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Node Date Estimation of Diversified Species of Ray-Finned Fish Based on Morphological and Molecular (Vitellogenin 3) Characters Using Bayesian Analysis

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Abstract

Fish and other oviparous and ovoviviparous animals contain vitellogenin (Vtg), an egg yolk precursor phospholipoglycoprotein, which is the prerequisite for oocyte growth during oogenesis. Vtg is also employed as a biomarker to assess the reproductive health of female fish. In this study, we select 34 ray-finned fish under the class Actinopterygii to investigate the evolutionary time scale of their diversification age based on the molecular (vtg3 gene) as well as the combined (morphological and vtg3 gene) characters using different evolutionary models in Bayesian analysis. The analysis indicates that the species of different orders evolved in different epochs. In the case of molecular-based analysis, the orders Cyprinodontiformes and Perciformes are diversified in early Eocene to Oligocene, Anabantiformes in late Eocene, Cypriniformes in Oligocene & Salmoniformes Miocene. In the case of morpho-molecular based analysis the order Cyprinodontiformes is diversified in early Eocene to Oligocene, Anabantiformes in late Eocene, Perciformes in late Eocene to Oligocene, Cypriniformes in Oligocene to Miocene & Salmoniformes Oligocene to Pliocene. However, both analyses suggest that most of the selected species are diversified in Miocene, Oligocene, Eocene, and Paleocene Epoch between 5 – 65 MYA.

Introduction

Vitellogenin (Vtg) is an egg yolk precursor protein found in female fish and nearly all oviparous and ovoviviparous species (Biscotti et al., 2018). It is the egg yolk precursor glycolipophosphoprotein, which is the prerequisite for oocyte growth during oogenesis (Mahapatra et al., 2017). It is synthesized in the liver under the influence of ovarian estradiol-17β (E2). Then it is secreted into circulation to reach the ovary and get incorporated into the growing oocytes by receptor-mediated endocytosis (Sawaguchi et al., 2006 and references therein). Vtg is required as a prior condition for oocyte growth during oogenesis and is also used as a biomarker for evaluating the reproductive condition in female fish (Ling et al., 2015). Fish vitellogenin is mainly synthesized in the female liver but in some cases, with the presence of estrogenic endocrine disruptive chemicals (EDCs), male fish can express the vitellogenin protein in a dose-dependent manner (Zhang et al., 2015). It can be induced in either sex in any condition by exposure to estrogen (specially estradiol-17β). Vertebrate chordates (Akasaka et al., 2013) and invertebrates including mollusks (Agnese et al., 2013; Chen et al., 2018) and arthropods (Hannas et al., 2011; Wu et al., 2018) produce vitellogenin as well.

An experiment on tetrapods that concentrated on the loss of vitellogenin genes in placental mammals has proposed a theory for the evolution of this family that is based on the presence of an ancestral cluster and gene

duplication events (Brawand et al., 2008). According to this theory, there would have only been two genes present before the reptiles and amphibians split: vitI (also known as vtgI in Babin's nomenclature) and vitanc (also known as vtg ancestral), the latter of which would have evolved vtgII and vtgIII through duplication events in different taxonomic groups. More than half of all vertebrate species are ray-finned fish (Actinopterygii). Actinopterygii consists of five main clades: Polypterids (such as *Polypterus bichir*), Chondrosteans (such as paddlefish), Lepisosteids (such as *Lepisosteus osseus*), Amiids (such as Bowfin, Amia), and Teleosts (e.g., Seahorses). Although all other ray-finned fishes are regularly grouped with the polypterids as their sister group, there are significant disagreements over the relationships between the other divisions. Lepisosteids, Amiids, and Teleosts are all grouped as the Neopterygii in morphology-based phylogenies (PATTERSON, 1982; Regan, 1923), although it is unclear what the neopterygian sister group to the Teleostei is. Although once more, relationships within the Neopterygii are unstable, the majority of nuclear gene investigations (Crow et al., 2006; Hoegg et al., 2004; Kikugawa et al., 2004; Le et al., 1993; Lecointre et al., 1993) suggest a neopterygian topology. The neopterygian theory, however, has been refuted by recent studies of the nuclear gene RAG-1 (Venkatesh et al., 2001) and the entire mitochondrial genome sequences (Inoue et al., 2003). Instead, both contain a monophyletic group known as the "Ancient Fish Clade," which connects Chondrosteans, Lepisosteids, and Amiids. Although likelihood ratio analyses of the same data cannot rule out Neopterygian monophyly, the phylogenetic study of mitochondrial genomes provides substantial support for the "Ancient Fish Clade" topology in both Bayesian and maximum-parsimony statistical frameworks (Inoue et al., 2003). Other writers contend that the "Ancient Fish Clade" structure is a product of low taxon sampling (Cavin and Suteethorn, 2006).

