Sound-Generating and -Detecting Motor System in Catfish: Design of Swimbladder Muscles in Doradids and Pimelodids

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ABSTRACT
Catfishes have evolved a diversity of swimbladder muscles serving in the generation of different sounds and probably other acoustic functions. In order to find out if anatomical and acoustical differences are paralleled by fine structural differences, I examined the sonic muscles of the doradid Platydoras and the pimelodid Pimelodus by gross dissections and ultrastructural methods. In Platydoras, the sound-generating (drumming) muscle (DM) inserts on a dorsal bony plate that vibrates the swimbladder. In pimelodids, the large DM attaches directly on the ventral surface of the swimbladder, whereas the small tensor tripodis muscle (TT) inserts on the rostral surface near the tripus, the most caudal Weberian ossicle. Fibers of all three muscles possess an extensive development of sarcoplasmatic reticulum (SR) in association with very thin myofibrils (MF) but differed widely in their arrangement. In Platydoras, ribbons of MFs are arranged radially around a central core. Mitochondria were found within the core and the peripheral sarcoplasm. Pimelodus does not have a differentiated core and the cross-sectional area of DM-MFs is about 15% larger as determined by stereological measurements. The TT possesses shorter sarcomeres and more mitochondria than DMs, which were primarily found between MFs. This suggests faster contraction properties and greater resistance to fatigue compared with sonic muscles. Data indicate that the higher amount of DM-myofibrils in pimelodids might result in stronger muscle contractions and, presumably, in higher sound intensities. The fine structure of the TT reveals that contractions most likely prevent transmission of swimbladder vibrations to the inner ear via the Weberian ossicles during vocalization. Annu. Rec. 263:297–306, 2001. © 2001 Wiley-Liss, Inc.

Key words: fish; sonic organs; drumming muscles; fine structure; intraspecific differences; hearing

Teleost fishes have evolved a diversity of sound-generating structures among which swimbladder vibration mechanisms are most widespread. Such structures are found in non-related taxa such as mormyrids, siluriforms, characids, batrachoidids, triglids, gadids, and sciaenids. They consist of a set of fast-contracting striated muscles (drumming muscles) that variously vibrate the swimbladder. Drumming muscles are either entirely attached to the lateral wall of the bladder (intrinscic type: toadfishes and triglids; Bass and Baker, 1991) or they have additional attachments on structures such as the vertebral column or occipital bones (extrinsic type: characids, Markl, 1971; sciaenids, Ono and Poss, 1982). All of these muscles are characterized by their ability to contract at very high rates (100–250 Hz) (Skoglund, 1961; Markl, 1971; Kastberger, 1977; Fine, 1981). The contraction rate usually determines the fundamental frequency of drumming sounds.

Grant sponsor: Austrian National Bank; Grant number: 6789.
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Received 7 April 2000; Accepted 8 February 2001
Published online 22 May 2001

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Several investigators revealed that rapidly contracting swimbladder musculature is associated with a characteristic fine structure. Contrary to locomotory muscles, drumming muscles possess thin myofibrils and an elaborate development of the sarcoplasmic reticulum (Fawcett and Revel, 1961; Eichelberg, 1977; Ono and Foss, 1981; Bass and Marchaterre, 1989; Fine et al., 1993; Leisner et al., 1997). These features are linked to an unusually rapid calcium cycling necessary for fibers to operate at such high frequencies (Appelt et al., 1991; Rome et al., 1996). Fehrer et al. (1998) relate the extensive sarcoplasmic reticulum to calcium capacity, which allows the muscle to keep contracting even though calcium is not completely recycled. Similarly fast-operating sound-producing muscles are also encountered in invertebrates. The tymbal muscle of male cicadas can operate at a frequency up to 500 Hz, and its ultrastructure resembles drumming muscle fibers (Josephson and Young, 1985, 1987).

