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Research Article

Evolutionary History and Taxonomic Reclassification of the Critically Endangered Daggernose Shark, a Species Endemic to the Western Atlantic

Luis Fernando da Silva Rodrigues-Filho [1], **Paula da Costa Nogueira** [1], **Davidson Sodré** [2], **José Rafael da Silva Leal** [1], **Jorge Luiz Silva Nunes** [3], **Getulio Rincon** [4], **Rosangela Paula Teixeira Lessa** [5], **Iracilda Sampaio** [6], **Marcelo Vallinoto** [6], **Jonathan S. Ready** [7], and **João Bráullio Luna Sales** [7]

[1]Federal Rural University of Amazonia, Research Group for Marine and Coastal Studies in the Amazon (GEMCA), Capanema Campus, 68600-030 Capanema, Pará, Brazil
[2]Federal Rural University of Amazonia, Capitão Poço Campus, 68650-000 Capitão Poço, Pará, Brazil
[3]Federal University of Maranhão, Laboratory of Aquatic Organisms, Department of Oceanography and Limnology, Avenida Portugueses, 1968, Bacanga, 65080-805 São Luis, Maranhão, Brazil
[4]Federal University of Maranhão, Campus Pinheiro, 65200-000 Pinheiro, Maranhão, Brazil
[5]Marine Population Dynamics Laboratory (DIMAR), Department of Fisheries and Aquaculture, Federal Rural University of Pernambuco, 52171-900 Recife, Pernambuco, Brazil
[6]Federal University of Pará, Faculty of Biological Sciences, Alameda Leandro Ribeiro, 68600-000 Bragança, Pará, Brazil
[7]Federal University of Pará, Integrated Biology Research Group, Center for Advanced Biodiversity Studies, Av. Perimetral 01, PCT-Guamá, Terreno 11, CEP: 66075-110 Belém, Pará, Brazil

Correspondence should be addressed to João Bráullio Luna Sales; braullio@ufpa.br

The family Carcharhinidae includes the most typical and recognizable sharks, although its internal classification is the subject of extensive debate. In particular, the type genus, *Carcharhinus* Blainville, 1816, which is also the most speciose, appears to be paraphyletic in relation to a number of morphologically distinct taxa. *Isogomphodon oxyrhynchus* (Valenciennes, 1839) (the daggernose shark) is a carcharinid, which is endemic to a limited area of the Western Atlantic between Trinidad and Tobago and the Gulf of Maranhão in northern Brazil, one of the smallest ranges of any New World elasmobranch species. In recent decades, *I. oxyrhynchus* populations have been decimated by anthropogenic impacts, which has led to the classification of the species as critically endangered by the IUCN. However, there is considerable debate on both the validity of the species (*I. oxyrhynchus*) and the status of *Isogomphodon* Gill, 1862 as a distinct entity from the genus *Carcharhinus*. The present study is based on a molecular assessment of the genetic validity of the *I. oxyrhynchus* that combines mitochondrial and nuclear markers, which were used to identify the biogeographic events responsible for the emergence and dispersal of the species in northern Brazil. The genetic distance analyses and phylogenetic trees confirmed the paraphyly of the genus *Carcharhinus*, recovering a clade comprising *Carcharhinus+I. oxyrhynchus+Prionace glauca* (Linnaeus, 1758). Our results indicate not only that the daggernose shark is actually a member of the genus *Carcharhinus*, but that it is genetically more closely related to *Carcharhinus porosus* (Ranzani, 1839) than it is to the other *Carcharhinus* species analyzed. Given this, *I. oxyrhynchus* and *P. glauca* are therefore reclassified and recognized as *Carcharhinus oxyrhynchus* and *Carcharhinus glaucus*. The daggernose shark, *Carcharhinus oxyrhynchus*, diverged from *C. porosus* during the Miocene, when significant geomorphological processes occurred on the northern coast of South America, in particular in relation to the configuration of the Amazon River. It is closely associated with the area of the Amazon plume, and its distinctive morphological features represent autapomorphic ecological adaptations to this unique habitat and do not reflect systematic distinction from *Carcharhinus*.

1. Introduction

Most phylogenetic studies of elasmobranchs have focused on higher taxonomic levels, such as order and family, rather than lower levels, such as genera and species. This results in major drawbacks for the understanding of the phylogenetic relationships among the members of given elasmobranch families, such as the Carcharhinidae Jordan and Evermann, 1896 [1–5].

In recent years, the use of molecular methods has greatly improved the potential for the resolution of evolutionary questions, providing more accurate interpretations of phylogenetic arrangements, as well as important input for the establishment of conservation priorities [6–10]. Molecular data can also provide important insights into the relationship between diversification patterns and biogeographic events [8, 11, 12]. However, the management of elasmobranch stocks, and in particular the conservation of species, is still widely hindered by gaps in both basic and applied researches. These shortfalls include key data on species biology, population status, the scale and intensity of threats, and conflicts with human activities, including public safety [13], especially in the case of endemic species with limited geographic ranges [14–16].

The dispersal capacity of species is one of the principal factors that determine animal biodiversity and distribution patterns [17]. Hard barriers—land masses that prevent gene flow, such as the Isthmus of Panama or the closure of the Tethys Sea [18, 19]—are important components of the speciation process in aquatic environments, whereas soft barriers are permeable, formed by environmental discontinuities or geographical features that restrict connectivity and gene flow between areas connected physically by bodies of water [18, 20–23]. Although they do not have a planktonic life stage, many elasmobranch species undertake major migrations [24–26]. This means that dispersal is the responsibility of the adults, whereas juveniles are dependent on nursery areas [27]. However, the relationships between biogeographical events and the speciation process are still mostly unclear in this group and have been elucidated only in some cases [8, 9, 25, 28, 29].

In fact, the classification of many species within the Carcharhinidae is still unresolved, and there is extensive debate on the potential for paraphyly of genera inside the family, as also found in other families such as the Triakidae Gray, 1851 and the Scyliorhinidae Gill, 1862 [10, 30–32]. López et al. [33] detected a paraphyletic arrangement within the carcharinids, based on DNA sequences, and noted a close relationship with the Sphyrnidae Rafinesque, 1810 and Hemigaleidae Compagno [56]. These authors recovered *Galeocerdo cuvier* (Péron & Lesueur, 1822) in the Hemigaleidae, in a branch external to the clade formed by the carcharhinid and sphyrnid species, which is consistent with the findings of Naylor et al. [30] and Amaral et al. [31], who identified *Galeocerdo* Müller and Henle, 1837 as a basal taxon and sister to the Carcharhinidae + Sphyrnidae clade.

Using nuclear markers to assess the phylogenetic relationships between *Carcharhinus* Blainville, 1816 and other carcharhinid genera, Dosay-Akbulut [34] recovered potential paraphyly of *Carcharhinus*, with *Prionace glauca* (Linnaeus, 1758) recovered inside *Carcharhinus* as sister to the group (*Carcharhinus falciformis* (Bibron, 1839)+*Carcharhinus altimus* ([35])), which lead the authors to suggest that *Prionace* Cantor, 1849 may not be distinct from *Carcharhinus*. However, they cited divergence in results of different analyses as a motive for not making any changes to the taxonomic classification.

The daggernose shark, *Isogomphodon oxyrhynchus* (Valenciennes, 1839), the type species of the genus *Isogomphodon* Gill, 1862, is a critically endangered carcharhinid, which has one of the most restricted geographic ranges of any elasmobranch, inhabiting waters off the coast of Venezuela, Trinidad and Tobago, Guyana, Suriname, French Guyana, and northern Brazil [3, 4, 16]. The most conspicuous characteristic of this species is its elongated and flattened snout, which resembles a dagger. The genus *Isogomphodon* was synonymized with *Carcharhinus* [36] but separated again due to its distinct morphological characteristics resurrecting the genus *Isogomphodon* [35]. Furthermore, the only extant congener *Isogomphodon maculipinnis* Poey, 1865 was subsequently synonymized with *Carcharhinus brevipinna* (Valenciennes, 1839) [37]. Compagno [37] proposed the designation of four tribes (Carcharhinini, Rhizoprionodontini, Triaenodontini, and Isogomphodontini) within the subfamily Carcharhinidae, based on the morphological characteristics, which implies distancing of *I. oxyrhynchus* from the other genera of this subfamily. These morphological differences led Garrick [38] to exclude *I. oxyrhynchus* from their analysis, which aimed to define the limits of the genus *Carcharhinus*. However, in a study of the molecular identification of the shark species harvested by fisheries using only mitochondrial 12S-16S sequences (1380 bp), Rodrigues-Filho et al. [4] found evidence that *I. oxyrhynchus* belongs to the genus *Carcharhinus* Blainville, 1816, challenging the distinction of the genus *Isogomphodon*, but did not make any changes to the taxonomic classification. Similarly, although other studies since then have shown paraphyly of *Carcharhinus*, the analyses of their studies also showed weak support [10, 39] or had poor taxonomic coverage [16] and also did not make any changes to the classifications. Other recent studies using mitogenomes have also shown paraphyly of *P. glauca* and probably *Triaenodon obesus* but did not include *I. oxyrhynchus* and focusing on other results did not reclassify *P. glauca* or *T. obesus* [40, 41].

