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## Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 1—Redescription of *Centrophorus granulosus* (Bloch & Schneider), a senior synonym of *C. acus* Garman and *C. niaukang* Teng

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### Abstract

The genus *Centrophorus* is one of the most taxonomically complex and confusing elasmobranch groups. A revision of this group is currently underway and this first paper sets an important foundation in this process by redescribing the type species of the genus—*Centrophorus granulosus*. This taxon name has been previously applied to two different morphotypes: a large species >1.5 m TL and a smaller species ~1 m TL. *Centrophorus acus* and *C. niaukang* are the most commonly used names applied to the larger morphotype. The original description of *C. granulosus* was based on a large specimen of ~1.5 m TL, but subsequent redescrptions were based on either of the large or small morphotypes. *Centrophorus granulosus* is herein redescribed as a large species and a neotype is designated. *Centrophorus acus* and *C. niaukang* are found to be junior synonyms of *C. granulosus*. *Centrophorus granulosus* is distinguishable from its congeners by its large size, dermal denticle shape, colouration and a number of morphological and biological characteristics. Ontogenetic changes in morphology, dentition and denticle shape for this species are described in detail.

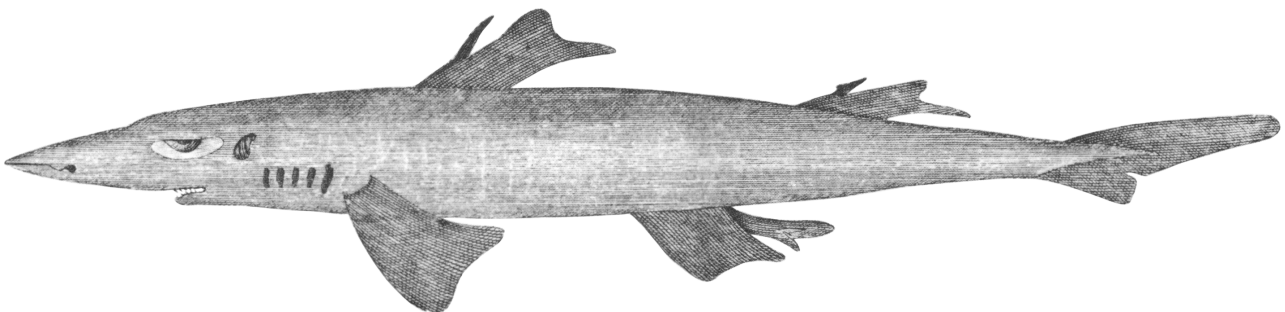
**Key words:** *Centrophorus*, type species, nomenclature, taxonomy, neotype

### Introduction

The family Centrophoridae Bleeker, 1859 (Chondrichthyes: Squaliformes) consists of two genera, *Centrophorus* Müller & Henle, 1837 and *Deania* Jordan & Snyder, 1902, both of which have a complex taxonomic history. For the purposes of this paper, only the genus *Centrophorus* will be discussed. The genus *Centrophorus* was proposed by Müller & Henle (1837) and Müller & Henle (1839) treated this as one of the four shark genera lacking an anal fin and possessing a spine before each dorsal fin, i.e. *Acanthias* Bonaparte, 1838 (objective synonym of *Squalus* Linnaeus, 1758), *Spinax* Cuvier, 1816 (synonym of *Etmopterus* Rafinesque, 1810), *Centrina* Cuvier, 1816

(objective synonym of *Oxynotus* Rafinesque, 1810) and *Centrophorus*. This genus was proposed for *Squalus granulosus* Bloch & Schneider, 1801 based on the following features of the dentition: lower jaw teeth indistinctly serrated and strongly oblique; upper jaw teeth without serrations and erect. Müller & Henle (1839) included both *C. granulosus* and *Squalus squamosus* Bonnaterre, 1788, in the genus *Centrophorus* and provided a more detailed description of the type species.

Günther (1870) expanded the diagnosis of the genus *Centrophorus* to include 6 additional squaloid species: four species described by Barbosa du Bocage & de Brito Capello, 1864 as *Centrophorus lusitanicus*, *C. crepidater*, *Scymnodon ringens*, *Centroscymnus coelolepis*, plus *Machephilus dumerilii* (Johnson, 1868) and *Acanthidium calceus* (Lowe, 1839). However, Garman (1906) opposed this view and stated that four distinct genera were involved as originally designated: *Acanthidium* Lowe, 1839 for *A. calceus*; *Centroscymnus* Barbosa du Bocage & de Brito Capello, 1864 for *C. coelolepis*; *Scymnodon* Barbosa du Bocage & de Brito Capello, 1864 for *S. ringens* and *Centrophorus* for *Squalus granulosus* Bloch & Schneider, 1801. Garman (1906) also described two new species of *Centrophorus*, i.e. *C. acus* and *C. tessellatus*. He also added *Squalus uyato* Rafinesque, 1810 to *Centrophorus*, in contrast to Müller & Henle (1839) who considered it as *Acanthias uyatus* and Bonaparte (1841) who considered it as *Spinax uyatus*. Garman (1913) provided a more detailed description of *Centrophorus uyato* based on a specimen (MCZ 943). However, the original description and illustration of *S. uyato* by Rafinesque (1810; Figure 1) depicts a *Squalus* species that is recognisable by its sharp snout, narrowly rounded pectoral free rear tip, large first dorsal fin spine, second dorsal fin much lower than the first and with a deeply incised posterior margin, very large claspers with prominent spines or spurs (which are very small in *Centrophorus*, with relatively inconspicuous spurs), a short abdomen, an elongated precaudal tail, and no subterminal notch on caudal fin. Thus, although *Centrophorus uyato* has been commonly used in the literature since Garman (1906), the original species description of *Squalus uyato* by Rafinesque (1810) was actually based on an undetermined *Squalus* species and arguably should therefore not be used to designate any *Centrophorus* species. Muñoz-Chápuli & Ramos (1989) provided the same argument for the exclusion of *uyato* from the genus *Centrophorus*. However, Böhlke (1984) regarded Bonaparte's (1834) treatment of *Spinax uyatus* as a new name proposal (with ANSP 483 as the holotype). This requires further investigation to determine whether Bonaparte's name is a valid new name proposal or whether it represents a homonym of a *nomen nudum* species, i.e. *Squalus uyato*.



**FIGURE 1.** Original illustration of *Squalus uyato* in Rafinesque (1810) from off Sicily, Italy, which shows the species to be clearly a *Squalus* species and not a *Centrophorus* species, as once considered.

Garman (1913) described *Centrophorus atromarginatus* from Japan and provided a short treatment on *Centrophorus moluccensis* Bleeker, 1860 from Indonesia. In this publication, Garman also placed those species with leaf-like denticles into the genus *Lepidorhinus* Bonaparte, 1838, which was established for *Squalus squamosus*. However, many subsequent authors placed *Squalus squamosus* back into the genus *Centrophorus* (Bigelow & Schroeder, 1957; Compagno, 1984). Much of the taxonomic confusion within *Centrophorus* is attributable to flux in assignment of species to a variety of genera and the lack of detailed descriptions in the earliest described taxa. It has been well recognised for a number of decades that the genus *Centrophorus* requires an extensive global revision (see e.g. Compagno, 1984). Muñoz-Chápuli & Ramos (1989) provided an excellent revision of the Eastern Atlantic *Centrophorus* species, but issues remain regarding which species are valid and whether any new taxa exist.

A central issue requiring resolution is the identity of the type species for the genus, *Centrophorus granulosus*. There has been much confusion in the literature, including recent publications, as to what constitutes

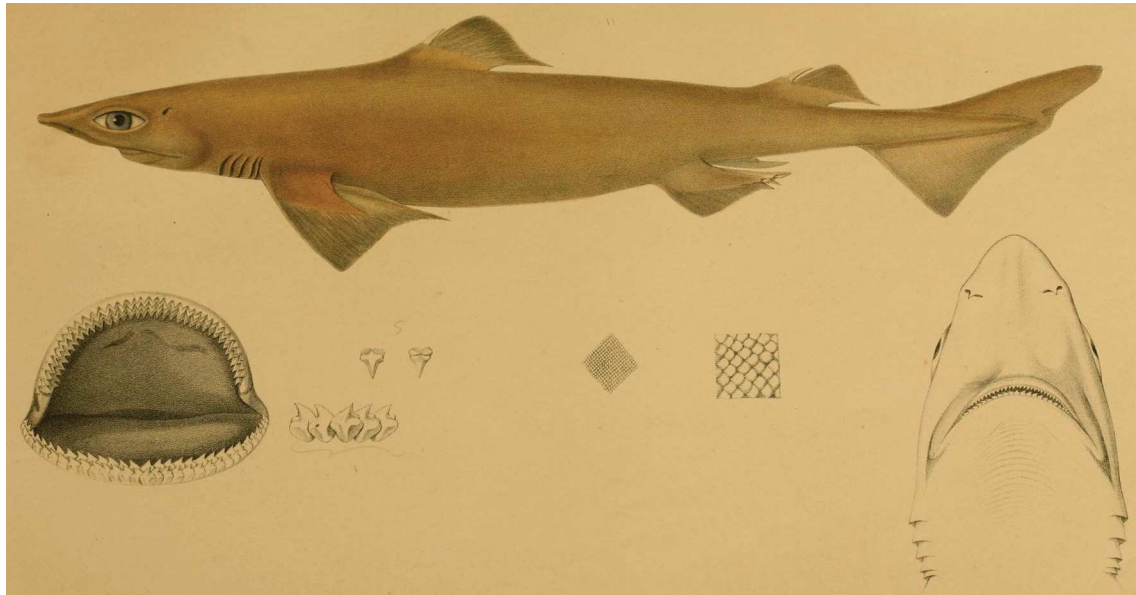
*C. granulatus*. A number of authors refer to *C. granulatus* as a large species attaining over 1.5 m total length (TL) following the original species description of Bloch & Schneider (1801), e.g. Cadenat & Blache (1981); Compagno, (1984, in part); Last & Stevens (1994); Bañón *et al.* (2008). But, the more recent opinion has been that *C. granulatus* is a small species attaining about 110 cm TL (e.g. Muñoz-Chápuli & Ramos, 1989; Compagno *et al.*, 2005). The large species that was considered by some to be *C. granulatus* has more recently been referred to as *Centrophorus niaukang* Teng, 1959 (Compagno *et al.*, 2005; Last & Stevens, 2009; Castro, 2011). Furthermore, no type locality was given for *C. granulatus* in the original description and the whereabouts of the dried holotype, originally deposited at the Museum für Naturkunde, Zoologisches Museum (ZMB) in Berlin, is unknown (confirmed with P. Bartsch, 26<sup>th</sup> September 2012). Müller & Henle (1837, 1839) examined Bloch & Schneider's type specimen of *S. granulatus*, along with several other specimens from the Mediterranean Sea off Sicily, in their account of this species and based on this material they proposed the genus *Centrophorus*.

Although Bloch & Schneider's description of *S. granulatus* was brief and mostly restricted to a description of the fin spines, it holds an important clue to the identity of this species. The type specimen used for this description was 5 feet (~152 cm) long and had a circumference of 2.3 feet (~70 cm). According to Compagno *et al.* (2005), only three species of *Centrophorus* attain such length – *C. squamosus*, *C. niaukang* and *C. acus*. The fact that Müller & Henle (1837, 1839) provide accounts of both *C. granulatus* and *C. squamosus* as distinct species, and that Bloch & Schneider (1801) also included *Squalus squamosus* in their publication, excludes *C. squamosus* as a potential candidate for the type specimen of *S. granulatus*. However, it is not possible to exclude *C. acus* or *C. niaukang* which are also robust species that can attain a similar size as the type specimen of *S. granulatus*. *Centrophorus acus* and *Centrophorus niaukang* are both commonly used names in the literature for large members of this genus. The feature used to differentiate between these two species is the shape of the dermal denticles: juveniles with more upright denticles have often been considered to be *C. acus* (e.g. Garman, 1906; Last & Stevens, 2009), while adults with lower, flatter denticles have often been referred to as *C. niaukang* (e.g. Teng, 1959; Last & Stevens, 2009). However, the species name used appears to be related to the country, for example, *C. acus* is commonly used for a large species in Japan, while in neighbouring Taiwan, *C. niaukang* is most commonly used.

In their excellent review of the nomenclature of squaliform sharks, Bigelow & Schroeder (1957) suggested that Müller & Henle (1841 [=1839]) should be considered the authority for *C. granulatus*, and that the type locality should be the Mediterranean Sea, since Müller & Henle provided a more detailed description of this species. However, this assumes that the specimens from the Mediterranean Sea examined by Müller & Henle are conspecific with the type of Bloch & Schneider's. Indeed, the illustrations of *C. granulatus* in Müller & Henle (1839) do not appear to be conspecific with the true *C. granulatus* as recognised and redescribed in this paper. The most significant differences are the pale brown colouration, the short first dorsal fin, short first dorsal-fin inner margin, and the pavement-like denticles (Figure 2). Furthermore, from the measurements provided by Müller & Henle (1839) for the specimen from Sicily, it is estimated that the specimen is ~800 mm TL and the illustration shows that it is a mature male. This is much smaller than the size at maturity for males for *C. granulatus* based on current information and as redescribed herein, i.e. 1050–1180 mm TL (see Size section below). Thus, it appears the species described by Müller & Henle (1839) is a small species and this reference is likely the root cause of the confusion over whether *C. granulatus* is a large or small species. Moreover, there are currently no known records of a large *Centrophorus* species from the Mediterranean Sea. It is possible that the true *C. granulatus* does not occur in this region. This highlights the need for examination of a large number of specimens for members of this genus from a wide size range and from different geographic regions.

This paper is the first in a series that will provide an extensive revision of the genus *Centrophorus*. Due to the complexity of taxonomic issues, multiple papers are considered the most effective way to proceed. In this first paper, we examine a large number of specimens originally identified as *C. acus*, *C. granulatus* and *C. niaukang* from a wide geographic area and a wide size range, using morphological and molecular data. We demonstrate that *Centrophorus acus* and *Centrophorus niaukang* are conspecific, and represent distinct ontogenetic stages of *Centrophorus granulatus*. The separation of *C. acus* and *C. niaukang* was based on ontogenetic differences, and the two species should thus be synonymised using the senior designation of *C. granulatus* (Bloch & Schneider 1801). We also provide a redescription of *Centrophorus granulatus* (Bloch & Schneider, 1801) and designate a neotype. Bloch & Schneider (1801) did not provide any location information for the holotype of *C. granulatus*, thus it was not possible to allocate a neotype from the same location. A large female specimen from the Eastern

Atlantic was considered the most suitable candidate for the neotype of *C. granulosis* given that the earliest work on this species, e.g. Müller & Henle (1837, 1839), was based on material from the North East Atlantic, and the original type was likely a female based on its size. *Centrophorus acus* Garman, 1906 and *C. niaukang* Teng, 1959 are herein considered as junior synonyms of *C. granulosis*. One of the previously considered lost syntypes of *Centrophorus steindachneri* was also located and is designated as a lectotype for this species, also a junior synonym of *C. granulosis*. The nomenclature of the small morphotype previously referable to *C. granulosis* is briefly discussed and from herein the name *C. granulosis* is used only for the large morphotype, i.e. the true *granulosus*.



**FIGURE 2.** Müller & Henle's (1839) illustrations of '*Centrophorus granulosis*' based on an ~800 mm TL adult male specimen from off Sicily, Italy.

## Methods

The 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 measuring methodologies adopted are frequently not specified. In this paper, morphometrics for all but one of the specimens of *C. granulosis* measured were taken by the senior author. 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 – 1<sup>st</sup> dorsal-fin midpoint to pectoral-fin insertion, D1SL – 1<sup>st</sup> dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), D2SL – 2<sup>nd</sup> dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), DPO – 1<sup>st</sup> dorsal-fin midpoint to pelvic-fin origin, PDI – pelvic-fin midpoint to 1<sup>st</sup> dorsal fin insertion, and PDO – pelvic-fin midpoint to 2<sup>nd</sup> 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 neotype and 57 other specimens of *C. granulosis* (including specimens referred to as *C. acus* or *C. niaukang*) were measured (Table 1). In the descriptions of *C. granulosis*, morphometric values for the neotype are given first, followed in parentheses by the ranges of the other specimens. For some characteristics, ranges are provided for small individuals (<700 mm TL) vs. larger individuals (>820 mm TL) to highlight ontogenetic differences.

**TABLE 1.** Proportional dimensions as percentages of total length for the neotype of *Centrophorus granulosis* (AMNH 78263), holotype of *Centrophorus acus* (MCZ S-1049), 12 other specimens less than 700 mm TL and 44 other specimens >820 mm TL of *Centrophorus granulosis*.

