

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3241, 25 pp., 10 figures, 1 table Month 00, 1998

Homology of Intermuscular Bones in Acanthomorph Fishes

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ABSTRACT

Myosepta of selected representatives of the following acanthomorph taxa were investigated: *Polymixiiformes*, *Lampridiformes*, *Paracanthopterygii*, *Beryciformes*, *Atherinomorpha*, and *Percomorpha*. A new technique, microdissection of alcohol-stored specimens and polarized-light microscopy, was applied to study the three-dimensional architecture of connective tissue fibers in epaxial parts of myosepta. Several invariable similarities were present in all taxa: an epineural series of tendons or bones and a tendinous series of lateral bands in the epaxial part of the myoseptum, and an epicentral series of tendons or bones in the horizontal septum.

Patterson and Johnson's (1995) hypothesis that the single bony series of intermusculars in higher acanthomorphs is the homolog of epineurals of lower teleosts is tested. Our results contradict their hypothesis at essential points because we discovered epineural tendons in the normal epaxial position in different acanthomorphs that were considered to lack these. We conclude that the first intermuscular bone of *Polymixia* is an epicentral, the single series of intermuscular bones of *Holacanthopterygii* are epicentrals, and the neoneurals of some percomorphs are normal epineurals. Phylogenetic implications of our results are discussed.

INTRODUCTION

Since Owen's initial studies (1846, 1866), three series of intermuscular bones of teleosts have been known as epineurals, epicentrals, and epipleurals. In some teleosts two additional bony series are developed and are

known as myorhabdoi (Chapman, 1944). Recently, Johnson and Patterson (1993) and Patterson and Johnson (1995) studied intermuscular bones among major teleostean groups. One important result of their exten-

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sive investigation is that the bony intermusculars are usually continued by fiber bundles of connective tissue in the same series as the bones. They extended the terms epineural, epicentral, and epipleural to include these intermuscular fiber bundles that they named intermuscular ligaments. They concluded that the single bony series found in higher acanthomorphs is not composed of epipleurals as generally assumed, but is the homolog of the epineural series of lower teleosts that is shifted ventrally into the horizontal septum.

They conceded that “recording details of the form and distribution of those structures [i.e., intermuscular bones and fiber bundles] in cleared and stained specimens can be extremely difficult . . .” (1995: 1) and that “observations of ligaments . . . include an unknown quantity of subjectivity, and we will be glad to see all or any of them checked by others” (1995: 4).

Doubts concerning their homology of acanthomorph intermusculars with epineurals arose during the doctoral study of Gemballa (1995). He developed a technique to study individual myosepta and reliably identify intermuscular fiber bundles by polarized light. This new technique revealed epineural fiber bundles in taxa declared to lack them by Patterson and Johnson (1995). Thus, it appeared to us that their applied technique misled Patterson and Johnson into homologizing the single series of intermuscular bones in acanthomorphs with the epineural series of lower teleosts.

The aim of our paper is to reinvestigate myoseptal structures of representatives of major acanthomorph subgroups using Gemballa’s technique (1995) to test Patterson and Johnson’s hypothesis. Anatomical data obtained by this technique form the basis for unequivocal identification of the bony series in acanthomorphs as the homolog either of the epineural or the epicentral series of lower teleosts. This is valuable because these structures are incorporated in phylogenetic hypotheses (Johnson and Patterson, 1993) that are weakened or strengthened depending on the homologization (see Discussion).

A detailed anatomical description of myoseptal structures is also of interest to functional morphologists because these structures are involved in transmission of muscular

forces during locomotion (Nursall, 1956, Willemse, 1972, Wainwright, 1983, Westneat et al., 1993). Collagenous fiber bundles as components of myosepta were not described in detail or well understood until recently (Gemballa, 1995). Descriptions for the diverse group of acanthomorph fishes are still lacking and some are presented here for the first time. The functional significance of the results presented here is the topic of a forthcoming paper.

ACKNOWLEDGMENTS

We thank Karsten Hartel (MCZ, Harvard), and Norma Feinberg, Barbara Brown, Melanie Stiassny, and Gareth Nelson (AMNH, New York) for the loan of study material. We express deepest gratitude to Dave Johnson and Colin Patterson for providing a copy of their interesting and stimulating paper on teleost intermusculars before publication. Their enormous survey facilitated our work and was the basis for constant checking of our data. We enjoyed discussion with Dave Johnson during a short visit to the Division of Fishes, National Museum of Natural History, Washington. We thank Gareth Nelson and Radford Arindell for inviting RB to join them for fieldwork in Alabama and for their interest in our “intermuscular problem”. We are grateful to Bob Shipp and the numerous individuals who helped in many ways during the 64th Annual Deep Sea Fishing Rodeo, 1996, on Dauphin Island, Alabama. Eduard Serrat and fishermen from Palamós (Catalunya, Spain) made fishing boat trips possible for SG. We thank Wolfgang Maier, Lehrstuhl für Spezielle Zoologie, Universität Tübingen, for his interest in our project, and Melanie Stiassny for her support. Barbara Brown, Radford Arindell, and Martina Hohloch provided technical assistance. The paper profited from the critical reading and commenting by Peter Bartsch, Gareth Nelson, and Marcelo Sánchez-Villagra and the reviews of Anthony Gill (BMNH, London) and Mark W. Westneat (FMNH, Chicago). MWW drew our attention to the terminology problems with tendons and ligaments.

This work was supported by the SFB 230 and a collection study grant from the American Museum of Natural History to SG, a

TABLE 1
Investigated Specimens^a

Specimen	SL(mm)	Family
<i>Polymixia lowei</i> AMNH 49674	103	POLYMIXIIDAE (c&s)
<i>Polymixia lowei</i> AMNH 086102	97	POLYMIXIIDAE (c&s)
<i>Velifer hypselopterus</i> AMNH 49575	115	VELIFERIDAE (c&s)
<i>Metavelifer multiradiatus</i> AMNH 92080	~279	VELIFERIDAE (skel.)
<i>Lampris guttatus</i> AMNH 79669	~820	LAMPRIDAE (skel.)
<i>Aphredoderus sayanus</i> AMNH 55089	74	APHREDODERIDAE (c&s)
<i>Molva dipterygia</i> personal coll.	220	GADIDAE (c&s, part)
<i>Gephyroberyx philippinus</i> AMNH 49701	85	TRACHICHTHYIDAE (c&s)
<i>Hoplostethus mediterraneus</i> personal coll.	106	TRACHICHTHYIDAE (c&s)
<i>Holocentrus rufus</i> AMNH 25919	124	HOLOCENTRIDAE (c&s)
<i>Holocentrinae</i> indet. MCZ 85252	11	HOLOCENTRIDAE (c&s)
<i>Holocentrinae</i> indet. MCZ 85252	11.5	HOLOCENTRIDAE (c&s)
<i>Holocentrinae</i> indet. MCZ 85252	13.5	HOLOCENTRIDAE (c&s)
<i>Holocentrinae</i> indet. MCZ 51911	18	HOLOCENTRIDAE (c&s)
<i>Holocentrinae</i> indet. MCZ 51911	26	HOLOCENTRIDAE (c&s)
<i>Bedotia geayi</i> personal coll.	98	BEDOTIIDAE (c&s)
<i>Scomberesox saurus</i> personal coll.	240	SCOMBERESOCIDAE (c&s)
<i>Channa obscura</i> personal coll.	121	CHANNIDAE (c&s)
<i>Channa obscura</i> personal coll.	126	CHANNIDAE (c&s)
<i>Anthias pleurotaenia</i> AMNH 38119	100	SERRANIDAE (c&s)
<i>Serranus hepatus</i> personal coll.	72	SERRANIDAE (c&s)
<i>Lates calcarifer</i> AMNH 37836	80	CENTROPOMIDAE ^b (c&s)
<i>Centropomus robalito</i> AMNH 32925	99	CENTROPOMIDAE (c&s)
<i>Morone americana</i> AMNH 57453	112	MORONIDAE (c&s)
<i>Percopsis omiscomaycus</i> AMNH 27265	86	PERCOPSIDAE (c&s)
<i>Oligoplites saurus</i> AMNH 45080	132	CARANGIDAE (c&s)
<i>Parupeneus barberinoides</i> AMNH 43106	61	MULLIDAE (c&s)
<i>Kuhlia rupestris</i> AMNH 17954	96	KUHLIIDAE (c&s)
<i>Arnoglossus laterna</i> personal coll.	53	BOTHIDAE (c&s)

^ac&s = cleared and double stained, skel = skeletonized specimens, SL = standard length.

^b Mooi and Gill (1995) gave full familial status to the centropomid Latinae.

dissertational grant to RB from the Landes-graduierntenförderung Baden-Württemberg and subsequently a postdoctoral fellowship in the Department of Herpetology and Ichthyology, American Museum of Natural History, New York.

MATERIAL AND METHODS

Most specimens (see table 1) were cleared and double-stained according to the procedure of Dingerkus and Uhler (1977). A few data were gathered from large, skeletonized specimens. Length is given as standard length in millimeters.

Glycerin-stored cleared and stained specimens were transferred to 100% or 70% ethanol because connective tissue elements are

much easier to identify in ethanol. A retransfer into glycerin is possible whenever necessary. After a close examination, individual myosepta were removed with fine iris spring scissors by cutting close to their insertion on the axial skeleton. Removed myosepta were mounted on slides, and studied under a stereomicroscope in transmitted light and under a light microscope using transmitted light or difference-interference contrast. Storage of individual myosepta was in 100% ethanol.

Polarized light microscopy has an advantage in visualizing fiber pathways within a myoseptum, because of double-refraction of collagen fibers. Collagen fibers are observed as bright strands against a black background. We photographed myosepta with a polarized

light microscope (ZEISS Axioplan with camera MC-100). Several photographs were taken to cover the epaxial part of a myoseptum. Prints were later mounted on black cardboard to show the complete epaxial myoseptum.

Polarized light has some disadvantages. Thick intermuscular bones are not translucent, appear black, and thus are difficult to recognize. Thin intermuscular bones may be hard to distinguish from tendons in the photographs. However, ossifications were easy to identify by their red Alizarin stain during dissection. There are problems when collagen fibers at angles of about 45 or 135° cross, because of double refraction of collagen. One of the two directions then appears almost black and may seem to be lost in these crossing areas. Closer differential interference contrast (DIC) examination revealed this to be an artifact and fiber directions were always continuous. Nevertheless, it was sometimes difficult to find an orientation that revealed all fiber directions to the same extent.

Individual myosepta of the following freshly caught species supplement the list in table 1: *Caranx hippos* (Carangidae) and *Sphyræna barracuda* (Sphyrænidae). Myosepta were removed from adult specimens of the two species during the 64th Annual Alabama Deep Sea Fishing Rodeo on Dauphin Island, July 19–21, 1996. First, the muscle tissue was scooped out with a spoon. Then individual myosepta were cut close to the axial skeleton and preserved in 4% formalin. Remnants of muscle tissue were digested in a trypsin solution and the myosepta rinsed in water and photographed with incident light in front of a blackboard.

TERMINOLOGY

Distinct bundles of connective tissue fibers occur in epaxial and hypaxial parts of myosepta and in the horizontal septum. Patterson and Johnson (1995) applied different terms to these fiber bundles naming them epineural, epipleural and epicentral ligaments and posterior oblique tendons (POTs). Westneat (personal commun.) pointed out to us the fact that the proper anatomical term for these fiber bundles is tendon and not ligament. Tendons connect muscle to bone, whereas liga-

ments connect bone to bone. Therefore we use the term “intermuscular tendons” instead of Patterson and Johnson’s “intermuscular ligaments.” Accordingly, individual fiber bundles are named epineural tendons, epicentral tendons (= anterior oblique tendons), epipleural tendons, and posterior oblique tendons.

