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„Hängt das Hörvermögen der Dornwelse
(Familie Doradidae) von der Morphologie
der Schwimmblase ab?“

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Abstract

Background: Thorny catfishes (Doradidae) exhibit impressive variations in swimbladder morphology: simple apple-shaped to cordiform, with simple straight walls, or with branched diverticulae. The swimbladder plays an important role in otophysans because it enhances their hearing sensitivity especially at higher frequencies. Sound pressure changes are transmitted to the inner ear by the Weberian ossicles, a bony connection from the swimbladder to the inner ear.

Methodology/Principal Findings: To investigate a form-function-relationship the swimbladder morphologies and hearing abilities were determined in six species. The morphology of the swimbladder was quantified by measuring the length, width and height and calculating a standardized swimbladder length (sSBL), which was then used to calculate the relative swimbladder length (rSBL). Hearing was measured using the auditory evoked potential (AEP) recording technique. Two thorny catfish species had simple apple-shaped and one a heart-shaped swimbladder with small, simple formed diverticula on the terminal margin. Three additional species possessed cordiform bladders. Two of these species had a secondary bladder and two many long branched diverticula. The rSBL differed significantly between most of the species. All species were able to detect frequencies between 70 Hz and 6 kHz with lowest thresholds found between 0.5 and 1 kHz (60 dB re 1 μ Pa). Hearing curves were U-shaped except in *Hemidoras* sp. in which it was ramp-like. Mean hearing thresholds of species possessing smaller rSBLs were slightly higher (maximum 8.5 dB) than of species having larger rSBLs. A positive correlation between the rSBL and hearing threshold was found at four out of twelve frequencies.

Conclusions/Significance: The current findings reveal a relationship between swimbladder form and its function. Relatively smaller swimbladders resulted in relatively better hearing. This is in contrast to a prior study on catfishes in which species with large unpaired swimbladders possessed higher sensitivity at higher frequencies than species having small paired and encapsulated bladders.

Keywords: Swimbladder morphology; hearing abilities; thorny catfishes, auditory evoked potential audiometry

Introduction

Already Aristotle was thinking about the hearing abilities of fishes. Pliny the Elder quoted the first written description in the 1st century CE and described observations about fleeing fish while clapping with hands (Popper & Fay, 2010; Popper, 2011). Fishes possess inner ears and associated structures, an auditory system that enables them to get important information about sounds, water movements and balance (Ladich & Popper, 2004; Lu, 2011; Zeddies et al., 2011). The anatomical description by Weber in the early 19th century (1820) reveals a special feature between the inner ears and the swimbladder. The Weberian ossicles, which are named after their discoverer, are a series of small bones in the otophysan fishes (a group of fish comprising Cypriniformes, Siluriformes, Characiformes and Gymnotiformes), which are involved in hearing improvement and are responsible for sound transmissions from the swimbladder to the ear (Weber, 1820; Hawkins, 1993; Ladich, 1999; Ladich & Wysocki, 2003).

The swimbladder plays an important role in buoyancy, in a few species in respiration and in the detection of sound pressure changes-and in sound production (Hall, 1924; Harden Jones & Marshall, 1952; Sand & Enger, 1973; Ladich & Fine 2006; Holbrook & Burt de Perera, 2011; Kaatz & Stewart, 2012). Due to these different functions, the swimbladder is an organ, which appears in different variations and underlies specialisation and modification. In non-otophysans such as clupeids (Clupeiformes), holocentrids (Beryciformes) and cichlids (Perciformes) some species possess rostral swimbladder extensions. A large diversity in these extensions is especially known in the sciaenids (Perciformes) (Alexander, 1964; Ramcharitar et al., 2006; Bird & Hernandez, 2007; Braun & Grande, 2008).

Otophysines evolved an impressive variation in swimbladder morphologies and Weberian ossicles, in particular in Siluriformes and to a smaller degree in Cypriniformes (Chranilov, 1929; Alexander, 1964; Chardon & Vandewalle, 1997; Chardon et al., 2003; Ladich, 2001; Chardon et al., 2003; Lechner & Ladich 2008). The form of the gas filled bladder can vary from basic ones with heart shaped swimbladders and encapsulated ones to swimbladders with diverticula at the posterior margins of the walls or around the whole swimbladder. Considering the diverse biotopes catfishes inhabit, it is not surprising that especially catfishes are highly specialized and remarkable developed. The gas bladder morphology was investigated in several catfish families. Bumblebee Catfish (family Pseudopimelodidae) have large cordiform and also tiny gas bladders, which are partially divided into two lateral sacs (Birindelli & Shibatta, 2011). Sea Catfishes (Ariidae) and Driftwood Catfishes (Auchenopteridae) reveal similar modifications (Marceniuk, & Birindelli, 2010; Birindelli et al., 2012).

Free heart-shaped swimbladders were found in the families Malapteruridae, Heptapteridae and Mochokidae, whereas bony encapsulated ones were found in the families Loricariidae and Callichthyidae (Ladich & Lechner, 2008). Thorny catfishes exhibit an impressive series of swimbladder modifications. These range from simple apple-shaped ones to large cordiform bladder with many branched diverticula. The swimbladders in thorny catfish are always unpaired single bladders which possess sometimes a caudal sac, termed secondary bladder (Birindelli et al., 2009; Kaatz and Stewart 2012).

At the beginning of the 20th century scientists demonstrated experimentally that fish are able to detect sound (Parker 1903, 1918, v. Frisch 1923, 1936, v. Frisch & Stetter, 1932). V. Frisch and colleagues demonstrated that the connection of the inner ear to air-filled cavities improves the hearing abilities in fishes. Among catfishes hearing abilities were measured in representatives of eleven fish families: in doradids, pimelodids, callichthyids, ariids, pseudopimelodids, malapterurids, heptapterids, mochokids, auchenipterids, silurids and ictalurids (Ladich, 1999, 2000; Lechner & Ladich, 2008; Wysocki et al., 2009; Lechner & Ladich, 2010; for a review see Ladich & Bass, 2003). Lechner and Ladich (2008) showed that catfish species which have large unpaired swimbladders and a higher number of Weberian ossicles possess higher hearing abilities at higher frequencies than species having tiny paired and encapsulated swimbladders. This was the case across eight different catfish families. Relationships between the morphological variations in accessory hearing structure and hearing abilities were furthermore analysed in squirrelfishes (Holocentridae) and drums or croakers (Sciaenidae) fishes (Coombs & Popper, 1979; Yan et al., 2000; Ramcharitar et al., 2006; Ramcharitar et al., 2006; Popper & Fay, 2011). Among squirrelfishes *Myripristis kuntze* showed lower hearing thresholds and a wider detectable frequency range than other species. The anterior part of the swimbladder of *M. kuntze* possesses extensions which directly contact the inner ear (Coombs & Popper, 1979; Parmentier et al., 2011). Within sciaenids Ramcharitar et al. (2006a, b) showed that species having anterior swimbladder horns possessed a wider detectable frequency-range than species lacking these structures. However, Horodysky et al.'s (2011) data do not support this observation in sciaenids.

Thorny catfishes seem to be a good model to investigate the relationship between different swimbladder forms and hearing abilities. The aim of this study was to find out if differences in swimbladder morphology affect hearing in thorny catfish. Therefore, six different species were dissected, swimbladder dimensions determined and their hearing abilities measured using the non-invasive auditory evoked potentials (AEP) recording technique.

Materials & Methods

Animals

Six species of the catfish family Doradidae were used for this study: *Acanthodoras spinosissimus* (Talking catfish), *Agamyxis pectinifrons* (Whitebarred catfish), *Hemidoras* sp., *Megalodoras uranoscopus*, *Oxydoras niger* (Ripsaw catfish) and *Platydoras hancokii* (Blue-eye catfish). Three specimen of each species were used for morphological investigations and three to nine for hearing measurements (Tab. 1)

All fish were purchased from a tropical fish supplier (Transfish, Munich, Germany). Fish were kept in aquaria, which were equipped with sand on the bottom, plants, roots, and various shelters. The tanks of *P. hancokii* and *A. spinosissimus* were 70 x 35 x 40 cm in size (width x height x depth), those of *A. pectinifrons* was 90 x 30 x 30 cm, of *Hemidoras* sp. 70 x 40 x 50 cm, of *M. uranoscopus* 100 x 50 x 50 cm and of *O. niger* 100 x 35 x 50 cm. In order to reduce noise only external filters were used. Temperature was maintained at $25 \pm 1^\circ\text{C}$ and a 12·h:12·h L:D cycle was provided. Fish were fed four to six times per week frozen chironomid larvae or artificial food. The study protocol was approved by the Austrian Federal Ministry of Science and Research, permit number GZ 66.006/0023-II/10b/2008.

