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A Review of the Mitogenomic Phylogeny of the Chondrichthyes

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Abstract

The phylogenetic analysis of the Chondrichthyes has been the subject of intense debate over the past two decades. The principal relationships within the group based on the analysis of morphological traits are inconsistent with the available molecular topologies, and the phylogeny of these animals is highly controversial, at all levels, ranging from superorders to families and even the genera within families. With the recent development of new generation sequencing (NGS), many phylogenies are now being inferred based on the complete genome of the species. In 2015 and 2016 alone, around 21 new elasmobranch genomes were made available in GenBank. In this context, the principal objective of the present study was to infer the phylogeny of the sharks and rays based on the complete mitochondrial genomes available in the literature. A total of 73 mitogenomes of chondrichthyan species were analyzed. The phylogenetic trees generated rejected the “Hypnosqualea” hypothesis and confirmed the monophyly of the Neoselachii and Batoidea as sister groups of the sharks. These mitogenomic analyses provided ampler and more complete insights into the relationships between the sharks and rays, in particular, the topologies obtained by the analyses revealed a number of incongruities in certain groups of sharks and rays, and the interrelationships between them.

Keywords: phylogeny, Chondrichthyes, mitogenomic, sharks and rays

1. Introduction

The Chondrichthyes (sharks, rays, and chimeras) are a diverse group of animals that occupy a key position in the phylogeny of the vertebrates, as one of their most ancient lineages

[1, 2]. Estimates of the diversification of the group based on DNA sequences are of the order of 300–460 million years ago. The class Chondrichthyes currently includes 14 orders and 60 families with approximately 1200 species [3–5]. The group of chondrichthyans with the greatest species diversity is the Batoidea (approximately 494 species), followed by the sharks, with around 500 species [4, 5]. The systematics of the Chondrichthyes have been the subject of considerable debate over the past two decades, and the phylogeny of these animals is still controversial, at all levels, ranging from superorders to families and even the genera within families [6].

Most of the hypotheses on the phylogenetic relationships among chondrichthyan species are based on morphological traits, in particular, the “Hypnosqualea” hypothesis [7, 8], which proposes that the batoids are derived sharks related intimately to the sawfish and angel sharks. However, most molecular phylogenies have rejected the “Hypnosqualea” hypothesis emphatically [3, 9–11].

A large number of morphological hypotheses have also been proposed to account for the arrangement of the shark orders, such as Ref. [12], which grouped the Squalomorphii and Squatinomorphii together, based on the synapomorphic nature of the orthostatic suspension of the maxilla within the ocular orbit, with the sharks of this clade being referred to as the “orthopedic” forms. In the case of the Galeomorphii and Squalimorphii, a number of studies, both molecular and morphological, have revealed a variety of controversial relationships within each group, and even the relationships among the orders vary between studies. One major example is the position of the Heterodontiformes, which has yet to be resolved [3, 7, 9, 10, 13, 14].

One other unresolved question is the phylogenetic position of the orders within the Galeomorphii, in which the available morphological inferences place Lamniformes as the sister order of the Carcharhiniformes [7, 15], although molecular studies have confirmed that the Orectolobiformes is the sister group of the Carcharhiniformes [13]. The topologies generated in other studies have nevertheless placed Lamniformes as the sister order of the Carcharhiniformes. On a more basal taxonomic level, there is even less agreement among the studies, and the taxonomic status of many Carcharhiniformes families is still unclear, such as the paraphyletism of the hammerhead sharks (*Sphyrna*) [14, 16, 17].

Another important question is the evidence of extensive paraphyly between the families of the Carcharhiniformes. Winchell et al. [18] concluded that the Scyliorhinidae is paraphyletic, a hypothesis confirmed by Refs. [12, 19]. Based on nuclear and mitochondrial sequences, these authors also proposed that the family Triakidae is paraphyletic, an arrangement confirmed by Ref. [20] based on a number of mitochondrial markers and the nuclear RAG1 gene, which contradicts the hypothesis of monophyly for the Triakidae. Similarly, the relationships among the members of the Batoidea remain unclear [15, 21–23]. In general, for example, four groups are recognized, the stingrays (*Myliobatiformes*), electric rays (*Torpediniformes*), sawfish (*Pristiformes*), skates, and guitarfish (*Rajiformes*), although the relationships among these groups are still undefined [21–25]. In addition, a number of new species of ray have been described recently, and the radiation patterns of this group have been better identified [25–29].