Among major groups of sonic fishes so far studied, catfishes exhibit the largest diversity in sonic organ design. Catfishes are especially well-studied because the mechanism and representatives of several families possess additional extrinsic drumming muscles that differ widely in origin and insertion and in the way the swimbladder is put into vibration (Tavolga, 1962; Abu-Gideiri and Nasr, 1973; Kastberger, 1977). This diversity is paralleled by a divergence in the organization of somatic/vocal motor nuclei (Ladich and Fine, 1994; Ladich and Bass, 1996, 1998) and by pronounced differences in the sounds produced. A comparison between acoustic signals emitted by representatives of catfish families revealed that drumming sounds in pimelodids tended to have a higher fundamental frequency and a higher sound pressure level than in doradids (Ladich, 1997).

In addition to the ventral sound-generating muscle, the pimelodid species examined revealed a small dorsal swimbladder muscle (tensor tripodiis), inserting near the triptis Weberi, the most caudal of the Weberian ossicles. Although the function of the tensor tripodiis muscle has not been examined physiologically, Bridge and Haddon (1892) and Schachner (1977) stated that it dampens oscillations of the triptis during swimbladder vibrations. It should, therefore, contribute to synchrony of the drumming muscle to protect the ear during sound production.

The goal of the present study is threefold. First to determine (1) whether ultrastructural properties of drumming muscles differ between closely related fishes, (2) whether the small tensor tripodiis muscle resembles fast-contracting sound-generating muscles ultrastructurally, and (3) in which way differences in the fine structure of these muscles can be related to differences in vocalization and presumed acoustic function. To accomplish this goal, representatives of two families were chosen that differ in the sound-producing mechanisms (direct attachment of the drumming muscles in pimelodids vs. indirect vibration of the swimbladder by bony plates in doradids) and in characteristics of sounds generated (fundamental frequency, sound pressure level). New descriptions of the anatomy of swimbladder muscles are presented in doradids and pimelodids. This complements an earlier description in these families (Ladich and Bass, 1998). This is followed by a detailed analysis of the fine structure of these three “acoustic” swimbladder muscles (drumming muscles in Platydoras and Pimelodus spp. and tensor tripodiis in Pimelodus spp.). Finally, to quantify differences between muscle types, morphometrical and in particular stereological measurements were performed.

**MATERIALS AND METHODS**

Five Striped Raphael Catfish *Platydoras costatus* (family Doradidae) (7.1–17.3 g) and five Pictus Catfish *Pimelodus pictus* (family Pimelodidae) (4.4–6.6 g) were used during this study. Fish were obtained commercially and maintained at 28°C in aerated, filtered, and planted aquaria. Gross examination of gonads suggested that all specimens were sexually immature.

**Tissue Preparation and Transmission Electron Microscopy**

Animals were deeply anesthetized with MS 222 and cold fixative (2.5% glutaraldehyde/2% paraformaldehyde in 0.1 M cacodylate buffer) was immediately dropped onto swimbladder muscles, the muscles excised, sliced into 1–2-mm blocks and fixed for an additional 2 hr in the above fixative. Secondary fixation was in 1% osmium tetroxide in 0.1 M cacodylate buffer for 1 hr. Tissue was then stored overnight in 0.1 M buffer before it was taken through a graded series of alcohol and embedded in epon-araldite.

Semithin sections for light microscopy observations were stained with methyleneblue-azur II (Richardson et al., 1980). Ultrathin sections were picked up on 200-square mesh grids or formvar-coated slot grids, were uranyl acetate–lead citrate double-stained, and observed under a Zeiss EM 902 (Oberkochen, Germany) transmission electron microscope.

For comparative purposes, additional samples of swimbladder muscles were prepared as described above for TEM for the following species: one *P. blochii* (9.5 g) and one *P. ornatus* (5.7 g).

**Quantitative Analysis and Stereological Measurements**

All measurements were taken from two randomly chosen blocks of each muscle type. Selected subsets of sections from each block were used for quantitative studies of muscle fiber and myofibril dimensions, sarcomere length, and volume densities. The diameters of muscle fibers were determined from semithin sections under a light microscope using an ocular micrometer. In order to avoid measuring oblique muscle fiber sections, only the smallest fiber diameter was determined. Fifty to one hundred muscle fibers were measured per block.

