Evolutionary Patterns in Sound Production across Fishes

Aaron N. Rice[1], Stacy C. Farina[2], Andrea J. Makowski[3], Ingrid M. Kaatz[4], Phillip S. Lobel[5], William E. Bemis[6], and Andrew H. Bass[3]

Sound production by fishes has been recognized for millennia, but is typically regarded as comparatively rare and thus yet to be integrated into broader concepts of vertebrate evolution. We map the most comprehensive dataset of sound production yet assembled onto a family-level phylogeny of ray-finned fishes (Actinopterygii), a clade containing more than 34,000 extant species. Family-, rather than species-, level analyses allowed broad investigation of sound production mostly based on illustrations of acoustic recordings and morphological specializations (82%) strongly indicative of sound production along with qualitative descriptions (18%), and a conservative estimate of the distribution and ancestry of a character that is likely more widespread than currently known. Compilation of sonic-related morphological characters shows 60 families exhibiting muscles coupled to swim bladder vibration and 39 families that employ movement of skeletal parts against each other, i.e., stridulation. Eighteen of these families, mostly catfishes (13), include individual species exhibiting both mechanisms. The results show that families with soniferous species contain nearly two-thirds of actinopterygian species, including a clade originating circa 155 Ma, and that sound production has independently evolved approximately 33 times within Actinopterygii. Despite the uncertainties of presence-only data records and incomplete evidence of absence, under-sampling species, and assuming family-level conservation of sound production, sensitivity analyses show that these patterns of shared ancestry are robust. In aggregate, these findings offer a new perspective on the ancestry and convergent evolution of sound production among actinopterygians, a clade representing more than half of extant vertebrate species.

THE use of sound as a communication channel is widely recognized in terrestrial species of vertebrates and marine mammals (Bradbury and Vehrencamp, 2011; Ladich and Winkler, 2017). Less well known is its prevalence among fishes, despite multiple early accounts (Dufossé, 1874; Abbott, 1877; Darwin, 1878; Aristotle, 1883; Tower, 1908; Pauly, 2004). Actinopterygii, or ray-finned fishes, includes more than half of extant vertebrate diversity and is one of two extant radiations of bony vertebrates together with Sarcopterygii, which includes coelacanths, lungfishes, and tetrapods (Nelson et al., 2016). Here, we use a quantitative, phylogenetic approach to test the hypothesis that sound production is an ancient behavior that has evolved more than once among actinopterygians, as recently shown for tetrapods (Chen and Wiens, 2020). We assess the distribution of sound production as a behavioral character that is "the result of actions taken by organisms" ("non-structural" character of Wiley, 1981: 319; also see Lauder, 1986; Wenzel, 1992; Greene, 1999; Lapiedra et al., 2018; Travis and Reznick, 2018). Soniferous behavior is associated with a communication function within or between species rather than a by-product of feeding or locomotion. Although the available data are less comprehensive, this includes the mapping of morphological features ("structural" character of Wiley, 1981: 319) known to underlie sound production or soniferous behavior.

As von Frisch (1938: 11) commented, "We know many species of sound-producing fish. There may be many more . . . . [and] much to discover in the future about the language of fishes". Since then, catalyzed by advancements in recording and analytical technology (Mann et al., 2016), and increased understanding of actinopterygian evolutionary relationships (e.g., Miya et al., 2003; Betancur-R. et al., 2013, 2017; Rabosky et al., 2013, 2018; Miya and Nishida, 2015; Sanciangco et al., 2016; Hughes et al., 2018), a growing body of evidence shows the role of sound production in social communication contexts ranging from reproductive tactics and resource defense to group cohesion, individual recognition and predator avoidance (Ladich, 2015). Although there are ever-increasing examples of sound production in actinopterygians (Ladich et al., 2006; Ladich, 2015) and studies demonstrating underlying morphological and physiological mechanisms similar to those of tetrapods (Bass, 2014; Zhang and Ghazanfar, 2020), more widespread recognition of sound production among fishes, and its integration into broader concepts of vertebrate evolution, are still lacking.

We recognize the challenge of assessing the ancestry of soniferous behavior within a clade of more than 34,000 valid extant species (Fricke et al., 2020). Thus, we chose a family level of analysis to be conservative in conclusions drawn regarding the distribution and ancestry of a behavioral character that is likely far more widespread in actinopterygians than is currently known. Combining stochastic character mapping with the most recent comprehensive phylogeny, our analyses show that soniferous behavior in Actinopterygii has evolved approximately 33 times but is ancestral for several radiations that together comprise nearly 29,000 species. We also show that sound production

[1] K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, New York; Email: arice@cornell.edu. Send reprint requests to this address.
[2] Department of Biology, Howard University, 415 College St. NW, Washington, D.C.
[3] Department of Neurobiology and Behavior, Cornell University, 215 Tower Road, Ithaca, New York; Email: (AHB) ahb3@cornell.edu.
[4] Stamford, Connecticut.
[5] Department of Biology, Boston University, 5 Cummington Street, Boston, Massachusetts.
[6] Department of Ecology and Evolutionary Biology and Cornell University Museum of Vertebrates, Cornell University, 215 Tower Road, Ithaca, New York.

appeared in actinopterygians circa 155 Ma, as it did in some tetrapods (Chen and Wiens, 2020).

In aggregate, we conclude that our results strongly support the hypothesis that soniferous behavior is ancient, but independently evolved in multiple clades of Actinopterygii, as it is among tetrapods (Chen and Wiens, 2020). Together, these findings highlight the strong selection pressure favoring the evolution of this character across vertebrate lineages.

MATERIALS AND METHODS

Family-level documentation of the occurrence of sound production.—One hundred and forty-one references derived from the published technical and scientific literature (journal articles, books, unpublished dissertations and theses, conference proceedings, and technical reports) were used to build a family-level database on the occurrence of fish sounds. This resulted from an extensive search employing three methods to find documentation of sounds at the family level. First, we reviewed a series of seminal works and comprehensive reviews in the area of fish bioacoustics to populate the initial family-level list (e.g., Dufossé, 1874; Sörensen, 1894–1895; Tavolga, 1968, 1971; Fish and Mowbray, 1970; Fine et al., 1977; Tavolga et al., 1981; Amorim, 2006). Second, we employed a series of standardized search terms in scientific search engines ("All Databases" in Web of Science, Google Scholar) using the search operator: "(fish* AND (sound production OR acoustic OR vocal* OR bioacoustic* OR sonic OR soniferous OR sound*))". Third, a heuristic approach similar to "snowball sampling" (*sensu* Johnson, 2014; Doohan et al., 2019) was adopted to track both citing literature and the literature cited of papers. Lastly, in cases where there was no evidence for sound production for a particular family returned through the broader keyword-based search, targeted searches were conducted in species or family guides (e.g., FishBase, FAO Guides) for any information on the occurrence of sound production. Documented evidence for the absence of soniferous behavior based on attempts to record sounds from such species with hydrophones was very limited (Fish and Mowbray, 1970; Kaatz et al., 2010).

The above search resulted in three principal sets of evidence identifying the occurrence of a single character—soniferous behavior (see Table S1 for summary, including sources; see Data Accessibility): 1) quantitative or pictorial documentation of acoustic recordings; 2) morphological characters strongly predictive of sonic ability (Fine and Parmentier, 2015); 3) qualitative descriptions of acoustics or morphological characters indicative of sonic ability.

