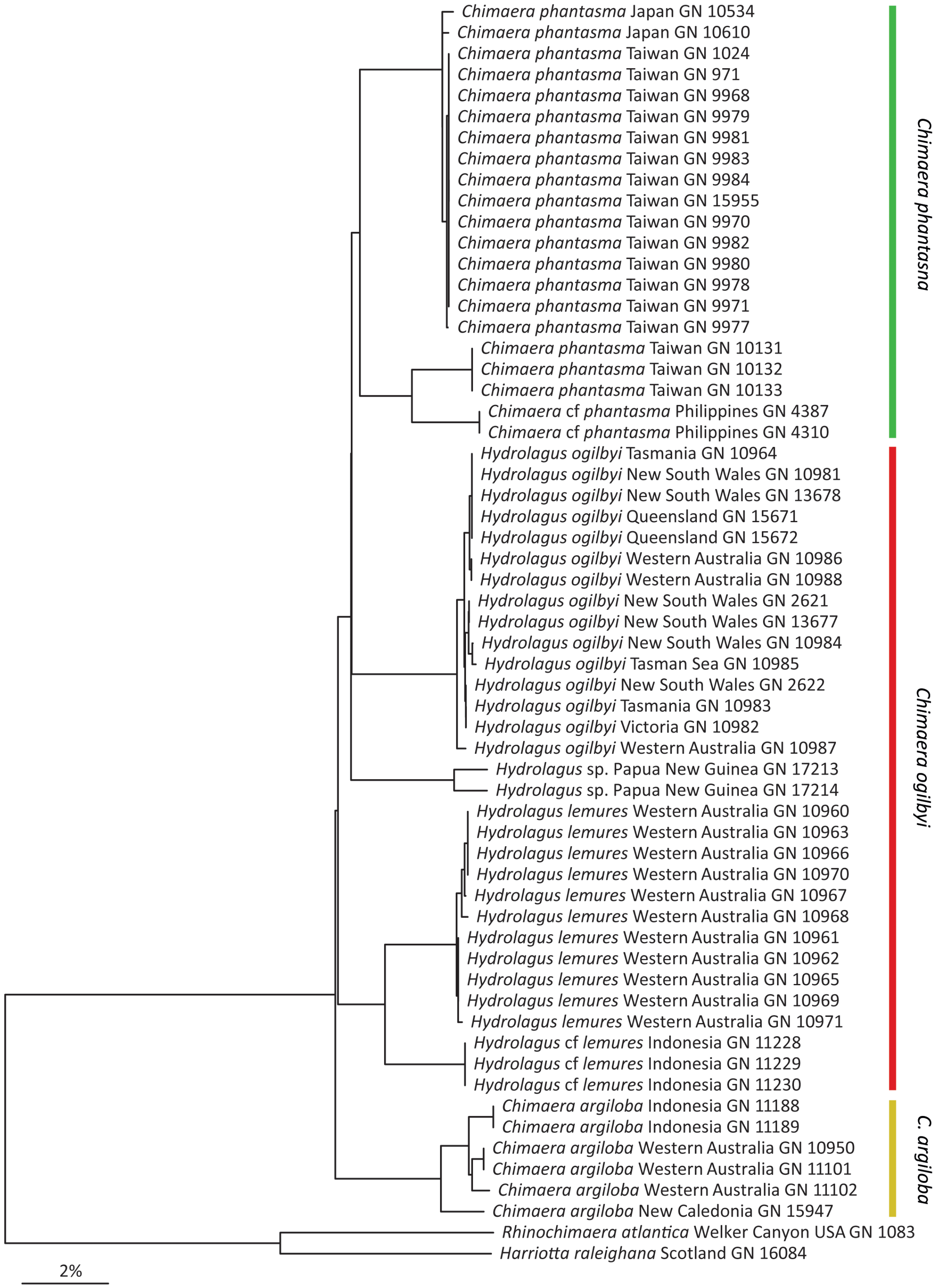

FIGURE 2. Neighbour-joining tree topology using Kimura 2 Parameter distance based on nucleotide sequence divergence in aligned nucleotide NADH2 sequences for *Chimaera ogilbyi* and closely related species. Outgroup is represented by *Rhinochimaera atlantica* and *Harriotta raleighana*. Sequence labels are based on operational taxonomic units defined in paper. GenBank accession numbers follow sequence labels. Scale bar represents 2% K2P distance.

Nuclear data. A full molecular phylogeny for the Chimaeriformes is currently in preparation by one of us (JK), which also includes extensive nuclear genetic data. Preliminary examination of these data show a strong discordance with the mitochondrial data and does not corroborate any of the differences seen between the four OTU's examined in the mitochondrial data.

Morphological data. Measuring preserved chimaeroid specimens is difficult due to several aspects of their morphology. The snout tips are quite gelatinous and after preservation are more restricted than when fresh. The caudal filament is also regularly damaged. Thus, total length is not a very useful character for this group. Body length (gill opening to the dorsal caudal-fin origin) is considered the best standard length measurement to use for chimaeroids (Inada & Garrick, 1979; Compagno *et al.*, 1990) to overcome these issues. The issue still remains that characters around the snout, e.g. preorbital, and caudal fin (e.g. caudal filament length) are difficult to capture with morphometric measurements.

Specimens assigned to the Australian OTU's, *H. lemures* and *H. ogilbyi*, were very similar in morphology and could not be separated based on external morphology. Furthermore, all of the measurements taken from the two OTU's overlapped (Table 1). Characters that were previously thought to separate these two species are: first dorsal fin uniformly brownish or bluish black in *H. ogilbyi* (vs. with a black posterior margin in *H. lemures*), dark margin of second dorsal fin broader than a third of fin height (vs. narrower than a third of fin height), and juveniles with dark brown stripes (vs. silvery or white) (Last & Stevens, 2009). When all measured specimens were examined, all were shown to have considerable variation in these characters. The first dorsal fin varied from uniformly dark to paler with a dark posterior margin, although mostly it was uniformly dark. The dark margin of the second dorsal varied greatly, from more than half of fin height in some individuals to very narrow in other specimens. Juveniles also were mostly banded, sometimes strongly, and only weakly banded in other individuals.

Specimens assigned to *H. lemures* were also very similar to *H.* cf *lemures* from Indonesia, but were found to differ slightly in the following measurements: pre-first dorsal length 32.9–36.1 vs. 29.1–32.7% BDL; prepelvic length 64.3–69.2 vs. 58.6–62.6% BDL; pectoral-fin length 25.2–28.6 vs. 22.8–24.7% BDL. There was no overlapping distances, however, between specimens of *H. ogilbyi* and *H.* cf *lemures* (Table 1). An additional 34 specimens of Australian *lemures-ogilbyi* were measured to determine what intraspecific variation may occur in the above characters that differ between *H. lemures* and *H.* cf *lemures.* In each case, the additional specimens expanded the ranges for these measurements: pre-second dorsal length 54.0–63.0% BDL (mean 58.9% BDL), prepelvic length 57.4–72.8% BDL (mean 65.2% BDL), and pectoral-fin length 22.3–29.5% BDL (mean 26.1% BDL).

Similarly, the two juvenile specimens of *H.* sp. PNG did not differ in any measurements with similar sized specimens from Australia. A number of differences were apparent between the similarly sized holotype of *H. lemures* from southwestern Australia and the two PNG specimens, e.g. snout-vent length (60.6 vs. 64.3–68.0% BDL), prepectoral length (36.9 vs. 34.8–35.0% BDL), pectoral-fin length (27.5 vs. 31.3–31.4% BDL), pelvic-fin anterior margin length (23.7 vs. 18.1–20.7% BDL), second dorsal-fin origin to pectoral-fin origin (33.5 vs. 28.0–29.9% BDL), eye length (9.3 vs. 10.9–13.2% BDL). Most of the above measurements overlap, however, when compared to the total range for the *H. lemures* OTU. The remaining measurements, i.e. eye length and pectoral-fin length, still differ between the PNG specimens and the measured Australian OTU's. When compared with five Australian specimens (CSIRO H 2031-01, CSIRO H 648-05, and CSIRO H 2591-03) of similar size (98–123 mm BDL), there was no difference in these measurements, i.e. eye length 10.9–13.2% BDL in the PNG specimens (vs. 10.3–14.6% BDL in Australian specimens), and pectoral-fin length 31.3–31.4% BDL (vs. 28.7–39.9% BDL). Thus, the morphometric differences reflect ontogenetic differences, with juveniles having proportionally larger eyes and pectoral fins.

