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Comparative Anatomy, Homologies and Evolution of the Pectoral Muscles of Bony Fish and Tetrapods: A New Insight

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ABSTRACT The Osteichthyes, including bony fishes and tetrapods, is a highly speciose group of vertebrates, comprising more than 42,000 living species. The anatomy of osteichthyans has been the subject of numerous comparative studies, but most of these studies concern osteological structures; much less attention has been paid to muscles. The most detailed comparative analyses of osteichthyan pectoral muscles that were actually based on a direct observation of representatives of various major actinopterygian and sarcopterygian groups were provided several decades ago by authors such as Howell and Romer. Despite the quality of their work, these authors did not have access to much information that is now available. In the present work, an updated discussion on the homologies and evolution of the osteichthyan pectoral muscles is provided, based on the authors' own analyses and on a survey of the literature, both old and recent. It is stressed that much caution should be taken when the results obtained in molecular and developmental studies concerning the pectoral muscles of model actinopterygians such as the teleostean zebrafish are discussed and compared with the results obtained in studies concerning model sarcopterygians from clades such as the Amphibia and/or the Amniota. This is because, as shown here, as a result of the different evolutionary routes followed within the actinopterygian and the sarcopterygian clades none of the individual muscles found, for example, in derived actinopterygians such as teleosts is found in derived sarcopterygians such as tetrapods. It is hoped that the information provided in the present work may help in paving the way for future analyses of the pectoral muscles in taxa from different osteichthyan groups and for a proper comparison between these muscles in those taxa. J. Morphol. 268:504–517, 2007. © 2007 Wiley-Liss, Inc.

KEY WORDS: Actinopterygii; comparative anatomy; evolution; morphology; mycology; Osteichthyes; pectoral muscles; Sarcopterygii

The Osteichthyes, including bony fishes and tetrapods, is a highly speciose group of gnathostomes, comprising more than 42,000 living species. Two main osteichthyan groups are usually recognized (Fig. 1): the Sarcopterygii (lobefins and tetrapods), with an estimate of more than 24,000 living species, and the Actinopterygii (rayfins), including more than 28,000 extant species (e.g., Nelson, 2006). The extraordinary taxonomic diversity of osteichthyans is accompanied by a remarkable variety of morphological features and adaptations to very different habitats, from miniature freshwater fishes to enormous terrestrial tetrapods.

The anatomy of osteichthyans has been the subject of numerous comparative studies. However, as stressed by Diogo (2004a,b, in press), most of the works dealing with osteichthyan comparative anatomy concern skeletal structures, with much less attention being paid to muscles. There are, of course, several works providing information on the musculature of osteichthyans, but the great majority of those works are focused on a specific taxon from one of the two main osteichthyan groups, the Actinopterygii and the Sarcopterygii, and not on taxa of both these groups (e.g., Allis, 1897: *Amia*; Danforth, 1913: *Polyodon*; Allis, 1922: *Polypterus*; Millot and Anthony, 1958: *Latimeria*; Jessen, 1972: Actinopterygii; Winterbottom, 1974: Teleostei; Brosseau, 1978a,b: Ostariophysi; Carroll and Holmes, 1980: Urodela; Bemis, 1986: Dipnoi; Abdala and Moro, 2003: Squamata; etc.). In fact, as explained by Diogo (in press), the most recent detailed comparative analyses of osteichthyan muscles that were actually based on a direct observation of actinopterygian and sarcopterygian taxa as varied as, e.g., Teleostei, Halecomorphi, Ginglymodi, Chondrostei, Cladistia, Dipnoi, Amphibia and Amniotes (see Fig. 1), and not mainly on a recompilation from the literature, were provided several decades ago in works of authors such as Edgeworth (1902, 1911, 1923, 1926a–c, 1928, 1935), Luther (1913, 1914), Romer (1922, 1924, 1944), Howell (1933a,b, 1935, 1936a,b), and Kesteven (1942–1945). Most of these works were essentially

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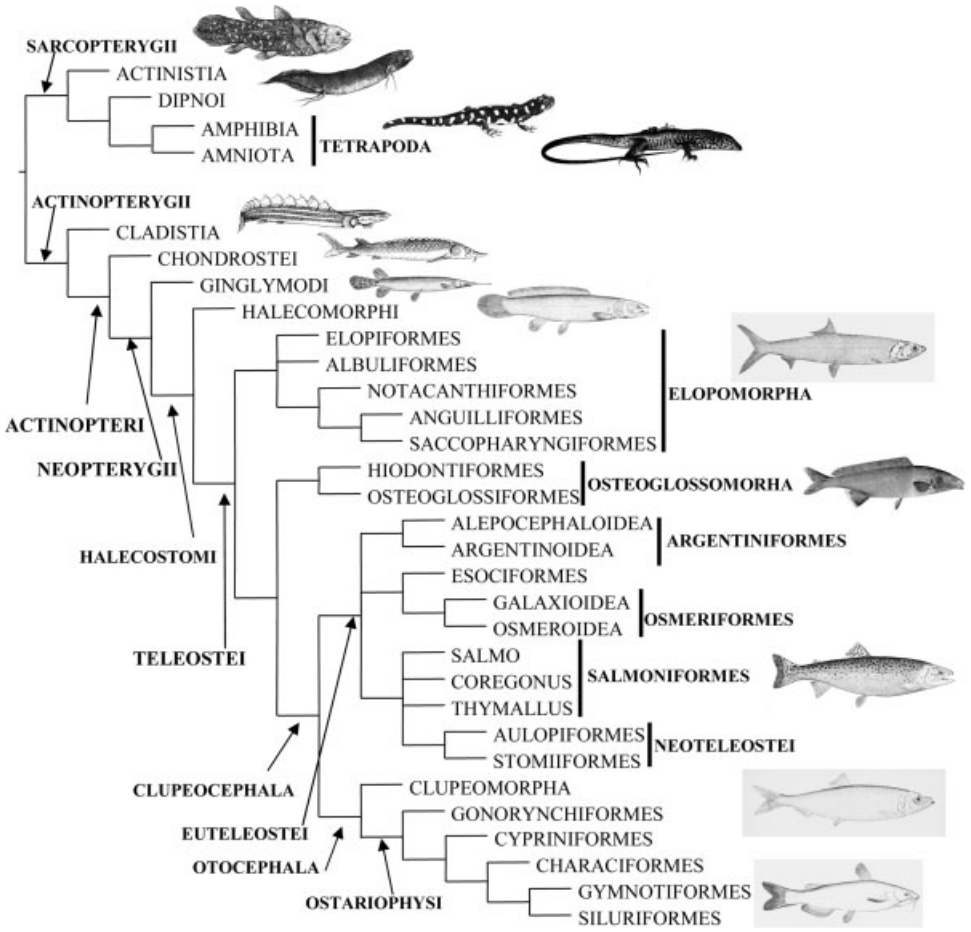

Fig. 1. Phylogenetic relationships among the major extant osteichthyan groups, according to the results of the cladistic analysis of Diogo (in press) (for more details, see text).

focused on cranial muscles, the exception being the studies of authors such as Howell (1933a,b, 1935, 1936a,b) and Romer (1922, 1924, 1944), which were mainly dedicated to pectoral muscles.

Due to their quality, these latter studies continue to be fundamental works on the comparative anatomy of osteichthyan pectoral muscles. However, as noted by Diogo (in press), one should keep in mind that they were written more than 60 years ago. Thus, despite the quality of these studies, their authors could not have access to information that is now available. For example, they had no access to such information on the muscles of the coelacanth *Latimeria chalumnae*, since this taxon had not yet been discovered. Also, they could not access the data provided in the last few decades by developmental studies supporting, for instance, the essential role of neural crest cells in the development and patterning of vertebrate cranial (e.g., Le Lièvre and Le Douarin, 1975; Noden, 1983, 1984, 1986; Couly et al., 1992; Köntges and Lumsden, 1996; Schilling and Kimmel, 1997; Olsson et al., 2001; Ericsson and Olsson, 2004; Ericsson et al., 2004) and seemingly also pectoral (e.g., McGonnell, 2001) muscles. It is also important to stress that some of the hypotheses advanced by authors such as Howell and Romer concerning the homologies and evolution of the pectoral muscles they examined were based on phylogenetic scenarios that have since been contradicted by numerous studies. For instance, according to Romer (1944) the cladistian *Polypterus* is more closely related to tetrapods than are the extant dipnoans, a view to which very few authors would adhere nowadays (see, e.g., Fig. 1).