Morphology underlying sonic behavior.—As stated above, morphological characters strongly predictive of sonic ability were one source of evidence identifying the occurrence of soniferous behavior within a family (Table S1; see Data Accessibility). Although the database was not as large as that available for acoustic recordings, it was still formidable. Given this, we separately mapped the phylogenetic distribution of three major categories of sonic mechanisms based on morphological (structural) characters reported in the literature that are considered to produce soniferous behavior (Table S1; see Data Accessibility). (1) Swim bladder vibration resulting from contractions of striated muscle attached to the swim bladder either directly or indirectly via movement of another skeletal part in close proximity. Examples include contraction of "drumming" muscles directly attached to the walls of the swim bladder of toadfishes and the sonic muscles of catfishes that indirectly induce swim bladder vibration via an elastic spring mechanism (Fine and Parmentier, 2015). (2) Stridulation resulting from movement of skeletal parts against each other. Examples include movements of oral jaw or pharyngeal teeth in anemonefish (Fine and Parmentier, 2015), fin spines in catfish (Fine and Parmentier, 2015), and pectoral girdle parts in sculpin (Barber and Mowbray, 1956; Fine and Parmentier, 2015). Other skeletal elements were also included, such as the snapping of pectoral fin tendons in croaking gouramis (*Trichopsis vittata*, family Osphronemidae; see Ladich et al., 1992; categorized as "buckling" by Bradbury and Vehrencamp, 2011). (3) Non-swim bladder vibration resulting from vibration of the entire body, large parts of the body, or of muscles not associated with the swim bladder. In some families, multiple sonic mechanisms have been identified (e.g., Kaatz, 2002), and these were included in analyses.

Ancestral-state reconstruction.—The presence or absence of soniferous behavior was scored as a binary character (Table S1; see Data Accessibility). To be conservative, we coded all families lacking such evidence as 0 (silent). Ancestral states were calculated using stochastic character mapping with the make.simmap function in the phytools package for R (version 0.7-70; Revell, 2012), with 1,000 MCMC generations, and the ARD ("All Rates Different") model to not assume that rates of behavioral evolution are the same among all clades. Clade values and transition rates were calculated by simulation, and posterior probabilities were mapped using the densityMap function in phytools (Revell, 2012; Figs. 1, 2). Probability values ≥50% were considered to be indicative of soniferous behavior being ancestral for a clade.

Next, we mapped the presence of soniferous behavior onto a recent phylogeny of the Actinopterygii that included species from 470 families (Rabosky et al., 2018; Fig. 1, Table S1; see Data Accessibility). All species included in the phylogeny (Rabosky et al., 2018) were assigned to their currently recognized families using Eschmeyer's Catalog of Fishes (Fricke et al., 2020). The Rabosky et al. (2018) tree was then pruned to include only one member of each family based on genus, using a list of valid genera in each family from the Eschmeyer Catalog of Fishes (Fricke et al., 2020). A rapidly expanding body of work has demonstrated that in actinopterygian families where sound production has been investigated, most species examined to date are soniferous, including toadfishes (Batrachoididae; e.g., Mosharo and Lobel, 2012), drums (Sciaenidae; e.g., Ramcharitar et al., 2006), damselfishes (Pomacentridae; e.g., Parmentier et al., 2016), butterflyfishes (Chaetodontidae; e.g., Tricas and Boyle, 2015), sturgeons (Acipenseridae; e.g., Johnston and Phillips, 2003), gobies (Gobiidae; e.g., Zeyl et al., 2016), cichlids (Cichlidae; e.g., Lobel et al., 2021), squirrelfishes (Holocentridae; e.g., Parmentier et al., 2011), and cods (Gadidae; e.g., Hawkins and Picciulin, 2019). Based on the existing and abundant evidence for extensive soniferous behavior within families, we decided that it was reasonable to assume that this behavior is conserved at the family level.
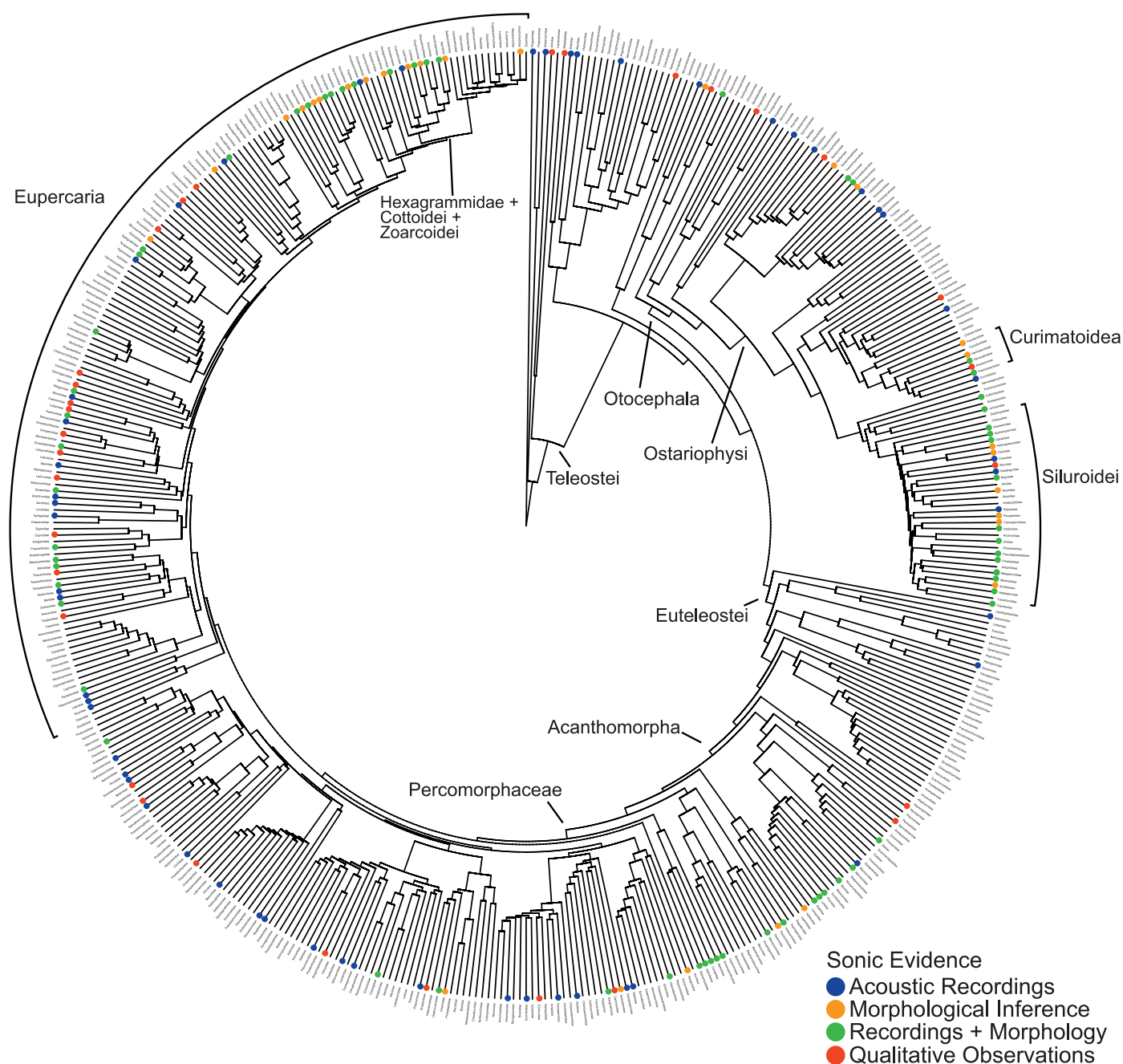
Fig. 1. Soniferous behavior mapped onto phylogenetic tree of actinopterygian families. Tree shows three different lines of evidence for soniferous behavior used here and its phylogenetic distribution. Tree is pruned from species-level phylogeny of Rabosky et al. (2018) to family-level here.

