Evolution and Ecology in Widespread Acoustic Signaling Behavior Across Fishes

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Abstract

Acoustic signaling by fishes has been recognized for millennia, but is typically regarded as comparatively rare within ray-finned fishes; as such, it has yet to be integrated into broader concepts of vertebrate evolution. We map the most comprehensive data set of volitional sound production of ray-finned fishes (Actinopterygii) yet assembled onto a family level phylogeny of the group, a clade representing more than half of extant vertebrate species. Our choice of family-level rather than species-level analysis allows broad investigation of sonifery within actinopterygians and provides a conservative estimate of the distribution and ancestry of a character that is likely far more widespread than currently known. The results show that families with members exhibiting soniferous behavior contain nearly two-thirds of actinopterygian species, with potentially more than 20,000 species using acoustic communication. Sonic fish families also contain more extant species than those without sounds. Evolutionary analysis shows that sound production is an ancient behavior because it is present in a clade that originating circa 340 Ma, much earlier than any evidence for sound production within tetrapods. Ancestral state reconstruction indicates that sound production is not ancestral for actinopterygians; instead, it independently evolved at least 27 times, compared to six within tetrapods. This likely represents an underestimate for actinopterygians that will change as sonifery is recognized in ever more species of actinopterygians. Several important ecological factors are significantly correlated with sonifery – including physical attributes of the environment, predation by members of other vertebrate clades, and reproductive tactics – further demonstrating the broader importance of sound production in the life history evolution of fishes. These findings offer a new perspective on the role of sound production and acoustic communication during the evolution of Actinopterygii, a clade containing more than 34,000 species of extant vertebrates.

Keywords: acoustic communication, sound production, convergent evolution, Actinopterygii, key innovation

Introduction

While spoken language is regarded as a uniquely human attribute, the use of sound as a vertebrate communication channel also occurs in other terrestrial species and marine mammals (Bradbury and Vehrencamp 2011, Ladich and Winkler 2017). Less well known is its prevalence among fishes, despite multiple early descriptions of anatomy, physiology or behavior (Dufossé 1874, Tower 1908), including von Frisch's comments on its widespread distribution as early as 1938:

> It may well be asked for what purpose fishes are able to hear so well in silent water. … We know many species of sound-producing fish. There may be many more species of sound-producing fishes not yet known. … [and] much to discover in the future about the language of fishes. (von Frisch 1938)

Since then, a growing body of evidence shows the importance of volitional sound production in social communication and reproduction especially among ray-finned fishes (Actinopterygii) (Ladich 2015), a group that includes more than half of extant vertebrate diversity. Together with Sarcopterygii (coelacanths, lungfishes, and tetrapods, which includes amphibians, reptiles, birds, and mammals), Actinopterygii is one of two extant radiations of bony vertebrates(Nelson et al. 2016). Although there is evidence for soniferous behavior in 800-1000 species of actinopterygians (Ladich 2015, Ladich et al. 2006) and numerous studies of neural and hormonal mechanisms that are similar to those of tetrapods (Bass 2014, Zhang and Ghazanfar 2020), more widespread recognition of acoustic behavior among fishes and its integration into broader concepts of vertebrate evolution are still lacking. This is, in part, because sound production is not externally obvious in fishes, nor can those sounds be easily detected underwater without specialized technology (Mann et al. 2016).

A recent study on the evolution of acoustic communication focused on tetrapods, recognized the important need for a comparable study of fishes (Chen and Wiens 2020). Using evolutionary modelling, combined with the most recent comprehensive phylogeny, we show that volitional sound production is ancestral for several speciose radiations that together comprise nearly two-thirds of the 34,000 valid extant species of actinopterygians (Fricke et al. 2020). We also show that sound production has evolved at least 27 times among actinopterygians, including the basal clade that diverged in the Carboniferous Period (~340 Ma). Thus, actinopterygian sonifery is likely an ancient communication mode that originated earlier than estimates for the origin of acoustic communication in tetrapods where it is proposed to have evolved six times (Chen and Wiens 2020). Nocturnality was identified as the one ecological factor contributing to the evolution of acoustic communication among tetrapods (Chen and Wiens 2020). We show that actinopterygian families with soniferous species are correlated with multiple ecological factors, including reproductive and mating tactics, trophic levels and complexity of habitats that vary in depth, substrate composition, and salinity.

In aggregate, our evidence strongly supports the hypothesis that, like tetrapods, acoustic communication is an ancient but also convergently evolved innovation across actinopterygian fishes. Unlike tetrapods, we find that actinopterygian soniferous behavior is associated with a broad range of abiotic and biotic factors, which may explain its repeated and independent evolution nearly 30 times in clades that include many of the most species-rich groups. The demonstration of repeated evolution of acoustic communication in tetrapods and now in ray-finned fishes highlights the strong selection pressure favoring this signaling modality across vertebrates.

Materials and Methods

We operationally define acoustic signaling, or soniferous behavior (we use these terms interchangeably) as volitional sound production associated with acoustic communication rather than by-products of feeding or locomotion. Like Chen and Wiens (2020), we score the presence or absence of soniferous behavior at a family level, in this case for valid extant species of actinopterygians in 461 families represented by species in Rabosky et al. (2018) with the assumption that sonifery is conserved and characteristic at the family level (Fricke et al. 2018). We use three lines of evidence from one or more reports to demonstrate the presence of soniferous behavior in 167 of the 461 families in our analysis (Fig. S1, Tables S1, S2): 1) quantitative or pictorial documentation of acoustic recordings (107 families); 2) the presence of specialized morphology strongly predictive of sonic ability (Fine and Parmentier 2015) (26 families); or 3) qualitative descriptions of sounds strongly predictive of sonic ability and behaviorally-relevant acoustic signals (Hubbs 1920, von Frisch 1938) (34 families). To be conservative, we code as 0 (silent) all families lacking such evidence.

Data on fish sound production were obtained from journals, technical reports, conference proceedings, theses, and books (Table S1). We mapped the presence (= 1) or absence (i.e. silent, = 0) of soniferous behavior onto Rabosky et al.'s (2018) recent phylogeny of Actinopterygii that includes species from 461 families (Fig. S1, Table S1). Species included in the phylogeny by Rabosky et al. (2018) were assigned to families using Catalog of Fishes (Fricke et al. 2018). Since Rabosky et al. (2018), new species have been described and familial designations changed (Fricke et al. 2020). We note that four families in our analyses (Abyssocottidae, Comephoridae, Cynolebiidae, Hapalogenyidae) were merged into other families, and approximately 14 new families were recognized (Fricke et al. 2020).

We scored the presence or absence of soniferous behavior as a binary character (Table S2). Ancestral states were calculated using stochastic character mapping with the make.simmap function in the *phytools* (Revell 2012) package for R, with 1,000 MCMC generations, sampling every 100 generations. Root node values and transition rates were calculated by simulation and posterior probabilities were mapped using the densityMap function in *phytools* (Revell 2012) (Figs 1, 2). Phylogenetic signal was calculated using the *D* statistic (Fritz and Purvis 2010) with the *caper* R package (Orme et al. 2013).

Ecological attributes for all 461 families were downloaded from FishBase(Froese and Pauly 2019) using *rfishbase* 3.04 R package (Boettiger et al. 2012) (see SI Appendix, Table S2 for complete data). Ecological parameters predictive of soniferous behavior were determined using logistic regression with a phylogenetic generalized linear model (Ives and Garland 2010) in *phylolm* 2.6 R package (Ho and Ané 2014). Since we tested several models for each set of parameters, we used Bonferroni correction to reduce Type I error (Rice 1989). Data on species number per family are from the Eschmeyer Catalog of Fishes (Fricke et al. 2020).

Results

Ancestral States. Stochastic character mapping simulates the distribution of a character along branches of a phylogeny (Bollback 2006, Revell 2012) and summaries of many simulations (N = 1000 in this study) are used to compute probabilities of a character being ancestral at nodes. Figure 1 reconstructs ancestral states of soniferous behavior across actinopterygian phylogeny, showing the probabilities of soniferous behavior being ancestral, ranging from 0% (silent) to 100% (soniferous); Table 1 presents probability values at key nodes.

Although sonifery occurs in the three extant clades of non-teleostean actinopterygians (Polypteriformes, Acipenseriformes, and Holostei) (Fig. 1), this reconstruction reveals that soniferous behavior is unlikely ancestral for Actinopterygii (29.4% probability). Teleostei, which comprises > 99.8% of actinopterygian species, also has low support (15.2% probability) that soniferous behavior is the ancestral state. Likewise, Osteoglossomorpha, an early diverging clade of teleosts, contains several soniferous families, but only a 25.5% probability that soniferous behavior is ancestral. Otocephala, a speciose subclade of actinopterygians exhibiting morphological adaptations to enhance hearing (Braun and Grande 2008), has an even lower probability that soniferous behavior is ancestral, 9.6%. Ostariophysi, a large subgroup of otocephalans well known for the Weberian apparatus (chain of bony elements that enhance hearing), has the lowest value among the groups analyzed that soniferous behavior is ancestral, 8.5%. A second large subclade of Teleostei, Euteleostei, includes two-thirds of living fish species, but here, too, there is little support that soniferous behavior is ancestral, 9.6%.

