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Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (Order Siluriformes): Ecomorphological implications

Ingrid M. KAATZ[1*], Donald J. STEWART[1], Aaron N. RICE[2**], Phillip S. LOBEL[3]

[1] Department of Environmental and Forest Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY 13210, USA
[2] Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA
[3] Department of Biology, Boston University, Boston, MA 02215, USA

Abstract Stridulatory sound-producing behavior is widespread across catfish families, but some are silent. To understand why, we compared spine morphology and ecotype of silent and vocal clades. We determined vocal ability of laboratory specimens during disturbance behavior. Vocal families had bony (not flexible or segmented) spines, well-developed anterior and/or posterior serrations, and statistically significantly longer spines. We compared morphology of the proximal end of the pectoral spine between vocal and silent species. For vocal taxa, microscopic rounded or bladed ridges or knobs were present on the dorsal process. Most silent species had reduced processes with exclusively smooth, convoluted, or honeycombed surfaces very similar to spine-locking surfaces, or they had novel surfaces (beaded, vacuolated, cobwebbed). Most callichthyids had ridges but many were silent during disturbance. All doradid, most auchenipterid and most mochokid species were vocal and had ridges or knobs. Within the Auchenipteridae, vocal species had spines with greater weight and serration development but not length. Silent auchenipterids had thin, brittle, distally segmented spines with few microscopic serrations on only one margin and a highly reduced dorsal process lacking any known vocal morphology. Silent auchenipterids are derived and pelagic, while all vocal genera are basal and benthopelagic. This is the first phylogenetic evidence for stridulation mechanism loss within catfishes. Phylogenetic mapping of vocal ability, spine condition, and ecotype revealed the repeated presence of silence and vocal taxa, short and long spines, and ecotype shifts within clades. The appearance and loss of vocal behavior and supporting morphologies may have facilitated diversification among catfishes [*Current Zoology* 56 (1): 73–89 2010].

Key words Bioacoustic, Defense mechanisms, Historical biology, Stridulation

Studies of sound-producing behavior in catfishes (Teleostei: Siluriformes) highlight the importance of sound signals in reproductive and agonistic behavioral contexts (Kaatz, 2002; Fine and Ladich, 2003). Pfeiffer and Eisenberg (1965) hypothesized that catfishes with weaponized pectoral spines produce disturbance sounds as a form of acoustic aposematism, but an experimental study of one species did not support this hypothesis (Bosher et al., 2006). Disturbance sounds are produced when a catfish is physically restrained in a way similar to an interspecific or predatory attack and can indicate the presence of stridulation signaling in undisturbed intraspecific contexts (Kaatz, 1999). Heyd and Pfeiffer (2000) observed that chemical alarm signals were weakened or absent from species that were vocal during disturbance. These findings suggest that disturbance could function as a vocal in place of a chemical alarm signal. Thus, sound production is a widespread and potentially important aspect of catfish behavior. Determining the distribution and evolutionary patterns of vocal behavior and morphology in catfishes is essential to understanding communication in these fishes.

The phylogenetic distribution of vocal swimbladder mechanisms in catfishes suggests multiple independent origins within the order (Parmentier and Diogo, 2006). Repeated, isolated origins of sound production suggest patterns of vocal mechanism acquisition, elaboration and possible loss and reacquisition. In addition to having the ability to vocalize with their swimbladders, many catfishes use pectoral spines to produce stridulation sounds, also associated with disturbance, agonistic behavior, and male courtship display (Kaatz, 1999;

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* Corresponding author. E-mail: ingridmkaatz1@yahoo.com. Current address: 40 Apple Valley Road, Stamford, CT 06903

** Present Address: Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850

Pruzsinszky & Ladich 1998; Kaatz and Lobel 1999; Fine and Ladich, 2003). The evolution of pectoral spine stridulation in catfishes is unexplored.

The structures employed for sound production in pectoral spine stridulating catfishes are part of a synapomorphic complex of characters that define the Order Siluriformes (Alexander, 1965). The functional role of this complex in catfishes is known to serve a locking function for a passive predator defense that deters gape-limited predators (Alexander, 1981). The structures involved are the pectoral girdle groove, the spine locking processes (Gainer, 1967), and, specifically, the dorsal process of the proximal end of the pectoral spine (Fine et al., 1997). The vocal mechanism includes microscopic bony ridges on the pectoral spine proximal surfaces that articulate with the pectoral girdle (Burkenroad, 1931; Agrawal and Sharma, 1965; Goel, 1966; Schachner and Schaller, 1981; Kaatz and Stewart, 1997; Fine et al., 1997; Teugels et al., 2001; Fabri et al., 2007; Parmentier et al. In Press). These ridges are hypothesized to be responsible for the production of pulsed, broad-band frequency “creaking” sounds (Tavolga 1960; Winn 1964; Fine et al. 1997) and are analogous to the stridulatory mechanisms of vocal communicating arthropods (Ewing, 1989). Determining if vocal morphology, the presence of ridges, is a reliable indicator of vocal ability would allow the mapping of vocal compared to non-vocal or silent taxa and provide an insight into the evolution of this stridulation mechanism.

What are the evolutionary constraints or selection pressures that might lead to loss of vocal behavior and morphology within a vocal clade? While sound production appears to be a relatively specialized behavior among fishes (Demski, et al., 1973; Ladich et al. 2006; Senter, 2008), reasons for the loss of vocal ability remain enigmatic. The causes of vocal mechanism loss have been examined in anurans (Martin, 1972), and sound production within an arthropod species can be lost rapidly (Zuk et al., 2006). Based on investigations of their vocal behavior or morphology, it has been found that more than ten families of vocal fishes include silent taxa (Moulton, 1958; Nelson, 1965; Hawkins and Rasmussen, 1978; Schuster, 1984-1985; Stewart, 1986; Chen and Mok, 1988; Kaatz, 1999; Ladich and Popper, 2001; Johnston and Vives, 2003). Absence of vocal ability was shown by a lack of muscles or bones specific to the vocalization mechanism in some species. Four of these families are catfishes, suggesting either ancestral absence or evolutionary loss of the swimbladder drumming mechanism in ariids (Kulongowski, 2001), pimelodids (Stewart, 1986), pangasiids (Parmentier and Diogo, 2006), and heptapterids (Heyd and Pfeiffer, 2000), although cladistic analysis, an explicit comparison of primitive versus derived taxa, was not conducted in all cases. Among fishes in general, many authors have speculated on the types of selection pressures that may produce silent lineages. The major areas these hypotheses cover are (reviewed in Kaatz, 1999): social behavior (Protasov et al., 1965), predator-prey interactions (Hawkins and Rasmussen, 1978), sensory ability (Ladich, 1999), and ecomorphology (Marshall, 1967). In this paper, we consider possible ecomorphological factors leading to the loss of sound production in catfishes.

Ecological selection pressures, differences between habitats among these, could effect fin spine morphology. Fin spine lengths differ between pelagic and littoral habitats in freshwater sunfishes (Robinson et al., 2008) and between marine shallow and deeper water ecotypes of groupers (Carvalho-Filho et al., 2009). Among catfishes, a shift from a bottom-dwelling habit to a burrowing habit in clariids correlates with a significant reduction of the pectoral spine, even to the point of complete loss in some individuals (Adriaens et al., 2002). A sub-benthic or burrowing habit, thus, appears to pose a constraint on using the pectoral spine for sound production. Multiple-use anatomical structures such as pectoral fins in catfishes play important functional roles in locomotion, brood care (Ochi and Yanagisawa, 2001), and defense, as well as in sound production (Fine and Ladich, 2003). We propose that there may be structural differences in the pectoral fin spine associated with these different functions and that some roles may conflict with others, imposing constraints on vocal mechanism design. Specifically, we hypothesize that shifts in pectoral fin use between different ecotypes may alter the use of the pectoral spine in vocal behavioral display, and we evaluate this hypothesis in this paper.

1 Materials and Methods

1.1 Literature review of pectoral spine distal morphology: Inter-familial variation

We conducted a survey of the vocal abilities of catfishes for all extant catfish families. The vocal or silent status of catfish families was based on previous reviews from the literature (Kaatz, 1999; Heyd and Pfeiffer, 2000). We categorized all species within a family as vocal if at least one species was known to be vocal. In order to determine if there were any differences between the gross morphology of pectoral spines of vocal and silent catfishes, we conducted a literature review of gross spine morphology by obtaining measurements of pectoral spine lengths from descriptions of type specimens in the literature for 351 references and 993 species (Teugels, 1996; All Catfish Species Inventory Database, Sabaj et al., 2003-2006). We recognized the 34 living families cited in Ferraris (2007) and four additional living families (Auchenoglanididae, Heteropneustidae, Lacantuniidae, and Horabagridae) identified by molecular techniques (Sullivan et al., 2006; Lundberg et al., 2007).

From these publications we extracted the quantitative and qualitative morphology of the anterior-most lepidotrichium of the pectoral fin, henceforth referred to as the "pectoral spine", for each species. We noted pectoral spine length, fish specimen standard length (SL), and the location and development of the anterior and posterior serrations on the pectoral spine for each species. For most species only one data point was obtained for each species (i.e., the holotype), but when available, we also used the range for paratypes as reported in the literature. We also noted the predominant habitat specializations or ecotypes for the majority of species within each family as described in the literature.

We applied and extended the comparative technique and classification scheme of Fernandez (1980) for ranking families by percent standard length of the pectoral spine (Appendix 1). Differences in spine length between vocal and silent taxa were evaluated with an analysis of covariance, with standard length as the covariate to account for differences in body size. This covariance analysis was performed using the JMP 5.0.1.2 statistical package (SAS Institute, Cary, NC).

1.2 Vocal disturbance behavior for laboratory specimens

The disturbance behavioral context in fishes, that simulates a predation attack and releases many fishes' agonistic vocal repertoires, provides a valuable tool for sampling fish sounds (Fish and Mowbray, 1970; Kaatz, 1999; Lin et al., 2007). In total, we evaluated 143 species in 23 families (Appendix 2). Disturbance sounds for vocal members of 81 species (for sample sizes see Kaatz, 1999) were recorded with a VHS Panasonic video camera while the fish was held by hand underwater within 3 to 6 cm of a suspended hydrophone (left side facing the hydrophone), either in the field or in a glass aquarium (see Kaatz, 1999; Kaatz and Lobel, 2001). For all remaining species, individuals were held in the air, and only the presence of disturbance stridulation was noted. For these remaining 62 species, one to 57 individuals per species were evaluated (mean 13 ±12 SD). Standard length (cm) and weight (g) were recorded for each individual immediately after recordings or observations were made for all individuals.

