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Myotomal Myogenesis of Axial Muscle in the Sturgeon *Acipenser baeri* (Chondrostei, Acipenseriformes)*

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Compared to teleost fishes, a unique character of the myogenesis of the plesiomorphic *A. baeri* is the fusion of myoblasts derived from the somite, leading to the formation of multinucleate muscle lamellae. Then, the lamellae are converted into cylindrical muscle fibres. The mechanism of transformation of lamellae into fibres is still debatable. Early embryonic muscle growth is mainly due to the hypertrophy of somite-cell derived stock. After hatching, hypertrophic growth occurs parallel to hyperplastic growth. Proliferatively active mesenchymal cells, which migrate from the intermyotomal space into the myotomes, participate in both processes.

Key words: Myogenesis, mesenchymal cells, muscle lamellae, sturgeon.

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The development and growth of skeletal muscles in fish is a multistage process during which undifferentiated cells of paraxial mesoderm acquire myogenic identity as a result of the coordinated action of various intrinsic and extrinsic factors.

Studies on the development of trunk muscles in fish have dealt with several species, and mainly with the hypertrophy and hyperplasy of muscle fibres. Hypertrophy consists of growth of preexisting muscle fibres, whereas hyperplasy is the formation of new muscle fibres (ROWE & GOLDSPINK 1969; KOUMANS & AKSTER 1995). Two hypotheses have been proposed to explain the increase of muscle mass in fish. According to the first, myosatellite cells are involved in hypertrophy and hyperplasy (NAG & NURSALL 1972; STOIBER & SÄNGER 1996; JOHNSTON *et al*. 1998). According to the second, new muscle fibres arise as a result of the division or splitting of preexisting fibres (WILEMSE & LIEUWMA-NOORDANAUUS 1984; FINE *et al.* 1993).

The term "myosatellite cell" has been defined in frogs on the basis of location and morphological criteria by MAURO (1961). In fully differentiated muscle fibres, myosatellite cells are situated between the basal lamina and the sarcolemma. Myosatellite cells are spindle-shaped, with a nucleus containing mainly electron-dense chromatin and a small amount of cytoplasm (KOUMANS *et al*. 1990). In adult muscle they do not divide mitotically and remain "dormant". External stimuli trigger the re-entry of myosatellite cells into the cell cycle. The descendants of these cells, myoblasts, fuse to form new multinucleated myofibres during regeneration (COSSU *et al*. 1980; BISCHOFF 1994; YABLONKA-REUVENI *et al*. 1994; CORNELISON & WOLD 1997). Little attention has been given to satellite cells and muscle growth in phylogenetically old taxa, such as Chondrostei.

The aim of this study was to analyse the differentiation of myotomal muscles in a plesiomorphic fish, *A. baeri,* and to trace the origin and morphology of cells which participate in hypertrophic and hyperplastic growth of muscles.

Material and Methods

Embryos of the Siberian sturgeon (*Acipenser baeri*) were obtained from the Experimental Fish Stocking Center of the Institute of Inland Fishery

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in Giżycko (Poland). Spawning took place on the 20th of January, 2000. Fertilized eggs and embryos of *A. baeri* were incubated at 14-16 °C according to SZCZEPKOWSKI & KOLMAN (2001). The studies on myotomal myogenesis in *A. baeri* encompassed developmental stages from the neurula to the 26th day after hatching. Until hatching (stage 35), stages were determined according to the developmental table for *Acipenser gueldenstaedti* (DETLAF *et al*. 1981).

Egg envelopes were removed with forceps and embryos were anaesthetised with Tricaine (MS 222) and placed in fixing solution. The kind of fixing solution depended on the technique subsequently applied.

Transmission Electron Microscope

TEM material was fixed for 24 hrs in modified Karnowsky's liquid (1% paraformaldehyde, 1% glutaraldehyde in 0.1 M phosphate buffer). The material was repeatedly rinsed in the same buffer and postfixed for 2 hrs in 1% OsO_4 in phosphate buffer, pH 7.4. After rinsing in 0.1 M phosphate buffer, the material was dehydrated in a graded alcohol series and in acetone, and embedded in epoxy resin Epon 812. The Epon blocks were cut on a Reihert Ultracut E ultramicrotome. Semithin sections (0.6 μm) were stained with methylene blue in 1% borax and examined under a light microscope (Olympus BHS). Ultrathin sections were contrasted with uranyl acetate and lead citrate according to the standard method of REYNOLDS (1963), and examined with a TEM Zeiss EM 900 at an accelerating voltage of 80 kV.

