



23 **Abstract**

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

45 communication during the evolution of Actinopterygii, a clade containing more than 34,000  
46 species of extant vertebrates.

47

48 **Keywords:** acoustic communication, sound production, convergent evolution, Actinopterygii,

49 key innovation

## 50 **Introduction**

51 While spoken language is regarded as a uniquely human attribute, the use of sound as a  
52 vertebrate communication channel also occurs in other terrestrial species and marine mammals  
53 (Bradbury and Vehrencamp 2011, Ladich and Winkler 2017). Less well known is its prevalence  
54 among fishes, despite multiple early descriptions of anatomy, physiology or behavior (Dufossé  
55 1874, Tower 1908), including von Frisch's comments on its widespread distribution as early as  
56 1938:

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

61 Since then, a growing body of evidence shows the importance of volitional sound production in  
62 social communication and reproduction especially among ray-finned fishes (Actinopterygii)  
63 (Ladich 2015), a group that includes more than half of extant vertebrate diversity. Together with  
64 Sarcopterygii (coelacanths, lungfishes, and tetrapods, which includes amphibians, reptiles, birds,  
65 and mammals), Actinopterygii is one of two extant radiations of bony vertebrates (Nelson et al.  
66 2016). Although there is evidence for soniferous behavior in 800-1000 species of  
67 actinopterygians (Ladich 2015, Ladich et al. 2006) and numerous studies of neural and hormonal  
68 mechanisms that are similar to those of tetrapods (Bass 2014, Zhang and Ghazanfar 2020), more  
69 widespread recognition of acoustic behavior among fishes and its integration into broader  
70 concepts of vertebrate evolution are still lacking. This is, in part, because sound production is not  
71 externally obvious in fishes, nor can those sounds be easily detected underwater without  
72 specialized technology (Mann et al. 2016).

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

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

95

## 96 **Materials and Methods**

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

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

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

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

133

## 134 **Results**

135 **Ancestral States.** Stochastic character mapping simulates the distribution of a character along  
136 branches of a phylogeny (Bollback 2006, Revell 2012) and summaries of many simulations (N =  
137 1000 in this study) are used to compute probabilities of a character being ancestral at nodes.  
138 Figure 1 reconstructs ancestral states of soniferous behavior across actinopterygian phylogeny,  
139 showing the probabilities of soniferous behavior being ancestral, ranging from 0% (silent) to  
140 100% (soniferous); Table 1 presents probability values at key nodes.

141           Although sonifery occurs in the three extant clades of non-teleostean actinopterygians  
142 (Polypteriformes, Acipenseriformes, and Holostei) (Fig. 1), this reconstruction reveals that  
143 soniferous behavior is unlikely ancestral for Actinopterygii (29.4% probability). Teleostei, which  
144 comprises > 99.8% of actinopterygian species, also has low support (15.2% probability) that  
145 soniferous behavior is the ancestral state. Likewise, Osteoglossomorpha, an early diverging clade  
146 of teleosts, contains several soniferous families, but only a 25.5% probability that soniferous  
147 behavior is ancestral. Otocephala, a speciose subclade of actinopterygians exhibiting  
148 morphological adaptations to enhance hearing (Braun and Grande 2008), has an even lower  
149 probability that soniferous behavior is ancestral, 9.6%. Ostariophysii, a large subgroup of  
150 otocephalans well known for the Weberian apparatus (chain of bony elements that enhance  
151 hearing), has the lowest value among the groups analyzed that soniferous behavior is ancestral,  
152 8.5%. A second large subclade of Teleostei, Euteleostei, includes two-thirds of living fish  
153 species, but here, too, there is little support that soniferous behavior is ancestral, 9.6%.

154           We find much stronger support for soniferous behavior as a character at the base of some  
155 key nodes. Siluroidei, a subclade of catfishes, and Curimatoidea, a subclade of characins, have  
156 96.7% and 67% probabilities, respectively, that soniferous behavior is ancestral (Figs. 1, 2a.  
157 Acanthomorpha, which includes 85% of fish species in marine habitats (Wainwright and Longo  
158 2017), has a low probability (31.4%) sonifery is ancestral. However, two of its subclades,  
159 Eupercaria (e.g., “surgeonfish”, “drums”, “grunts”, scorpaenoids) and Anabantaria + Carangaria  
160 + Ovalentaria (e.g., gouramis [Osphronemidae], jacks [Carangidae], cichlids [Cichlidae]) have  
161 88.6% and 64.1% probabilities, respectively (Fig. 2b, c). An even higher probability value,  
162 97.5%, supports soniferous behavior as ancestral for a crown group within Eupercaria,  
163 Hexagrammidae (greenlings) + Zoarcoidei (e.g., wolffishes) + Cottoidei (e.g., sculpin) (Fig. 2b).



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

168  
169 **Phylogenetic signal.** Patterns of ancestral states alone do not predict evolutionary processes  
170 underlying character evolution, making it necessary to evaluate phylogenetic signal (Blomberg et  
171 al. 2003). We use the  $D$  statistic for binary characters (Chen and Wiens 2020, Fritz and Purvis  
172 2010), in this case soniferous or silent, to calculate phylogenetic signal. For each clade, we  
173 computed  $D$  and the probability that character evolution results from Brownian phylogenetic  
174 structure, which can be visualized by the proximity of the clade's observed  $D$ -value to the center  
175 of the distribution of simulated  $D$ -values assuming Brownian evolutionary processes (Fig. S3).  
176 Where  $D$  is > 0.0, the evolution of soniferous behavior is phylogenetically random and not  
177 conserved within a group. Where  $D$  is close to or < 0.0, evolution of soniferous behavior results  
178 primarily from Brownian evolutionary processes and phylogenetic structure, and is conserved  
179 within a group.

