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Comparative anatomy, homologies and evolution of mandibular, hyoid and hypobranchial muscles of bony fish and tetrapods: a new insight

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Abstract

The Osteichthyes, including bony fishes and tetrapods, is a highly speciose group of vertebrates, comprising more than 42000 living species. The anatomy of osteichthyans has been the subject of numerous comparative studies, but these mainly concern osteological structures; much less attention has been paid to muscles. In fact, the most detailed and comprehensive myological comparative analyses that were actually based on a direct observation of representatives of various major osteichthyan groups were provided various decades by authors such as Luther, Kesteven and principally Edgeworth. The present work provides an updated discussion of the homologies and evolution of the osteichthyan mandibular, hyoid and hypobranchial muscles, based on the author's own analyses and on a survey of the literature, both old and recent. The risks of discussing muscle homologies on the basis of a single line of evidence, even when it concerns innervation or development, is emphasized. It is stressed that only by taking into consideration various lines of evidence (e.g. developmental biology, comparative anatomy, functional morphology, paleontology, molecular biology, experimental embryology, innervation and/or phylogeny) it is possible to establish well-grounded hypotheses of muscle homology.

Keywords

Actinopterygii; bony fish; comparative anatomy; cranial muscles; evolution; hyoid; hypobranchial; mandibular; Osteichthyes; Sarcopterygii; Tetrapods.

Introduction

The Osteichthyes, including bony fishes and tetrapods, is a highly speciose group of gnathostomes, with more than 42000 living species. Two main osteichthyan subgroups are usually recognized (fig. 1): the Sarcopterygii (lobefins and tetrapods, > 24000 living species) and the Actinopterygii (rayfins, > 28000 extant species) (e.g. Nelson 2006).

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The extraordinary taxonomic diversity of osteichthyans is associated with a remarkable variety of morphological features and adaptations to very different habitats, from miniature freshwater fishes to enormous tetrapods. The anatomy of osteichthyans has been the subject of numerous comparative studies, but these mainly deal with skeletal structures (Diogo, in press). There are, of course, several sources of information about the musculature of osteichthyans, but the majority of those focus on a specific taxon (e.g. Allis 1897: *Amia*; Danforth 1913: *Polyodon*; Allis 1922: *Polypterus*; Millot and Anthony 1958: *Latimeria*; Winterbottom 1974: Teleostei; Carroll and Holmes 1980: Urodela; Bemis 1986: Dipnoi; Abdala and Moro 2003: Squamata; etc.). In fact, the most detailed and comprehensive myological comparative analyses based on a direct observation of a variety of osteichthyan taxa as, e.g., Teleostei, Halecomorphi, Ginglymodi, Chondrostei, Cladistia, Dipnoi, Amphibia and Amniotes (fig. 1), and not mainly on a recompilation from the literature, were provided decades ago in works such as Luther (1913–1914), Kesteven (1942–1945), and principally Edgeworth (1935).

Edgeworth’s 1935 volume continues to be a fundamental source of information on vertebrate muscles. However, because that volume was written more than 70 years ago,

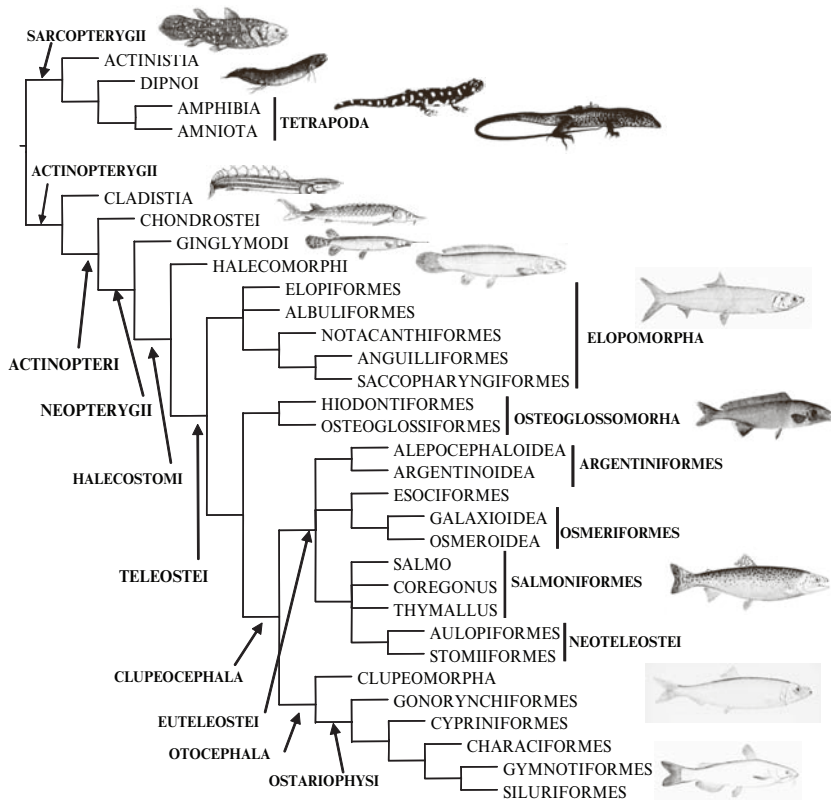


Figure 1. Phylogenetic relationships among the major extant osteichthyan groups, according to the results of the cladistic analysis of Diogo (in press) (for more details, see text).

Edgeworth could not, for instance, study the muscles of the at the time undiscovered coelacanth *Latimeria chalumnae* (Millot and Anthony 1958), or know of the essential role of neural crest cells in the development and patterning of vertebrate cranial muscles (e.g., Le Lièvre and Le Douarin 1975; Noden 1983, 1984, 1986; Couly et al. 1992; Köntges and Lumsden 1996; Schilling and Kimmel 1997; Olsson et al. 2001; Ericsson and Olsson 2004; Ericsson et al. 2004). Furthermore, some of Edgeworth's hypotheses concerning muscular homologies were based on phylogenetic scenarios that have been contradicted by subsequent research. For instance, according to Edgeworth (1935) the chondrichthyans, the tetrapods and actinopterygians *sensu* this work (fig. 1) were derived from an 'early dipnoan stock'; birds are the sister-group of a taxon including all his 'reptiles'; his clade Reptilia + Aves and his clade Mammalia were independently originated from amphibians; and the Teleostei is the sister-group of an assemblage including all non-teleostean actinopterygians (his 'Ganoidei'). It is thus opportune to re-evaluate the work of researchers such as Edgeworth in order to check the extent to which their hypotheses concerning the homologies and evolution of osteichthyan muscles are, or not, supported by more up-to-dated information.

About 15 years ago, Miyake et al. (1992) published an analysis of the cranial muscles of chondrichthyan batoids, in which they re-examined and discussed various hypotheses proposed by Edgeworth (1935). For instance, they noted that "Noden (1983, 1984, 1986) elegantly demonstrated with quail-chick chimeras that cranial muscles are embryologically of somitic origin, and not as commonly thought, of lateral plate origin, and in doing so corroborated the nearly forgotten work of Edgeworth" (Miyake et al. 1992: 214). They also pointed out that molecular developmental studies such as Hatta et al. (1990, 1991) "have corroborated one of Edgeworth's findings: the existence of one premyogenic condensation (the constrictor dorsalis) in the cranial region of teleost fish" (Miyake et al. 1992: 214).

As explained by Miyake et al. (1992), Edgeworth, based on his detailed observations of ontogenetic series - from very early to late stages - of members of all major vertebrate groups, recognized various presumptive premyogenic condensations, which he included in five main cranial muscle plates: mandibular, hyoid, branchial, epibranchial, and hypobranchial. Edgeworth viewed development of cranial muscles in the light of developmental pathways leading from these condensations to different states in each cranial arch. According to him these pathways involve migration of premyogenic cells, differentiation of myofibers, directional growth of myofibers and possibly interactions with surrounding structures. These events occur in very specific locations, e.g. dorsal, medial or ventral areas of each cranial arch, as shown in the scheme of figure 2. This scheme is similar to that recently proposed by Mallat (1997), the main differences being, in fact, mainly nomenclatural ones (e.g. the "hoyoidean and mandibular superficial constrictors" of Edgeworth correspond to the "hoyoidean and mandibular interbranchial muscles" of Mallat - see e.g. Mallat's table 2). According to Edgeworth, although exceptions may occur (see below), his mandibular muscles are generally innervated by the Vth nerve, his hyoid muscles by the VIIth nerve, and his branchial muscles by the IXth and Xth nerves. The epibranchial and hypobranchial muscles are "developed from the anterior myotomes of the body" and thus "are intrusive elements of the head"; they "retain

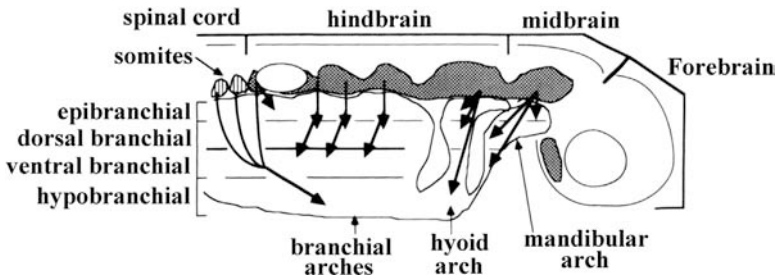


Figure 2. Schematic presentation of embryonic origin of cranial muscles in gnathostomes based on Edgeworth's (1902, 1911, 1923, 1926a,b,c, 1928, 1935) works; premyogenic cells originate from the paraxial mesoderm (hatched areas) and several somites (areas with vertical bars); large arrows indicate a contribution of cells in segments of the mesoderm to muscle formation of different cranial arches (modified from Miyake et al. 1992; the nomenclature of the structures illustrated basically follows that of these authors). For more details, see text.

a spinal innervation" and "do not receive any branches from the Vth, VIIth, IXth and Xth nerves" (Edgeworth 1935: 189). It is worth noting that apart the mandibular, hyoid, hypobranchial, epibranchial and branchial arches Edgeworth (1935: 5) referred to a primitive "premandibular arch" in "which passed the IIIrd nerve". This IIIrd nerve, together with the IVth and VIth nerves - which according to Edgeworth (1935: 5) are "not segmental nerves; they innervate muscles of varied segmental origin and are, phylogenetically, of later development than are the other cranial nerves" - innervate the external ocular muscles of most extant osteichthyans.

The main aim of this study is to provide an up-to-dated discussion on the homologies and evolution of the osteichthyan mandibular, hyoid and hypobranchial muscles (i.e., the 'superficial cranial muscles' sensu Diogo and Vandewalle 2003; note: the epibranchial muscles sensu Edgeworth are absent in extant osteichthyans). This discussion is based on the author's analyses of these muscles (e.g. of their topology, functional morphology, innervation and/or development) in key representative taxa of various major osteichthyan groups and on a survey of the literature, both recent and old. It is hoped that the present work may contribute for a better understanding of the cranial muscles of osteichthyans, as well as pave the way for future works concerning the comparative anatomy, functional morphology, ontogeny, evolution and phylogeny of these gnathostomes and of vertebrates in general.

Materials and methods

The phylogenetic framework for the discussions provided in the present paper is based on the results of a recent cladistic analysis of osteichthyan higher-level phylogeny including 356 phylogenetic osteological and myological characters and 80 extant and fossil terminal taxa (Diogo, in press; fig. 1).

The information provided in the text and the figures of the present work complements that provided in Miyake et al.'s (1992) study, which, as referred above, is mainly focused on chondrichthyans. Thus, figures 3–8 provide an up-dated version of the

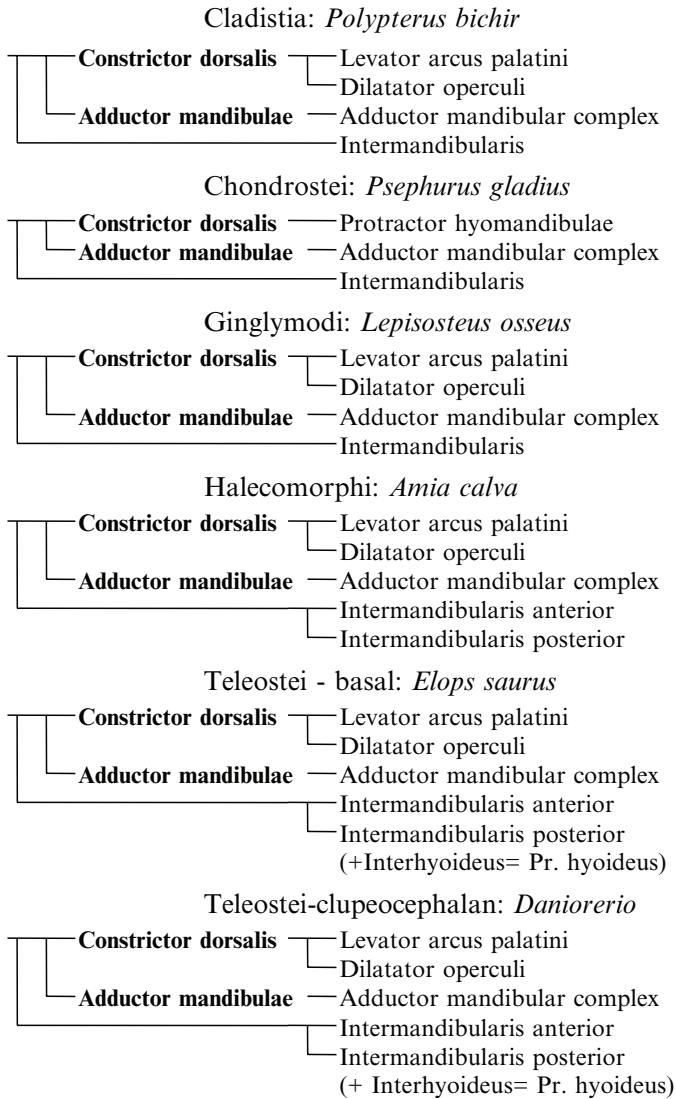


Figure 3. Developmental lineages of mandibular muscles in actinopterygians. In this figure, as well as in figures 4–8, Edgeworth's presumptive premyogenic condensations are in a bold face (modified from Miyake et al. 1992); the data is compiled from evidence provided by developmental biology, comparative anatomy, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers); the nomenclature of the muscles listed on the right of the figure follows that of the present work. "Pr. hyoideus" means protractor hyoideus; for more details, see text.

schemes provided in Miyake et al.'s (1992) table 1. The schemes illustrated in these figures include representatives of some osteichthyan groups not considered in Miyake et al.'s paper, e.g. amphibians and amniotes; the chondrichthyans, not analyzed in the present work, are excluded from those schemes. The information provided in these

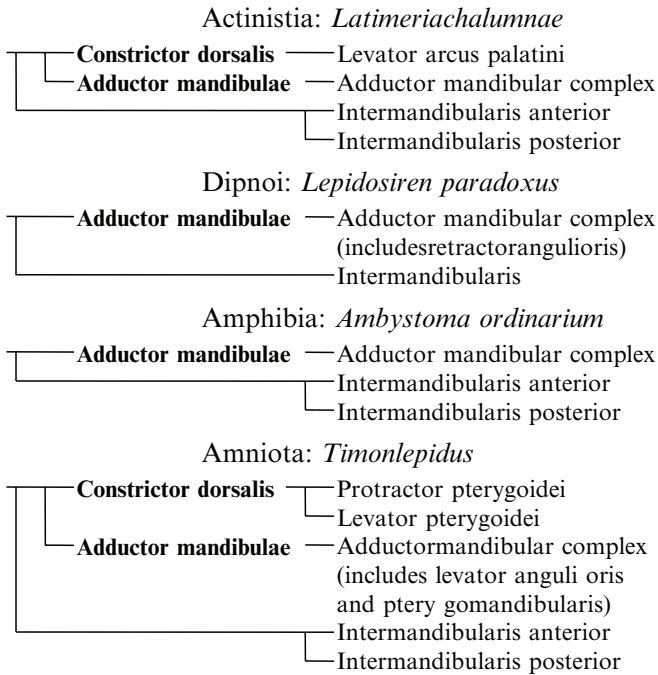


Figure 4. Developmental lineages of mandibular muscles in sarcopterygians. For more details, see text.

figures is complemented with that given in tables 1–6, respectively. As can be seen in those tables, when a same muscle is given a name X by researchers working with e.g. plesiomorphic bony fishes and a name Y by researchers working with e.g. tetrapods, I opted to use the name X. This option is methodologically more appropriate than to continue to designate that muscle by both names Y and X, as this is precisely one of the main reasons for the historical confusions concerning the homologies and evolution of osteichthyan muscles. This option makes more evolutionary sense than to use only the name Y, because tetrapods were originated from bony fishes, and not the reverse.

