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Resurrection and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae)

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Abstract

A taxonomic re-evaluation of the status of the North Pacific *Squalus suckleyi* (Girard, 1854) combining the use of meristic, morphological and molecular data reveal this species to be clearly distinct from the widespread *Squalus acanthias* (Linneaus, 1758). Differences in the external morphology between *S. acanthias* and *S. suckleyi* are subtle and are likely to be masked by intraspecific variation within individuals. However, we found *S. suckleyi* to differ from *S. acanthias* based on the following morphological and meristic characteristics: a short, broadly-rounded to acute snout; first dorsal-fin midpoint more posterior to pectoral-fin insertion; pelvic-fin origin closer to second dorsal fin than first dorsal fin; total vertebral counts average 99 (97–106). Molecular analysis of approximately 650 bp of the CO1 mitochondrial gene (DNA barcode region) showed separation of *S. suckleyi* and *S. acanthias* into two distinct genetic clades with 98% bootstrap support. Within species genetic diversities were 0.109±0.036% and 0.176±0.041% for *S. suckleyi* and *S. acanthias* respectively; between species diversity was 5– 6 fold greater at 0.765±0.307%. *Squalus suckleyi* is thus resurrected and a neotype for this endemic North Pacific *Squalus* species is designated.

Key words: Squalidae, *Squalus suckleyi*, morphometrics, meristics, DNA barcode, neotype, endemic

Introduction

The family Squalidae (Chondrichthyes: Squaliformes) is one of the more taxonomically problematic shark groups. The family includes two currently recognized genera, *Cirrhigaleus* with three species and *Squalus* with 24 species subdivided among three well define species subgroups as detailed in Ward *et al*. (2007) (Table 1). These subgroups include the *Squalus acanthias* group (Group A of Bigelow & Schroeder, 1948), with one species generally recognized, *Squalus acanthias* Linnaeus, 1758, but with numerous synonyms. Regional subspecies have been proposed within this subgroup for the North Atlantic, North Pacific, Black Sea, and the west coast of southern Africa. The *Squalus mitsukurii* group (Group B of Bigelow & Schroeder, 1948) was formerly termed the *blainville-fernandinus* group, *S. fernandinus* group, or *S. blainville* group, but changed due to identification problems with *S. blainville* (Risso, 1827) and the synonym of *S. fernandinus* Molina, 1782 with *S. acanthias*. This group includes at least 15 species including the nominal *S. blainville sensu* Chen *et al*. (1979) from the western North Pacific. The *Squalus megalops* group (Group C of Bigelow & Schroeder, 1948) also termed the *brevirostris-cubensis* group, with *S. megalops* (Macleay, 1881) possibly representing a species complex, *S. cubensis* Howell Rivero, 1936 from the North Atlantic, *S. acutipinnis* Regan, 1908 from

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southern Africa, *S. crassispinus* Last, Edmunds & Yearsley, 2007a from Australia, *S. brevirostris* Tanaka, 1917 from Japan, a Papua-New Guinea dogfish close to *S. crassispinus* that may represent yet another undescribed species, and an undescribed giant dogfish from Mauritius, dubbed "Frankenspine" and known from a single stuffed specimen in the Natural History Museum, London. Recent DNA barcoding of 16 *Squalus* species supports the three major subdivisions within the genus (Ward *et al*., 2007).

TABLE 1. Nominal *Squalus* species within each subgroup of genus.

Squalus acanthias subgroup (Cluster C of Ward *et al*., 2007)	
Squalus acanthias	Linnaeus, 1758
Squalus suckleyi	(Girard, 1854)
Squalus mitsukurii subgroup (Cluster A of Ward *et al*., 2007)	
Squalus albifrons	Last, White, & Stevens, 2007
Squalus altipinnis	Last, White, & Stevens, 2007
Squalus blainvillei	(Risso, 1826)
Squalus chloroculus	Last, White, & Motomura, 2007
Squalus crassispinus	Last, Edmunds, & Yearsley, 2007
Squalus edmundsi	White, Last, & Stevens, 2007
Squalus grahami	White, Last, & Stevens, 2007
Squalus griffini	Phillipps, 1931
Squalus hemipinnis	White, Last, & Yearsley, 2007
Squalus japonicus	Ishikawa, 1908
Squalus melanurus	Fourmanoir & Rivaton, 1979
Squalus mitsukurii	Jordan & Synder, in Jordan & Fowler, 1903
Squalus montalbani	Whitley, 1931
Squalus nasutus	Last, Marshall, & White, 2007
Squalus notocaudatus	Last, White, & Stevens, 2007
Squalus rancureli	Fourmanoir & Rivaton, 1979
Squalus megalops subgroup (Cluster B of Ward *et al*., 2007)	
Squalus acutipinnis	Regan, 1908
Squalus brevirostris	Tanaka, 1912
Squalus bucephalus	Last, Seret, & Pogonoski, 2007
Squalus cubensis	Howell-Rivero, 1936
Squalus megalops	(Macleay, 1881)
Squalus raoulensis	Duffy & Last, 2007

The *Squalus acanthias* group has been problematic as to whether it is monospecific or contains more than one species. Myagkov & Kondyurin (1986) proposed that *S. acanthias* may comprise at least four subspecies; *S. acanthias acanthias* from the North Atlantic, *S. a. africana* from southern Africa, *S. a. ponticus* from the Black Sea, and *S. a*. subspecies from Australia and New Zealand. However, the descriptions provided by Myagkov & Kondyurin (1986) are brief, often based on embryos, and rely heavily on characteristics that are subject to allometric changes with growth. Compagno *et al*. (1991) synonymized the subspecies *S. a. africana* with *S. acanthias*, but the giant Black Sea *S. a. ponticus* is considered a valid subspecies of *S. acanthias* (Eschmeyer, 2008). *Squalus acanthias africana* may be a valid species also, but would require a replacement name as it is a junior homonym of *S. africanus* Gmelin, 1789 (= *Poroderma africanum*, Scyliorhinidae).

Pacific Ocean species that are occasionally recognized within the *Squalus acanthias* subgroup and frequently appear in the literature include *S. fernandinus* Molina, 1782 from Chilean waters, *S. suckleyi* (Girard, 1854) from the North Pacific and *S. tasmanienesis* Howell Rivero, 1936 from southeastern Australia. The Chilean *S. fernandinus* is generally considered a junior synonym of *S. acanthias* (Garrick, 1960; Compagno, 1984; Eschmeyer, 2008), and a recent taxonomic reevaluation of the status of *S. tasmaniensis* revealed it also to be conspecific with *S. acanthias* (White *et al*., 2007). However, the taxonomic status of the North Pacific *S. suckleyi* has remained somewhat enigmatic.