	Neotype	Holotype of <i>C. acus</i>	<700 mm (n = 12)		>820 mm (n = 44)	
			Min.	Max.	Min.	Max.
Total length (mm)	1241	820	308	688	874	1623
Precaudal length	81.5	80.4	76.4	79.8	79.9	83.1
Pre-second dorsal length	61.8	63.7	59.7	62.9	62.0	67.8
Pre-first dorsal length	30.3	–	27.9	33.7	28.3	36.0
Pre-first dorsal length (horiz.)	30.2	27.7	27.1	33.1	27.8	35.7
Pre-vent length	59.8	60.1	56.6	59.8	59.3	64.6
Prepelvic length	58.5	57.2	55.4	58.4	57.5	63.2
Prepectoral length	25.4	20.5	23.1	26.5	19.9	24.8
Head length	24.6	–	23.2	26.1	20.6	24.9
Head length (horiz.)	23.7	22.2	22.9	25.9	20.2	23.7
Prebranchial length	20.8	19.1	20.4	23.3	17.8	20.9
Prespiracular length	12.5	12.6	13.6	15.9	11.4	13.7
Preorbital length	7.0	–	7.3	8.5	5.9	7.6
Preorbital length (horiz.)	5.7	5.7	6.7	8.1	4.8	7.1
Snout to inner nostril	4.5	–	5.1	5.9	3.6	5.0
Prenarial length (horiz.)	4.2	3.4	4.8	5.4	3.4	4.7
Preoral length	9.6	8.7	9.9	12.1	8.0	10.1
Inner nostril–labial furrow space	6.5	–	6.4	7.8	5.2	6.3
Mouth width	9.0	7.1	6.8	10.4	7.6	9.8
Upper labial furrow length	2.1	2.0	1.6	2.6	1.2	2.3
Nostril width	1.6	1.6	1.9	2.5	1.4	2.0
Internarial space	3.5	3.8	3.4	4.3	3.1	3.9
Interorbital space	7.8	7.2	8.5	10.0	7.2	9.1
Eye length	5.9	4.6	5.9	7.5	4.3	5.8
Eye height	1.4	1.2	1.7	2.3	1.1	2.4
Spiracle diameter - greatest	1.6	1.7	1.9	2.5	1.4	2.0
First gill-slit height	2.4	2.1	2.1	3.3	1.9	3.1
Fifth gill-slit height	3.6	2.7	2.5	3.7	2.4	4.0
Interdorsal space	17.5	20.4	14.6	18.9	16.8	21.1
Dorsal–caudal space	6.1	5.9	5.9	7.4	4.9	7.5
Pectoral–pelvic space	34.0	31.7	27.4	31.6	32.0	39.2
Pelvic–caudal space	13.5	14.6	10.1	12.5	10.3	14.1
First dorsal length	23.0	23.8	17.6	22.2	17.9	26.9
First dorsal soft fin length	15.9	–	11.0	13.2	12.3	16.6
First dorsal anterior margin	12.5	12.8	9.8	15.0	9.2	14.2
First dorsal base length	14.5	16.6	11.8	16.4	11.5	17.3
First dorsal height	5.9	5.7	4.4	5.7	4.8	6.5
First dorsal inner margin	8.5	6.8	5.4	6.5	6.0	8.7

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**TABLE 1** (continued)

	Neotype	Holotype of <i>C. acus</i>	<700 mm (n = 12)		>820 mm (n = 44)	
			Min.	Max.	Min.	Max.
First dorsal posterior margin	12.2	12.1	7.9	10.0	9.3	13.1
First dorsal exposed spine length	1.1	1.7	0.8	1.9	0.8	1.9
First dorsal spine base width	0.6	–	0.5	0.7	0.4	0.8
Second dorsal length	17.9	15.1	14.7	16.8	14.2	17.8
Second dorsal soft fin length	10.9	–	9.3	10.4	9.7	11.6
Second dorsal anterior margin	11.4	8.9	9.3	12.1	7.6	11.3
Second dorsal base length	12.6	10.6	10.4	12.1	9.7	13.7
Second dorsal height	5.9	5.4	4.8	6.1	4.8	6.5
Second dorsal inner margin	5.3	4.3	4.0	5.0	3.8	5.5
Second dorsal posterior margin	8.7	8.7	7.4	8.8	8.0	10.5
Second dorsal exposed spine length	1.4	2.2	1.8	2.6	0.7	1.8
Second dorsal spine base width	0.6	–	0.5	0.9	0.4	0.7
Pectoral anterior margin	13.1	11.6	9.8	11.1	10.5	13.6
Pectoral inner margin	13.4	9.5	8.7	10.6	9.8	14.0
Pectoral base length	5.5	5.9	4.4	5.1	3.8	6.0
Pectoral height	11.1	7.9	7.5	9.6	8.9	11.9
Pectoral free rear tip extension	4.0	–	0.9	2.2	1.7	4.1
Pectoral posterior margin	9.9	7.9	6.0	8.8	7.4	10.9
Pelvic length	12.4	11.0	9.4	10.9	10.3	12.7
Pelvic height	6.2	5.2	3.7	5.1	4.7	6.7
Pelvic inner margin	7.0	5.5	4.6	6.2	5.8	8.5
Dorsal caudal margin	18.1	19.0	18.6	22.1	16.2	19.6
Preventral caudal margin	13.9	10.6	13.8	15.2	11.6	14.6
Upper postventral caudal margin	7.9	6.7	6.7	10.4	6.8	9.1
Lower postventral caudal margin	3.8	3.7	2.8	5.1	3.2	5.2
Caudal fork width	7.8	–	6.9	8.1	6.6	8.1
Caudal fork length	13.6	10.7	13.7	15.6	10.9	14.2
Caudal terminal lobe	8.6	8.0	7.4	10.6	6.5	9.5
Caudal subterminal fin margin	2.7	2.9	3.2	4.6	2.0	3.7
Head width at anterior of nostrils	6.3	–	6.4	7.8	5.5	6.9
Head width at mouth	9.7	–	10.5	12.5	9.2	11.4
Head width	13.8	10.7	10.8	14.8	11.0	14.8
Trunk width	9.4	8.2	9.2	11.7	8.2	13.2
Abdomen width	8.3	–	8.7	11.7	7.4	14.6
Tail width	5.0	–	3.4	4.9	4.3	6.0
Caudal peduncle width	2.7	2.2	1.7	2.5	2.0	2.8
Head height	12.7	10.1	7.8	11.6	8.4	13.9
Trunk height	14.9	10.9	10.5	13.5	8.3	14.5
Abdomen height	14.9	–	10.4	13.8	8.6	16.2
Tail height	8.3	–	5.2	7.7	6.6	8.4
Caudal peduncle height	4.2	4.0	3.5	4.7	3.6	4.6
Clasper outer length	–	–	–	–	3.4	4.4
Clasper inner length	–	–	–	–	7.2	11.5
Clasper base width	–	–	–	–	0.8	1.2
First dorsal midpoint–pectoral insertion	10.6	9.3	7.7	10.9	10.4	15.2
First dorsal midpoint–pelvic origin	20.2	22.1	15.6	20.8	18.4	24.8
Pelvic midpoint–first dorsal insertion	17.0	16.3	11.9	16.0	15.5	20.1
Pelvic midpoint–second dorsal origin	1.2	4.6	0.5	4.4	0.9	4.1

Morphometric measurements, as % TL, were subjected to non-metric multidimensional scaling (MDS) ordination (Primer v6.0 package) (Clarke & Gorley, 2006), to determine the relative level of ontogenetic changes reflected by morphology. 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 10 specimens of *C. granulosus* (CSIRO H 788–01, CSIRO H 2543–05, CSIRO H 2543–06, CSIRO H 2543–10, CSIRO H 2572–01, CSIRO H 4632–05, CSIRO H 5353–01, CSIRO H 5343–07, CSIRO H 7029–01 and CSIRO H 7035–03). For comparison, counts were also taken from *C. atomarginatus* ( $n = 7$ ), *C. harrissoni* ( $n = 32$ ), *C. isodon* ( $n = 9$ ), *C. moluccensis* ( $n = 23$ ), *C. squamosus* ( $n = 14$ ), *C. westraliensis* ( $n = 6$ ) and *C. zeehaani* ( $n = 22$ ) (Table 2). 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. Counts for specimens of some species were also taken during dissection. 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 9 of the individuals examined (CSIRO H 2543–10, CSIRO H 2572–01, CSIRO H 4632–05, CSIRO H 5851–01, CSIRO H 5851–03, CSIRO H 5851–05, CSIRO H 5851–06, CSIRO H 5851–11 and DAE 882711). Tooth counts were also taken from 19 western North Atlantic specimens by two of us (AV, CC) following the methods used by Compagno (1988) for carcharhiniform sharks. Skin patches were removed from the right side (below the second dorsal fin) of a subsample of females and males of varying sizes to highlight ontogenetic changes in denticle morphology. Dermal folds on the ventral surface of the head were counted following Duffy (2007).

Specimen registration numbers are prefixed by the following abbreviations: CSIRO, Australian National Fish Collection, Hobart, Australia; AMNH, American Natural History Museum, New York; AMS, Australian Museum, Sydney; ASIZP, Biodiversity Research Center, Academia Sinica, Taipei; BMNH, British Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; FRIP (or TFRI), Fisheries Research Institute, Keelung, Taiwan; HUI, Hebrew University of Jerusalem, Israel; MCZ, Museum of Comparative Zoology, Harvard; NMMB-P, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan; NMW, Naturhistorisches Museum, Vienna; RMNH, Naturalis – National Natuurhistorisch Museum, Leiden; SAM, South African Museum, Cape Town; SU, Stanford University (now housed at CAS); SUML, Silliman University, Philippines; ZMH, Biozentrum Grindel und Zoologisches Museum, Universität Hamburg, Hamburg.

### Molecular analysis

Specimens originally identified in the field as *C. acus* (Japan), *C. granulosus* (western North Atlantic, Gulf of Mexico, Portugal and Australia), *C. lusitanicus* (Mauritius) and *C. niaukang* (Japan, Taiwan, Australia) were sampled for liver or muscle tissue by the authors and/or their collaborators, or by fishermen (see Supplementary Table S1 for details on each individual sampled). Additional tissues from one specimen each of *C. moluccensis* (southwest Indian) and *C. zeehaani* (Australia) were also obtained to serve as outgroup taxa. Samples were temporarily stored in 95% alcohol or in dimethyl sulphoxide solution (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  $-20^{\circ}\text{C}$  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  $\mu\text{l}$  tubes by adding 1–2  $\mu\text{l}$  of DNA template containing 1 unit of Takara Taq (Clontech, 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  $94^{\circ}\text{C}$  for 3 minutes, after which it was subjected to 35 cycles of denaturation at  $94^{\circ}\text{C}$  for 30s, annealing at  $48^{\circ}\text{C}$  for 30s and extension at  $72^{\circ}\text{C}$  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 corresponding final alignment was imported into MEGA version 5.0 (Tamura *et al.*, 2011) and used to construct a neighbour-joining tree based on genetic *p*-distances among haplotypes. Support for individual clades was evaluated with 10000 bootstrap replicates. The resulting topology, being based on a neighbour-joining analysis of simple *p*-distances is not to be interpreted as a phylogenetic tree of relationships among taxa, but is presented to help with the delineation of species based on sequence differences among specimens. It is also important to note that, because the analyses are based solely on mitochondrial genes, it is not possible to detect, and therefore rule out, potential hybridisation events between species given the strict maternal inheritance of mitochondrial DNA. This is not meant to suggest that hybridisation among forms has taken place, but simply to state that this hypothesis cannot be tested with the molecular data included here.

**TABLE 2.** Vertebral counts for various species of *Centrophorus*: A. monospondylous centra; B. precaudal centra; C. total centra. Total numbers and means are also provided for each species.

A												
Monospondylous centra	51	52	53	54	55	56	57	58	59	#	Mean	
<i>Centrophorus atromarginatus</i>			2	4	1					7	54	
<b><i>Centrophorus granulosis</i></b>	1	1	1	3	1	2	1			10	54	
<i>Centrophorus harrissoni</i>			1		7	7	8	6	3	32	56	
<i>Centrophorus isodon</i>					2	3	2	1	1	9	57	
<i>Centrophorus moluccensis</i>	1	1		4	4	8	4			22	55	
<i>Centrophorus squamosus</i>						4	3	5	2	14	57	
<i>Centrophorus westraliensis</i>					2	3	1			6	56	
<i>Centrophorus zeehaani</i>			2	3	5	7	2	1		20	55	

B																				
Precaudal centra	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	#	Mean
<i>Centrophorus atromarginatus</i>						2	4	1											7	82.9
<b><i>Centrophorus granulosis</i></b>	2			3	1	1		2	1										10	81
<i>Centrophorus harrissoni</i>									2	2	3	5	6	7	3	3		1	32	89.1
<i>Centrophorus isodon</i>									2	2	2	1	2						9	87.9
<i>Centrophorus moluccensis</i>									2	1	4	1	3	7	2	2		1	23	89.3
<i>Centrophorus squamosus</i>						1	4	2	2	5									14	84.4
<i>Centrophorus westraliensis</i>									1	1	2	2							6	86.8
<i>Centrophorus zeehaani</i>						1		9	4	3	4		1						22	85.1

C																											
Total centra	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128	#	Mean		
<i>Centrophorus atromarginatus</i>			1			1	3	1																	6	111	
<b><i>Centrophorus granulosis</i></b>	1		1	3	1	1		1		2															10	111	
<i>Centrophorus harrissoni</i>												2	2	4	2	5	6	6	2		1		1		31	122	
<i>Centrophorus isodon</i>								1	1	3			1	2	1										9	116	
<i>Centrophorus moluccensis</i>									2	1		3	2	1	2	3	4	1	3	1					23	120	
<i>Centrophorus squamosus</i>					1		1	2	2	1	2	1	2												12	115	
<i>Centrophorus westraliensis</i>							1		1		2	2													6	115	
<i>Centrophorus zeehaani</i>								1	1	7	8	2	2		1										22	116	



## Genus *Centrophorus* Müller & Henle 1837

**Type species.** *Squalus granulosus* Bloch & Schneider, 1801, by monotypy.

*Lepidorhinus* Bonaparte, 1838. Type species: *Squalus squamosus* Bonnaterre, 1788, by original description and monotypy.

*Entoxychirus* Gill, 1863. Type species: *Squalus uyato* Rafinesque, 1810, by original description and monotypy.

*Macephilus* Johnson, 1868: 713. Type species: *Macephilus dumerilii* Johnson, 1868, by monotypy.

*Atractophorus* Gilchrist, 1922: 48. Type species: *Atractophorus armatus* Gilchrist, 1922, by monotypy.

*Atractophorus* Gilchrist, 1922: 48. Probable error for *Atractophorus* Gilchrist, 1922.

*Gaboa* (subgenus of *Centrophorus*) Whitley, 1940: 146. Type species: *Centrophorus harrissoni* McCulloch, 1915, by original designation and monotypy.

*Somnispinax* (subgenus of *Centrophorus*) Whitley, 1940: 146. Type species: *Centrophorus nilsoni* Thompson, 1930, by original designation and monotypy.

*Somnispinax* Neave, 1950: 252. Probable error for *Somnispinax* Whitley, 1940.

*Encheiridiodon* Smith, 1967: 128. Type species: *Encheiridiodon hendersoni* Smith, 1967, by original description.

*Atractophorus* Bass, D'Aubrey & Kistnasamy, 1976: 27. Apparent error for *Atractophorus* Gilchrist, 1922.

*Encheiridiodon* Shiino, 1976: 11. Apparent error for *Encheiridiodon* Smith, 1967.

*Pseudocentrophorus* Chu, Meng & Liu, 1981: 100, 102. Type species: *Pseudocentrophorus isodon* Chu, Meng & Liu, 1981, by original description and monotypy.

**Definition.** Deepwater sharks with cylindrical body and very tough skin. Snout flattened and broadly rounded to slightly pointed in dorsoventral view, angular to rounded-angular in lateral view; snout short to moderately long with preoral length less than distance from mouth to pectoral origin, and half of head length or less. Labial furrows not extended anteriomedially as elongate preoral grooves. Eyes very large and iridescent green in life. Upper and lower teeth with broad, thick crowns and roots, often undergoing ontogenetic changes and sexually dimorphic in some species. upper and lower tooth rows 30 to 45 and 24 to 35, respectively; number of tooth rows somewhat greater in upper jaw than lower; lower teeth imbricated, blade-like and much larger than uppers, with vertical basal grooves on their lingual roots and with broader cusps than the upper teeth; edges of lower teeth often serrated in adults; upper teeth upright to strongly oblique. Dermal denticles with low, flat, ridged crowns, varying from leaf-shaped with low pedicels and posterior cusps, to cusp-less, block-shaped and without pedicels; denticle crowns flat and not elevated or pitch fork-like, with a short medial cusp (sometimes absent), lateral cusps short or absent and with one or multiple ridges; denticle bases broader and quadrangular; vary ontogenetically in most species, sometimes dramatically. Surface of skin rough with denticles on pedicels in *Centrophorus squamosus* and juvenile *Centrophorus granulosus* but smooth in species with sessile crowns and low bases. Pectoral fins with free rear tips varying from squared-off and angular to elongated and acutely pointed, not broadly lobate. Claspers with a lateral spine. Two dorsal fins with strong, grooved spines on both fins; second dorsal fin smaller than first and with its base about half to 3/4 length of first dorsal-fin base; second dorsal-fin origin varying from over last third of pelvic-fin bases to slightly posterior to pelvic free rear tips; second dorsal-fin spine equal to or slightly larger than first dorsal-fin spine but not greatly enlarged, spine moderately curved. Caudal fin with a strong subterminal notch. No anal fin. Vertebral counts: total vertebral counts 106 to 131, monospondylous precaudal vertebral count 49 to 64, total precaudal vertebral count 77 to 92. Intestinal valve with 10 to 29 turns. Adults are small to moderately large from 900 to 1725 cm TL. **Colour:** light to dark grey, greyish brown to black above, usually lighter below but some species uniformly dark; depending on the species fin edges may be plain to light or dark-edged.

### *Centrophorus granulosus* (Bloch & Schneider, 1801)

Gulper Shark

(Figures 3–9, 15a, Tables 1–2)

*Squalus granulosus* Bloch & Schneider, 1801: 135 (Type locality: not stated)

*Centrophorus acus* Garman, 1906: 204 (Type locality: Yokohama market, Japan) – Regan, 1908: 51; Jordan *et al.*, 1913: 21 (Japan); Kamohara, 1958: 6 (Japan); Garrick, 1959: 127, fig. 1b (Japan); Chen & Cheng, 1982: 143, fig. 2 (Taiwan); Masuda *et al.*, 1984: 10 (Japan); Yano & Tanaka, 1986: 372 (Japan); Chen & Yu, 1986: 112 (Taiwan); Yu, 1988: 3 (Taiwan); Shen *et al.*, 1993: 36, pl. 1 (Taiwan); Nakabo, 2002: 153, fig. (Japan); Compagno *et al.*, 2005: 82, pl. 4; Last & Stevens, 2009: 61, fig. 10, pl. 5 (fig. 9.1) (Australia); Shen & Wu, 2011: 82, fig. (Taiwan).

*Centrophorus steindachneri* Pietschmann, 1907: 394 (Type locality: Yokohama, Japan) – Pietschmann, 1908: 663, fig. 3, pl. 1 (fig. 1) (Japan).

*Centrophorus niaukang* Teng, 1959: 1, pl. 1, figs 1 and 2 (Type locality: Tou-cheng, northeastern Taiwan) – Teng, 1962: 159, fig. 40; Yang, 1979: 205, fig. 1 (Taiwan); Chen & Cheng, 1982: 143, fig. 5 (Taiwan); Chen & Yu, 1986: 112 (Taiwan); Yu, 1988: 3 (Taiwan); Muñoz-Chápuli & Ramos, 1989: 65, figs 1c, 3c, 4e, 5b, 6c, 7c (Eastern Atlantic); Yano & Kugai, 1993: 41, fig. 1 (Japan); Brito, 2002: 47, fig. 39 (Canary Islands); Nakabo, 2002: 153, fig. (Japan); Kiraly *et al.*, 2003: 10, figs 8–10; Compagno *et al.*, 2005: 86, pl. 4; White *et al.*, 2006: 54, fig. (Indonesia); Freitas & Bischoff, 2007: 5, fig. 3 (Madeira); Last & Stevens, 2009: 61, fig. 12, pl. 5 (fig. 9.4) (Australia); White & Dharmadi, 2010: 1364 (Indonesia); Castro, 2011: 73, figs 13a–e; Ho & Shao, 2011: 9 (Taiwan); Shen & Wu, 2011: 83, fig..

*Centrophorus lusitanicus* Barbosa du Bocage & de Brito Capello, 1864 – Bass *et al.*, 1976: 28, 32, fig. 23 (southern Africa); Compagno, 1984 (in part): 36, 39 (southern Africa); Bass *et al.*, 1986: 49, 50, fig. 5.2 (southern Africa); Compagno *et al.* (1989): 24, fig. (southern Africa).

*Centrophorus harrissoni* Chen, 1963: 93 (placed *C. niaukang* as a junior synonym of this species).

*Centrophorus robustus* Deng, Xiong & Zhan, 1985: 103 (English p. 106), Fig. 2 (Type locality: East China Sea); based on illustrations in original description.

*Centrophorus* c.f. *ascus* Garman, 1906 (misspelling) – McEachran & Feckhelm, 1998: 106, 107 (Gulf of Mexico)

**Neotype.** AMNH 78263, female 1241 mm TL, off Puerto Santa Cruz de Tenerife, Canary Islands, Spain, 28°19.0–21.55' N, 16°19.4–13.45' W, 731–1075 m depth, 27 Sep 1986.

