Evolutionary transformations of myoseptal tendons in gnathostomes

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Axial undulations in fishes are powered by a series of three-dimensionally folded myomeres separated by sheets of connective tissue, the myosepta. Myosepta have been hypothesized to function as transmitters of muscular forces to axial structures during swimming, but the difficulty of studying these delicate complex structures has precluded a more complete understanding of myoseptal mechanics. We have developed a new combination of techniques for visualizing the three-dimensional morphology of myosepta, and here we present their collagen-fibre architecture based on examination of 62 species representing all of the major clades of notochordates. In all gnathostome fishes, each myoseptum bears a set of six specifically arranged tendons. Because these tendons are not present outside the gnathostomes (i.e. they are absent from lampreys, hagfishes and lancelets), they represent evolutionary novelties of the gnathostome ancestor. This arrangement has remained unchanged throughout 400 Myr of gnathostome evolution, changing only on the transition to land. The high uniformity of myoseptal architecture in gnathostome fishes indicates functional significance and may be a key to understanding general principles of fish swimming mechanics. In the design of future experiments or biomechanical models, myosepta have to be regarded as tendons that can distribute forces in specific directions.

Keywords: myosepta; tendons; vertebrate evolution; swimming mechanics

1. INTRODUCTION

Fish muscle has become a model system for integrative studies of muscle function, from the level of gene expression to whole organism performance, ecology and evolution (Rome *et al.* 1993; Jayne & Lauder 1995; Altringham & Ellerby 1999; Katz *et al.* 1999; Shadwick *et al.* 1999; Cole & Johnston 2001; Ellerby & Altringham 2001). A missing link in this chain of integration is the biomechanics of force transmission within the architecturally complex axial musculoskeletal system. When fishes perform axial undulatory swimming, the forces developed by myomere muscles have to be transferred to axial structures, such as the vertebral column, to generate lateral bending moments along the trunk. The skin and horizontal septum (HS) have been implicated in force transmission in some fishes (Wainwright *et al.* 1978; Hebrank 1980; Hebrank & Hebrank 1986; Westneat *et al.* 1993), as have myosepta (Nursall 1956; Wainwright 1983), but the development of a generalized model has been hampered by the lack of anatomical information on the complex three-dimensional (3D) architecture of myomeres and the collagenous myosepta onto which the muscle fibres of the myomeres insert. So far, we have direct evidence of force transmission by myosepta neither from experiments, nor from morphology.

We have developed a new combination of techniques for visualizing the 3D shape of myomeres and the collagen-fibre architecture within myosepta. This is an

adequate technique to survey the axial musculoskeletal systems in representatives of all major clades of extant notochordates (from lancelets to tetrapods). The comparative analysis of the collagen-fibre architecture of myosepta presented here contributes to answering some long-standing questions of functional, evolutionary and ecological aspects of the locomotory system in vertebrates. The gnathostome ancestor evolved a specific set of tendons in its myosepta, which has been retained with remarkable fidelity through 400 Myr of evolution. These tendons distribute forces in specific directions. Their conservatism indicates that general pathways of force transmission in fish trunks exist. This system was lost only in the transition to tetrapods, when functional demands changed from aquatic to terrestrial locomotion.

2. MATERIAL AND METHODS

Comparative analysis of myosepta (3D shape, relation to axial structures, orientation and attachment of myoseptal tendons) was achieved by a new combination of several techniques: clearing and staining, alcohol visualization, microdissections, polarized light, scanning electron microscopy (SEM) and 3D reconstruction. Formalin-fixed specimens were skinned, and a modified version of the classic clearing and double-staining method (Dingerkus & Uhler 1977) was performed. Cleared and stained specimens were transferred to 99% ethanol to visualize better the connective-tissue system of the trunk. Attachment of myosepta to axial structures, and orientation and attachment sites of myoseptal tendons were inspected *in situ*. Myosepta were removed using fine iris spring scissors (Vannas-Mini, 3 mm × 1.2 mm, or Vannas Tübingen, 5 mm × 1.2 mm). Excised

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Table 1. List of investigated specimens. Total length (mm) of each specimen is listed.