Squalus acanthias was originally described by Linnaeus (1758) from European waters ("Habitat in Oceano Europaeo") and is considered one of the widest ranging shark species with an anti-tropical distribution in the North and South Atlantic, and North and South Pacific oceans (Compagno, 1984). It is also known from the Mediterranean Sea and Black Sea (Compagno, 1984). The North Pacific *Squalus suckleyi* was described from several specimens, all measuring about 750 mm total length (TL), collected by Dr George Suckley, a naturalist with the United States Pacific Railroad Survey, from off Fort Steilacom, Puget Sound, formerly Washington Territory now Washington State, U.S.A. The number and sex of these specimens were not provided in the original description (Girard, 1854) that was brief and did not provide any details separating it from the North Atlantic *Squalus acanthias*. Furthermore, the original 1854 description did not mention whether any specimens upon which the original description was made had been retained as type specimens. Girard (1858) later provided a more detailed description of his new species, but again did not clarify its status relative to the North Atlantic *S. acanthias*. However, in his later description, Girard (1858) listed 15 specimens deposited at the United States National Museum (USNM catalogue numbers 994, 997, 998, & 999). Seven of the 15 specimens were collected in 1853 while the remaining eight were collected in 1855, a year after the original description. Of the seven specimens that could possibly represent potential type specimens six were listed as young and in fact are embryos (Jerry Finan, US National Museum, pers. comm.). The only specimen that may represent a type specimen is USNM 994. However, this specimen(s) appears to have been lost (J. Finan, pers. comm.), a conclusion reached by previous authors (Compagno, 1984; Eschmeyer, 2008).

Subsequent authors have cited the lower dorsal-fin spines, the position of the first dorsal-fin spine which is opposite or slightly posterior to the inner free rear tip of the pectoral fin as distinguishing characters separating it from the North Atlantic *S. acanthias* (Jordan & Evermann, 1896; Garman, 1913). Other authors (Starks, 1917; Walford, 1935; Schultz, 1936; Clemens & Wilby, 1946, 1961) tended to recognize both species as being separate or subspecies (Lindberg & Legeza, 1956, 1959), but in the 1950s most authors began to synonymize *S. suckleyi* as a junior synonym of *S. acanthias*. The 1960 addition of the American Fisheries Society list of common and scientific names synonymized these two species as *S. acanthias* (American Fisheries Society, 1960). This was no doubt influenced by the works of Bigelow & Schroeder (1948, 1957) who found the primary characters distinguishing both species to be variable and to exhibit considerable overlap. Thus, they considered both the North Atlantic and North Pacific populations to be the same species. This conclusion was further supported by Jones & Geen (1976) who conducted a taxonomic reevaluation of the North Atlantic and North Pacific populations and concluded that *S. acanthias* comprised one of several discontinuous populations. Interestingly, however, they found statistically significant differences between meristic and biochemical characteristics between North Atlantic and North Pacific forms.

Recently, Ward *et al*. (2007) used DNA barcoding to confirm the existence of 11 newly described *Squalus* species and to support the concept that barcoding can be useful in specimen identification in groups that are morphologically very similar and difficult to distinguish to species by non-experts. They examined 127 specimens from 14 described *Squalus* species and two as-yet undescribed species. Their findings confirmed three major subgroups within the genus *Squalus*. However, within the supposed monospecific *Squalus acanthias* group (Cluster C of Ward *et al*., 2007; Figs 1, 4, & 7) they found two distinct clusters within this subgroup. These two groups included the North Pacific, including samples from Japan and North America, and a cluster consisting of the remainder of its distribution throughout the Atlantic and South Pacific, from a variety of locations.

Here we reevaluate the status of, resurrect and redescribe, the endemic North Pacific *Squalus suckleyi* incorporating meristic, morphological and molecular data. A neotype for *S. suckleyi* is also designated.

Material and methods

Numerical characters were selected to enable morphological and meristic comparisons with the morphologically similar *Squalus acanthias*, which it has been previously synonomised with. Morphometric methodology follows Compagno (2001) and Last *et al.* (2007b). Detailed description and illustrations of the measurements taken are provided in Last *et al.* (2007b). Seven specimens of *S. suckleyi* were collected during research surveys in Puget Sound, Washington, in 2007, which is the type locality for this species (Girard, 1854). The newly designated neotype and six other recently collected specimens of *S. suckleyi* from the type locality for this species were all measured in full and expressed as percentages of total length (Table 2). For comparison, five specimens of *S. acanthias* the South-west Pacific were also measured in full and ranges and means for these measurements provided in Table 2. In the description, morphometric values for the neotype are given first followed in parentheses by the ranges for the other six measured specimens. Tooth row counts were taken *in situ* from the seven new specimens prior to preservation.

Specimens examined are deposited in the ichthyological collection of the California Academy of Sciences (CAS); their registration numbers are prefixed with this acronym.

Molecular methodology. A small piece of muscle tissue (<0.5g) was subsampled from each of the seven specimens and stored in 20% dimethylsulfoxide-saturated salt buffer (Seutin *et al.*, 1991) or 95% ethanol until extraction. DNA was extracted using a salting-out protocol adapted from Sunnucks & Hales (1996). Approximately 650 base pairs of the mitochondrial cytochrome oxidase I gene were amplified from each sample using the heavy strand primer (5′-TAAACTTCAGGGTGACCAAAAAATCA -3′) and the light strand primer (5′-GGTCAACAAATCATAAAGATATTGG -3′) designed by Folmer *et al.* (1994).

10 µL PCR reactions consisted of 0.1 U Biolase *Taq* DNA polymerase (Bioline; Randolph, Massachusetts), 1x *Taq* buffer, 1.0 µM of each primer, 200 µm each dNTP, and 2.0 mM $MgCl_2$. PCR amplification on a MyCycler (Bio-Rad; Hercules, California) consisted of an initial denaturation at 95˚C for 4 min, followed by 30 cycles of 1 min at 95˚C, 30 s at 40˚C, (Folmer *et al.* 1994) and 30 s at 72˚C, followed by a final extension at 72˚C for 20 min. Excess oligonucleotide primers were removed with exonuclease I and shrimp alkaline phosphatase (ExoSAP; USB Corp., Cleveland OH) by incubating at 37°C for 30 min followed by deactivation at 80°C for 60 min.

PCR products were sequenced on an ABI 3130XL automated DNA sequencer (Applied Biosystems, Foster City, California) at the Hawaii Institute of Marine Biology EPSCoR Sequencing Facility, aligned by eye, and edited using Sequencher v4.6 (Gene Codes Corporation, Ann Arbor MI).

The nucleotide sequence of the DNA barcode region (Hebert *et al.*, 2003) of the mitochondrial gene cytochrome c oxidase I (COI) was obtained for the seven specimens (including the neotype), and supplemented with sequences from 21 further specimens of *S. suckleyi* and 32 specimens of *S. acanthias* from throughout the remainder of its distribution. Methodology for most sequencing runs followed the methodology of Ward *et al.* (2005, 2007). GenBank numbers and Barcode of Life Database (BOLD) numbers are in Appendix I. Sequence divergences among pairs of sequences were estimated using the Kimura 2 parameter model (Kimura, 1980) and a neighbour-joining tree (1000 bootstraps) derived from these values. These calculations utilized the software package MEGA4 (Tamura *et al.*, 2007).

Comparative material examined in this study: *Squalus acanthias*. 18 specimens: CAS 11226, male 183 mm, Massachusetts Bay, Massachusetts, USA; CAS 11227, female 155 mm TL, Massachusetts Bay, Massachusetts, USA; CAS 11228, male 180 mm TL, Massachusetts Bay, Massachusetts, USA; SU–CAS 3990, male 155 mm TL, Massachusetts Bay, Massachusetts, USA; 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.