Myofibril dimensions and sarcomere length were determined from randomly chosen ultrathin sections, which were subsequently photographed at magnifications of 12,000× and 7,000×. Prints were enlarged to give a final magnification of 20,000× and 10,900×. Because of their ribbon-like character, two myofibrillar measures were determined on cross-sections: length and width. Sarcomere length was measured as the distance between the midpoints of two successive Z-lines. As tissue preparation did not permit controlling for shrinkage, sarcomere lengths are probably underestimated but still robust enough to allow for comparison between muscles and species. Five measurements of myofibril width and sarcomere length and ten measurements of myofibril length were taken per block per individual. Means for each muscle type were used for further calculations.
Stereological analyses were used to determine volume densities of myofibrils, sarcoplasmic reticulum, mitochondria, and cytoplasm. Nuclei were avoided in this analysis because of their irregular occurrence. Morphometry was done by projecting 80 × 80 mm negative films on the screen of a microfilm reader (Micro Design 425A), using a point counting technique (Weibel, 1979). A transparent grid ruled at 1-cm intervals was laid over the screen and the number of grid intersections lying on selected fiber components was counted. The total number of grid intersections lying on a particular component, for example mitochondria, divided by the total number of intersection in the whole field gave the fractional volume of the muscle. With the grid used, approximately 420 intersections lay within the bound of each negative film, so the final volume density values for each muscle are based on approximately 3,400 individual counts as eight negative films (4 per block) were analyzed per muscle type and individual. The relative volumes of myofibrils (MF), cytoplasm (CP), mitochondria (MI), and sarcoplasmic reticulum (SR) were determined.

Statistics
Statistical differences between muscles were examined by one-way analysis of variance (ANOVA; SPSS 7.0) followed by Tukey’s multiple comparison procedure. All statistics were based on comparisons between average values calculated for each animal. Analysis of data distributions revealed no departures from normality for variables examined.

RESULTS

Gross Anatomy of Sound-Generating Organs
The sound-producing organ in P. costatus consists of an elastic spring mechanism. The swimbladder is vibrated by a thin, disc-shaped, bony plate (elastic spring or Ramus Mulleri), a transverse or lateral process of the fourth vertebra. The drumming muscle (DM) originates at the supracleithral and dorsosupracleithral bone (SO, DSO, Fig. 1) and inserts dorsally at the elastic spring (RM). The elastic spring is connected laterally via a short ligament with the first lateral dermal scute (scute 1, Fig. 1). The drumming muscles are never in direct contact with the swimbladder, although their contractions cause the swimbladder and first lateral dermal plate to vibrate.

All three pimelodid species examined possess two swimbladder muscles. Contrary to P. costatus, the drumming muscles (DM, Fig. 2) originate at the large transverse process of the vertebral column and insert ventrally and ventrolaterally at the swimbladder. The left and right drumming muscle completely cover the ventral surface of the rostral swimbladder.

The tensor tripodis (TT, Fig. 2), on the other hand, is a small conical muscle that originates on the occipital bone (SO, DSO, Fig. 2) of the skull and inserts via a long tendon on the rostrocaudal surface of the swimbladder near the tripos Weberi, the most caudal of the Weberian ossicles (T, Fig. 2). The caudal part of the tripos is firmly connected with the dorsal wall of the swimbladder.

Muscle Fibers
Swimbladder muscle fibers were round or polygonal in cross-sections and differed significantly in size (ANOVA, F_{2,12} = 19.2, P < 0.001). The mean diameter of the drumming muscle fiber of P. pictus was about twice that of P. costatus (29.7 vs. 16.0 μm), whereas there was no significant difference between the dorsal and ventral swimbladder muscle fibers in Pimelodus (24.5 vs. 29.7 μm) (Fig. 3).

