



EDITORS: P. R. LAST › W. T. WHITE › J. J. POGONOSKI

DESCRIPTIONS *of*
NEW DOGFISHES
of the genus *Squalus* (Squaloidea: Squalidae)



CSIRO MARINE AND ATMOSPHERIC RESEARCH PAPER NO. 014

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Part 1 — Application of a rapid taxonomic approach to the genus *Squalus*

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ABSTRACT.— The Indo–West Pacific appears to be a centre of speciation for the squaloid genus *Squalus*. In the following series of papers, a rapid taxonomic approach is used to formally describe 11 new species and rediagnose another 4 nominal *Squalus* species from the region. The approach focuses on delivering a good characterisation of each species in a minimalist sense to increase the cost effectiveness of the research and shorten timelines. Strong diagnoses are complemented by a thorough use of digital images to demonstrate key morphological features. This approach is useful for identifying new taxa and making names available quickly but is not recommended as a replacement for formal group revisionary studies. Morphometric characters are often poorly defined so all of the measurements taken in this study are clearly explained and illustrated. This approach also includes the use of molecular analyses to support morphological observations.

Key words. Squaloidea – Squalidae – background – new species – Indo–West Pacific – DNA barcode

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INTRODUCTION

Members of the squalid genus *Squalus* Blainville, 1816 (type species *Squalus acanthias* Linnaeus, 1758, by subsequent designation of Gill, 1862), otherwise known as spurdogs, dogsharks and dogfishes, are one of the most taxonomically problematic shark groups. Presently, 14 species of *Squalus* are recognised as valid (Compagno *et al.*, 2005): *S. acanthias* Linnaeus, 1758; *S. blainvillei* (Risso, 1827); *S. cubensis* Howell Rivero, 1936; *S. japonicus* Ishikawa, 1908; *S. megalops* (Macleay, 1881); *S. melanurus* Fourmanoir and Rivaton, 1979; *S. mitsukurii* Jordan and Snyder, in Jordan and Fowler, 1903; *S. rancureli* Fourmanoir and Rivaton, 1979; and 6 undescribed species from Australia (Last and Stevens, 1994). At least two other nominal species, *S. brevirostris* Tanaka, 1917 and *S. lalannei* Baranes, 2003, also appear to be valid taxa. The status of *S. acutirostris* Chu, Meng and Li, 1984 and *S. probatovi* Myagkov and Kondyurin, 1986 need to be determined. *Squalus asper* Merrett, 1973 has been placed in a related genus, *Cirrhigaleus*.

Squalus species have been divided into four assemblages based on their morphology: the ‘acanthias group’, the ‘blainvillei group’, the ‘megalops-cubensis group’, and the ‘asper-barbifer group’ (Bigelow and Schroeder, 1957; Garrick, 1960; Garrick and Paul, 1971). Members of the ‘asper-barbifer group’ are now assigned to the genus *Cirrhigaleus* (Compagno *et al.*, 2005). Other subgroups, whose members are considered to reside in the ‘blainvillei group’, can be identified based on the morphology of their

component species. These include: the slender, long-snout spurdogs (the ‘japonicus group’), the relatively short-snout spurdogs with a tall first dorsal fin, white edged caudal fin, and tricuspid denticles (the ‘highfin megalops group’), and the spurdogs with a moderate-sized snout, low dorsal fins, tricuspid denticles, and a well-defined dark caudal bar (the ‘mitsukurii group’). These groups may or may not represent monophyletic groups and more research is needed to understand their relationships. Members within groups are often very similar and have been confused in the literature.

In recent years, exploratory surveys of the continental slopes of Australasia and the nearby Indo–Malay Archipelago, as well as an increasing regional interest in elasmobranchs for conservation and fishery purposes, has led to the discovery of many new chondrichthyan fishes. Some of these have been discussed in important regional works. Last and Stevens (1994) identified 9 Australian *Squalus* species of which 6 had not yet been formally described. Four species of spurdogs were collected during recent surveys of fish markets in eastern Indonesia, of which two appear to be conspecific with undescribed Australian species and the other two could not be identified to species level (White *et al.*, 2006). Similarly, additional undescribed spurdogs were collected by French, Australian and New Zealand surveys in the Tasman and Coral Seas. The Indo–West Pacific region appears to be rich in species of *Squalus* with more than three-quarters of the known species occurring there.

In the following series of papers (presented as Parts 2–12 of this issue), 11 new species are formally described and another 4 nominal species are rediagnosed using a rapid taxonomic approach. The basis of this multi-author approach is to standardise morphometric methods, restrict the number of specimens examined in detail, provide only moderate length descriptions but give detailed diagnoses, and provide detailed images showing the key features of each species. Muscle tissue samples from 8 of these species, and an additional 5 regional taxa, have been analysed using a molecular barcoding method as part of a broader international project that aims to DNA barcode all fish species (FISH-BOL, see www.fishbol.org). The results of this research (Part 12) supported the findings of morphological studies in Parts 2–11.

METHODS

Morphometric characters were selected to discriminate new taxa and enable comparisons to be made with published information on nominal *Squalus* species from other regions. Methods generally followed a widely adopted scheme for elasmobranchs (Compagno 1984, 2001), but focused on direct (point-to-point) rather than horizontal measurements. Shark researchers have made unspecified use of both approaches, so data in the literature are often unreliable for comparative purposes. Also, because the way in which some measurements are taken can vary slightly from one shark group to another, authors need to carefully define their methods for the group in question. Primary measurements are explained in Table 1 and illustrated in Figs 1–3. Important dimensions of the snout, head, predorsal, precaudal and prenarial regions were also taken horizontally so comparisons between our material and literature specimens could be made when direct measurements were unavailable. Measurements of the first and second dorsal-fin heights and shape of the exposed portions of the first and second dorsal-fin spines follow the concept proposed by Yamakawa *et al.* (1986). Several new measurements, some of which were used but not fully-defined in Springer and Burgess (1985) and then adopted by Last *et al.* (2002), need clarification: pre-first dorsal and pre-second dorsal lengths are direct measurements taken between the tip of the snout and the embedded anterior edge of the respective dorsal spine (just forward of the exposed spine and detectable by pushing into the adjacent muscle tissue); pre-vent length is taken from the snout tip to the anterior margin of the main opening of the vent; spiracle length is the maximum diameter of the opening (usually measured through the vertical axis); entire lengths of the first and second dorsal fins are measured from the buried anterior edge of the spine to the apex of the free rear tip of the fin; soft dorsal-fin lengths are measured horizontally from where the rear edge of the spine joins the soft part of the fin, to the free rear tip of the fin. The lower labial furrow of spurdogs is not obvious externally and was not measured.

Black and white markings on the caudal fin are important for distinguishing *Squalus* species and these characters are usually embellished in late embryos and early juveniles. The most important markings and their disposition on the fin are illustrated in Fig. 4: the ‘caudal bar’ refers to the dark marking along the posterior edge of the fin in some species (it may be subvertical, extending dorsally along the postdorsal caudal margin from the caudal fork, or obliquely, from the origin of the ventral lobe to the caudal fork); a dark ‘basal marking’ is sometimes present near the origin of the ventral lobe; a dark ‘upper caudal blotch’ and/or ‘upper caudal fringe’ may exist on the upper lobe (these markings may be sharply defined or diffuse edged); a dark ‘caudal stripe’, which occurs rarely, is a narrow longitudinal stripe extending from near the origin of either the upper or lower fin lobe, along the dorsal or ventral edge of the fleshy portion of the fin. Other non-specific dark markings exist in some species. Similarly, large portions of the fin can be white, notably the distal portion of the dorsal and ventral lobes, and the posterior margin of the fin. In adults, white areas usually become less obvious and dark areas become dusky or merge with the main fin coloration.

The rapid approach used in this project involved producing minimal treatments of each new species and restricting the number of specimens measured and radiographed from the type series. The aim was to provide names and good diagnoses for species rather than to adopt a full revisionary approach. We attempted to provide a solid description of each species to enable it to be distinguished from related taxa without examining every specimen available in collections. For example, skeletal details were not included and only extreme intraspecific variations were discussed. Ideally, the holotype and at least 5 post-juvenile paratypes were measured in full, and vertebral counts were obtained, optimally for 10 types. In species descriptions, morphometric and meristic values for the holotype are given first, followed in parentheses by the ranges of the paratypes.

Meristics were obtained separately for trunk (monospondylous), precaudal (monospondylous + diplospondylous to origin of the caudal-fin upper lobe) and caudal (centra of the caudal fin) vertebrae. Tooth row counts, which are difficult to obtain from radiographs, were taken directly from specimens by making incisions at the jaw angles to expose the teeth. Type specimens are deposited in ichthyological collections mainly in the Indo–Pacific region. Acronyms for all repositories follow Leviton *et al.* (1985).

DNA barcoding of the *Squalus* specimens involved the amplification and sequencing of an approximately 655 base pair region of the mitochondrial gene cytochrome oxidase 1 (coxI). The premise is that each species will have a unique sequence for that coxI region, or a unique cluster of closely-related sequences (Hebert *et al.* 2003a). Preliminary results from nearly all animal groups showed

Table 1. Definition of the main morphometric characters taken for *Squalus*. Abbreviations and definitions are adapted from Compagno (2001).

Morphometric character	Methodology
TL – Total length	Greatest direct distance between snout tip and caudal-fin apex
PCL – Precaudal length	Direct distance from snout tip to origin of upper caudal lobe
PD2 – Pre-second dorsal length	Direct distance from snout tip to second dorsal-fin origin
PD1 – Pre-first dorsal length	Direct distance from snout tip to first dorsal-fin origin
SVL – Pre-vent length	Direct distance from snout tip to anterior end of cloaca
PP2 – Prepelvic length	Direct distance from snout tip to pelvic-fin origin (use finger to find origin)
PP1 – Prepectoral length	Direct distance from snout tip to exposed base of pectoral fin
HDL – Head length	Direct distance from snout tip to upper edge of the fifth gill slit
PG1 – Prebranchial length	Direct distance from snout tip to upper edge of the first gill slit
PSP – Prespiracular length	Direct distance from snout tip to anterior margin of spiracle
POB – Preorbital length	Direct distance from snout tip to fleshy, anterior margin of orbit
PRN – Prenarial length	Direct distance from snout tip to anterior edge of outer nostril
POR – Preoral length	Direct distance from snout tip to upper jaw (including teeth)
PINL – Pre-inner nostril length	Direct distance from snout tip to inner edge of nostril
INLF – Inner nostril-labial furrow space	Shortest distance between nostrils and upper labial furrow
MOW – Mouth width	Distance between apices of labial pleats (junction of labial furrows and postoral grooves)
ULA – Labial furrow length	Distance from apex of labial pleat to anterior edge of furrow
INW – Internarial space	Shortest distance between the two nostrils
INO – Interorbital space	Distance between soft interorbit in natural state (taken at mid-length of eye)
EYL – Eye length	Length of eye, not including eye socket
EYH – Eye height	Height of eye
SPL – Spiracle length	Maximum width of opening
GS1 – First gill-slit height	Vertical height of first gill slit (not following profile of gill)
GS5 – Fifth gill-slit height	Vertical height of fifth gill slit (not following profile of gill)
IDS – Interdorsal space	Shortest distance between first dorsal-fin insertion and second dorsal-fin origin
DCS – Dorsal-caudal space	Shortest distance between second dorsal-fin insertion and origin of upper caudal lobe
PPS – Pectoral-pelvic space	Direct distance from pectoral-fin insertion to pelvic-fin origin (taken on ventral side)
PCA – Pelvic-caudal space	Direct distance from pelvic-fin insertion to origin of lower caudal lobe (taken on ventral side)
D1L – First dorsal length	Distance from first dorsal-fin origin (use thumbnail to find origin) to apex of free rear tip
D1A – First dorsal anterior margin	Distance from first dorsal-fin origin (use thumbnail to find origin) to point of greatest curvature of apex of fin
D1B – First dorsal base length	Distance from first dorsal-fin origin (use thumbnail to find origin) to first dorsal-fin insertion
D1H – First dorsal height	Greatest vertical height from fin base to apex of fin
D1I – First dorsal inner margin	Distance from first dorsal-fin insertion to apex of free rear tip
D1P – First dorsal posterior margin	Distance from points of greatest curvature of the first dorsal-fin apex and apex of free rear tip
D1ES – First dorsal spine length	Distance from junction of exposed portion of spine and soft part of dorsal fin to spine apex
D1BS – First dorsal spine base width	Width of exposed spine at its junction with soft dorsal fin
D2L – Second dorsal length	Distance from second dorsal-fin origin (use thumbnail to find origin) to apex of free rear tip

Table 1. cont'd.

Morphometric character	Methodology
D2A – Second dorsal anterior margin	Distance from second dorsal-fin origin (use thumbnail to find origin) to point of greatest curvature of apex of fin
D2B – Second dorsal base length	Distance from second dorsal-fin origin (use thumbnail to find origin) to first dorsal-fin insertion
D2H – Second dorsal height	Greatest vertical height from fin base to apex of fin
D2I – Second dorsal inner margin	Distance from second dorsal-fin insertion to apex of free rear tip
D2P – Second dorsal posterior margin	Distance from points of greatest curvature of the second dorsal-fin apex and apex of free rear tip
D2ES – Second dorsal spine length	Distance from junction of exposed portion of spine and soft part of dorsal in to spine apex
D2BS – Second dorsal spine base width	Width of exposed spine at its junction with soft dorsal fin
P1A – Pectoral anterior margin	Distance from pectoral-fin origin to apex of fin (measured from ventral surface)
P1I – Pectoral inner margin	Distance from pectoral-fin insertion to apex of free rear tip (measured from ventral surface)
P1B – Pectoral base length	Distance from pectoral-fin origin to pectoral-fin insertion (measured from ventral surface)
P1P – Pectoral posterior margin	Distance between points of greatest curvature of pectoral-fin apex and free rear tip (measured from ventral surface)
P2L – Pelvic length	Distance from pelvic-fin origin (use finger to find origin) to point of greatest curvature of apex (measured from ventral surface)
P2H – Pelvic height	Greatest width of pelvic fin (measured from ventral surface)
P2I – Pelvic inner margin	Distance from pelvic-fin insertion to apex of free rear tip (measured on ventral surface)
CDM – Dorsal caudal margin	Distance from origin of upper caudal lobe to point of greatest curvature of apex of dorsal caudal lobe
CPV – Preventral caudal margin	Distance from origin of lower caudal lobe to point of greatest curvature of apex of ventral caudal lobe
CPU – Upper postventral caudal margin	Distance from greatest angle of caudal fork to point of greatest curvature of apex of dorsal caudal lobe
CPL – Lower postventral caudal margin	Distance from greatest angle of caudal fork to point of greatest curvature of apex of ventral caudal lobe
CFW – Caudal fork width	Perpendicular distance from greatest angle of caudal fork to dorsal caudal margin
CFL – Caudal fork length	Distance from greatest angle of caudal fork to origin of lower caudal lobe
HANW – Head width at nostrils	Width of head at anterior margin of nostrils (use straight edge through anterior edge of nostrils)
HAMW – Head width at mouth	Width of head at level of anterior margin of mouth
HDW – Head width	Width of head at fifth gill slit
TRW – Trunk width	Width of body at pectoral-fin insertions
ABW – Abdomen width	Width of body at first dorsal-fin insertion
TAW – Tail width	Width of body at pelvic-fin insertions
CPW – Caudal peduncle width	Width of caudal peduncle in front of caudal groove
HDH – Head height	Vertical height of head at fifth gill slit
TRH – Trunk height	Vertical height of body at pectoral-fin insertions
ABH – Abdomen height	Vertical height of body at first dorsal-fin insertion
TAH – Tail height	Vertical height of body at pelvic-fin insertions
CPH – Caudal peduncle height	Vertical height of caudal peduncle in front of caudal groove
CLO – Clasper outer length	Distance between lateral junction of pelvic-fin inner margin to apex of clasper
CLI – Clasper inner length	Distance between connection of the clasper base dorsally with the tail to apex of clasper
CLB – Clasper base width	Width of clasper at pelvic-fin insertion

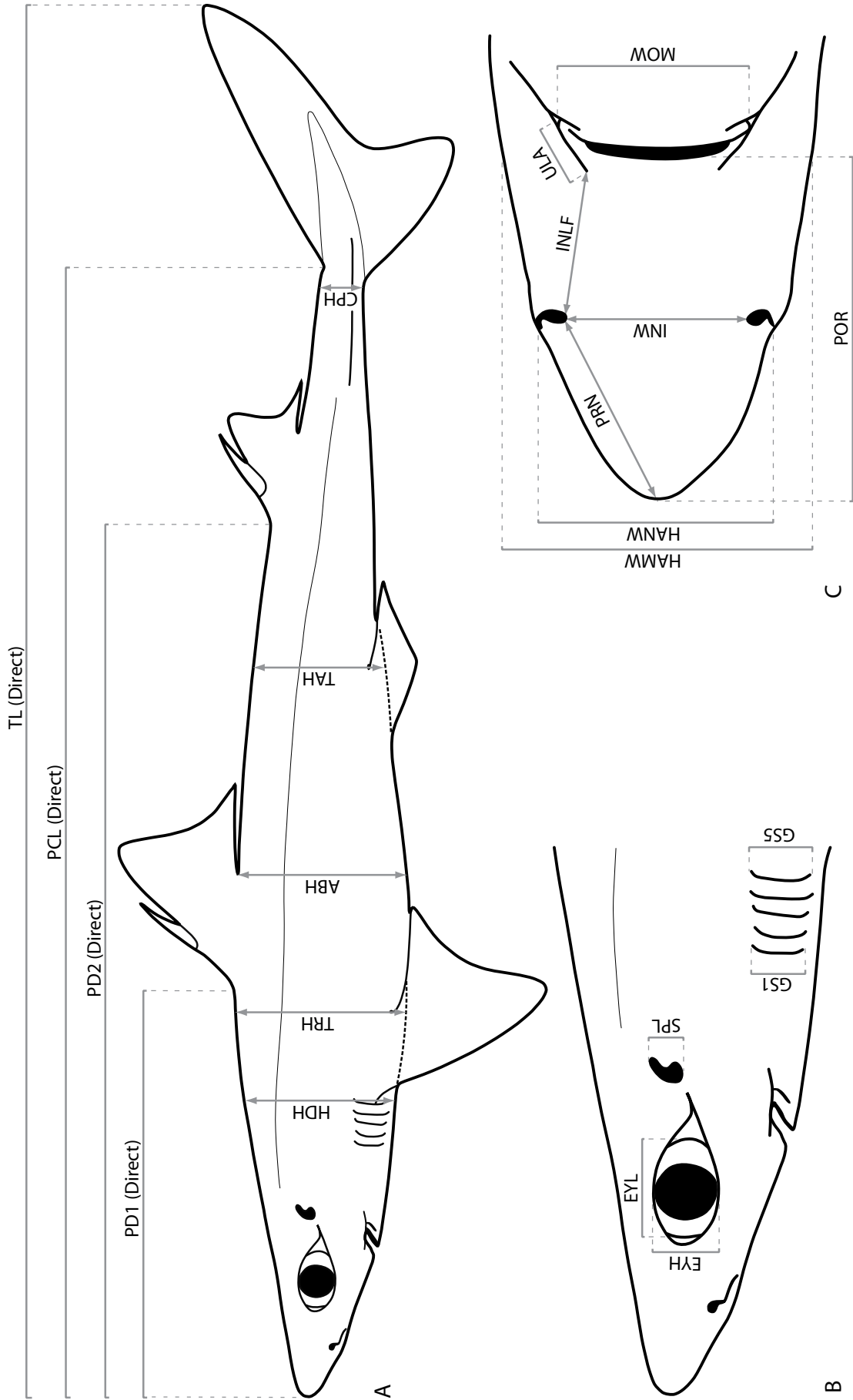


Figure 1. Diagrammatic representation of the morphometric characters used for *Squalus*: A. lateral view; B. lateral head; and C. ventral head. Refer to Table 1 for definitions of abbreviations and explanations of measurements.

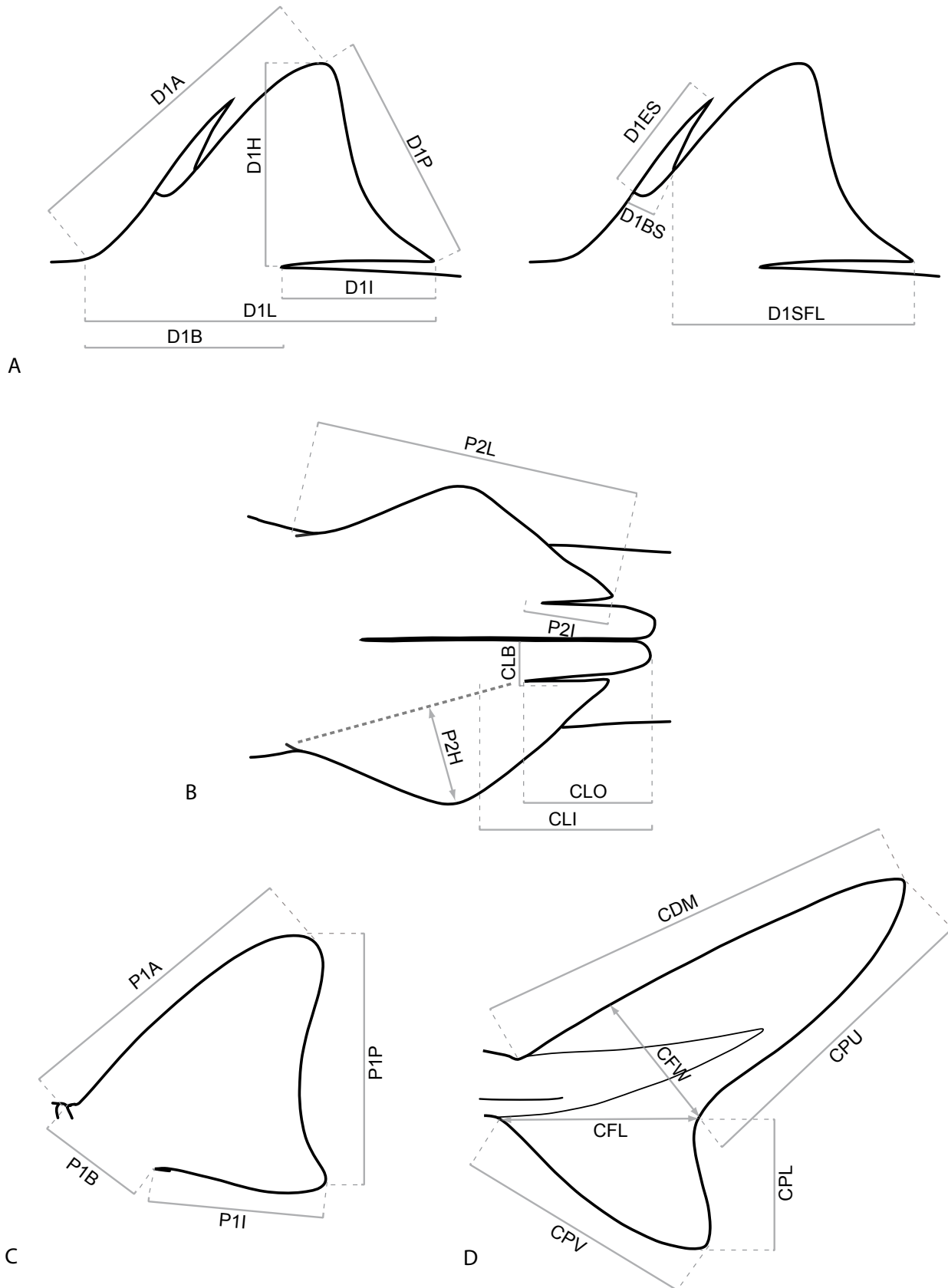


Figure 2. Diagrammatic representation of the morphometric characters used for *Squalus*: A. first dorsal fin (same method used for second dorsal fin); B. pelvic fin and claspers; C. pectoral fin; and D. caudal fin. Refer to Table 1 for definitions of abbreviations and explanations of measurements.

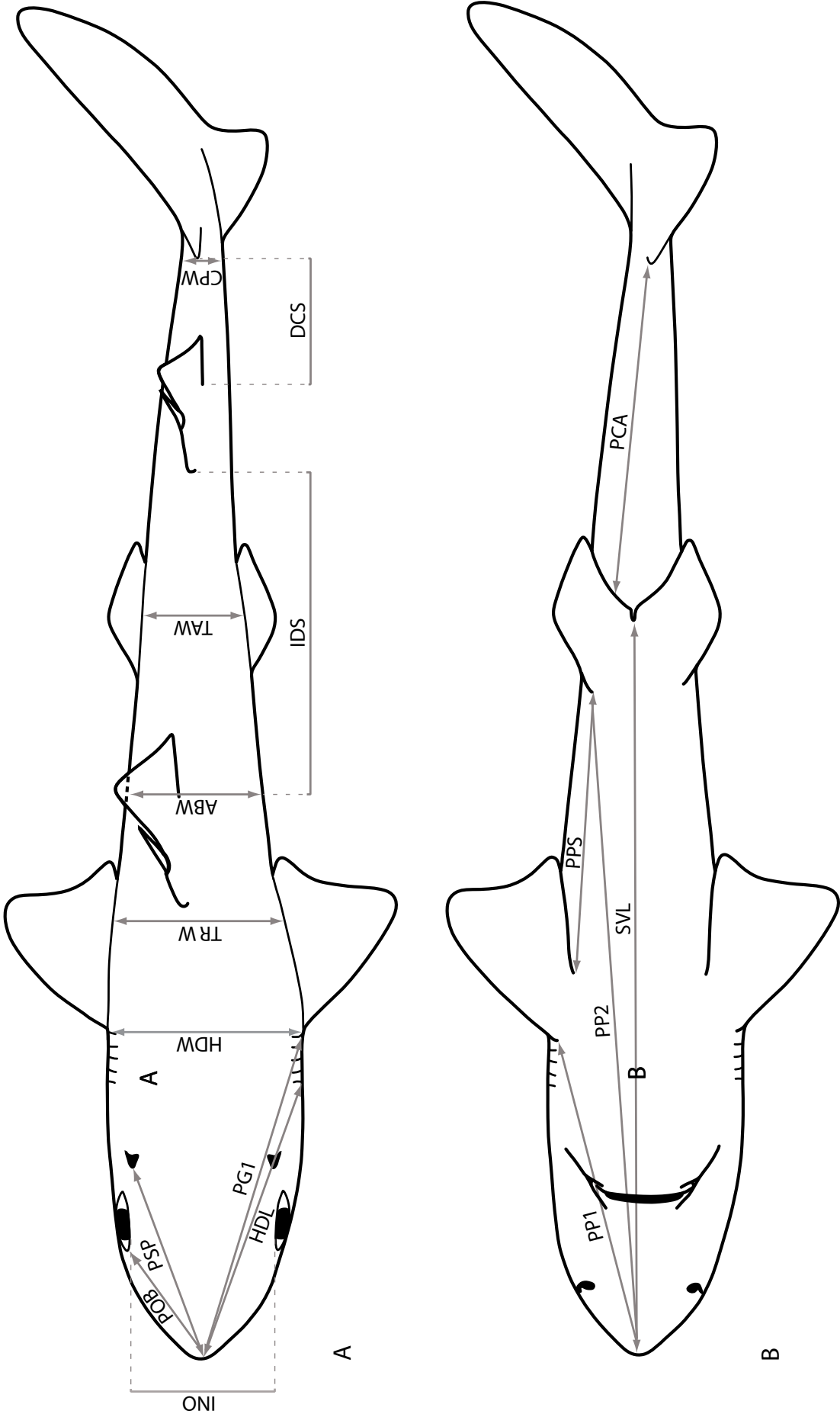


Figure 3. Diagrammatic representation of the morphometric characters used for *Squalus*: A. dorsal; and B. ventral view. Refer to Table 1 for definitions of abbreviations and explanations of measurements.

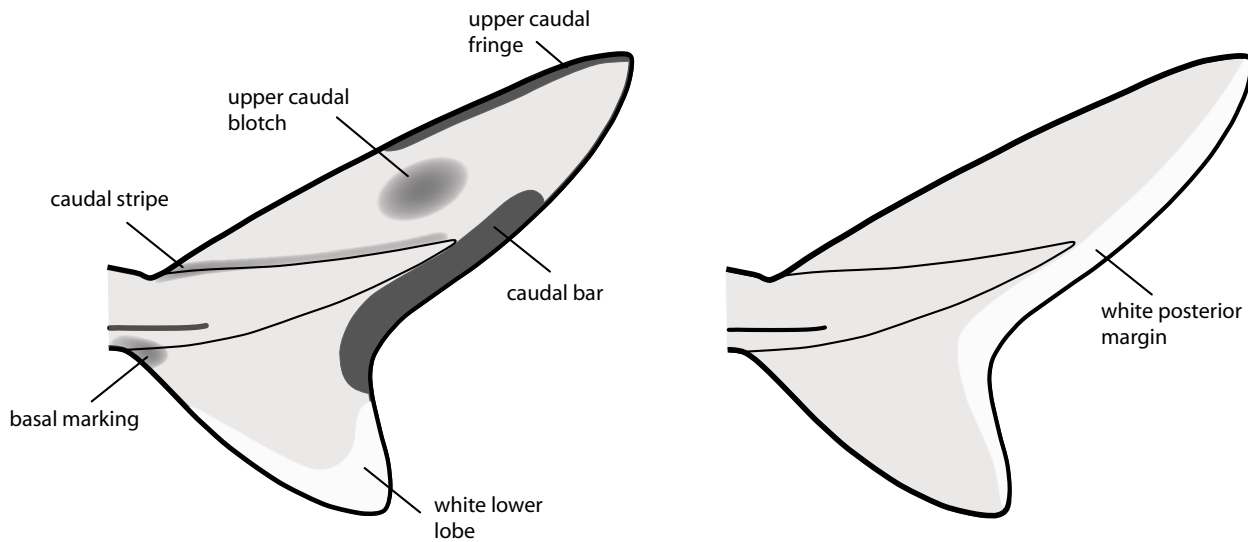


Figure 4. Terminology used for common caudal fin markings observed in *Squalus*.

that the chosen *coxI* gene region is indeed highly species-specific – exceptions include some invertebrate groups such as cnidarians (Hebert *et al.* 2003b). Methods for barcoding *Squalus* follow Ward *et al.* (2005), where the barcoding of about 200 fish species showed that the technique is indeed highly effective at discriminating fish species.

DISCUSSION

Providing more effective support to stakeholders (i.e. conservation managers, industry, scientists, and the public) is one of the major challenges for 21st Century taxonomists. Taxonomic research is often criticised because it is considered to be too slow. Taxonomists have been trained to focus on detail so most would prefer to complete a comprehensive review of a family or genus, rather than provide published names and simple diagnoses of each species. Unfortunately, this philosophy is at odds with the needs of most stakeholders who simply wish to know what species exist, their names, and how to distinguish them. The need for a ‘simple fix’ has increased with the expansion of conservation science and biodiversity management. Also, surveys to fill gaps in our knowledge of the biota on both land and in aquatic environments, have led to the discovery of increasing numbers of unidentifiable taxa, many of them new to science. Molecular approaches, such as the international Barcode of Life project campaign (see below), have led to the discovery of cryptic species and sister species pairs, often confirming suspicions that morphological differences between regional morphs are more likely to be interspecific than population differences. In summary, the delineation of operational taxonomic units (OTU’s) is important but stakeholders require more.

Research for the monograph *Sharks and Rays of*

Australia (Last and Stevens, 1994) led to the discovery of 97 unidentifiable taxa from the region; however less than a third of these have been formally described and named since its publication. Some of these species, such as the undescribed Maugean Skate (*Dipturus* sp. L), are now regarded as endangered and have been placed on national threatened species lists and the *IUCN Red List of Threatened Animals* (IUCN, 2006). The unavailability of names and full descriptions of these taxa have acted as impediments to stakeholders (scientists, fishery and conservation managers) and have arguably, retarded progress in other fields of biological science. Increasing demands on the services of a dwindling taxonomic community means that faster, more efficient approaches are needed for describing and naming taxa. In this series of papers, we have attempted to achieve this outcome by using a minimalist approach but without compromising authenticity and creating ambiguity. Electronic publishing enables a greater use of colour illustrations without serious cost implications. New electronic journals, such as *Zootaxa*, have led the way by providing high quality PDF’s with a rapid post-submission turn-around of manuscripts. In the following papers, the use of adequate descriptions and good diagnoses helped characterise taxa and provided the information needed to distinguish them without over-embellishment. Skeletal information, essential for systematic and revisionary studies, was largely ignored. Similarly, the sizes of morphometric and meristic datasets are kept to a minimum. Using this approach, undescribed taxa were treated relatively quickly. Still, we stress that this approach will never replace the need for full revisionary studies.

We supplemented this approach with DNA barcoding to add a new level of taxonomic rigor. Newly described and the re-described species had unique *coxI* barcodes and these can be linked with full confidence to type material and validated identifications of these taxa. Sequences

for these species have been deposited in the Barcode of Life Database (www.boldsystems.org) and in GenBank (www.ncbi.nlm.nih.gov). Their species-specificity and public availability means that unknown specimens of these taxa can be correctly identified by sequencing the COI region and searching either database for a match. Only a minute quantity of tissue is required, which can be sent to the most convenient molecular laboratory for sequencing. Classical morphological methods and molecular barcoding are complementary approaches that, when used together, have the potential to change the course of taxonomy.

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Part 2 — *Squalus crassispinus* sp. nov., a new spurdog of the ‘megalops-cubensis group’ from the eastern Indian Ocean

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ABSTRACT.— A new species of spurdog, *Squalus crassispinus* sp. nov., from the lower continental shelf and upper continental slope off Western Australia, is described. It belongs to the ‘megalops-cubensis group’, the members of which share a short snout, low dorsal fins, unicuspid denticles, and a white posterior caudal margin. The relationships of this species to other members of the ‘megalops-cubensis group’ are discussed. *Squalus crassispinus* can be distinguished from all other nominal *Squalus* species by a combination of fin coloration, dorsal-fin spine shape, denticle morphology, meristics, and morphometrics of the head, trunk and pectoral fins. Populations of *S. megalops*, a related, sympatric congener that was thought to be widely distributed outside the Australian region, are compared on an intraregional basis. Characters once considered to be intraspecifically variable are found to be conservative within this region suggesting that the species may be more restricted in distribution than first thought. *Squalus megalops* is re-diagnosed based on new material.

Key words. Squaloidea – Squalidae – *Squalus crassispinus* – *Squalus megalops* – new species – Indo–West Pacific.

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INTRODUCTION

Last and Stevens (1994) identified 9 *Squalus* species from Australian waters of which 6 appeared to be formally undescribed. One of these undescribed species belongs to the ‘megalops-cubensis group’, which includes *S. megalops* (Macleay, 1881), the first spurdog described from Australian seas. The group presently contains two valid nominal species, *S. megalops* (northeastern and southeastern Atlantic, southwestern Indian Ocean, western North Pacific, and Australia) and *S. cubensis* Howell Rivero, 1936 (western Atlantic). Two other nominal species, *S. acutipinnis* Regan, 1908 (southwest Indian Ocean) and *S. probatovi* Myagkov and Kondyurin, 1986 (tropical eastern Atlantic), are listed as likely synonyms of *S. megalops* (Eschmeyer, 2006). Members of the group share a short snout, low dorsal fins, unicuspid denticles, and a white posterior caudal-fin margin. In 1991, during an exploratory survey of deepwater off Western Australia, another member of the ‘megalops-cubensis group’ was collected with *S. megalops*. This species is formally described and an updated diagnosis of *S. megalops* is also provided.

METHODS

Methods follow those outlined in Part 1 of this issue (Last

et al., 2007). The holotype (CSIRO H 2547–06) and 6 paratypes (CSIRO CA 4074, CSIRO H 1035–12, CSIRO H 1035–14, CSIRO H 1035–15, WAM P 26223–001 and WAM P 26207–005) of the new species were measured in full (Table 1). In the description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the paratypes. Meristics were taken from radiographs of the 11 type specimens of the new species as well as 37 specimens of *S. megalops*. Populations of *S. megalops* from Queensland (n=3), southeastern Australia (n=6) and Western Australia (n=4), were compared morphometrically (Table 2). Type specimens are deposited in the Australian National Fish Collection, Hobart (CSIRO), and ichthyological collections of the Museum of Comparative Zoology, Boston (MCZ), the Australia Museum, Sydney (AMS) and the Western Australian Museum, Perth (WAM); their registration numbers are prefixed with these acronyms.

Squalus crassispinus sp. nov.

Figs 1–4; Table 1

Squalus sp. D: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 48, 95, figs 18, 8.34, pl. 6; Compagno, Dando and Fowler, 2005, *Sharks of the World*, p 80, figs, pl. 2.

Holotype. CSIRO H 2547–06, female 580 mm TL, west of North West Cape, Western Australia, 21°37' S, 113°59' E, 215 m, 24 Jan 1991.

Paratypes. 10 specimens. CSIRO CA 4074, female 497 mm TL, north of Nickol Bay, Western Australia, 19°11' S, 116°44' E, 194 m; CSIRO H 1035–12, female 565 mm TL, CSIRO H 1035–14, female 563 mm TL, CSIRO H 1035–15, adult male 476 mm TL, north of Dampier Archipelago, Western Australia, 19°08' S, 116°54' E, 196 m; CSIRO H 4649–03, female 400 mm TL, CSIRO H 4649–04, adult male 449 mm TL, north of Nickol Bay, Western Australia, 19°06' S, 117°01' E, 187 m; CSIRO H 4031–86, female 541 mm TL, CSIRO H 4031–87, female 543 mm TL, north of Cape Lambert, Western Australia, 18°57' S, 117°14' E, 248 m; WAM P 26207–005, adult male 457 mm TL, southwest of Rowley Shoals, Western Australia, 18°42' S, 117°40' E, 262 m; WAM P 26223–001, female 489 mm TL, north of Rowley Shoals, Western Australia, 16°32' S, 120°52' E, 210 m.

DIAGNOSIS.— A small species of *Squalus* of the 'megalops-cubensis group' with the following combination of characters: head width at mouth 9.9–11.3% TL; mouth width 2.1–2.4 times horizontal prenarial length; direct pre-second dorsal length 3.7–4.2 times pectoral-fin anterior margin, 2.6–2.8 times dorsal caudal margin; preoral length 2.7–3.0 times horizontal prenarial length, 8.3–9.2% TL; anterior nasal flap strongly bifurcate; first dorsal fin upright to raked; exposed bases of dorsal-fin spines very broad, 1.2–1.5% TL; both dorsal fins with short inner margins, first dorsal-fin height 1.3–1.7 times its inner margin length, second dorsal-fin height 1.1–1.3 times its inner margin length; pectoral-fin anterior margin 1.9–2.2 times its inner margin length; preventral caudal margin 2.4–4.6 times inner margin of pelvic fin; caudal fin pale with poorly demarcated, whitish posterior margin, no caudal bar; flank denticles unicuspid; 39–42 (mainly 40–41) monospondylous centra, 82–86 precaudal centra, 107–111 (mainly 109–110) total centra; adult maximum size at least 58 cm TL.

DESCRIPTION.— Body fusiform, stout (elongate in smallest paratypes), nape very prominently humped; deepest at belly (deepest at first-dorsal spine origin in smallest paratypes), maximum depth 1.03 (0.95–1.21 in paratypes) times width; trunk depth 1.01 (0.86–1.16) times abdomen depth; head short 21.4 (21.0–22.3)% TL; caudal peduncle robust (less so in smallest paratypes), elongate, 27.2 (26.6–28.4)% TL. Head not especially broad, width 1.03 (1.17–1.23) times trunk width, 1.04 (1.09–1.32) times abdomen width, depressed forward of spiracles, becoming subcylindrical towards pectoral-fin origin, length 2.28 (2.06–2.22) in pre-vent length; height 0.84 (0.76–0.93) times width. Snout short, narrowly triangular in lateral view, apex sharply pointed, lateral prenarial margin somewhat angular (less so in some paratypes); bluntly pointed in dorsal view, horizontal length 1.32 (0.94–1.26) times eye length, 0.57 (0.51–

0.66) times interorbital space; horizontal prenarial length 2.70 (2.66–2.94) times in preoral length. Eye broadly oval, size moderate, length 5.66 (4.53–4.89) in head, 1.81 (1.72–2.05) times height; strongly notched posteriorly, weakly connected to anteroventral margin of spiracle. Spiracle moderate, crescentic; broad lobe-like fold on posterior margin; greatest diameter 3.02 (2.80–3.23) in eye length. Gill openings slightly oblique, directed slightly anterodorsally from bottom to top (sometimes upright), first four subequal in size, fifth longest, height of fifth slit 2.5 (2.0–2.5)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.27 (1.11–1.27) in preoral length; upper labial furrows about twice length (or much more) of lower furrows, prominent postoral groove, subequal in length to upper labial furrows (longer in some paratypes), extending posterolaterally from angle of jaws; two series of functional teeth in upper jaw, 3 (2 or 3) series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, slightly oblique; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe narrow, thalate; internarial space 2.21 (2.13–2.27) in preoral length, 2.47 (2.08–2.61) times nostril length. Dermal denticles (based on paratypes CSIRO H 1035–14, CSIRO H 1035–15) on flank very small, unicuspid, not imbricated, crown quadrangular, width subequal to length, with pronounced median ridge, median ridge commencing well anterior of rest of crown, with a mesial furrow developing anteriorly and converging towards posterior tip of crown; cusp pungent, elongate; lateral extensions with a weak ridge, cusps absent; in paratype CSIRO H 1035–12, cusps arrowhead-shaped, broader than in other paratypes, more densely arranged, posterior cusp more obtuse. First dorsal fin relatively low, raked in holotype (paratypes taller, more upright), narrowly rounded apically; anterior margin moderately convex; upper posterior margin almost straight, not vertical, directed slightly anterodorsally from bottom to top (more extreme in some paratypes), moderately concave (almost straight in CSIRO H 4649–04) near free rear tip; free rear tip relatively thick basally, short; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior to free rear tip of pectoral fin; fin-spine origin above pectoral-fin insertion; spine base very broad, exposed anteriorly well below junction of spine and soft portion of fin; soft portion of fin connected distally above mid-point of total spine length; spine tapering rapidly distally, anterior margin almost straight, subequal in length to second dorsal-fin spine, tip almost level with apex of soft portion of fin in undamaged types; pre-first dorsal length 3.73 (3.52–3.78) times in TL, first dorsal-fin length 1.78 (1.62–2.00) times its height, 1.21 (1.07–1.15) times second dorsal-fin length; first dorsal-fin height 1.68 (1.56–1.89) times second dorsal-fin height; exposed first dorsal spine length (0.56–0.78, holotype damaged) times height of fin. Second dorsal fin of moderate size, strongly raked; anterior margin moderately convex, apex narrowly angular, posterior



Figure 1. Lateral view of *Squalus crassispinus* sp. nov. holotype (CSIRO H 2547–06, female 580 mm TL).



Figure 2. Ventral view of the head of *Squalus crassispinus* sp. nov. holotype (CSIRO H 2547–06, female 580 mm TL).

margin deeply concave, maximum concavity slightly distal to mid-point of margin (variable); upper portion directed slightly dorsoposteriorly strongly from bottom to top; free rear tip thick basally, moderately elongate, inner margin length 0.93 (0.77–0.90) times fin height; second dorsal-fin length 2.49 (2.60–2.85) times its height; spine length 1.08 (0.96–1.11) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, not exposed at level of junction with spine and fin; interdorsal space 0.94 (0.91–0.96) in length from snout tip to pectoral-fin origin, 1.16 (1.14–1.22) in pre-first dorsal length; second dorsal-fin spine with extremely broad base, subequal to width of exposed base of first dorsal-fin spine; spine slender, sharply pointed distally, tapering very rapidly just above

point of exposure, tip level with apex of soft portion of fin (taller than fin in some paratypes); no obvious interdorsal ridge or groove. Pectoral fin moderate, anterior margin moderately convex; inner margin moderately convex, length 7.0 (6.9–7.8)% TL; apex narrowly rounded (broadly rounded in CSIRO H 1035–12), lobe-like but not falcate; posterior margin moderately concave, free rear tip bluntly angular; base very short, 2.45 (2.38–2.78) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip angular, obtuse. Caudal peduncle long, tapering evenly to caudal fin; subcircular in cross-section anteriorly, broadly semicircular posteriorly, ventral groove well developed with weak median ridge; lateral

Table 1. Proportional dimensions as percentages of total length for the holotype (CSIRO H 2547–06) and ranges for the 6 paratypes of *Squalus crassispinus* sp. nov. and two paratypes of *Squalus cubensis*.

	<i>S. crassispinus</i> sp. nov.		<i>S. cubensis</i>		
	Holotype	Paratypes		MCZ	MCZ
		Min.	Max.	1462-S	1461-S
TL – Total length	580	457	565	282	683
PCL – Precaudal length	78.6	76.1	78.9	76.2	77.9
PD2 – Pre-second dorsal length	59.9	57.8	60.2	59.2	63.4
PD1 – Pre-first dorsal length	26.8	26.5	28.4	27.6	28.2
SVL – Pre-vent length	48.8	45.5	47.5	–	49.0
PP2 – Prepelvic length	46.7	44.0	46.0	–	49.8
PP1 – Prepectoral length	21.7	21.6	22.5	22.2	21.8
HDL – Head length	21.4	21.0	22.3	21.5	21.9
PG1 – Prebranchial length	17.6	17.8	18.6	18.1	18.4
PSP – Prespiracular length	11.2	11.7	12.4	13.1	12.6
POB – Preorbital length	6.9	6.9	7.3	7.2	7.6
PRN – Prenarial length	4.3	4.4	4.7	4.8	4.6
POR – Preoral length	8.6	8.3	9.2	10.8	9.6
MOW – Mouth width	6.8	6.9	7.8	7.5	6.7
ULA – Labial furrow length	1.8	1.8	2.2	2.2	2.1
INW – Internarial space	3.9	3.9	4.3	3.7	4.5
INO – Interorbital space	8.8	8.6	8.8	7.9	8.3
EYL – Eye length	3.8	4.5	4.9	5.5	–
EYH – Eye height	2.1	2.3	2.8	1.6	1.6
SPL – Spiracle length	1.2	1.4	1.7	1.7	1.9
GS1 – First gill-slit height	2.0	1.9	2.3	1.5	1.8
GS5 – Fifth gill-slit height	2.5	2.0	2.5	1.5	2.1
IDS – Interdorsal space	23.2	23.1	24.2	22.5	25.9
DCS – Dorsal-caudal space	11.0	10.1	11.4	11.5	8.5
PPS – Pectoral-pelvic space	20.4	17.5	20.7	18.0	–
PCA – Pelvic-caudal space	27.2	26.6	28.4	22.4	23.8
D1L – First dorsal length	14.9	14.3	15.0	14.9	15.1
D1A – First dorsal anterior margin	13.6	12.3	13.3	12.7	12.3
D1B – First dorsal base length	9.9	8.8	9.8	8.6	9.6
D1H – First dorsal height	8.4	7.2	8.9	6.4	7.6
D1I – First dorsal inner margin	5.0	5.0	5.5	6.1	5.9
D1P – First dorsal posterior margin	8.4	8.5	10.7	–	9.5
D1ES – First dorsal spine length	–	4.5	5.9	2.3	–
D1BS – First dorsal spine base width	1.3	1.2	1.3	0.7	1.1
D2L – Second dorsal length	12.3	12.5	13.7	12.1	11.3
D2A – Second dorsal anterior margin	11.4	11.7	13.0	11.3	10.5
D2B – Second dorsal base length	8.4	8.9	9.1	7.0	6.5
D2H – Second dorsal height	5.0	4.5	5.3	3.8	3.8
D2I – Second dorsal inner margin	4.6	3.5	4.3	5.5	5.4
D2P – Second dorsal posterior margin	5.8	4.8	5.4	3.9	3.9
D2ES – Second dorsal spine length	5.4	4.5	5.0	4.6	6.5
D2BS – Second dorsal spine base width	1.5	1.3	1.4	0.9	0.9

Table 1. cont'd.

	<i>S. crassispinus</i> sp. nov.			<i>S. cubensis</i>	
	Holotype	Paratypes		MCZ	MCZ
		Min.	Max.	1462-S	1461-S
P1A – Pectoral anterior margin	15.3	14.2	15.7	14.0	15.7
P1I – Pectoral inner margin	7.0	6.9	7.8	9.0	11.1
P1B – Pectoral base length	6.3	5.4	6.2	4.6	4.6
P1P – Pectoral posterior margin	11.2	9.9	11.5	8.1	11.2
P2L – Pelvic length	9.3	9.3	10.6	11.5	10.8
P2H – Pelvic height	5.5	4.5	5.5	3.6	5.1
P2I – Pelvic inner margin	4.4	2.5	4.8	3.2	6.1
CDM – Dorsal caudal margin	21.2	20.9	22.3	23.0	22.1
CPV – Preventral caudal margin	11.7	11.6	12.6	12.5	11.7
CPU – Upper postventral caudal margin	16.9	15.3	16.9	15.4	13.9
CPL – Lower postventral caudal margin	5.9	4.8	6.2	4.2	5.8
CFW – Caudal fork width	6.8	6.8	7.4	6.4	6.3
CFL – Caudal fork length	8.7	9.0	10.0	11.0	9.4
HANW – Head width at nostrils	6.6	6.7	7.2	7.5	6.5
HAMW – Head width at mouth	10.5	9.9	11.3	11.5	11.3
HDW – Head width	13.1	11.8	13.3	11.3	13.3
TRW – Trunk width	12.8	9.1	11.3	–	–
ABW – Abdomen width	12.6	8.3	11.8	–	–
TAW – Tail width	8.4	6.7	7.8	–	6.8
CPW – Caudal peduncle width	3.3	2.1	3.0	2.6	2.7
HDH – Head height	11.0	9.8	11.7	8.9	8.8
TRH – Trunk height	13.1	10.1	12.9	–	–
ABH – Abdomen height	13.0	8.9	11.7	–	–
TAH – Tail height	8.4	7.3	8.2	4.8	7.0
CPH – Caudal peduncle height	2.5	2.4	2.8	2.6	2.5
CLO – Clasper outer length	–	3.7	4.1	–	–
CLI – Clasper inner length	–	6.9	7.1	–	–
CLB – Clasper base width	–	1.2	1.6	–	–

keels well developed, originating posterior to insertion of second dorsal fin, terminating much less than an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.75 (0.62–0.75) in pectoral–pelvic space, 0.80 (0.77–0.83) in prepectoral length; dorsal–caudal space 2.10 (2.13–2.34) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit weak. Caudal fin relatively long, upper lobe not especially broad, upper postventral margin undulate to moderately convex; lower lobe angular (narrowly rounded in some); dorsal caudal margin 1.01 (0.94–1.05) in head length; length of lower caudal lobe 1.81 (1.72–1.88) in upper lobe length. Vertebral centra 110 (107–111 in 10 paratypes, mainly 109–110), monospondylous 41 (39–42, mainly 40–41), precaudal 85 (82–86) and caudal 25 (24–27, mainly 25–26). Teeth in upper jaw (of paratype, CSIRO CA 4074) 14+13=27, lower jaw 12+11=23.

COLOUR.— When fresh: uniform pale grey dorsally; much paler, white on ventral surface; light and dark areas poorly differentiated, pale areas forward of eye and between eye and spiracle, prominent dark area below spiracle abutting hind margin of eye and extending just forward of anteroventral margin of eye; fins relatively pale. Dorsal-fin spines dusky, darker grey over basal membrane; basal half of soft portion whitish, most pronounced adjacent to fin spine; distal half pale grey with narrow, black apical margin; first dorsal-fin posterior margin with equal, weakly demarcated pale basal and darker distal portions; second dorsal-fin posterior margin pale, black apical streak confined to outer anterior margin near tip of fin spine. Caudal fin pale, posterior margin and ventral lobe white; narrow dusky fringe along dorsal caudal margin. Pectoral fin dusky on dorsal surface, anterior margin darker greyish, posterior margin white;

ventral surface uniformly pale. Pelvic fin uniformly pale dorsally and ventrally. In preservative: coloration similar to above except pale and darker areas on dorsal fins less contrasted, except for basal part of soft portion of fins; dark streak stripe extending obliquely from caudal pit along dorsal fleshy portion of caudal fin; dark blotch present on lower lobe of caudal fin about a spiracle width behind fin insertion. In preservative (based on female paratype CSIRO H 4649–03): similar to holotype, border between pale and dark tonal areas extending from snout, near ventral margin of eye, above gill slits, then directed towards ventral margin, united near origin of pectoral fin;



Figure 3. Cusps of the flank denticles of *Squalus crassispinus* sp. nov. paratype (CSIRO H 1035–12, female 565 mm TL). Field of view width 1.0 mm.

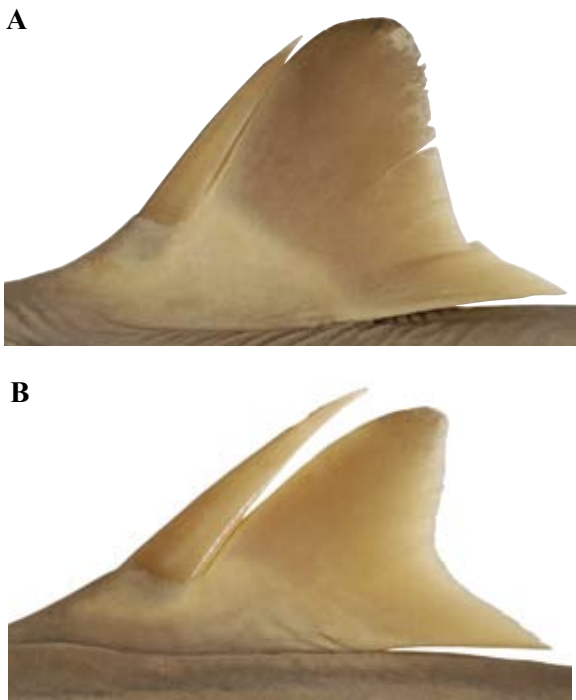


Figure 4. Lateral view of the dorsal fins of *Squalus crassispinus* sp. nov. paratype (CSIRO H 1035–12, female 565 mm TL) – A. first dorsal fin, B. second dorsal fin.

dorsal and caudal-fin coloration similar, distinct stripe extending above fleshy portion of caudal fin; anterior margin of upper caudal-fin lobe black, lobe with a median central blotch; lower lobe of caudal fin mostly uniformly pale, evidence of a darker basal marking.

SIZE.— Females attain at least 580 mm TL; males probably smaller, 3 adult male paratypes 449–476 mm TL.

DISTRIBUTION.— Endemic to the lower continental shelf and upper continental slope off northwestern Australia. Known from North West Cape (ca. 21°S, 114°E) to north of Rowley Shoals (ca. 16°30' S, 121° E) in 187–262 m depth, but probably occurs more widely in the eastern Indian Ocean.

ETYMOLOGY.— The epithet *crassispinus*, which is a combination of the Latin *crassus* (meaning fat or stout) and *spinus* (thorn), refers to the unusually stout dorsal-fin spines.

VERNACULAR.— Fatspine Spurdog.

REMARKS.— *Squalus crassispinus* is sympatric with its closest regional relative, *S. megalops*, off Western Australia. Both species are small with a short snout, low dorsal fins, unicuspid denticles, and the posterior margin of their caudal fins are mostly white. However, they differ mainly in the relative size and shape of the dorsal fins and their associated spines, and their pectoral fin shapes. *Squalus crassispinus* has a more upright first dorsal fin, with very robust fin spines (exposed base of first dorsal-fin spine 1.2–1.3 vs. 0.6–0.8% TL in *S. megalops*; exposed base of second dorsal-fin spine 1.3–1.5 vs. 0.7–0.9% TL), taller fins with short inner margins (first dorsal-fin height 1.32–1.70 vs. 1.00–1.33 times its inner margin length, second dorsal-fin height 1.08–1.30 vs. 0.71–1.04 times its inner margin length), and pectoral-fin anterior margin 1.92–2.19 (vs. 1.41–1.88) times its inner margin length. It also varies from *S. megalops* in the mouth width 2.12–2.36 (vs. 2.58–3.40) times horizontal prenarial length; direct pre-second dorsal length 3.67–4.21 (vs. 4.06–4.97) times pectoral-fin anterior margin, 2.59–2.84 (vs. 2.84–3.24) times dorsal caudal margin; preoral length 2.66–2.94 (vs. 2.93–3.84) times horizontal prenarial length, 8.3–9.2 (vs. 9.3–9.9)% TL; preventral caudal margin 2.44–4.55 (vs. 1.56–2.53) times inner margin of pelvic fin. *Squalus crassispinus* also has slightly more vertebrae: 39–42 (mainly 40–41) vs. 37–40 (mainly 39–40) monospondylous centra; 82–86 vs. 78–84 precaudal centra; and 107–111 (mainly 109–110) vs. 102–110 (mainly 105–106) total centra. The coloration of both species is similar (rather pale dorsally and ventrally) although some southern Australian species are much darker dorsally than ventrally. The posterior margin of the caudal fin in *S. crassispinus* is pale, but unlike *S. megalops*, it is not sharply demarcated from the rest of the fin, nor does it have a dusky bar through the ventral lobe.

Squalus megalops (Macleay, 1881)

Figs 5–9, Table 2

Acanthias megalops Macleay, 1881. *Proc. Linn. Soc. NSW*, 6(2): 367 [1882]. Holotype AMS I 16255–001, Port Jackson, New South Wales, Australia.

