Zootaxa 5155 (1): 001–051
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5155.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:D13EBD69-7110-44F7-AEFA-04582EE21551

Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 3—Redescription of *Centrophorus uyato* (Rafinesque) with a discussion of its complicated nomenclatural history

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Abstract

Centrophorus uyato (Rafinesque, 1810) has a complicated nomenclatural history which has led to multiple scientific names being ascribed to this species. In the Mediterranean Sea, and elsewhere in its range, this species was previously referred to as *C. granulosus* (Bloch & Schneider, 1801). The first paper in this revision series clarified that *C. granulosus* refers to a much larger species of gulper shark which attains at least 1.7 m length and is absent from the Mediterranean Sea. Further complicating the nomenclature of this species is the fact that the original description clearly refers to a *Squalus* species, and not a *Centrophorus* species. In this third part of the revision of the genus *Centrophorus*, this problematic species is redescribed. A detailed synonymy is provided and it is confirmed that *C. machiquensis*, *C. bragancae* and *C. zeehaani* are junior synonyms of this species. To preserve nomenclatural stability within the genus, the name *Centrophorus uyato* is retained for this species with a neotype from close to the original type locality off Italy being designated. Intraspecific variation within *Centrophorus uyato* is also discussed, particularly relating to denticle morphology and body morphology.

Key words: gulper sharks, Mediterranean, Indo-Pacific, genetics, morphology, nomenclature, neotype

Introduction

In complicated nomenclatural cases, it is important to work through the literature to investigate where the issues have arisen. In many cases, it is also beneficial to understand the reasons that have led to misinterpretations, which have subsequently generated confusion in the taxonomy of some taxa. Thus, it is important to begin with examina-

Accepted by M. de Carvalho: 23 May 2022; published: 20 Jun. 2022

tion of the original description of *Squalus uyato* Rafinesque, 1810 based on a specimen caught off Sicily in Italy (referred to as *S. uyatus* in pl. 14 in the description). The main characters presented in Rafinesque's brief description (pp. 13–14) are: grey coloration; fins with sharp spines; snout sharp and depressed; big eyes and very small acute teeth. It also states that it resembles *Galeus mustelus* (=*Mustelus mustelus*) in colour, shape and size. This information does not conform to a 'typical' *Centrophorus* species (with the exception of the "big eyes"), as was noted by a number of authors who doubted the generic placement of Rafinesque's *S. uyato* (e.g. Maurin, 1968; Tortonese, 1969; Cadenat & Blache, 1981; Bass *et al*., 1986). Instead, the data provided conforms better to a *Squalus* species than to any other squaliform species, which was also suggested previously by several authors (see e.g. Muñoz-Chápuli & Ramos, 1989; Serena, 2005; White *et al*., 2013).

The illustration provided by Rafinesque (1810; Fig. 1) offers some additional insights into the species identity. Despite it being a relatively poor depiction of a squaloid, it clearly depicts strong dorsal-fin spines, a long and pointed snout, a large spiracle and no anal fin confirming it as a squaloid species. Other possibly useful characters from the illustration include pectoral-fin free rear tips not elongate, caudal fin without a terminal lobe and more anteriorly placed pelvic fins (i.e. relatively short pectoral-pelvic space and a relatively long anal-caudal space). These characters, in combination with those in the description, provide reasonably strong evidence for this described specimen(s) being a *Squalus* species. Three species of *Squalus* are known from the Mediterranean Sea, *Squalus acanthias* Linnaeus, 1758, *Squalus blainville* (Risso, 1827) and *Squalus megalops* (Macleay, 1881) (Ebert & Stehmann, 2013), although the identity of at least one of these species needs resolving (e.g. Serena, 2005; Bonello *et al.*, 2016; Veríssimo *et al.*, 2017; Ferrari *et al.*, 2021). It is interesting to note at this point that the common name 'ujato' has been used in Italy for *S. acanthias* (e.g. Costa, 1991), although the official Italian common name for this species is 'spinarolo'. However, Bonaparte (1834) also refers to *Spinax uyatus* from Palermo in Sicily as 'ujatu'. The original description by Rafinesque contains limited information to distinguish which *Squalus* species it best matches. For instance, the long and depressed snout better matches *S. acanthias*, but the positioning of the dorsal fin in the illustration appears too far forward for this species. However, it is difficult to discern much from this image since it is a poor illustration.

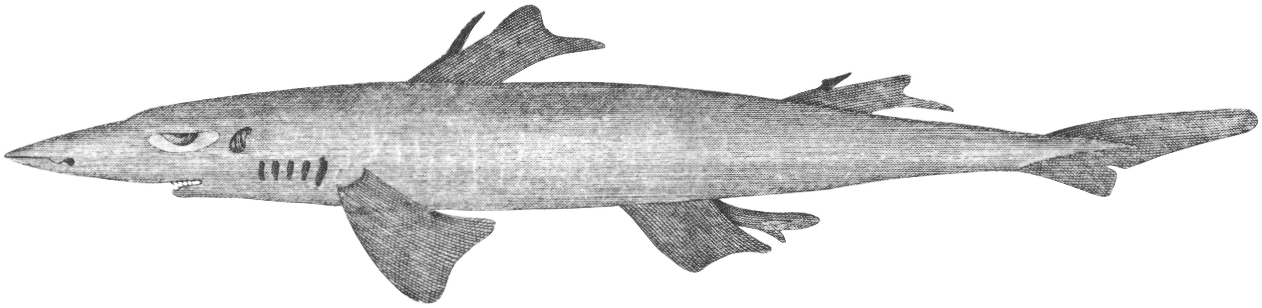

FIGURE 1. Original illustration of *Squalus uyatus* in Rafinesque (1810) from off Sicily, Italy.

Cuvier *et al.* (1834) erroneously stated that Rafinesque's *Squalus uyatus* "does not differ from *Spinax*, and is probably *Sq. spinax* [=*Etmopterus spinax* (L.]". Instead, Bonaparte (1834) provided a much more detailed redescription of *S. uyato* using the name combination *Spinax uyatus*. In this redescription, it is evident that, based on the synonymy, Bonaparte's intent was to provide more detailed information on the identity of Rafinesque's *S. uyatus*. He noted some additional characters that are considered strange to have not been mentioned by Rafinesque, e.g. inside of mouth black in colour. This suggests that Bonaparte redescribed under the name of *uyatus* a different species from that originally described by Rafinesque that does not align with a *Squalus* species. Bonaparte also considered *Squalus infernus* Blainville, 1825 as a junior synonym of this species. In Bonaparte's redescription of *Spinax uyatus*, it is likened and compared to what he considered to be a congener, *Spinax acanthias*, but the good quality illustration of *Spinax uyatus* clearly depicts a *Centrophorus* species (Fig. 2A). In contrast, the plate of *Spinax* (=*Squalus*) *blainvillei* clearly depicts a *Squalus* species. Moreover, Bonaparte describes the pectoral fins of *S. uyatus* to have an elongate rear tip and the very detailed illustration shows the lateral grooves in the dorsal-fin spines, which are also characteristics of *Centrophorus* species (vs. pectoral-fin free rear tips not produced and no lateral grooves on dorsal-fin spines in *Squalus* species). Böhlke (1984) recorded one alcohol preserved specimen from Bonaparte's collection in the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP 483; Fig. 2B) and the size of this specimen is consistent with the one used for the description of *Spinax uyatus* by Bonaparte (1834). Böhlke (1984) incorrectly referred this specimen as the holotype of *Spinax uyatus* Bonaparte, 1834. Although Bonaparte provides a new name combination, he did not intend to describe a new species but instead redescribe Rafinesque's species. As such, *Spinax uyatus* is not an available name if renaming this species is considered, as discussed later.

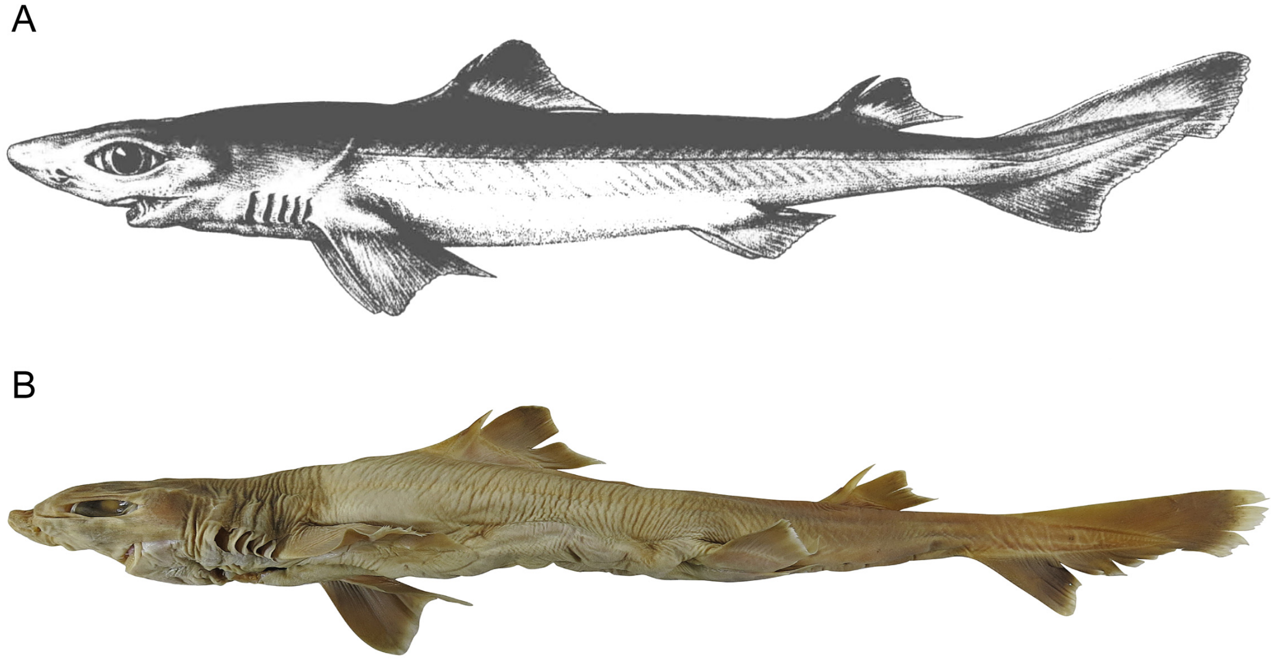

FIGURE 2. Lateral view of *Spinax uyatus* of Bonaparte (1834): (A) original illustration; (B) 'holotype' ANSP 483 (female 512 mm TL) designated by Böhlke (1984).

Squalus infernus was included in the synonymy of both *Spinax uyatus* by Bonaparte (1834) and *Acanthias uyatus* by Müller & Henle (1839). Blainville (1825) described this species based on two 'mutilated' individuals from the Mediterranean Sea off France and in the literature *S. infernus* has been allocated to both *Centrophorus uyato* and *Etmopterus spinax* (see Compagno, 1984a). In his description, Blainville states that it is perhaps the same as Rafinesque's *S. uyatus* although the black snout and shape of teeth suggest they are different. The characters in the description which are key for identifying this taxon are: upper teeth with a narrow, acute, long cusp flanked by a cusplet on each side; lower teeth similar to *Acanthias* species [=strongly oblique, blade-like]; strong spines on dorsal fins; mouth completely black inside; and body uniformly dark. These characters are enough to determine the generic placement of this species as *Etmopterus* and concur with Ebert & Stehmann (2013) in its placement as a junior synonym of *E. spinax*.

The genus *Centrophorus* was proposed by Müller & Henle (1837) in a review of the elasmobranch genera existing at that time. They proposed to separate the previous genus *Acanthorhinus* Blainville (1816), species with spiracles, fins with anterior spines and without anal fin, into four different genera: *Acanthias* Bonaparte (objective synonym of *Squalus* L.); *Spinax* Bonaparte (synonym of *Etmopterus* Rafinesque, 1810); *Centrina* Cuvier (synonym of *Oxynotus* Rafinesque, 1810); and a new genus *Centrophorus* (type species *Squalus granulosus* Bloch & Schneider, 1801). The main criterion used for genus separation was dentition, primarily morphology of the upper teeth. Several years later, Müller & Henle (1839) provided the first detailed description for two species belonging to the new genus *Centrophorus*, i.e. *C. granulosus* (Fig. 3) and *C. squamosus* (Bonnaterre, 1788). In the same publication, Müller & Henle allocated Rafinesque's species to *Acanthias*, together with *A. vulgaris* (=*S. acanthias*) and *A. blainvillii* (= *S. blainville*), and also included *Squalus infernus* in its synonymy. These authors distinguished the genus *Acanthias* (=*Squalus*) from *Centrophorus* by the upper teeth being strongly oblique vs. almost straight (following Müller & Henle, 1837). It is interesting that Müller & Henle (1839) did not include *Spinax uyatus* of Bonaparte (1834) in the genus *Centrophorus*. The likely reason for this is that one of the main generic characters used by Müller & Henle (1837) was the morphological shape of the upper teeth, and, under this criterion and with the somewhat inaccurate description of Bonaparte's *S. uyatus*, the latter clearly could not be included in the genus *Centrophorus*. However, dentition cannot be considered a robust diagnostic character to separate these genera, as juveniles of some *Centrophorus* species can have upper teeth with strongly oblique cusps which become almost straight in adults (Ledoux, 1970; Guallart, 1998; White *et al.*, 2013). At the present, the best characters to separate *Squalus* and *Centrophorus* are: absence of a caudal terminal lobe in *Squalus* (vs. a strong terminal lobe present in *Centrophorus*), caudal peduncle with lateral keels in *Squalus* (vs. without lateral keels), and dorsal-fin spines without lateral grooves in *Squalus* (vs. enamel restricted to an anterior longitudinal keel that creates lateral grooves with respect to the main trunk of the spine) (Garman, 1913; Bigelow & Schroeder, 1957; Cadenat, 1959; Bass *et al.*, 1976; Compagno, 1984a).

FIGURE 3. Illustration of *Centrophorus granulosus* in Müller & Henle (1839).

Müller & Henle (1839) appears to use the information for *A. uyato* from Bonaparte's (1834) redescription of *S. uyatus*, and it is possible they did not examine specimens. It is important to bring attention that although the lateral illustration of *Spinax uyatus* (as well as *S. blainvillei*) in Bonaparte (1834) is excellent, the associated illustrations of the teeth and dermal denticles are poor and apparently inaccurate. For example, the central upper teeth for *S. uyatus* are drawn with strongly oblique crowns, in a shape almost identical to those for *S. blainvillei* in the same plate. However, this is likely a mistake or simply an inaccurate drawing for several reasons. Firstly, the author notes in the text the differences between these two species ("*I denti sono conformati alquanto diversamente da quelli dello* Spinax Acanthias *e del* Blainvillii" = "teeth have a shape quite different to those of *Spinax acanthias* or that of *S. blainvillei*", p. 50). Secondly, the drawing does not agree with those of the specimen that was likely used for the description (ANSP 483) in which the central upper teeth are quite erect and not at all oblique. The description of the dermal denticles is also poor and probably inaccurate, at least when comparing Bonaparte's description and the shape of the denticles of the ANSP specimen. Bonaparte describes them as being oval, depressed and not very acute with slight grooves on the outer side ("*ovali, depressi, non, molto acuti, segnati dal lato esteriore da due leggeri solchi parte*", p. 50). However, this shape and the drawing provided by the author doesn't match with the shape of dermal denticles of ANSP 483 or other similar-sized *Centrophorus uyato* (e.g. Fig. 4E, F). It is difficult to reconcile the highly accurate whole lateral illustrations of the specimen and inaccurate illustrations of small denticles and teeth but it could be related to a limited availability of sufficient magnification equipment at the time. It is possible different illustrators were involved, drawings were made without suitable material or there was a predetermined decision to include them in the same genus. Thus, based on Bonaparte's description of *S. uyatus* and criteria established by Müller & Henle (1837) for characterisation of the genus *Centrophorus*, it is understandable that Müller & Henle (1839) chose not to include this species in the genus *Centrophorus*.

Garman (1906, p. 204) was the first to suggest that *S. uyato* of Rafinesque should be included in the genus *Centrophorus*. Garman (1913) treated this taxon as *Centrophorus uyatus* based on a 20 inch (~51 cm TL) juvenile specimen from Nice (Mediterranean Sea) and provided a more detailed definition of the genus *Centrophorus* and stated that "This species is very distinct from others of the genus [*Centrophorus*], but is a true *Centrophorus*, and cannot be placed in *Squalus*, as […]", p. 198. Garman (1913) agreed that the figure provided by Bonaparte (1834) for *Spinax uyatus* is a *Centrophorus* species but, in reference to the picture of the teeth, he simply stated that "the teeth figured [by Bonaparte] with it are those of a *Squalus*", without further comment. Bigelow *et al.* (1953) examined Garman's specimen (reported as 48 cm TL, MCZ 943) and some other specimens from the Gulf of Mexico, all of them juveniles of 42.0–44.2 cm TL. A more detailed discussion about the genus presented by Bigelow & Schroeder (1957) based on these small-sized specimens further contributed to the assignment of juvenile characters to the binomium *C. uyato*.

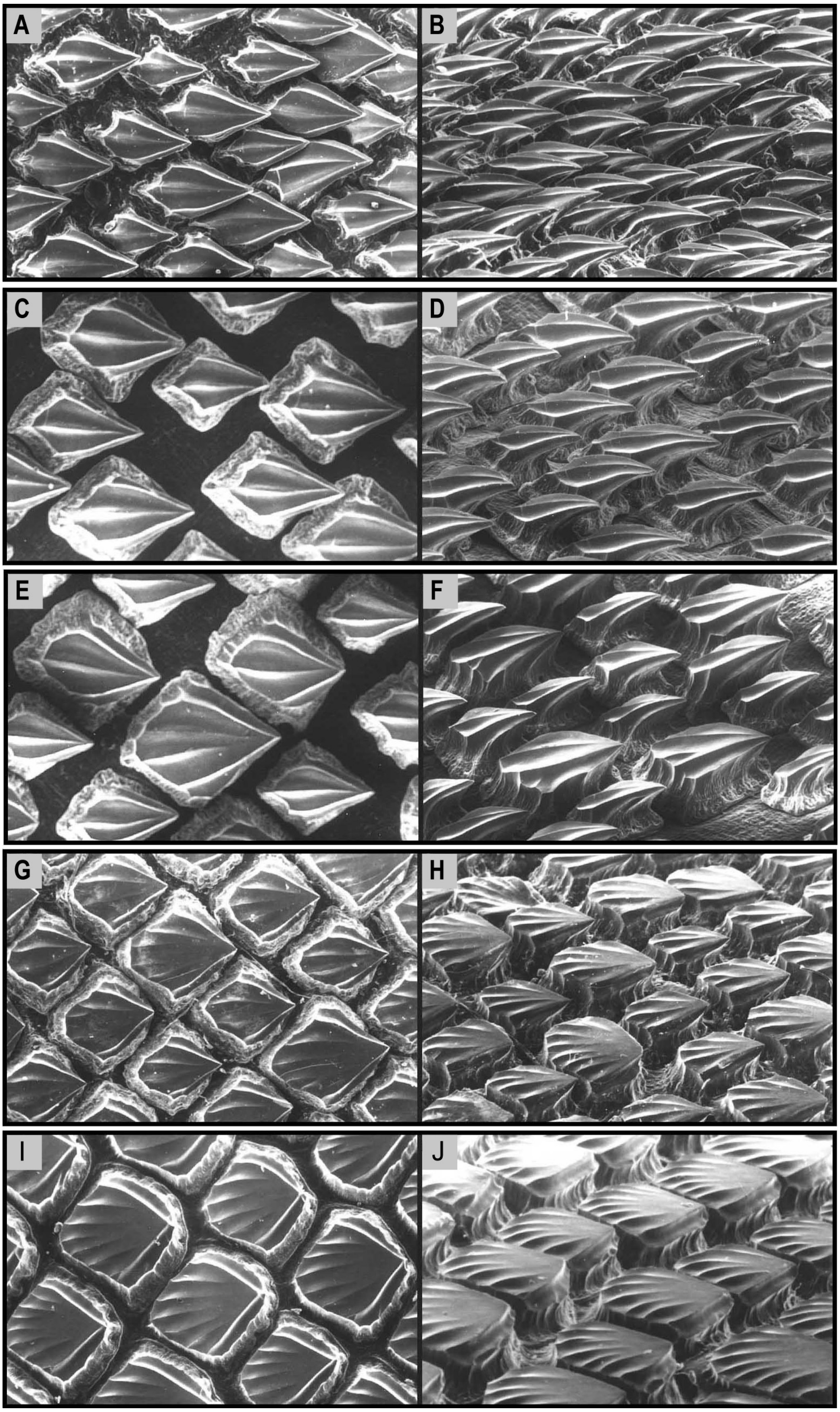

FIGURE 4. Scanning electron micrographs (SEMs) of the lateral trunk denticles in females of *Centrophorus uyato*: (A, B) late-term embryo 406 mm TL; (C, D) neonate 407 mm TL; (E, F) juvenile 591 mm TL; (G, H) juvenile 808 mm TL; (I, J) adult 973 mm TL. All photos parallel to the longitudinal axis of the body, in the direction of head to the left and tail to the right in each image. Images A, C, E,G, I were taken perpendicular to the body; images column B, D, F, H and J were taken at an approximately 30º angle from the horizontal.

As a result, juvenile characters have up to this point in time been considered as characteristic for the species without knowledge of adult characters. As a result, many authors suggested that *C. uyato* was synonymous with *C. granulosus* (e.g. Griffini, 1903; Lozano Rey; 1928; Maurin, 1968; Tortonese, 1969; Ledoux, 1970; Maurin & Bonnet, 1970; Quignard & Capapé, 1971; Capapé, 1985). In fact, some of these authors initially considered both species as separate but later considered that there was a single species, assigning the name *uyato* to juveniles and the name *granulosus* to adults (e.g. Maurin, 1968 vs. Maurin, 1962; Tortonese, 1956 vs. Tortonese, 1969). The findings of these papers have not been referred to by many subsequent authors, possibly because they were not written in English.

Bass *et al*. (1976) was the first work to provide adult and juvenile characters to this taxon, based on specimens caught off the southern Mozambique coast. They tentatively identified them as *Centrophorus uyato* and compared them to Bigelow *et al.*'s (1953) description. However, the authors did not present any argument as to why they chose the name *C. uyato* for these adults, with characters so different from those of juveniles previously assigned to this species. In Bass *et al*. (1986), the authors subsequently corrected the identification of these specimens to *C. granulosus* (Bloch & Schneider, 1801). But they noted that the assignment of this name follows the description of Muller and Henle (1839), following a reasoning similar to that indicated by Bigelow and Schroeder (1957), or based on it. Indeed, Bass *et al.* (1986) noted that they now regard *Squalus uyato* Rafinesque, 1810 as *nomen dubium*. The characters presented in Bass *et al*. (1976) undoubtedly contributed to confusion in the taxonomy of this genus and were used in subsequent publications, e.g. Compagno (1984a) and McEachran & Branstetter (1984). For example, Compagno's (1984a) treatment of *C. uyato* included a lateral drawing and dermal denticle drawing which appears to be reproduced from the adult presented in Bass *et al*. (1976; figs 22 and 24F, p. 82 and 83) but it also included drawings of teeth from a juvenile (42.9 cm TL) reproduced from Bigelow *et al*. (1953; fig. 4, p. 271) and other juvenile characters. McEachran & Branstetter (1984) also reproduced the figure of an adult presented by Bass *et al*. (1976), mixed with other juvenile characters. Based on this composite information, the result was a mixture of characters making it impossible to identify or assign a correct name to a *Centrophorus* species in some regions. It is noteworthy that the correction made by Bass *et al*. (1986) on the use of the specific name had much less impact in later work. Although several studies have improved the taxonomic understanding of this group (e.g. Muñoz-Chapuli & Ramos, 1989), the confusion detailed above is still repeated in recent publications (e.g. Serena, 2005).