TABLE 2. Proportional dimensions as percentages of total length for the neotype (CAS 227267), and means and ranges for all 7 measured specimens of *Squalus suckleyi* and 5 specimens of *Squalus acanthias.* Means and ranges are also provided.

	Neotype	*S. suckleyi* (n = 7)			*S. acanthias* (n = 5)		
	CAS 227267	Mean	Min.	Max.	Mean	Min.	Max.
Total length (mm)	674	724	674	805	558.0	429	678
Precaudal length	80.6	79.6	78.7	81.8	78.5	77.7	79.1
Prenarial length	4.2	4.5	4.2	4.6	3.9	3.5	4.1
Prenarial length (direct)	5.0	5.1	4.7	5.1	4.6	4.2	5.0
Preoral length	9.1	9.1	8.6	9.5	9.1	8.5	9.8
Preorbital	6.4	6.7	6.3	7.0	6.1	5.6	6.5
Preorbital (direct)	7.7	7.7	7.2	7.8	7.0	6.8	7.2
Prespiracle length	11.4	11.8	10.3	12.2	–	–	–
Prespiracle length (direct)	11.9	12.1	11.2	12.4	11.3	10.8	12.0
Prebranchial length	18.0	17.9	15.7	18.2	18.1	17.6	19.2
Head length	23.0	22.0	21.1	23.0	21.4	20.7	22.4
Prepectoral length	22.3	22.1	20.5	22.8	21.6	20.7	22.9
Prepelvic length	51.5	51.9	49.9	54.2	50.1	48.7	50.8
Snout-vent length	54.9	54.9	54.3	58.0	51.7	50.6	52.4
Pre-first dorsal length	34.1	33.8	33.2	35.6	33.9	32.8	35.2
Pre-second dorsal length	64.5	62.1	59.5	64.6	60.2	58.8	61.0
Interdorsal space	23.6	22.4	19.0	23.6	20.4	19.8	21.2
Dorsal–caudal space	11.4	11.1	10.7	11.6	11.3	10.8	12.0
Pectoral–pelvic space	27.3	26.9	23.4	28.0	23.6	21.3	24.9
Eye length	3.6	3.8	3.2	3.9	3.7	3.4	3.9
Eye height	1.5	1.7	1.4	2.3	1.7	1.4	2.2
Interorbital space	7.0	7.0	6.6	7.5	7.4	6.8	8.5
Nostril width	1.2	1.1	1.0	1.2	1.2	1.2	1.3
Internarial space	4.2	3.9	3.4	4.2	3.6	3.3	4.0
Anterior nasal flap length	0.7	0.6	0.5	0.7	–	–	–
Spiracle length	1.5	1.4	1.0	1.8	1.1	0.9	1.4
Eye–spiracle space	2.2	1.5	1.0	2.2	–	–	–
Mouth length	0.9	1.2	0.7	1.7	–	–	–
Mouth width	6.2	6.4	5.2	6.8	7.5	7.0	8.7
Upper labial furrow length	2.2	2.2	2.0	2.5	2.2	1.5	2.6
Lower labial furrow length	2.1	1.4	1.1	2.1	–	–	–
First gill-slit height	1.9	1.9	1.7	2.0	1.6	1.4	1.9
Second gill-slit height	1.8	1.9	1.7	2.1	–	–	–
Third gill-slit height	1.9	1.9	1.7	2.0	–	–	–
Fourth gill-slit height	1.9	2.0	1.9	2.2	–	–	–
Fifth gill-slit height	2.1	2.2	2.0	2.6	2.0	1.7	2.4
Head height	6.5	6.5	5.9	7.2	9.0	8.4	9.6
Head width	11.0	11.2	9.8	11.8	11.3	10.2	12.3

continued next page

TABLE 2. (continued)

		S. suckleyi (n = 7)			*S. acanthias* (n = 5)		
	Neotype CAS 227267	Mean	Min.	Max.	Mean	Min.	Max.
Trunk height	9.9	10.8	8.3	12.0	9.8	8.8	10.3
Trunk width	10.5	11.1	9.2	12.4	9.6	8.2	11.4
Caudal peduncle height	2.2	2.3	2.1	2.5	2.5	2.3	2.7
Caudal peduncle width	2.4	2.6	2.0	3.0	2.6	2.2	2.9
Pectoral length	12.2	12.2	11.9	12.8	–	–	–
Pectoral anterior margin	12.9	15.8	12.9	17.0	14.9	13.6	16.2
Pectoral base	6.4	6.3	6.1	6.7	5.4	4.7	6.0
Pectoral height	11.3	11.8	10.3	12.7	10.4	9.2	11.0
Pectoral inner margin	6.5	6.5	5.6	7.4	6.3	4.4	7.3
Pectoral posterior margin	11.0	11.0	9.6	12.3	9.4	8.1	11.0
Pelvic length	11.7	11.6	10.6	12.1	10.4	10.0	11.3
Pelvic anterior margin	7.6	7.3	6.7	8.5	–	–	–
Pelvic base	5.6	5.2	4.9	6.4	–	–	–
Pelvic height	3.6	3.6	3.2	4.2	4.7	4.2	5.0
Pelvic posterior margin	6.5	6.3	5.4	6.5	–	–	–
Clasper outer length	6.4	5.8	5.1	6.4	5.9	5.6	6.2
Clasper inner length	11.4	11.0	9.9	11.4	10.9	10.7	11.1
Clasper base length	1.3	1.3	1.0	1.5	1.3	1.2	1.3
D1 length	11.6	12.0	11.4	13.3	12.8	12.4	13.1
D1 anterior margin	8.8	9.9	8.8	10.4	9.8	9.3	10.2
D1 base	6.2	7.0	6.2	7.9	7.4	7.0	7.8
D1 height	6.2	5.9	5.2	6.8	6.2	5.9	6.8
D1 inner margin	7.7	5.4	4.6	7.7	5.4	5.0	5.7
D1 posterior margin	5.2	6.8	5.2	7.5	7.2	6.5	8.4
D1 spine height	n.a.	n.a.	n.a.	n.a.	2.2	1.7	2.7
D2 length	11.1	11.2	9.5	12.7	12.8	12.3	13.3
D2 anterior margin	7.9	8.0	7.5	9.8	9.6	9.2	10.6
D2 base	5.9	6.5	4.8	7.1	7.9	7.5	8.4
D2 height	3.0	3.0	2.5	3.5	3.8	3.2	4.1
D2 inner margin	4.9	4.6	4.1	5.0	4.9	4.8	5.0
D2 posterior margin	5.6	4.9	4.4	5.6	5.3	4.7	5.7
D2 spine height	n.a.	n.a.	n.a.	n.a.	3.1	2.6	3.7
Dorsal caudal margin	19.4	19.9	19.4	21.1	20.6	20.0	21.9
Preventral caudal margin	10.4	10.9	10.4	11.8	10.7	10.6	10.9
Lower postventral caudal margin	4.6	4.3	3.8	4.8	4.1	3.2	4.6
Upper postventral caudal margin	14.2	14.9	14.2	15.9	14.8	14.3	15.1
Terminal caudal lobe	8.0	6.7	5.2	8.0	–	–	–
DPI	10.4	11.2	9.7	12.4	–	–	–
DPO	15.0	14.7	12.0	15.0	–	–	–
PDI	15.1	14.0	13.2	15.1	–	–	–
PDO	7.6	7.6	5.0	9.1	–	–	–

