Evolutionary Trends of Swimbladder Sound Mechanisms in Some Teleost Fishes

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ABSTRACT

Many teleosts are able to emit sounds with their swimbladder. This chapter reviews the various sonic mechanisms involving the swimbladder and the intrinsic and extrinsic muscles, comparing them from a morphological, biochemical, morphofunctional and physiological point of view. Close attention is paid to the Siluriformes and Ophidiiformes in which different cases of parallelism and/or convergence are examined.

Key Words: Fishes; Evolution; Ophidiiformes; Morphology; Siluriformes; Swimbladder sound mechanisms.

1. INTRODUCTION

In teleosts, the ability to emit sounds was developed independently in distant phylogenetic taxa. Currently, taxa of more than 50 families include species with this capacity (Hawkins, 1993). Although certain sounds are not produced intentionally (for example, while consuming food or swimming), the majority of sonic emissions are used for communication between individuals in various behavioural contexts such as aggressive behaviour (territorial defence,
agonistic activities), reproductive activities (partner identification and choice, courtship, discouraging male competitors, etc.) (Winn, 1964; Tavolga 1971; Demski et al., 1973; Hawkins, 1993; Chapters 5 and 6, this book).

Two general types of sonic mechanisms may be listed in fishes (Fine et al., 1977, Hawkins and Myrberg, 1983, Chapter 1, this book). The first is a stridulatory mechanism wherein sounds are emitted by rubbing bony parts of the body against each other. Members of the grunt family (Haemulidae) produce calls by grating pharyngeal teeth and in the triggerfish (Balistidae) the spines of the dorsal fin produce a grating sound when moved in their socket. Numerous catfishes (Siluriformes) produce a squeak when their enlarged pectoral spines are moved. Other fish clap the operculum of their pectoral girdle against it. The stridulatory sounds are non-harmonic with a wide range of frequencies, from less than 100 Hz to more than 8000 Hz (Tavolga, 1971).

In the second class, sound production results from rhythmical vibration of the swimbladder by deformation of its wall under the action of the so-called ‘drumming muscles’ (Demski et al., 1973; Loesser et al., 1997). Drumming muscles produce characteristic sounds recognisable by their harmonic structure because they have fundamental frequencies, generally from 50 to 300 Hz depending on the species in which they are found. However, teleost groups possessing these muscles developed various mechanisms (Marshall, 1962; Alexander, 1966; Tavolga, 1967; Popper and Coombs, 1980; Hawkins, 1993; Ladich, 2000; Ladich and Fine, this volume) independently in distant phylogenetic taxa (Schneider, 1967; Carlson and Bass, 2000). This chapter reviews the different kinds of mechanisms in order to show their diversity and concomitantly highlight various cases of parallel and convergent evolution.

2. SWIMBLADDER AND ASSOCIATED MUSCLES

2.1. Bladder Wall Tissues

The swimbladder can be defined as a hollow organ, a diverticulum of the digestive tract, which implies that it is made of the same tissues. Three membranes are usually described (e.g. Fange, 1953, 1966; Demski et al., 1973): 1) The *tunica externa* (covered by the peritoneum = serosa) consists of a sheet of highly extensible elastic fibers and short needles of ichtyocol, a form of collagen; 2) The middle layer or *submucosa* consists of a loose fibrous connective tissue; 3) The *tunica interna* consists of a very thin inner endodermic epithelium and a smooth muscle layer (*muscularis mucosa*) of longitudinally and circulatory bundles with some ordinary collagen.

2.2. Sound Production Mechanisms

The sonic emission by the swimbladder in teleost fishes has already been inventoried by many authors (e.g. Jones and Marshall, 1953; Alexander, 1966;
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Schneider, 1967; Tavolga, 1971; Hawkins and Myrberg, 1983; Hawkins, 1993). It can be divided into three mechanisms:

2.2.1. Resonance of the Swimbladder

In triggerfish (Balistes) or sea horses (Hippocampus), the swimbladder may act as a resonator and can amplify and change the quality of the sounds emitted by stridulation (Fish, 1953; Jones and Marshall, 1953; Demski et al., 1973; Myrberg et al., 1993). On the other hand, fish such as some eels or catfishes are able to emit sounds by eructing gas bubbles from the swimbladder via the pneumatic duct (Fish and Mowbray, 1970; Tavolga, 1971). These emissions could be simply functional since they empty the swimbladder gases. However, the spectral structure of the sounds does not change over the course of time, which ought to be the case were the swimbladder emptied. This implies that the eel must compensate for the gas losses during the emission of bubbles and thus the phenomenon is not simply passive.

2.2.2. Intrinsic Sonic Muscles

This term could be confusing since smooth muscles form part of the swimbladder tissues. The intrinsic muscles of the swimbladder wall are striated muscles, however. The sonic muscles are completely attached to the wall of the swimbladder, as for example in the Batrachoïdidae Opsanus sp. (Demski et al., 1973; Fine et al., 1990) or Porichthys notatus (Greene, 1924; Bass and Marchaterre, 1989), in the Triglidae Prionotus sp., Bellator sp. (Evans, 1973), Eutrigla sp. (Hawkins and Myrberg, 1983) and in representatives of families Dactylopteridae (e.g. Dactylopterus volitans) and Zeidae (e.g. Zeus faber) (Dufossé, 1874).