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

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

197

198   **Hearing specializations.** Novel auditory morphologies, generally referred to as hearing  
199   specializations, e.g., the Weberian apparatus or swim bladder extensions contacting the otic  
200   capsule, may have evolved 20 times within Teleostei (Braun and Grande 2008). Families with  
201   these adaptations (Braun and Grande 2008, Colley et al. 2019, Radford et al. 2013) (Table S2),  
202   62 of 119, are highly correlated with soniferous behavior (phylogenetic logistic regression;  $P =$   
203   0.004).

204

205   **Habitat Complexity.** Actinopterygian families with soniferous taxa live in habitats that vary in  
206   complexity depending on one or more of the following: water salinity, depth and substrate  
207   composition (Boettiger et al. 2012, Froese and Pauly 2019) (Table S2). Freshwater and brackish  
208   water are more likely than marine habitats to have families with soniferous taxa ( $P < 0.000$ ,  $<$   
209   0.000,  $> 0.05$ , respectively; values here and below based on logistic regression with a

210 phylogenetic generalized linear model(Ives and Garland 2010) after Bonferroni correction).  
211 Marine families in shallow intertidal (< 5 m depth) and neritic (< 200 m depth) zones are more  
212 likely to have soniferous taxa ( $P < 0.000$ ) than families with oceanic (i.e. marine pelagic) fishes  
213 ( $P > 0.05$ ). Within families with freshwater species, there is no significant correlation of  
214 soniferous behavior with depth (littoral zone, sublittoral zone, caves;  $P$  values  $> 0.05$ ). Habitats  
215 with coarse ( $P = 0.008$ ), but not fine ( $P > 0.05$ ), sediment are also more likely to have families  
216 with soniferous taxa. Soniferous families are not more likely to live in any one particular climate  
217 (polar, temperate, boreal, tropical, subtropical;  $P$  values  $> 0.05$ ).

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

224

225 **Feeding and Reproductive Ecologies.** Actinopterygian families exhibiting acoustic signaling  
226 are associated with several other behavioral phenotypes (Table S2). Marine families with grazing  
227 species are more likely to contain soniferous taxa ( $P = 0.011$ ), as are families with mating tactics  
228 and reproductive modes ranging from batch spawning ( $P < 0.0001$ ) and internal fertilization ( $P =$   
229  $0.005$ ), to nest guarding ( $P = 0.001$ ), parental care ( $P = 0.004$ ) and alternative reproductive  
230 tactics (17 of 23 families identified by Mank and Avise (2006);  $P < 0.0001$ ). Families showing  
231 sex reversal (protogyny, protandry, hermaphroditism) are not more likely to contain soniferous  
232 taxa ( $P > 0.05$ ). Consistent with field observations, actinopterygian families with soniferous taxa

233 are significant prey for birds (Elliott et al. 2003) and elasmobranchs (Navia et al. 2007) ( $P =$   
234 0.002, 0.001, respectively; cetaceans (McCabe et al. 2010) and pinnipeds (Lance and Jeffries  
235 2009) are known predators, but  $P$  values  $> 0.05$ ).

236

## 237 **Discussion**

238 Although actinopterygian fishes have long been known capable of volitional sound production  
239 (Popper and Casper 2011), few studies integrate their acoustic communication ability into a  
240 broad evolutionary context across bony vertebrates (Bass et al. 2015, Fine and Parmentier 2015).  
241 We show evidence for soniferous behavior in 167 families, containing nearly two-thirds of the  
242 estimated 34,000 valid extant species of actinopterygians (Figs. 1, 2; Tables S1, S2).  
243 Actinopterygians independently evolved soniferous ability at least 27 times (Fig. S2, Table S3).  
244 To our knowledge, all species studied to date that are capable of volitional sound production  
245 have been shown to use sound in a signaling context to either conspecific or heterospecific  
246 individuals (Ladich 2015, Ladich et al. 2006). Consequently, sound production is likely an  
247 important communication modality in most actinopterygian species. This includes two species of  
248 polypterids (Ladich and Tadler 1988), members of a family that diverged from the  
249 actinopterygian stem circa 340 Ma during the Carboniferous Period (Giles et al. 2017). This  
250 suggests that acoustic communication in actinopterygians may have similarly ancient origins,  
251 predating its emergence within tetrapods, which occurred circa 100-200 Ma (Chen and Wiens  
252 2020). We further show significant correlations between families with soniferous species and  
253 diverse freshwater and marine habitats, predation by birds and elasmobranchs, and many  
254 reproductive and mating tactics. In parallel with recent findings for tetrapods (Chen and Wiens

255 2020), our results indicate strong selection to exploit acoustic signaling for communication and  
256 ecological success across vertebrate evolution.