We find much stronger support for soniferous behavior as a character at the base of some key nodes. Siluroidei, a subclade of catfishes, and Curimatoidea, a subclade of characins, have 96.7% and 67% probabilities, respectively, that soniferous behavior is ancestral (Figs. 1, 2a. Acanthomorpha, which includes 85% of fish species in marine habitats (Wainwright and Longo 2017), has a low probability (31.4%) sonifery is ancestral. However, two of its subclades, Eupercaria (e.g., “surgeonfish”, “drums”, “grunts”, scorpaenoids) and Anabantaria + Carangaria + Ovalentaria (e.g., gouramis [Osphronemidae], jacks [Carangidae], cichlids [Cichlidae]) have 88.6% and 64.1% probabilities, respectively (Fig. 2b, c). An even higher probability value, 97.5%, supports soniferous behavior as ancestral for a crown group within Eupercaria, Hexagrammidae (greenlings) + Zoarcoidei (e.g., wolffishes) + Cottoidei (e.g., sculpin) (Fig. 2b).

In aggregate, our results indicate that acoustic signaling, or soniferous behavior, has a high probability (>75%) of being ancestral for at least 27 nodes across Actinopterygii (Fig. S2). We interpret this as evidence of widespread, independent evolution of volitional sound production.

Phylogenetic signal. Patterns of ancestral states alone do not predict evolutionary processes underlying character evolution, making it necessary to evaluate phylogenetic signal (Blomberg et al. 2003). We use the *D* statistic for binary characters (Chen and Wiens 2020, Fritz and Purvis 2010), in this case soniferous or silent, to calculate phylogenetic signal. For each clade, we computed *D* and the probability that character evolution results from Brownian phylogenetic structure, which can be visualized by the proximity of the clade's observed *D*-value to the center of the distribution of simulated *D*-values assuming Brownian evolutionary processes (Fig. S3). Where *D* is > 0.0, the evolution of soniferous behavior is phylogenetically random and not conserved within a group. Where *D* is close to or < 0.0, evolution of soniferous behavior results primarily from Brownian evolutionary processes and phylogenetic structure, and is conserved within a group.

Actinopterygii and Teleostei have *D* values of 0.404 and 0.368, respectively (see Table 1 for all *D* values). The next set of large clades, Otocephala, Ostariophysi and Euteleostei, have *D* values of 0.328, 0.208, and 0.200, respectively. These values indicate that soniferous behavior is not conserved within these groups, in agreement with the relatively low to intermediate probabilities that it is ancestral for these groups (8.5% - 29.4%; Table 1). For Siluroidei, a large subclade of Otocephala, *D* is -0.469, consistent with the high probability that this character is ancestral for Otocephala (96.7%, Table 1).

Acanthomorpha has $D = 0.270$, in agreement with the relatively low probability that sonifery is ancestral for this group (Table 1). However, within Acanthomorpha, several nested groups show negative D values or values very close to 0.0, in agreement with the high probabilities that soniferous behavior is ancestral for these groups (Table 1). This includes two large acanthomorph clades, Eupercaria and Anabantaria + Carangaria + Ovalentaria, with D values of -0.066 and 0.075, respectively. Within Eupercaria, Hexagrammidae + Zoarcoidei + Cottoidei, $D = -0.676$. The two smallest subclades studied, Osteoglossomorpha and Curimatoidea, have D values of 1.680 and -31.388, respectively, that agree with low (Osteoglossomorpha) and high (Curimatoidea) probabilities sonifery is ancestral for these groups (Table 1).

Hearing specializations. Novel auditory morphologies, generally referred to as hearing specializations, e.g., the Weberian apparatus or swim bladder extensions contacting the otic capsule, may have evolved 20 times within Teleostei (Braun and Grande 2008). Families with these adaptations (Braun and Grande 2008, Colleye et al. 2019, Radford et al. 2013) (Table S2), 62 of 119, are highly correlated with soniferous behavior (phylogenetic logistic regression; $P = 0.004$).

Habitat Complexity. Actinopterygian families with soniferous taxa live in habitats that vary in complexity depending on one or more of the following: water salinity, depth and substrate composition (Boettiger et al. 2012, Froese and Pauly 2019) (Table S2). Freshwater and brackish water are more likely than marine habitats to have families with soniferous taxa ($P < 0.000$, < 0.000, > 0.05, respectively; values here and below based on logistic regression with a phylogenetic generalized linear model(Ives and Garland 2010) after Bonferroni correction). Marine families in shallow intertidal (< 5 m depth) and neritic (< 200 m depth) zones are more likely to have soniferous taxa ($P < 0.000$) than families with oceanic (i.e. marine pelagic) fishes ($P > 0.05$). Within families with freshwater species, there is no significant correlation of soniferous behavior with depth (littoral zone, sublittoral zone, caves; P values > 0.05). Habitats with coarse ($P = 0.008$), but not fine ($P > 0.05$), sediment are also more likely to have families with soniferous taxa. Soniferous families are not more likely to live in any one particular climate (polar, temperate, boreal, tropical, subtropical; P values > 0.05).

Grosberg et al. (2012) consider the complexity of freshwater and marine environments, and how more structurally complex habitats are associated with higher biodiversity. Of the 27 independent evolutionary events of soniferous behavior we describe (Fig. S2, Table S3), 18 clades are primarily freshwater, and nine are either marine, anadromous, or mixed. With the exception of Myctophidae, 26 of the 27 clades live in shallow waters or demersal/benthic habitats.

Feeding and Reproductive Ecologies. Actinopterygian families exhibiting acoustic signaling are associated with several other behavioral phenotypes (Table S2). Marine families with grazing species are more likely to contain soniferous taxa ($P = 0.011$), as are families with mating tactics and reproductive modes ranging from batch spawning ($P < 0.0001$) and internal fertilization ($P = 0.005$), to nest guarding ($P = 0.001$), parental care ($P = 0.004$) and alternative reproductive tactics (17 of 23 families identified by Mank and Avise (2006); $P < 0.0001$). Families showing sex reversal (protogyny, protandry, hermaphroditism) are not more likely to contain soniferous taxa ($P > 0.05$). Consistent with field observations, actinopterygian families with soniferous taxa are significant prey for birds (Elliott et al. 2003) and elasmobranchs (Navia et al. 2007) (*P* = 0.002, 0.001, respectively; cetaceans (McCabe et al. 2010) and pinnipeds(Lance and Jeffries 2009) are known predators, but *P* values > 0.05).

Discussion

Although actinopterygian fishes have long been known capable of volitional sound production (Popper and Casper 2011), few studies integrate their acoustic communication ability into a broad evolutionary context across bony vertebrates (Bass et al. 2015, Fine and Parmentier 2015). We show evidence for soniferous behavior in 167 families, containing nearly two-thirds of the estimated 34,000 valid extant species of actinopterygians (Figs. 1, 2; Tables S1, S2). Actinopterygians independently evolved soniferous ability at least 27 times (Fig. S2, Table S3). To our knowledge, all species studied to date that are capable of volitional sound production have been shown to use sound in a signaling context to either conspecific or heterospecific individuals (Ladich 2015, Ladich et al. 2006). Consequently, sound production is likely an important communication modality in most actinopterygian species. This includes two species of polypterids (Ladich and Tadler 1988), members of a family that diverged from the actinopterygian stem circa 340 Ma during the Carboniferous Period (Giles et al. 2017). This suggests that acoustic communication in actinopterygians may have similarly ancient origins, predating its emergence within tetrapods, which occurred circa 100-200 Ma (Chen and Wiens 2020). We further show significant correlations between families with soniferous species and diverse freshwater and marine habitats, predation by birds and elasmobranchs, and many reproductive and mating tactics. In parallel with recent findings for tetrapods(Chen and Wiens

2020), our results indicate strong selection to exploit acoustic signaling for communication and ecological success across vertebrate evolution.

Pattern and process. Within Actinopterygii, soniferous behavior occurs across the most speciose clades and has evolved independently at least 27 times, compared to only six within tetrapods (Chen and Wiens 2020). This high frequency of convergent evolution suggests that "the interplay of historical contingency and natural selection" (Blount et al. 2018) has a prominent role in the evolution of vertebrate acoustic communication behavior. A comparable degree of convergent evolution among actinopterygians is reported for alternative reproductive tactics (Mank and Avise 2006), suggesting that extensive convergence may be an evolutionary attribute of behavioral and reproductive ecology as well as other characters in actinopterygians (e.g., venom (Smith and Wheeler 2006), restricted gill openings (Farina et al. 2015), vertebrae (Ward and Brainerd 2007), adipose fins (Stewart et al. 2014), migratory behavior (Burns and Bloom 2020), bioluminescence (Davis et al. 2014)).