The main aim of the present work, thus, is to provide an updated discussion on the homologies and evolution of the osteichthyan pectoral muscles (sensu Diogo, in press). This discussion is based both on our own analyses of these muscles in key representative taxa of various major osteichthyan groups (see later) and on a survey of the literature, both recent and old. It is hoped that the present work may contribute to a better understanding of the pectoral muscles of osteichthyans, as well as pave the way for future works concerning the comparative anatomy, functional morphology, ontogeny, evolution, and phylogeny of these gnathostomes and of vertebrates in general.

MATERIALS AND METHODS

As a phylogenetic framework for the discussion provided in the present paper, we basically follow the scenario shown in the tree of Figure 1, which is based on the results of the recent cladistic analysis of Diogo (in press). This cladistic analysis includes a total of 356 phylogenetic characters, concerning both osteological and myological features, and 80 terminal taxa, both extant and fossil, being thus the most extensive morphological cladistic analysis published so far on osteichthyan higher-level phylogeny.

As mentioned earlier, the discussions provided here are based on a survey of the literature and also on our own observations of representatives of various major osteichthyan groups. It is important to stress that we have opted to pay special attention to taxa belonging to the major basal groups of the sarcopterygian and actinopterygian osteichthyan lineages, and not of derived extant groups such as the actinopterygian teleosts and the sarcopterygian tetrapods. That is, we have personally observed, for the present work, some representatives of these two groups (see later) in order to investigate and discuss the homologies between their muscles and the muscles of members of other major osteichthyan groups (see Tables 1 and 2). But we did not observe representatives of all the numerous extant teleostean and tetrapod subgroups. This is because the main aim of the present work is to discuss the homologies and evolution of the pectoral muscles within the major extant osteichthyan groups (i.e., Actinistia, Dipnoi, Amphibia, Amniota, Cladistia, Chondrostei, Ginglymodi, Halecomorphi, and Teleostei; see Tables 1 and 2), and not within all these numerous teleostean and tetrapod subgroups.

Of the nine major extant osteichthyan groups referred to in the paragraph earlier, the only group for which we could not obtain and thus personally examine extant representative specimens is the Actinistia. As is well known, the single living actinistian genus is *Latimeria*, and it is rather difficult to obtain specimens of this genus for muscular dissection. Fortunately, both the osteology and myology of *Latimeria* have been extensively described in the impressive and beautifully illustrated work of Millot and Anthony (1958). Concerning the provenience of the specimens that were examined for the present work, these are from the Laboratory of Functional and Evolutionary Morphology of the University of Liège (LFEM), the Museo Nacional de Ciencias Naturales de Madrid (MNCN), the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia (ANSP), the Chinese Academy of Sciences at Wuhan (CASW), the California Academy of Sciences (CAS), the Illinois Natural History Survey (INHS), the Centro Nacional Patagónico de Argentina (CONICET), the Macquarie University of Australia (MU), the Musée Royal de l'Afrique Centrale (MRAC), the Colección Mamíferos Lillo of the Universidad Nacional de Tucumán (CML), the Fundación Miguel Lillo de Argentina (FML), the San Diego State University (SDSU), and the National Museum of Natural History (USNM). Dissections and anatomical drawings of these specimens were made using a Wild M5 dissecting microscope equipped with a camera lucida. The nomenclature of the osteological and myological structures illustrated in these drawings basically follows that of Diogo (in press). It should be noted that, as explained by Diogo (in press), in those cases in which the same muscle is often given in the literature a name X by researchers working with, e.g., plesiomorphic bony fishes and a name Y by researchers working with, e.g., tetrapods, he has opted to use the name X. He considered that this option is methodologically more appropriate than to continue to designate that muscle by both the names Y and X, as this latter procedure is precisely one of the main reasons for the historical confusion concerning the homologies and evolution of osteichthyan muscles. Also, he considered that this option makes more evolutionary sense than to opt to use the name Y, because tetrapods originated from bony fishes, not the reverse. Thus, in his opinion it makes no evolutionary sense to consider, for instance, the muscles of amniotes (and in some cases even of humans) as the "base to follow" and then derive the names of the muscles of other osteichthyans from the amniote names. Therefore, as a general rule, when two different names are frequently used to designate the same muscle by researchers

TABLE 1. Pectoral muscles of adults of representative actinopterygian taxa

Plesiomorphic osteichthyan condition	Cladistia: *Polypterus bichir*	Chondrostei: *Psephurus gladius*	Ginglymodi: *Lepisosteus osseus*	Halecomorphii: *Amia calva*	Teleostei - basal: *Elops saurus*	Teleostei - clupeocephalan: *Danio rerio*
Abductor (of pectoral fin)	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**
Adductor (of pectoral fin)	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**
—	—	—	**Arrector dorsalis**	**Arrector dorsalis**	**Arrector dorsalis**	**Arrector dorsalis**
—	—	—	—	—	**Arrector ventralis**	**Arrector ventralis**
—	—	—	—	—	—	**Arrector 3** (= large external bundle of superficial abductor of e.g. Brosseau, 1978a,b)

The nomenclature of the muscles shown in bold follows that of the present work (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle are indicated in front of that muscle). For more details, see text (see also Figs. 2–8).

working in two different groups, Diogo employed the name used in the group that is phylogenetically more plesiomorphic. Lastly, it should be noted that, as mentioned earlier, the definition of pectoral muscles that is used here follows that of Diogo (in press). That is, it does not refer to all the muscles attaching to the pectoral girdle and/or to the pectoral fins/limbs, but to the so-called "appendicular" muscles of authors such as Kardong and Zalisko (1998) and Kardong (2002). Therefore, hypobranchial muscles such as the sternohyoideus and branchial muscles such as the protractor pectoralis, as well as muscles such as the hypoaxialis and the epaxialis, which usually attach to these skeletal structures, are not discussed in the present paper. The list of specimens examined for the present work is given later; the alcohol fixed (alc) condition of these specimens is indicated in parentheses following the number of specimens observed.

Chondrostei: *Acipenser sturio*. MNCN 152172, 3 (alc). *Psephurus gladius*: CASW, uncatalogued, 1 (alc). **Cladistia:** *Polypterus bichir*: MNCN 1579, 7 (alc). **Dipnoi:** *Lepidosiren paradoxa*: CONICET, uncatalogued, 1 (alc). *Neoceratodus forsteri*: MU, uncatalogued, 2 (alc). **Ginglymodi:** *Lepisosteus osseus*: ANSP 107961, 2 (alc); ANSP 172630, 1 (alc). *Lepisosteus platyrhincus*: AMNH 74789, 2 (alc). **Halecomorphi:** *Amia calva*: MNCN 35961, 1 (alc). **Teleostei:** *Albula vulpes*: MNCN 52124, 2 (alc). *Alepocephalus rostratus:* MNCN 108199, 2 (alc). *Anguilla anguilla*: MNCN 41049, 3 (alc). *Astronesthes niger:* MNCN 1102, 1 (alc). *Aulopus filamentosus:* MNCN 1170, 6 (alc). *Brycon guatemalensis:* MNCN 180536, 3 (alc). *Brycon henni:* CAS 39499, 1 (alc). *Chanos chanos:* USNM 347536, 1 (alc), LFEM, 1 (alc). *Conger conger*: MNCN 1530, 5 (alc). *Danio rerio:* LFEM, 5 (alc). *Denticeps clupeoides:* MRAC 76-032-P-1, 2 (alc). *Diplomystes chilensis:* LFEM, 3 (alc). *Elops lacerta*: LFEM, 2 (alc). *Elops saurus*: MNCN 48752, 2 (alc). *Engraulis encrasicolus:* MNCN 68048, 2 (alc); MNCN 65097, 8 (alc); MNCN 1099, 3 (alc). *Esox lucius:* MNCN 197706, 5 (alc). *Eurypharynx pelecanoides*: AMNH 44315, 1 (alc); AMNH 44344, 1 (alc). *Galaxias maculatus:* USNM 344889, 2 (alc). *Gymnotus carapo:* INHS 35493, 2 (alc). *Hiodon tergisus*: MNCN 36019, 3 (alc). *Mormyrus niloticus*: LFEM, 1 (alc). *Mormyrus tapirus*: MNCN 80593, 3 (alc); MNCN 85283, 1 (alc). *Notacanthus bonaparte*: MNCN 107324, 3 (alc). *Salmo trutta:* MNCN 136179, 2 (alc), 1 (c&s); MNCN 16373, 2 (alc); MNCN 40685, 2 (alc). *Opsariichthys uncirostris:* MNCN 56668, 3 (alc). *Xenomystus nigri*: MNCN 227824, 25 (alc). **Tetrapoda:** *Ambystoma texanum*: FML 03402, 1 (alc). *Ambystoma ordinarium*: MNCN, uncatalogued, 2 (alc). *Ambystoma mexicanum*: MNCN, uncatalogued, 2 (alc). *Anisolepis longicaudus*: FML, uncatalogued, 1 (alc). *Anolis allogus*: SDSU 2136, 1 (alc). *Anolis lineatopus*: SDSU 2157, 1 (alc). *Anolis macrolepis*: SDSU 2183, 1 (alc). *Anolis notopholis*: SDSU 2188, 1 (alc). *Anolis sagrei*: SDSU 2175, 1 (alc). *Bufo arenarum*: FML 01352-1, 1 (alc). *Didelphis albiventris:* CML 5971, 1 (alc). *Homonota fasciata*: FML, uncatalogued, 1 (alc). *Liolaemus cuyanus*: FML 13891, 1 (alc). *Liolaemus donosobarrosi*: FML 02871, 1 (alc). *Liolaemus riojanus*: FML 02876, 1 (alc). *Lutreolina crassicaudata:* CML 4114, 1 (alc). *Monodelphis dimidiata:* CML 4118, 1 (alc). *Pantodactylus schreibersi*: FML, uncatalogued, 1 (alc). *Phymaturus* sp.: FML 13834 1(alc). *Polychrus acutirostris*: FML 00140, 1 (alc). *Pristidactylus valeriae*: FML 9592, 1 (alc). *Teius suquiensis*: FML 03628, 1 (alc). *Teyous ocelatus*: FML 03633, 1 (alc). *Thylamys venustus:* CML 5586, 1 (alc). *Timon lepidus*: MNCN, 32544, 1 (alc), MNCN, uncatalogued, 1 (alc). *Tropidurus plica*: FML 6660, 1 (alc).