Cephalochordates	
<i>Branchiostoma lanceolatum</i> L., 1758	53, 55, 56, 58, 60
Petromyzontiformes	
<i>Mordacia mordax</i> (Richardson 1846)	277
<i>Geotria australis</i> (Gray 1851)	400, 568
Chondrichthyes	
<i>Chimaera monstrosa</i> L., 1758	508, 523, 533
<i>Galeus melastomus</i> (Rafinesque 1810)	282, 315
<i>Scyliorhinus canicula</i> L., 1758	306
Coelacanth	
<i>Latimeria chalumnae</i> (J. Smith 1939)	297, ca. 1100
Dipnoi	
<i>Neoceratodus forsteri</i> (Krefft 1870)	302
<i>Protopterus annectens</i> (Owen 1839)	321
Lissamphibia	
<i>Ambystoma mexicanum</i> (Shaw 1789)	200, 213
<i>Necturus maculosus</i> (Rafinesque 1818)	275
<i>Amphiuma tridactylum</i> (Cuvier 1827)	597
Actinopterygii (non-teleosts)	
<i>Polypterus ornatipinnis</i> (Boulenger 1902)	145, 229
<i>P. delhezi</i> (Boulenger 1899)	179
<i>P. senegalus</i> (Cuvier 1829)	175
<i>P. palmas</i> (Ayres 1850)	94, 158, 186, 197
<i>Acipenser ruthenus</i> L., 1758	145
<i>A. gueldenstaedtii</i> (Brandt & Ratzeberg 1833)	273
<i>Lepisosteus platyrhincus</i> (De Kay 1842)	166, 173, 218
<i>Amia calva</i> L., 1766	422
Actinopterygii (teleosts, non-acanthomorphs)	
<i>Arapaima gigas</i> (Cuvier 1829)	214
<i>Notopterus notopterus</i> (Pallas 1769)	182, 191
<i>Pappyrocranus afer</i> (Günther 1861)	181
<i>Megalops cyprinoides</i> (Broussonet 1782)	185
<i>Conger conger</i> L., 1758	298
<i>Engraulis encrasicolus</i> L., 1758	106
<i>Hoplias malabaricus</i> (Bloch 1794)	151
<i>Hydrocynus forskålii</i> (Cuvier 1819)	192
<i>Salmo trutta</i> L., 1758	130, 208
<i>Osmerus eperlanus</i> L., 1758	84
<i>Lampanyctus crocodilus</i> (Risso 1810)	116 standard length (SL)
Actinopterygii (teleosts, acanthomorphs)	
<i>Phycis blennoides</i> (Brünnich 1768)	143, 151
<i>Beryx splendens</i> (Lowe 1834)	323
<i>Scomber scombrus</i> L., 1758	275, 325
<i>Channa obscura</i> (Günther 1861)	139, 143, 148, 157
<i>Trachurus trachurus</i> L., 1758	216, 225
<i>Lepomis gibbosus</i> L., 1758	143, 149
<i>Scorpaena porcus</i> L., 1758	223
<i>Blennius ocellaris</i> L., 1758	127
<i>Trigla lyra</i> L., 1758	236

myosepta were spread out on microscope slides and viewed and photographed under a polarized light stereomicroscope (Zeiss Polarizer S and Analyzer A53) to visualize the collagen-fibre pathways. For some images, a difference-interference-contrast (DIC) device was used instead of polarized light. Selected pieces of myosepta were imaged with SEM (Cambridge Stereoscan 250 MK-2). The 3D shape of myosepta was reconstructed from horizontal histological sections by either the use of graphic methods or computer-based reconstruction (SURFDRIIVER v. 1.1). Furthermore, we used histological techniques to visualize certain aspects of myoseptal anatomy (paraffin embedding, slice thickness of 20 µm; Azan-Domagk or Azan- Heidenhain staining procedure).

We investigated 62 specimens representing all of the major

clades of notochordates. Forty-one species and 36 genera are listed in table 1. The dataset for our evolutionary analysis is completed by data from further species (acanthomorph fishes: 19 species from 19 genera listed in Gemballa & Britz (1998) and three species of myxinid and petromyzontid genera listed in Vogel & Gemballa (2000)).