Sensitivity analyses.—We recognize that our use of presence-only categorical character data, rather than continuous data, greatly limits the different types of phylogenetic comparative methods suitable to calculate and evaluate our data. We also recognize that the sampling of soniferous fishes represents a possible sampling bias (e.g., pelagic, deep-water, or rare species are undersampled) and that our results may be sensitive to uncertainties in character data that can influence outcomes using comparative methods in phylogenetic analysis (Paterno et al., 2018). Two principal sources of error may influence our interpretations: 1) soniferous behavior is conserved at the family level (Type I error, or false positive, where we incorrectly infer that soniferous behavior is conserved at the family

level), and 2) absences of data represent true absences of soniferous behavior and not just the result of sampling bias in previous studies (Type II error, or false negative, where we incorrectly infer that soniferous behavior is absent at the family level). Missing or uncertain character-state data is recognized to create uncertainty in phylogenetic inference and interpreting evolutionary patterns and processes through ancestral-state reconstruction (e.g., Maddison, 1993; Kearney, 2002). There have been several approaches to dealing with character state uncertainty, ranging from conservatively coding uncertain data as "absent" (e.g., Baliga and Law, 2016; Chen and Wiens, 2020) to modeling the probability of uncertainty or misclassification (Paterno et al., 2018). To account for possible uncertainties about
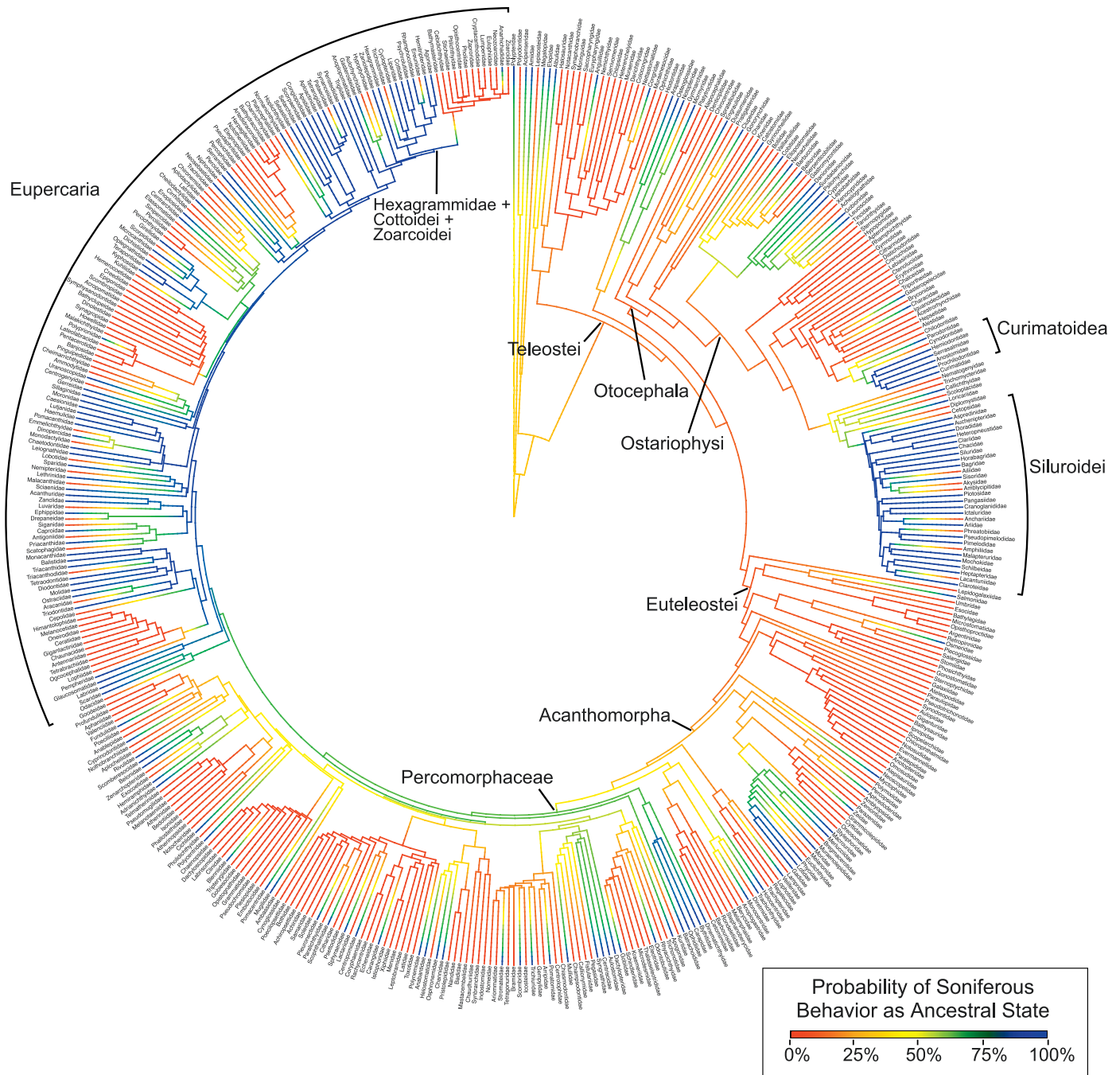
Fig. 2. Family-level phylogenetic tree of actinopterygians depicting evolution of soniferous behavior. Shown here are probabilities from ancestral-state reconstruction using stochastic character mapping. Probability is represented as a gradient, where blue indicates a high probability and red a low probability of soniferous behavior, and yellow is ~50% probability. Tree is pruned from species-level phylogeny (Rabosky et al., 2018) to family-level here.

our inference that sound production is conserved at the family level, we performed a sensitivity analysis (*sensu* Grant and Kluge, 2003) to evaluate the robustness of our stochastic character mapping results to changes in the underlying data. Following an approach similar to Odom et al. (2014), we conducted an iterative set of simulations where we artificially varied the proportion of families having or lacking evidence of soniferous behavior. We chose the range of 0–12% for sensitivity analysis for ancestral-state reconstruction, because clade values tended to converge on 50% probability for all clades at or beyond

12% uncertainty, especially for the false absence tests. We randomly assigned 2, 4, 6, 8, 10, and 12% of those missing families as having (false absence, or Type II error) or not having (false presence, or Type I error) evidence for sound production, and used stochastic character mapping (as above) to simulate character evolution with these missing data with 1,000 iterations for each permutation. With new ancestor reconstructions based on those randomizations, we then qualified our ancestral-state probability for key clades (Table 1).

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

Clade	Number of extant families in Figure 2	Number of soniferous families	Estimated number of valid extant species[a]	Probability soniferous behavior is ancestral to clade[b]
Actinopterygii	470	172	34,030	32.3%
Teleostei	464	169	33,970	16.6%
Osteoglossiformes	5	4	248	54.3%
Otocephala	97	41	11,720	9.8%
Ostariophysi	88	39	11,160	9.1%
Curimatoidea	6	5	420	63.6%
Siluroidei	29	22	2,340	93.9%
Euteleostei	340	119	20,930	10.7%
Acanthomorpha	305	116	19,470	24.8%
Percomorphaceae	268	102	17,759	75.3%
Eupercaria	149	66	6,970	78.1%
Hexagrammidae + Zoarcoidei + Cottoidei	23	9	1,280	97.8%

[a] Rounded to nearest 10 based on 04 April 2020 download of Fricke et al. (2020).
[b] Clade percentages summarize 1,000 stochastic character mapping simulations.

RESULTS

Evidence of soniferous behavior (direct or indirect) was identified in 175 of the 470 families represented in the phylogenetic hypothesis presented by Rabosky et al. (2018; Fig. 1, Table S1; see Data Accessibility) based on our three sources of evidence (Fig. 2, also see Materials and Methods): 52 families were supported by acoustic recordings or analysis, 26 families by inference based on morphological characters well known to be associated with sound production, 66 families by both acoustic and morphological evidence, and 31 families by qualitative descriptions indicative of soniferous behavior.

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 ($n = 1,000$ in this study) are used to compute probabilities of a character being ancestral for clades (also see Materials and Methods). Figure 2 reconstructs ancestral states of soniferous behavior across actinopterygian phylogeny showing probabilities ranging from 0% to 100% that the family is characterized by sound production; Table 1 presents a summary of probability values at key nodes.

Although soniferous behavior occurs in the three extant clades of non-teleostean actinopterygians (Polypteriformes, Acipenseriformes, Holostei; Fig. 2), the reconstruction reveals that it is unlikely to be ancestral with probability values of only 32.3% for Actinopterygii and 16.6% for Teleostei, which comprises >99.8% of actinopterygian species (Nelson et al., 2016). Otocephala, a species-rich subclade of actinopterygians exhibiting morphological adaptations to enhance hearing (Braun and Grande, 2008), and Ostariophysi, a large subgroup of Otocephala, have even lower probabilities of 9.8% and 9.1%, respectively, that soniferous behavior is ancestral. Euteleostei, a second large subclade of Teleostei that includes two-thirds of living fish species, also shows a low probability of 10.7% that soniferous behavior is ancestral.