Depending on the dataset and the method used, either the early Permian or the lower Carboniferous; (Inoue et al., 2003), the crown teleost date ranges between 285 and 334 million years (MYA) in the most recent mitochondrial genome data. however, fossil evidence places the minimum date for the genesis of crown group teleosts at 151 million years ago (MYA) (Upper Jurassic; Arratia 2000). According to fossil evidence from the Lower Triassic, the earliest crown-group neopterygian appeared 245 MYA ago. However, estimates based on mitochondrial genome data place the divergence of teleosts from amiids at between 417 and 390 MYA (Late Silurian or Middle Devonian, depending on the dataset and the method used; (Yamanoue et al., 2006)). The chondrostean (crown Actinopteri) and polypterid (crown Actinopterygii) total groups have successive fossil-based divergence estimations dating from 345 (early Carboniferous) and 392 MYA ago, respectively. However, because node dates have been determined using the "Ancient Fish Clade" tree topology, comparable mitochondrial estimations do not yet exist (Inoue et al., 2005). In conclusion, fossil evidence indicates that the current variety of actinopterygians is the result of numerous, widely spaced pre-teleost radiations that occurred in the second half of the Palaeozoic and Mesozoic eras. Molecular studies, on the other hand, place the teleost crown divergence at least 35 MYA before the Mesozoic, placing all of these events firmly within the Palaeozoic. In this study, we will try to know the phylogenetic relationship as well as the diversification ages of different ray-finned fish based on Bayesian analysis using the vtg3 gene sequence and morphological data.

Materials and Methods

Collection of the Morphological Character of Ray-finned Fish

The morphological characters of 34 ray-finned fish were collected from the literature (Larouche et al., 2018; Sallan, 2014). The study selected six body parts of the ray-finned fish mouth, head, abdomen, fins, lateral line, and swim bladder. Among six body parts, we chose 20 characters (Table 1).

Collection of the Molecular Character of Ray-finned Fish

The vtg3 gene sequences of 34 ray-finned fish were collected from the National Centre for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/). The species name, name of the gene, and gene bank accession number are listed in Table 2. The sequence was exported to FASTA format from NCBI and then edited using the Bio edit software program to eliminate any unwanted names and sequences that could not be used to pinpoint the analysis (Sharif S and Sung YY, 2015).

Sequence Editing, Alignment, and Analysis

Multiple alignments of nucleotide sequences of the vtg3 gene were constructed using the Clustal-MUSCLE program within MEGA X software. The MEGA X is used to determine the nucleotide diversity (π), estimated values of transition/transversion bias (R) for each nucleotide pair, and cluster analysis among the 34 ray-finned fish. We also used the maximum composite likelihood (MCL) method to estimate the pattern of nucleotide substitution (Kumar et al., 2018).

