

Functional study of the pectoral spine stridulation mechanism in different mochokid catfishes

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SUMMARY

Mochokidae are able to produce pectoral spine stridulation sounds. During sound production, high speed videos were used to study the pectoral fin movements to identify the mechanisms involved. A call consisted of a series of pulses and occurred during a spine sweep, which was in fact made up of a series of jerky movements. The morphology of the pectoral spines and associated muscles was also observed in different species. The contractions of adductor profundus and superficial adductor allows adduction and abduction movements (sweep) of the spine, respectively. Simultaneously, the contraction of the arrector ventralis or the arrector 3 of the pectoral spine allows the pulling and pressing the ridges of the dorsal process, against the rough lateral face of the spinal fossa. This results in the rubbing of the ridges of the dorsal process, producing sounds. In *Synodontis* the analogy for sound production would be a brake shoe pressing against a wheel.

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Key words: Mochokidae, acoustics, catfish, sound production, spine.

INTRODUCTION

Catfishes are well known to produce sounds during courtship and agonistic behaviour (Pfeiffer and Eisenberg, 1965; Abu-Gideiri and Nasr, 1973; Ladich and Fine, 1994; Kaatz, 1999; Wysocki and Ladich, 2003) and during disturbance (Abu-Gideiri and Nasr, 1973; Fine et al., 1997; Heyd and Pfeiffer, 2000; Fine and Ladich, 2003). Of the >30 extant catfish families, 22 at least are sonic while 16 are not currently known to produce any sounds. Of the vocal families, 18 produce pectoral spine stridulation sounds. These sounds are typically produced by two sonic mechanisms (Müller, 1857; Ladich, 1997; Heyd and Pfeiffer, 2000). Drumming sounds result from the contraction of sonic muscles in relation to the swimbladder (Ladich, 1997; Parmentier and Diogo, 2006). In the second mechanism, the majority of catfish families use their pectoral spines, and one family, the sisorids, use their dorsal spine only (Mahajan, 1963), to produce stridulatory sounds (Sørensen, 1895; Gainer, 1967; Schachner and Schaller, 1981; Fine and Ladich, 2003; Friel and Vigliotta, 2006).

Sounds are produced by friction of the first pectoral spine within the pectoral girdle (Pfeiffer and Eisenberg, 1965; Fine et al., 1997; Ladich, 1997; Heyd and Pfeiffer, 2000). Taverne and Aloulou-Triki (Taverne and Aloulou-Triki, 1974) point out that friction would be due to ridges on certain parts of the articulation. In *Ictalurus punctatus*, stridulation sounds are produced during spine abduction when ridges on the ventrolateral surface of the dorsal process of the pectoral spine contact the spinal fossa of the ventrolateral wall of the cleithrum (Fine et al., 1996; Fine et al., 1997; Fine et al., 1999). These stridulatory sounds contain groups of pulses that vary in frequency, amplitude, duration and pulse patterns. Based on stridulation mechanisms in crickets and other insects, Fine et al. (Fine et al., 1997) hypothesized that individual pulses in a fin sweep could be generated by ridges successively contacting the spinal fossa.

In this case, pulse rates should vary with the speed of pectoral-fin motion (Fine et al., 1997; Vance, 2000) and the distance between ridges (Fine et al., 1996). Silent species lack microscopic bony ridges or edge knobs on the dorsal process (Kaatz et al., 2010) and are often found nested within vocal clades, further supporting the role of microscopic ridges in sound production.

The Mochokidae constitute the most important family of African catfish, with 11 genera and more than 170 species (Burgess, 1989; Nelson, 2006). The genus *Synodontis* contains approximately 120 valid species (Poll, 1971; Burgess, 1989; Friel and Vigliotta, 2006), distributed in 52 basins and lakes of Megapotamic Africa. They extend from the freshwaters of sub-Saharan Africa to the Nile River system (Poll, 1971; Friel and Vigliotta, 2006). Pfeiffer and Eisenberg (Pfeiffer and Eisenberg, 1965) demonstrated that sound is produced when the pectoral spines are abducted as well as adducted in *Synodontis* spp. The abduction movement is slower than the adduction movement and the signal is accordingly longer. They also showed that the greatest energy of the sound is between 2000 and 4000 Hz in *Synodontis nigriventris* and *S. nigrita*. The work by Abu-Gideiri and Nasr (Abu-Gideiri and Nasr, 1973) on *S. schall* indicated that sounds lasted from 1 to 3 s and that the movements started and ended sharply. Ladich (Ladich, 1997) observed in *S. eupterus* and *S. schoutedeni* that adduction sounds were shorter and of lower sound pressure than abduction sounds.

Stridulation sounds in mochokids have been observed during agonism in undisturbed aquarium populations. However, they are more abundant during disturbance than during intraspecific social interactions (Kaatz, 1999; Kaatz, 2002) and thus may also serve as a warning signal to predators [an acoustic aposematic function (Pfeiffer and Eisenberg, 1965)], although very few *Synodontis* species have been acoustically monitored long term. In channel catfish, stridulation could function as distress calls, as it was found

to occur only when a catfish was held in the mouth of a largemouth bass (Bosher et al., 2006). A stridulation warning signal would be expected to show reduced species specificity across closely related and sympatric species, whereas a social signal, where sounds are used for species recognition, would show significant species differences in the call temporal parameters. Acoustic activity level can be a measure of signal strength which would communicate condition or ability to defend in either an intraspecific agonistic or predator defence context.

The relationship between morphology and the precise mechanism of pectoral stridulation sounds in catfish are not yet completely understood (Pruzinszky and Ladich, 1998; Fine et al., 1999). Kaatz and Stewart (Kaatz and Stewart, 1997) reported differences in ridge number, shape and width for several catfish families. The purpose of our study was to explain more precisely the functional morphology of the sound production mechanism involving pectoral spines in different *Synodontis*. The study of specimens of different species will show whether the fishes of this genus use the same kind of mechanism. The mechanism of sound production in six *Synodontis* species was investigated by examining the skeletal morphology and simultaneously studying the pectoral fin movements and their respective stridulatory sounds. Two other catfish families (Pangasiidae and Ariidae) known to be silent, and one soniferous catfish species were used for comparison with the Mochokidae.