The daggernose shark has been overfished since the 1980s and catches collapsed in the mid-1990s [15]. Since this time, the total biomass of the species harvested decreased by 90%, due to the intense targeting of juveniles, which has hampered recruitment [15]. In the 1980s and 1990s, Stride et al. [42] found that the juveniles, which are vulnerable due to the small mesh sizes of the gillnets [43], were the age class harvested most intensively in the state of Maranhão, northern Brazil. This pressure, combined with the restricted distribution of the species and its *K*-type life history strategy (slow growth, late sexual maturation, and reduced fecundity [2]), has led to the classification of *I. oxyrhynchus* as critically endangered (CR) since 2006 by the IUCN [44]. More recent demographic studies have indicated
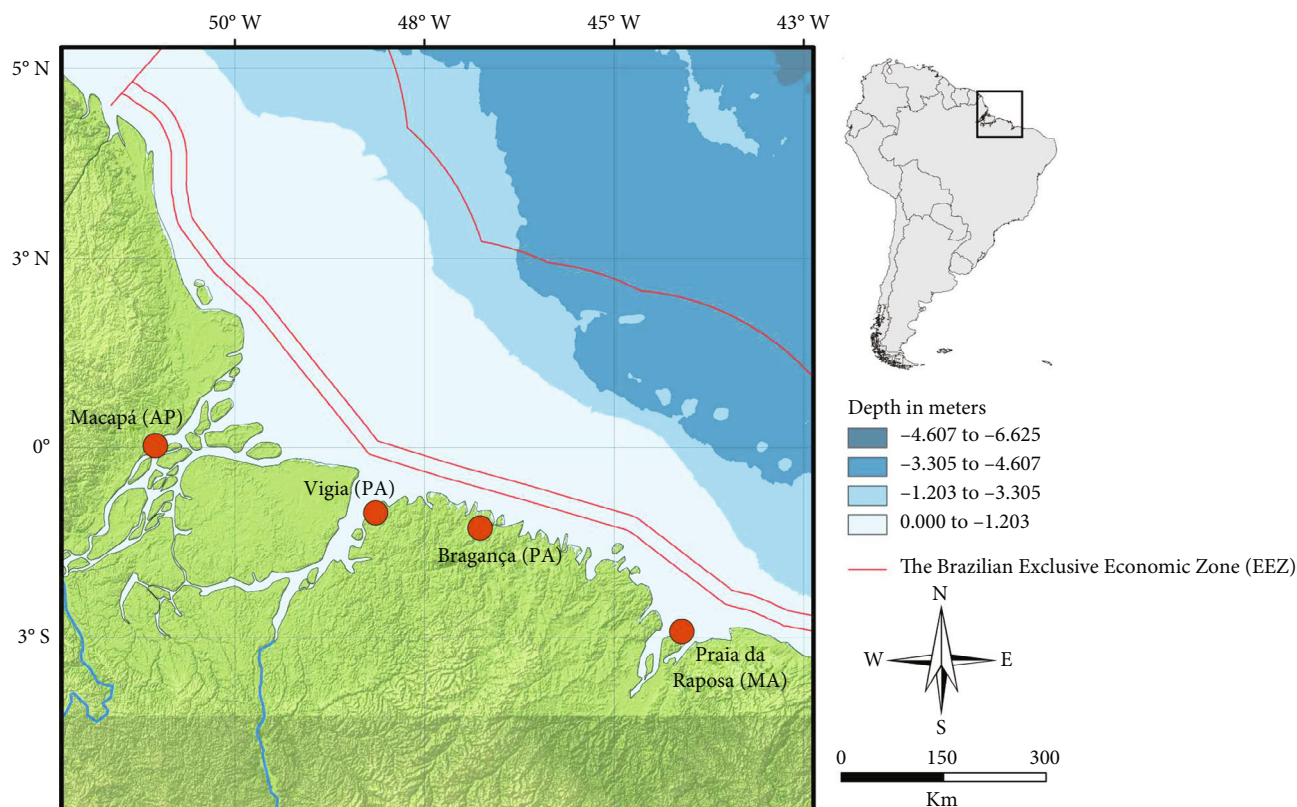
FIGURE 1: Study area in northern Brazil. The red dots represent the sampling locations in the Brazilian states of Amapá (AP), Pará (PA), and Maranhão (MA). The insets show the Brazilian states of the north coast and their location within Brazil.

that *I. oxyrhynchus* populations have been decreasing by approximately 18% per annum in recent years [15, 45, 46].

The present study is aimed at updating the taxonomic classifications in the Carcharhinidae by using data from mitochondrial and nuclear markers to confirm the phylogenetic position of *I. oxyrhynchus* and evaluate the evolutionary history of this critically endangered species in relation to other carcharhinids.

2. Material and Methods

2.1. *Study Area and Sampling.* All samples utilized in the present study were collected along the northern coast of Brazil. This is one of the five distinct regions of the Brazilian coast, classified according to their climatological and oceanographic characteristics [47]. It ranges from the mouth of the Oiapoque River, in the northernmost extreme of the Brazilian state of Amapá, to São Marcos Bay, in the state of Maranhão [44, 48] (Figure 1).

Samples of muscle tissue were obtained from *I. oxyrhynchus* and other sharks taken as bycatch and landed at Raposa Beach ($n = 1$ sample), in the Brazilian state of Maranhão, Bragança ($n = 10$) and Vigia ($n = 5$), both in the state of Pará, and Macapá ($n = 2$), in the state of Amapá (Table 1 and Figure 1). Some of the samples are whole individuals which were identified following the diagnostic key of Compagno [49]. Additional sequences represent muscle tissue samples that were sequenced in previous studies [4, 16]. All samples

were placed in microtubes containing 70% ethanol and stored at -20°C at the Genetics and Biotechnology Laboratory of the Capanema campus of the Federal Rural University of Amazonia. The collection of samples was authorized by the Biodiversity Authorization and Information System (*Sistema de Autorização e Informação da Biodiversidade*—SISBIO, Permanent License 12773-1) and the National Management System for Brazilian Genetic Heritage and Associated Traditional Knowledge (*Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado*—SISGen) through authorization number AD61D8E.

Publicly available sequences of species representing genera from the families Carcharhinidae (*Carcharhinus* Blainville, 1816; *Glyphis* Agassiz, 1843; *Lamiopsis* Gill, 1862; *Loxodon* Müller and Henle, 1838; *Nasolamia* Compagno and Garrick [62]; *Negaprion* Whitley, 1940; *Prionace* Cantor, 1849; *Rhizoprionodon* Whitley, 1929; *Scoliodon* Müller and Henle, 1838; and *Triaenodon* Müller and Henle, 1837), Triakidae (*Mustelus* Link, 1970), Scyliorhinidae (*Scyliorhinus* Blainville, 1816), Galeocerdonidae (*Galeocerdo* Müller and Henle, 1837), and Sphyrnidae (*Sphyrna* Griffith and Smith, 1834) were also included in the phylogenetic analyses after download from GenBank (Table 1).

2.2. *Extraction, Amplification, and Sequencing of the DNA.* The genomic DNA was extracted using the Wizard Genomic DNA Purification Kit (Promega Corporation), following the

mouse-tail protocol. The final product of each extraction was run at 60 V in 1% agarose gel for 20 minutes and photographed under ultraviolet light. For the phylogenetic analysis, fragments of three mitochondrial loci and one nuclear locus were amplified by polymerase chain reaction (PCR). These PCRs were run using the following primers for the mitochondrial loci: fish F1 and fish R2 [50] for the cytochrome C oxidase subunit 1 gene (COI), ND4 F and Leu-Scyliorhinus [3] for the NADH dehydrogenase subunit 4 gene (ND4), and 12SA and 16SA [51] for a region encompassing the 12S rRNA, valine tRNA, and 16S rRNA genes (12S–16S). The nuclear locus was Recombination Activating Gene 1 (RAG1), for which the primers were Chon-Rag1-S026 and Chon-Rag1-R025 [3].

The PCRs were run in a final volume of 12.5 μL, containing 0.5 μM of each primer, 0.8 mM of MgCl$_2$, 0.2 mM of each deoxynucleoside triphosphate (dNTP), 1x buffer (Tris-HCl (Invitrogen) and KCl, pH 7.8), 1 U of Taq polymerase (Invitrogen: 5 U/μL), and approximately 100 ηg/μL of the DNA, with ultrapure water to complete the final volume. Two internal primers were developed in the present study to sequence RAG1: Rag-Tuba-For (5$'$-TAGATGAGTTTGTG AGTGGRCCG-3$'$) and Rag-Tuba-Ver (5$'$-GGGTCTTGT GCAGRTAGTTGGGTG-3$'$).

The following PCR protocol was used to amplify all the samples: 5 minutes for initial denaturation at 94°C, followed by 30 cycles of 30 seconds at 94°C, 40 seconds at 50–60°C, and 1 minute at 72°C, with a final extension of 5 minutes at 72°C. The resulting amplicons were purified using the polyethylene glycol 20% protocol (20% PEG), adapted from Dun and Blattner [52]. The purified material was then precipitated and sequenced using the BigDye kit (ABI Prism™ Dye Terminator Cycle Sequencing Reading Reaction—Applied Biosystems, Foster City, CA, USA) and sequenced using an ABI 3500 Genetic Analyzer at the Phylogenomics Laboratory on the UFPA Bragança campus. The additional internal primers for RAG1 (Chon-Rag1-S030 and Chon-Rag1-S031 [3]) and 12S–16S [51] were used to sequence RAG1 and 12S–16S, respectively.

2.3. Phylogenetic and Genetic Distance Analyses.
The sequences generated during this initial processing were edited, aligned, and corrected using the automatic ClustalW alignment tool [53], run in BioEdit 7.0.5 [54]. The Gblocks 0.91b program [55] was used to process the 12S–16S ribosomal regions to avoid errors of homology in the portions of this fragment that are subject to indels and other variable positions, which were removed following preestablished criteria [56]. After the alignment and sequencing corrections, all available sequences were analyzed separately for each of the four loci (four single marker datasets) and a further dataset of concatenated mitochondrial sequences was produced for phylogenetic analyses (hereafter referred to as the "mtDNA dataset"). The mtDNA dataset included one sequence representing each of the 37 species for which all three mitochondrial loci were available for concatenation.

The nucleotide composition and the numbers of conserved, variable, and parsimonious sites, as well as the most

suitable nucleotide substitution models, were calculated in MEGA X [57] for each dataset as partitioned (COI: HKY+ G(1.0428)+I(0.6049), 12S-16S: GTR+G(0.4122)+I(0.3388), ND4: TN93+G(1.1641)+I(0.5130), mtDNA: GTR+G (0.5093)+I(0.4665), and RAG1: TN93+G(0.0963)). The number of transitions and transversions was plotted against the divergence of each region in DAMBE 7 to verify the saturation levels of the markers [58]. Nucleotide distance matrices, based on both the corrected and uncorrected p distances, were generated in MEGA X for all datasets [57]. Four different methods of phylogenetic inference were used to construct the phylogenetic trees, according to the evolutionary models identified for each dataset. The maximum likelihood (ML) approach was run in PhyML 3.0 [59], while Bayesian inference (BI) was applied in MrBayes 3.2 [60]. The maximum parsimony (MP) and neighbor joining (NJ) trees were generated in MEGA X [57]. The robustness of the clades generated by the ML, NJ, and MP analyses was estimated using 1000 bootstrap replicates [61].

For the concatenated dataset, BI analyses used all the concatenated fragments as separate unlinked partitions with their respective models as previously calculated. The Bayesian inference was based on MCMC (Markov chain Monte Carlo) sampling, with four simultaneous runs of four chains (one cold and three warm) and 50 million generations, with two runs. The a posteriori probabilities were defined using the 80% consensus rule, with samples being taken every 1000 generations and 10% of the initial trees being discarded as burn-in. The log-likelihood files generated by each run were visualized in Tracer v.1.7.1 [62], considering only the runs with a minimum effective sample size (ESS) of at least 200 (i.e., ESS ≥ 200).

2.4. Divergence Time Estimates.
Divergence times were estimated in BEAST 2.5 [63]. The Yule calibration model was selected as the tree prior parameter, using the relaxed molecular clock with uncorrelated rates, which assumes heterogeneous rates on the different branches [64]. This analysis was conducted using the mtDNA dataset using clock models and the unlinked evolutionary models for the concatenated fragments as previously calculated. This dataset was used given that most of the sequences used as calibration points are available for the taxa investigated here.

Three calibration points based on the fossil record were used to estimate the time of the most recent common ancestor (MRCA) of the principal clades, deployed a priori as the age of the nodes in the tree. The ancestral node is associated with the origin of the Carcharhiniformes, estimated at approximately 148.5 million years ago (mya), and the divergence times of Carcharhinus and Sphyrna were dated to ~38–42 mya and ~16–23 mya, respectively [65, 66].

The pretrees were modeled based on the Yule speciation process calibration, with all the other parameters being based on the BEAST 2.5 default values. The MCMC analyses were based on a run of 60 million generations, with four simultaneous runs of four chains (one cold and three heated) sampled every 6000 generations, with 10% of the samples being discarded as burn-in. The results were inspected using

TABLE 1: Species used for phylogenetic analyses with the GenBank code for each employed marker.