Immunocytochemistry

Embryos for immunocytochemical studies using the immunoperoxidase method ABC were fixed in formalin and buffered according to Lillie (PEARSE 1960). Immunocytochemical analysis for PCNA included stages 28 till the 26th day after hatching. The material was embedded in paraffin according to standard histological procedure and cut into 5 μm sections using a rotary microtome (E. Leitz, Wetzlar). Following deparaffination in xylene and a graded alcohol series, endogenous peroxidase was blocked with a 1% solution of H_2O_2. After repeated rinsing in PBS, non-specific protein binding was blocked with Protein Block Serum Free (DAKO). The sections were incubated with an antibody against proliferating cell nuclear antigen (PCNA) (clone PC10, DAKO), for 12 hrs at 4 °C, using a commercially available concentration. Afterwards the sections were rinsed in PBS, superimposed with a biotinylated antibody (LSAB 2 KIT, DAKO), and incubated with a streptavidin-peroxidase complex (LSAB 2 KIT, DAKO). The immunocytochemical reaction was triggered with 3,3'-diaminobenzidine tetrahydrochloride (DAB) solution (DAKO). Next, the sections were rinsed with running tap water and dehydrated in a graded alcohol series. The material was cleared in xylene, embedded in Depex and examined under a light microscope (Olympus BHS) at different magnifications. As a negative control, the primary antibody reaction step was omitted.

Results

Differentiation of muscles before hatching (developmental stages 25-35)

Somitogenesis

During somitogenesis, cell blocks (somites) detach from unsegmented mesoderm (stage 25). Somitogenesis in early sturgeon embryos shows a cephalo-caudal gradient. In longitudinal sections through *A. baeri* embryos, the somite contains a layer of tightly adjoining circumferential cells covering loosely organized round cells located centrally (Fig. 1). In somite cells numerous mitotic figures were observed, while yolk platelets were noticed in the cytoplasm.

