

# Bioacoustic variation of swimbladder disturbance sounds in Neotropical doradoid catfishes (Siluriformes: Doradidae, Auchenipteridae): Potential morphological correlates

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**Abstract** Swimbladder disturbance sounds of doradoid catfishes (Doradidae and Auchenipteridae) demonstrated striking waveform and spectrographic variation. We surveyed sounds of 25 doradoid species in 20 genera comparing these to sounds of four vocal outgroup catfish families. Sounds were either continuous waveforms (lacking interpulses) or pulsed (groups of pulses repeated at fixed temporal intervals). This is the first evidence for swimbladder calls with fixed interpulse patterns in catfishes. Vocal mechanism components that were similar between doradids and auchenipterids included: swimbladder shape, swimbladder dimensions and sonic muscle-somatic index. Morphological traits that showed variation among taxa and were evaluated for potential correlates of call diversity are: 1) diverticula (marginal outpocketings of the swimbladder with no connection to inner ear) and 2) elastic spring apparatus Müllerian rami (ESA-Mr). Within the doradid subfamilies and within the Auchenipteridae most species differed significantly in dominant frequency with frequency ranges overlapping to some extent for most. Doradid swimbladder diverticula did not explain dominant frequency variation within the doradoid superfamily. Some doradids with conical ESA-Mr had the highest dominant frequency sounds. Auchenipterids included both relatively lower and higher dominant frequency sound producers but lacked diverticula and had discoidal ESA-Mr. Comparing a phylogeny of doradoid genera with outgroup taxa, we infer that complex diverticula and conical ESA-Mr are derived characters within the Doradidae. Species representing outgroup families produced either continuous lower dominant frequency sounds (aspredinids, mochokids and pseudopimelodids) or pulsed higher dominant frequency sounds (pimelodids) [*Current Zoology* 58 (1): 171–188, 2012].

**Keywords** Catfishes, Communication, Signal evolution, Vocal mechanisms

Fish vocal signal diversity encompasses differences in bioacoustic properties including amplitude, frequency, temporal characteristics and waveform envelope (Amorim, 2006; Amorim and Vasconcelas, 2008). The role of call variation in speciation is supported by evidence for geographic variation of calls and female mate choice based on preference tests (e.g., pomacentrids, Myrberg et al., 1978; batrachoidids, McKibben and Bass, 1998; cichlids, Verzijden et al., 2010). Different factors that can influence bioacoustic properties of fish sounds include: pacemaker motor neuron circuits and muscle firing rate, subcellular muscle physiology, temperature, hormone condition of signaler and seasonal variation in the condition of vocal muscles (Fine et al., 1978; Bass and Clark, 2003; Ladich et al., 2006). Aspects of swimbladder vocal mechanisms that are functionally linked with call parameters in fishes are: single contraction of vocal muscle and single pulse production (Sprague,

2000), swimbladder rocker bone apparatus and pulse patterns (Parmentier et al., 2010), rate of muscle contraction and waveform interpulse variation (Mann et al., 2008), muscle contraction rate and frequency (Fine et al., 2001; Rome, 2006), swimbladder plate associated with a snapping swimbladder fenestra and frequency (Parmentier et al., 2006), and muscle mass and calling rate (Amorim et al., 2010). These examples highlight the role of vocal muscles and associated bony elements in producing call patterns. However they do not indicate how structural variation of vocal mechanism components within taxonomic clades might affect call variation. We examine that question in this paper.

Catfishes are a highly diverse group of fishes that offer an excellent opportunity to test hypotheses of vocal diversity and morphological correlates of sound signal design (Kaatz, 1999). Neotropical doradoid (Doradidae + Auchenipteridae) catfishes in particular exhibit diverse

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vocal morphology (Kaatz, 2002; Kaatz et al., 2010) and their phylogenetic relationships are becoming reasonably well resolved (Sullivan et al., 2006; Birindelli, 2010). These catfishes produce sounds in agonistic, reproductive and disturbance contexts (Kaatz and Lobel, 2001; Kaatz, 2002) and they exhibit sound discrimination abilities for their own sounds (Wysocki and Ladich, 2003; Lechner and Ladich, 2008). The swimbladder vocal mechanism of doradoid catfishes involves a novel form of elastic spring apparatus, ESA (Bridge and Haddon, 1894; Ladich and Bass, 1997; Ladich, 2001; Parmentier and Diogo, 2006). Ladich (1997) described harmonic, frequency modulated, low fundamental frequency (species differences present), continuous swimbladder “drumming” sounds of two doradids. Kastberger (1977, 1978) illustrated differences in waveforms among species and found differences in ESA components (ligaments and exomembranes) among doradoids. We were interested in determining if there is any relationship between signal design and variation in the structural components of the vocal mechanisms of these catfishes. We thus conducted an evaluation of bioacoustic variation among doradoids to identify any possible morphological correlates.

We recorded disturbance context swimbladder sounds of doradoids and evaluated their waveform and spectrographic patterns to assess their diversity. Our morphological hypothesis was that aspects of sound producing mechanism structures that are different among taxonomic groups could influence call variation. We examined the following characteristics of the catfish vocal apparatus: swimbladder dimensions, presence or absence of swimbladder diverticula, vocal muscle mass and ESA morphology. In general, our goal is to improve understanding of how vocal communication may have evolved among catfishes and to generate testable hypotheses that merit further investigation.

## 1 Materials and Methods

### 1.1 Species maintenance and taxa sampled

Monospecific aquarium populations of imported juveniles were raised to sexual maturity in laboratories at SUNY-ESF and maintained for an observational period from 1991 to 1998. Fishes were maintained on diets of dried flakes or pellet foods commercially formulated for aquarium fishes, and frozen blood worms for reproductive conditioning. We used an artificial light cycle of approximately 12 h light and 12 h dark. Temperatures were held between 24 and 28 °C using submersible heaters. Doradoid specimens included 20 species in 15

genera for Doradidae and five species in five genera for Auchenipteridae (see Appendix 1) for acoustic data, and additionally, included the auchenipterids *Tocantinsia piresi* and *Trachelyopterichthys taeniatus* for morphological samples. Taxa were chosen to represent a wide range of behavioral and ecomorphological differences, including territorial to socially schooling and benthic to pelagic habits in order to examine the potential full range of diversity of vocal communication in this group of fishes. We compared Neotropical doradoid sounds to recordings of four vocal outgroup catfish families: Pseudopimelodidae (*Batrochoglanis raninus*), Aspredinidae (*Bunocephalus verrucosus*), Pimelodidae (*Phractocephalus hemiliopterus*) and Mochokidae (*Synodontis robbianus*). We compared an ictalurid, a pimelodid, an ariid and other mochokids to doradoids solely for morphological comparisons; those taxa were as follows: Ictaluridae (*Ictalurus nebulosus*), Pimelodidae (*Pimelodus pictus*), Ariidae (*Sciades seemani*), and Mochokidae (*Synodontis angelica*, *S. decora*, *S. euptera*, *S. nigriventris*, *S. notata*, *S. ocellifer*, *S. pardalis*, and a multi-spotted undescribed species). The ariid, pimelodid and mochokids have swimbladder mechanisms, while the ictalurid lacks a swimbladder mechanism but can stridulate with pectoral spines.

### 1.2 Specimen condition

We describe sounds for adult fishes. Individuals of several species were judged to be sexually mature based on various indicators, including: 1) the presence of presumed to be gravid females based on the development of increased girth and cloacal papillae in aquarium populations that had been stimulated with water condition changes simulating rainy season conditions (*Platydoras* spp., *Agamyxis pectinifrons*, *Amblydoras affinis*); 2) well developed eggs in dissected specimens (*Orinocodoras eigenmanni*); 3) well developed sperm sacs in dissected individuals (*Trachelyopterus galeatus*); 4) copulation attempts by males of females (*Liosomadoras morrowi*); or 5) successful spawning that produced larval fishes (*Tatia aulopygia*). The sexual maturity of all other species is an assumption based on similar body sizes. It was not possible to reproductively condition most of the species or maintain reproductive condition for very long in those that were responsive to conditioning. Only three *Platydoras costatus* individuals appeared to be becoming gravid (no papillae) during the time period where we took individuals into the field to record their sounds. Species that spawned had passed their reproductive prime by the time they were recorded in the field. It is thus our assumption that the sounds we

recorded in the field for this study were for non-peak spawning condition individuals. However, any individual could have been at some level of reproductive conditioning, but we could not determine that precisely without physiological markers. All doradoid species included individuals that were found to be vocal when handled during disturbance and when un-disturbed during social interactions in aquarium populations. Miniaturization characterized some species (i.e., *T. aulopygia* and *Trachelyichthys exilis*) and for two larger bodied species, individuals we studied were not close to maximum adult size (i.e., *Megalodoras uranoscopus* and *Pterodoras granulatus*).