We maintain that fiber bundles fit the definition of tendon, not ligament, e.g., epineural tendons connect epaxial musculature to the axial skeleton. Intermuscular tendons transfer muscular forces from myomeres to the axial skeleton and thus act as tendons. When parts of the tendons ossify, the resulting intermuscular bones may sometimes be connected to the axial skeleton via a short bundle of fibers. Patterson and Johnson (1995) stressed that in such case the exact term for this proximal part is ligament because then it connects bone to bone, i.e., intermuscular bone to axial skeleton. Ontogenetically, however, it is the proximal portion of a tendon and we see no necessity to apply a different term to the same structure at a later point in ontogeny.

NUMBERING SEGMENTALLY ARRANGED STRUCTURES

The area of attachment of one myoseptum encompasses several vertebrae and thus numbering a myoseptum is problematic. For convenience, we number a given myoseptum according to the most anterior vertebra attached to the anterior cone of the myoseptum. In all investigated specimens this is the same vertebra attached to the epineural bone or epineural tendon.

ABBREVIATIONS

BL	Baudelot’s ligament
DAC	dorsal anterior cone
DPC	dorsal posterior cone
ecb	epicentral bone
ect	epicentral tendon
enb	epineural bone
ent	epineural tendon
EFP	epaxial flanking part
ESP	epaxial sloping part
HFP	hypaxial flanking part
HSP	hypaxial sloping part
lb	lateral band
SH	horizontal septum

VAC ventral anterior cone
VPC ventral posterior cone

CONNECTIVE TISSUE FIBERS IN EPAXIAL MYOSEPTUM

RESULTS

THREE-DIMENSIONAL SHAPE OF MYOSEPTUM

Patterson and Johnson (1995) pointed out that intermuscular bones ossifying in the myoseptum are associated with strands of strong fibers of connective tissue, their "intermuscular ligaments." These fiber bundles of connective tissue that we call intermuscular tendons (see above), are only parts of the complete myoseptum.

Our description of a typical myoseptum from the midbody region is based on findings of Gemballa (1995) and on additional data from our study. Gemballa investigated representatives of all major actinopterygian subgroups and found several invariable similarities in the basic architecture of the myoseptum, i.e., the three dimensional shape and arrangement of connective tissue fibers. We have confirmed his results. Terminology for the different parts of the myoseptum is partly adopted and modified from Alexander (1969), Willemse (1972) and Westneat et al. (1993).

The myoseptum is attached to the axial skeleton medially. Its area of attachment extends over several vertebrae, commonly three, sometimes up to five. The lateral area of attachment is the integument. When superimposed in lateral view (fig. 1A), both areas of attachment have the shape of ($\approx$). The myoseptum extends between the two areas of attachment. It is separated by the horizontal septum into epaxial and hypaxial parts. Both epaxial and hypaxial parts of the anterior myoseptum point into dorsal and ventral anterior cones (DAC and VAC) close to the horizontal septum (SH). The posterior tips of the ($\approx$) point into dorsal and ventral posterior cones (DPC and VPC). The relative size of anterior and posterior cones varies along the body and among taxa. Between anterior and posterior cones are epaxial or hypaxial sloping parts (ESP or HSP). From the posterior cones the myoseptum flexes anteriorly in the epaxial and hypaxial regions and forms epaxial and hypaxial flanking parts (EFP or HFP).

When the epaxial part of the myoseptum between the horizontal septum and the dorsal posterior cone is removed and spread out, usually two fiber bundles are recognized. They are illustrated schematically in figure 1B and are shown for several species in subsequent figures. One bundle of fibers originates on the neural arch of the vertebra, frequently as a distinct tendon, and extends posterolaterally toward the integument, where it fans out distally. This bundle is the epineural ligament of Patterson and Johnson (1995) and is here referred to as epineural tendon (see paragraph on terminology above). The second bundle originates at the dorsal anterior cone and also runs posterolaterally but then curves dorsally and fans out into the dorsal posterior cone. We call this structure the lateral band because it never shows the characteristic convergence of fibers that appear as a distinct tendon. It is more or less prominent and resembles an aponeurosis in some species. Such a structure was not reported by Patterson and Johnson (1995) for any teleost that they studied.

Ossifications can be found in both of the two fiber bundles or only in one of them. Ossification in both fiber bundles results in a characteristic Y-shaped bone with proximal forking. The anteromedial branch of the bone is embedded in the epineural tendon. This bone is attached either directly or via the proximal part of the epineural tendon to the respective vertebra. The anterolateral branch of the bone is embedded in the anterior part of the lateral band and ends free in the dorsal anterior cone. Ossification in only one fiber bundle causes the regular slightly curved splint of bone. Both types of ossifications are referred to as epineural bones by Patterson and Johnson (1995).

CONNECTIVE TISSUE FIBER BUNDLES IN HORIZONTAL SEPTUM

The horizontal septum separates hypaxial and epaxial parts of the myosepta and myomeres. Two distinct fiber bundles with different orientations may be developed in the horizontal septum. They were called anterior oblique tendons (AOTs) and posterior

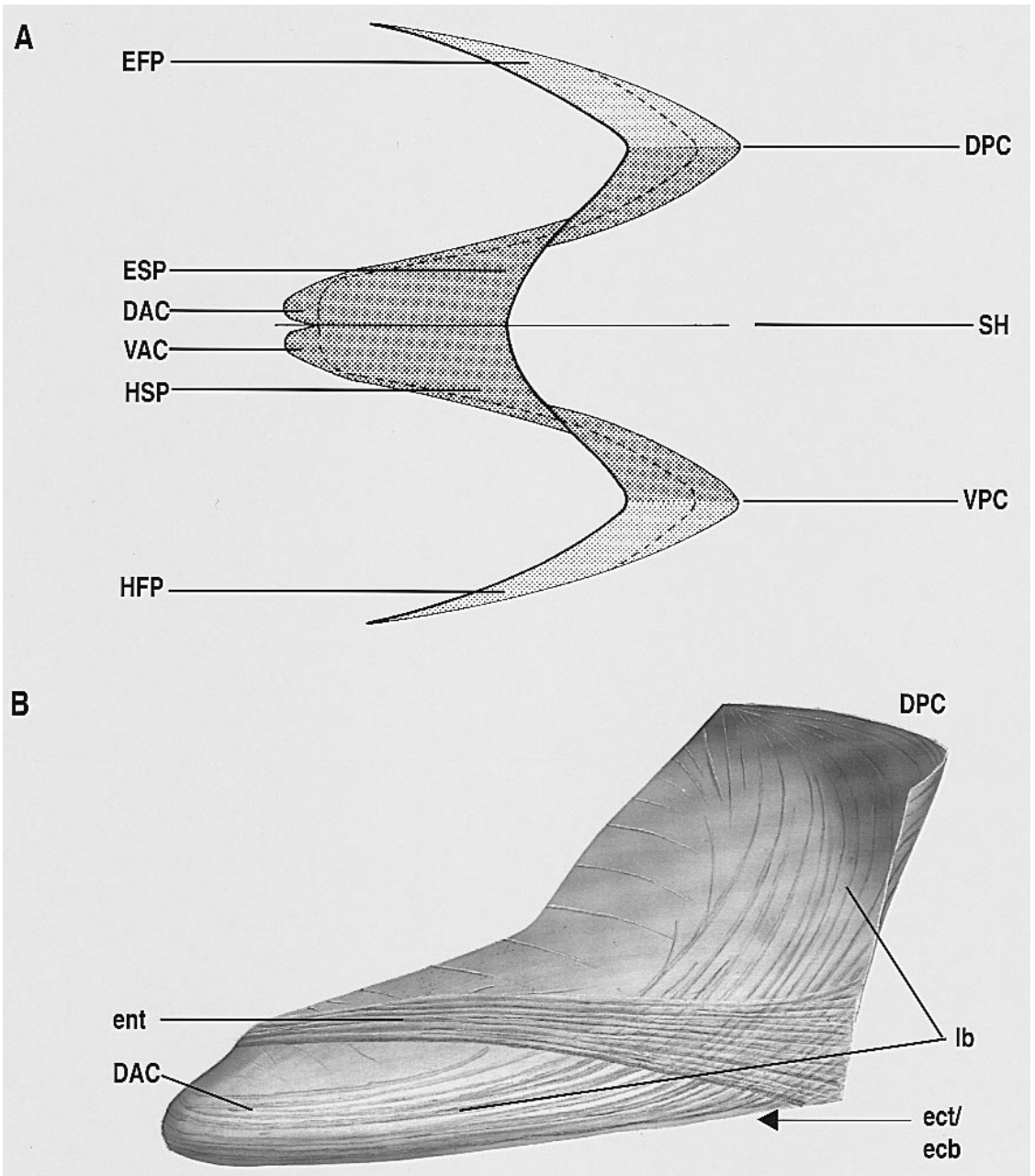


Fig. 1. **A**, Schematic representation of typical myoseptum from midbody in lateral view, anterior to the left. Position of cones in epaxial part (DAC, DPC) and hypaxial part (VAC, VPC) and epaxial and hypaxial flanking parts (EFP, HFP) are shown. Areas of attachment are $\geq$ -shaped. Dashed line represents medial area of attachment at axial skeleton; solid line lateral, area of attachment at integument. Area between anterior and posterior cone is called epaxial sloping part (ESP) and hypaxial sloping part (HSP), respectively (after Gemballa, 1995). **B**, Schematic representation of ESP of midbody myoseptum of left side, anterodorsal view. Arrangement of epineural tendon (ent) and lateral band (lb) is shown. Arrow points to position of epicentral bone or tendon that runs in horizontal septum. Its proximal part covered by DAC.

oblique tendons (POTs) (Kafuku, 1950, as cited in Patterson and Johnson, 1995). The AOTs were called epicentral ligaments by Patterson and Johnson (1995), here referred to as epicentral tendons (see above). The ossifications within these tendons are the epicentral bones. Epicentral bones or tendons are oriented posterolaterally. They are crossed by the POTs that are oriented antero-laterally.

CONNECTIVE TISSUE FIBERS IN HYPAXIAL MYOSEPTUM

The hypaxial part of the myoseptum is basically a mirror image of the epaxial part. This is not the case in the more anterior myosepta, where the abdominal cavity occupies more space and restricts the hypaxial musculature to narrow strips lateral to the ribs. Exactly as in the epaxial part, the hypaxial part of the myoseptum shows two prominent fiber bundles. One bundle originates on the rib or the dorsal part of the hemal arch and runs posterolaterally to the integument. It was called epipleural ligament by Patterson and Johnson (1995) but, for reasons given, is termed epipleural tendon. The other bundle originates more dorsally and extends likewise posterolaterally and ventrally into the ventral posterior cone. There it flexes into the hypaxial flanking part. We call this the lateral band of the hypaxial myoseptum. Ossifications can be developed in both bundles resulting in a proximally forked bone, or only in one bundle resulting in a slightly curved unforked bone. Both types are referred to as epipleural bones by Patterson and Johnson (1995).

FIBER BUNDLES IN FLANKING PARTS (EFP, HFP)

There are no distinct tendons in either the epaxial or the hypaxial flanking parts of the myoseptum. The fibers commonly run longitudinally forming broad bands. These bands may partly ossify in some teleosts and the resulting bones are called myorhabdoi after Chapman (1944).

INTERMUSCULAR BONES AND TENDONS IN ACANTHOMORPHS

In the following paragraphs we present a detailed description of the arrangement of

connective tissue fibers in the epaxial part of myosepta of selected taxa. We describe a typical myoseptum from the midbody region of a given taxon and then record changes that occur in anterior myosepta.