The present study pays more attention to basal sarcopterygian and actinopterygian groups than to derived extant taxa such as the actinopterygian teleosts or the sarcopterygian tetrapods. That is, some representatives of these two latter groups were observed in order to investigate and discuss the homologies between their muscles and the muscles of other major osteichthyan groups (tables 1–6). But not all the representatives of all the numerous extant teleostean and tetrapod subgroups were examined. This because the main aim of the present work is to discuss the homologies and evolution of the mandibular, hyoid and hypobranchial muscles within the major extant osteichthyan groups (i.e. Actinistia, Dipnoi, Amphibia, Amniota, Cladistia, Chondrostei, Ginglymodi, Halecomorphi and Teleostei), and not within all these numerous teleostean and tetrapod subgroups. It is however hoped that the present work will precisely help paving the way for detailed comparative analyses of these muscles within the Teleostei and/or the Tetrapoda.

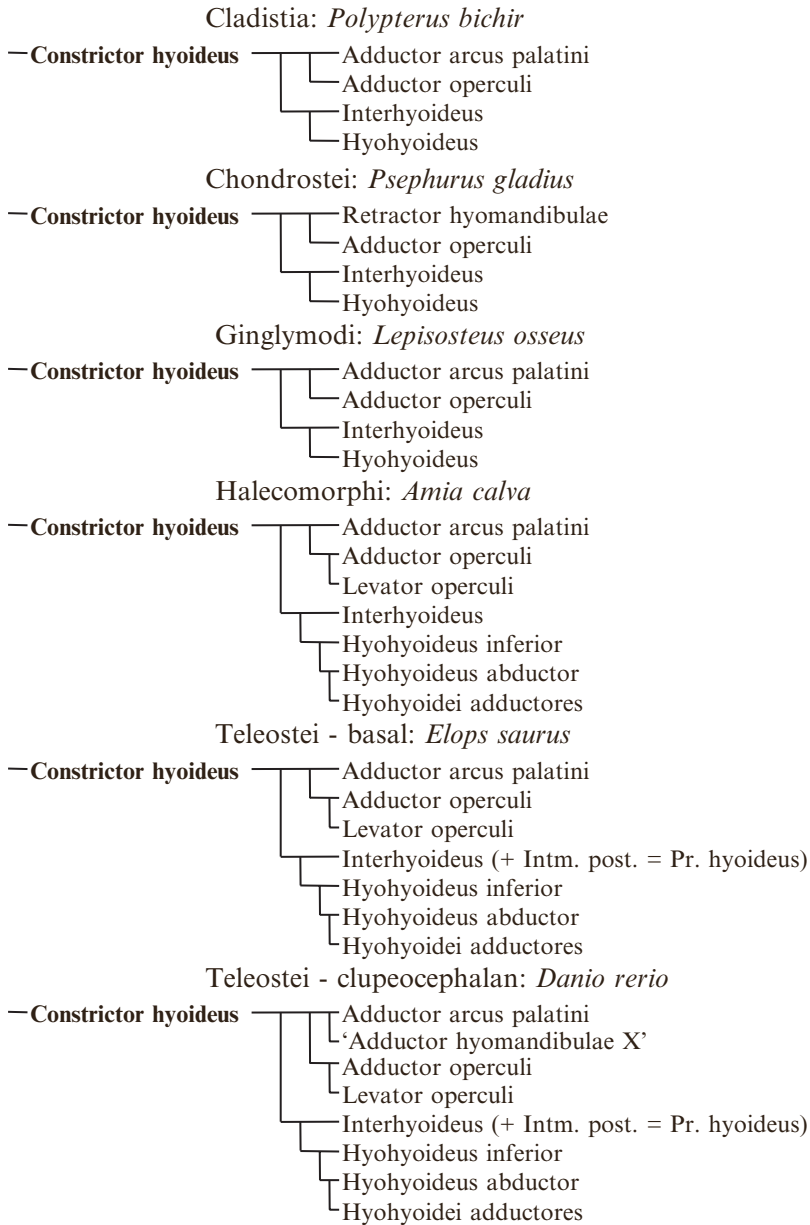


Figure 5. Developmental lineages of hyoid muscles in actinopterygians. “Pr. hyoideus” means protractor hyoideus and “Intm. post.” means intermandibularis posterior; for more details, see text.

Of the nine major extant osteichthyan groups listed in the paragraph above, the only group for which it was not possible to obtain representative specimens is the Actinistia, due to the difficulty to obtain *Latimeria* specimens for dissection. Fortunately, the cranial muscles of *Latimeria* have been described in detail by Millot and Anthony (1958). The specimens examined for the present study are from the Laboratory of Functional

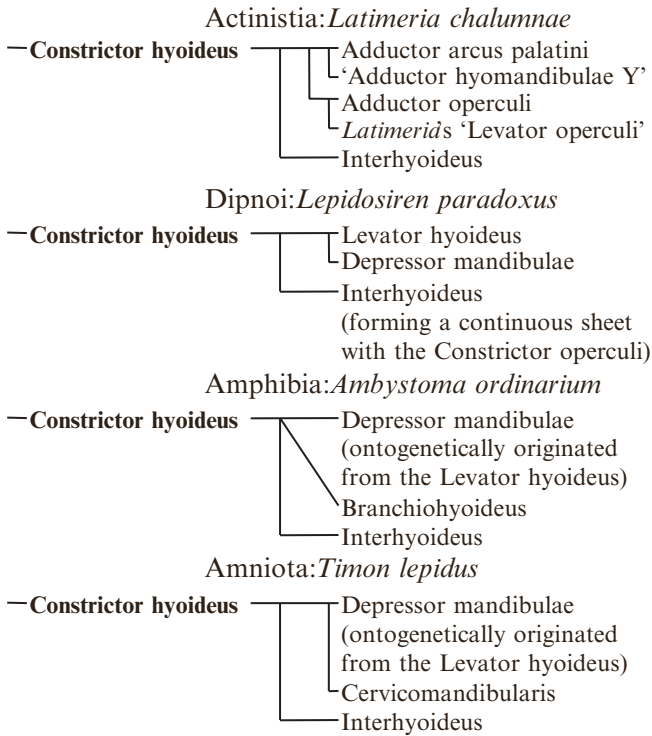


Figure 6. Developmental lineages of hyoid muscles in sarcopterygians. For more details, see text.

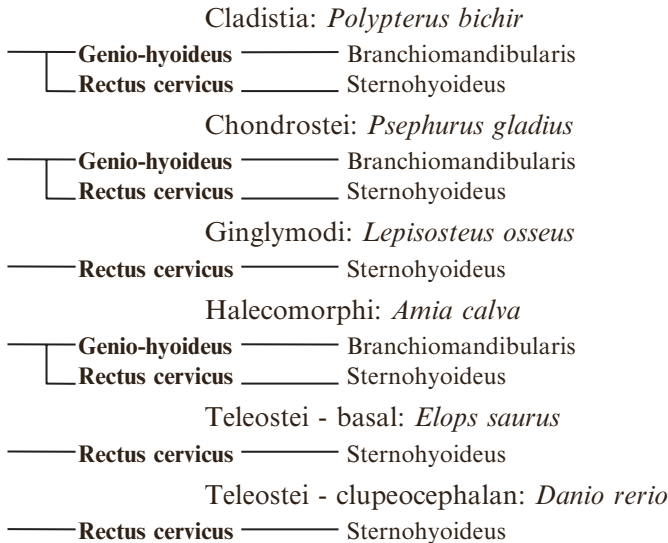


Figure 7. Developmental lineages of hypobranchial muscles in actinopterygians. For more details, see text.

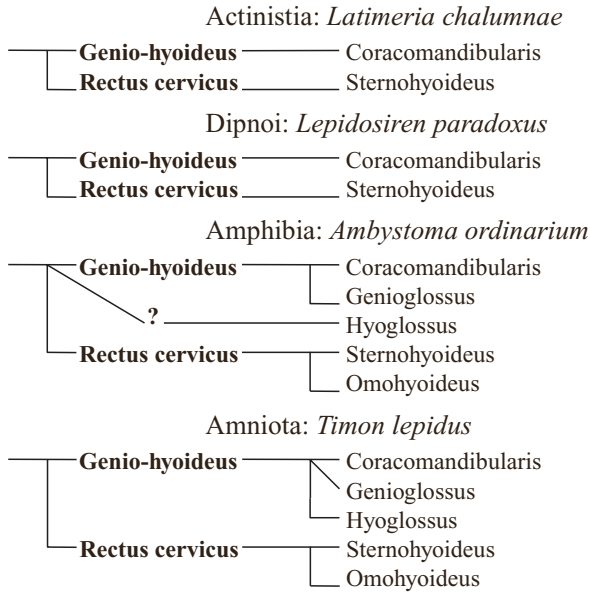


Figure 8. Developmental lineages of hypobranchial muscles in sarcopterygians. For more details, see text.

and Evolutionary Morphology of the University of Liège (LFEM), the Museo Nacional de Ciencias Naturales de Madrid (MNCN), the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia (ANSP), the Chinese Academy of Sciences at Wuhan (CASW), the California Academy of Sciences (CAS), the Illinois Natural History Survey (INHS), the Centro Nacional Patagónico de Argentina (CONICET), the Macquarie University of Australia (MU), the Musée Royal de l'Afrique Centrale (MRAC), the National Museum of Natural History (USNM), and the George Washington University (GWU). The list of specimens is given below; their alcohol fixed (alc) or formalin embalmed (for) condition is indicated in parentheses following the number of specimens observed. Dissections and anatomical drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The nomenclature of the skeletal structures illustrated in these drawings follows that of Diogo (in press).

Chondrostei: *Acipenser sturio*: MNCN 152172, 3 (alc). *Psephurus gladius*: CASW, uncatalogued, 1 (alc). **Cladistia:** *Polypterus bichir*: MNCN 1579, 7 (alc). **Dipnoi:** *Lepidosiren paradoxa*: CONICET, uncatalogued, 1 (alc). *Neoceratodus forsteri*: MU, uncatalogued, 2 (alc). **Ginglymodi:** *Lepisosteus osseus*: ANSP 107961, 2 (alc); ANSP 172630, 1 (alc). *Lepisosteus platyrhincus*: AMNH 74789, 2 (alc). **Halecomorphi:** *Amia calva*: MNCN 35961, 1 (alc). **Teleostei:** *Albula vulpes*: MNCN 52124, 2 (alc). *Alepocephalus rostratus*: MNCN 108199, 2 (alc). *Anguilla anguilla*: MNCN 41049, 3 (alc). *Astronesthes niger*: MNCN 1102, 1 (alc). *Aulopus filamentosus*: MNCN 1170, 6 (alc). *Brycon guatemalensis*: MNCN 180536, 3 (alc). *Brycon henni*: CAS 39499, 1 (alc).

Table 1.

Mandibular muscles of adults of representative actinopterygian taxa; the nomenclature of the muscles shown in bold follows that of the present work, “ad. mand.” meaning adductor mandibulae (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle/bundle are given in front of that muscle/bundle); data compiled from evidence provided by developmental biology, comparative anatomy, functional morphology, paleontology, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers). For more details, see text (see also fig. 3).

| | Cladistia: | Chondrostei: | Ginglymodi: | Halecomorphi: | Teleostei - basal: | Teleostei - |
|---------------------------------------------------------------------------------------------------------------------|-----------------------------------|----------------------------------------------|------------------------------------------|----------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | <i>Polypterus bichir</i> (Bichir) | <i>Pepihurus gladius</i> (Chinese swordfish) | <i>Lepisosteus osseus</i> (Longnose gar) | <i>Amia calva</i> (Bowfin) | <i>Elops saurus</i> (Ladyfish) | Teleostei - clupecocephalan: <i>Danio rerio</i> (Zebrafish) |
| Intermandibularis (* intermandibularis anterior and posterior plesiomorphically present in osteichthyans? See text) | Intermandibularis | Intermandibularis | Intermandibularis | Intermandibularis | Intermandibularis | Intermandibularis |
| dibularis anterior | dibularis | dibularis | dibularis | dibularis | dibularis | dibularis |
| and posterior | | | | anterior | anterior | anterior |
| plesiomorphically present in osteichthyans? See text) | | | | | | |
| Intermandibularis | ----- | ----- | ----- | Intermandibularis | Intermandibularis | Intermandibularis |
| dibularis | | | | dibularis | dibularis | dibularis |
| posterior (* see cell above) | | | | posterior | posterior (* forming, together with interhyoideus, the protractor hyoideus) | posterior (* see cell on the left) |
| ----- | ----- | ----- | ----- | ----- | Protractor hyoideus (* including intermandibularis posterior and interhyoideus; it is thus derived from both the mandibular and hyoid muscle plates) | Protractor hyoideus (* see cell on the left) |

Table 1. (cont.)

| | Cladistia: | Chondrostei: | Ginglymodi: | Halecomorphi: | Teleostei - basal: | Teleostei - |
|-----------------------------------------------|-------------------------------------------------------------------|---------------------------------------------------------------|------------------------------------------------------------------|-------------------------------------|--------------------------------|------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | <i>Polypterus bichir</i> (Bichir) | <i>Psephurus gladius</i> (Chinese swordfish) | <i>Lepisosteus osseus</i> (Longnose gar) | <i>Amia calva</i> (Bowfin) | <i>Elops saurus</i> (Ladyfish) | Teleostei - clupeocephalan: <i>Danio rerio</i> (Zebrafish) |
| Ad. mand. A3' | Ad. mand. A3' (ad. mand. of e.g. Lauder, 1980a) | ---- | Ad. mand. A3' (preorbitalis superficialis of e.g. Lauder, 1980a) | Ad. mand. A3' | ---- | ---- |
| Ad. mand. A3'' | Ad. mand. A3'' (ad. mand. pterygoideus of e.g. Lauder, 1980a) | ---- | Ad. mand. A3'' (preorbitalis profundus of e.g. Lauder, 1980a) | Ad. mand. A3'' | ---- | ---- |
| Ad. mand. A2 | Ad. mand. A2 (ad. mand. of postero-lateral of e.g. Lauder, 1980a) | Ad. mand. A2 (ad. mand. of e.g. Carroll and Wainwright, 2003) | Ad. mand. A2 (ad. mand. posterolateral of e.g. Lauder, 1980a) | Ad. mand. A2 | Ad. mand. A2 | Ad. mand. A2 |
| ---- | ---- | ---- | Palatoman-dibularis minor and major | ---- | ---- | ---- |
| ---- | ---- | ---- | ---- | Levator maxillae superioris 3 and 4 | ---- | ---- |
| ---- | ---- | ---- | ---- | ---- | ---- | Ad. mand. A1-OST |
| Ad. mand. A ω | Ad. mand. A ω | ---- | ---- | Ad. mand. A ω | Ad. mand. A ω | Ad. mand. A ω |

Table 1. (cont.)

| | | | | | | |
|-----------------------------------------------|-------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------|---------------------------------------------|------------------------------------------------------|------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Cladistia: <i>Polypterus bichir</i> (Bichir) | Chondrostei: <i>Psephurus gladius</i> (Chinese swordfish) | Ginglymodi: <i>Lepisosteus osseus</i> (Longnose gar) | Halecomorphi: <i>Amia calba</i> (Bowfin) | Teleostei - basal: <i>Elops saurus</i> (Ladyfish) | Teleostei - clupeocephalan: <i>Danio rerio</i> (Zebrafish) |
| Levator arcus palatini | Levator arcus palatini | Protractor hyomandibulae (* seemingly originated from the portion of the hyoid muscle plate from which originate the adductor arcus palatini and dilator operculi of other actinopterygians) | Levator arcus palatini | Levator arcus palatini | Levator arcus palatini | Levator arcus palatini |
| ----- | Dilator operculi | ----- (* dilator operculi absent as a separate element, but see cell above) | Dilator operculi | Dilator operculi | Dilator operculi | Dilator operculi |

Table 2.