Family/genus	Species			
		mtDNA		nuDNA
	COI (GenBank)	12S16S (GenBank)	ND4 (GenBank)	RAG1 (GenBank)
Carcharhinidae Carcharhinus	C. acronotus (**OK092567**)	C. acronotus (**OK169912**)	C. acronotus (**OK094394**)	C. acronotus (**OK104478**)
	C. falciformis (FJ519607)	C. falciformis (**OK169913**)	C. falciformis (**OK094395**)	C. falciformis (**OK104479**)
	C. leucas (**OK092568**)	C. leucas (**OK169914**)	C. leucas (**OK094396**)	C. leucas (**OK104480**)
	C. limbatus (**OK092569**)	C. limbatus (**OK169915**)	C. limbatus (**OK094397**)	C. limbatus (**OK104481**)
	C. perezi (MH9111298)	C. perezi (**OK169916**)	C. perezi (**OK094398**)	C. perezi (**OK104482**)
	C. plumbeus (FJ519154)	C. plumbeus (**OK169917**)	C. plumbeus (**OK094399**)	C. plumbeus (**OK104483**)
	C. porosus (**OK092570**)	C. porosus (**OK169918**)	C. porosus (**OK094400**)	C. porosus (**OK104484**)
	C. albimarginatus (HQ171610)	—	—	—
	C. altimus (FJ519046)	C. altimus (AY830722)	C. altimus (HM446375)	—
	C. amblyrhynchoides (GQ227287)	C. amblyrhynchoides (NC023948)	C. amblyrhynchoides (GQ227276)	—
	C. amblyrhynchos (KP193415)	—	C. amblyrhynchos (KX713064)	—
	C. amboinensis (JF493047)	C. amboinensis (KM921745)	C. amboinensis (HM446377)	—
	C. brachyurus (FJ519061)	—	—	—
	C. brevipinna (KM244770)	C. brevipinna (AY830723)	C. brevipinna (HM446389)	—
	C. cautus (EU398605)	—	—	—
	C. coatesi (JN313265)	—	—	—
	C. dussumieri (FJ519078)	—	C. dussumieri (GQ227279)	—
	C. fitzroyensis (KU366616)	—	C. fitzroyensis (HM446402)	—
	C. galapagensis (FJ519090)	—	—	—
	C. isodon (FJ519104)	C. isodon (AY830727)	—	—
	C. leiodon (JN034903)	—	—	—
	C. longimanus (EU396227)	C. longimanus (AY830733)	—	—
	C. macloti (EU398629)	C. macloti (KJ865755)	C. macloti (HM446410)	—
	C. melanopterus (FJ519127)	C. melanopterus (KJ720818)		—
	C. obscurus (KC470543)	C. obscurus (AY830737)	C. obscurus (KJ004551)	—
	C. sealei (EU398644)	—	—	—
	C. signatus (MH911151)	C. signatus (AY830744)	—	—
	C. sorrah (NC023521)	C. sorrah (KF612341)	C. sorrah (HM446413)	—
	C. tilstoni (GQ227285)	—	C. tilstoni (HM446458)	—
	C. tjutjot (KP091436)	C. tjutjot (KP091436)	—	—
Glyphis	G. fowlerae (KT698062)	G. fowlerae (KT698062)	G. fowlerae (KT698062)	—
	G. gangeticus (KT698058)	G. gangeticus (KT698058)	G. gangeticus (KT698058)	—
	G. garricki (KT698059)	G. garricki (KT698059)	G. garricki (KT698059)	—
	G. glyphis (KT698055)	G. glyphis (KT698055)	G. glyphis (NC021768)	—
	G. siamensis (KT698052)	G. siamensis (KT698052)	G. siamensis (KT698052)	—
Lamiopsis	L. temminckii (KT698048)	L. temminckii (KT698048)	L. temminckii (KT698048)	—
	L. tephrodes (KT698047)	L. tephrodes (KT698047)	L. tephrodes (KT698047)	—
Negaprion	N. acutidens (KP193438)	—	—	—
	N. brevirostris (FJ519235)	N. brevirostris (AY830756)	—	—
Prionace	P. glauca (NC0222819)	P. glauca (**OK169919**)	P. glauca (**OK094401**)	P. glauca (**OK104485**)
Isogomphodon	**I. oxyrhynchus (OK092571)**	**I. oxyrhynchus (OK169920)**	**I. oxyrhynchus (OK094402)**	**I. oxyrhynchus (OK104486)**

TABLE 1: Continued.

Family/genus		mtDNA		nuDNA
	COI (GenBank)	12S16S (GenBank)	ND4 (GenBank)	RAG1 (GenBank)
			Species	
Rhizoprionodon	*R. acutus* (FJ519253)		*R. acutus* (HQ530209)	—
	R. lalandii (FJ519255)	*R. lalandii* (**OK169921**)	*R. lalandii* (**OK094403**)	*R. lalandii* (**OK104487**)
	R. oligolinx (MH429295)	—	—	—
	R. porosus (**OK092572**)	*R. porosus* (**OK169922**)	*R. porosus* (**OK094404**)	*R. porosus* (**OK104488**)
	R. taylori (EU399001)		—	—
	R. terraenovae (FJ519275)	*R. terraenovae* (AY830763)	—	—
Loxodon	*L. macrorhinus* (HQ171691)	*L. macrorhinus* (NC029843)	*L. macrorhinus* (NC029843)	—
Triaenodon	*T. obesus* (FJ519288)	*T. obesus* (KJ748376)	*T. obesus* (KJ748376)	—
Scoliodon	*S. laticaudus* (NC042504)	*S. laticaudus* (NC042504)	*S. laticaudus* (NC042504)	—
	S. macrorhynchos (NC018052)	*S. macrorhynchos* (NC018052)	*S. macrorhynchos* (NC018052)	
Galeocerdo	*G. cuvier* (**OK092573**)	*G. cuvier* (**OK169923**)	*G. cuvier* (**OK094405**)	*G. cuvier* (**OK104489**)
	S. tudes (**OK092574**)	*S. tudes* (**OK169924**)	*S. tudes* (**OK094406**)	*S. tudes* (**OK104492**)
Sphyrnidae *Sphyrna*	*S. mokarran* (**OK092576**)	*S. mokarran* (**OK169926**)	*S. mokarran* (**OK094408**)	*S. mokarran* (**OK104491**)
	S. lewini (**OK092577**)	*S. lewini* (**OK169927**)	*S. lewini* (**OK094409**)	*S. lewini* (**OK104490**)
	S. tiburo (**OK092575**)	*S. tiburo* (**OK169925**)	*S. tiburo* (**OK094407**)	*S. tiburo* (**OK104493**)
	S. zygaena (**OK092578**)	*S. zygaena* (**OK169928**)	*S. zygaena* (**OK094410**)	*S. zygaena* (**OK104494**)
Triakidae *Mustelus*	*M. mustelus* (JN641215)		*M. mustelus* (KU523365)	—
	M. higmani (**OK092579**)	*M. higmani* (**OK169929**)	*M. higmani* (**OK094411**)	*M. higmani* (**OK104495**)
Scyliorhinidae *Scyliorhinus*	*S. canicula* (Y16067)	*S. canicula* (Y16067)	*S. canicula* (Y16067)	—
	S. torazame (AP019520)	*S. torazame* (AP019520)	*S. torazame* (AP019520)	—

mtDNA: mitochondrial DNA; nuDNA: nuclear DNA; COI: cytochrome oxidase subunit I; 12S16S: region comprising the 12S rRNA, tRNA valine, and 16S rRNA genes; ND4: NADH dehydrogenase subunit 4; RAG1: recombinant activation gene 1. The GenBank codes in bold are from specimens sampled in this study.

Tracer v1.7.1 [62], and only runs with an ESS of at least 200 for all the marginal parameters were used. After discarding the burn-in, the results of the MCMC runs were submitted to TreeAnnotator v1.7 [67] for the inclusion of calibration times in the branches of the final tree.

3. Results

3.1. Genetic Distances. The mitochondrial markers (COI: 599 base pairs (bp), NAD4: 813 bp, and 12S16S: 1,252 bp) grouped in the single mtDNA dataset resulted in a matrix with 2,664 bp, including 1,050 variable sites, 830 sites that were informative for parsimony, and 219 unique mutation sites. The nucleotide composition of this concatenated fragment was 28.4% thymine, 23.9% cytosine, 32.1% adenine, and 15.5% guanine.

The RAG1 sequence had 1,110 bp, with 122 variable sites, 72 informative sites, and 50 unique mutations. The nucleotide composition was 24.9% thymine, 17.7% cytosine, 33.0% adenine, and 24.4% guanine. None of the segments were saturated, given that the observed transition rates were higher than the transversion rates in all cases (Supplementary Figure S1).

The *p* (distP) and corrected (distC) distance matrices were generated for the mtDNA and RAG1 datasets (Table 2) to calculate the pairwise divergence intervals between the study species (Supplementary Tables S1 and S2). In the case of the corrected distances, the best nucleotide substitution model for the mtDNA dataset was the GTR+G(0.5093)+I(0.4665) model, and the best fit for the RAG1 data was the TN93+G(0.0963) model. In the case of the distP matrix, the genetic distances between *I. oxyrhynchus* and the other carcharhinid species ranged from 4.8% to 11.2% for the mtDNA and from 0.5% to 3.4% for RAG1. In the comparisons based on the distC matrix, the distances ranged from 5.8% to 19.3% for the mtDNA dataset and from 0.6% to 5% for RAG1.

The lowest mean intergeneric genetic distances were recorded between *I. oxyrhynchus* and the *Carcharhinus* species, for both the mtDNA (distP = 5.65% and distC = 7.06%) and RAG1 (distP = 0.77% and distC = 0.87%) datasets (Table 2 and Supplementary Tables S1 and S2). The mean values recorded between *I. oxyrhynchus* and the *Carcharhinus* species are consistent with those recorded within the genus *Carcharhinus*, that is, 3.6–6.8% for the mtDNA and 1.4–7.9% for RAG1 datasets (Supplementary Table S1 and S2). Much greater genetic distance values were recorded between *I. oxyrhynchus* and the species of the other genera analyzed in the present study, that is, *Rhizoprionodon*, *Loxodon*, and *Scoliodon* (Carcharhinidae) and *Galeocerdo* (Galeocerdonidae) (Table 2 and Supplementary Tables S1 and S2).

TABLE 2: Mean p (distP) and corrected (distC) distances calculated for the comparisons between *I. oxyrhynchus* and the other carcharhinid species analyzed in the present study. The analyses were based on the GTR+G(0.5093)+I(0.4665) model for the mtDNA dataset (COI, ND2, and 12S16S) and the TN93+G(0.0963) model for the RAG1 gene.