257

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

269 The presence and absence of soniferous behavior among actinopterygians likely includes  
270 secondary loss, suggested elsewhere to drive speciation (Miles and Fuxjager 2019). Within  
271 speciose clades where sonifery has a high probability of being ancestral (Siluroidei, Eupercaria,  
272 Anabantaria + Carangaria + Ovalentaria, Hexagrammidae + Zoarcoidei + Cottoidei), non-  
273 soniferous clades may have secondarily lost this character. Hexagrammidae + Zoarcoidei +  
274 Cottoidei have 97.9% probability that sound production is ancestral, and a very low  $D$  value (-  
275 0.676, Table 1, Fig. 2b). Within this group, Cottoidei comprises an estimated 850 species  
276 (compared to 9 hexagrammid and 405 zoarcoid species) with a very high probability that  
277 soniferous behavior is ancestral (98.8%). This correlates with a low  $D$  value (-0.330), suggesting

278 that the evolution of soniferous behavior within Cottoidei results primarily from Brownian  
279 evolutionary processes. Fish and Mowbray (1970) comment on the absence of sound production  
280 in Zoarcidae [their Zoarchidae]. If further research provides conclusive evidence for absence,  
281 then our tree (Fig. 2c) likely indicates secondary loss. Other places to investigate potential loss of  
282 soniferous capacity are between sister groups where one is coded as silent (e.g., Lophiiformes)  
283 and the other is soniferous (Tetraodontiformes; Fig. 2c). A particularly fascinating case of  
284 secondary loss concerns catfishes in the genus *Synodontis*; some species are only soniferous and  
285 others only weakly electric (Boyle et al. 2014). Weakly electric *Synodontis* have reduced sonic  
286 muscle characters, but share characters with myogenic electric organs (Kéver et al. 2020).  
287 Further demonstration of the loss of sonifery would support the hypothesis that losses can be as  
288 important in generating diversity as gains of complexity (Miles and Fuxjager 2019).

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

297       Plotting the relationship between ancestral state estimation and phylogenetic signal may  
298 indicate a broader conceptual link between pattern (ancestral states) and process (phylogenetic  
299 signal) in character evolution (Fig. 3b). Some cases deviate from this relationship. For example,  
300 it is unlikely that soniferous behavior is ancestral for Ostariophysii, yet the character is relatively

301 conserved within this clade. Exceptions indicate that the relationship is not necessitated  
302 mathematically, but instead is governed by evolutionary principles. Characters that vary  
303 enormously in phylogenetic signal throughout lineages and are characterized by repeated gains  
304 and losses, such as soniferous behavior, may be more likely to exhibit a relationship between  
305 ancestral state and phylogenetic signal.

306

307 **Ecological success.** Our results provide compelling evidence that soniferous evolution contributes  
308 to ecological success in many actinopterygian clades, as it does in tetrapods and insects (Miles et  
309 al. 2018, Wilkins et al. 2013). For example, we can now add soniferous behavior to the suite of  
310 traits considered as evolutionary drivers in Acanthomorpha, which account for 85% of fish  
311 species in marine habitats (Wainwright and Longo 2017), because many soniferous species  
312 belong to basal acanthomorph groups, e.g., Beryciformes, Ophidiiformes, and Gadiformes (Fig.  
313 1). Soniferous behavior may be a convergent evolutionary innovation contributing to ecological  
314 success in rapidly evolving and speciose subclades of actinopterygians for which sonifery is  
315 ancestral. For example, Eupercaria and Siluroidei are nested within rapidly evolving lineages in  
316 Actinopterygii (Table 1) (Alfaro et al. 2009), and it is intriguing to hypothesize that sonifery may  
317 promote diversification through sexual selection. This also appears to be the case for soniferous  
318 tetrapods, including birds and eutherian mammals (Alfaro et al. 2009, Chen and Wiens 2020).  
319 Molecular phylogenetic support for Curimatoidea, a clade recently recognized (Arcila et al.  
320 2017, Betancur-R. et al. 2019) within Characiformes (Figs 1, 2), is bolstered by our evidence that  
321 soniferous behavior is ancestral for this clade. Intriguingly, the relationship between repeated  
322 evolution of soniferous behavior in clades that live in shallow water or structurally complex or

323 fragmented habitats where diversification is more likely to occur (Grosberg et al. 2012), suggests  
324 a strong selection for acoustic communication within biodiverse communities.

325         Urlick (1975) points out at the very beginning of his classic text, Principles of Underwater  
326 Sound, that water is an excellent medium for sound transmission compared to other modalities:  
327         Of all the forms of radiation ... sound travels through the sea the best. In the turbid,  
328         saline water of the sea, both light and radio waves are attenuated to a far greater degree  
329         than is that form of mechanical energy known as sound. (Urlick 1975)

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

342         We report a correlation between families exhibiting soniferous behavior and hearing  
343 specializations that enhance sound detection. This enhances the efficacy of other physiological  
344 mechanisms for audio-vocal coupling that support acoustic communication. Actinopterygians  
345 share with tetrapods (and insects) two hallmarks of audio-vocal coupling: auditory encoding of



346 the spectral and temporal properties of conspecific and heterospecific vocalizations (Bass et al.  
347 2005, Rohmann et al. 2013), and a central vocal corollary discharge, whereby vocal pattern  
348 generator neurons inform auditory neurons about the spectral and temporal attributes of one's  
349 own vocalizations (Chagnaud and Bass 2013).

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

358

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

367

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534

535 **Acknowledgements**

536 Research supported, in part, by National Science Foundation awards OCE-1736936 (ANR),  
537 DBI-1523836 (SCF), and IOS-1656664 (AHB), the Tontogany Creek Fund (WEB), and Cornell  
538 Lab of Ornithology (AJM). Thanks to K. Bemis, T. Grande, H. W. Greene, L. Hughes, G. Ortí,  
539 L. Page, E. Schuppe, M. Wilson and K. R. Zamudio for discussion and helpful comments on the  
540 manuscript. Thanks also to Rick Grosberg for helpful feedback on complexity of aquatic  
541 habitats.

