The protractor pectoralis muscle and the classification of teleost fishes

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Introduction

The protractor pectoralis muscle is currently thought to be one of the shared derived features characterizing certain neoteleostean fishes. Further investigation shows, however, that a protractor pectoralis muscle occurs in many taxa throughout the Teleostei, the Dipnoi, the Palaeopterygii and other lower actinopterygians, and, probably, in the Elasmobranchiomorphi as well.

Since the protractor pectoralis is apparently homologous with the trapezius muscle of tetrapods it therefore would appear to be a derived feature of the Gnathostomata as a whole and not just a synapomorphy of a group (the Eurypterygii) within the Teleostei.

In his paper on the interrelationships of the higher Euteleostei, Rosen (1973) considered the presence of a protractor pectoralis muscle to be one of the synapomorphies characterizing the section Eurypterygii of his subdivision Neoteleostei. Rosen also included in the Neoteleostei, as the primitive sister group of the Eurypterygii, the section Stenopterygii (=Stomiatiformes). Although lacking a protractor pectoralis muscle, the Stomiatiformes share other derived features with their apomorph sister taxa, *viz.* the Aulopiformes, Myctophiformes, Protacanthopterygii and Acanthopterygii (Rosen, 1973 : 505).

According to Rosen (who based his conclusions involving the protractor pectoralis largely on the then unpublished work of Winterbottom) this muscle does not occur in any other group of teleostean fishes. When that work was published the following year, Winterbottom (1974 : 269) repeated the claim that '. . . the protractor pectoralis appears to be confined to the neoteleosts', despite the fact that he described and illustrated the muscle in three non-neoteleostean taxa, the ostariophysans *Brycon, Cyprinus* and *Diplomystus.*

This *lapsus* is probably explained by Winterbottom's definition of the concepts 'neoteleosts' and 'non-neoteleosts' (Winterbottom, 1974 : 227). He uses the term neoteleost '. . . in the sense proposed by Rosen & Patterson (1969 : 460)' but uses its antithesis, the non-neoteleosts, '. . . to designate Divisions I and II, and the salmoniforms (less myctophoids) of Division III of the Greenwood *et al.* (1966) classification'. Thus the Ostariophysi and the Gonorynchiformes of Greenwood *et al.* were left in limbo, neither neoteleosts nor non-neoteleosts, and were overlooked.

A further complication is introduced by Winterbottom's report in some clupeomorphs (*sensu* Greenwood, Rosen, Weitzman & Myers, 1966) of a muscle which, in his opinion (1974 : 269) '. . . seems to be analogous to the protractor pectoralis', and with which '. . . the muscle in the neoteleosts would appear to be a homologous structure, and indicative of common ancestry'.

These incongruities in recently published accounts, coupled with the fact that a muscle apparently identical to the protractor pectoralis in neoteleosts has been described in

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chondrichthyans (=Elasmobranchiomorphi), dipnoans and non-teleostean actinopterygians (see Allis, 1917; Edgeworth, 1911 & 1935), led us to review and reconsider the value of this muscle as a character in reconstructing gnathostome phylogenies, especially those of teleostean fishes.

As a first step we have reviewed the literature dealing with the protractor pectoralis (*ie* essentially the cucullaris and cephaloclavicularis muscles of Edgeworth and the trapezius of Allis) in lower gnathostomes, and have compared these findings with our dissections covering a wider range of taxa than any previously examined (see Table 1).

Allis (1917 : 343–350, and 402) gives a detailed summary of the situation at that time with respect to gnathostome fishes, and includes a critique of Edgeworth's earlier (1911) paper, the only wide-ranging review of cranial musculature in vertebrates then available. Later, Edgeworth (1935) expanded his earlier essay. Apart from these three works, and Winterbottom's (1974) recent contribution, there are no other papers dealing with the prime question we wished to review, namely the homology of the protractor pectoralis both within and outside the teleostean fishes.

Allis (1917) concludes that amongst gnathostome fishes the protractor pectoralis (his trapezius) is always innervated by the vagus, and that it is derived, embryologically, from the muscle plate of the last branchial arch. Thus, at least implicitly, Allis would consider the muscle to be homolgous in these animals. Edgeworth (1911; 1935) reaches a similar conclusion regarding the muscle's homology, and extends it even beyond the limits of the gnathostome fishes. According to Edgeworth (1935 : 151) the protractor pectoralis (which he calls cucullaris) 'In Dipnoi, Teleostomi, Amphibia, Reptilia and Mammalia . . . is developed as a backgrowth of the most caudal branchial muscle plate', and more specifically, (p. 151), 'The similar primary innervation of the Cucullaris from the most caudal fibres of the Vagus shows that the muscle has had a continuous phyletic history and is to be regarded as a homologous structure whatever its source'.

Ontogenetically, Edgeworth considered that in Dipnoi and other teleostomes the protractor pectoralis is derived from the posterior margin of the levator arcuum branchialium anlage (which would be topologically equivalent to Allis' muscle plate of the last branchial arch). However, in the Elasmobranchiomorphi (except the rays, Batoidei), he believed that the muscle is formed from the dorsal ends of all the embryonic branchial muscle plates (*ie* the embryonic branchial constrictors since in these animals no levator muscles are differentiated; see Edgeworth, 1935 : 232–233). In the Batoidei, according to Edgeworth, the protractor develops from the dorsal end of the fifth muscle plate alone, a condition which he thought was '. . . probably secondary to that in the Selachii and without any genetic relationship to that of the Teleostomi' (see Edgeworth: 152, and also 140 & 142). In other words, the batoid condition was derived from the selachian one which, in turn, Edgeworth considered to be derived from that basic to the gnathostomes, and characterized by the failure of the levator muscles to develop from the branchial muscle anlage (Edgeworth, 1911 : 193; 1935 : 152).

Allis (1917 : 346–7) contested Edgeworth's general conclusions (first published in 1911) regarding the derivation of the protractor pectoralis in elasmobranchiomorphs. In his opinion (based on personal observations and the literature available) the muscle in selachians '. . . is simply a differentiation of the constrictor superficialis of the ultimate branchial arch'. Allis took further support for his views from Dohrn's (1884; 1885) failure to find that the muscle in selachians was developed from the dorsal ends of all the branchial muscle plates.

This discrepancy between the viewpoints of Allis and Edgeworth has, as far as we can determine, never been resolved. It is of interest to note that in Edgeworth's 1935 account of the muscle and its development he entirely ignores Allis' comments. In part, their difference in viewpoints may be attributable to the fact that Edgeworth's approach was primarily embryological whilst Allis' first-hand information was derived from the dissection of post-embryonic fishes. Further and more critical work needs to be done before the problem can be resolved.

Until this uncertainty has been eliminated we must have some reservations about accepting the homology of the protractor pectoralis in elasmobranchiomorphs with the muscle identified as the protractor pectoralis in lower Teleostomi.

As far as the teleostome fishes are concerned, the results of both Allis' and Edgeworth's reviews strongly indicate the homology of the muscle throughout the group, at least with respect to those members of the Dipnoi and Actinopterygii which they had studied or which had been reported upon by others.

Winterbottom (1974 : 269) has clarified the confusion surrounding Edgeworth's (1935 : 131 & 143) account of the muscle in teleosts, especially the confusion stemming from his use of two names for a morphologically identical muscle. From our own experience we would endorse fully the conclusions reached by Winterbottom, and we therefore also treat Edgeworth's cucullaris and cephaloclavicularis muscles as synonymous, and thus, in turn, as a synonym of Winterbottom's protractor pectoralis muscle. We have also been able to check and clarify certain claims for the absence of the muscle, made by Allis (1917) and Vetter (1878). These are discussed below (p. 228).

None of our anatomical investigations on post-larval specimens would seem to refute the hypothesis that the protractor pectoralis muscle is homologous throughout the lower gnathostomes (with, of course, the reservations noted above regarding that muscle in the Elasmobranchiomorphi). We are very conscious that our research has only involved an investigation of post-embryonic material; the absence of detailed ontogenetic studies is a serious drawback in any attempt to investigate homologies.

Since Winterbottom (1974 : 269) expressed some uncertainty about the homology of the muscle he called the protractor pectoralis in the Clupeomorpha, that problem will be considered now.

Our observations (Table 1), based on 21 non-engraulid clupeoid taxa (the muscle apparently is absent in engraulids), lead us to believe that Winterbottom's difficulty stems partly from his mis-identification of a muscle as being entirely the fourth levator externus, and partly from the extreme postero-lateral displacement of the origin for the protractor pectoralis and consequently its very close association with the cranial insertion point of some epaxial body muscles (see Fig. 3).

We agree with Winterbottom in identifying the thin, strap-like muscle, running from the pterotic to the shoulder girdle, as the protractor pectoralis (see Winterbottom, 1974, fig. 24). But, we would identify the usually thin, sheet-like but somewhat expanded muscle lying ventral to it as the levator posterior muscle and not, as he does, a muscle composed entirely of the expanded 4th levator externus; we have not found, even in *Clupea harengus,* such an expansive and continuous muscle sheet lying between the protractor pectoralis and the main levator muscle mass as is shown in Winterbottom's figure 24. In other words, we believe that Winterbottom included the posterior levator, the 4th levator externus, and some non-muscular tissue lying above and between these muscles, in the 'muscle' he identified as the 4th levator externus.