Thirteen vocal species representing four families that were studied for disturbance behavior were also studied in undisturbed social settings. Observations on vocal behaviors associated with reproductive and agonistic interactions in aquaria demonstrated that the presence of disturbance stridulation correlated with the use of the same vocal mechanism in undisturbed contexts (Kaatz, 1999). Thus, when we observe disturbance sounds in a species of catfishes, it is a likely indicator of the presence of another vocal communication context that employs this mechanism. Lack of disturbance sounds is not necessarily an indicator of total silence, as some vocal fishes, such as cichlids, are not known to produce any disturbance sounds. For one additional species, *Ageneiosus magoi*, we also monitored behavior for seven individuals, including both adult males and females (*n* = 34, 10 - 20 min observations). In order to determine the extent of vocal ability in catfishes we particularly focused our survey of vocal disturbance behavior within several clades: (1) Mochokidae (18 species, 3 genera), (2) the doradoids, which include the Doradidae (24 species, 17 genera) and Auchenipteridae (12 species, 8 genera); and (3) Callichthyidae (48 species, 9 genera). To determine whether or not vocal behavior was evolutionarily derived for the species we sampled within each of the above families, we referred to genus level phylogenetic hypotheses for all families except the mochokids for which cladograms representing all the taxa we evaluated are lacking (Ferraris, 1988; Higuchi, 1992; Reis, 1998).

1.3 Microscopic analyses of pectoral spine proximal morphology for laboratory specimens

In order to determine if there were any differences in the surface structures on the proximal end of the pectoral spine, we conducted a microscopy survey of these structures (1 – 22 individuals per species; Appendix 2) for the same individuals whose social and disturbance behaviors were documented. Experimental fishes were euthanized following standard techniques (ASIH, AFS, and AIFRB, 1988) and skeletonized by water maceration. The cleaned bones were then air-dried. Morphology of the pectoral spine base was observed for 14 mochokid, 16 doradid, 12 auchenipterid, and 48 callichthyid species. We observed an additional 34 species in 19 other catfish families. Spine morphology was studied with a scanning electron (JEOL 5800, 15–20 KV, 30x–2,000x) or stereoscopic (Leica Zoom 2000, 30x–45x) microscope. Scanning electron microscopy samples were sputter-coated with gold palladium. Lateral surfaces of the pectoral spine dorsal process were imaged and documented for surface morphology patterns. The locking surfaces of the dorsal spine as well as the locking anterior and ventral processes of the pectoral spine were viewed for callichthyid, mochokid, doradid, and auchenipterid specimens (1–3 species per family, $n = 12$). We compared pectoral spine length (measured with digital calipers to nearest 0.01 mm) and weight (electronic microbalance to the nearest 0.001 g) for two vocal (*Liosomadoras morua* and *Trachelyopterus* cf. *galeatus*, $n = 8$ individuals for each species) and three silent species (*Ageneiosus* spp., $n = 10$ individuals) within the Auchenipteridae; differences in length and weight were statistically analyzed using ANOVA with Statistica (Ver. 6.0).

1.4 Historical biology of pectoral spine vocalization

In order to evaluate ecological patterns in relationship to vocal ability we mapped these character states onto the maximum parsimony siluriform phylogeny using unordered parsimony reconstruction in Mesquite (Ver. 2.5; Maddison and Maddison, 2009). We recognized the established families and general topology of Sullivan et al. (2006). Following Lundberg et al. (2007), we accepted the topology for African families whose relationships had been re-assessed relative to the new family Lacantuniidae. We did not make any changes for families in the Asian clade, as the family status of different genera of the Amblycipitidae is not yet fully resolved (Sullivan et al., 2008). Combination of the topologies for the different phylogenetic trees allowed for mapping of relationships for all 19 vocal families and for a total of 37 families. Austroglanididae is not mapped in Sullivan et al. (2006) and is silent.

For comparing shortened versus lengthened catfish pectoral spines relative to a phylogenetic standard, we calculated an average based on other bony fishes. We used the average length for the anterior-most lepidotrichium of the pectoral fin or “spine” (homologous to the catfish pectoral spine) for bony fishes that do not use their fin rays for sound production but do use them for locomotion, a functional difference we were trying to contrast. This average was calculated from a review of bony fish fin lengths reported in the literature and represented a wide range of taxa: 128 species, 54 families, and 19 orders (primarily Teleostei, one Chondrostei, one Holostei). We noted “spine” length for all newly described bony fish species, excluding catfishes, published in the journal *Copeia* between 1992 and 2008. We found this average estimate of “spine” length to be 14.3% SL ±6.4 *SD*. This value was used to map “short” (≤ 14.3%) versus “long” (> 14.3%) pectoral fin spines on a cladogram of catfish families. An alternative measure would be to use the Diplomystidae as a reference value for spine length, as it is the most basal family to the Siluroidei clade, which includes the majority of catfish families. However, diplomystid spine lengths are not an appropriate comparison for catfish families outside the Siluroidei superfamily (Sullivan et al. 2006). The range of spine standard length for diplomystids was 14.9% – 21.3% with a mean of 19.7% +0.03 *SD* ($n = 6$ species). This measure at its lowest estimate is very similar to the broader bony fish estimate from the "other bony fish" literature review. The upper range, above 19.7% SL, identifies eight families with very long spines relative to the Diplomystidae within the Siluroidei super family.

2 Results

2.1 Literature review of pectoral spine distal morphology: Inter-familial variation

Pectoral spine condition for a given species was either ossified, bony and rigid, or slender (described as filamentous in the literature) and flexible with a distally cartilaginous or segmented tip. Only three families (all silent) lacked fully ossified and serrated pectoral spines (Appendix 1): Astroblepidae, Cetopsidae and Trichomycteridae. Filamentous or flexible tips were found in some species in seven other families (Amblycipitidae, Amphiliidae, Lacantuniidae, Loricariidae, Pimelodidae, Plotosidae, Siluridae), all of whom are known as silent except the loricariids, pimelodids and plotosids.

The shortest spine length was 0.8 mm for a clariid (0.2% SL), and the longest was 144.7 mm for a doradid (26.3% SL), both vocal families (Appendix 1). Species in vocal catfish families had significantly longer pectoral spine lengths than did those in silent families (ANCOVA: $df = 2$, $F = 1071.05$, $P < 0.0001$). Of the eight longest spines, six were vocal families and mean % SL spines ranging from 20.6% – 27.8%. Their rank order from lowest to highest is: Pseudopimelodidae, Mochokidae, Aspredinidae, Callichthyidae, Loricariidae, and Doradidae. Other vocal families were found interspersed among silent families.

Silent families had spines with mean % SL across the full spectrum of lengths, ranging from the longest, 36.5% ±8.7 *SD*, for astroblepids, to the shortest, 7.0% ±0.6 *SD*, for malapterurids (Appendix 1). Vocal families similarly were not restricted to any narrow range of spine lengths (8.0 ±4.4 *SD* to 27.8 ±7.1 *SD* for % SL for clariids and doradids, respectively). Only nine families had short spines (< 14.3% SL) relative to our bony fish reference value, and five of these were vocal. A similar number of silent (13) and vocal (14) families had long spines (> 14.3% SL). The eight families above 19.7% SL, that have spines shorter than the average Diplomystidae, are predominantly vocal (6 of 8). In contrast, the group of families with the shortest spines had slightly more silent families (6 of 11) based on the lower diplomystid spine value (14.9% SL). The families with intermediate spine lengths relative to diplomystids also had similar numbers of vocal (8 of 18) compared to silent (10 of 18) families.

Variation of serration morphology on the pectoral spine (Appendix 1) included: (1) serrations present on both sides or present on only one side; (2) well-developed serrations that were regularly hook-shaped to irregularly shaped; and (3) serrations visible without a microscope to weakly developed serrations requiring a microscope to count. There was a relationship between spine serrations and vocal behavior. Six families (all silent) lacked serrations entirely: Malapteruridae, Trichomycteridae, Cetopsidae, Amblycipitidae, Lacantuniidae, and Astroblepidae. The silent amphiliids mostly lacked serrations, but one genus does have them. Among the silent sisorids, some lacked and some had serrations. There was a relationship between spine secondary serration ornamentation and vocal behavior. Of the nine families that have both anterior and posterior strongly developed spine serrations, eight are vocal, and one is silent. Six of the dual-sided serrated families also had among the highest % SL for spine length (20.6% – 27.8%). A total of 23 families (except pimelodids, that had the full range of serration variation) had only one side serrated, with the other often entirely smooth or weakly serrated.

2.2 Microscopic analyses of pectoral spines for laboratory specimens and vocal characteristics

Of the 23 families we surveyed, seven were silent and 16 were vocal (Table 1). The silent malapterurid, silurid, cetopsid, and schilbid specimens (Fig. 1) had pectoral spines that were relatively short (< 1 cm) and lightweight (< 1 mg). Malapterurids had the most reduced spine, with a proximal end that was entirely smooth, opaque bone, and whose structures were not clearly homologous to processes in any other catfish species. The dorsal process was so thin in the Schilbidae that it was translucent. In contrast, the silent erethistids, heptapterids, and sisorids had longer spines. Three silent families had dorsal process morphology unique to the silent species surveyed: (1) *Ageneiosus* in the Auchenipteridae, vacuolated (Fig. 1A, B); (2) Cetopsidae, cobwebbed (Fig. 1C, D); and (3) Erethistidae, beaded rows (Fig. 1E, G). Flat convolutions (Fig. 1E, F) were also exclusively present in the Schilbidae and four other silent taxa as well as in the vocal Heteropneustidae. Other structures found in both vocal and silent taxa that were not documented with SEM were shingled teeth (e.g., loricariids and sisorids) and hemispheres (e.g., silurids and ictalurids; Table 1). Silent individuals of silent species in five families had a limited numbers of edge knobs, but most individuals had none.

Vocal species always had either or both ridges (Fig. 2A, B) or knobs (Fig. 2C, D) present on the dorsal process. Honeycombed patches were present on the dorsal process to the right and left of centrally located ridges or knobs in several vocal families (Fig. 2C, D; Table 1), although only silent species had this structure solely covering the process.

Articulating surfaces of the anterior and ventral locking process of the pectoral spine proximal end, located below the dorsal process, had only either honeycombed or convoluted surface structures (Fig. 2E). Dorsal spine locking surfaces articulating with the vertebrae had only convolutions (Fig. 2F).