Taxonomic conclusions. The mitochondrial molecular data (NADH2 and CO1) provide strong evidence for separation of four distinct OTU's in the *lemures-ogilbyi* group, i.e. *H. lemures* from Western Australia; *H. ogilbyi* from Australia (widespread); *H.* cf *lemures* from southern Indonesia; and *H.* sp. PNG from northern Papua New Guinea. However, nuclear DNA data does not support this and instead supports the hypothesis that it is a single species, and thus the four OTU's are not supported as being different species. Discordance between nuclear and mitochondrial DNA analyses has been previously reported for fish. Rabone *et al.* (2015) found that analyses of microsatellite data for triplefins (Tripterygiidae) in New Zealand revealed far less structure than in the mtDNA data, suggesting extensive gene flow over tens of kilometres. Similar discordance has been recorded in other marine fishes (e.g. Sala-Bozano *et al.*, 2009; DiBattista *et al.*, 2012).

The detailed morphological data and examination of a large number of specimens also failed to find any significant differences between the four OTU's suggested by the mitochondrial DNA data. Since the nuclear DNA data and morphological data do not support the hypothesis of there being four distinct OTU's within the *lemures-ogilbyi* group, despite mitochondrial DNA support, it is herein suggested that this group is represented by only a single species, with *H. ogilbyi* the oldest available name. *Hydrolagus lemures* is placed into the synonymy of *H. ogilbyi* and one of the syntypes of *H. ogilbyi* (AMS I.3736) is designated as a lectotype. A full redescription of this species is presented below.

The presence or absence of an anal fin is not a reliable character within the Chimaeridae, evidenced by specimens of one species, *C. argiloba*, which have been found to either have or lack an anal fin. A full taxonomic revision is required for this family, but it is likely to reveal only a single genus is valid. In this case of the *lemures-ogilbyi* group, molecular data places its members close to *C. argiloba* and *C. phantasma*. Based on a lack of morphological differences and insights from the molecular data, *H. ogilbyi* is herein placed back into the genus *Chimaera*, pending a full revision of the Chimaeridae.

Taxonomic account

Chimaera ogilbyi Waite, 1898

Ogilby's Chimaera
Table 1; Figs 3 –7

Chimaera ogilbyi Waite, 1898: 56, pl. 11 (off Sydney, New South Wales, Australia; syntypes AMS I.3732, 3734, 3736, 3737)
Hydrolagus (Psychichthys) waitei Fowler, 1907: 419, Fig. 1 (Victoria, Australia; holotype ANSP 33119, dry, poor condition)
Chimaera waitei—Garman, 1911: 91 (Victoria, Australia)
Phasmichthys lemures Whitley, 1939: 261, pl. 22 (Fig. 2) (Great Australian Bight, off Eucla, Western Australia; holotype AMS E.3591, paratype AMS E.3592)
Hydrolagus ogilbyi—Bigelow & Schroeder, 1953: 534, 537 (southern Australia, Tasmania)
Hydrolagus lemures—Bigelow & Schroeder, 1953: 534
Hydrolagus cf *lemures*—White *et al.*, 2006: 310, fig. (Indonesia)

Lectotype. AMS I.3736, female 500 mm BDL, off Port Hacking, New South Wales, Australia, 34°04.8' S, 151°12' E, 22–38 fathoms (40–70 m) depth, 10 Mar 1898.

Paralectotypes. (2 specimens) AMS I.3732, female, AMS I.3734, female (tail damaged, similar size to lectotype), off Botany Bay, New South Wales, Australia, 34°01.8' S, 151°15' E, 50–52 fathoms (91–95 m) depth, 11 Mar 1898.

Other specimens: New South Wales (20 specimens): CSIRO CA 114, female 647 mm TL, 258 mm BDL, east northeast of Sydney, 33°33' S, 151°57' E, 265–305 m depth, 2 Feb 1977; CSIRO CA 3226, adolescent male 722 mm TL, 324 mm BDL, CSIRO CA 3227, female 709 mm TL, 345 mm BDL, northeast of Port Stephens, 32°23' S, 152°59' E, 278 m depth, 30 Jan 1982; CSIRO H 2692-01, female 807 mm TL, 490 mm BDL, east of Yamba, 29°24' S, 153°46' E, 153–175 m depth, 22 May 1991; CSIRO H 2967-01, adult male 618 mm TL, 385 mm BDL, east of Coffs Harbour, 30°21' S, 153°24' E, 139–154 m depth, 11 Mar 1992; CSIRO H 3586-01, female 722 mm TL, 348 mm BDL, east of Wollongong, 34°25' S, 151°11' E, 141–145 m depth, 31 Aug 1993; CSIRO H 4472-03, female 896 mm TL, 402 mm BDL, CSIRO H 4472-04, female 839 mm TL, 365 mm BDL, northeast of Batemans Bay, 35°40' S, 150°41' E, 541–585 m depth, 4 Dec 1996; CSIRO H 4682-05 (tissue accession GN10981; Genbank accession DQ108122), male 675 mm TL, 318 mm BDL, east of Broken Bay, 33°35' S, 151°58' E, 324–329 m depth, 10 Sep 1997; CSIRO H 4760-01, juvenile male 631 mm TL, 273 mm BDL, east of Eden, 37°12' S, 150°22' E, 373–401 m depth, 29 Oct 1996; CSIRO H 4704-03, adolescent male 658 mm TL, 325 mm BDL, east of Sydney, 33°40' S, 151°53' E, 326–331 m depth, 24 Sep 1996; CSIRO H 7029-02 (Genbank accession KY260632), adult male 906 mm TL, 429 mm BDL, east of Wooli, 29°58.72' S, 153°38.98' E, 500 m depth, 5 Sep 2009; CSIRO H 7041-09, female 682 mm TL, 324 mm BDL, east of Port Stephens, 32°32' S, 152°54' E, 510 m depth, 9 Sep 2009; CSIRO H 7043-07 (tissue accession GN13677; Genbank accession KY260650), adult male 717 mm TL, 432 mm BDL, east of Ballina, 28°59.87' S, 153°53.20' E, 440 m depth, 3 Sep 2009; CSIRO H 7048-02 (tissue accession GN13678; Genbank accession KY260637), adult male 822 mm TL, 433 mm BDL, east of Tweed Heads, 28°17.64' S, 153°53.54' E, 455 m depth, 2 Sep 2009; CSIRO H 7053-09 (Genbank accession KY260631), female 691 mm

TL, 374 mm BDL, CSIRO H 7053-10 (Genbank accession KY260633), adult male 736 mm TL, 408 mm BDL, east of Terrigal, 33°21’ S, 152°11’ E, 560 m depth, 14 Sep 2009; CSIRO H 7063-01 (tissue accession GN10984; Genbank accession KY260628), female 908 mm TL, 439 mm BDL, east of Jervis Bay, 35°12’ S, 150°59’ E, 385–520 m depth, 21 Sep 2009; CSIRO H 8058-01 (Genbank accession KY260627), adult male 897 mm TL, 432 mm BDL, east of Sydney, 34°03.16’ S, 151°36.86’ E, 450 m depth, 16 Sep 2009; CSIRO H 8058-02 (Genbank accession KY260630), adult male 884 mm TL, 450 mm BDL, Taupo Seamount, 33°05’ S, 156°16’ E, 525 m depth, 11 Sep 2009; not retained (Genbank accession DQ108121), east of Ulladulla, 33°25’ S, 151°11’ E, 141 m depth, 3 Nov 1994; not retained (Genbank accession DQ108123), east of Broken Bay, 33°32’ S, 152°00’ E, 329 m depth, 26 Sep 1996.

