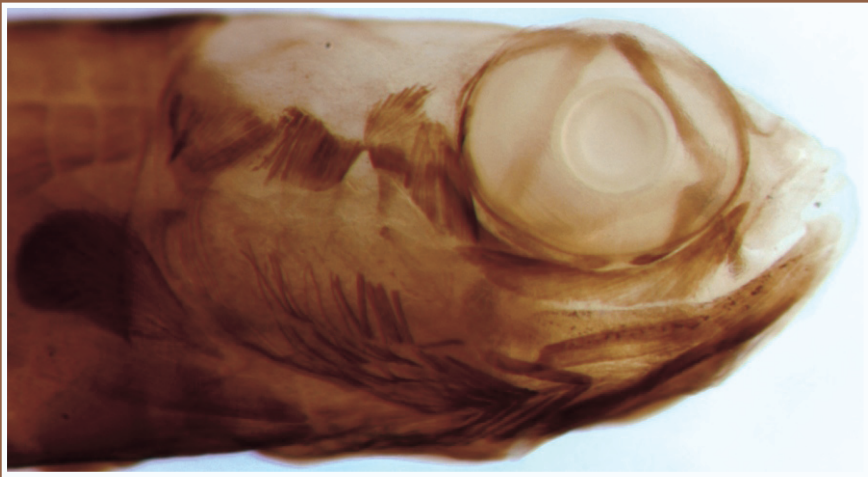


MUSCLES OF VERTEBRATES

**Comparative Anatomy, Evolution,
Homologies and Development**



**Rui Diogo
Virginia Abdala**



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Homologies and Development

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Preface

The vertebrates are members of the largest clade of chordates, the Vertebrata, and are characterized for having features such as backbones and spinal columns. More than 58,000 species of vertebrates have been described so far, making up about 5% of all described animal species. Several studies have provided information on the head, neck, pectoral and forelimb musculature of the Vertebrates, but most of them concentrated on a single taxon or a specific subgroup of muscles. The few more inclusive comparative analyses that were actually based on dissections of taxa representing sarcopterygian fish, amphibians, reptiles, monotremes and therian mammals, including modern humans, were published at least half a century ago, and some much earlier than that. Those authors did not have access to information that is now available about, for example, the cephalic and the pectoral muscles of the coelacanth *Latimeria chalumnae*, the role played by neural crest cells in the development and patterning of the vertebrate muscles, or the molecular and other evidence that has accumulated about phylogenetic relationships of Vertebrates. The main aims of the present volume are thus to summarize all the information obtained from our dissections of numerous specimens from vertebrate groups as varied as the Teleostei, Halecomorphi, Ginglymodi, Chondrostei, Cladistia, Dipnoi, Gymnophiona, Anura, Caudata, Testudines, Lepidosauria, Crocodylia, Aves, Monotremata, Marsupialia, Rodentia, Scandentia, Dermoptera and Primates, including *Homo sapiens*, to compare this new information with the data available in the literature, and then to collate and synthesize all of the new and existing data. To our knowledge, this is the most detailed account that has been published so far on the head, neck, pectoral and forelimb musculature of Vertebrates, because it includes information about the mandibular, hyoid, branchial, hypobranchial, epibranchial, pectoral, arm, forearm and hand muscles of each of the major vertebrate taxa. The book also includes hundreds of illustrations (drawings and photographs) of, as well as numerous tables showing the homologies between the muscles of all the major extant vertebrate taxa. It also provides a list of more than a thousand synonyms that have been used by other authors to designate these muscles in the literature, from more than two centuries ago until

the present date. Importantly, it also reviews data obtained in the fields of evolutionary developmental biology, embryology and genetics, and explains how this data helps to understand the evolution and homologies of vertebrate muscles. Chapters 1 and 2 provide an introduction to the main aims of the book and the methodology and material used. Chapter 3 deals with the muscles of non-osteichthyan vertebrates. Chapters 4 and 8 are focused on the head, neck, pectoral and pectoral fin/forelimb muscles of actinopterygians and basal sarcopterygians. Chapters 5 and 9 discuss the evolution and homologies of these muscles, from sarcopterygian fish such as coelacanth to mammals such as modern humans, while Chapters 6, 7 and 10 deal with the muscles of non-mammalian tetrapods. Chapter 11 provides a general discussion of the data presented in Chapters 3 to 10, addressing subjects such as the use of myological characters in phylogenetic reconstructions, the relationship between muscular splittings, fusions, paedomorphism, evolutionary reversions and anatomical complexity, the study of muscles in the context of evolutionary developmental biology, and the proposal of a unifying nomenclature for the head, neck, pectoral and forelimb muscles of the vertebrates as a whole. We thus hope that the information provided in this book will be useful to teachers, students, and researchers working in different fields such as functional morphology, ecomorphology, evolutionary developmental biology, embryology, molecular biology, zoology, evolution, and phylogeny. As the book includes crucial information about the anatomy, development, homologies, evolution and muscular abnormalities of our own species, *Homo sapiens*, it will also be helpful to physicians and medical students.

February 2010

Rui Diogo and Virginia Abdala

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R. Reis, R. Winterbottom, C. Borden, B. Richmond, , M. Fabrezi, M.J. Tulli, and A. Russell and many other colleagues for their helpful advice and assistance and for their discussions on vertebrate anatomy, functional morphology, development, phylogeny and evolution in the last years. Also, thanks to all those who have been involved in administering the various grants and other awards that we have received during the last years, without which this work would really not have been possible.

RD wants to thank P. Vandewalle and M. Chardon, for accepting him in the Laboratory of Functional and Evolutionary Morphology in 1998 and for thus giving him the opportunity to begin his research on the anatomy, functional morphology, phylogeny and evolution of Vertebrates. He also wants to thank E. Parmentier, as well as R. Vari and his colleagues S. Weitzman, J. Williams and S. Jewett from the National Museum of Natural History, for accepting him in that amazing museum during two academic years and for providing numerous specimens analyzed in the present work. He also wants to thank I. Doadrio, who received him in the Museo Nacional de Ciencias Naturales de Madrid, and has made available many specimens of the vast fish collection of this museum. Another particularly bright scientist who received RD in his lab for several months was S. Hughes, who RD thanks very, very much. In his lab, at the prestigious MRC Centre for Developmental Neurobiology of the King's College of London, RD took his first steps in Evolutionary Developmental Biology ("Evo-Devo"). He greatly enjoyed the availability, interest, and continuous questioning and curiosity of S. Hughes. RD also wants to take this occasion to thank B. Wood, for inviting him to continue his research at the Anthropology Department of the George Washington University and expand his studies to groups such as the Primates, including modern humans. RD is particularly thankful to all his friends, particularly to Pedro Brito, Claudia Oliveira, Henry Evrard and Diego Alarcon Reina, and, above all, to Alejandrita Pelito Lindo, to the amazing and adorable Tots Pelluda, and to his parents, Valter and Fatima, his brothers, Hugo and Luis, and to his late grandparents Raul and Amélia. He would also like to thank R. Primlani, who kindly invited him and VA to publish this book, as well as other books, with the prestigious Science Publishers (Enfield, USA).

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Contents

<i>Preface</i>	v
<i>Acknowledgements</i>	vii
1. Introduction and Aims	1
2. Methodology and Material	6
3. Muscles of Non-Osteichthyan Vertebrates	20
4. Head and Neck Muscles of Actinopterygians and Basal Sarcopterygians	61
5. From Sarcopterygian Fish to Modern Humans: Head Muscles and Neck	108
6. Head and Neck Muscles of Amphibians	205
7. Head and Neck Muscles of Reptiles	228
8. Pectoral and Pectoral Fin Muscles of Actinopterygian and Sarcopterygian Fishes	271
9. From Sarcopterygian Fish to Modern Humans: Pectoral and Forelimb Muscles	287
10. Pectoral and Forelimb Muscles of Limbed Amphibians and Reptiles	359
11. General Comments	421
11.1. Muscular splittings, fusions, paedomorphism, reversions and anatomical complexity	421
11.2. Myological characters and phylogenetic reconstructions	426
11.3. Myology, evolutionary developmental biology, model organisms, and the zebrafish	434
11.4. Proposal of a unifying nomenclature for the muscles of vertebrates	443
<i>References</i>	451
<i>About the Authors</i>	
<i>Color Plate Section</i>	

Chapter 1

Introduction and Aims

The vertebrates are members of the largest clade of chordates, the Vertebrata, and are characterized for having features such as backbones and spinal columns. More than 58,000 species of vertebrates have been described so far, making up about 5% of all described animal species, and representing over 5000 million years of evolution. Phylogenetically (see Fig. 1.1; see also Figs. 3.1, 4.1., 5.1 and 9.1), extant vertebrates may be divided into cyclostomes (including hagfish and lampreys: see Chapter 3) and Gnathostomes, the latter clade being, in turn, subdivided into chondrichthyans (including holocephalans and elasmobranchs) and osteichthyans. However, according to most authors there is a group of fossil fishes that is more closely related to osteichthyans than are the chondrichthyans: the †Acanthodii, which, together with the Osteichthyes, form a group usually named Teleostomi (e.g., Kardong 2002). In addition, apart from the Teleostomi and Chondrichthyes, there is another group that is usually included in the gnathostomes and that is usually considered the sister-group of teleostomes + chondrichthyans: the †Placodermi (e.g., Kardong 2002).

The Osteichthyes, including bony fishes and tetrapods, is a highly speciose group of animals, comprising more than 42,000 living species. Two main osteichthyan groups are usually recognized: the Sarcopterygii (lobefins and tetrapods), with an estimate of more than 24,000 living species (e.g., Stiassny et al. 2004), and the Actinopterygii (rayfins), including more than 28,000 extant species (e.g., Nelson 2006). The Polypteridae (included in the Cladistia) are commonly considered the most basal extant actinopterygian taxon. The Acipenseridae and Polyodontidae (included in the Chondrostei) are usually considered the sister-group of a clade including the Lepisosteidae (included in the Ginglymodi) and the Amiidae (included in Halecomorphi) plus the Teleostei. Regarding the Teleostei, four main living clades are usually recognized in recent works: the Elopomorpha,

Osteoglossomorpha, Otocephala (Clupeomorpha + Ostariophysi) and Euteleostei. The Sarcopterygii includes two groups of extant fishes, the coelacanth (Actinistia) and lungfishes (Dipnoi), and the Tetrapoda. Within tetrapods, Amphibia is the sister-group of Amniota, which includes the Mammalia and the Reptilia (note: when we use the term 'reptiles' we refer to the group including lepidosaurs, birds, crocodylians and turtles, which, despite some controversy, continues to be considered a monophyletic taxon by most taxonomists: see, e.g., Gauthier et al. 1988; Kardong 2002; Dawkins 2004; Diogo 2007; Conrad 2008). The Amphibia include three main extant groups: caecilians (Gymnophiona or Caecilia), frogs (Anura), and salamanders (Caudata or Urodela), the two latter groups being possibly more closely related to each other than to the caecilians (see, e.g., the recent review of Carroll 2007). The Reptilia include four main extant groups: turtles (Testudines), lepidosaurs (Lepidosauria), crocodylians (Crocodylia) and birds (Aves). The Lepidosauria, Crocodylia and Aves are probably more closely related to each other than to Testudines, being thus usually included in the clade Diapsida; crocodylians are considered to be the closest living relatives of birds, these two groups being included in the clade Archosauria (see, e.g., Gauthier et al. 1988; Dilkes 2000; Kardong 2002; Meers 2003; Dawkins 2004; Conrad 2008). The Lepidosauria comprises the Rhynchocephalia, which includes a single extant genus, *Sphenodon*, and the Squamata, which according to the recent study of Conrad (2008) includes amphisbaenians, mosasaurs, snakes and 'lizards' (as explained by this author, 'lizards' do not form a monophyletic group, because some 'lizards' are more closely related to taxa such as snakes than to other 'lizards': see Conrad 2008 for more details on the interrelationships of squamates). The Mammalia includes the Monotremata and Theria, which comprises marsupials and placentals. Within the latter, the Primates (including modern humans), Dermoptera (including colugos or 'flying lemurs') and Scandentia (including tree-shrews) are included in the clade Euarchonta and are placed in an unresolved trichotomy in Fig. 1.1, because the relationships between these three groups remains mainly unresolved (some authors continue to group colugos with tree-shrews, others group tree-shrews with primates, and yet others group colugos with primates: see, e.g., Sargis 2002ab, 2004; Dawkins 2004; Marivaux et al. 2006; Janecka et al. 2007; Silcox et al. 2007; Diogo 2009).