We employed combined morphological & molecular data to determine the node date & time scale of diversified species using MrBayes. For the Bayesian analysis, we used 10,000,000 generations. Each time, 1000 generations of the chain were sampled. Several chains were run for each analysis to verify convergence (Huelsenbeck and Ronquist, 2005, 2001). MrBayes supports relaxed clock models in which we used the

Table 1. Morphological character and character's state of ray-finned fish

Body parts of fish	Character	Character State
Mouth	Opening Size	Small=0, Large=1
	Jaw teeth	Without teeth=0, With teeth=1
	Snout	Small=0, Large=1, Blunt=2, Round=3
Head	Size	Small=0, Large=1
	Barbels	Without barbels=0 One pair of barbels=1, Two pair of barbels=2, Three pair of barbels=3
	Operculum	Absent=0, Present=1
Body	Scales	Without Scale=0, Cycloid=1, Ctenoid=2, Ganoid=3
	Body size	Short=0, Normal=1, Elongated=2
Fins	Pairs fin	One Pair=0, Two Pair=1
	Dorsal fin division	Not divided=0, Divide=1
	Dorsal fin numbers	One=0, Two=1
	Pelvic fin	Absent=0, Present=1
	Caudal fin shape	Round=0, Fork=1, Straight=2
	Anal fin types	Ray=0, Spine=1, Both=2
	Adipose fin	Absent=0, Present=1
Lateral line	Numbers	One=0, Two=1, Three=2
	Nature	Complete=0, Interrupted=1
	Scales on lateral line	Absent=0, Present=1
Swim bladder	Presentation	Absent=0, Present=1
	Duct	Without duct=0, With duct=1

Table 2. List of species and their gene bank accession no

Sl. No.	Fish Name	Gene	Gene bank Accession No.
1	*A. ocellaris*	vitellogenin 3	XM_023299650.1
2	*A. testudineus*	vitellogenin 3	XM_026345770.1
3	*A. anguilla*	vitellogenin 3	XM_035414662.1
4	*B. splendens*	vitellogenin 3	XM_029148744.2
5	*C. rostratus*	vitellogenin 3	XM_041934601.1
6	*C. lumpus*	vitellogenin 3	XM_034530674.1
7	*C. carpio*	vitellogenin 3	XM_042766001.1
8	*D. rerio*	vitellogenin 3	NM_131265.1
9	*E. electricus*	vitellogenin 3	XM_035523077.1
10	*G. affinis*	vitellogenin 3	XM_044129574.1
11	*G. aculeatus*	vitellogenin 3	XM_040185348.1
12	*K. marmoratus*	vitellogenin 3	XM_017413379.3
13	*M. cyprinoides*	vitellogenin 3	XM_036519547.1
14	*M. boesemani*	vitellogenin 3	XM_042005840.1
15	*M. saxatilis*	vitellogenin 3	XM_035653536.1
16	*N. whitei*	vitellogenin 3	XM_037698245.1
17	*O. gorbuscha*	vitellogenin 3	XM_046299305.1
18	*O. keta*	vitellogenin 3	XM_035774609.1
19	*O. tshawytscha*	vitellogenin 3	XM_024378647.2
20	*O. aureus*	vitellogenin 3	XM_031756179.1
21	*O. melastigma*	vitellogenin 3	XM_024278314.2
22	*P. hypophthalmus*	vitellogenin 3	XM_034308787.1
23	*P. promelas*	vitellogenin 3	XM_039653628.1
24	*P. georgianus*	vitellogenin 3	XM_034080783.1
25	*P. nattereri*	vitellogenin 3	XM_017702240.2
26	*S. salar*	Vitellogenin 3	XM_014215683.2
27	*S. namaycush*	vitellogenin 3	XM_039002060.1
28	*S. lucioperca*	Vitellogenin 3	XM_031307352.2
29	*S. umbrosus*	vitellogenin 3	XM_037769187.1
30	*S. chuatsi*	Vitellogenin 3	XM_044201124.1
31	*S. senegalensis*	vitellogenin 3	XM_044044449.1
32	*S. acus*	vitellogenin 3	XM_037250220.1
33	*T. jaculatrix*	vitellogenin 3	XM_041040165.1
34	*X. gladius*	Vitellogenin 3	XM_040128159.1

Independent Gamma Rate (Lepage et al., 2007) models. The stepping stone algorithm Markov chain Monte Carlo (MCMC) uses in MrBayes to perform this study.

