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Bones and Muscles of the Suspensorium in the Galaxioids and *Lepidogalaxias salamandroides* (Teleostei: Osmeriformes) and their Phylogenetic Significance

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ABSTRACT. The phylogenetic position of the south-western Australian endemic, *Lepidogalaxias salamandroides*, has been controversial since its description by Mees in 1961. Some workers place this tiny fish with the galaxioids of the southern end of the Southern Hemisphere, one considered it to be an esocoid (a group otherwise restricted to the northern end of the Northern Hemisphere), while another hypothesises that it may be the sister group of the Neoteleostei. My study of the suspensorium and its muscles in associated euteleosts supports the hypothesis that the galaxioids are monophyletic and include *Lepidogalaxias*. Data from the bones and muscles of the suspensorium suggests the following pattern: ([Retropinnidae + Prototroctidae] + [*Lepidogalaxias* + (Galaxiidae + Aplochitonidae)]). *Lepidogalaxias* is the sister group of Galaxiidae + Aplochitonidae based particularly on synapomorphies of the adductor mandibulae. The suspensorium and its muscles in *Lepidogalaxias* and the other galaxioids are described in detail for the first time. I also critically evaluate competing hypotheses of galaxioid relationships and comment on paedomorphosis in the group.

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The salmoniform fishes endemic to the Southern Hemisphere, the galaxioids, include the Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae (all *sensu* McDowall, 1969). Although the familial arrangement may vary, except for Rosen (1974) most recent workers consider the galaxioids to be monophyletic (e.g., McDowall, 1969, 1984; Nelson, 1972; Fink, 1984; Howes & Sanford, 1987; Williams, 1987; Begle, 1991; Nelson, 1994). In contrast, Rosen

(1974) linked the Galaxiidae + Aplochitonidae (his Galaxiidae) with the Salmonidae, and the Retropinnidae + Prototroctidae (his Retropinnidae) with the Osmeridae + Plecoglossidae + Salangidae.

Although most agree that the galaxioids are monophyletic, the phylogenetic position of the tiny galaxioid-like south-western Australian endemic, *Lepidogalaxias salamandroides*, is controversial. When Mees (1961) first described this highly unusual fish he

placed it in its own genus within the Galaxiidae, but suggested that it might occupy a separate subfamily. Scott (1966) reviewed the features of *Lepidogalaxias* and compared them to the Galaxiidae. He tentatively left it in the Galaxiidae but suggested that it may belong in a new family. McDowall (1969), in a review of Southern Hemisphere salmoniforms stated that it was not a galaxiid. Frankenberg (1969) described the osteology and some soft anatomy of *Lepidogalaxias*. Although he noted that it shared several morphological similarities with the esocoids of the Northern Hemisphere, he concluded that the overall evidence favoured a galaxiid relationship. He placed it in its own family, Lepidogalaxiidae, and suggested dividing Galaxioidei (of Greenwood *et al.*, 1966) into two superfamilies, one to contain *Lepidogalaxias* (Lepidogalaxioidea), and the other the remaining galaxioids (Galaxioidea). In a study of cephalic sensory canals and pit lines Nelson (1972: 38) concluded that "The relationships of *Lepidogalaxias* remain obscure" but noted that it shared similarities with both the Galaxiidae and Aplochitonidae (*sensu* McDowall, 1969) and the esocoid *Dallia*. Rosen (1973) placed the Lepidogalaxiidae in the suborder Salmonoidei of the order Salmoniformes, but did not discuss its relationship to the other salmonoids (Salmonidae, Galaxiidae, Aplochitonidae, Retropinnidae, Salangidae, Osmeridae, and Plecoglossidae).

In a radical departure, Rosen (1974) presented evidence that *Lepidogalaxias* was an esocoid, and placed it in the Esocoidei as a separate superfamily, Lepidogalaxioidea, along with the Esocoidea (Esocidae + Umbridae). The Esocoidea are restricted to the northern part of the Northern Hemisphere. Fink & Weitzman (1982) were not convinced that *Lepidogalaxias* was an esocoid and recommended further study. Roberts (1984) hypothesised that *Lepidogalaxias* might be a highly specialised galaxiid or galaxioid derivative. Emphasising its uniqueness and uncertain phylogenetic position, in 1984 Nelson placed *Lepidogalaxias* in its own suborder, the Lepidogalaxioidei, within the order Salmoniformes (with the Esocoidei, Argentinoidei, and Salmonoidei).

McDowall & Pusey (1983) provided a new description of *Lepidogalaxias*, briefly reviewed the controversy, but provided no new evidence concerning its relationships. Fink (1984) was also unconvinced of Rosen's (1974) hypothesis that *Lepidogalaxias* is an esocoid, and using new characters, placed it, the Salmonidae, and the Neoteleostei in an unresolved trichotomy. He noted, however, that (p. 205) "more work remains to be done before we can be really confident in [its] phylogenetic placement." Apparently because of the uncertainty, Rosen (1985) excluded *Lepidogalaxias* from his cladogram of clupeocephalan relationships, and stated only that evidence supporting either a neoteleost, galaxiid or esocoid relationship was available. More recently, Begle (1991) presented a cladistic analysis of the lower euteleosts. He hypothesised that *Lepidogalaxias* is the sister group of a clade made up of (Salangidae + [*Lovettia* + (*Aplochiton* + Galaxiidae)]) and that Retropinnidae + Prototroctidae is the sister group of

these five taxa. In Nelson's (1994) current classification *Lepidogalaxias* is placed in its own family, Lepidogalaxiidae, within superfamily Galaxioidea of the suborder Osmeroidei (with superfamily Osmeroidea) within the order Osmeriformes (with suborder Argentinoidei). Most recently, Johnson & Patterson (1995, 1996) hypothesise that *Aplochiton* and Galaxiidae are sister taxa, that *Lovettia* and *Lepidogalaxias* are sister taxa, and that the sister group of these two clades is the Retropinnidae (*Retropinna* + *Stokellia* + *Prototroctes*).

I examined the galaxioids and *Lepidogalaxias* as part of a comprehensive study of the suspensorium and its muscles in the salmoniforms and their relatives (Williams, 1987). This study yielded considerable new osteological and myological information. Some of this information constitutes evidence bearing on galaxioid intrarelationships and the phylogenetic position of *Lepidogalaxias*. In the present paper I describe in detail the suspensorium and its muscles in the galaxioids and *Lepidogalaxias*, and discuss the phylogenetic relationships that are suggested by the new data on bones and muscles of the suspensorium. The suggested phylogeny should not be considered definitive since it is based on data from a single character complex. Evidence from other anatomical systems as well as from other sources such as molecular sequences will have to be considered before a definitive hypothesis emerges. Nevertheless, the suspensorium provides critical new information potentially helpful for solving the riddle of galaxioid relationships.

Materials and methods

Specimens were cleared and stained for cartilage and bone using Taylor & Van Dyke's (1985) method. Radiographs of some fish were taken using a "Torrex 150 Radiographic-Fluoroscopic System." Dissections and drawings were made using a Wild M7A stereomicroscope equipped with a camera lucida. The standard length of each specimen was measured with Helios needle-pointed dial callipers. Osteological nomenclature follows Norden (1961) and Harder (1975). Muscle nomenclature follows Winterbottom (1974). The term tendon is frequently synonymised with ligament, not because they are difficult to distinguish, but because they are often homologous. The term endochondral refers to an ossification having a cartilaginous precursor. On cleared and stained specimens this is seen as a thickened bone (red) with a cartilaginous (blue) core. A dermal ossification does not arise from cartilage and is stained only red. The palatine has an endochondral component (the autopalatine) and a dermal component (the dermopalatine). The metapterygoid, quadrate, symplectic, and hyomandibular are endochondral but can have membranous laminae that are stained only red. The ectopterygoid, mesopterygoid, and preoperculum are dermal bones.

Unless noted, in the following text I use the name Salmoniformes in its traditional way (*sensu* Nelson, 1984) because of the prevalent usage of this name in

the literature, and because the relationships of its members are still controversial. In Nelson's (1994) new classification Salmoniformes refers only to the family Salmonidae. Otherwise names of taxa follow Nelson 1994 except that: Esocoidei = Esocidae + Umbridae; Salangidae = Salangidae + Sundasalangidae; osmeroids = Osmeridae (*Hypomesus* + *Mallotus* + *Allosmerus* + *Osmerus* + *Spirinchus* + *Thaleichthys* + *Plecoglossus*) + Salangidae; and Retropinnidae (*Retropinna* + *Stokellia*), Prototroctidae (*Prototroctes*), Galaxiidae, and Aplochitonidae (*Aplochiton* + *Lovettia*) are each *sensu* McDowall (1969). Contrary to Nelson (1994) I do not use the term Esociformes (= my Esocoidei) nor Osmeriformes (= Argentinoidei + my osmeroids + my galaxioids which include *Lepidogalaxias*).

I evaluated galaxioid intrarelationships as part of a larger study involving all Salmoniformes (Williams, 1987). The cladistic relationships of galaxioids were studied using evidence from the bones and muscles of the suspensorium. Characters were selected, their states were documented, and outgroup analysis was used to decide polarity.

The traditional galaxioids (Retropinnidae + Prototroctidae + Galaxiidae + Aplochitonidae, all *sensu* McDowall, 1969) + *Lepidogalaxias* were considered to be the ingroup. Monophyly is supported by Williams (1987), Begle (1991), and Johnson & Patterson (1995, 1996). The monophyly of the galaxioids excluding *Lepidogalaxias* is supported by numerous earlier workers (e.g., McDowall, 1969, 1984; Nelson, 1970, 1972; Fink, 1984). These workers either did not examine *Lepidogalaxias*, placed it elsewhere, or considered its position uncertain. The monophyly of the Retropinnidae (*Retropinna* + *Stokellia*) is based on McDowall (1969, 1979, 1984) and Begle (1991). The Prototroctidae contains only *Prototroctes* (McDowall, 1969, 1976, 1984). There is substantial evidence that the family Galaxiidae itself is monophyletic (e.g., McDowall, 1969, 1984; Nelson, 1972; Rosen, 1974; Fink, 1984). Although McDowall (1969, 1971, 1984) expressed some uncertainty about monophyly of the Aplochitonidae, monophyly is supported by Williams (1996). However, some workers claim that the family is paraphyletic (Begle, 1991; Johnson & Patterson, 1995, 1996).

I examined several outgroups before deciding on the polarity of a character since the character states in the outgroup for a given set of characters are not necessarily primitive relative to the ingroup (Stiassny, 1986; Sanford, 1990). The first outgroup was the osmeroids. This choice is supported by numerous recent studies, including Fink & Weitzman (1982), Williams (1987), Sanford (1990), Begle (1991, 1992), Wilson & Williams (1991), and Johnson & Patterson (1995). More remote outgroups are problematical since there is no consensus of salmoniform intra- and interrelationships. However, based on Williams (1987), Fink & Weitzman (1982), Sanford (1990), and Begle (1991, 1992), the Argentinoidei are the second outgroup. Based on my larger study, the outgroup of the osmeroids + galaxioids + argentinoids is the Neoteleostei, and outgroups of these four taxa are the Ostariophysii and the Salmonidae + Esocoidei.

I also studied representatives of other, phylogenetically more primitive teleostean taxa.

For most characters used all immediate outgroups had the same character state, judged to be primitive, and the polarity could be reliably estimated. In a few cases I used a character state as a synapomorphy if all the outgroups did not have the same state, but if the exception in the outgroups was restricted to a derived lineage. These exceptions are noted in the list of characters.

I also carried out a cladistic analysis using the branch-and-bound algorithm of PAUP 3.1.1. (Swofford, 1993). There were 21 characters with 26 apomorphic states. I treated all characters as unordered. Appendix 1 presents the input data matrix used in the numerical analysis.

Specimens from all the major salmoniform groups and the outgroups were examined. All taxa examined are listed in Appendix 2. The following museum acronyms are used on the figures: AMS—The Australian Museum, Sydney; CAS—California Academy of Sciences, San Francisco; NMC—National Museum of Natural Sciences, National Museums of Canada, Ottawa; UAMZ—The University of Alberta Museum of Zoology, Edmonton; WAM—Western Australian Museum, Perth. Other figure abbreviations are as follows: Aa—angulo-articular; AAP—adductor arcus palatini; A2—lateral section of adductor mandibulae; A2 α , A2 β —subdivisions of section A2 of adductor mandibulae; A2.dm—dorsomedial subdivision of A2; Aw—section of adductor mandibulae filling Meckelian fossa; AO—adductor operculi; Bb.tp—basibranchial tooth-plate; Bh.tp—basihyal tooth-plate; Ch—ceratohyal; D—dentary; DO—dilator operculi; Ec—ectopterygoid; E.lo—lamina orbitonasalis of ethmoid cartilage; Ep—epaxial muscles; E.pr—lateral prenasal process of ethmoid cartilage; Fr—frontal; Hh—hypohyal; Hm—hyomandibular; Hm.al—anterior lamina of hyomandibular; Hm.fl—lateral foramen for hyomandibular branch of facial nerve; Hm.fm—medial foramen for hyomandibular branch of facial nerve; Hm.h—head of hyomandibular; Hm.ls—lateral strut of hyomandibular; Hm.op—opercular arm of hyomandibular; Hm.v—ventral arm of hyomandibular; L—ligament; L.A2—tendon connecting section A2 of adductor mandibulae with angulo-articular in *Umbralimi* and *U. pygmaea*; L.cm—coronoid-maxilla ligament in Esocoidei; L.m—new ligament extending from maxilla to mandible in Aplochitonidae; L.mm—maxillo-mandibular ligament; L.smx—supramaxillary ligament; L.w, L.x, L.y, L.z—sections of maxillo-mandibular ligament; LAP—levator arcus palatini; Le—lateral ethmoid; LJ—lower jaw; LO—levator operculi; LO.p—posterior subdivision of levator operculi; md V—mandibular branch of trigeminal nerve; mm—millimetre(s); Ms—mesopterygoid; Ms.a—anterior end of mesopterygoid; Ms.t—mesopterygoid teeth; Mt—metapterygoid; Mx—maxilla; Op—operculum; Pa—parietal; Pl—palatine; Pl.a—autopalatine; Pl.ac—anterior cartilage of autopalatine; Pl.d—dermopalatine; Pl.ec—fused palatine and ectopterygoid; Pmx—premaxilla; Po—preoperculum; Po.af—anterior flange of preoperculum; Po.al—anterior lamina of preoperculum; Po.d—dorsal limb of preoperculum; Po.v—ventral limb of

preoperculum; Pq—palatoquadrate cartilage; Pr—proethmoid; Pro—prootic; Pt—pteroptic; Pts—pterosphenoid; Ptt—posttemporal; Q—quadrate; Q.b—body of quadrate; Q.c—condyle of quadrate; Q.j—quadratojugal arm of quadrate; Smx—supramaxilla; Sp—sphenotic; Sy—symplectic; Sy.l—lamina of symplectic; t.AM—tendinous aponeurosis extending to lower jaw.