FIGURE 3. Lateral view of the lectotype (AMS I.3736) of *Chimaera ogilbyi* (female 500 mm BDL). Photo: Mark Allen © Australian Museum.

FIGURE 4. Lateral view of the holotype (AMS E.3591) of *Phasmichthys lemures* (female 212 mm BDL). Photo: Mark Allen © Australian Museum.

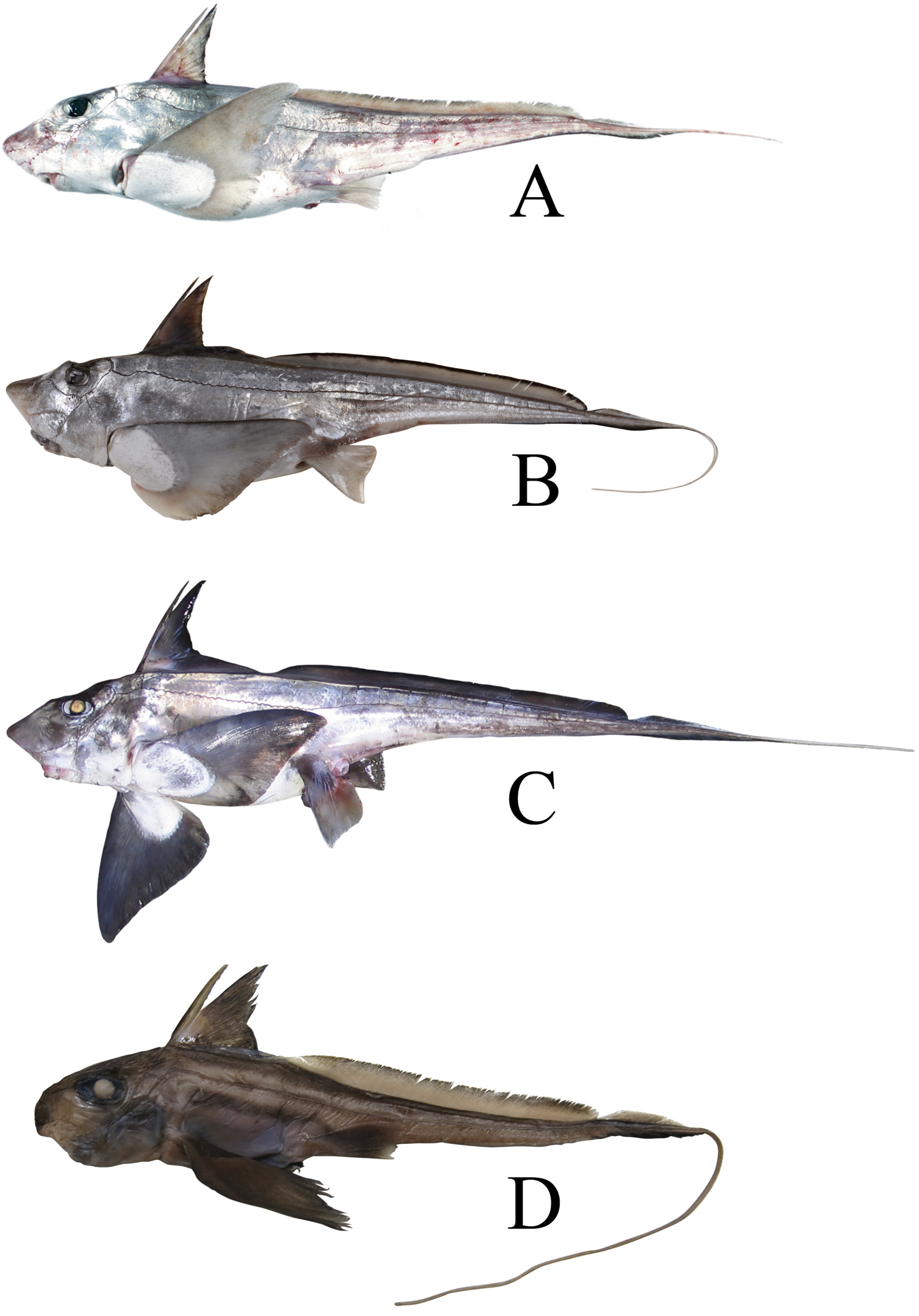

FIGURE 5. Lateral view of the four OTU's of *Chimaera ogilbyi*: (A) *Hydrolagus lemures*; (B) *Hydrolagus ogilbyi* (CSIRO H 7060-05, female 479 mm BDL); (C) *Hydrolagus* cf *lemures* (CSIRO H 7774-02, female 483 mm BDL); and (D) *Hydrolagus* sp. PNG (NTUM 10333, female 109 mm BDL).

Northern Territory (2 specimens): CSIRO CA 1262, juvenile male 351 mm TL, 165 mm BDL, CSIRO CA 1263, female 374 mm TL, 162 mm BDL, CSIRO CA 1264, female 166 mm TL, 83 mm BDL, north of Bathurst Island, Arafura Sea, 10°02' S, 130°03' E, 216 m depth, 8 Jul 1980.

South Australia (1 specimen): CSIRO H 2867-06, female 977 mm TL, 541 mm BDL, Great Australian Bight, 33°25' S, 129°54' E, 490–514 m depth, 13 Mar 1992.

Queensland (14 specimens): CSIRO H 648-05, female 296 mm TL, 108 mm BDL, east of Townsville, 18°59.7' S, 149°28.7' E, 452–453 m depth, 26 Nov 1985; CSIRO H 713-4, adolescent male 716 mm TL, 314 mm BDL, south of Saumarez Reef, 22°34.5' S, 153°37.4' E, 314–319 m depth, 16 Nov 1985; CSIRO H 1167-03 (2 embryos), 155 and 235 mm TL, 67.5 and 83 mm BDL, west of Lihou Reef and Cays, Queensland Plateau, 17°02.1' S, 151°03.7' E, 696 m depth, 6 Dec 1985; CSIRO H 2278-1, female 728 mm TL, 308 mm BDL, east of Flinders Reefs, 17°32.8' S, 149°31.9' E, 500–504 m depth, 3 Dec 1985; CSIRO H 2279-1, female 496 mm TL, 234 mm BDL, east of Hinchinbrook Island, Queensland Trough, 17°59.1' S, 147°09.6' E, 400–402 m depth, 29 Nov 1985; CSIRO H 2280-1, juvenile male, 442 mm TL, 180 mm BDL, Townsville Trough, 18°59.7' S, 149°28.7' E, 452–453 m depth, 26 Nov 1985; CSIRO H 2281-1, juvenile male 511 mm TL, 221 mm BDL, Saumarez Reef, 22°35.3' S, 153°46.7' E, 345–350 m depth, 17 Nov 1985; CSIRO H 2282-1, female 619 mm TL, 258 mm BDL, Marian Plateau, 19°29.2' S, 150°16.5' E, 324–328 m depth, 15 Nov 1985; CSIRO H 2283-1, female 530 mm TL, 194 mm BDL, Saumarez Reef, 22°40' S, 154°05.5' E, 416–419 m depth, 17 Nov 1985; CSIRO H 7569-01 (tissue accession GN15671), female 571 mm TL, 301 mm BDL, CSIRO H 7569-02 (tissue accession GN15672), juvenile male 659 mm TL, 307.5 mm BDL, Swain Reefs, 23°46.40' S, 152°30.96' E, 227–234 m depth, 2 Jun 2011; CSIRO H 7720-01, 774 mm TL, 434 mm BDL, Swains Reef, 22°38.82' S, 152°49.32' E, 135 m depth, 8 Oct 2010; not retained (Genbank accession KY260640, KY260642, KY260647, KY260251, KY260253), Swains Reef, 23°39.34' S, 152°24.22' E, 234 m depth, 2 Jun 2011.

