

# Functional Morphology of the Sonic Apparatus in *Ophidion barbatum* (Teleostei, Ophidiidae)

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**ABSTRACT** Most soniferous fishes producing sounds with their swimbladder utilize relatively simple mechanisms: contraction and relaxation of a unique pair of sonic muscles cause rapid movements of the swimbladder resulting in sound production. Here we describe the sonic mechanism for *Ophidion barbatum*, which includes three pairs of sonic muscles, highly transformed vertebral centra and ribs, a neural arch that pivots and a swimbladder whose anterior end is modified into a bony structure, the rocker bone. The ventral and intermediate muscles cause the rocker bone to swivel inward, compressing the swimbladder, and this action is antagonized by the dorsal muscle. Unlike other sonic systems in which the muscle contraction rate determines sound fundamental frequency, we hypothesize that slow contraction of these antagonistic muscles produces a series of cycles of swimbladder vibration. *J. Morphol.* 267:1461–1468, 2006. © 2006 Wiley-Liss, Inc.

**KEY WORDS:** sonic muscle; Ophidiiformes; rocker bone; swimbladder

In teleosts, the ability to emit sounds developed independently in phylogenetically distant taxa (Schneider, 1967; Ladich, 1997; Carlson and Bass, 2000). Two general types of sonic mechanisms occur commonly in fishes (Fine et al., 1977; Hawkins and Myrberg, 1983; Ladich and Fine, 2006; Parmentier and Diogo, 2006). The first is a stridulatory mechanism wherein sounds are emitted by rubbing bony parts of the body against each other (Ladich and Fine, 2006). In the second type of sonic mechanism, sound production results from contraction and relaxation of specialized sonic muscles that cause rapid movements of the swimbladder, resulting in vibrations of the swimbladder wall. However, teleost groups possessing these muscles have developed various mechanisms independently in phylogenetically unrelated taxa (Tavolga, 1967; Hawkins, 1993; Ladich, 2000). Sonic muscles may be intrinsic, i.e., completely attached to the swimbladder wall (Schneider, 1967; Demski et al., 1973), whereas extrinsic muscles have a distant origin and insert on the swimbladder or neighboring structures such as the ribs (Tavolga, 1971; Ladich and Fine, 2006).

Some Ophidiiformes present a highly specialized sound production mechanism. To the best of our

knowledge, these fish are unique in having more than one pair of sonic muscles (Courtenay, 1971; Howes, 1992; Parmentier et al., 2003a). The sonic muscles originate on the neurocranium and insert on the first ribs (which are connected to the swimbladder by ligaments) or directly on the swimbladder. Moreover, the anterior part of the tunica externa of some Ophidiiformes is thickened by sclerifications or ossifications existing in various forms: the outer wall can form a flap (Howes, 1992) or dorsal plates that merge with the ribs of the vertebral column (Parmentier et al., 2003a,b) or a “rocker bone” in some *Ophidion* (Ophidiidae) and *Onuxodon* (Carapidae) (Rose, 1961; Markle and Olney, 1990; Casadevall et al., 1996).

These structures appear to be modified for sound production. This assumption is reinforced by the sexual dimorphism in the sound-producing apparatus of different members of the Ophidiidae (Rose, 1961; Courtenay, 1971; Carter and Music, 1985) and Carapidae (Lagardère et al., 2005). These differences are found in the anterior vertebrae and ribs, the swimbladder configuration, and the associated muscles. Sounds have been recorded in a few Carapidae (Parmentier et al., 2003a,b; Lagardère et al., 2005) and in one species of Ophidiidae, *Ophidion marginatum* (Mann et al., 1997; Rountree and Bowers-Altman, 2002). Sounds of carapids are produced when two or more fish encounter each other inside an invertebrate host (Parmentier et al., 2003a, 2006; Lagardère et al., 2005), and sounds produced by *O. marginatum* have been recorded during courtship while cusk-eels are burrowed (Mann et al., 1997) or after emerging from the sand (Rountree and Bowers-Altman, 2002). In both case,

Contract grant sponsor: Fonds National de la Recherche Scientifique, Belgium; Contract grant number: 2.4574.01.

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Published online 13 November 2006 in  
Wiley InterScience (www.interscience.wiley.com)  
DOI: 10.1002/jmor.10496

these sounds may be an important means of communication because they are produced in shadow or in a completely dark environment.