The presence and absence of soniferous behavior among actinopterygians likely includes secondary loss, suggested elsewhere to drive speciation (Miles and Fuxjager 2019). Within speciose clades where sonifery has a high probability of being ancestral (Siluroidei, Eupercaria, Anabantaria + Carangaria + Ovalentaria, Hexagrammidae + Zoarcoidei + Cottoidei), non-soniferous clades may have secondarily lost this character. Hexagrammidae + Zoarcoidei + Cottoidei have 97.9% probability that sound production is ancestral, and a very low *D* value (-0.676, Table 1, Fig. 2b). Within this group, Cottoidei comprises an estimated 850 species (compared to 9 hexagrammid and 405 zoarcoid species) with a very high probability that soniferous behavior is ancestral (98.8%). This correlates with a low *D* value (-0.330), suggesting that the evolution of soniferous behavior within Cottoidei results primarily from Brownian evolutionary processes. Fish and Mowbray (1970) comment on the absence of sound production in Zoarcidae [their Zoarchidae]. If further research provides conclusive evidence for absence, then our tree (Fig. 2c) likely indicates secondary loss. Other places to investigate potential loss of soniferous capacity are between sister groups where one is coded as silent (e.g., Lophiiformes) and the other is soniferous (Tetraodontiformes; Fig. 2c). A particularly fascinating case of secondary loss concerns catfishes in the genus *Synodontis*; some species are only soniferous and others only weakly electric (Boyle et al. 2014). Weakly electric *Synodontis* have reduced sonic muscle characters, but share characters with myogenic electric organs (Kéver et al. 2020). Further demonstration of the loss of sonifery would support the hypothesis that losses can be as important in generating diversity as gains of complexity (Miles and Fuxjager 2019).

Together, *D* values show soniferous behavior is highly conserved (low *D*) in some lineages, but less in others (high *D*). Comparisons of ancestral state probabilities and *D* values show that clades with a higher probability of soniferous ability in the common ancestor also tend to have lower *D* values (Table 1, Fig. 3a), indicating that when it is ancestral, it has a higher probability of being conserved within a clade. This relationship becomes even clearer when plotting ancestral state probabilities against the probability that phylogenetic signal results from Brownian phylogenetic structure (Fig. 3b). It may intuitively follow that an ancestral trait is more likely to be conserved, but these two metrics are independently derived.

Plotting the relationship between ancestral state estimation and phylogenetic signal may indicate a broader conceptual link between pattern (ancestral states) and process (phylogenetic signal) in character evolution (Fig. 3b). Some cases deviate from this relationship. For example, it is unlikely that soniferous behavior is ancestral for Ostariophysi, yet the character is relatively conserved within this clade. Exceptions indicate that the relationship is not necessitated mathematically, but instead is governed by evolutionary principles. Characters that vary enormously in phylogenetic signal throughout lineages and are characterized by repeated gains and losses, such as soniferous behavior, may be more likely to exhibit a relationship between ancestral state and phylogenetic signal.

Ecological success. Our results provide compelling evidence that soniferous evolution contributes to ecological success in many actinopterygian clades, as it does in tetrapods and insects (Miles et al. 2018, Wilkins et al. 2013). For example, we can now add soniferous behavior to the suite of traits considered as evolutionary drivers in Acanthomorpha, which account for 85% of fish species in marine habitats (Wainwright and Longo 2017), because many soniferous species belong to basal acanthomorph groups, e.g., Beryciformes, Ophidiiformes, and Gadiformes (Fig. 1). Soniferous behavior may be a convergent evolutionary innovation contributing to ecological success in rapidly evolving and speciose subclades of actinopterygians for which sonifery is ancestral. For example, Eupercaria and Siluroidei are nested within rapidly evolving lineages in Actinopterygii (Table 1) (Alfaro et al. 2009), and it is intriguing to hypothesize that sonifery may promote diversification through sexual selection. This also appears to be the case for soniferous tetrapods, including birds and eutherian mammals (Alfaro et al. 2009, Chen and Wiens 2020). Molecular phylogenetic support for Curimatoidea, a clade recently recognized (Arcila et al. 2017, Betancur-R. et al. 2019) within Characiformes (Figs 1, 2), is bolstered by our evidence that soniferous behavior is ancestral for this clade. Intriguingly, the relationship between repeated evolution of soniferous behavior in clades that live in shallow water or structurally complex or fragmented habitats where diversification is more likely to occur (Grosberg et al. 2012), suggests a strong selection for acoustic communication within biodiverse communities.

Urick (1975) points out at the very beginning of his classic text, Principles of Underwater Sound, that water is an excellent medium for sound transmission compared to other modalities:

> Of all the forms of radiation … sound travels through the sea the best. In the turbid, saline water of the sea, both light and radio waves are attenuated to a far greater degree than is that form of mechanical energy known as sound. (Urick 1975)

The relationship between physical sound transmission in an aquatic medium with acoustic communication has previously been identified as promoting this modality in underwater habitats (Grosberg et al. 2012, Wilkins et al. 2013). Our analyses show that sonifery is correlated with families living in fresh or brackish waters, marine intertidal or neritic zones, and habitats with coarse as opposed to fine sediment bottoms. Salinity, water depth and substrate composition are all physical properties of the environment that impact acoustic properties (Forrest et al. 1993, Urick 1975). For example, transmission loss due to absorption (“conversion of acoustic energy into heat”; Urick 1975) is greater in seawater and shallow water. Sound speed is greater in bottoms with coarse substrates, but unpredictable in shallow water because of salinity, currents and changes in temperature at the surface. To more completely understand how physical properties of the environment combine to impact acoustic communication, direct measurements are needed in a range of habitats (Bass and Clark 2003, Lugli 2015).

We report a correlation between families exhibiting soniferous behavior and hearing specializations that enhance sound detection. This enhances the efficacy of other physiological mechanisms for audio-vocal coupling that support acoustic communication. Actinopterygians share with tetrapods (and insects) two hallmarks of audio-vocal coupling: auditory encoding of the spectral and temporal properties of conspecific and heterospecific vocalizations (Bass et al. 2005, Rohmann et al. 2013), and a central vocal corollary discharge, whereby vocal pattern generator neurons inform auditory neurons about the spectral and temporal attributes of one's own vocalizations (Chagnaud and Bass 2013).

Perhaps the most compelling evidence that acoustic signaling behavior contributes to ecological success within Actinopterygii is the evidence we present of its association with alternative mating tactics and multiple modes of reproduction, including nest guarding, batch spawning, internal fertilization, and parental care. These findings point to many taxa of soniferous actinopterygians as providing new testing grounds for investigating the influence of sexual and ecological selection, and drift on the evolution of acoustic communication systems (Amorim et al. 2018, Bose et al. 2018, Emlen and Oring 1977, Lee and Bass 2006, Myrberg and Riggio 1985, Wilkins et al. 2013).

Concluding Comments. The remarkable ecological, behavioral, and morphological diversity of actinopterygian fishes provides opportunities to test evolutionary trajectories, constraints or roles of acoustic communication. Because several key functional innovations have been associated with diversification and evolutionary success in actinopterygians (e.g., acanthomorphs; Wainwright and Longo 2017), we argue that sound production and acoustic signaling may be similar key innovations in actinopterygian evolution. In a broader sense, and together with recent demonstrations of acoustic communication in tetrapods (Chen and Wiens 2020), our findings highlight the important role that acoustic communication has played in the history of vertebrates.

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Author Contributions

A.H.B., W.E.B., A.N.R. (listed alphabetically) conceived the study. All authors aggregated data. A.H.B., W.E.B., S.C.F., A.N.R. (listed alphabetically) analyzed the data. S.C.F. and A.N.R. conducted statistical analyses. A.N.R. wrote initial draft; A.H.B., W.E.B., S.C.F., A.N.R. (listed alphabetically) revised, and all authors approved, final version of the manuscript.

Competing Interests

None

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Table 1. Probabilities sound production is ancestral state, and phylogenetic signal for Actinopterygii (ray-finned fishes) and some of its sub-clades.

Clade	**Number of Extant Families in Figure 2**	**Estimated Number of Valid Extant Species[1]**	**Probability Soniferous Behavior is Ancestral to Clade[2,3]**	**Phylogenetic Signal**	
				D statistic	**Probability of Brownian Phylogenetic Structure[2]**
Actinopterygii	461	34,030	29.4%	0.404	0.037
Teleostei	456	33,970	15.2%	0.368	0.057
Osteoglossomorpha	6	250	25.5%	1.680	0.165
Otocephala	96	11,720	9.6%	0.328	0.288
Ostariophysi	88	11,160	8.5%	0.208	0.400
Curimatoidea	6	420	67.0%	-31.388	0.809
Siluroidei	30	2,340	96.7%	-0.469	0.609
Euteleostei	333	20,930	9.6%	0.200	0.231
Acanthomorpha	298	19,470	31.4%	0.270	0.164
Eupercaria	142	6,970	88.6%	-0.066	0.589
Anabantaria + Carangaria + Ovalentaria	81	7,300	64.1%	0.075	0.489
Hexagrammidae + Zoarcoidei + Cottoidei	25	1,280	97.9%	-0.676	0.760
Cottoidei	11	850	98.8%	-0.330	0.644

[1] Rounded to nearest 10 based on 04 April 2020 download of (Fricke et al. 2020).

[2] Probabilities for ancestral state and Brownian phylogenetic structure are represented differently to help distinguish them.

[3] Node percentages summarize 1000 stochastic character mapping simulations.

Figure Legends

Fig. 1. Family-level phylogenetic tree of actinopterygians depicting evolution of soniferous behavior. Shown here are posterior probabilities from ancestral state reconstruction using stochastic character mapping. Probability is represented as a gradient, where blue indicates a high probability and red a low probability of soniferous behavior, and yellow is equivocal. Tree is pruned from species-level phylogeny of Rabosky et al.(Rabosky et al. 2018) to family-level here.