Tasmania (17 specimens): CSIRO T 442, female 753 mm TL, 333 mm BDL, off Tranmers Point, 42°38' S, 148°36' E, 480 m depth, 12 Oct 1994; CSIRO T 1377-02, adult male 1002 mm TL, 496 mm BDL, west of Strahan, 42°19' S, 144°46' E, 548 m depth, 19 Jan 1979; CSIRO H 789-02, embryo 122 mm TL, west of Mawson Bay, 41°02.3' S, 143°49.6' E, 820–872 m depth, 15 May 1986; CSIRO H 1908-1, juvenile male 512 mm TL, 206 mm BDL, CSIRO H 1908-2, female 565 mm TL, 292 mm BDL, CSIRO H 1908-3, juvenile male 602 mm TL, 255 mm BDL, CSIRO H 1908-5, female 541 mm TL, 205 mm BDL, CSIRO H 1908-6, female 462 mm TL, 181 mm BDL, CSIRO H 1908-7, juvenile male 488 mm TL, 203.5 mm BDL, CSIRO H 1908-8, female 528 mm TL, 194 mm BDL, CSIRO H 1908-9, female 455 mm TL, 179 mm BDL, CSIRO H 1908-10, juvenile male 468 mm TL, 172 mm BDL, west of King Island, 40°53.9' S, 143°44.5' E, 496–524 m depth, 31 Aug 1994; CSIRO H 3500-08, female 929 mm TL, 480 mm BDL, CSIRO H 3500-09, female 1005 mm TL, 457 mm BDL, east of Maria Island, Darcy's Patch, 42°42' S, 148°25.7' E, 510–520 m depth, 24 Jul 1993; CSIRO H 5942-01 (tissue accession GN10983), female 1037 mm TL, 602 mm BDL, CSIRO H 5943-01 (tissue accession GN10964), adult male 854 mm TL, 436 mm BDL, south of Tasman Peninsula, 43°35' S, 147°55' E, 460 m depth, 1 Sep 2002; CSIRO H 7061-08 (Genbank accession KY260655), adult male 904 mm TL, 436 mm BDL, CSIRO H 7061-09 (Genbank accession KY260639), female 810 mm TL, 388 mm BDL, east of Cape Barren Island, 40°14' S, 148°54' E, 580 m depth, 4 Oct 2009.

Victoria (6 specimens): CSIRO H 3522-07, female 622 mm TL, 232 mm BDL, south of Cape Everard, 38°11.9' S, 149°16.5' E, 230–240 m depth, 6 Aug 1993; CSIRO H 3546-02, adult male 758 mm TL, 412 mm BDL, south of Cape Everard, 38°12.4' S, 149°16.6' E, 240–250 m depth, 7 Aug 1993; CSIRO H 3690-08, female 464 mm TL, 173 mm BDL, south of Cape Everard, 38°11.8' S, 149°17.9' E, 258–296 m depth, 24 Feb 1994; CSIRO H 5322-02 (tissue accession GN10982; Genbank accession DQ108108), female 604 mm TL, 243.5 mm BDL, south-southeast of Cape Everard, Victoria, Australia, 38°09.98' S, 149°38.33' E, 225–295 m depth, 23 Apr 2000; CSIRO H 7060-05 (Genbank accession KY260624), female 928 mm TL, 479 mm BDL, south of Gabo Island, 37°48.30' S, 150°11.64' E, 510–515 m depth, 1 Oct 2009; CSIRO H 7065-03 (Genbank accession KY260644), female 955 mm TL, 481 mm BDL, south of Gabo Island, 37°48' S, 150°10' E, 550 m depth, 30 Sep 2009.

Western Australia (44 specimens): AMS E.3591 (holotype of *Phasmichthys lemures*), female 458 mm TL, 212 mm BDL, AMS E.3590 (paratype of *Phasmichthys lemures*), female 446 mm TL, 172 mm BDL, southwest of Eucla, Great Australian Bight, 126°45.5' E, 190–320 fathoms (348–585 m) depth, 4 Apr 1913; CSIRO CA 407, juvenile male 412 mm TL, 176 mm BDL, south of Mermaid Reef, 10 Jun 1978; CSIRO CA 3500, adult male 712 mm TL, 448 mm BDL, Great Australian Bight, 33°23.2' S, 127°34.3' E, 296–300 m depth, 2 Dec 1981; CSIRO

CA 367, adolescent male 583 mm TL, 282 mm BDL, north-northwest of Port Hedland, 18°24' S, 118°03' E, 258–270 m depth, 20 May 1978; CSIRO H 822-20, juvenile male 269 mm BDL, southwest of Shark Bay, 27°03' S, 112°40' E, 402 m depth, 27 Oct 1986; CSIRO H 1652-5, female 397 mm TL, 186 mm BDL, northwest of Port Hedland, 18°25' S, 117°48' E, 375 m depth, 21 Aug 1988; CSIRO H 2007-3, female 586 mm TL, 281 mm BDL, southwest of Rowley Shoals, 17°50' S, 118°33' E, 420 m depth, 12 Feb 1989; CSIRO H 2031-1 (3 specimens; 2 males, 1 female), 204–297 mm TL, 98–123 mm BDL, northeast of Mermaid Reef, 16°54' S, 120°25' E, 396 m depth, 12 Apr 1989; CSIRO H 2366-1, juvenile male 531 mm TL, 284.5 mm BDL, west of Geraldton, 28°48' S, 113°37' E, 457 m depth, 27 Dec 1989; CSIRO H 2555-14 (tissue accession GN10961; Genbank accession EU398877), female 614 mm TL, 302 mm BDL, west of Alison Point, 23°25.4' S, 113°03.9' E, 297–311 m depth, 26 Jan 1991; CSIRO H 2567-11, juvenile male 503 mm TL, 271 mm BDL, west of Dorre Island, 25°07.5' S, 112°09.3' E, 312 m depth, 28 Jan 1991; CSIRO H 2575-22, female 380 mm TL, CSIRO H 2575-23, female 637 mm TL, 300 mm BDL, CSIRO H 2575-24 (tissue accession GN10986; Genbank accession EU398882), male 604 mm TL, 342 mm BDL, CSIRO H 2575-25 (tissue accession GN10987; Genbank accession EU398881), female 821 mm TL, 430 mm BDL, west of Freycinet Estuary, 26°40.4' S, 112°32.7' E, 456–478 m depth, 30 Jan 1991; CSIRO H 2587-12, female 521 mm TL, 202 mm BDL, CSIRO H 2587-14, female 474 mm TL, 252 mm BDL, CSIRO H 2587-15, female 422 mm TL, 194 mm BDL, southwest of Shark Bay, 27°08.8' S, 112°44.8' E, 370–438 m depth, 2 Feb 1991; CSIRO H 2590-08, adult male 613 mm TL, 328 mm BDL, CSIRO H 2590-09, adult male 658 mm TL, 337 mm BDL, CSIRO H 2590-10, adult male 664 mm TL, 392 mm BDL, CSIRO H 2590-13 (tissue accession GN10962; Genbank accession EU398878), female 581 mm TL, 298 mm BDL, CSIRO H 2590-14 (tissue accession GN10988; Genbank accession EU398880), male 644 mm TL, 375 mm BDL, CSIRO H 2590-15, adult male 581 mm TL, 342 mm BDL, west of Leander Point, 29°15.8' S, 113°56.8' E, 320–325 m depth, 6 Feb 1991; CSIRO H 2591-03, female 277 mm TL, 121 mm BDL, CSIRO H 2591-12, female 481 mm TL, 211 mm BDL, west of Leander Point, 29°20.5' S, 113°58.3' E, 490–505 m depth, 6 Feb 1991; CSIRO H 2898-01, female 527 mm TL, 251 mm BDL, southwest of Rowley Shoals, 18°03.8' S, 118°16.3' E, 357–361 m depth, 26 Sep 1991; CSIRO H 3071-04, adult male 721 mm TL, 360 mm BDL, southwest of Geraldton, 29°14.2' S, 113°52.2' E, 556 m depth, 28 Jan 1989; CSIRO H 3222-04, adult male 631 mm TL, 325 mm BDL, north of Dampier Archipelago, 19°12.1' S, 116°25.2' E, 190–203 m depth, 11 Oct 1990; CSIRO H 4031-03 (tissue accession GN10963; Genbank accession DQ108124), female 671 mm TL, 380 mm BDL, CSIRO H 4031-84, adult male 607 mm TL, 340 mm BDL, CSIRO H 4031-85, adult male 656 mm TL, 356 mm BDL, north of Cape Lambert, 18°58.2' S, 117°12.1' E, 248–253 m depth, 30 Aug 1995; CSIRO H 4664-32, female 428 mm TL, 195 mm BDL, Rowley Shoals area, 17°38.9' S, 119°00.3' E, 310 m depth, 31 Aug 1997; CSIRO H 5188-10, female 527 mm TL, 267 mm BDL, CSIRO H 5188-11, female 487 mm TL, 194 mm BDL, CSIRO H 5188-12, female 409 mm TL, 193 mm BDL, north of Dampier Archipelago, 19°11.14' S, 116°16.05' E, 256 m depth, 27 Oct 1998; CSIRO H 5194-01, female 432 mm TL, 260 mm BDL, CSIRO H 5194-02, female 454 mm TL, 214 mm BDL, southeast of Rowley Shoals, 17°40.57' S, 119°40.57' E, 235 m depth, 9 Nov 1998; CSIRO H 5196-01, juvenile male 526 mm TL, 256 mm BDL, north of Dampier Archipelago, 19°12.30' S, 116°20.70' E, 220 m depth, 17 Oct 1998; CSIRO H 7242-01, female 144 mm TL, 72 mm BDL, west of Perth, 31°36.53' S, 114°58.86' E, 329–370 m depth, 19 Nov 2005; NMV 29673-004 (tissue accession GN10960; Genbank accession KY260648), northwest of Cape Leveque, 14°53.28' S, 121°36.12' E, 285 m depth, 27 Jun 2007.