In the clupeoids we examined, the protractor pectoralis and the levator posterior share a common site of origin and often a common tendon of attachment to that site. Both muscles are closely apposed to the surface of the epaxial body muscles which lie dorsal and medial to them, and both are often difficult to locate.

The clupeoid fourth levator externus muscle is much thicker and more nearly spindle-shaped than are the protractor pectoralis and posterior levator muscles. Its origin is contiguous with those of the other levators and is thus well separated from the origin of the posterior levator. It inserts on the dorso-medial angle of the enlarged 4th epibranchial. In contrast, the posterior levator inserts broadly along and behind almost the entire dorsal margin of that epibranchial.

As in many other teleosts, the origin of the presumed protractor pectoralis in clupeoids is closely associated with the origin of the levator posterior, the muscle is well separated from the origins of the levatores externi and interni muscles, and it inserts onto the cleithrum. We therefore consider that, within the terms of reference available to us and other workers, the muscle in clupeomorphs is homologous with the muscle identified as a protractor pectoralis in other teleosts.

Clearly, the presence of a protractor pectoralis muscle cannot be taken as a synapomorphy for the eurypterygian neoteleosts (see Rosen, 1973), a conclusion which is supported by evidence from many other taxa, and which will be discussed further below (p. 232). Parenthetically we note that the interrelationships of the protractor pectoralis and the levator posterior muscles have been the cause of confusion on previous occasions, as is shown by Winterbottom's (1974 : 269) lucid unravelling of that problem in Edgeworth's account of the so-called cucullaris and cephaloclavicularis muscles (Edgeworth, 1935 : 131–143).

Materials and methods

The comparative anatomy of the protractor pectoralis muscle was examined in over 250 taxa of primitive gnathostomes. In Table I we list the species examined, the presence or absence of the protractor pectoralis in each taxon, an indication of whether further comments on the anatomy will be given in the text (see pp. 222–232), and the register number(s) for the specimen(s) examined. All specimens are from the British Museum (Natural History) fish collection unless otherwise noted: the abbreviation 'MCZ' before a number indicates a specimen in the collection of the Museum of Comparative Zoology, Harvard University, and 'I.O.S.' refers to the Institute of Oceanographic Sciences' *Discovery* collection station number. A figure in parenthesis after the register numbers indicates the number of specimens which were examined from that particular lot.

The protractor pectoralis muscle is often extremely thin, and great care must be exercised when dissecting to prevent accidental removal of the muscle. In particular, removal of gill filaments from the arches, and the superficial fascia covering the dorsal branchial muscles laterally, should be done with caution. Portions of the pectoral girdle, especially the post-temporal, supracleithrum, and dorsal aspect of the cleithrum, were often removed to enable obliquus superioris muscle fibres to be distinguished from those of the protractor pectoralis.

The muscle nomenclature in this paper follows that of Winterbottom (1974) because of its general acceptance by investigators of teleostean morphology. We realize, however, that in studies of other basal gnathostome groups use of the term 'trapezius' has become common for a muscle which we consider to be homologous with the protractor pectoralis.

Taxon	Protractor pectoralis Present	Absent	Annotations in text (pp. 222–232)	Register number
ELASMOBRANCHIOMORPHI			+	
Centrophorus sp. (embryo)	+			1973.7.12 : 18–21
Hexanchus sp. (embryo)	+			1973.7.12 : 1–3
Scyliorhinus caniculus	+			1961.10.10 : 1–11
ACTINISTIA			+	
Latimeria chalumnae		+		BMNH uncatalogued
DIPNOI			+	
Neoceratodus forsteri	+		+	1959.8.11 : 12
Protopterus aethiopicus	+		+	1957.6.11 : 1–4
ACTINOPTERYGII				
Acipenseriformes				
Acipenser schrencki	+		+	1925.8.6 : 3
Polypteriformes				
Calamoichthys calabaricus	+		+	1894.7.30 : 14–15
Polypterus bichir		+	+	1928.7.3 : 1
Polypterus ornatipinnis	+		+	BMNH uncatalogued
Polypterus senegalus		+		1969.3.17 : 1–3

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
GINGLYMODI				
Lepisosteus oculatus		+	+	MCZ 34650
Lepisosteus osseus		+	+	MCZ uncatalogued
HALECOMORPHI				
Amia calva	+		+	MCZ uncatalogued
TELEOSTEI				
Osteoglossomorpha			+	
Arapaima gigas		+		BMNH uncatalogued
Brienomyrus taverni		+		1976.10.12 : 299–302
Gnathonemus longibarbis		+		1971.6.22 : 20–27
Gymnarchus niloticus		+		1953.7.10 : 5
Heterotis niloticus		+		1969.3.26 : 43
Hiodon tergisus		+	+	BMNH uncatalogued
Hyperopisus bebe		+		1971.9.28 : 28
Mormyrops deliciosus		+		MCZ 50425
Mormyrops engystoma		+		1976.5.21 : 1–4
Mormyrus kannume		+		BMNH uncatalogued
Mormyrus macrophthalmus		+		1971.9.28 : 15–18
Notopterus kapirat		+		BMNH uncatalogued
Pantodon buchholzi		+		BMNH uncatalogued
Papyrocranus afer		+		1969.3.26 : 27
Papyrocranus afer		+		1977.11.8 : 16–18
Petrocephalus catostoma		+		1976.3.18 : 2372–2390
Scleropages formosus		+		1962.9.5 : 2–6 (2)
Xenomystus nigri		+		BMNH uncatalogued
Elopomorpha				
Albula vulpes		+		MCZ 18064
Albula vulpes		+		1955.9.19 : 875–878
Anguilla anguilla		+		1962.6.29 : 11–42
Elops hawaiensis		+		1962.4.3 : 1–25
Elops machnata		+		1962.3.26 : 1–8
Halosaurus guentheri		+		1966.10.14 : 1–2
Megalops atlanticus		+		BMNH uncatalogued
Nemichthys scolopaceus		+		1968.3.2 : 1
Notacanthus bonaparti		+		1973.10.29 : 161–183
Clupeomorpha			+	
Alosa pseudoharengus	+			1974.6.25 : 540–559
Alosa pseudoharengus	+			MCZ uncatalogued
Anchoa hepsetus		+		1974.6.26 : 1916–1945
Anchoa spinifer		+	+	1974.6.26 : 947–956
Anchoa spinifer		+		1974.7.29 : 10–13
Brevoortia tyrannus	+			1974.7.26 : 60–84
Chirocentrus dorab	+		+	1966.11.16 : 3–4
Clupea harengus	+		+	1970.2.17 : 2–20
Cynothrissa mento	+		+	1967.12.29 : 1–79
Denticeps clupeoides		+	+	1969.4.28 : 1–4
Dorosoma cepedianum	+			1974.7.20 : 90–95
Dussumieria acuta	+			1935.9.20 : 1–8
Dussumieria hasseltii	+			1964.12.14 : 1–24
Engraulis edentulus		+		1976.4.30 : 14–19

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
Engraulis japonica		+		1969.4.22 : 1667–1676
Etrumeus teres	+			1974.6.19 : 4–11
Gilchristella sp.		+		1973.2.9 : 1–30
Jenkinsia stolifera		+		1972.5.4 : 55–56
Nematalosa come	+			1974.5.25 : 21–26
Neopisthopterus sp.		+		1974.7.11 : 559–578
Odontognathus panamensis	+			1974.6.26 : 7–9
Odontognathus panamensis	+			1974.7.11 : 79–123
Opisthopterus dovi	+			1974.6.26 : 139–147
Pellonula afzeliusi		+		1970.9.24 : 64–83
Sardinella jussieu	+			1966.11.16 : 20–27
Sprattus sprattus	+			1939.2.21 : 5–7
Stolephorus commersonii		+		1969.4.22 : 333–341
Stolephorus indicus		+		1969.4.22 : 2–6
Stolephorus heterolobus		+		1967.11.13 : 310–318
OSTARIOPHYSI			+	
ANOTOPHYSI				
Chanos chanos	+		+	1964.12.18 : 382
Chanos chanos	+			MCZ uncatalogued
Gonorynchus gonorynchus	+		+	BMNH uncatalogued
Phractolaemus ansorgii	+		+	1979.3.5 : 217–219
OTOPHYSI				
Cypriniformes				
Abramis brama		+		1974.9.5 : 1–31
Aspius vorax		+		1920.1.22 : 127–146
Barbus barbus	+		+	1864.4.11 : 41–42
Barbus intermedius australis		+	+	1980.4.18 : 79–83
Barilius bendelisis		+		1970.12.14 : 208–228
Capoeta capoeta		+		1958.11.7 : 7–10
Carassius auratus	+			1973.1.22 : 91–100
Catostomus commersonii	+			1973.1.22 : 41–44
Cobitis caspia romanica	+			1957.12.9 : 293–297
Cyprinus carpio	+		+	1977.7.19 : 1–4
Cyprinus carpio	+			MCZ uncatalogued
Gyrinocheilus aymonieri	+			1957.2.26 : 8–107
Noemacheilus barbatulus	+			1969.6.12 : 13–24
Notemigonus crysoleucas		+		MCZ uncatalogued
Opsariichthys uncirostris	+			1923.3.5 : 6–12
Opsariichthys uncirostris	+			1902.5.30 : 45–54
Opsaridium ubangensis	+			1978.8.3 : 59–113
Oxygaster anomalura		+		1978.9.5 : 5–7
Rutilus rutilus		+		BMNH uncatalogued
Tinca tinca	+			1970.9.24 : 238–240
Characiformes				
Alestes nurse	+			BMNH uncatalogued
Alestes rutilus	+			1977.11.16 : 25–35
Brycon dentex	+			MCZ uncatalogued
Brycon falcatus	+			1972.10.17 : 1398–1411
Erythrinus erythrinus	+			1971.11.26 : 5–7
Hoplias malabaricus	+			1974.5.22 : 154–173
Pyrrhulina filamentosa	+			1926.3.2 : 74–90