Cadenat & Blache (1981) provided information on two "putative" species ("formes") in the Northeast Atlantic, that had similar dermal denticle morphology (i.e. not leaf-like as in *C. squamosus*) but that differed in size at maturity and maximum size. They noted some ontogenetic changes in both "formes", such as changes in shape of the dermal denticles, and did not repeat the mistake of assigning juvenile characters to one of the "species". The main distinguishing feature between the two was the maximum size and size at maturity. They referred to these as *C.* (forme) *granulosus* for the large form and *C.* (forme) *uyato-machiquensis* for the small form but did not provide characters to distinguish between the two. Muñoz-Chapuli & Ramos (1989) in their review of the taxonomy of the genus *Centrophorus* in the Northeast Atlantic and the Mediterranean Sea recognised these two forms as different species and proposed the name *C. niaukang* Teng, 1959 for the large species and *C. granulosus* for the small species. However, they raised doubts about the validity of their own use of the nomenclature by asking the question: "Which species was described by Bloch & Schneider (1801) as *C. granulosus*? Their reference to a five-foot [~150 cm] specimen suggests that it could have been *C. niaukang*" (p. 79). Since then, various publications have referred to the smaller species taxon as either *C. uyato* or *C. granulosus*. For example, Guallart & Vicent (2001) used *C. granulosus* for the smaller Mediterranean specimens examined but noted that the basic nomenclatural reference was the description by Müller & Henle (1839). A similar argument was used by Bass *et al.* (1986), i.e. "Our use of *C. granulosus* for this species is based on Müller & Henle (1839) who examined the type-specimen from Bloch's collection" (p. 50). In contrast, Bañón *et al*. (2008) used *C. granulosus* for the large species off Galician waters (NE Atlantic). Recently White *et al*. (2013) provided a redescription of *C. granulosus* and definitively concluded that this name refers to the large species and is a senior synonym of *C. niaukang* and *C. acus*. Thus, the taxonomy of the large species has been resolved, but the most suitable name for the smaller species is still not resolved. For example, despite White *et al.* (2013) clarifying the taxonomy of *C. granulosus*, including designating a neotype, some publications since have retained the use of *C. granulosus* for the small species in the Mediterranean (e.g. Carneiro *et al.*, 2014; Barría *et al.*, 2015a, 2015b; Cariani *et al.*, 2017), compounding the taxonomic confusion in this group.

This controversy also has conservation implications. The first IUCN assessments for *Centrophorus granulosus* were made by Guallart *et al*. (2006) for the Mediterranean Sea, considering this name as corresponding to the small species (the *C. uyato* of this paper) following the nomenclatural criteria of numerous authors of that time. After White *et al*. (2013), the assessments for *Centrophorus granulosus* at the European (Guallart *et al*., 2015) and global (Finucci *et al*., 2020a) levels correspond to a different species. For the smaller species, it was assessed under the name *C. uyato* at the European (Guallart & Walls, 2015) and global (Finucci *et al*., 2020b) levels, but noting that the use of this binomium was tentative and its nomenclature status required further work. This controversy may have led to confusion in the information provided to managers who must make decisions about the conservation this species.

Although *S. uyato* was likely intended for a *Squalus* species, the subsequent redescription of Bonaparte (1834), which clearly depicts a *Centrophorus* species, was likely the misidentification that has been perpetuated in the literature. This mistake was continued and amplified by subsequent descriptions of juvenile specimens under the name *C. uyato* by Garman (1906, 1913), then by Bigelow *et al.* (1953) and Bigelow & Schroeder (1957). Rafinesque's species has been considered as *C. uyato* in the literature more recently by some authors (e.g. Compagno, 1984a; Last & Stevens, 1994; Fricke *et al.*, 2007; Castro, 2011). Over the last few decades, a number of authors have highlighted the fact that Rafinesque's *Squalus uyato* is either a *Squalus* species or a doubtful species and some have indicated that a taxonomic revision of this species is required (e.g. Maurin, 1968; Tortonese, 1969; Cadenat & Blache, 1981; Bass *et al*., 1986; Muñoz-Chápuli & Ramos, 1989; Guallart, 1998; White *et al*., 2008, 2013). Based on this, many recent publications have referred to this species as *Centrophorus granulosus* (Bloch & Schneider, 1801), the type species for the genus (e.g. Muñoz-Chapuli & Ramos, 1989; Bass et al., 1986; Guallart & Vicent, 2001; Compagno *et al.*, 2005; Ebert & Stehmann, 2013). However, White *et al.* (2013) provided a detailed redescription of *C. granulosus* and confirmed this species as a large *Centrophorus* (up to 1.7 m TL), which is the senior synonym of *C. acus* and *C. niaukang*. Thus, *C. granulosus* is not an available name for this small species. White *et al.* (2013) showed that the confusion over whether *C. granulosus* is an available name for this species appears to have originated from Müller & Henle (1839). The latter authors redescribed Bloch & Schneider's *C. granulosus* and examined part of the type material. However, Müller & Henle (1839) primarily based their description on an adult male specimen from the Mediterranean Sea that is not conspecific with *C. granulosus* and refers to the smaller species. This led to the confusion in the literature as most subsequent authors followed Müller & Henle's more detailed definition as basic reference for the binomium *C. granulosus* rather than Bloch & Schneider's uninformative original description.

In this paper, the nomenclatural history of the smaller species that has been referred to as both *C. granulosus* and *C. uyato* is investigated. All available names for this taxon are investigated to determine the most appropriate for this species in order to avoid future taxonomic confusion and to best protect nomenclatural stability in this group that has proven so troublesome to taxonomists. A neotype from close to the type locality is also designated and the species redescribed based on specimens from throughout its range. The status of the recently described *C. zeehaani* White, Ebert & Compagno, 2008, is also investigated as several recent molecular studies have suggested it is likely conspecific with *C. uyato* (Veríssimo *et al*., 2014; Wienerroither *et al*., 2015).

Methods

Morphology. The morphometric measurements taken follow those for sharks detailed by Compagno (1984a, 2002), 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. pre-first dorsal length, head length, preorbital length, prenarial length. Data in the literature are often not suited for direct comparative purposes, as the measuring methodologies used are frequently not specified. Morphometric measurements were taken for all specimens in the present paper by the senior author (WW). Illustrations and descriptions of the measurements taken follow the methodology described by Last *et al*. (2007) for the genus *Squalus* with some additional measurements, i.e. caudal subterminal margin, caudal terminal lobe, 1st dorsal-fin midpoint to pectoral-fin insertion, 1st dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), 2nd dorsal soft fin length (from perpendicular to junction of exposed spine and soft fin base to free rear tip), 1st dorsal-fin midpoint to pelvic-fin origin, pelvic-fin midpoint to 1st dorsal fin insertion, and pelvic-fin midpoint to 2nd dorsal-fin origin, from Compagno (2002). 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 were located using the back of a finger or thumb against the midline to determine the approximate location of the fin origin and a pin used to mark the position (White *et al.*, 2013). Total length (TL) was taken horizontally from the tip of the snout to the tip of the caudal fin when lowered to be in line with snout, i.e. stretched total length.

The neotype (BMNH 2021.10.4.1) and 71 other specimens of this small species, referred to as *C. uyato* herein, were measured (Table 1). The other specimens include the lectotype (BMNH 1904.11.30.12) and paralectotype (BMNH 1904.11.30.11) of *C. bragancae* and the holotype and eight paratypes of *Centrophorus zeehaani.* The description of *C. uyato* provided herein is updated from that provided in White *et al.* (2008) for *C. zeehaani* to include a wider range of specimens from throughout its range. Morphometric values for the neotype are given first, followed in parentheses by the ranges of the other specimens measured.

TABLE 1. Proportional dimensions as percentages of total length for *Centrophorus uyato:* neotype (BMNH 2021.10.4.1), holotype of *Centrophorus zeehaani* (CSIRO H 6628-05), lectotype (BMNH 1904.11.30.12) and paralectotype (BMNH 1904.11.30.11) of *Centrophorus bragancae*, 16 other specimens less than 700 mm TL and 52 other specimens >700 mm TL.

	Neotype *C. uyato*	Holotype *C. zeehaani*	Lectotype *C. bragancae*	Paralectotype *C. bragancae*	Other specimens <700 mm TL (n = 16)		Other specimens >700 mm TL (n = 52)	
	BMNH 2021.10.4.1	CSIRO H 6628-05	BMNH 1904.11.30.12	BMNH 1904.11.30.11	Min.	Max.	Min.	Max.
Total length (mm)	983.0	893.0	467.5	488.0	393.5	666.0	731.0	1059.0
Precaudal length	79.3	79.7	77.4	78.1	75.9	79.6	78.3	83.1
Pre-second dorsal length	64.6	63.6	60.1	60.7	59.3	63.8	61.6	66.3
Pre-first dorsal length	28.7	29.8	28.9	30.3	28.2	31.5	27.5	32.0
Pre-first dorsal length (horiz.)	29.3	30.7	29.2	30.4	28.7	31.3	27.9	31.8
Pre-vent length	–	60.4	57.1	55.9	55.1	58.6	56.0	62.2
Prepelvic length	57.1	58.2	53.5	53.9	53.0	56.6	54.1	61.1
Prepectoral length	22.1	22.2	23.4	23.2	21.1	24.9	20.9	24.6
Head length	22.3	22.9	23.2	23.7	20.9	25.1	20.4	24.5
Head length (horiz.)	22.5	23.3	23.9	23.7	21.4	25.6	21.2	25.1
Prebranchial length	18.5	19.3	20.4	20.8	18.8	21.9	18.2	21.2
Prespiracular length	12.1	12.1	13.5	13.8	12.9	14.9	11.5	14.2
Preorbital length	5.3	5.6	5.9	6.2	5.7	7.2	4.8	6.9
Preorbital length (horiz.)	6.1	6.1	6.6	6.8	6.1	8.1	5.9	7.6
Snout to inner nostril	4.2	4.2	4.5	4.5	4.1	5.2	3.7	4.9
Prenarial length (horiz.)	3.7	3.8	4.0	4.0	3.7	4.7	3.3	4.5
Preoral length	9.5	9.4	10.4	10.3	9.4	11.8	8.2	11.2
Inner nostril–labial furrow space	6.5	5.9	6.8	6.9	6.3	7.5	5.4	7.0
Mouth width	8.3	8.9	8.0	8.3	7.9	10.1	7.7	9.8
Upper labial furrow length	1.8	2.0	2.5	1.6	1.7	2.6	1.3	2.7
Nostril width	1.6	1.6	1.8	1.8	1.6	2.3	1.3	2.0
Internarial space	3.8	3.6	3.8	3.9	3.0	4.4	3.0	4.0
Interorbital space	8.3	7.6	9.0	9.2	7.5	10.8	7.3	9.8
Eye length	5.3	5.8	6.5	6.7	6.0	7.3	5.3	6.7
Eye height	1.4	2.2	1.5	1.4	1.6	2.7	1.5	2.4
Spiracle diameter - greatest	1.2	2.1	1.5	1.4	1.5	2.3	1.2	2.0
First gill-slit height	2.0	2.8	2.1	2.0	1.7	2.8	1.7	2.7

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TABLE 1. (continued)

	Neotype *C. uyato*	Holotype *C. zeehaani*	Lectotype *C. bragancae*	Paralectotype *C. bragancae*	Other specimens <700 mm TL (n = 16)		Other specimens >700 mm TL (n = 52)	
	BMNH 2021.10.4.1	CSIRO H 6628-05	BMNH 1904.11.30.12	BMNH 1904.11.30.11	Min.	Max.	Min.	Max.
Interdorsal space	23.2	21.9	19.4	18.8	18.2	22.4	19.8	24.3
Dorsal–caudal space	6.4	6.9	7.8	7.6	6.6	8.7	6.0	8.8
Pectoral–pelvic space	31.3	32.4	27.9	28.1	24.4	30.6	27.6	36.1
Pelvic–caudal space	13.9	13.7	14.1	13.4	12.4	14.7	11.6	16.1
First dorsal length	19.0	17.8	17.7	18.1	16.8	20.8	17.2	21.9
First dorsal soft fin length	11.2	11.8	10.6	11.1	10.3	12.2	9.8	13.9
First dorsal anterior margin	12.6	10.9	13.0	13.0	11.5	14.9	11.1	14.6
First dorsal base length	13.5	11.8	11.9	11.7	10.9	13.9	11.6	16.0
First dorsal height	5.8	6.0	6.2	6.8	5.4	7.3	5.2	7.7
First dorsal inner margin	5.8	6.2	5.7	6.3	5.7	7.0	4.9	7.5
First dorsal posterior margin	9.3	9.5	7.9	9.4	8.0	10.6	7.7	12.1
First dorsal exposed spine length	2.4	2.6	2.4	2.0	2.1	3.2	1.1	3.1
First dorsal spine base width	0.9	0.9	0.9	1.0	0.7	1.2	0.7	1.2
Second dorsal length	12.0	14.2	14.0	15.3	11.8	14.9	12.2	14.9
Second dorsal soft fin length	7.7	8.3	7.7	8.2	7.3	9.0	7.3	8.9
Second dorsal anterior margin	8.6	9.4	10.8	11.9	9.0	11.8	8.9	11.4
Second dorsal base length	8.3	9.6	9.9	10.8	7.6	10.2	8.4	11.2
Second dorsal height	4.7	4.7	5.0	5.1	4.2	6.1	4.0	6.1
Second dorsal inner margin	4.1	4.5	4.3	4.6	3.5	5.2	3.6	5.2
Second dorsal posterior margin	6.3	7.2	6.1	6.4	5.7	8.7	5.9	8.1
Second dorsal exposed spine length	2.1	**2.2**	3.4	3.3	2.7	4.0	1.5	3.6
Second dorsal spine base width	0.6	0.9	0.9	1.0	0.8	1.3	0.6	1.0
Pectoral anterior margin	12.3	11.4	11.4	11.4	11.2	13.3	10.7	13.4
Pectoral inner margin	12.3	13.6	12.0	11.9	10.6	13.4	11.5	15.7
Pectoral base length	5.8	4.8	4.5	4.8	3.8	5.5	4.2	6.2
Pectoral height	8.4	8.4	–	–	7.8	9.2	7.8	9.3
Pelvic length	11.2	11.2	10.5	10.5	9.8	11.7	9.8	12.8
Pelvic height	5.6	6.5	5.1	5.0	4.5	5.8	5.3	7.4
Pelvic inner margin	5.8	6.7	5.0	5.5	5.0	6.7	5.3	7.7
Dorsal caudal margin	20.1	19.6	22.5	21.3	19.8	22.8	16.5	21.5
Preventral caudal margin	11.9	12.5	12.9	13.9	12.0	14.7	10.0	14.5
Upper postventral caudal margin	8.2	7.7	8.3	9.0	7.4	9.7	6.3	9.1
Lower postventral caudal margin	4.6	4.1	3.7	3.9	3.3	5.2	3.3	5.6
Caudal fork width	7.0	7.1	7.2	7.6	6.4	8.0	6.5	8.2
Caudal fork length	12.2	11.8	12.6	13.7	11.9	14.1	10.6	13.3
Caudal terminal lobe	8.9	8.8	8.7	7.8	7.4	9.9	6.5	10.0
Caudal subterminal margin	2.9	3.4	3.6	3.8	1.7	4.5	1.6	3.6
Head width at anterior of nostrils	6.1	5.5	6.6	7.1	6.1	7.8	5.3	7.2

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TABLE 1. (continued)

	Neotype *C. uyato*	Holotype *C. zeehaani*	Lectotype *C. bragancae*	Paralectotype *C. bragancae*	Other specimens <700 mm TL (n = 16)		Other specimens >700 mm TL (n = 52)	
	BMNH 2021.10.4.1	CSIRO H 6628-05	BMNH 1904.11.30.12	BMNH 1904.11.30.11	Min.	Max.	Min.	Max.
Head width	11.1	12.6	11.5	11.3	10.4	13.5	10.9	14.3
Trunk width	–	11.4	9.6	9.1	6.4	11.7	7.5	13.6
Abdomen width	–	11.7	7.1	8.8	6.6	10.6	6.6	12.7
Tail width	6.0	5.8	4.5	4.4	3.8	5.2	4.5	6.5
Caudal peduncle width	2.9	3.0	2.4	2.0	2.0	2.9	2.2	3.4
Head height	9.6	11.0	9.0	9.3	8.9	10.8	8.3	13.2
Trunk height	–	12.2	9.6	10.5	9.2	12.0	10.2	15.5
Abdomen height	–	12.1	8.2	9.7	10.0	12.8	10.4	15.2
Tail height	7.3	6.8	6.8	7.3	6.3	7.3	6.1	8.0
Caudal peduncle height	3.7	3.8	3.9	3.9	3.3	4.1	3.2	4.2
Clasper outer length	–	3.7	–	–	–	–	2.6	4.0
Clasper inner length	–	8.3	–	–	–	–	6.4	10.8
Clasper base width	–	1.1	–	–	–	–	0.8	1.4
First dorsal midpoint–pectoral insertion	9.9	8.2	8.9	9.0	5.9	10.5	6.9	12.9
First dorsal midpoint–pelvic origin	20.9	22.0	18.0	18.1	14.8	21.1	18.7	24.8
Pelvic midpoint–first dorsal insertion	17.7	17.9	15.6	15.8	13.2	17.5	14.5	20.5
Pelvic midpoint–second dorsal origin	5.7	3.8	3.3	2.9	1.8	5.7	2.7	7.1

Cranial morphometric measurements taken follow Munoz-Chapuli & Ramos (1989). In some crania, the origin of the rostral keel is difficult to differentiate from the subethmoidean ridge on the ectethmoid chamber. A total of 20 measurements were taken from 10 crania of *Centrophorus uyato*, 16 crania of *C. harrissoni*, 1 cranium of *C. moluccensis* and 1 cranium of *C. squamosus*. Focus was placed on comparison between *C. uyato* and *C. harrissoni* in Australian waters and *C. granulosus* and *C. uyato* in the Mediterranean, as they are commonly misidentified or confused with each other in these regions.

Scanning electron micrographs (SEMs) of the lateral trunk denticles were obtained from specimens collected off Balearic Islands by one of us (JG). Specimens included a late-term embryo, a neonate, two juvenile sizes and an adult.

Meristics. Vertebral counts were obtained from radiographs of the neotype and 29 other specimens of *C. uyato*, including all types of *C. bragancae* and *C. zeehaani.* 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 (1988a) for carcharhiniform sharks.

Tooth file counts were taken from 28 excised jaws of *C. uyato* from across its range.

Multivariate analyses. Morphometric measurements, as % TL, were subjected to non-metric multidimensional scaling (MDS) ordination (Primer v7.0 package) (Clarke & Gorley, 2006), to examine morphological differences at a geographical scale and at an ontogenetic level. 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 as zero values are not acceptable in the MDS analysis. Specimens for which four or more measurements could not be taken were also excluded from this analysis. Of the 73 individuals that morphometrics were taken from, 64 were subsequently included in the multivariate analyses using 57 morphometric measurements. 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).

Neurocranial measurements, as percentages of neurocranial total length (% CL), were also subjected to MDS ordination to examine differences in cranial morphology between several species as outlined above.

Synonyms. The synonymy provided for *C. uyato* is aimed to be comprehensive but is not a complete synonymy due to the large number of publications that include this species. The synonyms for species include authorship, year, pages and figures or plates when possible. Focus has been placed on key literature, important regional work and representing a diversity of geographic localities. Synonyms are listed in chronological order and citations within each synonym are also listed chronologically. For names which cannot be verified as referring to *C. uyato* but are possibly a synonym, a question mark is placed at the start of the name combination.

Molecular analysis. A total of 20 *Centrophorus uyato* specimens were sampled for liver or muscle tissue by the authors and/or their collaborators. 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 °C until used for amplification via the Polymerase Chain Reaction (PCR). Samples were amplified using Takara Taq with primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (NADH2). A single set of universal primers (Naylor *et al*., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome was used to amplify the target fragment. PCR reactions were generally carried out in 25 µl tubes by adding 1–2 µl of DNA template containing 1 unit of Takara Taq (Clonetech, Mountain View, Ca), 10 µl of PCR buffer comprising 2.5 mM of MgCL2, 1.0 mM of dNTPs, and 1.0 mM of each primer. The reaction cocktail was denatured at 94˚C for 3 minutes, after which it was subjected to 35 cycles of denaturation at 94° C for 30s, annealing at 48° C for 30s and extension at 72° C for 90s. PCR products were either purified by centrifugation through size-selective filters (Millipore, Bedford, MA) according to manufacturer's recommendations, or were purified using ExoSAP-IT from USB (Cleveland, Ohio). Purified PCR products were sent off to commercial sequencing centres for sequencing (Seq-Wright, Houston, TX; Beckman-Coulter Genomics, Beverly, MA; Retrogen, San Diego, CA). Sequence trace files were evaluated for quality, translated to amino acids, and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences, to yield a nucleotide alignment that was 1044 nucleotides long.

The alignment was imported into PAUP* (Swofford, 2002) and used to construct a Maximum Likelihood Tree using the GTR+I+G model. All phylogenetic analyses were carried out using Maximum Likelihood analyses of the aligned sequence data using the software package PAUP*4.0 version a168. Sequences have been uploaded to GenBank and relevant accession numbers are provided in Figure 7.

Institutional acronyms. Museum acronyms used follow Fricke & Eschmeyer (2021). In addition: BPS, collection de tissus de la Station de Biologie Marine de Concarneau; ERB, Elasmobranch Research Belgium, Bonheiden; PMH, private collection of Mark Harris; SBMC, Station de Biologie Marine de Concarneau, MNHN.

Results and discussion

Available names

As outlined in the Introduction, *S. uyato* of Rafinesque (1810) most likely refers to a *Squalus* species despite being long considered a valid *Centrophorus* species. Although *C. granulosus* has been considered by some as the valid name for this small species, White *et al.* (2013) clarified that *C. granulosus* is a much larger species based on the only relevant information on the original description of *Squalus granulosus* by Bloch & Schneider, a length of about 150 cm: "*Exemplare meum* […] *5 pedum est*". This nominal species is therefore the senior synonym of *C. acus* and *C. niaukang*. Thus, it is now important to investigate what names are available for this smaller, wide-ranging *Centrophorus* species (the only species of *Centrophorus* in the Mediterranean Sea) given its complicated nomenclatural history.

Bonaparte's (1834) redescription of Rafinesque's *S. uyato* as *Spinax uyatus* was considered by Böhlke (1984) to represent a valid new species name, i.e. *Spinax uyatus* Bonaparte, 1834. But, as mentioned previously, this represents a new combination of names and not a new species. Thus, it is not an available name for this taxon. One possibility is that Bonaparte (1834) misread Rafinesque's Plate 14 and mistook figure 3 (*Dalatias nocturnus*) for

Squalus uyatus instead of figure 2. It is impossible to determine whether this occurred, but it is a possible scenario for how *Squalus uyatus* was first mistakenly considered to be a *Centrophorus* species.

Dalatias nocturnus Rafinesque, 1810, was described based on a specimen(s) from off Sicily in Italy (no types known). The identity and validity of this species had been poorly investigated in the literature until Muñoz-Chápuli & Ramos (1989) suggested it refers to a *Centrophorus* species, possibly *C. granulosus* (*sensu* the present *C. uyato*). The main point of confusion over the identity of this species is probably related to the generic placement, *Dalatias*, proposed in the same publication by Rafinesque. The generic description includes the characters: no anal fin, two dorsal fins, 5 gill openings on each side, tail unequal and oblique, and no spiracles. These characters mostly indicate a squaloid species except for the lack of spiracles. Rafinesque (1810) included two new species in this genus, *Dalatias sparophagus* and *D. nocturnus*. The former species is currently considered the type species for the genus *Dalatias* and a junior synonym of *D. licha* (Bonnaterre, 1788). The description of *D. nocturnus* includes the following key characters: grey to fawn in colour; fin spines present; less than 3 feet in length; teeth are unequal and acute; denticles close together but each distinct, flat, round with a striated margin; and many pores on head. Furthermore, several important features are also evident from the, albeit poor, illustration (Fig. 5A): fin spines long and robust; pectoral fins have an elongate free rear tip; and upper caudal lobe which does not appear to have a terminal lobe but is broader, suggesting it is possibly present. Based on these characters *D. nocturnus* most likely refers to a *Centrophorus* species. It should be noted that the size of the eye depicted for *D. nocturnus* is much smaller than that for *Squalus uyato*, whereas *Centrophorus* specimens often have larger eyes than *Squalus* species. The type location of Sicily restricts the possible candidates to *C. uyato* (also in literature as *C. granulosus*; true *C. granulosus sensu* White *et al.*, 2013 does not occur in the Mediterranean) or *C. squamosus* (Bonnaterre, 1788). The latter species in fact is not present in the Mediterranean and the morphology of the denticles described in the text and the elongate pectoral-fin free rear tips exclude *C. squamosus*. The characters listed above match with those of the *C. uyato* species, but the placement of *D. nocturnus* in the genus *Dalatias* by Rafinesque suggests it did not have spiracles.

Cuvier (1829) suggests that the spiracles were missed by Rafinesque (1810), while Swainson (1838) questioned whether Rafinesque made an error when referring to the lack of spiracles in this genus and suggested that this genus name be abolished. Gill (1862) considered the genus *Dalatias* as synonymous with *Squalus* L. with the spiracles simply being overlooked while Duméril (1865) suggested it as another ‘imaginary’ Rafinesque species. Although the generic definition and allocation of *D. nocturnus* by Rafinesque (1810) is somewhat confusing, the characters available in the illustration (albeit poor) and species description agree well with the *C. uyato* species. Therefore, rather than considering it as *nomen nudum*, *D. nocturnus* could be considered as an available name for the small *C. uyato* species.