RESULTS AND DISCUSSION

Actinopterygii (Table 1 and Figs. 2–8)

As can be seen in Table 1, the plesiomorphic condition for actinopterygians clearly seems to be that where there are only two pectoral muscles related to the movements of the pectoral fins, the abductor and the adductor, which may be subdivided into different bundles. Such a condition is found, for example, in extant chondrosteans and in extant cladistians (Fig. 2). In fact, this condition seems to be plesiomorphic for the osteichthyans as a whole, since it is also found in extant actinistian and dipnoan sarcopterygians (Table 2; Figs. 9–11 and below) as well as in non-osteichthyan gnathostomes such as numerous extant chondrichthyans (e.g., Romer, 1924; Jarvik, 1965, 1980; Kardong and Zalisko, 1998; Kardong, 2002). In both actinopterygian (Fig. 8) and sarcopterygian (Fig. 9) fishes the adductor and the abductor of the pectoral fin are often subdivided into adductor superficialis and adductor profundus and into abductor superficialis and abductor profundus, respectively. As done in the recent work of Diogo (in press), in the present study the adductor superficialis and adductor profundus are considered as bundles of the adductor, and not as separate muscles; in the same way the abductor superficialis and abductor profundus are considered as bundles of the abductor, and not as individual muscles (see Tables 1 and 2). As their names indicate, in these fishes the adductor and the abductor are mainly related to the adduction and with the abduction of the pectoral fin, respectively (e.g., Bischoff, 1840; Owen, 1841; Pollard, 1892; Romer, 1924; Howell, 1933b; Millot and Anthony, 1958; Greenwood and Thomson, 1960; Jessen, 1972; Winterbottom, 1974; Kaseda and Nomura, 1975; Brosseau, 1978a,b; Lauder and Liem, 1983; Adriaens et al., 1993; Pough et al., 1996; Kardong and Zalisko, 1998; Diogo et al., 2001; Kardong, 2002; Westneat et al., 2004; Kisia and Onyango, 2005; Thorsen and Hale, 2005; Thorsen and Westneat, 2005).

Contrary to extant cladistians and chondrosteans, as well as to extant sarcopterygian fishes, the living ginglymodians, the living halecomorphs, and the vast majority of the living teleosts exhibit a separate, well-distinguished muscle arrector dorsalis, which may be subdivided into different bundles (Table 1; Figs. 3–5, 6B, and 8). This arrector dorsalis usually originates on the mesial surface of the pectoral girdle, lateral to the adductor and to the mesocoracoid arch (when this structure is present) and inserts on the proximal head of the first and eventually of the second pectoral fin rays (Figs. 3, 5, 6B, and 8). The arrector dorsalis is ontogenetically derived from the adductor of the pectoral fin (Jessen, 1972; Winterbottom, 1974; Thorsen and Hale, 2005). The arrector dorsalis was seemingly phylogenetically acquired in the node leading to the Neopterygii (see Fig. 1; Table 2).

Apart from the arrector dorsalis, other separate, well-distinguished arrector muscles may be present in neopterygians (Table 1). One of these muscles is the arrector ventralis, which is found in the great majority of extant teleosts, and which was seemingly phylogenetically acquired in the node leading to the Teleostei (Diogo, in press). The arrector ventralis usually originates lateral to the abductor and inserts on the first pectoral ray (Figs. 6A and 7). It is ontogenetically derived from the abductor of the

TABLE 2. Pectoral muscles of adults of representative sarcopterygian taxa

Plesiomorphic osteichthyan condition	Actinistia: *Latimeria chalumnae*	Dipnoi: *Lepidosiren paradoxa*	Amphibia: *Ambystoma ordinarium*	Amniota: *Timon lepidus*
Abductor (of pectoral fin)	**Abductor (of pectoral fin)**	**Abductor (of pectoral fin)**	— (*there is no separate muscle abductor)	— (*see cell on the left)
Adductor (of pectoral fin)	**Adductor (of pectoral fin)**	**Adductor (of pectoral fin)**	— (*there is no separate muscle abductor)	— (*see cell on the left)
—	—	—	**Pectoralis**	**Pectoralis**
—	—	—	**Supracoracoideus**	**Supracoracoideus**
—	—	—	**Procoracohumeralis**	**Procaracohumeralis** (deltoides clavicularis of e.g. Romer, 1944)
—	—	—	**Coracobranchialis longus**	**Coracobranchialis longus**
—	—	—	**Anconaeus coracoideus**	**Anconaeus coracoideus** (*seemingly present, making part of the triceps group of e.g. Romer, 1944)
—	—	—	**Anconaeus scapularis medialis**	**Anconaeus scapularis medialis** (*seemingly present, making part of the triceps group of e.g. Romer, 1944)
—	—	—	**Anconaeus humeralis lateralis**	**Anconaeus humeralis lateralis** (*seemingly present, making part of the triceps group of e.g. Romer, 1944)
—	—	—	**Anconaeus humeralis medialis**	**Anconaeus humeralis medialis** (*seemingly present, making part of the triceps group of e.g. Romer, 1944)
—	—	—	**Latissimus dorsi**	**Latissimus dorsi**
—	—	—	**Dorsalis scapulae**	**Dorsalis scapulae** (deltoides scapularis of e.g. Romer, 1944)
—	—	—	**Humeroantebranchialis**	**Humeroantebranchialis** (part, or totality, of biceps of e.g. Romer, 1944)
—	—	—	— (*seemingly absent in *Ambystoma*, but may be found in other salamanders)	**Brachialis inferior**
—	—	—	**Flexor digitorum communis**	**Flexor digitorum communis** (part, or totality, of flexor digitorum longus of e.g. Abdala and Moro, 2006)
—	—	—	**Flexor antebrachii et carpi radialis**	**Flexor antebrachii et carpi radialis** (flexor carpi radialis of e.g. Abdala and Moro, 2006)
—	—	—	—	**Pronator teres** (*seemingly differentiated from part of the flexor antebrachii et carpi radialis)
—	—	—	**Flexor antebrachii et carpi ulnaris**	**Flexor antebrachii et carpi ulnaris** (flexor carpi ulnaris of e.g. Abdala and Moro, 2006)
—	—	—	**Extensor digitorum communis**	**Extensor digitorum communis** (extensor digitorum longus of e.g. Abdala and Moro, 2006)
—	—	—	**Extensor antebrachii et carpi radialis**	**Extensor antebrachii et carpi radialis** (extensor carpi radialis of e.g. Abdala and Moro, 2006)
—	—	—	**Extensor antebrachii et carpi ulnaris**	**Extensor antebrachii et carpi ulnaris** (extensor carpi ulnaris of e.g. Abdala and Moro, 2006)
—	—	—	**Contrahentium caput longum**	— (*seemingly absent as an independent muscle in *Timon*, but may eventually be found in some other lizards)