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
Gymnotoidei				
Apteronotus albifrons	+			1972.7.27 : 536–537
Gymnotus anguillaris	+			1972.10.17 : 414–423
Hypopomus artedi	+			1972.7.27 : 447–450
Siluroidei				
Arius heudeloti	+			1971.9.28 : 118–121
Diplomystes papillosus	+			MCZ 8290
Mystus cavisus	+			1976.7.1 : 32–34
PROTACANTHOPTERYGII			+	
Alepocephalus agassizii		+		1977.6.23 : 1–6
Aplochiton zebra		+		1912.12.20 : 18–19
Argentina sphyraena		+		1971.7.21 : 22–24
Argentina sphyraena		+		1970.2.17 : 87–107
Bathylagus sp.		+		1930.1.12 : 50–59
Coregonus albula		+		1906.12.5 : 1–3
Dallia pectoralis	+		+	MCZ uncatalogued
Dallia pectoralis	+			1883.12.14 : 172
Esox americanus		+		1963.2.9 : 5–9
Esox niger		+		MCZ uncatalogued
Galaxias auratus		+		1972.1.27 : 15–18
Galaxias brevipinnis	+			1964.4.30 : 32
Galaxias maculatus		+		1894.4.13 : 51–59
Galaxias vulgaris	+			1965.12.16 : 37–46
Galaxias waitei		+		1914.8.20 : 44–45
Galaxias weedoni	+			1972.1.27 : 10–14
Novumbra hubbsi		+		1965.10.19 : 17–23
Opisthoproctus soleatus	+			1934.12.19 : 1
Osmerus eperlanus		+		1979.11.26 : 11–223
Osmerus mordax		+		1963.10.28 : 16–25
Plecoglossus altivelis		+		1923.2.26 : 121
Plecoglossus altivelis		+		1965.5.2 : 43–48
Retropinna retropinna		+		1035.3.14 : 14–27
Retropinna retropinna		+		1930.2.5 : 1
Salmo trutta		+		1936.11.13 : 1–2
Thymallus thymallus		+		1979.6.22 : 226–238
Umbra krameri		+		1883.12.14 : 172
Umbra limi		+		MCZ 33124
Umbra pygmaea		+		1966.10.14 : 5–14
STENOPTERYGII				
Stomiatiformes				
Astronesthes lucifer		+		1922.6.7 : 14–23
Astronesthes niger		+		MCZ 52868
Chauliodus sloani		+		1972.2.22 : 17–19
Diplophos taenia		+		MCZ uncatalogued
Gonostoma elongatum		+		MCZ 42184
Photichthys argenteus		+		1930.1.12 : 299–306
Sternoptyx diaphana		+		1969.6.26 : 425–434
Stomias boa		+		BMNH uncatalogued

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
CYCLOSQUAMATA				
Aulopiformes			+	
Aulopus filamentosus	+			1953.11.1 : 10–13
Bathysaurus agassizi	+			MCZ uncatalogued (2)
Chlorophthalmus agassizi	+			MCZ 40530
Evermanella atrata	+			I.O.S. 5420
Evermanella balbo	+			I.O.S. 7824, ♯24
Evermanella indica	+			I.O.S. 4947
Evermanella normalops	+			I.O.S. 7089, ♯24
Harpadon macrochir	+			MCZ 44232
Paralepis elongata	+			MCZ 43140
Saurida undosquamis	+			MCZ 56111
SCOPELOMORPHA				
Myctophiformes				
Diaphus fragilis		+		MCZ uncatalogued
Electrona antarctica	+			1970.8.11 : 1–2
Gymnoscopelus aphya		+		1970.8.11 : 99–112
Lampadena speculigera	+			1962.1.3 : 11–12
Neoscopelus microchir	+			1939.5.24 : 475–483
Notoscopelus kroyeri	+			MCZ 55532
Scopelopsis multipunctatus		+		1976.9.29 : 31–32
Scopelus humboldti	+			1926.6.30 : 6–8
PARACANTHOPTERYGII				
Amblyopsis spelaea	+			1858.5.10 : 1–5
Antennarius altipinnis	+			1969.8.26 : 308–310
Aphredoderus sayanus	+			1898.12.29 : 141–149
Carapus acus	+			1952.11.25 : 1–4
Coelorhynchus occa	+			1974.6.27 : 1–6
Gadus ogac	+			MCZ 52937
Gobiesox papillifer	+			MCZ 44836
Lophius budegassa	+			1928.9.18 : 91–92
Lycodonus mirabilis	+			MCZ 38301
Malacocephalus laevis	+			MCZ 44993
Muraenolepis microps	+			1937.7.12 : 11–17
Ophiodon rochei	+			1971.12.17 : 6–8
Percopsis omiscomaycus	+			MCZ 54922
Porichthys notatus	+			MCZ uncatalogued
Porichthys porosissimus	+			1961.9.4 : 171–173
ACANTHOPTERYGII				
Atherinomorpha			+	
Anableps anableps	+			1973.9.13 : 33–36
Aphanius dispar	+			1973.9.10 : 154–194
Atherina duodecimalis	+			1974.5.25 : 3681–3697
Cyprinodon pecosensis	+			1978.8.1 : 303–502
Exocoetus obtusirostris	+			MCZ 42538
Fundulus heteroclitus	+			MCZ 51871
Lamprichthys tanganicanus	+			1955.12.20 : 1449–1465
Melanotaenia nigrans	+			1975.3.20 : 119–186
Menidia menidia	+			MCZ uncatalogued
Neostethus lankesteri	+			1970.7.22 : 71–77

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
Oryzias latipes	+			1923.2.26 : 160–169
Parexocoetus brachypterus	+			1967.2.1 : 53–57
Poecilia reticulata	+			1972.9.27 : 95–129
Potamorrhaphis guianensis	+			1972.7.27 : 1014–1019
Scomberesox saurus	+			BMNH uncatalogued
Percomorpha				
Ammodytes hexapterus	+			1968.8.6 : 91–116
Anabas testudineus	+			1970.9.3 : 367–386
Archamia zosterophora	+			1974.5.25 : 1548–1560
Ariomma indicus	+			1979.7.4 : 5–8
Aulostomus chinensis	+			1960.3.10 : 7–14
Bothus podas	+			1938.11.15 : 54–55
Brachydeuterus auritus	+			1962.9.18 : 109–117
Callionymus lyra	+			1962.6.1 : 15–29
Capros aper	+			1963.5.14 : 230–239
Caranx malabaricus	+			1976.5.10 : 4–6
Centropyge bispinosus	+			BMNH uncatalogued
Congiopodus perorianus	+			1936.8.26 : 1100–1104
Cottus gobio	+			1974.9.20 : 45–55
Cyclopterus lumpus	+			1968.12.31 : 2
Dactylopterus volitans	+			1967.2.1 : 308–311
Epinephelus aeneus	+		+	1967.2.1 : 73–76
Eupomacentrus fasciolatus	+			1977.4.4 : 81–84
Gerres poeti	+		+	1974.5.25 : 2432–2436
Gobius niger	+			1971.2.16 : 1072–1081
Grammistes sexlineatus	+		+	1951.1.16 : 145–147
Gymnocephalus cernua	+			1961.4.19 : 106–115
Holocentrus spinifer	+			1960.3.15 : 170–172
Holocentrus suborbitalis	+			MCZ 43537
Hoplichthys acanthopleurus	+			1939.5.24 : 1684–1695
Hoplolatilus starcki	+		+	BMNH uncatalogued
Kutaflammeo sammara	+			1974.5.25 : 814–818
Kyphosus cuierasceus	+			1960.3.15 : 914–918
Lates microlepis	+		+	1975.8.15 : 16–33
Lepomis auritus	+			1973.1.22 : 105–112
Liparis liparis	+		+	1971.2.16 : 749–754
Lutjanus synagris	+			1976.7.14 : 209–212
Macrorhamphosus gracilis	+		+	1962.12.20 : 21–26
Mastacembelus albomaculatus	+			MCZ 49212
Monocirrhus polyacanthus	+			MCZ 46017
Monopterus albus	+		+	1976.4.2 : 77–83
Mugil cephalus	+			1975.8.15 : 204–212
Nandus nebulosus	+		+	1957.2.27 : 1–4
Notothenia larseni	+			1939.7.12
Ophioblennius steindachneri	+			1955.5.12 : 1–6
Ostichthys murdjan	+			1974.5.25 : 738–739
Pachypops fourcroi	+			1964.7.9 : 193–196
Parapercis cephalopunctata	+			1974.5.25 : 3288–3298
Pelates quadrilineatus	+			1974.5.25 : 839–855
Phanerodon furcatus	+			1979.10.16 : 16–29
Platycephalus mulleri	+		+	1974.5.25 : 4027–4028
Pleuronectes platessa	+			1971.2.16 : 1992–1993

Table 1 cont.