Mandibular muscles of adults of representative sarcopterygian taxa; the nomenclature of the muscles shown in bold follows that of the present work, “ad. mand.” meaning adductor mandibulae (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle/bundle are given in front of that muscle/bundle); data compiled from evidence provided by developmental biology, comparative anatomy, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers). For more details, see text (see also fig. 4).

| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren paradoxa</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
|-----------------------------------------------|-------------------------------------------------------------------------|-------------------------------------------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------------------|
| Intermandibularis anterior (* see table 1) | Intermandibularis anterior | Intermandibularis | Intermandibularis anterior | Intermandibularis anterior |
| Intermandibularis posterior (* see table 1) | Intermandibularis posterior | ----- | Intermandibularis posterior | Intermandibularis posterior |
| Ad. mand. A3' | Ad. mand. A3' (ad. mand. 'moyen' of e.g. Millot and Anthony, 1958) | Ad. mand. A3' (ad. mand. anterior of e.g. Bemis and Lauder, 1986) | Ad. mand. A3' (pseudotemporalis posterior of e.g. Lordansky, 1992) | Ad. mand. A3' (pseudotemporalis superficialis of e.g. Abdala and Moro, 2003) |
| Ad. mand. A3'' | Ad. mand. A3'' (ad. man. 'profond' of e.g. Millot and Anthony, 1958) | ----- | Ad. mand. A3'' (pseudotemporalis anterior of e.g. Lordansky, 1992) | Ad. mand. A3'' (pseudotemporalis profundus of e.g. Abdala and Moro, 2003) |
| Ad. mand. A2 | Ad. mand. A2 (ad. mand. 'superficial' of e.g. Millot and Anthony, 1958) | Ad. mand. A2 (part of ad. mand. posterior of e.g. Bemis and Lauder, 1986) | Ad. mand. A2 (ad. mand. externus of e.g. Lordansky, 1992) | Ad. mand. A2 (ad. mand. externus of e.g. Abdala and Moro, 2003) |
| ----- | ----- | Ad. mand. A2-PVM (part of ad. mand. posterior of e.g. Bemis and Lauder, 1986) | Ad. mand. A2-PVM (ad. mand. posterior of e.g. Lordansky, 1992) | Ad. mand. A2-PVM (ad. mand. posterior of e.g. Abdala and Moro, 2003) |

Table 2. (cont.)

| | | | | |
|-----------------------------------------------|--------------------------------------------------------------------------|----------------------------------------------------------------------------------|---------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren paradoxo</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
| ----- | ----- | Retractor anguli oris (* seemingly derived from lateral portion of ad. mand.) | ----- | ----- |
| ----- | ----- | ----- | ----- | Levator anguli oris (* present, somewhat mixed with A2; seemingly derived from lateral portion of ad. mand. it may eventually be derived/modified from the retractor anguli oris, or at least from the portion of the mandibular muscle plate originating that muscle in other osteichthyan taxa) Ad. mand. A ω (* in <i>Timon</i> the ad. mand. has an anteroventral section that is lodged in the adductor fossa and that is very similar to the A ω of other osteichthyan taxa: is this section homologous with the A ω of those taxa? See text) |
| Ad. mand. A ω | Ad. mand. A ω (intramandibular adductor of e.g. Lauder, 1980b) | ----- | ----- | |

Table 2. (cont.)

| | | | | |
|-----------------------------------------------|-----------------------------------------------------------|---------------------------------------------------------------------|---------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren paradoxo</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
| ----- | ----- | ----- | ----- | Prerygomandibularis (* seemingly derived from mesial portion of ad. mand.) |
| Levator arcus palatini | Levator arcus palatini | ----- | ----- | Levator pterygoidei (* it may well be derived/modified from the levator arcus palatini, or at least from the portion of the mandibular muscle plate originating that muscle in other osteichthyan taxa) |
| ----- | ----- | ----- | ----- | Protractor pterygoidei (* same as cell above) |

Table 3.

Hyoid muscles of adults of representative actinopterygian taxa; the nomenclature of the muscles shown in bold follows that of the present work (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle/bundle are given in front of that muscle/bundle); data compiled from evidence provided by developmental biology, comparative anatomy, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers). For more details, see text (see also fig. 5).

| | Cladistia: | Chondrostei: | Ginglymodi: | Halecomorphi: | Teleostei - basal: | Teleostei - |
|-----------------------------------------------|-----------------------------------|----------------------------------------------|------------------------------------------|------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------|------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | <i>Polypterus bichir</i> (Bichir) | <i>Psephurus gladius</i> (Chinese swordfish) | <i>Lepisosteus osseus</i> (Longnose gar) | <i>Amia calva</i> (Bowfin) | <i>Elops saurus</i> (Ladyfish) | clupeocephalan: <i>Danio rerio</i> (Zebrafish) |
| Interhyoideus | Interhyoideus | Interhyoideus | Interhyoideus | Interhyoideus | Interhyoideus (* forming, together with intermandibularis posterior, the protractor hyoideus; see table 1) | Interhyoideus (* see cell on the left) |
| ----- | Hyohyoideus | Hyohyoideus | Hyohyoideus | Hyohyoideus inferior | Hyohyoideus inferior | Hyohyoideus inferior |
| ----- | ----- | ----- | ----- | Hyohyoideus abductor (* often considered as part of a hyohyoideus superior) | Hyohyoideus abductor (* see cell on the left) | Hyohyoideus abductor (* see cell on the left) |
| ----- | ----- | ----- | ----- | Hyohyoidei adductores (* often considered as part of a hyohyoideus superior) | Hyohyoidei adductores (* see cell on the left) | Hyohyoidei adductores (* see cell on the left) |

Table 3. (cont.)

| | | | | | | |
|-----------------------------------------------|----------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------|-------------------------------------------------------------------------------------|---------------------------------------------------------|-------------------------------------------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Cladistia: <i>Polypterus bichir</i> (Bichir) | Chondrostei: <i>Psephurus gladius</i> (Chinese swordfish) | Ginglymodi: <i>Lepisosteus osseus</i> (Longnose gar) | Halecomorphi: <i>Amia calva</i> (Bowfin) | Teleostei - basal: <i>Elops saurus</i> (Ladyfish) | Teleostei - clupeocephalan: <i>Danio rerio</i> (Zebrafish) |
| Adductor operculi | Adductor operculi | Adductor operculi (opercularis of e.g. Carroll and Wainwright, 2003) | Adductor operculi | Adductor operculi | Adductor operculi | Adductor operculi |
| Adductor arcus palatini | Adductor arcus palatini | Retractor hyomandibulae (*seemingly originated from the portion of the hyoid muscle plate from which originates the adductor arcus palatini of other actinopterygians) | Adductor arcus palatini | Adductor arcus palatini | Adductor arcus palatini | Adductor arcus palatini |
| ----- | ----- | ----- | ----- | ----- | ----- | 'Adductor hyomandibulae X' (*seemingly not homologous with the 'adductor hyomandibulae Y' of table 4) |
| ----- | ----- | ----- | ----- | Levator operculi (*seemingly not homologous with the 'levator operculi' of table 4) | Levator operculi (* see cell on the left) | Levator operculi (* see cell on the left) |

Table 4.

Hyoid muscles of adults of representative sarcopterygian taxa; the nomenclature of the muscles shown in bold in the present work (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle/bundle) are given in front of that muscle/bundle; data compiled from evidence provided by developmental biology, comparative anatomy, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers). For more details, see text (see also fig. 6).

| | Actinistia: | Dipnoi: | Amphibia: | Amniota: |
|-----------------------------------------------|-------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | <i>Latimeria chalumnae</i> (Coelacanth) | <i>Lepidosiren paradoxo</i> (South American lungfish) | <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | <i>Timon lepidus</i> (Ocellated lizard) |
| Interthyoideus | Interthyoideus ('gêniohyoïdien', plus 'hyoïdyien' of e.g. Millot and Anthony, 1958) | Interthyoideus | Interthyoideus (inter-hyoïdeus anterior plus interthyoideus posterior of e.g. Bauer, 1992, and Ericsson and Olsson, 2004) | Interthyoideus (constrictor colli of e.g. Herrel et al. 2005) |
| ----- | ----- | ----- | Branchiohyoideus (branchiohyoideus externus of e.g. Edgeworth, 1935, and Ericsson and Olsson, 2004) | ----- (* as noted by e.g. Edgeworth, 1935, the 'branchiohyoideus' of reptiles seemingly corresponds to the branchial muscle subarcualis rectus 1 of amphibians, and not to the hyoid muscle branchiohyoideus of the present work) |
| Adductor arcus palatini | Adductor arcus palatini | ----- (* does the portion of the hyoid muscle plate that gives rise to the levator hyoideus/depressor mandibulae eventually correspond to that giving rise to the adductor arcus palatini of other osteichthyans? See text) | ----- (* see cell on the left) | ----- (* see cell on the left) |

Table 4. (cont.)

| | | | | |
|-----------------------------------------------|---------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren pardoxa</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
| ----- | ----- | Levator hyoideus | Depressor mandibulae posterior (* the fibers corresponding to those of the levator hyoideus of dipnoans become also attached on the mandible, forming the depressor mandibulae anterior thus seemingly corresponds to the depressor mandibulae of dipnoans) | Depressor mandibulae (part) (* the fibers corresponding to those of the levator hyoideus of dipnoans become also attached on the mandible, forming part of the depressor mandibulae) |
| ----- | ----- | Depressor mandibulae | Depressor mandibulae anterior (* see cell above) | Depressor mandibulae (part) (* see cell above) |
| ----- | ----- | 'Adductor hyomandibulae Y' (* seemingly not homologous with the 'adductor hyomandibulae X' of table 3) | ----- | Cervicomandibularis (* seemingly derived from the levator hyoideus/depressor mandibulae: see e.g. Edgeworth, 1935) |
| Adductor operculi | Adductor operculi | ----- (* absent as a separate element in adults, but see text) | ----- | ----- |
| ----- | <i>Latimeria's</i> 'levator operculi' (* seemingly not homologous with the levator operculi of table 3) | ----- | ----- | ----- |

Table 6.

Hypobranchial muscles of adults of representative sarcopterygian taxa; the nomenclature of the muscles shown in bold follows that of the present work (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle/bundle are given in front of that muscle/bundle); data compiled from evidence provided by developmental biology, comparative anatomy, experimental embryology and molecular biology, innervation and phylogeny (in studies of the author and of other researchers). For more details, see text (see also fig. 8).

| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren paradoxo</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
|-----------------------------------------------|-----------------------------------------------------------|---------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------|
| Coracomandibularis | Coracomandibularis | Coracomandibularis (geniothoracicus of e.g. Miyake et al. 1992) | Coracomandibularis (geniohyoideus of e.g. Bemis et al. 1983, and Lauder and Shaffer, 1988) | Coracomandibularis (geniohyoideus and/or at least part of mandibulohyoideus of e.g. Edgeworth, 1935, and Herrel et al. 2005) |
| ----- | ----- | ----- | Genioglossus* according to e.g. Edgeworth, 1935, the genioglossus of salamanders such as <i>Ambystoma</i> is derived from the coracomandibularis) | Genioglossus(* according to e.g. Edgeworth, 1935, the genioglossus of lizards such as <i>Timon</i> is derived from the coracomandibularis) |
| ----- | ----- | ----- | Hyoglossus(* the statements of Edgeworth, 1935, concerning the origin of this muscle in salamanders such as <i>Ambystoma</i> are somewhat confuse: in his page 196 he states that it originates from the sternohyoideus but in his page 211 he seems to indicate that, as in other amphibians as well as in amniotes, it derives from the coracomandibularis) | Hyoglossus (* according to e.g. Edgeworth, 1935, the hyoglossus of lizards such as <i>Timon</i> is derives from the coracomandibularis) |

Table 6. (cont.)

| | | | | |
|-----------------------------------------------|-----------------------------------------------------------|---------------------------------------------------------------------|---------------------------------------------------------------------------|--------------------------------------------------------|
| Probable plesiomorphic osteichthyan condition | Actinistia: <i>Latimeria chalumnae</i> (Coelacanth) | Dipnoi: <i>Lepidosiren paradoxa</i> (South American lungfish) | Amphibia: <i>Ambystoma ordinarium</i> (Michoacan stream salamander) | Amniota: <i>Timon lepidus</i> (Ocellated lizard) |
| Sternohyoideus | Sternohyoideus | Sternohyoideus (rectus cervicis of e.g. Bemis and Lauder, 1986) | Sternohyoideus (rectus cervicis of e.g. Lauder and Shaffer, 1988) | Sternohyoideus (rectus cervicis of e.g. Kardong, 2002) |
| ----- | ----- | ----- | Omohyoideus (* seemingly derived from the sternohyoideus) | Omohyoideus (* see cell on the left) |

Chanos chanos: USNM 347536, 1 (alc), LFEM, 1 (alc). *Conger conger*: MNCN 1530, 5 (alc). *Danio rerio*: LFEM, 5 (alc). *Denticeps clupeioides*: MRAC 76–032–P–1, 2 (alc). *Diplomystes chilensis*: LFEM, 3 (alc). *Elops lacerta*: LFEM, 2 (alc). *Elops saurus*: MNCN 48752, 2 (alc). *Engraulis encrasicolus*: MNCN 68048, 2 (alc); MNCN 65097, 8 (alc); MNCN 1099, 3 (alc). *Esox lucius*: MNCN 197706, 5 (alc). *Eurypharynx pelecanooides*: AMNH 44315, 1 (alc); AMNH 44344, 1 (alc). *Galaxias maculatus*: USNM 344889, 2 (alc). *Gymnotus carapo*: INHS 35493, 2 (alc). *Hiodon tergisus*: MNCN 36019, 3 (alc). *Mormyrus niloticus*: LFEM, 1 (alc). *Mormyrus tapirus*: MNCN 80593, 3 (alc); MNCN 85283, 1 (alc). *Notacanthus bonaparte*: MNCN 107324, 3 (alc). *Salmo trutta*: MNCN 136179, 2 (alc), 1 (c&s); MNCN 16373, 2 (alc); MNCN 40685, 2 (alc). *Opsariichthys uncirostris*: MNCN 56668, 3 (alc). *Xenomystus nigri*: MNCN 227824, 25 (alc). **Tetrapoda**: *Ambystoma andersoni*: MNCN, uncatalogued, 2 (alc). *Ambystoma ordinarium*: MNCN, uncatalogued, 2 (alc). *Ambystoma mexicanum*: MNCN, uncatalogued, 2 (alc). *Bufo arenarum*: MNCN, uncatalogued, 2 (alc). *Homo sapiens*: GWU, uncatalogued, 6 (for). *Lacerta oxycephala*: MNCN, uncatalogued, 2 (alc). *Timon lepidus*: MNCN, 32544, 1 (alc), MNCN, uncatalogued, 1 (alc).