542

543 **Author Contributions**

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

548

549 **Competing Interests**

550 None

551

552 **Materials and Correspondence**

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554



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

Clade	Number of Extant Families in Figure 2	Estimated Number of Valid Extant Species <sup>1</sup>	Probability Soniferous Behavior is Ancestral to Clade <sup>2,3</sup>	Phylogenetic Signal	
				D statistic	Probability of Brownian Phylogenetic Structure <sup>2</sup>
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

557 <sup>1</sup> Rounded to nearest 10 based on 04 April 2020 download of (Fricke et al. 2020).

558 <sup>2</sup> Probabilities for ancestral state and Brownian phylogenetic structure are represented differently  
 559 to help distinguish them.

560

561 <sup>3</sup> Node percentages summarize 1000 stochastic character mapping simulations.

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568 **Figure Legends**

569

570 **Fig. 1. Family-level phylogenetic tree of actinopterygians depicting evolution of soniferous**

571 **behavior.** Shown here are posterior probabilities from ancestral state reconstruction using

572 stochastic character mapping. Probability is represented as a gradient, where blue indicates a

573 high probability and red a low probability of soniferous behavior, and yellow is equivocal. Tree

574 is pruned from species-level phylogeny of Rabosky et al.(Rabosky et al. 2018) to family-level

575 here.

576

577 **Fig. 2. Posterior probability soniferous behavior within major actinopterygian clades. (a)**

578 Otocephala, **(b)** Anabantaria + Carangaria + Ovalentaria, and **(c)** Eupercaria. For phylogenetic

579 trees showing the ancestral state estimation and associated evolutionary probabilities of sound

580 production being ancestral by stochastic character mapping, probability is represented as a

581 gradient where blue indicates high and red is low probability of sound production; yellow is

582 equivocal.

583

584 **Fig. 3. Phylogenetic signal versus ancestral state estimation for evolution of actinopterygian**

585 **soniferous behavior. (a)**  $D$  statistic value (Fritz and Purvis 2010) versus ancestral state estimate

586 (using stochastic character mapping) probability that soniferous behavior is ancestral for a clade.

587 **(b)** Probability of Brownian phylogenetic structure (modelled from  $D$  statistic) versus stochastic

588 character mapping probability soniferous behavior is ancestral for a clade. Values for  $D$  statistic,

589 probability of Brownian structure, and ancestral state probabilities are listed in Table 1. Only

590 clades with >25 families are used, since inference of  $D$  is limited for clades with <25 taxa (Fritz

591 and Purvis 2010).

592 **Supplementary Information**

593

594 **Fig. S1. Soniferous behavior mapped onto phylogenetic tree of actinopterygian families.**

595 Tree shows three different lines of evidence for soniferous behavior used here and its  
596 phylogenetic distribution. Tree is pruned from species-level phylogeny of Rabosky et al. (2018)  
597 to family-level here. Some clades recovered using genomic (Betancur-R et al. 2017; Near et al.  
598 2012; Rabosky et al. 2018) and transcriptomic data (Hughes et al. 2018) are supported by well-  
599 accepted, anatomical synapomorphies, but others such as Ovalentaria (Hughes et al. 2018) are  
600 not.

601

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

604

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

612

613

614 **Table S1.** Evidence for sound production in actinopterygian families. Levels of evidence are  
 615 coded as audio recordings (1), morphological inference (2), or qualitative observations (3).  
 616 Representative references are included to support evidence of sound production. Families are  
 617 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	(Sørensen 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; Sørensen 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.	Batrachoidiformes	Batrachoididae	1	(Fish et al. 1952)
74.	Eupercaria	Scaridae	1	(Tricas and Boyle 2014)
75.	Eupercaria	Labridae	1	(Fish et al. 1952)
76.	Eupercaria	Glaucomatidae	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; Sørensen 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	(Sørensen 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	Hemipteridae	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)

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619

620 **Table S2. (separate excel file) Aggregated data for 461 families considered in this analysis.**

621 Showing soniferous behaviors, valid extant species, male alternative reproductive tactics (Mank  
622 and Avise 2006), ecological data aggregated from FishBase (Boettiger et al. 2012; Froese and  
623 Pauly 2019), including occurrence of families as a function of latitude, salinity, bottom type,  
624 habitat, trophic ecology, and reproductive mode.

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

634

635 **Table S3. Clades with independent evolution of sonifery in actinopterygian fishes and**  
 636 **associated habitats.** Nodes on the phylogenetic tree are labelled in Supplementary Figure 2.  
 637 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