2.2.3. Extrinsic Sonic Muscles

Extrinsic sonic muscles show a high diversity in their origins and different insertion points (e.g. Tower, 1908; Jones and Marshall, 1953; Alexander, 1966; Demski et al., 1973). Generally speaking, these paired muscles are inserted on the swimbladder and on a neighbouring structure or are inserted between two bones, of which one is associated with the swimbladder via ligaments. Table 2.1 summarizes different types of sonic muscle insertions in various fish taxa, but it should be kept in mind that: 1) it clearly does not suffice to account for diversity by stating the various origins and insertion points of these muscles since the number of implied ribs and/or parapophyses for example, can vary according to the species (Hawkins, 1993); and (2) all the species of a given family do not necessarily present exactly the same configuration since for example, some species of a certain family may even lack extrinsic muscles.

Some fishes have more than one pair of sonic muscles. In some Ophidiiformes for example, a pair originates on the neurocranium and inserts on the dorsal part of the swimbladder, while a second (and in some cases,
Table 2.1: Examples of origins and insertions of sonic muscles in different teleost taxa

<table>
<thead>
<tr>
<th>Family</th>
<th>Muscle origin</th>
<th>Muscles insertion</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perciformes</td>
<td>Terapontidae</td>
<td>Supracleithrum</td>
<td>Anterior part of swimbladder</td>
</tr>
<tr>
<td></td>
<td>Sciaenidae</td>
<td>Occipital region</td>
<td>Anterior part of swimbladder</td>
</tr>
<tr>
<td></td>
<td>Serranidae</td>
<td>Lateral body musculature</td>
<td>Aponeuris attached dorsally to swimbladder</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gadiformes</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gadidae</td>
<td>Anterior ribs</td>
<td>Swimbladder</td>
</tr>
<tr>
<td>Ophidiiformes</td>
<td>Ophididae</td>
<td>Occipital region</td>
<td>Anterior part of swimbladder</td>
</tr>
<tr>
<td></td>
<td>Carapidae</td>
<td>Orbital region (frontal)</td>
<td>Anterior part of swimbladder</td>
</tr>
<tr>
<td></td>
<td>Brotulidae</td>
<td>Ventral part of occipital region</td>
<td>Anterior part of swimbladder</td>
</tr>
<tr>
<td>Beryciformes</td>
<td>Holocentridae</td>
<td>Occipital region</td>
<td>Ventral ribs</td>
</tr>
<tr>
<td>Siluriformes</td>
<td>Pimelodidae</td>
<td>Occipital region</td>
<td>Ventral surface of swimbladder</td>
</tr>
<tr>
<td></td>
<td>Heptapterinae</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pseudopimelodinae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
</tr>
<tr>
<td></td>
<td>Ariidae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
</tr>
<tr>
<td></td>
<td>Doradidae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
</tr>
</tbody>
</table>
Table 2.1: (Contd.)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Region of Neurocranium</th>
<th>Transverse Process of 4th Vertebra</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>TCranoglanididae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
<td>Diogo et al., 2002</td>
</tr>
<tr>
<td>Auchenipteridae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
<td>Bridge and Haddon, 1894; Diogo et al., 2003</td>
</tr>
<tr>
<td>Malapteruridae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
<td>Bridge and Haddon, 1894; Howes, 1985</td>
</tr>
<tr>
<td>Pangasiidae</td>
<td>Posterior region of neurocranium</td>
<td>Transverse process of 4th vertebra</td>
<td>Bridge and Haddon, 1894</td>
</tr>
</tbody>
</table>
a third) pair originates on the neurocranium and inserts on the first ribs, which are connected to the swimbladder by ligaments (Bougis and Ruivo, 1954; Rose, 1961, Howes, 1992; Parmentier et al., 2003a). In Carapus acus (Carapidae, Ophidiiformes), contraction of the sonic muscles inserted directly on the swimbladder is very likely associated with sonic emission, while that of the muscles inserted on the first ribs is probably related to variation of the sounds produced. This could function to maintain a single frequency range by offsetting pressure differentials at various depths, or may allow the existence of a larger sonic repertoire (Parmentier et al., 2003a). A similar mechanism was described by Courtenay (1971) in Rissola marginata (Ophidiidae, Ophidiiformes).

3. EXAMPLES OF EVOLUTION OF SOUND-PRODUCING STRUCTURES BY THE SWIMBLADDER

The sonic structures related to the swimbladder have seemingly been acquired independently several times within different taxa, unless in a rather unsound scenario, these structures were already present in a common ancestor and a series of secondary losses occurred inside different groups. More likely, the members of the various taxa in which these structures were acquired could have shared a certain common patrimony, in which case the probability for their development would be much greater in these fish groups than in other vertebrates. We shall now focus on the sound-producing structures of members of two representative teleost orders, the Ophidiiformes and the Siluriformes.