Results and discussion

Mandibular muscles (tables 1, 2; figures 3, 4)

In this Section, as well as in the Sections below regarding the hyoid and hypobranchial muscle plates, I first provide a short introductory paragraph explaining Edgeworth hypotheses regarding the respective plate, and then discuss to which extent my own analyses and the works of other authors support, or not, those hypotheses. According to Edgeworth (1935), in numerous gnathostomes the embryonic mandibular muscle plate gives rise dorsally to the premyogenic condensation constrictor dorsalis, medially to the premyogenic condensation adductor mandibulae, and ventrally to the intermandibularis (no description of a ventral mandibular premyogenic condensation was given by Edgeworth) (figs. 2–4). He suggested that a constrictor dorsalis condensation is not found in extant gnathostome taxa such as holocephalan chondrichthyans, dipnoans and amphibians. Since he considered that the chondrichthyans, the actinopterygians and the tetrapods sensu this work were derived from an ‘early dipnoan stock’ (see above), he concluded that the constrictor dorsalis was plesiomorphically absent in Gnathostomata and independently acquired in some taxa of this clade.

This is one of those cases in which one of Edgeworth’s conclusions is put in question by the evidence now available. In fact, very few researchers would now accept that the chondrichthyans, actinopterygians and tetrapods were originated from basal dipnoans (e.g. Kardong 2002; Song and Boord 2003). According to the phylogenetic scenario shown in figure 1, the constrictor dorsalis was either independently lost within dipnoans and amphibians, or lost in the node leading to non-actinistian sarcopterygians and then reacquired in amniotes. Although these options appear as equally parsimonious, there are reasons to favor the first one, i.e. that the constrictor dorsalis condensation was independently lost in amphibians and dipnoans. This because this premyogenic

condensation is, in fact, very similar in amniotes and in non-dipnoan sarcopterygian fishes (e.g. Brock 1938). Thus it makes more sense to consider that such a condensation was lost in dipnoans and in amphibians than to consider that it was lost in non-actinistian sarcopterygians and that a strikingly similar condensation was then independently acquired in amniotes. Actually, it is important to stress that it is not only the condensation that is similar in amniotes and non-dipnoan bony fishes. The adult muscles derived from it in amniotes such as lizards, i.e. the levator and protractor pterygoideus, are also strikingly similar to the adult muscle derived from it in sarcopterygians such as *Latimeria*, i.e. the levator arcus palatini (they essentially occupy the same position, running from the neurocranium to the dorsal/dorsolateral margin of the palatoquadrate, and are thus usually related to the elevation of this latter structure: Diogo, in press). A detailed analysis of the presence/absence of dorsal mandibular muscles in well conserved, plesiomorphic dipnoan and amphibian fossils, as well as in other sarcopterygian fossils, is needed to clarify the actual taxonomic distribution of the dorsal mandibular muscles within the Sarcopterygii.

As stated by e.g. Edgeworth (1935) and Winterbottom (1974), and supported by molecular developmental studies such as Hatta et al. (1990, 1991), in most extant actinopterygians the constrictor dorsalis forms differentiates into a levator arcus palatini and a dilatator operculi (see table 1 and figs. 3, 9–11). The former muscle is usually related to the elevation/abduction of the suspensorium (a structural complex formed by the hyomandibula, quadrate and pterygoid bones); the latter is mainly associated with the abduction (opening) of the opercle (see e.g. Stiassny et al. 2000). However, in extant acipenseriforms the constrictor dorsalis gives rise to a single, peculiar muscle mainly related to the protraction of the hyomandibula, the protractor hyomandibulae (e.g. Danforth 1913; Luther 1913; Sewertzoff 1928; Edgeworth 1935; Kesteven 1942–1945; Miyake et al. 1992; Carroll and Wainwright 2003; this work; table 1, fig. 3). The presence of a separate dilatator operculi in adults could thus be seen as a feature acquired in the node leading to all extant actinopterygians and then reverted in a node leading to extant acipenseriforms or, instead, as a feature independently acquired in cladistians and in neopterygians (see fig. 1). I agree with authors such as Lauder (1980) and Lauder and Liem (1983) in that there are strong reasons to suggest that a separate dilatator operculi was present in the ancestor of extant actinopterygians. In fact, the dilatator operculi of *Polypterus* and the dilatator operculi of neopterygians have a similar developmental origin (the dorsal part of the mandibular muscle plate), a similar innervation (the Vth nerve), a similar function (essentially related to opercle abduction), and a similar overall configuration (e.g. Pollard 1892; Allis 1897, 1922; Edgeworth 1935; Winterbottom 1974; Lauder 1980a; Lauder and Liem 1983; Miyake et al. 1992; Piotrowski and Northcutt 1996; this work). The absence of a distinct dilatator operculi in adult extant acipenseriforms may well be related to the fact that these fishes peculiarly lack an opercular bone and/or to the fact that they seemingly are pedomorphic (e.g. Bemis et al. 1997; Findeis 1997). This latter point could effectively help to explain why, contrary to most other living actinopterygians in which the constrictor dorsalis becomes ontogenetically differentiated into two muscles, adult acipenseriforms retain a single, undivided dorsal mandibular muscle, the protractor hyomandibulae.

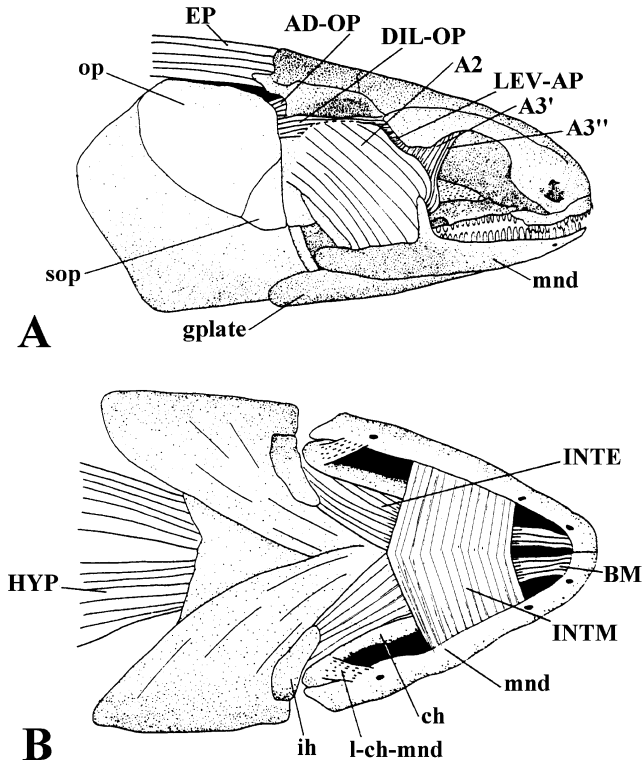


Figure 9. *Polypterus senegalus* (Cladistia): lateral (A) and ventral (B) views of the head after removal of the eye, suborbital bones, gular plates, and maxilla; in the ventral view the muscle hyohyoideus is not shown (modified from Lauder, 1980a; the nomenclature of the structures illustrated follows that used in the present work). A2, A3', A3'', adductor mandibulae A2, A3' and A3''; AD-OP, adductor operculi; BM, branchiomandibularis; ch, ceratohyal; DIL-OP, dilatator operculi; EP, epaxialis; gplate, gular plate; HYP, hypoaxialis; ih, interhyal; INTE, interhyoideus; INTM, intermandibularis; l-ch-mand, ligament between ceratohyal and mandible; LEV-AP, levator arcus palatini; mnd, mandible; op, opercle; sop, subopercle.

Miyake et al. (1992:221) stated: a “spiracularis was described in *Polypterus* by Edgeworth (1935), but confirmation of its actual existence in *Polypterus* is needed”. No spiracularis was found in the *Polypterus* specimens or in any other osteichthyan specimens I have examined.

In all major osteichthyan groups listed in tables 1 and 2 the ventral portion of the mandibular muscle plate gives rise to the intermandibularis. In adult extant members of the Actinistia, Chondrostei, Ginglymodi and Dipnoi the intermandibularis is mainly undivided (figs. 9, 12). In adult specimens of *Amia*, of *Latimeria*, and of numerous amphibian, amniote and teleostean genera this structure is divided into an intermandibularis anterior and an intermandibularis posterior (figs. 10, 13, 14). It is rather difficult to discern if the intermandibularis was divided or not in plesiomorphic adult osteichthyans (tables 1, 2). I tentatively hypothesize that it was (tables 1, 2), because a divided intermandibularis is found in numerous chondrichthyans, actinopterygians and sarcopterygians. However, a detailed analysis of the taxonomic distribution of this

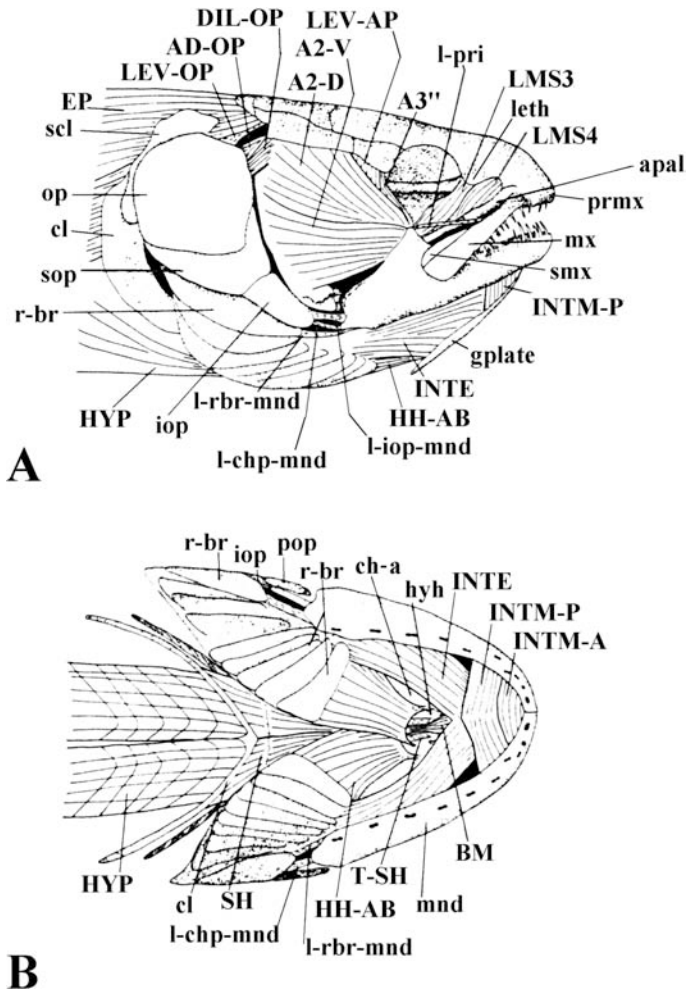


Figure 10. *Amia calva* (Halecomorphi): lateral (A) and ventral (B) views of the cephalic musculature after removal of the eye, dorsal portion of the preopercle, and gular plate; in the lateral view the A3' is not shown; in the ventral view the hyohyoideus inferior and the hyohyoidei adductores are not shown (modified from Lauder, 1980a; the nomenclature of the structures illustrated follows that used in the present work). A2-V, A2-D, A3'', adductor mandibulae A2-V, A2-D and A3''; AD-OP, adductor operculi; AD-SUP, adductor superficialis; apal, autopalatine; BM, branchiomandibularis; ch-a, anterior ceratohyal; cl, cleithrum; DIL-OP, dilatator operculi; EP, epaxialis; gplate, gular plate; HH-AB, hyohyoideus abductor; hyh, hypohyal; HYP, hypoaxialis; INTE, interhyoideus; INTM-A, INTM-P, intermandibularis anterior and posterior; iop, interopercle; l-chp-mand, ligament between posterior ceratohyal and mandible; l-iop-mand, ligament between interopercle and mandible; l-pri, primordial ligament; l-rbr-mand, ligament between branchiostegal rays and mandible; leth, lateral-ethmoid; LEV-AP, levator arcus palatini; LEV-OP, levator operculi; LMS3, LMS4, levator maxillae superioris 3 and 4; branchiomandibularis; mnd, mandible; mx, maxilla; op, opercle; pop, preopercle; prmx, premaxilla; r-br, branchiostegal rays; scl, supracleithrum; SH, sternohyoideus; smx, supramaxilla; sop, subopercle; T-SH, tendon of sternohyoideus.

