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NAYLOR ET AL.: DNA IDENTIFICATION OF SHARKS & RAYS

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A DNA SEQUENCE-BASED APPROACH TO THE  
IDENTIFICATION OF SHARK AND RAY SPECIES AND  
ITS IMPLICATIONS FOR GLOBAL ELASMOBRANCH  
DIVERSITY AND PARASITOLOGY

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G.J.P. NAYLOR, J.N. CAIRA, K. JENSEN,  
K.A.M. ROSANA, W.T. WHITE, AND P.R. LAST



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G.J.P. NAYLOR

*Department of Biology,  
College of Charleston, Charleston, SC 29401*

J.N. CAIRA

*Department of Ecology and Evolutionary Biology,  
University of Connecticut, Storrs, CT 06269-3043*

K. JENSEN

*Department of Ecology and Evolutionary  
Biology and the Biodiversity Institute,  
University of Kansas, Lawrence, KS 66045*

K.A.M. ROSANA

*Department of Scientific Computing/Department  
of Biological Science,  
Florida State University, Tallahassee, FL 32304*

W.T. WHITE

*CSIRO Marine and Atmospheric Research,  
Hobart, TAS, 7001, Australia*

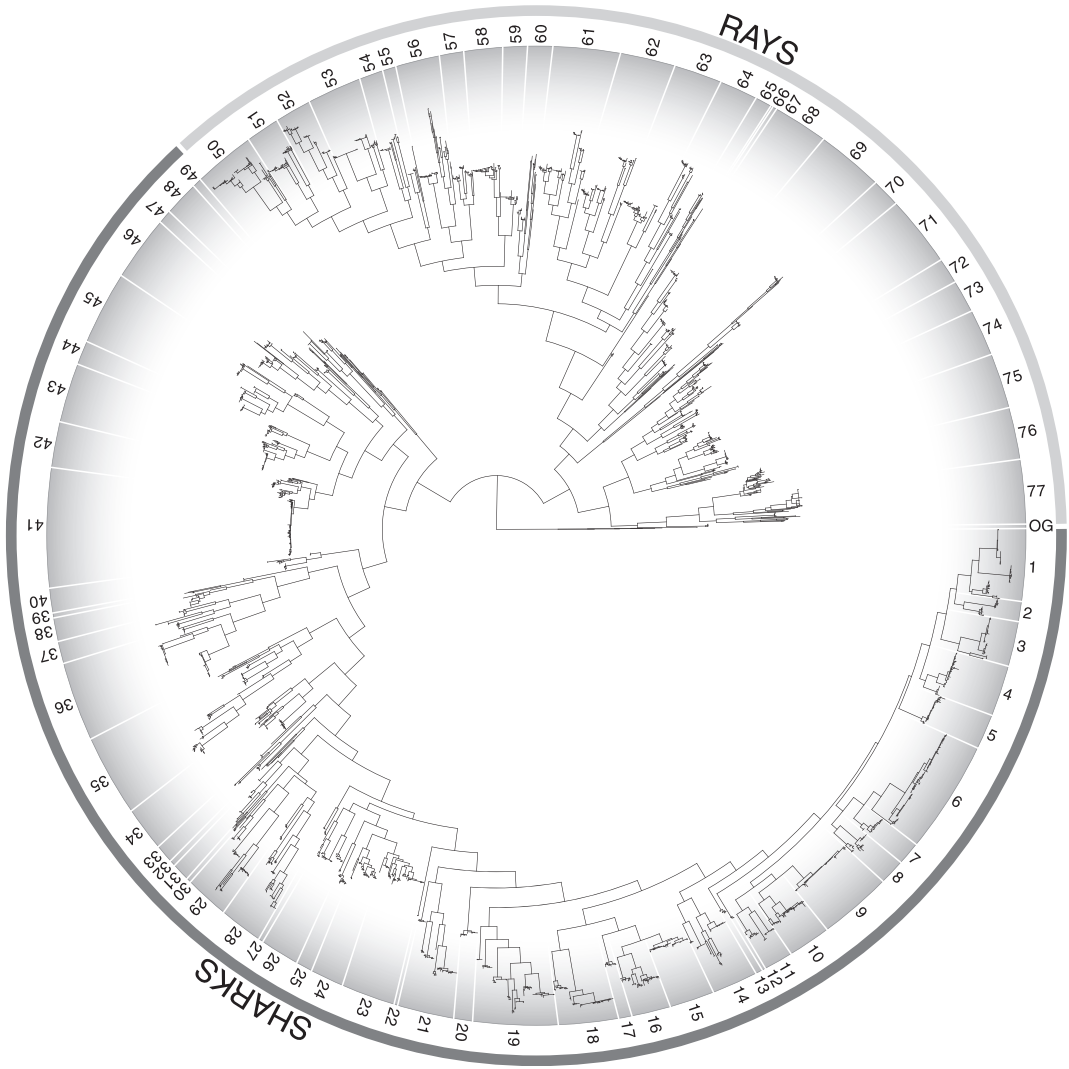
P.R. LAST

*CSIRO Marine and Atmospheric Research,  
Hobart, TAS, 7001, Australia*

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Overall tree topology resulting from neighbor-joining analysis of 4283 ingroup specimens based on ~1044 bp of NADH2 sequence data. Numbers refer to figures 1–77 illustrating the respective subtrees; OG, outgroup.

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## ABSTRACT

In an effort to provide a framework for the accurate identification of elasmobranchs, driven in large part by the needs of parasitological studies, a comprehensive survey of DNA sequences derived from the mitochondrial NADH2 gene was conducted for elasmobranchs collected from around the world. Analysis was based on sequences derived from 4283 specimens representing an estimated 574 (of ~1221) species (305 sharks, 269 batoids), each represented by 1 to 176 specimens, in 157 (of 193 described) elasmobranch genera in 56 (of 57 described) families of elasmobranchs (only Hypnididae was not represented). A total of 1921 (44.9%) of the samples were represented by vouchers and/or images available in an online host specimen database (<http://elasmobranchs.tapewormdb.uconn.edu>). A representative sequence for each of the 574 species identified in this survey, as well as an additional 11 sequences for problematic complexes, has been deposited in GenBank. Neighbor-joining analysis of the data revealed a substantial amount of previously undocumented genetic diversity in elasmobranchs, suggesting 79 potentially new taxa (38 sharks, 41 batoids). Within-species p-distance variation in NADH2-percent sequence divergence ranged from 0 to 2.12 with a mean of 0.27; within-genus p-distance variation ranged from 0.03 to 27.01, with a mean of 10.16. These values are roughly consistent with estimates from prior studies based on barcode COI sequences for elasmobranchs and fishes. While biogeographic influences have likely shaped the diversification of the entire group, the traces left by older influences tend to be overprinted by newer ones. As a result, the most clearly interpretable influences are those associated with recently diverged taxa. Among closely related elasmobranchs, four regions appear to be of particular importance: (1) the Atlantic Ocean, (2) Arabian Sea, Persian Gulf, and Red Sea, (3) Southeast Asia, and (4) Australia. Each of these regions has a substantial proportion of taxa that are genetically distinct from their closest relatives in other regions. These results suggest that great care should be taken in establishing the identities of elasmobranch hosts in parasitological studies. Furthermore, it is likely that many existing host records require confirmation.

## INTRODUCTION

Sharks, rays, and chimeras (chondrichthyan fishes) are widely recognized important constituents of vertebrate biodiversity. They constitute one of the two primary divisions of the gnathostome tree. Comparative anatomists, physiologists, and biochemists have long valued the basal phylogenetic position of chondrichthyans as a proxy for the primitive gnathostome condition. Yet, surprisingly, in spite of their phylogenetic importance, chondrichthyans remain poorly known in terms of their extant biodiversity relative to other vertebrate classes. This is reflected in the relative immaturity of chondrichthyan taxonomy. In the most recent comprehensive authoritative checklist of species of elasmobranchs, Compagno (2005a) recognized 1125 species. However, included in that list were tens of species that had not yet been described. Since 2005, more than 50 of these have been formally treated and named, while over 80 species not treated by Compagno (2005a) have also been described. This brings the total number of known

species of elasmobranchs to 1221. The fact that so many new species have been discovered and described over such a short time span, suggests that more remain to be discovered. Much of this increase is a result of reassessment of geographic variation; some of the increase represents recognition of subtle morphological variants among congeneric forms that nevertheless exhibit substantial molecular sequence divergence.

Recent advances in elasmobranch taxonomy have had a major impact on parasitological studies involving elasmobranch hosts. The accurate identification of hosts is of paramount importance in studies of any parasitological system if the results are to be meaningful. However, as our understanding of elasmobranch diversity has grown, so too has the number of instances in which longstanding concepts of host associations have been challenged (e.g., Caira et al., 2007; Jensen and Caira, 2008; Fyler and Caira, 2010; Desjardins and Caira, 2011; Koch et al., 2012; Cielocha and Jensen, 2011; White et al., 2010c). The current project grew out of a global survey of elasmobranch

TABLE 1

**Taxon coverage relative to known genera and species of elasmobranchs, by family**

The number in parentheses after number of species included indicates number of species potentially new to science recovered from the analysis.

Taxa	No. of described genera	No. of genera included	No. of known species	No. of species included
<b>Galeomorphi</b>				
Heterodontiformes				
Heterodontidae	1	1	9	6 (1)
Orectolobiformes				
Parascylliidae	2	1	8	1
Brachaeluridae	2	1 <sup>a</sup>	2	2
Orectolobidae	3	2	11	7
Hemiscylliidae	2	2	16	7 (1)
Ginglymostomatidae	3	3	3	4 (1)
Stegostomatidae	1	1	1	1
Rhincodontidae	1	1	1	1
Lamniformes				
Odontaspidae	2	2	3	3
Pseudocarchariidae	1	1	1	1
Mitsukurinidae	1	1	1	1
Megachasmidae	1	1	1	1
Alopiidae	1	1	3	3
Cetorhinidae	1	1	1	1
Lamnidae	3	3	5	5
Carcharhiniformes				
Scyliorhinidae	17	15	170	54 (8)
Proscylliidae	3	2	7	2 (1)
Pseudotriakidae	3	2	4	3 (1)
Leptochariidae	1	1	1	1
Triakidae	9	8	51	34 (4)
Hemigaleidae	4	3	8	6
Carcharhinidae	12	12	56	70 (10)
Sphyrnidae	2	2	8	10 (3)
<b>Squalomorphi</b>				
Hexanchiformes				
Chlamydoselachidae	1	1	2	1
Hexanchidae	3	3	4	5 <sup>b</sup>
Squaliformes				
Echinorhinidae	1	1	2	2
Squalidae	2	2	26	19 (4)
Centrophoridae	2	2	18	14 (4)
Etmopteridae	5	2	53	13
Somniosidae	7	6	18	10
Oxynotidae	1	1	5	2
Dalatiidae	7	4	10	5
Squatiniiformes				
Squatinae	1	1	23	7
Pristiophoriformes				
Pristiophoridae	2	2	9	3
<b>SHARK TOTAL</b>	<b>108</b>	<b>92</b>	<b>541</b>	<b>305 (38)</b>

TABLE 1  
(Continued)

Taxa	No. of described genera	No. of genera included	No. of known species	No. of species included
Rajiformes				
Pristidae	2	2	7	6
Rhinidae	1	1	1	1
Rhynchobatidae	1	1	7	4
Rhinobatidae	5	5	51	15 (3)
Platyrrhinidae	2	1	5	1
Zanobatidae	1	1	3	1
Narcinidae	4	1	35	3
Narkidae	5	2	14	2
Hypnidae	1	0	1	0
Torpedinidae	1	1	31	8 (1)
Arhynchobatidae	12	11	101	32
Rajidae	19	12	178	60 (7)
Anacanthobatidae	3	2	25	2
Plesiobatidae	1	1	1	1
Urolophidae	2	2	28	13
Urotrygonidae	2	2	15	6
Hexatrygonidae	1	1	1	1
Potamotrygonidae	6	3	30	8 (2)
Dasyatidae	8	8	89	62 (19)
Gymnuridae	2	1 <sup>c</sup>	12	9 (2)
Myliobatidae	4	4	23	20 (5)
Rhinopterae	1	1	11	8 (2)
Mobulidae	2	2	11	6
<b>RAY TOTAL</b>	<b>85</b>	<b>65</b>	<b>680</b>	<b>269 (41)</b>
<b>TOTAL</b>	<b>193</b>	<b>157</b>	<b>1221</b>	<b>574 (79)</b>

<sup>a</sup>*Heteroscyllium* is considered a synonym of *Brachaelurus*.

<sup>b</sup>*Hexanchus vitulus* is recognized as valid.

<sup>c</sup>*Aetoplatea* is considered a synonym of *Gymnura*.

tapeworms that was initiated in the mid-1980s by J.N.C. and was later substantially expanded through collaboration with K.J., in which a strategy to manage the issue of tracking the identities of novel (potentially undescribed) hosts was developed. Host tissue samples were routinely taken from each host individual examined, to serve as a voucher for subsequent sequence validation of host identity. The project was further expanded through collaboration with G.J.P.N. to include sequences from as diverse a set of chondrichthyans as possible, whether examined for parasites or not, with the goal of providing a baseline assessment of sequence variation among and within elasmobranch species in general. It is anticipated that this baseline will be useful to taxonomists, biogeographers, commercial fisheries, and conservation biologists. We hope this data set will

serve as a valuable resource to aid investigators working on elasmobranch parasites in the identification of their host taxa.

The fast-evolving protein-coding gene NADH dehydrogenase subunit 2 (NADH2) was selected by G.J.P.N. to provide a means of distinguishing among very closely related species, cryptic species, or geographic variants, while still ensuring that sequence alignments could be rigorously validated at the amino acid level. NADH2 is one of the fastest, if not the fastest, evolving of the 13 mitochondrial protein-coding genes when measured at the amino acid level (Broughton and Reneau, 2006). In elasmobranchs, it is generally between 347 and 349 amino acids (1041–1047 bp) long. Patterns of nucleotide substitution in NADH2 show a high transition bias as is typical for most protein-coding genes. The base composition is often hetero-



geneous among taxa especially at third codon positions.

#### TAXON COVERAGE

We have made every effort to include as much phylogenetic diversity as possible. However, the taxon coverage is most comprehensive at higher taxon levels. The analysis includes representation of 56 (98.3%) of the 57 families, 157 (81.4%) of the 193 genera, and as many as 574 species of elasmobranchs. Hypnidae is the only family for which no representatives were included. Also not included from Compagno (2005a) were representatives of the following 15 shark genera: *Aculeola*, *Cephalurus*, *Chaenogaleus*, *Cirrhoscyllium*, *Ctenacis*, *Euprotomicroides*, *Gogolia*, *Heteroscyminoides*, *Miroscyllium*, *Mollisquama*, new genus (Pseudotriakidae), *Pentanchus*, *Scymnodalatis*, *Sutorectus*, and *Trigonognathus*; and also the following 19 ray genera: *Anacanthobatis*, *Benthobatis*, *Breviraja*, *Crassinarke*, *Dactylobatus*, *Diplobatis*, *Discopyge*, *Fenestraja*, *Gurgesiella*, *Heteronarce*, *Hypnos*, n. gen. 1 (Potamotrygonidae), n. gen. 1 (Rajidae), n. gen. 2 (Potamotrygonidae), n. gen. 2 (Rajidae), *Platyrrhina*, *Plesiopygon*, *Pseudoraja*, and *Temera*. In total, the data set consists of NADH2 sequences for 4283 specimens; the number of replicate specimens of each species ranges from 1–176. Details of the taxon coverage are provided in table 1, as is a breakdown of elasmobranch species included by family of sharks versus rays. We anticipate that as researchers encounter additional species they will be able to contrast the sequences of their animals against those contained in our database and build on the initial data set to provide a more comprehensive understanding of the group.

#### DNA BARCODING

There has been much recent interest in exploring elasmobranch sequence variation using the barcode marker cytochrome oxidase 1 (COI) (e.g., Holmes et al., 2009; Moura et al., 2008; Toffoli et al., 2008; Ward et al., 2005, 2007, 2008, 2009; Ward and Holmes, 2007; Wong et al., 2009; Zemlak et al., 2009). While such barcode work will provide a useful parallel assessment of sequence variation, the

fragment of COI used is both shorter (650 vs. 1044 bp) and more slowly evolving in chondrichthyans than is the NADH2 fragment (Moore et al., 2011). As such, we feel it may not be as useful for distinguishing among some closely related forms. This is not intended as criticism of the barcode scheme. The fragment of COI used for barcoding was selected because of its utility across a broad suite of eukaryotes, rather than any particular group. Thus, while we expect results to be broadly concordant, we anticipate that NADH2 data will be generally better able to distinguish recently evolved elasmobranch sister species than the barcode COI fragment.

#### CAUTIONARY REMARKS

Just as COI barcode data are restricted in their utility so too are the NADH2 data we present. We emphasize at the outset that we regard mitochondrial sequence data as only a part of a suite of tools that can inform the biodiversity of any group. While we find them useful, they have shortcomings that can be misleading if not interpreted in context (see Moritz and Cicero, 2004). As a consequence, in selecting samples for inclusion here, we have strived, but not fully succeeded, to choose those for which images and/or voucher specimens were available. In the cases of some recently described species, sequence data were taken from holotype and/or paratype specimens. It is important to emphasize that the possibility of incorrect identification is greater for specimens that are not represented by images and/or vouchers.

**Hybridization.** In the event that two species hybridize, the mitochondrial sequence of the hybrid progeny will be identical to that of the mother. Hybridization between species that are morphologically different from one another can lead to situations in which the progeny are morphologically distinct from one or both parental species yet identical in mitochondrial sequence to the maternal species. Such discordance can lead to confusion. It is likely that some of the groupings in the current study have been affected by hybridization, especially where relationships implied by morphology or color pattern appear discordant with those implied by the sequence data. Where such cases are suspected to occur, it

will be important to target fast-evolving, single-copy nuclear markers such as introns (Lyons et al., 1997, Li et al., 2010) to allow for an independent assessment of relationships based on both parental genomes.

**Ancestral polymorphism.** If an ancestral polymorphism persists over more than two nodes in an evolutionary tree and is subsequently fixed differentially in descendant lineages, it is possible to have paraphyletically distributed alleles (Patton and Smith, 1994; Funk and Omland, 2003). This can yield what appear to be nonmonophyletic species, in which different populations of the same species appear not to be each others' closest relatives. This is more prevalent when populations are large, harboring substantial polymorphism and the time between vicariant events (i.e., internodal branch length) is short. When populations are small and the time between vicariant events is long, the alleles are more likely to coalesce and appear monophyletically distributed. Such differential coalescence is best identified using a suite of multiple independent nuclear markers (Liu et al., 2009; Degnan and Rosenberg, 2009).

**Rate variation among lineages.** Most surveys that employ mitochondrial sequence variation reveal substantial rate variation among lineages. Because rates vary among lineages, it is not possible to set a "sequence divergence threshold" for species distinctness. Among the data provided below there are a few cases in which species are clearly different based on multiple independent criteria such as morphology, color pattern, and/or reproductive isolation, but show little divergence at mitochondrial loci. At the other end of the spectrum, there are also cases in which distinct populations of a species exhibit greater sequence divergence than that seen among some species. These cases notwithstanding, we generally found that the more overall sequence divergence observed between forms, the more likely they are to be two different species.

**Missing data.** Clearly, gaps in sequence data induce differences in pairwise distances from which the neighbor-joining (Saitou and Nei, 1987) tree is derived. Missing data can also have topological and branch length consequences for phylogenetic reconstruction under parsimony and likelihood (unless the model is entirely consistent with the process that

generated the data, which is rarely, if ever, the case for real data sets). Because of these issues we have restricted our analysis to samples for which we have generated at least 1000 bp (the entire alignment is 1044 bases). Nevertheless, some of the variation observed among some of the closely related taxa may be the consequence of minor differences in pairwise distances induced by small sections of missing data.

**Experimental error.** Sequencing is prone to error at multiple levels. Errors can occur during PCR amplification due to imperfect Taq polymerase fidelity. The sequencing reaction itself can also be prone to error. The interpretation of chromatograms can be ambiguous and lead to assignment errors. Finally, errors can be introduced at the alignment stage. However, the use of a protein-coding gene, which can be aligned at both the nucleotide and amino acid level, goes a long way toward eliminating such problems, relative to markers based on nonprotein coding sequences.

#### CHOICE OF DISTANCE MEASURE

Several distance measures have been proposed to summarize divergence among sequences. Most accommodate the fact that as more distant comparisons are made, the probability of multiple hits at a site increases. The various measures differ in the assumptions they make about the molecular evolutionary process. Jukes-Cantor distance (Jukes and Cantor, 1969), for example, assumes that the rate of change from every nucleotide to every other nucleotide is equal and the base composition is even and stationary. The Kimura 2-parameter model (K2P) (Kimura, 1980) allows for a different rate of transitional changes relative to transversional changes but assumes equal base frequencies. The choice of distance measure is critically important if the goal is to use the distances obtained to estimate phylogeny. Indeed, if a distance could be found that perfectly captures the amount of evolutionary change that has taken place, the tree deduced from the resulting distance matrix would accurately reflect phylogeny. To date no such distance has been found.

In our case, we were interested in exploring the within-species (i.e., intraspecific) versus

**TABLE 2**  
**Summary p-distances and number of base pair differences in NADH2 within species and within genera of elasmobranchs**

	NADH2 (current study)				
	No. of contributing taxa (total number of taxa)	No. of comparisons	Mean ± SD	Min	Max
<b>Within-species</b> p-distance (%)	468 <sup>a</sup> (574)	468 <sup>d</sup>	0.27 ± 0.28	0	2.12
<b>Within-species</b> no. of base pair differences	468 <sup>a</sup> (574)	468	2.86 ± 2.93	0	22.00
<b>Within-genus</b> p-distance (%) (among congeneric species)	85 <sup>b</sup> (157)	2841 <sup>e</sup>	10.16 ± 4.89	0.03	27.01
<b>Within-genus</b> no. of base pair differences	85 <sup>b</sup> (157)	2841	106.05 ± 51.05	0.30	282.00
<b>Within-genus</b> p-distance (%) (among congeneric specimens) as calculated in BOLD	143 <sup>c</sup> (157)	331425 <sup>f</sup>	9.68 ± 3.65	0	27.09

<sup>a</sup>Number of species represented by two or more specimens.

<sup>b</sup>Number of genera represented by two or more species.

<sup>c</sup>Number of genera represented by two or more specimens.

<sup>d</sup>Number of comparisons among within-species means. See appendix 1.

<sup>e</sup>Number of pairwise comparisons among members of different species within genera, pooled over all genera.

<sup>f</sup>Number of pairwise comparisons among all specimens of all species in each genus, pooled across genera, as calculated in BOLD.

Abbreviations: SD, standard deviation; Min, minimum distance observed; Max, maximum distance observed.

within-genus (i.e., intragenetic) differences among closely related forms, and so have chosen to use p-distance (Jukes and Cantor, 1969). This simple measure represents the uncorrected distance, expressed as the number, or proportion when expressed as a percentage, of nucleotide differences between two sequences without estimating any unobserved changes (multiple hits) whatsoever. This has the effect of emphasizing differences among close relatives relative to differences among distant relatives. We also provide intragenetic p-distance summary statistics (table 2) as calculated in the Barcode of Life Data Systems (BOLD Systems; <http://www.boldsystems.org>) using all specimens from all genera represented by more than one specimen and K2P distances as calculated in the BOLD Systems (v. 2.5; <http://www.boldsystems.org>) for all intraspecific and intragenetic comparisons (appendix 1 and table 3, respectively).

**CLUSTERS DO NOT REFLECT  
 PHYLOGENETIC RELATIONSHIPS**

Our primary goal was to develop a molecular framework for the identification of

elasmobranch specimens to species. Neighbor-joining (Saitou and Nei, 1987) analysis, as employed here, provides an appropriate method of gauging specific identities based on sequence similarity from a single locus. There is, however, a tendency to interpret illustrations depicting cluster structure resulting from neighbor-joining analyses as faithful reflections of phylogenetic relationships. While there is undoubtedly some phylogenetic information in the clustering, it is almost entirely restricted to the tips of the tree. Larger, more inclusive clusters away from the tips cannot be reliably interpreted to reflect phylogenetic signal as the distance measure is inappropriate for such purposes. The neighbor-joining procedure is also known to be less reliable than character-based approaches to phylogenetic reconstruction such as parsimony and maximum likelihood. As a consequence, our results are not comparable with those of investigators looking to explore the phylogenetic relationships within or among one or more elasmobranch groups (e.g., Maisey et al., 2004 [molecules vs. morphology]; Naylor et al., 2005 [ordinal-level phylogeny]; Human et al., 2006 [Scyliorhinidae]; Cavalcanti, 2007

[supertree]; Lim et al., 2010 [Sphyrnidae]; López et al., 2006 [Triakidae]; Corrigan and Beheregarey, 2009 [Orectolobidae]; Stelbrink et al., 2010 [Squatinae]; Rocco et al., 2007 [Batoidea]). To avoid the temptation of interpreting our results in a phylogenetic context, the entire topology of the tree is presented in schematic form only (see frontispiece). Furthermore, individual figures have been designed to generally encompass only discrete clusters of specimens. However, the results and implications of a formal model-based phylogenetic analysis, of the NADH2 sequence data for one exemplar of each of the potential species examined here, are available in Naylor et al. (2012).

With these limitations in mind, we undertook a molecular survey of elasmobranchs using tissue samples acquired over the course of several different projects carried out over the past 24 years. Tissues were acquired primarily through field-collecting efforts undertaken by J.N.C., K.J., and G.J.P.N. in the waters of Australia, Azores, Belize, Chile, Gulf of Aqaba, Gulf of California, India, Indonesia, Madagascar, Malaysia, Philippines, Puerto Rico, South Africa, Taiwan, Thailand, the United States, and West Africa. These samples were supplemented by additional samples kindly provided by researchers around the globe (see Acknowledgments).

## MATERIALS AND METHODS

Liver or muscle tissue was sampled in the field from elasmobranch specimens that were either speared by the authors or their collaborators, collected on research vessels, purchased in local fish markets, or obtained in conjunction with local fishermen. A number of the samples collected by G.J.P.N. in the initial part of the survey were put in cryotubes, and placed in liquid nitrogen until they could be taken to the laboratory for storage at  $-80^{\circ}\text{C}$ . Samples collected later in the survey were stored in 95% alcohol or DMSO depending on availability. In early years, total DNA was extracted using phenol chloroform extraction (Sambrook et al., 1989), but in later years using High Pure PCR Template Preparation Kit by Roche Diagnostics (Indianapolis, IN). Extracted total DNA was stored at  $-20^{\circ}\text{C}$  until used

for PCR amplification. Samples were amplified using Fermentas Taq with primers designed to target the complete coding sequence for NADH dehydrogenase subunit 2 (NADH2). In most cases, a single set of universal primers (Naylor et al., 2005) designed to bind to the ASN and ILE tRNA regions of the mitochondrial genome were successful in amplifying the targeted fragment. However, for some taxa it was necessary to design taxon-specific primers. A complete list of primers for amplification and sequencing is shown in table 4. PCR products were purified by centrifugation through size-selective filters (Millipore, Bedford, MA) according to manufacturer's recommendations. Subsequent to 2008, samples were purified using ExoSAP-IT from USB (Cleveland, Ohio). The purified PCR products were sent off to commercial sequencing centers for sequencing (SeqWright, Houston, TX; Beckman-Coulter Genomics, Beverly, MA; Retrogen, San Diego, CA). The software packages Phred and Phrap (Ewing et al., 1998) were used to read sequence traces, assign quality values, make base calls, and produce output files for subsequent alignment. Sequences were translated to amino acids and aligned using the software package MUSCLE (Edgar, 2004). The aligned amino acid sequences were translated back, but in frame to their original nucleotide sequences, to yield a nucleotide alignment. The full protein-coding alignment was 1053 nucleotides long. Of the sequences that resulted, only those that were 1000 bp or greater were included in the alignment. To minimize the amount of missing data at the leading and trailing ends of some sequences, all sequences were truncated to a length of 1044 bp. Although our original goal was to generate 1044 bp of NADH2 sequence data for each of the 4283 specimens (of the 574 species) included in the analysis, in the end, we achieved this for 4220 (98.5%) of the specimens. Of the 63 remaining specimens, 45 had sequences that were three bases shorter and 18 had sequences that were up to 39 bases shorter; in such cases the missing data were mostly at the beginning and/or end of the sequence. We have not attempted to correct for this, given that the data generated for 99.5% of the specimens was between 1041 and 1044 bp in length.

TABLE 3  
**Mean intrageneric distances (%) for NADH2 (n = 85 genera)**

P-distance among species within a genus is given as the mean ± standard deviation, range, and number of congeners (*n*) included in the estimation. K2P distance is given as the mean ± standard deviation, range, and number of comparisons (*c*) of all constituent, nonconspecific specimens (as calculated in BOLD).

Genus	Figure(s)	p-distance	K2P distance
<b>Carcharhiniformes</b>			
Carcharhinidae	<i>Carcharhinus</i>	1–13 9.14 ± 1.88 (0.37–19.1; <i>n</i> = 40)	9.94 ± 2.49 (0–14.95; <i>c</i> = 216341)
Carcharhinidae	<i>Galeocerdo</i>	20 1.06 ( <i>n</i> = 2)	1.08 ± 0.18 (0.68–1.66; <i>c</i> = 198)
Carcharhinidae	<i>Glyphis</i>	14 7.41 ± 2.67 (0.72–9.84; <i>n</i> = 5)	7.82 ± 3.07 (0.48–11.16; <i>c</i> = 89)
Carcharhinidae	<i>Lamiopsis</i>	14 2.29 ( <i>n</i> = 2)	2.34 ± 0.08 (2.25–2.45; <i>c</i> = 26)
Carcharhinidae	<i>Loxodon</i>	18 2.86 ( <i>n</i> = 2)	2.94 ± 0.19 (2.45–3.26; <i>c</i> = 54)
Carcharhinidae	<i>Negaprion</i>	14 8.22 ( <i>n</i> = 2)	8.88 ± 0.11 (8.79–9.23; <i>c</i> = 84)
Carcharhinidae	<i>Rhizoprionodon</i>	15–17 6.88 ± 2.79 (0.96–11.25; <i>n</i> = 10)	7.66 ± 3.26 (0.77–13.21; <i>c</i> = 7597)
Carcharhinidae	<i>Scoliodon</i>	18 3.39 ± 0.42 (3.07–3.87; <i>n</i> = 3)	3.3 ± 0.33 (2.94–4.49; <i>c</i> = 646)
Hemigaleidae	<i>Hemigaleus</i>	21 9.06 ( <i>n</i> = 2)	9.86 ± 0.22 (9.34–10.36; <i>c</i> = 186)
Hemigaleidae	<i>Paragaleus</i>	21 11.8 ± 0.52 (11.3–12.35; <i>n</i> = 3)	12.8 ± 0.49 (12.24–14.15; <i>c</i> = 125)
Pseudotriakidae	<i>Gollum</i>	31 5.75 ( <i>n</i> = 2)	6.05 ( <i>c</i> = 1)
Scyliorhinidae	<i>Apristurus</i>	28, 30 13.96 ± 5.44 (1.87–19.73; <i>n</i> = 18)	15.66 ± 6.26 (1.85–23.56; <i>c</i> = 1701)
Scyliorhinidae	<i>Asymbolus</i>	31 8.04 ± 4.07 (3.35–10.68; <i>n</i> = 3)	9.85 ± 3.21 (3.45–11.84; <i>c</i> = 31)
Scyliorhinidae	<i>Atelomyxterus</i>	33 14.9 ( <i>n</i> = 2)	17.05 ± 0.16 (16.72–17.23; <i>c</i> = 30)
Scyliorhinidae	<i>Cephaloscyllium</i>	34 6.5 ± 2.57 (4.24–11.06; <i>n</i> = 7)	5.95 ± 1.94 (4.37–12.35; <i>c</i> = 213)
Scyliorhinidae	<i>Figaro</i>	31 1.85 ( <i>n</i> = 2)	1.88 ± 0.12 (1.75–2.15; <i>c</i> = 18)
Scyliorhinidae	<i>Galeus</i>	29 11.35 ± 4 (4.92–16.57; <i>n</i> = 5)	12.78 ± 5.75 (4.98–19.42; <i>c</i> = 177)
Scyliorhinidae	<i>Halaelurus</i>	29 10.81 ± 3.24 (5.8–13.61; <i>n</i> = 4)	12.75 ± 3.43 (6.05–15.64; <i>c</i> = 41)
Scyliorhinidae	<i>Parmaturus</i>	33 8.67 ( <i>n</i> = 2)	21.33 ± 0.12 (21.13–21.51; <i>c</i> = 30)
Scyliorhinidae	<i>Poroderma</i>	34 0.6 ( <i>n</i> = 2)	0.61 ± 0.08 (0.48–0.77; <i>c</i> = 192)
Scyliorhinidae	<i>Scyliorhinus</i>	34 6.44 ± 0.62 (5.51–7.02; <i>n</i> = 4)	6.35 ± 0.59 (5.74–8.21; <i>c</i> = 82)
Sphyrnidae	<i>Sphyrna</i>	19 9.9 ± 2.74 (1.28–12.8; <i>n</i> = 9)	11.18 ± 2.58 (0.97–14.72; <i>c</i> = 4754)
Triakidae	<i>Hemitriakis</i>	26 3.85 ± 1.89 (0.8–5.71; <i>n</i> = 5)	4.32 ± 2.2 (0.58–6.37; <i>c</i> = 122)
Triakidae	<i>Iago</i>	25 6.5 ± 5.64 (1.2–11.93; <i>n</i> = 4)	5.53 ± 5.63 (0.97–13.56; <i>c</i> = 157)
Triakidae	<i>Mustelus</i>	23–24 6.45 ± 2.5 (0.8–9.72; <i>n</i> = 18)	6.87 ± 2.59 (0.67–11.19; <i>c</i> = 7444)

TABLE 3  
(Continued)

	Genus	Figure(s)	p-distance	K2P distance
Triakidae	<i>Triakis</i>	27	8.29 ± 4.3 (3.78–12.36; n = 3)	11.45 ± 2.53 (9.2–15.32; c = 60)
<b>Heterodontiformes</b>				
Heterodontidae	<i>Heterodontus</i>	40	6.4 ± 2.64 (1.25–10.09; n = 6)	8.51 ± 1.72 (1.26–11.3; c = 695)
<b>Hexanchiformes</b>				
Hexanchidae	<i>Hexanchus</i>	49	8.87 ± 1.07 (7.73–9.87; n = 3)	10.12 ± 1.17 (8.29–11.64; c = 11)
<b>Lamniformes</b>				
Alopiidae	<i>Alopias</i>	35	10.72 ± 1.24 (9.29–11.5; n = 3)	11.68 ± 1.35 (9.94–13.4; c = 499)
Lamnidae	<i>Isurus</i>	35	10.57 (n = 2)	11.78 ± 0.41 (11.23–12.77; c = 144)
Lamnidae	<i>Lamna</i>	35	6.51 (n = 2)	6.96 ± 0.18 (6.63–7.18; c = 20)
Odontaspidae	<i>Odontaspis</i>	35	8.91 (n = 2)	9.72 (c = 2)
<b>Orectolobiformes</b>				
Brachaeluridae	<i>Brachaelurus</i>	38	10.87 (n = 2)	12.07 ± 0.81 (11.56–13.27; c = 4)
Ginglymostomatidae	<i>Ginglymostoma</i>	37	1.52 (n = 2)	1.55 ± 0.07 (1.46–1.66; c = 27)
Hemiscylliidae	<i>Chiloscyllium</i>	36	12.55 ± 3 (2.66–15.53; n = 6)	14.59 ± 2.29 (2.45–18.57; c = 4295)
Orectolobidae	<i>Orectolobus</i>	38	4.18 ± 1.69 (1.48–6.9; n = 6)	3.57 ± 1.56 (1.36–7.37; c = 276)
<b>Pristiophoriformes</b>				
Pristiophoridae	<i>Pristiophorus</i>	48	13.17 (n = 2)	14.95 ± 0.08 (14.89–15; c = 2)
<b>Squaliformes</b>				
Centrophoridae	<i>Centrophorus</i>	45	5.29 ± 1.99 (0.84–8.26; n = 10)	6.03 ± 1.65 (0.77–9.44; c = 2906)
Centrophoridae	<i>Deania</i>	44	5.06 ± 1.53 (2.16–6.37; n = 4)	5.38 ± 0.5 (2.15–7; c = 225)
Dalatiidae	<i>Squaliolus</i>	47	13.84 (n = 2)	15.28 ± 0.18 (15.05–15.55; c = 6)
Echinorhinidae	<i>Echinorhinus</i>	48	5.68 (n = 2)	6 ± 0.05 (5.96–6.07; c = 6)
Etmopteridae	<i>Etmopterus</i>	46	12.8 ± 4.29 (1.34–17.14; n = 12)	14.05 ± 5.59 (1.16–20.33; c = 3034)
Oxynotidae	<i>Oxynotus</i>	45	5.3 (n = 2)	5.55 ± 0.06 (5.52–5.73; c = 56)
Somniosidae	<i>Centroscyrmus</i>	45	9.22 ± 3.57 (7.16–13.34; n = 3)	8.04 ± 1.65 (7.46–15.09; c = 341)
Somniosidae	<i>Somniosus</i>	45	2.38 ± 1.29 (0.88–3.14; n = 3)	1.61 ± 1.09 (0.77–3.25; c = 29)
Squalidae	<i>Cirrhigaleus</i>	42	5.6 (n = 2)	5.94 ± 0.15 (5.83–6.04; c = 2)
Squalidae	<i>Squalus</i>	41–42	4.48 ± 1.74 (0.82–7.16; n = 17)	5.96 ± 1.84 (0.58–8.01; c = 15721)

TABLE 3  
(Continued)

	Genus	Figure(s)	p-distance	K2P distance
<b>Squatiniiformes</b>				
Squatinae	<i>Squatina</i>	48	10.58 ± 1.92 (4.41–13.12; n = 7)	11.58 ± 2.33 (4.07–14.83; c = 772)
<b>Rajiformes</b>				
Arhynchobatidae	<i>Atlantoraja</i>	77	6.97 ± 2.82 (3.72–8.62; n = 3)	6.3 ± 2.83 (3.75–9.39; c = 11)
Arhynchobatidae	<i>Bathyraja</i>	76	3.83 ± 0.68 (1.68–5.65; n = 14)	4 ± 0.77 (1.26–6.15; c = 1314)
Arhynchobatidae	<i>Brochiraja</i>	77	5.39 ± 2.73 (2.42–9.53; n = 6)	3.51 ± 1.9 (2.34–10.39; c = 566)
Arhynchobatidae	<i>Pavoraja</i>	77	5.14 (n = 2)	5.38 ± 0.12 (5.31–5.52; c = 3)
Arhynchobatidae	<i>Rhinoraja</i>	76	4.58 ± 1.37 (0.93–6.03; n = 5)	3.97 ± 1.81 (0.77–5.95; c = 36)
Arhynchobatidae	<i>Sympterygia</i>	77	12.4 (n = 2)	13.78 ± 0.06 (13.73–13.83; c = 4)
Dasyatidae	<i>Dasyatis</i>	55–56	14.56 ± 4.44 (1.96–22.53; n = 15)	18.67 ± 7.32 (1.95–27.96; c = 2572)
Dasyatidae	<i>Himantura</i>	50–54, 60	15.7 ± 3.37 (0.03–23.37; n = 30)	17.89 ± 3.37 (0–29.25; c = 41804)
Dasyatidae	<i>Neotrygon</i>	58	7.3 ± 3.82 (1.97–11.88; n = 6)	5.53 ± 3.83 (1.46–13.46; c = 850)
Dasyatidae	<i>Pastinachus</i>	57	8.91 ± 0.64 (7.78–9.68; n = 5)	9.87 ± 0.66 (7.82–11.44; c = 545)
Dasyatidae	<i>Taeniura</i>	55, 59	11.14 ± 7.76 (2.18–15.8; n = 3)	9.26 ± 8.35 (1.95–21.69; c = 340)
Dasyatidae	<i>Urogymnus</i>	54	2.39 (n = 2)	2.45 ± 0.11 (2.35–2.55; c = 8)
Gymnuridae	<i>Gymnura</i>	64	16.5 ± 2.76 (11.54–20.39; n = 9)	21.12 ± 4.03 (12.07–27.41; c = 1053)
Mobulidae	<i>Mobula</i>	61	11.72 ± 4.25 (3.01–14.52; n = 5)	14.35 ± 3.51 (3.04–16.82; c = 402)
Myliobatidae	<i>Aetobatus</i>	63	7.48 ± 4.74 (1.43–12.53; n = 7)	7.35 ± 5.22 (1.16–15.33; c = 1449)
Myliobatidae	<i>Aetomylaeus</i>	62	13.98 ± 5.8 (1.7–18.72; n = 6)	18.63 ± 5.29 (1.55–23.24; c = 433)
Myliobatidae	<i>Myliobatis</i>	62	8.41 ± 2.51 (4.68–12; n = 6)	8.45 ± 2.22 (4.71–13.45; c = 921)
Narcinidae	<i>Narcine</i>	70	20.65 ± 10.93 (8.03–27.01; n = 3)	22.61 ± 13.22 (8.6–33.79; c = 9)
Potamotrygonidae	<i>Potamotrygon</i>	60	7.04 ± 3.89 (0.24–12.21; n = 6)	8.5 ± 3.93 (0.19–13.55; c = 33)
Pristidae	<i>Pristis</i>	68	11.86 ± 3.45 (1.59–13.73; n = 5)	13 ± 2.65 (1.36–16.67; c = 828)
Rajidae	<i>Amblyraja</i>	74	3.08 ± 1.13 (1.79–3.86; n = 3)	3.5 ± 0.74 (1.36–4.58; c = 195)
Rajidae	<i>Dipturus</i>	71, 74	7.18 ± 2.73 (1.6–15.79; n = 17)	8.55 ± 3.95 (1.56–18.11; c = 1673)
Rajidae	<i>Leucoraja</i>	75	10.78 ± 3.54 (3.59–13.7; n = 6)	8.39 ± 4.74 (3.45–15.53; c = 841)
Rajidae	<i>Okamejei</i>	72, 75	13.35 ± 3.84 (9.2–17.84; n = 4)	12.44 ± 3.36 (9.73–21.19; c = 381)

TABLE 3  
(Continued)

	Genus	Figure(s)	p-distance	K2P distance
Rajidae	<i>Raja</i>	71, 73	12.57 ± 3.63 (2.21–17.75; n = 12)	13.91 ± 4.69 (1.85–21.17; c = 2244)
Rajidae	<i>Rajella</i>	74	5.01 ± 1.25 (3.16–6.49; n = 5)	5.43 ± 1.19 (3.25–7.02; c = 333)
Rajidae	<i>Zearaja</i>	71	2.35 ± 1.2 (0.99–3.25; n = 3)	2.01 ± 1.06 (0.67–3.55; c = 79)
Rhinobatidae	<i>Aptychotrema</i>	69	4.89 (n = 2)	5.09 ± 0.14 (4.99–5.19; c = 2)
Rhinobatidae	<i>Glaucostegus</i>	69	2.74 ± 0.71 (2.06–3.48; n = 3)	2.65 ± 0.44 (1.85–3.67; c = 132)
Rhinobatidae	<i>Rhinobatos</i>	68, 69	13.52 ± 4.29 (0.47–19.01; n = 8)	15.53 ± 5.26 (0.38–22.58; c = 1136)
Rhinopterae	<i>Rhinoptera</i>	61	7.45 ± 3.24 (0.44–10.69; n = 8)	8.36 ± 3.17 (0–12.71; c = 1068)
Rhynchobatidae	<i>Rhynchobatus</i>	68	2.84 ± 1.52 (0.29–4.24; n = 4)	3.71 ± 1.16 (0.19–4.5; c = 113)
Torpedinidae	<i>Torpedo</i>	70	13.26 ± 5.49 (0.53–17.92; n = 8)	15.32 ± 6.95 (0.48–21.32; c = 316)
Urolophidae	<i>Trygonoptera</i>	65	14.26 ± 1.51 (12.6–16.28; n = 4)	15.71 ± 1.55 (14–18.71; c = 15)
Urolophidae	<i>Urolophus</i>	65	13.69 ± 5.48 (1.44–21.07; n = 9)	15.2 ± 6.93 (1.46–25.6; c = 95)
Urotrygonidae	<i>Urobatis</i>	60	3.93 ± 6.69 (1.06–16.25; n = 4)	7.96 ± 6.04 (0.87–18.98; c = 153)
Urotrygonidae	<i>Urotrygon</i>	60	17.77 (n = 2)	20.96 ± 0.1 (20.89–21.03; c = 2)

#### CLUSTER ANALYSIS

The aligned sequences were subjected to a constrained neighbor-joining analysis using PAUP\* (v4.0b106). The constraint tree used for this analysis was derived from a maximum-likelihood analysis of a representative and phylogenetically diverse subset of 360 taxa that had previously been sequenced for multiple genes (Naylor, unpubl. data). A sequence for one individual representative of each of the 574 named clusters recognized in this study has been deposited in GenBank (see appendix 2), as have 11 additional sequences of species in particularly problematic complexes (e.g., *Bathyraja* spp.); in most instances, these exemplars are each represented by a museum specimen and/or one or more images. The resulting neighbor-joining tree was broken into subtrees of taxa; these taxa are treated on a case-by-case basis in the results section. This serves two purposes. First, it breaks up what would otherwise be an unwieldy amount of information into

manageable subunits and, second, it focuses the reader's attention on the relationships among close relatives (within and among closely related species) while excluding the frequently misleading inferences about relationships that occur at deeper nodes on the tree due to the shortcomings of this type of data and this type of analysis for estimating deeper phylogenetic relationships.

#### DISTANCE MEASURES

Distance measures were employed to assess both intraspecific and intrageneric variation. For all species represented by two or more specimens in the analysis, p-distances were calculated and are given as total number of base pair differences in individual species treatments, and as a percent of the 1044 base pairs (along with mean, standard deviation, and range) in appendix 1. P-distances were also calculated for all genera represented by two or more species in the analysis; these are presented as a percent of the 1044 base pairs



TABLE 4  
**Complete list of primers used for amplification and sequencing**

Location of first nucleotide of primer is given relative to first base of start codon in the multiple alignment. Negative numbers indicate that primer is upstream of start codon. Primer sequences are shown in the 5' to 3' direction even though their placement on the multiple alignment is numbered with respect to the coding strand.

Primer Name	Primer Sequence	Start	End	Notes
<b>External primers</b>				
ILEM	5'-AAGGAGCAGTTTGATAGAGT-3'	-124	-104	universal primer
ASNM	5'-AACGCTTAGCTGTTAATTAA-3'	1217	1237	universal primer
NZ_ND2_Fwd	5'-AGAGATCAAAAACYCTCCG-3'	-110	-92	for NZ <i>Apristurus</i> and <i>Parmaturus</i>
NZ_ND2_Rev	5'-GYRTCTGGGTTGCATTC-3'	1149	1166	for NZ <i>Apristurus</i> and <i>Parmaturus</i>
Torpedo_ND2_Fwd	5'-GCTAAATAAGCTTTTGGGCC-3'	-60	-38	for <i>Torpedo</i>
Torpedo_ND2_Rev	5'-AAGAGGTCGTAGGATCGAAGCC-3'	1197	1219	for <i>Torpedo</i>
Ilem-Mustelus	5'-AAGGACCACTTTGATAGAGT-3'	-194	-175	for <i>Mustelus</i> ; Naylor et al. (2005)
Asn-Mustelus	5'-AACGCTTAGCTGTTAATTAA-3'	1217	1237	for <i>Mustelus</i> ; Naylor et al. (2005)
<b>Internal primers</b>				
ILEM_C_carcharias_490	5'-GTAGGAGGATGAGGCGGATTA-3'	489	510	internal forward
ILEM_G_poecilura_490	5'-CTGAGGAGGCCTTAATCA-3'	497	515	internal forward
ILEM_H_gerrardi_490	5'-CAATTCTCATCGGCGGCTGA-3'	481	501	internal forward
ILEM_H_imbricata_490	5'-AATCCTTATTGGCGGTGAG-3'	482	502	internal forward
ILEM_Mustelus_mosis_490	5'-TTGGTGGATGAGGGGGACTTA-3'	490	511	internal forward
ILEM_P_septhen_490	5'-GGTGGTTGAGGGGTCTTAA-3'	492	512	internal forward
ILEM_R_javanica_490	5'-GGCGTCTCAACCAAAACACAA-3'	501	522	internal forward
ILEM_R_acutus	5'-CATTGGAGGATGAGGAGGGCTTA-3'	488	511	internal forward
ILEM_R_oligolinx	5'-GGAGGATGAGGAGGACTTAAC-3'	492	512	internal forward
L.smithiiTestFwd	5'-GGATCCCACTGACTTCTAG-3'	66	85	internal primer pair; use with ILEM/ ASNM
L.smithiiTestRev	5'-GAGGTGGTCAAGAGGATGAG-3'	970	990	internal primer pair; use with ILEM/ ASNM
Galeus-IntF	5'-CCAACCTCTGCCACACT-3'	274	291	Naylor et al. (2005)
Leptocharias-IntF	5'-CCAACATCTGCCACACT-3'	274	291	Naylor et al. (2005)
ND2-442-IF	5'-CCAACCTCCGCCACACT-3'	274	291	Naylor et al. (2005)
ND2-batoids-IFA	5'-CACTTYTGACTWCCAGAAAGT-3'	334	353	Naylor et al. (2005)
Aeto-IF	5'-CAACCAAGTATCCATCACACT-3'	270	291	Naylor et al. (2005)

(along with mean, standard deviation, and range) in table 3. It should be noted that the p-distance data in table 3 represent the average p-distance among species within a genus, rather than among all constituent specimens of all species in each genus as, for example, calculated in BOLD Systems (v. 2.5; <http://www.boldsystems.org>). We believe that the approach adopted here for summarizing intrageneric p-distances provides a more conservative and biologically reasonable assessment of intrageneric variation. Furthermore, comparisons made between or among

clusters or subclusters are presented as the mean of the mean p-distance of each cluster or subcluster.

Nonetheless, to facilitate comparisons with BOLD Systems-based studies (e.g., Ward et al., 2005; Ward and Holmes, 2007; Ward et al., 2007, 2008, 2009), intraspecific K2P distances (appendix 1) and intrageneric K2P distances (table 3), as calculated in BOLD, were also computed. Both of these distance measures are represented as a percent of the 1044 base pairs (along with mean, standard deviation, and range). As a consequence,

TABLE 5  
 Comparison of intraspecific and intrageneric K2P distances (%) for elasmobranchs between NADH2 (current study) and COI (Ward et al., 2008) sequences

	NADH2 (current study)				COI (Ward et al., 2008)			
	No. of contributing taxa (total number of taxa)	No. of comparisons	Mean $\pm$ SD	Min Max	No. of contributing taxa (total number of taxa)	No. of comparisons	Mean $\pm$ SD	Min Max
<b>Within-species</b> K2P distance	468 <sup>a</sup> (574)	468	0.27 $\pm$ 0.001	0 3.14	171 <sup>a</sup> (210)	2901	0.37 $\pm$ 0.02	0 10.91
<b>Within-genus</b> K2P distance (among congeneric specimens) as calculated in BOLD	143 <sup>b</sup> (157)	331425	10.81 $\pm$ 0.08	0 33.79	38 <sup>b</sup> (76)	16557	7.48 $\pm$ 0.04	0 24.18

<sup>a</sup>Number of species represented by two or more specimens.

<sup>b</sup>Number of genera represented by two or more specimens. Abbreviations: SD, standard deviation; Min, minimum distance observed; Max, maximum distance observed.

these intrageneric K2P distances were calculated, as in BOLD, based on comparisons among all specimens of all species in a particular genus. Summary statistics for intraspecific and intrageneric p-distances are presented in table 2. Similar statistics for intraspecific and intrageneric K2P distances are presented in table 5.

#### HAPLOTYPE NETWORKS

To augment interpretation of the p-distance data for the more problematic species complexes, we generated parsimony haplotype networks for the NADH2 sequences based on median joining networks as implemented in the Network 4.6 software package (Fluxus technology Ltd, 2010). Networks were generated for 27 species complexes, as well as for the least divergent pair of congeners (*Poroderma* species), and for one of the most genetically variable species (*Isurus oxyrinchus*) encountered in this study. We present paired versions for each haplotype network; one colored by phenotype, the other by geography (figs. 79–102). The colors were chosen to emphasize differences within each network and were not standardized across species. The number of base pair differences between haplotypes is shown in red on branches of the phenotype maps where haplotypes differ by more than two mutations. Branch lengths were selected for graphical clarity and are not directly proportional to the number of differences between haplotypes. In each case, circle diameter corresponds to haplotype frequency.

#### SPECIES BOUNDARIES AND NAMES

Specimens that formed distinct clusters in the neighbor-joining analysis were considered candidates for recognition as distinct species. However, only clusters that also exhibited distinct morphological and/or geographic differences relative to other clusters were assigned unique designations. For example, although *Isurus oxyrinchus* showed a substantial amount of genetic variation (figs. 35A and 91A), no geographic pattern to this variation was observed (fig. 91B), nor are we aware of any phenotypic differences consistent with this genetic variation. As a

consequence, we have treated *I. oxyrinchus* as a single species. In contrast, specimens of *Aetobatus* collected from Vietnam (fig. 101B) are both genetically distinct from their congeners in other parts of the world (figs. 63 and 101A) and exhibit a distinct color pattern. Accordingly, these specimens have been given a distinct species designation (*Aetobatus* sp.).

Based on these criteria, the analysis yielded evidence of 79 potentially undescribed species (see table 1). In a number of cases, candidate species names are available but are not in common use. Rather than resurrecting these names, we have used numerical designations to recognize potentially undescribed species in both the figures and text but have given candidate species names in the species treatments in an effort to further taxonomic work on these species. Examples include *Glyphis siamensis* for *G.* sp. 1, *Carcharhinus pleurotaenia* for the Indo-Pacific *C.* cf. *limbatus*, *C. japonicus* for the Indo-Pacific *C.* cf. *plumbeus*, *C. cerdale* for the eastern Pacific *C.* cf. *porosus*, *Rhizoprionodon crenidens* for *R.* cf. *acutus* 2, *Rhizoprionodon fissidens* for *R.* cf. *acutus* 1, *Rhizoprionodon walbeehmi* for *R.* cf. *acutus* 3, *Scoliodon muelleri* for *S.* cf. *laticaudus*, *Cephaloscyllium pictum* for *Cephaloscyllium* sp. 1, and *Scymnodalatias albicauda* for *Centroscymnus* sp. 1, *Galeocerdo arcticus* for the Atlantic form of *G. cuvier*, and *Okamejei meerdervoortii* for *O.* cf. *porosa*. In order to be as conservative as possible, we have not included these taxa in the count of potentially novel species revealed by the analysis, for the existence of possible names for these species attests to the fact that they may not, in fact, be new to science.

Among the novel taxa, are several species that have been previously treated in the literature but never formally described. In such instances, we have attempted to adhere to designations used by previous authors (e.g., Compagno, 2005a; Compagno et al., 2005b). In cases in which entirely novel species were encountered, the taxon label used reflects the nominal species the undescribed species most closely resembles. In cases in which complexes of multiple undescribed species were encountered, each designation was assigned a unique number. The classification follows Compagno (2005a). Common names for species described up to 2005 are generally those

formally presented by Compagno (2005a); for species described after 2005, common names were taken from original descriptions. Type locality data was taken from Eschmeyer and Fricke (2011).

#### SPECIMEN CHOICE AND VOUCHERING

In selecting elasmobranch specimens to include in the analysis, we emphasized those deposited in museums and/or those for which photo vouchers were available in our online Host Specimen Database (<http://elasmobranchs.tapewormdb.uconn.edu>). In total 1921 (44.9%) of the 4283 elasmobranch specimens are represented by images and/or vouchers. The inclusion of such vouchered specimens helped anchor the identities of the remaining specimens that did not come from museums or for which images were not available. We also made an effort to include specimens from as broad a range of the geographic distribution of each species as possible.

Each of the 4283 specimens has been given a unique GN number, which serves as the identifier for the associated molecular data. In the trees in figures 1–77 this number is provided near the end of the string of information given in each taxon label. Following the GN number, the collection code and collection number are provided for all specimens for which images and/or data are available in our host specimen database. The data and images for such specimens can be accessed by entering the collection code and collection number (e.g., BO-43, AF-106, etc.) in the online Host Specimen Database. Furthermore, specimens for which images are available are indicated with the designation “yes” at the end of the taxon label in figures 1–77; those for which images are not available have been given the designation “no.” An asterisk indicates the sample came from a museum specimen. Given the number of potentially new forms represented by our samples, rather than flood GenBank with provisional designations, we have elected to deposit sequence data for one specimen of each nominal taxon. Taxon labels of specimens for which NADH2 sequence data have been deposited in GenBank are indicated in bold in figs. 1–77 (also see appendix 2).

The outgroup consisted of a total of six specimens of four chimera species. These, and the GenBank accession numbers for their NADH2 sequence data are as follows: *Chimaera phantasma* (3 specimens: JQ518717, JQ518718, JQ518719), *Chimaera monstrosa* (1 specimen: JQ518716), *Hydrolagus collei* (1 specimen: JQ518720), and *Hydrolagus novaezealandiae* (1 specimen: JQ518721).

#### SPECIMEN DEPOSITION

In the cases of specimens deposited in museums, the accession numbers are provided in the section of the text treating each taxon. The museum abbreviations used are as follows:

AMNH	American Museum of Natural History, New York, New York	MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil
AMS	Australian Museum, Sydney, Australia	NMNZ	Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand
ANFC	CSIRO Australian National Fish Collection, Hobart, Tasmania, Australia	NTM	Northern Territories Museum (Darwin, Northern Territories), Australia
CAS	California Academy of Sciences, San Francisco	ROM	Royal Ontario Museum, Toronto, Canada
HUMZ	Hokkaido University Museum, Sapporo, Japan	SMEC	Zoology Department of the Sabah State Museum, Kota Kinabalu, Malaysia
IBUNAM	Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico	TCWC	Texas Cooperative Wildlife Collection, College Station, Texas
INIDEP	Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina	TU	Tulane University Museum of Natural History, New Orleans, Louisiana
IPMB	Universiti Malaysia Sabah, Kota Kinabalu, Malaysia	UFFC	University of Florida Fish Collection, Gainesville
IPPS	Institut Penyelidikan Perikanan Sarawak, Kuching, Malaysia	UMMZ	University of Michigan Museum of Zoology, Ann Arbor, Michigan
KAUM	Kagoshima University Museum, Kagoshima, Japan	UW	University of Washington Fish Collection, Seattle, Washington
KUI	University of Kansas Ichthyology Collection, Lawrence, Kansas	VIMS	Virginia Institute of Marine Sciences, Gloucester Point, Virginia
LACM	Los Angeles County Museum, Los Angeles, California	VN	Vietnam Natural Museum of Nature, Hanoi, Vietnam
MCZ	Museum of Comparative Zoology–Harvard, Cambridge, Massachusetts	WAM	Western Australian Museum, Welshpool, Western Australia, Australia
MMF	Museu de História Natural e Aquário, Funchal, Madeira	YPM	Yale Peabody Museum, New Haven, Connecticut.
MZB	Museum Zoologicum Bogoriense, Bogor-Cibinong, Indonesia		

In addition, the acronyms BRU, JPAG, MMLM, and RSE are used for unregistered specimens collected as part of a WWF-funded project, deposited in the SUML (Silliman University Marine Laboratories, Dumaguete City, Philippines) (see Compagno et al., 2005a).

#### RESULTS

The frontispiece provides a schematic overview of figures 1–77 as they relate to the topology of the full neighbor-joining tree. Given the taxonomic scope of this work and that, for some groups, our results suggest that congeners do not form monophyletic groups, we have treated taxa below in the order in which they appear in figures 1–77, regardless

of their current generic or familial placements. This allows readers to use the figures as a guide to locate species treatments within the text (also see table 3 and appendix 1).

CARCHARHINIFORMES (ground sharks)  
**Carcharhinidae (requiem sharks), in part**

*Carcharhinus falciformis* (silky shark) (fig. 1)

A total of 48 specimens representing much of the circumtropical distribution of this species were analyzed. These consisted of 30 specimens taken from Pacific regions including the Philippines, Hawaii, Gulf of California, Borneo, and India, and 18 from Atlantic regions including Senegal, Trinidad, Florida, Gulf of Mexico as well as coastal Georgia. The analysis yielded two weakly divergent subclusters. One subcluster was comprised primarily of specimens from the Pacific localities and the other was comprised of specimens from Atlantic localities. One of the specimens from the Philippines (i.e., GN2242 = RSE 001) was treated by Compagno et al. (2005a). The range in pairwise differences among specimens within the Pacific subcluster was 0–2, and among specimens within the Atlantic subcluster was 0–2. However, it should be noted that the Pacific cluster also included six specimens collected from Atlantic localities. The average of the pairwise differences between these two subclusters was 8.4. The range in pairwise differences among all specimens of *C. falciformis* was 0–10; the average of the pairwise differences among these specimens was 4.2. It should further be noted that a specimen (i.e., GN2214 = BRU 023) from the Philippines considered of uncertain identity but tentatively identified by Compagno et al. (2005a) as “*Hemitriakis* cf. *japanica* (var PP),” grouped among the specimens in the Pacific subcluster of *C. falciformis*.

*Prionace glauca* (blue shark) (fig. 1)

In total 23 specimens were included. These were collected from across much of the global distribution of this species, consisting of samples from specimens from the western North Atlantic, Gulf of California, Hawaii, and Tasmania. One sample in this cluster came from a specimen from Tasmania in the Australian National Fish Collection (GN4917 = ANFC H 4223-01). The range in pairwise

differences seen among specimens was 0–5; the mean was 2.5. No geographic structure was seen among specimens for this species. This species grouped among species of *Carcharhinus*, supporting the contention of previous authors (e.g., Compagno, 1988; Naylor, 1992; Dosay-Akbulut, 2008) that the monophyly of *Carcharhinus* is challenged by recognition of the monotypic *Prionace* as an independent genus.

*Carcharhinus amblyrhynchos* (gray reef shark) (fig. 1)

A total of 18 specimens, coming from Borneo, Philippines, Egypt, and Madagascar, and thus spanning much of the Indo-West and central Pacific distribution of this species, were analyzed. The analysis yielded a single cluster; one of the samples from Sarawak, Malaysia, is represented by a museum specimen (GN3672 = IPPS BO461). The range in pairwise differences seen among specimens in this cluster was 0–10; the mean was 3.8. Essentially no geographic structure was seen among specimens for this species.

*Carcharhinus wheeleri* (blacktail reef shark) (fig. 1)

A single specimen that was morphologically consistent with and collected from the type locality of *C. wheeleri* (i.e., the Red Sea) was included in the analysis. This specimen clustered most closely with but still outside the specimens of *C. amblyrhynchos*. The average of the pairwise differences between the specimen of *C. wheeleri* and those in the *C. amblyrhynchos* cluster was 16.8. This result provides support for the recognition of *C. wheeleri* as a species distinct from *C. amblyrhynchos* despite suggestions to the contrary (e.g., Compagno, 2005b).

*Carcharhinus albimarginatus* (silvertip shark) (fig. 1)

The analysis included five specimens, four from Taiwan and one from the Philippines, and thus represented only a subset of the Indo-Pacific distribution of this species. The analysis yielded two subclusters; one subcluster consisted of some specimens from Taiwan and the single specimen from the Philippines, the other subcluster consisted of the remaining specimens from Taiwan. The range in pairwise differences among specimens within these two subclusters was 0–1

and 2, respectively. The mean of the pairwise differences between subclusters was 19.3. The range in pairwise differences among all specimens of this species was 0–21; the mean was 12.

*Carcharhinus borneensis* (Borneo shark) (fig. 2)

A total of 13 specimens, all collected from Mukah on the island of Borneo, were analyzed. The range in pairwise differences seen among specimens was 0–5; the mean was 2.4. Six of these samples are represented by museum specimens (GN3638 = IPPS BO426, GN3639 = IPPS BO427, GN3660 = IPPS BO449, GN3667 = IPPS BO456, GN3670 = IPPS BO459, and GN3640 = ANFC H 6212-01). This species grouped most closely with the specimens in the *C. macroti* cluster.

*Carcharhinus macroti* (hardnose shark) (fig. 2)

A total of 13 specimens were analyzed. These came from the Gulf of Oman, India, Borneo, and northern Australia and thus spanned much of the Indo-West Pacific distribution of this species. The analysis yielded essentially three subclusters: one consisting of the specimens from India and the Gulf of Oman, one consisting of the specimens from Borneo, and one consisting of the Australian specimens. The range in pairwise differences within these subclusters was 0–4, 1–5 and 1, respectively. The mean of the pairwise differences between the Borneo and Australian cluster was 11.8; between the Gulf of Oman/India and Borneo cluster was 10.0, and between the Gulf of Oman/India and Australian cluster was 12.8. The range in pairwise differences among all 13 specimens was 0–14; the mean was 7.8. These results suggest that some consideration should be given to the existence of several distinct species of hard-nosed sharks.

*Carcharhinus sealei* (blackspot shark) complex (fig. 3)

A total of 51 specimens originally identified as *C. sealei* were included in the analysis. These were collected from the more eastern portions of the distribution of this species and included the Philippines, Borneo, Singapore, and a diversity of localities in western, northern, and eastern Australia. Two distinct subclusters resulted from the analysis, one consisting of all 16 specimens from Australia,

and the other consisting of the 35 specimens from the remaining areas in the Indo-West Pacific, including Malaysian Borneo. The range in pairwise differences within the latter subcluster was 0–8; the mean was 1.8. The range in pairwise differences within the Australian subcluster was 0–6; the mean was 1.6. The average of the pairwise differences between the two subclusters, however, was 20.8. Given that the type locality of this species is in eastern Malaysia, we have provisionally referred to the specimens in the Australian subcluster as *Carcharhinus* cf. *sealei*, reserving the name *Carcharhinus sealei* for those belonging to the subcluster that includes the type locality. Four samples of *C. sealei* from Borneo have voucher specimens (GN4454 = CAS 229028, GN2962 = IPPS HBO40, GN2960 = IPPS HBO35, and GN4188 = MZB 15.503). In addition, three samples of *C. cf. sealei* from Western Australia are vouchered (GN4904 = ANFC H4009-01, GN4905 = ANFC H6582-06, and GN4906 = ANFC H6582-09).

Further support for the recognition of these as separate species comes from the haplotype maps. These reveal two distinctly different tight clusters of haplotypes, one representing each species (fig. 79A), with no overlap in the geographic distribution of the haplotypes in these clusters (fig. 79B).

*Carcharhinus dussumieri* (whitecheek shark) complex (fig. 3)

The analysis included seven specimens initially identified as *C. dussumieri* from Borneo and the Persian Gulf. Two distinct subclusters resulted from the analysis, one consisting of the specimens from Borneo, and the other of the specimens from the Persian Gulf. The range in pairwise differences observed within the Borneo subcluster was 0–1 and within the Persian Gulf subcluster was 1. However, the mean of the pairwise differences between these widely divergent subclusters was substantial, at 54.7. In recognition of this difference we have designated specimens from the Persian Gulf as *Carcharhinus* cf. *dussumieri*, and referred to the specimens from Borneo as *C. dussumieri*. However, given that the type locality (Pondichéry, India) falls between these two regions, these designations

are essentially arbitrary. One of the specimens from Borneo was vouchered (GN4597 = CAS 229042).

The haplotype maps also support the recognition of two species of whitecheek sharks. The haplotype map colored by phenotype reveals two distinctly different tight clusters of haplotypes, one representing each species (fig. 79A), with no overlap in the geographic distribution of the haplotypes in these clusters (fig. 79B).

*Carcharhinus obscurus* (dusky shark) (fig. 4) and  
*Carcharhinus galapagensis* (Galapagos shark)  
(fig. 4)

The analysis yielded a cluster comprised of 46 specimens with evidence of two subclusters. Somewhat unexpectedly, the first subcluster consisted of a combination of specimens considered to represent two distinct species. Specifically, these were four specimens identified as *C. galapagensis*, all collected from Hawaii, as well as 35 specimens of *Carcharhinus obscurus* collected primarily from Indo-West Pacific localities (i.e., Taiwan, the northern half of Australia, including both west and east coasts, and South Africa), as well as a single specimen from Senegal. Two of the samples from Australia were taken from specimens in the Australian National Fish Collection (GN4908 = ANFC H 4778-01 and GN4909 = ANFC H 6358-01). This result suggests that, either the gene used here failed to resolve these two species, or it questions the distinctiveness of these two species. The defining characteristics for distinguishing these two species are habitat and precaudal vertebral counts (Garrick, 1982). The animals identified as *C. galapagensis* were fully consistent with these criteria. The range in pairwise differences among specimens identified as *C. galapagensis* was 1–4. However, the average of the pairwise differences between the four specimens identified as *C. galapagensis* and the specimens of *C. obscurus* in the first (i.e., Indo-West Pacific and Senegal) subcluster was 3; the average of the pairwise differences between the Atlantic and Indo-West Pacific/Senegal clusters of *C. obscurus* was 9.3 (see below). If the NADH2 data are correct, it is possible that *C. galapagensis* may merely represent the oceanic form of *C. obscurus*.

The second subcluster in this cluster was comprised of seven specimens, representing the majority of those collected from Atlantic localities including the Gulf of Mexico and the western Atlantic. The exception was that the specimen from Senegal clustered with the Indo-Pacific specimens. The ranges in pairwise differences seen within the primarily Indo-West Pacific (excluding specimens identified as *C. galapagensis*) and Atlantic subclusters were 0–15 and 0–2, respectively. The range of pairwise differences between the two subclusters of *C. obscurus* (i.e., excluding the specimens identified as *C. galapagensis*) was 7–21; the average of the pairwise differences (see above) was 9.3. The range in pairwise differences among all 46 specimens was 0–21; the average was 4.7. The range in pairwise differences among all 42 specimens of *C. obscurus* 0–21; the average was 4.8.

The haplotype map generated for *C. obscurus* and *C. galapagensis* (fig. 80A) underscores the lack of distinction between these two species. Not only were two of the three haplotypes exhibited by the four specimens of *C. galapagensis* shared by specimens of *C. obscurus*, but the third haplotype of *C. galapagensis* clustered among haplotypes of specimens identified as *C. obscurus*. Although the haplotypes of the Atlantic cluster of *C. obscurus* were divergent from those of the Indo-Pacific specimens, one of the latter specimens (collected from Taiwan) exhibited a haplotype that was conspicuously divergent relative to the other specimens in its cluster, (fig. 80B).

*Carcharhinus longimanus* (oceanic whitetip shark)  
(fig. 4)

Our analysis included seven specimens collected from Taiwan and Hawaii. Thus, these specimens represent only a very small portion of the global distribution of this species. These specimens grouped in a single cluster, with a range in pairwise differences among specimens of 0–3 and an average of 1.7. They grouped most closely with the cluster comprised of the specimens of *C. obscurus* and *C. galapagensis*. The average of the pairwise differences between specimens in the *C. longimanus* cluster and those in the *C. obscurus* and *C. galapagensis* cluster was 34.8.

*Carcharhinus perezii* (Caribbean reef shark) (fig. 4)

A total of 14 specimens, from Belize, the Bahamas, and the Gulf of Mexico, were included. These were found to comprise a single cluster with a range in pairwise differences of 0–10 among specimens. One of the specimens from Belize was responsible for much of this difference. If this specimen is excluded, the range in pairwise differences among specimens within the cluster was 0–1. The average of pairwise differences among all 14 specimens was 1.4.

*Carcharhinus sorrah* (spottail shark) complex (fig. 5)

The analysis included 46 specimens of this species that came from Borneo, India, Singapore, Philippines, Thailand, Vietnam, and northern Australia and thus span much of the eastern regions of the Indo-West Pacific distribution of this species. Three samples from Borneo are represented by vouchers (GN4449 = CAS 229026, GN2957 = IPPS HBO32, and GN4185 = MZB 15.504). The analysis yielded two subclusters, one consisting of the four specimens from Australia, and the other consisting of the remaining 42 specimens. The range in pairwise differences within the Australian subcluster was 1–5; the mean was 3. Within the second subcluster, the range in pairwise differences was 0–17, and the mean 3.8. The mean of the pairwise differences between the two clusters was 15.9, suggesting that this cluster may include two distinct taxa. Given the type locality of *C. sorrah* is Java, the specimens comprising the Australian subcluster have been provisionally referred to as *C. cf. sorrah*, reserving *C. sorrah* for the subcluster that includes specimens from Indonesia. The existence of genetic differences between Australian and Indonesian specimens of *C. sorrah* was also noted by Ovenden et al. (2009).

The haplotype map colored by phenotype (fig. 81A) shows two distinct clusters consistent with the existence of two species of spottail sharks. The haplotype map colored by geography (fig. 81B) shows interesting contrasting patterns of variation in *C. sorrah*. While several specimens collected from throughout Borneo and Vietnam share the same haplotype, specimens from Indian waters exhibit substantial variation.

*Carcharhinus limbatus* (blacktip shark) complex (fig. 6)

A total of 98 specimens identified as *C. limbatus* were analyzed. These specimens span much of the reported global distribution of this species and include a diversity of localities throughout the Indo-Pacific (i.e., Philippines, Taiwan, Borneo, Vietnam, northern Australia, India, Madagascar, Gulf of California, and Hawaii), as well as several localities in the eastern Atlantic (i.e., Sierra Leone and South Africa) and a diversity of localities in the western Atlantic (including the Gulf of Mexico, Belize, and Puerto Rico). The analysis yielded two distinct clusters, one consisting of the specimens collected from the western Atlantic, and the other consisting of the specimens collected throughout the Indo-Pacific Ocean and the eastern Atlantic. This result is fully consistent with that of Keeney and Heist (2006). The range in pairwise differences among the 39 specimens within the western Atlantic cluster was 0–5, and the average was 0.8; the range in pairwise differences among the 59 specimens within the second cluster was 0–18, and the average was 2.8. The specimens in the two clusters exhibited an average of pairwise differences of 22.2. However, of particular note was the fact that the specimens identified as *C. limbatus* did not comprise a single cluster independent of the other species of *Carcharhinus*. In fact, the two clusters of blacktip sharks were separated from one another by a cluster of the 36 specimens of *Carcharhinus amblyrhynchoides* included in the analysis. Given that the type locality of the blacktip shark is assumed to be Martinique Island, West Indies, specimens comprising the western Atlantic cluster have been given the provisional designation *Carcharhinus limbatus*, and those comprising the Indo-Pacific and eastern Atlantic cluster have been provisionally designated as *Carcharhinus cf. limbatus*. We note that one of the specimens from the Philippines was treated by Compagno et al. (2005a) as *C. limbatus* (i.e., GN2260 = JPAG 180). A detailed taxonomic revision of this group is required. If the Indo-Pacific *C. cf. limbatus* is deemed to be a valid species, *Carcharhinus pleurotaenia* (Bleeker, 1852) might need to be resurrected.

A haplotype map was generated that included *C. limbatus*, *C. cf. limbatus*, *C. tilstoni*, as



well as *C. amblyrhynchoides* given their similarities and the historical confusion surrounding these taxa. The haplotype map for phenotype (fig. 82A) shows four distinctive, relatively tight clusters of haplotypes that correspond to each of these four species. The greatest amount of variation within a species was seen in *C. cf. limbatus*. For example, that cluster included a specimen from the South China Sea near Borneo that was conspicuously divergent from its conspecifics. The haplotype map for geography (fig. 82B) illustrates the allopatric nature of *C. limbatus* and *C. cf. limbatus*. It also shows that three of these species (i.e., all but *C. limbatus*) cooccur in Australia.

*Carcharhinus amblyrhynchoides* (graceful shark)  
(fig. 6)

The analysis included a total of 36 specimens collected from northern Australia (17 specimens), Borneo (14 specimens), Vietnam (1 specimen), and India (4 specimens); these represent much of the eastern half of the Indo-West Pacific distribution of this species. The range in pairwise differences among the 36 specimens was 0–9; the average was 4.3. The analysis can be interpreted to yield three weak subclusters, one for each of these three regions. The range in pairwise differences within the subclusters was 0–4 for Australia, 0–4 for Borneo and Vietnam and 0 for India. The average of the pairwise differences between subclusters was 5.7 between the Australia and Borneo-Vietnam subclusters, 7.9 between the Borneo and India clusters, and 7.8 between the Australia and India clusters. One sample from northern Australia (GN1235 = NTM S.04689-006) and one from Borneo (GN2959 = IPPS HBO34) are represented by vouchers. As noted above, the specimens of this species grouped among specimens of the *C. limbatus* complex. The average of the pairwise differences between *C. amblyrhynchoides* specimens and those of *C. limbatus* was 20; and between *C. amblyrhynchoides* specimens and those of *C. cf. limbatus* was 17.3.

*Carcharhinus tilstoni* (Australian blacktip shark)  
(fig. 6)

Eleven specimens taken from the Timor Sea and the Arafura Sea, off northern Australia, were included in the analysis. A

single cluster consisting of these specimens was found. The range in pairwise differences within this cluster was 0–5; the mean was 2. The existence of this cluster, independently from that of the *C. limbatus* complex, supports *C. tilstoni* as a valid species (Stevens and Wiley, 1986; Lavery and Shacklee, 1991). However, the vertebral count data collected for these specimens failed to support this as a valid key characteristic for distinguishing between *C. tilstoni* and *C. limbatus*. The average of the pairwise differences between *C. tilstoni* and *C. limbatus* was 20.6, between *C. tilstoni* and *C. cf. limbatus* 24.2, and between *C. tilstoni* and *amblyrhynchoides* 19.1.

The haplotype map colored by phenotype in figure 82A underscores the distinctness of *C. tilstoni* from *C. limbatus*. The haplotypes of the 11 specimens of *C. tilstoni* included in the analysis are very similar to one another, but conspicuously different from those of specimens of both *C. limbatus* and *C. cf. limbatus*. Haplotypes consistent with *C. limbatus* appear to be restricted to Australia (fig. 82B). Our results suggest that additional work is required to identify morphological features that allow for the reliable distinction between *C. tilstoni* and the other species of blacktip sharks.

*Carcharhinus fitzroyensis* (creek whaler) (fig. 6)

A total of three specimens, all collected from Fog Bay, Australia, were included in the analysis. These comprised a single cluster; the sequences for these three specimens were identical. One of these samples is represented by a voucher in the Northern Territories Museum (GN1267 = NTM S.14690-002).

*Carcharhinus melanopterus* (blacktip reef shark)  
complex (fig. 7)

The analysis included a total of 26 specimens originally identified as this species. These were collected from the Philippines, Thailand, Borneo, the Timor Sea, the Gulf of Carpentaria in northern Australia, and Egypt. Despite our specimens being biased toward the eastern sector of the reported distribution of this species, the analysis yielded two subclusters; one consisting of the two specimens from Egypt, and the other consisting of the 24 specimens from a diversity of localities throughout the Indo-Pacific. The

specimens from Egypt differed from one another by one base; the range in pairwise differences within the larger subcluster was 0–9; the average was 4.3. The mean of the pairwise differences between the two subclusters was 15.3. In recognition of this difference, the subcluster from Egypt has been provisionally referred to as *Carcharhinus cf. melanopterus*, reserving *C. melanopterus* for the subcluster comprised of specimens more proximal to the type locality (i.e., eastern Indonesia).

*Carcharhinus cautus* (nervous shark) (fig. 7)

The five specimens of this species included in the analysis were collected from Buffalo Creek in northern Australia and were all identical in sequence. Two of these samples are represented by vouchers in the Northern Territory Museum (GN1233 and GN1234 = NTM S.14689-005). These specimens grouped most closely with specimens in the *C. melanopterus* complex. The average of the pairwise differences between *C. cautus* and those in the latter complex was 25.7.

*Carcharhinus leucas* (bull shark) complex (fig. 8)

A total of 24 specimens originally identified as *Carcharhinus leucas* were included in the analysis. These came from a diversity of localities that emphasize the Atlantic, rather than Pacific, elements of the distribution of this species, including the western North Atlantic (e.g., Alabama and Florida) as well as Belize, Sierra Leone, Senegal, and South Africa. In addition, seven of the specimens were collected in Borneo. The analysis yielded three potential subclusters, one consisting of the specimens from the western Atlantic, Belize, Senegal, and Sierra Leone, a second consisting of the three specimens from South Africa, and a third consisting of the seven specimens from Borneo. These results suggest that *C. leucas* may represent a complex of closely related species. Given that the type locality of *C. leucas* is in the western North Atlantic (i.e., the Antilles), we have used the provisional designation *C. leucas* for specimens comprising the primarily Atlantic subcluster. The specimens in the Borneo subcluster are referred to as *C. cf. leucas* 1. The three specimens in the South African subcluster are referred to as *C. cf. leucas* 2. The range of pairwise differences

among specimens in the *C. leucas* subcluster was 0–1, among specimens the *C. cf. leucas* 1 subcluster was 0–12, and among specimens in the *C. cf. leucas* 2 subcluster was 1–7. The average of pairwise differences within the *C. cf. leucas* 1 subcluster was 4.8, and within the *C. cf. leucas* 2 subcluster was 4.7. The average of the pairwise differences between specimens of *C. leucas* and *C. cf. leucas* 1 was 17.3, between specimens of *C. leucas* and *C. cf. leucas* 2 was 17.1, and between specimens of *C. cf. leucas* 1 and *C. cf. leucas* 2 was 13.1.

The haplotype map colored by phenotype (fig. 83A) shows that, although there is notable variation in haplotypes within each cluster, there is no overlap in haplotypes among the three potential species of bull sharks. The haplotype map for geography (fig. 83B) illustrates that the haplotypes of all three bullshark species are allopatrically distributed. Members of this complex would benefit greatly from further investigation.

*Carcharhinus amboinensis* (pigeon shark) complex (fig. 8)

The 10 specimens of this species included here were collected from India, South Africa, and several localities in western and northern Australia and thus represent much of the reported distribution of this species. The analysis yielded a single cluster consisting of two conspicuous subclusters. One subcluster consisted solely of specimens taken from western and northern Australia, whereas the other subcluster consisted of specimens from India, South Africa, and northern Australia. What makes this pattern somewhat puzzling is the occurrence of specimens from northern Australia in both subclusters, particularly given that some of these specimens were collected from the same exact locality on the same day. The range in pairwise differences within the solely northern Australian subcluster was 0–1, whereas range for the other subcluster was 0–10, with an average of 4. We note that one of the Australian samples came from a specimen deposited in the Australian National Fish Collection (GN4903 = ANFC H 6655-01). Given that the mean of the pairwise differences between these two subclusters was 26.6, it seems appropriate to nominally recognize both subclusters. In the absence of

specimens collected from the type locality (i.e., Ambon Island, Indonesia), we have used the designation *C. amboinensis* 2 for the solely Australian subcluster, and *C. amboinensis* 1 for the second subcluster.

The haplotype map for phenotype (fig. 83A) supports the notion that there are two distinct species of pignose sharks. There is no overlap in haplotypes between specimens of the two putative species. The haplotype map for geography (fig. 83B), illustrates that, although *C. amboinensis* 1 also occurs in South Africa, haplotypes of both species cooccur in Australia. This complex needs to be explored in more detail.

*Carcharhinus plumbeus* (sandbar shark) complex (fig. 9)

A total of 74 specimens originally identified as *C. plumbeus* were included in the analysis. These came from a diversity of localities in the western North Atlantic, as well as Hawaii, Borneo, Vietnam, the Philippines, and Taiwan. However, with respect to the overall reported distribution of *C. plumbeus*, our sample was conspicuous in its lack of representation from the Indian and eastern Atlantic oceans. Nonetheless, the analysis yielded two distinct clusters of sandbar sharks, one of which included the 22 specimens of *Carcharhinus altimus* in the analysis. The first cluster of sandbar sharks consisted solely of the 17 specimens from the Indo-Pacific. The second cluster consisted of 57 specimens originally identified as *C. plumbeus* from the western Atlantic localities, in addition to all of the specimens of *C. altimus*. The range in pairwise differences observed among the 17 specimens comprising the Indo-Pacific cluster of sandbar sharks was 0–8; the average within this cluster was 1.7. The range in pairwise differences seen among the 57 sandbar shark specimens comprising the western Atlantic cluster (excluding *C. altimus*) was 0–13; the average was 1.2. The average of the pairwise differences between the Indo-Pacific and the western Atlantic clusters of sandbar sharks (again, excluding *C. altimus*) was 14.9. Given this result, and the fact that the type locality of *C. plumbeus* is the Adriatic Sea, we have provisionally given specimens in the cluster collected from the western Atlantic the designation of *C. plumbeus* and those

from the Indo-Pacific the designation of *C. cf. plumbeus*. If further taxonomic investigation reveals this latter species to be valid, *Carcharhinus japonicus* (Temminck and Schlegel, 1850) might need to be resurrected. The affinities between Atlantic sandbar sharks and *C. altimus*, to the exclusion of the Pacific sandbar sharks, have been observed previously by a number of authors (e.g., Heist and Gold, 1999; Greig et al., 2005).

The haplotype map of phenotypes for all 74 sandbar shark specimens and the specimens of *C. altimus* (fig. 84A) supports recognition of the two sandbar shark species and *C. altimus* as distinct taxa. However, in the Atlantic *C. plumbeus* cluster, one specimen exhibited a particularly divergent haplotype relative to its conspecifics (fig. 84A). The geography haplotype map (fig. 84B) illustrates that *C. plumbeus* and *C. altimus* are sympatric in the western Atlantic and its environs, while *C. cf. plumbeus* appears to be restricted to the Indo-Pacific.

*Carcharhinus altimus* (bignose shark) (fig. 9)

The analysis included 22 specimens of this species, collected from the western North Atlantic, as well as the Gulf of Mexico, Hawaii, and Taiwan. These specimens, which admittedly lack representation of the eastern Atlantic, eastern Pacific, and Indian Ocean elements of the distribution of this species, were found to comprise a single cluster, exhibiting a range in pairwise differences among specimens of 0–9; the average was 1.8. However, as noted above, the *C. altimus* cluster was nested among the Atlantic specimens of *C. plumbeus*. Given the substantial morphological differences between *C. altimus* and the Atlantic form of *C. plumbeus*, we have treated them as distinct here.

*Carcharhinus brevipinna* (spinner shark) (fig. 10)

In total, 35 specimens of this species were included. Collectively, these specimens represent much of the distribution of this species, coming from the western Atlantic, Gulf of Mexico, Senegal, Sierra Leone, India, Philippines, Borneo, Vietnam, and Taiwan. The analysis yielded only a single cluster. The range in pairwise differences within the cluster was 0–20 and the average was 6.2.

*Carcharhinus brachyurus* (bronze whaler) complex (fig. 10)

In total, 10 specimens initially identified as this species were included in the analysis. These were collected from South Africa, Madeira (Portugal), southern Australia, and Taiwan, and thus span much of the distribution of this species, with the exception of the Americas. The analysis yielded two subclusters, one consisting of the specimen from Madeira and the seven specimens from South Africa, and the other consisting of the single specimen from each of Australia and Taiwan. The pairwise difference between the two specimens in the latter subcluster was 2; the range in pairwise differences among specimens within the African subcluster was 0–7, with an average of 2.4. The mean of the pairwise differences between these two subclusters was 23.3. Given that the type locality of *C. brachyurus* is New Zealand, we have provisionally referred to the smaller subcluster of specimens from Taiwan and southern Australia as *C. brachyurus*, and have given the specimens in the larger subcluster the designation *C. cf. brachyurus*. One specimen of *C. cf. brachyurus* from Portugal is represented by a voucher (GN6628 = MMF 39543). If further taxonomic investigation reveals the latter taxon as a distinct species, one of the species currently placed in the synonymy of *C. brachyurus* might need to be resurrected.

*Carcharhinus acronotus* (blacknose shark) (fig. 10)

All 11 specimens of this species were collected from the western Atlantic and the Gulf of Mexico. The analysis yielded a single cluster; the range in pairwise differences within this cluster was 0–5, with an average of 2.1.

*Nasolamia velox* (whitenose shark) (fig. 10)

The analysis included a single specimen of this species, collected from Panama. This specimen represents a southern element of the distribution of this species, which occurs from Baja to Peru. It grouped most closely with the specimens of *C. acronotus*; the average of the pairwise differences between specimens of these two species was 23.7.

*Carcharhinus isodon* (finetooth shark) (fig. 11)

All 16 specimens of this species included here were collected from the western North

Atlantic and the Gulf of Mexico and thus represent only the northeastern elements of the distribution of this species. The analysis yielded a single tight cluster. The range in pairwise differences within this cluster was 0–4, with a mean of 1.3.

*Isogomphodon oxyrhynchus* (daggernose shark) (fig. 11)

The five specimens included in the analysis were all collected from Maranhao, Brazil. As this species is apparently restricted in distribution to the northeastern regions of South America these specimens are representative of its range. A single cluster resulted from the analysis. Sequences of the five specimens were essentially identical (i.e., the maximum difference seen among specimens was 1).

*Carcharhinus porosus* (smalltail shark) complex (fig. 11)

Our analysis included a total of 18 specimens, 15 from Trinidad, and three from the Gulf of California. As this species is reported from much of the western Atlantic seaboard, and also from throughout the west coasts of Mexico, Columbia, and Ecuador, our sample is somewhat limited with respect to the overall distribution of this species. Nonetheless, the analysis resulted in two subclusters, one representing the Atlantic and one the Pacific localities. The range in pairwise differences within the Trinidad subcluster was 0–10, with an average of 4.4; the sequences of the three specimens comprising the Gulf of California subcluster were identical. The mean of the pairwise differences between the two subclusters was 18.5. Given these differences, and the fact that the type locality is Brazil, we have provisionally designated the specimens from Trinidad as *Carcharhinus porosus*, and refer to the specimens from Baja as *Carcharhinus cf. porosus*. One specimen of the latter taxon is represented by a voucher (GN1107 = IBU-NAM PE9494). A detailed taxonomic revision of this species is required and if the eastern Pacific population is deemed to be a valid species, *Carcharhinus cerdale* Jordan and Evermann, 1898, might need to be resurrected.

*Carcharhinus signatus* (night shark) (fig. 12)

Our analysis included a total of six specimens, all taken from the western North

Atlantic and the Gulf of Mexico. However, the south and eastern Atlantic elements of the distribution of this species were not sampled. The analysis yielded a single cluster; the range in pairwise differences among the six specimens of this cluster was 0–3, with a mean of 1.7.

*Triaenodon obesus* (whitetip reef shark) (fig. 13)

In total, the analysis included nine specimens of this species. These came from Hawaii (or possibly Christmas Island), Sulawesi, Borneo, and the Red Sea and Gulf of Aqaba, and thus span much of the distribution of this species with the exception of the eastern Pacific. The analysis resulted in essentially a single cluster. The range in pairwise differences among the specimens comprising this cluster was 0–9; the mean was 4.3

*Lamiopsis tephrodes* (Borneo broadfin shark) and  
*Lamiopsis temmincki* (broadfin shark) (fig. 14)

*Lamiopsis tephrodes* was originally collected by Fowler (1905), from the Baram River in Sarawak, Malaysia. Until recently, it has been considered to be a synonym of *Lamiopsis temmincki* (e.g., Compagno, 1984a, 1988), which was originally collected from India. However, *L. tephrodes* has recently been resurrected by White et al. (2010b) for the Indo-Malay form. Our sample included 26 specimens collected from Borneo (both Malaysian and Indonesian regions), as well as a single specimen collected from India; the analysis showed the 26 specimens from Borneo to cluster outside the specimen from India. Four of the Borneo specimens are represented by vouchers (GN4241 = CAS 229045, GN4240 = ANFC H 7083-01, GN4803 = ANFC H 7084-01, and GN3476 = IPPS BO259). The range in pairwise differences within the Borneo cluster was 0–3; the average of the pairwise differences between members of the Borneo cluster and the specimen from India was 23.9. Thus, our results support the decision to resurrect *L. tephrodes*.

*Glyphis* species (fig. 14)

Specific designations within this genus have recently come under much scrutiny. In these treatments (i.e., Compagno et al., 2008, 2010; Fahmi and Adrim, 2009), the genus has been considered to include a minimum of five valid species: *Glyphis garricki* recently de-

scribed by Compagno et al. (2008) from northern Australia and Papua New Guinea (= *Glyphis* sp. C of Compagno and Niem, 1998) and confirmed as distinct from *G. glyphis* by Wynen et al. (2009); *Glyphis glyphis*, recently redescribed by Compagno et al. (2008) from material from northern Australia and Papua New Guinea (and includes *Glyphis* sp. A of Compagno and Niem, 1998, and Last and Stevens, 1994); *Glyphis gangeticus* from the Ganges River, India (and possibly Pakistan see Compagno et al., 2005b); *Glyphis siamensis* (Steindachner, 1896) from the Irrawaddy River in Burma; and the recently described *Glyphis fowlerae* Compagno, White and Cavanagh, 2010 (*Glyphis* sp. B of Compagno and Niem, 1998), from the Kinabatangan River in Sabah, Malaysian Borneo. In addition, Fahmi and Adrim (2009) reported, as *Glyphis* sp., a specimen from Sampit, Kalimantan, Borneo, which may represent another undescribed taxon.

Our analysis included a total of 15 specimens of *Glyphis*: five from the West Alligator River, Australia, collected and identified by Louise McMahan of Charles Darwin University, Darwin, and consisting of three specimens of *G. garricki* and two of *Glyphis glyphis*; four specimens of *Glyphis fowlerae* consisting of the holotype (GN3376 = IPMB 38.14.02; also Fahmi and Adrim, 2009: fig. 7), a paratype (GN3377 = IPMB 38.14.03), and a third specimen, all from the Kinabatangan River in Sabah, Borneo, as well as one from Java, Indonesia; three specimens from Pakistan and India, which we have provisionally identified as *G. gangeticus*, primarily because Pakistan is included among the localities of this species; one specimen from the Bay of Bengal, off Bangladesh, and two from Malaysian Borneo, tentatively identified as *Glyphis* sp. 1.

The analysis yielded four primary clusters of specimens. One cluster consisted of a subcluster of the four specimens of *Glyphis fowlerae* and a subcluster of the three specimens identified as *Glyphis gangeticus*. A second cluster consisted of the three specimens of *Glyphis* sp. 1. A third cluster consisted of the three specimens of *G. garricki*. The fourth cluster consisted of the two specimens of *G. glyphis*. The range in pairwise differences among specimens of *G.*

*gangeticus* was 0–3, with an average of 2. The range in pairwise differences among specimens of *Glyphis fowlerae* was 0–6, with an average of 3. The range in pairwise differences among specimens of *Glyphis* sp. 1 was 5–7, with an average of six bases. The two specimens of *G. glyphis* differed by two bases, and the three specimens of *G. garricki* were identical in sequence. The means of the pairwise differences between clusters ranged from 7.5 (*G. gangeticus* vs. *G. fowlerae*) to 102.7 (*G. glyphis* vs. *G. sp. 1*). Pairwise differences among the five nominal species are as follows. The difference between *G. fowlerae* and *G. gangeticus* is 7.5, and *Glyphis* sp. 1 is 83.3, and *G. garricki* is 89, and *G. glyphis* is 85; the difference between *G. gangeticus* and *Glyphis* sp. 1 is 81.3, and *G. garricki* is 88, and *G. glyphis* is 83; the difference between *Glyphis* sp. 1 and *G. garricki* is 100.3, and between *Glyphis* sp. 1 and *G. glyphis* is 102.7; the difference between *G. garricki* and *G. glyphis* is 54.

In summary, our results support the distinction between *G. garricki* and *G. glyphis* despite their sympatry. While the correct name to apply remains uncertain, our results suggest that a species (perhaps *G. gangeticus*) occurs in Pakistan and India, and is very close to *G. fowlerae* from Borneo. Furthermore, our results suggest that there exists a species, distinct from all of those included here, that occurs in Bangladesh and Malaysian Borneo. Whether this represents a species new to science or is conspecific with one of those not included in our analysis (e.g., *G. siamensis*) remains to be determined. We have designated this specimen *Glyphis* sp. 1 to distinguish it from other recognized but as yet unnamed species of the genus.

*Negaprion acutidens* (sharptooth lemon shark) (fig. 14)

The analysis included 14 specimens of this lemon shark species, all collected from northern Australia, either the Gulf of Carpentaria or the Timor Sea. The analysis yielded a single tight cluster. The range in pairwise differences among specimens within this cluster was 0–5, with an average of 0.9. Unfortunately, our samples were relatively restricted in distribution and thus did not allow us to assess the variation among local-

ities seen in this species by Schultz et al. (2008).

*Negaprion brevirostris* (lemon shark) (fig. 14)

In total, six specimens were included in the analysis. These all came from the Gulf of Mexico, the east coast of Florida, and the Caribbean Sea. The analysis yielded a single cluster with a range in pairwise differences among specimens within the cluster of 0–4, with an average of 1.3. Once again, our samples represent only a small portion of the distribution of this species and thus did not allow us to assess variation among localities in this species reported by Schultz et al. (2008). The mean of the pairwise differences between specimens of *N. brevirostris* and *N. acutidens* was 85.8.

*Rhizoprionodon acutus* (milk shark) complex (fig. 15)

In total, 61 specimens originally identified as this species were included in the analysis. These samples were relatively representative of the complete distribution of this species, consisting of 14 specimens from the west coast of Africa, 7 from the Gulf of Oman, 7 from India, 20 from Borneo, 3 from the Philippines, and 10 from northern Australia. The analysis yielded four distinct subclusters. The first cluster consisted of the specimens from west coast of Africa. The second cluster consisted of the specimens from the Gulf of Oman and the majority of the specimens from India. The third subcluster consisted of the specimens collected from Australia, and the fourth of all the specimens from Borneo and the Philippines as well as two of the specimens from India. The ranges in pairwise differences within these subclusters were 0–2 (western Africa subcluster), 0–6 (Gulf of Oman etc. subcluster), 0–8 (Australia subcluster), and 0–8 (Borneo, etc.); the means were 0.6, 1.5, 2.4, and 3.2, respectively. The means of the pairwise differences among subclusters were as follows: 10 (western Africa vs. Gulf of Oman), 16.6 (western Africa vs. Australia), 17.6 (western Africa vs. Borneo), 15.6 (Gulf of Oman vs. Australia), 18.8 (Gulf of Oman vs. Borneo), and 15.3 (Australia vs. Borneo). Based on these differences we have given the four subclusters separate designations. Since the type locality of *R. acutus* is the Red Sea, the specimens in the

cluster from the Gulf of Oman and India have been given the designation *R. acutus*. The remaining three subclusters have been referred to as: *Rhizoprionodon* cf. *acutus* 1 (western Africa cluster), *Rhizoprionodon* cf. *acutus* 2 (Australia cluster), and *Rhizoprionodon* cf. *acutus* 3 (Borneo, etc., cluster). We note that two of the specimens of *R. cf. acutus* 2 came from specimens in the Australian National Fish Collection (GN4918 = ANFC H 4559-01 and GN4919 = ANFC H 6582-12) and one specimen of *R. cf. acutus* 3 came from the Institut Penyelidikan Perikanan Sarawak in Kuching, Malaysia (GN2955 = IPPS HBO30). This potential complex of species is in need of further investigation. If a taxonomic revision reveals that the three subclusters listed above are distinct from *R. acutus*, the following species currently placed in synonymy with *R. acutus* might need to be resurrected as valid species: *R. crenidens* (Klunzinger, 1880) for the Australian species; *R. fissidens* (Bennett, 1831) for the western Africa species; *R. walbeehmi* (Bleeker, 1856) for the western central Pacific species.

A haplotype map colored by phenotype (fig. 85A) supports the idea that *R. acutus* is a complex of four species. It shows four relatively tight haplotype clusters consistent with the four species treated above. The haplotype map colored by geography (fig. 85B) indicates that all four species are allopatric, with the exception of the cooccurrence of *R. acutus* and *R. cf. acutus* 3 in India.