Material examined. CSIRO H 1310–03, adult male 342 mm TL, south of Saumarez Reef, Queensland, 22°35' S, 153°40' E, 319 m; CSIRO H 1345–01, female 331 mm TL, CSIRO H 1345–02, adult male 386 mm TL, southeast of Swain Reef, Queensland, 22°53' S, 152°59' E, 325 m; CSIRO H 2688–03, adult male 400 mm TL, CSIRO H 2688–04, female 375 mm TL, CSIRO H 2688–05, immature male 312 mm TL, east of Coffs Harbour, New South Wales, 30°24' S, 153°23' E, 148 m; CSIRO C 3931, female 496 mm TL, CSIRO C 3932, female 471 mm TL, east of Laurieton, New South Wales, ca. 31°40' S, 152°52' E; AMS I 16255–001 (holotype), female 565 mm TL, Port Jackson, New South Wales,

ca. 33°50' S, 151°15' E; CSIRO H 3762–01, female 511 mm TL, south of Lakes Entrance, Victoria, 38°30' S, 148°25' E, 220 m; CSIRO H 624–02, adult male 417 mm TL, southeast of Eddystone Point, Tasmania, 41°04' S, 148°24' E, 80 m; CSIRO H 6449–01, immature male 245 mm TL, off Trial Harbour, Tasmania, ca. 42° S, 145° E; CSIRO H 1264–15, female 547 mm TL, CSIRO H 1264–16, female 520 mm TL, CSIRO H 1264–17, female 529 mm TL, north of Maria Island, Tasmania, 42°33' S, 148°15' E, 82 m; CSIRO T 1515, female 474 mm TL, CSIRO T 1516, female 442 mm TL, southeast of Maria Island, Tasmania, 42°49' S, 148°19' E, 118 m; CSIRO H 1403–01, female 494 mm TL, southeast Tasmania, 110 m; CSIRO H 2225–01, adult male 450 mm TL, CSIRO H 6482–01, adult male 415 mm TL, CSIRO H 6482–02, adult male 429 mm TL, Storm Bay, Tasmania, ca. 43° S, 147°30' E; CSIRO H 5737–02, female 482 mm TL, CSIRO H 5737–03, adolescent male 405 mm TL, west of Port Davey, Tasmania, 43°20' S, 145°35' E, 155 m; CSIRO CA 3287, female 537 mm TL, southeast of Point Culver, Great Australian Bight, Western Australia,

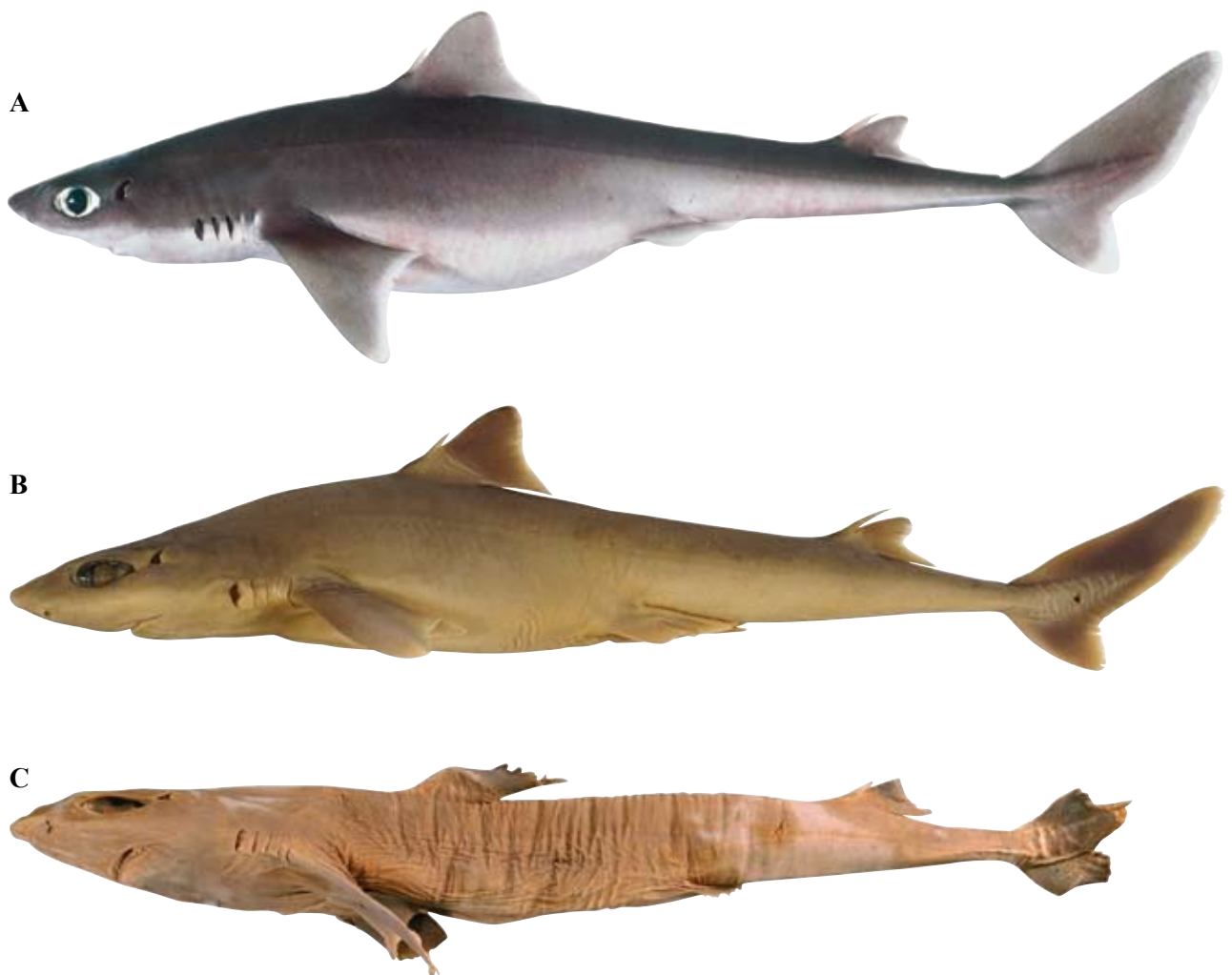


Figure 5. Lateral view of: A. *Squalus megalops* from Victoria (CSIRO H 3762–01, female 511 mm TL); B. *S. megalops* from Queensland (CSIRO H 1310–03, adult male 342 mm TL); C. *Squalus megalops* holotype (AMS I 16255–001, female 565 mm TL).

33°47' S, 125°24' E, 110 m; CSIRO H 2362–01, adult male 437 mm TL, CSIRO H 2365–01, female 507 mm TL, northwest of Cape Naturalist, Western Australia, 33°20' S, 114°30' E, 435 m; WAM P 27739–001 (1 of 2), adult female 540 mm TL, Western Australia, 32°00' S, 115°30' E, 128 m; CSIRO H 2605–08, female 542 mm TL, CSIRO H 2605–09, adult male 462 mm TL, northwest of Rottnest Island, Western Australia, 31°43' S, 114°58' E, 485 m; CSIRO H 2599–05, female 308 mm TL, west of Green Head, Western Australia, 29°58' S, 114°26' E, 490 m; CSIRO H 2270–03, immature male 292 mm TL, CSIRO H 2270–04, female 357 mm TL, southwest of Geraldton, Western Australia, 29°14' S, 113°52' E, 556 m; CSIRO H 6368–01, southwest of Shark Bay, Western Australia, 27°08' S, 112°45' E, 414 m; CSIRO H 2587–02, immature male 274 mm TL, southwest of Shark Bay, Western Australia, 27°06' S, 112°44' E, 370 m; CSIRO H 822–17, female 258 mm TL, CSIRO H 822–18, female 200 mm TL, southwest of Shark Bay, Western Australia, 27°03' S, 112°40' E, 402 m; CSIRO H 2575–19, female 345 mm TL, west of Freycinet Estuary, Western Australia, 26°42' S, 112°33' E, 456 m; CSIRO H 2567–09, adult male 415 mm TL, west of Dorre Island, Western Australia, 25°09' S, 112°09' E, 312 m; CSIRO H 2565–02, immature male 319 mm TL, CSIRO H 2565–11, immature male 343 mm TL, west of Bernier Island, Western Australia, 24°51' S, 112°06' E, 468 m.

DIAGNOSIS.— A small species of *Squalus* of the 'megalops-cubensis group' with the following combination of characters: mouth width 2.6–3.4 times horizontal prenarial length; direct pre-second dorsal length 4.1–5.0 times pectoral-fin anterior margin, 2.8–3.2 times dorsal caudal margin; preoral length 2.9–3.8 times horizontal prenarial length; anterior nasal flap strongly bifurcate; first dorsal fin raked; exposed bases of dorsal-fin spines narrow, 0.6–0.9% TL; both dorsal fins short with long inner margins, first dorsal-fin height 1.0–1.3 times its inner margin length, second dorsal-fin height 0.7–1.0 times its inner margin length; pectoral-fin anterior margin 1.4–1.9 times its inner margin length; preventral



Figure 6. Cusps of the flank denticles of *Squalus megalops* from NSW (CSIRO C 3931, female 496 mm TL). Field of view width 0.7 mm.

caudal margin 1.6–2.5 times inner margin of pelvic fin; caudal fin dusky with broad, sharply demarcated, whitish posterior margin, no caudal bar; flank denticles unicuspid; 37–40 (mainly 39–40) monospondylous centra, 78–84 precaudal centra, 102–110 (mainly 105–106) total centra; adult maximum size at least 57 cm TL.

REMARKS.— *Squalus megalops* appears to be widespread in Australian waters, with records from both temperate and tropical seas. It has been confirmed from east of the Whitsunday Islands in Queensland (ca. 20° S, 151° E) to the North West Shelf off Western Australia (ca. 19° S, 117° E), including off Tasmania (ca. 43° S) where it comes very close to the coast in only a few metres depth. In the northern part of its Australian range it occurs in greater depths, to at least 580 m. The

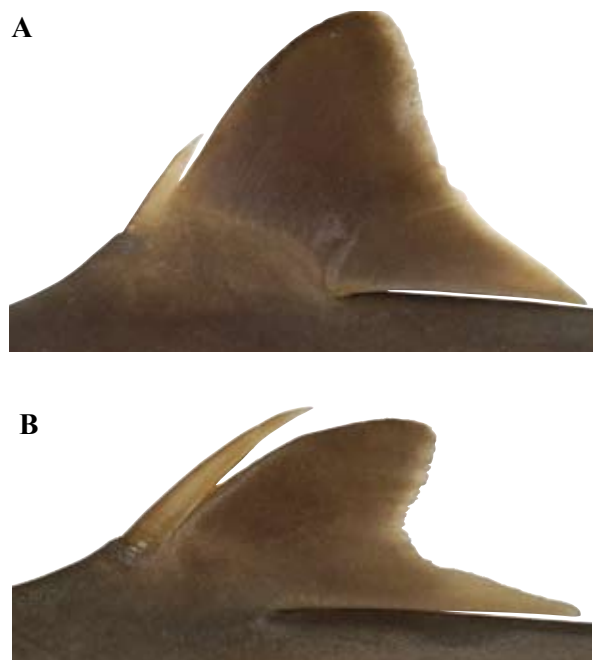


Figure 7. Lateral view of the dorsal fins of *Squalus megalops* from Victoria (CSIRO H 3762–01, female 511 mm TL) – A. first dorsal fin, B. second dorsal fin.



Figure 8. Juvenile coloration of the caudal fin of *Squalus megalops* from WA (CSIRO H 6368–01, female 210 mm TL).

Table 2. Proportional dimensions as percentages of total length for Australian specimens of *Squalus megalops* from southeastern Australia, Western Australia and Queensland.

	southeastern Australia (n = 6)			Queensland (n = 3)			Western Australia (n = 4)		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
TL – Total length	457	373	527	350	328	384	462	414	541
PCL – Precaudal length	77.7	76.1	79.3	78.5	77.8	78.9	78.4	77.7	79.2
PD2 – Pre-second dorsal length	61.6	60.6	62.3	61.2	60.5	62.4	61.4	60.2	62.1
PD1 – Pre-first dorsal length	30.2	29.1	31.6	30.6	29.9	31.6	29.6	29.1	30.2
SVL – Pre-vent length	48.5	47.6	50.1	46.5	46.1	47.2	47.9	45.9	50.4
PP2 – Prepelvic length	47.4	46.4	49.9	45.0	44.8	45.4	46.9	45.5	49.1
PP1 – Prepectoral length	21.5	20.4	23.2	22.6	22.2	22.9	21.9	20.9	23.0
HDL – Head length	21.9	21.0	23.7	22.8	22.6	23.0	22.0	21.4	23.2
PG1 – Prebranchial length	18.5	17.7	19.8	18.9	18.6	19.2	18.3	17.8	19.1
PSP – Prespiracular length	12.5	11.5	13.5	12.9	12.8	13.0	12.3	12.1	12.7
POB – Preorbital length	7.0	6.4	7.5	7.2	7.0	7.4	7.0	6.4	7.4
PRN – Prenarial length	3.9	3.7	4.1	4.3	4.2	4.4	4.2	3.9	4.4
POR – Preoral length	9.1	8.6	9.9	9.7	9.3	9.9	9.2	8.9	9.7
MOW – Mouth width	8.1	7.8	8.6	8.3	8.0	8.5	8.2	7.8	8.6
ULA – Labial furrow length	2.3	2.1	2.4	2.4	2.3	2.5	2.4	2.2	2.7
INW – Internarial space	4.5	4.3	4.7	4.7	4.6	4.9	4.5	4.2	4.8
INO – Interorbital space	8.8	8.4	9.8	9.1	8.8	9.3	8.4	7.6	9.0
EYL – Eye length	4.8	4.4	5.4	5.0	4.9	5.0	4.8	4.3	5.3
EYH – Eye height	2.2	1.9	2.6	2.3	2.1	2.5	2.5	2.3	2.9
SPL – Spiracle length	1.4	1.0	1.7	1.4	1.2	1.5	1.6	1.5	1.7
GS1 – First gill-slit height	2.3	2.0	2.4	1.9	1.8	1.9	2.2	1.9	2.4
GS5 – Fifth gill-slit height	2.4	2.1	2.5	2.5	2.3	2.6	2.2	1.8	2.4
IDS – Interdorsal space	24.8	24.0	25.3	24.6	23.2	25.8	25.3	23.7	26.0
DCS – Dorsal-caudal space	10.4	9.5	10.9	12.2	11.5	12.7	10.7	9.9	12.0
PPS – Pectoral-pelvic space	22.3	20.9	26.1	19.1	18.0	20.3	22.6	20.5	24.6
PCA – Pelvic-caudal space	25.6	24.5	27.0	29.0	28.7	29.4	26.9	25.7	27.8
D1L – First dorsal length	14.4	13.8	15.1	13.3	12.7	13.7	14.0	13.3	14.9
D1A – First dorsal anterior margin	11.5	11.1	12.4	11.1	10.3	12.2	11.5	10.8	12.2
D1B – First dorsal base length	8.2	7.9	8.9	7.6	7.2	8.0	8.3	7.7	8.9
D1H – First dorsal height	7.0	6.1	7.4	6.4	6.2	6.6	7.2	7.0	7.5
D1I – First dorsal inner margin	6.3	6.1	6.6	5.7	5.7	5.7	5.9	5.4	6.3
D1P – First dorsal posterior margin	8.3	6.6	9.0	7.9	7.6	8.1	7.9	7.5	8.1
D1ES – First dorsal spine length	3.0	2.4	3.3	3.0	2.9	3.2	3.3	3.0	3.4
D1BS – First dorsal spine base width	0.8	0.7	0.8	0.7	0.6	0.7	0.7	0.6	0.8
D2L – Second dorsal length	12.0	11.0	12.7	12.1	11.6	12.8	12.2	11.8	12.8
D2A – Second dorsal anterior margin	10.1	9.4	10.6	9.8	9.6	10.3	10.5	10.1	11.0
D2B – Second dorsal base length	7.1	6.4	7.5	7.2	6.9	7.6	7.5	7.1	8.2
D2H – Second dorsal height	4.0	3.6	4.6	3.7	3.2	4.0	3.9	3.7	4.3
D2I – Second dorsal inner margin	4.9	4.5	5.3	4.9	4.5	5.1	4.9	4.7	5.0
D2P – Second dorsal posterior margin	4.5	3.7	5.3	4.5	4.2	4.9	4.1	3.9	4.4
D2ES – Second dorsal spine length	4.3	3.6	5.0	4.6	4.0	5.0	4.5	4.2	4.6
D2BS – Second dorsal spine base width	0.8	0.8	0.9	0.8	0.7	0.8	0.8	0.8	0.9

Table 1. cont'd

	southeastern Australia (n = 6)			Queensland (n = 3)			Western Australia (n = 4)		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
P1A – Pectoral anterior margin	14.3	13.6	14.9	12.5	12.3	12.6	14.3	13.7	15.1
P1I – Pectoral inner margin	8.2	7.4	9.2	8.4	7.7	8.8	9.0	8.4	9.7
P1B – Pectoral base length	5.3	4.4	5.7	5.3	4.9	5.8	4.9	4.4	5.3
P1P – Pectoral posterior margin	11.6	10.8	12.7	10.4	9.6	10.9	11.2	10.3	12.3
P2L – Pelvic length	10.5	9.9	11.5	10.6	9.9	11.2	10.4	9.9	10.8
P2H – Pelvic height	4.8	4.3	5.2	4.7	4.5	5.1	4.9	4.7	5.2
P2I – Pelvic inner margin	5.5	4.2	6.8	5.8	5.1	6.8	5.9	4.8	6.6
CDM – Dorsal caudal margin	20.9	20.0	21.4	20.1	19.3	20.9	20.6	20.2	21.1
CPV – Preventral caudal margin	11.0	10.5	11.3	10.6	10.4	10.7	10.9	10.7	11.0
CPU – Upper postventral caudal margin	15.9	15.0	16.6	14.6	14.1	15.3	15.2	14.5	15.9
CPL – Lower postventral caudal margin	4.3	4.0	4.6	3.6	3.4	3.7	4.6	3.8	5.6
CFW – Caudal fork width	7.1	6.6	7.5	7.0	6.9	7.1	7.0	6.6	7.3
CFL – Caudal fork length	9.5	8.9	10.2	9.5	9.3	9.8	9.4	9.2	9.6
HANW – Head width at nostrils	6.7	6.3	7.6	6.9	6.7	7.2	6.7	6.3	7.1
HAMW – Head width at mouth	11.6	11.1	12.8	12.5	12.3	12.7	11.6	10.9	12.6
HDW – Head width	13.8	13.4	14.3	13.0	12.8	13.2	13.7	13.0	14.7
TRW – Trunk width	12.1	11.2	13.2	10.8	10.3	11.7	12.2	11.3	14.5
ABW – Abdomen width	10.9	10.1	12.2	10.0	9.1	11.0	10.8	10.0	11.5
TAW – Tail width	6.8	6.4	7.2	7.2	6.9	7.4	7.0	6.4	7.6
CPW – Caudal peduncle width	3.0	2.4	3.6	3.0	2.9	3.1	3.0	2.8	3.3
HDH – Head height	10.5	9.2	11.5	10.6	10.1	11.4	10.2	9.3	10.9
TRH – Trunk height	11.3	9.5	13.4	11.0	10.4	12.0	11.8	10.5	13.1
ABH – Abdomen height	11.3	9.1	14.4	11.7	10.4	13.4	11.5	9.5	13.3
TAH – Tail height	7.1	6.0	7.6	7.3	7.1	7.6	7.2	6.3	7.7
CPH – Caudal peduncle height	2.4	2.3	2.5	2.2	2.2	2.3	2.4	2.2	2.5
CLO – Clasper outer length	3.9	3.9	3.9	3.4	2.6	4.1	2.8	3.6	3.9
CLI – Clasper inner length	9.6	9.6	9.6	9.6	9.2	10.0	7.4	9.6	10.0
CLB – Clasper base width	1.8	1.8	1.8	1.6	1.5	1.6	1.1	1.4	1.6

type was collected from Port Jackson, New South Wales, but similar forms around the world have been identified as this species (Compagno *et al.*, 2005). In Australian seas, its closest relative is *S. crassispinus* from Western Australia. *Squalus megalops* has a more strongly raked dorsal fin and more delicate fin spines (exposed base of first dorsal-fin spine 0.6–0.8 vs. 1.2–1.3% TL in *S. crassispinus*; exposed base of first dorsal-fin spine 0.7–0.9 vs. 1.3–1.5% TL), shorter fins with longer inner margins (first dorsal-fin height 1.00–1.33 vs. 1.32–1.70 times its inner margin length, second dorsal-fin height 0.71–1.04 vs. 1.08–1.30 times its inner margin length), pectoral-fin anterior margin 1.41–1.88 (vs. 1.92–2.19) times its inner margin length, mouth width 2.58–3.40 (vs. 2.12–2.36) times horizontal preanial length; direct pre-second dorsal length 4.06–4.97 (vs. 3.67–4.21) times pectoral-fin anterior margin and 2.84–3.24 (vs. 2.59–2.84) times dorsal caudal margin, preoral length

2.93–3.84 (vs. 2.66–2.94) times horizontal preanial length, 9.3–9.9 (vs. 8.3–9.2)% TL; and preventral caudal margin 1.56–2.53 (vs. 2.44–4.55) times inner margin of pelvic fin. *Squalus megalops* also has slightly fewer vertebrae: 37–40 (mainly 39–40) vs. 39–42 (mainly 40–41) monospondylous centra; 78–84 vs. 82–86 precaudal centra; and 102–110 (mainly 105–106) vs. 107–111 (mainly 109–110) total centra.

The coloration of Australian *S. megalops* is variable. Northeastern forms resemble *S. crassispinus* being almost uniformly pale dorsally and ventrally, whereas southeastern Australian forms are much darker dorsally than ventrally. In *S. megalops*, the pale posterior margin of the caudal fin is usually sharply demarcated from the rest of the fin rather than weakly demarcated as in *S. crassispinus*. Juvenile *S. megalops* from Western Australia have a strong dark oblique bar extending from

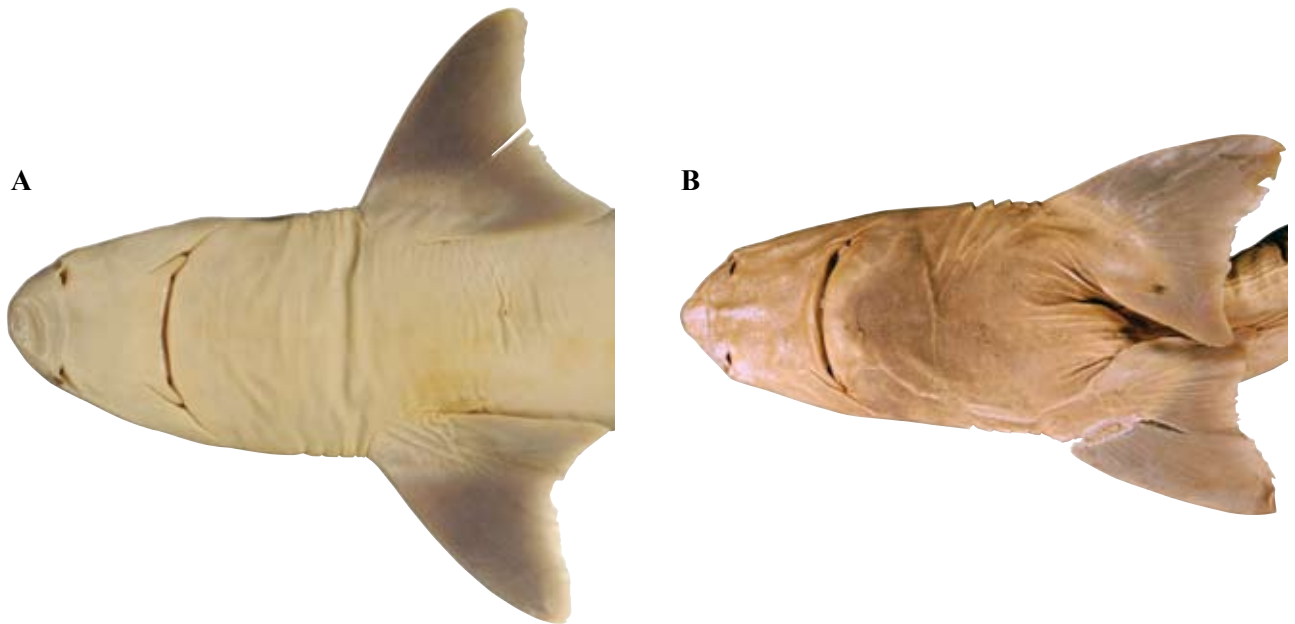


Figure 9. Ventral view of the head of: A. *Squalus megalops* from Victoria (CSIRO H 3762-01, female 511 mm TL); B. holotype (AMS I.16255-001, female 565 mm TL).

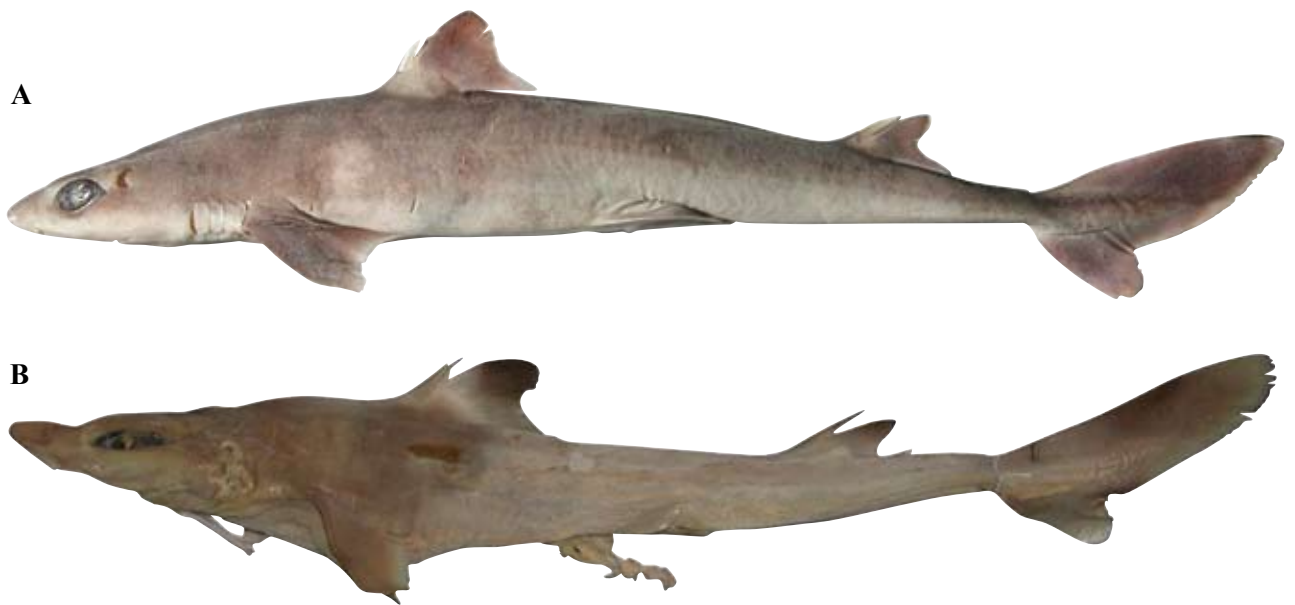


Figure 10. Lateral view of: A. *Squalus cubensis* from Santos, Brazil (NUPEC unregistered, ca. 460 mm TL); B. *Squalus cubensis* paratype (MCZ 1462-S, immature male 282 mm TL).

the base of the lower caudal lobe to the caudal fork (Fig. 8). In larger specimens, this bar fades but is often evident as a dusky margin at the caudal fork. There also appears to be some population based, intraspecific variation in the extent of dark markings on the dorsal fins and the strength of demarcation of posterior margins on the pectoral and caudal fins. Some regional differences in morphometrics exist between populations. Queensland *S. megalops* (n=3) have a shorter prepelvic length (44.8–45.4% vs. 45.5–49.9% TL), pectoral–pelvic space (18.0–20.3% vs. 20.5–26.1% TL), pectoral-fin anterior margin (12.3–12.6% vs. 13.6–15.1% TL), lower postventral

caudal margin (3.4–3.7% vs. 3.8–5.6% TL), and longer pelvic caudal space (28.7–29.4% vs. 24.5–27.8% TL) than populations from other regions (i.e. southeastern Australia and Western Australia, n=10). In addition, they differ in several other ratios: pectoral–pelvic space 0.63–0.69 vs. 0.74–1.04 times pelvic–caudal space, interdorsal space 1.83–2.17 vs. 2.15–2.51 times dorsal–caudal space, and pre-second dorsal length 4.82–4.97 vs. 4.06–4.57 times pectoral anterior margin length. Given this variability, a more comprehensive investigation of *S. megalops* populations is needed as more than one species may be represented.



Figure 11. Ventral view of the head of: A. *S. cubensis* (NUPEC unregistered, ca. 460 mm TL); B. *S. cubensis* paratype (MCZ 1461-S, female 683 mm TL).

Although *S. megalops* has been recorded from several localities outside Australia (i.e. southern Africa, eastern Atlantic and northwestern Pacific), some of these forms may prove to be non-conspecific. A larger, Atlantic member of the ‘megalops-cubensis group’, *Squalus cubensis* (Figs 10 and 11), has a relatively longer snout, darker dorsal-fin apices, more robust unicuspid denticles, and stronger dorsal-fin spines.

Other material.

Squalus cubensis: MCZ 1461-S (paratype), female 683 mm TL, MCZ 1462-S (paratype), immature male 282 mm TL, off Havana, Cuba.

ACKNOWLEDGEMENTS

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Part 3 — *Squalus bucephalus* sp. nov., a new short-snout spurdog from New Caledonia

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ABSTRACT.— A new species of spurdog, *Squalus bucephalus* sp. nov., is described from deepwater south of New Caledonia in the northern Tasman Sea. It belongs to the ‘megalops-cubensis group’ but differs from Australian forms of *S. megalops* in having a broader head, larger dorsal-fin spines and reaches a larger adult size. It also differs in several other meristic and morphometric details and is the only *Squalus* known to possess both unicuspid and multicuspid denticles in adults. It is morphologically similar to the newly described *S. crassispinus* from the eastern Indian Ocean, but differs in having a lower, strongly raked first dorsal fin, more vertebrae, and more slender dorsal-fin spines.

Key words. Squaloidea – Squalidae – *Squalus bucephalus* – new species – New Caledonia.

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INTRODUCTION

In recent decades, the French research institute IRD (formerly ORSTOM) has conducted a series of deepwater marine biodiversity surveys of the South Pacific (Richer de Forges, 1990, 1996; Séret, 1997). Some of these voyages have targeted the chondrichthyan fauna and these collections are presently under investigation (Séret and Last, unpubl. data). A preliminary list of chondrichthyan fishes published by Séret (1994), included new species. The total number of chondrichthyan fishes in the economic zone of New Caledonia is currently estimated at 73, comprising 51 sharks, 18 rays and 4 chimaeras (Séret, unpublished data). Two endemic species of *Squalus* have been recorded from the adjacent region. *Squalus melanurus* Fourmanoir and Rivaton, 1979 was described from material collected on the insular slopes of the Uatio and Bulari Passes near New Caledonia, and *S. rancureli* Fourmanoir and Rivaton, 1979 from insular slopes of nearby Vanuatu. In the recent surveys of this region, an undescribed, short-snout spurdog belonging to the ‘megalops-cubensis group’ was collected by one of us (B. Séret). This species is formally described and compared to other nominal members of the subgroup, i.e. *S. cubensis* Howell Rivero, 1936 and *S. megalops* (Macleay, 1881), and a new species described in this issue, *S. crassispinus* Last, Edmunds and Yearsley, 2007 (see Part 2).

METHODS

Methods generally follow those outlined in Part 1 of this issue (Last *et al.*, 2007b). Available material consisted of the holotype and three paratypes (Table 1). The largest specimens, two adult males (NMNZ P 34030), had been eviscerated so a smaller immature male in better condition was selected as the holotype. In the description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the measured paratypes. Measurements affected by damage to the largest paratypes were excluded so information for only one paratype is available in some instances. Meristics were taken from radiographs. Type specimens are deposited in the ichthyological collections of the Muséum national d’Histoire naturelle, Paris (MNHN) and National Museum of New Zealand, Wellington (NMNZ); their registration numbers are prefixed with these acronyms.

Squalus bucephalus sp. nov.

Figs 1–5; Table 1

Squalus sp. n.: Séret, 1994 (listed in Table A, p. 7); Séret in Grandperrin *et al.*, 1997 (listed in Annexe 11 – Liste des Poisons, p. 112)



Figure 1. Lateral view of *Squalus bucephalus* sp. nov. holotype (MNHN 2006–1754, immature male 556 mm TL).



Figure 2. Ventral view of the head of *Squalus bucephalus* sp. nov. holotype (MNHN 2006–1754, immature male 556 mm TL).

Holotype. MNHN 2006–1754, immature male 556 mm TL, Norfolk Ridge, south of New Caledonia, 23°43' S, 168°16' E, 405–411 m, 28 November 1993.

Paratypes. 3 specimens. MNHN 1997–3641, female 430 mm TL, Stylaster Seamount, Norfolk Ridge, New Caledonia, 23°37' S, 167°42', 420–470 m; NMNZ P 34030, two adult males 790, 808 mm TL, Stylaster Seamount, Norfolk Ridge, New Caledonia, 23°35' S, 167°42' E, 448–880 m.

DIAGNOSIS.— A large, broad-headed species of *Squalus* of the 'megalops-cubensis group' with the following combination of characters: head width at mouth 12.1–13.5% TL; mouth width 2.2–2.7 times

horizontal prenarial length; direct pre-second dorsal length 3.9–4.0 times pectoral-fin anterior margin, 2.7 times dorsal caudal margin; preoral length 2.7–3.1 times horizontal prenarial length, 9.2–10.5% TL; anterior nasal flap strongly bifurcate; first dorsal fin low, raked; exposed bases of dorsal-fin spines broad, 0.7–0.8% TL; both dorsal fins with short inner margins, first dorsal-fin height 1.4–1.5 times its inner margin length, second dorsal-fin height 0.8–1.0 times its inner margin length; pectoral-fin anterior margin 1.8–2.0 times its inner margin length; preventral caudal margin 1.8–2.2 times inner margin of pelvic fin; dorsal fins with dark distal portion, posterior margin of free rear tip pale; caudal fin upper posterior margin broadly white, lower lobe with dark base and

pale outer half, no caudal bar; flank denticles unicuspid or weakly tricuspid; 45 monospondylous centra, 86–89 precaudal centra, 113–118 total centra; adult maximum size at least 90 cm TL.

DESCRIPTION.— Body fusiform, relatively short, robust (small paratype more deep-bodied, mature males elongate), nape prominently humped; deepest near first dorsal-fin spine origin, maximum depth 0.97 (1.02 in paratype) times width; trunk depth 1.01 (1.04) times abdomen depth; head short 21.0 (21.8–22.9)% TL; caudal peduncle length relatively short, 23.3 (23.4–24.5)% TL. Head very robust, broad, slightly wider than trunk, width 1.17 (1.07) times trunk width, 1.33 (1.29) times abdomen width, depressed forward of spiracles, almost subtriangular in cross-section towards pectoral-fin origin, length 2.24 (2.08–2.31) in pre-vent length; height 0.72 (0.66–0.72) times width. Snout short, narrowly triangular in lateral view, apex bluntly pointed, lateral prenarial margin not angular; very broadly rounded in dorsal view, horizontal length 1.29 (1.12–1.18) times eye length, 0.61 (0.55–0.59) times interorbital space; horizontal prenarial length 2.73 (2.78–3.07) times in preoral length. Eye narrowly oval, size moderate, length 4.71 (4.72–4.93) in head, 2.25 (2.26–2.65) times height; strongly notched posteriorly, notch extending halfway to spiracle as a well-developed furrow. Spiracle small, crescentic; very broad, bulbous lobe-like fold on posterior margin; greatest diameter 3.11 (3.27–4.31) in eye length. Gill openings short, almost upright, first four subequal in size, fifth longest, height of fifth slit 2.1 (1.8–2.5)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.08 (1.13–1.25) in preoral length; upper labial furrow much longer than lower furrow; postoral groove prominent, much longer than upper labial furrows, extending posterolaterally from angle of jaws; one series of functional teeth in upper jaw (1–2 in paratypes), 1–2 series in lower jaw. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than

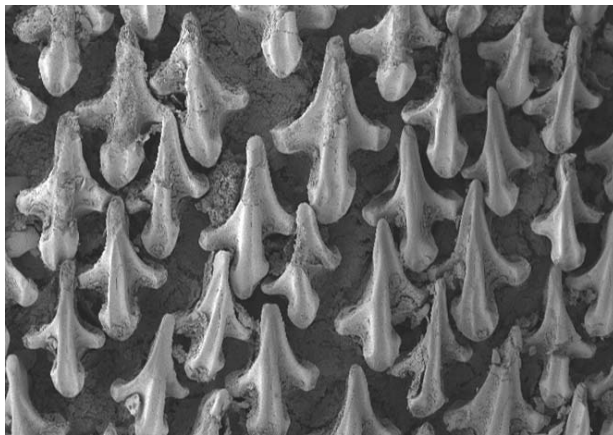


Figure 3. Cusps of the flank denticles of *Squalus bucephalus* sp. nov. paratype (NMNZ P 34030, adult male 808 mm TL). Field of view width 1.6 mm.

length of cusp. Nostrils small, slightly oblique; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe short, finger-like; internarial space 2.01 (1.75–2.11) in preoral length, 2.36 (2.71–2.77) times nostril length. Dermal denticles (based on holotype) on flank very small, not imbricated, varying in shape from weakly tricuspid to unicuspid. Largest denticles tricuspid, central cusp enlarged with strong median ridge; lateral cusps short, weakly pointed, without ridges. Smallest denticles extremely compressed, anvil shaped in lateral profile, central cusp with a narrow median ridge; bluntly pointed distally; often with short, nodular, lateral extensions; in mature male paratype NMNZ P 34030, denticles below dorsal fin mostly broadly unicuspid with long, broad central cusps and bulging lateral keels (keels sometimes expanded to form weak tricuspid crowns). Other denticles variable in shape, with rudimentary lateral cusps of varying sizes; apices usually sharply pointed. First dorsal fin low, raked slightly, narrowly rounded apically (more upright in adult male paratypes); anterior margin weakly convex; upper posterior margin almost straight, subvertical, strongly concave near free rear tip; free rear tip rather deep basally, short; inner margin of fin almost straight; insertion of base well forward of pelvic-fin origin, slightly posterior to free rear tip of pectoral fin; fin-spine origin above (just behind in one paratype) pectoral-fin insertion; spine base narrow,

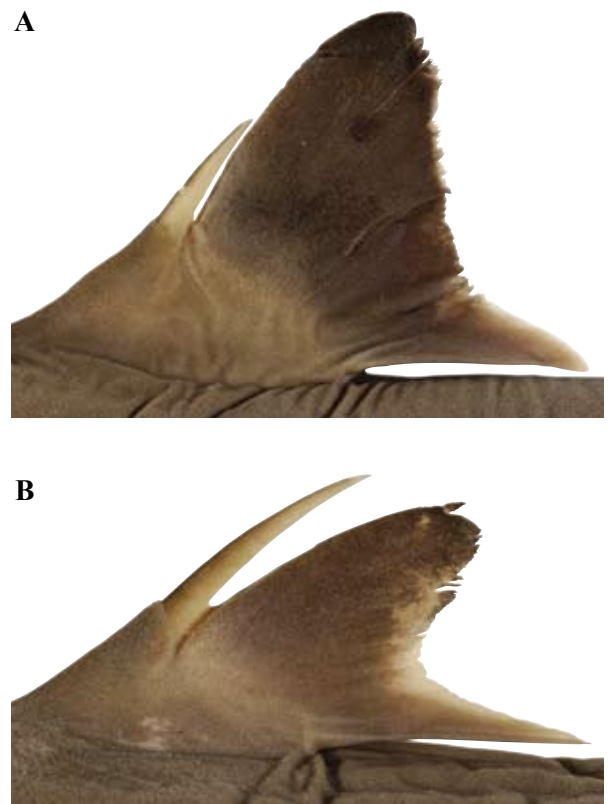


Figure 4. Lateral view of the dorsal fins of *Squalus bucephalus* sp. nov. holotype (MNHN 2006–1754, immature male 556 mm TL) – A, first dorsal fin, B, second dorsal fin.

exposed anteriorly near junction of spine and soft portion of fin; soft portion of fin connected near mid-point of total spine length (distal portion of spine usually abraded); spine tapering gradually distally, anterior margin almost straight, exposed portion tilted, shorter than length of exposed portion of second dorsal-fin spine; pre-first dorsal length 3.62 (3.47–3.54) times in TL; first dorsal-fin length 1.90 (1.75–1.93) times its height, 1.32 (1.23–1.34) times second dorsal-fin length; first dorsal-fin height 2.02 (1.69–2.22) times second dorsal-fin height; exposed first dorsal spine length 0.41 (0.32) times height of fin. Second dorsal fin small, very strongly raked; anterior margin weakly convex, apex narrowly rounded; posterior margin deeply concave, maximum concavity almost near mid-point of margin, upper portion directed dorsoposteriorly strongly from bottom to top; free rear tip elongate, inner margin length 1.18 (0.97–1.04) times fin height; second dorsal-fin length 2.90 (2.61–2.90) times its height; spine length 1.09 (0.82) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed about at level of junction with spine and soft portion of fin; second spine narrow based (broader in adult males), slender, sharply pointed distally, not tapering rapidly just above point of exposure, spine tip extending behind level of insertion of fin (when intact), much more strongly raked than first spine; interdorsal space 0.93 (0.89–1.01) in length from snout tip to pectoral-fin origin, 1.21 (1.13–1.29) in pre-first dorsal length; weak interdorsal groove. Pectoral fin moderate, anterior margin moderately convex; inner margin weakly convex, length 8.2 (7.4–8.2)% TL; apex narrowly rounded, lobe-like but not falcate; posterior margin weakly to moderately concave, free rear tip narrowly rounded; base very short, 3.14 (2.58–2.82) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight (sometimes weakly convex), apex broadly rounded, free rear tip bluntly pointed. Caudal peduncle short, pelvic–caudal space 23.3 (23.4–24.5)% TL; tapering evenly to caudal fin; subcircular in cross-section anteriorly, broadly semicircular posteriorly, ventral groove usually very well developed; lateral keels well developed, their origin obscure, about under insertion of second dorsal fin, terminating about half an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.86 (0.84–0.93) in pectoral–pelvic space, 0.91 (0.93–0.94) in prepectoral length; dorsal–caudal space 2.42 (2.24–2.72) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit rudimentary. Caudal fin relatively long, dorsal caudal margin 0.86 (0.98–1.00) in head length; length of lower caudal lobe 2.00 (1.92–2.05) in upper lobe length; upper posterior lobe moderately convex; lower lobe apex narrowly rounded. Vertebral centra 118 (113–117 in paratypes), monospondylous 45 (45), precaudal 88 (86–89) and caudal 30 (27–28). Teeth in upper jaw of holotype 13+1+13 = 27, lower jaw 11 (or 12)+11 (or 12) = 22 (or 23, 24), uncut side of jaw difficult to count, smaller symphyseal tooth with cusp directed slightly to right; in paratype, 13+13 = 26, lower jaw 11+12 = 23.

COLOUR.— In preservative: dorsal half uniformly dark brown; paler yellowish or white ventrally (paratypes with slightly darker, dusky tones on belly and ventral surface of tail, blotches on adult males); light and dark tones sharply demarcated on head (tones gradating on abdomen and tail), pale boundary extending around angle of snout just below eye and through upper two thirds of gill slits. First dorsal-fin base pale brown; outer fin dark grey to black (more pronounced in smallest paratype, NMNZ P34030), most pronounced at fin apex; free rear tip dusky with whitish posterior margin; adults with uniform dusky fins, upper posterior margins translucent. Second dorsal-fin base slightly paler than dorsal surface of body (more obvious in NMNZ P34030); outer portion of fin dark grey (distinctly black in NMNZ P34030); free rear tip greyish with narrow whitish margin extending to angle of fin. Caudal fin central fleshy portion brownish, upper lobe mostly darker, greyish to blackish; basal half of lower lobe with triangular dark grey to black bar; posterior margin of fin sharply demarcated pale yellow to white (more extensive and strongly pronounced in smallest paratype); light and dark interface extending from about middle of pre-ventral margin almost in a straight line dorsoposteriorly towards apex of upper lobe (anteroposterior margin of dorsal lobe pale in smallest paratype); posterior angle of caudal fin lacking black bar; adult males with more uniformly coloured fin, pale posterior margin strongly demarcated. Pectoral fin upper surface dark grey (darker than dorsal coloration) with a pronounced pale posterior margin; ventral surface with pale base and greyish outer fin, posterior margin pale. Pelvic fin brownish or greyish, of a similar tone or slightly darker than dorsal surface of body, posterior margin pale; ventral surface pale or blotched, similar to toning of belly.

SIZE.— Large species known from only a few individuals; two largest males both mature (790–808 mm TL); smallest male (556 mm TL) had undeveloped claspers. Additional non-type specimens in the MNHN



Figure 5. Caudal fin coloration of juvenile of *Squalus bucephalus* sp. nov. paratype (MNHN 1997-3641, female 430 mm TL).

Table 1. Proportional dimensions as percentages of total length for the holotype (MNHN 2006–1754) and ranges for the 3 paratypes of *Squalus bucephalus* sp. nov.

	<i>S. bucephalus</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
TL – Total length	556	430	808
PCL – Precaudal length	74.5	76.3	77.8
PD2 – Pre-second dorsal length	57.6	58.8	61.1
PD1 – Pre-first dorsal length	27.7	28.2	28.8
SVL – Pre-vent length	47.0	47.8	50.4
PP2 – Prepelvic length	46.9	45.6	48.8
PP1 – Prepectoral length	21.3	22.0	22.6
HDL – Head length	21.0	21.8	22.9
PG1 – Prebranchial length	18.5	18.5	20.1
PSP – Prespiracular length	13.0	12.6	13.9
POB – Preorbital length	7.7	7.1	7.9
PRN – Prenarial length	4.7	4.6	5.2
POR – Preoral length	9.2	9.2	10.5
MOW – Mouth width	8.5	8.1	8.4
ULA – Labial furrow length	2.1	2.2	2.4
INW – Internarial space	4.6	5.0	5.3
INO – Interorbital space	9.4	8.6	9.8
EYL – Eye length	4.4	4.4	4.9
EYH – Eye height	2.0	1.8	2.0
SPL – Spiracle length	1.4	1.1	1.4
GS1 – First gill-slit height	2.0	1.4	2.0
GS5 – Fifth gill-slit height	2.1	1.8	2.5
IDS – Interdorsal space	22.9	22.3	25.3
DCS – Dorsal-caudal space	9.5	9.3	9.9
PPS – Pectoral-pelvic space	20.0	20.0	21.7
PCA – Pelvic-caudal space	23.3	23.4	24.5
D1L – First dorsal length	16.1	14.8	15.7
D1A – First dorsal anterior margin	14.2	12.5	14.6
D1B – First dorsal base length	10.1	9.1	10.0
D1H – First dorsal height	8.5	8.1	8.4
D1I – First dorsal inner margin	6.1	5.4	5.8
D1P – First dorsal posterior margin	9.4	9.2	9.8
D1ES – First dorsal spine length	3.5	–	2.6
D1BS – First dorsal spine base width	0.8	0.8	0.8
D2L – Second dorsal length	12.2	11.0	12.7
D2A – Second dorsal anterior margin	10.7	9.4	11.4
D2B – Second dorsal base length	7.5	7.0	7.9
D2H – Second dorsal height	4.2	3.8	4.8
D2I – Second dorsal inner margin	5.0	4.0	4.8
D2P – Second dorsal posterior margin	5.0	4.1	5.2
D2ES – Second dorsal spine length	4.6	–	3.8
D2BS – Second dorsal spine base width	0.8	0.7	0.8

Table 1. cont'd

	<i>S. bucephalus</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
P1A – Pectoral anterior margin	15.8	14.3	15.7
P1I – Pectoral inner margin	8.2	7.4	8.2
P1B – Pectoral base length	5.0	5.1	5.9
P1P – Pectoral posterior margin	12.3	11.4	12.4
P2L – Pelvic length	9.4	9.0	11.0
P2H – Pelvic height	5.0	4.6	6.0
P2I – Pelvic inner margin	5.5	5.4	6.2
CDM – Dorsal caudal margin	24.5	21.9	23.5
CPV – Preventral caudal margin	12.3	11.4	11.5
CPU – Upper postventral caudal margin	18.3	17.1	17.7
CPL – Lower postventral caudal margin	5.2	4.8	5.5
CFW – Caudal fork width	7.1	7.1	7.3
CFL – Caudal fork length	9.6	9.3	9.7
HANW – Head width at nostrils	8.8	7.7	9.3
HAMW – Head width at mouth	13.0	12.1	13.5
HDW – Head width	13.8	13.7	14.2
TRW – Trunk width	11.8	–	12.9
ABW – Abdomen width	10.3	–	10.7
TAW – Tail width	6.6	6.3	6.6
CPW – Caudal peduncle width	3.1	3.0	3.3
HDH – Head height	9.9	9.3	10.0
TRH – Trunk height	11.5	–	13.1
ABH – Abdomen height	11.3	–	12.6
TAH – Tail height	6.9	6.6	6.9
CPH – Caudal peduncle height	2.7	2.6	2.8
CLO – Clasper outer length	1.0	2.5	2.9
CLI – Clasper inner length	3.2	8.7	8.8
CLB – Clasper base width	0.8	1.7	1.7

ranged in size from 301–900 mm TL; smallest adult male 662 mm TL.

DISTRIBUTION.— Known only from the northern Tasman Sea on the Norfolk Ridge (Stylaster Seamount), and off New Caledonia, in 448–880 m depth.

ETYMOLOGY.— Derived from the Latin *bu* (large) and Greek *kephalis* (of the head) in allusion to its relatively bulky head.

VERNACULAR.— Bighead Spurdog (English), Aiguillat à grosse tête (French).

REMARKS.— *Squalus bucephalus* can be distinguished from all other members of the ‘megalops-cubensis group’

by the combination of an unusually broad head, large dorsal-fin spines, and other meristic and morphometric details. It is the only *Squalus* known to possess both unicuspid and multicuspid denticles in adults. It differs from *S. megalops* in reaching a larger size (males about 800 vs. 470 mm TL in *S. megalops*), having different first dorsal fin (first dorsal-fin height 1.4–1.5 vs. 1.0–1.3 times its inner margin length) and preoral shapes (mouth width 2.2–2.7 vs. 2.6–3.4 times horizontal prenarial length), and more vertebrae (45 vs. 37–40 monospondylous centra, 86–89 vs. 78–84, and rarely more than 82, precaudal centra, and 113–119 vs. 102–110, and rarely more than 106, total centra). It is morphologically closer to *S. crassispinus* but differs in having a lower, more strongly raked first dorsal fin, broader head (width at mouth 12.1–13.5% vs. 9.9–11.3% TL in *S. crassispinus*), longer preoral length

(9.2–10.5% vs. 8.3–9.2% TL), less robust exposed bases of dorsal-fin spines (0.7–0.8% vs. 1.2–1.5% TL), a better demarcated, pale posterior caudal-fin margin, and more vertebrae (45 vs. 39–42 monospondylous centra, 86–89 vs. 82–86 precaudal centra, 113–119 vs. 107–111 total centra). The second dorsal-fin height is 0.9–1.0 (vs. 1.1–1.3) times its inner margin length and the preventral caudal margin is 1.8–2.2 (vs. 2.4–4.6) times the length of the inner margin of the pelvic fin. Another member of the ‘megalops-cubensis group’, *S. cubensis* from the Atlantic Ocean has a longer, narrower snout and darker dorsal fins (see Last *et al.*, 2007a, Part 2 of this issue).

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Part 4 — *Squalus raoulensis* sp. nov., a new spurdog of the ‘megalops-cubensis group’ from the Kermadec Ridge

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ABSTRACT.— A new species of spurdog, *Squalus raoulensis* sp. nov., is described from the upper insular slope of Raoul Island, Kermadec Islands, and the Kermadec Ridge north of Raoul Island, New Zealand. The new species belongs to a subgroup of *Squalus* whose members share a relatively short snout and unicuspid denticles. *Squalus raoulensis* differs from its closest congeners primarily in a combination of fin coloration, dorsal-fin shape, meristics, and morphometrics of the head, trunk and pectoral fins. The relationships of this species to other members of this subgroup are discussed.

Key words. Squaloidea – Squalidae – *Squalus raoulensis* – new species – south-west Pacific – Kermadec Ridge.

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INTRODUCTION

Squalus acanthias L. and *S. griffini* Phillipps, 1931 are the only *Squalus* species currently recognised from New Zealand waters (Garrick, 1960; Paulin *et al.*, 1989; Duffy and Last, 2007, Part 9 this issue). *Squalus acanthias* is widely distributed around the North and South Islands, Chatham Rise and Campbell Plateau, whereas *S. griffini* is restricted to waters north of the Subtropical Front. During an examination of *Squalus* held in the fish collection of the Museum of New Zealand, a third New Zealand species was identified based on a single female specimen collected by a scientific observer from the Kermadec Ridge, north of Raoul Island. Subsequently, the senior author collected two mature male specimens from the upper insular slope off Raoul Island in the Kermadec group. These specimens are described herein as a new species belonging to the ‘megalops-cubensis group’, and comparisons are made with similar species, *S. bucephalus* Last, Seret and Pogonoski, 2007 (Part 3, this issue) from the northern Tasman Sea, *S. crassispinus* Last, Edmunds and Yearsley, 2007 (Part 2, this issue) and *S. megalops* (Macleay, 1881) from off Australia.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007c). The only material, the holotype and two paratypes, of the new species were measured in full (Table 1). In the description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the paratypes. Meristics were

taken from radiographs of all types of the new species. Comparative data for closely related Australian and New Caledonian members of the ‘megalops-cubensis group’ were obtained from data presented in Parts 2 and 3 of this volume (Last *et al.*, 2007a, 2007b).

Type specimens are deposited in the ichthyological collection of the Museum of New Zealand, Wellington (NMNZ); their registration numbers are prefixed with this acronym. Comparative data for 5 specimens of *Squalus brevirostris* Tanaka, 1917, a Japanese member of this species group, are also presented. These specimens are deposited in the Kagoshima University Museum, Kagoshima, Japan (KAUM), and the Australian National Fish Collection, Hobart (CSIRO). Specimen registration numbers are prefixed by these acronyms.

Squalus raoulensis sp. nov.

Figs 1–4; Table 1

Holotype. NMNZ P 41678, adult male 651 mm TL, off Raoul Island, Kermadec Islands, New Zealand, 29°14' S, 177°53' W, 320 m, 8 November 2004.

Paratypes. 2 specimens. NMNZ P 42572, adult male 681 mm TL, collected with holotype; NMNZ P 34436, female 729 mm TL, Kermadec Ridge north of Raoul Island.

DIAGNOSIS.— A moderate-sized species of *Squalus* of the ‘megalops-cubensis group’ with the following combination of characters: mouth width 2.4–2.7 times



Figure 1. Lateral view of *Squalus raoulensis* sp. nov. holotype (NMNZ P 41678, adult male 651 mm TL).



Figure 2. Ventral view of the head of *Squalus raoulensis* sp. nov. holotype (NMNZ P 41678, adult male 651 mm TL).

horizontal prenarial length; direct pre-second dorsal length 3.6–4.0 times pectoral-fin anterior margin, 2.7–2.9 times dorsal caudal margin; preoral length 3.0–3.2 times horizontal prenarial length, 2.3–2.5 times internarial width; anterior nasal flap bifurcate; first dorsal fin upright and rounded apically; dorsal-fin spines not robust, width of exposed bases 0.6–0.7% TL; first dorsal-fin height 1.2–1.4 times its inner margin length; second dorsal-fin height 0.85–0.93 times its inner margin length; pectoral-fin anterior margin 1.7–1.8 times its inner margin length; preventral caudal margin 1.7–2.3 times inner margin of pelvic fin; caudal fin pale with strongly demarcated, whitish posterior margin, no caudal bar; flank denticles unicuspid; 41–43 monospondylous centra, 84–85 precaudal centra, 112–113 total centra; adult maximum size at least 73 cm TL.

DESCRIPTION.— Body fusiform, slender, nape not prominently humped, only marginally deeper at belly (uniformly deepest across abdomen), maximum depth 0.97 (0.93–1.00 in paratypes) times width; trunk depth 1.04 (1.02–1.08 in paratypes) times abdomen depth; head short 22.5 (22.3–22.9)% TL; caudal peduncle slender, 26 (23.2–26.4)% TL. Head not especially broad, width 1.24 (1.17–1.22) times trunk width, 1.37 (1.35–1.53) times abdomen width, slightly depressed forward of spiracles, becoming subtriangular towards pectoral-fin origin, length 2.1 (2.14–2.17) in pre-vent length; height 0.75 (0.73–0.74) times width. Snout short, narrowly triangular in lateral view, apex pointed, lateral prenarial margin somewhat angular; bluntly pointed in dorsal view, horizontal length 1.3 (1.19–1.25) times eye length, 0.7 (0.65–0.67) times interorbital length; horizontal

prealar length 3.15 (3.03–3.11) times in prealar length. Eye broadly oval, size moderate, length 4.95 (4.74–4.99) in head, 2.07 (1.97–2.74) times height; strongly notched posteriorly, weakly connected to anteroventral margin of spiracle. Spiracle small, strongly crescentic; lobe-like fold on posterior margin; a narrow subvertical fold present at anterior margin in holotype, fold covered in denticles (less obvious in female paratype NMNZ P 34436), greatest diameter 3.9 (3.51–4.28) in eye length. Gill openings slightly oblique, directed slightly anterodorsally from bottom to top (sometimes upright), first four subequal in size, fifth longest, height of fifth slit 1.8 (1.76–1.96)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.23 (1.12–1.32) in prealar length; upper labial furrow more than twice length of lower furrow, prominent postoral groove, slightly longer than upper labial furrow, extending posterolaterally from angle of jaws; two series of functional teeth in upper and lower jaws. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, slightly oblique; anterior nasal flap moderately bifurcate, upper lobe largest, broadest; posterior lobe short, digitiform; internarial space 2.26 (2.29–2.45) in prealar length, 2.52 (2.28–2.38) times nostril width. Dermal denticles on flank very small, unicuspid, not imbricated; crown quadrangular, width subequal to or slightly narrower than length, with pronounced median ridge; median ridge commencing well anterior of denticle base with a mesial furrow developing anteriorly and converging towards posterior tip of crown; cusp pungent, elongate; lateral extensions each with a weak ridge, cusps absent. First dorsal fin somewhat upright, broadly rounded apically; anterior margin weakly convex; posterior margin weakly concave, greatest curvature at or just below mid-length; free rear tip very thick basally, short, inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, just posterior to free rear

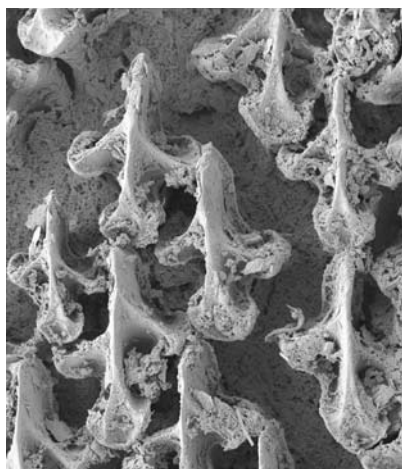


Figure 3. Cusps of the flank denticles of *Squalus raoulensis* sp. nov. paratype (NMNZ P 42572, adult male 681 mm TL). Field of view width 0.4 mm.

tip of pectoral fin; fin-spine origin well behind pectoral-fin insertion; spine base moderately robust, exposed anteriorly just below junction of spine and soft portion of fin; soft portion of fin connected distally at about mid-point of total spine length; spine tapering uniformly distally, anterior margin almost straight, subequal in length to second dorsal-fin spine, tip well below apex of soft portion of fin in undamaged holotype; pre-first dorsal length 3.39 (3.36–3.39) times in TL; first dorsal-fin length 1.75 (1.97–2.00) times its height, 1.02 (1.13) times second dorsal-fin length; first dorsal-fin height 1.62 (1.57–1.59) times second dorsal-fin height; exposed first dorsal-spine length 0.51 (0.36) times height of fin. Second dorsal fin of moderate size, not strongly raked; anterior margin weakly convex, apex narrowly rounded; posterior margin deeply concave, maximum concavity slightly near mid-point of margin, upper portion almost upright (directed slightly dorsoposteriorly from bottom to top in paratype NMNZ P 34436); free rear tip thin basally, elongate, inner margin length 1.07 (1.15–1.17) times fin height; second dorsal-fin length 2.79 (2.73–2.8) times its height; spine length 0.99 (0.98) in height of fin; fin-spine origin well behind free rear tip of pelvic fin; interdorsal space 0.97 (0.90–0.91) in length from snout tip to pectoral-fin origin, 1.27 (1.25–1.26) in pre-first dorsal length; second spine moderately robust, not extremely broad-based, subequal to width of exposed base of first dorsal-fin spine; spine slender, sharply pointed distally, tapering gradually just above point of exposure, tip just below level of apex of soft portion of fin; no obvious

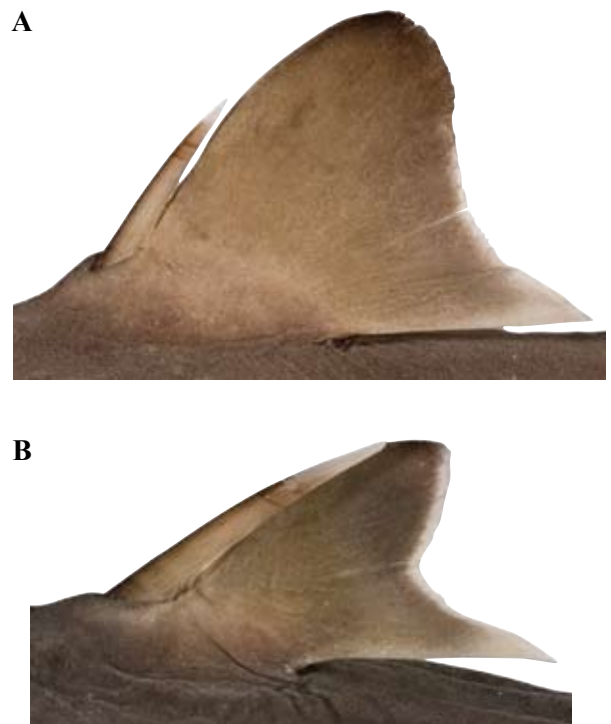


Figure 4. Lateral view of the dorsal fins of *Squalus raoulensis* sp. nov. holotype (NMNZ P 41678, adult male 651 mm TL) – A. first dorsal fin, B. second dorsal fin.

Table 1. Proportional dimensions as percentages of total length for the holotype (NMNZ P 41678) and ranges for the two paratypes of *Squalus raoulensis* sp. nov.