### 1.3 Sound recordings

We recorded disturbance sounds for 1–15 individuals per species (mean per species of  $4 \pm 3$  SD;  $n = 129$  total individuals for all species). Individuals were distinguished either by fin clipping, color patterns, fin and spine differences or sex for most species; standard length and weight or separately maintained aquaria with labels were used to identify individuals of the remaining species (*Acanthodoras cataphractus*, *P. costatus*, *L. morrowi* and all outgroup species). Disturbance sounds were elicited from individuals by holding them underwater next to a hydrophone. Individuals were positioned with their left side towards the hydrophone at a distance of 2.5 to 10 cm. Recordings were made with a Panasonic video camera and a BioAcoustics, Inc. hydrophone (for specifications see Kaatz and Lobel, 2001) in a shallow water environment. Fish were acclimated to field water and temperatures with incremental water changes in a holding container before being recorded. Recordings were conducted on Oneida Lake at the Cornell University Biological Field Station (Bridgeport, New York) from 1992 through 1996 and from June through September in late afternoon when natural and human noises were at a minimum. The hydrophone was suspended in a cotton mesh containment net 60 cm wide by 60 cm deep at a fixed location on the side of a wooden dock. The water column was 86 cm deep, and the substrate was mud and gravel covered with *Vallisneria* plant growth. Fishes were effectively recorded in a free field held 23 cm under the water surface and ~5 m from shore. Water temperatures ranged from 21 to 29 °C ( $26 \pm 2$  SD). Individuals recorded at water temperatures of  $\leq 25$  °C belonged to the species: *Acanthodoras spinosissimus* (3 individuals), *A. pectinifrons* (3 individuals), *L. morrowi* (2 individuals), *N. leporhinus* (1 individual, one of two recordings), *T. galeatus* (3 individuals) and *Oxydoras niger* (2 individuals). There were small but

significant differences in mean dominant frequency for one individual *Nemadoras leporhinus* recorded at 23 °C ( $388 \pm 69$  Hz) and 27 °C ( $417 \pm 85$  Hz), respectively (Kruskal-Wallis test,  $H_{1,130} = 8.2$ ,  $P = 0.004$ ), indicating a limited effect of temperature over this range. Outgroup ( $28.5 \pm 0.7$  °C), doradid ( $26.2 \pm 1.8$  °C) and auchenipterid ( $26.2 \pm 1.3$  °C) mean temperatures per individual recording were similar. A temperature increase of 11 °C correlated with a 60 Hz increase in dominant frequency in a vocal sciaenid (Connaughton et al., 2002; also see Gillooly and Ophir, 2010) further suggesting our recordings were conducted within a sufficiently narrow temperature range to limit effects on frequency. We also included *O. eigenmanni* data from Kaatz and Lobel (2001) in our analyses; they were studied under similar conditions.

Individuals representing genera taken to Lake Oneida were recorded under the same field conditions during two to four of four consecutive sampling years. Recordings were made in a 76 L glass aquarium in 1998 and 2003 for *Doras punctatus*, *Nemadoras humeralis*, *Rynchodoras xingui* and *Trachydoras brevis*; lab recordings were conducted in a sound-proof room at SUNY-ESF that was designed for bioacoustic studies. Recording close to a hydrophone in a glass aquarium limits artifacts, and aquaria of the size we used for recordings have resonance frequencies (Akamatsu et al., 2002) above the range of known frequencies for catfish swimbladder sounds (Kaatz, 1999). A direct comparison of recordings of doradid catfish swimbladder sounds in the field and in a glass aquarium found no artifacts (Kaatz and Lobel, 2001); thus, we followed the same methods for aquarium recordings in this study. Species observed in the Ecuadorian Amazon (*Hassar orestis*, *Leptodoras acipenserinus*, *Nemadoras trimaculatus*, and *P. hemiliopterus*) were recorded in plastic containers of 76 to 114 L with fish recorded a few centimeters below the water surface next to the hydrophone, immediately after being caught in nets. Amazonian species were recorded in the months of June and July of 1998 in lowland rivers of Ecuador (i.e., Napo, Yasuni and Yanayacu Rivers).

### 1.4 Bioacoustic analyses

Sounds were analyzed using Engineering Design SIGNAL 4.0 (Berkeley, CA). We examined each sound in RTS (real time spectrogram) and graphed waveforms and spectrograms simultaneously. We digitized sounds at a sampling rate of 25 kHz (FFT 128, Hanning Window). We determined waveform patterns, spectrographic patterns, potential repertoire size, audibility (based on a human observer holding a fish in the air

within 1 m of the ear, although this may not directly equate to underwater amplitude) and dominant frequency for each species. We characterized dominant frequency because it is an acoustic trait evaluated by vocal fishes when communicating (Ladich et al., 2006). Dominant frequency was determined from a power spectrum (amplitude versus frequency graph).

We visually examined individual sounds in SIGNAL RTS to characterize waveform and spectrogram patterns. We classified sounds into two categories: 1) pulsed (sounds regularly temporally patterned, separated by interpulses in a sequence), and 2) continuous (sounds lacking interpulse off-times between consecutive pulses; Lobel et al., 2010). For species where pulsed sound types were present in a sample, we only characterized the continuous types and used these in our data analysis because they were present in most species. For *M. uranoscopus* the majority of sounds were pulsed, so we had to include them to maintain sample size, however there was no significant difference for dominant frequency between call types (K-W test,  $H_{1,71} = 1.2$ ,  $P = 0.239$ ).

We examined expanded, simultaneous waveform and spectrogram graphs for individual sounds to interpret pulse patterns. We documented waveforms (Lobel, 2001) and described patterns of oscillation maxima (Parmentier et al., 2005) and evaluated them according to Kaatz and Lobel (2001). We cannot relate waveform patterns to functional aspects of the doradoid ESA sound producing mechanism without further studies, but our working hypothesis is that distinct, repeating waveform patterns represent individual pulses. We define a pulse as a basic patterned acoustic unit that can be related to some basic vocal mechanism action, such as a single muscle twitch (Sprague, 2000; Connaughton, 2004; Amorim, 2006; Ladich et al., 2006), and that will vary among different mechanisms. Identifying waveform patterns could reveal differences in mechanisms and signal design potentially important to future researchers. Waveforms were described according to the number of oscillation maxima per recurring pattern (i.e., number of peaks per pulse, Parmentier et al. 2005). Waveforms were characterized at the center of a call because the first and last pulses often had fewer, lower, less characteristic peaks per pulse.

We assigned descriptions (onomatopoeia, Appendix 1) to disturbance sounds that were audibly different to the human listener to provide an initial estimate of repertoire size in the disturbance context.

### 1.5 Morphological preparations

Specimens for morphological observations were ob-

tained from natural mortality of maintained populations monitored daily with the exception of *T. galeatus* whose individuals had been sacrificed for a separate study. These are the first measurements of structural components of the swimbladder vocal mechanism in this clade of fishes; thus, they provide a baseline for future studies.

Swimbladders were removed from specimens that had been preserved in 70% ethyl alcohol or fixed in 10% formalin (later transferred to 70% EtOH). We measured swimbladder dimensions for maximum length, width and depth. Swimbladders were photographed to document external shape when dried. We used swimbladder shape terminology from Birindelli et al. (2009). The specific terminology used by Eigenmann (1925) to describe the varied swimbladder wall extensions included: caeca (shallow outpocketings), horns (posterior or lateral pairs of diverticula), posterior caecum and diverticula consisting of multiple thin tubules. Birindelli et al. (2009) refer to well-developed posterior swimbladder extensions as the secondary bladder. We refer to all extensions from the swimbladder wall as “diverticula”. We were especially interested in diverticula that extend posteriorly and were not associated with the inner ear, because we wanted to omit any structures that might be functionally associated with hearing (Webb and Smith, 2006) rather than sound production. When present, diverticula were counted, their locations were noted (anterior, lateral, or posterior), and maximum length and width were measured for representative samples. We were not able to determine swimbladder condition for *H. orestis*, *L. acipenserinus*, *Doras micropoeus* and *Nemadoras trimaculatus*; for those taxa, we referred to Birindelli et al. (2009, 2011) and Sabaj (2005).

The ESA vocal mechanism for doradoids involves muscles attached to bony processes, Müllerian rami (hence, ESA-Mr), which are modifications of the 4<sup>th</sup> vertebral parapophyses (Sorenson, 1894–5, pg. 123; Ladich et al., 2006). The bilaterally symmetrical processes each insert into a pocket in the antero-dorsal wall of the swimbladder and are tightly connected to swimbladder tissue by their posterior surfaces. Vocal muscles originate on the posterior occipital region of the cranium and insert on the anterior surfaces of the ESA-Mr (Tavolga, 1962). Vocal muscles were dissected out from thawed frozen specimens and their total mass was measured to 0.0001 g using an analytical balance. Right and left side ESA-Mr muscles were individually removed and weighed, and the data combined for total mass. A sonic muscle-somatic index (SMSI) is defined as total sonic

muscle mass, divided by total body mass (measured to the nearest 0.01 g) times 100, for comparison to data of other vocal fishes (Connaughton et al., 1997).

We characterized ESA-Mr shapes (posterior surfaces inserting into the swimbladder) according to Higuchi (1992): 1) foliar (thin, leaf-like), 2) discoidal (thicker disc-shaped), 3) conical (cone-shaped); and we measured dimensions (dorso-ventral “height”, left to right body axis “width”, anterior-posterior “thickness”). ESA-Mr were photographically documented on skeletal preparations from water-macerated specimens after dissections and swimbladder removals were completed. We were not able to determine the ESA condition for *H. orestis*, *L. acipenserinus* or *N. trimaculatus* because we had no specimens. We quantified ESA-Mr dimensions using a digital micrometer for mochokid, doradid and auchenipterid species ( $n = 126$  total individuals; 1–27,  $6 \pm 5$  individuals per species). We measured one of the two processes depending on which one was most intact after skeletonization. For most species the ESA surface varied in thickness so we took one measurement from the thickest (maximum thickness) and one measurement from the thinnest (minimum thickness) area. In mochokids, we report the same value for both because the entire ESA surface was of even thickness and remeasurement risked damaging the specimen. *T. taeniatus* was the additional auchenipterid species included in dimensions measurements. *Platydoras armatulus*, *T. brevis*, *A. spinosissimus* and *N. leporhinus* were not included in the ESA dimensions measurements for doradids because of missing SL data or unresolved taxonomy.