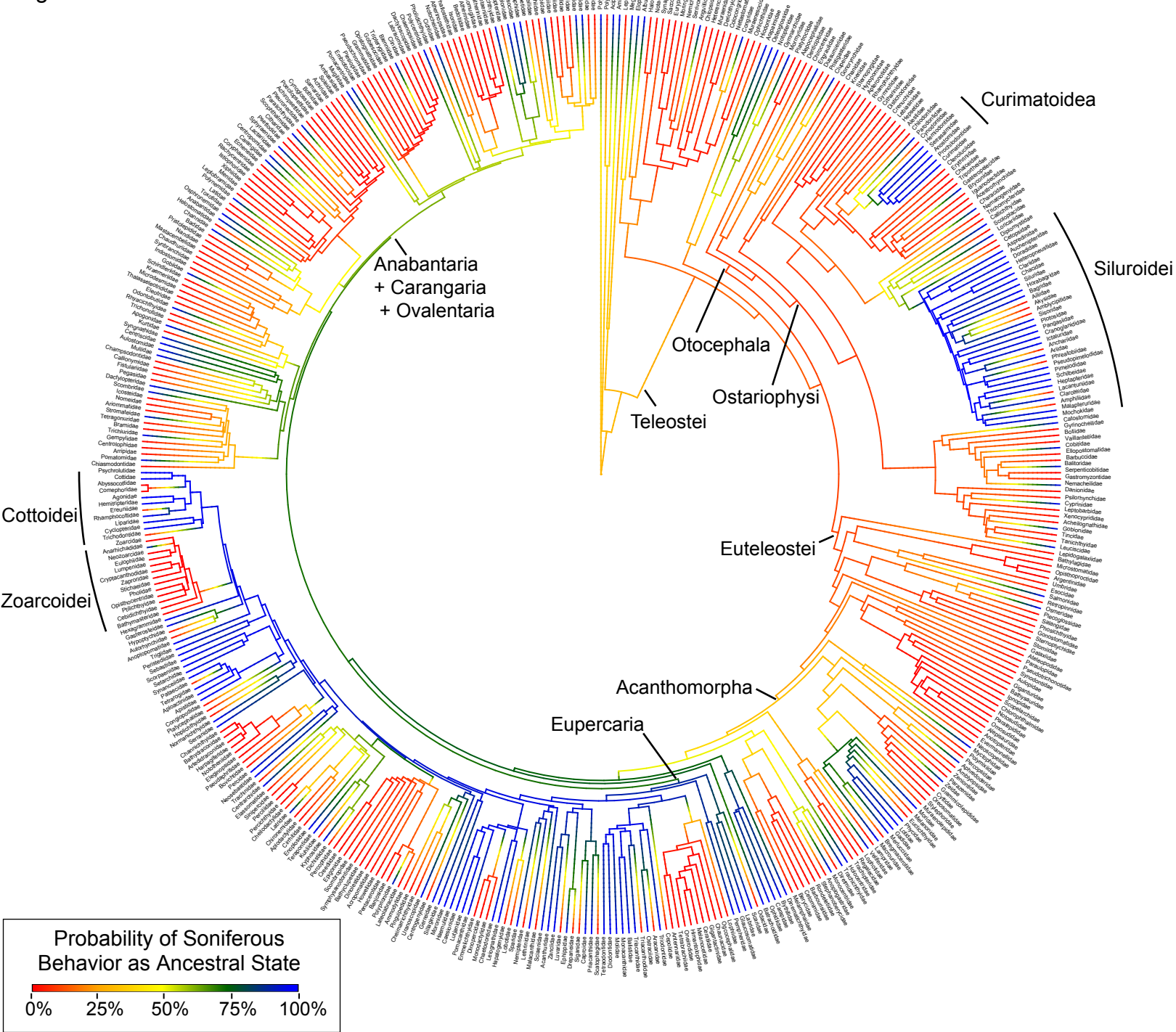
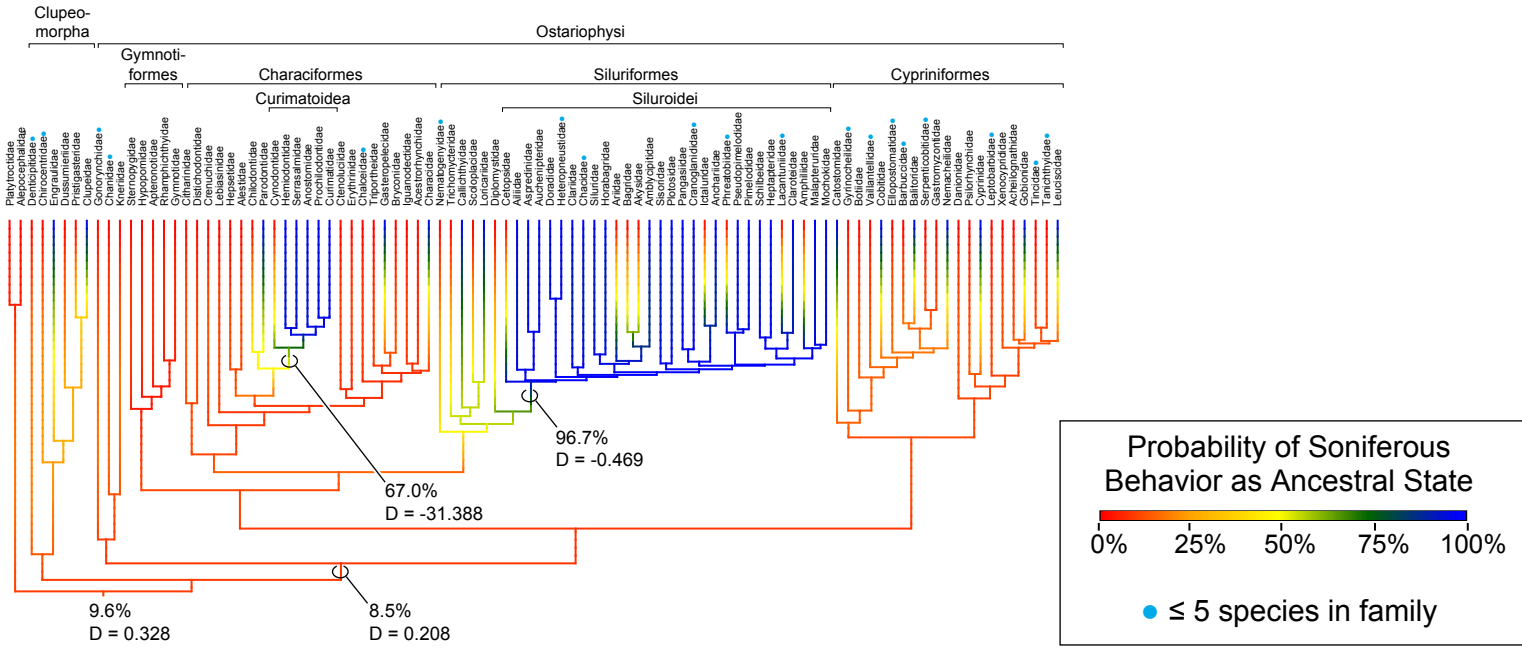
