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SYSTEMATIC IMPLICATIONS OF INNERVATION PATTERNS IN TELEOST MYOTOMES

QUENTIN BONE¹ AND R. DANA ONO²

ABSTRACT. The peripheral innervation patterns of the red and white myotomal muscles from over 230 species representing more than 125 families of teleosts were studied. A distributed, multiple innervation pattern of teleost red superficial myotomal muscles was found without exception in all groups examined. There is variability in the innervation patterns of the white myotomal muscles, however. A terminally innervated pattern seems to be present in the basal groups of teleosts, while a trend toward distributed innervation occurs in the Neoteleostei. Stomii-formes possess a rather different distributed pattern which we suggest is the early, transitional stage from terminal to distributed innervation patterns in teleosts. There appears to be a distinct functional difference in the distributed and terminal innervation patterns. The innervation of the white myotomal fibers should be considered a taxonomically useful character in elucidating familial relationships.

INTRODUCTION

In all fishes, there are two main muscle fiber types in the myotomes, usually readily visible to the naked eye when the fish is sectioned transversely. Small-diameter, well-vascularized red muscle fibers normally form a thin superficial layer covering the much more numerous, larger-diameter, poorly-vascularized white muscle fibers that make up the major portion of the myotome. In some fishes, but not in all, other myotomal fiber types are present. These minor myotomal components will not concern us here. In all fishes,

¹The Laboratory, Citadel Hill, Plymouth PL1 2PB, Devon, England.

²Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138.

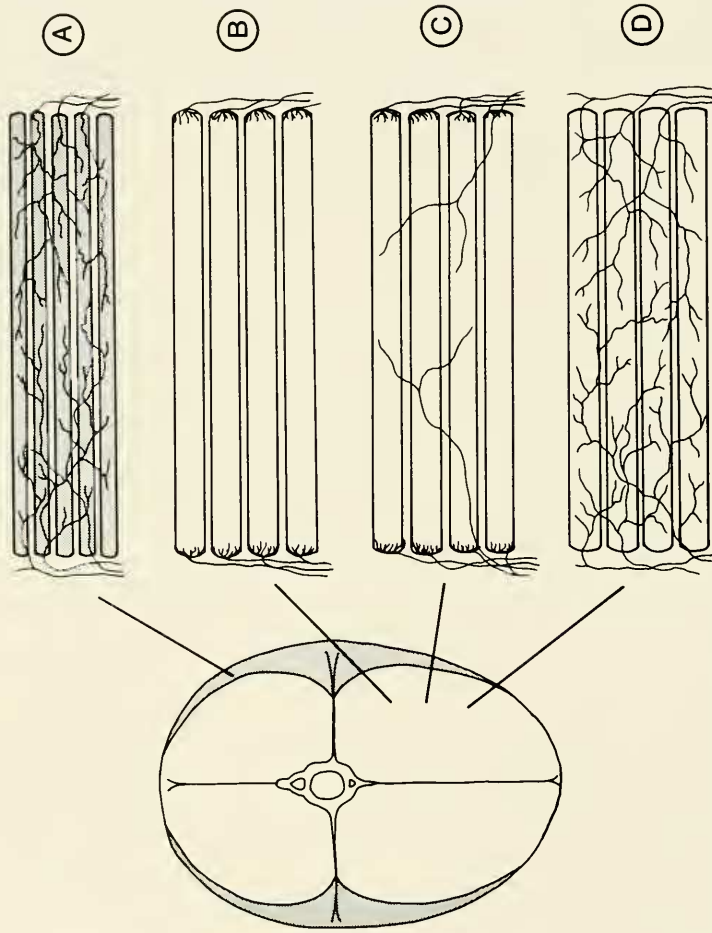


Figure 1. Cross section through hypothetical fish body depicting the larger white muscle mass and the superficial red muscle layer (supplied). A) distributed innervation of red muscle fibers; B) terminal innervation of white muscle fibers; C) terminal and small amount of distributed innervation of white muscle fibers in Stomifurmes; and D) distributed innervation of white muscle fibers.



Figure 2. Hypothetical relationship of the Teleostei modified from Fink and Weitzman (1982) and Fink and Fink (1981) to show the extent of the distributed innervation pattern in teleosts. **—** = distributed innervation in all. **□** = distributed innervation in some members.

the red muscle fibers are multiply innervated in a distributed fashion, so that each muscle fiber receives a number of motor terminations along its length (Fig. 1A). In most teleosts, the white muscle fibers are similarly innervated (Figs. 1D, 3, 6), but in some an entirely different innervation pattern is found. In such fishes the white muscle fibers are innervated only at their myoseptal ends, so that innervation is focal and terminal (Figs. 1B, 4, 5).