Papua New Guinea (2 specimens): NTUM 10332 (tissue accession GN17213), juvenile male 362 mm TL, 129 mm BDL, NTUM 10333 (tissue accession GN17214), female 287 mm TL, 109 mm BDL, west of Kairiru Island, East Sepik Province, Papua New Guinea, 3°20'S, 143°28'E, 378–495 m depth, 19 Dec 2012.

Indonesia (16 specimens): CSIRO H 5691-02, female 800 mm TL, 521 mm BDL, Kedonganan fish market, Bali, Indonesia, 6 Jul 2001; CSIRO H 5860-15 (tissue accession GN11228; Genbank accession KY260654), adult male 599 mm TL, 419 mm BDL, CSIRO H 5860-16 (tissue accession GN11229; Genbank accession KY260643), adult male 658 mm TL, 406 mm BDL, Cilacap fishing port, Central Java, Indonesia, 22 Mar 2002; CSIRO H 5889-32, adult male 705 mm TL, 514 mm BDL, CSIRO H 5889-33, female 850 mm TL, 481 mm BDL, CSIRO H 5889-34, adult male 794 mm TL, 434 mm BDL, Kedonganan fish market, Bali, Indonesia, Jul 2002; MZB 15111, female 663 mm TL, MZB 15112 (tissue accession GN11230; Genbank accession KY260626), female 630 mm TL, Cilacap fishing port, Central Java, Indonesia, 22 Mar 2002; CSIRO H 6410-04 (tissue accession GN10965; Genbank accession KY260634), adult male 736 mm TL, 346 mm BDL, west of Shark Bay, Western Australia, 25°31.5' S, 112°11.2' E, 256–326 m depth, 22 Apr 2006; CSIRO H 6570-01 (tissue accession GN10966; Genbank accession KY260638), female 668 mm TL, 312 mm BDL, northwest of Cape Leveque, Western Australia, 14°59.42' S, 121°39.15' E, 187–206 m depth, 26 Jun 2007; CSIRO H 6571-12 (tissue accession GN10967; Genbank accession KY260629), adult male 639 mm TL, 318 mm BDL, CSIRO H 6571-13 (tissue accession GN10968; Genbank accession KY260641), adult male 610 mm TL, 327 mm BDL, northwest of Cape Leveque, Western Australia, 15°00.86' S, 121°38.13' E, 205–211 m depth, 26 Jun 2007; CSIRO H 6574-19 (tissue accession GN10969; Genbank accession KY260635), female 824 mm TL, 481 mm BDL, northwest of Cape Leveque, Western Australia, 14°50.81' S, 121°26.44' E, 382–401 m depth, 26 Jun 2007; CSIRO H 6579-13 (tissue accession GN10970; Genbank accession KY260649), adult male 645 mm TL, 353 mm BDL, northwest of Cape Leveque, Western Australia, 14°53.49' S, 121°33.91' E, 285–302 m depth, 27 Jun 2007; CSIRO H 6581-26 (tissue accession GN10971; Genbank accession KY260625), female 517 mm TL, 339 mm BDL, northwest of Cape Leveque, Western Australia, 14°58.69' S, 121°40.18' E, 191–202 m depth, 28 Jun 2007; CSIRO H 7774-02, female 907 mm TL, 483 mm BDL, Tanjung Luar fish market, Lombok, Indonesia, 14 Jul 2005; not retained (Genbank accessions DQ108124, DQ108125, DQ108117 and DQ108118), north of Cape Lambert, Western Australia, 18°57' S, 117°14' E, 248 m depth, 30 Aug 1995.