TABLE 2. (Continued)

Plesiomorphic osteichthyan condition	Actinistia: *Latimeria chalumnae*	Dipnoi: *Lepidosiren paradoxa*	Amphibia: *Ambystoma ordinarium*	Amniota: *Timon lepidus*
—	—	—	**Flexor accessorius lateralis**	Present? It may eventually have given part, or the totality, of the pronator accessorius of e.g. Abdala and Moro, 2006
—	—	—	**Flexor accessorius medialis**	Present? It may eventually have given part, or the totality, of the pronator accessorius of e.g. Abdala and Moro, 2006
—	—	—	**Pronator profundus**	**Pronator profundus**
—	—	—	**Epitrochleoanconeus** (*our dissections indicate that it is seemingly present in at least some members of the genus *Ambystoma*)	**Epitrochleoanconeus**
—	—	—	**Flexores breves superficiales**	**Flexores breves superficiales** (flexores digiti brevis superficialis of e.g. Abdala and Moro, 2006)
—	—	—	**Intermetacarpales**	**Intermetacarpales I** (intermetacarpalis I of e.g. Abdala and Moro, 2006)
—	—	—	—	**Intermetacarpales II** (intermetacarpalis II of e.g. Abdala and Moro, 2006)
—	—	—	**Extensores digitorum breves**	**Extensores digitorum breves** (extensores digiti brevis of e.g. Abdala and Moro, 2006)
—	—	—	**Abductor et extensor digiti I**	**Abductor et extensor digiti I** (abductor longus pollici of e.g. Abdala and Moro, 2006)
—	—	—	**Extensor lateralis digiti IV**	**Abductor digitorum V** (*see text)
—	—	—	**Contrahentes digitorum**	**Contrahentes digitorum**
—	—	—	—	**Lumbricalis**
—	—	—	**Flexores breves profundi**	**Flexores breves profundi** (flexores digiti brevis profundus of e.g. Abdala and Moro, 2006)
—	—	—	—	**Abductor brevis pollicii**
—	—	—	—	**Dorsometacarpalis**
—	—	—	—	**Flexor digitorum V transversus I**
—	—	—	—	**Flexor digitorum V transversus II**

The nomenclature of the muscles shown in bold follows that of the present work (in order to facilitate comparisons, in some cases certain names often used by other authors to designate a certain muscle are indicated in front of that muscle). For more details, see text (see also Figs. 10–18). Note: the listing of the numerous pectoral muscles of the tetrapods *Ambystoma ordinarium* and *Timon lepidus* mainly follows the order used in Walthall and Ashley-Ross' (2006) Table 1, which is essentially ordered from the most proximal to the most distal regions of the pectoral girdle/forelimb.

pectoral fin (Jessen, 1972; Winterbottom, 1974; Thorsen and Hale, 2005). The other muscle is the small muscle arrector 3, which usually connects the pectoral girdle to the ventrolateral surface of the first pectoral ray (Fig. 7). This small muscle has been frequently neglected in the literature (Diogo, in press). That is, it has frequently been overlooked or considered as a bundle of the arrector ventralis or of the abductor of the fin (e.g., Brosseau, 1978a,b; see Table 1). However, the arrector 3 is found in numerous otocephalans (Fig. 7), and in at least some euteleosts, thus constituting a potential synapomorphy of the teleostean clade Clupeocephala (see Fig. 1; Table 1).

It should be noted that in previous works by Diogo and colleagues (e.g., Diogo et al., 2001; Diogo, 2004a,b) the arrector 3 of Diogo (in press) and of the present study was named "arrector ventralis." One of the main reasons for this confusion was precisely the fact that the small muscle arrector 3 was not described by authors such as Winterbottom (1974). Due to this confusion, the names attributed to the teleostean pectoral muscles by Diogo et al. (2001) and Diogo (2004a,b) were substantially different

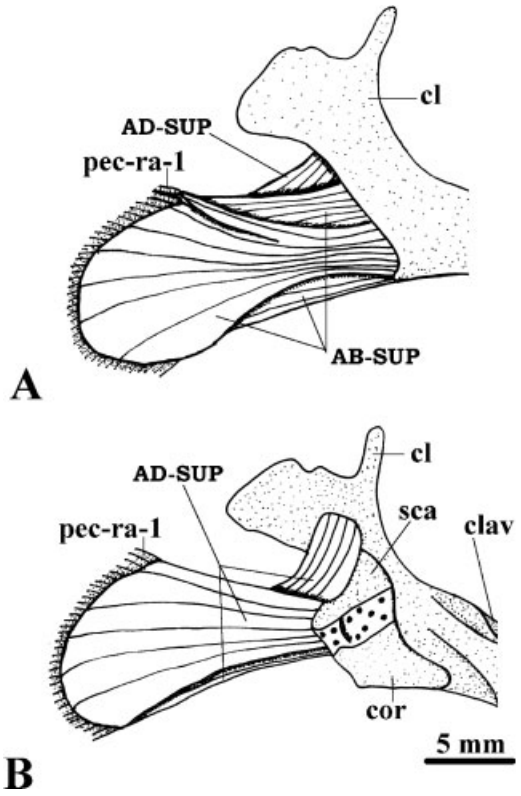

Fig. 2. *Polypterus bichir* (Cladistia): lateral (**A**) and mesial (**B**) views of the pectoral musculature; in the lateral view the adductor is also illustrated. AB-SUP, abductor superficialis; AD-SUP, adductor superficialis; cl, cleithrum; clav, clavicle; cor, coracoid; pec-ra-1, pectoral ray 1; sca, scapula.

from those proposed by Winterbottom (1974). In order to solve this problem, Diogo (in press) decided to name this small muscle as arrector 3, and to use the nomenclature proposed by Winterbottom (1974) to designate the other teleostean pectoral muscles.

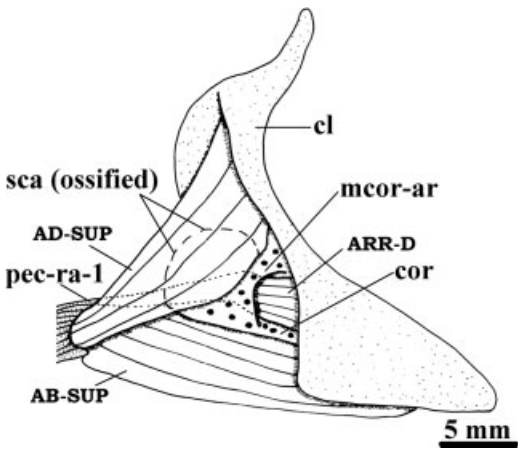

Fig. 3. *Lepisosteus osseus* (Ginglymodi): mesial view of the pectoral musculature; despite being a lateral structure, the abductor superficialis is also shown. AB-SUP, abductor superficialis; AD-SUP, adductor superficialis; ARR-D, arrector dorsalis; cl, cleithrum; cor, coracoid; mcor-ar, mesocoracoid arch; pec-ra-1, pectoral ray 1; sca, scapula.

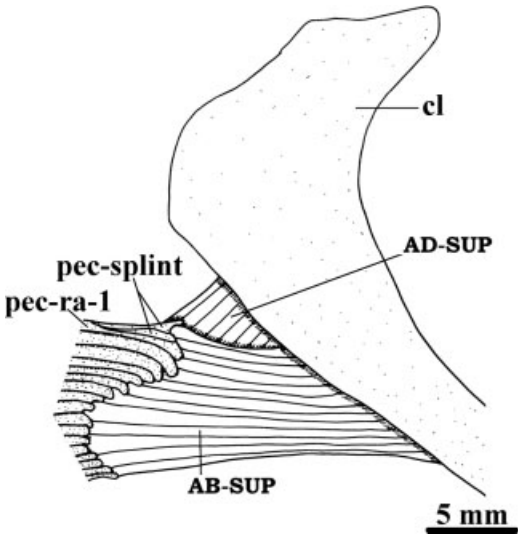

Fig. 4. *Amia calva* (Halecomorphi): lateral view of the pectoral musculature; despite being a mesial structure, the adductor superficialis is also shown. AB-SUP, abductor superficialis; cl, cleithrum; pec-ra-1, pectoral ray 1; pec-splint, pectoral splint.