Descriptions: bones of suspensorium

Palatine. The palatine and ectopterygoid are fused in *Retropinna* (Fig. 1). The area posterior to the last tooth is probably part of the original ectopterygoid since immediately behind this tooth the bone is slightly constricted, and the area posterior to this constriction is inclined at a slightly different angle. This part is also edentulous, flattened and blade-like, and overlaps the anterodorsal corner of the quadrate as in most salmoniforms. The area anterior to the central constriction is toothed and widens mediolaterally in an anterior direction to form a dorsally concave trough. The small autopalatine rests on its anterodorsal surface. The palatoquadrate cartilage emanating from the posterior end of the autopalatine is reduced. Unlike osmerids (Fig. 2), it does not extend dorsally to meet the lamina orbitonasalis of the ethmoid cartilage. The palatine and ectopterygoid are similar in *Prototroctes* (Fig. 3) except that the fused bone is straighter and the autopalatine is smaller, triangular and lacks an anterior cartilage. Unlike the other galaxioids, the palatine in *Lepidogalaxias* (Fig. 4) bears a row of teeth. The autopalatine and dermopalatine are fused. The cartilage at the anterior end of the palatine extends laterally as a finger-like hook that contacts the anteromedial surface of the maxilla. Salmonines have a similar hook. The lateral ethmoid contacts the dorsal surface of the cartilage at the anterior end of the palatine, unlike other salmoniforms. The palatoquadrate cartilage at the posterior end of the autopalatine is lost. The palatine in *Galaxias maculatus* lacks teeth and the dermopalatine is absent or greatly reduced (Fig. 5). The palatoquadrate cartilage at its posterior end is as in the Retropinnidae and Prototroctidae. The palatine is similar in other galaxiids (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974; Andrews, 1976). The palatine in *Aplochiton* resembles galaxiids but has an elongated anterior cartilage (Fig. 6). The palatine in *Lovettia* is poorly ossified, as are the other bones of the suspensorium.

Ectopterygoid. The palatine and ectopterygoid are fused in retropinnids and prototroctids (Figs 1, 3). The ectopterygoid in *Lepidogalaxias* is straight and short (Fig. 4). In galaxiids and aplochitonids it is absent and replaced by a ligament (Figs 5, 6: L). This ligament has never been described. Others have noted the absence of an ectopterygoid in these taxa, but none mention the ligament (e.g., Frankenberg, 1969; McDowall, 1969; Fink, 1984; Begle, 1991). A small, splint-like

ectopterygoid is reported in *Lovettia* by McDowall (1969) and by G. David Johnson (personal communication); however, I did not observe this element as a separate ossification in my specimens.

Mesopterygoid. As in the Osmeridae (Fig. 2), the medioventral surface of the mesopterygoid in *Retropinna* (Fig. 1) bears a series of large, ventrolaterally curving teeth. In two specimens there were 30–40 teeth on each bone: a medial row of 15–20 teeth and 15–20 irregularly distributed lateral teeth. The teeth are largest medially and posteriorly. All retropinnids bear similar teeth (McDowall, 1979). The mesopterygoid in *Prototroctes* has more teeth (Fig. 3). *Lepidogalaxias* has a small, elliptical, edentulous mesopterygoid (Fig. 4). The mesopterygoid in *Galaxias maculatus* bears seven or eight ventroanterolaterally curving teeth in a single row along the anteromedial edge (Fig. 5). It is similar in other galaxiids except that teeth are few and sometimes absent in *Galaxias cleaveri* (Andrews, 1976; McDowall & Frankenberg, 1981) and in *Neochanna* (personal observation; McDowall, 1970). The mesopterygoid in *Aplochiton* resembles *Galaxias maculatus* but is longer (Fig. 6). It is similar in *Lovettia* but has only four or five teeth.

Quadrate. Quadrates in *Retropinna* and *Prototroctes* are similar (Figs 1, 3). The condyle and quadratojugal arm in *Lepidogalaxias* are unusually large (Fig. 4). *Galaxias maculatus* is similar (Fig. 5). Differences among galaxiids are minor. The quadrate in *Aplochiton* (Fig. 6) and *Lovettia* has a small body and a very long quadratojugal arm.

Symplectic. The symplectic in *Retropinna* and *Prototroctes* is distinctly bent and has a large cartilaginous knob at its anterior end (Figs 1, 3). *Lepidogalaxias* has a slightly bent symplectic (Fig. 4). In *Galaxias maculatus* its posterodorsal edge rests in a groove on the ventral edge of the metapterygoid (Fig. 5). Differences among galaxiids are minor (see also Frankenberg, 1969). The symplectic in *Aplochiton* (Fig. 6) and *Lovettia* does not contact the metapterygoid.

Metapterygoid. The metapterygoid in *Retropinna* and *Prototroctes* is endochondral except for a narrow membranous lamina extending along its dorsal edge (Figs 1, 3). Projecting from its posterodorsal corner is a large cartilage that abuts the middle of the lateral strut of the hyomandibular. The metapterygoid in *Lepidogalaxias* is small, axe-shaped, and entirely endochondral (Fig. 4). The metapterygoid in *Galaxias maculatus* has an anterior, axe-shaped endochondral section and a posterior, rounded membranous lamina (Fig. 5). Its ventral edge is tightly braced against both the symplectic and hyomandibular. The metapterygoid in other galaxiids is variable (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). *Neochanna* for example has a square metapterygoid with a reduced

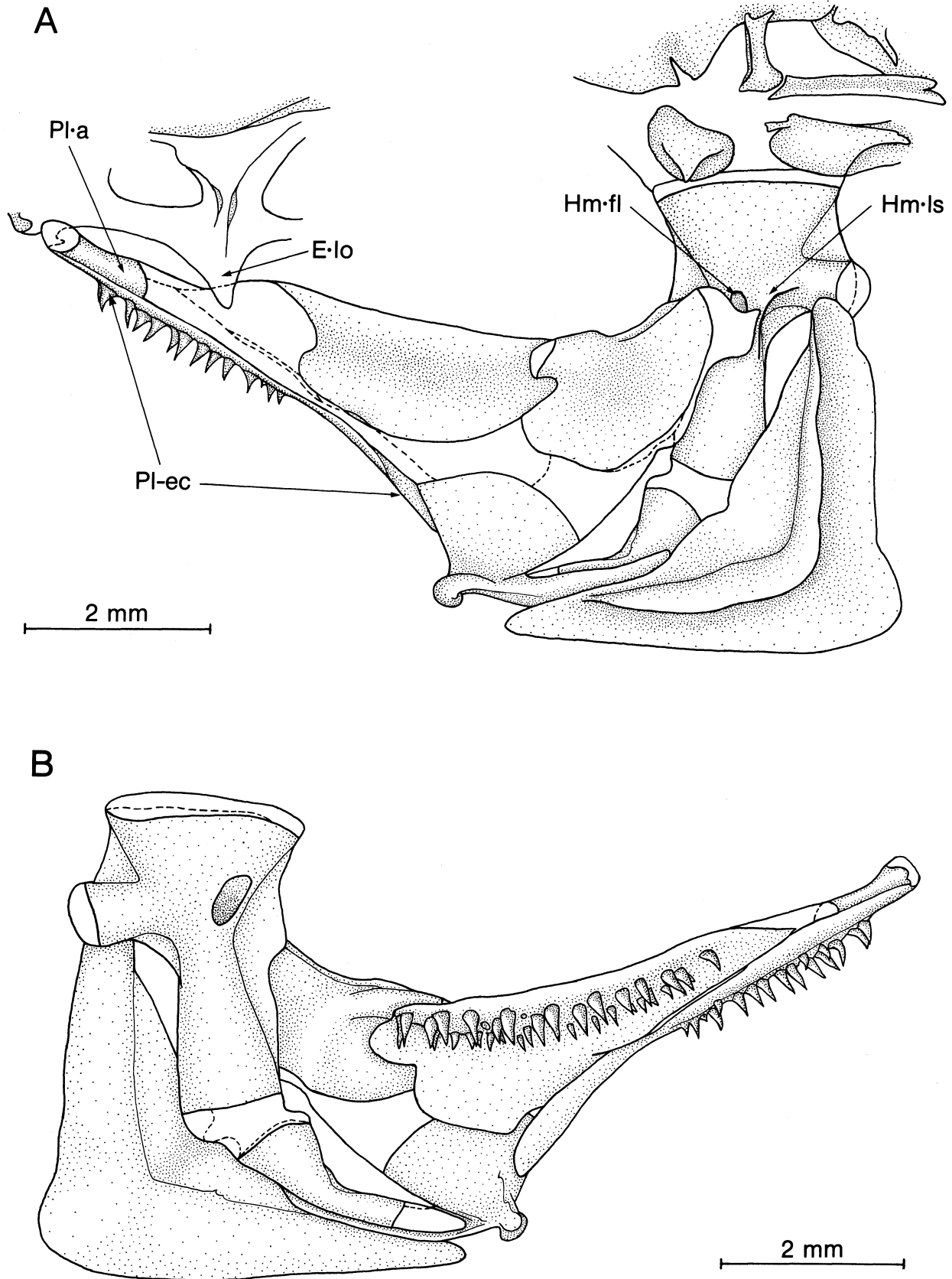


Fig. 1. Lateral (A) and medial (B) views of left suspensorium in *Retropinna retropinna* (UAMZ 4606, 71.5 mm). Stippling on Figs 1–6 and 17 indicates bone, while clear areas on and around bones bordered by lines indicate cartilage. Cartilaginous areas can be distinguished from bone by studying lateral and medial views.

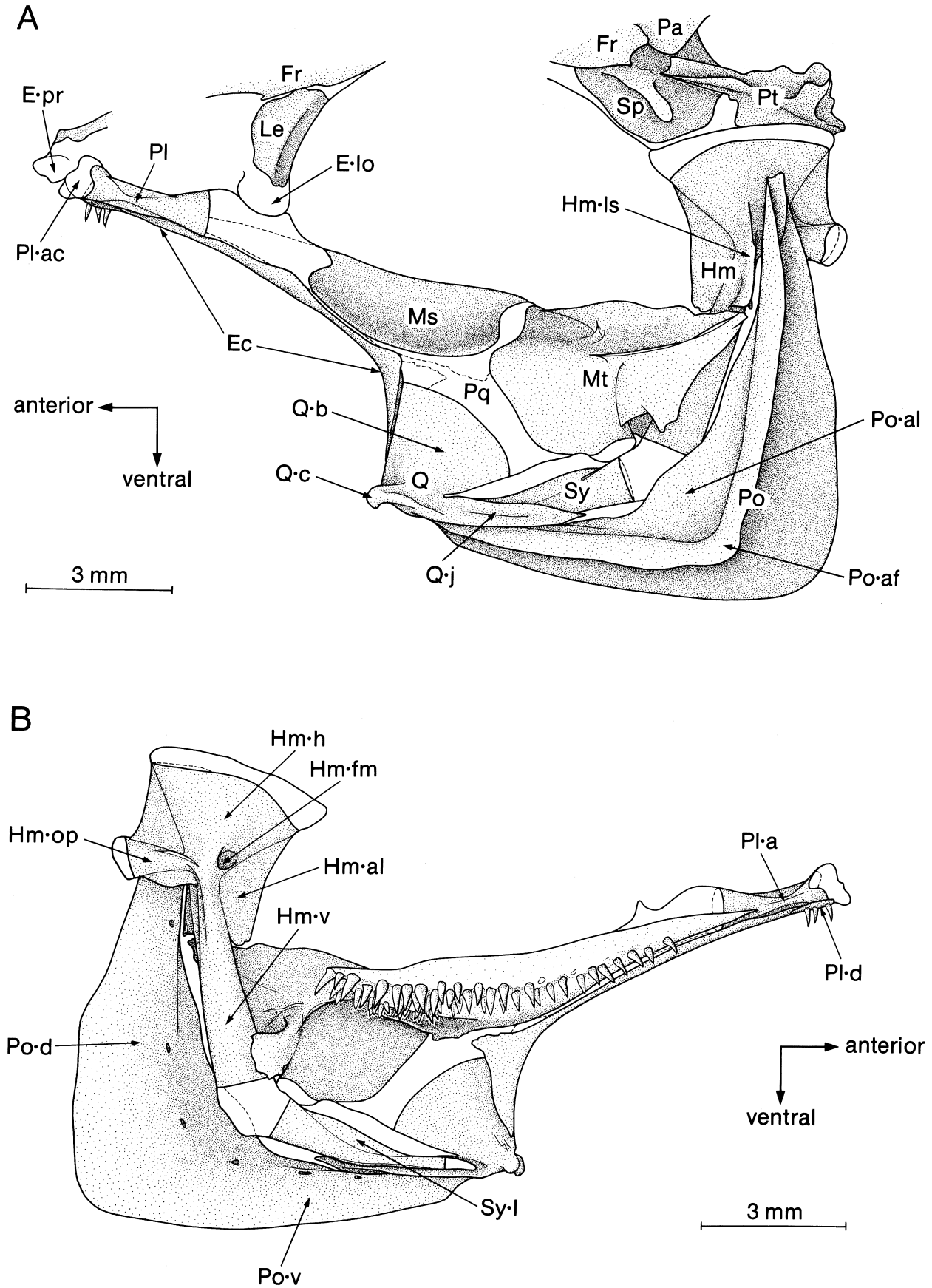


Fig. 2. Lateral (A) and medial (B) views of left suspensorium in *Hypomesus pretiosus* (UAMZ 874, 118.0 mm).