Fine Structure
All three muscles investigated revealed properties of fast-contracting muscles. Fibers were characterized by an abundance of very thin myofibrils (width 0.4–0.6 μm), which account for half or two-thirds of the cross-sectional area (Fig. 4). Myofibrils are for the most part flag-like structures with the long dimension oriented radially. The interfilibrillar clefs are occupied almost exclusively by the sarcoplasmic reticulum (SR, sarcotubules). Within sarcotubules, black granules—most likely glycogen granules—were found in all muscle types. Depending on the muscle type, mitochondria were present in the sarcoplasm as well as between myofibrils, whereas myonuclei were always arranged in the subsarcolemmal cytoplasm. All contractile elements were characterized by a pronounced cross-striation. Besides these general features, muscles differed in the arrangements and relative volumes of organelles as well as in the length of myofibrils and sarcosomes.

Organelle arrangement. In Platydoras, ribbons of long myofibrils were arranged radially around a central cytoplasmic core. Myofibrils were almost uniform in width and only broadened slightly or split at the periphery. Muscle fibers were furthermore characterized by a large volume of peripheral sarcoplasm (Figs. 4, 5). Within a muscle fiber, sometimes a second and third core could be distinguished. Cross-striation for the most part flag, ribbon between adjacent muscle fibers. Mitochondria were found within the central core and the peripheral subsarcolemmal sarcoplasm, but not between adjacent myofibrils (Figs. 4a, 5a).

Pimelodids differed from the doradid catfish by lacking a differentiated central core and extensive subsarcolemmal sarcoplasm. Myofibrils were mostly radially arranged. They were longer and narrower at the periphery and became wider and shorter in the center of the fiber. Mitochondria were present mainly in the subsarcolemmal cytoplasm and occasionally between myofibrils (Figs. 4b, 5b).

In the tensor tripodis muscle, myofibrils were short and radially arranged at the periphery but formed irregular patterns within the center of the fiber. In contrast to the sound-generating muscles, the tensor tripodis muscle possessed significantly more mitochondria, which were primarily clustered between myofibrils (Figs. 4c, 5c). These mitochondrial clusters were often associated with concentrations of sarcotubules. Occasionally, sarcotubules appeared to be continuous with circular stacks of double membranes, resembling whorl bodies (Fig. 5c).

The main characteristics of P. pictus swimbladder muscles, such as a lack of cores and abundant mitochondria in the tensor tripodis, were also found in both pimelodid species, P. blochii and P. ornatus.

Myofibril and sarcosome length. The maximum length of myofibrils as seen on cross-sections was significantly longer in drumming muscles than in the tensor tripodis (ANOVA, F_{2,12} = 5.104, P < 0.05). This was
mostly due to the lack of long ribbons of myofibrils at the periphery.

Transverse sections of muscle fibers revealed that all muscle types possessed one set of triads per sarcomere, which were located at the level of each Z-line. Each triad included the terminal cisternae of the SR and a central T-tubule (Fig. 5d–f). Average sarcomere length differed significantly among the swimbladder muscles examined (ANOVA, $F_{5,12} = 35.2, P < 0.001$). Sarcomere length was about 30% smaller in the tensor tripodis muscle vs. sonic muscles (Fig. 6).

**Volume densities of organelles.** The overall myofibrillar volume was significantly larger in the drumming muscle of *P. plectus* than the doradid catfish or the tensor tripodis, which did not differ from each other (ANOVA, $F_{2,12} = 31.29, P < 0.001$) (Fig. 7). As a consequence, the volume density of the sarcoplasmic reticulum was smaller by about 13% compared to both other muscle types (ANOVA, $F_{2,12} = 29.976, P < 0.001$) (Fig. 7). Correspondingly, mitochondrial volume density was also smallest in the drumming muscle of the pimelodid (ANOVA, $F_{2,12} = 43.35, P < 0.001$). No significant difference was found in the amount of SR among all three muscle types.