(a)

| | RAG1 *I. oxyrhynchus* | | | | | |
| | distP | | | distC | | |
Species in the genus	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Carcharhinus	0.77	0.5	1.1	0.87	0.6	1.2
Prionace	1.4	1.4	—	1.6	1.6	1.6
Galeocerdo	3.2	3.2	—	4.5	4.5	4.5
Rhizoprionodon	3.35	3.3	3.4	4.95	4.9	5.0

(b)

| | mtDNA *I. oxyrhynchus* | | | | | |
| | distP | | | distC | | |
Species in the genus	Mean	Minimum	Maximum	Mean	Minimum	Maximum
Carcharhinus	5.65	4.8	6.8	7.06	5.8	8.7
Prionace	6.4	6.4	—	8.4	8.4	8.4
Triaenodon	6.6	6.6	—	8.8	8.8	8.8
Lamiopsis	7.35	7.3	7.4	9.85	9.8	9.9
Glyphis	7.54	7.4	7.8	10.12	9.9	10.5
Rhizoprionodon	8.65	8.6	8.7	12.9	12.9	—
Galeocerdo	9.5	9.5	—	14.5	14.5	—
Loxodon	9.8	9.8	—	15.2	15.2	—
Scoliodon	11.15	11.1	11.2	19.1	18.9	19.3

3.2. Phylogenetic Analysis and Divergence Times. The phylogenetic inference trees generated separately for the concatenated mtDNA and RAG1 datasets (Figure 2) and for each locus (Supplementary Figures S7) resulted in generally similar topologies indicating paraphyly of *Carcharhinus*, with arrangements including *I. oxyrhynchus*, *Prionace glauca* (Linnaeus, 1758), and *Triaenodon obesus* (Rüppell, 1837), within the *Carcharhinus* clade. There was particularly strong support for the internal placement of *I. oxyrhynchus* and *Prionace glauca* within this clade in the BI analyses of the COI and 12S-16S loci (Figures S4a and S4b). The RAG1 nuclear tree showed *I. oxyrhynchus* within *Carcharhinus* but placed *P. glauca* as more closely related to *Rhizoprionodon* and *Galeocerdo* (Figure 2(b)), but taxon coverage for the nuclear data was lower (only seven *Carcharhinus* and no *T. obesus*), and the phylogenetic relationships were not significantly supported.

In addition to the previous phylogenetic analyses (Figure 2), the posterior probabilities for all the nodes of the time to most recent common ancestor (TMRCA, Figure 3) analysis are strong (PP > 0.9), placing *Isogomphodon* and *Prionace* conclusively within the genus *Carcharhinus*. *P. glauca* diversified from its sister species in the tree (*C. falciformis*) during the Miocene, approximately 16.61 mya (~9.68–23.98 mya), practically during the same timeframe that *I. oxyrhynchus* and *C. porosus* separated at

approximately 16.44 mya (9.38–23.74 mya). One other important feature of the TMRCA estimates is the subdivision of the genus *Carcharhinus* into at least three monophyletic subclades, all with high posterior probability values, which diverged during the Oligocene. The clade composed of *I. oxyrhynchus*, *C. porosus*, *Carcharhinus brevipinna* (Valenciennes, 1839), and *Carcharhinus acronotus* Poey, 1860 had an estimated TMRCA of approximately 26.37 mya (19.12–33.26). It is sister clade to the *Carcharhinus limbatus* (Valenciennes, 1839)+*Carcharhinus leucas* (Valenciennes, 1839)+*Carcharhinus amblyrhynchoides* (Bleeker, 1856) clade which has a TMRCA of around 22.29 mya (15.29–28.99) and the *P. glauca*+*C. falciformis*+*Carcharhinus obscurus* Lesueur, 1818+*Carcharhinus perezi* (Valenciennes, 1839)+*Carcharhinus sorrah* (Valenciennes, 1839) clade which has a TMRCA of around 26.01 mya (19.42–32.51).

There was weak support for a *Carcharhinus*+*Isogomphodon*+*Prionace* subclade within the *Triaenodon*+*Carcharhinus*+*Isogomphodon*+*Prionace* clade leaving the phylogenetic placement of *Triaenodon* as uncertain. The *Triaenodon*+*Carcharhinus*+*Isogomphodon*+*Prionace* clade shares a TMRCA with the *Glyphis*+*Lamiopsis* sister clade at approximately 48.24 mya (39.98–58). The genera *Rhizoprionodon*, *Loxodon*, and *Scoliodon* are then oldest components of the remaining carcharhinids, which diversified

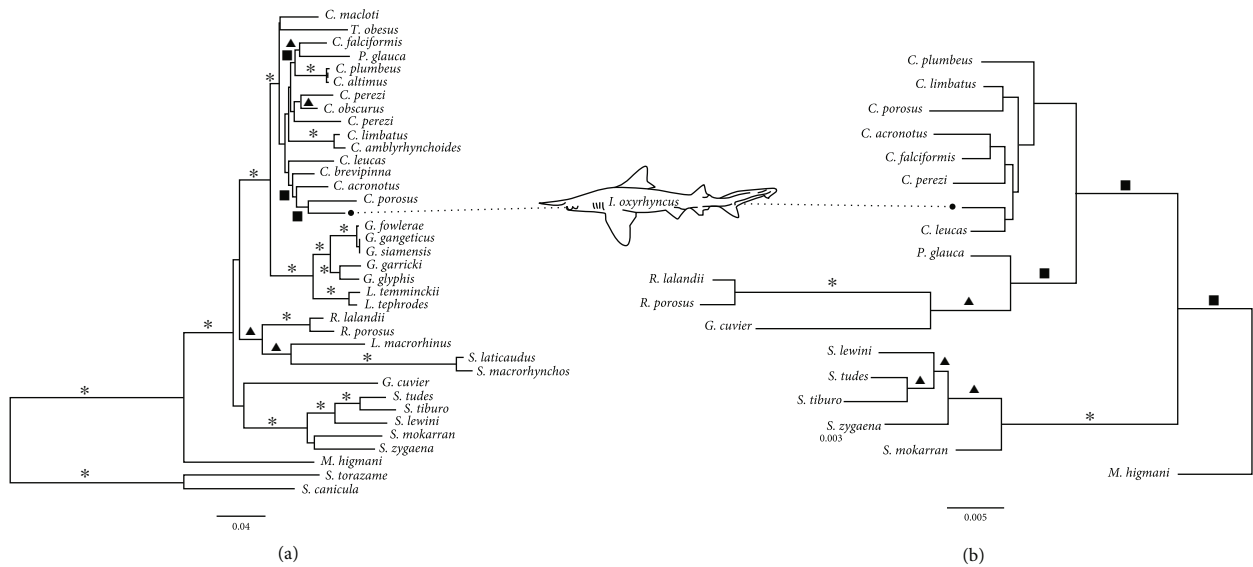(a)   (b)

FIGURE 2: Consensus trees showing the phylogenetic relationships of the species of the family Carcharhinidae, generated by the ML, NJ, MP, and BI methods, for (a) the mtDNA dataset (COI, ND2, and 12S-16S), based on the GTR+G(0.5093)+I(0.4665) nucleotide substitution model, and (b) RAG1 (based on the TN93+G(0.0963) model). The symbols represent three different levels of support: * = bootstrap > 90 %, posterior probability > 0.9; ▲ = bootstrap > 70%, posterior probability > 0.9; ■ = posterior probability > 0.7. The branches without symbols have support values of less than 70% (bootstrap) or 0.70 (posterior probability).
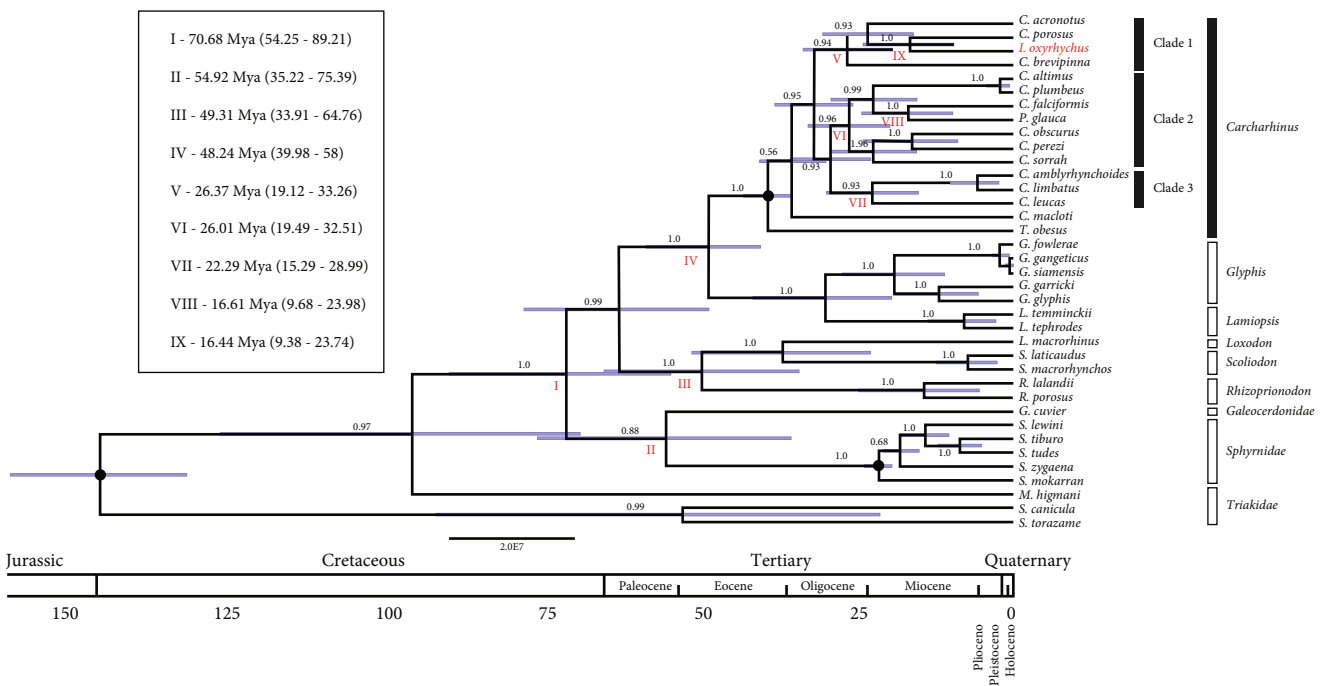

FIGURE 3: Consensus tree based on the mtDNA dataset showing the estimated divergence time of each ancestral node of the family Carcharhinidae, with the respective confidence limit (horizontal purple bars) and posterior probability support of each node. The insert shows the values recorded for each node marked with a Roman numeral. The calibration points are highlighted by black circles.

during the Eocene, around 49.31 mya (33.91–64.75 mya). Finally, there is a relatively weakly supported clade formed by *Galeocerdo* (Galeocerdonidae) and *Sphyrna* (Sphyrnidae) that appears as a sister group to the clade formed by the carcharhinid species, which separated toward the end of the Paleocene, approximately 54.92 mya (~35.22–75.39 mya). The estimated TMRCA for the Carcharhinidae+Galeocerdonidae+Sphyrnidae indicates that this group began to diversify in the late Cretaceous and early Paleocene, at around 70.68 mya (54.25–89.21 mya).

The subdivisions of *Carcharhinus* observed in the TMRCA analysis are also apparent in the phylogenetic inferences based on the mtDNA dataset (Figure 2(a)), albeit with no support, except for the *Carcharhinus+Prionace*

+*Triaenodon*+*Isogomphodon* clade (bootstrap > 70%, PP > 0.9). The genetic distances between these subclades were the same as those observed in the comparisons between *I. oxyrhynchus* and the *Carcharhinus* species (mtDNA: distP: 5.5–5.8%, distC: 5.9–6.2%; RAG1: distP and distC: 0.8–0.9%).