	<i>S. raoulensis</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
TL – Total length	651	681	729
PCL – Precaudal length	78.5	78.2	78.6
PD2 – Pre-second dorsal length	59.4	60.1	61.3
PD1 – Pre-first dorsal length	29.5	29.5	29.8
SVL – Pre-vent length	47.3	47.9	49.7
PP2 – Prepelvic length	45.2	46.5	48.8
PP1 – Prepectoral length	22.3	21.4	21.4
HDL – Head length	22.5	22.3	22.9
PG1 – Prebranchial length	18.8	18.2	18.7
PSP – Prespiracular length	13.0	13.3	13.7
POB – Preorbital length	7.2	7.1	7.3
PRN – Prenarial length	4.4	4.2	4.4
POR – Preoral length	9.6	8.9	9.6
MOW – Mouth width	7.8	7.3	7.9
ULA – Labial furrow length	2.4	2.0	2.3
INW – Internarial space	4.2	3.9	3.9
INO – Interorbital space	8.5	8.6	8.7
EYL – Eye length	4.5	4.5	4.8
EYH – Eye height	2.2	1.8	2.3
SPL – Spiracle length	1.2	1.1	1.3
GS1 – First gill-slit height	1.8	1.8	1.8
GS5 – Fifth gill-slit height	1.8	1.8	2.0
IDS – Interdorsal space	23.1	23.6	23.7
DCS – Dorsal-caudal space	10.8	9.6	10.0
PPS – Pectoral-pelvic space	21.3	22.0	22.0
PCA – Pelvic-caudal space	26.0	23.2	26.4
D1L – First dorsal length	13.9	14.4	14.8
D1A – First dorsal anterior margin	12.2	11.8	12.1
D1B – First dorsal base length	8.2	8.3	8.4
D1H – First dorsal height	8.0	7.2	7.5
D1I – First dorsal inner margin	5.9	6.3	6.3
D1P – First dorsal posterior margin	8.8	9.1	9.3
D1ES – First dorsal spine length	4.0	2.6	2.7
D1BS – First dorsal spine base width	0.7	0.6	0.7
D2L – Second dorsal length	13.7	12.7	13.1
D2A – Second dorsal anterior margin	11.6	10.1	10.5
D2B – Second dorsal base length	8.4	7.2	7.7
D2H – Second dorsal height	4.9	4.5	4.8
D2I – Second dorsal inner margin	5.3	5.2	5.6
D2P – Second dorsal posterior margin	5.5	5.4	6.2
D2ES – Second dorsal spine length	4.9	–	4.7
D2BS – Second dorsal spine base width	0.8	0.7	0.7

Table 1. cont'd

	<i>S. raoulensis</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
P1A – Pectoral anterior margin	15.3	15.0	16.9
P1I – Pectoral inner margin	9.1	8.8	9.1
P1B – Pectoral base length	5.1	5.1	5.4
P1P – Pectoral posterior margin	11.8	12.4	13.9
P2L – Pelvic length	11.5	10.1	10.6
P2H – Pelvic height	5.0	5.0	5.3
P2I – Pelvic inner margin	6.3	5.0	6.4
CDM – Dorsal caudal margin	22.0	20.9	21.4
CPV – Preventral caudal margin	11.5	11.3	11.4
CPU – Upper postventral caudal margin	15.9	15.8	16.0
CPL – Lower postventral caudal margin	5.4	4.9	5.2
CFW – Caudal fork width	7.1	7.1	7.7
CFL – Caudal fork length	9.8	9.7	10.0
HANW – Head width at nostrils	6.9	6.6	6.6
HAMW – Head width at mouth	11.4	11.1	11.9
HDW – Head width	12.7	13.3	13.5
TRW – Trunk width	10.3	10.9	11.5
ABW – Abdomen width	9.3	8.7	10.0
TAW – Tail width	7.0	6.2	7.0
CPW – Caudal peduncle width	3.0	3.2	3.3
HDH – Head height	9.6	9.8	9.8
TRH – Trunk height	10.0	10.7	10.8
ABH – Abdomen height	9.6	10.1	10.5
TAH – Tail height	7.1	6.5	7.2
CPH – Caudal peduncle height	2.5	2.4	2.7
CLO – Clasper outer length	3.5	–	3.1
CLI – Clasper inner length	9.7	–	9.8
CLB – Clasper base width	1.6	–	1.5

interdorsal ridge or groove (weak in paratype NMNZ P 34436). Pectoral fin moderately elongate, anterior margin moderately convex; inner margin moderately convex, length 9.1 (8.8–9.1)% TL; apex narrowly rounded to pointed, lobe-like but not falcate; posterior margin moderately to strongly concave, free rear tip usually angular; base 3.0 (2.95–3.11) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight (posterior margin slightly convex in female paratype NMNZ P 34436), apex broadly rounded, free rear tip angular (more obtuse in female paratype). Caudal peduncle long, tapering evenly to caudal fin; subcircular in cross-section anteriorly, slightly depressed posteriorly, ventral groove very well developed with weak median ridge; lateral keels well developed, originating under insertion of second dorsal fin, terminating much less than an eye diameter behind caudal-fin insertion; pelvic–

caudal space 0.82 (0.83–0.95) in pectoral–pelvic space, 0.86 (0.81–0.92) in prepectoral length; dorsal–caudal space 2.15 (2.36–2.46) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit weak. Caudal fin of moderate size, upper lobe not especially broad, upper postventral margin moderately convex; lower lobe well developed, narrowly rounded (angular in female paratype); dorsal caudal margin 1.03 (1.04–1.10) in head length; length of lower caudal lobe 1.92 (1.86–1.88) in upper lobe length. Vertebral centra 112 (112–113 in paratypes), monospondylous 41 (41–43), precaudal 84 (85) and caudal 28 (27–28). Teeth in upper jaw 13+13 (13+13)=26, lower jaw 12+12 (11–12 + 12)=24 (23–24).

COLOUR.— When fresh: uniform reddish brownish dorsally; much paler, white on ventral surface; light and

dark areas well differentiated; sharply demarcated border extending from snout tip, below eye, through middle of gill slits to pectoral fin origin; light and dark areas merging gradually on abdomen and tail; fins dark reddish brown. Dorsal-fin spines dusky, darkest anteriorly; base of soft portion slightly paler than distal portion of fin; first dorsal fin with very narrow black apical margin, extending to about distal third of posterior margin, lower two thirds of posterior margin and free rear tip with narrow white edge; second-dorsal fin similar colour to first dorsal fin, dark edge confined to fin tip, entire posterior margin with white edge, ventral margin of free rear tip brownish. Caudal fin mostly reddish brown; sharply defined white border extending along entire posterior margin of fin, its width subequal to half length of fifth gill slit. Pectoral and pelvic fin upper surfaces brownish, ventral surfaces pale, whitish; prominent, sharply defined white margins along posterior and inner margins of pectoral fin, and posterior margin of pelvic fin; claspers almost uniformly white. In preservative: coloration similar to above except reddish brown areas becoming greyish brown; pale and darker areas on dorsal fins remaining strongly contrasted; dark areas on upper surfaces of pectoral fin evident from ventral surface, most evident on lateral distal half of fin; mouth white; naked axils of fins white or dusky.

SIZE.— Females attain at least 729 mm TL; males probably smaller, maturity size unknown, male types adult at 651 and 681 mm TL.

DISTRIBUTION.— Known only from the upper insular slope west of Napier Island (off Raoul Island), and north of Raoul Island on the Kermadec Ridge. Not collected from the Kermadec Ridge south of Raoul Island.

ETYMOLOGY.— The epithet *raoulensis* is derived in reference to the type locality of Raoul Island.

VERNACULAR.— Kermadec Spiny Dogfish.

REMARKS.— *Squalus raoulensis* and the larger and more widely-distributed New Zealand spurdog *S. griffini*, are sympatric at Raoul Island in the northern sector of the Kermadec group. *Squalus raoulensis* can be readily distinguished from *S. griffini* by its unicuspid denticles (rather than tricuspid in *S. griffini*), shorter snout (preorbital length 7.1–7.3 vs. 7.4–8.8% TL), lower vertebral count (112–113 vs. generally 116–117, max. 121), and smaller size at maturity (males mature by 651 mm TL vs. 690–760 mm TL). Of members of the ‘megalops-cubensis group’, its closest regional relative is *S. bucephalus* from nearby New Caledonia. *Squalus raoulensis* mainly differs from this species in having a narrower head (maximum width 12.7–13.5 vs. 13.7–14.2% TL, width at anterior nostrils 6.6–6.9 vs. 7.7–9.3% TL in *S. bucephalus*), more slender body (trunk width 10.3–11.5 vs. 11.8–12.9% TL, trunk height 10.0–10.8 vs. 11.5–13.1% TL), and fewer vertebrae (41–43 vs. 45 monospondylous centra; 84–85 vs. 86–89 precaudal centra; and 112–113 vs.

113–119 total centra). It also has a shorter direct outer prenarial length (4.2–4.4 vs. 4.6–5.2% TL) and upper postventral caudal margin (15.8–16.0 vs. 17.1–18.3% TL), a relatively smaller first dorsal fin (first dorsal-fin base 8.2–8.4 vs. 9.1–10.1% TL, height 7.2–8.0 vs. 8.1–8.5% TL), a narrower exposed first dorsal-fin spine base (width of exposed base of first dorsal-fin spine 0.6–0.7 vs. 0.8% TL), a longer pre-first dorsal length (29.5–29.8 vs. 27.7–28.8% TL) and inner nostril-upper labial furrow space (5.2–5.4 vs. 4.5–5.0% TL), and a relatively larger second dorsal fin (second dorsal-fin length 12.7–13.7 vs. 11.0–12.7% TL, second dorsal-fin inner margin 5.2–5.6 vs. 4.0–5.0% TL).

Squalus raoulensis differs in morphology and meristics from the Australian members of the ‘megalops-cubensis group’, *S. crassispinus* and *S. megalops*. Its dorsal-fin spine bases are more slender than *S. crassispinus* (0.6–0.7 vs. 1.2–1.5% TL), its mouth width 2.4–2.7 times (rather than 2.1–2.4 times in *S. crassispinus*, n=7) the horizontal prenarial length, preoral length 3.0–3.2 times the horizontal prenarial length (rather than 2.7–3.0), the first dorsal fin more upright (first dorsal-fin height 1.2–1.4 vs. 1.3–1.7 times its inner margin length), second dorsal-fin height 0.9 times its inner margin length (rather than 1.1–1.3), pectoral-fin anterior margin 1.7–1.8 times its inner margin length (rather than 1.9–2.2), preventral caudal margin 1.8–2.3 times the inner pelvic-fin margin (rather than 2.4–4.6), and the white caudal fin posterior margin is strongly demarcated (rather than poorly demarcated). Compared to *S. megalops* from southeastern Australia (n=6), it has a narrower interdorsal space (23.1–23.7 vs. 24.0–25.3% TL), smaller gills (first gill-slit height 1.8 vs. 2.0–2.4% TL), and larger prenarial spaces (4.2–4.4 vs. 3.7–4.1% TL) and fins (pectoral-fin inner margin 15.0–16.9 vs. 13.6–14.9% TL; lower postventral caudal margin 4.9–5.2 vs. 4.0–4.6% TL; second dorsal-fin length 12.7–13.7 vs. 11.0–12.7% TL). The two species can be unambiguously distinguished by the ratio, preoral length/internarial width (2.3–2.5 vs. 1.9–2.2 in populations of *S. megalops* from southeastern Australia, 2.0–2.1 from Queensland, and 2.0–2.1 from Western Australia). *Squalus raoulensis* has more vertebrae (112–113, mean 112.3) than both *S. crassispinus* (107–111, mean 109.4, n=11) and *S. megalops* (102–110, mean 105.3, n=41).

Squalus raoulensis superficially resembles *S. brevirostris* Tanaka, 1917 from southern Japan (Figs 5 and 6). It can be distinguished from that species by the proportions of the head and gills, size and shape of the dorsal fins, coloration and denticle morphology. *Squalus raoulensis* has a longer head (head length 22.3–22.9 vs. 20.3–21.2% TL in *S. brevirostris*) and generally longer snout (pre-orbital length 7.1–7.3 vs. 6.6–7.1% TL), smaller gills (fifth gill height 1.8–2.0 vs. 2.2–2.8% TL), larger first (height 7.2–8.0 vs. 6.1–6.5% TL) and second dorsal fins (height 4.5–4.9 vs. 3.3–3.8% TL), second dorsal fin larger relative to the first (first dorsal height/second dorsal height about 1.6 vs. 1.7–1.9) and not strongly raked. In *S. brevirostris*



Figure 5. Lateral view of *Squalus brevirostris* (KAUM I 184, female 540 mm TL).



Figure 6. Ventral view of the head of *Squalus brevirostris* (KAUM I 184, female 540 mm TL).

the posterior margin of the second dorsal fin is deeply concave, and the apex of the second dorsal spine is located over or slightly beyond the notch in the posterior margin (cf. over or slightly beyond fin insertion in *S. raoulensis*). In *S. raoulensis* the dark dorsal coloration extends well down the side of the head, reaching the middle of the gills, and onto the pelvic-fin base and upper surface of the pelvic fin. In *S. brevirostris* the dorsal coloration is less extensive, only extending to the top of the gills, and the pelvic-fin base and upper pelvic fin surfaces are pale, similar in colour to the ventral abdomen (Pl. 364 Tanaka 1917). Adult *S. raoulensis* have unicuspid lateral dermal denticles which are arrow-shaped in *S. brevirostris*. Tanaka (1917) described the denticles of the 430 mm male holotype as having “a sharp median keel and a short blunt one on either side at a right angle to the former at the base, forming more or less a cross figure” (i.e. unicuspid). As the holotype is considerably smaller than material examined, shape differences observed are likely to be ontogenetic (see Garrick 1960).

Another large Atlantic member of the ‘megalops-cubensis group’, *Squalus cubensis*, has a shorter predorsal length (27.6–28.2 vs. 29.5–29.8% TL in *S. raoulensis*), longer

snout (prenarial length 4.6–4.8 vs. 4.2–4.4% TL), longer caudal fin (dorsal caudal margin 22.1–23.0 vs. 20.9–22.0% TL), and lower second dorsal fin (height 3.8 vs. 4.5–4.9% TL) (see Last *et al.*, 2007a, Part 2 of this issue).

Other material. *Squalus brevirostris*: KAUM 184, female 538 mm TL, KAUM 186, female 552 mm TL, KAUM 187, female 590 mm TL, KAUM 190, female 578 mm TL, KAUM 191, female 537 mm TL, CSIRO H 6483–01, adult male 451 mm TL, CSIRO H 6483–02, adult male 452 mm TL, CSIRO H 6483–03, female 542 mm TL, CSIRO H 6483–04, female 514 mm TL, East China Sea off Kasasa, Minamisatsuma, Kagoshima, Japan, 31°29' N, 130°02' E, 145–150 m.

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Part 5 — New species of *Squalus* of the ‘highfin megalops group’ from the Australasian region

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ABSTRACT.— Three new species of spurdogs, *Squalus albifrons*, *S. altipinnis*, and *S. notocaudatus*, are described based on material from the outer continental shelf and continental slope of Australia. These species belong to a subgroup of *Squalus*, known as the ‘highfin megalops group’, which have a short snout and white caudal-fin margin reminiscent of *S. megalops*. However, unlike *S. megalops*, they have a strong-spined, upright first dorsal fin and tricuspoid denticles. *Squalus altipinnis* is known from two specimens collected in about 300 m depth near the Rowley Shoals, off northwestern Australia. *Squalus albifrons* and *S. notocaudatus* appear to be endemic to the continental shelf and slope off eastern Australia. *Squalus albifrons* occurs widely from central New South Wales to central Queensland in 135–450 m depth. *Squalus notocaudatus* is known from the upper continental slope off central Queensland in 225–450 m depth. The species can be distinguished from each other based on meristics, morphometrics, denticle shape, and fin coloration.

Key words. Squaloidea – Squalidae – *Squalus albifrons* – *Squalus altipinnis* – *Squalus notocaudatus* – new species – Indo–West Pacific

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INTRODUCTION

Last and Stevens (1994) identified 9 Australian *Squalus* species of which 5 remain formally undescribed. Three of these species belong to a subgroup provisionally called the ‘highfin megalops group’. Australian members of this group are characterised by a short snout (preorbital length 6.4–7.0% TL), a tall and upright first dorsal fin (height 7.7–9.4% TL), robust dorsal-fin spines (exposed base width 0.7–1.1% TL), tricuspoid denticles, and a white posterior margin on the caudal fin. Members of the ‘megalops-cubensis group’ also have a short snout and white posterior margin on the caudal fin, but have distinctive unicuspid denticles and more strongly raked dorsal fins. The new members of the ‘highfin megalops group’, informally identified as *Squalus* sp. A, *Squalus* sp. B and *Squalus* sp. C (sensu Last and Stevens, 1994), are described based on material from Australia and eastern Indonesia. Other undescribed members of this subgroup may exist in the Indo-Pacific region.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007). For *Squalus albifrons* sp. nov., both morphometrics and meristics were taken from the holotype (CSIRO H 4627–01) and the following 5 paratypes: CSIRO H 644–04, CSIRO H 2487–01, CSIRO H 4704–02, CSIRO H 4705–01 and QM I 38077.

In addition, meristics were taken from the following 6 paratypes: CSIRO H 449, CSIRO H 2487–02, CSIRO H 2487–03, CSIRO H 2691–01, CSIRO H 3589–01 and QM I 19327. For *Squalus altipinnis* sp. nov., morphometrics and meristics were taken from the holotype (CSIRO CA 4111) and paratype (CSIRO CA 3297). For *Squalus notocaudatus* sp. nov., both morphometrics and meristics were taken from the holotype (CSIRO H 1368–02) and 3 paratypes (CSIRO H 1321–01, CSIRO H 1322–01 and CSIRO H 1323–01) (Table 1). In the species descriptions, morphometric and meristic values for the holotypes are given first, followed in parentheses by ranges for paratypes. Type specimens are deposited in the Australian National Fish Collection, Hobart (CSIRO) and the ichthyological collection of the Queensland Museum, Brisbane (QM); their registration numbers are prefixed with these acronyms.

Squalus albifrons sp. nov.

Figs 1–4; Table 1

Squalus sp. B: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 93, figs 20, 8.32, pl. 6; Compagno, Dando and Fowler, 2005, *Sharks of the World*, p 79, figs, pl. 2.

Holotype. CSIRO H 4627–01, adult male 618 mm TL, east of Broken Bay, New South Wales, 33°28' S, 152°05' E, 386 m, 18 Jun 1996.

Paratypes. 11 specimens. CSIRO H 644–04, adult male 643 mm TL, Saumarez Reef, Queensland, 22°49' S, 154°10' E, 450 m; CSIRO H 449, adult male 650 mm TL, northeast of Townsville Trough, Queensland, 17°57' S, 147°03' E, 300 m; QM I 38077, adult male 614 mm TL, east of Cairns, Queensland, 17°11' S, 146°41' E, 260 m; QM I 19327, adult male 618 mm TL, off Noosa, Queensland, 26°20' S, 153°53' E, 275 m; CSIRO H 2691–01, adult male 695 mm TL, northeast of Byron Bay, New South Wales, 28°30' S, 153°51' E, 153 m; CSIRO H 2487–01, female 647 mm TL, CSIRO H 2487–02, female 658 mm TL, CSIRO H 2487–03, female 681 mm TL, southeast of Ballina, New South Wales, 29°03' S, 153°49' E, 156 m; CSIRO H 3589–01, female 844 mm TL, east of Newcastle, New South Wales, 32°59' S, 152°14' E, 135 m; CSIRO H 4705–01, female 614 mm TL, east of Sydney, New South Wales, 33°28' S, 152°00' E, 230 m; CSIRO H 4704–02, female 596 mm TL, east of Sydney, New South Wales, 33°37' S, 151°55' E, 331 m.

Non-types. 3 specimens. CSIRO H 4704–01, female 656 mm TL, east of Sydney, New South Wales, 33°37' S, 151°55' E, 331 m; CSIRO H 3711–01, female 753 mm TL, northeast of Wollongong, New South Wales, 34°18' S, 151°12' E, 135 m; CSIRO H 4709–01, female 784 mm TL, east of Brush Island, New South Wales, 35°34' S, 150°44' E, 388 m.

DIAGNOSIS.— A large species of *Squalus* of the 'highfin megalops group' with the following combination of characters: abdomen depth 10.4–12.6% TL; pre-vent length 46.9–48.1% TL, 2.0–2.2 times dorsal caudal margin; pre-second dorsal length 3.7–4.3 times pectoral-fin anterior margin, 2.5–2.8 times dorsal caudal margin; head width 1.0–1.4 times abdomen width; preoral length 2.9–3.1 times horizontal prenarial length, 8.4–9.1% TL; head length 4.3–4.9 times eye length; mouth width 3.3–4.1 times length of upper labial furrow; interorbital width 1.5–1.7 times horizontal preorbital length; fifth gill slit height 2.1–2.5% TL; anterior nasal flap strongly bifurcate; first dorsal fin upright, upper posterior margin directed posteroventrally, greatest concavity about midway between free rear tip and fin apex; posterior margin of second dorsal fin deeply concave; second dorsal-fin spine with a broad base; pectoral fin of adult not falcate, anterior margin long, 14.2–15.8% TL; dorsal surface dark, sharply demarcated from paler ventral surface on side of head; dorsal fins dark with obvious darker tips; first dorsal-fin spine distinctly paler than base of soft portion of dorsal fin; caudal fin with broad white posterior margin, no caudal bar; flank denticles weakly tricuspid; 44–46 monospondylous centra, 89–93 precaudal centra, 116–122 total centra; adult maximum size at least 84 cm TL.

DESCRIPTION.— Body fusiform, moderately elongate (some similar-sized paratypes more robust), nape prominently humped; deepest near first dorsal-fin spine, maximum depth 0.96 (1.03–1.12 in paratypes) times width;

trunk depth 1.05 (0.92–1.01) times abdomen depth; head short 21.1 (20.4–21.6)% TL; caudal peduncle relatively robust, 25.6 (24.4–26.7)% TL. Head moderately robust, slightly wider than trunk, width 1.13 (1.08–1.27) times trunk width, 1.31 (1.03–1.38) times abdomen width, depressed forward of spiracles, becoming subtriangular towards pectoral-fin origin, length 2.24 (2.20–2.36) in pre-vent length; height 0.82 (0.80–0.87) times width. Snout short, narrowly triangular in lateral view, apex bluntly pointed, lateral prenarial margin not angular (weakly angular in some paratypes); broadly rounded in dorsal view (slightly more pointed in some paratypes), horizontal length 1.16 (1.16–1.35) times eye length, 0.62 (0.58–0.67) times interorbital space; horizontal prenarial length 2.97 (2.91–3.06) times in preoral length. Eye narrowly oval, size moderate, length 4.42 (4.33–4.88) in head length, 2.68 (2.01–2.79) times eye height; strongly notched posteriorly, notch extending halfway to spiracle as a well-developed furrow (fully connected to mid-anterior margin of spiracle in some paratypes). Spiracle moderate, subtriangular to crescentic; broad lobe-like fold on posterior margin; greatest diameter 3.36 (2.73–4.30) in eye length. Gill openings almost upright, first four subequal in size, fifth longest, height of fifth slit 2.3 (2.1–2.5)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.05 (1.04–1.17) in preoral length; upper labial furrows less than twice length of lower furrows; prominent post-oral groove, subequal in length to upper labial furrows, extending posterolaterally from angle of jaws; two series of functional teeth in upper jaw, two series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe narrow, finger-like; internarial space 2.08 (1.86–2.07) in preoral length, 2.40 (2.28–2.82) times nostril length. Dermal denticles (based on male paratypes CSIRO H 449 and CSIRO H 644–04) on flank very small, weakly to moderately tricuspid with pronounced median ridge; median ridge commencing well anterior of rest of crown, with a mesial furrow developing anteriorly and converging towards posterior tip of crown; lateral cusps weakly developed, blunt to rudimentary posteriorly, ridge extending distally, almost to tip of cusp, with a shallow mesial furrow; crown of female paratype more strongly tricuspid and more imbricated than that of male paratype. First dorsal fin elevated, upright, narrowly rounded apically; anterior margin moderately convex; upper posterior margin almost straight, not vertical, directed well anterodorsally from bottom to top, weakly concave (sometimes moderately concave) near free rear tip; free rear tip relatively thick basally, short (short to moderate in paratypes); inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, slightly posterior to free rear tip of pectoral fin; fin-spine origin above (sometimes just behind) pectoral-fin insertion; spine base broad, exposed anteriorly near junction of spine and soft portion of fin; soft portion of fin connected



Figure 1. Lateral view of: *Squalus albifrons* sp. nov. holotype (CSIRO H 4627–01, adult male 618 mm TL; image reversed).



Figure 2. Ventral view of the head of *Squalus albifrons* sp. nov. holotype (CSIRO H 4627–01, adult male 618 mm TL).

near mid-point of total spine length; spine tapering rapidly distally (less so in some paratypes), anterior margin slightly convex (sometimes almost straight); exposed portion of spine upright to tilted slightly, subequal in length to exposed portion of second dorsal-fin spine; pre-first dorsal length 3.66 (3.49–3.76) times in TL; first dorsal-fin length 1.69 (1.67–1.77) times its height, 1.16 (1.15–1.21) times second dorsal-fin length; first dorsal-fin height 1.78 (1.64–1.86) times second dorsal-fin height; exposed first dorsal-spine length 0.55 (0.53–0.63) times height of fin. Second dorsal fin of moderate size, strongly raked; anterior margin strongly convex, apex narrowly rounded; posterior margin deeply concave, maximum

concavity almost near mid-point of margin or slightly above, upper portion directed dorsoposteriorly strongly from bottom to top; free rear tip elongate, inner margin length 1.01 (0.86–1.00) times fin height; second dorsal-fin length 2.59 (2.36–2.69) times its height; spine length 1.01 (0.85–1.09) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed at about level of junction with spine and soft portion of fin; second spine moderately broad based, slender, sharply pointed distally, tapering rapidly (sometimes evenly) from point of exposure, spine tip extending behind level of insertion of fin (when undamaged), much more strongly raked than first spine; interdorsal space 0.87 (0.81–0.88)

in pre-pectoral length, 1.12 (1.08–1.11) in pre-first dorsal length; moderate interdorsal groove. Pectoral fin moderate, anterior margin weakly to moderately convex; inner margin weakly convex, length 7.7 (6.4–7.6)% TL; apex moderately rounded, lobe-like but not falcate; posterior margin moderately concave, free rear tip bluntly angular; base very short, 2.70 (2.56–2.92) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Caudal peduncle long, tapering slightly to caudal fin; subcircular in cross-section anteriorly, broadly semicircular posteriorly, ventral groove usually very well developed; lateral keels well developed, originating under insertion of second dorsal fin (more posterior in paratypes), terminating less than an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.82 (0.73–0.91) in pectoral–pelvic space, 0.83 (0.79–0.86) in prepectoral length; dorsal–caudal space 2.52 (2.29–2.59) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit rudimentary. Caudal fin relatively long, dorsal caudal margin 0.90 (0.86–1.01) in head length; length of lower caudal lobe 1.95 (1.86–1.96) in upper lobe length; upper posterior lobe moderately convex; lower lobe apex somewhat angular (narrowly rounded in some paratypes). Vertebral centra 119 (116–122 in 10 paratypes), monospondylous 45 (44–46), precaudal 89 (90–93) and caudal 30 (26–31). Teeth in upper jaw (in paratypes CSIRO H 2487–02, CSIRO H 2487–03) 13–14+13–14=27, lower jaw 11–12+11=22–23.

COLOUR.— When fresh (based on holotype and CSIRO H 3589–01): dorsal half slate grey, white ventrally; pale and dark tonal areas on head strongly demarcated before pectoral fin, their border extending from snout, under eye, through bottom half of gill slits; demarcation on trunk less evident, tail more uniformly grey ventrally. First dorsal fin dark greyish; holotype with a narrow black posterior margin extending from fin apex along the upper half of fin (not evident in paratype); free rear tip and base of fin dusky, not significantly paler than rest

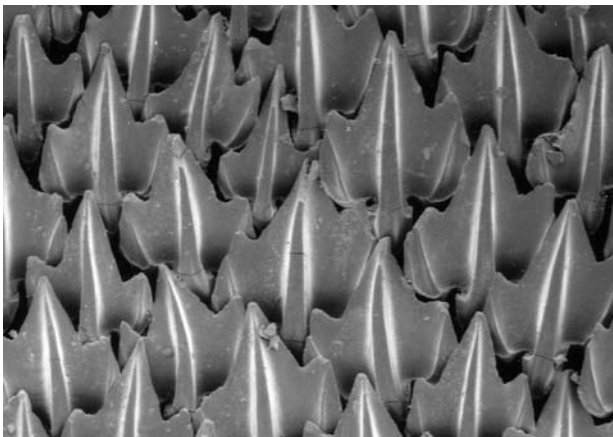


Figure 3. Cusps of the flank denticles of *Squalus albifrons* sp. nov. paratype (CSIRO H 644–04, adult male 643 mm TL). Field of view width 1.2 mm.

of fin; second dorsal fin almost uniformly dusky, apex barely darker than rest of fin; first dorsal-fin spine pale; second dorsal-fin spine dusky with dark anterior margin; skin below exposed spine bases distinctly darker than fins. Caudal fin greyish, posterior margin of upper lobe white; ventral lobe with a narrow, pale margin in holotype (weaker in paratype); base slightly darker than rest of fin. In preservative (based on holotype): body darker, more uniformly toned than in fresh condition; distinct pale and dark areas on head still evident; prominent white eyebrow above both eyes; pectoral and pelvic fins dark grey dorsally with narrow, pale posterior margins, fins similar ventrally apart from white basal portions; dorsal fins with persistent dark distal and upper posterior borders; free rear tips not paler than remaining fins; pale posterior margin of caudal fin persistent, bordered by a slightly darker submarginal bar.

SIZE.— Females reaching at least 844 mm TL (paratype); males probably smaller, largest male 695 mm TL (paratype), smallest adult male 614 mm TL (paratype). Females and males have been reported to attain 860 and 740 mm TL, respectively, off New South Wales (Graham, 2005).

DISTRIBUTION.— Known only from eastern Australia between the Townsville Trough, Queensland (ca. 17° S), and off Ulladulla, southern New South Wales (ca. 35° S), in 131–450 m depth.

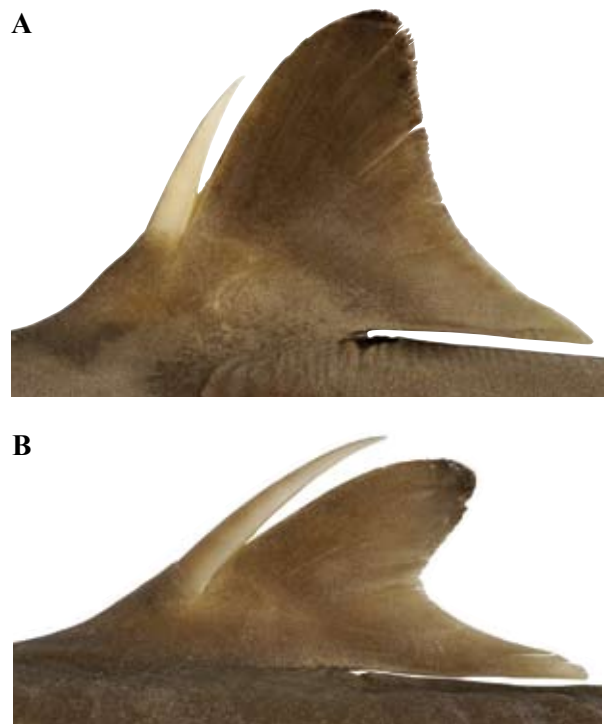


Figure 4. Lateral view of the dorsal fins of: *Squalus albifrons* sp. nov. holotype (CSIRO H 4627–01, adult male 618 mm TL) – A. first dorsal fin, B. second dorsal fin.

ETYMOLOGY.— Derived from the Latin *albi* (white) and *frons* (brow) in allusion to the white upper ocular margin in most specimens where denticles have been shed.

VERNACULAR.— Eastern Highfin Spurdog.

REMARKS.— Belongs to a group of spurdogs tentatively labeled as the ‘highfin megalops group’ that are distinguished by the combination of a short snout, robust dorsal-fin spines, tricuspid denticles, a white posterior caudal-fin margin, and a tall, upright first dorsal fin. Of the Australian species, *S. albifrons* is most similar morphometrically to another new spurdog described below in this paper (i.e. *S. sp. A: sensu* Last and Stevens, 1994), but differs in the following characters: head length 4.3–4.9 (3.8–4.3 in *S. sp. A*) times eye length; interorbital space 1.48–1.73 (1.39–1.47) times horizontal preorbital length; dorsal caudal margin 1.9–2.0 (2.0–2.1) times pre-ventral caudal margin; pre-vent length 2.0–2.4 (1.9–2.0) times length of dorsal caudal margin; first dorsal-fin length 1.7–1.8 (1.5–1.7) times its height; fifth gill-slit length 2.1–2.5 (1.9–2.1)% TL; pelvic-fin inner margin length 5.0–6.0 (4.4–5.1)% TL; upper labial furrow 2.1–2.4 (1.8–2.1)% TL; and caudal peduncle width 2.8–3.2 (2.1–2.6)% TL. *Squalus albifrons*, which appears to be more widely distributed than the sympatric *S. sp. A*, also has a relatively darker, more contrasted, dorsal surface, and fewer vertebrae (89–93 vs. 94–97 precaudal centra). The posterior margin of the first dorsal fin of *S. albifrons* is not strongly concave (rather than strongly concave) and the deepest part of the concavity is near the middle of the fin margin (rather than being situated more basally, closer to the free rear tip than the fin apex).

Squalus albifrons differs from a third new spurdog described in this paper, (i.e. *S. sp. C: sensu* Last and Stevens, 1994), in having a larger caudal fin (dorsal caudal margin 21.3–23.6 vs. 19.6–19.9% TL in *S. sp. C*; pre-ventral caudal margin 11.2–12.5 vs. 10.8–11.4% TL; caudal fork length 9.4–10.5 vs. 8.4–8.5% TL, larger pectoral fin (anterior margin 14.2–15.8 vs. 13.9–14.1% TL; posterior margin 10.8–11.7 vs. 10.2–10.4% TL) and shorter dorsal–caudal space (9.4–11.1 vs. 11.4–11.7% TL). Some other ratios appear to be useful for distinguishing these species: pre-second dorsal length 3.71–4.28 (vs. 4.32–4.36 in *S. sp. C*) times pectoral-fin anterior margin, 2.48–2.84 (vs. 3.07–3.08) times dorsal caudal margin, 3.18–3.89 (vs. 4.16–4.22) times upper postventral margin; mouth width 3.29–4.08 (vs. 3.11–3.26) times upper labial furrow; head length 2.52–2.73 (vs. 2.90–2.96) times mouth width; pre-vent length 2.00–2.24 (vs. 2.48) times dorsal caudal margin; dorsal caudal margin 1.94–2.48 (vs. 1.70–1.72) times dorsal–caudal space.

Squalus altipinnis sp. nov.

Figs 5–8; Table 1

Squalus sp. C: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 94, figs 21, 8.21, 8.33, pl. 6; Compagno, Dando and Fowler, 2005, *Sharks of the World*, p 79–80, figs, pl. 2.

Holotype. CSIRO CA 4111, adult male 586 mm TL, east of Rowley Shoals, Western Australia, 17°18' S, 120°09' E, 305 m, 4 Feb 1984.

Paratype. CSIRO CA 3297, adult male 589 mm TL, southwest of Rowley Shoals, Western Australia, 18°10' S, 118°20' E, 298 m.

DIAGNOSIS.— A moderate-sized species of *Squalus* of the ‘highfin megalops group’ with the following combination of characters: abdomen depth 9.0–10.6% TL; pre-vent length 48.6–49.2% TL, about 2.5 times dorsal caudal margin; pre-second dorsal length 4.3–4.4 times pectoral-fin anterior margin, about 3.1 times dorsal caudal margin; head width about 1.5 times abdomen width; preoral length 2.9–3.2 times horizontal preanial length, about 8.7% TL; head length 4.4–4.7 times eye length; mouth width 3.1–3.3 times length of upper labial furrow; interorbital width about 1.5 times horizontal preorbital length; fifth gill slit height 2.2–2.5% TL; anterior nasal flap strongly bifurcate; first dorsal fin upright, upper posterior margin directed posteroventrally, greatest concavity slightly closer to free rear tip than fin apex; posterior margin of second dorsal fin deeply concave; second dorsal-fin spine with a broad base; pectoral fin not falcate, anterior margin short, 13.9–14.1% TL; dorsal surface slightly darker than ventral surface, but tones not sharply demarcated on side of head; dorsal fins pale with paler tips; first dorsal-fin spine darker than base of soft portion of dorsal fin; caudal fin with broad white posterior margin, no caudal bar; flank denticles weakly to moderately tricuspid; 42–44 monospondylous centra, 88–92 precaudal centra, 114–120 total centra; adult maximum size at least 59 cm TL.

DESCRIPTION.— Body fusiform, slender, nape not prominently humped; barely deeper near first dorsal-fin spine, maximum depth 0.91 (0.90 in paratype) times width, trunk depth 1.03 (0.89) times abdomen depth; head short 22.0 (21.7)% TL; caudal peduncle slender, 27.1 (26.1)% TL. Head rather broad, much wider than trunk, width 1.23 (1.22) times trunk width, 1.53 (1.47) times abdomen width, moderately depressed forward of spiracles, becoming weakly subtriangular towards pectoral-fin origin, length 2.21 (2.27) in pre-vent length; height 0.71 (0.77) times width. Snout short, triangular in lateral view, apex bluntly pointed, lateral preanial margin not angular; broadly rounded in dorsal view, horizontal length 1.17 (1.23) times eye length, 0.69 (0.67) times interorbital space; horizontal preanial length 2.92 (3.18) times in preoral length. Eye oval, size moderate, length



Figure 5. Lateral view of: *Squalus altipinnis* sp. nov. holotype (CSIRO CA 4111, adult male 586 mm TL).



Figure 6. Ventral view of the head of *Squalus altipinnis* sp. nov. holotype (CSIRO CA 4111, adult male 586 mm TL).

4.41 (4.72) in head length, 2.76 (2.28) times depth; strongly notched posteriorly, notch more pronounced anteriorly, extending as a weak furrow to anteroventral margin of spiracle. Spiracle moderate, broadly crescentic; broad lobe-like fold on posterior margin; greatest diameter 3.28 (2.93) in eye length. Gill openings almost upright, first four subequal in size, fifth longest, height of fifth slit 2.2 (2.5)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.17 (1.15) in preoral length; upper labial furrows about twice length of lower furrows (slightly less in paratype); prominent postoral groove, subequal in length to upper labial furrow, extending posterolaterally from angle of jaws; two series of functional teeth in upper jaw, two series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of

tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe narrow, somewhat thalate; internarial space 2.13 (1.99) in preoral length, 2.31 (2.48) times nostril length. Dermal denticles (based on both types) on flank very small, weakly to moderately tricuspidate with pronounced median ridge; median ridge commencing slightly anterior of rest of crown, with a mesial furrow developing anteriorly and converging gently towards posterior tip of crown; lateral cusps short or indistinct, blunt or broadly rounded posteriorly, ridge extending distally, almost to tip of cusp, with low mesial furrow; strongly imbricated. First dorsal fin small, elevated, upright, relatively broadly rounded apically; anterior margin following profile of spine, strongly convex beyond spine tip; upper posterior margin almost

Table 1. Proportional dimensions as percentages of total length for the holotype (CSIRO H 4627–01) and ranges for the 5 paratypes of *Squalus albifrons* sp. nov. and the holotype (CSIRO CA 4111) and paratype (CSIRO CA 3297) of *Squalus altipinnis* sp. nov.

	<i>S. albifrons</i> sp. nov.			<i>S. altipinnis</i> sp. nov.	
	Holotype	Paratypes		Holotype	Paratype
		Min.	Max.		
TL – Total length	618	596	647	586	589
PCL – Precaudal length	76.4	75.9	78.1	79.9	80.0
PD2 – Pre-second dorsal length	59.1	58.6	61.0	60.4	61.0
PD1 – Pre-first dorsal length	27.3	26.6	28.6	27.6	27.0
SVL – Pre-vent length	47.2	46.9	48.1	48.6	49.2
PP2 – Prepelvic length	45.0	45.0	46.3	46.1	46.5
PP1 – Prepectoral length	21.3	20.2	21.8	22.2	21.7
HDL – Head length	21.1	20.4	21.6	22.0	21.7
PG1 – Prebranchial length	17.9	17.2	18.1	18.4	18.0
PSP – Prespiracular length	11.6	11.3	11.9	12.1	11.7
POB – Preorbital length	6.9	6.7	7.0	6.8	6.8
PRN – Prenarial length	4.3	4.4	4.5	4.4	4.5
POR – Preoral length	8.7	8.4	9.1	8.7	8.7
INLF – Inner nostril-labial furrow space	4.5	4.4	4.8	4.7	4.7
MOW – Mouth width	8.3	7.5	8.6	7.4	7.5
ULA – Labial furrow length	2.2	2.1	2.4	2.3	2.4
INW – Internarial space	4.2	4.3	4.6	4.1	4.3
INO – Interorbital space	8.9	8.3	9.4	8.5	8.5
EYL – Eye length	4.8	4.4	4.8	5.0	4.6
EYH – Eye height	1.8	1.7	2.2	1.8	2.0
SPL – Spiracle length	1.4	1.1	1.6	1.5	1.6
GS1 – First gill-slit height	2.2	1.9	2.1	2.0	2.0
GS5 – Fifth gill-slit height	2.3	2.1	2.5	2.2	2.5
IDS – Interdorsal space	24.4	24.4	26.1	23.8	24.8
DCS – Dorsal-caudal space	9.7	9.4	11.1	11.4	11.7
PPS – Pectoral-pelvic space	21.1	19.5	22.6	21.8	22.1
PCA – Pelvic-caudal space	25.6	24.4	26.7	27.1	26.1
D1L – First dorsal length	14.6	13.7	14.9	14.7	14.9
D1A – First dorsal anterior margin	12.7	10.9	12.5	12.6	12.0
D1B – First dorsal base length	8.9	8.5	9.3	9.6	9.6
D1H – First dorsal height	8.6	7.7	8.9	7.8	7.9
D1I – First dorsal inner margin	5.9	5.2	6.2	5.8	5.4
D1P – First dorsal posterior margin	10.1	9.9	10.6	8.9	9.6
D1ES – First dorsal spine length	4.8	4.4	5.4	4.9	5.3
D1BS – First dorsal spine base width	0.9	1.0	1.0	1.1	1.1
D2L – Second dorsal length	12.5	11.4	12.9	12.9	12.6
D2A – Second dorsal anterior margin	11.1	10.0	11.3	11.5	10.9
D2B – Second dorsal base length	7.7	7.3	8.3	8.5	7.9
D2H – Second dorsal height	4.8	4.3	5.1	4.5	4.8
D2I – Second dorsal inner margin	4.9	4.1	4.9	4.3	4.4
D2P – Second dorsal posterior margin	5.2	4.8	5.8	4.6	5.4
D2ES – Second dorsal spine length	4.9	3.8	5.2	4.7	4.8
D2BS – Second dorsal spine base width	0.7	0.7	0.9	0.9	0.9

Table 1. cont'd

	<i>S. albifrons</i> sp. nov.			<i>S. altipinnis</i> sp. nov.	
	Holotype	Paratypes		Holotype	Paratype
		Min.	Max.		
P1A – Pectoral anterior margin	15.2	14.2	15.8	13.9	14.1
P1I – Pectoral inner margin	7.7	6.4	7.6	7.1	6.6
P1B – Pectoral base length	5.6	5.4	6.0	5.2	5.1
P1P – Pectoral posterior margin	11.4	10.8	11.7	10.4	10.2
P2L – Pelvic length	10.6	9.2	9.8	10.4	10.0
P2H – Pelvic height	5.1	4.3	4.7	4.7	4.9
P2I – Pelvic inner margin	6.0	5.0	5.4	5.3	5.1
CDM – Dorsal caudal margin	23.4	21.3	23.6	19.6	19.9
CPV – Preventral caudal margin	12.0	11.2	12.5	10.8	11.4
CPU – Upper postventral caudal margin	17.0	15.7	18.4	14.5	14.4
CPL – Lower postventral caudal margin	4.4	3.9	4.9	4.0	4.3
CFW – Caudal fork width	6.5	6.8	7.3	6.4	6.8
CFL – Caudal fork length	9.9	9.4	10.5	8.5	8.4
HANW – Head width at nostrils	6.7	6.6	7.1	6.8	6.7
HAMW – Head width at mouth	11.5	11.2	12.1	10.6	11.4
HDW – Head width	12.8	12.4	13.0	12.6	12.7
TRW – Trunk width	11.3	10.0	12.0	10.2	10.5
ABW – Abdomen width	9.8	9.4	12.5	8.3	8.6
TAW – Tail width	6.2	6.1	6.7	5.7	6.9
CPW – Caudal peduncle width	3.2	2.8	2.9	2.6	2.6
HDH – Head height	10.4	10.2	11.3	9.0	9.8
TRH – Trunk height	10.8	10.9	12.3	9.3	9.4
ABH – Abdomen height	10.4	11.2	12.6	9.0	10.6
TAH – Tail height	6.5	6.2	7.2	5.7	6.2
CPH – Caudal peduncle height	2.6	2.5	2.7	2.3	2.2
CLO – Clasper outer length	3.6	3.2	3.6	3.1	3.2
CLI – Clasper inner length	6.8	6.3	6.3	6.3	6.3
CLB – Clasper base width	1.3	1.5	1.6	1.5	1.5

straight, not vertical, directed well anterodorsally from bottom to top, moderately concave near free rear tip (less so in paratype); free rear tip narrow basally (otherwise moderate); inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior (by about an eye diameter) to free rear tip of pectoral fin; fin-spine origin well posterior to pectoral-fin insertion; spine base broad, exposed anteriorly well below junction of spine and soft portion of fin (almost three-quarters of spine exposed); soft portion of fin connected slightly above mid-point of total spine length; spine tapering only slightly distally, anterior margin almost straight; exposed portion more upright, subequal in length to exposed portion of second dorsal-fin spine; pre-first dorsal length 3.63 (3.70) times in TL; first dorsal-fin length 1.89 (1.90) times its height, 1.14 (1.19) times second dorsal-fin length; first dorsal-fin height

1.72 (1.64) times second dorsal-fin height; exposed first dorsal spine length 0.64 (0.68) times height of fin. Second dorsal fin small, strongly raked; anterior margin moderately convex, apex narrowly rounded; posterior margin very deeply concave, maximum concavity almost near mid-point of margin, upper portion directed dorsoposteriorly strongly from bottom to top; free rear tip relatively short (or moderate), inner margin length 0.96 (0.92) times fin height; second dorsal-fin length 2.84 (2.61) times its height; spine length 1.03 (1.00) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed well below level of junction with spine and soft portion of fin, proximal part of spine base close to dorsal profile of body; second spine moderately broad based, slender, not sharply pointed distally (possibly with minor apical damage in both types), not tapering rapidly just above point of exposure, spine tip extending just

behind (otherwise over) level of insertion of fin, much more strongly raked than first dorsal spine; interdorsal space 0.93 (0.88) in pre-pectoral length, 1.16 (1.09) in pre-first dorsal length; moderate interdorsal groove. Pectoral fin small, anterior margin weakly convex; inner margin straight to slightly convex (otherwise moderately convex), length 7.1 (6.6)% TL; apex narrowly rounded, not lobe-like or falcate; posterior margin weakly concave (fin weakly falcate with concave posterior margin in paratype), free rear tip broadly rounded; base very short, 2.67 (2.76) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Caudal peduncle long, tapering slightly to caudal fin; subcircular in cross-section anteriorly, broadly semicircular posteriorly, ventral groove very well developed; lateral keels well developed, originating under insertion of second dorsal fin, terminating about half or less than an eye diameter behind caudal-fin insertion; pelvic-caudal space 0.81 (0.84) in pectoral–pelvic space, 0.82 (0.83) in prepectoral length; dorsal–caudal space 2.08 (2.11) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit rudimentary. Caudal fin short, dorsal caudal margin 1.12 (1.09) in head length; length of lower caudal lobe 1.81 (1.75) in upper lobe length; upper posterior lobe strongly convex, base of lobe broad; lower lobe apex narrowly rounded (more angular in paratype). Vertebral centra 120 (114 in paratype), monospondylous 44 (42), precaudal 92 (88) and caudal 28 (26). Teeth in upper jaw (of paratype, CSIRO CA 3297) 13+14=27, lower jaw 11+11=22.

COLOUR.— In preservative: dorsal half pale yellowish grey, off white ventrally; pale and dark areas on head and trunk not strongly demarcated, tones merging gradually. First dorsal-fin base off white, strongly demarcated from body and main portion of fin; soft portion of fin uniformly light grey, margin paler, no dark areas at fin apex; second dorsal fin similar to first dorsal, base also off white, strongly demarcated from rest of fin; both

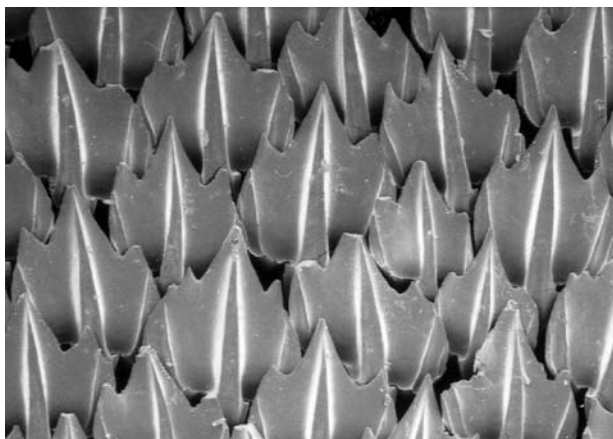


Figure 7. Cusps of the flank denticles of *Squalus altipinnis* sp. nov. paratype (CSIRO CA 3297, adult male 589 mm TL). Field of view width 1.4 mm.

dorsal-fin spines almost uniformly dark grey (slightly darker on anterior edge of first dorsal fin in holotype), much darker than base of soft portion of fin. Caudal fin light grey, paler along posterior margin in both lobes; no dark areas on fin. Pectoral and pelvic fins similar to first dorsal fin, uniformly light grey with a narrow, pale posterior margin; fin bases off white on ventral surface.

SIZE.— Presumably a small spurdog, known only from two adult male specimens, 586 and 589 mm TL.

DISTRIBUTION.— Continental slope off northwestern Australia in the vicinity of the Rowley Shoals (ca. 17–18° S) in about 300 m depth.

ETYMOLOGY.— Derived from the Latin combination of *altus* (high) and *pinna* (fin) in allusion to the upright dorsal fin, typical of members of this subgroup.

VERNACULAR.— Western Highfin Spurdog.

REMARKS.— *Squalus altipinnis* differs from *S. albifrons*, in having a smaller caudal fin (dorsal caudal margin 19.6–19.9 vs. 21.3–23.6% TL in *S. albifrons*; preventral caudal margin 10.8–11.4 vs. 11.2–12.5% TL; caudal fork length 8.4–8.5 vs. 9.4–10.5% TL), smaller pectoral fin (anterior margin 13.9–14.1 vs. 14.2–15.8% TL; posterior margin 10.2–10.4 vs. 10.8–11.7% TL)

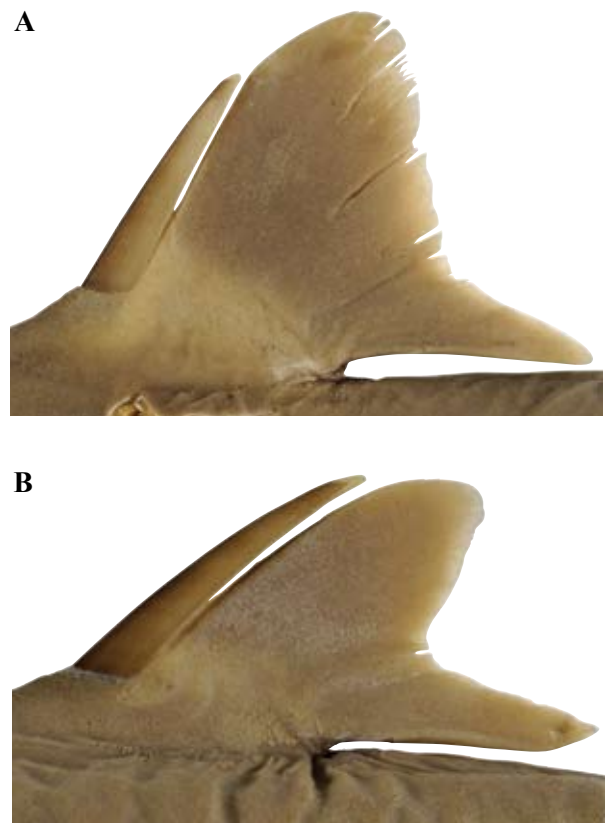


Figure 8. Lateral view of the dorsal fins of: *Squalus altipinnis* sp. nov. holotype (CSIRO CA 4111, adult male 586 mm TL) – A. first dorsal fin, B. second dorsal fin.

and longer dorsal-caudal space (11.4–11.7 vs. 9.4–11.1% TL). Some other ratios appear to be useful for distinguishing these species: pre-second dorsal-fin length 4.32–4.36 (3.71–4.28) times pectoral-fin anterior margin, 3.07–3.08 (2.48–2.84) times dorsal caudal margin, 4.16–4.22 (3.18–3.89) times upper post ventral margin; mouth width 3.11–3.26 (3.29–4.08) times upper labial furrow; head length 2.90–2.96 (2.52–2.73) times mouth width; pre-vent length about 2.48 (2.00–2.24) times dorsal caudal margin; dorsal caudal margin 1.70–1.72 (1.94–2.48) times dorsal-caudal space.

Squalus altipinnis differs from a third new highfin spurdog described in this paper, (i.e. *S. sp. A: sensu* Last and Stevens, 1994), in having a smaller caudal fin (dorsal caudal margin 19.6–19.9 vs. 23.3–24.0% TL in *S. sp. A*; pre-ventral caudal margin 10.8–11.4 vs. 11.5–11.9% TL; precaudal length 79.9–80 vs. 74.9–76.1% TL), smaller anterior pectoral-fin margin (13.9–14.1 vs. 14.6–16.4% TL), and longer dorsal caudal space (11.4–11.7 vs. 9.5–10.8% TL). Several other ratios appear to be useful for distinguishing these species: pre-second dorsal length 4.32–4.36 (vs. 3.60–3.98 in *S. sp. A*) times pectoral-fin anterior margin, 3.07–3.08 (vs. 2.39–2.57) times dorsal caudal margin, 4.16–4.22 (vs. 3.16–3.33) times upper post ventral margin; mouth width 3.11–3.26 (vs. 3.45–4.28) times upper labial furrow; head length 2.90–2.96 (vs. 2.63–2.79) times mouth width; pre-vent length about 2.48 (vs. 1.88–2.00) times dorsal caudal margin; dorsal caudal margin 1.70–1.72 (vs. 2.21–2.46) times dorsal-caudal space, 1.75–1.81 (vs. 2.01–2.09) times pre-ventral caudal margin; head length 4.41–4.72 (vs. 3.77–4.26) times eye length; 1.09–1.12 (vs. 0.85–0.89) times dorsal caudal margin; and first dorsal-fin length 1.89–1.90 (vs. 1.50–1.68) times its height.

***Squalus notocaudatus* sp. nov.**

Figs 9–12; Table 2

Squalus sp. A: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 48, 95, figs 19, 8.31, pl. 6; Compagno, Dando and Fowler, 2005, *Sharks of the world*, p 78–79, figs, pl. 2.

Holotype. CSIRO H 1368–02, immature male 619 mm TL, east of Flinders Reef, Queensland, 17°27' S, 149°46' E, 348 m, 3 Dec 1985.

Paratypes. 3 specimens. CSIRO H 1322–01, female 393 mm TL, east of Flinders Reef, Queensland, 17°28' S, 149°41' E, 402 m; CSIRO H 1323–01, immature male 368 mm TL, Queensland Plateau, east of Flinders Reef, Queensland, 17°32' S, 149°34' E, 454 m; CSIRO H 1321–01, female 495 mm TL, Capricorn Channel, east of Rockhampton, Queensland, 22°52' S, 152°42' E, 282 m.

DIAGNOSIS.— A moderate-sized or large species of *Squalus* of the 'highfin megalops group' with the following combination of characters: abdomen depth 8.6–

11.1% TL; pre-vent length 45.3–46.5% TL, 1.9–2.0 times dorsal caudal margin; pre-second dorsal length 3.6–4.0 times pectoral-fin anterior margin, 2.4–2.6 times dorsal caudal margin; head width 1.4–1.6 times abdomen width; preoral length 2.8–3.2 times horizontal preanial length, 8.4–9.5% TL; head length 3.8–4.3 times eye length; mouth width 3.4–4.3 times length of upper labial furrow; interorbital width 1.4–1.5 times horizontal preorbital length; fifth gill slit height 1.9–2.1% TL; anterior nasal flap strongly bifurcate; first dorsal fin upright, upper posterior margin almost vertical, greatest concavity closer to free rear tip than fin apex; posterior margin of second dorsal fin deeply concave; second dorsal-fin spine with a broad base; pectoral fin of adult weakly falcate, anterior margin long, 14.6–16.4% TL; both dorsal and ventral surfaces pale; dorsal fins pale with obvious dark tips; first dorsal-fin spine and base of soft portion of dorsal fin both pale; caudal fin with broad white posterior margin; prominent dark, diagonal subterminal streak parallel to the upper posterior margin; flank denticles strongly tricuspid; 47–49 monospondylous centra, 94–97 precaudal centra, 123–127 total centra; largest specimen immature at 62 cm TL.

DESCRIPTION.— Body fusiform, slender, nape not prominently humped; deepest near first dorsal-fin spine, maximum depth 1.06 (0.94–1.06 in paratypes) times width, trunk depth 1.08 (0.83–0.95) times abdomen depth; head short 19.7 (20.4–21.1)% TL; caudal peduncle slender, 25.6 (25.2–27.1)% TL. Head rather broad, much wider than trunk, width 1.34 (1.24–1.41) times trunk width, 1.46 (1.42–1.60) times abdomen width, depressed forward of spiracles, becoming subtriangular towards pectoral-fin origin, length 2.36 (2.18–2.22) in pre-vent length; height 0.74 (0.71–0.78) times width. Snout short, narrowly triangular in lateral view, apex bluntly pointed, lateral preanial margin slightly angular; narrowly rounded in dorsal view, distinct preanial notch (not evident in paratype CSIRO H 1321–01), horizontal length 1.19 (1.10–1.31) times eye length, 0.68 (0.68–0.72) times interorbital space; horizontal preanial length 2.87 (2.83–3.17) times in preoral length. Eye narrowly oval, size moderate, length 4.23 (3.77–4.26) in head length, 2.81 (2.32–3.45) times depth; strongly notched posteriorly, notch extending as a well-developed (less developed in two smallest paratypes, CSIRO H 1322–01 and CSIRO H 1323–01) furrow to anteroventral margin of spiracle. Spiracle moderate, subtriangular (variably closed in paratypes); narrow lobe-like fold on posterior margin, in paratypes more strongly produced with a convex anterior margin; greatest diameter 4.03 (3.60–4.44) in eye length. Gill openings almost upright (variable in paratypes), first four subequal in size, fifth usually slightly longer, height of fifth slit 1.9 (2.0–2.1)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.15 (1.19–1.26) in preoral length; upper labial furrows about twice or less length of lower furrows; prominent postoral groove, subequal in length to upper labial furrows, extending posterolaterally from angle of



Figure 9. Lateral view of: *Squalus notocaudatus* sp. nov. holotype (CSIRO H 1368–02, immature male 619 mm TL; image reversed).