Several studies have provided information on the head, neck, pectoral and forelimb/pectoral fin musculature of the Vertebrates, but most of them concentrate on a single taxon or a specific subgroup of muscles. The few more inclusive comparative analyses that were actually based on dissections of taxa comprising actinopterygians, sarcopterygian fish, amphibians, reptiles, monotremes and therian mammals, including modern humans, were published at least half a century ago, and some much earlier than

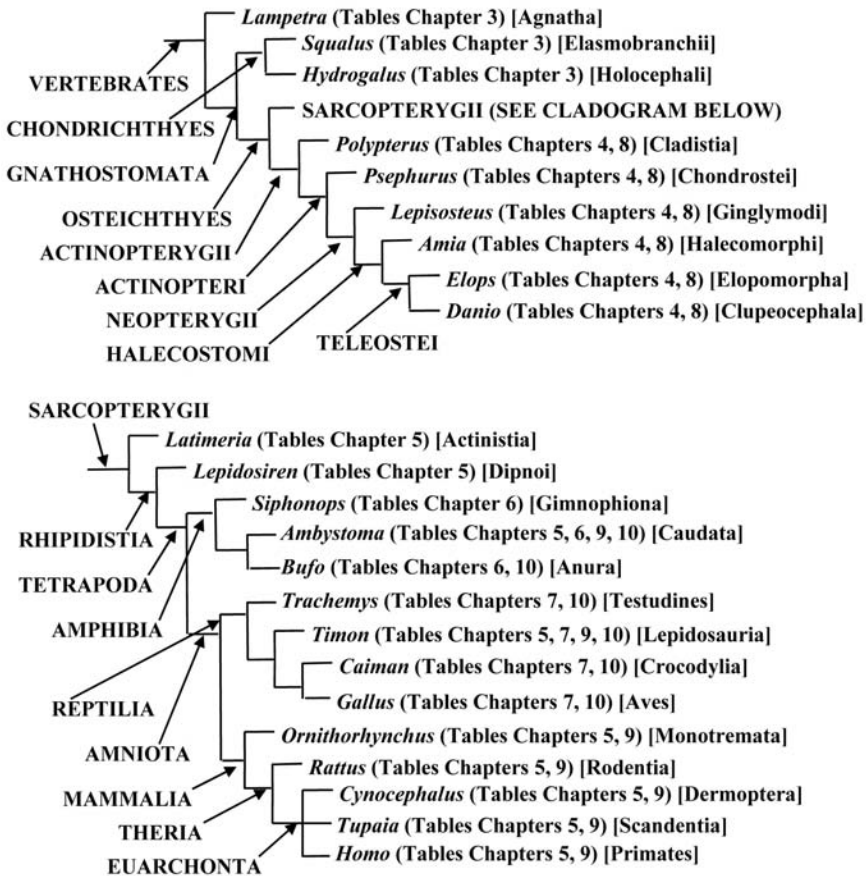


Fig. 1.1 Simplified phylogenetic framework for the discussions provided in this book and the comparison between the muscles of the genera listed in the tables of Chapters 3 to 10 (for more details about the phylogenetic relationships of the main vertebrate clades discussed in Chapters 3 to 10 and the literature from which this phylogenetic scenario is based, see text and Figs. 3.1, 4.1, 5.1, and 9.1).

that (e.g., Humphry 1872ab; Luther 1913–1914; Kesteven 1942–1945; Edgeworth 1902–1935; Huber 1930–1931; Brock 1938). However, none of these works actually covered in detail the whole head, neck, pectoral and forelimb/pectoral fin musculature of all these taxa. Moreover, the authors of these works did not have access to crucial information that is now available about, for example, the cephalic and the pectoral muscles of the coelacanth *Latimeria chalumnae* (discovered only in 1938), the important part played by neural crest cells in the development and patterning of the vertebrate muscles, or the molecular and other evidence that has

accumulated about the phylogenetic interrelationships of vertebrates (e.g., Millot and Anthony 1958; Jarvik 1963, 1980; Alexander 1973; Le Lièvre and Le Douarin 1975; Anthony 1980; Lauder 1980c; Rosen et al. 1981; Noden 1983, 1984, 1986; Hatta et al. 1990, 1991; Adamicka and Ahnelt 1992; Couly et al. 1992; Miyake et al. 1992; Köntges and Lumsden 1996; Pough et al. 1996; Schilling and Kimmel 1997; Kardong and Zalisko 1998; McGonnell 2001; Olsson et al. 2001; Hunter and Prince 2002; Kardong 2002; West-Eberhard 2003; Diogo 2004ab, 2007, 2008; Ericsson and Olsson 2004; Ericsson et al. 2004; Carroll et al. 2005; Thorsen and Hale 2005; Kisia and Onyango 2005; Noden and Schneider 2006; Diogo and Abdala 2007; see Chapters 3–11 and the list of references provided in the end of the book).

The main aims of the present volume are thus to summarize all the information obtained from our dissections of numerous specimens from vertebrate groups as varied as the Teleostei, Halecomorphi, Ginglymodi, Chondrostei, Cladistia, Dipnoi, Gymnophiona, Anura, Caudata, Testudines, Lepidosauria, Crocodylia, Aves, Monotremata, Marsupialia, Rodentia, Scandentia, Dermoptera and Primates, including *Homo sapiens*, to compare this new information with the data available in the literature, and then to collate and synthesize all of the new and existing data. To our knowledge, this is the most detailed account that has been published so far on the head, neck, pectoral and forelimb/pectoral fin musculature of Vertebrates, because it includes information about the mandibular, hyoid, branchial, hypobranchial, epibranchial, pectoral, arm, forearm and hand muscles of each of the major vertebrate taxa. As explained in the Preface, Chapters 1 and 2 provide a short introduction to the main aims of the book and to the methodology and material used. Chapter 3 deals with the muscles of non-osteichthyan vertebrates. Chapters 4 and 8 are focused on the head, neck, pectoral and pectoral fin/forelimb muscles of actinopterygians and basal sarcopterygians. Chapters 5 and 9 discuss the evolution and homologies of these muscles, from sarcopterygian fish such as coelacanth to mammals such as modern humans, while Chapters 6, 7 and 10 deal with the muscles of non-mammalian tetrapods. Chapter 11 provides a general discussion of the data presented in Chapters 1 to 10, addressing subjects such as the use of myological characters in phylogenetic reconstructions, the relationship between muscular splittings, fusions, paedomorphism, evolutionary reversions and anatomical complexity, the study of muscles in the context of evolutionary developmental biology, and the proposal of a unifying nomenclature for the head, neck, pectoral and forelimb/pectoral fin muscles of the vertebrates as a whole. As some readers will probably be particularly interested in a specific clade and/or a specific group of muscles (e.g., the head and neck muscles of amphibians), and, thus, in a specific chapter (e.g., in that case, Chapter 6), we decided that each chapter would follow a consistent organization internally (e.g.,

a short introduction, a main section with the results and discussion, and then some general remarks). So, some results and a few comments may thus be repeated in different chapters, but the book has more consistency of presentation throughout and the readers may quickly obtain the most important information about the taxon and/or group of muscles in which they are interested without having to read all the other parts of the book before that.

As stressed in our previous works (e.g., Diogo et al. 2008ab, 2009ab), one of the major problems researchers face when they compare the muscles of a certain vertebrate taxon with those of other taxa is the use of different names by different authors to designate the same muscle in the members of different clades, and even of the same clade. In order to reconcile the different nomenclatures we use a unifying nomenclature for the head, neck, pectoral and forelimb muscles of the vertebrates as a whole that takes into account the data compiled and discussed in this book. In fact, we are fully aware of the new, ambitious, and clearly needed ontological projects that are now being developed in different biological disciplines. Such ontologies are extremely important and are becoming increasingly popular, because they provide a vocabulary for representing and communicating knowledge about a certain topic and a set of relationships that hold among the terms in that vocabulary. Although we did not have in mind to build an ontology when we began this project, the fact is that we did it, and still do, in each of our works published in the context of comparative vertebrate myology, and particularly in this book. Therefore, we hope that the information provided here will stimulate researchers to develop a detailed ontology of the head, neck, pectoral and forelimb musculature of vertebrates, as well as to undertake future studies about the evolution, homologies, and development of these muscles and of other vertebrate anatomical structures in general. In fact, we sincerely hope that this volume will contribute to the revival of the field of vertebrate comparative myology, which was often neglected in the past few decades but remains crucial to understanding the evolution and phylogeny of vertebrates as a whole, as well as the evolutionary history, anatomical variations, ontogeny and numerous medical problems of modern humans in particular.

Chapter 2

Methodology and Material

Biological Material

The general phylogenetic framework for the comparisons provided in the present work is set out in Fig. 1.1 (see also Figs. 3.1, 4.1, 5.1, and 9.1). In order to facilitate the comparisons between the head, neck, pectoral and forelimb muscles of vertebrates, we carefully chose to include in the tables provided in Chapters 3–10: the lamprey *Lampetra japonica* (Agnatha), the shark *Squalus acanthias* (Elasmobranchii), the ratfish *Hydrolagus colliei* (Holocephali) [non-osteichthyan vertebrates: tables of Chapter 3]; the bichir *Polypterus bichir* (Cladistia), the swordfish *Xiphias gladius* (Chondrostei), the gar *Lepisosteus osseus* (Ginglymodi), the bowfin *Amia calva* (Halecomorphi), the basal teleostean *Elops saurus* and the clupeocephalan teleostean *Danio rerio* (Teleostei) [actinopterygian osteichthyans: tables of Chapters 4 and 8]. Regarding sarcopterygian osteichthyans [tables of Chapters 5, 6, 7, 9 and 10], we include the coelacanth *Latimeria chalumnae* (Actinistia), the lungfish *Lepidosiren paradoxa* (Dipnoi), the salamander *Ambystoma ordinarium* (Caudata or Urodela), the caecilian *Siphonops paulensis* (Gymnophiona), the frog *Bufo* (or *Rhinella*) *arenarum* (Anura), the ‘lizard’ *Timon lepidus* (Lepidosauria), the turtle *Trachemys scripta* (Testudines), the crocodylian *Caiman latirostris* (Crocodylia) and the bird *Gallus domesticus* (Aves). We also include a member of the phylogenetically most plesiomorphic extant mammal clade, the Monotremata (*Ornithorhynchus anatinus*, or ‘platypus’), a member of the Rodentia, the Norwegian rat (*Rattus norvegicus*; because rats are often considered as ‘anatomically generalized’ therian mammals but at the same time are somewhat closely related to primates), a member of the colugos (or ‘flying lemurs’) (*Cynocephalus volans*), and a member of the tree-shrews (*Tupaia* sp.). That is, we include in these tables members of the two groups that are usually considered the closest living relatives of primates (colugos and tree-shrews: Fig. 1.1). The latter group is represented in the tables by

our own species, *Homo sapiens*. It is important to explain that, apart from these taxa, we have dissected numerous specimens of other vertebrate taxa. The dissected specimens are from the Colección Mamíferos Lillo of the Universidad Nacional de Tucumán (CML), the Primate Foundation of Arizona (PFA), the Department of Anatomy (GWU-ANA) and the Department of Anthropology (GWU-ANT) of the George Washington University, the Department of Anatomy of Howard University (HU-ANA), the Smithsonian Institution's National Museum of Natural History (USNM), the Cleveland Metroparks Zoo (CMZ), the Yerkes National Primate Research Center (YNPRC), the Duke Lemur Center (DLC), the Museo Nacional de Ciencias Naturales de Madrid (MNCN), the Centro Nacional Patagónico de Argentina (CONICET), the Macquarie University of Australia (MU), the herpetological collection of Diamante-CONICET-Argentina (DIAMR), the Fundación Miguel Lillo of Argentina (FML), the San Diego State University (SDSU), the Laboratory of Functional and Evolutionary Morphology of the University of Liège (LFEM), 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 Field Museum of Natural History (FMNH), the Illinois Natural History Survey (INHS), the Museum National d'Histoire Naturelle de Paris (MNHN), the Musée Royal de l'Afrique Centrale (MRAC), the Université Nationale du Bénin (UNB), the collection of Anthony Herrel (AH), the herpetological collection of the Hebrew University of Jerusalem-Israel (HUJ), the "Museo de Zoología of the San Pablo University-Brasil" (MZUSP), the Tupinambis Project Tucumán-Argentina (PT), the personal collection of Richard Thomas in Puerto Rico University (RT), and the Peabody Museum of Natural History of Yale University (YPM). The list of specimens examined by us is given below; the number of specimens dissected is followed by an abbreviation that refers to the state of the specimen (alc = alcohol fixed; fre = fresh; for = formalin embalmed; c&s = trypsin-cleared and alizarine-stained). In our dissections, other than their color, there were no notable differences regarding the attachments, overall configuration and general appearance of the muscles of fresh, alcohol fixed, and formalin embalmed specimens.