### 1.6 Acoustic morphology correlates

To compare morphological character variation with call characteristics, we selected individuals of similar standard lengths (SL, Table 1) to minimize any possible effects of body size (Myrberg et al., 1993; Connaughton et al., 2002). For morphological data, outgroup and doradoid data sets did not differ significantly in SL except for comparisons of vocal muscles (Kruskal-Wallis test). Fishes compared for sex differences likewise did not differ significantly in SL (Kruskal-Wallis test). For all remaining cases, test groups differed significantly in length, hence we report SL for all test groups. Not all individuals that produced swimbladder sounds or all sounds produced could be evaluated for sound frequency because of noise by-products of a moving fish during recordings (see Appendix 1 for sample sizes). We only statistically analyzed sounds that had uninterrupted waveforms for the entire sound. We compared dominant frequency among groups differing in morphology of vocal mechanisms (i.e.,

diverticula and ESA-Mr). We tested for sexual dimorphism in vocal structures for *T. galeatus*, which could be sexed based on anal fin morphology.

### 1.7 Historical biology of swimbladder sound production systems

Outgroups were selected on the basis of a comprehensive family level phylogeny for catfishes (Sullivan et al., 2006). Phylogenetic analyses of doradoids based on morphology (Higuchi, 1992; Higuchi et al., 2007; Ferraris, 1988, 2007; Birindelli, 2010) were used to develop a simplified cladogram including only the genera that we sampled in this study. The molecular phylogeny of Moyer et al. (2004) agrees with many of these relationships. We mapped dominant frequency and key morphological traits onto the cladogram to determine whether traits were basal and likely ancestral to various taxa or derived, being found only in some terminal taxa in the cladogram.

### 1.8 Statistical analyses

We used STATISTICA 6.0 for descriptive statistics of dominant frequency and morphological traits (range, mean  $\pm$  standard deviation in text, and 95% confidence interval in cladogram lineage comparisons). We  $\log_{10}$  transformed, graphed residuals, and calculated variance, z-skew and z-kurtosis for data sets. We used z-skew and z-kurtosis scores of  $<2$  as indicative of a normal distribution. Non-parametric statistics (Kruskal-Wallis test) were used because various data sets violated assumptions of normality. Mann-Whitney U tests were additionally conducted for all two sample tests but because their P values had very similar significance levels to K-W P values and conclusions of significance were the same we do not report them. Statistical comparisons of species frequencies were for pooled individuals. Species differences were determined as significantly different based on the lack of overlap for  $\pm 95\%$  CI around the mean and Mann-Whitney U tests within but not between subfamilies and families. Mean dominant frequencies for individuals are graphed for vocal outgroup and selected doradoid species (two different SL size classes from different years were used for one individual of *P. armatulus* to increase the sample size). We excluded *T. brevis*, *N. trimaculatus*, *L. acipenserinus* and *H. orestis* from analyses beyond descriptive statistics because individuals were either not verified beyond one recording session, or they were recorded in the field in plastic containers for which resonance frequencies were not determined; *R. xingui* was excluded because there were no dominant frequency values available. We compared dominant frequencies of

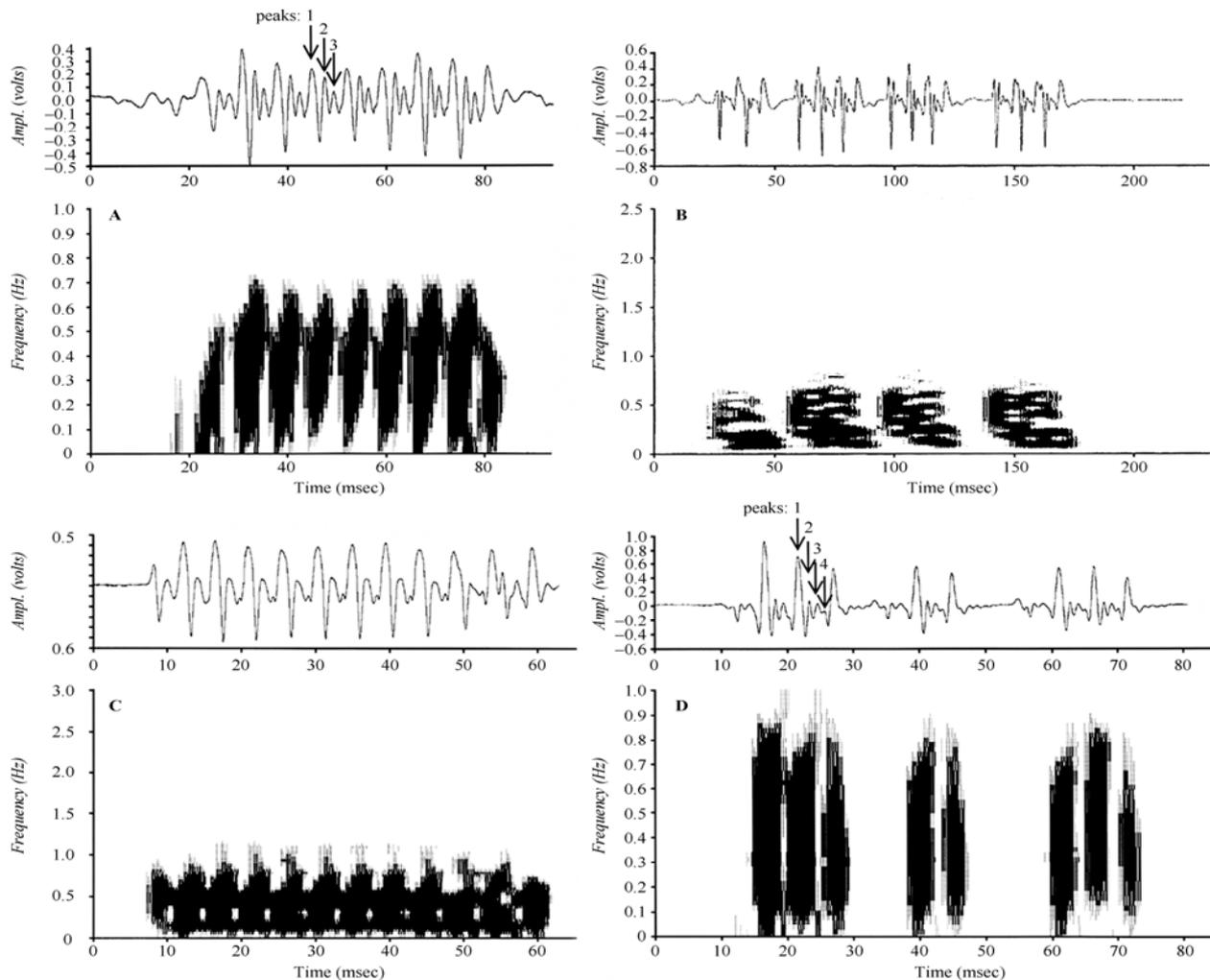
groups with different vocal mechanism morphotypes and ESA-Mr morphologies using the nonparametric Kruskal-Wallis test with significance level of  $P \leq 0.05$ . Comparisons were between selected out-groups and doradoids, doradoid families and among species within families or subfamilies.