Although this mode of innervation of white muscle fibers is rare in teleosts (Barets, 1961; Bone, 1964), investigations on other fish groups such as the Halecomorphi, Ginglymodi, Brachiopterygii,

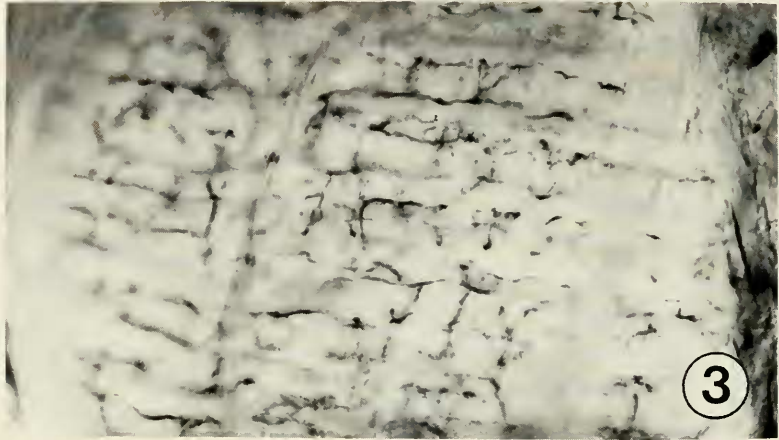


Figure 3. Distributed innervation pattern of motor endplates in white myotomal muscle fibers of *Morone labrax* as revealed by acetylcholinesterase (AChE) studies. (Mag. $\times 90$).



Figure 4. Terminal innervation pattern of motor endplates in white myotomal muscle fibers of the clupeomorph, *Sprattus sprattus*, as revealed by AChE studies. (Mag. $\times 90$).

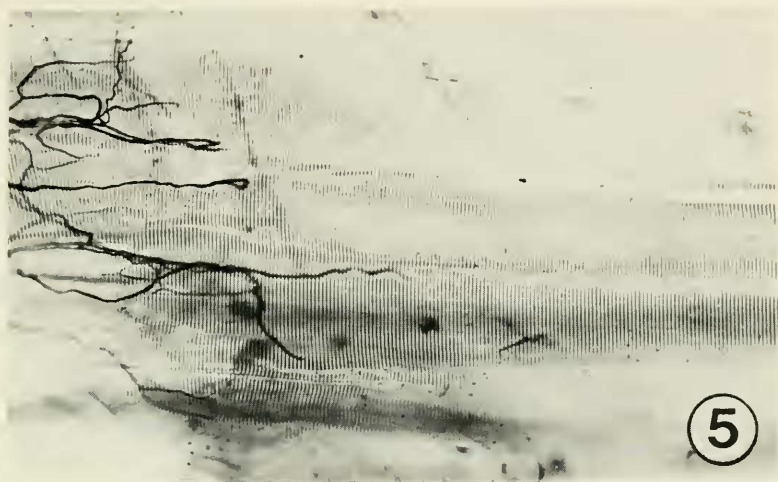


Figure 5. Silver impregnated axons of terminal innervation pattern in the white myotomal muscle fibers of the alepocephalid, *Xenodermichthys copei*. Winkelmann and Schmitt technique. (Mag. $\times 190$).



Figure 6. Silver impregnated axons of the distributed innervation pattern in the white myotomal muscle fibers of the gymnotid, *Eigenmannia virescens*. Winkelmann and Schmitt technique. (Mag. $\times 228$).

Chondrostei (Acipenseridae, Polydontidae), hagfish, Elasmobranchiomorpha, and *Latimeria chalumnae* have shown that terminal innervation is universal in non-teleost groups (Bone, 1964 and unpublished; Ono, unpublished; Sakharov and Kashapova, 1979). In addition, terminal innervation is found in the Dipnoi, in the myotomal musculature of adult urodeles, and in urodele and anuran larvae (Best and Bone, 1973; Bone, unpublished; Ono, unpublished).