Centrophorus bragancae Regan, 1906 was described from two specimens collected from off Portugal (BMNH 1904.11.30.11 and BMNH 1904.11.30.12), and has been considered as a questionable synonym of *C. uyato* (Garman, 1913; Bigelow *et al*., 1953; Bigelow & Schroeder, 1957) or *C. granulosus* (e.g. Lozano Rey, 1928; Krefft & Tortonese, 1973; Compagno, 1984a; McEachran & Branstetter, 1984). Examination of the types by one of us (WW) showed that they are clearly conspecific with the small *C. uyato* species, rather than the true *C. granulosus*, thus is another available name for the smaller species. Of the two syntypes, BMNH 1904.11.30.12 is in the best condition (Fig. 5B) as BMNH 1904.11.30.11 has a damaged mouth, a slightly squashed snout and damaged first dorsal-fin spine. Thus, BMNH 1904.11.30.12 is herein allocated as the lectotype of *Centrophorus bragancae*, with BMNH 1904.11.30.11 becoming the paralectotype.

Centrophorus machiquensis Maul, 1955 was described from a single specimen off Madeira (MMF 3767, skin only) and although considered valid with some doubts by Krefft & Tortonese (1973) and McEachran & Branstetter (1984), it was considered a questionable synonym of *C. granulosus* by Compagno (1984a). Cadenat & Blache (1981) referred to the small species in the NE Atlantic as *C.* (forme) *uyato-machiquensis*. Examination of the description and illustration of the holotype of *C. machiquensis* in Maul (1955) show that this species agrees well with the small *C. uyato* species rather than with the much larger *C. granulosus* (Fig. 5C). Thus, *C. machiquensis* is also an available name for this species.

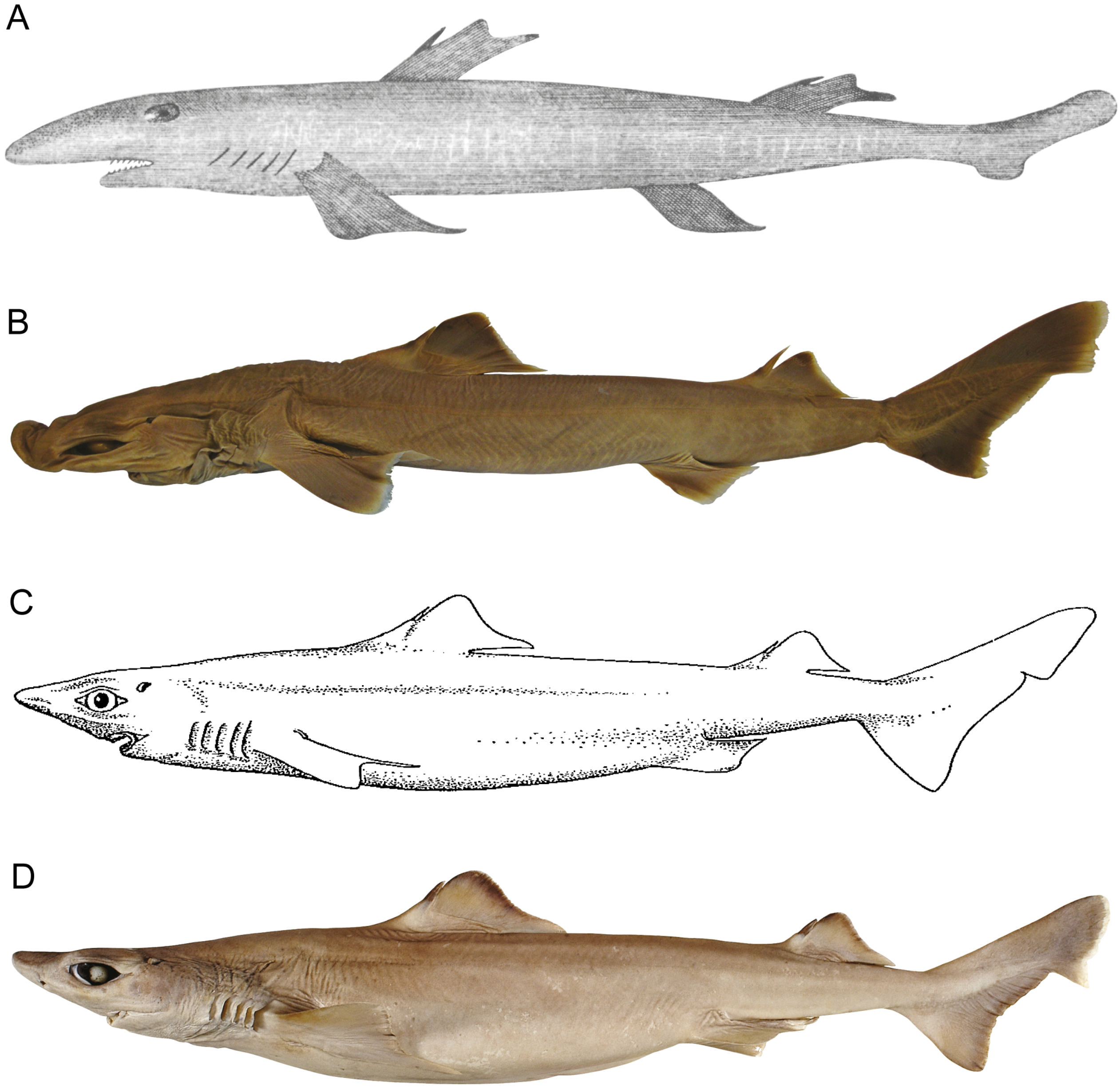

FIGURE 5. Lateral view of: (A) *Dalatias nocturnus*, original illustration from Rafinesque (1810); (B) preserved lectotype of *Centrophorus bragancae* (BMNH 1904.11.30.12, female 467 mm TL); (C) holotype of *Centrophorus machiquensis* (MMF 3767), original illustration from Maul (1955); (D) holotype (fresh) of *Centrophorus zeehaani* (CSIRO H 6628–05, adult male 893 mm TL).

White *et al.* (2008) described two new species of *Centrophorus* from Australian waters, including *C. zeehaani* White, Ebert & Compagno, 2008 which was previously considered to be *C. uyato* (Last & Stevens, 1994). These authors described this as a new species based on 9 type specimens and considered it endemic to southern Australian waters (Fig. 5D). Examination of more material and recent molecular analyses (see e.g. Naylor *et al.*, 2012; Veríssimo *et al*. 2014; Wienerroither *et al.*, 2015) have shown that this species is in fact conspecific with the small *C. uyato* species (synonymy discussed in more detail later). Thus, *C. zeehaani* is also an available name for this species.

Based on the above information, the following names are available for the small *C. uyato* species (in chronological order): *D. nocturnus* Rafinesque, 1810; *S. uyato* Rafinesque, 1810; *C. bragancae* Regan, 1906; *C. machiquensis* Maul, 1955; and *C. zeehaani* White, Ebert & Compagno, 2008. Although the oldest available name is *D. nocturnus*, this name has not been used since 1899 and thus, under Art. 23.9.1.1 of the ICZN code, prevailing usage can be argued if one of the other available names meets the criteria of Art. 23.9.1.2: the junior synonym has been used as its valid name in at least 25 works, published by at least 10 authors in the last 50 years and encompassing a span of at least 10 years. However, none of the available name combinations meet this requirement. In addition, the ICZN highlights the importance of nomenclatural stability thus, to protect prevailing usage. This is especially important if *Dalatias nocturnus* is considered a valid *Centrophorus* species as it would result in *Dalatias* being a senior synonym of *Centrophorus*, thus creating nomenclatural instability (see next section). It is herein argued that *Centrophorus uyato* (Rafinesque, 1810) should be conserved as the valid name for this species. Although the original description appears to refer to an undetermined *Squalus* species, selection of a neotype for *Centrophorus uyato* will result in conservation of the prevailing usage of this name and protect nomenclatural stability in this genus.

Protecting nomenclatural stability in the Squaliformes

The consideration of *D. nocturnus* as a valid species of *Centrophorus* does not in itself affect the generic structure of the Squaliformes as two species were allocated to this genus by Rafinesque (1810). The second species, *Dalatias sparophagus* Rafinesque, 1810, was described based on a specimen(s) from off Sicily, Italy (Fig. 6A). Cuvier (1829) suggested this species belongs to the genus *Scymnus* and Gray (1851) considered it to be a junior synonym of *Dalatias lichia* (Bonaparte, 1846) (=*Dalatias licha*). Regan (1908) also suggested it was probably either *Scymnorhinus lichia* (=*D. licha*) or *Somniosus rostratus* (Risso, 1827). Jordan *et al.* (1913) subsequently designated *D. sparophagus* as the type species of *Dalatias* and considered it a junior synonym of *D. licha* that has been perpetuated to present times. The original description of *D. sparophagus* includes the following important characters: grey above and white below; two dorsal fins, second very small (almost adipose); flat, long, acute teeth in two rows in upper jaw and one row in lower jaw, larger in lower jaw; eyes round, black and very small, iris greyish with a tawny inner circle; four to five feet long. Rafinesque's illustration (Fig. 6A) also shows the following additional characters: no anal fin; no dorsal-fin spines; no spiracles; pelvic fins almost opposite to the mid-interdorsal space; first dorsal-fin origin above pectoral-fin free rear tips; snout relatively long; and caudal fin narrow with ventral lobe barely evident. From these characters it is very difficult to determine how this species was considered synonymous with *D. licha*. The following characters of *D. licha* strongly conflict with the above characters: uniformly brownish to blackish; pelvic fin insertion about opposite second dorsal-fin origin; first dorsal-fin origin well behind pectoral fins; snout short; second dorsal fin larger than first; caudal fin large and broad; and large spiracles present (Fig. 6B). Thus, it is clearly not conspecific with *D. licha* and from the combination of characters mentioned above, it is impossible to determine what species Rafinesque was referring to.

If the lack of an anal fin is ignored, several characters (its colour, lack of dorsal spines, lack of spiracles, the smaller second dorsal fin and the anteriorly positioned pelvic and first dorsal fins) agree more readily with a carcharhinid species. It could be that the anal fin was simply removed from the specimen examined or was left off the illustration from which the description was subsequently based. Given the conflicting characters used to define this species and the lack of any type material, the only logical course of action would be to consider Rafinesque's *D. sparophagus* as *nomen dubium* and an application to suppress the name needs made to the ICZN. However, the issue then arises that since *D. nocturnus* is most likely a synonym of the small *C. uyato* species, and *D. sparophagus* is *nomen dubium*, the generic structure becomes unstable. The genus *Dalatias* Rafinesque, 1810, would become a senior synonym of *Centrophorus* Müller & Henle, 1837 and *Dalatias licha* requires a genus change also. In this case, it is important to protect prevailing usage of current literature as stated in the ICZN's code: "…the rules must enable the Principle of Priority to be set aside on occasions when its application would be destructive of stability or universality, or would cause confusion". In order to achieve this, a submission has been made to the ICZN Commission (White & Fricke) to change the type species of *Dalatias* to *D. licha* (Bonnaterre, 1788). Since the holotype of *D. licha* is considered lost (Fricke & Eschmeyer, 2021), a neotype for *D. licha* is designated (MNHN-IC 2021-0400). This neotype is a 901 mm TL juvenile male collected 23 April 2010 from off West Scotland (56°12.3'–56°32.1' N; 009°14.3'–009°09.8' W) in 623–673 m depth (Fig. 6B).

Molecular analyses

The Maximum Likelihood tree generated from the 22 *Centrophorus uyato ND2* sequences, together with 55 other sequences from available congeners, provide further support for a single, widespread species attributable to *Centrophorus uyato* (Fig. 7). The *Centrophorus uyato* samples form a distinct clade that is closest to *C. atromarginatus*, with both these species forming a group including samples of *C. moluccensis*. The same grouping was also reported by Veríssimo *et al.* (2014) and Wienerroither *et al.* (2015) based on *COI* sequences.

Based on *ND2* sequences, Naylor *et al.* (2012) found that *C. zeehaani* samples from southern Australia were nearly identical to those of two Eastern Atlantic specimens that were provisionally identified as *C. zeehaani*. They suggested this finding needed to be explored further. These results corroborate the findings of Veríssimo *et al.* (2014), using the *COI* and *16S* sequences, who also recorded a single wide ranging species which includes sequences from *C. zeehaani* from Australia. Wienerroither *et al.* (2015) also reported similar results and noted the conspecificity of *C. uyato* and *C. zeehaani*. A detailed investigation of the Mediterranean *Centrophorus*, as *C.* cf. *uyato* further corroborated previous molecular results by confirming a single gulper shark species in the Mediterranean Sea based on sequences of the *COI*, *ND2*, *16S* and a portion of a nuclear 28S ribosomal DNA gene (*28S*) (Bellodi *et al.*, 2022).

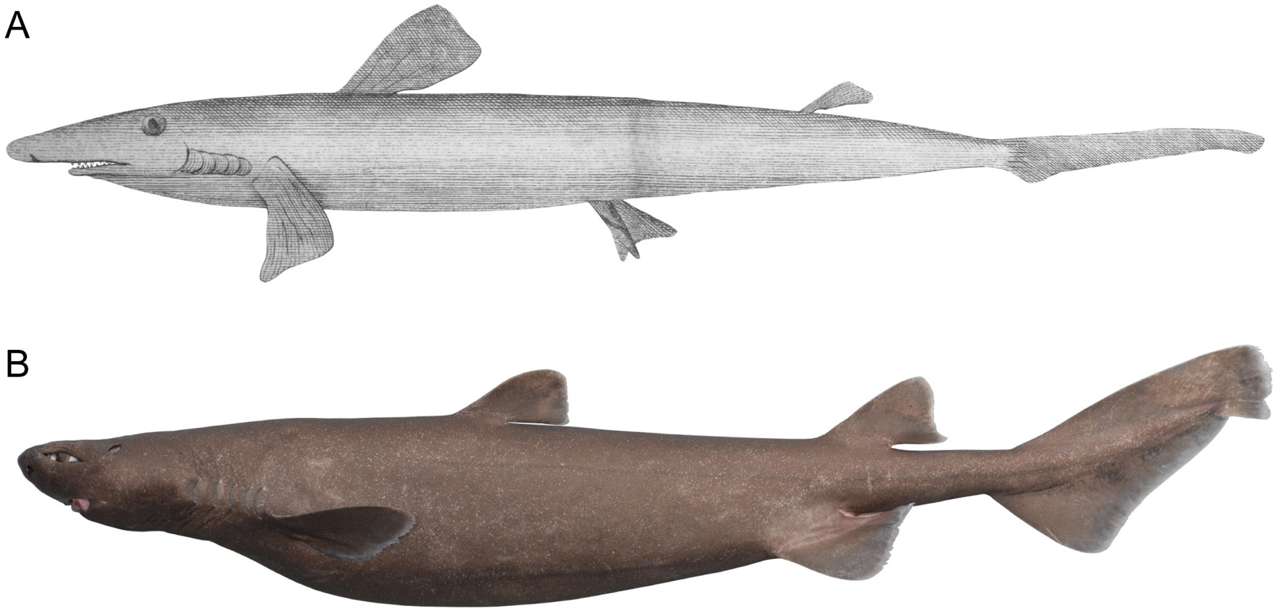

FIGURE 6. Lateral view of: (A) *Dalatias sparophagus*, original illustration from Rafinesque (1810); (B) neotype (fresh) of *Dalatias licha* (MNHN-IC 2021-0400, 901 mm juvenile male).

Taxonomic account

Centrophorus uyato **(Rafinesque, 1810)**

Little Gulper Shark

Synonymy.

Dalatias nocturnus Rafinesque, 1810: 11, pl. 14, fig. 3 (Type locality: Sicily, Italy)—Cuvier, 1818: 455; Cuvier, 1829: 392; Cuvier, 1837: 246; Swainson, 1838: 129, 160; Swainson, 1839: 313; Duméril, 1865: 436; Jordan & Evermann, 1917: 77; Bigelow & Schroeder, 1948: 500.

Spinax uyatus—Bonaparte, 1834: 49, fig. 2 (Italy); Bonaparte, 1846: 16 (Mediterranean); Böhlke, 1984: 158.

Acanthias uyatus—Müller & Henle, 1839: 85 (Mediterranean); Gray, 1851: vii, 71 (Mediterranean); Steindachner, 1864: 27; Duméril, 1865: 439 (Algerian coast, Mediterranean); Barbosa du Bocage & de Brito Capello, 1866: 7, 21; Günther, 1870: 419 (Mediterranean); Canestrini, 1872: 40; Steindachner, 1875: 466; Moreau, 1881: 346 (Mediterranean); Réguis, 1882: 72; Rochebrune, 1883: 47 (Senegal and Gambia); Hilgendorf, 1884: 518; Duncan, 1891: 35 (Mediterranean); Moreau, 1892: 39; Seeley, 1895: 35 (Mediterranean); Parona, 1898: 38 (Ligurian Sea); Duncker, 1914: 291; de Buen, 1916: 303, figs (Mediterranean coast of Morocco); Landolt, 1947: 353.

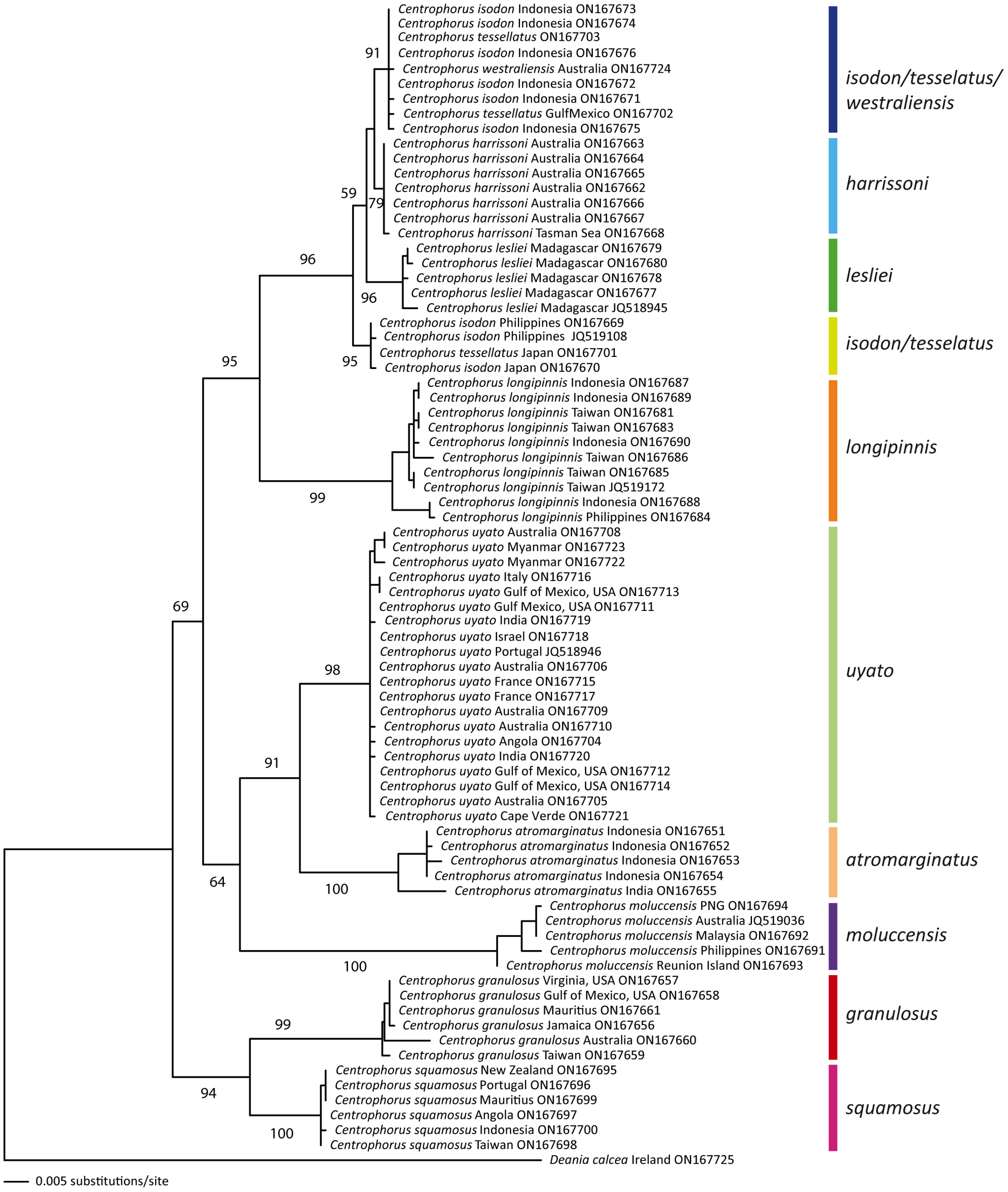

FIGURE 7. Maximum Likelihood tree estimated under the General Time Reversible model (GTR) with model terms to accommodate both Invariant site (I) and Gamma Distributed rates (G). Bootstrap support values are shown from a separate ML bootstrap analysis. GenBank accession numbers are provided.

Centrophorus granulosus—Müller & Henle, 1839: 89, pl. 33 (Sicily, Italy); Barbosa du Bocage & de Brito Capello, 1864: 261 (Portugal); Vinciguerra, 1883: 18 (482) (Gulf of Genoa); Goode & Bean, 1896: 12, pl. 3, fig. 11 (W Atlantic, Mediterranean and adjacent areas); Boutan, 1926: 1 (Algeria); Dieuzeide, 1928a: 15, figs (Algeria); Dieuzeide, 1928b: 1314 (Algeria?); Andr & Canal, 1929: 511 (Algeria); Arcidiacono, 1931: 609 (Gulf of Squillace, Italy); Gruvel, 1931: 74 (State of Syria [Syria, Lebanon, Israel]); Ranzi, 1932: 240 (Naples, Italy); Belloc, 1934: 146, fig. (Western Sahara, Morocco, Canary

Islands and Madeira); Ranzi, 1934: 343, 370 (Naples, Italy); Fowler, 1936: 73 (Mediterranean); Fowler, 1941 (in part): 231 (Mediterranean, inc. Italy); Šoljan, 1948: 66, figs (Adriatic Sea); Bigelow *et al.*, 1955: 6 (Gulf of Mexico); Kirinčić & Lepetić, 1955: 24 (southern Adriatic Sea); Tortonese, 1956: 176, figs 94-95 (Italy); Cadenat, 1959: 748, fig. 1b (West Africa); Maurin, 1968: 82 (Morocco to Algeria); Maurin & Bonnet, 1970: 147 (Canary Islands to Cape Verde); Karrer, 1975: 64 (Namibia); Karlovac, 1976: 601, fig. 4 (Adriatic Sea); Guitart, 1979: 67, fig. 46 (Cuba); Bouchet *et al.*, 1982: 577 (Tunisia); Zupanovic & El-Buni, 1982: 111 (Libya); Uyeno *et al.*, 1983: 62, figs (Suriname); Compagno, 1984a: 37, figs (Atlantic and Indo-West Pacific); Gilat & Gelman, 1984: 263 (Levant Sea, Israel); McEachran & Branstetter, 1984: 130, fig. (NE Atlantic and Mediterranean); Muñoz-Chapuli, 1984: 9 (NE Atlantic); ?Quéro, 1984: 43, fig.; Capapé, 1985: 97, fig. 1–7 (Eastern Atlantic); Jardas, 1985: 50 (Adriatic Sea); Anon, 1986: 93, fig. 22 (Atlantic Ocean); Bass *et al.*, 1986 (in part): 50, fig. 5.1 (Walvis Bay and Mozambique); Golani, 1986: 23, fig. 2 (Levantine Sea, Israel); Muñoz-Chapuli & Ramos, 1989: 65, figs 1a, 3a, 4b and c, 5a, 6a, 7a (NE Atlantic and Mediterranean); Compagno *et al.*, 1991: 54 (Hondeklip Bay to Namibia); Benli *et al.*, 1993: 133, figs 1 and 2 (Sea of Marmara); Pisanty & Golani, 1995: 388 (Levantine Sea, Israel); Lanfranco, 1996: 6, pl. 4 (Malta); Aldebert, 1997: 284 (Gulf of Lion, France); Guallart, 1998: 1, figs (Balearic Sea); Bello, 1999: 69 (Adriatic Sea); Hernández-Hamón & Núñez, 1998: 107 (Pacific Columbia); Ungaro *et al.*, 1999: 180 (Albania); Capapé *et al.*, 2000: 129 (Languedoc coast, France); Bertrand *et al.*, 2000: 5 (Gibraltar to Aegean Sea, Mediterranean); Golani & Pisanty, 2000: 71 (Levantine Sea, Israel); Baino *et al.*, 2001: 234 (Alboran Island to Aegean Sea, Mediterranean); Guallart & Vicent, 2001: 135, fig. 4 (Balearic Sea, Spain); Bilecenoglu *et al.*, 2002: 16 (Turkey); Schembri *et al.*, 2003: 76, fig. 3c (Malta); McLaughlin & Morrissey, 2004: 481, fig. 3 (Cayman Trench, Jamaica); Moreno García, 2004: 214 (in part, not figs) (Mediterranean Sea); Sion *et al.*, 2004: 155 (Ionian Sea, Greece); Golani, 2005: 11 (Levantine Sea, Israel); Lteif, 2015: 16, figs 9a, 14, (Lebanon); Serena, 2005: 27, figs, pl. I, 8 (Mediterranean Sea); Serét, 2005: 21 (Libya); Bessho, 2006: 28, figs 27–30, 33–35 (Japan, Namibia); Golani *et al.*, 2006: 38, fig. (eastern Mediterranean); Hadjichristophorou, 2006: 163 (Cyprus); Megalofonou & Chatzispyrou, 2006: 67, fig. 4 (Crete, Greece); Mejía-Falla *et al.*, 2007: 116 (Colombia); Psomadakis *et al.*, 2009: 200 (Gulf of Naples, Italy); D'Onghia *et al.*, 2010: 401 (Ionian Sea, Greece); Lipej & Dulĉić, 2010: 10 (Adriatic Sea); Damalas & Vassilopoulou, 2011: 145 (Aegean Sea, Greece); Colloca & Lelli, 2012: 12 (Lebanon); Costa *et al.,* 2012: 7 (Portugal); Guijarro *et al.*, 2012: 89 (Balearic Islands, Spain); Güven *et al.*, 2012: 278 (Antalya Bay, Turkey); Iglésias, 2013: 38, pl. 16 (France and Cape Verde); Carneiro *et al.*, 2014: 13 (Portugal); Farrugio & Soldo, 2014: 33 (Sicily, Italy and Tunisia); Veríssimo *et al.*, 2014: 6 (Gulf of Mexico); Goren & Galil, 2015: 510 (Levant Sea, Israel); Barría *et al.*, 2015a: 226 (Catalan Sea, Spain and Gulf of Lions, France); Barría *et al.*, 2015b: 114 (Catalan Sea, Spain and Gulf of Lions, France); Carpenter & De Angelis, 2016: 1170, figs (Eastern Atlantic); Ramírez-Amaro *et al.*, 2016: 639 (western Mediterranean); Cariani *et al.*, 2017: 5 (Mediterranean); ?Haroun *et al.*, 2017: 84 (Egypt); Gajić, 2019: 101, fig. 14 (Croatia, Montenegro and Albania); Bariche & Fricke, 2020: 17, fig. 12 (Lebanon).