*Rhizoprionodon terraenovae* (Atlantic sharpnose shark) (fig. 16)

Our analysis included a total of 24 specimens, which came from the western North Atlantic, Gulf of Mexico, Caribbean Sea, and Belize, and thus represent much of the distribution of this species. The range in pairwise differences among specimens within this relatively divergent cluster was 0–16; the mean was 4.9.

*Rhizoprionodon porosus* (Caribbean sharpnose shark) (fig. 16)

Two specimens were included. Both came from Trinidad, located in the northern region of the distribution of this species, which extends throughout the eastern coast of South America. These two specimens differed

in sequence by two bases. They were found to cluster most closely with the specimens of *R. terraenovae*. The average of the pairwise differences between specimens of *R. porosus* and those of *R. terraenovae* was 17.9.

*Rhizoprionodon longurio* (Pacific sharpnose shark) (fig. 16)

The eight specimens of this species included in the analysis were all collected from the Gulf of California and thus represent only the more northern region of the distribution of this species, which extends south from Baja along the western coast of North and Central America to Peru. These specimens comprised a relatively divergent cluster; two of the specimens (both collected from Bahia de Los Angeles) grouped together to the exclusion of the remaining six specimens (5 from Puertecitos and 1 from San Jose del Cabo). The range in pairwise differences among all eight specimens in the cluster was 1–8, with an average of 4.2; the two specimens from Puertecitos differed by 1; the range in pairwise differences among the remaining six specimens was 0–7.

*Rhizoprionodon lalandii* (Brazilian sharpnose shark) (fig. 16)

The six specimens of this species included in the analysis came from Trinidad. They represent the more northern regions of the distribution of this species. The analysis yielded a single cluster with the range in pairwise differences observed among specimens in this cluster being 0–2.

*Rhizoprionodon taylori* (Australian sharpnose shark) (fig. 16)

A total of 14 specimens, collected from the Timor Sea and the Gulf of Carpentaria off northern Australia, was included. The analysis yielded a single cluster, with a range in pairwise differences of 0–9 among specimens, with a mean of 4.4. One sample in this cluster was taken from a specimen in the Australian National Fish Collection (GN4920 = ANFC H 6655-02) and two from samples from specimens in the Northern Territory Museum (GN1254 and GN1255 = NTM S.14690-001).

*Rhizoprionodon oligolinx* (gray sharpnose shark) (fig. 17)

In total, 17 specimens were included; these came from Borneo and India and thus are

generally representative of the distribution of this species. These specimens comprised a loose cluster with some structure reflecting these two regions. The range in pairwise differences among all 17 specimens was 0–15, with an average of 5.8. Two specimens are represented by vouchers (GN3685 = IPPS BO474 and GN3686 = IPPS BO475).

*Scoliodon* species (fig. 18)

Our analysis included 61 specimens of *Scoliodon*: 29 from Borneo, 17 from Vietnam, 2 from Taiwan, 11 from India, and 2 from the Bay of Bengal, east of Thailand. Up until recently, this genus was considered monotypic (e.g., Compagno et al., 2005a), containing only *Scoliodon laticaudus*. However, White et al. (2010a) resurrected *Scoliodon macrorhynchus* from Java, Indonesia as a valid species. Our analysis yielded three distinct clusters of *Scoliodon*. The first cluster consisted of the *S. macrorhynchus* specimens from Borneo, Vietnam, and Taiwan; the range in pairwise differences among these specimens was 0–8, with an average of 2.2. Two of these specimens are deposited in the IPPS (GN3449 = IPPS BO222 and GN3450 = IPPS BO223). The second cluster consisted of the *S. laticaudus* specimens from India, which had a range in pairwise differences among specimens of 0–2. The third cluster consisted of the two specimens from the Bay of Bengal west of Thailand; their sequences differed by 5. Between-cluster differences were found to be substantial and not only supported *S. laticaudus* and *S. macrorhynchus* as separate species, but suggested the specimens from Thailand represent a distinct species. The latter have been given the designation *Scoliodon* cf. *laticaudus*, but taxonomic investigation is required to determine whether they represent an undescribed species or whether *S. muelleri* (Müller and Henle, 1839) should be resurrected as a valid species. The average of the pairwise differences between the *S. laticaudus* and *S. macrorhynchus* clusters was 32.1, between the *S. laticaudus* and *S. cf. laticaudus* clusters 33.8, and between the *S. macrorhynchus* and *S. cf. laticaudus* clusters 40.4.

The haplotype map colored by phenotype (fig. 86A) supports recognition of three species of *Scoliodon*; in each case haplotypes

of replicate specimens within a species are tightly clustered and conspicuously different from specimens in other species clusters. The haplotype map colored by geography (fig. 86B) illustrates that, although our specimens of *S. macrorhynchus* were collected from a diversity of localities in the central Indo-Pacific, they exhibit relatively little haplotype variation in NADH2.

*Loxodon macrorhinus* (sliteye shark) complex (fig. 18)

In total, 21 specimens of *Loxodon* were included in the analysis. These came from Borneo (14 specimens), India (4 specimens), the Philippines (2 specimens), and Madagascar (1 specimen). At present this genus is considered to include only the single valid species, *Loxodon macrorhinus*, with the type locality unknown (probably Indian Ocean). Our analysis yielded two clusters, one consisting of two of the specimens from India and all the specimens collected from Borneo and the Philippines (with a range in pairwise differences among specimens of 0–11, and an average of 4.6), and the other consisting of the remaining two specimens from India and a specimen from Madagascar (with a range in pairwise differences among specimens of 0–1). We have provisionally referred to specimens in the former cluster as *Loxodon macrorhinus*, whereas those in the latter cluster have been given the designation *L. cf. macrorhinus*; the average of the pairwise differences between these clusters was 29.9. Our results support the existence of a second species in this currently monotypic genus. Further taxonomic research is required to determine which species represents the true *L. macrorhinus*, and whether the second species truly represents an undescribed taxon.

### Sphyrnidae (hammerhead sharks)

Our analysis includes representation of seven of the eight described species of hammerhead sharks. However, we believe it also includes specimens of three undescribed species of hammerheads. To allow comparison of genetic variation across species, the haplotype maps presented for hammerheads (fig. 87A, B) include all 10 of these species. The implications of these maps for the three species complexes (*S. lewini*, *S. zygaena*, and



*S. tiburo*) are each treated separately below. However, from the standpoint of the family in general, it is interesting to note that the haplotype map colored by geography (fig. 87B) illustrates that hammerheads are among the most widely distributed species of elasmobranchs. For example, the same haplotype of *S. lewini* 1 is found in animals from the western Indian Ocean, India, and South China Sea. Similarly, the same haplotype of *S. zygaena* is found in animals from Taiwan, Borneo, and northern Australia. Little variation is seen in the haplotypes of individuals of *S. lewini* 2 that occur in Borneo, Taiwan, and the Gulf of California. Little variation is seen in the haplotypes of individuals of *S. zygaena* from the Gulf of Mexico, western North Atlantic, Senegal, Japan, Taiwan, Vietnam, and the Gulf of California. Nevertheless, it seems there is a great deal of sympatry. For example, the western Atlantic (including the Gulf of Mexico and Trinidad) is home to six species of hammerheads (*S. lewini* 2, *S. mokarran* 1, *S. tiburo*, *S. cf. tiburo*, *S. tudes*, and *S. zygaena*).

*Sphyrna lewini* (scalloped hammerhead) complex (fig. 19)

Our analysis included a total of 45 specimens initially identified as the scalloped hammerhead *S. lewini*. These came from the western North Atlantic (11 specimens), the Gulf of Mexico (6 specimens), Senegal (4 specimens), Madagascar (3 specimens), India (5 specimens), Borneo (10 specimens), Gulf of California (2 specimens), and Taiwan (4 specimens). Given that the type locality of this species is southern Australia, the unavailability of specimens from Australia was unfortunate. Our analysis yielded considerable structure among *S. lewini*. First, the analysis yielded two strongly divergent clusters, each with some substructure. However, at this time we have recognized only the two main clusters. The 32 specimens comprising the first cluster, from the western Atlantic, Gulf of Mexico, Senegal, Madagascar, India, and Malaysian Borneo, have been designated *Sphyrna lewini* 1, and the 13 specimens comprising the second cluster, from the Gulf of California, Borneo, and Taiwan, have been designated *Sphyrna lewini* 2; one specimen from the latter cluster is vouchered

(GN4187 = CAS 229024). Within the *S. lewini* 1 cluster, the specimens from the Gulf of Mexico and the western North Atlantic comprised a weak subcluster; the specimens from Senegal comprised a second weakly supported subcluster, and the specimens from India, Madagascar, and those from Malaysian Borneo comprised a third weakly supported subcluster. In addition, the specimens from Madagascar and India and three of the specimens from Borneo comprised a subcluster. Within the *Sphyrna lewini* 2 cluster, there was evidence of a subcluster consisting of a specimen from Taiwan and one from Malaysian Borneo. The range in pairwise differences among all 45 specimens of *S. lewini* was 0–78. The range in pairwise differences within the *S. lewini* 1 cluster was 0–12, with an average of 4.4. The range within the *S. lewini* 2 cluster was 0–21, with an average of 7.2. The average of the pairwise differences between specimens of *S. lewini* 1 and *S. lewini* 2 was 64.2. These results suggest that undescribed diversity exists among scalloped hammerheads, which may include sympatric species. This result is consistent with those of a number of previous authors who also reported genetic diversity within *S. lewini* (e.g., Abercrombie et al., 2005; Duncan et al., 2006; Quattro et al., 2006; Zemlak et al., 2009).

The haplotype map colored by phenotype (fig. 87A) supports recognition of *S. lewini* 1 and *S. lewini* 2 as they exhibit distinct, but relatively tight clusters of haplotypes. The haplotype map colored by geography (fig. 87B) illustrates the relatively broad distributions of both of these clusters of haplotypes (fig. 87B).

*Sphyrna tiburo* (bonnethead shark) complex (fig. 19)

All 14 specimens originally identified as *S. tiburo* were collected from the Gulf of Mexico (12 specimens) and Trinidad (2 specimens). As a consequence, our sample represents only a portion of the distribution of this species along the western Atlantic seaboard, and we have no representation of the eastern Pacific portions of the distribution of this species. The analysis yielded some geographic structure in that the specimens from the Gulf of Mexico clustered together as did those from Trinidad. The range in pairwise differences among bonnetheads overall was 0–28. The range in pairwise differences within the Gulf of Mexico

cluster was 0–3, with an average of 0.6, and the two specimens from Trinidad differed by 4. The average of the pairwise differences between the two clusters was 25.3. In recognition of the fact that the type locality of *S. tiburo* is America, we have given the Trinidad specimens the designation *Sphyrna* cf. *tiburo*. However, the type locality of *S. tiburo* is imprecise so the nomenclature of this group needs to be examined more thoroughly.

The haplotype map colored by phenotype (fig. 87A) supports the distinction between *S. tiburo* and *S. cf. tiburo*.

*Sphyrna tudes* (smalleye hammerhead) (fig. 19)

Our analysis included four specimens, all collected from Trinidad. Thus, our sample comes from a relatively northerly locality within the distribution of this species, which extends along the east coast of South American to Argentina. The analysis yielded a single cluster. The range in pairwise differences within the cluster was 0–6, with an average of 3.

*Sphyrna corona* (mallethead shark) (fig. 19)

The six specimens included in the analysis all came from the western coast of Panama. Thus, they represent the central region of the distribution of this species, which extends along the western seaboard of the Americas from the Gulf of California to Peru. The analysis yielded a single cluster. The range in pairwise differences within this cluster was 0–7, and the average was 3.3.

*Sphyrna mokarran* (great hammerhead) complex (fig. 19)

In total, 22 specimens were included. These were collected from the Gulf of Mexico (9 specimens), the western North Atlantic coast from Massachusetts to Florida (7 specimens), Malaysian Borneo (1 specimen; GN3471 = IPPS BO254), and northern Australia (5 specimens). Given that this species has been reported to occur in a global band (Last and Stevens, 2009), on continental shelves throughout the tropics and subtropics, our sample largely underrepresents the distribution of this species, and does not include the type locality (Red Sea). Nonetheless, the analysis yielded two distinct clusters: one comprised of the specimens collected from the Atlantic, which we refer to as *Sphyrna mokarran* 1,

and a second consisting of specimens from Australia and Borneo, which we refer to as *Sphyrna mokarran* 2. The range in pairwise differences among *S. mokarran* specimens overall was 0–16. The range in pairwise differences among specimens of *S. mokarran* 1 was 0–3 (with an average of 0.5) and the range in pairwise differences among specimens of *S. mokarran* 2 was 0–4 (with an average of 1.9). However, the average of the pairwise differences between these two clusters was 14.1.

Although they are not among the most divergent of the hammerhead species complexes treated here, there is no haplotype overlap between specimens of *S. mokarran* 1 and *S. mokarran* 2 (fig. 87A), which supports recognition of these as distinct allopatric species (fig. 87B).

*Sphyrna zygaena* (smooth hammerhead) (fig. 19)

The 16 specimens of this species were collected from the Gulf of California (4 specimens), western North Atlantic (6 specimens), Senegal (1 specimen), Vietnam (1 specimen), Taiwan (3 specimens), and Japan (1 specimen), and thus represent at least the longitudinal (if not the latitudinal) distribution of this species. The analysis yielded essentially a single cluster, with a range in pairwise differences among specimens of 0–8, with an average of 2.5. One of the specimens from the Gulf of California was vouchered (GN1097 = IBUNAM PE9519).

*Eusphyra blochii* (winghead shark) (fig. 19)

All nine of our specimens of this species were all collected from Fog Bay, in the Timor Sea of northern Australia and thus represent only a small portion of the distribution of this species, which includes much of the coastal regions of the Indo-West Pacific. The analysis yielded a single cluster of specimens with a very low range in pairwise differences among specimens (i.e., 0–2); one of these samples was vouchered (GN1256 = NTM S.14689-004).

### **Carcharhinidae (requiem sharks), continued**

*Galeocerdo cuvier* (tiger shark) complex (fig. 20)

Our 29 specimens of this species represent much of the longitudinal distribution of this species, having come from the western North

Atlantic and Gulf of Mexico (18 specimens), as well as the Gulf of California (1 specimen), Hawaii (1 specimen), Borneo (1 specimen), the Timor Sea off the coast of northern Australia (7 specimens), and the Red Sea (1 specimen). The specimen from the Gulf of California was deposited in the Texas Cooperative Wildlife Collection (GN5271 = TCWC 7574.01). The analysis yielded two clusters of tiger sharks. One of these consisted of specimens from the Atlantic localities, and the second consisted of the specimens from Australia, Hawaii, Borneo, Gulf of California, and Red Sea (i.e., the Pacific and Indian Ocean localities). The range in pairwise differences among all 29 tiger shark specimens was 0–17; the average was 6.2. The range in pairwise differences among specimens in the Atlantic cluster was 0–5 (with an average of 1.1), and among specimens in the Pacific and Indian Ocean cluster was 0–7 (with an average of 2.9). The average of the pairwise differences between the two clusters was 11.1. Given that the type locality of *G. cuvier* is northwestern Australia, we have given the 11 specimens comprising this cluster the designation *G. cuvier* and the 18 specimens in the second cluster the designation *G. cf. cuvier*.

Both haplotype maps for this genus (figs. 88A and B) support the above conclusions. There is no haplotype overlap among specimens of the two potential species of tiger sharks, and the haplotype map colored by geography clearly shows that the two species are allopatrically distributed. The notion that multiple species may exist within this genus needs to be further explored. If taxonomic investigation reveals that Atlantic populations are not conspecific with *G. cuvier*, *G. arcticus* (Faber, 1829), described from Iceland and Norway, might need to be resurrected.

### Hemigaleidae (weasel sharks)

*Hemigaleus microstoma* (sicklefin weasel shark) (fig. 21)

In total, 31 specimens of this species were included. They consist of one specimen collected from Singapore, six from the Philippines, and 24 from Borneo and thus represent only some of the more central elements of the Indo-West Pacific distribution of this species. Two of the specimens from the Philippines were treated by Com-

pagno et al. (2005a) (i.e., GN4324 = BRU 123 and GN4325 = JPAG 216) as *H. microstoma*. One of the specimens from Borneo was also vouchered (GN3694 = IPPS BO483). These 31 specimens comprised a single cluster, including a weakly supported subcluster comprised of a subset of specimens from Borneo. The range in pairwise differences among all 31 specimens of this species was 0–13 and the average was 4.9.

*Hemigaleus australiensis* (Australian weasel shark) (fig. 21)

Our analysis included six specimens of this newly described species (see White et al., 2005) from Western Australia, and the Timor and Arafura seas off the coast of northern Australia. Two of these specimens came from the Australian National Fish Collection (the holotype GN4913 = ANFC H 5949-01 and GN4914 = ANFC H 5949-02). Within this cluster, two specimens, one from Western Australia and one from the Arafura Sea, grouped together in a subcluster distinct from the other four specimens. The range in pairwise differences among all six specimens of this species was 0–11, with an average of 6.5. The two specimens in the former subcluster differed by one base, and the range in pairwise differences among the remaining four specimens was 0–5 (with an average of 3.2). The mean of the pairwise differences between the two subclusters of *H. australiensis* was 9.8. The mean of the pairwise differences between specimens of *H. australiensis* and those of *H. microstoma* was 94.6; this result strongly supports the distinction between these two congeners.

*Paragaleus* sp. (fig. 21)

A single specimen of *Paragaleus* from Phuket, Thailand, grouped outside both of the known species of *Paragaleus*, along with the two species of *Hemigaleus*. The average of the pairwise differences between this specimen and those of *P. randalli* was 128.9. The average of the pairwise differences between this specimen and those of *P. pectoralis* was 122.7. We have given this specimen the designation *Paragaleus* sp. It possibly represents an undescribed *Paragaleus* species, however, comparisons with the two described species of *Paragaleus* not included here would also be valuable. Given

its substantial difference from the other two *Paragaleus* species, it may, however, be a case of incorrect generic identification, and the possibility that it represents a species of *Chaenogaleus* should be explored.

*Paragaleus randalli* (slender weasel shark) (fig. 21)

Our analysis included a total of 17 specimens belonging to this species, two of which were vouchered (GN4182 = MZB 15.506 and GN4191 = MZB 15.507). The analysis yielded a single cluster. The specimens in this cluster included 16 samples from Borneo and a single specimen from the Philippines. The range in pairwise differences among specimens in this cluster was 0–9; the average of pairwise differences among specimens of this species was 2.9. All of the localities sampled in this study fall well outside the originally described range of *Paragaleus randalli* (i.e., Bahrain and western Indian Ocean), but within the range of the similar looking congener *Paragaleus tengi* (straighttooth weasel shark) which might lead to the suspicion that these tissue samples were actually derived from specimens of *P. tengi*. However, unpublished sequence data from NADH2 indicate no significant differences in sequence between specimens identified as *P. randalli* from the Persian Gulf and those of the 17 specimens from Southeast Asia used in the current study. Furthermore, vertebral counts examined (by PL and WW) from three specimens originally identified as *Paragaleus tengi* from Borneo, range in number between 164 and 171 which is outside the reported range for *P. tengi* (131–135) but consistent with the range given for *P. randalli* (165–186). Taken together, these observations suggest that *P. randalli* has a more extensive distribution than suggested in its original description (Compagno et al., 1996) extending from the western Indian Ocean to Southeast Asia. They also suggest that *P. randalli*, rather than *P. tengi*, is the dominant form of *Paragaleus* in Borneo.

*Paragaleus pectoralis* (Atlantic weasel shark) (fig. 21)

The analysis yielded a cluster consisting of six specimens of this species, all from western Africa (i.e., from Mauritania, Senegal, and Sierra Leone). These specimens are generally representative of the distribution of this species, which extends throughout the northern half

of the western coast of Africa. The range in pairwise differences among specimens within this cluster was 0–5, with an average of 2.9. The average of the pairwise differences between specimens of *P. pectoralis* and *P. randalli* was 118.

*Hemipristis elongata* (snaggletooth shark) (fig. 21)

Our analysis included a total of 14 specimens of this monotypic genus, nine from Borneo and five from the Arafura Sea off northern Australia; these represent only a subset of the distribution of this species which includes much of the Indo-West Pacific, with the Red Sea as the type locality. One of these specimens is represented by a voucher (GN4195 = CAS 229035). The analysis yielded a single cluster. The range in pairwise differences among specimens was 0–5; the average was 2. There is some evidence of geographic substructure within this cluster with the Australian specimens grouping apart from the Borneo specimens, however the signal is weak as the average of the pairwise differences between specimens from the two localities was only 3.5.

#### Leptochariidae (barbeled houndsharks)

*Leptocharias smithii* (barbeled houndshark) (fig. 22)

All three of our specimens were collected off of Senegal and represent the northern region of the distribution of this species which extends south from there along the coast of western Africa to Angola. The analysis yielded a single cluster; the range in pairwise differences among these three specimens was 0–1.

#### Triakidae (houndsharks)

*Mustelus* (smoothhounds) (figs. 23, 24)

This was among the most problematic of genera included in our analysis. At present, the genus includes ~31 species of which five have been described since 2005; clearly a substantial amount of diversity in this genus remains to be explored. Analysis of 129 specimens yielded 18 clusters, each of which we believe represents a distinct species of *Mustelus*. However, assigning correct names to clusters without vouchers was problematic; particularly challenging were the specimens collected from the Gulf of California. For nine clusters, photo vouchers are available for one or more of the included

specimens. For three additional clusters, identifications were based on one or more museum specimens. In the remaining six cases we have relied on geographical range and/or the taxonomic expertise of individuals providing samples. Ultimately, while we are confident in the existence of 18 species among these specimens, the specific identifications of many of the clusters remain to be confirmed. We hope that the generation of comparable sequence data for additional specimens of known identity will serve to place the data presented here into a broader perspective. Each of the 18 species clusters is treated separately below.

*Mustelus widodoi* (whitefin smoothhound) and *Mustelus ravidus* (Australian gray smoothhound) (fig. 23)

In total, 31 specimens were analyzed, consisting of 30 specimens of *M. widodoi* from Borneo and one specimen of *M. ravidus* from a specimen deposited in the Australian National Fish Collection (GN4898 = ANFC H 5947-01). The analysis yielded a cluster consisting of the 30 *M. widodoi* specimens from Borneo, with the *M. ravidus* specimen from Australia grouping outside. The specimens from Borneo were consistent morphologically with *M. widodoi* of White and Last (2006); however, they were collected further north than the type specimens and represent a distributional extension for this species (see Last et al., 2010c). The range of pairwise differences among the *M. widodoi* specimens was 0–5; the average was 1. The average of the pairwise differences between *M. widodoi* and *M. ravidus* was 8.5. We note that *M. ravidus* was referred to as *Mustelus* sp. A by Last and Stevens (1994) and Gardner and Ward (2002).

*Mustelus mosis* (Arabian smoothhound) (fig. 23)

The three specimens included in the analysis were collected from India and thus represent the eastern region of the distribution of this species, which extends from India, westward to Somalia, and possibly as far southwest as South Africa. The analysis yielded a single cluster. The range in pairwise differences within this cluster was 3–9; the average was 6.7. This is one of only two species of *Mustelus* known to occur in India. These specimens were found to group well outside those of the other Indian species, *M.*

*manazo*, the identity of which is grounded by specimens.

*Mustelus mustelus* (smoothhound) (fig. 23)

In total, nine specimens of this species were included in our analysis, three from Senegal, one from Angola, and five from South Africa. Thus, these specimens come from much of the known distribution of this species, which extends from the North Sea along the coast of Europe and the western coast of Africa to South Africa. The analysis yielded a single cluster, with some evidence of substructure. The range in pairwise differences among all nine specimens was 0–8; the average was 3.4. The range in pairwise differences among the specimens from Senegal was 1–3 (with an average of 2). The range among the other five specimens was 0–1 (with an average of 0.3). The average of the pairwise differences between specimens from Senegal and those from southern Africa was 6.2. The identities of a number of specimens in this cluster are grounded with photographs.

*Mustelus* cf. *lumulatus* (sicklefin smoothhound) (fig. 23)

The analysis yielded a cluster of eight specimens that we have tentatively identified as *M.* cf. *lumulatus*. The range in pairwise differences among specimens was 0–7, with an average of 2.9. The identity of this cluster is problematic. All eight specimens were collected from the Gulf of California and all possess teeth with low, rounded cusps. They were initially identified as *M. lumulatus*, but dissections and x-rays revealed a number of inconsistencies. For example, while two of the specimens (BJ-802 and BJ-796) have precaudal vertebral counts (77 and 81, respectively) that are within the range for this species (74–82) presented by Heemstra (1973), their monospondylic vertebral count (37 in both cases) is outside the range for *M. lumulatus* (28–34) presented by Heemstra (1973). Moreover, the cluster includes a specimen (BJ-803) that has a precaudal vertebral count (87) that falls within the range for *M. intermedius* (83–93) of Heemstra (1973) but has a monospondylous vertebral count (41) that falls within the range (41–44) for Heemstra's "*M. platyrhinus*." The identity of this cluster should be considered

tentative until confirmed specimens of *M. lumulatus* can be included in the analysis.

*Mustelus canis* (dusky smoothhound) (fig. 23)

The analysis included eight specimens identified as this species; seven were collected from the western North Atlantic coast from Rhode Island to North Carolina and one from the Bahamas. Only some of the Northern Hemisphere elements of the distribution of this species are represented and the Southern Hemisphere elements are unrepresented. The analysis yielded a single cluster, with the specimen from the Bahamas grouping outside those from the more northern latitudes. The range in pairwise differences among the eight specimens within this cluster was 0–23; the average was 7.9. Some consideration should be given to the possibility that additional species of *Mustelus* may be represented by these specimens. Heemstra's (1997) recognition of *Mustelus canis insularis* from several islands of the Caribbean, may, for example be relevant to the identity of the specimen included here from the Bahamas.

*Mustelus* sp. 2 (fig. 23)

The analysis yielded a cluster of four specimens from the Gulf of California with a range in pairwise differences among specimens of 0–5 and an average of 2.5. We have been unable to definitively identify this cluster to species. Like candidate species from the Gulf of California, these specimens possess teeth with low rounded cusps. However they lack the white posterior margins of the dorsal, pectoral, pelvic, and anal fins described by Castro-Aguirre et al. (2005) in *M. albipinnis* and also described by Pérez-Jiménez et al. (2005) in *M. hacat*, a potential junior synonym of the former species (Eschmeyer and Fricke, 2011). Moreover, all four specimens were collected by artisanal fishermen using bottom gill nets and thus, unlike specimens of *M. albipinnis*, came from waters substantially shallower than 100 m. While one of the specimens (GN1565 = BJ-671) in this cluster has a monospondylic vertebral count (41) that is generally consistent with that of *M. albipinnis* (40), it has a precaudal vertebral count (97) that is above that reported by Castro-Aguirre et al. (2005) for *M. albipinnis* (i.e., 92), and slightly lower

than the range (101–102) reported in the original description of *M. hacat*. The possibility that this species represents one of the two undescribed species from the Gulf of California treated by Heemstra (1973) should not be ruled out.

*Mustelus henlei* (brown smoothhound) (fig. 23)

Material from the Gulf of California also included six specimens of *Mustelus henlei*. These specimens represent only a small portion of the distribution of this relatively easy to identify species, which has been reported from as far north as Washington state and as far south as Peru. Analysis of these specimens yielded a single cluster with a range in pairwise differences of 2–9, and an average of 5.6. The identity of this cluster is grounded with images.

*Mustelus norrisi* (narrowfin smoothhound) (fig. 23)

A single specimen, collected and identified by NOAA Fisheries biologist Lisa Jones, was included in the analysis. This specimen grouped independently of all of the other specimens of *Mustelus* included in the analysis. However, clearly this specimen represents only one point in the distribution of this species which extends along the eastern coast of North and South America, from Florida to Venezuela, and Argentina.

*Mustelus californicus* (gray smoothhound) (fig. 23)

Our analysis included 15 specimens of this species, all collected from the Gulf of California. Given that this species occurs along coastal California, the Gulf of California, and possibly as far south as Puerto Vallarta, our specimens represent the center of the relatively limited overall distribution of this species. Three of these specimens were deposited in the Texas Cooperative Wildlife Collection (GN2284 = TCWC 7561.03, GN5291 = TCWC 7561.05, and GN5292 = TCWC 7561.04). The analysis yielded a single tight cluster. The range in pairwise differences among specimens within this cluster was 0–2 and the average of the pairwise differences among specimens was 1.4. The identity of this cluster is grounded not only with photographs, but also in that dissections and/or x-rays revealed that specimens had an extra symphyseal cartilage on

the palatoquadrate, which other sympatric *Mustelus* species lack (Compagno, 1984a).

*Mustelus* sp. 1 (fig. 23)

The analysis yielded an additional cluster of two specimens from the Gulf of California, which were identical in sequence. We have been unable to definitively identify this cluster to species. These specimens, like those of *Mustelus* sp. 2, possess teeth with low, rounded cusps and lack the white posterior margins of the dorsal, pectoral, pelvic and anal fins described by Castro-Aguirre et al. (2005) in *M. albipinnis* as well as in its potential junior synonym *M. hacat* (see Pérez-Jiménez et al., 2005). Like the four specimens of *Mustelus* sp. 2, both specimens were also collected by artisanal fishermen using bottom gill nets and thus, unlike *M. albipinnis*, came from waters substantially shallower than 100 m. The possibility that these specimens represent one of the two undescribed species from the Gulf of California treated by Heemstra (1973) can also not be ruled out. These specimens clustered together, independent of the remaining *Mustelus* species. They clustered most closely with *M. californicus*; the average of pairwise differences between these two species was 40.1.

*Mustelus antarcticus* (gummy shark) (fig. 24)

A total of nine specimens of this species were included in the analysis. All nine came from southeastern and southwestern Australia and are representative of much of the range of this species. The analysis yielded a single cluster, with a range in pairwise differences of 0–4 and an average of 1.9. The identity of this cluster is based on a specimen in the Australian National Fish Collection (GN4902 = ANFC H 6571-03).

*Mustelus lenticulatus* (spotted estuary smoothhound) (fig. 24)

This species occurs throughout New Zealand, which was the site of collection of all three specimens included in the analysis. The range in pairwise differences seen within the cluster that resulted from the analysis was 0–1. The identity of this cluster is based on two specimens in the Australian National Fish Collection (GN4896 = ANFC H 5551-01 and GN4897 = ANFC H 5551-02).

*Mustelus stevensi* (whitespotted gummy shark) (fig. 24)

Two specimens of this recently described species (see White and Last, 2006) were included in the analysis. Both specimens were collected from the type locality, from the Dampier Archipelago off northwestern Australia. These clustered together, independently of the remaining *Mustelus* species. The sequences of the two specimens differed by 2. The identity of this cluster is confirmed given that one of the samples comes from a paratype (GN4900 = ANFC H 4650-01); the second sample comes from a voucher (GN4899 = ANFC H 4649-08). The average of the pairwise differences between *M. stevensi* and *M. lenticulatus* was 14.3, between *M. stevensi* and *M. antarcticus* was 17.2, and between *M. stevensi* and *M. ravidus* was 83. Our results support the clear distinctions reported by Gardner and Ward (2002) between *M. stevensi* (= *Mustelus* sp. B of Last and Stevens, 1994, and Gardner and Ward, 2002) and each of *M. lenticulatus*, *M. antarcticus*, and *M. ravidus* (= *Mustelus* sp. A of Last and Stevens, 1994, and Gardner and Ward, 2002).

*Mustelus manazo* (starspotted smoothhound) (fig. 24)

In total, 13 specimens of this species were included in the analysis. These consist of seven specimens from Taiwan, two from Vietnam, three from Japan, and one specimen that was landed in Borneo. The analysis yielded a single cluster. The range in pairwise differences within this cluster is 0–6 and the average was 2.8. However, our specimens represent only the eastern central elements of the distribution of this species. Four samples from this cluster are represented by specimens (GN972, GN989, GN1019 and GN1020 = UMMZ 231357).

*Mustelus palumbes* (whitespot smoothhound) (fig. 24)

Six specimens of this species, all collected from South Africa, were included. These are representative of the distribution of this species which occurs from Namibia to central Natal. The range in pairwise differences of this cluster was 0–4, and the average was 2.6.

*Mustelus asterias* (starry smoothhound) (fig. 24)

The analysis included two specimens, both collected from the eastern North Atlantic. The sequences of these two specimens differed by one base. However, our specimens represent only the northernmost region of the distribution of this species, which extends along the coast as far south as Senegal. These specimens clustered most closely with those of *M. palumbes*. The average of the pairwise differences between specimen of these two species was 8.3.

*Mustelus schmitti* (narrownose smoothhound) (fig. 24)

In total, seven specimens of this species, all collected and identified by Gustavo Chiaramonte of the Museo Argentino de Ciencias Naturales, Buenos Aires, were included. The analysis yielded a single cluster, with a range in pairwise differences among specimens of this species of 0–4 and an average of 1.9. These specimens are fairly representative of the distribution of this species, which extends along the coasts of southern Brazil, Uruguay, and Argentina.

*Scylliogaleus queckettii* (flapnose houndshark) (fig. 24)

The analysis included four specimens of this species, all from South Africa; one donated by Mark Harris and three others by Jeremy Cliff of the KwaZulu-Natal Sharks Board. The analysis resulted in a single cluster of all four specimens of this monotypic genus. These specimens are representative of the distribution of this species, which is known only from the southeastern coast of South Africa. The range in pairwise differences among specimens within this cluster was 0–2 and the average was 1.2.

*Triakis megalopterus* (spotted gulley shark) (fig. 24)

Two specimens of this species were included in the analysis; both from South Africa and are representative of the distribution of this species, which occurs only along the coast of South Africa. These specimens clustered together, well away from the other two species of *Triakis* included in the analysis. The two specimens of *T. megalopterus* differed by two bases. The average of the pairwise differences between *T. megalopterus* and *T. semifasciata* (fig. 27) was

129, and the average of the pairwise differences between *T. megalopterus* and *T. scyllium* (fig. 27) was 139.5. Differences between *T. megalopterus* and *T. semifasciata* relative to *T. scyllium* were noted earlier by Compagno (1988) who suggested that *Triakis* may constitute two subgenera: *T. (Triakis)* containing *T. semifasciata* and *T. scyllium*, and *T. (Cazon)* containing not only *T. megalopterus* but also *T. maculata* and *T. acutipinna*, neither of which is represented here. Our results suggest that these two clades are likely not each other's closest relatives and thus should be considered as independent genera, rather than subgenera of *Triakis*.

*Iago omanensis* (bigeye houndshark) complex (fig. 25)

A total of 19 specimens was included in the analysis, which yielded three clusters, each of which corresponds to the geographic origins of the included specimens: Gulf of Oman (11 specimens), the Red Sea (6 specimens), and India (2 specimens). Unfortunately, the identities of these clusters are difficult to assign to nominal taxa. At present, only two species of *Iago* have been formally described (Compagno, 1984a). These are *Iago omanensis*, occurring from the Red Sea and Gulf of Oman to Pakistan, and *Iago garricki* from the western central Pacific. However, additional forms, mostly from the northeastern Indian Ocean, but also one from the Philippines, have been reported in the literature (e.g., Compagno, 1988). Based on available morphological data (i.e., images), the specimens comprising the Gulf of Oman subcluster appear to be consistent with *I. omanensis*, so we have used this designation for the members of this cluster. Although several additional informal names have been applied to additional forms from the Gulf of Oman (e.g., Compagno, 1988: 240, referred to “*Iago* sp. nov., low fins”; Compagno et al., 2005b, included an *Iago* sp. A from the Gulf of Aden to India), we are uncomfortable applying any of these names to the Indian or Red Sea clusters in the absence of additional morphological data. Thus, specimens within these clusters have been referred to as *Iago* cf. *omanensis* 1 and *Iago* cf. *omanensis* 2, respectively. The range in pairwise differences among specimens in



the *I. omanensis* cluster was 0–8 (with an average of 3.5); the two specimens of *I. cf. omanensis* 1 differed by seven bases, and the range in pairwise differences among the specimens of the *I. cf. omanensis* 2 cluster was 0–3 (with an average of 1.5). The averages of the pairwise differences between clusters were as follows: 12.5 (between *I. omanensis* and *I. cf. omanensis* 1), 13 (between *I. omanensis* and *I. cf. omanensis* 2), and 17.2 (between *I. cf. omanensis* 1 and *I. cf. omanensis* 2).

The haplotype map for *Iago* species colored by phenotype (fig. 89A) shows no overlapping haplotypes among specimens of the three forms of *Iago omanensis*. The haplotype map colored by geography (fig. 89B) confirms that haplotypes are restricted to the Gulf of Oman, the Red Sea, or India. Also shown on these maps is the clearly distinctive *I. garricki* from the Sulu and China Seas.

*Iago garricki* (longnose houndshark) (fig. 25)

Samples from three specimens collected from the Philippines and treated by Compagno et al. (2005b), were included in the analysis (i.e., GN2224 = JPAG 083, GN2228 = JPAG 152, and GN4330 = JPAG 346). These specimens clustered together, grouping most closely with the other specimens of *Iago* species. We have followed the identification indicated by Compagno et al. (2005b) for these specimens, who considered the Philippine specimens to be conspecific with those of *I. garricki* from Australia and New Caledonia. The range of pairwise differences among these specimens was 4–6 (with an average of 4.7). The average of the pairwise differences between *I. garricki* and those of the other *Iago* species are as follows: 124.5 (between *I. garricki* and *I. omanensis*), 123.5 (between *I. garricki* and *I. cf. omanensis* 1), and 116.7 (between *I. garricki* and *I. cf. omanensis* 2).

*Galeorhinus galeus* (topeshark) (fig. 26)

Our analysis included 18 specimens of this species, which were found to comprise a single cluster. These came from South Africa (5 specimens), the Tasman Sea off Australia (1 specimen), New Zealand (7 specimens), California (3 specimens), the Azores (1 specimen), and the eastern North Atlantic (1 specimen); as such they represent much

of the reported global distribution of this species, with the exception of South America and the western coast of Africa. The range in pairwise differences among all 18 specimens was 0–13, with an average of 4.9. The analysis yielded a group composed of three weak subclusters. The first subcluster consisted of the specimens from New Zealand, Australia, and South Africa with a range in pairwise differences among specimens of 0–4. The second consisted of the specimens from California with a range in pairwise differences of 0–1, and the third subcluster consisted of the specimens from Atlantic Ocean localities that were identical in sequence. At present only the single species, *Galeorhinus galeus*, with the type from European waters, is recognized in this genus. However, our results are consistent with those of others, for example, Compagno (1988) and Chabot and Allen (2009), who found variation in vertebral counts and genetic structure, respectively, among populations. Nonetheless, we have used the designation *G. galeus* for specimens from all three subclusters but note that the average of the pairwise differences between the New Zealand/Australia and California clusters is 6.7, between the New Zealand/Australia and Atlantic clusters 10.4, and between the California and Atlantic clusters 8.3. It seems likely that further investigation will result in the resurrection of synonyms of *G. galeus* for some of these regional subclusters.

*Hypogaleus hyugaensis* (blacktip topeshark) (fig. 26)

Thirteen specimens of this species, collected and identified by Adrian Kitchingman of Western Australian Fisheries, were included in the analysis. These all came from southwestern Australia and thus represent only a small region of the distribution of this species, which also includes Japan, Taiwan, the Persian Gulf, and the east coast of Africa. The analysis yielded a single tight cluster. The range in pairwise differences within the cluster was 0–2, with an average of 0.9. These belong to what is currently considered a monotypic genus.

*Hemistriakis japonica* (Japanese topeshark) (fig. 26)

In total, our analysis included nine specimens of this species collected from Japan, Taiwan,

and Vietnam, thus well representing the western North Pacific distribution of this species. Many of these specimens were sent to us by Kazuhiro Nakaya from the Hokkaido University Museum (GN2597 = HUMZ 162467, GN2598 = HUMZ 162468, GN2599 = HUMZ 162469, and GN2600 = HUMZ 176993). The four specimens from Taiwan are deposited at the University of Michigan Museum of Zoology (GN1000, GN1008, GN1009, and GN1010 = UMMZ 231964). The analysis yielded essentially a single cluster with the range in pairwise differences within the cluster being 0–7, with an average of 3.6.

*Hemitriakis leucoperiptera* (whitfin topeshark) (fig. 26)

The analysis included three specimens of this species collected from the Philippines and treated by Compagno et al. (2005b). The analysis yielded a single cluster; the range in pairwise differences among these specimens was 0–1. This result may help to eliminate concerns over the identification of Philippine *H. leucoperiptera* raised by Compagno et al. (2005b). Their samples included a specimen (GN2232 = JPAG 169) with a low vertebral count identified as *H. leucoperiptera*, a specimen (GN2225 = JPAG 161) of unknown vertebral count and thus included by those authors among a series of specimens of uncertain identity, tentatively considered to be *H. leucoperiptera*, and also a specimen (GN4366 = JPAG 139) of unknown vertebral count, tentatively identified by those authors as “*Hemitriakis* cf. *japanica* (var PP).” Our results suggest that all three specimens are conspecific. These specimens grouped most closely with those of *H. japonica*. The average of the pairwise differences between specimens of *H. leucoperiptera* and those of *H. japonica* was 8.3.

*Hemitriakis complicofasciata* (ocellate topeshark) (fig. 26)

Our analysis was based on five samples, all taken from museum specimens (GN2592 = HUMZ 165233, GN2593 = HUMZ 165255, GN2594 = HUMZ 162464, GN2595 = HUMZ 162465, and GN2596 = HUMZ 162466) cited by Takahashi and Nakaya (2004) in the original description of this species from the Ryuku Islands, Japan. The analysis yielded a single cluster; the range in pairwise differences

among these specimens was 0–3, with an average of 1.4.

*Hemitriakis falcata* (sicklefin houndshark) (fig. 26)

The single specimen of this species that was included in our analysis was taken from a specimen (GN4894 = ANFC H 5946-01) from Western Australia. This specimen grouped most closely with those of *H. complicofasciata*. The average of the pairwise differences between these two species was 10.8.

*Hemitriakis* sp. (fig. 26)

Interestingly, one of the specimens originally identified as *Hemitriakis complicofasciata* and also referenced in the original description of the species by Takahashi and Nakaya (2004), was found to group outside the cluster consisting of the specimens of *H. complicofasciata* and *H. falcata*. The average of the pairwise differences between this sample and those from the five specimens in the *H. complicofasciata* cluster was 29.8. The difference between this specimen and that of *H. falcata* was 27. The sample was taken from a specimen deposited in the Hokkaido University Museum (GN2591 = HUMZ 165225); this specimen needs to be more closely examined in light of these findings. It is possible this specimen represents an undescribed species.

*Furgaleus macki* (whiskery shark) (fig. 26)

Two specimens, both collected from Western Australia, were included in the analysis. These are fairly representative of the distribution of this species, which is known only from the western and southern regions of Australia. These two specimens comprised a single cluster; they were identical in sequence.

*Triakis scyllium* (banded houndshark) (fig. 27)

Six specimens of this species, all collected from the Izu Peninsula in Japan, and identified by Sho Tanaka, were included. The analysis yielded a single cluster with the range in pairwise differences among specimens in this cluster being 0–4, with an average of 2.1.

*Triakis semifasciata* (leopard shark) (fig. 27)

In total six specimens, one from the Gulf of California and five from coastal California, were included in the analysis. These represent much of the distribution of this species. The analysis yielded a single cluster; the range in pairwise differences within the cluster was

0–1. The average of the pairwise differences between *T. scyllium* and *T. semifasciata* was 91. Given that our specimens from western California all came from the same locality, our data did not allow us to examine the differences seen by Lewallen et al. (2007) between northern and southern specimens of this species.

### Scyliorhinidae (catsharks): group 1

*Apristurus melanoasper* (black roughscale catshark) complex (fig. 28)

The analysis included 10 specimens initially identified as *Apristurus melanoasper*; two from the western North Atlantic, three from Australia, and five from New Zealand. The analysis yielded two clusters, one consisting of the two Atlantic specimens (which differed from one another by three bases, one of which was deposited in the Yale Peabody Museum [GN1076 = YPM ICH.010136]) and a second cluster comprised of the eight specimens from Australia and New Zealand (all of which were identical in sequence). The average of the pairwise differences between members of these two clusters was 19.5. Given that *A. melanoasper* was described from the North Atlantic, we have given the specimens in the Atlantic cluster the designation of *A. melanoasper*. Although recent work extended the known distribution of this species to include Australia and New Zealand (Nakaya et al., 2008), the results in this paper do not fully support this decision, so the Australasian cluster has been given the provisional designation of *Apristurus* cf. *melanoasper*. Several of the samples in the latter cluster came from specimens in the Australian National Fish Collection (GN4868 = ANFC H 1391-01 and GN4869 = ANFC H 1391-03), and several from specimens in the Museum of New Zealand, Te Papa Tongarewa (GN6723 = NMNZ P.041310, GN6738 = NMNZ P.042336, GN6740 = NMNZ P.042569, GN6754 = NMNZ P.045140). Detailed taxonomic revision of this complex is required in the future.

*Apristurus brunneus* (brown catshark) (fig. 28)

The two specimens of this species were collected from California and thus generally represent the northern, but not the potential

southern hemisphere elements of this species, which has been reported from Panama, Ecuador, and Peru. These specimens clustered together, independently from the other species of *Apristurus* included in the analysis; pairwise difference between these two specimens was three bases.

*Apristurus laurussonii* (Iceland catshark) (fig. 28)

A total of seven specimens, all collected from the North Sea off the coast of Scotland, were included in the analysis. These specimens represent only one of the eastern components of the rather disjunct distribution of this species, which also includes isolated localities off northwestern Africa, Iceland, Massachusetts, and the Gulf of Mexico. The seven specimens were found to comprise a single cluster. The range in pairwise differences seen among these specimens was 0–3, with a mean of 1.4.

*Apristurus* cf. *sinensis* (South China catshark) (fig. 28)

A total of six samples taken from specimens collected from New Zealand, mostly from the Museum of New Zealand, Te Papa Tongarewa (GN6728 = NMNZ P.042126, GN6749 = NMNZ P.045142, GN6757 = NMNZ TMP004690, GN6745 = NMNZ P.044309, and GN6752 = NMNZ P.045139), were included in the analysis. They yielded a single cluster with a range in pairwise differences among specimens of 0–3 (with an average difference of 1). These specimens were originally identified as *A. sinensis* by Kazuhiro Nakaya. However, no specimens from near the type locality of this species (South China Sea) were included in this analysis. Given that a thorough taxonomic revision of this complex is required, the New Zealand form is provisionally referred to here as *A. cf. sinensis*.

*Apristurus* sp. 1 (fig. 28)

This sample, collected from Western Australia, came from a museum specimen (GN4863 = ANFC H 6411-02). It clustered most closely with *A. cf. sinensis*; the range in pairwise differences between these two taxa was 21.2. This result suggests that it represents either an undescribed species, or a known species that was not otherwise represented in the analysis.

*Apristurus platyrhynchus* (spatulasnout catshark) (fig. 28)

The analysis included three specimens collected from deepwater near Bass Strait, Australia. It yielded a single cluster with a pairwise difference of 1–2. Although recent taxonomic work on this species extended its known distribution to include Australia (Kawauchi et al., 2008), it would be ideal to obtain specimens from the type locality for this species, i.e., Japan, for comparison with the Australian specimens. Thus, the specific designation used here is provisional until such time as its identity can be examined in more detail.

*Apristurus* sp. 2 (fig. 28)

This specimen was collected from near Bass Strait, Australia, and clustered most closely with *A. platyrhynchus*; the range in pairwise differences between these two taxa is 33.3. This result suggests that it too represents either an undescribed species, or a known species that was not otherwise represented in the analysis.

*Apristurus exsanguis* (flaccid catshark) (fig. 28)

The analysis included nine samples, five of which came from specimens at the Museum of New Zealand, Te Papa Tongarewa (GN6753 = NMNZ P.045130, GN6743 = NMNZ TMP004689, GN6736 = NMNZ P.042520, GN6733 = NMNZ P.042176, and GN6732 = NMNZ P.042519). These specimens are representative of the distribution of this species, which appears to be endemic to New Zealand. Essentially a single cluster resulted from the analysis. The range in pairwise differences within the cluster was 0–4, with an average of 1.9.

*Apristurus macrorhynchus* (flathead catshark) (fig. 28)

Our sample included a total of four samples all taken from specimens in the University of Michigan Museum of Zoology (GN1013, GN1014, GN1015, and GN1016 = UMMZ 231973), and all of which were collected from Taiwan. These specimens are generally representative of the distribution of this species, which is known only from Taiwan and southern Japan. The analysis yielded a single cluster; the range in pairwise differences

among specimens within this cluster was 2–6; the average of pairwise differences among specimens was 4.7.

*Apristurus amplexiceps* (roughskin catshark) complex and *Apristurus manis* (fig. 28)

The relatively newly described species *A. amplexiceps* from Australia and New Zealand (see Sasahara et al., 2008), was represented by eight New Zealand samples, all of which came from specimens deposited in the Museum of New Zealand, Te Papa Tongarewa. Also included in the analysis was a single specimen from the Atlantic Ocean, tentatively identified as *Apristurus manis*. The analysis yielded two clusters, one consisting solely of five New Zealand specimens of *A. amplexiceps* (with a range of pairwise differences among specimens of 0–3 and an average of 1.6), the other consisting of three specimens from New Zealand (with a range of pairwise differences among these three specimens of 4–6 and an average of 5.5) and the specimen of *A. manis*. The average of the pairwise differences between members of the two clusters of *A. amplexiceps* (excluding the *A. manis* specimen) was 21.5 suggesting that conspecificity of specimens in these two clusters is doubtful. However, it is unclear which of the two clusters represents the true *A. amplexiceps*. Similarly, the identity of the *A. manis* specimen remains to be confirmed. Until such time as this subgroup of *Apristurus* can be examined in more detail, we have designated specimens comprising the first cluster as *A. amplexiceps* 1 and those comprising the second cluster as *A. amplexiceps* 2. We have, however, provisionally retained the designation *A. manis* for the Atlantic specimen in the second cluster. The average of pairwise differences between *A. manis* and *A. amplexiceps* 1 was 27.2; the average of pairwise differences between *A. manis* and *A. amplexiceps* 2 was 20.7. All five specimens of *Apristurus amplexiceps* 1 were vouchered (GN6726 = NMNZ P.041688, GN6724 = NMNZ P.041689, GN6725 = NMNZ P.041994, GN6735 = NMNZ P.042385, and GN6751 = NMNZ P.045206); this is also the case for the three specimens of *Apristurus amplexiceps* 2 (GN6727 = NMNZ P.041993, GN6742 = NMNZ TMP004687, GN6744 = NMNZ TMP004691).

*Apristurus profundorum* (deepwater catshark)  
(fig. 28)

Our material included two specimens that we have tentatively identified as *A. profundorum*. Both specimens were collected from the western North Atlantic but neither is vouchered or represented by images and thus the identity of this cluster remains to be verified; these specimens differed by 2.0.

*Galeus sauteri* (blacktip sawtail catshark) (fig. 28)

The five specimens of this species included in our analysis were all collected from Taiwan and thus represent the center of the distribution of this species, which is also known from southern Japan and the Philippines. All five samples came from specimens deposited in the University of Michigan Museum of Zoology (GN1021, GN1022, and GN1023 = UMMZ 231966 and GN991 and GN993 = UMMZ 231974). The analysis yielded a single cluster, with a range of pairwise difference among specimens of 0–5, with an average difference of 3.2 bases. It is interesting to note that this cluster occurred well outside those containing the other species of *Galeus* included in the analysis (see fig. 29). The average pairwise differences between these were as follows: 173 (between *G. sauteri* and *G. melastomus*), 154.4 (between *G. sauteri* and *G. arae*), 149.4 (between *G. sauteri* and *G. murinus*), and 166.0 (between *G. sauteri* and *G. polli*).

*Parmaturus xaniurus* (filetail catshark) (fig. 28)

The five specimens of *Parmaturus xaniurus* included in the analysis are generally representative of the distribution of this species given that they were collected from Monterey Bay, California, and this species occurs only in the eastern Pacific from California to Mexico. The analysis yielded a single cluster. The range in pairwise differences among members of this cluster was 1–5, with an average of 3.4.

*Haploblepharus edwardsii* (puffadder shyshark)  
(fig. 29)

The analysis included 19 specimens, all collected from South Africa and identified as *Haploblepharus edwardsii*. The range in pairwise differences among specimens within this cluster were 0–12, with an average of 4.4. This identification requires confirmation.

*Halaehurus buergeri* (blackspotted catshark) (fig. 29)

The analysis included five specimens from the Philippines (GN2219 = JPAG 005, GN2220 = JPAG 008, GN2222 = JPAG 115, GN2234 = JPAG 114, and GN2252 = RSE 003), examined by Compagno et al. (2005b). It yielded a single cluster; the range in pairwise differences among specimens was 0–4; the average was 2. Compagno et al. (2005b) noted that, while these specimens resembled *Halaehurus buergeri*, they differed somewhat in body shape and spotting pattern from those collected elsewhere (e.g., Taiwan, Indonesia, and Japan) and thus gave their specimens the designation *H. cf. buergeri*. However, as a result of work conducted in conjunction with the description of *Halaehurus maculosus* from Indonesia by White et al. (2007b), W.W. now considers these Philippine specimens to represent *H. buergeri*.

*Halaehurus sellus* (speckled catshark) (fig. 29)

This species was represented in the analysis by only a single specimen collected from Western Australia. This specimen was deposited in the Australian National Fish Collection (GN4893 = ANFC H 6367-01). It was identified by P.L. as *H. sellus*, a species recently described from northwestern Australia by White et al. (2007b). This specimen clustered most closely with those of *H. maculosus*; the average of the pairwise differences between specimens of these two species was 60.6.

*Halaehurus natalensis* (tiger catshark) (fig. 29)

The analysis included three specimens of this South African endemic species. The range in pairwise differences among specimens in this cluster was 3–5, with an average of 4.

*Halaehurus lineatus* (lined catshark) (fig. 29)

Both of the specimens of this species included in the analysis were collected from KwaZulu-Natal in South Africa and identified by Jeremy Cliff. They were found to comprise a single cluster; their sequences differed from one another by 4. These specimens are representative of the relatively limited distribution of this species. This species clustered most closely with *H. natalensis*. The average of the pairwise differences between these two species was 80.3.

*Holohalaelurus regani* (Izak catshark) (fig. 29)

All 17 specimens of this species included in the analysis were collected off the coast of Western Cape Province and the western regions of Eastern Cape Province, South Africa. The range in pairwise differences among specimens was 0–6, with an average of 2. Our analysis did not include specimens, formerly considered as the “Natal” form of this species, which were described as *Holohalaelurus favus* by Human et al. (2006).

*Galeus melastomus* (blackmouth catshark) (fig. 29)

A total of eight specimens identified as this species were included in this analysis. These were collected from a diversity of localities in the eastern Atlantic including Ireland, Scotland, and Madeira and thus represent the northwestern elements of the distribution of this species. The sample from Madeira was taken from a specimen in the Museu de História Natural e Aquário in Funchal (GN6627 = MMF 36798). The analysis yielded a single cluster; the range in pairwise differences among specimens in this cluster was 0–4; the average of pairwise differences was 2.

*Galeus polli* (African sawtail catshark) (fig. 29)

The six specimens of this species, all collected from western South Africa were included. These represent only a small portion of the distribution of this species, which occurs throughout the west coast of Africa, and also in the Mediterranean Sea. The range in pairwise differences among specimens of this species was 0–3. This species clustered most closely with *G. melastomus*. The average of the pairwise differences between these two species was 51.4.

*Galeus arae* (rougtail catshark) (fig. 29)

The analysis included a single Atlantic specimen identified provisionally as this species by Jose Castro. It was divergent from all other included *Galeus* species. For example, the average pairwise differences between the species with which it clustered most closely were 72.8 (*A. melastomus*) and 81.5 (*A. polli*).

*Galeus murinus* (mouse catshark) (fig. 29)

Both specimens of this species included in the analysis were collected from the central to eastern Atlantic; one of these was identified

by Neils Roar Hareide. The specimens clustered together independent of the other species of *Galeus*. The sequences of these two specimens differed by 2.

*Apristurus* species (second major cluster) (fig. 30)

Seven additional specimens belonging to the genus *Apristurus* were included in the analysis. These clustered together, but well outside the 56 specimens considered to represent ~14 other species of *Apristurus* (see fig. 28), questioning the integrity of this genus as currently circumscribed.

Three of the seven specimens in this cluster were identified as one of the long-snouted catsharks, *Apristurus australis* (pinocchio catshark). These specimens are representative of the known distribution of this Australian endemic species as they were collected from Tasmania and Western Australia. Both samples from Western Australia came from museum specimens (GN4877 = ANFC H 2573-01 and GN4878 = ANFC H 2600-04) and clustered with a specimen from Tasmania. The range of pairwise differences among these three specimens was 2–8 (with an average of 6).

Also included in the analysis was a single specimen from New Zealand. While this specimen clustered most closely with the specimens identified as *Apristurus australis*, the average of the pairwise differences between it and the specimens in the latter subcluster was 62.3. Thus, we have given this specimen the distinct designation *Apristurus* sp. 3 as it may represent an undescribed species. Although there are no photographs or retained specimens of this catshark, it could be another long-snout species; it could be the long-snouted *Apristurus* sp. A of Paulin et al. (1989), which has also been informally referred to as *A. cf. herklotsi* in unpublished checklists of New Zealand fishes. This cluster is most likely referable to the *A. longicephalus* group defined by Nakaya and Sato (1999).

Two specimens collected from the north-eastern Atlantic clustered together (with a sequence difference of 5), independently from all four of the above specimens. The average of the pairwise differences between these Atlantic specimens and those of *A. australis* was 153.8, and between the Atlantic specimens and *Apristurus* sp. 3 was 161.5. Thus, specimens

in the Atlantic cluster have been given the provisional designation *Apristurus* sp. 4; it is possible they also represent an undescribed species. Clustering with, but well outside these two specimens was a single specimen from the University of Kansas Ichthyology Collection (GN2533 = KUI 29258), collected from California and identified as *Apristurus kampae*. The average of the pairwise differences between the specimen of *A. kampae* and the two specimens of *Apristurus* sp. 4 was 69.

*Asymbolus rubiginosus* (orange spotted catshark) (fig. 31)

Three specimens from Ken Graham, identified as *Asymbolus rubiginosus*, from off New South Wales, Australia, were included in the analysis. These specimens clustered together and had a range in pairwise differences of 0–4, with an average of 2.7.

*Asymbolus parvus* (dwarf catshark) (fig. 31)

Both samples of this species included in the analysis came from museum specimens (GN4879 = ANFC H 6415-01 and GN4880 = ANFC H 6415-02) collected from Western Australia. These specimens are representative of the distribution of this species, which is endemic to Western Australia. The sequences of these specimens differed from one another by 4. The specimens of this species grouped most closely with those of *A. rubiginosus*; the average of the pairwise differences between these two species was 35.

*Asymbolus analis* (gray spotted catshark) (fig. 31)

All five specimens of this Australian endemic species included in the analysis were collected in the central part of its range. The analysis yielded a single tight cluster with a range in pairwise differences among specimens of 0–2.

*Figaro boardmani* (Australian sawtail catshark) complex (fig. 31)

The nine specimens included in the analysis are generally representative of the distribution of this Australian endemic; six come from southeastern Australia and three from Western Australia. The analysis yielded two distinct clusters: one consisting of specimens from southeastern Australia and one consisting of specimens from Western Australia. The range in pairwise differences among specimens within the southeastern cluster was 0–6, with an

average of 2.8; the range for the Western Australian cluster was 1–2, with an average of 1.3. The average of the pairwise differences between clusters was 19.3 suggesting that, as noted by Gledhill et al. (2008), regional variation occurs within this species. In recognition of this variation, we have given the specimens from Western Australia the designation *Figaro* cf. *boardmani*, reserving the designation *Figaro boardmani* for those in the southeastern cluster. The three samples of *F.* cf. *boardmani* were taken from specimens in the Australian National Fish Collection (GN4890 = ANFC H 6414-07, GN4891 = ANFC H 6414-08, and GN4892 = ANFC H 6414-10). Taxonomic revision of this species complex is currently being undertaken by researchers at the Australian National Fish Collection.

*Bythaelurus dawsoni* (New Zealand catshark) (fig. 31)

Six specimens of this New Zealand endemic were included in the analysis and they yielded a single tight cluster. The range in pairwise differences among specimens in the cluster was 0–1. The specimens from which five of these six samples were taken are deposited in the Museum of New Zealand, Te Papa Tongarewa (GN6731 = NMNZ P.042162, GN6737 = NMNZ P.042731, GN6739 = NMNZ P.042162, GN6746 = NMNZ P.044374, and GN6748 = NMNZ P.044375).

### Pseudotriakidae (false catsharks)

*Pseudotriakis microdon* (false catshark) (fig. 32)

Our analysis included three specimens of this species, all from the mid-Atlantic ridge. Thus, our material represents only one element of the wide and patchy distribution of this monotypic genus. The analysis yielded a single cluster with the three specimens being identical in sequence.

*Gollum* species (fig. 32)

At present this genus formally includes only the New Zealand endemic, *Gollum attenuatus*. However, Compagno et al. (2005b) noted that a second, potentially undescribed species (*Gollum* sp. 1), occurs in the Philippines (treated as *Gollum* sp. A by Compagno et al., 2005a). Our analysis included one specimen of *G. attenuatus* from New Zealand,

and one specimen (GN2440 = JPAG 229) of the potentially undescribed species, *Gollum* sp. 1, from the Philippines. These two *Gollum* specimens were found to group together, but their sequences differed by 60, thus this supports the notion of these being separate species.

### Proscylliidae (finback catsharks)

*Proscyllium habereri* (graceful catshark) (fig. 32)

Four specimens of this species collected and identified by Kazuhiro Nakaya from Okinawa and the East China Sea were included in the analysis. The specimen from Okinawa is deposited in the Hokkaido University Museum (GN2601 = HUMZ 175853). These specimens represent the more northern elements of the distribution of this species, which extends as far south as Java. The analysis yielded a single cluster. The sequences of the three specimens from the East China Sea were identical. The average of the pairwise differences between these three specimens and the one from Okinawa was 6.

*Eridacnis* sp. 1 (Philippine ribbontail catshark) (fig. 32)

A single specimen, provisionally identified as belonging to the genus *Eridacnis*, from the Philippines was included in the analysis. This specimen was identified as “?*Eridacnis* sp. 1” by Compagno et al. (2005b) and who considered it (GN2212 = BRU 004) potentially represented a new species. This specimen grouped potentially most closely with the specimens of *Proscyllium habereri*, but the average pairwise difference between specimens of these two species was 164.5.

### Scyliorhinidae (catsharks): group 2

*Atelomycteris marmoratus* (coral catshark) (fig. 33)

In total, 10 specimens of this species were included in the analysis: nine were collected from Malaysian Borneo and one from the Philippines. These specimens represent eastern elements of the distribution of this species, which extends as far west as Pakistan. The analysis yielded a single cluster. The range in pairwise differences within the cluster was 0–11, with an average of pairwise differences of 3.8. There was some evidence of geographic structure within the cluster in that the spe-

cimens from Borneo grouped together. The average of the pairwise differences between specimens in the Borneo cluster and the specimen from the Philippines was 9.9. We note that the sample from the Philippines, which came from a museum specimen (GN2235 = JPAG 044), was treated by Compagno et al. (2005b); one of the specimens from Borneo was deposited in the IPPS (GN3705 = IPPS BO495).

*Aulohalaelurus labiosus* (blackspotted catshark) (fig. 33)

The three specimens of this species were all collected from Western Australia and are thus representative of the distribution of this Western Australian endemic. Two samples came from specimens deposited in the Western Australian Museum (GN2268 = WAM P 31670-001 and GN2269 = WAM P 31671-001). The analysis yielded a single cluster. The range in pairwise differences among specimens in this cluster was 4–7, with an average of 5.3.

*Atelomycteris marnkalha* (eastern banded catshark) (fig. 33)

All three specimens of this species were collected from the Torres Strait, off Australia, and represent the central elements of its distribution, which extends eastward to New Guinea. All three samples were taken from specimens in the Australian National Fish Collection (GN4881 = ANFC H 6144-01, GN4882 = ANFC H 6145-01, and GN4883 = ANFC H 6146-01). The analysis yielded a single tight cluster, with a range in pairwise differences among members of this cluster of 2–4, and an average of 2.7. It was interesting that this species clustered with *Aulohalaelurus labiosus*. The average of the pairwise differences between these two species was 158.3 and between *A. marnkalha* and its congener *A. marmoratus* 155.6.

*Parmaturus* sp. (fig. 33)

Six samples, all collected from New Zealand and deposited in the Museum of New Zealand, Te Papa Tongarewa (GN6734 = NMNZ P.045528, GN6730 = NMNZ P.042517, GN6741 = NMNZ P.044582, GN6747 = NMNZ P.044583, GN6750 = NMNZ P.044578, and GN6755 = NMNZ P.042524), were identified only to genus. The



analysis yielded a single cluster with the range in pairwise differences among specimens being 0–3, with an average of 1.2. This taxon grouped well away from the cluster comprised of its congener, *Parmaturus xaniurus* (see fig. 28); the average of pairwise differences between these two species was 190.5. This suggests that the identity of these specimens needs to be examined more closely, both at the specific and generic levels. The only other species of *Parmaturus* currently known from New Zealand is *P. macmillani*. This taxon is currently under taxonomic investigation by P.L., Bernard Séret, and Keiichi Sato.

*Schroederichthys bivius* (narrowmouth catshark) (fig. 33)

Both specimens of this species were collected from Argentina and thus represent the eastern elements of the distribution of this species, which extends throughout much of coastal Chile and Argentina. The sequences of these two specimens were identical.

*Poroderma* species

Given they exhibited the least amount of intrageneric variation seen in the analysis, a haplotype map was generated for the two sympatric species of *Poroderma*. This map (fig. 90) shows two relatively tight haplotype clusters, with no overlap between species, suggesting that although divergence is low the species are distinct.

*Poroderma pantherinum* (leopard catshark) (fig. 34)

In total, 16 specimens of this species were included in the analysis. These specimens came from a diversity of localities throughout South Africa and thus represent much of the distribution of the species. The analysis yielded a single cluster. The range in pairwise differences among specimens was 0–6, with an average of 3.

*Poroderma africanum* (striped catshark) (fig. 34)

The 12 specimens of this species were collected from South Africa and thus are representative of the distribution of this South African endemic. The analysis yielded a single cluster, which was tightly allied with the cluster of specimens of *P. pantherinum*. The range in pairwise differences among specimens in the *P. africanum* cluster was 0–2, with an average of 1.3. The

average of the pairwise differences between specimens of the two *Poroderma* species was 6.3.

*Scyliorhinus capensis* (yellowspotted catshark) (fig. 34)

A total of 15 specimens of this southern Africa endemic were included. The range of pairwise differences among these specimens was 0–2; the average was 0.6.

*Scyliorhinus canicula* (smallspotted catshark) (fig. 34)

The single specimen of this species was collected from the eastern Atlantic. It grouped most closely with the specimens of the southern Africa endemic *S. capensis*. The average of the pairwise differences between specimens of these two species was 57.5.

*Scyliorhinus retifer* (chain catshark) (fig. 34)

Also included in the analysis were three specimens preliminarily identified as *Scyliorhinus retifer*. One of these came from a specimen in the University of Kansas Ichthyology Collection (GN2530 = KUI 26984) that was collected from the mid-Atlantic bight. The others were collected from the northwestern Atlantic and Gulf of Mexico. The analysis yielded a single, divergent cluster. However, the range in pairwise differences among these specimens was substantial, at 9–22, and the average was 14.7.

*Scyliorhinus stellaris* (nursehound) (fig. 34)

A single specimen of *S. stellaris*, collected from the eastern Atlantic, was included. This specimen grouped along with, but outside its congeners. The average pairwise difference between the specimen of *S. stellaris* and those in the *S. retifer* cluster was 73.3, between *S. stellaris* and the specimen of *S. canicula* 73, and between *S. stellaris* and *S. capensis* 66.5.

*Cephaloscyllium variegatum* (saddled swellshark) (fig. 34)

The analysis included six specimens of this species from Australia, one of which was included among the other material examined by Last and White (2008c) in the original description of this species (GN4889 = ANFC H 3580-01). The range in pairwise differences among specimens in this cluster was 0–2, with an average of 0.9.

*Cephaloscyllium albiginum* (whitefin swellshark) (fig. 34)

The three samples of this species included in the analysis were taken from the holotype (GN4887 = ANFC H 5314-11), a paratype (GN4888 = ANFC H 5940-01), and an additional examined specimen (GN4886 = ANFC H 3588-01) included in the original description of this relatively new species from New South Wales and Tasmania, Australia (see Last et al., 2008b). The range in pairwise differences among these three specimens was 1–2, with an average of 1.3.

*Cephaloscyllium hiscosellum* (Australian reticulate swellshark) (fig. 34)

The specimen of this species included in our analysis was a paratype of this Western Australian species (GN4884 = ANFC H 6419-01), described by White and Ebert (2008). It clustered outside but along with the specimens of *C. albiginum*. The average of the pairwise differences between this specimen and those of *C. albiginum* was 44.3.

*Cephaloscyllium umbratile* (Japanese swellshark) (fig. 34)

The four samples for this species included in the analysis come from specimens in the University of Michigan Museum of Zoology (GN981 = UMMZ 231960 and GN982, GN1017, and GN1018 = UMMZ 231967) originally identified as *C. isabellum*. These specimens were all collected from Taiwan. However, Schaaf-Da Silva and Ebert (2008) clarified the status of *C. umbratile* as a valid species having been previously placed in synonymy with *C. isabellum*. Thus, the specimens included here have been provisionally identified as *C. umbratile*. As such, they represent the southern portion of the western North Pacific distribution of this species. The range in pairwise differences among specimens of was 0–4, with an average of 2.7. Schaaf-Da Silva and Ebert (2008) also described two new species of *Cephaloscyllium* from Taiwan, so the identity of these specimens should be confirmed.

*Cephaloscyllium* sp. 1 (Philippine swellshark) (fig. 34)

Our analysis included two specimens of *Cephaloscyllium* collected from the Philippines, both of which were treated by Com-

pagno et al. (2005b) (GN4361 = JPAG 231 and GN4352 = JPAG 232) as *Cephaloscyllium* sp. 1. These specimens clustered together and their sequences differed from one another by three bases. However, this species needs to be critically compared with *C. pardelotum* and *C. maculatum* both described by Schaaf-DaSilva and Ebert (2008) from Taiwan, as well as with *C. pictum*, recently described from Indonesia by Last et al. (2008c). These specimens clustered mostly closely with specimens of *C. umbratile*. However, the average of the pairwise differences between these two clusters was 47.8.

*Cephaloscyllium laticeps* (Australian swellshark) (fig. 34)

In total, six specimens, all collected from southeastern Australia were included in the analysis. One of these samples was taken from a museum specimen (GN4885 = ANFC H 3581-01). The range in pairwise differences among specimens in this cluster was 0–5, with an average of 1.9.

*Cephaloscyllium ventriosum* (swellshark) (fig. 34)

One sample of this species, taken from a specimen in the University of Kansas Ichthyology Collection (GN2529 = KUI 28129) collected from California, was included in the analysis. This specimen was grouped with all other *Cephaloscyllium* species, but was by far the most divergent species. The average of the pairwise differences between this specimen and those of the six other *Cephaloscyllium* species was 109.

#### LAMNIFORMES (mackerel sharks)

##### Lamnidae (mackerel sharks)

*Isurus oxyrinchus* (shortfin mako) (fig. 35)

In total, 24 specimens of *I. oxyrinchus* were included in the analysis, which yielded a well-defined cluster. The range in pairwise p-differences among specimens was 0–21, with an average of 10.6. This cluster consisted of two fairly well-defined subclusters, one of which exhibited more sequence heterogeneity than the other; this is also reflected in the haplotype map for phenotype (fig. 91A). However, as illustrated by the haplotype map of geography (fig. 91B) there was no apparent geographic pattern to these subclusters, each of which was comprised of

specimens from the western North Atlantic, Gulf of Mexico, California, Gulf of California, and Taiwan; one subcluster also included a specimen from South Africa and the other also included a specimen from Vietnam. The range in pairwise differences among specimens in the subcluster including the specimen from South Africa was 0–4, with an average of 2.4. The range in pairwise differences among specimens in the other subcluster was 0–14, with an average of 6.8. The average of the pairwise differences between specimens in the two subclusters was 17.2. In the absence of morphological or geographic data to support this distinction, we have tentatively identified all 24 members of the cluster as *I. oxyrinchus*. Nonetheless, these results are interesting in light of previous workers (e.g., Moreno and Morón, 1992; Heist et al., 1996; Schrey and Heist, 2003), all of who provided evidence of population structure among makos globally.

*Isurus paucus* (longfin mako) (fig. 35)

A total of six specimens of this species were included in the analysis, four from the western North Atlantic, one from the Caribbean Sea, and one from the Gulf of Mexico. These specimens comprised a single cluster; the range in pairwise differences among specimens in this cluster was 0–8, with an average of 3.3. The average of the pairwise differences between the six specimens of this species and the 24 specimens of *I. oxyrinchus* was 110.3.

*Carcharodon carcharias* (great white shark) (fig. 35)

The 17 specimens of this species included in the analysis were collected from South Africa, the western North Atlantic, California, and South Australia. The analysis yielded a single cluster, with two subclusters. The range in pairwise differences among all 17 specimens was 0–20, with an average of 4.2. One subcluster was comprised of the specimens from South Africa and the western North Atlantic, the other comprised of specimens from California and South Australia (i.e., from localities in the Pacific Ocean). The range in pairwise differences among specimens in the former subcluster was 0–2; the two specimens in the latter subcluster differed from one another by seven

bases. On average, pairwise difference between specimens of the two subclusters was 16.3. This intriguing result, which is consistent at least in part with the findings of Pardini et al. (2001) and Jorgensen et al. (2009), suggests that some consideration should be given to the potential lack of conspecificity of *C. carcharias* from the Atlantic and Indian oceans, and those from the Pacific Ocean.

*Lamna nasus* (porbeagle shark) (fig. 35)

The analysis of 10 specimens yielded a single relatively divergent cluster with some evidence of two subclusters within. The range in pairwise differences among all 10 specimens was 0–15, with an average of 6.8. One subcluster consisted of the two specimens from Tasmania, both vouchered (GN2261 = AMS I32756-002 and GN2262 = AMS I32756-001), and the other consisted of specimens collected from the northeastern and northwestern Atlantic. The two specimens from Tasmania differed from one another by nine bases. The range in pairwise differences among specimens in the other subcluster was 0–8. The average of the pairwise differences between specimens from the Tasmanian subcluster and those from the Atlantic Ocean subcluster was 14. These results suggest that some consideration should be given to the possibility of the existence of taxonomic variation among porbeagles between ocean basins.

*Lamna ditropis* (salmon shark) (fig. 35)

Two specimens of this north Pacific-dwelling species, both from Japan, were included. They differed by 4. The average of the pairwise differences between *L. ditropis* and *L. nasus* was 68.

### Cetorhinidae (basking sharks)

*Cetorhinus maximus* (basking shark) (fig. 35)

Two specimens of this widely distributed species were included in the analysis. These samples differed from one another by five bases. As the locality of one of the two specimens is unknown, our results do not allow us to expand on the work of Hoelzel et al. (2006), who found relatively low genetic diversity among specimens from different ocean basins.

### **Odontaspidae (sand tiger sharks): group 1**

*Carcharias taurus* (sand tiger shark) (fig. 35)

All six specimens of this species included in the analysis were collected from the western North Atlantic. The range in pairwise differences among these specimens was 0–4, with an average of 1.7. As our specimens represented only a very small portion of the range of this widely distributed species, they were not conducive to examining the genetic variation seen, for example, by Ahonen et al. (2009) in this taxon.

### **Alopiidae (thresher sharks)**

*Alopias pelagicus* (pelagic thresher) (fig. 35)

The analysis yielded a cluster with weak evidence of two subclusters. The range in pairwise differences among all 20 specimens was 0–12; the average was 6. One subcluster consisted of a total of 10 specimens collected from Borneo, Taiwan, the Philippines, and India. The range in pairwise differences among these specimens was 0–3. The second subcluster consisted of 10 specimens from the Gulf of Mexico and the Gulf of California, as well as one specimen from Taiwan. One of the samples from the Gulf of California was vouchered (GN5402 = IBUNAM PE9512). The range in pairwise differences among these specimens was 0–7. The average of the pairwise differences between specimens in the two subclusters was 9.9. Although these results do not support the potential existence of a cryptic species of *Alopias* off Baja California as suggested by Eitner (1995), they do provide some support for the existence of greater diversity in this genus than currently thought. We note that included here is a specimen (GN4309 = JPAG 117B) treated by Compagno et al. (2005b) as the first record of *A. vulpinus* from the Philippines, which clusters among specimens of *A. pelagicus*. This result suggests that the identity of this specimen should be reconsidered.

*Alopias vulpinus* (thresher shark) (fig. 35)

The 11 specimens of this species included in the analysis were collected from both the western North Atlantic and the eastern Pacific oceans. While our analysis lacked

representation from throughout much of the distribution of this species, it revealed no evidence of structure between the eastern and western regions of North America. The range in pairwise differences among specimens in this cluster was 0–2, with an average of 0.9. However, the average of the pairwise differences between specimens of *A. vulpinus* and those identified as *A. pelagicus* was 97.

*Alopias superciliosus* (bigeye thresher) (fig. 35)

Little difference was seen among the nine specimens in the analysis, which included specimens from Virginia, Florida, Taiwan, Senegal, Gulf of California, and the Philippines, and thus represented much of the global distribution of this species. The range in pairwise differences among these specimens was 0–8, with an average of pairwise differences of 2.8. For comparative purposes we note that the average of the pairwise differences between specimens of *A. superciliosus* and those of *A. pelagicus* was 120.1 and between specimens of *A. superciliosus* and those of *A. vulpinus* 118.7.

### **Megachasmidae (megamouth sharks)**

*Megachasma pelagios* (megamouth shark) (fig. 35)

The six specimens included in the analysis came from California, Indonesia, Japan, and Taiwan, and thus represent essentially only the Pacific elements of the distribution of this species. The range in pairwise differences among these specimens was 0–10, with an average of pairwise differences of 3.5.

### **Odontaspidae (sand tiger sharks): Group 2**

*Odontaspis ferox* (smalltooth sand tiger) (fig. 35)

Both of the included specimens of this species were collected from the Azores and thus represent only a very small portion of the distribution of this species. Nonetheless, these specimens were identical in sequence.

*Odontaspis noronhai* (bigeye sand tiger) (fig. 35)

Only a single specimen of this species, collected from Brazil, was included in the analysis. The average of the pairwise differences between the specimens of this species, and those of *Odontaspis ferox* was 93.

### **Pseudocarchariidae (crocodile sharks)**

*Pseudocarcharias kamoharui* (crocodile shark) (fig. 35)

The four specimens of this species included in the analysis were collected from Taiwan and Hawaii, and thus represent only the Pacific elements of the distribution of this species. The range in pairwise differences among all four specimens was 1–18 (with an average of 9 bases). The analysis yielded a subcluster comprised of both specimens from Taiwan and a specimen from Hawaii. The range in pairwise differences among these specimens was 1–2. However, the second specimen collected from Hawaii, grouped outside this subcluster, with an average pairwise difference of 16.7 relative to the members of the cluster.

### **Mitsukurinidae (goblin sharks)**

*Mitsukurina owstoni* (goblin shark) (fig. 35)

All three specimens of this species included in the analysis were collected from localities in the Pacific Ocean (i.e., California, Tasmania, and Japan), and thus they represent only a relatively small portion of the distribution of this species. These specimens differed from one another by only 0–2, with an average of 1.3 bases. One of the samples was taken from a specimen at the Los Angeles County Museum (GN1798 = LACM 47362-1).

## **ORECTOLOBIFORMES (carpet sharks)**

### **Hemiscylliidae (longtailed carpetsharks)**

*Chiloscyllium punctatum* (brownbanded bambooshark) complex (fig. 36)

A total of 56 specimens originally identified as *Chiloscyllium punctatum* were included in the analysis. These were collected from Thailand, Singapore, Malaysian and Indonesian Borneo, Vietnam, and Australia. The analysis yielded two distinct clusters, one consisting of the two specimens from Australia; the other consisting of the 54 specimens from the remaining localities. One sample from Borneo was vouchered (GN4446 = CAS 229025). The two specimens in the Australian cluster differed from one another by a single base. The range in pairwise differences among the 54 specimens in the

second cluster was 0–10, with an average of 3.3. While some structure within the second cluster was observed, the averages of these differences (e.g., 5 between a group comprised of 3 of the specimens from Sabah and a group comprised of specimens primarily from Sarawak) were determined to be too small to warrant further mention at this time. The average of the pairwise differences between specimens of the two main clusters was 27.8. Given that the type locality of *C. punctatum* is Jakarta, the cluster comprised of specimens collected from Thailand, Singapore, and Borneo was given that provisional designation.

The haplotype map colored by phenotype (fig. 92A) supports the distinction between these two species in that there is no overlap in haplotypes among specimens of these two species. The haplotype map colored by geography (fig. 92B) illustrates the allopatric nature of the distribution of these two taxa. Although Last and Stevens (2009) provisionally referred to Australian populations as *C. punctatum*, this analysis suggests these specimens may represent an undescribed species. Thus, the specimens in the Australian cluster have been referred to here as *Chiloscyllium* cf. *punctatum*. Taxonomic revision of this species is currently being undertaken by W.W., P.L., and Gordon Yearsley.

*Chiloscyllium indicum* (slender bambooshark) (fig. 36)

The 42 specimens of this species included in the analysis were all collected from either Malaysian or Indonesian Borneo and thus represent only a portion of the Indo-West Pacific distribution of this species. Eleven of the specimens from Borneo were vouchered (GN4467 = CAS 229031, GN4471 = CAS 229032, GN3440 = ANFC H 6123-01, GN3676 = ANFC H 6213-01, GN3692 = ANFC H 6214-01, GN3693 = ANFC H 6214-02, GN3511 = IPPS BO294, GN3470 = IPPS BO253, GN3488 = IPPS BO271, GN3679 = IPPS BO468, and GN4276 = MZB 15.505). The analysis yielded essentially a single cluster, with a range of pairwise differences among specimens in this cluster of 0–11, with an average of 1.5. Significant morphological variation exists among specimens of *C. indicum*, even from the same

collection locality, and a more thorough investigation of the material is needed. The average of the pairwise differences between *C. indicum* and *C. punctatum* was 132.1, and between specimens of *C. indicum* and those of *C. cf. punctatum* 132.2.

*Chiloscyllium plagiosum* (whitespotted bambooshark) (fig. 36)

The analysis included three specimens of this species, which were collected from Singapore and Malaysian and Indonesian Borneo, and were identical in sequence. The average of the pairwise differences seen between these specimens and those of *C. indicum* was 115.9, those of *C. punctatum* 128.2, and those of *C. cf. punctatum* 128.5.

*Hemiscyllium ocellatum* (epaulette shark) (fig. 36)

This genus was relatively poorly represented in our analysis. Only three specimens of a single species were included and all three of these were of *H. ocellatum* collected from Cairns, Australia. These were identical in sequence and of particular interest is the fact that this cluster grouped among species of *Chiloscyllium*.

*Chiloscyllium hasseltii* (Indonesian bambooshark) (fig. 36)

The analysis included 13 specimens of this species, 12 from Borneo, and one from Singapore. The analysis yielded a single tight cluster. Three of the specimens from Borneo were vouchered (GN4458 = CAS 229029, GN3416 = ANFC H 6122-01, and GN3704 = IPPS BO494.) The range in pairwise differences among members of this cluster was 0–4, with an average of 0.7. The average of the pairwise differences between specimens of this species and those of *C. punctatum* was 142.3, between this species and *C. cf. punctatum* 143.5, between those of *C. indicum* 157.6, and between those of *C. plagiosum* 150.9.

*Chiloscyllium griseum* (gray bambooshark) (fig. 36)

Two specimens collected from Maharashtra, India, and preliminarily identified as *C. griseum* were included in the analysis. These specimens differed from one another by one base and clustered most closely with the specimens of *C. hasseltii*. The averages of the pairwise differences between this species and

its congeners were as follows: 137.8 from *C. punctatum*, 140 from *C. cf. punctatum*, 162.1 from *C. indicum*, 147.5 from *C. plagiosum*, and 119.6 from *C. hasseltii*. We have no images or retained specimens of this taxon, so their identity is somewhat uncertain. However, given that two of the three other described species of *Chiloscyllium* not included here occur only in localities well outside India (i.e., Madagascar for *C. caeruleopunctatum* and Burma for *C. burmensis*), and that the specimens from India lacked the dorsal ridges typical of *C. arabicum* and lacked the dark marks on the fins seen in *C. burmensis*, this identification is likely to be correct. Alternatively, these specimens may represent an as yet undescribed species of *Chiloscyllium*. NADH2 data for the three remaining described species of the genus would do much to help confirm this identification.

#### Stegostomatidae (zebra sharks)

*Stegostoma fasciatum* (zebra shark) (fig. 37)

Eleven of the 12 specimens included in the analysis were collected from Borneo; the remaining specimen came from Mozambique, and thus our specimens span much of the distribution of this species. The analysis yielded essentially a single cluster. The range in pairwise differences among specimens in this cluster was 0–7, with an average of 3.8. The relatively low level of variation seen here is interesting in view of the results of Dudgeon et al. (2009), given that our specimens included a specimen from Mozambique, as well as the Indo-West Pacific.

#### Rhincodontidae (whale sharks)

*Rhincodon typus* (whale shark) (fig. 37)

A total of six specimens were included in the analysis. These came from Taiwan, California, Borneo, and Mozambique and thus represent much of the Indo-Pacific distribution of this species, but do not include any representatives from the Atlantic Ocean. The analysis yielded a single very tight cluster with all six specimens identical in sequence. The comparatively small size of our sample makes our results difficult to compare with those of previous studies on genetic variation

of this species (e.g., Schmidt et al., 2009; Castro et al., 2007).

### Ginglymostomatidae (nurse sharks)

*Pseudoginglymostoma brevicaudatum* (shorttail nurse shark) (fig. 37)

The three specimens of this eastern Africa endemic species included here all came from Kenya. They were identical in sequence. This species clustered most closely with *Rhincodon typus*, but a model-based formal phylogenetic analysis is required to resolve their relationships more definitively. The average of the pairwise differences among specimens of these two species was 148.

*Ginglymostoma cirratum* (nurse shark) complex (fig. 37)

The 12 specimens originally identified as this species included in the analysis were collected from the Gulf of Mexico, the western Atlantic off the coasts of Florida and Virginia, and the Gulf of California. The analysis yielded two distinct clusters: one consisting of the Atlantic specimens and one consisting of the three specimens from the Gulf of California. The nine specimens in the Atlantic cluster exhibited a range in pairwise differences of 0–2, with an average of 1. The cluster comprised of the specimens from the Gulf of California had a range of pairwise differences of 0–1. However, the average of the pairwise differences between the members of these two clusters was 15.9. This finding lends some support to the suggestion that the nurse sharks occurring off of Baja may not be conspecific with those occurring along the eastern seaboard of North America. One of the specimens from the Gulf of California was vouchered (GN3561 = TCWC 7585.01 = IBUNAM PE9492). Given that the type locality of *G. cirratum* is Jamaica, we have referred to specimens in the Atlantic cluster as *G. cirratum* and to those in the Gulf of California cluster as *Ginglymostoma* cf. *cirratum*. Both the haplotype map for phenotype (fig. 93A), which shows no haplotype overlap among specimens of the two taxa, and that for geography (fig. 93B) support the distinction between these two allopatric species.

*Nebrius ferrugineus* (tawny nurse shark) (fig. 37)

Both specimens of this species included in the analysis were collected from northern Australia, and thus are not fully representative of the Indo-West to central Pacific distribution of this species. These specimens differed from one another by three base pairs.

### Orectolobidae (wobbegongs)

*Orectolobus hutchinsi* (western wobbegong) (fig. 38)

The 10 specimens of this relatively newly described Western Australian endemic species (see Last et al., 2006) included three paratypes (GN4847 = ANFC H 6189-01, GN4848 = ANFC H 6189-02, and GN4849 = ANFC H 6189-03). All 10 specimens were identical in sequence but differed substantially from all five of the other included species of this genus.

*Orectolobus parvimaaculatus* (dwarf spotted wobbegong) (fig. 38)

All three specimens included in the analysis were paratypes (GN4854 = ANFC H 5633-07, GN4855 = ANFC H 6172-01, and GN4856 = ANFC H 6192-01) of this recently described species found only off southwestern Australia (see Last and Childlow, 2008). These three specimens were identical in sequence and they clustered most closely with specimens of *O. hutchinsi*, but the average of the pairwise differences among specimens of these two species was 30.

*Orectolobus halei* (gulf wobbegong) (fig. 38)

Seven specimens of this Australian species, which was recently resurrected and redescribed by Huvneers (2006), an action supported by Corrigan et al. (2008), were included in the analysis; all seven were collected from New South Wales and Western Australia. The two samples from New South Wales came from voucher specimens deposited in the Australian National Fish Collection (GN4845 = ANFC H 6278-01, and GN4846 = ANFC H 6278-02). The seven specimens formed a tight cluster with a range in pairwise differences of 0–2, with an average of 1.

*Orectolobus maculatus* (spotted wobbegong) (fig. 38)

The three samples of this species included in the analysis came from voucher specimens

deposited in the Australian National Fish Collection (GN4851 = ANFC H 5765-01, GN4852 = ANFC H 5766-01, and GN4853 = ANFC H 5766-02). These specimens were identical in sequence. They clustered most closely with those of *O. halei*; the average of the pairwise differences between specimens of these two species was 15.4.

*Orectolobus ornatus* (ornate wobbegong) (fig. 38)

A single sample of this species, taken from a voucher specimen deposited in the Australian National Fish Collection (GN4857 = ANFC H 5763-01) was included. The average of pairwise differences between *O. ornatus* and *O. hutchinsi* was 58, *O. parvimaculatus* 60, *O. halei* 54.4, and *O. maculatus* 50.

*Orectolobus floridus* (floral banded wobbegong) (fig. 38)

All three of the specimens of this southwestern Australian endemic included in the analysis were paratypes (GN4858 = ANFC H 5936-01, GN4859 = ANFC H 6168-01, and GN4860 = ANFC H 6490-01). Like most other wobbegong species, these specimens were identical in sequence. They clustered along with, but outside their five congeners included in the analysis; the average of the pairwise differences between this species and the others were as follows: *O. hutchinsi* 59, *O. parvimaculatus* 59, *O. halei* 50.4, *O. maculatus* 46, and *O. ornatus* 72.

*Eucrossorhinus dasypogon* (tasselled wobbegong) (fig. 38)

The two specimens included in the analysis, both of which were collected in Australia, were identical in sequence. They represent the more southern elements of the distribution of this species, which is also known from Indonesia, Papua New Guinea, and possibly Malaysia. Specimens of this species grouped along with, but outside the six *Orectolobus* species.

#### **Brachaeluridae (blind sharks)**

*Brachaelurus colcloughi* (bluegray carpetshark) (fig. 38)

A total of four specimens of this Australian endemic species were included in the analysis. All came from Queensland, Australia; two were specimens deposited in the Australian National Fish Collection (GN6782 = ANFC H 6849-01 and GN6785 = ANFC H 6849-

04). A remarkable amount of variation was seen among these specimens. The range in pairwise differences was 0–21, with an average of 10.5. Thus, this species is worthy of further investigation.

*Brachaelurus waddi* (blind shark) (fig. 38)

The single sample of this Australian endemic species was taken from a specimen collected from New South Wales, Australia, and deposited in the Australian Museum, Sydney (GN2265 = AMS I31253-005). The average of the pairwise differences between this specimen and those of *B. colcloughi* was 113.5. These two species are considered congeneric by Last and Stevens (2009) and distinct genera (i.e., *Heteroscyllium* and *Brachaelurus*) by Compagno (1984b, 2005a). The placement of these species requires further attention.

#### **Parascylliidae (collared carpetsharks)**

*Parascyllium collare* (collared carpetshark) (fig. 39)

A total of six specimens of this Australian endemic, collected from Victoria and New South Wales, were included in the analysis. They were found to comprise a tight cluster. The range in pairwise differences among specimens was 0–2, with an average of pairwise differences of 0.9.

#### **HETERODONTIFORMES (bullhead sharks)**

##### **Heterodontidae (bullhead sharks)**

*Heterodontus mexicanus* (Mexican hornshark) (fig. 40)

The 22 samples of this species included in the analysis were all collected from the Gulf of California, and thus represent only the more northern elements of an eastern Pacific distribution of this species. Three of these specimens were deposited in the Texas Cooperative Wildlife Collection (GN5178 = TCWC 7572.01, GN5224 = TCWC 7576.02, and GN5231 = TCWC 7583.01) and two in the Instituto de Biología, Universidad Nacional Autónoma de México (GN5390 = IBUNAM PE9509 and GN5397 = IBUNAM PE9511). The range in pairwise differences among these specimens was 0–6, with an average of 1.8.



*Heterodontus portusjacksoni* (Port Jackson shark) (fig. 40)

The seven specimens of this species included in the analysis were collected from Australia in New South Wales and Western Australia and thus span the western and eastern elements of the Australian distribution of this species. The sequences of all seven specimens were identical. Three of these specimens are deposited in the Australian National Fish Collection (GN4841 = ANFC H 6340-01, GN4842 = ANFC H 6354-09, and GN4843 = ANFC H 6354-11).

*Heterodontus zebra* (zebra bullhead shark) complex (fig. 40)

A total of three specimens originally identified as *H. zebra* were included in the analysis. These were collected from Australia, Malaysian Borneo, and Japan. The sample from Australia, taken from a specimen in the Australian National Fish Collection (GN4844 = ANFC H 6581-01), was found to cluster with the specimens of *H. portusjacksoni*, away from the other two specimens identified as *H. zebra*. Whereas the average of the pairwise differences between the Australian specimen and those in the *H. portusjacksoni* cluster was 13, the average of the pairwise differences between the Australian specimen and those of *H. zebra* from Japan and Malaysian Borneo was 24. Specimens from Japan and Malaysian Borneo differed from one another by two bases. The average of the pairwise differences between the two specimens from Japan and Malaysian Borneo and those of *H. portusjacksoni* was 19. These results suggest that the specimen from Australia probably represents an undescribed species distinct from both *H. zebra* and *H. portusjacksoni*. Given that the type locality of *H. zebra* is China, we have referred to specimens from Japan and Malaysian Borneo as *H. zebra*, and used the designation *H. cf. zebra* for the Australian form. A taxonomic revision of this group is currently being undertaken by P.L. and W.W.

*Heterodontus galeatus* (crested bullhead shark) (fig. 40)

The analysis included four specimens of this eastern Australian endemic, all collected from New South Wales, Australia. The sequences of these four specimens were

identical. The average of their pairwise differences from *H. portusjacksoni* was 59, and from *H. zebra* was 64.

*Heterodontus francisci* (horn shark) (fig. 40)

The nine specimens of this species included in the analysis were all collected from the Gulf of California, and thus represent only the more northern elements of the disjunct eastern Pacific distribution of this species. Two of these specimens were deposited in the Texas Cooperative Wildlife Collection (GN5225 = TCWC 7576.01 and GN5254 = TCWC 7567.06). The range in pairwise differences among these specimens was 0–1. The average of the pairwise differences between this species and the other included described species were as follows: between *H. mexicanus* was 82.9, between *H. portusjacksoni* was 76.3, between *H. zebra* was 74.4, between *H. cf. zebra* was 77.3, and between *H. galeatus* was 95.3.

#### SQUALIFORMES (dogfish sharks)

##### **Squalidae (dogfish sharks)**

*Squalus* species

The genus *Squalus* has recently undergone intensive scrutiny and revision with, for example, 11 new species being described in 2007 alone (e.g., see Last et al., 2007d), and with multiple species having been resurrected in the last several years (e.g., see Last et al., 2007d; Ebert et al., 2010). In our treatment of species in this genus, we have attempted to follow this new taxonomy as closely as possible.

*Squalus acanthias* (piked dogfish) (fig. 41)

The analysis included a total of 176 specimens of this species, collected from the western North Atlantic off several states including Rhode Island and Maryland, the western South Pacific off New Zealand, Tasmania, and the eastern South Pacific off Chile. The three specimens from Tasmania were vouchered (GN4956 = ANFC H 2921-03, GN4957 = ANFC H 4266-01, and GN4958 = ANFC H 4876-01). The analysis yielded a single cluster with a range in pairwise differences among specimens of only 0–10, and an average of 2.2. This relatively low variation is one of the most striking results of our analysis given the small size of

this essentially benthic species, which belongs to a genus that otherwise shows rather extensive regional diversification.

*Squalus suckleyi* (spotted spiny dogfish) (fig. 41)

A total of eight specimens, collected from the eastern North Pacific were included in the analysis. These specimens clustered independently from the specimens of *S. acanthias*. The specimens of *S. suckleyi* had a range of pairwise differences of 2–15, with an average pairwise difference of 6.5. The average of the pairwise differences between the specimens of *S. suckleyi* and those of the *S. acanthias* was 11.9. This result is consistent with the work of Ward et al. (2007), Hauser (2009), and Verissimo et al. (2010) regarding the distinct nature of specimens from the North Pacific, and thus also supports the resurrection of *S. suckleyi* for specimens previously identified as *S. acanthias* collected from localities in the North Pacific as implemented by Ebert et al. (2010).

*Squalus* sp. (fig. 42)

In total, eight specimens collected from the western South Atlantic off the coast of Brazil were included in the analysis. The range in pairwise differences among these specimens was 0–7, with an average of 3.1. These specimens have been referred to here preliminarily as *Squalus* sp. This identity remains to be explored further in the context of the species known to occur off the coast of Brazil (e.g., see Gadig, 2001).

*Squalus* cf. *mitsukurii* (shortspine spurdog) (fig. 42)

Six specimens, originally identified as the *Squalus mitsukurii*, a species described from Japan, all collected from South Africa, were included in the analysis. The range in pairwise differences among these specimens was 0–2, with an average of 0.9. Conversations with Dave Ebert lead us to believe these specimens represent an undescribed species, which resembles but is distinct from *S. mitsukurii*. Thus, we have designated this specimen as *S. cf. mitsukurii* at this time. A taxonomic treatment of this species is currently underway by Dave Ebert. This species clustered with *Squalus* sp., *Squalus cubensis*, and *Squalus montalabani*. The average of the pairwise differences between *S. cf. mitsukurii*

and these three species was 8.5, 13, and 15 bases, respectively.

*Squalus cubensis* (Cuban dogfish) (fig. 42)

Two specimens, collected by John Morrissey from Jamaica and identified as *S. cubensis*, were included in the analysis. These specimens differed from one another by five bases. They represent the more northern elements of the range of this species, which is distributed as far south as the Falkland Islands. The average of the pairwise differences between *S. cubensis*, and *Squalus* sp., also from the western Atlantic Ocean, was 12.

*Squalus montalbani* (Philippine spurdog) (fig. 42)

The analysis included two samples of this recently resurrected (see Last et al., 2007c) Indo-Pacific species, both of which were collected from voucher specimens deposited in the Australian National Fish Collection (GN4981 = ANFC H 2609-07 and GN4982 = ANFC H 4623-05). These specimens differed from one another by one base.

*Squalus chloroculus* (greeneye spurdog) (fig. 42)

Four specimens of this relatively newly described (see Last et al., 2007c) Australian endemic species, collected from Western Australia, Victoria, and Tasmania, and thus from throughout much of its range, were included in the analysis. These samples all came from specimens deposited in the Australian National Fish Collection (GN4962 = ANFC H 2564-24, GN4963 = ANFC H 4775-01, GN4964 = ANFC H 594-01, and GN4980 = ANFC H 2606-06). The range in pairwise differences among these specimens was 0–3, with an average of 1.5.