MATERIALS AND METHODS

Different mochokid species were studied to try to confirm similarity in the mechanism across species. Three specimens of *Synodontis eupterus* Boulenger 1901 (38.8, 51.7 and 94.4 mm standard length; *SL*), one *S. decorus* Boulenger 1899 (94.2 mm *SL*), one *S. nigrita* Valenciennes 1840 (73.0 mm *SL*), one *S. nigriventris* David 1936 (49.5 mm *SL*), one *S. njassae* (76.2 mm *SL*), one *S. petricola* Matthes 1959 (79.1 mm *SL*), two *Acanthodoras cataphractus* (Linnaeus 1758) (Doradidae; 53.1 and 58.2 mm *SL*), two *Pangasianodon hypophthalmus* (Sauvage 1878) (Pangasiidae; 43.7 and 94.4 mm *SL*) and two *Sciades seemanni* (Günther 1864) (Ariidae; 54.0 and 57.8 mm *SL*) used in this study were obtained from aquarium stores. They were maintained in 300 l tanks in our laboratory. Temperature was kept at $24 \pm 1^\circ\text{C}$ with a 12 h:12 h light:dark cycle. Sex of fishes was not determined because they were mostly immature.

The anatomy of the pectoral spine in two silent species (*Pangasianodon hypophthalmus* and *Sciades seemanni*) and one soniferous species (*Acanthodoras cataphractus*) was used to gain a better understanding of the sound-producing mechanism. The comparison between the different mochokids should help to better understand relationships between the morphology and the produced sounds.

The study of the pectoral spine mechanism was accomplished in two steps. First, the stridulatory sounds and the related movements of the pectoral spine were simultaneously recorded. Second, the sound-producing pectoral fin was dissected to observe its morphology.

In air, the catfish was picked up by hand then placed next to the microphone and above the camera lens on a glass plate. The right pectoral spine was immobilized against the body while the left pectoral spine was free to move. In this position, the catfish directly produced stridulatory sounds. All sound recordings were made at temperatures between 22°C and 23°C . Stridulatory sounds were recorded in air with a Sennheiser ME62 microphone (frequency range 20 Hz–20 kHz ± 2.5 dB, sensitivity $32 \text{ mV Pa}^{-1} \pm 2.5$ dB) coupled with a Sennheiser K6 modulatory system onto

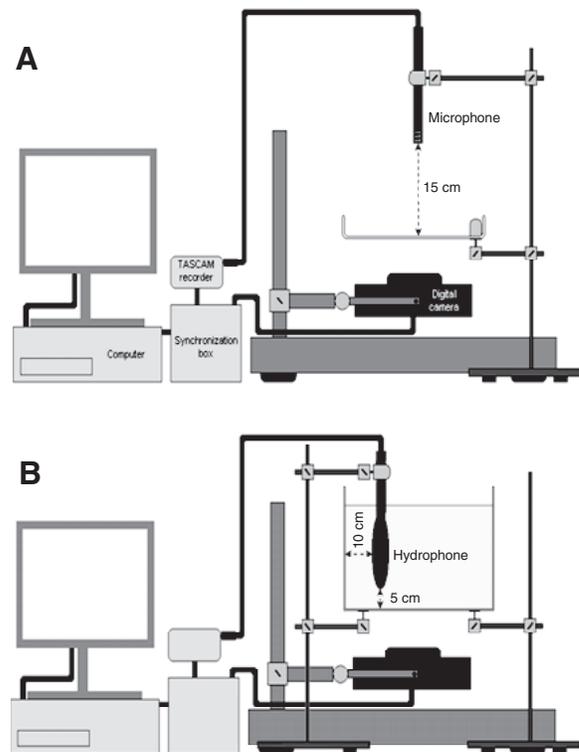


Fig. 1. Recording systems and setting to synchronize film and audiotape. The high-speed camera (RedLake MotionPro 2000 Color) recorded movements and (A) the microphone (Sennheiser ME62) was placed 15 cm in front of the specimen and the digital camera, or (B) the hydrophone (B&K type 8106) was placed 5 cm from the bottom and 10 cm from the wall of the aquarium. Two signals were synchronized and compiled in the computer.

a Tascam recorder (Fig. 1A). This methodology avoids reflection and resonance problems usually associated with aquaria (Parvalescu, 1964; Akamatsu et al., 2002) and allows the placement of each specimen at the same distance (15 cm) from the microphone.

Underwater, one catfish (*Synodontis decorus*) was also carried by hand and placed next to a hydrophone (Brüel & Kjær type 8106; sensitivity: $-173 \text{ dB re } 1 \text{ V } \mu\text{Pa}^{-1}$) coupled with a NexusTM conditioning amplifier (type 2690; amplification 10 V Pa^{-1}) and connected to a NI BNC-2110 connector block (synchronisation box in Fig. 1A,B). This system has a flat frequency response over a wide range, between 7 Hz and 80 kHz. *Synodontis decorus* were recorded in a glass tank (49 cm \times 24 cm \times 18 cm) with a transparent bottom above the camera lens (Fig. 1B). Sounds recordings were kept at water temperatures between 27°C and 28°C .

Simultaneously with sound recordings, pectoral fin movements were recorded with a high speed camera (RedLake MotionPro 2000 Color) at a rate of 500, 1000 or 1250 frames per second (frames s^{-1}). Two halogen lamps of 1000 W each were used to light the fish in a direct and indirect way by the use of a mirror.

Sounds were digitized at 44.1 kHz (16 bit resolution) and analysed with Avisoft-SasLab Pro 4.33 software (1024 point Hamming window fast Fourier transform, FFT). Temporal features were measured from oscillograms, and frequency variables were obtained from power spectra (filter bandwidth 300 Hz, FFT size 256 points, time overlap 96.87% and a flat top window; Fig. 2). According to Ladich (Ladich, 1997), a single pectoral sound, or call, is emitted

