Zootaxa 3752 (1): 020–034
www.mapress.com/zootaxa/

Article

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

http://dx.doi.org/10.11646/zootaxa.3752.1.4
http://zoobank.org/urn:lsid:zoobank.org:pub:E80EC148-F538-492A-994D-28B2EAF64845

Redescription of *Hexanchus nakamurai* Teng 1962, (Chondrichthyes: Hexanchiformes: Hexanchidae), with designation of a neotype

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Abstract

Hexanchus nakamurai Teng, 1962 is one of two valid nominal species in the genus *Hexanchus*; the other being *H. griseus*. The taxonomic history of *H. nakamurai* is somewhat convoluted due to questions about the validity of whether it constituted a publication or an unpublished dissertation. The issue appeared to have been resolved once it was determined that the Teng's original description met the criteria under the International Commission on Zoological Nomenclature code (Article 8a) of a publication. However, recent molecular studies have indicated that the western North Atlantic *H. nakamurai* (=?*H. vitulus*) may be distinct from western Indian Ocean *H. nakamurai*. Compounding the issue is the loss of the holotype of *H. nakamurai* from Taiwan. A neotype is herein designated and the species redescribed based on the neotype and eight additional Taiwanese specimens.

Key words: Hexanchidae, *Hexanchus nakamurai*, sixgill shark, neotype, Taiwan

Introduction

The genus *Hexanchus* Rafinesque 1810 is one of three genera recognized within the family Hexanchidae and comprises two widely recognized species. The members of this genus are separated from the other two monotypic genera *Heptranchias* Rafinesque, 1810 and *Notorynchus* Ayres, 1855 by having six paired gill openings as opposed to seven paired gill openings for these latter two genera. The sixgill shark species, *Hexanchus griseus* Bonnaterre, 1788 and *H. nakamurai* Teng, 1962 are separable by the presence of six distinctly comb-shaped lower teeth in the former and five comb-shaped lower teeth in the latter species. The well-known and wide-ranging *H. griseus* has a short, blunt, broadly rounded snout and a dorsal-caudal distance about equal to its dorsal fin base. The little known *H. nakamurai* has a relatively longer snout that is more pointed and narrow, and has a dorsal-caudal space that is much greater than the dorsal-fin base.

The recognition and taxonomic history of *Hexanchus nakamurai* species is somewhat convoluted. The large *Hexanchus griseus* was long regarded as the only member of the genus and the presence of a second species of *Hexanchus* was overlooked even though illustrations and records of its presence are frequently found in the literature (Nakamura, 1936; Desbrosses, 1938; Bigelow & Schroeder, 1948; Fourmanoir, 1961; Cervigon, 1966). Teng (1962) first described a subspecies of sixgill shark, *H. griseus nakamurai*, based on a couple of specimens collected at a fish market in northeastern Taiwan. He distinguished this subspecies from the only previously known member of the genus *Hexanchus* at the time, *H. griseus*, by having a concave versus straight pectoral-fin posterior margin, a long caudal peduncle, a long interspace between pelvic and anal fins, the position of the anal–fin origin

Accepted by M.R. de Carvalho: 16 Dec. 2013; published: 24 Dec. 2013

relative to the dorsal fin base, tricuspid dermal denticles with a strong and large central cusp, and a first dorsal-fin origin slightly anterior to the mid-body.

The presence of a second species, and Teng's (1962) description, went largely unrecognized until Springer & Waller (1969) recognized a distinct sixgill species from the Bahamas and described it as *H. vitulus*, but without commenting on Teng's (1962) earlier description. Compagno (1984) commented on the status of these two species, noting that Teng's (1962) work had been cited as an unpublished dissertation, thus invalidating his name. However, Ogawa Press (Maizuru, Kyoto Prefecture, Japan) published approximately 100 copies of Teng's dissertation, with copies deposited into institutional libraries and being made available to the public (K. Nakaya, Hokkaido University, Japan, pers. comm.). Ebert (1990) investigated the issue and concluded that Teng's (1962) "dissertation" met the criteria under the International Commission on Zoological Nomenclature code (Article 8a) of a publication, thus validating the species name *H. nakamurai*. Taniuchi & Tachikawa (1991) later investigated the issue and reached the same conclusion as Ebert (1990) regarding Teng's dissertation meeting the criteria of a publication.

The original description of *Hexanchus nakamurai* was based on two specimens, a holotype (TFRI 2515, immature male 750 mm TL) and a paratype (TRFI 3280, immature female 970 mm TL) both collected at the Keelung fish market, Taiwan. As part of an ongoing biodiversity study on Taiwanese chondrichthyans, the authors have attempted to locate the type specimens of *H. nakamurai*, but both appear to have been lost, as searches for them at the Taiwan Fisheries Research Institute where they were housed and at other Taiwanese institutions failed to locate these specimens.

Ebert (1990) examined in detail and compared morphological and meristic characteristics of *H. nakamurai* from a wide range of geographic regions, including all three major ocean basins, and concluded that morphologically this appears to be a single wide ranging species, although not nearly as common as *H. griseus*. However, recent molecular information has suggested that the western North Atlantic *H. vitulus* may be a distinct species from the Indo-Pacific species (Naylor *et al*., 2012a, 2012b). Therefore, since the type specimens of *H. nakamurai* have been lost, and questions as to the validity of the western North Atlantic *H. vitulus* have arisen, *H. nakamurai* is herein redescribed and a neotype is designated from Taiwanese waters. This paper represents the first part of a series redescribing and revising the family Hexanchidae.

Methods

The neotype and eight other specimens of *H. nakamurai*, all from Taiwanese waters, were measured in full and are described. Measurements modified after Ebert (1990; Appendix 1) and Compagno (2001) were taken to the nearest 0.1 mm and are presented as a proportion of total length (TL). Detailed meristic measurements were taken from one specimen (DAE 881504) that was skeletonised through dissection and hot-water maceration, with the vertebral centra and pectoral, pelvic, anal, and dorsal fin radial counts being taken. The cranium was removed from this specimen and measured following Ebert (1990; Appendix 2). Spiral valve and tooth counts were also taken opportunistically from several individuals. Morphological measurements of the holotype of *H. vitulus* from the Bahamas is compared. Tissue samples from two specimens (NMMBP–15835, GN–12888; NMMBP–15782, GN–12889) were taken and sequenced, and have been accessioned. Detailed morphological, meristic, and molecular comparison of the neotype with other regional *H. nakamurai* (= ?*H. vitulus*) specimens will be the subject of a separate paper.