We find much stronger support for soniferous behavior as a character at the base of several key clades within teleosts. Osteoglossiforme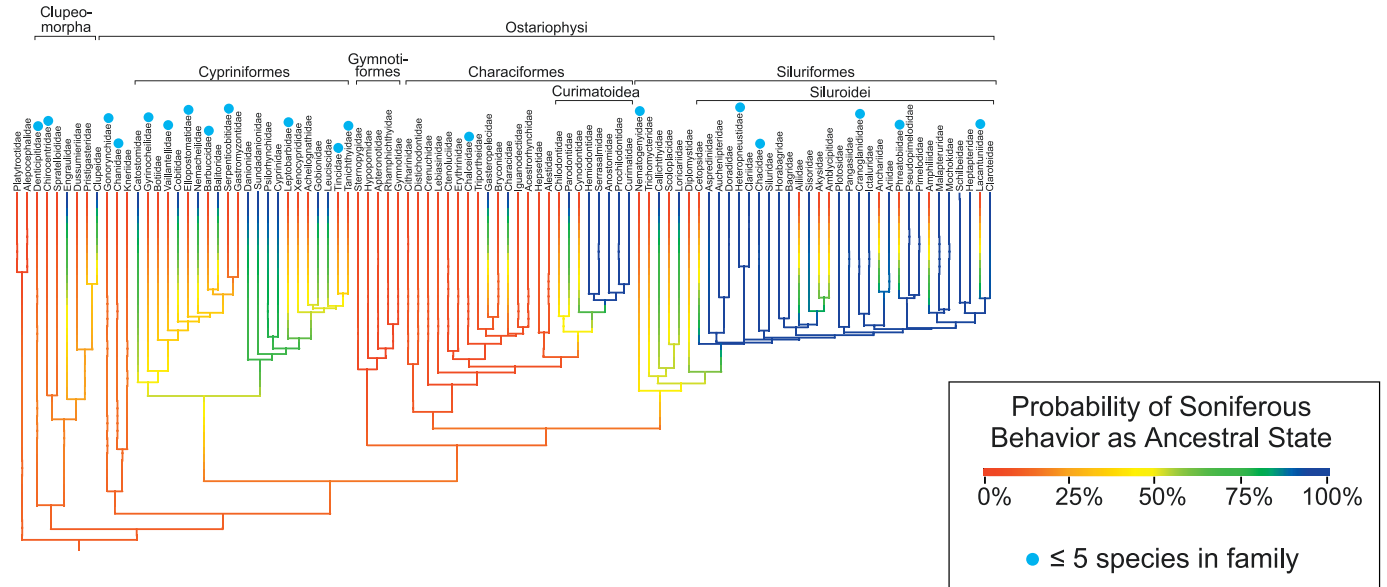s, an early-diverging clade of teleosts, contains four soniferous families and has a 54.3% probability that soniferous behavior is ancestral. Siluroidei, a subclade of catfishes, and Curimatoidea, a subclade of the Characiformes, have probabilities of 93.9% and 63.6%, respectively, that soniferous behavior is ancestral (Figs. 2, 3A). Acanthomorpha, which includes 85% of actinopterygian species in marine habitats (Wainwright and Longo, 2017), has a low probability of 24.8%, but the subclades Percomorphaceae and Eupercaria (e.g., "surgeonfishes," "drums," "grunts," scorpaenoids) have probabilities of 75.3% and 78.1%, respectively, that soniferous behavior is ancestral (Fig. 3B). An even higher probability of 97.8% supports soniferous behavior as ancestral for a crown group within Eupercaria (Fig. 3B)—Hexagrammidae (greenlings) + Cottoidei (e.g., sculpins) + Zoarcoidei (e.g., wolffishes).

In aggregate, our results indicate that soniferous behavior has a high probability, i.e., more than 50%, of being ancestral for approximately 33 independent clades across Actinopterygii identified in our analyses (Fig. S1; see Data Accessibility). We interpret this as evidence of widespread, independent evolution of sound production in actinopterygian fishes.

Morphology underlying sonic behavior.—Morphological information on three broad categories of sonic mechanisms (see Materials and Methods for more clarification) was available for 89 actinopterygian families. As illustrated in Figure 4 and listed in Table S1 (see Data Accessibility), families with more than one mechanism have two filled circles in different colors (one color/mechanism; see legend and Table S1; see Data Accessibility). A single mechanism is reported for 67 families; swim bladder vibration (SBV) is the most common ($n = 41$ families), followed by stridulation (STR, $n = 19$ families) and non-swim bladder vibration (non-SBV, $n = 7$ families). The following families with a non-SBV mechanism include identified species within the family that have lost their swim bladder: Hexagrammidae ($n = 4$, Shinohara, 1994), Aploactinidae ($n = 4$, Matsubara, 1943; Imamura, 2004), and Synanceiidae ($n = 4$, Matsubara, 1943; Imamura, 2004).

Swim bladder vibration occurs with a second mechanism in an additional 22 families (Fig. 4). Both SBV and STR occur
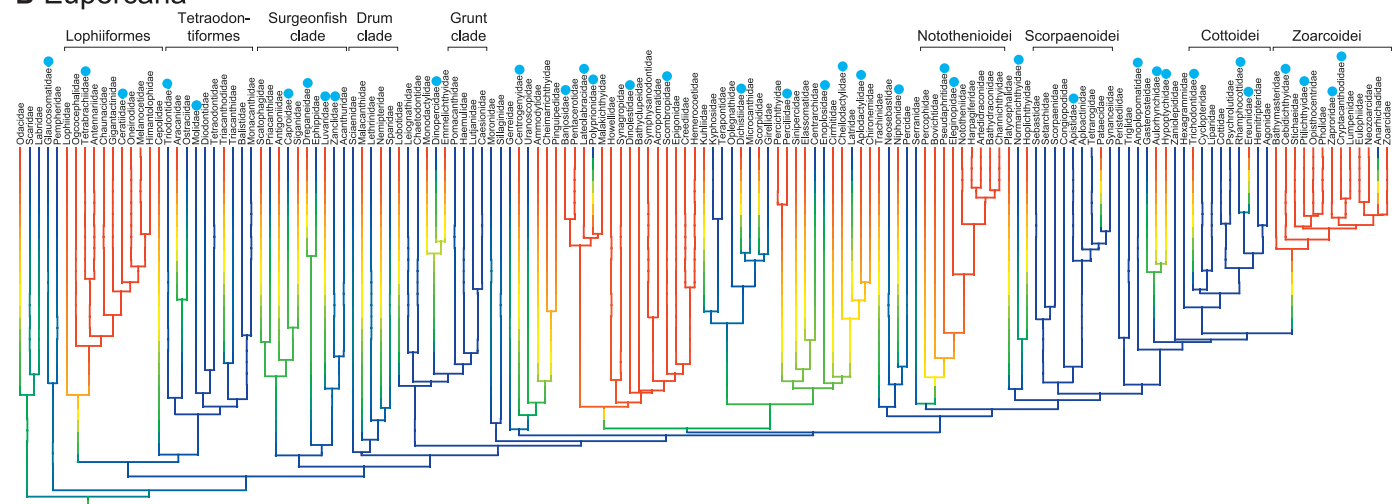
Fig. 3. Probability of soniferous behavior being ancestral within major actinopterygian clades. (A) Otocephala and (B) Eupercaria. For phylogenetic trees showing the ancestral-state estimation and associated evolutionary probabilities of sound production being ancestral by stochastic character mapping, probability is represented as a gradient where blue indicates high and red is low probability of sound production; yellow is equivocal.

within 18 of these families: Tetraodontidae, Balistidae, Tetrarogidae, and 15 families in the Siluroidei (see Fig. 4 for family names); individual species exhibiting both mechanisms are found in Balistidae and the 15 siluroid families. Both SBV and non-SBV are reported for four families: Aploactinidae, Synanceiidae, Hexagrammidae, Rhamphocottidae.

