

Review

Is there any phylogenetic relationship between teleosts and the elasmobranchs?

MINE Dosay-Akbulut

Afyon Kocatepe University, Veterinary Faculty, Medical Biology and Genetics Department, AFYON/TURKEY. Phone: 00902722281311/148. . E-Mail: minedosay@hotmail.com.

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There is still disagreement with regard to identifying the sister group of the tetrapods? Different hypotheses were suggested for this relationship. The aim of this article was to present and summarize some of these studies, which were based on the possible phylogenetic relationship between Chondrichthyes and land vertebrates (tetrapods).

Key words: Phylogenetic, relationship, Chondrichthyes and tetrapods.

INTRODUCTION

For many years, numerous investigators have been trying to better understand the evolution of the vertebrates, especially the phylogeny of the tetrapods or land vertebrates. Most of the information comes from paleontological or anatomic work. Nucleic acid and protein sequence analyses are very recent techniques and are providing new information on the subject (Bernardi et al., 1992). The relationship of the Chondrichthyes to other groups of fishes has been a topic of discussion for more than a century. For example, Schaeffer and Williams (1977) suggest that the Elasmobranchii and the Holocephalii are sister groups, and that the Chondrichthyes are more closely related to the Teleostomi than the Placodermi based on certain characteristics of the skull, skeleton, fin supports and fins.

THE SYSTEMATIC POSITIONS OF THE CHONDRICHTHYES AND TELEOSTS

The vertebrates are divided into two main groups, Agnathans (jawless vertebrates, including hagfishes and lampreys) and gnathostomata (jawed vertebrates). The current phylogenetic theory divides the recent gnathostomes (jawed fishes) into two groups which are the cartilaginous fishes and bony fishes (osteichthyes). Cartilaginous fishes include sharks, skates, rays and chimeras, which have a soft, firm tissue in the endoskeleton. They have a prismatic calcified cartilage instead of bone and together form a group in the class

Chondrichthyes. It is commonly known that cartilaginous fishes, Chondrichthyes, have a place among the Gnathostomata, and their relation could be viewed as the sister group of all other gnathostomes (i.e., osteichthyans) (Miller and Loates, 1997; Rasmussen and Arnason, 1999a; Rasmussen et al., 1998).

As mentioned above current phylogenetic theory divide recent gnathostomes into two major groups, the Chondrichthyes and the Osteichthyes (bony fishes). This separation based on the absence of typical bony fish characteristics in the Chondrichthyes such as a swimbladder and bony skeleton, teeth/tooth plates not fused to the jaw and separate gill openings. Osteichthyes split further into Actinopterygii (ray-finned fish) and Sarcopterygii (lobe-finned fish). Actinopterygii divide into the Cladistia (bichirs) and all other actinopterygians (teleostii), while on the other hand Sarcopterygians include the coelacanth (only one living species, *Latimeria chalumnae*), lungfish (dipnoans) and tetrapods. Sarcopterygians (lobe-finned fishes) have bony fins and some of them have lungs for respiration; therefore it is commonly accepted that sarcopterygians are closely related to the ancestral tetrapods (Rasmussen and Arnason, 1999a; Cao et al., 1998).

SUMMARY OF SOME PREVIOUS RESEARCH

Recently, nucleic acid and protein sequences have provided new information about where the cartilaginous

fishes are placed within the tree of bony fishes. For example, Rasmussen and Arnason (1999a) sequenced 12 mitochondrial protein-coding genes from the following fishes: sea lamprey, lungfish, bichir, coelacanth (*Latimeria chalumnae*), cod, loach, rainbow trout and a Chondrichthyes, represented by the spiny dogfish (*Squalus acanthias*). They used as an outgroup the echinoderms, represented by one starfish and two sea urchins and sea lamprey. In the same research, they also did analyses with the addition of four amniotes. These authors sought phylogenetic relationships among gnathostomes using the sea lamprey, which is the closest relative of the gnathostomes, as an outgroup. These analyses included the following fishes: lungfish, bichir, coelacanth, cod, rainbow trout and spiny dogfish and four amniotes: chicken, ostrich, wallaroo and cow (Rasmussen and Arnason, 1999a).