Abbreviations for institutions and field numbers are as follows: California Academy of Sciences (CAS); National Museum of Marine Biology, Pingtung, (NMMB-P); National Taiwan University, Department of Zoology, Taipei, Taiwan (NTUM); Taiwan Fisheries Research Institute, Keelung (FRIP); Tunghai University, Department of Zoology, Taichung, Taiwan (this institutional collection is now combined into NMMB-P); United States National Museum of Natural History (USNM); David A. Ebert field numbers (DAE). Institutional abbreviations follow Sabaj Pérez (2013).

Hexanchus nakamurai Teng, 1962
Bigeyed sixgill shark
(Figures 1–8, Tables 1–2)

Hexanchus griseus (*partim*) Günther, 1870: 397; Nakamura, 1936: 7, fig. 1, pl. 1; Desbrosses, 1938: *partim*, fig.; Bigelow & Schroeder, 1948: 80, figs. 8–9; Fourmanoir, 1961: 8, figs. 3–4, pl. 1; Chen, 1963: 6; Cervigon, 1966: 375, fig.; Shen & Wu, 2011: 77, fig. [figure is of a *H. nakamurai*].
Hexanchus griseus nakamurai Teng, 1962: 30, fig. 5.
Hexanchus nakamurai Boeseman *in* Whitehead *et al*., 1984: 74, fig.; Ebert, 1990: 54, fig. 3.13; Taniuchi & Tachikawa, 1991: 57; Herman *et al*., 1994: 152; Last & Stevens, 1994: 41, fig. pl. 1; Last & Stevens, 2009: 39, fig. 6.3, pl. 1; Compagno, 1998: 1210; 1999: 472; 2005: 504; Compagno *in* Randall & Lim, 2000: 577; Shinohara *et al*., 2001: 288; 2005: 394; Nakabo, 2002: 142; Espinosa Pérez *et al*., 2004: 88; Nelson *et al*., 2004: 49; Compagno *et al*., 2005a: 67, fig., pl. 1; Compagno *et al*., 2005b: 48; Nelson, 2006: 65; Shao *et al*., 2008: 237; Fricke *et al*., 2009: 11; 2011: Ho & Shao, 2011: 9, 18; 346; Shen & Wu, 2011: 77, fig.; Barnett *et al*., 2012: 967; Ebert & Stehmann, 2013: 48, fig.
Hexanchus vitulus Springer & Waller, 1969: 160, figs. 1, 2a, 3–4; Boeseman *in* Hurean & Monod, 1973: 74; Bass *et al*., 1975: 9, fig. 6, pl. 2; Cadenat & Blache, 1981: 22, fig. 10; Forester *et al*., 1970: 390; Tortonese, 1985: 137; Kemp, 1978: 61, pl. 12; Maisey & Wolfram, 1984: 170; Castro, 1983: 38; Compagno, 1984: 20, fig.; Bass *et al*., 1986: 46, fig. 2.3; Robins *et al*., 1986: 17, pl. 2; Castro-Aguirre & Garcia-Dominguez, 1988: 100; Yu, 1988: 3; Compagno *et al*., 1989: 18, pl. 1; Compagno & Smale, 1989: 200; Chen & Joung, 1993: 34, fig. 1–5; McEachran & Fechhelm, 1998: 101; McLaughlin & Morrissey, 2004: 482.

FIGURE 1. Neotype of *Hexanchus nakamurai* (NMMBP–15835), mature male 1565 mm TL.

Neotype. NMMBP 15835 (Figure 1), mature male 1565 mm TL, Cheng-gong, Taiwan, 22º58’ N, 120º08’ E, 29 Mar 2011, collected at fish market from shark dealer by H.C. Ho. Neotype herein designated. [Holotype originally TFRI 2515, male 750 mm TL; type locality: Keelung, Taiwan, 5 Sept 1955, but now lost]

Other Taiwanese material: (8 specimens) NMMB-P15782, mature female, 1683 mm TL, Cheng-gong, Taiwan, 22º58’ N, 120º08’ E, 25 Dec 2010, collected at fish market from shark dealer by H.C. Ho; CAS 235382, juvenile female 958 mm TL, 24°50' N, 121°22' E, Da-xi fish market, 25 May 2005; DAE 881504, juvenile male 482 mm TL, Su-ao fish market, 24°33' N, 121°48' E, 15 Apr 1988; DAE 880704, juvenile male 845 mm TL, Keelung fish market, 25°00' N, 121°50' E, 7 Apr 1988; TFRI uncat., juvenile female 860 mm TL, Dong-gang fish market, 22°26' N, 120°30' E, 23 Apr 1988; TFRI uncat., female 1155 mm TL, Liuchiu Island, 28 Apr 1988, 22°36' N, 120°17' E; TFRI uncat., adult male 1526 mm TL, Liuchiu Island, 28 Apr 1988, 22°36' N, 120°17' E; TFRI uncat., female 1230 mm TL, Liuchiu Island, 28 Apr 1988, 22°36' N, 120°17' E.

Diagnosis. A slender-bodied shark readily distinguished from its larger congener by a narrower head, relatively larger eyes, five large lower comb-shaped anterolateral teeth, a long slender dorsal–caudal space, with the distance from the dorsal origin to the upper caudal origin being at least twice the length of the dorsal fin base; upper and lower caudal postventral margins forming a strong arch. Color of dorsum in life a uniform pale brown without a light line extending along the lateral body trunk; trailing fin edges are white in some specimens; ventral surface lighter.

Description. Proportional measurements expressed as a percentage of total length (TL) are given for the neotype followed in parenthesis by the range for eight other Taiwanese specimens (Table 1).

TABLE 1. Morphometric data for the neotype of *Hexanchus nakamurai*, with ranges provided for eight other Taiwan specimens. Measurements are expressed as percentage of total length.

	Neotype	Others from Taiwan	
	NMMB–P15835	Min.	Max.
Total length (mm)	1565	482	1683
Pre-caudal length	69.4	62.8	69.4
Pre-narial length	2.0	1.0	1.9
Pre-oral length	4.6	4.2	6.2
Pre-orbital	4.6	3.6	4.8
Pre-spiracle length	11.8	9.8	13.0
Pre-gill length	15.7	11.9	15.7
Pre-pectoral length	18.3	16.0	18.8
Pre-pelvic length	43.3	39.8	45.3
Snout-vent length	47.4	42.7	49.0
Pre-dorsal length	51.9	48.1	51.9
Dorsal-caudal space	11.6	10.9	12.5
Pre-anal length	58.0	51.6	57.4
Pectoral-pelvic space	19.9	16.8	21.9
Pelvic-anal space	7.2	4.9	8.1
Anal-caudal space	7.3	7.6	9.0
Pelvic-caudal length	18.8	17.2	
Eye length	3.3	2.6	5.2
Eye height	1.9	1.5	2.9
Interorbital length	7.0	6.5	8.7
Nostril width	1.1	0.8	1.2
Internarial width	4.0	3.5	4.6
Anterior nasal flap	0.5	0.3	0.6
Spiracle length	0.5	0.1	0.5
Eye-spiracle length	4.7	3.4	4.7
Mouth length	6.6	3.5	6.0
Mouth width	9.3	5.6	10.0
Upper labial furrow		1.0	2.0
Lower labial furrow		1.2	2.7
1st Gill height	7.4	4.7	6.2
2nd Gill height	6.6	4.5	5.5
3rd Gill height	6.0	4.1	5.1
4th Gill height	5.4	4.0	4.5
5th Gill height	4.6	3.1	4.0
6th Gill height	3.4	2.4	3.1
Head height	9.3	7.1	9.1
Head width	10.6	10.7	10.9
Trunk height	10.0	10.3	10.6
Trunk width	9.5	9.4	10.1
Caudal peduncle height	3.6	3.4	4.1
Caudal peduncle width	3.3	2.8	3.6
Pectoral length	9.6	9.0	10.4