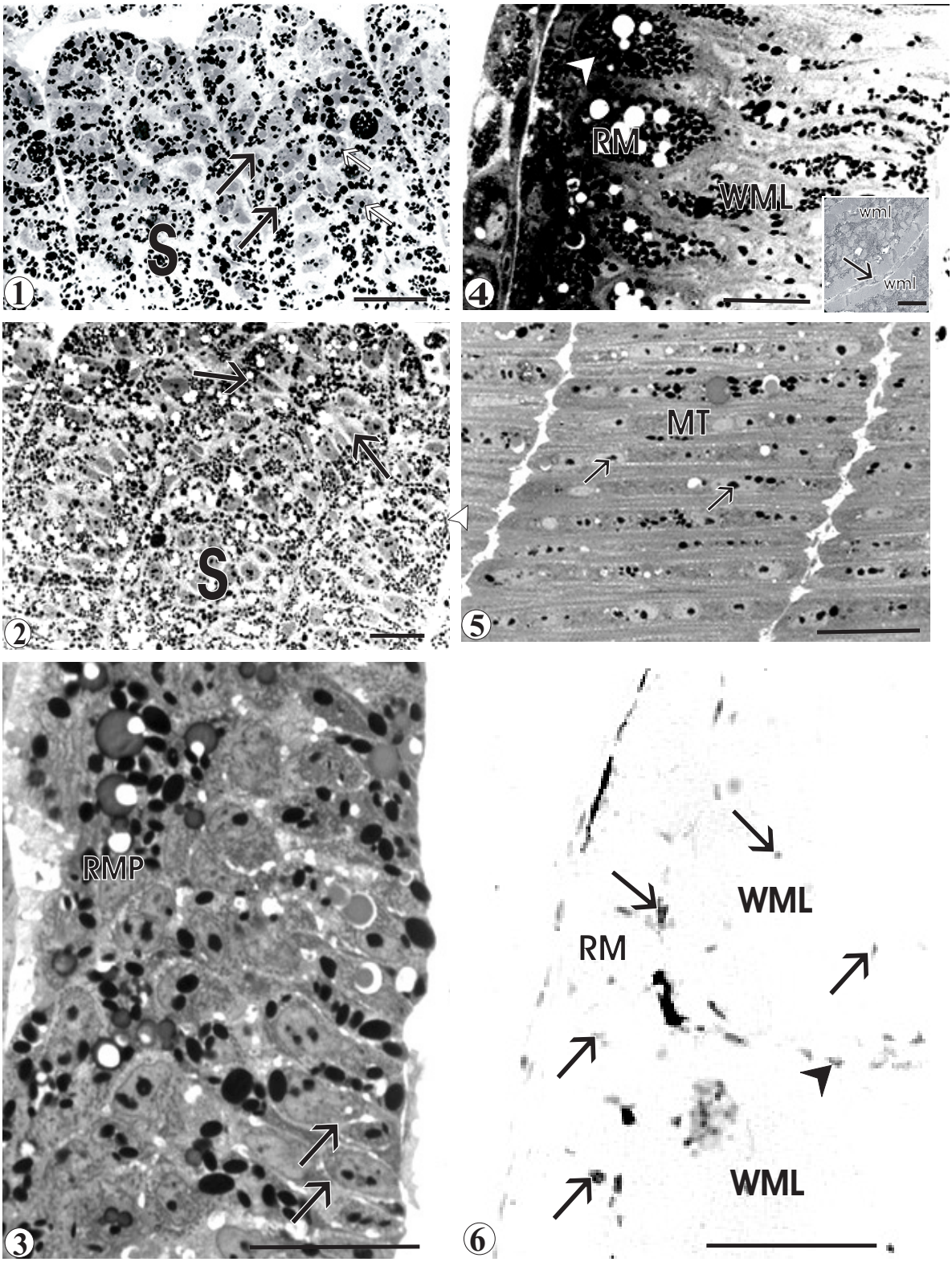
Early events in myogenesis

A morphological manifestation of the initiation of myogenesis in *A. baeri* (stage 27) is the elongation of somite cells. The cells acquire a conical shape and then fuse to form multinucleated muscle lamellae (Fig. 2). A linear arrangement of presumptive white muscle cells can be observed in cross sections through the embryo (Fig. 3). The multinucleated lamellae of the white muscle area are perpendicular to the notochord (Fig. 4). Long processes of the superficial red muscle lamellae are inserted between the underlying white muscle lamellae (Fig. 4, inset). The precursors of both lamellae types contain numerous yolk platelets.

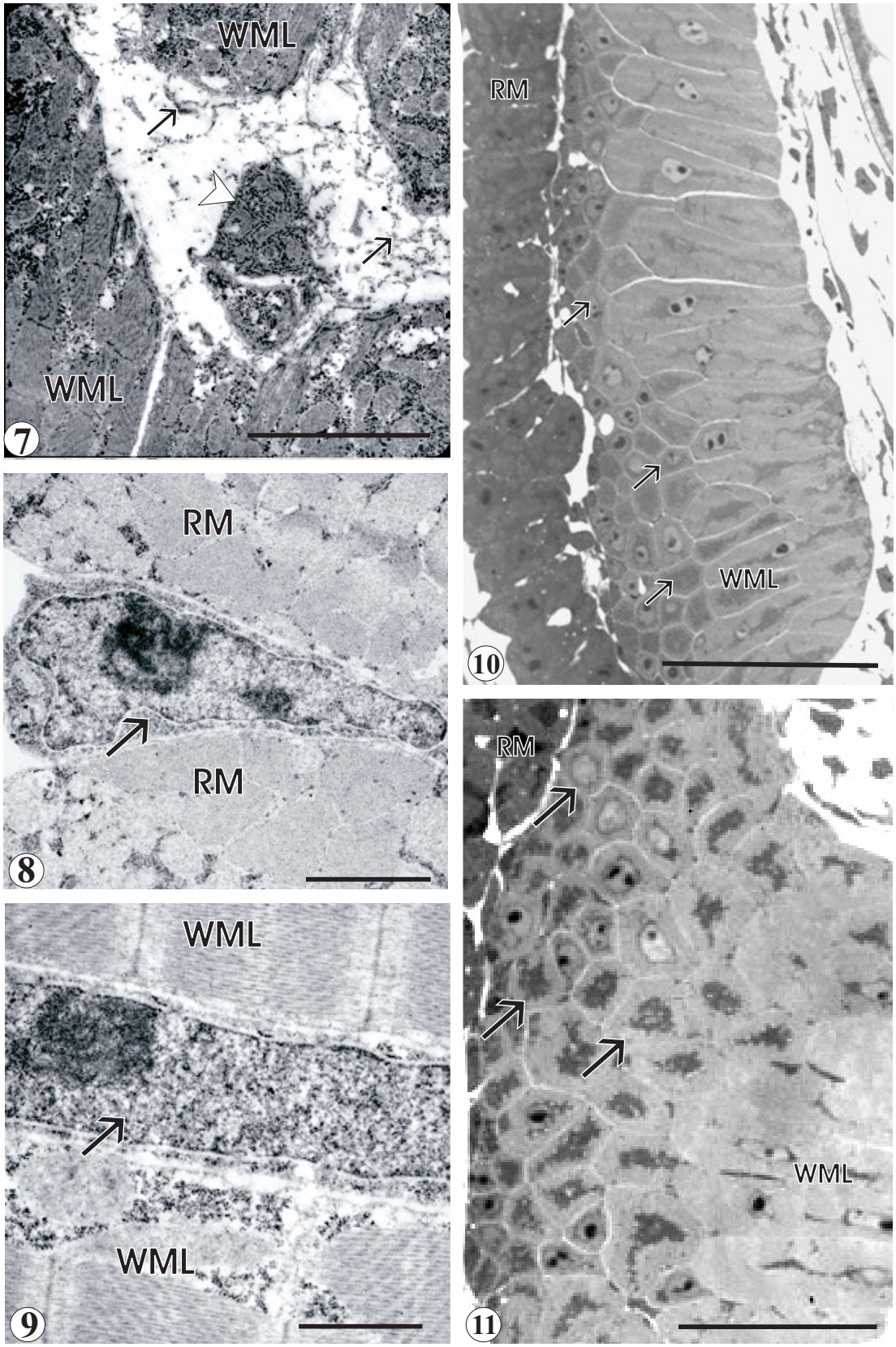
At stage 30 the first myofibrils can be observed in the multinucleated lamellae. Nuclei of the white muscle lamellae are located centrally (Fig. 5).