3. RESULTS

We present our results in the light of the vertebrate phylogeny (figure 1) that is used in recent publications or textbooks (e.g. Janvier 1996; Donoghue *et al.* 2000; Liem *et al.* 2001; Purnell 2002). Two major evolutionary transitions in the structure of myosepta become evident when

Figure 1. Collagen-fibre architecture of myosepta in notochordates. (a) Evolutionary transformations. Successive nodes on the cladogram represent ancestors of notochordates, craniates, myopterygii, gnathostomes, teleostomes, sarcopterygians (dipnoans + tetrapods) and tetrapods. For explanations of characters 3–9 (evolutionary novelties) and the transformations or reduction of these (characters 10–16) see § 3a,b,d,e and figures 2–5. For characters 1 and 2, see Vogel & Gemballa (2000). (b–g) Schematic representations of myosepta of specific notochordate groups; left body side, lateral view. Pathways of myoseptal tendons are indicated by black lines. Part of the hypaxial myoseptum of hagfishes (c) is omitted.

mapping the features of the myoseptal system onto this phylogeny. The first transition is completed in the gnathostome ancestor (figure 1a, characters 4–9). This ‘gnathostome condition’ (figure 1e) has been retained with remarkable fidelity through 400 Myr of evolution of the cartilaginous fishes (Chondrichthyes), ray-finned fishes (Actinopterygii) and coelacanth (*Latimeria*). In a second major evolutionary event, the gnathostome condition was lost upon the transition to land in tetrapods (figure 1a, characters 10–16).

(a) The ‘gnathostome condition’: 3D morphology

The most conserved features of segmented musculature in the gnathostome condition are the 3D folding of myosepta into cones and the presence of six discrete tendons in a myoseptum (figure 2). A gnathostome myoseptum is attached laterally to the skin, and medially to the connective-tissue sheet of the vertebral column and to the median septum (figure 2). Both lines of attachment form a median forward flexure and dorsal and ventral backward flexures, resembling a ‘W’ turned through 90° (figure 1e). The lateral line of attachment follows one of the two directions of the collagen fibres in the stratum compactum of the skin. The medial line of attachment spans at least three vertebral segments (figure 2a,b, dashed line along vertebrae; figure 1a, character 7). A myoseptum runs between these two lines and is drawn out into a dorsal

posterior cone (DPC) and a ventral posterior cone (VPC) at the backward flexures and a dorsal anterior cone (DAC) and a ventral anterior cone (VAC) at the forward flexure (figure 1a, character 8; figure 2a,b). Cones of successive myosepta are nested within each other. The part dorsal to the DPC is termed the epaxial flanking part and the part ventral to the VPC is the hypaxial flanking part. The parts between the DPC and the DAC, and the VPC and the VAC, respectively, are termed epaxial sloping parts (ESP) and hypaxial sloping parts (HSP) (figure 2a,b). A myoseptum is intersected in the medial horizontal plane by the HS (figure 1a, character 9; figure 2a,b). In the postanal region, epaxial and hypaxial myosepta are mirrored by the HS in terms of spatial arrangement and collagen-fibre architecture (figure 2b).

The attachment of a single epaxial myoseptum can be followed best starting from its lateral-most point at the HS. From here it runs craniomedially along the HS and proceeds dorsally along the anterior corner of a vertebra. It turns caudally and generally traverses three segments (four or more in *Chimaera*) at the level of the neural arches or centra. Owing to this horizontal pathway of the medial part of the ESPs, subsequent myoseptal sheets are densely packed in this region and form a horizontal sheet. We term this region the ESP multilayer, and the corresponding part of the hypaxial myoseptum the HSP multilayer. These horizontal multilayers are situated dorsal and ventral to