...... continued on the next page

TABLE 1 (continued)

	Neotype	Others from Taiwan	
	NMMB–P15835	Min.	Max.
Pectoral anterior margin	10.7	10.4	12.6
Pectoral base	6.3	6.0	6.4
Pectoral height	8.7	8.3	10.1
Pectoral inner margin	4.3	2.9	4.6
Pectoral posterior margin	8.0	6.7	9.4
Pelvic length	13.5	7.3	12.9
Pelvic anterior margin	4.7	3.3	4.9
Pelvic base	7.5	4.8	8.3
Pelvic height	4.7	1.4	4.1
Pelvic inner margin	6.6	0.8	6.6
Pelvic posterior margin	10.7	4.7	10.0
Outer clasper length	4.0		
Inner clasper length	5.4		
Clasper base	1.6		
Dorsal fin length	7.3	5.9	8.1
Dorsal fin anterior margin length	7.0	5.6	7.6
Dorsal fin base length	5.9	4.9	6.5
Dorsal fin height	4.6	2.6	4.6
Dorsal fin inner margin length	1.4	0.6	1.6
Dorsal fin posterior margin length	4.7	2.3	4.8
Anal fin length	6.2	4.4	6.5
Anal fin anterior margin	3.9	2.5	3.8
Anal fin base	4.6	3.3	5.0
Anal fin height	2.5	1.2	2.6
Anal fin inner margin	1.6	1.3	1.8
Anal fin posterior margin	3.6	2.5	3.8
Dorsal caudal margin	30.4	30.0	36.5
Preventral caudal margin	8.5	6.9	9.1
Lower postventral caudal margin	4.3	2.7	4.1
Upper postventral caudal margin	15.7	17.0	21.3
Subterminal caudal margin	3.3	3.0	4.4
Terminal caudal margin	5.9	4.3	6.3
Terminal caudal lobe	7.3	6.6	8.3
Caudal fork length	7.7	6.3	8.0
Dorsal-anal fin origin	5.5	3.4	5.6
Dorsal-anal fin insertion	4.4	2.8	4.0

Body trunk slender, tapering posteriorly to caudal peduncle. Head moderately flattened, narrowly parabolic or bluntly pointed in dorsoventral view; length to sixth gill opening 0.7 (0.6–0.9) times pectoral–pelvic space. Snout relatively narrow, rounded to angular in dorsoventral view, acutely pointed at apex; length of preoral snout 2.0 (1.3–1.9) times mouth width.

Eyes relatively large, rounded, orbits longer than high, their lengths about equal to length of snout in front of eye; anterior edge of orbit in advance of mouth; eye length about 5.7 (4.9–6.2) times in head length; eyes a bright iridescent green in life. Spiracles small, slit-like. Gill openings number six paired, with each successive gill opening becoming progressively shorter from the first to sixth gill; sixth gill opening about 2.2 (1.7–2.2) times length of first. Nostrils nearer the snout than to the forward edges of mouth, inner posterior part with single valve-like anterior nasal flap; nostril width 4.0 (3.3–4.4) in internarial width and 3.3 (2.7–3.5) in eye length. Mouth relatively large, strongly arched, length about 1.4–2.4 times in mouth width. Labial furrows not visible when mouth closed; lower labials slightly shorter than upper labial length.

Teeth differ in upper and lower jaws (Figure 2); upper jaw with two medial teeth each having a single high smooth–edged cusp, without serrations or cusplets; first anterolateral with a single large smooth-edged cusp, followed by six to seven anterolaterals each with a single large cusp with one to five smaller cusplets; number of cusplets increases with growth; serrations present on mesial edge; posterolateral commissural teeth small and granular. Lower jaw with central medial tooth, with a strong medial cusp flanked by three to five cusplets on either side; single cusp variably high or short depending on sex and maturity; larger comb–shaped anterolaterals with a single cusp followed by six to ten cusplets on either side of apical length; cusp is variably high or short depending on sex and maturity; posterolateral commissural teeth small and granular. Total tooth counts variable, ranging between 18 (18–33) upper jaw, 11 (9–12) for lower jaw. Upper jaw with two medial teeth followed by seven or eight anterolateral teeth per side; upper posterolateral commissural teeth number between 7–15, with a slight increase number of teeth associated with growth. Lower jaw consists of a single median tooth followed by five large comb–shaped anterolateral teeth per side; number of lower posterolateral commissural teeth ranged from 4–19; number of posterolateral commissural teeth varied, but did not appear to be associated with growth. Sexual dental dimorphism is strong in this species with the upper and lower anterolateral tooth cusp of adult males becoming higher than those of adult females; this increase in height only occurs at the onset of sexual maturity in males.

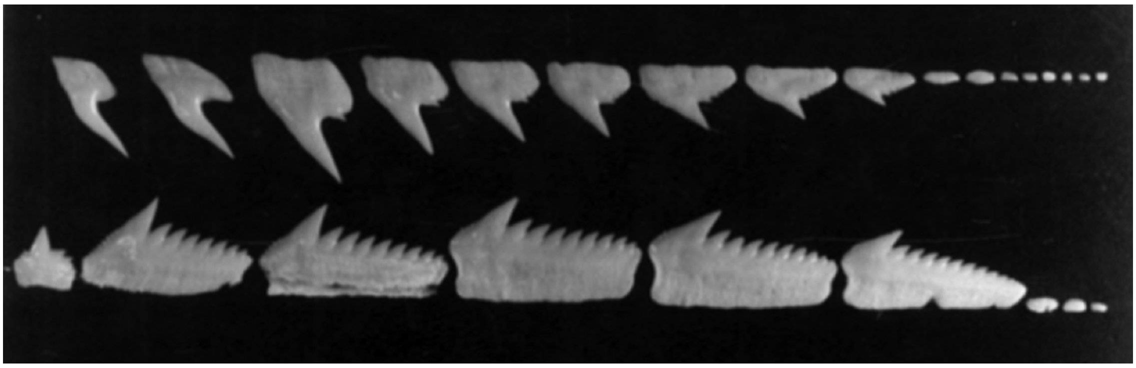

FIGURE 2. Upper and lower teeth of *Hexanchus nakamurai*, adult male 1553 TL (SAIAB 6897).