Overall, phylogenetic methods (21 trees representing NJ, ML, MP, BI, and TMRCA divergence time analyses) generated in the present study define a paraphyletic arrangement for the genus *Carcharhinus* in relation to what was previously classified as *I. oxyrhynchus* and *P. glauca* and possibly also *Triaenodon*. Given this molecular evidence, we officially recognize the previous combination *Carcharhinus oxyrhynchus* (vs. *I. oxyrhynchus*) and propose the new combination *Carcharhinus glaucus* (vs. *P. glauca*).

4. Discussion

4.1. Carcharhinus, Isogomphodon, and the Carcharhinidae. These results of this study reflect the long, controversial history of the taxonomic classification of *C. oxyrhynchus*, originally described as *Carcharias oxyrhynchus*, reassigned to *Isogomphodon* and then assigned as *Carcharhinus*, before Springer [35] and later studies resurrected the genus *Isogomphodon* (see [37]). Gill (1862) created the genus *Isogomphodon* to accommodate *I. oxyrhynchus. Isogomphodon maculipinnis* Poey, 1865, added subsequently, is now considered a synonym of *Carcharhinus brevipinna* [37]. Rodrigues-Filho et al. [4] raised the hypothesis that the daggernose shark was in fact a member of the genus *Carcharhinus*, based on a weakly supported phylogeny with low taxonomic coverage, a result of the fact that the study focused primarily on species identification rather than phylogenetic inference and did not make classification changes.

Compagno [37] proposed the allocation of tribes within the Carcharhinidae, in which case, *C. oxyrhynchus* would be assigned to the tribe Isogomphodontini, based on its unique morphological features. These differences led Garrick [38] to exclude *C. oxyrhynchus*, together with five other species, from a study that aimed to define the limits of *Carcharhinus* [38], based on the evidence of variables such as external morphology, morphometric and meristic parameters, and coloration. Garrick concluded that the use of these characteristics for the assessment of the systematics of this genus should be reconsidered, given that, despite their importance at the species level, they are inconclusive for the definition of subgeneric arrangements or inferences on the relationships between *Carcharhinus* and other, similar genera.

Carcharhinus oxyrhynchus is a demersal shark that inhabits shallow, muddy waters in coastal and estuarine areas, although few data are available on its basic biological characteristics [68]. This species nevertheless has a number of unique morphological features that distinguish it from all other carcharhinids, such as its pectoral fin to body size ratio, as well as its flattened and elongated snout, and the significantly reduced size of its eyes [37], which is probably associated with the muddy waters this shark inhabits, and its predation of benthic and nektonic organisms [37, 42]. The head and fins are also sexually dimorphic [69], which

may be associated with mating behavior patterns [70]. Silva [71] presented an anatomical description of *C. oxyrhynchus* based on an analysis of skeletal traits, including the dental series and morphology of the neurocranium, mandibular and brachial arches, claspers, fins, and the dermal denticles, which was used for systematic comparisons with other members of the family Carcharhinidae. Silva [71] initially compared *C. oxyrhynchus* with the fossil species attributed to the genus *Isogomphodon*, including *Isogomphodon acuarius* (Probst, 1879), *Isogomphodon lerichei* (Darterville and Casier, 1943), *Isogomphodon gracilis* (Jonet, 1966), *Isogomphodon caunellensis* ([65]), and *Isogomphodon aikenensis* (Cicimurri and Knight, 2019), affirming that only the fossil taxa *C. aikenensis* and *C. acuarius* should be maintained in *Isogomphondon* while other taxa were assigned to *Carcharhinus. I. aikenensis* and *I. acuarius* should therefore now also be recognized as *Carcharhinus aikenensis* n. comb. and *Carcharhinus acuarius* n. comb. Sorenson et al. [39] also found that *C. porosus* and *T. obesus* are the carcharhinid species that are most similar to *C. oxyrhynchus*. Although no exclusive similarities were found between *C. oxyrhynchus* and *C. porosus*, 26 (58%) of the 45 traits analyzed were highly similar, including the morphology of the lower teeth, which have an elongated crown, with narrow roots in the anterior rows [71]. The distinctive morphology of *C. oxyrhynchus* does not exclude this species from the genus *Carcharhinus*, however, given that the tree topology and genetic distances found in the present study emphatically support the inclusion of this species in *Carcharhinus*. The results are also consistent with previous findings of the paraphyletic arrangement of *Carcharhinus* considering *C. glaucus* [4, 10, 30, 31, 34, 37, 40, 41, 72], but this is the first time that it is recognized as a new combination and all fossil taxa in *Prionace* (*Prionace antiquus* (Agassiz, 1856), *Prionace egertoni* (Agassiz, 1843), and *Prionace tenuis* (Agassiz, 1843)) should also be reallocated to *Carcharhinus* or recognized as new combinations. The relatively large dataset employed in the present study, together with the robust phylogenetic approaches applied in the analyses, supports this conclusion. However, further research using more nuclear data and more complete taxon coverage will be needed to reevaluate the classification of *Triaenodon*, as well as the phylogenetic structure of the genus *Carcharhinus*.

The well-supported subdivisions of the genus *Carcharhinus* established in the TMRCA analysis are consistent with the findings of Springer [35, 73], Garrick [38], and Compagno [74]. Springer [35, 73] suggested the division of *Carcharhinus* into two groups of sharks, those with smooth backs and those with ridged backs. In the present study, the TMRCA estimates also support a division between the smooth-backed sharks (clade 1: *C. acronotus*, *C. brevipinna*, *C. porosus*, and *C. oxyrhynchus* and clade 3: *C. leucas*, *C. limbatus*, and *C. amblyrhynchoides*) and the ridge-backed forms (clade 2: *C. glaucus*, *C. falciformis*, *C. obscurus*, *C. plumbeus*, *C. perezi*, and *C. sorrah*). Naylor [75] referred to a monophyletic clade of large sharks with interdorsal dermal crests, which included *C. sorrah*, *C. longimanus*, *C. falciformis*, *C. plumbeus*, *C. altimus*, *C. perezi*, and *C. glaucus* (clade 2 in our study). The results of the present study further refine

this arrangement by recognizing two distinct clades (1 and 3) of smooth-backed sharks (Figure 3), of which, clade 3 is the more recent sister group of the ridge-backed shark clade (2). Garrick [38] and Compagno [74] suggested other groups within *Carcharhinus*, based on their morphological similarities, such as (i) *C. porosus, Carcharhinus dussumieri, Carcharhinus macloti, C. sorrah*, and *Carcharhinus sealei*; (ii) *Carcharhinus albimarginatus, Carcharhinus amblyrhynchos, C. perezi*, and *Carcharhinus wheeleri*; and (iii) *C. limbatus, C. amblyrhynchos*, and *C. brevipinna*. However, none of these arrangements were recognized by Naylor [75] or Lavery [49], and no evidence was found to support them in the present study. Naylor [75] argued that the morphological similarities found between the species of each group must be the result of convergent evolution and that there is a need for further studies of the phylogenetic structure of *Carcharhinus*. Future reclassifications based on these subdivisions are possible considering, but even with the full mitogenome datasets of Kousteni et al. [40] and Wang et al. [41], these arrangements are currently uncertain.

Based on an electrophoretic study of allozymes, Naylor [75] concluded that Carcharhinidae as described at the time was a paraphyletic group which included the hammerhead sharks of the genus *Sphyrna*, with *Galeocerdo* and *Rhizoprionodon* as the most basal genera of this family. Using DNA sequences, López et al. [33] reported paraphyly in the Carcharhinidae as classified at that time, showing marginal but consistent support for a clade corresponding to carcharhinids+sphyrnids to the exclusion of the Hemigaleidae+*Galeocerdo cuvier*, although only three carcharhinid species were included. However, these findings were corroborated by Naylor et al. [30] and Amaral et al. [31], who defined *Galeocerdo* as a basal group and a sister taxon to the Carcharhinidae+Sphyrnidae clade. Rodrigues-Filho et al. [4] also observed the phylogenetic proximity of *Galeocerdo* and *Sphyrna*, with *Rhizoprionodon* as the sister group of this clade. These authors highlighted the genetic divergence of *G. cuvier* and *Rhizoprionodon* from the other carcharhinid species included in the analyses and suggested that these two genera may represent distinct carcharhiniform families. In the present study, *Rhizoprionodon* was recovered as a more basal sister group of the clade formed by *Scoliodon* and *Loxodon*. Naylor et al. [30] obtained similar findings, recovering the same arrangement for these genera, but placing them all within the carcharhinid clade. Vélez-Zuazo and Agnarsson [10] recovered *Scoliodon* as a sister genus of *Rhizoprionodon*, although their study included no representatives of the genus *Loxodon*. Poey [76] allocated *Galeocerdo* in its own family Galeocerdonidae, based on morphology, and some of these (large eyes, very long lip folds, and large spiracles) and its ovoviviparous reproductive mode are not observed in more derived taxa [37, 75–79], demonstrating the considerable divergence from the Carcharhinidae. Despite Poey's allocation, *Galeocerdo* was until recently attributed to the Carcharhinidae, only recently being widely recognized as the only member of the Galeocerdonidae [76, 79]. This recent adoption of the use of the family Galeocerdonidae is strongly supported by the phylogenetic results of the present study.

4.2. Adaptations of the Daggernose Shark and Insights into the Speciation Process.

The TMRCA analysis indicates that *C. oxyrhynchus* diverged from its closest sister lineage in the analysis (*C. porosus*) during the Miocene, with a confidence interval ranging from approximately 9.38 to 23.74 mya. The geographic distribution of this species is closely associated with the area of the Amazon plume, which corresponds to more than 80% of its area of occurrence [16]. During the transition from the Oligocene to the Miocene, the proto-Amazon drained northward along the paleo-Orinoco basin to discharge into the Caribbean Sea near the present-day Lake Maracaibo, with an increase in the turbidity of the local coastal waters due to the intense deposition of sediments [80, 81]. Between the early and late Miocene, river drainage patterns in northern South America changed significantly [82], with increasingly large amounts of Andean sediments being deposited into the Atlantic Ocean from the mouth of the Amazon River [83].

The uplifting of the Andes during the Miocene (~10 mya) also contributed to the formation of the Amazon River, as well as increasing the outflow of the paleo-Orinoco River system towards the Caribbean, decreasing the transparency of the water [84]. The most recent evidence indicates the occurrence of three distinct phases of sediment deposition related to the formation of the Amazon plume: (i) relatively low deposition rates (~11.8–6.8 mya), (ii) increasing volume (~6.8–2.4 mya), and (iii) high deposition rates, from ~2.4 mya to the present day [82]. The Amazon River discharges approximately $6300\,km^3$ of water per year [85], creating a sediment-laden freshwater plume that extends approximately 200 km offshore from the mouth of the river, reaching the 30 m isobath in the middle sector of the continental shelf [86, 87]. This plume represents a soft barrier (the Amazon River Barrier) to the dispersal of many marine species [18, 88–91], which has been recently shown to have an indirect influence on elasmobranch speciation processes [92].