Specimens dissected

ACTINOPTERYGII—Non-teleostean actinopterygians: *Acipenser sturio*: MNCN 152172, 3 (alc). *Amia calva*: MNCN 35961, 1 (alc), 1 (c&s). *Lepisosteus osseus*: ANSP 107961, 2 (alc); ANSP 172630, 1 (alc); MNCN 246557, 1 (c&s). *Lepisosteus platyrhincus*: AMNH 74789, 2 (alc). *Polypterus bichir*: MNCN 1579, 7 (alc), 1 (c&s). *Psephurus gladius*: CASW, uncatalogued, 1 (alc). **Clupeomorpha:** *Denticeps clupeoides*: MRAC 76-032-P-1, 2 (alc). *Engraulis encrasicolus*: MNCN 68048, 2 (alc); MNCN 65097, 8

(alc); MNCN 1099, 3 (alc). *Engraulis* sp: MNCN 48896, 3 (alc). *Ethmalosa fimbriata*: MNCN 48865, 3 (alc). *Ilisha fuerthii*: MNCN 49338, 8 (alc). *Thryssa setirostris*: MNCN 49294, 2 (alc). **Elopomorpha**: *Albula vulpes*: MNCN 52124, 2 (alc). *Anguilla anguilla*: MNCN 41049, 3 (alc). *Elops lacerta*: LFEM, 2 (alc). *Elops saurus*: MNCN 48752, 2 (alc). *Conger conger*: MNCN 1530, 5 (alc). *Eurypharynx pelecanooides*: AMNH 44315, 1 (alc); AMNH 44344, 1 (alc). *Megalops cyprinoides*: MNCN 48858, 3 (alc). *Notacanthus bonaparte*: MNCN 107324, 3 (alc). **Euteleostei**: *Alepocephalus rostratus*: MNCN 108199, 2 (alc). *Argentina brucei*: USNM 239005, 2 (alc). *Argentina sphyraena*: MNCN 001134, 12 (alc); MNCN 78530, 5 (alc). *Astronesthes niger*: MNCN 1102, 1 (alc). *Aulopus filamentosus*: MNCN 1170, 6 (alc). *Bathylagus euryops*: MNCN 124597, 1 (alc). *Bathylagus longirostris*: USNM 384823, 2 (alc). *Bathylagus tenuis*: MNHN 2005-1978, 2 (alc). *Chlorophthalmus agassizi*: MNCN 1193, 3 (alc); MNCN 1182, 5 (alc). *Coregonus lavaretus*: MNCN 75424, 1 (alc). *Coregonus tugun*: MNCN 75422, 2 (alc). *Esox lucius*: MNCN 197706, 5 (alc). *Galaxias maculatus*: USNM 344889, 2 (alc). *Osmerus eperlanus*: MNCN 193795, 11 (alc). *Osmerus mordax*: USNM 32565, 2 (alc). *Plecoglossus altivelis*: MNCN 192036, 1 (alc). *Retropinna retropinna*: AMNH 30890, 1 (alc). *Salmo trutta*: MNCN 136179, 2 (alc), 1 (c&s); MNCN 16373, 2 (alc); MNCN 40685, 2 (alc). *Salmo* sp: MNCN 48863, 2 (alc). *Searsia koefoedi*: USNM 206896, 2 (alc). *Stokellia anisodon*: AMNH 31037, 1 (alc). *Stomias boa*: MNCN 74444, 8 (alc); MNCN 74456, 4 (alc). *Thymallus thymallus*: MNCN 115147, 1 (alc); MNCN 114992, 1 (alc). *Umbra limi*: MNCN 35672, 2 (alc); 36072, 2 (alc). *Umbra krameri*: MNCN 36659, 3 (alc). *Xenodermichthys copei*: MNCN 78950, 2 (alc); MNCN 1584, 2 (alc); USNM 215527, 2 (alc). **Ostariophysi**: *Bagrus bajad*: LFEM, 1 (alc), 1 (c&s). *Bagrus docmak*: MRAC 86-07-P-512, 1 (alc). *Barbus barbuis*: LFEM, 1 (c&s). *Barbus guiraonis*: MNCN 245730, 3 (alc). *Brachyhyppopomus brevirostris*: LFEM, 2 (alc). *Brachyhyppopomus* sp: INHS 89761, 2 (alc). *Brycon guatemalensis*: MNCN 180536, 3 (alc). *Brycon henni*: CAS 39499, 1 (alc). *Callichthys callichthys*: USNM 226210, 2 (alc). *Catostomus commersonii*: MNCN 36124, 10 (alc). *Citharinus* sp.: 86-016-P-72, 3 (alc). *Cetopsis coecutiens*: USNM 265628, 2 (alc). *Chanos chanos*: USNM 347536, 1 (alc), LFEM, 1 (alc). *Chrysichthys auratus*: UNB, 2 (alc). *Chrysichthys nigrodigitatus*: LFEM, 1 (c&s). *Cobitis paludica*: MNCN 248076, 7 (alc). *Cromeria nilotica*: MRAC P.141098, 2 (alc). *Danio rerio*: MNCN, 10 (alc). *Diplomystes chilensis*: LFEM, 3 (alc). *Distichodus notospilus*: MRAC A0-048-P-2630, 3 (alc). *Gonorynchus gonorynchus*: LFEM, 2 (alc). *Gonorynchus greyi*: FMNH 103977, 1 (alc). *Grasseichthys gabonensis*: MRAC 73-002-P-264, 3 (alc). *Gymnotus carapo*: INHS 35493, 2 (alc). MNCN 115675, 2 (alc). *Kneria wittei*: MRAC P-33512, 2 (alc). *Nematogenys inermis*: USNM 084346, 2 (alc). *Opsariichthys uncirostris*: MNCN 56668, 3 (alc). *Parakneria abbreviata*: MRAC 99-090-P-703, 3 (alc). *Phractolaemus ansorgii*: MRAC P.137982, 3 (alc). *Pimelodus blochii*: LFEM, 2 (alc), 1 (c&s). *Silurus aristotelis*: LFEM, 2 (alc). *Silurus glanis*: LFEM, 2 (alc). *Sternopygus macrurus*: CAS 48241, 1 (alc); INHS 62059, 2 (alc). *Trichomycterus areolatus*: LFEM, 2 (alc). *Xenocharax spilurus*: MRAC A0-048-P-2539, 3 (alc). [†*Chanooides macropoma*, †*Clupavus maroccanus*, †*Lusitanichthys characiformis*, †*Santanichthys diasii*, and †*Sorbininardus apulienensis*, not directly observed by the author, were also included in the cladistic analysis: see above]. **Osteoglossomorpha**: *Hiodon tergisus*: MNCN 36019, 3 (alc). *Mormyrus niloticus*: LFEM, 1 (alc). *Mormyrus tapirus*: MNCN 80593, 3 (alc); MNCN 85283, 1 (alc). *Pantodon buchholzi*: MNCN 73493, 4 (alc). *Xenomystus nigri*: MNCN 227824, 25 (alc).

SARCOPTERYGII—Amphibia: *Ambystoma mexicanum*: MNCN, uncatalogued, 2 (alc). *Ambystoma ordinarium*: MNCN, uncatalogued, 2 (alc). *Ambystoma texanum*:

FML 03402, 1 (alc). *Bufo arenarum*: FML 01352-1, 3 (alc). *Chtonerpethon indistinctum*: JC, uncatalogued, 1 (alc). *Leptodactylus fuscus*: FML, uncatalogued, 2 (alc). *Litoria caerulea*: DIAM 0313, 1 (alc). *Phyllomedusa sauvagi*: FML 04899, 2 (alc), and DIAM 0337, 1 (alc). *Siphonops paulensis*: FML, uncatalogued, 1 (alc); *Siphonops* sp.: DB, uncatalogued, 2 (alc). *Telmatobius laticeps*: FML 3960, 1 (alc). **Aves**: *Cairina moschata*: FML w/d, 1 (alc). *Coturnyx coturnyx*: FML w/d, 2 (alc). *Gallus domesticus*: FML w/d, 3 (alc). *Nothura* (alc). FML w/d 1 (alc). *Pitangus sulphuratus*: FML w/d, 1 (alc). *Thraupis sayaca*: FML w/d, 1 (alc). **Crocodylia**: *Caiman latirostris*: FML w/d, 1 (alc), and CCyTTP w/d, 4 (alc). **Dipnoi**: *Lepidosiren paradoxa*: CONICET, uncatalogued, 1 (alc). *Neoceratodus forsteri*: MU, uncatalogued, 2 (alc). **Lepidosauria**: *Ameiva ameiva*: FML 03637, 4 (alc). *Amphisbaena alba*: FML uncatalogued, 2 (alc). *Anisolepis longicauda*: UNNEC no number, 1 (alc). *Basiliscus vittatus*: SDSU 02097, 1 (alc). *Bogertia lutzae*: MZU(ALC) 54747, 1 (alc). *Briba brasiliana*: MZU(ALC) 73851, 1 (alc). *Callopiastes maculatus*: MZU(ALC) 58107, 1 (alc). *Calyptommatius leiolepis*: MZU(ALC) 71339, 1 (alc). *Chalcides chalcides*: FML 03712, 1 (alc). *Cnemidophorus ocellifer*: FML 03389, 2 (alc); FML 03409, 4 (alc), without data, 1 (alc), and FML 17606, 1 (alc). *Cordylus tropidosternon*: AH no number, 1 (alc). *Crocodylurus lacertinus*: MZU(ALC) 12622, 1 (alc). *Dicrodon guttulatum*: FML 02017, 1 (alc). *Diplolaemus bibroni*: MACN 35850, 1 (alc). *Dracaena paraguayensis*: MZU(ALC) 52369, 1 (alc). *Echinosaura horrida*: MZU(ALC) 54452, 1 (alc). *Enyalius iheringii*: MZU(ALC) 74901, 1 (alc). *Garthia gaudichaudii*: MZU(ALC) 45329, 1 (alc). *Garthia penai*: MZU(ALC) 60937, 1 (alc). *Gekko vittatus*: AH no number, 2 (alc). *Gerrohsaurus major*: AH no number, 1 (alc). *Gymnodactylus geckoides*: MZ(ALC) 48128, 1 (alc). *Hemidactylus garnoti*: AH no number, 2 (alc). *Hemidactylus mabouia*: FML 02142, 1 (alc), and FML 02421, 1 (alc). *Homonota fasciata*: FML 02137, 1 (alc), and FML 00915, 2 (alc). *Leiosaurus paronae*: MACN 4386, 1 (alc). *Liolaemus cuyanus*: FML 02021, 7 (alc). *Mabuya frenata*: FML 00277, 1 (alc), and FML 01713, 1 (alc). *Microlophus theresioides*: FML 03674, 1 (alc). *Phelsuma madagascariensis*: AH no number, 2 (alc). *Phyllodactylus gerrophygus*: FML 01563, 2 (alc). *Phyllopezus pollicaris*: FML 02913, 2 (alc). *Phymaturus* (alc): FML 13834-13844, 3 (alc). *Phymaturus punae*: FML 2942, 4 (alc). *Podarcis sicula*: FML 03714, 1 (alc). *Polychrus acutirostris*: MZU(ALC) 48151, 1 (alc). MZU(ALC) 08605, 1 (alc). *Pristidactylus achalensis*: MACN 32779, 1 (alc). *Proctoporus guentheri*: FML 02010, 1 (alc). *Teius teyous*: FML 00290, 2 (alc). *Stenocercus caducus*: FML 00260, 1 (alc), and FML 00901, 1 (alc). *Thecadactylus rapicauda*: MZU(ALC) 11476, 1 (alc). *Tropidurus etheridgei*: FML 03562, 2 (alc). *Tropidurus hygoni*: FML 08796, 1 (alc). *Tropidurus oreadicus*: FML 08771, 1 (alc). *Tropidurus (alc)inulosus*: FML 00129, 2 (alc), and FML 03559, 2 (alc). *Tupinambis rufescens*: PT 0084, 1 (alc), PT 0085, 1 (alc), FML 06412, 1 (alc), FML 06425, 1 (alc), and FML 07420, 1 (alc). *Vanzoia klugei*: MZU(ALC) 59130, 1 (alc). *Varanus* (alc): AH no number, 1 (alc). *Xantusia* (alc): AH no number 1, 1 (alc). *Zonosaurus* (alc): AH no number, 1 (alc). **Mammalia**: *Cynocephalus volans*: USNM, 144941, 1 (alc); USNM, uncatalogued, 1 (alc). *Didelphis albiventris*: CML 5971, 1 (alc). *Homo sapiens*: GWU-ANA, 1-16, 16 (for). *Hylobates lar*: HU-ANA, H01, 1 (for). *Lepilemur ruficaudatus*: HU-ANA, L01, 1 (for). *Lutreolina crassicaudata*: CML 4114, 1 (alc). *Macaca mulatta*: HU-ANA, M01, 1 (for); YNPRC, M1-9, 9 (for). *Monodelphis dimidiata*: CML 4118, 1 (alc). *Otolemur garnettii*: DLC, OG1-10, 10 (for). *Otolemur crassicaudatus*: DLC, OC1-12, 12 (for). *Ornithorhynchus anatinus*: USNM, 13678, 1 (alc); USNM, uncatalogued, 1 (alc). *Pan troglodytes*: PFA, 1016, 1 (fre); PFA, 1009, 1 (fre); PFA, 1051, 1 (alc.); HU-ANA, C104, 1 (for); GWU-ANT, 01, 1 (for);

GWU-ANT, 02, 1 (for); YNPRC, C1-2, 2 (for); CMZ, C1-2, 2 (for). *Pongo pygmaeus*: HU-ANA, O01, 1 (for); GWU-ANT, 01, 1 (for). *Rattus norvegicus*: USNM, uncatalogued, 2 (alc). *Thylamys venustus*: CML 5586, 1 (alc). *Tupaia sp.*: USNM, 87244, 1 (alc), USNM, uncatalogued, 1 (alc). **Testudines:** *Cuora amboinensis*: YPM R 14443 1 sp. *Cuora galbinifrons*: YPM R 12735, 1 sp. *Geochelone chilensis*: DIAMR-038, 2 sp., DIAMR-039, 2 sp., DIAMR-040, 1 sp., FML 16879, 1 sp., FML 16880, 1 sp., FML16595, 1 sp., FML 00005, 1 sp., and FML 16978, 1 sp. *Glyptemys insculpta*: YPM R 5952, 1 sp. *Mauremys caspica rivulata*: YPM R 16233-36, 2 sp. *Phrynops hilarii*: DIAMR-044, 1 sp., DIAMR-042, 1 sp., DIAMR-041, 1 sp., DIAMR-043, 1 sp., DIAMR-037, 1 sp., DIAMR-005, 1 sp., DIAMR-006 1 sp., and DIAMR-007, 1 sp. *Podocnemys unifilis*: DIAMR-078, 6 sp. *Rhinoclemmys pulcherrima*: AH uncatalogued, 1 sp. *Sacalia bealei*: YPM R 14670-71 2 sp. *Terrapene carolina*: YPM R 13624 1 sp. YPM R 13622 1 specimen. *Testudo graeca*: HUI-R 22843; HUI-R 22845 2 sp. *Trachemys scripta*: RT uncatalogued, 2 sp.