The most recent molecular analyzed the complete mitochondrial genomes of 48 elasmobranch species, and rejected the “Hypnosqualea” hypothesis. The authors of this study recuperated the monophyly of the Lamnidae, with the families arranged as (Mitsukurinidae (Alopiidae, Megachasmidae) (Odontaspidae (Cetorhinidae (Lamnidae))) [6]. It is important to note that most chondrichthyan topologies are based on DNA sequences from only a few markers, such as a single nuclear or mitochondrial gene, or a combination of these two genes, and the sequences rarely exceed a length of 6 kb [3, 9–11], except for Ref. [6]. More recently, however, improvements in the speed and accuracy of new generation sequencing (NGS), and the reduction of laboratory costs, have provided a large number of molecular markers, amplifying considerably the analytical perspectives in the fields of phylogenetic and phylogenetic research, and the potential for the study of molecular ecology in a wide range of organisms [30–32]. In 2015 and 2016 alone, around 21 new elasmobranch genomes were made available in GenBank.

Mitochondrial markers are widely used in phylogenetic analyses in a diversity of organisms due to the relatively simple sequencing procedures and the high rates of nucleotide substitution [33]. However, the analysis of the complete mtDNA genome may provide a much richer source of genetic information for phylogenetic inferences in comparison with the more traditional approach, based on the analysis of single or multiple genes [32]. In this context, the principal objective of the present study was to provide phylogenetic inferences on the Chondrichthyes based on the complete mitochondrial genome, and a more comprehensive understanding of the relationships among the species of sharks and rays.

Order/species	Family	GenBank
Carcharhiniformes		
<i>Carcharhinus leucas_G1</i>	Carcharhinidae	NC023522
<i>Carcharhinus leucas</i>	Carcharhinidae	KJ210595
<i>Carcharhinus macloiti</i>	Carcharhinidae	NC024862
<i>Carcharhinus sorrah</i>	Carcharhinidae	NC024055
<i>Carcharhinus acronotus</i>	Carcharhinidae	NC024596
<i>Carcharhinus plumbeus</i>	Carcharhinidae	KF801102
<i>Carcharhinus falciformis</i>	Carcharhinidae	KF801102
<i>Carcharhinus obscurus</i>	Carcharhinidae	NC020611
<i>Carcharhinus melanopterus</i>	Carcharhinidae	NC024284
<i>Carcharhinus amblyrhyncooides</i>	Carcharhinidae	NC023948
<i>Carcharhinus longimanus</i>	Carcharhinidae	KM434158.1
<i>Carcharhinus brevipinna</i>	Carcharhinidae	KM244770.1
<i>Triaenodon obesus</i>	Carcharhinidae	KJ748376.1
<i>Prionace glauca</i>	Carcharhinidae	NC022819
<i>Glyphis garricki</i>	Carcharhinidae	NC023361
<i>Glyphis glyphis</i>	Carcharhinidae	KF006312