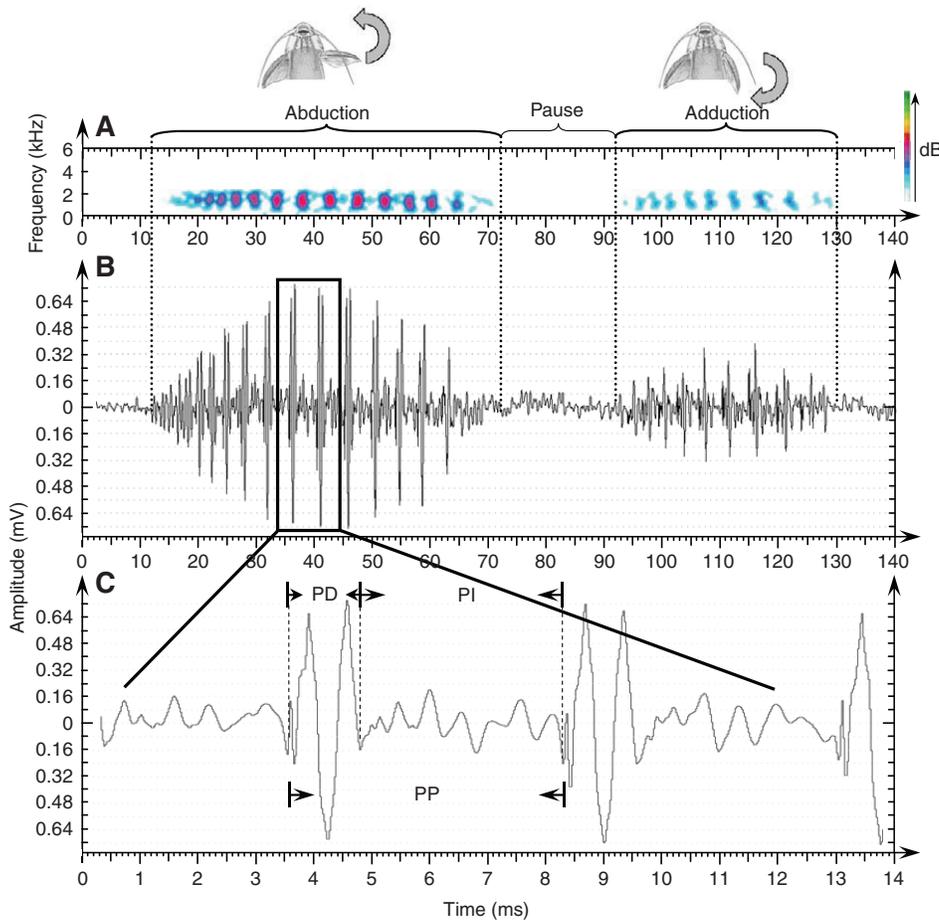


Fig. 2. Spectrogram (A) and corresponding oscillogram (B) of two sounds in *Synodontis eupterus*. (C) An enlargement of part of the oscillogram of two pulses showing the three acoustical parameters used in this study. Dotted lines indicate beginning and termination of a sound. The colour scale in A corresponds to the relative intensity of the sound. PP, pulse period; PD, pulse duration; PI, pulse interval.

during the sweep of the spine in one direction. A call consists of a series of pulses, each being a discrete acoustic waveform (Vance, 2000). This study will show that the sweep is not steady but consist of a series of jerky movements.

Abduction (AB) and adduction (AD) sounds were distinguishable (Fig. 2). The following sound variables were measured (Fig. 2C): pulse duration (PD), i.e. the time interval between the onset of one pulse and its end; pulse number; pulse interval (PI), i.e. the time

Table 1. Mean, minimum and maximum number of jerks and pulses produced during abduction and adduction of pectoral spine in different *Synodontis* species

	Number of jerks per movement					Number of pulses per movement				N ridges
	N1	N2	Min.	Max.	Mean ± s.d.	N3	Min.	Max.	Mean ± s.d.	
Abduction										
<i>S. eupterus</i> (38.8 mm SL)	34	287	7	12	10±1	36	8	11	9±1	13
<i>S. eupterus</i> (51.7 mm SL)	9	101	2	12	9±3	87	2	11	8±3	15
<i>S. eupterus</i> (94.4 mm SL)	10	120	6	15	12±3	120	6	15	12±3	17
<i>S. nigrita</i>	3	37	4	11	7±3	32	4	11	8±3	11
<i>S. nigriventris</i>	4	52	5	13	10±3	52	5	13	10±3	14
<i>S. njassae</i>	3	29	7	12	10±2	29	7	13	10±3	15
<i>S. petricola</i>	6	54	2	12	7±4	53	2	16	8±5	17
<i>S. decorus</i>	3	34	–	17	17	34	–	17	17	17
Adduction										
<i>S. eupterus</i> (38.8 mm SL)	30	150	1	12	5±4	41	7	13	10±3	13
<i>S. eupterus</i> (51.7 mm SL)	8	73	8	10	9±1	61	6	9	8±1	15
<i>S. eupterus</i> (94.4 mm SL)	6	60	2	11	9±3	58	2	11	8±3	17
<i>S. nigrita</i>	2	22	2	11	7±5	21	1	11	7±5	11
<i>S. nigriventris</i>	4	25	4	9	6±2	21	4	7	5±1	14
<i>S. njassae</i>	2	21	6	9	7±2	15	6	15	10±6	15
<i>S. petricola</i>	5	40	4	10	6±3	35	4	10	7±2	17
<i>S. decorus</i>	2	22	10	12	11	22	10	12	11	17

N1, number of movements; N2, total number of jerks; N3, total number of pulses; N ridges, number of ridges found on the medial face of the dorsal process of the pectoral spine.

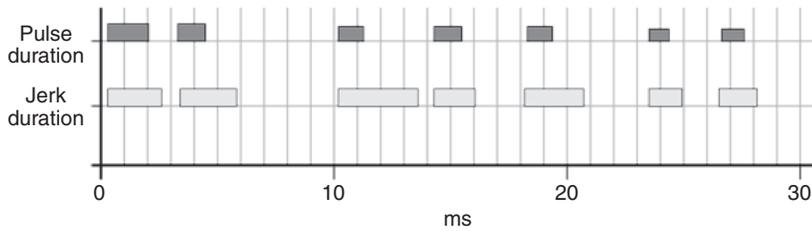


Fig. 3. Comparison between pulse duration (in dark grey) and jerk duration (in light grey) in *Synodontis decorus*.

from the end of one pulse to the beginning of the next; pulse period (PP), measured as the average peak to peak interval between consecutive pulse units in the entire sound and the dominant frequency (Fig. 2A). From the movie (supplementary material Movie 1), jerk duration, i.e. the time interval between the onset of one jerk and its end and jerk number was also measured.

After recording, fish were killed in a solution of tricaine methanesulfonate (MS-222). The left pectoral girdle and spine were dissected under a binocular dissecting microscope (Wild M5) to observe the pectoral girdle morphology and muscles associated with the pectoral spine. The muscle nomenclature is based on the work of Diogo and Abdala (Diogo and Abdala, 2007). Spines and pectoral girdles were then cleaned in distilled water and dehydrated through an ethanol series (50%, 75% and 100%), critical-point dried and platinum sputter-coated (20 nm) in a Balzers SCD-030 sputter unit. Photographs were taken using a scanning electron microscope JEOL JSM-840A under a 19-kV accelerating voltage. Spine articulations were compared between species and the number of ridges was counted on the lateral side of each dorsal process.

Two *Synodontis eupterus* specimens were fixed in 7% formaldehyde, dehydrated in butanol, decalcified, embedded in paraffin and serially sectioned with a Reichert microtome (15 µm). Cross sections were stained in Haematoxylin and Eosin (Gabe, 1976). The different sections were observed with a Leica DM 1000 microscope.