***Squalus suckleyi* (Girard, 1854)**
Spotted spiny dogfish
Fig. 1; Table 2

Spinax (Acanthias) suckleyi Girard, 1854: p. 196. "Specimens about twenty nine inches long." (Girard, 1854) from Fort Steilacomb, Puget Sound, Washington Territory, United States of America.
***Acanthias suckleyi*:** Suckley, 1860: p. 367.
***Acanthias sucklii*:** Girard, 1858: p. 368.
***Acanthias vulgaris*:** Bleeker, 1853: p. 21; Ishikawa & Matsuura, 1897: p. 61.
***Squalus acanthias*:** Jordan & Gilbert, 1881: p. 458; Jordan & Gilbert, 1883: p. 17; Schmidt, 1904: p. 287; Pavlenko, 1910: p. 11; Berg, 1911: p. 71; Soldatov & Lindberg, 1930: p. 16; Bigelow & Schroeder, 1934: p. 17, fig. 16; Roedel & Ripley, 1950: p. 27, 61, fig. 45; Herald & Ripley, 1951: 321–322; Roedel, 1953: p. 23, fig. 20; Okada, 1955: p. 21, fig.; Roedel, 1962: p. 22; Jensen, 1966: p. 527–554, fig. 1; Ueno, 1971: p. 69; Ketchen, 1972: 1717; Miller & Lea, 1972: pp. 34, 38, fig.; Hart, 1973: pp. 44–47, fig.; Ketchen, 1975: 43; Anderson *et al*., 1979: 257; Hubbs *et al*., 1979: p. 3; Castro, 1983: p. 55, fig.; Eschmeyer *et al.*, 1983: p. 23, pl. 2; Masuda *et al*., 1984: p. 9, pl. 10–G; Ketchen, 1986: p. 1–88, fig. 1; Amaoka *et al*., 1989: p. 256.; Orlov, 1998: tab. 2; Mecklenburg *et al*., 2002: p. 88, fig.; Nakabo, 2002: p. 155; Ebert, 2003: p. 63–66, fig.; Tok, 2004: tab. 2, p. 132; Compagno *et al*., 2005: p. 73, plate 3; Stevenson *et al*., 2007: 20
***Squalus mitsukurii*:** Tanaka, 1908: p. 236; Tanaka, 1917: pp. 471–474, pl. 130 (368, 369, 370); Jordan & Metz, 1913: p. 4, fig. 2.
Squalus suckleyi: Jordan & Hubbs, 1925: 105; Fang & Wang, 1932: p. 246; Walford, 1935: p. 42, fig. 40; Schultz, 1936: p. 131; Clemens & Wilby, 1946: p. 59, fig. 19; Mori, 1952: p. 22; Clemens & Wilby, 1961: p. 81, fig.22.
***Squalus sucklii*:** Gill, 1862: p. 499; Jordan & Starks, 1895: p. 789; Jordan & Evermann, 1896: p. 54; Jordan & Gilbert, 1899: p. 434; Evermann & Goldsborough, 1907: p. 228; Starks & Morris, 1907: p. 168; Garman, 1913: pp. 194–195; Halkett, 1913: p. 41; Starks, 1917: p. 152, fig. 62; Daniel, 1934: pp. 37, 154, fig. 147.
***Squalus wakiyae*:** Tanaka, 1918: p. 475.

Neotype. CAS 227267, adult male 674 mm TL, Hood Canal, Puget Sound, Washington, USA, 30 m depth, 47°22′ N, 123°05′ W, 55 m, 03 August 2007.

Other material. 11 specimens. CAS 227268, adult male 760 mm TL, CAS 227269, adult male 691 mm TL, CAS 227270, adult male 703 mm TL, CAS 227271, adult male 805 mm TL, CAS 227272, adult male 725 mm TL, Central/South Puget Sound, Washington, USA, 15 m depth, 47°22′ N, 122°24′ W, 110 m, 28 September 2007; CAS 227273, adult male 707 mm TL, North Puget Sound, Washington, USA, 2007; CAS 21424, male 380 mm TL, San Francisco Bay, California; CAS 25319, female 213 mm TL, Puget Sound, Washington State, USA; DAE 990624–01, male 360 mm TL, Monterey Bay, California, USA; DAE 990624–02, female 316 mm TL, Monterey Bay, California, USA; DAE 990624–03, female 332 mm TL, Monterey Bay, California, USA.

Diagnosis. A large-sized, slender bodied *Squalus* with the following combination of characters: body slender, trunk height 10.8 (8.3–12.0)% TL; snout rounded, somewhat blunted at apex, relatively short, prenarial length 1.4 (1.3–1.5) times mouth width, preoral length 2.0 (2.1) times prenarial length, 9.1 (8.6–9.5)% TL; eye moderate-sized, length 3.8 (3.2–3.9)% TL; anterior nasal flap simple, secondary lobe absent; dorsal fins small, raked; first dorsal originates just posterior to free-rear tip of pectoral fin, first dorsal-fin spine moderate, relatively narrow-based; pectoral fin lobe-like, not or weakly falcate; flank denticles broadly unicuspidate to weakly tricuspidate; adult maximum size at least 1300 mm TL.

Description. Body fusiform, slender, nape somewhat humped; deepest near first dorsal-fin spine, maximum trunk height equal to trunk width; head short 23.0 (21.1–23.0)% TL; dorsal–caudal space, 11.1 (10.7–11.6)% TL. Head somewhat broad, its width 1.0 (1.0–1.1) times trunk width; depressed forward of spiracles, becoming somewhat subtriangular towards pectoral-fin origin; length 3.8 (3.6–3.9) in pre-vent length; height 0.6 times width. Snout relatively short, rounded, somewhat blunted at apex; prenarial length 1.4 (1.3–1.5) times mouth width, prenarial length 1.2 (1.2–1.3) times eye length, 0.6 times interorbital space; prenarial length 2.0 (2.1–2.1) in preoral length.

Eye oval, moderate-sized, length 3.8 (4.1–4.4) in head, 2.3 (1.7–2.2) times its height; strongly notched posteriorly. Spiracle moderate-sized, broadly crescentic, with a shallow lobe-like fold on posterior margin, and about equidistant between snout tip and pectoral-fin origin, 0.5; greatest diameter nearly equidistant to eye-spiracle length. Gill slits directed slightly anterodorsally from bottom to top; first four near equal in size, fifth slightly longer, height of fifth slit 2.2 (2.0–2.6)% TL. Mouth almost transverse, upper jaw weakly concave, width 1.4 (1.4–1.6) in preoral length; upper labial furrows about 1.6 (1.2–1.7) times length of lower furrows; prominent postoral groove, subequal in length to upper labial furrows, extending posterolaterally from angle of jaws. Teeth oblique, bladelike, and 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; two series of functional teeth in upper jaw, three (sometimes two) series in lower jaw; teeth in upper jaw (range from left to right including median tooth if present) (13–15) – (0–1) – (12–14), total upper tooth counts range from 26–29; lower jaw (11–14) – (9–13), total lower tooth counts range from 20–27. Nostrils small, almost transverse; anterior nasal flap single lobed; lobe broadly triangular and somewhat flattened; internarial space 2.3 (2.3–2.5) in preoral length, 3.5 (3.4–3.5) times nostril length.