POLYMIXIIFORMES: *Polymixia lowei*. Patterson and Johnson (1995) described the intermusculars of *Polymixia* in detail. There are two series, partly bony and partly tendinous (epineurals and epipleurals), and one tendinous series of epicentrals. The first intermuscular bone of *Polymixia* is stronger than the others, lies in the horizontal septum, and articulates in a groove on the neural arch of the first vertebra.

Myoseptum 13 (fig. 2A) bears a short but well-developed epicentral tendon in the horizontal septum. The epineural tendon is stout and its posterior part approaches the lateral band. Individual fibers diverge along its length from the epineural tendon and cross the lateral band. The lateral band is broad without any condensations of fibers to distinct bundles.

Rostrally, epineural tendon 13 is well in line with the epineural tendons or bones of the more anterior myosepta. Both bones and tendons insert on the neural arch of the respective vertebrae. Epicentral tendon 13 is likewise in line with epicentrals of anterior segments up to 2. In the first myoseptum we find a different situation (fig. 2B, C). When observed in alcohol under the stereomicroscope, or with polarized light under the microscope, a distinct tendinous structure is present in the epineural position of myoseptum 1. It is in line with epineurals of all subsequent vertebrae (fig. 2C). We therefore consider this tendon to be the epineural of myoseptum 1. It inserts dorsal to the intermuscular bone of the first vertebra. The intermuscular bone is in the epicentral position in the horizontal septum and is in line with epicentral tendons of posterior segments. We consider this to be the bony epicentral of myoseptum 1 (see below).

LAMPRIDIFORMES: *Velifer hypselopterus*. *Velifer* is a deep-bodied fish and, as is frequently the case in myosepta of such fishes, anterior cones are not developed. We show myoseptum 11 (fig. 3A) of the midbody region. There is an epineural tendon with a stout proximal end that inserts on the neural

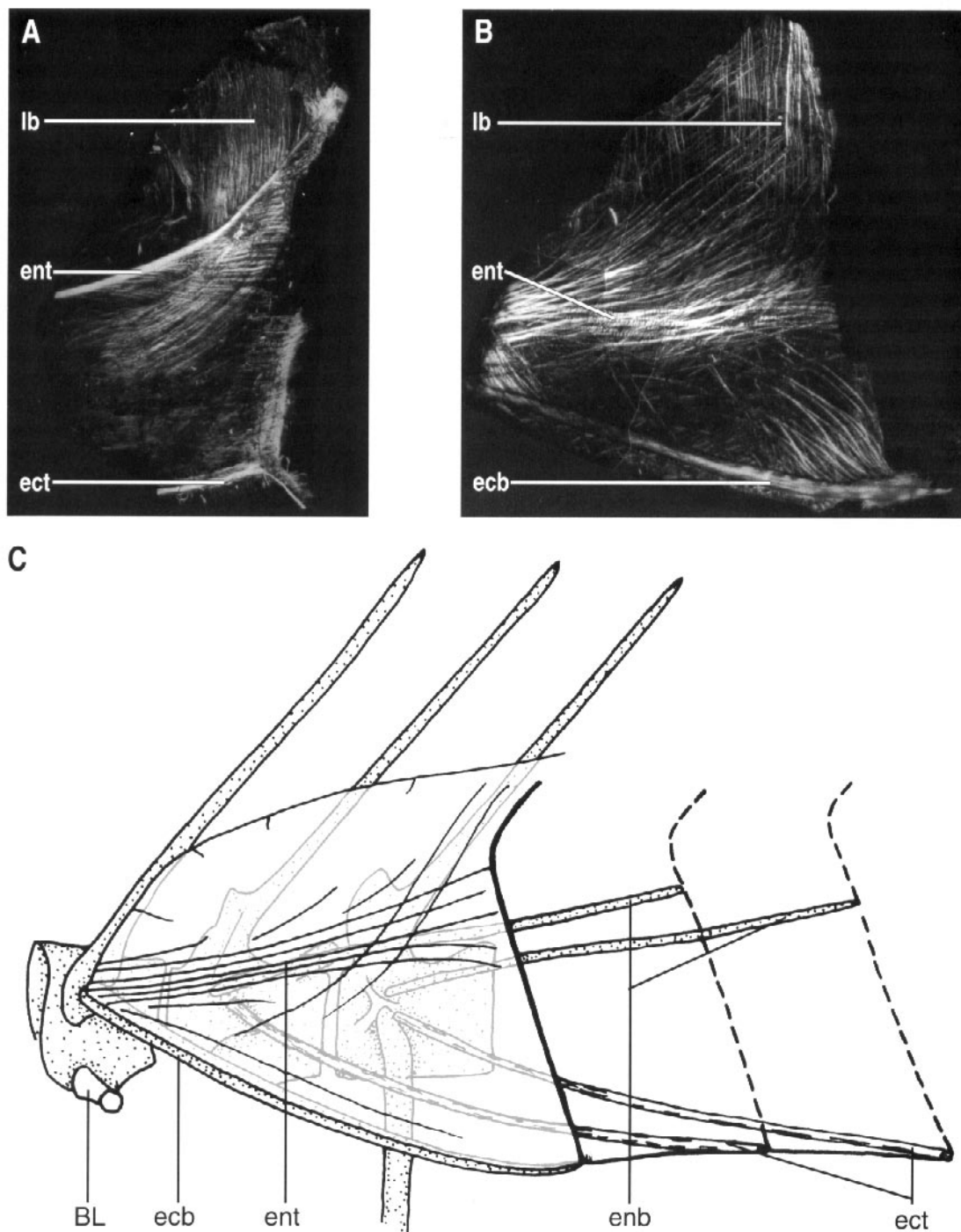


Fig. 2. *Polymixia lowei*. **A, B.** Micrographs of epaxial myosepta. Here and in all subsequent micrographs myosepta spread out; medial area of attachment to the left. **A,** Myoseptum 13. **B,** Myoseptum 1. **C,** Spatial relationship of epaxial myoseptum 1 and axial skeleton, lateral view, parts behind myoseptum illustrated in gray, modified after Patterson and Johnson (1995).

spine and with a distal end that fans out. The broad lateral band coming from the DPC crosses the epineural tendon and inserts along the height of the centrum. It appears to be of equal thickness. In the horizontal septum there is an epicentral tendon that is crossed by three POTs.

In anterior myosepta some gradual changes can be noticed. They are shown by photographs of myosepta 9, 4, and 1 (fig. 3B–D). Epineural tendon 11 is aligned with the series of epineural bones. The site of attachment shifts from the neural spine in 9 to the neural arch in 1. Epineural bones 10–7 insert with a short proximal tendinous sheath and those of 6 to 1 articulate directly with vertebrae. We identified epicentral tendons for myosepta 11–2 (see fig. 3B, C for myosepta 9 and 4) but failed to do so for myoseptum 1. There it seems to be represented by a diffuse bundle of fibers at the level of Baudelot's ligament (fig. 3D).

Lampris guttatus. We were not able to study myosepta of this lampridiform but found differences from Patterson and Johnson's (1995) account of its intermusculars. The two anterior intermuscular bones of our large specimen of *L. guttatus* (AMNH 79669) are attached to centra and not to neural arches or spines. As already noted by Patterson and Johnson, all following intermuscular bones are attached to proximal portion of ribs.

BERYCIFORMES: *Hoplostethus mediterraneus*. Examination of myosepta 9–1 reveals the basic arrangement of the lateral band, epineural, and epicentral tendons. Myoseptum 8 of *Hoplostethus* (fig. 4A) is thus similar to myosepta of the midbody region of *Velifer* (9, 11, fig. 3A, B) or *Polymixia* (13, fig. 2A). It has a broad epicentral tendon in the horizontal septum. In this area of the trunk, vertebrae have long hemal spines. The horizontal septum and epicentral tendons are displaced ventrally and attach at their distal ends. Epineural tendon 8 inserts on the centrum dorsal to the epicentral. Its fibers diverge in its middle part and eventually fan out at its distal end. The remaining part of the myoseptum consists of very fine, thin fibers that can be recognized only under polarized light. Consequently, they form a very faint lateral band when compared to the for-

mation in *Velifer* or *Polymixia*. Epineural tendon of myoseptum 6 (fig. 4B) is not as distinct in its proximal part as that of 8. In addition, distance between the insertions of epicentral and epineural has doubled compared to 8. This is caused by a dorsal shift of the insertion of the epineural from the centrum in 8 to the neural arch in 6. In myoseptum 3 (fig. 4C) the epicentral tendon attaches to the ventral part of the centrum and the distance between the insertions of epineural and epicentral tendons has increased further. Epicentral tendons 8–3 are in line with epicentral bones in 2 and 1 (fig. 4D). Also epineural tendons 1–8 are aligned and thus two complete series are present.

We observed a ventral shift of the epineural and epicentral series toward the midbody region in our specimen of *Hoplostethus mediterraneus*. The shift starts approximately at vertebra 6, which bears the first hemal spine. As the hemal spine lengthens in subsequent segments, the epicentral series shifts further ventrally to the level of the distal end of the hemal spines. Insertion of epineural elements shifts ventrally from the neural arch to the centrum. Further caudally we recorded a dorsal shift of the two series. The epineural tendon is attached from vertebra 14 to the neural arch. The insertion of the epicentral gradually shifts up to the centrum from vertebra 16.

Gephyroberyx philippinus (not figured). The pattern of tendons and bones in *Gephyroberyx* is similar to that in *Hoplostethus*. There is ventral shift of the middle part of the whole series. The bony epicentrals of the first two myosepta attach to the neural arch, followed by a series of epicentral tendons. We failed to remove myoseptum 1 for a closer examination but we were able to detect epineural tendons dorsal to epicentrals in all remaining myosepta. There is also a lateral band in the normal position in each myoseptum.

Holocentrus rufus. Epineural 10 (fig. 5A) is completely tendinous as in the posterior segments. It inserts on the neural arch of vertebra 10. There is an epicentral tendon in the horizontal septum. We found the same arrangement in myosepta 9, 8, and 7. In 8 (fig. 5B) the epineural tendon bears a small ossification in its distal part, whereas the proxi-