Statistical analyses were performed using GraphPad Prism (version 5.00). Non-parametric Kruskal–Wallis' tests were used to calculate the significant differences among and between each studied parameter. Dunn's post-test (multiple comparisons of the medium ranks) was also performed. Experiments were performed under control of the ethical commission of the University of Liège.

RESULTS

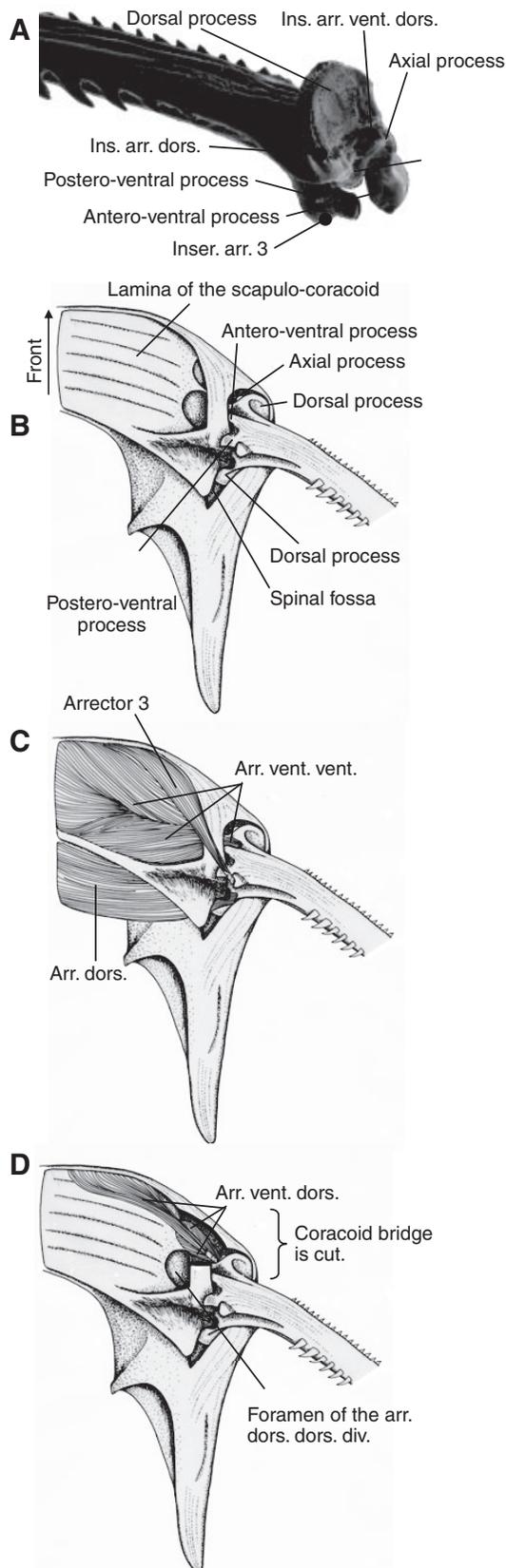
Film recordings

In Mochokidae, the sound production occurs during movements of the pectoral spine. However, the pectoral movements do not always produce sounds. Sounds are produced during adduction and abduction movements. The high speed video indicated in each case that sweeps

Table 2. Comparison of pulse characteristics produced during abduction or adduction of the pectoral spine in different *Synodontis*

	N	Pulse duration (ms)			Pulse interval (ms)			Pulse period (ms)			Dominant frequency (Hz)		
		Min.	Max.	Mean ± s.d.	Min.	Max.	Mean ± s.d.	Min.	Max.	Mean ± s.d.	Min.	Max.	Mean ± s.d.
Abduction													
<i>Synodontis eupterus</i> (38.8 mm SL)	36	1.05	1.68	1.5±0.1	0.29	8.27	3.4±1.6	1.34	9.73	4.8±1.6	–	–	–
<i>Synodontis eupterus</i> (51.7 mm SL)	87	1.70	2.84	2.4±0.2	0.89	6.01	3.5±1.2	2.86	8.55	5.9±1.2	689.9	3103	1922±759
<i>Synodontis eupterus</i> (94.4 mm SL)	11	1.20	2.88	1.7±0.2	0.13	4.35	2.2±1.2	1.74	5.94	3.9±1.2	–	–	–
<i>Synodontis nigrita</i>	32	0.91	1.61	1.3±0.2	0.02	3.94	0.7±1.1	1.04	5.17	2±1.1	689.9	1380	713.7±128
<i>Synodontis nigriventris</i>	52	1.11	1.71	1.3±0.1	1.08	6.28	3±1.1	2.43	7.71	4.4±1.1	2756	3449	2895±276
<i>Synodontis njassae</i>	23	1.43	2.11	1.9±0.1	0.36	6.41	3.4±1.7	2.29	8.30	5.3±1.6	2070	2756	2383±143
<i>Synodontis petricola</i>	41	1.11	3.02	1.7±0.3	0.63	2.81	1.8±0.6	1.92	4.54	3.6±0.6	2070	3449	2624±565
<i>Synodontis decorus</i>	37	0.60	1.80	1±0.2	1.30	2.90	2.3±0.4	2.30	4.20	3.2±0.4	–	–	–
Adduction													
<i>Synodontis eupterus</i> (38.8 mm SL)	41	0.97	2.44	1.3±0.2	0.36	2.29	0.8±0.5	1.50	3.58	2.1±0.5	–	–	–
<i>Synodontis eupterus</i> (51.7 mm SL)	61	1.52	2.77	2.3±0.3	0.39	6.78	2.9±1.4	2.93	9.04	5.2±1.3	346.6	1036	521±248
<i>Synodontis eupterus</i> (94.4 mm SL)	58	0.24	3.02	1.9±0.4	0.34	4.38	1.8±0.9	1.39	6.44	3.8±1.2	–	–	–
<i>Synodontis nigrita</i>	22	0.86	1.97	1.3±0.3	0	2.26	1±0.9	0.86	4.10	2.3±1.3	689.9	1380	804±247
<i>Synodontis nigriventris</i>	20	0.95	1.45	1.2±0.1	0.23	3.87	1.4±0.9	1.30	5.19	2.6±1	346.6	689.9	673±75
<i>Synodontis njassae</i>	17	1.24	1.57	1.4±0.1	0.93	1.66	1.3±0.2	2.18	3.08	2.7±0.3	1380	1380	1380
<i>Synodontis petricola</i>	36	1.17	2.02	1.6±0.2	0.50	3.88	1.7±1	1.68	5.67	3.3±1	2070	3454	2742±468
<i>Synodontis decorus</i>	26	0.90	1.20	1±0.1	1.60	5.60	2.8±1.1	2.60	6.50	3.8±1	–	–	–

of the pectoral spine are not uniform but made of a series of jerky movements corresponding to small increments of movement during the realisation of the sweep. The number of jerks in a sweep varied



between 1 and 17 (Table 1). High speed video recordings also showed that a basic sound unit corresponded to one single fin sweep. Each pulse within one basic sound unit corresponded directly to a single jerk movement, and a full sweep was composed of two or more pulses (Table 1). The video recordings at 500 and 1000 frames s^{-1} were insufficient but 1250 frames s^{-1} allowed us to determine that a pulse always begins with the onset of a jerk in *S. decorus* (Fig. 3). Moreover, the jerk periods and durations were not constant and the pulse duration was always shorter than the jerk duration (Fig. 3).