Both phylogenetic analyses placed the spiny dogfish representing the chondrichthyes, among the bony fishes. Both the amino acid and nucleotide data sets support this position. The lungfish was in the most basal position among all gnathostome fishes, while the bichir in the second most basal position. The coelacanth/shark/teleostean clade was high and phylogenetic analysis values ranged from 84 to 99% in different studies. The spiny dogfish was placed as the sister group of the teleosts within the same clade (without amniotes) (Rasmussen and Arnason, 1999a).

In the same year in a different study, the same authors concluded that cartilaginous fishes have a terminal position in the piscine tree. To better understand vertebrate evolution and clarify the gnathostome relationship, Rasmussen and Arnason (1999b) sequenced complete mtDNA from starry skate (*Raja radiata*) with 3 squalomorph chondrichthyans, the common dogfish (*Scyliorhinus canicula*), the spiny dogfish (*Squalus acanthias*) and star spotted dogfish (*Mustelus manazo*) with several bony fishes and amniotes. In this study, the most closely related nongnathostome species, sea lamprey was used as an outgroup (Rasmussen and Arnason, 1999b).

In unrooted ML analysis, the teleosts and the chondrichthyans form sister groups, and the NJ analysis places the chondrichthyans in a terminal position in the piscine tree with support values for the sister group relationship between chondrichthyans and teleosts are 78% (ML), 79% (NJ), and 70% (MP). These results suggest that the origin of the amniote lineage is older than oldest extant bony fishes (the lungfishes). The oldest lungfish fossils go back 400 million years, and by using this as a calibration point, the squalomorphs and batomorphs were separated about 190 million years before the present (MYBP). This dating was also supported by the first appearance of batomorph (skates and rays) fossils in paleontological records. In these records, the origin of the Chondrichthyes goes back ~290 MYBP. The gnathostome fishes and the amniote lineage

were split about 420 MYBP. The divergence of the coelacanth and the teleost/chondrichthyan branch occurred ~ 310 MYBP, and of the cladistian (bichir) and coelacanth/teleost/chondrichthyans ~ 380 MYBP. These results offer different explanations for the relationship between gnathostome and cartilaginous fishes with regard to the same main morphological characteristics, lung/swimbladder, bone/cartilage, and the exoskeleton, rather than the commonly accepted gnathostome relationship based on the same characters (Rasmussen and Arnason, 1999b).

Bernardi et al. (1992) sequenced 18S rRNA from two teleostean fish species, *Fundulus heteroclitus* and *Sebastolobus* and two sharks, *Squalus acanthias* and *Echinorhinus cookei*. After that, the sequences were compared with 18S rRNA sequences of the coelacanth *Latimeria chalumnae*, the frog *Xenopus laevis*, and humans for phylogenetic conclusion. Maximum parsimony analyses consistently grouped the two teleosts and two sharks together (Bernardi, et al., 1992).

Mallatt and Sullivan (1998) also tried to establish the relationship between the lamprey and hagfish, and they wanted to test the classical hypothesis of monophyly of the cyclostomes (lampreys plus hagfishes), which is very similar to the Stock and Whitt study, to provide more results. For this work, 92-97% complete 28S and partial 5.8S rDNA sequences were obtained from five chordate species, the lancelet *Branchiostoma floridae*, the hagfish *Eptatretus stouti*, the lamprey *Petromyzon marinus* and the cartilaginous fishes *Hydrolagus colliei* (the chimaeroid) and dogfish shark *Squalus acanthias* which were then analysed with previously reported 28S and 18S rDNA sequences from other chordates from Genbank. Additionally, one trout *Oncorhynchus mykiss* was used to provide a small segment of the 28S gene. However, in this research, the interrelationship of the major groups of jawed bony fishes and tetrapod vertebrates (Osteichthyes) was not found as expected. For example, the frog never grouped with the coelacanth. Maybe because of region, they choose to work. On the other hand, in all trees, where both cartilaginous fishes (shark and chimaera) grouped together and were placed with the bony fishes (Stock and Witt, 1992; Mallatt and Sullivan, 1998).