**Other material.** *Western Atlantic:* AMNH 78262, adult male 1151 mm TL, AMNH 78266, adult male 1198 mm TL, offshore of Brevard county, Florida, USA, 28°37.4–37.2' N, 78°28.7–25.4' W, 899–917 m depth, 26 Aug 1986; ZMH 119881, juvenile male 450 mm TL, east of Florida, 29°11' N, 77°7' W, 3 Nov 1979. *Eastern Atlantic:* AMNH 78296, female 1474 mm TL, between Tenerife and Gran Canaria, Canary Islands, Spain, 28°13.5–13.8' N, 15°40.5–38.5' W, 760–800 m depth, 4 Oct 1986; BMNH 2013.9.20.30, adult male 1075 mm TL, Northeast Atlantic (no other data); SAM 36184, juvenile female 392 mm TL, west of Saldanha, South Africa, 32°16' S, 16°18' E, 10 Feb 2002; ZMH 120700, juvenile male 457 mm TL, west of Scotland, 57°40' N, 9°35' W, 1 Apr 1982. *Western Indian:* BMNH 1973.7.12.13–17 (5 embryos and skin patch of adult), 4 females and 1 male, 303–352 mm TL, 12 miles off Cerf Island, Seychelles, ~5° S, 55° E, 22 Jan 1969; BMNH 1973.7.9.16, adult male 1100 mm TL, Seychelles, 5 Feb 1969; BMNH 1973.7.9.18–21 (4 embryos), 3 males and 1 female, 333–354 mm TL, west side of Providence Atoll, Seychelles, ~9° S, 51° E, 366 m depth, 21 Jan 1969; BMNH 1973.7.12.9, embryo 348 mm TL, west side of Providence Atoll, Seychelles, ~9° S, 51° E, 330 m depth, 20 Jan 1969; CSIRO H 5343–06, female 1179 mm TL, CSIRO H 5343–07, adult male 1176 mm TL, South West Indian Ridge, 36°39' S, 52°05' E, 801–1027 m depth, 29 Oct 1999; CSIRO H 5353–01, female 1096 mm TL, South West Indian Ridge, 37°03' S, 51°57' E, 824–1060 m depth, 2 Nov 1999; CSIRO H 5851–01 (head only), female 1540 mm TL, CSIRO H 5851–02 to –12, 11 embryos from 1650 mm TL pregnant female, 370–420 mm TL, South West Indian Ridge, 38°37' S, 48°19' E, 524 m depth, 15 Mar 2001; CAS 234914, female 1138 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 34°30' S, 44°05' E, 800–1300 m depth, 7 Mar 2012; CAS 234915, female 1248 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 34°30' S, 44°05' E, 800–1300 m, 7 Mar 2012; CAS 234916, immature male 436 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 34°30' S, 44°05' E, 800–1300 m, 7 Mar 2012; CAS 234917, immature male 1170 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 34°10' S, 45°05' E, 900–1200 m, 9 Mar 2012; CAS 234920, female 1080 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 36°50' S, 52°05' E, 900–1100 m, 20 Mar 2012; CAS 234921, adult male 1240 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 36°50' S, 52°05' E, 900–1200 m, 20 Mar 2012; CAS 234922, adult male 1261 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 35°10' S, 54°20' E, 900–1100 m, 21 March 2012; CAS 234924, immature male 1170 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 34°10' S, 45°05' E, 900–1200 m, 16 Apr 2012; CAS 234925, female 1470 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 2012; CAS 234926, female 1350 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 2012; DAE 882711 (specimen possibly lost or in LJVC collection at SAM), pregnant female 1560 mm TL, northern Natal, South Africa, 27 Nov 1988; HJ 18636, adult male 1055 mm TL, Alphonse Group, Seychelles, ~7° S, 52°40' E, 20 Dec 1998. *Eastern Indian & South-west Pacific:* CSIRO H 788–01, female 1575 mm TL, northeast Queensland, Australia, 1985 or 1986; CSIRO H 2543–05, adult male 1124 mm TL, CSIRO H 2543–06, adult male 1131 mm TL, CSIRO H 2543–10, juvenile female 489 mm TL, Exmouth Plateau, Western Australia, 20°07.8' S, 112°55.1' E, 854–868 m depth, 23 Jan 1991; CSIRO H 2572–01, juvenile female 688 mm TL, west of Dirk Hartog Island, Western Australia, 26°05.3' S, 111°46.7' E, 874–882 m depth, 30 Jan 1991; CSIRO H 4632–05, juvenile male 465 mm TL, west of Montebello Islands, Western Australia, 20°25.4' S, 114°40.2' E, 806 m depth, 13 Aug 1997; CSIRO H 5860–05,

male embryo 350 mm TL, Cilacap fish landing site, Central Java, Indonesia,  $\sim 07^{\circ}50'$  S,  $109^{\circ}00'$  E, 22 Mar 2002; CSIRO H 7029–01, female 1519 mm TL, east of Woolli, New South Wales, Australia,  $29^{\circ}57.83'$  S,  $153^{\circ}39.71'$  E, 470–500 m depth, 5 Sep 2009; CSIRO H 7035–03, female 1532 mm TL, east of Fraser Island, Queensland, Australia,  $24^{\circ}58'$  S,  $153^{\circ}42'$  E, 390 m depth, 3 Jun 2009. *North-west Pacific*: CAS 234955, newborn or aborted embryo male 321 mm TL (308 mm TL preserved), Da-xi fish market, Yilan, north-eastern Taiwan,  $24^{\circ}48'$  N,  $122^{\circ}10'$  E, 26 May 2005; CSIRO H 6292–13, newborn female 392 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan,  $24^{\circ}48'$  N,  $122^{\circ}10'$  E, 21 May 2005; FRIP 3674, adult male 1167 mm TL, northeastern Taiwan; MCZ S-1049 (Holotype of *Centrophorus acus*), subadult male 820 mm TL, Yokohama fish market, Japan, 5 May 1903; NMMBP 15807, immature female 952 mm TL, NMMBP 15808, juvenile female 874 mm TL, NMMBP 15809, female 1194 mm TL, NMMBP 15810, female 1429 mm TL, NMMBP 15811, juvenile female 1121 mm TL, NMMBP 15812, juvenile female 1052 mm TL, NMMBP 15815, subadult female 1350 mm TL, NMMBP 15816 subadult male 1036 mm TL, NMMBP 15817 adult male 1114 mm TL, NMMBP 15818, subadult female 1345 mm TL, NMMBP 15819, subadult female 1460 mm TL, NMMBP 15820, subadult female 1410 mm TL, NMMBP 15821, pregnant female 1623 mm TL, off Taitung, eastern Taiwan, between 300 and 800 m depth, 18 Jul 2011; NMMBP 15822, adult male 1117 mm TL, NMMBP 15823, adult male 1124 mm TL, NMMBP 15824, adult male 1160 mm TL, NMMBP 15825, juvenile female 1226 mm TL, NMMBP 15826, adult male 1051 mm TL, NMMBP 15827, adult male 1117 mm TL, NMMBP 15828, adult male 1094 mm TL, NMMBP 15829, subadult male 1078 mm TL, NMMBP 15830, juvenile male 900 mm TL, NMMBP 15831, adult male 1076 mm TL, NMMBP 15832, adult male 1130 mm TL, NMMBP 15833, adult male 1144 mm TL, off Taitung, eastern Taiwan, between 300 and 800 m depth, 27 Apr 2011; NMW 61300 (lectotype of *Centrophorus steindachneri*), juvenile male 426 mm TL, Yokohama, Japan; SU 35472 (deposited at CAS), juvenile female 378 mm TL, Yenoshima, Japan.

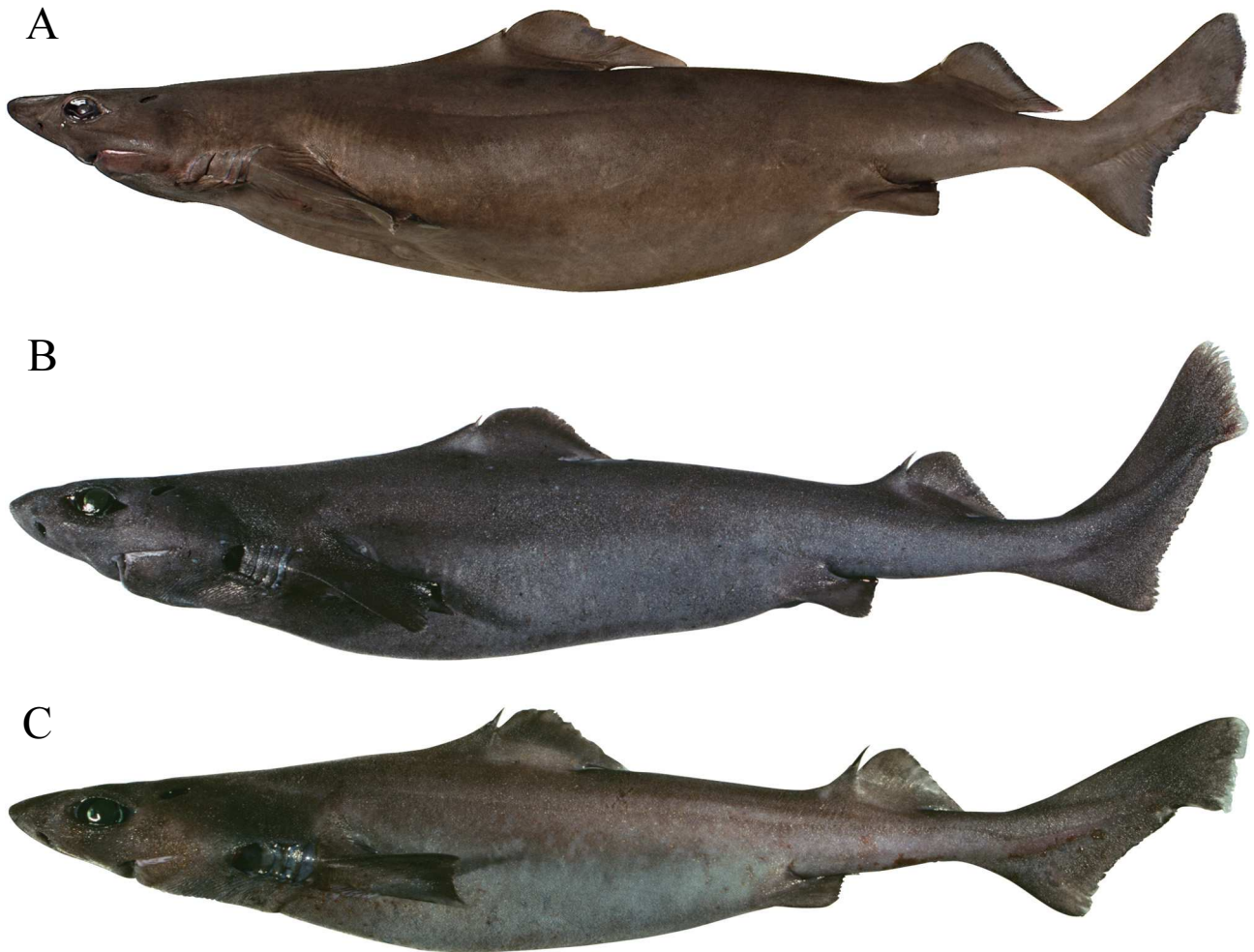
**Diagnosis.** A large ( $>1.5$  m maximum total length) species of *Centrophorus* with the following combination of characters: body moderately robust (see Fig. 3); head moderately long (20.6–24.9% TL, 3.9–4.9 times in total length) and very robust; snout relatively short (horizontal preorbital length 4.8–8.1% TL) and moderately rounded in dorsal view; first dorsal fin low and long (height 4.4–6.5% TL, its soft length 11.0–16.6% TL), inner margin very long (more than length from insertion of exposed spine to fin insertion); second dorsal fin large, similar in height to first dorsal fin; pectoral fins large (anterior margin length 9.8–13.6% TL), free rear tip varying from slightly elongate in small individuals (free rear tip extension 0.9–2.2% TL in individuals  $<700$  mm TL) to moderately elongate in adults (1.9–4.1% TL); lateral trunk denticles elevated on low, broad pedicel with strongly tricuspidate crowns in juveniles  $<700$  mm TL; denticles of large individuals low, not on pedicels, crown tear-drop shaped with one long posterior cusp; upper teeth of juveniles  $<500$  mm TL strongly oblique; upper teeth of individuals  $>700$  mm TL with erect to slightly oblique cusps; lower teeth of all sizes much larger than upper teeth, strongly oblique, blade-like; body uniformly brownish (sometimes greyish to greyish brown), slightly paler ventrally; total vertebral centra 106–115; teeth 30–37/27–32.



**FIGURE 3.** Lateral view of the neotype of *Centrophorus granulosus* (AMNH 78263, female 1241 mm TL). The black line denotes the join of the anterior and posterior halves of the neotype which were imaged separately, but joined for this figure.

**Description.** Body fusiform, robust, nape somewhat humped; deepest near first dorsal-fin spine, trunk height 1.59 (1.00–1.28 in specimens  $<700$  mm TL; 0.76–1.56 in specimens  $>820$  mm TL) times width, 1.00 (0.84–1.09; 0.79–1.20) times abdomen height; no lateral ridges; a low, rounded ridge along predorsal midline from about level of pectoral-fin base gradually rising posteriorly and joining into first dorsal-fin origin; interdorsal ridge usually present (more obvious in smaller specimens); pre-first dorsal length 3.30 (2.97–3.58; 2.78–3.53) in TL; interdorsal

space 1.45 (1.32–1.71; 0.98–1.46) in prepectoral length, 1.73 (1.50–2.17; 1.41–2.04) in pre-first dorsal length; pelvic–caudal space 2.51 (2.20–3.01; 2.17–3.51) in pectoral–pelvic space, 1.88 (1.85–2.46; 1.40–2.17) in prepectoral length; dorsal–caudal space 2.86 (2.25–2.89; 2.61–4.12) in interdorsal space. Caudal peduncle moderately short and deep, moderately compressed, its length 13.5 (10.1–12.5; 10.3–14.6)% TL, its height 1.55 (1.60–2.06; 1.40–2.09) times its width; tapering slightly towards caudal fin; ventral midline sometimes a very weak ridge; ventral groove weak (better developed in some paratypes); a shallow, weak dorsal groove often present; no lateral keels; precaudal pits absent.



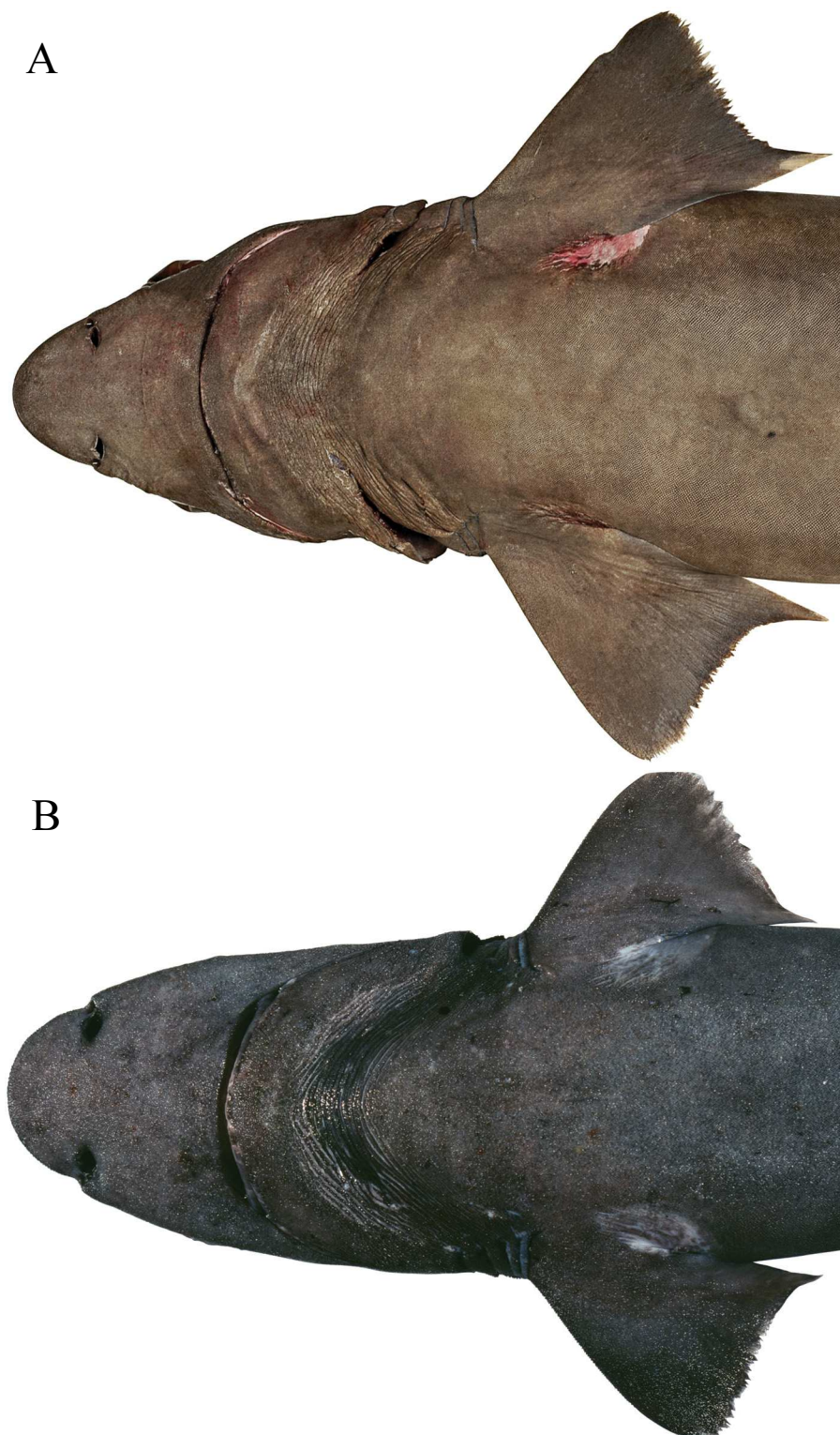
**FIGURE 4.** Lateral view of *Centrophorus granulatus*: A. mature female, CSIRO H 7029–01 (1519 mm TL); B. juvenile female, CSIRO H 2572–01 (688 mm TL); C. juvenile female, CSIRO H 2543–10 (489 mm TL).