*Squalus grahamsi* (eastern longnose spurdog) (fig. 42)

The two specimens of this newly described, Australian endemic species (see White et al., 2007c) included in the analysis consisted of one paratype (GN4973 = ANFC H 4682-02) and one voucher (GN4972 = ANFC H 4623-03) in the Australian National Fish Collection. Both specimens were collected from New South Wales, Australia; they were identical in sequence.

*Squalus edmundsi* (Edmund's spurdog) (fig. 42)

Three specimens of this newly described species (see White et al., 2007c) were included

in the analysis. They consisted of a paratype (GN4969 = ANFC H 2605-05) and two voucher specimens (GN4968 = ANFC H 2591-17 and GN4970 = ANFC H 3969-15) in the Australian National Fish Collection. All three specimens were collected from Western Australia and thus represent the more southern elements of the distribution of this species, which also occurs in Indonesia and Malaysia. These specimens clustered together; the range in pairwise differences among specimens was 1–4, with an average of 2.7.

*Squalus cf. megalops* (fig. 42)

A total of 17 specimens, all from southern Africa, and originally identified as *S. megalops*, were included in the analysis. The range of pairwise differences among these specimens was 0–7, with an average of 2.9. These specimens comprised a cluster distinct from the Australian endemic *S. megalops*. The average of the pairwise differences among specimens of this cluster and those of *S. megalops* was 13.2. At this time, these specimens are considered to represent a distinct, and possibly undescribed species, and have been given the designation *Squalus cf. megalops*. They clustered most closely with *S. breviostris*. The average of the pairwise differences between specimens of *S. cf. megalops* and *S. breviostris* was 10.1.

*Squalus breviostris* (Japanese shortnose spurdog) (fig. 42)

Two samples of this species, both taken from specimens deposited in the Kagoshima University Museum (GN4996 = KAUM I 186 and GN4995 = KAUM I 187), were included in the analysis. Both specimens came from the waters off Japan and thus represent the more northern elements of the distribution of this species, which extends to the South China Sea. These two specimens were identical in sequence and clustered most closely with the specimens of *S. cf. megalops*.

*Squalus megalops* (shortnose spurdog) (fig. 42)

The analysis included seven specimens of this species, all but one of which is deposited in the Australian National Fish Collection (GN4974 = ANFC H 2605-08, GN4975 = ANFC H 3762-01, GN4978 = ANFC H

6581-23, GN4976 = ANFC H 4649-05, GN4977 = ANFC H 6581-22, and GN4979 = ANFC H 6581-24). These specimens were collected from Western Australia, Victoria, and New South Wales and thus represent much of the distribution of this species, which is now considered an Australian endemic (see Last and Stevens, 2009). The analysis yielded a single cluster of these specimens. The range in pairwise differences among specimens in this cluster was 0–6, with an average of 1.9.

*Squalus formosus* (Taiwan spurdog) (fig. 42)

Three specimens of this recently described species (White and Iglésias, 2011) from Taiwan were included in the analysis. The range in pairwise differences among these specimens was 0–2, with an average of 1.3. All three specimens are deposited in the University of Michigan Museum of Zoology (GN969 = UMMZ 231956 and GN976 and GN980 = UMMZ 231963). These specimens clustered most closely with the specimens of *S. albifrons*. The average of the pairwise differences between specimens in these two clusters was 29.3. Ward et al. (2007) also found that specimens of this species (as “sp. Taiwan highfin”) clustered most closely with *S. albifrons* from eastern Australia.

*Squalus albifrons* (eastern highfin spurdog) (fig. 42)

The three specimens of this newly described (see Last et al., 2007e) eastern Australian endemic consist of a holotype (GN4960 = ANFC H 4627-01), a paratype (GN4959 = ANFC H 3589-01), and a voucher (GN4961 = ANFC H 4704-01), all deposited in the Australian National Fish Collection. The range in pairwise differences among these specimens was 1–2, with an average of 1.3.

*Squalus japonicus* (Japanese spurdog) (fig. 42)

All three specimens of this species included in the analysis were collected from Taiwan and thus represent only the more northern elements of the distribution of this species. One of the specimens was deposited in the University of Michigan Museum of Zoology (GN975 = UMMZ 231962). All three specimens were identical in sequence.

*Squalus nasutus* (western longnose spurdog) (fig. 42)

The two specimens of this newly described species (see Last et al., 2007b) included in the analysis were collected from Western Australia. One of these was deposited in the Australian National Fish Collection (GN4983 = ANFC H 6413-01). These specimens differed from one another by one base. They clustered most closely to the *S. japonicus* cluster, as was also seen by Ward et al. (2007). The range of pairwise differences between specimens in these two species was 9.5.

*Squalus crassispinus* (fatspine spurdog) (fig. 42)

The analysis included three specimens of this newly described (see Last et al., 2007a) species, two of which are paratypes (GN4965 = ANFC H 4649-03 and GN4966 = ANFC H 4649-04) and one a voucher (GN4967 = ANFC H 6412-01), all deposited in the Australian National Fish Collection. The analysis yielded a single cluster; the range in pairwise differences among these specimens was 1–8, with an average of 5.3.

*Cirrhigaleus australis* (southern Mandarin dogfish) (fig. 42)

The two specimens of this newly described species (see White et al., 2007a) included in the analysis consisted of the holotype (GN4944 = ANFC H 5789-01) from Tasmania, Australia, and a voucher collected from New Zealand. These specimens differed by four bases. We believe this result supports the suggestion of White et al. (2007a) that *C. australis* occurs in New Zealand.

*Cirrhigaleus asper* (roughskin spurdog) (fig. 42)

A single specimen of *C. asper* collected off Florida was included in the analysis. This specimen clustered with the two specimens of *C. australis*. The average of the pairwise differences between this specimen and those comprising the cluster of *C. australis* was 58.5.

### Centrophoridae (gulper sharks)

*Centrophorus squamosus* (leafscale gulper shark) (fig. 43)

The analysis included 50 specimens of *Centrophorus squamosus*. These came from several localities in the North Atlantic including the mid-Atlantic ridge, the Azores, Madeira, and Scotland, as well as New Zealand,

Australia, and the southwest Indian Ocean, and thus represent much of the global distribution of this species. Only two of these samples come from museum specimens (GN4926 = ANFC H 5343-06 and GN6614 = MMF 36123). The range in pairwise differences among these 50 specimens was 0–9, with an average of 1.3. It is interesting to note that 28 of the specimens were identical in sequence and these came from the Azores, Scotland, the mid-Atlantic ridge, Australia, New Zealand, and the southwest Indian Ocean.

*Centrophorus granulatus* (gulper shark) (fig. 43)

In combination, the 13 specimens of this species included in the analysis were collected from the western North Atlantic, the Gulf of Mexico, Caribbean Sea, Madeira, the coast of mainland Portugal, and New South Wales, Australia. The overall distribution of this species is uncertain pending a taxonomic revision of this group. The two samples from Australia came from specimens deposited in the Australian National Fish Collection (GN4924 = ANFC H 5343-06 and GN4925 = ANFC H 5343-07); the two samples from mainland Portugal came from specimens in the museum in Funchal (GN6613 = MMF 36122 and GN6615 = MMF 36124). The range in pairwise differences seen among these 13 specimens was 0–2, with an average of 0.6. The mean of the pairwise differences between specimens of *C. granulatus* and those of *C. squamosus* was 37.8. A similar lack of divergence between these two species was reported by Moura et al. (2008).

*Centrophorus cf. lusitanicus* (fig. 43)

Four specimens taken from the Mozambique Channel off Madagascar were included in the analysis. The images for these specimens most closely resemble the illustration of *C. lusitanicus* from southern Africa in Bass et al. (1986). However, since no specimens from near the type locality for this species are included (i.e., Portugal) this species is referred to as *C. cf. lusitanicus*. The range in pairwise differences among these specimens was 1–5, with an average of pairwise differences of 3.2. Taxonomic revision of this complex is being undertaken by W.W. and Dave Ebert.

*Centrophorus* sp. 1 (fig. 43)

Two specimens collected from Jamaica by John Morrissey were included in the analysis and were identical in sequence. They clustered most closely with, but independently from, the four specimens of *Centrophorus* cf. *lusitanicus* collected from Madagascar. The average of the pairwise differences between these specimens and those of *C. cf. lusitanicus* was 8.8. Unfortunately, images are not available for these specimens. We have referred to them as *Centrophorus* sp. 1 until their identity can be examined in more detail. It is possible these specimens represent an undescribed species.

*Centrophorus harrissoni* (longnose gulper shark) (fig. 43)

Three specimens of this Australian/New Zealand endemic were included in the analysis. The range in pairwise differences among these three specimens was 1–5; the mean was 3.3. All three came from specimens collected from Tasmania (see White et al., 2008) and deposited in the Australian National Fish Collection (GN4941 = ANFC H 6307-07, GN4942 = ANFC H 6309-05, and GN4943 = ANFC H 6500-01).

*Centrophorus isodon* (blackfin gulper shark) (fig. 43)

Two specimens identified as *C. isodon* were included in the analysis. Both specimens (GN4338 = JPAG 227 and GN4392 = JPAG 225) were collected from the Philippines and were treated by Compagno et al. (2005b) as new records of this species from this region. These specimens differed in sequence by only one base. The average of the pairwise differences between these specimens and those of *C. harrissoni*, with which they were closely clustered, was 11.5.

*Centrophorus* sp. 2 (fig. 43)

The analysis included three specimens, all from Taiwan, two of which came from vouchers (GN973 = UMMZ 231976 and GN974 = UMMZ 231959). This species belongs to the *C. lusitanicus* complex but likely represents an undescribed species. The range in pairwise differences among these specimens was 0–3, with an average of 2. Taxonomic revision of this complex is being undertaken by W.W. and Dave Ebert.

*Centrophorus* sp. 3 (fig. 43)

A single specimen collected from the Philippines that resembles *C. lusitanicus* was included in the analysis. This specimen (GN4348 = JPAG 226) was considered by Compagno et al. (2005b) to represent a new record of *C. lusitanicus* for the Philippines. The average of the pairwise differences between this specimen and the three specimens of *Centrophorus* sp. 2 from Taiwan was 13.7. This species is possibly conspecific with specimens off Indonesia that were tentatively referred to as *C. cf. lusitanicus* by White et al. (2006). However, this species likely represents an undescribed species. Taxonomic revision of this complex is being undertaken by W.W. and Dave Ebert.

*Centrophorus zeehaani* (southern dogfish) complex (fig. 43)

The analysis yielded a single cluster, consisting of a total of five specimens, three of which were paratypes of the newly described species *C. zeehaani* deposited in the Australian National Fish Collection (GN4932 = ANFC H 6628-01, GN4933 = ANFC H 6628-03, and GN4934 = ANFC H 6628-07) (see White et al., 2008). The remaining two specimens were collected from Angola and Madeira. The range in pairwise differences among all five specimens was 0–1. As *C. zeehaani* is currently considered an endemic of southern Australia, we have used the provisional designation *C. cf. zeehaani* for the specimens from Madeira and Angola until this unusual finding can be explored further. We note that photographs of the specimen from Madeira are available in the database; it is superficially similar morphologically to the Australian specimens.

*Centrophorus moluccensis* (smallfin gulper shark) (fig. 43)

Ten specimens, which were morphologically consistent with *C. moluccensis*, were included in the analysis: one specimen came from the southwestern Indian Ocean, one from Malaysian Borneo, six specimens were deposited in the Australian National Fish Collection (GN4921 = ANFC H 3599-04, GN4922 = ANFC H 6410-01, GN4923 = ANFC H 6410-02, GN4927 = ANFC H 5343-07, GN4928 = ANFC H 4873-03, and GN4929 = ANFC H 2575-26), five of these

were collected from Australian and one from New Zealand localities, while three samples came from the Philippines. These specimens thus represent a large portion of the Indo-West Pacific distribution of this species. Two of the three specimens from the Philippines (GN4329 = JPAG 257 and GN4351 = JPAG 258) were among those treated by Compagno et al. (2005b) as *Centrophorus cf. moluccensis*. The analysis yielded a cluster consisting of two potential subclusters. The range in pairwise differences among all 10 specimens was 0–14, with an average of 6.4. One of the subclusters consisted of the specimens collected from Borneo and Australia; the other consisted of the three specimens from the Philippines. The range in pairwise distances among specimens in the former subcluster was 0–8 and among specimens in the latter subcluster was 5–11. The average of the pairwise distances among specimens in the two subclusters was 9.9.

*Deania calcea* (birdbeak dogfish) (fig. 44)

A total of 26 specimens of this species were included in the analysis. These came from the mid-Atlantic ridge, Ireland, Scotland, southern Africa, New Zealand, Tasman Sea, and southwest Indian Ocean, and thus represent much of the distribution of this species. Three of these specimens were from the Australian National Fish Collection (GN4945 = ANFC H 4873-02, GN4946 = ANFC H 5343-08, and GN4947 = ANFC H 5365-01). The analysis yielded essentially a single cluster. The range of pairwise differences among specimens in the cluster was 0–11, with an average of 3.3.

*Deania cf. profundorum* (fig. 44)

The analysis included five specimens preliminarily identified as *D. cf. profundorum*, all taken from the coast of mainland Portugal and the Azores, but the identities of which remain to be confirmed. The range in pairwise differences among specimens in this cluster was 0–10, with an average of 5.4. Images are available only for the specimen from the Azores and they suggest that at least this specimen is not fully consistent with existing descriptions of *Deania profundorum* (e.g., Compagno, 1984b). For example, this specimen has a second dorsal fin that differs substantially in shape from that of the true *D.*

*profundorum*. Further taxonomic work, including specimens definitively identified as *D. profundorum*, and preferably taken from throughout the extensive distribution of that species is required.

*Deania quadrispinosa* (longsnout dogfish) complex (fig. 44)

Three specimens identified as *D. quadrispinosa* were included in the analysis. These were all collected from New South Wales, Australia, and represent only the eastern portion of the distribution of this species, which extends from east of New Zealand to the west coast of South Africa. However, while two of these specimens exhibited sequences that differed from one another by only a single base, the average of the pairwise differences between these two specimens and the third specimen was 22.5, suggesting that they may represent more than a single species. We have given these specimens separate designations (i.e., *D. quadrispinosum* 1 and *D. quadrispinosum* 2) in order to call attention to this interesting result.

**Somniosidae (sleeper sharks), in part**

*Centroscymnus coelolepis* (Portuguese dogfish) (fig. 45)

A total of 18 specimens of this species were included in the analysis. These came from the western North Atlantic, mid-Atlantic ridge, Madeira, Scotland, and Tasmania, and thus represent all but the South Atlantic and North Pacific elements of the distribution of this species. The three specimens from Madeira are deposited in the Museu de História Natural e Aquário in Funchal (GN6616 = MMF 36129, GN6626 = MMF 36784, and GN6606 = MMF 36090). Despite the disparate localities from which these specimens came, they were remarkably homogeneous in NADH2 sequence; the range in pairwise differences among these 18 specimens was 0–2, with an average of 1.1.

*Centroscymnus owstonii* (roughskin dogfish) (fig. 45)

The 17 included specimens of this species were collected from the mid-Atlantic Ridge, Madeira, coastal mainland Portugal, and New Zealand. The analysis yielded a single

cluster. The range of pairwise differences among these 17 specimens was 0–6, with an average of 1.8. A number of specimens taken from Portugal and New Zealand were identical in sequence. The six specimens collected from Madeira are deposited in the Museu de História Natural e Aquário in Funchal (GN6598 = MMF 36021, GN6599 = MMF 36044, GN6600 = MMF 36058, GN6623 = MMF 36739, GN6619 = MMF 36142, and GN6625 = MMF 36741). This species clustered most closely with *C. coelolepis*. The average of the pairwise differences between *C. owstonii* and *C. coelolepis* was 74.7 (or 7.15%). This result is somewhat more conservative than that of Moura et al. (2008) who found the genetic divergence between these two species to be 12.8%.

### Oxynotidae (roughsharks)

*Oxynotus bruniensis* (prickly dogfish) (fig. 45)

A total of 14 specimens of this species were included in the analysis. These were collected from New Zealand and New South Wales in Australia and thus are representative of the temperate Australasian distribution of this species. The analysis yielded one cluster. The range in pairwise differences seen among the 14 specimens was 0–6, with an average of 1.6.

*Oxynotus paradoxus* (sailfin roughshark) (fig. 45)

The four specimens of this species included in the analysis were all collected from the eastern North Atlantic, including off Scotland, and were all identical in sequence. These specimens represent the northern elements of this species, which is distributed southward to Senegal. The average of the pairwise differences between this species, and *O. bruniensis* was 55.3. It is of note that both of these oxynotid species grouped within the cluster containing the somniosids.

### Somniosidae (sleepers), continued

*Proscomnodon plunketi* (plunket shark) (fig. 45)

The 12 specimens of this species included in the analysis were all collected from New Zealand and thus represent the more eastern elements of the distribution of this species. Most of these specimens were identical in sequence, but one specimen differed from the others by one base.

*Scymnodon ringens* (knifetooth dogfish) (fig. 45)

All five specimens identified as this species included in the analysis were collected from Ireland and thus represent the northeastern elements of the distribution of this species. These specimens were identical in sequence. They clustered most closely with specimens of *P. plunketi*; the average of the pairwise differences between these two species was 59.1.

*Centroselachus crepidater* (longnose velvet dogfish) (fig. 45)

The analysis included 27 specimens of this currently monotypic genus. These specimens were collected from the mid-Atlantic ridge, Madeira, Scotland, southern Africa, Tasman Sea, and New Zealand and thus represent only the western Pacific and eastern Atlantic portions of the distribution of this species. The specimen collected from the Tasman Sea came from the Australian National Fish Collection (GN4940 = ANFC H 4873-01). The two specimens from Madeira are deposited in the Museu de História Natural e Aquário in Funchal (GN6617 = MMF 36134 and GN6618 = MMF 36136). The analysis yielded a single cluster and, in fact, several specimens from Madeira, Scotland, and New Zealand were identical in sequence. However, the range of pairwise differences among all 27 specimens was 0–17, with an average of 2.4.

*Zameus squamulosus* (velvet dogfish) (fig. 45)

Four specimens identified as *Zameus squamulosus* were included in the analysis. Two were collected from southern Africa and two from Tasmania and thus represent only a portion of the southern hemisphere distribution of this essentially cosmopolitan species. The range in pairwise differences among specimens was 0–6 bases, with an average of 4.6. They clustered most closely with *C. crepidater*. The average of the pairwise differences between specimens of these two species was 107.3.

*Centroscymnus* sp. 1 (fig. 45)

The analysis included a specimen collected from New Zealand, and preliminarily identified as *Centroscymnus* sp. by Di Tracey. This specimen clustered provisionally along with, but outside the group comprised of the two specimens of *Zameus squamulosus* and the 27 specimens of *Centroselachus crepidater* (well

away from the specimens of the two species of *Centroscymnus* included in the analysis). The average of the pairwise differences between this specimen and those of *Z. squamulosus* was 166. The average of the pairwise differences between this specimen and those of *C. crepidater* was 160.7. We have referred to this specimen here as *Centroscymnus* sp. 1. However, it should be noted that results from barcode (COI) data, which show similar results within the Somniosidae, include a clade consisting of *Z. squamulosus*, *C. crepidater*, and a single specimen of *Scymnodalatias albicauda* from New Zealand. Thus, it is highly likely that this species actually refers to *S. albicauda*, but additional samples are required to confirm this.

*Somniosus microcephalus* (Greenland shark) (fig. 45)

Four of the five specimens of this species included here came from the Northwest Territories in northern Canada, the remaining specimen was from the eastern Atlantic. Thus, our sample represents much of the breadth of the distribution of this species. The range in pairwise differences among specimens was 0–1.

*Somniosus pacificus* (Pacific sleeper shark) (fig. 45)

All four specimens of this species included in the analysis were collected from Alaska and thus represent only the eastern Pacific elements of the distribution of this species, which also includes the western Pacific. The range in pairwise differences among these specimens was 0–2, with an average of 1.2. The average of the pairwise differences between specimens of this species and those of *S. microcephalus* was 9.2. This result is consistent with that of Murray et al. (2008) with respect to the distinction between the latter two species.

*Somniosus rostratus* (little sleeper shark) (fig. 45)

The single specimen of this species included in the analysis was collected from the coast of France, and thus is representative of the eastern North Atlantic distribution of this species. The average of the pairwise differences between this specimen and the specimens comprising the cluster of *S. microcephalus* was 32.4, and between those comprising the cluster of *S. pacificus* was 32.8.

### **Etmopteridae (lantern sharks)**

*Etmopterus spinax* (velvet belly) (fig. 46)

All but one of the 21 specimens of this species included in the analysis were collected from the Azores; the remaining specimen came from Scotland. Thus, our sample represents only some of the more northern elements of the distribution of this species, which occurs throughout the eastern Atlantic from Norway to Gabon. The analysis yielded essentially a single cluster. The range in pairwise differences among specimens in this cluster was 0–8, with an average of pairwise differences of 2.5.

*Etmopterus princeps* (great lanternshark) (fig. 46)

The seven specimens of this species included in the analysis were collected from throughout much of the distribution of this species, consisting of Connecticut in the western North Atlantic, Madeira, and the eastern North Atlantic. The two specimens from Madeira were deposited in the Museu de História Natural e Aquário in Funchal (GN6608 = MMF 36093 and GN6611 = MMF 36103). The analysis yielded essentially a single cluster. The range in pairwise differences among specimens within this cluster was 0–6, with an average of 3.4.

*Etmopterus* cf. *unicolor* complex (fig. 46)

Four specimens originally identified as *Etmopterus unicolor* were included in the analysis. Two of these were collected by Peter Smith from New Zealand. The other two specimens are from the Australian National Fish Collection (GN4952 = ANFC H 5673-02 and GN4954 = ANFC H 5674-08), both of which were collected from the eastern Indian Ocean. These four specimens grouped together but in two distinct clusters, one consisting of the specimens from New Zealand, the other of specimens from the eastern Indian Ocean. The specimens from New Zealand differed from one another by base; those in the latter cluster differed from one another by seven bases. The average of the pairwise differences between specimens in these two clusters was 14. Given the type locality of this species is Japan, a locality not represented by our specimens, we have referred to the specimens from New Zealand as *E. cf. unicolor* 1 and those from the eastern



Indian Ocean as *E. cf. unicolor* 2. However, some consideration should be given to the specimens in the first of these clusters being conspecific with the newly described *Etmopterus viator* of Straube et al. (2011). The second cluster could represent one of the many species of this genus not nominally represented in the analysis.

*Etmopterus baxteri* (New Zealand lanternshark) (fig. 46)

In total, 11 specimens of this possibly southern global species, all from New Zealand, were included in the analysis, which yielded a single cluster. Ten of the specimens were almost identical in sequence, but one of the specimens differed from the remaining nine by seven or eight bases. The average of pairwise differences among the 11 specimens was 1.5.

*Etmopterus virens* (green lanternshark) (fig. 46)

A single specimen of this species, collected from the western North Atlantic, was included in the analysis.

*Etmopterus gracilispinis* (broadband lanternshark) (fig. 46)

A single specimen of this species, collected from the western North Atlantic was included in the analysis. This specimen clustered with the specimen of *E. virens*. However, the difference between the specimens of these two species was 126.

*Etmopterus pusillus* (smooth lanternshark) (fig. 46)

The analysis included 20 specimens of this species. These were collected from a diversity of localities in the eastern North Atlantic, including the Azores, Madeira, and the coast of mainland Portugal, as well as from New South Wales in Australia. However, given the extent of the reported distribution of this species, these localities represent only a small portion of its patchy global distribution. Three specimens from Portugal (GN6603 = MMF 36075, GN6620 = MMF 36530, and GN6624 = MMF 36740), and one from Australia (GN4951 = ANFC H 5956-01) were vouchered. The analysis yielded essentially a single cluster. The range in pairwise differences among these specimens was 0–11, with an average of 3.5.

*Etmopterus bigelowi* (blurred smooth lanternshark) (fig. 46)

The four specimens of this species included in the analysis represent only a very small portion of the patchy global distribution of this species, having come from the Gulf of Mexico and the mid-Atlantic Ocean. The analysis yielded a single cluster and the range in pairwise differences among specimens in this cluster was 0–2, with an average of 1.

*Etmopterus splendidus* (splendid lanternshark) (fig. 46)

Both samples of this species included in the analysis were collected from Taiwan, from specimens deposited in the University of Michigan Museum of Zoology (GN994 and GN995 = UMMZ 231969). These specimens differed from one another by two bases. They clustered together, most closely allied with the *E. pusillus* and *E. bigelowi* clusters. The average of the pairwise differences between *E. splendidus* and *E. pusillus* was 128.1 and between *E. splendidus* and *E. bigelowi* was 105.5.

*Etmopterus lucifer* (blackbelly lanternshark) (fig. 46)

All 10 specimens of this species were collected from the eastern portions of the relatively extensive, but poorly defined, distribution of this species, having come from New South Wales in Australia and also from New Zealand. The analysis yielded a single cluster. The range in pairwise differences among these specimens was 0–6, with an average of 2.

*Etmopterus molleri* (slendertail lanternshark) (fig. 46)

The four specimens of this species included in the analysis were collected from Taiwan and thus represent only a very small portion of the distribution of a possible species complex (G. Burgess, personal commun.). All four specimens are deposited in the University of Michigan Museum of Zoology (GN996, GN997, GN998, and GN999 = UMMZ 231971). The analysis yielded a single cluster. The range in pairwise differences among these specimens was 0–6, with an average of 3. These specimens clustered most closely with those of *E. lucifer*, with an average of the pairwise differences among specimens of these two species was 110.5. However, given that *E. burgessi* is also known from Taiwan (Schaaf-DaSilva and

Ebert, 2006) and was not included in our analysis, the identity of the *E. molleri* cluster should be confirmed by careful comparison of the deposited specimens with verified specimens of *E. burgessi*.

*Centroscyllium fabricii* (black dogfish) (fig. 46)

The 10 specimens of this species included here represent the North Atlantic elements of the distribution of this Atlantic species having come from Connecticut, the Azores, and Scotland. The southern Atlantic elements of the distribution were not represented. The analysis yielded a single cluster; the range of pairwise differences among specimens in this cluster was 0–8, with an average of 3.6.

### Dalatiidae (kitefin sharks)

*Dalatias licha* (kitefin shark) (fig. 47)

The analysis included 17 specimens of this broadly distributed monotypic genus, taken from the eastern North Atlantic (i.e., the Azores and Scotland), the western North Pacific (i.e., Taiwan) and the western South Pacific (i.e., New South Wales, Australia, and New Zealand). However, much of its distribution (e.g., the Indian Ocean elements), was not represented. One of the specimens from Taiwan is deposited at the University of Michigan Museum of Zoology (GN985 = UMMZ 231958). The analysis yielded essentially a single relatively homogeneous cluster given the breadth of geographic regions from which these specimens came. The range in pairwise differences among specimens in this cluster was 0–5, with an average of 1.9.

*Isistius brasiliensis* (cookiecutter shark) (fig. 47)

The analysis included a total of three specimens of this remarkably broadly distributed species. These were collected from the central Pacific and Atlantic oceans. The analysis yielded essentially a single cluster with the specimen from the Pacific Ocean clustering outside the two specimens collected from the Atlantic Ocean. The range in pairwise differences among these three specimens was 4–10, with an average of 8.

*Squaliolus aliae* (smalleye pygmy shark) (fig. 47)

The three specimens included in the analysis were collected from Western Aus-

tralia and Taiwan and thus are relatively representative of the distribution of this species. The specimen from Western Australia is in the Australian National Fish Collection (GN4955 = ANFC H 6416-02). The analysis yielded essentially a single cluster comprised of these specimens. However, the specimen from Australia was relatively divergent from the two specimens from Taiwan. The range in pairwise differences among all three specimens was 5–14, with an average difference of 10 bases.

*Euprotomicrus bispinatus* (pygmy shark) (fig. 47)

The analysis included a single specimen of this broadly distributed species collected from the North Pacific. This species clustered among the two species of *Squaliolus*, most closely allied with *S. aliae*, suggesting that the generic placement of this, the only species in its genus, might warrant closer scrutiny. The average of the pairwise differences between this specimen and those of *S. aliae* was 89.3.

*Squaliolus laticaudus* (spined pygmy shark) (fig. 47)

The two specimens included in the analysis were collected from the Azores, and thus represent only a very small portion of the distribution of this almost circumtropical species. These specimens clustered together and differed from one another by eight bases. The average of the pairwise differences between specimens of *S. laticaudus* and those of *S. aliae* was 140.8 and between *E. bispinatus* was 187.7.

## SQUATINIFORMES (angel sharks)

### Squatinae (angel sharks)

*Squatina oculata* (smoothback angelshark) (fig. 48)

The 12 specimens included in the analysis were all taken from Senegal and Sierra Leone and thus represent the center of the distribution of this species, which extends coastally from France to Namibia. The analysis yielded a single cluster; all 12 specimens were identical in sequence.

*Squatina formosa* (Taiwan angelshark) (fig. 48)

The analysis included three specimens of this species which is possibly endemic to Taiwan. These specimens comprised a single cluster with a pairwise difference among specimens of 0–1. However, this genus includes

several similar species from Taiwan not included in the analysis (e.g., *S. japonica* and *S. nebulosus*) (see Walsh and Ebert, 2007). The identity of this cluster requires confirmation in the context of these other taxa.

*Squatina tergocellatoides* (ocellated angelshark) (fig. 48)

The analysis included two specimens collected from Malaysian Borneo that represent the distinctive *S. tergocellatoides*. These specimens were identical in sequence to one another and clustered most closely with the specimens of *S. formosa*. The average of the pairwise differences between this species and *S. formosa* from Taiwan was 88.3.

*Squatina aculeata* (sawback angelshark) (fig. 48)

The 11 specimens of this species included in the analysis were all collected from Senegal and thus represent the center of the distribution of this species, which extends coastally from the western Mediterranean to Namibia. The analysis yielded a single cluster. The range in pairwise differences seen among specimens was 0–3, however, the majority of these specimens were identical in sequence. The average of the pairwise differences among the 11 specimens was 0.7.

*Squatina dumeril* (sand devil) (fig. 48)

The analysis included eight specimens representing the more northern elements of the distribution of this species including New Jersey and the northern Gulf of Mexico. The analysis yielded a single cluster, with pairwise differences seen among these specimens of 0–12, with an average of 5.6.

*Squatina californica* (Pacific angelshark) (fig. 48)

The seven specimens included were collected from California and the Gulf of California and thus represent much of the distribution of this species. The range in pairwise differences among specimens was 0–6, with an average of pairwise differences of 3.8. This species clustered most closely with *S. dumeril*, a result consistent with the findings of Stelbrink et al. (2010). The average of the pairwise differences among specimens of these two species was 46.

*Squatina albipunctata* (eastern angelshark) (fig. 48)

A single specimen of this newly described eastern Australian endemic species (see Last

and White, 2008b) was included in the analysis. It clustered most closely with *S. dumeril* and *S. californica*. The mean of the pairwise differences between this specimen and those of the former species was 112.5, and between this specimen and those of the latter species 109.1.

### Echinorhinidae (bramble sharks)

*Echinorhinus brucus* (bramble shark) (fig. 48)

Three specimens of this species, all collected from the western North Atlantic (i.e., Louisiana and North Carolina), were included in the analysis. One of these specimens came from the University of Florida Fish Collection (GN1983 = UFFC 103000), and the other a specimen deposited in the Tulane University Museum of Natural History (GN1067 = TU 172379). These specimens represent only a very small portion of the distribution of this species. The range in pairwise differences among these specimens was 2–5, with an average of 4.

*Echinorhinus cookei* (prickly shark) (fig. 48)

In total, two specimens of this species were included in the analysis. One came from the Australian National Fish Collection (GN4998 = ANFC H 6115-01) collected from Queensland, and the other was collected from California. These specimens thus represent only some of the more southern elements of the Pacific distribution of this species. These specimens differed by one base, clustering most closely with those of *E. brucus*. The average pairwise difference between specimens of these species was 59.3.

### PRISTIOPHORIFORMES (sawsharks)

#### Pristiophoridae (sawsharks)

*Pliotrema warreni* (sixgill sawshark) (fig. 48)

Two specimens of this southern Africa endemic were included in the analysis. The specimens were identical in sequence.

*Pristiophorus japonicus* (Japanese sawshark) (fig. 48)

The single specimen of this species was collected from Japan. It clustered most closely with the specimens of *P. warreni*; the average of the pairwise differences between these two species was 130.

*Pristiophorus cirratus* (longnose sawshark) (fig. 48)

The two specimens of this southern Australian endemic species were both collected from New South Wales and differed by a single base. The average of the pairwise differences between this species and *P. warreni* was 152.5, and between this species and *P. japonicus* 137.5.

**HEXANCHIFORMES (cow and frilled sharks)**  
**Hexanchidae (sixgill and sevengill sharks)**

*Hexanchus nakamurai* (bigeye sixgill shark) and  
*Hexanchus vitulus* (fig. 49)

The analysis included three specimens collected from Madagascar, the Philippines (GN2246 = JPAG 053 of Compagno et al., 2005b), and New South Wales in Australia as well as one specimen from the Bahamas in the Caribbean Sea. It yielded a cluster consisting of the three specimens from the Indo-Pacific localities grouping with the specimen from the Bahamas. The range of pairwise differences among the three Indo-Pacific specimens was 5–15, with an average of 11.3; the average of the pairwise differences between the specimen from Australia and those from Madagascar and the Philippines was 14.5. However, the average of the pairwise differences between the specimen from the Bahamas and the three Indo-Pacific specimens was 80.7. *Hexanchus nakamurai* and *H. vitulus* have been considered to be synonyms (e.g., Compagno, 1984b; Taniuchi and Tachikawa, 1991) with a relatively broad distribution, occurring throughout the tropics and subtropics globally (Last and Stevens, 2009). However, our results suggest that both may actually represent valid species. Given the type locality of *H. vitulus* is Bimini in the Bahamas and the type locality of *H. nakamurai* is Taiwan, the specimen from the Bahamas has been identified as *H. vitulus*, and those from Indo-Pacific localities have been given the designation *H. nakamurai*. Clearly, the conspecificity of the bigeye sixgill sharks should be examined in more detail.

*Hexanchus griseus* (bluntnose sixgill shark) (fig. 49)

Specimens of this species included here were both collected from the eastern and central sectors of the North Atlantic. They differed from one another by two bases and

clustered most closely with their two congeners. The average of pairwise differences between *H. griseus* and *H. nakamurai* was 103, and between *H. griseus* and *H. vitulus* 94.

*Heptranchias perlo* (sharpnose sevengill shark) (fig. 49)

All four specimens of this monotypic genus included in the analysis came from Taiwan and thus represent only essentially a single locality of this global species. These four specimens were identical in sequence. All but one of these specimens are deposited in the University of Michigan Museum of Zoology (GN977, GN978, and GN979 = UMMZ 231961).

*Notorhynchus cepedianus* (broadnose sevengill shark) (fig. 49)

The four specimens of this species included in the analysis were all collected from localities in the Pacific Ocean (e.g., California and Australia) and thus represent only a portion of the distribution of this essentially global species. The range in pairwise differences among these specimens was 0–6, with an average of 3.8.

**Chlamydoselachidae (frilled sharks)**

*Chlamydoselachus anguineus* (frilled shark) (fig. 49)

The three specimens of this species included in the analysis were collected from the mid-Atlantic ridge, Scotland, and Japan. Despite the geographic breadth of our samples, they represent only a relatively small portion of the distribution of this species. The range in pairwise differences among these three specimens was 2–5, with an average of 4.

**BATOIDS**

**RAJIFORMES (batoids)**

**Dasyatidae (whiptail stingrays)**

*Himantura gerrardi* (whitespotted whipray) complex (fig. 50)

As has been suggested by a number of authors (e.g., Manjaji, 2004; White et al., 2006; Ward et al., 2008), there is reason to believe that *Himantura gerrardi* represents a complex of species that urgently requires taxonomic revision. Our analysis included 71 specimens exhibiting the basic color pattern

of *H. gerrardi*. However, these rays display considerable morphological variability within forms, without obvious differences between forms. In the absence of a formal taxonomic treatment and also material from the type locality of India, we have assigned numerical designations to the five clusters of these specimens that we believe, based in large part, on their genetic distances, may represent distinct species. The haplotype map colored by phenotype (fig. 94A) generally supports the distinct identity of each cluster, with no haplotypes shared among specimens with different species designations. However, there is considerable haplotype variation among specimens of *H. cf. gerrardi* 1, and also among the specimens of *H. cf. gerrardi* 2. The geographic haplotype map (fig. 94B) supports the notion that at least two species of *H. cf. gerrardi* (*H. cf. gerrardi* 1 and *H. cf. gerrardi* 2) cooccur in the Indo-Pacific.

*Himantura cf. gerrardi* 1 (fig. 50)

The analysis included a cluster of 39 specimens that have been given the designation *H. cf. gerrardi* 1. These specimens were collected from throughout the coasts of Malaysian and Indonesian Borneo as well as Thailand. One of the Borneo specimens has been deposited in the California Academy of Sciences (GN4521 = CAS 229036). Given that the range in pairwise differences seen among specimens in this cluster was 0–22, with an average of 5.5, this designation is very conservative. It is possible that this cluster includes representation of perhaps two species. For example, within this cluster there was a distinct subcluster comprised of two of the specimens collected from Sabah in eastern Malaysian Borneo.

*Himantura cf. gerrardi* 5 (fig. 50)

One specimen, collected from Vietnam, clustered along with but outside the 39 specimens of *Himantura cf. gerrardi* 1. The average of the pairwise differences between specimens of these two taxa was 34.8.

*Himantura cf. gerrardi* 2 (fig. 50)

The analysis yielded a second cluster comprised of, at least conservatively, 29 specimens. However, as circumscribed here, this cluster includes one specimen (GN3022) that is relatively more divergent from the

remaining specimens in the cluster. The range in pairwise differences among the 29 specimens in this cluster was 0–19 if this specimen is included (with an average of 3.4); the range is 0–8 if this specimen is excluded. Like *H. cf. gerrardi* 1, specimens of *H. cf. gerrardi* 2 were also collected from throughout the coasts of Malaysian and Indonesian Borneo; two of these specimens were vouchered (GN3426 = IPPS BO158 and GN3431 = IPPS BO163). At least two sympatric species of whitespotted whiprays may exist on the island of Borneo, given that the average of the pairwise differences between specimens comprising the clusters of *H. cf. gerrardi* 1 and *H. cf. gerrardi* 2 was 64.4.

*Himantura cf. gerrardi* 3 (fig. 50)

A single specimen collected from the Gulf of Oman was included in the analysis. This specimen grouped independently from the other clusters of whitespotted whiprays. Thus, this specimen has also been given a distinct numerical designation. The averages of the pairwise differences between this specimen and those comprising the clusters of *H. cf. gerrardi* 1, *H. cf. gerrardi* 2, and *H. cf. gerrardi* 5 were 74.7, 20.4, and 70, respectively. Additional specimens of whitespotted whiprays from the Gulf of Oman need to be investigated using both morphological and molecular methods.

*Himantura cf. gerrardi* 4 (fig. 50)

The analysis also included a specimen collected from the Mozambique Channel off Madagascar. This specimen grouped outside all three of the above clusters of whitespotted whiprays. The averages of the pairwise differences between this specimen and those of *H. cf. gerrardi* 1, *H. cf. gerrardi* 2, *H. cf. gerrardi* 3, and *H. cf. gerrardi* 5 were 67.2, 35.7, 47, and 65, respectively. Additional collections of whitespotted whiprays from the Mozambique Channel are required.

*Himantura astra* (blackspotted whipray) (fig. 50)

The analysis included nine specimens identified as this newly described Australasian species (see Last et al., 2008a). Six of these specimens were collected from the Arafura Sea, two from the Gulf of Carpentaria, and one from Moreton Bay. The range in pairwise differences among all nine specimens was

0–32, with an average of 7.9. One of the specimens collected from the Gulf of Carpentaria and the specimen from Moreton Bay clustered outside the six specimens from the Arafura Sea and one of the specimens from the Gulf of Carpentaria; the range in pairwise differences among the former six specimens was 0–3. The identities of the specimens in this cluster should be examined in more detail as some variation in morphology, such as dorsal surface spot pattern, were also observed among the nine specimens.

*Himantura pastinacoides* (round whiplay) complex (fig. 50)

Five specimens originally identified as belonging to the Indo-Pacific species *Himantura pastinacoides* were collected from Malaysian Borneo. However, the analysis yielded two distinct, very divergent clusters of these specimens, with an average pairwise difference among specimens in the two clusters of 72. Given that the type locality of *H. pastinacoides* is Java, and none of our material came from that locality, and the clusters overlap in distribution, we have used numerical designations for specimens from both clusters. They have been referred to as *Himantura pastinacoides* 1 and *H. pastinacoides* 2 until such time as the identity of these clusters can be examined in more detail. The three specimens comprising the former cluster were identical in sequence. The two specimens comprising the latter cluster differed from one another by eight bases.

*Himantura* sp. B (Arabian banded whiplay) (fig. 50)

The analysis included two specimens of whiplays collected from the Gulf of Oman that, while they had a banded tail, lacked spots on their disc; they appear conspecific with *Himantura* sp. B of Manjaji (2004). These specimens differed by three bases, and clustered most closely to but well outside specimens of *Himantura pastinacoides* 1 and *H. pastinacoides* 2. However, the average of the pairwise differences between these specimens and those of the former cluster was 136.3 and of the latter cluster was 111.5. While the Gulf of Oman form has been confused with *H. gerrardi* (see Randall, 1995), it clearly represents a distinct taxon.

It is currently being described by Manjaji-Matsumoto, Last, and Moore (in prep.).

*Himantura uarnacoides* (whitenose whiplay) complex (fig. 51)

In total, 32 specimens identified as the Indo-Malay species *Himantura uarnacoides* were included in the analysis, all collected from around the coast of Borneo. Two of these specimens were deposited in museums (GN4588 = CAS 229041 and GN3418 = IPPS BO149). The analysis yielded essentially a single cluster, although one of the specimens from Kalimantan (GN4781) was slightly divergent. The range of pairwise differences within this cluster was 0–20, with an average of 6.3, if this specimen was included.

An additional specimen (GN3366), collected from Sabah in Malaysian Borneo, resembling *H. uarnacoides* at least superficially, was also included in the analysis. This specimen clustered along with but well outside the main *H. uarnacoides* group. The average of the pairwise differences between this specimen and the 32 specimens in the *H. uarnacoides* cluster was 92.7. As this specimen is likely to represent a distinct species, it has been given the designation *H. cf. uarnacoides* until its identity can be examined in more detail.

*Himantura jenkinsii* (pointed-nose stingray) (fig. 51)

The analysis included a total of 13 specimens consistent with *H. jenkinsii*. The majority of these specimens were collected from Borneo and the Philippines; two specimens were collected in Vietnam. Four specimens collected from the Arafura Sea bear dark spots along the posterior margin of their disc which Last and Stevens (2009) noted is consistent with a color morph described as *H. draco* from South Africa (Compagno and Heemstra, 1984). The analysis yielded essentially a single cluster comprised of all 13 specimens. The range in pairwise differences among all 13 specimens was 0–16, with an average of 5.5. A specimen from the Philippines is deposited at the Philippines National Museum (GN2250 = JPAG 038).

*Himantura fai* (pink whiplay) (fig. 51)

Four specimens resembling *H. fai* were included in the analysis; two from Australia, one from the Philippines, and one from

Malaysian Borneo. They represent the eastern portion of the distribution of this Indo-West Pacific ray, which has also been reported from the Arabian Peninsula and possibly as far south as South Africa. Although the specimens from Australia differed from one another by 11 bases, those from the other localities were identical to one another. Thus, the range in pairwise differences among all four specimens was 0–12, with an average of 9.5. The specimen from the Philippines (i.e., GN2231 = BRU 083) was treated by Compagno et al. (2005b).

*Himantura uarnak* (reticulate whipray) complex (fig. 52)

The analysis yielded four distinct clusters of specimens that were generally consistent in morphology and color pattern with *Himantura uarnak* as defined by Last and Stevens (2009) based on Australian material (i.e., disc with a pale yellow background with a dense pattern of brown, fine reticulations). However, members of this species complex undergo multiple ontogenetic changes in coloration and these stages need to be described in detail for each of the forms. Unfortunately, such data were not available to inform the identifications of the specimens included here. Moreover, our analysis did not include specimens from the type locality of *H. uarnak*, the Red Sea, and thus it is unclear which, if any, of the four clusters truly represents *H. uarnak*. As a consequence, all four of the clusters have been given numerical designations of *Himantura uarnak* from 1 to 4; each of these is treated separately below.

The haplotype map of phenotypes (fig. 95A), which for comparative purposes also includes the similarly colored *H. undulata* and *H. leoparda*, shows no overlap in haplotypes among any of these six species. The haplotype map colored by geography (fig. 95B) indicates that *H. undulata*, *H. leoparda*, and as many as three of the four species in the *Himantura uarnak* complex (i.e., all but *H. uarnak* 2) may cooccur in Borneo. The *H. uarnak* species complex is currently being revised by P.L. and B. Mabel Manjaji-Matsumoto.

*Himantura uarnak* 1 (fig. 52)

The 12 specimens comprising the cluster referred to as *Himantura uarnak* 1 were

collected from Malaysian and Indonesian Borneo and the Philippines. They exhibited a disc with a yellow background and fine brown reticulations comprised of brown lines and some spots. The two specimens (i.e., GN2934 and GN3006) collected from Lahad Datu in Malaysian Borneo were most divergent among the specimens in this cluster; these individuals exhibited a somewhat darker disc and spots. The range of pairwise differences among all 12 of the specimens of this cluster was 0–25, with an average of 8. We note that the Philippine specimens (GN2237 = JPAG 035, GN2238 = JPAG 036, and GN2249 = BRU 027) were treated by Compagno et al. (2005b) as *Himantura uarnak*.

*Himantura uarnak* 2 (fig. 52)

The 12 specimens comprising the second cluster, referred to as *Himantura uarnak* 2, were collected from several localities off northern Australia. Their disc exhibits dark, crisp lines and some spots that may resemble joined hexagons. The range of pairwise differences among specimens of this cluster was 0–6, with an average of 2.6. The average of the pairwise differences between specimens in the *H. uarnak* 1 and *H. uarnak* 2 clusters was 54.9. These two clusters grouped together, well away from the third cluster of specimens with this general color pattern.

*Himantura undulata* (honeycomb whipray) (fig. 52)

A total of 11 specimens of this species were included in the analysis and were found to comprise a single tight cluster. These rays were collected from Malaysian and Indonesian Borneo. Our specimens include juveniles with discs of light background and brown spots (rhomboids) that were light/open internally, to very large, mature animals with discs that exhibit a light background and brown reticulations rather than brown spots. Manjaji-Matsumoto and Last (2008) and Manjaji (2004) considered this to be a senior synonym of *H. fava*. The range of pairwise differences among specimens in this cluster was 0–3, with an average of 1.5. These specimens were found to group with two of the clusters of *Himantura uarnak*, i.e., *H. uarnak* 1 and *H. uarnak* 2.

*Himantura leoparda* (leopard whipray) (fig. 52)

In total, four specimens of this newly described Indo-Pacific species (see Manjaji-Matsumoto and Last, 2008) were included in the analysis. These were collected from the Arafura Sea off northern Australia, Singapore, and Indonesian Borneo. These specimens comprised a single cluster. The range in pairwise differences among specimens in this cluster was 1–12, with an average of 7.8.

*Himantura uarnak* 3 (fig. 52)

The third *H. uarnak* cluster, which is referred to here as *Himantura uarnak* 3, was comprised of 15 specimens from Singapore and Malaysian and Indonesian Borneo. These specimens had a disc with a yellow background with fine brown reticulations or small brown spots. The range in pairwise differences among specimens in this cluster was 0–5, with an average of 1.8. However, two other species of *Himantura* (namely, *H. undulata* and *H. leoparda*) grouped more closely with the clusters comprised of specimens identified as *H. uarnak* 1 and *H. uarnak* 2 than did specimens of *H. uarnak* 3. The averages of the pairwise differences between specimens of *H. uarnak* 3 and those of *H. uarnak* 1 and *H. uarnak* 2, were 122.9 and 121.3, respectively.

*Himantura uarnak* 4 (fig. 52)

One of the specimens, also bearing a disc with dorsal spots and/or reticulations, clustered along with but outside all of the other specimens of the *H. uarnak* complex. This specimen also came from Malaysian Borneo. The average of the pairwise differences between this specimen and those of *H. uarnak* 1 was 140.7, from those of *H. uarnak* 2 was 148.3, and from *H. uarnak* 3 was 136.3. Thus, it was given the separate numerical designation of *Himantura uarnak* 4. This species also grouped outside the *H. undulata* and *H. leoparda* clusters.

*Himantura oxyrhyncha* (longnose marbled whipray) complex (fig. 53)

In total, 42 specimens identified as this species were included in the analysis. All of these were taken from the west coast of Indonesian Borneo and thus represent the more southern portion of the distribution of this species, which has also been reported

from Cambodia and Thailand. Two specimens from Kalimantan were deposited in the California Academy of Sciences (GN4534 = CAS 229037 and GN4540 = CAS 229038). The analysis yielded a single cluster with a range in pairwise differences among members of this cluster was 0–6, with an average of 0.6. It is interesting to note, however, that included among these specimens was one animal (GN4483) that differed conspicuously from the remaining specimens in form, denticle pattern, and color pattern. In recognition of these morphological distinctions, we have referred to this specimen as *Himantura* cf. *oxyrhyncha*.

*Himantura signifer* (white-edge freshwater whipray) (fig. 53)

The 21 specimens of this species included in the analysis were all collected from the Kapuas River in West Kalimantan, Indonesia, and thus represent only a portion of the distribution of this species, which has also been reported from freshwaters in Thailand. One sample has been deposited in the California Academy of Sciences (GN4552 = CAS 229039). The analysis yielded a single cluster with a range of pairwise differences among specimens in this cluster of 0–7, with an average of pairwise differences of 1.6.

*Himantura* cf. *kittipongi* (fig. 53)

One specimen, collected from the Pawan River in West Kalimantan, Indonesia, was included in the analysis. This specimen is generally consistent in morphology with the relatively recently described but morphologically variable *H. kittipongi* (see Vidthayanon and Roberts, 2005). However, as *H. kittipongi* is known only from Thailand, this specimen has been given the designation *H. cf. kittipongi* until additional material from Borneo can be examined in more detail. This specimen clustered most closely with specimens of *H. signifer*; however, the average of the pairwise differences between this specimen and those in the *H. signifer* cluster was 45.3.

*Himantura imbricata* (scaly whipray) (fig. 53)

In total, seven specimens of this species were included in the analysis. One of these was collected from the west coast of India and the remaining six came from the Persian Gulf and Gulf of Oman. Thus, our specimens



represent the western and central elements of the distribution of this species, the range of which is not well defined in the Indo-West Pacific. The analysis yielded essentially a single cluster. The range in pairwise differences among specimens in this cluster was 0–11, with an average of 5.3.

*Himantura walga* (dwarf whipray) (fig. 53)

The six specimens of this species included in the analysis were all collected from western Malaysian Borneo and thus represent only a small portion of the distribution of this species, which is more widespread in the Indo-West Pacific. These six specimens were found to comprise a single cluster, however, the range in pairwise differences among specimens in this cluster was relatively broad at 2–17, with an average of 8.5. These specimens clustered most closely with those of *H. imbricata*, but the average of the pairwise differences among specimens of these two species was 95.8.

*Himantura lobistoma* (tubemouth whipray) (fig. 54)

The analysis included 20 specimens of this relatively newly described (see Manjaji-Matsumoto and Last, 2006) Borneo endemic species. These specimens include the holotype (GN2972 = SMEC 369), a paratype (GN2965 = SMEC 370), and four vouchers (GN4609 = CAS 229043, GN3691 = ANFC H 6214-03, and GN3465 = IPPS BO248, and GN4211 = MZB 15.508). The analysis yielded a single tight cluster with a range in pairwise differences among these specimens was 0–4, with an average of 0.9.

*Himantura granulata* (mangrove whipray) (fig. 54)

In total, three specimens of this Indo-West Pacific species were included in the analysis, from Malaysian and Indonesian Borneo and the Gulf of Carpentaria in northern Australia. The analysis yielded a single cluster. The range of pairwise differences among these specimens was 1–3; the average of the pairwise differences was 2.

*Himantura* sp. 1. (fig. 54)

The analysis included a single specimen (GN2103) of a very large species of *Himantura* (161 cm disc width), collected from the Arafura Sea off northern Australia, the identity of which is uncertain. While this

animal clustered most closely with the specimens of *H. granulata*, the average of the pairwise differences between this specimen and those of *H. granulata* was 65.3. This specimen has been referred to here as *Himantura* sp. 1. It should be noted that this specimen was host to five new cestodes described by Fyler et al. (2009) and was referred to by those authors as *Himantura* sp. The NADH2 sequence data for this animal were deposited in GenBank (No. FJ896004) by those authors as an aid to establishing the identity, if not the name, of this host species.

*Himantura polylepis* (giant freshwater whipray) (fig. 54)

All seven of the specimens of this species included in the analysis were collected from eastern Borneo, specifically from the Kinabatangan River in Malaysian Borneo, and the Mahakam River and the Sulawesi Sea in Indonesian Borneo. The analysis yielded a single cluster of specimens with a range of pairwise differences among specimens of 0–6, with an average of 1.7. However, it would be interesting to include specimens collected from elsewhere in the distribution of this species, which includes the Cho Phraya River basin in Thailand and the Mekong River basin in Cambodia. As noted by Last and Manjaji-Matsumoto (2008), it is likely that records from New Guinea actually refer to *Himantura dalyensis*, specimens of which were not included in the analysis.

*Urogymnus asperrimus* (porcupine ray) complex (fig. 54)

The analysis included six specimens originally identified as belonging to this relatively broadly distributed species. However, the analysis yielded two distinct clusters. One consisted of four specimens collected from northern and Western Australia that were identical in sequence. The second cluster consisted of two specimens collected from the Philippines. These specimens differed from one another by two bases. However, the average of the pairwise differences among specimens in the two clusters was 25, suggesting that more than one species may be involved. The genus currently includes only two species. Our analysis did not include representation of the second described species, *Urogymnus ukpam*, which is known only

from rivers in western Africa. Given that our analysis also did not include representation from the type locality of *U. asperrimus* (i.e., India), we have referred to the Australian form as *Urogymnus asperrimus* 1 and the Philippines form as *Urogymnus asperrimus* 2 until the identity of *Urogymnus* from these regions has been studied in more detail. We note that both specimens from the Philippines (GN2259 = JPAG 191 and GN4385 = JPAG 170) were treated by Compagno et al. (2005b) as *U. asperrimus*. Also of interest is the fact that all specimens of *Urogymnus* clustered among species of *Himantura*.

*Dasyatis margarita* (daisy stingray) (fig. 55)

The 11 specimens of this species included in the analysis were identical in sequence. All were collected from the coast of Senegal and thus represent the more northern elements of the distribution of this species, which extends as far south as Angola.

*Dasyatis margaritella* (pearl stingray) (fig. 55)

The analysis included five specimens of this species, all of which were collected from Senegal, and all of which comprised a single cluster. The range in pairwise differences among specimens in this cluster was 0–6, with an average of 2.6. These specimens also represent only the more northern elements of the distribution of this species, which extends south to Angola. This species grouped most closely with the sympatric species *D. margarita*. The average of the pairwise differences between specimens of these two species was 75.4.

*Taeniura grabata* (round fantail stingray) (fig. 55)

The two specimens of this species included in the analysis were identical in sequence. Both were collected from Senegal, and thus represent only the northwestern elements of the distribution of this species, which may occur throughout much of the coast of Africa, and as far east as the Red Sea. These specimens clustered among *Dasyatis* species, most closely with *D. microps*. However, the average of the pairwise differences between specimens of these two species was 161.5. It should be noted that the generic placement of this species is questionable.

*Dasyatis microps* (thickspine giant stingray) (fig. 55)

Two specimens of this species, one from the Arafura Sea off northern Australia and one from Mozambique, were included in the analysis. These specimens represent the eastern and western margins of the Indo-West Pacific distribution of this species. The specimens clustered together, differing by only a single base.

*Dasyatis zugei* (pale-edged stingray) complex (fig. 56)

The analysis included 24 specimens from Borneo and 12 from Vietnam and thus represents only the central elements of the distribution of this species, which is considered to occur widely throughout the Indo-West Pacific. The analysis yielded two clusters. One consisted of the specimens from Borneo with a range of pairwise differences among specimens of 0–7, with an average of 3.2; the other consisted of the specimens from Vietnam with a range of pairwise differences among specimens of 0–5, and an average of 1.5. These clusters differed substantially from one another, with an average of the pairwise differences among specimens in the two clusters of 33.7 and likely represent two distinct taxa. Given that the type locality of *D. zugei* is Macau, China, the specimens from Vietnam have been designated as *D. zugei*. The specimens in the cluster from Borneo have been designated as *D. cf. zugei* until such time as this complex can be examined in more detail. Two specimens of the latter taxon have been deposited (GN4450 = CAS 229027 and GN3437 = IPPS BO169).

*Dasyatis centroura* (rougtail stingray) (fig. 56)

Two specimens of this Atlantic species were included in the analysis. These were collected from Virginia and differed from one another by one base.

*Dasyatis ushieii* (cow stingray) (fig. 56)

A single specimen identified as *D. ushieii* was included in the analysis. This species was also reported in Indonesia, as *D. cf. ushieii*, by White et al. (2006) and has since been validated as conspecific with specimens from Taiwan (Last et al., 2010c). This specimen clustered most closely with the specimens of *D. centroura*, with an average of the pairwise

differences between specimens of these two species of 20.5.

*Dasyatis breviceaudata* (shorttail stingray) (fig. 56)

The single specimen of this species included is deposited in the Australian National Fish Collection (GN4652 = ANFC H 6346-25). It was collected from Western Australia and thus represents only a small portion of the distribution of this southern temperate Indo-West Pacific species. This specimen grouped most closely with *D. ushiei* and *D. centroura*. The averages of the pairwise differences between *D. breviceaudata* and the latter two species were 49 and 58.5, respectively.

*Pteroplatytrygon violacea* (pelagic stingray) (fig. 56)

The specimen of this species included in the analysis was collected off California and thus represents a single locality from the global distribution of this oceanic species. It clustered most closely with a grouping consisting of *D. breviceaudata*, *D. ushiei*, and *D. centroura* with an average of the pairwise differences between the *P. violacea* and specimens in the latter grouping of 81.8. It should be noted that this species clustered among *Dasyatis* species. Its placement has alternated between *Pteroplatytrygon* and *Dasyatis* in the last few decades and based on our findings, this needs to be revisited.

*Dasyatis marmorata* (marbled stingray) (fig. 56)

A single specimen, collected from Senegal, of this African species was included in the analysis. It clustered along with several other species of this genus. Following Eschmeyer and Fricke (2011), we have referred to this Senegalese specimen as *D. marmorata*.

*Taeniurops meyeri* (fantail stingray) (fig. 56)

Two specimens of this species were included in the analysis. These came from the Arafura Sea off northern Australia and the eastern coast of Malaysian Borneo, and thus represent only a small portion of the Indo-West Pacific distribution of this species. These specimens differed from one another by one base. It is of note that this species clustered among species of *Dasyatis* suggesting that its generic placement should be revisited. The average of the pairwise differences between this species and the other five with which it clustered was 108.

*Dasyatis dipterura* (diamond stingray) (fig. 56)

All four specimens of this species included in the analysis were collected from the Gulf of California and thus represent a more northern element of the distribution of this species, which extends coastally from southern California to Chile. These specimens differed from one another by 1–2 bases; the average of the pairwise differences was 1.5. We have followed Ebert (2003) here in referring to these specimens as *D. dipterura*, rather than *D. brevis*, because the latter is a junior synonym of the former.

*Dasyatis say* (bluntnose stingray) (fig. 56)

The three specimens of this species included in the analysis were all collected from the Gulf of Mexico, and thus represent only the northern elements of the distribution of this species, which extends south to Brazil. The range in pairwise differences among these specimens was 0–1. The cluster comprised of specimens of this species grouped most closely with those of *D. dipterura*. The average of the pairwise differences among specimens of these two species was 52.6.

*Dasyatis longa* (longtail stingray) (fig. 56)

Four specimens of this species, all from the Gulf of California, were included in the analysis. They were identical in sequence. However, they represent only the most northern elements of the distribution of this species, which occurs as far south as Ecuador.

*Dasyatis* sp. (fig. 56)

Two adults and one juvenile specimen from Senegal, which were identical in sequence, grouped close to but independently from the Pacific-dwelling *D. longa* with an average pairwise difference of 26. The adult of this unidentified species exhibited a median row of conspicuous thorns on the midline of the disc that extended onto the tail and a shorter row of smaller spines on either side of the median row. In this respect, this species appears to be inconsistent with species known from this region. Its identity remains uncertain and it possibly represents an undescribed species.

*Dasyatis americana* (southern stingray) (fig. 56)

The analysis included three specimens of this western Atlantic species, two collected

from the western Atlantic Ocean and one from the Gulf of Mexico. Although these specimens grouped together, the range of pairwise differences among them was high at 15–29, with an average of 21.7. Unfortunately no specimens were retained; clearly the identity of *D. americana* from the western Atlantic seaboard would be interesting to explore in more detail.

*Dasyatis sabina* (Atlantic stingray) (fig. 56)

The two specimens of this species included in the analysis differed by 15 bases. Both were collected from the Gulf of Mexico at the center of the distribution of this species, which occurs coastally from North Carolina to Belize. They comprised a single cluster and differed substantially from all other closely grouped taxa. For example, the ranges of pairwise differences between this species and its sympatric congeners *D. say* and *D. americana* were 149 and 163.3, respectively.

*Pastinachus* species

The fact that this genus has recently been expanded from one or two species to include five valid species led us to generate phenotype and geography haplotype networks for the 29 specimens in the analysis that we believe constitute five distinct species. The phenotype haplotype map (fig. 96A) illustrates that, collectively, these specimens exhibit five distinct, tight (except for *P. stellurostris*, which is represented by only a single specimen) clusters of haplotypes that correspond to the species recognized here. The haplotype map showing the geographic origin of the specimens (fig. 96B) emphasizes that four of these species cooccur throughout the island of Borneo. *Pastinachus atrus* appears widely distributed, with a relatively tight clustering of haplotypes among specimens in different parts of its distribution.

*Pastinachus atrus* (cowtail stingray) (fig. 57)

In total, 14 specimens identified as this species were included in the analysis, which yielded a single cluster. These specimens came from eastern Malaysian and Indonesian Borneo, the Philippines, Madagascar, and Australia. The range of pairwise differences among specimens in this cluster was 0–14, with an average of 5.8. This species has long been confused with *P. sephen*, originally

described from Saudi Arabia and the Red Sea. However, Last and Stevens (2009) resurrected *P. atrus* and it is now considered to have a broad Indo-Pacific distribution (Last et al., 2010c). The average of the pairwise differences between specimens of *P. atrus* and those of *P. solocirostris* was 93, *P. stellurostris* 101.1, *P. gracilicaudus* 95, and *P. cf. sephen* 84.1. We note that the specimen from the Philippines (GN2226 = JPAG 167) was treated by Compagno et al. (2005b) as *P. cf. sephen*.

*Pastinachus gracilicaudus* (narrowtail stingray) (fig. 57)

The analysis yielded a cluster comprised of nine specimens of this recently described species (see Last and Manjaji-Matsumoto, 2010), collected from throughout the island of Borneo. These included three paratypes (GN4498 = ANFC H 7107-01, GN4503 = ANFC H 7108-01, and GN4456 = MZB 18227). The range of pairwise differences among the specimens in this cluster was 1–8, with an average of 4.1.

*Pastinachus cf. sephen* (fig. 57)

Three specimens collected from the Gulf of Oman off the coast of Iran were included in the analysis; the range of pairwise differences among specimens in this cluster was 1–4, with an average of 2.7. These specimens exhibited a deep ventral fin fold consistent with that seen in *P. sephen* and also in *P. atrus*. The specimens from the Gulf of Oman grouped well away from the specimens of *P. atrus*, and thus are not likely conspecific with the latter species. Given that no specimens definitely identified as *P. sephen* were included here, this cluster has provisionally been designated as *P. cf. sephen* until the required morphological and molecular comparisons with *P. sephen* can be made. These specimens clustered most closely with *P. gracilicaudus*. The average of the pairwise differences between specimens in these two clusters was 86.8.

*Pastinachus solocirostris* (roughnose stingray) (fig. 57)

The analysis included 12 specimens identified as this relatively newly described species (see Last et al., 2005). These specimens were collected from Malaysian and Indonesian

Borneo and represent the core parts of its distribution; it is also known to occur elsewhere in Indonesia. Three of these specimens are paratypes (GN3432 = ANFC H 6123-03, GN3433 = ANFC H 6123-02, and GN3441 = ANFC H 6219-01) and one is a voucher deposited in the California Academy of Sciences (GN4612 = CAS 229044). The analysis yielded a single cluster comprised of these specimens. The range of pairwise differences among 11 of these specimens was 0–8. However, one specimen from western Malaysian Borneo was particularly divergent; this specimen extended the upper boundary of the range of pairwise differences within this cluster to 18. However, this specimen did not differ conspicuously morphologically from the other specimens in the cluster. The average of pairwise differences among all 12 specimens in this cluster was 6.2.

*Pastinachus stellurostris* (starrynose stingray)  
(fig. 57)

One specimen of this recently described species (see Last et al., 2010b) was collected from western Indonesian Borneo. It clustered most closely with specimens of *P. solocirostris*; the average of the pairwise differences between this specimen and those of *P. solocirostris* was 81.2.

*Neotrygon kuhlii* (bluespotted maskray) complex  
(fig. 58)

In total, 47 specimens of maskrays with blue spots were included in the analysis. Conservatively, the resulting group includes four distinct clusters, suggesting that *N. kuhlii* actually represents a complex of species as reported by Last et al. (2010c). Unfortunately, our specimens do not include the localities of any of the syntype material of *N. kuhlii* (i.e., India, Solomon Islands, or New Guinea). As a consequence, we have referred to these clusters as *N. kuhlii* 1 through 4. These species are treated separately below. A taxonomic revision of this complex is being undertaken by P.L. and W.W. and a detailed molecular phylogenetic study is being undertaken by Melody Puckridge.

The phenotype and geography haplotype networks generated for *Neotrygon* include these four forms as well as *N. picta* and a specimen we have identified as *N. cf. ningalooensis* (see below). The haplotype

network colored by phenotype (fig. 97A) shows no overlap in haplotypes among any of these six forms. *Neotrygon kuhlii* 1 showed the greatest amount of haplotype variation, but also was represented by the greatest number of specimens. The sympatry of three species (*N. picta*, *N. cf. ningalooensis*, and *N. kuhlii* 4) in Australia, and two species in Borneo (*N. kuhlii* 1 and *N. kuhlii* 2) is clearly illustrated in the geography network (fig. 97B).

*Neotrygon kuhlii* 1 (fig. 58)

The 33 specimens given this designation were collected from throughout Borneo and also the Philippines. In general, these specimens are typical of members of the *N. kuhlii* complex, bearing a dark mask and blue spots of several sizes. Six of the specimens from Borneo were vouchered (GN4475 = CAS 229033, GN3445 = IPPS BO218, GN3446 = IPPS BO219, GN3684 = IPPS BO473, GN3697 = IPPS BO486, and GN3698 = IPPS BO487). The range of pairwise differences among specimens comprising this cluster was 0–16, with an average of 7. While some structure was seen within this cluster, particularly with respect to four specimens collected from South and Central Kalimantan, to be conservative we have refrained from using a different designation for these specimens. We note that the two Philippine specimens (GN2216 = BRU 029 and GN2211 = BRU 001) were treated by Compagno et al. (2005b) as *Dasyatis kuhlii*.

*Neotrygon kuhlii* 2 (fig. 58)

This designation was employed for a cluster comprised of eight specimens collected from western Borneo, Thailand, Vietnam, and Taiwan. These animals either lacked spots entirely, or possessed only a few small blue spots. One of the specimens from Borneo was vouchered (GN3621 = IPPS BO409). We note that the relatively large range in pairwise differences among specimens in this cluster (i.e., 0–19, with an average of 6.6) can be accounted for by the specimen from Thailand. Nonetheless, we have again taken the conservative approach of assigning only a single designation to the members of this cluster at this time. These specimens grouped most closely to the cluster consisting of specimens of *N. kuhlii* 1. However, the average of the pairwise differ-

ences between specimens of *N. kuhlii* 2 and those of *N. kuhlii* 1 was 20.6.

*Neotrygon kuhlii* 3 (fig. 58)

Also unique, was a single specimen collected from the western coast of Madagascar in the Mozambique Channel. This specimen also exhibited the color pattern typical of *Neotrygon kuhlii*, with a dark mask and blue spots of several sizes. The averages of the pairwise differences between this specimen and *N. kuhlii* 1 and *N. kuhlii* 2, were 29.3 and 30.4, respectively.

*Neotrygon kuhlii* 4 (fig. 58)

This designation was employed for the cluster comprised of the five specimens collected from northern Australia. These specimens also exhibited the color pattern typical of *Neotrygon kuhlii*. The range of pairwise differences among specimens in this cluster was 0–10, with an average of 5.8. The averages of the pairwise differences between specimens in this cluster and those of species *Neotrygon kuhlii* 1, *N. kuhlii* 2, and *N. kuhlii* 3 were 30.3, 32.4, and 36.4, respectively.

*Neotrygon picta* (speckled maskray) (fig. 58)

The specimens of this newly described Australian endemic species (see Last and White, 2008a) that were included in the analysis consisted of the holotype (GN4654 = ANFC H 5771-01) and five additional specimens. The analysis yielded essentially a single cluster with a range in pairwise differences among specimens of 0–9, with an average of pairwise differences of 3.8. The average of the pairwise differences between specimens of this cluster and the 46 specimens in the *Neotrygon kuhlii* complex overall was 95.1.

*Neotrygon* cf. *ningalooensis* (fig. 58)

A single specimen, collected from the Gulf of Carpentaria in northern Australia, which is similar in appearance to the recently described *N. ningalooensis* from northwestern Australia (see Last et al., 2010d) was included in the analysis. This specimen clustered along with but outside all the other *Neotrygon* species. The average of the pairwise differences between this specimen and all other *Neotrygon* taxa included in the analysis was 111.4. Until this specimen

can be compared with the types of *N. ningalooensis*, it has been given the designation *N. cf. ningalooensis*.

*Taeniura lymma* (bluespotted fantail ray) complex (fig. 59)

In total, 33 specimens of bluespotted fantail rays were included in the analysis. The analysis yielded a group exhibiting a substantial amount of substructure indicating that more than a single species is represented by these specimens. However, because much of this molecular variation was not associated with any immediately apparent phenotypic variation or geographic distribution, we have given separate designations to only the two most conspicuous clusters until bluespotted fantail rays can be examined in more detail. Given that the type locality of *T. lymma* is the Red Sea and our analysis included no specimens from that region, we have given specimens in the two clusters the numerical designations *T. lymma* 1 and *T. lymma* 2 as it is unclear which, if either, represents the original *T. lymma*.

The haplotype maps reflect the uncertainty associated with specific designations in this complex. While there is no haplotype overlap among specimens identified as *T. lymma* 1 and *T. lymma* 2 (fig. 98A), there is substantial haplotype variation among specimens within both of these clusters. The geography haplotype map (fig. 98B) suggests that these two species are not entirely allopatric with respect to one another for one or more specimens of both species came from Kalimantan.

*Taeniura lymma* 1 (fig. 59)

The 28 specimens comprising this cluster were collected from a diversity of localities throughout Borneo, Vietnam, and the Philippines. While many of the specimens from Sabah in northeastern Borneo are identical in sequence, the range in pairwise differences among all the specimens in this cluster was 0–21, with an average of 3.8 bases. The upper end of this range can be accounted for by a specimen from Sabah and also by several specimens from West Kalimantan. We note that the four specimens from the Philippines (GN2243 = JPAG 033, GN2255 = RSE 007, GN2257 = RSE 008, and GN2215 = BRU 028) were treated by Compagno et al. (2005b) as *Taeniura lymma*.

*Taeniura lymma* 2 (fig. 59)

The seven specimens comprising the second cluster of bluespotted fantail rays were collected from northern Australia, Sulawesi, and Indonesian Borneo. The range in pairwise differences among the specimens in this cluster was 0–17, with an average of 9.5. However, within this cluster, the four specimens from Australia grouped independently from the remaining specimens. The average of the pairwise differences between the Australian specimens and those from the Sulawesi and Borneo cluster was 14.7. The average of the pairwise differences between specimens of the *T. lymma* 1 cluster and those of the *T. lymma* 2 cluster was 22.8.

**Urotrygonidae (round stingrays)***Urobatis concentricus* (bullseye stingray) (fig. 60)

Five specimens of this species were included in the analysis, which yielded a single cluster. These specimens were collected from the Gulf of California and are thus representative of the distribution of this species. One of these specimens was deposited in the Texas Cooperative Wildlife Collection (GN2275 = TCWC 7580.01). The range in pairwise differences among these specimens was 0–4, with an average of 1.6.

*Urobatis maculatus* (Cortez round stingray) (fig. 60)

All five specimens of this species included in the analysis were collected from the Gulf of California and thus are representative of the distribution of this species in general. The analysis yielded a single cluster. The range of pairwise differences among specimens in this cluster was 0–6, with an average of 2.8. This cluster grouped closely with that comprised of the specimens of *U. concentricus*. The average of the pairwise differences among specimens of these two species was 11.1.

*Urobatis halleri* (round stingray) (fig. 60)

The nine specimens included in the analysis all came from the Gulf of California and thus are representative of the more northern elements of the distribution of this species, which occurs as far south as Panama. The range in pairwise differences among these specimens was 0–8, with an average of 4. This cluster grouped outside that consisting of specimens of *U. concentricus* and *U. macula-*

*tus*. The average of the pairwise differences between specimens of this species and those of *U. concentricus* was 53.2 and between this species and *U. maculatus* was 58.8.

*Urotrygon rogersi* (lined round stingray) (fig. 60)

Two specimens of this species were included in the analysis, both collected from the Gulf of California and thus represent the northern portion of the distribution of this species, which occurs as far south as Ecuador. One of these specimens was deposited in the Texas Cooperative Wildlife Collection (GN5250 = TCWC 7567.04). The specimens differed by five bases.

*Urotrygon* cf. *simulatrix* (fig. 60)

One specimen of this species was included in the analysis. The specimen clustered along with, but outside the two specimens of *U. rogersi*. The average of the pairwise differences between specimens of these two species was 185.5.

*Urobatis jamaicensis* (yellow stingray) (fig. 60)

Both specimens of this species included in the analysis were collected from the Cayman Islands and thus come from essentially the center of the distribution of this species, which occurs throughout much of the subtropical and tropical western seaboard of the Atlantic Ocean including the Caribbean Sea and Bahamas. These specimens were identical in sequence. They clustered most closely with the specimens of *U. rogersi* and *U. cf. simulatrix*; the average of the pairwise differences between specimens of *U. jamaicensis* and the latter two species was 180.5 and 184, respectively.

**Potamotrygonidae (river stingrays)***Potamotrygon* species (fig. 60)

Much confusion surrounds the identities of the potamotrygonid stingrays from the rivers of South America. In total, the analysis included nine specimens of the South American freshwater stingray genus *Potamotrygon*, five of which were collected from the Madre de Dios River in Peru. The results of the analysis suggest that these nine specimens represent perhaps as many as six distinct lineages. However, the molecular results are not necessarily congruent with the color patterns of the specimens involved. Given this, in combination with the fact that only

two of the nine specimens have been deposited in a museum (GN5881 = MZUSP 95411 and GN5880 = MZUSP 107670), and in light of the concerns raised by Toffoli et al. (2008), we have only limited confidence in the identifications of the specimens included here.

The analysis yielded a group comprised of all nine specimens, with a cluster comprised of five specimens collected from the Madre de Dios River in Peru. Within the Madre de Dios cluster, the genetic identities of three specimens were much closer to one another than to either of the other two specimens in the cluster. These three specimens had a range of pairwise differences of 2–3 (with an average of 2.7). However, the color patterns of these five specimens are inconsistent with their genetic identities. Given the issues raised by Toffoli et al. (2008), the identities of these specimens have been assigned here are based in large part on color pattern. We are confident that GN5880 is *P. tatianae* because it was among the voucher specimens examined by da Silva and de Carvalho (2011) in their description of *P. tatianae*, which is known only from the Madre de Dios River. Two specimens have been identified as *P. cf. tatianae* because, although they are consistent with the color pattern of that species, they differ from it by 26.5 bases. The color pattern of the remaining two specimens resembles that of *P. motoro*. However, in the absence of definitively identified specimens of *P. motoro*, in combination with the fact that these specimens differ from one another by 37 bases, we have given these specimens the designations *Potamotrygon cf. motoro* 1 and *P. cf. motoro* 2. The remaining four specimens were purchased from pet stores and, as a consequence, are of unknown provenance and their identities are uncertain. These have been given the designation *Potamotrygon* sp. 1 and *Potamotrygon* sp. here, but it is important to note that these specimens may represent described species that were not included in the analysis. The two specimens of *Potamotrygon* sp. 1 differed from one another by one base and the two specimens of *Potamotrygon* sp. 2 differed from one another by one base. The average of the pairwise differences between specimens of *Potamotrygon* sp. 1 and those of *Potamotrygon* sp. 2 was 104. Clearly, much work

remains to be done to resolve the identities of these specimens relative to confirmed material.

*Paratrygon aiereba* (discus ray) (fig. 60)

A single specimen of this currently monotypic genus, also collected from Peru, was included in the analysis. This grouped along with but outside the *Potamotrygon* specimens. This specimen is deposited in the Zoology Museum in Sao Paulo, Brazil (GN5874 = MZUSP 95406).

*Himantura schmardae* (Chupare stingray) (fig. 60)

A single specimen of this species, collected from Guyana, was included in the analysis. This specimen clustered along with, but outside those of *Potamotrygon* and *Paratrygon*. This specimen was deposited at the Royal Ontario Museum (GN6488 = ROM 66845). The grouping of this species with the Potamotrygonidae rather than with the Dasyatidae warrants further taxonomic investigation.

### Rhinopteridae (cownose rays)

*Rhinoptera* species

In total, 52 specimens of cownose rays were included in the analysis. The identities of most of these specimens were difficult to determine using either morphological or molecular criteria, because the taxonomy of this genus remains so relatively poorly known. Even key characters such as tooth shape and number appear to be intraspecifically variable. Hence, in assigning names to taxa we have taken a conservative approach. Morphology, molecular differences, and geographic location were used in combination to make these determinations. In general, only in instances in which at least two of these three criteria were congruent, were the specimens comprising a cluster assigned a unique name. In total we believe our specimens represent as many as eight species of *Rhinoptera*.

The phenotype and geography haplotype maps for the 52 specimens of *Rhinoptera* included here are illustrated in figure 99A and 99B, respectively. The phenotype map supports the validity of at least seven of these species in that their haplotypes are distinct and, in the cases of species represented by multiple specimens, the haplotypes of their members are tightly clustered. However, it



also serves to highlight issues with *R. steindachneri* and *R. bonasus*, which are addressed in the sections treating these species below.

*Rhinoptera steindachneri* (Pacific cownose ray) complex (fig. 61)

The analysis yielded a cluster comprised of seven specimens of *Rhinoptera steindachneri* from the Gulf of California, seven specimens from the Gulf of Mexico, and one from North Carolina all originally identified as *Rhinoptera bonasus*. The range of pairwise differences among the 15 members of this cluster was 0–9 (with an average of 3.8). However, these specimens differ from one another morphologically in a number of respects. For example, the specimens from the Gulf of California appear to be fully consistent with the eastern Pacific species, *Rhinoptera steindachneri*, the type locality of which is in the Gulf of California. In contrast, the configuration of the tooth plates of the specimens from the Gulf of Mexico and North Carolina resemble those of *Rhinoptera brasiliensis*, even more than they do those of *R. bonasus*. Furthermore, these specimens clustered well outside specimens from the western Atlantic considered to be morphologically consistent with *R. bonasus* (see below). Unfortunately, no confirmed specimens of the southwestern Atlantic *R. brasiliensis* were included in the analysis. Until such time as the New World members of this genus can be examined in more detail, despite the mixed nature of this cluster, we have retained the designation *Rhinoptera steindachneri* for the specimens from the Gulf of California and have adopted *Rhinoptera* cf. *steindachneri* for the members of this cluster that occur in the other localities.

However, the haplotype map colored by phenotype (fig. 99A) does not support this line of reasoning. Not only is one haplotype shared by specimens identified as *R. steindachneri* and *R. cf. steindachneri*, but the haplotypes of specimens of these two taxa are very similar and, in fact, comprise a single group. This suggests the alternative interpretation that *R. steindachneri* occurs not only in the eastern Pacific, but also in the Gulf of Mexico, and possibly also the western

Atlantic Ocean, where it is sympatric with *Rhinoptera bonasus*.

*Rhinoptera* sp. 1 (fig. 61)

Clustering along with but outside the specimens in the *Rhinoptera steindachneri* complex was a specimen collected from Senegal (GN5978). The average of the pairwise differences between this specimen and those in the former cluster of 15 specimens was 20.8. Given its degree of genetic divergence and disparate locality, this specimen has been given a separate designation until such time as additional specimens from the eastern Atlantic can be examined in more detail.

*Rhinoptera jayakari* (Oman cownose ray) (fig. 61)

The analysis also yielded a cluster comprised of 10 specimens collected from a diversity of localities including Borneo, Mozambique, and the Gulf of Oman. The range of pairwise differences among specimens in this cluster was 0–17, with an average of 8.3. While there was some evidence of two subclusters within this cluster, the specimens in these two subclusters overlapped in geography and had an average of the mean pairwise differences of 13.7. At this time, all specimens in this cluster have been referred to as *Rhinoptera jayakari* following Last et al. (2010c).

*Rhinoptera bonasus* (cownosed ray) complex (fig. 61)

The analysis yielded a cluster comprised of 18 specimens from a diversity of localities in the western Atlantic including Virginia, North Carolina, and South Carolina. The range in pairwise differences among members of this cluster was 0–8, with an average of 1. The fact that these specimens grouped away from those comprising the *R. cf. steindachneri* cluster, which also included a specimen from the western Atlantic, as noted above, suggests that this region may be home to two sympatric species of *Rhinoptera*. These specimens have been given the designation *R. bonasus*, based on their morphology and because the type locality of this species is New York. The average of the pairwise differences between *R. bonasus* and its sympatric congener *R. cf. steindachneri* was 86.

Grouping along with but outside the members of the former cluster was a second

specimen collected from Senegal. The average of the pairwise differences between this specimen and those of the *R. bonasus* cluster was 19.4. Thus, while this specimen from Senegal exhibited a tooth pattern similar to that of *R. bonasus*, given its geography and genetic difference, it has been referred to here as *R. cf. bonasus*. The difference between this specimen and that of the other from Senegal (*Rhinoptera* sp. 1) was 80. This suggests that Senegal may also be home to two sympatric species of *Rhinoptera*.

The haplotype map (fig. 99A) supports the contention that *R. cf. bonasus* from Senegal is distinct from *R. bonasus*. However, it also confirms that a second species (*Rhinoptera* sp. 1) occurs sympatrically with *R. cf. bonasus* in Senegal.

*Rhinoptera neglecta* (Australian cownose ray) (fig. 61)

The analysis also yielded a cluster comprised of five specimens of *R. neglecta* from northern Australia. One of these specimens came from the Australian National Fish Collection (GN4662 = ANFC H 3915-01). The range of pairwise differences among these specimens was 0–3, with an average of 1.2.

*Rhinoptera javanica* (Javanese cownose ray) (fig. 61)

Two specimens identified as *R. javanica* (see Last et al., 2010c), one from eastern Malaysian Borneo and one from Vietnam, grouped immediately outside the *R. neglecta* cluster. These specimens differed from one another by nine bases. The average of the pairwise differences between these specimens and those of *R. neglecta* was 22.6.

### Mobulidae (devil rays)

*Mobula japanica* (spinetail devilray) (fig. 61)

In total, 12 specimens of this species were included in the analysis. Given that 10 of these specimens were collected from the Gulf of California and two from Vietnam, they represent two disparate elements of the distribution of this widely distributed species. One of the specimens was deposited in the Texas Cooperative Wildlife Collection (GN5273 = TCWC 7568.01). The analysis yielded a single cluster; the range of pairwise

differences among specimens in this cluster was 0–5, with an average of 2.3.

*Manta birostris* (manta) (fig. 61)

The two specimens of this species included in the analysis were collected from Indonesia and the Philippines and thus represent only a very small portion of the distribution of this global species. The sequences of these specimens differed by seven bases. It is interesting that this species clustered among *Mobula* species; most closely with *Mo. japanica*. The average of the pairwise differences among specimens of *Ma. birostris* and *Mo. japanica* was 125.8. The recent resurrection of *Manta alfredi* by Marshall et al. (2009) has caused doubt over the identifications of manta species in published literature and other records. The specimen from Indonesia can be accurately confirmed as *M. birostris* based on photographic evidence. There is a possibility that the specimen from the Philippines may represent *M. alfredi*; acquisition of more specimens confirmed as *M. alfredi* in the future will be required to confirm this. The Philippine specimen is deposited in the Philippines (GN4356 = BRU 043). At this stage we retain *M. birostris* as the designation for both specimens.

*Mobula thurstoni* (smoothtail devilray) (fig. 61)

The analysis included eight specimens of this relatively widely distributed species, all collected from the Gulf of California and thus representing only a very small portion of its distribution. One of these specimens was deposited in the Texas Cooperative Wildlife Collection (GN5284 = TCWC 7565.01). The range in pairwise differences among these specimens was 0–7, with an average of pairwise differences of 2.5.

*Mobula kuhlii* (shortfin devilray) (fig. 61)

Three specimens, two from the Philippines and one from eastern Malaysian Borneo, were included in the analysis. The specimens from the Philippines (GN4337 = BRU 031 and GN4327 = JPAG 303) were treated by Compagno et al. (2005b) as representing a new record of *M. kuhlii* for that region. The range of pairwise differences among all three specimens was 0–1. The analysis yielded a single cluster that grouped most closely with the specimens of *M. thurstoni*. The average of

the pairwise differences between specimens of these two species was 46.8.

*Mobula munkiana* (pygmy devilray) (fig. 61)

Eight specimens of this species, all collected from the Gulf of California, were included in the analysis. These specimens represent the northern part of the eastern Pacific distribution of this species, which has been reported as far south as Ecuador. One of these specimens was deposited in the Texas Cooperative Wildlife Collection (GN2286 = TCWC 7589.03). The range of pairwise differences among these specimens was 0–3, with an average of 0.8.

*Mobula hypostoma* (Atlantic devilray) (fig. 61)

Both specimens of this species included in the analysis were collected from the Gulf of Mexico and thus represent one of the more northern parts of the distribution of this species, which occurs from New Jersey to Argentina. These specimens differed by four bases and they clustered most closely with *M. munkiana*, with an average of the pairwise differences among specimens between these two species of 31.4.

### Myliobatidae (eagle rays)

*Pteromylaeus bovinus* (duckbill ray) (fig. 61)

A single specimen of this species was included in the analysis. This specimen was collected from Senegal and thus represents a northeastern element of the distribution of this species, which occurs from Portugal, throughout the western coast of Africa, around the cape and as far north as Mozambique. It clustered away from other myliobatids and along with, but outside all of the species of *Rhinoptera* and *Mobula*.

*Myliobatis californica* (bat ray) (fig. 62)

The 18 specimens of this species were collected from throughout the Gulf of California and thus represent the southern parts of the distribution of this species, which has been reported to occur from Oregon to Baja, with a rare report from the Galapagos Islands (Grove and Lavenberg, 1997). One of these specimens was deposited in the Texas Cooperative Wildlife Collection (GN5203 = TCWC 7564.03). The analysis yielded a single cluster with a range in pairwise differences among the 18 specimens of 0–12, with an average of 5.6.

*Myliobatis aquila* (common eagle ray) (fig. 62)

The seven specimens of this eastern Atlantic-dwelling species were all collected from South Africa. The range of pairwise differences among specimens in this cluster was 0–2, with an average of 0.7.

*Myliobatis tobijei* (kite ray) (fig. 62)

The analysis included three specimens of this species, which occurs from Japan to Indonesia, one of which came from Taiwan and two from the Philippines. The specimens from the Philippines (GN4384 = JPAG 130 and GN4357 = JPAG 147) were treated by Compagno et al. (2005b) as *M. cf. tobijei*. However, given that the range in pairwise differences among specimens from both localities was only 1–7, with an average of 4.7, we have used the designation *M. tobijei* for all three specimens in this cluster. These specimens grouped most closely with those of *M. aquila*. The average of the pairwise differences among specimens in these two clusters was 48.9.

*Myliobatis longirostris* (longnose eagle ray) (fig. 62)

Sixteen specimens of this Gulf of California endemic were included in the analysis, which yielded a single cluster. Five of these specimens were deposited in the Texas Cooperative Wildlife Collection (GN5200 = TCWC 7564.04, GN5201 = TCWC 7564.06, GN5241 = TCWC 7589.04, GN5269 = TCWC 7587.01, and GN1570 = IBUNAM PE9517). Although many of the specimens were identical in sequence, the range in pairwise differences among all specimens in this cluster was 0–11, with an average of 2.5.

*Myliobatis freminvillei* (bullnose ray) (fig. 62)

The two specimens identified as *M. freminvillei* included in the analysis differed by a single base. They were both collected from the western North Atlantic and thus represent more northern elements of the amphitropical distribution of this species, which has been reported as far south as Argentina. This species grouped most closely with *M. longirostris*; the average of the pairwise differences among specimens of these two species was 52.8.

*Myliobatis australis* (southern eagle ray) (fig. 62)

The analysis included four specimens of this species, all collected from the Tasman Sea in Australia. They thus represent a more eastern

element of the distribution of this species, which has been reported from southern Australia and possibly New Zealand (Last and Stevens, 2009). The range in pairwise differences among these specimens was 0–4, with an average of pairwise difference of two bases.

#### *Aetomylaeus* species

The analysis included specimens of six nominal species of *Aetomylaeus*. A haplotype map for phenotype (fig. 100A) and also one for geography (fig. 100B) was generated for the five most similar of these species (i.e., all but *A. vespertilio*). The phenotype map supports recognition of three distinct species in the *A. nichofii* complex because it shows no overlap in haplotypes among specimens of the different species and also illustrates the substantial amount of divergence between the sympatric *A. nichofii* and *A. maculatus*. However, additional specimens from the Persian Gulf would help to confirm the distinction between *A. cf. nichofii* 1 and *A. nichofii*. The haplotype map for geography illustrates the allopatric nature of these three species.

#### *Aetomylaeus nichofii* (banded eagle ray) complex (fig. 62)

Eighteen specimens that were generally consistent with the color morph of *Aetomylaeus nichofii* were included in the analysis. The majority of these came from a diversity of localities around the island of Borneo, but they also included one specimen from the Persian Gulf and two from the Arafura Sea off northern Australia. The analysis yielded a group consisting of these 18 specimens. However, the 15 specimens from Borneo represented a cluster within this group; five of these specimens were vouchered (GN4264 = CAS 229046, GN2968 = ANFC H 6209-01, GN2969 = ANFC H 6209-02, GN3444 = IPPS BO180, and GN3696 = IPPS BO485). The range of pairwise differences among the 15 specimens in the Borneo cluster was 0–10, with an average of 3.3. The Persian Gulf and Arafura Sea specimens grouped along with but outside the Borneo specimens. The two specimens from the Arafura Sea differed by one base. The average of the pairwise difference between the specimens from Borneo and the specimen from the Persian Gulf was 17.7, and between the specimens from Borneo and those from the Arafura Sea was 74. Furthermore, pairwise

difference between the specimens from the Persian Gulf and Arafura Sea was 72. These results suggest that our sample may include three distinct taxa. Until this issue can be addressed in more detail, we have provisionally referred to the specimens in the Borneo cluster as *Aetomylaeus nichofii* as the type locality for this species is Indonesia. The specimen from the Persian Gulf has been referred to as *Aetomylaeus cf. nichofii* 1, and the specimen from the Arafura Sea referred to as *Aetomylaeus cf. nichofii* 2. A taxonomic revision of this complex is currently being undertaken by P.L. and W.W.

#### *Aetomylaeus maculatus* (mottled eagle ray) (fig. 62)

In total, 10 specimens consistent with the color pattern of *A. maculatus* were included in the analysis. The analysis yielded a single cluster, but with evidence of two subclusters; one comprised primarily of specimens from Malaysian Borneo and one of specimens from Indonesian Borneo. Three of the samples from Borneo come from museum specimens (GN2993 = ANFC H 6220-01, GN3423 = ANFCH 6123-04 and H 6122-02, and GN3442 = ANFC H 6219-02). The range in pairwise differences among all 10 specimens in the cluster was 0–17, with an average of 8.3. The range of pairwise differences among specimens within the Malaysian subcluster was 0–5; the three specimens in the Indonesian subcluster were identical in sequence. The average of the pairwise differences among specimens in the two subclusters was 15.2. However, in the absence of consistent morphological or geographic differences, we have made no formal distinction between the two subclusters. It should be noted that our specimens represent only a small portion of the distribution of this species, which has been reported from throughout much of the Indo-West Pacific.

#### *Aetomylaeus milvus* (ocellate eagle ray) (fig. 62)

Two specimens collected from the Persian Gulf were included in the analysis. These specimens were identical in sequence to one another. They grouped most closely with specimens of *Aetomylaeus maculatus*. However, the average of the pairwise differences between specimens of these two species was 95.2. This result supports the validity of this species, which has been questioned by some previous authors (e.g., Compagno, 1999).

*Aetomylaeus vespertilio* (ornate eagle ray) (fig. 62)

The five specimens of this species included here were collected from the Arafura Sea and Gulf of Carpentaria, off northern Australia, and from the Philippines. These specimens represent eastern elements of the distribution of this Indo-West Pacific species, which has been reported from as far west as the Mozambique Channel. The Philippine specimen (GN4344 = JPAG 324) was treated as *A. vespertilio* by Compagno et al. (2005b). The analysis yielded a single cluster of these specimens, which had a range of pairwise differences of 0–5, with an average of pairwise differences of 2.8 bases.

*Aetobatus* species

Until recently, a great deal of confusion has existed with respect to the identity of the various color morphs of “spotted eagle rays.” Several authors (e.g., Last and Stevens, 2009; Richards et al., 2009) have noted that the genus may include more species than currently recognized. The taxonomy of the spotted eagle ray group was recently partially revised by White et al. (2010c), who resurrected a number of existing names for the various color morphs that appear to represent distinct valid taxa. The treatment of this genus here follows the taxonomy proposed by White et al. (2010c). The haplotype maps for our *Aetobatus* specimens provide support for the recognition of all seven of the nominal species treated below. Specimens of these species share no haplotypes (fig. 101A). Furthermore, the majority of these species exhibit relatively restricted and allopatric geographic distributions (fig. 101B).

*Aetobatus ocellatus* (whitespotted eagle ray) complex (fig. 63)

The analysis yielded a cluster comprised of 34 specimens from throughout the Indo-West Pacific (i.e., Malaysian and Indonesian Borneo as well as from Taiwan, Thailand, Vietnam, Singapore, the Philippines, and northern Australia). The range of pairwise differences among specimens in this cluster was 0–16, with an average of 5.8. These specimens are morphologically consistent with previous accounts of *A. ocellatus* (e.g., see White et al., 2010c), the type locality of which is Java in Indonesia. One of the specimens from the Philippines (GN4364 = JPAG 314) was

treated by Compagno et al. (2005b) as *Aetobatus* cf. *narinari*. Two of the specimens from Borneo were also deposited (GN3550 = IPMB 38.01.08 and GN3513 = IPPS BO296).

However, three additional specimens, one from the Mozambique Channel and two from off Qatar in the Persian Gulf, clustered along with but outside these 34 specimens. Specimens from the Mozambique Channel and Qatar are genetically different from one another, and also from those from the Indo-West Pacific. The average of the pairwise differences between the specimen from the Mozambique Channel (*A. cf. ocellatus* 1) and those from the Indo-West Pacific (*A. ocellatus*) was 20.2; the average of pairwise differences between the specimen from the Mozambique Channel and the two from Qatar (*A. cf. ocellatus* 2) was 29. The average of the pairwise differences between the specimens from Qatar (*A. cf. ocellatus* 2) and the Indo-West Pacific (*A. ocellatus*) was 26.8. Unfortunately, photographs are unavailable for any of the three specimens from the Mozambique Channel and Qatar. Nonetheless, they have been referred to here as *Aetobatus* cf. *ocellatus* 1 and *Aetobatus* cf. *ocellatus* 2, respectively, based on their genetic differences. The two specimens of *A. cf. ocellatus* 2 differed by two bases.

*Aetobatus narinari* (spotted eagle ray) (fig. 63)

Fourteen specimens identified as this species were included in the analysis. These specimens came from the Florida Keys and Gulf of Mexico, as well as from Puerto Rico. Three of the specimens from the Florida Keys came from vouchers (GN5675 and GN5676 = AMNH 251703 and GN5678 = AMNH 251704). The analysis yielded essentially a single cluster with a range in pairwise differences of 0–18, and an average of 4.4. However, one of the specimens from Puerto Rico (GN2118) differed conspicuously from the other 13 specimens in the cluster. The average of the pairwise differences between this specimen and the other 13 was 14.6. The specimens in this cluster are morphologically generally consistent with *A. narinari*, the type locality of which is St. Barthélemy in the Caribbean Sea and Brazil. We have included the more divergent Puerto Rican specimen under this name, but note that it differs, for example, from the other Puerto Rican

specimen (GN2119), in that many more of its white spots are ocellate, rather than solid.

*Aetobatus laticeps* (Pacific whitespotted eagle ray) (fig. 63)

The analysis also yielded a cluster comprised of four specimens collected from Loreto in the Gulf of California. These specimens are generally consistent with *Aetobatus laticeps*, described from California by Gill (1867). The range of pairwise differences among these specimens was 0–2, with an average of 1. These specimens clustered most closely with those of *A. narinari*; the average of the pairwise differences between specimens of these two species was 14.9.

*Aetobatus* sp. (fig. 63)

Nine specimens from Vietnam, that differed conspicuously morphologically from the five other species of eagle rays included here, were also found to comprise a cluster that was genetically distinct from the five other species. The range of pairwise differences among specimens in this cluster was 0–2, with an average of 0.4. Unlike other species in the genus, these specimens lacked white spots from the dorsal surface and exhibited a relatively short head. These specimens likely represent an undescribed species. Two of these specimens were deposited in the Vietnam Natural Museum of Nature (GN7014 = VN-z-v.000394 and GN7050 = VN-z-v.000309).

*Aetobatus flagellum* (longheaded eagle ray) (fig. 63)

The two specimens of this species included in the analysis were collected from Indonesian Borneo and Maharashtra, India, and they differed from one another by 11 bases. These specimens are consistent with *A. flagellum*, whose type locality is the coast of Coromandel off India. They clustered most closely with *Aetobatus* sp. from Vietnam. The average of the pairwise differences between *A. flagellum* and those of *Aetobatus* sp. was 93.7.

### Gymnuridae (butterfly rays)

*Gymnura* species

The analysis included a total of 50 specimens of *Gymnura*. This was among the most problematic genera with respect to specific identifications of specimens. We have treated these specimens as representing nine distinct

species. The haplotype map for phenotype (fig. 102A) supports this level of diversity, in that there are no overlapping haplotypes among the specimens of any of these nine species. The haplotype map for geography (fig. 102B) provides support for the notion that two species of *Gymnura* (*G. crebripunctata* and *G. marmorata*) cooccur in the Gulf of California, two species cooccur in the Indo-Pacific (*G. zonura* and *G. cf. poecilura* 1), and that potentially three species cooccur in northern Australia (*G. australis*, *G. micrura*, and *Gymnura* sp. 1). Furthermore, our analyses are consistent with the suggestion that butterfly rays in the Persian Gulf are distinct from those in the other localities sampled here. However, clearly this genus would benefit greatly from additional taxonomic work.