Vocal and silent species were both present in a group of eight families (Table 1). Ridges and or knobs were present in all vocal species. Ridges and knobs were present in silent species in the genera *Corydoras*, *Tatia*, *Ameiurus*, *Noturus*, and *Otocinclus*, while all other silent species lacked ridges entirely and had either edge knobs or predominantly convoluted or honeycombed surface morphology. Within the vocal families that we surveyed at the species level, very few silent species were found. From 8 to 11% were silent per clade: 3 of 32 doradoids (Auchenipteridae + Doradidae), 2 of 18 mochokids, and 4 of 48 callichthyids (ridged and knobbed species scored as vocal). Ridges and knobs on the shelf of the dorsal process were present in all vocal species.

Ridge and/or knob morphology was present in all individuals of eight (e.g., doradids, horabagrids, pimelodids, ariids, aspredinids, heteropneustids, pangasiids, and auchenoglanidids) of the vocal families that had vocal behavior present in each species sampled in the family (Table 1). Two of these families are categorized as "strongly vocal", as each individual produced disturbance stridulation sounds in great numbers, with multiple sweeps of the pectoral fin as opposed to single

Table 1 Microscopic pectoral spine surface structures for catfishes that are vocal or silent during disturbance

Family: Genus	Vocal ability	Dorsal process surface structures (lateral side)		
		Ridges	Knobs	Other morphology
Silent				
Cetopsidae: *Denticetopsis*		none	none	cobwebbed
Erethistidae: *Hara*		none	0 – few	smooth, convolutions, beaded
Heptapteridae: *Pimellodella*		none, round	0 – edge	Convol
Malapteruridae: *Malapterurus*		none	none	smooth opaque bone
Schilbidae: *Pareutropius*		none	none	flat convolutions
Siluridae: *Kryptopterus*		none	none	hemispheres, translucent bone
Sisoridae: *Bagarius* (2 sp.)		none	none	shingled teeth, convolutions
Vocal and silent species both present in family (“weakly” or “strongly” vocal, see below)				
Auchenipteridae: (7 sp.)	V	round	on shelf	honeycomb
Tatia perugiae	S	round	on shelf	none
Ageneiosus (3 sp.)	S	none	none	vacuolated, bony arches
Bagridae: *Mystus, Pelteobagrus*	V	round	0 – on shelf	honeycomb
Bagrichthys	S	none	few, edge	honeycomb
Hemibagrus	S	none	few	flat convolutions
Callichthyidae: *Corydoras* (16 sp.)	V	round, bladed	on shelf	none
Corydoras (23 sp.)	S	round, bladed	on shelf	none
Brochis multradiatus	V	round, bladed	on shelf	none
Aspidoras pauciradiatus	V	round	none	none
Dianema	V	none	on edge	flat convolutions, convolutions
Aspidoras spp.	S	none	none	convolutions
*Brochis splend*ens	S	round, bladed	on shelf	none
Scleromystax	S	round, bladed	on shelf	none
Callichthys	S	none	none	flat or rugose convol.
Megalechis	S	none	none	flat or rugose convol.
Hoplosternum	S	none	none	flat or rugose convol.
Chacidae: *Chaca chaca*	V	round	rectangular	none
Chaca (2 sp.)	S	none	few, edge	flat convolutions, honeycombed
Ictaluridae: *Ictalurus*	V	round	on shelf	hemispheres, flat convol.
Ameiurus	S	round	on shelf	hemispheres, convolutions
Noturus	S	round	none	none
Loricariidae: *Panaque, Peckoltia*	V	round, bladed	none	none or shingled teeth
Ancistrus	S	0–bladed	square	flat convolutions
Otocinclus	S	round, bladed	none	none
Rhineloricaria	S	none	square	convolutions
Sturisoma	S	none	none	flat convol., convol
Mochokidae: *Synodontis* (15 sp.)	V	round	on shelf	honeycombed
Hemisynodontis	V	none	edge	convolutions
Microsynodontis	S	none	on edge	honeycomb
Pseudopimelodidae: *Microglanis*	V	none	on shelf	honeycomb
Batrochoglanis	V	none	on shelf	honeycomb
Pseudopimelodus	S	none	0 – few	smooth, honeycombed
“Weakly vocal” (<1/2 of individ. vocal, single ‘squeeks’ or irregular multi-sweep ‘creaks’)				
Ariidae: *Arius*		bladed	none	honeycomb
Aspredinidae: *Agmus*, *Bunocephalus*		none	on shelf	honeycomb
Auchenoglanididae: *Parauchenoglanis*		none	few	convolutions, honeycombed
Heteropneustidae: *Heteropneustes*		none, bladed	none	flat convolutions
Pangasiidae: *Pangasius*		none	0 – few	convolutions
Pimelodidae: *Pimelodus* (2 sp.)		round	on shelf	honeycombed
“Strongly vocal” (most individ. vocal, regularly pulsed multi-sweep ‘creaks’)				
Doradidae: (16 sp.)		round	on shelf	honeycombed
Horabagridae: *Horabagrus*		round	none	none

Ridges may be round or bladed and are linear, extending from process edge to >1/2 of process shelf. Knobs are short ridges found only at the process edge or onto <1/2 of process shelf. See Appendix 2 for lists of species where more than one species per family is indicated by a number in parentheses. Abbreviations: S = Silent; V = Vocal.

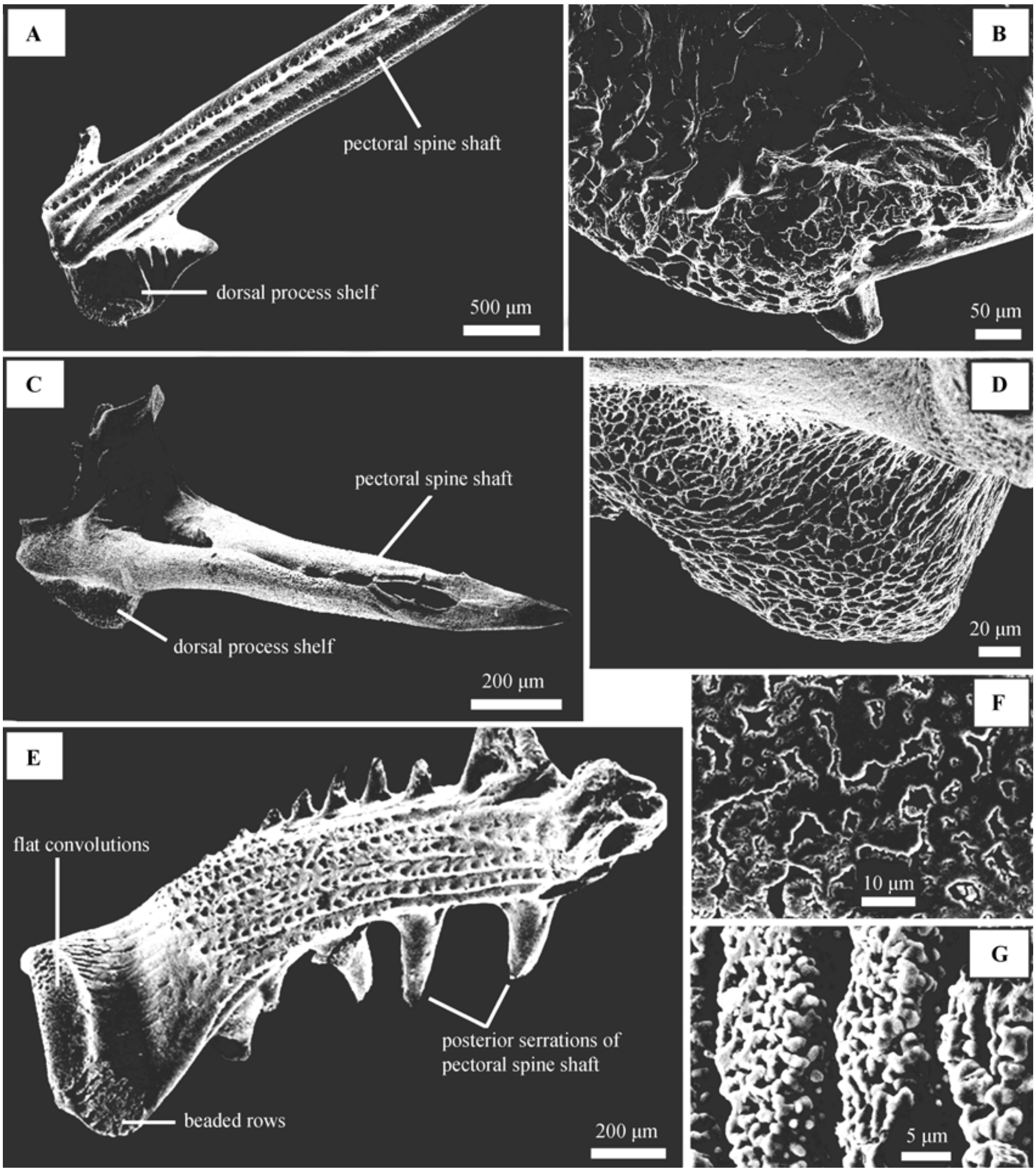

Fig. 1 Electron micrographs of pectoral spine surface structures, dorsal view of dorsal process (lateral side) in "silent" species
A. *Ageneiosus sp.,* whole spine with ribbed spine shaft, irregularly vacuolated surface of process (30×). **B**. *Ageneiosus sp.,* further magnified vacuolated surface (230×). **C**. *Denticetopsis praecox*, whole needle-shaped spine, cobwebbed surface of process (85×). **D**. *Denticetopsis praecox*, further magnified cobwebbed surface (550×). **E**. *Hara jerdoni*, whole spine with anterior and posterior serrations, smooth base, curled process edge (65×). **F**. *Hara jerdoni*, magnified flat convolutions (1,000×). **G**. *Hara jerdoni*, beaded lines present at both ends of process (2,000×).

sweeps. Their sounds and the sounds of most vocal species we recorded produced "creaks" whose spectrograms indicated pulsed broadband frequency sounds that were audible, temporally even-spaced pulses (Fig. 3A). Of the six "weakly vocal" families that had a reduced capacity for stridulation (less than half of individuals tested produced sounds, and these were often few in number, sometimes only one sweep), three produced sounds audibly different from all other catfishes recorded: *Parauchenoglanis* sp., *Pangasius sutchi*, and *Heteropneustes fossilis*. The spectrograms were of frequency modulated "squeaks" (Fig. 3B) with few broad-band pulses, and individuals rarely could be stimulated to produce any sounds during disturbance even as adults. The "squeaks" were narrower in frequency band than were "creaks" and weakly pulsed, lacking regular spaces between pulses. Only one individual each of the Heteropneustidae and Pangasiidae produced a single "squeak" by abduction and adduction of the pectoral spine. Ariid, aspredinid, auchenoglanidid and pimelodid individuals produced “creaks” by weakly audible multiple sweeps of pectoral fin spine abduction and adduction. Raised linear ridges (rounded or bladed), that extended from the edge of the dorsal process to at least half of the shelf of the dorsal process (Fig. 2A, B), were present in both “strongly vocal” families as well as in Ariidae, Heteropneustidae, and Pimelodidae. Short knobs at the edge of the process (Fig. 2C) were present to the exclusion of ridges in auchenoglanidids and pangasiids. Knobs that reached onto the dorsal process (Fig. 2D) were present in aspredinids and pimelodids.

