# Distribution of the Lampriformes in the Mediterranean Sea

Subjects: Biodiversity Conservation

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Lampriformes are circumglobally distributed and contain several families of strictly marine bony fishes that have a peculiar morphology. Lampriformes systematics is affected by limitations in biometric, meristic, and molecular data; for this reason, it underwent several rearrangements in the past. Knowledge scarcity is due to their solitary nature, in addition to their low to absent economic value. Despite this, the order Lampriformes represents a taxon of high biological and ecological importance. The high depth range of distribution characterizes their lifestyle. In the Mediterranean Sea, four families are present—Lampridae, Lophotidae, Regalecidae, and Trachipteridae—with the following species respectively, *Lampris guttatus* (Brünnich, 1788), *Lophotus lacepede* (Giorna, 1809), *Regalecus glesne* (Ascanius, 1772), *Trachipterus arcticus* (Brünnich, 1788), *T. trachypterus* (Gmelin, 1789), and *Zu cristatus* (Bonelli, 1819).

Keywords: zoological records ; teleost ; deep-sea fishes ; phylogeny ; marine environment

## 1. Introduction

The order Lampriformes is a globally distributed taxon that contains several families of strictly marine bony fishes with a peculiar morphology [1][2]. Despite their wide distribution, they are not commonly reported due to their rarity and life cycle that result in their elusiveness [3][4]. The scarcity of reports in the literature results in little information regarding their presence and distribution. Indeed, even if they are biologically interesting species, they represent fishing waste from a commercial point of view. Therefore, they are not retained and reported, leading to a significant gap in data collection [5]. Their morphological aspects led to characteristic common names of these species (ribbonfish, velifers, tube-eye, crestfish, oarfish, dealfish, tapertails, unicornfish, and inkfish). Due to the distinctive shape of most of these species, jointly with their iridescent colors, these fishes became historically involved in several legends and popular myths [4]. Moreover, the larval stages of these species are often very different from the adult stages, both in morphology and lifestyle aspects [6]. All these factors contribute to the interest of zoological researchers and public curiosity.

The research interest in this order is linked to the ecological role of lampriform species that are involved in many bathypelagic food webs interactions. Moreover, during evolution, deep-sea species have developed highly specialized features to inhabit deep-sea environments, such as the maintenance of a vertical position in the water column during predation, which was reported also for some Lampriformes species [7][8]. This feature may help these fish in the visualization of prey against downwelling light, and, at the same time, allow these elongate fish to minimize their appearance [9]. However, studies that are related to adaptations of Lampriformes species to deep-sea life are scarce and, in consideration of their morphological features, require further in-depth investigations, especially from functional and genetic points of view [10][11]. Studying the adaptation to deep-sea life is essential both from an anatomical and physiological point of view, in relation to their ecological features [12]. Moreover, this group is quite important from a phylogenetic point of view, due to their ancient origins among teleosts [13][14].

Lampriformes systematics is affected by limitations in biometric, meristic, and molecular data; for this reason, it underwent several rearrangements in the past. Some researchers have included other deep-sea fish families (e.g., Ateleopodidae, Megalomycteridae, Mirapinnidae, and Stylephoridae) based on morphological identifications of the group. Still, recent phylogenetic analyses, which were also based on molecular approaches, excluded these additional families that are currently considered unrelated [15][16]. However, this aspect is under continuous debate, and few phylogenetic studies of species-level relationships have been carried out on Lampriformes. Hence, to better assess the phylogenetic relationship of the group, more in-depth molecular data on families, genera, and species are required.

Environmental evolution in global marine ecosystems leads to continuous rearrangement of faunal stands [17]. In recent years, it is known that global climate changes have contributed to modifying several important environmental parameters of aquatic ecosystems, such as salinity, temperature, and pH (for the strong influence on dissolved $CO_2$) [18][19]. Currently, the scientific community is working on understanding how these changes could affect aquatic organisms by trying to develop further predictive models [20][21]. The influences on marine faunal assemblages are various, and not only attributable to climate change. It is known that reproductive behaviors, habitat preferences, feeding behaviors, genetic adaptation, and especially anthropic pressure (with its double impacts of fishing and pollution) [22][23], lead to complex biocenotics dynamics. These cannot be explained without considering all these factors that impact the species. Biological monitoring assumes a pivotal role, through maintaining records of previously undiscovered species, new records of invasive alien species, and rare or uncommon, rarely reported ones [24][25][26].