The wide distribution of the terminal innervation pattern of white muscle fibers led to a preliminary attempt (Bone, 1970) to link the occurrence of the terminal pattern in teleosts with the systematic position of the families in which it was found. This attempt was unsuccessful since relatively few families were examined. In this study, we report the results of a more detailed survey of the innervation pattern of white muscle fibers in different teleost groups that suggests that this character may be of interest to systematists.

MATERIALS AND METHODS

The innervation pattern of white muscle fibers was studied either by supravital staining with methylene blue in teleost Ringer solution, or by silver staining of 10% unbuffered formalin and Bouin-fixed material using the methods of Palmgren (1948) and Winkelmann and Schmitt (1957). During the last several years, we have collected marine fish material from the Caribbean, the Indian Ocean, the North Atlantic Ocean, and the Bay of Biscay. The freshwater fish material was collected by us from North American and European waters. In addition, we have been much assisted by other workers who have provided specially fixed or museum material from the waters of South America, Africa, Japan, New Zealand, and several deep-sea localities. We owe a particular debt of gratitude to Dr. P. H. Greenwood (BMNH) and to Mr. J. B. Badcock and Mr. N. Merrit (IOS) who have generously provided material from their collections.

TELEOST GROUPS AND THEIR INNervation PATTERNS

The status of the different groups of teleosts is still subject to review, and different authors have adopted different systems of classification to indicate their views of the relationships of the

various groups. In this paper we have adopted the classification scheme of Rosen (1973) and Fink and Weitzman (1982). A complete checklist showing the teleosts examined is given in Table 1.

1) Osteoglossomorpha

Nine genera from this group were examined. With the exception of the two *Hiodon* species, all possess the distributed pattern of white muscle innervation.

2) Elopomorpha

We have examined 12 genera from this group representing the Elopiformes, Anguilliformes, and Notacanthiformes. All possess the terminal innervation pattern. Both the adults and leptocephali of *Elops* sp. and *Albula* sp. have the terminal pattern of white muscle innervation.

3) Clupeomorpha

Twenty-one species of clupeids belonging to 16 genera were studied. All possess the terminal innervation pattern with the sole exception of *Denticeps*, in which the white myotomal muscle has a distributed innervation.

4) Ostariophysi

We have examined 32 genera of ostariophysans representing the Gonorynchiformes, Characiformes, Cypriniformes, and Siluriformes. Some ostariophysans possess the terminal pattern (some siluroids and all gonorynchids), but the majority have the distributed pattern of innervation.

5) Protacanthopterygii

There is considerable uncertainty about the limits of this group, which has been reduced from its original size (Fink and Weitzman, 1982). The 16 species representing 14 genera listed in Table 1 are provisionally placed in this group.

6) Stomiiformes

Fifteen genera representing the two Infraorders Gonostomata and Photichthya (Weitzman, 1974) were studied. Two innervation patterns are found in these two lineages of Stomiiformes. While the Gonostomata possess the usual distributed innervation pattern found in other teleosts, members within the Photichthya have the white zone of the myotome innervated in a different way. Terminal endplates are seen on many fibers which are probably innervated at

both ends. In addition, some axons pass from the myosepta into the midregions of the myotome to form a sparsely distributed innervation pattern. Thus, the Photichthya possess a third type of innervation pattern (Fig. 1C), distinct from either the terminal or distributed patterns, apparently combining elements of both.

7) Eurypterygii

All 125 species representing 99 genera examined in the Aulopiformes, Myctophiformes, Paracanthopterygii, and Acanthopterygii possess the distributed innervation pattern (see Table 1 for list of eurypterygians examined).

DISCUSSION

All non-teleost fishes possess terminally innervated white muscle fibers (Ono, unpublished). It is reasonable to suppose therefore that this pattern is the primitive condition and that the distributed pattern of innervation is derived. The universal occurrence of the distributed pattern in the Eurypterygii supports this view.

Two questions arise. First, is there a functional advantage in the distributed pattern that has led to its universal appearance in "higher" teleosts? Secondly, can white muscle innervation prove useful in dealing with the controversial questions of the limits and interrelationships of different teleost groups?