Figure 2. (a,b) Schematic representations of spatial arrangement and collagen-fibre architecture of gnathostome myosepta; part of left body side. Pathways of myoseptal tendons are indicated by black lines; dashed line: attachment of myoseptum to axial structures and HS. (a) Epaxial part, oblique dorsal and anterior view. A set of three tendons (ENT, LT, MT) is present. Red indicates possible membranous ossifications of these tendons (ENB, LB, MB; not labelled). (b) Hypaxial part, oblique ventral and anterior view. A set of three tendons (EPT, LT, MT) is present. Red indicates possible membranous ossifications of these tendons; VR, ventral ribs. (c,d) Sagittal sections. (c) *Acipenser gueldenstaedtii*, anterior to left. Arrows indicate the horizontal pathway of successive ESPs that form the ESP multilayer. (d) *Channa obscura*, level of DPC, anterior to left. Arrows indicate horizontal fanlike projections of lateral tendon into musculature. (e-i) Midbody myoseptum of *Channa obscura*. (e) ESP under polarized light. Myoseptum is cut at DPC (dotted line); dashed line: medial attachment of myoseptum. Positions of (f-i) indicated. (f) DIC micrograph of robust ENT fibres and adjacent weak ESP. (g-i) Sectional views of (g) robust part of ENT and (h) robust part of LT, in contrast to (i) thin ESP region. Scale bars: (e) 2 mm, (f-i) 50 µm.

the HS (figure 2c). At the third vertebra the medial attachment line leaves the multilayer and follows the dorsocaudal course of a neural spine (figure 2a, dashed line). At the level of the dorsal backward flexure the medial attachment line of a myoseptum takes a sharp turn towards its anterior end at the dorsal midline.

(b) The 'gnathostome condition': 3D arrangement of myoseptal tendons

Our microdissections and polarized-light analyses revealed a conserved set of six tendons in each myoseptum of three gnathostome groups (chondrichthyans, actinopterygians and *Latimeria*, figures 1e, 2a,b,e, 3a-d): two

myorhabdoid tendons (MT) (figure 1a, character 3), two lateral tendons (LT) (figure 1a, character 6), an epineural tendon (ENT) and an epipleural tendon (EPT) (figure 1a, characters 4 and 5). These myoseptal tendons cause the robustness of the myoseptum. Collagen fibres of the remaining parts of the myoseptum are remarkably thin or are of a lower density (figure 2e-i). A single (epaxial) LT and ENT are present in an ESP (figures 2a, 3a-d). The corresponding elements in the HSP are the EPT and a (hypaxial) LT (figure 2b). LTs (figure 1a, character 6) connect the DAC and the DPC, and the VAC and the VPC. They take a curved pathway along the lateral part of the ESP (HSP) in a posterodorsal (posteroventral)

Figure 3. Examples of epaxial midbody myosepta of elasmobranchs, basal actinopterygians and tetrapods under polarized light. Position of myoseptum between anterior ($a = 0.0$) and posterior ($a = 1.0$) ends of specimens indicated. Dashed line, medial attachment of myoseptum. Myosepta in (a) and (b) are cut at DPC (dotted line) and ESP (lower part) and epaxial flanking part (upper part) are spread out separately. (a) *Galeus melastomus*, (b) *Acipenser gueldenstaedtii*, (c) *Chimaera monstrosa*, (d) *Amia calva* and (e) *Ambystoma mexicanum*. Scale bars, 2 mm.

direction and attach to the skin in their middle part (figure 2a,b). The LTs are broad but not very distinct structures of remarkable thickness (figure 2h). At both ends they are usually drawn out into horizontal fanlike projections (figure 2a,d), which proceed into the musculature and serve as additional attachment sites for white muscle fibres (see Alexander 1969). They are most pronounced in the posterior body region. LTs are not fixed to any axial structures such as the vertebral column or the median plane.

The ENT (figure 1a, characteristic 4) of the ESP and the EPT (figure 1a, characteristic 5) of the HSP connect the body axis and the integument. Their proximal ends form a distinct tendon that is firmly attached to the centrum, neural arch or neural spine of a vertebra (figure 2a,e-g). On their posterolateral pathway towards the skin the collagen fibres of the ENT and EPT diverge markedly. The ENT and EPT together wrap around the anterior myoseptal cones and are fixed at the skin and vertebral column (figures 1e, 2a,b). Thus, ENTs and EPTs are situated in the ESP and HSP multilayers and cause the robustness of these horizontal layers (figure 2c). MTs (figure 1a, characteristic 3) are longitudinal tendinous elements of the flanking parts, which reach from the anterior tips to the posterior cones (figures 2a,b, 3a,b). Here they fan out into the horizontal fanlike projections together with the LTs (figure 2a).