Figure 10. Ventral view of the head of *Squalus notocaudatus* sp. nov. holotype (CSIRO H 1368–02, immature male 619 mm TL).

jaws; two series of functional teeth in upper jaw, two series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe narrow, finger-like; internarial space 1.91 (1.92–2.25) in preoral length, 2.47 (2.19–2.56) times nostril length. Dermal denticles (based on paratypes CSIRO H 1321–01 and CSIRO H 1322–01) on flank very small, strongly tricuspidate with pronounced median ridge; median ridge commencing well anterior to rest of crown, with a mesial furrow developing anteriorly and converging towards posterior tip of crown; lateral cusps well to very well developed, acute posteriorly, ridge anterior, not distal or extending toward tip of cusp; weakly or not imbricated, more regular on snout tip. First dorsal fin elevated, upright, narrowly rounded apically; anterior margin strongly convex; upper posterior margin

almost straight, subvertical, not directed anterodorsally from bottom to top (slightly anterodorsally in paratype CSIRO H 1321–01), moderately concave near free rear tip; free rear tip moderately short (less well developed in some paratypes), moderately thick basally; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, slightly posterior to free rear tip of pectoral fin; fin-spine origin more-or-less above pectoral-fin insertion; spine base broad, exposed anteriorly just below junction of spine and fin; soft portion of fin connected near mid-point of total spine length (skin covering smallest paratypes extending toward spine apex, in paratype CSIRO H 1323–01 exposed height of spine equivalent to height of spiracle); spine tapering weakly distally (variable in paratypes), anterior margin weakly convex (more strongly convex in paratype CSIRO H 1321–01); exposed portion raked slightly, shorter in length to exposed portion of second dorsal-fin spine; pre-first dorsal length 3.81 (3.64–3.73) times in TL; first

dorsal-fin length 1.68 (1.50–1.66) times its height, 1.13 (1.10–1.19) times second dorsal-fin length; first dorsal-fin height 1.74 (1.71–1.77) times second dorsal-fin height; exposed first dorsal spine length 0.55 (0.40–0.47) times height of fin. Second dorsal fin of moderate size, strongly raked; anterior margin strongly convex, apex narrowly rounded; posterior margin deeply concave, angle about 90° or slightly more, maximum concavity almost near mid-point of margin, upper portion directed dorsoposteriorly strongly from bottom to top; free rear tip elongate, inner margin length 0.98 (0.86–1.01) times fin height; second dorsal-fin length 2.59 (2.22–2.65) times its height; spine length 1.20 (0.90–0.99) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed just below level of junction with spine and soft portion of fin; second spine moderately broad based, slender, partially covered anteriorly by skin in two smallest paratypes), sharply pointed distally, tapering evenly from point of exposure, spine tip extending behind level of insertion of fin (over in paratype CSIRO H 1323–01), much more strongly raked than first spine; interdorsal space 0.78 (0.87–0.89) in length from snout tip to pectoral-fin origin, 1.04 (1.11–1.17) in pre-first dorsal length; moderate interdorsal groove (weaker in paratypes). Pectoral fin well developed, anterior margin weakly convex; inner margin moderately convex, length 7.3 (7.5–7.8)% TL; apex narrowly rounded, lobe-like, somewhat falcate (less pronounced in smallest paratypes); posterior margin strongly concave, free rear tip bluntly angular; base very short, 3.00 (2.67–3.26) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Caudal peduncle long, tapering slightly to caudal fin; subcircular in cross-section anteriorly, almost semicircular posteriorly, ventral groove very well developed; lateral keels poorly developed, originating anterior to (under in some paratypes) insertion of second dorsal fin, terminating about half an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.85 (0.73–0.83)

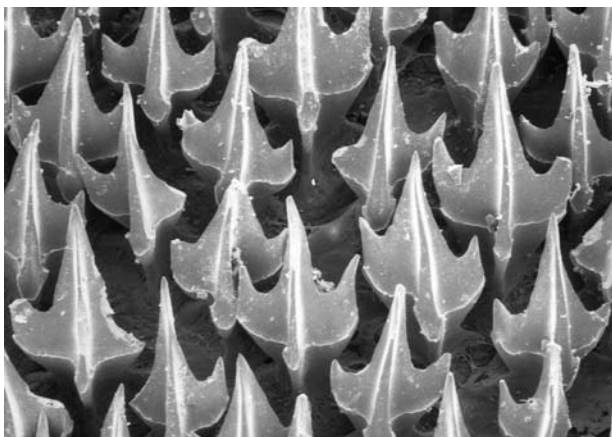


Figure 11. Cusps of the flank denticles of *Squalus notocaudatus* sp. nov. paratype (CSIRO H 1322–01, female 393 mm TL). Field of view width 0.8 mm.

in pectoral–pelvic space, 0.76 (0.78–0.83) in prepectoral length; dorsal–caudal space 2.66 (2.15–2.40) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit rudimentary. Caudal fin relatively elongate, dorsal caudal margin 0.85 (0.85–0.89) in head length; length of lower caudal lobe 2.01 (2.02–2.09) in upper lobe length; upper posterior lobe moderately convex; lower lobe apex somewhat angular (more rounded in paratypes). Vertebral centra 127 (123–125 in 3 paratypes), monospondylous 49 (47–49), precaudal 97 (94–96) and caudal 30 (29). Teeth in upper jaw (of paratype, CSIRO H 1321–01) 14+13=27, lower jaw 12+11=23.

COLOUR.— When fresh (based on holotype): uniform pale grey dorsally; not significantly paler on ventral surface, dorsal and ventral tonal areas merging gradually, not sharply demarcated. First dorsal fin pale grey, anterior basal half whitish, narrow black edge to upper anterior margin; second-dorsal fin pale greyish, slightly paler through base and free rear tip, thin black margin along anterior, apical and posterior margins; first dorsal-fin spine pale; second dorsal-fin spine dusky, anterior margin darkest. Caudal fin upper lobe with thin black anterior fringe; posterior margin broadly white, remaining upper lobe pale grey; ventral lobe pale; prominent blackish, diagonal, bar-like marking extending from near anterior

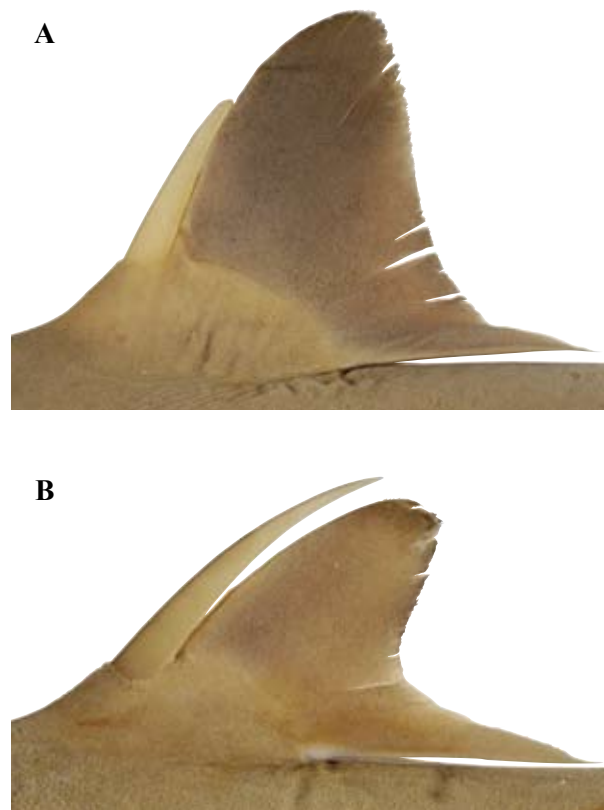


Figure 12. Lateral view of the dorsal fins of: *Squalus notocaudatus* sp. nov. holotype (CSIRO H 1368–02, immature male 619 mm TL) – A. first dorsal fin, B. second dorsal fin.

Table 2. Proportional dimensions as percentages of total length for the holotype (CSIRO H 1368–02) and ranges for the 3 paratypes of *Squalus notocaudatus* sp. nov.

	<i>S. notocaudatus</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
TL — Total length	619	368	495
PCL — Precaudal length	75.9	74.9	76.1
PD2 — Pre-second dorsal length	59.8	57.4	58.2
PD1 — Pre-first dorsal length	26.2	26.8	27.5
SVL — Pre-vent length	46.5	45.3	46.1
PP2 — Prepelvic length	44.9	44.2	44.8
PP1 — Prepectoral length	19.6	20.6	21.2
HDL — Head length	19.7	20.4	21.1
PG1 — Prebranchial length	17.0	17.6	18.3
PSP — Prespiracular length	11.3	12.1	12.2
POB — Preorbital length	6.4	6.9	7.0
PRN — Prenarial length	4.3	4.5	5.0
POR — Preoral length	8.4	9.3	9.5
INLF — Inner nostril-labial furrow space	4.5	4.6	4.9
MOW — Mouth width	7.3	7.3	8.0
ULA — Labial furrow length	2.0	1.8	2.1
INW — Internarial space	4.4	4.2	4.8
INO — Interorbital space	8.1	8.8	9.2
EYL — Eye length	4.7	4.8	5.5
EYH — Eye height	1.7	1.6	2.1
SPL — Spiracle length	1.2	1.2	1.4
GS1 — First gill-slit height	1.8	2.0	2.1
GS5 — Fifth gill-slit height	1.9	2.0	2.1
IDS — Interdorsal space	25.2	23.4	24.2
DCS — Dorsal-caudal space	9.5	10.1	10.8
PPS — Pectoral-pelvic space	21.6	19.1	20.9
PCA — Pelvic-caudal space	25.6	25.2	27.1
D1L — First dorsal length	13.7	13.6	14.1
D1A — First dorsal anterior margin	11.9	12.9	13.7
D1B — First dorsal base length	8.5	7.9	9.0
D1H — First dorsal height	8.2	8.3	9.4
D1I — First dorsal inner margin	5.6	5.0	5.7
D1P — First dorsal posterior margin	9.1	8.8	10.5
D1ES — First dorsal spine length	4.5	3.6	4.4
D1BS — First dorsal spine base width	1.0	0.7	0.9
D2L — Second dorsal length	12.1	11.8	12.5
D2A — Second dorsal anterior margin	10.2	10.5	11.5
D2B — Second dorsal base length	7.6	7.2	8.2
D2H — Second dorsal height	4.7	4.7	5.3
D2I — Second dorsal inner margin	4.6	4.5	4.7
D2P — Second dorsal posterior margin	5.4	4.7	5.7
D2ES — Second dorsal spine length	5.6	4.2	5.3
D2BS — Second dorsal spine base width	0.9	0.8	0.8

Table 1. cont'd

	<i>S. notocaudatus</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
P1A — Pectoral anterior margin	16.4	14.6	16.0
P1I — Pectoral inner margin	7.3	7.5	7.8
P1B — Pectoral base length	5.5	4.9	5.5
P1P — Pectoral posterior margin	10.6	9.9	11.4
P2L — Pelvic length	9.4	9.1	9.6
P2H — Pelvic height	4.4	4.3	4.8
P2I — Pelvic inner margin	4.7	4.4	5.1
CDM — Dorsal caudal margin	23.3	23.4	24.0
CPV — Preventral caudal margin	11.6	11.5	11.9
CPU — Upper postventral caudal margin	17.9	17.5	18.2
CPL — Lower postventral caudal margin	4.1	3.7	4.7
CFW — Caudal fork width	6.3	6.5	6.9
CFL — Caudal fork length	9.1	8.6	9.9
HANW — Head width at nostrils	6.7	6.7	7.1
HAMW — Head width at mouth	10.9	10.9	11.5
HDW — Head width	11.8	12.7	12.7
TRW — Trunk width	8.9	9.0	10.2
ABW — Abdomen width	8.1	7.9	9.0
TAW — Tail width	5.7	5.5	6.1
CPW — Caudal peduncle width	2.1	2.5	2.6
HDH — Head height	8.7	8.9	10.0
TRH — Trunk height	9.4	9.2	10.2
ABH — Abdomen height	8.6	10.3	11.1
TAH — Tail height	5.9	6.1	7.1
CPH — Caudal peduncle height	2.4	2.5	2.6
CLO — Clasper outer length	1.4	0.6	0.6
CLI — Clasper inner length	3.2	2.7	2.7
CLB — Clasper base width	0.7	0.5	0.5

margin of lower lobe towards caudal fork and on to sub-basal portion of upper lobe. In preservative (based on holotype): holotype more uniformly toned than in fresh condition, somewhat yellowish brown; fins with dark markings less evident; pectoral and pelvic fins uniform (possibly with indistinct pale edges on both fins); tip of snout with irregular blackish marking. In small paratype (CSIRO H 1323–01), black snout marking absent, dark areas on fins more strongly developed than on fresh holotype; free rear tip of first dorsal fin whitish, distinctly paler than non-basal portion of fin; blackish area on second dorsal fin more pronounced, free rear tip pale; dark anterior marking on upper lobe of caudal fin broader than on holotype; dark streak through lower half of fin well defined, strongly contrasted with broad whitish margin at caudal fork.

SIZE.— Known from limited material. Largest specimen is the 619 mm TL, immature male holotype (CSIRO H 1368–02). The 3 paratypes range from 368 to 495 mm TL.

DISTRIBUTION.— Based on a few specimens collected off central Queensland near Flinders Reef (ca. 17° S) and off Rockhampton (ca. 23° S) in 225–454 m depth.

ETYMOLOGY.— Derived from a combination of the Latin *nota* (mark) and *cauda* (tail) with reference to the dark bar on the caudal fin.

VERNACULAR.— Bartail Spurdog.

REMARKS.— *Squalus notocaudatus* is most similar morphometrically to *S. albifrons*, but differs in the

following characters: head length 3.8–4.3 (4.3–4.9 in *S. albifrons*) times eye length; interorbital space 1.39–1.47 (1.48–1.73) times horizontal preorbital length; dorsal caudal margin 2.0–2.1 (1.9–2.0) times pre-ventral caudal margin; pre-vent length 1.9–2.0 (2.0–2.4) times length of dorsal caudal margin; first dorsal-fin length 1.5–1.7 (1.7–1.8) times its height; fifth gill-slit length 1.9–2.1 (2.1–2.5)% TL; pelvic-fin inner margin length 4.4–5.1 (5.0–6.0)% TL; upper labial furrow 1.8–2.1 (2.1–2.4)% TL; and caudal peduncle width 2.1–2.6 (2.8–3.2)% TL. *Squalus notocaudatus* is much paler coloured on the dorsal surface than *S. albifrons*, and the side of the head does not display sharp tonal differences. It also has more vertebrae (94–97 vs. 89–93 precaudal centra), and the posterior margin of the first dorsal fin of *S. notocaudatus*, which is oriented almost vertically (rather than being directed posteroventrally), is more strongly concave with the deepest part of the concavity situated more basally (i.e. closer to the free rear tip than the fin apex rather than about midway between the free rear tip and the fin margin).

Squalus notocaudatus differs from *S. altipinnis*, in having a much larger caudal fin (dorsal caudal margin 23.3–24.0 vs. 19.6–19.9% TL in *S. altipinnis*; pre-ventral caudal margin 11.5–11.9 vs. 10.8–11.4% TL; precaudal length 74.9–76.1 vs. 79.9–80% TL), larger anterior pectoral-fin margin (14.6–16.4 vs. 13.9–14.1% TL), and shorter dorsal–caudal space (9.5–10.8 vs. 11.4–11.7% TL). Some other ratios appears to be useful for distinguishing these species: pre-second dorsal length 3.60–3.98 (vs. 4.32–4.36 in *S. altipinnis*) times pectoral-fin anterior margin, 2.39–2.57 (vs. 3.07–3.08) times dorsal caudal margin, 3.16–3.33 (vs. 4.16–4.22) times upper post ventral margin; mouth width 3.45–4.28 (vs. 3.11–3.26) times upper labial furrow; head length 2.63–2.79 (vs. 2.90–2.96) times mouth width; pre-vent length 1.88–2.00 (vs. 2.48) times dorsal caudal margin; dorsal caudal margin 2.21–2.46 (vs. 1.70–1.72) times dorsal–caudal space, 2.01–2.09 (vs. 1.75–1.81) times pre-ventral caudal margin; head length 3.77–4.26 (vs. 4.41–4.72) times eye length; 0.85–0.89 (vs. 1.09–1.12) times dorsal caudal margin; and first dorsal-fin length 1.50–1.68 (vs. 1.89–1.90) times its height.

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Part 6 — Description of *Squalus chloroculus* sp. nov., a new spurdog from southern Australia, and the resurrection of *S. montalbani* Whitley

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ABSTRACT.— A new spurdog, *Squalus chloroculus* sp. nov., is described based on specimens from the upper continental slope off southern Australia. This species and a closely related Indo–West Pacific species, *S. montalbani* Whitley, have been consistently confused with each other and misidentified as a western North Pacific spurdog, *S. mitsukurii* Jordan and Snyder. In this paper, the new species is described and *Squalus montalbani* is resurrected and rediagnosed based on material from the Philippines, Indonesia, and tropical and warm temperate Australia. Intraspecific variation between populations of *S. montalbani* across these regions is discussed. These species are compared to *S. mitsukurii* and belong to a subgroup of *Squalus*, the ‘mitsukurii group’, whose members have a moderately elongate snout, stocky body, and a dark caudal bar on the posterior notch of the caudal fin. These spurdogs are very similar morphologically but can be distinguished using molecular techniques and through a combination of caudal-fin coloration, meristics, and morphometrics of the head, trunk and fins.

Key words. Squaloidea – Squalidae – *Squalus chloroculus* – new species – *Squalus montalbani* – resurrected species – southern Australia

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INTRODUCTION

Squalus mitsukurii Jordan and Snyder in Jordan and Fowler, 1903, which has long been considered to be a very wide ranging dogfish in temperate and tropical oceans (Compagno, 1984), is now thought to be a species complex (Last and Stevens, 1994; Compagno *et al.*, 2005). Members of this complex, referred to here as the ‘mitsukurii group’, are characterised by their large relative size, a dark caudal bar, low dorsal-fin spines, and a small, raked first dorsal fin. An Australian form referable to *S. mitsukurii* was reported by Last and Stevens (1994) from the temperate and tropical continental slope of Australia between Townsville (Queensland) and Shark Bay (Western Australia). Molecular studies (see Ward *et al.*, 2007, Part 12 of this issue) of Australian members of this complex revealed the existence of two species. One of these spurdogs has a temperate distribution off southern Australia, whereas the other species occurs primarily in subtropical and tropical latitudes off both eastern and western Australia. These species are very similar morphologically to each other and to *S. mitsukurii*.

Market surveys at various landing sites in the Philippines (late 1990’s) and eastern Indonesia (April 2001 to March 2006) produced a wide variety of sharks, rays and chimaeras, including many squaloids, for research. This material included multiple species of *Squalus*, one

of which appeared to be conspecific with an Australian member of the ‘mitsukurii group’. A Philippine species, which was provisionally identified as *S. cf. mitsukurii*, was thought to be non-conspecific with *S. mitsukurii* (Compagno *et al.*, 2005). Smith and Radcliffe in Smith (1912) described *Squalus philippinus* (a junior homonym of *S. philippinus* Shaw, 1804 = *Heterodontus portusjacksoni* (Meyer, 1793)) from the west coast of Luzon Island, Philippines. This species, which was later renamed *Squalus montalbani* by Whitley (1931), was considered to be a likely junior synonym of *S. mitsukurii* (Compagno, 1984).

In the following paper, the temperate Australian spurdog is described as a new species and *Squalus montalbani* is resurrected and rediagnosed. These species are compared to the types and other material, from near the type locality (off Japan), of *Squalus mitsukurii*.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007). Diagnoses are provided for *S. montalbani* and the new species; mean values for diagnostic ratios and counts are given in parentheses after their ranges. In the new species description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the measured paratypes.

Table 1. Proportional dimensions as percentages of total length for the holotypes of *Squalus montalbani* (USNM 70256) and *Squalus mitsukurii* (SU 12793) and ranges for additional material measured.

	<i>S. montalbani</i>			<i>S. mitsukurii</i>		
	n = 14			n = 4		
	Holotype	Min.	Max.	Holotype	Min.	Max.
TL – Total length	311	520	843	719	266	855
PCL – Precaudal length	76.5	77.1	79.9	76.6	78.2	79.0
PD2 – Pre-second dorsal length	57.6	59.1	62.8	59.8	58.6	61.2
PD1 – Pre-first dorsal length	30.7	26.5	30.0	30.9	28.5	32.3
SVL – Pre-vent length	47.2	48.6	52.7	51.5	48.9	52.2
PP2 – Prepelvic length	43.8	47.2	50.8	48.5	47.4	50.1
PP1 – Prepectoral length	22.8	20.8	22.9	23.3	19.9	23.9
HDL – Head length	23.2	21.3	23.4	23.4	20.9	23.5
PG1 – Prebranchial length	20.3	17.6	19.7	19.5	18.0	20.1
PSP – Prespiracular length	13.4	11.3	13.6	12.8	12.1	13.3
POB – Preorbital length	7.1	6.7	8.1	7.5	7.3	7.9
PRN – Prenarial length	4.6	4.0	5.3	5.5	5.0	5.4
POR – Preoral length	10.1	8.7	10.6	10.8	9.4	10.6
INLF – Inner nostril-labial furrow space	5.3	4.2	4.9	4.4	4.2	4.7
MOW – Mouth width	6.5	7.1	8.5	6.2	6.3	7.5
ULA – Labial furrow length	2.5	1.9	2.5	2.4	2.1	2.5
INW – Internarial space	5.2	4.1	5.0	4.8	4.0	4.9
INO – Interorbital space	8.7	7.5	9.6	8.1	7.9	8.4
EYL – Eye length	4.3	3.8	5.2	3.4	3.8	4.7
EYH – Eye height	1.6	1.5	2.3	1.3	1.8	2.5
SPL – Spiracle length	1.5	1.3	1.9	1.2	1.2	1.5
GS1 – First gill-slit height	1.6	1.7	2.5	1.9	1.6	1.7
GS5 – Fifth gill-slit height	2.0	1.7	2.4	2.1	1.8	2.0
IDS – Interdorsal space	21.7	22.1	25.9	21.3	18.7	25.2
DCS – Dorsal-caudal space	11.2	9.7	11.2	9.8	9.9	11.2
PPS – Pectoral-pelvic space	18.9	19.8	25.4	22.5	21.3	24.5
PCA – Pelvic-caudal space	26.3	22.9	26.0	22.7	22.3	27.4
D1L – First dorsal length	14.2	12.8	15.9	14.5	12.5	15.7
D1A – First dorsal anterior margin	12.4	10.4	12.6	12.0	10.5	11.1
D1B – First dorsal base length	8.3	7.6	9.8	8.3	7.8	7.8
D1H – First dorsal height	6.1	5.7	7.4	8.5	4.5	8.3
D1I – First dorsal inner margin	6.2	4.9	6.8	6.3	4.9	6.4
D1P – First dorsal posterior margin	6.7	6.9	8.8	9.7	4.6	7.9
D1ES – First dorsal spine length	2.1	2.2	4.0	3.3	3.5	4.8
D1BS – First dorsal spine base width	0.7	0.5	0.6	0.8	0.6	0.8
D2L – Second dorsal length	13.4	11.1	13.9	12.7	12.0	13.9
D2A – Second dorsal anterior margin	10.2	8.5	10.8	10.2	10.4	10.7
D2B – Second dorsal base length	8.1	7.0	8.5	7.2	8.0	9.2
D2H – Second dorsal height	4.2	3.4	4.6	4.5	3.0	4.6
D2I – Second dorsal inner margin	5.9	4.0	5.7	5.1	4.2	5.4
D2P – Second dorsal posterior margin	5.2	4.5	6.3	5.2	4.1	4.4
D2ES – Second dorsal spine length	3.6	2.0	3.9	3.8	3.8	5.0
D2BS – Second dorsal spine base width	0.8	0.5	0.6	0.7	0.7	0.9

Table 1. cont'd.

	<i>S. montalbani</i>			<i>S. mitsukurii</i>		
		n = 14			n = 4	
	Holotype	Min.	Max.	Holotype	Min.	Max.
P1A – Pectoral anterior margin	13.6	12.8	15.5	15.0	11.7	16.1
P1I – Pectoral inner margin	8.9	6.8	8.8	8.2	7.0	7.5
P1B – Pectoral base length	5.0	5.1	6.2	6.8	5.0	6.1
P1P – Pectoral posterior margin	9.6	8.5	11.8	11.0	7.6	11.4
P2L – Pelvic length	10.1	8.6	11.0	10.8	9.6	10.3
P2H – Pelvic height	3.3	3.6	4.8	5.6	4.0	4.9
P2I – Pelvic inner margin	3.7	3.6	5.9	5.8	2.0	3.1
CDM – Dorsal caudal margin	22.6	19.8	23.3	22.6	21.2	21.3
CPV – Preventral caudal margin	12.2	10.9	13.2	12.3	10.2	12.2
CPU – Upper postventral caudal margin	15.9	14.5	17.8	16.4	13.2	16.2
CPL – Lower postventral caudal margin	3.6	3.9	5.9	4.8	3.4	5.6
CFW – Caudal fork width	6.7	6.4	7.7	6.7	5.9	6.7
CFL – Caudal fork length	10.8	9.0	10.8	9.2	9.3	10.3
HANW – Head width at nostrils	7.7	7.0	8.7	7.7	7.6	7.7
HAMW – Head width at mouth	10.6	9.7	11.9	11.5	10.1	10.8
HDW – Head width	12.1	11.3	13.9	14.8	11.5	13.8
TRW – Trunk width	10.9	9.3	12.5	–	8.2	10.7
ABW – Abdomen width	8.2	8.1	13.2	–	6.4	9.6
TAW – Tail width	5.3	5.6	7.0	6.3	4.7	6.7
CPW – Caudal peduncle width	2.7	2.6	3.5	2.5	2.4	3.1
HDH – Head height	9.1	9.0	12.1	8.5	7.5	11.7
TRH – Trunk height	12.0	8.9	13.4	–	7.9	9.1
ABH – Abdomen height	12.6	9.3	13.0	–	7.7	8.4
TAH – Tail height	6.6	6.0	7.3	7.2	5.3	6.2
CPH – Caudal peduncle height	2.5	2.2	2.8	2.6	2.3	2.5
CLO – Clasper outer length	1.4	4.5	5.6	–	1.7	2.6
CLI – Clasper inner length	5.4	7.8	8.8	–	5.2	6.0
CLB – Clasper base width	0.8	1.4	1.9	–	0.9	1.1

Morphometric and meristic data were taken from 9 specimens of *S. montalbani* (CSIRO H 2575–02, CSIRO H 2606–02, CSIRO H 2606–05, CSIRO H 5857–06, CSIRO H 5875–07, CSIRO H 5888–03, CSIRO H 5889–20, SUML F 1198 and SUML unreg BRU 136); morphometrics only from another 6 specimens (USNM 70256 (holotype), CSIRO H 2605–04, CSIRO H 4623–04, CSIRO H 4623–05, QM I 38075 and AMS I 43982–001); and meristics only from another 10 specimens (CSIRO H 1203–02, CSIRO H 1290–02, CSIRO H 1348–01, CSIRO H 2606–06, CSIRO H 4623–02, CSIRO 4708–01, CSIRO H 5889–10, CSIRO H 5889–19, QM I 21518 and WAM P 32843–001). Morphometric and meristic details were taken from the holotype (CSIRO H 4775–01) and two paratypes of the new species (CSIRO H 1405–01, CSIRO H 1662–01); morphometrics only from 7 other paratypes (CSIRO H 2867–02, CSIRO

H 2867–03, CSIRO H 2867–04, CSIRO H 2867–05, CSIRO H 2966–01, CSIRO H 5941–01 and NMV A 29563–001); and meristics from 5 other paratypes (CSIRO CA 121, CSIRO H 1350–02 (4 embryos)).

Specimens examined are deposited in the Australian National Fish Collection, Hobart (CSIRO), the Australian Museum, Sydney (AMS), the National Museum of Victoria (NMV), the Queensland Museum (QM), the Western Australian Museum (WAM), the Museum Zoologicum Bogoriense, Jakarta (MZB), the Hokkaido University, Faculty of Fisheries, Hakodate (HUMZ), the California Academy of Sciences, San Francisco (CAS, inc. SU) and the National Museum of Natural History, Washington, D.C. (USNM); their registration numbers are prefixed with these acronyms.

Squalus montalbani Whitley, 1931

Figs 1a–c, 2a,b, 3–5a; Table 1, 2

Squalus philippinus Smith and Radcliffe, 1912 (junior homonym of *S. philippinus* Shaw, 1804 = *Heterodontus portusjacksoni* (Meyer, 1793)). In: Smith 1912: 677, pl. 51, fig. 1, *Proc. U. S. Natl. Mus.* v. 41 (no. 1877). Holotype (unique): USNM 70256. *Squalus montalbani* Whitley 1931:310. In: *Aust. Zool.* v. 6 (pt 4). Replacement name for *Squalus philippinus* Smith and Radcliffe 1912.

Squalus sp. 1: White *et al.*, 2006, *Economically Important Sharks and Rays of Indonesia*, pp 68–69.

Holotype. USNM 70256, immature male 311 mm TL, off Sombrero I., west coast of Luzon Island, 13°45' N, 120°46' E, Philippines, Albatross sta. 5111, ca. 425 m.

Other material. 32 specimens. CSIRO H 1290–02, immature male 592 mm TL, east of Flinders Reef, Queensland, 17°38' S, 149°23' E, 600 m; CSIRO H 1348–01, female 375 mm TL, north-west of Saumarez Reef, Queensland, 21°20' S, 153°32' E, 502 m; QM

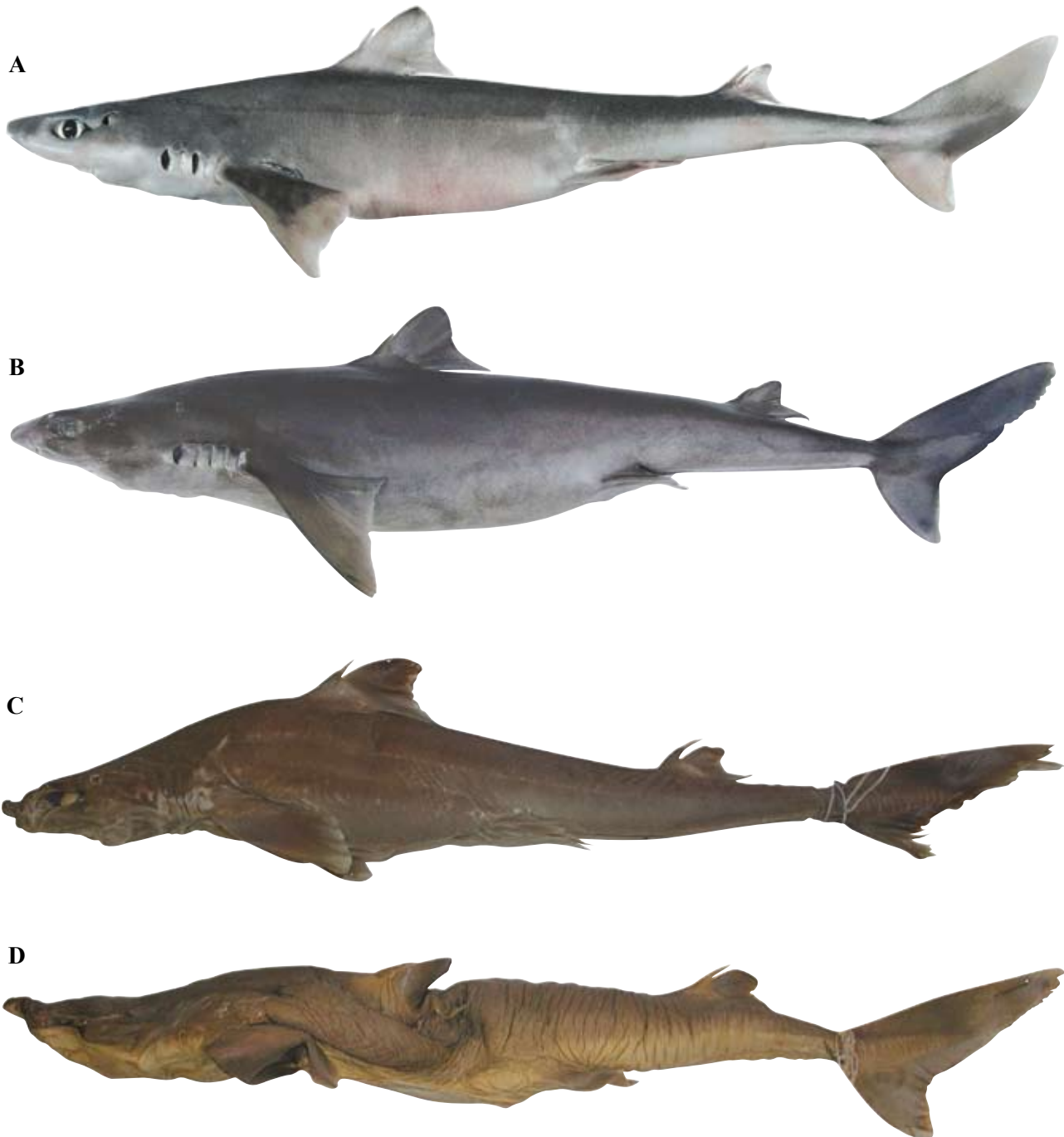


Figure 1. Lateral view of: A. *Squalus montalbani* from NW Australia (CSIRO H 2575–02, adult male 681 mm TL); B. *Squalus montalbani* from Indonesia (MZB 15424, female 945 mm TL); C. *Squalus philippinus* (=montalbani) holotype (USNM 70256, immature male 311 mm TL); d. *Squalus mitsukurii* holotype (SU 12793, female 719 mm TL).

I 21518, female 370 mm TL, east of Capricorn Group, Queensland, 23°21' S, 153°56' E, 460 m; AMS I 20301–027, 310 mm TL, east of Woolli, New South Wales, 29°53' S, 153°42' E, 502 m; CSIRO H 4623–02, female 485 mm TL, CSIRO H 4623–04, adult male 811 mm TL, CSIRO H 4623–05, female 760 mm TL, east of Terrigal, New South Wales, 33°28' S, 152°04' E, 383 m; CSIRO H 2606–02, female 557 mm TL, CSIRO H 2606–05, female 607 mm TL, CSIRO H 2606–06, adolescent male 440 mm TL, west of Rottnest Island, Western Australia, 32°02' S, 114°54' E, 670 m; CSIRO H 2605–04, female 825 mm TL, north-west of Rottnest Island, Western Australia, 31°44' S, 114°59' E, 485 m; WAM P 32843–001, immature male 440 mm TL, west of Greenhead, Western Australia, 29°59' S, 114°26' E, 490 m; CSIRO H 2574–04, immature female 221 mm TL, west of Freycinet Estuary, Western Australia, 26°35' S, 112°29' E, 508 m; CSIRO H 2575–02, adult male 681 mm TL, west of Freycinet Estuary, Western Australia, 26°40' S, 112°32' E, 478 m; CSIRO H 1203–02, embryo 208 mm TL, north of Sahul Banks, Timor Sea, Western Australia, 11°33' S, 124°58' E, 415 m; MZB 15018, female 862 mm TL, MZB 15019, adult male 862 mm TL, Cilacap fish landing site, Central Java, Indonesia, 07°40' S, 109°00' E; CSIRO H 5857–06, adult male 678 mm TL, CSIRO H 5889–20, adult male 627 mm TL, CSIRO H 5888–03, female 801 mm TL, CSIRO H 5889–10, female 495 mm TL, CSIRO H 5889–19, female 481 mm TL, AMS I 43982–001, adult male 564 mm TL, QM I 38075, female 801 mm TL, QM I 38076, immature male 463 mm TL, MZB 15421, female 912 mm TL, MZB 15424, female 945 mm TL, NMV A 29561–001, female 528 mm TL, Kedonganan fish landing site, Bali, Indonesia, 08°45' S, 115°10' E; CSIRO H 5875–07, female 843 mm TL, MZB 15099, female 781 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E; SUML F 1198, female 694 mm TL, SUML unreg BRU 136, female 520 mm TL, Aliguay Island, Philippines.

DIAGNOSIS.— A large species of *Squalus* of the 'mitsukurii group' with the following combination of characters: body elongate to robust, trunk depth 8.9–13.4% TL (mean 11.4% TL, n=14); snout broadly triangular, mouth width 1.69–2.32 (1.85) times horizontal prenarial length; pre-first dorsal length 26.5–30.7 (29.0)% TL; pre-second dorsal length 57.6–62.8 (60.8)% TL; interdorsal space 21.7–25.9 (23.7)% TL; low raked dorsal fins; second dorsal-fin length 11.1–13.9 (12.4)% TL, height 3.4–4.6 (4.0)% TL, inner margin length 4.0–5.9 (4.8)% TL; second dorsal-fin base 15.8–21.3 (20.8) times base of second dorsal spine; prepectoral length 20.8–22.9 (22.0)% TL; pelvic–caudal space 22.9–26.0 (24.0)% TL; caudal bar almost upright, extending broadly from the caudal fork up the posterior margin of the upper lobe for about 0.6 of its length in immatures, upper caudal fringe forming a deep saddle along mid-length of lobe; flank denticles tricuspid; 41–47 (mainly 42–44) monospondylous centra, 79–85 precaudal centra, 105–114 total centra; adult size more than 84 cm TL.

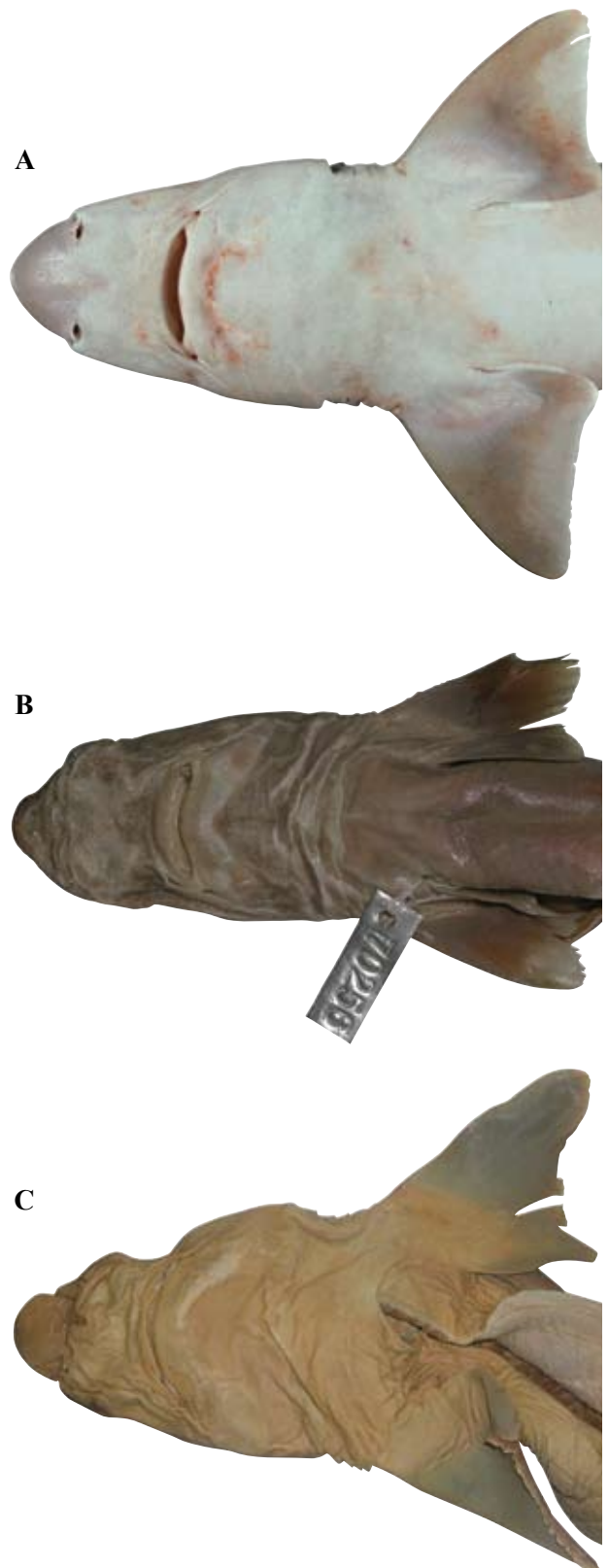


Figure 2. Ventral view of the head of: A. *Squalus montalbani* (CSIRO H 2575–02, adult male 681 mm TL); B. *Squalus philippinus* (=montalbani) holotype (USNM 70256, immature male 311 mm TL); C. *Squalus mitsukurii* holotype (SU 12793, female 719 mm TL).

REMARKS.— *Squalus montalbani* is similar in appearance to *S. mitsukurii* and both species occur together in the same general geographic region. Hence, it is not unsurprising that these forms have been considered to be conspecific (Compagno, 1984). These species differ subtly in caudal fin coloration and these markings are more strikingly obvious in young (Fig. 5) than in adult specimens. The dark caudal bar, which extends diagonally as a linear marking from the origin of the lower lobe to the axil of the caudal fork in *S. mitsukurii* (exposed along the posterior caudal margin for about half an eye diameter), is less developed than in *S. montalbani* (extending broadly from the caudal fork and following the posterior margin of the upper lobe for 0.6–0.7 of its length to an upper level typically demarcated by a posterior projection of the distal part of a fleshy portion of the fin). Also, the dark blotch on the upper caudal lobe is located more distally than in *S. montalbani* which is represented as a saddle-like extension of the upper caudal fringe. The late embryo paratypes of *S. mitsukurii* (SU 7748, 228–237 mm TL) are slightly larger than the post-natal young of *S. montalbani* (CSIRO H 1203–02, 207 mm TL) suggesting that they are born at different sizes. These specimens also display slight differences in the form of the anterior nasal flap and pectoral fin which are either attributable to interspecific or ontogenetic differences. It should be noted that, although paratype SU 7748 consists of 8 late-term embryos labeled as “from uterus of type”, the literature suggests that it may actually contain embryos from several individuals collected with the holotype (Jordan and Snyder, 1903). However, the 5 (of 8) embryos examined in this study all appear to be conspecific based on their morphology and coloration and as such are representative of *S. mitsukurii*.

These species also differ morphometrically (Table 1). The female holotype (SU 12793, 719 mm TL, Fig. 1d, 2c) and immature male paratype (SU 7184, 266 mm TL) of *Squalus mitsukurii* differ from the holotype (USNM 70256, 311 mm TL, Fig. 1c, 2b) and other material of

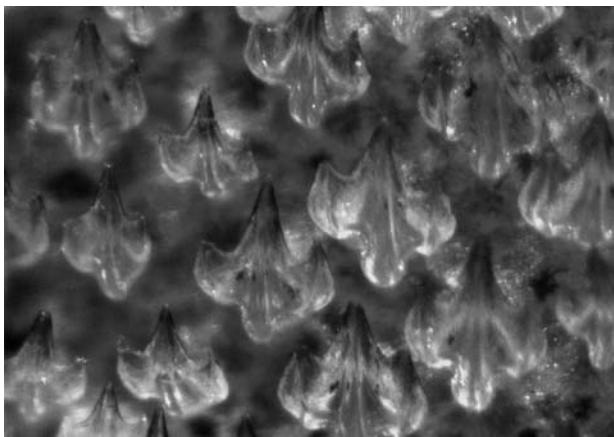


Figure 3. Cusps of the flank denticles of *Squalus montalbani* (CSIRO H 2575–02, adult male 681 mm TL). Field of view width 1.0 mm.

S. montalbani in the following ratios: total length 3.10–3.23 vs. 3.26 (3.33–3.78, n=14) times pre-first dorsal length in *S. montalbani*; pre-first dorsal length 1.45–1.73 vs. 1.42 (1.10–1.30) times interdorsal space; prepectoral length 1.09–1.28 vs. 1.05 (0.85–1.00) times interdorsal space; prepectoral length 1.02–1.07 vs. 0.87 (0.85–0.99) times pelvic–caudal space; and head height 0.58–0.65 vs. 0.76 (0.66–0.96) times its width. *Squalus mitsukurii* also appears to have slightly longer head measurements (direct head length 23.4–23.5 vs. 23.2 (21.3–23.4)% TL, prepectoral length 23.3–23.9 vs. 22.8 (20.8–22.9)% TL, prenarial length 5.4–5.5 vs. 4.6 (4.0–5.3)% TL, preoral length 10.6–10.8 vs. 10.1 (8.7–10.6)% TL) and a more slender body (head height 7.5–8.5 vs. 9.1 (9.0–12.1)% TL, trunk height 7.9 vs. 12.0 (8.9–13.4)% TL, abdomen height 7.7 vs. 12.6 (9.3–13.0)% TL, trunk width 8.2 vs. 10.9 (9.3–12.5)% TL, abdomen width 6.4 vs. 8.2 (8.1–13.2)% TL, and caudal peduncle width 2.4–2.5 vs. 2.7 (2.6–3.5)% TL). The mouth of *S. mitsukurii* appears to be relatively narrow compared to *S. montalbani* (mouth width 6.2–6.3 vs. 6.5 (7.1–8.5)% TL) but this may be due to methodological inconsistencies. Differences between the species also exist in the number of vertebral centra. Chen *et al.* (1979) provided counts and morphometrics for 54 specimens of *S. mitsukurii* from central and northeastern Japan, close to the type locality (Misaki). Their counts for *S. mitsukurii* are higher (45–51 monospondylous centra, 87–93 precaudal centra, 118–127 total centra) than those

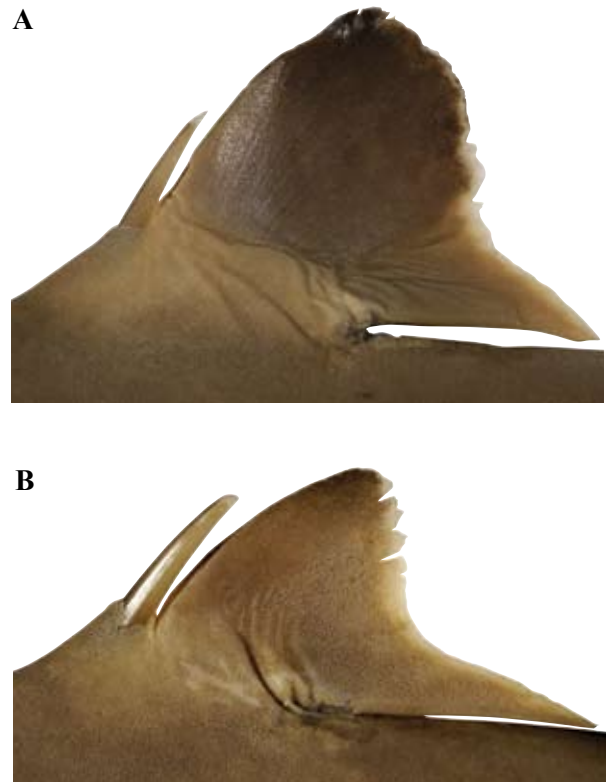


Figure 4. Lateral view of the dorsal fins of *Squalus montalbani* (CSIRO H 2575–02, adult male 681 mm TL) – A. first dorsal fin, B. second dorsal fin.

Table 2. Proportional dimensions as percentages of total length for *S. montalbani* from the Philippines including holotype (USNM 70256), Indonesia and Australia.

	Philippines				Indonesia			Australia		
	Holotype	n = 2			n = 6			n = 6		
		Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
TL – Total length	311	607	520	694	719	564	843	707	557	825
PCL – Precaudal length	76.5	78.3	78.2	78.3	78.2	77.3	79.9	77.9	77.1	78.9
PD2 – Pre-second dorsal length	57.6	60.4	60.2	60.6	61.4	59.8	62.8	60.3	59.1	62.1
PD1 – Pre-first dorsal length	30.7	29.8	29.8	29.9	29.0	28.6	30.0	28.6	26.5	29.4
SVL – Pre-vent length	47.2	48.8	48.6	49.0	50.4	48.8	52.7	50.3	48.7	51.5
PP2 – Prepelvic length	43.8	48.1	47.7	48.4	48.7	47.2	50.8	48.7	47.5	50.5
PP1 – Prepectoral length	22.8	21.5	20.8	22.3	22.1	21.2	22.9	22.1	21.0	22.8
HDL – Head length	23.2	22.0	21.7	22.4	22.4	21.7	23.2	22.6	21.3	23.4
PG1 – Prebranchial length	20.3	18.2	17.9	18.4	18.7	17.6	19.3	19.2	18.3	19.7
PSP – Prespiracular length	13.4	11.6	11.3	11.8	12.0	11.4	12.5	12.7	11.9	13.6
POB – Preorbital length	7.1	6.9	6.8	7.1	7.4	6.7	7.7	7.7	7.3	8.1
PRN – Prenarial length	4.6	4.3	4.0	4.5	4.9	4.6	5.1	5.2	4.9	5.3
POR – Preoral length	10.1	9.0	8.7	9.4	9.6	9.2	10.2	10.0	9.3	10.6
INLF – Inner nostril-labial furrow space	5.3	4.3	4.2	4.5	4.6	4.5	4.9	4.7	4.5	4.9
MOW – Mouth width	6.5	7.7	7.6	7.8	7.5	7.1	7.8	8.0	7.5	8.5
ULA – Labial furrow length	2.5	2.2	2.2	2.2	2.2	1.9	2.5	2.2	2.1	2.2
INW – Internarial space	5.2	4.4	4.3	4.5	4.3	4.1	4.5	4.6	4.2	5.0
INO – Interorbital space	8.7	7.8	7.6	8.0	8.2	7.5	9.1	9.0	8.7	9.6
EYL – Eye length	4.3	4.0	3.8	4.2	4.9	4.8	5.2	4.2	4.0	4.6
EYH – Eye height	1.6	1.9	1.9	1.9	1.7	1.5	1.9	2.0	1.8	2.3
SPL – Spiracle length	1.5	1.3	1.3	1.3	1.7	1.5	1.8	1.7	1.6	1.9
GS1 – First gill-slit height	1.6	1.7	1.7	1.7	2.0	1.8	2.2	2.0	1.8	2.5
GS5 – Fifth gill-slit height	2.0	1.8	1.7	1.8	2.2	2.0	2.4	2.1	1.9	2.3
IDS – Interdorsal space	21.7	23.4	22.9	24.0	24.4	22.8	25.9	23.0	22.1	24.1
DCS – Dorsal-caudal space	11.2	10.1	9.7	10.4	10.6	9.7	11.2	10.4	9.9	10.6
PPS – Pectoral-pelvic space	18.9	22.4	21.9	22.9	23.0	19.8	25.1	23.0	22.2	25.4
PCA – Pelvic-caudal space	26.3	23.6	23.4	23.7	24.4	23.0	26.0	23.8	22.9	25.3
D1L – First dorsal length	14.2	13.5	13.0	14.0	14.2	12.8	15.1	14.9	14.5	15.9
D1A – First dorsal anterior margin	12.4	11.3	11.0	11.6	11.6	10.4	12.5	12.2	11.6	12.6
D1B – First dorsal base length	8.3	7.9	7.6	8.3	8.9	8.2	9.3	9.3	8.7	9.8
D1H – First dorsal height	6.1	6.5	6.5	6.6	6.3	5.7	6.7	6.8	6.4	7.4
D1I – First dorsal inner margin	6.2	5.6	5.5	5.8	5.5	4.9	6.2	5.8	5.1	6.8
D1P – First dorsal posterior margin	6.7	7.6	7.4	7.9	7.3	6.9	8.0	8.1	7.5	8.8
D1ES – First dorsal spine length	2.1	2.7	2.4	3.0	2.9	2.2	4.0	3.0	2.5	3.5
D1BS – First dorsal spine base width	0.7	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.5	0.6
D2L – Second dorsal length	13.4	12.3	11.4	13.2	11.8	11.1	12.6	13.0	12.2	13.9
D2A – Second dorsal anterior margin	10.2	9.8	9.2	10.3	8.9	8.5	9.4	10.0	9.0	10.8
D2B – Second dorsal base length	8.1	7.5	7.0	7.9	7.2	7.0	7.5	8.0	7.1	8.5
D2H – Second dorsal height	4.2	4.0	4.0	4.1	3.9	3.4	4.3	4.1	3.5	4.6
D2I – Second dorsal inner margin	5.9	4.8	4.3	5.3	4.5	4.0	5.1	5.1	4.7	5.7
D2P – Second dorsal posterior margin	5.2	5.1	5.0	5.1	5.3	4.5	6.0	5.7	5.0	6.3
D2ES – Second dorsal spine length	3.6	2.9	2.7	3.2	2.9	2.0	3.8	3.3	2.6	3.9
D2BS – Second dorsal spine base width	0.8	0.6	0.6	0.6	0.6	0.5	0.6	0.6	0.5	0.6

Table 1. cont'd.

	Philippines				Indonesia			Australia		
	Holotype	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
P1A – Pectoral anterior margin	13.6	14.2	14.0	14.3	13.9	12.8	15.2	14.5	13.7	15.5
P1I – Pectoral inner margin	8.9	7.8	7.4	8.1	7.3	6.8	7.7	8.2	7.7	8.8
P1B – Pectoral base length	5.0	5.7	5.7	5.7	5.4	5.1	5.8	5.9	5.5	6.2
P1P – Pectoral posterior margin	9.6	10.8	10.8	10.8	10.0	8.5	11.4	11.0	9.1	11.8
P2L – Pelvic length	10.1	8.8	8.6	9.0	9.9	9.2	10.4	10.2	9.7	11.0
P2H – Pelvic height	3.3	4.7	4.6	4.8	4.1	3.6	4.5	4.5	4.3	4.8
P2I – Pelvic inner margin	3.7	3.9	3.6	4.3	4.9	3.9	5.9	4.9	4.4	5.6
CDM – Dorsal caudal margin	22.6	21.8	21.6	22.0	21.0	19.8	21.8	22.2	20.9	23.3
CPV – Preventral caudal margin	12.2	12.2	11.9	12.5	11.6	10.9	12.1	12.6	11.5	13.2
CPU – Upper postventral caudal margin	15.9	15.9	15.8	16.1	15.4	14.5	16.4	16.8	15.6	17.8
CPL – Lower postventral caudal margin	3.6	4.9	4.9	4.9	4.8	3.9	5.9	5.0	4.4	5.5
CFW – Caudal fork width	6.7	6.8	6.8	6.8	6.7	6.4	7.0	7.3	7.0	7.7
CFL – Caudal fork length	10.8	9.9	9.4	10.4	9.5	9.0	9.8	10.1	9.4	10.8
HANW – Head width at nostrils	7.7	7.5	7.1	7.8	7.2	7.0	7.4	8.1	7.5	8.7
HAMW – Head width at mouth	10.6	10.4	10.0	10.8	10.4	9.7	11.4	11.4	10.6	11.9
HDW – Head width	12.1	13.7	13.5	13.9	12.2	11.3	13.0	12.7	11.8	13.2
TRW – Trunk width	10.9	10.6	10.5	10.7	10.5	9.3	11.7	11.0	9.9	12.5
ABW – Abdomen width	8.2	8.9	8.9	9.0	10.3	8.1	12.6	10.7	8.9	13.2
TAW – Tail width	5.3	6.0	5.9	6.2	6.4	5.6	7.0	6.5	5.7	7.0
CPW – Caudal peduncle width	2.7	2.7	2.6	2.9	3.2	3.1	3.4	3.3	3.2	3.5
HDH – Head height	9.1	9.3	9.2	9.4	10.8	9.2	12.0	10.6	9.0	12.1
TRH – Trunk height	12.0	9.9	9.2	10.7	11.6	10.1	13.1	11.6	8.9	13.4
ABH – Abdomen height	12.6	10.6	10.2	10.9	11.3	9.3	13.0	11.8	9.5	12.9
TAH – Tail height	6.6	6.5	6.4	6.7	6.6	6.0	7.3	6.8	6.2	7.2
CPH – Caudal peduncle height	2.5	2.5	2.5	2.6	2.4	2.2	2.6	2.7	2.6	2.8
CLO – Clasper outer length	1.4	–	–	–	4.9	4.4	5.3	5.0	4.5	5.6
CLI – Clasper inner length	5.4	–	–	–	7.6	7.4	7.9	8.3	7.8	8.8
CLB – Clasper base width	0.8	–	–	–	1.6	1.4	1.9	1.5	1.4	1.7

of *S. montalbani* (41–47 monospondylous centra, 79–85 precaudal centra, 105–114 total centra, n=30).

Some minor differences exist between populations of *S. montalbani* across the Indo–West Pacific. Vertebral counts varied slightly between material from Indonesia (41–45 (mean 42.8) monospondylous centra, 79–83 (mean 80.5) precaudal centra, 105–111 (mean 107.6) total centra, n=12) and northern Australia (42–47 (mean 43.6) monospondylous centra, 81–85 (mean 83.1) precaudal centra, 110–114 (mean 112.2) total centra, n=14). Morphometrics from the three populations are reasonably consistent (Table 2) with minor variation in eye length, first dorsal-fin base length, pelvic-fin inner margin length, spiracle length, caudal peduncle width, and head width at the anterior nostrils. Indonesian material is darker in overall coloration than Australian

material but the general morphology of specimens from both regions and the Philippines is similar.

Squalus chloroculus sp. nov.

Figs 6–10; Table 3

Squalus mitsukurii: (not Jordan and Snyder) Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 101, figs 8.24, 8.39, pl. 5; Gomon, Glover and Kuiter, 1994, *The Fishes of Australia's South Coast*, pp 105, 107, 108, figs 56, 57.

Holotype. CSIRO H 4775–01, adult male 753 mm TL, off Portland, Victoria, 38° S, 141° E, 17 April 1998.

Paratypes. 14 specimens. CSIRO CA 121, female 731 mm TL, off Ulladulla, New South Wales, 35°27' S, 150°51' E, 400 m; NMV A 29563–001, adult male



Figure 5. Juvenile coloration of the caudal fin of: A. *Squalus montalbani* (CSIRO H 1203–02, immature female 207 mm TL); B. *Squalus mitsukurii* paratype (CAS SU 7748, female embryo 237 mm TL).

856 mm TL, off St Helens, Tasmania, ca. 42° S, 148° E, 550 m; CSIRO H 5941–01, adult male 762 mm TL, west of Cape Sorell, Tasmania, 42°10' S, 144°45' E, 460 m; CSIRO H 1662–01, adult male 722 mm TL, east of Maria Island, Tasmania, 42°40' S, 148°24' E, 468 m; CSIRO H 1350–02, 4 embryos 217–238 mm TL, northwest of Macquarie Harbour, Tasmania, 41°52' S, 144°23' E, 1370 m; CSIRO H 1405–01, adult male 760 mm TL, south of King Island, Tasmania, 40°46' S, 143°42' E, 216 m; CSIRO H 2966–01, female 832 mm TL, Great Australian Bight, South Australia, 33°47' S, 131°27' E, 780 m; CSIRO H 2867–02, adult male 733 mm TL, CSIRO H 2867–03, adult male 685 mm TL, CSIRO H 2867–04, female 797 mm TL, CSIRO H 2867–05, female 789 mm TL, Great Australian Bight, South Australia, 33°25' S, 129°54' E, 514 m.

DIAGNOSIS.— A large species of *Squalus* of the 'mitsukurii group' with the following combination of characters: body moderately robust, trunk depth 10.4–13.8% TL (mean 11.7% TL, n=9); snout broadly triangular, mouth width 1.72–2.48 (2.07) times horizontal prenarial length; pre-first dorsal length 29.2–31.8 (30.2)% TL; pre-second dorsal length 60.7–63.6 (61.7)% TL; interdorsal

space 23.7–27.5 (24.9)% TL; low raked dorsal fins; second dorsal-fin length 10.9–12.2 (11.6)% TL, height 3.4–4.0 (3.7)% TL, inner margin length 3.9–5.0 (4.4)% TL; second dorsal-fin base 15.1–20.0 (17.2) times base of second dorsal spine; prepectoral length 21.1–24.3 (22.2)% TL; pelvic–caudal space 21.8–25.0 (23.5)% TL; caudal bar almost upright, extending broadly from the caudal fork up the posterior margin of the upper lobe for 0.6–0.7 of its length in immatures, upper caudal fringe forming a narrow saddle along mid-length of lobe; flank denticles tricuspid; 43–46 monospondylous centra, 84–86 precaudal centra, 111–115 total centra; adult maximum size at least 85 cm TL.