## 2 Results

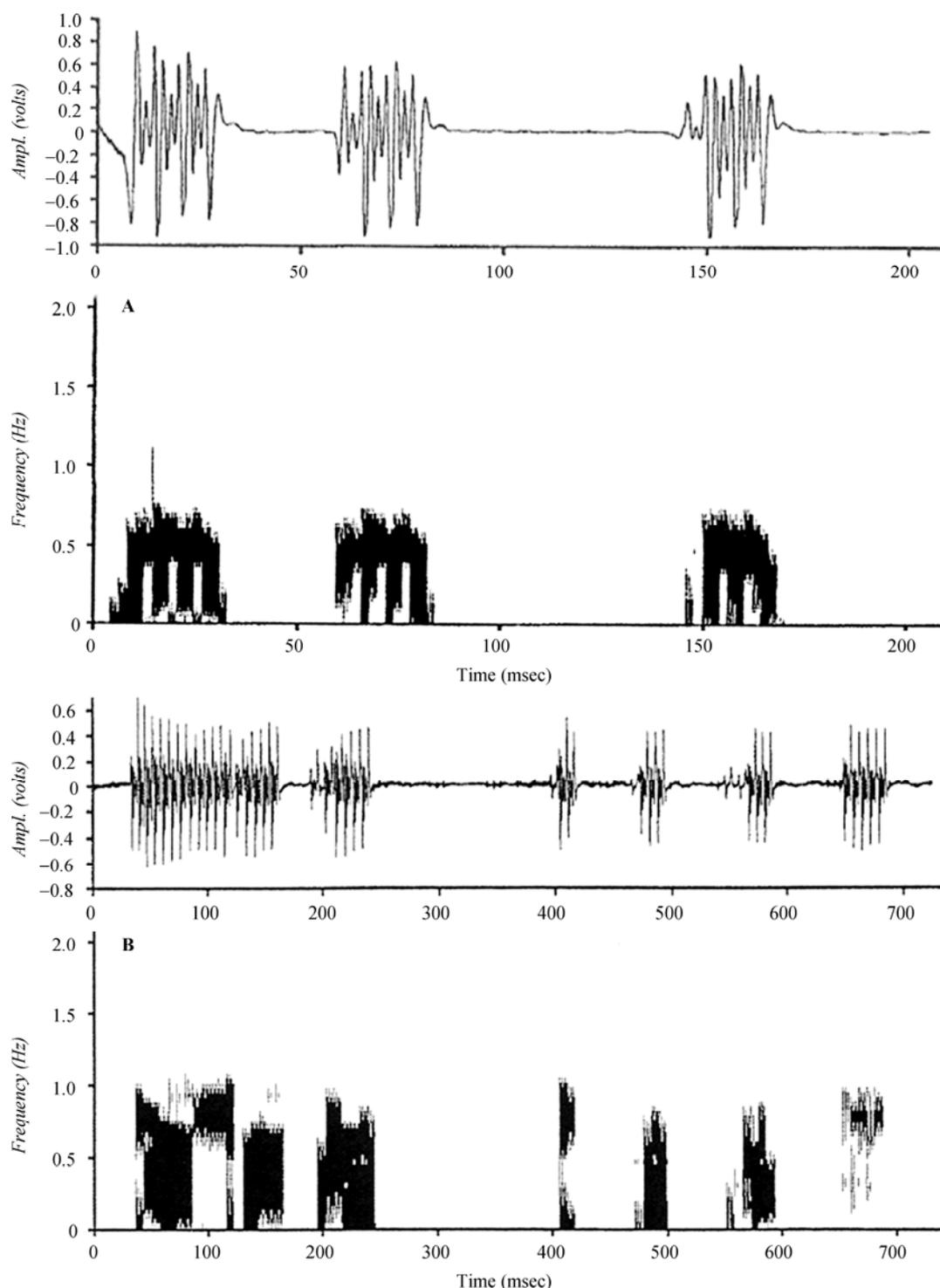
### 2.1 Bioacoustic variation

Sound patterns of up to 337 sounds per individual ( $36 \pm 48$ ) and up to 577 sounds per species ( $160 \pm 139$  sounds/species;  $n = 4,644$  total sounds) for 29 species in four outgroup and two doradoid families were examined spectrographically (distinct sound units of pulsed series sounds were measured separately). Continuous disturbance sounds were present in all species sampled except *P. hemiliopterus*. Pulsed sounds were present in *P. hemiliopterus* and three doradoid species (Appendix 1).

The survey of doradoid sounds indicates waveform and spectrographic variation among the Doradidae (Fig. 1 A, B) and Auchenipteridae (Fig. 1 C, D). Distinct sounds were produced in sequences with irregular inter-sound intervals by all species (e.g., Fig. 2 A, B). Waveform patterns differed according to the number of oscillation maxima per recurring pattern, or pulse, at the call center (range 1 to 4) and relative amplitude or peak heights (Appendix 1). Waveform peak patterns were either: a) alternating in a relatively fixed pattern (Fig. 1 A, first amplitude peak highest, second peak approximately twice height of third lowest peak) with relatively similar maximum peak heights across repeating waveform; b) single uniform amplitude peaks; or c) complexly varying in peak numbers and relative heights (Fig. 1 D, first two pulse groups with declining maximum peak heights) with the greatest peak heights generally more than twice the height of other peaks within one pulse.



**Fig. 1** Waveforms (upper image) and spectrograms (lower image) of doradoid swimbladder disturbance sounds **A.** Doradid continuous “growl”, *Nemadoras leporhinus*. **B.** doradid fixed interval pulse groups, *Megalodoras uranoscopis*; **C.** auchenipterid continuous “growl”, *Trachelyichthys exilis*; and **D.** auchenipterid fixed interval pulse groups, *Tatia aulopygia*. “Peak numbers” = consecutive oscillation maxima within a characteristic waveform or pulse.



**Fig. 2** Field recordings of irregular sound series produced during disturbance

**A.** Three sounds, doradid *Doras micropoeus*. **B.** Six sounds, auchenipterid *Trachelyopterus galeatus*.

Repertoire size ranged from one to two per species (Appendix 1). Audibility of these sounds, to a human listener, was within 1 m in the air for most species. Exceptions were: 1) very low-amplitude for *B. verrucosus*, when holding the fish sounds were very weak and difficult to hear; and 2) high-amplitude for *L. morrowi*, with sounds audible up to 3 m away for a breeding group

whose sounds were not included in this study. Most species sounds were inaudible to the researcher outside of an aquarium. In the field, swimbladder sounds of low-amplitude species (i.e., *P. costatus* and *A. pectinifrons*) were detectable with a hydrophone at a minimum distance of 1 m (I. M. Kaatz, pers. obs.).

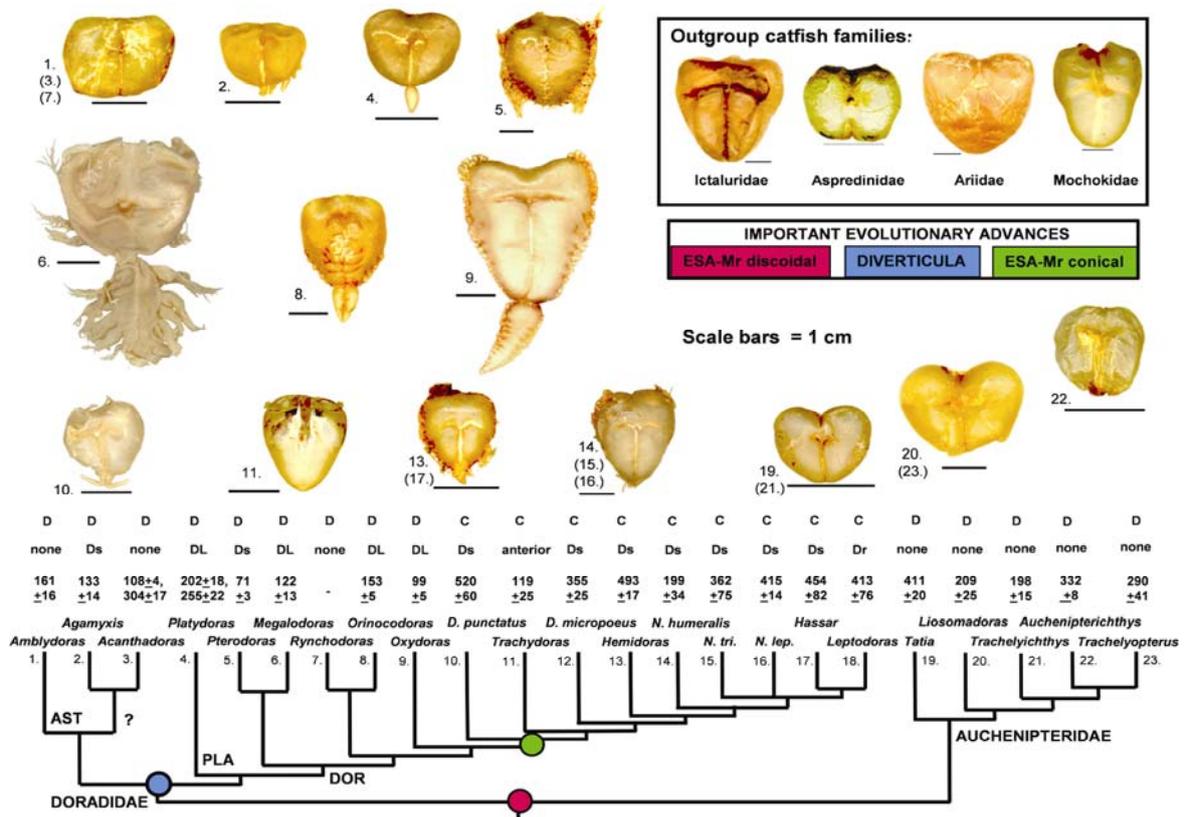
Dominant frequency was significantly different among

species within doradid clades (Fig. 3): 1) for the Astrodoradinae and un-named sister group, all four species were significantly different ( $H_{3,381} = 91.6, P < 0.001$ , and also based on lack of 95% CI overlap); 2) in the Platydoradinae, both species were significantly different ( $H_{1,129} = 13.5, P < 0.001$ , and based on lack of 95% CI overlap); and 3) in the Doradinae, species were significantly different ( $H_{8,803} = 606.4, P < 0.001$ ), and based on lack of 95% CI overlap, all species pairs were significantly different from each other except *D. punctatus* and *Hemidoras stenopeltis*. Auchenipterids differed significantly among species ( $H_{4,381} = 167.6, P < 0.001$ ), with 95% CI overlap found for: 1) *L. morrowi* and *T. exilis*; and 2) *Auchenipterichthys thoracatus* and *T. galeatus*. Mann-Whitney *U* tests found the same significant differences ( $P < 0.045$ ) between doradid species except for the following pairs that were not significantly different: 1) *A. pectinifrons* and *A. spinosissimus*; and 2) *O. eigenmanni*

and *N. humeralis*, while *D. punctatus* and *H. stenopeltis* were different. The auchenipterids *T. galeatus* and *A. thoracatus* were significantly different (Mann-Whitney *U*,  $P = 0.018$ ). Frequency ranges overlapped among most species to some degree (Appendix 1). The lowest dominant frequencies among doradids were 48 Hz for *T. brevis* and 58 Hz for *P. granulatus*, *M. uranoscopus* and *N. humeralis*. Lowest dominant frequency values for auchenipterid species were >100 Hz. The highest dominant frequency, 817 Hz for *L. acipenserinus*, was also found among doradids.