Tab. 1. Species, number of specimens and size range of thorny catfishes used in this study. AM, auditory measurements; BM, body mass (g); MM, morphological measurements; SL, standard length (mm).

| Species | AM | | | MM | | |
|--|----|--------------|-------------|----|---------------|-------------|
| | N | SL | BM | N | SL | BM |
| <i>Acanthodoras spinosissimus</i> (Eigenmann & Eigenmann, 1888) | 3 | 15.4 - 16.8 | 67.8 - 87.9 | 3 | 61.3 - 113.2 | 7.1 - 24.4 |
| <i>Agamyxis pectinifrons</i> (Cope, 1870) | 7 | 54.8 - 59.3 | 6.7 - 9.1 | 3 | 57.5 - 59.4 | 7.0 - 8.1 |
| <i>Platyodoras hancokii</i> (Valenciennes, 1840) | 7 | 53.0 - 69.8 | 3.85 - 10.7 | 3 | 54.4 - 71.2 | 8.9 - 9.7 |
| <i>Hemiodoras</i> sp. | 9 | 71.0 - 79.5 | 5.3 - 6.7 | 3 | 78.3 - 87.3 | 6.4 - 6.8 |
| <i>Megalodoras uranoscopus</i> (Eigenmann & Eigenmann, 1888) | 9 | 69.6 - 107.1 | 24.1 - 31.6 | 3 | 101.5 - 122.7 | 34.2 - 41.6 |
| <i>Oxydoras niger</i> (Valenciennes, 1821) | 3 | 15.4 - 16.8 | 67.8 - 87.9 | 3 | 105.0 - 127.7 | 23.3 - 23.8 |

Morphological Measurements

Fish were euthanized using an overdose of tricaine methanesulfonate (MS 222) and were directly fixed in alcohol (70%) for conservation. Swimbladder dissections were made following Bridge and Haddon (1893). Fishes were cut open ventrally and laterally and stomach, intestine, liver and associated structures were removed to bare the swimbladder. Dissections were performed using a dissecting microscope (Wild M7).

Fish length and swimbladder measures were taken using digital callipers. All measures were taken including the secondary bladders but excluding the diverticula. The swimbladder form was described following the terminology by Birindelli et al. (2009) (Fig. 2). Standardized swimbladder length (sSBL) was calculated using the formula $sSBL = (l+h+w)/3$, where l is length, h is height and w is width. The relative swimbladder length (rSBL) was calculated following the formula $rSBL = sSBL/SL$, where SL is the standard length.

Hearing Measurements

Hearing sensitivity was measured using the auditory evoked potentials (AEP) recording technique developed by Kenyon et al. (1998) and modified by Ladich and Wysocki (2005).

The thorny catfish were mildly immobilized with Flaxedil (gallamine triethiodide; Sigma Aldrich Handels GmbH, Vienna, Austria). The dosage used was $3.07 - 3.27 \mu\text{g g}^{-1}$ for *A. spinosissimus*, $3.99 - 5.38 \mu\text{g g}^{-1}$ for *A. pectinifrons*, $0.86 - 3.26 \mu\text{g g}^{-1}$ for *P. hancockii*, $1.73 - 2.82 \mu\text{g g}^{-1}$ for *Hemidoras* sp., $3.8 - 7.01 \mu\text{g g}^{-1}$ for *M. uranoscopus* and $1.73 - 2.06 \mu\text{g g}^{-1}$ for *O. niger*. The lowest dosage that immobilized fish while enabling slight movement of the opercula during the experiments was applied. All auditory measurements were carried out in a bowl-shaped plastic tub (diameter 33 cm, water depth 13 cm, 1 cm layer of gravel) which was lined inside with acoustically absorbent material (air-filled packing wrap) to decrease resonances and reflections. The tub was positioned on an air table (TMC Micro-g 63-540, Technical Manufacturing Corporation, Peabody, MA, USA), which rested on a vibration-isolated plate of concrete. A sound proof chamber, constructed as a Faraday cage (interior dimensions: 3.2 m x 3.2 m x 2.4 m) enclosed the whole setup (Fig. 1).

Test subjects were positioned in the centre of the tub, so that the nape of the head was at the water surface. For respiration a pipette was inserted into the fish's mouth and respiration was effected by a simple, temperature-controlled ($25 \pm 1 \text{ }^\circ\text{C}$), gravity-fed water system. The area of the head above the water surface was covered with a small piece of Kimwipes® tissue paper to keep moist. Silver wire electrodes (diameter 0.38 mm) were used for recording AEPs. The recording electrode was placed in the midline of the skull over the region of the medulla, the reference electrode cranially between the nares. Both electrodes were pressed firmly against the skin (Fig. 1).

Both presentation of sound stimuli and AEP waveform recording were achieved using a modular rack-mount system (Trucker-Davis Technologies (TDT) System 3, Gainesville, FL, USA) controlled by a PC containing a TDT digital signal processing board and running TDT BioSig RP software.

Hearing thresholds were determined for the following frequencies: 0.07, 0.1, 0.3, 0.5, 1, 2, 3, 4, 5 and 6 kHz. Sound stimuli waveforms were created using TDT SigGen RP software. For tone bursts, two speakers (Fostex PM-0.5 Sub and PM-0.5 MKII, Fostex Corporation, Tokyo, Japan) installed 0.5 m above the fish, were used. Tone bursts at different frequencies were presented in random order. A hydrophone (Brüel and Kjaer 8101, Naerum,

Denmark; frequency range 1 Hz to 80 kHz \pm 2 dB; voltage sensitivity – 184 dB re 1 V μ Pa⁻¹) was placed 2 cm from the right side of the animal to determine absolute sound pressure levels (SPLs) under water in the immediate vicinity of the test subject. A second custom-built pre-amplifier was used to amplify the hydrophone signal (1000x). Sound stimuli consisted of tone bursts played at a repetition rate of 21 s⁻¹ and at opposite polarities (90° and 270°). One thousand stimuli of each polarity were presented and the corresponding AEPs averaged by BioSig RP software to eliminate stimulus artefacts. The SPL was reduced in 4 dB steps until the AEP waveform was no longer identifiable. By overlaying replicate traces, the lowest SPL yielding a repeatable AEP trace was determined and regarded as threshold.