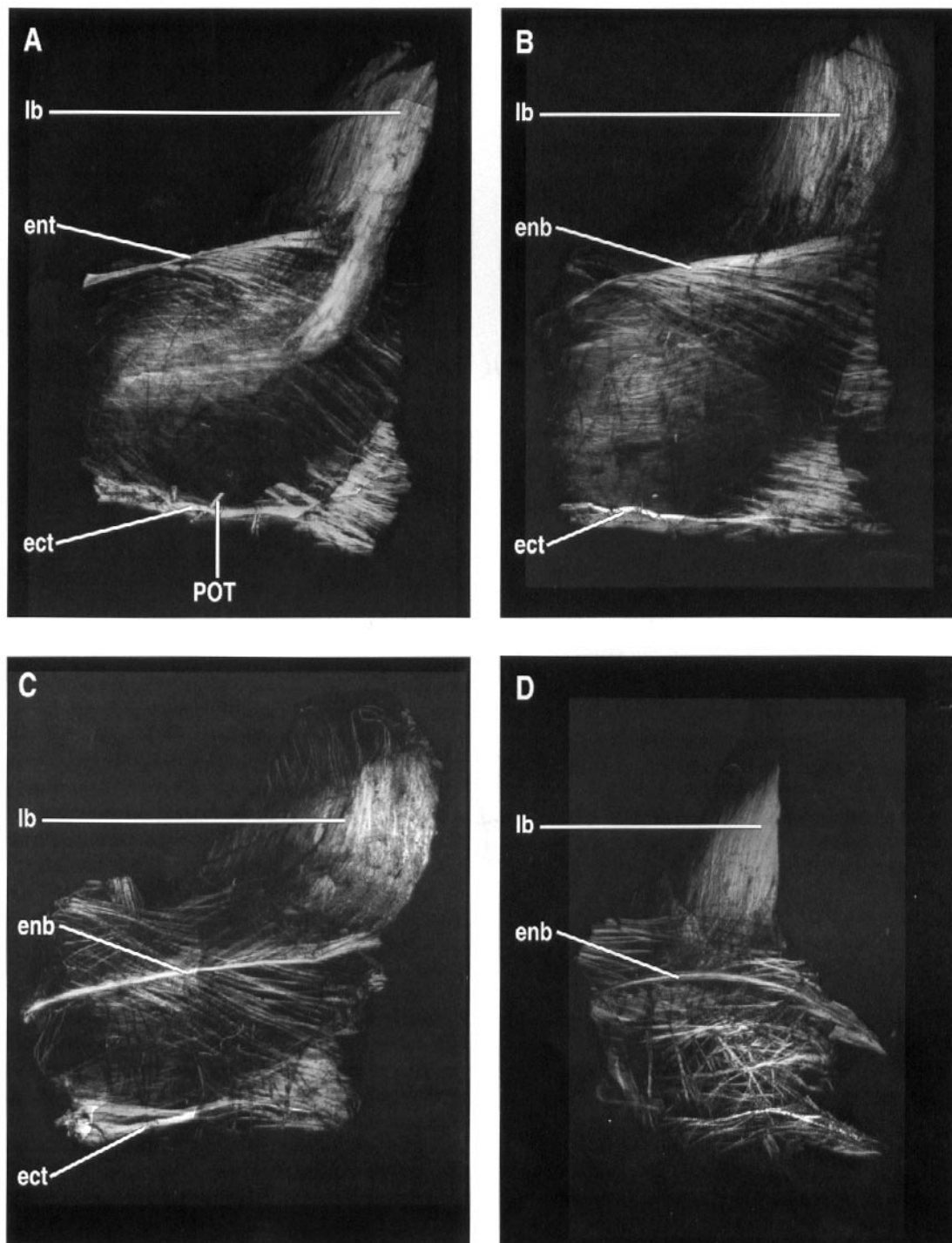


Fig. 3. *Velifer hypselopterus*. Micrographs of epaxial myosepta **A**, Myoseptum 11. **B**, Myoseptum 9. **C**, Myoseptum 4. **D**, Myoseptum 1.

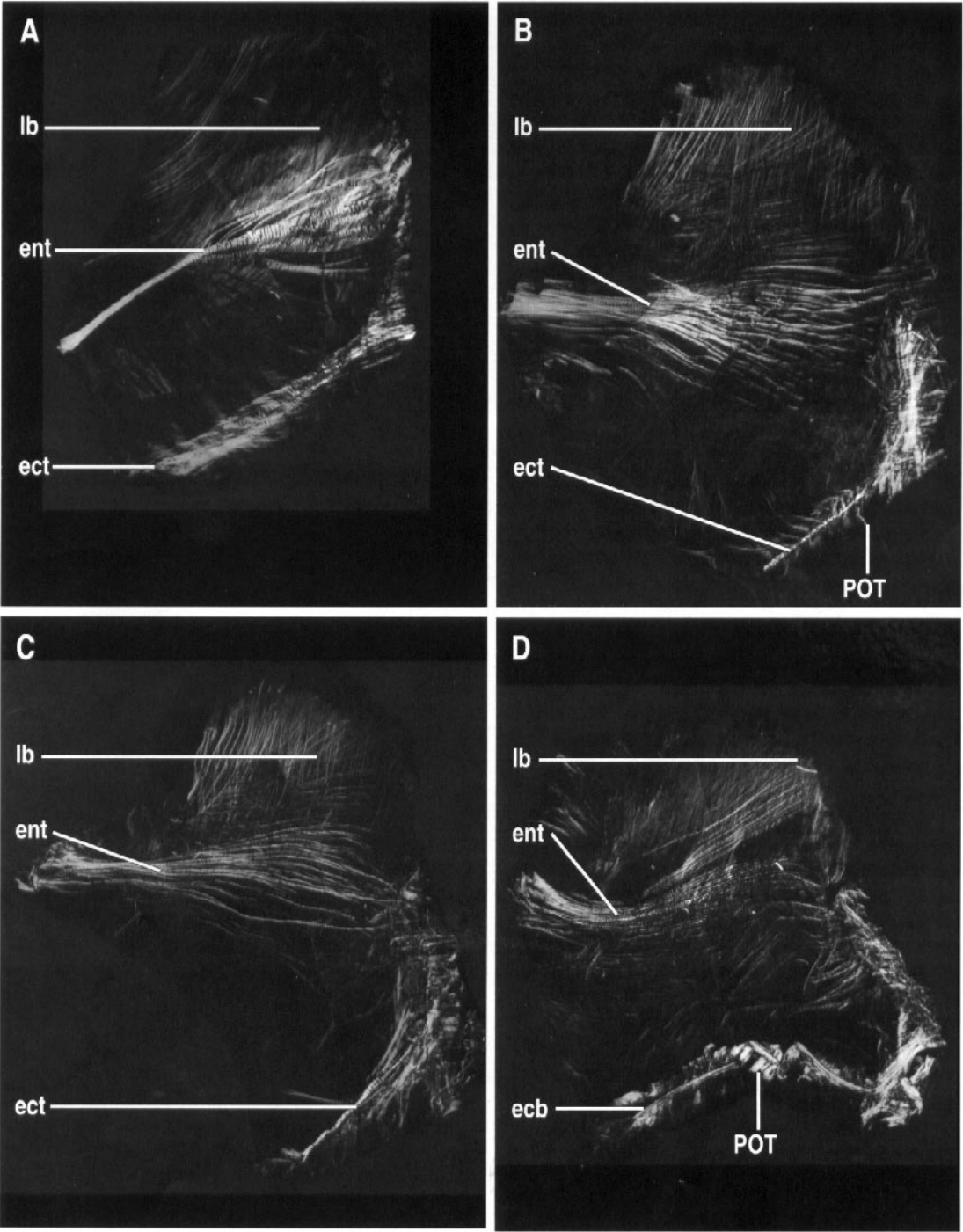


Fig. 4. *Hoplostethus mediterraneus*. Micrographs of epaxial myosepta. **A**, Myoseptum 8. **B**, Myoseptum 6. **C**, Myoseptum 3. **D**, Myoseptum 1, epicentral bone broken twice.

mal part remains tendinous. In 7 (fig. 5C) the epineural bone is attached directly to the axial skeleton. The site of insertion is shifted ventrally from the neural arch in 10, and the centrum in 9, to the proximal part of the ventral rib in 8 and 7. The basic arrangement of fibers in these myosepta of the midbody region is almost identical to that described for *Polymixia* (13, fig. 2A), *Velifer* (9, 11; fig. 3A, B), and *Hoplostethus* (8, fig. 4A).

Anteriorly, each myoseptum from 6 to 3 bears an epicentral tendon (see fig. 5D–F). In myosepta 2 and 1, epicentrals are ossified. We found some peculiar changes of the intermuscular bones in myosepta 6 (fig. 5D) to 1, which we did not observe in other teleosts. Starting with 6, a ventral shift of the epineural bone can be noticed that involves the proximal part of the bone. This intermuscular bone 6 is located in the lateral band but still attached to the rib as in 7. In myosepta 5, 4, and 3 (marked by *, see fig. 5E, F) the bones have lost contact with the axial skeleton and are shifted further ventrally. They are in a position neither epineural nor epicentral but somewhat intermediate. There is still an epicentral tendon beneath these bones. The strong epineural tendon of the midbody myosepta is not present here. Inserting at the centrum, there is a set of fibers that resembles the epineural fiber direction but the fibers do not extend to the integument. Bones of myosepta 2 and 1 (fig. 5G, H) are strongly developed in sharp contrast to those of 5, 4, and 3. They attach to centrum 2 or to neural arch 1. They are in the horizontal septum and therefore we consider them epicentrals.

This positional difference of intermuscular bones 1 and 2 (epicentrals) from those of 3, 4, and 5 and from posterior ones (epineurals 6 on) is reflected also by an ontogenetic difference. In a series of five specimens of undetermined Holocentrinae ranging from 11 to 26 mm SL, we found that intermuscular bones 1 and 2 are well ossified in all specimens and attach to the neural arch. However, bones posterior to 2 are not developed until the 26 mm stage. At this length we found six additional ossifications (3–8), none of them reaching the vertebral column.

PARACANTHOPTERYGII: *Aphredoderus sayanus*. We found some differences from Patterson and Johnson's (1995) report of the in-

termusculars of this species. Our specimen had nine bony intermusculars in the horizontal septum that represent the epicentral series. Bones 1 and 2 insert on the neural arch and posterior bones on the rib. This bony series is continued caudally by well-developed epicentral tendons. Myoseptum 15 (fig. 6A) is an example from the midbody region. There is a strong epicentral tendon with few POTs attached to it, a lateral band of evenly distributed fibers, and an epineural tendon with converging fibers. The myoseptum is thin, and the epineural tendon is visible only under a microscope.

Molva dipterygia. As in *Aphredoderus*, there is a bony epicentral series in the horizontal septum. We show a myoseptum from the midbody region (fig. 6B). It bears a small epicentral ossification in the horizontal septum that is embedded in a tendinous sheath and not attached to the axial skeleton. Well above the horizontal septum there is a broad epineural tendon with the fibers converging slightly. They cross fibers of an aponeurosis-like, elongated lateral band.

ATHERINOMORPHA: *Bedotia geayi*. As recorded by Patterson and Johnson (1995), there is a long series of bones in the horizontal septum of *Bedotia*. We show myoseptum 15 (fig. 6C). There is a well-developed bony epicentral in the horizontal septum with POTs crossing it. The lateral band is broad. The epineural is present but inconspicuous.

Scomberesox saurus. All myosepta of this elongate species exhibit long DACs and DPCs which is reflected by the presence of a very long lateral band. As in *Bedotia* there is a long series of epicentrals in the horizontal septum. We show myoseptum 11 (fig. 6D) of this species. A bony epicentral is present and a conspicuous lateral band. The epineural is a faint structure consisting only of few strands of fibers.

PERCOMORPHA: *Lates calcarifer*. As described by Patterson and Johnson (1995), *Lates* has a short series of four intermuscular bones in the horizontal septum of the first four vertebra which we homologize with epicentrals (see below). Bones 1 and 2 attach to neural arches and 3 and 4 to ribs. These bones are continued by epicentral tendons that are hard to recognize from 4 through 9. In figure 6E the weak tendon of 8 is shown.