## 2. Biological and Ecological Features of Lampriformes

Morphologically, most Lampriformes are characterized by bright silvery colors and very colorful fins that are mainly shades of red [2][4]. Sometimes, the first ray of the dorsal fin is quite elongated and evident, characterizing the appearance as in the case of *Zu cristatus* (Bonelli, 1819) [27]. As members of Subphylum Vertebrata and Subclass Teleostei, lampriform fishes are characterized by a developed axial skeleton. The elongate form, such as that of trachipterids, has a highly variable number of vertebrae comprising between 60 and 150 [1][28]. In contrast, the most compressed body species possess fewer vertebrae (33 to 46), such as the case of lamprids. Notably, this order features quite different patterns of small bones and ligaments associated with their anterior vertebrae, which probably evolved as a result of their characteristic swimming behavior and deep-sea life [1][29][30]. Other structural differences with the common teleost are mainly found in the head structure, with its lack of a ligamentous link between the cheekbones and the upper jaws (maxillae), supported by the nasal cartilage placed in the frontal region of the skull in a hollow [1]. These peculiar features are significant from a functional point of view for lampriform species, because they enable the upper jaws to be stretched forward during feeding behavior.

This extreme jaw protrusion in some species permits the expansion of the mouth of up to 40 times in dimension during predation, allowing capture of even the most evasive of planktonic prey items in darkness. Indeed, lampriforms feed mainly on small Polychaeta, medium/small-sized pelagic cephalopods, and crustaceans, Malacostraca included [31][32]. Moreover, they prey on small fishes that are not easy to capture in the dark deep-sea environment [31][32]. Borme and Voltolina also reported the occurrence in the stomach of *Trachipterus trachypterus* of some macroalgae, such as *Ulva intestinalis* (Linnaeus, 1753) and *Cystoseira compressa* ((Esper) Gerloff and Nizamuddin, 1975); this shows the fascinating omnivorous, opportunistic nature of the species [32]. Regarding feeding interactions as prey, lampriform fishes have been sporadically found in the stomachs of cetaceans, such as the sperm whale (*Physeter macrocephalus,* Linnaeus, 1758), chondrichthyans such as blue shark (*Prionace glauca*, Linnaeus, 1758), or large-sized bony fish predators such as tunas [33][34]. Moreover, some typical enteric parasites of fishes, such as *Ascaris capsularia* (Rudolphi, 1802), *Scolex polymorphus*, (Rudolphi, 1819), and *Anisakis physeteris* (Baylis, 1923), have been reported in some Lampriformes species [35].

Information about the reproduction of Lampriformes is very scarce due to their elusive nature [36]. Even though spawning has never been observed, lampriform fishes are considered broadcast spawners because the eggs are planktonic, and several authors have used them to record the presence of some species [6][37]. The eggs have a diameter of about 2–6 mm and remind of the species' coloration with their bright with reddish hues. At hatching, the larvae have fully developed mouths and digestive tracts, and begin to feed immediately on minute plankton [6]. The larval stages of lampriforms are beautiful and identifiable fishes characterized by their evident, ornamented dorsal and pelvic long fin rays. It is known that trachipterids undergo metamorphosis, passing from the larval to the juvenile form [38][39].

Moreover, from a habitat point of view, some species prefer shallow water during larval/juvenile stages, eventually moving to the deep-sea environment during adult life. These transitions from shallow, nearshore habitats, to the deep open ocean, is one of the two significant events that were hypothesized to characterize evolution of the order Lampriformes [13]. The family of Veliferidae is a moderate-sized coastal fish group that inhabits shallow waters for their entire life cycle. Some authors have reported finding it at a maximum depth of 110 m. It seems to be the most ancient group within the Lampriformes order [40]. In the adult stage, all other lampriforms are open-ocean, epipelagic, mesopelagic, or bathypelagic fishes. Some adult specimens of the Lampridae family were also detected in shallow waters near the surface, but, apart from these occasional events, it is not considered a coastal water group [4]. An essential event in the evolution of the lampriform lineage is represented by the colonization of deep-sea environments made by other families of the group as a result of the necessary functional adaptations [41][42]. The second significant evolutionary transition relates to body shape, which passes from oval-shaped and deep-bodied veliferids and lamprids, to elongate forms of oar-ribbon fishes (Regalecidae, Trachipteridae) [39].