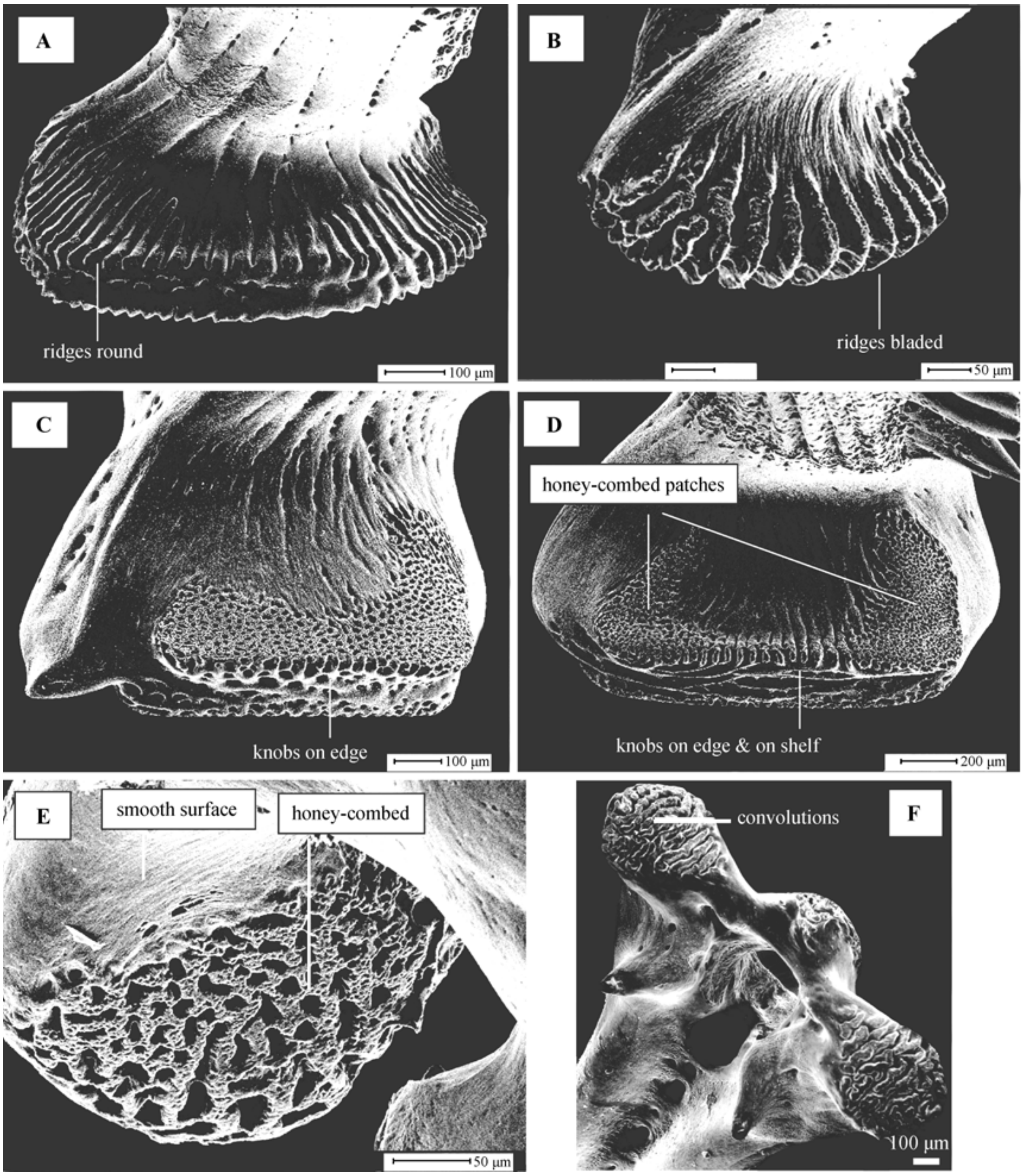

Fig. 2 Electron micrographs of pectoral spine bony surface structures, dorsal view of the dorsal process (lateral side) in vocal species

A. *Corydoras habrosus*, rounded ridges in center and bladed ridges at process ends (140×). **B**. *Heteropneustes fossilis*, bladed ridges (200×). **C**. *Mystus carcio*, knobs on edge with extensive honeycombed surface, smooth spine shaft base (110×). **D**. *Batrochoglanis raninus*, knobs on edge and on process shelf, two honeycombed patches (65×); Articulating surfaces of spine structures not associated with sound production. **E**. *Batrochoglanis raninus*, honeycombed surface, pectoral spine locking surface, anterior process (350×). **F**. *Corydoras paleatus*, convolutions, proximal end of dorsal spine locking surface.

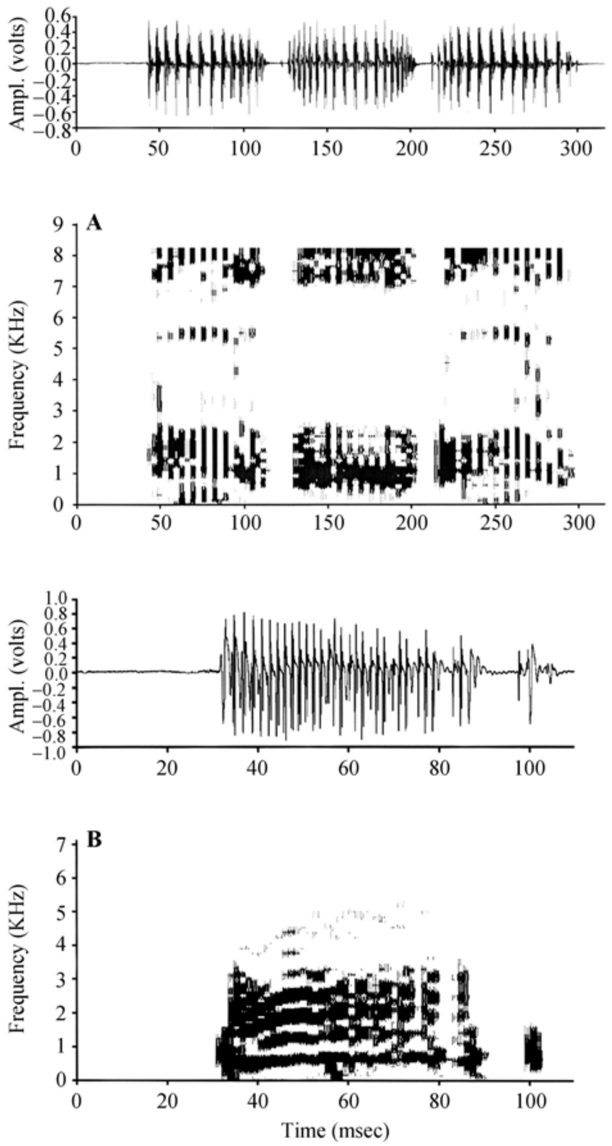

Fig. 3 Spectrograms of disturbance pectoral spine stridulation sounds recorded from two species in the Mochokidae
A. "creaking", *Synodontis eupterus* (above), and B. "squeaking" *Hemisynodontis membranaceus* (below). The "creaking" species has numerous ridges that cover more than half of the dorsal process shelf, while the "squeaking" species only has short knobs at the edge of the process.

2.3 Pectoral spine variation within three clades for laboratory specimens and their ecotypes

All doradid species had both rounded ridges and knobs that reached onto the shelf of the dorsal process, and were vocal, producing broad-band, pulsed "creaks" (Fig. 3A). Spines of doradid species were very thick, with strong serrations on both the anterior and posterior surfaces. Their spine weights ranged from 0.011 to 2.074 g (mean 0.279 ± 0.294 *SD*, n = 23), and lengths ranged from 10 to 58 mm (mean 28.07 ± 12.18 *SD*, n = 23). All species of Auchenipteridae, the sister group of Doradidae, were vocal as well, except species in the genus *Ageneiosus*, which did not produce pectoral stridulation disturbance sounds and lacked any known vocal morphology on the dorsal process. *Ageneiosus* pectoral spines were thin, translucent, and brittle, with segmented distil ends. In contrast, vocal doradid spines were solid opaque bone and non-brittle, with a sharp distal point. Spine weight (6 – 46 mg, mean 17 ± 13 *SD*, n = 10), but not spine length (12 – 36 mm, mean 23 ± 8 *SD*, n = 10), of three *Ageneiosus* species was significantly less (ANOVA df = 2, F = 15.9, $P < 0.0001$) compared to two disturbance-stridulating genera in the same family. The spines of the two vocal genera did not differ from each other: A. *Parauchenipterus* cf. *galeatus* spine weight range 210 – 918 mg (mean 502 ± 242 *SD*, n = 8) and spine length range 19 – 35 mm (mean 29 ± 5 *SD*, n = 8); B. *Liosomadoras morhua* spine weight range 28 – 764 mg, (mean 447 ± 275 SD, n = 8) and spine length range 16 – 36 mm (mean 27 ± 8 *SD*, n = 8). *Ageneiosus* species also lacked serrations along the anterior margin of the pectoral spine and had few (< 10), very low-aspect microscopic serrations on the posterior margin. All vocal species of both families had strongly curved, numerous, and visibly countable serrations on both margins of the spine. All doradids species were predominantly bentho-pelagic while active. Within the Auchenipteridae all species are benthopelagic except *Ageneiosus* species which are pelagic piscivores.

In our survey of the Mochokidae, one species, *Hemisynodontis membranaceus*, a pelagic zooplanktivore, produced weak, poorly pulsed and rare "squeaks" (Fig. 3B). Its pectoral spine had a largely smooth surface with a few shallow anterior and posterior serrations and was longer and heavier (20.0% SL, 43 mm, 811 mg, n = 1) than those in all *Synodontis* species (3 – 444 mg, mean 90 ± 99 SD; 8 - 41 mm, mean 19 ± 9 SD; n = 69). The dorsal process surface morphology was smooth except for two patches of convolutions and had knobs only on the edge. All *Synodontis* species were benthopelagic and vocal, and spines had numerous serrations that were large and hook-shaped on both margins. All species in the genus *Synodontis* produced loudly audible, pulsed, broad-band frequency "creaking" sounds (Fig. 3A), and had a dorsal process with well-defined, rounded ridges. The "creaking" species have numerous ridges that cover more than half of the dorsal process shelf, while the "squeaking" species only has short knobs at the edge of the process.