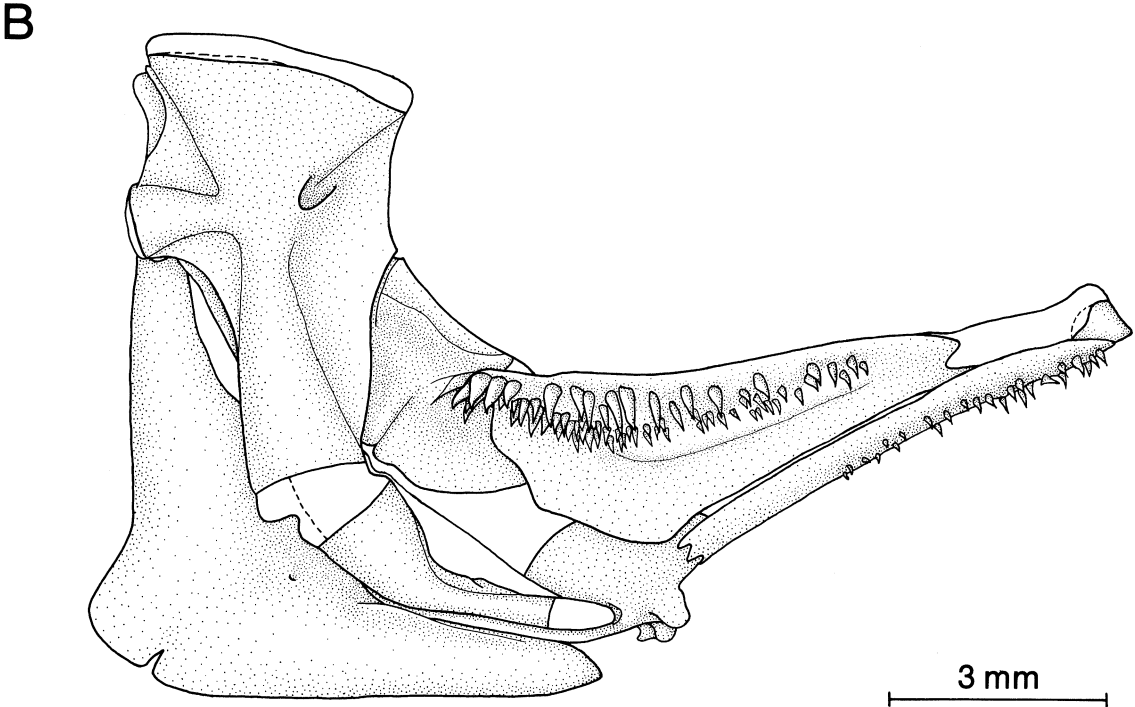
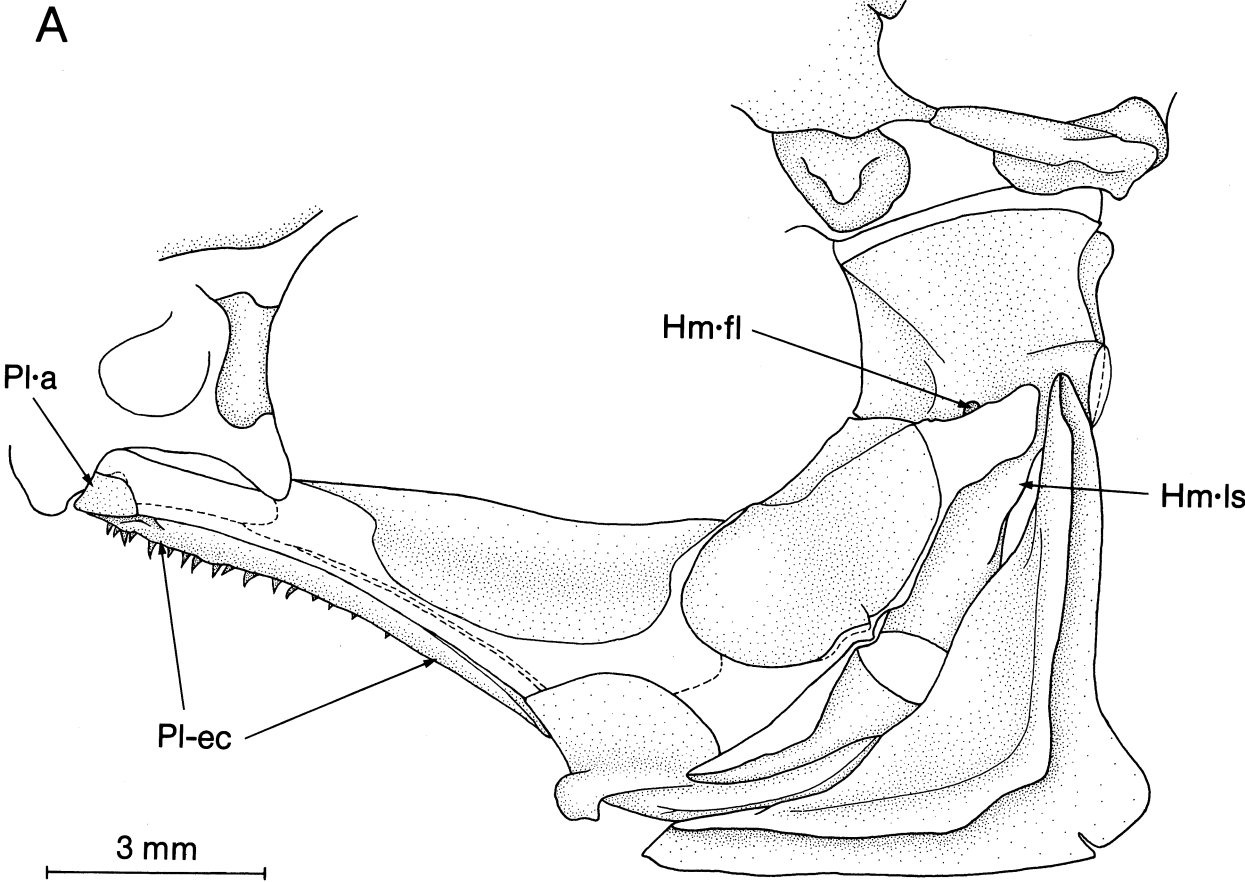


Fig. 3. Lateral (A) and medial (B) views of left suspensorium in *Prototroctes maraena* (UAMZ 6325, 117.0 mm).

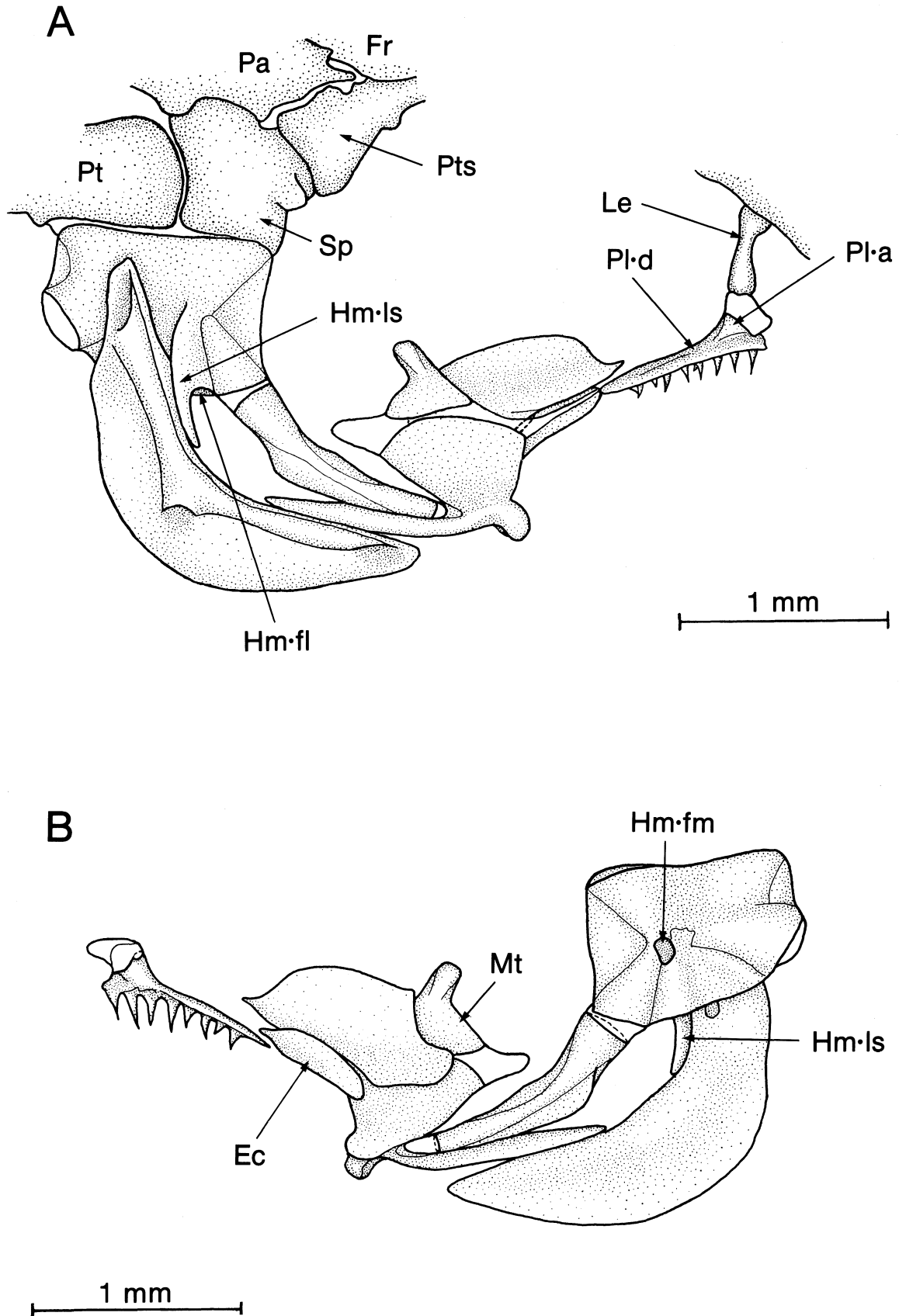


Fig. 4. Lateral (A) and medial (B) views of right suspensorium in *Lepidogalaxias salamandroides* (WAM P. 7578-81, 34.6 mm).

lamina. In *G. brevipinnis* the endochondral portion is small while the lamina is large. The metapterygoid in *G. paucispondylus* is widely separated from the mesopterygoid and quadrate and does not contact the hyomandibular; a feature shared with *Galaxiella pusilla* and *G. nigrostriata* (Frankenberg, 1969). The metapterygoid in *Aplochiton* (Fig. 6) and *Lovettia* is small, with a posteriorly extending finger-like projection, and is posterodorsal to the body of the quadrate.

Hyomandibular. The hyomandibular in *Retropinna* and *Prototroctes* is deeper than it is wide (Figs 1, 3). The small lateral strut is convex anteriorly as it arches posterodorsally from the ventral arm to the opercular arm (Fig. 1A: Hm.ls). The lateral foramen for the hyomandibular branch of the facial nerve is anterior to the middle of the lateral strut (Figs 1, 3: Hm.fl). The hyomandibular in *Lepidogalaxias* is wider than it is deep (Fig. 4). The ventral arm is very short. A vertical lateral strut (Fig. 4: Hm.ls) abuts the preoperculum. The lateral foramen (Fig. 4: Hm.fl) is on the mid-ventral edge of the hyomandibular at the ventral end of the lateral strut. The hyomandibular in *Galaxias maculatus* is about as wide as it is deep (Fig. 5). A wide, shelf-like lateral strut (Fig. 5A: Hm.ls) arches posterodorsally from the ventral arm to the opercular arm. The lateral foramen (Fig. 5A: Hm.fl) is posterior to the ventral end of the lateral strut. The hyomandibular in the other galaxiids is moderately variable (see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). For example, in *Neochanna* and *G. brevipinnis* it is wider than in *G. maculatus* and has a shorter ventral arm. The lateral strut in *G. paucispondylus* and *Brachygalaxias* is larger than in the other species examined. The lateral foramen in *Neochanna* is at the ventral end of the lateral strut. The hyomandibular in *Aplochiton* is deeper than it is wide (Fig. 6). The lateral strut resembles galaxiids but is less robust (Fig. 6: Hm.ls). The lateral foramen (Fig. 6: Hm.fl) is anterior to the ventral end of the lateral strut. The hyomandibular in *Lovettia* is about as wide as it is deep. The ventral arm is shorter than in *Aplochiton* and only slightly expanded ventrally. Although a lateral strut is absent the lateral foramen occupies the same position.

Preoperculum. In *Retropinna* the ventral limb of the preoperculum is longer than the dorsal limb (Fig. 1). The lateral sensory canal is completely open posterior to a flange that runs along the entire length of the anterolateral surface of the preoperculum. *Retropinna* lacks a suprapreoperculum (like all galaxioids). The preoperculum in the Prototroctidae, Galaxiidae, and Aplochitonidae resembles *Retropinna* (Figs 3, 5, 6; see also Frankenberg, 1969; McDowall, 1969; Rosen, 1974). *Lepidogalaxias* has dorsal and ventral limbs of equal length (Fig. 4). A bone-enclosed lateral sensory canal runs the length of its anterior surface and gives off three pores, one at each end of the bone, and one at the intersection of the two limbs.

Descriptions: muscles of suspensorium

Adductor mandibulae. The adductor mandibulae in *Retropinna* has a posterior A2 section and an anterior Aw section (Fig. 7). The mandibular branch of the trigeminal nerve (Fig. 7: md V) passes lateral to the anterodorsal end of the adductor mandibulae at the division of A2 and Aw before running lateral to Aw and then medial to the lower jaw. Section A2 originates from the preoperculum, hyomandibular, metapterygoid, symplectic, and quadrate. The medial fibres insert on the lateral surface of a tendinous aponeurosis (Fig. 7: t.AM) that overlies the quadrate and metapterygoid. This aponeurosis bifurcates when it passes medial to the lower jaw, the ventral tendon attaching to the coronomeckelian bone and the longer dorsal tendon attaching farther anteriorly along and next to Meckel's cartilage. Section Aw fills the Meckelian fossa on the medial side of the lower jaw. It originates primarily from the dorsal tendon (anterior to A2) and inserts onto the dorsal border of Meckel's cartilage and the angulo-articular and dentary. The dorsolateral fibres of A2 converge onto a flattened tendon that extends anteriorly to join the posterodorsal part of the maxillo-mandibular ligament (Fig. 7: L.mm). This tendon is continuous with the dorsal part of the tendinous aponeurosis. The maxillo-mandibular ligament extends from the angulo-articular to the maxilla. Like all galaxioids there are no supramaxillae. *Prototroctes* (Fig. 8) has a similar adductor mandibulae except that ligament L.mm is shorter. The mandibular branch of the trigeminal nerve also passes medial to the anterior end of the adductor mandibulae before running medial to the lower jaw, a feature shared with *Lepidogalaxias*, galaxiids, and aplochitonids.

The adductor mandibulae in *Lepidogalaxias* extends unusually far dorsally, originating from the levator arcus palatini, dilatator operculi, hyomandibular, symplectic, and quadrate (Fig. 9). The medial fibres of A2 insert onto a long, flat, narrow tendinous aponeurosis that overlies the quadrate and extends anteriorly medial to the lower jaw to attach to the coronomeckelian. This aponeurosis does not bifurcate anteriorly. There is no Aw. The lateral fibres of A2 insert tendinously on both the maxilla and lower jaw. They converge anteriorly to fit into a tendinous "glove" that opens posteriorly. The glove, in turn, inserts onto the medial and lateral surfaces of the coronoid process (dentary) of the lower jaw. Extending anteriorly from the anterodorsal part of the tendinous "glove" is a short, flattened tendon that inserts onto the dorsal edge of the posterior third of the maxilla. This tendon and "glove" are not continuous with the aponeurosis extending to the coronomeckelian. A short ligament (Fig. 9: L) joins the posteromedial surface of the maxilla with the coronoid process anterior to the insertion of the adductor mandibulae. It is also present in galaxiids and aplochitonids.