?Acanthias nigrescens Nardo, 1860: 70, 96 (Type locality: Venice, Italy).

Entoxychirus uyatus—Gill, 1862: 498; Whitley, 1934: 199 (Australia).

Acanthias ujatus—Döderlein, 1878: 30 (Sicily, Italy); Döderlein, 1881: 92 (Italy).

Centrophorus uyatus—Goode & Bean, 1896: 508; Garman, 1906: 204; Garman, 1913: 9, 196.

Squalus uyatus—Garman, 1899: 28.

Squalus uyato—Garman, 1906: 204.

Centrophorus bragancae Regan, 1906: 438 (Type locality: Cezimbra, Portugal)—Regan, 1908: 53 (coast of Portugal); Strand, 1908: 83.

Centrophorus uyato—Fowler, 1936: 72, fig. 21 (Mediterranean and eastern Atlantic); Tortonese, 1938: 310 (Mediterranean); Poll 1951: 64, figs 33–34 (Angola and Namibia); Bigelow *et al*., 1953: 227, fig. 4 (Gulf of Mexico; Nice, Mediterranean Sea); Aksiray, 1954?: 233 (Turkish Seas); Bigelow *et al*., 1955: 5, 9; Springer & Bullis, 1956: 42 (Gulf of Mexico); Bigelow & Schroeder, 1957: 54, 66, 69, 72, 79–84, fig. 8e (Gulf of Mexico); Springer & Garrick, 1964: 81, 91; Krefft & Tortonese, 1973: 39 (NE Atlantic and Mediterranean); Bass *et al*., 1976: 31, figs 22, 24E, 24F, pl. 7 (southern Mozambique); Bridger, 1978: 26 (west of Ireland and Britain); Compagno, 1981: 8 [sharks] (Eastern Central Atlantic); Castro, 1983: 54, figs (Gulf of Mexico); Allu *et al*., 1984: 125 (Namibia); Compagno, 1984a: 45, figs (Atlantic, Indo-West Pacific); Compagno, 1984b: 9 [sharks] (Western Indian Ocean); McEachran & Branstetter, 1984: 132, fig. (NE Atlantic and Mediterranean); Lloris, 1986: 96, fig 24 (Namibia); Turón *et* al., 1986: 63 (Namibia); Fischer *et al*., 1987: 823 (Mediterranean); Compagno, 1988b: 603 (Comoro Islands); Compagno *et al*., 1989: 24, fig. (Hondeklip Bay, South Africa to Namibia); ?Clark & Kristof, 1990: 277, fig. 9 (Caribbean); Springer, 1990: 11 (Gulf of Mexico, Mediterranean, and Natal, South Africa); Applegate *et al*., 1993: 35 (Atlantic Mexican waters); Gomon *et al*., 1994: 92, 94, figs 30, 31 (southern Australia); Last & Stevens, 1994: 60, figs, pl. 4 (fig. 8.5) (southern Australia); Meriç, 1995: 192 (Sea of Marmara, Turkey); Perry *et al*., 1995: 139 (Gulf of Mexico); Reiner, 1996: 22, fig. (Cape Verde); Bonfil, 1997: 105 (Veracruz, Mexico); Joseph, 1999: [unpaginated] (Sri Lanka); Cervigón & Alcalá, 1999 (Venezuela); Clarke, 2000: 377 (Rockall Trough, NE Atlantic); Baino *et al*., 2001: 234 (Alboran Island to Aegean Sea, Mediterranean); Graham *et al*., 2001: 551 (south-eastern Australia); Yearsley *et al*., 2001: 35, 360 (southern Australia); Bilecenoglu *et al*., 2002: 17 (Turkey); Daley *et al*., 2002: 53 (southern Australia); Ali & Saad, 2003: 58, fig. (Syria); Schembri *et al*., 2003: 77, fig. 3d (Malta); Serena, 2005: 28, figs, pl. I, 9 (Mediterranean Sea, NE Atlantic, Western Indian, Gulf of Mexico and Taiwan); Meriç *et al*., 2007: 31 (Turkey); White, 2008: 87, figs (southern Australia); Scacco *et al*., 2010: 39, fig. 3f (Mediterranean Sea); Castro, 2011: 81, figs 16a-e (north-western Atlantic); Davenport *et al*.: 2011: 557 (north-western Atlantic, USA); White *et al*., 2013: 36, fig. 2, 15, 16 (Atlantic); Veríssimo *et al*., 2014: 6, fig. 5 (Gulf of Mexico); Hipes, 2015: 1, fig. 11 (Gulf of Mexico, USA); Wienerroither *et al*., 2015: 834, fig.

2 (northern Norway); Farrag, *et al*., 2016: 481, fig. 2a (Egypt); Driggers *et al*., 2017: 52 (Gulf of Mexico); Haroun *et al*., 2017: 84 (Egypt); Lteif *et al*., 2017: 1491 (Lebanon); Biscoito *et al*., 2018: 471, fig. 7 (Madeira, Portugal); Carneiro *et al*., 2019: 36 (Portugal); Ehemann *et al*., 2019: 4 (Venezuela); Fernando *et al*., 2019: 231, figs 5e, 18d-f (Mutur, Sri Lanka); Follesa *et al*., 2019: 85 (Mediterranean); Psomadakis *et al*., 2019: 162, figs, pl. X (fig. 70) (Myanmar); Iglésias, 2020: 46, pl. 21 (France and Cape Verde); Ebert & Dando, 2021: 217, figs (NE Atlantic and Mediterranean); Kousteni *et al*., 2021: 1, figs 2 and 3 (Cypriot waters).

Centrophorus machiquensis Maul, 1955: 5, figs 13–16 (Type locality: Madeira)—Krefft & Tortonese, 1973: 39 (Madeira); Ali & Saad, 2003: 57, fig. (Syria); Biscoito *et al*., 2018: 470, fig. 6 (Madeira, Portugal); Almeida & Biscoito, 2019: 99 (Canary Islands and Madeira); Carneiro *et al*., 2019: 36 (Portugal).

Centrophorus ujato—Tortonese, 1956: 178, fig. 96 (Genova, Italy); Bini, 1967: 97, fig. (Italy); Sara, 1968: 1, figs 1–3 (west of Sicily); FAO, 1971: no pagination (Mediterranean Sea).

Centrophorus spp. (*granulosus* group)—Forster *et al,* 1970 (in part): 388 (Western Indian Ocean).

Centrophorus (forme) *uyato-machiquensis*—Cadenat & Blache, 1981: 58, figs. 36, 37 and 40 (NE Atlantic).

Centrophorus spp.—Peyronel *et al*., 1984: 643 (Bay of Ajaccio, Corsica, France).

Centrophorus cf. *harrissoni* (Undescribed gulper shark #2)—Kiraly *et al*., 2003: 2 (Puerto Rico, US Virgin Islands, Virginia, North Carolina and Florida Straits to Dry Tortugas).

Centrophorus bragance—Hernández-Hamón & Núñez, 1998: 108 (as questionable synonym of *C. granulosus*).

Centrophorus sp. (*uyato*?)—Morón *et al*., 1998: 144 (Beruwela, Sri Lanka).

Centrophorus sp. cf. *uyato*—Saad, *et al*., 2004: 430 (Syria).

?Centrophorus sp. (non *uyato*)—Serét, 2005: 21 (Libya).

Centrophorus zeehaani White, Ebert & Compagno, 2008: 1, figs 8-10 (Type locality: South Australia)—Last & Stevens, 2009: 68, pl. 9.7, figs (southern Australia); Pethybridge *et al*., 2010: 1369 (Tasmania and Great Australian Bight, Australia); Pethybridge *et al*., 2011: 2743 (Tasmania and Victoria, Australia); Graham & Daley, 2011: 583 (southern Australia); Daley *et al*., 2012: 708 (southern Australia); White *et al*., 2013: 41 (southern Australia); Daley *et al*., 2015:127 (southern Australia); Wienerroither *et al*., 2015: 834, fig. 2 (northern Norway); Bineesh *et al*., 2016: 461 (Kollam, India).

Centrophorus cf. *uyato*—McLaughlin & Morrissey, 2005: 1185, figs 2, 3 (Cayman Trench, Jamaica); Veríssimo *et al*., 2014: 7 (Gulf of Mexico); Serena *et al*., 2020: 502, 509 (Mediterranean); Bellodi *et al*., 2022: 2 (Mediterranean Sea).

Centrophorus zeehani—Daley *et al*., 2012: fig. 2 (misspelling; southern Australia); Bineesh *et al*., 2016: 466 (misspelling; Kollam, India).

Centrophorus ‘uyato’—White *et al*., 2017: 86 (Eastern Atlantic); Almeida & Biscoito, 2019: 100 (Mediterranean Sea, Canary Islands and Madeira).

Centrophorus cf. *granulosus*—Follesa *et al*., 2019: 85 (Mediterranean); FAO, 2018: unpaginated, fig. (Mediterranean Sea).

?*Centrophorus granulosus*—Parenti, 2019: 102 (Sicily).

Material examined. Neotype: BMNH 2021.10.4.1 (eviscerated; GenBank accession ON167716), female 983 mm TL, between Gorgona and Capraia islands, Ligurian Sea, 43°19.8′ N, 9°56.1′ E, 180 m, 20 Dec. 2012.

Other specimens: *Australia*: AMS I 44310–001 (paratype of *Centrophorus zeehaani*; GenBank accession ON167706), adult male 826 mm TL, southwest 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, 4 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 6307–01 (skeletal parts), female 1027 mm TL, 12 July 2004, east of Flinders Island, Tasmania, ~40° S, ~149° E, 350–430 m; CSIRO H 6309–01 (skeletal parts; GenBank accession ON167708), adult male 865 mm TL, CSIRO H 6309–02 (skeletal parts), adult male 876 mm TL, CSIRO H 6309–04 (skeletal parts), adult male 906 mm TL, east of Flinders Island, Tasmania, ~40° S, ~149° E, 400–450 m, 1 Aug. 2004; CSIRO H 6310–04 (skeletal parts), female 970 mm TL, northeast of Flinders Island, Tasmania, 39°04′ S, 148°39′ E, 500–680 m, 24 Jul. 1986; CSIRO H 6311–01 (skeletal parts), female 655 mm TL, east of St. Helens, Tasmania, 41°27′ S, 148°44′ E, 850–860 m, 5 Jun. 1987; CSIRO H 6500-02, adult male 862 mm TL, east of Flinders Island, Tasmania, 40°15′ S, 148°45′ E, 329–512 m, 21 Aug. 2003; CSIRO H 6503–02 (skeletal parts), female 991 mm TL, CSIRO H 6503–03 (skeletal parts; GenBank accession ON167709), female 1023 mm TL, CSIRO H 6503–04 (skeletal parts; GenBank accession ON167710), female 987 mm TL, CSIRO H 6503–05 (skeletal parts), female 957 mm TL, northeast of Flinders Island, Tasmania, 39°20′ S, 148°45′ E, 370–420 m, 7 Apr. 2003; CSIRO H 6504–02, adult male 854 mm TL, CSIRO H 6504–03, female 817 mm TL, CSIRO H 6504–04, juvenile male 666 mm TL, 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; CSIRO H 6628–01 (paratype of *Centrophorus zeehaani*), immature male 506 mm TL, CSIRO H 6628–02 (paratype of *Centrophorus zeehaani*; GenBank accession ON167705), immature male 645 mm TL, CSIRO H 6628–03 (paratype of *Centrophorus zee-*

haani), adult male 875 mm TL, CSIRO H 6628–04 (paratype of *Centrophorus zeehaani*), adult male 910 mm TL, CSIRO H 6628–05 (holotype of *Centrophorus zeehaani*), adult male 893 mm TL, CSIRO H 6628–06 (paratype of *Centrophorus zeehaani*), adult male 852 mm TL, CSIRO H 6628–07 (paratype of *Centrophorus zeehaani*), adult male 906 mm TL, NMV A 29736–001 (paratype of *Centrophorus zeehaani*), adult male 820 mm TL, southwest of Coffin Bay, South Australia, 35°14′ S, 134°29′ E, 360–600 m, 28 July 2005; CSIRO unreg. (DB 02/181), Great Australian Bight, adult male 857 mm TL; CSIRO unreg. (LJVC 880517), female 840 mm TL, unknown location; PMH095-11 (jaws only), female 104 cm TL, Albany, Western Australia.

Eastern Atlantic (including Mediterranean): AMNH 78267, female 922 mm TL, AMNH 78269, female 937 mm TL, AMNH 78271, female 1016 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 1862.4.22.29, female 449 mm TL, Madeira, Portugal; BMNH 1864.7.18.1, female 894 mm TL, Madeira, Portugal; BMNH 1904.11.30.9-10 (2 specimens), female 1036 mm TL, adult male 888 mm TL, west of Faro, Portugal, 662 m depth; BMNH 1904.11.30.11 (paralectotype of *Centrophorus bragancae*), juvenile male 488 mm TL, off Sesimbra, Portugal, 841 m depth; BMNH 1904.11.30.12 (lectotype of *Centrophorus bragancae*), female 467.5 mm TL, off Sesimbra, Portugal, 505 m depth; BMNH 2013.9.20.34, female 875 mm TL, BMNH 2013.9.20.35, female 930 mm TL, BMNH 2013.9.20.36, female 935 mm TL, BMNH 2013.9.20.37, female 731 mm TL, BMNH 2013.9.20.38, adult male 843 mm TL, BMNH 2013.9.20.39, adult male 865 mm TL, northeast Atlantic; CSIRO H 7471-01 (GenBank accession ON167715), adult male 853 mm TL, east of Corsica, France, 42°05.8′ N, 9°44.5′ E, 550–565 m, 30 May 2012; CSIRO H 7472-01, juvenile male 440 mm TL, southeast of Corsica, France, 41°47.9′ N, 9°30.5′ E, 466–480 m, 31 May 2012; ERB 1288, male 770 mm TL, Concarneau fish-market, France, 9 Sep. 2000; ERB 0763, male, 850 mm TL, Concarneau, France, 13 May 2009; HUJ 10885, female 760 mm TL, Hadera, Israel, 13 Sep. 1982; HUJ 11339, adult male 796 mm TL, Haifa Bay, Israel, 1 Mar. 1983; HUJ 17029, female 476 mm TL, Haifa, Israel, 16 Mar. 1983; HUMZ 151304, juvenile male 578 mm TL; HUMZ 151306, female 978 mm TL, Namibia; HUJ 21135 (GenBank accession ON167718), female 753 mm TL, Haifa fishing port, Israel, 29 July 2013; MNHN-IC 1905-0568, juvenile male 454 mm TL, Portugal, 460 m depth, June 1903; MNHN-IC 1969-0269, juvenile male 499 mm TL, southwest of Monrovia, Liberia, 6°08′ N, 10°56′ W, 400 m depth, 27 Apr. 1964; MNHN-IC 0000-1224, female 537 mm TL, Naples, Italy; MNHN-IC 2005-0169, adult male 892 mm TL, west of Ireland, 28 Apr. 2005; NMW 15009, female 889 mm TL, Nice; NMW 63020, adult male 880 mm TL, Nice, France, 1902; PMH095-13 (jaws only), male 860 mm TL, Lisbon fish auction, Portugal; PMH095-14 (jaws only), female 905 mm TL. Algeciras fish market, Spain; SBMC unreg (BPS-0488), female 670 mm TL, Cape Verde, 15°27.75’ N, 23°25.91’ W, 100–300 m depth, 16 Jun. 2005; ZMB 22737, female 456 mm TL, Naples, Italy; ZMB 22993, juvenile male 432 mm TL, South Atlantic Ocean; ZMH 120700, adult male 803 mm TL, northwest of Scotland, 57°40’ N, 09°35’ W, Apr. 1982, 680 m depth.

In addition, 506 specimens studied by Guallart (1998) from Balearic Sea (Western Mediterranean); only some samples and photographic material preserved.

Western Atlantic: AMNH 33442, adult male 857 mm TL, off Mississippi, Gulf of Mexico, USA, 24 Aug. 1962; AMNH 33443, juvenile male 539 mm TL, off Mississippi River mouth, Gulf of Mexico, USA, 29°11′ N, 88°08′ W, 20 Dec. 1962; CAS 60861, female 987 mm TL, south of St. Thomas Harbor, US Virgin Islands, 18°11′12” N, 64°55′30” W, 340–460 m depth, 22 Sep. 1987; PMH095-1 (jaws only), male 850 mm TL, northern Gulf of Mexico, USA; PMH095-2 (jaws only), male 855 mm TL, northern Gulf of Mexico, USA; PHM095-3 (jaws only), male 900 mm TL, northern Gulf of Mexico, USA; PHM095-4 (jaws only), male 910 mm TL, northern Gulf of Mexico, USA; PMH095-7 (jaws only), female 870 mm TL, northern Gulf of Mexico, USA; PMH095-8 (jaws only), female 875 mm TL, northern Gulf of Mexico, USA; PMH095-9 (jaws only), female 1010 mm TL, northern Gulf of Mexico, USA; PMH095-11 (jaws only), female 1080 mm TL, northern Gulf of Mexico, USA; PMH095-12 (jaws only), female 1090 mm TL, northern Gulf of Mexico, USA; SAM unreg (*Oregon II* 37238), female 500 mm TL, SAM unreg (*Oregon II* 11281), female 393.5 mm TL, Gulf of Mexico, USA; ZMH 119879, juvenile male 808 mm TL, east of Florida, USA, 29°08′ N, 78°57′ W, 4 Nov. 1979.

Western Indian Ocean: BMNH 1973.7.9.17, female 735 mm TL, east of settlement on Aldabra Island, Seychelles, 878 m depth, 7 January 1969; CAS 29287, female 1024 mm TL, Vailhev Shoal, off Grand Comoro Island, 220–440 m depth, 30 Aug. 1973.

Unknown location: HUMZ 102985, adult male 868 mm TL; HUMZ 124764, female 1013 mm TL.

Genetic material (specimens not retained). *Indian Ocean*: specimen #589 (GenBank accession ON167722), specimen #782 (GenBank accession ON167723), Myanmar waters of Andaman Sea, 2015; specimen J78 (GenBank accession ON167720), specimen J81 (GenBank accession ON167719), Kochi, India.

Eastern Atlantic: AZ-17 (GenBank accession JQ518946), male 860 mm TL, Funchal, Madeira, Portugal, 32°38′ N, 16°56′ W, 1 Jun. 2009; specimen #15, off central Angola, 11°30.95′ S, 13°21.24′ E, 22 Apr. 2010.

Western Atlantic: AM-1102-008-002-Csp (GenBank accession ON167711), off Pascagoula, Mississippi, northern Gulf of Mexico, USA, 29°2.78′ N, 88°32.27′ W, 26 Mar. 2011; OM-1009-005-002 (GenBank accession ON167712), OM-1009-005-005 (GenBank accession ON167713), off Pascagoula, Mississippi, northern Gulf of Mexico, USA, 29°8.74′ N, 88°16.6′ W, 15 Jan. 2011; OM-1009-XXX-002 (GenBank accession ON167714), off Pascagoula, Mississippi, northern Gulf of Mexico, USA.

Diagnosis. This species undergoes important morphoanatomic changes during ontogeny in many of the characters used for its identification. Comparison between pregnant females and the full-term embryos they contain, which are undoubtedly conspecific, provides the strongest evidence for such changes. The most notable changes are in coloration, morphology of the dermal denticles and morphology of the teeth. In addition, many morphological measurements show allometric trends, so their percentage value with respect to TL varies with body size. This pattern broadly follows that described for various species of sharks by Bass (1973). Thus, the description of characters which vary ontogenetically are provided first for full-term embryos and neonates and then for adults. Large juveniles and sub-adults present characters with intermediate values or morphologies. If nothing is indicated, the range of values includes the entire length range from newborn to adults even although there may be a trend in the values within this range

A medium-sized (112 cm maximum total length) species of *Centrophorus* with the following combination of characters: head long (length 20.4–25.1% TL) and moderately robust (width 10.4–14.3% TL); snout relatively short (horizontal preorbital length 4.8–7.2% TL), narrowly rounded in dorsal view; first dorsal fin relatively short (base length 10.9–16.0% TL; soft fin length 9.8–13.9% TL), moderately tall (height 5.2–7.7% TL); second dorsal fin slightly smaller than first (height of second dorsal fin 1.1–1.6 in that of first dorsal fin, soft fin length of second dorsal fin 1.2–1.6 in that of first dorsal fin); pectoral fins large (anterior margin length 10.7–13.4% TL), free rear tip moderately elongated in newborns, very elongate in larger individuals (sometimes with a damaged tip); dorsal and lateral surfaces medium greyish in newborns and small juveniles becoming pale brownish with a reddish tinge in large adults (some large adult males can have a uniform medium brown colour on entire body); inside of mouth almost black in newborns and small juveniles, whitish or pale grey in adults; dorsal fins newborns and small juveniles distinctly black apically with a white margin on free rear tips, the white margin lost in adults and dark markings less distinct but usually still present; central upper teeth erect, lateral teeth with oblique cusps and a marked notch; the number of erect (not asymmetric) teeth increases from a few (3–8) in newborns and small juveniles to most of them (>15) in adults and almost all (>25 in large dark-brown males); lower teeth much larger than upper teeth, strongly oblique, blade-like with margin slightly serrated (only visible under magnification in small juveniles); lateral trunk denticles sessile (not raised on pedicels), changing from pointed in newborns and small juveniles to almost block-like in subadults and adults, not overlapping or elevated, margin scalloped; total vertebral centra 113–120 (mean 116); teeth 33–44 / 26–32.

Description. Body fusiform, moderately elongate, nape moderately humped (Figs 8, 9); deepest near first dorsal-fin spine; head moderately elongate, length 22.5% TL in neotype (21.2–25.6% TL in 71 other specimens, from small juveniles to large adults); caudal peduncle moderately slender, pelvic-caudal space 13.9 (11.6–16.1)% TL. Head moderately robust, broad; depressed forward of spiracles, becoming somewhat semicircular in cross-section towards pectoral-fin origin; length 3.5 (3.0–3.8) in precaudal length; height 0.9 (0.7–1.0) times width. Snout relatively short, narrowly rounded in lateral view, apex bluntly pointed; lateral prenarial margin angular; narrowly rounded in dorsal view (Fig. 10); horizontal preorbital length 1.0 (0.8–1.2) times eye length, 0.6 (0.6–0.9) times interorbital space; horizontal prenarial length 2.6 (2.2–2.8) times in preoral length.