Nomenclature

The myological nomenclature used in the present work essentially follows that of Diogo (2004a, 2007, 2008) and Diogo et al. (2008ab, 2009ab), with a few exceptions, which will be mentioned in the text and tables provided in the following chapters. Regarding the pectoral and forelimb musculature, we recognize five main groups of muscles: the axial muscles of the pectoral girdle, the appendicular muscles of the pectoral girdle and arm, the appendicular muscles of the ventral forearm, the appendicular muscles of the hand, and the appendicular muscles of the dorsal forearm. The appendicular musculature of the pectoral girdle, arm, forearm and hand (see, e.g., Tables 9.2–9.3) derives from the adductor and abductor muscles of the pectoral fin of sarcopterygian fish, and essentially corresponds to the ‘abaxial musculature’ sensu Shearman and Burke (2009). The axial pectoral girdle musculature (see, e.g., Table 9.2) is derived from the postcranial axial musculature and, together with most of the remaining epaxial and hypaxial muscles of the body (with the exception of, e.g., various muscles of the pectoral girdle and hind limb), form the ‘primaxial musculature’ sensu Shearman and Burke (2009). As explained by these authors, the muscles of the vertebrate body are classically described as epaxial or hypaxial according to the innervation from either the dorsal or ventral rami of the spinal nerves, respectively, while the terms ‘abaxial musculature’ and ‘primaxial musculature’ reflect embryonic criteria that are used to distinguish domains relative to embryonic patterning. The ‘primaxial’ domain comprises somitic cells that develop within somite-derived connective tissue, and the ‘abaxial’ domain includes muscle and bone that originates from somites but then mixes with, and develops within, lateral plate-derived connective tissue.

Concerning the head and neck musculature, the main groups of muscles recognized here correspond to those proposed by Edgeworth (1902–1935): external ocular, mandibular, hyoid, branchial, epibranchial, and hypobranchial. Edgeworth (1935) viewed the development of these muscles in the light of developmental pathways leading from presumptive premyogenic condensations to different states in each cranial arch (see Fig. 2.1; the condensations of the first and second arches corresponding respectively to Edgeworth's 'mandibular and hyoid muscle plates', and those of the more posterior, 'branchial' arches corresponding to his 'branchial muscle plates'). According to him these developmental 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 Fig. 2.1: for instance, the 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); the hyoid condensation usually gives rise to dorso-medial and ventral derivatives; the hypobranchial condensation gives rise to the 'genio-hyoideus' and to the 'rectus cervicis' (as noted by Miyake et al. 1992, it is not clear whether Edgeworth's 'genio-hyoideus' and 'rectus cervicis' represent separate premyogenic condensations or later states of muscle development).

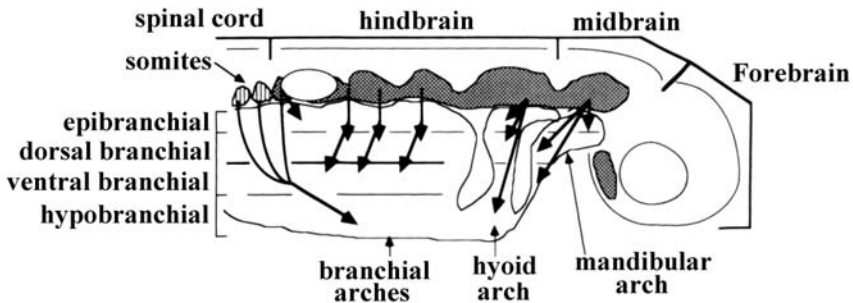


Fig. 2.1 Schematic presentation of embryonic origin of cranial muscles in gnathostomes based on Edgeworth's works (e.g., Edgeworth 1902, 1911, 1923, 1926abc, 1928, 1935); premyogenic cells originate from the paraxial mesoderm (hatched areas) and several somites (areas with vertical bars); large arrows indicate a contribution of cells in segments of the mesoderm to muscle formation of different cranial arches; for more details, see text (modified from Miyake et al. 1992; the nomenclature of the structures illustrated basically follows that of these authors).

According to Edgeworth (1935), although exceptions may occur (see below), the mandibular muscles are generally innervated by the Vth nerve, the hyoid muscles by the VIIth nerve and the branchial muscles by the IXth and Xth nerves. Diogo et al. (2008b) divided the branchial muscles *sensu lato* (that is, all the branchial muscles *sensu* Edgeworth 1935) into three main groups. The first comprises the 'true' branchial muscles, which are subdivided into: (1) the branchial muscles *sensu stricto* that are directly associated with the movements of the branchial arches and are usually innervated by the glossopharyngeal nerve (CNIX) and (2) the protractor pectoralis and its derivatives, which are instead mainly associated with the pectoral girdle and are primarily innervated by the spinal accessory nerve (CNXI). The second group consists of the pharyngeal muscles, which are only present as independent structures in extant mammals. They are considered to be derived from arches 4–6, and they are usually innervated by the vagus nerve (CNX). As will be seen in Chapter 5, the mammalian stylopharyngeus is considered to be derived from the third arch and is primarily innervated by the glossopharyngeal nerve, being thus grouped with the 'true' branchial muscles, and not with the pharyngeal muscles. The third group is made up of the laryngeal muscles, which are considered to be derived from arches 4–6 and are usually innervated by the vagus nerve (CNX). Regarding the epibranchial and hypobranchial muscles, according to Edgeworth these are "developed from the anterior myotomes of the body" and thus "are intrusive elements of the head"; they "retain a spinal innervation" and "do not receive any branches from the Vth, VIIth, IXth and Xth nerves" (Edgeworth 1935: 189). It is worth mentioning that apart from the mandibular, hyoid, branchial, hypobranchial, and epibranchial musculature, 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 vertebrates. These external ocular muscles will not be discussed in the present volume.

Some of the hypotheses defended by Edgeworth have been contradicted by recent studies (e.g., certain phylogenetic hypotheses that he used to formulate his theories: see, e.g., Chapters 4 and 5). However, many of his conclusions have actually been corroborated by more recent developmental and genetic studies. For instance, Miyake et al. (1992) published a paper that reexamined, discussed and supported some of the general ideas proposed by Edgeworth (1935). For example, 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). Actually, the existence of this and other condensations (e.g., the hyoid condensation) has received further support in developmental studies published more recently (e.g., Knight et al. 2008; Kundrat et al. 2009). For instance, in the zebrafish engrailed immunoreactivity is only detected in the levator arcus palatini + dilatator operculi muscles, i.e., in the two muscles that are derived from the dorsal portion of the mandibular muscle plate (constrictor dorsalis *sensu* Edgeworth 1935) (see Chapter 4). Interestingly, in mammals such as the mouse engrailed immunoreactivity is detected in mandibular muscles that are very likely derived from a more ventral ('adductor mandibulae') portion of that plate, i.e., in the masseter, temporalis, pterygoideus medialis and/or pterygoideus lateralis (see Chapter 5). Also interestingly, Tzahor (2009) and other authors have shown that, among members of a single species, muscles from a particular type of arch (e.g., from the mandibular arch) might originate from different types of cells. For instance, the mandibular 'adductor mandibulae complex' and its derivatives (e.g., masseter) derive from cranial paraxial mesoderm, while the more ventral mandibular muscle intermandibularis and its derivatives (e.g., mylohyoideus) originate from medial splanchnic mesoderm.

As stated by Miyake et al. (1992) and more recently by Diogo et al. (2008b), Edgeworth's (1935) division of the head and neck muscles in external ocular, mandibular, hyoid, branchial, epibranchial, and hypobranchial muscles continues to be widely used by both comparative anatomists and developmental biologists. For instance, Edgeworth's scheme is similar to that proposed in Mallat's anatomical studies (e.g., 1997; the differences between the two schemes are actually mainly nomenclatural ones, for example, the "hyoidean and mandibular superficial constrictors" *sensu* Edgeworth correspond to the "hyoidean and mandibular interbranchial muscles" *sensu* Mallat: see table 2 of Mallat 1997 and Chapter 3 below), as well as to the schemes used in numerous recent developmental and molecular works, such as Holland et al. (1993, 2008), Kuratani et al. (2002, 2004), Trainor et al. (2003), Kuratani (2004, 2005ab, 2008), Kusakabe and Kuratani (2005), Olsson et al. (2005), Kuratani and Ota (2008), and Kuratani and Schilling (2008). However, as expected, some researchers do prefer to catalog the head and neck muscles into groups that do not always correspond to those proposed by Edgeworth (1935). For instance, Noden and Francis-West (2006) refer to three main types of head and neck muscles (Fig. 2.2): the 'extra-ocular' muscles, which

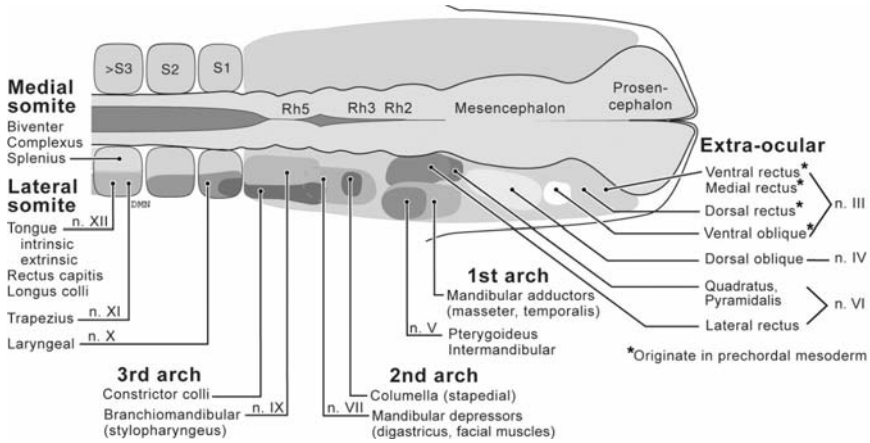


Fig. 2.2 Noden and Francis-West's (2006) scheme showing the locations and main groups of muscle primordia within chick (Reptiles, Aves, Gallus) cephalic paraxial mesoderm, based on their interpretations of the results of recent developmental and molecular studies using techniques such as quail-chick transplants and retroviral injections; names in parentheses indicate some mammalian homologues; the first arch, second arch and third arch muscles shown in the scheme form the 'branchial muscles' sensu Noden and Francis-West 2006, while part of the 'lateral somite' muscles shown in the figure (namely the intrinsic and extrinsic muscles of the tongue, the trapezius, and the laryngeal muscles) form the 'laryngoglossal' musculature sensu these authors (see text) [modified from Noden and Francis-West 2006; the nomenclature of the structures illustrated basically follows that of these authors]. It is remarkable that the use of these new techniques has confirmed a great part of Edgeworth's hypotheses (e.g., Edgeworth 1902, 1911, 1923, 1926abc, 1928, 1935) about the origin and homologies of the vertebrate head and neck muscles, for instance: that the 'adductor mandibulae complex' ('mandibular adductors'), the pterygomandibularis ('pterygoideus') and the intermandibularis derive from the first arch (mandibular muscles sensu Edgeworth 1935); that the masseter and temporalis of mammals correspond to part of the 'adductor mandibulae complex' of non-mammalian groups such as birds; that the levator hyoideus ('columella') and the depressor mandibulae ('mandibular depressors') derive from the second arch (hyoid muscles sensu Edgeworth 1935); that the mammalian stapedius ('stapedial') corresponds to the levator hyoideus of non-mammalian groups such as birds; that part of the 'digastricus' of mammals (i.e., the digastricus posterior) derives from the depressor mandibulae of non-mammalian groups such as birds; that the hyobranchialis ('branchiomandibularis') derives from the third arch, i.e., that it is a branchial muscle sensu Edgeworth 1935; that the intrinsic and extrinsic tongue muscles are derived from somites and they migrate anteriorly during the ontogeny in order to make part of the craniofacial musculature, i.e., that they are hypobranchial muscles sensu Edgeworth (1935). As explained in the text, the main difference between Edgeworth's (1935) and Noden and Francis-West's (2006) schemes is that these latter authors include the laryngeal muscles and the trapezius in their 'laryngoglossal' musculature, which also includes the hypobranchial muscles sensu Edgeworth; that is, they do not consider the trapezius and the laryngeal muscles as part of the 'branchial musculature, as did Edgeworth (see text) [NB: another difference between these schemes is that Noden and Francis-West 2006 consider (probably erroneously in our opinion: see Chapter 4-7) that the 'constrictor colli' (which is part of the interhyoideus sensu the present volume) is not a second arch muscle, i.e., is not a hyoid muscle sensu Edgeworth].

correspond to Edgeworth's extra-ocular muscles, the 'branchial' muscles, which correspond to the mandibular, the hyoid, and most of the branchial muscles sensu Edgeworth, and the 'laryngoglossal' muscles, which include the hypobranchial muscles but also part of the branchial muscles sensu Edgeworth (namely the laryngeal muscles sensu Diogo et al. 2008b). A main advantage of recognizing these three groups is to stress that, in at least vertebrate taxa such as salamanders, chickens and mice, laryngeal muscles such as the dilatator laryngis and constrictor laryngis receive a contribution of somitic myogenic cells (e.g., Noden 1983; Noden et al. 1999; Yamane 2005; Piekarski and Olsson 2007), as do the hypobranchial muscles sensu Edgeworth (see above, and also Chapters 3–7 and 11). That is, the main difference between the 'branchial' and 'laryngoglossal' groups sensu Noden and Francis-West (2006) is that, contrary to the former, the latter receive a contribution of these somitic cells. However, recent developmental studies have shown that some of the 'branchial' muscles sensu Noden and Francis-West (2006), as for instance some 'true' (non-laryngeal) branchial muscles sensu Diogo et al. (2008) such as the protractor pectoralis and the levatores arcuum branchialium of salamanders and the trapezius of chickens and mice, and even some hyoid muscles such as the urodelan interhyoideus, do also receive a contribution of somitic myogenic cells (see, e.g., Piekarski and Olsson 2007; NB: Edgeworth 1935 included the protractor pectoralis and its derivatives—which include the trapezius of amniotes—in the branchial musculature, but he was already aware that these muscles were at least partially originated from somites). Moreover, while it might seem appropriate to designate the laryngeal and hypobranchial muscles of derived vertebrate clades such as birds as 'laryngoglossal' muscles, it would be less suitable to use the name 'laryngoglossal' to designate the hypobranchial muscles of taxa such as lampreys or sharks, because these latter muscles are not functionally associated with a larynx or with a tongue (see Chapter 3). That is why authors who usually work with non-osteichthyan clades often prefer to follow the names that Edgeworth (1935) used to designate the main groups of head and neck muscles, i.e., external ocular, mandibular, hyoid, branchial, hypobranchial, and epibranchial (see, e.g., Holland et al. 1993, Kuratani et al. 2002, 2004, Kuratani 2004, 2005ab, 2008, Kusakabe and Kuratani 2005, Olsson et al. 2005, Kuratani and Ota 2008, Kuratani and Schilling 2008, Holland et al. 2008; see also Chapter 3). As one of the main goals of this volume is precisely to propose a unifying nomenclature for muscles of the Vertebrata as a whole, we will also use these names throughout the book.