Order/species	Family	GenBank
<i>Galeocerdo cuvier cuvier</i>	Carcharhinidae	NC022193
<i>Scoliodon macrorhynchus</i>	Carcharhinidae	JQ693102
<i>Sphyrna zygaena</i>	Sphyrnidae	KM489157
<i>Sphyrna lewini</i>	Sphyrnidae	NC022679
<i>Sphyrna tiburo</i>	Sphyrnidae	KM453976
<i>Eusphyrna blochii</i>	Sphyrnidae	KU892590.1
<i>Mustelus griseus</i>	Triakidae	NC023527
<i>Mustelus manazo</i>	Triakidae	NC000890
<i>Scyliorhinus canicula</i>	Scyliorhinidae	NC022415
Lamniformes		
<i>Carcharodon carcharias</i>	Lamnidae	NC022691
<i>Lamna ditropis</i>	Lamnidae	NC024269
<i>Isurus oxyrinchus</i>	Lamnidae	NC022691
<i>Isurus paucus</i>	Lamnidae	NC024101
<i>Cetorhinus maximus</i>	Cetorhinidae	NC024101
<i>Carcharias taurus</i>	Odontaspidae	NC023266
<i>Alopias pelagicus</i>	Alopiidae	NC023520
<i>Alopias superciliosus</i>	Alopiidae	NC021443
<i>Megachasma pelagios</i>	Megachasmidae	NC021442
<i>Mitsukurina owstoni</i>	Megachasmidae	NC011825
Orectolobiformes		
<i>Orectolobus japonicus</i>	Orectolobidae	KF111729
<i>Rhincodon typus</i>	Rhincodontidae	NC023455
<i>Chiloscyllium griseum</i>	Hemiscylliidae	NC017882
<i>Chiloscyllium plagiosum</i>	Hemiscylliidae	NC012570
<i>Chiloscyllium punctatum</i>	Hemiscylliidae	NC016686
<i>Stegostoma fasciatum</i>	Stegostomatidae	KU057952.1
Heterodontiformes		
<i>Heterodontus francisci</i>	Heterodontidae	NC003137
<i>Heterodontus zebra</i>	Heterodontidae	NC021615
Squatiniiformes		
<i>Squatina formosa</i>	Squatinaidae	NC025328
<i>Squatina japonica</i>	Squatinaidae	NC024276
<i>Squatina nebulosa</i>	Squatinaidae	NC025578
<i>Squatina formosa</i>	Squatinaidae	NC025328

Order/species	Family	GenBank
Squaliformes		
<i>Squalus acanthias</i>	Squalidae	NC002012
<i>Cirrhigaleus australis</i>	Somniosidae	KJ128289
<i>Squaliolus aliae</i>	Dalatiidae	KU873080.1
<i>Somniosus pacificus</i>	Somniosidae	NC022734
Pristiophoriformes		
<i>Pristiophorus japonicus</i>	Pristiophoridae	NC_024102
Hexanchiformes		
<i>Hexanchus griseus</i>	Hexanchidae	KF894491
Myliobatiformes		
<i>Gymnura poecilura</i>	Gymnuridae	NC_024102
<i>Dasyatis akajei</i>	Dasyatidae	NC021132.1
Torpediformes		
<i>Narcine entemedor</i>	Narcinidae	KM386678
Rajiformes		
<i>Rhinobatos schlegelii</i>	Rhinobatidae	NC023951
<i>Rhinobatos hymnicephalus</i>	Rhinobatidae	NC022841
<i>Rhina ancylostoma</i>	Rhinobatidae	KU721837.1
<i>Zearaja chilensis</i>	Rajidae	KJ913073
<i>Hongoe koreana</i>	Rajidae	NC021963
<i>Dipturus kwangtungensis</i>	Rajidae	NC023505
<i>Raja pulchra</i>	Rajidae	NC025498
<i>Raja rhina</i>	Rajidae	KC914434
<i>Okamejei hollandi</i>	Rajidae	KP756687
<i>Okamejei kenojei</i>	Rajidae	NC007173
<i>Atlantoraja castelnaui</i>	Arhynchobatidae	NC025942
<i>Pavoraja nitida</i>	Arhynchobatidae	NC024599
Pristiformes		
<i>Anoxypristis cuspidata</i>	Pristidae	NC026307
<i>Pristis clavata</i>	Pristidae	KF381507
<i>Pristis pectinata</i>	Pristidae	NC027182
Chimaeriformes		
<i>Callorhynchus milli</i>	Callorhynchidae	NC014285
<i>Chimaera monstrosa</i>	Chimaeridae	AJ310140

Table 1. Complete mitochondrial genome of the elasmobranch species analyzed in the present study.