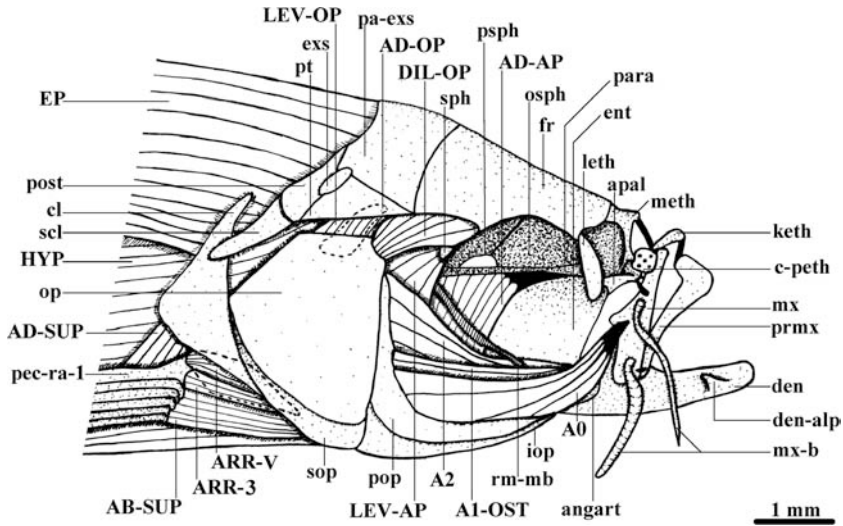


Figure 11. *Danio rerio* (Teleostei): lateral view of the cephalic musculature; all muscles are exposed, the maxillary barbels and the mesial branch of the ramus mandibularis are also illustrated; the nasals, infraorbitals and postcleithra were removed. A0, A1-OST, A2, adductor mandibulae A0, A1-OST and A2; AB-SUP, abductor superficialis; AD-AP, adductor arcus palatini; AD-OP, adductor operculi; AD-SUP, adductor superficialis; angart, angulo-articular; apal, autopalatine; ARR-3, arrector 3; ARR-V, arrector ventralis; c-peth, pre-ethmoid cartilage; cl, cleithrum; den, dentary bone; den-alp, anterolateral process of dentary bone; DIL-OP, dilatator operculi; ent, entopterygoid; EP, epaxialis; exs, extrascapular; fr, frontal; HYP, hypoaxialis; iop, interopercle; keth, kinethmoid; leth, lateral-ethmoid; LEV-AP, levator arcus palatini; LEV-OP, levator operculi; meth, mesethmoid; mx, maxilla; mx-b, maxillary barbel; op, opercle; osph, orbitosphenoid; pa-exs, parieto-extrascapular; para, parasphenoid; pec-ra-1, pectoral ray 1; pop, preopercle; post, posttemporal; prmx, premaxilla; psph, pterosphenoid; pt, pterotic; rm-mb, mesial branch of ramus mandibularis; scl, supracleithrum; sop, subopercle; sph, sphenotic.

feature in Chondrichthyes, and, if this would be possible, in key osteichthyan and non-osteichthyan gnathostome fossils such as the Acanthodii, is needed to clarify this issue. As its name indicates, the intermandibularis is usually a transversal muscle connecting the two mandibles. In most teleosts the intermandibularis posterior forms, together with the interhyoideus (see below), the protractor hyoideus (fig. 15), which is thus derived from both the mandibular and hyoid muscle plates (e.g. Edgeworth 1935; Winterbottom 1974; Schilling and Kimmel 1997; Hernandez et al. 2002, 2005; pers. obs.). The protractor hyoideus is innervated by both the Vth and the VIIth nerves and functionally it is a complex muscle: authors such as Osse (1969) demonstrated that its anterior and posterior portions may contract differently during different phases of respiration. Nonetheless, as stated by Stiassny (2000), as a broad generality it can be said that the protractor hyoideus plays a primary role in the elevation (protraction) of the hyoid bars and in the depression of the mandible. According to my own phylogenetic results (fig. 1), although a protractor hyoideus is not found in a few teleost taxa such as *Albula* and *Mormyrus* (e.g. Greenwood 1971, 1977; Winterbottom 1974; this work), the ancestors of extant teleosts did seemingly have a protractor hyoideus. Based on the altered morphology of the protractor hyoideus in morpholino-mediated Hox PG2 (*hoxa2b* and

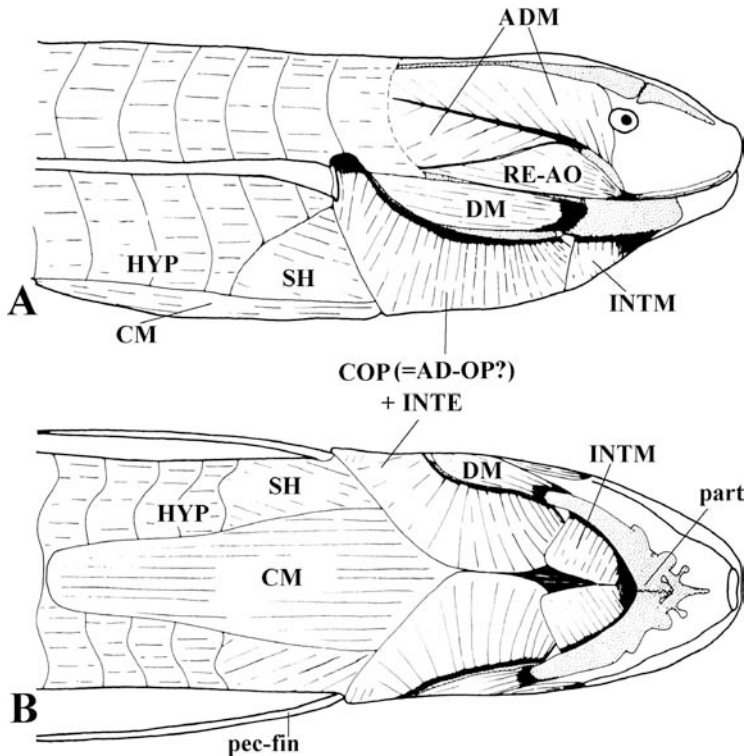


Figure 12. *Lepidosiren paradoxa* (Dipnoi): Lateral (A) and ventral (B) views of the cephalic musculature (modified from Bemis and Lauder, 1986; the nomenclature of the structures illustrated follows that used in the present work). ADM, adductor mandibulae complex; AD-OP, adductor operculi; CM, coracomandibularis; COP, constrictor operculi; DM, depressor mandibulae; HYP, hypoaxialis; INTE, interhyoideus; INTM, intermandibularis; part, prearticular; RE-AO, retractor anguli oris; SH, sternohyoideus.

hoxa2a) knock-down larvae, Hunter and Prince (2002: 378) suggested that in the zebrafish “the basihyal (cartilage) may be important for the proper ontogenetic organization” of the intermandibularis posterior and the interhyoideus, and, thus, for the association of their fibers and the formation of the protractor hyoideus. Further studies are needed to check if this is so and if it is a general feature within the Teleostei.

The adductor mandibulae condensation is found in members of all major osteichthyan groups (tables 1, 2; figs. 3, 4). The number of structures originated from this condensation is highly variable within these groups (tables 1, 2). The adductor mandibulae A3’ and A3” sensu the present work (which correspond to the “mesial adductor mandibulae divisions” of Lauder 1980a) are seemingly found plesiomorphically in osteichthyans (Lauder 1980a; tables 1, 2; figs. 9–10, 16–20). One of these bundles, or both, may however be missing in osteichthyan taxa as e.g. dipnoans, acipenseriforms and various teleosts (tables 1, 2; figs. 21, 22). The adductores mandibulae A2 and A ω were seemingly also found in basal osteichthyans (e.g. Lauder 1980a,b; tables 1, 2; figs. 17, 19, 22). The A ω may be missing in extant osteichthyans such as chondrosteans, ginglymodians, various teleosts and most tetrapods (tables 1, 2; figs. 18, 20, 21). In the adult specimens of the lizard *Timon* that I have analyzed the adductor mandibulae has

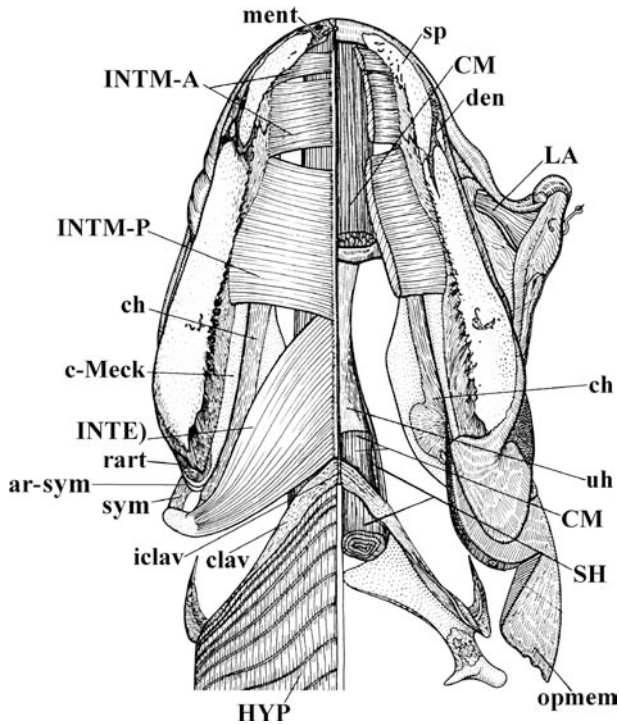


Figure 13. *Latimeria chalumnae* (Cladistia): ventral view of the cephalic musculature; on the left side are shown the most superficial cephalic muscles, after removal of the gular plate; on the right side are shown these most muscles were removed or cut in order to shown muscles that are situated more dorsally (modified from Millot and Anthony 1958; the nomenclature of the structures illustrated follows that used in the present work). ar-sym, articular facet for symplectic; c-Meck, Meckelian cartilage; ch, ceratohyal; clav, clavicle; CM, coracomandibularis; dent, dentary bone; HYP, hypoaxialis; iclav, interclavicle; INTE, interhyoideus; INTM-A, INTM-P, intermandibularis anterior and posterior; LA, labialis; ment, mentomeckelian bone; opmem, opercular membrane; rart, retroarticular; SH, sternohyoideus; sp, splenial bone; sym, symplectic, uh, urohyal.

a large anteroventral portion lodged in the ‘adductor fossa’ (sensu e.g. Lauder 1980b), which is remarkably similar to the A ω of bony fishes. Such an anteroventral portion of the adductor mandibulae was also described in other extant reptiles (e.g. *Crocodylus*: Edgeworth 1935). In view of the data available, it is difficult to discern if this anteroventral portion of the adductor mandibulae is effectively homologous to the A ω of bony fishes (table 2). I plan to promote a detailed analysis on this issue in a future work.

In Lauder’s (1980a) table 2 it is suggested that the palatomandibularis minor and major of extant ginglymodians (fig. 18) are likely homologous to the levator maxillae superioris 3 and 4 of living halecomorphs (fig. 10), since these structures represent an ‘anterior division’ of the adductor mandibulae. However, the overall configuration, position and attachments of the ginglymodian palatomandibularis minor and major are markedly different from those of the halecomorph levator maxillae superioris 3 and 4. For instance, the *Lepisosteus* palatomandibularis minor and major of *Lepisosteus* insert dorsally on the ectopterygoid/entopterygoid and ventrally on the mandible (fig. 18), while

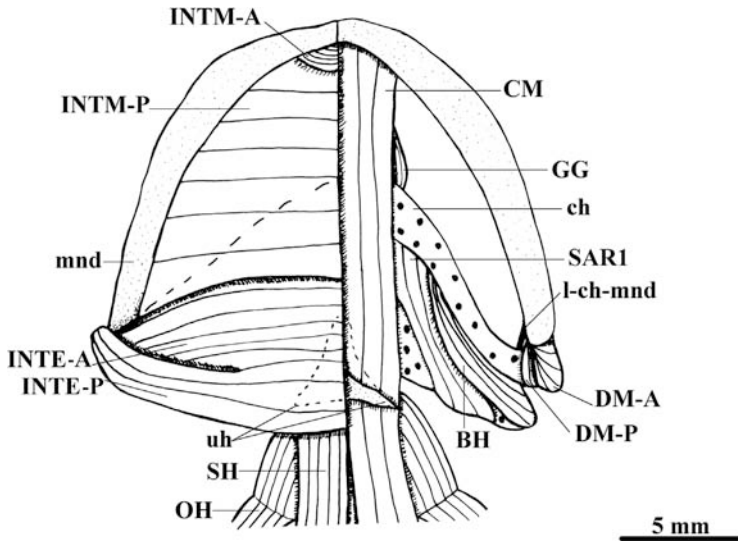


Figure 14. *Ambystoma ordinarium* (Amphibia): ventral view of the cephalic musculature; on the right side the most ventral muscles were removed. BH, branchiohyoideus; ch, ceratohyal; CM, coracomandibularis; DM-A, DM-P, depressor mandibulae anterior and posterior; GG, genioglossus; INTE-A, INTE-P, interhyoideus anterior and posterior; INTM-A, INTM-P, intermandibularis anterior and posterior; l-ch-mand, ligament between ceratohyal and mandible; mnd, mandible; OH, omohyoideus; SAR1, subarcualis rectus 1; SH, sternohyoideus; uh, urohyal.

the section 3 of the levator maxillae superioris of *Amia* inserts dorsally on the neurocranium and orbital bones and ventrally mainly on the autopalatine (fig. 10). The results of my cladistic analyses (fig. 1) strongly support a close relationship between the Halecomorphi and the Teleostei (fig. 1), contradicting that ginglymodians and halecomorphs are sister-groups. These phylogenetic results thus indicate that the ginglymodian palatomandibularis minor and the halecomorph levator maxillae 3 and 4 may well be non-homologous (table 1).

Apart the adductor mandibulae divisions mentioned above, other divisions may eventually be found in adult osteichthyans, e.g. the A1-OST and A0 (sensu Diogo and Chardon 2000; e.g. fig. 11), the A2-PVM (e.g. figs. 20, 21), the retractor and levator anguli oris (e.g. figs. 12, 16) and the pterygomandibularis (e.g. fig. 23) (tables 1, 2). It is important to stress that I found, in the adult dipnoan specimens analyzed, a peculiar section of the adductor mandibulae that has some fibers associated with those of the A2 but is well-differentiated from it. As this section is somewhat posterior, ventral, and medial to the main body of the A2, I call it adductor mandibulae A2-PVM (the PVM thus meaning posteroventromesial: fig. 21). Authors as Edgeworth (1935), Bemis (1986), Bemis and Lauder (1986) and Miyake et al. (1992) did not mention the presence of such an adductor mandibulae section in extant dipnoans (the A2-PVM should not be confused with the retractor anguli oris of these fishes, which is usually situated posteroventrolaterally to the A2, being mainly superficial, and not mesial, to the A2; in fact both bundles can be found in the same taxon, e.g. in *Lepidosiren*). The A2-PVM of dipnoans seemingly corresponds to the structure that is often named ‘adductor mandibulae posterior’ by researchers working with amphibian and amniote tetrapods (e.g. Brock 1938; Carroll and Holmes 1980;

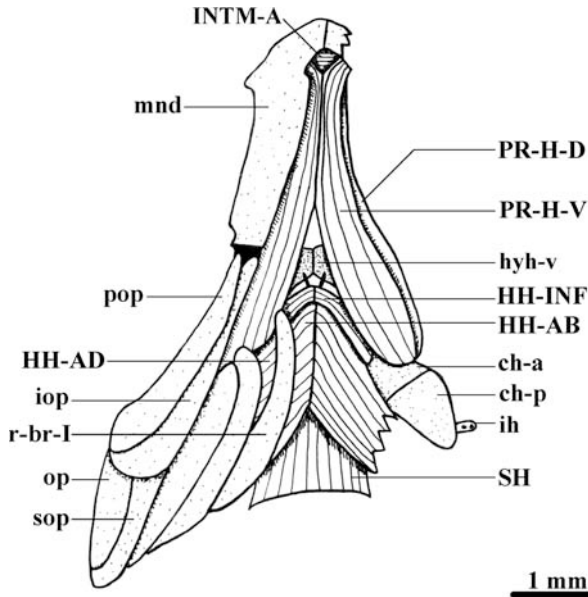


Figure 15. *Danio rerio* (Teleostei): ventral view of the ventral cephalic musculature; on the right side a portion of the hyohyoidei adductores, as well as of the mandible, was cut, and the opercle, interopercle, subopercle and preopercle are not represented. ch-a, ch-p, anterior and posterior ceratohyals; HH-AB, hyohyoideus abductor; HH-AD, hyohyoidei adductores; HH-INF, hyohyoideus inferior; hyh-v, ventral hypohyal; ih, interhyal; INTM-A, anterior intermandibularis; iop, interopercle; mnd, mandible; op, opercle; pop, preopercle; PR-H-D, PR-H-V, sections of protractor hyoideus; r-br-I, branchiostegal ray I; SH, sternohyoideus; sop, subopercle.