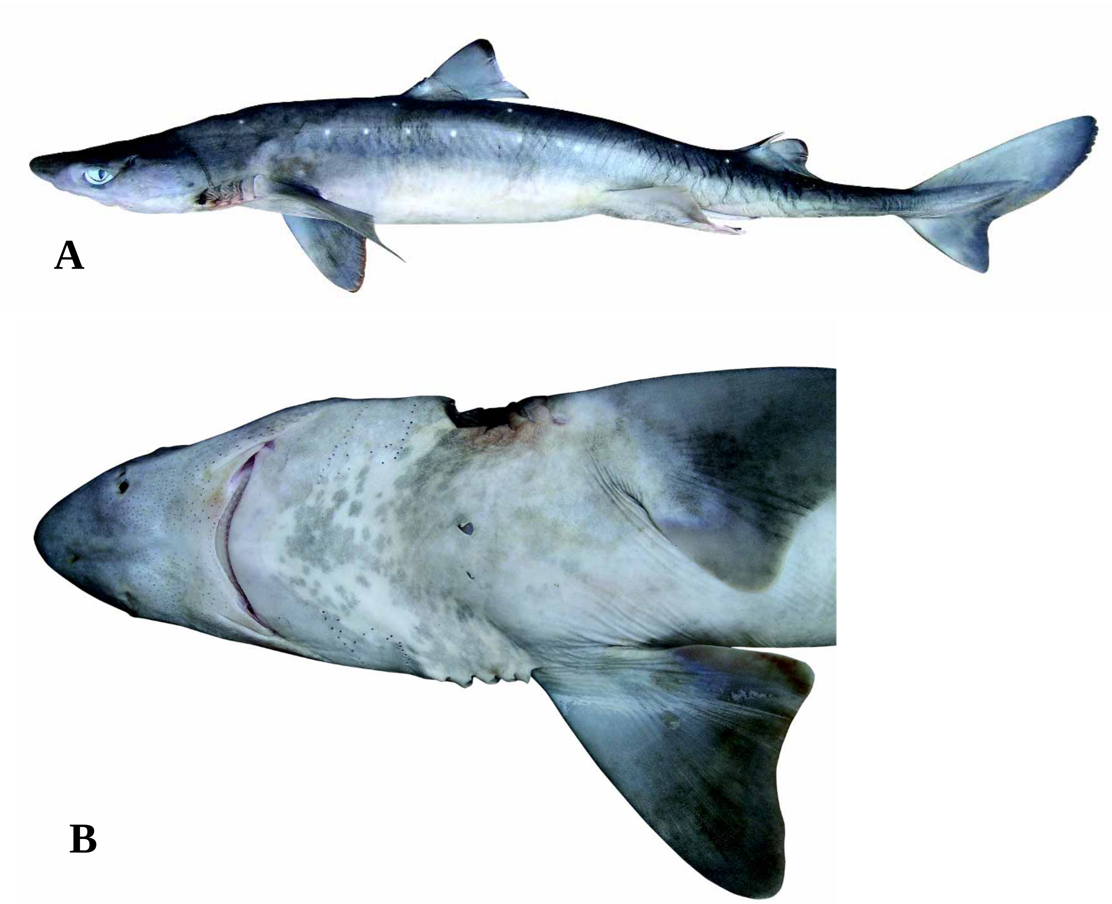

FIGURE 1. *Squalus suckleyi*, neotype (CAS 227267, adult male 674 mm TL). A, Lateral view; B, Ventral view of the head.

Dermal denticles on flank below first dorsal fin very small, loosely spaced and non-imbricate; crowns elevated, quadrate, broadly unicuspidate with pronounced median ridge; median ridge commencing 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; denticles mostly unicuspidate with some weakly tricuspidate.

First dorsal fin small, raked, broadly rounded apically; anterior margin relatively straight; upper posterior margin almost straight, not vertical, instead directed very slightly anterodorsally from bottom to top, very weakly concave near free rear tip; free rear tip very thick basally, short; inner margin of fin almost straight; origin posterior to free-rear tip of pectoral fins; first dorsal-fin midpoint pectoral-fin insertion closer to pectoral-fin origin than to pelvic-fin origin; fin-spine origin slightly posterior to pectoral-fin free rear tips; spine base relatively narrow, exposed anteriorly well below junction of spine and soft portion of fin; spine tapering slightly distally, anterior margin almost straight; spine shorter than exposed portion of second dorsal-fin spine; pre-first dorsal length 2.9 (2.8–3.0) times in TL; first dorsal-fin length 2.0 (2.0–2.2) times its height, 1.1 (1.0–1.2) times second dorsal-fin length; first dorsal-fin height 2.0 (2.0–2.1) times second dorsal-fin height.

Second dorsal fin small, strongly raked; anterior margin moderately convex, apex broadly rounded; posterior margin moderately concave; free rear tip moderately elongate, inner margin length 1.5 (1.4–1.6) times fin height; second dorsal-fin length 3.8 (3.7–3.8) times its height; exposed spine length 1.1 (1.0–1.2) in height of fin; fin-spine origin over free rear tip of pelvic fins; exposed second spine broad-based; spine robust, acutely pointed distally, curving slightly posteriorly, tapering rapidly just above point of exposure, spine tip not extending to level of insertion of fin; interdorsal space about equidistant in prepectoral length, 1.5 (1.5–1.8) in pre-first dorsal length; interdorsal ridge weak.

Pectoral fin moderate, anterior margin slightly greater than length, moderately convex; inner margin moderately convex, length 6.5 (5.6–7.4)% TL; apex broadly rounded, lobe-like, not or weakly falcate; posterior margin moderately concave, free rear tip broadly rounded; fin base very short, 2.5 (2.1–2.5) in length of anterior margin. Pelvic fins moderate-sized, anterior and posterior margins nearly straight, apex broadly rounded, free rear tip somewhat acute. Caudal peduncle very long, tapering slightly to caudal fin; subcircular in cross-section anteriorly, slightly depressed and broadly semicircular posteriorly; dorsal precaudal pit weakly developed, ventral pit absent; lateral keels well developed, originating below or slightly posterior to second dorsal-fin insertion, terminating just posterior to lower caudal-fin insertion; pelvic–caudal space 0.9 (0.9–1.1) in pectoral–pelvic space, 1.1 (1.0–1.2) in prepectoral length; dorsal–caudal space 2.0 (1.8–2.0) in interdorsal length. Caudal fin relatively short, dorsal margin nearly straight, apex broadly rounded; apex of lower lobe narrowly angular; dorsal caudal margin 1.4 (1.3–1.4) in head length; length of lower caudal lobe 1.8 (1.8–1.9) in upper lobe length. Spiral valve count range from non-voucher specimens: 12–13. Vertebral count range from non-voucher specimens: 97–106.