Sound analyses

Sound duration was significantly longer during abduction (40 ± 2 ms) than adduction (27 ± 2 ms) in the different *Synodontis* species (see also Ladich, 1997). However, this duration is highly dependent on the number of jerks and there is large variation between and within species and, even in the same specimen. In all the fishes, sound signals or calls showed considerable variation in most acoustic parameters (Table 2) and it was not possible within the context of this study to determine the specificity of sounds because of the degree of overlap in sonic data for the small sample size of individuals available per species (Table 2). Mean pulse duration did not differ between abduction and adduction movement (Kruskal–Wallis, $P < 0.05$). There were between 2 and 17 pulses in a sound (Table 1). The pulse duration ranged from 0.6 to 3 ms according to the species. The pulse interval durations varied between 0 ms and 8.27 ms (Table 2). The outcome is that pulse periods, corresponding to the sum of pulse duration and pulse interval time are really short (< 10 ms) and it is quite impossible for the human ear to distinguish the different pulses of a sound. The dominant frequency of stridulation sounds also shows high variability. Average dominant central frequency ranged from 520 to 2900 Hz, and maximum frequency was reached at approximately 3.5 kHz.

Morphology

The general morphology of the pectoral spines is very similar in all studied species, and has been previously described in different species (Fine et al., 1997; Diogo et al., 2001). Consequently, the following description is brief. The first pectoral ray is a strong serrated spine with a highly modified base that forms an articulation with the pectoral girdle (Fig. 4). The spine base possesses four processes (Fig. 4). This study concentrated mainly on the dorsal process, known to be at the origin of stridulatory sounds. In all the fishes, the dorsal process possesses numerous small cavities that form a honey-combed surface, known as spongy bone (Figs 5, 6). In *Synodontis* species and *Acanthodoras cataphractus*, however, the pores are smaller and many of them seem to be filled, giving a more compact aspect to the whole surface. All these fish also possess small lateral ridges on the lateral faces of the processes. These ridges are found only on certain parts of the dorsal process edges (Fig. 5A,B). The widths of the ridges and their spacing are given in Table 3 (see also Fig. 5C). There is no relationship between the width of the ridge and pulse duration, and between the spacing between ridges and the pulse interval duration

Fig. 4. Pectoral ray morphology of *Synodontis nigriventris*. (A) Scanning electron micrographs of the left pectoral spine, (B–D) ventral view of the skeleton (B) and of the musculature (C,D) of the left scapular girdle. In D, arrector ventralis ventral division, arrector dorsalis and arrector 3 were removed. arr. dors., arrector dorsalis; arr. vent. dors., arrector ventralis, dorsal division; arr. vent. vent., arrector ventralis, ventral division; inser. arr. 3, insertion of the arrector 3; ins. arr. dors., insertion of the arrector dorsalis; ins. arr. vent. dors., insertion of the arrector ventralis, dorsal division.

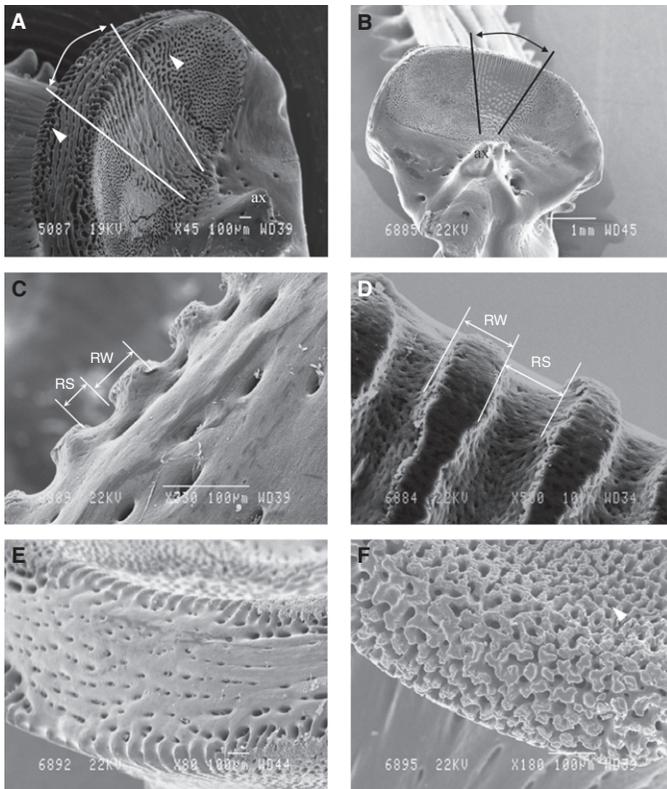


Fig. 5. Scanning electron micrographs (SEM) of (A) the dorsal process in dorsomedial view in *Acanthodoras cataphractus* and (B) in medial view in *Synodontis decorus*. (C,D) SEM of the ridges situated on the medial face of the dorsal process in *Synodontis decorus*. Double-headed arrows indicate the parts of the dorsal process having ridges. Ridge spacing (RS) and ridge widths (RW) are shown. (E) A view showing that the ridges are only found on the lateral faces of the dorsal process in *S. decorus*. (F) The dorsal process of *Pangasius hypophthalmus* does not have ridges. ax, axial process. Arrowheads indicate spongy bone.

(Fig. 7). Also, the average number of pulses in a sound does not correspond to the number of ridges (Table 1). However, the number of jerks never exceeded the total number of ridges, except in *S. decorus*.