**DISCUSSION**

**Comparison Between Drumming Muscles**

Comparison between drumming muscles of the pimelodid *P. plectus* and the doradid *P. costatus* reveals that differences in the gross anatomy of sonic organs is paralleled by pronounced differences in the fine structure. The main differences are the muscle fiber diameters and the arrangement of myofibrils, which constitute a contractile cylinder in the doradid, leaving a mitochondria-rich sarcoplasmic core in the center. Similar differences were briefly mentioned by Dorn (1976) who compared the doradid *Doras hancocki* and *D. pectinifrons* to the pimelodid.
Rhamdia sebae. In the present study, significantly larger fiber diameters were found in the smaller species *P. pic- tus*, indicating that differences are species- or even family-dependent and not growth-dependent. Fine et al. (1990) showed that fiber diameters increased as the oyster toadfish *Opsanus tau* grows. Mochokid catfishes, which are closely related to doradids—both constitute the taxon “do- radoids” (Lundberg, 1993)—possess a very similar contractile cylinder and are similar in fiber diameter (20 vs. 16 μm in *Platydoras*) (Hagedorn et al., 1996; for a discussion of the sonicelectric muscle in *Synodontis*, see Ladich and Bass, 1996). Because *Pimelodus* differs from *Platydo- ras* in organelle arrangement and in several other mor- phometrical measures (larger muscle fiber diameter, larger myofibril volume density) a typical “catfish pattern” of sonic muscle fiber organization does not exist.

A common feature of all otophysans described so far (catfishes and characids) is that only one triad is found per sarcomere at the level of the Z-line (present study; Dorn, 1976; Eichelberg, 1977). This is similar to the sciaenid *Cynoscion* (Ono and Pass, 1982) but contrasts with the toadfishes *Porichthys* and *Opsanus* and the tigerperch *Therapon*, which possess two triads at the A-I-band border (Eichelberg, 1976; Bass and Marchaterre, 1989; Loesser et al., 1997). However, the number of triads is not necessarily a taxonomic characteristic because both sciaenids and
tigerperches (grunts) belong to the order Perciformes. It might rather be related to sarcomere length. A pair of triads would optimize conduction of excitation in muscle fibers with long sarcomeres such as in toadfishes (2.0—3.4 \( \mu \text{m} \); Bass and Marchaterre, 1989) and grunts (2.2 \( \mu \text{m} \); Eichelberg, 1976). One triad per sarcomere is primarily found in species having shorter sarcomeres such as \textit{Serrasalmus} (1.3 \( \mu \text{m} \); Eichelberg, 1977) and \textit{Cynodon} (1.5 \( \mu \text{m} \); Ono and Poss, 1982). However, this relationship does not seem to hold for the catfishes described in the present study. Catfishes possess only one triad despite having relatively long sarcomeres (2.2—2.3 \( \mu \text{m} \)). Although the above comparisons may be influenced by shrinkage of tissues, relationships might be lacking in general. Kilarski (1967), comparing cardiac, skeletal and eye muscles in six families of teleosts, stated that no correlation between triad and morphology or contraction physiology of muscle fibers exists.

**Fine Structure and Contraction Frequency**

Besides differences in the arrangement of organelles, drumming muscle fibers in both species reveal properties of fast-contracting muscles: thin myofibrils (0.4—0.6 \( \mu \text{m} \)) were surrounded by layers of sarcotubules, which minimize the distance and, thus, the transport time of calcium to the contractile proteins and back to the SR. This design is not restricted to vertebrates (fishes and reptiles), but has also been found in sound-generating (tympanic) muscles in cicadas (Josephson and Young, 1985). Physiological investigations in toadfishes, piranhas, and doradids as well as cicadas demonstrated that the fundamental frequency of drumming sounds corresponds to an unusually high contraction frequency of these muscles (Skoglund, 1961; Tuvolga, 1982; Markl, 1971; Kastberger, 1977; Josephson and Young, 1985). Therefore, this is assumed to also be the case in pinelodids although electrophysiological data are currently lacking.