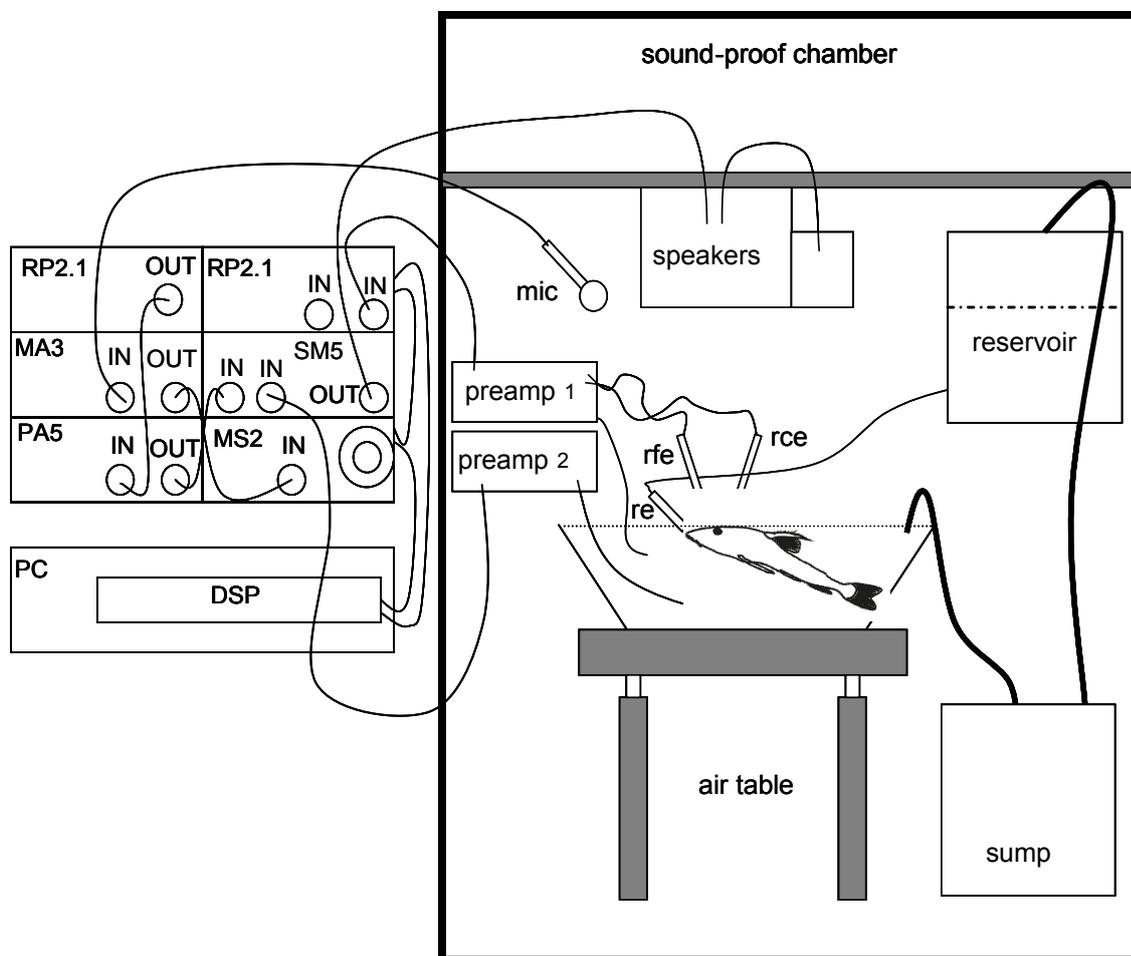


Fig. 1. Auditory evoked potential (AEP) recording and tone bursts presentation setup, modified after Kenyon et al. (1998). DSP, digital signal processing card; hyd: hydrophone; MA3, microphone amplifier; mic, microphone; MS2, monitor speaker; PA5, programmable attenuator; PC, personal computer; preamp, preamplifier; re, respiratory pipette; rce, recording electrode; rfe, reference electrode; RP 2.1, realtime processor.

Statistical Analysis

All morphological and physiological data were normally distributed (Kolmogorov-Smirnov-Test). For statistic analysis of the morphological data an One-way ANOVA was calculated to find out if rSBLs differ between the species. Differences between the hearing sensitivities of the six different species were calculated using a two-way ANOVA followed by a Bonferroni Post Hoc test. In order to find out if rSBL affects hearing sensitivities the mean thresholds of species having small rSBLs were compared to those having large rSBLs calculating another two-way ANOVA. Pearson's correlation coefficient was calculated for correlating the mean hearing thresholds to rSBL of each species.

All statistical tests run by using SPSS 19.0 (SPSS Inc., Chicago, USA).

Results

Swimbladder morphology

The swimbladders were free, the morphology of the examined species were classified as apple-shaped, cordiform and abbreviated cordiform (Fig. 2). *A. spinosissimus* and *P. hancockii* showed apple-shaped swimbladders without any lateral and caudal diverticulae (Fig. 3). *A. pectinifrons* possessed abbreviated heart-shaped swimbladders with small, simple formed diverticulae on the caudal end of the swimbladder. The swimbladders of *M. uranoscopus*, *O. niger* and *Hemidoras* sp. were cordiform. The swimbladders in *M. uranoscopus* and *Hemidoras* sp. had many long branched diverticula anteriorly, laterally and caudally. *M. uranoscopus* and *O. niger* possessed a small secondary swimbladder (Fig. 2, 3).

The rSBL varied between 0.129 in *Hemidoras* sp. and 0.201 in *A. spinosissimus*. They differed significantly between most of the species (One-way ANOVA; $F_{5,17} = 31.351$; $p < 0.001$) except for *A. spinosissimus* and *A. pectinifrons*, *A. pectinifrons* and *M. uranoscopus*, *Hemidoras* sp. and *O. niger* and *M. uranoscopus* and *P. hancockii*, and between *O. niger* and *P. hancockii*, *Hemidoras* sp. and *M. uranoscopus* (Tab. 2).

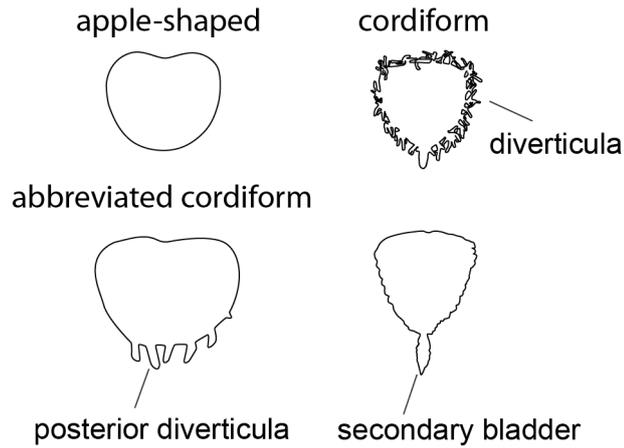


Fig. 2. Terminology of shapes and morphological features of swimbladders of species examined.

Tab. 2. Swimbladder forms, morphological measures of species and their swimbladders. rSBL, relative swimbladder length; SB, swimbladder; s.e.m., standard error of mean; sSBL, standardized swimbladder length; SL, standard length; TL, total length.

| Species | N | SB form | SL mean \pm s.e.m (mm) | TL mean \pm s.e.m (mm) | sSBL mean \pm s.e.m (mm) | rSBL mean \pm s.e.m |
|-------------------------|---|---|--------------------------|--------------------------|----------------------------|-----------------------|
| <i>A. spinosissimus</i> | 3 | apple-shaped | 83.02 \pm 15.57 | 95.45 \pm 16.38 | 16.64 \pm 2.89 | 0.201 \pm 0.003 |
| <i>P. hancockii</i> | 3 | apple-shaped | 64.83 \pm 5.26 | 54.2 \pm 7.2 | 10.36 \pm 1.05 | 0.158 \pm 0.005 |
| <i>A. pectinifrons</i> | 3 | abbreviated cordiform with diverticula | 58.15 \pm 0.62 | 68.70 \pm 1.17 | 11.48 \pm 0.28 | 0.197 \pm 0.003 |
| <i>M. uranoscopus</i> | 3 | cordiform with diverticulae and secondary bladder | 112.40 \pm 6.13 | 138.21 \pm 6.39 | 19.44 \pm 0.62 | 0.174 \pm 0.006 |
| <i>O. niger</i> | 3 | cordiform with secondary chamber | 119.06 \pm 7.10 | 136.38 \pm 7.99 | 17.96 \pm 1.64 | 0.150 \pm 0.006 |
| <i>Hemidoras sp.</i> | 3 | cordiform with diverticulae | 81.94 \pm 2.72 | 94.36 \pm 1.87 | 10.50 \pm 0.15 | 0.129 \pm 0.006 |