Eye large, oval, length 4.2 (3.0–4.4) in head, 3.8 (2.4–4.7) times height; strongly notched posteriorly, notch not extending towards spiracle. Spiracle moderately-sized, semicircular; no lobe-like fold on posterior margin.

Gill openings directed slightly anteroventrally from top to bottom; first four subequal in size, fifth longest, height of fifth slit 2.9 (2.3–4.1)% TL. Nostrils small, almost transverse; anterior nasal flap formed as a large subtriangular lobe with a somewhat rudimentary secondary lobe mesially; internarial space 2.5 (2.5–3.5) in preoral length, 2.5 (1.5–2.7) times nostril length. Mouth almost transverse (Fig. 10), upper jaw slightly concave, width 1.2 (0.9–1.4) in preoral length; upper labial furrows subequal to or slightly longer than lower furrows; prominent postoral groove, more than twice length of upper labial furrows, extending posterolaterally from angle of jaws.

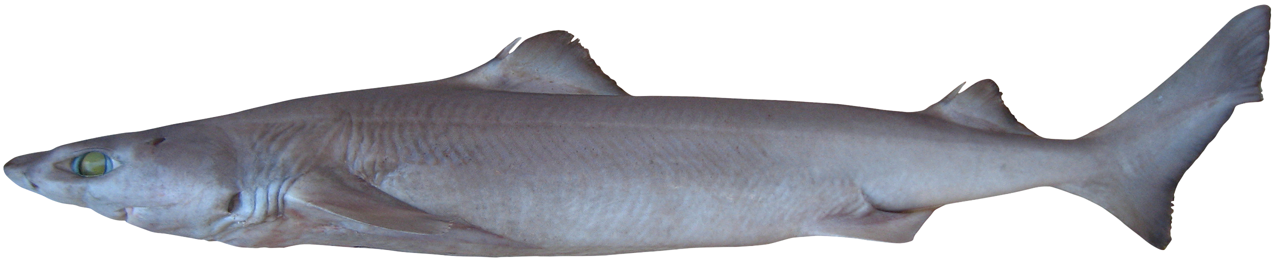

FIGURE 8. Lateral view of the adult neotype of *Centrophorus uyato* (BMNH 2021.10.4.1, adult male 983 mm TL; image flipped, right side shown).

FIGURE 9. Lateral view of juvenile of *Centrophorus uyato* CSIRO H 7472-01, 440 mm TL juvenile male): (A) lateral view; (B) dorsal view.

Dignathic heterodonty strongly evident; monognathic heterodonty noticeable in upper jaw and lesser so in the lower jaw; ontogenetic heterodonty non-existent in females, slight in males; sexual dimorphism evident in some adult males. Upper teeth mostly smooth in males, finely serrated in females (Fig. 11A, C); no discernable symphyseal teeth present but with 3 to 6 very symmetrical, large and similarly-sized medial teeth with straight crowns and gradient merging into anterior files; upper tooth shape conical and somewhat narrow with peg-shaped roots and a distinct apron along basal face; anterior teeth with somewhat straight crowns and a very slight distal heel present and becoming more oblique antero-laterally; lateral teeth increasingly more oblique, deeply notched with a distinct distal bifurcation of basal and apical crown sections and a very distinct distal heel present; mesial crown portion of lateral teeth slightly concave with apical portion of crown slightly reflexed mesially; posterior files very strongly oblique and with heavily notched distal margins and straight mesial edges. Lower teeth with very well-developed serrations on mesial cutting edge, more so in adult females (Fig. 11B, D); lower jaw with no discernable symphyseal or medial teeth; teeth compressed and interlocked with strongly oblique crowns forming an even cutting edge across lower jaw; anteroposterior files similar except for smaller size and lower crown height in posteriors; root asymmetrical with the distal edge slightly convex and the mesial edge concave and a very weakly developed apron at centre; crowns heavily notched distally with strong bifurcation of basal and apical crown sections and well-developed distal heels; mesial edge convex with apical portion directed distally; last file of teeth in posterior section usually with a very elongated distal root and basal crown section.

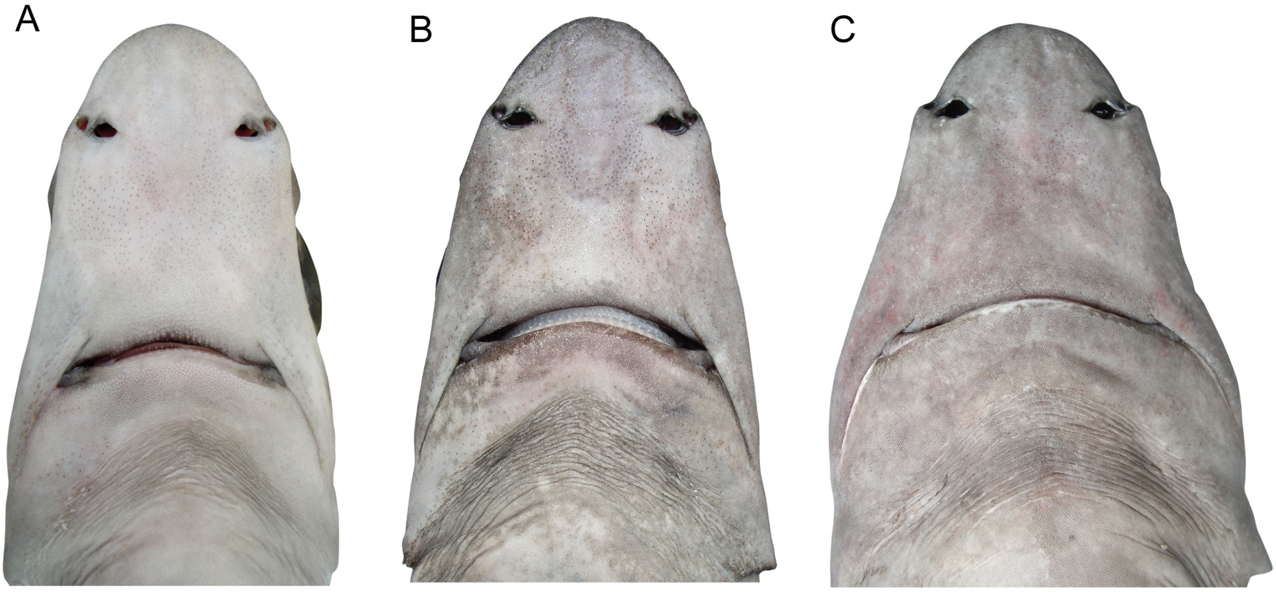

FIGURE 10. Ventral view of the head of *Centrophorus uyato*: (A) juvenile (BPS-0489, newborn male 470 mm TL); (B) juvenile (BPS-0488, female 687 mm TL); (C) adult (MNHN-IC 2005-0169, male 892 mm TL).

Dermal denticles on flank small, flat, pavement-like, not overlapping (Fig. 4); medial cusp relatively blunt; no lateral cusps; ridges present on anterior crown, not extending onto cusp. Denticles of newborns and small juveniles smaller, more pointed (Fig. 4A, B); crowns with narrowly pointed medial cusp; a single central ridge distinct and extending to tip of cusp. Mid-sized juveniles with skin covered by small white flecks which under magnification are decalcified dermal denticles in a replacement phase.

First dorsal fin moderately small, raked, broadly rounded apically; anterior margin moderately convex; upper posterior margin straight to slightly convex, slanting strongly posteroventrally from top to bottom, moderately concave near free rear tip; free rear tip relatively thick basally, moderately long; inner margin of fin almost straight to weakly concave; insertion of base extremely well forward of pelvic-fin origin, posterior to or opposite free rear tip of pectoral fin; fin-spine origin above mid pectoral-fin inner margin (in newborns and small juveniles near the much shorter free tip apex); spine base broad, exposed anteriorly just below junction of spine and soft portion of fin; soft portion of fin connected about level of two thirds of total spine length; spine rapidly tapering distally when not damaged, anterior margin almost straight to weakly convex; exposed portion of spine sloping strongly posterodorsally from base to apex, usually shorter than exposed portion of second dorsal-fin spine; first dorsal soft-fin length 1.9 (1.5–2.3) times its height, 1.5 (1.2–1.6) times second dorsal soft-fin length; first dorsal-fin height 1.2 (1.1–1.6) times second dorsal-fin height; exposed first dorsal spine length 2.4 (2.0–4.6) in height of fin.

Second dorsal fin moderately small, slightly raked; anterior margin slightly convex, apex moderately to narrowly rounded; posterior margin weakly to moderately concave, sloping strongly posteroventrally from apex; free rear tip greatly elongated, inner margin length 0.9 (0.7–1.1) times fin height; second dorsal soft-fin length 1.6 (1.4–2.0) times its height; exposed spine length 2.3 (0.9–4.0) in height of fin; fin-spine origin above or just anterior to free rear tip of pelvic fin, exposed just below level of junction with spine and soft portion of fin; second dorsal spine moderately broad based, tapering distally, sharply pointed when undamaged; second dorsal-fin spine has a lateral expansion of enamel at apex that gives it an "arrowhead" appearance (not observed when the apex is eroded); interdorsal space 1.0 (0.9–1.3) in prepectoral length, 1.2 (1.2–1.7) in pre-first dorsal length; interdorsal groove weak.

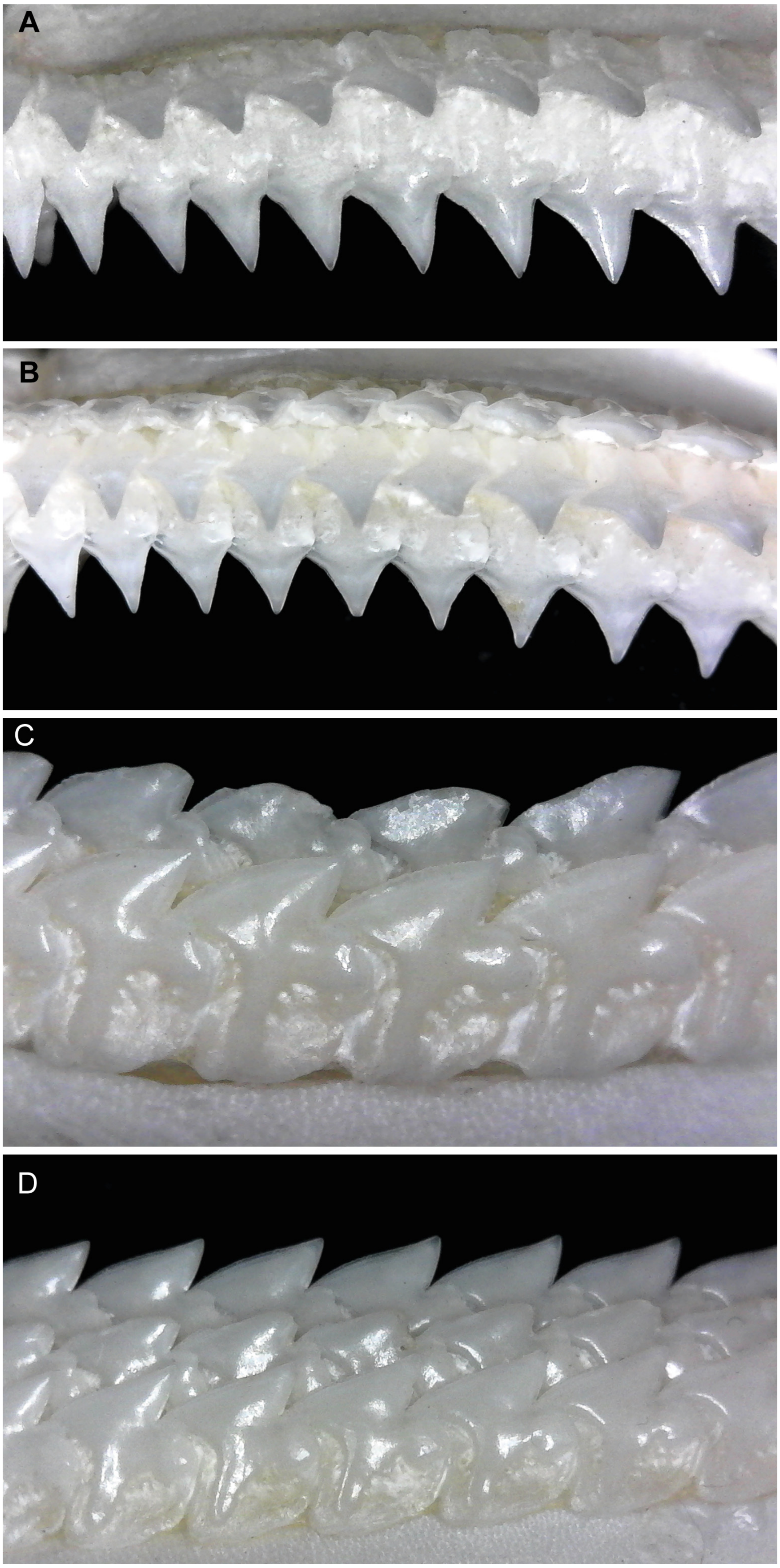

FIGURE 11. Upper (A, B) and lower (C, D) teeth of *Centrophorus uyato*: (A, C) adult female 1090 mm TL (PMH 095-12); (B, D) adult male 910 mm TL (PMH 095-4).

Pectoral fin moderately large, anterior margin weakly convex; inner margin weakly convex anteriorly, almost straight posteriorly, anterior margin length 12.3 (10.7–13.4)% TL; apex moderately rounded to somewhat angular, lobe-like but not falcate; posterior margin almost straight from apex to free rear tip; inner margin length 12.3 (10.6–15.7)% TL; free rear tip only slightly elongate in newborns and small juveniles (Fig. 12A), barely passing the origin of the spine of first dorsal fin, but greatly elongated in adults (Fig. 12B), extending to posterior half of first dorsal-fin base; base very short, 2.1 (1.9–3.3) in anterior margin length.

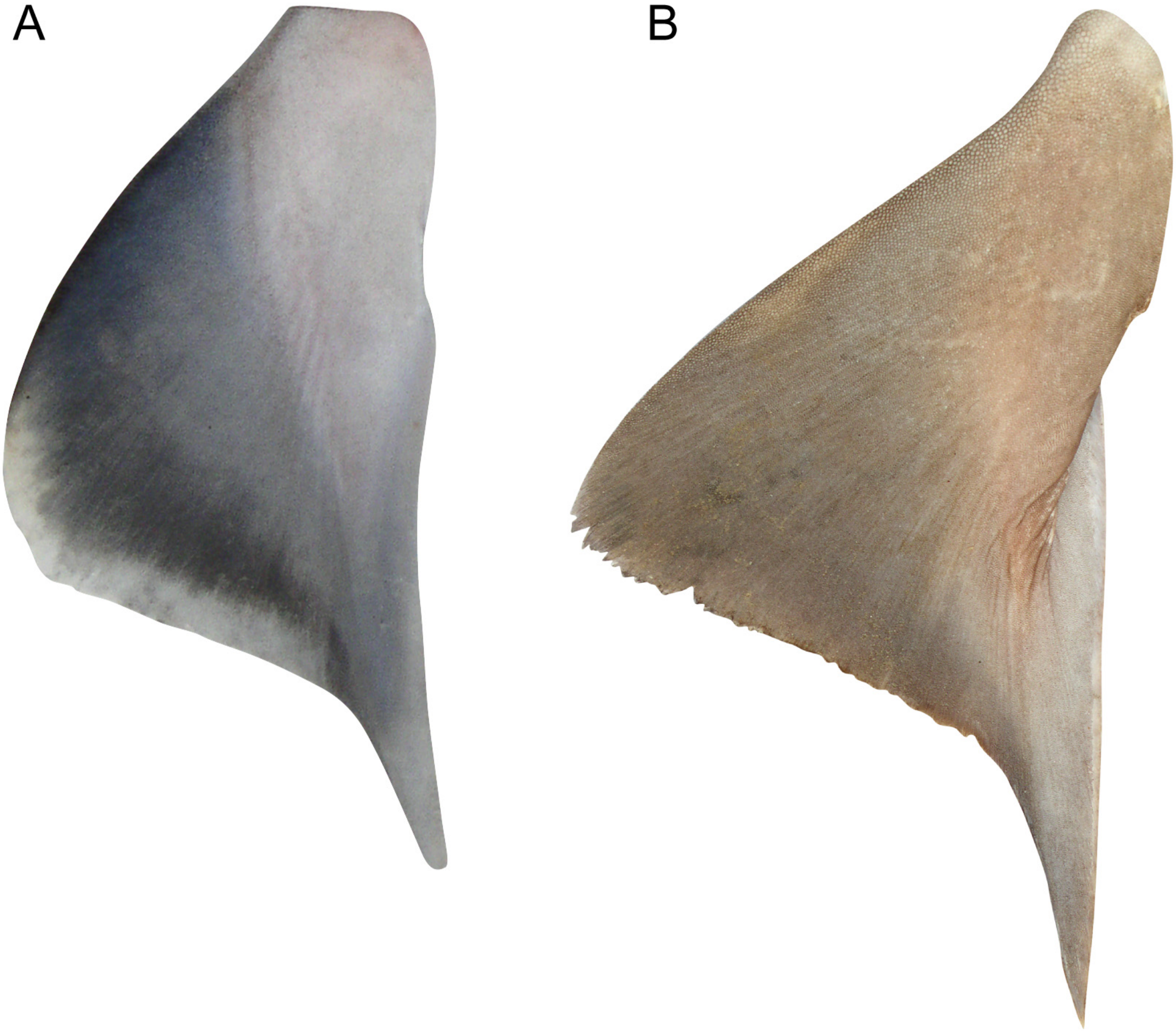

FIGURE 12. Pectoral fin of *Centrophorus uyato* in ventral view: (A); juvenile (BPS-0489, newborn male 470 mm TL); (B) adult (not retained, male 870 mm TL).

Pelvic fins moderately large, length 11.2 (9.8–12.8)% TL, anterior margin straight to weakly convex, posterior margin weakly concave to nearly straight, apex moderately rounded to bluntly angular, free rear tip acute to narrowly rounded. Claspers of adult males relatively short, outer length 2.6–4.0% TL, attached along inner margin of pelvic fin for most of their length, inner length 1.0–1.6 times pelvic-fin inner margin; area of attachment to pelvic fin markedly thickened; compressed dorsoventrally, only extended slightly beyond free rear tips of pelvic fin; clasper groove long, longitudinal and dorsomedially; apopyle and hypopyle not pronounced; rhipidion elongate, blade-like, mostly concealing the accessory terminal cartilage (spur); spur originating at about level of insertion of clasper and pelvic fin (Fig. 13).

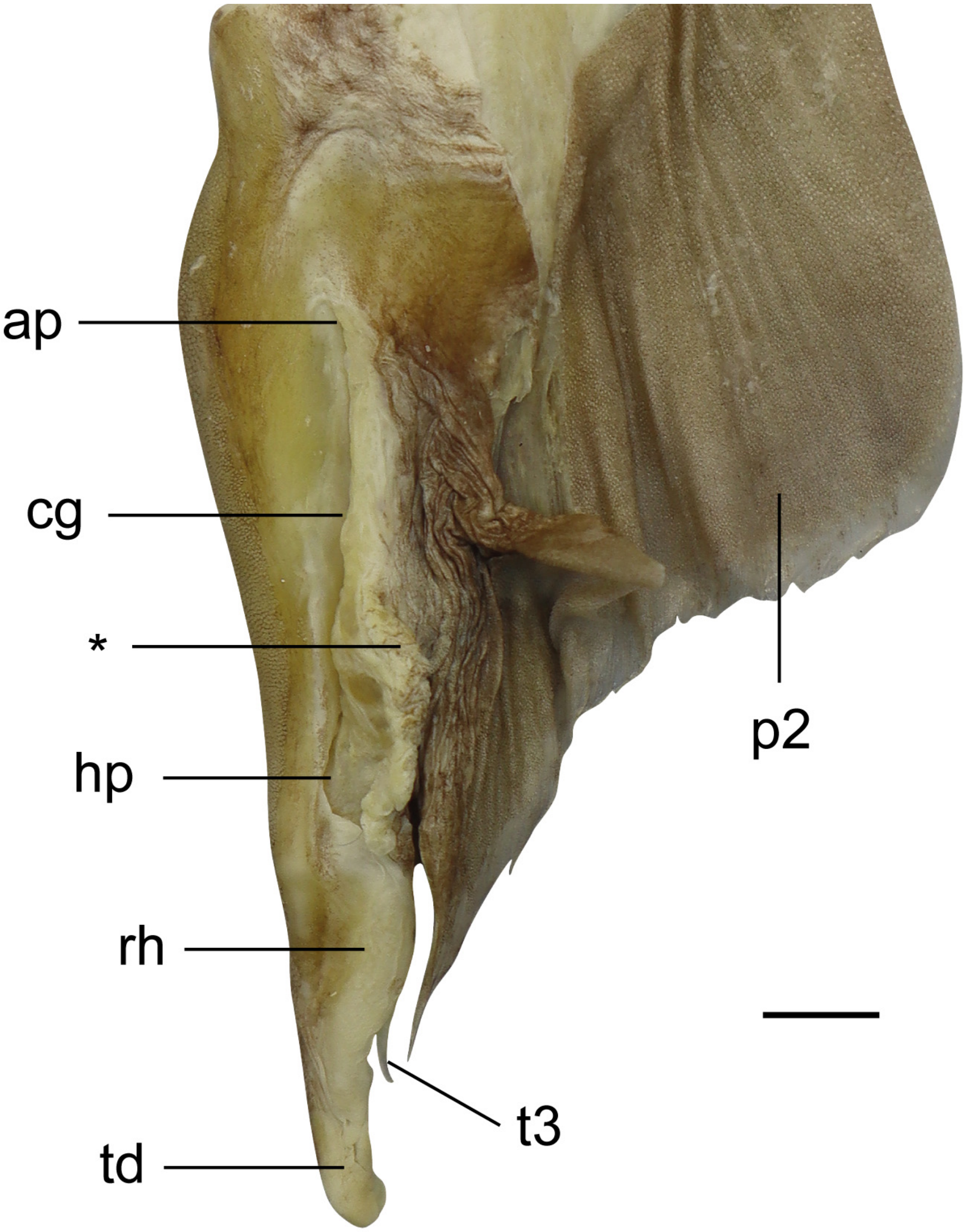

FIGURE 13. Right clasper of *Centrophorus uyato* in dorsal view (CSIRO H 6309-01, adult male 865 mm TL). Abbreviations: ap, apopyle; cg, clasper groove; hp, hypopyle; p2, pelvic fin; rh, rhipidion; td, dorsal terminal cartilage; t3, accessory terminal cartilage (spur); ***** thickened portion at attachment area of clasper and pelvic fin. Scale bar: 10 mm.

Caudal peduncle moderately long, compressed, tapering slightly towards caudal fin; ventral groove weak; no lateral keels; pelvic–caudal space 2.3 (1.7–2.9) in pectoral–pelvic space, 1.6 (1.4–2.0) in prepectoral length; dorsal–caudal space 3.6 (2.3–3.5) in interdorsal length; precaudal pits absent. Caudal fin relatively long, postventral margin mostly moderately concave, terminal lobe moderately large, deep; apex of lower lobe narrowly to moderately rounded; dorsal caudal margin 1.1 (0.9–1.5) in head length; length of lower caudal lobe 1.8 (1.4–2.6) in upper lobe length.

Total vertebral centra 118 (113–120), monospondylous precaudal centra 56 (53–59), diplospondylous precaudal centra 30 (27–31), precaudal centra 86 (82–89) and diplospondylous caudal centra 32 (28–33). Tooth file count: upper jaw 16–22 (n = 25) + 17–22 (n = 27), 33–44 (n = 40); lower jaw 13–17 (n = 28) + 13–16 (n = 28), 26–33 (n = 37).

Coloration. Dorsal and lateral surfaces uniformly medium grey (newborns and small juveniles, Fig. 9, and some subadults and adults) to pale brown with a distinct pale reddish tinge (in larger adults, Fig. 8) or uniform medium to dark brown (in some large adult males, Fig. 14); ventral surfaces paler; waterline between dorsal and ventral colour shades very diffuse on lower sides, well demarcated on head, extending just below lower margin of eye and just below upper margin of gill slits, pectoral-fin origin pale; eye–spiracle space often with a distinct pale whitish blotch anteriorly, less distinct near spiracle. A diffuse white spot in the centre of the dorsal surface of the head in front of the eyes in both juveniles (Fig. 9B) and adults. In subadults and adults, dorsal fins pale with a distinct, broad, diffuse-edged, dusky margin extending from about level of fin-spine apices to just posterior of the maximum concavity of the posterior margin; dorsal fin spines ivory coloured with a dark anterior longitudinal ridge covered with enamel; pectoral and pelvic fins darker distally, with narrow whitish posterior margins; caudal fin mostly greyish or brownish, postventral margin darker distally, terminal lobe usually darker than rest of fin. In newborns and small juveniles, a distinct dark greyish blotch over upper portion of gill slits, extending dorsally to level of upper margin of spiracle; dorsal fins blackish distally with a whitish free rear tip; pectoral fin upper surfaces dark grey with a distinct white posterior margin; pelvic fins pale with whitish posterior margin, blackish border on central edge of anterior margin; caudal fin with a broader white postventral margin, terminal lobe with very broad white margin and often with a darkish blotch extending to margin on lower third of terminal margin, preventral margin with a very narrow blackish border.