*Gymnura* cf. *poecilura* complex (fig. 64)

The analysis, which included 17 specimens showing a resemblance to *Gymnura poecilura*, yielded two clusters. Given that no specimens from India, the type locality of this species, were included, we have given the clusters numerical designations. One, designated *Gymnura* cf. *poecilura* 1, contained 12 specimens collected from throughout Borneo; two of these specimens were vouchered (GN3641 = IPPS BO430 and GN4507 = CAS 229034). The range of pairwise differences among specimens in this cluster was 0–13, with an average of 5.3. The second cluster, designated *Gymnura* cf. *poecilura* 2, consisted of the other five specimens, all of which were collected from the Gulf of Oman. Specimens comprising the latter cluster had a range of pairwise differences of 1–8, with an average of 4.8. The average of the pairwise differences between specimens the two clusters was 120.5. It is likely that at least one of these forms is an undescribed species.

*Gymnura zonura* (zonetail butterfly ray) (fig. 64)

Seven specimens identified as this species were included in the analysis. These came from Borneo, Singapore, and the Philippines and thus represent eastern elements of the Indo-West Pacific distribution of this species. The Philippine specimen (GN4369 = BRU 105) was treated by Compagno et al. (2005b) as *Aetoplatea zonura*. These specimens were generally consistent with *G. zonura*; however, they varied in dorsal color pattern from the typical patterned form of *G. zonura* (GN4838) to plain (GN4830). The

analysis yielded a single cluster comprised of these specimens. The range in pairwise differences among specimens in this cluster was 1–14, with an average of 6; the upper end of this range was accounted for by a specimen from the Philippines. Specimens in this cluster grouped among other *Gymnura* species, supporting the placement of this species in *Gymnura* (see White et al., 2006; Last et al., 2010c) rather than in the separate genus *Aetoplatea*. It is closest to *Gymnura* sp. 1; the average of the pairwise differences between specimens of *G. zonura* and *Gymnura* sp. 1 was 129.2; between those of *G. cf. poecilura* 1 was 159.5, and between those of *G. cf. poecilura* 2 was 143.6.

*Gymnura* sp. 1 (fig. 64)

The analysis included three specimens from the western North Atlantic that had preliminarily been identified as *Gymnura altavela*, but that grouped well outside specimens identified as *G. altavela* from the eastern Atlantic. Given that the type locality of *G. altavela* is in the eastern Atlantic, specimens comprising that cluster (see below) have been provisionally identified as *G. altavela*, and those comprising the genetically divergent western Atlantic cluster, as *Gymnura* sp. 1. Unfortunately, images of material from the western Atlantic are not available. In the interim, these have been identified as *Gymnura* sp. 1, but it should be recognized that they may refer to a *Gymnura* species not represented in this analysis. These specimens differed from one another by 0–1 bases. They clustered along with *G. zonura*. The average of the pairwise differences between *Gymnura* sp. 1 and those of *G. zonura* is 129.2, between *Gymnura* sp. 1 and *G. cf. poecilura* 1 150.3, and between the *G. cf. poecilura* 2 cluster 141.3.

*Gymnura australis* (Australian butterfly ray) (fig. 64)

A single specimen of this, the only species of its genus reported from Australia, was included in the analysis. This specimen was collected from the Arafura Sea off northern Australia. It represents a northwestern element of the distribution of this species. It clustered most closely with *G. zonura* and *Gymnura* sp. 1, with average pairwise differences of 158.4 and 131.3, respectively.

*Gymnura crebripunctata* (longsnout butterfly ray) (fig. 64)

In total, seven specimens of this species were included in the analysis. These comprised a single cluster, and exhibited a range of pairwise differences of 1–10, with an average of 5. These specimens, which were collected in the Gulf of California, are representative of the northern portion of the distribution of this species, which is known to occur coastally as far south as Panama.

*Gymnura marmorata* (California butterfly ray) (fig. 64)

The four specimens of this species included here comprised a single cluster and exhibited a range of pairwise differences of 1–3, and an average of pairwise differences of 1.5. These specimens, collected in the Gulf of California, are representative of the northern elements of the distribution of this species, which has been reported as far south as Peru. The average of the pairwise differences between specimens of this species, and those of their sympatric congener, *G. crebripunctata*, was 180.3. This is consistent with the work of Smith et al. (2009) in supporting the recognition of *G. marmorata* as a taxon distinct from *G. crebripunctata*.

*Gymnura micrura* (smooth butterfly ray) (fig. 64)

One specimen identified as this species, collected from the western Atlantic, was included in the analysis. Unfortunately, images of this specimen are not available, and thus the identity of this specimen has not been confirmed. However, field notes (K. Cleason, personal commun.) indicate that this specimen lacked a tail spine. This specimen clustered most closely with the specimens of *G. marmorata*, but the average of the pairwise differences between specimens of these two species was 160.8. This specimen represents only a portion of the western Atlantic distribution of this species, which occurs throughout much of the central western and eastern seaboard of the Atlantic Ocean.

*Gymnura altavela* (spiny butterfly ray) (fig. 64)

Ten specimens that are generally morphologically consistent with this species were included in the analysis. All 10 specimens came from Senegal and thus represent only a small portion of the distribution of this species, which has been reported from throughout much of the central

western and eastern seaboard of the Atlantic Ocean. The range of pairwise differences among these specimens was 0–5, with an average of 1.9 bases. Specimens in this cluster and those of their sympatric congener *Gymnura* sp. 1 had an average pairwise difference of 196.5.

#### **Plesiobatidae (giant stingarees)**

*Plesiobatis daviesi* (giant stingaree) (fig. 64)

The three specimens of this species included in the analysis were collected from Malaysian Borneo and the Philippines and thus represent only a central portion of the distribution of this species, which has been reported from southeastern Africa to Hawaii. The specimen from the Philippines was vouchered (GN4346 = MMLM 017). The sequences of all three specimens were identical.

#### **Urolophidae (stingarees)**

*Urolophus paucimaculatus* (sparsely spotted stingaree) (fig. 65)

Four specimens of this southern Australian endemic were included in the analysis. The analysis yielded a single tight cluster; the range in pairwise differences among these specimens was 1–5, with an average of pairwise differences of three bases.

*Urolophus cruciatus* (crossback stingaree) (fig. 65)

The analysis included three specimens identified as this distinctively colored southeastern Australian endemic species. The range of pairwise differences among these specimens was 1–2, with an average of 1.3. These specimens grouped most closely with those of *U. paucimaculatus*; the average of the pairwise differences between these two species was 76.5.

*Urolophus westraliensis* (brown stingaree) (fig. 65)

A single specimen of this Australian endemic was included. It is deposited in the Australian National Fish Collection (GN4637 = ANFC H 4649-23).

*Urolophus expansus* (wide stingaree) (fig. 65)

The single specimen of this southwestern Australian endemic species included in the analysis is deposited in the Australian National Fish Collection (GN4656 = ANFC H 6414-12).

*Urolophus viridis* (greenback stingaree) (fig. 65)

A single specimen of this species, a south-eastern Australian endemic, was included in the analysis. This specimen is deposited in the Australian National Fish Collection (GN4661 = ANFC H 2444-04). This species clustered most closely with the specimen of *U. expansus*, but the sequences of these specimens differed by 44 bases.

*Urolophus kapalensis* (Kapala stingaree) (fig. 65)

A single specimen of this relatively newly described Australian endemic (see Yearsley and Last, 2006) was also included. It was taken from a specimen (GN4658 = H6153-02) listed among “other material examined” in the original description of this species.

*Urolophus lobatus* (lobed stingaree) (fig. 65)

The analysis included one specimen of this Australian endemic, which is in the Australian National Fish Collection (GN4659 = ANFC H 6346-15).

*Urolophus flavomosaicus* (patchwork stingaree) (fig. 65)

Two specimens of this Australian endemic, both in the Australian National Fish Collection (GN4636 = ANFC H 1036-6 and GN4657 = ANFC H 1036-37) were included. These specimens were identical in sequence.

*Urolophus bucculentus* (sandyback stingaree) (fig. 65)

The analysis included a single specimen of this southeastern Australian endemic. This specimen is deposited in the Australian National Fish Collection (GN4655 = ANFC H 1269-01). It clustered most closely with *U. flavomosaicus*. Although these two species were considered to bear a strong morphological resemblance to one another and to be sympatric in Southern Queensland by Last and Stevens (1994), the distinction between these two species both morphologically and geographically is made clear by Last and Stevens (2009). The average of the pairwise differences between the two species was 15.

*Trygonoptera imitata* (eastern shovelnose stingaree) (fig. 65)

The four specimens of this newly described southeastern Australian endemic species (see Yearsley et al., 2008) included in the analysis were collected from New South Wales. The range in pairwise differences among these



specimens was 1–3, with an average of 1.7. The analysis yielded a single tight cluster comprised of these specimens.

*Trygonoptera testacea* (common stingaree) (fig. 65)

A single specimen of this eastern Australian endemic species was included in the analysis. This specimen grouped most closely with the cluster of *T. imitata* specimens. The average of the pairwise differences between this specimen and those of *T. imitata* was 141.

*Trygonoptera personata* (masked stingaree) (fig. 65)

The analysis included one specimen of this western Australian endemic; this specimen is in the Australian National Fish Collection (GN4635 = ANFC H 6347-20). This species clustered along with but outside two of its three congeners included in the analysis. The average of the pairwise differences between this species and *T. imitata* was 131.5, and between *T. testacea* was 162.

*Trygonoptera ovalis* (striped stingaree) (fig. 65)

A single specimen of this western Australian endemic was included in the analysis. This specimen is in the Australian National Fish Collection (GN4634 = ANFC H 6347-13). It grouped most closely with but outside its three congeners included in the analysis. The average of the pairwise differences between this species and *T. imitata* was 155, *T. testacea* 170, and *T. personata* 134.

### Hexatrygonidae (sixgill stingrays)

*Hexatrygon bickelii* (sixgill stingray) (fig. 66)

Two specimens of this unusual ray were included in the analysis. Both specimens came from Taiwan. They differed from one another by one base. These specimens represent only a small portion of the distribution of this species, which is patchily distributed from southern Africa to Hawaii.

### Zanobatidae (panrays)

*Zanobatis schoenleinii* (striped panray) (fig. 67)

Eight specimens of this species, all collected from Senegal, were included in the analysis. These specimens thus represent a more northern element of the distribution of this species, which extends from Morocco to the Gulf of Guinea. The range of pairwise

differences among specimens of this species was 0–10, with an average of 3.6.

### Pristidae (modern sawfishes): genus *Pristis*

*Pristis pectinata* (smalltooth sawfish) (fig. 68)

In total, 20 specimens of this species were included in the analysis. These were collected from the Gulf of Mexico off Florida and the Bahama Islands in the Caribbean Sea. The analysis yielded a single cluster and the range of pairwise differences among these specimens was 0–12, with an average of pairwise differences of 2.2. Given the reported breadth of the distribution of this species, these specimens represent only the northwestern elements of its distribution.

*Pristis zijsron* (green sawfish) (fig. 68)

All six specimens of this species included in the analysis were collected from northern Australia and thus represent only a small part of the original Indo-West Pacific distribution of this species, which has been reported from fresh, brackish, and marine habitats. Two of these specimens are vouchered (GN3155 = NTM S.14689-001 and GN3159 = NTM S.14689-003). The range of pairwise differences among these specimens was 0–5, with an average of pairwise differences of 1.7. The analysis yielded a single cluster that grouped most closely with the cluster of *P. pectinata* specimens. The average of the pairwise differences between specimens of these two species was 108.8.

*Pristis clavata* (dwarf sawfish) (fig. 68)

Four specimens of this species, which is now considered restricted to northern Australia, were included here. One of these specimens is vouchered (GN3158 = NTM S.14689-002). All four of these specimens were collected from Buffalo Creek in northern Australia. The analysis yielded a single cluster and the range in pairwise differences among these specimens was 0–4, with an average of pairwise differences of 2. The average of the pairwise differences between specimens of this species and those of *P. pectinata* was 119.6, and between those of *P. zijsron* was 116.7.

*Pristis perotteti* (largetooth sawfish) (fig. 68)

The 17 specimens of this coastal Atlantic-dwelling species all came from Belem in Brazil. The range of pairwise differences among these specimens was 0–11, with an

average of pairwise differences of 3.7. The average of the pairwise differences between specimens of this species and those of *P. pectinata*, which were also collected from the western Atlantic, was 123.1

*Pristis microdon* (freshwater sawfish) (fig. 68)

The analysis yielded a single cluster comprised of two specimens of this species, both from the Norman River in Queensland, Australia. The sequences of these specimens were identical and they grouped most closely with specimens of *Pristis perotteti*. The average of the pairwise differences between specimens of these two species was 16.6.

#### Rhinobatidae (guitarfishes): group 1

*Rhinobatos productus* (shovelnose guitarfish) and *Rhinobatos glaucostigma* (speckled guitarfish) (fig. 68)

The analysis included 11 specimens identified as *R. productus* and eight identified as *R. glaucostigma*, all but one of which came from the Gulf of California; one of the specimens of *R. productus* was collected from the coast of California. The analysis yielded a single cluster comprised of specimens of both species with no clear subclustering of species within this cluster. The range in pairwise differences among the 19 specimens was only 0–7, with an average of 3.6. Nonetheless, these species differ markedly in morphology, most conspicuously in maximum length and color pattern. Thus, we have retained the specific identities of specimens within this cluster in order to call attention to the discrepancy between the molecular and morphological results in this case. The average of the pairwise differences between specimens identified as *R. productus* and *R. glaucostigma* was 4.9.

#### Pristidae (modern sawfishes): genus *Anoxypristis*

*Anoxypristis cuspidata* (narrow sawfish) (fig. 68)

The seven specimens of this species included in the analysis all came from northern and eastern Australia and the range in pairwise differences was 0–1. Given the relatively broad distribution of this species, which includes much of the Indo-West Pacific, these specimens represent the only the eastern parts of its distribution. It is interesting to note that these specimens grouped conspicuously away from the five other species of

sawfishes of the genus *Pristis* included in the analysis. Furthermore, the range of pairwise differences between specimens of *A. cuspidata* and *P. pectinata*, *P. zijsron*, *P. clavata*, *P. perotteti*, and *P. microdon* was 159.2, 155.3, 151.4, 168.7, and 166.1, respectively.

#### Rhynchobatidae (wedgfishes)

*Rhynchobatus* species

The taxonomy of the genus *Rhynchobatus* is in need of full revision. Recent descriptions of two new Indo-West Pacific species (Compagno and Last, 2008, 2010) has partly resolved some of the issues but further taxonomic work is required. We have attempted to employ the revised taxonomy in naming the specimens in the clusters resulting from the analysis conducted here. Our treatment was further informed by the morphological information presented for these Indo-West Pacific species by Last and Stevens (2009) and Last et al. (2010c).

*Rhynchobatus australiae* (whitespotted shovelnose ray) (fig. 69)

The analysis yielded a cluster comprised of 12 specimens collected from a diversity of localities throughout the island of Borneo, as well as from northern Australia, Singapore, Vietnam, and Thailand. One specimen is in the Australian National Fish Collection (GN2996 = ANFC H 6221-01). These 12 specimens were generally morphologically consistent with *R. australiae* (see Last and Stevens, 2009). Most conspicuously, the majority of these specimens exhibited the single well-defined black pectoral fin spot, surrounded by four smaller white spots on either side of their body and lacked dark spots behind their eyes. The one exception was a relatively large specimen from Sarawak (GN2893) in which the pectoral fin spot configuration was not as distinct. The range in pairwise differences among these specimens was 0–7, with an average of 3.3.

*Rhynchobatus* cf. *laevis* and *Rhynchobatus palpebratus* (eyebrow wedgfish) (fig. 69)

The analysis yielded a cluster comprised of five Australian specimens identified as *R.* cf. *laevis* and two specimens identified as *R. palpebratus*. One of the specimens of *R.* cf. *laevis* is vouchered in the Australian National

Fish Collection (GN4627 = ANFC H 6319-01). The range of pairwise differences among the seven specimens in this cluster was only 0–4, with an average of 2.3. Within the cluster there was no evidence of the existence of subclusters of specimens of either species. Nonetheless, specimens identified as *R. cf. laevis* are morphologically consistent with that species as defined by Last and Stevens (2009). For example, not only do these specimens possess a diffuse black pectoral fin spot surrounded by scattered small white spots on each side of their body, but they also lack dark spots or markings near their eyes, whereas the specimens identified as *R. palpebratus* exhibit a well-defined black pectoral fin spot surrounded by four smaller white spots on each side of the body and also have dark spots behind their eyes. Thus, we have retained the different species designations of these specimens in order to call attention to the apparent discrepancy between color pattern and molecular data in this instance. The average of the pairwise differences between *R. palpebratus* and *R. cf. laevis* was 3. This cluster grouped within a larger cluster containing *R. australiae*. The average of pairwise differences between specimens identified as *R. cf. laevis* and those of *R. australiae* was 41.6 and between specimens identified as *R. palpebratus* and *R. australiae* was 41.

*Rhynchobatus laevis* (smoothnose wedgefish) (fig. 69)

Another specimen (GN3004 = ANFC H 6221-02) of this genus included in the analysis, collected from western Borneo, grouped along with but outside the cluster containing *R. cf. laevis* and *R. palpebratus*. The average of the pairwise differences between this specimen and those of *R. australiae* was 44.3, from those of *R. cf. laevis* 25 and from those of *R. palpebratus* 23.

### Rhinidae (sharkrays)

*Rhina ancylostoma* (sharkray) (fig. 69)

The six specimens included here came from northern Australia and northern Borneo and thus represent only a small portion of the distribution of this widespread Indo-West Pacific species. They were found to comprise a single cluster, which grouped along with but outside the specimens of *Rhynchobatus*. The range of

pairwise differences among specimens in this cluster was 0–4, with an average of 2.1.

### Rhinobatidae (guitarfishes): group 2

*Glaucostegus typus* (giant shovelnose ray) complex (fig. 69)

Fifteen specimens identified as *G. typus* were included in the analysis. These were collected from northern Australia and eastern and southern Borneo and thus represent the more eastern parts of the distribution of this species, which occurs as far west as India. One of these specimens was vouchered (GN4214 = ANFC H 7085-02). These specimens comprised a single cluster; the range of pairwise differences among specimens in this cluster was 0–3, with an average of 1.

Two additional specimens from Borneo clustered along with, but outside the specimens of *G. typus*. Although morphologically indistinguishable, these specimens exhibited an average pairwise difference from the specimens of *G. typus* of 20.5. In recognition of this molecular result, these two specimens, which were identical in sequence, have been given the designation *G. cf. typus*. Taxonomic investigation of these specimens needs to be undertaken.

*Glaucostegus thouin* (clubnose guitarfish) (fig. 69)

The six specimens of this species were collected from localities in western and southern Borneo. These specimens represent the central portion of the distribution of this species, which has been reported as far west as the Red Sea and eastward to New Guinea. The analysis yielded a single tight cluster with the range of pairwise differences among these specimens being 0–1. These specimens clustered most closely with those of *G. typus* and *G. cf. typus*; the average of the pairwise differences between these specimens and those of *G. typus* was 27.9, and between those of *G. cf. typus* was 36.3.

*Rhinobatos cemiculus* (blackchin guitarfish) (fig. 69)

The two specimens of this species included here, both collected from Senegal, were identical in sequence. They clustered along with but outside *G. typus* with an average of the pairwise differences relative to *G. typus* of 106.9, relative to *G. cf. typus* 106, and relative

to *G. thouin* 116.3. Our specimens represent only a relatively small portion of the distribution of this species, which is distributed throughout much of the northern and western coasts of Africa.

*Rhinobatos rhinobatos* (common guitarfish) (fig. 69)

All 20 specimens included in the analysis were collected from Senegal and thus represent the central part of the distribution of this species, which is known from the Mediterranean Sea to Angola. The analysis yielded a single tight cluster and the range of pairwise differences among these specimens was 0–6, with an average of 2.

*Rhinobatos annulatus* (lesser guitarfish) (fig. 69)

The five specimens of this southern African species all came from South Africa, and their sequences were identical. This species grouped most closely with *R. rhinobatos*, but the average of the pairwise differences among specimens of these two species was substantial at 122.2.

*Rhinobatos* cf. *schlegelii* (fig. 69)

The analysis included four specimens from the Philippines (GN4388 = BRU 071, GN2244 = BRU 073, GN2253 = MMLM 001, and GN2254 = MMLM 012), identified by Compagno et al. (2005b) as *Rhinobatos* cf. *schlegelii* and considered to represent an undescribed species. However, the cluster also included a specimen (GN4326 = JPAG 310) collected from the Philippines, and originally identified by Compagno et al. (2005b) as *Rhinobatos* sp. 1, in recognition of the fact that it was a specimen of uncertain identity. Since these specimens form a single cluster, we have used the designation of *R. cf. schlegelii* for this Philippine species. The range of pairwise differences among these five specimens was 0–3, with an average of pairwise differences of 1.8.

*Rhinobatos* sp. 1 (fig. 69)

Two specimens collected from Malaysian Borneo clustered along with but outside their congeners from the Philippines. These differed from one another by one base. This species is very similar morphologically and in color to *R. formosensis* from Taiwan and was considered to be conspecific with that species by Last et al. (2010c), but this analysis

suggests that it likely represents an undescribed species. The average of the pairwise differences between these specimens and those of *R. cf. schlegelii* was 24.9.

*Rhinobatos formosensis* (Taiwan guitarfish) (fig. 69)

One specimen from Taiwan clustered along with, but outside the specimens from the Philippines and Malaysian Borneo. The color pattern and morphology of this specimen is consistent with *R. formosensis*. The average of the pairwise differences between this specimen and those of *R. cf. schlegelii* was 105.2, and between this specimen and those of *Rhinobatos* sp. 1 was 109.5.

*Aptychotrema rostrata* (eastern shovelnose ray) (fig. 69)

Two specimens of this eastern Australian endemic were included in the analysis. These specimens differed from one another by four bases.

*Aptychotrema vincentiana* (southern shovelnose ray) (fig. 69)

The analysis included one specimen of this southwestern Australian endemic species, from the Australian National Fish Collection (GN4625 = ANFC H 6348-06). It grouped along with but outside those of *A. rostrata*. The average of the pairwise differences between this specimen and those of *A. rostrata* was 51.

*Zapteryx exasperata* (banded guitarfish) (fig. 69)

Two specimens of this species, both collected from the Gulf of California, were included; they differed from one another by a single base.

*Trygonorrhina dumerilii* (southern fiddler ray) (fig. 69)

A single sample of this southwestern Australian endemic species was included in the analysis. The specimen is in the Australian National Fish Collection (GN4626 = ANFC H 6346-22).

### Torpedinidae (Torpedo rays)

*Torpedo fuscumaculata* (blackspotted torpedo) (fig. 70)

A total of 11 specimens of this species, which is considered to occur off the southern regions of Africa and possibly elsewhere in the Indian Ocean, were included. The range

of pairwise differences among the specimens of this species, which were all collected off South Africa, was 0–6, with an average of pairwise differences of 2.6.

*Torpedo torpedo* (ocellate torpedo) (fig. 70)

A single specimen from Senegal provisionally identified by Marcelo de Carvalho (personal commun.) as this species was included. This specimen grouped most closely with *T. fuscomaculata*, with an average of the pairwise differences between species of 45.4.

*Torpedo sinuspersici* (gulf torpedo) (fig. 70)

Two specimens of this western Indian Ocean species, both collected in the Persian Gulf off Iran, were included. These clustered together, but differed by 22 bases. They grouped most closely with but outside *T. fuscomaculata* and *T. torpedo*; the average of the pairwise differences between *T. sinuspersici* and the latter two species was 52.7 and 64.5, respectively.

*Torpedo mackayana* (ringed torpedo) (fig. 70)

The single specimen of this species, which has been reported from Senegal to Angola, was included in the analysis. This specimen was collected from Senegal and thus represents only a northern element of the distribution of this species. The identification of this specimen was provided by M. de Carvalho (personal commun.).

*Torpedo marmorata* (spotted torpedo) (fig. 70)

The specimen included was collected from Senegal and thus represents only one element of the distribution of this species, which occurs throughout much of the western coast of Europe, the Mediterranean, and also much of Africa. Although this specimen resembles *T. bauchotae*, it has tentatively been identified as *T. marmorata* by M. de Carvalho (personal commun.) at this time.

*Torpedo nobiliana* (Atlantic torpedo) (fig. 70)

The analysis included eight specimens of *T. nobiliana*, all collected from the western Atlantic. These specimens represent only the western part of the distribution of this species, which, at present, is considered to occur in both the western and eastern Atlantic Ocean and Mediterranean Sea. However, the western Atlantic form has been considered by some to represent the distinct species *T. occidentalis* (see Storer, 1843). It is unfortu-

nate that our analysis did not include specimens from the eastern Atlantic and thus did not allow comparison across this distribution. Until this issue can be investigated in more detail, we have used the name in common use for this species here. However, given that syntypes of *T. nobiliana* come from Italy, the name *T. occidentalis* may be more appropriate for the western Atlantic cluster if detailed study confirms the nonconspecificity of the western and eastern Atlantic Ocean forms. The range in pairwise differences among these eight specimens was 0–5, with an average of pairwise differences of 1.7.

*Torpedo macneilli* (Australian torpedo) and *Torpedo* cf. *nobiliana* (fig. 70)

The analysis included four specimens of the Australian endemic *T. macneilli* and a single specimen from South Africa initially identified as *T. nobiliana*. These specimens were found to group together well away from the specimens of *Torpedo nobiliana* collected from western Atlantic localities. The specimens of *T. macneilli* differed from one another by 0–2 bases, with an average of 1. This supports the work of Dave Ebert suggesting that the South African form, referred to here as *T. cf. nobiliana*, is not conspecific with its western Atlantic counterpart. The average of the pairwise differences between *T. macneilli* and *T. cf. nobiliana* was 5.5. The average of the pairwise differences between the South African specimens of *T. cf. nobiliana* and those of *T. nobiliana* from the western Atlantic was 27.6. The formal description of this species is currently underway (D. Ebert, personal commun.).

#### Narkidae (sleepers): genus *Typhlonarke*

*Typhlonarke aysoni* (blind legged torpedo) (fig. 70)

Two specimens of this New Zealand endemic were included in the analysis; both were vouchered (GN6758 = NMNZ P.041329 and GN6759 = NMNZ P.042187). They differed from one another by three bases. These specimens were found to comprise a cluster that grouped most closely with the *Torpedo* species.

#### Narcinidae (numbfishes)

*Narcine tasmaniensis* (Tasmanian numbfish) (fig. 70)

The four specimens of this Australian endemic included here all came from New

South Wales, Australia. The range of the pairwise differences among these specimens was 0–9, with an average of 4.5.

*Narcine lasti* (western numbfish) (fig. 70)

A single specimen of this western Australian species was included in the analysis. It is in the Australian National Fish Collection (GN4628 = ANFC H 6418-01). It grouped most closely with the specimens of *N. tasmaniensis*. The average of the pairwise differences between this specimen and those of the latter species was 83.8.

*Narcine entemedor* (Cortez electric ray) (fig. 70)

The analysis included a single specimen of this species, which was collected from the Gulf of California and thus represents the more northern part of the distribution of this species, which has been reported as far south as Peru. This specimen grouped with *Narke capensis* outside all the other species and genera of electric rays included in the analysis. The average of the pairwise differences between this species and *N. tasmaniensis* was 282 bases, and between *N. entemedor* and *N. lasti* is 281 bases.

#### **Narkidae (sleepers): genus *Narke***

*Narke capensis* (Cape sleeper ray) (fig. 70)

A single specimen of this southern African endemic was included. It grouped most closely with the specimen of *Narcine entemedor*. However, the specimens of these two species differed by 245 bases.

#### **Platyrrhinidae (thornbacks and fanrays)**

*Platyrrhinoidis triseriata* (thornback) (fig. 70)

Both of the specimens of this monotypic genus included in the analysis were collected from California, and thus are generally representative of the distribution of this species, which also includes the Gulf of California. The sequences of these two specimens were identical.

#### **Rajidae (skates)**

*Dipturus innominatus* (New Zealand smooth skate) (fig. 71)

In total, 11 specimens of this New Zealand endemic were included in the analysis. They were found to comprise a single cluster and

the range in pairwise differences among specimens in this cluster was 0–6, with an average of 2.2.

*Dipturus gudgeri* (bight skate) (fig. 71)

The differences between sequences of the three specimens of this Australian endemic that were included in the analysis ranged from 1–7, with an average of 4.7. These grouped most closely with the specimens of *D. innominatus*. The average of the pairwise differences between specimens of these two species was 29.2.

*Dipturus* sp. 4 (fig. 71)

The analysis included two skate specimens collected from the Philippines (GN4339 = BRU 096 and GN4353 = JPAG 091) that were treated by Compagno et al. (2005b) as *Dipturus* sp. 4. These specimens differed from one another by 13 bases. As noted by Compagno et al. (2005b) these specimens may represent an undescribed species in this genus.

*Dipturus healdi* (Heald's skate) complex (fig. 71)

Two specimens, both of which had provisionally been identified as *Dipturus healdi*, were included in the analysis. These specimens differed from one another by 56 bases. Two morphs referable to *D. healdi* were discussed by Last et al. (2008d), and a specimen of each morph was included in this analysis. The specimen of the northern morph (GN6788 = ANFC H 6574-20) is consistent with *D. healdi* and clusters well away from the southern morph (GN6789 = ANFC H 6419-04), which is provisionally referred to as *Dipturus* cf. *healdi*; these forms are indisputably separate species. *Dipturus healdi* clustered most closely with *Dipturus* sp. 4, with an average of the pairwise differences between these two taxa of 39.5.

*Dipturus tenuis* (acutenose skate) (fig. 71)

The analysis included one specimen identified as this species, collected from Taiwan. If this identification is correct, this specimen is representative of a central element of the distribution of this species, which is known to occur from Japan to the Philippines.

*Dipturus springeri* (roughbelly skate) (fig. 71)

The four specimens of this species, all collected from South Africa, were identical in sequence.

They represent the central southwestern elements of the distribution of this species, which occurs along the coast of Africa from Angola to Somalia as well as Madagascar.

*Dipturus australis* (Sydney skate) (fig. 71)

Six specimens of this species, which is endemic to eastern Australia, were included in the analysis. They formed a single cluster. The range of pairwise differences among these specimens was 0–2, with an average of 0.7.

*Dipturus cerva* (whitespotted skate) (fig. 71)

Three specimens of this South Australian endemic were included in the analysis. They were identical in sequence.

*Dipturus confusus* (longnose skate) (fig. 71)

Two specimens of this recently described (see Last, 2008) southeastern Australian endemic species were included here. They were identical in sequence and clustered most closely with the two specimens of *D. cerva*. The average of the pairwise differences among specimens of these two Australian endemic species was 18, and between this species and its other Australian congener, *D. australis*, was 30.3.

*Zearaja chilensis* (yellownose skate) (fig. 71)

The eight specimens of this species included here had a range of pairwise differences of 0–5, with an average of 2; they comprised a single cluster. These specimens all came from a single locality in Chile and thus represent the western part of the distribution of this species, which occurs throughout the coastal regions of southern South America and the Falkland Islands.

*Zearaja nasuta* (New Zealand rough skate) (fig. 71)

Five specimens of this New Zealand endemic were included in the analysis. These specimens had a range of pairwise differences of 1–5, with an average of 3.2. They comprised a cluster that grouped most closely with the specimens of *Z. chilensis*. The average of the pairwise differences between specimens of these two species was 10.3.

*Zearaja flavirostris* (Falklands skate) (fig. 71)

All three specimens identified as this species included in the analysis, were provid-

ed by Joost Pompert, of the Falkland Islands Fisheries Department, extending the range of this species from central Chile to the Falkland Islands. They comprised a single cluster, with a range of pairwise differences among specimens of 0–3 and an average of 2. They grouped most closely with the cluster consisting of *Z. chilensis* and *Z. nasuta*. The average of the pairwise differences between specimens of *Z. flavirostris* and those of *Z. chilensis* was 29.5, and those of *Z. nasuta* was 33.9. Given these differences, we have recognized *Z. flavirostris* as a species distinct from *Z. chilensis*, despite the suggestion that these two species may be synonyms (e.g., Last and Gledhill, 2007).

*Dipturus leptocauda* (thintail skate) (fig. 71)

Both specimens identified as this species were collected from the Falkland Islands, extending the range of this species from Brazil and Uruguay south to include the Falkland Islands. The sequences of these specimens were identical to one another.

*Dipturus batis* (gray skate) and *Dipturus oxyrinchus* (sharpnose skate) complex (fig. 71)

The analysis included a total of 12 specimens originally identified as *D. batis* and two identified as *D. oxyrinchus*. These specimens come from several localities in the eastern North Atlantic and were found to comprise a single group, exhibiting considerable internal structure. The largest cluster consisted of eight specimens from the eastern North Atlantic and three from the Azores. The range of pairwise differences among the 11 specimens in this cluster was 0–8, with an average of 4.3. However, there was evidence of structure within this cluster, with six of the specimens from the eastern North Atlantic (identified as *D. batis* by Bernard Séret) comprising a subcluster distinct from that consisting of the three specimens from the Azores identified locally as *D. batis* and two specimens from the eastern North Atlantic identified as *D. oxyrinchus*, also by Bernard Séret. The average of the pairwise differences among specimens in these two subclusters was 7.5. In order to call attention to this discrepancy, we have retained the original identifications of these specimens. This result suggests that the identity of specimens of *D.*

*batis* from the Azores needs to be investigated in more detail.

One specimen, also collected from the eastern North Atlantic, grouped outside this subcluster of 11 specimens. The average of the pairwise differences between this specimen and those in the *D. batis* and *D. oxyrinchus* subcluster was 23.7. This specimen has been given the designation *Dipturus* cf. *batis* 1. Finally, two specimens, both collected from Norway, grouped outside all 12 other specimens in the cluster overall; these two specimens were identical with one another in sequence. The average of the pairwise differences between these specimens and those in the *D. batis* and *D. oxyrinchus* subcluster was 16.7, and between *D. cf. batis* 1 was 37. These two specimens have been given the designation *Dipturus* cf. *batis* 2.

These results suggest that it is likely these specimens represent several distinct species, all of which bear a morphological resemblance to *Dipturus batis*. Recent published work by Iglésias et al. (2009) reveals that the *D. batis* complex likely consists of two species, both of which should be considered as valid, i.e., *D. cf. flossada* and *D. cf. intermedia*. Following these designations and morphological characters provided by Iglésias et al. (2009), the specimens with images in the second subcluster (GN5160, GN5165 and GN6546) are consistent with *D. cf. intermedia*. Thus, this second subcluster, which includes the two *D. oxyrinchus* specimens, may represent *D. cf. intermedia*. There is a possibility that one of the other subclusters represents *D. cf. flossada* and one represents *D. oxyrinchus*. Another species which Iglésias et al. (2009) reported as very close to these species is the Norwegian skate *D. nidarosiensis*, and it is possible the two specimens from Norway may represent that species. Additional specimens, with designated vouchers and confirmed identifications based on the work of Iglésias et al. (2009), are required to resolve this issue. The lack of specific locality data for our eastern North Atlantic specimens makes it difficult for us to compare our results with those of Griffiths et al. (2010), except to note that, like these authors, we found specimens identified as *D. oxyrinchus* to cluster among specimens identified as *D. batis*.

*Dipturus laevis* (barndoor skate) (fig. 71)

The three specimens of this unusually large skate included in the analysis all came from the western North Atlantic and are thus generally representative of the distribution of this species. One of these specimens is in the Harvard Museum of Comparative Zoology MCZ (GN2603 = MCZ 159202 and TCWC 11021.01). The range of the pairwise differences among these specimens was 0–1. These specimens grouped along with, but outside the 14 specimens in the *Dipturus batis* and *Dipturus oxyrinchus* complex.

*Dipturus pullopunctatus* (slime skate) (fig. 71)

Three specimens of this southern African endemic, all collected from South Africa, were included. These specimens were identical in sequence.

*Spiniraja whiteleyi* (Melbourne skate) (fig. 71)

Two specimens of this southern Australian endemic species were included in the analysis. These differed from one another by two bases and they grouped along with but outside the *Dipturus* and *Zearaja* species.

*Raja* sp. 1 (fig. 71)

A single specimen collected from Taiwan clustered independently from all specimens of *Dipturus*, *Zearaja*, *Spiniraja*, and *Raja*. It is possible that this specimen, for which an image is available, represents a known species, but we have been unable to assign a specific identification with confidence at this time; its generic designation also requires confirmation.

*Raja rhina* (longnose skate) (fig. 71)

This northeastern Pacific species was represented by 17 specimens; the analysis yielded a single cluster. The range of pairwise differences among the specimens in this cluster was 0–8, with an average of 1.3. Two of these specimens are deposited in the University of Washington Fish Collection (GN6712 = UW 47645 and GN6713 = UW 49457). This species grouped well away from the specimens of most of the other *Raja* species included in the analysis (see figs. 73, 75). This is consistent with McEachran and Dunn (1998) and Compagno (2005b), who listed this species, among others, as comprising a “North Pacific Assemblage” that may represent an undescribed genus.



*Raja binocularata* (big skate) (fig. 71)

The analysis included two specimens of this northeastern Pacific species. These specimens differed by six bases. This species, like *Raja rhina*, grouped well outside specimens of the other *Raja* species included in the analysis (see figs. 73, 75). This is consistent with McEachran and Dunn (1998) and Compagno (2005b) who listed these two species, among others, as comprising a “North Pacific Assemblage” that may represent an undescribed genus. The average of the pairwise differences between specimens of this species and those of *Raja rhina* was 111.2.

*Okamejei cairae* (Borneo sand skate) (fig. 72)

Thirteen specimens of this recently described species (see Last et al., 2010a) were included in the analysis. These were all collected from Sarawak in Malaysian Borneo, Pontianak in West Kalimantan (Indonesia), or Vietnam. The specimens from Vietnam extend the northern boundary of the distribution of this species. They comprised a single cluster and the range of pairwise differences among them was 0–4, with an average of 2.1. All nine specimens from Kalimantan were vouchered (GN4730 = ANFC H 7099-07, GN4731 through GN4735 = ANFC H 7099-01 through ANFC H 7099-05, GN4737 = ANFC H 7099-06, GN4729 = MZB 17176, and GN4736 = MZB 17177).

*Okamejei* cf. *porosa* (fig. 72)

Five specimens collected from Japan were included in the analysis. While the range of pairwise differences among these specimens was only 0–8 (with an average of 3.9) there was substantial morphological variation among these specimens (e.g., in color pattern, disc shape, etc.), based on images for four of the five specimens. These specimens, although they also resemble *Okamejei meerdervoortii*, are provisionally referred to here as *Okamejei* cf. *porosa* until their identities can be examined in more detail. These specimens grouped most closely with those of *Okamejei cairae*. However, the average of the pairwise differences between the two species was 96.

*Okamejei hollandi* (yellow-spotted skate) (fig. 72)

A total of 14 specimens, identified as *O. hollandi* by Last et al. (2010c), were included in the analysis. These specimens were all collected from Pontianak in West Kalimantan

(Indonesia); one was vouchered (GN4738 = ANFC H 7099-08). The range of pairwise differences among these 14 specimens was 0–13, with an average of six bases. The average of their pairwise differences relative to specimens of *Okamejei cairae* was 106.9; the average of their pairwise differences relative to specimens of *Okamejei* cf. *porosa* was 107.6.

*Raja miraletus* (brown skate) complex (fig. 73)

In total, 23 specimens that were generally consistent with the color pattern of *R. miraletus* (i.e., in their possession of small dark spots and a pair of distinctive ocelli on their discs) were included. These consisted of 17 specimens from Senegal and six from South Africa. The analysis yielded three distinct clusters. Two of these clusters consisted of specimens from Senegal and the third of specimens from South Africa. The average of the pairwise differences between specimens in the two Senegal clusters was 99.3. Morphologically, specimens of these two clusters differed most conspicuously in coloration; in one form the small dark disc spots were interspersed with numerous white spots, whereas specimens of the other form exhibited few, if any, small white spots. Specimens of the first Senegal cluster exhibiting the latter color pattern were designated *R. miraletus*. The more heavily spotted specimens comprising the second cluster of specimens from Senegal were given the designation *Raja* cf. *miraletus* 2. The range of pairwise differences among specimens in the *R. miraletus* cluster was 0–7 (with an average of 2) and among specimens in the *R. cf. miraletus* 2 cluster was 1–4 (with an average of 2.4).

The cluster of specimens from South Africa had a range of pairwise differences of 0–2 (with an average of 1.2). They most closely resembled *R. cf. miraletus* 2 in color pattern. However, they clustered more closely with the specimens of *R. miraletus*. These specimens have been given the designation *Raja* cf. *miraletus* 1 until such time as the taxonomy of this complex can be examined in more detail. The average of the pairwise differences between *R. cf. miraletus* 1 and *R. cf. miraletus* 2 was 85.2 and between *R. cf. miraletus* 1 and *R. miraletus* was 49.1. Our results suggest that the differences seen among these three forms may reflect the existence of several distinct

species in these regions as was observed by McEachran et al. (1989). However, it is important to note that several known species from one or more of these regions (e.g., *R. herwigi* and *R. ocellifera*) were not included in the analysis.

*Raja clavata* (thornback skate) (fig. 73)

Eight of the specimens of this species were collected from the eastern North Atlantic and the Azores; the ninth specimen came from the Black Sea. The range in pairwise differences among all nine specimens was 0–11, with an average of 6.1. The analysis yielded some evidence of a subcluster comprised of the specimens from the Azores, and the other comprised of the specimens from the eastern North Atlantic and Black Sea. The average of the pairwise differences among specimens in these two subclusters was 9.5. The range within the Azores subcluster was 0–3, and within the North Atlantic subcluster 1–3. These results parallel the situation in the *D. batis* complex, which provides evidence that the fauna of the Azores may differ somewhat from that of their mainland counterparts. This result is consistent with that of Chevolut et al. (2006) who found regional differentiation between specimens from the European continental shelf and the Azores.

*Raja straeleni* (biscuit skate) (fig. 73)

The nine specimens of this species, which occurs throughout much of the western coast of Africa, were all collected off South Africa. The range in pairwise differences among specimens of this species was 0–3, with an average of 1.6. This species grouped most closely with *Raja clavata*. The average of the pairwise differences between these two species was 23.1.

*Raja asterias* (Atlantic starry skate) (fig. 73)

The analysis included three specimens of this species, all collected from Spain and generally representative of the eastern elements of this primarily Mediterranean-dwelling species. The range of pairwise differences among specimens was 1–4, with an average of 2.7. The analysis yielded a single cluster, which grouped most closely with that consisting of *R. clavata* and *R. straeleni*. The average of the pairwise differences between *R. asterias* and *R. clavata* was 62.1, and between *R. asterias* and *R. straeleni* was 66.1.

*Raja montagui* (spotted skate) (fig. 73)

A single specimen of this species was included here. This specimen was collected from the coast of England and thus represents a northerly element of the distribution of this species, which extends throughout the Mediterranean Sea and northern coast of Africa. It grouped most closely with but outside the *Raja clavata*, *Raja straeleni*, and *Raja asterias* specimens. The average of the pairwise differences between this specimen and those of *R. clavata* was 66.1, between this specimen and those of *R. straeleni* 70.3, and between this specimen and those of *R. asterias* 78.3.

*Rajella fyllae* (round skate) (fig. 74)

The analysis included 18 specimens from the eastern North Atlantic (identified by Bernard Séret) and three from Norway. These were found to comprise a single cluster and the range of pairwise differences among these 21 specimens was 0–6, with an average of pairwise differences of 1.7. These specimens represent the more eastern parts of the distribution of this species, which occurs throughout the entire North Atlantic.

*Rajella* sp. (fig. 74)

Two specimens from the Harvard Museum of Comparative Zoology (GN4664 = MCZ 167899 and GN4665 = MCZ 167900), both collected on the continental shelf off New England, were included. These two specimens were identical in sequence. They grouped most closely with the two specimens of *Rajella caudospinosa*; these two species were, in turn, most closely allied with *Rajella fyllae*. The average of the pairwise differences between *Rajella* sp. and *R. caudospinosa* was 33, and between the specimens of *Rajella* sp. and those of *R. fyllae* 33.3. We believe these specimens represent a western Atlantic relative of *R. caudospinosa*.

*Rajella caudospinosa* (munchkin skate) (fig. 74)

Two specimens of this southern African endemic, all collected from South Africa, were included. These specimens were identical in sequence. They clustered most closely with *Rajella* sp. As noted above, the average of the pairwise differences between these two species was 33.

*Rajella leopardus* (leopard skate) (fig. 74)

Five specimens of this southern African endemic, all collected from South Africa, were included in the analysis. The range

in pairwise differences among specimens in this cluster was 0–3, with an average of 1.2.

*Rajella kukujevi* (mid-Atlantic skate) (fig. 74)

The four specimens of this species included in the analysis, all collected from the North Atlantic, comprised a single cluster. The range of pairwise differences among these specimens was 0–3, with an average of 1.5. These specimens grouped most closely with those of *Rajella leopardus*. The average of the pairwise differences between these two species was 49.

*Dipturus linteus* (sailskate) (fig. 74)

A total of five specimens identified as this species, all collected from the eastern North Atlantic and off Norway, and thus representing the eastern portions of the distribution of this species, were included in the analysis. The range in pairwise differences among these specimens was 0–1. They comprised a single cluster, which grouped most closely with the clusters of the three *Rajella* species. This *Dipturus* species clustered well away from all 15 of its congeners included in the analysis (see fig. 69), lending support to Compagno (2005b) who listed this species as “*Dipturus? linteus*” and noted that its generic placement needs investigating.

*Amblyraja radiata* (thorny skate) (fig. 74)

In total, the analysis included 14 specimens identified as this species, one of which is in the Harvard Museum of Comparative Zoology (GN2602 = MCZ 159184). These were found to comprise a single cluster. Although there was evidence of structure within this cluster, and the range of pairwise differences among the members of this cluster was 0–15, with an average of 8.5, there was no obvious pattern to this variation; all specimens within this cluster have thus been given the same designation. These specimens represent the more eastern part of the distribution of this species, which occurs throughout the North Atlantic.

*Amblyraja hyperborea* (Arctic skate), *Amblyraja jenseni* (Jensen’s skate), *Amblyraja badia* (broad skate), and *Amblyraja* sp. complex (fig. 74)

The analysis yielded a somewhat confusing cluster of nine specimens, five of which are deposited in museums. This cluster consists of four specimens from the Barents Sea identified as *A. hyperborea* by Age Hoines, one specimen from California identified as *A. badia* deposited at the University of Washington (GN6681

= UW 115021), one specimen from the mid-Atlantic identified as *A. jenseni* by Chip Cotton, and deposited at Virginia Institute of Marine Sciences (GN5040 = VIMS 11757), as well as two specimens deposited at the Harvard Museum of Comparative Zoology (MCZ GN4666 = MCZ 167944 and GN4667 = MCZ 167945), both identified only as *Amblyraja* sp., and a specimen from the Tasman Sea, identified as *Amblyraja hyperborea*, from the Australian National Fish Collection (GN4650 = ANFC H 5944-01). These specimens differ somewhat in morphology. The range of pairwise differences among the nine specimens comprising this cluster was 0–11, with an average of 5.7. As none of the specimens comprising this cluster have been definitively identified, we have retained the original identifications as they serve to draw attention to the uncertainty associated with the identity of the members of this cluster.

*Amblyraja doellojuradoi* (southern thorny skate) (fig. 74)

Three specimens of this species, all collected from the Falkland Islands, were included in the analysis. They represent the more eastern parts of the distribution of this species, which occurs throughout the southern regions of South America. The range of pairwise differences among specimens was 4–8, with an average of 5.3. These specimens grouped most closely with the *A. hyperborea*, etc., cluster. The average of the pairwise differences between the specimens of these two clusters was 18.7.

*Leucoraja naevus* (cuckoo skate) (fig. 75)

In total, 29 specimens of this species were included in the analysis. These were all collected from localities in the eastern North Atlantic and thus represent the northern portions of the distribution of this species, which has been reported from as far south as Senegal. The range of pairwise differences among the specimens in this species was 0–6, with an average of pairwise differences of 1.5.

*Leucoraja wallacei* (yellowspot skate) (fig. 75)

The 12 specimens of this southern African species, all collected from South Africa, were found to comprise a single cluster. The range in pairwise differences among specimens was 0–8, with an average of 3.7. This species grouped most closely with the eastern

North Atlantic species *Leucoraja naevus*; the average of the pairwise differences between these two species was 37.5.

*Leucoraja fullonica* (shagreen skate) (fig. 75)

The analysis included two specimens collected from the Azores and two from the eastern North Atlantic. These specimens thus represent some of the southern and western elements of this species, which occurs as far eastward as Murmansk, Russia. The range in pairwise differences among these specimens was 0–3, with an average of 2. The analysis yielded a single cluster, which grouped most closely with the cluster consisting of *L. naevus* and *L. wallacei*. The average of the pairwise differences among specimens of *L. fullonica* and *L. naevus* was 72.4, and *L. wallacei* was 65.4.

*Leucoraja erinacea* (little skate) (fig. 75)

In total, four specimens of this western Atlantic species were included in the analysis, which yielded a single cluster with a range of pairwise differences among specimens of 3–8 and an average of pairwise differences of 5.3. One of these specimens is in the University of Kansas Ichthyology Collection (GN2505 = KUI 26967).

*Leucoraja ocellata* (winter skate) (fig. 75)

The two specimens of this western Atlantic species included differed by two bases. They grouped most closely with the specimens of *L. erinacea*; the average of the pairwise differences between specimens of these two species was 45.5.

*Leucoraja garmani* (rosette skate) (fig. 75)

The single specimen of this species, collected from the western North Atlantic, represents a more northern element of the distribution of this species, which occurs as far south as Venezuela. It grouped outside all four other species of this genus included here. The averages of the pairwise differences between this specimen and its congeners were: *L. naevus* 130.3, *L. wallacei* 130.9, *L. fullonica* 132.5, *L. erinacea* 142.8, and *L. ocellata* 143.

*Rostroraja alba* (white skate) (fig. 75)

A total of six specimens of this species was included in the analysis. These specimens were all collected from South Africa and thus represent only a central element of the distribution of this species, which has been reported

from Great Britain, the Mediterranean Sea, much of the coast of Africa, and the Red Sea. These specimens were identical in sequence. This species grouped most closely with the specimens identified as *Raja velezi*. The average of the pairwise differences between *Ro. alba* and *Ra. velezi* was 86. This grouping is generally consistent with the affinities reported by McEachran and Dunn (1998) and Compagno (2005b) who listed these species, among others, as comprising an “Amphi-American Assemblage.” However, these results suggest that some consideration should be given to *Rostroraja* as the generic name to apply to the species comprising this entire assemblage.

*Raja velezi* (rasptail skate) (fig. 75)

All three specimens of this species were identical in sequence. All three were collected from the Gulf of California and thus represent a northern distribution of this species, which has been reported from as far south as Peru. These specimens grouped most closely with those of *Ro. alba*.

*Raja eglanteria* (clearnose skate) (fig. 75)

Four specimens, identified as *R. eglanteria*, collected from the western North Atlantic and the Gulf of Mexico off Florida, were included in the analysis. These represent much of the distribution of this species, which occurs from Massachusetts to Florida. The range in pairwise differences among specimens was 0–12, with an average of 8.2. This species grouped with *Ra. velezi* and *Rostroraja alba*, well outside specimens of the other *Raja* species included in the analysis (see figs. 71, 73), which is consistent with McEachran and Dunn (1998) and Compagno (2005b) who listed *Ra. eglanteria* and *Ra. velezi*, among other species, as comprising an “Amphi-American Assemblage” that may represent an undescribed genus.

*Okamejei jensenae* (Philippine ocellate skate) (fig. 75)

The analysis included two specimens of the recently described *Okamejei jensenae* (see Last and Lim, 2010) from the Philippines, which were treated by Compagno et al. (2005b) (GN4343 = BRU 171 and GN4382 = JPAG 328) as *Okamejei* sp. 1. These differed from one another by one base. It is of note that this species grouped most closely

with specimens in the *R. eglanteria* and *R. velezi* clusters, well away from its congeners (see fig. 70). The generic placement of this species requires additional taxonomic investigation when adult males of this species are collected as clasper cartilages are needed to assign this taxon to a genus.

*Malacoraja senta* (smooth skate) (fig. 75)

All three specimens of this species were found to be identical in sequence. These specimens were collected from the western North Atlantic and are largely representative of the distribution of this species, which occurs from Newfoundland to New Jersey.

*Neoraja caerulea* (blue pygmy skate) (fig. 75)

Two specimens of this eastern North Atlantic endemic were included in the analysis; they were identical in sequence. They clustered most closely with the specimens of *M. senta* and the average of the pairwise differences among specimens of these two species was 80.

#### Arhynchobatidae (softnose skates)

*Bathyrāja* spp. (includes *Bathyrāja* sp., *B. interrupta*, *B. kincaidi*, *B. kincaidilinterrupta*, *B. mariposa*, *B. taranetzi*, *B. violacea*) (fig. 76)

The analysis yielded a cluster comprised of 19 specimens whose identities are uncertain. The range of pairwise differences among these specimens was 0–24, with an average of pairwise differences of 7.6. These specimens were collected from a diversity of localities in the eastern North Pacific Ocean, including the Gulf of Alaska, Bering Sea, and Strait of Juan de Fuca. Their specific designations, assigned by their original collectors, varied wildly and include *Bathyrāja* sp., *B. interrupta*, *B. kincaidi*, *B. kincaidilinterrupta*, *B. mariposa*, *B. taranetzi*, and *B. violacea*. The original field identifications have been retained for all specimens, regardless of current thoughts on generic placements and specific synonymies, because their identities of these specimens could not be confirmed. This draws attention to the need for voucher specimens and/or images to confirm species designations and problems created when they are unavailable. It should be noted that only three of these samples come from museum specimens (i.e., *B. interrupta* GN6689 = UW 111883, *B. violacea* GN6707 = UW 48757, and *B.*

*mariposa* GN6694 = UW 47201). In addition, as indicated in figure 76, at least some images are available for another eight specimens. We suspect that the mixed nature of this cluster may reflect either extensive hybridization among closely related forms with different color patterns or complex polymorphism that has hindered accurate identification in the field.

*Bathyrāja minispinosa* (smallthorn skate) (fig. 76)

The three specimens of this North Pacific species included here were collected from the eastern North Pacific. All three are deposited at the University of Washington (i.e., GN6696 = UW 47049, GN6697 = UW 117948, GN6698 = UW 117950). The range of pairwise differences among the specimens comprising this cluster was 0–4, with an average of 2.7. These grouped most closely with the specimens comprising the *Bathyrāja* spp. cluster; the average of the pairwise differences between specimens of *B. minispinosa* and those in the *Bathyrāja* spp. cluster was 24.1.

*Bathyrāja pallida* (pallid skate) (fig. 76)

Four samples from skates identified by their collectors as *B. pallida* were included in the analysis. Two of these specimens are deposited in museums (GN4668 = MCZ 167975 and GN5039 = VIMS 11758). The analysis yielded a single cluster comprised of these four specimens, however, the range of pairwise differences among these specimens was 4–21, with an average of 17.3. We note, however, that while *B. pallida* is known only from the Bay of Biscay, the specimens included here come from a diversity of localities that include the western Atlantic off New England, the mid-Atlantic, and the Barents Sea. Further investigation of the identity of skates from these regions is required.

*Bathyrāja shuntovi* (narrownose skate) (fig. 76)

A single specimen of this New Zealand endemic was included in the analysis. This specimen clustered most closely with those of *Bathyrāja pallida*. The average of the pairwise differences between those comprising the latter cluster and the specimen of *B. shuntovi* was 30.5.

*Bathyrāja trachura* (rougtail skate) (fig. 76)

The specimen of this eastern North Pacific endemic included in the analysis was collected from the Gulf of Alaska.

*Bathyraja aleutica* (Aleutian skate) (fig. 76)

This cluster consisted of a specimen from the Gulf of Alaska and one from the Bering Sea; they differed from one another by 10 bases. The identity of these specimens was confirmed by D. Ebert (personal commun.) following examination of the images of GN5722.

*Rhinoraja macloviana* (Patagonian skate) (fig. 76)

Three specimens of this southeastern South American endemic skate, all from the Falkland Islands, were included in the analysis. The range of pairwise differences among the specimens in this cluster was 0–1.

*Rhinoraja albomaculata* (whitedotted skate) (fig. 76)

Three specimens of this southern South American endemic species, all collected from the Falkland Islands, were included here. The range of pairwise differences among these specimens was 1–4, with an average of 2.7; they clustered most closely with specimens of *R. macloviana*, with an average pairwise difference among specimens of 9.7. We note that this was one of several species of *Rhinoraja* that grouped among the clusters of species of *Bathyraja*.

*Bathyraja brachyurops* (broadnose skate) (fig. 76)

The four specimens of this species included in the analysis were found to comprise a single cluster with a range of pairwise differences among specimens of 0–10, and an average of pairwise differences of 7. All four of these specimens came from the Falkland Islands and thus represent a southeastern part of the distribution of this species, which is known from Chile to northern Argentina.

*Rhinoraja magellanica* (Magellan skate) (fig. 76)

A single specimen of this species, collected from the Falkland Islands, was included. This southern South American endemic clustered along with but outside the specimens of *B. brachyurops*, *R. macloviana*, and *R. albomaculata*.

*Bathyraja* sp. 1 (fig. 76)

Three unidentified *Bathyraja* specimens from the Falkland Islands clustered together. The range of pairwise differences among specimens in this cluster was 0–5, with an average of 3.3.

*Bathyraja griseocauda* (graytail skate) (fig. 76)

The analysis included two specimens, both from the Falkland Islands, of this southern South American and Antarctic endemic. These specimens differed from one another by a single base. They grouped most closely with the specimens of *Bathyraja* sp. 1. The average of the pairwise differences between specimens of what we believe are two distinct species was 22.2.

*Bathyraja scaphiops* (cuphead skate) (fig. 76)

The analysis included two specimens of this southwestern Atlantic endemic. These specimens differed from one another by two bases.

*Bathyraja* cf. *taranetzi* (fig. 76)

The analysis included a single specimen collected from the Bering Sea that was originally identified as *B. taranetzi*, a species currently known only from the Kuril Islands in the western North Pacific. This specimen grouped most closely with the *Bathyraja scaphiops* cluster; the average of the pairwise differences between these two species was 42. Several other specimens also identified by their collectors as *B. taranetzi* clustered elsewhere in the analysis (see above). Thus, we have given this specimen the tentative designation of *B. cf. taranetzi*. The grouping of this specimen among *Bathyraja* species is noteworthy in the context of the generic distinctions between *Rhinoraja* and *Bathyraja*.

*Rhinoraja multispinis* (multispine skate) (fig. 76)

Three specimens of this South American endemic species, all collected from the Falkland Islands, were included in the analysis. All three specimens had identical sequences.

*Bathyraja parmifera* (Alaska skate) (fig. 76)

Eight specimens tentatively identified as *B. parmifera*, two of which are deposited at the University of Washington (GN6699 = UW 111889 and GN6721 = UW 117306), were included in the analysis. These specimens were all collected from localities in the eastern North Pacific Ocean, including the Bering Sea, and are generally representative of the distribution of this species. The range of pairwise differences among these specimens was 0–12, with an average of 3. The upper end of this range was accounted for by the second specimen in the UW collection. Given that

some of the specimens in this cluster were originally identified as *B. aleutica*, and none of the specimens in this cluster have been firmly established to represent *B. parmifera*, the identity of this cluster remains to be confirmed. Our results are consistent with those of Spies et al. (2011) and suggest that this species should be recognized as a member of the generic group level taxon *Arctoraja*.

*Bathyraja smirnovi* (golden skate) (fig. 76)

A single specimen of this western North Pacific Ocean species was included. It clustered most closely with the specimens of *B. parmifera*. The average of the pairwise differences between specimens of these two species was 17.5. Our results are consistent with those of Spies et al. (2011) and suggest that this species should also be recognized as a member of the generic group level taxon *Arctoraja*.

*Bathyraja bergi* (bottom skate) (fig. 76)

A single specimen of this western North Pacific species was included in the analysis. It clustered along with but outside those of *B. parmifera* and *B. smirnovi*; the averages of the pairwise differences between this species and the specimens comprising the clusters of each of the latter two species were 45.5 and 40, respectively. Our analysis suggests that it would also be interesting to explore the generic placement of this species relative to *Arctoraja* species.

*Bathyraja maculata* (whiteblotched skate) (fig. 76)

The analysis included four specimens of this Bering Sea endemic. The range of pairwise differences among these specimens was 1–5, with an average of 3.8.

*Brochiraja asperula* (prickly deepsea skate) complex (fig. 77)

The analysis yielded a group that included two clusters, one of which was comprised of 19 specimens of the New Zealand endemic, *Brochiraja asperula*; 13 of these came from the Museum of New Zealand, Te Papa Tongarewa (GN6803 = NMNZ P.040505, GN6804 = NMNZ P.040506, GN6809 = NMNZ P.040512, GN6811 = NMNZ P.040514, GN6812 = NMNZ P.040515, GN6820 = NMNZ P.041493, GN6818 = NMNZ P.041491, GN6795 = NMNZ P.040465, GN6798 = NMNZ P.040467,

GN6801 = NMNZ P.040469, GN6802 = NMNZ P.040470, GN6821 = NMNZ P.041494, and GN6817 = NMNZ P.041490). These specimens were collected from a diversity of localities throughout the waters of New Zealand, including the Chatham Islands, Chatham Rise, Campbell Plateau, and the South Island. The range of pairwise differences among the 19 specimens in this cluster was 0–2, with an average of 0.3. However, the analysis yielded a second smaller cluster in this group comprised of two specimens also in the National Museum of New Zealand, Te Papa Tongarewa (GN6807 = NMNZ P.040510 and GN6808 = NMNZ P.040511), collected off Westland on New Zealand's South Island. The sequences of these two specimens differed from one another by a single base and were somewhat divergent relative to those comprising the specimens of the first cluster. The average of the pairwise differences between specimens of these two clusters was 27.7. The specimens in the smaller cluster have been referred to as *Brochiraja* cf. *asperula*.

*Brochiraja spinifera* (spiny deepsea skate) (fig. 77)

Sixteen specimens of this New Zealand endemic, all collected from localities in and around New Zealand (e.g., North Island, South Island, Stewart Island, Campbell Island, Auckland Islands, Chatham Rise), were found to comprise essentially a single cluster. A total of 12 of these are from the Museum of New Zealand, Te Papa Tongarewa (GN6794 = NMNZ P.040464, GN6826 = NMNZ P.041752, GN6822 = NMNZ P.041748, GN6827 = NMNZ P.041753, GN6805 = NMNZ P.040508, GN6836 = NMNZ P.045193, GN6806 = NMNZ P.040509, GN6810 = NMNZ P.040513, GN6823 = NMNZ P.041749, GN6824 = NMNZ P.041750, GN6797 = NMNZ P.040466, and GN6828 = NMNZ P.041754). The range of pairwise differences among the 16 specimens in this cluster was 0–13, with an average of 6.1. While there was some evidence of substructure within this cluster, this remains to be explored in more detail. These specimens have all been referred to here as *B. spinifera*, but this identity needs to be confirmed. This cluster grouped most closely with the specimens of *B. asperula* and *B.* cf. *asperula*. The average of the pairwise differences between specimens of *B.*

*spinifera* and those of *B. asperula* was 25.3, and those of *B. cf. asperula* 31.1.

*Brochiraja leveneta* (smooth blue skate) (fig. 77)

Three specimens of this recently described New Zealand endemic (see Last and McEachran, 2006) were included in the analysis. All three specimens are deposited in the Museum of New Zealand, Te Papa Tongarewa (GN6835 = NMNZ P.045192, GN6815 = NMNZ P.040676, and GN6830 = NMNZ P.041985). The range of pairwise differences among these three specimens was 4–12, with an average of 9.3.

*Brochiraja albilabiata* (whitelipped skate) (fig. 77)

This relatively newly described New Zealand endemic (see Last and McEachran, 2006) was represented by a single specimen from the Museum of New Zealand, Te Papa Tongarewa (GN6833 = NMNZ P.042691). This specimen grouped most closely with the specimens of *B. leveneta*. The average of the pairwise differences between specimens of these two species was 28.7.

*Insentiraja subtilispinosa* (velvet skate) (fig. 77)

A specimen of this species from the Australian National Fish Collection (GN4629 = ANFC H 6417-03), collected from Western Australia, was included in the analysis. This specimen clustered outside those of the *Brochiraja* species. The generic placement of this species follows Last and Stevens (2009).

*Notoraja azurea* (blue skate) (fig. 77)

A paratype (GN4631 = ANFC H 6409-02) of this recently described Tasmanian endemic (see McEachran and Last, 2008) was included in the analysis. This specimen clustered with the specimen of *Insentiraja subtilispinosa*, but the sequences of these two species differed by 34 bases.

*Brochiraja microspinifera* (small prickly skate) (fig. 77)

The single specimen of this relatively recently described New Zealand endemic (see Last and McEachran, 2006) was included in the analysis. This specimen is in the Museum of New Zealand, Te Papa Tongarewa (GN6816 = NMNZ P.041321). It was found to belong to a cluster consisting of the other *Brochiraja* species, but also of the

specimens of *Insentiraja subtilispinosa* and *Notoraja azurea*.

*Pavoraja nitida* (peacock skate) (fig. 77)

The analysis included three specimens of this Australian endemic species. These specimens differed from one another by 0–4 bases, with an average of pairwise differences of 2.7.

*Pavoraja alleni* (Allens skate) (fig. 77)

This Australian endemic was represented by a single specimen from the Australian National Fish Collection (GN4632 = ANFC H 6419-03). This specimen clustered with those of its congener, *P. nitida*. The average of the pairwise differences between specimens of these two species was 53.7.

*Irolita waitii* (southern round skate) (fig. 77)

The analysis included a single specimen of this southwestern Australian endemic species (GN4630 = ANFC H 6350-01). This sample clustered along with, but outside all of the specimens representing species of *Brochiraja*, *Insentiraja*, *Notoraja*, and *Pavoraja*.

*Psammobatis* sp. (fig. 77)

In total, 10 specimens of an as yet unidentified species of *Psammobatis*, all collected from the Falkland Islands, were included in the analysis. They were found to comprise a single cluster and the range of pairwise differences among these specimens was 0–6, with an average of 2.2. It is likely this represents one of the seven *Psammobatis* species occurring in the western South Atlantic.

*Sympterygia bonapartii* (smallnose fanskate) (fig. 77)

Two specimens of this southern South American endemic were included in the analysis. Both specimens came from Argentina and were identical in sequence.

*Arhynchobatis asperrimus* (longtailed skate) (fig. 77)

One specimen of this New Zealand endemic was included in the analysis. This specimen is in the Museum of New Zealand, Te Papa Tongarewa (GN6831 = NMNZ P.042403). It grouped most closely with the specimens of *S. bonapartii* and the average of the pairwise differences between specimens of these two species was 130.



*Sympterygia acuta* (bignose fanskate) (fig. 77)

The two specimens of this southeastern South American species included in the analysis were both collected from Argentina, and are deposited in the Instituto Nacional de Investigación y Desarrollo Pesquero (GN4726 = INIDEP T 0405 and GN4727 = INIDEP T 0407). These differed from one another by six bases. They grouped most closely with but outside the specimens of *S. bonapartii* and *A. asperrimus*, which suggests that the distinctions between *Sympterygia* and the currently monotypic *Arhynchobatis* needs to be explored in more detail. The average of the pairwise differences between *S. acuta* and *S. bonapartii* was 129.5; the average of the pairwise differences between *S. acuta* and *A. asperrimus* was 137.

*Atlantoraja cyclophora* (eyespot skate) (fig. 77)

Three specimens of this species, which is known from Argentina and Brazil, were included in the analysis. These were all collected from Argentina and are deposited in the Instituto Nacional de Investigación y Desarrollo Pesquero (GN4717 = INIDEP T 0469, GN4718 = INIDEP T 0471, and GN4719 = INIDEP T 0474). They were found to comprise a single cluster; the range of pairwise differences among these specimens was 1–4, with an average of 2.7.

*Atlantoraja platana* (La Plata skate) (fig. 77)

The analysis included two specimens of this southwestern Atlantic species, both collected from Argentina and both from the Instituto Nacional de Investigación y Desarrollo Pesquero (GN4721 = INIDEP T 0425 and GN4722 = INIDEP T 0426). They differed from one another by one base. They grouped most closely with the specimens of *A. cyclophora* and the average of the pairwise differences between these two species was 38.8.

*Atlantoraja castelnaui* (spotback skate) (fig. 77)

The analysis included a single specimen of this southeastern South American species (GN4720 = INIDEP T 0406). It clustered along with but outside the specimens of its two congeners. The average of the pairwise differences between *A. castelnaui* and *A. cyclophora* was 90, and the average of the pairwise differences between *A. castelnaui* and *A. platana* was 89.5.

*Rioraja agassizii* (Rio skate) (fig. 77)

This monotypic genus was represented by two specimens in the analysis, both collected from Argentina and deposited in the Instituto Nacional de Investigación y Desarrollo Pesquero (GN4724 = INIDEP T 0404 and GN4725 = INIDEP T 0408). These specimens thus represent a central element of the distribution of this species, which has been reported from throughout much of the eastern coast of South America. These specimens differed from one another by 10 bases and they grouped most closely with the three species of *Atlantoraja*.

### Anacanthobatidae (Legskates)

*Cruiriraja hulleyi* (roughnose legskate) (fig. 77)

Ten specimens of this southern African endemic, all collected from South Africa, were included in the analysis. The range in pairwise differences among specimens in this cluster was 0–8, with an average of 1.9.

*Sinobatis bulbicauda* (western legskate) (fig. 77)

Both specimens of this newly described skate (see Last and Séret, 2008) included here were collected from localities in Western Australia. One was a paratype (GN6775 = ANFC H 6417-04), the other a voucher (GN6776 = ANFC H 6578-02). These differed from one another by a single base.

## DISCUSSION

The foregoing results give a first approximation of intraspecific and intrageneric differentiation seen across a broad spectrum of elasmobranchs. When these data are combined with other sources of information (morphological, distributional, ecological, and tagging data) they can enrich our understanding of species ranges, life histories, gene flow, and the incidence of philopatry, and thereby give us a better sense of the operational evolutionary units that characterize extant diversity. There are, for example, species such as *Rhincodon typus* that appear genetically homogeneous for NADH2 across their entire range (see fig. 37), while others, like *Carcharodon carcharias*, appear distinct in different parts of their range (see fig. 37). We might hypothesize that those that are genetically homogeneous are likely to exhibit more movement and gene flow across their range than those with regionally distinct

populations. Tagging data can be invaluable to test such hypotheses.

#### INTRASPECIFIC P-DISTANCES (AVERAGE OF % PAIRWISE DIFFERENCES)

The average of the intraspecific p-distances for the 468 species for which replicate specimens were included was  $0.27\% \pm 0.28\%$ ; the range was  $0\%–2.12\%$  (table 2). The distribution of mean % p-distances for these 468 species is illustrated in fig. 78. In terms of base pairs, on average, specimens of a species differed by  $2.86 \pm 2.93$  (0–22) base pairs. For comparative purposes, the overall average of the intraspecific K2P distance for 468 taxa, as calculated in BOLD, was  $0.27\% \pm 0.001\%$ ; with a range of  $0\%–3.14\%$  (table 5).

Of the 468 species for which greater than a single specimen was included in the analysis, replicate specimens of 60 species were identical in sequence (i.e., there was no intraspecific variation). Although 25 of these 60 species were represented by only two specimens and 19 by only three specimens, 16 were represented by four to 12 specimens. Those with 10 or more specimens were the western Australian endemic *Orectolobus hutchinsi* (10 specimens), as well as *Dasyatis margarita* (11 specimens) and *Squatina oculata* (12 specimens), the latter two represented by specimens from the eastern Atlantic elements of their distributions.

The mean p-distances calculated as the average of all pairwise comparisons among specimens within each recognized species (appendix 1) allow us to make the following observations. The most variable species (i.e., those with average p-distances of  $>1\%$ ) were *Brachaelurus colcloughi* (mean p =  $1.01\%$ ), *Isurus oxyrinchus* (mean p =  $1.02\%$ ), *Aetobatus flagellum* (p =  $1.05\%$ ), *Hexanchus nakamurai* (mean p =  $1.10\%$ ), *Carcharhinus albimarginatus* (mean p =  $1.15\%$ ), *Dipturus* sp. 4 (p =  $1.25\%$ ), *Scyliorhinus retifer* (mean p =  $1.41\%$ ), *Dasyatis sabina* (p =  $1.44\%$ ), *Bathyraja pallida* (mean p =  $1.66\%$ ), *Dasyatis americana* (mean p =  $2.08\%$ ), and *Torpedo sinuspersici* (p =  $2.12\%$ ). This result does not appear to be tied to the number of specimens examined because all but one of these species were represented by only 2–5 specimens. *Isurus oxyrinchus* was the exception in that 24 specimens were included in the analysis. In

some cases the relatively substantial divergence seen among specimens may be attributable to geographic variation. For example, the three specimens of *H. nakamurai* came from Australia, Madagascar, and India; the 24 specimens of *I. oxyrinchus* came from the Atlantic, Pacific, and Indian Ocean basins; one specimen of *A. flagellum* came from Borneo, the other from India; the three specimens of *S. retifer* were collected from mid-Atlantic bight, the northwestern Atlantic and the Gulf of Mexico; the four specimens of *B. pallida* were collected from the Barents Sea, mid-Atlantic, and the western Atlantic off New England. However, in the cases of other species, the replicate specimens were collected from locations of relatively close proximity, and thus an alternate explanation for the divergence seen may need to be invoked. For example, all four specimens of *B. colcloughi* came from Queensland, both specimens of *Dipturus* sp. 4 were collected in the Philippines, both specimens of *D. sabina* came from the Gulf of Mexico, as did all three specimens of *D. americana*; both specimens of *T. sinuspersici* were collected in the Persian Gulf, and the five specimens of *C. albimarginatus* came from Taiwan and the Philippines. It is of further note that in the majority of these cases, the relatively substantial divergence seen among specimens of a species was the result of a single divergent specimen.

#### INTRAGENERIC P-DISTANCES (AVERAGE OF % PAIRWISE DIFFERENCES)

The average of the intrageneric (i.e., interspecific) p-distances for the 85 (of 157 included) genera represented by two or more species in the analysis was  $10.16\% \pm 4.89\%$ , the range was  $0.03\%–27.01\%$  (table 2). The distribution of mean % p-distances for these 85 genera is illustrated in fig. 78. In terms of base pairs, on average, congeners differed from one another by  $106.05 \pm 51.05$  (0.3–282) base pairs. For comparative purposes, the overall average of the congeneric p-distances calculated using BOLD for 143 genera was  $9.68\% \pm 3.65$  (0–27.09) (table 2), and the overall average for the congeneric K2P distances for all 143 taxa was  $10.81\% \pm 0.08\%$  with a range of  $0\%–33.79\%$  (table 5).

The mean p-distances calculated as the average of all pairwise comparisons among

species within each recognized genus (table 3) allow us to make the following observations. The genera found to be least variable were each represented by only two species. These were *Poroderma* ( $p = 0.6\%$ ), *Galeocерdo* ( $p = 1.06\%$ ), *Ginglymostoma* ( $p = 1.52\%$ ), and *Figaro* ( $p = 1.85\%$ ). Although the two species of *Poroderma* included here (i.e., *P. africanum* and *P. pantherinum*) are routinely recognized as distinct (e.g., Compagno 1984a, 2005a, 2005b), the existence of two species in each of the latter three genera is not without controversy. Given the strong geographic signal for the clusters of specimens in each of these three genera, the possibility that the analysis has detected regional variation, rather than distinct taxa, should be explored in more detail. The relatively low amount of variation seen within these genera is unlikely to be attributed to the small number of species, for, as described below, some of the genera exhibiting the greatest intrageneric variation were also represented by only two species.

The genera exhibiting the greatest average amount of variation among species (i.e., those with average intrageneric p-distances of  $>14\%$ ) were *Trygonoptera* ( $p = 14.26\%$ ; 4 species), *Dasyatis* ( $p = 14.56\%$ ; 15 species), *Atelomycterus* ( $p = 14.90\%$ ; 2 species), *Himantura* ( $p = 15.7\%$ ; 30 species), *Gymnura* ( $p = 16.50\%$ ; 9 species), *Urotrygon* ( $p = 17.77\%$ ; 2 species), and *Narcine* ( $p = 20.65\%$ ; 3 species). In some instances, all included species were relatively divergent from one another. For example, the range of p-values for comparisons among *Gymnura* species was  $11.54\%$ – $20.39\%$ . In other instances, subsets of species were conspicuously divergent from one another. For example, the range of p-values for comparisons among *Himantura* species was  $0.03\%$ – $23.7\%$  and the 30 species were distributed across two different sets of clusters (i.e., figs. 50–54 and fig. 60). In such instances, this divergence may be indicative of generic nonmonophyly. For example, the Atlantic species *Himantura schmardae*, which clustered with the potamotrygonids rather than with its Indo-Pacific congeners, is largely responsible for the intrageneric p-distance disparity observed in *Himantura*. Species in the following genera also exhibited substantial % p-value ranges and were distributed across two groupings: *Dasyatis* (p-values  $1.96\%$ – $22.53\%$ ; figs. 55, 56), *Apristurus* (p-

values  $1.87\%$ – $19.73\%$ ; figs. 28, 30), *Taeniura* (p-values of  $2.18\%$ – $15.8\%$ ; figs. 55, 59), as well as the skate genera *Dipturus* (p-values of  $1.6\%$ – $15.79\%$ ; figs. 71, 74) and *Raja* (p-values of  $2.21\%$ – $17.75\%$ ; figs. 71, 73). The monophyly of each of these genera, as currently circumscribed, bears further investigation.

In a number of cases, the divergence seen between individuals in populations of a nominal species (i.e., intraspecific variation) was as large as or larger than divergences seen between congeneric species that are traditionally recognized as distinct (i.e., interspecific variation). For example, the upper end of the range of p-distance values among conspecific specimens was  $2.01\%$  in *Carcharhinus albimarginatus*, *C. brevipinna*, and *C. obscurus*, whereas the p-distance value between specimens of *C. galapagensis* and *C. obscurus* was only  $0.37\%$  and between *C. altimus* and *C. plumbeus* only  $0.42\%$ . In fact, comparison of table 3 and appendix 1 shows that intraspecific variation among specimens of 25 other species of *Carcharhinus* also exceeded  $0.42\%$ . Similarly, for example among rays, the p-distance value between *Himantura oxyrhyncha* and *H. signifer* was  $1.03\%$ , while the upper end of the range of p-distance values for conspecific specimens of 10 of the 21 species of *Himantura* exceeded this value. Instances of intraspecific p-distance values greater than the low end of the range of interspecific p-distance values were also seen for two species of *Rhizoprionodon*, *Sphyrna lewini*, 2, 3 species of *Mustelus*, 2 species of *Centrophorus*, 2 species of *Squalus*, 2 species of *Bathyraja*, 2 species of *Aetobatus*, *Aetomylaeus maculatus*, 3 species of *Rhinobatos*, 4 species of *Rhinoptera*, 2 species of *Rhynchobatus*, and 2 species of *Torpedo*. These results suggest that there may be considerably more diversity in elasmobranchs than hitherto supposed, and also than recognized here. While much of the divergence uncovered in this study likely reflects the presence of cryptic or as yet undocumented species, it is always possible that some of the differentiation is due to the differential fixing of ancestral polymorphisms. Before we can be sure that these are distinct and different species, in addition to morphological work, we will need to look at nuclear markers for the same set of taxa. This is work that is currently underway by G.J.P.N.

A number of unnamed potentially novel species were also recovered from the analysis. While it is possible from a molecular standpoint that some represent named species for which NADH2 signatures are not currently available, examination of the images and/or vouchers, in combination with the geographic localities from which these specimens were collected, suggests otherwise. In total the analysis yielded 79 such taxa; these consist of 38 species of sharks and 41 species of rays. The distribution of these species among elasmobranch families is provided in table 1. This hitherto undiscovered diversity in elasmobranchs logically begs the question: How many species are there? The fact that so many new species have been described from Australian waters alone in the past 10 years (see Last and Stevens, 2009) might suggest that our current estimates are woefully low, which has obvious implications for conservation policy and the effective management of marine resources. Indeed it is impossible to manage elasmobranch marine resources effectively without an accurate species level characterization of the standing diversity. For example, policies designed to manage scalloped hammerheads globally need to be cognizant of the fact that *Sphyrna lewini* appears to consist of two evolutionarily distinct species. This said, the Australian case may be atypical. Australia has a high degree of endemism and, as noted below, is one of the four regions identified in this study for which there is clear evidence of population divergence within existing nominal species. It is, however, likely that undiscovered concentrations of global elasmobranch diversity occur in other regions with comparable endemism, particularly those regions that have not yet been rigorously surveyed such as the Red Sea, the Persian Gulf, and the Indian Ocean. The east coast of Africa remains particularly poorly sampled. The phylogenetic groups most likely to reveal previously hidden diversity are those for which there is high endemism and which are as yet poorly characterized, such as the catsharks, dogfish sharks, and skates.

#### BIOGEOGRAPHY

There are clear biogeographic footprints seen in the patterns of genetic cohesion among close relatives in this study. These influences are

modulated by patterns of migration and gene flow. At one extreme, there are endemic species with highly restricted ranges, such as the South African endemic catshark (*Poroderma pantherinum*), that do not reveal much about historical biogeography, because they are not distributed across multiple regions. At the other extreme there exist a few globally distributed pelagic species such as *Centrophorus squamosus* that are genetically so homogeneous across their range that they reveal little about biogeography. Most species, however, lie somewhere between these two extremes and exhibit patterns of divergence that reflect biogeographic influences at a range of scales. In this section, we restrict our attention to broad-based patterns that are shared across multiple species. Patterns characterizing individual species or closely related groups of species are dealt with in the results section. We restrict our treatment to four regional patterns that are particularly conspicuous among closely related groups but acknowledge that biogeography has shaped the distribution of the taxa at all levels of relatedness. However, the older influences are harder to detect and interpret as they are often “overprinted” by newer influences with the passage of time.

**Atlantic Ocean.** Populations of several species in the Atlantic appear to be clearly differentiated from those in other parts of the world. For example, specimens of the nurse shark *Ginglymostoma cirratum* in the Atlantic are distinctly different from specimens taken in the Gulf of California. The smalltail shark *Carcharhinus porosus*, the sandbar shark *Carcharhinus plumbeus*, the tiger shark *Galeocerdo cuvier*, and the great hammerhead *Sphyrna mokarran* all have Atlantic populations that appear distinct from their counterpart populations in the Pacific Ocean, Indian Ocean, Southeast Asia, and/or Australia.

**Arabian Sea, Persian Gulf, and Red Sea.** In a number of cases, populations in the Arabian Sea, Persian Gulf, and Red Sea appear genetically distinct from those of conspecifics in Southeast Asia, the Pacific, and Australia. While our sample does not include many specimens from the Arabian Sea, Persian Gulf, or Red Sea, many of those that have been included in this study appear distinct from conspecific counterparts elsewhere in the world (e.g., *Carcharhinus* cf. *dussumieri*, *Carcharhi-*

*nus* cf. *melanopterus*, *Rhizoprionodon acutus* 1, *Aetomylaeus* cf. *nichofii* 1, *Aetobatus* cf. *ocellatus* 2, *Pastinachus* cf. *sephen*, and *Gymnura* cf. *poecilura* 2). Interestingly, there is also evidence of biogeographic subdivision at the scale of the Persian Gulf, Arabian Sea, Bay of Bengal, and South China Sea. For example, the Arabian Sea, Bay of Bengal, and South China Sea each contain a distinct species of *Scoliodon* (*S. laticaudus* in the Arabian Sea, *S. cf. laticaudus* in the Bay of Bengal, and *S. macrorhynchus* in the South China Sea). Similarly, at a somewhat finer scale, the Gulf of Oman, the Red Sea, and the Arabian Sea each have a distinct form of *Iago omanensis*. However, a denser sampling of populations throughout the region will be required before boundaries among subregions can be determined with any confidence.

**Southeast Asia.** Much of elasmobranch diversity, like teleost diversity, is centered in Southeast Asia. While several nominal species are found exclusively in that region, there are some that are more widespread but exhibit distinct population-level differentiation in Southeast Asian waters. Indeed, some are sufficiently different to warrant recognition as distinct species relative to their sister groups from other regions (e.g., *Carcharhinus sealei*, *Carcharhinus dussumieri*, *Carcharhinus* cf. *leucas* 1, *Aetomylaeus nichofii*, and *Himantura* cf. *uarnak* 1, 3, and 4).

**Australia.** This region appears to be a long-standing region of elasmobranch diversification and endemism. For example, about 40% of the species diversity in the order Orectolobiformes is unique to Australian waters. In the past 10 years more than 100 new species of sharks and rays have been described from the region. While much of the elasmobranch fauna of Australia is endemic, there are several instances where species with distributions that are globally widespread have distinctive subpopulations in Australia relative to other regions (see Zemlak et al., 2009, for similar patterns in teleosts). In most cases we have recognized the distinctiveness of these populations as likely novel species using unique designations. Examples include variants of *Carcharhinus sealei* (i.e., *C. cf. sealei*), *Carcharhinus sorrah* (i.e., *C. cf. sorrah*), *Rhizoprionodon acutus* (i.e., *R. cf. acutus* 2), *Aetomylaeus nichofii* (i.e., *A. cf. nichofii* 2), and *Neotrygon kuhlii* (i.e., *N. kuhlii* 4).

**Other biogeographic patterns.** While the above four regional patterns stand out, there are other regional patterns that are noteworthy. In the case of the white shark, *Carcharodon carcharias*, for example, we see that animals taken from the KwaZulu-Natal coast in the southwestern Indian Ocean are more similar to those taken from the western North Atlantic (New Jersey and New York) than they are to specimens from Australia, which, in turn seem to be genetically similar to although distinct from animals from the eastern Pacific. This result is consistent with the work of previous authors (e.g., Jorgensen et al., 2009). The implication is that migration does not occur across the Indian Ocean for this species. However, Bonfil et al. (2005) have shown that movement of individual animals between South Africa and Australia is possible. *Carcharhinus limbatus* also shows an unusual pattern of genetic cohesion in the Pacific. Specimens ranging from the eastern (Gulf of California), central, and western Pacific, Southeast Asia, northern Australia, India, southeastern Africa, and West Africa are reasonably homogeneous while the populations in the western North Atlantic and Gulf of Mexico are strikingly distinct, so much so that we recognize them as a distinct species. The pattern observed is consistent with the earlier studies of population differentiation in *Carcharhinus limbatus* by Keeney and Heist (2006).

**Anomalies.** Some deepwater species are found to have wide ranges with little divergence evident. For example, *Centrophorus squamosus* specimens in the Atlantic Ocean, Australia, and New Zealand are genetically identical. Also, *Centrophorus zeehani*, considered to be a southern Australian endemic, was found to be genetically identical to a specimen identified as *Centrophorus granulosus* in the Atlantic. Such patterns are provocative. On the one hand, it is possible that these species are capable of moving tremendous distances and exchanging genetic material with individuals across their ranges, perhaps by taking advantage of deep water marine superhighways that link regions together (e.g., Broecker, 1991). On the other hand, it is possible that the rate of molecular evolution has slowed down in these taxa such that populations seem more homogeneous than might otherwise be expected. One possible source of a reduction in

molecular rate would be long generation times. It is not inconceivable that some of these organisms may be extremely long-lived and have associated long generation times. Nonetheless, groups, such as *Centrophorus*, are clearly in need of taxonomic revision.

#### COMPARISONS TO COI BARCODE DATA

Several molecular surveys of elasmobranchs have been conducted using the 650 bp COI barcode sequence fragment (Holmes et al., 2009; Moura et al., 2008; Toffoli et al., 2008; Ward et al., 2005, 2007, 2008, 2009; Ward and Holmes, 2007; Wong et al., 2009; Zemlak et al., 2009). These studies have used the K2P rather than the p-distance measure we have chosen to use for the current study. In order to provide a means of comparison between the NADH2 sequence data presented herein and those of previously published COI barcode sequences, we computed pairwise K2P distances for our NADH2 data set using the same methods that were used to compute these measures for the barcode COI studies. The mean, standard deviation, and range of intraspecific K2P distances are given for species (appendix 1) and of intrageneric K2P distances of genera (table 3) to allow for direct comparisons across taxa. We have also carried out an overall comparison of the variation averaged across species and genera using K2P distance (see table 5) to allow direct comparison with the statistics provided by the Ward et al. (2008) study, which was based on 945 samples of COI sequences representing 210 species of chondrichthyans and is thus especially appropriate for direct comparison with the current study.

These comparisons suggest that within-taxon divergences are comparable for the two genes, although they are slightly lower for NADH2 (0.27%) than they are for the COI barcode fragment (0.37%) for the within-species comparisons, and somewhat higher for NADH2 (10.81%) than they are for the COI barcode fragment (7.48%) for the within-genus comparisons. This may be as much due to the differences in taxon sampling between the two studies as it is to anything else. The current NADH2 survey includes a larger proportion of instances where multiple genetically similar individuals are used to represent a single species (176 in the case of *Squalus acanthias*) and has a

broader sampling of taxa within genera and across elasmobranchs in general. A more precise measure of the differences associated with the divergences between NADH2 and the COI barcode fragment would require a comparison among exactly the same set of individual specimens across a range of species. Nonetheless, it is clear that the percent divergences are roughly comparable as might be expected given that both are linked genes inherited as a unit on the mitochondrial genome and subject to equivalent changes in population size and migration influences even if not the exact same profiles of selection. It should also be noted that the within-species COI divergences seen in elasmobranchs appear to be similar to those seen in actinopterygians (Ward and Holmes, 2007).

#### IMPLICATIONS FOR PARASITOLOGY

This work highlights the importance of establishing accurate identifications for hosts from which parasites are collected. Furthermore, it illustrates that the rewards from such endeavors far outweigh the time and effort they require. The hitherto undiscovered elasmobranch diversity revealed by this study is of relevance to parasitologists in several ways. In some cases the novel host taxa are morphologically cryptic and every effort in the field should be made to include the collection of tissue samples appropriate for molecular work, in addition to photographs. This is the case, for example, for many of the species pairs of *Carcharhinus* (i.e., *C. plumbeus* and *C. cf. plumbeus*, *C. sealei* and *C. cf. sealei*, *C. sorrah*, and *C. cf. sorrah*, etc.). In other cases, the species comprising a complex exhibit some morphological feature that initially encourages rapid, unfortunately superficial, identifications. For example, that "*Aetobatus narinari*" actually consists of a complex of species, all of which exhibit dorsal coloration consisting of white spots on a black background, has only recently been firmly established (White et al., 2010c). As a consequence, it is now clear that the distinction among species in the complex can be made based on relatively conspicuous morphological criteria, as well as on the basis of molecular differences. Although its taxonomic complexity has not yet been formally resolved, the bluespotted maskray (*Neotrygon*

*kuhlii*) represents a second example of the latter scenario. Analysis of NADH2 yielded four distinct lineages that, although they are all currently identified as *N. kuhlii* in their respective countries of origin, exhibit variation in, for example, the size and distribution of their blue spots.

When working with host groups in which the taxonomy is rapidly changing, it is essential that parasitologists become familiar with developments in host taxonomy through collaboration with host taxonomists because in many host groups, taxonomic advancements may far outpace published knowledge. We note, for example, that the transformation in the taxonomy of Australian elasmobranchs that occurred between the first edition of *Sharks and Rays of Australia* (Last and Stevens, 1994) and the second edition (Last and Stevens, 2009) was, unfortunately, not reflected in the host identifications of work on Australian elasmobranch parasites over the intervening time (see Fyler and Caira, 2010). In collaborations between parasitologists and host taxonomists, it is, however, important to recognize that while their interests are mutually compatible, the methods employed in field situations may differ. To the parasitologist, the accurate identification of each individual host specimen is paramount if the hosts of all parasites discovered are to be accurately determined. In instances in which host identities cannot definitely be made in the field, sufficient data and samples must be collected to allow the identities to be confirmed when data from different sources can be generated and integrated. In contrast, host taxonomists, particularly those exploring novelty, typically focus their efforts on a subset of specimens, generally those that are most complete, and often of a size appropriate for deposition in museums. The host specimen database we have developed was aimed at serving the interests and needs of both parasite and host taxonomists.

To date, hundreds of species of parasites have been reported from elasmobranchs (Caira et al., 2012); these records suggest that most elasmobranch species harbor a distinct fauna of parasites. At present, many of the parasites of elasmobranchs, and in particular cestodes (see Caira and Jensen, 2001), are considered to be remarkably host specific. However, a reevaluation of the host associations of many

elasmobranch parasite species would be interesting to undertake in light of the results presented here. Furthermore, the parasite faunas of hundreds of species of elasmobranchs (both described and novel elasmobranch species) remain to be characterized. The assumption that hosts have been accurately identified, when in fact they have not, has implications for assessments of host specificity, estimation of global elasmobranch parasite biodiversity, explorations of the relationship between parasite and host phylogenies, and the establishment of trophic links as illuminated by life-cycle studies. At this point it is unclear whether elasmobranchs are unique among vertebrate host groups in this respect, or if the host identity issues raised here are more widespread. We suspect that a similar situation may exist in other, even more speciose host groups such as teleosts, the taxonomy of which is currently also rapidly expanding.

## OUTLOOK AND FUTURE WORK

**BIOGEOGRAPHY:** We have presented a survey of DNA sequence variation in a single mitochondrial gene for a phylogenetically balanced and dense taxon sample of elasmobranchs. While this represents a fairly comprehensive treatment in terms of taxon sampling we regard it as only a first step in understanding the diversification of this group. There are several regions of the world that remain poorly sampled in the current study that likely harbor more diversity than described herein. One such region is that encompassing the Red Sea, the Persian Gulf, Arabian Sea, Bay of Bengal, and Indian Ocean. The limited geographic sampling that we have for this vast area suggests there is probably more diversity that remains to be discovered. The recently expanded deep sea fishery off the southwest coast of India has yielded several specimens that appear distinct from congeners in other parts of the world (D. Ebert, personal commun.). Other regions that may also warrant further exploration are the South Pacific, from which several new taxa have recently been described, and also deepwater and abyssal faunas worldwide (e.g., Straube et al., 2011).

**PHYLOGENY:** While patterns of species level mitochondrial cohesion are evident in this study, a rigorous estimate of the overall phylogeny among the taxa is conspicuously

absent. There will be many who will wonder why we have not subjected these sequences to methods of phylogenetic analysis in order to estimate the phylogenetic relationships among the taxa sampled. Our reasons for not doing so are twofold. First, the primary goal of this study was to carry out a DNA-based global survey of species diversity. Second, we feel strongly that such an analysis would likely not yield a phylogenetic estimate that is either accurate or reliable. These mitochondrial sequences evolve at such a high rate that any historical signal present in the data set is likely to have been overridden by multiple substitutions, changing substitutional dynamics, and lineage-specific effects that put them beyond the reach of any of the commonly used independent and identically distributed (IID) nucleotide-based models, no matter how parameter rich. While it is clear that there is historical signal among close relatives the deeper phylogenetic relationships are probably unrecoverable. This said, an analysis of a comprehensive subset of the current data set has been carried out by Naylor et al. (2012) to explore the depth at which the phylogenetic signal is recoverable for the data set. An effort is also underway by G.J.P.N. to sample more slowly evolving single-copy nuclear genes to estimate relationships among the taxa identified in this study and to estimate the temporal component of lineage diversification.

**FUNCTIONAL DIVERSITY:** We anticipate that other workers will contribute toward our efforts to complete a full characterization of standing extant elasmobranch biodiversity. A rigorous characterization of diversity at the species level will provide a framework for a more fine-grained understanding of life-history traits and their variation across species and geography. For example, the current study indicates that the scalloped hammerhead, *Sphyrna lewini*, which is generally considered to be a single, globally distributed species, constitutes two evolutionarily distinct species. Now that we are aware of this, we can better appreciate that there may be differences in the life-history traits, depth distributions, and behaviors between the two species. This type of information will provide a foundation for a functional characterization of biodiversity that will not only advance scientific understanding of the role of these animals in ocean

ecosystems, but will also allow us to better manage stocks, understand regional variation in susceptibility to fishing pressure, recognize units for conservation, and be better stewards of ocean resources.

#### AUTHOR CONTRIBUTIONS

This project was originally conceived by J.N. Caira and K. Jensen in collaboration with G.J.P. Naylor as a result of discussions of how best to validate and verify host identifications for parasitological studies. G.J.P. Naylor was responsible for expanding its scope to include representation of as broad a spectrum of elasmobranchs as possible to serve the needs of both parasitologists and elasmobranch biologists. G.J.P. Naylor oversaw the sequencing and initial analysis of the distance data and wrote sections of the Introduction and sections of the Discussion. J.N. Caira (in close collaboration with K. Jensen) wrote the results section as well as portions of the Introduction and Discussion; she also supervised the design and population of the host specimen database. K. Jensen (in close collaboration with J.N. Caira) generated the distance data, and prepared the figures, tables, and appendices; she also took the majority of the photographs of elasmobranchs presented in the host specimen database. J.N. Caira and K. Jensen collected 53% of the tissue samples; G.J.P. Naylor collected and/or solicited tissues for the remainder. K.A.M. Rosana carried out 90% of the laboratory work involved in generating the sequence data. W.T. White and P.R. Last contributed key tissue samples from rare taxa and provided valuable input on the species treatments.