In all the species, the dorsal process articulates in a depression of the cleithrum, the spinal fossa (infundibulum). The fossa is rough and coarse and did not present ridges or other structure that can collide with the ridge of the dorsal process. Moreover, the

Table 3. Width and spacing between adjacent ridges of the dorsal process of the pectoral spine in different *Synodontis*

	Ridge width (μm)	N	Ridge spacing (μm)	N
<i>S. eupterus</i> (38.8 mm SL)	47 \pm 11	8	101 \pm 11	8
<i>S. eupterus</i> (51.7 mm SL)	23 \pm 2	9	37 \pm 6	9
<i>S. eupterus</i> (94.4 mm SL)	38 \pm 8	12	60 \pm 10	11
<i>S. nigrita</i>	–	–	–	–
<i>S. nigriventris</i>	26 \pm 4	7	29 \pm 4	7
<i>S. njassae</i>	39 \pm 7	11	24 \pm 8	11
<i>S. petricola</i>	37 \pm 6	13	43 \pm 12	13
<i>S. decorus</i>	51 \pm 5	12	43 \pm 7	8

Values are means \pm s.d.

histological cross sections of the infundibulum did not allow observing ridges in the spinal fossa. However, the spinal fossa has lacunae which make the lateral faces appear rough (Fig. 6). *Pangasianodon hypophthalmus* (Pangasiidae) and *Sciades seemanni* (Ariidae) were found to be different from the mochokid species. Their dorsal processes do not have any ridges (Fig. 5F), and these fish do not produce any stridulatory sound with their pectoral fins. Another difference is found at the level of the axial process. The species in this study with ridges on the dorsal process (all the mochokids and *Acanthodoras cataphractus*) also possessed a more developed axial process (Fig. 5A). The two species without ridges had a very small axial process.

Different muscles insert on the spine in the *Synodontis* species (Fig. 4). The ventral division of the arrector ventralis is divided into two bundles that originate on both surfaces of the lamina of the scapulocoracoid and insert between the basis of the anteroventral process and the anterior basis of the dorsal process. The arrector dorsalis, originates on the posterior surface of the coracoid, passes through the mesocoracoid arch, and inserts on the posterior basis of the dorsal process. The arrector 3 originates on the ventral surface of the cleithrum and inserts on the basis of the posteroventral process of the spine. The dorsal division of the arrector ventralis is shorter and thinner than other muscles, it originates on the ventral surface of the cleithrum and inserts on the axial process. This muscle is called the ventral rotator by Gainer (Gainer, 1967). The Pangasiidae, Ariidae and Doradidae specimens in this study show differences in the insertions and thickness of their muscles. The aim here was not to give a complete and accurate description of all species, but see Diogo et al. (Diogo et al., 2001; Diogo et al., 2004) and Oliveira et al. (Oliveira et al., 2002) for descriptions. *Acanthodoras* have the same organisation. In the Pangasiidae and Ariidae, the *arrector ventralis* is inserted on the margin of the dorsal process.

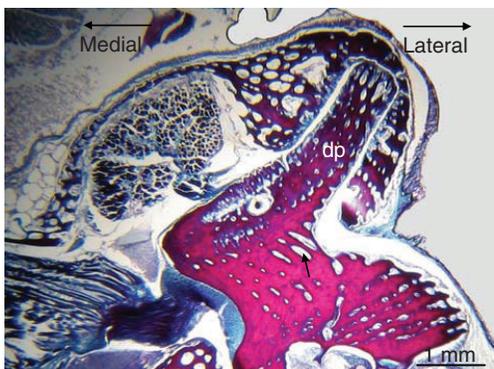


Fig. 6. Two histological cross sections at different scales, at the level of the dorsal process of the spine in *Synodontis eupterus*. Arrows indicate the honeycomb structure and the lacunae. dp, dorsal process; pg, pectoral girdle; sf, spinal fossa.

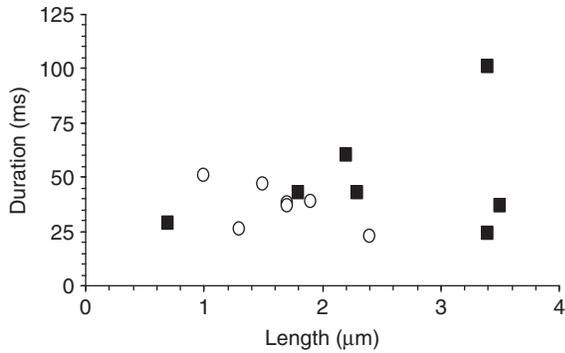


Fig. 7. Plots of means of ridge width against pulse duration (white circles), and means of ridge spacing against pulse interval duration (black squares) in *Synodontis* species.

DISCUSSION

Synodontis is an important genus having around 130 species. Although it cannot be definitely generalized for all the species, it seems that the mechanism used by the six *Synodontis* species studied is based on the same kind of mechanism, giving the same kinds of sounds (Tables 1 and 2). The mean and maximum pulse periods and frequency are consistent with the results of Ladich (Ladich, 1997). The pulse duration in our study tended to be longer, 1.8 ms ($N=3$ fishes) vs 0.91 ms ($N=10$ fishes) in Ladich (Ladich, 1997).

Stridulation of the pectoral spine within the pectoral girdle has been shown in different catfish taxa. Sweep movement of the pectoral spine consists of a number of discrete pulses, each being a discrete acoustic waveform (Fine et al., 1997). According to Vance (Vance, 2000), they are created by the ridges lining the base of the pectoral spine as they pass over the rough surface of the spinal fossa of the cleithrum. The image used to explain sound production in the catfish *Ictalurus punctatus* is that the different pulses of a sweep are produced in a fashion similar to the rubbing of a finger over a succession of teeth of a plastic comb. The number of pulses per sweep remains constant as does the number of ridges in growing fish and the pulse repetition rate decreases, correlating with the increasing distance between ridges in larger fish (Fine et al., 1996; Fine et al., 1999). In *Ictalurus punctatus*, it seems also that pulses and pulse interval durations increased toward the end of each sweep, suggesting the speed of the spine decreases towards the end of each sweep (Vance, 2000). Fine et al. (1997) estimated the raising and lowering contractions would both have to take place in 0.75 ms, giving a cycle contraction–relaxation rate of 1333 Hz. No known vertebrate muscle can complete a twitch at this speed. Although Fine and colleagues (Fine et al., 1997) concluded that the slightly convex shape of the spinal process and concave shape of the fossa wall must allow ridge impacts to occur in a continuous motion, they did not rule out the possibility that pulses are generated by several ridges simultaneously striking the wall of the spinal fossa. In *Synodontis*, the data indicate a somewhat different mechanism. The comparison of different species clearly shows that ridges on the dorsal process are necessary to produce sounds. The ridges move over the rough surface of the spinal fossa, but one without ridges. However, unlike in *Ictalurus punctatus* (Fine et al., 1999), the ridges are restricted to a small part of the dorsal process in *Synodontis* species (Fig. 5). If each pulse was produced by each ridge successively, the sound would be produced only during small parts of the whole sweep. This is not the case; the videos highlighted that pulses were produced all along the abduction or adduction