DESCRIPTION.— Body fusiform, moderately elongate to robust, nape prominently humped; deepest near first dorsal-fin spine, maximum depth 0.89 (0.88–1.13 in paratypes) times width; trunk depth 1.03 (0.98–1.11) times abdomen depth; head moderately elongate, 23.0 (22.1–23.8)% TL; caudal peduncle robust, 24.0 (21.8–25.0)% TL. Head robust, rather broad, width 1.12 (1.07–1.32) times trunk width, 1.30 (1.05–1.37) times abdomen width, slightly depressed forward of spiracles, becoming subtriangular in cross-section towards pectoral-fin origin, length 2.21 (2.15–2.33) in pre-vent length; height 0.77 (0.67–0.85) times width. Snout moderately elongate, narrowly triangular in lateral view, apex bluntly pointed, lateral prenarial margin weakly angular; narrowly pointed in dorsal view, horizontal length 1.64 (1.61–1.62) times eye length, 0.90 (0.76–0.81) times interorbital space; horizontal prenarial length 2.20 (2.16–2.23) times in preoral length. Eye oval, of moderate size, length 5.25 (4.98–5.37) in head, 2.13 (1.90–2.20) times height; strongly notched posteriorly, notch deep anteriorly, becoming shallow near anteroventral margin of spiracle (not connected to spiracle in some paratypes). Spiracle moderate, broadly crescentic but variable; broad, lobe-like fold on posterior margin; greatest diameter 2.68 (2.22–3.69) in eye length. Gill openings almost upright, first 4 subequal in size, fifth longest, height of fifth slit 2.1 (1.9–2.5)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.28 (1.09–1.30) in preoral length; prominent postoral groove, much longer than upper labial furrows (rarely subequal), extending posterolaterally from angle of jaws; 1 (1–2) series of functional teeth in upper jaw, 2 (2–3) series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap weakly bilobed or single-lobed; anterior lobe large, narrowly rounded, subtriangular (flattened in some paratypes); posterior lobe of nasal flap either indistinguishable, rudimentary or weak in paratypes (sometimes variable within an individual); internarial space 2.23 (2.93–2.21) in preoral length, 2.65 (2.48–2.83) times nostril length. Dermal denticles (based on adult male CSIRO H 1405–01) on flank very small, strongly imbricate, tricuspidate; crown broad with pronounced median ridge; median ridge



Figure 6. Lateral view of *Squalus chloroculus* sp. nov. holotype (CSIRO H 4775–01, adult male 753 mm TL).



Figure 7. Ventral view of the head of *Squalus chloroculus* sp. nov. holotype (CSIRO H 4775–01, adult male 753 mm TL).

commencing well anterior of rest of crown, with a mesial furrow developing anteriorly and converging towards posterior tip of crown; distal ridge extending laterally along crown, lateral cusps short or variably developed, low, weak, with very narrow mesial furrow. First dorsal fin small, low, strongly raked, very broadly rounded apically; anterior margin strongly convex; posterior margin weakly concave, upper portion subvertical (usually directed slightly or strongly anterodorsally from bottom to top in paratypes); lower half almost straight or weakly concave; free rear tip relatively thick basally, very short; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior to free rear tip of pectoral fin; fin-spine origin slightly posterior to pectoral-fin insertion (more

posterior in some paratypes); spine base moderately broad, 0.7 (0.6–0.8)% TL, exposed anteriorly well below junction of spine and soft portion of fin; soft portion of fin connected well above mid-point of total spine length (spine often damaged); spine tapering distally (often abraded apically), anterior margin almost straight; exposed portion only slightly raked, much shorter in length than exposed portion of second dorsal-fin spine (also marginally abraded apically); pre-first dorsal length 3.43 (3.15–3.42) times in TL; first dorsal-fin length 2.41 (2.14–2.41) times its height, 1.25 (1.17–1.26) times second dorsal-fin length; first dorsal-fin height 1.50 (1.59–1.78) times second dorsal-fin height; exposed first dorsal spine length 0.56 (0.39–0.50) times height of fin. Second dorsal fin small, strongly raked; anterior margin

Table 3. Proportional dimensions as percentages of total length for the holotype (CSIRO H 4475–01) and ranges for the 9 paratypes of *Squalus chloroculus* sp. nov.

	<i>S. chloroculus</i> sp. nov.			
	Holotype	Paratypes		
		Min.	Max.	Mean
TL – Total length	753	721	856	783
PCL – Precaudal length	78.8	77.9	79.7	78.6
PD2 – Pre-second dorsal length	61.8	60.7	63.6	61.7
PD1 – Pre-first dorsal length	29.2	29.3	31.8	30.2
SVL – Pre-vent length	50.7	49.5	52.1	50.8
PP2 – Prepelvic length	49.0	47.9	51.0	49.3
PP1 – Prepectoral length	22.3	21.1	24.3	22.2
HDL – Head length	23.0	22.0	23.8	22.7
PG1 – Prebranchial length	19.4	18.5	20.1	19.2
PSP – Prespiracular length	13.0	12.3	13.6	12.8
POB – Preorbital length	7.5	7.5	8.1	7.7
PRN – Prenarial length	5.3	4.7	5.3	5.0
POR – Preoral length	9.9	9.5	10.1	9.8
INLF – Inner nostril-labial furrow space	5.0	4.4	4.9	4.7
MOW – Mouth width	7.7	7.7	9.1	8.1
ULA – Labial furrow length	2.4	2.0	2.5	2.3
INW – Internarial space	4.5	4.5	5.1	4.8
INO – Interorbital space	8.0	8.3	9.5	8.8
EYL – Eye length	4.4	4.3	4.5	4.4
EYH – Eye height	2.1	2.0	2.3	2.2
SPL – Spiracle length	1.6	1.2	2.0	1.5
GS1 – First gill-slit height	1.9	1.7	2.8	2.1
GS5 – Fifth gill-slit height	2.1	1.9	2.5	2.2
IDS – Interdorsal space	25.2	23.7	27.5	24.9
DCS – Dorsal-caudal space	10.2	9.3	10.7	10.1
PPS – Pectoral-pelvic space	24.0	21.6	25.2	23.2
PCA – Pelvic-caudal space	24.0	21.8	25.0	23.5
D1L – First dorsal length	14.5	13.1	14.8	14.2
D1A – First dorsal anterior margin	12.2	10.6	12.5	11.5
D1B – First dorsal base length	9.3	8.1	9.6	8.7
D1H – First dorsal height	6.0	5.9	6.8	6.2
D1I – First dorsal inner margin	5.3	5.1	6.1	5.4
D1P – First dorsal posterior margin	6.7	6.8	8.2	7.4
D1ES – First dorsal spine length	3.4	2.3	3.3	2.9
D1BS – First dorsal spine base width	0.7	0.6	0.8	0.7
D2L – Second dorsal length	11.6	10.9	12.2	11.6
D2A – Second dorsal anterior margin	8.9	8.0	9.6	8.9
D2B – Second dorsal base length	7.4	6.5	7.4	7.2
D2H – Second dorsal height	4.0	3.4	3.9	3.7
D2I – Second dorsal inner margin	4.5	3.9	5.0	4.4
D2P – Second dorsal posterior margin	5.1	4.8	6.1	5.2
D2ES – Second dorsal spine length	4.0	2.5	3.9	3.2
D2BS – Second dorsal spine base width	0.7	0.6	0.8	0.7

Table 1. cont'd.

	<i>S. chloroculus</i> sp. nov.			
	Holotype	Min.	Max.	Mean
P1A – Pectoral anterior margin	14.9	13.7	16.9	14.9
P1I – Pectoral inner margin	7.6	7.0	8.6	7.8
P1B – Pectoral base length	5.4	5.1	6.0	5.6
P1P – Pectoral posterior margin	11.0	10.2	12.8	11.2
P2L – Pelvic length	10.5	9.2	10.5	9.8
P2H – Pelvic height	5.1	4.4	5.4	5.0
P2I – Pelvic inner margin	5.3	1.9	4.6	3.3
CDM – Dorsal caudal margin	20.9	19.2	21.7	21.0
CPV – Preventral caudal margin	12.2	11.0	12.8	11.7
CPU – Upper postventral caudal margin	15.8	14.7	16.5	15.8
CPL – Lower postventral caudal margin	5.1	5.2	6.3	5.5
CFW – Caudal fork width	7.1	6.6	7.2	7.0
CFL – Caudal fork length	9.5	9.1	9.7	9.4
HANW – Head width at nostrils	7.9	7.6	8.5	7.9
HAMW – Head width at mouth	11.1	10.8	12.5	11.6
HDW – Head width	13.3	12.7	14.9	13.7
TRW – Trunk width	11.8	10.5	13.0	11.7
ABW – Abdomen width	10.2	10.1	13.2	11.5
TAW – Tail width	6.1	4.8	7.3	6.3
CPW – Caudal peduncle width	3.3	3.0	3.7	3.2
HDH – Head height	10.2	9.4	11.5	10.3
TRH – Trunk height	10.5	10.4	13.8	11.7
ABH – Abdomen height	10.3	10.1	13.5	11.5
TAH – Tail height	6.4	6.0	6.8	6.4
CPH – Caudal peduncle height	2.7	2.3	2.6	2.5
CLO – Clasper outer length	3.8	4.1	4.6	4.3
CLI – Clasper inner length	7.2	6.9	8.8	7.7
CLB – Clasper base width	1.5	1.5	1.7	1.6

convex, apex broadly rounded; posterior margin strongly concave, maximum concavity just above mid-point of margin (variable in paratypes), upper portion almost vertical (directed slightly dorsoposteriorly in paratypes CSIRO H 2867–05 and H 2966–01); free rear tip very elongate, inner margin length 1.12 (1.06–1.39) times fin height; second dorsal-fin length 2.89 (2.97–3.44) times its height; spine length 1.01 (0.68–1.06) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed near level of junction with spine and soft portion of fin (connected slightly above in some paratypes); second spine moderately broad based, 0.7 (0.6–0.8)% TL, sharply pointed distally when undamaged, usually abraded; spine tip when undamaged extending to about level of insertion of fin; soft portion and spine apices subequal in height; interdorsal space 0.89 (0.81–0.99) in length

from snout tip to pectoral-fin origin, 1.16 (1.10–1.30) in pre-first dorsal length; interdorsal ridge rudimentary or absent, more obvious posteriorly. Pectoral fin large, more so in large females (anterior margin 15.7–16.9% TL, n=3) than males (anterior margin 13.7–14.9% TL, n=7 inc. holotype), anterior margin weakly convex; inner margin moderately convex, length 7.6 (7.0–8.6)% TL; apex narrowly rounded (variable in some male paratypes, significantly broader), weakly lobe-like and not falcate; posterior margin weakly to moderately concave; free rear tip narrowly rounded to weakly angular; base very short, 2.76 (2.35–3.08) in length of anterior margin. Pelvic fins large, subtriangular, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Clasper extending well beyond free rear tip of pelvic fin. Tail long, subcircular in cross-section anteriorly,

tapering slightly to second dorsal fin, beyond second dorsal fin tapering more rapidly, moderately depressed, broadly semicircular posteriorly; ventral groove well developed, broad, shallow, with obvious medial ridge (better developed posteriorly); lateral keels very well developed, originating under (or slightly posterior to) insertion of second dorsal fin, terminating about half an eye diameter behind caudal-fin insertion; pelvic–caudal space 1.00 (0.94–1.11) in pectoral–pelvic space, 0.93 (0.87–1.11) in prepectoral length; dorsal–caudal space 2.46 (2.31–2.65) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit moderate to weak. Caudal fin relatively long; upper lobe relatively broad, tip narrowly rounded, postventral margin weakly convex (much more pronounced in CSIRO H 5941–01); lower lobe acute (more broadly rounded in CSIRO H 1662–01); dorsal caudal margin 1.10 (1.03–1.16) in head length; length of lower caudal lobe 1.71 (1.66–1.89) in upper lobe length. Vertebral centra 114 (111–115 in 7 paratypes), monospondylous 43 (43–46), precaudal 84 (84–86) and caudal 30 (27–30). Teeth in upper jaw (in paratype CSIRO H 1662–01) 14+15=29, lower jaw 12+12=24.

COLOUR.— When fresh (based on holotype): rather uniformly greyish; undersurface of head paler grey, light and dark tonal areas sharply demarcated, significantly paler ventrally from snout to outer edge of spiracle, along subocular ridge to mid-gill slits; rest of belly paler than dorsal surface, almost white. Dorsal fins mostly pale grey, distinct blackish margin extending from above fin spine and along outer margin to notch in posterior margin (some variation as dark margin not obvious in some paratypes). Second dorsal fin similar with variable defined blackish extremity; no obvious pale areas at anterior base of fins; fin spines pale, greyish brown to opaque white. Caudal fin mostly greyish; broad dark area at notch, extending dorsally for slightly longer than an eye diameter along upper postdorsal margin (usually to a position demarcated by a line through the tail vertebrae where it meets the

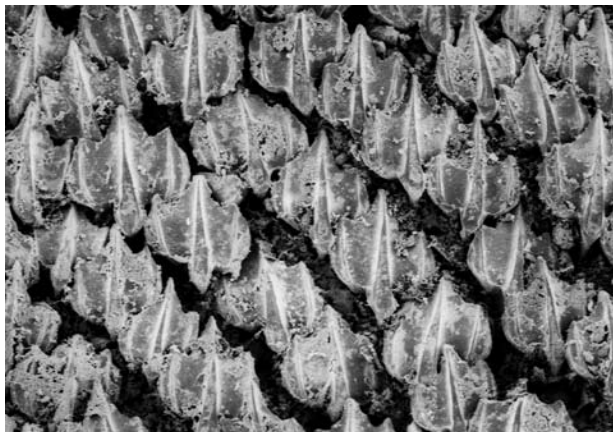


Figure 8. Cusps of the flank denticles of *Squalus chloroculus* sp. nov. paratype (CSIRO H 1405–01, adult male 760 mm TL). Field of view width 1.3 mm.

upper posterior caudal margin); tip of upper lobe and upper posterior margin pale; outer margin of lower lobe pale. Pectoral fin upper surface greyish with narrow pale posterior margin and apex; ventral surface paler, with less well demarcated outer margin. Pelvic fin upper surface similar to upper surface of pectoral fin; posterior margin strongly demarcated pale; ventral surface uniformly pale. Claspers mostly pale, basal dorsal half of clasper greyish. Eye greenish in life, otherwise bluish black. In preservative (based on holotype): similar, more uniformly medium grey above; ventral surface somewhat mottled, slightly paler grey; undersurface of snout off-white, to mottled grey. Pectoral and pelvic fins greyish dorsally with slightly paler posterior margins. Late embryo paratypes from Tasmania (CSIRO H 1350–02, Fig. 10) with more strongly demarcated pale and dark tonal areas on head; apical two-thirds of dorsal fins black, anterior basal half of fins and free rear tip white; skin on anterior dorsal-fin spines blackish. Caudal fin pattern strong, black and white; broad black caudal bar over caudal fork, extending up the dorsal lobe for more than half its length (as a posterior projection of distal part of fleshy portion of fin), then extending slightly above fleshy portion to join large, diffuse-edged, black blotch on central anterior portion of upper lobe; large black blotch at base of lower lobe narrowly connected to caudal bar below fleshy portion of fin; apical third of upper lobe and most of ventral lobe vivid white.

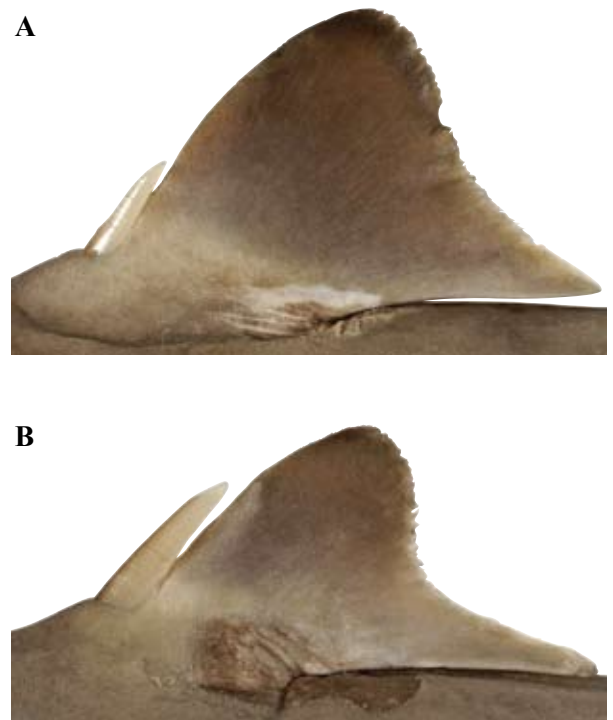


Figure 9. Lateral view of the dorsal fins of *Squalus chloroculus* sp. nov. paratype (CSIRO H 5941–01, adult male 762 mm TL) – A. first dorsal fin, B. second dorsal fin.

SIZE.— Females and males reach at least 832 (paratype) and 856 mm TL (paratype), respectively; males mature by 685 mm TL.

DISTRIBUTION.— Upper to mid continental slope off southern Australia from New South Wales (ca. 35° S) to the Great Australian Bight (33° S, 129° E). Known from depths of 216–1360 m.

ETYMOLOGY.— Derived from the Greek *choloros* meaning ‘green’ and the Latin *oculus* meaning ‘eye’ in allusion to the vivid green eyes evident on this species when fresh.

VERNACULAR.— Greeneye Spurdog.

REMARKS.— *Squalus chloroculus* differs from *S. montalbani* in the structure of the CO1 gene (see Ward *et al.*, 2007, Part 12) but the two species are very similar morphologically. Minor differences in coloration were detected in Australian ‘mitsukurii’-like spurdogs during investigations for the Australian shark and ray guide (Last and Stevens, 1994) but these forms were provisionally grouped under *S. mitsukurii*. Three shape characters distinguish Australian populations of the two species: pre-first dorsal length 2.41–2.77 vs. 1.91–2.41 times second dorsal-fin length in *S. montalbani*; horizontal pre-second dorsal length 5.03–5.81 vs. 4.20–4.92 times second dorsal-fin length; and second dorsal-fin length 10.9–12.2 vs. 12.2–13.9% TL. In addition, *S. chloroculus* has smaller dorsal fins (the mean values for all 6 measurements of both dorsal fins are higher for *S. montalbani*) with broader fin spine bases (means 0.68 vs. 0.58% TL for first dorsal-fin spine, 0.68 vs. 0.60% TL for second dorsal-fin spine), shorter adult claspers (outer length 3.8–4.6, mean 4.3% TL vs. 4.5–5.6, mean 5.0%

TL), and the upper postventral caudal margin is short relative to the lower postventral margin (ratio 2.54–3.15, mean 2.88 vs. 2.92–3.89, mean 3.36). Vertebral counts are very similar, with *S. chloroculus* having a marginally higher average precaudal count (84–86, mean 84.8, n=8 vs. 81–85, mean 83.1, n=14). *Squalus chloroculus* differs from *S. mitsukurii* in caudal fin coloration (caudal bar upright and marginal rather than oblique) and by having slightly lower vertebral counts (43–46 vs. 45–51 monospondylous centra, 84–86 vs. 87–93 precaudal centra, 111–115 vs. 118–127 total centra).

Squalus chloroculus displays some intraspecific variability in shape. A large adult male paratype from off St Helens, Tasmania (NMV A 29563–001), has a much broader upper caudal lobe, more broadly rounded lower caudal lobe, more robust head, and is more uniformly dark ventrally and dorsally than other types. Its pectoral fin is also less falcate with a more broadly rounded apex.

Other material.

Squalus mitsukurii: SU 7184 (paratype), immature male 266 mm TL, SU 7748 (paratypes), 5 of 8 embryos examined 228–237 mm TL, SU 12793 (holotype), 719 mm TL, Misaki, Honshu Island, Japan; HUMZ 79797, female 855 mm TL, HUMZ 79798, female 854 mm TL, Kyushu–Palau Ridge, Japan, 320–640 m; HUMZ 101719, adult male 657 mm TL, northwest of Okinawa, Japan.

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Figure 10. Juvenile coloration of the caudal fin of *Squalus chloroculus* sp. nov. paratype (CSIRO H 1350–02, immature male 225 mm TL).

Nurhakim (RCCF), Ian Potter (Murdoch University), Cathy Dichmont and Steve Blaber (CSIRO).

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Part 7 — Two new species of *Squalus* of the ‘mitsukurii group’ from the Indo–Pacific

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ABSTRACT. — Two new species of spurdog, *Squalus edmundsi* sp. nov. and *Squalus grahami* sp. nov., are described based on specimens from the upper continental slope off western and eastern Australia respectively. The new species, one of which has been confused with *S. mitsukurii* from the western North Pacific, belong to a subgroup of *Squalus*, the ‘mitsukurii group’, whose members all have tricuspid denticles, a moderately elongate snout, a dark bar on or reaching the posterior notch of the caudal fin, and a moderately slender body. The two species are clearly separable from each other and their closely related congeners by a combination of coloration, meristics and morphometrics.

Key words. Squaloidea – Squalidae – *Squalus edmundsi* – *Squalus grahami* – new species – Indo–West Pacific

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INTRODUCTION

Last and Stevens (1994) identified 9 Australian *Squalus* species of which 6 appear to be formally undescribed. Two of these species, referred to as *Squalus* sp. C and *Squalus* sp. F (Compagno *et al.*, 2005), belong to the ‘mitsukurii group’ but are more slender than most other group members. Recent work on *S.* sp. C (*sensu* Last and Stevens, 1994) from Western Australia revealed two distinct undescribed species: *S. altipinnis* Last, White and Stevens, 2007 (Part 5 of this issue), which has a high dorsal fin and short snout reminiscent of the ‘megalops group’, and a second species also with an upright dorsal fin similar to *S. altipinnis*, but with a longer and more pointed snout and a ‘mitsukurii-like’ dark bar on the posterior notch of the caudal fin. Market surveys at various landing sites in eastern Indonesia between April 2001 and March 2006 produced a variety of sharks, skates, rays and chimaeras, including several squalid species (White *et al.*, 2006). Amongst this material were four species of *Squalus*, one of which (i.e. *Squalus* cf. sp. C, *sensu* White *et al.*, 2006) appears to be conspecific with the second undescribed, northwestern Australian species. *Squalus* sp. F from eastern Australia, which was identified by research to produce an Australian faunal guide (Last and Stevens, 1994), remains undescribed. These two new members of the ‘mitsukurii group’ are described herein based on Australian material and comparisons are made with other similar congeners.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007). For *Squalus edmundsi* sp. nov., both morphometrics and meristics were taken from the holotype (CSIRO H 2566–01) and the following 5 paratypes: CSIRO H 2605–05, CSIRO H 2605–06, CSIRO H 2605–07, CSIRO H 2608–16 and CSIRO H 2590–11 (Table 1). In addition, meristics were taken from the following 5 paratypes: CSIRO H 822–16, CSIRO H 1207–06, CSIRO H 2567–10, CSIRO H 2575–18 and CSIRO H 2599–01. For *Squalus grahami* sp. nov., both morphometrics and meristics were taken from the holotype (CSIRO H 4476–01) and the following 5 paratypes: CSIRO H 4476–08, CSIRO H 4682–01, CSIRO H 4682–02, CSIRO H 4682–03 and CSIRO H 4682–04 (Table 1). In addition, meristics were taken from the following 23 paratypes: CSIRO H 452, CSIRO H 453, CSIRO H 454, CSIRO H 455, CSIRO H 456, CSIRO H 457–01, CSIRO H 602–02, CSIRO H 644–03, CSIRO H 644–05, CSIRO H 644–06, CSIRO H 1311–03, CSIRO H 1312–06, CSIRO H 1312–07, CSIRO H 1312–08, CSIRO H 1312–09, CSIRO H 1344–03, CSIRO H 1346–01, CSIRO H 1347–01, CSIRO H 1406–01, CSIRO H 2468–02, CSIRO H 2469–04, CSIRO H 2469–05 and CSIRO H 2688–02. In each description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the paratypes.

Type specimens are deposited in the Australian National

Fish Collection, Hobart (CSIRO), and at the Australian Museum, Sydney (AMS) and National Museum of Victoria (NMV); their registration numbers are prefixed with these acronyms.

***Squalus edmundsi* sp. nov.**

Figs 1–5; Table 1

Squalus sp. C (in part): Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 94, fig. 8.33, pl. 6.

Squalus sp. C: Compagno, Dando and Fowler, 2005, *A Field Guide to the Sharks of the World*, pp 79–80, fig. pl 2.

Squalus cf. sp. C: White *et al.*, 2006, *Economically Important Sharks and Rays of Indonesia*, pp 72–73.

Holotype. CSIRO H 2566–01, adult male 614 mm TL, west of Bernier Island, Western Australia, 24°55' S, 112°11' E, 344 m, 28 January 1991.

Paratypes. 11 specimens. CSIRO H 2608–16, female 732 mm TL, Rottneest Canyon, Western Australia, 31°55' S, 115°10' E, 850 m; CSIRO H 2605–05, female 649 mm TL, CSIRO H 2605–06, female 560 mm TL, CSIRO H 2605–07, female 508 mm TL, northwest of Rottneest Island, Western Australia, 31°44' S, 114°58' E, 485 m; CSIRO H 2599–01, adult male 585 mm TL, west of Green Head, Western Australia, 30°00' S, 114°27' E, 490 m; CSIRO H 2590–11, adult male 627 mm TL, west of Leander Point, Western Australia, 29°15' S, 113°56' E, 325 m; CSIRO H 822–16, immature male 541 mm TL, southwest of Shark Bay, Western Australia, 27°03' S, 112°40' E, 402 m; CSIRO H 2575–18, female 499 mm TL, west of Freycinet Estuary, Western Australia, 26°40' S, 112°32' E, 478 m; CSIRO H 6410–03, immature male 459 mm TL, west of Shark Bay, Western Australia, 25°31' S, 112°10' E, 326 m; CSIRO H 2567–10, female 448 mm TL, west of Dorre Island, Western Australia, 25°07' S, 112°09' E, 312 m; CSIRO H 1207–06, female 305 mm TL, northwest of Port Hedland, Western Australia, 18°20' S, 117°50' E, 430 m.

Non-types. 16 specimens. CSIRO H 2619–10, female 650 mm TL, west of Bunbury, Western Australia, 33°22' S, 114°31' E, 204 m; CSIRO H 3969–15, female 600 mm TL, southwest of Fremantle, Western Australia, 33°00' S, 114°30' E, 324 m; CSIRO H 2591–17, adult male 610 mm TL, west of Leander Point, Western Australia, 29°18' S, 113°56' E, 505 m; CSIRO H 2264–03, adult male 610 mm TL, west of Geraldton, Western Australia, 28°30' S, 113°27' E, 212 m; CSIRO H 2014–01, adult male 597 mm TL, north of Abrolhos Islands, Western Australia, 28°11' S, 113°15' E, 450 m; AMS I 31165–003 (2 specimens), female 461 mm TL and immature male 426 mm TL, northwest of Shark Bay, Western Australia, 24°00' S, 112°09' E, 312 m; CSIRO CA 4071, immature male 278 mm TL, southwest of Rowley Shoals, Western Australia, 18°45' S, 117°09' E, 356 m; CSIRO H 5786–01, female 715 mm TL, CSIRO H 5876–04, female 639 mm TL, CSIRO H 5875–05, adult male 573 mm TL,

CSIRO H 5875–06, adult male 589 mm TL, Tanjung Luar fish landing site, Lombok, Indonesia, 08°45' S, 116°35' E; CSIRO H 5857–09, adult male 537 mm TL, CSIRO H 5857–10, female 697 mm TL, CSIRO H 5857–11, adult male 563 mm TL, CSIRO H 5857–12, female 650 mm TL, Kedongan fish landing site, Bali, Indonesia, 08°45' S, 115°10' E.

DIAGNOSIS.— A moderate-sized species of *Squalus* of the 'mitsukurii group' with the following combination of characters: body moderately elongate, depth 9.9–11.5% TL; snout narrowly triangular, moderately long, preoral length 2.20–2.44 times horizontal preanial length, 10.3–10.8% TL, mouth width 1.56–1.81 (1.73) times horizontal preanial length; pre-first dorsal length 27.7–30.0 (28.5)% TL; pre-second dorsal length 60.2–62.9 (61.3)% TL; interdorsal space 23.5–25.6 (24.7)% TL; anterior nasal flap weakly bifurcate; first dorsal fin large, upright, first dorsal-fin height 7.0–8.0% TL; first dorsal-fin spine strong, upright and broad-based; second dorsal-fin spine long, moderately broad-based; prepectoral length 21.9–23.1 (22.6)% TL; pelvic–caudal space 25.0–26.7 (25.9)% TL; pectoral fin of adult not falcate; pectoral-fin inner margin relatively short, 6.4–7.1% TL; caudal bar oblique, extending along base of lower lobe to caudal fork, less than 0.1–0.2 of posterior margin of upper lobe, upper caudal fringe narrow, with a large dark saddle situated distinctly closer to tip of lobe than its base; flank denticles strongly tricuspidate; 43–44 monospondylous centra, 86–91 precaudal centra, 113–120 total centra; adult maximum size at least 73 cm TL.

DESCRIPTION.— Body fusiform, moderately long, nape moderately humped (most pronounced in largest female, CSIRO H 2608–16); deepest near first dorsal-fin spine (more posterior in smallest paratypes), maximum depth 1.02 (0.92–1.01 in 5 paratypes) times width; trunk depth 1.01 (0.87–1.01) times abdomen depth; head moderately elongate 22.4 (22.5–23.1)% TL; caudal peduncle slender, 26.2 (25.0–26.7)% TL. Head not broad, width 1.20 (1.14–1.24) times trunk width, 1.37 (1.12–1.40) times abdomen width; depressed forward of spiracles, becoming subtriangular in cross-section towards pectoral-fin origin; length 2.14 (2.13–2.26) in pre-vent length; height 0.77 (0.71–0.76) times width. Snout elongate, narrowly triangular in lateral view, apex bluntly pointed; lateral preanial margin not angular (slightly angular); very pointed in dorsal view (bluntly pointed in some paratypes); horizontal length 1.52 (1.23–1.45) times eye length, 0.83 (0.82–0.85) times interorbital space; horizontal preanial length 2.20 (2.25–2.44) times in preoral length. Eye narrowly oval, size moderate, length 4.88 (4.03–4.63) in head, 2.81 (2.17–2.57) times height; strongly notched posteriorly, notch extending as a well-developed furrow half the distance to spiracle (rarely reaching spiracle). Spiracle size moderate, broadly crescentic (variable); broad lobe-like fold on posterior margin; greatest diameter 3.85 (3.28–4.42) in eye length. Gill openings directed slightly



Figure 1. Lateral view of *Squalus edmundsi* sp. nov. holotype (CSIRO H 2566–01, adult male 614 mm TL).



Figure 2. Ventral view of the head of *Squalus edmundsi* sp. nov. holotype (CSIRO H 2566–01, adult male 614 mm TL).

anterodorsally from bottom to top (sometimes upright); first four subequal in size (first on left side distinctly smaller in CSIRO H 2605–05), fifth longest, height of fifth slit 2.1 (2.1–2.3)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.41 (1.33–1.38) in preoral length; upper labial furrows less than twice length of lower furrows; prominent postoral groove, longer than upper labial furrows, extending posterolaterally from angle of jaws; in paratypes, two series of functional teeth in upper jaw, two or three series in lower. Teeth in paratypes similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap weakly bifurcate, upper lobe greatly enlarged; posterior lobe rudimentary to short (variable), flattened; internarial space 2.19 (2.06–2.28) in preoral length, 2.63 (2.58–3.06) times nostril length. Dermal denticles (based on holotype) on flank very small, strongly imbricate; crowns broad, strongly tricuspidate with pronounced median ridge; median ridge commencing well forward of

rest of crown, with a mesial furrow developing anteriorly and converging towards posterior tip of crown; lateral cusps well developed, ridges not visible (in female paratype CSIRO H 2608–16, lateral cusps less well developed, with evidence of ridges). First dorsal fin moderate, elevated, upright, broadly rounded apically; anterior margin very strongly convex; upper posterior margin straight, not vertical, directed well anterodorsally from bottom to top, weakly (rarely moderately) concave near free rear tip; free rear tip relatively thick basally, short; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior to free rear tip of pectoral fin; fin-spine origin above pectoral-fin insertion (slightly posterior in CSIRO H 2608–16); spine base broad, exposed anteriorly well below junction of spine and soft portion of fin; soft portion of fin connected above (or near) mid-point of total spine length; spine tapering distally, anterior margin almost straight; exposed portion upright, subequal in length to exposed portion of second dorsal-fin spine; unexposed base only slightly longer than unexposed base of second

dorsal-fin spine; pre-first dorsal-fin length 3.53 (3.34–3.61) times in TL; first dorsal-fin length 1.88 (1.82–2.00) times its height, 1.17 (1.11–1.25) times second dorsal-fin length; first dorsal-fin height 1.67 (1.63–1.78) times second dorsal-fin height; exposed first dorsal spine length 0.65 (0.66–0.82) times height of fin. Second dorsal fin of moderate size, strongly raked; anterior margin convex, apex narrowly rounded; posterior margin very deeply concave, maximum concavity almost near mid-point of margin, upper portion directed dorsoposteriorly strongly from bottom to top; free rear tip elongate, inner margin length 0.96 (0.93–1.04) times fin height; second dorsal-fin length 2.68 (2.60–2.80) times its height; spine length 1.11 (1.09–1.27) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed well below (variable) level of junction with spine and soft portion of fin; second dorsal spine moderately broad based, slender, sharply pointed distally, tapering rapidly just above point of exposure, spine tip extending to about level of insertion of fin (slightly posterior in some); interdorsal space 0.87 (0.86–0.98) in prepectoral length, 1.11 (1.09–1.21) in pre-first dorsal length; interdorsal groove weak. Pectoral fin small, anterior margin moderately convex; inner margin weakly convex, length 6.4 (6.4–7.1)% TL; apex narrowly rounded (sometimes angular), lobe-like but not falcate; posterior margin moderately concave, free rear tip broadly rounded; base very short, 2.60 (2.57–3.02) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Caudal peduncle long, tapering slightly to caudal fin; subcircular in cross-section anteriorly, moderately semicircular posteriorly; ventral groove well developed; lateral keels well developed, originating under insertion of second dorsal fin, terminating less than an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.79 (0.78–0.95) in pectoral–pelvic space, 0.84 (0.85–0.90) in prepectoral length; dorsal–caudal space 2.51 (2.15–2.60) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit moderate. Caudal fin relatively long, upper postventral margin moderately convex; apex of

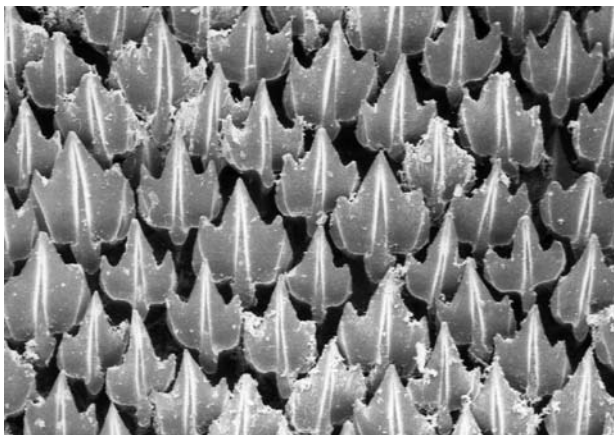


Figure 3. Cusps of the flank denticles of *Squalus edmundsi* sp. nov. paratype (CSIRO H 822–16, immature male 541 mm TL). Field of view width 1.3 mm.

lower lobe somewhat angular; dorsal caudal margin 1.07 (1.07–1.14) in head length; length of lower caudal lobe 2.00 (1.84–1.94) in upper lobe length. Vertebral centra 113 (115–120 in 10 paratypes), monospondylous 43 (43–44), precaudal 87 (86–91) and caudal 26 (24–30). Teeth in upper jaw (in paratype CSIRO H 2605–05) 12+13=25, lower jaw 11+11=22.

COLOUR.— When fresh (based on holotype): head greyish to greyish brown dorsally, paler off-white to light grey ventrally; light and dark tonal areas sharply demarcated, interface extending from snout to below eye, through middle of gill slits to pectoral-fin base; entire trunk mostly dark, similar to dorsal coloration of head. First dorsal fin dusky, free rear tip slightly paler, apical margin black-tipped; second dorsal fin dusky, apical margin black-tipped, mid- and lower posterior margin pale (abruptly demarcated from black apex); dorsal spines dusky, darkest anteriorly. Caudal fin mostly dusky; black upper caudal fringe very narrow; white margin on upper and lower lobes of caudal fin well-demarcated; evidence of an oblique, blackish caudal bar along base of anterior lower lobe, confined to notch on posterior fin margin. Pectoral and pelvic-fin upper surfaces greyish. In juvenile paratype (CSIRO H 2567–10), body coloration similar, with slightly paler ventral surface; dark margins on dorsal fins more pronounced; free rear tip of first dorsal fin white (much paler than holotype), strongly contrasted

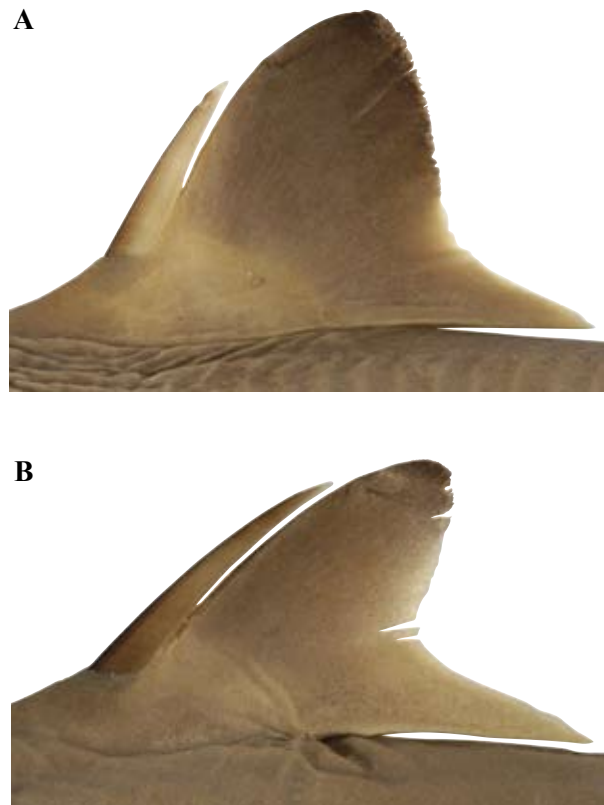


Figure 4. Lateral view of the dorsal fins of *Squalus edmundsi* sp. nov. paratype (CSIRO H 2605–05, female 649 mm TL) – A. first dorsal fin, B. second dorsal fin.

with black apex; pale area on posterior margin of second dorsal fin extending almost to apex of fin, very strongly contrasted; caudal fin with a distinctive white posterior margin; lower caudal lobe white distally, bordered basally with a well-defined, oblique, diffuse-edged, blackish caudal bar (not quite touching posterior margin of fin at fork); blackish upper caudal fringe better defined than in holotype; no obvious black margin on anterior margin of pectoral fin; evidence of large, upper caudal blotch on central upper lobe (more pronounced in smaller juvenile non-type, CSIRO CA 4071). In preservative (based on holotype): coloration similar, more uniformly greyish, light and dark tonal areas on head remaining evident; pale margins on caudal fin distinct and caudal bar still evident.

SIZE.— Females and males reach at least 866 (not retained) and 700 mm TL (not retained), respectively; smallest adult male 537 mm TL (non-type), immature males ranging from 278 to 541 mm TL; smallest post-natal female and male 305 and 278 mm TL, respectively.

DISTRIBUTION.— Upper continental slope off Western Australia, southwest of Fremantle, Western Australia (ca. 33° S, 114° E) to east of Rowley Shoals, Western Australia (ca. 18° S, 118° E). Occurs in depths of 204–850 m (mostly 300–500 m). Also recorded off eastern Indonesia between Kedonganan, Bali (ca. 09° S, 115° E) and Tanjung Luar, Lombok (ca. 09° S, 116° E).

ETYMOLOGY.— Named after Matt Edmunds for his high-quality, preliminary research on Australian *Squalus* undertaken as part of a summer vacation scholarship at the CSIRO Marine Laboratories in the early 1990's.

VERNACULAR.— Edmunds' Spurdog.



Figure 5. Juvenile coloration of the caudal fin of *Squalus edmundsi* sp. nov. (CSIRO CA 4071, immature male 278 mm TL).

REMARKS.— *Squalus edmundsi* can be distinguished from all other regional members of the 'mitsukurii group' in having an oblique caudal bar through the base of the lower caudal-fin lobe rather than a vertical bar along the posterior fin margin. It also differs in a combination of snout length, dorsal fin shape, dorsal-fin spine robustness, and other meristic and morphometric details. It differs from the morphologically similar *S. chloroculus*, *S. mitsukurii* and *S. montalbani*, in having more upright dorsal fins with more robust spines (first dorsal-fin spine base width 1.0–1.2 vs. 0.5–0.8% TL), and a smaller maximum size (males attaining 70 cm TL vs. >85 cm TL in the other three species). *Squalus edmundsi* differs from the three superficially-similar species belonging to the 'highfin megalops group', *S. albifrons*, and *S. altipinnis* (Last, White and Stevens, 2007; Part 5 of this issue) in having a dark caudal bar that either extends or almost reaches to the caudal-fin posterior margin at the caudal fork vs. an entirely pale posterior margin, and these species and *S. notocaudatus* (Last, White and Stevens, 2007; Part 5 of this issue) by a longer, more pointed snout (preoral snout 10.3–10.8 vs. 8.4–9.5% TL; prenarial length 5.6–5.8 vs. 4.3–5.0% TL).

***Squalus grahami* sp. nov.**

Figs 6–10; Table 1

Squalus sp. F: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 97, fig. 8.26, 8.36, pl. 5; Compagno, Dando and Fowler, 2005, *A Field Guide to the Sharks of the World*, p 81, fig, pl 2.

Holotype. CSIRO H 4476–01, adult male 602 mm TL, northeast of Batemans Bay, New South Wales, 35°29' S, 150°46' E, 234 m, 4 December 1996.

Paratypes. 30 specimens. CSIRO H 1347–01, female 380 mm TL, east of Flinders Reefs, Queensland, 17° 29' S, 149°32' E, 504 m; CSIRO H 1406–01, female 221 mm TL, Queensland Trough, east of Hinchinbrook Island, Queensland, 17°55' S, 147°06' E, 402 m; CSIRO H 453, adult male 526 mm TL, CSIRO H 457–01, female 623 mm TL, northeast of Hinchinbrook Island, Queensland, 17°57' S, 147°03' E, 300 m; CSIRO H 2468–02, female 653 mm TL, east of Hinchinbrook Island, Queensland, 17°57' S, 147°02' E, 306 m; CSIRO H 2469–04, female 649 mm TL, CSIRO H 2469–05, female 631 mm TL, east of Hinchinbrook Island, Queensland, 17°58' S, 147°01' E, 264 m; CSIRO H 454, adult male 550 mm TL, CSIRO H 455, female 635 mm TL, CSIRO H 456, adult male 550 mm TL, Townsville Trough, Queensland, 17°58' S, 147°00' E, 220 m; CSIRO H 1311–03, female 653 mm TL, Marian Plateau, east of Whitsunday Islands, Queensland, 19°29' S, 150°17' E, 328 m; CSIRO H 1346–01, immature male 294 mm TL, North East Slope, Queensland; CSIRO H 602–02, female 367 mm TL, CSIRO H 1312–06, female 286 mm TL, CSIRO H 1312–07, female 340 mm TL, CSIRO H 1312–08, female 282 mm TL, CSIRO H 1312–09, immature

male 279 mm TL, south of Saumarez Reef, Queensland, 22°42' S, 154°05' E, 419 m; CSIRO H 644-03, adult male 520 mm TL, CSIRO H 644-05, adult male 531 mm TL, CSIRO H 644-06, adult male 523 mm TL, CSIRO H 1344-01, female 232 mm TL, CSIRO H 1344-02, juvenile male 238 mm TL, CSIRO H 1344-03, immature male 327 mm TL, south of Saumarez Reef, Queensland, 22°49' S, 154°10' E, 450 m; CSIRO H 452, female 624 mm TL, southwest of Saumarez Reef, Queensland, 22°52' S, 152°42' E, 225 m; CSIRO H 2688-02, adult male 572 mm TL, east of Coffs Harbour, New South Wales, 30°24' S, 153°23' E, 148 m; CSIRO H 4682-01, adult male 558 mm TL, CSIRO H 4682-02, female 689 mm TL, CSIRO H 4682-03, female 702 mm TL, CSIRO H 4682-04, adult male 571 mm TL, east of Broken Bay, New South Wales, 33°32' S, 152°00' E, 329 m; CSIRO H 4476-08, female 578 mm TL, collected with holotype.

Non-types.— 18 specimens. CSIRO H 5635-13, female 643 mm TL, east of Rockingham Bay, Queensland, 18°08' S, 147°09' E, 248 m; CSIRO H 602-13, female 355 mm TL, south of Saumarez Reef, Queensland, 22°42' S, 154°05' E, 419 m; CSIRO H 4623-03, female 607 mm TL, east of Terrigal, New South Wales, 33°26' S, 152°06' E, 383 m; NMV A 29562-001, female 675 mm TL, east of Sydney, New South Wales, 33°28' S, 152°00' E, 230 m; CSIRO H 4476-02, female 595 mm TL, CSIRO H 4476-03, adult male 522 mm TL, CSIRO H 4476-04, adult male 525 mm TL, CSIRO H 4476-05, female 580 mm TL, CSIRO H 4476-06, female 592 mm TL, CSIRO H 4476-07, female 552 mm TL, CSIRO H 4476-09, female 594 mm TL, CSIRO H 4476-10, female 556 mm TL, CSIRO H 4476-11, adult male 542 mm TL, collected with holotype; CSIRO H 4771-01, adult male 516 mm TL, east of Brush Island, New South Wales, 35°30' S, 150°45' E, 333 m; CSIRO H 4477-01, female 663 mm TL, CSIRO H 4477-02, female 598 mm TL, CSIRO H 4709-02, female 711 mm TL, east of Brush Island, New South Wales, 35°34' S, 150°44' E, 388 m; CSIRO H 4708-01, immature male 549 mm TL, east of Batemans Bay, New South Wales, 35°48' S, 150°34' E, 291 m.

DIAGNOSIS.— A moderate-sized species of *Squalus* of the 'mitsukurii group' with the following combination of characters: body very elongate, depth 10.1–12.6% TL; snout narrow, moderately long, preoral length 2.38–2.53 times horizontal prenarial length, 10.5–11.3% TL, mouth width 1.54–1.77 (1.66) times horizontal prenarial length; pre-first dorsal length 28.9–31.3 (30.0)% TL; pre-second dorsal length 60.2–62.7 (61.2)% TL; interdorsal space 22.3–24.7 (23.8)% TL; dorsal fins small, raked, first dorsal-fin height 6.3–7.2% TL; first dorsal-fin spine short, weak; second dorsal-fin spine slender with moderately broad base; prepectoral length 21.7–23.6 (22.4)% TL; pelvic-caudal space 24.0–26.5 (25.4)% TL; pectoral fin of adult slightly falcate; pectoral-fin inner margin relatively short, 7.1–7.8% TL; caudal bar almost upright, extending narrowly from the caudal fork up the

posterior margin of the upper lobe for usually about 0.4 (rarely to 0.6) of its length in immatures, upper caudal fringe narrow, sometimes with a narrow central blotch on upper lobe; flank denticles weakly tricuspidate; 37–42 monospondylous centra, 80–87 precaudal centra, 105–116 total centra; adult maximum size up to 71 cm TL.

DESCRIPTION.— Body fusiform, elongate (more robust in large female paratypes), nape slightly humped (more pronounced in largest paratypes); deepest near first dorsal-fin spine, maximum depth 0.94 (0.88–1.00 in paratypes) times width; trunk depth 0.97 (0.86–0.98) times abdomen depth; head short 22.0 (22.6–24.0)% TL; caudal peduncle moderately slender, 26.3 (24.0–26.5)% TL. Head somewhat narrow, width 1.08 (1.05–1.14) times trunk width, 1.25 (1.10–1.28) times abdomen width; depressed forward of spiracles, becoming subtriangular in cross-section towards pectoral-fin origin; length 2.15 (2.07–2.21) in pre-vent length; height 0.82 (0.74–0.84) times width. Snout long, narrowly triangular in lateral view, apex bluntly pointed; lateral prenarial margin somewhat angular; pointed in dorsal view; horizontal length 1.59 (1.46–1.56) times eye length, 1.00 (0.90–1.01) times interorbital space; horizontal prenarial length 2.38 (2.43–2.53) times in preoral length. Eye oval, size moderately large, length 4.47 (4.21–4.68) in head, 2.55 (2.24–2.58) times height; strongly notched posteriorly, notch extending as a well-developed furrow to anteroventral margin of spiracle (usually more pronounced anteriorly, sometimes barely extending to spiracle). Spiracle size small to moderate, broadly (sometimes narrowly) crescentic; broad lobe-like fold on posterior margin; greatest diameter 3.89 (3.33–4.11) in eye length. Gill openings almost upright; first four subequal in size, fifth longest, height of fifth slit 2.1 (1.9–2.3)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.55 (1.43–1.53) in preoral length; upper labial furrows about twice length of lower furrows (or less); prominent postoral groove, much longer than upper labial furrows (usually longer in paratypes), extending posterolaterally from angle of jaws; two series of functional teeth in upper jaw, two series in lower. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like; cusps directed strongly laterally, low; base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate, upper lobe largest, broadest; posterior lobe narrow, thallate (variable in paratypes); internarial space 2.23 (2.11–2.28) in preoral length, 2.74 (2.67–3.04) times nostril length. Dermal denticles (based on the holotype) on flank very small; crown weakly tricuspidate with pronounced median ridge, median cusp apex broadly triangular; median ridge origin slightly anterior to rest of crown; ridge with mesial furrow converging towards posterior tip of crown; lateral cusps weakly developed, blunt to rudimentary, distal ridges not evident. First dorsal fin somewhat raked, broadly rounded apically; anterior margin weakly convex; upper posterior margin weakly convex, not vertical, directed slightly anterodorsally from



Figure 6. Lateral view of *Squalus grahami* sp. nov. holotype (CSIRO H 4476–01, adult male 602 mm TL).



Figure 7. Ventral view of the head of *Squalus grahami* sp. nov. holotype (CSIRO H 4476–01, adult male 602 mm TL).

bottom to top, moderately concave near free rear tip; free rear tip moderately thick basally, short; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior to free rear tip of pectoral fin; fin-spine posterior to pectoral-fin insertion; spine base narrow, exposed anteriorly below junction of spine and soft portion of fin; soft portion of fin connected slightly above mid-point of total spine length (in paratype CSIRO H 4682–03 close to spine apex); spine tapering distally, anterior margin almost straight; exposed portion of spine raked, shorter than exposed portion of second dorsal-fin spine; pre-first dorsal length 3.44 (3.19–3.46) times in TL; first dorsal-fin length 1.97 (2.04–2.28) times its height, 1.12 (1.09–1.19) times second dorsal-fin length; first dorsal-fin height 1.50 (1.25–1.66) times second dorsal-fin height; exposed first dorsal spine length 0.56 (0.49–0.67) times height of fin. Second dorsal fin

of moderate size, strongly raked; anterior margin slightly convex, apex narrowly rounded; posterior margin deeply concave, maximum concavity well below mid-point of margin, upper portion directed slightly dorsoposteriorly from bottom to top; free rear tip very elongate, inner margin length 1.15 (0.98–1.18) times fin height; second dorsal-fin length 2.64 (2.53–3.08) times its height; spine length 1.03 (0.86–1.14) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, usually exposed at level of junction with spine and soft portion of fin; second dorsal spine moderately broad based (more pronounced in largest paratypes), slender, anterior margin slightly convex, weakly recurved distally, apex sharply pointed, tapering just above point of exposure; spine tip extending behind level of insertion of fin (over in some paratypes); interdorsal space 0.88 (0.91–1.06) in pre-pectoral length, 1.18 (1.22–1.39) in pre-first dorsal length; interdorsal

Table 1. Proportional dimensions as percentages of total length for the holotypes and 5 paratypes of *Squalus edmundsi* sp. nov. (holotype CSIRO H 2566–01) and *Squalus grahami* sp. nov. (holotype CSIRO H 4476–01).

	<i>S. edmundsi</i> sp. nov.			<i>S. grahami</i> sp. nov.		
	Holotype	Paratypes		Holotype	Paratypes	
		Min.	Max.		Min.	Max.
TL – Total length	614	508	738	602	558	702
PCL – Precaudal length	78.8	78.4	79.8	78.2	77.8	80.5
PD2 – Pre-second dorsal length	61.1	60.2	62.9	59.1	58.8	62.0
PD1 – Pre-first dorsal length	28.4	27.7	30.0	28.4	28.6	30.5
SVL – Pre-vent length	47.9	48.8	51.6	47.3	47.8	50.9
PP2 – Prepelvic length	45.9	47.0	49.5	45.3	45.5	50.1
PP1 – Prepectoral length	22.1	21.9	23.1	21.7	22.1	23.6
HDL – Head length	22.4	22.5	23.1	22.0	22.7	24.0
PG1 – Prebranchial length	19.2	19.3	19.9	19.0	19.5	20.5
PSP – Prespiracular length	13.3	13.2	13.6	12.9	12.9	14.0
POB – Preorbital length	8.0	7.9	8.1	8.3	8.3	9.0
PRN – Prenarial length	5.8	5.6	5.8	5.6	5.7	6.3
POR – Preoral length	10.3	10.4	10.8	10.5	10.8	11.3
INLF – Inner nostril-labial furrow space	4.8	4.5	5.0	4.7	4.5	5.0
MOW – Mouth width	7.3	7.8	7.9	6.8	7.1	7.9
ULA – Labial furrow length	2.2	2.0	2.3	2.2	2.3	2.8
INW – Internarial space	4.7	4.6	5.0	4.7	4.7	5.4
INO – Interorbital space	8.4	8.2	8.8	7.8	7.6	8.5
EYL – Eye length	4.6	4.9	5.7	4.9	4.9	5.5
EYH – Eye height	1.6	2.0	2.3	1.9	1.9	2.3
SPL – Spiracle length	1.2	1.2	1.5	1.5	1.3	1.7
GS1 – First gill-slit height	1.6	1.4	2.0	1.5	1.4	1.8
GS5 – Fifth gill-slit height	2.1	2.1	2.3	2.1	1.9	2.3
IDS – Interdorsal space	25.5	23.5	25.6	23.7	20.6	23.8
DCS – Dorsal-caudal space	10.2	9.6	10.9	10.8	9.9	11.1
PPS – Pectoral-pelvic space	20.7	20.8	23.8	20.6	20.3	24.8
PCA – Pelvic-caudal space	26.2	25.0	26.7	26.3	24.0	26.5
D1L – First dorsal length	14.6	13.8	14.8	14.1	14.8	15.2
D1A – First dorsal anterior margin	11.9	11.3	12.8	11.7	12.0	13.0
D1B – First dorsal base length	9.3	8.3	9.6	8.6	9.1	10.1
D1H – First dorsal height	7.7	7.0	8.0	7.0	6.3	7.2
D1I – First dorsal inner margin	5.5	4.9	5.6	5.9	5.1	6.0
D1P – First dorsal posterior margin	9.2	8.5	9.1	8.0	7.5	8.6
D1ES – First dorsal spine length	5.0	4.8	5.7	3.9	3.1	4.2
D1BS – First dorsal spine base width	1.2	1.0	1.2	0.6	0.6	0.8
D2L – Second dorsal length	12.5	11.6	13.0	13.9	12.4	14.4
D2A – Second dorsal anterior margin	11.0	10.2	11.8	11.2	10.2	12.2
D2B – Second dorsal base length	8.1	7.5	8.6	8.5	8.0	9.6
D2H – Second dorsal height	4.6	4.2	4.9	4.6	4.0	5.1
D2I – Second dorsal inner margin	4.5	4.1	4.6	5.3	4.3	5.1
D2P – Second dorsal posterior margin	5.0	4.4	5.0	5.6	4.8	6.2
D2ES – Second dorsal spine length	5.2	5.0	5.5	4.8	3.5	5.4
D2BS – Second dorsal spine base width	0.8	0.8	1.0	0.7	0.7	0.8

Table 1. cont'd.

	<i>S. edmundsi</i> sp. nov.			<i>S. grahamsi</i> sp. nov.		
	Holotype	Paratypes		Holotype	Paratypes	
		Min.	Max.		Min.	Max.
P1A – Pectoral anterior margin	14.0	14.3	15.1	14.4	14.1	15.0
P1I – Pectoral inner margin	6.4	6.4	7.1	7.5	7.1	7.8
P1B – Pectoral base length	5.4	4.9	5.9	5.0	5.3	6.1
P1P – Pectoral posterior margin	9.9	10.0	11.2	10.0	10.6	12.0
P2L – Pelvic length	10.4	8.9	10.4	11.2	10.5	11.5
P2H – Pelvic height	4.7	3.9	5.1	3.9	4.1	4.6
P2I – Pelvic inner margin	5.5	3.7	5.6	5.7	5.0	6.4
CDM – Dorsal caudal margin	21.0	20.0	21.1	21.7	19.2	22.0
CPV – Preventral caudal margin	10.5	10.8	11.4	11.9	11.0	12.1
CPU – Upper postventral caudal margin	15.7	15.0	15.9	16.4	14.2	16.5
CPL – Lower postventral caudal margin	4.3	3.6	5.0	5.1	4.0	5.0
CFW – Caudal fork width	6.5	6.2	6.9	6.3	6.2	7.2
CFL – Caudal fork length	8.6	8.3	9.2	9.2	9.3	10.0
HANW – Head width at nostrils	6.8	6.8	7.3	8.2	8.1	8.9
HAMW – Head width at mouth	10.8	11.1	11.7	10.3	11.2	11.5
HDW – Head width	12.0	11.8	13.3	11.2	11.4	13.2
TRW – Trunk width	10.0	9.8	11.7	10.4	10.3	12.1
ABW – Abdomen width	8.7	8.4	11.9	9.0	9.5	11.7
TAW – Tail width	6.4	5.7	6.7	5.8	6.5	7.1
CPW – Caudal peduncle width	3.0	2.4	3.0	2.8	2.9	3.2
HDH – Head height	9.3	8.3	10.0	9.2	9.1	10.3
TRH – Trunk height	10.2	9.2	10.7	9.8	9.8	11.5
ABH – Abdomen height	10.1	9.9	11.5	10.1	10.5	12.6
TAH – Tail height	6.6	6.2	6.6	6.0	6.2	7.3
CPH – Caudal peduncle height	2.3	2.2	2.4	2.4	2.3	2.6
CLO – Clasper outer length	3.4	3.0	3.0	4.0	4.0	4.0
CLI – Clasper inner length	6.2	6.1	6.1	7.2	7.7	8.2
CLB – Clasper base width	1.1	1.2	1.2	1.6	1.3	1.6

ridge obvious (variable in paratypes). Pectoral fin small, length 7.5 (7.1–7.8)% TL; anterior margin weakly convex, apex narrowly rounded, slightly falcate; posterior margin moderately concave, inner margin convex, free rear tip bluntly angular; fin base very short, 2.89 (2.46–2.83) in length of anterior margin. Pelvic fins moderate, anterior and posterior margins almost straight, apex broadly rounded, free rear tip acute. Caudal peduncle long, tapering very slightly to caudal fin; subcircular in cross-section anteriorly, broadly semicircular posteriorly; ventral groove well developed (variable in paratypes); lateral keels well developed, originating under insertion of second dorsal fin (or slightly behind), terminating less than an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.78 (0.76–1.03) in pectoral–pelvic space, 0.83 (0.85–0.94) in prepectoral length; dorsal–caudal space 2.28 (2.04–2.43) in interdorsal length; dorsal

caudal pit well developed, ventral caudal pit rudimentary. Caudal fin moderate, posterior margin of upper lobe very strongly convex, base broad; apex of lower lobe narrowly rounded to somewhat angular; dorsal caudal margin 1.01 (1.03–1.21) in head length; length of lower caudal lobe 1.83 (1.64–1.81) in upper lobe length. Vertebral centra 113 (108–116), monospondylous 40 (38–42), precaudal 86 (80–87) and caudal 27 (26–32). Teeth in upper jaw (in paratype CSIRO H 2469–05) 13+14=27, lower jaw 12+11=23.