In *Galaxias maculatus* the adductor mandibulae has an A2 section that originates from the preoperculum, metapterygoid, hyomandibular, symplectic, and quadrate (Fig. 10). It has a small dorsomedial subdivision that

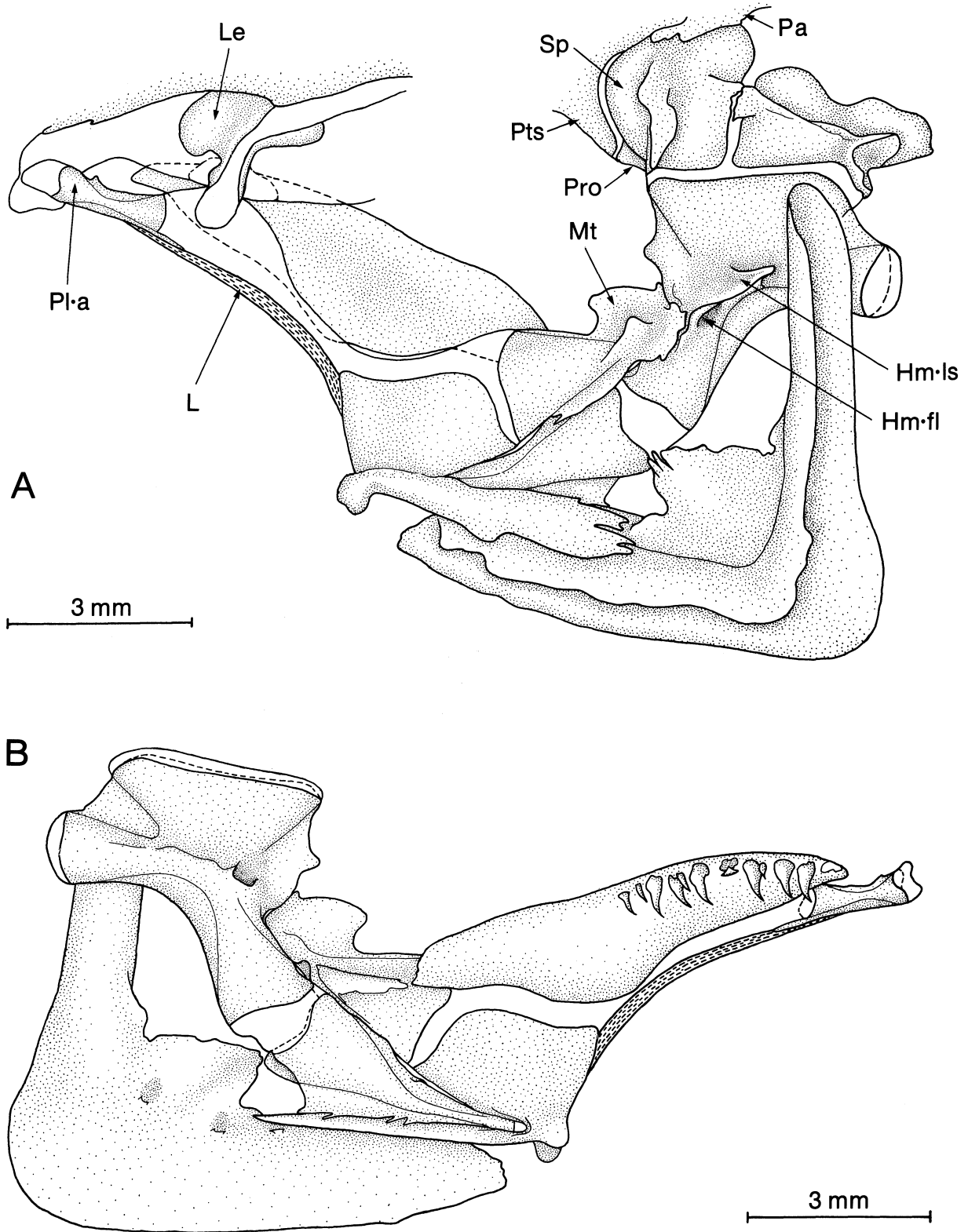


Fig. 5. Lateral (A) and medial (B) views of left suspensorium in *Galaxias maculatus* (UAMZ 4609, 117.9 mm).

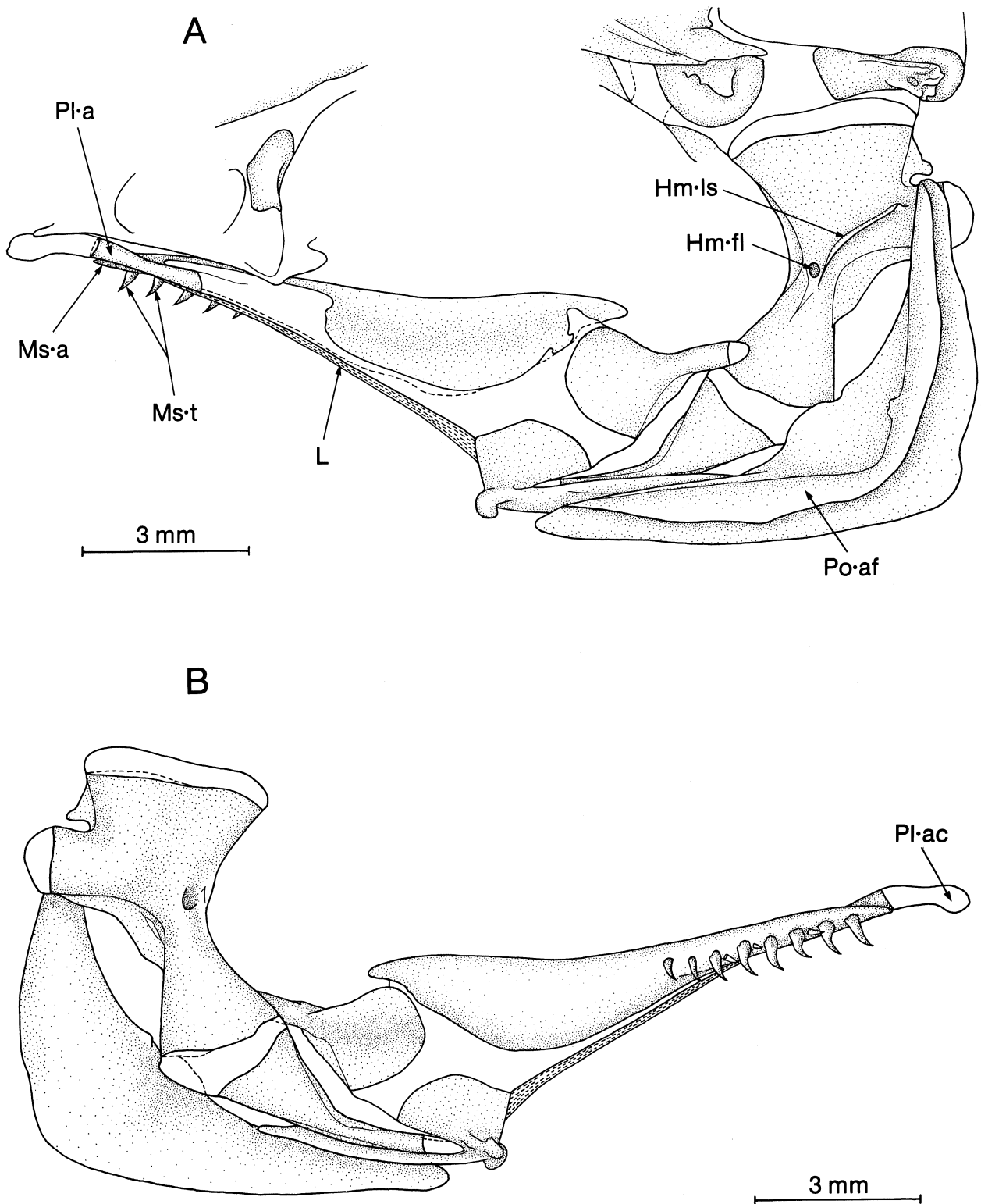


Fig. 6. Lateral (A) and medial (B) views of left suspensorium in *Aplochiton taeniatus* (NMC 76-0393, 110.5 mm).

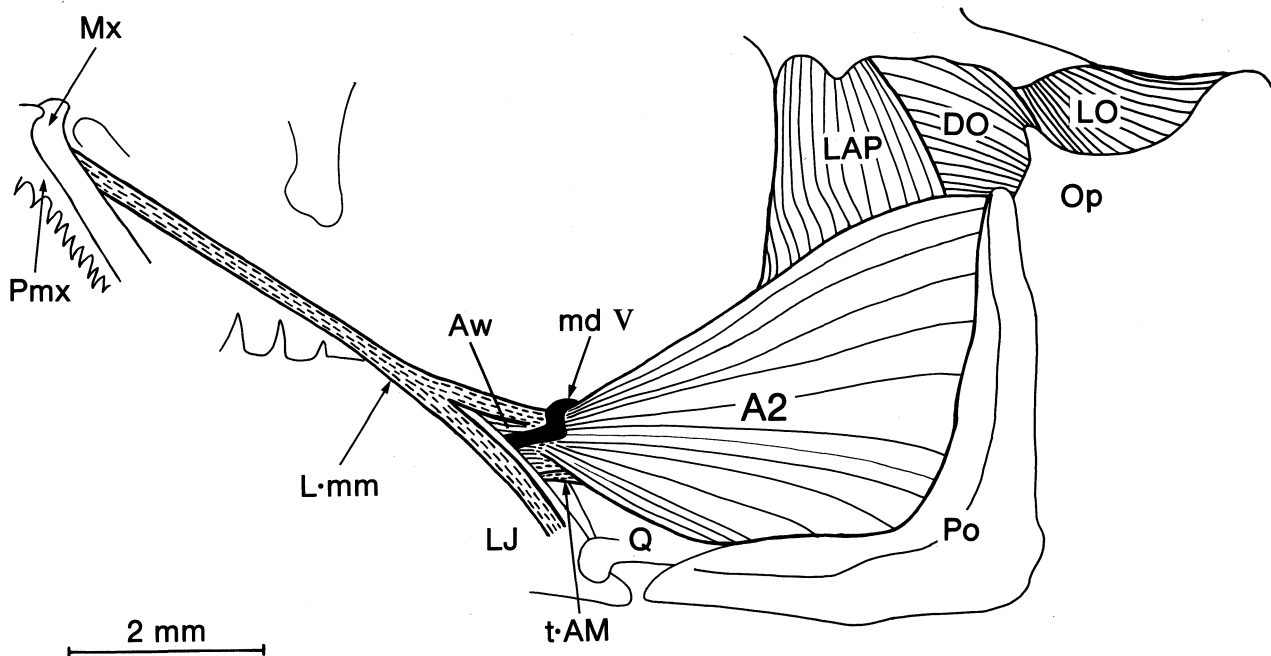


Fig. 7. Lateral view of external muscles of left suspensorium in *Retropinna retropinna* (UAMZ 4606, 77.0 mm). On Figs 7–12, 14–16, 18, and 19 muscles are indicated by closely spaced parallel lines; ligaments and tendons are short, closely spaced dashes; bones are outlined or stippled.

passes medial to the levator arcus palatini and originates from the metapterygoid. Its anteroventral fibres are continuous with those of A2. The medial and posterodorsal fibres of A2 (including the subdivision) insert on a tendinous aponeurosis similar to that in *Lepidogalaxias* except that it bifurcates when passing medial to the lower jaw: the ventral tendon attaches to the coronomeckelian and the longer, narrower dorsal tendon attaches to Meckel's cartilage and the angulo-articular. An Aw section fills the Meckelian fossa. It originates from the dorsal tendon of the aponeurosis and inserts on the dorsomedial surface of the lower jaw. The fibres of A2 converge on a flattened tendon that extends anteriorly to the dorsolateral surface of the middle of the maxilla. Removing the anterolateral fibres of A2 reveals a unique tendinous arrangement attaching A2 to the lower jaw (see Fig. 10B). A short and narrow tendon (L.y) extends ventrally from the posteriormost end of tendon L.x to the angulo-articular. Another narrow tendon (L.w) extends anteroventrally from the intersection of tendons L.x and L.y to the coronoid process (dentary) of the lower jaw. The adductor mandibulae in other galaxiids is similar to *Galaxias maculatus* but can differ in relative size, shape, and length and degree of development of the tendons connecting it to the upper and lower jaws. In *G. fasciatus* (Fig. 11), *G. brevipinnis* and *Neochanna* it is shorter anteroposteriorly and thicker than in the other galaxiids. The very large adductor mandibulae in *Neochanna* entirely covers the levator arcus palatini and dilatator operculi. Tendon L.x is longest and inserted farthest anteriorly in *G. maculatus*. In *G. paucispondylus*, and *Neochanna* L.x is short but broad, and inserts about

a third of the way from the posterior end of the maxilla. It is longer in *Brachygalaxias*, *G. brevipinnis*, and *G. fasciatus* and inserts farther anteriorly. Tendon L.y in *Brachygalaxias*, *G. paucispondylus*, *G. brevipinnis*, and *G. fasciatus* is similar to *G. maculatus*. Tendon L.w is variable and in some species resembles the tendinous "glove" in *Lepidogalaxias*. In *G. paucispondylus* L.w is broader and shorter than in *G. maculatus*. In *Brachygalaxias*, *G. brevipinnis*, and *G. fasciatus* (Fig. 11B: L.w) it is even shorter and forms a tendinous sheath that inserts broadly on the coronoid process. In *Neochanna* this broad sheath extends ventrally to both angulo-articular and dentary. A vestige of tendon L.y was present at the posteroventral corner of the sheath on one side of each specimen.

The adductor mandibulae in *Aplochiton* (Fig. 12) resembles *Galaxias maculatus* but is thinner and does not extend as far anteriorly. There is a partial dorsomedial subdivision whose dorsolateral fibres are separable from the main muscle. The subdivision does not pass medial to the levator arcus palatini. Section Aw is also larger. Section L.x is longer, L.w is thinner, and the posterodorsal corner of L.x is barely continuous with the aponeurosis that extends medial to the lower jaw. *Aplochiton* has a separate ligament (Fig. 12: L.m) extending from the ventral end of L.y to the anterior end of L.x of the maxillo-mandibular ligament. The adductor mandibulae in *Lovettia* resembles *Aplochiton* but there may not be a partial dorsomedial subdivision of A2, and I am uncertain whether the posteriormost end of the tendon extending from the adductor mandibulae to the maxilla joins the tendinous aponeurosis. It has ligament L.m.

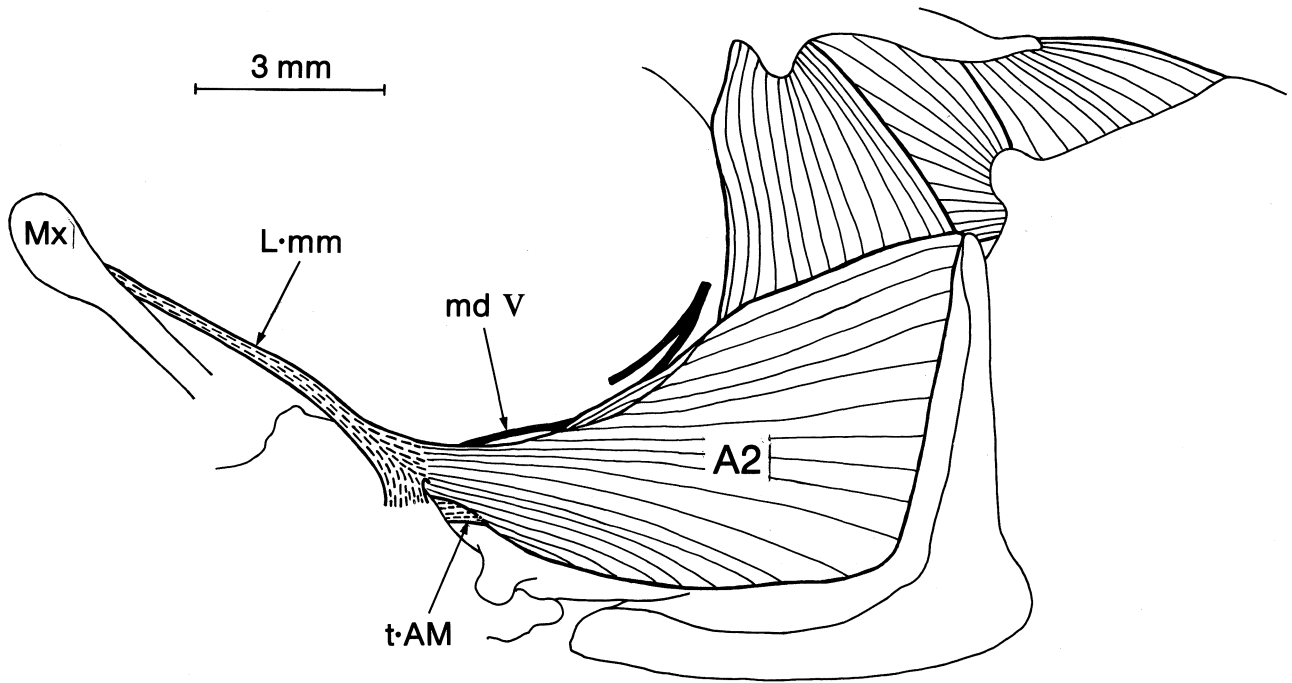


Fig. 8. Lateral view of external muscles of left suspensorium in *Prototroctes maraena* (UAMZ 6325, 122.1 mm).