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APPENDIX 1  
 Mean intraspecific p-distance (%) and K2P distance (%) for NADH2 given as the mean, standard deviation, range, and number of specimens (n) as calculated in BOLD (n = 468 species)

	Figure(s)	p-distance	K2P distance
<b>Carcharhiniformes</b>			
Carcharhinidae			
Carcharhinus acronotus	10	0.2 ± 0.12 (0-0.48; n = 11)	0.2 ± 0.12 (0-0.48; n = 11)
Carcharhinus albigmarginatus	1	1.15 ± 0.91 (0-2.01; n = 5)	1.17 ± 0.93 (0-2.05; n = 5)
Carcharhinus altimus	9	0.17 ± 0.2 (0-0.86; n = 22)	0.17 ± 0.2 (0-0.87; n = 22)
Carcharhinidae			
Carcharhinus amblyrhynchoides	6	0.41 ± 0.27 (0-0.86; n = 36)	0.42 ± 0.28 (0-0.87; n = 36)
Carcharhinidae			
Carcharhinus amblyrhynchos	1	0.37 ± 0.27 (0-0.96; n = 18)	0.37 ± 0.27 (0-0.97; n = 18)
Carcharhinidae			
Carcharhinus amboinensis 1	8	0.38 ± 0.31 (0-0.96; n = 5)	0.39 ± 0.32 (0-0.97; n = 5)
Carcharhinidae			
Carcharhinus amboinensis 2	8	0.06 ± 0.05 (0-0.1; n = 5)	0.06 ± 0.05 (0-0.1; n = 5)
Carcharhinidae			
Carcharhinus borneensis	2	0.23 ± 0.14 (0-0.48; n = 13)	0.23 ± 0.14 (0-0.48; n = 13)
Carcharhinidae			
Carcharhinus brachyurus	10	0.19 (n = 2)	0.19 (n = 2)
Carcharhinidae			
Carcharhinus brevipinna	10	0.59 ± 0.32 (0-2.01; n = 35)	0.59 ± 0.32 (0-2.04; n = 35)
Carcharhinidae			
Carcharhinus cautus	7	0 (n = 5)	0 (n = 5)
Carcharhinidae			
Carcharhinus cf. brachyurus	10	0.23 ± 0.2 (0-0.67; n = 8)	0.23 ± 0.2 (0-0.67; n = 8)
Carcharhinidae			
Carcharhinus cf. dussumieri	3	0.1 (n = 2)	0.1 (n = 2)
Carcharhinidae			
Carcharhinus cf. leucas 1	8	0.46 ± 0.41 (0-1.16; n = 7)	0.46 ± 0.42 (0-1.17; n = 7)
Carcharhinidae			
Carcharhinus cf. leucas 2	8	0.45 ± 0.3 (0.1-0.67; n = 3)	0.45 ± 0.31 (0.1-0.67; n = 3)
Carcharhinidae			
Carcharhinus cf. limbatus	6	0.27 ± 0.24 (0-1.72; n = 59)	0.27 ± 0.25 (0-1.75; n = 59)
Carcharhinidae			
Carcharhinus cf. melanopterus	7	0.1 (n = 2)	0.1 (n = 2)
Carcharhinidae			
Carcharhinus cf. plumbeus	9	0.16 ± 0.19 (0-0.77; n = 17)	0.16 ± 0.19 (0-0.77; n = 17)
Carcharhinidae			
Carcharhinus cf. porosus	11	0 (n = 3)	0 (n = 3)
Carcharhinidae			
Carcharhinus cf. sealai	3	0.15 ± 0.13 (0-0.57; n = 16)	0.15 ± 0.13 (0-0.58; n = 16)
Carcharhinidae			
Carcharhinus cf. sorrah	5	0.29 ± 0.13 (0.1-0.48; n = 4)	0.29 ± 0.13 (0.1-0.48; n = 4)
Carcharhinidae			
Carcharhinus dussumieri	3	0.04 ± 0.05 (0-0.1; n = 5)	0.04 ± 0.05 (0-0.1; n = 5)
Carcharhinidae			
Carcharhinus falciformis	1	0.4 ± 0.39 (0-0.96; n = 48)	0.41 ± 0.39 (0-0.97; n = 48)
Carcharhinidae			
Carcharhinus fitzroyensis	6	0 (n = 3)	0 (n = 3)
Carcharhinidae			
Carcharhinus galapagensis	4	0.24 ± 0.13 (0.1-0.38; n = 4)	0.24 ± 0.13 (0.1-0.38; n = 4)
Carcharhinidae			
Carcharhinus isodon	11	0.13 ± 0.1 (0-0.38; n = 16)	0.13 ± 0.1 (0-0.38; n = 16)
Carcharhinidae			
Carcharhinus leucas	8	0.04 ± 0.05 (0-0.1; n = 14)	0.04 ± 0.05 (0-0.1; n = 14)
Carcharhinidae			
Carcharhinus limbatus	6	0.08 ± 0.09 (0-0.48; n = 39)	0.08 ± 0.09 (0-0.48; n = 39)
Carcharhinidae			
Carcharhinus longimanus	4	0.16 ± 0.09 (0-0.29; n = 7)	0.16 ± 0.09 (0-0.29; n = 7)
Carcharhinidae			
Carcharhinus macloiti	2	0.75 ± 0.45 (0-1.34; n = 13)	0.76 ± 0.45 (0-1.36; n = 13)
Carcharhinidae			
Carcharhinus melanopterus	7	0.41 ± 0.23 (0-0.86; n = 24)	0.41 ± 0.24 (0-0.87; n = 24)
Carcharhinidae			
Carcharhinus obscurus	4	0.46 ± 0.37 (0-2.01; n = 42)	0.47 ± 0.38 (0-2.05; n = 42)
Carcharhinidae			
Carcharhinus perezii	4	0.14 ± 0.3 (0-0.96; n = 14)	0.14 ± 0.31 (0-0.97; n = 14)
Carcharhinidae			
Carcharhinus plumbeus	9	0.11 ± 0.2 (0-1.25; n = 57)	0.11 ± 0.2 (0-1.26; n = 57)

APPENDIX 1  
(Continued)

	Figure(s)	p-distance	K2P distance
Carcharhinidae			
<i>Carcharhinus porosus</i>	11	0.42 ± 0.28 (0-0.96; n = 15)	0.43 ± 0.29 (0-0.97; n = 15)
Carcharhinidae			
<i>Carcharhinus sealiei</i>	3	0.17 ± 0.14 (0-0.77; n = 35)	0.18 ± 0.14 (0-0.77; n = 35)
Carcharhinidae			
<i>Carcharhinus signatus</i>	12	0.17 ± 0.14 (0-0.29; n = 6)	0.17 ± 0.14 (0-0.29; n = 6)
Carcharhinidae			
<i>Carcharhinus sorrah</i>	5	0.37 ± 0.32 (0-1.63; n = 42)	0.37 ± 0.32 (0-1.65; n = 42)
Carcharhinidae			
<i>Carcharhinus tilstoni</i>	6	0.19 ± 0.17 (0-0.48; n = 11)	0.19 ± 0.17 (0-0.48; n = 11)
Carcharhinidae			
<i>Galeocerdo cf. cuvier</i>	20	0.1 ± 0.11 (0-0.48; n = 18)	0.1 ± 0.11 (0-0.48; n = 18)
Carcharhinidae			
<i>Galeocerdo cuvier</i>	20	0.28 ± 0.17 (0-0.67; n = 11)	0.28 ± 0.18 (0-0.68; n = 11)
Carcharhinidae			
<i>Glyphis fowlerae</i>	14	0.29 ± 0.2 (0-0.57; n = 4)	0.29 ± 0.2 (0-0.58; n = 4)
Carcharhinidae			
<i>Glyphis gangeticus</i>	14	0.19 ± 0.17 (0-0.29; n = 3)	0.19 ± 0.17 (0-0.29; n = 3)
Carcharhinidae			
<i>Glyphis garricki</i>	14	0 (n = 3)	0 (n = 3)
Carcharhinidae			
<i>Glyphis glyphis</i>	14	0.19 (n = 2)	0.19 (n = 2)
Carcharhinidae			
<i>Glyphis sp. 1</i>	14	0.57 ± 0.1 (0.48-0.67; n = 3)	0.58 ± 0.1 (0.48-0.68; n = 3)
Carcharhinidae			
<i>Isogomphodon oxyrinchus</i>	11	0.04 ± 0.05 (0-0.1; n = 5)	0.04 ± 0.05 (0-0.1; n = 5)
Carcharhinidae			
<i>Lamiopsis tephrodes</i>	14	0.1 ± 0.08 (0-0.29; n = 26)	0.1 ± 0.08 (0-0.29; n = 26)
Carcharhinidae			
<i>Loxodon cf. macrorhinus</i>	18	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Carcharhinidae			
<i>Loxodon macrorhinus</i>	18	0.44 ± 0.31 (0-1.05; n = 18)	0.44 ± 0.31 (0-1.06; n = 18)
Carcharhinidae			
<i>Negaprion acutidens</i>	14	0.08 ± 0.12 (0-0.48; n = 14)	0.08 ± 0.12 (0-0.48; n = 14)
Carcharhinidae			
<i>Negaprion brevirostris</i>	14	0.13 ± 0.14 (0-0.38; n = 6)	0.13 ± 0.14 (0-0.38; n = 6)
Carcharhinidae			
<i>Prionace glauca</i>	1	0.24 ± 0.15 (0-0.48; n = 23)	0.24 ± 0.15 (0-0.48; n = 23)
Carcharhinidae			
<i>Rhizoprionodon acutus</i>	15	0.14 ± 0.15 (0-0.58; n = 12)	0.15 ± 0.15 (0-0.58; n = 12)
Carcharhinidae			
<i>Rhizoprionodon cf. acutus 1</i>	15	0.06 ± 0.06 (0-0.19; n = 14)	0.06 ± 0.06 (0-0.19; n = 14)
Carcharhinidae			
<i>Rhizoprionodon cf. acutus 2</i>	15	0.23 ± 0.2 (0-0.77; n = 10)	0.23 ± 0.2 (0-0.77; n = 10)
Carcharhinidae			
<i>Rhizoprionodon cf. acutus 3</i>	15	0.3 ± 0.18 (0-0.77; n = 25)	0.3 ± 0.18 (0-0.77; n = 25)
Carcharhinidae			
<i>Rhizoprionodon lalandii</i>	16	0.09 ± 0.06 (0-0.19; n = 6)	0.09 ± 0.06 (0-0.19; n = 6)
Carcharhinidae			
<i>Rhizoprionodon longurio</i>	16	0.4 ± 0.24 (0.1-0.77; n = 8)	0.4 ± 0.24 (0.1-0.77; n = 8)
Carcharhinidae			
<i>Rhizoprionodon oligolinx</i>	17	0.56 ± 0.35 (0-1.44; n = 17)	0.56 ± 0.35 (0-1.45; n = 17)
Carcharhinidae			
<i>Rhizoprionodon porosus</i>	16	0.19 (n = 2)	0.19 (n = 2)
Carcharhinidae			
<i>Rhizoprionodon taylori</i>	16	0.42 ± 0.21 (0-0.86; n = 14)	0.42 ± 0.21 (0-0.87; n = 14)
Carcharhinidae			
<i>Rhizoprionodon terraenovae</i>	16	0.47 ± 0.33 (0-1.53; n = 24)	0.47 ± 0.33 (0-1.55; n = 24)
Carcharhinidae			
<i>Scoliodon cf. laticaudus</i>	18	0.48 (n = 2)	0.48 (n = 2)
Carcharhinidae			
<i>Scoliodon laticaudus</i>	18	0.05 ± 0.06 (0-0.19; n = 11)	0.05 ± 0.06 (0-0.19; n = 11)
Carcharhinidae			
<i>Scoliodon macrorhynchus</i>	18	0.21 ± 0.14 (0-0.77; n = 48)	0.21 ± 0.14 (0-0.77; n = 48)
Carcharhinidae			
<i>Triakonodon obesus</i>	13	0.41 ± 0.25 (0-0.86; n = 9)	0.42 ± 0.25 (0-0.87; n = 9)
Hemigaleidae			
<i>Hemigaleus australiensis</i>	21	0.63 ± 0.37 (0-1.05; n = 6)	0.63 ± 0.37 (0-1.06; n = 6)
Hemigaleidae			
<i>Hemigaleus microstoma</i>	21	0.47 ± 0.32 (0-1.25; n = 31)	0.47 ± 0.32 (0-1.26; n = 31)
Hemigaleidae			
<i>Hemipristis elongata</i>	21	0.19 ± 0.16 (0-0.48; n = 14)	0.19 ± 0.16 (0-0.48; n = 14)

APPENDIX 1  
(Continued)

	Figure(s)	p-distance	K2P distance
Hemigaleidae	21	0.28 ± 0.16 (0-0.48; n = 6)	0.28 ± 0.16 (0-0.48; n = 6)
Hemigaleidae	21	0.25 ± 0.24 (0-0.86; n = 17)	0.25 ± 0.24 (0-0.87; n = 17)
Leptochariidae	22	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Proscylliidae	32	0.29 ± 0.31 (0-0.57; n = 4)	0.29 ± 0.32 (0-0.58; n = 4)
Pseudotriakidae	32	0 (n = 3)	0 (n = 3)
Seyliorhinidae	28	0.16 ± 0.09 (0-0.29; n = 5)	0.16 ± 0.09 (0-0.29; n = 5)
Seyliorhinidae	28	0.51 ± 0.11 (0.38-0.57; n = 3)	0.51 ± 0.12 (0.38-0.58; n = 3)
Seyliorhinidae	30	0.58 ± 0.33 (0.19-0.77; n = 3)	0.58 ± 0.33 (0.19-0.77; n = 3)
Seyliorhinidae	28	0.29 (n = 2)	0.29 (n = 2)
Seyliorhinidae	28	0 (n = 8)	0 (n = 8)
Seyliorhinidae	28	0.1 ± 0.14 (0-0.29; n = 6)	0.1 ± 0.14 (0-0.29; n = 6)
Seyliorhinidae	28	0.18 ± 0.11 (0-0.38; n = 9)	0.18 ± 0.11 (0-0.38; n = 9)
Seyliorhinidae	28	0.14 ± 0.1 (0-0.29; n = 7)	0.14 ± 0.1 (0-0.29; n = 7)
Seyliorhinidae	28	0.45 ± 0.13 (0.19-0.57; n = 4)	0.45 ± 0.13 (0.19-0.58; n = 4)
Seyliorhinidae	28	0.29 (n = 2)	0.29 (n = 2)
Seyliorhinidae	28	0.13 ± 0.05 (0.1-0.19; n = 3)	0.13 ± 0.05 (0.1-0.19; n = 3)
Seyliorhinidae	28	0.19 (n = 2)	0.19 (n = 2)
Seyliorhinidae	30	0.48 (n = 2)	0.48 (n = 2)
Seyliorhinidae	31	0.08 ± 0.1 (0-0.19; n = 5)	0.08 ± 0.1 (0-0.19; n = 5)
Seyliorhinidae	31	0.38 (n = 2)	0.38 (n = 2)
Seyliorhinidae	31	0.25 ± 0.22 (0-0.38; n = 3)	0.25 ± 0.22 (0-0.38; n = 3)
Seyliorhinidae	33	0.37 ± 0.33 (0-1.05; n = 10)	0.37 ± 0.33 (0-1.06; n = 10)
Seyliorhinidae	33	0.25 ± 0.11 (0.19-0.38; n = 3)	0.25 ± 0.11 (0.19-0.38; n = 3)
Seyliorhinidae	33	0.51 ± 0.15 (0.38-0.67; n = 3)	0.51 ± 0.15 (0.38-0.67; n = 3)
Seyliorhinidae	31	0.03 (n = 6)	0.03 ± 0.05 (0-0.1; n = 6)
Seyliorhinidae	34	0.13 ± 0.05 (0.1-0.19; n = 3)	0.13 ± 0.05 (0.1-0.19; n = 3)
Seyliorhinidae	34	0.18 ± 0.16 (0-0.48; n = 6)	0.18 ± 0.16 (0-0.48; n = 6)
Seyliorhinidae	34	0.29 (n = 2)	0.29 (n = 2)
Seyliorhinidae	34	0.25 ± 0.16 (0-0.38; n = 4)	0.25 ± 0.16 (0-0.38; n = 4)
Seyliorhinidae	34	0.09 ± 0.06 (0-0.19; n = 6)	0.09 ± 0.06 (0-0.19; n = 6)
Seyliorhinidae	31	0.27 ± 0.15 (0-0.57; n = 6)	0.27 ± 0.15 (0-0.58; n = 6)
Seyliorhinidae	31	0.13 ± 0.05 (0.1-0.19; n = 3)	0.13 ± 0.05 (0.1-0.19; n = 3)
Seyliorhinidae	29	0.19 ± 0.12 (0-0.38; n = 8)	0.19 ± 0.12 (0-0.38; n = 8)
Seyliorhinidae	29	0.19 (n = 2)	0.19 (n = 2)
Seyliorhinidae	29	0.17 ± 0.15 (0-0.29; n = 6)	0.17 ± 0.15 (0-0.29; n = 6)
Seyliorhinidae	28	0.31 ± 0.22 (0-0.48; n = 5)	0.31 ± 0.22 (0-0.48; n = 5)

APPENDIX 1  
(Continued)

	Figure(s)	p-distance	K2P distance
Scyliorhinidae	29	0.19 ± 0.11 (0-0.38; n = 5)	0.19 ± 0.11 (0-0.38; n = 5)
Scyliorhinidae	29	0.38 (n = 2)	0.38 (n = 2)
Scyliorhinidae	29	0.38 ± 0.1 (0.29-0.48; n = 3)	0.39 ± 0.1 (0.29-0.48; n = 3)
Scyliorhinidae	29	0.42 ± 0.24 (0-1.15; n = 19)	0.42 ± 0.25 (0-1.16; n = 19)
Scyliorhinidae	29	0.2 ± 0.12 (0-0.57; n = 17)	0.2 ± 0.12 (0-0.58; n = 17)
Scyliorhinidae	33	0.12 ± 0.08 (0-0.29; n = 6)	0.12 ± 0.08 (0-0.29; n = 6)
Scyliorhinidae	28	0.33 ± 0.12 (0.1-0.48; n = 5)	0.33 ± 0.12 (0.1-0.48; n = 5)
Scyliorhinidae	34	0.13 ± 0.07 (0-0.19; n = 12)	0.13 ± 0.07 (0-0.19; n = 12)
Scyliorhinidae	34	0.28 ± 0.16 (0-0.57; n = 16)	0.28 ± 0.16 (0-0.58; n = 16)
Scyliorhinidae	33	0 (n = 2)	0 (n = 2)
Scyliorhinidae	34	0.06 ± 0.06 (0-0.19; n = 15)	0.06 ± 0.06 (0-0.19; n = 15)
Scyliorhinidae	34	1.41 ± 0.64 (0.86-2.11; n = 3)	1.42 ± 0.65 (0.87-2.14; n = 3)
Sphyrmidae	19	0.07 ± 0.06 (0-0.19; n = 9)	0.07 ± 0.06 (0-0.19; n = 9)
Sphyrmidae	19	0.38 (n = 2)	0.38 (n = 2)
Sphyrmidae	19	0.31 ± 0.24 (0-0.67; n = 6)	0.31 ± 0.24 (0-0.67; n = 6)
Sphyrmidae	19	0.42 ± 0.32 (0-1.15; n = 32)	0.42 ± 0.32 (0-1.16; n = 32)
Sphyrmidae	19	0.67 ± 0.52 (0-2.01; n = 13)	0.68 ± 0.53 (0-2.04; n = 13)
Sphyrmidae	19	0.05 ± 0.07 (0-0.29; n = 16)	0.05 ± 0.07 (0-0.29; n = 16)
Sphyrmidae	19	0.19 ± 0.15 (0-0.38; n = 6)	0.19 ± 0.15 (0-0.38; n = 6)
Sphyrmidae	19	0.06 ± 0.08 (0-0.29; n = 12)	0.06 ± 0.08 (0-0.29; n = 12)
Sphyrmidae	19	0.29 ± 0.31 (0-0.57; n = 4)	0.29 ± 0.32 (0-0.58; n = 4)
Sphyrmidae	19	0.24 ± 0.23 (0-0.77; n = 16)	0.24 ± 0.23 (0-0.77; n = 16)
Triakidae	26	0 (n = 2)	0 (n = 2)
Triakidae	26	0.47 ± 0.38 (0-1.25; n = 18)	0.48 ± 0.38 (0-1.26; n = 18)
Triakidae	26	0.14 ± 0.08 (0-0.29; n = 5)	0.14 ± 0.08 (0-0.29; n = 5)
Triakidae	26	0.34 ± 0.19 (0-0.67; n = 9)	0.34 ± 0.19 (0-0.68; n = 9)
Triakidae	26	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Triakidae	26	0.09 ± 0.06 (0-0.19; n = 13)	0.09 ± 0.06 (0-0.19; n = 13)
Triakidae	25	0.67 (n = 2)	0.68 (n = 2)
Triakidae	25	0.14 ± 0.09 (0-0.29; n = 6)	0.14 ± 0.09 (0-0.29; n = 6)
Triakidae	25	0.44 ± 0.11 (0.38-0.57; n = 3)	0.45 ± 0.12 (0.38-0.58; n = 3)
Triakidae	25	0.34 ± 0.21 (0-0.77; n = 11)	0.34 ± 0.21 (0-0.77; n = 11)
Triakidae	24	0.19 ± 0.14 (0-0.38; n = 9)	0.19 ± 0.14 (0-0.38; n = 9)
Triakidae	24	0.1 (n = 2)	0.1 (n = 2)
Triakidae	23	0.13 ± 0.08 (0-0.19; n = 15)	0.13 ± 0.08 (0-0.19; n = 15)
Triakidae	23	0.75 ± 0.62 (0-2.2; n = 8)	0.76 ± 0.63 (0-2.24; n = 8)

APPENDIX I  
(Continued)

	Figure(s)	p-distance	K2P distance
Triakidae			
	23	0.28 ± 0.18 (0-0.67; n = 8)	0.28 ± 0.18 (0-0.67; n = 8)
Triakidae			
	23	0.54 ± 0.19 (0.19-0.86; n = 6)	0.54 ± 0.2 (0.19-0.87; n = 6)
Triakidae			
	24	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Triakidae			
	24	0.27 ± 0.14 (0-0.58; n = 13)	0.27 ± 0.14 (0-0.58; n = 13)
Triakidae			
	23	0.64 ± 0.31 (0.29-0.86; n = 3)	0.64 ± 0.31 (0.29-0.87; n = 3)
Triakidae			
	23	0.33 ± 0.28 (0-0.77; n = 9)	0.33 ± 0.28 (0-0.77; n = 9)
Triakidae			
	24	0.25 ± 0.13 (0-0.4; n = 6)	0.25 ± 0.13 (0-0.4; n = 6)
Triakidae			
	24	0.18 ± 0.09 (0-0.38; n = 7)	0.18 ± 0.09 (0-0.38; n = 7)
Triakidae			
	23	0 (n = 2)	0 (n = 2)
Triakidae			
	23	0.24 ± 0.16 (0-0.48; n = 4)	0.24 ± 0.16 (0-0.48; n = 4)
Triakidae			
	24	0.19 (n = 2)	0.19 (n = 2)
Triakidae			
	23	0.1 ± 0.09 (0-0.48; n = 30)	0.1 ± 0.09 (0-0.48; n = 30)
Triakidae			
	24	0.11 ± 0.07 (0-0.19; n = 4)	0.11 ± 0.07 (0-0.19; n = 4)
Triakidae			
	24	0.19 (n = 2)	0.19 (n = 2)
Triakidae			
	27	0.2 ± 0.17 (0-0.38; n = 6)	0.2 ± 0.17 (0-0.38; n = 6)
Triakidae			
	27	0.03 (n = 6)	0.03 ± 0.05 (0-0.1; n = 6)
<b>Heterodontiformes</b>			
Heterodontidae			
	40	0.05 ± 0.05 (0-0.1; n = 9)	0.05 ± 0.05 (0-0.1; n = 9)
Heterodontidae			
	40	0 (n = 4)	0 (n = 4)
Heterodontidae			
	40	0.17 ± 0.13 (0-0.57; n = 22)	0.17 ± 0.13 (0-0.58; n = 22)
Heterodontidae			
	40	0 (n = 7)	0 (n = 7)
Heterodontidae			
	40	0.19 (n = 2)	0.19 (n = 2)
<b>Hexanchiformes</b>			
Chlamydoselachidae			
	49	0.38 ± 0.17 (0.19-0.48; n = 3)	0.38 ± 0.17 (0.19-0.48; n = 3)
Hexanchidae			
	49	0 (n = 4)	0 (n = 4)
Hexanchidae			
	49	0.2 (n = 2)	0.2 (n = 2)
Hexanchidae			
	49	1.1 ± 0.53 (0.49-1.46; n = 3)	1.12 ± 0.55 (0.49-1.48; n = 3)
Hexanchidae			
	49	0.37 ± 0.26 (0-0.59; n = 4)	0.37 ± 0.26 (0-0.59; n = 4)
<b>Lamniformes</b>			
Alopiidae			
	35	0.57 ± 0.42 (0-1.25; n = 20)	0.58 ± 0.42 (0-1.26; n = 20)
Alopiidae			
	35	0.27 ± 0.21 (0-0.77; n = 9)	0.27 ± 0.21 (0-0.77; n = 9)
Alopiidae			
	35	0.09 ± 0.09 (0-0.19; n = 11)	0.09 ± 0.09 (0-0.19; n = 11)
Cetorhinidae			
	35	0.48 (n = 2)	0.48 (n = 2)
Lamnidae			
	35	0.4 ± 0.65 (0-1.92; n = 17)	0.41 ± 0.65 (0-1.95; n = 17)
Lamnidae			
	35	1.02 ± 0.69 (0-2.02; n = 24)	1.04 ± 0.7 (0-2.06; n = 24)

APPENDIX 1  
(Continued)

	Figure(s)	p-distance	K2P distance
Lamnidae			
<i>Isurus paucus</i>	35	0.32 ± 0.26 (0-0.78; n = 6)	0.32 ± 0.26 (0-0.79; n = 6)
Lamnidae			
<i>Lamna ditropis</i>	35	0.38 (n = 2)	0.39 (n = 2)
Lamnidae			
<i>Lamna nasus</i>	35	0.65 ± 0.59 (0-1.44; n = 10)	0.66 ± 0.6 (0-1.46; n = 10)
Megachasmidae			
<i>Megachasma pelagios</i>	35	0.35 ± 0.33 (0-0.98; n = 6)	0.35 ± 0.33 (0-0.99; n = 6)
Mitsukurinidae			
<i>Mitsukurina owstoni</i>	35	0.13 ± 0.11 (0-0.19; n = 3)	0.13 ± 0.11 (0-0.19; n = 3)
Odontaspidae			
<i>Carcharias taurus</i>	35	0.17 ± 0.12 (0-0.39; n = 6)	0.17 ± 0.12 (0-0.39; n = 6)
Odontaspidae			
<i>Odontaspis ferox</i>	35	0 (n = 2)	0 (n = 2)
Pseudocarchariidae			
<i>Pseudocarcharias kamoharui</i>	35	0.87 ± 0.81 (0.1-1.73; n = 4)	0.88 ± 0.83 (0.1-1.76; n = 4)
<b>Orectolobiformes</b>			
Brachaeluridae			
<i>Brachaelurus colcloughi</i>	38	1.01 ± 0.9 (0-2.01; n = 4)	1.02 ± 0.92 (0-2.04; n = 4)
Ginglymostomatidae			
<i>Ginglymostoma cf. cirratum</i>	37	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Ginglymostomatidae			
<i>Ginglymostoma cirratum</i>	37	0.1 ± 0.06 (0-0.19; n = 9)	0.1 ± 0.06 (0-0.19; n = 9)
Ginglymostomatidae			
<i>Nebrius ferrugineus</i>	37	0.29 (n = 2)	0.29 (n = 2)
Ginglymostomatidae			
<i>Pseudoginglymostoma brevicaudatum</i>	37	0 (n = 3)	0 (n = 3)
Hemiscylliidae			
<i>Chiloscyllium cf. punctatum</i>	36	0.1 (n = 2)	0.1 (n = 2)
Hemiscylliidae			
<i>Chiloscyllium griseum</i>	36	0.1 (n = 2)	0.1 (n = 2)
Hemiscylliidae			
<i>Chiloscyllium hasseltii</i>	36	0.07 ± 0.09 (0-0.38; n = 13)	0.07 ± 0.09 (0-0.38; n = 13)
Hemiscylliidae			
<i>Chiloscyllium indicum</i>	36	0.13 ± 0.11 (0-0.58; n = 42)	0.13 ± 0.11 (0-0.58; n = 42)
Hemiscylliidae			
<i>Chiloscyllium plagiosum</i>	36	0 (n = 3)	0 (n = 3)
Hemiscylliidae			
<i>Chiloscyllium punctatum</i>	36	0.31 ± 0.24 (0-0.96; n = 54)	0.31 ± 0.24 (0-0.96; n = 54)
Hemiscylliidae			
<i>Hemiscyllium ocellatum</i>	36	0 (n = 3)	0 (n = 3)
Orectolobidae			
<i>Eucrossorhinus dasyptegon</i>	38	0 (n = 2)	0 (n = 2)
Orectolobidae			
<i>Orectolobus floridanus</i>	38	0 (n = 3)	0 (n = 3)
Orectolobidae			
<i>Orectolobus halei</i>	38	0.09 ± 0.1 (0-0.19; n = 7)	0.09 ± 0.1 (0-0.19; n = 7)
Orectolobidae			
<i>Orectolobus hutchinsi</i>	38	0 (n = 10)	0 (n = 10)
Orectolobidae			
<i>Orectolobus maculatus</i>	38	0 (n = 3)	0 (n = 3)
Orectolobidae			
<i>Orectolobus parvimaculatus</i>	38	0 (n = 3)	0 (n = 3)
Parascylliidae			
<i>Parascyllium collaris</i>	39	0.09 ± 0.06 (0-0.19; n = 6)	0.09 ± 0.06 (0-0.19; n = 6)
Rhincodontidae			
<i>Rhincodon typus</i>	37	0 (n = 6)	0 ± 0 (0-0; n = 6)
Stegostomatidae			
<i>Stegostoma fasciatum</i>	37	0.36 ± 0.22 (0-0.67; n = 12)	0.36 ± 0.23 (0-0.67; n = 12)
<b>Pristiophoriformes</b>			
Pristiophoridae			
<i>Pliotrema warreni</i>	48	0 (n = 2)	0 (n = 2)
Pristiophoridae			
<i>Pristiophorus cirratus</i>	48	0.1 (n = 2)	0.1 (n = 2)
<b>Squaliformes</b>			
Centrophoridae			
<i>Centrophorus cf. lusitanicus</i>	43	0.3 ± 0.14 (0.1-0.48; n = 4)	0.3 ± 0.14 (0.1-0.48; n = 4)



APPENDIX I  
(Continued)

	Figure(s)	p-distance	K2P distance
Centrophoridae	43	0.06 ± 0.06 (0-0.19; n = 13)	0.06 ± 0.06 (0-0.19; n = 13)
Centrophoridae	43	0.32 ± 0.2 (0.1-0.48; n = 3)	0.32 ± 0.2 (0.1-0.48; n = 3)
Centrophoridae	43	0.1 (n = 2)	0.1 (n = 2)
Centrophoridae	43	0.61 ± 0.4 (0-1.34; n = 10)	0.62 ± 0.41 (0-1.36; n = 10)
Centrophoridae	43	0 (n = 2)	0 (n = 2)
Centrophoridae	43	0.19 ± 0.17 (0-0.29; n = 3)	0.19 ± 0.17 (0-0.29; n = 3)
Centrophoridae	43	0.12 ± 0.15 (0-0.86; n = 50)	0.12 ± 0.15 (0-0.87; n = 50)
Centrophoridae	43	0.04 ± 0.05 (0-0.1; n = 5)	0.04 ± 0.05 (0-0.1; n = 5)
Centrophoridae	44	0.32 ± 0.29 (0-1.05; n = 26)	0.32 ± 0.3 (0-1.06; n = 26)
Centrophoridae	44	0.52 ± 0.3 (0-0.96; n = 5)	0.52 ± 0.3 (0-0.97; n = 5)
Centrophoridae	44	0.1 (n = 2)	0.1 (n = 2)
Dalatiidae	47	0.18 ± 0.17 (0-0.48; n = 17)	0.18 ± 0.17 (0-0.48; n = 17)
Dalatiidae	47	0.77 ± 0.33 (0.38-0.96; n = 3)	0.77 ± 0.34 (0.38-0.97; n = 3)
Dalatiidae	47	0.96 ± 0.44 (0.48-1.34; n = 3)	0.97 ± 0.45 (0.48-1.36; n = 3)
Dalatiidae	47	0.77 (n = 2)	0.77 (n = 2)
Echinorhinidae	48	0.38 ± 0.17 (0.19-0.48; n = 3)	0.38 ± 0.17 (0.19-0.48; n = 3)
Echinorhinidae	48	0.1 (n = 2)	0.1 (n = 2)
Etmopteridae	46	0.34 ± 0.21 (0-0.77; n = 10)	0.34 ± 0.21 (0-0.77; n = 10)
Etmopteridae	46	0.14 ± 0.26 (0-0.77; n = 11)	0.14 ± 0.26 (0-0.77; n = 11)
Etmopteridae	46	0.1 ± 0.1 (0-0.19; n = 4)	0.1 ± 0.1 (0-0.19; n = 4)
Etmopteridae	46	0.1 (n = 2)	0.1 (n = 2)
Etmopteridae	46	0.67 (n = 2)	0.67 (n = 2)
Etmopteridae	46	0.19 ± 0.2 (0-0.57; n = 10)	0.2 ± 0.2 (0-0.58; n = 10)
Etmopteridae	46	0.29 ± 0.25 (0-0.57; n = 4)	0.29 ± 0.25 (0-0.58; n = 4)
Etmopteridae	46	0.33 ± 0.23 (0-0.57; n = 7)	0.33 ± 0.23 (0-0.58; n = 7)
Etmopteridae	46	0.33 ± 0.23 (0-1.05; n = 20)	0.34 ± 0.23 (0-1.06; n = 20)
Etmopteridae	46	0.24 ± 0.23 (0-0.77; n = 21)	0.24 ± 0.23 (0-0.77; n = 21)
Etmopteridae	46	0.19 (n = 2)	0.19 (n = 2)
Oxynotidae	45	0.15 ± 0.17 (0-0.57; n = 14)	0.15 ± 0.17 (0-0.58; n = 14)
Oxynotidae	45	0 (n = 4)	0 (n = 4)
Somniosidae	45	0.11 ± 0.07 (0-0.19; n = 18)	0.11 ± 0.07 (0-0.19; n = 18)
Somniosidae	45	0.18 ± 0.15 (0-0.57; n = 17)	0.18 ± 0.15 (0-0.58; n = 17)
Somniosidae	45	0.23 ± 0.3 (0-1.63; n = 27)	0.23 ± 0.3 (0-1.65; n = 27)
Somniosidae	45	0.02 ± 0.04 (0-0.1; n = 12)	0.02 ± 0.04 (0-0.1; n = 12)
Somniosidae	45	0 (n = 5)	0 (n = 5)
Somniosidae	45	0.06 ± 0.05 (0-0.1; n = 5)	0.06 ± 0.05 (0-0.1; n = 5)

APPENDIX 1  
(Continued)

	Figure(s)	P-distance	K2P distance
Somniosidae			
<i>Somniosus pacificus</i>	45	0.11 ± 0.07 (0-0.19; n = 4)	0.11 ± 0.07 (0-0.19; n = 4)
Somniosidae			
<i>Zameus squamulosus</i>	45	0.41 ± 0.22 (0-0.57; n = 4)	0.42 ± 0.23 (0-0.58; n = 4)
Squalidae			
<i>Cirrhigaleus australis</i>	42	0.39 (n = 2)	0.39 (n = 2)
<i>Squalus acanthias</i>	41	0.21 ± 0.16 (0-0.96; n = 176)	0.22 ± 0.16 (0-0.97; n = 176)
<i>Squalus albifrons</i>	42	0.13 ± 0.05 (0.1-0.19; n = 3)	0.13 ± 0.05 (0.1-0.19; n = 3)
<i>Squalus brevirostris</i>	42	0 (n = 2)	0 (n = 2)
<i>Squalus cf. megalops</i>	42	0.28 ± 0.15 (0-0.67; n = 17)	0.28 ± 0.15 (0-0.67; n = 17)
<i>Squalus cf. mitsukurini</i>	42	0.09 ± 0.06 (0-0.19; n = 6)	0.09 ± 0.06 (0-0.19; n = 6)
<i>Squalus chloroculus</i>	42	0.15 ± 0.1 (0-0.29; n = 4)	0.15 ± 0.1 (0-0.29; n = 4)
<i>Squalus crassispinus</i>	42	0.51 ± 0.36 (0.1-0.77; n = 3)	0.52 ± 0.36 (0.1-0.77; n = 3)
<i>Squalus cubensis</i>	42	0.48 (n = 2)	0.48 (n = 2)
<i>Squalus edmundsi</i>	42	0.26 ± 0.14 (0.1-0.38; n = 3)	0.26 ± 0.14 (0.1-0.38; n = 3)
<i>Squalus formosus</i>	42	0.13 ± 0.11 (0-0.19; n = 3)	0.13 ± 0.11 (0-0.19; n = 3)
<i>Squalus grahami</i>	42	0 (n = 2)	0 (n = 2)
<i>Squalus japonicus</i>	42	0 (n = 3)	0 (n = 3)
<i>Squalus megalops</i>	42	0.18 ± 0.18 (0-0.57; n = 7)	0.18 ± 0.18 (0-0.58; n = 7)
<i>Squalus montalbani</i>	42	0.1 (n = 2)	0.1 (n = 2)
<i>Squalus nasutus</i>	42	0.1 (n = 2)	0.1 (n = 2)
<i>Squalus sp.</i>	42	0.3 ± 0.2 (0-0.67; n = 8)	0.3 ± 0.2 (0-0.68; n = 8)
<i>Squalus suckleyi</i>	41	0.62 ± 0.31 (0.19-1.44; n = 8)	0.63 ± 0.31 (0.19-1.45; n = 8)
<b>Squatiniformes</b>			
<i>Squatina aculeata</i>	48	0.07 ± 0.08 (0-0.29; n = 11)	0.07 ± 0.08 (0-0.29; n = 11)
<i>Squatina californica</i>	48	0.36 ± 0.18 (0-0.57; n = 7)	0.37 ± 0.19 (0-0.58; n = 7)
<i>Squatina dumeril</i>	48	0.54 ± 0.4 (0-1.15; n = 8)	0.55 ± 0.4 (0-1.16; n = 8)
<i>Squatina formosa</i>	48	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
<i>Squatina oculata</i>	48	0 (n = 12)	0 (n = 12)
<i>Squatina tergocellatoides</i>	48	0 (n = 2)	0 (n = 2)
<b>Rajiformes</b>			
Anacanthobatidae			
<i>Cruriraja hulleyi</i>	77	0.18 ± 0.29 (0-0.77; n = 10)	0.18 ± 0.29 (0-0.77; n = 10)
Anacanthobatidae			
<i>Sinobatis bulbicauda</i>	77	0.1 (n = 2)	0.1 (n = 2)
Arhynchobatidae			
<i>Atlantoraja cyclophora</i>	77	0.26 ± 0.14 (0.1-0.38; n = 3)	0.26 ± 0.14 (0.1-0.38; n = 3)
Arhynchobatidae			
<i>Atlantoraja platana</i>	77	0.1 (n = 2)	0.1 (n = 2)
Arhynchobatidae			
<i>Bathyraja brachyurops</i>	76	0.67 ± 0.34 (0-0.96; n = 4)	0.68 ± 0.34 (0-0.97; n = 4)
Arhynchobatidae			
<i>Bathyraja aleutica</i>	76	0.96 (n = 2)	0.96 (n = 2)
Arhynchobatidae			
<i>Bathyraja griseocauda</i>	76	0.1 (n = 2)	0.1 (n = 2)

APPENDIX I  
(Continued)

	Figure(s)	p-distance	K2P distance
Arhynchobatidae	76	0.37 ± 0.14 (0.1-0.48; n = 4)	0.37 ± 0.14 (0.1-0.48; n = 4)
Arhynchobatidae	76	0.25 ± 0.22 (0-0.38; n = 3)	0.26 ± 0.22 (0-0.39; n = 3)
Arhynchobatidae	76	1.66 ± 0.64 (0.38-2.01; n = 4)	1.69 ± 0.65 (0.38-2.05; n = 4)
Arhynchobatidae	76	0.29 ± 0.46 (0-1.15; n = 8)	0.29 ± 0.46 (0-1.16; n = 8)
Arhynchobatidae	76	0.19 (n = 2)	0.19 (n = 2)
Arhynchobatidae	76	0.32 ± 0.28 (0-0.48; n = 3)	0.32 ± 0.28 (0-0.48; n = 3)
Arhynchobatidae	76	0.73 ± 0.59 (0-2.3; n = 19)	0.74 ± 0.6 (0-2.35; n = 19)
Arhynchobatidae	77	0.03 ± 0.05 (0-0.19; n = 19)	0.03 ± 0.05 (0-0.19; n = 19)
Arhynchobatidae	77	0.1 (n = 2)	0.1 (n = 2)
Arhynchobatidae	77	0.89 ± 0.44 (0.38-1.15; n = 3)	0.9 ± 0.45 (0.38-1.16; n = 3)
Arhynchobatidae	77	0.59 ± 0.5 (0-1.25; n = 16)	0.6 ± 0.5 (0-1.26; n = 16)
Arhynchobatidae	77	0.25 ± 0.22 (0-0.38; n = 3)	0.25 ± 0.22 (0-0.38; n = 3)
Arhynchobatidae	77	0.21 ± 0.21 (0-0.57; n = 10)	0.21 ± 0.21 (0-0.58; n = 10)
Arhynchobatidae	76	0.26 ± 0.14 (0.1-0.38; n = 3)	0.26 ± 0.14 (0.1-0.38; n = 3)
Arhynchobatidae	76	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Arhynchobatidae	76	0 (n = 3)	0 (n = 3)
Arhynchobatidae	77	0.96 (n = 2)	0.97 (n = 2)
Arhynchobatidae	77	0.57 (n = 2)	0.58 (n = 2)
Arhynchobatidae	77	0 (n = 2)	0 (n = 2)
Dasyatidae	56	2.08 ± 0.67 (1.44-2.78; n = 3)	2.11 ± 0.69 (1.46-2.83; n = 3)
Dasyatidae	56	0.1 (n = 2)	0.1 (n = 2)
Dasyatidae	56	0.31 ± 0.14 (0-0.67; n = 24)	0.31 ± 0.15 (0-0.68; n = 24)
Dasyatidae	56	0.15 ± 0.05 (0.1-0.19; n = 4)	0.15 ± 0.05 (0.1-0.19; n = 4)
Dasyatidae	56	0 (n = 4)	0 (n = 4)
Dasyatidae	55	0 (n = 11)	0 (n = 11)
Dasyatidae	55	0.25 ± 0.17 (0-0.57; n = 5)	0.25 ± 0.17 (0-0.58; n = 5)
Dasyatidae	55	0.1 (n = 2)	0.1 (n = 2)
Dasyatidae	56	1.44 (n = 2)	1.45 (n = 2)
Dasyatidae	56	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Dasyatidae	56	0 (n = 3)	0 (n = 3)
Dasyatidae	56	0.14 ± 0.14 (0-0.48; n = 12)	0.14 ± 0.14 (0-0.48; n = 12)
Dasyatidae	50	0.76 ± 0.86 (0-3.07; n = 9)	0.77 ± 0.87 (0-3.14; n = 9)
Dasyatidae	50	0.49 ± 0.47 (0-2.11; n = 39)	0.49 ± 0.48 (0-2.15; n = 39)
Dasyatidae	50	0.33 ± 0.37 (0-1.82; n = 29)	0.33 ± 0.38 (0-1.84; n = 29)
Dasyatidae	51	0.91 ± 0.45 (0-1.15; n = 4)	0.92 ± 0.45 (0-1.16; n = 4)
Dasyatidae	54	0.19 ± 0.1 (0.1-0.29; n = 3)	0.19 ± 0.1 (0.1-0.29; n = 3)

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(Continued)

	Figure(s)	p-distance	K2P distance
Dasyatidae	53	0.51 ± 0.44 (0-1.05; n = 7)	0.52 ± 0.44 (0-1.06; n = 7)
Dasyatidae	51	0.53 ± 0.34 (0-1.53; n = 13)	0.53 ± 0.34 (0-1.55; n = 13)
Dasyatidae	52	0.75 ± 0.42 (0.1-1.15; n = 4)	0.76 ± 0.42 (0.1-1.16; n = 4)
Dasyatidae	54	0.09 ± 0.09 (0-0.38; n = 20)	0.09 ± 0.09 (0-0.38; n = 20)
Dasyatidae	53	0.06 ± 0.11 (0-0.57; n = 41)	0.06 ± 0.11 (0-0.58; n = 41)
Dasyatidae	50	0 (n = 3)	0 (n = 3)
Dasyatidae	50	0.77 (n = 2)	0.77 (n = 2)
Dasyatidae	54	0.16 ± 0.18 (0-0.58; n = 7)	0.16 ± 0.18 (0-0.58; n = 7)
Dasyatidae	53	0.16 ± 0.15 (0-0.67; n = 21)	0.16 ± 0.15 (0-0.67; n = 21)
Dasyatidae	50	0.29 (n = 2)	0.29 (n = 2)
Dasyatidae	51	0.61 ± 0.37 (0-1.92; n = 32)	0.61 ± 0.37 (0-1.95; n = 32)
Dasyatidae	52	0.77 ± 0.77 (0-2.39; n = 12)	0.78 ± 0.78 (0-2.45; n = 12)
Dasyatidae	52	0.25 ± 0.16 (0-0.57; n = 12)	0.25 ± 0.16 (0-0.58; n = 12)
Dasyatidae	52	0.17 ± 0.12 (0-0.48; n = 15)	0.17 ± 0.12 (0-0.48; n = 15)
Dasyatidae	52	0.14 ± 0.09 (0-0.29; n = 11)	0.14 ± 0.09 (0-0.29; n = 11)
Dasyatidae	53	0.82 ± 0.4 (0.19-1.63; n = 6)	0.82 ± 0.41 (0.19-1.65; n = 6)
Dasyatidae	58	0.67 ± 0.35 (0-1.53; n = 33)	0.67 ± 0.35 (0-1.56; n = 33)
Dasyatidae	58	0.63 ± 0.61 (0-1.82; n = 8)	0.64 ± 0.62 (0-1.85; n = 8)
Dasyatidae	58	0.56 ± 0.46 (0-0.96; n = 5)	0.56 ± 0.46 (0-0.97; n = 5)
Dasyatidae	58	0.36 ± 0.37 (0-0.86; n = 6)	0.37 ± 0.38 (0-0.87; n = 6)
Dasyatidae	57	0.56 ± 0.31 (0-1.34; n = 14)	0.56 ± 0.31 (0-1.36; n = 14)
Dasyatidae	57	0.26 ± 0.14 (0.1-0.38; n = 3)	0.26 ± 0.14 (0.1-0.38; n = 3)
Dasyatidae	57	0.39 ± 0.2 (0.1-0.77; n = 9)	0.4 ± 0.2 (0.1-0.77; n = 9)
Dasyatidae	57	0.59 ± 0.44 (0-1.72; n = 12)	0.59 ± 0.45 (0-1.74; n = 12)
Dasyatidae	55	0 (n = 2)	0 (n = 2)
Dasyatidae	59	0.37 ± 0.44 (0-2.01; n = 28)	0.37 ± 0.44 (0-2.04; n = 28)
Dasyatidae	59	0.91 ± 0.65 (0-1.63; n = 7)	0.92 ± 0.65 (0-1.66; n = 7)
Dasyatidae	56	0.1 (n = 2)	0.1 (n = 2)
Dasyatidae	54	0 (n = 4)	0 (n = 4)
Dasyatidae	54	0.19 (n = 2)	0.19 (n = 2)
Gymnuridae	64	0.18 ± 0.14 (0-0.48; n = 10)	0.18 ± 0.14 (0-0.48; n = 10)
Gymnuridae	64	0.51 ± 0.29 (0-1.25; n = 12)	0.52 ± 0.29 (0-1.26; n = 12)
Gymnuridae	64	0.46 ± 0.2 (0.1-0.77; n = 5)	0.46 ± 0.2 (0.1-0.77; n = 5)
Gymnuridae	64	0.47 ± 0.22 (0.1-0.96; n = 7)	0.48 ± 0.22 (0.1-0.96; n = 7)
Gymnuridae	64	0.15 ± 0.1 (0-0.29; n = 4)	0.15 ± 0.1 (0-0.29; n = 4)
Gymnuridae	64	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)

APPENDIX I  
(Continued)

	Figure(s)	p-distance	K2P distance
Gymnuriidae	64		
Hexatrygonidae	66	0.58 ± 0.44 (0.1-1.39; n = 7)	0.59 ± 0.44 (0.1-1.41; n = 7)
Mobulidae	61	0.1 (n = 2)	0.1 (n = 2)
Mobulidae	61	0.72 (n = 2)	0.72 (n = 2)
Mobulidae	61	0.38 (n = 2)	0.38 (n = 2)
Mobulidae	61	0.22 ± 0.17 (0-0.48; n = 12)	0.22 ± 0.17 (0-0.48; n = 12)
Mobulidae	61	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Mobulidae	61	0.07 ± 0.09 (0-0.29; n = 8)	0.07 ± 0.09 (0-0.29; n = 8)
Mobulidae	61	0.24 ± 0.18 (0-0.67; n = 8)	0.24 ± 0.19 (0-0.68; n = 8)
Myliobatidae	63	0.19 (n = 2)	0.19 (n = 2)
Myliobatidae	63	1.05 (n = 2)	1.06 (n = 2)
Myliobatidae	63	0.1 ± 0.1 (0-0.19; n = 4)	0.1 ± 0.1 (0-0.19; n = 4)
Myliobatidae	63	0.42 ± 0.44 (0-1.73; n = 14)	0.42 ± 0.45 (0-1.76; n = 14)
Myliobatidae	63	0.55 ± 0.32 (0-1.53; n = 34)	0.56 ± 0.32 (0-1.55; n = 34)
Myliobatidae	63	0.04 ± 0.06 (0-0.19; n = 9)	0.04 ± 0.06 (0-0.19; n = 9)
Myliobatidae	62	0.1 (n = 2)	0.1 (n = 2)
Myliobatidae	62	0.8 ± 0.64 (0-1.64; n = 10)	0.81 ± 0.65 (0-1.67; n = 10)
Myliobatidae	62	0 (n = 2)	0 (n = 2)
Myliobatidae	62	0.31 ± 0.23 (0-0.96; n = 15)	0.32 ± 0.23 (0-0.96; n = 15)
Myliobatidae	62	0.27 ± 0.2 (0-0.48; n = 5)	0.27 ± 0.2 (0-0.48; n = 5)
Myliobatidae	62	0.07 ± 0.06 (0-0.19; n = 7)	0.07 ± 0.06 (0-0.19; n = 7)
Myliobatidae	62	0.19 ± 0.15 (0-0.38; n = 4)	0.19 ± 0.15 (0-0.38; n = 4)
Myliobatidae	62	0.54 ± 0.24 (0-1.15; n = 18)	0.54 ± 0.25 (0-1.16; n = 18)
Myliobatidae	62	0.1 (n = 2)	0.1 (n = 2)
Myliobatidae	62	0.24 ± 0.27 (0-1.05; n = 16)	0.24 ± 0.28 (0-1.06; n = 16)
Myliobatidae	62	0.45 ± 0.3 (0.1-0.67; n = 3)	0.45 ± 0.31 (0.1-0.67; n = 3)
Narcinidae	70	0.43 ± 0.4 (0-0.86; n = 4)	0.44 ± 0.41 (0-0.87; n = 4)
Narkidae	70	0.29 (n = 2)	0.29 (n = 2)
Platyrhinidae	70	0 (n = 2)	0 (n = 2)
Plesiobatidae	64	0 (n = 3)	0 (n = 3)
Potamotrygonidae	60	0.29 (n = 2)	0.29 (n = 2)
Potamotrygonidae	60	0.1 (n = 2)	0.1 (n = 2)
Potamotrygonidae	60	0.1 (n = 2)	0.1 (n = 2)
Pristidae	68	0.03 (n = 7)	0.03 ± 0.05 (0-0.1; n = 7)
Pristidae	68	0.2 ± 0.15 (0-0.38; n = 4)	0.2 ± 0.15 (0-0.38; n = 4)
Pristidae	68	0 (n = 2)	0 (n = 2)
Pristidae	68	0.21 ± 0.26 (0-1.15; n = 20)	0.21 ± 0.26 (0-1.16; n = 20)

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(Continued)

	Figure(s)	p-distance	K2P distance
Pristidae			
<i>Pristis perotteti</i>	68	0.36 ± 0.32 (0-1.06; n = 17)	0.36 ± 0.32 (0-1.06; n = 17)
Pristidae			
<i>Pristis zijsron</i>	68	0.16 ± 0.23 (0-0.48; n = 6)	0.16 ± 0.23 (0-0.48; n = 6)
Rajidae			
<i>Amblyraja doellojuradoi</i>	74	0.51 ± 0.23 (0.38-0.77; n = 3)	0.51 ± 0.23 (0.38-0.77; n = 3)
Rajidae			
<i>Amblyraja hyperboreal/jensenilbadia<sup>a</sup></i>	74	0.52 ± 0.28 (0-1.05; n = 9)	0.53 ± 0.28 (0-1.06; n = 9)
Rajidae			
<i>Amblyraja radiata</i>	74	0.82 ± 0.33 (0-1.44; n = 14)	0.83 ± 0.33 (0-1.46; n = 14)
Rajidae			
<i>Dipturus australis</i>	71	0.07 ± 0.06 (0-0.19; n = 6)	0.07 ± 0.06 (0-0.19; n = 6)
Rajidae			
<i>Dipturus batis/oxyrinchus<sup>a</sup></i>	71	0.41 ± 0.34 (0-0.77; n = 11)	0.42 ± 0.34 (0-0.77; n = 11)
Rajidae			
<i>Dipturus cerva</i>	71	0 (n = 3)	0 (n = 3)
Rajidae			
<i>Dipturus cf. batis 2</i>	71	0 (n = 2)	0 (n = 2)
Rajidae			
<i>Dipturus confusus</i>	71	0 (n = 2)	0 (n = 2)
Rajidae			
<i>Dipturus gudgeri</i>	71	0.45 ± 0.31 (0.1-0.68; n = 3)	0.45 ± 0.31 (0.1-0.68; n = 3)
Rajidae			
<i>Dipturus innominatus</i>	71	0.19 ± 0.15 (0-0.57; n = 11)	0.19 ± 0.15 (0-0.58; n = 11)
Rajidae			
<i>Dipturus laevis</i>	71	0.07 ± 0.06 (0-0.1; n = 3)	0.07 ± 0.06 (0-0.1; n = 3)
Rajidae			
<i>Dipturus leptocauda</i>	71	0 (n = 2)	0 (n = 2)
Rajidae			
<i>Dipturus linteus</i>	74	0.04 (n = 5)	0.04 ± 0.05 (0-0.1; n = 5)
Rajidae			
<i>Dipturus pullopunctata</i>	71	0 (n = 3)	0 (n = 3)
Rajidae			
<i>Dipturus sp. 4</i>	71	1.25 (n = 2)	1.26 (n = 2)
Rajidae			
<i>Dipturus springeri</i>	71	0 (n = 4)	0 (n = 4)
Rajidae			
<i>Leucoraja erinacea</i>	75	0.51 ± 0.19 (0.29-0.77; n = 4)	0.51 ± 0.19 (0.29-0.77; n = 4)
Rajidae			
<i>Leucoraja fullonica</i>	75	0.19 ± 0.15 (0-0.29; n = 4)	0.19 ± 0.15 (0-0.29; n = 4)
Rajidae			
<i>Leucoraja naevus</i>	75	0.14 ± 0.17 (0-0.57; n = 29)	0.14 ± 0.17 (0-0.58; n = 29)
Rajidae			
<i>Leucoraja ocellata</i>	75	0.19 (n = 2)	0.19 (n = 2)
Rajidae			
<i>Leucoraja wallacei</i>	75	0.36 ± 0.2 (0-0.77; n = 12)	0.36 ± 0.2 (0-0.77; n = 12)
Rajidae			
<i>Malacoraja senta</i>	75	0 (n = 3)	0 (n = 3)
Rajidae			
<i>Neoraja caerulea</i>	75	0 (n = 2)	0 (n = 2)
Rajidae			
<i>Okamejei cairae</i>	72	0.2 ± 0.11 (0-0.38; n = 13)	0.2 ± 0.11 (0-0.38; n = 13)
Rajidae			
<i>Okamejei cf. porosa</i>	72	0.38 ± 0.29 (0-0.77; n = 5)	0.38 ± 0.29 (0-0.77; n = 5)
Rajidae			
<i>Okamejei hollandi</i>	72	0.58 ± 0.29 (0-1.25; n = 14)	0.58 ± 0.3 (0-1.26; n = 14)
Rajidae			
<i>Okamejei jensenae</i>	75	0.1 (n = 2)	0.1 (n = 2)
Rajidae			
<i>Raja asterias</i>	73	0.26 ± 0.14 (0.1-0.38; n = 3)	0.26 ± 0.14 (0.1-0.38; n = 3)
Rajidae			
<i>Raja binoculata</i>	71	0.58 (n = 2)	0.58 (n = 2)
Rajidae			
<i>Raja cf. miraletus 1</i>	73	0.12 ± 0.06 (0-0.19; n = 6)	0.12 ± 0.06 (0-0.19; n = 6)
Rajidae			
<i>Raja cf. miraletus 2</i>	73	0.23 ± 0.09 (0.1-0.38; n = 5)	0.23 ± 0.09 (0.1-0.38; n = 5)
Rajidae			
<i>Raja clavata</i>	73	0.58 ± 0.38 (0-1.05; n = 9)	0.59 ± 0.38 (0-1.06; n = 9)
Rajidae			
<i>Raja eglanteria</i>	75	0.78 ± 0.43 (0-1.15; n = 4)	0.79 ± 0.43 (0-1.16; n = 4)
Rajidae			
<i>Raja miraletus</i>	73	0.2 ± 0.18 (0-0.67; n = 12)	0.2 ± 0.18 (0-0.67; n = 12)

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(Continued)

	Figure(s)	p-distance	K2P distance
Rajidae	<i>Raja rhina</i>	71	0.12 ± 0.19 (0-0.77; n = 17)
Rajidae	<i>Raja straeleni</i>	73	0.16 ± 0.09 (0-0.29; n = 9)
Rajidae	<i>Raja velezi</i>	75	0 (n = 3)
Rajidae	<i>Rajella caudaspinosa</i>	74	0 (n = 2)
Rajidae	<i>Rajella fyllae</i>	74	0.17 ± 0.17 (0-0.57; n = 21)
Rajidae	<i>Rajella kukujevi</i>	74	0.15 ± 0.1 (0-0.29; n = 4)
Rajidae	<i>Rajella leopardus</i>	74	0.12 ± 0.1 (0-0.29; n = 5)
Rajidae	<i>Rajella</i> sp.	74	0 (n = 2)
Rajidae	<i>Rostroraja alba</i>	75	0 (n = 6)
Rajidae	<i>Spiriraja whiteleyi</i>	71	0.1 (n = 2)
Rajidae	<i>Zearaja chilensis</i>	71	0.19 ± 0.14 (0-0.48; n = 8)
Rajidae	<i>Zearaja flavirostris</i>	71	0.19 ± 0.17 (0-0.29; n = 3)
Rajidae	<i>Zearaja nasuta</i>	71	0.31 ± 0.11 (0.1-0.48; n = 5)
Rhinidae	<i>Rhina ancylostoma</i>	69	0.21 ± 0.15 (0-0.38; n = 6)
Rhinobatidae	<i>Aptychotrema rostrata</i>	69	0.38 (n = 2)
Rhinobatidae	<i>Glaucostegus cf. typus</i>	69	0 (n = 2)
Rhinobatidae	<i>Glaucostegus thouni</i>	69	0.05 ± 0.05 (0-0.1; n = 6)
Rhinobatidae	<i>Glaucostegus typus</i>	69	0.09 ± 0.11 (0-0.29; n = 15)
Rhinobatidae	<i>Rhinobatos annulatus</i>	69	0 (n = 5)
Rhinobatidae	<i>Rhinobatos cemicutis</i>	69	0 (n = 2)
Rhinobatidae	<i>Rhinobatos cf. schlegelii</i>	69	0.17 ± 0.15 (0-0.29; n = 5)
Rhinobatidae	<i>Rhinobatos glaucostigma</i>	68	0.17 ± 0.22 (0-0.57; n = 8)
Rhinobatidae	<i>Rhinobatos productus</i>	68	0.23 ± 0.17 (0-0.57; n = 11)
Rhinobatidae	<i>Rhinobatos rhinobatos</i>	69	0.19 ± 0.14 (0-0.57; n = 20)
Rhinobatidae	<i>Rhinobatos</i> sp. 1	69	0.1 (n = 2)
Rhinobatidae	<i>Zapteryx exasperata</i>	69	0.1 (n = 2)
Rhinopteridae	<i>Rhinoptera bonasus</i>	61	0.1 ± 0.21 (0-0.77; n = 18)
Rhinopteridae	<i>Rhinoptera cf. steindachneri</i>	61	0.26 ± 0.18 (0-0.67; n = 8)
Rhinopteridae	<i>Rhinoptera javanica</i>	61	0.86 (n = 2)
Rhinopteridae	<i>Rhinoptera jayakari</i>	61	0.79 ± 0.57 (0-1.63; n = 10)
Rhinopteridae	<i>Rhinoptera neglecta</i>	61	0.12 ± 0.1 (0-0.29; n = 5)
Rhinopteridae	<i>Rhinoptera steindachneri</i>	61	0.28 ± 0.15 (0.1-0.67; n = 7)
Rhynchobatidae	<i>Rhynchobatus australiae</i>	69	0.31 ± 0.29 (0-0.67; n = 12)
Rhynchobatidae	<i>Rhynchobatus cf. laevis</i>	69	0.16 ± 0.14 (0-0.38; n = 5)
Rhynchobatidae	<i>Rhynchobatus palpebratus</i>	69	0.19 (n = 2)
Torpedinidae	<i>Torpedo fuscomaculata</i>	70	0.25 ± 0.15 (0-0.58; n = 11)

APPENDIX 1  
(Continued)

	Figure(s)	p-distance	K2P distance
Torpedinidae			
<i>Torpedo macneilli</i>	70	0.1 ± 0.1 (0-0.19; n = 4)	0.1 ± 0.1 (0-0.19; n = 4)
<i>Torpedo nobilitana</i>	70	0.16 ± 0.14 (0-0.48; n = 8)	0.16 ± 0.14 (0-0.48; n = 8)
Torpedinidae			
<i>Torpedo sinuspersici</i>	70	2.12 (n = 2)	2.16 (n = 2)
Urolophidae			
<i>Trygonoptera imitata</i>	65	0.16 ± 0.08 (0.1-0.29; n = 4)	0.16 ± 0.08 (0.1-0.29; n = 4)
Urolophidae			
<i>Urobatis jamaicensis</i>	60	0 (n = 2)	0 (n = 2)
Urolophidae			
<i>Urolophus cructatus</i>	65	0.13 ± 0.05 (0.1-0.19; n = 3)	0.13 ± 0.05 (0.1-0.19; n = 3)
Urolophidae			
<i>Urolophus flavomosaiicus</i>	65	0 (n = 2)	0 (n = 2)
Urolophidae			
<i>Urolophus paucinaculatus</i>	65	0.29 ± 0.13 (0.1-0.48; n = 4)	0.29 ± 0.14 (0.1-0.48; n = 4)
Urotrygonidae			
<i>Urobatis concentricus</i>	60	0.15 ± 0.2 (0-0.38; n = 5)	0.15 ± 0.2 (0-0.38; n = 5)
Urotrygonidae			
<i>Urobatis halleri</i>	60	0.38 ± 0.2 (0-0.77; n = 9)	0.38 ± 0.2 (0-0.77; n = 9)
Urotrygonidae			
<i>Urobatis maculatus</i>	60	0.27 ± 0.18 (0-0.57; n = 5)	0.27 ± 0.19 (0-0.58; n = 5)
Urotrygonidae			
<i>Urotrygon rogersi</i>	60	0.48 (n = 2)	0.48 (n = 2)
Zanobatidae			
<i>Zanobatus schoenleinii</i>	67	0.34 ± 0.32 (0-0.96; n = 8)	0.34 ± 0.32 (0-0.96; n = 8)

<sup>a</sup>May represent a species complex.



## APPENDIX 2

## Representative specimens of named clusters recognized in this study deposited in GenBank (n=585)

Voucher information is presented as (1) availability of images (yes or no), (2) Collection Code and Collection number (e.g., BO-43, AF-106, etc.) for specimens collected by JNC and KJ and for which data (incl. images) are available in the on-line host specimen database (<http://elasmobranchs.tapewormdb.uconn.edu>), (3) and museum accession numbers for samples with physical vouchers (see Materials and Methods for museum abbreviations).

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
<b>Carcharhiniformes</b>					
Carcharhinidae	GN5801	JQ518620	yes; KC-5	male	Atlantic Ocean, U.S.A.
Carcharhinidae	GN287	JQ518609	no	female	South China Sea, Pacific Ocean, Philippines
Carcharhinidae	GN120	JQ518603	no	female	Norfolk Canyon, Atlantic Ocean, U.S.A.
Carcharhinidae	GN2959	JQ519102	yes; HBO-34; IPPS HBO34	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN3672	JQ519095	yes; BO-461; IPPS BO461	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN1246	JQ518604	yes; AU-72	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN5120	JQ518618	yes; AU-102	male	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN3639	JQ519094	yes; BO-427; IPPS BO427	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN3	JQ518611	no	female	South Australia, Great Australian Bight, Indian Ocean, Australia
Carcharhinidae	GN6214	JQ518625	yes; MS05-5	female	Mississippi, Gulf of Mexico, U.S.A.
Carcharhinidae	GN1233	JQ519153	yes; AU-46; NTM S.14689-005	male	Northern Territory, Buffalo Creek, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN6628	JQ519130	no; MMF-39543; MMF 39543	unknown	Madeira, Atlantic Ocean, Portugal
Carcharhinidae	GN6585	JQ518628	yes; MM-302	male	Persian Gulf, Iran
Carcharhinidae	GN3368	JQ518613	yes; BO-97	female	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN642	JQ518627	no	female	KawZulu-Natal, Indian Ocean, South Africa
Carcharhinidae	GN5061	JQ518616	yes; AU-26	male	Northern Territory, Buffalo Creek, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN5	JQ518615	no	female	Gulf of Aquaba, Egypt

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Carcharhinidae	GN7098	JQ518629	yes; VN-100	unknown	South China Sea, Pacific Ocean, Vietnam
Carcharhinidae	GN1107	JQ519077	yes; BJ-525; IBUNAM PE9494	male	Baja California, Gulf of California, Pacific Ocean, Mexico
Carcharhinidae	GN1264	JQ518606	yes; AU-109	male	Northern Territory, Fog Bay Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN1258	JQ518605	yes; AU-93	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN4597	JQ519073	yes; KA-303; CAS 229042	female	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Carcharhinidae	GN6059	JQ518622	yes; SE-218	male	Atlantic Ocean, Senegal
Carcharhinidae	GN1267	JQ519154	yes; AU-112; NTM S.14690-002	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN544	JQ518619	yes	female	Hawaii, Pacific Ocean, U.S.A.
Carcharhinidae	GN6247	JQ518626	yes; MS05-495	female	Florida, Indian Pass, Gulf of Mexico, U.S.A.
Carcharhinidae	GN6083	JQ518623	yes; SE-243	male	Atlantic Ocean, Senegal
Carcharhinidae	GN5802	JQ518621	yes; KC-7	male	Atlantic Ocean, U.S.A.
Carcharhinidae	GN611	JQ518624	no	male	Hawaii, Pacific Ocean, U.S.A.
Carcharhinidae	GN2982	JQ518610	yes; HBO-72	unknown	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN1269	JQ518607	yes; AU-114	male	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN3213	JQ518612	yes; SE-59	female	Atlantic Ocean, Senegal
Carcharhinidae	GN233	JQ518608	no	male	Grand Bahama Island, Caribbean Sea, Atlantic Ocean, Bahamas
Carcharhinidae	GN903	JQ518632	no	unknown	South Carolina Atlantic Ocean, U.S.A.
Carcharhinidae	GN481	JQ518614	no	female	Caribbean Sea, Atlantic Ocean, Trinidad
Carcharhinidae	GN4454	JQ519065	yes; KA-160; CAS 229028	male	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Carcharhinidae	GN899	JQ518631	no	unknown	South Carolina, Atlantic Ocean, U.S.A.
Carcharhinidae	GN2957	JQ519101	yes; HBO-32; IPPS HBO32	female?	Sarawak, South China Sea, Pacific Ocean, Malaysia

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Carcharhinidae	GN5086	JQ518617	yes; AU-64	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN8	JQ518630	no	male	Red Sea, Egypt
Carcharhinidae	GN239	JQ518633	no	male	Maryland, Atlantic Ocean, U.S.A.
Carcharhinidae	GN5271	JQ519164	yes; BJ-382; TCWC 7574.01	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Carcharhinidae	GN3377	JQ519085	yes; BO-107; IPMB 38.14.03	female	Sabah, Kinabatangan River, Malaysia
Carcharhinidae	GN2669	JQ518634	no	unknown	northern Indian Ocean, Pakistan
Carcharhinidae	GN6502	JQ518636	no	unknown	Northern Territory, West Alligator River System, Australia
Carcharhinidae	GN6505	JQ518637	no	unknown	Northern Territory, West Alligator River System, Australia
Carcharhinidae	GN3682	JQ518635	yes; BO-471	unknown	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN1543	JQ518638	no	male	Maranhao, Atlantic Ocean, Brazil
Carcharhinidae	GN1670	JQ518639	no	male	Maharashtra, Indian Ocean, India
Carcharhinidae	GN4240	JQ519056	yes; KA-67; ANFC H 7083-01	male	South Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Carcharhinidae	GN2014	JQ518640	yes; GA-13	female	Mozambique Channel, Indian Ocean, Madagascar
Carcharhinidae	GN3646	JQ518641	yes; BO-435	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN1056	JQ518642	no	female	Pacific Ocean, Panama
Carcharhinidae	GN5055	JQ518644	yes; AU-17	male	Northern Territory Buffalo Creek
Carcharhinidae	GN25	JQ518643	no	female	Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN5435	JQ518645	yes; BJ-780	female	Florida Atlantic Ocean, U.S.A. Baja California Sur, Gulf of California Pacific Ocean, Mexico
Carcharhinidae	GN6632	JQ518653	yes; MM-4	female	Gulf of Oman, Iran
Carcharhinidae	GN6060	JQ518652	yes; SE-219	male	Atlantic Ocean, Senegal
Carcharhinidae	GN5137	JQ518649	yes; AU-120	male	Northern Territory Fog Bay Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN2955	JQ519100	yes; HBO-30; IPPS HBO30	male	Sarawak, South China Sea, Pacific Ocean, Malaysia

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Carcharhinidae	GN487	JQ518646	no	female	Caribbean Sea, Atlantic Ocean, Trinidad
Carcharhinidae	GN5298	JQ518650	yes; BJ-529	unknown	Baja California, Gulf of California, Pacific Ocean, Mexico
Carcharhinidae	GN3686	JQ519096	yes; BO-475; IPPS BO475	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN510	JQ518648	no	female	Caribbean Sea, Atlantic Ocean, Trinidad
Carcharhinidae	GN5087	JQ518647	yes; AU-65	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Carcharhinidae	GN5662	JQ518651	yes; DEL-5	male	Florida, Atlantic Ocean, U.S.A.
Carcharhinidae	GN6769	JQ518655	no	unknown	Bay of Bengal, Indian Ocean, Thailand
Carcharhinidae	GN1677	JQ518654	no	female	Maharashtra, Indian Ocean, India
Carcharhinidae	GN3450	JQ519090	yes; BO-223; IPPS BO223	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Carcharhinidae	GN4420	JQ518656	yes; KA-126	unknown	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Hemigaleidae	GN1263	JQ518657	yes; AU-108	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Hemigaleidae	GN3694	JQ519097	yes; BO-483; IPPS BO483	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Hemigaleidae	GN4195	JQ519069	yes; KA-22; CAS 229035	male	East Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Hemigaleidae	GN3212	JQ518659	yes; SE-129	female	Atlantic Ocean, Senegal
Hemigaleidae	GN4191	JQ519132	yes; KA-18; MZB 15.507	female	East Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Hemigaleidae	GN2301	JQ518658	no	unknown	Phuket, Indian Ocean, Thailand
Leptochariidae	GN1213	JQ518660	no	female	Atlantic Ocean, Senegal
Proscylliidae	GN2212	JQ519061	no; BRU 004	female	Sulu Sea, Pacific Ocean, Philippines
Proscylliidae	GN2601	JQ519076	no; HUMZ 175853	unknown	Okinawa, North Pacific Ocean, Japan
Pseudotriakidae	GN1470	JQ518661	no	female	South Island, Pacific Ocean, New Zealand
Pseudotriakidae	GN2440	JQ519110	no; JPAG 229	male	Sulu Sea, Pacific Ocean, Philippines
Pseudotriakidae	GN1418	JQ518662	no	male	Mid-Atlantic Ridge, northern Atlantic Ocean

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Scyliorhinidae					
<i>Apristurus ampliceps</i> 1	GN6751	JQ519148	no; NMNZ P.045206	unknown	Pacific Ocean, New Zealand
<i>Apristurus ampliceps</i> 2	GN6742	JQ519149	no; NMNZ TMAP004687	unknown	Pacific Ocean, New Zealand
<i>Apristurus australis</i>	GN4877	JQ518995	no; ANFC H 2573-01	unknown	Western Australia, Indian Ocean, Australia
Scyliorhinidae					
<i>Apristurus brunneus</i>	GN1539	JQ518667	no	unknown	California, Monterey Bay, Pacific Ocean, U.S.A.
Scyliorhinidae					
<i>Apristurus cf. melanoasper</i>	GN4869	JQ518993	no; ANFC H 1391-03	unknown	Bass Strait, Australia
Scyliorhinidae					
<i>Apristurus cf. sinensis</i>	GN6728	JQ519141	no; NMNZ P.042126	unknown	Pacific Ocean, New Zealand
Scyliorhinidae					
<i>Apristurus exsanguis</i>	GN6732	JQ519144	no; NMNZ P.042519	unknown	Pacific Ocean, New Zealand
Scyliorhinidae					
<i>Apristurus kampaе</i>	GN2533	JQ519119	no; KUI 29258	unknown	California, Pacific Ocean, U.S.A.
Scyliorhinidae					
<i>Apristurus laurussonii</i>	GN1478	JQ518666	no	female	North Sea, Atlantic Ocean, Scotland
Scyliorhinidae					
<i>Apristurus macrohynchus</i>	GN1013	JQ519180	no; UMMZ 231973	female	Pacific Ocean, Taiwan
Scyliorhinidae					
<i>Apristurus manis</i>	GN1089	JQ518663	no	female	northern Atlantic Ocean, U.S.A.
Scyliorhinidae					
<i>Apristurus melanoasper</i>	GN1076	JQ519193	no; YPM ICH.010136	male	Connecticut, Atlantic Ocean, U.S.A.
Scyliorhinidae					
<i>Apristurus platyrhynchus</i>	GN4865	JQ518670	no	unknown	Bass Strait, Australia
Scyliorhinidae					
<i>Apristurus profundorum</i>	GN4672	JQ518668	no	male	northern Atlantic Ocean, U.S.A.
Scyliorhinidae					
<i>Apristurus sp. 1</i>	GN4863	JQ519037	no; ANFC H 6411-02	female	Western Australia, Indian Ocean, Australia
Scyliorhinidae					
<i>Apristurus sp. 2</i>	GN4861	JQ518669	no	unknown	Bass Strait, Australia
Scyliorhinidae					
<i>Apristurus sp. 3</i>	GN1446	JQ518664	no	female	North Island, Pacific Ocean, New Zealand
Scyliorhinidae					
<i>Apristurus sp. 4</i>	GN1473	JQ518665	no	male	Atlantic Ocean, Scotland or Ireland
Scyliorhinidae					
<i>Asymbolus analis</i>	GN2478	JQ518672	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Scyliorhinidae					
<i>Asymbolus parvus</i>	GN4880	JQ519041	no; ANFC H 6415-02	male	Western Australia, Indian Ocean, Australia
Scyliorhinidae					
<i>Asymbolus rubiginosus</i>	GN1936	JQ518671	no	female	New South Wales, Pacific Ocean, Australia
Scyliorhinidae					
<i>Atelomycterus marmoratus</i>	GN3705	JQ519099	yes; BO-495; IPPS BO495	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Scyliorhinidae					
<i>Atelomycterus marnkalla</i>	GN4883	JQ519017	no; ANFC H 6146-01	female	Queensland, Torres Strait, Pacific Ocean, Australia
Scyliorhinidae					
<i>Autohalecturus labiosus</i>	GN2268	JQ519192	no; WAM P 31670-001	unknown	Western Australia, Indian Ocean, Australia
Scyliorhinidae					
<i>Bythaelurus dawsoni</i>	GN6746	JQ519146	no; NMNZ P.044374	unknown	Pacific Ocean, New Zealand

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Scyliorhinidae	GN4886	JQ518999	no; ANFC H 3588-01	unknown	New South Wales, Tasman Sea, Pacific Ocean, Australia
Scyliorhinidae	GN4884	JQ519045	no; ANFC H 6419-01	male	Western Australia, Indian Ocean, Australia
Scyliorhinidae	GN4885	JQ518998	no; ANFC H 3581-01	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Scyliorhinidae	GN4361	JQ519111	no; JPAG 231	unknown	South China Sea, Pacific Ocean, Philippines
Scyliorhinidae	GN982	JQ519177	no; UMMZ 231967	female	Pacific Ocean, Taiwan
Scyliorhinidae	GN4889	JQ518997	no; ANFC H 3580-01	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Scyliorhinidae	GN2529	JQ519118	no; KUI 28129	unknown	California, Pacific Ocean, U.S.A.
Scyliorhinidae	GN1946	JQ518673	no	male	New South Wales, Pacific Ocean, Australia
Scyliorhinidae	GN4892	JQ519039	no; ANFC H 6414-10	female	Western Australia, Indian Ocean, Australia
Scyliorhinidae	GN1892	JQ518675	no	unknown	Atlantic Ocean
Scyliorhinidae	GN6627	JQ519129	no; MMF-36798; MMF 36798	unknown	Madeira, Atlantic Ocean, Portugal
Scyliorhinidae	GN1417	JQ518674	no	male	Mid-Atlantic Ridge, northern Atlantic Ocean
Scyliorhinidae	GN7116	JQ518676	no	unknown	Atlantic Ocean, Angola
Scyliorhinidae	GN991	JQ519181	no; UMMZ 231974	female	Pacific Ocean, Taiwan
Scyliorhinidae	GN2222	JQ519104	no; JPAG 115	male	Sulu Sea, Pacific Ocean, Philippines
Scyliorhinidae	GN1198	JQ518677	no	unknown	KwaZulu-Natal, Indian Ocean, South Africa
Scyliorhinidae	GN7306	JQ518678	yes; AF-153	unknown	Indian Ocean, South Africa
Scyliorhinidae	GN4893	JQ519034	no; ANFC H 6367-01	female	Western Australia, Indian Ocean, Australia
Scyliorhinidae	GN7237	JQ518679	yes; AF-84	unknown	Indian Ocean, South Africa
Scyliorhinidae	GN7178	JQ518680	yes; AF-24	unknown	Indian Ocean, South Africa
Scyliorhinidae	GN6741	JQ519147	no; NMNZ P.044582	unknown	Pacific Ocean, New Zealand
Scyliorhinidae	GN1536	JQ518681	no	female	California, Monterey Bay, Pacific Ocean, U.S.A.
Scyliorhinidae	GN1772	JQ518682	no	male	Indian Ocean, South Africa

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Scyliorhinidae	GN7325	JQ518683	yes; AF-172	unknown	Indian Ocean, South Africa
Scyliorhinidae	GN2305	JQ518684	no	unknown	Atlantic Ocean, Argentina
Scyliorhinidae	GN2346	JQ518686	no	unknown	eastern Atlantic Ocean
Scyliorhinidae	GN7186	JQ518687	yes; AF-32	unknown	Indian Ocean, South Africa
Scyliorhinidae	GN2530	JQ519117	no; KUI 26984	unknown	Mid-Atlantic Bight, Atlantic Ocean, U.S.A.
Scyliorhinidae	GN2339	JQ518685	no	unknown	eastern Atlantic Ocean
Sphyrnidae	GN1256	JQ519152	yes; AU-83; NTM S.14689-004	male	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Sphyrnidae	GN501	JQ518689	no	female	Manzanilla Bay, Atlantic Ocean, East Trinidad
Sphyrnidae	GN2642	JQ518688	no	male	Pacific Ocean, Panama
Sphyrnidae	GN5663	JQ518691	yes; DEL-6	male	Florida, Atlantic Ocean, U.S.A.
Sphyrnidae	GN4187	JQ519063	yes; CAS 229024	unknown	East Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Sphyrnidae	GN5804	JQ518692	yes; KC-9	female	Atlantic Ocean, U.S.A.
Sphyrnidae	GN3471	JQ519091	yes; BO-254; IPPS BO254	unknown	Sarawak, South China Sea, Pacific Ocean, Malaysia
Sphyrnidae	GN5825	JQ518693	yes; MS05-405	male	Florida, Crooked Island Bay, Gulf of Mexico, U.S.A.
Sphyrnidae	GN502	JQ518690	no	male	Manzanilla Bay, Atlantic Ocean, East Trinidad
Sphyrnidae	GN1097	JQ519079	yes; BJ-784; IBUNAM PE9519	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN1522	JQ518694	no	female	Western Australia, Indian Ocean, Australia
Triakidae	GN7236	JQ518695	yes; AF-83	unknown	Indian Ocean, South Africa
Triakidae	GN2595	JQ519074	no; HUMZ 162465	female	Pacific Ocean, Japan
Triakidae	GN4894	JQ519014	no; ANFC H 5946-01	female	Western Australia, Indian Ocean, Australia
Triakidae	GN1000	JQ519176	no; UMMZ 231964	female	Pacific Ocean, Taiwan
Triakidae	GN2225	JQ519106	no; JPAG 161	female	Sulu Sea, Pacific Ocean, Philippines
Triakidae	GN2591	JQ519075	no; HUMZ 165225	male	Pacific Ocean, Japan
Triakidae	GN1819	JQ518696	no	female	Western Australia, Indian Ocean, Australia

APPENDIX 2  
(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Triakidae	GNI1669	JQ518697	no	female	Kerala, Indian Ocean, India
Triakidae	GNI1951	JQ518698	no	male	Red Sea, Israel
Triakidae	GN4330	JQ519114	no; JPAG 346	unknown	South China Sea, Pacific Ocean, Philippines
Triakidae	GN6659	JQ518699	yes; MM-31	female	Gulf of Oman, Iran
Triakidae	GN4902	JQ519050	no; ANFC H 6571-03	male	Western Australia, Indian Ocean, Australia
Triakidae	GN2351	JQ518705	no	unknown	eastern Atlantic Ocean
Triakidae	GN5291	JQ519158	no; BJ-446; TCWC 7561.05	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN917	JQ518711	no	unknown	Virginia, Atlantic Ocean, U.S.A.
Triakidae	GN1101	JQ518700	yes; BJ-792	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN1564	JQ518701	yes; BJ-642	unknown	Baja California, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN4896	JQ519008	no; ANFC H 5551-01	male	Pacific Ocean, New Zealand
Triakidae	GN1020	JQ519171	no; UMMZ 231357	female	Pacific Ocean, Taiwan
Triakidae	GN1687	JQ518703	no	male	Maharashtra, Indian Ocean, India
Triakidae	GN7218	JQ518709	yes; AF-65	unknown	Indian Ocean, South Africa
Triakidae	GN2414	JQ518706	no	unknown	Mississippi, Gulf of Mexico, U.S.A.
Triakidae	GN7322	JQ518710	yes; AF-169	unknown	Indian Ocean, South Africa
Triakidae	GN4898	JQ519015	no; ANFC H 5947-01	male	Western Australia, Indian Ocean, Australia
Triakidae	GN2311	JQ518704	no	unknown	Atlantic Ocean, Argentina
Triakidae	GN5308	JQ518708	yes; BJ-546	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN1565	JQ518702	yes; BJ-671	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Triakidae	GN4899	JQ519003	no; ANFC H 4649-08	male	Western Australia, Indian Ocean, Australia
Triakidae	GN3609	JQ518707	yes; BO-354	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Triakidae	GN2293	JQ518712	no	unknown	Indian Ocean, South Africa
Triakidae	GN712	JQ518715	no	male	Cape Province, Indian Ocean, South Africa



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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Triakidae	GN2454	JQ518714	no	female	Izu Peninsula, Pacific Ocean, Japan
Triakidae	GN1038	JQ518713	no	female	California, Pacific Ocean, U.S.A.
<b>Heterodontiformes</b>					
Heterodontidae	GN4844	JQ519052	no; ANFC H 6581-01	female	Western Australia, Indian Ocean, Australia
Heterodontidae	GN5225	JQ519165	yes; BJ-233; TCWC 7576.01	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Heterodontidae	GN1939	JQ518722	no	male	New South Wales, Pacific Ocean, Australia
Heterodontidae	GN5224	JQ519166	yes; BJ-232; TCWC 7576.02	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Heterodontidae	GN4843	JQ519033	no; ANFC H 6354-11	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Heterodontidae	GN2905	JQ518723	yes; BOD-38	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
<b>Hexanchiformes</b>					
Chlamydoselachidae	GN1403	JQ518724	no	female	Mid-Atlantic Ridge, northern Atlantic Ocean
Hexanchidae	GN978	JQ519173	no; UMMZ 231961	female	Pacific Ocean, Taiwan
Hexanchidae	GN2342	JQ518727	no	unknown	eastern Atlantic Ocean
Hexanchidae	GN2015	JQ518726	yes; GA-14	male	Mozambique Channel, Indian Ocean, Madagascar
Hexanchidae	GN1988	JQ518725	no	female	Caribbean Sea, Atlantic Ocean, Bahamas
Hexanchidae	GN1	JQ518728	no	female	South Australia, Great Australian Bight, Indian Ocean, Australia
<b>Lamniformes</b>					
Alopiidae	GN5402	JQ519078	yes; BJ-721; IBUNAM PE9512	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Alopiidae	GN1125	JQ518729	yes; BJ-716	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Alopiidae	GN6200	JQ518730	no; TWB-42	unknown	Long Island Sound, Atlantic Ocean, U.S.A.
Cetorhinidae	GN1058	JQ518731	no	unknown	Atlantic Ocean, England

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Lamnidae	GN1428	JQ518732	no	male	KwaZulu-Natal, Indian Ocean, South Africa
Lamnidae	GN7069	JQ518734	yes; VN-71	unknown	South China Sea, Pacific Ocean, Vietnam
Lamnidae	GN614	JQ518733	no	unknown	Florida Keys Gulf of Mexico, U.S.A.
Lamnidae	GN1069	JQ518735	no	unknown	Pacific Ocean, Japan
Lamnidae	GN2261	JQ518990	no; AMS I32756-002	unknown	Tasmania, Tasman Sea, Pacific Ocean, Australia
Megachasmidae	GN2724	JQ518736	no	unknown	California, Pacific Ocean, U.S.A.
Mitsukurinidae	GN1798	JQ519120	no; LACM 47362-1	unknown	California, Pacific Ocean, U.S.A.
Odontaspidae	GN907	JQ518737	no	unknown	North Carolina, Atlantic Ocean, U.S.A.
Odontaspidae	GN1085	JQ518738	no	male	Azores, Atlantic Ocean, Portugal
Odontaspidae	GN1422	JQ518739	no	unknown	Atlantic Ocean, Brazil
Pseudocarchariidae	GN2634	JQ518740	no	male	Hawaii, Pacific Ocean, U.S.A.
<b>Orectolobiformes</b>					
Brachaeluridae	GN6782	JQ519055	no; ANFC H 6849-01	unknown	New South Wales, Pacific Ocean, Australia
Brachaeluridae	GN2265	JQ518989	no; AMS I31253-005	unknown	New South Wales, Pacific Ocean, Australia
Ginglymostomatidae	GN3561	JQ519168	no; BJ-425; TCWC 7585.01; IBUNAM PE9492	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Ginglymostomatidae	GN5681	JQ518741	yes; FY-7	female	Florida, Atlantic Ocean, U.S.A.
Ginglymostomatidae	GN1252	JQ518742	yes; AU-81	female	Northern Territory, Fog Bay, Timor Sea, Indian Ocean, Australia
Ginglymostomatidae	GN7111	JQ518743	no	unknown	Indian Ocean, Kenya
Hemiscylliidae	GN2590	JQ518745	yes; JO-17	male	Queensland, Pacific Ocean, Australia
Hemiscylliidae	GN1702	JQ518744	no	female	Maharashtra, Indian Ocean, India
Hemiscylliidae	GN4458	JQ519066	yes; KA-164; CAS 229029	male	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Hemiscylliidae	GN4467	JQ519067	yes; KA-173; CAS 229031	female	West Kalimantan, Java Sea, Pacific Ocean, Indonesia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Hemiscylliidae	GN4616	JQ518746	yes; KA-322	unknown	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Hemiscylliidae	GN4446	JQ519064	yes; KA-152; CAS 229025	female	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Hemiscylliidae	GN2587	JQ518747	yes; JO-1	female	Queensland, Pacific Ocean, Australia
Orectolobidae	GN2582	JQ518748	yes; JO-14	female	Queensland, Pacific Ocean, Australia
Orectolobidae	GN4860	JQ519048	no; ANFC H 6490-01	female	Western Australia, Indian Ocean, Australia
Orectolobidae	GN4845	JQ519025	no; ANFC H 6278-01	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Orectolobidae	GN4847	JQ519020	no; ANFC H 6189-01	female	Western Australia, Indian Ocean, Australia
Orectolobidae	GN4852	JQ519011	no; ANFC H 5766-01	female	Queensland, Pacific Ocean, Australia
Orectolobidae	GN4857	JQ519010	no; ANFC H 5763-01	male	Queensland, Pacific Ocean, Australia
Orectolobidae	GN4855	JQ519019	no; ANFC H 6172-01	male	Western Australia, Indian Ocean, Australia
Parascylliidae	GN1927	JQ518749	no	male	New South Wales, Pacific Ocean, Australia
Rhincodontidae	GN929	JQ518750	no	unknown	Pacific Ocean, Taiwan
Stegostomatidae	GN3700	JQ518751	yes; BO-490	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
<b>Pristiophoriformes</b>					
Pristiophoridae	GN7303	JQ518752	yes; AF-150	unknown	Indian Ocean, South Africa
Pristiophoridae	GN1977	JQ518754	no	female	New South Wales, Pacific Ocean, Australia
Pristiophoridae	GN1049	JQ518753	no	unknown	Pacific Ocean, Japan
<b>Squaliformes</b>					
Centrolophoridae	GN2011	JQ518945	yes; GA-8	female	Mozambique Channel, Indian Ocean, Madagascar
Centrolophoridae	GN6515	JQ518946	yes; AZ-17	male	Madeira, Atlantic Ocean, Portugal
Centrolophoridae	GN6615	JQ519126	no; MMF-36124	unknown	Madeira, Atlantic Ocean, Portugal
Centrolophoridae	GN4943	JQ519049	no; ANFC H 6500-01	male	Bass Strait, Australia
Centrolophoridae	GN4392	JQ519108	no; JPAG 225	unknown	South China Sea, Pacific Ocean, Philippines

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Centrolophidae	GN4922	JQ519036	no; ANFC H 6410-01	male	Western Australia, Indian Ocean, Australia
Centrolophidae	GN1966	JQ518944	no	female	Caribbean Sea, Atlantic Ocean, Jamaica
Centrolophidae	GN974	JQ519172	no; UMMZ 231959	male	Pacific Ocean, Taiwan
Centrolophidae	GN4348	JQ519109	no; JPAG 226	unknown	South China Sea, Pacific Ocean, Philippines
Centrolophidae	GN6514	JQ518947	yes; AZ-16	unknown	Madeira, Atlantic Ocean, Portugal
Centrolophidae	GN4933	JQ519054	no; ANFC H 6628-03	male	South Australia, Great Australian Bight, Indian Ocean, Australia
Centrolophidae	GN4946	JQ519007	no; ANFC H 5343-08	male	southwestern Indian Ocean
Centrolophidae	GN6544	JQ518950	yes; AZ-46	female	Azores, Atlantic Ocean, Portugal
Centrolophidae	GN2619	JQ518949	no	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Centrolophidae	GN2543	JQ518948	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Dalatiidae	GN6576	JQ518951	yes; AZ-79	male	Azores, Atlantic Ocean, Portugal
Dalatiidae	GN3749	JQ518952	no	unknown	North Pacific Ocean
Dalatiidae	GN3748	JQ518953	no	unknown	central South Pacific Ocean
Dalatiidae	GN6176	JQ518955	yes; TW-5	female	Pacific Ocean, Taiwan
Dalatiidae	GN1981	JQ518954	no	female	Azores, Atlantic Ocean, Portugal
Echinorhinidae	GN1983	JQ519170	no; UFFC 103000	unknown	Louisiana, Gulf Of Mexico, U.S.A.
Echinorhinidae	GN4988	JQ519016	no; ANFC H 6115-01	male	Queensland, Pacific Ocean, Australia
Etmopteridae	GN6558	JQ518956	yes; AZ-61	male	Azores, Atlantic Ocean, Portugal
Etmopteridae	GN5591	JQ518962	yes; CR-17	female	Chatham Rise, Pacific Ocean, New Zealand
Etmopteridae	GN3582	JQ518959	no	female	Gulf of Mexico
Etmopteridae	GN2674	JQ518957	no	unknown	Pacific Ocean, New Zealand
Etmopteridae	GN4954	JQ519009	no; ANFC H 5674-08	male	Indian Ocean
Etmopteridae	GN3723	JQ518960	no	female	western North Atlantic Ocean
Etmopteridae	GN5594	JQ518963	yes; CR-20	male	Chatham Rise, Pacific Ocean, New Zealand
Etmopteridae	GN997	JQ519179	no; UMMZ 231971	female	Pacific Ocean, Taiwan
Etmopteridae	GN6608	JQ519125	no; MMF-36093; MMF 36093	unknown	Madeira, Atlantic Ocean, Portugal

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Etmopteridae					
<i>Etmopterus pusillus</i>	GN6552	JQ518964	yes; AZ-55	female	Azores, Atlantic Ocean, Portugal
<i>Etmopterus spinax</i>	GN5162	JQ518961	yes; AZ-7	female	Azores, Atlantic Ocean, Portugal
Etmopteridae					
<i>Etmopterus splendidus</i>	GN995	JQ519178	no; UMMZ 231969	male	Pacific Ocean, Taiwan
<i>Etmopterus virens</i>	GN3564	JQ518958	no	female	western North Atlantic Ocean
Oxynotidae					
<i>Oxynotus brunianus</i>	GN1844	JQ518965	no	female	Pacific Ocean, New Zealand
<i>Oxynotus paradoxus</i>	GN1852	JQ518966	no	unknown	Atlantic Ocean, Scotland
Somniosidae					
<i>Centroscymnus coelepis</i>	GN6626	JQ519128	no; MMF-36784; MMF 36784	unknown	Madeira, Atlantic Ocean, Portugal
Somniosidae					
<i>Centroscymnus owstonii</i>	GN6600	JQ519124	no; MMF-36058; MMF 36058	unknown	Madeira, Atlantic Ocean, Portugal
Somniosidae					
<i>Centroscymnus</i> sp. 1	GN1451	JQ518967	no	female	North Island, Pacific Ocean, New Zealand
Somniosidae					
<i>Centroscymnus crepidater</i>	GN6617	JQ519127	no; MMF-36134; MMF 36134	unknown	Madeira, Atlantic Ocean, Portugal
Somniosidae					
<i>Proscymnodon plunketi</i>	GN5607	JQ518968	yes	female	Chatham Rise, Pacific Ocean, New Zealand
Somniosidae					
<i>Scymnodon ringens</i>	GN1703	JQ518969	no	female	Atlantic Ocean, Ireland
Somniosidae					
<i>Somniosus microcephalus</i>	GN1156	JQ518970	no	male	Northwest Territories, Victor Bay, Canada
Somniosidae					
<i>Somniosus pacificus</i>	GN1528	JQ518971	no	female	Alaska, Prince William Sound, Gulf of Alaska, Pacific Ocean, U.S.A.
Somniosidae					
<i>Somniosus rostratus</i>	GN2651	JQ518972	no	male	Atlantic Ocean, France
Somniosidae					
<i>Zameus squamulosus</i>	GN4986	JQ518973	no	unknown	Tasmania, Pacific Ocean, Australia
Squalidae					
<i>Cirrhigaleus asper</i>	GN4624	JQ518974	no	female	Florida, Atlantic Ocean, U.S.A.
Squalidae					
<i>Cirrhigaleus australis</i>	GN4944	JQ519012	no; ANFC H 5789-01	female	Bass Strait, Australia
Squalidae					
<i>Squalus acanthias</i>	GN6336	JQ518978	yes; RDM-65	female	Atlantic Ocean, U.S.A.
Squalidae					
<i>Squalus albifrons</i>	GN4961	JQ519005	no; ANFC H 4704-01	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Squalidae					
<i>Squalus brevirostris</i>	GN4995	JQ519115	no; KAUM I 187	female	Minamisatsuma Kagoshi, East China Sea, Pacific Ocean, Japan
Squalidae					
<i>Squalus</i> cf. <i>megalops</i>	GN7179	JQ518979	yes; AF-25	unknown	Indian Ocean, South Africa
Squalidae					
<i>Squalus</i> cf. <i>mitsukurii</i>	GN7253	JQ518980	yes; AF-100	unknown	Indian Ocean, South Africa
Squalidae					
<i>Squalus chloroculus</i>	GN4963	JQ519006	no; ANFC H 4775-01	male	Bass Strait, Australia
Squalidae					
<i>Squalus crassispinus</i>	GN4966	JQ519002	no; ANFC H 4649-04	male	Western Australia, Indian Ocean, Australia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Squalidae	GN1969	JQ518976	no	female	Caribbean Sea, Atlantic Ocean, Jamaica
Squalidae	GN4969	JQ518996	no; ANFC H 2605-05	female	Western Australia, Indian Ocean, Australia
Squalidae	GN976	JQ519175	no; UMMZ 231963	female	Pacific Ocean, Taiwan
Squalidae	GN4972	JQ519000	no; ANFC H 4623-03	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Squalidae	GN975	JQ519174	no; UMMZ 231962	female	Pacific Ocean, Taiwan
Squalidae	GN4979	JQ519053	no; ANFC H 6581-24	female	Western Australia, Indian Ocean, Australia
Squalidae	GN4982	JQ519001	no; ANFC H 4623-05	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Squalidae	GN4983	JQ519038	no; ANFC H 6413-01	Female	Western Australia, Indian Ocean, Australia
Squalidae	GN1167	JQ518975	no	female	Rio Grande do Sul, Atlantic Ocean, Brazil
Squalidae	GN5688	JQ518977	yes; GOA-8	female	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
<b>Squatiformes</b>					
Squatimidae	GN5926	JQ518985	yes; SE-5	female	Atlantic Ocean, Senegal
Squatimidae	GN2573	JQ518981	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Squatimidae	GN5234	JQ518984	no; BJ-256	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Squatimidae	GN4692	JQ518983	no	male	New Jersey, Atlantic Ocean, U.S.A.
Squatimidae	GN986	JQ518987	no	female	Pacific Ocean, Taiwan
Squatimidae	GN5968	JQ518986	yes; SE-48	male	Atlantic Ocean, Senegal
Squatimidae	GN3038	JQ518982	no; HBO-144	female	Sabah, South China Sea, Pacific Ocean, Malaysia
<b>Rajiformes</b>					
Anacanthobatidae	GN7164	JQ518755	yes; AF-10	unknown	Indian Ocean, South Africa
Anacanthobatidae	GN6775	JQ519043	no; ANFC H 6417-04	unknown	Western Australia, Indian Ocean, Australia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Arhynchobatidae	GN6831	JQ519143	no; NMNZ P.042403	unknown	North Island, North Auckland, Pacific Ocean, New Zealand
Arhynchobatidae	GN4720	JQ519082	no; INIDEP T 0406	male	Atlantic Ocean, Argentina
Arhynchobatidae	GN4719	JQ519084	no; INIDEP T 0474	male	Atlantic Ocean, Argentina
Arhynchobatidae	GN4722	JQ519083	no; INIDEP T 0426	female	Atlantic Ocean, Argentina
Arhynchobatidae	GN5722	JQ518766	no; GOA-58	male	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
Arhynchobatidae	GN5789	JQ518769	yes; JN-24	female	Pacific Ocean, Japan
Arhynchobatidae	GN2368	JQ518756	no	female	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN2436	JQ518761	no	unknown	Alaska, Bering Sea, Pacific Ocean, U.S.A.
Arhynchobatidae	GN2378	JQ518757	no	male	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN5691	JQ518764	yes; GOA-12	male	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
Arhynchobatidae	GN6689	JQ519182	yes; UW 111883	unknown	eastern North Pacific Ocean, U.S.A.
Arhynchobatidae	GN6497	JQ518770	no	unknown	eastern North Pacific Ocean, U.S.A.
Arhynchobatidae	GN2437	JQ518762	no	unknown	Alaska, Bering Sea, Pacific Ocean, U.S.A.
Arhynchobatidae	GN6694	JQ519186	yes; UW 47201	unknown	eastern North Pacific Ocean, U.S.A.
Arhynchobatidae	GN6697	JQ519185	yes; UW 117948	unknown	eastern North Pacific Ocean, U.S.A.
Arhynchobatidae	GN5039	JQ519190	no; VIMS 11758	female	Mid-Atlantic Ocean
Arhynchobatidae	GN6699	JQ519183	yes; UW 111889	unknown	North Pacific Ocean, U.S.A.
Arhynchobatidae	GN2384	JQ518758	no	male	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN5617	JQ518763	no; CR-48	female	Chatham Rise, Pacific Ocean, New Zealand
Arhynchobatidae	GN5788	JQ518768	yes; JN-23	male	Pacific Ocean, Japan
Arhynchobatidae	GN5697	JQ518765	no	female	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN2385	JQ518759	yes; GOA-18	female	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
Arhynchobatidae	GN2433	JQ518760	no	unknown	Alaska, Bering Sea, Pacific Ocean, U.S.A.