The described set of tendons is present in postanal epaxial and hypaxial myosepta and in preanal epaxial myosepta. By contrast, the collagen-fibre architecture of preanal hypaxial myosepta mainly consists of homogeneously distributed fibres that run mediolaterally and never form distinct tendons. Owing to the outbulging of the body cavity, preanal hypaxial myosepta are restricted to narrow oblique planes without cones.

(c) The 'gnathostome condition': patterns of membrane bones in teleosts

Slight variations of the described overall pattern were detected. ENTs and EPTs are usually more distinct in teleosts than they are in elasmobranchs and lower actinopterygians (figures 2e, 3a-d, 4b-d). Ossifications of myoseptal tendons occur only within teleosts (figure 4). The most complete pattern of ossified tendons (membrane bones; red area in figure 2) includes rodlike myorhabdoid bones in the flanking parts, and a 'Y'-shaped bone in the ESP (HSP) representing the ossifi-

Figure 4. ESPs of teleost myosepta under polarized light. Scale bars, 2 mm. (a-c) *Megalops cyprinoides*. Ossification pattern changes from (a) anterior via (b) midbody to (c) posterior myosepta. Miniaturized outlines show ossifications (red) and tendinous areas (white stippled) only. (d) *Salmo trutta*, no ossifications.

Figure 5. Polarized-light micrographs of horizontal septa; top view, left side, top side of figures represent attachment to vertebral axis, bottom side of figures represent attachment to skin. Scale bars, 2 mm. The mechanical properties of the HS are achieved by a cross array of caudolateral and caudomedial collagen fibres. The caudolateral orientation is represented by collagen fibres of the ECT. ECTs mark the intersection line of HS with the epaxial and hypaxial myoseptum. The caudomedial orientation is represented by POT. ECTs and POTs connect the vertebral axis and the skin. (a) The chondrichthyan *Scylliorhinus canicula*. ECT and POT directions are represented by homogeneously distributed fibres. (b) The basal actinopterygian *Polypterus ornatipinnis*. The ECT direction is represented by ossified dorsal ribs (dri); the POT direction is represented by homogeneously distributed fibres. (c) The basal actinopterygian *Amia calva*. The ECT direction is condensed to tendon-like ECTs; the POT direction is represented by homogeneously distributed fibres. (d) The teleost *Scomber scombrus*. In teleosts both directions are represented by condensed tendon-like ECTs and POTs. The anterior elements of an ECT series are frequently ossified, whereas POTs are always collagenous.

cations of the LT and ENT (EPT). Its anteromedial branch represents the ossified epineural (termed epineural bone, ENB) and is attached to the vertebral axis. The anterolateral and posterior branches represent the ossified LT (termed lateral bone, LB) (figure 2*a,b*).

This typical ossification pattern of midbody myosepta changes in a rostrocaudal gradient. Towards the posterior myosepta, the epineural remains collagenous and the remaining rodlike bone represents the ossified LT (figure 4*c*). Towards the anterior myosepta (figure 4*a*), the anterior part of the LT remains collagenous. The remaining 'C'-like bony element is attached to the vertebral column and represents the ossification of the posterior LT and the ENT. This correspondence of myoseptal tendons and intermuscular bones allows us to homologize unambiguously ossification patterns in teleosts that have been interpreted in different ways before (Patterson & Johnson 1995; Gemballa & Britz 1998) and to include these as characteristics in phylogenetic studies on teleosts.

(d) The 'gnathostome condition': HS

All horizontal septa investigated exhibited a cross-fibre texture of postero- and anterolateral orientated collagen fibres. We term the posterolateral fibres epicentral tendons (ECT) and the anterolateral fibres posterior oblique tendons (POT). In elasmobranchs and lower actinopterygians fibres are distributed homogeneously (figure 5*a-c*). The fibre directions are maintained in teleosts, but form distinct tendons (figure 5*d*). The ECT-POT fibre array in the HS is regarded as homologous throughout gnathostomes and is a synapomorphic gnathostome feature (figure 1*a*, character 9).