In teleosts, swimbladder sounds have a fundamental frequency ranging from 75 to 300 Hz, which corresponds to the muscle contraction rate, placing sonic muscles among the fastest in vertebrates (Rome et al., 1996; Loesser et al., 1997; Connaughton et al., 2000; Fine et al., 2001). Young and Rome (2001) have shown that the sonic muscles of the swimbladder in *Opsanus tau* can generate power at 10 times the maximum frequency of white epaxial muscles. Additional studies on sonic muscles in *Cynoscion regalis* (Sciaenidae), *Prionotus scitulus* (Triglidae), *Arius felis* (Ariidae), *Bagre marinus* (Ariidae), and *Terapon jarbua* (Terapontidae) place them among the “champions” of contraction speed (Schneider, 1967; Tavolga, 1967; Sprague, 2000). However, Parmentier et al. (in press) recently discovered that some Carapidae fishes produce sound with slow sonic muscles that tetanize at about 10 Hz. This discovery implies that another kind of mechanism is required to produce sounds.

The aim of this study is to describe the highly specialized sonic mechanism in *Ophidion barbatum* and the role of the rocker bone. This fish lives in sand in the Eastern Atlantic Ocean and Mediterranean Sea at depths between 5 and 1500 m (Matalanas, 1980; Goren and Galil, 2002).

## MATERIALS AND METHODS

Fifty-two specimens of *O. barbatum* (TL: 126–242 mm,  $X = 173 \pm 22$  mm) were caught on the Costa Brava (Spain, 41°40'30" N, 2°47'53" E) on sandy ground at a depth varying from 90 to 120 m during October 1987, September 2004, and May 2005. Forty-eight fish were fixed in 7% formaldehyde or in 100% ethanol for dissection, and two were fixed in Bouin's solution for serial histological sections.

The general morphology of the sonic apparatus was examined with a Wild M10 (Leica) binocular microscope equipped with a camera lucida and a digital camera (Canon Power Shot S50).

Two *O. barbatum* specimens were dehydrated in butanol, decalcified, embedded in paraffin, and serially sectioned using a Reichert microtome (10- $\mu$ m thick). Three stains were used (Gabe, 1968): Romer's cartilage and bone distinctive stain, Gallego's ferric fushin stain for elastic fibers, and Masson's trichrome stain for collagen. Sections were observed using a polarizing Olympus microscope (Leica DM 100) coupled with a digital camera (Canon Power Shot S50). Fiber diameter in the ventral, intermediate and dorsal sonic muscles and epaxial muscles were measured. Fiber diameters were compared using analysis of variance followed by multiple range test.

A freshly obtained specimen was manipulated to assess the action of the various muscles, skeletal components, and the rocker bone on bladder movement.

## RESULTS

The sound-producing mechanism of *O. barbatum* is composed of three pairs of sonic muscles (ventral, intermediate, and dorsal), the swimbladder, the first four vertebrae, and the rocker bone (Figs. 1 and 2).

## Vertebral Modifications

The first neural arch (neural rocker) is specialized to pivot in the anterior–posterior plane (Fig. 1B): it is shaped like a horseshoe whose two branches articulate with the first vertebral body. The neural rocker has two large epipleural ribs modified into transverse plates (the wing-like process), which connect to the rocker bone by a ligament (Fig. 1D).

The third epineural ribs (Fig. 1A) are composed of a widespread wedge-shaped bony plate (swimbladder plate), which surrounds the rocker bone and connects to the anterior part of the swimbladder dorsolaterally. An osseous mace (Figs. 1C and 2C) on the medial face of each swimbladder plate presents an alveolar structure that firmly attaches to the swimbladder (Fig. 1C). Moreover, right and left maces delimit a longitudinal corridor filled by the rocker bone (Fig. 2C).

The fourth and fifth vertebrae possess two short lateroventral plates (Fig. 1A) that connect to form a triangular plate prolonging the swimbladder plate caudally.

## Rocker Bone

The rocker bone (see Fig. 2) is kidney-shaped, and its anterior end protrudes from the front of the swimbladder. Its anterior part curves, ending in a dorsal and ventral dome (Fig. 2A). Its posterior hilum (Fig. 2A) is narrower, and contains the insertion point for the tendon of the ventral muscle and the ligaments of the wing-like process (see Fig. 3). The right and left ligament form a virtual transverse axis around which the rocker bone pivots (Figs. 2B and 3).