Fig. 2. Posterior probability soniferous behavior within major actinopterygian clades. (**a**) Otocephala, (**b**) Anabantaria + Carangaria + Ovalentaria, and (**c**) Eupercaria. For phylogenetic trees showing the ancestral state estimation and associated evolutionary probabilities of sound production being ancestral by stochastic character mapping, probability is represented as a gradient where blue indicates high and red is low probability of sound production; yellow is equivocal.

Fig. 3. Phylogenetic signal versus ancestral state estimation for evolution of actinopterygian soniferous behavior. (**a**) *D* statistic value (Fritz and Purvis 2010) versus ancestral state estimate (using stochastic character mapping) probability that soniferous behavior is ancestral for a clade. (**b**) Probability of Brownian phylogenetic structure (modelled from *D* statistic) versus stochastic character mapping probability soniferous behavior is ancestral for a clade. Values for *D* statistic, probability of Brownian structure, and ancestral state probabilities are listed in Table 1. Only clades with >25 families are used, since inference of *D* is limited for clades with <25 taxa (Fritz and Purvis 2010).

Supplementary Information

Fig. S1. Soniferous behavior mapped onto phylogenetic tree of actinopterygian families. Tree shows three different lines of evidence for soniferous behavior used here and its phylogenetic distribution. Tree is pruned from species-level phylogeny of Rabosky et al. (2018) to family-level here. Some clades recovered using genomic (Betancur-R et al. 2017; Near et al. 2012; Rabosky et al. 2018) and transcriptomic data (Hughes et al. 2018) are supported by well-accepted, anatomical synapomorphies, but others such as Ovalentaria (Hughes et al. 2018) are not.

Fig. S2. Count of occurrences of the evolution of sonifery. Independent origins of soniferous behavior in actinopterygian fishes, inferred from node values calculated in Fig. 1.

Fig. S3. Observed *D*-values for each clade. The observed *D*-values (vertical lines) indicate the strength of phylogenetic signal, based on their value relative to the distribution of simulated *D*-values assuming Brownian evolutionary processes (histograms) for each clade. Values that fall closer to the center of the distribution indicate higher phylogenetic signal within a clade. Some observed *D*-values were closer to (although not near the center of) the simulated distribution based on models of random character evolution with respect to phylogeny (red histograms in upper right plot).

Table S1. Evidence for sound production in actinopterygian families. Levels of evidence are coded as audio recordings (1), morphological inference (2), or qualitative observations (3). Representative references are included to support evidence of sound production. Families are arranged in sequence following their phylogenetic placement in Figure 1, arranged clockwise.

Number	**Higher Taxonomy**	**Family**	**Sonic Evidence**	**Representative References**
1.	Cladistia	Polypteridae	1	(Ladich and Tadler 1988)
2.	Chondrostei	Acipenseridae	1	(Johnston and Phillips 2003)
3.	Amiiformes	Amiidae	3	(Fülleborn 1894)
4.	Elopomorpha	Megalopidae	1	(Fish and Mowbray 1970)
5.	Elopomorpha	Elopidae	1	(Fish and Mowbray 1970)
6.	Elopomorpha	Albulidae	1	(Fish and Mowbray 1970)
7.	Elopomorpha	Anguillidae	1	(Fish et al. 1952)
8.	Elopomorpha	Congridae	3	(Moulton 1963)
9.	Osteoglossomorpha	Arapaimidae	1	(Olsen 2014)
10.	Osteoglossomorpha	Osteoglossidae	2	(Sörensen 1894-1895)
11.	Osteoglossomorpha	Notopteridae	3	(Greenwood 1963)
12.	Osteoglossomorpha	Mormyridae	1	(Crawford et al. 1997)
13.	Clupeiformes	Engraulidae	1	(Kuznetsov and Kuznetsov 2012)
14.	Clupeiformes	Clupeidae	1	(Fish et al. 1952; Wilson et al. 2004)
15.	Characiformes	Parodontidae	2	(Moreira et al. 2019)
16.	Characiformes	Hemiodontidae	2	(Netto-Ferreira and Moreira 2019)
17.	Characiformes	Serrasalmidae	1	(Millot et al. 2011)
18.	Characiformes	Anostomidae	3	(Reynalte-Tataje et al. 2013)
19.	Characiformes	Prochilodontidae	1	(Godinho et al. 2017)
20.	Characiformes	Curimatidae	1	(Borie et al. 2019)
21.	Characiformes	Gasteropelecidae	3	(Weitzman 1954)
22.	Characiformes	Characidae	1	(Meschkat 1957)

23.	Siluriformes	Callichthyidae	1	(Kaatz and Lobel 1999)
24.	Siluriformes	Loricariidae	1	(Heyd and Pfeiffer 2000)
25.	Siluriformes	Aspredinidae	1	(Kaatz and Stewart 2012)
26.	Siluriformes	Auchenipteridae	1	(Kaatz and Stewart 2012)
27.	Siluriformes	Doradidae	1	(Ladich 2001)
28.	Siluriformes	Heteropneustidae	3	(Kaatz et al. 2010)
29.	Siluriformes	Clariidae	3	(Goel 1966)
30.	Siluriformes	Chacidae	3	(Kaatz et al. 2010)
31.	Siluriformes	Siluridae	3	(Moulton 1963)
32.	Siluriformes	Horabagridae	3	(Kaatz et al. 2010)
33.	Siluriformes	Bagridae	1	(Heyd and Pfeiffer 2000)
34.	Siluriformes	Sisoridae	3	(de Pinna 1996; Mahajan 1963)
35.	Siluriformes	Plotosidae	3	(Burgess 1989)
36.	Siluriformes	Pangasiidae	3	(Marshall 1966; Sorensen 1890)
37.	Siluriformes	Cranoglanididae	2	(Diogo et al. 2002)
38.	Siluriformes	Ictaluridae	1	(Fine et al. 1997)
39.	Siluriformes	Ariidae	1	(Breder 1968)
40.	Siluriformes	Pseudopimelodidae	1	(Kaatz and Stewart 2012)
41.	Siluriformes	Pimelodidae	1	(Kaatz and Stewart 2012)
42.	Siluriformes	Schilbeidae	2	(Mo 1991)
43.	Siluriformes	Heptapteridae	1	(Heyd and Pfeiffer 2000; Schachner and Schaller 1981)
44.	Siluriformes	Claroteidae	1	(Kaatz et al. 2010; Skelton and Skelton 1993)
45.	Siluriformes	Malapteruridae	2	(Howes 1985; Sörensen 1894-1895)
46.	Siluriformes	Mochokidae	1	(Kaatz and Stewart 2012)

47.	Cypriniformes	Catostomidae	1	(Straight et al. 2014)
48.	Cypriniformes	Cobitidae	1	(Rigley and Marshall 1971)
49.	Cypriniformes	Balitoridae	3	(Dufossé 1874)
50.	Cypriniformes	Nemacheilidae	3	(Dufossé 1874)
51.	Cypriniformes	Cyprinidae	1	(Winn and Stout 1960)
52.	Cypriniformes	Gobionidae	1	(Scholz and Ladich 2006)
53.	Cypriniformes	Leuciscidae	1	(Johnston and Vives 2003; Protasov 1965)
54.	Protacanthopterygii	Salmonidae	1	(Johnson et al. 2017; Neproshin 1972; Neproshin 1974)
55.	Osmeriformes	Osmeridae	1	(Neproshin et al. 1980)
56.		Myctophidae	1	(McCauley and Cato 2016)
57.	Percopsiformes	Aphredoderidae	3	(Abbott 1877)
58.	Zeiformes	Zeidae	1	(Onuki and Somiya 2004)
59.	Gadiformes	Moridae	1	(Marshall 1967; Tavolga 1964)
60.	Gadiformes	Phycidae	1	(Fish and Mowbray 1970)
61.	Gadiformes	Lotidae	1	(Hawkins and Rasmussen 1978; Rountree and Juanes 2010)
62.	Gadiformes	Gadidae	1	(Fish et al. 1952)
63.	Gadiformes	Merlucciidae	1	(Fish 1954)
64.	Gadiformes	Macrouridae	2	(Marshall 1965)
65.	Lampriformes	Veliferidae	2	(Walters 1960)
66.	Holocentriformes	Holocentridae	1	(Bright and Sartori 1972; Moulton 1958)
67.	Trachichthyiformes	Trachichthyidae	2	(Shimizu 1977)
68.	Trachichthyiformes	Monocentridae	1	(Onuki et al. 2010)
69.	Ophidiiformes	Dinematichthyidae	1	(Campagna 1973; Howes 1992)
70.	Ophidiiformes	Bythitidae	1	(Campagna 1973)