FIGURE 14. Variation in colour of adult male *Centrophorus uyato* from the Balearic Sea (Western Mediterranean): medium grey in top and bottom individuals, uniformly medium brown in middle individual.

Skeletal morphology. *Neurocranium* (Fig. 15; based on CSIRO H 6310-04). Measurements of the neurocranium are presented in Table 2. Neurocranium greatest width at level of postorbital processes (44.4–49.8% CL), narrower at interorbital region (29.0–33.4% CL). Rostrum elongate (precerebral fossa length 27.8–32.3% CL, its width 9.4–13.1% CL); lateral rostral appendages thick, short and hook-like; median rostral prominence small; rostral keel conspicuous and elongate, extending anterior to nasal capsules (its length 38.2–42.5% CL). Anterior fontanelle almost pear-shaped, located at base of rostrum and anterior to cerebrum; two short, broad protuberances anteriorly adjacent to nasal capsules. Nasal capsules almost spherical, moderately large, width across nasal capsules 40.8%–47.0% CL; inner anterior nasal margins with a small nasal protuberance; subnasal fossa moderately larger and suboval, located ventrally on each side of posterior rostral keel; a prominent, triangular, slightly curved process on anterolateral edge of each subnasal fossa.

TABLE 2. Cranial measurements of *Centrophorus uyato*, *C. harrissoni*, *C. moluccensis* and *C. squamosus* expressed as a percentage of neurocranium total length (% CL). N: number of specimens.

	C. uyato				*C. harrissoni*				*C. moluccensis*		*C. squamosus*	
	N	Min.	Max.	Mean	N	Min.	Max.	Mean	N	CSIRO H 3599-04	N	CSIRO H 1358-01
Total length of neurocranium (CL) (mm)	9	107.2	157.7	140.6	16	101.6	181.7	147.3	1	108.0	1	180.9
Postcerebral length	9	60.8	66.7	63.7	16	57.1	61.9	59.5	1	65.4	1	62.8
Precerebral fossa length	9	27.8	32.3	30.6	16	33.6	39.7	36.9	1	30.5	1	31.9
Precerebral fossa width	9	9.4	13.1	10.9	16	9.3	12.7	10.8	1	9.2	1	11.6
Width across nasal capsules	9	40.8	47.0	44.3	16	36.9	44.9	42.4	1	38.9	1	46.0
Interorbital width	9	29.0	33.4	31.5	16	25.3	28.0	26.6	1	25.3	1	27.0
Width across preorbital processes	9	34.7	40.2	37.6	16	31.8	36.9	34.0	1	40.6	1	41.1
Width across postorbital processes	9	44.4	49.8	47.0	16	36.1	44.0	38.8	1	38.2	1	44.8
Width across prootic processes	9	40.0	45.2	42.3	16	35.3	40.9	38.0	1	41.2	1	46.0
Nasobasal length	9	61.6	65.2	63.4	16	48.0	58.2	53.2	1	63.0	1	62.5
Rostral keel length	9	38.2	42.5	40.5	16	46.7	54.9	50.3	1	43.2	1	40.5
Subethmoidean width	9	5.4	7.9	6.9	16	7.6	8.9	8.4	1	3.5	1	6.9
Basal plate length	9	33.4	40.2	36.3	16	28.8	35.2	32.1	1	36.1	1	36.4
Distance between postorbital and prootic processes	9	19.9	23.1	21.7	16	18.5	22.0	19.7	1	22.1	1	26.4
Width of basal angle	9	15.3	17.4	16.1	16	12.3	16.4	14.6	1	16.0	1	22.6
Width across 1st cartilaginous process	9	25.0	28.3	26.5	16	23.1	26.9	24.9	1	26.9	1	30.0
Width across 2nd cartilaginous process	9	30.2	34.4	32.0	16	27.5	30.6	28.7	1	31.2	1	34.8
Maximum sagittal height	9	26.3	29.2	27.7	16	23.6	27.4	25.1	1	28.2	1	27.5
Width of foramen magnum	9	4.1	6.3	5.3	16	3.7	6.1	5.0	1	6.9	1	4.8

Cranial roof strongly concave medially of interorbital region (forming a deep longitudinal sulcus on either side), moderately convex medially; a prominent lateral supraorbital crest present; preorbital canals large, tear-drop shaped, placed anteriorly to a series of foramina; canal for the ophtalmicus profundus small, rounded, located anterior to the preorbital canal and adjacent to ethmoidal canal; foramen of the epiphysial organ large, circular, located medially just posterior to anterior fontanelle; no supraethmoidal processes. Preorbital processes small, neurocranium broad between them. Postorbital processes prominent and triangular, not elongate, distance between processes 34.7–40.2% CL. Prominent ectethmoid process on each side of ethmoidal chamber; inconspicuous subethmoidal ridge, posterior to rostral keel, extending almost to subethmoidal region; subethmoidal region elongate and narrow, its width 5.4–7.9% CL.

Otic capsules relatively narrow; dorsally, two conspicuous anterior and two posterior semicircular canals; anterior canals with a strong ridge anteriorly; endolymphatic fossa oval and large, with two anterior endolymphatic foramina, slightly oblique, and two larger, posterior and vertical perilymphatic foramina; moderately strong otic crest located posteriorly to endolymphatic fossa; prominent sphenopterotic ridge at sides of otic capsules; opisthotic process at distal portion of sphenopterotic ridge small; laterally, otic wall delimited by a prominent lateral semicircular canal below the sphenopterotic ridge; width across hyomandibular facets 40.0–45.2% CL.

Orbital region narrow with concave preorbital wall, with orbitonasal canal at base; optic foramen (II) large, placed midventrally in interorbital wall; trochlear foramen (IV) small dorsal to optic foramen (II); eye-stalk located posteriorly, between the oculomotor foramen (III) and abducens foramen (VI); a broad foramen prooticum for trigeminal (V) and facial (VII) nerves positioned in the posterior edge of the interorbital wall, just anterior to the postorbital process; the foramen prooticum also opens posteriorly for the hyomandibular branch of the facial nerve (VII) at the base of hyomandibular facet; transbasal canal ventroposterior to anterior opening of foramen prooticum.

Basal plate flattened and large (length 33.4–40.2% CL), only slightly narrower anteriorly at basitrabecular process, broader posteriorly with its width 25.0–28.3% CL; basitrabecular processes conspicuous and elongate, slightly oblique to basal plate axis; basal angle width 15.3–17.4% CL; a small, shallow lateral prominence on each side at posterior of basitrabecular processes; two sets of cartilaginous processes on each side of the basal plate, first set small and below postorbital processes, second set prominent and below otic region, width across 2nd posterior cartilaginous processes 30.2–34.4% CL; single foramen for carotid artery anteromedially located in basal plate; foramina for orbital artery with its ventral opening in the anterior base of the cartilaginous process and its lateral opening in the lateral otic wall.

Occipital region with two distinct, triangular occipital condyles distally, and a wide foramen magnum between them, its width 4.1–6.3% CL; vagus foramen (X) large, lateral to occipital condyles; narrow glossopharyngeal base located more laterally in the occipital region, with a narrow, oval foramen for glossopharyngeal nerve (IX).

First dorsal fin (Fig. 16; based on CSIRO H 6503-04). Spine long and moderately wide basally, curving dorsoposteriorly. Dorsal fin with 6 basal plates bearing 8 proximal radials and 10 distal radials; first basal plate largest with 2 broad proximal radials anteriorly; a small triangular inter-basal plate at posterior of first basal plate bearing broad proximal radial which is divided distally with two separate distal radials; posterior 5 basal plates short and subequal in width, each bearing a single long proximal radial and a shorter distal radial; two posteriormost proximal radials curving posteriorly; penultimate proximal radial bearing two distal radials.

Guallart (1998) recorded first dorsal-fin radial counts of 5–11, mostly 7–9 (n = 154), and second dorsal-fin radial counts of 3–5, mostly 4 (n = 154).

Pectoral fin and girdle (Fig. 17; based on CSIRO H 6310-04). Coracoid bar convex anteriorly with a short, rounded projection on its medial portion (Fig. 17A); posterior margin concave and with a faint medial notch; two conspicuous, posteriorly orientated triangular processes present on laterointernal coracoid bar; base of the scapula, on its junction with the coracoid bar, is expanded and provided with a rounded diazonal foramen located just anterior of the articular region; condyle for articulation of the pectoral basals is wide. Scapula forming a U-shaped scapulacoracoid cartilage; scapular process on each side relatively long and narrowly pointed. Pectoral fin with two pectoral basals: a wide and broadly subtriangular meso+mesopterygium and a shorter, narrow, subtriangular, distally enlarged propterygium; meso+mesopterygium mostly fused together but separation visible distally (Fig. 17B). Pectoral radials: propterygium with one segmented radials consisting of a distal and proximal radial elements; mesopterygium with 9 segmented radials, two with only a distal and proximal radial element, remaining with distal, medial and proximal elements; metapterygium with 6 radials with 3 elements, 2 free radials, and a metapterygial axis with 3 radials. Guallart (1998) recorded pectoral-fin radial counts of 19–23, mostly 21 (n = 26).

Pelvic fin (Fig. 18; based on female CSIRO H 6503-04). Anterior pelvic fin basal element short and broad with 5 radials, distal one shortest; radials longer basally, becoming broader and shorter posteriorly; an additional rudimentary radial distal to other radials. Basipterygium elongate, slender, somewhat cylindrical, with 17 segmented radials; proximal elements of fourth and fifth radials fused distally; terminal axis with a broad, moderate-sized, cylindrical proximal cartilage element and an elongate triangular, flattened distal element. Pelvic radials thin and long, cylindrical, and segmented into a long proximal element and much shorter distal element; 22 total pelvic radials. Guallart (1998) recorded pelvic-fin radial counts of 18–20 in males (n = 9) and 22–24 in females (n = 7).

Claspers (Fig. 19; based on right clasper of CSIRO H 6309-02). Axial cartilage slender, long, curved along its length; dorsal marginal cartilage slim, located dorsolaterally to axial cartilage; dorsal terminal cartilage elongate, reaching almost to distal end of clasper, connected proximally to dorsal marginal cartilage and axial cartilage; dorsal terminal 2 cartilage wider, flattened, also elongate, with concave lateral margin, attached medially to dorsal terminal cartilage, and proximally to dorsal marginal cartilage; ventral marginal cartilage flat and quadrangular, emerging as a folded plate at insertion of accessory terminal cartilage; ventral terminal cartilage large, elongate, slender, curved distally with a bluntly rounded distal tip; accessory terminal 3 cartilage (or spur) slim and elongate with an evident dorsal groove, distally pointed, partially attached to ventral margin and ventral terminal cartilages. Additional information on clasper morphology is available in Guallart (1998).

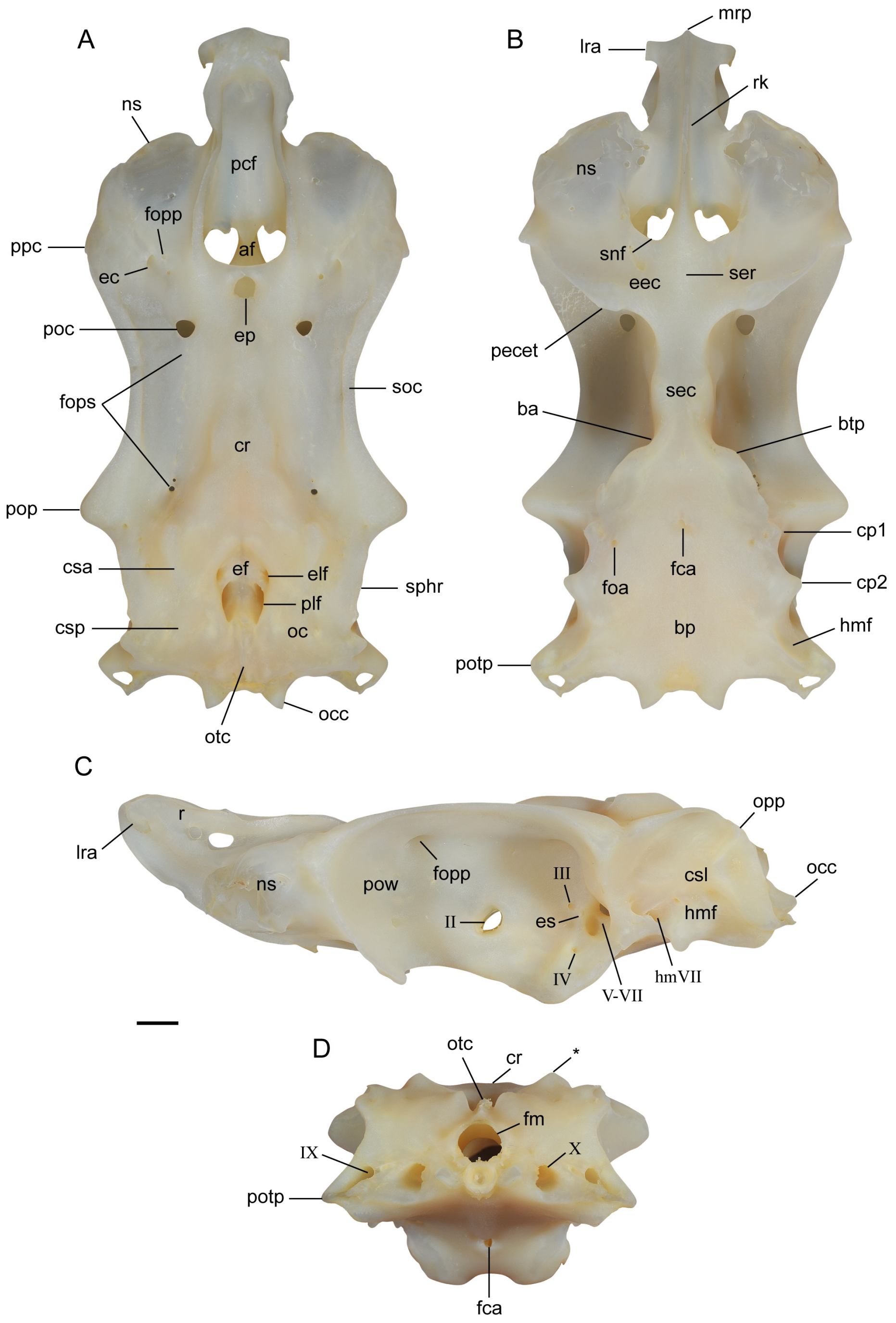

FIGURE 15. Neurocranium of *Centrophorus uyato* (CSIRO H 6310-04, female). (A) dorsal view; (B) ventral view; (C) lateral view; (D) posterior view. Abbreviations: af, anterior fontanelle; ba, basal angle; bp, basal plate; btp, basitrabecular process; cp1, first cartilaginous process; cp2, second cartilaginous process; cr, cranial roof; csa, anterior semicircular canal; csl, lateral semicircular canal; csp, posterior semicircular canal; ec, ethmoidal canal; eec, ectethmoid chamber; ef, endolymphatic fossa; elf, endolymphatic foramen; ep, epiphysial pit; es, eye-stalk (base only); fca, foramen for carotid artery; fm, foramen magnum; foa, foramen for orbital artery; fopp, profundus canal; fops, series of foramina for superficial ophthalmic branch of trigeminal and facial nerves; hmf, hyomandibular facet; hmVII, foramen for hyomandibularis facialis; lra, lateral rostral appendage; mrp, median rostral prominence; ns, nasal capsule; oc, otic capsule; occ, occipital condyle; opp, opisthotic process; otc, otic crest; pcf, precerebral fossa; pecet, ectethmoid process; plf, perilymphatic foramen; poc, preorbital canal; pop, postorbital process; potp, prootic process; pow, preorbital wall; ppc, preorbital process; r, rostrum; rk, rostral keel; sec, subethmoid chamber; ser, subethmoidean ridge; snf, subnasal fenestra; soc, supraorbital crest; sphr, sphenopterotic ridge; II, optic foramen ; III, oculomotor foramen; IV, trochlear foramen; V, VII, foramen prooticum; VI, abducens foramen; IX, foramen for glossopharyngeal nerve; X, vagus foramen; *, ridge at anterior of csa. Scale bar: 10 mm.

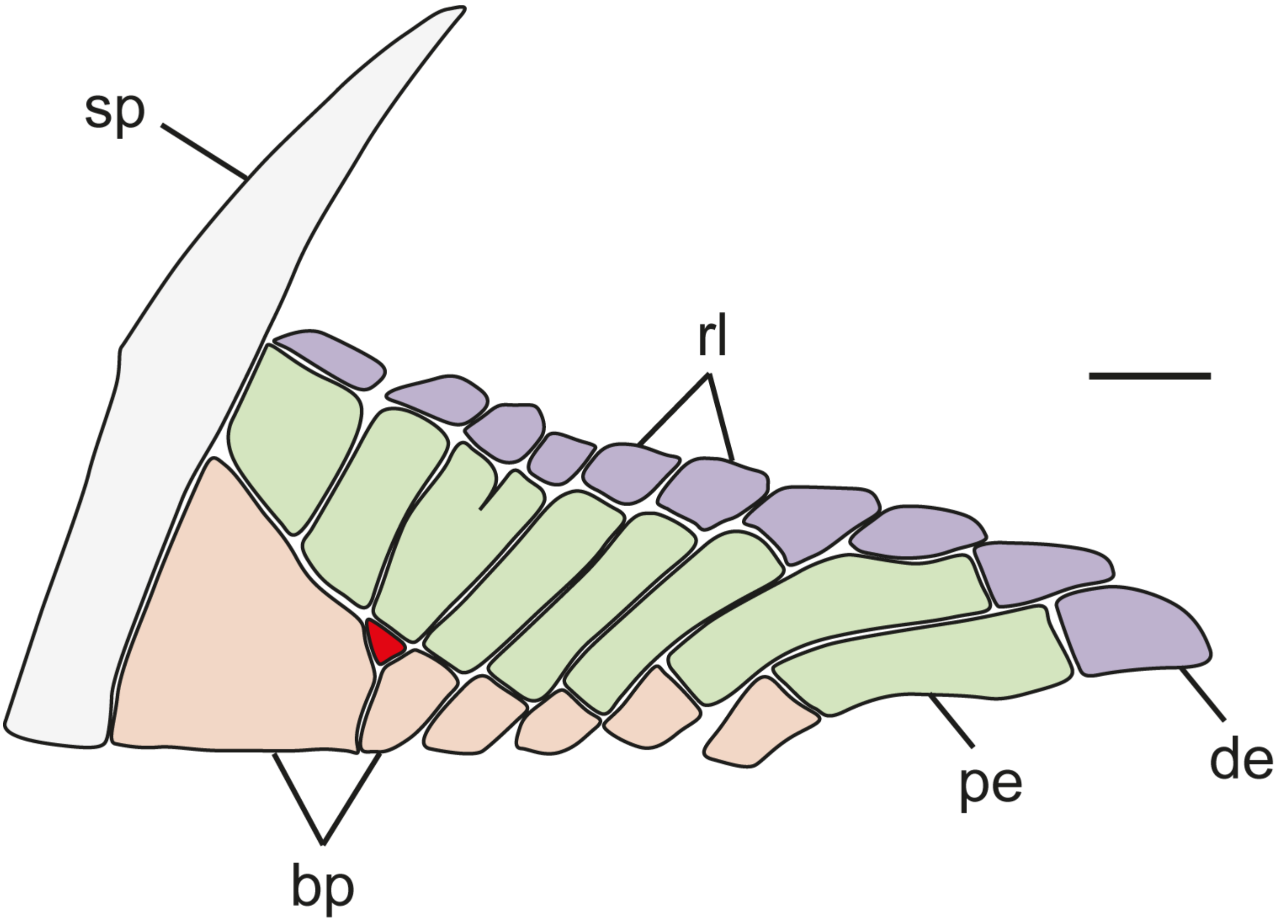

FIGURE 16. First dorsal-fin skeleton of *Centrophorus uyato* (CSIRO H 6503-04). Abbreviations: bp, basal plates (pale orange; small inter-basal plate in red); rl, segmented radials consisting of proximal elements (pe, pale green) and distal elements (de, pale purple); sp, spine. Scale bar: 10 mm.

Size. The largest specimen examined in this study was a 1059 mm TL individual from the Canary Islands. In the Mediterranean, this species has been recorded to 1125 mm TL by Guallart (1998) and in Australia it has been reported to 1110 mm TL by Graham & Daley (2001). Although Capapé (1985) recorded a maximum size of 1280 mm TL for this species in the Mediterranean Sea, it did not appear in any of the graphs provided in that publication and we consider is a doubtful maximum size for this species. Minimum size at maturity recorded for *C. uyato* appears to be relatively consistent across its range: Capapé (1985) and Megalofonou & Chatzispyrou (2006) reported a size at maturity of 745–800 mm TL for males and 850–940 mm TL for females in the Mediterranean; likewise, Guallart (1998) reported size range of maturation of 790–850 mm TL for males (L_{50} = 799 mm TL) and 893–994 mm TL for females (L_{50} = 935 mm TL) in the Mediterranean; size at maturity off southern Australia is 790 mm TL for males and 960 mm TL for females. Size at birth 330–461 mm TL in the Mediterranean (Capapé, 1985; Guallart & Vicent, 2001) and 380–450 mm TL in southern Australia.

Distribution. Known from scattered localities around the world (Fig. 20): Indo-Pacific: southern Australia (Forster in New South Wales to Freycinet Estuary in Western Australia, including Tasmania) (White *et al.*, 2008); Taiwan (Compagno, 1984a; Serena, 2005); East China Sea, Japan (Bessho, 2006); Okinawa, Japan (G. Naylor, unpubl. data - GN10528); Andaman Sea, Myanmar (GenBank accession ON167722); Sri Lanka (Morón *et al.*, 1998; Fernando *et al.*, 2019); Kochi, India (GenBank accession ON167719 and ON167720); Kollam, India (Bineesh *et al.*, 2016); Comoro Islands (Compagno, 1988a); Mozambique Channel, Madagascar (G. Naylor, unpubl. data - GN5684); southern Mozambique (Bass *et al.*, 1976); and Natal, South Africa (Springer, 1990). Eastern Atlantic: Hondeklip Bay, South Africa (Compagno *et al.*, 1991); Namibia (Compagno, 1984a; Bessho, 2006); Angola (Poll, 1951; GenBank accession ON167704); Cape Verde (Reiner, 1996; GenBank accession ON167721); Angola to Ivory Coast, Senegal to Gibraltar (Compagno, 1984a); Senegal and Gambia (Rochebrune, 1883); Western Sahara (Belloc, 1934); Madeira, Portugal (Maul, 1955; Biscoito *et al.*, 2018); Canary Islands (Maurin & Bonnet, 1970; Pajuelo *et al.*, 2010); Atlantic slope off Morocco (Belloc, 1934); continental coast of Portugal (Costa *et al.*, 2012); Rockall Trough, NW of Ireland (Clarke, 2000); west of Britain (Bridger, 1978); northern Norway (Wienerroither *et al.*, 2015). Mediterranean Sea (where it is the only species of *Centrophorus* present): Spain (Guallart, 1998; Guijarro *et al.*, 2012; Barría *et al.*, 2015a, b); France (Rancurel, 1983; Capapé *et al.*, 2000; Barría *et al.*, 2015a, b); Italy (Tortonese, 1956; Parenti, 2019); Croatia (Gajić, 2019); Montenegro (Gajić, 2019); Albania (Ungaro *et al.*, 1999; Gajić, 2019); Malta (Lanfranco, 1996; Schembri *et al.*, 2003); Greece (Megalofonou & Chatzispyrou, 2006); Turkey (Bilecenoglu *et al.*, 2002; Meriç *et al.*, 2007); Syria (Gruvel, 1931; Ali & Saad, 2003); Lebanon (Colloca & Lelli, 2012; Lteif, 2015; Bariche & Fricke, 2020); Israel (Golani & Pisanty, 2000; Goren & Galil, 2015); Cyprus (Hadjichristophorou, 2006; Kousteni *et al.*, 2021); Eypgt (Farrag *et al.*, 2016); Libya (Zupanovic & El-Buni, 1982; Serét, 2005); Tunisia (Farrugio & Soldo, 2014); Algeria (Duméril, 1865; Boutan, 1926; Maurin, 1962); Morocco (Maurin, 1962; 1968). Western Atlantic: Suriname and French Guiana (Uyeno *et al.*, 1983); Venezuela (Cervigón & Alcalá, 1999; Ehemann *et al.*, 2019); Caribbean Colombia (Hernández-Hamón & Núñez, 1998); Mexico (Applegate *et al.*, 1993; Bonfil, 1997); Cuba (Guitart, 1979); Louisiana to Florida, Gulf of Mexico, USA (Perry *et al.*, 1995; Veríssimo *et al.*, 2014; Hipes, 2015; Driggers *et al.*, 2017); Florida Straits to Dry Tortugas and South Carolina, USA (Davenport *et al.*, 2011); North Carolina and Virginia, USA (Kiraly *et al.*, 2003); and US Virgin Islands (Kiraly *et al.*, 2003).