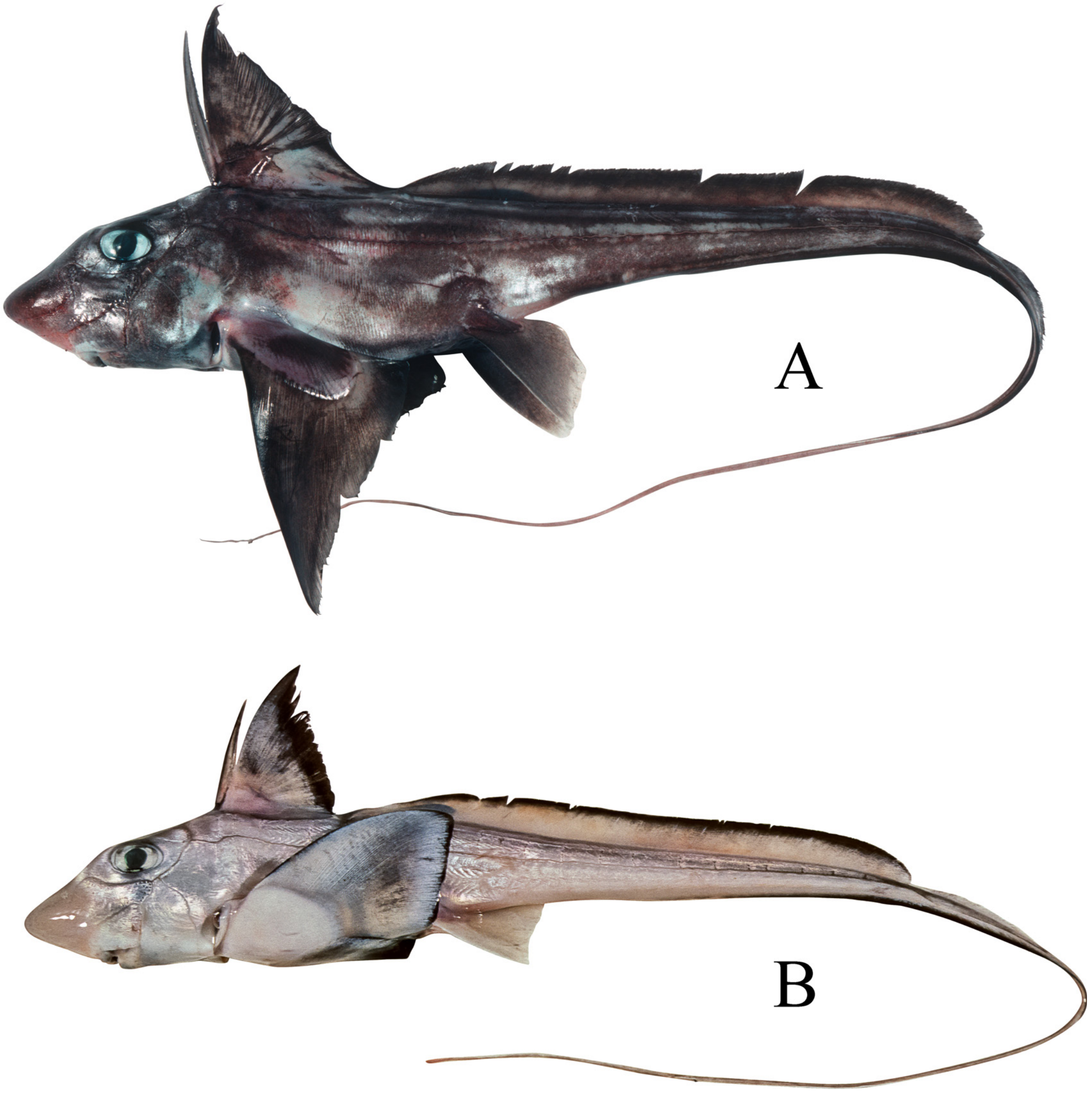

FIGURE 6. Lateral view of juvenile *Chimaera ogilbyi* from off Victoria highlighting colour variation in juveniles: (A) CSIRO H 3522-07, female 232 mm BDL; (B) CSIRO H 3690-08, female 173 mm BDL.

FIGURE 7. Lateral anterior view of *Chimaera ogilbyi* (CSIRO H 7060-05, female 479 mm BDL) highlighting the wavy lateral line, a distinguishing feature of this group.

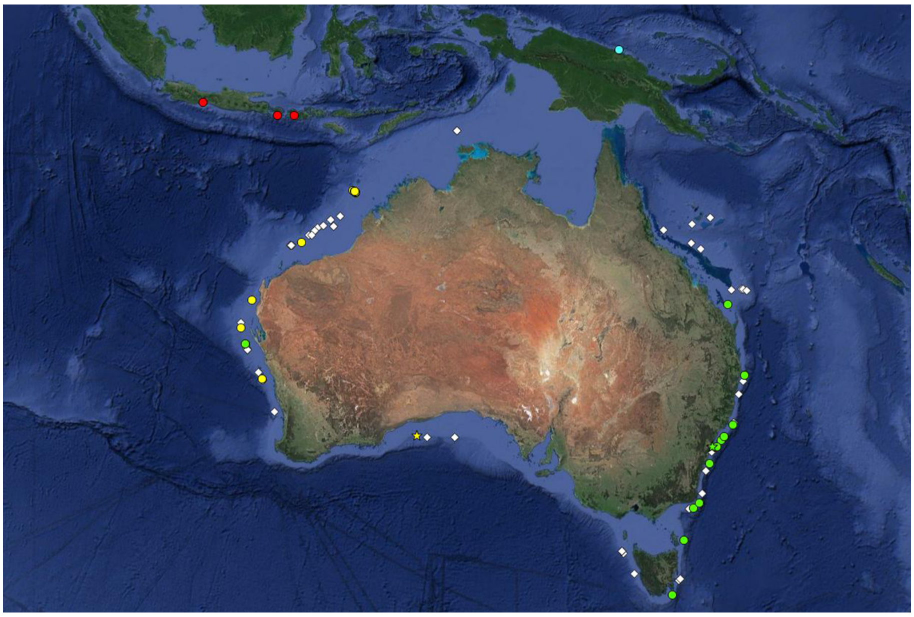

FIGURE 8. Map of the Indo-Australasian region showing the collection localities for the *Chimaera ogilbyi* specimens examined in this study. The coloured circles represent the specimens of the four OTU's which have supporting molecular data (yellow = *Hydrolagus lemures*; green = *Hydrolagus ogilbyi*; red = *Hydrolagus* cf *lemures*; blue = *Hydrolagus* sp. PNG). The yellow star and green star denote the primary types of *H. lemures* and *H. ogilbyi*, respectively. The white diamonds denote other specimens without supporting molecular data. (Image © NASA, TerraMetrics, Google Earth).

Diagnosis. *Chimaera ogilbyi* is distinguished from its congeners by the following combination of characters: no anal fin; lateral line with tight sinuous undulations; moderately long, narrow snout; relatively thick, non-deciduous skin; uniformly silvery greyish dorsally and laterally, paler ventrally; first dorsal fin mostly uniformly dark; second dorsal fin even height for whole length; preopercular and oral lateral line canals usually not sharing a common branch; dorsal spine long, usually longer than first dorsal fin; claspers slender, trifurcate, divided for more than half their length, not bulbous distally.

Description. Trunk very short and slightly compressed; deep groove on interdorsal space which partly receives depressed first dorsal fin; a low membrane connects soft elements of first and second dorsal fins; precaudal tail tapering evenly from pelvic fins to caudal base; anal insertion usually connected to ventral origin of caudal fin by a very low membrane. Skin smooth, leathery, relatively thick; usually intact, not deciduous. Dermal denticles absent.

Snout moderately long, preorbital snout 6.8 in lectotype (4.9–7.2 in other specimens) in body length; tip broadly pointed in lateral view, narrowly pointed in dorsoventral view. Postorbital head compressed. Eyes moderately large, horizontally oval, parallel to body axis (not directed anterodorsally); horizontal length 3.6 (3.4–4.7) in head length, vertical height 0.7 (0.5–0.7) times horizontal length; almost lateral on head (very slightly dorsolateral), without subocular ledges. Gill openings large, broadly separated, with prominent posterior flap which stands outwards from base of head and forms a short tube with rear end of gill cover. Gular flap between gill openings low. Nostrils, lips and mouth slightly expanded below ventral contour of snout. Nostrils with incurrent apertures close together on underside of snout located close to mouth, separated by a narrow septum; a deep blind dermal pocket between incurrent apertures; anterior nasal flaps extending posteriorly from incurrent apertures lateral to tooth plates of upper jaw and delimiting ventromedial surfaces of nasal cavities; nasal cavities delimited ventrolaterally by high, narrow, longitudinal vertical flap with a lobular distal end; excurrent apertures posterior to incurrent apertures and vertical flap, lateral to tooth plates of upper jaw, and inside pockets formed by large upper labial folds.

Mouth narrow, short; upper labial folds and furrows prominent; upper and lower furrows deep; lower lip with a deep pocket between mandibular tooth plates and its outer edge. Upper anterior tooth plates (vomerine tooth plates) small, incisor-like with 8–10 tritor rods visible (sometimes very weakly defined); posterior upper tooth plates (palatine) with 3 prominent tritor pads on wear surface, up to 8 prominent weak tritor rods on anterior margins; lower tooth plates (mandibular) incisor like with 3 or 4 tritor rods visible at the beak like tip, and more than 8 tritor rods visible posteriorly; upper anterior and lower tooth plates pale yellowish, upper posterior tooth plates pale greyish to yellowish.