**2.3 Morphological variation: comparisons to outgroups and between families**

Swimbladder shape was cordiform for the nonvocal outgroup Ictaluridae as well as for species representing vocal outgroup families, including an ariid, pimelodid, pseudopimelodid and mochokids (Fig. 3). The aspredinid had a non-rigid, non-cordiform, translucent



**Fig. 3 Cladogram of doradoid swimbladders (orientation = top of page anterior) for taxa whose sounds were recorded, with examples from outgroup catfish families**

The best, intact, side of dissected swimbladders are shown with ventral views indicated by a tripartite indentation and dorsal views showing two insertion points anteriorly for elastic spring apparatus processes (ESA-Mr). Numbers in parentheses next to images indicate other species with similar shaped swimbladders. *Doras micropoeyes* (#12 in figure) has a single thin posterior diverticulum (swimbladder type not shown, see Birindelli et al., 2009). The swimbladder character state for *N. trimaculatus* (#15) was determined from Birindelli et al. (2009), for *H. orestis* (#17) from Birindelli et al. (2011) and for *L. acipenserinus* (#18) from Sabaj (2005). Hypothesized origins for diverticula and conical ESA-Mr are indicated by color coded circles on cladogram nodes and in boxes, upper right. Species designations are listed in Appendix 1. ESA-Mr = “C” conical, and “D” discoidal. Diverticula are coded: “DL” length >1/3 swimbladder and posterior, “Ds” short, thin or fringed lateral, “Dr” highly reduced swimbladder with anterior and posterior horns. Numbers = mean dominant frequency in Hz per species ± 95% CI. “AST” = Astrodoradinae; “PLA” = Platydoradinae; “DOR” = Doradinae; “?” un-assigned subfamily status (Birindelli, 2010); “-” character state unavailable; and scale bar = 1 cm.

swimbladder that was spherical with a constriction along its central body axis. Doradids and most auchenipterids shared a relatively rigid, cordiform swimbladder that had an opaque tunic except for *A. thoracatus* whose tunic was translucent and non-rigid. Swimbladders were apple-shaped in *A. affinis*, *Acanthodoras* spp. and *R. xingui*. Abbreviated cordiform swimbladders are exemplified by *A. pectinifrons* and *Platydoras* spp. and auchenipterid genera. The most longitudinally oblong, cordiform swimbladders were found in the doradids *M. uranoscopus*, *O. niger* and *O. eigenmanni* (Fig. 3).

Swimbladder dimensions of doradoids (doradids,  $n = 88$  individuals, 16 species; auchenipterids,  $n = 56$  individuals, eight species) were compared to mochokids ( $n = 18$  individuals, nine species, SL 3.7–14.3 cm,  $9.1 \pm 3.5$ ) (Table 1). Outgroup swimbladder length ( $H_{1,162} = 0.3$ ,  $P = 0.323$ ) and depth ( $H_{1,162} = 2.0$ ,  $P = 0.157$ ) were not significantly different from doradoids, while mochokids had reduced widths ( $H_{1,162} = 4.9$ ,  $P = 0.027$ ). Doradid (SL 2.8–26.0 cm,  $9.1 \pm 4.1$ ) and auchenipterid (SL 2.8–23.0 cm;  $12.8 \pm 5.3$ ) swimbladder dimensions were significantly different in length ( $H_{1,144} = 10.3$ ,  $P < 0.001$ ), width ( $H_{1,144} = 7.7$ ,  $P < 0.005$ ) and depth ( $H_{1,144} = 8.1$ ,  $P = 0.004$ ). Auchenipterid swimbladder dimensions were wider, longer and deeper.

Diverticula were absent in all outgroup taxa and auchenipterids. Diverticula were present in species of two of three doradid subfamilies (i.e., Platydoradinae and Doradinae, but not Astrodoradinae) that we sampled and in the un-named sister group of the Astrodoradinae. Diverticula were present in ten genera (i.e., *Platydoras*, *Agamyxis*, *Orinocodoras*, *Pterodoras*, *Megalodoras*, *Oxydoras*, *Nemadoras*, *Doras*, *Trachydoras* and *Hemidoras*) that we examined and are described as present for *H. orestis*, *L. acipenserinus* and *D. micropoews*, which we did not examine (see Birindelli et al., 2010).

The number and lengths of diverticula were species specific (we were not able to sample the swimbladders of both *Platydoras* spp.) and varied from shorter diverticula less than a few mm in length (e.g., *A. pectinifrons*) to longer diverticula,  $\geq 1/3$  swimbladder length (e.g., *O. niger*; Fig. 3).

The pimelodid outgroup ( $n = 23$  individuals; SL 5.2–7.9 cm,  $6.3 \pm 0.9$ ; *P. pictus*), had significantly less total vocal muscle mass ( $H_{1,75} = 19.4$ ,  $P < 0.001$ ) than doradoids. Doradids ( $n = 23$  individuals; SL 5.4–25.0 cm,  $11.0 \pm 5.1$ ; five species) had a lower vocal muscle mass than auchenipterids ( $n = 29$  individuals; SL 11.9–22.9 cm,  $17.0 \pm 2.5$ ; two species) ( $H_{1,52} = 16.5$ ,  $P < 0.001$ ). SMSI was higher in the out-group and similar for doradoid families (Table 1).

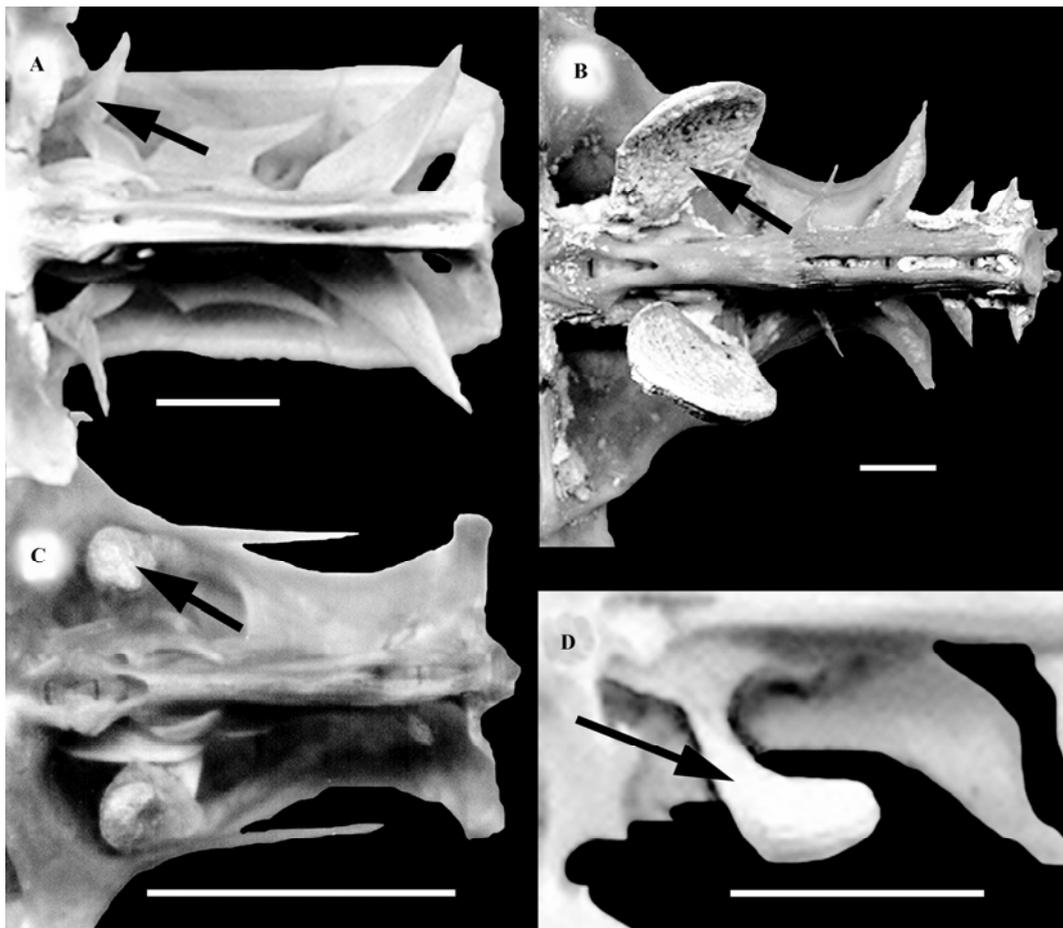
For catfish outgroup families, ESA-Mr were absent in a pimelodid, an aspredinid and an ictalurid. ESA-Mr present in the outgroup Mochokidae were foliar in shape (Fig. 4A), translucent and paper-thin in some specimens, with a flexible narrow stalk attaching them to the vertebral column. Pseudopimelodids have an ESA, but we did not examine it (see Parmentier and Diogo, 2008).

The most derived members of the doradid subfamily Doradinae have conical ESA-Mr that extend from a reduced disc-shaped base and end in posteriorly-directed protrusions of various shapes as follows: *D. punctatus* have a moderate disc base with an acutely tapering end (Fig. 4 C); *D. micropoews* have a hemi-spherical plug; *H. stenopeltis* have a highly-reduced round-ended plug; *N. leporhinus* have an elongated cylindrical plug with a narrow, dorsally attaching stalk (Fig 4 D); *N. humeralis* have a spherical plug; *N. trimaculatus* are conical (J. Birindelli, pers. com.); *H. orestis* have an anterior bony base and postero-ventral end with spherical cartilage (J. Birindelli, pers. com.); *L. acipenserinus* have a shortened plug-like cylinder (M. Sabaj, pers. com.)

**Table 1** Measurements of standard body length and morphological features related to sound production system (range, mean, standard deviation $\pm$ SD)

Character	Outgroups	Doradidae	Auchenipteridae	Sample size (n)
Standard length	4.7–14.2 (7.7 $\pm$ 2.8)	4.9–18.7 (9.4 $\pm$ 2.8)	5.4–16.0 (8.4 $\pm$ 2.1)	129
Swimbladder length	0.7–2.9 (1.7 $\pm$ 0.7)	0.4–4.5 (1.7 $\pm$ 0.7)	0.3–4.3 (2.2 $\pm$ 1.0)	162
Swimbladder width	0.7–1.9 (1.3 $\pm$ 0.4)	0.5–3.3 (1.6 $\pm$ 0.6)	0.3–3.7 (2.0 $\pm$ 0.9)	162
Swimbladder depth	0.4–1.3 (0.8 $\pm$ 0.3)	0.2–2.0 (0.8 $\pm$ 0.3)	0.2–2.5 (1.1 $\pm$ 0.5)	162
Vocal muscle mass	0.0429 $\pm$ 0.03	0.1841 $\pm$ 0.3	0.3264 $\pm$ 0.1	75
SMSI	0.19–1.88 (1.05 $\pm$ 0.4)	0.03–0.68 (0.256 $\pm$ 0.2)	0.11–0.86 (0.26 $\pm$ 0.2)	75

Standard length is for all individuals that produced swimbladder sounds; for vocal muscle mass only mean and SD are given). All lengths are in cm; swimbladder dimensions exclude diverticula when present; total wet muscle mass is in g; SMSI is total sonic muscle mass as percentage of total body mass.