Thus, in order to facilitate comparisons with previous works such as Diogo et al. (2001) and Diogo (2004a,b), it is worth noting that the "arrector ventralis," "arrector dorsalis," "abductor superficialis 1," "abductor superficialis 2," "adductor superficialis 1," "adductor superficialis 2" and "abductor profundus" of those previous works correspond respectively to the arrector 3, arrector ventralis, abductor superficialis, abductor profundus, adductor superficialis, adductor profundus and arrector dorsalis of Diogo (in press) and of the present work.

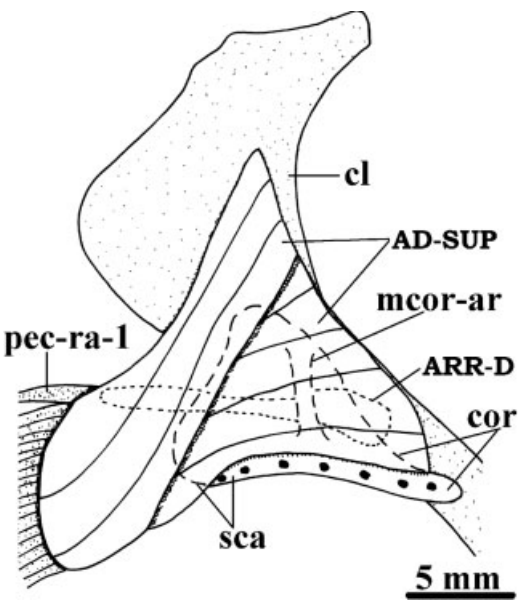

Fig. 5. *Amia calva* (Halecomorphi): mesial view of the pectoral musculature. AD-SUP, adductor superficialis; ARR-D, arrector dorsalis; cl, cleithrum; cor, coracoid; mcor-ar, mesocoracoid arch; pec-ra-1, pectoral ray 1; sca, scapula.

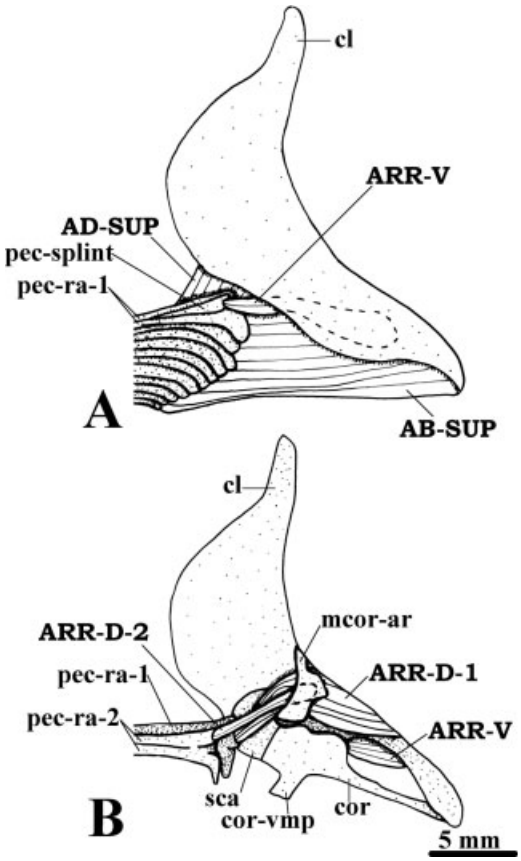

Fig. 6. *Elops saurus* (Teleostei): lateral (**A**) and mesial (**B**) view of the pectoral musculature; in the mesial view the adductor superficialis and abductor superficialis are not shown. AB-SUP, abductor superficialis; AD-SUP, adductor superficialis; ARR-D-1, 2, arrector dorsalis 1 and 2; ARR-V, arrector ventralis; cl, cleithrum; cor, coracoid; cor-vmp, ventromesial process of coracoid; mcor-ar, mesocoracoid arch; pec-ra-1, 2, pectoral rays 1 and 2; pec-slint, pectoral splint; sca, scapula.

As explained in the recent paper of Thorsen and Hale (2005: p 149) the arrectors of the pectoral fin "initiate the movement of the fin at the leading edge" while the adductor and the abductor "power the upstroke and downstroke." Besides the abductor, the adductor and the arrector muscles, some derived teleosts (e.g., certain neoteleosts) may eventually exhibit other pectoral muscles, such as the coracoradialis, adductor radialis, interradialis pectoralis and adductor medialis (Winterbottom, 1974).

Sarcopterygii (Table 2 and Figs. 9–18)

The plesiomorphic condition for sarcopterygians seems also to be that in which there are only two distinct pectoral muscles associated to the movements of the pectoral fins, the abductor and the adductor; this condition is found in extant dipnoans (Figs. 10 and 11) and seemingly in extant actinistians (Fig. 9; see later). However, contrarily to the configuration found in actinopterygians and in non-osteichthyan gnathostomes such as living chondrichthyans, in these two sarcopterygian groups the adductor and the abductor extend far into the pectoral fin, thus giving to this fin its characteristic "lobed" or "fleshy" appearance (Figs. 9–11; see also, e.g., Bischoff, 1840; Owen, 1841; Romer, 1924; Howell, 1933b; Millot and Anthony, 1958; Jessen,

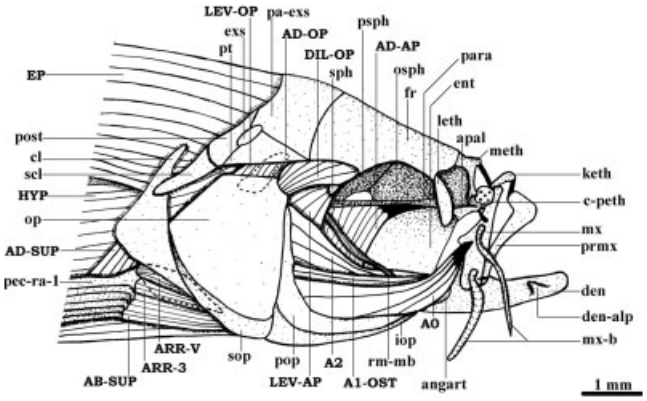

Fig. 7. *Danio rerio* (Teleostei): lateral view of the cranial and pectoral musculature; all muscles are exposed, the maxillary barbels and the mesial branch of the ramus mandibularis are also illustrated; the nasals, infraorbitals, and postcleithra were removed. A0, A1-OST, A2, adductor mandibulae A0, A1-OST and A2; AB-SUP, abductor superficialis; AD-AP, adductor arcus palatini; AD-OP, adductor operculi; AD-SUP, adductor superficialis; angart, angulo-articular; apal, autopalatine; ARR-3, arrector 3; ARR-V, arrector ventralis; c-peth, pre-ethmoid cartilage; cl, cleithrum; den, dentary bone; den-alp, anterolateral process of dentary bone; DIL-OP, dilatator operculi; ent, entopterygoid; EP, epaxialis; exs, extrascapular; fr, frontal; HYP, hypoaxialis; iop, interopercle; keth, kinethmoid; leth, lateral-ethmoid; LEV-AP, levator arcus palatini; LEV-OP, levator operculi; meth, mesethmoid; mx, maxilla; mx-b, maxillary barbel; op, opercle; osph, orbitosphenoid; pa-exs, parieto-extrascapular; para, parasphenoid; pec-ra-1, pectoral ray 1; pop, preopercle; post, posttemporal; prmx, premaxilla; psph, pterosphenoid; pt, pterotic; rm-mb, mesial branch of ramus mandibularis; scl, supracleithrum; sop, subopercle; sph, sphenotic.

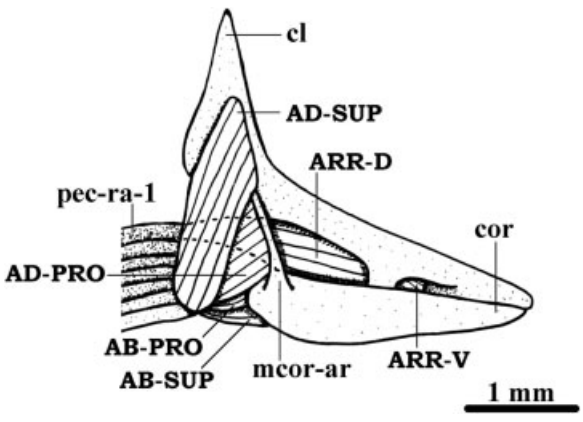

Fig. 8. *Danio rerio* (Teleostei): mesial view of the pectoral musculature; despite being lateral structures, the abductor superficialis and abductor profundus are also shown. AB-PRO, abductor profundus; AB-SUP, abductor superficialis; AD-PRO, adductor profundus; AD-SUP, adductor superficialis; ARR-D, arrector dorsalis; ARR-V, arrector ventralis; cl, cleithrum; cor, coracoid; mcor-ar, mesocoracoid arch; pec-ra-1, pectoral ray 1.