Genetics. The average length of the COI region sequenced was 650.4 bp, with lengths ranging from 593–652 bp (the large majority of samples were sequenced for all 652 bp of the DNA barcode region). The neighbour joining tree of K2P distances (Figure 2) clearly shows separation into two clades, one comprising *S. suckleyi* and one comprising *S. acanthias*, with 98% bootstrap support for the two clades. The *S. suckleyi* clade included all the North Pacific specimens, from Japan and from the west coast of Canada and the United States. The *S. acanthias* clade included all specimens from the North Atlantic (Iceland, the United Kingdom, and the east coast of the United States), the South Atlantic (Uruguay and Argentina) and the South Pacific (Chile, New Zealand and Australia). Within species genetic diversities were 0.109±0.036% and 0.176±0.041% for *S. suckleyi* and *S. acanthias* respectively. There was no evidence of spatial structuring within either clade, although the potential for structuring is limited given the low diversities. The most common haplotype in *S. acanthias*, the species with the higher within species diversity, is found in specimens from all localities, from Iceland to Tasmania. Between–species diversity was 5–6 fold greater at 0.765±0.307%. Within the 652 bp COI region, there were four fixed and therefore diagnostic nucleotide base substitutions between the species, all for third-base synonymous mutations. These were, *S. suckleyi* followed by *S. acanthias*, at positions 226 A–G, 406 G–A, 514 C–T and 628 G–A (all positions numbered within the 652 bp barcode region).

Coloration. Gray dorsally, with conspicuous white spots present on their flanks, becoming lighter ventrally; the fins adults and juveniles are without white edges or other prominent markings. Coloration is similar in neonates and younger juveniles except for white-edge along posterior margin of pectoral–fins, on apex and posterior margin of dorsal-fins, and along caudal–fin margins.

Distribution. Endemic to the North Pacific, from the Koreas and Japan, northward to Russia (Kamchatka, Sea of Okhotsk and Sakhalin), the Bering Sea and the Aleutian Islands, and eastwards in the Gulf of Alaska, British Columbia and Washington south to southern Baja California. In North America, *S. suckleyi* is extremely common off British Columbia and Washington, but decline in abundance off the Oregon and California coasts. It occurs in a wide depth range from very shallow waters in some areas down to depths of at least 1236 m (Ebert, 2003). *Squalus suckleyi* appears to prefer water temperatures between 7 and 15°C, and often makes longitudinal and depth migrations to follow this temperature preference (Ebert, 2003).

Etymology. The species name is in honor of George Suckley who collected the specimens used by Charles Girard in his original description.

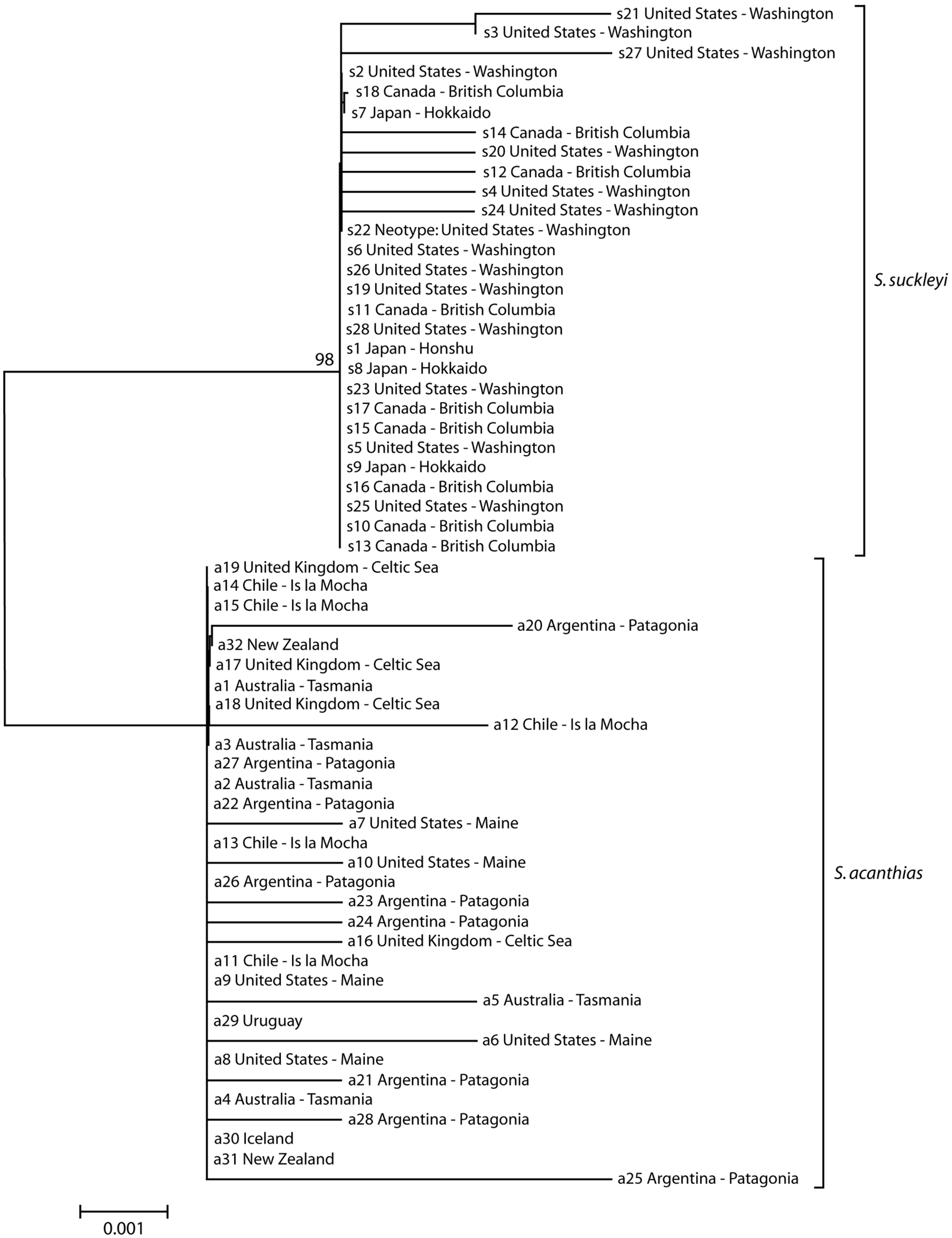

FIGURE 2. Neighbour joining tree for COI divergences of specimens of *Squalus suckleyi* and *S. acanthias*. Kimura 2 parameter distances used and distance bar given. Bootstrap values >70% shown. Specimen designations as in Appendix I.

Common names. North Pacific spiny dogfish, spotted spiny dogfish, or spiny dogfish.

Size and sexual maturity. *Squalus suckleyi* is a viviparous species with yolk-sac dependency, with litters of up to 20, but with most averaging between 2–12. Litter size and size at birth are correlated with the size of the female. Males mature between 700–800 mm total length (TL) and for females 800–1000 mm TL. Maximum size is about 1070 mm for males and at least 1300 mm for females (Ebert, 2003).