Lateral line canal originating at fork between occipital and otic head canals at level of upper eye; notched anteriorly, then strongly elevated below first dorsal spine, extending posteriorly with tight sinuous undulations, becoming slightly wavy below anterior half of second dorsal-fin base, nearly straight posterior to second dorsal-fin mid base; line directed strongly posteroventrally to ventral margin of tail just posterior to origin of dorsal caudal lobe; line running along ventral margin of tail to caudal filament. Occipital canals short, only slightly longer than half eye length, directed anterodorsally, arched posteriorly, united to supratemporal and supraorbital canals about half distance between eye and dorsal-fin spine origin, near dorsal margin of head when viewed laterally. Supratemporal canals short, curved anteriorly, united at dorsal midline about half an eye length forward of dorsal-fin spine. Supraorbital canal extending anteriorly from supratemporal junction, curving slightly anteroventrally then becoming straight parallel to dorsal margin of eye, strongly notched slightly forward of eye, following profile of snout tip apically to join infraorbital canal. Otic canal longer than occipital canal, slightly longer than eye, united to infraorbital and origin of oral and preopercular canals below hind margin of eye. Preopercular and oral canals connected separately from infraorbital-otic junction, not sharing a common branch. Preopercular canal extending posteroventrally; terminating at about mid gill. Oral canal short, extending very slightly anteroventrally, divided into mandibular and angular canals below posterior 2/3 of eye. Mandibular canal extending slightly ventrolaterally, almost straight, joined to post-oral pores near mouth. Angular canal directed slightly anteroventrally, with prominent sensory pores, divided into nasal and subrostral canals near ventral margin of snout when viewed laterally; nasal canals strongly arched ventrally, then directed anterodorsally to unite on midline of snout slightly more than a nostril length from nostril; subrostral canal parallel to anterior portion of nasal canal. Infraorbital canal long, from otic junction following ventral contour of eye; forming a prominent S-shaped, double loop forward of eye; united to supraorbital canal close to snout tip near ventral midline of snout. Ampulla pores, not particularly numerous, present anterior to occipital and mandibular canals, at angle of infraorbital and oral canals, below upper margin of infraorbital canal, and concentrated on snout tip.

Dorsal-fin spine long, mostly straight, about subequal (slightly taller or slightly shorter in some specimens) to first dorsal-fin anterior margin; spine length 1.2 (1.1–1.4) in head length, (0.9–1.4) times first dorsal fin height; origin over pectoral-fin origin; anterior margin of spine forming a very narrow keel, not serrated; upper half of posterior margin of spine finely serrated. Soft portion of first dorsal fin with a relatively short base, subequal to snout length; posterior margin of fin moderately concave.

Second dorsal long-based, margin not incised centrally, mostly uniform in height, length of longest elements about two thirds eye length, base length 73.4 (69.7–79.1)% BDL; origin posterior of midpoint of depressed dorsal-fin spine; united to upper lobe of caudal fin by a low membrane.

Pectoral fins very long, broad, not falcate; anterior margin moderately convex distally; apex narrowly pointed to narrowly rounded; posterior margin almost straight to weakly concave; inner margin, free-rear tip and ventral portion of posterior margin broadly-rounded; anterior margin 35.8–48.5% BDL; apex when laid adpressed to body usually extending well posterior to insertion of pelvic fin. Pelvic fin large, broadly triangular; anterior margin convex; apex angular; posterior margin, free rear tip and inner margin broadly convex.

Frontal tenaculum of adult male with a relatively short, broad neck (about equal to nostril opening), and a prominent distal knob; distal knob with 8 longitudinal rows of up to 8 large, pointed, relatively slender, posteriorly directed, unicuspidate spines on its sides and ventral surface. Pelvic claspers of adult males large, broad, extending well posterior to distal edge of the pelvic fins; trifurcate; forked for the distal 1/2 to 2/3 of their length, with slightly bulbous, pale yellowish tips covered in fine denticles. Prepelvic tenaculae of adult male blade-like, concealed in pouches anterior to the pelvic fins, with about 9 very stout, pointed denticles along the medial edge. Large females with fleshy anal pad posterior to the cloaca, lacking in males.

Caudal fin short, much lower than second dorsal fin, margins of dorsal and ventral lobes moderately convex; dorsal and ventral lobes subequal in height; origin of ventral lobe difficult to ascertain, joins with a fleshy ridge which extends anteriorly to about level with mid second dorsal-fin base; caudal filament very long (when undamaged), slender.

Colour. Preserved specimens: Silvery to pale greyish or brownish dorsally and laterally, paler ventrally; dorsal surface of body above lateral line often somewhat marbled or with pale longitudinal stripes (may be distinct or faint and poorly differentiated); juveniles usually with more distinct dark longitudinal stripes on body (some juveniles more uniformly silver); first dorsal fin uniformly blackish or with outer half blackish and basal portion slightly paler (somewhat variable across all specimens); dorsal spine yellowish or greyish; pectoral fins greyish to brownish usually with broad, dusky posterior margins; pelvic fins greyish with whitish posterior margins; second dorsal fin pale basally, upper quarter to half of fin dark greyish to blackish; dorsal caudal lobe greyish, often darker distally; ventral caudal lobe mostly dark greyish with a narrow, pale basal marking; caudal filament white; claspers uniformly pale yellowish. When fresh: Silvery dorsally and laterally, white ventrally; markings on fins more prominent.

Size. Largest specimen examined was a female 602 mm BDL (1037 mm TL); largest male examined was 450 mm BDL (904 mm TL). Smallest mature male was 325 mm BDL (631 mm TL), largest adolescent male was also 325 mm BDL (658 mm TL). Thus, males mature at about 325 mm BDL.

Distribution. Found in the Indo-Australasian region (Fig. 8) in depths of 139–872 m (mostly 200–500 m). In Australia, recorded from off Queensland Plateau (~17° S, 151° E) south to off New South Wales, Victoria and Tasmania, east to South Australia and Western Australia north to the Arafura Sea off the Northern Territory (~10° S, 130° E). In Indonesia, recorded from fish landing sites at Cilacap in Central Java, Bali, and Lombok. In Papua New Guinea, recorded from the East Sepik province.

Etymology. Waite (1898) named this species after James Douglas Ogilby (1853–1925) in recognition of the research he had undertaken on the fishes of Australia.

Conclusions

An integrated taxonomic approach, combining both morphological and molecular data, is critical for resolving the taxonomy of the chimaeriform fishes. In this case, single mitochondrial markers (CO1 and NADH2) provided supporting evidence for the separation of multiple species in the *ogilbyi-lemures* group in the Indo-Australasian region. However morphological data and nuclear DNA data failed to support these differences and, together with the morphological data, supported the hypothesis that only a single species in this group was present in the Indo-Australian region. A revision of the generic placement of species within the Chimaeridae is required.

TABLE 1. Morphometric data for the lectotype and ranges for other specimens of *Hydrolagus ogilbyi*; the holotype, paratype and ranges for 10 other specimens of *Hydrolagus lemures*; ranges for 7 specimens of *Hydrolagus* cf *lemures* (Indo); and the two specimens of *Hydrolagus* sp. PNG. Measurements expressed as a percentage of body length.