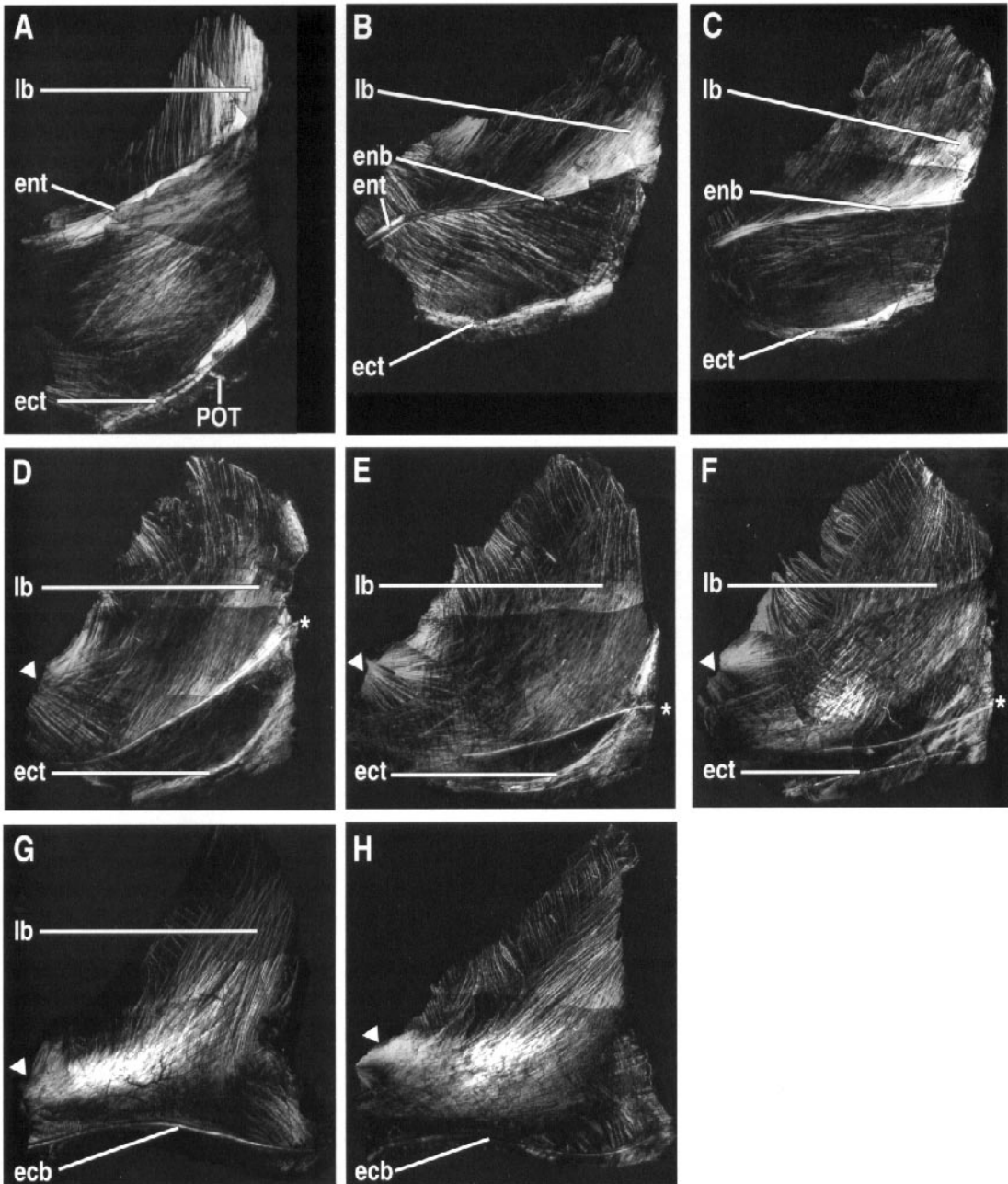
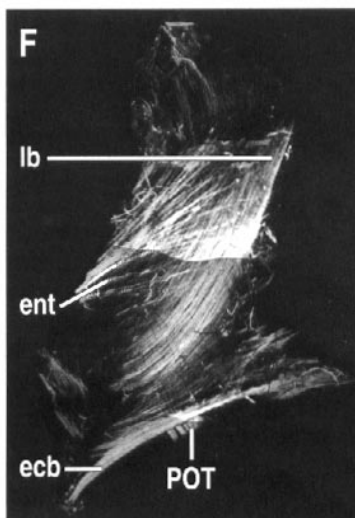
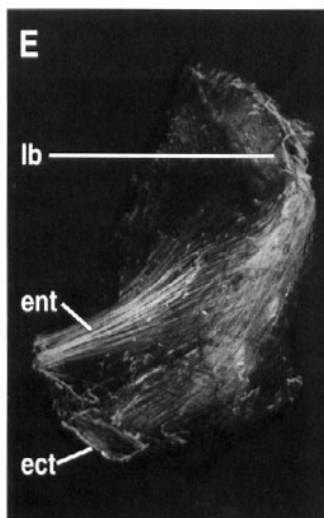
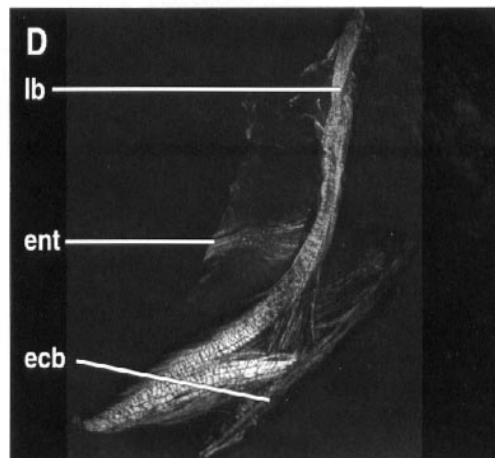
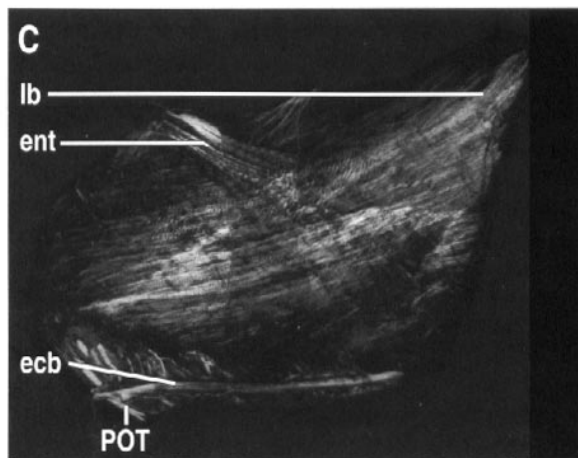
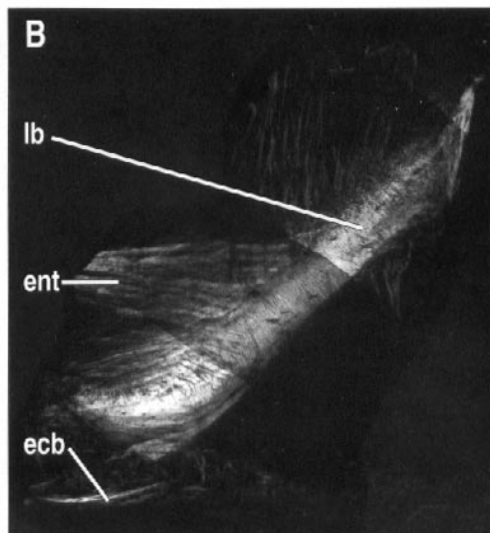
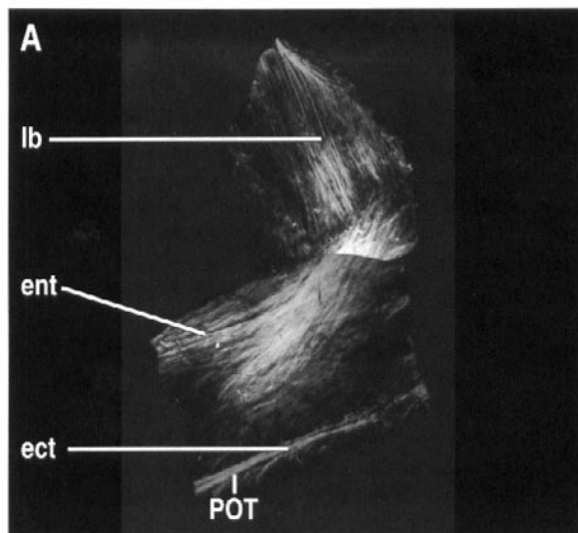


Fig 5. *Holocentrus rufus*. Micrographs of epaxial myosepta. **A**, Myoseptum 10. **B**, Myoseptum 8. **C**, Myoseptum 7. **D**, Myoseptum 6. **E**, Myoseptum 5. **F**, Myoseptum 4. **G**, Myoseptum 2. **H**, Myoseptum 1. Note bony element (distal end marked by asterisk) shifting ventrally from margin of lateral band in D to area between epicentral tendon and lateral band in F (see discussion). Proximal ends of epineural tendons in D–H marked by arrowhead.



More posteriorly, these tendons become more pronounced and were recorded by Patterson and Johnson (1995) for vertebra 12 and posterior segments. In addition to this epicentral series there is an epineural series dorsal to the former. In myoseptum 8, an example for the midbody region, the epineural tendon consists of numerous converging fibers. The lateral band is developed as the normal broad band of evenly distributed fibers. This series of epineural tendons is continued anteriorly as shown by myoseptum 2 (fig. 6F). Here the epineural tendon consists of fewer fibers than the epineural tendon on vertebra 8. The epicentral bone is located below the epineural and crossed by few POTs.

Centropomus robalito. *Centropomus* has a pattern of intermuscular bones and tendons like that of *Lates*. Epicentral bones are restricted to the anterior eight vertebrae with 1 and 2 attached to neural arches and the subsequent ones to ribs. Bony epicentrals are continued by tendons that are weakly developed. We show myoseptum 9 (fig. 7A) as an example of this region. In contrast, epineural tendons are conspicuous and consist of numerous converging fibers. They are accompanied by a broad lateral band. Anteriorly, epineural tendons gradually change from distinct tendons to broad bands with fibers converging only slightly. This can be noted in myoseptum 3 in figure 7B. Below the epineural tendon there is an epicentral bone.

Morone americana. Intermusculars of *M. americana* strongly resemble those of *Lates* and *Centropomus*. The seven anterior myosepta have epicentral bones in the horizontal septum that are continued posteriorly by tendons, as shown by myoseptum 11 (fig. 7C). Epicentral and epineural tendons can be easily recognized. The lateral band is present. In myoseptum 6 (fig. 7D), the epicentral is bony and the epineural tendon consists of fewer fibers than that of 11. In myoseptum 2 (fig. 7E), the epicentral bone is longer than in 6 and attached to the neural arch. The epineural tendon is well-developed and inserts

above the epicentral. Myoseptum 1 (fig. 7F) has the same arrangement as 2, but the epineural tendon has a more diffuse appearance.

Serranus hepatus and *Pseudanthias pleurotaenia*. We found 11 epicentral bones in the horizontal septum in *Serranus* and 12 in *Pseudanthias*. Figure 8A shows myoseptum 15 of *Serranus*. There is a distinct epineural tendon with strongly converging fibers. The epicentral tendon is weakly developed. Both epicentral and epineural series are continued anteriorly. In myosepta 8 (fig. 8B) and 2 (fig. 8C), the epicentral is ossified but there is no remarkable change in the epineural tendon. The situation is very similar in *Pseudanthias*. In both myosepta 8 (fig. 8D) and 3 (fig. 8E) the epineural tendon is well above the epicentral bone. The lateral band is only weakly developed.

Parupeneus barberinoides. Our specimen of *Parupeneus* bears a series of 14 epicentral bones in the horizontal septum. Their site of attachment on the axial skeleton is the same as reported for intermuscular bones (there termed epineurals) of *Upeneus* by Patterson and Johnson (1995). In both genera this series is continued by tendons. There is a second series of intermusculars above the horizontal septum, the epineural tendons, which can be traced rostrally to the second segment.

Kuhlia rupestris. *Kuhlia* has a series of seven epicentral bones in the horizontal septum. As evidenced by myoseptum 5 (fig. 9A), there is an epineural tendon above the epicentral bone. It consists of several strong converging fibers. Myoseptum 8 (fig. 9B) is almost identical to 5 but the epicentral is tendinous here.