Life history. Considerable differences exist in published vital rate estimates for *Squalus acanthias* (Fordham *et al.*, 2006). Age and growth studies have shown large discrepancies in growth rates from different geographic locations. For example, in the northwest Atlantic Nammack *et al.* (1985) provided a growth coefficient (k) of 0.11 yr^{-1} and 0.15 yr^{-1} for females and males, respectively. In the North Pacific, several age and growth studies have been conducted providing growth coefficients ranging from 0.031 to 0.034 yr^{-1} for females and from 0.067 to 0.092 yr^{-1} for males (Ketchen, 1975; Jones & Geen, 1977). Saunders & McFarlane (1993) provided a growth coefficient for *Squalus acanthias* (= *S. suckleyi*) off British Columbia for the sexes combined of 0.044 yr^{-1}. Growth coefficients from other geographic locations such as the Black Sea are similar to those from the North Atlantic, ranging from 0.13 to 0.17 yr^{-1} and 0.17 to 0.2 yr^{-1} for females and males, respectively (Avsar, 2001; Demirhan & Sehyan, 2007).

Accompanying the differences in growth rates are differences in longevity and in age at first reproduction. In the northwest Atlantic the median age at maturity is 12 and six years for females and males, respectively (Nammack *et al.*, 1985), while median age at maturity in the North Pacific is 35.5 and 18.5 for females and males, respectively (Saunders & McFarlane, 1993; Cindy Tribuzio, NOAA Fisheries Auke Bay Laboratory, pers. comm.).

The order of magnitude in the differences in growth rates between the North Pacific and other geographic locations around the world cannot be explained by differences in techniques or be due to a lack of validation. In fact, ages have been validated with OTC and bomb radiocarbon dating for *S. suckleyi* in the eastern North Pacific (McFarlane & Beamish, 1987; McFarlane & King, 2009; Campana *et al.*, 2006) and for *S. acanthias* via bomb radiocarbon in the northwest Atlantic (Campana *et al.*, 2006). Similarly, the significant differences at median age at maturity that accompany these different growth rates cannot be explained by differing assessment techniques.

The reason for such differences in vital rates between the North Pacific and other geographic locations has never been elucidated. Discussions have centered on potential environmental or ecosystem differences, however, no data have been brought to bear for that argument. Our data show a much more parsimonious and viable explanation for these differences; that *Squalus acanthias* group species in the North Pacific constitute a different species (= *S. suckleyi*) than *S. acanthias* in other geographic locations. Tagging studies show that *S. suckleyi* in the North Pacific can migrate thousands of miles from British Columbia to Japan and Mexico (McFarlane & King, 2003). This information suggests that *S. suckleyi* in the North Pacific are a single stock, which is supported by our genetic analysis.

Remarks. The *Squalus acanthias* subgroup is one of the more taxonomically problematic shark groups as its members are very similar in external appearance. Differences in external morphology between *S. acanthias* (Fig. 3) and *S. suckleyi* (Fig. 1) are subtle and intraspecific variations within individuals of the same maturity class are likely to mask these differences. The broad geographic ranges of these two species, particularly *S. acanthias*, are likely to contribute to the intraspecific variation and future research should focus on defining this variation across the known ranges. There are few external morphometric characters to separate these two nominal species, e.g. lower dorsal-fin spines, position of the first dorsal-fin spine relative to the inner rear tip of the pectoral fin. In the present study we found that *S. suckleyi* had a slightly shorter, more broadly–rounded to acute snout than *S. acanthias* which tends to have a slightly longer and more acute snout. Also, we found the following morphometric ratios to differ between *S. suckleyi* and *S. acanthias*: pelvic–fin midpoint to first dorsal-fin insertion (PDI) 14.0 (13.2–15.1)% versus 9.3 (8.7–9.8)%, pelvic-fin midpoint to second dorsal-fin insertion (PDO) 7.6 (5.0–9.1)% versus 10.0 (9.3–10.4)%, first dorsal-fin midpoint to pectoral–fin insertion (DPI) 11.2 (9.7–12.4)% versus 9.8 (9.3–10.7)%, and first dorsal-fin midpoint to pelvic–fin origin (DPO) 14.7 (12.0–15.0)% versus 12.4 (10.7–13.5)%. The DPI and DPO ratios found in the present study indicate that although there may be some overlap the first dorsal-fin midpoint is proportionally slightly more posterior to the pectoral-fin insertion and pelvic fin origin. This finding is somewhat consistent with that of Jordan & Evermann (1896), although these authors observed that the position of the first dorsal-fin spine was more posterior to the pectoral-fin. Our findings also indicate that the pelvic-fin is proportionally closer to the second dorsal-fin in *S. suckleyi* while in *S. acanthias* it is closer to the first dorsal fin. This finding is consistent with those of Bigelow & Schroeder (1957) and Garrick (1960). Jones & Geen (1976) found similar results, but concluded that these differences were due to the effects of length and sex for individual specimens.