3.1. Sound Production by the Swimbladder in Ophidiiformes

In Carapus (Ophidiiformes), the swimbladder is shaped like a closed oblong tube characterised by a thinner zone of its forward wall (Fig. 2.1). Parmentier and colleagues (2003a) called this zone, the swimbladder fenestra. Cross-sections taken from the thicker part of the swimbladder show the presence of several layers of tissue. The swimbladder is composed from the inner to the outer part of (1) an endodermic tissue (= mucosa), (2) a thin fibrous layer made of collagen fibres (= muscularis mucosa), (3) a thick layer of elastic fibres (= submucosa) and (4) an epidermic tissue (= serosa). The swimbladder fenestra displayed by the swimbladder structure is composed, from the inner to the outer side, of (1) an endodermic tissue (mucosa), (2) a thicker muscularis mucosa and (3) the serosa attached to the bone. The swimbladder fenestra corresponds to the lack of submucosa (Fig. 2.1).

Traction made by the primary sonic muscles (i.e. pulling and releasing of the front of the swimbladder) might be responsible for the sound emissions of these three species by provoking the frontward movement of the forepart of the swimbladder and extending and ‘flapping’ the swimbladder fenestra.
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Fig. 2.1: Schematic, frontal view of the anterior part of the swimbladder and associated ligaments and muscles in the Carapidae (Ophidiiformes) species: A—Carapus boraborensis; B—Echiodon cryomargarites; C—Onuxodon fowleri.
On the other hand, the sonic muscles could progressively draw the swimbladder fenestra which emits sound when rapidly released in a spring-like manner (Parmentier et al., 2003b).

Moreover, carapids (Ophidiiformes) of the *Onuxodon* genus also show a so-called ‘rocker bone’ in front of the swimbladder (Courtenay and McKittrick, 1970; Tyler, 1970; Markle and Olney, 1990; Parmentier and Vandewalle, 2003). The primary sonic muscles insert on this ‘rocker bone’ in this genus but insert directly on the swimbladder in other Carapidae (Parmentier and Vandewalle 2003). The histological nature of this structure is not still known, however. In all carapids but *Onuxodon*, both the primary sonic muscles and the ligaments of the first epineural ribs (Fig. 2.1C) insert on the swimbladder tunica in front of the fenestra; in the genus *Onuxodon*, the same muscles and ligaments insert on the rocker bone in front of the swimbladder fenestra (Fig. 2.1A, B), while the anterior region seems to be absent (Parmentier et al., 2002). Moreover, in both cases the anterior region and the rocker bone are situated in front of the swimbladder fenestra. This hypothesis receives some support from observation of the anterior region in two species of the sister genus *Echiodon* (Williams, 1984; Markle and Olney, 1990): (1) region 1 has developed more hard and fibrous tissue on the outer part of the swimbladder in *Echiodon cryomargarites* (Fig. 2.1B), possibly as a response to the mechanical stress of the traction transmitted by the ligaments of the first and second epipleural ribs; (2) the confluence of the ligaments of the first epineural ribs on region 1 in *Echiodon rendhali* could be a first evolutionary step towards formation of a rocker bone and a ligamentary axis. By comparing the swimbladder in different Carapidae, it is hypothesised that this ‘rocker bone’ is homologous to the anterior part of the swimbladder as a response to the mechanical stress of the traction transmitted by the various ligaments and muscles inserted on it (Markle et al., 1983; Parmentier et al., 2002, 2003a, b).

A ‘rocker bone’ is also present in certain Ophidiidae however, such as *Ophidion* and *Brotula* (Rose, 1961; Stevovidov, 1961; Howes, 1992; Casadevall et al., 1996). But Markle and Olney (1990) do not consider the presence of a ‘rocker bone’ as constituting a synapomorphy of the order Ophidiiformes since there are at least six synapomorphies supporting a closer relationship between carapids with a ‘rocker bone’ and those lacking a ‘rocker bone’ than between the former and those ophidiids also presenting a ‘rocker bone’.

In Ophidiidae, comparison of various genera allowed postulating a hypothesis concerning formation of the ‘rocker bone’, which could somewhat parallel that realised in Carapidae.

According to Howes (1992), the anterodorsal surface of the swimbladder is sclerified in the ophidiid *Hypopleuron*. In the ophidiid *Cherublemma*, the anterior part of the swimbladder shows a mobile plate that results from ossification of the tunica externa. A ligament attached to the first pair of ribs inserts on this plate. The ophidiid genus *Ophidion* presents a ligament between the first pair of ribs and the rocker bone that is situated in front of the
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swimbladder. As the phylogeny of family Ophidiidae is still poorly known, it is imprudent to claim that the latter three genera could be sister groups. However, it is indeed interesting to note that in two families of the same order there are different intermediary stages leading to formation of a ‘rocker bone’. A comparative study based on the morphology and development of the sonic muscle, the swimbladder and the ‘rocker bone’ of both genera would surely be highly interesting in order to ascertain how this latter structure appeared homoplastically at least two times in the evolutionary history of order Ophidiiformes.