In another study, Delarbre et al. (1998) worked with another dogfish species and sequenced the complete genome of the mitochondrial DNA of the dogfish *Scyliorhinus canicula*. In addition, they compared it with the mtDNA genomic map of carp (*Cyprinus carpio*), chicken (*Gallus gallus*), coelacanth (*Latimeria chalumnae*), lancelet (*Branchiostoma lanceolatum*), loach (*Crossostoma lacustre*), rainbow trout (*Oncorhynchus mykiss*) and sea lamprey (*Petromyzon marinus*). The phylogenetic analyses using the NJ method with Kimura's two parameter distance from Phylip shows that the Chondrichthyes are the sister group of the Osteichthyes and the dogfish placed with a gnathostome monophyly,

while with a significantly different position with regard to the sea lamprey (agnathans) (Delarbre et al., 1998).

In another study, molecular phylogenetics of gnathostomous (jawed) fishes investigated via understanding of the relationship between Holocephali (as represented by the ratfish, *Chimaera monstrosa*) and

Neoselachii in analyses based on the data set of 12 mt protein-coding genes by Arnason et al. (2001). The mtDNA of the *Chimaera* is 18 580 nt long as being the largest vertebrate mtDNA described so far. In the result of this study, the phylogenetic analyses identified Chondrichthyes as a monophyletic (ratfish, *Chimaera monstrosa*; starry skate, *Raja radiata*; horn shark, *Heterodontus francisci*; spiny dogfish, *Squalus acanthias*; spotted dogfish, *Scyliorhinus canicula*; common dogfish, *Mustelus manazo*) in a terminal position in the piscine tree, with maximum support of a basal chondrichthyan divergence between holocephalans (the ratfish) and neoselachians (the sharks and the skate) and a basal neoselachian divergence between selachians (sharks) and batomorphs (the skate) and the monophyly of the teleostean group (ranging from the Arctic char [top] to the loach [bottom]) but without supporting the traditionally accepted basal position of cartilaginous fishes among extant gnathostomes. These findings put into question the phylogenetic validity of the taxonomic nomenclature attributed to various vertebrate, notably piscine, clades (Arnason et al., 2001).

Another study based on the same elasmobranchs position within the piscine tree but from different angle of this subject, was carried out with sequence characterization of gamma-crystallins, a common lens protein of most vertebrate eye lenses and the major protein component in lenses of fishes and in many mammalian species during embryonic and neonatal stages by Chuang et al. (1997). Comparison of protein sequences of two shark cDNAs with published sequences of gamma-crystallins from mouse, bovine, human, frog, and carp lenses indicated that there is about 61-80% sequence homology between different species of the piscine class, whereas only 47-66% is found between mammals and shark. A phylogenetic tree revealed the close relatedness between shark gamma M2-crystallin and mammalian gamma-crystallins and that between shark gamma M1 and teleostean gamma-crystallins. This results indicated that ancestral precursors of gamma-crystallins were present in the sharp lens long before the appearance of modern-day mammalian and teleostean gamma-crystallins (Chuang et al., 1997).

CONCLUSION

All the above mentioned studies, hypotheses and proposals suggest to us that the relationship between the class Chondrichthyes and teleosts is unresolved and ambiguous. All these studies indicate that there is still disagreement in establishing the sister group of the tetrapods. Some of these investigations suggest the possibility of Chondrichthyes being the sister group to the tetrapods, but it is still early to tell whether the Chondrichthyes are the sister group of the tetrapods, because of the dissimilar results obtained from different studies.

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