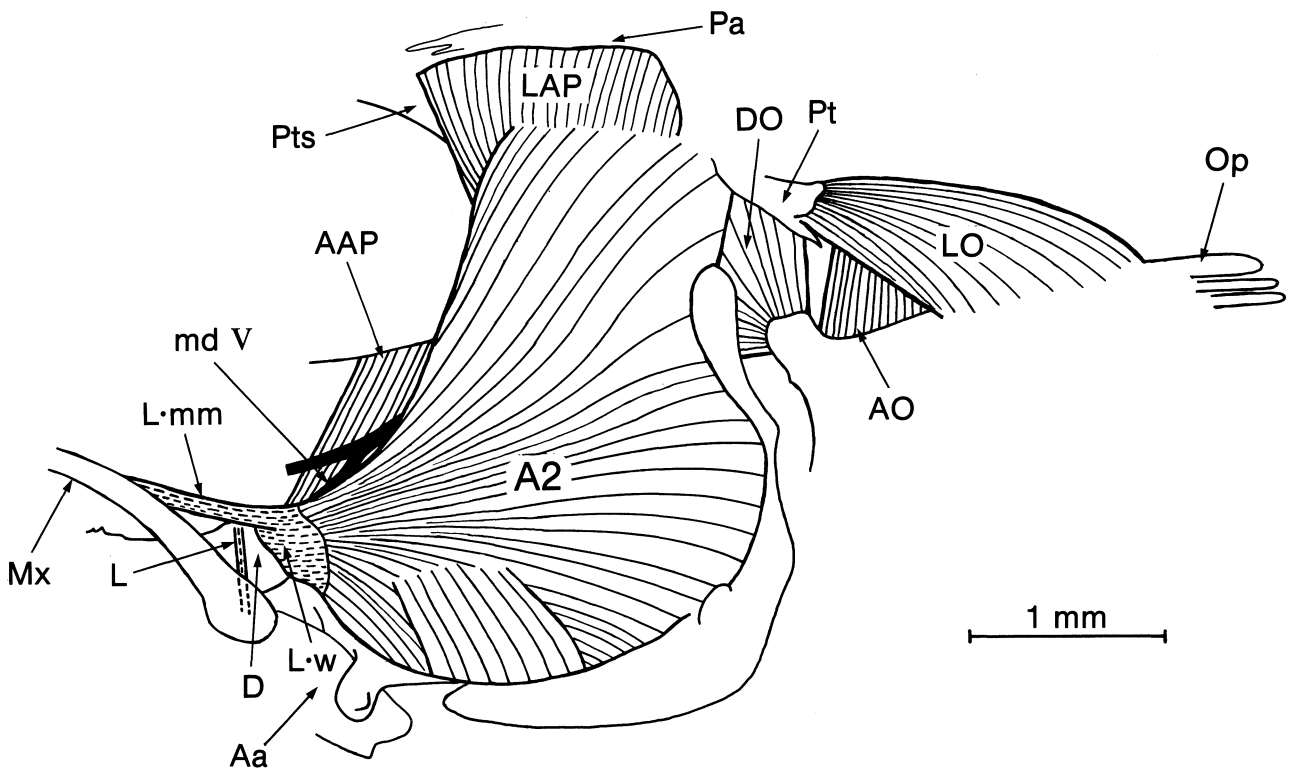


Fig. 9. Lateral view of external muscles of left suspensorium in *Lepidogalaxias salamandroides* (WAM P. 8124-31, 39.7 mm).

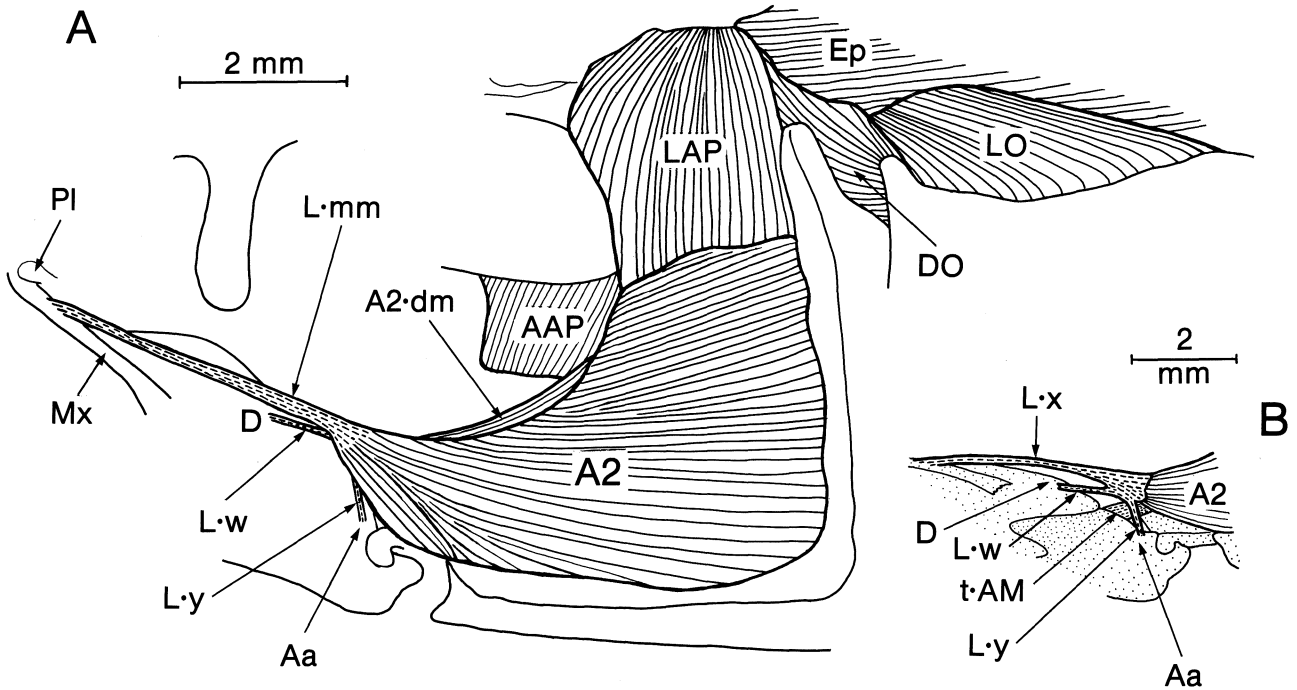


Fig. 10. *Galaxias maculatus* (UAMZ 4609, 92.6 mm): (A) lateral view of external muscles of left suspensorium; (B) ventrolateral (slightly posterior) view of tendons/ligaments attaching section A2 of adductor mandibulae onto maxilla and lower jaw, anterolateral fibres of section A2 inserting onto tendons/ligaments are removed. Ligament L (see Fig. 9) is not drawn.

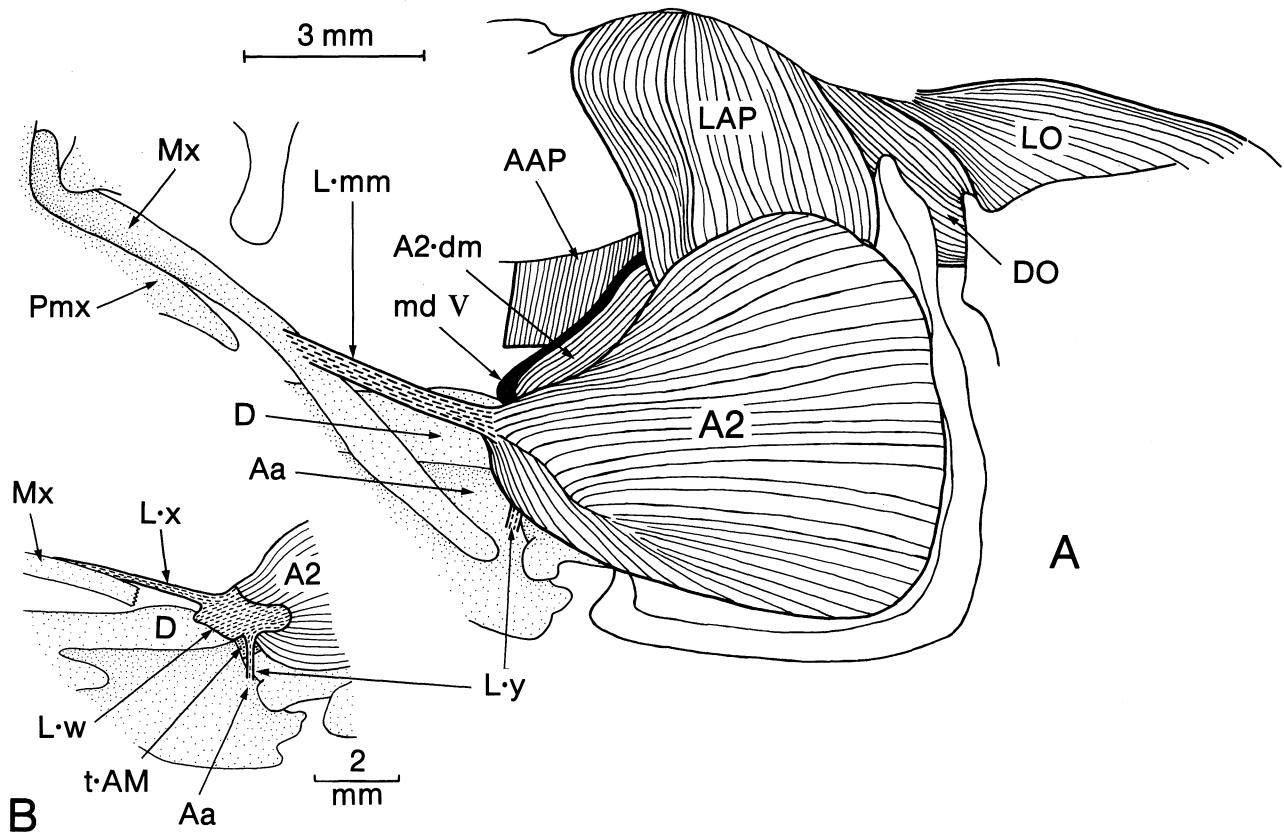


Fig. 11. *Galaxias fasciatus* (UAMZ 5122, 95.2 mm): (A) lateral view of external muscles of left suspensorium; (B) ventrolateral (slightly posterior) view of tendons/ligaments attaching section A2 of adductor mandibulae onto maxilla and lower jaw, anterolateral fibres of section A2 inserting onto tendons/ligaments are removed. Ligament L (see Fig. 9) is not drawn.

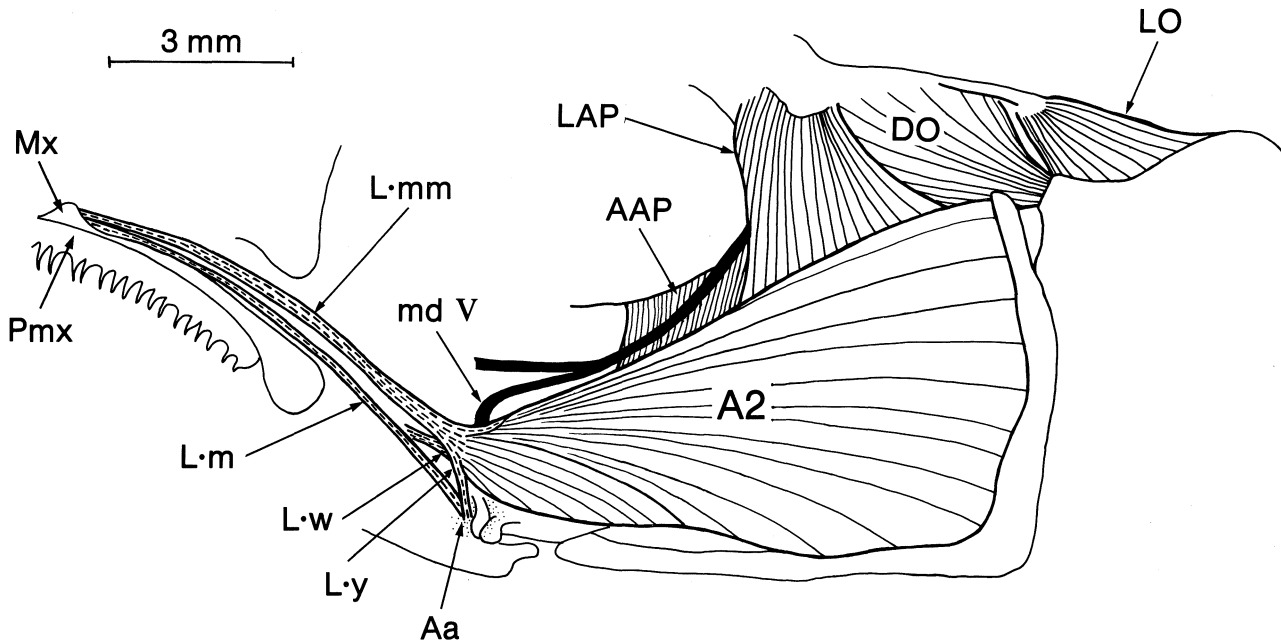


Fig. 12. Lateral view of external muscles of left suspensorium in *Aplochiton taeniatus* (NMC 76-0393, 104.1 mm). Ligament L (see Fig. 9) is not drawn.

Levator arcus palatini. The levator arcus palatini (LAP) in *Retropinna* and *Prototroctes* is conical and slightly bulbous (Figs 7, 8). It originates from the sphenotic and inserts on the hyomandibular and metapterygoid. The LAP in *Lepidogalaxias* is barrel-shaped and mostly covered by the adductor mandibulae (Fig. 9). It originates from the pterosphenoid, sphenotic, frontal, parietal, and possibly the prootic and pterotic. It inserts on the hyomandibular, symplectic, and palatoquadrate cartilage. The LAP in *Galaxias maculatus* (Fig. 10), *G. paucispondylus*, *G. brevipinnis*, and *G. fasciatus* (Fig. 11) resembles *Lepidogalaxias* except the origin excludes the pterotic and the insertion is on the hyomandibular and metapterygoid. In *Neochanna* it is covered by the greatly enlarged adductor mandibulae and has a broad area of origin primarily along the edges of the frontal and pterosphenoid. The LAP in *Brachygalaxias* is smaller than in the other galaxiids, conical, and not expanded dorsally onto the skull (the origin includes only the sphenotic). The LAP in *Aplochiton* resembles *Retropinna* (Fig. 12). It is similar in *Lovettia* except that the insertion includes the symplectic, not the metapterygoid.

Dilatator operculi. The conical dilatator operculi (DO) in *Retropinna* (Fig. 7) originates from the head of the hyomandibular, sphenotic, and pterotic, and inserts broadly on the articular process of the operculum. It is similar in other galaxioids (Figs 8–12).