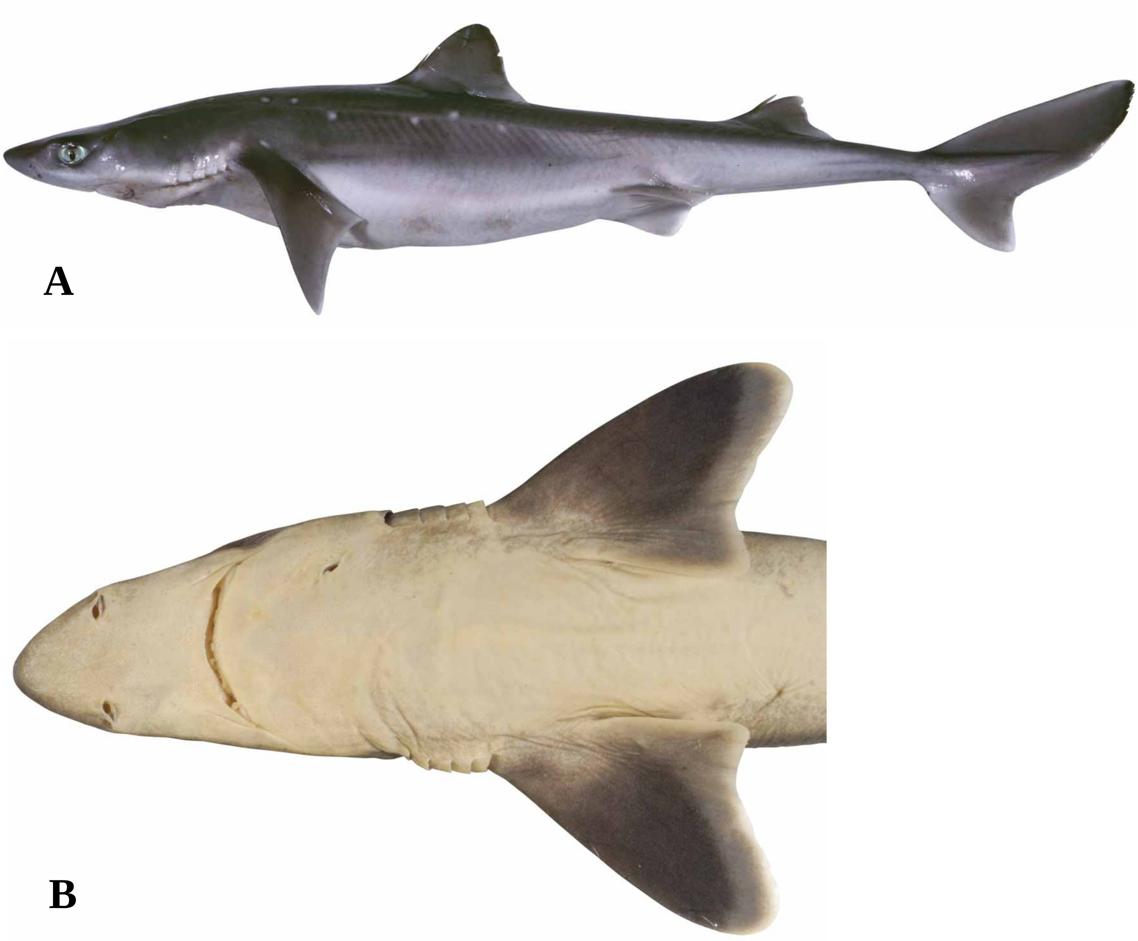

FIGURE 3. *Squalus acanthias*: A, Lateral view of CSIRO H 1214 (female 678 mm TL); B, Ventral view of head of CSIRO H 4876–01 (adult male 616 mm TL).

Although most external morphological characters appeared to overlap between North Pacific and North Atlantic forms, meristic characters such as vertebral counts consistently reveal a distinct separation between these two forms. In the present study we found the total number of vertebral counts to be slightly lower in *S. suckleyi* (mean = 99, range = 97–106) than those found in *S. acanthias* (mean =112, range = 109–116); a finding consistent with other studies (Springer & Garrick, 1964; Jones & Geen, 1976).

In this study, we designate a recently collected specimen as the neotype for *Squalus suckleyi* (CAS 227267). We have followed the requirements of the International Code of Zoological Nomenclature in designating the holotype. The designated neotype was collected from the type locality of Puget Sound, the syntypes are lost and not available, a detailed diagnosis and description is provided, and differences between the closest related species (*S. acanthias*) are provided. Given that the *Squalus acanthias* group requires further taxonomic revision, particularly the Black Sea population, the designation of a neotype for this species will be beneficial for future taxonomic work.

The results of our molecular analysis were congruent with results from other studies comparing within- and between-species diversity at CO1 in the genus *Squalus* (5-6X difference in magnitude; Ward *et al*. 2005). The use of molecular tools in recent years has helped to shed light on many difficult taxonomic questions

(Hillis 1987; Avise 2004; Hauser 2009), including problematic elasmobranchs. Two North Pacific shark species, *Somniosus pacificus* Bigelow & Schroeder, 1944 and *Lamna ditropis* Hubbs & Follet, 1947, were long thought to be synonymous with the morphologically similar, but taxonomically distinct North Atlantic species *S. microcephalus* (Bloch & Schneider, 1801) and *L. nasus* (Bonnaterre, 1788), respectively (Ebert, 2003). Interestingly, both these species were not considered to be distinct from their North Atlantic congeners until the middle of the last century while *S. suckleyi* had been described as distinct nearly 100 years earlier. Subsequent molecular studies have shown both *S. pacificus* and *L. ditropis* to be genetically distinct (Naylor *et al.*, 1997; Murray *et al.*, 2008).

The present study is a descendant of Ward *et al.* (2005, 2007), which was part of a large-scale project to revise the taxonomy of the genus *Squalus* in the Indo-Australasian region using both morphological and molecular techniques. Despite the lack of evidence in a 1976 allozyme paper (Jones and Green), newer studies have argued for the taxonomic distinction of *S. acanthias* in the North Pacific based on molecular evidence (Hauser 2009; Verissimo *et al.* 2010). In particular, a recent analysis of the global population structure of this species using both mitochondrial and nuclear markers recovered a unique genetic clade in the North Pacific (Verissimo *et al.* 2010), results that are highly consistent with ours.

Future research on this subgroup of *Squalus* needs to address the conservation and management implications emanating from the results of this study. *Squalus acanthias* is currently listed as Vulnerable by the IUCNs *Red List of Threatened Animals* (Fordham *et al.*, 2006). The North Pacific populations included in this assessment should now be treated as a separate species, *Squalus suckleyi*, and should be assessed separately, while the assessment for *S. acanthias* should be updated to reflect this change. Current management strategies for these two species, especially in North American waters, should be revised in light of these findings.

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Appendix 1: GenBank accession numbers and Barcode of Life Database (BOLD) numbers for the specimens in Figure 2.

Designation	GenBank	BOLD
S. suckleyi		
s1	-	ABRZ1
s2	EF539277	BW-A2327
s3	EF539276	BW-A2328
s4	EF539275	BW-A2329
s5	EF539274	BW-A2330
s6	EF539273	BW-A2331
s7	EF539272	BW-A2332
s8	EF539271	BW-A2333
s9	EF539270	BW-A2334
s10	FJ165376	TZ-06-RICKER-465
s11	FJ165369	TZ-06-RICKER-559
s12	FJ165370	TZ-06-RICKER-582
s13	FJ165371	TZ-06-RICKER-590
s14	FJ165372	TZ-06-RICKER-610
s15	FJ165375	TZ05-FROSTI-051
s16	FJ165374	TZ05-FROSTI-114
s17	FJ165368	TZ05-FROSTI-141
s18	FJ165373	TZ05-FROSTI-168
s19	-	UWO47291
s20	-	UWO47708
s21	-	UWO47709
s22 (Neotype)	FJ379928	(SS1)
s23	FJ379929	(SS2)
s24	FJ379930	(SS3)
s25	FJ379931	(SS4)
s26	FJ379932	(SS5)
s27	FJ379933	(SS6)
s28	FJ379934	(SS7)
S. acanthias		
a1	DQ108279	BW-A083
a2	DQ108280	BW-A084
a3	DQ108281	BW-A085
a4	DQ108282	BW-A086
a5	DQ108267	BW-A087

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Appendix I. (continued)

Designation	GenBank	BOLD
a6	EF539291	BW-A2312
a7	EF539290	BW-A2313
a8	EF539289	BW-A2314
a9	EF539288	BW-A2315
a10	EF539287	BW-A2316
a11	EF539286	BW-A2317
a12	EF539285	BW-A2318
a13	EF539284	BW-A2319
a14	EF539283	BW-A2320
a15	EF539282	BW-A2321
a16	EF539281	BW-A2322
a17	EF539280	BW-A2323
a18	EF539279	BW-A2324
a19	EF539278	BW-A2325
a20	EU074609	INIDEP-T 0199
a21	EU074607	INIDEP-T 0201
a22	EU074601	INIDEP-T 0202
a23	EU074605	INIDEP-T 0203
a24	EU074606	INIDEP-T 0204
a25	EU074608	INIDEP-T 0205
a26	EU074603	INIDEP-T 0227
a27	EU074604	INIDEP-T 0228
a28	EU074599	INIDEP-T 0255
a29	EU074602	INIDEP-T 0333
a30	NC_002012	-
a31	-	P42571
a32	-	Fe119