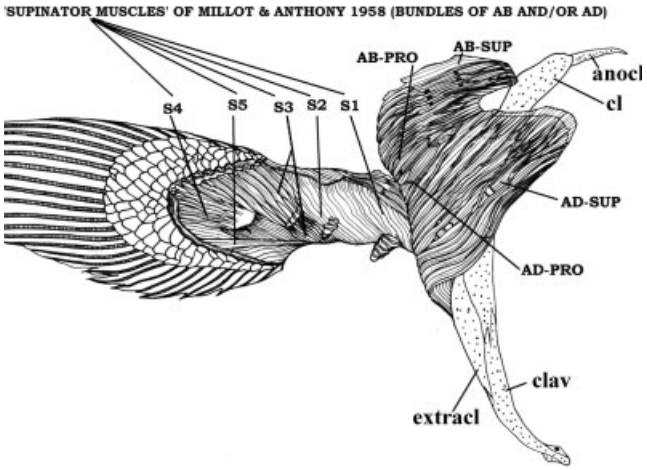

Fig. 9. *Latimeria chalumnae* (Cladistia): lateral view of pectoral musculature (modifed from Millot and Anthony, 1958). AB-PRO, abductor profundus; AB-SUP, abductor superficialis; AB-PRO, abductor profundus; AD-SUP, adductor superficialis; anocl, anocleithrum; cl, cleithrum; clav, clavicle; extracl, extracleithrum; S1, S2, S3, S4, S5, "supinator muscles" of Millot and Anthony (1958) (bundles of the abductor and/or adductor of the fin sensu the present work).

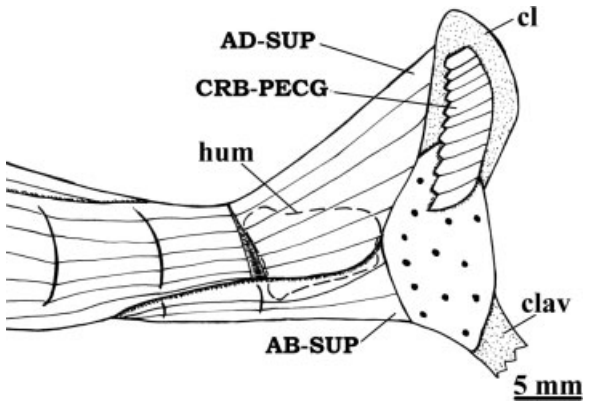

Fig. 11. *Neoceratodus forsteri* (Dipnoi): mesial view of pectoral musculature; despite being a lateral structure, the abductor superficialis is also shown; in relation to the lateral view illustrated in Figure 10, the anocleithrum, the Baudelot's ligament, and the protractor pectoralis were removed and the muscle between the cranial rib and the pectoral girdle was cut. AB-SUP, abductor superficialis; AD-SUP, adductor superficialis; cl, cleithrum; clav, clavicle; CRB-PECG, muscle between cranial rib and pectoral girdle; hum, humerus.

1972; Pough et al., 1996; Kardong and Zalisko, 1998; Kardong, 2002; Kisia and Onyango, 2005).

Millot and Anthony (1958) suggested that apart from the adductor and the abductor of the pectoral fin, *Latimeria* exhibits various "pronator" and "supinator" muscles (Fig. 9). As explained earlier, we could not undertake a detailed dissection of *Latimeria* due to the difficulty of finding specimens of this taxon that are available for muscular examination. However, from the textual descriptions and the illustrations provided in Millot and Anthony's (1958) work, it seems that their "pronator" and "supinator" muscles are not well-separated, functionally independent muscles, but are, instead, bundles of the adductor and of the abductor (Table 1; see, e.g., in Fig. 9 the seemingly poor differentiation between Millot and Anthony's "supinators" 1 and 2). As is the case in extant dipnoans (Figs. 10 and 11), these adductor and abductor bundles may eventually resemble certain tetrapod pectoral muscles, but are not as distinct and as functionally independent as are these latter muscles (Romer, 1924; Diogo, in press; this work). This view is indirectly supported by Diogo's (in press) recent cladistic analysis, which strongly supports that tetrapods are more closely related to dipnoans than to actinistians (see Fig. 1). Thus, according to these results it would seem rather unsound that *Latimeria* may effectively exhibit several distinct pectoral muscles as those found in extant tetrapods, since this would implicate: 1) that such muscles were independently acquired twice in evolution; or 2) that such muscles were acquired only once and were present in the last common ancestor of actinistians, dipnoans and tetrapods, but were secondarily lost within the Dipnoi (see Fig. 1). As explained by Diogo (in press), a more plausible scenario would be to consider that in this last common ancestor of actinistians, dipnoans and tetrapods the abductor and the adductor were eventually already differentiated in certain subdivisions, but that these subdivisions, as well as other subdivisions acquired later in evolution, only became well-separated, independent muscles during the subsequent evolutionary transitions leading to the origin of tetrapods. However, only a detailed, up-dated analysis of the pectoral muscles of *Latimeria* may clarify whether the members of this taxon exhibit (as suggested by Millot and Anthony, 1958), or not (as suggested here), well-differentiated pecto-

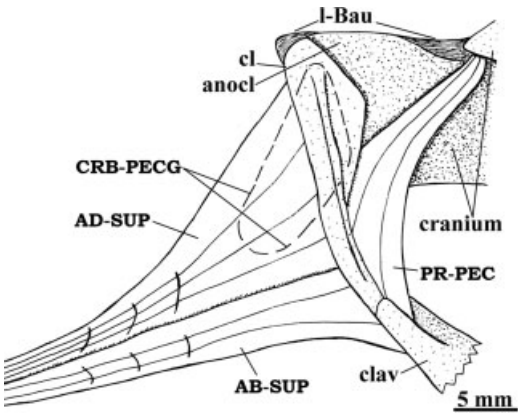

Fig. 10. *Neoceratodus forsteri* (Dipnoi): lateral view of pectoral musculature. AB-SUP, abductor superficialis; AD-SUP, adductor superficialis; anocl, anocleithrum; cl, cleithrum; clav, clavicle; CRB-PECG, muscle between cranial rib and pectoral girdle; l-Bau, Baudelot's ligament; PR-PEC, protractor pectoralis.

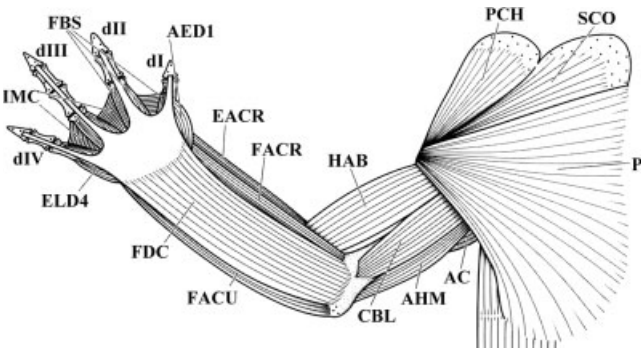

Fig. 12. *Taricha torosa* (Amphibia): ventral view of the superficial musculature of the forelimb; anterior is toward the top of the figure (modifed from Walthall and Ashley-Ross, 2006). AC, anconaeus coracoideus; AED1, abductor et extensor digiti I; AHM, anconaeus humeralis medialis; CBL, coracobrachialis longus; dI, dII, dIII, dIV, digits I, II, III and IV; EACR, extensor antebrachii et carpi radialis; ELD4, extensor lateralis digiti IV; FACR, flexor antebrachii et carpi radialis; FACU, flexor antebrachii et carpi ulnaris; FBS, flexores breves superficiales; FDC, flexor digitorum communis; HAB, humeroantebrachialis; IMC, intermetacarpales; P, pectoralis; PCH, procoracohumeralis; SCO, supracoracoideus.