2. Materials and methods

All 73 mitogenomes analyzed in the present study were obtained from the GenBank public database (**Table 1**). The sequences were aligned automatically by Clustal and colleagues [34], run in the BioEdit sequence editor [35], which was used for visual inspection and possible corrections. The phylogenetic trees were rooted with the species *Callorhincus milli* and *Chimaera monstrosa*, which are considered to be most closely related to the sharks and rays, based on the results of previous studies [3, 10, 11]. The Bayesian inference was run in Mr. Bayes 3.0b4 [36], using the GTR + I + G model, which was selected by jModelTest 2 [37], based on the Bayesian information criterion (BIC) [38]. A Metropolis-coupled Markov chain Monte Carlo (MCMCMC) was executed with four chains run for 100,000,000 generations, using the default parameters. The quality of the run was verified in Tracer v1.6 [39]. The maximum likelihood tree was generated in PhyML 3.0 [40], using the GTR + I + G model, selected by jModelTest 2 [37], based on the Akaike information criterion (AIC), with the confidence interval being established by a bootstrap of 1000 replicates [41]. All the trees were visualized and edited in FigTree v.1.4.3 [42]. The distances among the taxa were calculated using NeighborNet, run in SplitsTree [43].

3. Results and discussion of the phylogenetic relationships

The phylogenetic analyses of the 73 shark and ray mitogenomes supports a basic division into four major groups, the Galeomorphii, Squalomorphii, Squatinomorphii, and Batoidea (**Figure 1**), as suggested in previous molecular studies, based on both mitochondrial and nuclear genes [3, 6, 9–11, 13]. The Bayesian and the maximum likelihood phylogenetic trees of the mitochondrial genomes had highly similar topologies, with the Batoidea being placed as the most basal group, sister group to all the others [3, 6, 11, 13]. The results of this analysis reject emphatically the “Hypnosqualea” hypothesis based on morphological data, which proposes that the Batoidea is part of the shark group, and represents a highly derived lineage of this group (see [7, 8, 44]). The molecular and morphological data are highly divergent with regard to this question.

The phylogenetic reconstruction obtained in the present study confirms the monophyly of the modern sharks (neoselachian), although another controversial question is the existence of the superorders proposed by Ref. [44], based on cladistic analyses of morphological data, which indicated the existence of four superorders—Galeomorphii, Squalomorphii, Squatinomorphii, and Batoidea. While the results of the present study confirm the existence of these four major groups, there are some differences in their arrangement (**Figure 1**) [6, 9, 11, 13].

The data support the monophyly of the order Squaliformes, with *Hexanchus griseus* (Hexanchiformes) at the base of the clade, followed by squaliformes as the sister taxon of the Squatiniformes and Pristiophoriformes. An important feature of the arrangement of the species within the Squatiniformes is the position of *Squatina nebulosa* as sister taxon of *S. formosa*, with *S. japonica* in a basal position in the clade. *Pristiophorus japonicus* is a sister group