Results

Information of Vtg3 Gene Sequences

For phylogenetic analysis, the nucleotide sequences of selected species were collected from NCBI. The length of these gene sequences varies from 2420 to 3667 bp and the alignment length is 3725 bp. During alignment, we got 647 bp of the conserved site, 3045 bp variable sites, 425 bp Singleton site, and 2608 bp Parsimony-informative sites throughout the 3725-nucleotide sequence (Table 3). Among the 3725 nucleotide sequences, G+C contains 46.8% and A+T contains 53.2%. Here, A+T is more unstable than G+C (Hershberg, 2016) for that reason so many variable sites contain out of 3725 bp. Here 3045 bp segregating sites (S) are present.

As far as we know, the range of nucleotide diversity was between 0.00000 and 0.01993 with a mean of 0.00388 which was a little bit higher than the median (0.00356) found in animal nucleotides regularly (Goodall-Copestake et al., 2012). Thus, the nucleotide diversity value in our finding is 0.294483 (Table 3), which is higher than the average value. Our calculated value of 1:163 (Table 3) for the Overall transition/transversion bias ratio (R) corresponds to the typical transition/transversion bias ratio for animal nucleotides.

Node-Date Estimation Based on Molecular (Vtg3 Gene) Data Using Bayesian Analysis

Based on molecular data we construct a Bayesian estimation of the phylogenetic tree (BEPT) to find out the time scale of diversified species. This phylogenetic tree shows the Erathem era, system period, and Series Epoch of the diversified species (Figure 1). In this tree, the branches are divided into many nodes, each of which underwent changes through time and became isolated from its forebears. We observed that all the species are diversified into two eras such as Mesozoic and Cenozoic, three periods such as Cretaceous, Paleogene & Neogene, and five epochs such as Paleocene, Eocene Oligocene Miocene, and Pliocene. Here, we mention the minimum to the maximum age of the diversified branch by highlighting the blue colour of each branch node, and this diversified branch developed within 100 to 3 MYA. To demonstrate how long evolution takes for diversification we divided the BEPT into four clusters.

Node-date Estimation Based on Morpho-molecular Data Using Bayesian Analysis

Based on Morphological and molecular data we construct another BEPT to find out the accuracy of Bayesian analysis. From this tree, we observed that all the species are diversified as that diversified in vtg3-based BEPT. Here, we mention the minimum to the maximum age of the diversified branch by highlighting the blue colour of each branch node, and this diversified branch developed within 100 to 1 MYA. The BEPT was divided into four clusters. All the species of the four clusters are systematically situated in the same position as the species that are found in vtg3-based BEPT.

Discussion

Discussion on Bayesian Estimation of the Phylogenetic Tree Based on Molecular (Vtg3) Data

Cluster 1

This group of seven species includes *Oryzias melastigma* diversified 73 million years ago (MYA) in the late Mesozoic, *Melanotaenia boesemani* diversified 65 MYA in the Paleocene, *Amphiprion ocellaris* and *Oreochromis aureus* diversified 59 MYA on their own during the same Epoch, *Gambusia affinis* diversified 51 MYA in the early Eocene. *Nematolebias whitei* and *Kryptolebias marmoratus* diversified in 33 MYA in the Oligocene (Figure 1).