Differences in the sound output of doradids and pinelodids can only partly be explained by differences in the fine structure of these muscles. Swimbladder sounds of pinelodids differ from those of doradids in two sound characteristics. The fundamental frequency (and thus contraction rate) is higher in pinelodids than in doradids (177 vs. 96 Hz), as is the sound pressure level (SPL) (Ladich, 1997). Josephson and Young (1985) argue that higher myofibril volume is associated with an increase in the muscle force per cross-sectional area and the mechanical power output per gram muscle in cicadas. In addition, Pite et al. (1993) observed that muscle fibers were smaller in juvenile toadfish and that their grunts had a significantly lower SPL than those of adults. Both reports are in agreement with observations in catfishes. \textit{Pimelodus pictus} possesses thicker muscle fiber (30 vs. 16 \( \mu \text{m} \)) and a higher myofibril volume density (65 vs. 50\% of \textit{Platy-}

doras). In addition, the higher SPL of \textit{P. pictus} compared to similarly-sized doradids might be due to differences in the sound-producing mechanisms. In pinelodids, the drumming muscle is inserting ventrally on the swimbladder and covers its ventral part almost totally, whereas in doradids only a small elastic bony plate (elastic spring) touches the bladder cranially (Ladich and Bass, 1988).

Contraction frequency, on the other hand, seems to be inversely related to the size (width) of myofibrils and the relative myofibril volume per muscle fiber or the ratio of fibrils to SR. In cicadas, such an inverse relationship exists between contraction frequency (50—220 Hz) and myofibril volume (41—22 \% (Josephson and Young, 1985, 1987). No such relationships were found in catfishes. \textit{Pimelodus pictus} has a higher myofibril volume (65 vs. 50\%) and thus a higher fibril/SR-ratio (2.3 vs. 1.8 for total SR; 2.3 vs. 2.1 for the interribellar SR alone) than \textit{Platy-}

doras and sounds are of higher fundamental frequency. Also, myofibrils are not smaller in faster-contracting muscles in catfishes (vs. cicadas; Josephson and Young, 1985). Although only two catfish species were studied quantitatively, it is concluded that differences in the contraction frequency cannot be explained based on morphological differences in the fine structural design of muscle fibers. Besides differences in the morphology of sonic organs, other differences between both families probably exist in the contraction kinetics of sonic muscle fibers, for example differences in speeds of calcium transients, crossbridge detachment rates, and probably kinetic off-rates of calcium from troponin (Rome et al., 1996).

**Musculus Tensor Tripodis**

The second (dorsal) swimbladder muscle of pinelodids is unique among all sound-generating fishes. Because of its small size and minute insertion point on the swimbladder, it very unlikely serves in sound production. The close proximity of its insertion to the tibias Weberi led earlier investigators to speculate about a protection function of the inner ear similar to the musculus tensor tympani in mammals (Bridge and Haddon, 1892; Schachner, 1977). Therefore, it was termed musculus tensor tripodis. This function in hearing seems to be reasonable, especially in otophysans utilizing the swimbladder to generate high-amplitude sounds and concurrently enhancing their hearing ability (Ladich, 1997, 1999).

Does the fine structural design support such an assumption? Clearly, the tensor tripodis of pinelodids resembles fast-contracting, sound-generating muscles in its high content of thin myofibrils and SR. However, it differs from sonic muscles in three major features. First, the tensor tripodis has significantly more mitochondria, which are not restricted to the subsarcomembran region or a central...
core but occur mainly between muscle fibers. This arrangement considerably decreases the maximum distance between the energy-generating and utilizing parts of the fibers compared with sonic muscles. Second, the ribbons of myofibrils are shorter and the contractile elements and sarcotubules appear to be less regularly arranged. Occasionally, stacks of membranes, similar to whorl bodies in toadfishes (Loesser et al., 1997), were found between myofibrils. These whorl bodies were continuous with the SR. Third, the sarcomere length was significantly shorter than in sonic muscles (1.6 vs. 2.2 μm).