A species belonging to a third genus in the family, *Microsynodontis* sp., was silent, but its disturbance behavior is in question, since only one specimen in poor condition was available. Its habit was benthic. Its spine was 7 mm long and weighed 5 mg and had anterior and posterior serrations that were strongly hooked. The dorsal process surface had a smooth and convoluted surface morphology, and the process itself was strongly curled in toward the spine shaft instead of closer to a 90° angle from it as in most vocal taxa examined.

Callichthyid catfishes we sampled had spine lengths that ranged from 3 to 23 mm (mean 15 ± 6 *SD*, *n* = 10) and weights from 3 to 200 mg (mean 54 ± 60 *SD*, *n* = 10). The subfamily Corydoradinae had rounded or blade-like ridges plus some areas of convolution, but within the basal genus *Aspidoras*, some individuals lacked ridges, having only convoluted surfaces. In the genus *Corydoras*, all 39 species had ridge morphology and knobs. All *Corydoras* with blade-like or rounded ridges produced pulsed, broad-band frequency, grating “creak” sounds. Unlike in other catfishes, disturbance stridulation was difficult to elicit even in species for which social sound communication is well documented. The majority of *Corydoras* species produced no sounds during disturbance. Species of the subfamily Callichthyinae typically had raised convolutions or flat convoluted surfaces. Some individuals had knoblike extensions of convolutions exposed only on the edge of the process. Only *Dianema* produced typical pulsed disturbance “creaks”, while all individuals of other genera were silent (e.g., *Megalechis*, *Hoplosternum*, and *Callichthys*). Within the entire family, pelagic, benthopelagic, and benthic species exhibited both silent and vocal behavior.

2.4 Historical biology of pectoral spine vocalizations, ecotype, and spine length

Phylogenetic patterns of sound production show repeated groupings of vocal and silent lineages within clades. Of eight well-defined clades consisting of two or more families, five included both vocal and silent families (Fig. 4). Silent families in the Loricarioid clade were basal, while the Siluroidei clade also had one silent basal family with many vocal lineages representing higher order clades.

Ecotypes, or typical habitats (Appendix 1), for the majority of species within a family were different between vocal and silent families (Fig. 4). The majority of vocal families (13 of 19) were predominantly benthopelagic (Appendix 1). Among silent families, only Claroteidae, Malapteruridae, Lacantuniidae, Austroglanididae, and Cranoglanididae were benthopelagic. Silent taxa were mostly benthic. Of the 14 benthic families, only five were vocal (e.g., Aspredinidae, Auchenoglanididae, Chacidae, Heptapteridae, and Loricariidae), while nine were silent (e.g., Astroblepidae, Nematogenyidae, Amblycipitidae, Amphiliidae, Scoloplacidae, Akysidae, Sisoridae, Anchariidae, and Erethistidae). One predominantly sub-benthic family, Trichomycteridae, was also silent and included some parasitic species. Only four families were predominantly pelagic, and of these, only pangasiids were “weakly” (Table 1) and “rarely” (Appendix 1) vocal. The other three pelagic families were silent (Cetopsidae, Siluridae, and Schilbidae). The Cetopsidae also included sub-benthic or burrowing species.

Spines were long (> 14.3% SL) for the majority of families. Only nine catfish families had short (< 14.3% SL) spines. Four of the short-spined families were silent, and five of the short-spined families were vocal. Three clades showed variation in spine length, with both short (< 14.3% SL) and long (> 14.3% SL) spines representing different families within the clade.

3 Discussion

3.1 Patterns in vocal behavior and morphology in catfish families

Catfish families with the longest spines in terms of % SL were predominantly vocal, although many vocal families had proportionally shorter spines. Silent families are represented in some cases by highly reduced spines (ie. Cetopsidae, Malapteruridae) both in terms of length, weight and serration development. In the auchenipterids we found evidence that the strong degree of ossification (i.e., weight) and defensive morphology of the pectoral spine (i.e., presence of secondary serrations on spine margins) may also correlate with the presence of audible stridulation ability, supporting Pfeiffer and Eisenberg (1965), who originally observed this phenomenon. This is explicable if a locking defensive spine is an exaptation for audible stridulation, as hypothesized by Alexander (1981).

Not all catfishes are alike in disturbance sound intensity, number of vocalizations produced, or defensive morphology (Kaatz, 1999). Members of “strongly vocal” families (Table 1) as well as loud vocalizing species with strong serrations (e.g. *Synodontis*) could be acoustically aposematic. Many catfish families have venom gland cells in the pectoral fin tissues (Wright 2009). Only some families include species with the ability to envenomate and cause painful symptoms in a human handler (Kaatz pers. observ.), and all these are both vocal during disturbance (except *Noturus insignis*) and found within vocal families, suggesting that sounds could have preceded envenomation. However, many envenomators were “weakly vocal” in disturbance (Table 1), implying constraints on envenomators for being vocal. Other families are quiet vocalizers and produce sounds of very low amplitude (inaudible to humans underwater without a hydrophone) predominantly in social contexts, rarely during disturbance (e.g. *Corydoras* species; Kaatz 1999). Catfish families currently hypothesized as “weakly vocal” in disturbance (Table 1) or silent in this study could fall into this latter category.

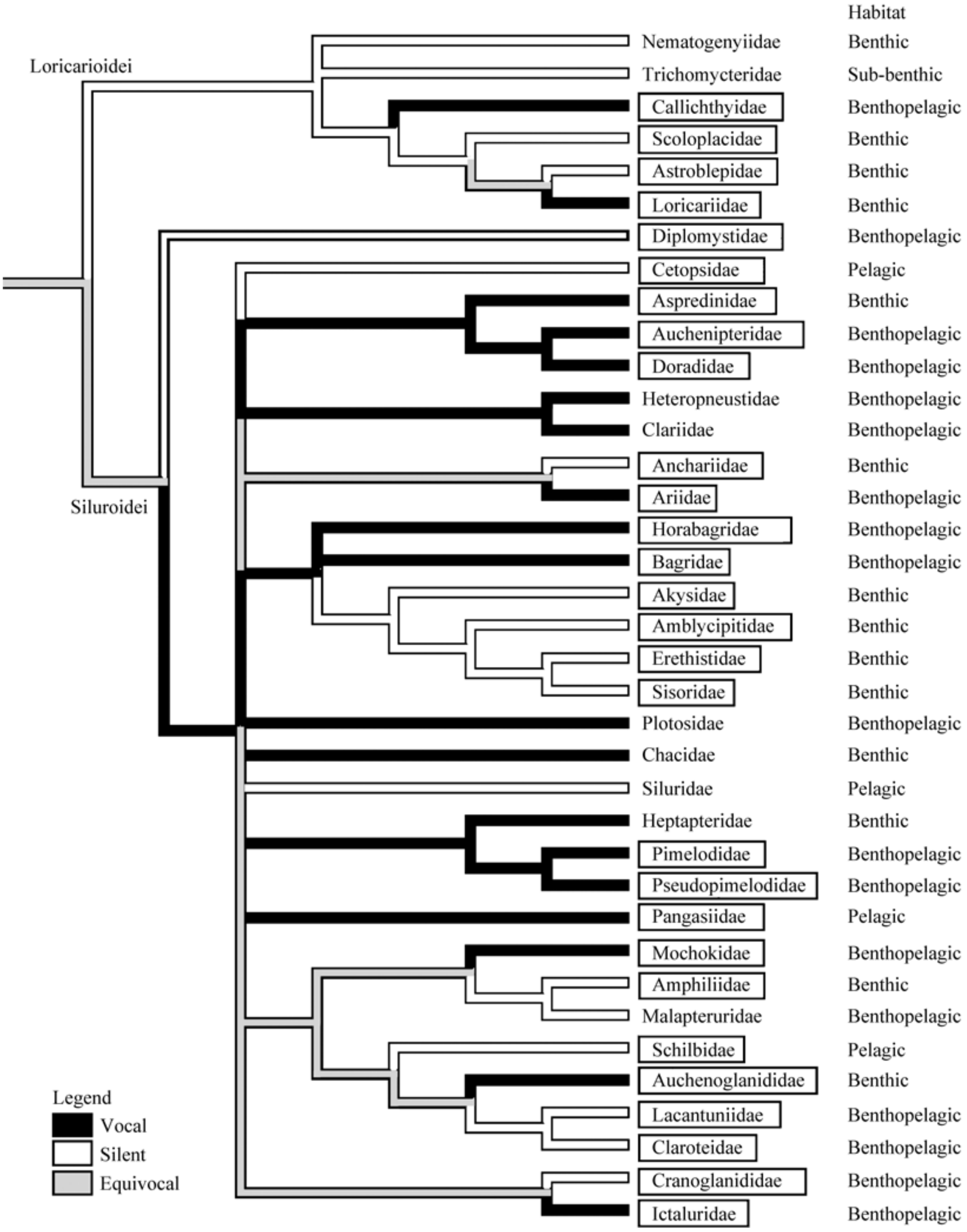

Fig. 4 Phylogenetic relationships of catfish families based on a modified topology (Sullivan et al., 2006; Lundberg et al., 2007) showing the evolution of vocal taxa within the order Siluriformes

Black branches represent vocal taxa, white branches represent silent taxa, and gray represents equivocal cases. Family names with boxes indicate taxa that have a pectoral spine length greater than 14.3% SL (long spine), and family names without boxes have a pectoral spine less than 14.3% SL (short spine). The column to the right of family names indicates the predominant habitat for members of each taxon.

3.2 Microscopic vocal morphology: disturbance versus non-disturbance stridulation

The well-known microscopic, vocal ridges on the dorsal process of the pectoral fin spine (Burkenroad, 1931; Schachner and Schaller, 1981; Fine et al., 1997) were found to be widely distributed among the catfish families we surveyed and present in all species that produced disturbance sounds (Table 1). Thus ridge or knob morphology could serve as a valuable morphological indicator for the presence of sound communication in a species. Recognizing morphologies associated with vocal behavior allows inferences about vocalizations where behavior cannot be observed, such as for rare species only represented by museum specimens or for fossils.