71.	Ophidiiformes	Carapidae	1	(Parmentier et al. 2003)
72.	Ophidiiformes	Ophidiidae	1	(Courtenay and McKittrick 1970; Parmentier et al. 2010)
73.	Batrichoidiformes	Batrachoididae	1	(Fish et al. 1952)
74.	Eupercaria	Scaridae	1	(Tricas and Boyle 2014)
75.	Eupercaria	Labridae	1	(Fish et al. 1952)
76.	Eupercaria	Glaucosomatidae	1	(Mok et al. 2011; Parsons et al. 2013)
77.	Eupercaria	Pempheridae	1	(Takayama et al. 2003)
78.	Eupercaria	Triodontidae	3	(Breder and Clark 1947)
79.	Eupercaria	Ostraciidae	1	(Fish and Mowbray 1970; Lobel 1996)
80.	Eupercaria	Triacanthidae	3	(Breder and Clark 1947; Bridge 1904)
81.	Eupercaria	Balistidae	1	(Fish et al. 1952; Salmon et al. 1968)
82.	Eupercaria	Monacanthidae	1	(Fish et al. 1952)
83.	Eupercaria	Molidae	1	(Fish and Mowbray 1970)
84.	Eupercaria	Diodontidae	1	(Fish et al. 1952)
85.	Eupercaria	Tetraodontidae	1	(Fish et al. 1952)
86.	Eupercaria	Priacanthidae	1	(Salmon and Winn 1966)
87.	Eupercaria	Caproidae	3	(Bridge 1904; Fish 1948; Sörensen 1894-1895)
88.	Eupercaria	Ephippidae	1	(Fish et al. 1952)
89.	Eupercaria	Zanclidae	1	(Tricas and Boyle 2014)
90.	Eupercaria	Acanthuridae	1	(Fish and Mowbray 1970)
91.	Eupercaria	Sciaenidae	1	(Tower 1908)
92.	Eupercaria	Lethrinidae	3	(Moulton 1964)
93.	Eupercaria	Sparidae	1	(Fish et al. 1952)

94.	Eupercaria	Leiognathidae	3	(Fish 1948; Uchida 1934)
95.	Eupercaria	Chaetodontidae	1	(Tricas and Boyle 2015)
96.	Eupercaria	Pomacanthidae	1	(Fish and Mowbray 1970; Moyer et al. 1983)
97.	Eupercaria	Lutjanidae	3	(Fish and Mowbray 1970)
98.	Eupercaria	Caesionidae	3	(Yokoyama et al. 1994)
99.	Eupercaria	Haemulidae	1	(Burkenroad 1930)
100.	Eupercaria	Moronidae	3	(Fish 1954; Fish et al. 1952; Fish and Mowbray 1970)
101.	Eupercaria	Sillaginidae	1	(McKay 1985; Walls 1964)
102.	Eupercaria	Gerreidae	3	(Fish and Mowbray 1970)
103.	Eupercaria	Uranoscopidae	3	(Mikhailenko 1973)
104.	Eupercaria	Polyprionidae	1	(Clark and Allen 2018)
105.	Eupercaria	Kyphosidae	1	(Fish and Mowbray 1970)
106.	Eupercaria	Terapontidae	1	(Dorai Raj 1960)
107.	Eupercaria	Enoplosidae	3	(Graham 1992)
108.	Eupercaria	Latridae	3	(Castelnau 1872)
109.	Eupercaria	Centrarchidae	1	(Gerald 1971)
110.	Eupercaria	Neosebastidae	2	(Hallacher 1974; Ishida 1994; Matsubara 1943)
111.	Eupercaria	Percidae	1	(Johnston and Johnson 2000)
112.	Eupercaria	Serranidae	1	(Fish et al. 1952)
113.	Eupercaria	Normanichthyidae	2	(Yabe and Uyeno 1996)
114.	Eupercaria	Apistidae	2	(Imamura 2004)
115.	Eupercaria	Aploactinidae	1	(Matsubara 1943; Walls 1964)
116.	Eupercaria	Tetrarogidae	1	(Walls 1964)
117.	Eupercaria	Synanceiidae	1	(Imamura 2004; Walls 1964)

118.	Eupercaria	Setarchidae	2	(Imamura and Yabe 2002; Ishida 1994)
119.	Eupercaria	Scorpaenidae	1	(Fish and Mowbray 1970; Hallacher 1974)
120.	Eupercaria	Sebastidae	1	(Širović and Demer 2009)
121.	Eupercaria	Peristediidae	2	(Evans 1969; Evans 1970)
122.	Eupercaria	Triglidae	1	(Fish et al. 1952)
123.	Eupercaria	Anoplopomatidae	1	(Riera et al. 2020)
124.	Eupercaria	Gasterosteidae	2	(Bridge 1904; Fish 1954)
125.	Eupercaria	Hexagrammidae	1	(Yamato et al. 2018)
126.	Eupercaria	Anarhichadidae	2	(Sörensen 1884; 1894-1895)
127.	Eupercaria	Cyclopteridae	1	(Fish and Mowbray 1970)
128.	Eupercaria	Liparidae	2	(Hallacher 1974)
129.	Eupercaria	Rhamphocottidae	1	(Imamura and Yabe 2002; Yabe 1985)
130.	Eupercaria	Hemitripteridae	2	(Fish and Mowbray 1970)
131.	Eupercaria	Agonidae	2	(Imamura and Yabe 2002; Yabe 1985)
132.	Eupercaria	Cottidae	1	(Barber and Mowbray 1956; Fish et al. 1952)
133.	Eupercaria	Psychrolutidae	2	(Hallacher 1974; Yabe 1985)
134.	Pelagiaria	Pomatomidae	1	(Fish and Mowbray 1970)
135.	Pelagiaria	Trichiuridae	3	(Moulton 1963)
136.	Pelagiaria	Stromateidae	1	(Fish et al. 1952)
137.	Pelagiaria	Scombridae	1	(Fish and Mowbray 1970)
138.	Sygnatharia	Dactylopteridae	1	(Fish and Mowbray 1970)
139.	Sygnatharia	Mullidae	1	(Fish and Mowbray 1970)
140.	Sygnatharia	Aulostomidae	3	(Bright 1972)

141.	Sygnatharia	Centriscidae	3	(Knudsen et al. 1948)
142.	Sygnatharia	Syngnathidae	1	(Fish 1953)
143.	Gobiaria	Apogonidae	3	(Kuwamura 1985)
144.	Gobiaria	Odontobutidae	1	(Horvatić et al. 2019)
145.	Gobiaria	Gobiidae	1	(Protasov et al. 1965)
146.	Anabantaria	Mastacembelidae	3	(Sörensen 1894-1895)
147.	Anabantaria	Channidae	2	(Sörensen 1894-1895)
148.	Anabantaria	Anabantidae	3	(Kratochvil 1985)
149.	Anabantaria	Osphronemidae	1	(Ladich et al. 1992)
150.	Carangaria	Polynemidae	1	(Fish and Mowbray 1970)
151.	Carangaria	Carangidae	1	(Fish et al. 1952; Moulton 1960; Taylor and Mansueti 1960)
152.	Carangaria	Centropomidae	1	(Fish and Mowbray 1970)
153.	Carangaria	Sphyraenidae	1	(Fish and Mowbray 1970)
154.	Carangaria	Scophthalmidae	3	(Fish and Mowbray 1970; Lagardère et al. 2004)
155.	Carangaria	Pleuronectidae	1	(Fish et al. 1952)
156.	Ovalentaria	Mugilidae	1	(Barros 1993)
157.	Ovalentaria	Pomacentridae	1	(Avidor 1974; Myrberg 1972; Spanier 1979)
158.	Ovalentaria	Blenniidae	1	(Tavolga 1958)
159.	Ovalentaria	Polycentridae	3	(Barlow 1967)
160.	Ovalentaria	Cichlidae	1	(Myrberg et al. 1965)
161.	Ovalentaria	Adrianichthyidae	1	(Kang et al. 2017)
162.	Ovalentaria	Belonidae	3	(Dufossé 1874)
163.	Ovalentaria	Scomberesocidae	1	(Protasov 1965)
164.	Ovalentaria	Hemiramphidae	3	(Burkenroad 1931)
165.	Ovalentaria	Cynolebiidae	2	(Costa 2009; Costa et al. 2010)

165.	Ovalentaria	Fundulidae	1	(Drewry 1962)
166.	Ovalentaria	Cyprinodontidae	1	(Johnson 2000)

Table S2. (separate excel file) Aggregated data for 461 families considered in this analysis. Showing soniferous behaviors, valid extant species, male alternative reproductive tactics (Mank and Avise 2006), ecological data aggregated from FishBase (Boettiger et al. 2012; Froese and Pauly 2019), including occurrence of families as a function of latitude, salinity, bottom type, habitat, trophic ecology, and reproductive mode.

Nocturnality is strongly correlated with the evolution of acoustic communication within tetrapods (Chen and Wiens 2020). We considered including nocturnality as part of this analysis. Although there are many examples of robust nocturnal chorusing by actinopterygians (Feng and Bass 2016; Mann and Jarvis 2004; McCauley and Cato 2016; Rice et al. 2017), there are no comprehensive analyses of photoperiod-related activity patterns for the soniferous families that are the basis of our study. Assessment of nocturnality in fishes is complicated by potential sampling biases (Dornburg et al. 2017), including seasonal and diel shifts in soniferous and other behaviors coupled to peak times of spawning and reproduction (Feng and Bass 2016; Mann and Jarvis 2004; McCauley and Cato 2016; Rice et al. 2017).