Sensitivity analyses.—Sensitivity analysis incorporating uncertainty in the number of soniferous families did not change the outcomes of our principal findings (Fig. 5). Clades in which there is a high probability that sound production is ancestral, namely Osteoglossiformes, Curimatoidea, Siluroidei, Percomorphaceae, Eupercaria, and Hexagrammidae + Cottoidei + Zoarcoidei, still had a >50% probability of sound production as an ancestral character even when up to 12% of soniferous families are removed (Table 1, Fig. 5). Assignment of ancestral-state probability for key clades did not change

significantly, even with up to 12% of Type I or Type II error, which is less likely than perhaps 1% or 5% of families with missing data that may ultimately be found to be acoustic.

DISCUSSION

The results presented here for actinopterygians, in combination with recent ones for tetrapods (Chen and Wiens, 2020), broadly indicate strong selection to exploit sound production as a behavioral character across vertebrate evolution. Our findings are significant for several reasons. First, we show that sound production is likely as ancient in Actinopterygii as it is in Tetrapoda (~100–200 Ma, Chen and Wiens, 2020), given its presence in Acipenseridae, a family originating circa 155 Ma (Shen et al., 2020), and in Osteoglossiformes, a single order of five families (Nelson et al., 2016) with origins circa 100 Ma (see Lavoué et al., 2012). Polypteriformes are also an ancient lineage (Giles et al., 2017) that exhibit soniferous
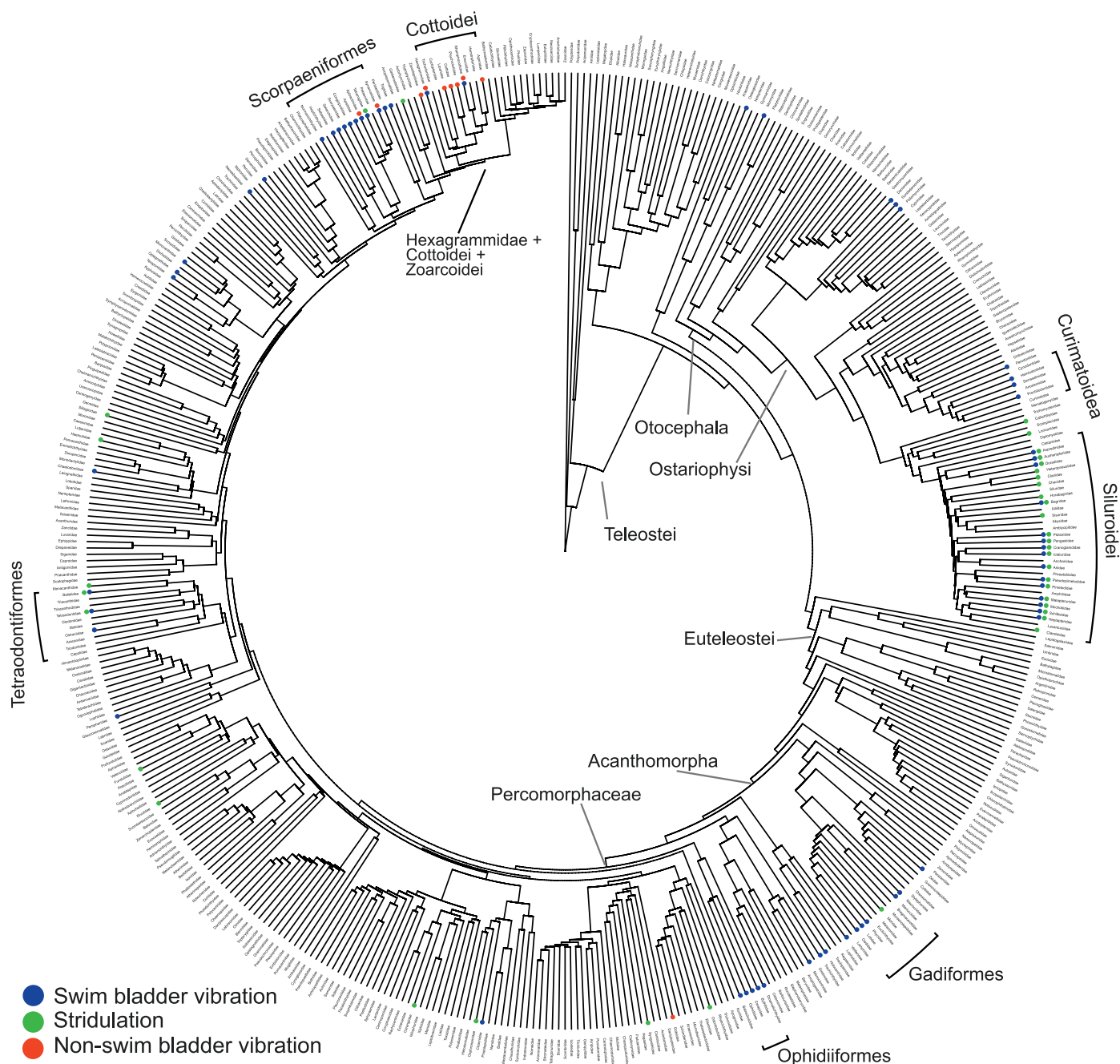
Fig. 4. Family-level phylogenetic tree of actinopterygians as shown in Figure 1, but in this case mapping the distribution of three categories of soniferous mechanisms for 88 families: SBV, swim bladder vibration; STR, stridulation; non-SBV, non-swim bladder vibration (see Results section for details).

behavior, but extant species of Polypteridae share a more recent origin, 15–25 Ma (Near et al., 2014; Hughes et al., 2018). Second, evidence for (or strongly suggestive of) soniferous behavior is present in a surprising number of families ($n = 175$) that contain nearly 85% of the estimated 34,000 valid extant species of actinopterygians spread across the tree (Fig. 1; Table S1; see Data Accessibility). Last, the results suggest that actinopterygians independently evolved soniferous ability approximately 33 times (Fig. S1; see Data Accessibility), an estimate that may change as soniferous behavior is either found or not in more species.