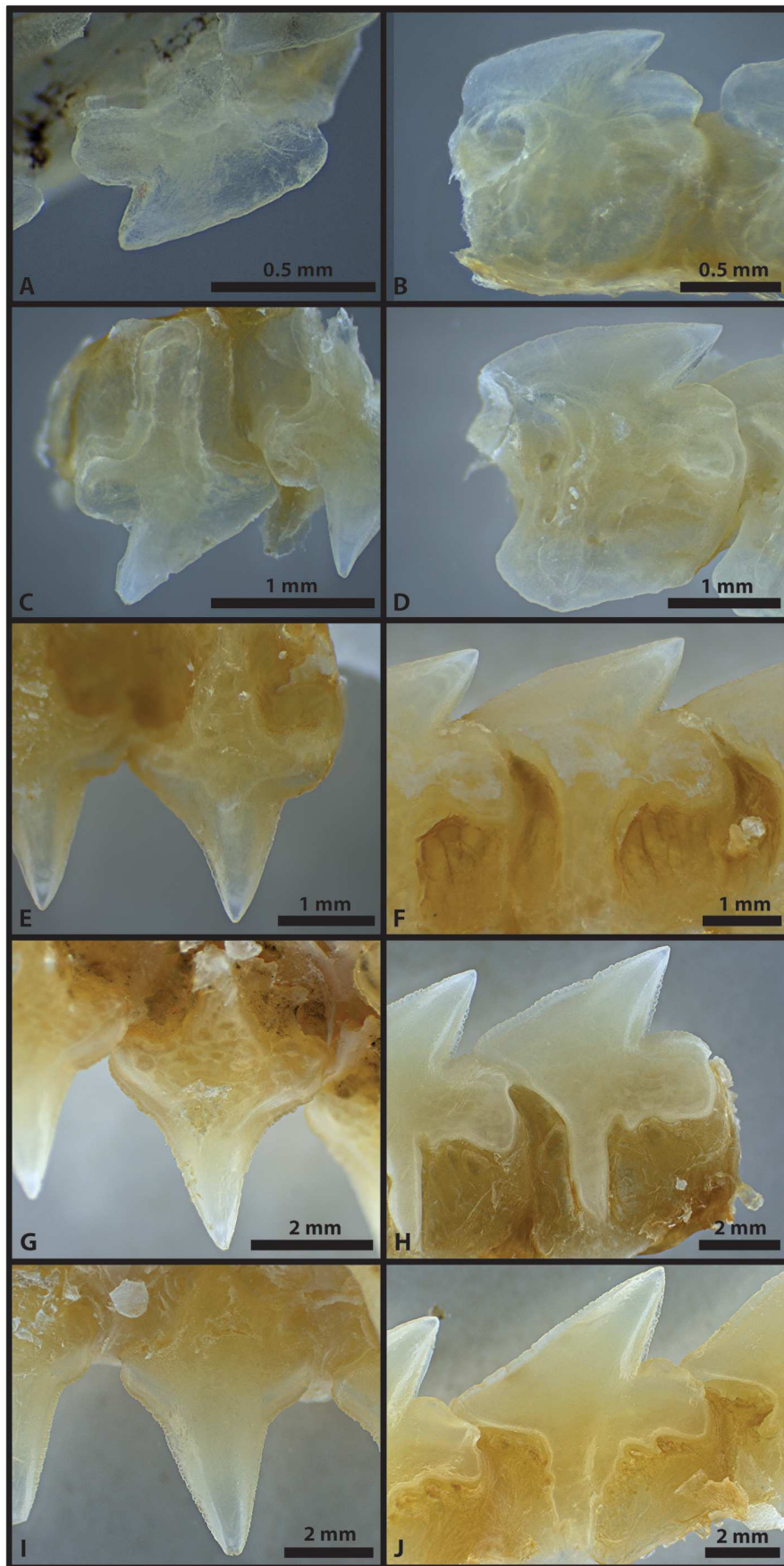
**FIGURE 5.** Lateral view of the holotype of *Centrophorus acus* (MCZ S-1049, subadult male 820 mm TL).

Head moderately long, robust (less robust in juveniles <700 mm TL), broad, width 1.47 (1.19–1.40; 0.97–1.54)

times trunk width, 1.67 (1.20–1.47; 0.89–1.72) times abdomen width, length 24.6 (23.2–26.1; 20.6–24.9)% TL, 2.43 (2.21–2.46; 2.46–2.97) in pre-vent length, height 0.92 (0.66–1.00; 0.63–1.05) times width; slightly depressed forward of spiracles, somewhat 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 three or four gill slits on either side; usually about 14 folds present.



**FIGURE 6.** Ventral view of the head and pectoral fins of *Centrophorus granulosus*: A. mature female, CSIRO H 7029–01 (1519 mm TL); B. juvenile female, CSIRO H 2572–01 (688 mm TL).



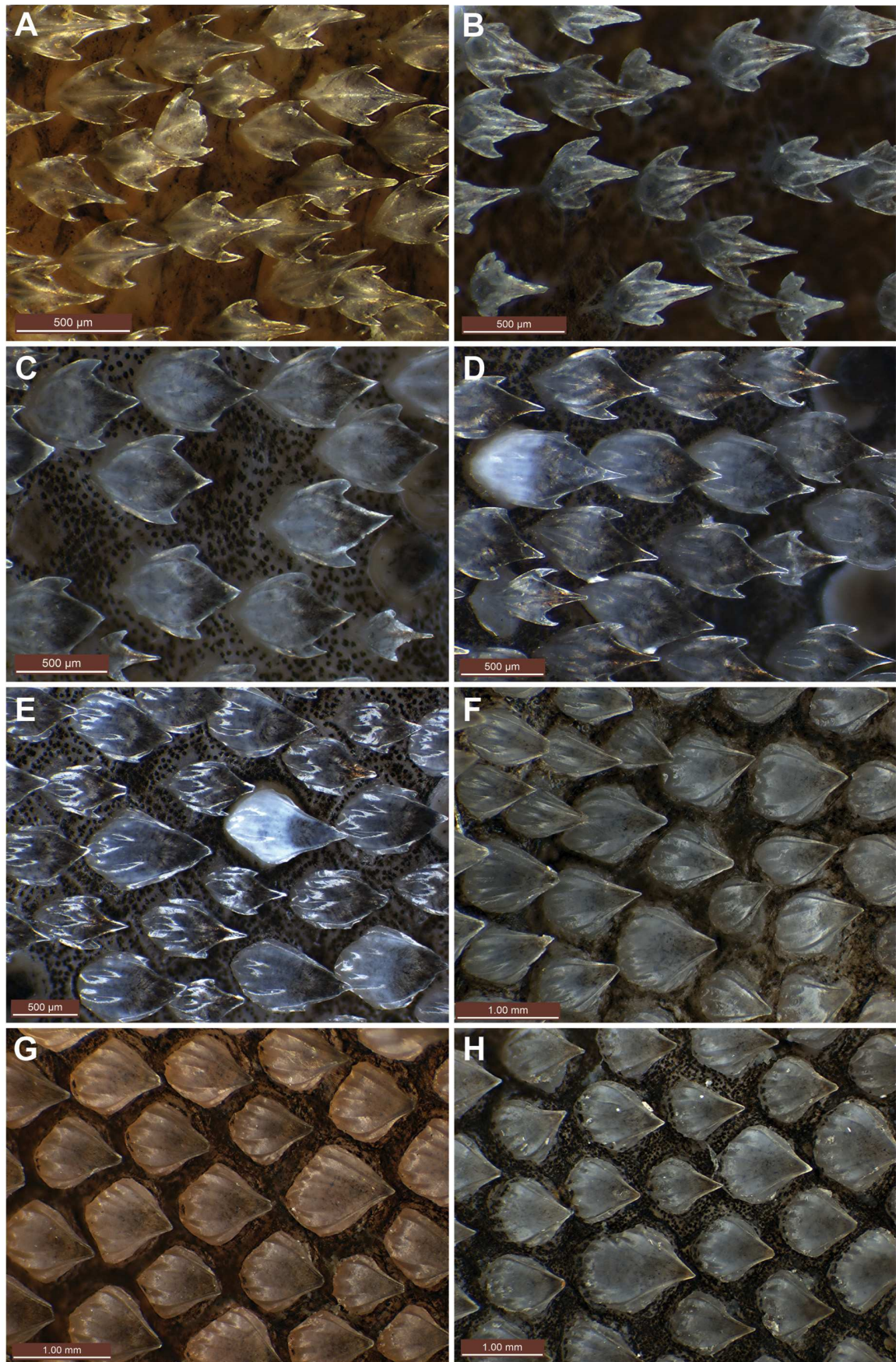
**FIGURE 7.** Upper (A, C, E, G, I) and lower (B, D, F, H, J) teeth of *Centrophorus granulosus*: A, B: CSIRO H 5851–06, male embryo 392 mm TL; C, D: CSIRO H 4632–05, juvenile male 465 mm TL; E, F: CSIRO H 2572–01, female 688 mm TL; G, H: CSIRO H 5343–07, adult male 1176 mm TL; I, J: CSIRO H 5851–01, female 1540 mm TL.

Snout relatively short, very robust (less so in juveniles <700 mm TL), narrowly triangular in lateral view, apex bluntly pointed; lateral prenarial margin rounded; moderately rounded in dorsal view; horizontal length 0.96 (0.92–1.19; 0.91–1.44) times eye length, 0.73 (0.72–0.92; 0.63–0.86) times interorbital space; horizontal prenarial length 2.26 (1.96–2.47; 2.09–2.55) times in preoral length. Nostrils small, slightly oblique; anterior nasal flap with a large, broadly triangular lobe, and usually with a very small, somewhat rudimentary, pale lobe at inner corner of large lobe; internarial space 2.75 (2.62–3.22; 2.29–2.80) in preoral length, 2.15 (1.41–2.25; 1.70–2.67) times nostril length. Eye moderately large, elongate, length 4.14 (3.26–4.37; 4.08–5.46) in head, 4.22 (2.62–3.84; 2.06–4.90) 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 3.66 (2.58–3.98; 2.34–4.06) 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 3.6 (2.5–3.7; 2.5–4.0)% TL.

Mouth almost transverse, upper jaw slightly concave, width 1.07 (1.05–1.66; 0.90–1.22) in preoral length; lower labial furrows slightly longer than upper furrows; prominent postoral groove, usually more than twice length of upper labial furrows, extending slightly posterolaterally from angle of jaws. Teeth strongly differentiated in upper and lower jaws, with upper teeth much smaller than lower teeth. Upper teeth moderately large, changing with size: near-term embryos (392 mm TL, (CSIRO H 5851–06) with strongly oblique cusps, almost blade-like, somewhat similar in shape to lower teeth, bases overlapping (Figure 7a); a juvenile 465 mm TL (CSIRO H 4632–05) with oblique cusps, less strongly oblique than in embryos, especially anterior-most teeth (Figure 7c); a juvenile 688 mm TL (CSIRO H 2572–01) with mostly erect to slightly oblique cusps, posteriormost teeth semi-oblique (Figure 7e); larger specimens with more erect cusps, becoming slightly oblique posteriorly towards mouth corners, bases slightly overlapping, similar in both adult females and males (Figure 7g, 7i). Lower teeth much larger than uppers: cusps of small juveniles very strongly oblique, blade-like, overlapping, without serrations (Figures 7b, 7d, 7f); in larger specimens, cusp becoming more upright and edges of cusp with regular, fine serrations (Figures 7h, 7j). Sexual dimorphism in dentition was not observed based on the specimens examined.

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 near-term embryos and juveniles (less than 700 mm) raised on low, broad pedicels and tricuspidate; crowns with a long central cusp with a pair of strong lateral cusps, and a low medial ridge; about 0.4–0.5 mm long; often relatively widely spaced, sometimes slightly overlapping (Figures 8a, 8b). Denticles of larger juveniles (874 and 900 mm TL) with lower pedicels, less upright; central cusp shorter and much broader; developing ridges on anterior margin; about 0.6–0.8 mm long; less widely spaced (Figures 8c, 8d). Denticles of a subadult male (1036 mm TL) mostly weakly tricuspidate, 0.5–0.8 mm long; some denticles much larger, flat, tear-drop shaped with one long posterior cusp, no lateral cusps, about 0.8–0.9 mm long (Figure 8e). Denticles of a subadult female (1110 mm TL) flat, tear-drop shaped, varying in size from 0.7–1.0 mm long; some denticles much broader; mostly not overlapping, but close set (Figure 8f). Denticles of larger specimens (>1200 mm TL) with mostly broader, tear-drop shaped crowns; anterior margin with low blunt ridges; varying in size and proportions, some with more pointed cusps and some with wider interspaces; mostly close-set and not overlapping (Figures 8g, 8h).

First dorsal fin relatively low, long; length 3.89 (3.50–4.39; 3.11–4.73) times its height, 1.28 (1.10–1.43; 1.17–1.57) times second dorsal-fin length; soft-fin length 2.69 (2.15–2.82; 2.20–2.96) times its height; height 1.01 (0.85–1.00; 0.83–1.17) times second dorsal-fin height; anterior margin strongly convex; apex broadly rounded; posterior margin weakly concave to nearly straight, slanting well posteroventrally from top to bottom; free rear tip long, relatively thick basally; inner margin of fin straight to very weakly concave, 1.86 (1.81–2.33; 1.79–2.15) in soft-fin length, 1.45 (1.04–1.42; 1.08–1.55) times its height; insertion extremely well forward of pelvic-fin origin, pelvic-fin midpoint to first dorsal-fin insertion 17.0 (11.9–16.0; 15.5–20.1)% TL; base of exposed fin spine anterior to pectoral-fin free rear tip in adults (slightly posterior in the smallest juveniles); spine base broad, exposed anteriorly just above junction of spine and soft portion of fin; exposed fin spine short (longer in juveniles), robust, tapering distally (tip often damaged in adults), anterior margin almost straight; exposed portion of spine sloping strongly posterodorsally from base (of exposed portion) to apex, subequal in length to exposed portion of second dorsal-fin spine in adults (much shorter in juveniles), exposed first dorsal spine length 0.19 (0.14–0.35; 0.13–0.33) times height of fin.



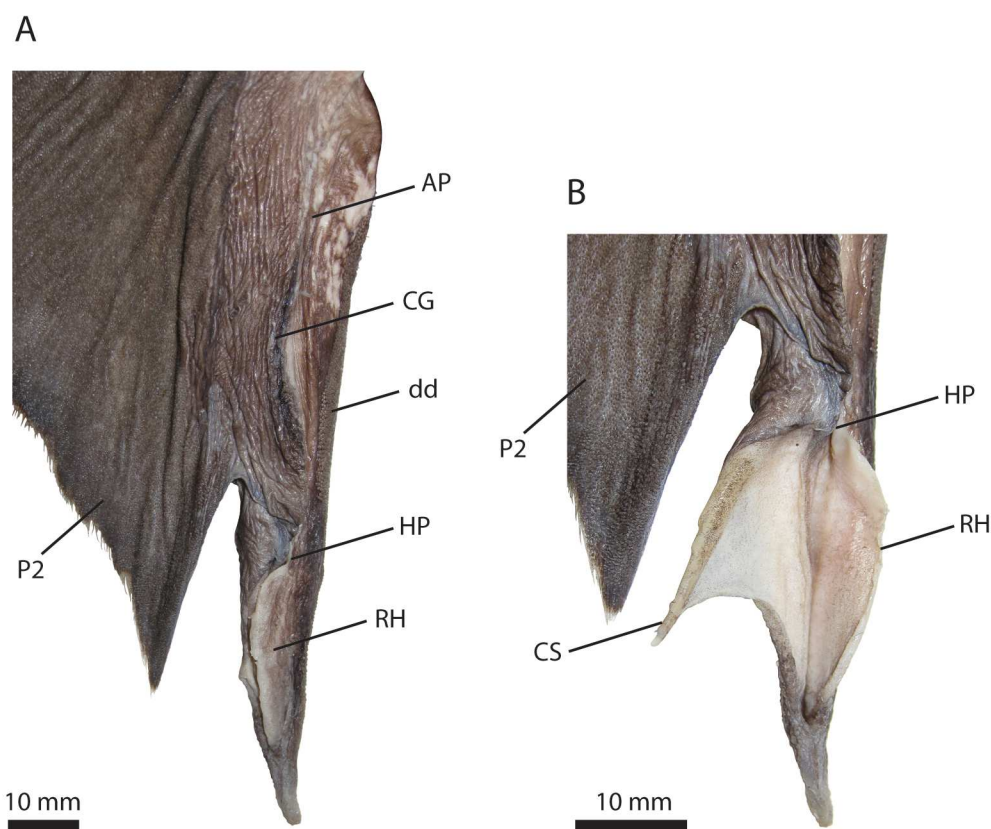
**FIGURE 8.** Lateral trunk denticles (from below first dorsal fin) of *Centrophorus granulosus*: A. CSIRO H 5860–05, male embryo 350 mm TL; B. CSIRO H 4632–05, juvenile male 465 mm TL; C. NMMBP 15808, juvenile female 874 mm TL; D. NMMBP 15830, juvenile male 900 mm TL; E. NMMBP 15816, subadult male 1036 mm TL; F. CAS 234914, female 1138 mm TL; G. CAS 234922, adult male 1261 mm TL; H. CAS 234926, female 1350 mm TL.



Second dorsal fin large, only slightly smaller in area compared to first dorsal fin, moderately long; second dorsal-fin length 3.05 (2.53–3.35; 2.48–3.43) times its height; anterior margin slightly to moderately convex; apex rounded; posterior margin weakly concave to weakly convex, sloping strongly posteroventrally from apex; free rear tip long, thick basally, inner margin length 2.04 (2.07–2.44; 1.97–2.66) in soft-fin length, 1.10 (1.08–1.43; 1.02–1.44) times fin height; spine length 0.23 (0.31–0.50; 0.13–0.41) in height of fin; base of exposed fin spine anterior to or level with pelvic-fin free rear tip, exposed just above level of junction with spine and soft portion of fin; exposed fin spine short (longer in juveniles; 1.8–2.6% TL in individuals <700 mm TL vs. 0.7–1.8% TL in specimens >820 mm TL), robust, broad based, tapering rapidly distally, pointed in juveniles and smaller subadults, eroded with rounded tips in large specimens.

Pectoral fins large (moderately large in juveniles <700 mm TL; anterior margin 9.8–11.1% TL in individuals <700 mm TL vs. 10.5–13.6% TL in individuals >820 mm TL); anterior margin weakly convex, its length 13.1 (9.8–11.1; 10.5–13.6)% TL; base very short, 2.40 (2.07–2.40; 1.98–3.16) 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; free rear tip moderately elongate in adults (only slightly produced in small juveniles; 0.9–2.2% TL in individuals <700 mm TL vs. 1.7–4.1% TL in individuals >820 mm TL), free rear tip 3.38 (4.03–11.1; 3.15–6.03) in inner margin, extending past level of exposed first dorsal-fin spine in adults; origin situated at level of mid-fifth gill slit, partially obscured by gill membrane.

Pelvic fins moderately large, length 12.4 (9.4–10.9; 10.3–12.7)% TL, 1.14 (0.92–1.09; 0.97–1.18) times second dorsal-fin soft length; anterior margin almost straight; apex moderately rounded; posterior margin weakly to moderately concave; free rear tip angular, inner margin almost straight to weakly convex. Claspers of adult males moderately long, slender; tapering to a fleshy, narrowly rounded tip; outer length 3.4–4.4% TL, 3.04–4.51 times its base length (n = 18); clasper glans about 0.4 in clasper inner length; apophyle and hypophyle connected by long clasper groove; rhipidion large, laterally expanded, extended from hypophyle to anterior of clasper tip; lateral edge with a large, straight spine; dermal denticles mostly absent from dorsal surface, except on lateral edges (Figure 9).



**FIGURE 9.** Clasper (left) of *Centrophorus granulatus* (CSIRO H 5343–07, adult male 1176 mm TL). A, Glans not dilated; B, Glans spread. Abbreviations: AP, apophyle; CG, clasper groove; CS, clasper spine; dd, dermal denticles; HP, hypophyle; P2, pelvic fin; RH, rhipidion.

Caudal fin relatively long, deep, broad; dorsal margin almost straight, 1.36 (1.10–1.35; 1.07–1.43) in head length, 1.31 (1.31–1.56; 1.19–1.79) times preventral margin; preventral margin weakly convex, apex moderately rounded; upper postventral margin weakly convex, lower postventral margin almost straight, angle between postventral margins moderately concave; terminal lobe moderately large, lobe length 2.10 (1.87–2.96; 1.94–2.57) in dorsal caudal margin, terminal margin almost straight to slightly undulating; apex of upper lobe moderately rounded.

**Meristic data.** Total vertebral centra 106–115 (n = 10), monospondylous precaudal centra 51–57, diplospondylous precaudal centra 25–30, total precaudal centra 77–85 and diplospondylous caudal centra 28–32. Teeth count (n = 9): 16–19 + 16–18 / 13–16 + 14–17; total 30–37/27–32.