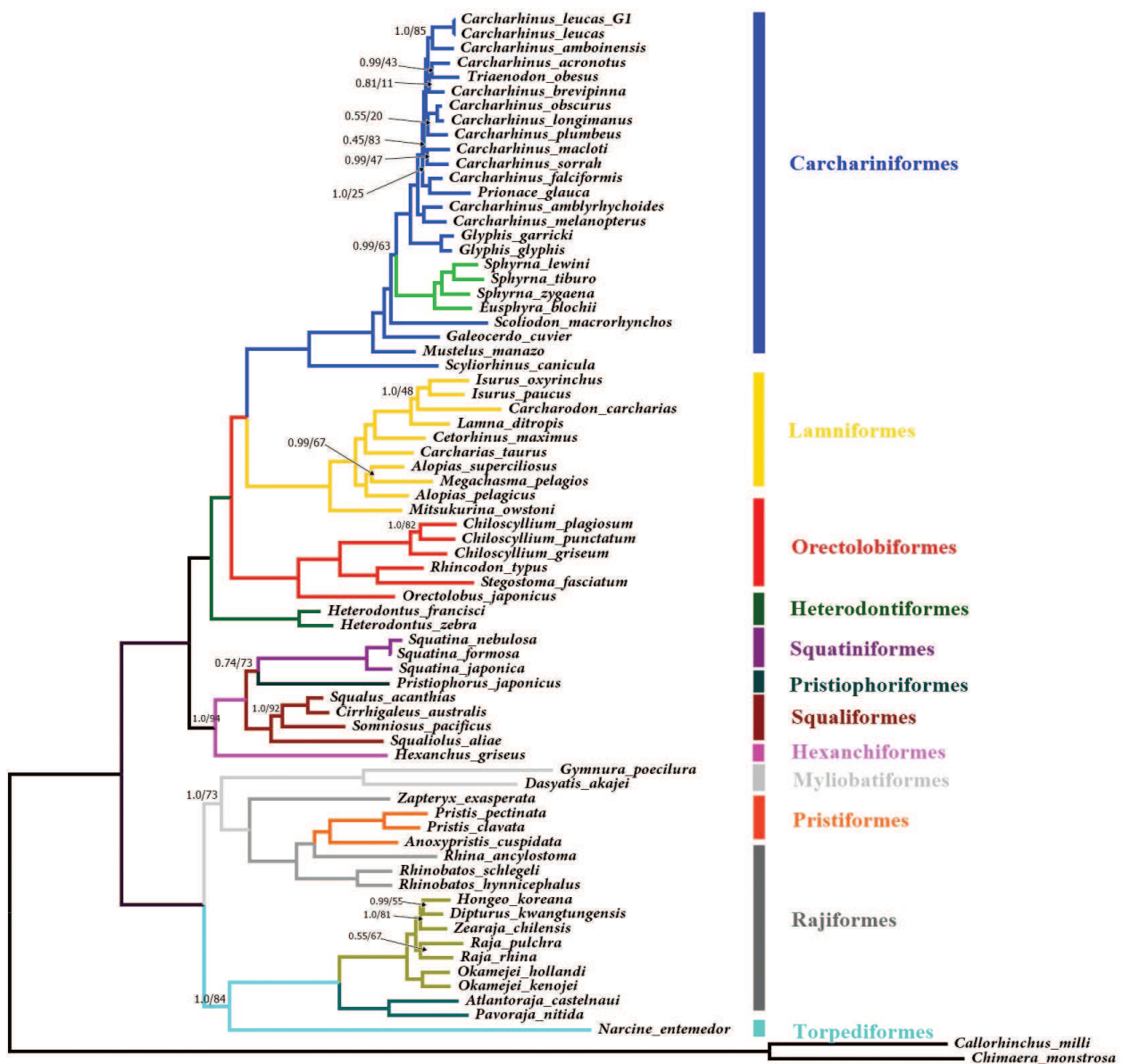


Figure 1. Bayesian inference and maximum likelihood generated from the complete mitochondrial genome of the Chondrichthyes. Only branches with bootstrap values below 100% are shown.

of this same clade, which highlights the paraphyletism of the two orders (Squatiniforme and Pristiophoriformes), an arrangement proposed by Ref. [13], who were nevertheless unable to define the position of *S. nebulosa*. The close relationship between the orders Squaliformes and Squatiniformes is consistent with [12], who used the projection of the cartilage of the upper mandible into the ocular orbit as a synapomorphic trait, with the sharks of this clade being denominated “orbitostylic” sharks. This arrangement confirms the findings of previous studies based on molecular markers [3, 6, 13, 18].

In the case of the Galeomorphii, it is important to note that the Heterodontiformes was identified as the most basal taxon of this superorder, in a clade supported by high probability values

(**Figure 1**). The Lamniformes is the sister group of Carcharhiniformes, which is placed as sister group of the Orectolobiformes with strong statistical support. The taxonomic position of the order Heterodontiforme within the Galeomorphii is considered to be extremely controversial [13]. Some studies have identified the Heterodontiformes as the most basal order, with Orectolobiformes being more closely related to the Lamniformes and Carcharhiniformes, a grouping supported by both morphological [7, 8] and molecular studies [3, 6, 9]. However, Ref. [18], using 5.8 kb of nuclear gene sequences (major and minor rRNA subunits), and Ref. [14], who analyzed mitochondrial data, indicated a closer relationship between the Orectolobiformes and Lamniformes [6, 10, 13].