Cluster 2

Before cluster 2, there was a first diversification in the Cretaceous period, 90 MYA, during which one branch evolved into cluster 1 and another into cluster 2. In the late Cretaceous period, 81 MYA, *Syngnathus acus* separately split off into a distinct clade, making up one of the fourteen species that make up Cluster 2. In the same period, another clade was divided into two groups, such as 2a and 2b, in 74 MYA. Then, about 64 MYA during the Paleocene, the 2a group once more split into two branches. (Figure 1). Among two branches one branch contains five species such as *Pseudochaenichthys georgianus*, *Sander lucioperca*, *Sebastes umbrosus, Gasterosteus aculeatus,* and *Cyclopterus lumpus* that were separated in 58 MYA in Paleocene, in 51 MYA in early Eocene, in 47 MYA in Early Eocene and 35 MYA in late Eocene Epoch respectively. The other branch contains three species such as *Siniperca chuatsi, Chelmon rostratus & Morone saxatilis* where *Siniperca chuatsi*, separated from *Chelmon rostratus & Morone saxatilis* in 61 MYA in Paleocene as well as *Chelmon rostratus* & *Morone saxatilis* separate from each other in 31 MYA in Oligocene Epoch (Figure 1). Then the 2b group again diversified in 61 MYA in Paleocene. In this group, *Xiphias gladius* and *Toxotes jaculatrix* separated from one another in 31 MYA, and *Solea senegalensis* separated from both of them in 48 MYA in the Early Eocene. On the other hand, in the late Eocene, *Betta splendens* diverged from *Anabas testudineus* at approximately 37 MYA. (Figure 1).

Table 3. Analysis of vtg3 gene sequence of different ray-finned fish

Number of Taxa	34
Sequence alignment length (bp)	3725
Sequence length (bp)	2420-3667
Conserved sites (bp)	647
Variable sites (bp)	3045
Parsimony-informative sites (bp)	2608
Singleton sites (bp)	425
Number of segregating sites (S)	3045
G+C content (%)	46.8
Nucleotide diversity (π)	0.294483
Overall transition/transversion bias ratio (R)	1:163