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Arhynchobatidae	GN5751	JQ518767	no; GOA-121	unknown	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
Arhynchobatidae	GN6707	JQ519187	yes; UW 48757	unknown	eastern North Pacific Ocean, U.S.A.
Arhynchobatidae	GN4629	JQ519042	no; ANFC H 6417-03	unknown	Western Australia, Indian Ocean, Australia
Arhynchobatidae	GN4630	JQ519032	no; ANFC H 6350-01	unknown	Western Australia, Indian Ocean, Australia
Arhynchobatidae	GN4631	JQ519035	no; ANFC H 6409-02	unknown	Tasmania, Tasman Sea, Pacific Ocean, Australia
Arhynchobatidae	GN4632	JQ519046	no; ANFC H 6419-03	unknown	Western Australia, Indian Ocean, Australia
Arhynchobatidae	GN2574	JQ518771	no	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Arhynchobatidae	GN2392	JQ518772	no	male	southwestern Atlantic Ocean
Arhynchobatidae	GN2366	JQ518775	no	male	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN2360	JQ518773	no	male	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN2364	JQ518774	no	female	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN2377	JQ518776	no	male	South Atlantic Ocean, Falkland Islands
Arhynchobatidae	GN4724	JQ519080	no; INIDEP T 0404	female	Atlantic Ocean, Argentina
Arhynchobatidae	GN4726	JQ519081	no; INIDEP T 0405	female	Atlantic Ocean, Argentina
Arhynchobatidae	GN4716	JQ518777	no	unknown	Atlantic Ocean, Argentina
Dasyatidae	GN6232	JQ518789	yes; MS05-304	unknown	Mississippi, Gulf of Mexico, U.S.A.
Dasyatidae	GN4652	JQ519028	no; ANFC H 6346-25	unknown	Western Australia, Indian Ocean, Australia
Dasyatidae	GN4638	JQ518781	no	Male	Virginia, Atlantic Ocean, U.S.A.
Dasyatidae	GN3437	JQ519088	yes; BO-169; IPPS BO169	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasyatidae	GN5379	JQ518782	yes; BJ-675	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Dasyatidae	GN1599	JQ518778	yes; BJ-738	unknown	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Dasyatidae	GN6058	JQ518784	yes; SE-217	male	Atlantic Ocean, Senegal



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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Dasyatidae	GN6115	JQ518786	yes; SE-276	female	Atlantic Ocean, Senegal
Dasyatidae	GN6009	JQ518783	yes; SE-168	male	Atlantic Ocean, Senegal
Dasyatidae	GN2113	JQ518779	yes; NT-108	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Dasyatidae	GN6229	JQ518787	yes; MS05-253	female	Mississippi, Biloxi Ship Channel, Gulf of Mexico, U.S.A.
Dasyatidae	GN6230	JQ518788	yes; MS05-297	female	Mississippi, Gulf of Mexico, U.S.A.
Dasyatidae	GN6063	JQ518785	yes; SE-222	male	Atlantic Ocean, Senegal
Dasyatidae	GN2877	JQ518780	yes; BOD-10	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasyatidae	GN7025	JQ518790	yes; VN-27	unknown	South China Sea, Pacific Ocean, Vietnam
Dasyatidae	GN2063	JQ518793	yes; NT-47	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Dasyatidae	GN4521	JQ519070	yes; KA-227; CAS 229036	female	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Dasyatidae	GN3431	JQ519087	yes; BO-163; IPPS BO163	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasyatidae	GN6638	JQ518824	yes; MM-10	male	Gulf of Oman, Iran
Dasyatidae	GN2018	JQ518792	yes; GA-30	female	Mozambique Channel, Indian Ocean, Madagascar
Dasyatidae	GN7086	JQ518809	yes; VN-88	unknown	South China Sea, Pacific Ocean, Vietnam
Dasyatidae	GN4840	JQ518806	no; KA-439	unknown	West Kalimantan, Sungai Pawan, Indonesia
Dasyatidae	GN4483	JQ518801	yes; KA-189	male	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Dasyatidae	GN3366	JQ518795	yes; BO-95	male	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Dasyatidae	GN3627	JQ518799	yes; BO-415	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasyatidae	GN5569	JQ518808	yes; CM03-74	male	Queensland, Gulf of Carpentaria, Pacific Ocean, Australia
Dasyatidae	GN6640	JQ518825	yes; MM-12	male	Gulf of Oman, Iran

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(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Dasytidae	GN7101	JQ518810	yes; VN-103	unknown	South China Sea, Pacific Ocean, Vietnam
Dasytidae	GN4575	JQ518802	yes; KA-281	female	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Dasytidae	GN2972	JQ519156	yes; HBO-51; SMEC 369 (holotype)	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasytidae	GN4540	JQ519071	yes; KA-246; CAS 229038	female	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Dasytidae	GN3373	JQ518796	yes; BO-102	male	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Dasytidae	GN3452	JQ518797	yes; BO-235	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasytidae	GN4794	JQ518804	yes; KA-393	female	East Kalimantan, Sulawesi Sea, Pacific Ocean, Indonesia
Dasytidae	GN4552	JQ519072	yes; KA-258; CAS 229039	male	West Kalimantan, Kapuas River, Indonesia
Dasytidae	GN2103	FJ896004	yes; NT-96	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Dasytidae	GN6649	JQ518826	yes; MM-21	male	Gulf of Oman, Iran
Dasytidae	GN3418	JQ519086	yes; BO-149; IPPS BO149	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasytidae	GN4812	JQ518805	yes; KA-411	female	East Kalimantan, Sulawesi Sea, Pacific Ocean, Indonesia
Dasytidae	GN5561	JQ518807	yes; CM03-65	male	Queensland, Gulf of Carpentaria, Pacific Ocean, Australia
Dasytidae	GN4221	JQ518800	yes; KA-48	male	East Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Dasytidae	GN1740	JQ518791	no	female	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Dasytidae	GN4620	JQ518803	yes; KA-326	male	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Dasytidae	GN3456	JQ518798	yes; BO-239	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Dasytidae	GN2026	JQ518812	yes; NT-8	male	Northern Territory, Gulf of Carpentaria, Pacific Ocean, Australia



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(Continued)

	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Gymnuridae	GN6650	JQ518834	yes; MM-22	male	Gulf of Oman, Iran
Gymnuridae	GN1551	JQ518827	yes; BJ-676	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Gymnuridae	GN5448	JQ518832	yes; BJ-807	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Gymnuridae	GN4678	JQ518831	no	female	western North Atlantic Ocean
Gymnuridae	GN4640	JQ518830	no	female	Virginia, Atlantic Ocean, U.S.A.
Gymnuridae	GN2883	JQ518829	yes; BOD-16	female	Sarawak, South China Sea Pacific Ocean, Malaysia
Hexarhygonidae	GN6772	JQ518835	no	unknown	Yilan, Pacific Ocean, Taiwan
Mobulidae	GN4356	JQ519062	no; BRU 043	unknown	South China Sea, Pacific Ocean, Philippines
Mobulidae	GN5814	JQ518837	yes; MS05-391	female	Florida, St. Joseph Bay, Gulf of Mexico, U.S.A.
Mobulidae	GN5273	JQ519163	yes; BJ-391; TCWC 7568.01	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Mobulidae	GN3019	JQ518836	yes; HBO-122	male	Sabah, Celebes Sea, Pacific Ocean, Malaysia
Mobulidae	GN2286	JQ519169	yes; BJ-275; TCWC 7589.03	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Mobulidae	GN5284	JQ519161	yes; BJ-429; TCWC 7565.01	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Myliobatidae	GN4703	JQ518840	no	unknown	Indian Ocean, Mozambique
Myliobatidae	GN6793	JQ518841	no	unknown	Persian Gulf, Qatar
Myliobatidae	GN4510	JQ518839	yes; KA-216	female	West Kalimantan, Java Sea, Pacific Ocean, Indonesia
Myliobatidae	GN1605	JQ518838	yes; BJ-723	unknown	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Myliobatidae	GN5675	JQ518988	yes; FY-1; AMNH 251703	female	Florida, Atlantic Ocean, U.S.A.
Myliobatidae	GN3513	JQ519092	yes; BO-296; IPPS BO296	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Myliobatidae	GN7050	JQ519191	yes; VN-52; VN-z-v.000309	unknown	South China Sea, Pacific Ocean, Vietnam
Myliobatidae	GN6584	JQ518844	no; MM-400A	unknown	Persian Gulf, Iran

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Myliobatidae	GN2075	JQ518843	yes; NT-59	unknown	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Myliobatidae	GN3442	JQ519022	yes; BO-178; ANFC H 6219-02	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Myliobatidae	GN6594	JQ518845	no; AM-3	female	Persian Gulf, Qatar
Myliobatidae	GN3444	JQ519089	yes; BO-180; IPPS BO180	female	Sarawak, South China Sea, Pacific Ocean, Malaysia
Myliobatidae	GN2072	JQ518842	yes; NT-56	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Myliobatidae	GN7334	JQ518848	yes; AF-181	unknown	Indian Ocean, South Africa
Myliobatidae	GN2551	JQ518846	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Myliobatidae	GN5203	JQ519159	yes; BJ-144; TCWC 7564.03	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Myliobatidae	GN4697	JQ518847	no	male	western North Atlantic Ocean
Myliobatidae	GN5200	JQ519160	yes; BJ-141; TCWC 7564.04	male	Baja California, Gulf of California, Pacific Ocean, Mexico
Myliobatidae	GN4384	JQ519105	no; JPAG 130	unknown	South China Sea, Pacific Ocean, Philippines
Myliobatidae	GN6097	JQ518849	yes; SE-257	female	Atlantic Ocean, Senegal
Narcinidae	GN5446	JQ518851	yes; BJ-799	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Narcinidae	GN4628	JQ519044	no; ANFC H 6418-01	unknown	Western Australia, Indian Ocean, Australia
Narcinidae	GN2566	JQ518850	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Narkidae	GN7230	JQ518852	yes; AF-77	unknown	Indian Ocean, South Africa
Narkidae	GN6759	JQ519142	no; NMNZ P.042187	unknown	Pacific Ocean, New Zealand
Platyrimidae	GN1043	JQ518853	no	female	California, Pacific Ocean, U.S.A.
Plesiobatidae	GN4346	JQ519131	no; MMLM 017	unknown	South China Sea, Pacific Ocean, Philippines
Potamotrygonidae	GN6488	JQ519155	no; ROM 66845	unknown	Atlantic Ocean, Guyana
Potamotrygonidae	GN5874	JQ519134	yes; PU-10; MZUSP 95406	female	Madre de Dios River, Peru

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Potamotrygonidae	GN5881	JQ519135	yes; PU-20; MZUSP 95411	male	Madre de Dios River, Peru
Potamotrygonidae	GN5887	JQ518856	yes; PU-28	male	Madre de Dios River, Peru
Potamotrygonidae	GN5886	JQ518855	yes; PU-27	male	Madre de Dios River, Peru
Potamotrygonidae	GN2726	JQ518854	no; PU-2	unknown	(pet store), Peru
Potamotrygonidae	GN6169	JQ518857	no; TP-2	female	(pet store), South America
Potamotrygonidae	GN5880	JQ519133	yes; PU-17; MZUSP 107670	male	Madre de Dios River, Peru
Pristidae	GN2074	JQ518858	yes; NT-58	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Pristidae	GN3158	JQ519150	yes; AU-136;	unknown	Northern Territory, Buffalo Creek, Timor Sea, Indian Ocean, Australia
Pristidae	GN2866	JQ518861	yes; CM02-9	unknown	Queensland, Australia
Pristidae	GN2607	JQ518859	no	male	Florida, Lostman's River, U.S.A.
Pristidae	GN2754	JQ518860	no	unknown	Belem, Atlantic Ocean, Brazil
Pristidae	GN3159	JQ519151	yes; AU-137; NTM S.14689-003	unknown	Northern Territory, Buffalo Creek, Timor Sea, Indian Ocean, Australia
Rajidae	GN6681	JQ519184	no; UW 115021	unknown	North Pacific Ocean, U.S.A.
Rajidae	GN2381	JQ518862	no	female	southwestern Atlantic Ocean
Rajidae	GN4650	JQ519013	no; ANFC H 5944-01	unknown	Tasman Sea, Australia
Rajidae	GN5040	JQ519189	no; VIMS 11757	male	Mid-Atlantic Ocean
Rajidae	GN2602	JQ519121	no; MCZ 159184	unknown	North Atlantic Ocean, U.S.A.
Rajidae	GN4667	JQ519123	no; MCZ 167945	unknown	Atlantic Ocean, U.S.A.
Rajidae	GN6833	JQ519145	no; NMNZ P.042691	unknown	Tasman Sea, Pacific Ocean
Rajidae	GN6817	JQ519138	no; NMNZ P.041490	unknown	Chatham Islands, Pacific Ocean, New Zealand
Rajidae	GN6808	JQ519136	no; NMNZ P.040511	unknown	South Island, Westland Pacific Ocean, New Zealand
Rajidae	GN6830	JQ519140	no; NMNZ P.041985	unknown	Antipodes Islands, Pacific Ocean, New Zealand
Rajidae	GN6816	JQ519137	no; NMNZ P.041321	unknown	North Island, Bay of Plenty, Pacific Ocean, New Zealand
Rajidae	GN6826	JQ519139	no; NMNZ P.041752	unknown	Stewart Island, Pacific Ocean, New Zealand
Rajidae	GN6787	JQ518873	no	unknown	Australia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Rajidae					
Rajidae	GN6546	JQ518872	yes; AZ-48	male	Azores, Atlantic Ocean, Portugal
Rajidae	GN6790	JQ518874	no	unknown	Australia
Rajidae	GN2128	JQ518864	no	female	eastern North Atlantic Ocean
Rajidae	GN4152	JQ518870	no	unknown	North Sea, Atlantic Ocean, Norway
Rajidae	GN6789	JQ519047	no; ANFC H 6419-04	unknown	north Western Australia,
Rajidae	GN2467	JQ518867	no	unknown	Bass Strait, Australia
Rajidae	GN2631	JQ518868	no	male	New South Wales, Tasman Sea, Pacific Ocean, Australia
Rajidae	GN6788	JQ519051	no; ANFC H 6574-20	unknown	north Western Australia,
Rajidae	GN5614	JQ518871	yes; CR-45	male	Chatham Rise, Pacific Ocean, New Zealand
Rajidae	GN2603	JQ519157	no; TCWC 11021.01, MCZ 159202	unknown	North Atlantic Ocean, U.S.A.
Rajidae	GN2397	JQ518866	no	female	southwestern Atlantic Ocean
Rajidae	GN4149	JQ518869	no	unknown	North Sea, Atlantic Ocean, Norway
Rajidae	GN2181	JQ518865	no	female	eastern North Atlantic Ocean
Rajidae	GN7190	JQ518875	yes; AF-37	unknown	Indian Ocean, South Africa
Rajidae	GN4353	JQ519103	no; JPAG 091	unknown	South China Sea, Pacific Ocean, Philippines
Rajidae	GN7382	JQ518876	no	unknown	Atlantic Ocean, South Africa
Rajidae	GN1025	JQ518863	no	male	Pacific Ocean, Taiwan
Rajidae	GN2505	JQ519116	no; KUI 26967	unknown	Atlantic Ocean, U.S.A.
Rajidae	GN6547	JQ518880	yes; AZ-49	female	Azores, Atlantic Ocean, Portugal
Rajidae	GN4687	JQ518879	no	female	western North Atlantic Ocean
Rajidae	GN2150	JQ518877	no	male	North Atlantic Ocean
Rajidae	GN4686	JQ518878	no	male	western North Atlantic Ocean
Rajidae	GN7282	JQ518881	yes; AF-129	unknown	Indian Ocean, South Africa
Rajidae	GN4688	JQ518882	no	female	western North Atlantic Ocean
Rajidae	GN2182	JQ518883	no	unknown	Atlantic Ocean, Great Britain
Rajidae	GN4735	JQ519058	yes; KA-334; ANFC H 7099-05	male	West Kalimantan, South China Sea, Pacific Ocean, Indonesia
Rajidae	GN5794	JQ518884	yes; JN-89	female	Pacific Ocean, Japan
Rajidae	GN4738	JQ519059	yes; KA-337; ANFC H 7099-08	male	West Kalimantan, South China Sea, Pacific Ocean, Indonesia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Rajidae	GN4382	JQ519113	no; JPAG 328	unknown	South China Sea, Pacific Ocean, Philippines
Rajidae	GN2410	JQ518887	no	unknown	Atlantic Ocean, Spain
Rajidae	GN1611	JQ518885	yes; GOA-1	unknown	Alaska, Gulf of Alaska, Pacific Ocean, U.S.A.
Rajidae	GN7221	JQ518895	yes; AF-68	unknown	Indian Ocean, South Africa
Rajidae	GN5933	JQ518890	yes; SE-12	female	Atlantic Ocean, Senegal
Rajidae	GN6557	JQ518893	yes; AZ-60	male	Azores, Atlantic Ocean, Portugal
Rajidae	GN5834	JQ518889	yes; MS05-421	female	Florida, Indian Pass, Gulf of Mexico, U.S.A.
Rajidae	GN5936	JQ518891	yes; SE-15	female	Atlantic Ocean, Senegal
Rajidae	GN1957	JQ518886	no; SCOT-36	female	Atlantic Ocean, England
Rajidae	GN6713	JQ519188	yes; UW 49457	unknown	North Pacific Ocean, U.S.A.
Rajidae	GN6181	JQ518892	yes; TW-10	female	Pacific Ocean, Taiwan
Rajidae	GN7192	JQ518894	yes; AF-39	unknown	Indian Ocean, South Africa
Rajidae	GN5235	JQ518888	yes; BJ-257	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Rajidae	GN7371	JQ518899	no	unknown	Atlantic Ocean, South Africa
Rajidae	GN2135	JQ518897	no	male	North Atlantic Ocean
Rajidae	GN2122	JQ518896	no	unknown	North Atlantic Ocean
Rajidae	GN7366	JQ518898	no	unknown	Atlantic Ocean, South Africa
Rajidae	GN4664	JQ519122	no; MCZ 167899	unknown	Atlantic Ocean, U.S.A.
Rajidae	GN7302	JQ518900	yes; AF-149	unknown	Indian Ocean, South Africa
Rajidae	GN2472	JQ518901	no	unknown	Bass Strait, Australia
Rajidae	GN6416	JQ518904	yes; CHL-9	female	Pacific Ocean, Chile
Rajidae	GN2361	JQ518902	no	female	southwestern Atlantic Ocean
Rajidae	GN2708	JQ518903	no	unknown	Pacific Ocean, New Zealand
Rhinidae	GN3533	JQ518905	yes; BO-316	unknown	Sarawak, South China Sea, Pacific Ocean, Malaysia
Rhinobatidae	GN6773	JQ518906	no	unknown	Queensland, Pacific Ocean, Australia
Rhinobatidae	GN4625	JQ519031	no; ANFC H 6348-06	unknown	Western Australia, Indian Ocean, Australia
Rhinobatidae	GN4231	JQ518907	yes; KA-58	male	South Kalimantan, Makassar Strait, Pacific Ocean, Indonesia



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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Rhinobatidae	GN4243	JQ518908	yes; KA-70	female	South Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Rhinobatidae	GN4214	JQ519057	yes; KA-41; ANFC H 7085-01	female	East Kalimantan, Makassar Strait, Pacific Ocean, Indonesia
Rhinobatidae	GN7309	JQ518915	yes; AF-156	unknown	Indian Ocean, South Africa
Rhinobatidae	GN6004	JQ518912	yes; SE-163	female	Atlantic Ocean, Senegal
Rhinobatidae	GN4326	JQ519112	no; JPAG 310	unknown	South China Sea, Pacific Ocean, Philippines
Rhinobatidae	GN6187	JQ518914	yes; TW-16	female	Taiwan Strait, Pacific Ocean, Taiwan
Rhinobatidae	GN5423	JQ518911	yes; BF-761	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Rhinobatidae	GN1828	JQ518909	yes; BJ-670	unknown	Baja California, Gulf of California, Pacific Ocean, Mexico
Rhinobatidae	GN6136	JQ518913	yes; SE-297	male	Atlantic Ocean, Senegal
Rhinobatidae	GN3605	JQ518910	yes; BO-350	male	Sarawak, South China Sea, Pacific Ocean, Malaysia
Rhinobatidae	GN4626	JQ519027	no; ANFC H 6346-22	unknown	Western Australia, Indian Ocean, Australia
Rhinobatidae	GN5400	JQ518916	yes; BJ-711	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Rhinopteridae	GN5466	JQ518919	no; BNC-14	male	North Carolina, Core Sound, Atlantic Ocean, U.S.A.
Rhinopteridae	GN6089	JQ518923	yes; SE-249	female	Atlantic Ocean, Senegal
Rhinopteridae	GN5850	JQ518921	yes; MS05-440	female	Mississippi, Gulf of Mexico, Atlantic Ocean, U.S.A.
Rhinopteridae	GN7092	JQ518924	yes; VN-94	unknown	South China Sea, Pacific Ocean, Vietnam
Rhinopteridae	GN1623	JQ518917	yes; TH-27	unknown	Gulf of Thailand, Pacific Ocean, Thailand
Rhinopteridae	GN5545	JQ518920	yes; CM03-48	male	Queensland, Gulf of Carpentaria, Pacific Ocean, Australia
Rhinopteridae	GN5978	JQ518922	yes; SE-137	female	Atlantic Ocean, Senegal
Rhinopteridae	GN5440	JQ518918	yes; BF-793	male	Baja California Sur, Gulf of California, Pacific Ocean, Mexico

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Rhynchobatidae	GN2996	JQ519023	yes; HBO-87; ANFC H 6221-01	female	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Rhynchobatidae	GN2065	JQ518926	yes; NT-49	male	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Rhynchobatidae	GN3004	JQ519024	yes; HBO-104; ANFC H 6221-02	male	Sabah, Sulu Sea, Pacific Ocean, Malaysia
Rhynchobatidae	GN2044	JQ518925	yes; NT-27	female	Northern Territory, Arafura Sea, Pacific Ocean, Australia
Torpedinidae	GN7264	JQ518933	yes; AF-111	unknown	Indian Ocean, South Africa
Torpedinidae	GN7293	JQ518934	yes; AF-140	unknown	Indian Ocean, South Africa
Torpedinidae	GN6012	JQ518929	yes; SE-171	female	Atlantic Ocean, Senegal
Torpedinidae	GN2571	JQ518927	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Torpedinidae	GN6010	JQ518928	yes; SE-169	female	Atlantic Ocean, Senegal
Torpedinidae	GN6167	JQ518931	yes; TN-128	unknown	Rhode Island, Atlantic Ocean, U.S.A.
Torpedinidae	GN6655	JQ518932	yes; MM-27	unknown	Gulf of Oman, Iran
Torpedinidae	GN6013	JQ518930	yes; SE-172	unknown	Atlantic Ocean, Senegal
Urolophidae	GN2557	JQ518936	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Urolophidae	GN4634	JQ519029	no; ANFC H 6347-13	unknown	Western Australia, Indian Ocean, Australia
Urolophidae	GN4635	JQ519030	no; ANFC H 6347-20	unknown	Western Australia, Indian Ocean, Australia
Urolophidae	GN1627	JQ518935	yes; DF-3	female	Queensland, Moreton Bay, Pacific Ocean, Australia
Urolophidae	GN4655	JQ518992	no; ANFC H 1269-01	unknown	New South Wales, Tasman Sea, Pacific Ocean, Australia
Urolophidae	GN2546	JQ518937	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Urolophidae	GN4656	JQ519040	no; ANFC H 6414-12	unknown	Western Australia, Indian Ocean, Australia
Urolophidae	GN4657	JQ518991	no; ANFC H 1036-37	unknown	Western Australia, Indian Ocean, Australia
Urolophidae	GN4658	JQ519018	no; ANFC H 6153-02	unknown	Queensland, Pacific Ocean, Australia

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	Unique project no.	GenBank no.	Voucher information	Sex	Locality
Urolophidae	GN4659	JQ519026	no; ANFC H 6346-15	unknown	Western Australia, Indian Ocean, Australia
Urolophidae	GN2554	JQ518938	no	female	New South Wales, Tasman Sea, Pacific Ocean, Australia
Urolophidae	GN4661	JQ518994	no; ANFC H 2444-04	unknown	Tasmania, Tasman Sea, Pacific Ocean, Australia
Urolophidae	GN4637	JQ519004	no; ANFC H 4649-23	unknown	Western Australia, Indian Ocean, Australia
Urotrygonidae	GN2275	JQ519167	yes; BJ-443; TCWC 7580.01	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Urotrygonidae	GN5314	JQ518939	yes; BJ-559	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Urotrygonidae	GN5912	JQ518941	no; SAB-2	unknown	Atlantic Ocean, Cayman Islands
Urotrygonidae	GN5340	JQ518940	yes; BJ-605	female	Baja California, Gulf of California, Pacific Ocean, Mexico
Urotrygonidae	GN1585	JQ518942	no; BJ-804	unknown	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Urotrygonidae	GN5250	JQ519162	yes; BJ-309; TCWC 7567.04	female	Baja California Sur, Gulf of California, Pacific Ocean, Mexico
Zanobatidae	GN6014	JQ518943	yes; SE-173	male	Atlantic Ocean, Senegal

<sup>a</sup>member of *Bathyraja* spp. complex;

<sup>b</sup>member of *Amblyraja hyperborea*, *A. jenseni*, and *A. badia* complex;

<sup>c</sup>member of *Dipturus batis* and *D. oxyrhynchus* complex.

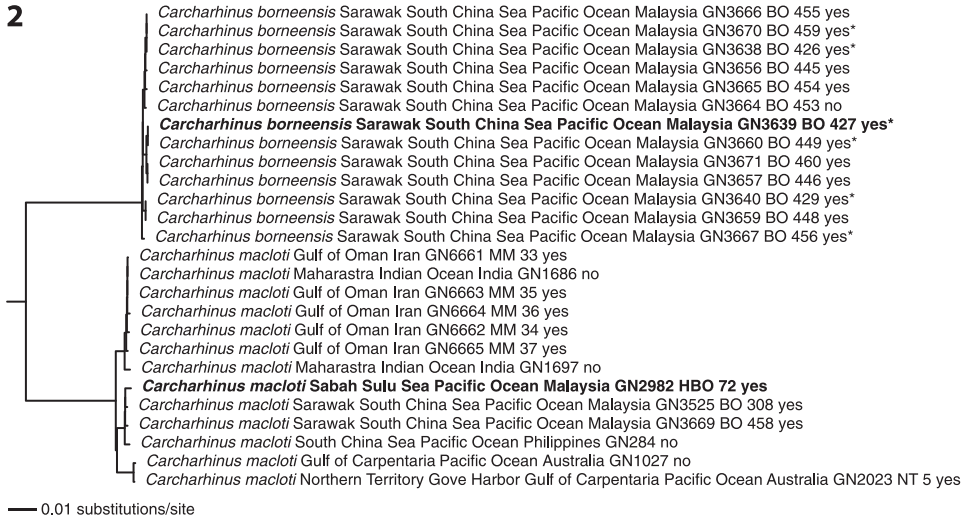
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Figs. 1–77. (following pages). Subtrees of elasmobranchs. **1.** Carcharhinidae (requiem sharks) (1 of 18); **2.** same (2 of 18); **3.** same (3 of 18); **4.** same (4 of 18); **5.** same (5 of 18); **6.** same (6 of 18); **7.** same (7 of 18); **8.** same (8 of 18); **9.** same (9 of 18); **10.** same (10 of 18); **11.** same (11 of 18); **12.** same (12 of 18); **13.** same (13 of 18); **14.** same (14 of 18); **15.** same (15 of 18); **16.** same (16 of 18); **17.** same (17 of 18); **18.** same (18 of 18); **19.** Sphyrnidae (hammerhead sharks); **20.** *Galeocerdo* (tiger sharks). **21.** Hemigaleidae (weasel sharks). **22.** Leptochariidae (barbeled houndsharks). **23.** Triakidae (houndsharks) (1 of 5); **24.** same (2 of 5); **25.** same (3 of 5); **26.** same (4 of 5); **27.** same (5 of 5). **28.** Scyliorhinidae (catsharks) group 1 (1 of 4); **29.** same (2 of 4); **30.** same (3 of 4); **31.** same (4 of 4). **32.** Pseudotriakidae (false catsharks) and Proscylliidae (finback catsharks). **33.** Scyliorhinidae (catsharks) group 2 (1 of 2). **34.** same (2 of 2). **35.** Lamniformes (mackerel sharks). **36.** Hemiscylliidae (longtailed catsharks). **37.** Stegostomatidae (zebra sharks), Rhincodontidae (whale sharks), and Ginglymostomatidae (nurse sharks). **38.** Orectolobidae (wobbegongs) and Brachaeluridae (blind sharks). **39.** Parascylliidae (collared carpetsharks). **40.** Heterodontiformes (bullhead sharks). **41.** Squalidae (dogfish sharks) (1 of 2). **42.** same (2 of 2). **43.** Centrophoridae (gulper sharks) (1 of 2); **44.** same (2 of 2). **45.** Somniosidae (sleepers) and Oxynotidae (roughsharks). **46.** Etmopteridae (lanternsharks). **47.** Dalatiidae (kitefin sharks). **48.** Squatiniformes (angelsharks), Echinorhinidae (bramble sharks), and Pristiophoridae (sawsharks). **49.** Hexanchidae (sixgill and sevengill sharks) and Chlamydoselachidae (frilled sharks). **50.** Dasyatidae (whiptail stingrays) (1 of 10); **51.** same (2 of 10); **52.** same (3 of 10); **53.** same (4 of 10); **54.** same (5 of 10); **55.** same (6 of 10); **56.** same (7 of 10); **57.** same (8 of 10); **58.** same (9 of 10); **59.** same (10 of 10). **60.** Urotrygonidae (round stingrays) and Potamotrygonidae (river stingrays). **61.** Rhinopteridae (cownose rays), Mobulidae (devilrays), and *Pteromylaeus* (duckbill ray); **62.** Myliobatidae (eagle rays) (1 of 2). **63.** same (2 of 2). **64.** Gymnuridae (butterfly rays) and Plesiobatidae (giant stingarees). **65.** Urolophidae (stingarees). **66.** Hexatrygonidae (sixgill stingrays). **67.** Zanobatidae (panrays). **68.** Pristidae (sawfishes) and Rhinobatidae (guitarfishes) Group 1. **69.** Rhynchobatidae (wedgfishes), Rhinidae (shark rays), and Rhinobatidae (guitarfishes) Group 2. **70.** Torpedinidae (torpedo rays), Narcinidae (numbfishes), and Platyrrhinidae (thornbacks and fanrays). **71.** Rajidae (skates) (1 of 5); **72.** same (2 of 5); **73.** same (3 of 5); **74.** same (4 of 5); **75.** same (5 of 5). **76.** Arhynchobatidae (softnose skates) (1 of 2); **77.** same (2 of 2) and Anacanthobatidae (legskates).

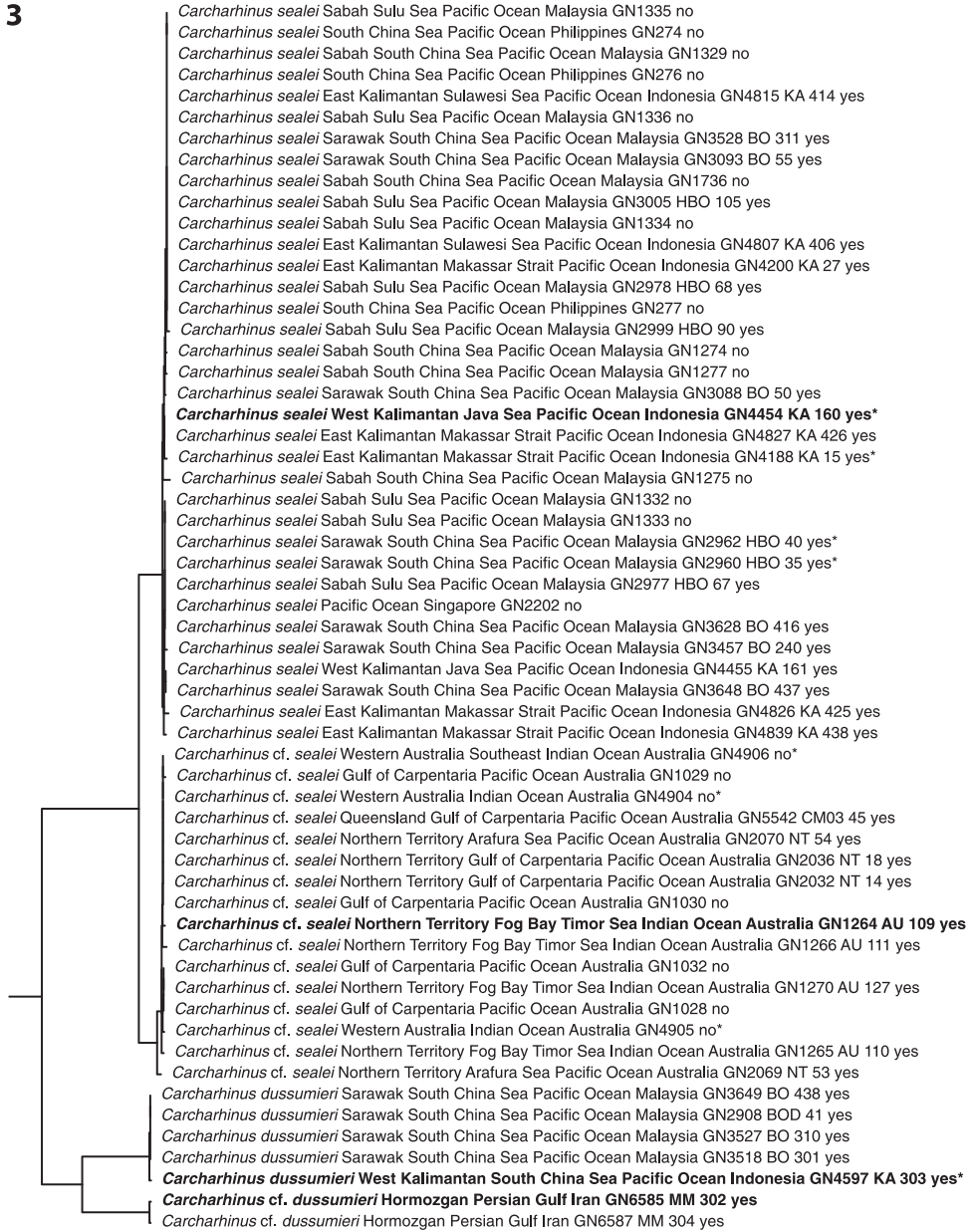
1

*Carcharhinus falciformis* Caribbean Sea Atlantic Ocean Trinidad GN490 no  
*Carcharhinus falciformis* Sabah South China Sea Pacific Ocean Malaysia GN1361 no  
*Carcharhinus falciformis* Luzon South China Sea Pacific Ocean Philippines GN260 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN331 no  
*Carcharhinus falciformis* Sabah South China Sea Pacific Ocean Malaysia GN1375 no  
*Carcharhinus falciformis* Hawaii Pacific Ocean U.S.A. GN129 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN332 no  
*Carcharhinus falciformis* Sabah South China Sea Pacific Ocean Malaysia GN1362 no  
*Carcharhinus falciformis* Sabah South China Sea Pacific Ocean Malaysia GN1373 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN330 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN333 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN335 no  
*Carcharhinus falciformis* Gulf of Mexico Mexico GN3137 no  
*Carcharhinus falciformis* Georgia Atlantic Ocean U.S.A. GN894 no  
*Carcharhinus falciformis* Sabah South China Sea Pacific Ocean Malaysia GN1374 no  
*Carcharhinus falciformis* Kerala Indian Ocean India GN1633 no  
*Carcharhinus falciformis* Gulf of Mexico Mexico GN3136 no  
*Carcharhinus falciformis* Kerala Indian Ocean India GN1658 no  
*Carcharhinus falciformis* Iloilo Sulu Sea Pacific Ocean Philippines GN2214 no\*  
*Carcharhinus falciformis* Gulf of Mexico Mexico GN3133 no  
*Carcharhinus falciformis* Baja California Gulf of California Pacific Ocean Mexico GN2282 BJ 207 no  
*Carcharhinus falciformis* Baja California Sur Gulf of California Pacific Ocean Mexico GN1094 BJ 783 no  
*Carcharhinus falciformis* Sabah Celebes Sea Pacific Ocean Malaysia GN3403 BO 133 yes  
*Carcharhinus falciformis* Kerala Indian Ocean India GN1632 no  
*Carcharhinus falciformis* Sabah Celebes Sea Pacific Ocean Malaysia GN3402 BO 132 yes  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN329 no  
*Carcharhinus falciformis* Mindanao South China Sea Pacific Ocean Philippines GN334 no  
*Carcharhinus falciformis* Gulf of Mexico Mexico GN3135 no  
*Carcharhinus falciformis* Siquijor Sulu Sea Pacific Ocean Philippines GN2242 no\*  
*Carcharhinus falciformis* Sabah Celebes Sea Pacific Ocean Malaysia GN3404 BO 134 yes  
*Carcharhinus falciformis* Gulf of Mexico U.S.A. GN621 no  
*Carcharhinus falciformis* Manzanilla Bay Atlantic Ocean East Trinidad GN505 no  
*Carcharhinus falciformis* Caribbean Sea Atlantic Ocean Trinidad GN509 no  
*Carcharhinus falciformis* Florida Atlantic Ocean U.S.A. GN3194 DEL 10 yes  
*Carcharhinus falciformis* Gulf of Mexico U.S.A. GN616 no  
*Carcharhinus falciformis* Atlantic Ocean U.S.A. GN3192 PE 11 no  
*Carcharhinus falciformis* Caribbean Sea Atlantic Ocean Trinidad GN506 no  
*Carcharhinus falciformis* Caribbean Sea Atlantic Ocean Trinidad GN474 no  
*Carcharhinus falciformis* Atlantic Ocean U.S.A. GN3191 PE 9 no  
*Carcharhinus falciformis* Atlantic Ocean U.S.A. GN3189 PE 5 no  
*Carcharhinus falciformis* Georgia Atlantic Ocean U.S.A. GN891 no  
*Carcharhinus falciformis* Gulf of Mexico U.S.A. GN612 no  
*Carcharhinus falciformis* Georgia Atlantic Ocean U.S.A. GN892 no  
*Carcharhinus falciformis* Caribbean Sea Atlantic Ocean Trinidad GN508 no  
***Carcharhinus falciformis* Atlantic Ocean Senegal GN6059 SE 218 yes**  
*Carcharhinus falciformis* Florida Atlantic Ocean U.S.A. GN608 no  
*Carcharhinus falciformis* Florida Atlantic Ocean U.S.A. GN3195 DEL 11 yes  
*Carcharhinus falciformis* Atlantic Ocean U.S.A. GN3190 PE 8 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN865 no  
*Pronace glauca* New York Long Island Sound Atlantic Ocean U.S.A. GN5908 RI 52 no  
*Pronace glauca* Baja California Sur Gulf of California Pacific Ocean Mexico GN5777 BJ 777 no  
***Pronace glauca* Baja California Sur Gulf of California Pacific Ocean Mexico GN5435 BJ 780 yes**  
*Pronace glauca* western South Pacific Ocean GN4915 no  
*Pronace glauca* Hawaii Pacific Ocean U.S.A. GN2001 no  
*Pronace glauca* Maryland Atlantic Ocean U.S.A. GN920 no  
*Pronace glauca* New Jersey Atlantic Ocean U.S.A. GN12 no  
*Pronace glauca* New York Long Island Sound Atlantic Ocean U.S.A. GN5907 RI 51 no  
*Pronace glauca* western South Pacific Ocean GN4916 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN866 no  
*Pronace glauca* Tasmania Pacific Ocean Australia GN4917 no\*  
*Pronace glauca* Atlantic Ocean Portugal GN6516 AZ 18 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN870 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN867 no  
*Pronace glauca* California Pacific Ocean U.S.A. GN1037 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN868 no  
*Pronace glauca* Baja California Sur Gulf of California Pacific Ocean Mexico GN5275 BJ 402 no  
*Pronace glauca* New York Long Island Sound Atlantic Ocean U.S.A. GN6476 RI 55 no  
*Pronace glauca* Baja Peninsula Gulf of California Pacific Ocean Mexico GN1098 BJ 785 yes  
*Pronace glauca* New Jersey Atlantic Ocean U.S.A. GN416 no  
*Pronace glauca* Virginia Atlantic Ocean U.S.A. GN869 no  
*Pronace glauca* Maryland Atlantic Ocean U.S.A. GN921 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1285 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1286 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1287 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1370 no  
*Carcharhinus amblyrhynchos* Sarawak South China Sea Pacific Ocean Malaysia GN3662 BO 451 yes  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1281 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1369 no  
*Carcharhinus amblyrhynchos* Sarawak South China Sea Pacific Ocean Malaysia GN3673 BO 462 yes  
***Carcharhinus amblyrhynchos* Sarawak South China Sea Pacific Ocean Malaysia GN3672 BO 461 yes\***  
*Carcharhinus amblyrhynchos* Hawaii Pacific Ocean U.S.A. GN545 no  
*Carcharhinus amblyrhynchos* Sabah South China Sea Pacific Ocean Malaysia GN1288 no  
*Carcharhinus amblyrhynchos* Sulawesi Sulawesi Sea Pacific Ocean Indonesia GN2196 no  
*Carcharhinus amblyrhynchos* West Kalimantan Java Sea Pacific Ocean Indonesia GN4422 KA 128 yes  
*Carcharhinus amblyrhynchos* Mindanao South China Sea Pacific Ocean Philippines GN327 no  
*Carcharhinus amblyrhynchos* Red Sea Gulf of Aqaba Egypt GN4 no  
*Carcharhinus amblyrhynchos* Indian Ocean Madagascar GN1222 MG 6 no  
*Carcharhinus amblyrhynchos* Camarines Norte South China Sea Pacific Ocean Philippines GN288 no  
*Carcharhinus amblyrhynchos* Camarines Norte South China Sea Pacific Ocean Philippines GN289 no  
***Carcharhinus wheeleri* Red Sea Egypt GN8 no**  
*Carcharhinus albimarginatus* Pacific Ocean Taiwan GN930 no  
*Carcharhinus albimarginatus* Pacific Ocean Taiwan GN933 no  
***Carcharhinus albimarginatus* Camarines Norte South China Sea Pacific Ocean Philippines GN287 no**  
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*Carcharhinus albimarginatus* Pacific Ocean Taiwan GN934 no

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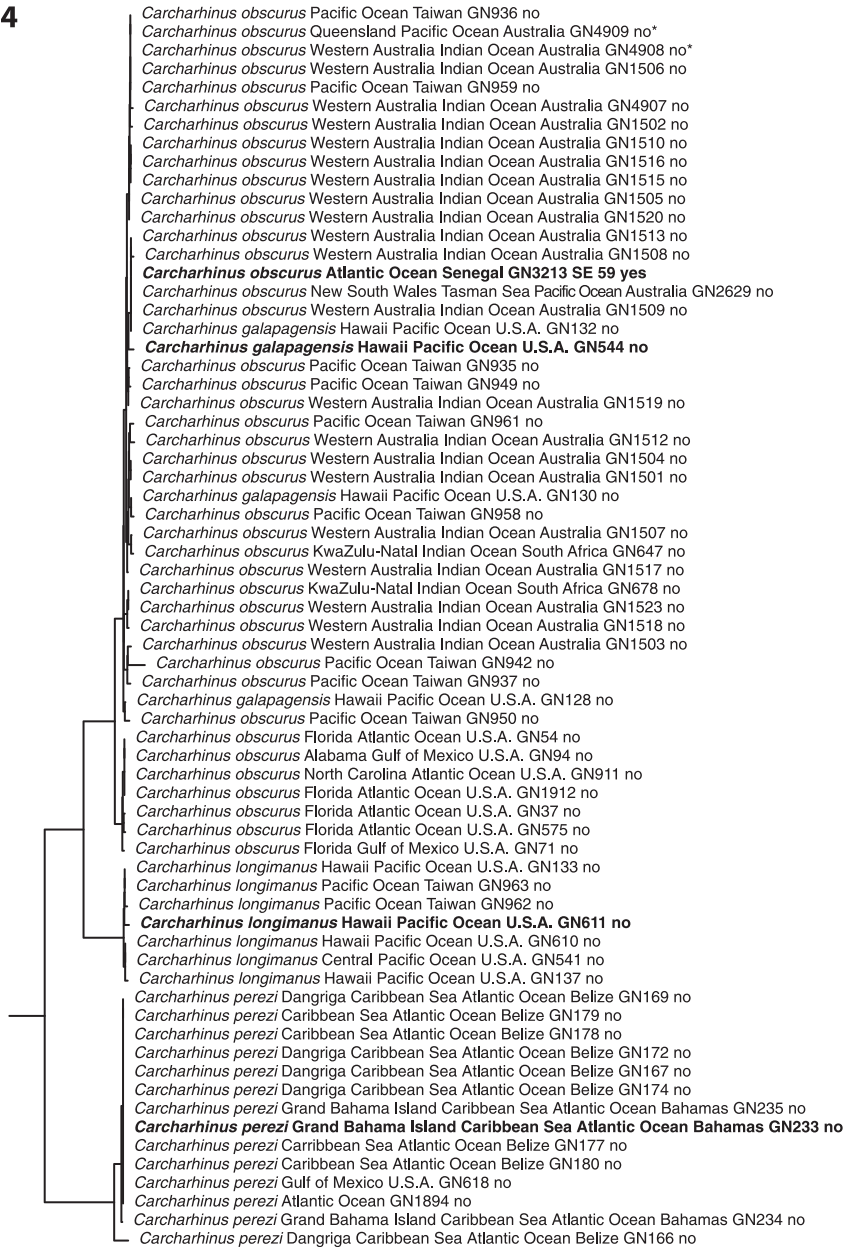


3



— 0.01 substitutions/site

4



— 0.01 substitutions/site



5

- Carcharhinus sorrah* South China Sea Pacific Ocean Vietnam GN7060 VN 62 yes  
*Carcharhinus sorrah* East Kalimantan Makassar Strait Pacific Ocean Indonesia GN4201 KA 28 yes  
*Carcharhinus sorrah* Sarawak South China Sea Pacific Ocean Malaysia GN3529 BO 312 yes  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1343 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1306 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1732 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1731 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1728 no  
*Carcharhinus sorrah* Pacific Ocean Singapore GN2209 no  
*Carcharhinus sorrah* West Kalimantan Java Sea Pacific Ocean Indonesia GN4449 KA 155 yes\*  
*Carcharhinus sorrah* East Kalimantan Makassar Strait Pacific Ocean Indonesia GN4180 KA 7 yes  
*Carcharhinus sorrah* South Kalimantan Makassar Strait Pacific Ocean Indonesia GN4234 KA 61 yes  
*Carcharhinus sorrah* Sabah Sulu Sea Pacific Ocean Malaysia GN3391 BO 121 yes  
*Carcharhinus sorrah* South Kalimantan Makassar Strait Pacific Ocean Indonesia GN4233 KA 60 yes  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1355 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1730 no  
***Carcharhinus sorrah* Sarawak South China Sea Pacific Ocean Malaysia GN2957 HBO 32 yes\***  
*Carcharhinus sorrah* West Kalimantan South China Sea Pacific Ocean Indonesia GN4767 KA 366 yes  
*Carcharhinus sorrah* East Kalimantan Makassar Strait Pacific Ocean Indonesia GN4186 KA 13 yes  
*Carcharhinus sorrah* East Kalimantan Makassar Strait Pacific Ocean Indonesia GN4185 KA 12 yes\*  
*Carcharhinus sorrah* East Kalimantan Sulawesi Sea Pacific Ocean Indonesia GN4805 KA 404 yes  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1662 no  
*Carcharhinus sorrah* Sarawak South China Sea Pacific Ocean Malaysia GN3504 BO 287 yes  
*Carcharhinus sorrah* Luzon South China Sea Pacific Ocean Philippines GN259 no  
*Carcharhinus sorrah* Sabah Sulu Sea Pacific Ocean Malaysia GN3384 BO 114 yes  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1663 no  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1638 no  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1664 no  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1636 no  
*Carcharhinus sorrah* Palawan South China Sea Pacific Ocean Philippines GN361 no  
*Carcharhinus sorrah* Kerala Indian Ocean India GN1637 no  
*Carcharhinus sorrah* Palawan South China Sea Pacific Ocean Philippines GN360 no  
*Carcharhinus sorrah* Palawan South China Sea Pacific Ocean Philippines GN358 no  
*Carcharhinus sorrah* Sarawak South China Sea Pacific Ocean Malaysia GN3108 BO 70 yes  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1716 no  
*Carcharhinus sorrah* Palawan South China Sea Pacific Ocean Philippines GN359 no  
*Carcharhinus sorrah* Pacific Ocean Thailand GN1176 TH 1 yes  
*Carcharhinus sorrah* Sarawak South China Sea Pacific Ocean Malaysia GN3048 BO 10 yes  
*Carcharhinus sorrah* Coast of Palawan South China Sea Pacific Ocean Philippines GN297 no  
*Carcharhinus sorrah* Sabah South China Sea Pacific Ocean Malaysia GN1368 no  
*Carcharhinus sorrah* South China Sea Pacific Ocean Vietnam GN7061 VN 63 yes  
*Carcharhinus sorrah* Coast of Palawan South China Sea Pacific Ocean Philippines GN296 no  
***Carcharhinus cf. sorrah* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN1258 AU 93 yes**  
*Carcharhinus cf. sorrah* Northern Territory Gulf of Carpentaria Pacific Ocean Australia GN2034 NT 16 yes  
*Carcharhinus cf. sorrah* Northern Territory Gulf of Carpentaria Pacific Ocean Australia GN2035 NT 17 yes  
*Carcharhinus cf. sorrah* Northern Territory Gulf of Carpentaria Pacific Ocean Australia GN2033 NT 15 yes

— 0.01 substitutions/site

6A

*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN3637 BO 425 yes  
*Carcharhinus cf. limbatus* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5079 AU 52 yes  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1239 no  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1224 AU 4 no  
***Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5061 AU 26 yes**  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1223 AU 3 yes  
*Carcharhinus cf. limbatus* Queensland Gulf of Carpentaria Indian Ocean Australia GN5558 CM03 62 yes  
*Carcharhinus cf. limbatus* Sabah South China Sea Pacific Ocean Malaysia GN1300 no  
*Carcharhinus cf. limbatus* Sabah South China Sea Pacific Ocean Malaysia GN1303 no  
*Carcharhinus cf. limbatus* Queensland Gulf of Carpentaria Indian Ocean Australia GN5504 CM03 5 yes  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN6263 BO 58 yes  
*Carcharhinus cf. limbatus* Sabah South China Sea Pacific Ocean Malaysia GN1340 no  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5068 AU 39 yes  
*Carcharhinus cf. limbatus* South Kalimantan Makassar Strait Pacific Ocean Indonesia GN4247 KA 74 yes  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN3092 BO 54 yes  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN3206 AU 38 yes  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1238 no  
*Carcharhinus cf. limbatus* Atlantic Ocean Sierra Leone GN223 no  
*Carcharhinus cf. limbatus* Atlantic Ocean Sierra Leone GN225 no  
*Carcharhinus cf. limbatus* Atlantic Ocean Sierra Leone GN211 no  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1227 AU 28 yes  
*Carcharhinus cf. limbatus* South China Sea Pacific Ocean Philippines GN301 no  
*Carcharhinus cf. limbatus* Sabah Sulu Sea Pacific Ocean Malaysia GN2983 HBO 73 yes  
*Carcharhinus cf. limbatus* South China Sea Pacific Ocean Philippines GN283 no  
*Carcharhinus cf. limbatus* Sabah Sulu Sea Pacific Ocean Malaysia GN2984 HBO 74 yes  
*Carcharhinus cf. limbatus* Sulu Sea Pacific Ocean Philippines GN2260 no\*  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN3477 BO 260 yes  
*Carcharhinus cf. limbatus* Sabah South China Sea Pacific Ocean Malaysia GN1346 no  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN3509 BO 292 yes  
*Carcharhinus cf. limbatus* KwaZulu-Natal Indian Ocean South Africa GN3360 no  
*Carcharhinus cf. limbatus* KwaZulu-Natal Indian Ocean South Africa GN3359 no  
*Carcharhinus cf. limbatus* Mozambique Channel Indian Ocean Madagascar GN2009 GA 5 yes  
*Carcharhinus cf. limbatus* Richards Bay Indian Ocean South Africa GN3362 no  
*Carcharhinus cf. limbatus* Kerala Indian Ocean India GN1657 no  
*Carcharhinus cf. limbatus* Maharashtra Indian Ocean India GN1691 no  
*Carcharhinus cf. limbatus* Kerala Indian Ocean India GN1631 no  
*Carcharhinus cf. limbatus* Kerala Indian Ocean India GN1656 no  
*Carcharhinus cf. limbatus* Kerala Indian Ocean India GN1647 no  
*Carcharhinus cf. limbatus* Kerala Indian Ocean India GN1646 no  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN3508 BO 291 yes  
*Carcharhinus cf. limbatus* South China Sea Pacific Ocean Philippines GN280 no  
*Carcharhinus cf. limbatus* South China Sea Pacific Ocean Philippines GN282 no  
*Carcharhinus cf. limbatus* South China Sea Pacific Ocean Philippines GN302 no  
*Carcharhinus cf. limbatus* Pacific Ocean Taiwan GN960 no  
*Carcharhinus cf. limbatus* South China Sea Vietnam GN7084 VN 86 yes  
*Carcharhinus cf. limbatus* Taiwan Strait Pacific Ocean Taiwan GN6194 TW 24 yes  
*Carcharhinus cf. limbatus* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1240 no  
*Carcharhinus cf. limbatus* KwaZulu-Natal Indian Ocean South Africa GN3361 no  
*Carcharhinus cf. limbatus* KwaZulu-Natal Indian Ocean South Africa GN3358 no  
*Carcharhinus cf. limbatus* Baja California Sur Gulf of California Pacific Ocean Mexico GN3196 BJ 737 yes  
*Carcharhinus cf. limbatus* Gulf of California Pacific Ocean Mexico GN3354 no  
*Carcharhinus cf. limbatus* Gulf of California Pacific Ocean Mexico GN3357 no  
*Carcharhinus cf. limbatus* Baja California Sur Gulf of California Pacific Ocean Mexico GN1140 BJ 805 yes  
*Carcharhinus cf. limbatus* Gulf of California Pacific Ocean Mexico GN3355 no  
*Carcharhinus cf. limbatus* Gulf of California Pacific Ocean Mexico GN3356 no  
*Carcharhinus cf. limbatus* Queensland Gulf of Carpentaria Pacific Ocean Australia GN5565 CM03 69 yes  
*Carcharhinus cf. limbatus* Gulf of California Pacific Ocean Mexico GN3353 no  
*Carcharhinus cf. limbatus* Hawaii Pacific Ocean U.S.A. GN1926 no  
*Carcharhinus cf. limbatus* Sarawak South China Sea Pacific Ocean Malaysia GN2909 BOD 42 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Timor Sea Indian Ocean Australia GN1249 no  
*Carcharhinus amblyrhynchoides* Northern Territory Timor Sea Indian Ocean Australia GN1261 no  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5117 AU 97 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5119 AU 101 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Timor Sea Indian Ocean Australia GN1260 no  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5111 AU 91 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5112 AU 92 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5118 AU 100 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Timor Sea Indian Ocean Australia GN1259 no  
*Carcharhinus amblyrhynchoides* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5054 AU 16 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Timor Sea Indian Ocean Australia GN1262 no  
*Carcharhinus amblyrhynchoides* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1235 AU 47 yes\*  
*Carcharhinus amblyrhynchoides* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5090 AU 68 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5051 AU 7 no  
*Carcharhinus amblyrhynchoides* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5056 AU 18 yes  
*Carcharhinus amblyrhynchoides* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1236 AU 49 yes  
*Carcharhinus amblyrhynchoides* Queensland Gulf of Carpentaria Pacific Ocean Australia GN5574 CM03 80 yes  
*Carcharhinus amblyrhynchoides* Maharashtra Indian Ocean India GN1700 no  
*Carcharhinus amblyrhynchoides* Maharashtra Indian Ocean India GN1671 no  
*Carcharhinus amblyrhynchoides* Maharashtra Indian Ocean India GN1672 no  
*Carcharhinus amblyrhynchoides* Maharashtra Indian Ocean India GN1699 no  
*Carcharhinus amblyrhynchoides* Sabah South China Sea Pacific Ocean Malaysia GN3031 HBO 134 yes  
*Carcharhinus amblyrhynchoides* Sabah South China Sea Pacific Ocean Malaysia GN1360 no  
*Carcharhinus amblyrhynchoides* Sabah South China Sea Pacific Ocean Malaysia GN1338 no  
*Carcharhinus amblyrhynchoides* Sabah Sulu Sea Pacific Ocean Malaysia GN2915 BOD 48 yes  
*Carcharhinus amblyrhynchoides* Sabah South China Sea Pacific Ocean Malaysia GN1367 no  
*Carcharhinus amblyrhynchoides* Sabah South China Sea Pacific Ocean Malaysia GN1339 no  
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*Carcharhinus amblyrhynchoides* Sulu Sea Pacific Ocean GN1337 no  
*Carcharhinus amblyrhynchoides* Sarawak South China Sea Pacific Ocean Malaysia GN3668 BO 457 yes  
*Carcharhinus amblyrhynchoides* Sarawak South China Sea Pacific Ocean Malaysia GN3532 BO 315 yes  
*Carcharhinus amblyrhynchoides* South Kalimantan Makassar Strait Pacific Ocean Indonesia GN4246 KA 73 yes  
*Carcharhinus amblyrhynchoides* South China Sea Pacific Ocean Vietnam GN7099 VN 101 yes  
***Carcharhinus amblyrhynchoides* Sarawak South China Sea Pacific Ocean Malaysia GN2959 HBO 34 yes\***  
*Carcharhinus amblyrhynchoides* Sarawak South China Sea Pacific Ocean Malaysia GN3531 BO 314 yes  
*Carcharhinus amblyrhynchoides* Sarawak South China Sea Pacific Ocean Malaysia GN3506 BO 288 yes

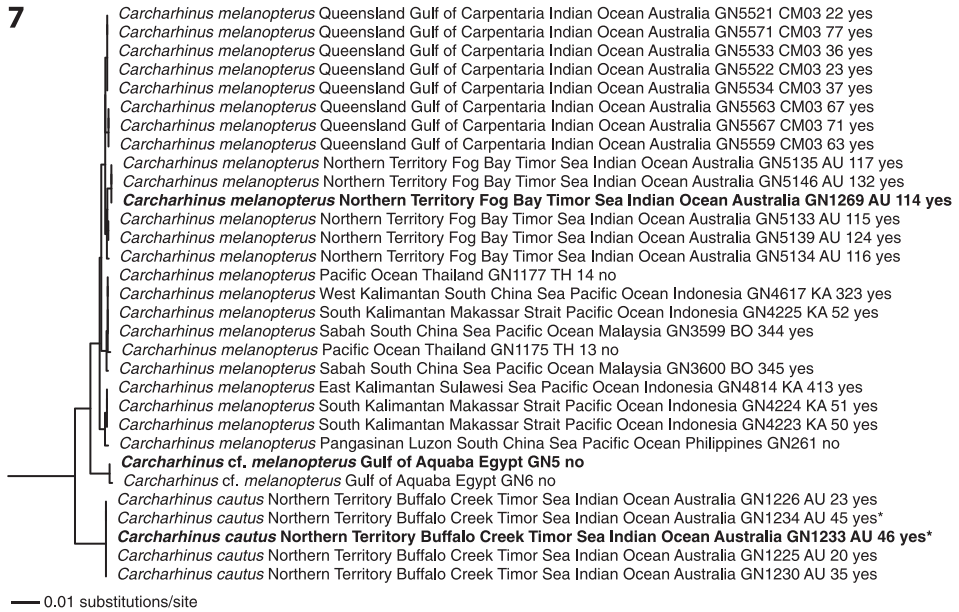
6B

## 6B

6A

- 
- Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN162 no  
*Carcharhinus limbatus* Virginia Atlantic Ocean U.S.A. GN880 no  
*Carcharhinus limbatus* Mississippi Gulf of Mexico U.S.A. GN6224 MS05 87 yes  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN5667 DEL 12 yes  
*Carcharhinus limbatus* Florida St. Andrews Bay Gulf of Mexico U.S.A. GN5847 MS05 435 yes  
*Carcharhinus limbatus* Florida Indian Pass Gulf of Mexico U.S.A. GN6243 MS05 481 yes  
*Carcharhinus limbatus* Florida St. Joseph Bay Gulf of Mexico U.S.A. GN5816 MS05 393 yes  
*Carcharhinus limbatus* Florida Gulf of Mexico U.S.A. GN74 no  
***Carcharhinus limbatus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5802 KC 7 yes**  
*Carcharhinus limbatus* Virginia Atlantic Ocean U.S.A. GN881 no  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN65 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN157 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN159 no  
*Carcharhinus limbatus* Florida Indian Pass Gulf of Mexico U.S.A. GN6242 MS05 480 yes  
*Carcharhinus limbatus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5803 KC 8 yes  
*Carcharhinus limbatus* Florida Indian Pass Gulf of Mexico U.S.A. GN5835 MS05 422 yes  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN444 no  
*Carcharhinus limbatus* Florida Indian Pass Gulf of Mexico U.S.A. GN6244 MS05 482 yes  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN5665 DEL 8 yes  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN153 no  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN446 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN156 no  
*Carcharhinus limbatus* Florida Indian Pass Gulf of Mexico U.S.A. GN6245 MS05 485 yes  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN29 no  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN5768 JMT 2 no  
*Carcharhinus limbatus* Gulf of Mexico GN6761 no  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN5666 DEL 9 yes  
*Carcharhinus limbatus* Florida Crooked Island Bay Gulf of Mexico U.S.A. GN5824 MS05 403 yes  
*Carcharhinus limbatus* Dangriga Caribbean Sea Atlantic Ocean Belize GN170 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN143 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN154 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN155 no  
*Carcharhinus limbatus* Alabama Gulf of Mexico U.S.A. GN158 no  
*Carcharhinus limbatus* Mississippi Gulf of Mexico U.S.A. GN6217 MS05 22 yes  
*Carcharhinus limbatus* Mississippi Gulf of Mexico U.S.A. GN6237 MS05 351 no  
*Carcharhinus limbatus* Mississippi Gulf of Mexico U.S.A. GN6219 MS05 24 yes  
*Carcharhinus limbatus* Mississippi Gulf of Mexico U.S.A. GN6236 MS05 350 no  
*Carcharhinus limbatus* Florida Atlantic Ocean U.S.A. GN23 no  
*Carcharhinus limbatus* Puerto Rico Caribbean Sea Atlantic Ocean U.S.A. GN1921 PR 6 no  
*Carcharhinus tilstoni* Northern Territory Arafura Sea Pacific Ocean Australia GN2071 NT 55 yes  
*Carcharhinus tilstoni* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5063 AU 29 yes  
***Carcharhinus tilstoni* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5086 AU 64 yes**  
*Carcharhinus tilstoni* Northern Territory Arafura Sea Pacific Ocean Australia GN2053 NT 36 yes  
*Carcharhinus tilstoni* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN1237 AU 50 yes  
*Carcharhinus tilstoni* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN3207 AU 53 yes  
*Carcharhinus tilstoni* Northern Territory Indian Ocean Australia GN4910 no  
*Carcharhinus tilstoni* Northern Territory Timor Sea Indian Ocean Australia GN1250 no  
*Carcharhinus tilstoni* Northern Territory Indian Ocean Australia GN4912 no  
*Carcharhinus tilstoni* Northern Territory Arafura Sea Pacific Ocean Australia GN2039 NT 22 yes  
*Carcharhinus tilstoni* Northern Territory Indian Ocean Australia GN4911 no  
***Carcharhinus fitzroyensis* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN1267 AU 112 yes\***  
*Carcharhinus fitzroyensis* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN1268 AU 113 yes  
*Carcharhinus fitzroyensis* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN1241 AU 51 yes

— 0.01 substitutions/site



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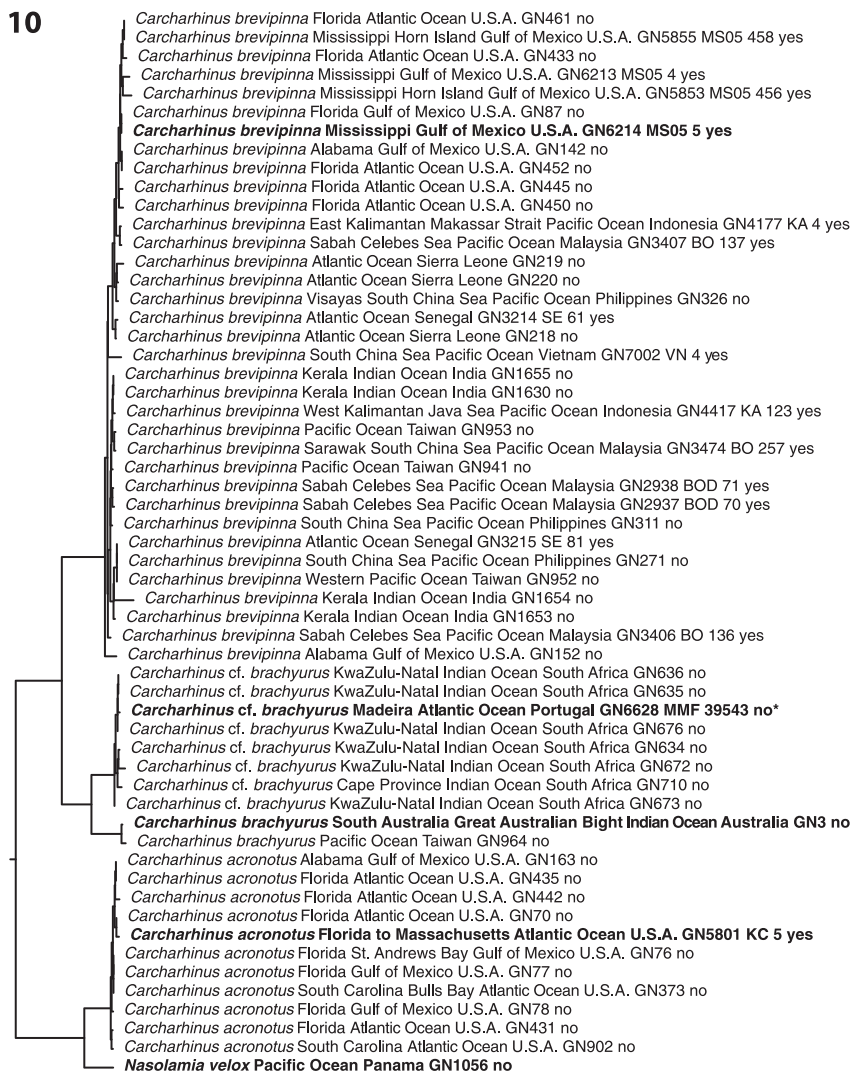
— 0.01 substitutions/site

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*Carcharhinus plumbeus* Florida Gulf of Mexico U.S.A. GN84 no  
*Carcharhinus plumbeus* Atlantic Ocean U.S.A. GN104 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN52 no  
***Carcharhinus plumbeus* South Carolina Atlantic Ocean U.S.A. GN903 no**  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN51 no  
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*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN439 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN55 no  
*Carcharhinus plumbeus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5799 KC 2 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN56 no  
*Carcharhinus plumbeus* Atlantic Ocean U.S.A. GN5863 PE 3 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN50 no  
*Carcharhinus plumbeus* Maryland Atlantic Ocean U.S.A. GN236 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN20 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN36 no  
*Carcharhinus plumbeus* New Jersey Atlantic Ocean U.S.A. GN14 no  
*Carcharhinus plumbeus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5810 KC 17 no  
*Carcharhinus plumbeus* Georgia Atlantic Ocean U.S.A. GN893 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN19 no  
*Carcharhinus plumbeus* Florida Gulf of Mexico U.S.A. GN88 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN448 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN43 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN449 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN44 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN61 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN27 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN42 no  
*Carcharhinus plumbeus* New York Atlantic Ocean U.S.A. GN419 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN438 no  
*Carcharhinus plumbeus* North Carolina Atlantic Ocean U.S.A. GN913 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN62 no  
*Carcharhinus plumbeus* New Jersey Atlantic Ocean U.S.A. GN15 no  
*Carcharhinus plumbeus* North Carolina Atlantic Ocean U.S.A. GN912 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN49 no  
*Carcharhinus plumbeus* New Jersey Atlantic Ocean U.S.A. GN414 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN447 no  
*Carcharhinus plumbeus* Virginia Magoth Bay Atlantic Ocean U.S.A. GN363 no  
*Carcharhinus plumbeus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5808 KC 15 no  
*Carcharhinus plumbeus* North Carolina Atlantic Ocean U.S.A. GN909 no  
*Carcharhinus plumbeus* New York Atlantic Ocean U.S.A. GN421 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN41 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN47 no  
*Carcharhinus plumbeus* Atlantic Ocean U.S.A. GN105 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN26 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN69 no  
*Carcharhinus plumbeus* New Jersey Atlantic Ocean U.S.A. GN415 no  
*Carcharhinus plumbeus* Maryland Atlantic Ocean U.S.A. GN242 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN48 no  
*Carcharhinus plumbeus* New York Atlantic Ocean U.S.A. GN417 no  
*Carcharhinus plumbeus* Maryland Atlantic Ocean U.S.A. GN243 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN437 no  
*Carcharhinus plumbeus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5805 KC 10 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN40 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN45 no  
*Carcharhinus plumbeus* Florida Atlantic Ocean U.S.A. GN60 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN106 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN108 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN116 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN117 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN113 no  
*Carcharhinus altimus* Gulf of Mexico U.S.A. GN625 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN115 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN118 no  
***Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN120 no**  
*Carcharhinus altimus* Gulf of Mexico U.S.A. GN626 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN112 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN121 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN111 no  
*Carcharhinus altimus* Florida Keys Gulf of Mexico U.S.A. GN563 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN110 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN114 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN109 no  
*Carcharhinus altimus* Norfolk Canyon Atlantic Ocean U.S.A. GN119 no  
*Carcharhinus altimus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5811 KC 18 no  
*Carcharhinus altimus* Florida Atlantic Ocean U.S.A. GN885 no  
*Carcharhinus altimus* Hawaii Keawaula Bay Pacific Ocean U.S.A. GN127 no  
*Carcharhinus altimus* Pacific Ocean Taiwan GN965 no  
*Carcharhinus plumbeus* Florida to Massachusetts Atlantic Ocean U.S.A. GN5807 KC 14 no  
*Carcharhinus cf. plumbeus* Visayas South China Sea Pacific Ocean Philippines GN323 no  
*Carcharhinus cf. plumbeus* South China Sea Pacific Ocean Vietnam GN7068 VN 70 yes  
*Carcharhinus cf. plumbeus* Hawaii Pacific Ocean U.S.A. GN1923 no  
*Carcharhinus cf. plumbeus* Hawaii Pacific Ocean U.S.A. GN1924 no  
*Carcharhinus cf. plumbeus* Pacific Ocean Taiwan GN957 no  
*Carcharhinus cf. plumbeus* Sabah South China Sea Pacific Ocean Malaysia GN1273 no  
*Carcharhinus cf. plumbeus* Hawaii Central Pacific Ocean U.S.A. GN1813 no  
*Carcharhinus cf. plumbeus* Hawaii Central Pacific Ocean U.S.A. GN1922 no  
*Carcharhinus cf. plumbeus* Hawaii Central Pacific Ocean U.S.A. GN1837 no  
***Carcharhinus cf. plumbeus* South China Sea Pacific Ocean Vietnam GN7098 VN 100 yes**  
*Carcharhinus cf. plumbeus* Sabah South China Sea Pacific Ocean Malaysia GN1272 no  
*Carcharhinus cf. plumbeus* Hawaii Pacific Ocean U.S.A. GN131 no  
*Carcharhinus cf. plumbeus* Pacific Ocean Taiwan GN955 no  
*Carcharhinus cf. plumbeus* Hawaii Pacific Ocean U.S.A. GN126 no  
*Carcharhinus cf. plumbeus* Hawaii Pacific Ocean U.S.A. GN136 no  
*Carcharhinus cf. plumbeus* Pacific Ocean Taiwan GN956 no  
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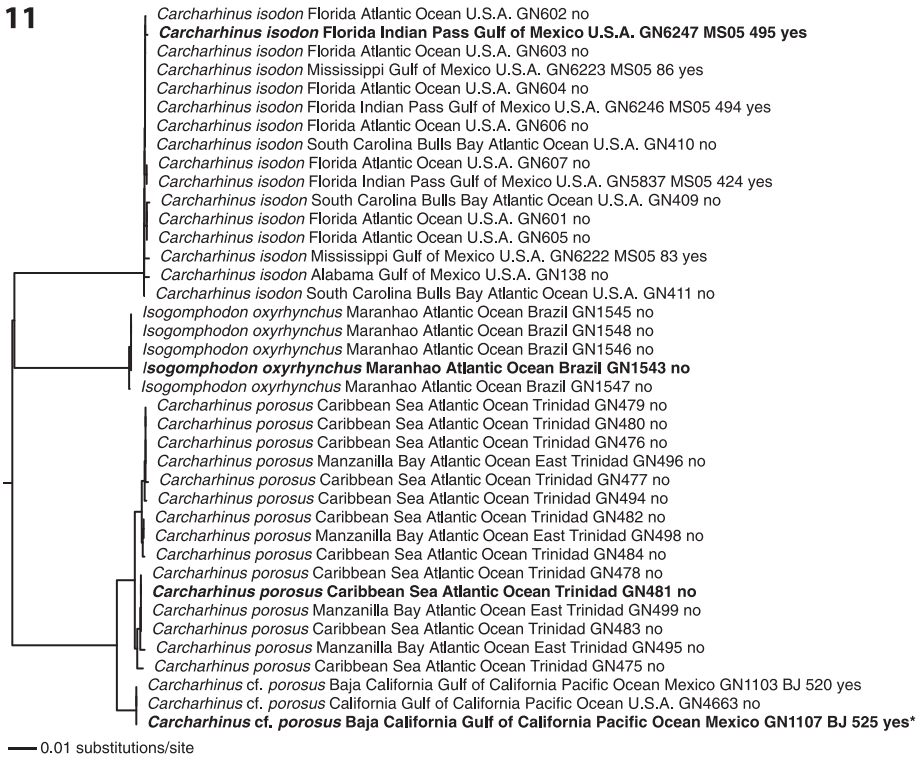
— 0.01 substitutions/site

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— 0.01 substitutions/site

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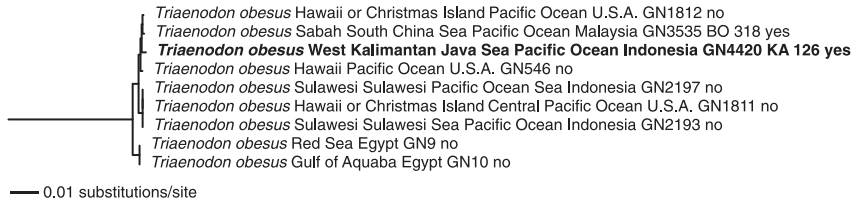




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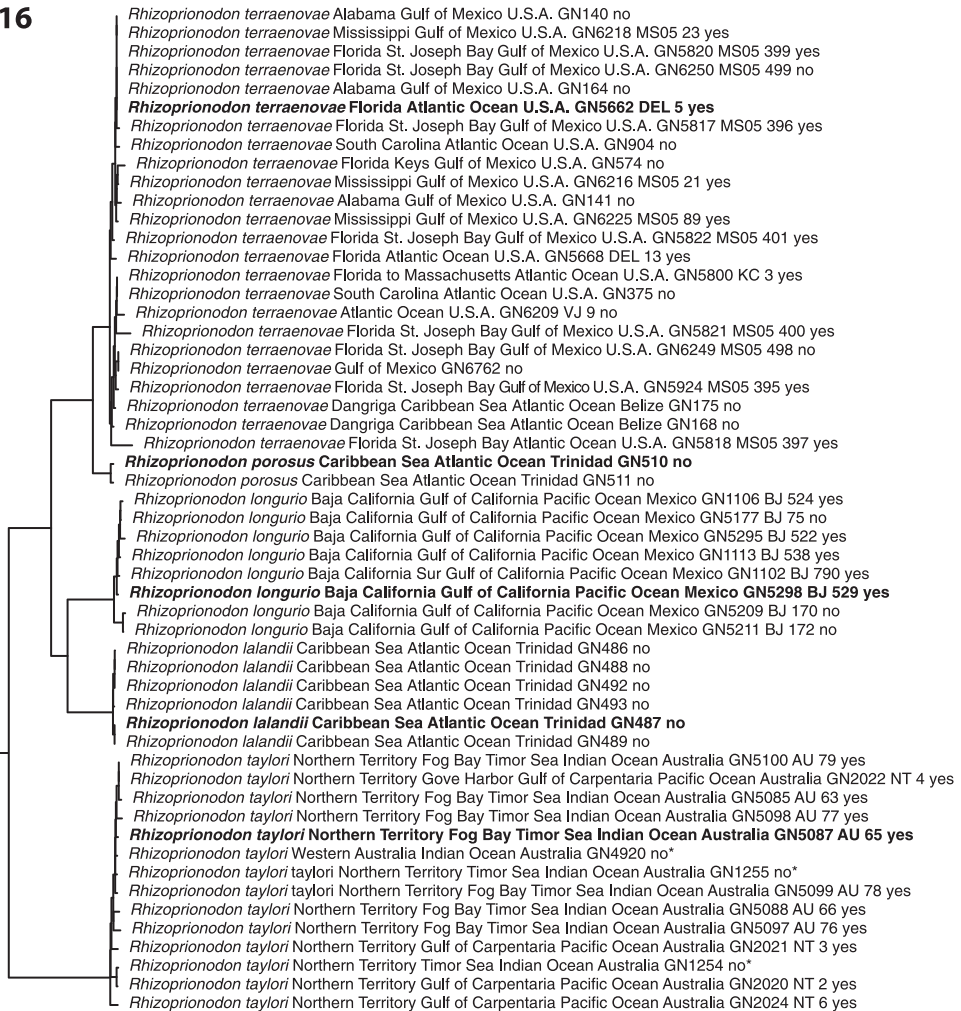
— 0.01 substitutions/site

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- Rhizoprionodon cf. acutus* 1 Atlantic Ocean Sierra Leone GN214 no  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN6154 SE 315 yes  
*Rhizoprionodon cf. acutus* 1 Casamance Atlantic Ocean Senegal GN6103 SE 263 yes  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Sierra Leone GN212 no  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN5965 SE 45 yes  
***Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN6060 SE 219 yes**  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN6062 SE 221 yes  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Sierra Leone GN213 no  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN6064 SE 223 yes  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN5922 SE 2 yes  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Senegal GN6157 SE 318 yes  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Sierra Leone GN216 no  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Angola GN7130 no  
*Rhizoprionodon cf. acutus* 1 Atlantic Ocean Sierra Leone GN215 no  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6652 MM 24 yes  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6637 MM 9 yes  
***Rhizoprionodon acutus* Gulf of Oman Iran GN6632 MM 4 yes**  
*Rhizoprionodon acutus* Kerala Indian Ocean India GN1645 no  
*Rhizoprionodon acutus* Kerala Indian Ocean India GN1644 no  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6630 MM 2 yes  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6674 MM 46 yes  
*Rhizoprionodon acutus* Maharastra Indian Ocean India GN1688 no  
*Rhizoprionodon acutus* Kerala Indian Ocean India GN1643 no  
*Rhizoprionodon acutus* Kerala Indian Ocean India GN1639 no  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6629 MM 1 yes  
*Rhizoprionodon acutus* Gulf of Oman Iran GN6669 MM 41 yes  
*Rhizoprionodon cf. acutus* 2 Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5138 AU 123 yes  
*Rhizoprionodon cf. acutus* 2 Queensland Gulf of Carpentaria Pacific Ocean Australia GN5547 CM03 50 yes  
*Rhizoprionodon cf. acutus* 2 Queensland Gulf of Carpentaria Pacific Ocean Australia GN5578 CM03 84 yes  
***Rhizoprionodon cf. acutus* 2 Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5137 AU 120 yes**  
*Rhizoprionodon cf. acutus* 2 Northern Territory Arafura Sea Pacific Ocean Australia GN2081 NT 68 yes  
*Rhizoprionodon cf. acutus* 2 Queensland Torres Strait Pacific Ocean Australia GN4918 no\*  
*Rhizoprionodon cf. acutus* 2 Western Australia Indian Ocean Australia GN4919 no\*  
*Rhizoprionodon cf. acutus* 2 Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5115 AU 95 yes  
*Rhizoprionodon cf. acutus* 2 Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5114 AU 94 yes  
*Rhizoprionodon cf. acutus* 2 Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5057 AU 19 yes  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1292 no  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1294 no  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1290 no  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1289 no  
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*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1291 no  
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***Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN2955 HBO 30 yes\***  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3619 BO 407 yes  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3616 BO 404 yes  
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*Rhizoprionodon cf. acutus* 3 Sabah Sulu Sea Pacific Ocean Malaysia GN2981 HBO 71 yes  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3617 BO 405 yes  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3614 BO 402 yes  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3613 BO 401 yes  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1282 no  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3534 BO 317 yes  
*Rhizoprionodon cf. acutus* 3 Sarawak South China Sea Pacific Ocean Malaysia GN3615 BO 403 yes  
*Rhizoprionodon cf. acutus* 3 South China Sea Pacific Ocean Philippines GN312 no  
*Rhizoprionodon cf. acutus* 3 Sabah South China Sea Pacific Ocean Malaysia GN1284 no  
*Rhizoprionodon cf. acutus* 3 Kerala Indian Ocean India GN1661 no  
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— 0.01 substitutions/site

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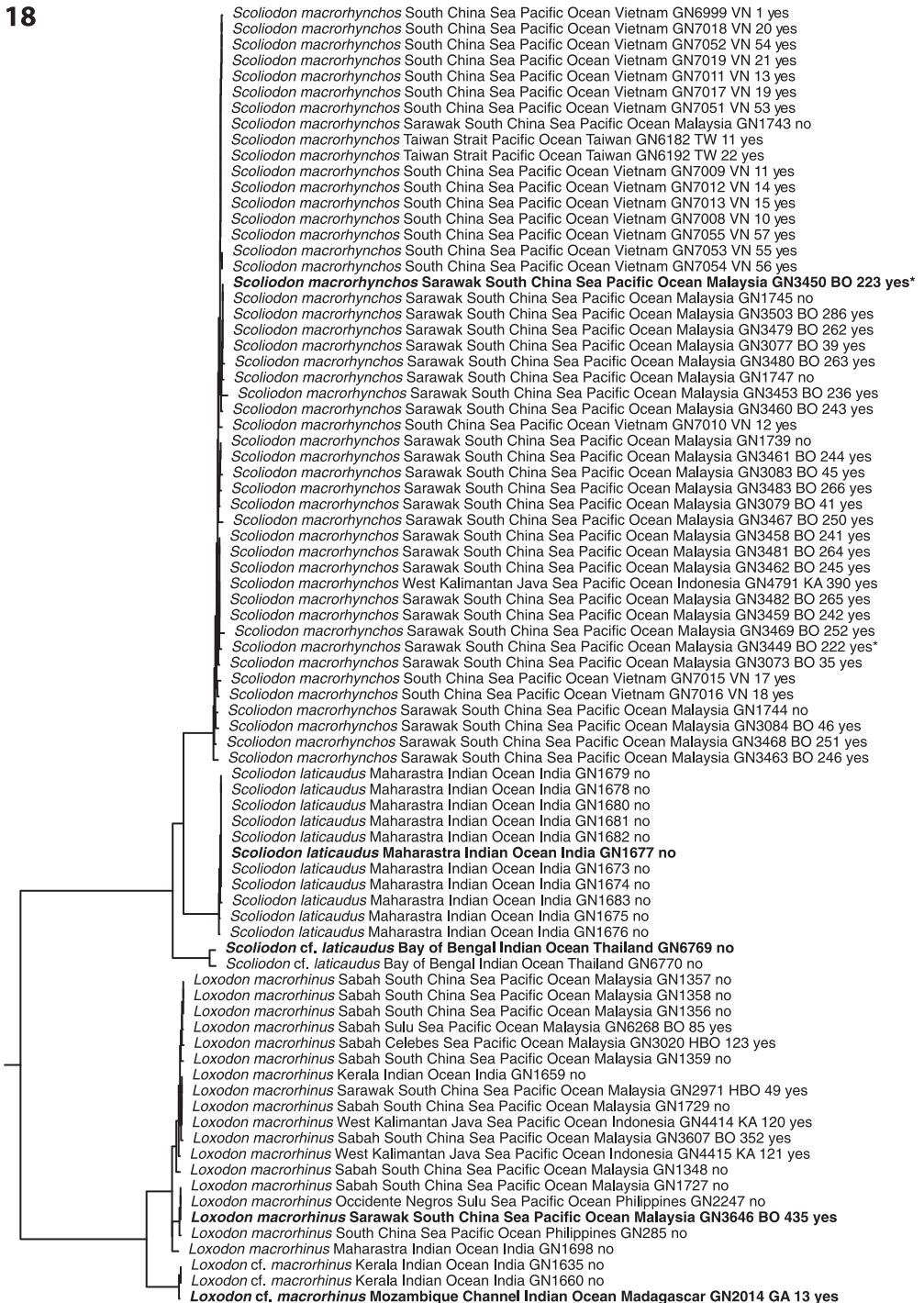
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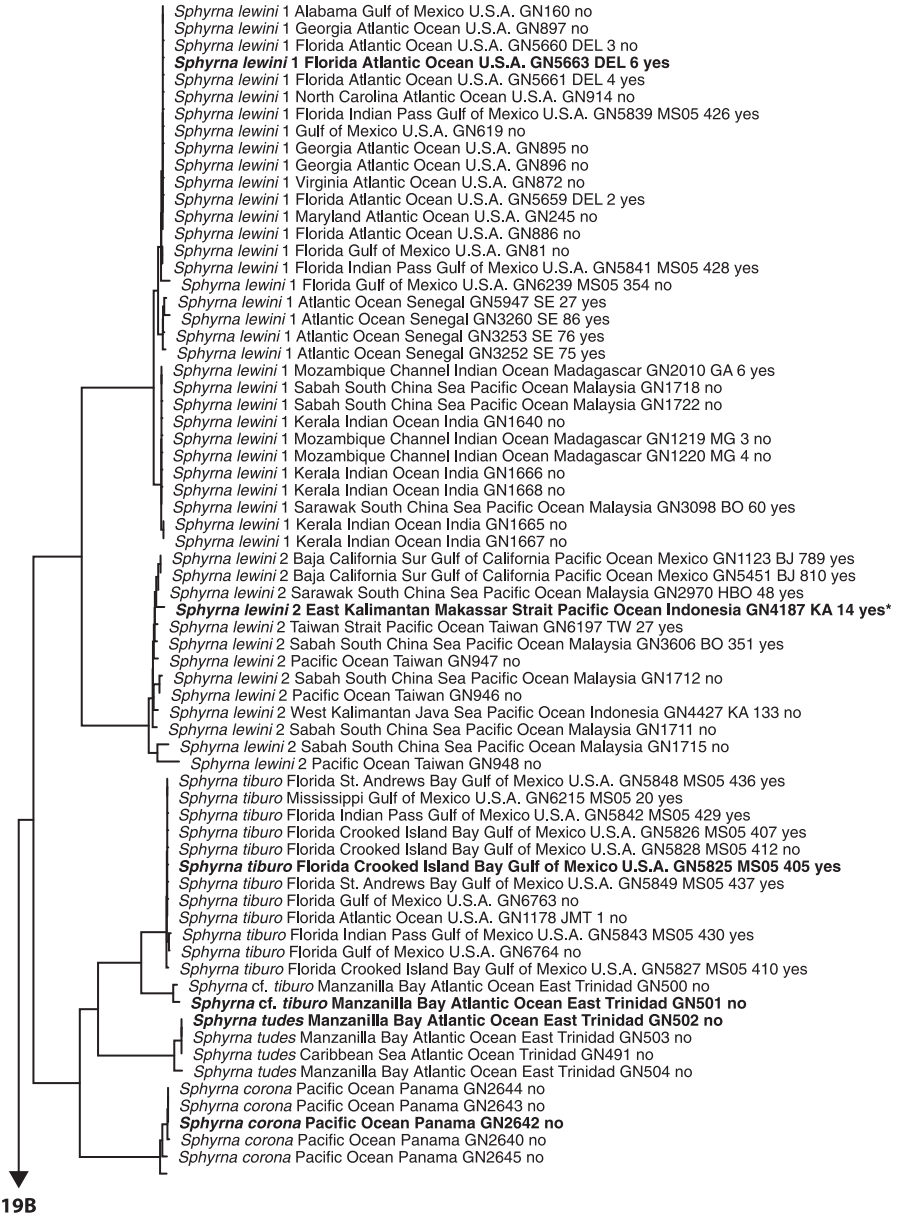
- Rhizoprionodon oligolinx* West Kalimantan Java Sea Pacific Ocean Indonesia GN4496 KA 202 yes
- Rhizoprionodon oligolinx* Sarawak South China Sea Pacific Ocean Malaysia GN3685 BO 474 yes\*
- Rhizoprionodon oligolinx* South Kalimantan Makassar Strait Pacific Ocean Indonesia GN4260 KA 87 yes
- Rhizoprionodon oligolinx* Sarawak South China Sea Pacific Ocean Malaysia GN3686 BO 475 yes\***
- Rhizoprionodon oligolinx* West Kalimantan Java Sea Pacific Ocean Indonesia GN4495 KA 201 yes
- Rhizoprionodon oligolinx* East Kalimantan Sulawesi Sea Pacific Ocean Indonesia GN4806 KA 405 yes
- Rhizoprionodon oligolinx* Sabah South China Sea Pacific Ocean Malaysia GN1371 no
- Rhizoprionodon oligolinx* Sabah South China Sea Pacific Ocean Malaysia GN1372 no
- Rhizoprionodon oligolinx* Sabah Celebes Sea Pacific Ocean Malaysia GN2939 BOD 72 yes
- Rhizoprionodon oligolinx* Kerala Indian Ocean India GN1649 no
- Rhizoprionodon oligolinx* Kerala Indian Ocean India GN1651 no
- Rhizoprionodon oligolinx* Kerala Indian Ocean India GN1634 no
- Rhizoprionodon oligolinx* Maharastra Indian Ocean India GN1685 no
- Rhizoprionodon oligolinx* Maharastra Indian Ocean India GN1684 no
- Rhizoprionodon oligolinx* Kerala Indian Ocean India GN1652 no
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- Rhizoprionodon oligolinx* Kerala Indian Ocean India GN1641 no

— 0.01 substitutions/site

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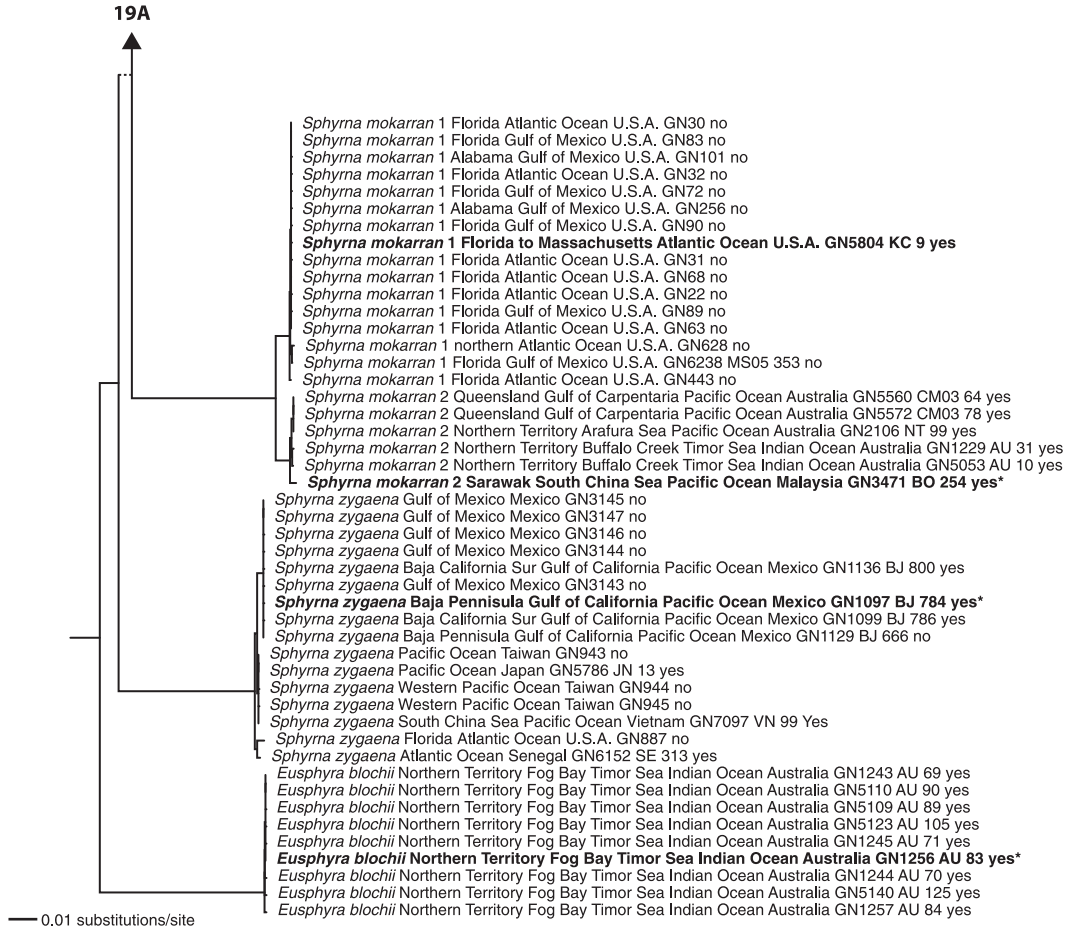


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19B

19B





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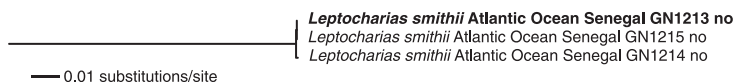
- Galeocerdo cf. cuvier* Virginia Atlantic Ocean U.S.A. GN877 no
- Galeocerdo cf. cuvier Maryland Atlantic Ocean U.S.A. GN239 no***
- Galeocerdo cf. cuvier* Florida Atlantic Ocean U.S.A. GN46 no
- Galeocerdo cf. cuvier* Virginia Atlantic Ocean U.S.A. GN876 no
- Galeocerdo cf. cuvier* Alabama Gulf of Mexico U.S.A. GN96 no
- Galeocerdo cf. cuvier* Florida Gulf of Mexico U.S.A. GN91 no
- Galeocerdo cf. cuvier* Virginia Atlantic Ocean U.S.A. GN878 no
- Galeocerdo cf. cuvier* Florida Gulf of Mexico U.S.A. GN85 no
- Galeocerdo cf. cuvier* Alabama Gulf of Mexico U.S.A. GN98 no
- Galeocerdo cf. cuvier* Florida Atlantic Ocean U.S.A. GN34 no
- Galeocerdo cf. cuvier* Alabama Gulf of Mexico U.S.A. GN102 no
- Galeocerdo cf. cuvier* Alabama Gulf of Mexico U.S.A. GN97 no
- Galeocerdo cf. cuvier* Gulf of Mexico U.S.A. GN6240 MS05 355 no
- Galeocerdo cf. cuvier* Virginia Atlantic Ocean U.S.A. GN879 no
- Galeocerdo cf. cuvier* Florida Atlantic Ocean U.S.A. GN35 no
- Galeocerdo cf. cuvier* Florida Atlantic Ocean U.S.A. GN59 no
- Galeocerdo cf. cuvier* Alabama Gulf of Mexico U.S.A. GN252 no
- Galeocerdo cf. cuvier* Florida Atlantic Ocean U.S.A. GN888 no
- Galeocerdo cuvier* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5050 AU 6 no
- Galeocerdo cuvier* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5059 AU 21 yes
- Galeocerdo cuvier* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5071 AU 44 no
- Galeocerdo cuvier* Hawaii Pacific Ocean U.S.A. GN135 no
- Galeocerdo cuvier* Red Sea Gulf of Aqaba Egypt GN7 no
- Galeocerdo cuvier* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5101 AU 80 yes
- Galeocerdo cuvier Baja California Sur Gulf of California Pacific Ocean Mexico GN5271 BJ 382 yes\****
- Galeocerdo cuvier* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5143 AU 129 yes
- Galeocerdo cuvier* Northern Territory Fog Bay Timor Sea Indian Ocean Australia GN5144 AU 130 yes
- Galeocerdo cuvier* West Kalimantan Java Sea Pacific Ocean Indonesia GN4418 KA 124 yes
- Galeocerdo cuvier* Northern Territory Buffalo Creek Timor Sea Indian Ocean Australia GN5049 AU 5 yes