Oligoplites saurus. The epicentral series of *Oligoplites* consists of nine bony elements continued caudally by tendons. We show myosepta 10 from the midbody and 2 from the anterior region. Myoseptum 2 (fig. 9C) has a bony epicentral. The lateral band is broad and consists of thick fibers. The epineural tendon is conspicuous and inserts on the neural arch. Myoseptum 10 (fig. 9D) is different

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Fig. 6. Micrographs of epaxial myosepta. **A**, *Aphredoderus sayanus*, myoseptum 15. **B**, *Molva dipterygia*, myoseptum of midbody region. **C**, *Bedotia geayi*, myoseptum 15. **D**, *Scomberesox saurus*, myoseptum of midbody region. **E**, **F**, *Lates calcarifer*. **E**, Myoseptum 8. **F**, Myoseptum 2.

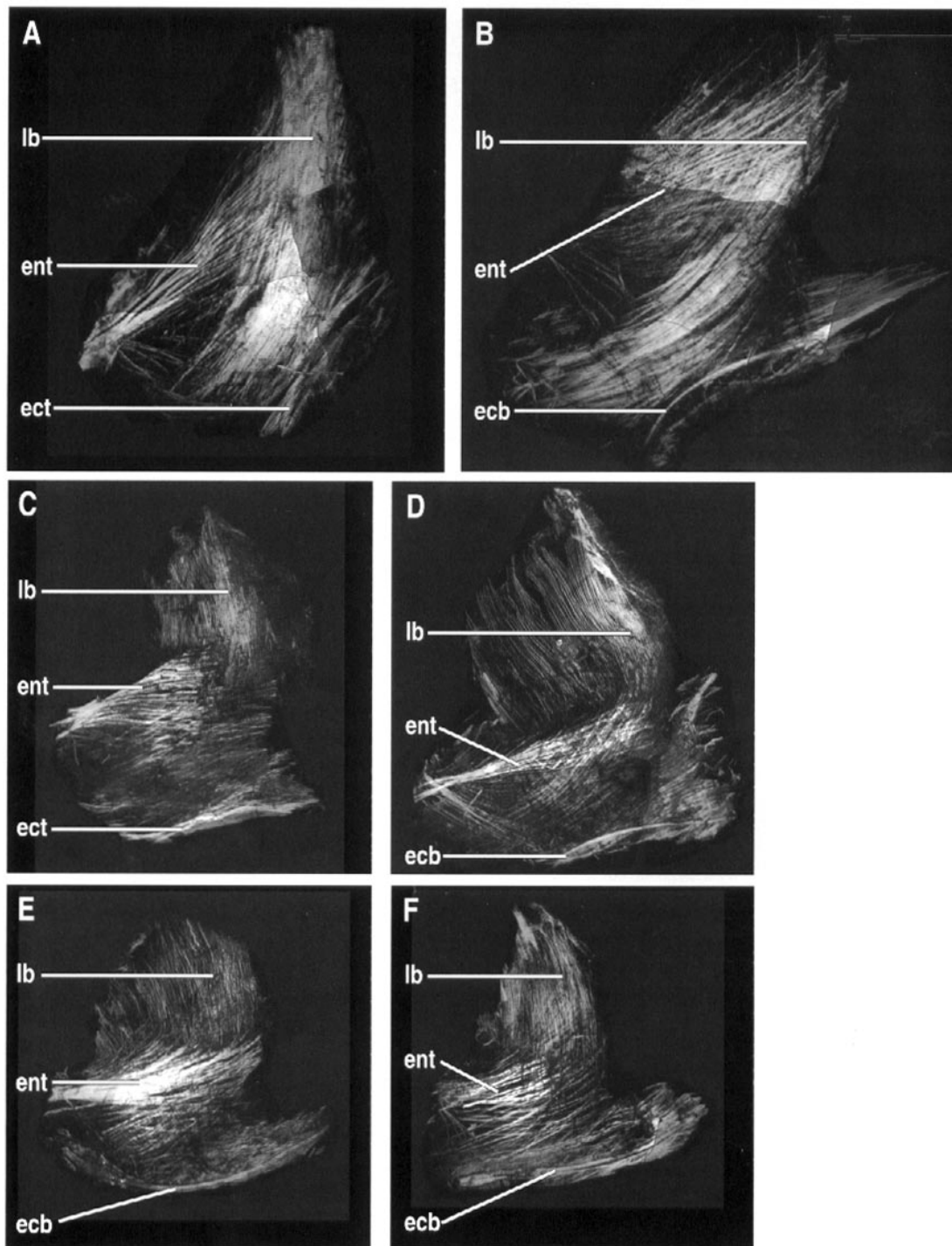


Fig 7. Micrographs of epaxial myosepta. **A, B.** *Centropomus robalito*. **A,** Myoseptum 9. **B,** Myoseptum 3. **C–F.** *Morone americana*. **C,** Myoseptum 11. **D,** Myoseptum 6. **E,** Myoseptum 2. **F,** Myoseptum 1.

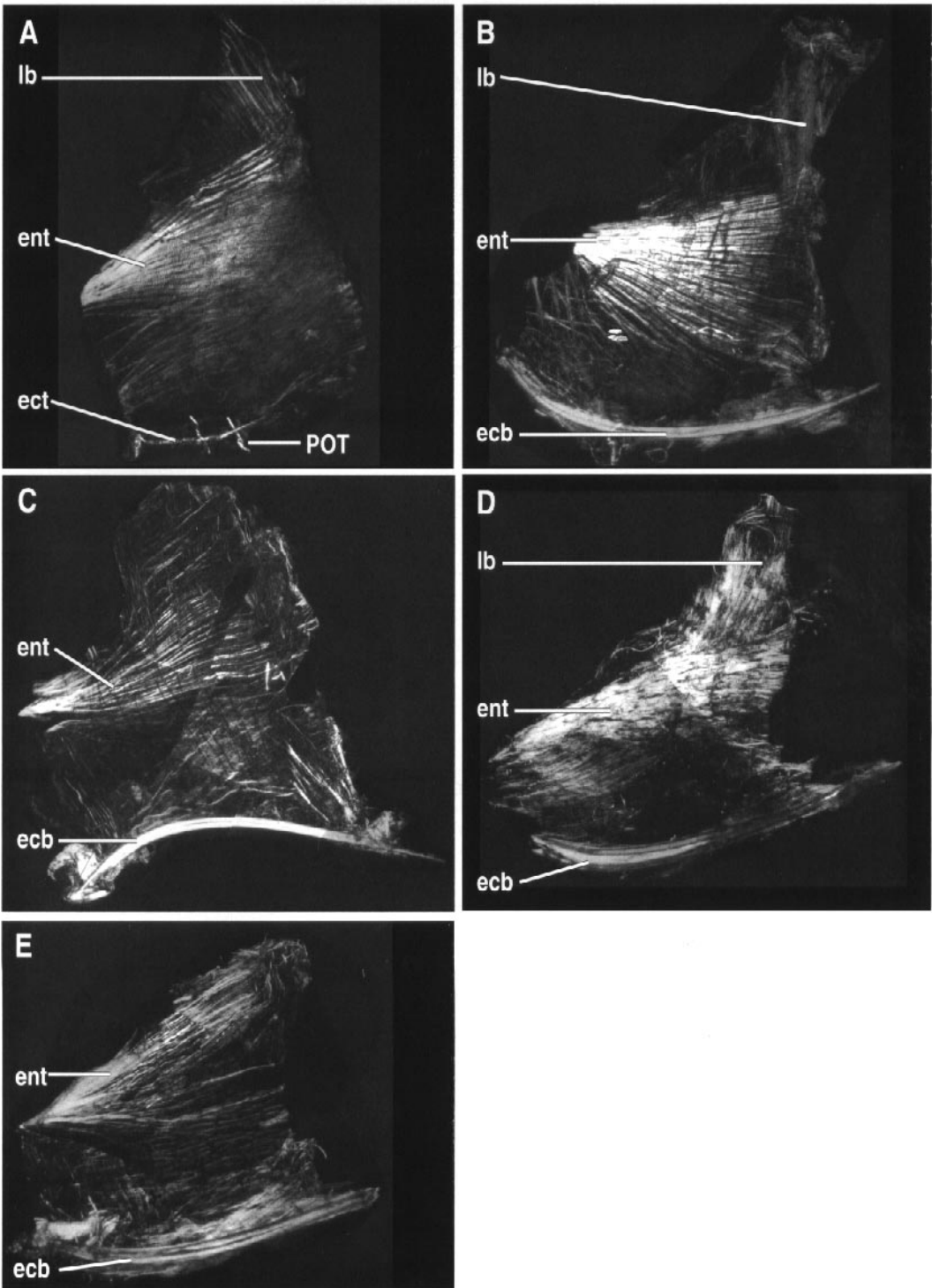


Fig 8. Micrographs of epaxial myosepta. A–C. *Serranus hepatus*. A, Myoseptum 15. B, Myoseptum 8. C, Myoseptum 2. D, E. *Pseudanthias pleurotaenia*. D, Myoseptum 8. E, Myoseptum 3.

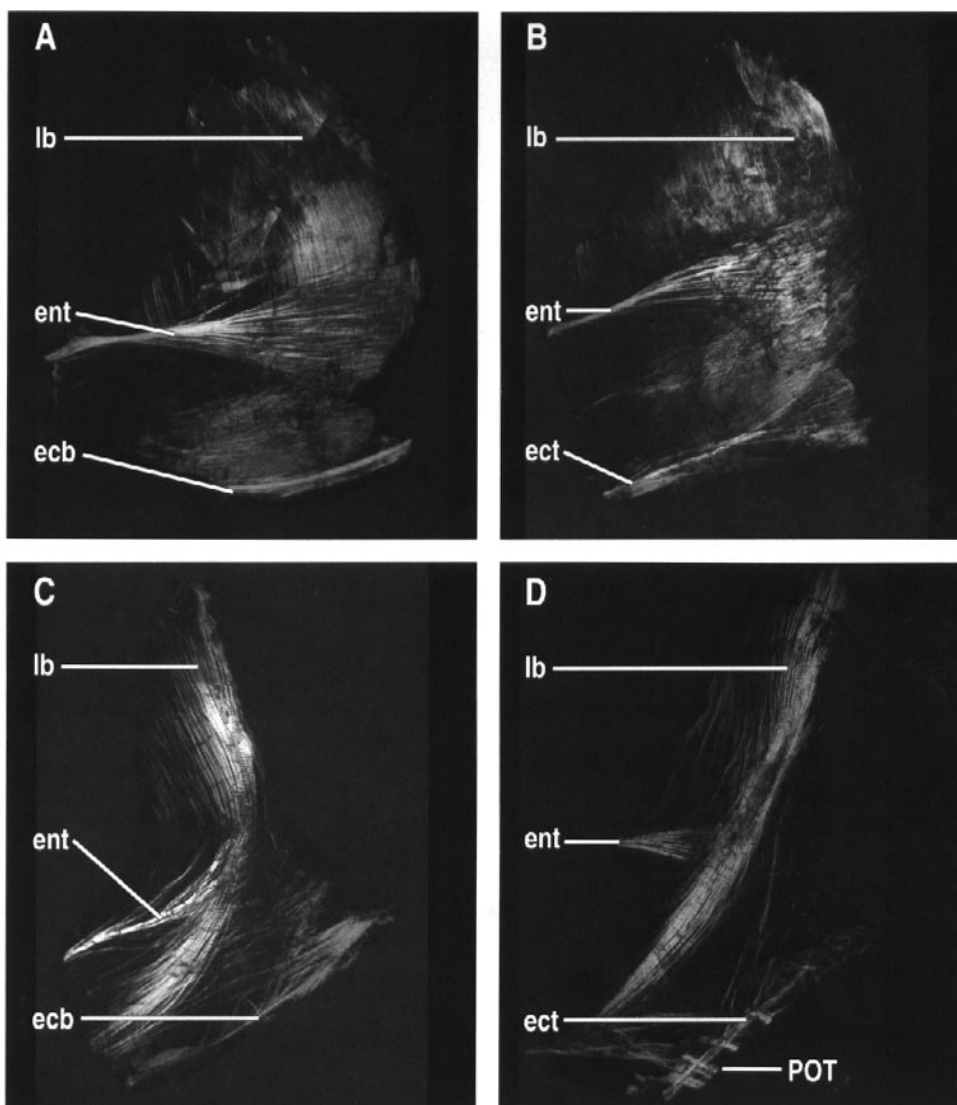


Fig 9. Micrographs of epaxial myosepta. **A, B.** *Kuhlia rupestris*. **A,** Myoseptum 5. **B,** Myoseptum 8. **C, D.** *Oligoplites saurus*. **C,** Myoseptum 2. **D,** Myoseptum 10.

from 2 in that it is more elongate and has a distinct DAC. The epicentral is tendinous and has numerous POTs crossing it. The lateral band is a long and strong fiber bundle. The epineural tendon consists of several thick converging fibers that attach to the neural spine.

