

## B R E V I O R A

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**ON THE EVOLUTION OF THE JAW ADDUCTOR  
MUSCULATURE IN PRIMITIVE GNATHOSTOME FISHES**GEORGE V. LAUDER, JR.<sup>1</sup>

**ABSTRACT.** The primitive condition of the adductor mandibulae musculature in gnathostomes is a large unsubdivided, fan-shaped muscle mass originating from the palatoquadrate and inserting on the lateral aspect of the mandible. Unspecialized suborbital fibers extend posteriorly from the palatoquadrate to insert laterally on the lower jaw, and an intramandibular adductor division is absent. The Actinopterygii, Actinistia, Dipnoi, and Choanata primitively possess three distinct components of the adductor mandibulae: a suborbital division, a medial division, and a posterolateral division, as well as medial intramandibular adductor fibers. The suborbital division of the adductor mandibulae has been lost in teleosts and, independently, in coelacanths and living lungfishes. Devonian lungfishes and early choanates possessed both the suborbital and intramandibular adductor muscle components.

## INTRODUCTION

Towards the end of the nineteenth and in the first half of the twentieth century, a large number of investigators were concerned with the homologies of the jaw musculature between the different vertebrate classes (Allis, 1897, 1917, 1923; Edgeworth, 1935; Kesteven, 1942, 1943, 1944; Lightoller, 1939; Luther, 1913; Souché, 1932; Vetter, 1874). The musculature of the mandibular arch was the subject of special attention and several attempts were made to precisely link each branchial arch muscle with its serial homologue on the mandibular arch [see Lightoller (1939) for an example of this procedure carried to an extreme]. In recent years, little work has been done on the evolution of the musculature in primitive gnathostomes, despite the discovery of significant new fossil material that allows more accurate reconstruction of the musculature in extinct taxa.

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Lauder (1980) has proposed that the primitive condition of the jaw musculature in the Actinopterygii (ray-finned fishes) is a tripartite division into distinct components: an anterior or suborbital division, a medial division, and a posterolateral division. In this paper, the consideration of adductor muscle components, including the intramandibular division, is extended to other primitive gnathostome taxa to elucidate the evolution and homologies of the gnathostome jaw adductor musculature.

## COMPARATIVE ANATOMY

### *Elasmobranchiomorphi*

The adductor musculature in the primitive living selachian *Chlamydoselachus anguineus* has been described by Allis (1923) and Smith (1937). Based on their descriptions and on the comparative anatomy of the adductor mandibulae in other living sharks, the adductor musculature in the primitive Devonian selachian *Cladodus* has been reconstructed (Fig. 1A).

In living selachians, the adductor musculature is divided into two main components. The adductor mandibulae proper [= quadrato-mandibularis of Kesteven (1942) and Lightoller (1939)] is a single unsubdivided muscle mass having a fan-shaped origin on the palatoquadrate. The fibers converge to a tendinous inscription before fanning out ventrally to insert on the lower jaw. The adductor insertion is on the lateral aspect of the mandible and no intramandibularis division is present.

A suborbitalis muscle [= pterygoideus of Kesteven (1942), adductor  $\beta$  of Vetter (1874), levator labii superioris of Allis (1923), preorbitalis of Luther (1913)] originates tendinously from the "ectethmoidal process" (Allis, 1923) of the cranium anteriorly and inserts onto the upper labial cartilage and the skin of the lip. In *Cladodus* this muscle is represented as distinct suborbital fibers of the adductor mandibulae originating from the palatoquadrate (Fig. 1A: SO). Some fibers may also have originated from the nasal capsule, as in living sharks, and inserted onto the labial cartilages, when present.