Recorded from depths of 208–701 m, usually greater than 400 m, off Australia (White *et al.*, 2008). In the Mediterranean Sea, abundant commercial fishing catches have been reported by Boutan (1926) at 150–500 m in Algeria; Rancurel (1983) at 150–600 m in Corsica; Guallart (1998) at 150–650 m depth in the Balearic Sea. Guallart (1998) reported that catches of up to 900 subadult and adult specimens could be landed in a single day (Fig. 21). Muñoz-Chapuli (1984) reported the uncommon catch of a juvenile in the continental shelf at "<100 m depth" in NE Atlantic. Compagno *et al.* (1989) reported a depth range of 274–480 m off southern Africa. Maximum depths reported for this species is 1490 m (Gilat & Gelman, 1984) and in some other cases about 1400 m (e.g. FAO, 2018; Psomadakis *et al.*, 2019), but rarely deeper than 600 m (Baino *et al.*, 2001).

Intraspecific variation. The MDS plot for *C. uyato* coded by size classes shows a trend from smaller size classes to the left of plot to larger size classes to the right of the plot (Fig. 22). The samples for the larger size classes show considerable overlap, but those for size class 1 (<500 mm TL) and 2 (500–699 mm TL) are grouped away from the larger size class samples. ANOSIM showed size classes were significantly different overall (P<0.01), albeit with relatively low support (R^2 = 0.466). Pairwise comparisons were only significantly different (P<0.01) between size class 1 (<500 mm TL) and all other size classes, and between size class 2 (500–699 mm TL) and size classes 4 (800–899 mm TL) and 5 (>900 mm TL). The measurements shown by SIMPER to be the most responsible for differences between size class 1 and the other size classes are (in order of importance): pectoral–pelvic space (e.g. 24.4–29.3 vs. 28.8–33.1% TL in size class 4), dorsal caudal margin (e.g. 20.3–22.8 vs. 17.2–21.1% TL in size class 5), pectoral-fin inner margin length (10.6–12.9 vs. 11.5–15.7% TL in size class 4), and head width (e.g. 10.4–12.9 vs. 12.5–14.2% TL in size class 3). The measurements shown by SIMPER to be most responsible for differences between size class 2 and the size classes 4 and 5 are (in order of importance): pectoral–pelvic space (27.4–30.6 vs. 27.6–36.1% TL), pelvic-fin height (4.5–5.5 vs. 5.3–7.4% TL) and dorsal caudal margin (19.8–22.5 vs. 17.2–21.1% TL). It is important to note that the characters found by SIMPER to distinguish between the size classes mostly overlap considerably.

The most notable differences between juveniles and larger specimens of *C. uyato* are coloration and dermal denticle morphology. Juveniles have very distinct markings on the dorsal and caudal fins, which adults lack, and body coloration changes from medium grey in juveniles to brown in adults (Fig. 23). The lateral trunk denticles of juveniles have far more pointed cusps than larger specimens, which have more pavement-like, flat denticles (Fig. 4).

The ontogenetic differences in morphology within members of this genus are well illustrated in Fig. 24A, which incorporates the four species so far investigated in this revision series (i.e. *C. granulosus*, *C. lesliei*, *C. longipinnis* and now *C. uyato*). Small individuals of *C. granulosus* (<700 mm TL) were found to differ significantly from individuals >820 mm TL in having a longer head, larger eyes, paired fins closer together, a taller second dorsal-fin spine and different denticles morphology (White *et al.*, 2013). Small individuals of *C. uyato* also differ in denticle morphology and in having the paired fins closer together and a slightly taller second dorsal-fin spine compared to larger individuals. However, there were no difference in measurements associated with a longer head (i.e. preoral length, preorbital length, prespiracular and prenarial length) or eye size. Similarly, small individuals of *C. lesliei* and *C. longipinnis* (<524 mm TL) differed from the larger individuals in having a longer head, shorter pectoral-pelvic space and eye length (White *et al.*, 2017). The smaller size classes of these two species also differed from larger individuals in having a longer caudal fin and pectoral-fin inner margin, which was also the case for *C. uyato.* Thus, ontogenetic shift in morphology in this genus appears to be driven by a relatively small number of features. Examination of this ontogenetic variation should be included in future studies of not only this genus, but all groups where possible. In general, variation within species of sharks is poorly understood despite adequate specimens often available for investigation.

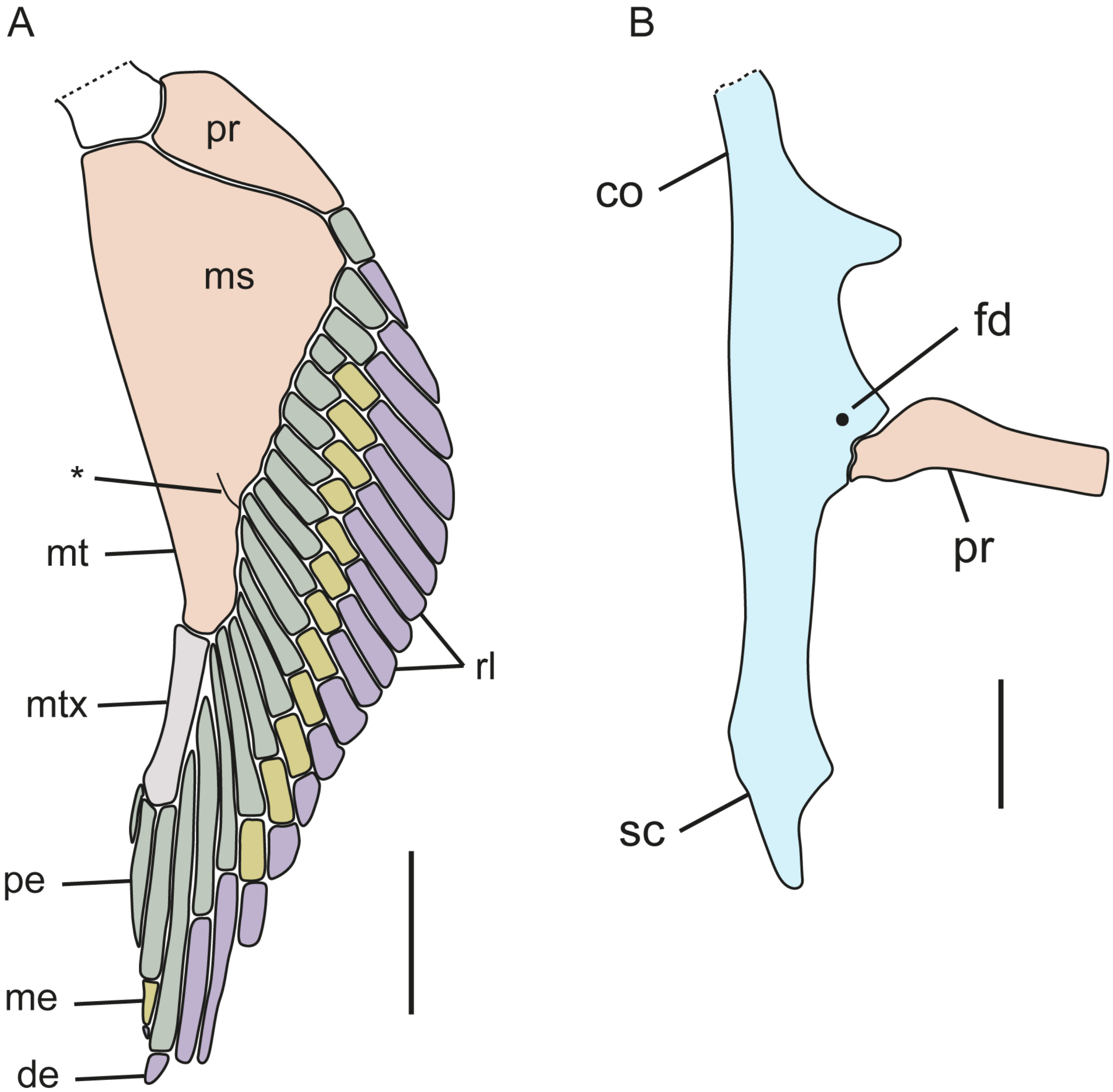

FIGURE 17. Left pectoral fin skeleton in ventral view (A) and pectoral girdle in lateral view (B) of *Centrophorus uyato* (CSIRO H 6310-04). Abbreviations: co, coracoid bar; fd, diazonal foramen; ms, mesopterygium; mt, metapterygium; mtx, metapterygial axis; pr, propterygium; rl, segmented radials consisting of proximal elements (pe, pale green), medial elements (pale yellow) and distal elements (de, pale purple); sc, scapula; *, distal separation between mesopterygium and metapterygium. Scale bar: 10 mm.

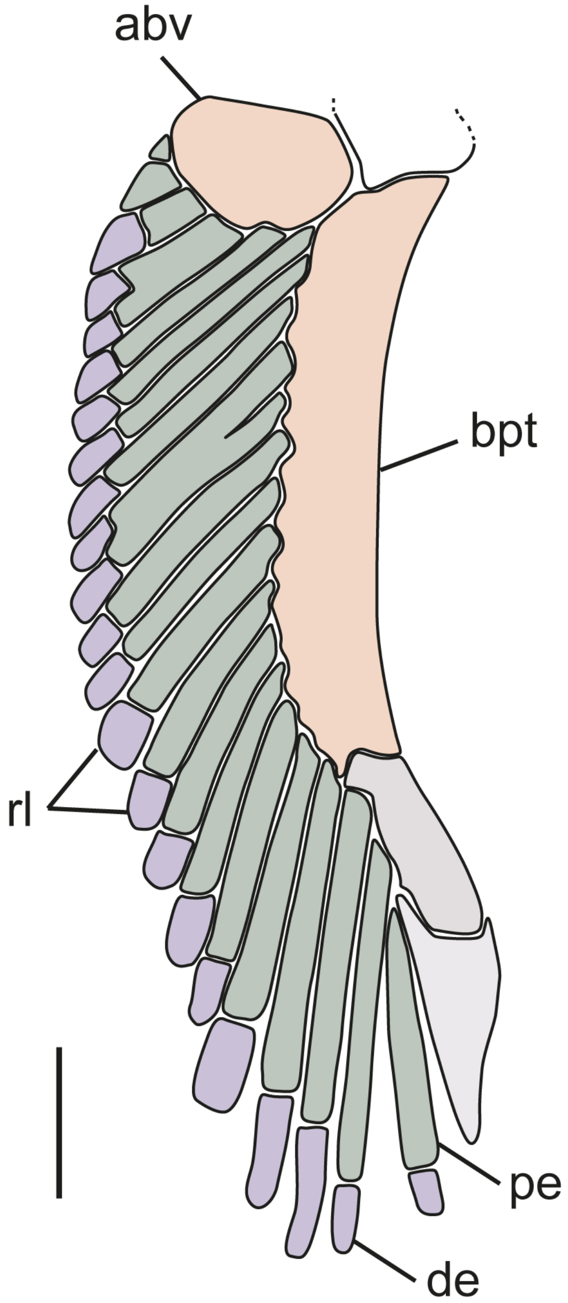

FIGURE 18. Left pelvic fin skeleton of *Centrophorus uyato* (CSIRO H 6503-04) in dorsal view. Abbreviations: abv, anterior pelvic basal; bpt, basipterygium; rl, segmented radials consisting of proximal elements (pe, pale green) and distal elements (de, pale purple); basipterygium elements (grey). Scale bar: 10 mm.

Comparison between species. *Centrophorus uyato* differs from the two large species of *Centrophorus*, i.e. *C. granulosus* and *C. squamosus* in the following key characters: denticles of adults flat, pavement-like (vs. raised on pedicels or tear-drop shaped) in subadults and adults; pectoral-fin free rear tip in subadults and adults elongate (vs. not or only slightly produced); body medium brown to greyish above, paler below (vs. mostly uniform dark brown, except in juvenile *C. granulosus*). It differs from *C. moluccensis* in having a taller second dorsal fin (its height 4.0–6.1 vs. 2.9–3.9% TL, 1.1–1.6 vs. 1.6–2.2 times, respectively, in first dorsal-fin height). *Centrophorus uyato* can be readily distinguished from *C. lesliei* and *C. longipinnis* in having a much shorter first dorsal fin (first dorsal soft fin length 9.8–13.9 vs. 16.0–20.2% TL, 1.2–1.6 vs. 1.7–2.3 times in second dorsal soft fin length).

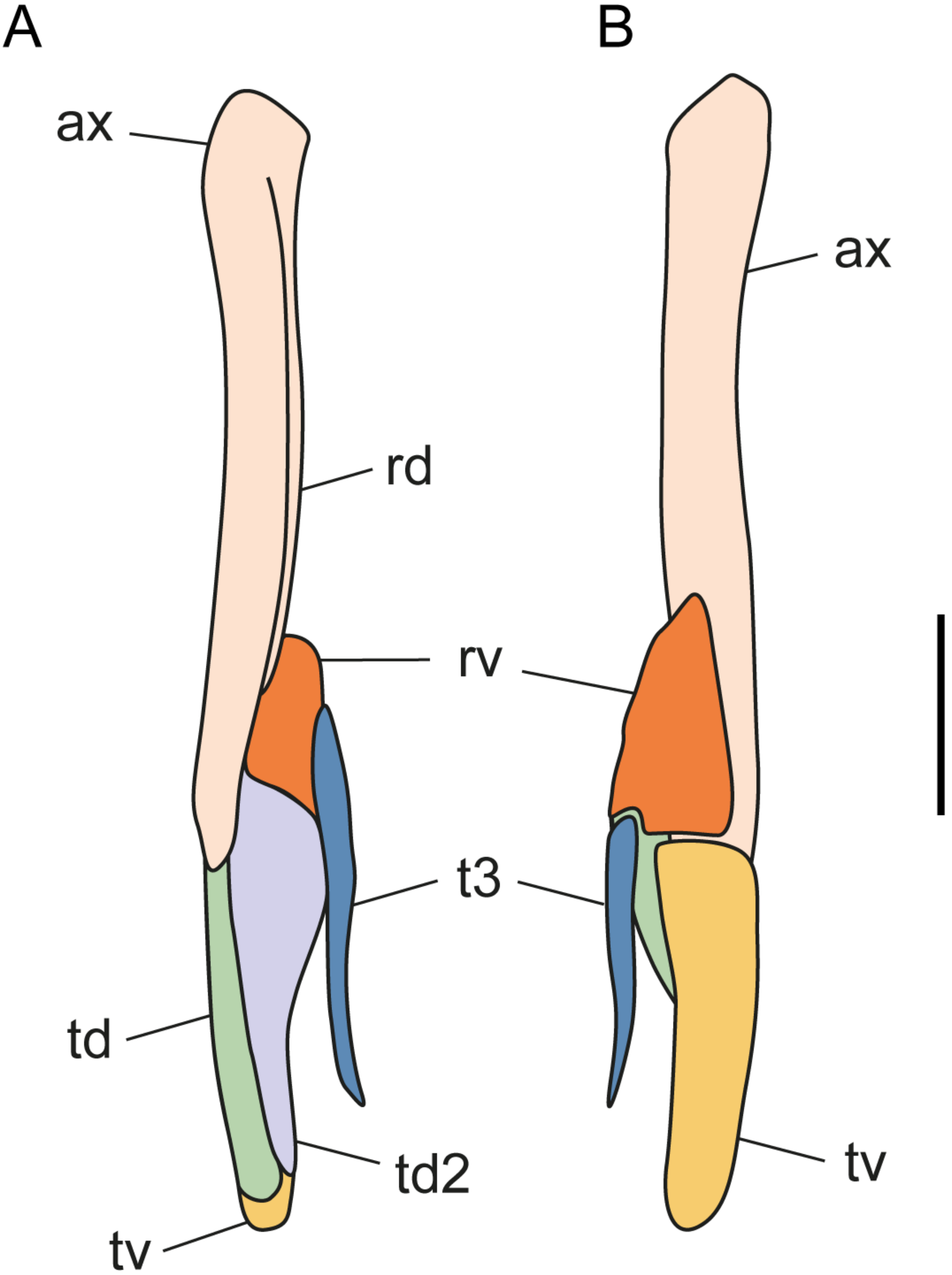

FIGURE 19. Clasper cartilages, right side, of *Centrophorus uyato* (CSIRO H 6309-02, adult male). Detail of terminal cartilages in (A) dorsal view; (B) ventral view. Abbreviations: ax, axial cartilage; rd, dorsal marginal cartilage; rv, ventral marginal cartilage; td, dorsal terminal cartilage; td2, dorsal terminal 2 cartilage; tv, ventral terminal cartilage; t3, accessory terminal cartilage (spur). Scale bars: 10 mm.

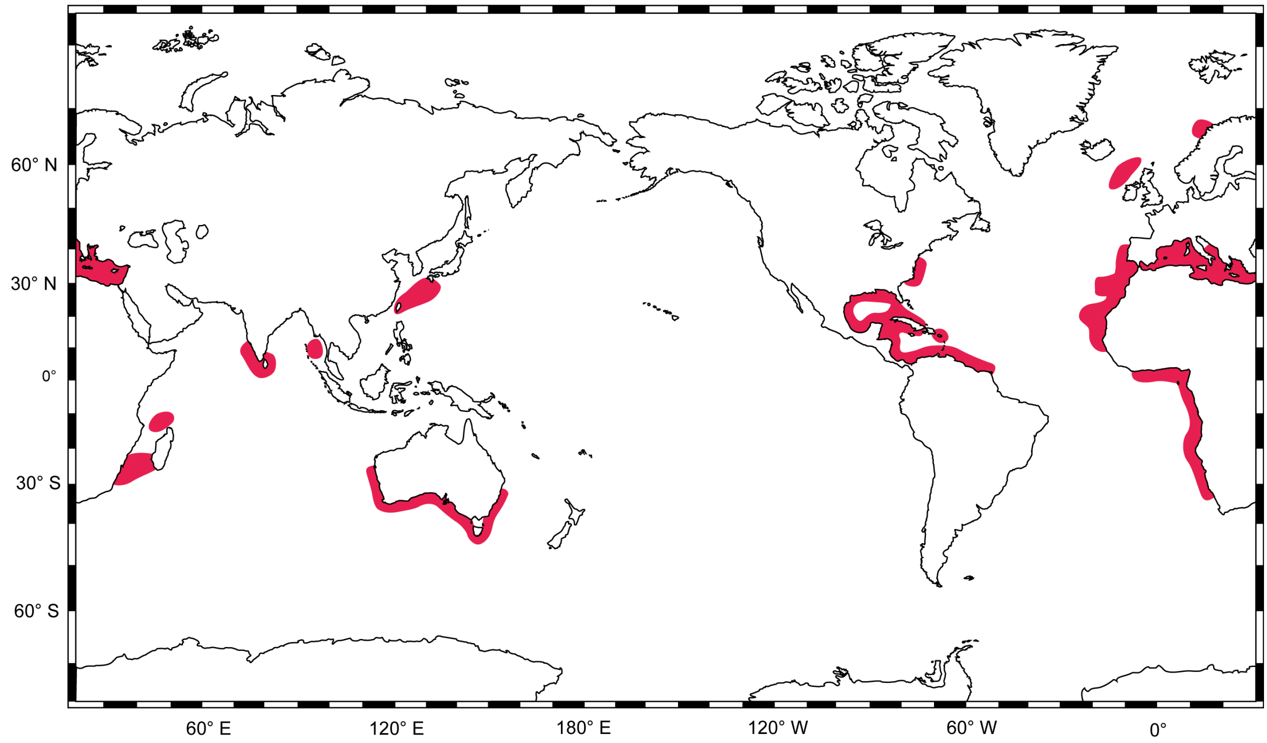

FIGURE 20. Distribution of *Centrophorus uyato* based on specimens examined, genetic tissue samples or validated literature records.

FIGURE 21. Large catches of *Centrophorus uyato* off Mallorca, Spain, in 1995.

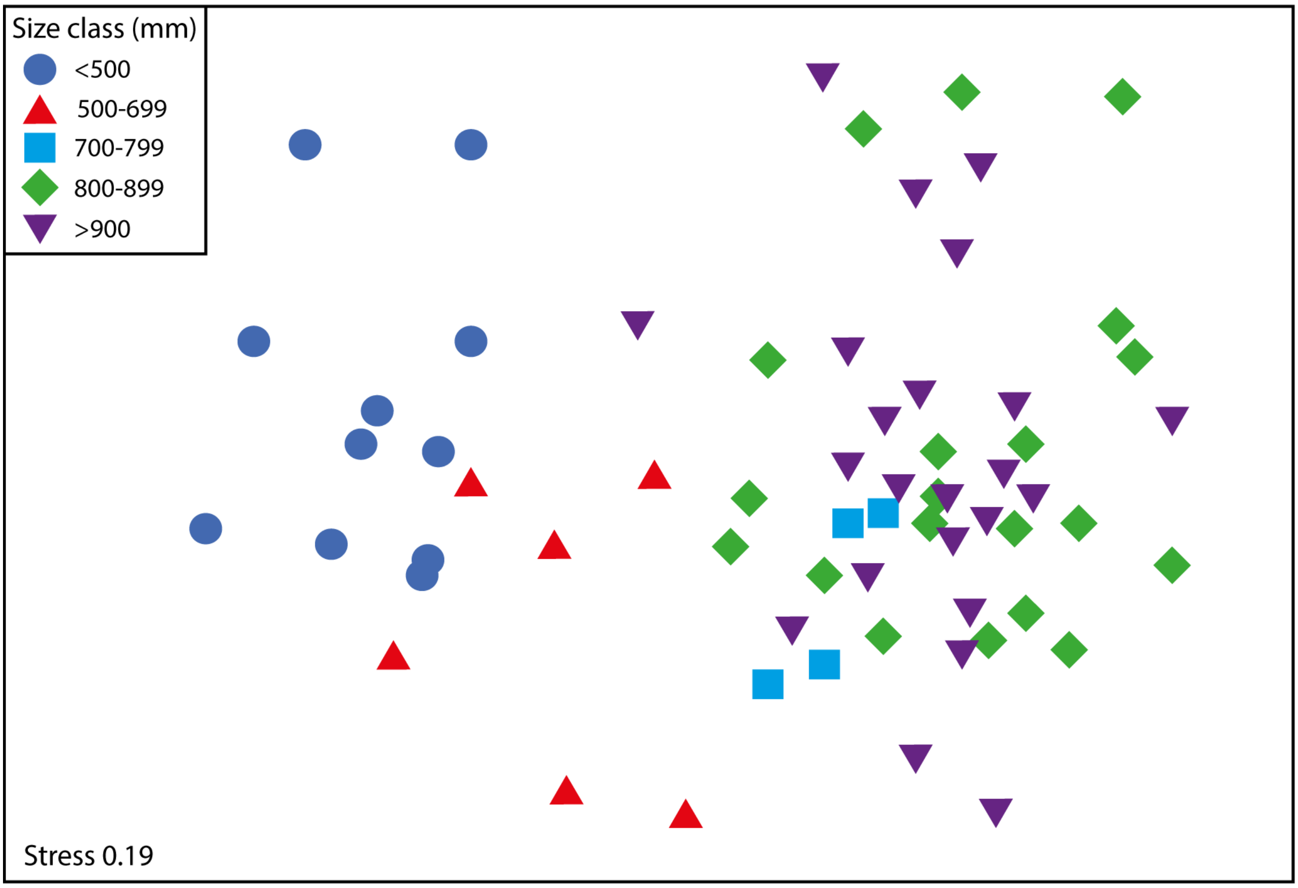

FIGURE 22. Non-metric multidimensional (MDS) ordination of morphometric percentages (%TL) of *Centrophorus uyato* in each of the five size classes used: 1 (<500 mm TL), 2 (500–699 mm TL), 3 (700–799 mm TL), 4 (800–899 mm TL) and 5 (>900 mm TL).

Centrophorus uyato is superficially similar to members of the long-snouted species complex that consists of *C. harrissoni*, *C. isodon*, *C. seychellorum*, *C. westraliensis* and possibly *C. tesselatus*. A revision of the long-snouted complex is currently in progress and will be presented as another part of this series of revision papers for the genus *Centrophorus*. *Centrophorus uyato* is sympatric with *C. harrissoni* and *C. westraliensis* in Australian waters and their similarity has led to these species being commonly mis-identified. It differs from these two species in having a shorter snout (preorbital length 4.8–7.2 vs. 7.5–8.6% TL, prenarial length 3.3–4.7 vs. 5.9–5.8% TL); shorter preoral length (in adults, 8.2–11.2 vs. 10.9–12.4% TL); dorsal fins of subadults and adults with a blackish apical marking (usually obvious when fresh) vs. without a dark apical marking but with narrow white posterior margin (sometimes indistinct in large adults); dorsal fins of juveniles with distinct, broad blackish apical markings and pale free rear tips vs. a black anterior blotch and white posterior blotch.