— 0.01 substitutions/site

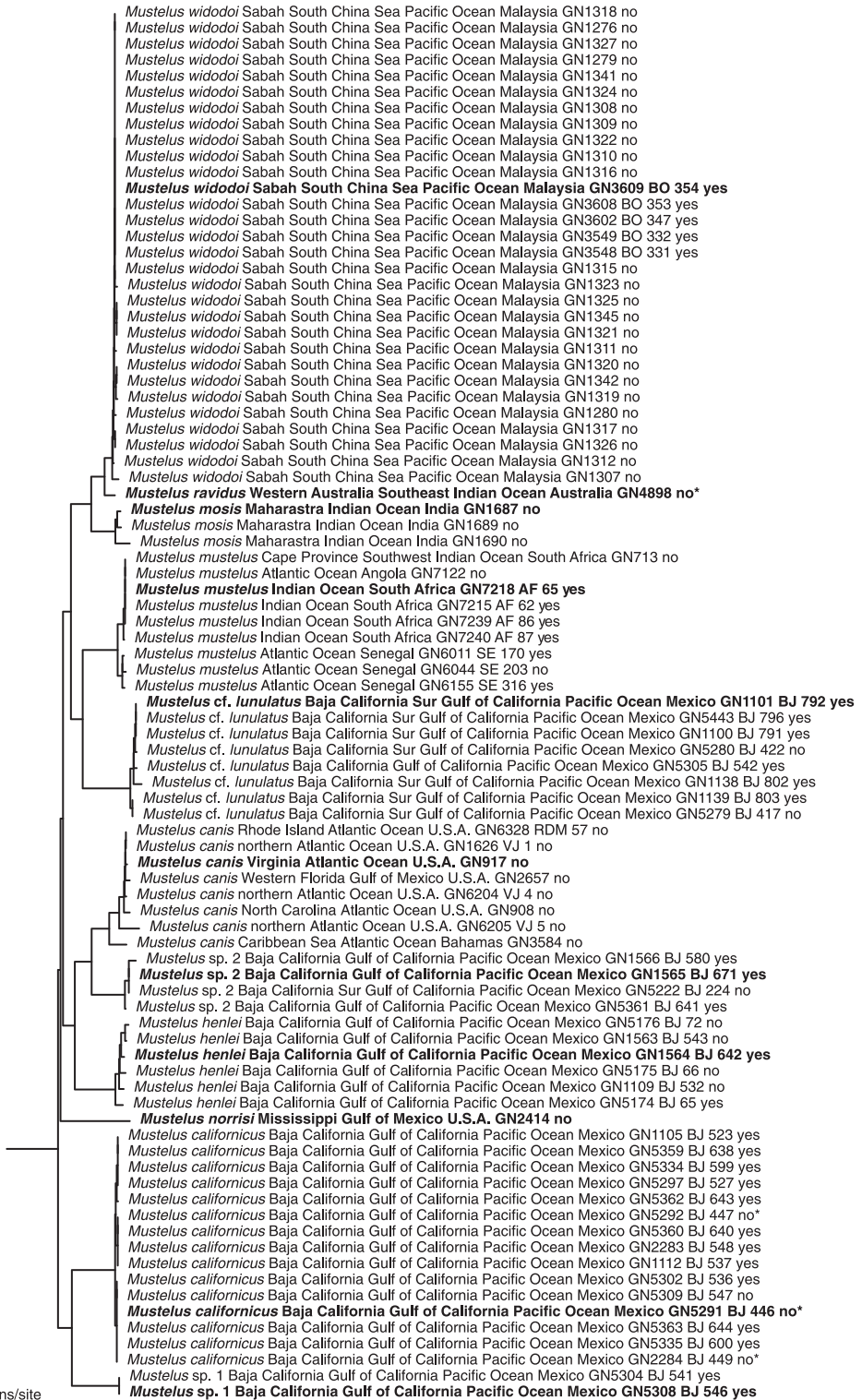
21



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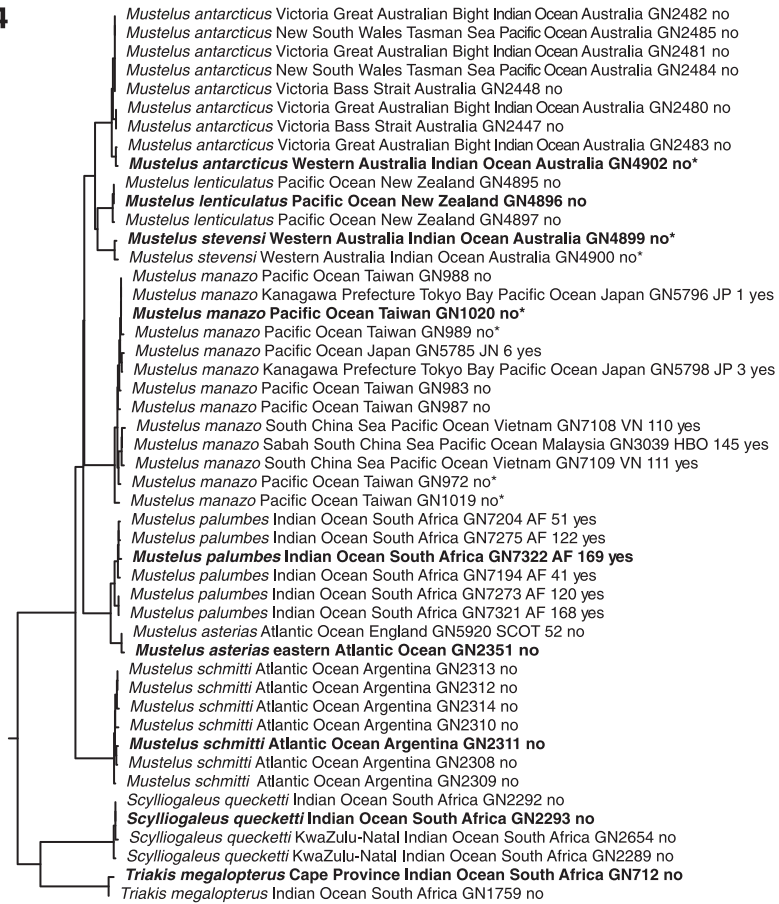


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— 0.01 substitutions/site

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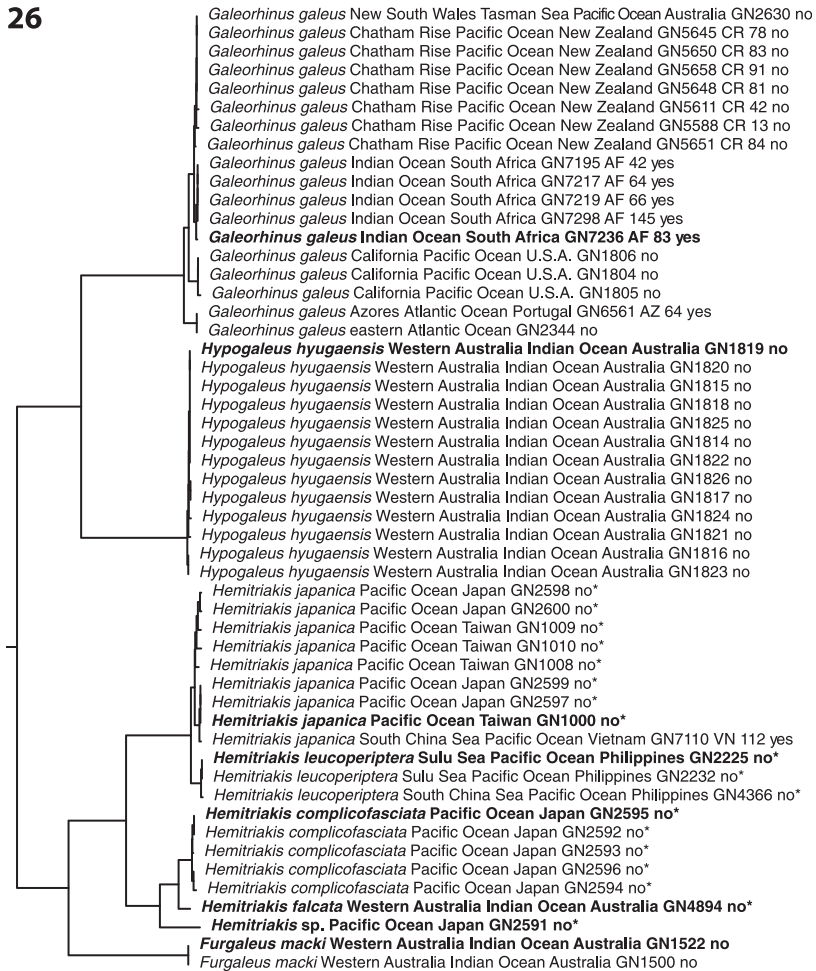


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— 0.01 substitutions/site

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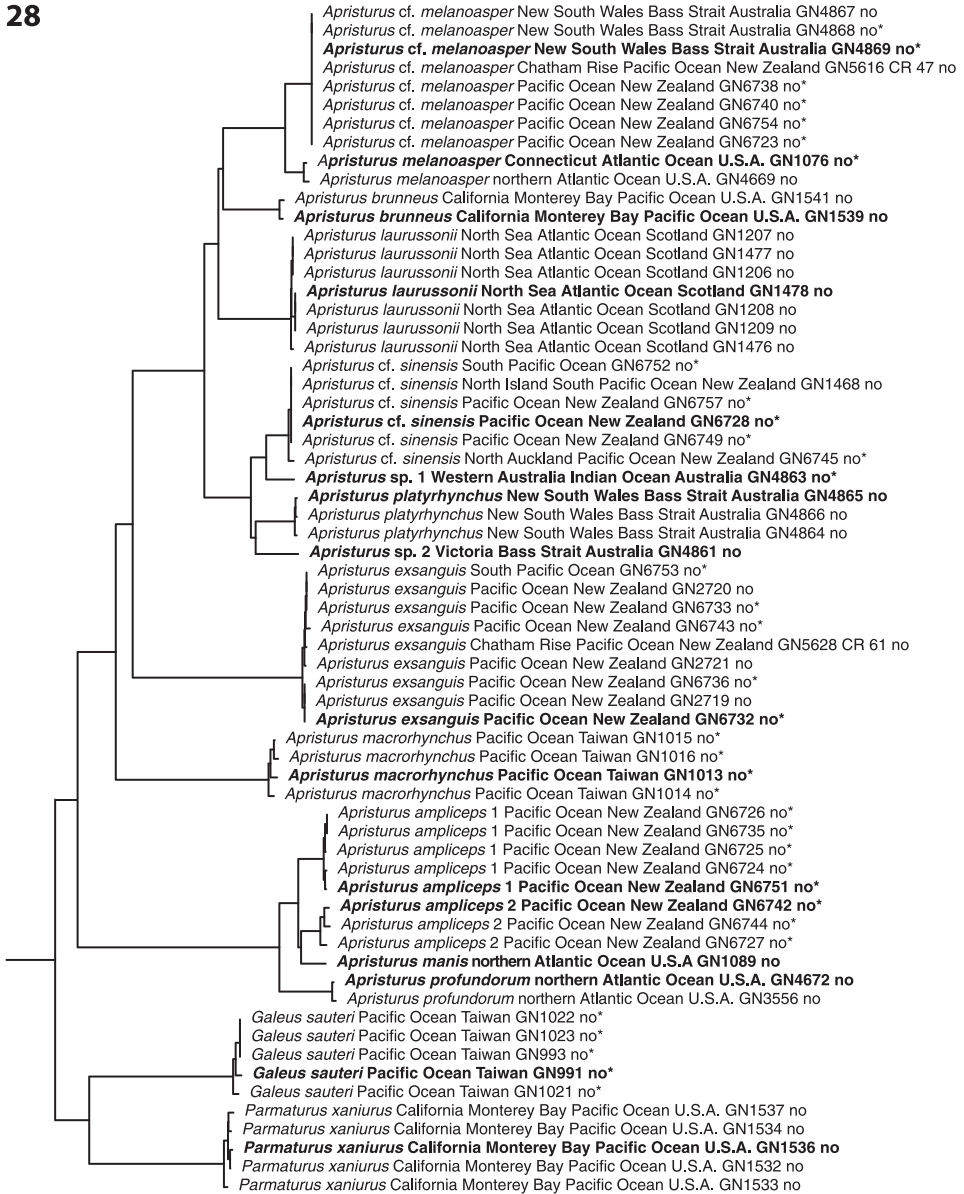
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— 0.01 substitutions/site

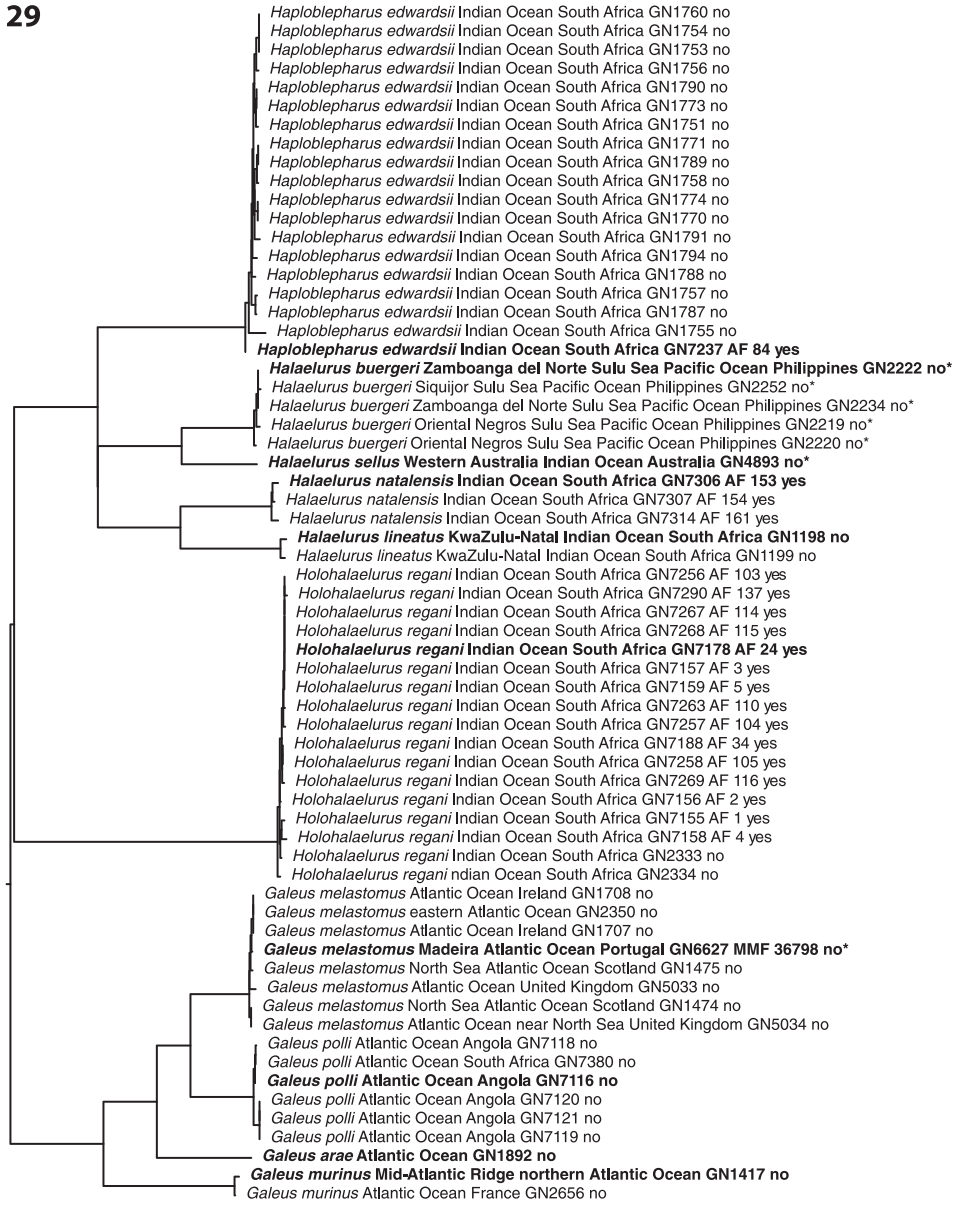
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— 0.01 substitutions/site



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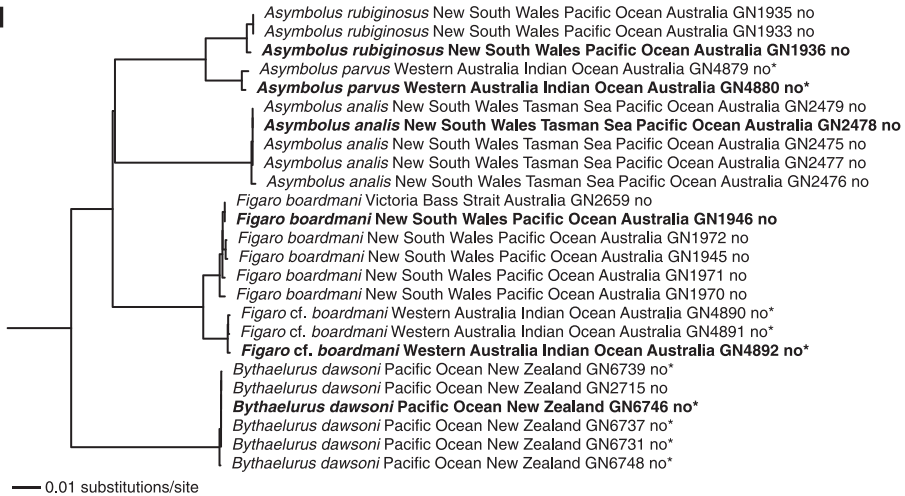


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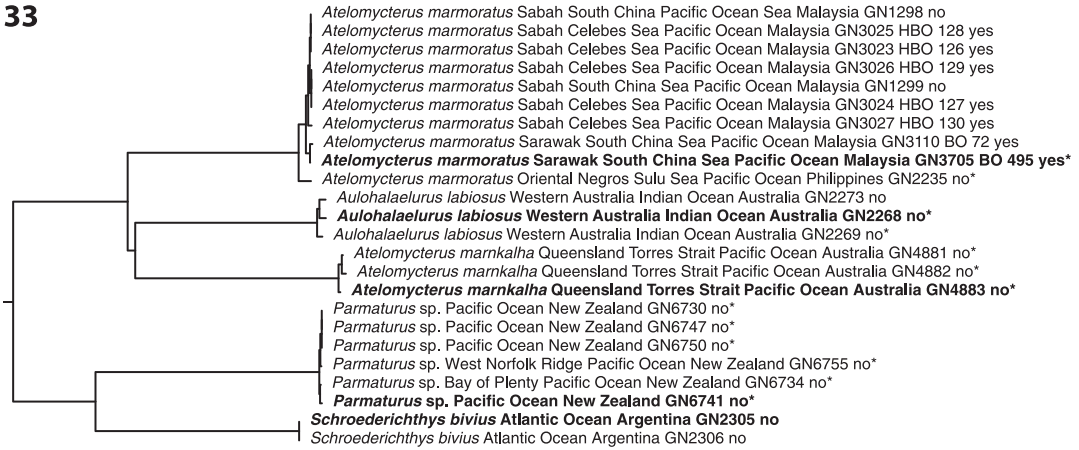
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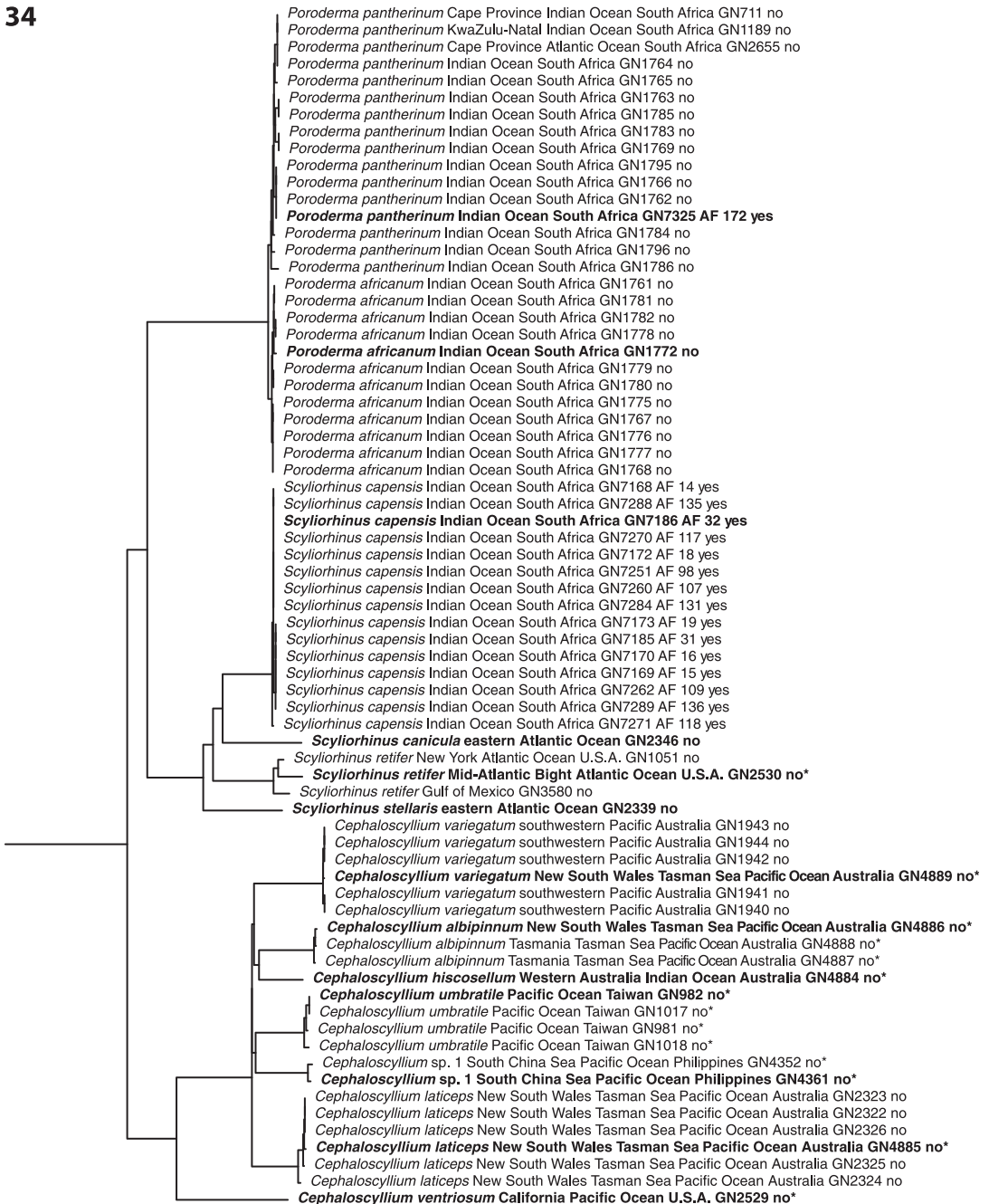


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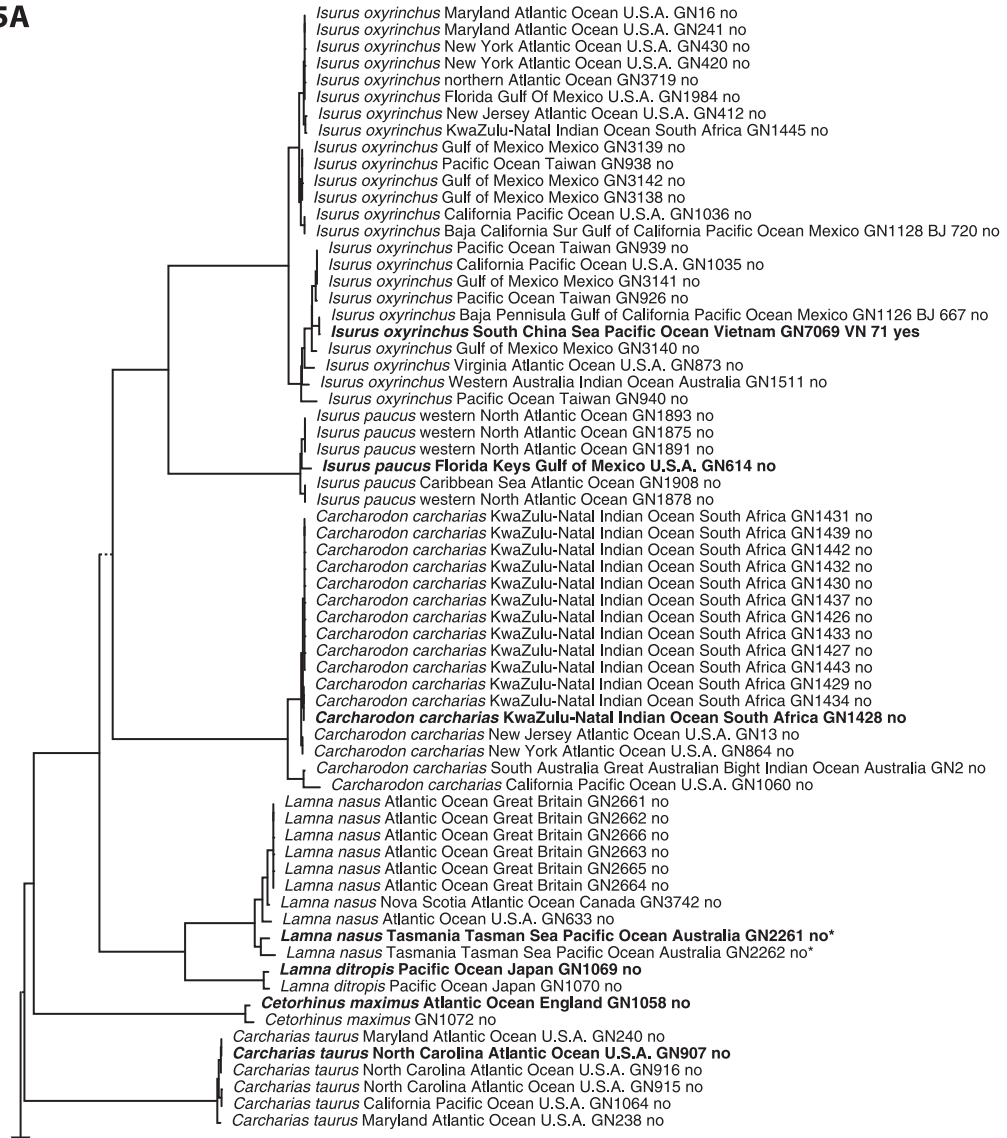
— 0.01 substitutions/site

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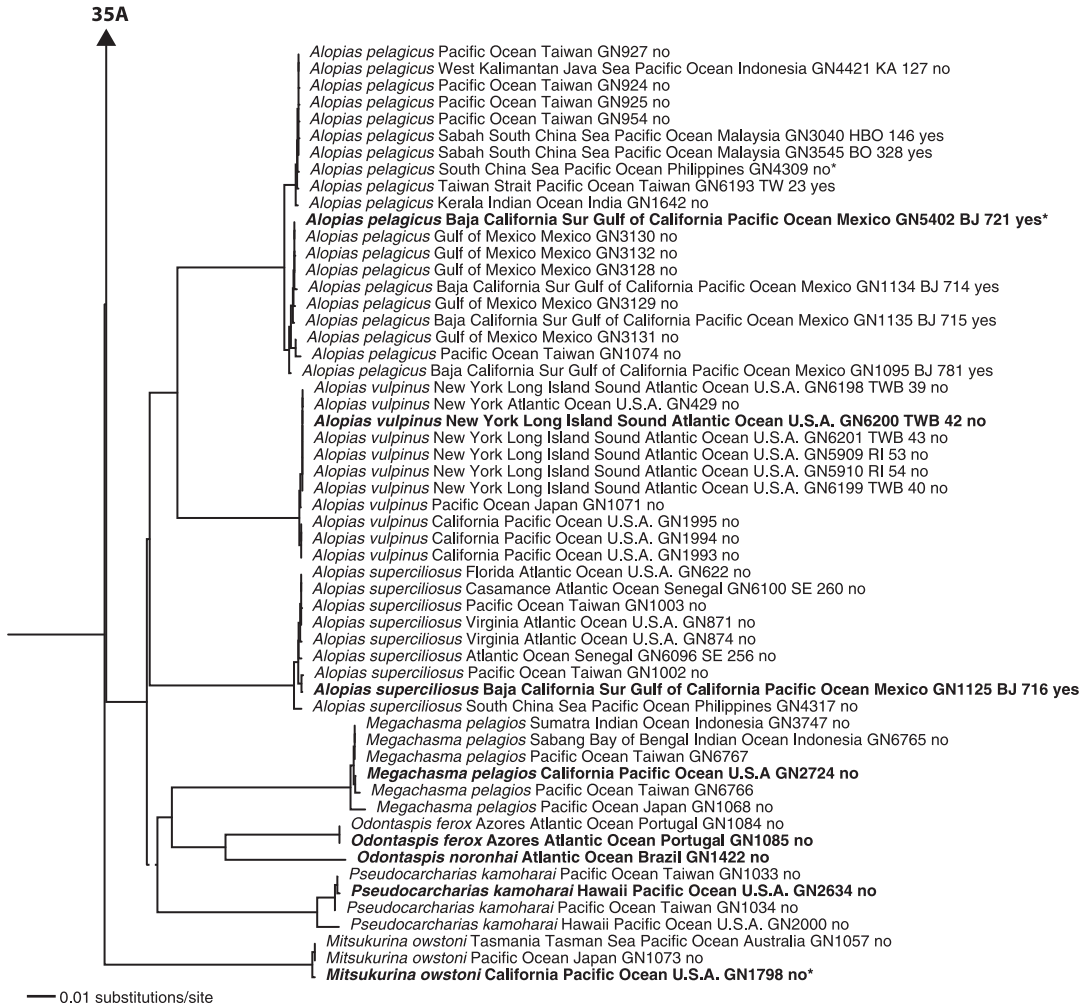
— 0.01 substitutions/site

35A



35B

35B

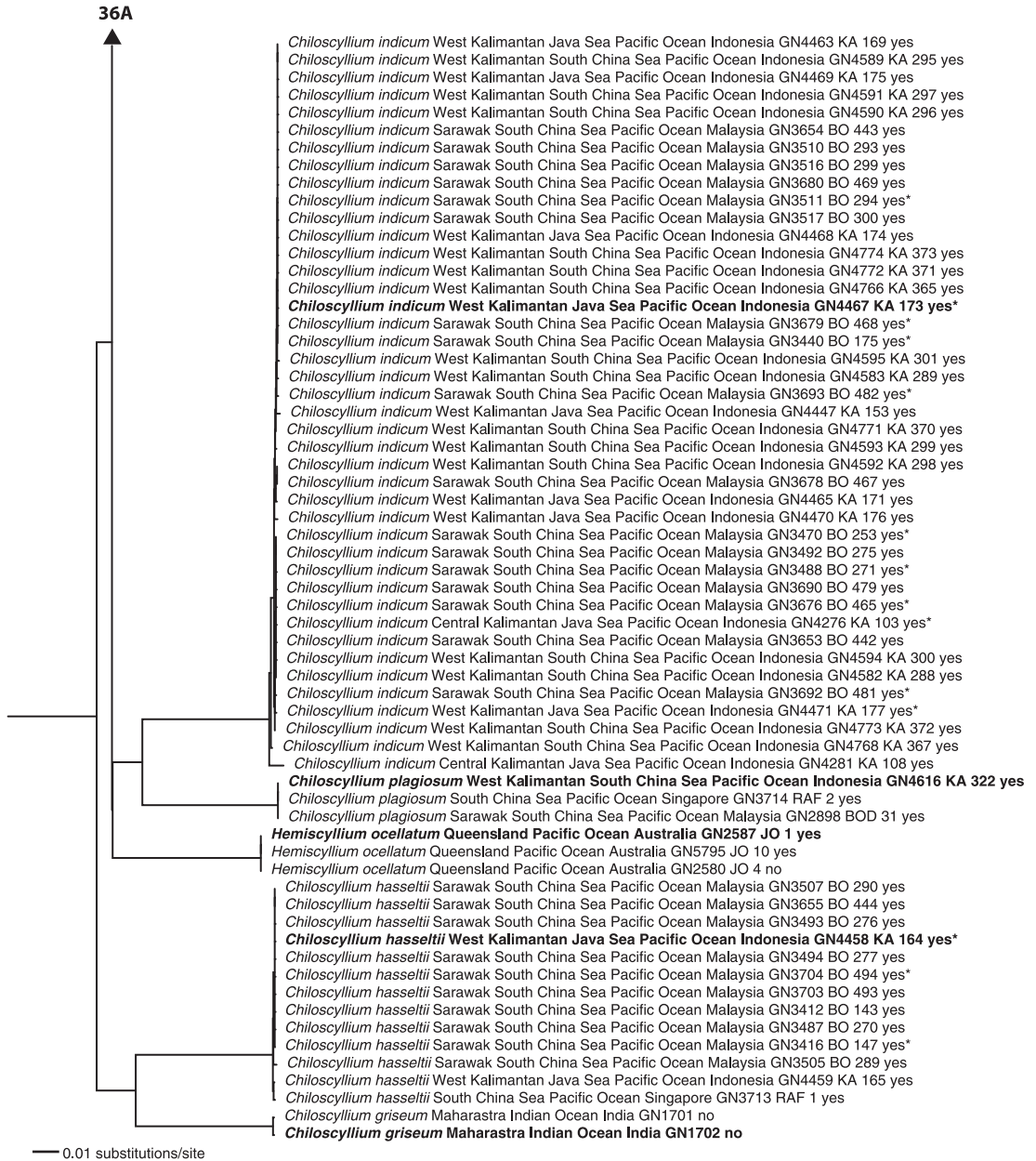


36A

*Chiloscyllium punctatum* South China Sea Pacific Ocean Vietnam GN7090 VN 92 yes  
*Chiloscyllium punctatum* South China Sea Pacific Ocean Vietnam GN7094 VN 96 yes  
*Chiloscyllium punctatum* Pacific Ocean Thailand GN1169 TH 2 no  
*Chiloscyllium punctatum* Pacific Ocean Thailand GN1173 TH 7 yes  
*Chiloscyllium punctatum* Pacific Ocean Thailand GN1172 TH 6 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4444 KA 150 yes  
*Chiloscyllium punctatum* West Kalimantan South China Sea Pacific Ocean Indonesia GN4615 KA 321 yes  
*Chiloscyllium punctatum* Pacific Ocean Thailand GN1170 TH 3 yes  
*Chiloscyllium punctatum* Central Kalimantan Java Sea Pacific Ocean Indonesia GN4285 KA 112 yes  
*Chiloscyllium punctatum* South China Sea Pacific Ocean Singapore GN3715 RAF 3 yes  
*Chiloscyllium punctatum* Central Kalimantan Java Sea Pacific Ocean Indonesia GN4274 KA 101 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4453 KA 159 yes  
***Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4446 KA 152 yes\***  
*Chiloscyllium punctatum* West Kalimantan South China Sea Pacific Ocean Indonesia GN4574 KA 280 yes  
*Chiloscyllium punctatum* South China Sea Pacific Ocean Vietnam GN7095 VN 97 yes  
*Chiloscyllium punctatum* South China Sea Pacific Ocean Vietnam GN7093 VN 95 yes  
*Chiloscyllium punctatum* South China Sea Pacific Ocean Vietnam GN7096 VN 98 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4443 KA 149 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3658 BO 447 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3520 BO 303 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN2902 BOD 35 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3519 BO 302 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4445 KA 151 yes  
*Chiloscyllium punctatum* West Kalimantan South China Sea Pacific Ocean Indonesia GN4596 KA 302 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4452 KA 158 yes  
*Chiloscyllium punctatum* West Kalimantan Java Sea Pacific Ocean Indonesia GN4466 KA 172 yes  
*Chiloscyllium punctatum* Pacific Ocean Singapore GN2192 no  
*Chiloscyllium punctatum* Sabah Celebes Sea Pacific Ocean Malaysia GN3028 HBO 131 yes  
*Chiloscyllium punctatum* Sabah South China Sea Pacific Ocean Malaysia GN1296 no  
*Chiloscyllium punctatum* Sabah Sulawesi Sea Pacific Ocean Malaysia GN3029 no  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3663 BO 452 yes  
*Chiloscyllium punctatum* Sabah Sulu Sea Pacific Ocean Malaysia GN3382 BO 112 yes  
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*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3500 BO 283 yes  
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*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3491 BO 274 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3498 BO 281 yes  
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*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3489 BO 272 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3495 BO 278 yes  
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*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN2900 BOD 33 yes  
*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3522 BO 305 yes  
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*Chiloscyllium punctatum* Sarawak South China Sea Pacific Ocean Malaysia GN3642 BO 431 yes  
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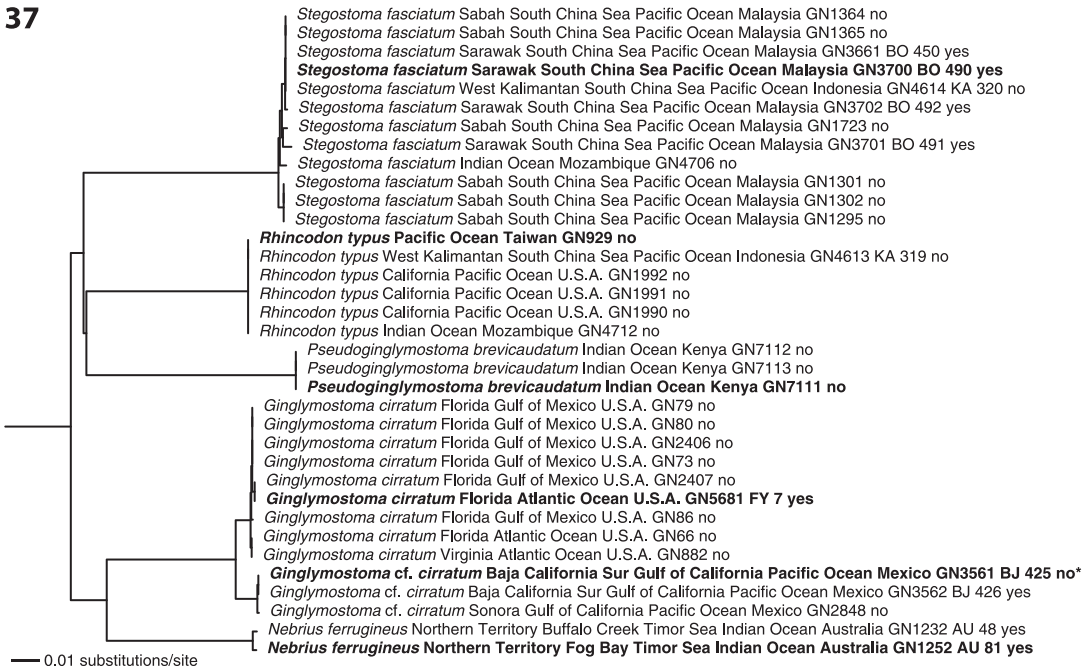
36B

36B

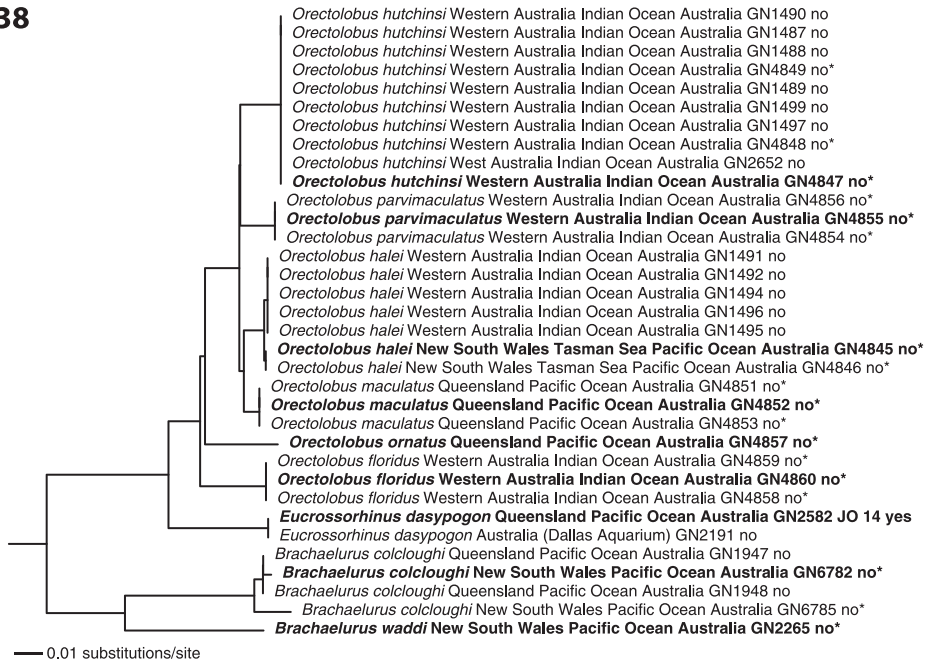




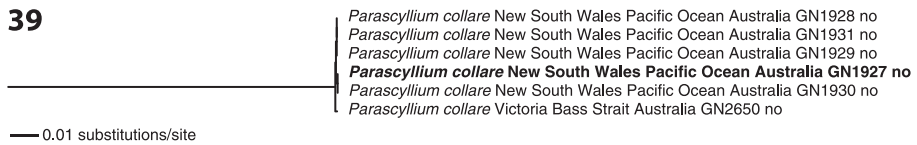
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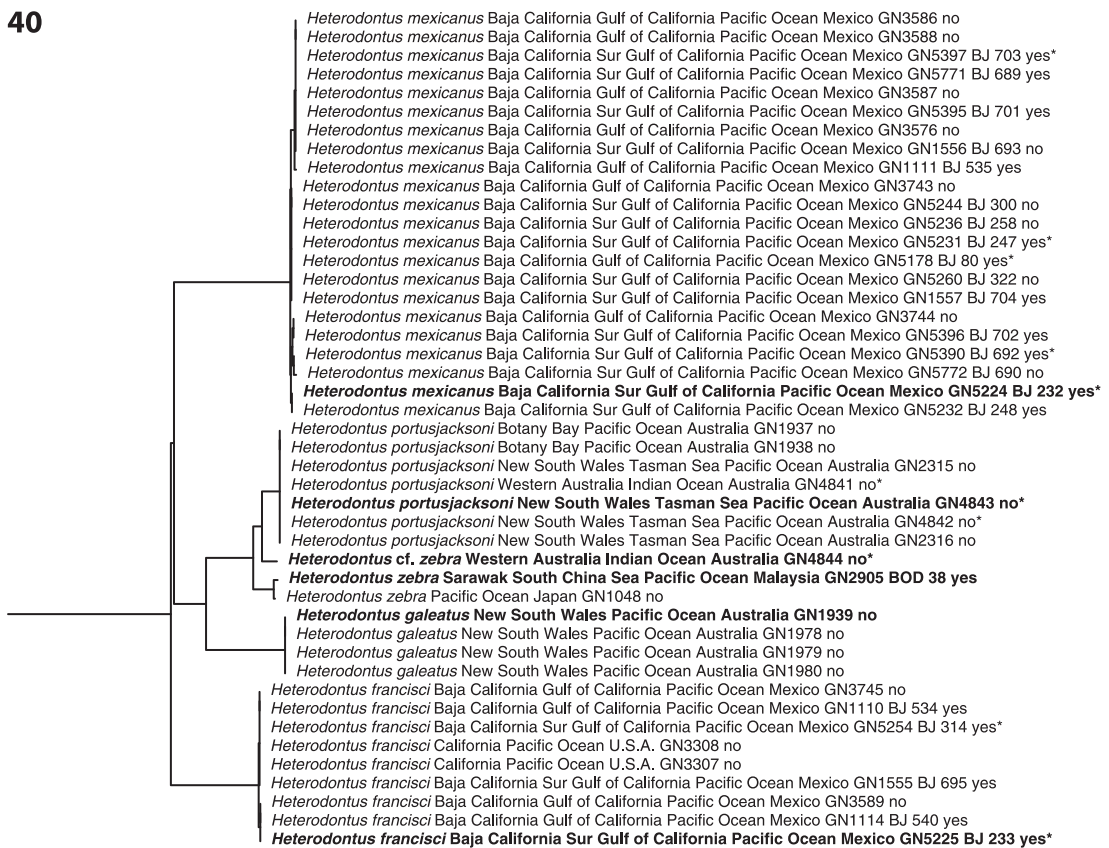
38



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— 0.01 substitutions/site

## 41A

*Squalus acanthias* Chatham Rise Pacific Ocean New Zealand (3 spcms.)†  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. (38 spcms.)‡  
*Squalus acanthias* Pacific Ocean Chile (9 spcms.)§  
*Squalus acanthias* Tasmania Western South Pacific Australia GN4958 no\*  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN5906 RDM 32 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6322 RDM 51 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN5894 RDM 20 no  
*Squalus acanthias* Maryland Atlantic Ocean U.S.A. GN919 no  
*Squalus acanthias* Pacific Ocean Chile GN2399 CI 1 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6310 RDM 39 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6453 RDM 160 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6371 RDM 104 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6404 RDM 138 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6391 RDM 124 yes  
*Squalus acanthias* Pacific Ocean Chile GN5673 no  
*Squalus acanthias* Pacific Ocean Chile GN6421 CHL 14 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6355 RDM 85 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6304 RDM 33 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6363 RDM 93 yes  
*Squalus acanthias* Pacific Ocean Chile GN5674 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6388 RDM 121 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6312 RDM 41 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6386 RDM 119 yes  
*Squalus acanthias* Pacific Ocean Chile GN5672 no  
*Squalus acanthias* Pacific Ocean Chile GN6414 CHL 7 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6331 RDM 60 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6446 RDM 153 yes  
*Squalus acanthias* Pacific Ocean Chile GN6419 CHL 12 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN5893 RDM 19 no  
*Squalus acanthias* Tasmania Pacific Ocean Australia GN4957 no\*  
*Squalus acanthias* Chatham Rise Pacific Ocean New Zealand GN5653 CR 86 no  
*Squalus acanthias* Pacific Ocean Chile GN6412 CHL 5 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6325 RDM 54 no  
*Squalus acanthias* Florida to Massachusetts Atlantic Ocean U.S.A. GN1187 KC 20 no  
*Squalus acanthias* Pacific Ocean Chile GN6435 CHL 28 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN5895 RDM 21 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6326 RDM 55 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6345 RDM 74 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN5904 RDM 30 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6362 RDM 92 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6392 RDM 125 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6324 RDM 53 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6389 RDM 122 yes  
*Squalus acanthias* Pacific Ocean Chile GN6423 CHL 16 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6369 RDM 102 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6443 RDM 150 yes  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6313 RDM 42 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6329 RDM 58 yes  
*Squalus acanthias* Pacific Ocean Chile GN5670 no  
***Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6336 RDM 65 yes**  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6385 RDM 118 yes

## 41B

† Specimen details: GN4302 CR 10 no; GN4303 CR 11 no; GN5654 CR 87 no.

‡ Specimen details: GN4290 RDM 3 yes; GN4291 RDM 4 yes; GN4292 RDM 5 yes; GN4293 RDM 6 yes; GN4297 RDM 10 yes; GN5901 RDM 27 no; GN5903 RDM 29 no; GN6307 RDM 36 yes; GN6308 RDM 37 yes; GN6317 RDM 46 no; GN6318 RDM 47 no; GN6320 RDM 49 no; GN6327 RDM 56 no; GN6330 RDM 59 yes; GN6335 RDM 64 yes; GN6337 RDM 66 yes; GN6340 RDM 69 yes; GN6342 RDM 71 no; GN6343 RDM 72 no; GN6349 RDM 79 no; GN6354 RDM 84 yes; GN6364 RDM 94 yes; GN6368 RDM 101 no; GN6377 RDM 110 yes; GN6379 RDM 112 yes; GN6380 RDM 113 yes; GN6382 RDM 115 yes; GN6384 RDM 117 yes; GN6390 RDM 123 yes; GN6393 RDM 126 yes; GN6395 RDM 128 yes; GN6402 RDM 136 no; GN6406 RDM 141 no; GN6407 RDM 142 no; GN6408 RDM 145 no; GN6442 RDM 149 yes; GN6449 RDM 156 yes; GN6456 RDM 163 yes.

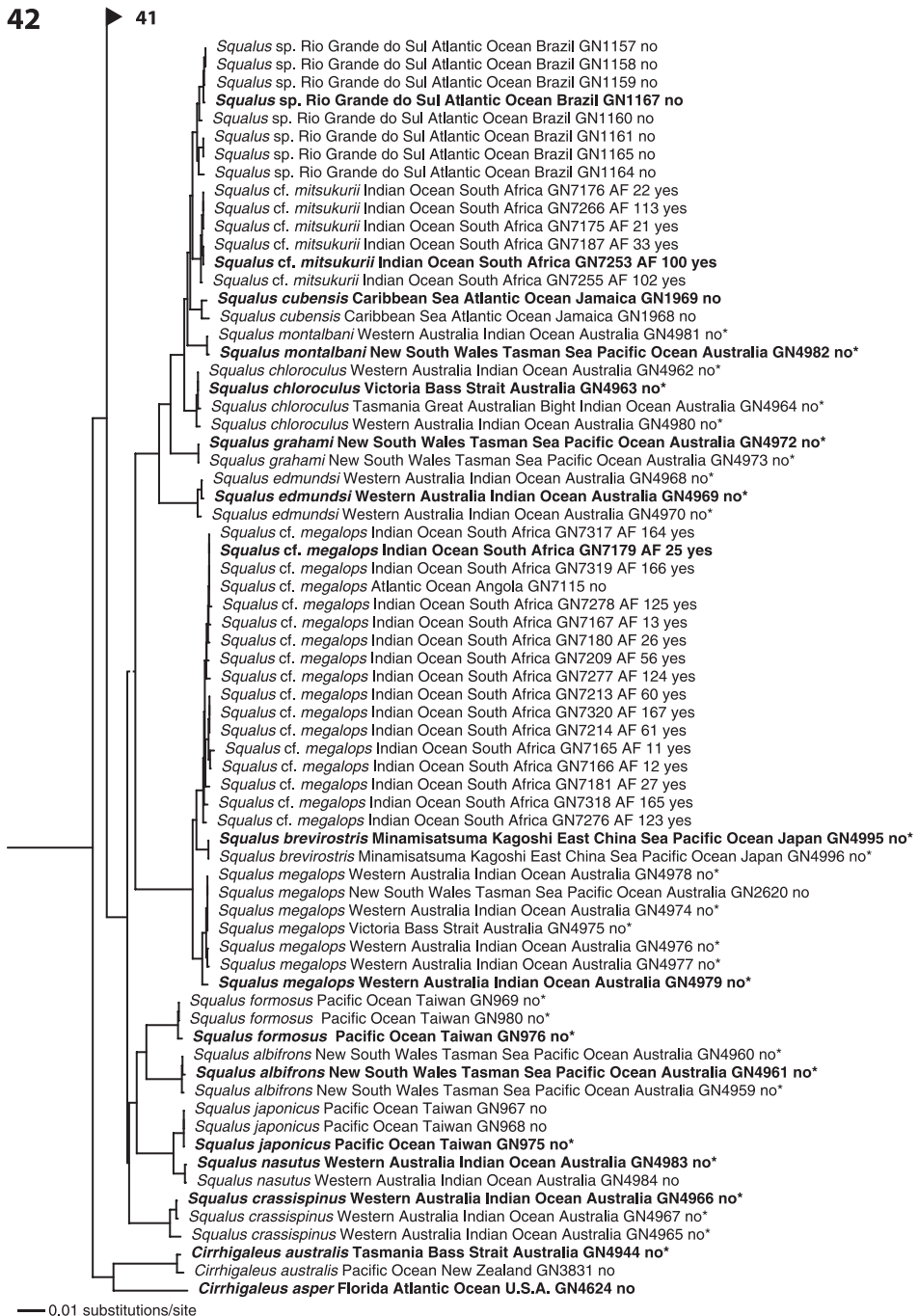
§ Specimen details: GN5669 FS 5 no; GN5671 FS 7 no; GN6409 CHL 2 no; GN6417 CHL 10 yes; GN6418 CHL 11 yes; GN6420 CHL 13 yes; GN6431 CHL 24 yes; GN6432 CHL 25 yes; GN6433 CHL 26 yes.

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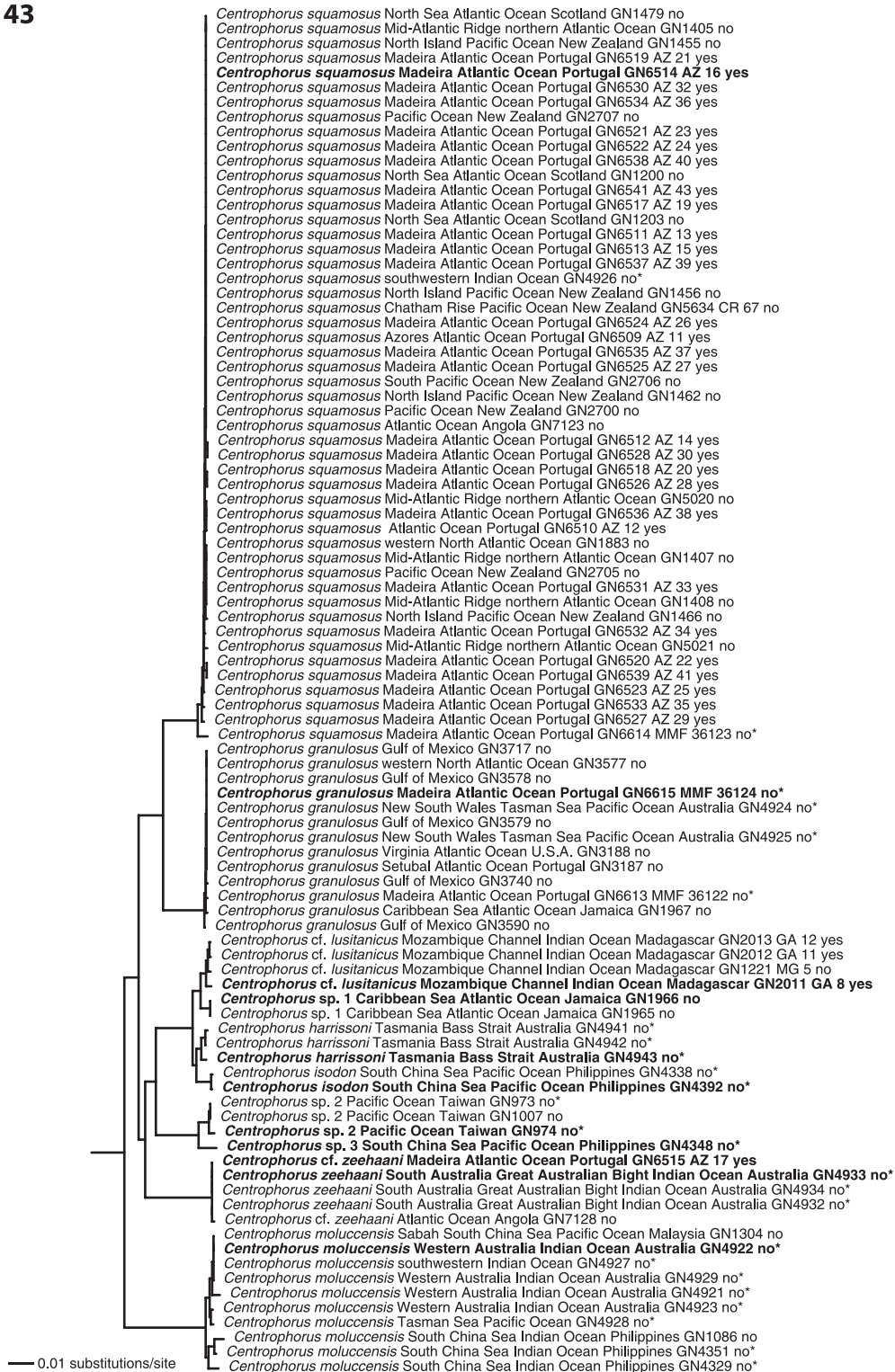
41A

- Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6319 RDM 48 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6367 RDM 97 no  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6378 RDM 111 yes  
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*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6333 RDM 62 yes  
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*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6348 RDM 78 no  
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*Squalus acanthias* Tasmania Pacific Ocean Australia GN4956 no\*  
*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6315 RDM 44 no  
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*Squalus acanthias* Rhode Island Atlantic Ocean U.S.A. GN6401 RDM 134 yes  
*Squalus acanthias* Chatham Rise Pacific Ocean New Zealand GN4304 CR 35 no  
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*Squalus suckleyi* Alaska Gulf of Alaska Pacific Ocean U.S.A. GN1185 GOA 52 yes  
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— 0.01 substitutions/site



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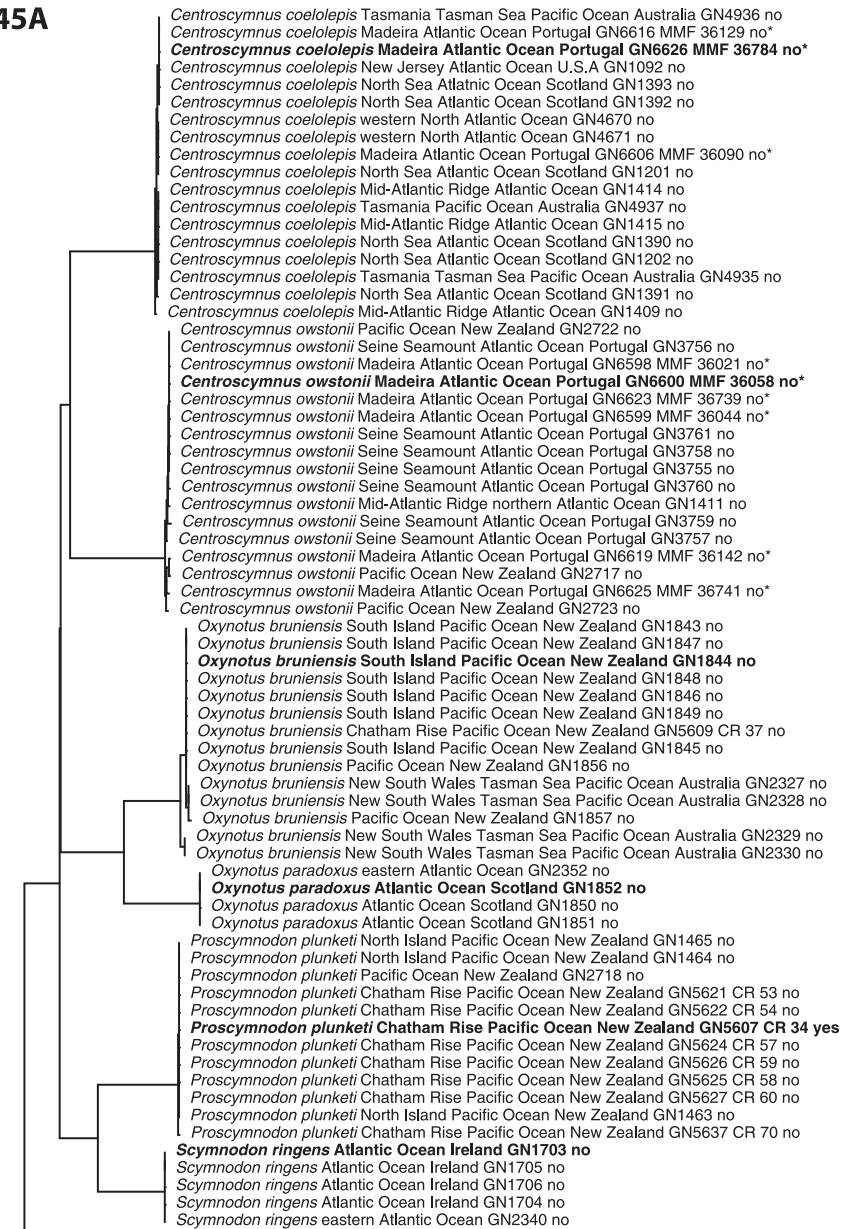


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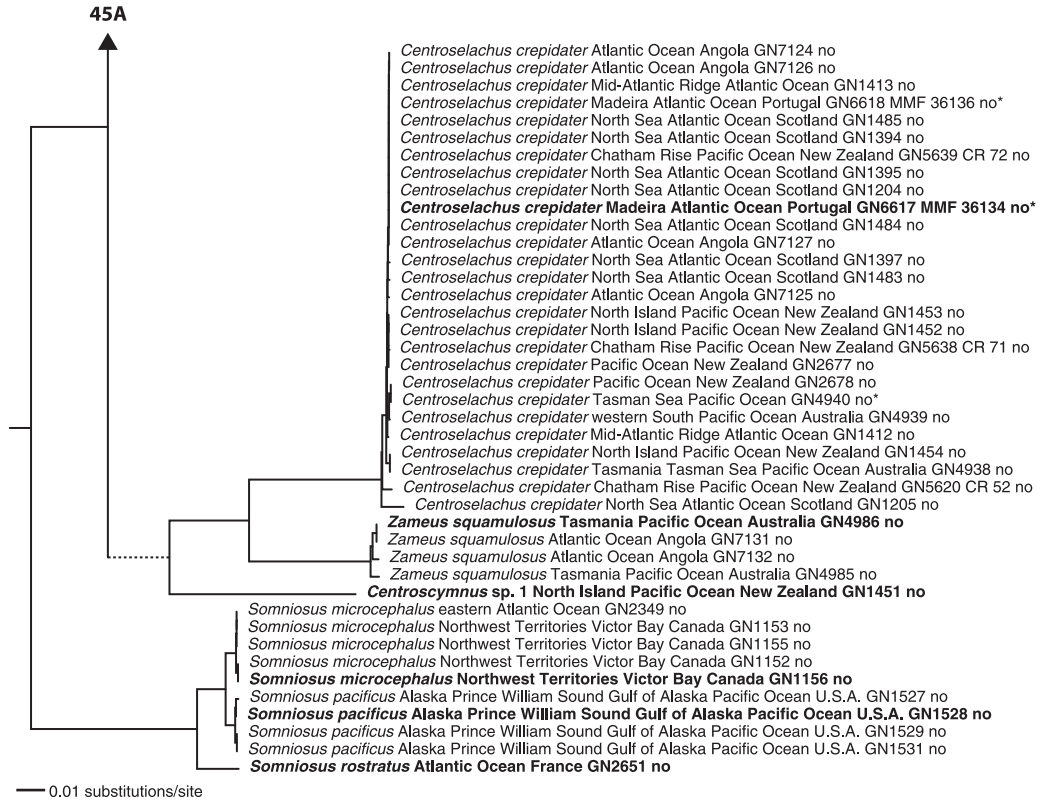


45A



45B

45B

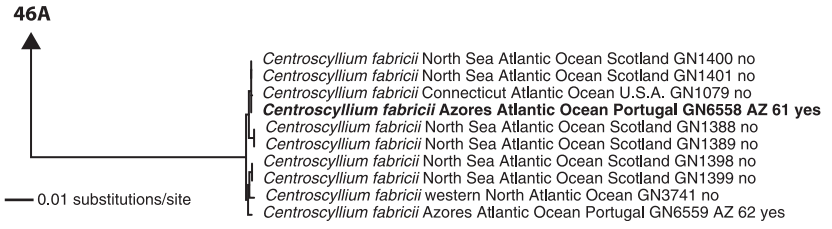


46A

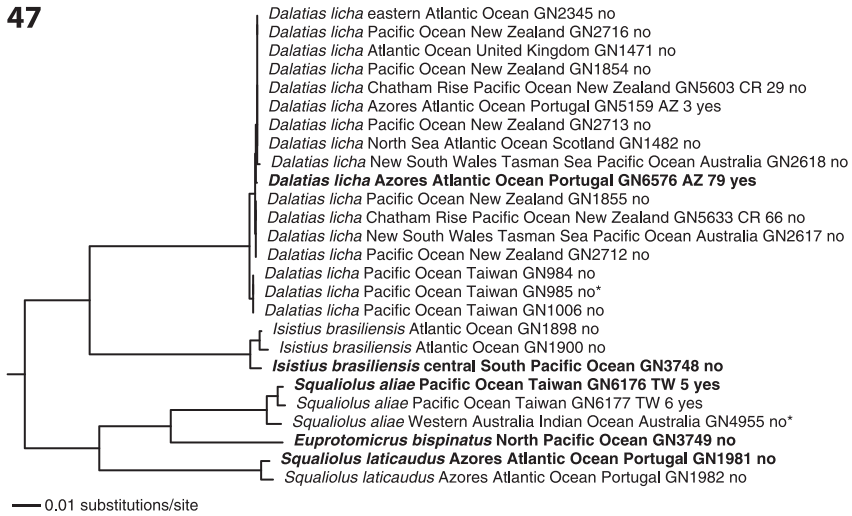


46B

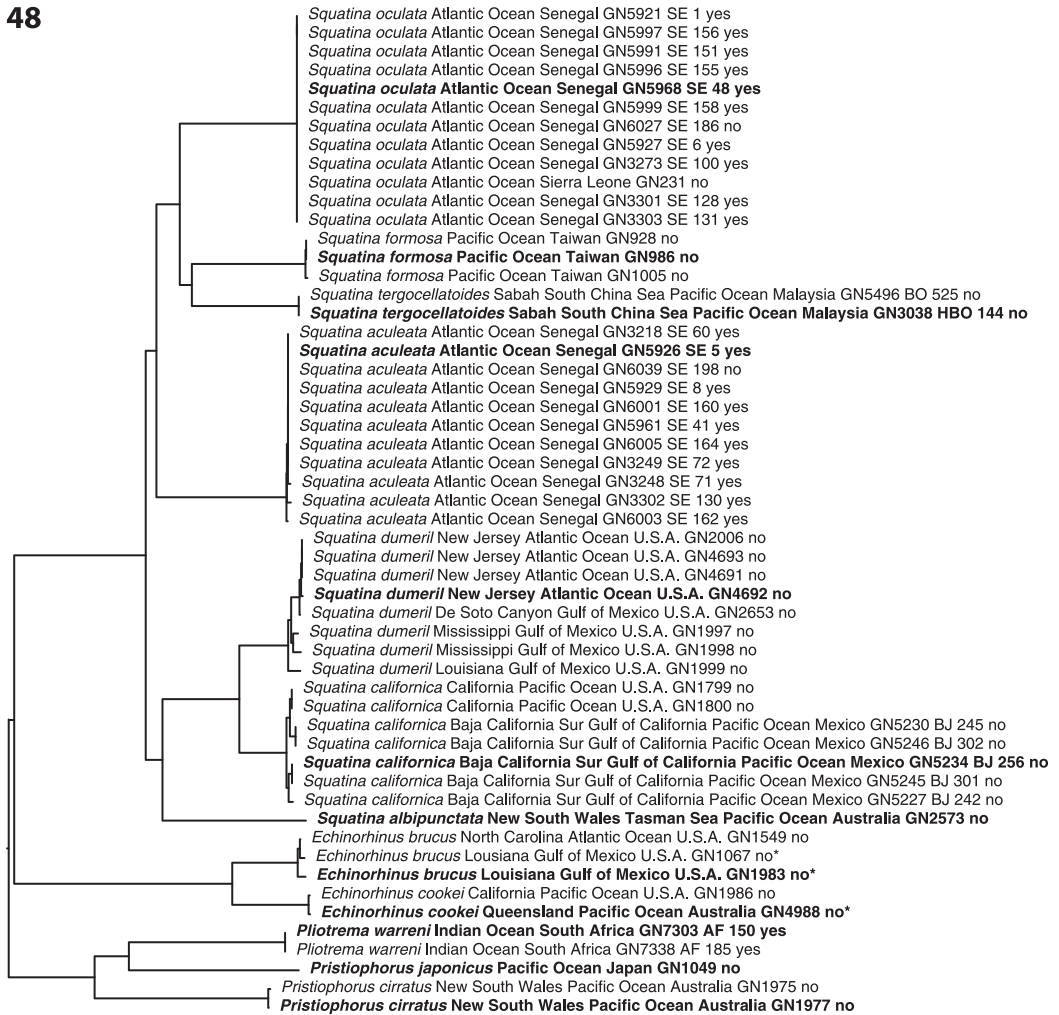
**46B**



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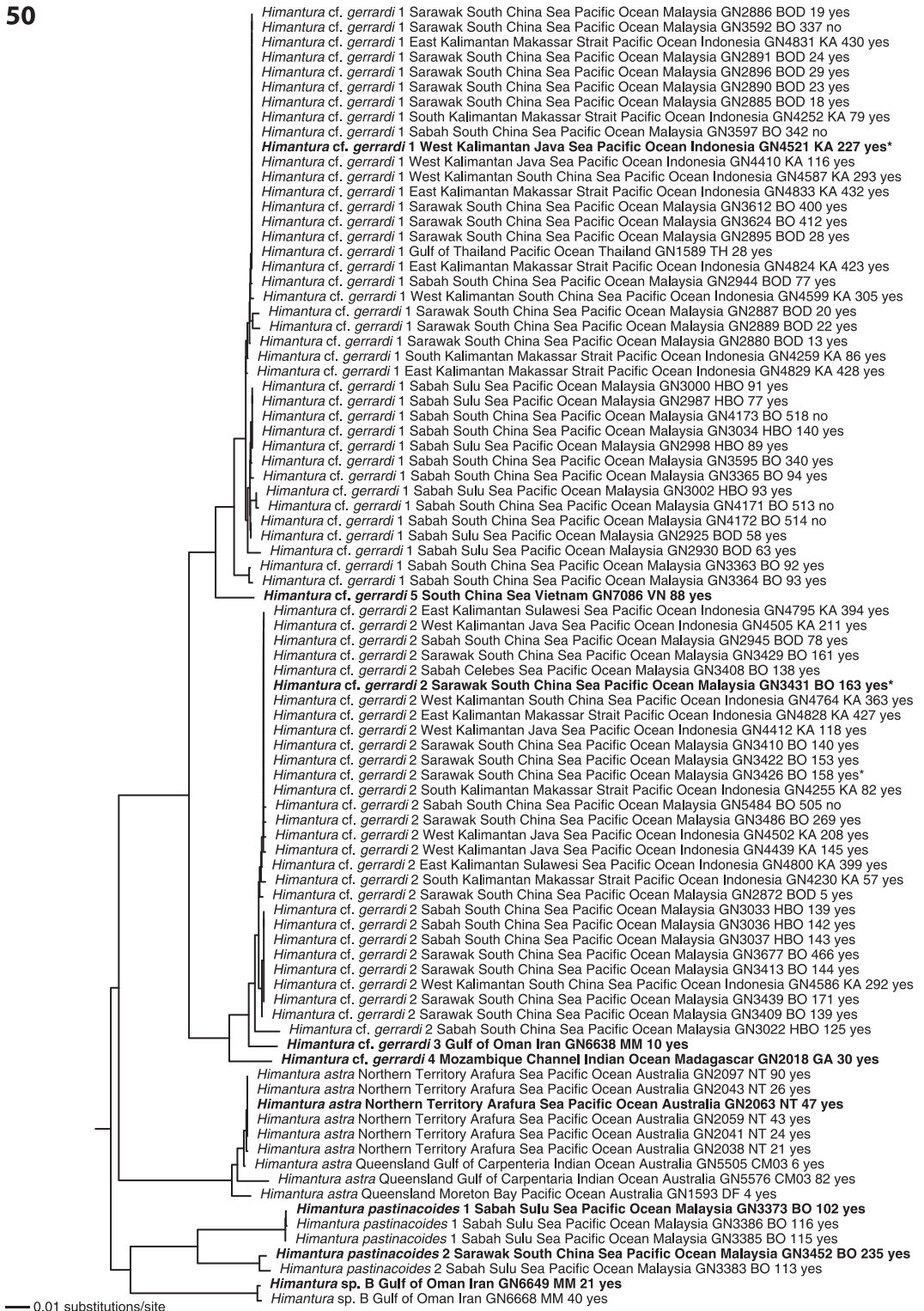
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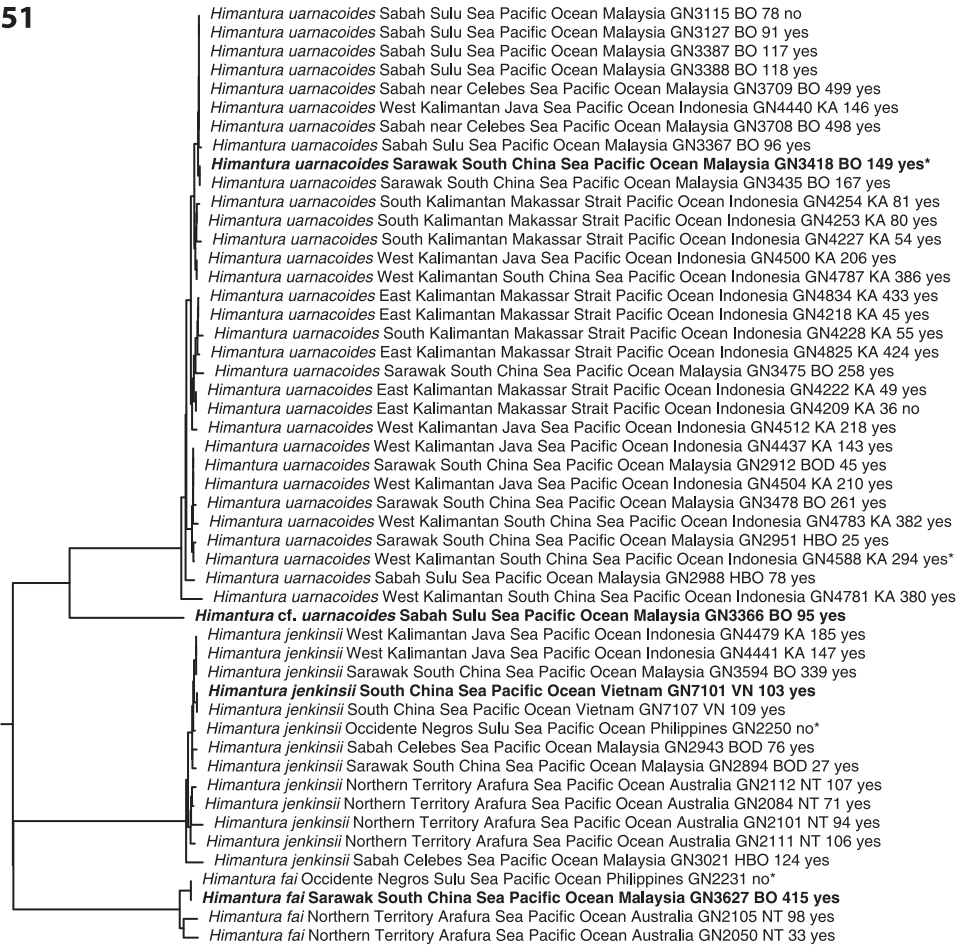


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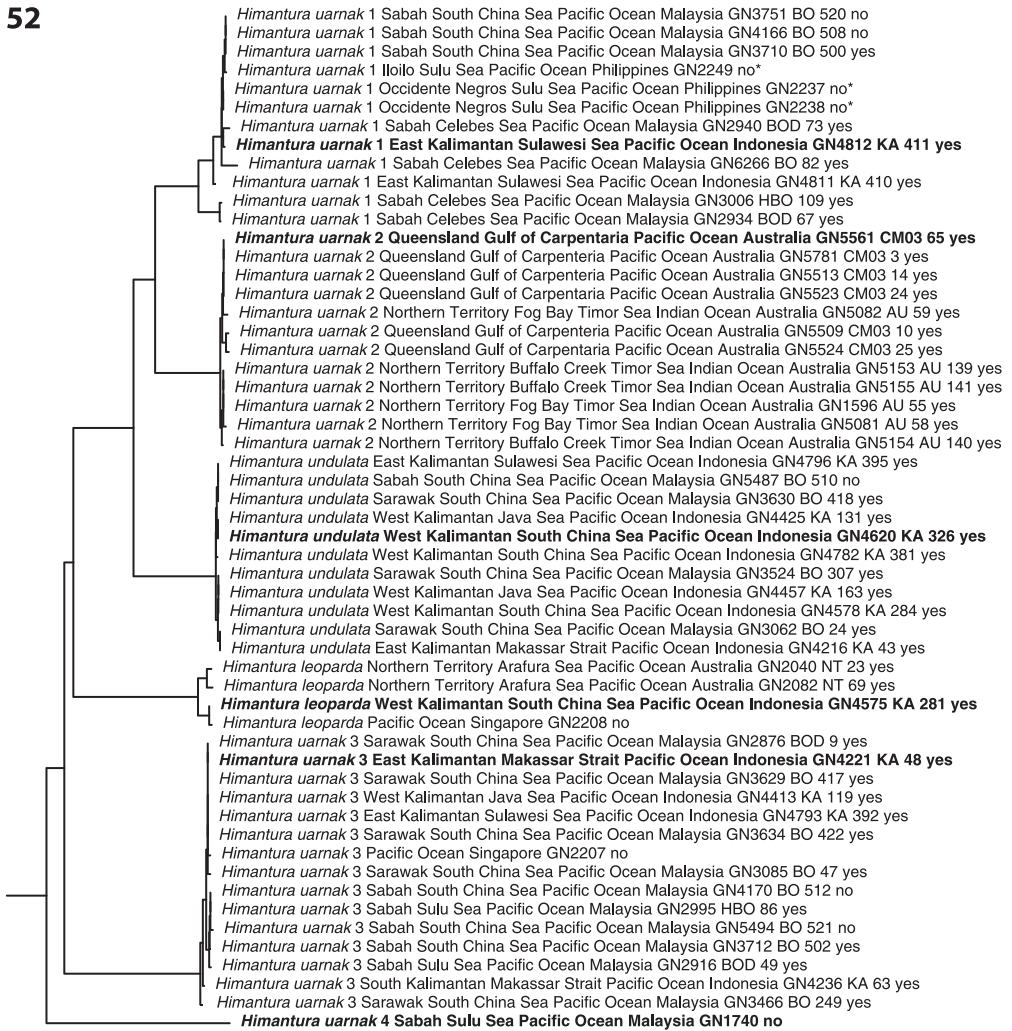


51



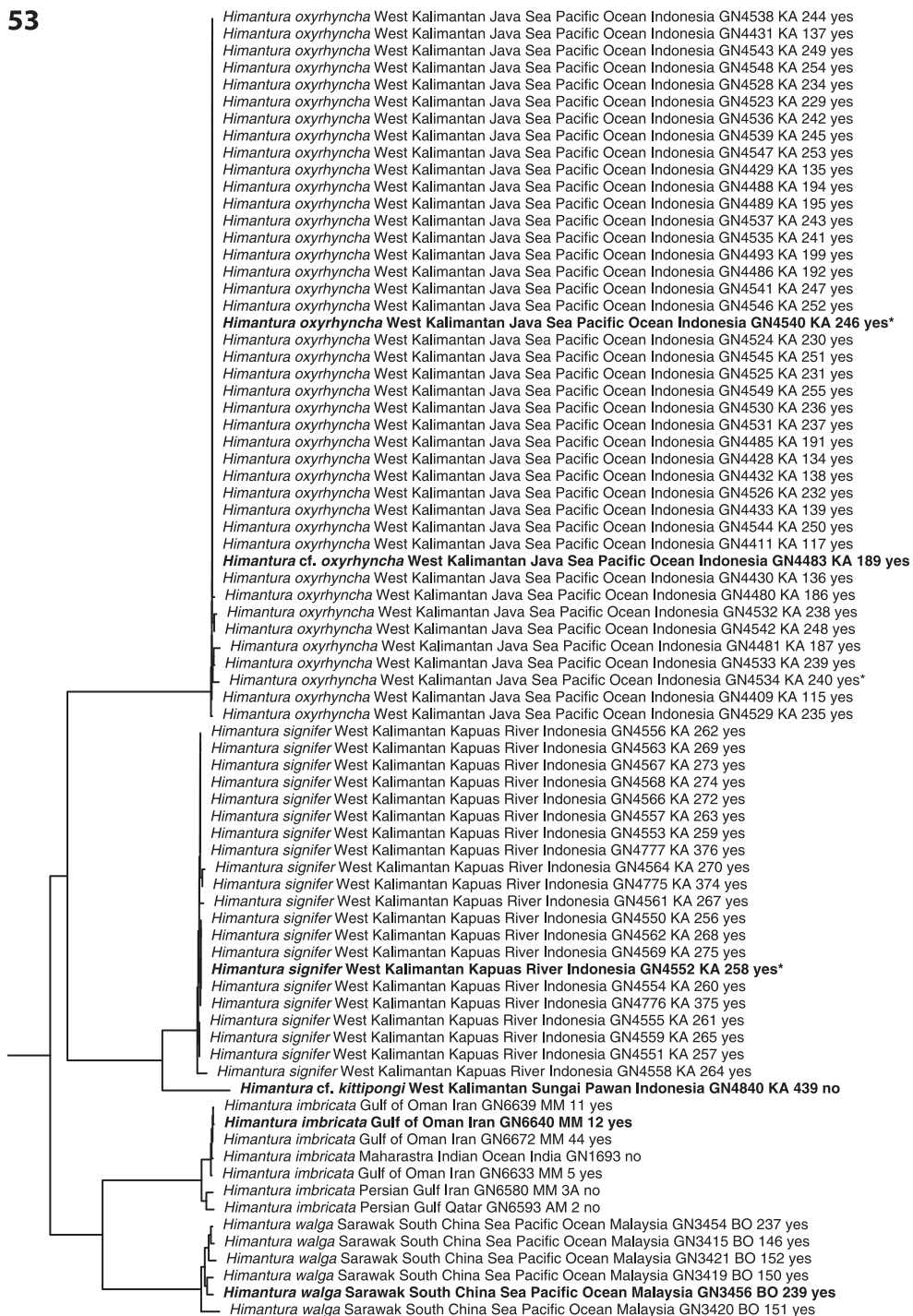
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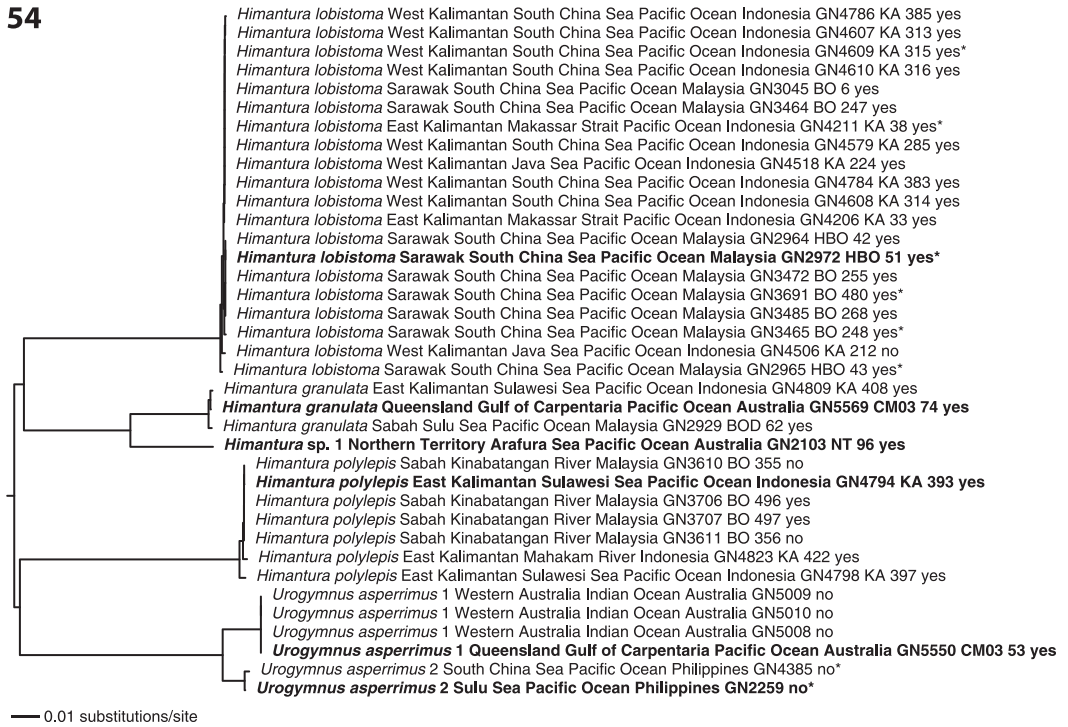
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— 0.01 substitutions/site

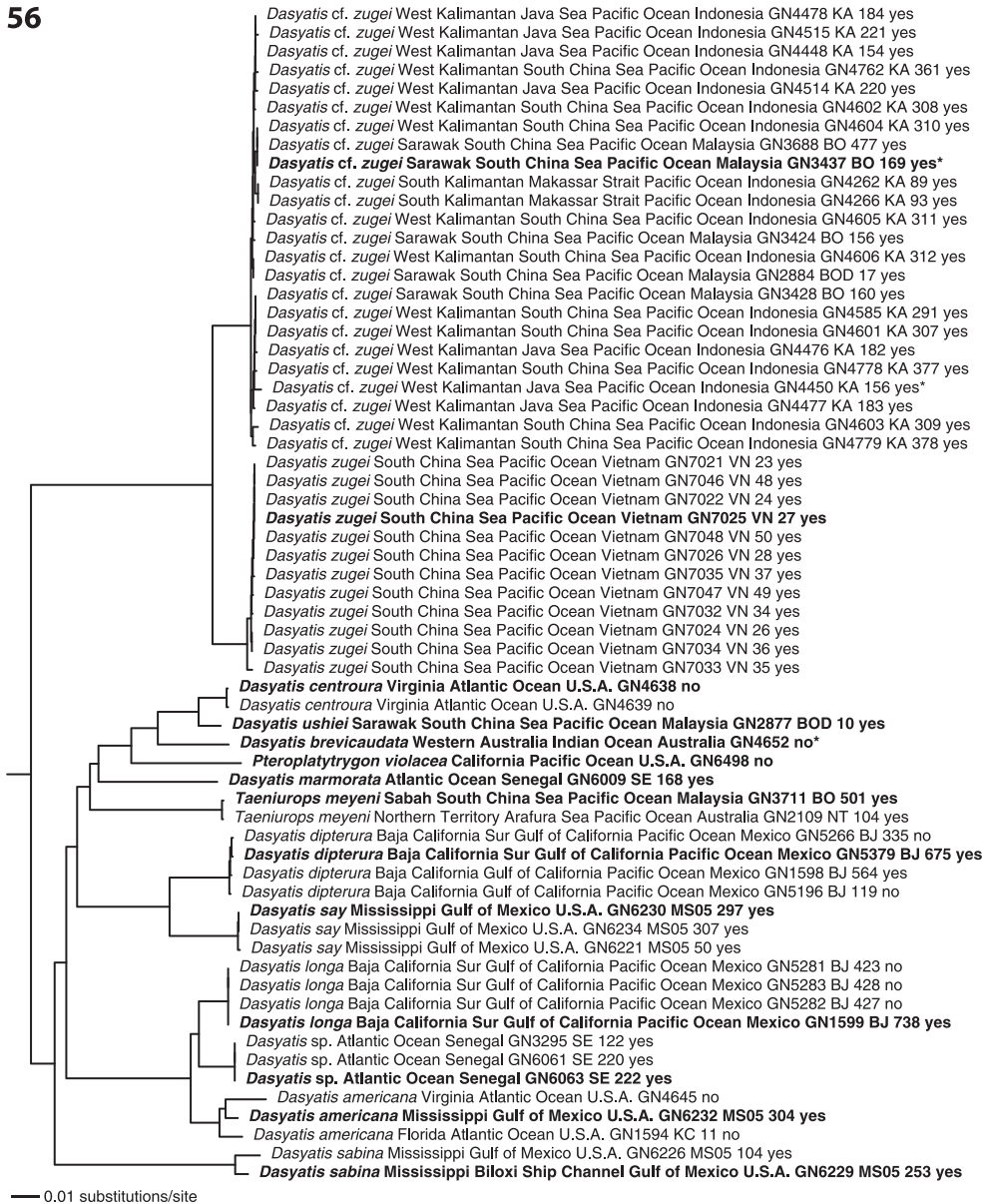
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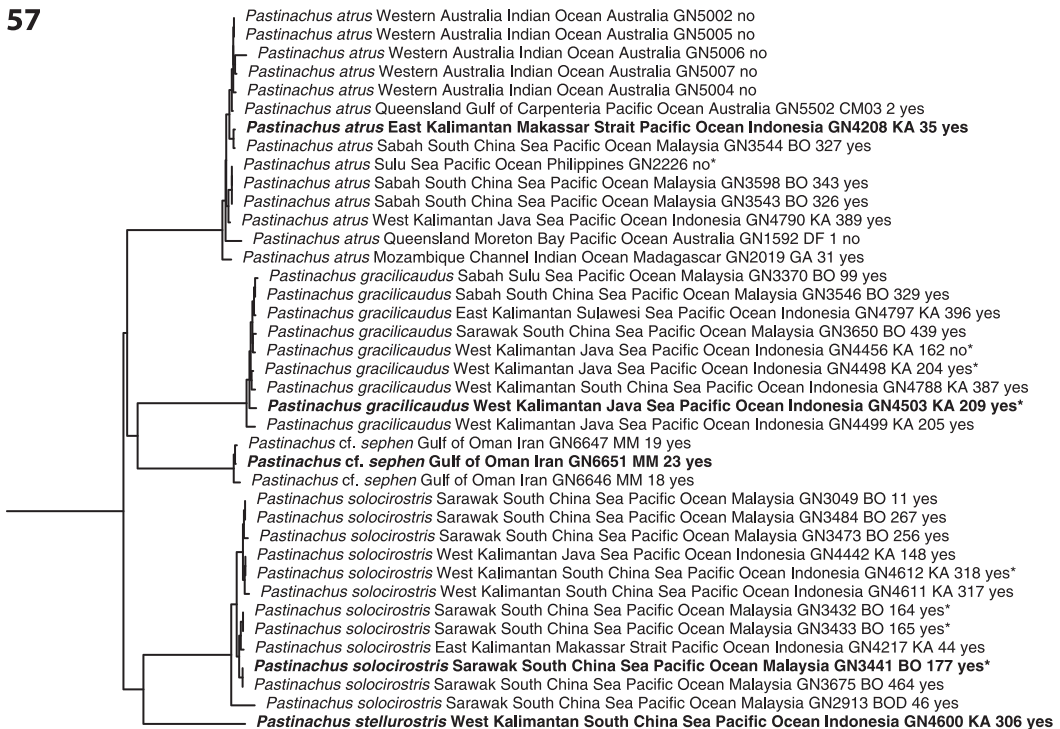
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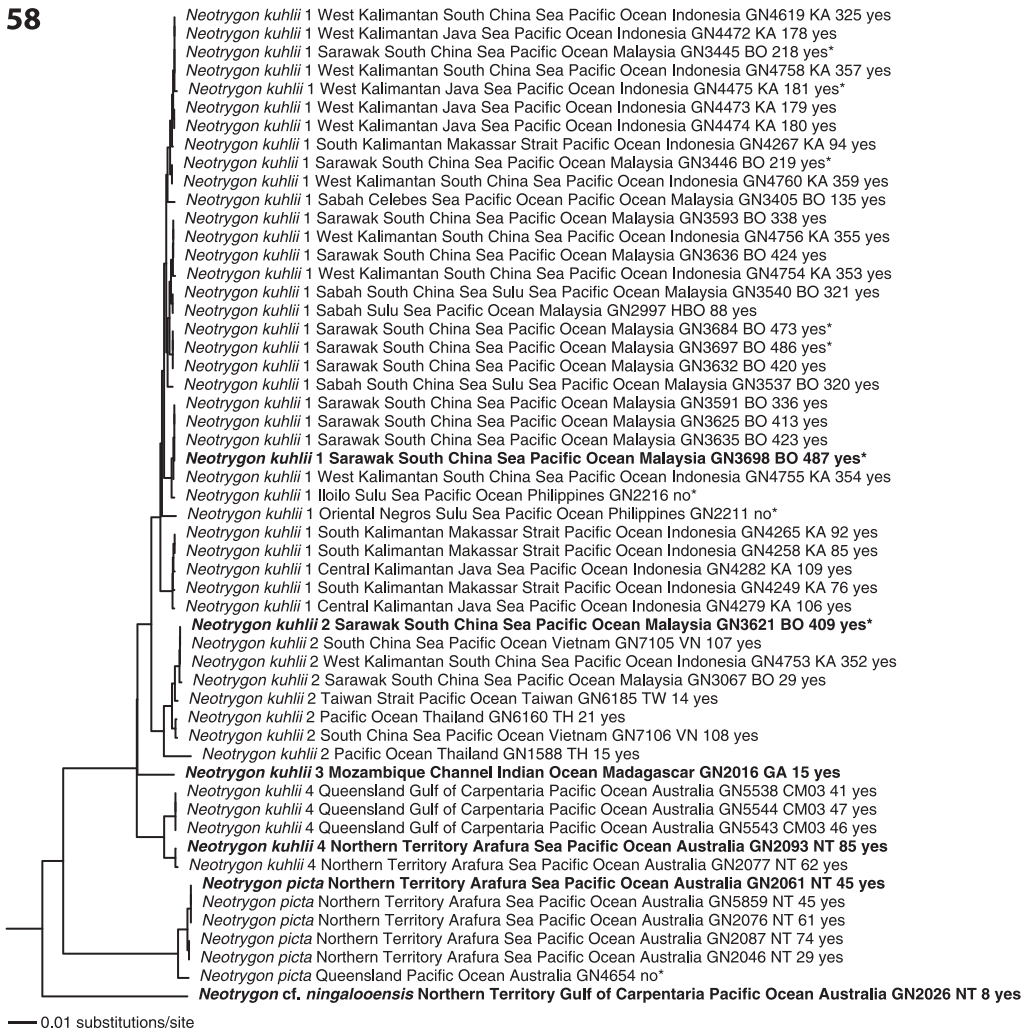
56