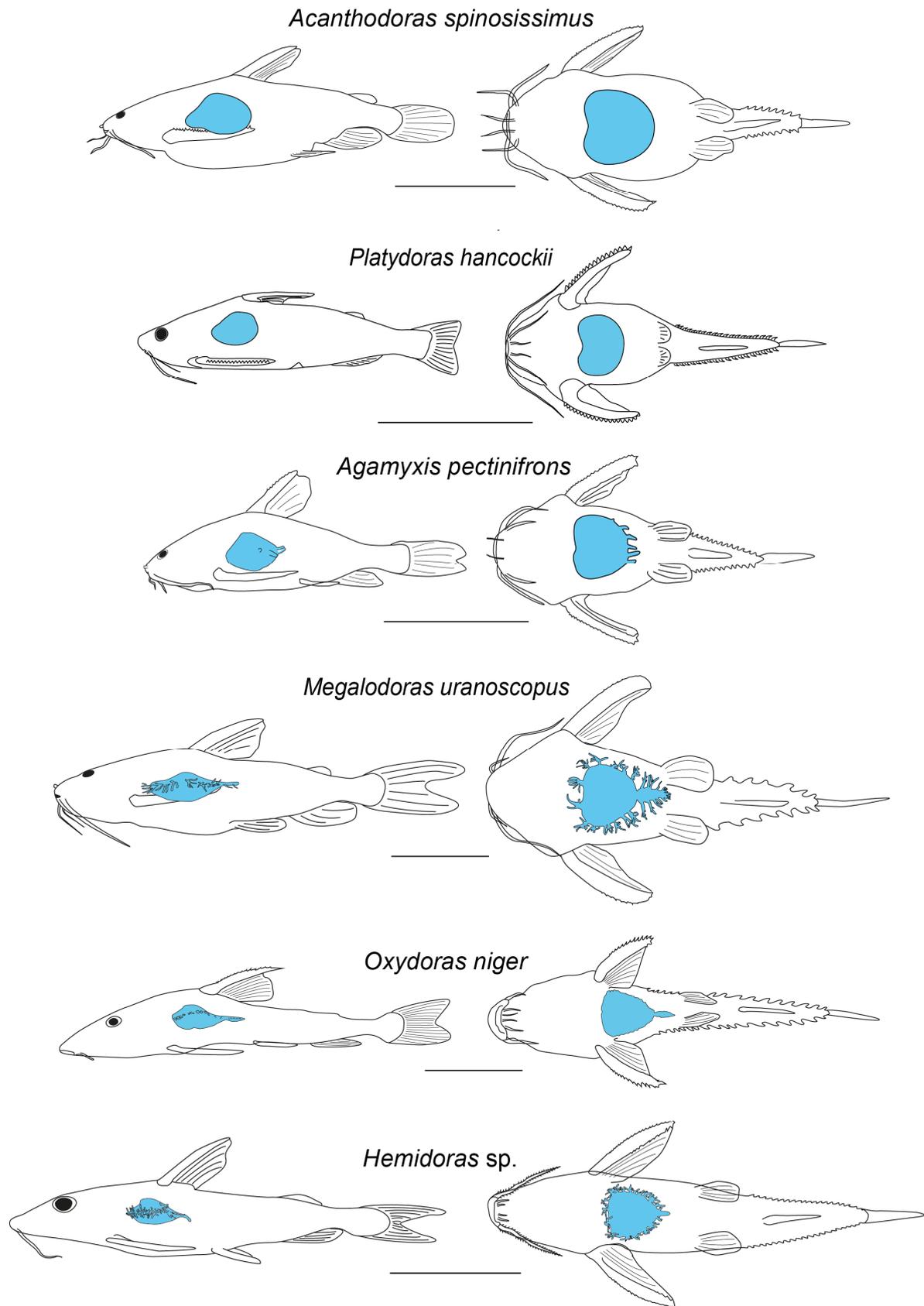


Fig. 3. Lateral (left) and ventral (right) view of the six thorny catfish species investigated. The swim-bladders are given in blue. Scale bar 3 cm.

Tab. 3. Mean difference in rSBLs between catfish species investigated. Asterisks indicate statistical significant differences as calculated by a Bonferroni Post-Hoc test. *A. s.*, *Acanthodoras spinosissimus*; *A. p.*, *Agamyxis pectinifrons*; *H. sp.*, *Hemidoras sp.*; *M. u.*, *Megalodoras uranoscopus*; *O. n.*, *Oxydoras niger*; *P. h.*, *Platydoras hancockii*.

| | <i>A. s.</i> | <i>A. p.</i> | <i>P. h.</i> | <i>H. sp.</i> | <i>M. u.</i> | <i>O. n.</i> |
|-------------------------|--------------|--------------|--------------|---------------|--------------|--------------|
| <i>A. spinosissimus</i> | - | 0.004 | 0.042 * | 0.073 * | 0.028 * | 0.051 * |
| <i>A. pectinifrons</i> | | - | 0.038 * | 0.069 * | 0.024 | 0.047 * |
| <i>P. hancockii</i> | | | - | 0.031 * | 0.014 | 0.009 |
| <i>Hemidoras sp.</i> | | | | - | 0.045 * | 0.022 |
| <i>M. uranoscopus</i> | | | | | - | 0.023 |
| <i>O. niger</i> | | | | | | - |

Hearing Sensitivity

All species detected tone bursts between 70 Hz and 6 kHz. Hearing curves were typically U-shaped with best hearing sensitivity located between 0.5 and 1 kHz except for *Hemidoras sp.* Hearing thresholds decreased by approximately 15-20 dB from 70 Hz to 0.5 - 1 kHz and increased at higher frequencies. In contrast, the hearing curve of *Hemidoras sp.* showed an almost constant increase in sensitivity up to 6 kHz. Interestingly, *Hemidoras sp.* revealed better hearing abilities at low and high frequencies than the other species and lower abilities in the mid-frequency range from 0.5 - 1 kHz. *O. niger* showed the best hearing sensitivity at 0.3 kHz and a decrease in sensitivity above 1 kHz. *A. pectinifrons* and *M. uranoscopus* showed best hearing sensitivity at 1 kHz. The lowest absolute thresholds were found in *P. hancockii* (59.6 dB re 1 μ Pa at 0.5 kHz) (Fig. 4, Tab. 4).

Hearing curves differed significantly between species (Two-way ANOVA: $F_{5, 320} = 50.913$, $p < 0.001$) and differences were furthermore frequency-dependent ($F_{45, 324} = 12.476$, $p < 0.001$) indicating that auditory sensitivities showed different trends at different frequencies (Tab. 4).

According to table 2 rSBL was smaller in *Hemiodoras* sp., *O. niger* and *P. hancockii* than in *A. spinosissimus*, *A. pectinifrons* and *M. uranoscopus*. Hearing thresholds were significantly higher in species with smaller swimbladders than in species with larger swimbladders (Two-way ANOVA: $F_{1,40} = 16.245$, $p < 0.001$). Differences between both groups were not frequency-dependent indicating a similar trend at all frequencies (Two-way ANOVA: $F_{1,40} = 0.854$, $p > 0.05$) (Fig. 5).

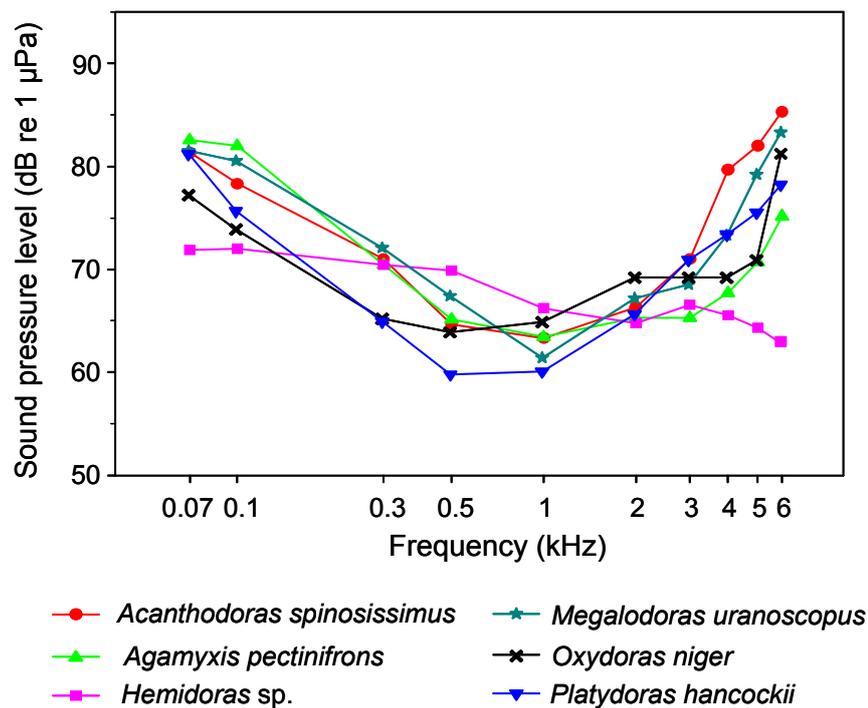


Fig. 4. Mean auditory sensitivities of the thorny catfish species investigated.

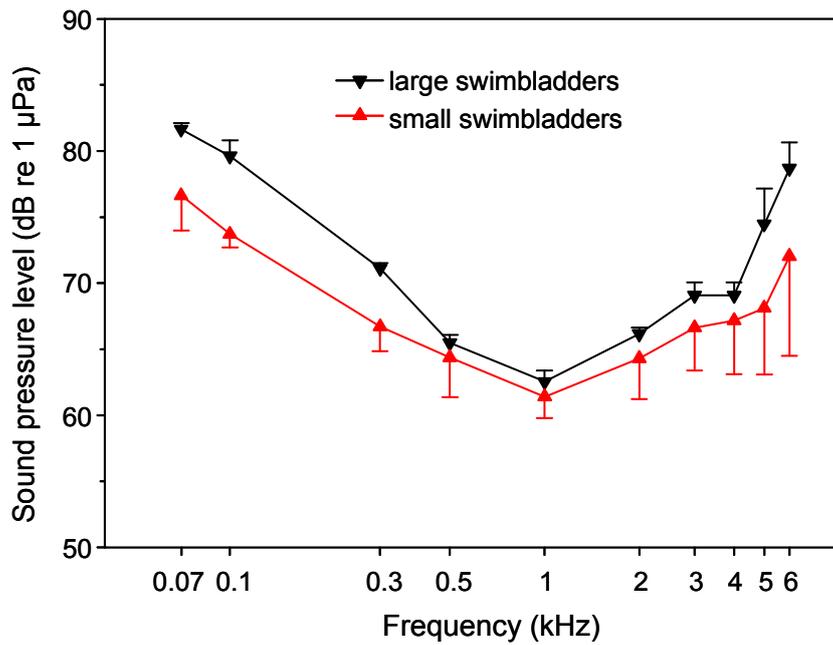


Fig. 5. Mean hearing thresholds of thorny catfish species with large and small swimbladders. Standard errors were only drawn in one direction to avoid overlap.