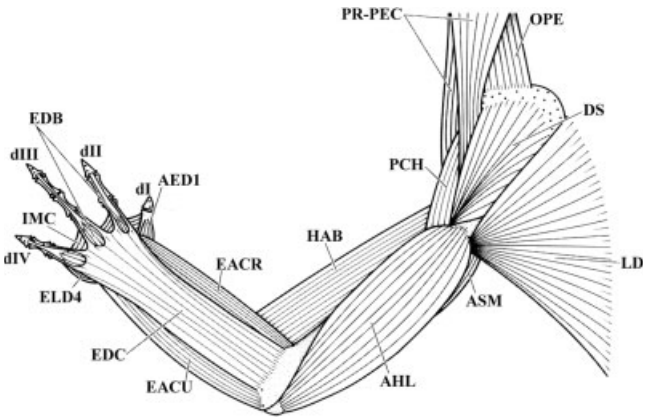

Fig. 13. *Taricha torosa* (Amphibia): dorsal view of the superficial musculature of the forelimb; anterior is toward the top of the figure (modifed from Walthall and Ashley-Ross, 2006). AED1, abductor et extensor digiti I; AHL, anconaeus humeralis lateralis; ASM, anconaeus scapularis medialis; dI, dII, dIII, dIV, digits I, II, III and IV; DS, dorsalis scapulae; EACR, extensor antebrachii et carpi radialis; EACU, extensor antebrachii et carpi ulnaris; EDB, extensores digitorum breves; EDC, extensor digitorum communis; ELD4, extensor lateralis digiti IV; HAB, humeroantebrachialis; IMC, intermetacarpales; LD, latissimus dorsi; OPE, opercularis; PR-PEC, protractor pectoralis; PCH, procoracohumeralis.

ral muscles other than the abductor and the adductor of the fin.

As explained in the section Material and Methods, we will not provide here a detail account on the configuration and function of each of the numerous tetrapod pectoral muscles (Table 2; Figs. 12, 13, 15–18). Detailed, up-dated accounts on the pectoral muscles of members of the representative amphibian and amniote groups shown in Table 2 of the present paper work, i.e., of urodeles and lizards, are, for instance, given in the recent studies of Walthall and Ashley-Ross (2006) and of Abdala and Moro (2006), respectively. For the purpose of the present paper, we prefer instead to focus on the major differences between the pectoral musculature of these representative amphibian and amniote groups. In fact, contrary to what the rather different names generally used in amphibian and amniote literature to designate the pectoral muscles of the members of these groups might indicate, our observations and comparisons have pointed out that the overall configuration of these muscles in amphibians such as urodeles and in amniotes such as lizards is in reality very similar (Table 2). In order to simplify the comparisons between these two groups, we will use the recent works of Walthall and Ashley-Ross (2006) and of Abdala and Moro (2006) (see earlier) as a main example of how different nomenclatures are effectively applied to designate homologous muscles in the amphibian and the amniote literature (Table 2).

Some major differences between the pectoral musculature of adult members of a representative urodele species, *Ambystoma ordinarium*, and of adult members of a representative lizard species, *Timon lepidus*, are summarized in Table 2. As can be seen in that table, a few muscles found in the lizard are absent in the urodele, e.g., the intermetacarpales II, the flexor digitorum V transversus I, the flexor digitorum V transversus II, the branchialis inferior, the pronator teres, the abductor brevis pollici, and the

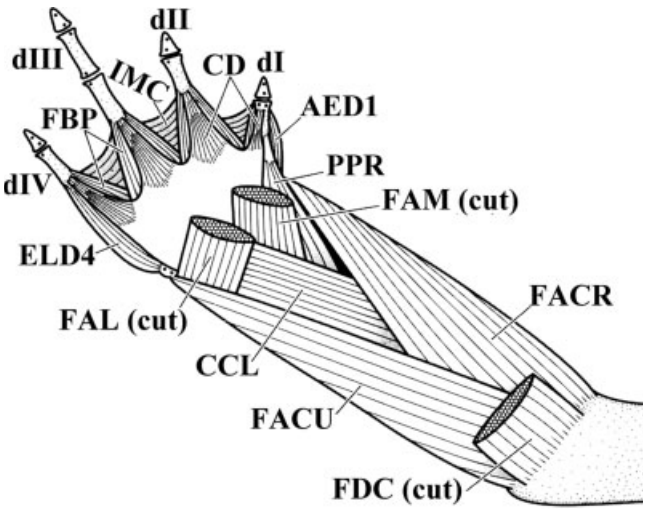

Fig. 14. *Taricha torosa* (Amphibia): ventral view of the deep musculature of the forearm; anterior is toward the top of the figure (modifed from Walthall and Ashley-Ross, 2006). AED1, abductor et extensor digiti I; CD, contrahentes digitorum; CCL, contrahentium caput longum; dI, dII, dIII, dIV, digits I, II, III and IV; ELD4, extensor lateralis digiti IV; FACR, flexor antebrachii et carpi radialis; FACU, flexor antebrachii et carpi ulnaris; FAL, flexor accessorius lateralis; FAM, flexor accessorius medialis; FBP, flexores breves profundi; FDC, flexor digitorum communis; IMC, intermetacarpales; PPR, pronator profundus.

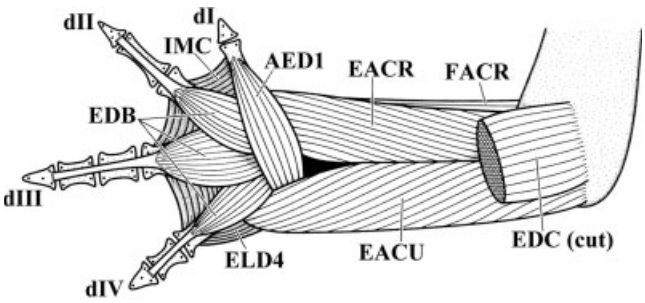

Fig. 15. *Taricha torosa* (Amphibia): dorsal view of the deep musculature of the forearm; anterior is toward the top of the figure (modifed from Walthall and Ashley-Ross, 2006). AED1, abductor et extensor digiti I; dI, dII, dIII, dIV, digits I, II, III and IV; EACR, extensor antebrachii et carpi radialis; EACU, extensor antebrachii et carpi ulnaris; EDB, extensores digitorum breves; EDC, extensor digitorum communis; ELD4, extensor lateralis digiti IV; FACR, flexor antebrachii et carpi radialis; IMC, intermetacarpales.

dorsometacarpal and lumbrical muscles. In turn, the contrahentium caput longum, present in the urodele (Fig. 14), is apparently missing as an independent muscle in the lizard *Timon*. However, as noted in Table 2, this muscle does seem to be present in some other lizards examined by us, connecting the flexor plate to the carpus (e.g., *Liolaemus*, *Teius*). Other muscles found in the urodele that may eventually be missing in the lizard *Timon* are the flexor accessorius lateralis and/or the flexor accessorius medialis (Fig. 14). Our observations and comparisons, however, indicate that at least part of these muscles may well have given part, or the totality, of the muscle that is often named pronator accessorius in amniote literature; this latter muscle is present in the lizard *Timon* (Fig. 18; Table 2).

It should be noted that contrary to what seems to be the case in certain other urodele genera (e.g., *Taricha*: Walthall and Ashley-Ross, 2006) our dissections pointed out that a muscle epitrochleoanconeus as that found in lizards is also found in at least some members of the genus *Ambystoma* (e.g., *Ambystoma texanum*). It should also be noted that the muscle extensor lateralis digiti IV of the urodele clearly seems to correspond to the lizard muscle that is frequently named abductor digitorum V in amniote literature (Abdala and Moro, 2006). However, in contrast to what we have done for other muscles in Table 2, in this case we prefer to not attribute the name frequently used in the amphibian literature to designate the corresponding lizard muscle. This is because the lizard muscle is attached to digit V, and not to digit IV, as is the case in the urodele (which has four digits, and not five as the lizard; see Fig. 14). Thus, in this case, we consider inappropriate to designate a muscle that in

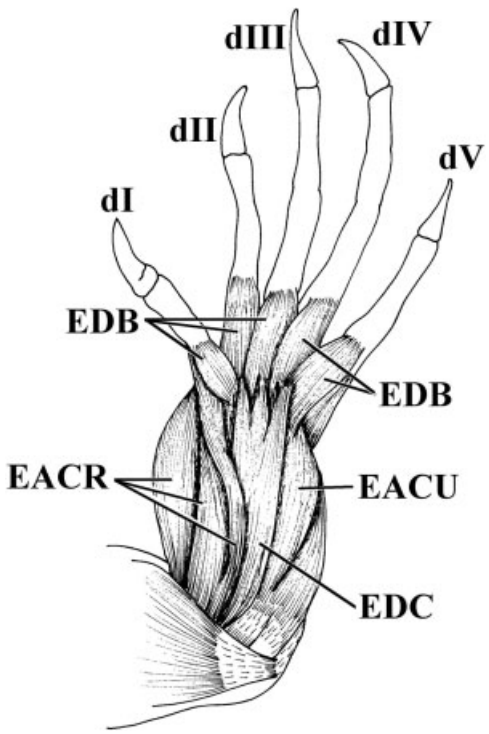

Fig. 16. *Phymaturus* sp. (Amniota): dorsal view of the superficial musculature of the forearm; anterior is toward the top of the figure (modifed from Abdala and Moro, 2006). dI, dII, dIII, dIV, dV, digits I, II, III, IV and V; EACR, extensor antebrachii et carpi radialis; EACU, extensor antebrachii et carpi ulnaris; EDB, extensores digitorum breves; EDC, extensor digitorum communis.