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58



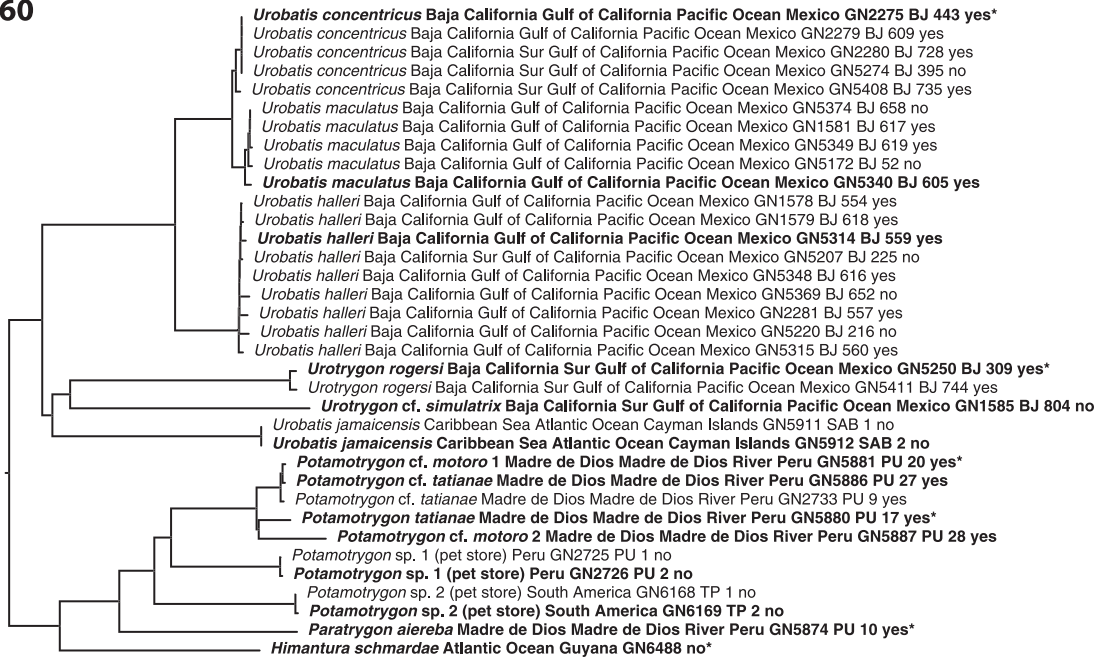


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— 0.01 substitutions/site

60



— 0.01 substitutions/site

61



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—0.01 substitutions/site

62

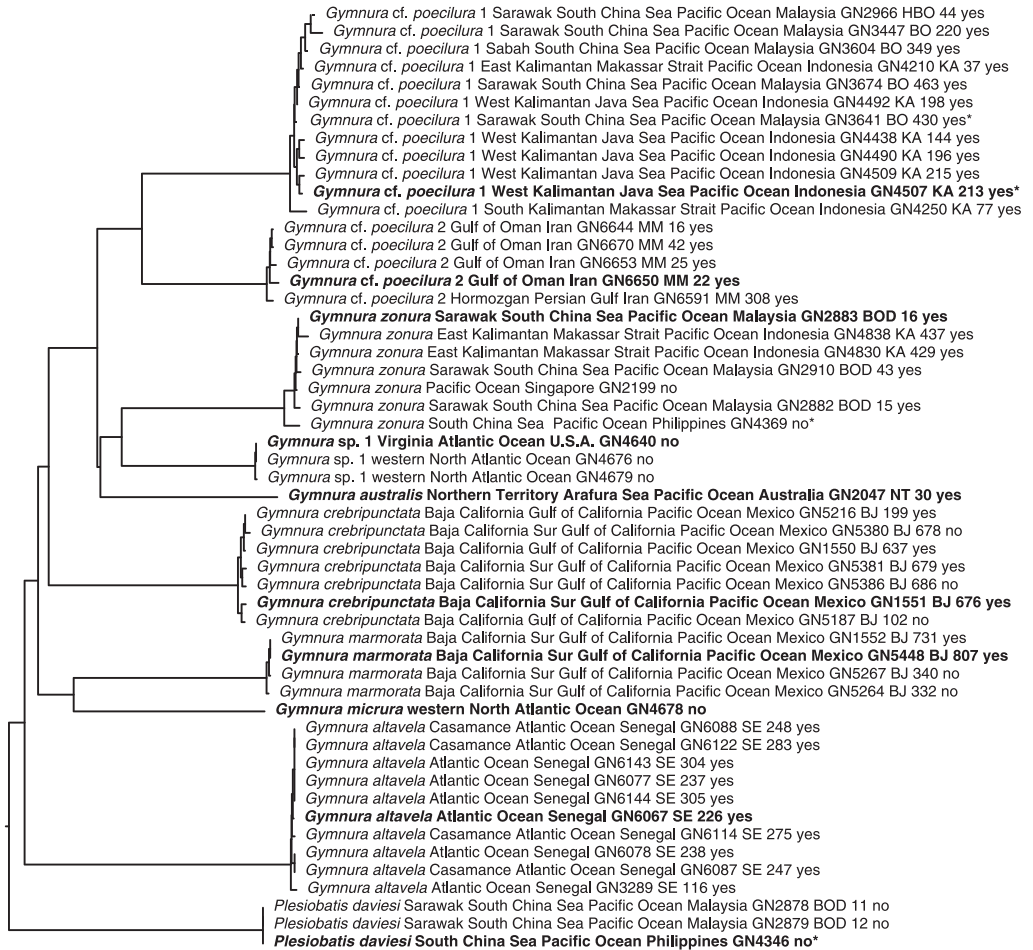
61



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64



65



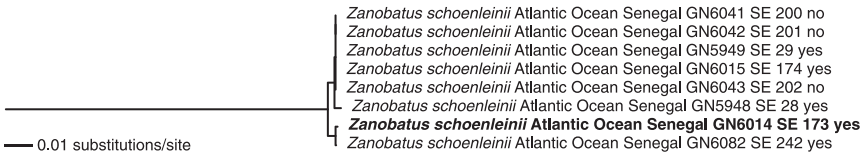
— 0.01 substitutions/site

66



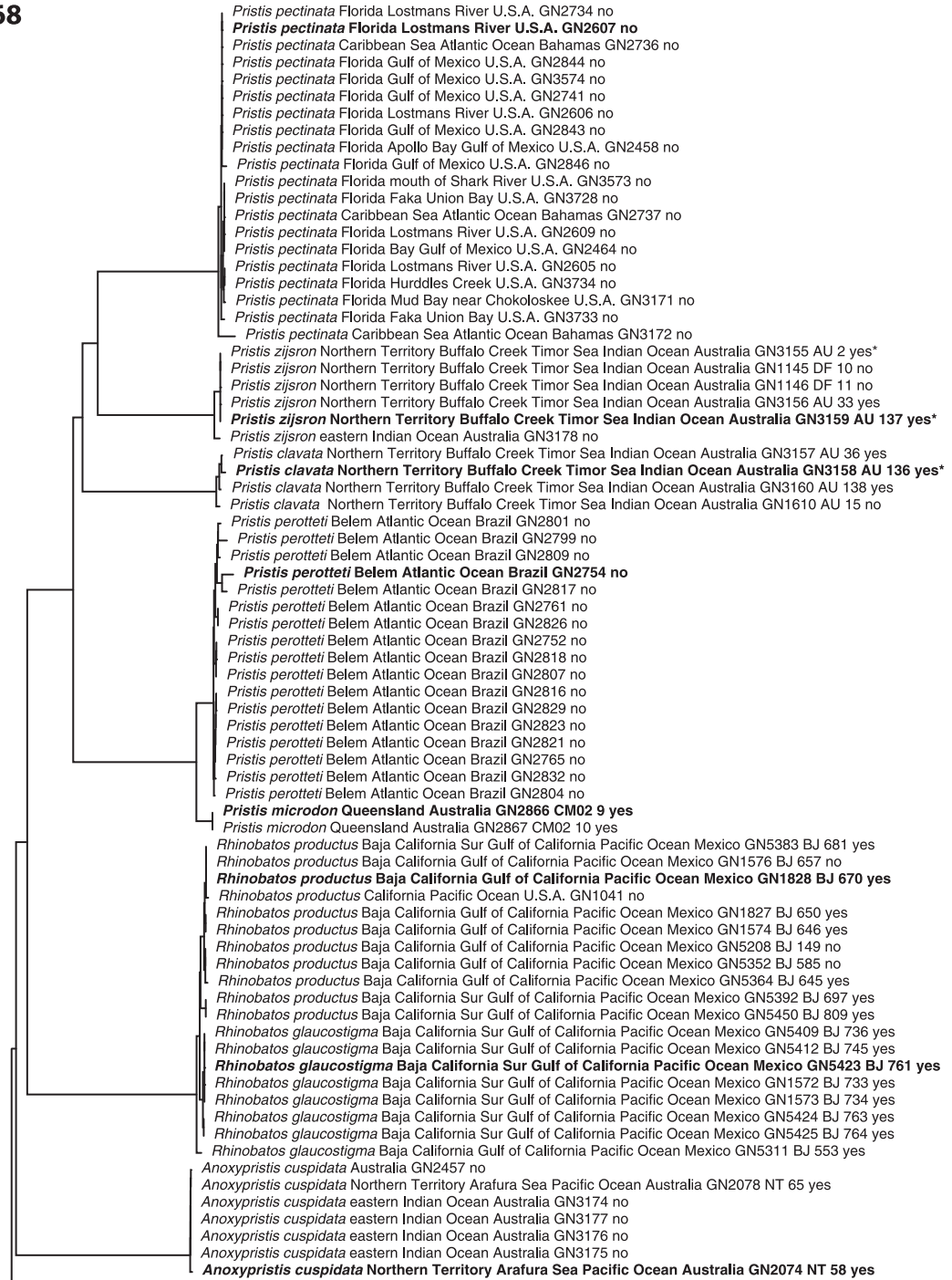
— 0.01 substitutions/site

67



— 0.01 substitutions/site

68



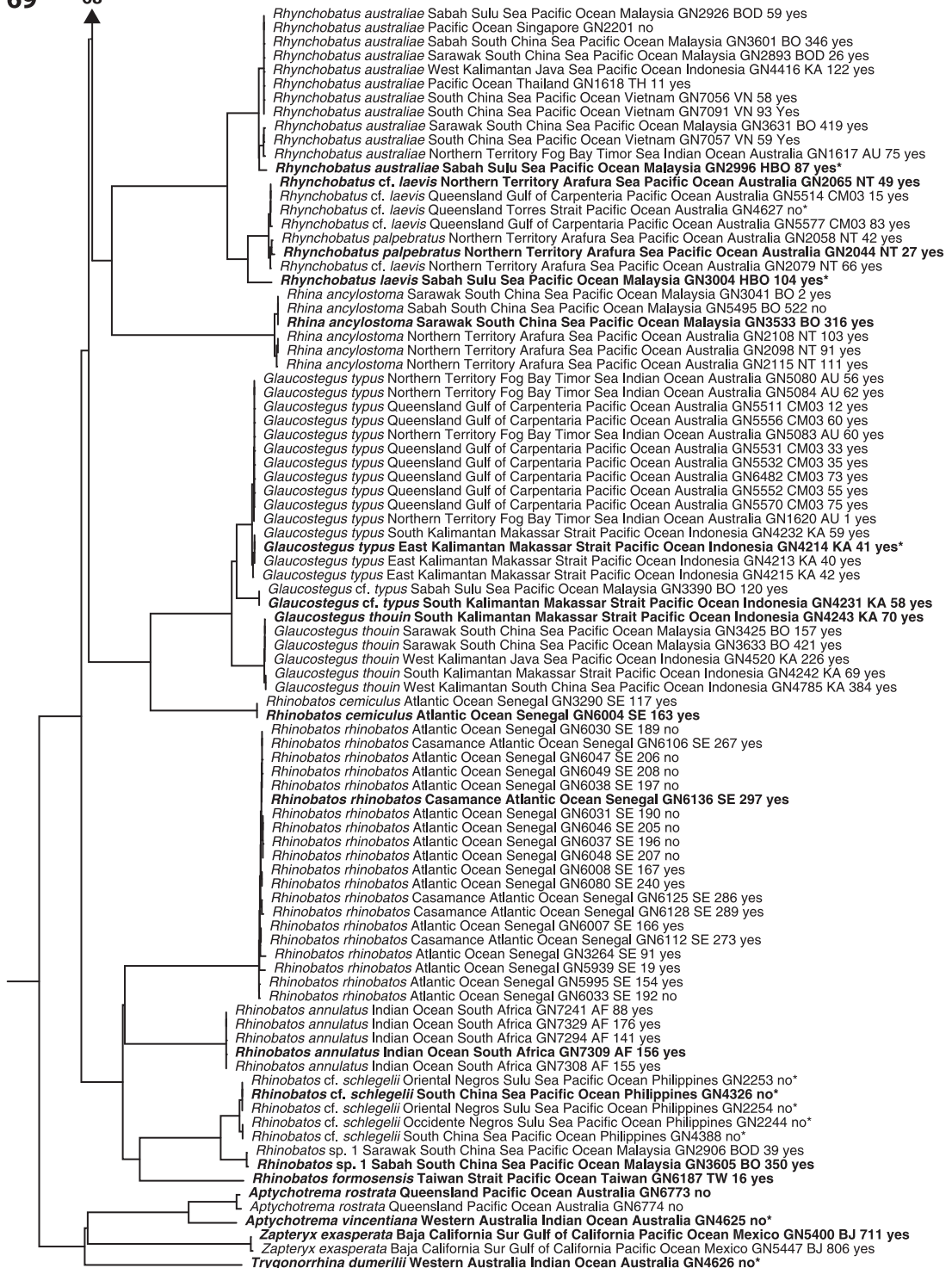
69

— 0.01 substitutions/site



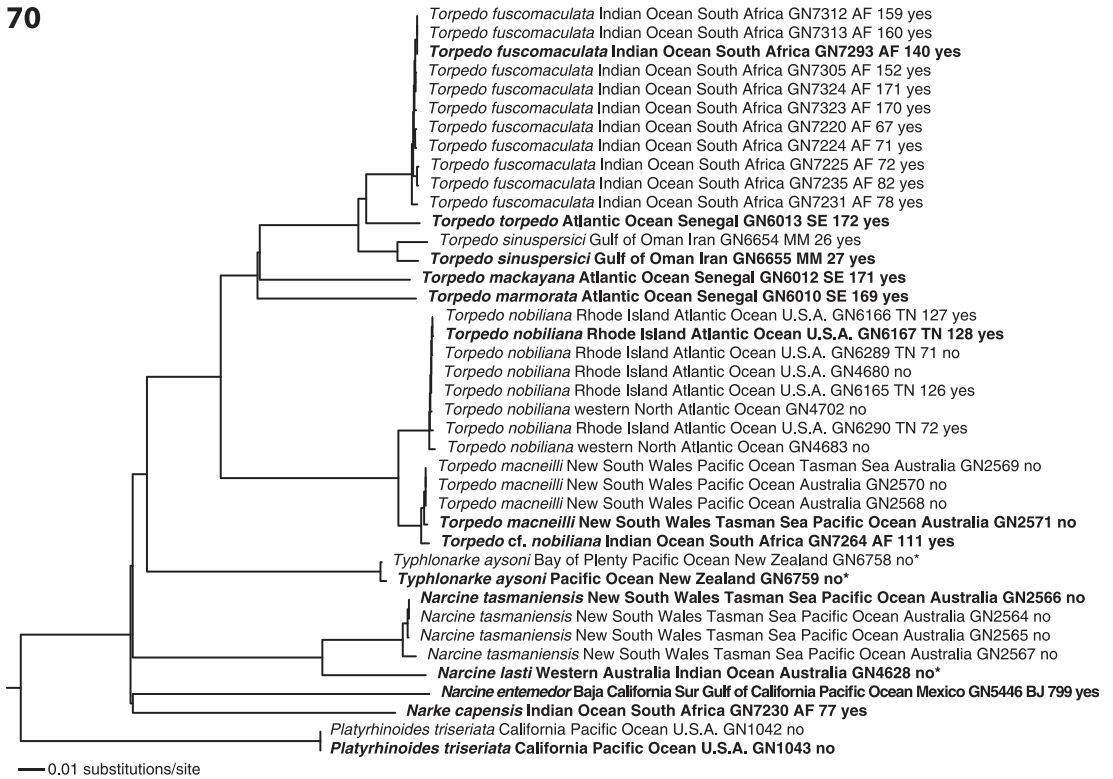
69

68

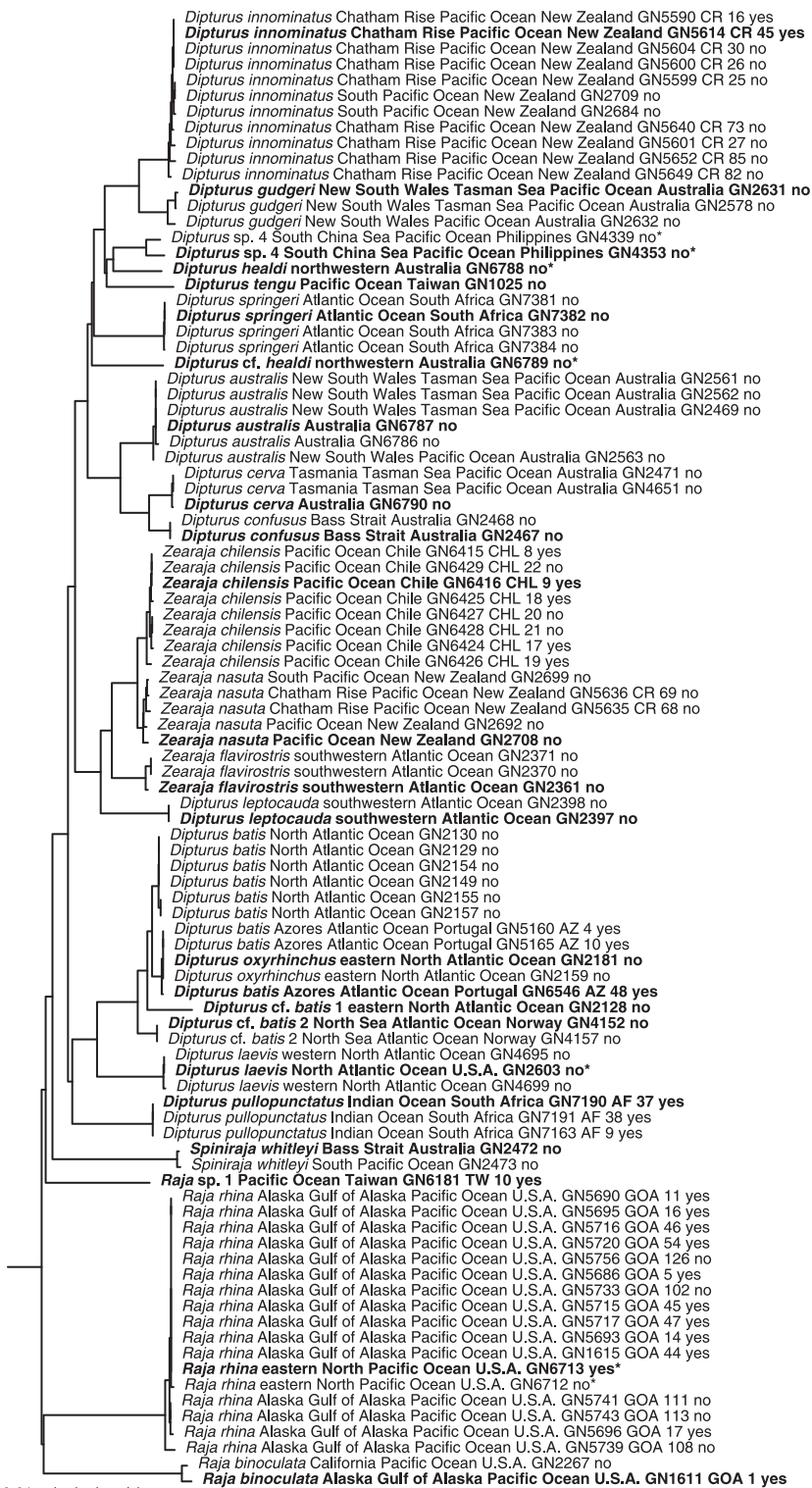


—0.01 substitutions/site

70

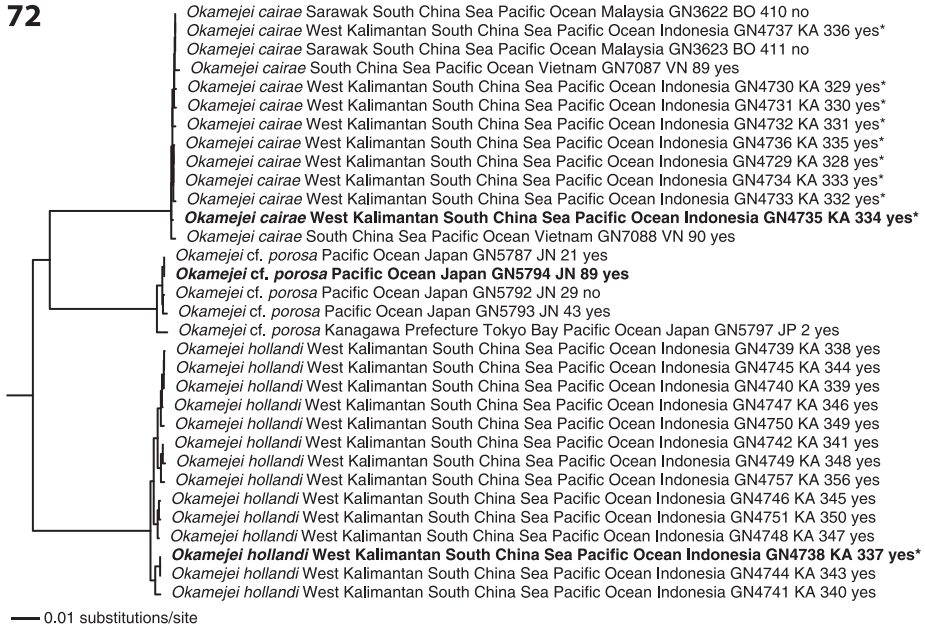


71

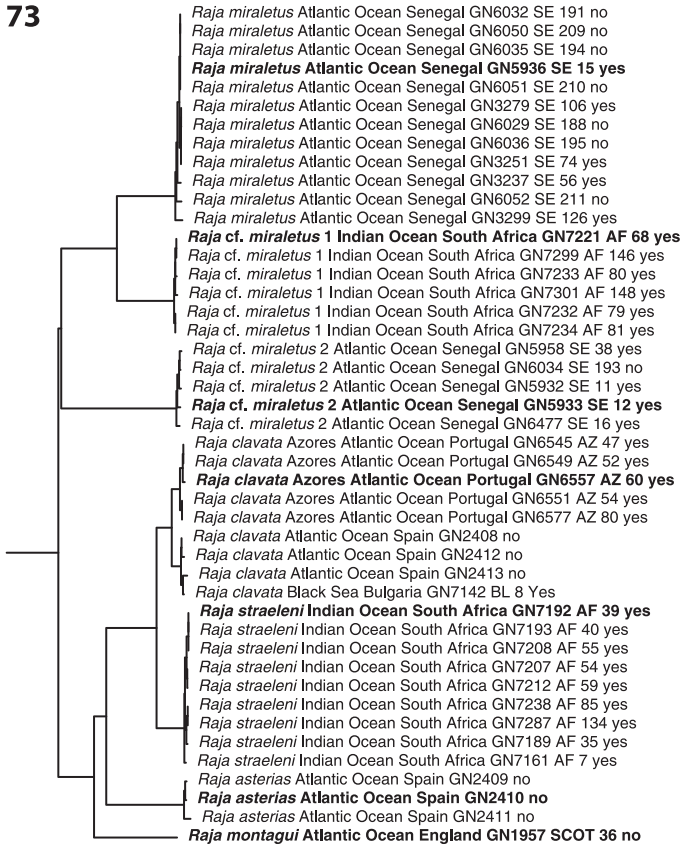


— 0.01 substitutions/site

72

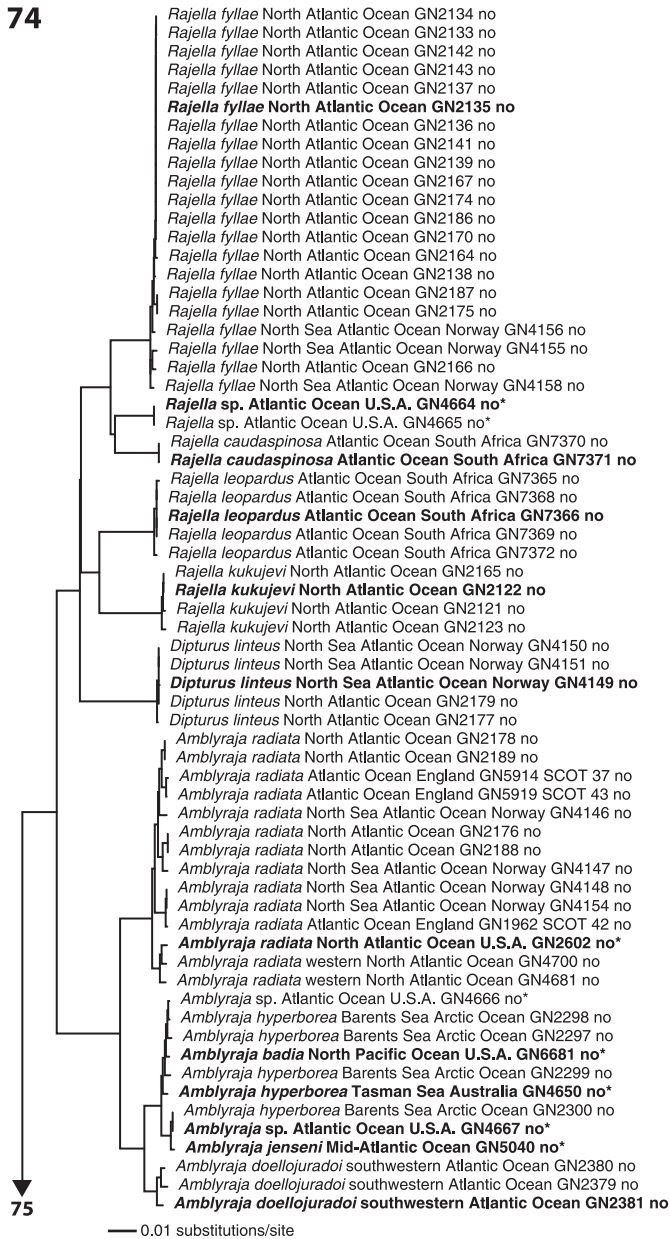


73

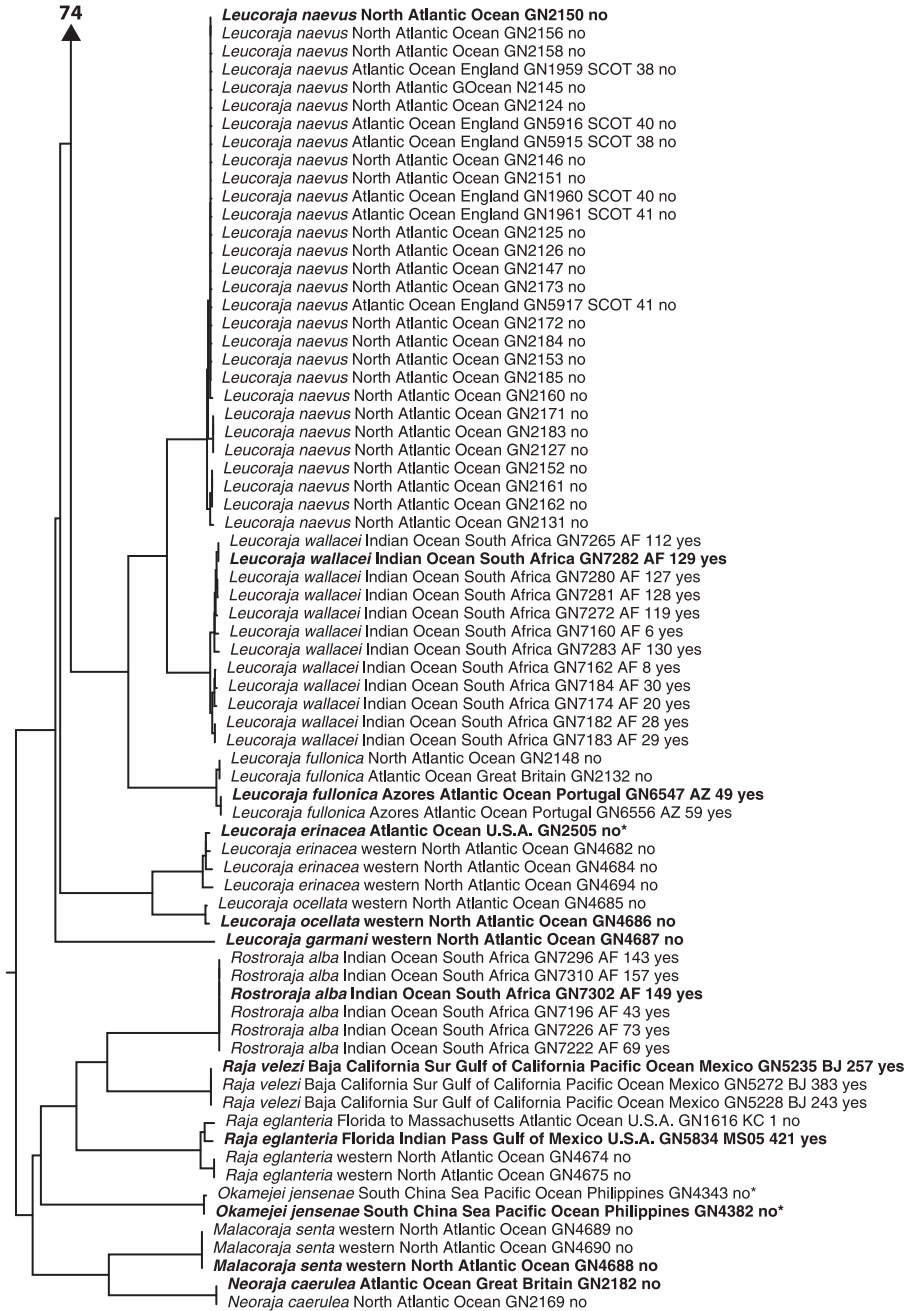


— 0.01 substitutions/site

74

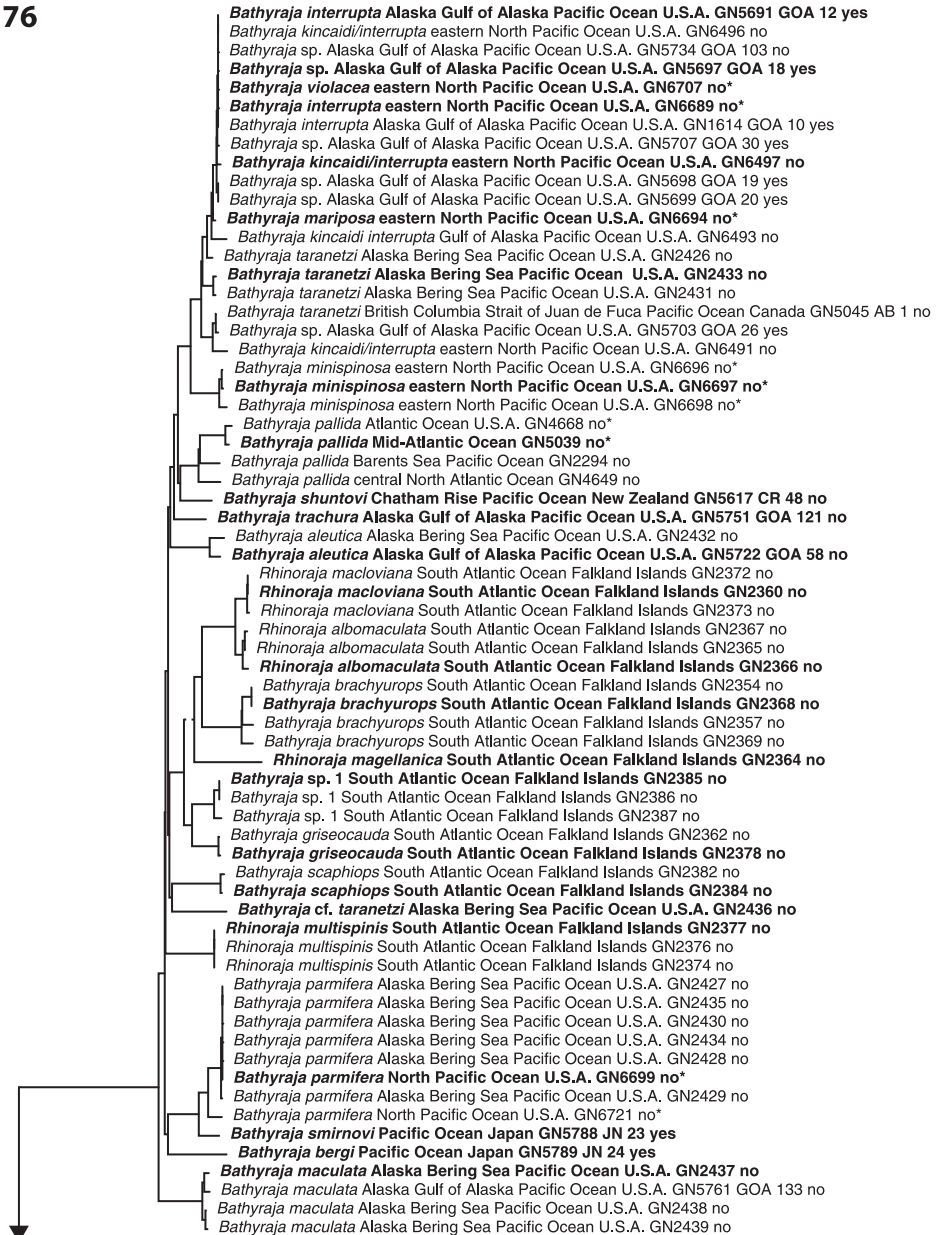


75



— 0.01 substitutions/site

76



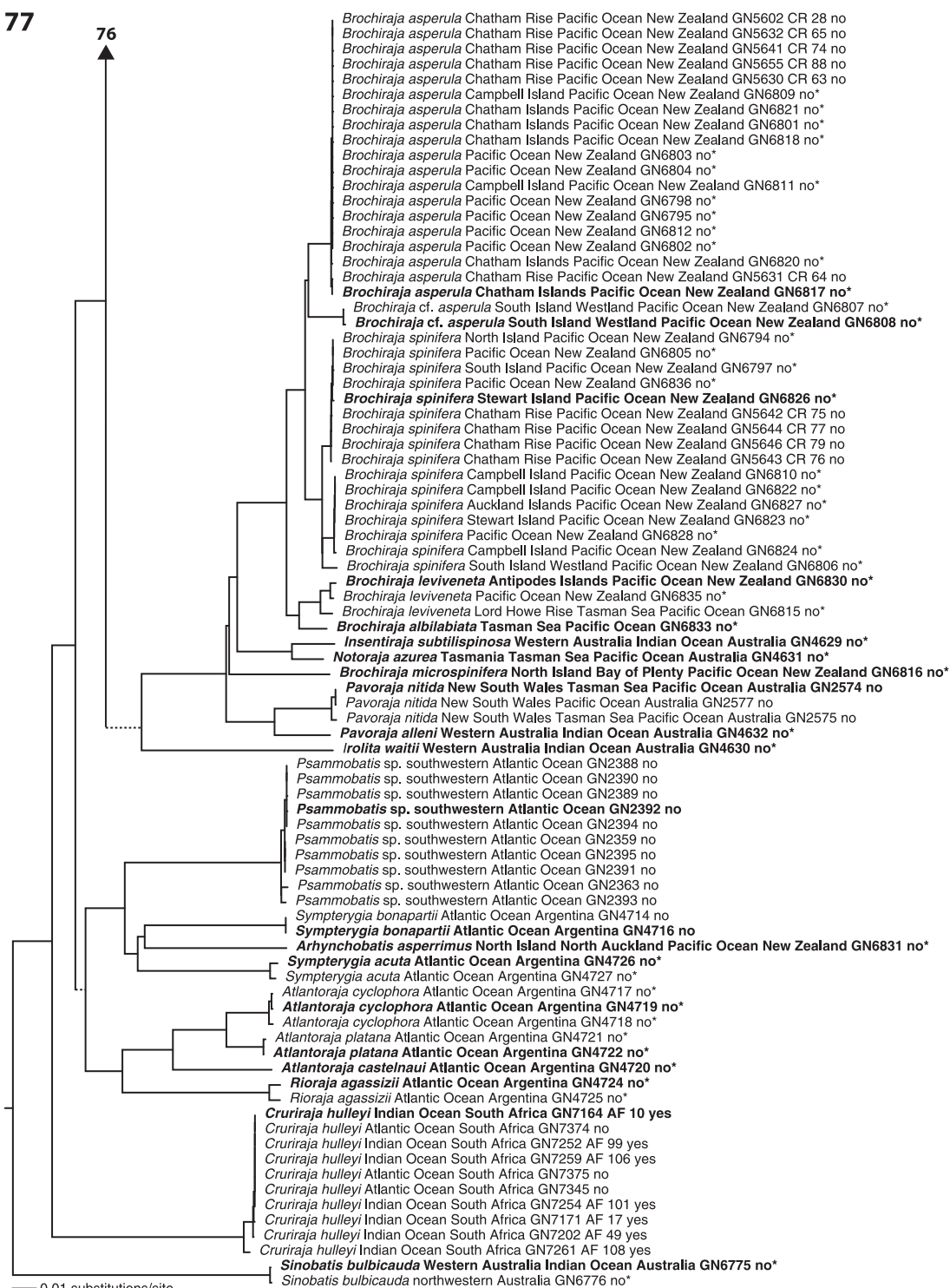
77

— 0.01 substitutions/site



77

76



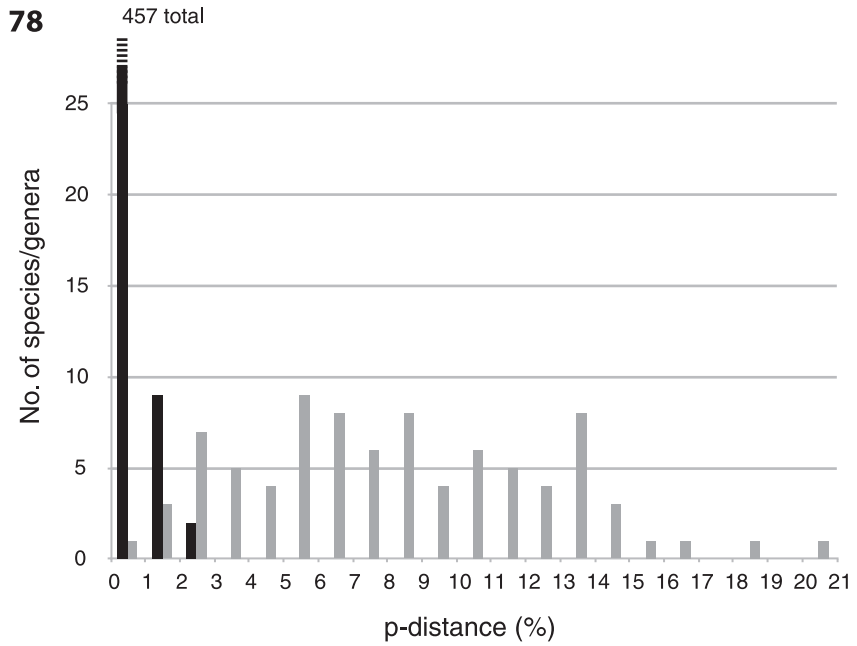
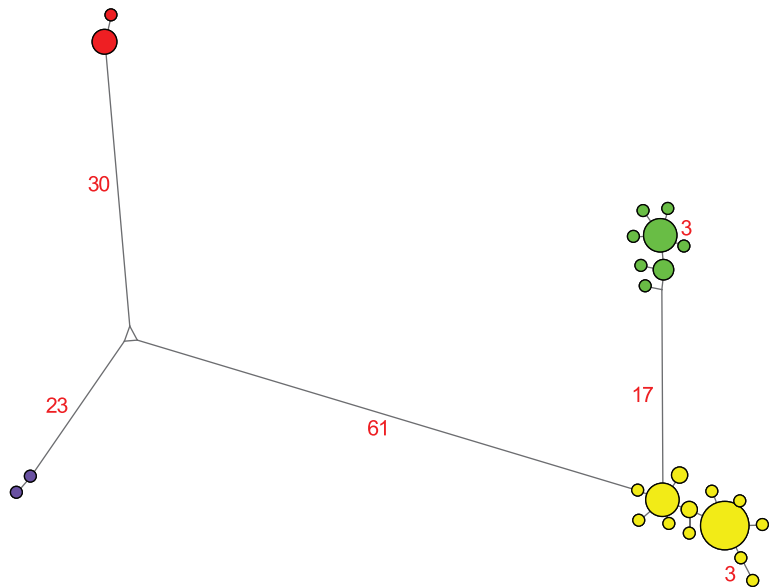


Fig. 78. Distribution of mean p-distances (%) for NADH2; within species (black); within genera (grey).

**A Phenotype**

- *Carcharhinus sealei*
- *Carcharhinus cf. sealei*
- *Carcharhinus dussumieri*
- *Carcharhinus cf. dussumieri*



**B Geography**

- Sulu Sea
- South China Sea
- Kalimantan
- Western Australia
- northern Australia
- Gulf of Carpentaria
- Persian Gulf

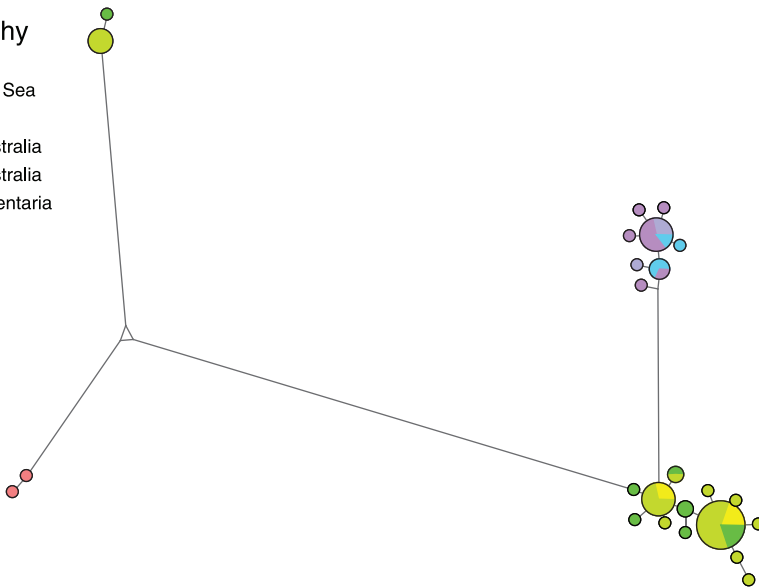
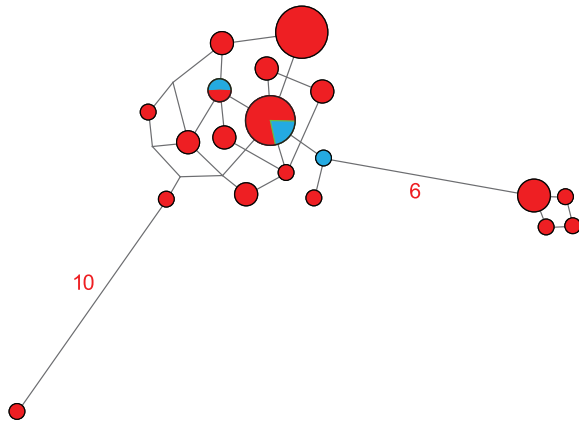


Fig. 79. Parsimony haplotype network for *Carcharhinus sealei*, *C. cf. sealei*, *C. dussumieri*, and *C. cf. dussumieri* color coded by phenotype (A) and geography (B). For this illustration and all successive illustrations, circle diameter corresponds to haplotype frequency; number of base pair differences between haplotypes is indicated in red; only differences  $\geq 3$  bp are indicated.

**A Phenotype**

- *Carcharhinus obscurus*
- *Carcharhinus galapagensis*



**B Geography**

- Western Australia
- eastern Atlantic Ocean
- Tasman Sea
- Hawaii
- South Africa
- Taiwan
- Queensland
- western North Atlantic Ocean
- Gulf of Mexico

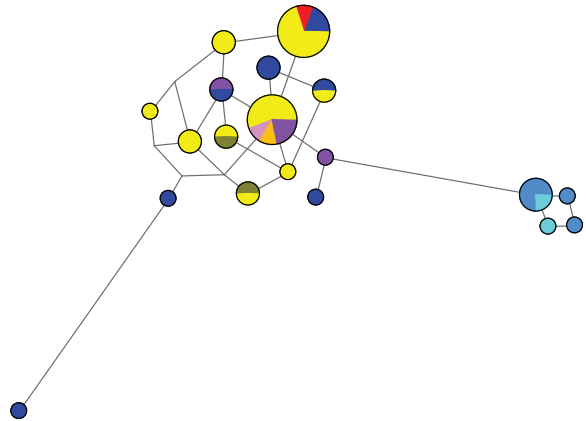


Fig. 80. Parsimony haplotype network for *Carcharhinus obscurus* and *C. galapagensis* color coded by phenotype (A) and geography (B).

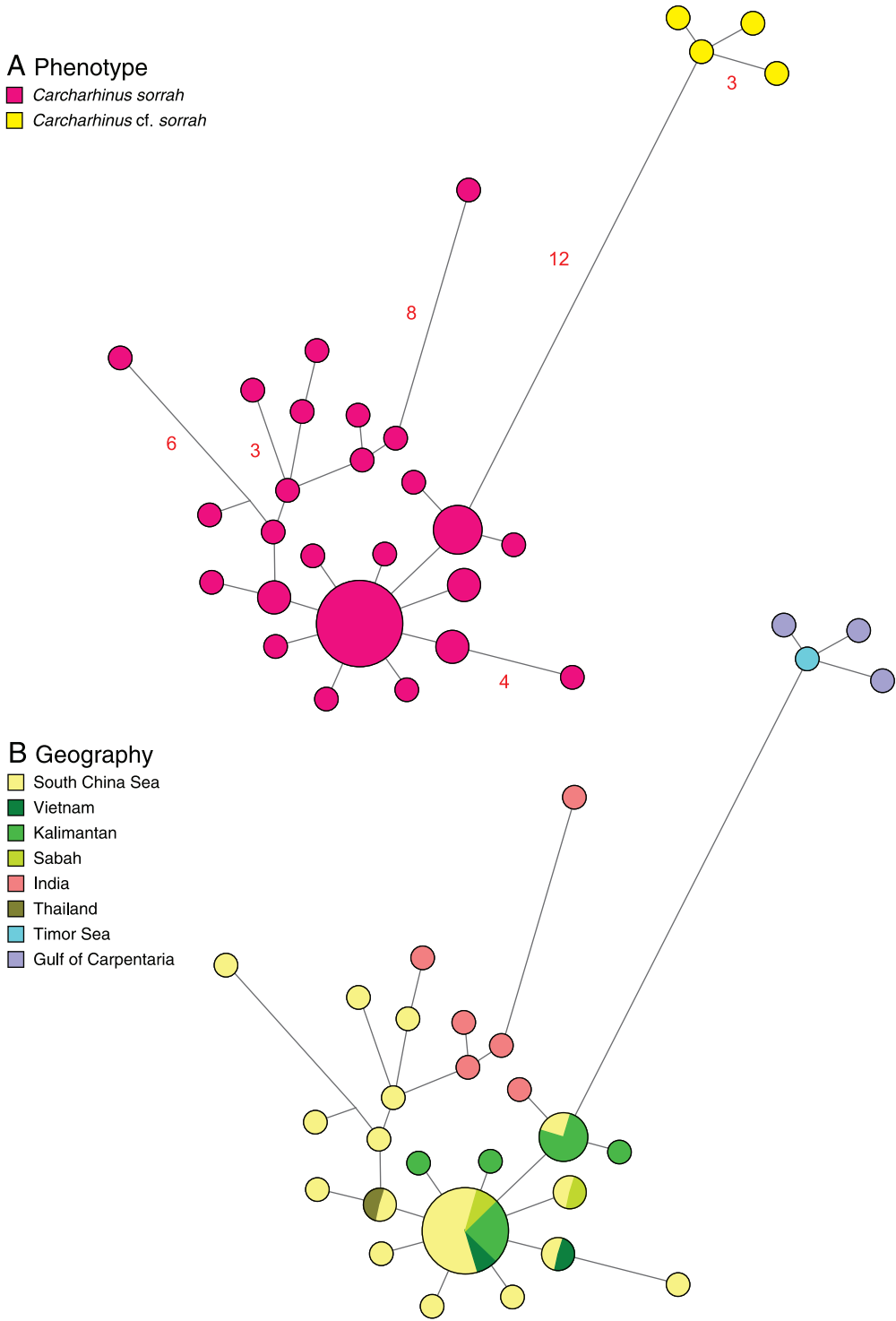


Fig. 81. Parsimony haplotype network for *Carcharhinus sorrah* and *C. cf. sorrah* color coded by phenotype (A) and geography (B).

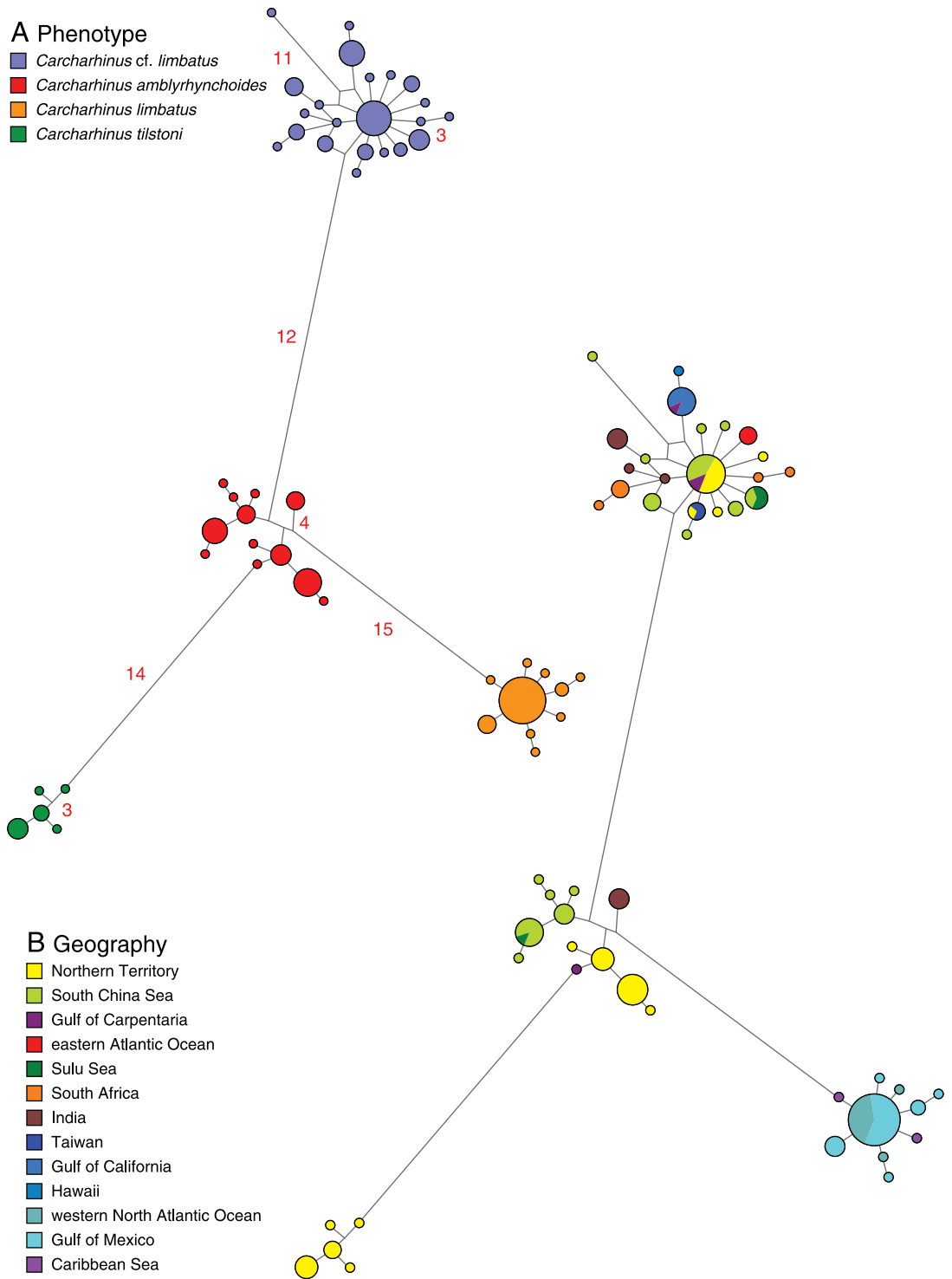
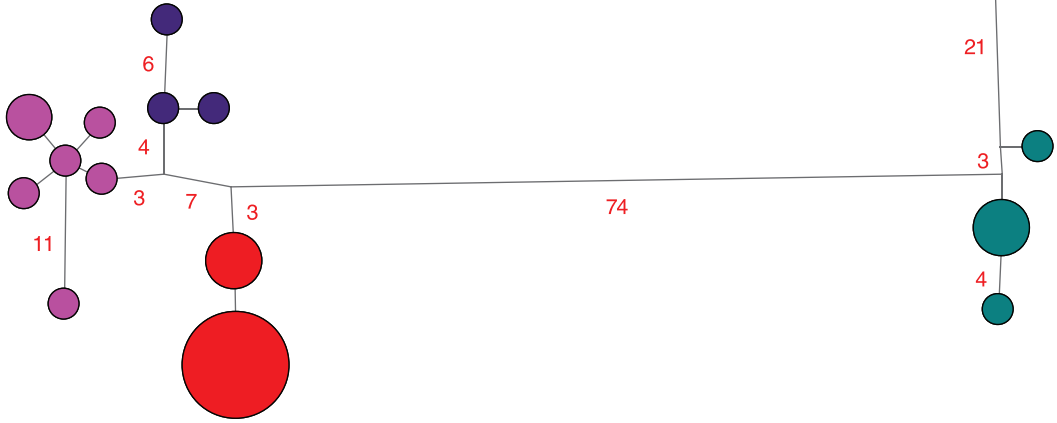


Fig. 82. Parsimony haplotype network for *Carcharhinus limbatus*, *C. cf. limbatus*, *C. amblyrhynchooides*, and *C. tilstoni* color coded by phenotype (A) and geography (B).

### A Phenotype

- *Carcharhinus leucas*
- *Carcharhinus cf. leucas* 1
- *Carcharhinus cf. leucas* 2
- *Carcharhinus amboinensis* 1
- *Carcharhinus amboinensis* 2



### B Geography

- western North Atlantic Ocean
- Gulf of Mexico
- Caribbean Sea
- eastern Atlantic Ocean
- South China Sea
- Sulu Sea
- Java Sea
- South Africa
- Timor Sea
- India
- Western Australia

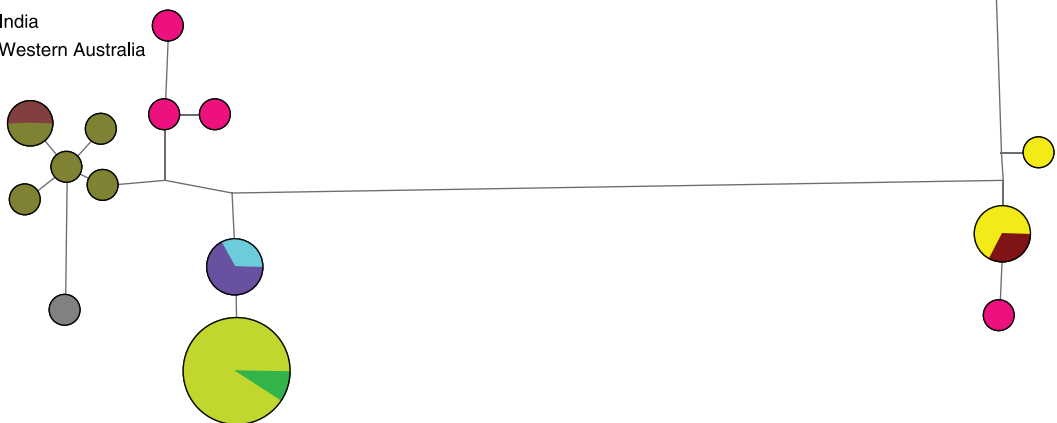
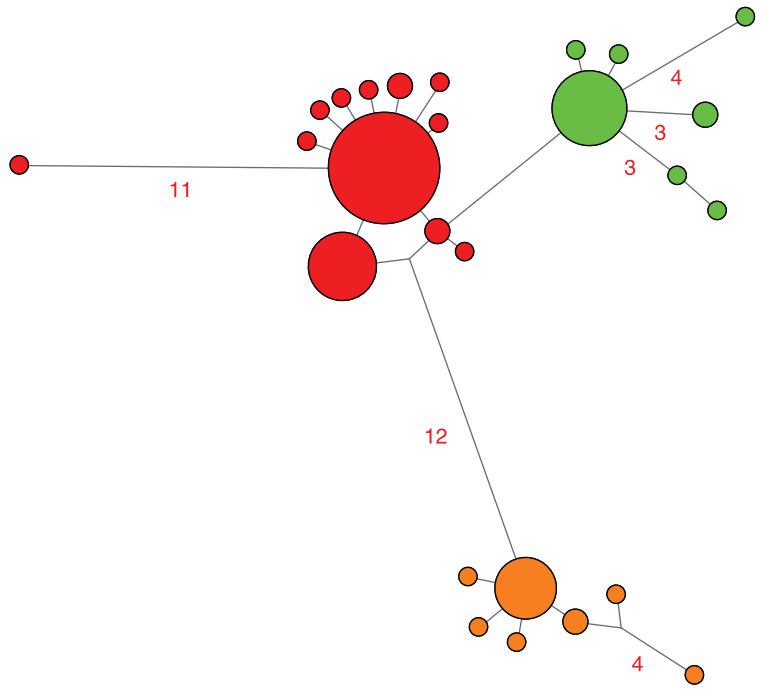


Fig. 83. Parsimony haplotype network for *Carcharhinus leucas*, *C. cf. leucas* 1, *C. cf. leucas* 2, *C. amboinensis* 1, and *C. amboinensis* 2 color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Carcharhinus plumbeus*
- *Carcharhinus altimus*
- *Carcharhinus cf. plumbeus*



**B Geography**

- western North Atlantic Ocean
- Gulf of Mexico
- Caribbean Sea
- Hawaii
- South China Sea
- Taiwan
- Vietnam

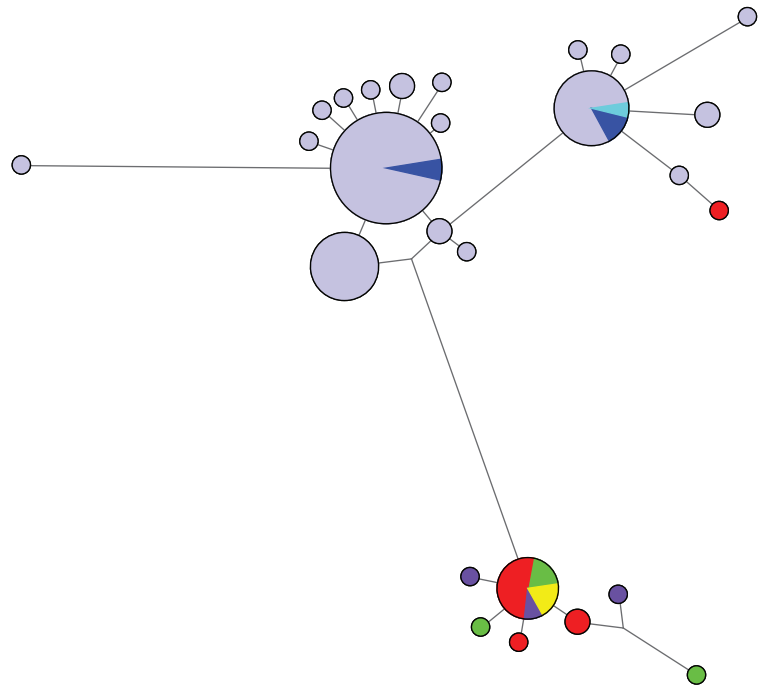
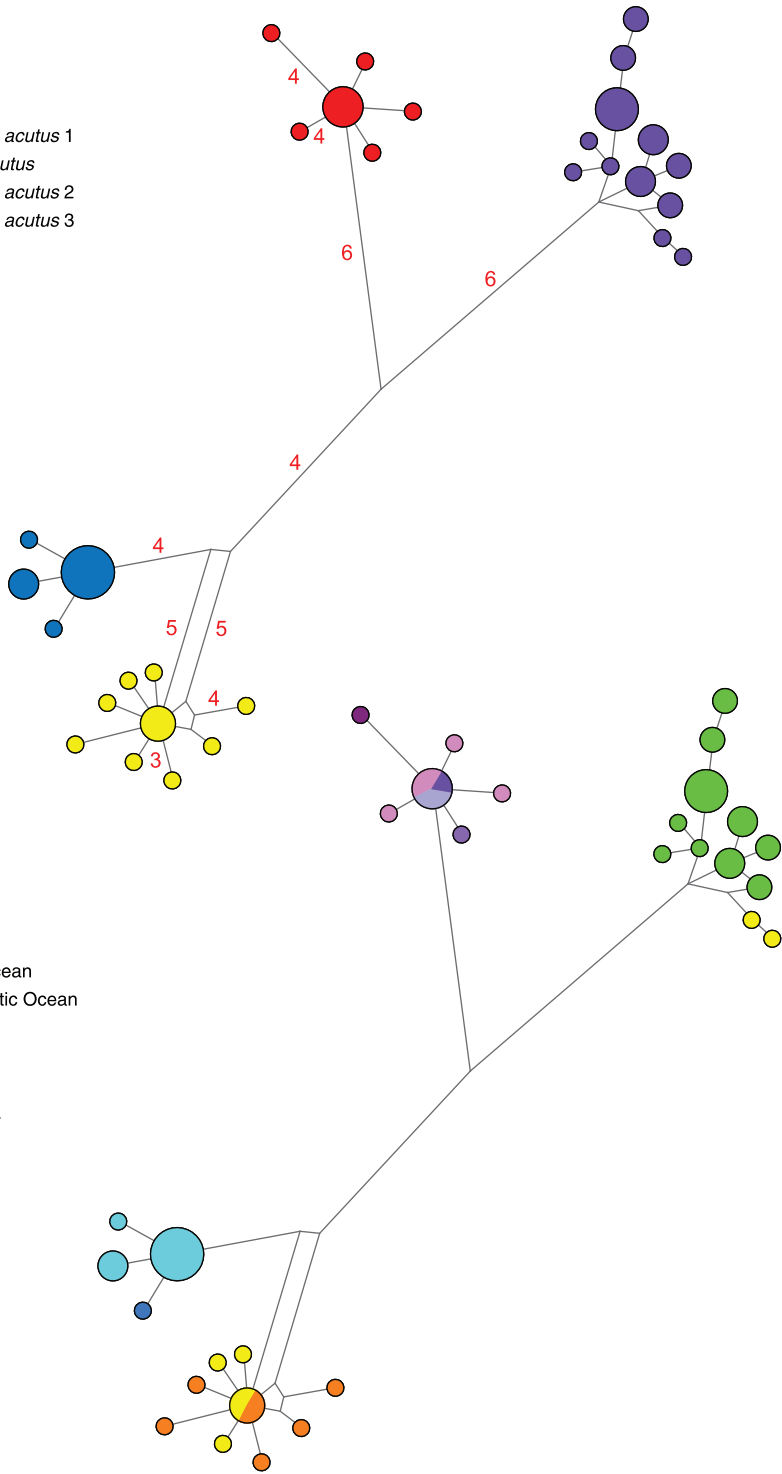


Fig. 84. Parsimony haplotype network for *Carcharhinus plumbeus*, *C. cf. plumbeus*, and *C. altimus* color coded by phenotype (A) and geography (B).



**A Phenotype**

- *Rhizoprionodon* cf. *acutus* 1
- *Rhizoprionodon* *acutus*
- *Rhizoprionodon* cf. *acutus* 2
- *Rhizoprionodon* cf. *acutus* 3



**B Geography**

- eastern Atlantic Ocean
- southeastern Atlantic Ocean
- India
- Gulf of Oman
- Timor Sea
- Gulf of Carpentaria
- Arafura Sea
- Torres Strait
- Western Australia
- South China Sea

Fig. 85. Parsimony haplotype network for *Rhizoprionodon acutus*, *R. cf. acutus* 1, *R. cf. acutus* 2, and *R. cf. acutus* 3 color coded by phenotype (A) and geography (B).

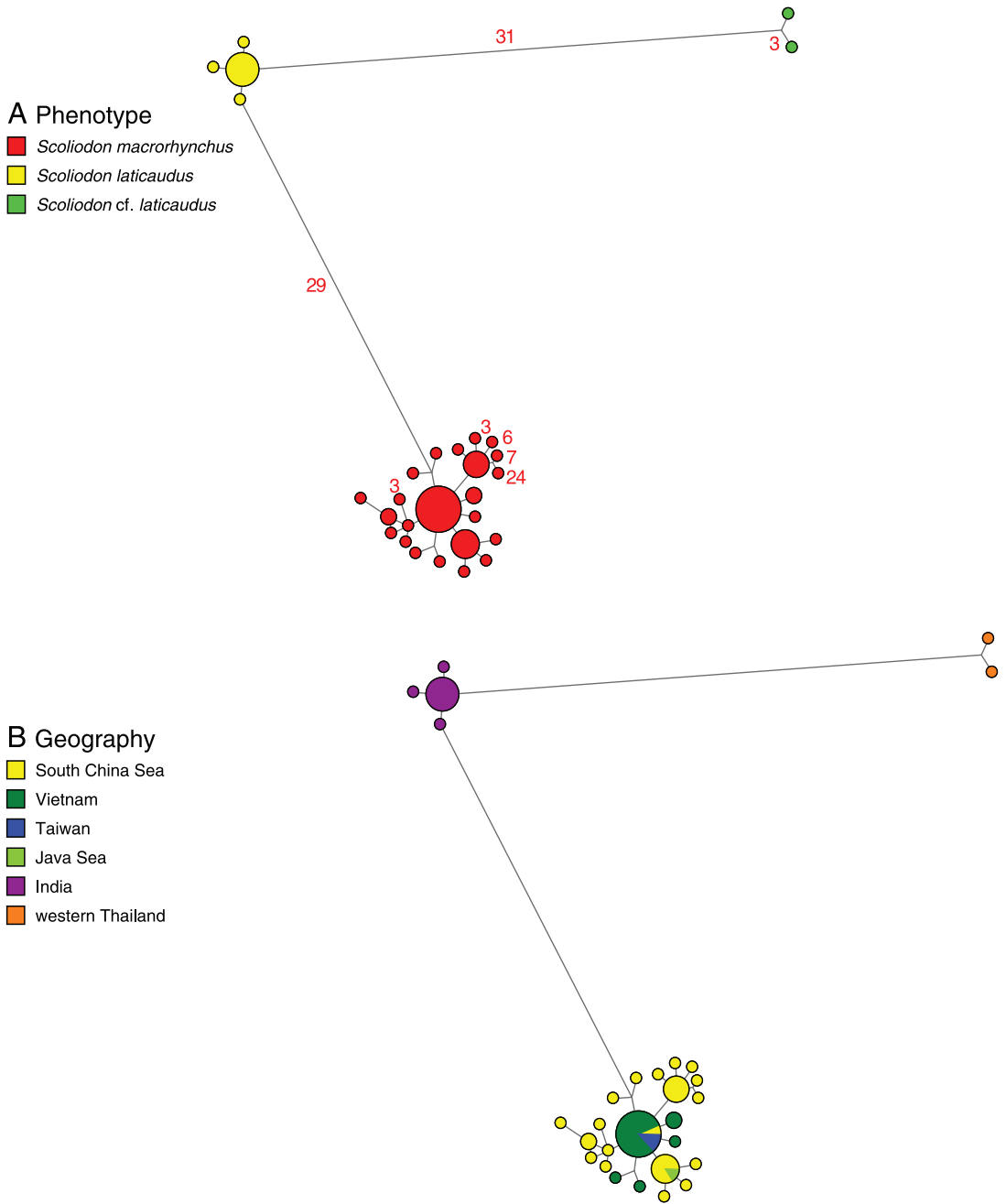
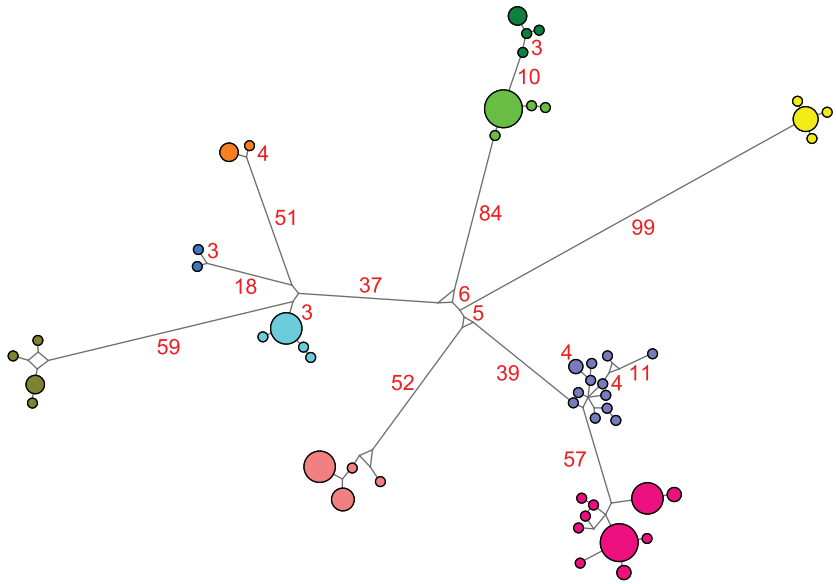


Fig. 86. Parsimony haplotype network for *Scoliodon macrorhynchus*, *S. laticaudus*, and *S. cf. laticaudus* color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Sphyrna lewini* 2
- *Sphyrna lewini* 1
- *Sphyrna tiburo*
- *Sphyrna cf. tiburo*
- *Sphyrna tudes*
- *Sphyrna corona*
- *Sphyrna zygaena*
- *Sphyrna mokarran* 1
- *Sphyrna mokarran* 2
- *Eusphyrna blochii*



**B Geography**

- Gulf of Mexico
- western North Atlantic Ocean
- Senegal
- western Indian Ocean
- South China Sea
- India
- Gulf of California
- Kalimantan
- Taiwan
- Trinidad
- eastern Central Pacific Ocean
- Japan
- Gulf of Carpentaria
- Arafura Sea
- Timor Sea

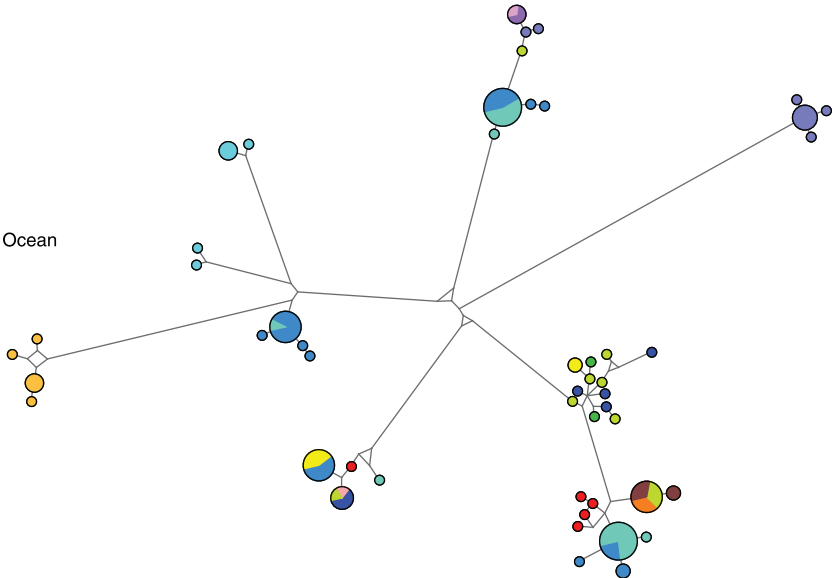
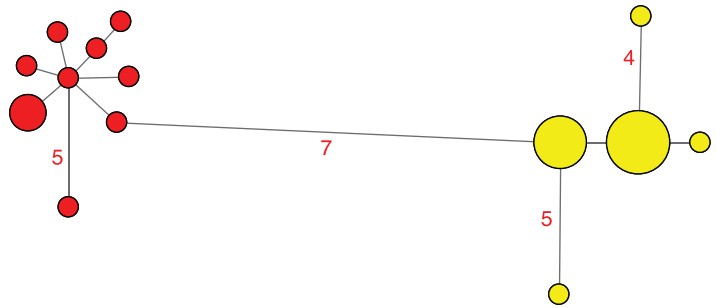


Fig. 87. Parsimony haplotype network for species of Sphyrindae color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Galeocerdo cf. cuvier*
- *Galeocerdo cuvier*



**B Geography**

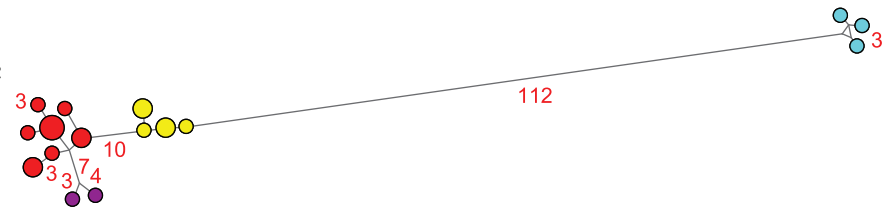
- western North Atlantic Ocean
- Gulf of Mexico
- Timor Sea
- Hawaii
- Red Sea
- Gulf of California
- Kalimantan



Fig. 88. Parsimony haplotype network for *Galeocerdo cuvier* and *G. cf. cuvier* color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Iago omanensis*
- *Iago cf. omanensis* 1
- *Iago cf. omanensis* 2
- *Iago garricki*



**B Geography**

- Gulf of Oman
- India
- Red Sea
- South China Sea
- Sulu Sea

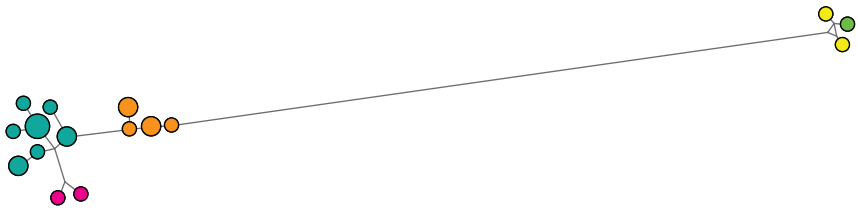


Fig. 89. Parsimony haplotype network for *Iago omanensis*, *I. cf. omanensis* 1, *I. cf. omanensis* 2, and *I. garricki* color coded by phenotype (A) and geography (B).

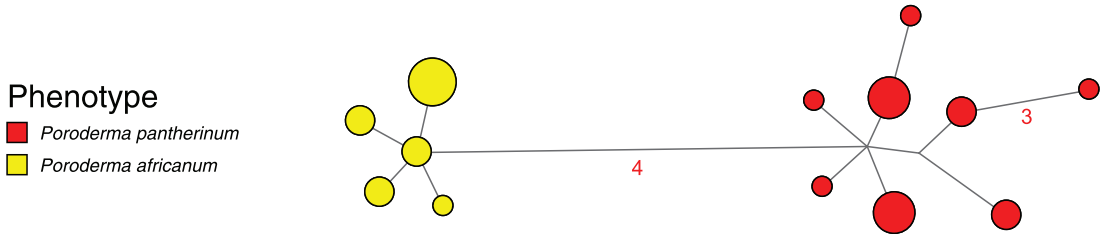


Fig. 90. Parsimony haplotype network for *Poroderma pantherinum* and *P. africanum* color coded by phenotype.

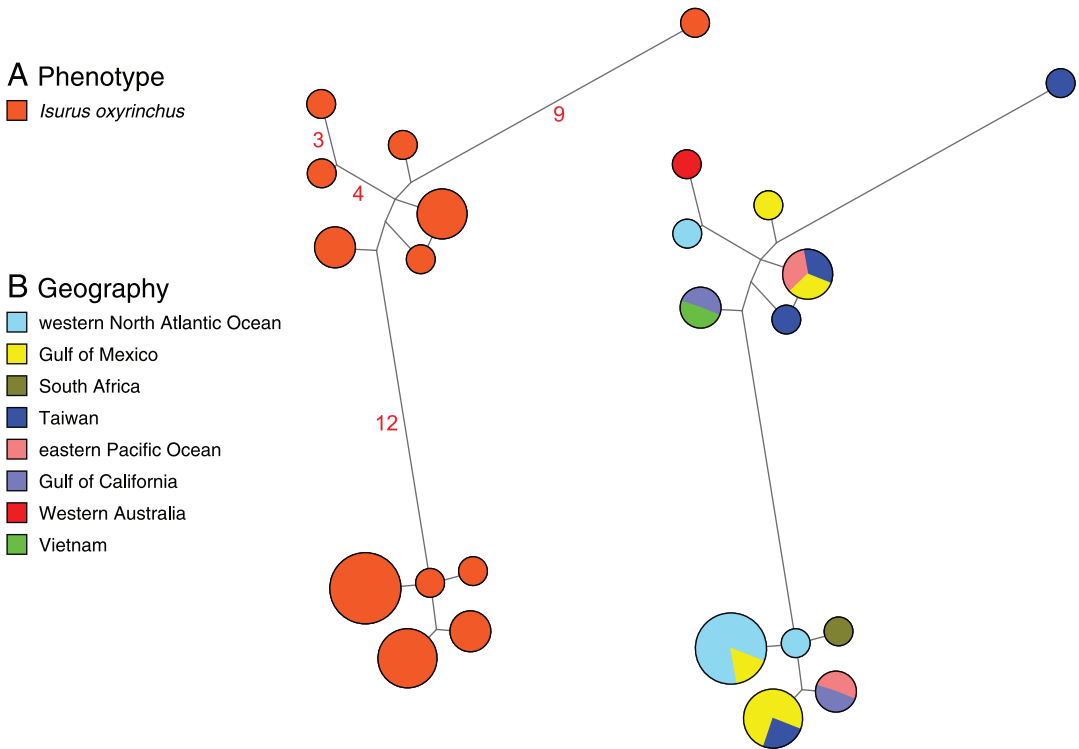


Fig. 91. Parsimony haplotype network for *Isurus oxyrinchus* color coded by phenotype (A) and geography (B).

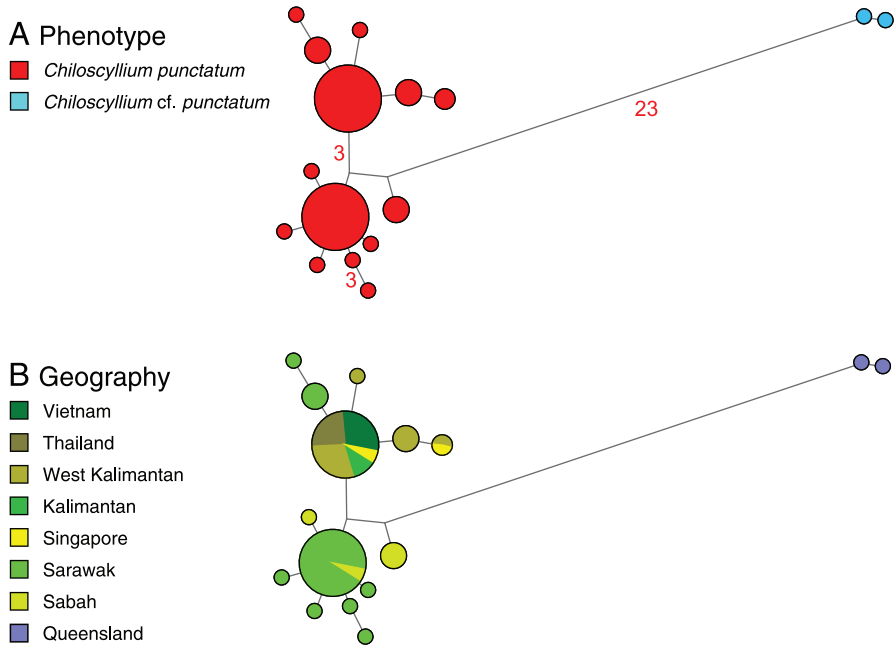


Fig. 92. Parsimony haplotype network for *Chiloscyllium punctatum* and *C. cf. punctatum* color coded by phenotype (A) and geography (B).

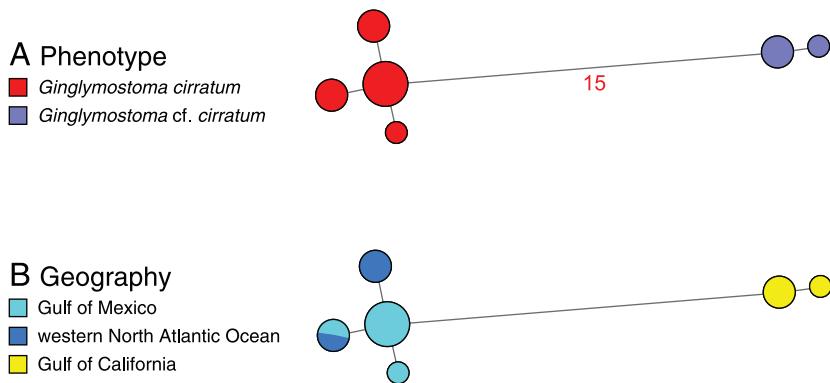
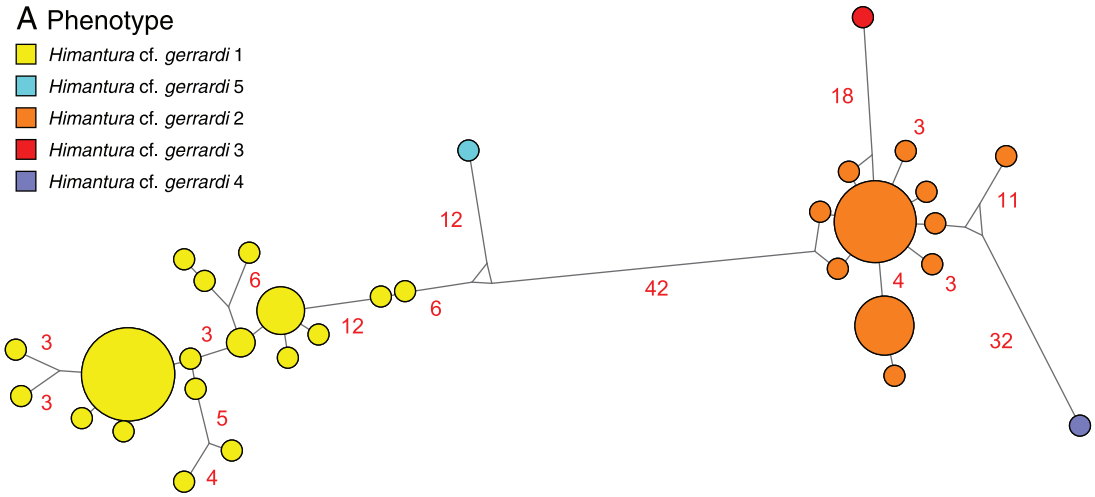


Fig. 93. Parsimony haplotype network for *Ginglymostoma cirratum* and *G. cf. cirratum* color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Himantura cf. gerrardi* 1
- *Himantura cf. gerrardi* 5
- *Himantura cf. gerrardi* 2
- *Himantura cf. gerrardi* 3
- *Himantura cf. gerrardi* 4



**B Geography**

- Sarawak
- Kalimantan
- Sabah
- Thailand
- Vietnam
- Gulf of Oman
- Madagascar

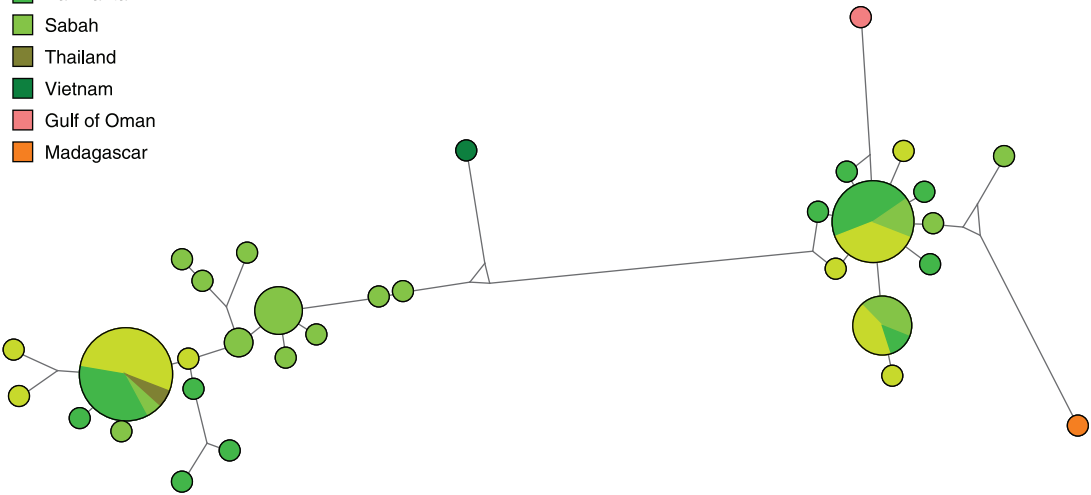


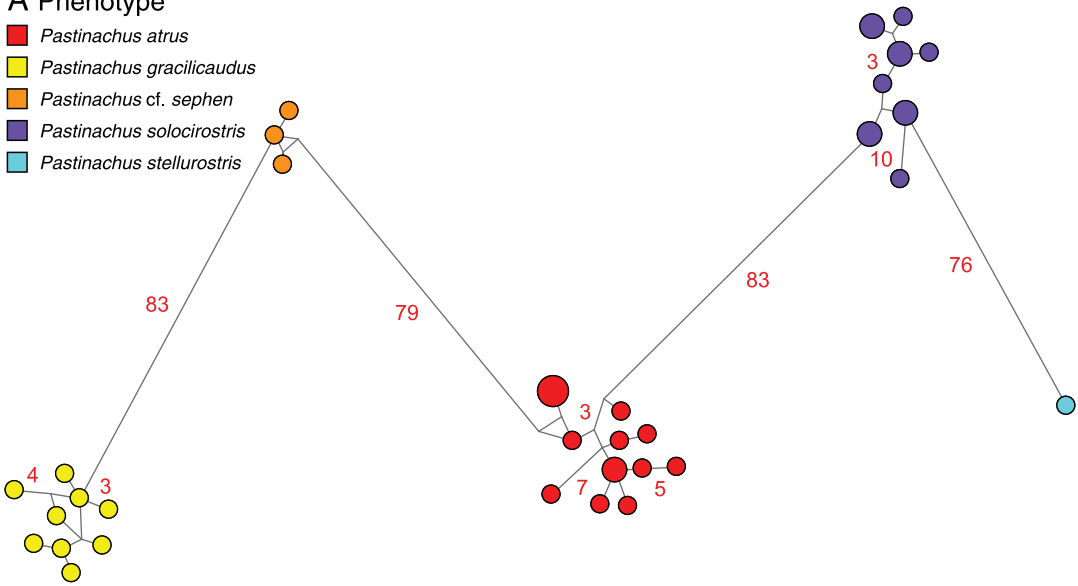
Fig. 94. Parsimony haplotype network for *Himantura cf. gerrardi* 1, 2, 3, 4, and 5 color coded by phenotype (A) and geography (B).





**A Phenotype**

- *Pastinachus atrus*
- *Pastinachus gracilicaudus*
- *Pastinachus* cf. *sephen*
- *Pastinachus solocirostris*
- *Pastinachus stellurostris*



**B Geography**

- Western Australia
- Gulf of Carpentaria
- Kalimantan
- Sabah
- Philippines
- Queensland
- Madagascar
- Sarawak
- Gulf of Oman

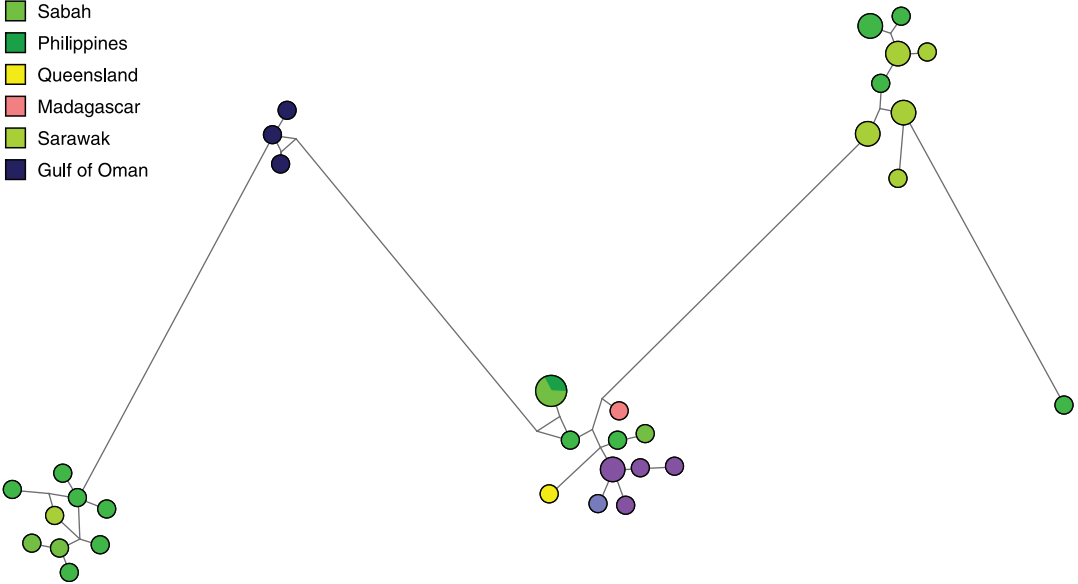


Fig. 96. Parsimony haplotype network for species of *Pastinachus* color coded by phenotype (A) and geography (B).

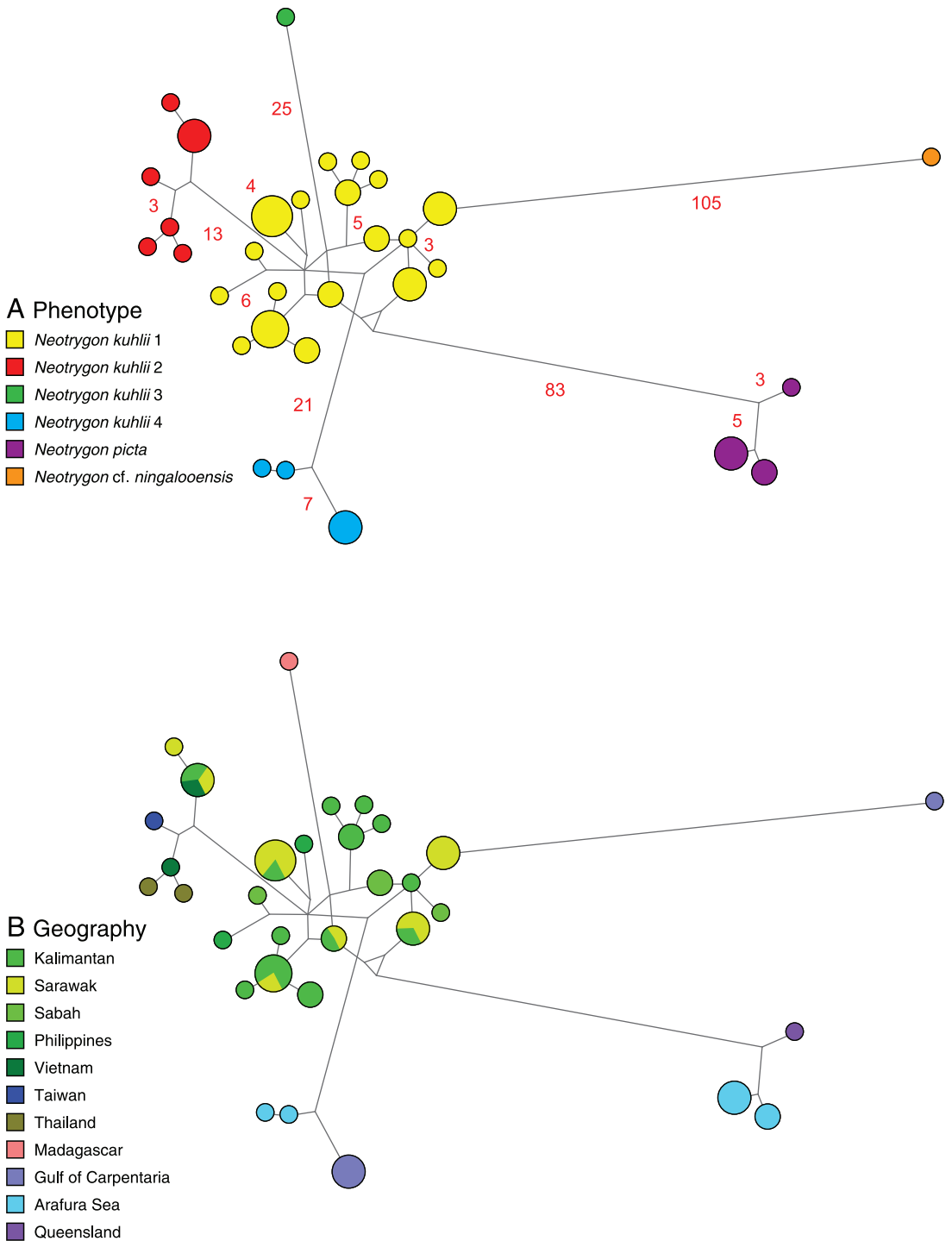
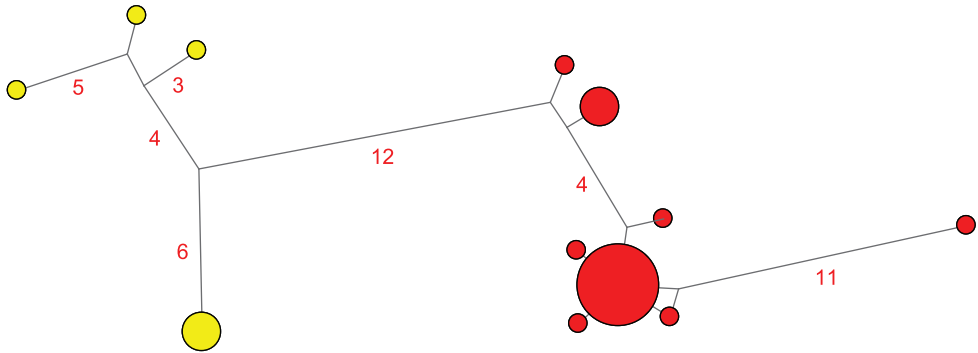


Fig. 97. Parsimony haplotype network for *Neotrygon kuhlii* 1, 2, 3, and 4, and *N. picta* and *N. cf. ningalooensis* color coded by phenotype (A) and geography (B).

A Phenotype

- Taeniura lymma 1
- Taeniura lymma 2



B Geography

- Kalimantan
- Sabah
- Philippines
- Vietnam
- Gulf of Carpentaria
- Sulawesi

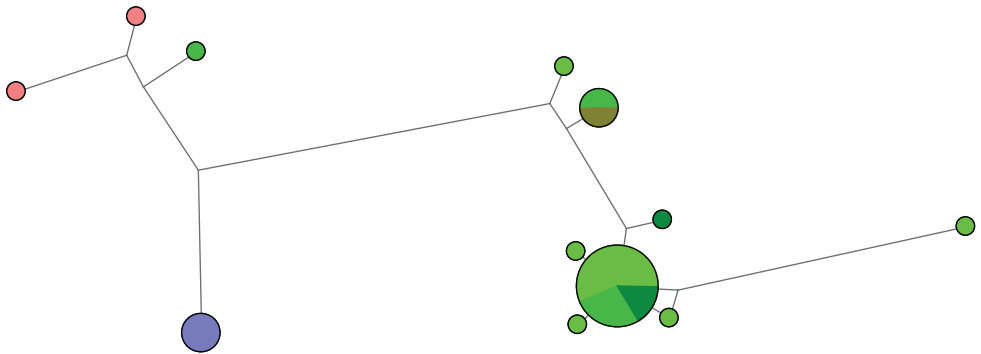
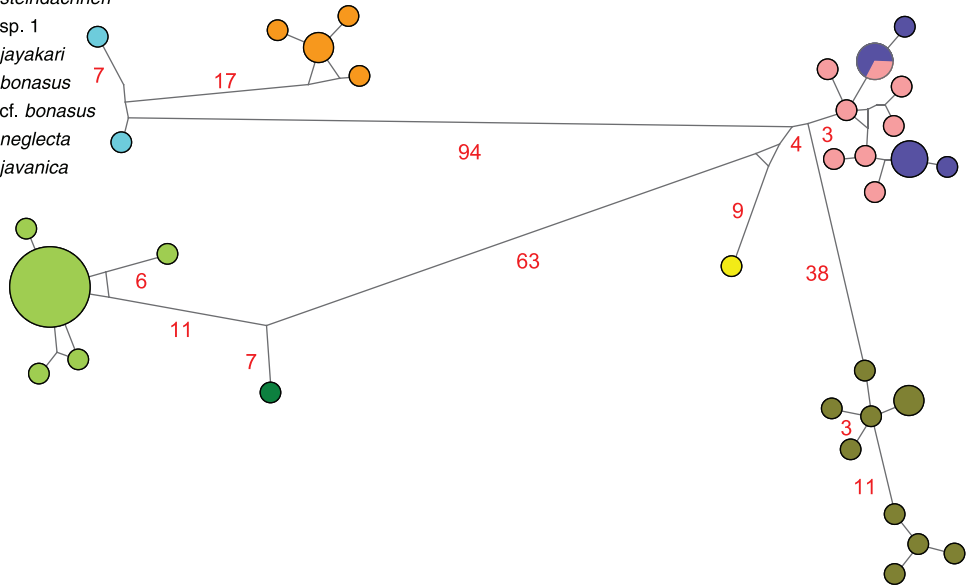


Fig. 98. Parsimony haplotype network for *Taeniura lymma* 1 and 2 color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Rhinoptera cf. steindachneri*
- *Rhinoptera steindachneri*
- *Rhinoptera sp. 1*
- *Rhinoptera jayakari*
- *Rhinoptera bonasus*
- *Rhinoptera cf. bonasus*
- *Rhinoptera neglecta*
- *Rhinoptera javanica*



**B Geography**

- Gulf of Mexico
- Gulf of California
- western North Atlantic Ocean
- Senegal
- Sabah
- Mozambique
- Kalimantan
- Gulf of Oman
- Thailand
- Timor Sea
- Gulf of Carpentaria
- Arafura Sea
- Vietnam

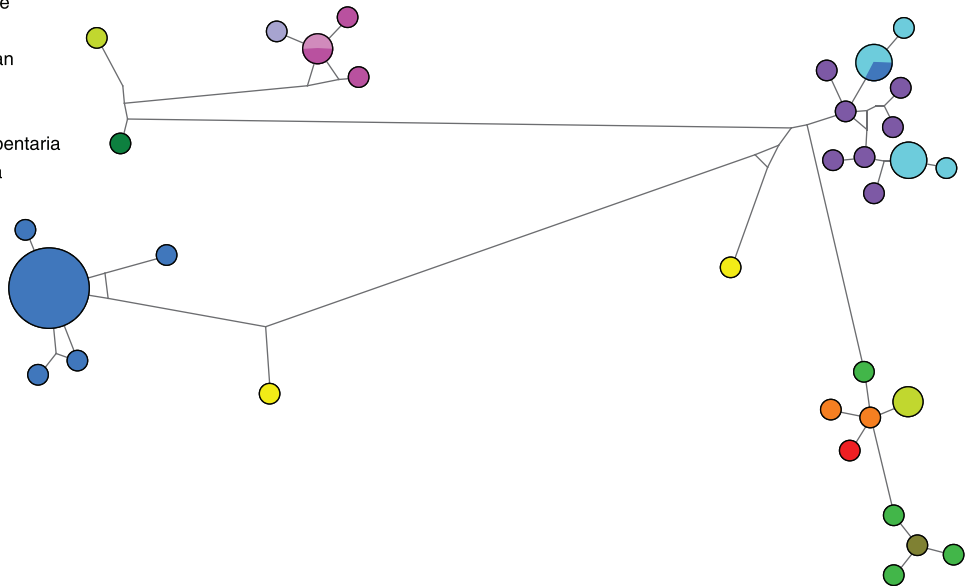


Fig. 99. Parsimony haplotype network for species of *Rhinoptera* color coded by phenotype (A) and geography (B).

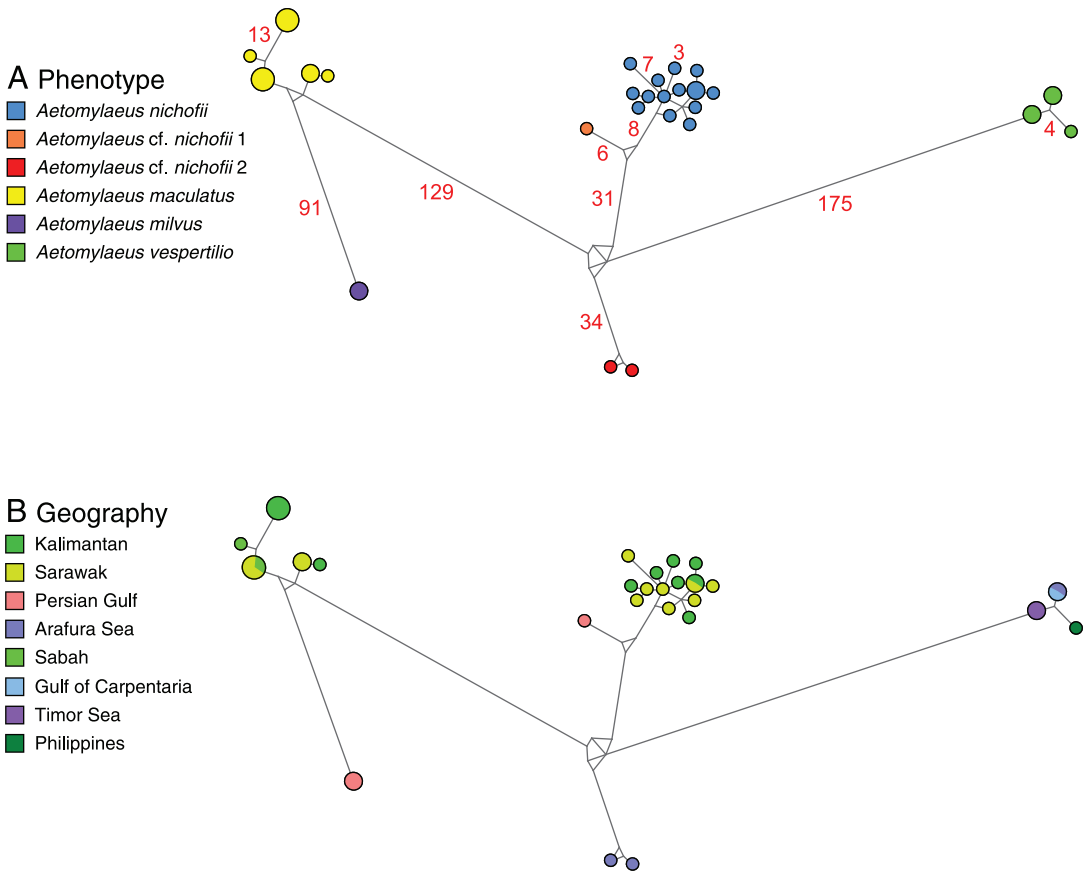
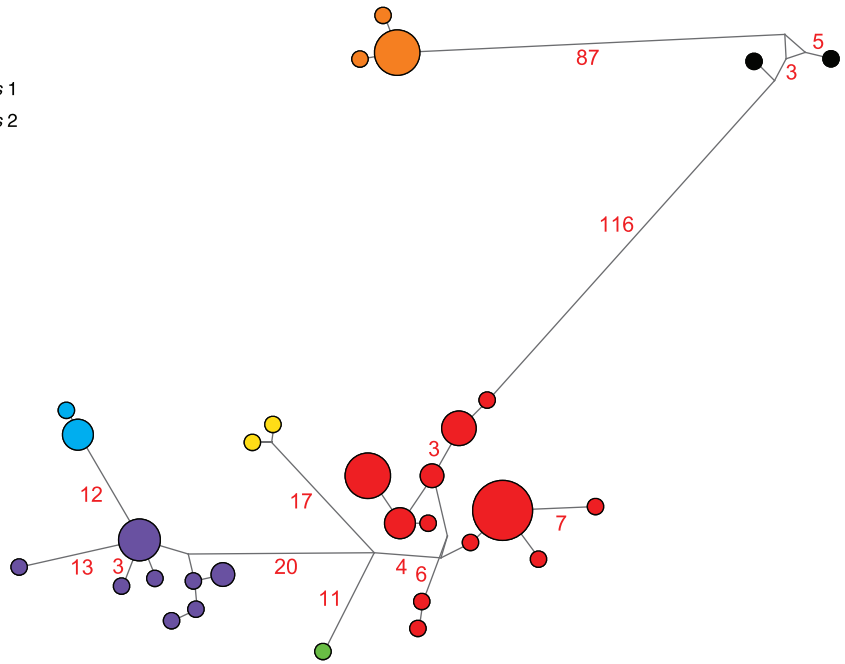


Fig. 100. Parsimony haplotype network for species of *Aetomylaeus* color coded by phenotype (A) and geography (B).

**A Phenotype**

- *Aetobatus ocellatus*
- *Aetobatus cf. ocellatus 1*
- *Aetobatus cf. ocellatus 2*
- *Aetobatus narinari*
- *Aetobatus laticeps*
- *Aetobatus sp.*
- *Aetobatus flagellum*



**B Geography**

- Gulf of Carpentaria
- Kalimantan
- Sarawak
- Philippines
- Sabah
- Arafura Sea
- Timor Sea
- Taiwan
- Thailand
- Vietnam
- Singapore
- Mozambique
- Qatar
- Gulf of Mexico
- Caribbean Sea
- western Atlantic Ocean
- Gulf of California
- India

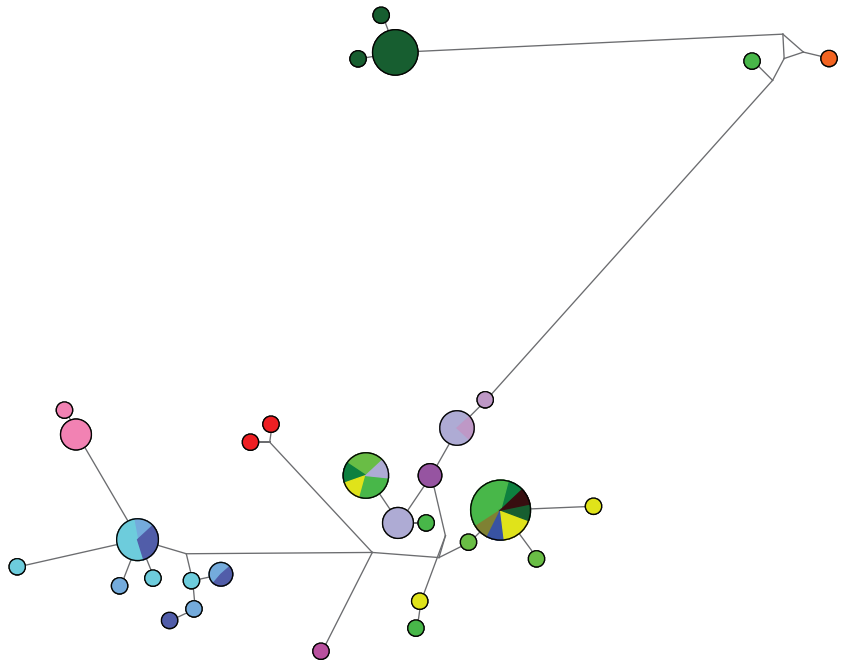


Fig. 101. Parsimony haplotype network for species of *Aetobatus* color coded by phenotype (A) and geography (B).