Tab. 4. Absolute differences between species in mean hearing thresholds (dB). Asterisks indicate statistically significant differences calculated by the two-way ANOVA and Bonferroni's post hoc tests. Abbreviations see table 3.

| | <i>A. s.</i> | <i>A. p.</i> | <i>P. h.</i> | <i>H. sp.</i> | <i>M. u.</i> | <i>O. n.</i> |
|-------------------------|--------------|--------------|--------------|---------------|--------------|--------------|
| <i>A. spinosissimus</i> | - | 3.07 | 3.99 * | 8.47 * | 2.26 | 4.48 * |
| <i>A. pectinifrons</i> | | - | 3.12 * | 6.38 * | 1.95 | 3.32 * |
| <i>P. hancockii</i> | | | - | 6.25 * | 3.35 * | 2.6 |
| <i>Hemidoras. sp.</i> | | | | - | 7.34 * | 5.46 * |
| <i>M. uranoscopus</i> | | | | | - | 4.21 * |
| <i>O. niger</i> | | | | | | - |

Tab. 5. Hearing threshold values (dB re 1 μ Pa) of species investigated. f, frequency; s.e.m. standard error of mean.

| f kHz | <i>A. spinosissimus</i> | <i>A. pectinifrons</i> | <i>A. hancockii</i> | <i>Hemidoras</i> sp. | <i>M. uranoscopus</i> | <i>O. niger</i> |
|----------|-------------------------|------------------------|---------------------|-------------------------|-----------------------|-------------------|
| | Mean \pm s.e.m. | Mean \pm s.e.m. | Mean \pm s.e.m. | Mean \pm s.e.m. | Mean \pm s.e.m. | Mean \pm s.e.m. |
| 0.07 | 81.33 \pm 0.33 | 82.57 \pm 0.81 | 81.00 \pm 1.45 | 71.89 \pm 1.21 | 81.33 \pm 0.78 | 77.00 \pm 0.00 |
| 0.1 | 78.33 \pm 0.33 | 82.00 \pm 0.58 | 75.43 \pm 0.90 | 72.00 \pm 1.29 | 80.33 \pm 1.87 | 73.67 \pm 0.33 |
| 0.3 | 71.00 \pm 2.52 | 70.43 \pm 0.78 | 64.71 \pm 1.11 | 70.44 \pm 0.75 | 71.89 \pm 0.72 | 65.00 \pm 1.53 |
| 0.5 | 64.67 \pm 1.33 | 65.14 \pm 1.28 | 59.57 \pm 0.78 | 69.89 \pm 0.61 | 67.22 \pm 1.12 | 63.67 \pm 1.33 |
| 1 | 63.33 \pm 0.67 | 63.43 \pm 0.87 | 59.86 \pm 0.88 | 66.22 \pm 1.02 | 61.22 \pm 0.63 | 64.67 \pm 2.73 |
| 2 | 66.33 \pm 1.67 | 65.29 \pm 0.68 | 65.43 \pm 1.63 | 64.78 \pm 0.85 | 67.00 \pm 0.33 | 69.00 \pm 1.53 |
| 3 | 71.00 \pm 1.00 | 67.71 \pm 1.19 | 70.71 \pm 1.41 | 66.56 \pm 0.69 | 68.33 \pm 0.71 | 69.00 \pm 1.00 |
| 4 | 79.67 \pm 1.76 | 70.71 \pm 0.18 | 73.14 \pm 1.98 | 65.56 \pm 0.84 | 73.11 \pm 0.99 | 69.00 \pm 1.53 |
| 5 | 82.00 \pm 2.65 | 75.14 \pm 0.55 | 75.29 \pm 1.32 | 64.33 \pm 0.82 | 79.00 \pm 0.94 | 70.67 \pm 2.60 |
| 6 | 85.33 \pm 1.87 | 80.86 \pm 0.94 | 78.00 \pm 1.22 | 62.78 \pm 1.00 | 83.11 \pm 0.70. | 81.00 \pm 1.53 |

Correlations between morphological structures and hearing sensitivities

The rSBL was positively correlated to the hearing thresholds at 70 and 100 Hz (Pearson's correlation: 70 Hz: $r = 0.87$, $p < 0.05$; 100 Hz: $r = 0.92$, $p < 0.05$) and at 4 and 5 kHz (Pearson's correlation: 4 kHz: $r = 0.82$, $p < 0.05$; 5 kHz: $r = 0.85$, $p < 0.05$).

Discussion

Swimbladder morphology in catfishes

Thorny catfish comprise 77 species out of 30 genera (Ferraris, 2007) and exhibit the largest variety of swimbladder modifications among catfishes (Birindelli et al., 2009). The morphology of the swimbladders described in the present study resemble mostly those described by Birindelli et al. (2009). The swimbladder of *Platydoras hancockii*, which was not described by the authors, is similar to that of *Platydoras bolivarensis*. The bladder was apple-shaped with completely smooth walls. Another apple-shaped bladder was found in *Acanthodoras spinosissimus*, which is comparable to the bladder of *Acanthodoras cataphractus*. The swimbladder of *M. uranoscopus* from the current study resembles the gasbladder of *M. uranoscopus* and *M. guayoensis*; the gasbladders are cordiform, have a secondary bladder and many well developed and often branched diverticula. Birindelli et al. (2009) showed that swimbladders from small specimen of *M. uranoscopus* possess anterior diverticula, while they are lacking in larger ones, while the size of the secondary chamber and the number of diverticula is increasing with growth. *Hemidoras* sp. revealed a cordiform swimbladder with many branched diverticula. Birindelli et al. (2009) mentioned that these diverticula became thinner and more branched in larger species of *Hemidoras*. In *A. pectinifrons* there were three to five small posterolateral diverticula, whereas in *Agamyxis albomaculatus* there was only a single posterolateral diverticulum on either side of the terminal diverticulum (Birindelli et al. 2009). Kaatz and Stewart (2012) described the swimbladder shape of 20 representatives of doradids. The swimbladder morphology were described similar to Birindelli et al. (2009), except that all extensions including secondary bladders were termed diverticula. In contrast to Birindelli et al. (2009), Kaatz and Stewart (2011) gave absolute swimbladder measures. Swimbladders varied from 0.4 to 4.5 cm in length, from 0.5 to 3.3 cm in width and from 0.2 to 2.0 cm in depth. The number and lengths of diverticula were species specific and varied from shorter diverticula less than a few mm in length (e.g. *A. pectinifrons*) to longer diverticula of about 1/3 of the swimbladder length (e.g. *O. niger*) (Kaatz & Stewart, 2012).

Recent studies on swimbladder morphology in other catfish families also revealed differences in gross morphology but these were smaller than in thorny catfishes (Marceniuk & Birindelli, 2010; Birindelli & Shibatta, 2011; Birindelli et al., 2012). Gasbladders in Auchenopteridae, which are closely related to Doradidae (Diogo et al., 2004; Sullivan et al., 2006), varied to a lesser extent than in doradids, but more than in other catfish families such as Pseu-

dopimelodidae and Ariidae (Marceniuk & Birindelli, 2010; Birindelli & Shibatta, 2011; Birindelli et al., 2012). Auchenipterids possessed either cordiform swimbladders with smooth walls (*Glanidium*, *Pseudauchenipterus*), or almost apple-shaped bladders (*Centromochlus* spp.) or gasbladders reduced in size and partially or completely ossified (*Ageneiosus inermis*). *Tocantinsia piresi* and *Asterophysus batrachus* had distinctive looking bladders with either two or many diverticula. Variations were also found within genera: *Trachycorystes menezesi* had a simple cordiform swimbladder, whereas *Trachycorystes trachycorystes* had a pair of lateral diverticula and a well developed terminal diverticulum. The bladder of the genus *Auchenipterichthys* was characterized by having a secondary bladder (Birindelli et al., 2012). Birindelli et al. (2012) discussed that variation in swimbladder morphology may be related to the elastic spring apparatus. The diversity of swimbladder shapes in ariids is moderate as compared to the high diversity in doradids. In ariids most species had a cordiform bladder with smooth external walls (*Bagre*), a few species have well-developed secondary bladders (*Sciades* spp.) and some species apple-shaped bladders (*Galeichthys ater*, *G. feliceps* and *G. peruvianus*) (Marceniuk & Birindelli, 2010). In contrast to the diversity in the swimbladder form in thorny catfishes swimbladders in pseudopimelodids varied only to a small extent. The gasbladder in pseudopimelodids is large and cordiform (*Cephalosilurus albomarginatus*, *Batrochoglanis*) or moderately sized apple-shaped (*Lophiosilurus alexandri*). Gasbladders either completely lack diverticula or possess rounded bulges or blister-like swellings (e. g. *Aspistor quadriscutis*). Representatives of the genera *Pseudopimelodus* and *Cruciglanis* had a diminutive swimbladder partially divided into two lateral sacs, where the parapophyses of the fourth vertebra partially covering the bladder anteroventrally (Birindelli & Shibatta, 2011). Due to the fact that thorny catfishes or siluriforms in general, inhabit different habitats and live under different environmental conditions, high variations are not surprising and were described in numerous anatomical studies (Bridge & Haddon, 1889, 1892, 1893; Chronilov, 1929; Alexander, 1964).