## Swimbladder

The swimbladder (Fig. 4A) is a closed oblong tube situated dorsally in the abdominal cavity and firmly attached to the vertebral bodies by connective fibers. Sagittal and transverse sections of the posterior swimbladder indicate several layers of tissue (see Fig. 4). From the inside out, the swimbladder is composed of (1) an epithelial layer (mucosa), (2) a thick layer of elastic fibers (submucosa), and (3) a second epithelial layer (serosa). The submucosa is composed of two layers of fibers: internal ones traveling longitudinally and external circular fibers transverse to the fish axis.

The anterior part of the swimbladder presents different modifications.

- The submucosa is intimately connected to the rocker bone. It thickens medially, penetrates and ramifies into different branches in the rocker bone (Fig. 4B,C).
- The serosa completely surrounds the rocker bone and delimits a large gap in which the rocker bone

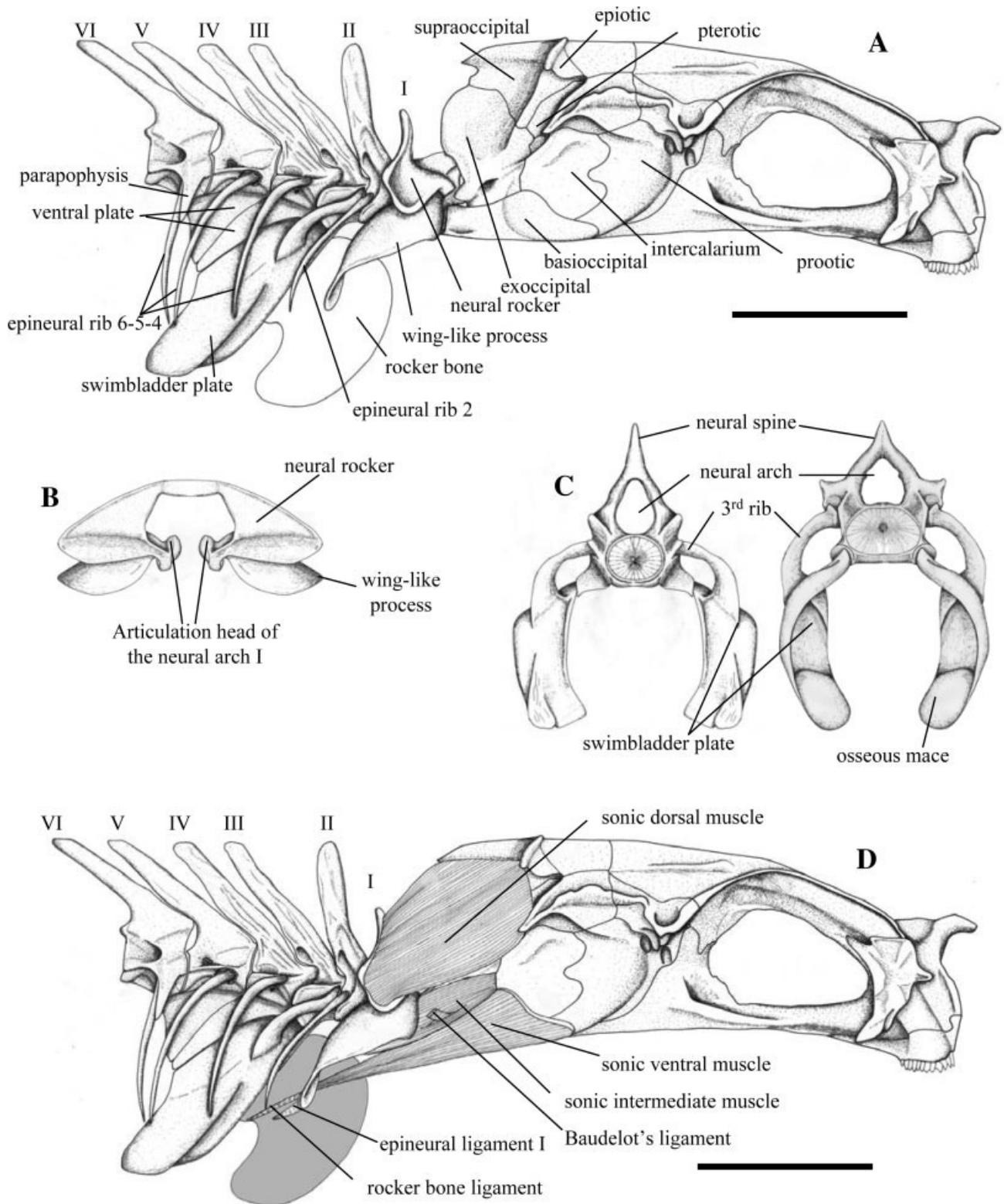


Fig. 1. Sound producing mechanism in *Ophidion barbatum*. Left lateral view of the skeleton (A), anterior view of the modified pivoting first neural arch (= neural rocker, (B), anterior (left) and posterior (right) view of the third vertebra and associated epineural ribs (C), left lateral view of the sonic muscles (D).