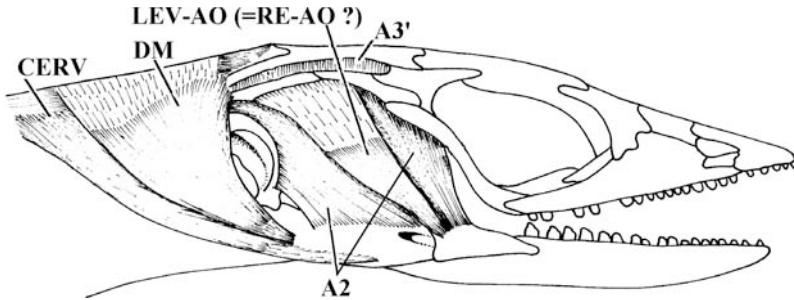


Figure 16. *Euspondylus acutirostris* (Amniota): lateral view of the cephalic musculature; the adductor mandibulae sections A2-PVM and A3'' are not shown (modified from Montero et al. 2002; the nomenclature of the structures illustrated follows that used in the present work). A2, A3', adductor mandibulae A2 and A3'; CERV, cervicomandibularis; DM, depressor mandibulae; LEV-AO, levator anguli oris; RE-AO, retractor anguli oris.

Iordansky 1992; Moro and Abdala 2000; Montero et al. 2002; Abdala and Moro 2003; table 2). All extant non-dipnoan bony fishes I examined lack an A2-PVM. The textual descriptions and illustrations of the adductor mandibulae complex of *Latimeria* provided by Millot and Anthony (1958) and Adamicka and Ahnelt (1992) indicate that such an A2-PVM is also missing in that taxon.

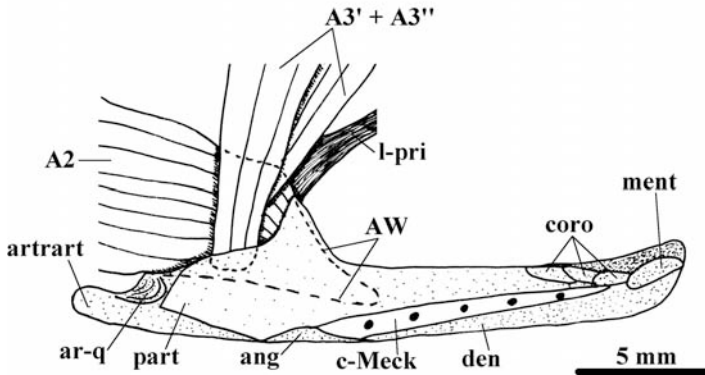


Figure 17. *Polypterus bichir* (Cladistia): mesial view of adductor mandibulae and mandible; mandibular teeth are not illustrated. A2, A3', A3'', AW, adductor mandibulae A2, A3', A3'' and Aw; ang, angular; ar-q, articular facet for quadrate; artrart, articulo-retroarticular; c-Meck, Meckelian cartilage; coro, coronoids; den, dentary bone; l-pri, primordial ligament; ment, mentomeckelian bone; part, prearticular.

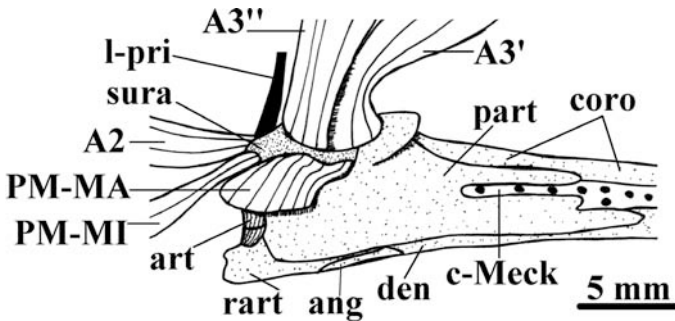


Figure 18. *Lepisosteus osseus* (Ginglymodi): mesial view of adductor mandibulae and mandible; mandibular teeth are not illustrated. A2, A3', A3'', adductor mandibulae A2, A3', A3''; ang, angular; art, articular; c-Meck, Meckelian cartilage; coro, coronoids; den, dentary bone; l-pri, primordial ligament; part, prearticular; PM-MA, PM-MI, palatmandibularis major and minor; rart, retroarticular; sura, surangular.

Although the adductor mandibulae divisions are usually related with the adduction of the mandible, this is not always the case. For instance, some of them may attach to structures other than the mandible as e.g. the maxilla (e.g. the adductor mandibulae A0: fig. 11) and thus not be directly related to lower jaw adduction (see e.g. Alexander 1966; Winterbottom 1974; Stiassny 2000). Certain divisions of the adductor mandibulae may inclusively be related with the opening, and not the closing, of the mouth, as is the case of the 'abductor mandibulae' of saccopharyngiform teleosts (e.g. Tchernavin 1947a,b, 1953; this work).

Hyoid muscles (tables 3, 4; figures 5, 6)

According to Edgeworth (1935) the constrictor hyoideus condensation usually gives rise to dorso-medial and ventral derivatives throughout the major groups of gnathostomes. As shown in tables 3 and 4, two dorso-medial hyoid muscles were seemingly

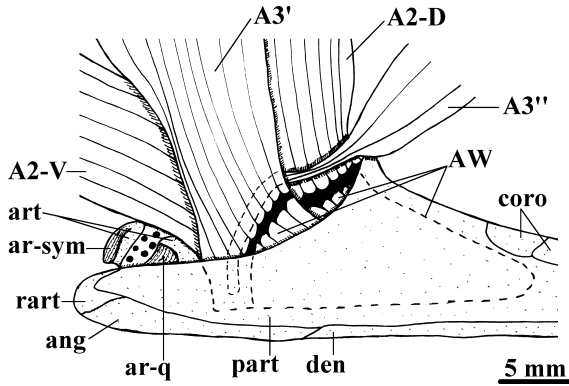


Figure 19. *Amia calva* (Halecomorphi): mesial view of mandible and of adductor mandibulae sections A2, A3', A3'' and Aw; the levator maxillae superioris 3 and 4 and the mandibular teeth are not illustrated. A2-D, A2-V, A3', A3'', AW, adductor mandibulae A2-D, A2-V, A3', A3'' and Aw; ang, angular; ar-q, ar-sym, articular facets for quadrate and for symplectic; art, articular; coro, coronoids; den, dentary bone; part, prearticular; rart, retroarticular.

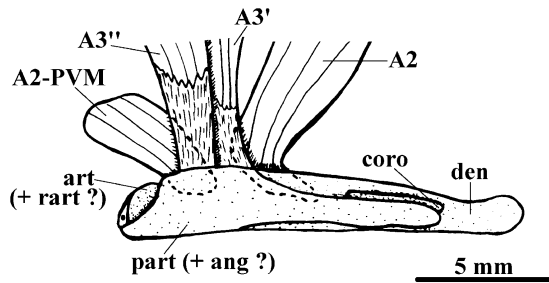


Figure 20. *Ambystoma ordinarium* (Amphibia): mesial view of the mandible and adductor mandibulae; the mandibular teeth are not illustrated. A2, A2-PVM, A3', A3'', adductor mandibulae A2, A2-PVM, A3' and A3''; art, articular; coro, coronoids; den, dentary bone; part, prearticular.

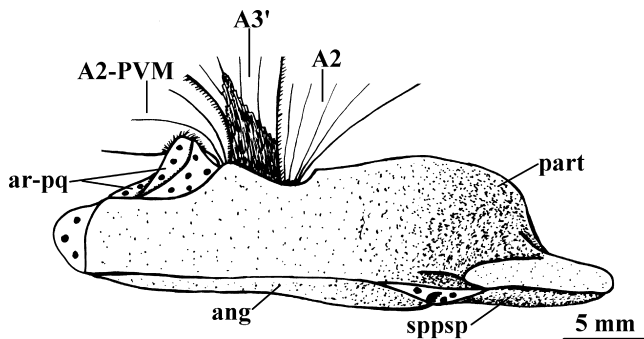


Figure 21. *Neoceratodus forsteri* (Dipnoi): mesial view of adductor mandibulae and mandible; the mandibular tooth-plates are not illustrated. A2, A2-PVM, A3', adductor mandibulae A2, A2-PVM and A3'; ang, angular; ar-pq, articularity facet for palatoquadrate; part, prearticular; sppsp, splenio-postsplenial bone.

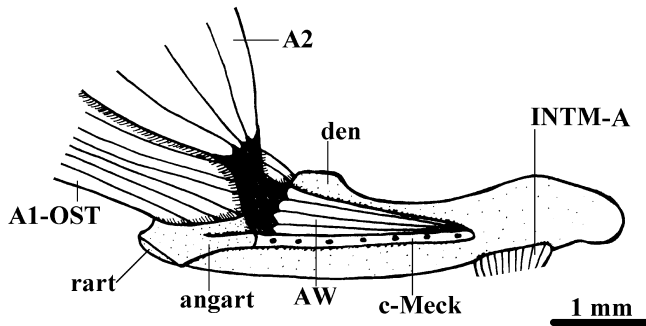


Figure 22. *Danio rerio* (Teleostei): mesial view of the left mandible and adductor mandibulae, the anterior intermandibularis is also shown; the adductor mandibulae A0 was removed. A1-OST, A2, adductor mandibulae A1-OST, A2 and A0; angart, angulo-articular; c-Meck, Meckelian cartilage; coro, coronoids; den, dentary bone; INTM-A, intermandibularis anterior; rart, retroarticular.

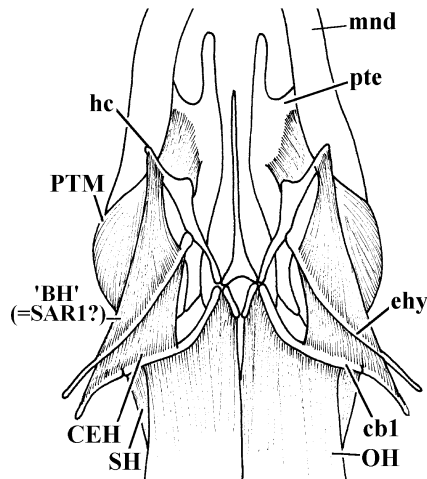


Figure 23. *Euspondylus acutirostris* (Amniota): ventral view of the deep ventral cephalic musculature; muscles such as the intermandibularis, the interhyoideus, the coracomandibularis, the genioglossus and the hyoglossus are not shown (modified from Montero et al. 2002; the nomenclature of the structures illustrated basically follows that used in the present work). 'BH', 'branchiohyoideus'; cb1, ceratobranchial 1; CEH, ceratohyoideus; ehy, epihyal; hc, hyoid cornu; mnd, mandible; OH, omohyoideus; pte, pterygoid; PTM, pterygomandibularis; SAR1, subarcualis rectus 1; SH, sternohyoideus.

found in plesiomorphic osteichthyans: the adductor arcus palatini and the adductor operculi (fig. 11). These two muscles, which as their name indicates are usually related to the adduction of the suspensorium/palatoquadrate and of the opercle, are found in *Latimeria* and in most living actinopterygians (tables 3, 4; figs. 5, 6). Some actinopterygians may however lack an adductor operculi (e.g. saccopharyngiform teleosts: Tchernavin 1947a,b, 1953; this work). In living chondrosteans the dorso-medial portion of the hyoid muscle plate gives rise to a peculiar retractor hyomandibulae, and not to an adductor arcus palatini similar to that found in most other actinopterygians

(e.g. Danforth 1913; Luther 1913; Edgeworth 1935; Kesteven 1942–1945; Miyake et al. 1992; Carroll and Wainwright 2003; this work; table 3, fig. 5).

As stressed by Winterbottom (1974: 239), apart from the adductor arcus palatini, some osteichthyans have other muscles connecting the neurocranium to the palatoquadrate/suspensorium and promoting the adduction of these latter structures. Examples of this are the muscles described by him under the name “adductor hyomandibulae”. I have found well-differentiated muscles “adductor hyomandibulae” sensu Winterbottom in various teleosts (table 3; fig. 5); an “adductor hyomandibulae” is seemingly also found in *Latimeria* (see Millot and Anthony 1958). As stressed by Winterbottom (1974: 239), at least some of these “adductor hyomandibulae” muscles were seemingly acquired independently (i.e. they are non-homologous), since they may be originated “1) either from the posterior region of the adductor arcus palatini or 2) from the anterior fibers of the adductor operculi”. This is for example the case of the “adductor hyomandibulae” found in *Latimeria* and in teleosts such as *Danio*, which are designated in tables 3 and 4 as “adductor hyomandibulae Y” and “adductor hyomandibulae X”, respectively. Miyake et al. (1992) suggested that, apart these taxa, other key osteichthyan genera listed in tables 3 and 4 as e.g. *Amia* and *Lepisosteus* also have an “adductor hyomandibulae” sensu Winterbottom (note: the muscles named “adductor hyomandibulae” and “adductor arcus palatini” in Winterbottom’s work and in the present study correspond respectively to the muscles named “adductor arcus palatini” and “adductor hyomandibulae” in Miyake et al.’s paper). However, in the *Amia* and *Lepisosteus* specimens I examined there is no separate, well-differentiated “adductor hyomandibulae” sensu Winterbottom. This is also the case in the specimens of these genera analyzed by e.g. Lauder (1980a), who stated that “in *Lepisosteus* the adductor arcus palatini (= Winterbottom’s “adductor hyomandibulae”) and the adductor hyomandibulae (= Winterbottom’s “adductor arcus palatini”) form a continuous sheet of parallel-fibered muscle” and that “the adductor arcus palatini (= Winterbottom’s “adductor hyomandibulae”) is absent in *Amia*” (Lauder 1980a: 289). [As explained by Winterbottom (1974), the reason why some authors use the name “adductor hyomandibulae” to designate his “adductor arcus palatini” is that in various osteichthyans the mesial insertion of this muscle is exclusively on the hyomandibula. However, as he pointed out, the name “adductor hyomandibulae” becomes clearly inappropriate in the numerous cases in which the muscle is expanded anteriorly along the floor of the orbit and attaches on more anterior elements of the suspensorium such as the metapterygoid and/or entopterygoid.]