Caranx hippos. We show myoseptum 2 and one from the anterior abdominal region (precise segment unknown; fig. 10A, B) removed from an adult specimen. The arrange-

ment of bones and tendons in the two myosepta is very similar. There is a strong epicentral bone in both. The epineural tendon is distinct at its proximal end and fans out toward its distal part. The lateral band is distinct and has the appearance of an aponeurosis.

Sphyræna barracuda. We show a myoseptum of the anterior body region of a large adult (fig. 10C). There is an epicentral bone with one POT attached to it. Similarly as in

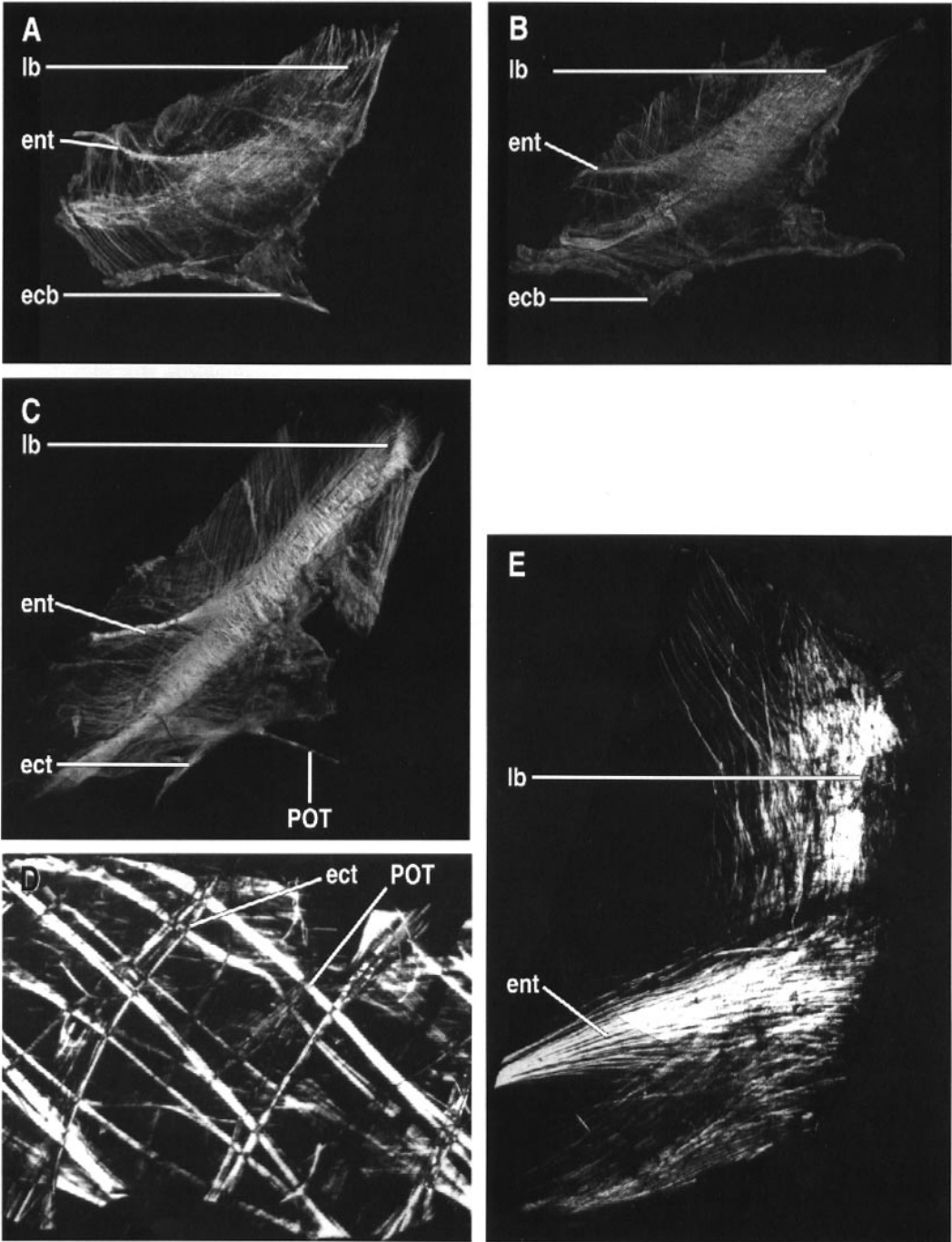


Fig. 10. A–C. Photographs of epaxial myosepta. A, B. *Caranx hippos*. A, Myoseptum 2. B, Myoseptum from anterior body. C, *Sphyaena barracuda*, myoseptum from midbody. D–E. *Channa obscura*. D, Micrograph of horizontal septum from midbody, dorsal view, right side, anterior to the left. E, Micrograph of epaxial myoseptum 19.

Caranx, the epineural tendon is distinct at its proximal end and fans out toward its distal part. The lateral band is a well-defined broad band of dense fibers.

Channa obscura. This species bears a series of about 19 epicentral bones that is continued posteriorly by a series of epicentral tendons. As shown by the micrograph of the horizontal septum (fig. 10D), the series is crossed by POTs. Above the series in the epaxial part of each myoseptum we again can demonstrate epineural tendon and lateral band (fig. 10E). Even if less pronounced, they are present in all body segments.

Arnoglossus laterna. This is the only percomorph we investigated bearing epineural ossifications. There are Y-shaped epineural ossifications in the anterior 12 segments. In subsequent myosepta only the lateral band (but not the anteromedial branch) is ossified. Thus the ossifications are C-shaped. Epicentrals of the first 12 segments are ossified.

DISCUSSION

Johnson and Patterson (1993) and Patterson and Johnson (1995) concluded that the single bony series of intermusculars of most acanthomorphs is not the homolog of the epipleural series of non-acanthomorphs as was generally thought. We agree with this conclusion. Primitively, in acanthomorphs there are three separate series of intermusculars, which in their unmodified state are easy to distinguish by their position: epineurals are in the epaxial myoseptum, epicentrals in the horizontal septum, and epipleurals in the hypaxial myoseptum. However, that criterion does not work in most acanthomorph fishes because there is only a single series of bones. Even assuming that bony series may shift during phylogeny, as already noted by Owen (1846, 1866), one problem of homology remains: Is the single bony series in most acanthomorphs the homolog of the epicentral or of the epineural series of lower teleosts?

In each series, a bone or a tendon corresponds to a bone or a tendon in about the same position in the adjacent myosepta. (Only *Holocentrus* seems to be an exception, see discussion below.) We present evidence that there are two series, either tendinous or bony, in all acanthomorph species investi-

gated. One series is situated in the horizontal septum, and the other dorsal to that in the epaxial part of the myosepta. Thus we can use the position as a simple criterion and homologize the series in the horizontal septum of acanthomorphs (anterior elements usually bony) with the epicentral series of lower teleosts. The series (usually tendinous) in the epaxial myosepta dorsal to the epicentral series is homologized with the epineural series of lower teleosts.

These homologies stand in contrast to the findings of Patterson and Johnson (1995) who hypothesized that the single bony series in the horizontal septum is the epineural series that is shifted ventrally. In the subsequent discussion we explain our line of evidence and discuss their hypothesis in light of our findings.

PATTERSON AND JOHNSON'S (1995)

HYPOTHESIS:

VENTRAL SHIFT OF EPINEURALS
INTO HORIZONTAL SEPTUM

Patterson and Johnson (1995) compared the situation of intermusculars in *Polymixia* (considered the primitive euacanthomorph pattern), *Holocentrus* (primitive acanthopterygian pattern), *Lates* (primitive percomorph pattern), and *Pseudanthias* (derived percomorph pattern). *Polymixia* was hypothesized to show the most primitive state among euacanthomorphs, because there are three series of intermusculars: an epineural series, predominantly bony, an epicentral series, completely tendinous, and an epipleural series, partly bony and partly tendinous. However, compared to what they take to be primitive for acanthomorphs, *Polymixia* shows one derived feature: The first intermuscular bone, which they homologized with the epineural of the first vertebra, no longer lies in the epaxial myoseptum but is shifted ventrally into the horizontal septum. In *Holocentrus*, considered by them to exemplify the primitive state for acanthopterygians, not only one but the first five to seven intermuscular bones, which they consider epineurals, are shifted ventrally into the horizontal septum.

Eventually, in percomorphs all intermuscular bones, which they claim to be epineu-

rals, lie in the horizontal septum. Therefore, they hypothesized that all epineurals are shifted ventrally into the horizontal septum. Accordingly, this ventral displacement of the epineurals into the horizontal septum has taken place in three steps, which Johnson and Patterson also used to define monophyletic groups (see below).

The first step, ventral displacement of the first epineural into horizontal septum (Johnson and Patterson, 1993: 601, character 8), is considered a synapomorphy for their Eucanthomorpha (*Acanthomorpha* minus *Lampridiformes*). The second step, ventral shift of anterior epineurals into horizontal septum (*ibid.*, p. 603, character 14), is considered a synapomorphy for their Holacanthopterygii (*Acanthomorpha* minus *Lampridiformes* and *Polymixiiformes*). The final step, ventral displacement of all epineurals into horizontal septum (*ibid.*, p. 615, character 32), is considered a synapomorphy of their Percomorpha (which includes *Atherinomorpha*).

They discovered, unexpectedly, a series of tendinous structures above the epineural series in a number of percomorph taxa. According to their hypothesis, this dorsal series is not an epineural series because that series is located in the horizontal septum. Consequently, they concluded that the tendinous series above the epineurals is a neoformation—the so-called “neoneural ligaments.” These “neoneural ligaments” may even ossify in some bothid and samarid species and then represent “neoneural bones.”

Patterson and Johnson had doubts concerning their method of recognizing tendons in glycerin-stored cleared-and-stained specimens (1995: 4): “. . . we cannot pretend that observing and recording intermuscular ligaments is an entirely objective procedure. . .”. On the other hand they also found that “Transferring cleared-and-stained specimens to alcohol may render the ligaments more opaque, and so more visible” (1995: 4).

We used alcohol along with microdissection, light- and DIC-microscopy, and polarized light to demonstrate the presence of various tendinous structures apparently overlooked by them. We consider our method more objective, which leads to reproducible results.

HOMOLOGY OF INTERMUSCULAR BONE ON FIRST VERTEBRA IN *POLYMIXIA*

Patterson and Johnson (1995) identified the first intermuscular bone of *Polymixia* as an epineural that is displaced ventrally from its position in the epaxial part of the myoseptum into the horizontal septum. They based their homology on two lines of evidence (1995: 33): (1) the first intermuscular “develops in series with the epineurals and is fully formed at 12 mm SL, before the epicentrals are recognizable” and (2) “there is no lower teleost in which the epicentral series contains just one bone on V1 followed by a series of ligaments”.