Lateral trunk denticles small, closely imbricate, with a strong central ridge and two short lateral ridges, apical points not strong (Figure 3). A series of 1–3 enlarged denticles on upper surface of caudal dorsal margin.

Pectoral fins broad based, short, anterior margin slightly convex, rounded at apex; origin below and posterior to midpoint of sixth gill opening; posterior margin slightly concave, tips rounded and triangular. Pectoral–fin skeleton (Figure 4) with radials extending about 2.2 times pectoral anterior margin length into fin. Total radial count for a single individual was 26; propterygium small without radials, mesopterygium with 10 radials, metapterygium with 16 radials; radials divided into 6 segments.

Pelvic–fin anterior margins slightly concave in males, nearly straight in females; posterior margins straight in females, but concave in males due to elongated scrolling of clasper folds with clasper development. Pelvic–fin skeleton (Figure 5) consists of a long basipterygium with two segments from which 23 radials extend diagonally from its axis; each radial with 3 segments, except for 4 posterior-most radials that are unsegmented. Claspers with long axial cartilage and basal segments combined with calcified terminal cartilage in adult males; last radial cartilages form the clasper scroll; spurs and spines absent. Clasper skeleton consists of an elongated axial cartilage connected to basipterygium by an intermediate segment, followed by the beta cartilage; end style joined by terminal cartilage element in adults.

Dorsal–fin origin set above pelvic–fin midbase; anterior margin nearly straight, apex rounded subtriangular, posterior margin slightly concave; base length 2.0 (1.7–2.6) times into dorsal–caudal space. Dorsal–fin skeleton (Figure 6) with an elongate basal cartilage that is convex ventrally and slightly concave dorsally where the radial cartilages attach; a single specimen had 13 radials attached to the basal cartilage, each with 3 segments per radial. Anal fin small, subtriangular at apex, anterior and posterior margins nearly straight; anal–fin base 1.6 (1.5–2.7) times in anal caudal space. Anal–fin skeleton (Figure 7) composed of an elongate basal cartilage with 13 radials, each consisting of 3 segments. Caudal fin elongated, slightly convex, about 2.3 (1.7–2.3) times precaudal length; preventral caudal margin slightly convex; subterminal lobe strongly notched; upper and lower postventral caudal margins strongly concave; terminal caudal lobe moderately concave.

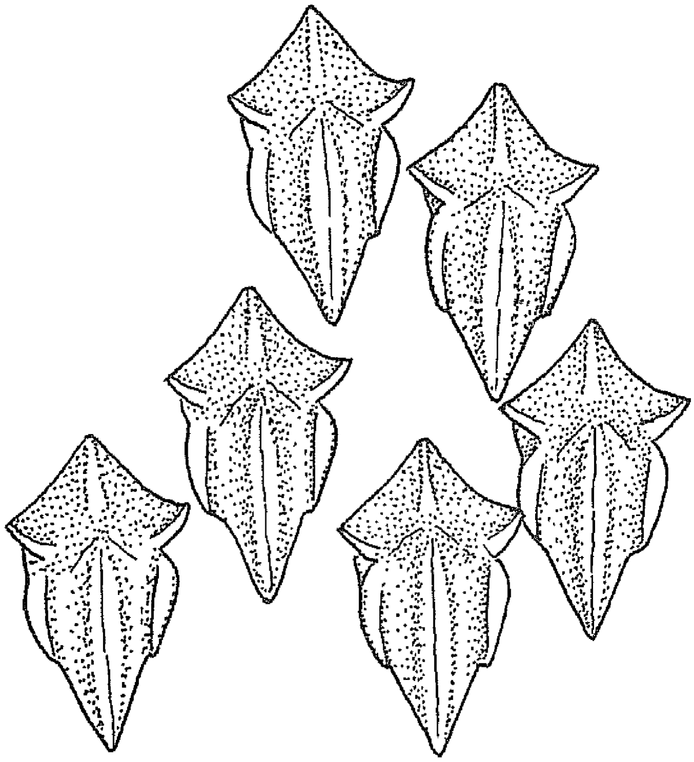

FIGURE 3. Lateral trunk denticles of *Hexnachus nakamurai*, adult male 1553 TL (SAIAB 6897).

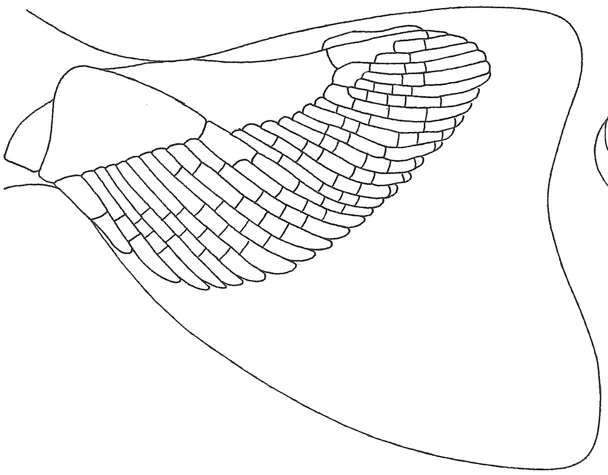

FIGURE 4. Pectoral fin radial skeleton of *Hexanchus nakamurai*, immature male 482 mm TL (DAE 881504).

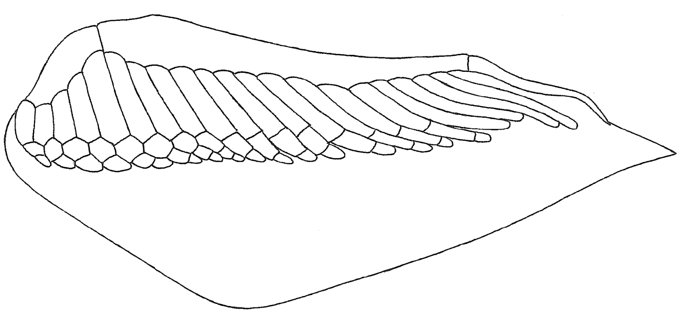

FIGURE 5. Pelvic fin radial skeleton of *Hexanchus nakamurai*, immature male 482 mm TL (DAE 881504).