Not all taxa known to produce sounds with pectoral stridulation in intra-specific social contexts produced disturbance sounds in this study. At least five *Corydoras* have been documented to produce sounds with pectoral stridulation during male courtship (Kaatz and Lobel, 1999), but the majority of *Corydoras* handled during disturbance were silent, although vocal ridge structures were present. Disturbance sounds might not be useful to such small fishes, which can be readily swallowed by a variety of predators. The ictalurid, *Ameiurus nebulosus*, is known to produce sounds in agonistic contexts (Rigley and Muir, 1979); individuals of this species that we tested were silent in disturbance as well but did have dorsal process ridges. For such fishes, morphology may be a more useful indicator of vocal ability than disturbance context observations. We infer that the following taxa may fit into this category of vocal behavior because they were silent during disturbance but have vocal ridges: *Corydoras* spp., *Ancistrus* sp., *Noturus insignis*, *Tatia perugia*, *Otocinclus* sp., *Scleromystax barbatus*, and *Brochis splendens*. These individuals may not have been reproductively conditioned or sexually mature enough to produce disturbance sounds. Many *Corydoras* species that were vocal during reproduction subsequently failed to produce disturbance sounds outside the breeding season (Kaatz, personal observation).

Catfishes may be able to produce pectoral spine stridulation sounds without the presence of either ridges or knobs. *Megalechis* and *Hoplosternum* species had flat and convoluted surfaces (Fig. 1) with no knobs or ridges, suggesting the lack of ability to produce typical “creaking” stridulation sounds. *Megalechis thoracata* is reported to produce undisturbed stridulation sounds with the pectoral spine in social contexts (Mayr, 1987). The absence of disturbance vocalization in this species may reflect its lack of importance in predator-prey interactions.

Vocal mechanism morphology may have evolved from the friction-locking surface structures (Fig. 2), although in some taxa ridges from the primary spine shaft extend directly onto the dorsal process surface, indicating an alternative origin for vocal structures. The absence of ridges and knobs and the presence of other novel surface morphologies in some silent species suggest a functional bifurcation between sound production for the former and spine locking for the latter structure types. Convoluted or honey-combed surfaces on the dorsal process may serve some function in the binding phase of spine locking (Fine et al., 1997).

3.3 Ecomorphological implication of vocal ability in catfishes

Marshall (1967) observed differences in ecotype between silent and vocal fishes; swimbladder mechanisms are present in coastal and deep-sea benthic taxa and absent in bathy- and meso-pelagic taxa. Like Marshall (1967), we found that for catfishes, vocal families were associated with bottom habitats and that the vocal ability of some highly specialized pelagic species was reduced or absent. Heyd and Pfeiffer (2000) note that some vocal species are solitary and nocturnal while some silent species are pelagic, diurnal and schooling. Ladich (1997) has observed the widespread importance of agonistic sound production in fishes that could be advantageous during territorial disputes in substrate-associated habitats. However, many silent families are benthic, more strongly restricted to the bottom than benthopelagic species which we found to be the ecotype more predominantly vocal (Fig. 4). The silent and benthic association is not explained by any hypothesis in the literature.

Phylogenetic relations among auchenipterid genera we studied (Ferraris, 1988) indicate that pelagic habit correlated directly with an altered and reduced pectoral spine vocal mechanism for three species of *Ageneiosus*. This suggests differences in the functional role of the pectoral fin and its spine in the silent *Ageneiosus* species compared to all other auchenipterids we studied. Silent *Ageneiosus* species are specialized pelagic piscivores. Doradids and other auchenipterids, that are active just above the bottom or in the water column during the night, typically rest under cover on the bottom diurnally, and are territorial, competing vocally and aggressively for cover sites (Kaatz, 1999). There was a notable difference in the way the silent *Ageneiosus* moved their pectoral fins. The locking mechanism was never observed to hold spines at 90° to the body, as was common in vocal doradoids. Doradids and basal auchenipterids have fins that are rigid with fewer pectoral fin rays and used in inter- and intra-specific defensive behaviors, often “hooking” other individuals with their pectoral spine and engaging in lateral thrashing (Kaatz pers. obs.). The pelagic *Ageneiosus* had pectoral fins that had numerous fin rays, were highly flexible and engaged in locomotion, especially hovering behavior in aquarium populations; they aggregated with conspecifics and did not engage in pectoral spine “hooking” behaviors. A reduced vocal capacity in disturbance stridulation was also found in a the pelagic mochokid catfish, *Hemisynodontis membranaceus*. However, its pectoral fin was robust, and the spine was similar to those of all vocal Mochokidae species, although unlike all *Synodontis* species, *Hemisynodontis* only produced “squeek” sounds. Pangasiid individuals were silent except for one individual who only produced a single spine sweep “squeek”. Such “squeak” sounds, in these and other catfishes observed in this study, were irregularly pulsed or not pulsed at all, providing limited temporal information for a signal (Fig. 3).

Other ecomorphological and behavioral specializations that correlated with currently known silent families were: electrogenesis (malapterurids), psammophilly (dwelling in sand; trichomycterids), phreatic or interstitial (in wells or between gravel/rocks; cetopsids), pelagic (cetopsids, silurids, schilbids), and possibly troglobitic (cave dwellers; ictalurids).

3.4 Historical biology of pectoral spine morphology and vocalization ability

Knowing the phylogenetic distribution of vocal and silent catfishes (Fig. 4) allows us to better understand sound communication in this diverse and ecologically important group of fishes. Questions that can be addressed include: (1) When did vocal ability arise? Was there a single basal origin for stridulation mechanisms or has it arisen independently multiple times? and (2) What are the patterns of vocal ability acquisition and loss? Catfishes evolved an ossified pectoral spine that locks in a defensive position, and this morphology is lacking in the most likely sister groups within the Ostariophysi, the soft-rayed Gymnotiformes and Characiformes (Fink and Fink, 1996; Saitoh et al., 2003; Peng et al., 2006). Hence, pectoral spine stridulation most likely arose within the catfishes either once basally or multiple times independently in the evolution of this fish order.

There are two generally differing topologies for the evolutionary trajectory of catfish vocal ability based on either morphological or molecular cladograms. Two morphological catfish phylogenies (DePinna, 1998; Diogo, 2004) identify the family Diplomystidae as the most primitive extant family. Diplomystids have a long, bony, hypertrophied pectoral spine with serrations on both margins and structures that look similar to vocal ridges on the dorsal process (Gayet and Meunier, 1998). Whether or not the dorsal process and these structures can be used by diplomystids for vocal behavior is currently unknown. They are currently considered silent, supporting the hypothesis of a later origin for pectoral stridulation, however if they are vocal an unequivocal early single origin for stridulation is indicated. The most recent molecular phylogeny, modified from Sullivan et al. (2006) identifies the vocal ability of the hypothetical ancestor for the entire catfish order as equivocal (Figure 4). In this phylogeny the superfamily Loricarioidei is the most basal catfish group. Loricarioids have reduced spine length and are basally represented by silent families indicating that sounds are not a basal trait. Two independent origins of stridulation mechanisms among derived families within the superfamily Loricarioidei are suggested by this cladogram. The second major clade within this phylogeny is rooted by the Diplomystidae whose vocal status, as noted above, is currently uncertain. The basal condition for the remaining families in this catfish super family, the Siluroidei, is vocal suggesting an early origin for sound with silent families within this group having secondarily lost vocalization ability. The majority of derived lineages in the Siluroidei also form a polytomy, so it is not possible to discern a clear pattern of evolutionary radiation for the pectoral spine and associated vocal morphologies at higher levels within this clade, which includes the majority of catfish families. Spine vocalization mechanisms thus appear to have evolved independently at least three times between the two super families. Whether additional independent origins also occurred within the Siluroidei awaits better phylogenetic resolution of inter-familial relations and a more complete understanding of catfish vocal biology.

From our parsimony analysis, we can also infer repeated transitions between silent and vocal ability within five distinct clades for the entire order. We also observe variation in spine length and ecotype (benthic vs. benthopelagic) repeatedly occurring. This pattern points to new opportunities for studying the origin of stridulation and its loss as well as the possible relationships between habitat and vocal abilities in catfishes.

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References

Adriaens D, Devaere S, Teugels GG, Dekegel B, Verraes W, 2002. Intraspecific variation in limblessness in vertebrates: A unique example of microevolution. Biol. J. Linn. Soc. 75: 367–377.

Agrawal VP, Sharma RS, 1965. Sound producing organs of an Indian catfish *Heteropneustes fossilis*. Ann. Mag. Nat. Hist. 13: 339–344.

Alexander RM, 1965. Structure and function in the catfish. J. Zool. Lond. 148: 88–152.

Alexander RM, 1981. The Chordates. Cambridge: Cambridge University Press.

ASIH, AFS, AIFRB, 1988. Guidelines for use of fishes in field research. Fisheries 13: 16–23.

Bosher BT, Newton SH, Fine ML, 2006. The spines of the channel catfish *Ictalurus punctatus* anti-predator adaptation: An experimental study. Ethology 112: 188–195.

Burkenroad MD, 1931. Notes on the sound-producing marine fishes of Louisiana. Copeia 1931: 20–28.

Carvalho-Filho A, Ferreira CEL, Craig M, 2009. A shallow water population of *Pronotogrammus martinicensis* (Guichenot 1868) (Teleostei: Serranidae: Anthiinae) from South-western Atlantic, Brazil. Zootaxa 2228: 29–42.

Chen KC, Mok HK, 1988. Sound production in the anemonefishes *Amphiprion clarkii* and *A. frenatus* (Pomacentridae), in captivity. Jap. J. Ichthyol. 35: 90–97.

De Pinna MCC, 1998. Phylogenetic relationships of Neotropical Siluriformes (Teleostei: Ostariophysi): Historical overview and synthesis of hypotheses. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS, Lucena CAS ed. Phylogeny and Classification of Neotropical Fishes. Porto Alegre: EDIPUCRS, 279–330.

Demski LS, Gerald JW, Popper AN, 1973. Central and peripheral mechanisms of teleost sound production. Amer. Zool. 13: 1141–1167.

Diogo R, 2004. Phylogeny, origin and biogeography of catfishes: Support for a Pangean origin of 'modern teleosts' and reexamination of some Mesozoic Pangean connections between the Gondwanan and Laurasian supercontinents. Anim. Biol. 54: 331–351.

Ewing AW, 1989. Arthropod Bioacoustics: Neurobiology and Behavior. Ithaca, NY: Comstock Publishing Associates, 42–57.

Fabri G, Mauguit Q, Vandewalle P, Parmentier E, 2007. Sound production by *Synodontis* (Mochokidae): A morphological study. J. Morphol. 268: 1071.

Fernandez JM, 1980. Morfologia y Evolución de las Espinas de las Aletas en los Bagres de la Familia Pimelodidae (Teleostei, Siluriformes). Ph.D. Disseration. Caracas, Venezuela: Universidad Central de Venezuela.