**Fig. 4** Elastic spring apparatus Müllerian rami (ESA-Mr) types

All insert dorso-anteriorly into the swimbladder (ventral view of skulls, anterior to left).

**A.** Foliar, mochokid *Synodontis decora*. **B.** Discoidal, auchenipterid *Tocantinsia piresi*, the ESA-Mr dimensions of this species were not included in statistical tests. **C.** Conical, acute plug extending from reduced disc, doradid *Doras punctatus*. **D.** Conical, cylindrical plug, doradid *Nemadoras leporhinus*. Arrows indicate ESA-Mr; scale bars = 5 mm.

and *T. brevis* have a wider disc base tapering into an acute posterior plug. Bony, thicker, rigid discoidal ESA-Mr, with a wide attachment dorsally to the vertebral column, were present in all other doradoid species (Fig. 4 B).

ESA-Mr of the outgroup mochokid *S. robbianus* (SL 8.0–14.3 cm,  $11.1 \pm 2.1$ ) had significantly thinner and narrower processes compared to doradoids (SL 4.0–30.0 cm,  $12.6 \pm 5.4$ ) but were similar in height (Table 2). Doradid (SL 4.8–30.0 cm,  $11.8 \pm 5.8$ ; 13 species) and auchenipterid (SL 4.0–22.1 cm,  $13.5 \pm 4.6$ ; six species) ESA-Mr dimensions did not differ significantly in height or maximum thickness, while auchenipterids had wider processes with greater minimum thickness than doradids (Table 2). Among doradoids, conical (i.e., non-discoidal) ESA-Mr (SL 5.4–11.4 cm,  $8.2 \pm 2.1$ ) were significantly different from discoidal (SL 4.0–30.0 cm,  $13.0 \pm 5.4$ ) for all traits except minimum thickness

(Table 2). In the auchenipterid *T. galeatus*, there were no significant differences in ESA-Mr dimensions between males (SL 13.8–23.0 cm,  $18.1 \pm 2.1$ ) and females (SL 14.6–22.1 cm,  $17.4 \pm 2.0$ ) (Table 2).

#### 2.4 Acoustic morphological correlates

Doradids ( $204 \pm 132$  Hz; SL 5.2–17.0 cm,  $9.2 \pm 2.4$ ) had a significantly lower dominant frequency than auchenipterids ( $282 \pm 110$  Hz; SL 5.4–16.0 cm,  $8.1 \pm 1.8$ ) ( $H_{1,1528} = 196.9$ ,  $P < 0.001$ ). Auchenipterids lacked diverticula (Fig. 3) except for one specimen of *T. galeatus* with two posterior threads ~2 cm in length. Doradids with diverticula had a significantly higher dominant frequency ( $209 \pm 137$  Hz; SL 5.2–11.8 cm,  $9.0 \pm 2.4$ ) than those lacking diverticula ( $166 \pm 81$  Hz; SL 6.5–12.0 cm,  $10.5 \pm 1.8$ ) ( $H_{1,1147} = 5.6$ ,  $P = 0.017$ ). Four doradid species were responsible for the highest mean dominant frequencies within the statistically analyzed, diverticulated swimbladder group: *H. stenopeltis*,

**Table 2** Morphological variation in dimensions (mm) of the Müllerian ramus of the elastic spring apparatus among mochokid and doradoid catfishes (mean  $\pm$  SD)

Taxon	Width	Height	Minimum thickness	Maximum thickness	# individuals
<b>Mochokid and Doradoid (doradid and auchenipterid) differences: Kruskal-Wallis (<math>df = 1, n = 126</math>)</b>					
Mochokidae	3.29 $\pm$ 0.8	4.36 $\pm$ 1.2	0.19 $\pm$ 0.1	0.19 $\pm$ 0.1	8
Doradidae	5.45 $\pm$ 2.8	5.16 $\pm$ 2.4	0.54 $\pm$ 0.3	0.94 $\pm$ 0.6	63
Auchenipteridae	6.57 $\pm$ 2.7	5.82 $\pm$ 2.1	0.63 $\pm$ 0.2	0.92 $\pm$ 0.4	55
H	8.0, $P = 0.005$	2.2, $P = 0.137$	21.4, $P < 0.001$	22.3, $P < 0.001$	
<b>Doradid and Auchenipterid differences: Kruskal-Wallis (<math>df = 1, n = 118</math>)</b>					
H	4.6, $P < 0.032$	2.6, $P = 0.105$	6.2, $P = 0.013$	1.1, $P = 0.285$	
<b>Doradoid process morphotype differences: Kruskal-Wallis (<math>df = 1, n = 118</math>)</b>					
Non-discoidal	1.87 $\pm$ 1.0	2.43 $\pm$ 1.7	0.73 $\pm$ 0.3	2.11 $\pm$ 0.5	9
Discoid	6.31 $\pm$ 2.7	5.72 $\pm$ 2.1	0.57 $\pm$ 0.2	0.83 $\pm$ 0.4	109
H	20.8, $P < 0.001$	14.8, $P < 0.001$	3.4, $P = 0.065$	24.0, $P < 0.001$	
<b>Auchenipterid sex differences: Kruskal-Wallis (<math>df = 1, n = 25</math>)</b>					
Male	8.26 $\pm$ 1.0	6.93 $\pm$ 1.0	0.86 $\pm$ 0.2	1.22 $\pm$ 0.2	15
Female	8.42 $\pm$ 1.3	7.26 $\pm$ 1.0	0.78 $\pm$ 0.1	1.21 $\pm$ 0.3	10
H	0.1, $P = 0.803$	0.9, $P = 0.332$	1.4, $P = 0.232$	0.2, $P = 0.677$	

*N. leporhinus*, *D. micropoeus* and *D. punctatus* (Appendix 1). Doradids with posterior, larger diverticula ( $\geq 1/3$  of swimbladder length) had a lower dominant frequency (166  $\pm$  89 Hz; SL 5.2–14.7 cm, 8.7  $\pm$  2.0) than species with smaller or fringed diverticula (276  $\pm$  167 Hz; SL 5.7–17.0 cm, 9.5  $\pm$  3.0;  $H_{1, 1013} = 47.5$ ,  $P < 0.001$ ). However, taxa producing the lowest dominant frequencies included *P. granulosus* with short, fringelike diverticula as well as *M. uranoscopus* with large, complex posterior diverticula. Taxa producing the highest dominant frequencies had either fringed or small, posterior diverticula.

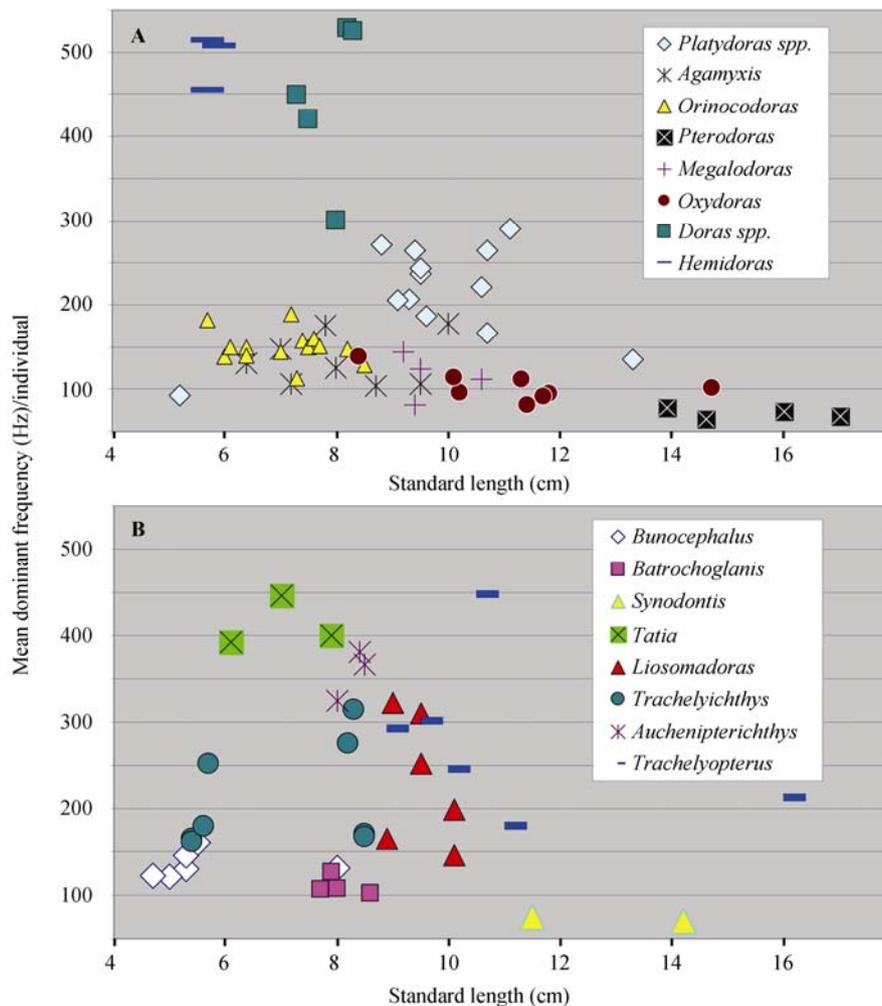
Doradids with conical ESA-Mr (i.e., *H. stenopeltis*, *N. humeralis*, *N. leporhinus*, *D. micropoeus* and *D. punctatus*; SL 5.7–11.2 cm, 8.3  $\pm$  1.2) have a higher dominant frequency (383  $\pm$  129 Hz; 58–576 Hz) compared to doradids with a discoidal ESA-Mr (147  $\pm$  68 Hz; 58–345 Hz; SL 5.2–17.0 cm, 9.4  $\pm$  2.6) ( $H_{1, 1147} = 415.0$ ,  $P < 0.001$ ). However, one species with a conical ESA-Mr had a low mean dominant frequency below 200 Hz (i.e., *N. humeralis*). Three species with conical ESA-Mr not included in the statistical analysis (i.e., *N. trimaculatus*, *H. orestis* and *L. acipenserinus*) had high, >300 Hz, mean dominant frequencies (Fig. 3), while another (i.e., *T. brevis*) did not. Among auchenipterids *T. aulopygia*, *T. galeatus* and *A. thoracatus* had higher mean dominant frequencies than the remaining two auchenipterid species (Appendix 1), but all of these