Table S3. Clades with independent evolution of sonifery in actinopterygian fishes and associated habitats. Nodes on the phylogenetic tree are labelled in Supplementary Figure 2. Habitat data are from FishBase (Froese and Pauly 2019)

Clade	**Marine/Freshwater**	**Habitat**
Polypteridae	Freshwater	Demersal
Acipenseridae	Anadromous	Demersal spawning and feeding
Amiidae	Freshwater	Demersal
Megalopidae+Elopidae	Marine	Demersal
Albulidae	Marine	Demersal
Anguillidae	Anadromous	Demersal in Freshwater
Congridae	Marine	Demersal
Arapaimidae+Mormyridae+ Gymnarchidae+Notopteridae +Osteoglossidae	Freshwater	Rivers
Engraulidae	Marine	Some demersal, some pelagic
Clupeidae	Marine	Some demersal, some pelagic
Curimatoidea	Freshwater	Rivers
Gasteropelecidae	Freshwater	Rivers
Characidae	Freshwater	Demersal
Siluroidei	Mostly Freshwater, some marine	Mostly benthic or demersal
Catostomidae	Freshwater	Demersal
Cobitidae	Freshwater	Demersal
Balitoridae	Freshwater	Demersal
Nemacheilidae	Freshwater	Demersal
Cyprinidae	Freshwater	Many with demersal spawning and feeding
Gobionidae	Freshwater	Rivers, some demersal
Leuciscidae	Freshwater	Rivers
Salmonidae	Anadromous	Demersal spawning
Osmeridae	Anadromous	Demersal and pelagic
Myctophidae	Marine	Bathypelagic
Aphredoderidae	Freshwater	Demersal spawning
Zeidae	Marine	Demersal
Gadiformes	Mostly marine	Demersal

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Figure 1

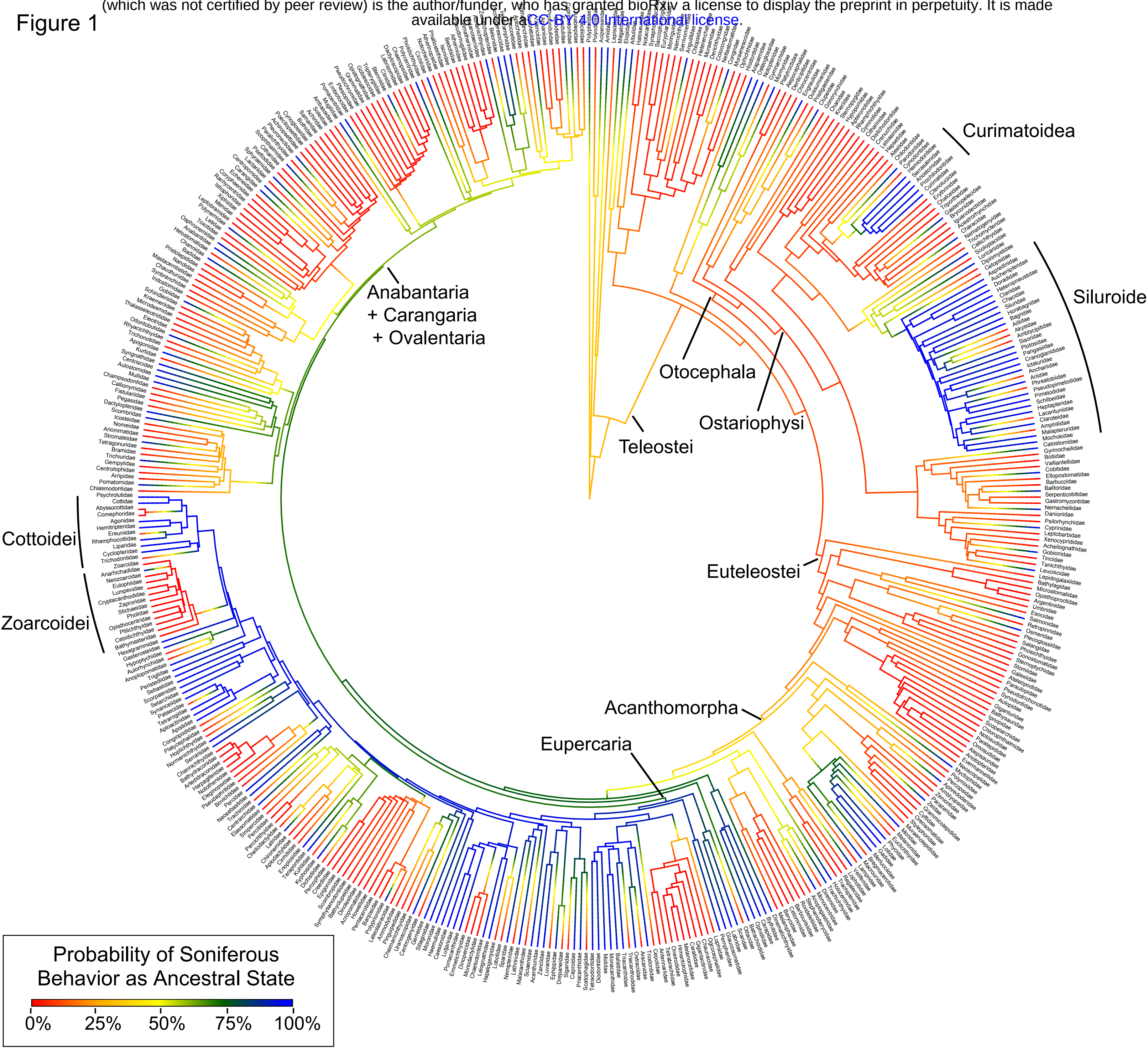

Curimatoidea
Siluroidei
Anabantaria
+ Carangaria
+ Ovalentaria
Otocephala
Ostariophysi
Teleostei
Euteleostei
Cottoidei
Zoarcoidei
Acanthomorpha
Eupercaria
Probability of Soniferous
Behavior as Ancestral State
0%
25%
50%
75%
100%