Taxon	Protractor pectoralis Present	Protractor pectoralis Absent	Annotations in text (pp. 222–232)	Register number
Polymixia nobilis	+			1862.4.22 : 17–18
Pomacanthus arctifrons	+			1938.12.12 : 90–94
Psettodes erumei	+			1933.7.31 : 1–2
Scomber japonicus	+			1967.2.1 : 41–44
Scorpaenodes insularis	+			1979.1.5 : 234–236
Sebastes crameri	+		+	1967.3.5 : 298–318
Solea solea	+			1971.2.16 : 118–127
Sphyraena chrysotaenia	+			1973.7.26 : 2–13
Stephanoberyx monae		+	+	1972.10.24 : 2–3
Synbranchus marmoratus	+		+	1925.10.28 : 24
Syngnathus acus	+			1971.2.16 : 322–327
Tautogolabrus sp.	+			BMNH uncatalogued
Thalassoma purpureum	+			1978.9.15 : 4–8
Trachipterus taenia	+		+	1891.8.31 : 27–35
Trichogaster pectoralis	+			1970.9.3 : 418–427
Uranoscopus scaber	+			1978.1.17 : 57–61
Zaniolepis latipinnis	+			1967.3.5 : 354–385
Zeus faber	+		+	MCZ 41388
Zeus faber	+			1971.7.21 : 86–90

Comments on the protractor pectoralis muscle in certain taxa

ELASMOBRANCHIOMORPHI

In selachians the protractor pectoralis (=trapezius or cucullaris of authors) originates from the fascia covering the epaxial muscles laterally (Fig. 1). The fibres extend posteroventrally to insert on the pectoral girdle. Medial to the protractor pectoralis, another muscle, which appears to be an epaxialis derivative, extends anteriorly from the dorsal aspect of the pectoral girdle to merge with epaxial muscle fibres. The fibres of this muscle lie at 90° to those of the protractor pectoralis.

Anterior to the protractor pectoralis a muscle runs posteroventrally from the epaxialis fascia to insert on the posterodorsal aspect of the last gill arch (Fig. 1). We consider this muscle to represent an anterior division of the protractor pectoralis, as did Allis (1917) and Edgeworth (1935 : 141).

The protractor pectoralis lies medial to the branchial constrictor muscles although both share a common origin from the epaxial muscle fascia. Levator arcuum branchialum muscles are absent in selachians.

ACTINISTIA

Millot & Anthony (1958 : 63, fig. 29) do not describe a protractor pectoralis muscle (or a muscle with the anatomical relationships of the protractor) in adult *Latimeria chalumnae.* We have dissected and made observations on a 32 cm foetus, and also find no trace of the muscle.

DIPNOI

Neoceratodus forsteri. The protractor pectoralis is a well-developed and distally expansive muscle (Fig. 2). Its narrow origin lies immediately posterior to the common origin of the 3rd

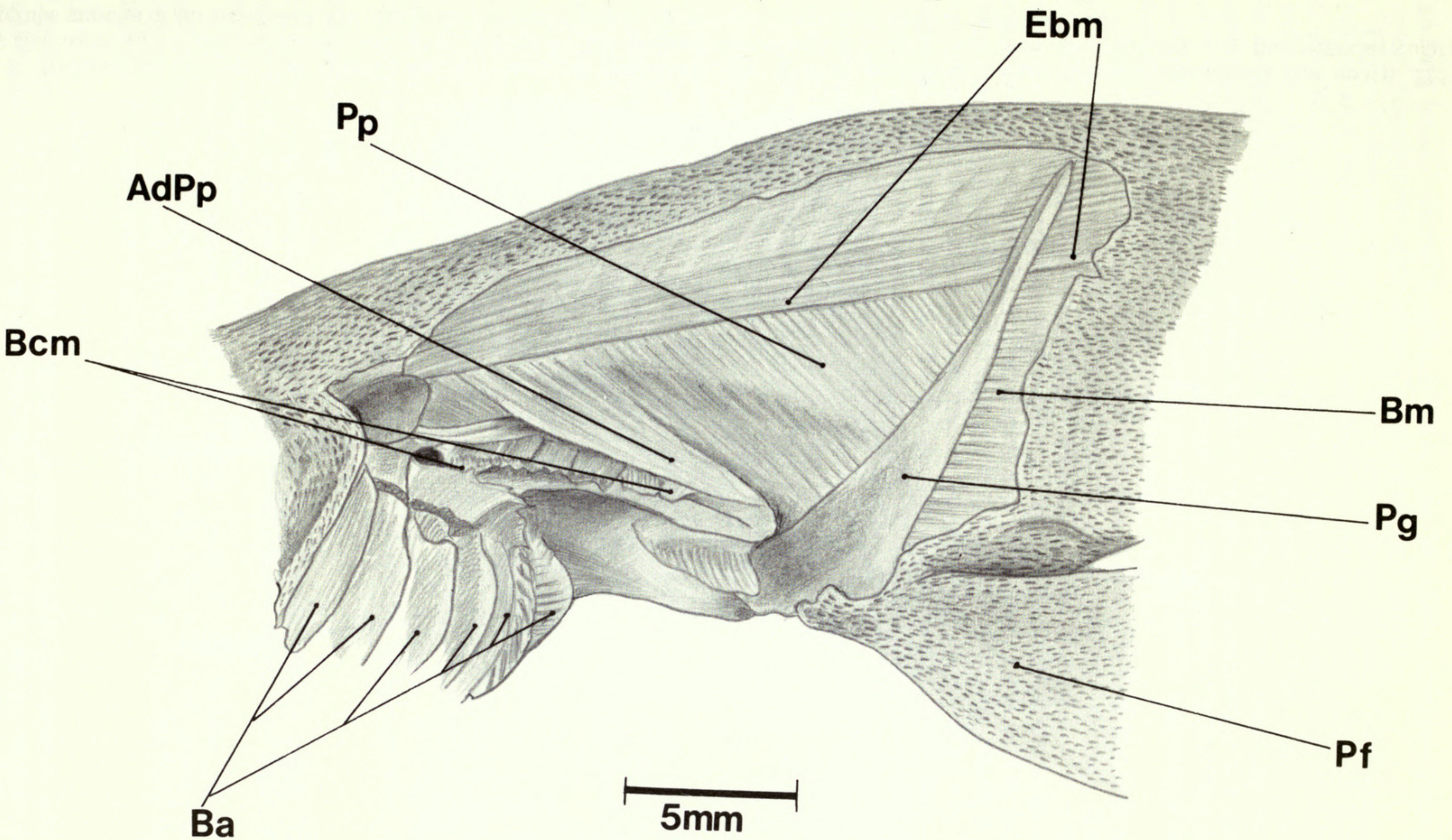

Fig. 1 *Hexanchus* sp., foetus *ca* 382 mm total length (oblique dorsolateral view, left side; first five gill arches reflected forwards). AdPp: anterior division of the protractor pectoralis muscle inserting onto 6th gill arch. Ba: branchial arches 1–6, cut dorsally and reflected forward. Bcm: cut dorsal ends of branchial muscles. Bm: body muscles. Ebm: epaxial body muscles. Pf: pectoral fin. Pg: pectoral girdle. Pp: protractor pectoralis muscle. Drawn from specimen BMNH 1973.7.12 : 1–3.