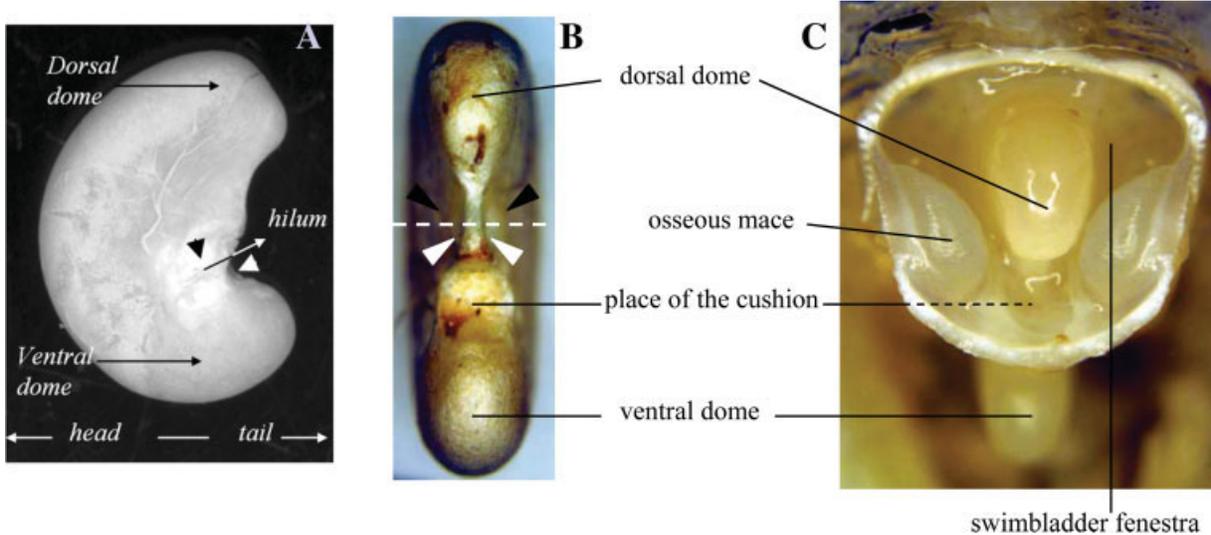


Fig. 2. Rocker bone of *O. barbatum* in right lateral (A) and posterior view (B). In C, the swimbladder was transversally sectioned behind the rocker bone to illustrate the swimbladder fenestra and the place devoted to the osseous masses of the third epineural ribs. Black arrow-head: insertion of the epineural ligament I; white arrow-head: insertion of the rocker bone ligament. In B, the white dotted line represents the virtual axis around which the rocker bone pivots.

is free to pivot. At the level of the hilum, the serosa thickens and forms a cushion of dense connective fibers (Fig. 4B,C).

- The submucosa does not cover the posterior part of the dorsal dome of the rocker bone: it inserts dorsally onto the triangular shape of the fifth vertebra and it enters ventrally into the rocker bone. As a result, the anterior swimbladder comprised only the thin serosa and the mucosa, forming a thin swimbladder fenestra, which allows movement of the rocker bone.
- A line of buckling occurs on the anteroventral part of the swimbladder (see Fig. 3). This line allows the inwards and outwards displacements of the ventral wall of the swimbladder.

### Sonic Muscles

Three pairs of sonic muscles are involved in the sound-producing system (Fig. 1D). The ventral sonic muscle originates on the base of the skull (basioccipital, the intercalarium, and the prootic) and ends in a tendon that inserts on the rocker bone (see Fig. 3). The intermediate sonic muscle originates on the exoccipital and inserts on the ventral face of the wing-like process. Baudelot's ligament, which connects the basioccipital to the pectoral girdle, penetrates the intermediate muscle. The dorsal sonic muscle originates in the neurocranium (exoccipital, supraoccipital, and epiotic) and inserts on the neural rocker of the first vertebra. Note that the dorsal muscle is considerably more massive than the ventral muscle (Fig. 1D).