One of the largest limitations with our analysis was our ability to confidently infer the absence of sound production within a family, since the absence of evidence is not evidence of absence. There have been relatively few published studies that specifically report on lack of soniferous behavior despite recording attempts or morphological investigation (e.g., Fish and Mowbray, 1970; Kaatz et al., 2010; Hawkins and Picciulin, 2019). For example, over the development of the field of fish bioacoustics, there have been examples of certain taxa being categorized as silent (*Sebastes* in Fish and Mowbray, 1970) that later recording attempts demonstrated to be soniferous (Širović and Demer, 2009); consequently, if sounds are not recorded during an initial set of observations, it does not always represent definitive proof that the focal species is incapable of soniferous behavior. While phyloge-
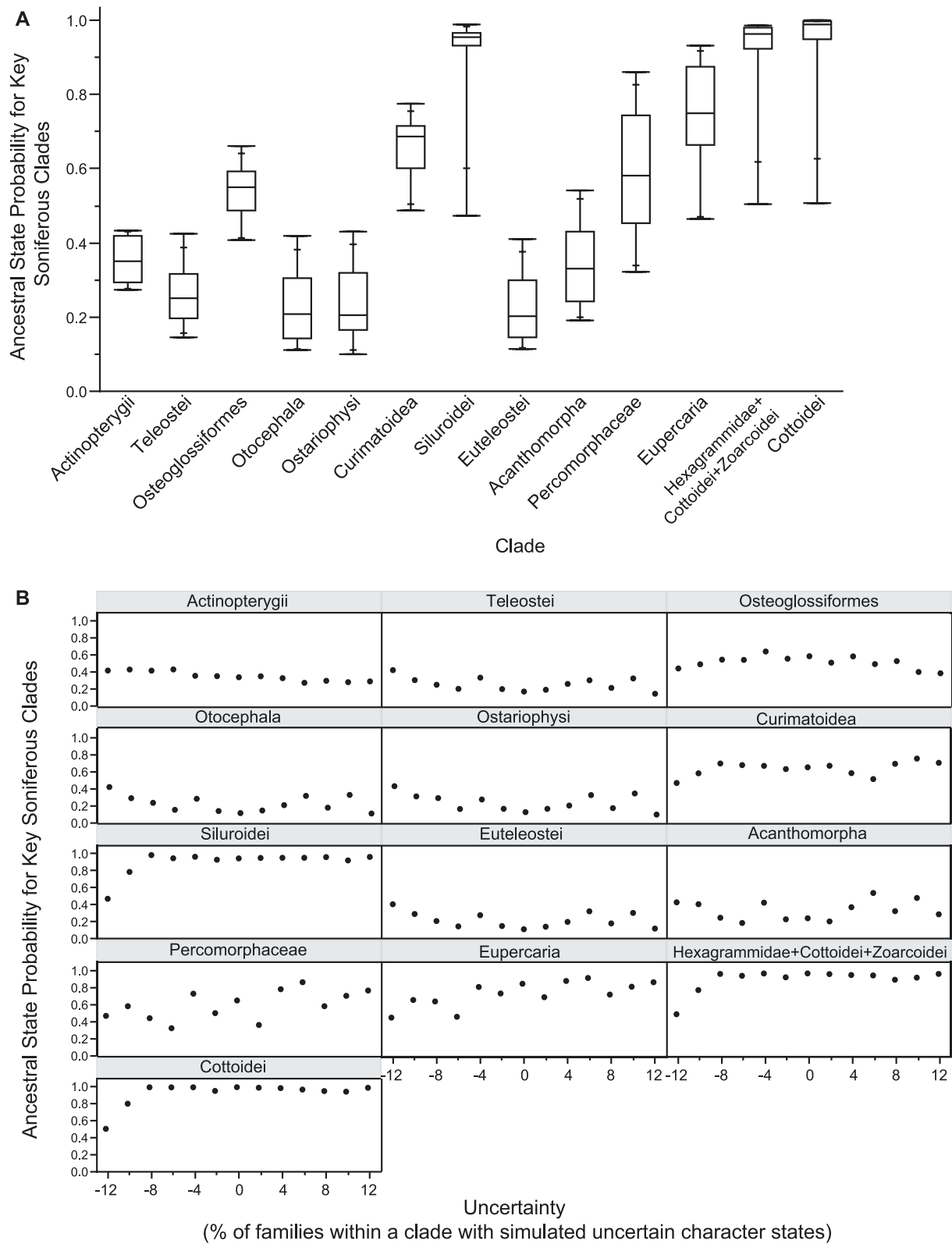
Fig. 5. Sensitivity of ancestral-state reconstruction of soniferous fish clades to uncertainty of character states. (A) Box and whisker plot showing median and interquartile range of ancestral probabilities for different actinopterygian clades included in Table 1 related to increases or decreases in the number of soniferous fish families. (B) Variation in ancestral probabilities for each clade related to sampling uncertainty (the percentage of families within each clade with simulated uncertainty in character state).

netic comparative methods offer extensive power to quantitatively analyze evolutionary patterns, these approaches are limited for categorical data compared to continuous data. Further, our data should be considered a "presence-only" dataset rather than presence–absence. There is a precedent within the paleontological literature for inferring trait evolution using phylogenetic comparative methods that use either presence-only datasets or datasets with unclear patterns of trait absence (e.g., Finarelli and Flynn, 2006; Benton, 2015; Hunt and Slater, 2016), particularly where appropriate trait data may be limited, such as behavior (Hsieh and Plotnick, 2020), physiology (e.g., Legendre et al., 2016), or development (Organ et al., 2015; Jablonski, 2020). Our method for the ability to infer the identity of non-soniferous families offers an opportunity to further explore these families for the potential of soniferous behavior. We envision that many additional fish species will be shown to produce sounds in the coming years, further supporting our demonstration of the widespread nature of soniferous behavior across fishes.

Morphology underlying sonic behavior.—Our survey of sonic mechanisms based on morphological characters would lead one to conclude that swim bladder vibration (SBV) is the ancestral character state for soniferous actinopterygians, occurring in 63 of the 89 families included in our survey; SBV occurs with a second mechanism for the same or different species within a family in about one-third of these families (Fig. 4, Table S1; see Data Accessibility; see Results for definitions). Tetrapods also exhibit examples where the most prevalent sonic organ—larynx or syrinx in non-avian and avian taxa, respectively—occurs together with a second mechanism of sound production (see Bass and Chagnaud, 2012).

If sound production in two sister taxa is achieved through two different mechanisms defined by different morphological characters, this could be an indication that sound production has independently evolved in these two sister taxa because the mechanism is different. While the evidence remains somewhat limited, we find no such support for this possibility in our survey. As such, the mapping of morphological mechanisms presented here does not change our estimate regarding the approximate number of times (33) sound production has independently evolved among actinopterygians. We recognize, however, that it remains important for establishing ancestral character states to look at close relatives of some of the soniferous clades identified here to see if they exhibit similar morphologies for sound production, especially where one is coded as silent and the other as soniferous, e.g., among the Otocephala and Eupercaria (Fig. 3A, B). We further recognize that evidence of one sonic morphology in a single family or species does not necessarily mean that it is the only one because any one study may have only focused on identifying the presence of that character.

Convergent evolution and secondary loss.—The presence and absence of soniferous behavior among actinopterygians likely includes secondary loss (Miles and Fuxjager, 2019). Within speciose clades where soniferous behavior has a high probability of being ancestral, non-soniferous clades may have secondarily lost this character. For example, the clade Hexagrammidae + Cottoidei + Zoarcoidei have 97.8% probability that sound production is ancestral. Fish and

Mowbray (1970) comment on the absence of sound production and swim bladders in Zoarcidae (their Zoarchidae). If further research provides conclusive evidence for absence, then our tree (Fig. 3B) likely indicates secondary loss. As an additional example, sound production is likely ancestral for Gadiformes (Hawkins and Picciulin, 2019), which use specialized swim bladder muscles to make sounds. Yet several species of gadiforms have reduced swim bladder muscles and do not produce sounds, likely representing secondary loss of this behavior (Hawkins and Picciulin, 2019). Other places to investigate potential loss of soniferous capacity are between sister groups where one is coded as silent and the other as soniferous (e.g., Fig. 3).

A particularly fascinating case of secondary loss concerns mochokid catfishes in the genus *Synodontis*; some species are only soniferous and other more recently diverged species are both soniferous and weakly electric or only weakly electric (Boyle et al., 2014). Weakly electric species of *Synodontis* have reduced sonic muscles, but share features of myogenic electric organs (Kéver et al., 2020, 2021). Neuroanatomical studies show that the general pattern of central nervous system organization of populations of neurons is highly conserved among all species of Mochokidae so far investigated (Kéver et al., 2020, 2021). How the electrophysiological properties (physiological characters of Wiley, 1981) of these neuronal populations vary depending on their role in sound production or electric organ discharges has only begun to be explored (see Kéver et al., 2020).

Concluding comments.—Our results indicate that within Actinopterygii, soniferous behavior occurs across the most speciose clades and is estimated to have evolved independently about 33 times. This is a quickly expanding field (Lobel et al., 2010; Lindseth and Lobel, 2018), and there are surely more soniferous fish species and families to be recorded. In a broader sense, together with the recent report showing evolutionary patterns of sound production in tetrapods (Chen and Wiens, 2020), our findings highlight the important role that this behavior has played in the history of vertebrates.

DATA ACCESSIBILITY

Supplemental material, including Table S1, Figure S1, and PDF versions of all figures, is available at https://www.ichthyologyandherpetology.org/i2020172. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

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LITERATURE CITED

Abbott, C. C. 1877. Traces of a voice in fishes. American Naturalist 11:147–156.

Amorim, M. C. P. 2006. Diversity of sound production in fish, p. 71–105. *In:* Communication in Fishes. Vol. 1. F. Ladich, S. P. Collin, P. Moller, and B. G. Kapoor (eds.). Science Publishers, Enfield, New Hampshire.

Aristotle. 1883. Historia Animalium (Aristotle's History of Animals, Translated by R. Creswell). George Bell & Sons, London.

Baliga, V. B., and C. J. Law. 2016. Cleaners among wrasses: phylogenetics and evolutionary patterns of cleaning behavior within Labridae. Molecular Phylogenetics and Evolution 94:424–435.

Barber, S. B., and W. H. Mowbray. 1956. Mechanism of sound production in the sculpin. Science 124:219–220.