3.2. Sound Production by the Swimbladder in Siluriformes

Generally speaking, siluriforms, or catfishes, show three main types of sound-producing mechanisms by the swimbladder.

3.2.1. Elastic Spring Apparatus

The ‘elastic spring apparatus’ is formed by the modified, flexible transverse process of the fourth vertebra (Müllerian process), which is attached to the anterior surface of the swimbladder, and by a ‘protractor’ muscle (Bridge and Haddon, 1893, 1894; Sörensen, 1894; Chranilov, 1929; Schneider, 1961; Tavolga, 1962; Alexander, 1964, 1965; Chardon, 1968; Howes, 1983, 1985). It is commonly accepted however, that such an ‘elastic spring apparatus’ is a homoplastic feature (e.g. Chardon, 1968; de Pinna, 1998; Mo, 1998; Diogo, in press), which seems to have evolved at least 5 times within the order Siluriformes (Fig. 2.2: dark blue). ‘When this muscle contracts it pulls the anterior process of the parapophysis forwards (the elastic spring), enlarging the swimbladder; when it relaxes, it allows the spring to recoil; …, the swimbladder is thus caused to pulsate, emitting sound’ (Alexander, 1965). An ‘elastic spring apparatus’ is found in members of eight different extant catfish families, namely Doradidae, Auchenipteridae, Mochokidae, Malapteruridae, Ariidae, Cranoglanididae, some Pangasiidae, and the pimelodid subfamily Pseudopimelodinae (Fig. 2.2: dark blue). However, these fish show differences in the insertion of the Müllerian protractor muscle and in the shape, size and flexibility of the Müllerian process. The Müllerian protractor is always inserted on the Müllerian process. Its origin is usually on the neurocranium (see e.g. Arius and Platydoras in Fig. 2.3), but in catfishes such as mochokids it originates on the epaxial musculature near the dorsal fin (see e.g. Synodontis in Fig. 2.3).

In an excellent, unfortunately still unpublished Bachelor’s thesis on the morphology and evolution of the siluriform dorsal fin and related structures, Royero (1987) provided interesting evidence to support the ‘Müllerian protractor muscle’ as likely the result of differentiation of the supracarinalis anterior (sensu Winterbottom, 1974).

As noted by Royero (1987: 38–39), the common function of this muscle in catfishes, which usually runs from ‘the posterior margin of the neurocranium
Fig. 2.2: Strict-consensus cladogram of the phylogenetic relationships between the 87 genera representing the 32 extant siluriform families in Diogo’s (in press) cladistic analysis. Dark blue: presence of an ‘elastic spring apparatus’; Green: presence of a ‘protractor post-temporalis’ mechanism; Orange: presence of drumming muscles; Celestial blue: ambiguity (for more details, see text).
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Fig. 2.3: Lateral view of the swimbladder-vibrating mechanisms in fishes of four catfish families: A—*Platydoras*, Doradidae (elastic spring apparatus); B—*Synodontis*, Mochokidae (elastic spring apparatus); C—*Pimelodus*, Pimelodidae (drumming muscle mechanism); D—*Arius*, Ariidae (elastic spring apparatus). Modified from Fine and Ladich, 2003 (for more details, see text).

to the supraneural’ is ‘seemingly to maintain the rigidity and position of the dorsal fin’. Thus, as also noted by this author, the ‘Müllerian protactor’ muscle usually originates in a position similar to that of the supracarinalis anterior, with this latter muscle apparently absent in those groups presenting a well-developed ‘elastic spring apparatus’ and its respective ‘protractor’. However, the study of Royero (1987) did only include four of the eight extant groups possessing ‘elastic spring apparatus’, namely the Ariidae, Mochokidae, Doradidae and Auchenipteridae. Thus, as recognised by Royero, his observations do not necessarily apply to the other four catfish groups having members with an ‘elastic spring apparatus’, since the presence of this apparatus
in at least some of those groups clearly seems to be the result of homoplasy (see above).

For example, according to Royero (1987), the ‘Müllerian protractor muscle’ of the Malapteruridae described by other authors does not seem to be homologous with that of the Ariidae, Doradidae, Auchenipteridae and Mochokidae directly observed by him: contrary to these groups, in Malapterurus both this muscle and the supracarinalis anterior are well developed. In fact, it should be noted that even inside the clade Mochokidae + Doradidae + Auchenipteridae, the ‘Müllerian protractor muscle’ exhibits rather different configurations. For example, in Centromochlus the muscle is markedly subdivided into two well-distinguished divisions, while in Mochokus and Synodontis it does not originate as usual on the posterior surface of the cephalic region but instead, as mentioned above, on the region of the dorsal fin and its support.