**Colour.** Uniformly brownish to greyish brown dorsally (near-term embryos greyish, slightly paler ventrally; waterline between dorsal and ventral colour shades very diffuse on lower sides; sometimes with numerous white (deciduous) denticles; sometimes a pale, central blotch on dorsal surface of snout at level of anterior eye (most obvious in smaller specimens). Fins without distinct markings in adults; dorsal and caudal fins of juveniles usually much darker and sometimes with a white posterior margin (usually only the posterior margin of the caudal terminal lobe and ventral lobe white); pectoral-fin free rear tip whitish in the smallest juveniles; fin spines greyish to brownish. Eyes greenish in life.

**Size and biology.** The females and males examined in this study ranged in length from 321–1650 mm and 308–1237 mm, respectively; 11 of the embryos examined were from a 1650 mm TL pregnant female that was not retained. The largest specimen (1650 mm TL) examined is close to that previously recorded for this species (designated as *C. niaukang*), i.e. 1660 mm TL by Bañón *et al.* (2008), and 1700 mm TL by Compagno *et al.* (2005) and Last & Stevens (2009). Cotton (2010) recorded a maximum size for females and males of 1725 and 1240 mm TL, respectively. Four females between 1345 and 1460 mm TL were adolescent females and five females examined between 1500 and 1650 mm TL were pregnant. This agrees with Bañón *et al.* (2008) who recorded a length at 50% maturity for females of 1470 mm TL, with the smallest mature female 1380 mm TL. Cotton (2010) reported a size at 50% maturity for females of 1430 mm TL from the western North Atlantic, with the smallest mature female 1460 mm TL and largest immature female 1630 mm TL, based on 111 females examined. Compagno *et al.* (2005) stated that females are mature at 1300–1400 mm TL (as *C. niaukang*), but this is likely an underestimate of female maturity size for this species. Two males of 1036 and 1078 mm TL were adolescent, i.e. possessed partially calcified claspers, and 19 males between 1051 and 1237 mm TL were adult, i.e. possessed fully calcified claspers. Bañón *et al.* (2008) stated that the smallest mature male they examined was 1180 mm TL and largest immature male was 1150 mm TL. Cotton (2010) reported a size at 50% maturity for males of 1100 mm TL from the western North Atlantic, based on 20 specimens examined. Thus, the length at maturity for males of *C. granulatus* is about 1050–1180 mm. The length at maturity of 900–1100 mm given by Compagno *et al.* (2005) is too small for this species.

A total of 12 near-term embryos were examined in this study ranging from 350–420 mm TL; newborn individuals with yolk-sac scars ranged from 378 to 393 mm TL. Bañón *et al.* (2008) recorded 13 near-term embryos ranging from 350 to 470 mm TL (mean 400 mm TL). Size at birth in this species is thus between 350 and 470 mm TL. Compagno *et al.* (2005) reported a litter size of 4–6 for this species (as *C. niaukang*), and Bañón *et al.* (2008) reported up to 6 pups per litter. A 1650 mm TL pregnant female from the southwestern Indian Ocean, which was not retained, contained a litter of 11 pups (CSIRO H 5851–02 to –12). Two females examined off South Africa by one of the authors of this paper (DAE) were pregnant and each contained 6 large freshly fertilised eggs *in utero* (80–94 mm diameter). Six pregnant females were examined by an author (DAE) from Da-xi fish market in Taiwan in 1988 which contained about 3–6 large yolked eggs *in utero*. In the western North Atlantic, pregnant females had litters of 4–8 with no relationship between female size and fecundity; mating appears to be asynchronous, with concurrent ovarian development; ripe oocytes about 100 mm in diameter; pregnant females tend to segregate from the rest of the population (Cotton, 2010).

**Distribution.** *Centrophorus granulatus* has a wide distribution in all ocean basins except the Eastern Pacific (Figure 10). Although its currently reported distribution is somewhat scattered, this is likely due to the difficulties in accurately identifying *Centrophorus* species. The distribution for *C. granulatus* given below is based on specimen records or published records that could be verified by images. *Western Atlantic:* reported from off Puerto Rico and the U.S. Virgin Islands in the Caribbean Sea; one specimen observed north of the Hudson Canyon, off New Jersey (L. Natanson, pers. comm.); from off Norfolk and Washington Canyons, Virginia (37.5° N) and off

Cape Hatteras, North Carolina (34.5° N) to off southern Florida (26.5° N) in the U.S. Atlantic; from offshore of the Mississippi River Delta (90.5° W), off the Florida panhandle (Desoto Canyon), off Tampa Bay (26°55' N, 84°53' W) to the Florida Straits (Dry Tortugas, 83.8° W) in the Gulf of Mexico (Kiraly *et al.*, 2003; Castro, 2011; Cotton, unpubl. data, as *C. niaukang*); reports of this species off Brazil (e.g. Soto, 2001) need to be confirmed and possibly are misidentifications; the image of this species in Uyeno *et al.* (1983) from off Suriname and French Guinea are not conspecific with the true *C. granulatus*. *Eastern Atlantic*: probably wide ranging but commonly confused with *C. lusitanicus* and *C. niaukang* in the literature; recorded from west of Scotland (57°40' N, ZMH specimen); on the Galicia Bank, Spain (42°67' N) (Bañón *et al.*, 2008); off Sesimbra, Portugal (A. Veríssimo, pers. obs.); off the Canary Islands, North Africa (28° N) (specimens examined in this study; Brito, 2002); off Western Sahara (26° 10' N) (Iglésias pers. comm.); SAM specimen collected off Saldanha, South Africa (32°16' S). *Western Indian*: off KwaZulu-Natal in South Africa and Mozambique (Bass *et al.*, 1986; Compagno *et al.*, 1989, as *C. lusitanicus*; DAE unpubl. data); BMNH and HJ specimens collected from off Providence Atoll, Cerf Island and Alphonse Group, Seychelles; CAS and CSIRO specimens collected from southern Madagascar Ridge and the South West Indian Ridge (36–39° S, 48–52° E); off the northeast end of Thaa and Laamu Atolls in the Maldives (~02°20' N, 73°40' E) (Adam *et al.*, 1998, as *C. niaukang*). *Eastern Indian & South-west Pacific*: in Indonesia based on a specimen from off Cilacap, Central Java (~07°50' S, 109°00' E) and record from off Lombok (~08°50' S, 116°35' E) (White *et al.*, 2006, as *C. niaukang*); in Australia, specimens from west of Dirk Hartog Island (26°05' S) to west of Montebello Islands (20°25' S) in Western Australia, and from off Wooli in New South Wales (29°58' S) to northeast Queensland. *North-west Pacific*: from the East China Sea (30°35' N, 128°54' E) (Deng *et al.*, 1985, as *C. robustus*); off eastern and southern Taiwan; in Japan from the Okinawa Trough (~25°30' S) (Yano & Kugai, 1993, as *C. niaukang*) north to Sagami-Nada (~34°50' S) (Nakabo, 2002, as *C. acus*). Recorded from depths of 98–1700 m (Nakabo, 2002; Last & Stevens, 2009).

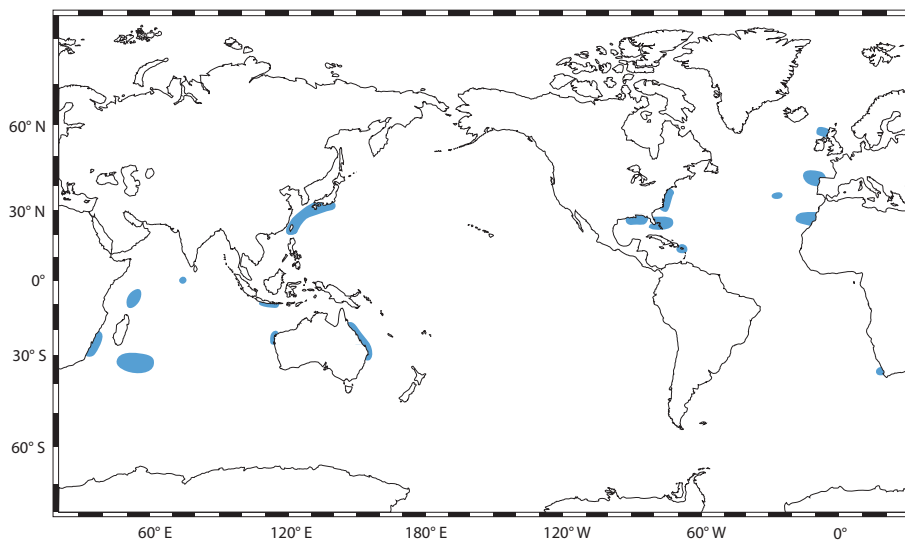
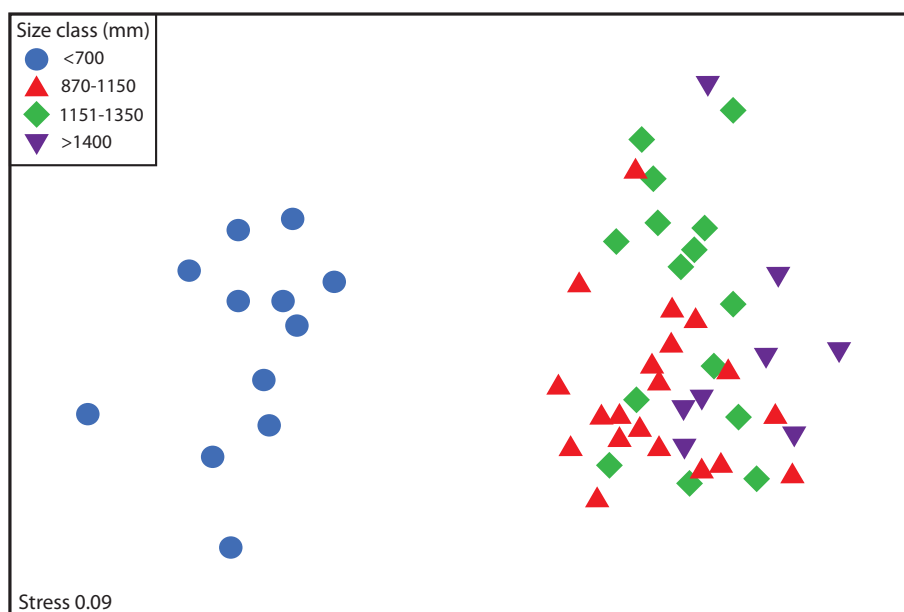


FIGURE 10. Distribution of *Centrophorus granulatus* based on specimens examined or validated literature records.

**Non-metric multidimensional scaling (MDS) ordination of morphometric characters.** The MDS analysis of the measured *Centrophorus granulatus* individuals showed clear differences between the size classes (Figure 11), particularly between the smallest individuals (<700 mm TL) and larger individuals >820 mm TL. Individuals in the smallest size class (<700 mm TL) grouped to the left of the plot, while those in the larger size classes were located on the right of the plot with a clear distinction between these size classes. Within the larger size classes, a similar left to right trend was also apparent albeit with many overlapping data points within the three size classes. ANOSIM showed the size classes were significantly different overall ( $P < 0.01$ ;  $R^2 = 0.548$ ); pairwise comparisons were significantly different for the <700 mm size class vs. the three larger size classes ( $P < 0.01$ ;  $R^2 = 0.985-1$ ). The pairwise comparisons for the 870–1150 mm vs. 1151–1350 and >1400 mm size classes were also significantly different ( $P < 0.5$ ), but with very low  $R^2$  values (0.190 and 0.253 respectively). The measurements shown by SIMPER to be the most responsible for the differences between the smallest size class and the three larger ones are

(in order of importance): pectoral–pelvic space; first dorsal midpoint–pelvic origin; first dorsal midpoint–pectoral insertion; prepelvic length; pelvic midpoint–first dorsal insertion; and pre-second dorsal length.



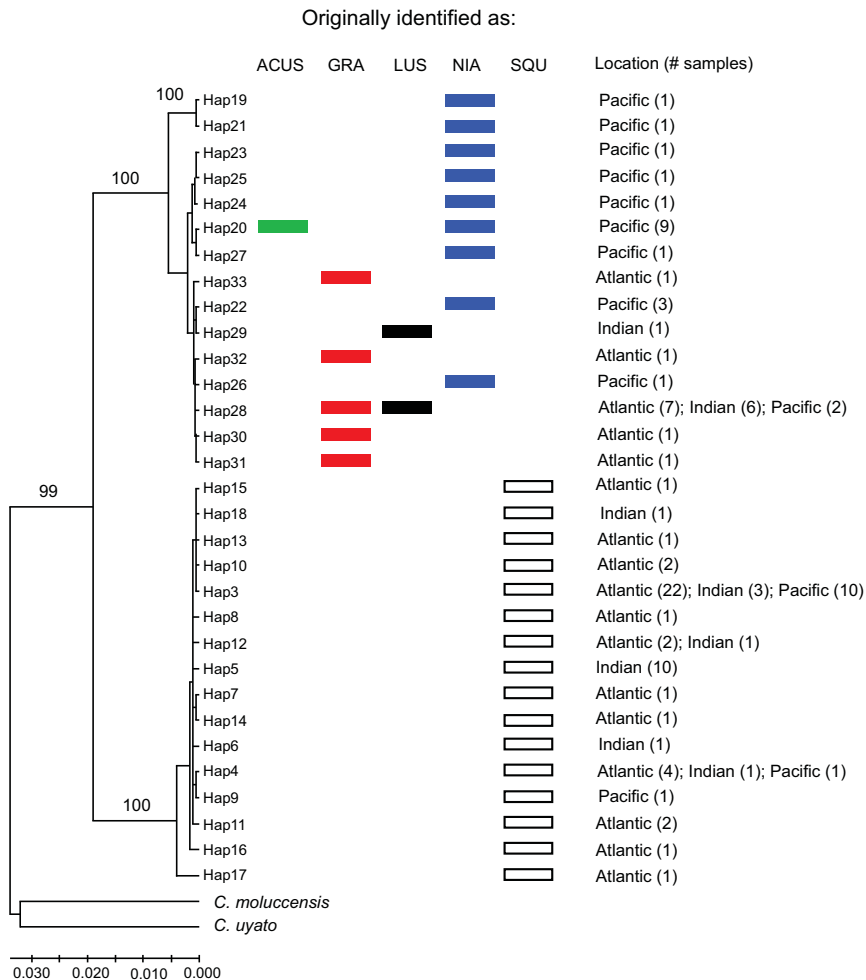
**FIGURE 11.** Non-metric multidimensional scaling (MDS) ordination of *Centrophorus granulosus* morphometric percentages (% TL) by size class.

**Molecular analyses.** All specimens originally assigned to *C. acus*, *C. lusitanicus*, *C. niaukang* and *C. granulosus* have similar sequences, and as a result fall in the same clade together (Figure 12). Some haplotypes were shared between *C. acus* and *C. niaukang* (e.g. Hap20), and between *C. granulosus* and *C. lusitanicus* (e.g. Hap28). The bootstrap support for this clade was 100%, and the average number of differences among sequences was  $3.1 \pm 0.9$  (minimum – maximum: 0–13;  $n=39$ ). All subclades had low bootstrap support values except for two relatively well differentiated haplotypes from Australia (Hap19 and Hap21; 100% bootstrap support), which exhibited between 10 and 13 nucleotide differences to the remaining haplotypes. By contrast, all specimens identified as *C. squamosus* clustered together in a distinct clade to the exclusion of specimens assigned to any other species. The *C. squamosus* clade also exhibited a high bootstrap support value (e.g. 100%), with an average number of differences among sequences of  $1.3 \pm 0.3$  (minimum – maximum: 0–9;  $n=62$ ). Both clades included representatives from the Atlantic, Indian and Pacific Ocean basins.

## Discussion

### Intraspecific morphological variation

*Centrophorus granulosus* undergoes substantial ontogenetic changes in morphology which have not been thoroughly investigated previously. The MDS analysis of the morphometric characters highlighted a major ontogenetic shift in morphology between the smallest juveniles (<700 mm TL) and larger juveniles, subadults and adults (>820 mm TL) (Figure 11). This also coincides with the sizes at which the upper teeth and denticle morphology undergo the biggest changes. The upper teeth of a near-term embryo and small juvenile (392 and 465 mm TL) had strongly oblique cusps, whilst those of a 688 mm TL individual and larger individuals had mostly erect to slightly oblique cusps. The lateral trunk denticles of near-term embryos and individuals <700 mm TL were raised on low, broad pedicels and had strongly tricuspidate crowns. Large individuals >1100 mm TL had low, flat, tear-drop shaped denticles with one long posterior cusp. Individuals with lengths between 874 and 1036 mm TL usually had a mixture of denticle types, some small and tricuspid, some large and tear-drop shaped, and some intermediate of the two. Since denticle morphology is considered an important character for identification of squaloid species, this highlights the critical importance of understanding the changes in denticle morphology throughout life of such species.



**FIGURE 12.** Neighbour-Joining tree of p-distances among unique ND2 haplotypes. Bootstrap support values based on 10000 replicates are indicated over tree branches if >90%. Haplotypes found in specimens originally identified as *Centrophorus acus* (ACUS, green blocks), *Centrophorus granulosus* (GRA, red blocks), *Centrophorus lusitanicus* (LUS, black blocks), *Centrophorus niauakang* (NIA, blue blocks) and *Centrophorus squamosus* (SQU, open blocks). Location and number of duplicate haplotypes are indicated in the rightmost column.

Small individuals (<700 mm TL) of *Centrophorus granulosus* differed from larger individuals (>820 mm TL) in the following morphological characters: longer anterior head and snout (prespiracular length 13.6–15.9 vs. 11.4–13.7% TL; snout to inner nostril 5.1–5.9 vs. 3.6–5.0; horizontal prenarial length 4.8–5.4 vs. 3.4–4.7% TL; preoral length 9.9–12.1 vs. 8.0–10.1% TL); larger eyes (eye length 5.9–7.5 vs. 4.3–5.9% TL); paired fins closer together (pectoral–pelvic space 27.4–31.6 vs. 32.0–39.2% TL; first dorsal midpoint–pectoral insertion 7.7–10.9 vs. 10.4–15.2% TL; pelvic midpoint–first dorsal insertion 11.9–16.0 vs. 15.5–20.1% TL); taller second dorsal spine (exposed spine length 1.8–2.6 vs. 0.7–1.8% TL); shorter pre-vent length (56.6–59.8 vs. 59.3–64.6% TL).

#### Status of *Centrophorus acus*

Garman's (1906) description of the holotype of *Centrophorus acus* (MCZ S-1049) commences with the statement that its outline, dentition and squamation resemble those of *C. granulosus*, but no distinguishing features between the two species are provided. Although the description is brief and lacks an illustration, it does contain the following key characters: 'hinder angles of pectorals and ventrals slightly produced', 'Scales small, with stout stalks, and with several keels on the crowns, the median one of which ends in a sharp cusp; lateral cusps rudimentary...', and 'Brown, nearly uniform, sprinkled with white single scales.'. The slightly produced pectoral-fin free rear tip differentiates this species from *C. squamosus*, which doesn't have a produced free rear tip. In fact, *C. squamosus* has a far shorter pectoral-fin free rear tip than the majority of other *Centrophorus* species. The length of the free rear tip of the 820 mm TL *C. acus* holotype matches similar-sized specimens of *C. granulosus* that were

previously identified as *C. niaukang*, i.e. inner margin length of *C. acus* holotype 9.5%TL vs. 9.7 and 9.8% TL for a 688 and an 874 mm TL individual, respectively.