COLOUR.— When fresh (based on holotype): dorsal surface dark grey, off-white to greyish below; light and dark tonal areas well demarcated on head, extending from snout to below eye, through middle of gill slits to pectoral-fin base; not obviously demarcated on belly; tail almost uniformly greyish above and below. First dorsal

fin almost uniformly dark grey, base slightly paler, narrow black apical margin; second dorsal fin uniformly greyish, no evidence of darker markings; dorsal-fin spines dusky. Caudal bar blackish, pronounced, extending dorsally from fork, covering basal half of upper lobe posteriorly; distal half of posterior margin of upper lobe pale, remainder of lobe dusky; ventral lobe almost uniformly pale; fleshy portion of fin bordered above and below by dark, diagonal, greyish caudal stripes. Small paratype (CSIRO H 602–02) significantly paler than holotype, greyish above, almost white below; light and dark tonal areas less strongly demarcated with more pronounced dark margins along dorsal fins; a broad dark edge on first dorsal fin extending from upper anterior margin along fin towards free rear tip; second dorsal fin similar, dark marking very broad, not extending onto free rear tip; dark caudal bar very distinct, strongly demarcated from white areas on upper and lower lobes; upper caudal fringe forming a well-developed saddle on middle of lobe, faint upper caudal blotch on mid-outer lobe; upper caudal stripe narrow, lower stripe appearing as a prominent black basal blotch; narrow black anterior margin on pectoral fin. In preservative (based on holotype): narrow dark margins on dorsal fins more evident than in fresh state; dorsal surface of pectoral fin similar to upper body, posterior margins only slightly paler; ventral surface of pectoral fins dusky with a whitish base; upper pelvic fins greyish with broad, pale posterior margin, more uniformly pale ventrally. Neonatal paratype (CSIRO H 1406–01) similar to fresh paratype (CSIRO H 602–02), more yellowish, dark coloration on fins similarly disposed; upper caudal blotch and upper caudal stripe prominent.

SIZE.— Females and males reach at least 711 (non-type) and 602 mm TL (holotype), respectively; smallest adult male 516 mm TL, immature males ranging from 238 to 327 mm TL; smallest post-natal specimen 232 mm TL. Graham (2005) provides basic biological data for several *Squalus* species including *S. grahami* (as *S. sp. F*) and reports maximum sizes of 730 and 620 mm TL for

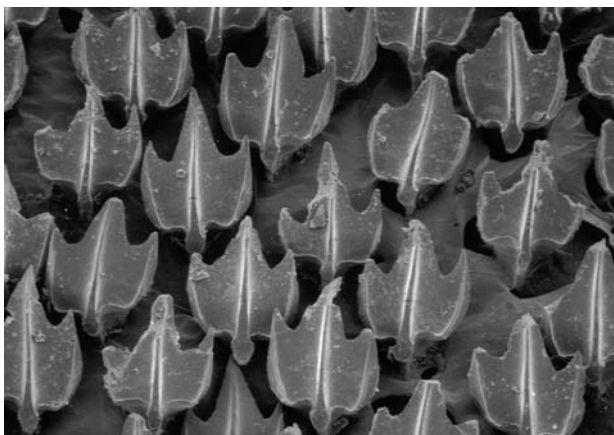


Figure 8. Cusps of the flank denticles of *Squalus grahami* sp. nov. (CSIRO H 602–02, female 367 mm TL). Field of view width 0.9 mm.

females and males, respectively.

DISTRIBUTION.— Upper continental slope off eastern Australia, from north of Brush Island, New South Wales (ca. 35°S, 150°E) to Cape York, Queensland (ca. 10°S, 144°E). Known from depths of 148–504 m but trawled mainly in depths of 220–450 m.

ETYMOLOGY.— Named after prominent Australian

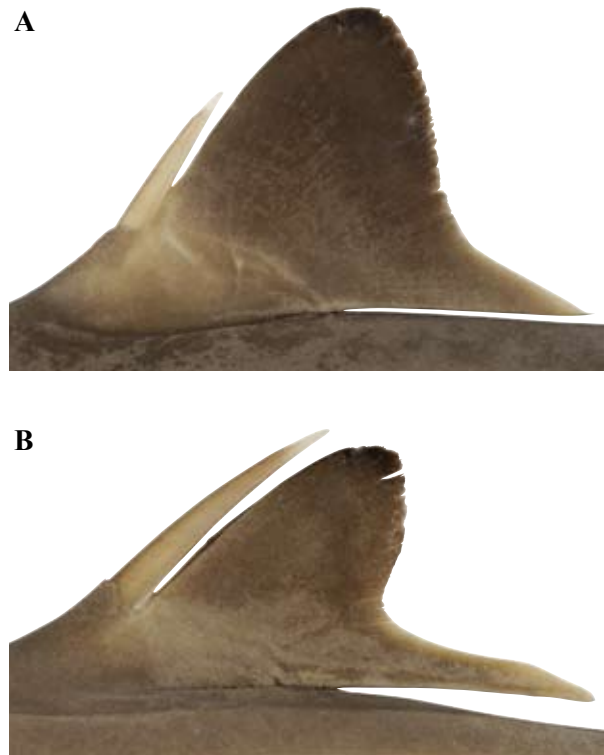


Figure 9. Lateral view of the dorsal fins of *Squalus grahami* sp. nov. holotype (CSIRO H 4476–01, adult male 602 mm TL) – A. first dorsal fin, B. second dorsal fin.



Figure 10. Juvenile coloration of the caudal fin of *Squalus grahami* sp. nov. (CSIRO H 1406–01 female 221 mm TL).

ichthyologist, Ken Graham (NSW Department of Primary Industries, Cronulla), who has contributed greatly to our knowledge of the sharks and rays of southeastern Australia, and who collected the primary type, as well as the majority of New South Wales material of this species.

VERNACULAR.— Eastern Longnose Spurdog.

REMARKS.— *Squalus grahami* can be distinguished from all other members of the ‘mitsukurii group’ by the combination of a narrow, moderately long snout, small raked dorsal fins, small dorsal-fin spines, and other meristic and morphometric details. It differs from the morphologically similar *S. montalbani*, *S. chloroculus* and *S. mitsukurii* in having a much smaller maximum size (ca. 600 vs. >850 mm TL for males), a slightly longer snout (preoral length 10.5–11.3 vs. 9.5–10.1, 9.3–10.6 and 9.4–10.8% TL respectively), and fewer monospondylous centra (37–42 vs. 41–47, 43–46 and 45–51 respectively). *Squalus grahami* differs from *S. edmundsi* in having an upright caudal bar (rather than oblique), more strongly raked dorsal fins with short, narrow spines (exposed first dorsal spine length 3.1–4.2 vs. 4.8–5.7 TL), a slightly longer snout (preorbital length 8.3–9.0 vs. 7.9–8.1% TL), and slightly less precaudal centra (80–87 vs. 86–92).

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Part 8 — *Squalus nasutus* sp. nov., a new long-snout spurdog of the ‘japonicus group’ from the Indian Ocean

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ABSTRACT.— A new species of spurdog, *Squalus nasutus* sp. nov., is described based on specimens from the upper continental slope off Western Australia. The new species, which has been confused with *S. japonicus* from the western North Pacific, belongs to a subgroup of *Squalus* whose members all have a very elongate snout. *Squalus nasutus* differs from its closely related congeners in a combination of fin coloration, meristics and morphometrics of the head, trunk and pectoral fins. It appears to occur outside Australian seas and intraspecific variation between populations across the Indo–West Pacific is discussed.

Key words. Squaloidea – Squalidae – *Squalus nasutus* – new species – Indo–West Pacific

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INTRODUCTION

Last and Stevens (1994) identified 9 *Squalus* species from Australian waters of which 6 appear to be formally undescribed. One of these species belongs to the ‘japonicus group’. The group presently contains three nominal species, *S. japonicus* Ishikawa, 1908 from the western North Pacific, and *S. melanurus* Fourmanoir and Rivaton, 1979 and *S. rancureli* Fourmanoir and Rivaton, 1979 from New Caledonia. These species are characterised by a very slender body and a very long snout. A new species of the ‘japonicus group’, informally identified as *Squalus* sp. E (sensu Last and Stevens, 1994), is described based on Australian material and comparisons are made with similar forms from the Indian Ocean.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007). Morphometrics and meristics were taken from the holotype (CSIRO H 2590–12) and the following 5 paratypes: CSIRO H 1652–02, CSIRO H 2032–01, CSIRO H 2567–08, CSIRO H 2598–07 and CSIRO H 2898–07 (Table 1). In addition, meristics were taken from the following 13 paratypes: CSIRO CA 3290, CSIRO CA 4055, CSIRO CA 4110, CSIRO H 1207–07, CSIRO H 1207–08, CSIRO 1652–01, CSIRO H 1693–01, CSIRO H 1693–02, CSIRO H 1694–01, CSIRO H 2032–02, CSIRO H 2608–15 and WAM P 28086–006 (2 specimens). Shape data was obtained from an additional 4 specimens from Indonesia and 3 specimens from the Philippines of a ‘japonicus group’ *Squalus* thought to be conspecific with the new species. A subset of morphometric characters possibly useful in discriminating members of

the ‘japonicus group’ were obtained from the remaining post-juvenile paratypes. In the formal description, morphometric and meristic values for the holotype are given first followed in parentheses by the ranges of the paratypes. Meristics were taken from radiographs of 17 Australian, 4 Indonesian and 5 Philippine specimens of the new species as well as 4 specimens of *S. japonicus*. Type specimens are deposited in the Australian National Fish Collection, Hobart, Australia (CSIRO) and Western Australian Museum, Perth (WAM). Other material used in this study are deposited in the ichthyological collections of the Australian Museum, Sydney (AMS), National Museum, Victoria (NMV), Silliman University Marine Laboratory, Philippines (SUML), University of Florida, USA (UF) and Hokkaido University, Japan (HUMZ); their registration numbers are prefixed with these acronyms.

***Squalus nasutus* sp. nov.**

Figs 1a, 2a, 3, 4, 5a; Table 1

Squalus sp. E: Last and Stevens, 1994, *Sharks and Rays of Australia*, pp 49, 96, fig. 8.25, 8.36, pl. 5; Compagno, Dando and Fowler, 2005, *Sharks of the World*, p 80–1, figs, pl. 2; White *et al.*, 2006, *Economically Important Sharks and Rays of Indonesia*, pp 74–75.

Holotype. CSIRO H 2590–12, female 508 mm TL, west of Leander Point, Western Australia, 29°15' S, 113°56' E, 325 m, 6 Feb 1991.

Paratypes. 18 specimens. CSIRO H 2608–15, female 411 mm TL, Rottnest Canyon, Western Australia, 31° 57' S, 115°08' E, 850 m; CSIRO H 2598–07, female

465 mm TL, west of Green Head, Western Australia, 29°58' S, 114°27' E, 380 m; CSIRO H 2567–08, adult male 470 mm TL, west of Dorre Island, Western Australia, 25°09' S, 112°09' E, 312 m; CSIRO 1652–01, female 315 mm TL, CSIRO H 1652–02, female 459 mm TL, northwest of Port Hedland, Western Australia, 18°25' S, 117°48' E, 375 m; CSIRO H 1207–07, female 537 mm TL, CSIRO H 1207–08, female 496 mm TL, northwest of Port Hedland, Western Australia, 18°20' S, 117°50' E, 430 m; CSIRO CA 3290, female 549 mm TL, southwest of Rowley Shoals, Western Australia, 18°10' S, 118°20' E, 300 m; CSIRO CA 4055, female 527 mm TL, southwest of Rowley Shoals, Western Australia, 18°11' S, 118°04' E, 400 m; CSIRO H 2898–07, adolescent male 452 mm TL, north-northwest of Port Hedland, Western Australia, 18°07' S, 118°12' E, 361 m; WAM P 28086–006 (2 specimens), female 452 mm TL and immature male 380 mm TL, Rowley Shoals, Western Australia, 17°49' S, 118°41' E, 310 m; CSIRO CA 4110, adult male 497 mm TL, east of Rowley Shoals, Western Australia, 17°18' S, 120°09' E, 305 m; CSIRO H 1693–01, immature male 361 mm TL, CSIRO H 1693–02, female 306 mm TL, Rowley Shoals, Western Australia, 17°02' S, 120°05' E, 409 m; CSIRO H 1694–01, female 425 mm TL, Rowley Shoals, Western Australia, 16°57' S, 120°14' E, 413 m; CSIRO H 2032–01, adult male 461 mm TL, CSIRO H 2032–02, female 404 mm TL, northeast of Mermaid Reef, Rowley Shoals, Western Australia, 16°54' S, 120°25' E, 392 m.

Non-types. 17 specimens. CSIRO H 6413–01, female 590 mm TL, west of Shark Bay, Western Australia, 25°03' S, 112°08' E, 340 m; AMS I 43986–001, female 570 mm TL, NMV A 29560–001, female 531 mm TL, WAM P 32841–001 (2 specimens), adult male 499 mm TL and female 472 mm TL, northwest of Shark Bay, Western Australia, 23°40' S, 112°47' E, 337 m; CSIRO H 6125–04, adult male 468 mm TL, Kedonganan fish landing site, Bali, Indonesia, 08°45' S, 115°10' E; CSIRO H 5860–01, female 546 mm TL, CSIRO H 5860–02, female 546 mm TL, CSIRO H 5860–03, female 549 mm TL, CSIRO H 6484–01, female 575 mm TL, WAM P 32842–001, female 520 mm TL, Cilacap fish landing site, Central Java, Indonesia, 07°40' S, 109°00' E; CSIRO H 4132–02, male 473 mm TL, CSIRO H 4132–03, female 479 mm TL, CSIRO H 4132–04, female 541 mm TL, SUML F 1131, adult male 443 mm TL, SUML F 1151, female 486 mm TL, Bolinao evening market, Philippines.

DIAGNOSIS.— A small species of *Squalus* of the 'japonicus group' with the following combination of characters: body very elongate, depth 9.4–11.4% TL; snout narrow, long, preoral length 1.85–2.01 times horizontal preanial length, 11.1–11.7% TL; eye large, 4.3–5.1% TL; secondary lobe of anterior nasal flap well developed; dorsal fins small, raked; first dorsal-fin spine short, weak; second dorsal-fin spine short with strong base; pectoral fin of adult not falcate; pectoral-fin inner margin short, 6.6–7.1% TL; caudal bar almost upright, short, broad, extending from the caudal fork up the

posterior margin of the upper lobe for 0.4–0.5 of its length, upper caudal blotch somewhat linear, located near dorsal margin of fin lobe; flank denticles weakly tricuspidate; 36–39 monospondylous centra, 78–81 precaudal centra, 103–109 total centra; adult size at least 60 cm TL.

DESCRIPTION.— Body elongate fusiform to slightly compressed (bulging marginally at belly, maximum depth 1.03 (1.04–1.13) times width); head long 23.6 (23.0–24.1 in paratypes)% TL; caudal peduncle elongate, narrow, depressed slightly 24.9 (25.2–26.6)% TL. Head very depressed forward of spiracles, decreasingly less so towards pectoral origin, length 2.19 (2.00–2.10) in pre-vent length; height 0.77 (0.74–0.79) times width. Snout very long, narrowly triangular in lateral view, acutely angular in dorsal view, horizontal length 1.85 (1.61–1.84) times eye length, 0.98 (0.95–1.01) times interorbital space; horizontal preanial length 1.85 (1.88–2.01) times in preoral length; apex narrowly rounded. Eye broadly oval, relatively large, length 5.17 (4.77–5.44) in head, 1.53 (2.13–2.63) times height. Spiracle small, horseshoe-shaped; broad lobe-like fold on posterior margin; greatest diameter 3.23 (2.68–3.89) in eye length. Gill openings slightly oblique directed slightly posteroventrally, subequal in size, height of fifth slit 1.98 (1.7–2.2)% TL. Mouth almost transverse, upper jaw strongly arched, its width 1.92 (1.72–1.91) in preoral length; three series of functional teeth in upper jaw, two series in lower; upper labial furrows about twice length of lower furrows, prominent groove extending posterior-laterally from angle of jaws. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low, base of tooth broader than length of cusp. Nostrils small, almost transverse; anterior nasal flap bifurcate, upper lobe largest; posterior lobe narrow, skirt-like; internarial space 2.56 (2.33–2.82) in preoral length, 2.61 (2.20–3.14) times nostril length. Dermal denticles on back very small, weakly tricuspidate with pronounced median ridge; lateral cusps varying from barely detectable to short, weakly angular; on dorsal and caudal fins leaf-shaped, strongly imbricated, more regular on snout tip; interorbit primarily with unicuspidate denticles, sharply pointed posteriorly, with three broad lobe-like expansions on lateral and anterior margin, median ridge pronounced; on belly very strongly imbricated, pungent distally, unicuspidate to weakly tricuspidate, ridges appear less pronounced; dorsal fins entirely covered with closely spaced denticles; denticles present over gill membranes; denticles around spiracle unicuspidate, extending into cavity anteriorly, fold covered with denticles. First dorsal fin low, raked slightly, weakly rounded apically; anterior margin moderately convex; posterior margin moderately concave, upper portion directed slightly anterodorsally; free rear tip relatively thick, short; inner margin almost straight; insertion of base well forward of pelvic-fin origin; fin-spine origin above pectoral-fin rear tip; spine base moderately broad, exposed anteriorly well below junction of spine and fin; spine tapering rapidly distally, smaller than second



Figure 1. Lateral view of: A. *Squalus nasutus* sp. nov. holotype (CSIRO H 2590–12, female 508 mm TL); B. *Squalus japonicus* (CSIRO H 6294–31, female 571 mm TL).

dorsal-fin spine; pre-first dorsal length 3.06 (3.03–3.22) times in TL; first dorsal-fin length 2.11 (1.89–2.11) times its height, 1.25 (1.18–1.23) times second dorsal-fin length; first dorsal-fin height 1.77 (1.47–1.74) times second dorsal-fin height; exposed first dorsal spine length 0.48 (0.36–0.54) times height of fin. Second dorsal fin small, strongly raked; posterior margin deeply concave, upper portion directed slightly dorsoposteriorly; free rear tip long, inner margin length 1.43 (1.01–1.34) times fin height; second dorsal-fin length 2.98 (2.53–3.00) times its height; spine length 1.07 (0.97–1.17) in height of fin; fin-spine origin well behind insertion of pelvic fin, exposed at level of junction with spine and fin; interdorsal space 1.02 (0.92–0.99) in length from snout tip to pectoral-fin origin, 1.31 (1.21–1.36) in pre-first dorsal length; second spine with very broad base, slender distally, tapering very rapidly just above point of exposure. Pectoral fin small, anterior margin weakly convex; inner margin moderately convex, length 7.1 (6.6–7.7)% TL; apex narrowly rounded, lobe-like but not falcate; posterior margin moderately convex, free rear tip bluntly angular; base very short, 2.74 (2.85–3.11) in length of anterior margin. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip narrow, acute. Caudal peduncle long, tapering slightly to caudal fin, pelvic-caudal space 0.88 (0.70–0.82) in pectoral–pelvic space, 1.03 (0.87–0.96) in prepectoral length; dorsal–caudal space 2.26 (2.06–2.47) in interdorsal length; lateral folds extending from below insertion of second dorsal fin to about a pupil diameter posterior of caudal pits. Caudal fin relatively short, dorsal caudal margin 1.28 (1.14–1.26) in head length; length of lower caudal lobe 1.60 (1.59–1.79)

in upper lobe length. Vertebral centra 107 (103–109 in 18 paratypes), monospondylous 39 (36–39), precaudal 81 (78–83) and caudal 26 (23–28). Teeth in upper jaw (of paratype, CSIRO H 2598–07) 13+13=26, lower jaw 11+11=22.

COLOUR.— When fresh (based on holotype): dorsal surface greyish brown, much paler ventrally; light and dark tonal areas strongly demarcated on head, their border extending from snout, beneath eye, through top of gill slits to pectoral-fin origin; tonal areas poorly demarcated on trunk. Dorsal fins uniformly greyish brown, anterior bases and free rear tip slightly paler; spines dusky, anterior margins slightly darker; skin at base of exposed spine black. Caudal fin mostly dusky; black caudal bar subvertical, prominent, broad, extending from fork to about halfway along posterior margin of upper lobe; upper halves of dorsal and ventral lobes off-white; black blotches at base of upper and lower lobes. Pectoral fin greyish dorsally, with well-defined white posterior margin; pelvic fins similar, ventral surface pale grey with a white base and posterior margin. Juvenile paratype (CSIRO H 1652–01) similar to holotype, but with much more pronounced fin markings; dorsal fins with black outer halves. Caudal bar relatively short, broad, black, slightly taller than eye length; upper caudal-fin lobe with well-defined black blotch on anterior margin and weak upper median dusky blotch; ventral lobe paler than apex of upper lobe. In preservative: holotype similar, but light and dark tonal areas on body less distinct; dark markings on fins faint but evident; broad, pale posterior borders on pectoral and pelvic fins well-defined.



Figure 2. Ventral view of the head of A. *Squalus nasutus* sp. nov. holotype (CSIRO H 2590-12, female 508 mm TL); B. *Squalus japonicus* (HUMZ 80224, female 641 mm TL).

SIZE.— Australian females and males attain at least 590 (non-type) and 499 mm TL (non-type), respectively; smallest adult male 461 mm TL, still adolescent at 452 mm TL. Ten adult males from Indonesia and the Philippines ranged from 464–539 mm TL; 25 females from 470–634 mm TL.

DISTRIBUTION.— Upper continental slope off Western Australia, north of the Rottnest Canyon (ca 32°S, 115°E) to the Rowley Shoals (ca 17°S, 120°E). Occurs in depths of 300–850 m but trawled mainly in depths of 300–400 m. Appears to be distributed through the Indonesian Archipelago to the Philippines but depth

Table 1. Proportional dimensions as percentages of total length for the holotype (CSIRO H 2590–12) and 5 paratypes of *Squalus nasutus* sp. nov., with comparisons with Indonesian and Philippines material.

	Western Australia		Indonesia		Philippines		
	Holotype	Paratypes		n = 4		n = 3	
		Min.	Max.	Min.	Max.	Min.	Max.
TL – Total length	508	452	470	468	576	473	541
PCL – Precaudal length	81.7	79.4	80.9	80.6	81.0	80.4	81.0
PD2 – Pre-second dorsal length	65.4	63.1	64.4	64.5	66.3	63.4	64.1
PD1 – Pre-first dorsal length	32.7	31.0	33.0	31.7	34.4	31.8	33.5
SVL – Pre-vent length	51.8	46.9	50.5	48.4	49.3	47.8	49.7
PP2 – Prepelvic length	48.8	45.3	47.7	45.5	47.9	45.5	48.4
PP1 – Prepectoral length	25.6	23.3	24.2	23.7	24.7	24.6	25.2
HDL – Head length	23.6	23.0	24.1	23.2	24.1	23.5	24.5
PG1 – Prebranchial length	21.0	19.4	20.8	19.2	20.5	19.6	20.7
PSP – Prespiracular length	14.9	13.4	14.8	13.3	14.7	14.0	14.9
POB – Preorbital length	9.9	8.5	9.3	8.3	9.1	9.3	10.1
PRN – Prenarial length	7.3	6.4	6.7	5.9	6.6	6.8	7.5
POR – Preoral length	12.7	11.4	12.3	11.1	12.0	11.7	12.4
INLF – Inner nostril-labial furrow space	4.9	4.8	5.2	4.7	5.1	4.6	5.1
MOW – Mouth width	6.6	6.3	7.2	6.0	6.6	5.8	6.2
ULA – Labial furrow length	2.3	1.8	2.2	1.9	2.3	1.8	2.2
INW – Internarial space	5.0	4.2	5.1	4.3	4.5	4.3	4.7
INO – Interorbital space	8.6	7.8	8.6	7.3	7.5	7.3	7.9
EYL – Eye length	4.6	4.3	5.1	4.5	5.0	4.5	4.9
EYH – Eye height	3.0	1.9	2.1	1.8	2.2	1.9	2.1
SPL – Spiracle length	1.4	1.3	1.6	1.3	1.7	1.5	1.7
GS1 – First gill-slit height	1.7	1.3	1.6	1.4	1.6	1.1	1.6
GS5 – Fifth gill-slit height	2.0	1.7	2.2	2.0	2.2	1.7	1.9
IDS – Interdorsal space	25.0	24.4	25.6	25.8	28.0	25.6	26.1
DCS – Dorsal-caudal space	11.1	10.4	12.0	9.8	10.8	10.4	11.5
PPS – Pectoral-pelvic space	21.9	18.7	20.8	18.4	22.5	17.8	22.0
PCA – Pelvic-caudal space	24.9	25.2	26.6	25.2	27.7	25.4	26.2
D1L – First dorsal length	12.5	12.0	12.8	10.6	11.6	11.1	11.8
D1A – First dorsal anterior margin	10.6	10.4	10.6	8.9	10.0	9.3	10.1
D1B – First dorsal base length	7.1	6.8	7.7	5.6	6.9	6.4	6.9
D1H – First dorsal height	5.9	5.7	6.8	5.9	6.2	6.2	6.5
D1I – First dorsal inner margin	5.6	4.9	5.5	4.7	5.3	4.5	5.3
D1P – First dorsal posterior margin	7.2	6.6	8.4	6.8	7.4	7.5	7.7
D1ES – First dorsal spine length	2.8	2.2	3.4	3.8	3.8	3.2	3.4
D1BS – First dorsal spine base width	0.9	0.7	1.0	0.6	0.9	0.7	0.8
D2L – Second dorsal length	10.0	9.9	10.9	9.3	9.9	9.5	10.3
D2A – Second dorsal anterior margin	8.3	7.5	8.9	7.1	8.3	8.0	8.9
D2B – Second dorsal base length	5.4	5.2	6.6	4.9	6.0	5.9	6.4
D2H – Second dorsal height	3.3	3.3	4.2	3.3	3.8	3.7	4.2
D2I – Second dorsal inner margin	4.8	3.9	5.0	3.8	4.5	3.4	4.4
D2P – Second dorsal posterior margin	4.6	4.4	5.3	3.9	4.8	4.3	4.9
D2ES – Second dorsal spine length	3.6	3.5	4.7	3.2	3.9	4.0	4.5
D2BS – Second dorsal spine base width	1.1	0.9	1.1	0.7	0.9	0.6	0.9

Table 1. cont'd.

	Western Australia		Indonesia		Philippines		
	Holotype	Paratypes		n = 4		n = 3	
		Min.	Max.	Min.	Max.	Min.	Max.
P1A – Pectoral anterior margin	12.9	12.0	13.3	11.4	13.9	12.0	13.0
P1I – Pectoral inner margin	7.1	6.6	7.7	5.9	6.4	5.9	6.8
P1B – Pectoral base length	4.7	4.0	4.3	3.9	4.9	4.5	4.8
P1P – Pectoral posterior margin	8.2	7.0	8.5	8.4	10.4	7.7	8.7
P2L – Pelvic length	10.2	9.0	12.1	9.8	12.0	8.3	11.2
P2H – Pelvic height	4.3	4.0	4.9	3.9	6.0	4.2	4.4
P2I – Pelvic inner margin	4.7	3.8	6.6	4.6	6.6	3.8	7.3
CDM – Dorsal caudal margin	18.5	19.0	20.1	18.8	19.2	19.4	19.7
CPV – Preventral caudal margin	11.6	10.6	12.3	10.6	11.2	10.7	10.9
CPU – Upper postventral caudal margin	13.2	13.2	14.3	13.5	13.8	13.6	14.4
CPL – Lower postventral caudal margin	4.7	3.8	4.5	4.2	5.1	4.1	5.1
CFW – Caudal fork width	6.7	6.3	6.7	6.2	6.5	6.3	6.4
CFL – Caudal fork length	9.3	8.5	9.7	8.0	8.8	7.9	9.2
HANW – Head width at nostrils	8.3	8.1	8.5	7.6	8.0	7.8	8.0
HAMW – Head width at mouth	11.0	10.7	11.5	9.8	10.9	9.8	10.3
HDW – Head width	12.6	11.4	11.9	11.5	12.4	11.5	11.9
TRW – Trunk width	11.0	8.6	9.6	8.9	10.6	8.3	9.2
ABW – Abdomen width	9.7	7.9	9.6	8.3	9.9	6.9	8.7
TAW – Tail width	6.9	5.9	6.6	5.0	6.9	6.0	6.5
CPW – Caudal peduncle width	3.0	2.9	3.5	2.8	3.0	2.9	3.1
HDH – Head height	9.6	8.7	9.1	8.2	9.2	8.7	9.7
TRH – Trunk height	11.4	9.4	10.2	9.2	10.5	10.1	11.2
ABH – Abdomen height	12.2	8.6	10.8	7.8	10.9	10.4	10.6
TAH – Tail height	7.0	6.0	7.7	5.4	6.7	6.1	7.5
CPH – Caudal peduncle height	2.2	2.2	2.3	2.0	2.1	2.3	2.6
CLO – Clasper outer length	–	2.5	4.5	4.4	4.4	–	4.6
CLI – Clasper inner length	–	9.3	12.2	11.4	11.4	–	11.4
CLB – Clasper base width	–	1.3	1.6	1.5	1.5	–	1.5

distribution unknown as examined material was collected from fish markets.

ETYMOLOGY.— Derived from the Latin *nasutus* meaning ‘large-nosed’ in allusion to its elongated prenarial snout.

VERNACULAR.— Western Longnose Spurdog.

REMARKS.— The type series of *Squalus nasutus* is based on Australian material because minor differences in morphometrics (Table 1) and meristics exist between populations across the Indo–West Pacific. Apart from having slightly higher total vertebral counts in Philippine specimens (109–111, n=3 vs. 103–109 in Australian forms, n=10), the Indo–Philippine specimens appear to have a slightly longer interdorsal space (25.6–28.0 vs.

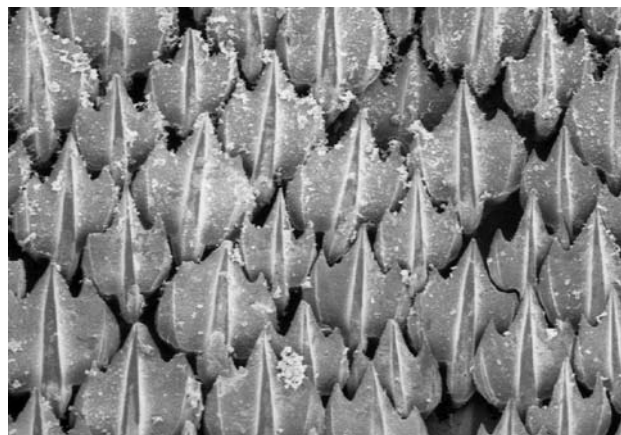


Figure 3. Cusps of the flank denticles of *Squalus nasutus* sp. nov. paratype (CSIRO H 1207–08, female 496 mm TL). Field of view width 1.2 mm.

24.4–25.6% TL), slightly narrower interorbit (7.3–7.9 vs. 7.8–8.6% TL) and head (width at nostrils 7.6–8.0 vs. 8.1–8.5% TL), and a marginally shorter pectoral-fin inner margin (5.9–6.8 vs. 6.6–7.7% TL) and first dorsal fin (length 10.6–11.8 vs. 11.1–12.8% TL). More material is needed to understand the extent of interregional variation between populations.

The new species belongs to a subgroup of *Squalus* that includes 3 other, long-snouted species: *S. japonicus* (western North Pacific), *S. melanurus* (New Caledonia) and *S. rancureli* (New Caledonia). *Squalus nasutus* is much smaller than these species, attaining only 63 cm TL with males maturing at about 45 cm TL, whereas the other species are reported to reach at least 91 cm, 75 cm, and 77 cm TL, respectively, and have females that mature larger than 65 cm TL (Compagno, 1984). Of these species, *Squalus nasutus* appears closest to *S. japonicus* (Figs 1b, 2b, 5b) from the western North Pacific with which it appears to have been confused in the Philippines (Compagno *et al.*, 2005b). These species differ significantly from the two New Caledonian endemics: from *S. melanurus* in lacking prominent dark markings on the dorsal and caudal fins; and from *S. rancureli* in having a more acutely pointed snout, a longer ventral caudal lobe and possessing a well-developed secondary lobe on the anterior nasal flap.

Squalus nasutus differs from *S. japonicus* in both morphometrics and meristics. Chen *et al.* (1979) gives

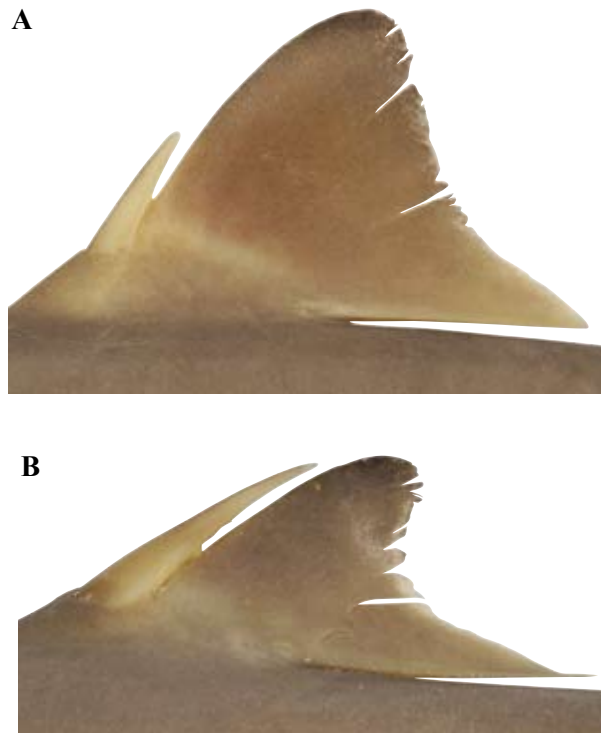


Figure 4. Lateral view of the dorsal fins of: *Squalus nasutus* sp. nov. paratype (CSIRO H 2598-07, female 465 mm TL) – A. first dorsal fin, B. second dorsal fin.

relatively higher vertebral counts for *S. japonicus* (40–45 vs. 36–39 monospondylous centra for *S. nasutus* from Australia; 82–91 vs. 78–81 precaudal centra; and 110–119 vs. 103–109 total centra). There also appears to be a difference in the ratio of diplospondylous trunk to monospondylous centra (0.8 based on one of Chen *et al.*'s specimens vs. 1.1–1.2 in the 10 types of *S. nasutus*). Teeth counts appear similar, in one paratype with 26 in the upper jaw (vs. 25–27, mainly 27 in 33 specimens) and 22 in the lower jaw (vs. 23–24, mainly 23 in 33 specimens). The most obvious morphometric differences exist around the head, pectoral fin and trunk. The pectoral fin of adult *S. japonicus* is much larger, much more falcate with a more concave posterior margin (Fig 2b), and a longer inner margin (8.6–11.1 vs. 6.6–7.1% TL in *S. nasutus*). The preoral length (10.2–11.4 vs. 11.1–11.7% TL) and eye (length 3.8–4.2 vs. 4.3–5.1% TL) of *S. japonicus* are relatively smaller, and the trunk appears to be more depressed (trunk height 8.2–9.5 vs. 9.4–11.4% TL; trunk width 12.0–12.6 vs. 8.6–11.0% TL in *S. nasutus*). Key

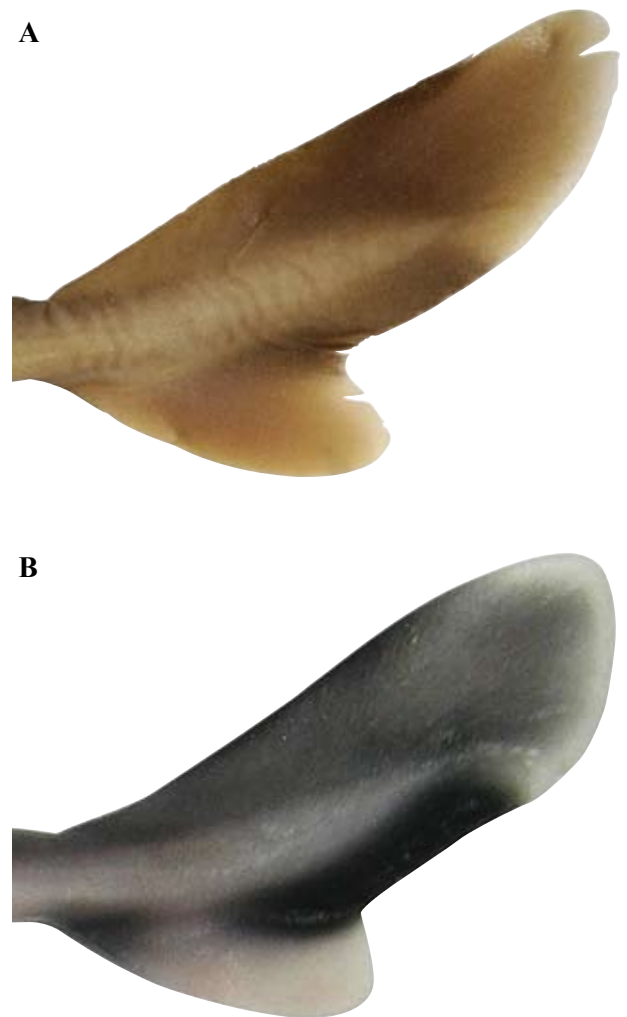


Figure 5. Juvenile coloration of the caudal fin of: A. *Squalus nasutus* sp. nov. (CSIRO H 1693-02, female 306 mm TL); B. *Squalus japonicus* (UF 148932, male embryo 247 mm TL).

measurements taken by Ishikawa (1908) of the male holotype of *S. japonicus* (700 mm TL) conformed well to the ranges provided by Chen *et al.* (1979) for this species. He recorded a preoral length of 75 mm (10.7% TL) and a 26 mm eye (3.7% TL), both of which conform to the ranges listed above.

Other material.

Squalus japonicus: HUMZ 39455, female 535 mm TL, HUMZ 48406, female 339 mm TL, HUMZ 80501, immature male 291 mm TL, HUMZ 97257, adult male 602 mm TL, Mimase fish market, Kochi, Japan; HUMZ 80224, female 641 mm TL, Okinawa Trough, Japan, 310 m; CSIRO H 6294–26, male 456 mm TL, CSIRO H 6294–27, female 380 mm TL, CSIRO H 6294–31, female 571 mm TL, UF 148932, male embryo 247 mm TL, Tashi fish market, north-east Taiwan.

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Part 9 — Redescription of the Northern Spiny Dogfish *Squalus griffini* Phillipps, 1931 from New Zealand

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ABSTRACT.— The Northern Spiny Dogfish, *Squalus griffini* Phillipps, from central and northern New Zealand is resurrected based upon detailed re-examination of the holotype and new material collected from throughout its range. Comparisons are made with *S. griffini* and other large Indo-Pacific species of *Squalus*, including *S. mitsukurii* from the western North Pacific, and newly recognised members of the ‘mitsukurii group’ from Australia. *Squalus griffini* differs from members of the ‘mitsukurii group’ in having a white posterior caudal-fin margin without a dark caudal bar. It also appears to be atypically variable in body and fin shapes, adult coloration and denticle morphology.

Key words. Squaloidea – Squalidae – *Squalus griffini* – resurrected species – New Zealand – Australasia

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INTRODUCTION

Two species of *Squalus* are recognised from New Zealand waters. *Squalus acanthias* (Linnaeus, 1758), known as the Spotted Spiny Dogfish (New Zealand) or Whitespotted Dogfish (Australia), is widely distributed around North and South Islands of New Zealand, as well as over the Chatham Rise and Campbell Plateau, where it is most abundant south of 40° S (Anderson *et al.*, 1998). The Northern Spiny Dogfish, presently referred to as *S. mitsukurii* Jordan and Snyder in Jordan and Fowler, 1903 (Paulin *et al.*, 1989), is restricted to waters north of the Subtropical Front. It occurs along the continental margin off the west coasts of the North and South Islands from about 34° S to 44° S, with some isolated records from research trawls on the central Challenger Plateau. Off the east coast, it has been recorded southward to almost 45° S but is rarely caught south of 38° S, except around the Chatham Islands between 175° and 179° W (Anderson *et al.*, 1998).

The Northern Spiny Dogfish was originally recorded erroneously from the Northland as *S. megalops* by Regan (1914) but was later described as a new species, *S. griffini*, by Phillipps (1931). Phillipps’ description, based upon two specimens from the Hauraki Gulf, was meager and unaccompanied by an illustration. He noted that a description of *S. griffini* and two new Australian species was being published elsewhere and simply described it as showing no sign of spots and having a relatively massive compressed spine in front of the second dorsal fin. He distinguished *S. griffini* from *S. megalops* primarily by a heavier, more compressed and unpolished appearance of

the second dorsal spine, a somewhat shorter head, and a more posterior location of the pelvic fin. Whitley (1940) provided a slightly more detailed description of *S. griffini*, reporting three proportional measurements and repeating Phillipps’ (1931) description of the second dorsal spine and morphological comparison with *S. megalops*. He also figured the species for the first time, reproducing a copy of a painting of *S. griffini* provided by Phillipps. Phillipps’ (1946) account of the species figured the original painting of the type specimen by E. H. Atkinson but added little to the description, noting only that the centre of the pelvic-fin base is midway between the posterior orbit and the caudal-fin tip (rather than midway between the snout and caudal tip as in *S. megalops*).

Garrick (1960) reviewed the Australasian species of *Squalus* and incorrectly synonymised *S. griffini* and *S. fernandinus* Molina, 1782 (*sensu* Bigelow and Schroeder, 1948, 1957) with *S. blainvillii* (incorrect spelling of *S. blainville* (Risso, 1827), Eschmeyer, 1998). Garrick recognised *S. acanthias* and *S. blainville* from New Zealand, and *S. acanthias*, *S. blainville* and *S. megalops* from Australia. *Squalus blainville* was thought to be widespread in the Atlantic, Indian and Pacific Oceans (Bigelow and Schroeder, 1948, 1957; Garrick 1960). However, in a review of Japanese *Squalus*, Chen *et al.* (1979) defined *S. blainville* as a species with high dorsal fins and long dorsal-fin spines based upon examination of Japanese material and descriptions of *S. blainville* purportedly from its type locality, the Mediterranean. They observed that *Squalus*, referred to *S. fernandinus* and *S. blainville* by Bigelow and Schroeder (1948) and Garrick (1960), had short dorsal-fin spines

and were more similar to *S. mitsukurii* from Japan, and suggested that nominal *S. blainville* from New Zealand could be identical to *S. mitsukurii*. Compagno (1984) also noted that dogfishes resembling *S. mitsukurii* occurred off Australia and New Zealand, and did not recognise *S. blainville* from the Southern Hemisphere. Although none of the above authors made direct comparisons between *S. mitsukurii* and New Zealand material, the Northern Spiny Dogfish has subsequently been widely synonymised with *S. mitsukurii* (Paulin *et al.* 1989; Yano in Amaoka *et al.*, 1990; Roberts, 1991; Paul and Heath, 1997; Cox and Francis, 1997; Anderson *et al.*, 1998; Compagno *et al.*, 2005). Last and Stevens (1994) provisionally mapped New Zealand populations as *S. mitsukurii* but suggested that regional forms may represent a species complex.

We examined the holotype of *S. griffini* and additional material held in the New Zealand and Australian National Fish Collections, and concluded that these are specifically distinct from Australian material once incorrectly referred to as *S. mitsukurii* (see Part 6 of this issue, Last *et al.*, 2007a), as well as material of *S. mitsukurii* from the western North Pacific. In this paper, *S. griffini* is redescribed based upon a reexamination of the holotype and additional material collected from the Louisville Ridge, Kermadec Ridge, Wanganella Bank, Chatham Rise, and North and South Islands of New Zealand.

METHODS

Morphometric characters were selected to enable comparisons to be made with other *Squalus* taxa treated in the series of papers in this issue (Part 1 of this issue, Last *et al.*, 2007b). The holotype and 16 specimens from the North and South Islands of New Zealand, the Wanganella Bank, Chatham Rise, and southern Kermadec and Louisville Ridges were measured in full (Table 1). Vertebral counts were taken from X-rays of 10 specimens (including the holotype). Tooth row counts were taken directly from specimens. Morphometric and meristic values for the holotype are given, followed by ranges for other specimens in parentheses. The holotype and a large collection of specimens are held at the National Fish Collection, Museum of New Zealand, Te Papa Tongarewa, Wellington (NMNZ); 3 additional specimens used in this study are held at the Australian National Fish Collection, Hobart (CSIRO). Specimen registration numbers are prefixed by these acronyms.

Squalus griffini Phillipps, 1931

Figs 1–5; Table 1

Squalus megalops: (not Macleay) Regan, 1914: 14; Phillipps, 1927: 9.

Squalus griffini Phillipps, 1931: 360; Phillipps, 1946: 16, fig. 5;

Moreland, 1957; Parrott, 1958: 114, incorrectly illustrated with a figure of *S. megalops* from McCulloch (1922).

Flakeus griffini: Whitley, 1940: 136, fig. 149; Powell, 1951: 61, fig. 295.

Squalus blainvillii: (not Risso) Garrick, 1960: 532–537, figs 1D–F, 3A–F, 6A–F.

Squalus blainville: (not Risso) Garrick, 1961; Doogue *et al.*, 1966; York, 1970; Paul, 1985: 21, fig. 7; Ayling and Cox, 1982: 65, fig.

Squalus mitsukurii: (not Jordan and Snyder) Compagno, 1984: 121–122, figs; Paulin *et al.*, 1989: 13, fig. 7.3; Roberts, 1991: 8, fig. 4; Last and Stevens, 1994: 101–102, 8.39, Plate 5; Paul and Heath, 1997: 2, fig.; Cox and Francis, 1997: 45, fig.

Holotype. NMNZ P 662, adult female 972 mm TL, Hauraki Gulf, North Island, New Zealand, 1931.

Other material. 20 specimens. NMNZ P 2646, female 1025 mm TL, off Foxton, New Zealand, 40°28' S, 175°14' E, 55 m; NMNZ P 2649, female 955 mm TL, off Kapiti Island, New Zealand, 40°51' S, 174°52' E, 37 m; NMNZ P 2759, immature female 539 mm TL, off Lottin Point, 37°32' S, 178°10' E, New Zealand, 137 m; NMNZ P 5176, female 929 mm TL, near Cuvier Island, New Zealand, 36°26' S, 175°46' E, 77 m; NMNZ P 20965, female 482 mm TL, east of the Chatham Islands, New Zealand, 43°20' S, 176°36' W, 136 m; NMNZ P 22549, adult male 794 mm TL, Louisville Ridge, New Zealand, 32°00' S, 172°00' W; NMNZ P 35270, adult male 867 mm TL, Chatham Rise, New Zealand, 43°43' S, 175°22' W, 543 m; NMNZ P 35973, female 823 mm TL, southern Kermadec Ridge, New Zealand, 32°43' S, 179°20' W, 333 m; NMNZ P 39893, female 1018 mm TL, NMNZ P 39899, near-term male embryo 227 mm TL, off Volkner Rocks, White Island, Bay of Plenty, New Zealand, 37°28' S, 177°08' E, 265 m; NMNZ P 40888, adult female 1070 mm TL, off Napier Island, Kermadec Islands, New Zealand, 29°14' S, 177°53' E, 350 m; NMNZ P 41774, adult male 693 mm TL and 4 females 737–835 mm TL, Southern Challenger Plateau, New Zealand, 41°28' S, 171°06' E, 175m; NMNZ P 41775, immature female 418 mm TL, Wairarapa, New Zealand, 40°15' S, 177°01' E, 616 m; CSIRO H 6057–12, female 836 mm TL, Tasman Sea, West Norfolk Ridge, 33° 45' S, 167°17' E, 259 m; CSIRO H 5002–06, adult male 819 mm TL, CSIRO H 5002–07, female 974 mm TL, Wanganella Bank, Norfolk Ridge, 31°49' S, 167°47' E, 351 m; CSIRO H 6006–11, immature male 473 mm TL, Norfolk Ridge, south of Norfolk Island, 29°42' S, 168° 02' E, 344 m; CSIRO H 6066–08, immature male 262 mm TL, Wanganella Bank, Norfolk Ridge, 32°33' S, 167°38' E, 362 m; CSIRO H 6069–02, adult male 789 mm TL, Wanganella Bank, Norfolk Ridge 32°35' S, 167°41' E, 497 m; NMV A 25109–007, immature male 531 mm TL, mid-Norfolk Ridge 29°42' S, 168°02' E, 344 m.

DIAGNOSIS.— A large species of *Squalus* with the following combination of characters: body slender, depth 8.6–13.9% TL; snout long, preoral length greater than mouth width, 2.4–2.6 times horizontal preanial length, 8.8–11.4% TL; eye large, 3.6–5.3% TL; secondary

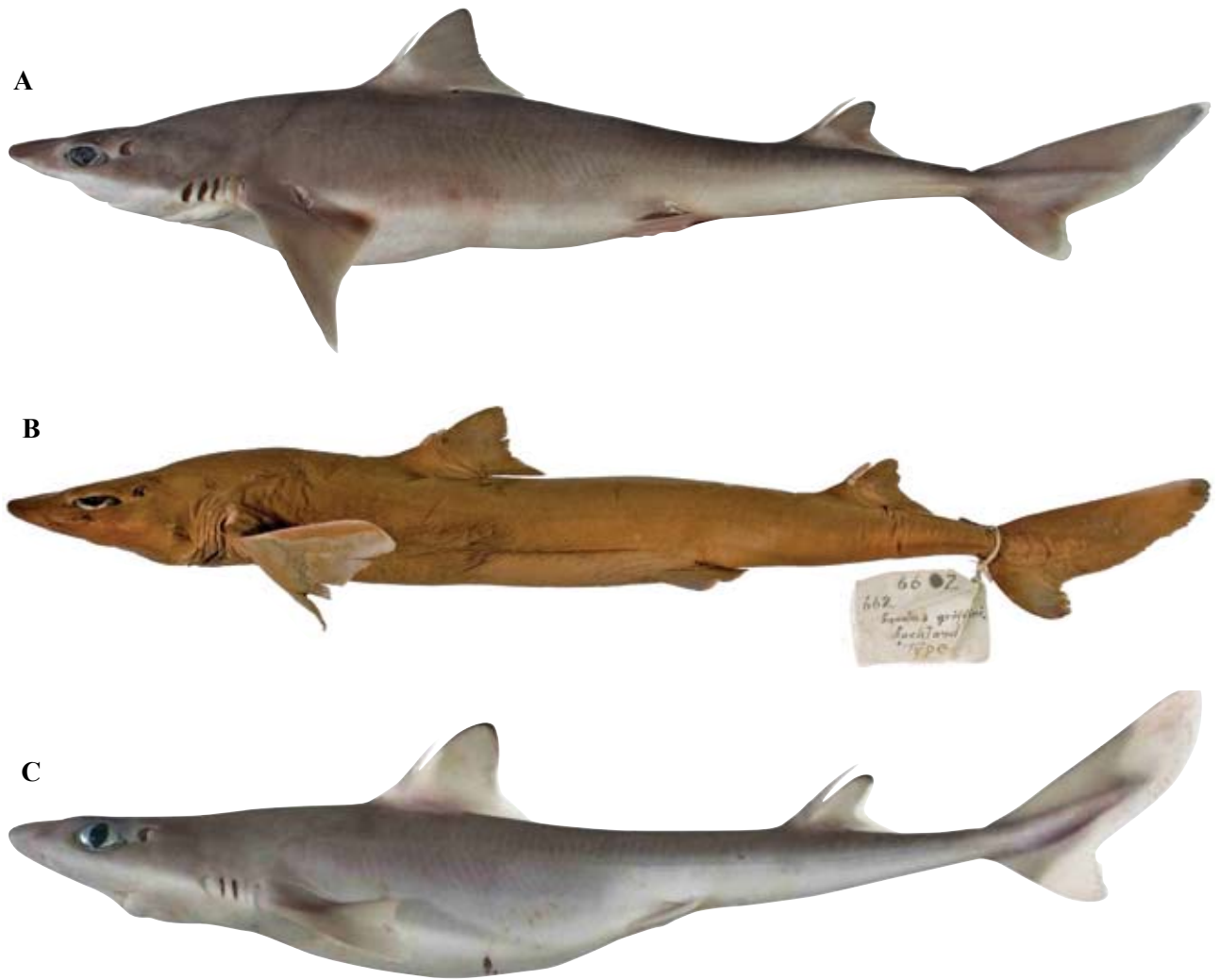


Figure 1. Lateral view of: A. *Squalus griffini* (NMNZ P 39893, female 1018 mm TL); B. *Squalus griffini* holotype (NMNZ P 662, female 972 mm TL); C. *Squalus griffini* (CSIRO H 6006–11, immature male 473 mm TL).

lobe of anterior nasal flap well developed; first dorsal fin moderate-sized, height 6.3–8.7% TL, triangular, posterior margin almost straight, spine short and heavy; second dorsal fin raked, posterior margin deeply concave, height up to 4.2–5.8% TL, spine long with strong base; pectoral fin of adult not falcate; pectoral-fin inner margin short, 5.4–7.7% TL; caudal fin with broad pale posterior margin and lower lobe in all but largest adults, dark caudal bar absent, well-defined stripes above and below soft portion of fin in juveniles; flank denticles tricuspid; 45–47 monospondylous centra, 86–91 precaudal centra, 113–121 total centra; adult maximum size at least 110 cm TL.

DESCRIPTION.— Body elongate fusiform to slightly compressed; head long 21.0 (20.2–24.3)% TL; caudal peduncle elongate, narrow, depressed slightly, 23.8 (21.7–26.0)% TL. Head depressed forward of spiracles, length 2.48 (2.07–2.51) in pre-vent length; height 0.76 (0.60–0.82) width. Snout long, triangular in lateral view,

narrowly rounded in dorsal view, horizontal length 1.87 (1.16–1.92) times eye length, 0.94 (0.67–0.88) times interorbital space; horizontal prenarial length 2.42 (2.37–2.65) in preoral length; apex narrowly rounded. Eye broadly oval, relatively large, length 5.88 (4.29–5.91) in head, 2.60 (1.83–3.46) times height. Spiracle small, broadly crescentic; broad lobe-like fold on posterior margin; greatest diameter 2.43 (2.25–3.61) in eye length. Gill openings small, oblique, directed slightly posteroventrally; subequal in size, height of first gill slit 2.06 (1.73–2.50)% TL; fifth gill slit wrapping around pectoral fin origin. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate, weakly bifurcate in some other material; posterior lobe narrow, skirt-like; internarial space 2.09 (1.97–2.31) times in preoral length, 3.03 (2.48–3.22) times nostril length. Mouth arched, width 1.62 (1.43–1.88) in preoral length; upper labial furrows 2.2 (1.8–2.7)% TL, continued as prominent grooves extending posterior-laterally from angle of jaws; lower furrows about half the length of the uppers, generally not

visible in ventral view. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like; cusps directed strongly laterally, low, base of tooth broader than length of cusp. Dermal denticles on flank below first dorsal fin of holotype broad, strongly imbricated, tricuspid, with weak lateral cusps and well-developed, grooved lateral ridges; variable in other material, denticles often weakly imbricate with long cusps with weak lateral ridges, even in adult males and large females of similar size to the holotype; present on gill membranes. First dorsal fin of moderate size, broadly rounded apically, posterior margin almost upright, strongly convex near fin base; free rear tip base relatively thick, short; inner margin almost straight; insertion of fin base well forward

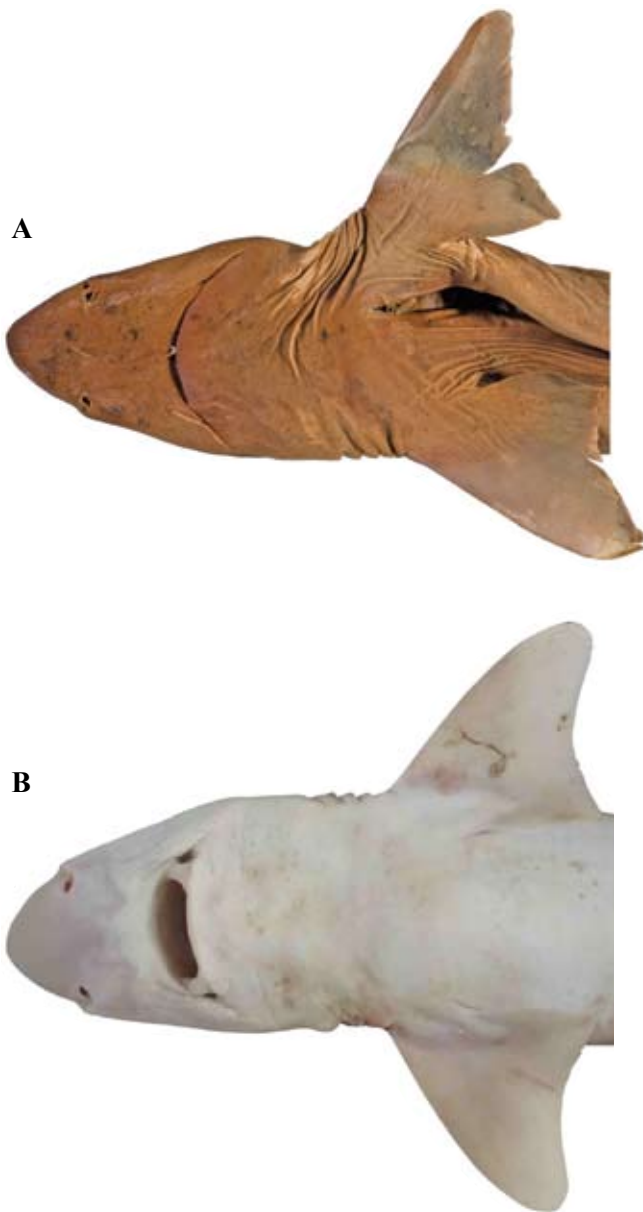


Figure 2. Ventral view of the head of: A. *Squalus griffini* holotype (NMNZ P 662, female 972 mm TL); B. *Squalus griffini* (CSIRO H 6006-11, immature male 473 mm TL).

of pelvic-fin origin; spine origin over pectoral-fin inner margin; spine base broad, exposed anteriorly well below junction of spine and fin; shorter than second dorsal-fin spine; pre-first dorsal fin length 3.43 (3.17–3.70) in TL; first dorsal-fin length 2.16 (1.78–2.36) times its height, 1.26 (1.10–1.38) times second dorsal-fin length; first dorsal-fin height 1.51 (1.42–1.71) times second dorsal-fin height; first dorsal spine broken in holotype, often damaged but usually about half of fin height in other material. Second dorsal fin smaller than first, strongly to weakly raked; subtriangular in holotype and a few large specimens (i.e. NMNZ P 39908) with broadly rounded apex, weakly concave posterior margin and long free rear tip; most other specimens retain fin form similar to juveniles, being relatively taller, more strongly raked with a deeply concave posterior margin, and shorter free rear tip; inner margin length 0.89 (0.84–1.20) times fin height; second dorsal-fin length 2.57 (2.16–2.88) times its height; second dorsal spine broken in holotype, spine length 0.7–1.2 in fin height in other material; fin-spine origin well behind free rear tip of pelvic fin, exposed below level of junction with spine and fin; second spine with broad base, slender distally, tapering above point of

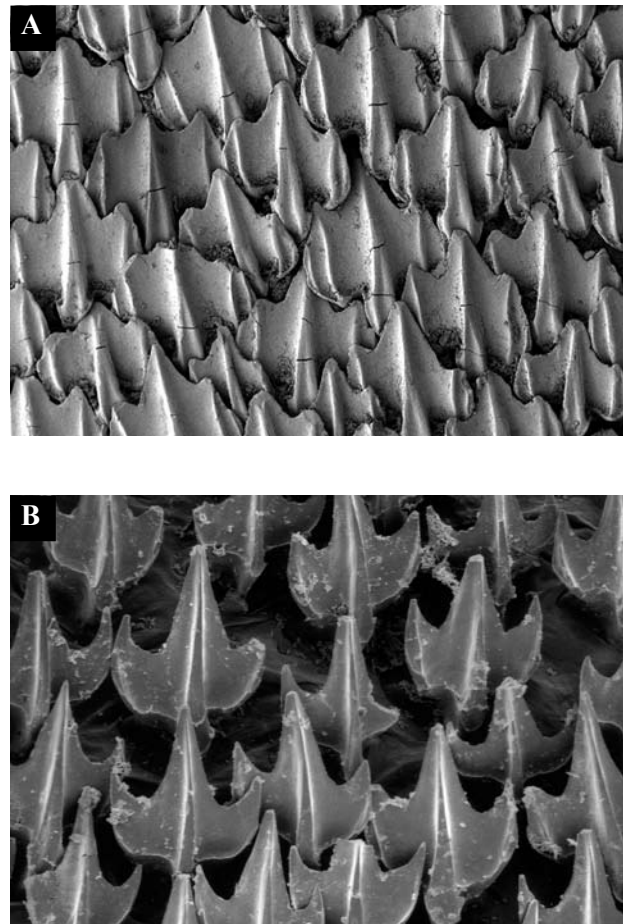


Figure 3. Cusps of the flank denticles of: A. *Squalus griffini* holotype (NMNZ P 662, female 972 mm TL); and B. *Squalus griffini* (NMNZ P 20965, female 482 mm TL). Field of view width 0.8 mm.

Table 1. Proportional dimensions as percentages of total length for the holotype (NMNZ P 662) and ranges for the 16 paratypes of *Squalus griffini*. Note that those measurements in *italics* are horizontal rather than direct measurements.