Although there are similarities to sonic muscles in some morphometric measures (muscle fiber diameter, volume density of myofibrils, and SR), the differences described above point to different contraction kinetics and strongly indicate a different function of the tensor tripodis muscle in catfishes. Especially, the regular occurrence of interfibrillar mitochondria is very unusual for drumming muscles in fishes.

Short sarcomeres are usually associated with fast contraction speed, whereas long sarcomeres are associated with high force production. Gronenberg et al. (1997) described differences in the sarcomere length in the mandible closer muscle fiber of ants, which are inversely correlated to the maximal velocity of the closing movements of mandibles. This indicates a faster onset of contraction in the tensor tripodis muscle. Assuming that the ear protection function of the tensor tripodis is correct and that motoneurons innervating the tensor and the sonic muscle fire synchronously, which is very likely because motor nuclei are connected in the medulla (Ladich and Fine, 1994), then the tripus might be inactivated before the first contraction of the drumming muscle puts the bladder wall into vibration. This might efficiently prevent transmission of a large, self-generated oscillation of the bladder wall to the endolymph of the inner ear. The greater number of mitochondria in the sarcoplasm and their shorter distance to the contractile proteins suggest that this muscle can sustain a higher level of oxidative metabolism and is, thus, more resistant to fatigue. This would, in addition, reduce swimbladder wall vibrations near the Weberian ossicle during and after drumming to a minimum.

Although it remains to be demonstrated that the contractions of both swimbladder muscles in pimelodids are synchronized, the fine structure of the tensor tripodis supports the notion that it is able to protect the ears from sensory overload during vocalization.

**Evolutionary Considerations**

Phylogenetic analysis revealed that the direct attachment of sound-generating muscles onto the swimbladder in *Pimelodus* is probably the ancestral condition, because pimelodids are currently regarded as the most primitive group (Lundberg, 1993). In other families, the drumming muscles insert onto the bony elastic spring (ramus Müller), which vibrates the swimbladder indirectly. Families possessing an elastic spring mechanism are classified as "aroidids" by Lundberg (1993). Among "aroidis," aruids are separated from "doradoids" (doradids and mochokids) by
Fig. 5. High-power electron micrographs of sonic muscle fibers of *P. costatus* (a, d), *P. pictus* (b, e), and tensor tripodiis fibers of *P. pictus* (c, f). Transverse sections are shown to the left, longitudinal sections to the right. Scale bar = 1 μm. C, central core; MF, myofibrils; SR, sarcoplasmic reticulum; T, triad; W, whorl body; Z, Z-line.
the shape of the elastic spring. Interestingly, no such mechanism is known from charraciforms, the sister group of Siluriformes (Fink and Fink, 1996). Fine structural data support these phylogenetic considerations. Pimelodids and the characid Serrasalmus possess larger muscle fiber diameters and lack a central core. Eichelberg (1977) states that in the sonic muscle of the piranha S. nattereri "mitochondria lie almost without exception, in the periphery of the fibers." A cylinder-like arrangement of myofibrils as found in the "doradoide," where mitochondria are arranged outside and inside but not within the contractile cylinder, appears to be a derived organizational pattern. The fine structural organization of organelles of the dora
did Platydoras resembles that of sonic muscles in toadfishes (Bass and Marchaterre, 1989; Fine et al., 1993) and sciænids (Ono and Poss, 1982). In both nonrelated groups, mitochondria are found outside and within the radially arranged ribbons of myofibrils. Although it is unclear which constraints resulted in this organelle arrangement, it demonstrates that similar patterns of sonic muscle fiber organization evolved independently in several fish taxa.

ACKNOWLEDGMENTS

Thanks go to M.L. Fine for numerous comments on the manuscript and for discussion on this topic; H. Grillitech for the line drawings; G. Rothe for fixatives; C. Beisser for cutting, staining, and final photography; A. Sänger for introducing me to stereology and D. Moser for stereological studies; and the staff of the ultrastructure lab for technical assistance.

LITERATURE CITED