Compagno and Compagno et al. [37, 74, 93] and Ebert et al. [77] evaluated a total of 24 traits to support the status of *Isogomphodon* as a genus distinct from *Carcharhinus*. However, most of these characteristics were shared with *C. oxyrhynchus* with only six distinct traits: (1) snout acutely triangular or subtriangular in the dorsoventral view and very elongated (preoral length much greater than internarial space or the width of the mouth); (2) extremely small eyes that lack posterior notches; (3) the teeth are not strongly differentiated in either the upper or lower jaws, with anteroposterior narrow acute cusps, and no cusplets or proximal or distal blades; (4) teeth in the upper jaw with broad, flat cusps, and those in the lower jaw with slenderer cusps and smooth edges; (5) a total of 49–60/49–56 rows of teeth; and (6) broad and triangular pectoral fins, whose length from the origin to the free posterior tip is approximately 3/4 of that of the anterior pectoral margins.

These distinctive features of *C. oxyrhynchus* almost certainly represent adaptations to the conditions found in the Amazon plume, and Compagno [37] already proposed that the distinct characteristics of this species are the result of a process of adaptation to the turbid waters of the coastal and estuarine environments associated with the discharge

of the Amazon River. These adaptations include changes in the structure of the snout and an associated increase in the area of the Lorenzini ampullae that enhances its function, facilitating movement and feeding in turbid water [37]. The need to adapt to murky environments with poor visibility in northern South America would have favored the enhancement of the snout of *C. oxyrhynchus* to the detriment of its visual system, with this sensory, dental, and mandibular morphology favoring the predation of small prey [16, 42, 93].

4.3. Conservation of Carcharhinus oxyrhynchus. Given the importance of the role played by most elasmobranchs in the ecosystems they inhabit and increasing fishery pressures around the world, conservation efforts are urgently needed to ensure the protection of this prominent group of fishes. The principal threat to their survival is the progressive expansion of fishery operations. Sharks and rays started to attract attention from conservationists in the 1990s, when research institutions began to assess this fishery resource more systematically. In Brazil, there were two prominent initiatives during this period—the REVIZEE Program (Program for the Assessment of the Potential Sustainability of Resources in the Exclusive Economic Zone), created by the Ministry of the Environment in 1994 [94], and the establishment of the Brazilian Society for Elasmobranch Studies (SBEEL), founded in 1997, that is active in the promotion of the conservation of sharks and rays in Brazil [95].

The increasing evidence of the vulnerability of elasmobranchs led to the establishment, in 1998, of the International Action Plan for the Conservation and Management of Sharks (IPOA-SHARK), with the support of the United Nations Food and Agriculture Organization (FAO). During this same period, Brazil implemented its first federal antifinning legislation, which prohibited the removal of the fins of sharks and rays (the most expensive byproducts) without the subsequent utilization of the carcass. However, landing shark and ray catches with the fins still attached to the body only became mandatory in 2012 [96, 97]. Furthermore, the ability of *C. oxyrhynchus* to recover health after stressful interactions may result in greater survival risks compared to other Carcharhiniformes even if released alive after accidental capture [98].

The decline observed in Brazilian elasmobranch populations was considered to be an alert and provided an incentive for the implementation of the National Action Plan for the Conservation of Endangered Sharks and Marine Rays in Brazil (PAN-Tubarões), which was created by federal ordinance no. 575 of December 5th, 2014 [99–101]. This plan focuses on 12 species, including *C. oxyrhynchus*, with the support of technical advisory groups.

An associated initiative is the National Action Plan for the Conservation of Endangered and Socioeconomically Important Species in the Mangrove Ecosystem (PAN-Manguezal), which aims to protect the Brazilian mangroves, including the species contemplated by PAN-Tubarões (including *C. oxyrhynchus*), while respecting local traditions, which are reconciled with scientific knowledge. The PAN-Manguezal action plan encompasses the conservation of 74 elasmobranch species, 20 of which are threatened with extinction in Brazil, including *C. oxyrhynchus* [102].

Recently, the coastal and marine protected area (GEF-Mar) project was implemented to protect the biodiversity of marine and coastal areas from the impacts of bycatch. This project is aimed at identifying priority coastal areas in northern Brazil for both endangered species and artisanal fisheries and, in particular, the establishment of marine protected areas that can contribute to the recovery of the most threatened species, in particular, through the protection of nursery areas. This has led to the imposition of restrictions on fisheries in the estuaries of the states that make up the northern Brazil region [103].

Clearly, the strategies employed to ensure the conservation of Brazilian elasmobranchs, in particular, the most endangered species, such as the daggernose shark, will not be altered significantly in response to the present study, which refers specifically to a question of scientific nomenclature. It is nevertheless important to note that this species inhabits the shallow waters of the western Atlantic, in regions in which hot and rainy conditions predominate, where it prefers the turbid, brackish waters of estuaries dominated by mangroves and has a viviparous reproduction, late sexual maturity, and a biannual reproductive cycle [37, 104]. These characteristics, together with habitat loss and fishing pressure, combine to threaten the survival of the species intensely, reinforcing its classification as critically endangered by the IUCN [44].

Data Availability

The set of sequences used and analyzed in this study is available on the GenBank website, identified by the access codes listed in Table 1.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Authors' Contributions

Luis Fernando da Silva Rodrigues-Filho was responsible for the laboratory procedures, data analysis and interpretation, intellectual and methodological development, manuscript writing, and approval of the final version. Davidson Sodré was responsible for the sample acquisition, laboratory procedures, data analysis and interpretation, intellectual development, and manuscript revision. Paula da Costa Nogueira was responsible for the laboratory procedures and manuscript writing. José Rafael da Silva Leal was responsible for the laboratory procedures and manuscript writing. Jorge Luiz Silva Nunes was responsible for the data interpretation and manuscript revision. Getulio Rincon was responsible for the analysis and interpretation of data, intellectual and methodological development, and writing and revision of the manuscript. Rosangela Paula T. Lessa was responsible for the data interpretation and manuscript writing and revision. Iracilda Sampaio was responsible for the data interpretation and writing and revision of the manuscript. Marcelo

Supplementary Materials

Supplementary 1. Figure S1: plots of the number of transitions and transversions versus the divergence found in the RAG and mtDNA datasets, used to determine saturation levels.

Supplementary 2. Figure S2: phylogenetic inference, based on the maximum likelihood (ML) approach, for each mitochondrial locus independently, with the respective bootstrap values. The evolutionary models used for the different mitochondrial loci were (a) COI: HKY+G(1.0428)+I(0.6049), (b) 12S-16S: GTR+G(0.4122)+I(0.3388), and (c) ND4: TN93+G(1.1641)+I(0.5130). Only the bootstrap values of over 50% are presented in the plots.

Supplementary 3. Figure S3: phylogenetic inference, based on the neighbor joining (NJ) approach, for each mitochondrial locus independently, with the respective bootstrap values. The evolutionary models used for the different mitochondrial loci were (a) COI: HKY+G(1.0428)+I(0.6049), (b) 12S-16S: GTR+G(0.4122)+I(0.3388), and (c) ND4: TN93+G(1.1641)+I(0.5130). Only the bootstrap values of over 50% are presented in the plots.

Supplementary 4. Figure S4: phylogenetic inference, based on the Bayesian inference (BI) approach, for each mitochondrial locus independently, with the respective bootstrap values. The evolutionary models used for the different mitochondrial loci were (a) COI: HKY+G(1.0428)+I(0.6049), (b) 12S-16S: GTR+G(0.4122)+I(0.3388), and (c) ND4: TN93+G(1.1641)+I(0.5130). Only the bootstrap values of over 50% are presented in the plots.

Supplementary 5. Figure S5: phylogenetic inference, based on the maximum parsimony (MP) approach, for each mitochondrial locus independently, with the respective bootstrap values. Only the bootstrap values of over 50% are presented in the plots.

Supplementary 6. Figure S6: phylogenetic inferences from the mtDNA dataset, with the respective bootstrap and posterior probability values. The GTR+G(0.5093)+I(0.4665) nucleotide substitution model was used for the maximum likelihood (ML), neighbor joining (NJ), maximum parsimony (MP), and Bayesian inference (BI) approaches. Only the bootstrap values of over 50% are presented in the plots.

Supplementary 7. Figure S7: phylogenetic inferences from the RAG1 dataset, with the respective bootstrap and posterior probability values. The TN93+G(0.0963) nucleotide substitution model was used for the maximum likelihood (ML), neighbor joining (NJ), maximum parsimony (MP), and Bayesian inference (BI) approaches. Only the bootstrap values of over 50% are presented in the plots.

Supplementary 8. Table S1: genetic distance (%) matrix for the species of the family Carcharhinidae based on the mtDNA dataset. The *p* distances are presented below the diagonal, while the corrected distances (GTR+G(0.5093)+I(0.4665)) are shown above the diagonal, in bold script.

Supplementary 9. Table S2: genetic distance (%) matrix for the species of the family Carcharhinidae based on the RAG1 dataset. The *p* distances are presented below the diagonal, while the corrected distances (TN93+G(0.0963)) are shown above the diagonal, in bold script.

References

[1] K. A. Dunn and J. F. Morrissey, "Molecular phylogeny of elasmobranchs," *Copeia*, vol. 1995, no. 3, pp. 526–531, 1995.

[2] C. J. Winchell, A. P. Martin, and J. Mallatt, "Phylogeny of elasmobranchs based on LSU and SSU ribosomal RNA genes," *Molecular Phylogenetics and Evolution*, vol. 31, no. 1, pp. 214–224, 2004.

[3] G. J. P. Naylor, J. A. Ryburn, O. Fedrigo, and A. Lopez, "Phylogenetic relationships among the major lineages of modern elasmobranchs," *Reproductive biology and phylogeny*, vol. 3, no. 1, p. 25, 2005.

[4] L. F. Rodrigues-Filho, T. C. Rocha, P. S. Rêgo, H. Schneider, I. Sampaio, and M. Vallinoto, "Identification and phylogenetic inferences on stocks of sharks affected by the fishing industry off the northern coast of Brazil," *Genetics and Molecular Biology*, vol. 32, no. 2, pp. 405–413, 2009.

[5] C. J. Douady, M. Dosay, M. S. Shivji, and M. J. Stanhope, "Molecular phylogenetic evidence refuting the hypothesis of Batoidea (rays and skates) as derived sharks," *Molecular Phylogenetics and Evolution*, vol. 26, no. 2, pp. 215–221, 2003.

[6] P. R. Last, G. J. P. Naylor, and B. M. Manjaji-Matsumoto, "A revised classification of the family Dasyatidae (Chondrichthyes: Myliobatiformes) based on new morphological and molecular insights," *Zootaxa*, vol. 4139, no. 3, pp. 345–368, 2016.

[7] W. T. White and G. J. P. Naylor, "Resurrection of the family Aetobatidae (Myliobatiformes) for the pelagic eagle rays, genus Aetobatus," *Zootaxa*, vol. 4139, no. 3, pp. 435–438, 2016.

[8] J. B. L. Sales, C. N. de Oliveira, W. C. R. dos Santos et al., "Phylogeography of eagle rays of the genus Aetobatus: Aetobatus narinari is restricted to the continental western Atlantic Ocean," *Hydrobiologia*, vol. 836, no. 1, pp. 169–183, 2019.

[9] F. F. Petean, G. J. Naylor, and S. M. Lima, "Integrative taxonomy identifies a new stingray species of the genus Hypanus Rafinesque, 1818 (Dasyatidae, Myliobatiformes), from the tropical southwestern Atlantic," *Journal of Fish Biology*, vol. 97, no. 4, pp. 1120–1142, 2020.