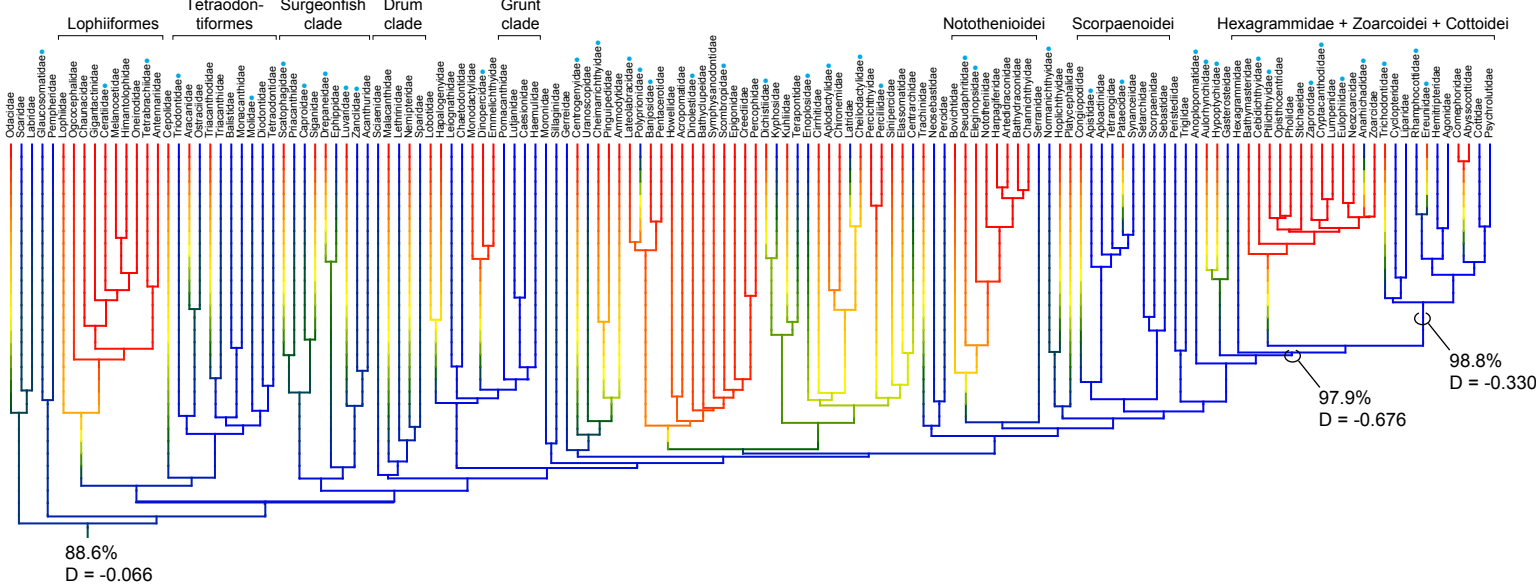