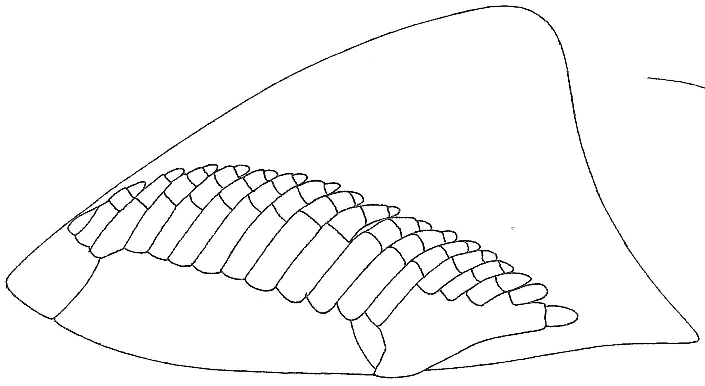

FIGURE 6. Dorsal fin radial skeleton of *Hexanchus nakamurai*, immature male 482 mm TL (DAE 881504).

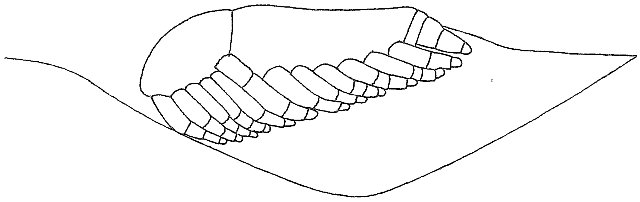

FIGURE 7. Anal fin radial skeleton of *Hexanchus nakamurai*, immature male 482 mm TL (DAE 881504).

Vertebral column counts were made from a single specimen. Total vertebral count for a single specimen was 155, precaudal vertebral count 87, monospondylous precaudal vertebral (MP) counts 57, diplospondylous precaudal vertebral (DP) count 30, caudal vertebral (DC) count 68. The rib closure occurred at the 54^{th} centra. The transition between MP-DP occurred three centra beyond the closure of the rib cage. The percentage of total vertebral centra was MP 36.8%, DP 19.4%, and DC 43.9%. Ratios were 0.5 DP/MP and 1.2 DC/MP. Spiral valve turn counts were 22 for three Taiwanese individuals.

The cranium from a 482 mm TL immature male was removed and examined with the measurements expressed as percentages of the nasobasal length (Table 2). Cranium (Figure 8) with short blunt rostral cartilage, not hypercalcified. Length of medial rostral cartilage about 29.8 times in nasobasal length, width across bases of lateral rostral cartilages about 0.2 times in length of medial rostral cartilage. Nasal capsules large, rounded, width about 3.8 in nasobasal length. Nasal apertures large, oval, and separated by a space 1.6 times their widths. Anterior fontanelle rounded, slightly longer than wide. cranial roof 1.4 times orbital length. Orbital notches 6.7 times orbital length. Suborbital shelves 1.1 times orbital length. Otic capsules 1.5 times orbital length.

TABLE 2. Cranial measurements expressed as percentage of the nasobasal length from a 482 mm TL immature male *H. nakamurai* (DAE 881504) from Taiwan.

Nasobasal length (mm)	59.5
Medial rostral cartilage length	3.4%
Width between bases of lateral rostral cartilage	14.3%
Width across nasal capsules	55.5%
Nasal capsule length	26.1%
Nasal capsule width	26.9%
Nasal aperture width	20.2%
Width between nasal apertures	12.6%
Rostral base to edge of anterior fontanelle length	30.3%
Anterior fontanelle width	10.1%
Cranial height	31.9%
Basal plate width at orbital notches	6.7%
Cranial roof width over orbital notches	28.6%
Orbital length	40.3%
Pre-orbital process length	21.8%
Post-orbital process length	15.1%
Width across sub-orbital shelves	35.3%
Otic capsule length	27.7%
Width across otic capsule	26.9%
Width across pre-orbital processes	47.9%
Width across post-orbital processes	63.9%

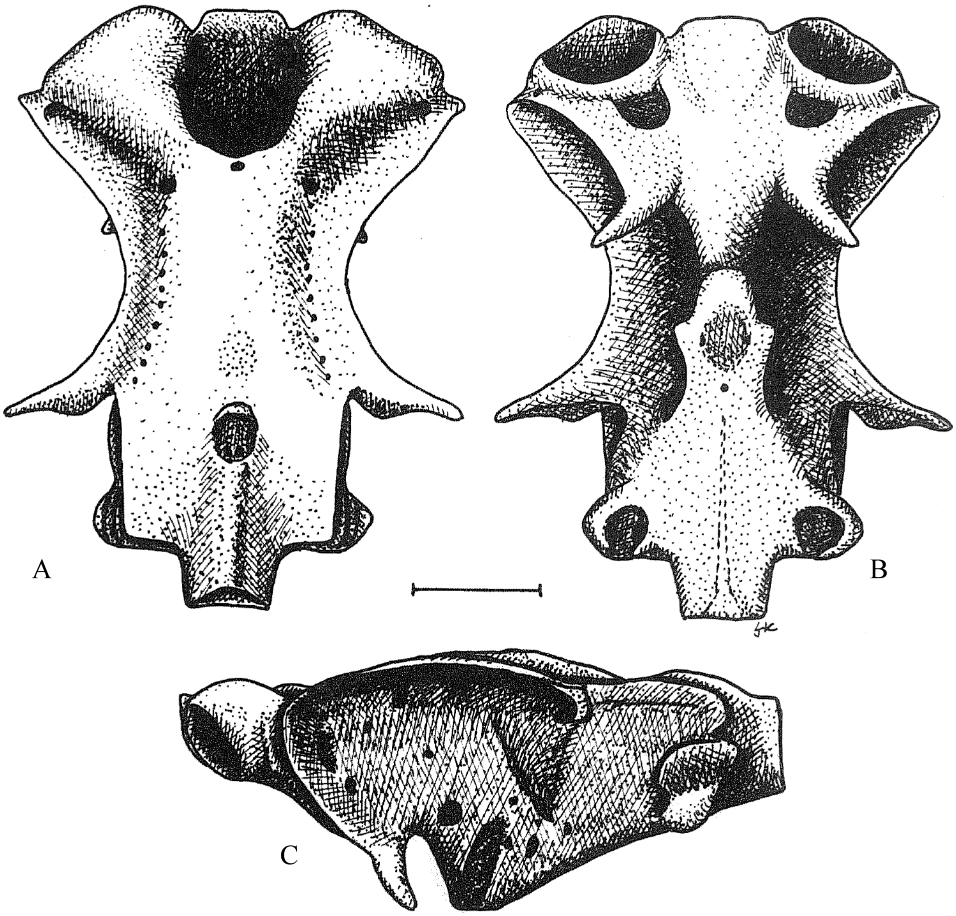

FIGURE 8. Cranium of *Hexanchus nakamurai*, immature male 482 mm TL (DAE 881504). Cranial terminology and measurement provided in Appendix 2. A. dorsal view. B. ventral view. C. lateral view..