The fiber diameters of all three sonic and the epaxial muscles are different ( $F_{3,749} = 802$ ;  $P < 0.001$ ) (see Fig. 5), but they can be divided into two categories. Ventral and dorsal sonic muscle fibers

are smaller ( $14.29 \pm 3.46 \mu\text{m}$ ,  $n = 374$  and  $29.9 \pm 11.13 \mu\text{m}$ ,  $n = 306$  respectively) than the intermediate and epaxial muscles ( $90.51 \pm 33.52 \mu\text{m}$ ,  $n = 29$  and  $81.36 \pm 22.31 \mu\text{m}$ ,  $n = 40$  respectively).

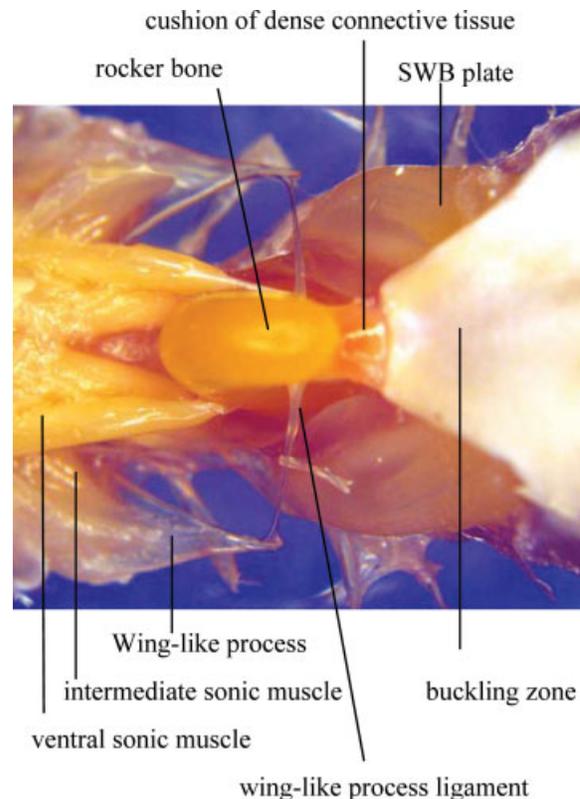


Fig. 3. Ventral view of the sound-producing apparatus.