The family-level phylogenetic inferences within the Carcharhiniformes reinforced the paraphyly of this order, with the clade of the hammerhead sharks (Sphyrnidae) being placed as a sister group of the sharks (Carcharhinidae). *Scyliorhinus canicula* (Scyliorhinidae) was the most basal of the Carcharhiniformes, with *Mustelus manazo* (Triakidae) and *Galeocerdo cuvier* (Carcharhinidae) being placed close to all the other sharks, with high levels of statistical support (**Figure 1**). This arrangement is inconsistent with the results of Ref. [6], who used the complete mtDNA genome, and placed *Scoliodon macrorhincos* as a sister group of the sharks, with the sphyrnas as a sister group of this same clade. However, the arrangement observed here is in agreement with the studies of Refs. [3, 11, 13]. The most likely explanation for the lack of agreement between the results of the present study and those of Ref. [6] may be the difference in the number of species analyzed, given that an additional 24 mitogenomes were included in the present study. In addition, the pairs of species *Carcharhinus sorrah*/*C. macloti*, *C. amblyrhynchoides*/*C. leucas*, and *C. brevipania*/*Triaenodon obesus*/*C. acronotus* were involved in a polytomy. The polytomic pattern within Carcharhinidae is probably related to the low-levels of intrinsic genetic variability of sharks (**Figure 2**) [47]. The results of the present study are consistent with those of other molecular phylogenies [10, 13, 17, 24]. The analyses support the monophyly of the Lamniformes, with high probability values. The genus *Lamna* is the sister group of *Carcharodon* and *Isurus*, the most derived taxa of this group. This arrangement is supported by both the morphological data (Compagno 1990) and molecular inferences [6, 13, 17].

The monophyly of the rays was also supported by high probability values [3, 6, 9, 10, 16]. The analysis revealed the formation of four well-defined groups—Torpediformes, Rajiformes, Pristiformes, and Myliobatiformes—with branches supported by high bootstrap values (**Figure 1**). These results are consistent with previous studies based on the analysis of morphological and molecular data [21–25]. One other important finding of the present study was the arrangement of the orders Torpediniformes and Rajiformes close to the root of the tree (**Figure 2**). At the family level, two clades were observed, one containing the Narcinidae (the electric rays) as the most primitive taxon of the group, with the Rajidae (skates) and Arhynchobatidae grouped in the same clade, all on branches with high statistical support. The arrangement of the Narcinidae (Torpediniformes) is inconsistent with the morphological inferences, which assume that Pristiformes is the most basal order of the Batoidea [11, 15, 24]. However, the principal phylogenies based on mitochondrial and nuclear markers indicate that the Rajoidei is the sister group of all the other members of the Batoidea [3, 6, 16, 21, 22].