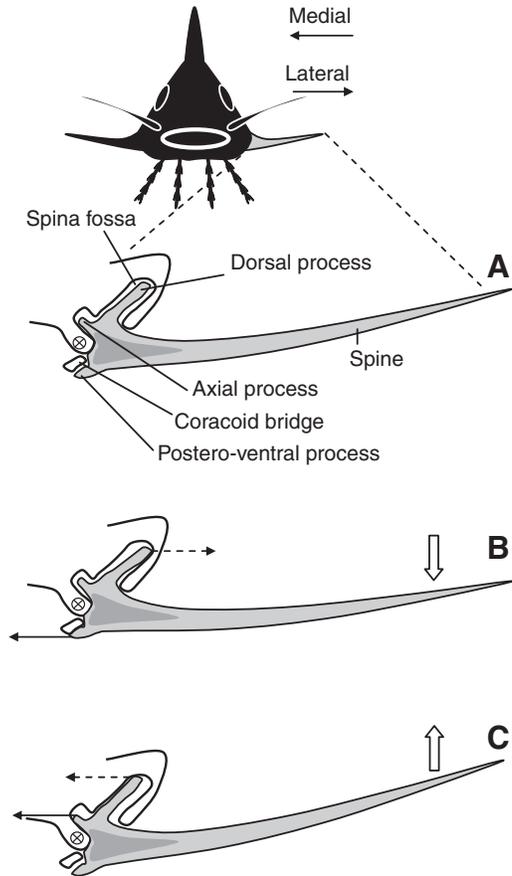


Fig. 8. Frontal schematic view of a mochokid catfish showing the left pectoral spine and the position of its dorsal process in the spinal fossa. (A) The spine in neutral position. (B) The contraction of the arrector 3 (arrow) causes the flexion of the spine so that it presses (dotted arrow) on the lateral face of the dorsal process. (C) The contraction of the arrector ventralis, dorsal division (arrow), causes the extension of the spine so that it presses (dotted arrow) on the medial face of the dorsal process. The circle with a cross in it indicates the articulation head of the scapulo-coracoid.

movement. This study shows, for the first time, that sweep movement during sound production is not continuous but made of a series of distinct movements or ‘jerks’. These jerks are of irregular duration and are longer than the pulses. The pulse and the jerk periods are highly variable and there is not relationship between them. It means the sweep is not steady and that the sound does not seem to correspond with each ridge rubbing in a regular fashion on the spinal fossa. If this was the case, the jerks would have the same period or should not be detectable. In *Synodontis*, sounds could be produced by several ridges simultaneously.

In the different *Synodontis* species in this study, the pulse period ranged from 0.86 ms to 9.73 ms, corresponding to a maximum contraction–relaxation rate of 1160 Hz, which is not possible in vertebrate muscles. The different pulses in a sound cannot result from successive contraction because muscles are not able to reach these contraction speeds. The spine can move without making sound, sliding within the spinal fossa without resistance. These movements of adduction or abduction of the pectoral spine can be realised by the contractions of the adductor profundus (or arrector ventralis) of the spine and superficial adductor (or arrector dorsalis) of the spine,

respectively. Manual traction of adductor profundus and arrector dorsalis allows the spine to articulate on the head articulation of the scapula-coracoid, giving abduction and adduction of the spine, respectively (Fig. 8). An additional muscle is required for the production of sound. The dorsal process has to rub against the spinal fossa to make sound.

In the banjo catfish (*Bunocephalus* sp.), the sweep of the pectoral spine is produced by maintained tension which is developed by continuous excitation of the muscle motor unit (Gainer, 1967). Schachner and Schaller (Schachner and Schaller, 1981) supposed that the stridulation in *Rhamdia sebae* (Pimelodidae) is caused by contraction of the arrector 3, which allows the spine to pivot dorsally and presses the lateral ridged dorsal process of the spine against the spinal fossa (Fig. 8). In *Ictalurus punctatus*, the dorsomedial surface of the process has a honeycombed surface, and the ventrolateral surface bears a series of ridges, supporting the friction by the medial face (Fine et al., 1999). However, from a functional point of view, the rubbing of the dorsal face against the spinal fossa could also be due to the dorsal division of the arrector ventralis. Its contraction allows the pulling and pressing of the dorsal process against the medial face of the spinal fossa (Fig. 8). The medial face of the dorsal process is usually worn in soniferous species of this study, supporting its role in the sound production. Generally speaking, the contractions allowing the abduction or adduction movements should be regular. However, the contraction of the arrector ventralis pulls the dorsal process against the rough surface of the spinal fossa, holding back the displacement and creating jerks and corresponding sonic pulses when the different ridges rub simultaneously. In *Synodontis* the analogy for sound production would be a brake shoe pressing against a wheel. This assumption could be reinforced by the more developed axial process found in the stridulating species of this study. *Ictalurus punctatus* (Fine et al., 1997) and other soniferous fish such as *Pimelodella cristata*, a member of the Pimelodidae (personal observation) do not possess a developed axial process. It is interesting to note that these fish seem able to make sounds only during abduction of the fins (Fine et al., 1996; Ladich, 1997). The Mochokidae and Doradidae species in this study have a developed axial process and are able to make sounds during abduction and adduction movements. Observations in a wider range of species are necessary to confirm the hypothesis that the dorsal division of the arrector ventralis is involved in sound production and its insertion point is important.