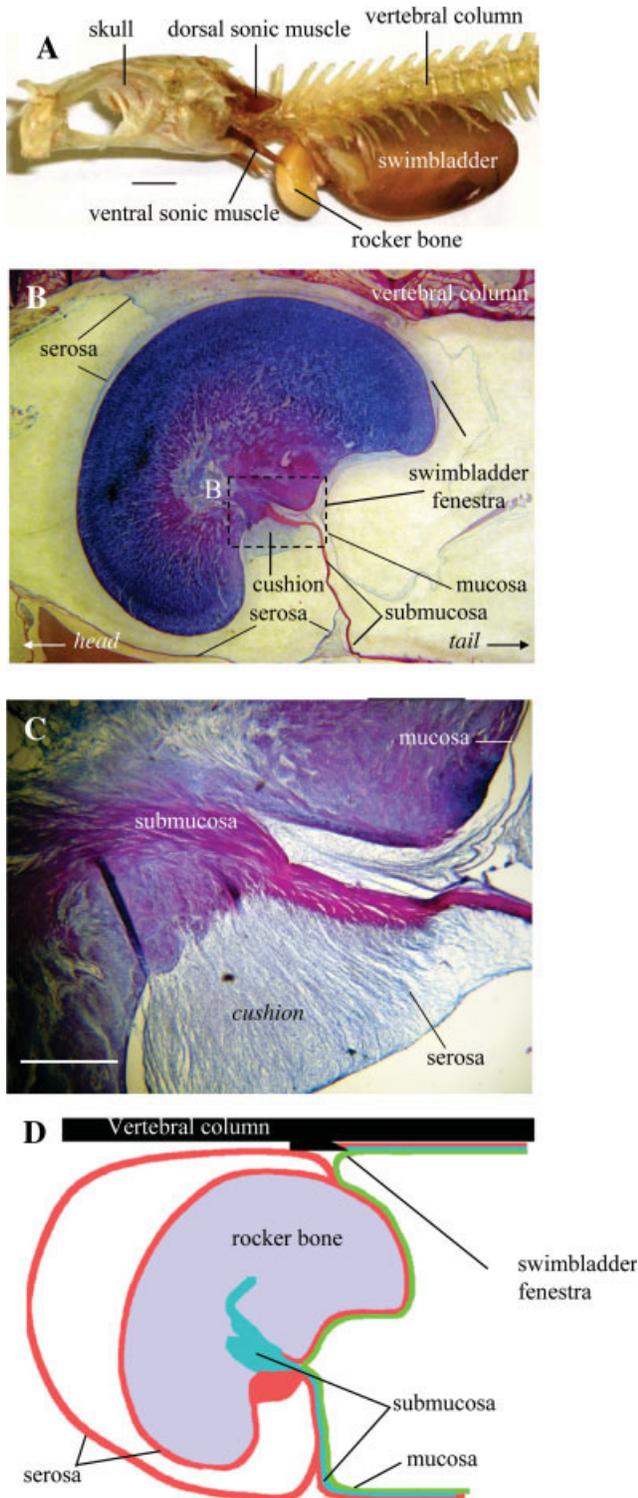


Fig. 4. Left lateral view of the skull and the sound-producing apparatus in *Ophidion barbatum* (A, scale bar = 5 mm). Sagittal section in the region of the rocker bone in *O. barbatum* (B) and enlarged view (C) of the junction between the rocker bone and the swimbladder showing that the rocker bone seems to be continuous with the submucosa. In D, panel B is schematized to show the position of the different tissues of the swimbladder. The swimbladder fenestra is made up of the mucosa and the serosa. The serosa delimits a large space in which the rocker is able to pivot.

## Functional Features

Sounds appear to be produced with antagonistic muscle pairs that exert opposite forces on the swimbladder utilizing the rocker, neural rocker, and wing-like process. 1) Manually pulling the ventral muscles causes the rocker bone to swivel counter clockwise (Fig. 6B1). The cushion of serosa and the ventral dome rotate caudally causing rapid compression of the swimbladder at the buckling zone. This process also stretches the swimbladder fenestra, which is anchored to the dorsal dome. 2) Pulling on the dorsal sonic muscles (Fig. 6B2) causes the first neural arch (neural rocker) to pivot rostrally around its articulations on the first vertebral body. This movement causes the tips of the wing-like process to rise, which rotates the rocker bone clockwise. As a result, the rocker bone pivots backwards, and the dorsal dome pushes the swimbladder fenestra into the swimbladder as the ventral dome of the rocker bone pulls forward causing the buckling zone to be displaced outside the swimbladder. At rest the buckling zone assumes a horizontal position. 3) The contraction of the intermediate muscles involves the forward and outward displacement of the wing-like processes, forming a rigid transverse axis by stretching the left and right epineural ligaments attached on the lateral faces of the rocker bone. The formation of the rigid axis allows a better rotation of the rocker bone.

## DISCUSSION

Extrinsic sonic muscles are found in phylogenetically distant taxa (Ladich and Fine, 2006; Parmentier and Diogo, 2006). Typically, one pair of muscles is involved in sound production, and the mechanism is relatively simple: contraction and relaxation of the sonic muscles cause rapid movements of the swimbladder, resulting in sound production. However, speed in fish sonic muscles is necessary because sound frequency is determined as a forced response to muscle contraction. As a result, the rate of sonic muscle contraction determines fundamental frequency in calls of long duration (Fine et al., 2001;

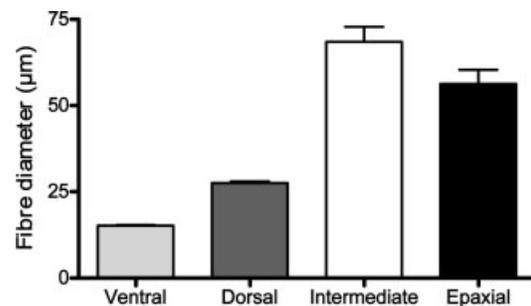


Fig. 5. Diameter of fibers of sonic and epaxial muscles in *O. barbatum*. Mean fiber diameter of all muscles are significantly different.