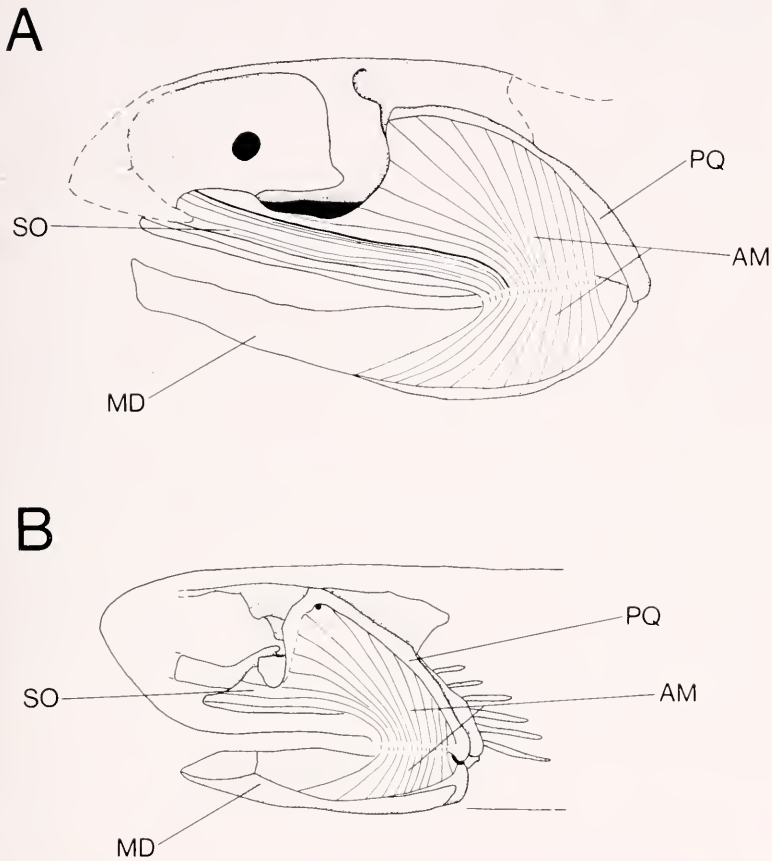


Figure 1. A. Reconstruction of the adductor mandibulae musculature in a primitive shark (*Cladodus*). Osteological features after Gross (1938). B. Reconstruction of adductor mandibulae musculature in an acanthodian (*Acanthodes*). Osteological features after Jarvik (1977) and Miles (1973). Abbreviations: AM, adductor mandibulae; MD, mandible; PQ, palatoquadrate; SO, suborbital fibers of the adductor mandibulae (separated into a distinct muscle in *Cladodus*).

In many living sharks, but not in *Chlamydoselachus*, a small superficial muscle overlies part of the adductor mandibulae. This muscle, the adductor mandibulae superficialis of Edgeworth (1935), adductor  $\gamma$  of Smith (1937), Vetter (1874), and Allis (1923), originates from the skin overlying the adductor mandibulae and inserts onto the posterior aspect of the palatoquadrate and mandible. There is currently no evidence to indicate whether the lack of this muscle in *Chlamydoselachus* is a specialization or if the primitive elasmobranchiomorph condition (absence of this muscle) has simply been retained. This muscle represents a small superficial component of the main adductor muscle, and I have reconstructed *Cladodus* (Fig. 1) with an unsubdivided adductor.

#### *Acanthodii*

The structure of the adductor mandibulae in acanthodians appears to have been very similar to that hypothesized to be primitive for elasmobranchiomorphs (Fig. 1). The large adductor mandibulae had a fan-shaped origin from the palatoquadrate and a lateral insertion on the mandible. An intramandibular division is hypothesized to have been absent since the "adductor fossa" is located on the lateral aspect of the mandible and the medial surface is convex in shape (Jarvik, 1977; Miles, 1973).

The adductor mandibulae is proposed to have extended anteriorly ventral to the orbit (Fig. 1B: SO); the suborbital fibers originating from the palatoquadrate and extending posteriorly to join the other adductor fibers at a tendinous inscription before inserting on the mandible.

#### *Actinopterygii*

In ray-finned fishes, the adductor mandibulae complex may be divided into three separate divisions each inserting on the lower jaw, and an intramandibular adductor component (Fig. 2; Lauder, 1980). Suborbital adductor fibers are present in *Amia*, *Lepisosteus*, and *Polyodon*. In *Amia*, these suborbital fibers have been called the levator maxillae superioris by Allis (1897) while the homologous adductor component in *Lepisosteus* is the palatomandibularis minor and major. *Polyodon* possesses a large separate anterior adductor

division originating on the palatoquadrate (Danforth, 1913). The suborbitalis adductor component has been lost in all teleosts (Fig. 2: character 6; also see Winterbottom, 1974).

In palaeoniscoid actinopterygians, the suborbital fibers were enclosed in the anterior part of the maxillary—palatoquadrate chamber (Schaeffer and Rosen, 1961) and extended posteroventrally to insert in the mandibular fossa.

The medial adductor division represents one of two components of the primitive unsubdivided postorbital adductor fibers. Homologies of the medial division in actinopterygians are given in Lauder (1980). The medial adductor fibers in *Polypterus* are called the “pterygoideus” and “temporalis” muscles by Allis (1922). The “pterygoideus” of Allis (1922) is not homologous to the “pterygoideus” of Kesteven (1942), which represents the suborbital division.