In fact, a main advantage and strength of using and expanding the nomenclature proposed by Diogo (2004a, 2007, 2008) and Diogo et al. (2008ab, 2009ab) is that it combines, and thus creates a bridge between, names that are normally used in human anatomy and names that are more

typically used in works dealing with other vertebrate taxa, including bony fishes but also phylogenetically more plesiomorphic vertebrates such as agnathans, elasmobranchs and holocephalans. For instance, coracomandibularis, intermandibularis, and interhyoideus are names that are often used in the literature to designate the muscles of non-osteichthyan vertebrates. As some of these muscles are directly homologous to muscles that are present in osteichthyans and particularly in phylogenetically plesiomorphic sarcopterygian and actinopterygian groups such as cladistians, actinistians and dipnoans, it makes sense to use these names in the descriptions of these latter groups. At the same time, this nomenclature allows us to keep almost all the names that are currently used to designate the muscles of humans (see, e.g., Terminologia Anatomica 1998) and also takes into account major nomenclatural reviews that have been done for other groups of tetrapods (e.g., Nomina Anatomica Avium: Baumel et al. 1979; see Chapter 7). To maintain the stability of the names used in human anatomy is an important aspect of our nomenclature, because these names have been employed for various decades in thousands of publications dealing with human anatomy and medicine and by thousands of teachers, physicians and practitioners. As one of the main goals of using this unifying nomenclature is precisely to avoid the confusion created by the use of different names to designate the same muscles in distinct vertebrate groups, some of the names that we use to designate the muscles of certain taxa do not correspond to the names that are more usually used in the literature for those taxa. So, using the muscles of dipnoans as an example, the adductor mandibulae A3', the adductor mandibulae A2, the adductor mandibulae A2-PVM, the protractor pectoralis, the coracomandibularis and the sternohyoideus sensu this volume correspond respectively to the 'adductor mandibulae anterior', the 'more anterior/lateral part of the adductor mandibulae posterior', the 'more posterior/mesial part of the adductor mandibulae posterior', the 'cucularis', the 'geniothoracicus' and the 'rectus cervicis' sensu Miyake et al. (1992) and Bemis and Lauder (1986) (see Chapters 4 and 5). When we cite works that use a nomenclature that differs from that proposed here, the respective synonymy is given in the tables provided throughout the book. It should be noted that the muscles listed in these tables are those that are usually present in adults of the respective taxa; we do not list all the muscles that occasionally appear as variants in the members of these taxa (e.g., although a few adult modern humans may have a platysma cervicale, in the vast majority of cases this muscle is lacking: see Chapter 5). When we use the terms anterior, posterior, dorsal and ventral, we do so in the sense the terms are used for pronograde tetrapods (e.g., in mammals the eye, and thus the muscle orbicularis oculi, is usually anterior to the ear, and thus to the muscle auricularis superior, and dorsal to the mandible, and thus

to the muscle orbicularis oris: see Chapter 5). Although there is obviously some subjectivity concerning the identification of separate muscles, we followed as strictly as possible Edgeworth's (1935) criteria for analyzing the evidence acquired by others and ourselves, including, for instance, the degree of separation of muscular fibers, the differences regarding the function, orientation and insertions of these fibers, and the innervation of the various myological structures being investigated, among others (see Diogo, 2007, 2008; Diogo et al., 2008ab, 2009ab).

Phylogeny and Homology

The definition of homology and its use in systematics and comparative anatomy has been discussed by several authors (e.g., Patterson 1988; de Pinna 1991; Agnarsson and Coddington 2007). The simplest meaning of homology is equivalence of parts (e.g., De Pinna 1991). In the present work we follow the phylogenetic definition of homology, as proposed by Patterson (1988): homology is equal to synapomorphy. Therefore, following De Pinna (1991), we recognize two main types of muscular homology. 'Primary homology' hypotheses are conjectures or hypotheses about common origin of muscular characters that are established after a careful analysis of criteria such as function, topology and ontogeny (i.e., after the so-called test of similarity). In this volume we follow the same methodology that we have employed and carefully explained in previous works (e.g., Diogo, 2007, 2008, and Diogo et al., 2008ab, 2009ab; Abdala and Diogo in press) and thus take into account all the lines of evidence obtained from our dissections and gleaned from the literature in order to formulate such 'primary homology' hypotheses (e.g., the innervation of the muscles; their relationships with other muscular structures; their relationships with hard tissues; the configuration/orientation of their fibers; their development; their function; the configuration or absence/presence of the muscles in embryos of model organisms that were previously the subject of genetic manipulations, e.g., the knock-down of certain *hox* genes or the induction of *C-met* mutations; etc.).

This is because, as noted Edgeworth (1935), none of these lines of evidence is infallible. For instance, although the innervation of a muscle generally 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 single muscle may have 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 the same muscle may originate 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 “cucullaris”), 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”. As stressed by 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 there are also cases in which “similar secondary developments occur in separate genera or phyla”, i.e., cases of convergence and parallelism (see, e.g., Diogo 2004a, 2005 for a recent discussion of these two concepts; see also Chapters 3–10).

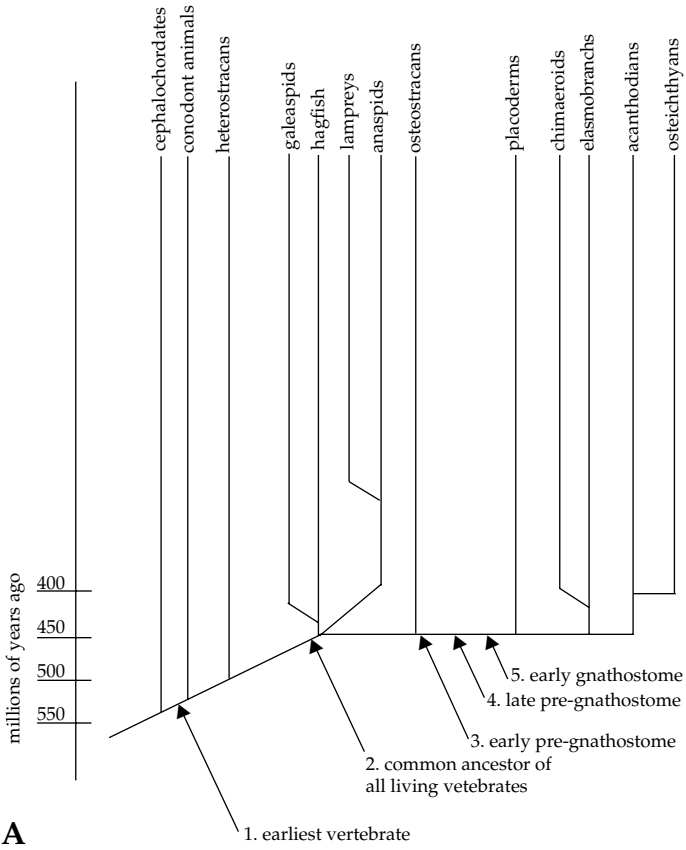
Following De Pinna (1991), the ‘primary homology’ hypotheses have however to pass the second, or “hard”, test of homology, i.e., the test of phylogenetic conjunction and congruence (agreement in supporting the same phylogenetic relationships) before they can actually be considered as solid hypotheses of homology, i.e., as ‘secondary homology’ hypotheses. The important point is, thus, that under the phylogenetic definition of homology it is the test of phylogenetic conjunction and congruence that ultimately determines if a hypothesis can, or cannot, be considered a solid hypothesis of homology. So, if for instance a muscle A of a taxon X and a muscle B of a taxon Y have a similar innervation, function, topology and development but the phylogenetic data available strongly supports the idea that muscles A and B were the result of convergent evolution (i.e., that they were acquired independently in evolution and do not correspond to a structure that was present in the last common ancestor of A and B), then the phylogenetic criterion has preponderance over the other criteria. As explained above, in the specific case of the present work the phylogenetic framework that we use to investigate and discuss the evolution and homologies of the vertebrate muscles of the taxa listed in the tables provided in the book is shown in Fig. 1.1. So, following the methodology explained above, if for example an analysis of the data provided by some lines of evidence (e.g., innervation, function and relationships with other muscular and hard structures) indicates that muscles C and D could be homologous (‘primary homology’ hypothesis), but within all mammals muscle C is only present in monotremes and muscle D in modern humans, then

we would consider that muscles C and D were likely independently acquired in monotremes and modern humans, respectively, i.e., that these muscles are likely not homologous (i.e., the 'primary homology' hypothesis did not pass the "hard" test of homology, that is the test of phylogenetic conjunction and congruence). So, the hypotheses of homology that are shown in the tables provided in the present work are hypotheses that are phylogenetically congruent with the scenario shown in the cladogram of Fig. 1.1, i.e., they are 'secondary homology' hypotheses sensu De Pinna (1991).

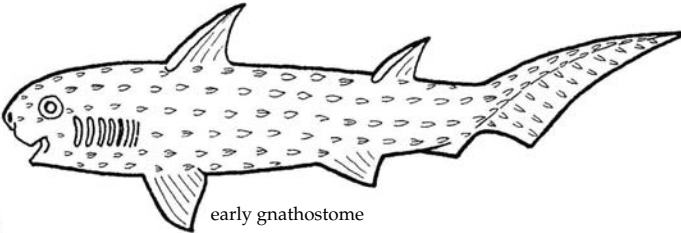
Chapter 3

The Muscles of Non-Osteichthyan Vertebrates

In this chapter, we briefly compare the muscles of living lampreys, living hagfishes, living elasmobranchs, living holocephalans, and basal living osteichthyans and discuss which muscles were probably present in the last common ancestor of the extant vertebrates, in the last common ancestor of the extant gnathostomes, and in the last common ancestor of the extant osteichthyans (Fig. 3.1). This will pave the way for the discussions provided in Chapters 4–10, which are mainly concerned with the muscles of actinopterygian and sarcopterygian osteichthyans. As explained in Chapters 1 and 2, as a base for the data presented in this book, we have literally dissected thousands of specimens of vertebrate taxa as diverse as dipnoans, anurans, caecilians, ‘lizards’, turtles, birds, monotremes, rodents, tree shrews, flying lemurs, primates, polypteriforms, chondrosteans, lepisosteiforms, amii-forms, and teleosts, but we did not dissect chondrichthyans (including holocephalans and elasmobranchs) nor cyclostomes (including hagfish and lampreys). Therefore, unlike in the remaining chapters, the comparisons and discussions provided in Chapter 3 are essentially based on a review of the data available in the literature. However, as in all chapters, we made an effort to take into account as much information as possible, from classic anatomical descriptions such as those provided by Bischoff (e.g., 1840), Owen (e.g. 1841), Gegenbaur (e.g., 1872), Huxley (e.g., 1876), Cole (e.g., 1896), Allis (e.g., 1897, 1917, 1919, 1922, 1923, 1931), Alcock (e.g., 1898), Edgeworth (e.g., 1902, 1911, 1923, 1926abc, 1928, 1935) and Luther (e.g., 1913, 1914, 1938) to more recent reviews by authors Miyake et al. (1992), Mallat (1996, 1997) Anderson (2008), and others, including, importantly, the developmental and molecular data obtained in evo-devo studies undertaken in the past few decades (e.g., Holland et al. 1993; Kuratani et al. 2002, 2004; Graham 2003; Manzanares and Nieto 2003; Santagati and



A



B

Fig. 3.1 (A) Phylogenetic relationships of non-osteichthyan taxa discussed in Chapter 3, according to Mallat (1996). As explained by Mallat (1996), “the long, almost horizontal line at 450 million years ago indicates a rapid radiation, and is not meant to be interpreted as an unresolved branching scheme”. It should be noted that the results of various recent molecular studies indicate that Tunicates (or Urochordates, including ascidians) are actually the closest living relatives of the Vertebrates, and that the Cephalochordates (including amphioxus) are thus the most basal extant Chordates (see, e.g., Garcia-Fernández and Benito-Gutiérrez 2009). **(B)** Hypothetical, thelodont-scaled, early gnathostome, based on Mallat’s (1996) reconstruction (modified from Mallat 1996).