PCNA estimation

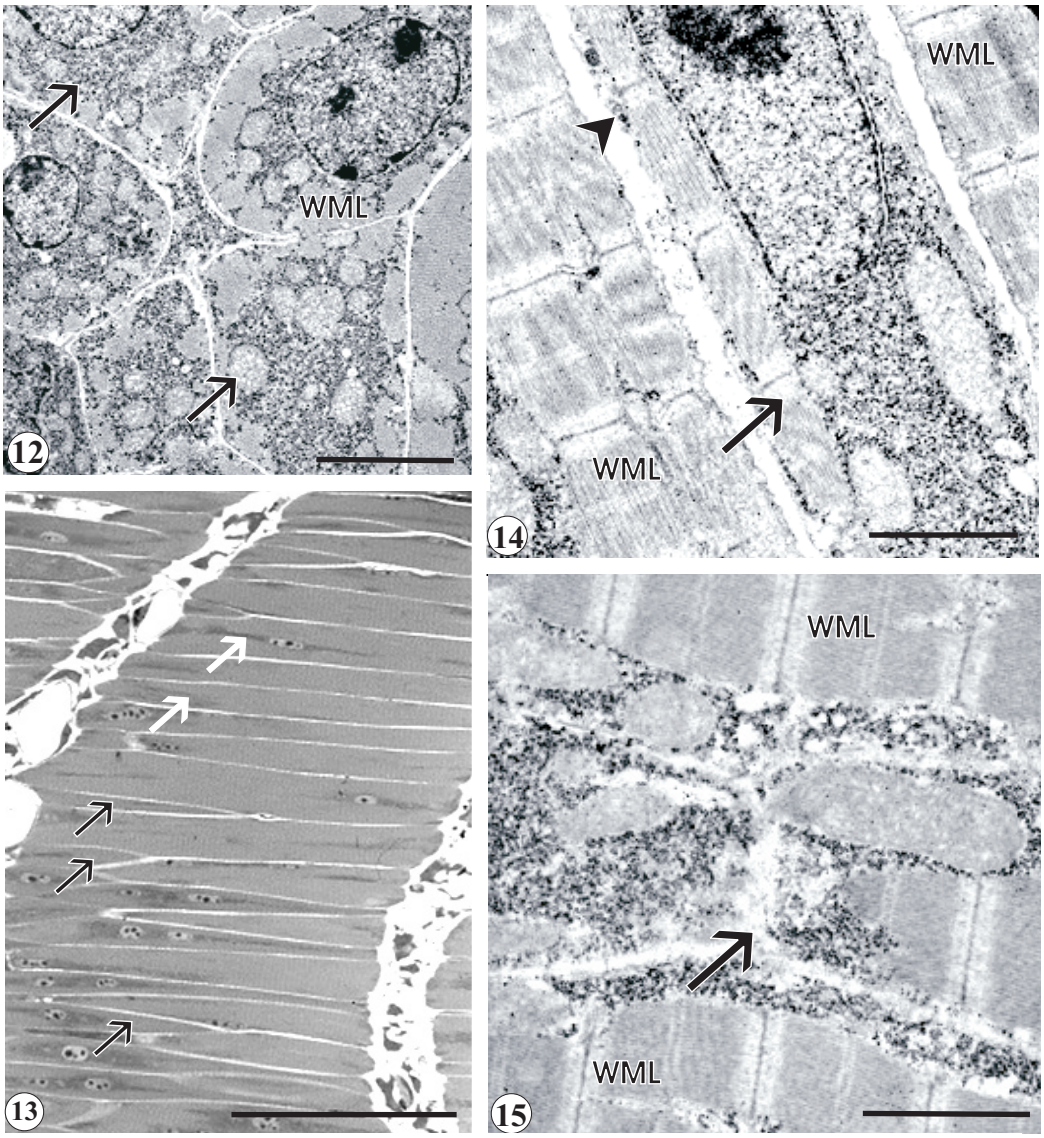
Before hatching (stage 32-33), mononucleated undifferentiated cells of unknown origin were for the first time observed in the intermyotomal space and subsequently in the myotomes. Immunocytochemical detection of PCNA showed that proliferatively active cells are present in the area of the intermyotomal space and horizontal septum, white muscle lamellae, and subsequently between the red muscle lamellae (stages 33-35) (Fig. 6). No