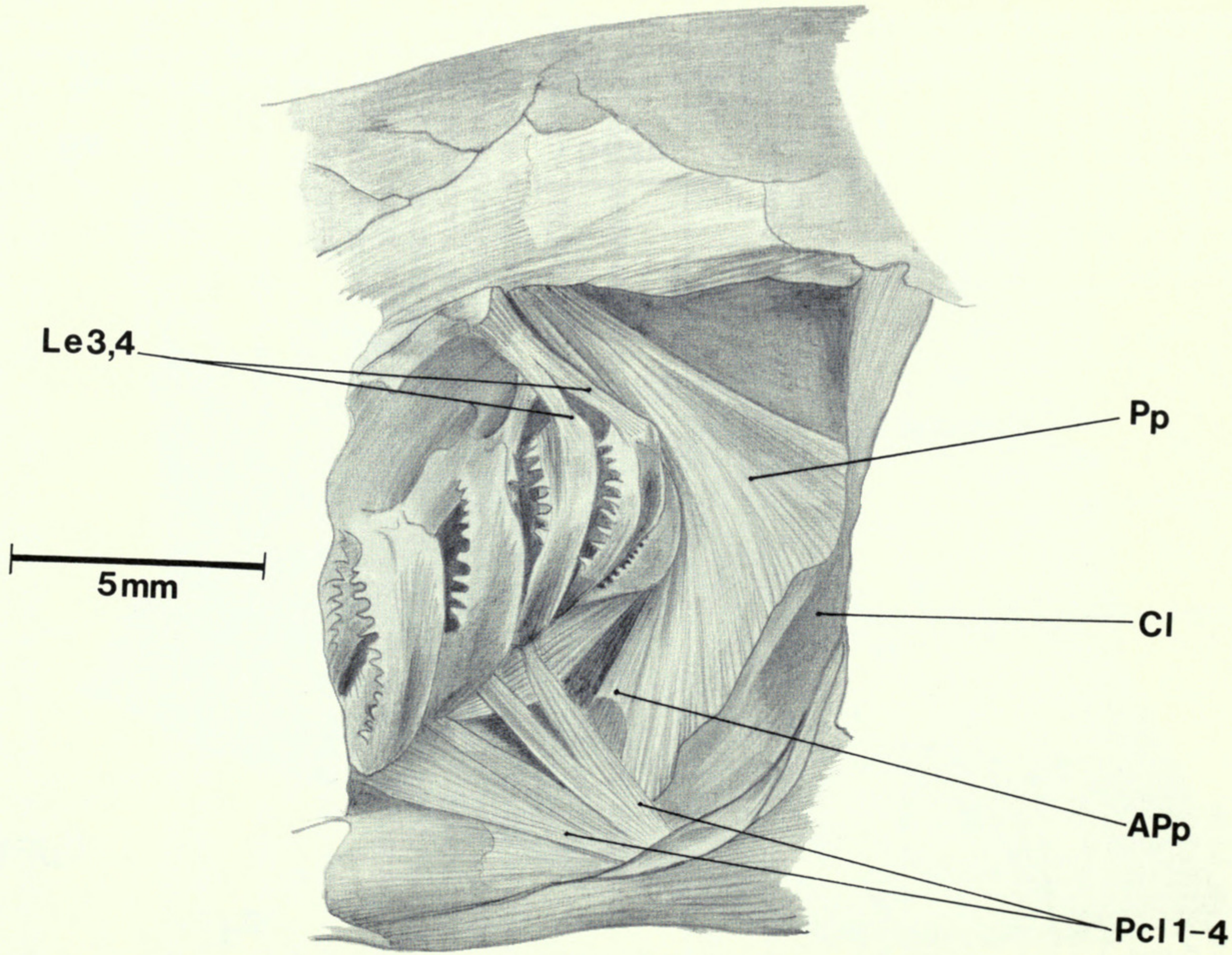

Fig. 2 *Neoceratodus forsteri* (left lateral view; gill filaments removed). APp: anterior portion of protractor pectoralis muscle (see text p. 225). Cl: cleithrum. Le3,4: external levator muscles of 3rd and 4th gill arches (those of arches 1 and 2 have been removed). PcL 1–4: pharyngoclavicularis internus muscles of gill arches 1–4. Pp: protractor pectoralis muscle. Drawn from specimen BMNH 1969.8.11 : 12.

and 4th levator externi muscles; it has a wide, musculose insertion onto the cleithrum, its antero-posterior orientation being almost in the sagittal plane.

From its apparent anterior face some fibres attach dorsally to the posterior aspect of the 5th gill arch, immediately above the origin of the subarcualis rectus of Wiley (1979 : fig. 4). Unlike Wiley, we cannot identify a separate pharyngoclavicularis internus muscle associated with the 5th gill arch. Possibly the muscle he illustrates is what, in our specimen, appears to be the anterior portion of the protractor pectoralis. In other words, the two muscles in this specimen are so closely contiguous that they give the appearance of a single muscle. The fibre orientation of this anterior muscle (if it be separate) is like that in the protractor pectoralis itself, and its attachment to the cleithrum is medial and ventral to the attachment area of the pharyngoclavicularis muscles from arches 1–4.

Protopterus aethiopicus. A protractor muscle, originating from the posterior margin of the cartilaginous skull broadens out from its narrow point of origin to insert, tendinously, on the cleithrum. The muscle, as compared with that in *Neoceratodus*, is narrow and instead of having a simple inverted fan-shape has a slightly concave and twisted anterior margin which, again unlike *Neoceratodus*, is aligned almost at right angles to the sagittal plane; posteriorly a short length of the muscle lies in that plane. Continuous with the muscle's posterior margin are several much more expansive muscle bundles. These are apparently derived from the hypaxial body musculature; dorsally the muscles attach to the horizontal septum, and posteriorly they continue beyond the girdle but give off fibres which insert on the anterior face of the cleithrum as the main muscle mass passes below that bone. Careful dissection shows that the apparent continuity of fibres from the branchial protractor pectoralis with those of the hypaxial pseudo-protractor is in fact false; the two muscles are separated by a very narrow hiatus obscured by the rather dense tissue overlying them.

ACTINOPTERYGII

Acipenseriformes

Acipenser schrencki. The very well-developed, broad and thick protractor pectoralis originates along the posterior transverse region of the skull and inserts on the cleithrum. Its origin is clearly separated from that of the muscle plate representing the levators of the 3rd and 4th gill arches.

Sewertzoff's (1928) embryological studies of the cranial muscles in *Acipenser ruthenus* clearly demonstrate the common origin of the branchial levators, and the derivation of the protractor pectoralis, from the posterior part of the same plate.

The muscle's ontogenetic history in other chondrosteans is less clear (see Edgeworth, 1935 : 142) and would repay further investigations on both embryological and adult material. According to Edgeworth *(loc. cit.)* the muscle is absent in *A. sturio* '. . . possibly by atrophy during developmental stages owing to the fixation of the pectoral girdle'.

Polypteriformes

Polypterus ornatipinnis. The protractor in this species in a thin, largely tendinous muscle which shares its origin with the 3rd and 4th levatores externi, and inserts on the cleithrum near its point of maximum curvature.

Calamoichthys calabaricus. In this species, unlike *P. ornatipinnis*, the protractor is large and noticeably broader distally than proximally. As in *P. ornatipinnis* it has a common origin with the 3rd and 4th levatores externi but inserts onto the cleithrum at a point slightly dorsal to the bone's region of maximum curvature.

GINGLYMODI

Lepisosteus osseus lacks both protractor pectoralis and levator posterior muscles. Just dorsal to the origin of the fourth levator externus, the obliquus superioris inserts tendinously on the skull. In *Lepisosteus oculatus* some lateral fibres of the obliquus superioris insert on a medial flange of the supracleithrum, but no protractor pectoralis is present.

HALECOMORPHI

Amia calva possesses a well-developed protractor pectoralis (=fifth levator externus of Allis, 1897). The protractor pectoralis originates from the otic region of the skull and inserts *via* a long tendon onto the cleithrum.

TELEOSTEI

OSTEOGLOSSOMORPHA

The osteoglossomorph fishes lack both a protractor pectoralis (Table 1) and a levator posterior muscle. Winterbottom (1974 : 252) noted that the levator posterior is confined to the neoteleosts (in his usage of the category) with the exception of *Hiodon.* We find that *Hiodon* lacks the levator posterior and possesses a posteriorly displaced origin of the fourth levator externus due to the large swimbladder extension in the otic region.

CLUPEOMORPHA

Some comments on the protractor pectoralis of clupeomorph fishes have been made already (p. 215).

In none of the clupeid and chirocentrid species we have examined is the muscle well-developed; usually it is mainly tendinous, flat and narrow, and invariably it is closely applied to the ventro-anterior face of the overlying body muscles. Often part of the protractor pectoralis inserts on the supracleithrum.

A protractor pectoralis muscle is absent in all the engraulid species examined, and apparently, in the sole extant representative of the Denticipitoidei, *Denticeps clupeoides.* However, because the only specimens of *Denticeps* available are small (*ca* 50 mm SL), a narrow, thin muscle could easily be overlooked. The muscle is present in a large proportion of the Clupeidae *(sensu lato)* we examined (Fig. 3).

A levator posterior muscle occurs in the majority of clupeomorph taxa we dissected. Its origin is shared with, or is very close to, that of the protractor pectoralis. In general it too is a thin, narrow and partly tendinous muscle, and is always closely applied to the ventro-anterior face of the body musculature (Fig. 3).

No levator posterior was found in the engraulid *Anchoa spinifer* (although the muscle is present in *A. heterolobus).* It also appears to be absent in the chirocentrid *Chirocentrus dorab,* unless, atypically, it is closely associated with the 4th external levator muscle which, in this species, seems to be composed of two very closely contiguous parts. We are uncertain about the condition in the denticipitoids because of the small size of the available specimens.

The presence of a levator posterior in many clupeomorph fishes contradicts Winterbottom's (1974 : 252) statement about the occurrence of that muscle within the teleosts, namely, that apart from its occurrence in the osteoglossomorph *Hiodon,* it is a neoteleostean feature (see also above). It also contradicts his suggestions about a possible origin for the posterior levator from a condition like that supposedly occurring in the clupeomorphs (Winterbottom, *loc. cit.*). As noted already (p. 215), and in contradistinction to Winterbottom's observations, none of the clupeoids we examined showed any continuity of fibres between the 4th external levator and '. . . a thin sheet of muscle whose origin extends to the posterolateral tip of the pterotic' (the condition which Winterbottom considered to be the typical clupeomorph one). Our interpretation of the clupeomorph condition is that part of Winterbottom's 'thin sheet of muscle . . .' is the levator posterior muscle, but that the area of tissue between it and the 4th levator externus is devoid of muscle fibres, and consequently the two muscles are distinct from one another (see also p. 215).