Rijli 2003; Trainor et al. 2003; Cerny et al. 2004; Kuratani 2004, 2005ab, 2008; Takio et al. 2004; Helms et al. 2005; Kusakabe and Kuratani 2005; Northcutt 2005; Olsson et al. 2005; Shigetani et al. 2005; Kuratani and Ota 2008; Kuratani and Schilling 2008; Holland et al. 2008). However, because we did not dissect chondrichthyan and cyclostome specimens, because osteichthyans, cyclostomes and chondrichthyans have been evolving separately for various hundreds of millions of years (see Fig. 3.1) and also because each of these three lineages has given rise to remarkably peculiar and unique phenotypes, the hypotheses of homology proposed in Chapter 3 are clearly not as solid as those proposed in Chapters 4–10.

In the discussions presented in this chapter, we follow the now commonly accepted phylogenetic hypothesis that living hagfishes and lampreys are more closely related to each other than to other living vertebrates, which has been consistently supported by recent molecular cladistic studies (see, e.g., Kuratani et al. 2002; Fig. 3.1). Therefore, following this phylogenetic framework, when a certain muscle A is absent in non-vertebrate animals and is present in both living lampreys and living gnathostomes, then there are two phylogenetically equally parsimonious solutions: that muscle A was present in the LCA of vertebrates and then secondarily lost in hagfishes, or that the muscle was independently acquired in lampreys and in gnathostomes. We should, however, stress that, in such cases, although these solutions are theoretically equally parsimonious in a cladistic context, if there is detailed information about muscle A of lampreys and of gnathostomes, and if the innervation, topology, blood supply, development, and other features of this muscle in these two groups is actually very similar or identical, we would tend to see the secondary loss in hagfishes as more likely than the independent evolution of a muscle innervated by exactly the same nerves, supplied by exactly the same arteries, surrounded by exactly the same anatomical structures, attached to the same elements, and so on, in lampreys and gnathostomes. If future studies would indicate that hagfishes are in reality phylogenetically closer to gnathostomes than to lampreys, these evolutionary interpretations would not really change so much, because theoretically we would have again the same two equally parsimonious solutions (i.e., a secondary loss of muscle A in hagfishes versus an independent acquisition of muscle A in lampreys and gnathostomes). However, if future studies would instead indicate that lampreys and gnathostomes are phylogenetically more closely related to each other than to hagfishes, as was often defended in the past (see, e.g., Kuratani et al. 2002), the interpretations would be different. That is, in this case we would have a single, most parsimonious solution, i.e., that muscle A was not present in the LCA of vertebrates, and that it was only acquired after the evolutionary split between the hagfishes and the remaining vertebrates (thence

its absence in hagfishes and its presence in lampreys + gnathostomes). Before passing to the discussion of the origin, evolution, ontogeny, functional morphology and homologies of the muscles of non-osteichthyan vertebrates, we would like to clarify that a great part of the functional hypotheses mentioned below, as well as of the figures used in this chapter, are based on Mallat's detailed studies of these vertebrates (e.g., Mallat 1996, 1997). In our opinion, this is one of the best ways to pay a special, and totally deserved, tribute to such a remarkable anatomist.

According to Mallat (1996), the biting, mandibular-arch jaws of gnathostomes evolved primarily through changes in ventilation. In his view, the jawless ancestors of all living vertebrates were benthonektonic predators that ate slow-moving invertebrates, grasping their prey in a ring of oral cartilage that was squeezed by an oral sphincter muscle (Figs. 3.2, 3.3). Initially, the activity level and ventilatory rate of these vertebrates were low. The expiratory phase of their ventilatory cycle resulted from peristaltic contraction of the pharyngeal-wall musculature, whereas inspiration resulted from the passive recoil of unjointed internal and external branchial arches. Then, as 'pre-gnathostomes' (Fig. 3.1) became more active foragers, both expiration and inspiration were strengthened and a capacity for active, forceful inspiration evolved. Correspondingly, many new ventilatory muscles evolved and were attached to the internal arches, which became large, jointed, and highly mobile (Fig. 3.5). The most powerful of these ventilatory muscles closed the mouth during forceful expiration to prevent leakage (the adductor mandibulae: see, e.g., Fig. 3.5 and below), and opened the mouth wide during forceful inspiration (the myotomal hypobranchial muscles: see, e.g., Fig. 3.9 and below), and the branchial arch on which these powerful muscles inserted became the largest, forming the mandibular-arch jaws (Figs. 3.5, 3.8). Now, for the first time, gnathostomes could capture evasive prey, by sucking it in through forceful 'inspiration' and clamping it with biting jaws during 'expiration', the way living gnathostome fish often feed.

Both ammocoetes (lamprey larvae; Fig. 3.4) and sharks (Fig. 3.5) propel ventilatory water through the pharynx unidirectionally, in through the mouth and out through the external gill openings. Each ventilatory cycle consists of an expiratory then an inspiratory phase. Expiration is effected by the branchial superficial constrictor and the interbranchial muscles, the former being a circular sheet that squeezes water through the pharynx by peristalsis (Figs. 3.4, 3.5), the latter running in the gill septa and acting to decrease the height of the pharynx and compress the gill pouches (Fig. 3.6). These expiratory muscles are aided in ammocoetes by a pumping velum and in sharks by muscles to the internal branchial arches. During quiet ventilation, after the expiratory muscles relax, inspiration results from a passive recoil of the pharyngeal skeleton: recoil of

the external arches in ammocoetes versus a recoil of the extrabranchial cartilages, internal arches, and various fibroelastic membranes in sharks. During forceful ventilation, in sharks only, inspiration is aided by the hypobranchial ventilatory muscles, which actively enlarge the pharynx. According to Mallat, lamprey and shark ventilation thus share two main features: (1) expiration through the peristaltic action of branchial superficial constrictor and interbranchial muscles and (2) inspiration through passive recoil of the branchial arches. Consequently, the LCA of verte-

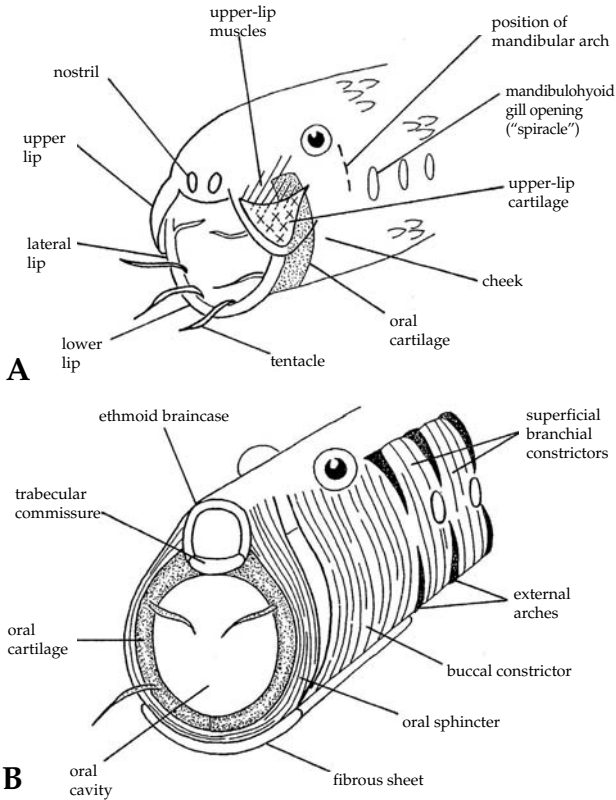


Fig. 3.2 Lips and mouth of the common ancestor of all living vertebrates, according to Mallat (1996). (A) External view, but also showing some cartilages and the muscles in the upper lip. (B) View with the skin and the snout removed, emphasizing the muscles around the oral cavity and pharynx. As stressed in the text, further studies are needed to clarify if the mandibular musculature was already differentiated into 'labial muscles' such as the oral sphincter, buccal constrictor, and the upper-lip muscles sensu Mallat (1996), as proposed by this author, or if the so-called 'labial muscles' of vertebrate groups such as elasmobranchs, holocephalans, cyclostomes, and osteichthyans are instead the result of an independent differentiation of the mandibular mesoderm in these taxa (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

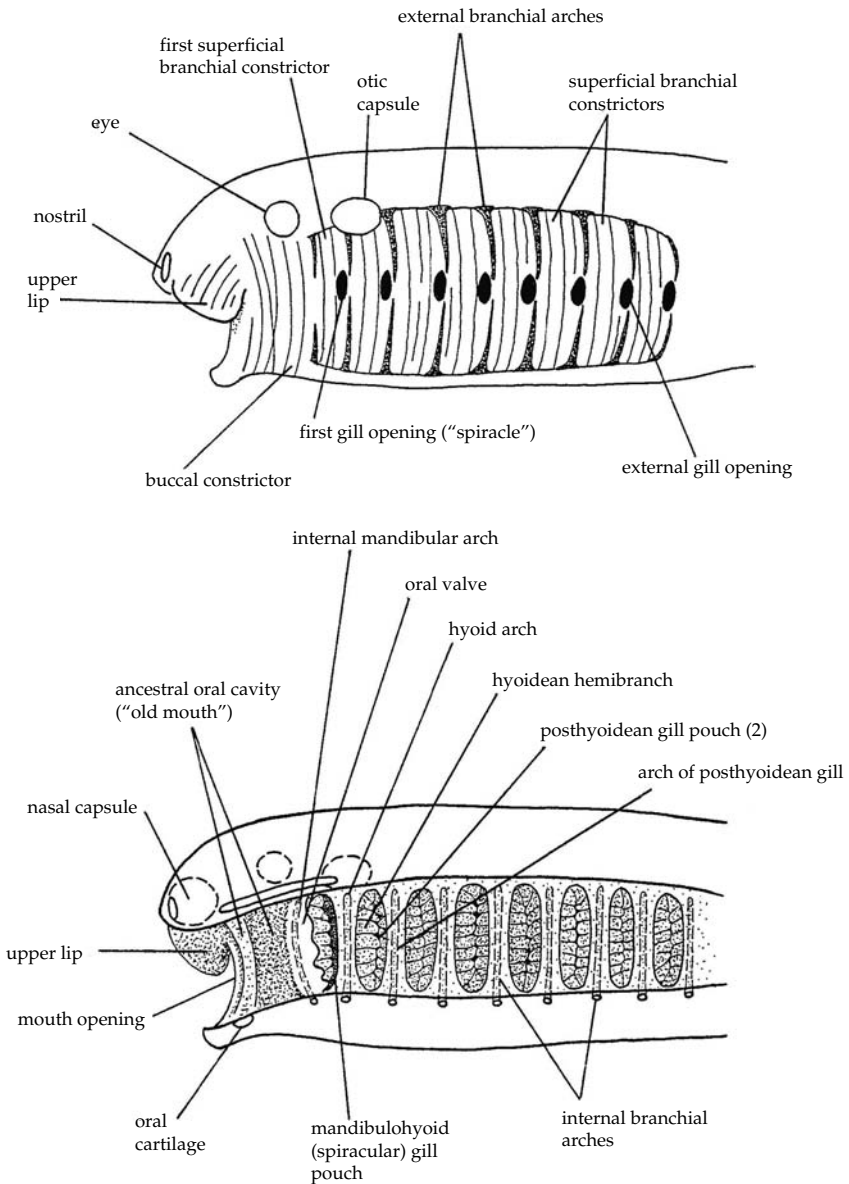


Fig. 3.3 Head and pharynx of the reconstructed common ancestor of all living vertebrates, according to Mallat (1996). External and mid-sagittal views; numbers such as '(1)' and '(2)' are used to identify the ancestral/embryonic gill pouches. According to Mallat (1996) this ancestor may have had more gill pouches than the eight illustrated in this figure (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

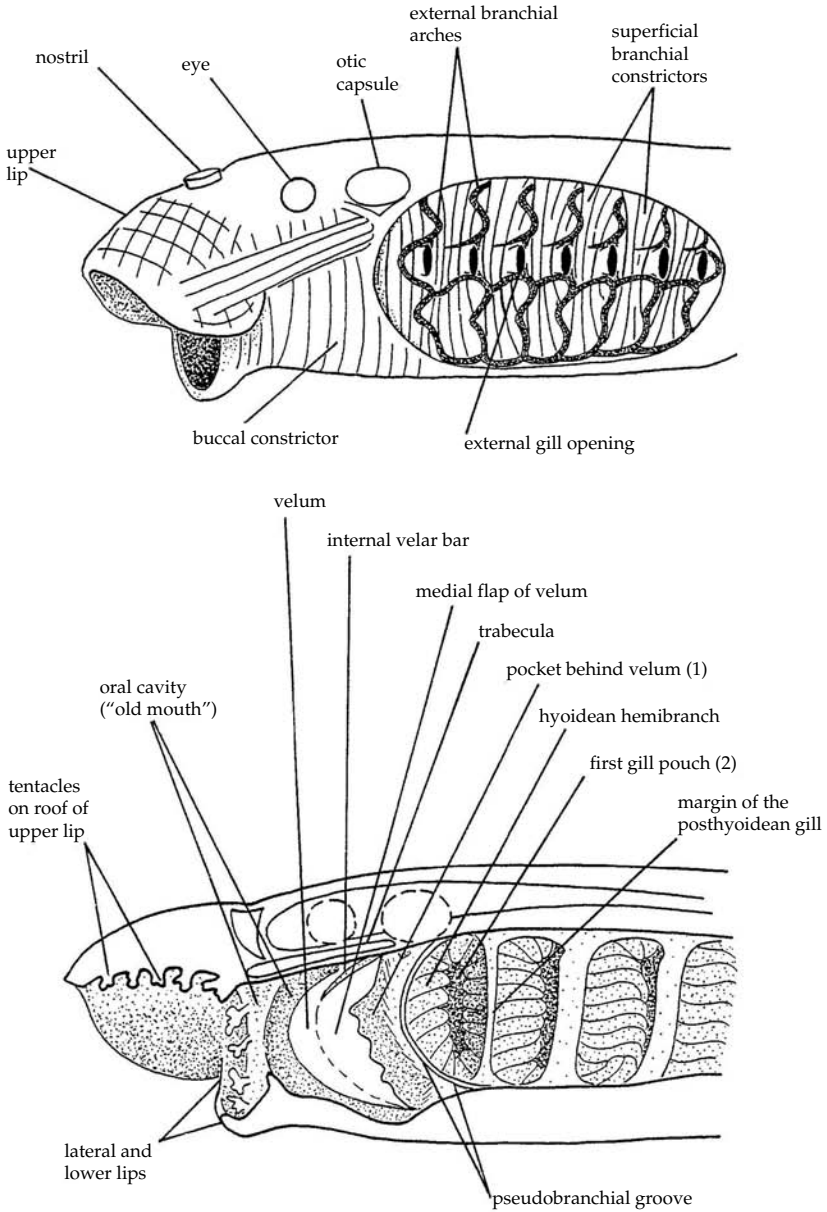


Fig. 3.4 Head and pharynx of ammocoete lampreys (Cyclostomata), according to Mallat (1996); numbers such as '1' and '2' are used to identify the ancestral/embryonic gill pouches; external and mid-sagittal views. Top: *Lampetra planeri*. Bottom: *Ichthyomyzon fossor* (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