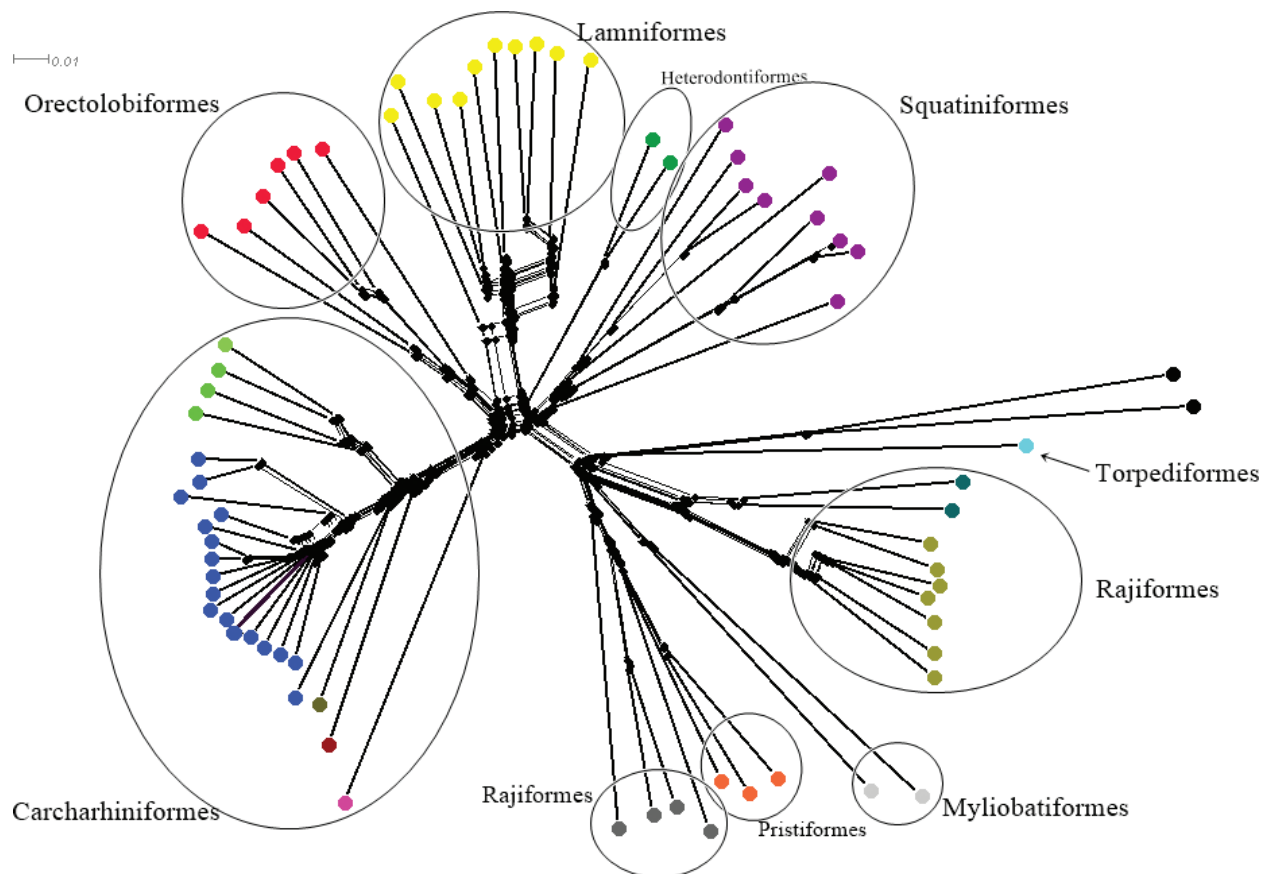


Figure 2. Genealogy showing the relationships between the orders of Chondrichthyes based on the complete mitochondrial genome of 73 species of sharks and rays. The two black circles on the right represent the out group.

The second clade includes *Zapteryx exasperata* (Rhinobatidae) as the most basal taxon, with *Rhinobatos hynnicephalus*/*R. schlegelii* as sister taxa. The family Rhinobatidae is placed as a sister group of the Pristidae, which is represented by *Anoxpristis cuspidata*, *Pristis clavata*, and *P. pectinata*, with all branches being supported by high probability values. The Myliobatidae is placed in this same clade as the sister group of the Rhinobatidae, an arrangement with high values in the Bayesian inference, and more moderate ones in the maximum likelihood analysis. The grouping of the sawfish (Pristiformes) with the guitarfish (Rhinobatidae) disagrees with the morphological phylogenies, which identifies the Pristiformes as the most primitive group of the Batoidea [23, 46]. However, this arrangement is supported by other molecular studies (see [3, 6, 16, 21]).

4. Conclusion

The analyses of the mitochondrial genome provided an ampler and more complete overview of the relationships within the Chondrichthyes, with the topologies highlighting a number of inconsistencies in some of the taxonomic groups of sharks and rays, principally in terms of the interrelationships among groups [13]. It is important to note that the phylogenetic relationships within the genera of these groups are still poorly understood, and that

a mitogenomic phylogeny, including a much broader diversity of taxa, may provide more comprehensive insights into the relationships among the species of these organisms. Among other conclusions, the phylogenetic trees rejected the “Hypnosqualea” hypothesis and confirmed the monophyly of the Neoselachii, and Batoidea as the sister group of the sharks [16, 21], in agreement with most of the available molecular phylogenies. The Batoidea is a monophyletic group, in which the Torpediniformes and Rajiformes are the most ancestral orders, contradicting the morphological analyses, which identifies the Pristiformes as the most basal order. The phylogenetic trees supported conclusively the division of the Batoidea into four groups, the Torpediniformes, Rajiformes, Pristiformes, and Myliobatiformes [45].

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