Levator operculi. The flattened, fan-shaped levator operculi (LO) in *Retropinna* and *Prototroctes* (Figs 7, 8) originates from the pterotic and inserts on the dorsal

third to quarter of the medial surface of the operculum. The LO in *Lepidogalaxias* is slightly bulbous, fan-shaped, and originates from the pterotic (Fig. 9). Unlike other galaxioids, it inserts only along the dorsal edge of the operculum (mostly along the dorsomedial edge but with the lateralmost fibres extending onto the dorsolateral surface). The LO in *Galaxias maculatus* is similar to *Lepidogalaxias* but inserts on the dorsal third of the medial surface of the operculum (Fig. 10). The LO in *G. brevipinnis*, *G. paucispondylus*, *G. fasciatus* (Fig. 11), and *Brachygalaxias* resembles *G. maculatus* except that its insertion covers a greater opercular surface. In *Neochanna* it covers the dorsal two-thirds of both sides of the operculum. The LO in *Aplochiton* and *Lovettia* is smaller than in galaxiids, and inserts onto only the dorsal quarter of the medial surface of the operculum (Fig. 12).

Adductor operculi. The adductor operculi (AO) in *Retropinna* and *Prototroctes* is conical to cylindrical, and completely covered by the anterior part of the LO. It originates from the pterotic and exoccipital medioventral to the origin of the LO and inserts on the medial surface of the anterodorsal corner of the operculum. The insertion is slightly ventral to the insertion of the anterior part of the LO, and lies medial to it. The AO in *Lepidogalaxias* is partly visible externally (Fig. 9). In galaxiids and aplochitonids it originates only from the pterotic.

Adductor arcus palatini. The adductor arcus palatini (AAP) in *Retropinna* and *Prototroctes* is flattened and rectangular. It originates primarily from the prootic and

inserts on the dorsomedial surface of the metapterygoid and on the medial surface of the hyomandibular. Next to its posterior end is an adductor hyomandibulae (AH) that originates on the pterotic and inserts along the dorsomedial edge of the opercular arm of the hyomandibular. The AAP in *Lepidogalaxias* is longer anteroposteriorly than in *Retropinna* and *Prototroctes* (Fig. 9). It originates from the parasphenoid, prootic, and pterotic. The insertion includes most of the medial surface of the hyomandibular, the dorsomedial edge of the palatoquadrate cartilage posterior to the metapterygoid, the lateral surface of the metapterygoid, and the posterodorsal surface of the mesopterygoid. The AAP in galaxiids is similar except the insertion includes less of the hyomandibular, does not include the palatoquadrate cartilage, and is from the medial surface of the metapterygoid (Figs 10, 11). The AAP in *Aplochiton* resembles the galaxiids (Fig. 12). The AAP in *Lovettia* resembles *Aplochiton* except that the insertion is as in *Lepidogalaxias*. Aplochitonids, galaxiids, and *Lepidogalaxias* lack an AH (I did not check *Brachygalaxias*).

Hypothesis of galaxioid intrarelationships

Figure 13 presents the galaxioid relationships suggested by the data from the suspensorium and its muscles. The

branch-and-bound algorithm of PAUP, which guarantees the most parsimonious tree(s), revealed a single shortest tree. The PAUP analysis included 21 characters with 26 apomorphic states. Since the most parsimonious tree had 27 steps only one character was incompatible (character 6), and the consistency index was 0.963.

What follows is a discussion of the synapomorphies supporting each clade. For each description the derived states are presented first, followed by taxa sharing this state if it is not unique, followed by the primitive state.

Galaxioids (Retropinnidae + Prototroctidae + *Lepidogalaxias* + Galaxiidae + Aplochitonidae)

- (1) *Autopalatine small* (shared with most Salmonidae, *Dallia*, and *Umbra*). Primitively, it is somewhat large with expanded ends.
- (2) *Palatoquadrate cartilage at posterior end of autopalatine reduced or absent*. Primitively it expands dorsally towards the lamina orbitonasalis.
- (3) *Ventral limb of preoperculum as long as, or longer than, dorsal limb* (shared with *Dallia*, Salangidae, and Argentinoidea). Primitively, the dorsal limb is longer than the ventral limb.

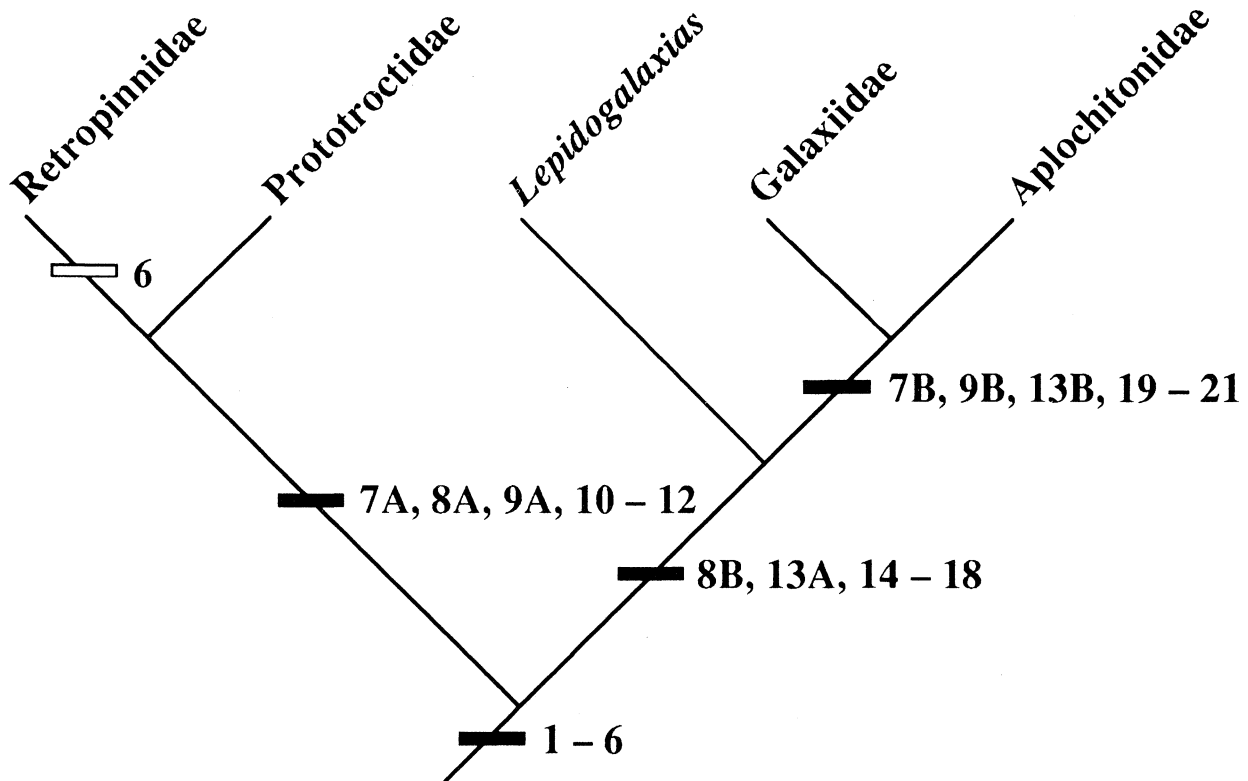


Fig. 13. Galaxioid relationships suggested by the suspensorium and its muscles. Synapomorphies correspond to those discussed in the text. The open bar indicates character 6 in its reversed state.

(4) *Supramaxillae and supramaxillary ligament absent* (shared with adult *Plecoglossus*, some Salangidae, and Argentinoidea). Primitively in Teleostei there are two supramaxillae, and a supramaxillary ligament extends from the anterior tip of the posterior one to the lower jaw.

(5) *Origin of adductor mandibulae includes most of lateral surface of preoperculum anterior to lateral sensory canal* (shared with Esocoidei and Argentinoidea). Primitively, the adductor mandibulae originates only along the anterolateral edge of the preoperculum.

(6) *Mandibular branch of trigeminal nerve passes medial to anterior end of section A2 of adductor mandibulae before running medial to lower jaw* (shared with Argentinidae and Bathylagidae). The assumption is that a reversal has occurred in *Retropinna* since it has the primitive state. Primitively, the nerve passes lateral to the anterior end of section A2 before running medial to the lower jaw (e.g., Figs 7, 14). Most lower teleosts (e.g., *Chanos*, *Clupea*, *Hiodon*, *Elops*) and primitive neoteleosts (e.g., *Diplophos*, *Vinciguerria*, *Aulopus*) have this state. Although the nerve technically passes medial to the anterior end of section A2 in *Umbra limi* and *U. pygmaea* this is related to a feature uniting them: the anterolateral fibres of section A2 converge onto a unique tendon (Fig. 15: L.A2) extending to the angulo-articular. The nerve rests lateral to the anterior end of section A2 at the division of sections A2 and Aw, as in all other esocoids, but is medial to the new tendon and the anterolateral fibres of section A2 that converge onto it. Hence it occupies the same relative position as the other esocoids and is the primitive state (compare Fig. 15 of *U. limi* with Fig. 16 of *U. krameri*, the sister species of *U. limi* + *U. pygmaea*; Wilson & Veilleux, 1982).

Retropinnidae + Prototroctidae

(7) *Ectopterygoid fused with palatine* (Fig. 13: 7A). *Dallia* questionably shares this state. It can be argued that in *Dallia* the ectopterygoid is lost, and the dermopalatine is greatly expanded posteriorly to nearly touch the anterodorsal corner of the quadrate (see also Wilson & Veilleux, 1982). However, even if the ectopterygoid and palatine are fused in *Dallia*, the so-called fused bone is unlike the one in the Retropinnidae and Prototroctidae because it is more robust, the teeth are larger and more numerous, and its posterior end does not overlap the quadrate. Primitively, palatine and ectopterygoid are separate. Galaxiidae and Aplochitonidae are united because they share an ectopterygoid that is greatly reduced or absent and largely or completely replaced by a prominent ligament (Fig. 13: 7B).

(8) *Lateral foramen for hyomandibular branch of facial nerve anterior to middle of lateral strut of hyomandibular* (Fig. 13: 8A). A lateral foramen at the ventral end of

the lateral strut unites *Lepidogalaxias*, Galaxiidae, and Aplochitonidae (Fig. 13: 8B). A lateral strut is absent in *Lovettia*. Primitively, it is posterior to the dorsal half of the strut (see also Williams, 1987).

(9) *Lateral strut of hyomandibular convex anteriorly as it arches posterodorsally from ventral to opercular arm* (Fig. 13: 9A). A robust, shelf-like lateral strut, somewhat similar to the above, unites Galaxiidae and Aplochitonidae (Fig. 13: 9B). A lateral strut is absent in *Lovettia*. Primitively, the strut is concave anteriorly and inclined vertically between the ventral arm and the base of the head.

(10) *Large cartilage at posterodorsal corner of metapterygoid*. Primitively this cartilage is either small or lacking (usually).

(11) *Symplectic prominently bent, with broad posterior expansion, and large anterior cartilaginous knob*. Primitively it has a slight bend, a slightly expanded posterior end, and a small anterior cartilage.

(12) *Adductor hyomandibulae (AH) present* (shared with Esocidae, *Dallia*, some osmerids [*Spirinchus* and *Thaleichthys*], and most Alepocephaloidea). Primitively there is no AH (see also Winterbottom, 1974).

Lepidogalaxias + Galaxiidae + Aplochitonidae

(8B) *Lateral foramen for hyomandibular branch of facial nerve at ventral end of lateral strut of hyomandibular* (see synapomorphy 8 for details). A lateral strut is absent in *Lovettia*.

(13) *Mesopterygoid teeth reduced in number or absent* (Fig. 13: 13A). These teeth are also absent in esocoids, salmonids, salangids, alepocephalids, and the Argentinoidea, and are few in platytroctids. Primitively in galaxioids (Retropinnidae + Prototroctidae) and osmerids the entire medioventral surface of the mesopterygoid bears numerous teeth (Williams, 1987).

(14) *Metapterygoid small with axe-shaped endochondral part* (shared with *Novumbra*, *Dallia*, and some Argentinoidea). It is smaller in the latter three taxa, and in *Novumbra* and *Dallia* overlaps a unique anteroventral wing of the hyomandibular. Primitively, the metapterygoid is somewhat large with a prominent rectangular or lunate endochondral section. Johnson & Patterson (1996) believe that a greatly reduced metapterygoid that fails to contact the symplectic and hyomandibular unites only *Lovettia* and *Lepidogalaxias*. However, the metapterygoid is also relatively small in *Aplochiton* and the Galaxiidae. Although the metapterygoid does not contact the hyomandibular and symplectic in *Lovettia* and *Lepidogalaxias*, this is also true of the equally small

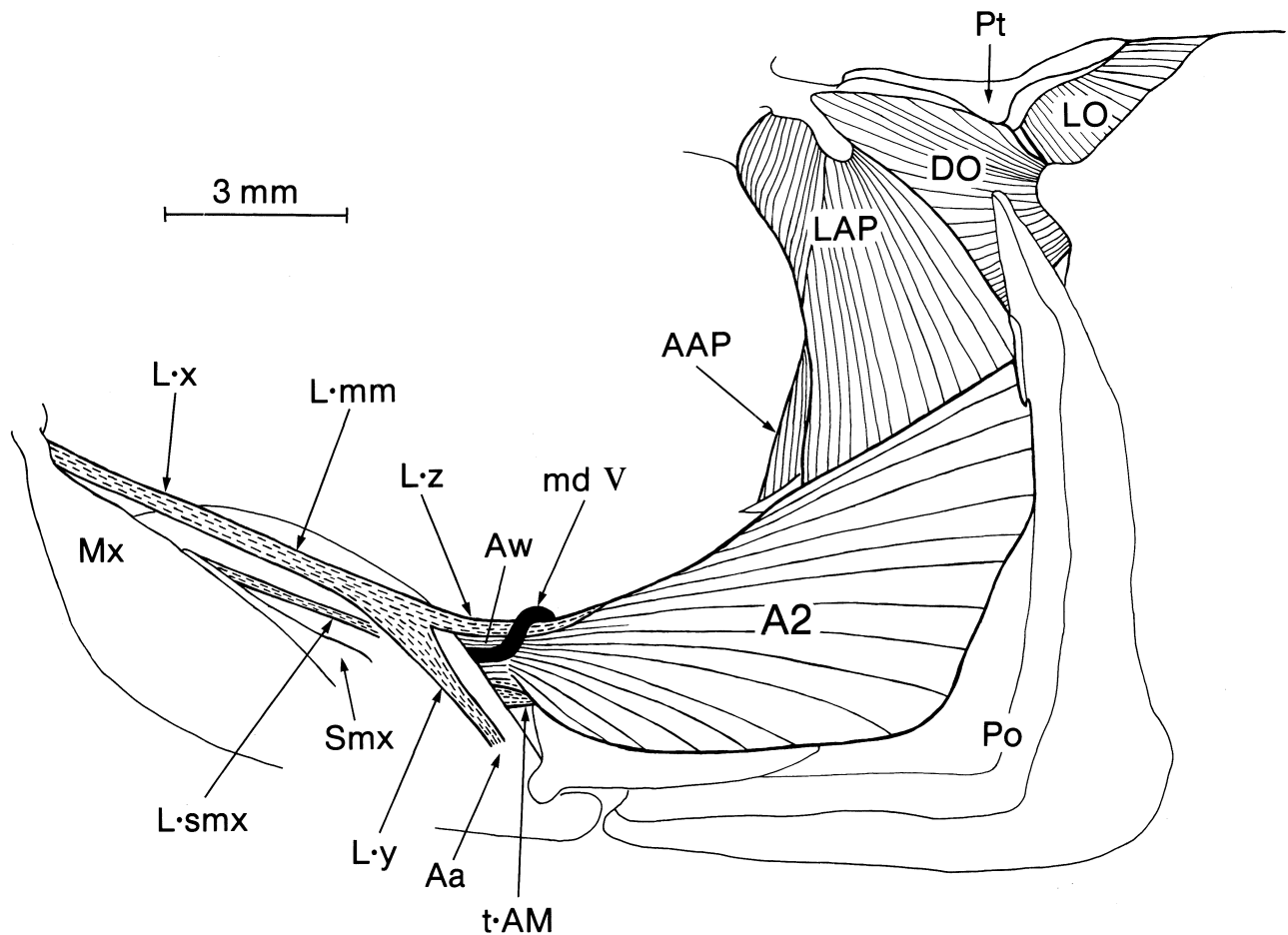


Fig. 14. Lateral view of external muscles of left suspensorium in *Hypomesus pretiosus* (UAMZ 3515, 135.4 mm) to illustrate elements commonly referred to in text.

galaxiids *Galaxias paucispondylus* (Williams, 1987), *Galaxiella pusilla* and *G. nigrostriata* (Frankenberg, 1969). Furthermore, the metapterygoid does not contact the symplectic and just barely contacts the hyomandibular in *Aplochiton taeniatus* (Fig. 6), and contacts neither the symplectic nor the hyomandibular in *A. zebra* (McDowall, 1969, fig. 3).