Figs 1-6. Fig. 1. Sagittal section through somites (S). Circumferential cells of somite wall (black arrows), round cells in the central part of the somite (white arrows). Semithin section, methylene blue. Stage 25. Bar = 0. 5 μm. Fig. 2. Sagittal section through *A. baeri* somites. Elongated cells of the somite wall (arrows), S (somite). Semithin section, methylene blue. Stage 27. Bar = 0. 5 μm. Fig. 3. Cross section through the *A. baeri* embryo. Precursors of red muscles (RMP), linear arrangement of precursor cells of white muscles (arrows). Semithin section, methylene blue. Stage 27. Bar = 0. 5 μm. Fig. 4. Cross section through the *A. baeri* myotome. RM (red muscles), WLM (white muscle lamellae), yolk platelets (arrow head). Semithin section, methylene blue. Stage 27. Scale bar 0. 5 μm. Inset - long processes of the superficial red muscle lamellae (RM) between white muscle lamellae (wml). TEM. Stage 27. Bar = 1. 1 μm. Fig. 5. Sagittal section through the *A. baeri* myotome. White muscle lamellae (arrows), MT (myotome). Semithin section, methylene blue. Stage 30. Bar = 0. 5 μm. Fig. 6. Immunocytochemical localisation of PCNA in *A. baeri*. Cross section through the embryo. Strong reaction in nuclei between red and white muscle lamellae, among white muscle lamellae (arrows) and in horizontal septum (arrow head), RM (red muscles), WML (white muscle lamellae). Stage 35. Bar = 0. 5 μm.



Figs 7-11. Fig. 7. Ultrastructure of mesenchymal cells in intermytomal space (arrow head), collagen fibres (arrows), WML (white muscle lamellae). Bar = 1. 1 μm. Fig. 8. Ultrastructure of mesenchymal cells between red muscles (arrow), RM (red muscles). Stage 35. Bar = 6 μm. Fig. 9. Ultrastructure of mesenchymal cells between white muscle lamellae (arrow), WML (white muscle lamellae). Stage 35. Bar = 4 μm. Fig. 10. Cross section through the *A. baeri* myotome, Cylindrical muscle fibres (arrows), RM (red muscles), WML (white muscle lamellae). Semithin section, methylene blue. 11th day after hatching. Bar = 0. 5 μm. Fig. 11. Cross section through the *A. baeri* myotome. Cylindrical muscle fibres in different stages of myofibrillogenesis (arrows) between red (RM) and white muscle lamellae (WML). Semithin section, methylene blue. 11th day after hatching. Bar = 0. 5 μm.



Figs 12-15. Fig. 12. Ultrastructure of cylindrical muscle fibres (arrows) next to white muscle lamellae (WML). Cross section through the embryo. 11th day after hatching. Bar = 0. 5 μm. Fig. 13. Sagittal section through the *A. baeri* myotome. White muscle lamellae spanning the whole length of the myotome (white arrows), wedge-shaped lamellae (black arrows). Semithin section, methylene blue. 11th day after the hatching. Bar = 0. 5 μm. Fig. 14. Ultrastructure of conical fibres (arrow head), myofibrillae (arrow), white muscle lamellae (WML). Sagittal section through the embryo. 11th day after hatching. Bar = 6 μm. Fig. 15. Ultrastructure of conical lamellae in contact with each other in the central part of the myotome (arrow), white muscle lamellae (WML). 11th day after hatching. Bar = 6 μm.

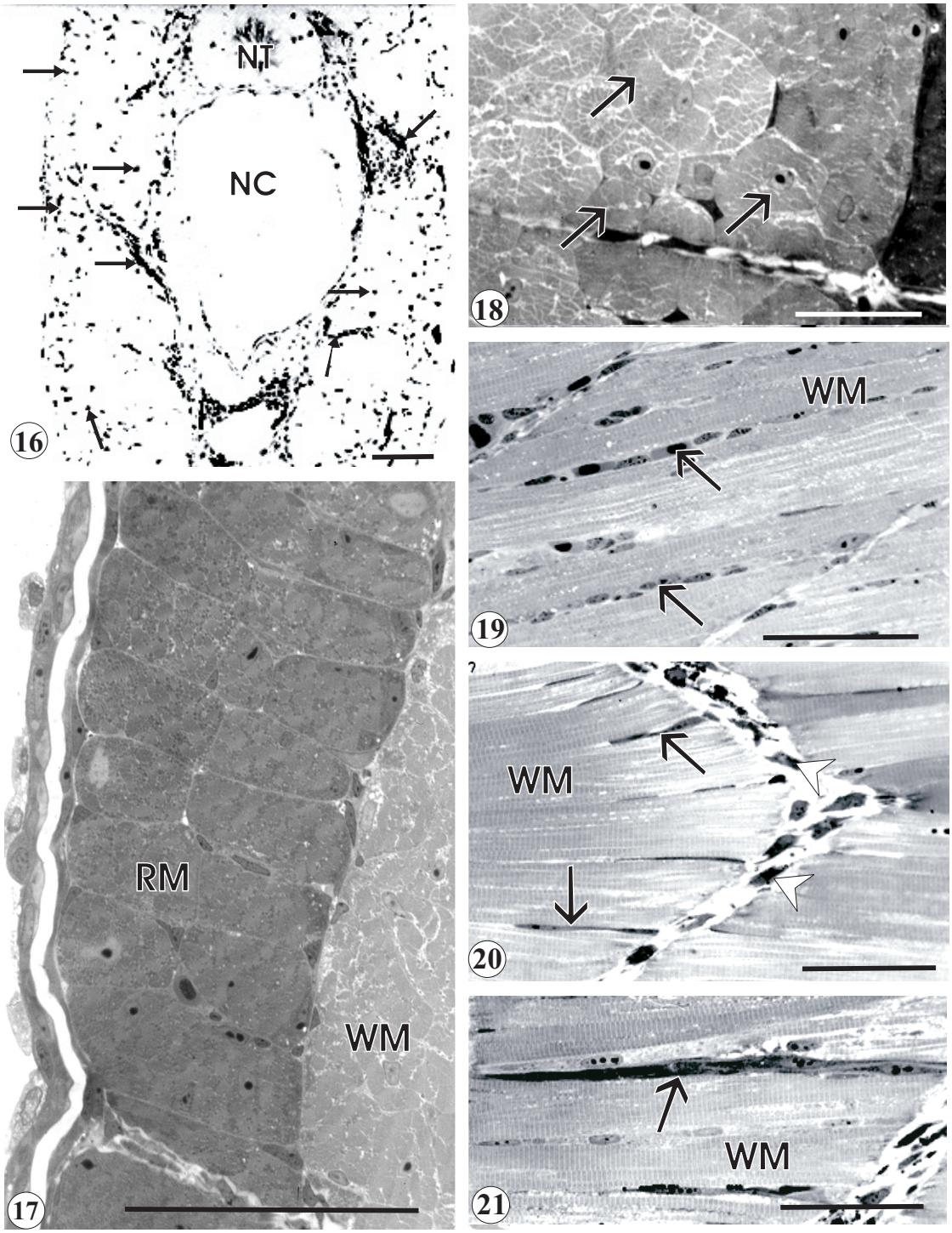
PCNA was detected in the nuclei of the red and white muscle lamellae.