species have discoidal ESA-Mr and lacked diverticula.

## 2.5 Historical biology: Evolution of swimbladder sound production systems

The sister group of doradoids, aspredinids, had a continuous waveform. Three of the outgroup species (*S. robbianus*, *B. raninus* and *B. verrucosus*) had dominant frequencies (112  $\pm$  5 Hz) that were significantly lower than doradoids (224  $\pm$  131 Hz) ( $H_{1, 1589} = 55.6$ ,  $P < 0.001$ ) (Appendix 1; Fig. 5 A, B). Among doradids relatively low (<200 Hz) and high ( $\geq 200$  Hz) mean dominant frequency sounds were found within each of the subfamilies. Basal genera of the Doradinae, *Pterodoras* and *Megalodoras*, had among the lowest mean dominant frequencies (i.e., 71 and 122 Hz) in the superfamily. Seven of the nine most derived taxa of the Doradinae (i.e., *D. punctatus* to *L. acipenserinus*) included the highest mean dominant frequencies (i.e., 355 to 520 Hz). The opposite pattern is found in the Auchenipteridae, where the basal *T. aulopygia* had a higher mean dominant frequency (i.e., 411 Hz) than more derived taxa.

All outgroups had cordiform swimbladders except the aspredinid sister group (Fig. 3). The most complex and longest (>1/3 of swimbladder length) diverticula (i.e., *M. uranoscopus*) were present in the doradinae. Short ( $\leq 1/3$  of swimbladder length) diverticula were present in two of the doradid subfamilies and absent in the Platydoradinae. Auchenipterids and vocal



**Fig. 5** Mean dominant frequency for individuals of different species

**A.** Doradids (*Platydoros* and *Doras* species pooled). **B.** Auchenipterids and outgroups: *Bunocephalus* (aspredinid), *Batrochoglanis* (pseudopimelodid), *Synodontis* (mochokid); see Appendix 1 for species designations. Two individuals of *O. eigenmanni* had the same overlapping values (7.0 cm, 144 Hz).

and nonvocal outgroup taxa lacked diverticula. Discoidal ESA-Mr were basal to the doradoids, and conical ESA-Mr distribution indicated a derived condition within the doradid subfamily Doradinae (Fig. 3).

### 3 Discussion

#### 3.1 Sound signal variation

We found exceptional waveform and frequency diversity among swimbladder disturbance sounds of doradoid catfishes (Fig. 1, Appendix 1). Swimbladder disturbance sounds of doradid and auchenipterid catfishes were first reported by Kastberger (1977) as harmonic “grunts”. Doradoid continuous swimbladder disturbance sounds are similar to agonistic sounds, while pulsed sounds are similar to male courtship sounds, both types sampled from undisturbed social contexts for the same

individuals that had been recorded in the field (Kaatz, 1999). Kaatz and Lobel (2001) described the sounds of *O. eigenmanni*, characterizing duration and waveform. Waveform can vary within a species depending on frequency (Fine et al., 2001). Although it is not known if fishes can detect waveform variation, sound components that determine waveform envelope vary among males of a marine toadfish and are proposed to play a role in individual recognition (Amorim and Vasconcelas, 2008). We report the first evidence of pulsed swimbladder sounds in catfishes (Fig. 1 B, D). These temporal characteristics are determined by neurological not gross morphological vocal traits (Kastberger, 1977). Species recognition in fishes has been demonstrated for pulsed sounds (Verzijden et al., 2010). It is likely that an examination of doradoid species in reproductive field con-

ditions could reveal larger repertoire sizes, more call types and higher amplitude calls because physiological condition can alter fish vocal mechanisms, modifying their vocal ability (Fine, 1978; Connaughton et al., 1997; Connaughton et al., 2002).

### 3.2 Vocal mechanism design: swimbladder shape and muscles

The relationship of vocal mechanism design to call variation is of key interest to fish bioacousticians (Demski et al., 1973; Ladich et al., 2006). Swimbladder shape can affect directionality of sounds in toadfishes (Barimo and Fine, 1998), but swimbladder resonant properties do not contribute to call frequency (Fine et al., 2001); neither do changes in swimbladder size (Fine et al., 2009). However, the resonance property of diverticula in vocal fishes has not been examined. Doradoids are a group in which this could be tested (Fig. 3) as the ESA of catfishes has been hypothesized to pulsate the swimbladder (Parmentier and Diogo, 2006), and the damping characteristics of those swimbladders have not been examined.

Muscle mass correlated with male mating success in a gadid (Rowe and Hutchinson, 2008). Total vocal muscle mass of doradoids (Table 1) exceeds that of similar sized ophidiids (Nguyen et al., 2008) and is similar to several sciaenid species (Hill et al., 1987). Doradoid SMSI was less than in sciaenids (Connaughton et al., 1997) but overlapped with *Porichthys notatus* (Brantley and Bass, 1994).

### 3.3 Hypothesized vocal mechanism components: diverticula

Three hypotheses have been proposed for diverticula function in vocalization of living poikilotherms. Dufosse (1874, translated in Sorenson, 1894–5, pg. 226) indicated an association between the largest diverticula of swimbladders in sciaenids and vocal muscles lacking aponeuroses, concluding that this association amplified call intensity. Sorenson (1894–5) similarly proposed that complex swimbladder diverticula enhance amplitude in the tropical doradid *Pterodoras granulosus* (reported as *Doras maculatus*). Marshall (1962) proposed that differences in swimbladder diverticula might contribute to interspecific call variation in vocal fishes. The third hypothesis is based on a terrestrial analog of diverticula function of a vocal reptile (Young, 1991). An experimentally tested model of the diverticulated esophagus of a snake demonstrated that the addition of diverticula altered resonance properties that caused a drop in dominant frequency.

Among doradoids the highest amplitude vocalizer, *L.*

*morrowi*, had a cordiform swimbladder with a tough opaque tunic that lacked diverticula, which runs counter to the amplitude enhancement hypothesis. One of the most complex calls was produced by a species with the most elaborate diverticula, *M. uranoscopus*. However two other species (*T. galeatus* and *T. aulopygia*) lacking diverticula also produced pulsed calls with complex waveforms. Some catfish taxa that we examined with swimbladder diverticula did produce lower dominant frequency sounds, supporting the frequency-drop hypothesis, but others did not (Fig. 3). If diverticula cause a drop in dominant frequency in some species, the adaptive function could be to produce sounds within a quiet window in an otherwise noisy, signal-masking aquatic environment (Lugli, 2010). Swimbladder variation of doradids includes internal chamber partitioning (Eigenmann, 1925), which we did not examine. How this aspect of swimbladder morphology might affect sound production resonance properties also remains unexamined.

### 3.4 Vocal mechanism design: elastic spring apparatus

ESA-Mr that are discoidal had a greater surface area for muscle attachment (greater width and height) compared to conical ESA-Mr (Table 2), supporting a hypothesis that the discoidal ESA-Mr species could have larger vocal muscles that would produce greater sound intensities (Fine et al., 2009). Tavalga (1962) illustrates with spectrograms that simultaneous stimulation of both ariid ESA vocal muscles increased intensity in higher harmonics, suggesting that frequency could be dynamically modified. Tavalga (1962) also hypothesized that species differences in ESA-Mr compliance determined differences in sound frequency. In our study, *Nemadoras leporhinus* consistently produced high dominant frequency sounds and its ESA-Mr (Fig. 4D) has the narrowest and most flexible attachment stalk of the conical forms that varied significantly among taxa (I. M. Kaatz, pers. obs.). In contrast to ariids, some doradids have elastic connections between the ESA and the body wall providing additional flexibility, what Kastberger (1978) describes as a compound oscillating system. Some high frequency sound producers also produced shorter calls (I. M. Kaatz, pers. obs.). Ophidiids and carapids can produce higher peak frequency sounds with slow vocal muscle contraction (Fine et al., 2007; Parmentier et al., 2006), the former involving specialized bones associated with the swimbladder. A triglid fish with dual swimbladder vocal mechanisms can double its fundamental frequency by alternate muscle contraction

(Connaughton, 2004). Doradoids have two separate ESA vocal muscles, but whether they act independently requires further investigation. Increases in fundamental frequencies are also determined by physiological properties of the vocal muscles (Rome, 2006), which we did not examine.