3.2.2. Drumming Muscle

The ‘drumming muscle’ (see e.g. Pimelodus in Fig. 2.3) originates from the parapophyses of the fourth vertebra and, in some cases, also from the posterior surface of the neurocranium, to the ventro and ventrolateral surfaces of the swimbladder (e.g. Bridge and Haddon, 1894; Ladich and Fine, 1994; Ladich and Bass, 1998; Ladich, 2001; Fine and Ladich, 2003). Interestingly, the presence of a ‘drumming muscle’ seems to be usually associated with that of a ‘tensor tripodis’, a small muscle running from the posterior surface of the neurocranium to the dorsal surface of the swimbladder near the tripus (e.g. Ladich, 2001; Fine and Ladich, 2003). According to Ladich (2001), ‘because its small size and minute insertion point on the swimbladder’, the tensor tripodis ‘very unlikely serves in sound production’. According to Ladich and Bass (2003: 718), ‘contraction of this muscle during sound production would thus serve to either attenuate or eliminate tripus vibrations and thus sound conduction to the inner ear, analogous to the tympanal reflex in mammals’. Therefore, in order ‘to effectively work as a “tympanal reflex”, the tensor tripodis muscle would have to contract synchronously with drumming muscle contractions’ (Ladich and Bass, 2003: 718).

Catfishes having a ‘drumming muscle’ do not possess an ‘elastic spring apparatus’. They belong to the pimelodid subfamily Pimelodinae and, according to the review of Fine and Ladich (2003), also to some members of the Pimelodidae subfamily Heptapterinae such as some species of Rhamdia (according to the original taxonomic determination of Schachner and Schaller 1981). Figure 2.2 (orange) indicates the presence of a ‘drumming muscle’ while celestial blue indicates that this character is ambiguous in Rhamdia since it is present in some species but absent in others. This character is inapplicable in the peculiar genus Hypophthalmus and the ambiguity of the phylogenetic distribution of this character within Siluriformes is shown below).
Although the functional signification of the ‘drumming muscle’ is somewhat clear, the evolutionary history of its origin is far from obvious. Plesiomorphically catfishes lack a drumming muscle but it is present in the Pimelodinae examined by the authors, except for the peculiar genus *Hypophthalmus*. In fact, this character was coded as ‘inapplicable’ (Fig. 2.2: celestial blue) in this peculiar pimelodin genus since, contrary to most other Pimelodinae, its swimbladder is almost completely encapsulated by the well-developed parapophyses of the complex vertebra, which prevents a priori, the presence of a well-developed muscle attaching to this swimbladder.

However, as mentioned above, the ‘drumming muscle’ is apparently not restricted to Pimelodinae catfishes since it was also reported in some species of *Rhamdia* (Fig. 2.2: celestial blue), a genus of Pimelodidae subfamily Heptapterinae (e.g. Schachner and Schaller, 1981). Also, in this case, there seems to be a relation between the presence of drumming muscles and encapsulation of the swimbladder, since in *Rhamdia sapo*, with a markedly encapsulated swimbladder, these muscles are lacking (Ladich, 2001). But the situation is still more complex since, as also noted by Ladich (2001), even in some Heptapterinae with a free swimbladder, such as those of genus *Pimelodella*, a genus not examined by the authors, these muscles are absent.

Therefore, it is difficult to discern the evolutionary history of the ‘drumming muscle’ within Siluriformes (Fig. 2.2: ambiguity represented by celestial blue). They could perhaps have evolved in the node leading to Heptapterinae + Pimelodinae, thus supporting the sister-group relationship between these two Pimelodidae subfamilies. However, this would imply a series of secondary losses within each of those two subfamilies and not only in species with an encapsulated swimbladder, since as noted above, those muscles are lacking in some species with an essentially free swimbladder, e.g. those of genus *Pimelodella*. But the alternative hypothesis, that is an independent origin of those muscles in some Pimelodinae and some Heptapterinae catfishes appears still more unlikely. As explained above, it would seem rather surprising that such a peculiar and rare muscle as the ‘tensor tripodis’, a muscle present seemingly in all those catfishes having a ‘drumming muscle’ and virtually absent in all other sound-generating fishes, would develop independently in two so closely related catfish groups.

Interestingly the first of these two evolutionary scenarios, i.e. an origin of the ‘drumming muscle’ in the node leading to Heptapterinae + Pimelodinae, would perhaps have intriguing evolutionary implications. In fact, as explained above, Pseudopimelodinae (Pimelodidae) present an ‘elastic spring apparatus’. As these catfishes are probably the most plesiomorphic Pimelodidae, this would indicate that the origin of the ‘drumming muscle’ and/or ‘tensor tripodis’ would perhaps be phylogenetically apomorphic within family Pimelodidae, in relation to the presence of an ‘elastic spring apparatus’ (Fig. 2.2).
3.2.3. *Protractor Post-temporalis Mechanism*