As mentioned, knowledge about this taxon is scarce in relation to difficulties in finding and monitoring live specimens, which rarely occurs. This difficulty is also due to their solitary nature, confirmed by the records present in the literature and collected, which mainly concern occurrences of single specimens, very rarely two or three [5]. Whereas the generalist fishing methods through which they are caught, such as through trawling nets or longline fisheries, the rare occurrence of one specimen highlights their solitary nature and already known rarity. Experimental studies are absent in the literature, and very little is known about the most suitable habitats of these species, their preferences or interactions in aquatic communities, and their role in deep-sea food webs. Occasional underwater surveys with ROVs, or with diver direct observations and video recordings, suggest that more elongated species such as the oar-ribbon fishes usually orientate their body vertically [17]. This characteristic head-up position involves vertically using all of their long fins through the water column, sometimes rapidly [43]. Indeed, their appearance as non-robust fishes has been confirmed through histological analysis revealing soft pale muscle tissues. When disturbed, these species can swim rapidly, but briefly. On the contrary, veliferids, and lampridids usually swim horizontally in the typical teleost way, confirming in this case, a different evolutionary story. These species are considered powerful swimmers, using their large pectoral fins for forward propulsion [44].

From the scarce data found in the literature, even if they are active predators, Lampriformes seem not to be aggressive fishes, and are provided with extraordinary features to offend prey or defend themselves from predators. The above-mentioned head-maxillae structure provides them efficacy in predation. At the same time, from a defensive point of view, fast swimming seems to be the primary mechanism of escape, with some exceptions. Particularly curious is the case of the regalecid *Agrostichthys parkeri* (Benham, 1904), which has been reported to give a mild electric shock if handled [45]. Moreover, some species of the genus *Lophotus* and *Radiicephalus* seem to have specialized organs that, as defense mechanisms, expel a dark, squid-like ink through the cloaca if disturbed [39][46]. *T. trachypterus* (Gmelin, 1789) showed a Batesian mimicry strategy when observed alive, and its feeding behavior seems to be strictly influenced by up-welling currents and the moon phases [17]. Moreover, the areal distribution of this species seems to be related to the movements of different aquatic masses within the water column [32]. Despite some cases of pathogenic infections that have been recorded in Lampriformes [35][47], no information in these species about the immune system and its role in organism defense is available [48][49][50].

Currently, no lampriform species are listed by the IUCN; however, it depends on the rarity of these fishes, and the scarcity of data about them. Considering the discussed role of Lampriformes in deep-sea food webs, fishermen and researchers should take more care in reporting the related data of their occurrence as by-catch [5][51], in order to deepen their stock evaluation, and consequently better assess if conservation measures are required.