Dorsal coloration a uniform light pale brown to gray with no conspicuous markings, except for white along trailing fin edges; ventral surface lighter. Juvenile coloration with noticeable white trailing fin edges on pectoral, pelvic, and dorsal fin tip. Caudal fin white–edged along dorsal caudal margin, upper postventral margin, and subterminal lobe; a black spot is located at the tip of the caudal fin; no light lateral line present.

Etymology. The species name was in honor of Dr. Hiroshi Nakamura.

Distribution. A wide-ranging, although patchily distributed, species found in warm temperate and tropical seas. In the Western Central Pacific the species occurs off Japan (including Kochi, Ogasawara Islands and Okinawa), Taiwan, the Philippines (Negros, possibly Luzon), Indonesia (Java, Bali, and Lombok), Australia (Western Australia, Queensland, northern New South Wales), New Caledonia, and French Polynesia (Tahiti). In the Western Indian Ocean it occurs off South Africa (kwaZulu-Natal), Kenya, Madagascar, Geyser and Zeleé Banks, Aldabra Islands and Mauritius. Eastern north and central Atlantic records include the Bay of Biscay, off France, Spain, Gibraltar, Morocco, and possibly the Ivory Coast and Nigeria, and also the western Mediterranean. Western Atlantic records range from off the Bahamas, coast of Florida, northern Cuba, Cayman and Virgin Islands, Gulf of Mexico to the Yucatan and Gulf coast of Mexico, Nicaragua, Costa Rica, Venezuela and the Guyanas (Ebert *et al*., 2013).

Size. A small sixgill shark species with a maximum total length of about 178 cm TL; males mature at about 123 cm TL and females mature at about 142 cm TL. Size at birth is about 40 to 43 cm TL. Barnett *et al*. (2012) provides an overview on the biology of this little known species.

Discussion

Compagno (1984) commented that comparison of the original descriptions of *H. griseus nakamurai* and *H. vitulus* strongly suggested that these two species were synonymous, but he did not have any specimens with which to compare these two nominal species directly. Ebert (1990) however in a revision of the family Hexanchidae examined specimens of *H. nakamurai* from Taiwan and compared morphometrics to the type specimens of *H. vitulus*, but found no distinct morphological differences between the two species. During his study, Ebert (1990) visited Taiwan and attempted to locate Teng's (1962) specimens, but without success and concluded that the type specimens may have been lost. A subsequent field trip to Taiwan by two of us (DE, WW) in 2005 also failed to locate the type specimens. Ho & Shao (2011) listed the type specimens, but did not comment on their status. During the present study, and as part of a broader study on the biodiversity of Taiwanese Chondrichthyans, the authors attempted to locate the type specimens, but again without success. Eschmeyer (2013) lists the type specimens as missing.

Ebert (1990) examined extensive material, from museum collections and collected fresh specimens in the field, from Australia, Bahamas, Florida, USA, Indonesia, Kenya, Philippines, South Africa, Taiwan, the northern Gulf of Mexico, and the U.S. Virgin Islands. The type specimens of *H. vitulus* from the Bahamas were also examined and compared to other regional material to determine whether *H. nakamurai* was a single wide-ranging species or may involve other additional species. Morphological comparison of regional *H. nakamurai* (=?*H. vitulus*) did not reveal any distinctive differences between those from the western North Atlantic and the western North Pacific (Ebert, 1990). Taniuchi & Tachikawa (1991) followed in synonymising the two species with *H. nakamurai* being the senior synonym and most subsequent authors considering the two species to be synonymous (Last & Stevens, 1994, 2009; Compagno *et al*., 2005; Barnett *et al*., 2012; Ebert & Stehmann, 2013; Ebert *et al*., 2013).

Herman *et al*. (1994) later resurrected *H. vitulus* as a valid species separable from *H. nakamurai* based on the following odontological differences. *Hexanchus vitulus*: lower anterolateral teeth with cusp much higher than distal cusplets and with mesial edges smooth; *H. nakamurai*: lower anterolateral teeth with cusp about as high or only slightly higher than distal cusplets and with mesial edges coarsely serrated.

Herman *et al*. (1994) based their findings on the jaws of four specimens of *H. vitulus* and four specimens of *H. nakamurai*. However, their findings were flawed since they did not take into account sexual dimorphism and ontogeny in the development of the teeth with maturation. Furthermore, two of the specimens Herman *et al*. (1994) examined were one in the same specimen (ORI 2822 and RUSI 6897). Ebert (1990) examined RUSI 6897, which had been originally designated ORI 2822, but when the fish collection at the Oceanographic Research Institute (ORI) was moved to the former J.L.B. Smith Institute of Ichthyology (now the South African Institute for Aquatic Biodiversity, SAIAB) the accession number changed; Herman *et al*. (1994) apparently was unaware of this change and inadvertently cited both accession numbers without realizing they were one in the same specimen. Furthermore, in reviewing the material examined and the conclusions reached by Herman *et al*. (1994) it is apparent that these authors did not examine a size range of individuals. As discussed by Ebert (1990) sexual dimorphism and ontogeny is strong in the family Hexanchidae and must be taken into consideration. For example, all of the specimens referred to as *H. vitulus* by Herman *et al*. (1994) were adult males, which have a significantly higher cusp relative to the distal cusplets, while adult females and juveniles of both sexes have a cusp that is nearly the same or slightly higher than the distal cusplets. In fact, Herman *et al*. (1994) concluded that the holotype of *H. vitulus* (an adult male) was a different species based exclusively on tooth morphology from its paratype (an adult female) that they referred to as *H. nakamurai*.

The question as to whether *H. nakamurai* and *H. vitulus* are distinctly different species remains somewhat enigmatic. Based on morphological and meristic data Ebert (1990) concluded that these two species are one in the same. However, Naylor *et al*. (2012a, 2012b) in analyzing molecular data of *H. nakamurai* specimens from the Bahamas (western North Atlantic) and Madagascar (western Indian Ocean) concluded that these two species are genetically separable. Therefore, since the holotype of *H. nakamurai* is now lost it is of taxonomic importance to designate a neotype for this species from its type location. Morphological and molecular comparison of specimens from these two regions and other geographic locations will be reported on elsewhere as data is still being added to and collected.