Bass, A. H. 2014. Central pattern generator for vocalization: Is there a vertebrate morphotype? Current Opinion in Neurobiology 28:94–100.

Bass, A. H., and B. P. Chagnaud. 2012. Shared developmental and evolutionary origins for neural basis of vocal-acoustic and pectoral-gestural signaling. Proceedings of the National Academy of Sciences of the United States of America 109:10677–10684.

Benton, M. J. 2015. Exploring macroevolution using modern and fossil data. Proceedings of the Royal Society B: Biological Sciences 282:2015069.

Betancur-R., R., R. E. Broughton, E. O. Wiley, K. Carpenter, J. A. López, C. Li, N. I. Holcroft, D. Arcila, M. Sanciangco, J. C. Cureton II, F. Zhang, T. Buser, M. A. Campbell, J. A. Ballesteros . . . G. Ortí. 2013. The tree of life and a new classification of bony fishes. PLoS Currents Tree of Life. 2013 Apr 18. Edition 1.

Betancur-R., R., E. O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre, and G. Ortí. 2017. Phylogenetic classification of bony fishes. BMC Evolutionary Biology 17: 162.

Bollback, J. P. 2006. SIMMAP: stochastic character mapping of discrete traits on phylogenies. BMC Bioinformatics 7:88.

Boyle, K. S., O. Colleye, and E. Parmentier. 2014. Sound production to electric discharge: sonic muscle evolution in progress in *Synodontis* spp. catfishes (Mochokidae). Proceedings of the Royal Society B: Biological Sciences 281: 20141197.

Bradbury, J. W., and S. L. Vehrencamp. 2011. Principles of Animal Communication. Second edition. Sinauer Associates, Sunderland, Massachusetts.

Braun, C. B., and T. Grande. 2008. Evolution of peripheral mechanisms for the enhancement of sound reception, p. 99–144. *In:* Fish Bioacoustics. J. F. Webb, R. R. Fay, and A. N. Popper (eds.). Springer, New York.

Chen, Z., and J. J. Wiens. 2020. The origins of acoustic communication in vertebrates. Nature Communications 11:369.

Darwin, C. 1878. The Descent of Man, and Selection in Relation to Sex. D. Appleton and Company, New York.

Doohan, B., S. Fuller, S. Parsons, and E. E. Peterson. 2019. The sound of management: acoustic monitoring for agricultural industries. Ecological Indicators 96:739–746.

Dufossé, M. 1874. Recherches sur les bruits et les sons expressifs que font entendre les poissons d'Europe et sur les organes producteurs de ces phénomènes acoustiques ainsi que sur les appareils de l'audition de plusieurs de ces animaux. Annales des Sciences Naturelles Cinquième Série: Zoologie et Paléontologie 20:1–134.

Finarelli, J. A., and J. J. Flynn. 2006. Ancestral state reconstruction of body size in the Caniformia (Carnivora, Mammalia): the effects of incorporating data from the fossil record. Systematic Biology 55:301–313.

Fine, M. L., and E. Parmentier. 2015. Mechanisms of fish sound production, p. 77–126. *In:* Sound Communication in Fishes. F. Ladich (ed.). Springer, Vienna.

Fine, M. L., H. E. Winn, and B. L. Olla. 1977. Communication in fishes, p. 472–518. *In:* How Animals Communicate. T. A. Sebeok (ed.). Indiana University Press, Bloomington, Indiana.

Fish, M. P., and W. H. Mowbray. 1970. Sounds of the Western North Atlantic Fishes. Johns Hopkins Press, Baltimore, Maryland.

Fricke, R., W. N. Eschmeyer, and J. D. Fong. 2020. Eschmeyer's Catalog of Fishes: Species by Family/Subfamily. https://researcharchive.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp (accessed 4 April 2020).

Giles, S., G.-H. Xu, T. J. Near, and M. Friedman. 2017. Early members of 'living fossil' lineage imply later origin of modern ray-finned fishes. Nature 549:265–268.

Grant, T., and A. G. Kluge. 2003. Data exploration in phylogenetic inference: scientific, heuristic, or neither. Cladistics 19:379–418.

Greene, H. W. 1999. Natural history and behavioural homology, p. 173–188. *In:* Novartis Foundation Symposium 222—Homology. G. K. Bock and G. Cardrew (eds.). John Wiley & Sons, West Sussex, England.

Hawkins, A. D., and M. Picciulin. 2019. The importance of underwater sounds to gadoid fishes. Journal of the Acoustical Society of America 146:3536–3551.

Hsieh, S., and R. E. Plotnick. 2020. The representation of animal behaviour in the fossil record. Animal Behaviour 169:65–80.

Hughes, L. C., G. Ortí, Y. Huang, Y. Sun, C. C. Baldwin, A. W. Thompson, D. Arcila, R. Betancur-R., C. Li, L. Becker, N. Bellora, X. Zhao, X. Li, M. Wang . . . Q. Shi. 2018. Comprehensive phylogeny of ray-finned fishes (Actino-

pterygii) based on transcriptomic and genomic data. Proceedings of the National Academy of Sciences of the United States of America 115:6249–6254.

Hunt, G., and G. Slater. 2016. Integrating paleontological and phylogenetic approaches to macroevolution. Annual Review of Ecology, Evolution, and Systematics 47:189–213.

Imamura, H. 2004. Phylogenetic relationships and new classification of the superfamily Scorpaenoidea (Actinopterygii: Perciformes). Species Diversity 9:1–36.

Jablonski, D. 2020. Developmental bias, macroevolution, and the fossil record. Evolution & Development 22:103–125.

Johnson, T. P. 2014. Snowball sampling: introduction. *In:* Wiley StatsRef: Statistics Reference Online. N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri, and J. L. Teugels (eds.). John Wiley & Sons.

Johnston, C. E., and C. T. Phillips. 2003. Sound production in sturgeon *Scaphirhynchus albus* and *S. platorynchus* (Acipenseridae). Environmental Biology of Fishes 69:59–64.

Kaatz, I. M. 2002. Multiple sound-producing mechanisms in teleost fishes and hypotheses regarding their behavioral significance. Bioacoustics 12:230–233.

Kaatz, I. M., D. J. Stewart, A. N. Rice, and P. S. Lobel. 2010. Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (order Siluriformes): ecomorphological implications. Current Zoology 56:73–89.

Kearney, M. 2002. Fragmentary taxa, missing data, and ambiguity: mistaken assumptions and conclusions. Systematic Biology 51:369–381.

Kéver, L., A. H. Bass, E. Parmentier, and B. P. Chagnaud. 2020. Neuroanatomical and neurophysiological mechanisms of acoustic and weakly electric signaling in synodontid catfish. Journal of Comparative Neurology 528:2602–2619.

Kéver, L., E. Parmentier, A. H. Bass, and B. P. Chagnaud. 2021. Morphological diversity of acoustic and electric communication systems in mochokid catfish. Journal of Comparative Neurology 529:1787–1809.

Ladich, F. 2015. Sound Communication in Fishes. Springer, Vienna.

Ladich, F., C. Bischof, G. Schleinzer, and A. Fuchs. 1992. Intra- and interspecific differences in agonistic vocalizations in croaking Gouramis (genus: *Trichopsis*, Anabantoidei, Teleostei). Bioacoustics 4:131–141.

Ladich, F., S. P. Collin, P. Moller, and B. G. Kapoor. 2006. Communication in Fishes. Science Publishers, Enfield, New Hampshire.

Ladich, F., and H. Winkler. 2017. Acoustic communication in terrestrial and aquatic vertebrates. Journal of Experimental Biology 220:2306–2317.

Lapiedra, O., T. W. Schoener, M. Leal, J. B. Losos, and J. J. Kolbe. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. Science 360:1017–1020.

Lauder, G. V. 1986. Homology, analogy, and the evolution of behavior, p. 9–40. *In:* Evolution of Animal Behavior: Paleontological and Field Approaches. M. H. Nitecki and J. A. Kitchell (eds.). Oxford University Press, New York.

Lavoué, S., M. Miya, M. E. Arnegard, J. P. Sullivan, C. D. Hopkins, and M. Nishida. 2012. Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. PLoS ONE 7:e36287.