Apart the levator operculi, the adductor operculi and the muscles “adductor hyomandibulae”, other dorso-medial hyoid muscles may be found in living osteichthyans (tables 3, 4; figs. 5, 6). For instance, *Amia* and most extant teleosts have a levator operculi (figs. 10, 11). The levator operculi of these fishes is usually related to a peculiar mechanism mediating lower jaw depression via the so-called ‘four-bar linkage system’ in which the force of contraction of this muscle is transmitted through the opercular series and the interoperculo-mandibular ligament to the lower jaw (e.g. Stiassny 2000). A levator operculi may be missing in certain teleosts, as for example saccopharyngiforms (e.g. Tchernavin 1947ab, 1953; this work). Millot and Anthony (1958) stated that

Latimeria has a “levator operculi”. As can be seen in the descriptions and the figures provided by these authors (see e.g. their plate VII), and as recognized in their page 61, the fibers of their “levator operculi” are deeply mixed with those of the adductor operculi. This has made authors such as Lauder (1980c) to be very skeptical about the presence, in *Latimeria*, of a distinct, well-differentiated levator operculi similar to that found in *Amia* and teleosts. However, Adamicka and Ahnelt (1992: 108) reaffirmed, seemingly based on their own observations of *Latimeria*, that this taxon “does have a levator operculi muscle differentiated out of the adductor (operculi)”. According to the results of my cladistic studies the “levator operculi” of *Latimeria* is probably non-homologous to the levator operculi of *Amia* and teleosts (tables 3, 4; fig. 1). It is important to stress that the function of the “levator operculi” of *Latimeria* is, in fact, not similar to that of the levator operculi of *Amia* and teleosts. This because, contrary to these fishes, *Latimeria* has no interoperculo-mandibular ligament and, consequently, has no opercular mechanism mediating mandible depression (e.g. Millot and Anthony 1958; Alexander 1973; Anthony 1980; Lauder 1980c). In order to distinguish the “levator operculi” of *Latimeria* and the levator operculi of *Amia* and teleosts the former muscle is named “*Latimeria*’s ‘levator operculi’” in table 4.

A muscle named ‘levator operculi’ is shown in an illustration of the dipnoan *Neoceratodus* by Kardong (2002: fig. 10.39B). However, in the dipnoan specimens I examined, as well as in those described by e.g. Bischoff (1840), Owen (1841), Luther (1913–1914), Edgeworth (1935), Kesteven (1942–1945), Bemis (1986), Bemis and Lauder (1986), and Bartsch (1994), there is no structure resembling the ‘levator operculi’ of *Latimeria* or the levator operculi of *Amia* and teleosts. In fact, the ‘levator operculi’ of Kardong (2002: fig. 10.39B) seemingly corresponds to the constrictor operculi of Bemis and Lauder (1986), which may correspond to the adductor operculi of other bony fishes but forms, in extant adult dipnoans, a continuous sheet of fibers together with other cranial muscles.

Examples of other dorso-medial hyoid muscles found in osteichthyans are e.g. the levator hyoideus and the depressor mandibulae (table 4; fig. 6). The levator hyoideus is usually related with the elevation of the posterodorsal portion of the ceratohyal (fig. 24), whereas the depressor mandibulae is often related with the opening of the mouth (figs. 12, 14, 16). These muscles are found in at least some developmental stages of extant dipnoans and of numerous extant tetrapods. Contrarily to what is suggested in table 4, Edgeworth (1935) stated that the depressor mandibulae of adult dipnoans such as *Protopterus* and *Lepidosiren* is not homologous with part of the depressor mandibulae of adult tetrapods. This because in the dipnoan developmental series observed by him the levator hyoideus and the depressor mandibulae seemingly appear at the same time, while in tetrapods the depressor mandibulae appears as a modification of part, or the totality, of the levator hyoideus. Authors such as Forey (1986) have however suggested that the depressor mandibulae/levator hyoideus of adult *Protopterus* and *Lepidosiren* are homologous with the depressor mandibulae/levator hyoideus of adult tetrapods, and that this actually provides support for a close relationship between dipnoans and tetrapods. My observations, comparisons and phylogenetic results strongly support Forey’s hypothesis: the innervation, position, relations with other structures,

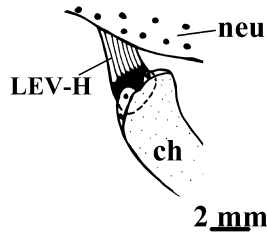


Figure 24. *Lepidosiren paradoxa* (Dipnoi): lateral view of levator hyoideus; the ventral portion of the ceratohyal was cut. LEV-H, levator hyoideus; neu, neurocranium.

and function of the depressor mandibulae of adult dipnoans are strikingly similar to those of the posterior part of the depressor mandibulae of adult tetrapods, and the results of my cladistic studies do strongly support that dipnoans are effectively the closest living relatives of tetrapods (fig. 1). Even authors that have adhered to Edgeworth's (1935) view do in fact admit that the depressor mandibulae of adult dipnoans is "functionally and topographically comparable" to the anterior part of the depressor mandibulae of adult tetrapods such as salamanders (e.g. Bauer 1997: 79).

The following hypothesis concerning the evolution of the levator hyoideus and depressor mandibulae may therefore be tentatively proposed. The first evolutionary step was probably the differentiation of the levator hyoideus (possibly from the portion of the hyoid muscle plate that gives rise to the adductor arcus palatini in other osteichthyans, but this is far from clear: table 4; see below). A configuration such as this, i.e. in which there is no depressor mandibulae and in which the levator hyoideus consists of a single mass of fibers attaching to the hyoid arch, is found for example in early development stages of the dipnoan *Neoceratodus* and of various tetrapods (e.g. Edgeworth 1935: fig. 313; Bartsch 1994: fig. 2B). The second evolutionary step may have been the attachment of some fibers of the levator hyoideus to the mandible and the ulterior differentiation of these fibers into a depressor mandibulae. A configuration such as this, i.e. in which the levator hyoideus and the depressor mandibulae inserting respectively to the hyoid arch and to the mandible, is found in early development stages of various tetrapods and of the dipnoans *Lepidosiren* and *Protopterus*, as well as in juveniles and adults of these two dipnoan genera and of amphibians as e.g. *Siren* (figs. 12, 24; Edgeworth 1935: fig. 327). These two evolutionary steps seemingly occurred before the phylogenetic splitting between dipnoans and tetrapods, since at least some members of these groups have depressor mandibulae fibers attaching on the mandible. In other words, the last common ancestors of dipnoans and tetrapods probably had, in at least some stages of their development, both a levator hyoideus and a depressor mandibulae. After that phylogenetic splitting, the evolution of these muscles has seemingly been rather diverse and complex. For instance, in the dipnoan *Neoceratodus* the levator hyoideus becomes ontogenetically mixed with other hyoid muscles, being absent as a separate element in adults; a separate depressor mandibulae is missing in early and late developmental stages of this taxon. In the dipnoans *Lepidosiren* and *Protopterus* and in tetrapods as e.g. *Siren* these two muscles remain as separate elements until the adult stages (figs. 12, 24). As in *Neoceratodus*, the levator hyoideus is also absent as a separate

element in numerous adult tetrapods, but for a different reason: because, as shown by e.g. Edgeworth (1935), in the course of their development all the fibers of this muscle become ontogenetically attached to the mandible, thus constituting the depressor mandibulae (table 4; figs. 14, 16).

Therefore the levator hyoideus of adult dipnoans such as *Protopterus* and *Lepidosiren* (fig. 24), as well as of adult tetrapods such as *Siren*, seemingly corresponds to the depressor mandibulae posterior of adult amphibians as e.g. *Ambystoma* (fig. 14) and to part of the depressor mandibulae of adult amniotes as e.g. *Timon* (fig. 16) (table 4). The depressor mandibulae of *Protopterus* and *Lepidosiren* (fig. 12) and of *Siren* seemingly corresponds to the depressor mandibulae anterior of adult amphibians as e.g. *Ambystoma* (fig. 14) and to part of the depressor mandibulae of adult amniotes as e.g. *Timon* (fig. 16) (table 4). The statements of Edgeworth regarding the ontogenetic differences between the dipnoan depressor mandibulae and the anterior part of the depressor mandibulae of tetrapods such as *Ambystoma* may thus be due to two main reasons: 1) the mode of appearance of these structures may effectively be somewhat different in dipnoans and in tetrapods (which, in view of the recent discoveries on the field of evolutionary developmental biology, does not completely invalidates the hypothesis that they are homologous: see e.g. Gould 2002; West-Eberhard 2003; Carroll et al. 2005; Kirschner and Gerhart 2005; see also below); 2) the mode of appearance of the depressor mandibulae of dipnoans is, in reality, similar to that of the anterior part of the depressor mandibulae of tetrapods (i.e. it appears ontogenetically after the levator hyoideus, resulting from the differentiation of part of its fibers), but the youngest dipnoan specimens observed by Edgeworth were too old to detect such a differentiation (i.e. the differentiation had already occurred and thus both the levator hyoideus and the depressor mandibulae were already present in those specimens, giving the idea that these structures were ontogenetically originated at the same time). Further detailed comparative analyses on the development of the hyoid muscles of dipnoans and of other osteichthyans are needed to clarify this issue.

Such detailed analyses are also needed to clarify if the portions of the constrictor hyoideus from which originate the levator hyoideus/depressor mandibulae and the constrictor operculi of extant dipnoans may eventually correspond to the portions that give rise to the adductor arcus palatini and the adductor operculi of other bony fishes, as suggested by e.g. Edgeworth (1935) and Diogo (in press). Edgeworth (1935: 102) stated that the levator hyoideus of dipnoans is derived from the portion of the constrictor hyoideus that gives rise to the retractor hyomandibulae in extant acipenseriforms, which seemingly corresponds to the adductor arcus palatini of other bony fishes (table 3; see above). It should be noted that in living dipnoans the hyomandibula is very reduced or even missing and the palatoquadrate is fused to the neurocranium, being thus much less mobile than that of most other bony fishes. Therefore, the portion of the hyoid muscle plate that gives rise to the adductor arcus palatini of other bony fishes may have lost its usual attachments to the hyomandibula and/or palatoquadrate and became attached to the ceratohyal. The dorsal surface of the ceratohyal actually is more dorsal in dipnoans than in most other bony fishes, occupying a position somewhat similar to that of the hyomandibula of these latter fishes (fig. 24; e.g. Rosen et al.

1981; Forey 1986; Bauer 1997; Diogo, in press; this work). My observations of juvenile and adult specimens of *Lepidosiren* pointed out that in these specimens the levator hyoideus attaches not only to the dorsal surface of the ceratohyal, but also to part of its dorsomesial margin (fig. 24). Thus, as the adductor arcus palatini of other bony fishes usually attaches on the dorsomesial margin of the hyomandibula/palatoquadrate in order to promote their adduction, it seems that the dipnoan levator hyoideus might promote not only an elevation, but also an adduction, of the dorsal portion of the ceratohyal. Regarding the dipnoan constrictor operculi (fig. 12), it could effectively be originated from the same portion of the constrictor hyoideus that gives rise to the adductor operculi in other bony fishes. This seems to be supported by the fact that some plesiomorphic fossil dipnoans exhibit well defined scars on the mesial margin of the opercle for the attachment of a muscular structure that seemingly corresponds to the adductor operculi of other fishes (e.g. Campbell and Barwick 1986). Be that as it may, in adult extant dipnoans the constrictor operculi forms a sheet of fibers that is continuous with other muscles as e.g. the interhyoideus. Therefore, even if the constrictor operculi of dipnoans is eventually derived from the portion of the constrictor hyoideus that gives rise to the adductor operculi in other bony fishes, in adult extant dipnoans there is no separate, distinct adductor operculi as that found in adult members of e.g. *Latimeria* and most actinopterygians (table 4).

Regarding the ventral portion of the hyoid muscle plate, the plesiomorphic condition for osteichthyans is seemingly that in which that portion gave rise to a single division, which is designated here as interhyoideus (tables 3, 4). In most extant actinopterygians part of the interhyoideus becomes ontogenetically differentiated into a distinct, separate muscle, the hyohyoideus (table 3, fig. 5). In *Amia* and most teleosts the hyohyoideus is subdivided into hyohyoideus inferior, hyohyoideus abductor and hyohyoidei adductores (fig. 15). The hyoideus abductor and hyohyoidei adductores are often considered parts of a hyohyoideus superior (table 3; fig. 5). As stated by Stiassny's (2000: 122), "there is little commentary in the literature regarding the function of HhI (hyohyoideus inferior) but adduction of the hyoid bar is suggested by its position and presumed line of action". Regarding the hyohyoideus abductor and the hyohyoidei adductores, they are usually related with the expansion and the constriction of the branchiostegal membranes, respectively (fig. 15). The interhyoideus, which as its name indicates usually connects the two hyoid bars, has become associated with the intermandibularis posterior in teleosts, forming the peculiar protractor hyoideus (tables 1, 3; see above).

Miyake et al.'s (1992) table 1 suggests that in extant cladistians, chondrosteans and ginglymodians the hyohyoideus is differentiated into two well-differentiated divisions, namely a hyohyoideus inferior and a hyohyoideus superior. However, in the adult specimens of these three groups that I examined the hyohyoideus is not divided into well-differentiated parts as is the case in *Amia* and teleosts. It is instead essentially constituted by a continuous sheet of fibers. These observations seem to be supported by those of other authors. For instance, Lauder (1980a: 293) wrote that "in *Lepisosteus* the hyohyoideus superioris (...) also (as in *Polypterus*) is continuous with the fibers of the hyohyoideus inferioris" (i.e. the fibers of the hyohyoideus form a continuous sheet, as

is the case in the *Lepisosteus* and *Polypterus* specimens I examined). The hyohyoideus of the chondrosteans described by e.g. Danforth (1913: *Polyodon*) and Carroll and Wainwright (2003: *Scaphirhynchus*) is also constituted by a continuous sheet of fibers, as is the case in the *Psephurus* and *Acipenser* specimens I analyzed (note: the interhyoideus of this work corresponds to the “geniohyoideus posterior” and the “constrictor ventralis posterior” of Danforth 1913, and of Carroll and Wainwright 2003, respectively).

There is seemingly no well-differentiated, separate hyohyoideus in extant Sarcopterygii (table 4, figs. 86, 91, 99, 6). That is, there are some sarcopterygians in which the portion of the hyoid muscle plate that gives rise to the interhyoideus and hyohyoideus in actinopterygians might eventually be somewhat differentiated into bundles that may resemble those two structures, but these bundles remain deeply mixed throughout all their lives. This is e.g. the case of the interhyoideus anterior and the interhyoideus posterior of various salamanders (table 4; fig. 14; see also e.g. Lubosch 1914; Luther 1913–1914; Edgeworth 1935; Kesteven 1942–1945; Jarvik 1963; Larsen and Guthrie 1975; Carroll and Holmes 1980; Bauer 1992; Haas 2001). This is seemingly also the case of the “géniohyoïdien” and the “hyohyoïdien” described by Millot and Anthony (1958) in *Latimeria*, which are deeply mixed in the adult members of this genus and which, thus, seem to correspond to the interhyoideus of the present work (table 4).