Figure 2

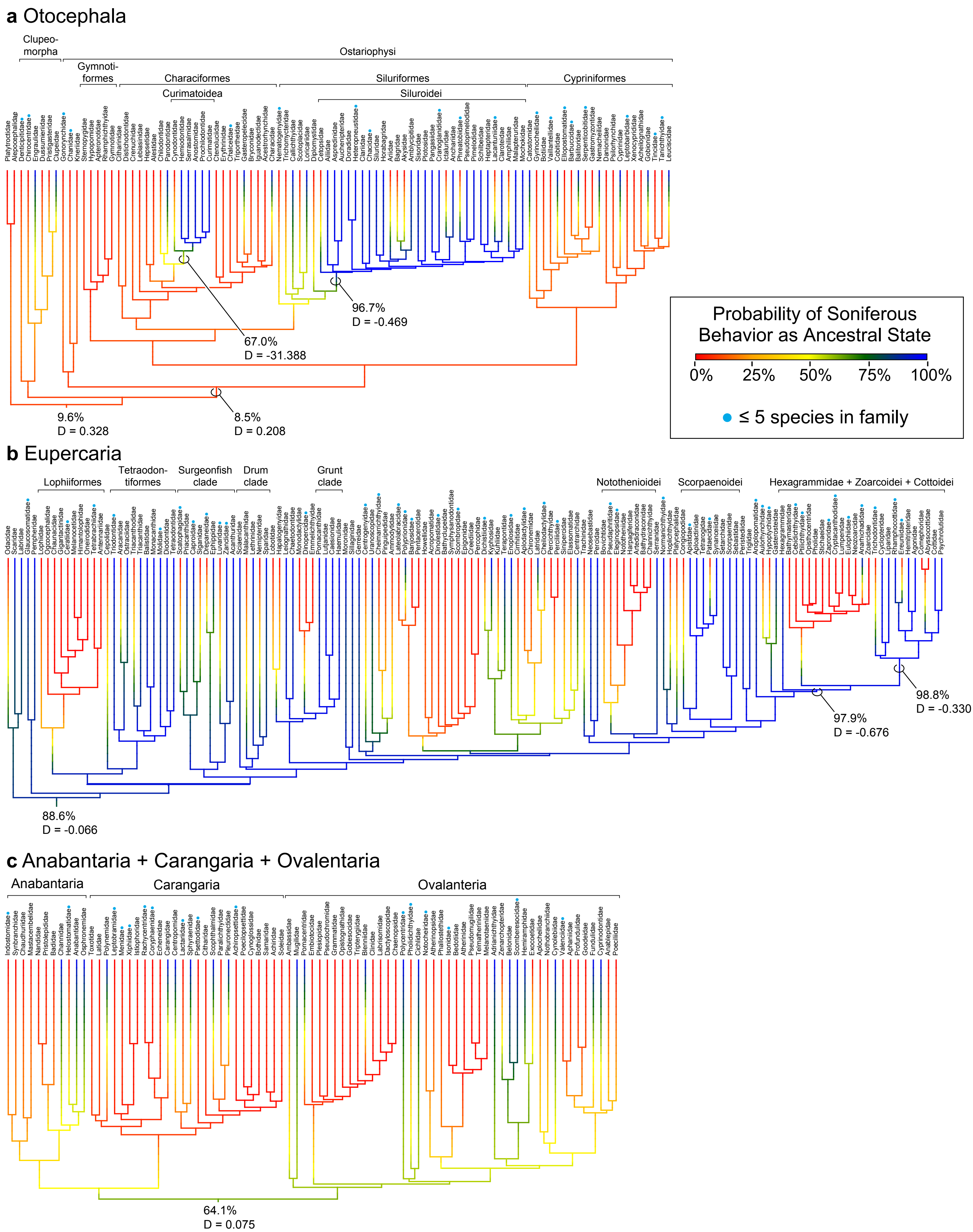
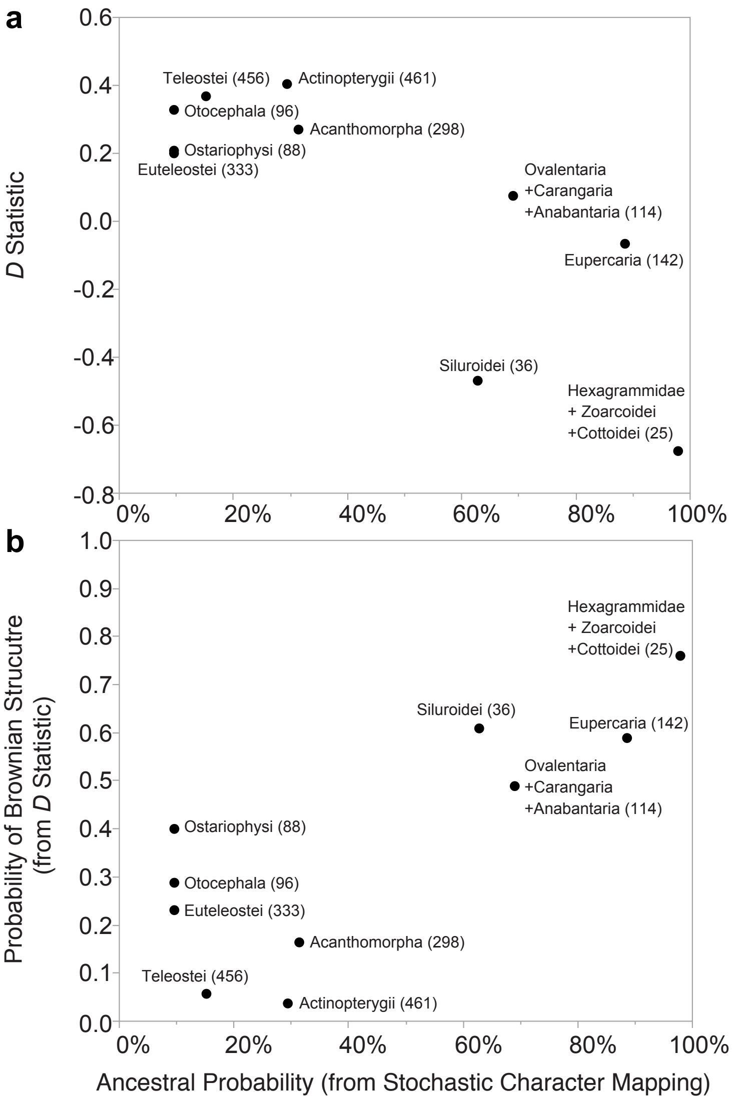
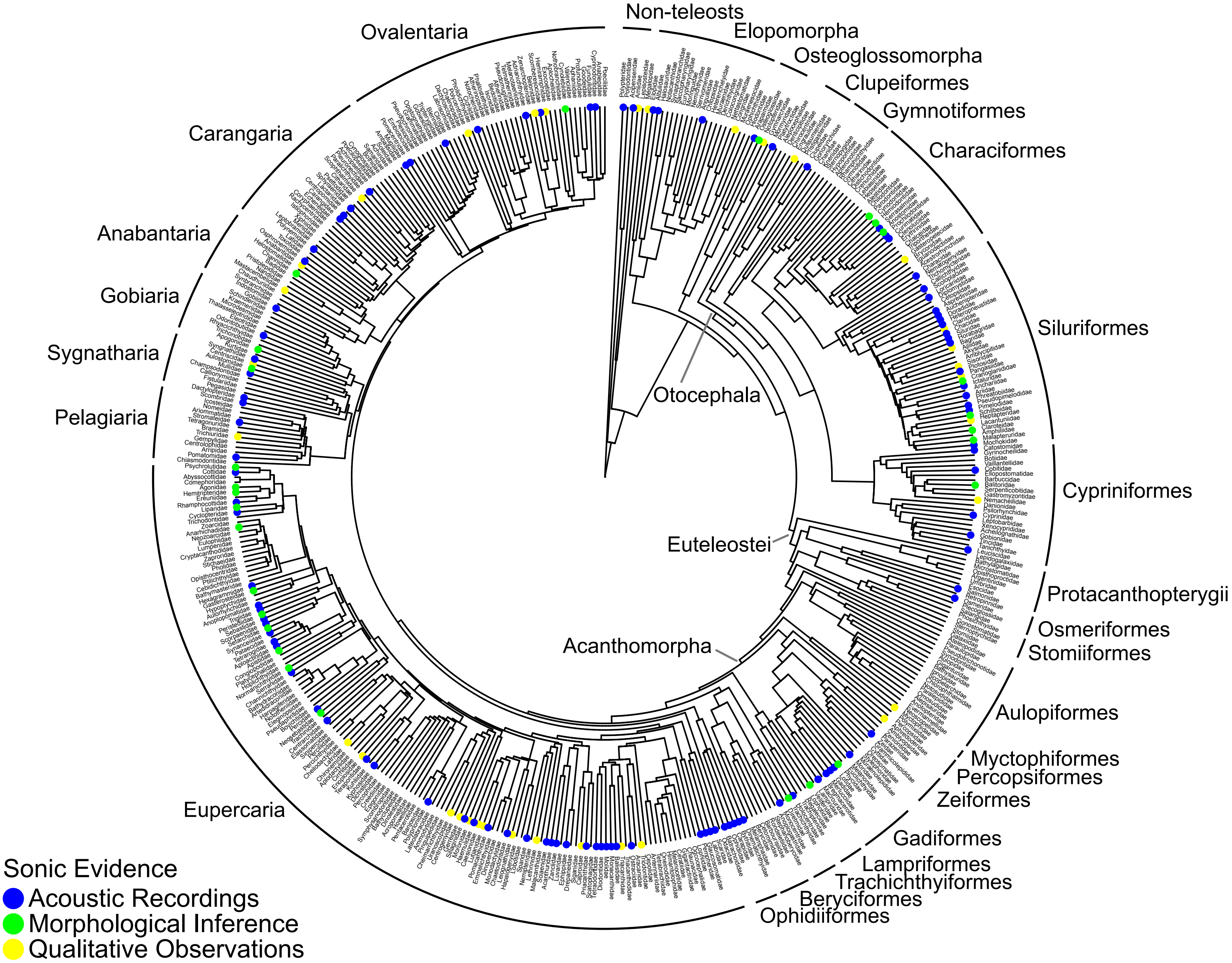