Legendre, L. J., G. Guenard, J. Botha-Brink, and J. Cubo. 2016. Palaeohistological evidence for ancestral high metabolic rate in archosaurs. Systematic Biology 65:989–996.

Lindseth, A., and P. Lobel. 2018. Underwater soundscape monitoring and fish bioacoustics: a review. Fishes 3:36.

Lobel, P. S., J. G. Garner, I. M. Kaatz, and A. N. Rice. 2021. Sonic cichlids, p. 443–502. *In:* The Behavior, Ecology and Evolution of Cichlid Fishes. M. E. Abate and D. L. G. Noakes (eds.). Springer, New York.

Lobel, P. S., I. M. Kaatz, and A. N. Rice. 2010. Acoustical behavior of coral reef fishes, p. 307–386. *In:* Reproduction and Sexuality in Marine Fishes: Evolutionary Patterns and Innovations. K. S. Cole (ed.). Elsevier Academic Press, San Diego.

Maddison, W. P. 1993. Missing data versus missing characters in phylogenetic analysis. Systematic Biology 42:576–581.

Mann, D., J. Locascio, and C. Wall. 2016. Listening in the ocean: new discoveries and insights on marine life from autonomous passive acoustic recorders, p. 309–324. *In:* Listening in the Ocean. W. W. L. Au and M. O. Lammers (eds.). Springer, New York.

Matsubara, K. 1943. Studies on the scorpaenoid fishes of Japan: anatomy, phylogeny and taxonomy. Transactions of the Sigenkagaku Kenkyusho 1:1–170.

Miles, M. C., and M. J. Fuxjager. 2019. Phenotypic diversity arises from secondary signal loss in the elaborate visual displays of toucans and barbets. American Naturalist 194:152–167.

Miya, M., and M. Nishida. 2015. The mitogenomic contributions to molecular phylogenetics and evolution of fishes: a 15-year retrospect. Ichthyological Research 62:29–71.

Miya, M., H. Takeshima, H. Endo, N. B. Ishiguro, J. G. Inoue, T. Mukai, T. P. Satoh, M. Yamaguchi, A. Kawaguchi, and K. Mabuchi. 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 26:121–138.

Mosharo, K. K., and P. S. Lobel. 2012. Acoustic signals of two toadfishes from Belize: *Sanopus astrifer* and *Batrachoides gilberti* (Batrachoididae). Environmental Biology of Fishes 94:623–638.

Near, T. J., A. Dornburg, M. Tokita, D. Suzuki, M. C. Brandley, and M. Friedman. 2014. Boom and bust: ancient and recent diversification in bichirs (Polypteridae: Actinopterygii), a relictual lineage of ray-finned fishes. Evolution 68:1014–1026.

Nelson, J. S., T. C. Grande, and M. V. H. Wilson. 2016. Fishes of the World. Fifth edition. John Wiley & Sons, Inc., Hoboken, New Jersey.

Odom, K. J., M. L. Hall, K. Riebel, K. E. Omland, and N. E. Langmore. 2014. Female song is widespread and ancestral in songbirds. Nature Communications 5:3379.

Organ, C. L., L. N. Cooper, and T. L. Hieronymus. 2015. Macroevolutionary developmental biology: embryos, fossils, and phylogenies. Developmental Dynamics 244:1184–1192.

Parmentier, E., D. Lecchini, and D. A. Mann. 2016. Sound production in damselfishes, p. 204–228. *In:* Biology of Damselfishes. B. Frédérich and E. Parmentier (eds.). CRC Press, Boca Raton, Florida.

Parmentier, E., P. Vandewalle, C. Brié, L. Dinraths, and D. Lecchini. 2011. Comparative study on sound production in different Holocentridae species. Frontiers in Zoology 8: 12.

Paterno, G. B., C. Penone, and G. D. A. Werner. 2018. sensiPhy: an R-package for sensitivity analysis in phylogenetic comparative methods. Methods in Ecology and Evolution 9:1461–1467.

Pauly, D. 2004. Darwin's Fishes: An Encyclopedia of Ichthyology, Ecology, and Evolution. Cambridge University Press, Cambridge, UK.

Rabosky, D. L., J. Chang, P. O. Title, P. F. Cowman, L. Sallan, M. Friedman, K. Kaschner, C. Garilao, T. J. Near, M. Coll, and M. E. Alfaro. 2018. An inverse latitudinal gradient in speciation rate for marine fishes. Nature 559: 392–395.

Rabosky, D. L., F. Santini, J. Eastman, S. A. Smith, B. Sidlauskas, J. Chang, and M. E. Alfaro. 2013. Rates of speciation and morphological evolution are correlated across the largest vertebrate radiation. Nature Communications 4:1958.

Ramcharitar, J., D. P. Gannon, and A. N. Popper. 2006. Bioacoustics of fishes of the family Sciaenidae (croakers and drums). Transactions of the American Fisheries Society 135:1409–1431.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Sanciangco, M. D., K. E. Carpenter, and R. Betancur-R. 2016. Phylogenetic placement of enigmatic percomorph families (Teleostei: Percomorphaceae). Molecular Phylogenetics and Evolution 94:565–576.

Shen, Y., N. Yang, Z. Liu, Q. Chen, and Y. Li. 2020. Phylogenetic perspective on the relationships and evolutionary history of the Acipenseriformes. Genomics 112: 3511–3517.

Shinohara, G. 1994. Comparative morphology and phylogeny of the suborder Hexagrammoidei and related taxa (Pisces: Scorpaeniformes). Memoirs of the Faculty of Fisheries Hokkaido University 41:1–97.

Širović, A., and D. A. Demer. 2009. Sounds of captive rockfishes. Copeia 2009:502–509.

Sörensen, W. 1894–1895. Are the extrinsic muscles of the air-bladder in some Siluroidae and the "elastic spring" apparatus of others subordinate to the voluntary production of sounds? What is, according to our present knowledge, the function of the Weberian ossicles? A contribution to the biology of fishes. Journal of Anatomy and Physiology 29:109–139; 205–229; 399–423; 518–552.

Tavolga, W. N. 1968. Fishes, p. 271–288. *In:* Animal Communication: Technique of Study and Results of Research. T. A. Sebeok (ed.). Indiana University Press, Bloomington, Indiana.

Tavolga, W. N. 1971. Sound production and detection, p. 135–205. *In:* Fish Physiology. Vol. 5. W. S. Hoar and D. J. Randall (eds.). Academic Press, New York.

Tavolga, W. N., A. N. Popper, and R. R. Fay. 1981. Hearing and Sound Communication in Fishes. Springer-Verlag, New York.

Tower, R. W. 1908. The production of sound in the drumfishes, the sea-robin and the toadfish. Annals of the New York Academy of Sciences 18:149–180.

Travis, J., and D. N. Reznick. 2018. Natural selection: how selection on behavior interacts with selection on morphology. Current Biology 28:R882–R884.

Tricas, T. C., and K. S. Boyle. 2015. Diversity and evolution of sound production in the social behavior of *Chaetodon* butterflyfishes. Journal of Experimental Biology 218:1572–1584.

von Frisch, K. 1938. The sense of hearing in fish. Nature 141: 8–11.

Wainwright, P. C., and S. J. Longo. 2017. Functional innovations and the conquest of the oceans by acanthomorph fishes. Current Biology 27:R550–R557.

Wenzel, J. W. 1992. Behavioral homology and phylogeny. Annual Review of Ecology and Systematics 23:361–381.

Wiley, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. Wiley Interscience, New York.

Zeyl, J. N., S. Malavasi, D. E. Holt, P. Noel, M. Lugli, and C. E. Johnston. 2016. Convergent aspects of acoustic communication in darters, sculpins, and gobies, p. 93–120. *In:* Fish Hearing and Bioacoustics: An Anthology in Honor of Arthur N. Popper and Richard R. Fay. J. A. Sisneros (ed.). Springer International Publishing, Cham.

Zhang, Y. S., and A. A. Ghazanfar. 2020. A hierarchy of autonomous systems for vocal production. Trends in Neurosciences 43:115–126.