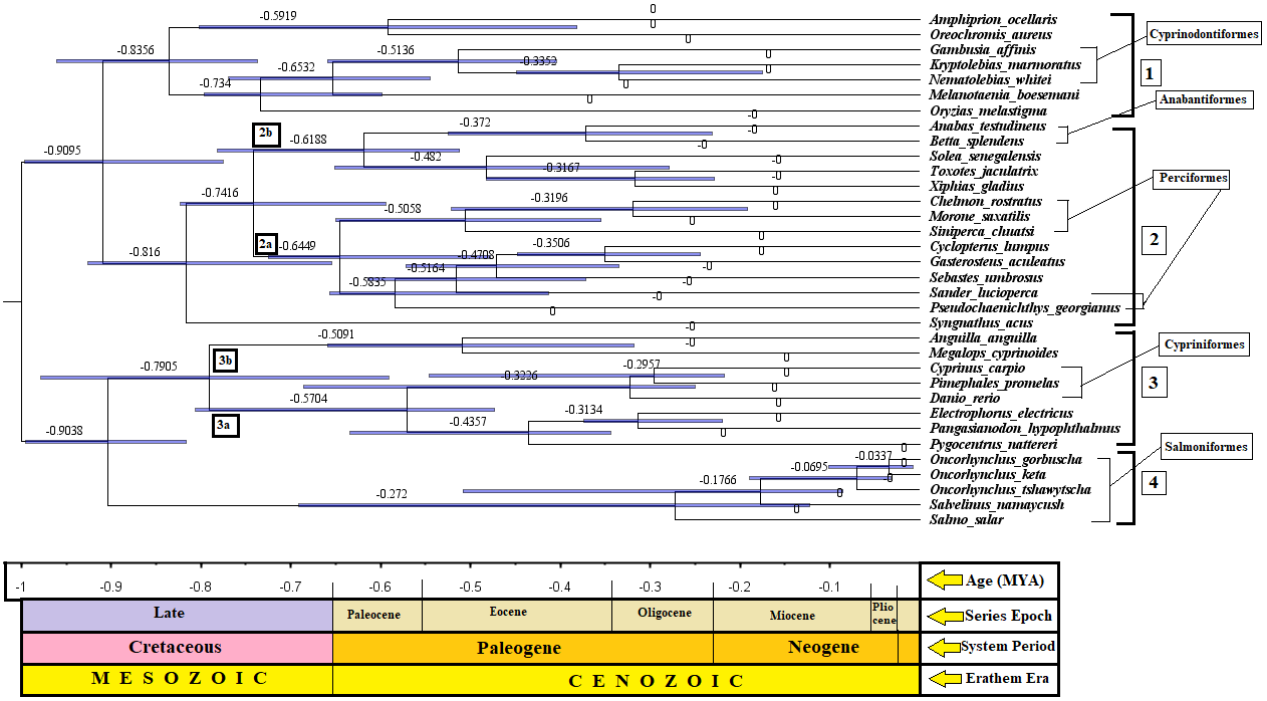

Figure 1. The phylogenetic tree of the ray-finned fish obtained from Bayesian Inference (BI) analysis of the vtg3 gene dataset. Different species are diversified in different ages which are indicated below by a colourful box. Each node depicts the diversifying age (MYA). The blue lines of each node indicate the range of diversifying age of that particular node. The species of the different order are creating different clades which are represented by arrow on the right side of the figure.

Cluster 3

Eight different species make up this cluster, which split into two groups called "3a" and "3b" in the late Cretaceous epoch (Figure 1). 57 MYA were further differentiated from the "3a" group. Containing six species, three of which, *Pygocentrus nattereri*, split out from *Pangasianodon hypophthalmus* and *Electrophorus electricus* in the late Eocene 43 MYA, and again in the Oligocene 31 MYA *Pangasianodon hypophthalmus* & *Electrophorus electricus* separate to each other. The next three species of the 3a group such as *Danio rerio* separated from *Cyprinus carpio* & *Pimephales promelas* in 32 MYA in the Oligocene and again *Cyprinus carpio* & *Pimephales promelas* separate from each other independently in 29 MYA in the same epoch. (Figure 1). The '3b'group diversified independently in 50 MYA into *Anguilla anguilla*, and *Megalops cyprinoides* in the early Eocene epoch (Figure 1).

Cluster 4

Five species make up this cluster, although three of them, *Oncorhynchus gorbuscha*, *Oncorhynchus keta*, and *Oncorhynchus tshawytscha*, are the most closely related. They diverged from one another between 3-6 MYA in the Pliocene and Miocene, respectively. *Salvelinus namaycush* and *Salmo salar*, two other species, split off in the Miocene (17 MYA) and Oligocene (27 MYA), respectively. (Figure 1).

The diversification of the ancestor and descendant started from 100 MYA, and the majority of the species diversified over the Paleocene, early Eocene, Late Eocene, Oligocene Epochs & Miocene epochs (Figure 1).