It is difficult to provide accurate data to compare *Centrophorus uyato* with *C. isodon*, *C. seychellorum* and *C. tesselatus* as they are, at present, poorly defined. The molecular data presented in White *et al.* (2017) shows *C. harrissoni* forming a group sister to samples consisting of specimens identified as *C. isodon* (Indonesia), *C. westraliensis* (Western Australia) and *C. tesselatus* (Gulf of Mexico). However, another group of samples containing *C. isodon* (Philippines) and *C. tesselatus* (Japan) is also present.

The dental morphology of *Centrophorus* species often passes through various stages of ontogenetic development, but this can be inconsistent at times often rendering dentition a difficult diagnostic tool for some species. In addition, sexual dimorphism in *Centrophorus uyato* is not always consistent, particularly in males. Immature males often have oblique, weakly developed cusps which may become very erect and conical in shape with maturity. However, this is sometimes only weakly developed and immature males quite often will have predeveloped teeth with small, very erect cusps. Adding to the confusion, juvenile males at times may have very small, erect lower tooth crowns with somewhat concave mesial margins, mesially reflexed cusp tips and heavy serrations. In some instances, this has led to the misidentification of immature specimens of larger species of *Centrophorus*.

Regarding the comparison of the dental morphology of *Centrophorus uyato* with other small species of *Centrophorus*, for the most part, female *Centrophorus uyato* will tend to have much longer, erect and better developed upper anterolateral tooth crowns than other species. For example, female *C. moluccensis*, *C. isodon* and *C. harrissoni* tend to have very oblique crowns, more reminiscent of *Squalus*. Additionally, the 3–6 straight and symmetrical upper medial teeth, as noted in the description, are seldom seen in other species of *Centrophorus* aside for *C. granulosus* and sometimes *C. squamosus*. A detailed comparison of dentition for species of *Centrophorus* is currently in preparation and is beyond the scope if this publication.

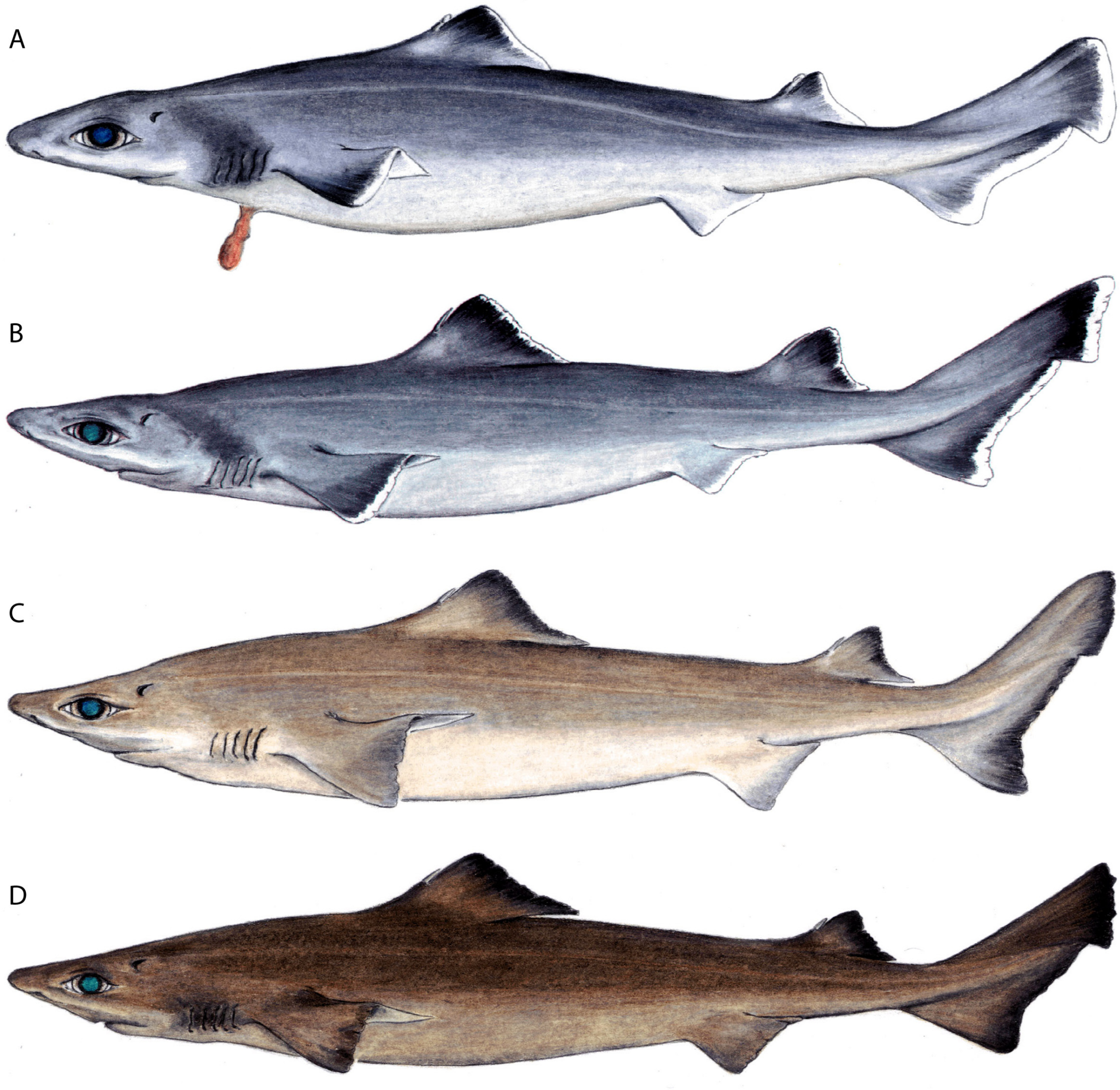

FIGURE 23. Colour variation in *Centrophorus uyato* (from Guallart, 1998): (A) female late-term embryo, 420 mm TL, found in the right uterus of (C) below; (B) juvenile female, 598 mm TL; (C) pregnant female, 978 mm TL; (D) adult male (var dark brown), 875 mm TL. Illustrations by Susana Rodríguez.

The MDS plot based on morphometric measurements of the four species of *Centrophorus* for which this series of revisions has included to date (i.e. *C. granulosus*, *C. lesliei*, *C. longipinnis* and now *C. uyato*) separated the species well (Fig. 24). Although the two-dimensional plot (Fig. 24A) shows two *C. granulosus* samples overlapping with *C. lesliei* samples, this is an artifact of the two-dimensional plot and the three-dimensional plot (Fig. 24B) shows clearer separation. ANOSIM showed morphological measurements were significantly different between species ($P<0.01$; $R^2 = 0.690$), and in all pairwise comparisons ($P<0.01$; $R^2 = 0.547$–0.994), except for *C. lesliei* vs. *C. longipinnis* which had only a weak significant difference ($P<0.5$; 0.254). The measurements shown by SIMPER to be most responsible for differences between *C. uyato* and both *C. lesliei* and *C. longipinnis* are not surprisingly related to length of the first dorsal fin: first dorsal-fin base (10.9–16.0 vs. 16.8–23.3% TL), first dorsal soft fin length (9.8–13.9 vs. 16.0–20.2% TL) and first dorsal-fin length (16.8–21.9 vs. 23.1–29.4% TL). The measurements shown by SIMPER to be most responsible for differences between *C. uyato* and *C. granulosus* are: second dorsal soft fin length (7.3–9.0 vs. 9.3–11.6% TL); pectoral–pelvic space (24.4–36.1 vs. 27.4–39.2% TL); interdorsal space (18.2–24.3 vs. 14.6–21.1% TL) and first dorsal soft fin length (9.8–13.9 vs. 11.0–16.6% TL). Although the range in measurements for each of these characters overlap in most cases, the high level of intraspecific variation in both species, particularly in relation to ontogenetic changes in morphology, is the likely the main cause.

TABLE 3. Morphological measurements shown by SIMPER that contribute the most to differences between *Centrophorus* species. Pale orange cells are based on only size class 1 for each species; pale blue is based on the remaining larger size classes. * denotes those characters which differ from the corresponding size class for a particular species pair.

	C. granulosus	***C. lesliei***	***C. longipinnis***	***C. uyato***
C. granulosus		Head width at ant. mouth First dorsal base	First dorsal base Head width at ant. mouth First dorsal length	Second dorsal soft length* Pectoral-pelvic space* First dorsal soft length*
C. lesliei	Head width at ant. mouth First dorsal base First dorsal soft length*		First dorsal base First dorsal length First dorsal soft length	First dorsal base First dorsal soft length First dorsal length
C. longipinnis	First dorsal base First dorsal length Head width at ant. mouth	First dorsal base Pectoral-pelvic space* First dorsal soft length		First dorsal base First dorsal soft length First dorsal length
C. uyato	Pectoral inner margin* Interdorsal space* First dorsal base*	First dorsal base First dorsal length First dorsal length	First dorsal base First dorsal length First dorsal soft length	

For each species, the smallest size class is located to the upper left of the remaining size classes. When only size class 1 is compared between the four species, ANOSIM showed a more significant difference between species ($P<0.01$; $R^2 = 0.962$) that when all size classes were included. Likewise, when all other size classes (i.e. excluding size class 1) where compared between species, ANOSIM also showed a more significant difference ($P<0.01$; $R^2 = 0.881$) than when all size classes included. Thus, ontogenetic differences in morphology are an important consideration when comparing species of *Centrophorus* (see previous section). The characters shown by SIMPER to contribute the most to the differences between species for both of the above analyses separated by size class are displayed in Table 3. There is little variation in the characters SIMPER found that best differentiated between species with the exception between *C. uyato* and *C. granulosus* where different characters best distinguished between size class 1 individuals and between large individuals (excluding size class 1).

The morphology of the neurocranium is also a useful character for separating *Centrophorus* species. While not a useful field character, neurocranium morphology in *Centrophorus* should be investigated further. For the four species examined, the MDS plot based on proportional neurocranium measurements separated the species well (Fig. 25). The samples for *C. harrissoni* grouped together on the right side of the plot, well away from the other three species. *Centrophorus uyato* samples grouped tightly together in the centre of the left side of the plot, with the single samples of *C. moluccensis* and *C. squamosus* located above and below the *C. uyato* samples, respectively. ANOSIM showed neurocranial measurements were significantly different between species ($P<0.01$; $R^2 = 0.994$), and in all pairwise comparisons. The measurements shown by SIMPER to be most responsible for differences between *C. uyato* and *C. harrissoni* are (in order of importance): nasobasal length (61.6–65.2 vs. 48.0–58.2% CL), rostral keel length (38.2–42.5 vs. 46.7–54.9% CL), width across postorbital processes (44.4–49.8 vs. 36.1–44.0% CL), and precerebral fossa length (27.8–32.3 vs. 33.6–39.7% CL). In addition, they also differ in interorbital width

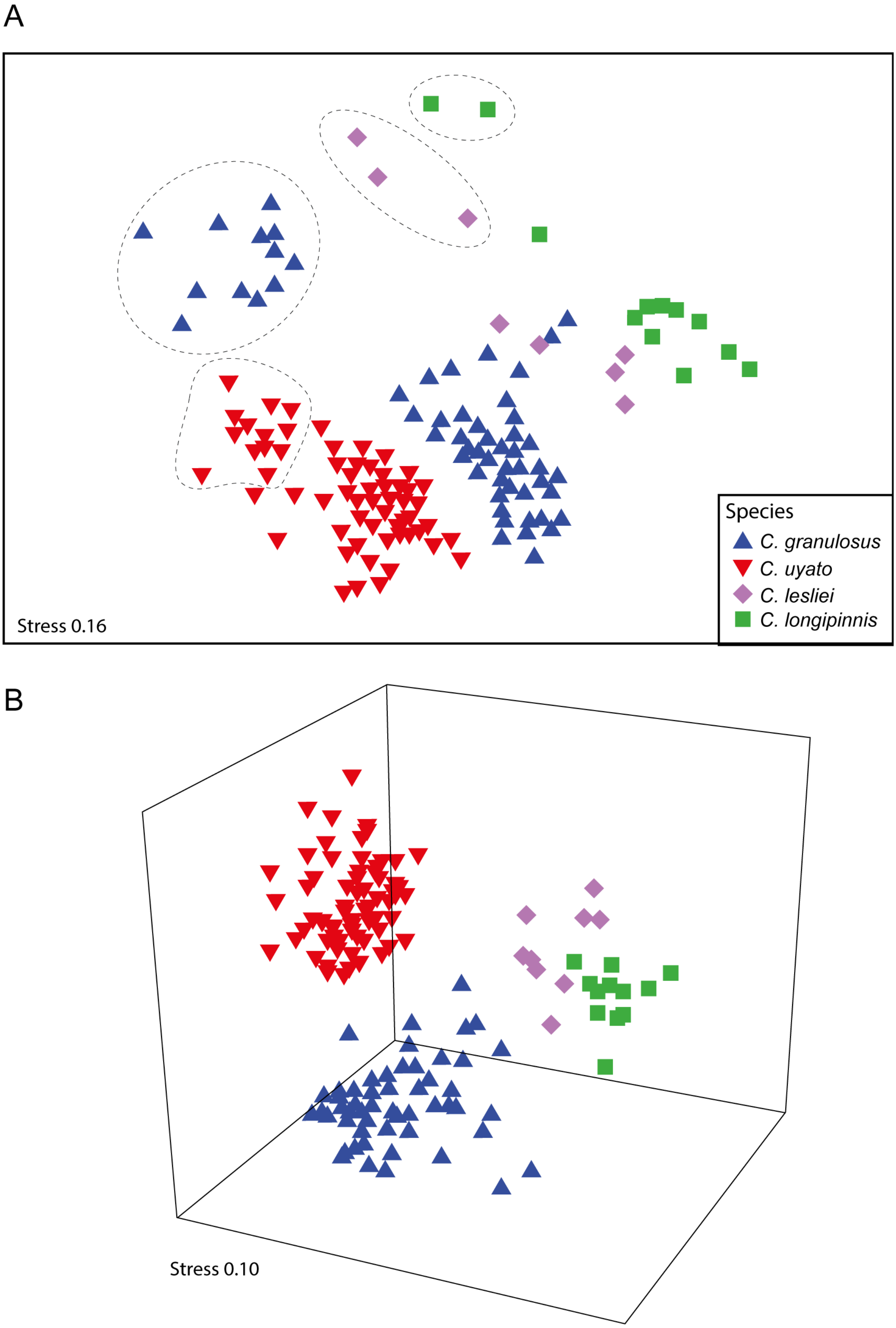

FIGURE 24. Non-metric multidimensional (MDS) ordination of morphometric percentages (%TL) of recently revised *Centrophorus* species: *C. granulosus* (blue triangles), *C. lesliei* (purple diamonds), *C. longipinnis* (green squares) and *C. uyato* (red triangles). The samples in size class 1 for each species is distinguished by a dashed line. (A) two-dimensional plot; (B) three-dimensional plot.

(29.0–33.4 vs. 25.3–28.0% CL). Muñoz-Chapuli & Ramos (1989) compared the neurocranium of *C. granulosus* (as *C. niaukang*), *C. uyato* (as *C. granulosus*) and *C. lesliei* (as *C. lusitanicus*). The main characters used to separate *C. uyato* from the other two species was width of the precerebral fossa and height of neurocranium. Based on seven specimens, Muñoz-Chapuli & Ramos (1989) recorded a mean precerebral fossa width for *C. granulosus* of 7.70% CL and a maximum sagittal height of 24.96% CL, vs. a mean of 12.19% CL and 28.97% CL in 18 specimens of *C. uyato*, respectively.

The measurements shown by SIMPER to be most responsible for differences between *C. uyato* and *C. moluccensis* are: postorbital width (44.4–49.8 vs. 38.2% CL), interorbital width (29.0–33.4 vs. 25.3% CL), and width across nasal capsule (40.8–47.0 vs. 38.9% CL). SIMPER found the main differences between *C. uyato* and *C. squamosus* are: width of basal angle (15.3–17.4 vs. 22.6% CL), postorbital to prootic processes (19.9–23.1 vs. 26.4% CL), and interorbital width (29.0–33.4 vs. 27.0% CL). Note for both *C. moluccensis* and *C. squamosus*, only a single neurocranium was measured. Thus, the differences noted above need to be investigated further when additional crania become available for these species.

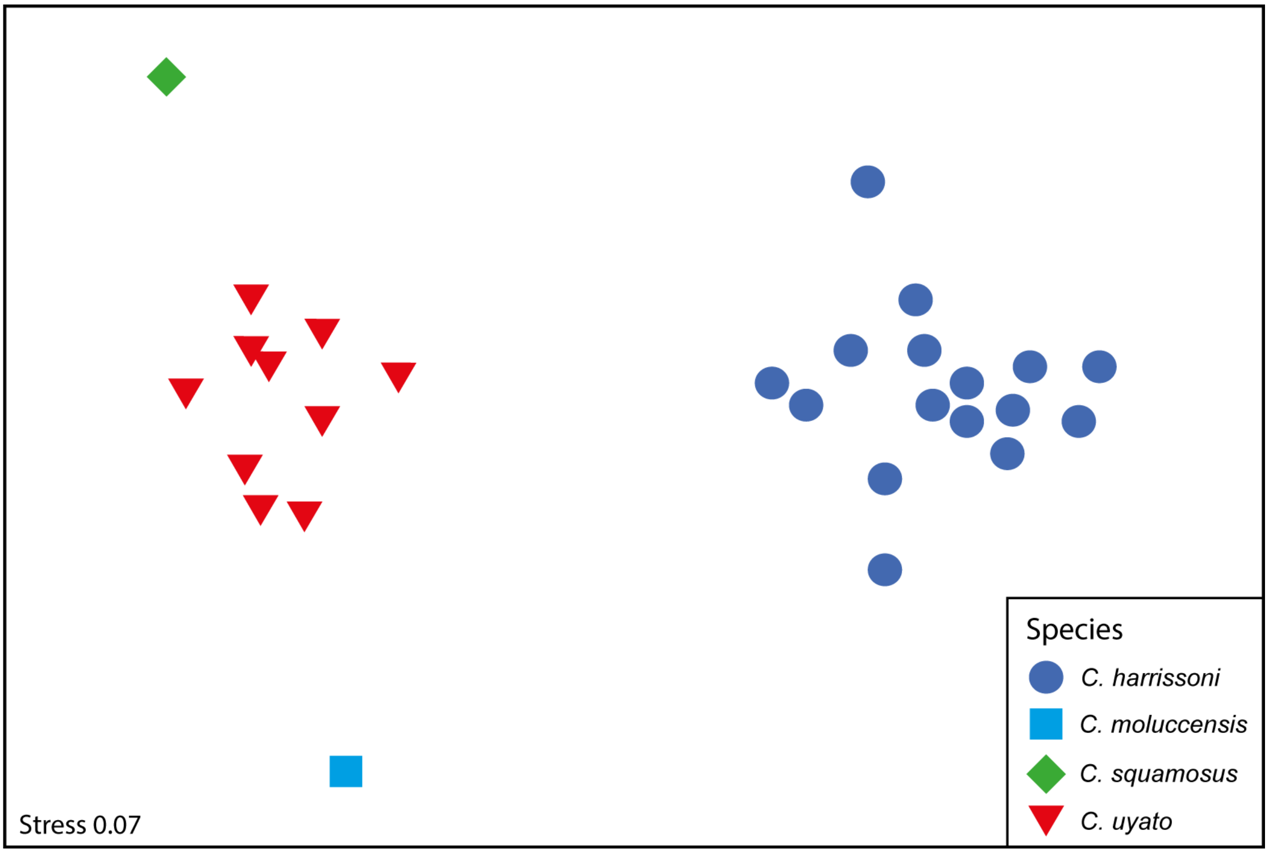

FIGURE 25. Non-metric multidimensional scaling (MDS) ordination of neurocranium morphometric percentages (% CL) of four *Centrophorus* species: *C. harrissoni* (dark blue circles), *C. moluccensis* (blue squares), *C. squamosus* (green diamonds) and *C. uyato* (red triangles).

Comparative material

Comparative material examined in this study is listed in White *et al.* (2013, 2017) in the material examined and comparative material sections. Additional comparative material is listed below:

Centrophorus harrissoni. CSIRO H 6307–02 (skeletal parts), female 1066 mm TL, CSIRO H 6307–03 (skeletal parts), juvenile male 557 mm TL, CSIRO H 6307–04 (skeletal parts), female 1025 mm TL, CSIRO H 6307–05 (skeletal parts), juvenile male 565 mm TL, CSIRO H 6307–06 (skeletal parts), female 933 mm TL, east of Flinders Island, Tasmania, ~40° S, ~149° E, 350–430 m, 12 Jul. 2004; CSIRO H 6308–02 (skeletal parts), female 1039 mm TL, CSIRO H 6308–03 (skeletal parts), female 716 mm TL, Banks Strait, Tasmania, ~40° S, ~148° E, 29 Jul. 2004; CSIRO H 6309–03 (skeletal parts), adult male 902 mm TL, east of Flinders Island, Tasmania, ~40° S, ~149° E, 400–450 m, 1 Aug. 2004; CSIRO H 6310–01 (skeletal parts), adult male 926 mm

TL, CSIRO H 6310–02 (skeletal parts), male 882 mm TL, CSIRO H 6310–03 (skeletal parts), female 870 mm TL, northeast of Flinders Island, Tasmania, 39°04′ S, 148°39′ E, 500–680 m, 24 Jul. 1986; CSIRO H 6498–02 (skeletal parts), adult male 909 mm TL, off southern Flinders Island, Tasmania, ~40° S, ~148° E, 300–500 m, 24 Jun. 2003; CSIRO H 6499–01 (skeletal parts), female 1080 mm TL, CSIRO H 6499–02 (skeletal parts), female 880 mm TL, CSIRO H 6499–03 (skeletal parts), female 1070 mm TL, off northeast Tasmania, ~41° S, ~149° E, 24 Jul. 2003; CSIRO H 6503–01 (skeletal parts), adult male 872 mm TL, CSIRO H 6503–06 (skeletal parts), adult male 867 mm TL, northeast of Flinders Island, Tasmania, 39°20′ S, 148°45′ E, 370–420 m, 7 Apr. 2003.

Centrophorus moluccensis. CSIRO H 3599–04 (skeletal parts), adult male, southwest of Shark Bay, Western Australia, 27°05′ S, 112°45′ E, 303–333 m, 3 Feb. 1991.

Centrophorus squamosus. CSIRO H 1358–01 (skeletal parts), east of Dunk Island, Queensland Trough, Queensland, 18°08′ S, 147°11′ E, 200 m, 9 Dec. 1985.

Acknowledgements

This project was supported by two National Science Foundation (NSF) grants (NSF-DEB-01132229 and NSF-DEB-1932759). WW would like to acknowledge CSIRO's National Research Collections Australia, in particular B. Deagle, L. Joseph and A. Young, for support. DAE would like to acknowledge additional funding support from the South African Shark and Ray Protection Project, implemented by the WILDTRUST, funded by the Shark Conservation Fund, Save Our Seas Foundation, and the South African Institute for Aquatic Biodiversity. AV was funded through national funds from Fundação para a Ciência e Tecnologia (DL57/2016).

We would like to acknowledge the following museum staff for their assistance accessing collection material examined during this study: A. Graham (CSIRO, Hobart); J. Maclaine and O. Crimmen (BMNH, London); F. Mollen (ERB, Belgium); R.D. Grubbs (Florida State University, USA); P. Pruvost and R. Causse (MNHN, Paris); P. Bartsch (ZMB, Berlin); I. Eidus and R. Thiel (ZMH, Hamburg); A. Palandačić and H. Wellendorf (NMW, Vienna); H. Imamura and K. Nakaya (HUMZ, Hokkaido); D. Golani (HUJ, Israel); M. McGrouther and A. Hay (AMS, Sydney); D. Bray and M. Gomon (NMV, Victoria);); D. Catania and J. Fong (CAS, San Francisco); R. Bills, N. Mazungula and M. Dwani (SAIAB, South Africa). We would also like to thank the following people for their important technical contributions to this paper: J. Pogonoski (CSIRO) for the radiographs and technical editing of the manuscript; H. O'Neill (CSIRO) for capturing images and providing detailed editorial comments; S. Corrigan and L. Yang (UF, Florida) for obtaining molecular data. Special thanks also goes to R. Fricke (Stuttgart) for his ever reliable nomenclatural advice, particularly for difficult cases such as this.

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