(15) *Adductor mandibulae with unique maxillo-mandibular ligament.* Osmerids (Fig. 14) and more generalised and primitive clupeomorphs and elopomorphs have the primitive state. The ostariophysan pattern is an autapomorphy (Fink & Fink, 1981; Howes, 1985). Primitively, there is one external division of the adductor mandibulae, section A2. There is also an Aw section (= intramandibularis) anterior to A2 that inserts in and fills the Meckelian fossa on the medial surface of the lower jaw. Section A2 inserts mainly on the medial surface of the lower jaw (via a tendinous aponeurosis) and connects with the maxilla and the posterolateral surface of the lower jaw via the maxillo-mandibular ligament (= ligamentum primordium, labelled L.x, L.y, and L.z on Fig. 14). In *Lepidogalaxias*, Galaxiidae and

Aplochitonidae the maxillo-mandibular ligament extends from the anterolateral end of section A2 to the maxilla. However, the part of the maxillo-mandibular ligament attaching onto the lower jaw is unlike the outgroups. The section extending to the angulo-articular (Figs 9–12: L.y) is reduced so there is almost no separate segment (Fig. 14: L.z) extending from the adductor mandibulae to the main part (L.x–L.y) of the maxillo-mandibular ligament. The maxillo-mandibular ligament also has a new section (Figs 9–12: L.w) extending anteroventrally from the intersection of L.x and L.y to the coronoid process (dentary).

(16) *Tendinous aponeurosis on which medial fibres of section A2 of adductor mandibulae insert not connected with posteriormost end of maxillo-mandibular ligament or barely connected with it* (shared with the argentinoid *Bathylagus*). The state in *Lovettia* could not be determined mainly because of small specimen size. Primitively, there is a distinct connection between the anterodorsal edge of the tendinous aponeurosis (before it bifurcates anteriorly) and the posteriormost end of the maxillo-mandibular ligament.

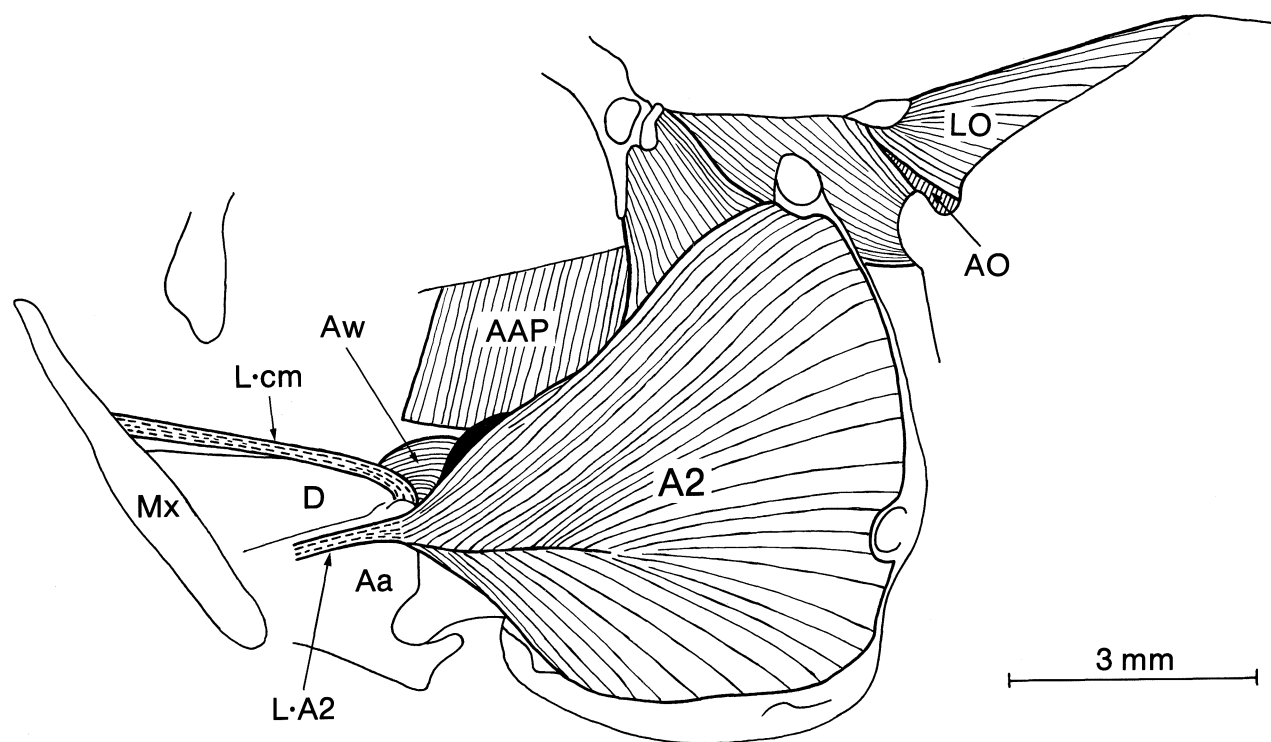


Fig. 15. Lateral view of external muscles of left suspensorium in *Umbra limi* (UAMZ 3752, 67.4 mm).

(17) Short ligament between posteromedial surface of maxilla and coronoid process of lower jaw (Fig. 9: L). Although the posteromedial surface of the maxilla is connected to the coronoid process via connective tissue in the other salmoniforms, none has a similar ligament. All esocoids have a ligament between the coronoid process and maxilla (Figs 15, 16, 18, 19: L.cm), but it is not the maxillo-mandibular ligament since both occur in *Esox* (Fig. 18). It is not homologous with the galaxioid ligament because it is much longer and flatter, extends anteroposteriorly, and inserts farther anteriorly on the maxilla. Also, connective tissue extends between the posteromedial surface of the maxilla and the coronoid process, but there is no ligament. This coronoid-maxilla ligament is a new esocoid synapomorphy (Williams, 1987).

(18) Adductor arcus palatini expanded anteriorly so insertion includes dorsal surface of mesopterygoid (shared with Esocoidei, Salmoninae, and Argentinoidea). Primitively, it is posterior and inserts on the hyomandibular, and usually the metapterygoid (see also Winterbottom, 1974).

Galaxiidae + Aplochitonidae

(7B) Ectopterygoid greatly reduced or absent and largely or completely replaced by prominent ligament (see also synapomorphy 7 for details). The replacement may not be complete in all specimens, in that a small, splint-like ectopterygoid can be present in *Lovettia* according to McDowall (1969) and G. David Johnson (personal communication); however, the character would still apply since the new ligament is found in *Lovettia*.

(9B) Lateral strut of hyomandibular robust, forming a lateral shelf (see synapomorphy 9 for details). A lateral strut is absent in *Lovettia*.

(13B) Mesopterygoid with large ventroanterolaterally curving teeth in single anteromedial row opposing large posterodorsally curving teeth around the edge of the basihyal (Fig. 17). Primitively in galaxioids (Retropinnidae + Prototroctidae) and osmerids the teeth are distributed over the entire medioventral surface of the mesopterygoid, they are ventrolaterally directed (see also Williams, 1987), and they oppose dorsomedially-directed teeth on the basihyal and basibranchials. Among other salmoniforms, some platytroctids have mesopterygoid teeth, but they are smaller than in

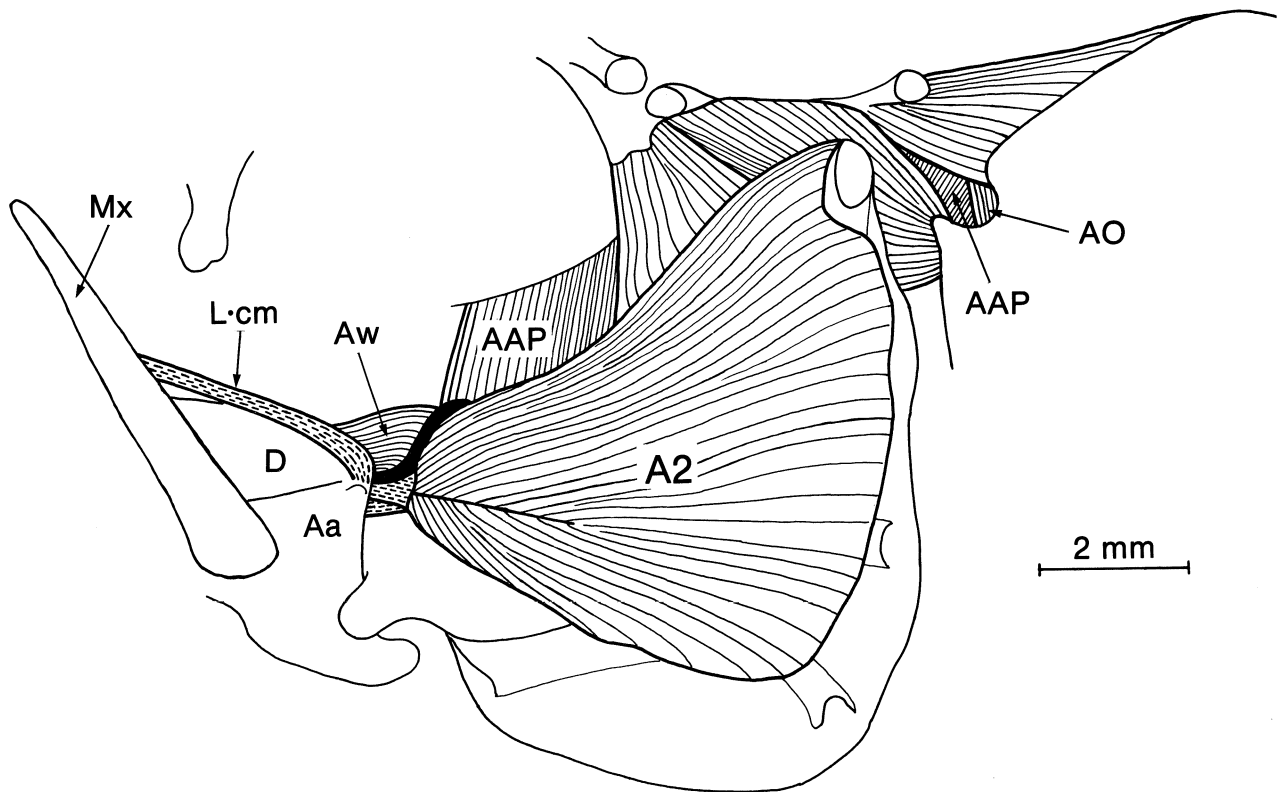


Fig. 16. Lateral view of external muscles of left suspensorium in *Umbra krameri* (UAMZ 3727, 63.3 mm).

galaxiids and aplochitonids and oppose small teeth on the basibranchials. Salmonines have enlarged basihyal teeth, but they are smaller than in galaxiids and aplochitonids and oppose large vomerine teeth (mesopterygoids and basibranchials are edentulous).

(19) *Palatine lacks teeth and the dermopalatine is absent or greatly reduced* (shared with adult *Plecoglossus* and some alepocephaloids; see also Markle, 1976 and Matsui & Rosenblatt, 1987). Primitively the palatine consists of a tubular, endochondral autopalatine, and a flattened, tooth-bearing dermopalatine.

(20) *Section A2 of adductor mandibulae has dorsomedial subdivision* (shared with *Plecoglossus* and possibly *Dallia*). Homology is suggested by a similar origin and insertion, and because the mandibular branch of the trigeminal nerve lies medial to the subdivision. The state in *Lovettia* could not be determined mainly because of small specimen size. Primitively in salmoniforms and lower teleosts A2 is not subdivided. The dorsomedial subdivision in *Plecoglossus* is not homologous with that in galaxioids because its fibres converge anteriorly on a separate tendon that extends anteriorly to join the tendon on which the dorsolateral fibres of the main muscle mass converge (Williams, 1987). *Dallia* has what might be interpreted as either a dorsomedial subdivision of section A2 (Fig. 19: A2.dm?) or a posteromedial

expansion of section Aw (Williams, 1987). Either way it is unlikely to be homologous with the muscle in galaxiids and aplochitonids because it originates mainly from the hyomandibular (versus metapterygoid) in a unique way, inserts on a separate tendon that inserts on the medial surface of the lower jaw, and because the mandibular branch of the trigeminal nerve is lateral to it (versus medial).

(21) *Section A2 of adductor mandibulae originates partly from posterior surface of lateral strut of hyomandibular* (shared with the alepocephalid *Leptoderma*). Although a lateral strut is absent in *Lovettia* the origin of Section A2 of the adductor mandibulae is the same as in *Aplochiton* and the Galaxiidae. Primitively it originates from the anterior face of the strut.