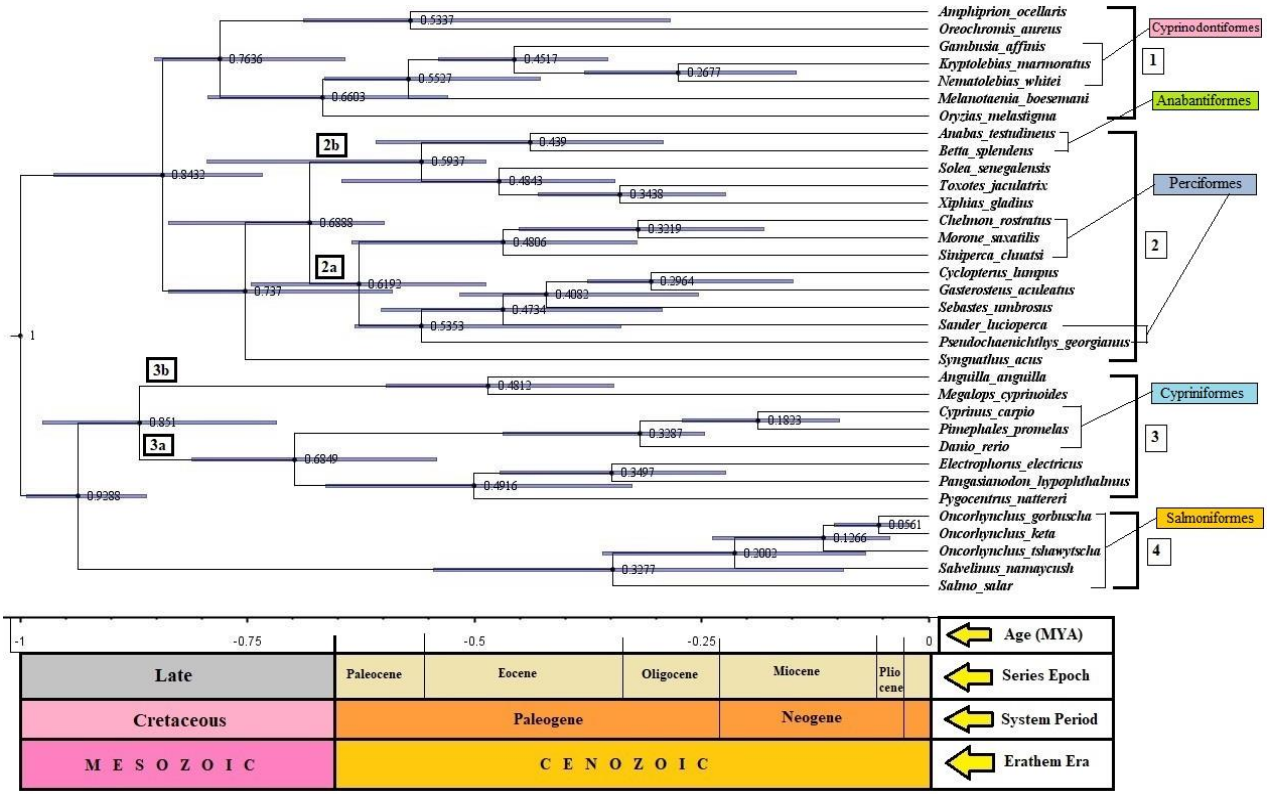

Figure 2. The phylogenetic tree of the ray-finned fish obtained from Bayesian Inference (BI) analysis of combined morphological data and vtg3 gene dataset. Different species are diversified in different ages which are indicated below by a colourful box.

Discussion on Bayesian Estimation of the Phylogenetic Tree Based on Combined Morpho-molecular Data

Cluster 1

This cluster consists of seven species, among them *O. melastigma* diversified in 66 MYA in the late Mesozoic, *M. boesemani* diversified in 55 MYA in the early Eocene, *A. ocellaris* & *O. aureus* diversified in 53 MYA autonomously in same Epoch, *G. affinis* diversified in 45 MYA in the early Eocene, *N. whitei, K. marmoratus* diversified in 26 MYA in the Oligocene (Figure 2).

Cluster 2

Before the formation of cluster 2, the first diversification occurred in 84 MYA in the Cretaceous period in which one branch converted into cluster 1 and another into cluster 2. Cluster 2 consists of fourteen species, among them, *S. acus* independently separated into a single clade in 73 MYA in the late Cretaceous. Another clade diversified into two groups such as 2a and 2b in 68 MYA in the same period. Then the 2a group again diversified into two branches in 61 MYA in Paleocene (Figure 2). Among two branches one branch contains five species such as *P. georgianus*, *S. lucioperca*, *S. umbrosus*, *G. aculeatus,* and *C. lumpus* that were separated in 53 MYA in Early Eocene, in 47 MYA in early Eocene, in 40 MYA in Late Eocene and 29 MYA in Oligocene Epoch respectively. The other branch contains three species such as *S. chuatsi*, *C. rostratus* & *M. saxatilis* where *S. chuatsi*, separated from *C. rostratus* & *M. saxatilis* in 48 MYA in early Eocene as well as *C. rostratus* & *M. saxatilis* separate from each other in 32 MYA in Oligocene Epoch. Then the 2b group again diversified in 59 MYA in Paleocene. In this group *S. senegalensis* separate from *X. gladius* & *T. jaculatrix* in 48 MYA in Early Eocene and again, *X. gladius* & *T. jaculatrix* separate from each other in 34 MYA. On the other hand, *B. splendens* separated from *A. testudineus,* in 43 MYA in late Eocene (Figure 2).