Finally, the increasing use of molecular tools to highlight potential cryptic species or species complexes has been gaining use in Chondrichthyan systematics. The present study is an example, where a DNA sequenced approach to identifying shark species has suggested that the bigeyed sixgill shark *Hexanchus* species from western North Atlantic (=?*H. vitulus*) is separable from the western Indian Ocean (=*H. nakamurai*) species. This example highlights the importance of type specimens and the importance of locating the type material. However, where type specimens have been lost it is also important to consider designating a neotype, when appropriate, and if possible to barcode the specimen. Poor taxonomic practices in which holotype specimens are not retained, where the description is based primarily on genetic sequences and or the nomenclature is not properly researched only creates taxonomic confusion, especially among complex species groups. The designation of a neotype along with associated genetic data on the other hand will only strengthen and clarify the taxonomic status of problematic groups and species.

Acknowledgements

We thank the following individuals for assistance on various aspects of this study: Leonard Compagno (South African Museum), Paul Cowley (South African Institute Aquatic Biodiversity), Tom Hecht (Rhodes University), Andrew Payne (Cefas), Shoou-Jeng Joung (National Taiwan Ocean University), Chuan-Cheng Wu, Hung-Chia Yang (Taiwan Fisheries Research Institute), Rob Leslie (Department Agriculture, Fisheries & Forestry, Cape Town, South Africa), John McCosker, Dave Catania and Jon Fong (California Academy Sciences), Mike Bougaardt (South African Museum), Kazuhiro Nakaya (Hokkaido University), Alastair Graham (CSIRO Marine and Atmospheric Research), George Burgess (University of Florida), Wade Smith (Oregon State University), Matthew Jew (CSU Monterey Bay and Pacific Shark Research Center, Moss Landing Marine Laboratories), Paul Clerkin (Pacific Shark Research Center, Moss Landing Marine Laboratories), and Kwang-Tsao Shao (Academia Sinica, Taiwan). Support for this project was provided by NOAA/NMFS to the National Shark Research Consortium and the David and Lucile Packard Foundation to the Pacific Shark Research Center, National Science Foundation grant (Jaws and backbone: Chondrichthyan phylogeny and a spine for the vertebrate tree of life, DEB 1132229) to Gavin Naylor, College of Charleston, and the National Science Council, Taiwan, and National Museum of Marine Biology and Aquarium (NMMBA 102200255), Taiwan, provided supported for this project.