Ultrastructure of mononucleated cells

Ultrastructural analysis of mononucleated cells in the intermyotomal space showed that their cytoplasm contained a system of rough endoplasmic reticulum. Numerous collagen fibrils, present in the neighborhood of the mononucleated cells, testify to their mesenchymal character (Fig.7). Cells occurring between red and white muscle lamellae are spindle-shaped with numerous ribosomes in their cytoplasm. These cells are characterized by nuclei with electron-dense chromatin beneath the nucleus envelope and reduced cytoplasm, no collagen fibres in the vicinity of these cells were observed (Figs 8, 9).

Differentiation of muscles after hatching (from the 3rd to the 26th day)

On the 11th day after hatching, red muscles located laterally in the myotome form a layer of muscle fibres, whereas white muscles located medially are still in the form of multinucleated muscle lamellae. The presence of oval sections through muscle fibres was observed between the layer of red and white muscles in cross sections through the embryo (Fig. 10). A myofibrylogenesis gradient



Figs 16-21. Fig. 16. Imunocytochemical localisation of PCNA in cross section through the embryo (arrows), neural tube (NT), notochord (NC). 11th day after hatching. Bar = 1 μm. Fig. 17. Cross section through the embryo. Two layers of red muscles (RM), white muscles (WM). Semithin section, methylene blue. 20th day after hatching. Bar = 0. 5 μm. Fig. 18. Cross section through white muscle fibre mass (arrows). Semithin section, methylene blue. 20th day after hatching. Bar = 0. 5 μm. Fig. 19. Saggital section through the myotome. Mesenchymal cells (arrows), white muscle fibres (WM). Semithin section, methylene blue. 26th day after hatching. Bar = 0. 5 μm. Fig. 20. Saggital section through the myotomes. Early secondary myotubes (arrows), mesenchymal cells in intermyotomal space (arrow heads), white muscle fibres (WM). Semithin section, methylene blue. 26th day after hatching. Bar = 0. 5 μm. Fig. 21. Saggital section through the myotomes. Secondary myotubes occupy the whole length of the myotome (arrow), white muscle fibres (WM). Semithin section, methylene blue. 26th day after hatching. Bar = 0. 5 μm.

was observed in cross sections among these cells. Fibres adjacent to the white muscle lamellae are characterized by a greater diameter and a more advanced myofibrilogenesis, in comparison with fibres adjacent to the red muscles (Fig. 11). These observations were confirmed by examining cross sections through the embryo in TEM (Fig. 12). The presence of two classes of white muscle lamellae

can be observed in longitudinal sections of myotomes (serial sections): the first class occupies the whole length of the myotome, and the second comprises conical lamellae which do not reach the end of the myotome (Fig. 13). TEM analysis of the conical lamellae revealed a less advanced myofibrilogenesis (Fig. 14). Ultrastructural examination revealed the probable splitting of white muscle lamellae; some of the conical lamellae make contact with each other in the central part of the myotome (Fig. 15).

Immunocytoreaction for PCNA was still present in the area of myotomes. Proliferatively active cells were observed in cross sections in dorsal, ventral, and lateral parts of the myotomes, as well as in the area of the horizontal septum (Fig. 16).

On the 20th day after hatching red muscle fibres are built of two layers and all white muscle fibres attain a cylindrical shape (Figs 17, 18).