Cluster 3

This cluster consists of eight species and all the species diversified into two groups such as '3a' & '3b' in the late Cretaceous period (Figure 2). The '3a' group was further divided into 68 MYA. Which contain six species among them three species such as *P. nattereri* separated from *P. hypophthalmus* & *E. electricus* in 49 MYA in early Eocene, and again *P. hypophthalmus* & *E. electricus* separate from each other in 34 MYA in the late Eocene. The next three species of the 3a group such as *D. rerio* separated from *C. carpio* & *P. promelas* in 32 MYA in the Oligocene and again *C. carpio* & *P. promelas* separate from each other independently in 18 MYA in the Miocene. (Figure 2). The '3b'group diversified independently in 48 MYA into *A. anguilla, M. cyprinoides* in the early Eocene epoch (Figure 2).

Cluster 4

This cluster consists of five species among them three species such as *O. gorbuscha, O. keta,* and *O. tshawytscha* are the most closely related taxa that were diversified from each other between 5-12 MYA in Pliocene and Miocene respectively (Figure 2). The rest of the species such as *S. namaycush* & *S. salar* separated in 20 MYA in Miocene & 32 MYA in Oligocene respectively (Figure 2).

The diversification of the ancestor and descendant started from 100 MYA, and the majority of the species diversified within the Paleocene, early Eocene, Late Eocene & Oligocene Epochs (Figure 2).

Conclusion

The Bayesian estimation of both the phylogenetic analysis revealed that molecular (vtg3) based BEPT is more robust than the Morpho-molecular based BEPT. Because the era and periods of diversified species are completely similar in both analyses, but a little bit of changes occurs in Epoch, for example in the case of morpho-molecular based BEPT the order Cyprinodontiformes is diversified in early Eocene to Oligocene, Anabantiformes in late Eocene, Perciformes in late Eocene to Oligocene, Cypriniformes in Oligocene to Miocene & Salmoniformes Oligocene to Pliocene. However, most of the selected species are diversified in the early as well as late Eocene, Oligocene, and Miocene Epoch between 5 – 56 MYA. In the case of molecular-based BEPT Cyprinodontiformes and Perciformes are diversified in the early Eocene to Oligocene, Anabantiformes in the late Eocene, Cypriniformes in Oligocene & Salmoniformes Miocene. However, most of the selected species are diversified in Miocene to Paleocene Epoch between 5 – 65 MYA. On the other hand, in morpho-molecular-based BEPT, there has no species diversification in Paleocene Epoch but in molecular-based BEPT, the four species were diversified such as *A. ocellaris, O. aureus, M. boesemani* & *P. georgianus*. Our analysis also revealed that, among the 34 species 2 species evolved in the Mesozoic and 32 species evolved in the Cenozoic era.

Ethical Statement

Not applicable. Because morphological characters of fishes were collected from different literature and all the sequences of the fishes were collected from NCBI.

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Author Contribution

Sk Kabita and Sk Nasim Ali both the authors collected the data and wrote the manuscript. Sk Md Abu Imam Saadi designed and corrected the manuscript. All authors read and approved the final manuscript.

Conflict of Interest

The author(s) declare that they have no known competing financial or non-financial, professional, or personal conflicts that could have appeared to influence the work reported in this paper.

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