Consideration of the habits of fishes possessing the two types of innervation pattern, for example, *Hiodon* and *Heterotis* or *Albula* and *Chanos*, shows no obvious correlation between habitat and innervation pattern, nor any obvious differences in locomotor ability. But studies of fishes swimming under controlled conditions have revealed a notable difference in locomotor ability between fishes where the white muscle is innervated terminally, and where it is innervated in the distributed manner. Few fishes have yet been studied in this way (where activity in different zones of the myotome is monitored by electromyography as the fish swims at different speeds), but results are consistent, and are probably generally applicable. In all fishes studied, the red muscle fiber zone of the myotome is active during slow cruise swimming that can be maintained indefinitely. In fishes where the white muscle fibers are terminally innervated, these are only active during bursts of rapid swimming, and are rapidly exhausted (Bone, 1966; Bone *et al.*,

1978). Where the white muscle fibers are innervated in the distributed manner, they operate quite differently, for they are active not only during bursts of rapid swimming, but also during cruise swimming at intermediate speeds (Hudson, 1973; Johnston *et al.*, 1977; Bone *et al.*, 1978).

Electromyographic records from the white muscle zone during cruise swimming in such fishes are different from those obtained during rapid swimming, and it appears that where the fibers receive distributed innervation, they can operate in two ways propagating action potentials only during rapid swimming (Bone *et al.*, 1978). Extracellular recordings cannot provide other than suggestive evidence on this point, and definite proof of the hypothesis that contraction of the same fast muscle fiber in such fishes can either follow local potentials or propagated action potentials awaits intracellular investigation.

However, the results of these electromyographic studies clearly show that fishes with the distributed pattern of innervation of the white muscles are able to recruit these fibers to give a wider range of sustainable cruising speeds than can be obtained when the white fibers are terminally innervated and are used only during burst swimming. Evidently, this ability to swim for long periods over a wide speed range could confer a significant advantage to fishes in some particular habitats. For example, it may be advantageous to fishes living in streams where flow varies and the fishes are required to keep stationary. This ability to swim over a wide speed range would be insignificant to benthic fishes, however, at least in the adult stage due to the relatively stable flow regime of the water column.

We conclude that the distributed pattern of innervation was derived in teleostean evolution when adults or larvae were pelagic, and has been retained in those groups where the adults today are relatively sedentary, so that the habits of the adults today are not correlated with the innervation pattern.

The first attempt to use the innervation pattern as a systematic character made the simple assumption that this derivation from the ancestral terminal pattern occurred only once during teleost phylogeny (Bone, 1970). The present more complete survey (unfortunately still lacking data on several important species) demonstrates that this assumption can no longer be justified. Figure

2 shows a current view of the relationships among teleost groups (Fink and Weitzman, 1982), and indicates points where transition from terminal to distributed innervation is assumed to have taken place. In this view of the relationships of the groups, the change presumably took place independently on at least eight occasions.

In general, our survey has shown that the more primitive groups possess the terminal innervation pattern, as expected. Thus in the Osteoglossomorpha, the Hiodontoidei is a phylogenetic relict in the sense that the two living *Hiodon* species form a lineage that has retained a large number of primitive features (Greenwood, 1970); only these members of the group possess the terminal pattern.

Both the Elopomorpha and Clupeomorpha (with the sole exception of *Denticeps*) also possess the terminal pattern. The freshwater *Denticeps* retains many primitive characters, (Greenwood, 1968), but is unique among clupeomorphs in having achieved the distributed innervation pattern. Since a wider sustainable speed range might be a distinct advantage in the fluvatile freshwater environment, we examined other African freshwater clupeids, but all five genera studied possessed terminally innervated white muscle fibers.

In the Ostariophysi, all Gonorynchiformes and some Siluriformes have the terminal innervation pattern, and if the scheme of ostariophysan relationships proposed by Fink and Fink (1981) is accepted, this implies that convergent origin of the distributed pattern has occurred in all lines except that leading to the Gonorynchiformes (Fig. 2). Certainly, although the phylogenetic position of Siluriform families is uncertain, the innervation pattern is terminal in the most primitive, the relict Diplomystidae.

Perhaps the most interesting group with respect to muscle innervation pattern is the Stomiiformes. This group has been less thoroughly studied than the Ostariophysi, and despite recent work by Fink and Weitzman (1982), and an earlier study by Weitzman (1974), relationships within the group are still uncertain. It is notable that the two major sister groups forming the Stomiiformes, the Gonostomata and Photichthya (Weitzman, 1974), have different innervation patterns. In the Gonostomata, innervation is distributed, but in the Photichthya, innervation of the white fibers is mixed. Relatively few axons course through the white portion of the myotome, and in addition there are axons terminating on the fiber

ends as in the terminal pattern. Perhaps in this group of teleosts, we witness the distributed innervation pattern at an early stage in its development. It would be interesting to see whether the mixed pattern of adult photichthyans develops from an initially terminal pattern in the larval stage.