Figure 2

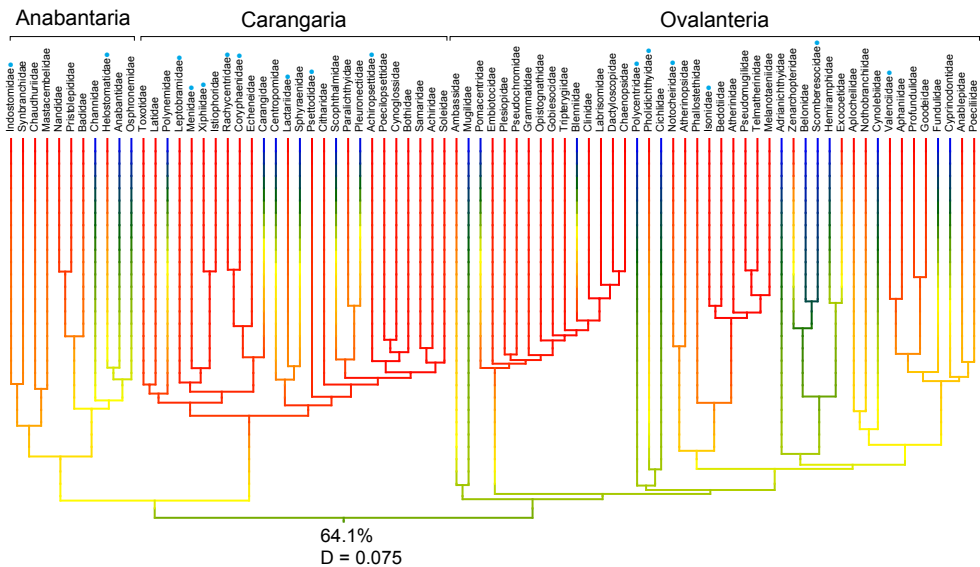
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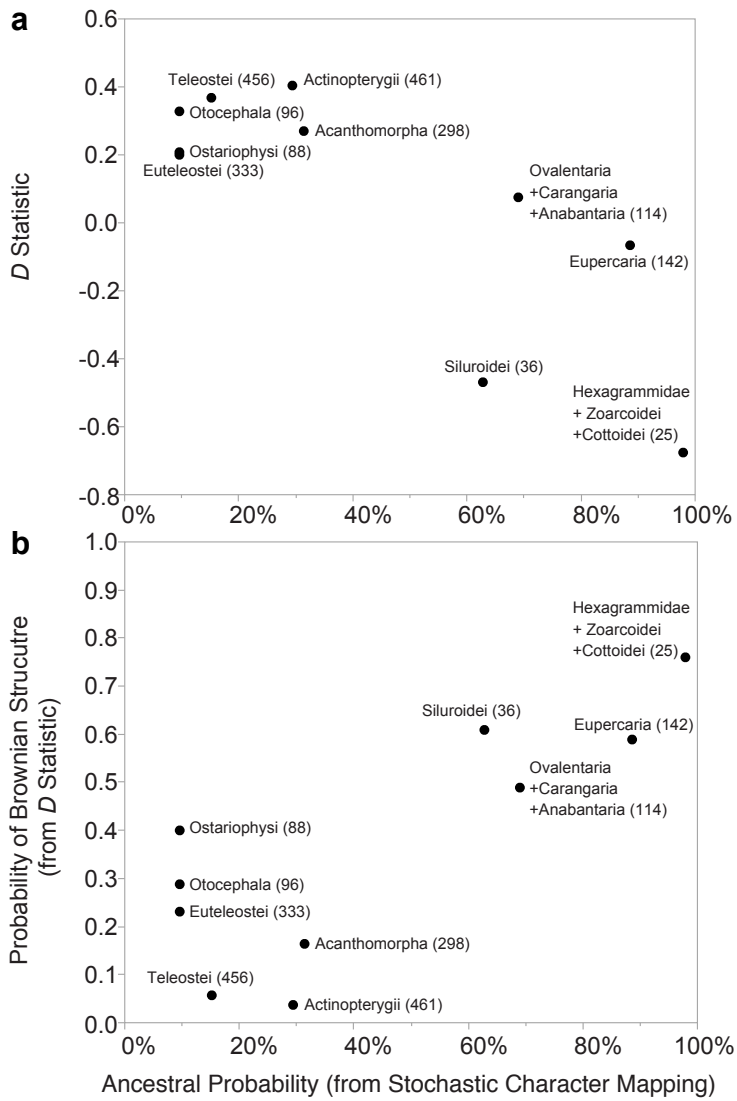
**b Eupercaria**



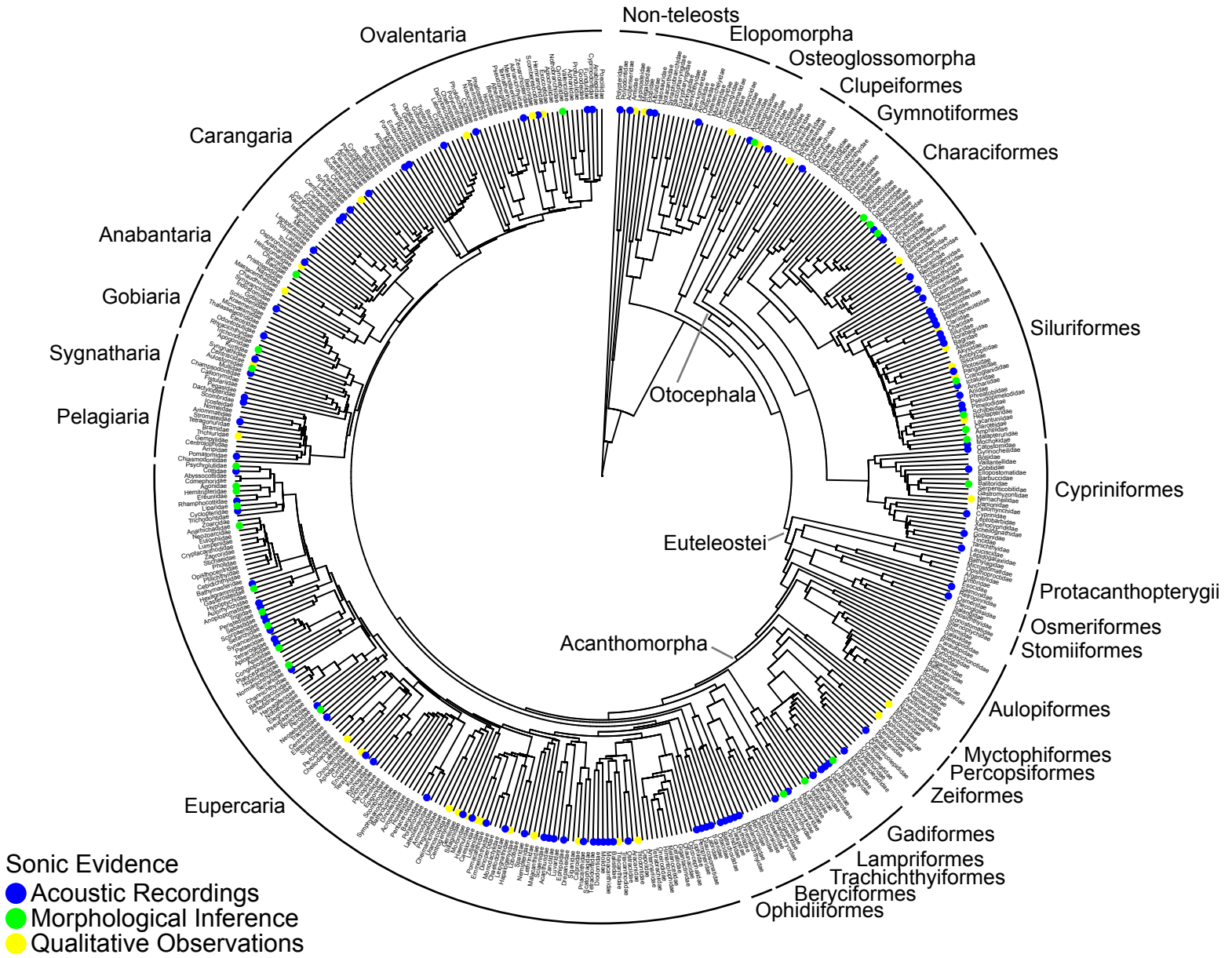
**c Anabantaria + Carangaria + Ovalentaria**