OSTARIOPHYSI

A protractor pectoralis is present in some or all taxa of every otophysan subdivision (see Table 1; also Winterbottom, 1974; figs 20, 21 & 22), and apparently is absent only in certain

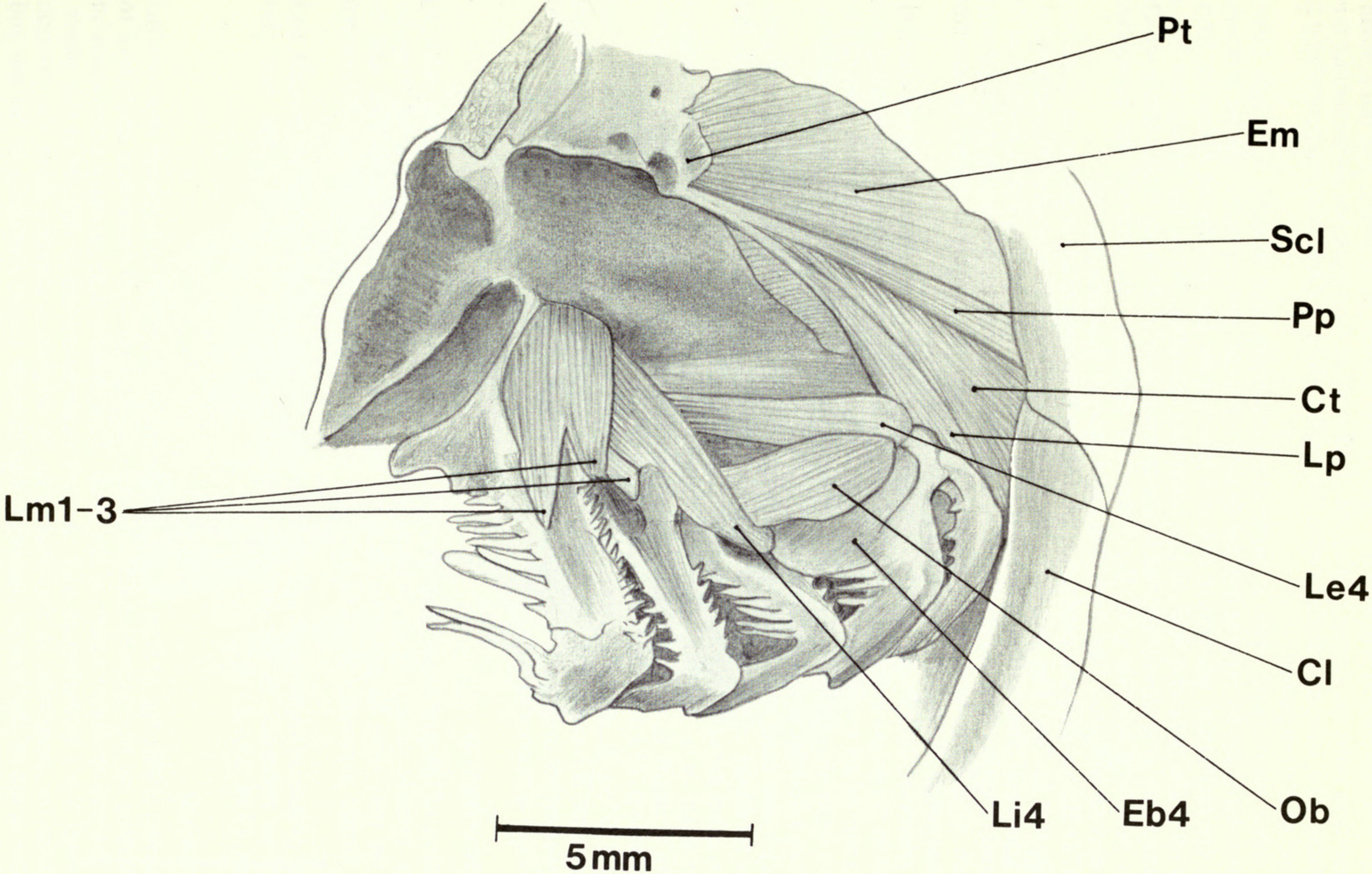

Fig. 3 *Cynothrissa mento* (slightly oblique ventrolateral view, left side; gill filaments removed). Cl: cleithrum. Ct: connective tissue overlying body musculature in posterior region of branchial cavity. Eb4: expanded 4th epibranchial bone. Em: epaxial body musculature. Le4: 4th external levator muscle. Li4: 4th internal levator muscle. Lm: 1–3: levator muscles of 1st–3rd gill arches. Lp: levator posterior muscle. Ob: obliquus dorsalis muscle. Pp: protractor pectoralis muscle. Pt: pterotic. Scl: supracleithrum. Drawn from specimen BMNH 1967.7.12.29 : 1–79.

cypriniform taxa. It is well-developed in the three members of the anotophysi we dissected, particularly in *Chanos chanos* where it is a thick, deep muscle proximally, and has a broad, tendinous insertion onto the upper half of the cleithrum; in *Gonorynchus gonorynchus* it is narrow and strap-like, inserting directly onto the girdle, while in *Phractolaemus ansorgii* it is broad, thin and partly tendinous.

Amongst those otophysans with a protractor pectoralis, the muscle, although intraspecifically constant, shows varying degrees of development; also, in some species it inserts directly onto the cleithrum, whereas in others it inserts onto the membrane extending from the girdle to form the posterior wall of the branchial chamber. When the protractor has a 'membrane insertion' it is closely applied to the anterior face of the body musculature which delimits the posterior boundary of the branchial chamber. In general, the protractor pectoralis is narrow and strap-like, and often has a near-vertical orientation.

Vetter (1878) claims that the protractor pectoralis (his trapezius), is absent in *Cyprinus carpio* and *Barbus barbus*. The muscle certainly is present in *C. carpio* (see Winterbottom, 1974, fig. 22; personal observations), but may have been overlooked by Vetter because of its slenderness and its rather tendinous nature. A short, fine, protractor pectoralis is also present in a specimen of *Barbus barbus* we dissected, although the muscle is absent in another member of that genus, *B. intermedius,* from Kenya, east Africa.

A levator posterior muscle appears to be absent in some anotophysans *(Chanos chanos)*, but is present in *Gonorynchus gonorynchus.* Its absence in *Chanos* could be correlated with the development of an expansive and complex suprabranchial organ in that genus. The muscle is seemingly also absent in *Phractolaemus ansorgii,* but the condition of our material does not permit a definite conclusion on that point.

All the otophysan taxa examined have a levator posterior muscle; it is particularly well-developed in members of the Cypriniformes (see also Winterbottom, 1974; 252–253, figs 20–22), but in other groups it is often a slender strap-like muscle.

The occurrence of a levator posterior muscle in the Ostariophysi further negates Winterbottom's claim that its presence is a neoteleostean feature (see above [Clupeomorpha], and also p. 213 regarding that author's handling of the category Ostariophysi).

Brousseau (1976*a* & *b*) has described parts of the branchial musculature in six ostariophysan taxa. It is clear from his descriptions and figures that, depending on the species involved, he has either misidentified the protractor pectoralis, or confused and compounded it with the levator posterior muscle.

PROTACANTHOPTERYGII

The distribution of the protractor pectoralis in this group is exceedingly irregular, with, in addition, the muscle occurring in relatively few taxa. As an example of its irregular occurrence, we may note its presence in some but not in other *Galaxias* species, and its presence in *Dallia pectoralis* (Fig. 4) but not in *Umbra limi, U. krameri* or *Novumbra hubbsi.*

None of the protacanthopterygian species we examined has a levator posterior muscle, and we can find no reference in the literature to its occurrence in these fishes (see also Winterbottom, 1974: 252–253).

ACANTHOPTERYGII

Lauder & Lanyon (1980: fig. 2) identified as a protractor pectoralis in *Lepomis macrochirus* a muscle inserting on the supracleithrum and posttemporal, and extending anteriorly to originate on the posterodorsal aspect of the skull. This muscle is apparently a derivative of the epaxialis and is not homologous with the protractor pectoralis as defined in this paper. The true protractor pectoralis in *Lepomis* (Fig. 5) originates dorsally from the pterotic adjacent to the origin of the levator posterior, and extends posteroventrally to fan out and insert in the connective tissue between the last gill arch and the cleithrum. No fibres of the protractor pectoralis contact the cleithrum.