a Otocephala
Clupeomorpha
Ostariophysi
Gymnotiformes
Characiformes
Curimatoidea
Siluriformes
Siluroidei
Cypriniformes
Platytroctidae
Alepocephalidae
Denticipitidae
Chirocentridae
Engraulidae
Dussumieriidae
Pristigasteridae
Clupeidae
Gonorynchidae
Chanidae
Kneriidae
Sternopygidae
Hypopomidae
Apteronotidae
Rhamphichthyidae
Gymnotidae
Citharinidae
Distichodontidae
Crenuchidae
Lebiasinidae
Hepsetidae
Alestidae
Chilodontidae
Parodontidae
Cynodontidae
Hemiodontidae
Serrasalmidae
Anostomidae
Prochilodontidae
Curimatidae
Ctenoluciidae
Erythrinidae
Chalceidae
Triportheidae
Gasteropelecidae
Bryconidae
Iguanodectidae
Acestrorhynchidae
Characidae
Nematogenyidae
Trichomycteridae
Callichthyidae
Scoloplacidae
Loricariidae
Diplomystidae
Cetopsidae
Ailiidae
Aspredinidae
Auchenipteridae
Doradidae
Heteropneustidae
Clariidae
Chacidae
Siluridae
Horabagridae
Ariidae
Bagridae
Akysidae
Amblycipitidae
Sisoridae
Plotosidae
Pangasiidae
Cranoglanididae
Ictaluridae
Anchariidae
Phreatobiidae
Pseudopimelodidae
Pimelodidae
Schilbeidae
Heptapteridae
Lacantuniidae
Claroteidae
Amphiliidae
Malapteruridae
Mochokidae
Catostomidae
Gyrinocheilidae
Botiidae
Vaillantellidae
Cobitidae
Ellopostomatidae
Barbuccidae
Balitoridae
Serpenticobitidae
Gastromyzontidae
Nemacheilidae
Danionidae
Psilorhynchidae
Cyprinidae
Leptobarbidae
Xenocyprididae
Acheilognathidae
Gobionidae
Tincidae
Tanichthyidae
Leuciscidae
67.0%
D = -31.388
96.7%
D = -0.469
9.6%
D = 0.328
8.5%
D = 0.208
Probability of Soniferous Behavior as Ancestral State
0%
25%
50%
75%
100%
● ≤ 5 species in family
b Eupercaria
Lophiiformes
Tetraodontiformes
Surgeonfish clade
Drum clade
Grunt clade
Notothenioidei
Scorpaenoidei
Hexagrammidae + Zoarcoidei + Cottoidei
Odacidae
Scaridae
Labridae
Glaucosomatidae
Pempheridae
Lophiidae
Ogcocephalidae
Chaunacidae
Gigantactinidae
Ceratiidae
Melanocetidae
Himantolophidae
Oneirodidae
Tetrabrachiidae
Antennariidae
Cepolidae
Triodontidae
Aracanidae
Ostraciidae
Triacanthodidae
Triacanthidae
Balistidae
Monacanthidae
Molidae
Diodontidae
Tetraodontidae
Scatophagidae
Priacanthidae
Caproidae
Siganidae
Drepaneidae
Ephippidae
Luvaridae
Zanclidae
Acanthuridae
Sciaenidae
Malacanthidae
Lethrinidae
Nemipteridae
Sparidae
Lobotidae
Hapalogenyidae
Leiognathidae
Chaetodontidae
Monodactylidae
Dinopercidae
Emmelichthyidae
Pomacanthidae
Lutjanidae
Caesionidae
Haemulidae
Moronidae
Sillaginidae
Gerreidae
Centrogenyidae
Uranoscopidae
Cheimarrichthyidae
Pinguipedidae
Ammodytidae
Lateolabracidae
Polyprionidae
Banjosidae
Pentacerotidae
Howellidae
Acropomatidae
Dinolestidae
Bathyclupeidae
Symphysanodontidae
Scombropidae
Epigonidae
Creediidae
Percophidae
Dichistiidae
Kyphosidae
Kuhliidae
Terapontidae
Enoplosidae
Cirrhitidae
Aplodactylidae
Chironemidae
Latridae
Cheilodactylidae
Percichthyidae
Perciliidae
Sinipercidae
Elassomatidae
Centrarchidae
Trachinidae
Neosebastidae
Percidae
Bovichtidae
Pseudaphritidae
Eleginopsidae
Nototheniidae
Harpagiferidae
Artedidraconidae
Bathydraconidae
Channichthyidae
Serranidae
Normanichthyidae
Hoplichthyidae
Platycephalidae
Congiopodidae
Apistidae
Aploactinidae
Tetrarogidae
Pataecidae
Synanceiidae
Setarchidae
Scorpaenidae
Sebastidae
Peristediidae
Triglidae
Anoplopomatidae
Aulorhynchidae
Hypoptychidae
Gasterosteidae
Hexagrammidae
Bathymasteridae
Cebidichthyidae
Ptilichthyidae
Opisthocentridae
Pholidae
Stichaeidae
Zaproridae
Cryptacanthodidae
Lumpenidae
Eulophiidae
Neozoarcidae
Anarhichadidae
Zoarcidae
Trichodontidae
Cyclopteridae
Liparidae
Rhamphocottidae
Ereuniidae
Hemitripteridae
Agonidae
Comephoridae
Abyssocottidae
Cottidae
Psychrolutidae
88.6%
D = -0.066
97.9%
D = -0.676
98.8%
D = -0.330
c Anabantaria + Carangaria + Ovalentaria
Anabantaria
Carangaria
Ovalanteria
Indostomidae
Synbranchidae
Chaudhuriidae
Mastacembelidae
Nandidae
Pristolepididae
Badidae
Channidae
Helostomatidae
Anabantidae
Osphronemidae
Toxotidae
Latidae
Polynemidae
Leptobramidae
Menidae
Xiphiidae
Istiophoridae
Rachycentridae
Coryphaenidae
Echeneidae
Carangidae
Centropomidae
Lactariidae
Sphyraenidae
Psettodidae
Citharidae
Scophthalmidae
Paralichthyidae
Pleuronectidae
Achiropsettidae
Poecilopsettidae
Cynoglossidae
Bothidae
Samaridae
Achiridae
Soleidae
Ambassidae
Mugilidae
Pomacentridae
Embiotocidae
Plesiopidae
Pseudochromidae
Grammatidae
Opistognathidae
Gobiesocidae
Tripterygiidae
Blenniidae
Clinidae
Labrisomidae
Dactyloscopidae
Chaenopsidae
Polycentridae
Pholidichthyidae
Cichlidae
Notocheiridae
Atherinopsidae
Phallostethidae
Isonidae
Bedotiidae
Atherinidae
Pseudomugilidae
Telmatherinidae
Melanotaeniidae
Adrianichthyidae
Zenarchopteridae
Belonidae
Scomberesocidae
Hemiramphidae
Exocoetidae
Aplocheilidae
Nothobranchiidae
Cynolebiidae
Valenciidae
Aphaniidae
Profundulidae
Goodeidae
Fundulidae
Cyprinodontidae
Anablepidae
Poeciliidae
64.1%
D = 0.075

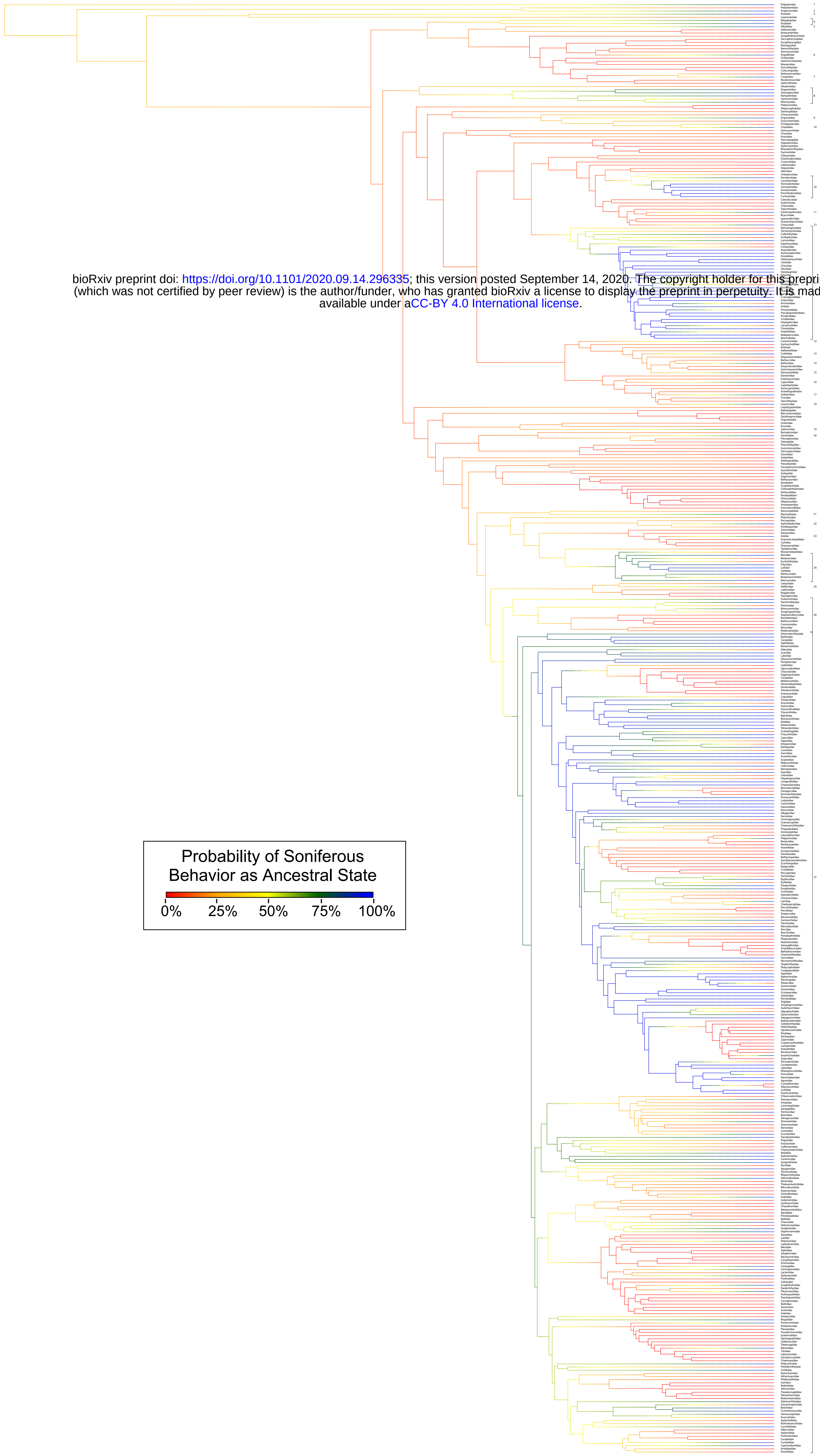
Figure 3


a
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
D Statistic
Teleostei (456)
Actinopterygii (461)
Otocephala (96)
Acanthomorpha (298)
Ostariophysi (88)
Euteleostei (333)
Ovalentaria
+Carangaria
+Anabantaria (114)
Eupercaria (142)
Siluroidei (36)
Hexagrammidae
+ Zoarcoidei
+Cottoidei (25)
0%
20%
40%
60%
80%
100%
b
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Probability of Brownian Strucutre
(from *D* Statistic)
Hexagrammidae
+ Zoarcoidei
+Cottoidei (25)
Siluroidei (36)
Eupercaria (142)
Ovalentaria
+Carangaria
+Anabantaria (114)
Ostariophysi (88)
Otocephala (96)
Euteleostei (333)
Acanthomorpha (298)
Teleostei (456)
Actinopterygii (461)
0%
20%
40%
60%
80%
100%
Ancestral Probability (from Stochastic Character Mapping)

Supplementary Figure 1



Supplementary Figure 2



Supplementary Figure 3