	<i>S. griffini</i>		
	Holotype	Paratypes	
		Min.	Max.
TL – Total length	972	473	1070
PCL – Precaudal length	80.2	76.8	80.3
PD2 – Pre-second dorsal length	63.2	59.4	63.2
PD1 – Pre-first dorsal length	29.1	27.0	31.5
SVL – Pre-vent length	52.2	50.0	54.9
PP2 – Prepelvic length	49.5	47.0	52.0
PP1 – Prepectoral length	20.1	19.3	24.4
HDL – Head length	21.0	20.2	24.3
PG1 – Prebranchial length	18.2	16.5	20.7
PSP – Prespiracular length	12.1	10.0	14.5
POB – Preorbital length	7.5	7.4	8.8
PRN – Prenarial length	5.2	5.0	5.9
POR – Preoral length	9.5	8.8	11.4
INLF – Inner nostril-labial furrow space	4.4	4.1	5.5
MOW – Mouth width	5.8	5.7	7.6
ULA – Labial furrow length	2.2	1.8	2.7
INW – Internarial space	4.5	4.4	5.2
INO – Interorbital space	7.1	7.3	9.6
EYL – Eye length	3.6	3.9	5.3
EYH – Eye height	1.4	1.4	2.4
SPL – Spiracle length	1.5	1.0	1.8
GS1 – First gill-slit height	2.3	1.4	2.3
GS5 – Fifth gill-slit height	2.1	1.7	2.5
IDS – Interdorsal space	25.3	22.6	26.0
DCS – Dorsal-caudal space	9.7	9.1	11.1
PPS – Pectoral-pelvic space	26.9	21.5	27.0
PCA – Pelvic-caudal space	23.8	21.7	26.0
D1L – First dorsal length	14.9	13.3	16.5
D1A – First dorsal anterior margin	11.5	11.5	14.6
D1B – First dorsal base length	9.7	8.3	10.4
D1H – First dorsal height	6.9	6.3	8.7
D1I – First dorsal inner margin	5.2	4.9	6.4
D1P – First dorsal posterior margin	8.2	7.5	10.4
D1ES – First dorsal spine length	–	1.9	4.0
D1BS – First dorsal spine base width	0.8	0.6	0.9
D2L – Second dorsal length	11.8	10.7	13.1
D2A – Second dorsal anterior margin	9.5	9.1	11.6
D2B – Second dorsal base length	7.7	6.7	8.1
D2H – Second dorsal height	4.6	4.2	5.8
D2I – Second dorsal inner margin	4.1	3.8	5.1
D2P – Second dorsal posterior margin	5.4	4.3	6.3
D2ES – Second dorsal spine length	–	3.1	5.3
D2BS – Second dorsal spine base width	0.7	0.6	0.9

Table 1. cont'd.

	<i>S. griffini</i>		
	Holotype	Paratypes	
		Min.	Max.
P1A – Pectoral anterior margin	13.6	13.4	16.5
P1I – Pectoral inner margin	6.5	5.4	7.7
P1B – Pectoral base length	5.3	5.0	6.2
P1P – Pectoral posterior margin	9.7	9.5	13.2
P2L – Pelvic length	10.2	9.0	11.5
P2H – Pelvic height	4.7	4.4	5.1
P2I – Pelvic inner margin	4.2	4.7	5.7
CDM – Dorsal caudal margin	19.4	19.4	22.5
CPV – Preventral caudal margin	10.0	9.8	11.7
CPU – Upper postventral caudal margin	14.8	14.7	17.2
CPL – Lower postventral caudal margin	3.2	3.4	4.8
CFW – Caudal fork width	6.2	6.0	7.1
CFL – Caudal fork length	8.4	8.5	10.1
HANW – Head width at nostrils	6.5	6.4	7.5
HAMW – Head width at mouth	10.4	10.4	12.4
HDW – Head width	11.6	12.2	14.9
TRW – Trunk width	11.7	8.3	13.7
ABW – Abdomen width	7.9	8.0	14.0
TAW – Tail width	6.0	5.3	7.2
CPW – Caudal peduncle width	3.1	2.1	4.8
HDH – Head height	8.8	7.9	11.0
TRH – Trunk height	9.4	8.6	13.9
ABH – Abdomen height	9.0	6.9	14.7
TAH – Tail height	6.7	4.9	6.8
CPH – Caudal peduncle height	2.3	2.2	2.6
CLO – Clasper outer length	–	0.8	4.6
CLI – Clasper inner length	–	5.0	9.7
CLB – Clasper base width	–	0.8	1.4

exposure, generally reaching level of insertion of fin when unbroken (slightly posterior in some); interdorsal space 0.79 (0.76–1.07) in pre-pectoral length, 1.15 (1.12–1.30) in pre-first dorsal fin length. Pectoral fin large, anterior margin weakly convex, apex rounded; posterior margin concave to nearly straight; inner margin convex, length 6.5 (5.4–7.7)% TL, free-rear tip narrowly rounded, not acute; base 2.59 (2.35–2.85) in anterior margin length. Pelvic fins small, anterior and posterior margins almost straight, apex broadly rounded, free rear tip narrow, acute. Precaudal tail tapering to caudal fin, broadly semicircular posteriorly, ventral groove well developed; prominent lateral keels extending posteriorly from below insertion of second dorsal fin past caudal fin insertion; pelvic–caudal space 1.13 (0.84–1.22) in pectoral–pelvic space, 0.85 (0.76–1.07) in pre-pectoral length; dorsal–

caudal space 2.61 (2.10–2.68) in interdorsal space; upper and lower precaudal pits present, upper pit better defined than lower pit. Caudal fin well developed, dorsal caudal margin 19.4 (19.4–22.5)% TL, 1.08 (0.94–1.19) in head length, without a subterminal notch; lower caudal lobe 1.93 (1.72–2.03) in dorsal caudal margin. Vertebral centra 121 (113–119), monospondylous 47 (45–47), precaudal 91 (86–90) and caudal 30 (26–29). Teeth missing from upper and lower jaws of holotype, 11 + 8 remaining in upper jaw, 8 + 10.5 remaining in the lower jaw; 13–14+13=26–27 in upper jaw, 10–12+10–12=21–24 in lower jaw of other material (NMNZ P 2759, NMNZ P 22549, NMNZ P 35270, NMNZ P 35973 and NMNZ P 41774).

COLOUR.— The female holotype is stained brown and

has lost all natural colour and markings. Large female with similar morphology to holotype (NMNZ P 39893, 1018 mm TL, based on fresh specimen): uniform grey-brown dorsally, white below; dorsal and ventral colours strongly demarcated on head, extending from snout below eye and through gill slits to pectoral-fin base, demarcation less distinct posteriorly; dorsal and caudal fins grey, first dorsal-fin anterior base and free rear tip paler than rest of fin, second dorsal-fin anterior base not darker than rest of fin, dorsal-fin tips and upper posterior margin with narrow black margin; first dorsal spine pale, second dorsal spine dark brown to dusky at base, becoming pale towards tip; pectoral, pelvic and caudal fins grey with white posterior margins and tips; naked axils of fins and pectoral origin dusky; eyes bright green in life. Some individuals with

scattered black spots on dorsal and ventral surfaces. A melanistic specimen (NMNZ P 5176) is black above, dark grey below with white spots scattered along the ventral surface from the mouth to the pelvic fins. Juvenile female (NMNZ P 41775, 418.5 mm TL): first and second dorsal-fin anterior bases and free rear tips distinctly paler than rest of body and fin, posterior margin of second dorsal-fin white almost to tip; first dorsal-fin upper anterior and upper posterior margins and tip black; second dorsal-fin upper anterior margin and tip black; caudal fin with broad white posterior margin, no caudal bar; basal half of upper caudal lobe with thin black fringe, upper caudal blotch faint, distal third of lobe white; distal half of lower caudal lobe white. Some adult specimens retaining juvenile colour pattern.

SIZE.— Females reach at least 1100 mm TL (specimen not retained) and males at least 898 mm TL (NMNZ P 39908); smallest mature male 693 mm TL (NMNZ P 41774); smallest pregnant female 865 mm TL, largest immature female 935 mm TL (specimens not retained).

DISTRIBUTION.— North and South Islands of New Zealand and Chatham Rise north of the Subtropical Front. Also occurs north of New Zealand on Wanganella Bank, Norfolk and Louisville Ridges, and southern Kermadec Ridge to at least Raoul Island.

REMARKS.— Garrick (1960) synonymised *S. griffini* with *S. blainville* (syn. *S. blainvillii*, *S. blainvillei*) based on the literature and an examination of the holotype of *S. griffini*, several specimens from New Zealand, and a presumed *S. blainville* specimen from the east coast of the United States. Use of the name *S. blainville* is problematic as there are no extant types and Risso's (1827) description and figure do not conform to any known species of *Squalus* (Chen *et al.* 1979; Muñoz-Chápuli and Ramos 1989). Consequently two regional taxonomic reviews have described morphologically disparate species from Japan and the eastern North Atlantic and Mediterranean as *S. blainville*. Although recognising that Risso's description was problematic, Chen *et al.* (1979) nonetheless identified a Japanese species as *S. blainville* on the basis of its high dorsal fins and long fin spines also depicted in Risso's figure. Muñoz-Chápuli and Ramos (1989) however observed that the only *Squalus* species known from the Mediterranean Sea (type locality of *S. blainville*) with long spines agrees well with their interpretation (erroneously) of *S. megalops*. Hence, rather than recognising this species as *S. blainville*, they identified it as *S. megalops*, and applied *S. blainville* to a less abundant short-spined species in order to maintain nomenclatural stability with Bigelow and Schroeder (1948, 1957), Garrick (1960) and Bass *et al.* (1976), who had applied this name to short-spined species from the Southern Hemisphere. Muñoz-Chápuli and Ramos (1989) concluded that the Japanese species referred by Chen *et al.* (1979) to *S. blainville* is probably undescribed.

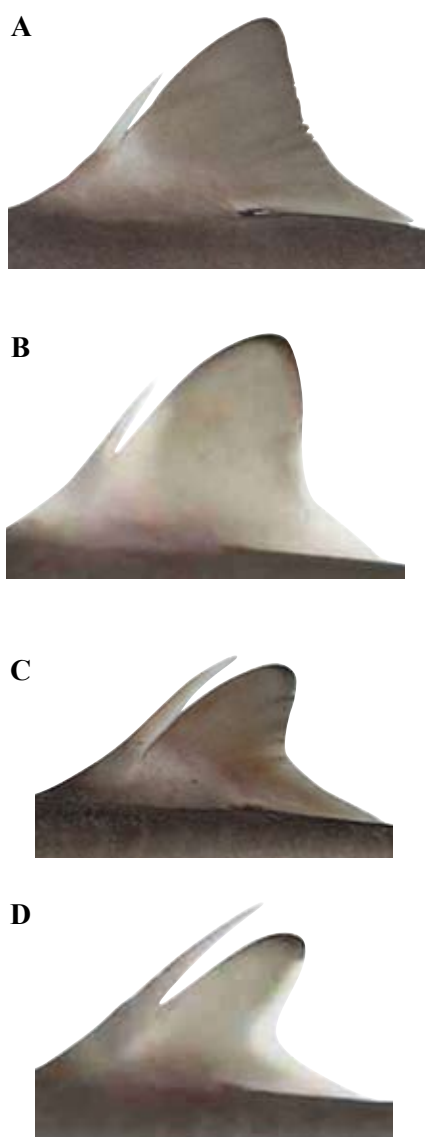


Figure 4. Lateral view of the dorsal fins of *Squalus griffini*: A. first dorsal fin, and C. second dorsal fin of NMNZ P 39893 (female 1018 mm TL); B. first dorsal fin, and D. second dorsal fin of CSIRO H 6006-11 (immature male 473 mm TL).

Notwithstanding the problems regarding correct application of the name *Squalus blainville* identified by Muñoz-Chápuli and Ramos (1989), *S. griffini* is distinguishable from ‘*S. blainville*’ from Japan on the basis of its much smaller first dorsal fin (height 6.4–8.7%, mainly less than 7.9% vs. 9.1–10.3% TL), more delicate dorsal-fin spines, and the first dorsal-fin base greater than its height (rather than less than its height). *Squalus griffini* is distinguishable from *S. blainville* from the eastern North Atlantic and Mediterranean by its longer snout (preoral length 8.8–11.4, mean 9.5% TL vs. 8.4–8.7% TL in *S. blainville*) and smaller first dorsal fin (first dorsal-fin height mainly less than 7.9%, mean 6.9% TL vs. 8.1–8.5% TL).

Squalus griffini is morphologically most similar to the short-spined ‘mitsukurii group’ *sensu* Chen *et al.* (1979) within what was formerly known as the ‘fernandinus-blainville group’ (Bigelow and Schroeder 1948, 1957; Garrick 1960). Members of the ‘mitsukurii group’ are characterised by having tricuspid denticles, pectoral fins not falcate with their inner margin rounded rather than pointed, a short first dorsal-fin spine, and relatively high vertebral counts (Chen *et al.* 1979; Muñoz-Chápuli and Ramos 1989). However, *S. griffini* is readily distinguished from members of the ‘mitsukurii group’ by the absence of a dark caudal bar. It differs from *S. mitsukurii* in having a lower vertebral count (113–121, mean 116 vs. 118–127, mean 121) and generally larger interdorsal space (distance 1.12–1.30 times in pre-first dorsal fin length vs. 1.45–1.73) (Chen *et al.* 1979; Last *et al.* 2007b, Part 6 of this issue). The absence of a dark caudal bar also separates *S. griffini* from the two Australian species, *S. chloroculus* Last, White and Motomura, 2007 and *S. montalbani* Whitley, 1931, previously referred to *S. mitsukurii*. These species also have a smaller second dorsal fin with a proportionally longer free rear tip, and much lower vertebral counts than *S. griffini*. *Squalus*

montalbani also has a shorter prenarial snout (4.0–5.3% vs. 5.0–5.9%, mean 5.4% TL in *S. griffini*) (Last *et al.* 2007b, Part 6 of this issue).

Five other *Squalus* species with characters typical of the ‘fernandinus-blainville group’ are described from Australia in this issue. *Squalus grahami* White, Last and Stevens, 2007 (Part 7 of this issue) is readily distinguished from *S. griffini* by the presence of a dark upright caudal bar, fewer monospondylous vertebrae (38–42 vs. 45–47 in *S. griffini*), a longer second dorsal-fin base and wider prenarial snout. *Squalus edmundsi* White, Last and Stevens, 2007 (Part 7 of this issue), *S. albifrons* Last, White and Stevens, 2007 (Part 5 of this issue) and *S. altipinnis* Last, White and Stevens, 2007 (Part 5 of this issue), all resemble *S. griffini* in having a predominately white posterior caudal margin (*S. edmundsi* has an oblique caudal bar that barely reaches the posterior fin margin). However, unlike *S. griffini*, they have a more erect first dorsal fin with a longer, fatter spine (exposed base width 0.9–1.2% vs. 0.6–0.9% TL, mean 0.7% TL in *S. griffini*) resembling that of *S. blainville sensu* Chen *et al.* (1979). *Squalus edmundsi* and *S. altipinnis* have fewer monospondylous vertebrae (42–44), and *S. altipinnis* has a shorter snout, smaller internarial space and longer caudal peduncle than *S. griffini*. *Squalus albifrons* also differs in having a shorter snout, horizontal prenarial length 2.91–3.06 times in preoral length (vs. 2.37–2.65 times in *S. griffini*), first dorsal-fin height 1.67–1.77 times in its length (vs. 1.78–2.36 times), and a slightly longer upper caudal-fin lobe (dorsal caudal margin 21.3–23.6% vs. 19.4–22.5%, mean 21% TL). *Squalus notocaudatus* Last, White and Stevens, 2007 also has an upright first dorsal fin with a relatively heavy spine (0.7–1.0% TL) but is most readily distinguished from *S. griffini* by its coloration (diagonal black caudal bar across base of lower caudal), short snout (preorbital length 6.4–7.0% vs. 7.4–8.8% TL), longer upper caudal (23.3–24.0% TL) and high vertebral count (123–127 total vertebrae).

The holotype of *Squalus griffini* is quite different in body shape to most specimens collected from the region. This morphotype, represented in the NMNZ collection by a few large individuals, is rather robust with broad, weakly tricuspid denticles, a relatively small, subtriangular second dorsal fin with a long free rear tip, and is possibly dark bodied. The more typical form of *S. griffini* caught in the region is less robust, has strongly tricuspid denticles, and a relatively tall, deeply notched second dorsal fin. Colour of the body and fins usually becomes darker and more uniform with growth, however some adults remain relatively pale overall, with a pale first dorsal-fin anterior base, prominent dark fin markings, and whitish dorsal-fin free rear tips and lower caudal-fin lobe. Molecular work supports conspecificity of these morphotypes (see Part 12 of this issue, Ward *et al.*, 2007) and no obvious morphometric or meristic differences exist between them. However, given such radical differences in the morphology of the denticles, and fin shape and colour,



Figure 5. Juvenile coloration of the caudal fin of *Squalus griffini* (CSIRO H 6066–08, immature male 262 mm TL).

this species requires further investigation across its distributional range.

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Part 10 — *Squalus hemipinnis* sp. nov, a new short-snout spurdog from eastern Indonesia

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ABSTRACT.— A new species of spurdog, *Squalus hemipinnis* sp. nov., is described based on specimens from eastern Indonesia. This species differs from other *Squalus* species in the region in a combination of coloration, meristics, and morphometrics of the head, trunk and fins. *Squalus hemipinnis* does not conform to any of the widely recognised *Squalus* subgroups, instead sharing characters with several groups. *Squalus hemipinnis* has a short snout typified by members of the ‘megalops-cubensis group’ but also has a dark caudal bar in juveniles typical of the ‘mitsukurii group’. Its low vertebral count is unusual within *Squalus*.

Key words. Squaloidea – Squalidae – *Squalus hemipinnis* – new species – Indonesia

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INTRODUCTION

Market surveys at various landing sites in eastern Indonesia between April 2001 and March 2006 produced a wide variety of new or poorly known sharks, skates, rays and chimaeras, including undescribed squalids (White *et al.*, 2006). Amongst this material were four members of the genus *Squalus*, including one particularly abundant species that is very distinct from its congeners and does not conform to any of the recognised *Squalus* complexes. This species, which can be distinguished from sympatric relatives by the combination of a relatively short snout, deeply forked second dorsal fin and the presence of a broad caudal bar in juveniles, is described based on available Indonesian material. Comparisons are made with other species of *Squalus* from the Indo–West Pacific.

METHODS

Methods follow those outlined in Part 1 of this issue (Last *et al.*, 2007). Both morphometrics and meristics were taken from the holotype (MZB 15040) and the following 5 paratypes: CSIRO H 5631–02, CSIRO H 5631–06, CSIRO H 5692–02, CSIRO H 5692–03 and CSIRO H 5692–06 (Table 1). In addition, meristics were taken from the following 9 paratypes: CSIRO H 5631–01, CSIRO H 5631–03, CSIRO H 5631–04, CSIRO H 5692–01, CSIRO H 5857–13, CSIRO H 5857–14, CSIRO H 5857–15, CSIRO H 5693–06 and CSIRO H 5693–07, and colour is described from the following paratype embryo: CSIRO H 5889–38 (1 of 3). In the description, morphometric and meristic values for the holotype are

given first followed in parentheses by the ranges of the paratypes.

Type specimens are deposited in the ichthyological collection of the Museum Zoologicum Bogoriense, Jakarta (MZB) and at the Australian National Fish Collection, Hobart (CSIRO); other material of the new species is deposited in the National Museum of Victoria (NMV); their registration numbers are prefixed with these acronyms.

Squalus hemipinnis sp. nov.

Figs 1–5; Table 1

Squalus sp. 3: White *et al.*, 2006, *Economically Important Sharks and Rays of Indonesia*, pp 70–71.

Holotype. MZB 15040, female 637 mm TL, Kedonganan fish landing site, Bali, Indonesia, 08°45' S, 115°10' E, July 2002.

Paratypes. 17 specimens. Collected at same locality as holotype. CSIRO H 5631–01, female 580 mm TL; CSIRO H 5631–02, female 575 mm TL; CSIRO H 5631–03, female 605 mm TL; CSIRO H 5631–04, female 580 mm TL; CSIRO H 5631–06, female 566 mm TL; CSIRO H 5692–01, adult male 418 mm TL; CSIRO H 5692–02, adult male 498 mm TL; CSIRO H 5692–03, adult male 484 mm TL; CSIRO H 5692–06, female 566 mm TL; CSIRO H 5693–06, female 550 mm TL; CSIRO H 5693–07, female 425 mm TL; CSIRO H 5857–13, female 640 mm TL; CSIRO H 5857–14, female 660 mm TL; CSIRO H 5857–15, female 625 mm TL;

CSIRO H 5889–38, 3 female embryos 162–166 mm TL. **Non-types.** 9 specimens. Collected at same locality as holotype. MZB 15039, adult male 493 mm TL; NMV A 29559–001, adult male 452 mm TL; NMV A 29559–002, female 580 mm TL; CSIRO H 5631–05, female 564 mm TL; CSIRO H 5692–05, four embryos 154–157 mm TL; CSIRO H 5889–29, adult male 449 mm TL.

DIAGNOSIS.— A moderately sized species of *Squalus* with the following combination of characters: body slender, depth 9.0–10.6% TL; snout relatively narrow, very short, horizontal prenarial length 2.0–2.2 times mouth width, preoral length 2.41–2.49 times horizontal prenarial length, 8.4–9.1% TL; eye large, its length 5.1–5.6% TL; secondary lobe of anterior nasal flap well developed; dorsal fins small, strongly raked; first dorsal-fin spine moderate, broad-based; second dorsal-fin spine moderate, robust and broad-based; pectoral fin of adult weakly falcate; pectoral-fin inner margin relatively short, 6.9–7.8% TL; caudal fin with a short, broad caudal bar, enlarged upper caudal blotch and fringe located distally on lobe in juveniles; flank denticles broadly unicuspidate to weakly tricuspidate; 35–38 monospondylous centra, 72–76 precaudal centra, 96–100 total centra; adult maximum size at least 78 cm TL.

DESCRIPTION.— Body fusiform, slender, nape prominently humped (less so in smallest paratypes); deepest near first dorsal-fin spine, maximum depth 1.14 (0.86–1.09 in 5 paratypes) times width; trunk depth 1.05 (0.84–0.98) times abdomen depth; head short 22.6 (20.9–22.5)% TL; caudal peduncle slender, 27.1 (26.4–28.4)% TL. Head not especially broad, width 1.30 (1.03–1.18) times trunk width, 1.27 (1.15–1.30) times abdomen width; depressed forward of spiracles, becoming somewhat subtriangular towards pectoral-fin origin; length 2.09 (2.15–2.37) in pre-vent length; height 0.85 (0.78–0.89) times width. Snout short, narrowly triangular in lateral view, apex bluntly pointed, broadly pointed in dorsal view; lateral prenarial margin not angular; horizontal length 1.07 (1.05–1.14) times eye length, 0.72 (0.70–0.74) times interorbital space; horizontal prenarial length 2.49 (2.41–2.47) in preoral length. Eye oval, large, length 4.23 (4.04–4.19) in head, 2.34 (2.10–2.72) times its height; strongly notched posteriorly, notch deep anteriorly, usually weakly connected to anteroventral margin of spiracle. Spiracle size moderate, broadly crescentic (sometimes subtriangular); broad lobe-like fold on posterior margin; greatest diameter 3.04 (2.98–3.33) in eye length. Gill openings directed slightly anterodorsally from bottom to top (more upright in some paratypes); first four subequal in size, fifth longest, height of fifth slit 2.0 (1.9–2.3)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.15 (1.14–1.22) in preoral length; upper labial furrows about 1.5 times length of lower furrows; prominent postoral groove, subequal in length to upper labial furrows, extending posterolaterally from angle of jaws; two series of functional teeth in upper jaw, three (sometimes two)

series in lower jaw. Teeth similar in upper and lower jaws; upper teeth unicuspid, interlocking, blade-like, cusps directed strongly laterally, low; tooth base broader than length of its cusp. Nostrils small, almost transverse; anterior nasal flap strongly bifurcate; anterior lobe broad, posterior lobe much shorter, narrow, somewhat flattened; internarial space 2.29 (2.10–2.42) in preoral length, 2.69 (2.38–2.56) times nostril length. Dermal denticles (based on holotype) on flank very small, non-imbricate; crowns well elevated, quadrate, broadly unicuspidate to weakly tricuspidate with pronounced median ridge; median ridge commencing very well anterior of rest of crown, with a mesial furrow developing anteriorly and converging rapidly towards posterior tip of crown; posterior portion of cusp strongly produced, pungent; lateral portion of crown very short, cusps weakly developed or forming an obtuse angle; circumorbital region easily abraded in holotype (and most paratypes). First dorsal fin small, strongly raked, narrowly rounded apically (sometimes angular); anterior margin moderately convex; upper posterior margin almost straight, not vertical, instead directed very slightly anterodorsally from bottom to top (vertical in most paratypes), weakly concave near free rear tip (variable, never strongly concave); free rear tip very thick basally, short; inner margin of fin almost straight; insertion of base extremely well forward of pelvic-fin origin, well posterior to free rear tip of pectoral fin; fin-spine origin slightly posterior to pectoral-fin insertion; spine base broad, exposed anteriorly well below junction of spine and soft portion of fin; soft portion of fin connected well above mid-point of total spine length (sometimes at about three-quarters of spine length from its base); spine tapering slightly distally, anterior margin almost straight; exposed portion raked; spine longer than exposed portion of second dorsal-fin spine (variable in paratypes, distinctly shorter in CSIRO H 5692–03), exposed base more elevated than exposed base of second dorsal-fin spine; pre-first dorsal length 3.52 (3.42–3.61) times in TL; first dorsal-fin length 1.89 (1.73–2.15) times its height, 1.15 (1.09–1.25) times second dorsal-fin length; first dorsal-fin height 2.10 (1.77–1.91) times second dorsal-fin height; exposed first dorsal spine length 0.60 (0.55–0.73) times height of fin. Second dorsal fin very small, very strongly raked; anterior margin moderately convex (less so in some paratypes), apex narrowly angular; posterior margin very deeply concave, maximum concavity forming a V-shape (mostly less than 90°) at about mid-point of margin, upper portion directed dorsoposteriorly very strongly from bottom to top; free rear tip moderately elongate, inner margin length 1.09 (1.03–1.18) times fin height; second dorsal-fin length 3.45 (2.94–3.22) times its height; spine length 1.01 (1.26–1.41) in height of fin; fin-spine origin well behind free rear tip of pelvic fin, exposed at about or slightly below level of junction with spine and soft portion of fin; exposed second spine broad based (broader than exposed base of first dorsal-fin spine); spine robust, bluntly pointed distally, tapering rapidly just above point of exposure, spine tip not extending to level of insertion



Figure 1. Lateral view of: A. *Squalus hemipinnis* sp. nov. holotype (MZB 15040, female 637 mm TL); B. *Squalus hemipinnis* (CSIRO H 5631-02, female 575 mm TL).



Figure 2. Ventral view of the head of *Squalus hemipinnis* sp. nov. holotype (MZB 15040, female 637 mm TL).

of fin (extending beyond insertion in paratypes); interdorsal space 0.97 (0.85–0.91) in length from snout tip to pectoral-fin origin, 1.19 (1.11–1.16) in pre-first dorsal length; interdorsal ridge weak (appearing as a shallow groove in some paratypes). Pectoral fin moderate (relatively smaller in smallest paratypes), anterior margin moderately convex; inner margin moderately convex, length 7.8 (6.9–7.3)% TL; apex narrowly rounded, lobe-

like, weakly falcate (not falcate in smallest paratypes); posterior margin moderately concave (otherwise weakly), free rear tip broadly angular; fin base very short, 3.18 (2.82–3.11) in length of anterior margin. Pelvic fins size moderate, anterior and posterior margins almost straight, apex broadly rounded, free rear tip broadly angular (more acute in mature males). Caudal peduncle very long, tapering slightly to caudal fin; subcircular in cross-section

Table 1. Proportional dimensions as percentages of total length for the holotype (MZB 15040) and ranges for the 5 paratypes of *Squalus hemipinnis* sp. nov.

	<i>S. hemipinnis</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
TL – Total length	637	484	575
PCL – Precaudal length	79.4	79.3	80.0
PD2 – Pre-second dorsal length	60.4	60.3	62.6
PD1 – Pre-first dorsal length	28.4	27.7	29.2
SVL – Pre-vent length	47.3	47.3	49.6
PP2 – Prepelvic length	45.8	45.5	48.3
PP1 – Prepectoral length	22.7	21.2	22.0
HDL – Head length	22.6	20.9	22.5
PG1 – Prebranchial length	18.8	17.1	18.9
PSP – Prespiracular length	11.7	10.6	12.4
POB – Preorbital length	6.6	6.4	6.7
PRN – Prenarial length	4.3	3.9	4.4
POR – Preoral length	8.8	8.4	9.1
INLF – Inner nostril-labial furrow space	5.2	4.8	5.3
MOW – Mouth width	7.6	6.9	7.7
ULA – Labial furrow length	2.0	1.9	2.1
INW – Internarial space	3.8	3.5	4.3
INO – Interorbital space	7.9	7.6	8.3
EYL – Eye length	5.3	5.1	5.6
EYH – Eye height	2.3	1.9	2.6
SPL – Spiracle length	1.8	1.5	1.8
GS1 – First gill-slit height	1.9	1.7	2.0
GS5 – Fifth gill-slit height	2.0	1.9	2.3
IDS – Interdorsal space	23.9	24.2	25.9
DCS – Dorsal-caudal space	10.6	10.9	11.4
PPS – Pectoral-pelvic space	20.9	20.9	24.4
PCA – Pelvic-caudal space	27.1	26.4	28.4
D1L – First dorsal length	14.4	12.8	15.3
D1A – First dorsal anterior margin	13.0	11.7	13.8
D1B – First dorsal base length	9.3	8.1	9.9
D1H – First dorsal height	7.7	6.7	7.4
D1I – First dorsal inner margin	5.4	4.9	5.4
D1P – First dorsal posterior margin	8.2	6.8	8.2
D1ES – First dorsal spine length	4.6	4.1	5.5
D1BS – First dorsal spine base width	0.9	0.7	0.8
D2L – Second dorsal length	12.6	11.4	12.5
D2A – Second dorsal anterior margin	11.4	10.7	11.6
D2B – Second dorsal base length	8.8	7.4	8.2
D2H – Second dorsal height	3.6	3.8	3.9
D2I – Second dorsal inner margin	4.0	4.1	4.6
D2P – Second dorsal posterior margin	3.7	3.6	4.4
D2ES – Second dorsal spine length	3.7	4.8	5.5
D2BS – Second dorsal spine base width	1.0	0.9	1.0

Table 1. cont'd.

	<i>S. hemipinnis</i> sp. nov.		
	Holotype	Paratypes	
		Min.	Max.
P1A – Pectoral anterior margin	15.7	13.4	14.8
P1I – Pectoral inner margin	7.7	6.9	7.3
P1B – Pectoral base length	4.9	4.4	5.1
P1P – Pectoral posterior margin	11.6	9.5	10.1
P2L – Pelvic length	10.0	9.0	10.1
P2H – Pelvic height	5.2	4.2	5.0
P2I – Pelvic inner margin	3.3	3.9	4.8
CDM – Dorsal caudal margin	20.6	19.5	20.7
CPV – Preventral caudal margin	11.3	11.1	11.8
CPU – Upper postventral caudal margin	15.3	13.7	15.1
CPL – Lower postventral caudal margin	5.8	4.6	6.0
CFW – Caudal fork width	7.1	6.1	6.9
CFL – Caudal fork length	8.7	8.6	9.3
HANW – Head width at nostrils	6.9	6.5	7.6
HAMW – Head width at mouth	9.3	8.9	10.0
HDW – Head width	12.1	10.5	12.0
TRW – Trunk width	9.3	9.4	10.6
ABW – Abdomen width	9.5	8.5	9.6
TAW – Tail width	6.6	5.7	6.5
CPW – Caudal peduncle width	2.9	2.5	2.9
HDH – Head height	10.2	8.5	9.7
TRH – Trunk height	10.6	9.0	10.2
ANH – Abdomen height	10.2	9.1	11.8
TAH – Tail height	7.0	6.1	7.0
CPH – Caudal peduncle height	2.2	2.2	2.5
CLO – Clasper outer length	–	4.5	4.5
CLI – Clasper inner length	–	7.1	7.3
CLB – Clasper base width	–	1.4	1.5

anteriorly, broadly semicircular posteriorly; ventral groove well developed; lateral keels well developed, originating slightly posterior to (or below) insertion of second dorsal fin, terminating about half an eye diameter behind caudal-fin insertion; pelvic–caudal space 0.77 (0.73–0.92) in pectoral–pelvic space, 0.84 (0.77–0.81) in prepectoral length; dorsal–caudal space 2.27 (2.12–2.38) in interdorsal length; dorsal caudal pit well developed, ventral caudal pit rudimentary. Caudal fin short, upper postventral margin almost straight (weakly convex in some paratypes), apex of lower lobe narrowly angular; dorsal caudal margin 1.10 (1.03–1.13) in head length; length of lower caudal lobe 1.83 (1.67–1.80) in upper lobe length. Vertebral centra 96 (96–100 in 14 paratypes), monospondylous 36 (35–38), precaudal 72 (72–76) and caudal 24 (22–26). Teeth in upper jaw (in paratype

CSIRO H 5692–06) 13+13=26, lower jaw 12+11=23.

COLOUR.— When fresh (based on paratype CSIRO H 5631–02): slate grey above, white below; light and dark tonal areas sharply demarcated on head, extending from snout adjacent suborbit, across head and through top part of gill slits; differentiation indistinct on trunk. First dorsal fin greyish, darker apical marking appearing as a weak blotch rather than a marginal marking; anterior base and extremity of rear tip slightly paler; skin-covered basal portion of spine and base of soft portion of first dorsal fin white; second dorsal-fin anterior base white, rest of fin greyish with a small prominent black blotch distally, free rear tip pale; dorsal-fin spines dusky with darker anterior margins. Caudal fin mainly greyish with a broad white posterior margin; pale edge extending along full length

of posterior margin, from near apex of upper lobe to near apex of lower lobe, its width constricted slightly at caudal fork; slightly darker black caudal stripe present; no obvious caudal bar or other prominent black blotches or markings. In preservative (based on holotype): similar to fresh paratype except fins distinctly more brownish than body; interface between light and dark tonal areas extends through mid-gill area; pectoral and pelvic fins brownish grey above with broad white posterior margins; pectoral and pelvic fins brownish below with broad pale posterior margins and white bases; upper caudal stripe evident, no other dark markings. Late-term embryo (CSIRO H 5889–38, female 166 mm TL) with strongly differentiated light and dark fin markings; light and dark tonal areas across head sharply defined. First dorsal fin with a prominent white anterior base and free rear tip, distal part of fin mostly black; second dorsal fin with oblique black bar extending from base to fin apex, anterior portion of fin base and free rear tip white; prominent median black stripe extending from insertion of second dorsal fin to origin of caudal fin. Caudal fin with a prominent black caudal bar at its fork; bar short extending from angle of fin diagonally over posterior half of base of ventral lobe, intersection with posterior fin margin short; upper caudal fringe pronounced, closer to tip of lobe than its origin; upper caudal blotch well defined, located in central distal portion of upper lobe near fin margin; most of lower lobe and posterior margin of upper lobe white. Pectoral fin with dark anterior margin and basal blotch; broad posterior white margin; fin more uniformly pale ventrally. Pelvic fins uniformly white dorsally and ventrally.

SIZE.— Females and males reach at least 780 and 522 mm TL, respectively; smallest mature male 432 mm TL, smallest post-natal male 395 mm TL; smallest post-natal female 325 mm TL; 6 pregnant females examined had between 7 and 10 late-term embryos, 140–175 mm TL.

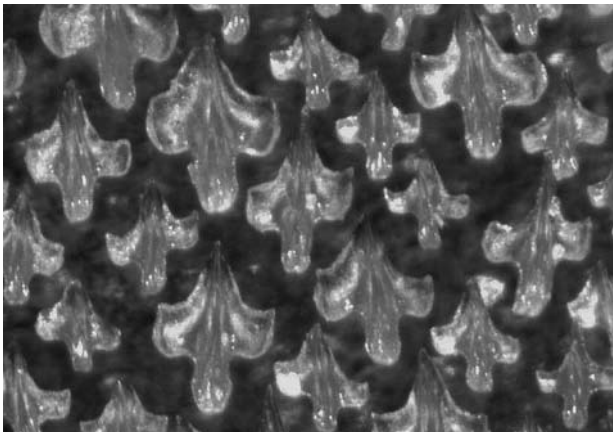


Figure 3. Cusps of the flank denticles of *Squalus hemipinnis* sp. nov. paratype (CSIRO H 5631–06, female 566 mm TL). Field of view width 1.0 mm.

DISTRIBUTION.— Known only from eastern Indonesia between Cilacap in Central Java (ca. 08°S, 109°E) and Tanjung Luar in eastern Lombok (ca. 09°S, 117°E) where it is the most abundant squaloid targeted by demersal longline fishers. Depth distribution unknown as existing material was collected from fish markets in eastern Indonesia, but likely to be deeper than 100 m.

ETYMOLOGY.— Derived from the combination of the Greek *hemi* (half) and the Latin *pinna* (fin) in allusion to its strongly notched, v-shaped posterior margin of the second dorsal fin.

VERNACULAR.— Indonesian Shortsnout Spurdog.

REMARKS.— *Squalus hemipinnis* can be distinguished from all other members of the genus by the combination of a short ‘megalops-like’ snout, deeply notched second dorsal-fin posterior margin, strongly demarcated dorsal coloration, very low number of precaudal centra, and other morphometric and colour details. *Squalus hemipinnis* has a fewer precaudal centra (72–75) than other *Squalus* species (more than 78), except *S. acanthias* Linnaeus, 1758 (74–79 in Australian specimens) and *S. lalannei* Baranes, 2003 (67–69). *Squalus hemipinnis* differs from *S. acanthias* in having a shorter snout, more anteriorly positioned dorsal fin, no white spots on the dorsal and lateral body surfaces, and a bifurcate nasal flap (vs. a single-lobed nasal flap). Although *S. lalannei*

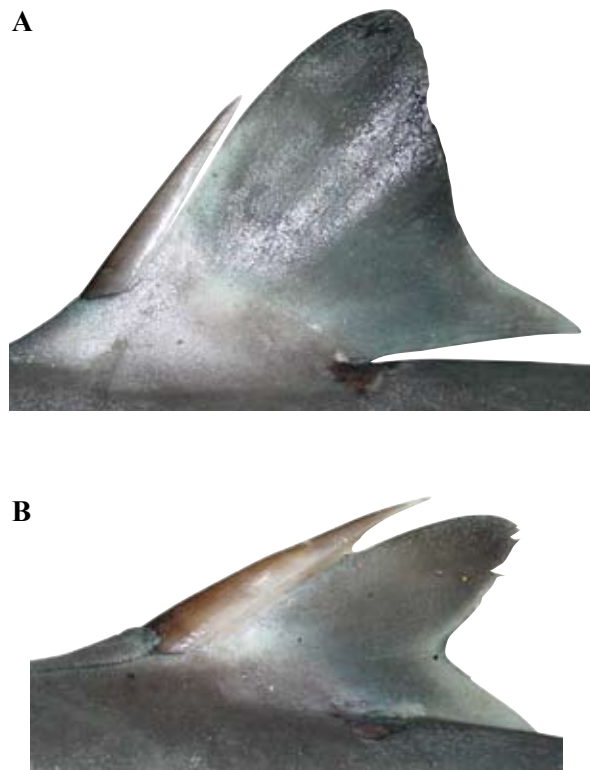


Figure 4. Lateral view of the dorsal fins of: *Squalus hemipinnis* sp. nov. paratype (CSIRO H 5631–02, female 575 mm TL) – A. first dorsal fin, B. second dorsal fin.

was not included in the recent book *Sharks of the World* (Compagno *et al.*, 2005), it differs from all other *Squalus* species in having an unusually low number of precaudal centra, i.e. 67–69 (vs. 72–75 in *S. hemipinnis*).

The snout shape of *S. hemipinnis* is similar to members of the ‘megalops-cubensis group’ and ‘highfin megalops group’ but it is clearly separable from all members of these *Squalus* subgroups. It possesses low, strongly raked dorsal fins (first dorsal-fin height 6.7–7.7% TL), which differ from the taller, more upright dorsal fins of *S. albifrons* Last, White and Stevens, 2007 (7.7–8.9% TL), *S. altipinnis* Last, White and Stevens, 2007 (7.8–7.9% TL), *S. bucephalus* Last, Séret and Pogonoski, 2007 (8.1–8.5% TL), *S. crassispinus* Last, Edmunds and Yearsley, 2007 (7.2–8.9% TL) and *S. notocaudatus* Last, White and Stevens, 2007 (8.2–9.4% TL). *Squalus hemipinnis* differs morphometrically from *S. cubensis* Howell Rivero, 1936, in having a shorter snout (preorbital length 6.4–6.7 vs. 7.2–7.6% TL; preoral length 1.14–1.21 vs. about 1.44 times mouth width, 8.4–9.1 vs. 9.6–10.8% TL), shorter pectoral-fin free rear tips (pectoral-fin inner margin 1.90–2.09 vs. 1.42–1.55 in its anterior margin) and a shorter second dorsal-fin free rear tip (second dorsal-fin inner margin 1.03–1.18 vs. 1.42–1.44 times its height). *Squalus hemipinnis* differs from *S. megalops* (Macleay, 1881) in having a narrower head (head width at anterior mouth 8.9–10.0 vs. 10.9–12.8% TL, head width 10.5–12.1 vs. 12.8–14.7% TL), a short, constricted snout (horizontal preanial length 2.02–2.17 vs. 2.58–3.40 times mouth width) and more robust dorsal-fin spines. The caudal fin of *S. hemipinnis*, which has a distinct black bar on its fork in juveniles that becomes unobvious in adults, differs from the northwestern Pacific species, *S. brevirostris* Tanaka, 1917, which has a pale caudal-fin posterior margin without a dark caudal bar.

Although *S. hemipinnis* is morphologically similar to some members of the ‘megalops-cubensis group’, it possesses



Figure 5. Juvenile coloration of the caudal fin of *Squalus hemipinnis* sp. nov. paratype (CSIRO H 5889–38, female embryo 166 mm TL).

a distinct caudal bar in juveniles typical of members of the ‘mitsukurii group’ and the ‘japonicus group’ but lacking in the ‘megalops-cubensis group’. *Squalus hemipinnis* differs from members of the ‘mitsukurii group’ and the ‘japonicus group’ in having a shorter snout (preoral length 8.4–9.1% TL vs. >11.4 % TL in *S. japonicus* Ishikawa, 1908 and *S. nasutus* Last, Marshall and White, 2007, and 9.3–11.5% in *S. chloroculus* Last, White and Motomura, 2007, *S. edmundsi* White, Last and Stevens, 2007, *S. grahami* White, Last and Stevens, 2007, *S. mitsukurii* Jordan and Snyder in Jordan and Fowler, 1903 and *S. montalbani* Whitley, 1931) and a strongly notched, v-shaped second dorsal-fin posterior margin. *Squalus griffini* Phillipps, 1931, has a much longer snout (preoral length 7.4–8.8% TL vs. 6.4–6.7 % TL), more strongly tricuspid denticles, and a different caudal coloration.

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Part 11 — Clarification of the status of *Squalus tasmaniensis* and a diagnosis of *Squalus acanthias* from Australia, including a key to the Indo–Australasian species of *Squalus*

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ABSTRACT.—*Squalus tasmaniensis* has been previously synonymised with *S. megalops* and *S. mitsukurii*. However, recent examination of the holotype revealed that it is a juvenile *S. acanthias* based on the position of the first dorsal fin and the narrow head. *Squalus acanthias* can be separated from all other known species of *Squalus* by the posterior location of the first dorsal fin (its origin behind the free rear tips of pectoral fins), a single-lobed anterior nasal flap, and the presence of white spots on the dorsal and lateral body surfaces. A diagnosis of southeastern Australian populations of *S. acanthias* and a key to the Indo–Australasian *Squalus* species are also presented.

Key words. Squaloidea – Squalidae – *Squalus tasmaniensis* – *Squalus acanthias* – key to species – Indo–Australasian.

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INTRODUCTION

Squalus tasmaniensis Howell Rivero, 1936a was described based on a single juvenile specimen collected off Hobart, Tasmania, in 1860. The author noted in his description that the specimen “resembles *Squalus acanthias* Linné in many aspects, and was identified as such by Garman”. Its nomenclatural affinity has remained unclear, having been synonymised with *S. mitsukurii* Jordan and Snyder, 1903 (Compagno, 1984) and with *S. megalops* (Macleay, 1881) by Last and Stevens (1994). Recent examination of the poorly preserved holotype of *S. tasmaniensis* by one of the authors (P. Last) revealed that this juvenile type specimen resembles *S. acanthias* Linnaeus, 1758 in a number of key characters.

Myagkov and Kondurin (1986) proposed that *S. acanthias* comprised at least 4 subspecies, *S. a. acanthias* from the northern Atlantic, *S. a. africana* from southern Africa, *S. a. ponticus* from the Black Sea and *S. a.* subsp. from Australia and New Zealand. However, the descriptions provided by Myagkov and Kondurin (1986) are very short, often based on embryos, and relied heavily on characters that are subjected to allometric changes with growth. Compagno *et al.* (1991) synonymised the subspecies *S. a. africana* with *S. acanthias*, but *S. a. ponticus* is considered a valid subspecies by Eschmeyer (2006). Apparently restricted to the Black Sea, *S. a. ponticus*, is much larger than other forms of

S. acanthias, attaining lengths of up to 180 cm TL (vs. <100 cm) with the females and males maturing at greater than 104 (vs. <60) and 120 (vs. <70) cm TL, respectively (Myagkov and Kondurin, 1986; Compagno *et al.*, 2005).

This paper proposes the synonymy of *S. tasmaniensis* with *S. acanthias* and provides a diagnosis of *S. acanthias* from southeastern Australia. A key to the Indo–Australian species of *Squalus* is also included.

METHODS

Methods follow those outlined in Part 1 of this publication (Last *et al.*, 2007). The holotype of *S. tasmaniensis* (MCZ 146-S) and five southeastern Australian specimens of *S. acanthias* (CSIRO T 712, CSIRO H 1214, CSIRO H 4226–01, CSIRO H 4876–01 and CSIRO H 6485–01) were measured in full (Table 1). For comparison with the juvenile (240 mm TL) holotype of *S. tasmaniensis*, selected measurements were also taken from similar-sized, juvenile/late term embryos of *S. acanthias* (n=4), *S. chloroculus* (n=3) and *S. megalops* (n=3) in the 200–271 mm TL size range. Meristics were taken from radiographs of 9 specimens of *S. acanthias*. Specimens examined are deposited in the Australian National Fish Collection, Hobart (CSIRO) and the ichthyological collection of the Museum of Comparative Zoology, Boston (MCZ); their registration numbers are prefixed with these acronyms.

Squalus acanthias Linnaeus, 1758

Figs 1, 2, Table 1

Squalus acanthias Linnaeus, 1758, *Systema Naturae*, ed. 10, 1: 233. Possible syntypes (2): Linnaean Collection in Uppsala, no. 159 (alcohol), no. 160 (dried), European Seas (“Habitat in Oceano Europaeo”).

Material examined. 15 specimens. MCZ 146-S (*Squalus tasmaniensis* holotype), female 240 mm TL, Hobart, Tasmania; CSIRO H 1214, female 678 mm TL, Dover or Southport, Tasmania, 30 m; CSIRO H 2921–01, female 606 mm TL, CSIRO H 2921–02, adolescent male 525 mm TL, CSIRO H 2921–03, female 698 mm TL, off Shark Point, Tasmania, 42°48' S, 147°29' E, 5.5 m; CSIRO H 4226–01, female 429 mm TL, Frederick Henry Bay, Tasmania, 42°50' S, 147°33' E, 6 m; CSIRO H 6205–01, immature male 271 mm TL, Battery Point, Tasmania, 42°53' S, 147°20' E; CSIRO T 1099, 4 late-term embryos 205–218 mm TL, Sandy Bay, Tasmania, 42°53' S, 147°20' E; CSIRO H 4876–01, adult male 616 mm TL, off Woodbridge, Tasmania, 43°10' S, 147°15' E, 20 m; CSIRO T 712, adult male 575 mm TL,

CSIRO H 6485–01, female 492 mm TL, CSIRO T 783, adult male 661 mm TL, off Port Davey, Tasmania.

DIAGNOSIS.— A moderately sized species of *Squalus* with the following combination of characters: body very slender, abdomen width 7.2–9.2% TL; head narrow, width at mouth 7.9–10.2% TL; mouth width 1.7–2.2 times horizontal prenarial length; snout moderately long, preoral length 2.2–2.5 times horizontal prenarial length, 8.5–9.8% TL; anterior nasal flap single-lobed; dorsal fins small and raked, first dorsal-fin height 1.1–1.3 times its inner margin length, second dorsal-fin height 0.7–0.9 times its inner margin length; first dorsal-fin origin located just posterior to pectoral-fin free rear tips; exposed bases of dorsal-fin spines relatively narrow, 0.4–0.7% TL; first dorsal-fin spine short, exposed length 1.7–2.7% TL; pectoral-fin anterior margin 1.9–3.1 times its inner margin length; preventral caudal margin 1.9–2.6 times inner margin of pelvic fin; caudal fin pale with poorly demarcated, whitish margin, blackish caudal blotch at apex of upper lobe, anterior margins of both lobes whitish in juveniles; no dark caudal bar; dorsal and lateral surfaces of body bluish grey with an irregular array of moderately-large white spots; flank denticles tricuspid;

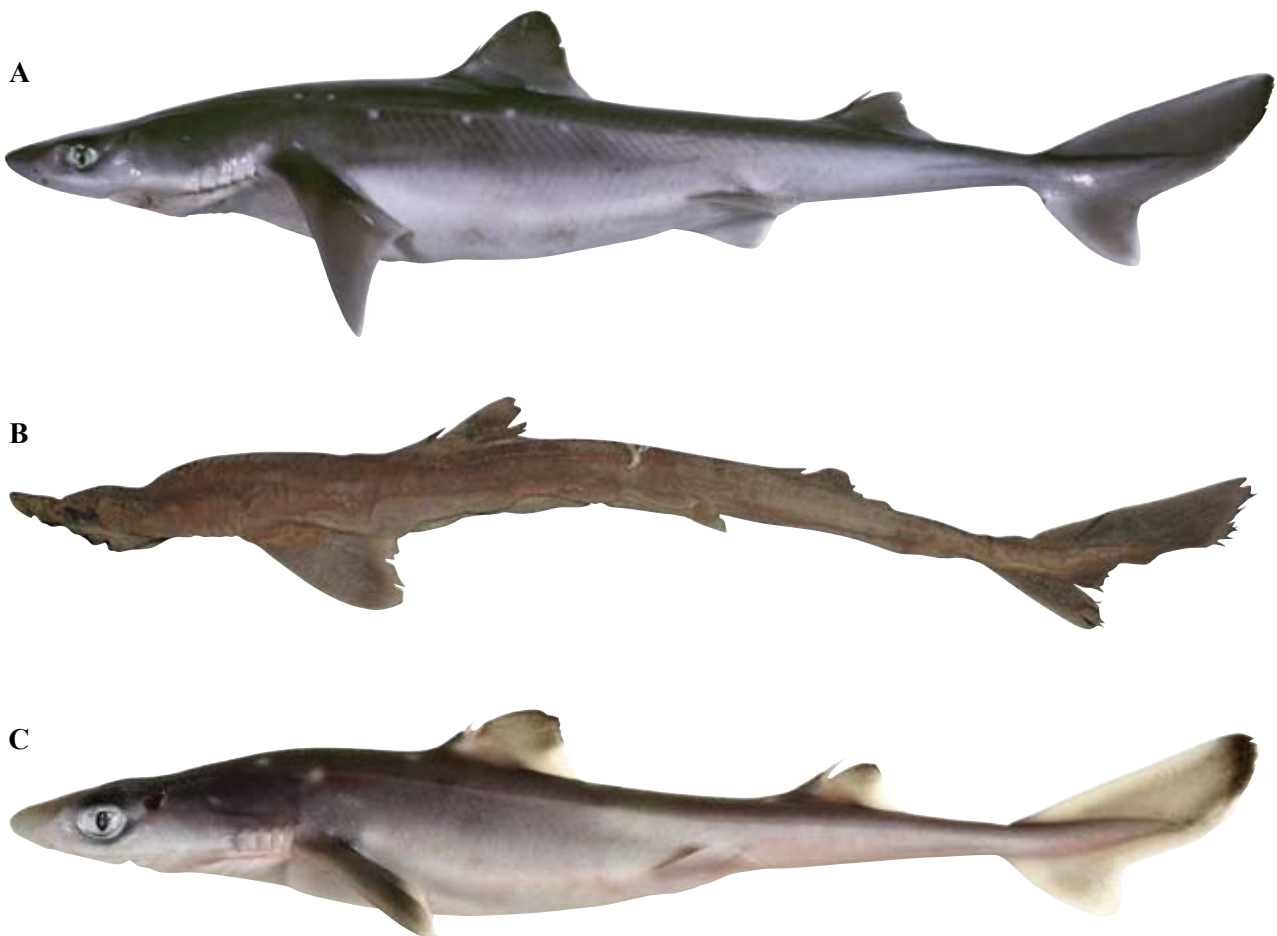


Figure 1. Lateral view of: A. *Squalus acanthias* (CSIRO H 1214, female 678 mm TL); B. *Squalus tasmaniensis* (MCZ 146-S, female 247 mm TL); C. *Squalus acanthias* (CSIRO H 6205–01, immature male 271 mm TL).

Table 1. Proportional dimensions as percentages of total length for 5 southeastern Australian specimens of *Squalus acanthias* and the holotype (MCZ 146-S) of *S. tasmaniensis*.

	<i>S. tasmaniensis</i>		<i>S. acanthias</i>	
	Holotype	Min.	Max.	(n = 5)
TL – Total length	240	429	678	
PCL – Precaudal length	78.2	77.7	79.1	
PD2 – Pre-second dorsal length	56.3	58.8	61.0	
PD1 – Pre-first dorsal length	29.5	32.8	35.2	
SVL – Pre-vent length	49.3	50.6	52.4	
PP2 – Prepelvic length	46.2	48.7	50.8	
PP1 – Prepectoral length	19.7	20.7	22.9	
HDL – Head length	20.1	20.7	22.4	
PG1 – Prebranchial length	15.7	17.6	19.2	
PSP – Prespiracular length	10.6	10.8	12.0	
POB – Preorbital length	6.1	6.8	7.2	
PRN – Prenarial length	3.2	4.2	5.0	
POR – Preoral length	7.5	8.5	9.8	
INLF – Inner nostril-labial furrow space	3.9	3.9	4.6	
MOW – Mouth width	6.2	7.0	8.7	
ULA – Labial furrow length	–	1.5	2.6	
INW – Internarial space	–	3.3	4.0	
INO – Interorbital space	–	6.8	8.5	
EYL – Eye length	3.5	3.4	3.9	
EYH – Eye height	1.0	1.4	2.2	
SPL – Spiracle length	1.3	0.9	1.4	
GS1 – First gill-slit height	1.7	1.4	1.9	
GS5 – Fifth gill-slit height	1.1	1.7	2.4	
IDS – Interdorsal space	18.7	19.8	21.2	
DCS – Dorsal-caudal space	12.3	10.8	12.0	
PPS – Pectoral-pelvic space	21.2	21.3	24.9	
PCA – Pelvic-caudal space	22.2	21.5	23.0	
D1L – First dorsal length	13.5	12.4	13.1	
D1A – First dorsal anterior margin	12.0	9.3	10.2	
D1B – First dorsal base length	8.1	7.0	7.8	
D1H – First dorsal height	4.3	5.9	6.8	
D1I – First dorsal inner margin	5.6	5.0	5.7	
D1P – First dorsal posterior margin	5.6	6.5	8.4	
D1ES – First dorsal spine length	1.9	1.7	2.7	
D1BS – First dorsal spine base width	0.5	0.4	0.6	
D2L – Second dorsal length	14.0	12.3	13.3	
D2A – Second dorsal anterior margin	10.4	9.2	10.6	
D2B – Second dorsal base length	9.3	7.5	8.4	
D2H – Second dorsal height	3.0	3.2	4.1	
D2I – Second dorsal inner margin	4.9	4.8	5.0	
D2P – Second dorsal posterior margin	5.2	4.7	5.7	
D2ES – Second dorsal spine length	3.7	2.6	3.7	
D2BS – Second dorsal spine base width	1.0	0.6	0.7	

Table 1. cont'd.

	<i>S. tasmaniensis</i>	<i>S. acanthias</i> (n = 5)	
	Holotype	Min.	Max.
P1A – Pectoral anterior margin	13.7	13.6	16.2
P1I – Pectoral inner margin	7.0	4.4	7.3
P1B – Pectoral base length	4.8	4.7	6.0
P1P – Pectoral posterior margin	8.5	8.1	11.0
P2L – Pelvic length	10.7	10.0	11.3
P2H – Pelvic height	3.2	4.2	5.0
P2I – Pelvic inner margin	3.8	4.1	5.6
CDM – Dorsal caudal margin	22.1	20.0	21.9
CPV – Preventral caudal margin	12.4	10.6	10.9
CPU – Upper postventral caudal margin	14.7	14.3	15.1
CPL – Lower postventral caudal margin	4.7	3.2	4.6
CFW – Caudal fork width	6.2	6.6	7.6
CFL – Caudal fork length	10.8	9.1	10.7
HANW – Head width at nostrils	6.6	5.6	6.7
HAMW – Head width at mouth	–	7.9	10.2
HDW – Head width	10.1	10.2	12.3
TRW – Trunk width	6.4	8.2	11.4
ABW – Abdomen width	4.2	7.2	9.2
TAW – Tail width	–	5.2	5.8
CPW – Caudal peduncle width	–	2.2	2.9
HDH – Head height	5.5	8.4	9.6
TRH – Trunk height	–	8.8	10.3
ABH – Abdomen height	–	8.6	10.9
TAH – Tail height	3.5	5.2	6.3
CPH – Caudal peduncle height	2.1	2.3	2.7
CLO – Clasper outer length	–	5.6	6.2
CLI – Clasper inner length	–	10.7	11.1
CLB – Clasper base width	–	1.2	1.3

41–45 monospondylous centra, 74–79 precaudal centra, 100–105 total centra; adult maximum size at least 100 cm TL.

REMARKS.— The holotype of *Squalus tasmaniensis* (Fig. 1b) resembles members of the ‘acanthias group’ in having a more posteriorly located first dorsal fin compared to all other *Squalus* species, i.e. the first dorsal-fin origin is situated just posterior to (rather than over or forward of) the pectoral-fin free rear tips and the interdorsal space is short (interdorsal space 18.7% TL in holotype, 17.9–18.6% TL in similar-sized *S. acanthias* vs. 20.7–23.9% TL in similar-sized *S. chloroculus* Last, White & Motomura, 2007 and *S. megalops*). The head of the holotype of *S. tasmaniensis* is also much narrower (Fig. 1b) than that of either *S. chloroculus* or *S. megalops*, with which it has

previously been synonymised (head width 10.1% TL in holotype, 10.9–11.5% TL in similar-sized *S. acanthias* vs. 12.5–14.2% TL in similar-sized *S. chloroculus* and *S. megalops*). Thus, although the holotype of *S. tasmaniensis* is in a poor condition, it shares a number of key features with *S. acanthias* and given its size appears to be a juvenile of this species. This specimen was originally identified by Garman as *S. acanthias* and the confusion that has followed seems to be related to the lack of any obvious white spots on the skin. The poor condition of the specimen has also possibly contributed to its previous misidentification.