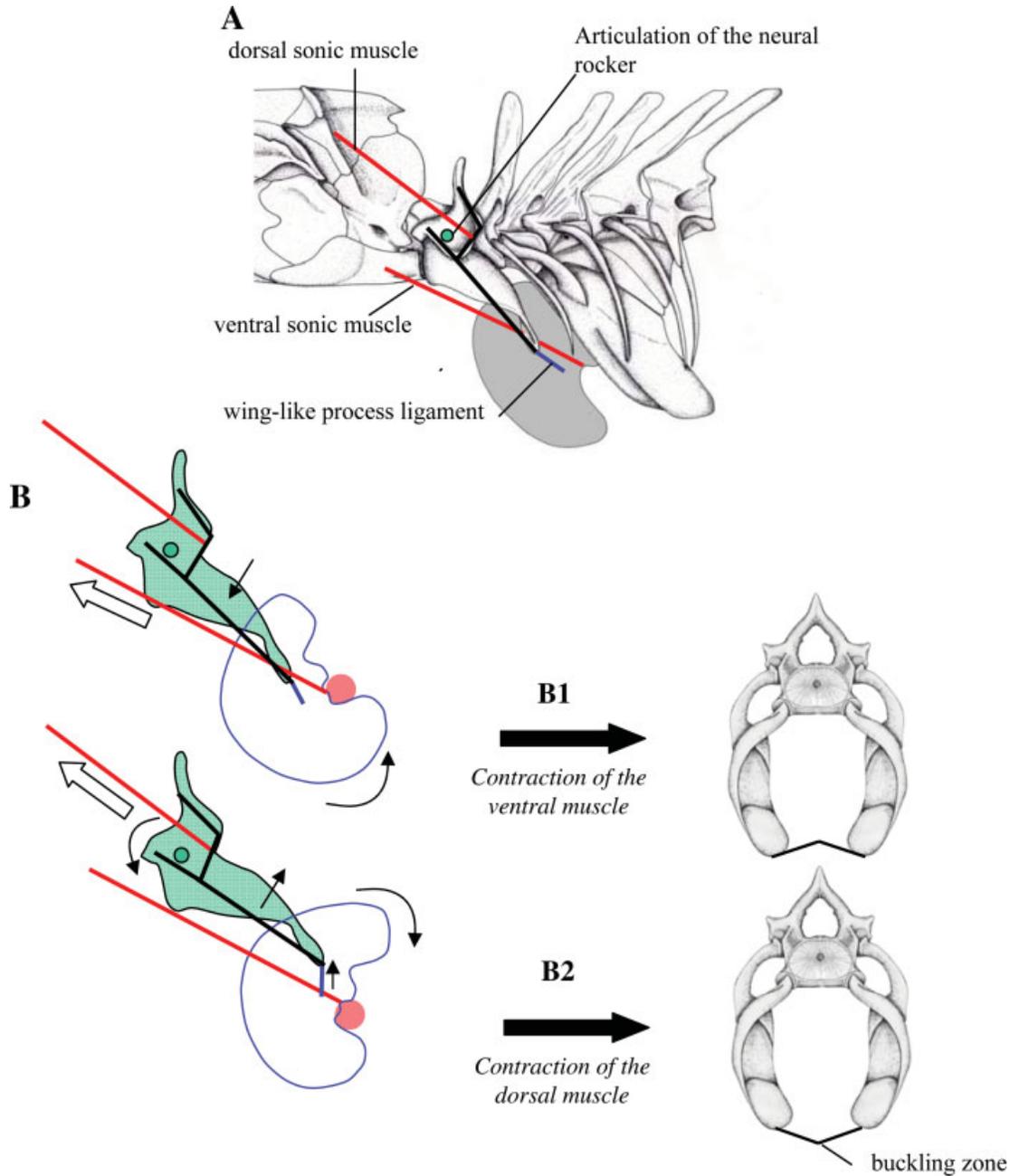


Fig. 6. Schematic of the sound-producing apparatus in *O. barbatum* (A). The main parts are used in panel B to illustrate the different movements of the rocker bone. The contraction of the ventral muscle (B1) originates the frontward rotation of the rocker bone and the internal buckling of the anterior part of the swimbladder. The contraction of the dorsal muscle (B2) originates the backward rotation of the rocker bone and the external buckling of the anterior part of the swimbladder.

Connaughton, 2004). In the oyster toadfish, for instance, a 250-Hz contraction rate generates a sound with a 250-Hz fundamental frequency, and slow bladder movements do not generate sound (Barimo and Fine, 1998; Fine et al., 2001). Similarly, in weakfish, which produce trains of individual pulses each caused by a single muscle twitch, the peak frequency of each pulse appears to be determined by the timing of contraction and relaxation

(Connaughton et al., 2000). In *O. barbatum*, the mechanism is more complicated. The contraction of two antagonistic muscles, the ventral and dorsal sonic muscles, causes respectively counter clockwise and then clockwise rotation of the rocker bone resulting in the inward and outward deformation of the swimbladder.