The relative size of swimbladders varied between different species of thorny catfishes. The largest rSBL was found in *A. spinosissimus* (0.201) and the smallest in *Hemidoras* sp. (0.129). Comparable data on relative swimbladder lengths are only found in Lechner & Ladich (2008) because Kaatz and Stewart (2012) did not calculate this ration. Lechner and Ladich (2008) found that the rSBL of free unpaired swimbladders which were ellipsoid or slightly heart-shaped, and rSBL varied from 0.084 in *Malapterurus beninensis* (family Malapteruridae) to 0.152 in *Synodontis schoutedeni* (family Mochokidae). In catfish species with tiny paired and encapsulated bladders the rSBL was much smaller and varied between 0.016

in *Hemiodontichthys acipenserinus* and 0.057 in *Ancistrus ranunculus* (family Loricariidae) (Lechner & Ladich, 2008). This comparison reveals that species possessing free unpaired swimbladders (Ariidae, Pseudopimelodidae, Malapteruridae, Heptapteridae, Mochokidae, Auchenipteridae and Doradidae) had relatively larger bladders than those having small, paired bladders (Loricariidae and Callichthyidae). Variation within doradids in rSBL (0.129 to 0.201) is much smaller than between families as described by Lechner and Ladich (2008). Siluriformes comprise the largest number of bottom-dwelling fishes, thus in the majority of species there is no need for the swimbladder to function in buoyancy or in respiration. But otophysines never completely lost their swimbladders due to its function as hearing and sometimes sound generating organ (Alexander, 1964).

Hearing sensitivity in catfishes

The hearing abilities of thorny catfishes differed significantly from each other, but showed similarities regarding their general characteristics in most of the species. The hearing curves were U-shaped with best sensitivities between 0.5 and 1 kHz. The lowest hearing threshold was measured in *P. hancockii* at 500 Hz (60 dB), while highest threshold was determined by *A. spinosissimus* with a mean of 85.33 dB. The hearing abilities of *Hemidoras* sp. differed from all other species because this species had lower thresholds at very low and very high frequencies and higher ones in the best hearing range as compared to the other species investigated. *Hemidoras* sp. was the only species which differed significantly from all other species. The largest difference was found between *Hemidoras* sp. and *A. spinosissimus* (mean overall difference: 8 dB). The differences between hearing thresholds of all species were frequency dependent, where high variations in thresholds at lower and higher frequencies.

The U-shaped hearing curve of *A. spinosissimus*, *A. pectinifrons*, *P. hancockii*, *M. uranoscopus* and *O. niger* resemble the audiogram gained previously gained in the Striped Raphael catfish *Platydoras armatulus* (formerly *P. costatus*) another representative of thorny catfishes (Ladich, 1999; Papes & Ladich, 2011) (Fig. 5). Surprisingly, the hearing threshold of *A. pectinifrons* was 10-30 dB higher in the previous (Ladich, 1999) than in the current study. Because the AEP protocols utilized in both studies were quite similar it is assumed that the fish's size might be responsible for this difference in sensitivity. The fish in the prior study were on average smaller (2.1-7.9 g) than in the present one (6.9 - 9.0 g). Thus, it is assumed that sensitivity improved during growth. Ladich (1999) demonstrated a significantly higher overall sensitivity (difference 18 dB) in *P. armatulus* than in *A. pectinifrons*. Com-

pared to the species tested in this study, the difference is more than twice of the difference for tested species in current study, where maximum mean difference of 8.47 dB was found.

Differences in hearing sensitivities were also found in other catfish families such callichthyids and loricariids. The mean difference between the two callichthyid species *Corydoras sodalis* and *Dianema urostriatum* was 7.5 dB (Ladich & Lechner, 2008) which is similar to the difference between *M. uranoscopus* and *Hemiodoras* sp. in current study. Somewhat higher differences were found within loricariids, where *Ancistrus ranunculus* and *Hemiodontichthys acipenserinus* differed by about 9 dB, *A. ranunculus* and *Hypoptopoma thoracatum* by about 12 dB. No significant difference was found among pimelodids (Ladich, 1999). Mean overall difference between *Pimelodus pictus* and *P. blochii* was about 1.6 dB.

When comparing different families with regard to differences in their hearing abilities, a general trend can be observed. Ladich (1999) found out that callichthyids had lower auditory sensitivities than pimelodids (*P. blochii* and *P. pictus*) and doradids (*P. armatulus*) whereas no difference was found between the latter two families. Lechner and Ladich (2008) observed that loricariids and callichthyids had lower sensitivities above 1 kHz than ariids, pseudopimelodids, malapterurids, heptapterids, mochokids and auchenipterids.

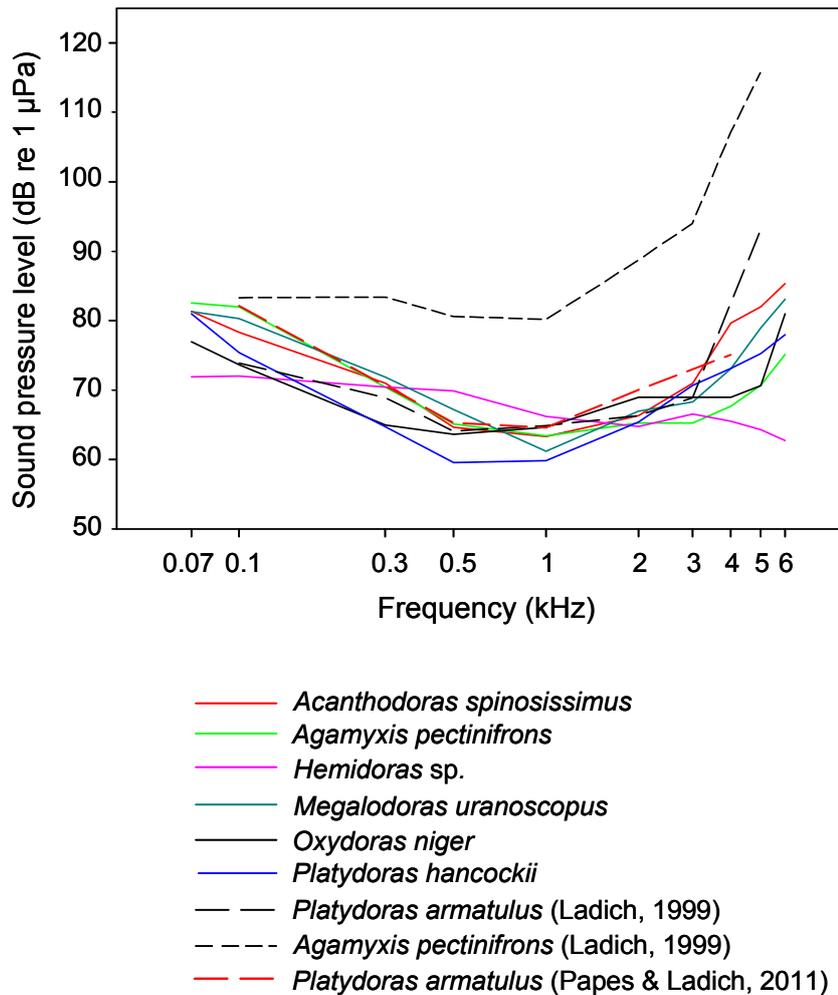


Fig. 6. Hearing sensitivities in thorny catfish species measured in the present and in prior studies (Ladich, 1999; Papes & Ladich, 2011).