Few studies involving the nervous system in fishes have been used in a comparative fashion to solve problems of classification. On the whole, our survey suggests that the innervation of white myotomal fibers, despite evident convergence in its origin, should be considered a systematically useful character, and may prove particularly helpful in elucidating interrelationships within the Siluriformes and the Stomiiformes, respectively.

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LITERATURE CITED

- BARETS, A. 1961. Contribution à l'étude des systèmes moteurs lent-et rapid du muscle latéral des téléostéens. *Arch. Anat. Morphol. Exp.*, **50** (suppl.): 91-187.
- BEST, A. C. G., AND Q. BONE. 1973. The terminal neuromuscular junctions of lower chordates. *Z. Zellforsch.*, **143**: 495-504.
- BONE, Q. 1964. Patterns of muscular innervation in the lower chordates. *Int. Rev. Neurobiol.*, **6**: 99-147.
- . 1966. On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. Mar. Biol. Ass. U.K.*, **46**: 321-349.
- . 1970. Muscular innervation and fish classification, pp. 369-377. *In* A. de Haro (ed.), *I Simposio Internacional de Zoofilogenia*, Fac. Ciencias, Univ. Salamanca, 492 pp.
- BONE, Q., J. KICENIUK, AND D. R. JONES. 1978. On the role of different fibre types in fish myotomes at intermediate swimming speeds. *Fish. Bull.*, **76**: 691-699.
- FINK, S. V., AND W. L. FINK. 1981. Interrelationships of the ostariophysan fishes (Teleostei). *Zool. J. Linn. Soc.*, **72**(4): 297-353.

- FINK, W. L., AND S. H. WEITZMAN. 1982. Relationships of the Stomiiform fishes (Teleostei) with a description of *Diplophos*. Bull. Mus. Comp. Zool., **150**: 31-93.
- GREENWOOD, P. H. 1968. The osteology and relationships of the Denticipitidae, a family of clupeomorph fishes. Bull. Br. Mus. Nat. Hist. (Zool.), **16**: 213-273.
- . 1970. On the genus *Lycoptera*, and its relationships with the family Hiodontidae (Pisces, Osteoglossomorpha). Bull. Br. Mus. Nat. Hist. (Zool.), **19**: 257-285.
- HUDSON, R. C. L. 1973. On the function of the white muscles in teleosts at intermediate swimming speeds. J. Exp., Biol., **58**: 509-522.
- JOHNSTON, I. A., W. DAVIDSON, AND G. GOLDSPIK. 1977. Energy metabolism of carp swimming muscles. J. Comp. Physiol., **114**: 203-216.
- PALMGREN, A. 1948. A rapid method for selective silver staining of nerve fibres and nerve endings in mounted paraffin sections. Acta Zool., **29**: 378-392.
- ROSEN, D. E. 1973. Interrelationships of higher euteleostean fishes, pp. 397-513. In P. H. Greenwood, R. S. Miles, and C. Patterson (eds.), London, Academic Press, 536 pp.
- SAKHAROV, D. A., AND L. A. KASHAPOVA. 1979. The primitive pattern of the vertebrate body muscle innervation: Ultrastructural evidence for two synaptic transmitters. Comp. Biochem. Physiol., **62(A)**: 771-776.
- WEITZMAN, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae with a new classification of stomioid families. Bull. Am. Nat. Hist., **153(3)**: 329-478.
- WINKELMANN, R. K., AND R. W. SCHMITT. 1957. A simple silver method for nerve axoplasm. Proc. Staff Meeting Mayo Clinic, **32**: 217-222.

Table 1. Patterns of Innervation in the White Myotomal Muscle Fibers of Teleosts.