### 3.5 Vocal signal diversity and evolution

Among vocal fishes, evolution of low frequency sound signals has been evaluated for gobies (Malavasi et al., 2008) and toadfishes (Rice and Bass, 2009). Goby species show differences in dominant frequency based on body size, a less likely explanation for most doradoid species differences over the ranges we sampled (Fig. 5). Variation in toadfish sounds and mechanisms indicated that a two-voice system in some species can significantly impact sound signals (Rice et al., 2011), a possibility for doradoids that also have two separate vocal muscles.

Diverticula are lacking in aspredinids (Friel, 1994), basal doradid genera (*Wertheimeria*, *Kalyptodoras*; Higuchi, 1992) and basal auchenipterids (Ferraris, 1988; but see Walsh, 1990, for derived taxa), so we infer that this condition is ancestral for doradoids. The prevalence of diverticula within doradids, in other vocal catfish families (ariid *Osteogeneiosus* sp., Marceniuk and Birindelli, 2010; Pimelodid *Calophysus macropterus*, Bridge and Haddon, 1894, reported as *Pimelodus macropterus*), and other non-siluriform vocal fish families (Evans, 1940; Evans, 1973; Ramcharitar et al., 2006; Fine et al., 2007; Paulin, 1988; Marshall, 1967) raises questions about their effect on vocalization, even though we did not find consistent evidence for effects. The great varieties of modifications of the derived conical ESA-Mr in doradids (Higuchi, 1992) raise similar questions about their effect on vocal signals. An ESA-enhanced vocal mechanism has independently evolved at least five times among catfishes (Parmentier and Diogo, 2006) indicating the recurrent adaptive value of these vocal structures to catfishes.

Swimbladder sounds of aspredinids suggest a low (i.e., mean of 133 Hz) ancestral dominant frequency for the superfamily including doradoids. Dominant frequency varied among doradoid families and species (Fig. 3). Some species' very low frequency sounds might be explained by larger body size (e.g., *P. granulosus*; Fig. 5 A), but for other species this does not seem to be the case (e.g., *T. galeatus*; Fig. 5 B). Differences in dominant frequency among doradoid species could be independently derived specializations that contribute to vocalization diversity and, in combination with other vocal

signal traits could facilitate individual (Amorim and Vasconcelas, 2008) or species recognition among these nocturnal fishes and/or those that live in turbid, light-limited environments. The low dominant frequencies in doradoid catfishes were present in some predominantly solitary, nocturnal and benthic species (e.g., *O. eigenmanni*, *N. humeralis*, *L. morrowi*; I. M. Kaatz, pers. obs.), while high dominant frequencies were found in significantly more socially aggregating (Ferraris, 1991) and mid-water species (I. M. Kaatz, pers. obs.) like *D. micropoeus*, *N. leporhinus* and *T. aulopygia*, although exceptions to this pattern can also be cited. Ariids produce sounds with fundamental frequencies of 400 Hz in nocturnal schools (potentially contact calls) and 150 Hz when restrained (Tavolga, 1962), indicating that they can modify their call frequency according to context and motivation. Doradoids produced a wide range of dominant frequencies during disturbance (Appendix 1), with some species having a greater range than others (e.g., *P. granulosus*, narrow range; *N. humeralis*, wide range), indicating flexibility in sound trait frequency. These findings emphasize the importance of investigating undisturbed vocal contexts among doradoids in order to further understand patterns of vocal trait diversity and evolution. Alternative evolutionary hypotheses for doradoid structural variation highlighted in this paper are: 1) that diverticula serve some nonvocal function, and 2) that ESA components have been modified under the constraints of an independent ecological adaptive radiation rather than for signal functions. The latter is especially interesting because it could reveal the design limits under which a functional vocal mechanism can persist in a fish lineage.

### 3.6 Future directions

New studies should further examine differences of sounds among taxa by considering additional bioacoustic traits and testing hypotheses with functional morphology analyses. Field work on the soundscape of Neotropical aquatic habitats is also lacking. Passive acoustic detection of taxon specific catfish sounds applied in the field could help in identifying spawning aggregations, assessing local fish species diversity, and monitoring local fish population abundances. Such field studies, thus could contribute to developing programs for conservation and management of ichthyofaunas (Lobel, 2002; Luczkovich et al., 2008; Mann et al. 2008).

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**Appendix 1 Swimbladder sounds produced by catfishes in the disturbance context, audible to an observer near a fish in the air**

Taxa (number of vocal individuals <sup>a</sup> )	Waveform: # peaks at center, pattern		Repertoire: Number of sound types "onomatopoeia" <sup>ab</sup>	Dominant frequency (Hz)	
	Continuous	Pulsed		Mean ± SD <sup>c</sup>	Number of sounds (number of individuals)
<b>Outgroup Families:</b>					
<i>Batrochoglanis raninus</i> (4)	2, complex variable	---	1 "hummm"	108 ±10 (92–127)	10 (4)
<i>Phractocephalus hemiliopterus</i> (1)	---	pulse series	1 "grunt"	310 ±49 (276–345)	2 (1)
<i>Synodontis robbianus</i> (2)	1-2, alternating amplitude	---	1 "hummm"	72 ±15 (58–92)	17 (2)
<i>Bunocephalus verrucosus</i> (6)	1, uniform wave peaks	---	2 "vrrrr, hum-buzz"	133 ±35 (69–196)	34 (6)
<b>Family Doradidae:</b>					
<i>Amblydoras affinis</i> (1)	2, alternating amplitude	---	1 "growl"	161 ±68 (92–386)	72 (1)
<i>Agamyxis pectinifrons</i> (8)	3, alternating amplitude	---	2 "brrr, growl"	133 ±64 (69–288)	81 (8)
<i>Acanthodoras cataphractus</i> (3)	1, uniform wave peaks	---	1 "growl"	304 ±40 (265–368)	20 (2)
<i>Acanthodoras spinosissimus</i> (3)	1, uniform wave peaks	---	1 "growl"	108 ±12 (81–127)	42 (3)
<i>Platydoras costatus</i> (9)	2, alternating amplitude	---	2 "drum, growl"	202 ±82 (69–322)	82 (9)
<i>Platydoras armatulus</i> (3)	2, alternating amplitude	---	1 "wooh"	255 ±74 (127–345)	47 (3)
<i>Pterodoras granulatus</i> (4)	1-2, alternating amplitude	---	1 "growl"	71 ±11 (58–104)	65 (4)
<i>Megalodoras uranoscopus</i> (5)	3-4, complex variable	pulse groups	2 "growl, rumble"	122 ±55 (58–253)	71 (4)
<i>Rhynchodoras xingui</i> (3)	continuous	---	1 "growl"	204 ±37 (106–684) <sup>d</sup>	46 (3)
<i>Orinocodoras eigenmanni</i> (15)	3, alternating amplitude	---	1 "growl"	153 ±44 (81–345)	315 (15)
<i>Oxydoras niger</i> (8)	2, alternating amplitude	---	1 "growl"	99 ±25 (69–230)	84 (8)
<i>Doras punctatus</i> (3)	4, alternating amplitude	---	1 "growl"	520 ±113 (115–576)	16 (3)
<i>Trachydoras brevis</i> (4)	3, unclear waveform	---	1 "growl"	119 ±35 (46–150)	10 (1)
<i>Doras micropoeus</i> (2)	3, alternating amplitude	---	1 "toot"	355 ±86 (138–506)	48 (2)
<i>Hemidoras stenopeltis</i> (3)	3, alternating amplitude	---	1 "pop"	493 ±46 (299–543)	30 (3)
<i>Nemadoras humeralis</i> (6)	3-4, complex variable	---	2 "toot, growl-hum"	199 ±112 (58–460)	44 (3)
<i>Nemadoras trimaculatus</i> (1)	2, unclear waveform	---	1 "toot"	362 ±136 (138–702)	15 (1)
<i>Nemadoras leporhinus</i> (1)	3, alternating amplitude	---	2 "bark, growl"	415 ±84 (115–541)	130 (1)
<i>Hassar orestis</i> (1)	3, unclear waveforms	---	1 "pop"	454 ±164 (196–771)	18 (1)
<i>Leptodoras acipenserinus</i> (2)	2, unclear waveforms	---	1 "toot"	413 ±172 (150–817)	22 (2)
<b>Family Auchenipteridae:</b>					
<i>Tatia aulopygia</i> (7)	3-4, complex variable	pulse groups	2 "drill, drill series"	411 ±60 (196–506)	36 (3)
<i>Liosomadoras morrowi</i> (6)	3-4, alternating amplitude	---	1 "boop"	209 ±72 (115–702)	35 (6)
<i>Trachelyichthys exilis</i> (8)	3-4, alternating amplitude	---	1 "growl"	198 ±80 (127–437)	112 (8)
<i>Auchenipterichthys thoracatus</i> (4)	3, alternating amplitude	---	2 "bark, growl"	332 ±47 (127–518)	141 (3)
<i>Trachelyopterus galeatus</i> (6)	3, alternating amplitude	pulse se- ries	2 "buzz, buzz-series"	290 ±154 (115–702)	57 (6)

"---" = none.

<sup>a</sup> Individuals that produced swimbladder sounds and whose waveforms and spectrograms were visually inspected.

<sup>b</sup> Audible to human next to fish in air except: *Bunocephalus verrucosus* barely audible; *Liosomadoras morrowi* audible up to 1 m from aquarium in non-reproductive condition.

<sup>c</sup> Minimum to maximum frequency range from dominant frequency measures in parentheses.

<sup>d</sup> Middle of frequency range values, not dominant frequency, is reported for *Rhynchodoras xingui*.