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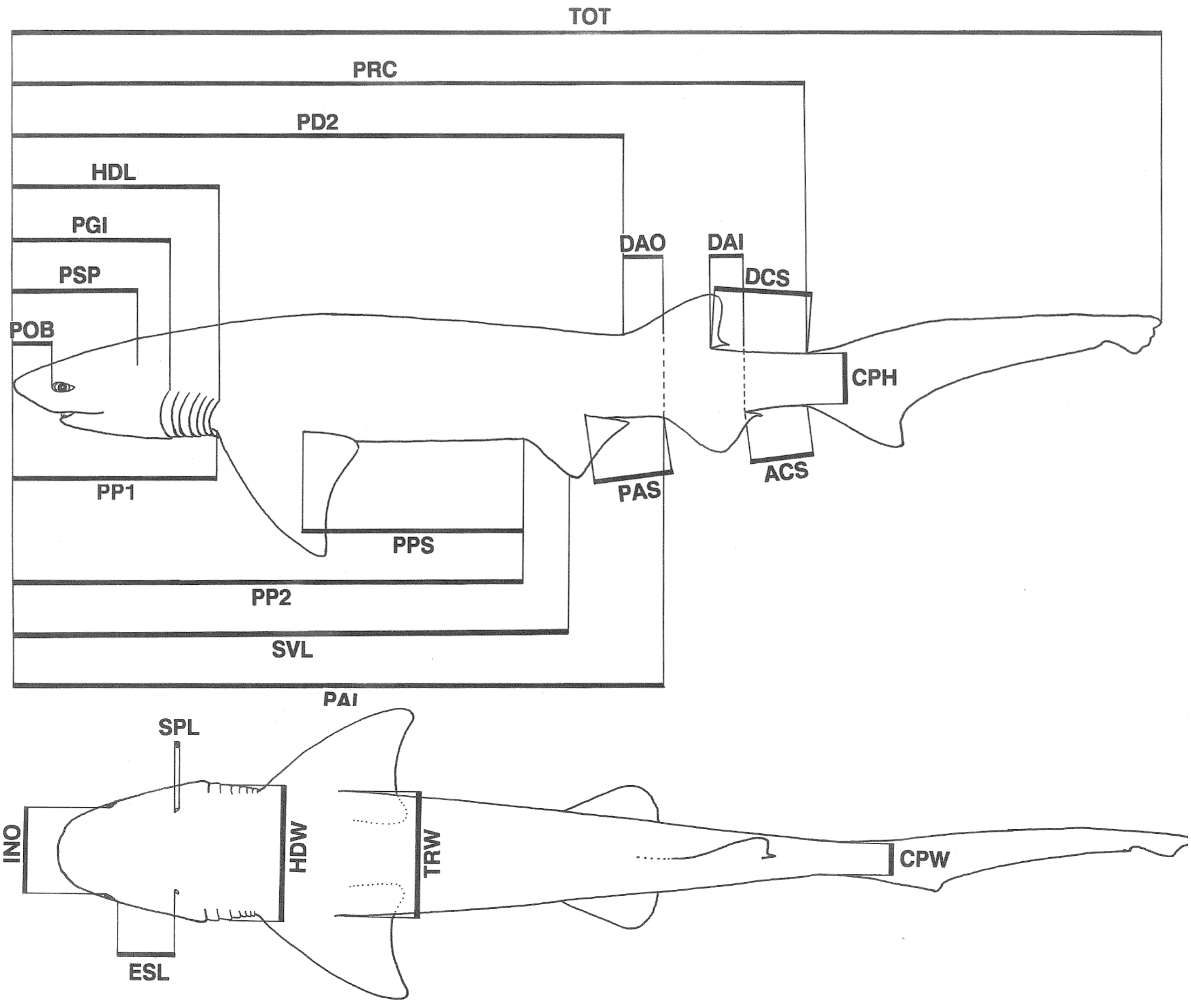
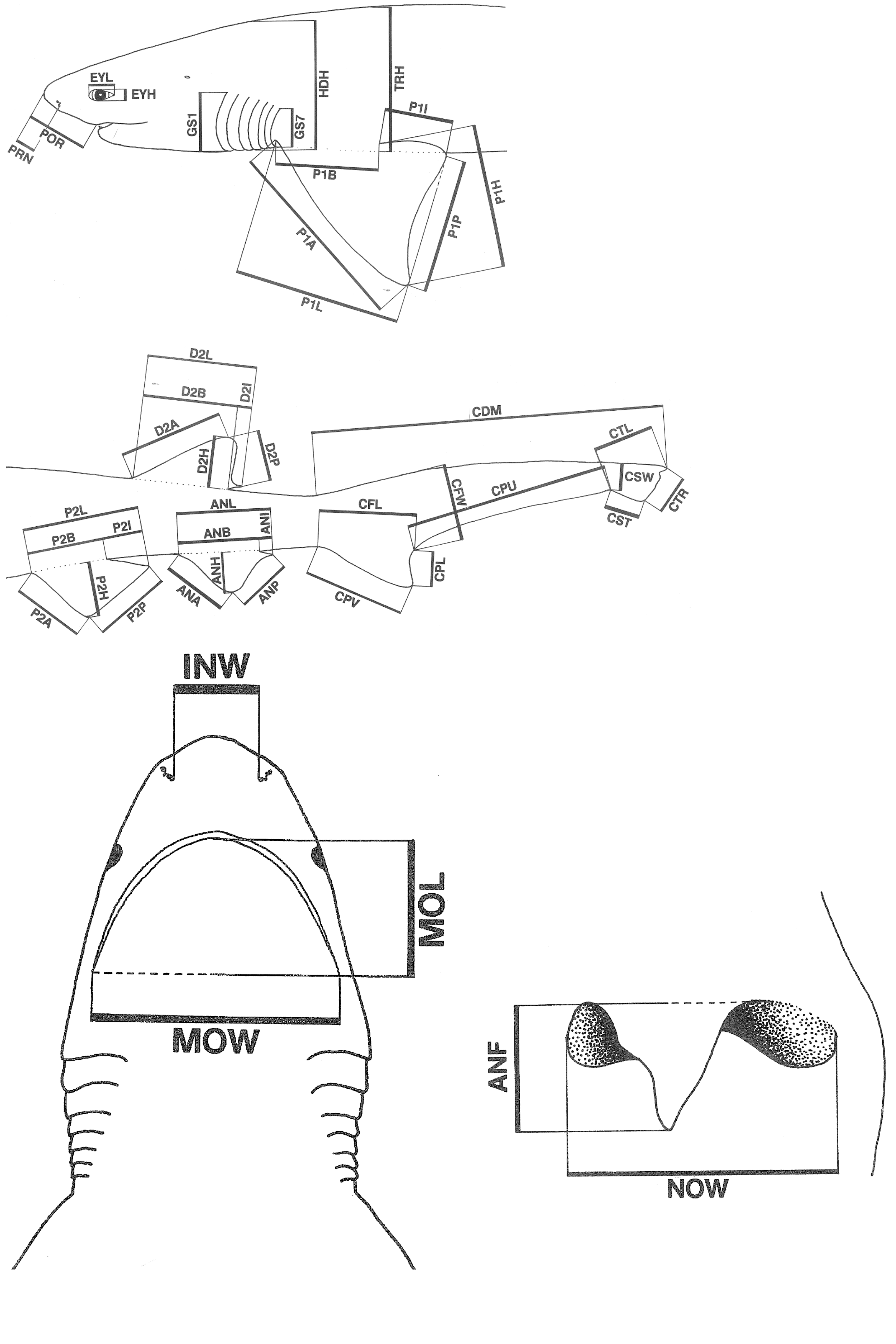
Appendix 1. Morphometric measurements for hexanchid sharks following Ebert (1990). Abbreviated terms are as follows: TOT, total length; PRC, pre-caudal length; PRN, pre-narial length; POR, pre-oral length; POB, pre-orbital length; PSP, pre-spiracle length; PGI, pre-gill length; PP1, pre-pectoral fin length; PP2, pre-pelvic fin length; SVL, snout-vent length; PD2, pre-dorsal fin length; DCS, dorsal-caudal space; PAL, pre-anal fin length; PPS, pectoral-pelvic space; PAS, pelvic-anal fin space; ACS, anal-caudal length; EYH, eye height; EYL, eye length; INO, interorbital length; NOW, nostril width; INW, internarial width; ANF, anterior nasal flap length; SPL, spiracle length; ESL, eye-spiracle length; MOL, mouth length; MOW, mouth width; GS1, first gill height; GS2, second gill height; GS3, third gill height; GS4, fourth gill height; GS5, fifth gill height; GS6, sixth gill height; GS7, seventh gill height (sevengill sharks only); HDH, head height; HDW, head width; TRH, trunk height; TRW, trunk width; CPH, caudal peduncle height; CPW, caudal peduncle width; P1L, pectoral fin length; P1A, pectoral fin anterior margin length; P1B, pectoral fin base length; P1H, pectoral fin height; P1I, pectoral fin inner margin; P1P, pectoral fin posterior margin length; P2L, pelvic fin length; P2A, pelvic fin anterior margin; P2B, pelvic fin base length; P2H, pelvic fin height; P2I, pelvic fin inner margin; P2P, posterior margin length; CLB, clasper base length; CLI, inner clasper length; CLO, outer clasper length; D2L, dorsal fin length; D2A, dorsal fin anterior margin; D2B, dorsal fin base length; D2H, dorsal fin height; D21, dorsal fin inner margin; D2P, dorsal fin posterior margin; ANL, anal fin length; ANA, anal fin anterior margin; ANB, anal fin base length; ANH, anal fin inner margin; ANI, anal fin inner margin; ANP, anal fin posterior margin; CDM, caudal dorsal fin margin; CPV, preventral caudal margin; CPL, lower postventral caudal margin; CPU, upper postventral caudal margin; CST, subterminal caudal margin; CTR, terminal caudal margin; CTL, terminal caudal lobe; CFL, caudal fork length; DAI, dorsal-anal fin insertions; DAO, dorsal-anal fin origins; not depicted in figure: Pelvic-caudal length; ULA, upper labial furrow; LLA, lower labial furrow.

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Appendix 2. Cranial measurements for hexanchid sharks following Ebert (1990). A) dorsal view, B) ventral view, and C) lateral view. Abbreviated terms are as follows: 1. nasobasal length; 2. medial rosral cartilage length; 3. width between bases of lateral rostral cartilage; 4. width across nasal capsules; 5. nasal capsule width; 6. nasal capsule length; 7. nasal aperture width; 8. width between nasal apertures; 9. rostral base to edge of anterior fontanelle length; 10. anterior fontanelle width; 11. cranial height; 12. width across post-orbital processes; 13. cranial roof width over orbital notches; 14. Orbital length; 15. pre-orbital process length; 16. post-orbital process length; 17. otic capsule length; 18. width across sub-orbital shelves; 19. width across otic capsule; 20. width across pre-orbital processes; 21. basal plate width at orbital notches.