	Hydrolagus ogilbyi			***Hydrolagus lemures***				***H.* cf. *lemures* (Indo)**		***H.* sp. PNG**	
		Min.	Max.			Min.	Max.	Min.	Max.	NTUM 10332	NTUM 10333
	Lectotype	n = 18		Holotype	Paratype	n = 10		n = 7			
TL	–	166.0	248.0	286.4	259.1	152.5	214.1	143.0	187.8	279.7	262.8
PCL	128.0	125.0	133.5	132.5	130.7	127.4	132.7	123.7	129.1	133.2	133.8
BDL	500.0	243.0	602.0	160.0	172.0	298.0	481.0	406.0	521.0	129.4	109.0
SVL	64.0	59.7	68.1	60.6	61.0	63.7	66.7	56.5	64.4	68.0	64.3
TRL	39.0	33.4	39.7	36.2	34.0	34.8	40.0	31.6	36.8	34.3	34.7
PD2	57.6	54.1	62.2	57.0	56.0	58.4	60.5	53.2	58.0	56.8	57.3
PD1	31.6	30.8	35.9	32.9	31.3	33.5	36.1	29.1	32.7	33.8	32.6
POB	14.6	15.0	20.3	15.5	15.2	16.3	19.4	13.8	16.3	15.8	14.1
POR	14.8	14.6	18.8	16.0	17.0	13.6	18.5	12.2	16.0	17.4	14.0
PRN	11.4	11.6	15.8	13.8	15.9	10.8	15.1	9.9	13.3	15.2	12.8
PP1	30.9	28.7	35.6	36.9	32.7	31.4	36.2	27.4	32.4	34.8	35.0
PP2	65.2	60.2	70.0	64.3	63.3	65.8	69.2	58.6	62.6	66.5	62.3
D2B	73.4	69.7	76.7	78.2	79.1	71.3	75.2	71.5	75.6	76.1	76.6
D2AH	2.5	2.3	4.7	6.2	5.7	2.7	4.1	2.3	3.3	6.5	6.8
D2PH	–	3.0	4.1	5.4	5.5	3.2	4.2	2.4	3.1	6.3	5.8
D1A	–	24.5	28.6	29.9	27.5	22.9	31.2	23.9	25.4	29.2	30.3
D1B	–	14.3	18.5	20.0	20.1	13.4	17.6	13.5	16.8	19.8	21.2
DSA	24.2	22.2	26.6	25.8	24.8	24.7	29.2	22.9	25.0	26.0	25.0
D1H	–	20.3	24.1	27.6	27.0	18.6	25.2	18.1	21.3	26.7	28.2
CDM	–	12.6	21.1	24.6	23.7	15.7	24.4	18.1	26.2	22.1	23.0
CDH	–	1.2	2.4	2.1	2.5	1.1	2.0	1.2	1.8	2.7	3.7
CTL	–	40.9	119.3	152.5	129.4	44.5	83.5	25.4	62.0	143.7	129.4
CVM	–	35.7	82.5	–	–	51.2	74.4	62.3	65.3	21.0	25.0
CVH	–	1.1	1.8	2.4	1.8	1.3	1.8	1.3	1.8	1.4	2.1
HDL	29.7	28.8	34.3	34.0	31.9	30.3	34.8	25.8	30.4	33.7	34.3
INO	6.1	5.8	8.4	8.3	7.8	7.5	9.4	5.8	6.6	7.0	7.0
MOW	6.4	5.1	7.5	7.7	7.9	6.0	8.3	5.4	6.8	6.5	7.1
GS1	–	6.1	8.9	8.1	8.0	5.9	8.8	6.3	9.1	10.1	9.2
P1A	–	38.6	43.6	44.4	43.7	38.5	44.1	35.8	39.7	48.5	45.8
P1L	–	23.2	28.6	27.5	27.3	25.2	28.6	22.8	24.7	31.3	31.4
P2A	17.8	17.4	21.2	23.7	23.0	18.3	20.4	16.4	18.0	20.7	18.1
IDS	–	7.3	15.1	5.1	7.8	10.0	12.7	9.7	15.1	5.4	7.1
DCS	–	0.0	1.5	0.0	0.0	0.0	1.4	0.6	1.1	0.0	0.0

......*continued on the next page*

TABLE 1. (Continued)

	Hydrolagus ogilbyi			***Hydrolagus lemures***				***H.* cf. *lemures* (Indo)**		***H.* sp. PNG**	
		Min.	Max.			Min.	Max.	Min.	Max.	NTUM 10332	NTUM 10333
	Lectotype	n = 18		Holotype	Paratype	n = 10		n = 7			
PPS	31.1	24.6	32.6	27.4	23.9	26.4	30.6	24.9	29.4	24.7	24.4
D1P1	21.1	17.7	22.6	24.9	23.5	18.8	24.4	17.0	20.3	22.1	21.2
D1P2	40.5	35.3	44.7	36.4	39.4	38.9	43.6	35.5	40.0	40.1	38.9
D2P1	35.0	29.7	34.8	33.5	31.5	31.3	36.1	31.1	34.3	29.9	28.0
D2P2	21.4	17.8	24.8	22.1	20.3	20.7	25.4	17.7	22.1	23.1	21.2
EYL	8.2	6.6	8.7	9.3	8.7	7.6	9.2	6.5	8.4	11.0	13.2
EYH	5.9	3.8	6.0	6.0	5.5	4.7	6.6	3.9	4.8	6.1	6.8
CLT	–	23.5	30.7	–	–	24.4	29.0	25.1	29.7	–	–
CLO	–	22.5	26.6	–	–	21.5	25.8	23.0	24.9	–	–
CLM	–	11.4	16.8	–	–	12.7	15.6	13.3	15.3	–	–
CLL	–	12.3	17.3	–	–	13.5	15.4	13.6	14.7	–	–

Comparative material

Chimaera argiloba: (14 specimens) CSIRO H 1207-09 (paratype), juvenile male 654 mm TL, 320 mm BDL, north-west of Port Hedland, Western Australia, 18°20′ S, 117°50′ E, 430 m, Oct 1987; CSIRO H 2585-01 (paratype), female 835 mm TL, 414 mm BDL, CSIRO H 2585-02 (holotype), late adolescent male 897 mm TL, 424 mm BDL, north-west of Geraldton, Western Australia, 28°16′ S, 113°17′ E, 520 m, 02 Feb 1991; CSIRO H 2586-08, female 782 mm TL, 379 mm BDL, CSIRO H 2586-10, female ~830 mm TL, 421 mm BDL, CSIRO H 2586–11, juvenile male 793 mm TL, 376 mm BDL, south-west of Shark Bay, Western Australia, 27°15′ S, 112°44′ E, 510– 520 m, 02 Feb 1991; CSIRO H 2587-16 (paratype; tissue accession GN10950; Genbank accession KY260646), female 822 mm TL, 413 mm BDL, south-west of Shark Bay, Western Australia, 27°06′ S, 112°44′ E, 370–438 m, 02 Feb 1991; CSIRO H 4071–17 (paratype), adult male 912 mm TL, 440 mm BDL, CSIRO H 4071-18 (paratype), female 877 mm TL, 448 mm BDL, south-west of Rowley Shoals, Western Australia, 18°02′ S, 118°14′ E, 388–392 m, 09 Sep 1995; CSIRO H 7140-06 (tissue accession GN11101; Genbank accession JN313180), 210 mm TL, CSIRO H 7140-07 (tissue accession GN11102; Genbank accession JN313181), 390 mm TL, northwest of Cape Leveque, Western Australia, 15°56′ S, 120°36′ E, 395–396 m depth, 7 Jun 2004; CSIRO H 8059-01 (Genbank accession KY260645), adult male 891 mm TL, Tanjung Luar fish market, Lombok, Indonesia, 8°45′ S, 116°35′ E, 11 Mar 2005; CSIRO H 8060-01 (tissue accession GN11188; Genbank accession KY260652), adult male 883 mm TL, CSIRO H 8060-02 (tissue accession GN11189; Genbank accession KY260636), adult male ~802 mm TL, Tanjung Luar fish market, Lombok, Indonesia, 8°45′ S, 116°35′ E, 26 Mar 2006.

Chimaera phantasma: (14 specimens) AMNH 258154 (tissue accession GN10132), female 159 mm PCL, Tongkang fish market, Taiwan, 19 Mar 2012; CSIRO H 6292-05, male 500 mm TL, CSIRO H 6292-06, female 493 mm TL, Da-xi fish market, Taiwan, 21 May 2005; CSIRO H 6294-16, juvenile male 200 mm TL, Da-xi fish market, Taiwan, 23 May 2005; CSIRO H 6295-23, juvenile male 556 mm TL, Da-xi fish market, Taiwan, 24 May 2005; CSIRO H 7395-03, female 290 mm TL, CSIRO H 7395-04, female 240 mm TL, CSIRO H 7395-31, juvenile male 200 mm TL, CSIRO H 7395-32, female 150 mm TL, CSIRO H 7395-33, female 212 mm TL, CSIRO H 7395-34 (tissue accession GN9983), female ~125 mm TL, CSIRO H 7395-35, juvenile male ~155 mm TL, Da-xi fish market, Taiwan, 14 Mar 2012; MNHN 2013-0398 (tissue accession GN10131), juvenile male 127 mm PCL, MNHN 2013-0399 (tissue accession GN10133), female ~139 mm PCL, Tongkang fish market, Taiwan, 19 Mar 2012.

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