SHARK

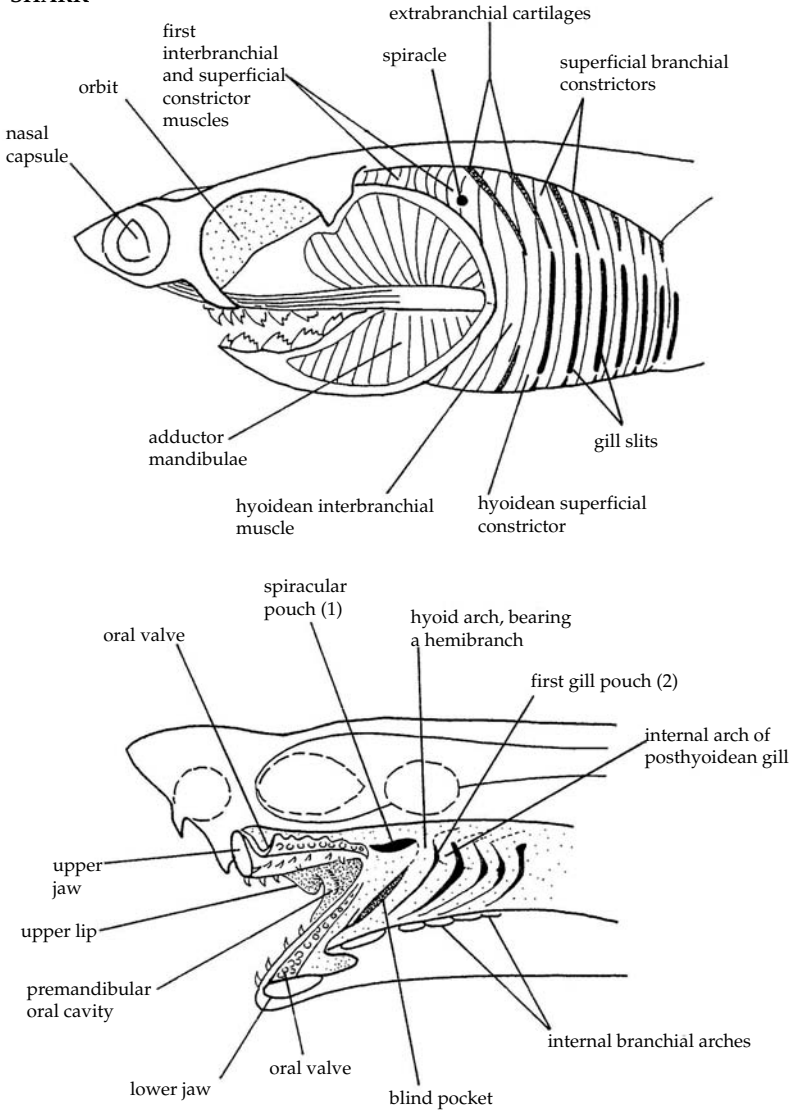


Fig. 3.5 Head and pharynx of sharks (Elasmobranchii), according to Mallat (1996); numbers such as '(1)' and '(2)' are used to identify the ancestral/embryonic gill pouches; external and mid-sagittal views. Top: *Heptanchus maculatus*; this species of shark is shown because, according to Mallat (1996), it has the primitive features of a short snout and a simple type of adductor mandibulae muscle. Bottom: *Triakis semifasciatus* (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

brates must have possessed the superficial constrictor and interbranchial muscles (Figs. 3.2, 3.3).

As also noted by Mallat (1996), the velum of lampreys is a pair of cupped, muscular paddles that push water posteriorly into the pharynx during the expiratory phase of each ventilatory cycle. It is a powerful, piston-like pump that can work against back pressure and force ventilatory water through the sand in which ammocoetes live. Projecting posteriorly from each velar paddle is a 'medial flap', which is supported by the internal velar bar (Fig. 3.4). When the velum starts to contract, its right and left medial flaps come together to form a seal that prevents reflux of water from the pharynx through the mouth. In the embryonic lamprey, the velum develops at the border between the mouth and pharynx, from the buccopharyngeal membrane. Its muscles belong to the mandibular branchial segment, being innervated by the mandibular branch (V3) of the trigeminal nerve. The lateral mouth plates of ammocoetes bear a

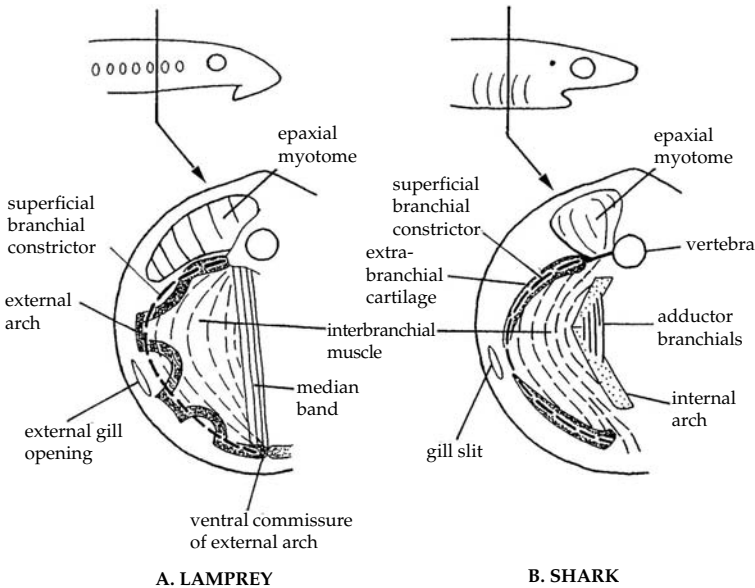


Fig. 3.6 Basic similarities between the gill muscles of lampreys (*Cyclostomata*) and sharks (*Elasmobranchii*), according to Mallat (1996): in both animals, the superficial branchial constrictors (broken lines) wrap around the pharynx externally and an interbranchial muscle occupies each gill septum; these two muscles are continuous, separated only by the external branchial arch; a straight band of muscle in the medial part of the lamprey gill ('median band') may correspond to the adductor branchialis of sharks (the adductor branchialis of the first arch corresponding to the adductor mandibulae of Fig. 3.5) (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

superficial resemblance to the branchial arches behind them and have been called a 'premandibular branchial arch' by some authors. However, as stressed by Olsson et al. (2005), "there is no clear fossil evidence that a complete gill arch skeleton ever existed anteriorly to the first gill arch", and most researchers now agree that no such complete 'premandibular' arch was present in the LCA of vertebrates or of gnathostomes. Another idea that was often accepted in the past and that has been contradicted by recent findings is that neural crest cells from the first mandibular arch form a dorsal, 'maxillary' and a ventral, 'mandibular' condensation, which later give rise to the upper jaw cartilage (palatoquadrate) and the lower jaw cartilage (Meckel's cartilage), respectively. In fact, recent developmental studies using vital-dye labeling in both the Mexican axolotl and the chicken embryo have shown that cells which form the ventral or 'mandibular' condensation give rise to both the upper and lower jaw cartilages (e.g. Cerny et al. 2004; Olsson et al. 2005). The dorsal or 'maxillary' condensation contributes to the trabecular cartilage, but not to the jaw joints as previously assumed. Interestingly, Cerny et al.'s (2004) developmental study provides evidence to support the idea that the jaw cartilages of gnathostomes are homologous to the lower lip and velum of lampreys.

It is, however, important to explain that the word 'mandibular' can be used in different contexts and different development stages, including the following: (1) the 'mandibular condensation' is an osteological term that refers to an early stage of development, and that thus seems to be inadequate, as it gives rise to both the upper and lower jaw cartilages, contrary to what was thought in the past; (2) the 'mandible', which is an osteological term that refers to both early and later stages of development, and essentially corresponds to the term 'lower jaw' (note that the 'mandible'/'lower jaw' does not necessarily correspond to 'lower jaw cartilages' and/or to the ossifications of these cartilages, because apart from these cartilages and their ossifications, the 'mandible'/'lower jaw' of adults may include, and often does, other structures, such as dermal bones); (3) the 'mandibular muscular plate' sensu Edgeworth (1935), which, as explained above, is a myological term and refers to an early stage of development (see Fig. 2.1); (4) the 'mandibular muscles' sensu Edgeworth (1935; and sensu this volume), which are myological structures that are found in both early and later stages of development, and that derive from the 'mandibular muscular plate' (see, e.g., Table 3.1); (5) the 'mandibular arch', which is an osteological term, refers to both early and latter stages, and corresponds to the 'first branchial arch', including both the 'palatoquadrate' and the 'lower jaw' (see, e.g., Fig. 3.8). For the reasons explained just above, in this work we avoid the use of the term 'mandibular condensation', but we continue to use the terms 'mandible', 'mandibular muscular plate',

Table 3.1 Mandibular muscles of adults of representative non-osteichthyan extant vertebrate 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, in round brackets; additional comments are given in front of that muscle/bundle, in round brackets (for more details, see text).

<p>Agnatha: <i>Lampetra japonica</i> (Japanese lamprey)</p>	<p>Probable plesiomorphic gnathostome condition</p>	<p>Elasmobranchii: <i>Squalus acanthias</i> (Spiny dogfish)</p>	<p>Holocephali: <i>Hydrolagus collieti</i> (Spotted ratfish)</p>
<p>— [a distinct, independent intermandibularis such as that found in chondrichthyans is seemingly not present in lampreys, but see velothyroideus below and also text]</p>	<p>Intermandibularis</p>	<p>Intermandibularis [probably corresponds to the intermandibularis (= csv1b'' + csv1a''b'') and possibly to the mandibularis [= csv1c] sensu Lightoller 1939, the latter structure thus corresponding to the intermandibularis posterior of some authors and being at least in some cases innervated by CN7, according to Lightoller 1939; however, it is quite possible that at least part of the intermandibularis sensu Lightoller 1939 corresponds in fact to part of the interhyoideus of osteichthyans, as it is innervated by CN7, and also because, in his table III, Lightoller states that this muscle gives rise to some of the facial muscles of mammals; Miyake et al. 1992 and Anderson 2008 describe a single intermandibularis in elasmobranchs, but they state that at least some elasmobranchs, e.g., electric rays, may have an</p>	<p>Intermandibularis [Anderson 2008 describes only one intermandibularis in <i>Hydrolagus</i>, but he explains that Kesteven 1942–1945 described this muscle (his ‘protractor labii inferioris’) as having two parts, and Edgeworth 1935 also states that some holocephalans have both an ‘intermandibularis anterior’ and an ‘intermandibularis posterior’; Edgeworth 1935 interprets the intermandibularis of holocephalans as the anterior-most remnant of the intermandibularis muscle-sheet in elasmobranchs]</p>

<p>— [a distinct, independent adductor mandibulae A2 such as that found in chondrichthyans is seemingly not present in lampreys: see text]</p>	<p>Ad. Mand. A2</p>	<p>‘intermandibularis superficialis’ and an ‘intermandibularis profundus’, as described by Edgeworth 1935 and other authors (see, e.g., his fig. 83)]</p>	<p>Ad. mand. A2 (levator mandibulae anterior and posterior sensu Miyake et al. 1992; adductor mandibulae anterior and posterior sensu Anderson 2008)</p>
<p>‘Labial muscles’ [see text]</p> <p>Velohydroideus [does the velohydroideus sensu Holland et al. 1993 really correspond to the levator arcus palatini of the LCA of gnathostomes? See text]</p>	<p>‘Labial muscles’ Levator arcus palatini</p>	<p>Ad. mand. A2 (adductor mandibulae sensu Adams 1919 and Anderson 2008; pars inscriptionalis, musculus quadrato-mandibularis or cs1b’ sensu Lightoller 1939; part of adductor mandibulae complex sensu Miyake et al. 1992)</p>	<p>‘Labial muscles’ [see text]</p> <p>— [see text]</p>
<p>Velohydroideus and velocranialis [if the velohydroideus is effectively derived from the constrictor dorsalis, are the other two muscles of the velum, i.e., the velohydroideus and velocranialis, also derived from the constrictor dorsalis, or do they possibly correspond to the intermandibularis and/or the adductor mandibulae of other vertebrates? See text]</p>	<p>—</p>	<p>—</p>	<p>—</p>

Table 3.1 contd...