Another interesting configuration is that found in Bagridae (Fig. 2.2: green). These catfishes exhibit a peculiar, seemingly autapomorphic, muscle protractor post-temporalis (first described by Mo, 1991 under the name ‘retractor post-temporalis’, which was subsequently modified by Diogo et al., 1999) running from the neurocranium to the anterior margin of the post-temporo-supracleithrum (see Fig. 2.4). The latter bone is in direct association with the anterior process of the 4th parapophyse, which is closely related to the swimbladder wall. Based on anatomical evidence and artificial manipulation, it seems plausible that the presence of a protactor post-temporalis is effectively related to the production of sound by the swimbladder (Diogo et al., 1999). So, contraction of this muscle would protract the post-temporo-supracleithrum and thus the anterior process of the 4th vertebra to which this bone is associated posteriorly (Fig. 2.4). Relaxation of the protactor post-temporalis and resiliency of the complex formed by the swimbladder, the anterior process of the 4th vertebra and the post-temporo-supracleithrum would thus provoke a rapid and strong posterior movement of this latter bone and consequently, of the anterior process of the 4th vertebra, against the fore end of the swimbladder (Fig. 2.4). The swimbladder and anterior process of the 4th vertebra would thus probably work in a mechanism somewhat similar to that found in those catfish groups with an ‘elastic spring apparatus’.

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**Fig. 2.4**: Schematic, lateral view of the protactor post-temporalis mechanism in the siluriform family Bagridae. Contraction of the muscle protactor post-temporalis protracts the posttemporo-supracleithrum and the anterior process of the 4th vertebra associated with it; subsequent relaxation of the muscle thus provokes a rapid and strong posterior movement of this anterior process of the 4th vertebra against the swim-bladder.
4. FINE STRUCTURAL AND PHYSIOLOGICAL CONSIDERATIONS OF THE TELEOST SONIC MUSCLES

Although belonging to distantly phylogenetic groups, the sonic muscles, either extrinsic or intrinsic, possess in common a whole set of features. We compare these characters here in order to ascertain whether distant phyletic fish show the same pattern of organisation. We have tried to determine whether analysis of the fine structure and physiology give some indication on the multiple origin of sonic muscles in fishes.

In two Batrachoidiformes toadfish (Opsanus tau and Porichthys notatus), the muscular contraction speed determines the fundamental frequency of sounds (Skoglund, 1961; Fine et al., 2001). With a fundamental frequency from 100 to 300 Hz, a contraction time between 3 and 8 ms, a relaxation time of 8 ms (Skoglund, 1959, 1961; Feher et al., 1998), and a resistance to tetanus until frequencies higher than 500, sonic muscles of Opsanus tau are among the fastest muscles known in vertebrates (Rome et al., 1996; Loesser et al., 1997; Fine et al., 2001). In Holocentrus rufus (Beryciformes), contraction and relaxation times for sonic muscles are 5 ms and 12 ms respectively, with a contraction time of 12 ms and a relaxation time of 25 ms for non-sonic muscles (Gainer and Klancher, 1965). Fast-contracting (white) muscles and low-contracting (red) muscles of vertebrates have a contraction speed of 20 ms and 50–80 ms respectively (Hamoir et al., 1980), and most of them will produce a tetanus at frequencies inferior to 50 Hz (Tavolga, 1971). In experimental conditions, Young and Rome (2001) showed that the sonic muscles of the swimbladder in Opsanus tau can generate power at 10 times the maximum frequency at which the white epaxial muscles do. Although less documented, studies done on the sonic muscles in Cynoscion regalis (Sciaenidae, Perciformes), Prionotus scitulus (Triglidae, Scorpaeniformes), Arius felis (Ariidae, Siluriformes), Bagre marinus (Ariidae, Siluriformes), and Terapon jarbua (Terapontidae, Perciformes) permit placing them among the ‘champions’ of contraction speed (Schneider, 1967; Tavolga, 1967 Sprague, 2000). These exceptional contraction speeds result from numerous morphological and biochemical adaptations as well as from the presence of important concentrations in intracellular metabolites.

4.1. Morphological Adaptations

Sonic muscles seem to be constructed to increase the exchange surfaces and to reduce the diffusion distances between the different parts intervening in muscular contraction. According to Rome and Lindstedt (1998), the enormous speed of the swimbladder muscles is due in part to their extremely fast relaxation rate, which in turn is due to three specific adaptations: the swimbladder muscles remove Ca$^{2+}$ from the cytoplasm 50-fold faster than the red muscles, troponin of the swimbladder muscles has a far faster Ca$^{2+}$
off-rate than that of red muscles, and crossbridges of the swimbladder muscles have a 50-fold faster constant detachment rate than red muscles.

Fibres of the fast-twitch sonic muscles are characterised by a smaller diameter than white fibres of the epaxial musculature (Table 2.2). Their sarcoplasmic reticulum is also more developed (Hamoir et al., 1980; Hamoir and Focant, 1981; Feher et al., 1998) than that of white fibres (Eichelberg, 1976). Moreover, in fishes belonging to different families such as *Opsanus tau*, *Cynoscion regalis*, *Porichthys notatus* and *Platydoras costatus*, the sonic fibres have a central core of sarcoplasm surrounded by a radially arranged contractile cylinder consisting of alternating ribbons of sarcoplasmic reticulum and myofibrils (Eichelberg, 1976; Ono and Poss, 1982; Fine and Pennypacker, 1988; Bass and Marchaterre, 1989; Appelt et al., 1991; Brantley et al., 1993; Fine et al., 1993; Connaughton et al., 1997; Loesser et al., 1997; Ladich, 2001). These characters give a higher surface-volume ratio that seemingly facilitates fast