Relationship between swimbladder morphology and hearing sensitivity

The aim of the present study was to investigate if the variation in swimbladder morphology affects hearing sensitivity in thorny catfishes. Regarding their rSBLs the doradids were divided into two groups: fish with relatively larger swimbladder (*A. spinosissimus*, *A. pectinifrons* and *M. uranoscopus*) and fish with relatively smaller swimbladder (*Hemidoras sp.*, *O. niger*, *P. hancockii*). Surprisingly, fish with smaller swimbladder had slightly better hearing abilities than fish with larger ones. This finding is in contrast to former studies. Lechner and Ladich (2008) described pronounced differences in rSBL in catfishes possessing large unpaired (mean rSBL of 0.121) and those having small paired swimbladders (mean rSBL of 0.037). These differences resulted in significantly better hearing abilities at frequencies above

1 kHz, with mean differences of about 5 dB at 1 kHz until up to more than 20 dB at 5 kHz (Lechner & Ladich, 2008). Due to the fact that differences in rSBLs between thorny catfishes having larger and smaller rSBLs was smaller (difference: 0.045) than between different catfish families, smaller differences in hearing sensitivities were expected. Nevertheless, a comparison of hearing sensitivities of the thorny catfish species with smaller rSBLs and larger rSPLs gave unexpected results. Doradids possessing relatively smaller swimbladders heard slightly better than fishes with larger ones. Obviously other factors besides swimbladder size affected hearing in thorny catfishes. Did swimbladder diverticula improve hearing sensitivities? This was obviously not the case. *P. hancockii*, a catfish with a simple apple-shaped swimbladder without any diverticula showed lowest auditory threshold at all, while species with a cordiform gasbladder and diverticula had poorer sensitivities. All swimbladders of thorny catfishes in this study were not covered by bones, thus enabling swimbladders to vibrate freely. The differences in hearing abilities could be explained by differences in accessory hearing structures (swimbladder, Weberian ossicles) or inner ear morphology or due to ontogenetic development (Chranilov, 1924; Lechner & Ladich, 2008; Lechner et al., 2010)

The effects of differences in the swimbladders size on hearing have not been studied in fishes except in catfishes. Typically, investigators concentrated on the distance between swimbladder including anterior extensions and the inner ear. Smaller distances positively affect the hearing sensitivities in squirrelfishes (Hococentridae) and to some degree in drums or croakers (Sciaenidae). The Hawaiian Squirrelfish *Myripristis kuntzei* showed lower auditory thresholds and detected a wider frequency range than *Adioryx xantherythrus* (Coombs & Popper, 1979; Hawkins, 1993). *M. kuntzei* possesses anterior swimbladder horns, which directly contact the ear, while the distance between the bladder and inner ear in *A. xantherythrus* is significant larger. However, the situation is more complicated in sciaenids. No clear differences in absolute hearing threshold were observed in sciaenid fishes. The weakfish (*Cynoscion regalis*) detects frequencies up to 2000 Hz while the spot (*Leiostomus xanthurus*) detects frequencies only up to 700 Hz. The hearing differences were explained by different swimbladder-inner ear configurations: In weakfish the swimbladder has a pair of anterior horns and terminates close to the ear while in the spot the bladder terminates at a greater distance from the ear (Ramcharitar et al., 2006a, b). Contrary, Horodysky et al. (2008) showed that among sciaenids *Menticirrhus saxatilis* which lacks swimbladders as adults is among the sciaenids which exhibit best hearing sensitivities below 600 Hz. They furthermore showed that thresholds of species with anterior extensions of their swimbladders (e.g. Atlantic

croaker, spotted seatrout) were not significantly lower than those of fishes lacking these projections (e.g. northern kingfish, red drum) (Horodysky et al., 2008).

The relationship between swimbladder extensions and hearing sensitivities were furthermore studied in the family Cichlidae. Schulz-Mirbach et al. (under revision), showed that cichlids with anterior swimbladder extensions have higher auditory sensitivities between 0.5 and 1 kHz than species lacking extensions. However, high frequency hearing in cichlids is not necessarily linked to the presence of anterior extensions. *Hemichromis guttatus*, which lacks anterior horns possesses similar auditory sensitivity as species in which the swimbladder directly contacts the inner ear.

Conclusion

The present investigation showed that thorny catfish with somewhat smaller swimbladders had slightly better hearing abilities than species with larger ones. Although this result is unexpected it points to the fact that the relationship between swimbladder morphology and auditory sensitivity is not always straightforward so that larger swimbladders and shorter distances between swimbladders and inner ear result in improved hearing. Horodysky et al. (2008) showed that among sciaenids swimbladder reduction and presence or absence of anterior extensions do not affect hearing sensitivity. Other factors such as the surrounding of the bladder (bony encapsulation) and thus its vibrations patterns, the fine structure of the swimbladder wall, morphological differences in the Weberian ossicles or in the inner ear morphology might influence hearing sensitivity in fishes in general and in thorny catfishes in particular.

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Zusammenfassung

Dornwelse weisen eine beeindruckende Variation ihrer Schwimmblasen-Morphologie auf: einfache apfelförmige bis herzförmige Schwimmblasen, mit einfachen glatten Wänden oder mit verzweigten Anhängen. Die Schwimmblase spielt bei Otophysen eine wichtige Rolle, da sie ihr Hörvermögen verbessert, besonders im höheren Frequenzbereich. Änderungen des Schalldrucks werden über die Weberschen Knöchelchen von der Schwimmblase ans Innenohr übertragen. Um eine Beziehung zwischen Form und Funktion heraus zu finden, wurde die Schwimmblasen-Morphologie und das Hörvermögen von sechs Dornwelsarten untersucht. Die Länge, Höhe und Breite der Schwimmblasen wurde gemessen um eine standardisierte Schwimmblasenlänge (sSBL) zu ermitteln. Die relative Schwimmblasenlänge (rSBL) wurde aus dem Quotient von sSBL und der Totallänge des Fisches errechnet. Das Hörvermögen wurde mittels der Ableitung von akustisch evozierten Potentialen (AEP) gemessen. Die AEP-Methode ist nicht invasiv, und leitet Potentiale ab, die in der Hörbahn von Tieren entstehen. Zwei Dornwelsarten hatten eine apfelförmige Schwimmblase und ein Art eine verkürzte herzförmige mit einfachen Anhängen am terminalen Rand. Die restlichen drei Arten hatten eine herzförmige Schwimmblase, zwei davon hatten zahlreiche, verzweigte Anhänge rund um die Schwimmblase. Die rSBL war signifikant unterschiedlich zwischen den meisten Arten. Alle Fische waren in der Lage Töne im Frequenzbereich von 70 Hz bis 6 kHz wahrzunehmen. Die niedrigste Hörschwelle wurde zwischen 0.5 und 1 kHz (60 dB re 1 μ Pa) gefunden. Die Hörkurven waren U-förmig mit Ausnahme von *Hemidoras* sp., wo sie gegen die höheren Frequenzen hin abfiel. Die mittlere Hörempfindlichkeit war bei den Dornwelsarten mit kleiner Schwimmblase etwas höher (maximal 8.5 dB) als bei von Arten mit großer Schwimmblase. Bei vier von zehn Frequenzen konnte ein positiver Zusammenhang zwischen rSBL und Hörschwelle nachgewiesen werden.

Das aktuelle Ergebnis zeigt einen Zusammenhang zwischen der Schwimmblasenform und ihrer Funktion. Relativ kleinere Schwimmblasen führen zu relativ einem relativ besseren Hörenvermögen. Die steht im Gegensatz zu einer früheren Studie, im Rahmen welcher gezeigt wurde, dass Welsarten mit großer, unpaarer Schwimmblase ein besseres Hörvermögen besitzen als Welse mit kleiner, verkapselter Schwimmblase.

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Curriculum vitae

| | | |
|----------------------------|---|--|
| Persönliche Daten | Name: | Angelika Zebedin |
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| | Adresse: | Linker Graben 6; 2384 Breitenfurt bei Wien |
| Schulbildung | 1987 - 1991 | Volksschule, Gundersheim |
| | 1991 - 1995 | Gymnasium, Lienz |
| | 1995 - 2002 | HLW, Lienz |
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| Beschäftigungsverhältnisse | 2002 – 2004 | Chef de Rang, Hotel Wulfenia, Kärnten |
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| | seit 2010 | Tutorin, Universität Wien |
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| | Mitglied im Vereinsvorstand „Austrian Biologist Association“ | |
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| | Mitglied im Heimausschuss im Tiroler Studentenwohnheim in Wien | |