## 3. Essential Systematics and Phylogeny of the Group

The taxonomy and systematics of Lampriformes passed through many insights in recent years, due to the advent of new molecular approaches to determining phylogenetic relationships [16][52][53][54]. For this reason, clarifying the taxonomy of the group is essential, to better evaluate and compare the literature in the field. Currently, the order Lampriformes comprises six families: Lampridae (Gill, 1862), Lophotidae (Bonaparte, 1845), Radiicephalidae (Osorio, 1917), Regalecidae (Gill, 1884), Trachipteridae (Swainson, 1839), and Veliferidae (Bleeker, 1859) [55][56]. The family Lampridae consists of the genus *Lampris* (Retzius, 1799), which contains five species, three of which are very recent discoveries: *Lampris australensis* (Underkoffler, Luers, Hyde and Craig, 2018), *Lampris guttatus* (Brünnich, 1788), *Lampris immaculatus* (Gilchrist, 1904), *Lampris incognitus* (Underkoffler, Luers, Hyde and Craig, 2018), and *Lampris megalopsis* (Underkoffler, Luers, Hyde and Craig, 2018) [44]. The family Lophotidae contains two genera, *Eumecichthys* (Regan, 1907), which includes a single species, *Eumecichthys fiski* (Günther, 1890), and the genus *Lophotus* (Giorna, 1809), which constitutes four species: *Lophotus capellei* (Temminck and Schlegel, 1845), *Lophotus guntheri* (Johnston, 1883), *Lophotus lacepede* (Giorna, 1809), and *Lophotus machadoi* (Miranda Ribeiro, 1927) [56][57]. The family Radiicephalidae is constituted by only one genus, *Radiicephalus* (Osório, 1917), which contains two species: *Radiicephalus elongatus* (Osório, 1917) and the recently annotated *Radiicephalus kessinger* (Koeda and Ho, 2018) [58]. The family Regalecidae passed through many rearrangements that, over time, added or deleted species and genera that were considered synonyms or sisters. Currently, the accepted classification attributes two genera to this family, *Agrostichthys* (Phillipps, 1924), with *Agrostichthys parkeri* (Benham, 1904) as unique species, and *Regalecus* (Ascanius, 1772), which contains the two species *Regalecus glesne* (Ascanius, 1772) and *Regalecus russellii* (Cuvier, 1816). These species have several synonyms (e.g., *Regalecus kinoi, Regalecus masterii, Regalecus woodjonesi, Gymnetrus hawkenii, Gymnetrus russellii*) [55][56]. Similarly, the family Trachipteridae consists of three genera, *Desmodema* (Walters and Fitch, 1960), which contains the two species, *Desmodema lorum* (Rosenblatt and Butler, 1977) and *Desmodema polystictum* (Ogilby, 1898), the genus *Zu* (Walters & Fitch, 1960) with two species, *Zu cristatus* (Bonelli, 1819) and *Zu elongatus* (Heemstra and Kannemeyer, 1984), and the most prominent genus, *Trachipterus* (Goüan, 1770), with its six species: *Trachipterus altivelis* (Kner, 1859), *Trachipterus arcticus* (Brünnich, 1788), *Trachipterus fukuzakii* (Fitch, 1964), *Trachipterus ishikawae* (Jordan and Snyder, 1901), *Trachipterus jacksonensis* (Ramsay, 1881), and *Trachipterus trachypterus* (Gmelin, 1789). Several species of the Trachipteridae family have synonyms (e.g., *Trachipterus misakiensis, Trachypterus altivelis, Trachypterus nigrifrons*) [55][56]. The family Veliferidae is constituted by the genus *Metavelifer* (Walters, 1960), with the species *Metavelifer multiradiatus* (Regan, 1907), and the genus *Velifer* (Temminck and Schlegel, 1850), which contains *Velifer hypselopterus* (Bleeker, 1879) as its unique species [55].

The older classification also comprised the family Stylephoridae, which was recently moved on the basis of molecular data into the new separate order of Stilephoriformes, which contains one monotypic genus, *Stylephorus* (Shaw, 1791) [15][59][60]. The current research manuscript represents one of the first documents based on this new classification.

Different phylogenetic surveys conducted with morphological and molecular approaches have placed the Lampriformes order within the Acanthomorpha clade [61][62]. Lampriform fishes are primitive compared to the Percomorpha, but their precise placement among basal Acanthomorpha remains undetermined [29]. The monophyly of Lampridiformes is based on four apomorphies, three of which are correlated, and involve evolutionary modifications of the unique feeding mechanism. In these species, the maxilla slides forward with the premaxilla during jaw protrusion [39]. The Veliferidae family is deemed the sister group of all other lampriforms, with the oarfish and related that evolved from a common velifer-like ancestor during the late Cretaceous or early Eocene [1]. Effectively, the order Lampriformes is considered one of the ancient sister taxa to approximately 60% of all known teleost species [29][39]. This pivotal systematic position makes the order essential to evolutionary researchers, considering the difficulty of establishing this kind of phyletic relationship in classifying Acanthomorpha fishes [63].