<table>
<thead>
<tr>
<th>Species</th>
<th>White fibres (µm)</th>
<th>Sonic fibres (µm)</th>
<th>References</th>
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<tr>
<td>Zeiformes</td>
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<td>30–32</td>
<td>11–13</td>
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<td><em>Opsanus tau</em></td>
<td>100–200</td>
<td>24</td>
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<tr>
<td></td>
<td>180</td>
<td>20</td>
<td>Fine et al., 1993</td>
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<td></td>
<td>11.5–29.1</td>
<td></td>
<td>Fine et al., 1990</td>
</tr>
<tr>
<td><em>Allenbatrachus grunniens</em></td>
<td>40</td>
<td>13</td>
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<td>131.7</td>
<td>29.6</td>
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<td></td>
<td>109.7</td>
<td>23.1-39.3</td>
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<td>50</td>
<td>17-20</td>
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<td>50</td>
<td>&lt; 27</td>
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<td>16</td>
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<td><em>Trigla hirundo corax</em></td>
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<td><em>Carpus acus</em></td>
<td>89</td>
<td>37</td>
<td>Parmentier et al., 2003b</td>
</tr>
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</table>
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flow of metabolites (glucose, lactic acid), oxygen, and calcium (Eichelberg, 1976; Fine et al., 1990; Feher et al., 1998). A central core is not present in all drumming muscles, however: it is lacking in *Carapus acus* and *Pimelodus pictus* (Ladich, 2001; Parmentier et al., 2003b). According to Fine and Ladich (2003), a greater myofibrillar volume could be required to provide sufficient force to deform a large portion of the swimbladder, as is the case in *Carapus acus* and *Pimelodus pictus*.

The position, number and size of the T system/SR (1 T tubule + 2 sarcoplasmic cisternae) would also limit the diffusion distance. The T system/SR of the white fibres is usually found at the Z-line level (Akster, 1981). In the sonic muscles of *Opsanus tau* (Batrachoidiformes) and *Terapon jarbua* (Perciformes), these are at the level of the A/I junctions (Eichelberg, 1976; Loesser et al., 1997), whereas they are at the level of both the Z-line and A/I junctions in the primary sound-producing muscles of *Carapus acus* (Ophidiiformes) (Parmentier et al., 2003b; Fig. 2.5). This T system/SR disposition would also be a factor limiting the diffusion time because the Ca²⁺ are nearer the contraction site.

### 4.2. Physiological Adaptations

#### 4.1.1. White Muscles, Red Muscles

Two kinds of fibres are generally described in fish muscles: red and white. However, there are actually 4 to 7 types in them (Johnston et al., 1974; Patterson et al., 1975; Korneliussen et al., 1978; Hamoir and focant, 1981; Meyer-Rochow et al., 1994, Devincenti et al., 2000). The fast-twitch white fibres do not usually contract for a long period of time, while the slow-twitch red fibres can usually sustain work during long periods (Akster and Osse, 1978; Johnston, 1981; te Kronnie, 1983). This dichotomy in properties is due to morphological and biochemical features that are used to evaluate, by comparison, the properties of sonic muscles. Unfortunately, few species have been studied from this point of view.

The importance of ATPase activity of the myosin and stability of these enzymes to different pHs correlated directly to the contraction speed of the muscular fibres (Johnston et al., 1975; Akster and Osse, 1978). White fibres (anaerobic metabolism) possess a high ATPase activity because alkali stable and acid labile, whereas slow red fibres (aerobic metabolism) have an activity 3 to 4 times lower than white fibres because alkali labile and acid stable (Mosse and Hudson, 1977; te Kronnie et al., 1983; Zawadowska and Kilarski, 1984; Devincenti et al., 2000).

The capacities of fatigue strength of muscle fibres can be evaluated by the presence and concentration of oxidative enzymes (e.g. succinic dehydrogenase), metabolites of aerobic metabolism (lipids, glycogen) and activity of glycolytic enzymes such as lactate dehydrogenase in anaerobic
metabolism. The abundance of mitochondria is also important because of their oxidative enzymes. Oxidative activity is high in red fibres and low in white fibres (Akster and Osse, 1978; Akster, 1983).