Ferraris C, 1988. The Auchenipteridae: putative monophyly and systematics, with a classification of the neotropical doradoid catfishes (Ostariophysi; Siluriformes). Ph.D. Dissertation. New York: City University of New York**.**

Ferraris CJ Jr., 2007. Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes), and catalogue of siluriform primary types. Zootaxa 1418: 1–628.

Fine ML, Friel JP, McElroy D, King CB, Loesser KE, Newton S, 1997. Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. Copeia 1997: 777–790.

Fine ML, Ladich F, 2003. Sound production, spine locking and related adaptations. In: Kapoor BG, Arratia G, Chardon M, Diogo R ed. Catfishes. Enfield, NH: Science Publishers, Inc, 248–290.

Fink SV, Fink WF, 1998. Interrelationship of Ostariophysan Fishes (Teleostei). In: Stiassny MJL, Parenti LR, Johnson GD ed. Interrelationships of Fishes. San Diego: Academic Press, 209–249.

Fish, MP and Mowbray, WH, 1970. Sounds of the Western North Atlantic Fishes. Baltimore: The Johns Hopkins Press.

Gainer H, 1967. Neuromuscular mechanisms of sound production and pectoral spine locking in the Banjo catfish *Bunocephalus* species. Physiol. Zool. 40: 296–306.

Gayet M, Meunier FJ, 1998. Maastrichtian to early Late Paleocene freshwater Osteichthyes of Bolivia: Additions and comments. In: Malabarba LR, Reis RE, Vari RP, Lucena ZMS , Lucena CAS ed. Phylogeny and Classification of Neotropical Fishes. Porto Alegre, Brasil: EDIPUCRS, 95–110.

Goel HC, 1966. Sound production in *Clarias batrachus* (Linnaeus). Copeia 1966: 622–624.

Hawkins AD, Rasmussen KJ, 1978. The calls of gadoid fish. J. Mar. Biol. Assoc. U.K. 58: 891–911.

Heyd A, Pfeiffer W, 2000. Ueber die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren zusammenhang mit der Phylogenie und der Schreckreaktion. Rev. Suisse Zool. 107: 165–211.

Higuchi, H, 1992. A phylogeny of the South American thorny catfishes (Osteichthyes; Siluriformes, Doradidae). Ph.D. Dissertation. Cambridge, MA: Harvard University.

Johnston CE, Vives SP, 2003. Sound production in *Codoma ornata* (Girard) (Cyprinidae). Environ. Biol. Fish. 68: 81–85.

Kaatz IM, 1999. The Behavioral and Morphological Diversity of Acoustic Communication Systems in a Clade of Tropical Catfishes (Pisces: Siluriformes). Ph.D. Dissertation. Syracuse: State University of New York.

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

Kaatz IM, Lobel PS, 1999. Intra- and interspecific differences in sound production in the Neotropical catfish genus *Corydoras* (Callichthyidae). Amer. Zool. 41: 1489.

Kaatz IM, Lobel PS, 2001. A comparison of sounds recorded from a catfish (*Orinocodoras eigenmanni*, Doradidae) in an aquarium and in the field. Biol. Bull. 201: 278–280.

Kaatz IM, Stewart DS, 1997. The evolutionary origin and functional divergence of sound production in catfishes: Stridulation mechanisms. J. Morphol. 232: 272.

Kulongoswki C, 2001. The Anatomy and Taxonomy of the Marine Catifsh Genus *Galeichthys* Valenciennes (Siluriformes: Ariidae). M.Sc. Thesis. Grahamstown: Rhodes University.

Ladich F, 1997. Agonistic behaviour and significance of sounds in vocalizing fish. Mar. Fresh. Behav. Physiol. 29: 87–108.

Ladich F, 1999. Did auditory sensitivity and vocalization evolve independently in otophysan fishes? Brain Behav. Evol. 53: 288–304.

Ladich F, Popper AN, 2001. Comparison of the inner ear ultrastructure between teleost fishes using different channels for communication. Hear. Res. 154: 62–72.

Ladich F, Collin SP, Moller P, Kapoor GP, 2006. Communication in Fishes. Enfield (NH): Science Publishers.

Lin YC, Mok HK, Huang BQ, 2007. Sound characteristics of big-snout croaker *Johnius macrorhynchus* (Sciaenidae). J. Acoust. Soc. Amer. 121: 586–593.

Lundberg JG, Sullivan JP, Rodiles-Hernández R, Hendrickson DA, 2007. Discovery of African roots for the Mesoamerican Chiapas catfish *Lacantunia enigmatica* requires an ancient intercontinental passage. Proc. Acad. Nat. Sci. Phila. 156: 39–53.

Maddison WP, Maddison DR, 2009. Mesquite: A modular system for evolutionary analysis. Version 2.71. http://mesquiteproject.org.

Marshall NB, 1967. Sound-producing mechanisms and the biology of deep-sea fishes. In: Tavolga WN ed. Marine Bioacoustics. Oxford: Pergamon Press, 123–133.

Martin WF, 1972. Evolution of vocalizations in the toad genus *Bufo*. In: Blair WF ed. Evolution in the Genus *Bufo*. Austin: University of Texas Press, 265–287.

Mayr M, 1987. Verhaltensbeobachtungen an *Hoplosternum thoracatum* (Cuvier & Valenciennes 1840), mit besonderer Berueksichtigung des Lautverhaltens. Ph.D. Dissertation. Vienna: University of Vienna.

Moulton JM, 1958. The acoustical behavior of some fishes in the Bimini area. Biol. Bull. 114: 357–374.

Nelson K, 1965. The evolution of a pattern of sound production associated with courtship in the characid fish *Glandulocauda inequalis*. Evolution 18: 526–540.

Ochi H, Kanda T, Yanagisawa Y, 2001. Nest building and brooding behavior of the bagrid catfish *Auchenoglanis occidentalis* (Valenciennes, 1840), in Lake Tanganyika. Copeia 2001: 566–570.

Parmentier E, Diogo R, 2006. Evolutionary trends of swimbladder sound mechanisms in some teleost fishes. In: Ladich F, Collin SP, Moller P, Kapoor BG ed. Communication in Fishes, Vol. 1. Enfield, NH: Science Publishers, 43–68.

Parmentier E, Fabri G, Kaatz I, Decloux N, Planes S et al. Functional study of the pectoral spine stridulation mechanisms in different mochokid catfishes. J. Exp. Biol. In press.

Peng Z, Shunping H, Wang J, Wang W, Diogo R, 2006. Mitochondrial molecular clocks and the origin of the major Otocephalan clades (Pisces:Teleostei): A new insight. Genes 370: 113–124.

Pfeiffer W, Eisenberg JF, 1965. Die lauterzeugung der Dornwelse (Doradidae) und der Fiederbartwelse (Mochokidae). Z. Morph. Oekol. Tiere 54: 669–679.

Protasov VR, 1965. Bioacoustics of Fishes, Moscow.

Pruzsinszky I, Ladich F, 1998. Sound production and reproductive behavior of the armored catfish *Corydoras paleatus* (Callichthyidae). Environ Biol. Fish. 53: 183–191.

Reis RE, 1998. Anatomy and phylogenetic analysis of the Neotropical Callichthyid catfishes (Ostariophysi, Siluriformes). Zool. J. Linn Soc. 124: 105–168.

Rigley L, Muir J, 1979. The role of sound production by the brown bullhead *Ictalurus nebulosus*. Proc. Penn. Acad. Sci. 53: 132–134.

Robinson BW, Januszkiewicz AJ, Koblitz JC, 2008. Survival benefits and divergence of predator-induced behavior between pumpkinseed sunfish ecomorphs. Behav. Ecol. 19: 263–271.

Sabaj MH, Armbruster JW, Ferraris CJ, Friel JP, Lundberg JG et al., 2003-2006. The All Catfish Species Inventory. http://silurus. acnatsci.org/.

Saitoh K, Masaki M, Jun GI, Ichiguro NB, Mutsumi N, 2003. Mitochondrial genomics of Ostariophysan fishes: Perspectives on phylogeny and biogeography. J. Mol. Evol. 56: 464–472.

Schachner G, Schaller F, 1981. Schallerzeugung und schallreaktionen beim Antennenwels (mandim) *Rhamdia sebae sebae*. Zool. Beitraege 27: 375–392.

Schuster S, 1984-1985. Untersuchungen zur bioakustik der zwergfaden fischen *Colisa lalia* (Perciformes, Belontiidae). Zool. Beitraege 292: 295–306.

Senter P, 2008. Voices of the past: A review of Paleozoic and Mesozoic animal sounds. Hist. Biol. 20: 255–287.

Stewart DJ, 1986. Revision of *Pimelodina* and description of a new genus and species from the Peruvian Amazon (Pisces: Pimelodidae). Copeia 1986: 653–672.

Sullivan JP, Lundberg JG, Hardman M, 2006. A phylogenetic analysis of the major groups of catfishes (Teleostei: Siluriformes) using *rag1* and *rag2* nuclear gene sequences. Mol. Phylogenet. Evol. 41: 636–662.

Sullivan JP, Peng Z, Lundberg JG, Shunping JP, 2008. Molecular evidence for diphyly of the Asian catfish family Amblycipitidae (Teleostei: Siluriformes) and exclusion of the South American Aspredinidae from Siluroidea. Proc. Acad. Nat. Sci. Phila. 157: 51–65.

Tavolga WN, 1960. Sound production and underwater communication in fishes. In: Lanyon WE, Tavolga WN ed. Animal Sounds and Communication. Washington, DC: American Institute of Biological Sciences, 93–136.

Teugels GG, 1996. Taxonomy, phylogeny and biogeography of catfishes (Ostariophysi, Siluroidei): An overview. Aquat. Liv. Res. 6: 9–34.

Teugels GG, Sudarto, Pouyaud L, 2001. Description of a new *Clarias* species from southeast Asia based on morphological and genetical evidence (Siluriformes, Clariidae). Cybium 25: 81–92.

Winn HE, 1964. The biological significance of fish sounds. In: Tavolga WN ed. Marine Bioacoustics. New York, Pergamon Press, 213–231.

Wright JJ, 2009. Diversity, phylogenetic distribution, and origins of venomous catfishes. BMC Evol. Biol. 9:282.

Zuk M, Rotenberry JT, Tinghitella RM, 2006. Silent night: Adaptive disappearance of a sexual signal in a parasitized population of field crickets. Biol. Lett. 2: 521–524.