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Osteoglossomorpha		
Notopteridae		
<i>Notopterus chitala</i>		+
<i>Xenomystus nigri</i>		+
Osteoglossidae		
<i>Heterotis niloticus</i>		+
<i>Osteoglossum bicirrosum</i>		+
Pantodontidae		
<i>Pantodon buchholzi</i>		+
Mormyridae		
<i>Mormyrus</i> sp.		+
<i>Mormyrops engystoma</i>		+
<i>Gnathonemus petersii</i>		+
Hiodontidae		
<i>Hiodon tergisus</i>	+	
<i>Hiodon alosoides</i>	+	
Elopomorpha		
Elopiformes		
Elopidae		
<i>Elops</i> sp.	+	
Albulidae		
<i>Albula</i> sp.	+	
Anguilliformes		
Anguillidae		
<i>Anguilla</i> sp.	+	
Muraenidae		
<i>Gymnothorax</i> sp.	+	
Congridae		
<i>Conger</i> sp. (2)	+	
<i>Paraconger</i> sp.	+	
Muraenesocidae		
<i>Muraenesox</i> sp.	+	
Ophichthidae		
<i>Ophichthus</i> sp.	+	

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Eurypharyngidae		
<i>Eurypharynx pelecanoïdes</i>	+	
Notacanthiformes		
Halosauridae		
<i>Halosaurus</i> sp.	+	
<i>Halosauropsis</i> sp.	+	
Notacanthidae		
<i>Polyacanthonotus</i> sp.	+	
Clupeomorpha		
Clupeidae		
<i>Clupea</i> sp.	+	
<i>Harengula</i> sp. (2)	+	
<i>Sardinella</i> sp.	+	
<i>Pellonula atzeliusi</i>	+	
<i>Opisthopterus</i> sp.	+	
<i>Limnothrissa miodon</i>	+	
<i>Thrissocles</i> sp.	+	
<i>Euplatygaster</i> sp.	+	
<i>Cynothrissa mento</i>	+	
<i>Poecilothrissa congicae</i>	+	
<i>Stolothrissa tanganiçae</i>	+	
<i>Microthrissa</i> sp.	+	
<i>Opisthopterus</i> sp.	+	
<i>Alosa pseudoharengus</i>	+	
<i>Alosa aestivalis</i>	+	
<i>Alosa</i> sp.	+	
<i>Sprattus sprattus</i>	+	
Engraulidae		
<i>Anchoa mitchilli</i>	+	
<i>Anchoa</i> sp.	+	
Chirocentridae		
<i>Chirocentrus dorab</i>	+?	
Denticipitidae		
<i>Denticeps clupeoides</i>		+
EUTELEOSTEI		
Ostariophysii		
Gonorynchiformes		

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Chanidae		
<i>Chanos chanos</i>	+	
Kneriidae		
<i>Kneria mitteï</i>	+	
Phractolaemidae		
<i>Phraetolaemus ansorgei</i>	+	
Gonorynchidae		
<i>Gonorynchus gonorynchus</i>	+	
Characiformes		
Characidae		
<i>Crenuchus spilurus</i>		+
<i>Hyphessobrycon flammeus</i>		+
<i>Hyphessobrycon serpaë</i> X		
<i>Hyphessobrycon collistus</i>		+
<i>Hyphessobrycon pulchrspinis</i>		+
<i>Astyanax mexicanus</i>		+
Lebiasinidae		
<i>Nannostomus nannostomus</i>		+
Gasteropelecidae		
<i>Gasteropelecus</i> sp.		+
Hemiodontidae		
<i>Hemiodus</i> sp.		+
Cypriniformes		
Cyprinidae		
<i>Notropis hudsonius</i>		+
<i>Cyprinus</i> sp.		+
Gyrinocheilidae		
<i>Gyrinocheilus aymonieri</i>		+
Catostomidae		
<i>Catostomus catostomus</i>		+
Cobitidae		
<i>Noemacheilus</i> sp.		+
Siluriformes		
Siluroidei		