Table 3.1 cont'd...

<p>Agnatha: <i>Lampetra japonica</i> (Japanese lamprey)</p> <p>—</p>	<p>Probable plesiomorphic gnathostome condition</p> <p>— [really absent in the LCA of gnathostomes?]</p>	<p>Elasmobranchii: <i>Squalus acanthias</i> (Spiny dogfish)</p> <p>Spiracularis, depressor palpebrae superioris, levator palpebrae nictitantis and retractor palpebrae superioris [according to Miyake et al. 1992, all these muscles may be found in sharks, being derived ontogenetically from the constrictor dorsalis anlage; the spiracularis sensu the present work corresponds to the 'constrictor superficialis dorsalis' sensu Adams 1919, and probably corresponds to the 'pars craniomaxillaris' (csd 1b'') sensu Lightoller 1939]</p>	<p>Holocephali: <i>Hydrolagus colliei</i> (Spotted ratfish)</p> <p>—</p>
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'mandibular muscles' and 'mandibular arch' as they are often used in the literature.

As described by Mallat (1996), in living Chondrichthyes, the robust internal arches are divided into five segments, connected by movable joints: pharyngo-, epi-, cerato-, hypo-, and basibranchial segments (Fig. 3.8). The segmentation and jointing allow muscles to attach and pull from many different directions. Unlike the extrabranchial cartilages (external branchial arches *sensu* Mallat 1996), which are embedded firmly in the pharyngeal wall, the internal arches have an extraordinary range of movement within the gnathostome pharynx. During ventilation in sharks, they are proposed to move as shown in Fig. 3.9. During expiration, to decrease pharyngeal volume and expel water, the arch segments are flexed by adductor branchialis and lateral interarcual muscles, and successive arches are pulled closer by dorsal and lateral interarcual muscles (Fig. 3.9A). At the same time, the lateral interarcuals swing the arches posteromedially (Fig. 3.9B), further decreasing pharyngeal volume. During quiet inspiration, the bent arches recoil passively like springs to help enlarge the pharynx and draw in water. On the other hand, active forceful inspiration is effected by the coracobranchial muscles, which rapidly swing the arches anterolaterally and abduct them (Fig. 3.9C). At this time, the mouth is opened wide by the coracomandibular and coracohyoid muscles (along with their common base, the coracoarcualis) (see Figs. 3.8–3.11).

Mallat (1996) stated that "the adductor branchialis, lateral interarcual, and coracobranchial muscles develop from 'branchial muscle plates' in the gill septa, indicating they evolved from the interbranchial muscles". In his opinion, the dorsal interarcuals, coracomandibular, and coracohyoid muscles develop from the anterior myotomes, and thus evolved from epibranchial and hypobranchial myotomes, which overlie much of the pharyngeal musculature in extant cyclostomes. It should, however, be noted that Johanson (2003) and other authors argue that the coracobranchiales of gnathostomes do not correspond to part of the interbranchials of lampreys, because, in their view, the interbranchiales are more likely to be homologous to gnathostome muscles involved in branchial arch constriction rather than expansion (see below). Also, Luther (1938), Lightoller (1939) and others defend the position that the adductor mandibulae of gnathostomes probably derived from a lateral part of the interbranchialis of the first arch (and not from a medial part of this muscle, as defended by Mallat, 1996), or even from the branchial superficial constrictor of this arch, because in gnathostomes the adductor mandibulae lies on the lateral, and not on the medial, surface of its branchial arch.

We agree with Edgeworth (1935), Lightoller (1939) and Lauder (1980ab) in that the 'labial' muscles *sensu* Anderson (2008) are, at least in some cases, likely related to the 'adductor mandibulae complex'. Mallat (1996)

calls these muscles 'oral muscles', but he recognized that at least some of them (e.g., his 'buccal constrictor') develop from the 'mandibular branchiomere' in lampreys. The 'labial muscles' sensu Anderson (2008) also seem to develop from the mandibular plate in elasmobranchs and osteichthyans (e.g., Edgeworth, 1935). Therefore, whether these muscles are called 'labial' (e.g., Anderson 2008), 'oral' (e.g., Mallat 1996) or 'preorbital/suborbital mandible adductors' (e.g., Edgeworth 1935; Lauder 1980a), the fact is that they do seem to develop from the mandibular mesoderm, as does the 'adductor mandibulae complex'. This idea was supported by the developmental work of Kuratani et al. (2004), who concluded that "experiments labeling the mandibular mesoderm of the early lamprey embryo, before the cheek process has differentiated into the upper lip anlage or the premandibular domain, indicate that a part of the mandibular mesoderm secondarily grows anteriorly and laterally and migrates into the upper lip domain". According to Mallat (1996), the muscles that are derived from this mandibular mesoderm in lampreys, and particularly their 'labial' portion (sensu Anderson 2008), was possibly innervated by both V2 and V3 in the LCA of vertebrates (within living vertebrates, innervation by V2 and V3 is said to occur in lampreys, holocephalans, and possibly hagfishes: see Fig. 3.12), the V2 innervation being secondarily lost in elasmobranchs and osteichthyans. However, it should be noted that according to Kuratani et al. (2004) the nerve that is often called V2 in cyclostomes such as lampreys possibly does not correspond to the V2 of gnathostomes.

Mallat (1996) discussed the homologies between the various 'labial' muscles (sensu Anderson 2008) present in Cephalochordates (Fig. 3.13), in hagfishes (Fig. 3.7), in lampreys (Fig. 3.14), in elasmobranchs (Fig. 3.10) and in holocephalans (Fig. 3.15), and summarized all his hypotheses of homology in a table (see Fig. 3.12). A brief description of these muscles, which is mainly based on Mallat (1996), is given below.

In ammocoetes, the oro-labial musculature is complex. In the upper lip, the largest and most important muscle is the buccalis anterior (Fig. 3.14A), which runs from the superolateral walls of the oral cavity, the superoanterior surface of the lateral mouth plate, the trabecular commissure just below the nasal capsule, and the nasal capsule itself. It forms most of the mass of the upper lip and inserts on to the entire undersurface of the rostro-dorsal plate and on to the lip mucosa. Functionally, the buccalis anterior retracts and constricts the upper lip. Other muscles surround the oral cavity and mouth opening of ammocoetes (Fig. 3.14B): buccal constrictor, elevator labialis ventralis, sublabialis, and basalis tentacularis (sensu Mallat 1996). According to Mallat, the buccal constrictor encircles the oral cavity from the external hyoid bar posteriorly to the front of the eye. It forms the bulk of the 'cheek'. Superiorly, it attaches to the trabeculae and the fibrous braincase. The elevator labialis ventralis surrounds the mouth opening;

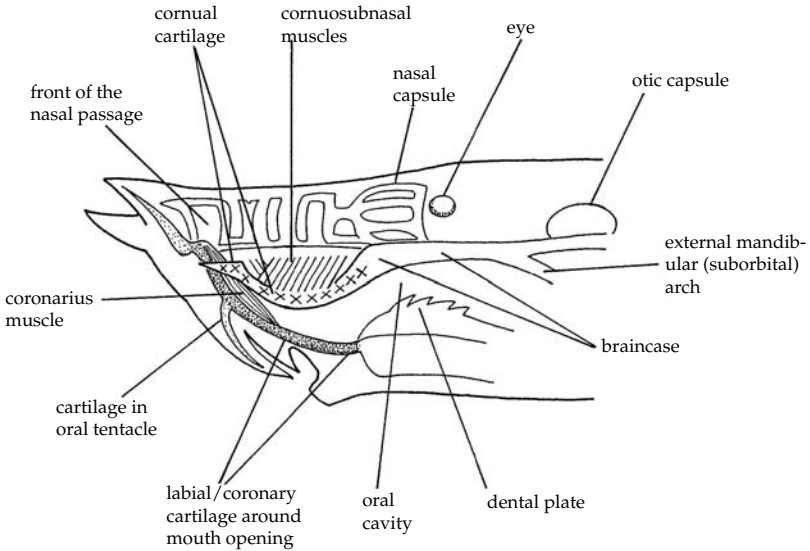


Fig. 3.7 Anterior part of the hagfish *Myxine glutinosa* (Cyclostomata). As explained in the text, according to Mallat (1996) the labeled cartilages and muscles may be homologous to structures in ammocoetes and gnathostomes (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

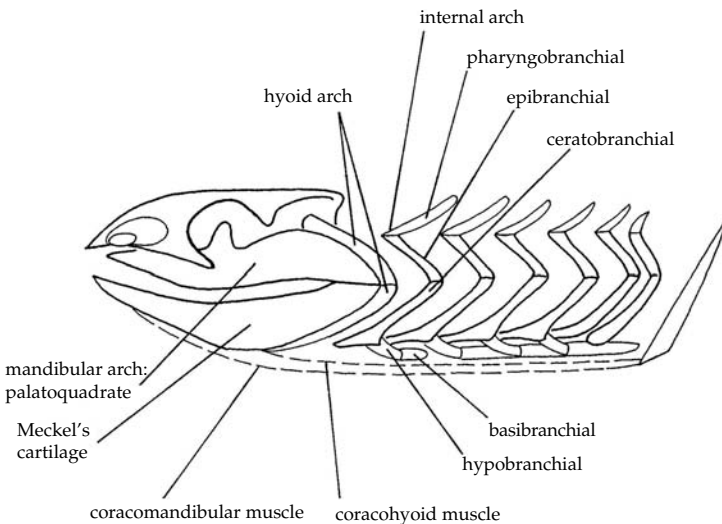


Fig. 3.8 Head and pharyngeal skeleton of the frilled shark *Chlamydoselachus anguineus* (Elasmobranchii); the five segments of an 'internal arch' (sensu Mallat 1996) are labeled; the extrabranchial cartilages are not shown; the coracomandibular and corachyoid muscles are shown ventrally as broken lines (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).

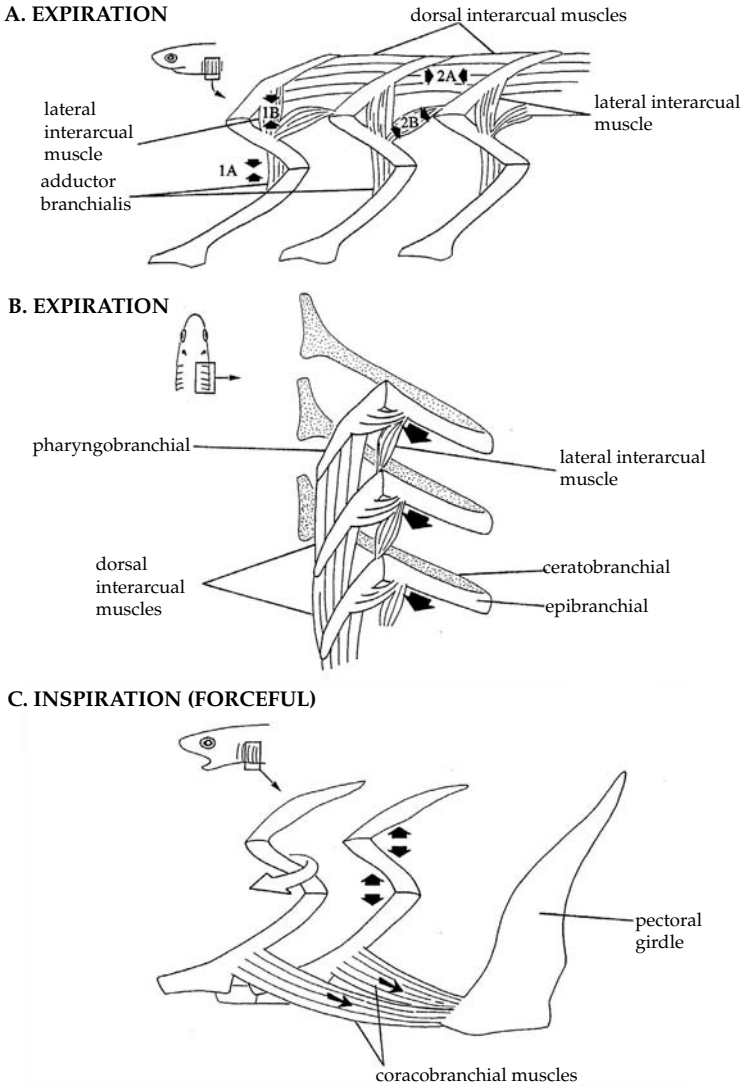


Fig. 3.9 Probable movements of the internal arches during the ventilatory cycle of sharks (Elasmobranchii), according to Mallat (1996). **(A)** expiratory movements, lateral view: the segments are flexed and pulled dorsally by adductor branchialis ('1A') and lateral interarcual muscles ('1B'), while successive arches are pulled closer together by the dorsal and lateral interarcuals ('2A' and '2B') (note: the dorsal interarcuales of sharks are considered to be epibranchial muscles *sensu* Edgeworth 1935). **(B)** expiratory movements, dorsal view: the lateral interarcual muscles swing the arches posteromedially (arrows). **(C)** forceful inspiration: the coracobranchial muscles swing the arches anterolaterally (large, curved arrow) and abduct the arch segments (dark, diverging arrows) (modified from Mallat 1996; the nomenclature of the structures illustrated basically follows that of this author).