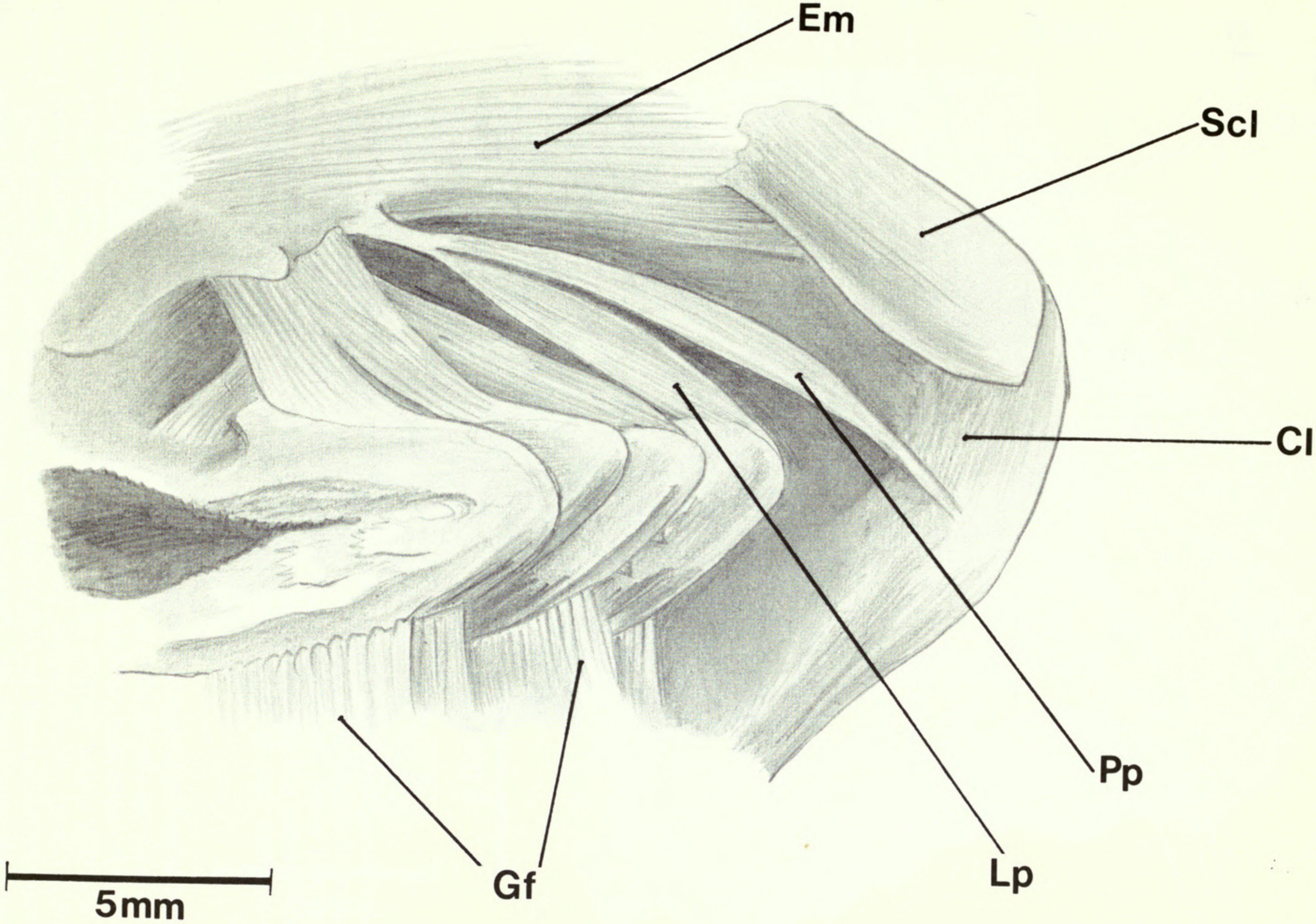

Fig. 4 *Dallia pectoralis* (slightly oblique ventrolateral view, left side, upper gill filaments removed). Cl: cleithrum. Em: epaxial body musculature. Gf: gill filaments. Lp: levator posterior muscle. Pp: protractor pectoralis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1883:12.12 : 172.

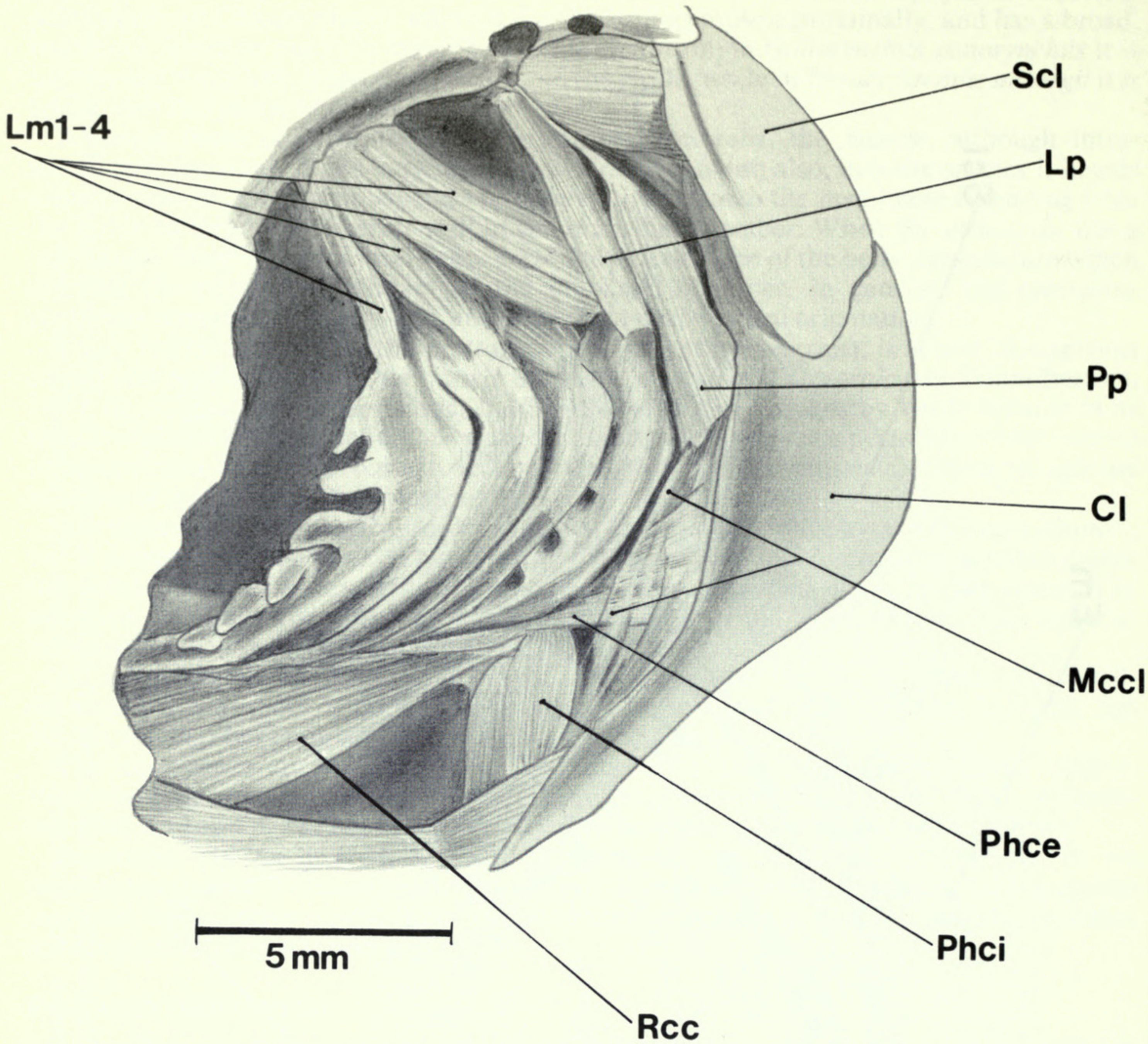

Fig. 5 *Lepomis auritus* (lateral view, left side; gill filaments removed). Cl: cleithrum. Lm 1–4: levator muscles of 1st–4th gill arches. Lp: levator posterior muscle. Mccl: membrane overlying cleithrum and distal part of pharyngocleithralis externus muscle. Phce & Phci: pharyngocleithralis internus and externus muscles, respectively. Pp: protractor pectoralis muscle. Rcc: rectus communis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1973.1.22 : 105–112.

Many other acanthopterygians also possess a thin protractor pectoralis muscle which does not insert directly on the cleithrum (*eg. Zeus, Nandus, Trachipterus, Macrorhamphosus, Sebastes*). Another common condition in the Acanthopterygii is the presence of a protractor pectoralis inserting either directly onto the cleithrum (*eg.* most atherinomorphs, cichlids, *Platycephalus, Liparis, Hoplolatilus*), or inserting onto both the connective tissue posterior to the 4th ceratobranchial and the cleithrum (*eg. Lates, Epinephalus, Grammistes, Gerres*).