The genetic component of this issue (Ward *et al.*, 2007; Part 12) found that the *Squalus acanthias* samples separated into two clearly distinct subgroups: a subgroup

consisting of 10 specimens from the North Pacific (Japan and U.S.A.); and larger subgroup from a much broader geographic range encompassing the Atlantic (U.K., U.S.A. and Iceland) and South Pacific Oceans (Australia, New Zealand and Chile). Populations belonging to the second subgroup are likely to conform to the current definition of *S. acanthias* because the holotype of *S. acanthias* was collected from European Seas. Additional morphological investigations are required to compare the regional forms of *S. acanthias*, in particular North Pacific populations vs. Atlantic and South Pacific populations. There are several junior synonyms of *S. acanthias* from the Atlantic (*Acanthias americanus* Storer, 1846, *A. antiquorum* Leach, 1818, *Squalus barbouri* Howell Rivero, 1936b, *A. commun* Navarrete, 1898, *A. linnei* Malm, 1877, *Spinax mediterraneus* Gistel, 1848, *Spinax (Acanthias) suckleyi* Girard, 1855, *A. vulgaris* Risso, 1827) and South Pacific (*S. fernandinus* Molina, 1782, *S. kirki* Phillipps, 1931, *A. lebruni* Vaillant, 1888, *S. whitleyi* Phillipps, 1931). *Squalus wakiyae* Tanaka, 1918 from Japan, which is the only available name from the North Pacific, may be resurrected as a valid species.

Other material. *Squalus chloroculus*: CSIRO H 1350–02, 4 embryos 217–238 mm TL, northwest of Macquarie

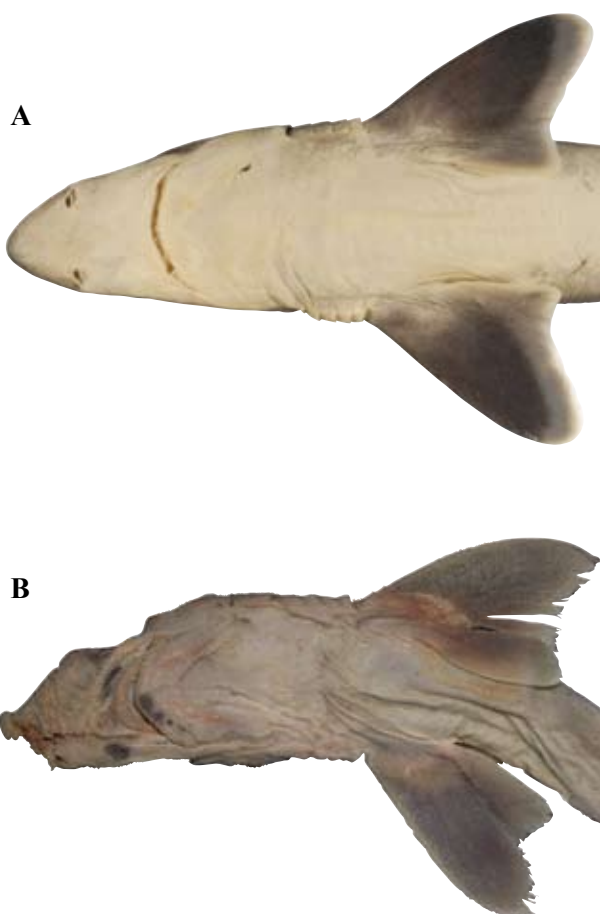


Figure 2. Ventral view of the head of A. *Squalus acanthias* (CSIRO H 4876–01, adult male 616 mm TL); B. *Squalus tasmaniensis* (MCZ 146–S, female 247 mm TL).

Harbour, Tasmania, 41°52' S, 144°23' E, 1370 m. *Squalus megalops*: CA 3176, immature female 255 mm TL, east of Gabo Island, New South Wales, 37°38' S, 150°14' E, 580 m; CSIRO H 5320–01, immature male 200 mm TL, south-southeast of Cape Everard, Victoria, 38°09' S, 149°38' E, 294 m; CSIRO H 6449–01, immature male 245 mm TL, off Trial Harbour, Tasmania, ca. 42° S, 145° E.

Key to *Squalus* of the Indo–Australasian region.

- 1a. First dorsal-fin spine origin distinctly behind free rear tips of pectoral fins; anterior nasal flap single-lobed; body typically bluish grey with white spots *S. acanthias* (circumglobal)
- b. First dorsal-fin spine origin over or anterior to free rear tips of pectoral fins; anterior nasal flap with two lobes; body typically greyish in colour, lacking white spots 2
- 2a. Snout long to very long, distance from snout tip to inner nostril longer than distance from inner edge of nostril to labial furrow.....3
- b. Snout short, distance from snout tip to inner nostril shorter or equal to distance from inner edge of nostril to labial furrow.....10
- 3a. Ventral lobe of caudal fin conspicuously black.....
..... *S. melanurus* (New Caledonia)
- b. Ventral lobe of caudal fin without a conspicuous black marking 4
- 4a. First dorsal fin and its associated spine almost upright..... 5
- b. First dorsal fin and its associated spine angled rearwards..... 6
- 5a. Snout acutely pointed, prenarial length more than 6.5% TL; 46 monospondylous vertebrae.....*S. rancureli* (Vanuatu)
- b. Snout narrowly triangular, prenarial length less than 6.5% TL; 43–44 monospondylous vertebrae ..
.....*S. edmundsi* (northwestern Australia, Indonesia)
- 6a. Snout narrow and long (preoral length 84–103% of head width); 36–42 (usually 37–40) monospondylous vertebrae 7
- b. Snout relatively broad and long (preoral length 62–81% of head width, ratio larger in specimens of *S. griffini* <550 mm TL); 41–47 (usually 43–47) monospondylous vertebrae 8
- 7a. Snout very long; preoral length <2.0 times horizontal prenarial length; undamaged first dorsal-fin spine much shorter than second dorsal-fin spine (first dorsal spine length 74–90% of second dorsal spine length); 78–84 (typically 81 or fewer) precaudal

- vertebrae..... *S. nasutus*
(northwestern Australia, Indonesia, Philippines)
- b. Snout long; preoral length >2.3 times horizontal prenarial length; undamaged first dorsal-fin spine slightly shorter than second dorsal-fin spine (first dorsal spine length about 96% of second dorsal spine length); 80–87 (typically 82 or more) precaudal vertebrae
..... *S. grahami* (eastern Australia)
- 8a. Caudal fin with a continuous broad pale posterior margin, lacking a dark caudal bar (most evident in juveniles and subadults; often indistinct in largest adults); 86–91 (usually 87–90) precaudal vertebrae..... *S. griffini* (New Zealand)
- b. Caudal fin with a dark caudal bar extending onto its posterior margin (most evident in juveniles and subadults); 79–86 (usually 79–84) precaudal vertebrae..... 9
- 9a. Second dorsal fin moderately large, its length 12.2–13.9% TL, 4.2–4.9 in pre-second dorsal length; adult claspers relatively long (outer length 4.5–5.6% TL)..... *S. montalbani*
(Australia, Indonesia, Philippines)
- b. Second dorsal fin relatively smaller, its length 10.9–12.2% TL, 5.0–5.8 in pre-second dorsal length; adult claspers shorter (outer length 3.8–4.6% TL)..... *S. chloroculus* (southern Australia)
- 10a. Dorsal body coloration strongly demarcated from ventral coloration; second dorsal-fin posterior margin strongly notched forming a distinct v-shape; 100 or less total vertebrae (range 96–100)..... *S. hemipinnis* (Indonesia)
- b. Dorsal body coloration only weakly demarcated from ventral coloration; second dorsal-fin posterior margin concave but not strongly notched and not forming a v-shape; 102 or more total vertebrae (range 102–127)..... 11
- 11a. Head enlarged, very broad (head width at anterior of nostrils 7.7–9.3% TL); denticles on flank both unicuspid and weakly tricuspid in adults..... *S. bucephalus* (New Caledonia)
- b. Head moderate, narrower (head width at anterior of nostrils 6.3–7.6% TL, usually less than 7.0% TL); denticles on flank either unicuspid or distinctly tricuspid 12
- 12a. Prominent dark bar along base of lower caudal-fin lobe (most evident in juveniles); 123–127 total vertebrae.....
..... *S. notocaudatus* (northeastern Australia)
- b. No dark oblique bar on base of lower caudal-fin lobe; usually less than 120 total vertebrae (range 102–122) 13
- 13a. First dorsal fin low (first dorsal-fin height 2.4–4.0% TL), usually angled rearwards 14
- b. First dorsal fin tall (first dorsal-fin height 4.4–5.9% TL), usually upright (sometimes angled rearwards in *S. crassispinus*) 15
- 14a. Interdorsal space 24–25% TL; preoral length 1.9–2.2 times internarial space; 37–40 monospondylous vertebrae..... *S. megalops* (Australia)
- b. Interdorsal space 23–24% TL; preoral length 2.3–2.5 times internarial space; 41–43 monospondylous vertebrae..... *S. raoulensis* (New Zealand)
- 15a. Dorsal spines very robust (second dorsal-spine base width 1.3–1.5% TL); denticles on flank unicuspid; 107–111 total vertebrae.....
..... *S. crassispinus* (northwestern Australia)
- b. Dorsal spines robust (second dorsal-spine base width 0.7–0.9% TL); denticles on flank tricuspid; 114–122 total vertebrae..... 16
- 16a. Caudal fin large (dorsal caudal margin >21% TL, <2.9 times in pre-second dorsal length); 44–46 (usually 45 or 46) monospondylous vertebrae *S. albifrons* (northeastern Australia)
- b. Caudal fin moderately large (dorsal caudal margin <20% TL, >3.0 times in pre-second dorsal length); 42–44 monospondylous vertebrae
..... *S. altipinnis* (northwestern Australia)

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Part 12 — DNA barcoding discriminates spurdogs of the genus *Squalus*

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ABSTRACT.— Sixteen species of *Squalus* were analysed (barcoded) for a 654 bp region of the mitochondrial cytochrome c oxidase I gene. These comprised four previously recognized species (*S. acanthias*, *S. brevirostris*, *S. japonicus* and *S. megalops*), two resurrected species (*S. griffini* and *S. montalbani*), eight new species (*S. albifrons*, *S. chloroculus*, *S. crassispinus*, *S. edmundsi*, *S. grahami*, *S. hemipinnis*, *S. nasutus* and *S. raoulensis*) and two species yet to be described, informally named here as the *Squalus* sp. (Taiwan highfin) and the *Squalus* sp. (Lombok highfin). A total of 127 individuals were barcoded. Average sequence divergences within and between the 15 species represented by multiple specimens were $0.17 \pm 0.05\%$ and $4.35 \pm 0.23\%$ respectively. Sequences of a particular species always clustered tightly together and away from clusters of other species. No instances of species sharing of sequences were observed, suggesting that these species were reproductively isolated from one another. DNA barcoding can be used to identify specimens of this genus with a high degree of certainty.

Key words. Squalidae – DNA barcode – mitochondrial DNA – cytochrome oxidase – species identification

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INTRODUCTION

Molecular approaches have long been used to assist species identification, beginning with protein electrophoresis in the early 1960s (Manwell and Baker, 1963) and mitochondrial DNA analyses in the late 1970s (Avice, 1994). A few years ago, it was proposed that a single gene sequence might be able to distinguish all, or the vast majority of, animal species, and that the mitochondrial gene cytochrome c oxidase I (COI) would be a good candidate gene (Hebert *et al.*, 2003). The species sequence of COI was likened to a barcode (Hebert *et al.*, 2003), although it was recognised from the start that species might each possess multiple sequences or barcodes. This does not matter from a species identification viewpoint providing that each sequence is unique to an individual species and clusters with (is more closely related to) other sequences of that species rather than with sequences from other species.

DNA barcoding of more than 200 species of Australian fishes (some imported) showed that COI barcoding does indeed permit the unambiguous resolution of this assortment of fish species (Ward *et al.*, 2005). While there may well be very closely related species pairs that cannot be discriminated by COI sequencing, these are likely to account for no more than 1 or 2% of all species.

Here we investigate whether DNA barcode analysis can contribute to a better understanding of the taxonomy and identification of *Squalus* species.

The taxonomy of Australian spurdogs was poorly known until Last and Stevens (1994) recognised 9 species of *Squalus* in Australian waters, 6 of which were previously undescribed (species A through F). The identity of the taxa found around northern New Zealand has also been uncertain and specimens have been variously (and incorrectly) recorded as *Squalus mitsukurii* (Paulin *et al.*, 2001; Tracey and Shearer, 2002) and *Squalus blainville* (Ayling and Cox, 1982; Paul, 2000).

The preceding papers in this special publication of the CSIRO Marine & Atmospheric Research Paper series formally describe 11 species from the Indo–Australasian region. In this final paper of the series, we use the approach of DNA barcoding to confirm that these newly described *Squalus* species do indeed have distinguishable COI sequences consistent with their being reproductively isolated species, and to support the concept that barcoding can be used for specimen identification in groups that are morphologically difficult to ascribe to species by non-experts. Some of these *Squalus* barcode data were briefly described in Ward *et al.* (2005), and subsequently in Hauser (in press), but in those publications many of

the species remained un-named. We also analyse barcode data from previously described species, including the widespread *S. acanthias*.

METHODS

Details of the individuals sequenced are provided in Table 1. Sixteen species of *Squalus* were analysed, comprising 4 previously recognised species (*S. acanthias*, *S. brevirostris*, *S. japonicus* and *S. megalops*), two resurrected species (*S. griffini* and *S. montalbani*), 8 new species (*S. albifrons*, *S. chloroculus*, *S. crassispinus*, *S. edmundsi*, *S. grahami*, *S. hemipinnis*, *S. nasutus* and *S. raoulensis*) and two species yet to be described, informally identified here as the *Squalus* sp. (Taiwan highfin) and the *Squalus* sp. (Lombok highfin).

DNA was sequenced from white muscle tissue samples stored at -80°C . DNA from most specimens was extracted using a Chelex dry release procedure (similar to Hajibabaei *et al.*, 2005), but New Zealand specimens were extracted using a phenol-chloroform-ethanol procedure (Taggart *et al.*, 1992). Approximately 655 base pairs (bp) were amplified from the 5' region of the COI gene from mitochondrial DNA using primers FishF2 and FishR2 and PCR procedures as in Ward *et al.* (2005), or primers LCO1490 and HCO2198 described by Folmer *et al.* (1994) and amplifications using an initial denaturation of 95°C for 60 s; 30 cycles of 95°C for 30 s, 45°C for 60 s, and 72°C for 60 s, followed by a final extension at 72°C for 10 min. Products were labeled using the BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Inc.) and sequenced bidirectionally using ABI 3730 or ABI 3100 capillary sequencers following manufacturer's instructions. Sequences were aligned using SeqScape v2.5 software (Applied Biosystems, Inc.).

GenBank numbers, where deposited, are given in Table 1. We sequenced all individuals except for a single *S. acanthias* sequence taken from GenBank. This was a specimen of *S. acanthias* taken off Iceland and whose entire mtDNA genome was sequenced (Rasmussen and Arnason, 1999, accession number Y18134); the COI portion of this sequence was added to our study.

Once sequences had been assembled for each specimen, sequence divergences were calculated using the Kimura two parameter (K2P) distance model (Kimura, 1980). Both neighbour-joining (NJ) and UPGMA trees of K2P distances were created to provide graphic representations of the patterning of divergence between species (Saitou and Nei, 1987). Bootstrapping was used to estimate standard errors of sequence divergence and reliability of tree branch points, as performed in MEGA3 (Kumar *et al.*, 2004) with 1000 replications. The latter values are given as percentages, and represent the percentage of times that interior branch is computed in the bootstrap resampling technique.

RESULTS

A total of 127 specimens from 14 species of *Squalus* (including those described in the previous papers of this issue) and two as-yet undescribed species was barcoded using the COI gene segment. The mean length of COI sequence across specimens was 645.5 bp, with a range of 573–654 bp. The average percentages of the four bases were thymine 33.8, cytosine 24.5, adenosine 25.1 and guanine 16.6.

The topology of the neighbour-joining K2P tree for all 127 sequences is given in Figs 1–4. All specimens of a particular species clustered together and away from clusters of other species. Note that one specimen of *S. grahami* (BW–A094) had been erroneously identified as a *S. mitsukurii* in Ward *et al.* (2005); subsequent morphological re-examination revealed the initial error in identification.

Figure 1 reveals three major *Squalus* clusters. Cluster A is a large complex of twelve species, with a bootstrap value of 95% (Fig. 2). It comprises one previously-recognised species (*S. japonicus*), two resurrected species (*S. griffini* and *S. montalbani*), 7 new species (*S. albifrons*, *S. chloroculus*, *S. crassispinus*, *S. edmundsi*, *S. grahami*, *S. hemipinnis* and *S. nasutus*), and two presumptive new species that require further study and description (informally known as *Squalus* sp. (Taiwan highfin) and *Squalus* sp. (Lombok highfin)). Cluster B comprises two previously recognised species (*S. brevirostris* and *S. megalops*) and a new species (*S. raoulensis*), with a bootstrap value of 100% (Fig. 3). Cluster C comprises a single previously recognised species (*S. acanthias*), again with a bootstrap value of 100% (Fig. 4).

Cluster A comprises 12 species. Fifteen specimens of *S. griffini* (Fig. 2) from the north and south islands of New Zealand formed a subcluster with a bootstrap value of 85% and a mean divergence of $0.03\pm 0.02\%$. Six specimens of *S. grahami*, all taken off the New South Wales coast of Australia, formed a subcluster with a bootstrap value of 60% and zero divergence. These two species appeared to be quite closely related sister species, forming a cluster with a bootstrap value of 95%. Five individuals of *S. japonicus* were sequenced, all from Taiwan. Two haplotypes were observed, which differed in a single synonymous mutation and appeared to make the taxon paraphyletic. Average sequence divergence was $0.11\pm 0.10\%$. This species grouped with *S. nasutus* forming a joint cluster with 94% bootstrap support. Eight specimens of *S. nasutus* (6 from Indonesia and two from an unrecorded location, most likely Australia), formed a subcluster with 84% bootstrap support and a mean divergence of $0.18\pm 0.13\%$. Two specimens of *S. crassispinus*, from northwestern Australia, had identical sequences and the pair had a bootstrap value

of 100%. Nine specimens of *S. montalbani*, from the east and west coasts of Australia and from Indonesia, formed a subcluster with 76% bootstrap support and a mean divergence of $0.42 \pm 0.16\%$. Seven specimens of *S. chloroculus*, from the Great Australian Bight to the Tasman Sea, formed a subcluster with 95% bootstrap support and a mean divergence of $0.11 \pm 0.07\%$. Fourteen specimens of *S. edmundsi* (Fig. 2), from Western Australia and Indonesia, formed a cluster with 65% bootstrap support and a mean divergence of $0.29 \pm 0.13\%$. This species cluster was paired (at 82% bootstrap support) with the *S. hemipinnis* species cluster (Fig. 2). This latter cluster comprised 6 specimens, all from Bali, Indonesia, with 56% bootstrap support and a mean divergence of $0.19 \pm 0.10\%$. Finally, there is a cluster of three species, *Squalus albifrons* and two undescribed species, with a bootstrap support of 95%. Five specimens of *S. albifrons* were sequenced, all from New South Wales, Australia, which all had identical sequences forming a cluster with 81% bootstrap support. The two undescribed species comprised two specimens of a *Squalus* sp. (Taiwan highfin), with bootstrap support of 81% and a divergence of $0.19 \pm 0.18\%$, and a single specimen of a *Squalus* sp. (Lombok highfin).

Cluster B comprises 3 species. Five specimens of *Squalus megalops*, all taken from Bass Strait between Victoria and Tasmania (Australia), formed a subcluster with a bootstrap value of 60% and a mean divergence of $0.44 \pm 0.19\%$ (Fig. 3). Eight specimens of *S. brevirostris*, from southern Japan and Taiwan, formed a subcluster with a bootstrap value of 89% and a mean divergence of $0.09 \pm 0.06\%$. Three specimens of *S. raoulensis*, from Raoul Island off the north of New Zealand, formed a subcluster with a bootstrap value of 93% and zero divergence.

Cluster C comprises the 31 individuals of *Squalus acanthias*, a globally distributed species (Fig. 4). Ten of these were from the North Pacific (3 from Japanese waters, 7 from North America) and 21 were from much of the remainder of its distribution (4 from the United Kingdom – the Celtic Sea, 5 from the United States – the Gulf of Maine, one from Iceland, 5 from mid-Chile – Isla Mocha, one from off the north island of New Zealand, and 5 from the east coast of Tasmania). Specimens of *S. acanthias* had a mean sequence divergence of $0.47 \pm 0.16\%$. Two subclusters were evident, the first comprising the 10 north Pacific fish (bootstrap 60% and sequence divergence of $0.10 \pm 0.05\%$) and the other the 21 Atlantic/south Pacific fish (bootstrap 89% and sequence divergence of $0.14 \pm 0.05\%$). The inter-subcluster divergence was $0.76 \pm 0.31\%$. One north Pacific fish (BW–A2328) differed from all other *S. acanthias* in having a triplet GAC rather than GAT about one-third into the barcode region. The GAC triplet is found in about 97.5% of all the other *Squalus* specimens barcoded, with GAT in the residual 2.5%. Both triplets code for the same amino acid, aspartic acid.

Average sequence divergences within and between 15 species were $0.17 \pm 0.05\%$ and $4.35 \pm 0.23\%$ respectively. This calculation omits the *Squalus* sp. (Lombok highfin), for which thus far only one specimen has been barcoded.

Sequences were also clustered using a UPGMA approach (Figs 5–7), which assumes that the rate of nucleotide substitution is the same for all evolutionary lineages. This assumption is not made by the NJ approach, except that the NJ tree shown here (Fig. 1) is rooted at the midpoint of the longest route connecting two sequences. The UPGMA tree retains all the major features described above from the NJ tree. One minor difference is that in the UPGMA tree, the *S. japonicus* specimens formed a single subcluster and no longer appeared paraphyletic. Another difference is that *S. crassispinus* now appeared basal within Cluster A.

DISCUSSION

All COI sequences, DNA barcodes, were found to be specific for particular species of *Squalus*. There was no evidence for sharing of barcodes among species. However, the number of specimens barcoded per species is currently small, ranging from one to 31 (mean of 7.94), and undoubtedly new barcodes will be described for these species as sample sizes increase. Nevertheless, barcode variation within species is currently very limited, and likely to remain so, and all barcodes thus far cluster by species. Hence, barcoded specimens can be identified to species with a high degree of certainty.

The lack of barcode sharing suggests that these species of *Squalus* are reproductively isolated from one another and this, together with the high bootstrap values for the species groups, supports the taxonomic revisions described in the earlier papers of this issue.

Barcode analyses of some of these species, prior to these taxonomic revisions, were outlined in Figure 6 of Ward *et al.* (2005). In this earlier paper, two clusters were labeled as *S. mitsukurii* – these are now known to be the resurrected species *S. montalbani* and the new species *S. chloroculus*. Further, one misplaced *S. mitsukurii* in Ward *et al.* (2005) was subsequently carefully reexamined morphologically and found to be *S. grahami* – consistent with its barcode identification.

The two subclusters in *S. acanthias* (north Pacific versus Atlantic and south Pacific) could suggest two cryptic species. In fact, the north Pacific form of *S. acanthias* was, pre-1960, given a different specific epithet, *S. suckleyi* (see Jensen, 1966). Hauser (in press) points out that while the COI data show reciprocal monophyly consistent with distinct species status, some north Pacific specimens analysed in his laboratory for the mitochondrial D-loop region fell into the north Atlantic/south Pacific cluster.

Further work is needed to resolve this issue, which should include the analysis of further specimens and perhaps nuclear DNA regions.

The average COI sequence divergence between *Squalus* species in this study, 4.35%, was about 25 times that within species, 0.17%. These values are lower than the average distances between species within genera (9.93%) and within species (0.39%) recorded in an examination of 207 species of elasmobranchs and teleosts (Ward *et al.*, 2005), but the within-genus divergence is very similar to a value of 3.6% found among 12 species of the skate genus *Bathyraja* (Spies *et al.*, 2006). This low degree of variation is consistent with the reduced levels of molecular evolution detected within cartilaginous fishes (Martin and Palumbi, 1993). However, some teleosts show lower congeneric divergence, for example tunas of the genus *Thunnus* (1.11%, Ward *et al.*, 2005). *Thunnus* species may have radiated more recently than these *Squalus* species.

The extremely high, often complete, COI sequence identity between *S. acanthias* from the North Atlantic (northeast and northwest), southeast Pacific (Chile), and southwest Pacific (Tasmania, New Zealand) suggests that these widely-divergent populations are in fact linked by present or recent gene flow, presumably through stepping-stone population links. In the western north Atlantic, this species undergoes seasonal migrations along the coast, from the Gulf of Maine and Canadian waters in the summer to southern New England and North Carolina in the winter, and in the east Atlantic, from Britain's northwest in summer to Norway in the winter (Jensen, 1966; McCauley *et al.*, 2004). While *S. acanthias* is more abundant in temperate regions, its distribution appears to extend throughout equatorial regions so stepping-stone gene flow is not unreasonable. Many marine fish – but not sharks – have pelagic larval stages that can assist dispersal. *Squalus acanthias* is viviparous, with yolk-sac dependency, and has 1 to 32 young per litter (Compagno *et al.*, 2005), and dispersal is likely to be mediated largely by adult movements. Northern Pacific Ocean *S. acanthias* have been recorded as making extensive migrations, from British Columbia to Japan (McFarlane and King, 2003), so the genetic homogeneity observed between Japan and the North American Pacific coast is entirely expected.

We wish to emphasise that barcoding is essentially a tool for specimen identification rather than phylogenetic reconstruction, and can also reveal likely new species. Its value in specimen identification became evident during the course of this work. The barcodes of several specimens were inconsistent with their original identifications, and subsequent morphological re-examination of those voucher specimens revealed their true identity – in every case consistent with the species attributed by the barcode. Barcoding, at least within this genus, gives higher taxonomic rigour than that afforded by non-expert taxonomists. Finally, within this paper we have described

related sequences as forming clusters, but we do not wish to imply that the trees shown necessarily represent the true evolutionary history of this group. Robust phylogenetic reconstructions need data from more than one gene region, and preferably from both mitochondrial and nuclear genes. Hence the relationships and species groups suggested here need to be confirmed (or refuted) with additional molecular data.

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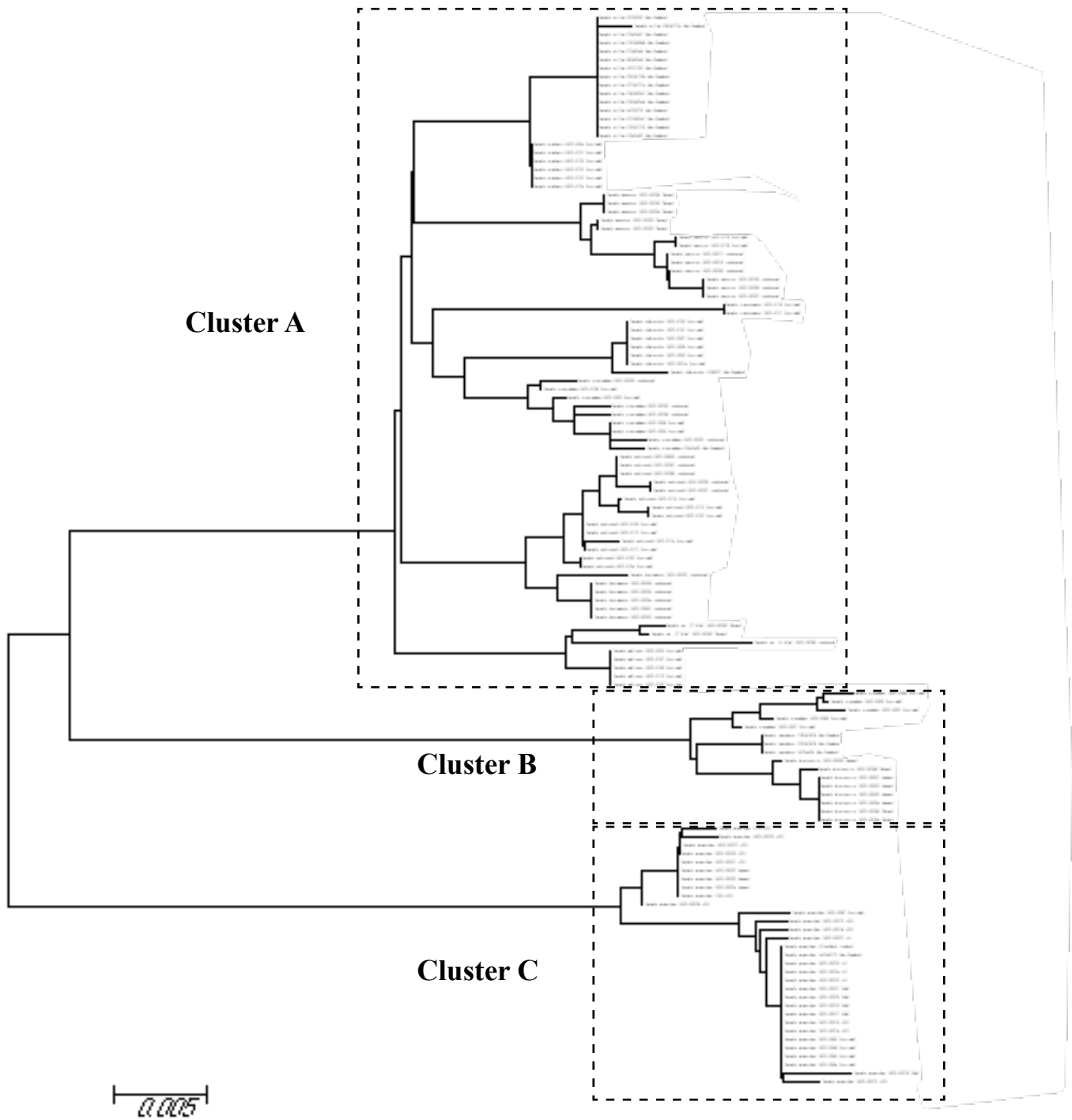


Figure 1. K2P distance neighbour joining tree for the 16 species of *Squalus* showing the three major clusters of species referred to in text and Figs 2–4. K2P distance bar given.

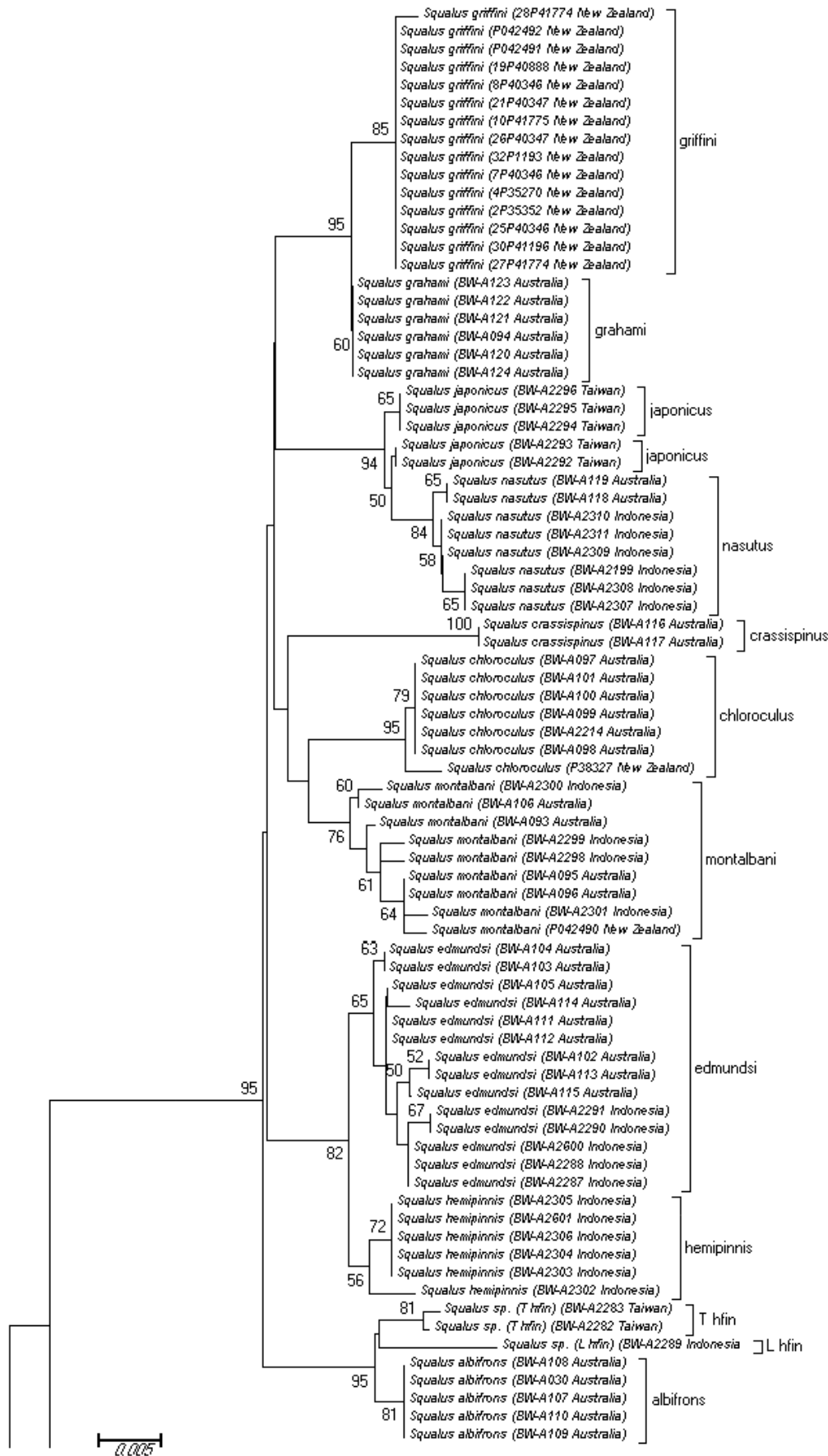


Figure 2. K2P distance neighbour joining tree for *Squalus* sequences in Cluster A. In this and figs 3–7, species, sample designation and country of origin are shown. T fin = Taiwan highfin, L hfin = Lombok highfin. Bootstrap values $\geq 50\%$ shown. K2P distance bar given.

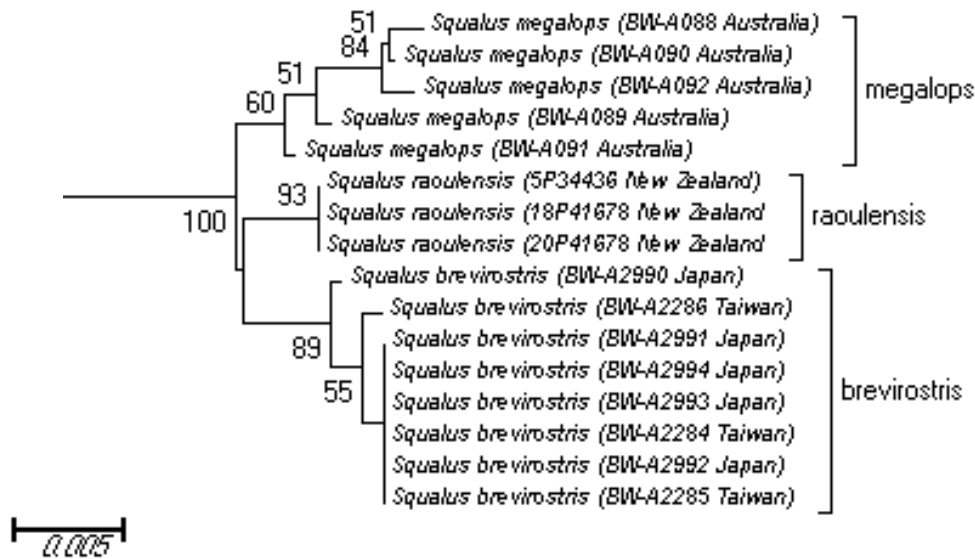


Figure 3. K2P distance neighbour joining tree for *Squalus* sequences in Cluster B. Bootstrap values $\geq 50\%$ shown. K2P distance bar given.



Figure 4. K2P distance neighbour joining tree for *Squalus* sequences in Cluster C. Bootstrap values $\geq 50\%$ shown. K2P distance bar given.

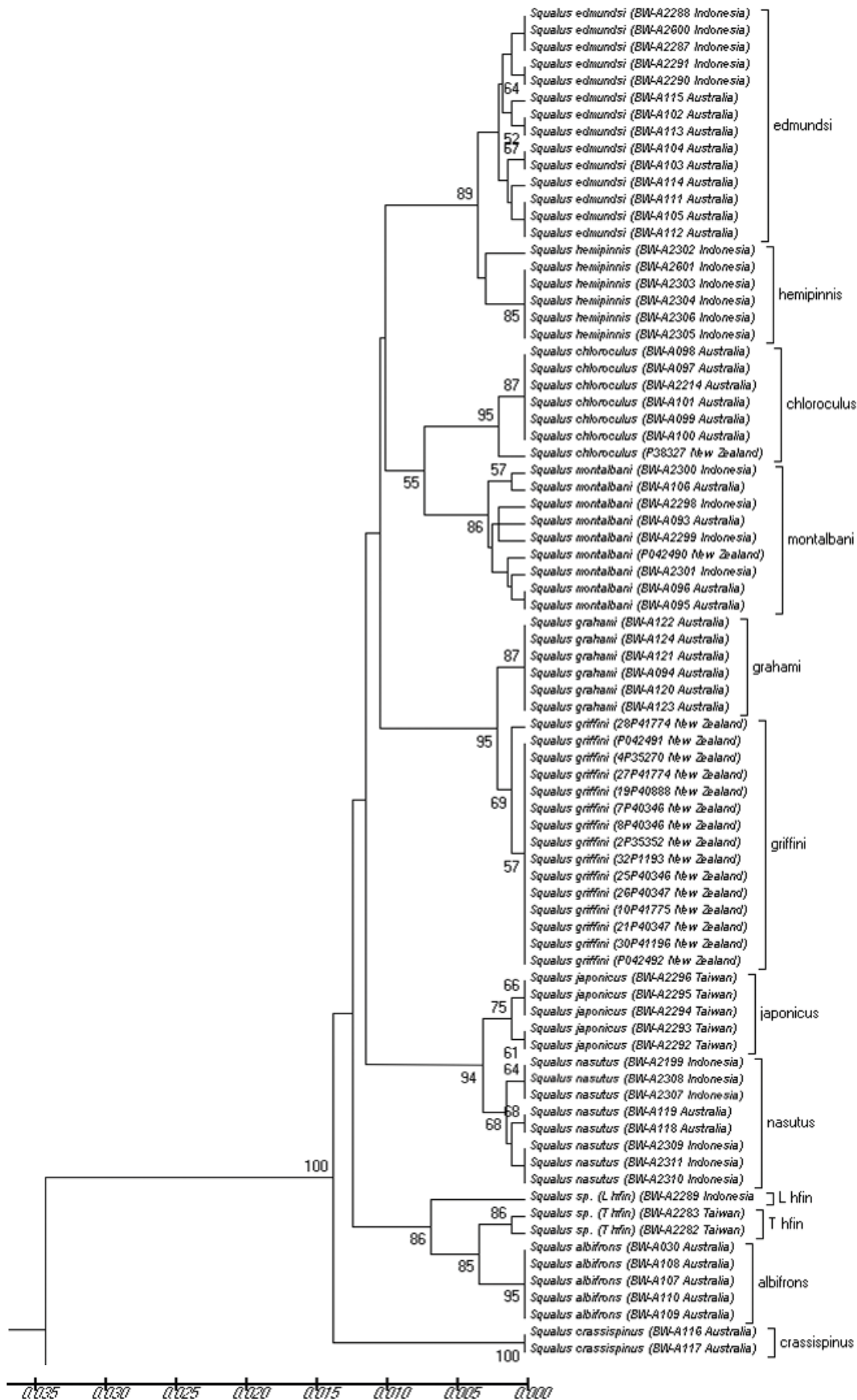


Figure 5. K2P distance UPGMA tree for *Squalus* sequences in Cluster A. T hfin = Taiwan highfin, L hfin = Lombok highfin. Bootstrap values $\geq 50\%$ shown. K2P distance axis given.

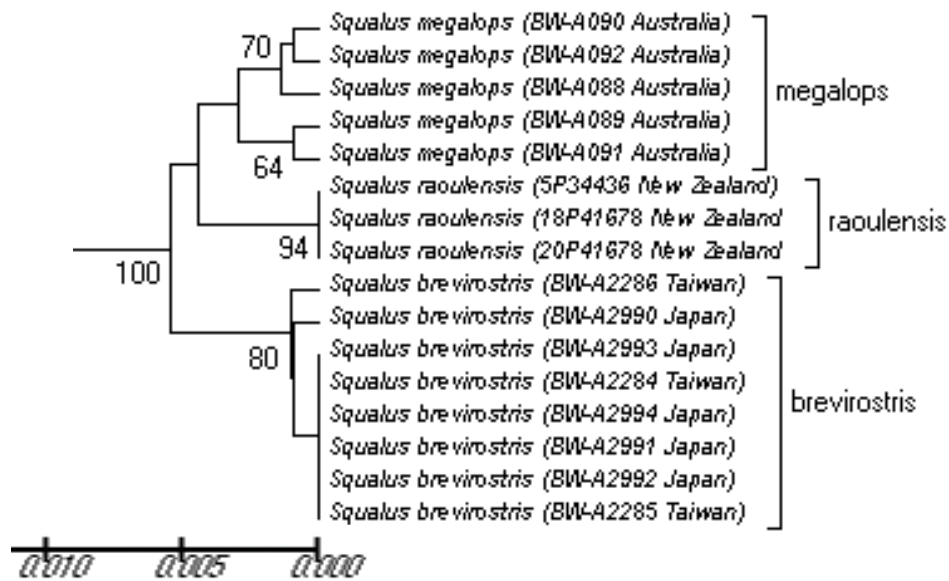


Figure 6. K2P distance UPGMA tree for *Squalus* sequences in Cluster B. Bootstrap values $\geq 50\%$ shown. K2P distance axis given.

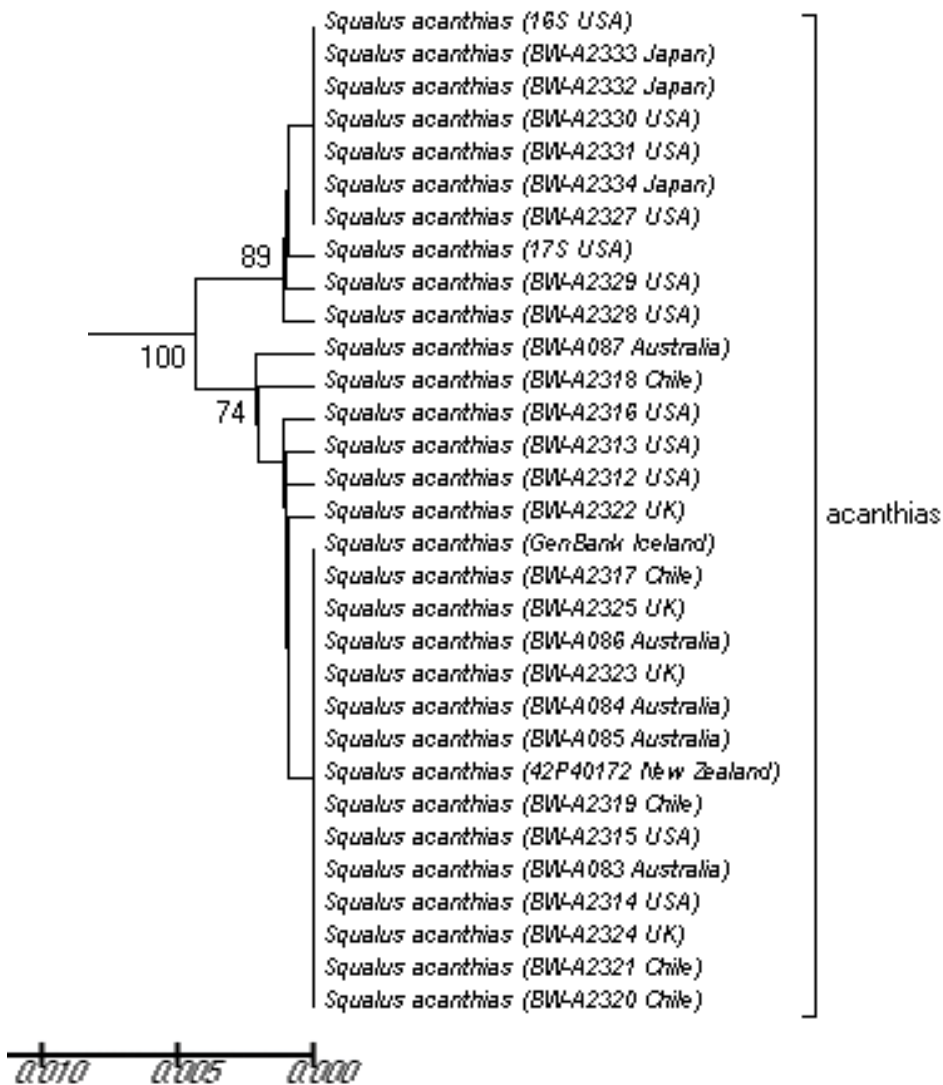


Figure 7. K2P distance UPGMA tree for *Squalus* sequences in Cluster C. Bootstrap values $\geq 50\%$ shown. K2P distance axis given.

Table 1. Summary details of the 127 specimens of *Squalus* sequenced for the barcode region of mtDNA COI. CSIRO = Australian National Fish Collection, CSIRO, Hobart, Australia; KAUM = Kagoshima University Museum, Kagoshima, Japan; MLML = Moss Landing Marine Laboratory, California, USA; MZB = Museum Zoologicum Bogoriense, Jakarta, Indonesia; NMNZ = National Fish Collection at the Museum of New Zealand, Te Papa Wellington, New Zealand; UF = University of Florida, Florida, USA.

Species	Sample ID number	GenBank No.	Voucher No.	Voucher location	Collection site
<i>S. acanthias</i>	16 S	–	not retained	–	USA, Washington coast
<i>S. acanthias</i>	17 S	–	not retained	–	USA, Washington coast
<i>S. acanthias</i>	BW–A2327	–	not retained	–	USA, Puget Sound
<i>S. acanthias</i>	BW–A2328	–	not retained	–	USA, Puget Sound
<i>S. acanthias</i>	BW–A2329	–	not retained	–	USA, Puget Sound
<i>S. acanthias</i>	BW–A2330	–	not retained	–	USA, Puget Sound
<i>S. acanthias</i>	BW–A2331	–	not retained	–	USA, Puget Sound
<i>S. acanthias</i>	BW–A2332	–	not retained	–	Japan, off Hokkaido Island
<i>S. acanthias</i>	BW–A2333	–	not retained	–	Japan, off Hokkaido Island
<i>S. acanthias</i>	BW–A2334	–	not retained	–	Japan, off Hokkaido Island
<i>S. acanthias</i>	42P40172	–	NMNZ P 40172	Wellington, NZ	New Zealand, North Island
<i>S. acanthias</i>	BW–A083	DQ108279	not retained	–	Australia, Tasmania
<i>S. acanthias</i>	BW–A084	DQ108280	not retained	–	Australia, Tasmania
<i>S. acanthias</i>	BW–A085	DQ108281	not retained	–	Australia, Tasmania
<i>S. acanthias</i>	BW–A086	DQ108282	not retained	–	Australia, Tasmania
<i>S. acanthias</i>	BW–A087	DQ108267	CSIRO H 4876–01	CSIRO, Hobart	Australia, Tasmania
<i>S. acanthias</i>	BW–A2312	–	not retained	–	USA, Gulf of Maine
<i>S. acanthias</i>	BW–A2313	–	not retained	–	USA, Gulf of Maine
<i>S. acanthias</i>	BW–A2314	–	not retained	–	USA, Gulf of Maine
<i>S. acanthias</i>	BW–A2315	–	not retained	–	USA, Gulf of Maine
<i>S. acanthias</i>	BW–A2316	–	not retained	–	USA, Gulf of Maine
<i>S. acanthias</i>	BW–A2317	–	not retained	–	Chile, Isla Mocha
<i>S. acanthias</i>	BW–A2318	–	not retained	–	Chile, Isla Mocha
<i>S. acanthias</i>	BW–A2319	–	not retained	–	Chile, Isla Mocha
<i>S. acanthias</i>	BW–A2320	–	not retained	–	Chile, Isla Mocha
<i>S. acanthias</i>	BW–A2321	–	not retained	–	Chile, Isla Mocha
<i>S. acanthias</i>	BW–A2322	–	not retained	–	UK, Celtic Sea
<i>S. acanthias</i>	BW–A2323	–	not retained	–	UK, Celtic Sea
<i>S. acanthias</i>	BW–A2324	–	not retained	–	UK, Celtic Sea
<i>S. acanthias</i>	BW–A2325	–	not retained	–	UK, Celtic Sea
<i>S. acanthias</i>	GenBank	Y18134	–	–	Iceland, Faxaflói
<i>S. albifrons</i>	BW–A030	–	CSIRO H 3589–01	CSIRO, Hobart	Australia, New South Wales
<i>S. albifrons</i>	BW–A107	DQ108254	CSIRO H 4627–01	CSIRO, Hobart	Australia, New South Wales
<i>S. albifrons</i>	BW–A108	DQ108255	CSIRO H 4704–01	CSIRO, Hobart	Australia, New South Wales
<i>S. albifrons</i>	BW–A109	DQ108256	CSIRO H 4704–02	CSIRO, Hobart	Australia, New South Wales
<i>S. albifrons</i>	BW–A110	DQ108257	CSIRO H 4705–01	CSIRO, Hobart	Australia, New South Wales
<i>S. brevirostris</i>	BW–A2284	–	CSIRO H 6293–29	CSIRO, Hobart	Taiwan
<i>S. brevirostris</i>	BW–A2285	–	CSIRO H 6293–30	CSIRO, Hobart	Taiwan
<i>S. brevirostris</i>	BW–A2286	–	CSIRO H 6293–31	CSIRO, Hobart	Taiwan
<i>S. brevirostris</i>	BW–A2990	–	KAUM I 184	KAUM, Kagoshima	Japan, East China Sea

Table 1. cont'd.

Species	Sample ID number	GenBank No	Voucher No	Voucher location	Collection site
<i>S. brevisrostris</i>	BW-A2991	–	KAUM I 185	KAUM, Kagoshima	Japan, East China Sea
<i>S. brevisrostris</i>	BW-A2992	–	KAUM I 186	KAUM, Kagoshima	Japan, East China Sea
<i>S. brevisrostris</i>	BW-A2993	–	KAUM I 187	KAUM, Kagoshima	Japan, East China Sea
<i>S. brevisrostris</i>	BW-A2994	–	KAUM I 377	KAUM, Kagoshima	Japan, East China Sea
<i>S. chloroculus</i>	BW-A100	DQ108263	not retained	–	Australia, South Australia
<i>S. chloroculus</i>	BW-A101	DQ108264	CSIRO H 4775-01	CSIRO, Hobart	Australia, Victoria
<i>S. chloroculus</i>	BW-A2214	–	CSIRO H 5941-01	CSIRO, Hobart	Australia, Tasmania
<i>S. chloroculus</i>	BW-A097	DQ108260	not retained	–	Australia, South Australia
<i>S. chloroculus</i>	BW-A098	DQ108261	not retained	–	Australia, South Australia
<i>S. chloroculus</i>	BW-A099	DQ108262	not retained	–	Australia, South Australia
<i>S. chloroculus</i>	P38327	–	NMNZ P 38327	Wellington, NZ	Tasman Sea, Norfolk Ridge
<i>S. crassispinus</i>	BW-A116	DQ108247	CSIRO H 4649-03	CSIRO, Hobart	Australia, Western Australia
<i>S. crassispinus</i>	BW-A117	DQ108248	CSIRO H 4649-04	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A102	DQ108265	CSIRO H 2608-16	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A103	DQ108266	CSIRO H 2605-05	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A104	DQ108251	CSIRO H 2605-06	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A105	DQ108252	CSIRO H 2605-07	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A111	DQ108258	CSIRO H 3969-15	CSIRO, Hobart	Australia, Western Australia
<i>S. edmundsi</i>	BW-A112	DQ108243	not retained	–	Australia, Western Australia
<i>S. edmundsi</i>	BW-A113	DQ108244	not retained	–	Australia, Western Australia
<i>S. edmundsi</i>	BW-A114	DQ108245	not retained	–	?
<i>S. edmundsi</i>	BW-A115	DQ108246	not retained	–	?
<i>S. edmundsi</i>	BW-A2287	–	CSIRO H 5857-09	CSIRO, Hobart	Indonesia, Bali
<i>S. edmundsi</i>	BW-A2288	–	CSIRO H 5857-10	CSIRO, Hobart	Indonesia, Bali
<i>S. edmundsi</i>	BW-A2290	–	CSIRO H 5875-05	CSIRO, Hobart	Indonesia, Lombok
<i>S. edmundsi</i>	BW-A2291	–	CSIRO H 5875-06	CSIRO, Hobart	Indonesia, Lombok
<i>S. edmundsi</i>	BW-A2600	–	not retained	–	Indonesia, Lombok
<i>S. grahami</i>	BW-A120	DQ108235	CSIRO H 4682-01	CSIRO, Hobart	Australia, New South Wales
<i>S. grahami</i>	BW-A121	DQ108236	CSIRO H 4682-02	CSIRO, Hobart	Australia, New South Wales
<i>S. grahami</i>	BW-A122	DQ108237	CSIRO H 4682-03	CSIRO, Hobart	Australia, New South Wales
<i>S. grahami</i>	BW-A123	DQ108238	CSIRO H 4682-04	CSIRO, Hobart	Australia, New South Wales
<i>S. grahami</i>	BW-A124	DQ108239	CSIRO H 4623-03	CSIRO, Hobart	Australia, New South Wales
<i>S. grahami</i>	BW-A94	DQ108273	CSIRO H 4623-02	CSIRO, Hobart	Australia, New South Wales
<i>S. griffini</i>	10P41775	–	NMNZ P 41775	Wellington, NZ	New Zealand, South Island
<i>S. griffini</i>	19P40888	–	NMNZ P 40888	Wellington, NZ	New Zealand, Raoul Island
<i>S. griffini</i>	21P40347	–	NMNZ P 40347, TS1029	Wellington, NZ	New Zealand, North Island
<i>S. griffini</i>	25P40346	–	NMNZ P 40346	Wellington, NZ	New Zealand, North Island
<i>S. griffini</i>	26P40347	–	NMNZ P 40346, TS1027	Wellington, NZ	New Zealand, North Island
<i>S. griffini</i>	27P41774	–	NMNZ P 41774, 765TL	Wellington, NZ	New Zealand, South Island

Table 1. cont'd.

Species	Sample ID number	GenBank No	Voucher No	Voucher location	Collection site
<i>S. griffini</i>	28P41774	–	NMNZ P 41774, TL690	Wellington, NZ	New Zealand, South Island
<i>S. griffini</i>	2P35352	–	NMNZ P 35352	Wellington, NZ	New Zealand, Kermadec Ridge
<i>S. griffini</i>	30P41196	–	NMNZ P 41196	Wellington, NZ	New Zealand, Chatham Rise
<i>S. griffini</i>	32P1193	–	NMNZ P 41993	Wellington, NZ	New Zealand, Chatham Rise
<i>S. griffini</i>	4P35270	–	NMNZ P 35270	Wellington, NZ	New Zealand, Chatham Rise
<i>S. griffini</i>	7P40346	–	NMNZ P 40346, 826TL	Wellington, NZ	New Zealand, North Island
<i>S. griffini</i>	8P4034	–	NMNZ P 40346, 807TL	Wellington, NZ	New Zealand, North Island
<i>S. griffini</i>	P042491	–	NMNZ P 42491, TS1732	Wellington, NZ	New Zealand, Challenger Plateau
<i>S. griffini</i>	P042492	–	NMNZ P 042492, TS1733	Wellington, NZ	New Zealand, Challenger Plateau
<i>S. hemipinnis</i>	BW–A2302	–	CSIRO H 5631–02	CSIRO, Hobart	Indonesia, Bali
<i>S. hemipinnis</i>	BW–A2303	–	CSIRO H 5631–01	CSIRO, Hobart	Indonesia, Bali
<i>S. hemipinnis</i>	BW–A2304	–	CSIRO H 5631–05	CSIRO, Hobart	Indonesia, Bali
<i>S. hemipinnis</i>	BW–A2305	–	CSIRO H 5631–03	CSIRO, Hobart	Indonesia, Bali
<i>S. hemipinnis</i>	BW–A2306	–	CSIRO H 5631–04	CSIRO, Hobart	Indonesia, Bali
<i>S. hemipinnis</i>	BW–A2601	–	not retained	–	Indonesia, Lombok
<i>S. japonicus</i>	BW–A2292	–	CSIRO H 6294–26	CSIRO, Hobart	Taiwan
<i>S. japonicus</i>	BW–A2293	–	CSIRO H 6294–27	CSIRO, Hobart	Taiwan
<i>S. japonicus</i>	BW–A2294	–	CSIRO H 6294–31	CSIRO, Hobart	Taiwan
<i>S. japonicus</i>	BW–A2295	–	UF 148938	UF, Florida	Taiwan
<i>S. japonicus</i>	BW–A2296	–	TAI–119	MLML, California	Taiwan
<i>S. megalops</i>	BW–A088	DQ108268	not retained	–	Australia, Bass Strait
<i>S. megalops</i>	BW–A089	–	not retained	–	Australia, Bass Strait
<i>S. megalops</i>	BW–A090	DQ108269	not retained	–	Australia, Bass Strait
<i>S. megalops</i>	BW–A091	DQ108270	not retained	–	Australia, Bass Strait
<i>S. megalops</i>	BW–A092	DQ108271	CSIRO H 3762–01	CSIRO, Hobart	Australia, Bass Strait
<i>S. montalbani</i>	BW–A106	DQ108253	CSIRO H 2606–05	CSIRO, Hobart	Australia, Western Australia
<i>S. montalbani</i>	BW–A2298	–	CSIRO H 5857–17	CSIRO, Hobart	Indonesia, Bali
<i>S. montalbani</i>	BW–A2299	–	CSIRO H 5857–18	CSIRO, Hobart	Indonesia, Bali
<i>S. montalbani</i>	BW–A2300	–	CSIRO H 5857–06	CSIRO, Hobart	Indonesia, Java
<i>S. montalbani</i>	BW–A2301	–	MZB 15022	MZB, Jakarta	Indonesia, Java
<i>S. montalbani</i>	BW–A093	DQ108272	CSIRO H 4623–01	CSIRO, Hobart	Australia, New South Wales
<i>S. montalbani</i>	BW–A095	DQ108274	CSIRO H 4623–04	CSIRO, Hobart	Australia, New South Wales
<i>S. montalbani</i>	BW–A096	DQ108259	CSIRO H 4623–05	CSIRO, Hobart	Australia, New South Wales
<i>S. montalbani</i>	P042490	–	NMNZ P 42490, TS1731	Wellington, NZ	New Zealand, Challenger Plateau
<i>S. nasutus</i>	BW–A118	DQ108249	not retained	–	Australia ?
<i>S. nasutus</i>	BW–A119	DQ108250	not retained	–	Australia ?
<i>S. nasutus</i>	BW–A2199	–	not retained	–	Indonesia, Lombok

Table 1. cont'd.

Species	Sample ID number	GenBank No	Voucher No	Voucher location	Collection site
<i>S. nasutus</i>	BW-A2307	–	MZB 15008	MZB, Jakarta	Indonesia, Bali
<i>S. nasutus</i>	BW-A2308	–	MZB 15009	MZB, Jakarta	Indonesia, Bali
<i>S. nasutus</i>	BW-A2309	–	CSIRO H 5860–01	CSIRO, Hobart	Indonesia, Java
<i>S. nasutus</i>	BW-A2310	–	CSIRO H 5680–03	CSIRO, Hobart	Indonesia, Java
<i>S. nasutus</i>	BW-A2311	–	CSIRO H 5680–02	CSIRO, Hobart	Indonesia, Java
<i>S. raoulensis</i>	18P41678	–	NMNZ P 41678	Wellington, NZ	New Zealand, Raoul Island
<i>S. raoulensis</i>	20P41678	–	NMNZ P 42572	Wellington, NZ	New Zealand, Raoul Island
<i>S. raoulensis</i>	5P34436	–	NMNZ P 34436	Wellington, NZ	New Zealand, Raoul Island
<i>S. sp.</i> (Lombok highfin)	BW-A2289	–	CSIRO H 5788–06	CSIRO, Hobart	Indonesia, Lombok
<i>S. sp.</i> (Taiwan highfin)	BW-A2282	–	TAI-001	Taiwan?	Taiwan
<i>S. sp.</i> (Taiwan highfin)	BW-A2283	–	CSIRO H 6292–10	CSIRO, Hobart	Taiwan