### Figure 3



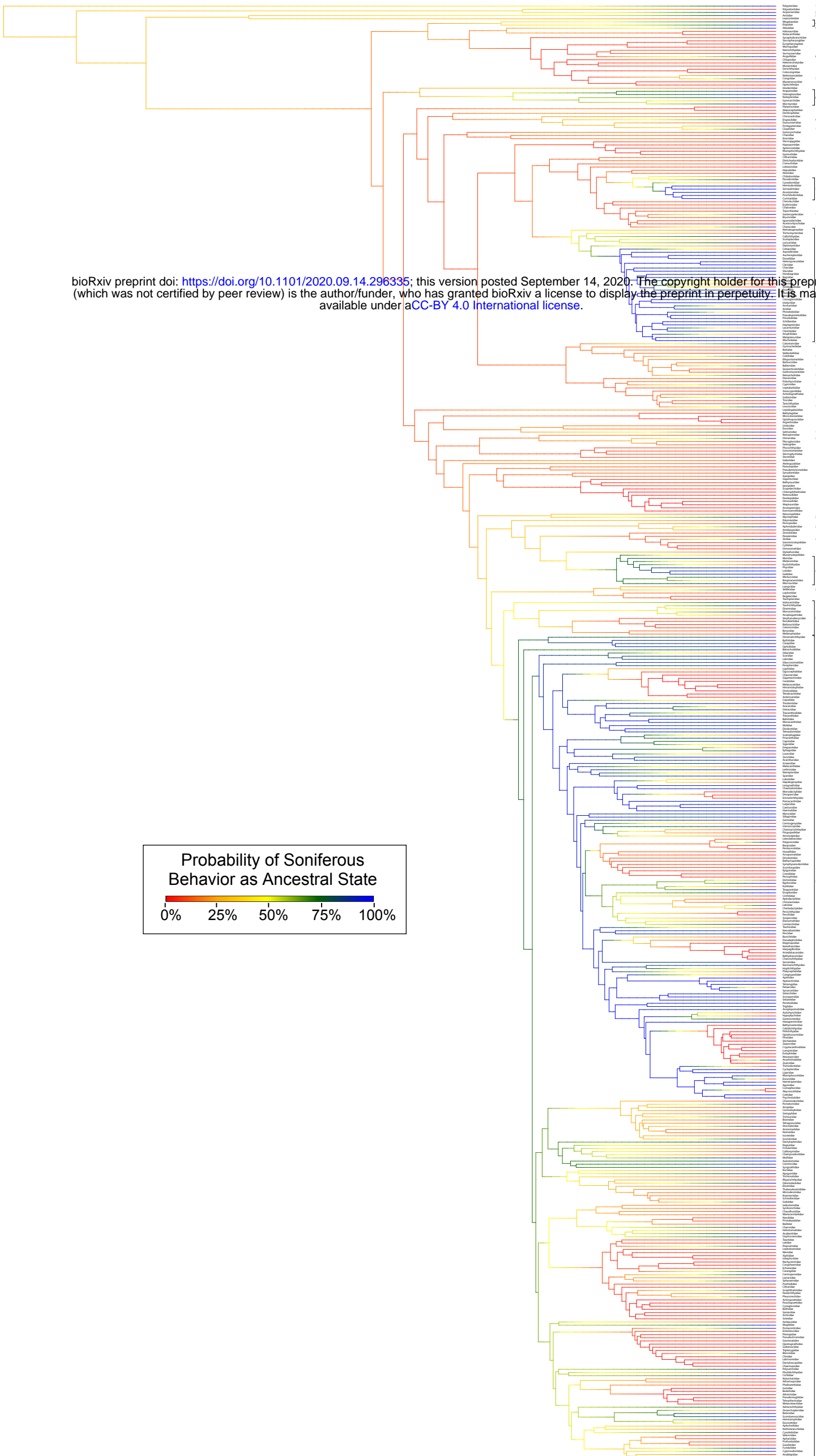
## Supplementary Figure 1





# Supplementary Figure 2

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Supplementary Figure 3