[10] X. Vélez-Zuazo and I. Agnarsson, "Shark tales: a molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes)," *Molecular Phylogenetics and Evolution*, vol. 58, no. 2, pp. 207–217, 2011.

[11] T. Bertozzi, M. S. Y. Lee, and S. C. Donnellan, "Stingray diversification across the end-Cretaceous extinctions," *Memoirs of Museum Victoria*, vol. 74, pp. 379–390, 2016.

[12] E. Villalobos-Segura and C. J. Underwood, "Radiation and divergence times of Batoidea," *Journal of Vertebrate Paleontology*, vol. 40, no. 3, article e1777147, 2020.

[13] S. J. Jorgensen, F. Micheli, T. D. White et al., "Emergent research and priorities for shark and ray conservation," *Endangered Species Research*, vol. 47, pp. 171–203, 2022.

[14] L. N. Davidson and N. K. Dulvy, "Global marine protected areas to prevent extinctions," *Nature ecology & evolution*, vol. 1, no. 2, pp. 1–5, 2017.

[15] R. Lessa, V. S. Batista, and F. M. Santana, "Close to extinction? The collapse of the endemic daggernose shark (Isogomphodon oxyrhynchus) off Brazil," *Global Ecology and Conservation*, vol. 7, pp. 70–81, 2016.

[16] L. M. Feitosa, A. P. B. Martins, R. P. T. Lessa, R. Barbieri, and J. L. S. Nunes, "Daggernose shark: an elusive species from northern South America," *Fisheries*, vol. 44, pp. 144–147, 2019.

[17] M. Hirschfeld, C. Dudgeon, M. Sheaves, A. Barnett, and A. MacNeil, "Barriers in a sea of elasmobranchs: from fishing for populations to testing hypotheses in population genetics," *Global Ecology and Biogeography*, vol. 30, no. 11, pp. 2147–2163, 2021.

[18] S. R. Floetter, L. A. Rocha, D. R. Robertson et al., "Atlantic reef fish biogeography and evolution," *Journal of Biogeography*, vol. 35, pp. 22–47, 2007.

[19] A. O'Dea, H. A. Lessios, A. G. Coates et al., "Formation of the Isthmus of Panama," *Science Advances*, vol. 2, no. 8, article e1600883, 2016.

[20] P. F. Cowman and D. R. Bellwood, "The historical biogeography of coral reef fishes: global patterns of origination and dispersal," *Journal of Biogeography*, vol. 40, no. 2, pp. 209–224, 2013.

[21] B. W. Bowen, Z. H. Forsman, J. L. Whitney et al., "Species radiations in the sea: what the flock?," *Journal of Heredity*, vol. 111, no. 1, pp. 70–83, 2020.

[22] P. R. Teske, S. Von der Heyden, C. D. McQuaid, and N. P. Barker, "A review of marine phylogeography in southern Africa," *South African Journal of Science*, vol. 107, no. 5/6, pp. 1–11, 2011.

[23] B. W. Bowen, L. A. Rocha, R. J. Toonen, and S. A. Karl, "The origins of tropical marine biodiversity," *Trends in Ecology & Evolution*, vol. 28, no. 6, pp. 359–366, 2013.

[24] M. Poortvliet, J. L. Olsen, D. A. Croll et al., "A dated molecular phylogeny of manta and devil rays (Mobulidae) based on mitogenome and nuclear sequences," *Molecular Phylogenetics and Evolution*, vol. 83, pp. 72–85, 2015.

[25] R. R. Domingues, A. W. Hilsdorf, M. M. Shivji, F. V. Hazin, and O. B. Gadig, "Effects of the Pleistocene on the mitochondrial population genetic structure and demographic history of the silky shark (Carcharhinus falciformis) in the western Atlantic Ocean," *Reviews in Fish Biology and Fisheries*, vol. 28, no. 1, pp. 213–227, 2018.

[26] B. C. Souza, V. P. Cruz, T. R. Almeida et al., "Genetic diversity assessment for the vulnerable migratory cownose ray Rhinoptera bonasus (Myliobatiformes: Rhinopteridae) from the southwestern Atlantic Ocean," *Neotropical Ichthyology*, vol. 19, no. 4, 2021.

[27] K. I. Flowers, M. J. Ajemian, K. Bassos-Hull et al., "A review of batoid philopatry, with implications for future research and population management," *Marine Ecology Progress Series*, vol. 562, pp. 251–261, 2016.

[28] J. Sandoval-Castillo and A. Rocha-Olivares, "Deep mitochondrial divergence in Baja California populations of an aquilopelagic elasmobranch: the golden cownose ray," *Journal of Heredity*, vol. 102, no. 3, pp. 269–274, 2011.

[29] D. S. Portnoy, C. M. Hollenbeck, C. N. Belcher et al., "Contemporary population structure and post-glacial genetic demography in a migratory marine species, the blacknose shark, Carcharhinus acronotus," *Molecular Ecology*, vol. 23, no. 22, pp. 5480–5495, 2014.

[30] G. Naylor, J. Caira, K. Jensen, K. Rosana, N. Straube, and C. Lakner, "Elasmobranch phylogeny: a mitochondrial estimate based on 595 species," in *Biology of Sharks and their Relatives*, J. C. Carrier, J. A. Musick, and M. R. Heithaus, Eds., pp. 31–56, Taylor & Francis, Boca Raton, 2nd edition, 2012.

[31] C. R. L. Amaral, F. Pereira, D. A. Silva, A. Amorim, and E. F. de Carvalho, "The mitogenomic phylogeny of the Elasmobranchii (Chondrichthyes). Mitochondrial DNA part A DNA mapping," *Sequential Analysis*, vol. 29, pp. 867–878, 2018.

[32] S. Johri, J. Solanki, V. A. Cantu et al., "'Genome skimming' with the MinION hand-held sequencer identifies CITES-listed shark species in India's exports market," *Scientific Reports*, vol. 9, no. 1, p. 4476, 2019.

[33] J. A. López, J. A. Ryburn, O. Fedrigo, and G. J. P. Naylor, "Phylogeny of sharks of the family Triakidae (Carcharhiniformes) and its implications for the evolution of carcharhiniform placental viviparity," *Molecular Phylogenetics and Evolution*, vol. 40, no. 1, pp. 50–60, 2006.

[34] M. Dosay-Akbulut, "La phylogenie a l'interieur du genre Carcharhinus," *Comptes Rendus Biologies*, vol. 331, no. 7, pp. 500–509, 2008.

[35] Springer, "A revision of North American sharks allied to the genus Carcharhinus," *American Museum Novitates*, vol. 1451, pp. 1–13, 1950.

[36] H. B. Bigelow and W. C. Schroeder, "Sharks in," in *Fishes of the Western North Atlantic*, J. Tee-Van, C. M. Breder, S. F. Hildebrand, A. E. Parr, and W. C. Schroeder, Eds., pp. 59–546, Yale University: Sears Foundation for Marine Research, New Haven, 1948.

[37] L. Compagno, *FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO series*, FAO, Rome, 1984.

[38] J. A. F. Garrick, *Sharks of the genus Carcharhinus*, vol. 445, NOAA Technical Report NMFS Circular, 1982.

[39] L. Sorenson, F. Santini, and M. E. Alfaro, "The effect of habitat on modern shark diversification," *Journal of Evolutionary Biology*, vol. 27, no. 8, pp. 1536–1548, 2014.

[40] V. Kousteni, S. Mazzoleni, K. Vasileiadou, and M. Rovatsos, "Complete mitochondrial DNA genome of nine species of sharks and rays and their phylogenetic placement among modern elasmobranchs," *Genes*, vol. 12, no. 3, p. 324, 2021.

[41] C. Wang, T. Lai, P. Ye et al., "Novel duplication remnant in the first complete mitogenome of Hemitriakis japanica and the unique phylogenetic position of family Triakidae," *Gene*, vol. 820, no. 8, p. 146232, 2022.

[42] R. Stride, V. Batista, and L. A. B. Raposo, *Pesca experimental de tubarão com redes de emalhar no litoral maranhense*, CORSUP/EDUFMA, São Luís, Brazil, 1992.

[43] G. A. Casselberry and J. K. Carlson, *Endangered species act status review of the argentine angel shark (Squatina argentina). Report to the National Marine Fisheries Service, Office of Protected Resources*, National Oceanic and Atmospheric Administration (NOAA), Panama City, Florida, 2015.

[44] R. Pollom, P. Charvet, V. Faria et al., *Isogomphodon oxyrhynchus. The IUCN red list of threatened species 2020: e.T60218A3094144*, IUCN, 2020.

[45] R. Lessa, F. M. Santana, and P. Duarte-Neto, "A critical appraisal of marginal increment analysis for assessing temporal periodicity in band formation among tropical sharks," *Environmental Biology of Fishes*, vol. 77, no. 3-4, pp. 309–315, 2006.

[46] L. M. Feitosa, A. P. B. Martins, T. Giarrizzo et al., "DNA-based identification reveals illegal trade of threatened shark species in a global elasmobranch conservation hotspot," *Scientific Reports*, vol. 8, no. 1, p. 3347, 2018.

[47] A. C. Z. Amaral and S. Jablonski, "Conservação da biodiversidade marinha e costeira no Brasil," in *MEGADIVERSIDADE*, J. M. C. Silva and M. Fonseca, Eds., pp. 43–51, Brasília, DF, Brasil, 1st edition, 2005.

[48] V. J. Isaac and R. B. Barthem, "Os recursos pesqueiros da Amazônia Brasileira," *Boletim do Museu Paraense Emílio Goeldi*, vol. 11, pp. 151–194, 1995.

[49] S. Lavery, "Electrophoretic analysis of phylogenetic relationships among Australian Carcharhinid sharks," *Australian Journal of Marine and Freshwater Research*, vol. 43, no. 1, pp. 97–108, 1992.

[50] R. D. Ward, T. S. Zemlak, B. H. Innes, P. R. Last, and P. D. N. Hebert, "DNA barcoding Australia's fish species," *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 360, no. 1462, pp. 1847–1857, 2005.

[51] T. W. Greig, M. K. Moore, C. M. Woodley, and J. M. Quattro, "Mitochondrial gene sequences useful for species identification of western North Atlantic Ocean sharks," *Fishery Bulletin*, vol. 103, pp. 516–523, 2005.

[52] I. S. Dun and F. R. Blattner, "Charons 36 to 40: multi enzyone, high capacity, recombination deficient replacement vectors with polylinkers and ploystuffers," *Nucleic Acids Research*, vol. 15, no. 6, pp. 2677–2698, 1987.

[53] J. D. Thompson, T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins, "The CLUSTAL X windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools," *Nucleic Acids Research*, vol. 25, no. 24, pp. 4876–4882, 1997.

[54] T. A. Hall, "Bio Edit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT," *Nucleic acids symposium series*, vol. 41, pp. 95–98, 1999.

[55] G. Talavera and J. Castresana, "Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments," *Systematic Biology*, vol. 56, no. 4, pp. 564–577, 2007.

[56] J. Castresana, "Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis," *Molecular Biology and Evolution*, vol. 17, no. 4, pp. 540–552, 2000.

[57] S. Kumar, G. Stecher, M. Li, C. Knyaz, and K. Tamura, "MEGA X: molecular evolutionary genetics analysis across computing platforms," *Molecular Biology and Evolution*, vol. 35, no. 6, pp. 1547–1549, 2018.