Sonic muscles are characterised by unusual contractile properties: their fibres show characters of both red and white fibres. In phylogenetically distant fishes possessing intrinsic muscles (e.g. *Opsanus tau*, Batrachoidiformes) or extrinsic muscles (e.g. *Terapon jarbua*, Perciformes; *Cynoscion regalis*, Perciformes; *Carapus acus*, Ophidiiformes), the sonic fibres are alkali stable. On the other hand, they also show, compared to fibres of white muscles, higher concentrations in glycogen and mitochondria, which supplies an important energetic inflow (Eichelberg, 1976; Ono and Poss, 1982; Fine et al., 1990, 1993; Connaughton et al., 1997; Chen et al., 1998; Parmentier et al., 2003b). These characters are in agreement with the fast capacities of work of these sonic muscles and may be more aerobic than white muscle.
4.1.2. Parvalbumins

Fast contractions of sonic muscles could also be associated with the parvalbumins (PA). Parvalbumins are globular, soluble, acid and thermostable proteins (~12 kDa). They act as the releasing factor that binds Ca$^{2+}$ before sarcoplasmic reticulum reaccumulation (Gerday, 1982). They are particularly abundant in white fast-twitch fibres of amphibians and fishes in which they could play an accelerator role in relaxation (Gerday and Gillis, 1976; Gillis, 1985) by sequestering Ca$^{2+}$ in order to carry it from the contractile apparatus to the sarcoplasmic reticulum (Gillis and Gerday, 1977; Rome and Klimov, 2000). Mammals have a single muscular isoform, while fishes can possess more than five. The isoform expression of the PA differs according to the kind of muscular fibre and development stage (Focant et al., 1994, 2000; Huriaux et al., 1996, 1997). The polymorphism of the PA in fishes could be a way to modulate contractile properties. To our knowledge, these proteins have only been studied in two different sonic muscles—the intrinsic muscles of *Opsanus tau* and the extrinsic muscles of *Carapus acus*.

The sonic muscles of *Opsanus tau* contain the same three isoforms of PA that are present in the white muscles, but the total concentration in PAs is three times higher in the sonic muscles than in the white ones (Hamoir and Focant, 1981; Appelt et al., 1991; Feher et al., 1998). This could be related to the fact that in these sonic muscles, the concentration of calcium is three times higher and the reticulum sarcoplasmic three times more developed than in the white epaxial muscles (Hamoir et al., 1980; Gillis, 1985).

In *Carapus acus*, the differences in PAs between the white and sonic muscles are both qualitative and quantitative (Parmentier et al., 2003b). PA I is present only in the sonic muscles, where it is present in a greater amount than PA II and PA III, which are also found in the white muscles. These differences could explain the different contractile properties between sonic and white muscles, since the expression of peculiar isoforms in a certain type of muscle seemingly corresponds to its functional requirements (Gerday, 1982; Huriaux et al., 1997; Focant et al., 2000).

5. CONCLUSION

Production of sound by muscular action on the swimbladder implies that during the evolutionary history of the sonic muscles, they have developed the capacity to contract in a fast and sustained way. Most of these muscles seemingly developed from different origins, at least epaxial, hypaxial or occipital. This would mean that the various sound mechanisms described above could be the result of evolutionary convergence. This fact could thus explain in part why the sonic muscles of distant phylogenetic species show a high number of common features at both a morphological and a physiological
level. There are probably not so many possibilities of increasing the velocity of muscles. A common strategy seems to be development of the sarcoplasmic reticulum (at the expense of the contractile apparatus, in terms of diameter and number of myofibrils), which allows the exchange surfaces and concentration of required metabolites for the contraction/relaxation cycles to increase. Other modifications seem to intervene also at the level of the binding protein isoform (PA) and the different isoforms of myosin, troponin and calcium pumps (Rome and Lidstedt, 1998; Parmentier et al., 2003b). However, not all teleost sonic muscles necessarily have exactly the same architecture, which is very likely linked to their different insertions. For example, insertion on a skeletal piece associated with the swimbladder or on a small point of the swimbladder seems to require a proportionally more developed contractile apparatus, in order to apply a powerful force on an accurate point. On the other hand, insertion of a sonic muscle on a wider area, as in *Opsanus tau* for example, seems to require a less powerful force since this muscle will act on several points of the swimbladder: the number of cross-bridges is less important, as shown by the important development of the sarcoplasmic reticulum. These two different kinds of work of the sonic muscles could reflect differences in muscular configuration. However, a comparative study on the number of myofibrils in intrinsic and extrinsic muscles could support the hypothesis dealing with the force.

Different modifications of the swimbladder wall may also be related to certain types of muscular insertions. For example, in fishes with intrinsic sonic muscles inserted on wide areas of the swimbladder, the latter is rather flexible. On the other hand, in groups with extrinsic sonic muscles inserting on a precise point of the swimbladder, modifications of the bladder wall (e.g. sclerification, ossification) or of the tendinous insertions on the swimbladder are possibly a response to the mechanical stress created by traction of the sonic muscles. In the same line of thought, the ‘elastic spring apparatus’ appears to be a homoplastic feature. Its development in various catfish families could also be a response to the mechanical stress imposed by the insertion of the sonic muscle on the swimbladder. Differences in the shape, size and flexibility of the Müllerian process could probably be linked to differences in the origin and surface of the muscle.

However, studies on the characterisation of teleost sonic muscles and their neighbouring pieces are definitely scarce or were done mainly for a few particular species (e.g. *Opsanus tau*); only future studies will enable obtaining new data to test the several hypotheses advanced in the present work. It is hoped that this work will stimulate further studies on this undoubtedly intriguing subject.
REFERENCES


Fish Communication


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