In Ophidiiformes, sounds have been recorded in different Carapidae species (Parmentier et al.,

2003a, 2006; Lagardère et al., 2005) and in one ophidiid, *O. marginatum* (Mann et al., 1997; Sprague and Luczkovich, 2001; Rountree et al., 2003). In carapids, manually pulling on the ventral sonic muscle in an anesthetized fish produces sounds with a peak frequency of 150 Hz (Parmentier et al., in press). Therefore, unlike other known sonic fishes, sounds can be produced by a slow muscle contraction, and the muscle contraction rate does not determine the fundamental frequency. In *O. marginatum*, sounds are composed of 1–27 pulses with a peak frequency of 1200 Hz, and muscle contraction at this frequency would be physiologically impossible. However, the pulse period is about 23 Hz. In this case, the muscular contraction does not correspond to the sound frequency but could be related to the pulse period. Cicada insects produce sound by rapid buckling of a pair of domed tymbals situated on the sides of the first abdominal segment (Pringle, 1954). During sound production, the posterior tymbal plate is pulled inwards by a large fast muscle, becoming concave (Simmons and Young, 1978). This rapid buckling movement and the resonant vibration of the tymbal plate produce a pulse of sound. This sound producing system acts as a mechanical resonator (Bennet-Clark, 1999). The tymbal also acts as a frequency multiplier, which converts the 117-Hz contraction frequency of each of the paired tymbal muscles into the 4.3 kHz frequency of the insect's song (Bennet-Clark, 1999; Bennet-Clark and Daws, 1999). As in cicadas, the buckling of the swimbladder in *O. marginatum* could be at the origin of the sounds whose frequency could be multiplied by the modified ribs (the swimbladder plate) and possibly swimbladder resonance. Movement of the rocker will transfer energy into the swimbladder and also stimulate the osseous maces on the swimbladder plate, whose vibrations could continue to stimulate the swimbladder after the muscles have returned to a resting state. If the former proves true, sound production would still be a force response to an external driver.

Fiber diameter in sonic muscle is typically smaller than in epaxial muscles (see Parmentier and Diogo, 2006). Smaller fibers have a higher surface–volume ratio, which increases the exchange surfaces and reduces the diffusion distances between the different cellular components during muscle contraction, thereby providing fatigue resistance during long calls (Pennypacker et al., 1985; Fine et al., 1990; Parmentier and Diogo, 2006). Many Ophidiiformes utilize different sonic muscles, which are more or less developed. A muscle analogous to the dorsal muscle of *Ophidion* species is not found in carapids, and the ventral muscle is responsible for sound production in the latter taxa (Parmentier et al., in press). In other Ophidiiformes, the ventral sonic muscle is directly connected to the swimbladder (Howes, 1992).

We hypothesize that the ventral sonic muscle contracts before the dorsal one for several reasons.

First, ventral sonic muscles occur in taxa without dorsal muscles (Parmentier et al. 2003a) and are thus likely to be capable of producing sound on their own. The ventral muscles have smaller fibers than the dorsal muscles, which suggests they are faster muscles likely to quickly impart energy to the bladder. Finally, the dorsal muscle is considerably larger than that of the ventral muscle and thus capable of greater force. Were the dorsal muscle to contract first, the ventral muscle would be unlikely to have sufficient force to reverse the direction of the rocker. For these reasons it is more parsimonious to assume that the ventral muscles contract first. The role of the intermediate muscle is not clear.

On the other hand, the diameter of intermediate sonic muscle fibers is larger than that in the dorsal and ventral muscles. Its point of insertion on the inner face of the wing-like process suggests its contraction compliments the ventral muscle, as in the case of *Ophidion holbrookii* (Rose, 1961) and the *Carapus* species (Parmentier et al., 2003a).

The sound-producing mechanism of *O. barbatum* exhibits highly specialized morphological adaptations. Three different pairs of muscles and the pivoting first neural spine (neural rocker) have evolved, and the swimbladder appears to secrete its own bone (the rocker), which is responsible for driving bladder movements. These modifications appear more or less developed in the Ophidiiform taxa (Bougis and Ruivo, 1954; Carter and Musick, 1985; Howes, 1992; Parmentier et al., 2002). Work on additional species will enable a better understanding of how the sound-producing apparatus evolved in this group.

## ACKNOWLEDGMENTS

The authors thank N. Decloux, and Dr P. Compère for their help in the microscopic study. We also thank M. Casadevall and M. R. Hernandez (University of Girona), and fishermen from the Blanes Harbor (Spain) for their help in collecting fishes.

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