[58] X. Xia, "DAMBE7: new and improved tools for data analysis in molecular biology and evolution," *Molecular Biology and Evolution*, vol. 35, no. 6, pp. 1550–1552, 2018.

[59] S. Guindon, J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel, "New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0," *Systematic Biology*, vol. 59, no. 3, pp. 307–321, 2010.

[60] F. Ronquist, M. Teslenko, P. Van Der Mark et al., "MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space," *Systematic Biology*, vol. 61, no. 3, pp. 539–542, 2012.

[61] J. Felsenstein, "Confidence limits on phylogenies: an approach using the bootstrap," *Evolution*, vol. 39, no. 4, pp. 783–791, 1985.

[62] A. Rambaut, A. Drummond, D. Xie, G. Baele, and M. Suchard, "Posterior summarization in Bayesian phylogenetics using Tracer 1.7," *Systematic Biology*, vol. 67, no. 5, pp. 901–904, 2018.

[63] R. Bouckaert, T. G. Vaughan, J. Barido-Sottani et al., "BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis," *PLoS Computational Biology*, vol. 15, no. 4, pp. 1–28, 2019.

[64] A. J. Drummond, S. Y. W. Ho, M. J. Phillips, and A. Rambaut, "Relaxed phylogenetics and dating with confidence," *PLoS Biology*, vol. 4, no. 5, pp. e88–710, 2006.

[65] H. Cappetta, "Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii," in *Handbook of Paleoichthyology*, H. P. Shultze, Ed., pp. 474-475, Verlag, Munich, 3rd edition, 1988.

[66] A. P. Martin, "Mitochondrial DNA sequence evolution in sharks: rates, patterns and phylogenetic inferences," *Molecular Biology and Evolution*, vol. 12, pp. 1114–1123, 1995.

[67] A. Rambaut and A. J. Drummond, "TreeAnnotator v1.7.0. Available as part of the Beast package," 2013, http://beast.bio.ed.ac.uk.

[68] R. P. Lessa, "Sinopse dos estudos sobre elasmobrânquios da costa do Maranhão," *Boletim do Laboratório de Hidrobiologia*, vol. 10, pp. 19–36, 1997.

[69] A. P. B. Martins, F. E. da Silva, L. Manir Feitosa, L. P. Nunes e Silva, Z. da Silva de Almeida, and J. L. Silva Nunes, "Sexual dimorphism of sharks from the Amazonian equatorial coast," *Universitas Scientiarum*, vol. 20, pp. 297–304, 2015.

[70] N. Crooks and C. P. Waring, "Sexual dimorphisms in the dermal structure of the lesser-spotted catshark, Scyliorhinus canicula (Linnaeus, 1758)," *Acta Zoologica*, vol. 94, no. 3, pp. 331–334, 2013.

[71] A. L. O. Silva, *Skeletal anatomical description of Isogomphodon oxyrhynchus (Müller & Henle, 1839) and discussion of its phylogenetic position within Carcharhinidae (Chondrichthyes, Carcharhiniformes)*, Masters Thesis, Museu Zoologia da Universidade de São Paulo, 2021.

[72] A. P. Martin, G. J. P. Naylor, and S. R. Palumbi, "Rates of mitochondrial DNA evolution in sharks are slow compared with mammals," *Nature*, vol. 357, no. 6374, pp. 153–155, 1992.

[73] Springer, "Correction for "A revision of North American sharks allied to the genus Carcharhinus"," *Copeia*, vol. 1951, pp. 1–244, 1951.

[74] L. J. V. Compagno, *Sharks of the Order Carcharhiniformes*, Princeton University Press, New Jersey, 1988.

[75] G. J. Naylor, "The phylogenetic relationships among requiem and hammerhead sharks: inferring phylogeny when thousands of equally most parsimonious trees result," *Cladistics*, vol. 8, no. 4, pp. 295–318, 1992.

[76] F. Poey, "Enumeratio piscium cubensium," *Anales de la Sociedad Española de Historia Natural*, vol. 4, pp. 75–161, 1875.

[77] D. A. Ebert, S. P. Wintner, and P. M. Kyne, "An annotated checklist of the chondrichthyans of South Africa," *Zootaxa*, vol. 4947, no. 1, pp. 1–127, 2021.

[78] W. T. White, L. Baje, B. Salub, S. A. Appleyard, J. J. Pogonoski, and R. R. Mana, "Sharks and rays of Papua New Guinea," in *ACIAR Monograph, 189*, p. 377, Canberra, Australian center for International Agricultural research, 2018.

[79] P. C. Heemstra, E. Heemstra, D. A. Ebert, W. Holleman, and J. E. Randal, *Coastal Fishes of the Western Indian Ocean*, South African Institute for Aquatic Biodiversity, South Africa, 2022.

[80] C. Hoorn, F. P. Wesselingh, J. Hovikoski, and J. Guerrero, "The Development of the Amazonian Mega-Wetland (Miocene; Brazil, Colombia, Peru, Bolivia)," in *Amazonia, Landscape and Species Evolution: A Look into the Past*, C. Hoorn and F. Wesselingh, Eds., p. 1230, Blackwell, New York, 1st edition, 2010.

[81] E. G. Leigh, A. O'Dea, and G. J. Vermeij, "Historical biogeography of the Isthmus of Panama," *Biological Reviews*, vol. 89, no. 1, pp. 148–172, 2014.

[82] J. Figueiredo, C. Hoorn, P. Van der Ven, and E. Soares, "Late Miocene onset of the Amazon River and the Amazon deepsea fan: evidence from the Foz do Amazonas Basin," *Geology*, vol. 37, no. 7, pp. 619–622, 2009.

[83] C. M. Hoorn, G. R. Bogotá-A, M. Romero-Baez et al., "The Amazon at sea: onset and stages of the Amazon River from a marine record, with special reference to Neogene plant turnover in the drainage basin," *Global and Planetary Change*, vol. 153, pp. 51–65, 2017.

[84] C. Hoorn, J. Guerrero, G. A. Sarmiento, and M. A. Lorente, "Andean tectonics as a cause for changing drainage patterns in Miocene northern South America," *Geology*, vol. 23, no. 3, pp. 237–240, 1995.

[85] J. D. Milliman and R. H. Meade, "World-wide delivery of river sediment to the oceans," *Journal of Geology*, vol. 91, no. 1, pp. 1–21, 1983.

[86] C. A. Nittrouer and D. J. DeMaster, "Sedimentary processes on the Amazon continental shelf: past, present and future research," *Continental Shelf Research*, vol. 6, no. 1-2, pp. 5–30, 1986.

[87] S. Masson and P. Delecluse, "Influence of the Amazon River runoff on the tropical Atlantic," *Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere*, vol. 26, no. 2, pp. 137–142, 2001.

[88] O. J. Luiz, J. S. Madin, D. Ross Robertson, L. A. Rocha, P. Wirtz, and S. R. Floeter, "Ecological traits influencing range expansion across large oceanic dispersal barriers: insights from tropical Atlantic reef fishes," *Proceedings of the Royal Society B: Biological Sciences*, vol. 279, no. 1730, pp. 1033–1040, 2012.

[89] J. L. Tourinho, A. M. Solé-Cava, and C. Lazoski, "Cryptic species within the commercially most important lobster in the tropical Atlantic, the spiny lobster Panulirus argus," *Marine Biology*, vol. 159, no. 9, pp. 1897–1906, 2012.

[90] J. T. Boehm, L. Woodall, P. R. Teske et al., "Marine dispersal and barriers drive Atlantic seahorse diversification," *Journal of Biogeography*, vol. 40, no. 10, pp. 1839–1849, 2013.

[91] I. Cord, L. T. Nunes, C. X. Barroso et al., "Brazilian marine biogeography: a multi-taxa approach for outlining sectorization," *Marine Biology*, vol. 169, no. 5, pp. 1–13, 2022.

[92] J. P. Fontenelle, F. Portella Luna Marques, M. A. Kolmann, and N. R. Lovejoy, "Biogeography of the Neotropical freshwater stingrays (Myliobatiformes: Potamotrygoninae) reveals effects of continent-scale paleogeographic change and drainage evolution," *Journal of Biogeography*, vol. 48, no. 6, pp. 1406–1419, 2021.

[93] L. Compagno, M. Dando, and S. Fowler, *Sharks of the World*, Princeton University Press, New Jersey, 2005.

[94] REVIZEE, *DECRETO No 1.203, DE 28 DE JULHO DE 1994*, 2020, April 2021, http://www.planalto.gov.br/ccivil_03/decreto/1990-1994/D1203.htm.

[95] SBEEL, "Sociedade Brasileira para estudos de elasmobrânquios," 2020, April 2021, http://www.sbeel.org.br.

[96] ICMBIO, *Instrução Normativa Interministerial Mpa/Mma N° 14, De 26 De Novembro De 2012*, 2012, April 2021, https://www.icmbio.gov.br/cepsul/images/stories/legislacao/Instrucao_normativa/2012/in_inter_mpa_mma_14_2012_normasprocedimentoscapturatubaroes_raias.pdf..

[97] FAO, *iSharkFin | International Plan of Action for Conservation and Management of Sharks | Food and Agriculture Organization of the United Nations*, 2020, April 2021, http://www.fao.org/ipoa-sharks/en/.

[98] N. Wosnick, A. P. Chaves, H. N. Dias, A. R. O. P. Nunes, J. L. S. Nunes, and R. A. Hauser-Davis, "Assessment of the physiological vulnerability of the endemic and critically endangered Daggernose shark: a comparative approach to other Carcharhiniformes," *Frontiers in Marine Science*, vol. 10, p. 1116470, 2023.

[99] ICMBIO, *Plano de ação nacional para a conservação dos cervídeos ameaçados de Extinção. Brasília: Instituto Chico Mendes de Conservação da Biodiversidade*, 2020, April 2021, https://www.icmbio.gov.br/portal/faunabrasileira/plano-de-acao-nacional-lista/2839-plano-de-acao-nacional-para-a-conservacao-dos-tubaroes.

[100] ICMBIO, *PORTARIA N° 125, DE 04 DE DEZEMBRO DE 2014*, 2014, April 2021, https://www.icmbio.gov.br/portal/images/stories/docs-pan/pan-tubaroes/1-ciclo/pan-tubaroes-portaria-aprovacao.pdf.

[101] ICMBIO, *PORTARIA N° 575, DE 05 DE DEZEMBRO DE 2014*, 2014, April 2021, http://extwprlegs1.fao.org/docs/pdf/bra148925.pdf.

[102] ICMBIO, *PORTARIA ICMBIO N° 09, DE 29 DE JANEIRO DE 2015*, 2015, April 2021, https://www1.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2015/p_icmbio_09_2015_aprova_pan_manguezais.pdf.

[103] M. L. Ruffino, "Identificação e caracterização das áreas rele-
        vantes para a pesca artesanal e das principais interações
        com espécies da megafauna marinha sensíveis biologica-
        mente na região norte (AP, PA, MA e PI)," 2018, MMA,
        Brasília.

[104] R. Lessa, F. M. Santana, V. Batista, and Z. Almeida, "Age and
        growth of the daggernose shark, Isogomphodon oxyrhyn-
        chus, from northern Brazil," *Marine and Freshwater
        Research*, vol. 51, no. 4, pp. 339–347, 2000.