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Bagridae		
<i>Parauchenoglanis macrostoma</i>		+
Siluridae		
<i>Kryptopterus bicirrhis</i>		+
Malapteruridae		
<i>Malapterurus electricus</i>		+
Pangasiidae		
<i>Pangasius sutchi</i>		+
Chacidae		
<i>Chaca chaca</i>		+
Mochokidae		
<i>Synodontis</i> sp.		+
Aspredinidae		
<i>Bunocephalus</i> sp.		+
Callichthyidae		
<i>Corydoras</i> sp.		+
<i>Hoplosternum</i> sp.		+
<i>Dianema</i> sp.		+
Loricariidae		
<i>Ancistrus</i> sp.		+
Ictaluridae		
<i>Ictalurus</i> sp.		+
Diplomystidae		
<i>Diplomystes</i> sp.	+	
Ariidae		
<i>Arius</i> sp.	+	
Doradidae		
<i>Doras</i> sp.	+	
Pimelodidae		
<i>Sorubim limas</i>	+	
<i>Pimelodella</i> sp.	+	
Gymnotoidei		
Rhamphichthyidae		
<i>Eigenmannia virescens</i>		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Protacanthopterygii		
Salmoniformes		
Esocidae		
<i>Esox niger</i>		+
<i>Esox americanus</i>		+
Umbridae		
<i>Umbra limi</i>		+
<i>Dallia pectoralis</i>		+
Salmonidae		
<i>Salmo trutta</i>		+
<i>Salmo</i> sp.		+
Retropinnidae		
<i>Retropinna</i> sp.		+
Galaxiidae		
<i>Galaxias</i> sp.		+
Osmeridae		
<i>Osmerus mordax</i>		+
Plecoglossidae		
<i>Plecoglossus altivelis</i>		+
Argentinidae		
<i>Argentina</i> sp.		+
Opisthoproctidae		
<i>Opisthoproctus</i> sp.		+
Alepocephalidae		
<i>Alepocephalus</i> sp.	+	
<i>Xenodermichthys copei</i>	+	
<i>Bathylaco nigricans</i>	+	
Searsiidae		
<i>Searsia</i> sp.	+	
Stomiiformes		
Gonostomata		
Gonostomatidae		
<i>Cyclothone obscura</i>		+
<i>Gonostoma elongatum</i>		+
<i>Maurolicus</i> sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Sternoptychidae		
<i>Argyropelecus</i> sp. (2)		+
<i>Sternoptyx</i> sp.		+
Photichthya		
Chauliodontidae		
<i>Chauliodus</i> sp.	+	+
Stomiidae		
<i>Stomias</i> sp.	+	+
<i>Macrostomias longibarbatu</i> s	+	+
Astronesthidae		
<i>Astronesthes</i> sp.	+	+
Melanostomiidae		
<i>Melanostomias</i> sp.		+
<i>Eustomias</i> sp.	+	+
<i>Echistoma barbatum</i>	+	+
Malacosteidae		
<i>Malacosteus</i> sp.	+	+
<i>Photostomias</i> sp.	+	+
Idiacanthidae		
<i>Idiacanthus</i> sp.	+	+
EURYPTERYGII		
Aulopiformes		
Aulopodidae		
<i>Aulopus</i> sp.		+
Synodontidae		
<i>Synodus</i> sp. (2)		+
Giganturidae		
<i>Gigantura</i> sp.		+
Bathypteroidae		
<i>Bathypterois</i> sp. (2)		+
Myctophiformes		
Myctophidae		
<i>Myctophum</i> sp.		+
<i>Diaphus</i> sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Paralepididae		
<i>Paralepis</i> sp.		+
Omosudidae		
<i>Omosudis</i> sp.		+
Evermannellidae		
<i>Coccorella</i> sp.		+
Scopelarchidae		
<i>Scopelarchus</i> sp.		+
Paracanthopterygii		
Gadiformes		
Moridae		
<i>Antimora</i> sp.		+
Macrouridae		
<i>Nematonurus</i> sp.		+
Lophiiformes		
Lophiidae		
<i>Lophius</i> sp.		+
Antennariidae		
<i>Antennarius hispidus</i>		+
<i>Antennarius scaber</i>		+
Acanthopterygii		
Atheriniformes		
Exocoetidae		
<i>Parexocoetus</i> sp.		+
<i>Cypselurus</i> sp.		+
<i>Hemiramphus</i> sp. (2)		+
Belonidae		
<i>Belone</i> sp.		+
<i>Platybelone</i> sp.		+
<i>Tylosurus</i> sp.		+
Cyprinodontidae		
<i>Belonesox belizanus</i>		+
Scomberesocidae		
<i>Scomberesox</i> sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Atherinidae		