Appendix 1 Catfish families (*n* = 38) ranked by mean pectoral spine length (as % SL) compared to vocal ability, typical habitat, and pectoral spine morphology (351 references, ACSI Database)

Family	Sampled specimens		Pectoral spine length		Vocal ability	Typical habitat, common (other[a])	Pectoral spine serrations (ant./post.[b])
	SL (mm)	# sp.	range (mm)	% SL±SD (range)			
Malapteruridae	70–1,020	3	20–20.1	7.0+0.6 (6–7)	silent	benthopelagic	none
Clariidae	28–1,050	57	0.8–125	8.0+4.4 (0.2–20)	str	benthopelagic, (S)	+ / –
Plotosidae	28–1,350	12	6.5–67.4	8.2+2.5 (6–14)	str	benthopelagic	none or weak / +
Siluridae	63–672	24	5.8–65.2	9.9+2.7 (4–14)	silent	pelagic	none or weak / +
Heptapteridae	28–138	18	1.8–19.2	10.5+3.0 (6–18)	str	benthic (S)	– / + or none
Nematogenyidae	100	1	10.6	10.6	silent	benthic	– / +
Trichomycteridae	13–101	17	2.3–13.4	11.5+4.8 (8–23)	silent	sub–benthic (PS, PA)	none
Chacidae	20–220	3	12–26.8	11.8+3.3 (8–15)	str	benthic	+ / –
Heteropneustidae	146–154	2	19.6	12.8	str	benthopelagic	– / + weak
Amblycipitidae	35–164	7	4.0–24.3	14.5+5.0 (8–21)	silent	benthic	none
Cetopsidae	10 – 264	40	2.1–23.3	14.6+11.0 (6–60)	silent	pelagic (B, S)	none
Ictaluridae	25 – 333	25	2.7–34.2	15.4+3.3 (9–22)	str	benthopelagic	+ / +
Lacantuniidae	223– 427	1	56.4–76.4	15.5	silent	benthopelagic	none
Pangasiidae	117–627	14	13.4–111	15.8+4.2 (6–19)	str (rare)	pelagic	none or weak / +
Austroglanididae	62–190	3	9.5–13.3	16.0+2.9 (14–20)	silent	benthopelagic	– / +
Auchenoglanididae	62–412	9	10.1–53.0	17.0+3.6 (8–23)	str	benthic	– / +
Bagridae	21–600	79	2.7–113.0	16.6+4.1 (9–26)	str	benthopelagic (B&P)	none or weak / +
Cranoglanididae	210	1	50	16.9	silent	benthopelagic	none or weak / weak
Schilbidae	10–297	27	7.5–56.7	17.3+2.8 (10–23)	silent	pelagic	weak / +
Ariidae	74–610	27	11.0–86.0	17.4+3.7 (13–23)	str	benthopelagic	weak / +
Amphiliidae	18–124	54	2.7–26.8	18.1+3.9 (8–26)	silent	benthic	– / + or none
Auchenipteridae	15–442	53	1.6–64.6	18.3+5.4 (10–41)	str	benthopelagic (B&P)	+ / + or weak or none
Horabagridae	56–118	2	8.7–25.0	18.4+2.4 (17–21)	str	benthopelagic	+ / +
Scoloplacidae	11–20	4	2.0–3.3	18.5+6.1 (10–23)	silent	benthic	– / rare
Akysidae	12–190	44	1.3–28.5	18.6+3.2 (11–23)	silent	benthic	none or weak / + or none
Claroteidae	20–490	27	5.0–73.6	18.7+4.5 (10–33)	silent	benthopelagic	– / +
Sisoridae	32–700	9	5.5–70.6	18.7+4.2 (10–24)	silent (dor)	benthic	none or serrated
Anchariidae	79–242	5	11.0–55.7	18.7+2.9 (14–23)	silent	benthic	weak / none or weak
Pimelodidae	21–1,607	52	1.7–254	19.3+8.3 (3–62)	str	benthopelagic (B&P)	highly variable
Diplomystidae	35–211	3	6.8–36.2	19.7+3.4 (13–21)	silent (?str)	benthopelagic	– / +
Pseudopimelodidae	27–137	10	3.5–27.7	20.6+3.6 (15–25)	str	benthopelagic	+ / +
Mochokidae	17–503	57	3.4–137	21.9+4.3 (13–32)	str	benthopelagic (B&P)	+ / +
Aspredinidae	14–110	14	2.6–23.7	23.5+7.6 (16–41)	str	benthic	+ / +
Callichthyidae	19–137	66	4.1–50.7	25.1+5.8 (8–37)	str	benthopelagic (B&P)	+ / + or none
Loricariidae	22–368	90	3.5–143	26.1+12.0 (12–89)	str	benthic	weak
Doradidae	65–201	80	2.7–144	27.8+7.1 (17–46)	str	benthopelagic	+ / +
Erethistidae	16–85	16	4.9–28.5	28.6+6.9 (17–43)	silent	benthic	+ / +
Astroblepidae	24–118	11	7.0–48.3	35.1+8.7 (19–46)	silent	benthic	none

[a] Codes for "other" less common habitats: S = sub–benthic, burrowing; PS = psammophillic, in sand; PA = parasitic; B&P = some species benthic only or pelagic only

[b] Codes for serration conditions: + present, – absent, weak = small or irregular

Abbreviations for vocal ability are as follows: "str" = pectoral spine stridulation (for at least one species in the family), "?str" = hypothesized vocal ability, ridges present on spine; "dor" = dorsal spine stridulation; and "silent" = no known sounds. Spines of all family members were bony except Astroblepidae and Amblycipitidae, which were soft and distally segmented. Among species of Pimelodidae, Trichomycteridae, Amphiliidae, and Cetopsidae there are both bony and flexible first pectoral elements.

Appendix 2 Families and included species of catfishes (*n* = 143) recorded or observed during disturbance by handling

Ariidae: *Arius jordani* (17)

Aspredinidae: *Agmus lyriformis* (6), *Bunocephalus coracoideus* (3)

Auchenipteridae: *Ageneiosus* sp. (2), *Ageneiosus inermis* (6), *Ageneiosus magoi* (3), *Auchenipterichthys thoracatus* (5), *Liosomadoras morua* (8), *Liosomadoras oncinus*, *Tatia aulopygia* (3), *Tatia perugiae* (3), *Tocantinsia perisi* (1), *Trachelyichthys exilis* (5), *Trachelyopterus* cf. *galeatus* (9), *Trachelyopterichthys taeniatus* (4)

Auchenoglanididae: *Parauchenoglanis* spp. (1)

Bagridae: *Bagrichthys hypselopterus* (1), *Hemibagrus whyckioides* (4), *Mystus carcio* (5), *Pelteobagrus fulvidraco* (1)

Callichthyidae: *Callichthys callichthys* (1), *Hoplosternum littorale* (5), *Dianema urostriatus* (3), *Megalechis thoracata* (4), *Aspidoras* sp. (3), *Aspidoras pauciradiatus* (3), *Brochis splendens* (6), *Brochis multiradiatus* (2), *Scleromystax barbatus* (3); *Corydoras* spp. (2 or more specimens for each species): *C. adolfoi*, *C. aeneus* (7), *C. agassizi*, *C. arcuatus*, *C. bondi*, *C. caudomaculatus*, *C. elegans*, *C. eques*, *C. gossei*, *C. guapore*, *C. habrosus* (3), *C. hastatus* (3), *C. imitator*, *C. leopardus*, *C. leucomelas*, *C. melanistus* (3), *C. melanotaenia*, *C. melini*, *C. metae*, *C. napoensis*, *C. nijsseni*, *C. ornatus*, *C. orphnopterus*, *C. paleatus* (7), *C. panda*, *C. punctatus* , *C. pygmaeus*, *C. rabauti*, *C. reticulatus*, *C. reynoldsi*, *C. robiniae*, *C. schwartzii*, *C. seussi*, *C. simulatus*, *C. sodalis*, *C. sterbai*, *C. sychri* (3), *C. trilineatus*, *C. virginiae*

Cetopsidae: *Denticetopsis praecox* (3)

Chacidae: *Chaca chaca* (4), *C. bankanensis* (2), *C. burmensis* (1)

Doradidae: *Acanthadoras cataphractus* (3), *Acanthadoras spinossisimus* (1), *Agamyxis pectinifrons* (6), *Amblydoras affinis*, *Amblydoras hancocki* (4), *Doras micropoeus* (1), *Doras punctatus* (1), *Hassar orestes*, *Hemidoras stenopletis* (1), *Leptodoras acipenserinus*, *Lithodoras* sp., *Megalodoras irwini* (3), *Nemadoras trimaculatus*, *Nemadoras elongatus*, *Nemadoras humeralis* (1), *Nemadoras leporhinus*, *Orinicodoras eigenmanni* (3), *Oxydoras niger* (3), *Physopyxis* sp. (1), *Platydoras armatulus*, *Platydoras costatus* (22), *Pterodoras granulosus* (4), *Rhynchodoras xingui* (3), *Trachydoras* sp. (1)

Erethistidae: *Hara jerdoni* (7)

Heptapteridae: *Pimellodella gracilis* (5)

Heteropneustidae: *Heteropneustes fossilis* (3)

Horabagridae: *Horabagrus brachysoma* (1)

Ictaluridae: *Noturus insignis* (2), *Ictalurus punctatus* (3), *Ameiurus nebulosus* (9)

Loricariidae: *Ancistrus* sp. (3), *Hypostomus* sp., *Otocinclus* sp. (1), *Panaque maccus* (8), *Peckoltia pulcher* (1), *Planiloricaria cryptodon*, *Rhineloricaria* sp. (2), *Sturisoma aureum* (7)

Malapteruridae: *Malapterurus electricus* (1)

Mochokidae: *Microsynodontis* sp. (1), *Hemisynodontis membrenaceus* (1), *Synodontis* species: *S. alberti* (3), *S. angelicus* (2), *S. decorus* (5), *S. eupterus* (7), *S. flavitaeniatus* (8), *S. multipunctatus* (1), *S. nigriventris* (16), *S. notatus* (2), *S. ocellifer* (7), *S. pardalus* (1), *S. petricola* (5), *S. pleurops* (3), *S. polystictus* (1), *S. robianus* (8), *S. schal*, *S. schoutedeni* (3), *S. sorex*

Pangasiidae: *Pangasius sutchi* (8)

Pimelodidae: *Phractocephalus hemioliopterus*, *Sorubim* sp., *Pimelodus ornatus* (1), *Pimelodus pictus* (10)

Pseudopimelodidae: *Microglanis iheringi* (1), *Batrochoglanis raninus* (6), *Pseudopimelodus* sp. (1)

Schilbidae: *Pareutropius debaui* (6)

Siluridae: *Kryptopterus bicirrhis* (5)

Sisoridae: *Bagarius yarelli* (2), *Bagarius bagarius* (1)

In parentheses is number of specimens for those particular species for which the base of the pectoral fin spine was examined microscopically.