Apart the muscles mentioned in the paragraphs above, osteichthyans may exhibit other hyoid muscles (tables 3, 4). For instance, in at least some developmental stages of various urodeles there is a peculiar muscle branchiohyoideus connecting the hyoid and branchial arches (fig. 14). Ontogenetically, this muscle appears between the interhyoideus and the levator hyoideus/depressor mandibulae, a position that “makes it difficult to determine if it belongs to the dorsal or ventral (hyoid) muscles” (Ericsson and Olsson 2004: 136) (see fig. 6). According to Lauder and Shaffer (1985: 308) the function of the branchiohyoideus is to “mediate hyoid retraction and possibly also produce ceratobranchial abduction in the absence of antagonistic activity”. Edgeworth (1935) and Lauder and Shaffer (1988) stated that the branchiohyoideus becomes lost after metamorphosis in most urodeles. However, the metamorphosed specimens of *Ambystoma ordinarium* I examined do have a distinct muscle branchiohyoideus (fig. 14). As explained by Edgeworth (1935), the structure that is often named “branchiohyoideus” in amniotes is seemingly homologous to the branchial muscle subarcualis rectus 1 of amphibians, and not to the hyoid muscle branchiohyoideus of the present work (which Edgeworth designated as “branchiohyoideus externus”) (figs. 14, 23). Jarvik (1963) suggested that a branchiohyoideus similar to that of urodeles may have been present in at least some of the sarcopterygian fossil fishes placed in his “porolepiform-stock”. However, as stressed by e.g. Rosen et al. (1981), some of Jarvik’s interpretations of fossils, principally those concerning soft structures, should be viewed with much caution, since they were profoundly influenced by certain strong, and rather heterodox, beliefs of this author. For instance, in this specific case regarding the eventual presence of a branchiohyoideus in his “porolepiforms”, this has much to do with his profound conviction that these latter fishes were the sister-group of urodeles, and, thus, that amphibians are not monophyletic, a view to which almost no authors would

adhere nowadays (“these great resemblances ... cannot possibly be due to parallel evolution and they prove definitively that the urodeles are closely related to and descendants of porolepiforms”: Jarvik 1963: 61). Therefore, a detailed, up-dated, and if possible less biased, comparative analysis is needed in order to clarify if a branchiohyoideus is, or not, present in sarcopterygian fish fossils.

Hypobranchial muscles (tables 5, 6; figures 7, 8)

According to Edgeworth (1935), there are two major lineages of muscles originated from the hypobranchial muscle plate: his genio-hyoideus and his rectus cervicis (figures 5, 6). As noted Miyake et al. (1992), it is not very clear if Edgeworth’s genio-hyoideus and rectus cervicis represent separate premyogenic condensations or later states of muscle development.

The plesiomorphic condition for osteichthyans is seemingly that found in adult members of Actinistia and Dipnoi, in which there is a coracomandibularis and a sternohyoideus (sensu this work: table 6; figs. 13, 14). According to e.g. Edgeworth (1935), Kesteven (1942–1945), Wiley (1979a,b), Jollie (1982), Mallat (1997), Wilga et al. (2000) and Johanson (2003), these muscles were originally mainly related with the opening of the mouth. Extant tetrapods exhibit various hypobranchial muscles that are not found in other living osteichthyans, as e.g. the omohyoideus and the specialized glossal muscles related with tongue movements (table 6; figs. 14, 23). The omohyoideus and the genioglossus are seemingly derived from the sternohyoideus and the coracomandibularis, respectively (Edgeworth, 1935; fig. 14). However, the statements of Edgeworth (1935) regarding the origin of the hyoglossus are somewhat confuse: in his page 196 it is stated that in amphibians such as salamanders this muscle originates from the sternohyoideus, but in his page 211 he affirmed that “the hypobranchial muscles of Amphibia, Sauropsida and Mammalia are essentially similar (..), a genioglossus and a hyoglossus are developed from the genio-hyoideus (= coracomandibularis of the present work)”. Jarvik (1963:41) reanalyzed this issue, and stated that the hyoglossus of salamanders “seems to be an anterior portion of the rectus cervicis (= sternohyoideus of this work)”. Larsen and Guthrie (1975) suggested that the hyoglossus of salamanders may eventually be originated from “part of the genioglossus complex” (and, thus, from the coracomandibularis of this work), but stated that it was not possible to confirm this hypothesis “without examining early ontogenetic stages”. The information provided in more recent publications referring to the cranial musculature of salamanders, as e.g. Carroll and Holmes (1980), Lauder and Shaffer (1985, 1988), Reilly and Lauder (1989, 1990, 1991), Iordansky (1992), Bauer (1992, 1997), Kardong and Zalisko (1998), Haas (2001), Kardong (2002), Ericsson and Olsson (2004) and Ericsson et al. (2004), does not allow to completely clarify if the hyoglossus of these amphibians is derived from the sternohyoideus or from the coracomandibularis (or eventually from both). The analysis of the salamander specimens examined in the present work does also not help to clarify this issue; minutiose comparative analyses of the development of the hyoglossus in salamanders and in other tetrapods are thus needed.

In extant cladistians, chondrosteans and halecomorphs the coracomandibularis is modified into a peculiar muscle branchiomandibularis connecting the branchial arches and the mandible (figs. 9, 10), which is missing in living ginglymodians and teleosts (fig. 15). Wiley (1979a,b) and Lauder and Liem (1983) defended that the ancestors of extant actinopterygians probably had a branchiomandibularis, and that the absence of this muscle in living ginglymodians and teleosts is due to a secondary loss. The phylogenetic results of Diogo (in press) strongly support this hypothesis.

General remarks

In view of the discussion above and of the information provided in tables 1–6 and figures 3–8, the evolution of the mandibular, hyoid and hypobranchial muscles within osteichthyans may be tentatively summarized as follows. In plesiomorphic osteichthyans the mandibular muscle plate gave rise to the levator arcus palatini, dorsally, to the adductor mandibulae A2, A3', A3'' and A ω , medially, and to a divided intermandibularis, ventrally. Within osteichthyan evolution, the posterior part of the intermandibularis become associated with the interhyoideus in teleosts, forming the peculiar muscle protractor hyoideus (table 1). The number of divisions of the adductor mandibulae complex has been variable during the evolutionary history of osteichthyans; some peculiar divisions are exclusively found in extant members of specific groups, e.g. the A1-OST (ostariophysans), the A0 (cypriniforms), the palatomandibularis minor and major (ginglymodians), the levator maxillae superioris 3 and 4 (halecomorphs) or the A2-PVM (non-actinistian sarcopterygians) (tables 1, 2). The number of dorsal mandibular muscles is also variable within adult osteichthyans: some taxa have a single muscle (e.g. *Latimeria*, in which there is only a levator arcus palatini; this seems to represent the plesiomorphic condition for osteichthyans); some have more than one muscle (e.g. the numerous actinopterygians exhibiting a levator arcus palatini and a dilatator operculi or the numerous amniotes exhibiting a levator pterygoidei and a protractor pterygoidei); and some have none (e.g. living dipnoans and amphibians) (tables 1 and 2).

Regarding the hyoid muscle plate, the plesiomorphic condition for osteichthyans is seemingly that in which this plate gave rise to a single ventral division, which is designated here as interhyoideus, and to the dorso-medial divisions adductor arcus palatini and adductor operculi (tables 3 and 4). In actinopterygians a portion of the interhyoideus became differentiated into a separate muscle, the hyohyoideus, which is divided into three distinct subdivisions in halecostomes, the hyohyoideus inferior, the hyohyoideus abductor and the hyohyoidei adductores (table 3). Other hyoid muscles may be present in osteichthyans, e.g. the branchiohyoideus of urodeles (table 4) and the levator operculi of halecostomes (table 3). *Latimeria* has a muscle 'levator operculi' that in certain aspects resembles, but is seemingly not homologous to, that of halecostomes (table 4). *Latimeria* also has an 'adductor hyomandibulae' somewhat similar, but that is seemingly also not homologous, to the muscles 'adductor hyomandibulae' found in osteichthyans such as actinopterygians (tables 3, 4). As explained above, there are many uncertainties concerning the homologies and evolution of the levator hyoideus/depressor mandibulae of dipnoans and tetrapods. According to the hypothesis proposed in the

present work both these muscles seem to have been found in at least some ontogenetic stages of the last common ancestors of dipnoans and tetrapods (table 4). Interestingly, Köntges and Lumsden (1996) showed that in tetrapods such as birds the posterior region of the mandible in which the depressor mandibulae attaches is constituted by neural crest derivatives of the hyoid arch, and not of the mandibular arch. This is, in fact, one of the various examples given by these authors to illustrate a highly constrained pattern of cranial skeletomuscular connectivity: each rhombomeric neural crest population remains coherent throughout ontogeny, forming both the connective tissues of specific muscles and their respective attachment sites onto the neuro- and viscerocranium. It would thus be interesting to investigate if the depressor mandibulae of dipnoans as e.g. *Protopterus* and *Lepidosiren* also attaches to a region of the mandible constituted by neural crest derivatives of the hyoid arch. If that is the case, and if further investigation would eventually point out that the mandible of extant non-dipnoan bony fishes is exclusively formed by mandibular neural crest derivatives, this would indicate that the presence of a depressor mandibulae in tetrapods and dipnoans might be related with an evolutionary change in which hyoid neural crest derivatives were incorporated in the formation of the lower jaw.

Concerning the hypobranchial muscles, the plesiomorphic osteichthyan condition seemingly corresponds to that found in extant actinistians and dipnoans, in which there is a coracomandibularis and a sternohyoideus (table 6). Changes to this plesiomorphic condition occurred during osteichthyan evolution. For instance, in actinopterygians the coracomandibularis became modified into a peculiar branchiomandibularis (table 5). In sarcopterygians such as tetrapods the hypobranchial muscle plate became differentiated in various muscles that are not found in other extant osteichthyans, as e.g. the omohyoideus and the glossal muscles of the tongue (table 6). In mammals, the hypobranchial muscle plate became divided into an even higher number of muscles; this is also the case of the mandibular and hyoid muscle plates, which in mammals usually give rise to a higher number of muscles than in other tetrapods (e.g. Edgeworth 1935; Brock 1938; Jarvik 1963, 1980; Gorniak 1985; Pough et al. 1996; Kardong and Zalisko 1998; Gibbs et al. 2000, 2002; Kardong 2002; Kisia and Onyango 2005).

It should be emphasized that, as mentioned above, the discussions provided in this paper are based on data compiled from evidence provided by developmental biology, comparative anatomy, functional morphology, paleontology, experimental embryology and molecular biology, innervation and phylogeny. As stressed by e.g. Edgeworth (1935: 222), in order to provide a well-grounded analysis of the homologies and evolution of a certain muscle within different taxa it is imperative to take all the lines of evidence into consideration, since “no one criterion is sufficient, not even two”. This because none of these lines of evidence is infallible. For instance, although the innervation of a muscle usually remains constant and corresponds to its segment of origin (e.g. Luther 1913–1914; Edgeworth 1935; Kesteven 1942–1945; Köntges and Lumsden 1996), there are cases in which a same muscle may exhibit different innervations in different taxa. One of the examples provided by Edgeworth (1935: 221) to illustrate this concerns the intermandibularis of extant dipnoans, which “is innervated by the Vth and VII nerves, though wholly of mandibular origin”.

Also, there are eventually cases in which a same muscle may be derived from different regions and/or segments of the body in different taxa. An example provided by Edgeworth (1935: 221) concerns the branchial muscle protractor pectoralis (his “cucularis”), which “has diverse origins in *Ornithorhynchus*, *Talusia* and *Sus*; in the first-named it is developed from the 3rd, in the second from the 2nd and in the last from the 1st branchial muscle-plate; these changes are secondary to the non-development of the branchial muscle-plates, from behind forwards; the muscles are homologous and have a constant primary innervation from the Xth nerve”. This is one of the reasons why I mentioned above that even if the development of the depressor mandibulae of dipnoans is not completely similar to that of the anterior part of the depressor mandibulae of tetrapods such as salamanders, this does not necessarily mean that these structures cannot be homologous. This because in this case there are actually several different lines of evidence supporting their homology, such as: 1) innervation (e.g. they are innervated by the VIIth nerve); 2) topology (e.g. they occupy a similar position and have similar relations to other structures); 3) functional morphology (e.g. they have a similar function, being mainly related with the depression of the lower jaw); 4) ontogeny (even if their development is eventually not completely similar, as stated Edgeworth, most aspects concerning this development are actually much alike, e.g. they originate from the dorso-medial portion of the hyoid muscle plate); 5) phylogeny (e.g. according to the phylogenetic scenario shown in figure 1 and defended by other authors the dipnoans are the closest living relatives of tetrapods).

As noted Edgeworth (1935: 224), there are also cases in which “an old structure may be lost” (e.g. the branchiomandibularis is lost in extant ginglymodians and teleosts), in which “new muscles may be developed” (e.g. the glossal muscles of tetrapods), and in which “an old structure or group of structures may be transformed” (e.g. the levator hyoideus “may be transformed, either partially or wholly, into a depressor mandibulae”). The occurrence of such phenomena thus raises further difficulties for comparative analyses within different clades. And, of course, there are also cases in which “similar secondary developments occur in separate genera or phyla”, i.e., convergences and parallelisms (see e.g. Diogo 2004a, 2005, for a recent discussion of these two concepts). Thence the importance to turn for aid to the evidence provided by phylogenetic analyses in order to recognize the occurrence of such cases. For instance, there are some similarities between the ‘levator operculi’ of *Latimeria* and the levator operculi of halecostomes (e.g. innervation, position, relations to other structures), but the phylogenetic results of Diogo (in press) and of other recent studies, together with other lines of evidence (e.g. functional morphology), indicate that these similarities are likely due to homoplasy (see above).

The discussions and examples provided in the paragraphs above point out the danger of discussing the homologies of structures such as muscles on the basis of a single line of evidence, even when this concerns innervation or development. Thus, to put it in simple words, because in my opinion it is important to stress this point, if for instance the innervation of a certain muscle seems to indicate that it is part of the adductor mandibulae complex, one should check if this is not contradicted by other lines of evidence, e.g.: if it originates ontogenetically from a muscle plate other than

the mandibular one (ontogeny); if its configuration in adults does indicate that it is not a mandibular muscle (adult anatomy/topology); if its function is very different from that of the adductor mandibulae sections of other taxa (functional morphology); if there is eventually palaeontological data available supporting that it is not part of the adductor mandibulae (paleontology); if there is eventually molecular and/or experimental data available supporting that it is a non-mandibular structure, e.g. if in an experimental work blocking the development of mandibular muscles this structure is nevertheless developed (molecular biology and/or experimental embryology); if there is eventually phylogenetic information supporting that it is not part of the adductor mandibulae, e.g. if this structure belongs to derived taxon of a large clade in which all the other taxa lack an adductor mandibulae (phylogeny). All this should therefore be taken into consideration. But the discussions and examples provided above also indicate that when this is done, i.e. when there are various lines of evidence available and when all these are carefully analyzed and taken into account, it is effectively possible to establish well-grounded hypotheses of homology. In other words, the hard work, in this case, does seem to be rewarding. In fact, a better understanding of the muscles of a certain taxon allows a much more detailed, integrative analysis of the comparative anatomy, functional morphology and evolution of that taxon. In the specific case of the present work, it is hoped that the information provided here may help to contribute to a better understanding of the muscles of osteichthyans, and, thus, to a better knowledge of the evolution of these gnathostomes and of vertebrates in general.

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