<i>Menidia menidia</i>		+
<i>Atherinomorus</i> sp.		+
Beryciformes		
Polymixiidae		
<i>Polymixia lowei</i>		+
<i>Polymixia japonica</i>		+
Holocentridae		
<i>Holocentrus</i> sp. (3)		+
Cetomimidae		
<i>Cetomimus</i> sp.		+
Melamphaeidae		
<i>Melanphaes</i> sp.		+
Dactylopteriformes		
Dactylopteridae		
<i>Dactylopterus</i> sp.		+
Zeiformes		
Zeidae		
<i>Zeus faber</i>		+
Sygnathiformes		
Aulostomidae		
<i>Aulostomus</i> sp.		+
Fistulariidae		
<i>Fistularia</i> sp. (2)		+
Sygnathidae		
<i>Nerophis</i> sp.		+
<i>Hippocampus</i> sp.		+
Scorpaeniformes		
Triglidae		
<i>Trigla</i> sp.		+
Cottidae		
<i>Cottus cognathus</i>		+
Perciformes		
Centrarchidae		
<i>Pomoxis nigromaculatus</i>		+
<i>Lepomis gibbosus</i>		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Priacanthidae		
<i>Priacanthus</i> sp.		+
Carangidae		
<i>Caranx</i> sp. (3)		+
<i>Oligoplites</i> sp.		+
<i>Seriola</i> sp.		+
Lutjanidae		
<i>Lutjanus</i> sp. (2)		+
<i>Ocyurus</i> sp.		+
Plectorynchidae		
<i>Gaterin</i> sp.		+
Pentapodidae		
<i>Monotaxis</i> sp.		+
Serranidae		
<i>Epinephelus</i> sp. (3)		+
<i>Petrometapon</i> sp.		+
<i>Serranus</i> sp.		+
<i>Cephalopholis</i> sp.		+
Pomadasyidae		
<i>Haemulon</i> sp. (2)		+
<i>Anisotremus</i> sp.		+
Percichthyidae		
<i>Morone labrax</i>		+
Sphyraenidae		
<i>Sphyraena</i> sp.		+
Grammistidae		
<i>Rypticus</i> sp.		+
Scaridae		
<i>Sparisoma</i> sp. (3)		+
Percidae		
<i>Etheostoma olmstedii</i>		+
Stromateidae		
<i>Stromateid</i> sp.		+
Istiophoridae		
<i>Makaira</i> sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Coryphaenidae		
<i>Coryphaena</i> sp.		+
Sciaenidae		
<i>Cynoscion regalis</i>		+
<i>Equetus</i> sp.		+
Cichlidae		
<i>Julidochromis</i> sp.		+
Belontiidae		
<i>Trichogaster trichopterus</i>		+
Channidae		
<i>Channa micropeltes</i>		+
Mullidae		
<i>Mullus surmuletus</i>		+
<i>Mulloidichthys</i> sp.		+
Kyphosidae		
<i>Kyphosus</i> sp.		+
Chaetodontidae		
<i>Chaetodon</i> sp. (6)		+
<i>Pomacanthus</i> sp.		+
<i>Pomacanthodes</i> sp.		+
Pomacentridae		
<i>Abudefduf</i> sp.		+
Cepolidae		
<i>Cepola rubescens</i>		+
Centropomidae		
<i>Centropomus</i> sp.		+
Acanthuridae		
<i>Adanthurus</i> sp. (4)		+
<i>Zanclus</i> sp.		+
Scombridae		
<i>Scomber</i> sp. (2)		+
<i>Thunnus</i> sp.		+
<i>Euthynnus</i> sp.		+
Gerreidae		
<i>Gerres</i> sp.		+
<i>Eugerres</i> sp.		+

Table 1. continued

List of Teleosts Examined for Innervation Pattern	White Myotomal Muscle Fibers	
	Terminal Pattern	Distributed Pattern
Siganidae		
<i>Siganus</i> sp.		+
Labridae		
<i>Halichoeres</i> sp.		+
<i>Lepidaplois</i> sp.		+
<i>Anampses</i> sp.		+
<i>Lachnolaimus maximus</i>		+
Gobiidae		
<i>Periophthalmus koelreuteri</i>		+
Ephippidae		
<i>Chaetodipterus</i> sp.		+
Tetraodontiformes		
Balistidae		
<i>Balistes</i> sp.		+
<i>Xanthichthys</i> sp.		+
<i>Melichthys</i> sp.		+
<i>Cantherhines</i> sp.		+
<i>Balistapus</i> sp.		+
Ostracioidae		
<i>Acanthostracion</i> sp. (2)		+
<i>Lactophrys</i> sp.		+
Diodontidae		
<i>Diodon</i> sp. (2)		+
<i>Chilomycterus</i> sp.		+
Tetradontidae		
<i>Sphoeroides</i> sp.		+

In all the fishes listed above, the red myotomal muscle fibers had the distributed pattern of innervation.