The morphology of the lateral trunk denticles of the holotype of *C. acus* are almost identical with those of a 874 mm TL specimen of *C. granulatus* (see Figure 8c) and represent the transitional phase between the strongly tricuspidate juvenile denticles and the broader, flatter, single cusped adult denticles. The reference to the stout stalks (=pedicels) is also an important feature which separates this species from *C. squamosus* which has taller, narrow pedicels. This feature is consistent with similar-sized *C. granulatus* specimens, and in larger specimens the pedicels become much reduced and the denticles become flattened and not on pedicels. The uniform brownish colouration is another character consistent with *C. granulatus*, and the white single scales refers to the scattering of deciduous denticles which many specimens of *C. granulatus* examined possessed.

Following examination of the immature holotype of *C. acus* (820 mm TL) and comparison with similar-sized specimens of *C. granulatus* (mostly previously identified as *C. niaukang*), it is concluded that these two species are conspecific and that *C. acus* should be considered a junior synonym of *C. granulatus*. Table 3 shows the ranges in measurements and vertebral counts between specimens of this taxon which were previously referred to as *C. granulatus*, *C. niaukang* or *C. acus*.

**TABLE 3.** Proportional dimensions as percentages of total length and vertebral counts for specimens originally identified as: *C. granulatus* (neotype and 4 other specimens); *C. niaukang* (specimen of same sex and size as lost holotype and 44 other specimens); *C. acus* (holotype and 7 other specimens).

	<i>C. granulatus</i>			<i>C. niaukang</i>			<i>C. acus</i>		
	Neotype	n = 4		CSIRO H 7035-03	n = 44		Holotype	n = 7	
		Min.	Max.		Min.	Max.		Min.	Max.
Total length (mm)	1241	1131	1575	1532	370	1623	820	308	688
Precaudal length	81.5	80.6	83.1	82.4	76.4	82.9	80.4	77.3	79.7
Pre-second dorsal length	61.8	62.0	64.7	64.7	60.2	67.8	63.7	59.7	62.9
Pre-first dorsal length	30.3	29.3	32.5	30.7	28.3	36.0	0.0	27.9	33.7
Pre-first dorsal length (horiz.)	30.2	29.2	30.3	30.4	27.8	35.7	27.7	27.1	33.1
Pre-vent length	59.8	60.2	64.4	63.4	57.1	64.6	60.1	56.6	59.8
Prepelvic length	58.5	57.7	62.1	61.5	55.4	63.2	57.2	55.5	58.0
Prepectoral length	25.4	21.2	22.3	22.4	19.9	25.2	20.5	23.1	26.5
Head length	24.6	21.6	22.7	22.2	20.6	25.9	-	23.2	26.1
Head length (horiz.)	23.7	21.3	22.2	21.4	20.2	25.4	22.2	22.9	25.9
Prebranchial length	20.8	18.5	19.3	19.0	17.8	23.0	19.1	20.4	23.3
Prespiracular length	12.5	11.6	11.8	11.4	11.6	15.7	12.6	13.6	15.9
Preorbital length	7.0	5.9	6.1	6.3	5.9	8.5	-	7.5	8.4
Preorbital length (horiz.)	5.7	4.8	5.6	5.5	5.3	7.5	5.7	6.8	8.1
Snout to inner nostril	4.5	3.6	4.3	4.3	4.0	5.8	-	5.1	5.9
Prenarial length (horiz.)	4.2	3.4	3.8	3.9	3.5	5.2	3.4	4.8	5.4
Preoral length	9.6	8.0	9.0	8.9	8.1	12.0	8.7	9.9	12.1
Inner nostril-labial furrow space	6.5	5.5	5.7	5.6	5.2	7.4	-	6.4	7.8
Mouth width	9.0	8.5	9.1	8.3	6.8	9.8	7.1	8.3	10.4
Upper labial furrow length	2.1	1.4	2.0	1.5	1.2	2.4	2.0	1.6	2.6
Nostril width	1.6	1.5	1.8	1.5	1.4	2.5	1.6	1.9	2.5
Internarial space	3.5	3.2	3.6	3.9	3.1	4.2	3.8	3.4	4.3
Interorbital space	7.8	7.6	8.7	8.3	7.2	9.4	7.2	8.5	10.0
Eye length	5.9	4.6	5.3	4.6	4.3	7.1	4.6	6.4	7.5
Eye height	1.4	1.4	2.2	1.7	1.1	2.4	1.2	1.7	2.3

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TABLE 3 (continued)

	<i>C. granulosis</i>			<i>C. niukang</i>			<i>C. acus</i>		
	Neotype	n = 4		CSIRO H 7035-03	n = 44		Holotype	n = 7	
		Min.	Max.		Min.	Max.		Min.	Max.
Spiracle diameter - greatest	1.6	1.6	2.0	1.6	1.4	2.3	1.7	1.9	2.5
First gill-slit height	2.4	1.9	2.6	2.6	1.9	3.3	2.1	2.1	2.9
Fifth gill-slit height	3.6	2.6	3.5	2.9	2.4	4.0	2.7	2.5	3.7
Interdorsal space	17.5	17.7	20.8	19.6	14.6	21.1	20.4	15.5	18.9
Dorsal-caudal space	6.1	5.8	6.7	5.1	4.9	7.5	5.9	6.0	7.4
Pectoral-pelvic space	34.0	32.1	39.1	39.2	28.9	38.2	31.7	27.4	31.5
Pelvic-caudal space	13.5	12.6	14.1	12.4	10.1	13.3	14.6	11.1	12.5
First dorsal length	23.0	20.7	22.6	-	17.9	26.9	23.8	17.6	21.0
First dorsal soft fin length	15.9	13.8	14.4	-	11.7	16.6	-	11.0	12.8
First dorsal anterior margin	12.5	12.0	13.1	11.3	9.2	15.0	12.8	9.8	13.6
First dorsal base length	14.5	13.6	15.5	13.2	11.5	17.3	16.6	11.8	15.3
First dorsal height	5.9	5.0	5.5	5.3	4.8	6.5	5.7	4.4	5.6
First dorsal inner margin	8.5	7.0	7.5	-	5.4	8.7	6.8	5.4	6.5
First dorsal posterior margin	12.2	10.0	11.4	-	9.3	13.1	12.1	7.9	9.7
First dorsal exposed spine length	1.1	0.0	0.0	-	0.8	1.9	1.7	0.8	1.7
First dorsal spine base width	0.6	0.5	0.8	-	0.4	0.8	-	0.5	0.6
Second dorsal length	17.9	15.8	16.4	-	14.2	17.8	15.1	14.7	16.3
Second dorsal soft fin length	10.9	9.9	10.9	-	9.6	11.6	-	9.3	10.3
Second dorsal anterior margin	11.4	8.1	10.4	9.2	7.6	12.1	8.9	9.3	11.7
Second dorsal base length	12.6	10.9	12.6	10.4	9.7	13.7	10.6	10.4	12.1
Second dorsal height	5.9	4.8	5.8	5.7	4.9	6.5	5.4	4.8	5.8
Second dorsal inner margin	5.3	4.0	4.6	-	3.8	5.5	4.3	4.0	4.9
Second dorsal posterior margin	8.7	8.4	9.6	-	7.4	10.5	8.7	7.4	8.8
Second dorsal exposed spine length	1.4	1.2	1.2	-	0.7	2.5	2.2	1.8	2.6
Second dorsal spine base width	0.6	0.5	0.6	-	0.4	0.7	0.0	0.5	0.9
Pectoral anterior margin	13.1	10.5	12.6	11.7	10.5	13.6	11.6	9.8	11.1
Pectoral inner margin	13.4	10.3	12.1	10.9	9.0	14.0	9.5	8.7	10.3
Pectoral base length	5.5	4.3	5.0	4.7	3.8	6.0	5.9	4.4	5.1
Pectoral height	11.1	9.3	11.2	10.5	8.1	11.9	7.9	7.5	9.6
Pectoral free rear tip extension	4.0	2.4	3.2	3.0	1.3	4.1	-	0.9	2.2
Pectoral posterior margin	9.9	8.5	9.5	9.0	7.4	10.9	7.9	6.0	8.6
Pelvic length	12.4	10.3	11.9	11.1	9.5	12.7	11.0	9.4	10.2
Pelvic height	6.2	5.4	5.9	6.3	4.3	6.7	5.2	3.7	4.9
Pelvic inner margin	7.0	5.9	6.4	6.2	4.7	8.5	5.5	4.6	5.5
Dorsal caudal margin	18.1	16.2	18.8	16.5	16.4	20.7	19.0	20.4	22.1
Preventral caudal margin	13.9	11.6	13.6	13.2	12.2	15.1	10.6	14.1	15.2
Upper postventral caudal margin	7.9	7.7	9.1	7.5	6.7	9.6	6.7	8.1	10.4
Lower postventral caudal margin	3.8	3.4	4.9	4.1	3.2	5.2	3.7	2.8	5.1
Caudal fork width	7.8	6.9	7.6	7.6	6.6	8.1	-	6.9	7.8
Caudal fork length	13.6	10.9	13.8	12.2	11.3	15.5	10.7	14.5	15.6
Caudal terminal lobe	8.6	6.5	8.2	8.5	7.2	10.6	8.0	7.4	9.0

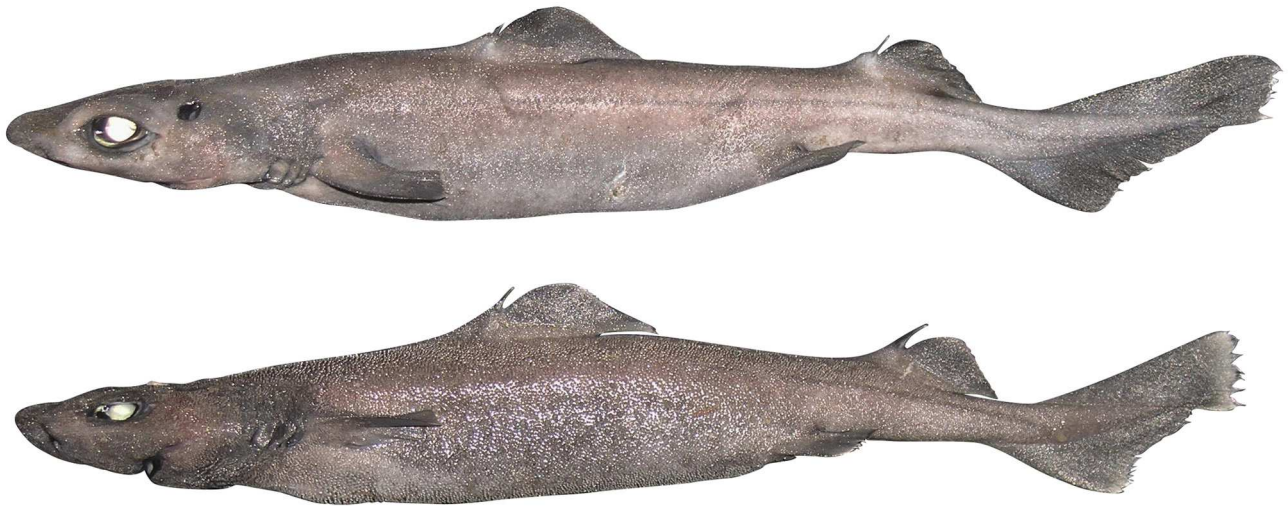
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TABLE 3 (continued)

	<i>C. granulosus</i>			<i>C. niaukang</i>			<i>C. acus</i>		
	Neotype	n = 4		CSIRO H 7035-03	n = 44		Holotype	n = 7	
		Min.	Max.		Min.	Max.		Min.	Max.
Caudal subterminal fin margin	2.7	2.6	3.0	2.9	2.0	4.2	2.9	3.4	4.6
Head width at anterior of nostrils	6.3	5.5	6.2	6.0	5.7	7.8	-	6.4	7.6
Head width at mouth	9.7	9.6	10.8	10.3	9.2	12.5	-	10.5	11.7
Head width	13.8	11.0	13.0	13.0	11.2	14.8	10.7	10.8	13.8
Trunk width	9.4	8.2	11.9	13.2	8.2	12.9	8.2	9.2	11.7
Abdomen width	8.3	7.4	13.8	14.6	7.4	14.1	-	8.7	9.9
Tail width	5.0	5.0	5.6	5.6	4.0	6.0	-	3.4	4.9
Caudal peduncle width	2.7	2.2	2.8	2.5	2.0	2.8	2.2	1.7	2.5
Head height	12.7	11.1	12.4	12.6	8.4	13.9	10.1	7.8	10.9
Trunk height	14.9	12.5	14.3	14.0	8.3	14.5	10.9	10.8	13.4
Abdomen height	14.9	12.4	15.7	15.9	8.6	16.2	-	10.4	13.0
Tail height	8.3	6.8	8.0	8.0	6.6	8.4	-	5.2	7.6
Caudal peduncle height	4.2	3.8	4.2	4.6	3.6	4.7	4.0	3.5	4.4
Clasper outer length	-	3.6	4.4	-	3.6	4.4	-	-	-
Clasper inner length	-	8.9	10.5	-	8.9	11.5	-	-	-
Clasper base width	-	0.9	1.1	-	0.9	1.2	-	-	-
First dorsal midpoint–pectoral insertion	10.6	10.5	12.6	12.9	9.4	15.2	9.3	7.7	10.7
First dorsal midpoint–pelvic origin	20.2	20.2	24.8	24.1	17.0	22.9	22.1	15.6	20.8
Pelvic midpoint–first dorsal insertion	17.0	15.7	20.1	19.7	13.1	18.8	16.3	11.9	16.0
Pelvic midpoint–second dorsal origin	1.2	1.9	2.4	1.2	0.5	4.1	4.6	1.8	4.4
<b>Vertebral counts</b>		n = 2			n = 4			n = 3	
Monospondulous	-	51	56	53	52	57	-	54	54
Diplospondylous - trunk	-	26	26	27	25	29	-	26	30
Diplospondylous - caudal	-	29	32	30	28	31	-	28	29
Precaudal	-	77	82	80	77	85	-	80	84
Total	-	109	111	110	106	115	-	108	113

*Centrophorus steindachneri* Pietschmann, 1907 is considered a synonym of *C. acus* (e.g. Compagno, 1984), but the two syntypes have been previously reported as lost. During a recent visit to the NMW fish collection in Vienna, one of the syntypes was located by the collection manager and was examined by one of us (WW). This specimen, NMW 61300, is juvenile male from Yokohama in Japan and has a length of 426 mm TL, which matches the size of the specimens described by Pietschmann (1907 and 1908), i.e. 426 and 431 mm TL. Thus, we agree that this specimen is a syntype of *C. steindachneri* and designate this specimen as the lectotype. This specimen (Figure 13) agrees with similar-sized *C. granulosus* specimens examined in this study and is thus considered a junior synonym of *C. granulosus*. *Centrophorus drygalskii* Engelhardt, 1912 was previously considered to be a possible synonym of *C. acus*, the types of which were destroyed during WWII (Neumann, 2006). Although no illustration was provided, the description includes the following (translated): “the surface is very rough. The denticles are coarse, stand-off strongly the skin and not close together” and “gill area, the centre line of the belly and the fins are coloured somewhat blackish”. These characters more closely align with *C. squamosus* than *C. granulosus*, with the exception of the denticles not close together which may be a translational or interpretation issue. Based on this, we consider *C. drygalskii* is probably a junior synonym of *C. squamosus*.





**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*.

#### Status of *Centrophorus niaukang*

During a recent visit by the senior author to the Taiwan Fisheries Research Institute (TFRI) in Keelung, the holotype of *Centrophorus niaukang* (TFRI 3612) could not be located and the only available specimen of this species was an adult male of 1167 mm TL (FRIP 3674). This specimen was presented to us as being the possible holotype but the type specimen of Teng (1959) was a mature female 1540 mm TL. It thus seems that the holotype of *Centrophorus niaukang* has been misplaced. Fortunately, several large females (1343–1623 mm TL) collected from Taiwan by one of us (HH) all agree well with the original description of *C. niaukang* by Teng. In his description, Teng (1959) states that the new *C. niaukang* is closely related to *C. acus*, especially in shape of pectoral-fin free rear tip, but differs in a number of characters. Firstly, the denticles of *C. niaukang* are considered to be thorn-like while in *C. acus* they are tricuspidate. This difference can be reconciled by changes in denticle morphology with growth, as shown in Figure 8. Juveniles have strongly tricuspid denticles, while a specimen of 874 mm TL possessed weakly tricuspid denticles and larger specimens had thorn-like denticles.

The second character used to distinguish these two species is the dorsal spines' length, with *C. acus* possessing prominent, well-exposed dorsal spines while *C. niaukang* possesses low and largely covered dorsal spines. This character is also attributable to ontogenetic differences with large specimens >1300 mm TL having very low and worn dorsal spines (<0.9% TL) compared to a well exposed spine length in the *C. acus* holotype (of 1.7% TL). Thirdly, Teng (1959) indicates that the second dorsal fin is much larger than ventrals (=pelvic fins) in *C. acus* while it is subequal in size in *C. niaukang*. Again, these differences are attributable to ontogenetic changes where juveniles possess smaller pelvic fins than adults. This is highlighted by the measurements taken in this study, i.e. pelvic-fin height in juveniles <820 mm TL (including *C. acus* holotype) 3.7–5.2 vs. 4.7–6.7% TL in specimens >820 mm TL. The final distinguishing character stated by Teng (1959) is the presence of only faint, irregular serrations on lower teeth in *C. acus* vs. distinct, regular, fine serrations on lower teeth in *C. niaukang*. This feature also varies between juveniles and adults. The lower teeth of adult specimens previously referred to as *C. niaukang* possessed regular, fine serrations, whilst those of small juveniles had very few or no serrations (see Figure 7).

Therefore, all of the differences proposed by Teng (1959) to distinguish between *C. acus* and *C. niaukang* can be attributed to ontogenetic differences. Thus *C. niaukang* is a junior synonym of *C. acus*, with both species being junior synonyms of *C. granulosus*.

#### Molecular analyses

Nucleotide sequences of the mitochondrial gene NADH2 of specimens assigned to *C. acus*, *C. granulosus*, *C. lusitanicus* and *C. niaukang* were very similar among specimens, and clustered together in a single well-supported clade. In fact, some of the NADH2 haplotypes were shared among specimens originally designated as distinct taxa sampled in different geographic localities (e.g. *C. acus* Japan and *C. niaukang* Taiwan). These results are consistent

with the idea that the names *C. acus*, *C. granulatus* and *C. niaukang* have been used to designate the same species and, thus, lend support to the synonymy proposed in this paper using the senior taxon name, *C. granulatus* (Bloch & Schneider 1801). It also highlights that this species has been misidentified as *C. lusitanicus* in some areas. This is likely due to the relatively long first dorsal fin of *C. granulatus*, which is a diagnostic feature of the true *C. lusitanicus*, but is much longer in the latter species which is also much smaller in size. By contrast, the comparison of NADH2 nucleotide sequences among specimens identified as *C. squamosus* sampled from various geographic locations have similar sequences. All sequences from specimens identified as *C. squamosus* cluster together in a distinct clade with high support values. Thus, the identification of *C. squamosus* specimens appears to have been more consistent across the species' range. Our results also show that *C. granulatus* and *C. squamosus* represent two distinct globally distributed lineages of large-sized *Centrophorus*.