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REFERENCES

- Abu-Gideiri, Y. B. and Nasr, D. H. (1973). Sound production by *Synodontis schall* (Bloch-Schneider). *Hydrobiologia* **43**, 415-428.
- Akamatsu, T., Okumura, T., Novarini, N. and Yan, H. Y. (2002). Empirical refinements applicable to the recording of fish sounds in small tanks. *J. Acoust. Soc. Am.* **112**, 3073-3082.
- Bosher, B. T., Newton, S. H. and Fine, M. L. (2006). The spines of the channel catfish, *Ictalurus punctatus*, as an anti-predator adaptation: an experimental study. *Ethology* **112**, 188-195.
- Burgess, W. E. (1989). *An Atlas of Freshwater and Marine Catfishes. A Preliminary Survey of the Siluriformes*. Neptune City, NJ: T.F.H. Publications Inc.
- Diogo, R. and Abdala, V. (2007). Comparative anatomy, homologies and evolution of the pectoral muscles of bony fish and tetrapods: a new insight. *J. Morph.* **268**, 504-517.
- Diogo, R., Oliveira, C. and Chardon, M. (2001). On the osteology and myology of catfish pectoral girdle, with a reflection on catfish (Teleostei: Siluriformes) plesiomorphies. *J. Morphol.* **249**, 100-125.
- Diogo, R., Chardon, M. and Vandewalle, P. (2004). On the osteology and myology of the cephalic region and pectoral girdle of *Franciscodoras marmoratus* (Lütken 1874), comparison with other doradids, and comments on the synapomorphies and phylogenetic relationships of the Doradidae (Teleostei: Siluriformes). *Animal Biol.* **54**, 175-193.
- Fine, M. L. and Ladich, F. (2003). Sound production, spine locking and related adaptations. In *Catfishes* (ed. B. G. Kapoor, G. Arratia, M. Chardon and R. Diogo), pp. 248-290. Enfield: Science Publishers.
- Fine, M. L., McElroy, D., Rafi, J., King, C. B., Loesser, K. E. and Newton, S. (1996). Lateralization of pectoral stridulation sound production in the channel catfish. *Physiol. Beh.* **60**, 753-757.
- Fine, M. L., Friel, J. P., McElroy, D., King, C. B., Loesser, K. E. and Newton, S. (1997). Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. *Copeia* **1997**, 777-790.
- Fine, M. L., King, C. B., Friel, J. P., Loesser, K. E. and Newton, S. (1999). Sound production and locking of the pectoral spine of the channel catfish. *Am. Fish. Soc. Symp.* **24**, 105-114.
- Friel, J. P. and Vigliotta, T. R. (2006). *Synodontis acanthoperca*, a new species from the Ogooué River system, Gabon with comments on spiny ornamentation and sexual dimorphism in mochokid catfishes (Siluriformes: Mochokidae). *Zootaxa* **1125**, 45-56.
- Gabe, M. (1976). *Histological Techniques*. New York: Springer Verlag.
- Gainer, H. (1967). Neuromuscular mechanisms of sound production and pectoral spine locking in the banjo catfish, *Bunocephalus* species. *Physiol. Zool.* **403**, 290-306.
- Heyd, A. and Pfeiffer, W. (2000). Über die lauterzeugung der welse (Siluroidei, Ostariophysi, Teleostei) und ihren zusammenhang mit der phylogenie und der schreckreaktion. *Rev. Suisse Zool.* **107**, 165-211.
- Kaatz, I. M. (1999). The behavioral and morphological diversity of acoustic communication systems in a clade of tropical catfishes (Pisces: Siluriformes, Super Family Arioidae). New York: University of New York.
- Kaatz, I. M. (2002). Multiple sound-producing mechanisms in teleost fishes and hypotheses regarding their behavioral significance. *Bioacoustics* **12**, 230-233.
- Kaatz, I. M. and Stewart, D. J. (1997). The evolutionary origin and functional divergence of sound production in catfishes: stridulation mechanisms. *J. Morph.* **232**, 272.
- Kaatz, I. M., Stewart, D. J., Rice, A. N. and Lobel, P. S. (2010). Differences in pectoral spine morphology between vocal and "silent" clades of catfishes: ecomorphological implications. *Curr. Zool.* **56**, 73-89.
- Ladich, F. (1997). Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. *Bioacoustics* **8**, 185-208.
- Ladich, F. and Fine, M. L. (1994). Localization of swimbladder and pectoral motoneurons involved in sound production in pimelodid catfish. *Brain, Behav. Evol.* **44**, 86-100.
- Mahajan, C. L. (1963). Sound producing apparatus in an Indian catfish *Sisor rhabdophorus* Hamilton. *J. Linn. Soc.* **44**, 721-724.
- Müller J. (1857). Über Fische, welche Töne von sich geben und die Entstehung dieser Töne. *Arch. Anat. Physiol. Wiss. Med.*, 249-279.
- Nelson, J. S. (2006). *Fishes of the World*. Hoboken, NJ: John Wiley & Sons, Inc.
- Oliveira, C., Diogo, R., Chardon, M. and Vandewalle, P. (2002). On the myology of the cephalic region and pectoral girdle of three ariid species, *Arius heudeloti*, *Genidens genidens* and *Bagre marinus*, and comparison with other catfishes (Teleostei: Siluriformes). *Belg. J. Zool.* **132**, 17-24.
- Parmentier, E. and Diogo, R. (2006). Evolutionary trends of swimbladder sound mechanisms in some teleost fishes. In *Communication in Fishes*, Vol. 1 (ed. F. Ladich, S. P. Collin, P. Moller and B. G. Kapoor), pp. 43-68. Enfield: Science Publishers.
- Parvalescu, A. (1964). Problems of propagation and processing. In *Marine Bio-Acoustics* (ed. W. N. Tavolga), pp. 87-100. Oxford: Pergamon Press.
- Pfeiffer, W. and Eisenberg, J. F. (1965). Die lauterzeugung der dornwelse (Doradidae) und der fiederbartwelse (Mochokidae). *Zoomorphology* **54**, 669-679.
- Poll, M. (1971). Révision des *Synodontis* africains (Famille Mochokidae). *Ann. Mus. Roy. Afr. Cent.* **191**, 1-497.
- Pruzsinszky, I. and Ladich, F. (1998). Sound production and reproductive behaviour of the armoured catfish *Corydoras paleatus* (Callichthyidae). *Env. Biol. Fishes* **53**, 183-191.
- Schachner, G. and Schaller, F. (1981). Schallerzeugung und schallreaktionen beim antennenwels (Mandim) *Rhamdia sebae sebae* Val. *Zool. Beit.* **27**, 375-392.
- Sörensen, W. (1895). Are the extrinsic muscles of the air-bladder in some Siluroideae and the "elastic spring" apparatus of others subordinate to the voluntary production of sounds? What is, according to our knowledge, the function of the Webberian ossicles? *J. Anat. Physiol.* **29**, 205-229.
- Taverne, L. and Aloulou-Triki, A. (1974). Étude anatomique, myologique et ostéologique du genre *Synodontis* Cuvier (Pisces: Siluriformes, Mochokidae). *Ann. Mus. Roy. Afr. Cent.* **210**, 1-69.
- Vance, T. (2000). Variability in stridulatory sound production in the channel catfish, *Ictalurus punctatus*. *BIOS* **71**, 79-84.
- Wysocki, L. E. and Ladich, F. (2003). The representation of conspecific sounds in the auditory brainstem of teleost fishes. *J. Exp. Biol.* **206**, 2229-2240.