Appendix

Morphometric data

| Art/Individuum | SL(mm) | TL(mm) | SB-Länge (mm) | SB-Breite (mm) | SB-Höhe (mm) | rSBL |
|-----------------------------------|--------|--------|------------------|-------------------|-----------------|-------------|
| <i>Acanthodoras spinosissimus</i> | | | | | | |
| <i>Acanthodoras</i> 1a | 74.5 | 86.73 | 16.99 | 19.01 | 9.86 | 0.205219985 |
| <i>Acanthodoras</i> 2a | 61.3 | 72.47 | 12.62 | 15.95 | 8.79 | 0.203021411 |
| <i>Acanthodoras</i> 3a | 113.2 | 127.15 | 23.65 | 26.64 | 16.27 | 0.195968161 |
| <i>Agamyxis pectinifrons</i> | | | | | | |
| <i>Agamyxis</i> 1a | 57.5 | 69.61 | 11.37 | 15.12 | 7.49 | 0.196848569 |
| <i>Agamyxis</i> 2a | 57.5 | 66.37 | 10.89 | 14.47 | 7.91 | 0.192730363 |
| <i>Agamyxis</i> 3a | 59.4 | 70.12 | 11.83 | 15.53 | 8.73 | 0.202578062 |
| <i>Amblyodoras hancockii</i> | | | | | | |
| <i>Amblyodoras</i> 1a | 54.4 | * | 8.46 | 10.71 | 5.73 | 0.152644919 |
| <i>Amblyodoras</i> 2a | 68.9 | * | 12.08 | 14.51 | 8.44 | 0.169431146 |
| <i>Amblyodoras</i> 3a | 71.2 | * | 11.14 | 15.34 | 6.89 | 0.156336379 |
| <i>Hassar sp.</i> | | | | | | |
| <i>Hassar</i> 1a | 87.3 | 97.6 | 13.87 | 10.75 | 6.04 | 0.117147405 |
| <i>Hassar</i> 2a | 80.3 | 94.36 | 14.48 | 10.70 | 6.94 | 0.133330566 |
| <i>Hassar</i> 3a | 78.3 | 91.11 | 15.08 | 10.38 | 6.27 | 0.135102139 |
| <i>Megalodoras uranoscopus</i> | | | | | | |
| <i>Megalodoras</i> 1a | 101.5 | 126.08 | 27.27 | 18.73 | 8.72 | 0.17973985 |
| <i>Megalodoras</i> 2a | 113.0 | 140.78 | 29.50 | 20.52 | 10.91 | 0.179706469 |
| <i>Megalodoras</i> 3a | 122.7 | 147.77 | 28.80 | 21.14 | 9.40 | 0.161215249 |
| <i>Oxydoras niger</i> | | | | | | |
| <i>Oxydoras</i> 1a | 105.0 | 120.53 | 15.54 | 14.46 | 7.36 | 0.11862577 |
| <i>Oxydoras</i> 2a | 127.7 | 142.49 | 18.50 | 17.55 | 10.56 | 0.12164631 |
| <i>Oxydoras</i> 3a | 124.5 | 146.13 | 19.93 | 20.14 | 10.81 | 0.136244768 |

* Caudalis beschädigt oder fehlt

Hearing thresholds

| Art/Individuum | Frequenz (kHz) | | | | | | | | | | | |
|-----------------------------------|----------------|------|-----|-----|-----|-----|----|----|----|----|----|----|
| | 0.05 | 0.07 | 0.1 | 0.3 | 0.5 | 0.8 | 1 | 2 | 3 | 4 | 5 | 6 |
| <i>Acanthodoras spinosissimus</i> | | | | | | | | | | | | |
| <i>Acanthodoras 1</i> | 81 | 81 | 78 | 68 | 66 | 65 | 62 | 63 | 70 | 77 | 83 | 83 |
| <i>Acanthodoras 2</i> | 81 | 82 | 79 | 69 | 62 | 62 | 64 | 68 | 70 | 79 | 77 | 84 |
| <i>Acanthodoras 3</i> | 80 | 81 | 78 | 76 | 66 | 63 | 64 | 68 | 73 | 83 | 86 | 89 |
| <i>Agamyxis pectinifrons</i> | | | | | | | | | | | | |
| <i>Agamyxis 1</i> | 81 | 82 | 83 | 72 | 66 | 66 | 64 | 66 | 69 | 71 | 74 | 82 |
| <i>Agamyxis 2</i> | 81 | 86 | 83 | 73 | 67 | 66 | 61 | 63 | 64 | 71 | 74 | 82 |
| <i>Agamyxis 4</i> | 81 | 80 | 79 | 69 | 71 | 66 | 64 | 64 | 69 | 71 | 74 | 76 |
| <i>Agamyxis 5</i> | 81 | 82 | 83 | 68 | 62 | 65 | 64 | 65 | 69 | 71 | 77 | 81 |
| <i>Agamyxis 6</i> | 85 | 85 | 82 | 71 | 66 | 66 | 67 | 68 | 68 | 70 | 76 | 84 |
| <i>Agamyxis 7</i> | 85 | 82 | 83 | 68 | 62 | 65 | 64 | 64 | 72 | 71 | 77 | 80 |
| <i>Agamyxis 8</i> | 85 | 81 | 81 | 72 | 62 | 63 | 60 | 67 | 63 | 70 | 74 | 81 |
| <i>Amblydoras hancokii</i> | | | | | | | | | | | | |
| <i>Amblydoras 1</i> | 85 | 83 | 71 | 65 | 64 | 60 | 64 | 64 | 73 | 76 | 78 | 81 |
| <i>Amblydoras 2</i> | 81 | 74 | 75 | 65 | 58 | 60 | 60 | 75 | 71 | 72 | 73 | 77 |
| <i>Amblydoras 3</i> | 84 | 83 | 76 | 62 | 59 | 62 | 60 | 64 | 76 | 76 | 75 | 78 |
| <i>Amblydoras 4</i> | 85 | 82 | 76 | 66 | 59 | 58 | 60 | 62 | 70 | 77 | 79 | 82 |
| <i>Amblydoras 5</i> | 85 | 79 | 76 | 70 | 60 | 62 | 60 | 64 | 72 | 76 | 78 | 78 |
| <i>Amblydoras 6</i> | 89 | 86 | 79 | 64 | 59 | 58 | 56 | 64 | 64 | 62 | 69 | 72 |
| <i>Amblydoras 7</i> | 80 | 80 | 75 | 61 | 58 | 61 | 59 | 65 | 69 | 73 | 75 | 78 |
| <i>Hassar sp.</i> | | | | | | | | | | | | |
| <i>Hassar 1</i> | 78 | 78 | 79 | 68 | 70 | 70 | 66 | 62 | 69 | 69 | 67 | 63 |
| <i>Hassar 2</i> | 70 | 70 | 66 | 69 | 69 | 69 | 62 | 64 | 66 | 62 | 64 | 59 |
| <i>Hassar 3</i> | 70 | 70 | 68 | 69 | 70 | 70 | 68 | 62 | 65 | 62 | 61 | 59 |
| <i>Hassar 4</i> | 70 | 70 | 71 | 68 | 66 | 65 | 64 | 63 | 63 | 65 | 64 | 64 |
| <i>Hassar 5</i> | 70 | 66 | 71 | 69 | 70 | 66 | 64 | 67 | 65 | 64 | 65 | 61 |
| <i>Hassar 6</i> | 70 | 70 | 72 | 73 | 71 | 70 | 68 | 69 | 69 | 67 | 63 | 66 |
| <i>Hassar 7</i> | 74 | 74 | 72 | 73 | 70 | 69 | 64 | 63 | 68 | 68 | 69 | 68 |
| <i>Hassar 8</i> | 74 | 74 | 73 | 72 | 70 | 65 | 68 | 67 | 66 | 67 | 62 | 62 |
| <i>Hassar 9</i> | 74 | 75 | 76 | 73 | 73 | 73 | 72 | 66 | 68 | 66 | 64 | 63 |
| <i>Megalodoras uranoscopus</i> | | | | | | | | | | | | |
| <i>Megalodoras 1</i> | 83 | 84 | 95 | 72 | 72 | 66 | 64 | 68 | 67 | 74 | 80 | 82 |
| <i>Megalodoras 2</i> | 82 | 81 | 78 | 69 | 67 | 64 | 62 | 68 | 68 | 70 | 77 | 84 |
| <i>Megalodoras 3</i> | 84 | 81 | 81 | 73 | 66 | 62 | 60 | 66 | 66 | 70 | 81 | 81 |
| <i>Megalodoras 4</i> | 84 | 81 | 78 | 73 | 66 | 62 | 62 | 66 | 70 | 69 | 80 | 83 |
| <i>Megalodoras 5</i> | 80 | 81 | 78 | 72 | 70 | 64 | 58 | 67 | 71 | 73 | 80 | 83 |
| <i>Megalodoras 6</i> | 84 | 82 | 79 | 73 | 71 | 69 | 59 | 68 | 72 | 78 | 82 | 85 |
| <i>Megalodoras 8</i> | 83 | 84 | 77 | 75 | 61 | 64 | 63 | 66 | 67 | 74 | 77 | 80 |
| <i>Megalodoras 9</i> | 79 | 76 | 78 | 72 | 66 | 61 | 60 | 66 | 67 | 74 | 73 | 83 |
| <i>Megalodoras 10</i> | 84 | 82 | 79 | 68 | 66 | 61 | 63 | 68 | 67 | 76 | 81 | 87 |
| <i>Oxydoras niger</i> | | | | | | | | | | | | |
| <i>Oxydoras 1</i> | 77 | 77 | 73 | 63 | 65 | 68 | 70 | 71 | 70 | 72 | 75 | 82 |
| <i>Oxydoras 2</i> | 80 | 77 | 74 | 64 | 65 | 62 | 63 | 70 | 70 | 68 | 71 | 83 |
| <i>Oxydoras 3</i> | 76 | 77 | 74 | 68 | 61 | 60 | 61 | 66 | 67 | 67 | 66 | 78 |