On the 26th day after hatching mesenchymal cells were still present in myotomes; they were arranged linearly and firmly adhered to the surface of myotubes. Their cytoplasm, compared to the myotube cytoplasm, was strongly stained by methylene blue (Fig. 19). Secondary muscle fibres were observed on the surface of myotubes for the first time in this stage. These either spanned the whole length of the myotome or occurred in the form of oligonucleated myotubes (Figs 20, 21).

Discussion

Somitogenesis

In longitudinal sections through the embryo, the emerging somites in *A. baeri* are built by a single layer of cells surrounding rounded cells located centrally. The structure of the somite of this phylogenetically ancient lineage resembles the arrangement of cells in teleost somites of *B. rerio* (WATERMAN 1969; VAN RAAMSDONK *et al*. 1974), *Oryzias latipes* (MARTINDALE *et al*. 1987), *Thymallus thymallus* (MERKEL 1995) as well as *Rutilus frisii meidingeri* (STOIBER & SÄNGER 1996).

Early events in myogenesis

Despite the morphological similarity between the somites of *A. baeri* and teleost fishes, in the initial phase of myogenesis in *A. baeri*, mononucleated myoblasts of the somite fuse to form multinucleated muscle lamellae, and not multinucleated muscle fibres. Lamellae of a similar structure have been observed in the myogenesis of another representative of Acipenseridae: *Acipenser stellatus* (FLOOD *et al*. 1987). In this species the myotome is built of wedge–shaped, flattened multinuclear lamellae, stacked on top of each other in a dorso-ventral direction. Successive lamellae within the stack have bases alternating in a medial or lateral direction. Multinuclear lamellae have also been observed in Australian lung-fish (*Neoceratodus forsteri*) (DACZEWSKA in preparation). Multinuclear muscle lamellae in Acipenseridae and Ceratodondidae resemble in structure mononucleated muscle lamellae present in the larval and adult musculature of amphioxus (*Branchiostoma lanceolatum*) (PEACHY 1961; FLOOD 1968). Like in amphioxus, lamprey larvae (ammocoetes) also have myotomes composed of lamellae stacked horizontally on top of each other, extending along the whole length and width of the myotome. Each muscle lamella has one nucleus. In adult lamprey the myotomes are built of slightly flattened multinucleated muscle fibres (NAKAO 1977; ROVAINEN 1979). Muscle lamellae remain in the adult musculature only in amphioxus, whereas in lamprey, *A. baeri* and *A. stellatus* multinucleated muscle lamellae are converted into multinucleated muscle fibres. In teleost fishes (*B. rerio*, *Th. thymallus*, *Rutilus frisii meidingeri*, *Oncorhynchus mykiss*) (VAN RAAMSDONK *et al*. 1978; MERKEL 1995; STOIBER & SÄNGER 1996), amphibians (*Xenopus laevis*, *Hymenochirus boettgeri*, *Bombina variegata*, *Pelobates fuscus*, *Rana lessonae*) (KIEŁBÓWNA 1966, 1981; KIEŁBÓWNA & KOŚCIELSKI 1979; DACZEWSKA & PAŁUCKA 1999; DACZEWSKA 2001), and birds (PRZYBYLSKI & BLUMBERG 1966) trunk muscles are built of multinucleated cylindrical muscle fibres. The presence of muscle lamellae has not been observed during the early stages of myogenesis in these vertebrates. Therefore, on the basis of the obtained results and information from the literature, it is suggested that the presence of multinucleated muscle lamellae is a plesiomorphic feature in the myotomal myogenesis of vertebrates.

Hypertrophic and hyperplastic growth of muscles

During further stages of myogenesis in *A. baeri* (just before hatching), the presence of mononucleated proliferatively active cells was observed in the intermyotomal space and subsequently between red and white muscles, which was confirmed by immunocytochemical studies with the application of an S phase marker (PCNA). What should be emphasized is the absence of PCNA in the nuclei of red and white muscle lamellae, which testifies that the nuclei of lamellae withdrew from the cell cycle in the G_1 phase. In the myogenesis of teleost fishes the presence of a similar population of proliferatively active cells (termed myosatellite cells) has been observed (JOHNSTON *et al.* 1998

according to JOHNSTON 2001). Teleost fish myosatellite cell nuclei contain a great amount of electron-dense chromatin and have a strongly reduced cytoplasm. In longitudinal sections through the embryo, spindle-shaped fish myosatellite cells are predominantly evenly dispersed along the muscle fiber (JOHNSTON *et al*. 1998 according to JOHNSTON 2001), as are nuclei in *A. baeri*. It is believed that myosatellite cells are involved in the process of hypertrophy and hyperplasia of muscle fibres in fish (GEER-WALKER 1970; STICKLAND 1983; KOUMANS 1993 according to JOHNSTON 2001).