#### Comparison with other species

*Centrophorus granulatus* is the largest member of this genus attaining up to 1.7 m TL. The only other *Centrophorus* species attaining a similar size is *C. squamosus*, i.e. 1.6 m TL, which is also the most morphologically similar species to *C. granulatus*. These two species can be easily distinguished by their denticle morphology at all sizes and several other characters are useful for species discrimination. The lateral trunk denticles of adult *Centrophorus squamosus* have leaf-shaped crowns with a serrated posterior margin which are raised on a narrow pedicel, and are imbricate. In contrast, the lateral trunk denticles of adult *C. granulatus* have flat, tear-drop shaped crowns with one long posterior cusp, and are not raised on pedicels or are overlapping. Juveniles of these two species are easily confused, but when observed side by side are clearly distinguishable (Figure 14). Juvenile *C. squamosus* have tricuspid lateral trunk denticles which are more bristle-like than those of the adults, but are also raised on narrow pedicels. Juvenile *C. granulatus* also have tricuspid denticles which are somewhat bristle-like, but they are not raised on narrow pedicels (short and broad pedicels only) and are much smaller in size than those of *C. squamosus*. The pectoral fin shape is also useful to distinguish between the two species. The pectoral fins of *Centrophorus granulatus* have short, slightly extended free rear tips. Juveniles have shorter, but distinct, free rear tips relative to larger specimens (see Figures 6b vs. 6a). In contrast, the pectoral fins of *C. squamosus* are not produced at any size. Furthermore, the second dorsal-fin spine of *C. squamosus* is slightly curved (most evident in juveniles), with a convex anterior margin, whereas *C. granulatus* typically has a short, straight spine (e.g. see Figure 14). The body of adult *C. granulatus* is also more robust than similar-sized specimens of *C. squamosus*.



**FIGURE 14.** Lateral view of neonate females of: A. *Centrophorus granulatus* (CSIRO H 6292–13, 392 mm TL); B. *Centrophorus squamosus* (CSIRO H 6292–14, 407 mm TL).

*Centrophorus granulatus* was previously considered to be a small species in the North Atlantic. As discussed below, this small species should be referred to as *C. uyato* until further taxonomic investigation can be carried out. Although the nomenclature of these two species has been previously confused, they are morphologically distinct from one another. Firstly, *C. uyato* is a much smaller species, attaining a maximum of about 1100 mm TL, with males mature by 800 mm TL. In contrast, *C. granulatus* attains 1700 mm TL with males becoming mature at about 1050–1180 mm TL. The pectoral-fin free tip is more extended in *C. uyato* than in *C. granulatus*, i.e. moderately long vs. short. The shape of the first dorsal fin is also a useful character to separate the two species. *Centrophorus granulatus* has a longer, lower first dorsal fin than *C. uyato* which has a shorter and more triangular first dorsal fin

(Figure 15); height 2.1–3.0 (n = 55) vs. 1.6–1.9 in soft-fin length (n = 12). The lateral trunk denticles of *C. uyato* are also different than those of *C. granulosis* in having flat, block-like denticles with only a short cusp which gives the skin a smooth feel rather than the granular texture associated with *C. granulosis*. This character also distinguishes *C. granulosis* from the other nominal congeners, i.e. *C. atromarginatus*, *C. harrissoni*, *C. isodon*, *C. lusitanicus*, *C. moluccensis*, *C. tessellatus*, *C. westraliensis* and *C. zeehaani*.



**FIGURE 15.** Lateral view of *Centrophorus uyato* (unregistered; Corsica, France; adult male ~790 mm TL).

Although counts of vertebral centra can be a very useful method for separating congeneric shark species, counts amongst various *Centrophorus* species largely overlap (Table 2). *Centrophorus granulosis* has lower vertebral counts than most of the other species for which vertebral counts were obtained, but there was considerable overlap in most counts. The greatest differences were found in total centra counts between *C. granulosis* (106–115; n=10) vs. *C. harrissoni* (117–128; n=31), *C. isodon* (113–120; n=9) and *C. moluccensis* (114–125; n=23) (Table 2). Also *C. granulosis* differed from some species in number of precaudal centra (77–85; n=10) vs. *C. harrissoni* (85–94; n=32), *C. isodon* (86–90; n=9), *C. moluccensis* (85–94; n=23) and *C. westraliensis* (85–88; n=6) (Table 2).

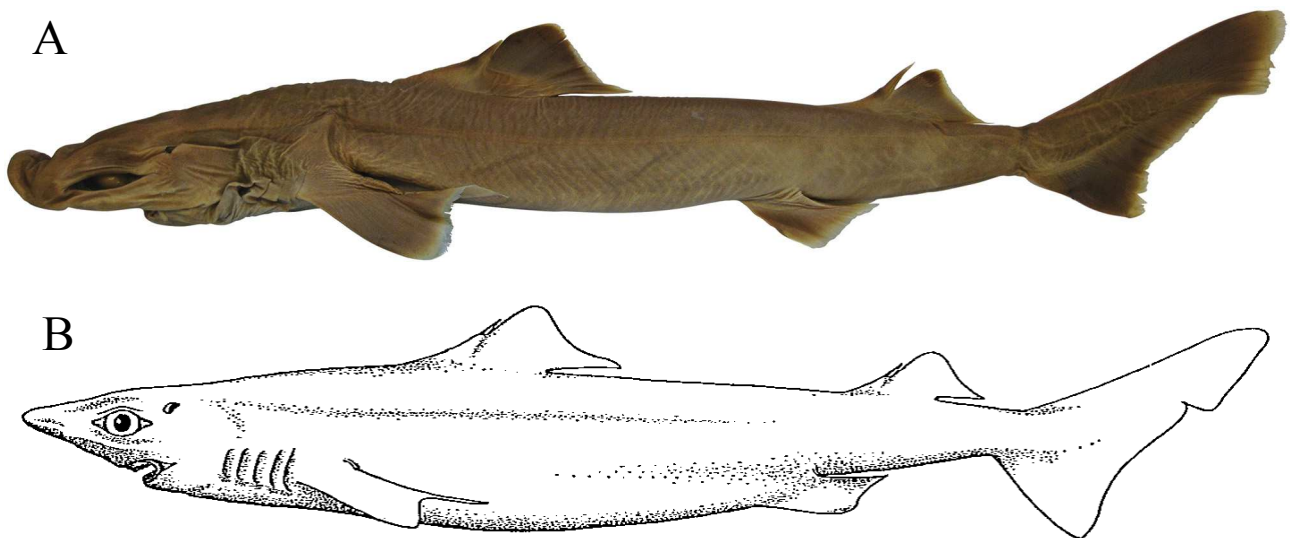
#### Other nomenclatural issues

Although the holotype of *Centrophorus robustus* Deng, Xiong & Zhan, 1985 was not examined in this study, the illustration and description of denticle morphology most closely matches *C. granulosis*. Examination of the holotype of *C. robustus* is required to confirm its identity but based on the information gleaned from the original description, it should be considered a probable junior synonym of *C. granulosis*.

The identity of the small species which has been referred to by many authors as *C. granulosis* warrants close scrutiny. As discussed above, the Mediterranean specimen examined by Müller & Henle (1839) in their redescription of *C. granulosis* is a smaller species, not conspecific with the true *C. granulosis* described herein. This small species has had a complicated nomenclatural history having been referred to for decades by many authors as *Centrophorus uyato* (see e.g. Garman, 1913; Bigelow & Schroeder, 1957; Cadenat & Blache, 1981; Compagno, 1984). As discussed in the Introduction, *Centrophorus uyato* is not a valid combination as it originally referred to an undetermined species of *Squalus*. Bonaparte's (1841) more detailed description of *Spinax uyatus* included an illustration that clearly refers to a *Centrophorus* species and the validity of his new name combination needs to be investigated further. Muñoz-Chápuli & Ramos (1989) discussed the complicated issue of *Dalatias nocturnus* Rafinesque, 1810, from the same publication as the *S. uyato* description. The description of this species, which has been neglected by most taxonomists, closely matches some *Centrophorus* species, e.g. less than three feet in length, teeth are dissimilar, large dorsal spines, and skin with many little tubercles closely set, ... rounded, with slightly striated margin (Muñoz-Chápuli & Ramos, 1989). The illustration by Rafinesque (1810) also appears to show an elongate pectoral-fin free rear tip, typical of some *Centrophorus* species. Based on the size, denticle morphology and the type locality (Sicily) it is possible that this species is the smaller species previously referred to variously as *C. uyato* and *C. granulosis* in the Mediterranean.

*Centrophorus bragancae* Regan, 1906 was described from two specimens collected from off Portugal, and has been considered as a questionable synonym of *C. granulosis* (small morphotype). The description and image of one of the syntypes (Figure 16a) agree well with the smaller species described by Müller & Henle (1839) mistakenly as *C. granulosis*. *Centrophorus machiquensis* Maul, 1955 was described based on a single specimen

from off Madeira, and has also been considered a questionable synonym of *C. granulatus* (small morphotype). Based on the illustration in Maul (1955), this species also agrees well with the smaller species from the Mediterranean and not the true *C. granulatus*, e.g. pectoral free rear tip very elongate, first dorsal fin short (Figure 16b). Thus, the identity of the small species which occurs in the Mediterranean needs to be critically investigated. If Rafinesque's *D. nocturnus* was determined to be conspecific with this species, it would be the oldest name available. However, the name *D. nocturnus* has been rarely, if at all, used in the literature since its first usage for the small morphotype previously called *C. granulatus*. In contrast, *C. uyato* has been used frequently and for a long period for this species and thus it may be advisable to make a submission to the ICZN to retain the usage of *C. uyato* for this small *Centrophorus* species. A revision of this species is currently in progress by the senior authors including an investigation into these nomenclatural issues. While it is likely that one of the above species names will need to be resurrected for this taxon, we do not want to introduce a new combination for this species at this stage. We thus recommend the use of the name *C. uyato* for this species until a full revision of this taxon is published.



**FIGURE 16.** A. *Centrophorus bragancae* syntype, BMNH 1904.11.30.12 (~440 mm TL) from off Sesimbra, Portugal; B. line drawing of the holotype of *Centrophorus machiquensis* MMF 3767 (female, ~1050 mm TL) from the original description (Maul, 1955).

Rafinesque (1810) also described *Dalatias sparophagus*, a junior synonym of *D. licha* (Bonnaterre, 1788), which is the type species of *Dalatias* by subsequent designation by Jordan *et al.* (1913). However, subsequent authors have stated that there are no grounds to synonymise these two species (see Muñoz-Chápuli & Ramos, 1989) and indeed the description and illustration of *D. sparophagus* does not appear to agree with *D. licha*. This has important implications for the nomenclature of these sharks since, if *D. nocturnus* is considered to be a valid *Centrophorus* species, then the genus *Dalatias* Rafinesque, 1810 would become a senior synonym of *Centrophorus* Müller & Henle (1837). It would be important to maintain nomenclatural stability if this was to occur by retaining the two genera as they are currently used. To do this, an application to the International Commission of Zoological Nomenclature would be required to change the type species of *Dalatias* to conserve its usage, and that of *Centrophorus*.

In summary, we have demonstrated that *C. acus* Garman 1906 and *C. niukang* Teng 1959 are conspecific, and represent distinct ontogenetic stages of *C. granulatus* (Bloch & Schneider 1801). The confusion over the identity of *C. granulatus* is not surprising given the high level of ontogenetic changes that occur throughout life, particularly in denticle morphology. This has contributed to the current taxonomic confusion in species identification. This study highlights the importance of having a comprehensive ontogenetic series of material available to address complex taxonomic questions, especially for *Centrophorus* species. Without a good understanding of how the various life stages differ, misidentification among members of this complicated group is likely to continue.

## Comparative material

*Centrophorus atromarginatus*: MCZ 1117-S (Holotype), female 837 mm TL, Suruga Bay, Japan, 9 Apr 1903; CAS 64520, 2 specimens, female 433 mm TL, adult male 564 mm TL, 1.5 km southwest of Bil Bil Island, north of the Gogol River, Ma Dang Province, Papua New Guinea, Bismarck Sea, 05°18' S, 145°46' E, 180–200 m, 10 May 1987; CAS 234956, adult male 583 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, 5 May 1988; CSIRO H 5788–01, female 502 mm TL, CSIRO H 5788–03, female 509 mm TL, CSIRO H 5788–04, female 743 mm TL, CSIRO H 5788–05, adult male 596 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 11 Apr 2002; CSIRO H 5889–07, female 722 mm TL, CSIRO H 5889–08, female 735 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 01 Jul 2002; CSIRO H 6125–01, female 762 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 27 Aug 2005; CSIRO H 6201–02, female 555 mm TL, CSIRO H 6201–03, female 562 mm TL, CSIRO H 6201–04, juvenile male 458 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 24 Apr 2004; unreg LJVC collection (currently housed at SAM), 6 specimens 288–560 mm TL, Gulf of Aden, Somalia, 11°12' N, 048°02'24" E, 335 m, 7 Jan 1987.

*Centrophorus bragancae*: BMNH 1904-11-30-12 (1 of 2 Syntypes), female 470 mm TL, off Sesimbra, Portugal, 276 fms (~500 m) [probably a synonym of *C. uyato*].

*Centrophorus harrissoni* (whole specimens): AMS E-5570 (Holotype) eviscerated female 736 mm TL, Gabo Island, Victoria, Australia; CSIRO CA 4103, adult male 843 mm TL, north of Flinders Island, Bass Strait, 39°05' S, 148°38' E, 444–468 m, 06 May 1984; CSIRO H 866–01, female 420 mm TL, CSIRO H 866–05, immature male 350 mm TL, CSIRO H 866–06, immature male 417 mm TL, east of Jervis Bay, New South Wales, 34°58' S, 151°09' E, 490–576 m, 10 Sep 1986; CSIRO H 987–01, immature female ca. 390 mm TL, north of Flinders Island, Bass Strait, 39°02' S, 148°37' E, 440–448 m, 29 Nov 1984; CSIRO H 2528–01, female 1049 mm TL, east of Maria Island, Tasmania, 42°39' S, 148°28' E, 500 m, 15 July 1990; CSIRO H 6310–05, adult male 874 mm TL, north-east of Flinders Island, Tasmania, 39°00' S, 148°38' E, 500–680 m; CSIRO H 6498–03, adult male 825 mm TL, CSIRO H 6498–04, adult male 925 mm TL, southern half of Flinders Island, Tasmania, 300–500 m, 24 June 2003; CSIRO H 6500–03, adult male 910 mm TL, off Flinders Island, Tasmania, 40°15' S, 148°45' E, 329–512 m, 21 Aug 2003; CSIRO H 6501–01, female 1114 mm TL, CSIRO H 6501–02, adult male 882 mm TL, CSIRO H 6501–03, adult male 907 mm TL, east of Flinders Island, Tasmania, ca. 41° S, ca. 149° E, 403–439 m, 18 June 2004; CSIRO H 6502–01, adult male 890 mm TL, CSIRO H 6502–02, female 940 mm TL, south of South East Cape, Tasmania, 43°45' S, 146°45' E, 329–549 m, 27 Aug 2002; CSIRO T 810, female 850 mm TL, Oct 1981, off St Helens, Tasmania, 580 m; QM I 35759, immature male 387 mm TL, QM I 35770, female 600 mm TL, Fraser Seamount, Queensland, 24°25' S, 155°17' E, 670 m;

*Centrophorus harrissoni* (skeletal specimens): CSIRO H 6307–03, immature male 557 mm TL, CSIRO H 6307–04, female 1025 mm TL, CSIRO H 6307–05, immature male 565 mm TL, CSIRO H 6307–06, female 933 mm TL, CSIRO H 6307–07, adult male 891 mm TL, east of Flinders Island, Tasmania, ca. 40° S, ca. 149° E, 350–430 m, 12 July 2004; CSIRO H 6308–01, adult male 900 mm TL, CSIRO H 6308–02, female 1039 mm TL, CSIRO H 6308–03, female 716 mm TL, Banks Strait, Tasmania, ca. 40° S, ca. 148° E, 29 July 2004; CSIRO H 6309–03, adult male 902 mm TL, CSIRO H 6309–05, adult male 939 mm TL, east of Flinders Island, Tasmania, ca. 40° S, ca. 149° E, 400–450 m, 01 Aug 2004; CSIRO H 6310–01, adult male 926 mm TL, CSIRO H 6310–03, female 870 mm TL, north-east of Flinders Island, Tasmania, 39°00' S, 148°38' E, 500–680 m, 24 July 1986; CSIRO H 6498–03, male 825 mm TL, southern half of Flinders Island, Tasmania, 300–500 m, 24 June 2003; CSIRO H 6499–01, female 1080 mm TL, CSIRO H 6499–02, female 880 mm TL, CSIRO H 6499–03, female 1070 mm TL, CSIRO H 6499–04, female 778 mm TL, north-east coast of Tasmania, ca. 41° S, 149° E, 24 July 2003; CSIRO H 6500–01, adult male 902 mm TL, off Flinders Island, Tasmania, 40°15' S, 148°45' E, 329–512 m, 21 Aug 2003.

*Centrophorus isodon*: CSIRO H 5857–01, immature male 540 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 9 Apr 2001; CSIRO H 5889–15, female 530 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, July 2002; CSIRO H 5875–04, female 989 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 26 Mar 2002; CSIRO H 6125–02, female 965 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 27 Aug 2005; CSIRO H 6138–01, female 952 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 25 Mar 2002; CSIRO H 6233–02, immature male 306 mm TL, CSIRO H 6233–03, immature male 304 mm TL, CSIRO H 6233–04, immature male

305 mm TL, CSIRO H 6233–05, female 241 mm TL, CSIRO H 6233–06, immature male 256 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 16 Mar 2005; SAM unregistered, Taiwan Fisheries Research Institute Fishery Researcher 1 sta. FR1–PHI–14–95, 950927, 435–451 m, 14°41'–42' N, 123°24'–21' E, adult male 905 mm TL, northern Luzon, Philippines.

*Centrophorus lusitanicus*: BMNH 1867.7.23.2 (Syntype), juvenile male 742 mm TL, Portugal.