A distinct posterolateral adductor component is also hypothesized to be primitive for actinopterygians (Lauder, 1980). This muscle represents the superficial lateral adductor fibers which run dorsoventrally from the palatoquadrate to insert in the adductor fossa.

An intramandibular adductor division is present in most teleosts and in *Amia*, *Polypterus*, *Polyodon*, and palaeoniscoids (as inferred by the presence of an adductor fossa). The presence of intramandibular fibers is thus proposed to be a primitive actinopterygian character (Fig. 2: character 4).

#### *Actinistia*

Millot and Anthony (1958) describe three adductor muscles in *Latimeria*. A superficial adductor arises posteroinferiorly from the quadrate and inserts on the mandible in the mandibular fossa. This muscle appears to represent the posterolateral adductor division.

The two remaining adductors arise from the ethmosphenoid portion of the cranium posterior to the orbit. Millot and Anthony (1958) note that these muscles appear to correspond to the “pterygoideus” and “temporalis” adductors of *Polypterus*, and thus are both comparable to the medial adductor complex in primitive actinopterygians. No anterior (suborbital) division is present in *Latimeria*; all jaw adductors extend dorsoventrally behind the orbit.

A large intramandibular adductor occurs in *Latimeria* (Millot and Anthony, 1958: Fig. 19).

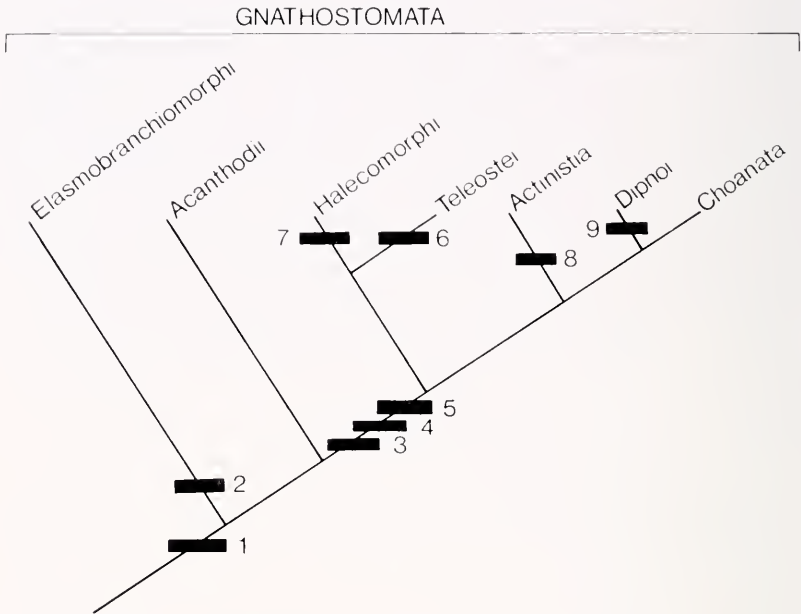


Figure 2. The distribution of various character states of the adductor mandibulae musculature in gnathostomes superimposed on one hypothesis of gnathostome phylogeny. For other characters supporting this phylogeny see Liem and Lauder (in press). Character 1: fan-shaped adductor mandibulae with unspecialized suborbital and postorbital fibers and a lateral insertion on the mandible; 2: suborbitalis muscle differentiated from suborbital fibers; 3: medial insertion of the adductor mandibulae on the mandible; 4: intramandibular adductor division present; 5: postorbital adductor component divided into medial and posterolateral divisions; 6: loss of suborbital adductor component; 7: specialization of suborbital fibers into the levator maxillae superioris 3 and 4 muscles (see Allis, 1897); 8: loss of the suborbital adductor component; 9: loss of suborbital component in living forms.

### *Dipnoi*

While extant dipnoans lack both intramandibular and suborbital adductor divisions, Devonian lungfishes appear to have possessed both. A space between the infraorbital bones laterally and the palatoquadrate medially may have housed the anterior adductor (suborbital) division, and an adductor fossa for the intramandibular adductor is found on the medial surface of the lower jaw (see Miles, 1977).

The main adductor mass in living lungfishes is divisible into posterolateral and medial components. The adductor mandibulae posterior (Edgeworth, 1935; = retractor anguli oris of Luther, 1913), corresponds to the posterolateral adductor division, and lies lateral to the ramus maxillaris and mandibularis V. The adductor mandibulae anterior (Edgeworth, 1935; = temporalis of Luther, 1913) is located anteromedially to the posterior adductor. In adult lungfishes the adductor mandibulae anterior is a large muscle with a broad postorbital origin from the skull. In larval lungfishes (Edgeworth, 1935), the anterior adductor is nearly equal in mass to the posterior adductor and lies medial to it, and lateral to the trabeculae.