In both the synbranchiform taxa examined, the protractor pectoralis is, however, a well-developed, strap-like muscle running horizontally from the skull to the pectoral girdle. In *Synbranchus marmoratus* (Fig. 6) its origin is shared with that of the branchial levator muscles, and it inserts onto the small, moveable supracleithrum. An insertion onto the cleithrum itself is precluded by the position of the gill arches, which are so positioned that

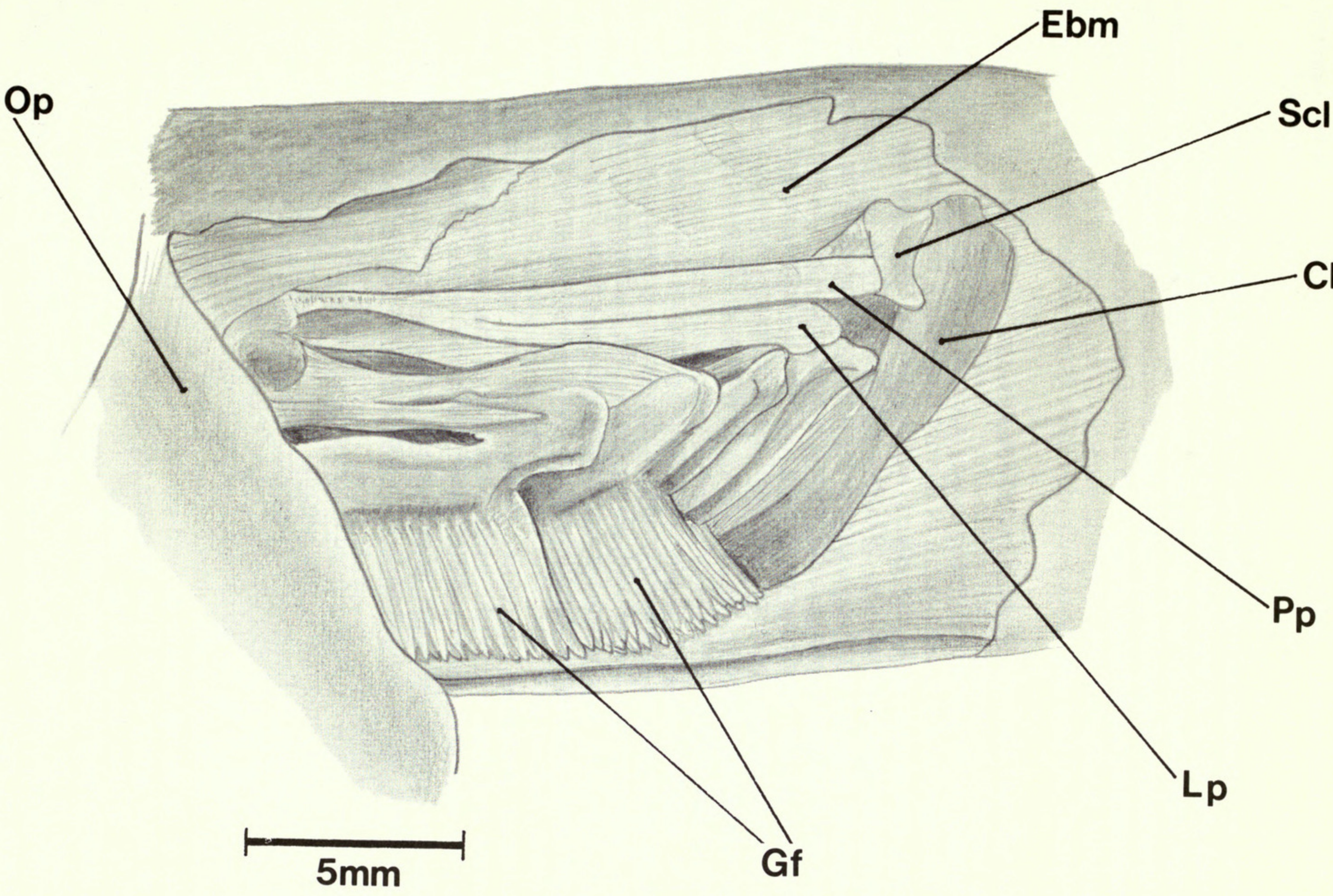

Fig. 6 *Synbranchus marmoratus* (lateral view, left side; gill filaments removed from upper parts of gill arches). Cl: cleithrum. Ebm: epaxial body muscles. Gf: gill filaments. Lp: levator posterior muscle. Op: opercular bones and membranes reflected forward. Pp: protractor pectoralis muscle. Scl: supracleithrum. Drawn from specimen BMNH 1925.10.28 : 24.

the path of the protractor is directed so as to lie above the dorsal extremity of the cleithrum. The origin of the protractor in *Monopterus albus* lies posterior to and well-separated from that of the levators, and its orientation is such that it inserts onto the dorsal tip of the cleithrum. The dorsoposterior margin of the protractor pectoralis is closely applied to the ventral margin of the supracleithrum, but no fibres from the muscle are inserted onto the bone.

The muscle in *Lepomis* identified by Lauder & Lanyon (1980, fig. 2) as a protractor pectoralis (see above), is of uncertain homology. It appears to be similar to the levator pectoralis of Winterbottom (1974: 270, and fig. 25) which has been found in batrachoids, lophiids, and tetraodontiforms. We have also found a similar muscle to the levator pectoralis in scorpaeniforms and nandids, and it may have a much wider distribution than is presently realized.

Summary and conclusions

Since our interest in the protractor pectoralis was stimulated initially by irregularities in its presumed phylogenetically based pattern of distribution within the Teleostei (see p. 213), our principal concern is with the effects additional data have on the phylogenetic conclusions reached previously (Rosen, 1973; Winterbottom, 1974).

Clearly, because of its occurrence in some or even many members of the Clupeomorpha, Ostariophysi and Protacanthopterygii, the protractor pectoralis is not, as was once thought, a feature restricted to the Neoteleostei (see pp. 217–219). Indeed, its overall pattern of occurrence extends beyond the current limits of the Euteleostei (of which the Neoteleostei are a major subdivision; Rosen, 1973; Patterson & Rosen, 1977) to include the Teleostei (*sensu* Patterson & Rosen) as a whole.

Taking the argument further: if one accepts the supposed homology of the muscle throughout the gnathostomes, the protractor pectoralis occurs in some or all members of the Neopterygii, Palaeopterygii, Dipnoi and, very probably, the Elasmobranchiomorphi as well (see pp. 214; 216–221). Amongst the major groups making up the lower gnathostomes, a protractor pectoralis is absent only in the extant Actinistia, a group represented by the single taxon *Latimeria chalumnae.*

The protractor pectoralis, therefore, would seem to be a synapomorphy of the Gnathostomata and thus, within the various lineages of that group, its presence must be treated as a plesiomorph character and not as a synapomorphy of the Teleostei in part.

Its distribution among the lower gnathostomes has a somewhat patchy pattern (see Table 1), a pattern whose patchiness is, in some respects, even more marked and more puzzling within the Teleostei.

A protractor pectoralis is not developed in the two lineages which are generally thought to be the most primitive amongst living teleosts, namely the Osteoglossomorpha and the Elopomorpha. Patterson & Rosen (1977) for example, consider the Osteoglossomorpha to be the plesiomorph sister group of all other living teleosts combined (*ie* the Elopocephala), and the Elopomorpha to be the plesiomorph sister group of the other Elopocephala (*ie* the Clupeocephala). The muscle is also absent in one 'higher' group, the Stomiatiformes, which, on the basis of its having certain derived characters, Rosen (1973: 505) identified as the plesiomorph sister group of all other lineages he brought together as the Neoteleostei (see also p. 213). Within those other lineages (*ie* the Aulopiformes, Myctophiformes, Paracanthopterygii and Acanthopterygii) a protractor pectoralis has been found in virtually all taxa placed in the supposedly 'higher' categories Paracanthopterygii and Acanthopterygii,[1] in the majority of Aulopiformes, and in many Myctophiformes as well (See Table I; also Winterbottom, 1974).

[1] The exceptional taxon is *Stephanoberyx monae;* no protractor was found in the two specimens we examined.

Among lineages which lie, cladistically speaking, between the plesiomorph Osteoglossomorpha + Elopomorpha on the one hand and the apomorphic Neoteleostei (*sensu* Rosen) on the other, the muscle occurs in most members of the Clupeomorpha and in many Ostariophysi (including the plesiomorphic Anotophysi), but is found in only a few members of the Protacanthopterygii.

An intriguing aspect of this pattern is the contrast between the absence of a protractor pectoralis (a derived condition) in the two most primitive lineages, and its presence (the primitive condition) in the more derived ones. Equally intriguing is the way the muscle, in taxa belonging to the 'intermediate' groups, may be absent in some species of a genus but not in others (for example in the protacanthopterygian genus *Galaxias*), or in some but not all members of seemingly closely related taxa (for example, again amongst the protacanthopterygians, its presence in *Dallia,* but its absence in *Umbra* and *Novumbra*). Similar patterns of presence or absence can be found within the Clupeomorpha and the Ostariophysi (see Table 1).

We can offer no explanation for these patterns, and must conclude that the presence or absence of a protractor pectoralis muscle is a feature of little value as an indicator of phyletic relationship except at a high level of universality. In other words, it is a synapomorphy of the Gnathostomata.

Within the Teleostei we are impressed by the constancy of its presence in the Paracanthopterygii and Acanthopterygii, and by the constancy of its absence in some other groups (for example, the Osteoglossomorpha). This pattern would suggest to us that in these lineages the ontogenetic canalization leading either to the development or to the suppression of a protractor pectoralis was fixed very early in the history of each lineage. In contrast, the irregular patterns seen in other lineages (for example the Ostariophysi and Protacanthopterygii) would seem to indicate the retention of a flexible linkage between the pathway of protractor pectoralis ontogeny and other elements of the total ontogenetic pattern. What significance, if any, this may have in tracing phyletic histories remains obscure.

All our conclusions (and speculations) are, of course, dependent on the hypothesis that the muscle is an homologous (*ie* synapomorphic) feature within the Gnathostomata. Our investigations provide no refutation of that hypothesis, but we are of the opinion that the only critical test will come from comparative embryological and ontogenetic studies on a larger scale than has been carried out so far.

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