*Centrophorus moluccensis*: CSIRO C 4894, female 610 mm TL, southeastern Australia; CSIRO CA 4067, adult male 813 mm TL, north-west of Port Hedland, Western Australia, 18°34' S, 117°27' E, 400–402 m, 16 Aug 1983; CSIRO H 459–01, female 756 mm TL, Townsville Trough, Queensland, 17°59' S, 147°06' E, 300 m, 11 Jan 1986; CSIRO H 461, female 639 mm TL, Townsville Trough, Queensland, 17°59' S, 147°06' E, 300 m, 11 Jan 1986; CSIRO H 462, female 656 mm TL, Townsville Trough, Queensland, 17°59' S, 147°06' E, 300 m, 10 Jan 1986; CSIRO H 600–04, female 712 mm TL, CSIRO H 600–05, juvenile male 478 mm TL, Saumarez Plateau, Queensland, 22°44' S, 154°12' E, 492 m, 17 Nov 1985; CSIRO H 709–01, adult male 680 mm TL, south of Saumarez Reef, Queensland, 21°57' S, 154°00' E, 400–403 m, 20 Nov 1985; CSIRO H 947–12, male 632 mm TL, Saumarez Plateau, Queensland, 22°54' S, 154°20' E, 590–606 m, 17 Nov 1985; CSIRO H 1203–01, juvenile male 377 mm TL, north of Sahul Banks, Western Australia, 11°33' S, 124°58' E, 415 m, Jan 1988; CSIRO H 2268–01, adult male 760 mm TL, west of Bunbury, Western Australia, 33°03' S, 114°25' E, 701 m, 10 Feb 1989; CSIRO H 2564–04, juvenile male 422 mm TL, CSIRO H 2564–07, adult male 767 mm TL, west of Bernier Island, Western Australia, 24°51' S, 112°07' E, 467–478 m, 28 Jan 1991; CSIRO H 2586–13, juvenile female 321 mm TL, south-west of Shark Bay, Western Australia, 27°17' S, 112°45' E, 510–520 m, 2 Feb 1991; CSIRO H 2608–17, female 865 mm TL, Rottneest Canyon, Western Australia, 31°55' S, 115°10' E, 320–850 m, 11 Feb 1991; CSIRO H 4683–01, juvenile male 335 mm TL, CSIRO H 4683–02, juvenile male 323 mm TL, east of Sydney, New South Wales, 33°47' S, 151°52' E, 600–614 m, 30 May 1996; CSIRO H 5670–02, male 684 mm TL, northeast Queensland, Nov 1985; CSIRO H 5692–04, female 543 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 10 Jul 2001; CSIRO H 5857–03, adult male 630 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 09 Apr 2001; CSIRO H 5875–03, female 961 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 26 Mar 2002; CSIRO H 5877–03, female 860 mm TL, CSIRO H 5877–04, adult male 813 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 07 Jun 2002; CSIRO H 5889–02, male 550 mm TL, CSIRO H 5889–06, female 862 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 01 Jul 2002; CSIRO H 6125–05, female 827 mm TL, Kedonganan fish market, Bali, Indonesia, 08°45' S, 115°10' E, 27 Aug 2005; CSIRO H 7403–01, female 587 mm TL, off Kaohsiung, Taiwan, 22°32' N, 120°07' E, 320 m, 21 Mar 2012; RMNH 7415 (Holotype), near-term embryo male 213 mm TL, Ambon, Indonesia; SUML JPAG 061, juvenile male 733 mm TL, Bohol Sea, Philippines, 8 Apr 1999; SUML JPAG 0088, female 449 mm TL, Bohol Sea, Philippines, 17 Apr 1999; SUML JPAG 254, adult male 777 mm TL, SUML JPAG 255, adult male 751 mm TL, SUML JPAG 257, female 709 mm TL, Bohol Sea, Philippines, 29 Mar 2000.

*Centrophorus squamosus*. ASIZP 0060842, female 350 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, probably 300–400 m; CAS 234957, juvenile male 374 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, 21 May 2005; CAS 234910, adult male 1090 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 33°50' S, 44°20' E, 500–1000 m, 3 Mar 2012; CAS 234911, adult male 1074 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 35°00' S, 44°15' E, 900–1100 m, 6 Mar 2012; CAS 234912, female 1165 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 35°00' S, 44°15' E, 500–600 m, 6 Mar 2012; CAS 234913, adult male 1080 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 37°00' S, 52°00' E, 800–1000 m, 6 Mar 2012; CAS 234918, adult male 1050 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 39°00' S, 46°30' E, 800–1200 m, 17 Mar 2012; CAS 234919, adult male 1110 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 37°00' S, 52°00' E, 800–1000 m, 19 Mar 2012; CAS 234923, immature male 966 mm TL, southern Madagascar Ridge, South-western Indian Ocean, 35°00' S, 44°15' E, 800–1200 m, 11 Apr 2012; CSIRO H 787–01, adult female 1285 mm TL, Tasmania, Jul 1987; CSIRO H 1191–01, juvenile female 414 mm TL, east of Sydney, New South Wales, 33°49' S, 151°54' E, 900–935 m, 12 Feb 1987; CSIRO H 4873–03, adult male 1100 mm TL, Cascade Plateau, Tasmania, 44°01' S, 150°28' E, 950 m, 9–12 Oct 1998; CSIRO H 4873–03, adult male 1100 mm TL, Cascade Plateau, Tasmania, 44°01' S, 150°28' E, 950 m, 9–12 Oct 1998; CSIRO H 5611–12, juvenile female 425 mm TL, CSIRO H 5611–13, juvenile male 436 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, 1 Aug 2000; CSIRO H 5860–09, adult female 1140 mm TL, Cilacap landing site, Central Java, Indonesia,

07°40' S, 109°00' E, 22 Mar 2002; CSIRO H 5862–01, female 750 mm TL, CSIRO H 5862–02, adult male 986 mm TL, Pelabuhanratu landing site, West Java, Indonesia, 07°00' S, 106°30' E, 1 Jul 2001; CSIRO H 5863–01, juvenile male 511 mm TL, Pelabuhanratu landing site, West Java, Indonesia, 07°00' S, 106°30' E, 18 May 2002; CSIRO H 6042–05, adult male 1063 mm TL, Lord Howe Rise, Tasman Sea, 32°41.80' S, 162°33.47' E, 855–874 m, 25 May 2003; CSIRO H 6042–05, adult male 1063 mm TL, Lord Howe Rise, Tasman Sea, 32°41.80' S, 162°33.47' E, 855–874 m, 25 May 2003; CSIRO H 6292–14, juvenile female 407 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, 21 May 2005; CSIRO H 7406–01, adult male 1022 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E, 4 Mar 2009; CSIRO H 7040–01, female 1192 mm TL, CSIRO H 7040–02, female 1072 mm TL, CSIRO H 7040–03, female 1229 mm TL, CSIRO H 7040–04, female 1056 mm TL, east of Tuross Heads or Cape Howe, New South Wales, Sep 2009; CSIRO H 7062–01, adult male 1063 mm TL, CSIRO H 7062–02, adult male 954 mm TL, east of Cape Howe, New South Wales, 37°25.86' S, 150°19.86' E, 475–500 m, 25 Sep 2009; CSIRO H 7395–01, juvenile male 374 mm TL, CSIRO H 7395–02, juvenile female 392 mm TL, Da-xi fish market, Yilan, north-eastern Taiwan, 24°48' N, 122°10' E, 14 Mar 2012.

*Centrophorus tessellatus*: MCZ 1031S (Holotype), adult male 875 mm TL, Sagami Bay, Japan, 35°08' N, 139°31' E, ca. 730 m, 09 Aug 1903.

*Centrophorus westraliensis*: CSIRO H 2625–06 (holotype), female 909 mm TL, west of Point D'Entrecasteaux, Western Australia, 35°00' S, 114°42' E, 738–750 m, 18 Feb 1991; CSIRO H 2357–03 (paratype), female 789 mm TL, south of Cape Leeuwin, Western Australia, 35°02' S, 115°02' E, 673 m, 23 Dec 1989; CSIRO H 2358–01 (paratype), juvenile male 371 mm TL, north-west of Geraldton, Western Australia, 28°13' S, 113°07' E, 616 m, 27 Dec 1989; CSIRO H 2580–01 (paratype), female 414 mm TL, south-west of Shark Bay, Western Australia, 27°05' S, 112°22' E, 713–714 m, 31 Jan 1991; CSIRO H 2606–01 (paratype), female 774 mm TL, west of Rottnest Island, Western Australia, 32°00' S, 114°55' E, 640–670 m, 10 Feb 1991; CSIRO H 2625–05 (paratype), female 866 mm TL, collected with holotype.

*Centrophorus zeehaani* (whole specimens): CSIRO H 6628–05 (holotype), adult male 893 mm TL, AMS I 44310–001 (paratype), adult male 826 mm TL, CSIRO H 6628–01 (paratype), immature male 506 mm TL, CSIRO H 6628–02 (paratype), immature male 645 mm TL, CSIRO H 6628–03 (paratype), adult male 875 mm TL, CSIRO H 6628–04 (paratype), adult male 910 mm TL, CSIRO H 6628–06 (paratype), adult male 852 mm TL, CSIRO H 6628–07 (paratype), adult male 906 mm TL, NMV A 29736–001 (paratype), adult male 820 mm TL, south-west of Coffin Bay, South Australia, 35°14' S, 134°29' E, 360–600 m, 28 July 2005; CSIRO CA 4104, adult male 843 mm TL, east of Gabo Island, Victoria, 37°40' S, 150°15' E, 504–508 m, 04 May 1984; CSIRO H 866–02, immature male 456 mm TL, CSIRO H 867–01, female 439 mm TL, east of Jervis Bay, New South Wales, 34°58' S, 151°09' E, 490–576 m, 10 Sep 1986; CSIRO H 2268–02, adult male 800 mm TL, west of Bunbury, Western Australia, 33°03' S, 114°25' E, 701 m, 10 Feb 1989; CSIRO H 6504–05, adult male 861 mm TL, east of Jervis Bay, New South Wales, 35°12' S, 150°58' E, 320–500 m, July to Aug 2003.

*Centrophorus zeehaani* (skeletal specimens): CSIRO H 6307–01, female 1027 mm TL, east of Flinders Island, Tasmania, ca. 40° S, 149° E, 350–430 m, 12 July 2004; CSIRO H 6309–01, adult male 865 mm TL, east of Flinders Island, Tasmania, ca. 40° S, 149° E, 400–450 m, 01 Aug 2004; CSIRO H 6503–01, adult male 872 mm TL, CSIRO H 6503–02, female 991 mm TL, CSIRO H 6503–03, female 1023 mm TL, CSIRO H 6503–04, female 987 mm TL, CSIRO H 6503–05, female 957 mm TL, CSIRO H 6503–06, adult male 867 mm TL, north-east of Flinders Island, Tasmania, 39°20' S, 148°45' E, 370–420 m, 07 Apr 2003.

*Centrophorus uyato* (Eastern Atlantic): AMNH 78267, female 922 mm TL, AMNH 78269, female 937 mm TL, AMNH 78271, female 922 mm TL, AMNH 78273, adult male 872 mm TL, AMNH 78277, adult male 895 mm TL, AMNH 78279, adult male 890 mm TL, between Tenerife and Gran Canaria, Canary Islands, Spain, 3 Oct 1986; AMNH 78280, female 996 mm TL, AMNH 78282, female 1059 mm TL, AMNH 78283, female 1056 mm TL, AMNH 78284, adult male 832 mm TL, AMNH 78285, female 921 mm TL, AMNH 78286, female 1004 mm TL, AMNH 78291, female 1034 mm TL, AMNH 78292, female 980 mm TL, AMNH 78294, adult male 891 mm TL, between Tenerife and Gran Canaria, Canary Islands, Spain, 4 Oct 1986; BMNH 1904.11.30.12 (Syntype of *Centrophorus bragancae*), ~440 mm TL, off Sesimbra, Portugal.

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SUPPLEMENTARY MATERIAL

TABLE S1. *Centrophorus* specimens used for the molecular analyses in this study.

Haplo-type no.	GN#	Original Species Identification	Proposed Species Identification	Country/Location	Ocean basin	Latitude	Longitude	Sex	Registration #	Collection #
1	4927	<i>C. moluccensis</i>	<i>C. moluccensis</i>	–	Indian	36° 38' S	52°04' E	male	CSIRO H 5343-07	CSIRO
2	10722	<i>C. zeehaani</i>	<i>C. zeehaani</i>	Australia	Pacific	35°12.06' S	150°59.34' E	male	CSIRO H 7039-01	GT 5268
3	7123	<i>C. squamosus</i>	<i>C. squamosus</i>	Angola	Atlantic	16°34.36' S	11°19.01' E	–		10
3	1405	<i>C. squamosus</i>	<i>C. squamosus</i>	Mid-Atlantic Ridge	Atlantic	42°51' N	29°06' W	male		N/A
3	1455	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific	42°45' S	179°58' W	female		NZ 10
3	1456	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific	42°45' S	179°58' W	female		NZ 11
3	1462	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific	42°45' S	179°58' W	female		NZ 17
3	2700	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific			–		
3	2706	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific			–		D5
3	2707	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific			–		D6
3	5634	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific	43°40' S	174°40' E	male		CR_67
3	10525	<i>C. squamosus</i>	<i>C. squamosus</i>	Japan	Pacific			–	200712171	
3	6509	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_11
3	6511	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_13
3	6513	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_15
3	6514	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_16
3	6517	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_19
3	6519	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_21
3	6521	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_23
3	6522	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_24
3	6524	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_26
3	6525	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_27
3	6530	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_32
3	6534	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_36
3	6535	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_37
3	6537	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_39
3	6538	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_40
3	6541	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_43
3	1200	<i>C. squamosus</i>	<i>C. squamosus</i>	Scotland	Atlantic	59°00' N	7°40' W	female		MHD 1
3	1203	<i>C. squamosus</i>	<i>C. squamosus</i>	Scotland	Atlantic	59°00' N	7°40' W	female		MHD 4
3	1479	<i>C. squamosus</i>	<i>C. squamosus</i>	Scotland	Atlantic			female		SAMS 9
3	10458	<i>C. squamosus</i>	<i>C. squamosus</i>	South Africa	Atlantic			female		CT-091
3	4926	<i>C. squamosus</i>	<i>C. squamosus</i>	southwestern Indian Ocean	Indian	36°38' S	52°04' E	female	CSIRO H 5343-06	
3	11706	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			–		1577
3	11997	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			–		1034
3	10049	<i>C. squamosus</i>	<i>C. squamosus</i>	Taiwan	Pacific			female	HO-162	
3	10050	<i>C. squamosus</i>	<i>C. squamosus</i>	Taiwan	Pacific			female	CSIRO H 7395-01	
4	1883	<i>C. squamosus</i>	<i>C. squamosus</i>	–	Atlantic			–		N/A
4	1407	<i>C. squamosus</i>	<i>C. squamosus</i>	Mid-Atlantic Ridge	Atlantic	42°51' N	29°06' W	male		N/A

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TABLE S1 (continued)

Haplo-type no.	GN#	Original Species Identification	Proposed Species Identification	Country/Location	Ocean basin	Latitude	Longitude	Sex	Registration #	Collection #
4	1408	<i>C. squamosus</i>	<i>C. squamosus</i>	Mid-Atlantic Ridge	Atlantic	42°51' N	29°06' W	male		N/A
4	2705	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific			–		D4
4	6531	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_33
4	11664	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			–		1729
5	12055	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			male		1372
6	12079	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			female		1525
7	5020	<i>C. squamosus</i>	<i>C. squamosus</i>	Mid-Atlantic Ridge	Atlantic	42°49.79' N	29°6.82' W	male		
7	6510	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_12
7	6536	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_38
7	10457	<i>C. squamosus</i>	<i>C. squamosus</i>	South_Africa	Atlantic			female		CT-090
8	5021	<i>C. squamosus</i>	<i>C. squamosus</i>	Mid-Atlantic Ridge	Atlantic	42 25.9' N	29 7.32' W	male		
9	1466	<i>C. squamosus</i>	<i>C. squamosus</i>	New Zealand	Pacific	42°45' S	179°58' W	female		NZ 21
10	6512	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_14
10	6528	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_30
11	6518	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_20
11	6526	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_28
12	6520	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_22
12	6539	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_41
12	11506	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			–		1112
13	6523	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	female		AZ_25
14	6527	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_29
15	6532	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_34
16	6533	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic	32°38' N	16°56' W	male		AZ_35
17	6614	<i>C. squamosus</i>	<i>C. squamosus</i>	Portugal	Atlantic			–		MMF_36123
18	11589	<i>C. squamosus</i>	<i>C. squamosus</i>	Mauritius	Indian			–		1953
19	10720	<i>C. niaukang</i>	<i>C. granulosus</i>	Australia	Pacific	29°58.72' S	153°38.98' E	female	CSIRO H 7029-01	GT 5432
20	7425	<i>C. acus</i>	<i>C. granulosus</i>	Japan	Pacific			–	ZSM-tissue-collection-P-CH_0076	04JAP
20	7427	<i>C. acus</i>	<i>C. granulosus</i>	Japan	Pacific			–	ZSM-tissue-collection-P-CH_0081	09JAP
20	10193	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15811	20110718ck004
20	10195	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	?	20110718ck006
20	10197	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15810	20110718ck015
20	10201	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15773	20110730ck006
20	10203	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15761	20110730ck008
20	10521	<i>C. niaukang</i>	<i>C. granulosus</i>	Japan	Pacific			–	200509153	
20	10523	<i>C. sp</i>	<i>C. granulosus</i>	Japan	Pacific			–	20081002	
21	10721	<i>C. niaukang</i>	<i>C. granulosus</i>	Australia	Pacific	24°58' S	153°42' E	female	CSIRO H 7035-03	GT 5431
22	10191	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15858	20110303ck003
22	10196	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	?	20110718ck007
22	10204	<i>C. niaukang</i>	<i>C. granulosus</i>	Taiwan	Pacific			–	NMMBP 15757	20110730ck009

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TABLE S1 (continued)

Haplo-type no.	GN#	Original Species Identification	Proposed Species Identification	Country/Location	Ocean basin	Latitude	Longitude	Sex	Registration #	Collection #
23	10194	<i>C. niaukang</i>	<i>C. granulosis</i>	Taiwan	Pacific			–	NMMBP 15815	20110718ck005
24	10200	<i>C. niaukang</i>	<i>C. granulosis</i>	Taiwan	Pacific			–	?	20110718ck022
25	10202	<i>C. niaukang</i>	<i>C. granulosis</i>	Taiwan	Pacific			–	NMMBP 15759	20110730ck007
26	10206	<i>C. niaukang</i>	<i>C. granulosis</i>	Taiwan	Pacific			–	NMMBP 15760	20110730ck011
27	10207	<i>C. niaukang</i>	<i>C. granulosis</i>	Taiwan	Pacific			–	NMMBP 15758	20110730ck012
28	3187	<i>C. granulosis</i>	<i>C. granulosis</i>	Portugal	Atlantic			female		N/A
28	3188	<i>C. granulosis</i>	<i>C. granulosis</i>	western North Atlantic	Atlantic	36°54' N	74°37' W	female		N/A
28	3577	<i>C. granulosis</i>	<i>C. granulosis</i>	western North Atlantic	Atlantic			female		NEFSC
28	3578	<i>C. granulosis</i>	<i>C. granulosis</i>	Gulf of Mexico	Atlantic			female		59
28	3579	<i>C. granulosis</i>	<i>C. granulosis</i>	Gulf of Mexico	Atlantic			female		54
28	3717	<i>C. granulosis</i>	<i>C. granulosis</i>	Gulf of Mexico	Atlantic			female		N/A
28	4924	<i>C. granulosis</i>	<i>C. granulosis</i>	Australia	Pacific	33°44' S	151°54' E	male	CSIRO H 4683-01	
28	4925	<i>C. granulosis</i>	<i>C. granulosis</i>	Australia	Pacific	33°44' S	151°54' E	male	CSIRO H 4683-02	
28	6615	<i>C. granulosis</i>	<i>C. granulosis</i>	Portugal	Atlantic			–		MMF_36124
28	11565	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1036
28	11583	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1124
28	11778	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1117
28	11779	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1000
28	11780	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1583
28	11777	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		2014
29	11582	<i>C. lusitanicus</i>	<i>C. granulosis</i>	Mauritius	Indian			–		1593
30	3590	<i>C. granulosis</i>	<i>C. granulosis</i>	Gulf of Mexico	Atlantic			female		N/A
31	3740	<i>C. granulosis</i>	<i>C. granulosis</i>	Gulf of Mexico	Atlantic			female		N/A
32	1967	<i>C. granulosis</i>	<i>C. granulosis</i>	Jamaica	Atlantic	18°29.58' N	77°15.8' W	female		JM #724991
33	6613	<i>C. granulosis</i>	<i>C. granulosis</i>	Portugal	Atlantic			–		MMF_36122