### *Choanata*

Olson (1961) and Thomson (1967) both provide partial reconstructions of the adductor mandibulae complex in primitive choanates. A suborbital component of the adductor mandibulae was located anteriorly and presumably had its origin from the palatoquadrate. This division was housed in a chamber formed between the palatoquadrate medially and the dermal skull bones laterally. Postorbitally, the lateral wall of the suborbital adductor chamber was formed by the postorbital and jugal bones; while anteriorly the prefrontal, jugal, and maxilla enclosed the suborbital adductor. The posterolateral and medial adductor divisions both appear to have been present (Thomson, 1967) and thus the configuration of the adductor mandibulae in primitive choanates closely resembles that of palaeoniscoid actinopterygians. An intramandibular adductor division is inferred to have been present by the occurrence of an adductor fossa in the lower jaw (see Romer, 1966).

## DISCUSSION

In figure 2, the various configurations of the adductor mandibulae complex are superimposed on one hypothesis of gnathostome phylogeny. Other characters supporting this hypothesis may be found in Liem and Lauder (in press). The primitive configuration of the adductor mandibulae in gnathostomes is hypothesized to be a single unsubdivided fan-shaped muscle mass with unspecialized suborbital fibers originating anteriorly from the palatoquadrate (Fig. 2: character 1). Elasmobranchiomorphs retain the fan-shaped adductor configuration but possess specialized suborbital fibers (Fig. 2:

character 2); these fibers originate, in most cases, from the nasal capsule. A fan-shaped adductor muscle is also hypothesized for acanthodians (Fig. 1B), and the main postorbital adductor mass is reconstructed as being unsubdivided.

One notable aspect of the adductor mandibulae in elasmobranchiomorphs and acanthodians is its lateral insertion on the lower jaw. This condition contrasts sharply with the medial adductor insertion in actinopterygians, actinists, dipnoans, and choanates (Fig. 2: character 3). The medial insertion correlates with the presence of an intramandibularis adductor division (Fig. 2: character 4) and the occurrence of an adductor fossa on the medial surface of the lower jaw, in contrast to the lateral fossa of elasmobranchiomorphs and acanthodians.

In the Actinopterygii, Actinistia, Dipnoi, and Choanata, an hypothesis of a tripartite division of the adductor mandibulae into suborbital, medial, and posterolateral components best fits the embryological data and morphological relationships of the musculature in the adult (Fig. 2: character 5). Although among living taxa, *Polypterus* lacks the suborbital adductor fibers and *Lepisosteus* the intramandibular division, other primitive actinopterygians (including palaeoniscoids) possess or show evidence of three extramandibular adductor components.

Teleost fishes have lost the suborbital adductor division (Fig. 2: character 6) but halecomorphs (*Amia*) retain specialized derivatives of the suborbital musculature, the levator maxillae superioris 3 and 4 of Allis (1897) (Fig. 2: character 7). The cylindrically-shaped suborbital muscles of *Amia* are not morphologically homologous to the similarly shaped and located suborbitalis muscle of elasmobranchiomorphs. Both muscles, however, are derived from the same geographical area of the adductor anlagen, and are thus homologous as suborbital fibers of the adductor mandibulae.

Coelacanth retain both the medial and posterolateral adductor components but have lost all suborbital fibers (Fig. 2: character 8).

The primitive condition for dipnoans and choanates is the presence of well-developed suborbital, medial, and posterolateral adductor divisions as well as an intramandibular section. Devonian dipnoans and early choanates appear to possess a very primitive configuration of the jaw adductor musculature, similar in all essential features to that of palaeoniscoids. Living lungfishes have lost all suborbital adductor fibers (Fig. 2: character 9).



Based on this analysis, the following classification of jaw adductor muscle states is proposed. The primitive gnathostome condition consisted of a jaw adductor composed of unspecialized suborbital and postorbital components. The presence of both suborbital and postorbital fibers defines the "fan-shaped" condition. Suborbital fibers occur in elasmobranchiomorphs as a distinct suborbitalis muscle while the postorbital component is divided into two divisions in actinopterygians, dipnoans, and choanates. The mandibular component represents the third adductor component. It lies lateral to the mandible in elasmobranchiomorphs and acanthodians, and medial to it in all other groups (Fig. 2).

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