We have demonstrated above that a distinct tendinous structure originates dorsal to the origin of the first intermuscular and is aligned with the subsequent epineural bones (fig. 2). We therefore interpret this tendon as the epineural of the first vertebra. It was not reported and apparently overlooked by them. This may be caused by the different technique that they applied, i.e., studying specimens in glycerin.

We think that an epineural tendon on the first vertebra in *Polymixia* is sufficient evidence that the bone ventral to this tendon is not a ventrally shifted epineural bone, and we want to address their argument briefly. The intermuscular bone on the first vertebra “develops in series with the epineurals and is fully formed at 12 mm SL, before the epicentrals are recognizable” (Patterson and Johnson, 1995: 33). We consider this argument to be invalid because the identification of epicentral tendons in 12 mm long cleared-and-stained specimens would be impossible with their technique. The fact that “there is no lower teleost in which the epicentral series contains just one bone on V1 followed by a series of ligaments” (1995: 33) is not evidence that this is impossible, but rather that *Polymixia* is unique in this respect.

In summary there is strong and unambiguous evidence that the first vertebra of *Polymixia* has an epineural tendon. Therefore, the first intermuscular bone of *Polymixia* is not an epineural, as claimed by Patterson and Johnson (1995), but an epicentral.

INTERMUSCULAR BONES IN LAMPRIDIFORMES

There is only a slight difference between our and Patterson and Johnson's (1995) specimen of *Velifer*. We could not identify the discrete epicentral tendon of the first vertebra as described by them. Both investigations reveal a tendinous epicentral series in the horizontal septum. The series dorsal to that is tendinous in its posterior part and bony in its anterior part. It is in an epineural position. We thus consider it an epineural series.

Differences between our and their specimen of *Lampris guttatus* in the attachment of the first two intermuscular bones are interesting. We found both anterior bones attached to the centrum. The first stout bone even articulates in a well-developed, deep groove of the centrum. All subsequent intermuscular bones attach to the proximal parts of the ribs. This arrangement of intermuscular bones is characteristic for the epicentral bones of higher acanthomorphs (see discussion below). In fact, they (Johnson and Patterson, 1993: 558) have already pointed out this resemblance but concluded that this placement is developed independently in *Lampris* and higher acanthomorphs. It would be worth investigating myosepta of this species to check the precise placement of intermuscular bones in the myoseptum and to reconsider their possible homology with epicentrals.

INTERMUSCULAR BONES IN
PARACANTHOPTERYGII

There are no difficulties in homologizing intermusculars in *Molva* and *Aphredoderus*, because in both genera there is a bony/tendinous epicentral series in the horizontal septum and a tendinous epineural series in the epaxial part of the myoseptum. Patterson and Johnson (1995) identified a single bony series in the horizontal septum of the paracanthopterygians, *Percopsis guttatus*, *Aphredoderus sayanus*, *Raniceps raninus*, and *Gaidropsaurus mediterraneus*, and homologized them with epineural bones shifted ventrally into the horizontal septum. We did not reinvestigate all species but our different findings in *Aphredoderus sayanus* led to the conclu-

sion that Patterson and Johnson must have overlooked the epineural tendons.

INTERMUSCULAR BONES IN BERYCIFORMES

We described a continuous tendinous series in the epineural as well as in the epicentral position (bony on V1 and V2) for *Hoplostethus* and *Gephyroberyx*. These results allow unequivocal homology. In Patterson and Johnson's (1995) *Hoplostethus* specimen, they recorded only a series of epicentral tendons from vertebra 9 backward and two bones on V1 and 2 in the epicentral position. They interpreted the two bones as epineural bones shifted ventrally into the horizontal septum. In light of our results, we think that they overlooked the real epineural tendons in the anterior 8 myosepta because they were unrecognizable in glycerin-stored cleared-and-stained specimens.

Homologization of intermuscular bones in our *Holocentrus* specimen is unambiguous for myosepta from 7 backward. We found a continuous series of tendons in the horizontal septum preceded by bones on V1 and V2, and we regard these as homologs of epicentral tendons or bones. The series dorsal to the epicentrals is the epineural series. In myosepta 6 to 1, these bony elements undergo a remarkable ventral shift. In myosepta 4 and 3, they are situated even ventral to the lateral band. It is not clear whether an epineural tendon is present as well. We are not sure how to interpret this pattern of bones lying between the epineural and epicentral position. Because we have not seen a similar arrangement in any other species, we are inclined to interpret these as autapomorphic for Holocentridae.

For the two bony elements in the horizontal septum, the question arises whether they are true epicentrals, as claimed above, or epineurals that have shifted further ventrally as claimed by Patterson and Johnson (1995), who investigated two species, *Holocentrus spinifer* and *Holocentrus vexillaris*. They failed to recognize tendinous epicentrals 3 to 8 but recorded them from 9 backward. They considered the two bones on V1 and V2 as epineurals because the bones are in line with other epineural elements. We have demonstrated that these bones on V1 and V2 are in

line with the epicentral series. Patterson and Johnson may have overlooked epicentral tendons 3 to 8 because the tendons are difficult to detect by examination of glycerin specimens but, according to our findings, more easily detected by dissection and microscopy.

Our interpretation that the first two intermuscular bones are epicentrals and thus differ from the posterior bones is further supported by ontogenetic differences that we found between the two bone groups. The first two intermuscular bones are already present in the smallest larva available (11 mm), whereas 3 to 6 ossify in line with true epineural bones of 7 backward, but not before the 26 mm stage.

INTERMUSCULAR BONES IN ATHERINOMORPHA

In none of the atherinomorphs (*Bedotia* sp., *Menidia peninsulae*, and *Exocoetus volitans*) they investigated did Patterson and Johnson (1995) record two intermuscular elements within a single myoseptum. With the exception of some posterior segments in *Menidia*, they reported only a bony series in the horizontal septum, which was interpreted as epineural shifted ventrally. Again, with our technique, we detected two intermuscular elements in a single myoseptum for *Bedotia geayi* and *Scomberesox saurus*. We consider the bony elements in the horizontal septum to be epicentrals, and the tendinous elements situated above the horizontal septum to be epineurals.

INTERMUSCULAR BONES IN PERCOMORPHA

In all percomorphs there is only one series of intermuscular bones, which has generally been referred to as epipleural. Patterson and Johnson (1995) pointed out that this series is not the homolog of the epipleural series of lower teleosts, and we agree with this statement.

We have demonstrated above that there are tendons in the position of epineurals dorsal to the intermuscular bones in all percomorphs that we investigated. The tendons insert on the neural arches of the respective vertebra and we homologize them with epineural tendons. Therefore, the intermuscular bone situated ventral to the tendons is not an epineural but an epicentral. This contradicts

the homology of Patterson and Johnson (1995). They claimed that the single series of intermuscular bones in percomorphs is the epineural series that has shifted ventrally. This homology is based on a comparison of intermusculars of *Polymixia*, *Holocentrus*, and *Centropomus*. They considered the position of the intermusculars in these three taxa to be a morphocline reflecting ventral displacement of epineurals into the horizontal septum during evolution.

However, we have seen that (1) the intermuscular bone on V1 of *Polymixia* is not an epineural, (2) other beryciforms like *Hoplostethus* have epineural tendons dorsal to their series of intermuscular bones, and (3) centropomids also possess a series of epineural tendons dorsal to their series of intermuscular bones. For these reasons we conclude that Patterson and Johnson (1995) were misled in homologizing the single series of intermuscular bones with epineurals of lower teleosts. Our results present unambiguous evidence that there are epineural tendons in Percomorpha and that their single bony series is actually the homolog of the epicentral series of lower teleosts.

Patterson and Johnson (1995) reported tendons in the position of epineurals of lower teleosts also in a number of percomorph representatives (Ammodytidae, Pomacentridae, Polynemidae, Mullidae) that even ossify in the pleuronectiforms *Samaris* and *Bothus* (and *Arnoglossus* according to our observations). Because they claimed that epineurals of percomorphs are ventrally displaced and located in the horizontal septum, Patterson and Johnson concluded that the series of tendons in the position of epineurals of lower teleosts is something different. They therefore called those tendons "neoneurals" and reported them in additional percomorph taxa: Teraponidae, Kuhliidae, Carangidae, Eche-neidae, Lutjanidae, Caesionidae, Gerreidae, Sparidae, Lethrinidae, Sciaenidae, Haemulidae, Labridae, and Scaridae.

In percomorphs, presence of tendinous structures that occur in the position of epineurals of lower teleosts is additional evidence for our hypothesis that intermuscular bones in percomorphs are epicentrals. We have checked myosepta of some of these taxa that are reported to possess "neoneurals"

(see above *Kuhlia*, *Parupeneus*, *Oligoplites*, *Caranx*) and found the same basic pattern of epineurals and epicentral bones in the myoseptum that we reported for other percomorphs (see above). We therefore have no doubt that percomorph “neoneurals” are normal epineurals and that percomorph “epineurals” are epicentrals.

PHYLOGENETIC IMPLICATIONS AND CONCLUDING REMARKS

We have presented convincing evidence that (1) the first intermuscular bone of *Polymixia* is an epicentral and (2) the single series of intermuscular bones in higher acanthomorphs is the homolog of the epicentral series of non acanthomorphs. If this interpretation is accepted then the synapomorphy “First epineural displaced ventrally into the horizontal septum” used by Johnson and Patterson (1993: 601, character 8) to support their Euacanthomorpha (Acanthomorpha minus Lampridiformes) is invalid. We think that the phylogenetic position of Lampridiformes basal to Polymixiiformes needs critical reexamination especially in the light of the sister-group relationship of *Polymixia* and all remaining acanthomorphs proposed by other authors (Rosen, 1985; Stiassny, 1986; Patterson and Rosen, 1989; Stiassny and Moore, 1992).

Accepting our hypothesis also invalidates the following characters as synapomorphies: “Epicentral ligaments absent anteriorly” (Johnson and Patterson, 1993: 603, character 13) and “Distal parts of anterior epineurals displaced ventrally into horizontal septum” (1993: 603, character 14) used by Johnson and Patterson to support their Holacanthopterygii. “Anterior epineurals displaced ventrally on to the ribs” (1993: 606, character

20) used to support a group Zeiformes + Euacanthopterygii and “Point of origin of all but the first two epineurals displaced ventrally, and the distal parts of all epineurals displaced ventrally into the horizontal septum” (1993: 615, character 32) used to support their Percomorpha (including Atherinomorpha).

A series of epicentral bones may turn out to be a synapomorphy for their Holacanthopterygii. However, further studies are needed to support such a hypothesis.

Our hypothesis explains several of their conflicting data.

1. The ventral position of the intermuscular bones of Paracanthopterygii, some Stephanoberyciformes, and Zeiformes need not be explained as a downward shift of epineurals acquired independently from that in Percomorpha (which include Atherinomorpha). Rather it is the plesiomorphic retention of an epicentral bony series.

2. In zeiforms and percomorphs the anterior POTs are thought (Patterson and Johnson, 1995: ii) to “acquire a new association, attaching to epineural bones secondarily positioned in the horizontal septum.” Our hypothesis does not need such an assumption because the bones in the horizontal septum are epicentrals and thus the situation of POTs in zeiforms and percomorphs is a retention of the plesiomorphic association between the two systems.

3. The concept of “neoneurals” in some percomorphs is superfluous because the “neoneurals” are true epineurals.

As Patterson and Johnson (1995) have stressed, intermusculars of teleosts hold much potential for resolution of phylogenetically problematic groups, and we hope that our improvement of their method will help in accomplishing this goal.

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