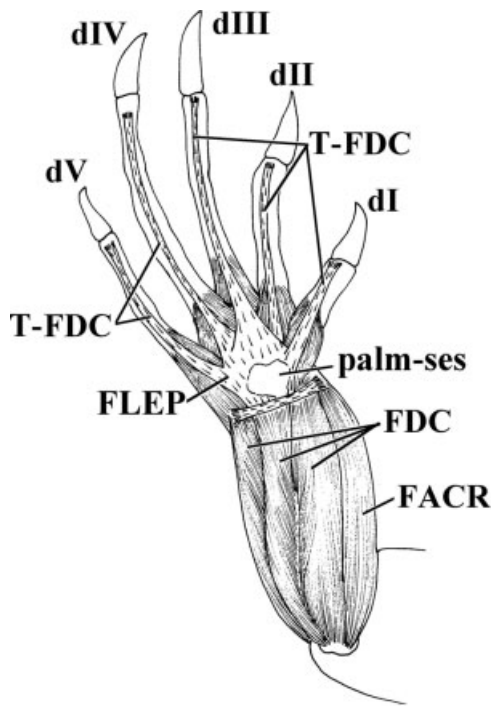

Fig. 17. *Phymaturus* sp. (Amniota): ventral view of the superficial musculature of the forearm; anterior is toward the top of the figure (modifed from Abdala and Moro, 2006). dI, dII, dIII, dIV, dV, digits I, II, III, IV and V; FACR, flexor antebrachii et carpi radialis; FDC, flexor digitorum communis; FLEP, flexor plate; palm-ses, palmar sesamoid; FDC, flexor digitorum communis; T-FDC, tendon of flexor digitorum communis.

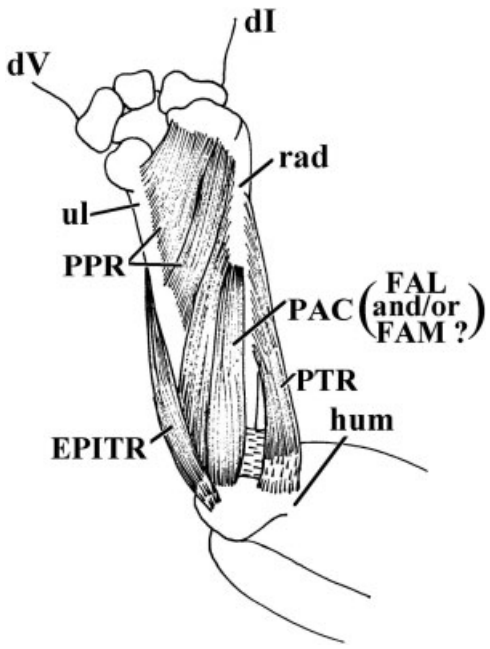

Fig. 18. *Phymaturus* sp. (Amniota): ventral view of the deep musculature of the forearm; anterior is toward the top of the figure (modifed from Abdala and Moro, 2006). dI, dV, digits I and V; EPITR, epitrochleoanconeus; FAL, flexor accessorius lateralis; FAM, flexor accessorius medialis; hum, humerus; PAC, pronator accesorius; PPR, pronator profundus; PTR, pronator teres; rad, radius; ul, ulna.

the lizard attaches on digit V as "extensor lateralis digiti IV." Consequently, in Table 2 we keep the name that is often used in amniote literature, i.e., abductor digitorum V, to designate this lizard muscle (see Table 2).

Apart from the differences mentioned earlier, there are some other differences concerning the configuration of certain homologous muscles in amphibians such as urodeles and in amniotes such as lizards. To give just an illustrative example, in urodeles the pronator profundus usually extends distally in order to attach on digit I (Fig. 14), while in lizards the proximal insertion of this muscle is usually on the radius, i.e. it does not reach the digits (Fig. 18). However, as stated earlier, in a general way it can be said that the overall configuration of the pectoral musculature of these taxa is rather similar. In fact, as shown in Table 2, the vast majority of the individual pectoral muscles found in urodeles are present in lizards (e.g., at least 26 of the 29 *Ambystoma* pectoral muscles listed in that table are seemingly present in *Timon*). It should be noted that apart from the muscles listed in that table, other pectoral muscles may be eventually found in extant tetrapods: for instance, Shellswell and Wolpert (1977) have mentioned that some birds may have about 50 distinct muscles in the wing, a number that is significantly greater than the number of pectoral muscles found in tetrapods such as urodeles and lizards (see Table 2; see also Romer, 1922, 1924, 1944; Howell, 1933a,b, 1935, 1936a,b; Sullivan, 1962; George and Berger, 1966; Jarvik, 1980; Pough et al., 1996; Kardong and Zalisko, 1998; Gibbs et al., 2000, 2002; Kardong, 2002; Abdala and Moro, 2003, 2006; Moro and Abdala, 2004; Kisia and Onyango, 2005; Walthall and Ashley-Ross, 2006). We plan to provide, in a future work, a detailed account on the pectoral musculature of all the major tetrapod subgroups.

General Remarks

In view of the discussion earlier and of the information summarized in Tables 1 and 2, it can thus be said that from a similar plesiomorphic overall configuration (i.e., the presence of only two pectoral muscles, the abductor and the adductor of the fin), the evolution of the pectoral musculature has been rather different within the actinopterygian and the sarcopterygian clades. Within the Actinopterygii, different arrector muscles were acquired at different evolutionary stages: an arrector dorsalis is only present in extant neopterygians, an arrector ventralis is only present in extant teleosts, and an arrector 3 is only present in extant clupeocephalans. These three arrector muscles, together with the adductor and the abductor are, for example, present in one of the model organisms that is most studied among actinopterygians, as well as among osteichthyan fishes in general (see Diogo, in press), the zebrafish *Danio rerio* (Table 1). As explained earlier, apart from these five muscles, other pectoral muscles may eventually be found in some derived actinopterygians, e.g., in certain neoteleosts. Within sarcopterygians, the most significant evolutionary transformations concerning the pectoral musculature occurred in the transitions that had led to the origin of the tetrapods: the configuration of the pectoral musculature of all living tetrapods is markedly different from that found in living sarcopterygian fishes (Table 2). As mentioned earlier, certain living tetrapods may seemingly have up to 50 individual pectoral muscles.

As a result of the different evolutionary routes followed within the actinopterygian and the sarcopterygian clades, none of the individual muscles found for example in derived actinopterygians such as teleosts is found in derived sarcopterygians such as tetrapods (Tables 1 and 2). Thus, concerning the pectoral musculature, much caution should be observed when, for instance, one takes a model actinopterygian organism such as the teleostean zebrafish to be representative of osteichthyan fishes as a whole or to be representative of the plesiomorphic condition found in these fishes, as is unfortunately done in some recent developmental and molecular studies (see Diogo, in press, for a recent discussion on this subject). Also, much caution should be taken when the results obtained in developmental and mo-

lecular studies concerning the pectoral muscles of a model actinopterygian such as the zebrafish are compared with those concerning the pectoral muscles of model sarcopterygians from clades such as the Amphibia and/or the Amniota (see, e.g., the recent work of Thorsen and Hale, 2005). A proper knowledge of the osteichthyan pectoral musculature, thus, is not only important to increase our general understanding of the comparative anatomy, functional morphology, and evolution of this group, but also to provide a solid basis for the comparisons and extrapolations made in such developmental and molecular studies. It is very much hoped that the present work may contribute to a better knowledge of the pectoral muscles of osteichthyans, as well as to help to pave the way for future comparative, functional, evolutionary, molecular and/or developmental works concerning this group.

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