(e) Evolution and loss of the 'gnathostome condition'

Myosepta represent an evolutionary novelty of notochordates (figure 1*a*, character 1), as no myosepta are present outside this group (Cloney & Burighel 1991). The gnathostome condition evolved from relatively simple and coneless myosepta in the notochordate-vertebrate ancestor that were devoid of a HS and tendons but bore an array of collagen fibres of specific orientations (Vogel & Gemballa 2000; figure 1*a-d*, characters 1 and 2). The discovered uniform myoseptal features (figure 1*a,e*, characters 3-9) in Chondrichthyes, Actinopterygii and *Latimeria*

clearly represent features of the gnathostome ground plan. Out of these only MTs are also present in petromyzontiforms and are therefore regarded as a myopterygian (petromyzontiformes + gnathostomes) synapomorphy (figure 1*a*, character 3). The remaining features are not present in any group outside the gnathostomes (Vogel & Gemballa 2000) and represent gnathostome synapomorphies (figure 1*a*, characters 4-9). Future experimental work will be necessary to clarify whether and in what respect these novel myoseptal structures differ in function from the MS in the non-gnathostome conditions.

The gnathostome condition is gradually lost within Sarcopterygii (Coelacanth + Dipnoi + Lissamphibia + Amniotes), starting with reduction of the HS (figure 1*a*, character 10; for gnathostome condition see figure 5). Further simplification in the common ancestor of dipnoans and tetrapods included reduction of ENTs and EPTs, and reduction of the medial line of attachment to fewer than three vertebrae (figure 1*a*, characteristics 11 and 12; see figure 2*a* for gnathostome condition). The myosepta of aquatic salamanders (figures 1*g*, 3*e*) are markedly different from the gnathostome myosepta, even though these species secondarily inhabit an aquatic environment. No homologous tendinous elements can be detected except for the longitudinal fibres in the epaxial flanking part, which correspond to the MTs in non-tetrapods. Myoseptal cones and LTs are reduced (figure 1*a*, characters 13 and 15) and the myoseptal attachment spans fewer than two vertebral segments (figure 1*a*, character 14). In amniotes, the segmented muscle system is replaced completely by a set of discrete muscles and tendons, which are derived from myomeres and myosepta (figure 1*a*, character 16). Further research on tetrapod myosepta will be necessary to clarify the details of evolutionary changes in the connective tissue during the conquest of land.

4. DISCUSSION AND CONCLUDING REMARKS

The high uniformity of myoseptal tendons in the trunk musculature of the vast majority of fully aquatic gnathostomes (and the breakdown of this system in the transition to land) indicates the functional importance of this system in axial undulatory swimming. We propose that myosepta are better regarded as tendons that can distribute forces in

specific directions, rather than as thin sheets of connective tissues. Myosepta have been proposed to transmit forces to the axial skeleton (Nursall 1956; Wainwright 1983), to control the shape changes of myomeres during contraction (Westneat *et al.* 1998; Azizi *et al.* 2002) and to act together with the myomeric musculature to modulate body stiffness (Long *et al.* 1994; McHenry *et al.* 1995; Long & Nipper 1996; Long 1998). Our discovery of conserved myoseptal tendons in aquatic gnathostomes provides new data for distinguishing between these hypotheses and opens new directions for *in vivo* experiments on muscle physiology and modelling of fish swimming.

Besides myoseptal architecture, another crucial point for further understanding of the complex 3D geometry and function of fish trunks is the 3D arrangement of muscle fibres and its relation to myoseptal tendons. It became clear only recently (Gemballa & Vogel 2002) that a certain spatial relationship between muscle fibres and myoseptal tendons exists in non-sarcompterygian gnathostomes. From this relationship it is hypothesized that LTs are involved in force transmission and ENTs and EPTs contribute to the generation of internal pressure. These suggestions are in accordance with recent dynamic modelling of fish swimming (Long *et al.* 2002). This dynamic model works best when longitudinal tendons are introduced. We suggest that the LTs described here for gnathostome fishes are the morphological correlatives. The conservatism in the myomeric architecture of gnathostome fishes indicates that general principles in fish swimming really exist.

We are grateful to Peter Bartsch, Elizabeth L. Brainerd, Ralf Britz, John H. Long Jr and Wolfgang Maier for their support and encouraging comments on our work. We are especially grateful to E. L. Brainerd for her comments on the manuscript. Wilhelm Harder, Peter Bartsch and Ralf Britz kindly provided specimens. The experience of Horst Schoppmann helped with the SEM technique.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.