In this regard, the inclusion of fossils in the analysis also assumes importance in phylogenetic studies since they deepen the knowledge of morphological characters and their evolution. During archaeological research in the Mediterranean area, some skeletal evidence of about another ten extinct Acanthomorpha species have been found in fossil findings [14][64][65]. These fossil relics have been related to ancestral Lampriformes [14][61][65][66]. In 1999, Sorbini and Sorbini described a fossil of the oldest known lampriform fish, *Nardovelifer altipinnis*, found in the Cretaceous deposits of Nardò, Italy [40]. Carnevale and Bannikov [67], and Papazzone et al. [68] described in Eocene deposits from Verona, Italy, two ancient species, *Bajaichthys elegans* and *Veronavelifer sorbinii*. Carnevale [64], reported about the first fossil of the ribbonfish *Trachipterus mauritanicus* from a Miocene locality in northwestern Algeria. Additional fossil taxa from other areas of the world reported the existence of some other Lampris-like species that were discovered in Miocene deposits in California (*Lampris zatima*) [69], two Oligocene lophotids, *Protomecicthys* and *Protolophotus* [65], and in Oligocene deposits from New Zealand (*Megalampris keyesi*) [70].

**Lampriformes Phylogenetic Relationships Based on mt-COI Sequences**

The taxonomy and systematics of the order Lampriformes are still affected by the absence of a wide database, especially from a molecular point of view, which currently represent the main goal [43]. Particularly for the rarest families, the few or incomplete descriptions joined to the morphological variation within, and similarities between Lampriformes species, lead to some uncertainty on phylogenetic relationships [71]. Molecular analysis will be essential to better assess the taxonomic status of these taxa, which will probably pass-through revisions in the coming years.

Researchers reported the results of the phylogenetic reconstruction of Lampriformes based on the currently available cytochrome oxidase subunit 1 (mt-COI) gene sequences revealed, with high posterior probability support that the topology of the tree is partially in accordance with the currently accepted taxonomic relationships amongst the families. All the coding sequences of mt-COI from 21 Lampriformes species, currently annotated in the GenBank database, were aligned with MUSCLE and then trimmed with Gblocks. A total of 542 positions were selected for Bayesian phylogenetic reconstruction using the GTR+I nucleotide substitution model. The consensus tree was built after burning 25% of the trees from 500,000 generations. Bayesian posterior probabilities are represented as percentages. This analysis was performed with the pipeline NGPhylogeny.fr [72]. Despite having chosen the most common gene used for phylogenetic analysis in teleosts, there remained six species included in the order (*L. guntheri, L. machadoi, R. elongatus, R. kessinger, T. fukuzakii, T. ishikawae*) that were without annotated mt-COI sequences, denoting the strong lack of data on the subject, and the need to deepen research in this topic.

Particularly, no available data were present for the entire family of Radiicephalidae. On the contrary, all the species of the Lampridae, Veliferidae, and Regalecidae families had mt-COI sequences available on NCBI. From the analysis, the members of the first two taxa clustered in accordance with the current taxonomy, on two monophyletic branches that are not distant from each other. On the other hand, the three species of the Regalecidae family were grouped in two separate branches from the same node, one related to the two species of the genus Regalecus, while the other one consisted only of *A. parkeri*. Beginning from the same node, there originated three other branches, two of which related to the Trachipteridae genera, *Trachipterus* and *Zu*, grouped as expected, and the other one concerning the species *E. fiski* was separate from the other Lophotidae. Indeed, the species of the genus *Lophotus* grouped somewhat distantly from *E. fiski,* in a branch near the Lampridae, as a well-defined clade. This represents the most important difference between the analysis and the accepted phylogeny of the order. Moreover, the two species of the genus *Desmodema* clustered separately from the rest of the Trachipteridae genera, without being too evolutionarily distant. It is also interesting to note how *T. arcticus* grouped separately from its congeners, on a shared clade with *Regalecus* species, which originated from the same node as the other *Trachipterus*. It can be found that the most interesting insight from analysis of the position within the Lophotidae and Trachipteridae families. Further and more complex analyses (e.g., phylogenomics) are necessary, in order to better assess these relationships, especially those that are between quite dissimilar organisms, both morphologically and biologically, such as Lophotidae [65].

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