Ultrastructural analysis of these cells in *A. baeri* showed that their differentiation depends on their position. Cells comprising intermyotomal areas differentiate into fibroblasts, evidenced by the clear presence of rough endoplasmic reticulum within their cytoplasm as well as collagen fibres in their vicinity. Cells that have migrated into the myotomes differentiate into secondary myoblasts and contribute to hypertrophic growth at this stage of myogenesis (stage 32-33). PCNA positive mononucleated cells are still observed in the area of myotomes during subsequent stages of myogenesis (on the 26th day after hatching). The presence of secondary muscle fibres associated with myotomes was found for the first time in this stage of *A. baeri* myogenesis. It is presumed that proliferatively active cells can be a source of new muscle fibres. Similar observations have been obtained by VEGGETII *et al*. (1990) in the myogenesis of *Dicetrarchus labrax*, and STOIBER & SÄNGER (1996) in rainbow trout (*Oncorhynchus mykis*), roach (*Rutilus rutilus*) Dunabe bleak (*Chalcalburnus chalcoides mento*) and pearlfish (*Rutilus frisii meidingeri*).The presence of multinucleated proliferatively active mesenchymal cells has not been demonstrated so far in muscle growth during myogenesis, in which an intermediate stage incorporates multinucleated muscle lamellae. Therefore, this study is the first to report this phenomenon.

The results obtained in *A. baeri* with anti-PCNA labelling also correspond to results obtained with other fishes using exogenous 5 bromo-deoxyuridine for proliferating nuclei (ROWLERSON *et al*. 1995; JOHNSTON *et al*. 1998). Ultrastructural examination confirmed that the labelled nuclei were present in myogenic cells (ROWLERSON *et al*. 1995). Moreover, detection of cell-cycle-dependent expression of nuclear proteins such as PCNA has been used to identify hyperplastic growth in fish muscle (ALFEI *et al*. 1993, 1994; AKSTER et al. 1995; JOHNSTON *et al*. 1995; ROWLERSON *et al*. 1995; VEGETTI *et al*. 1999 according to JOHNSTON 2001). In Atlantic herring (*Clupea harengus*) JOHNSTON *et al.* (1995) and in rainbow trout (*Oncorhynchus mykiss*) STOIBER & SÄNGER (1996) have found mitotically active cells appearing within myosepts and between established muscle fibres. VAN RAAMSDONK *et al.* (1974) have found high mitotic activity of the cells in the dorso-caudal and ventro-caudal tips of differentiating tail myotomes of *B. rerio.* Proliferatively active cells in *Salmo salar* have been observed in dorsal, ventral and lateral parts of the myotome (STICKLAND *et al*. 1988), under the surface of the red muscles (ROWLERSON *et al*. 1995) or mosaically distributed between the white muscle fibres (KOUMANS *et al*. 1995). The distribution of proliferatively active mesenchymal cells in *A. baeri* myotomes resembles that of the above mentioned species.

Conversion of muscle lamellae into fibres

Multinucleated white muscle lamellae were not found in the advanced stage of myogenesis in *A. baeri*. Exclusively oval sections across cylindrical muscle fibres were observed in cross sections. TEM images suggest that multinucleated muscle lamellae may undergo longitudinal division leading to the formation of cylindrical multinucleated muscle fibres. In sections across the myotomes of the studied species, two classes of muscle lamellae were observed: conical lamellae and lamellae spanning the whole length of the myotome. Some of the lamellae contact each other by way of their conical ends in the central parts of the myotome. The hyperplastic process *via* mechanical division of the muscle fibre has been observed in several fish species. In *A. stellatus*, multinucleated muscle lamellae undergo divisions leading to the formation of multinucleated muscle fibres (FLOOD *et al*. 1987), as in *A. baeri*. In the toadfish, FINE *et al.* (1993) consider an increase of muscle fiber number a result of the divisions of preexisting fibres. In representatives of Perciformes (*Patagontothen tessellata*, *Patagontothen longipes*, *Notothenia coriiceps*) hyperplasy of large-diameter fibres also occurs by division. Connective tissue that penetrates the fiber splits it into 2-6 fibres of smaller diameter (JOHNSTON *et al*. 2003). The mechanism of muscle fiber division has not been fully explained. According to BAUMEISTER *et al.* (1997) a morphological manifestation of the initiation of splitting is sarcolemma indentation into the sarcoplasm.

Analysis of static images of histological sections, serial longitudinal and transverse sections through embryos of *A. baeri* did not shed light on the problem of conversion of muscle lamellae into fibres. Cylindrical muscle fibres may arise *de novo* as a result of fusion of mesenchymal cells which have migrated into the myotomes, at a simultane-

ous re-organisation of the lamellae cytoskeleton. This problem requires a detailed analysis.

Analysis of myotomal myogenesis in the sturgeon showed that multinucleated muscle lamellae are formed as a result of fusion of myoblasts derived from somite cells. At first, early embryonic muscle growth is mainly due to the hypertrophy of somite-cell derived stock. After hatching, hypertrophic growth occurs parallel to hyperplastic growth. Proliferatively active mesenchymal cells which have migrated from the intermyotomal space into the myotomes, participate in both processes. White muscle lamellae are not observed in the further stages of myogenesis, myotomes within the whole section are filled with muscle fibres.

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