Critique of competing hypotheses of galaxioid relationships

Although substantial evidence supports the hypothesis that the Retropinnidae + Prototroctidae form a monophyletic group (McDowall, 1969; Patterson, 1970; Nelson, 1972; Rosen, 1974; Berra *et al.*, 1982; Fink, 1984; Nelson, 1984; Begle, 1991) and that the Galaxiidae + Aplochitonidae form a monophyletic group (McDowall,

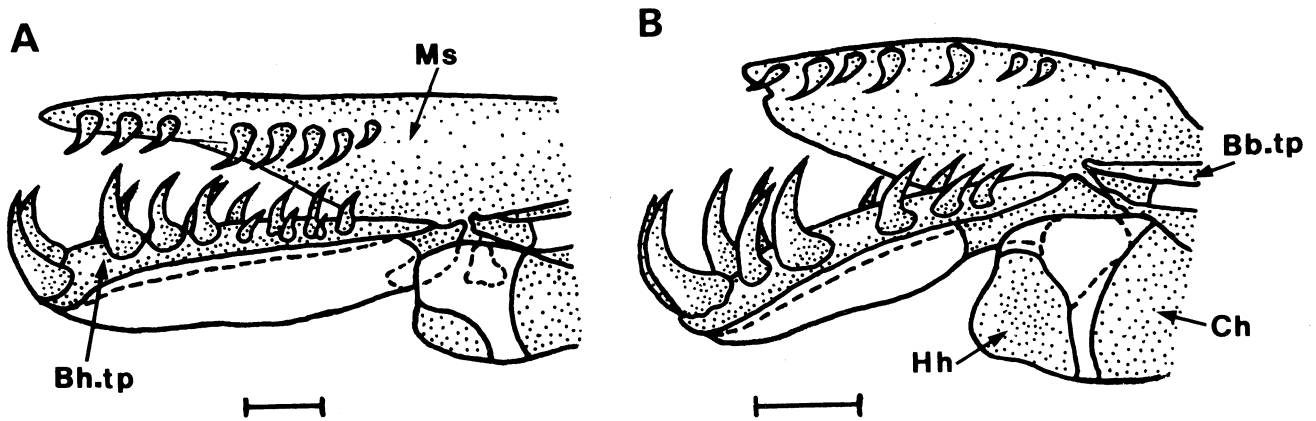


Fig. 17. Medial view of right mesopterygoid and basihyal, *in situ*, in (A) *Aplochiton taeniatus* (NMC 76-0393, 110.5 mm) and (B) *Galaxias brevipinnis* (UAMZ 4608, 93.0 mm) to show bite. Scale = 1.0 millimetre.

1969; Patterson, 1970; Nelson, 1972; Rosen, 1974; Fink, 1984; Begle, 1991), the relationship of each assemblage to other salmoniforms is debatable. As noted earlier, most workers place Retropinnidae, Prototroctidae, Galaxiidae, and Aplochitonidae in a monophyletic group. Rosen (1974) believed otherwise. He united the Retropinnidae, Prototroctidae, Osmeridae, and Salangidae partly because he claimed that they share a unique "stegural" formed by fusion of the rudimentary neural arch(es) of PU1 with the first uroneural. Fink & Weitzman (1982) analysed Rosen's (1974) evidence and noted exceptions: some of the above taxa have rudimentary neural arches fused with PU1 (in addition to fusion with the uroneural), and some galaxiids and aplochitonids have fusion of the rudimentary neural arches with the first uroneural (and PU1).

Rosen (1974) also used hyobranchial evidence to unite retropinnids, prototroctids, and osmeroids. It is hard to tell from his text what synapomorphies he is using (see also Fink & Weitzman, 1982). One is apparently (p. 313) "a blunt, somewhat elevated median ridge [on the basibranchial toothplate] except when [the] tooth plate is greatly expanded." I found that although the toothplate arches dorsally there is no "blunt ... median ridge." An arched, similarly shaped basibranchial toothplate is also present in many primitive teleosts (e.g., *Elops* and *Osteoglossum*). Another synapomorphy is (p. 313): "Basihyal fangs in forms with unreduced dentition [are] large, arranged in alternating positions on [the] right and left side, and tending to form a single large terminal tooth." I do not find this convincing. First, two osmeroids (*Mallotus* and *Plecoglossus*) have reduced basihyal

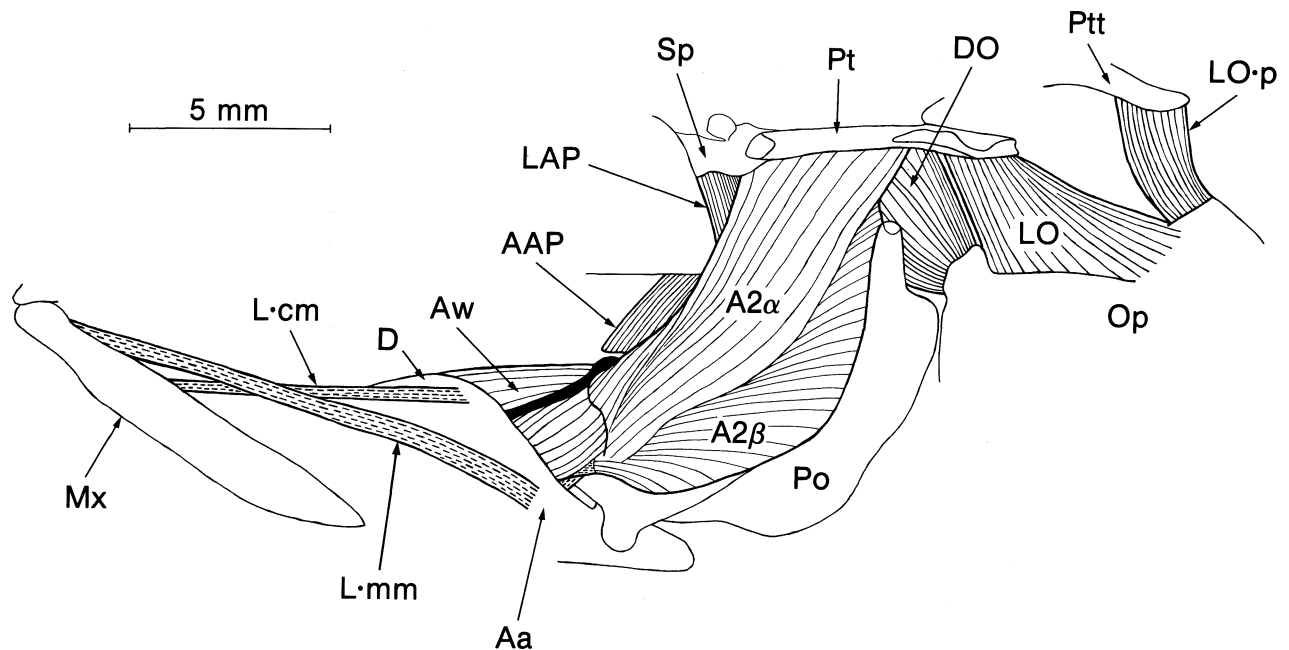


Fig. 18. Lateral view of external muscles of left suspensorium in *Esox lucius* (UAMZ 4878, 103.0 mm).

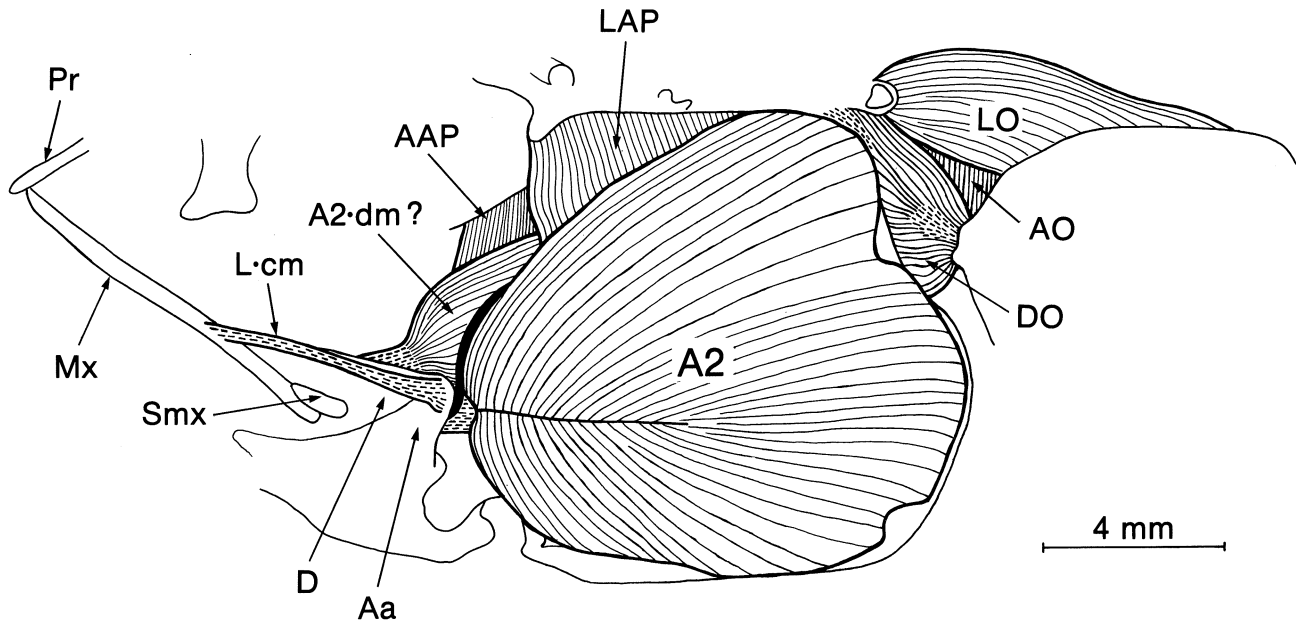


Fig. 19. Lateral (slightly dorsal) view of external muscles of left suspensorium in *Dallia pectoralis* (UAMZ 3737, 115.8 mm).

dentition and small teeth, and second, the teeth on the right and left sides of the basihyal do not alternate in all osmeroids (*sensu* Rosen, 1974), nor do they usually all alternate even when alternation is present. For example, in my specimens of *Thaleichthys* the teeth are arranged in right and left pairs (except the anteriormost pair), and except for the anteriormost pair resemble the pattern in the salmonines, galaxiids, and aplochitonids. Also, when the teeth alternate it is usually the anterior teeth; the posterior teeth are paired. The alternating anterior teeth may be the result of the anterior end of the basihyal being narrow, crowding the anterior teeth (not clearly illustrated by Rosen but visible in my specimens). A terminal tooth is absent in my specimens of *Hypomesus* and *Prototroctes*; instead, there is a terminal pair as in the salmonines, galaxiids, and aplochitonids. Some salmonines (*Salvelinus fontinalis*, *S. namaycush*) also have a terminal tooth. Another apparent Rosen synapomorphy is that in osmeroids the fifth epibranchial is fused ventrally to the posteroventral end of the fourth. Primitively, the fifth epibranchial is next to, but not fused with the posteroventral end of the fourth (Nelson, 1967a). However, there is no fusion of epibranchial five with epibranchial four (although they are adjacent) in several osmeroids illustrated by Rosen, including *Stokellia* and *Plecoglossus*. Epibranchial five is distinctly separate from epibranchial four in my specimens of *Prototroctes*, a taxon not illustrated by Rosen. Also, in my specimens of *Retropinna retropinna* the ventral end of epibranchial five closely abuts the posteroventral end of epibranchial four but there is a line between the two, suggesting no fusion (see Rosen's fig. 16F, in which he shows fusion in *R. retropinna*).

Rosen (1974) united the Galaxiidae (my Galaxiidae + Aplochitonidae) with the Salmonidae and placed them in their own superfamily, Salmonoidea. According to him they share enlarged, fang-like teeth around the margin of the basihyal (arranged in right and left pairs and terminating anteriorly as a single pair) and a basibranchial that is edentulous or has just a few teeth. This basihyal character is suspect for several reasons. First, other salmoniforms have enlarged marginal basihyal teeth, including the Retropinnidae, Prototroctidae, Osmeridae, and Argentinidae. As mentioned earlier, some members of the latter families also have basihyal teeth arranged in right and left pairs ending anteriorly in a terminal pair. Fink & Weitzman (1982) also noted that about half the galaxiids they examined had alternating tooth pairs along the margin of the basihyal and a single terminal tooth, a state similar to the condition Rosen claimed was an osmeroid (*sensu* Rosen, 1974) synapomorphy. Although the Salmoninae have paired basihyal teeth, some (*Salvelinus fontinalis*, *S. namaycush*) have a terminal tooth as in many osmeroids. Basibranchial teeth are also absent or few in salangids, *Lepidogalaxias*, the Argentinoidei, and stomiiforms. Rosen (1974) also noted that, unlike the condition in salmonines, the basibranchial toothplate in galaxiids and aplochitonids is not fused with the second endoskeletal basibranchial. Within the Salmonidae, only the Salmoninae exclusive of the Eocene fossil *Eosalmo* (Wilson & Williams, 1992) have enlarged basihyal teeth; the Thymallinae and Coregoninae have numerous small teeth scattered randomly over both the basihyal and basibranchials. Furthermore, numerous salmonines have basibranchial teeth (see Stearley & Smith, 1993), including

Oncorhynchus clarki, which has up to 52 according to Behnke (1992).

Rosen also cited epibranchial evidence. He claimed that fusion between the dorsal tip of the fifth epibranchial and the midpoint of the dorsolateral border of the fourth epibranchial was a galaxiid + salmonid synapomorphy. All galaxiids and aplochitonids illustrated by Rosen (and those examined by me) had this state. However, Rosen found such fusion only in one salmonid, *Prosopium cylindraceum*. All the other species possessed the primitive state in which the fifth epibranchial is separate from the fourth. None of the salmonids that I examined possessed fusion, including *P. williamsoni*. Another synapomorphy was the lack of an uncinete process on the fourth epibranchial. But not all galaxiids lack an uncinete process. It is present in *G. anomalus* (= *G. vulgaris*), *G. delfini* (= *G. platei*) (Fink & Weitzman, 1982), and in *G. paucispondylus* (personal observation). Besides salmonids, an uncinete process is absent in some umbrids (*Umbra*), some osmerids (*Hypomesus*, *Mallotus*, and possibly *Allosmerus*), salangids, prototroctids, some retropinnids (*Retropinna retropinna*), *Lepidogalaxias*, and many Argentinoidei (personal observation; see also Rosen, 1974; Greenwood & Rosen, 1971; Begle, 1992). Another synapomorphy was the absence of a levator process on the fourth epibranchial. According to Rosen, the process is the insertion area for the fourth external levator muscle. This character is difficult to interpret. Fink & Weitzman (1982) questioned Rosen's definition of a levator process noting (p. 82) that "In many primitive euteleosts [the dorsolateral surface of the fourth epibranchial] is separated from the ventrolateral extremity of the bone by a concavity, so that the area of [the insertion of the levator muscle] may be termed a process. Rosen's character, "absence of a levator process", might better be defined as loss of this concavity; the area of levator attachment remains unchanged, although in descriptive terms it is no longer a process." I concur with Fink & Weitzman's interpretation. As defined by Fink & Weitzman the "Absence of this concavity" is shared with salmonids, galaxiids (*sensu* Rosen, 1974), the retropinnids *R. retropinna* and *Stokellia*, prototroctids, *Salangichthys* (Salangidae), and all esocoids except *Umbra* (personal observation; Fink & Weitzman, 1982).

The neotenic salangids are sometimes placed with galaxioids. Greenwood *et al.* (1966) included them within the Galaxioidei, but why they did this is unclear from their text. Weitzman (1967) suggested placing salangids in a group separate from osmerids, galaxioids, and stomioids. Nelson (1970) noted similarities with the Argentinoidea. McDowall (1969) concluded that salangids are not galaxioids. Rosen (1974) placed them *incertae sedis* within his Osmeroidea. Howes & Sanford (1987) considered salangids to be the sister group of their Osmeridae. Roberts (1984) placed them in the superfamily Salangoidea within the order Salmoniformes (coordinate with Osmeroidea and Salmonoidea). Fink (1984) said that salangids were galaxioids if one accepted their shared reductive traits, or osmeroids if

one accepted their shared (p. 204) complex caudal skeleton character. Begle (1991) placed salangids with galaxioids after conducting a phylogenetic analysis using PAUP. Suspensorial evidence is equivocal, and I placed them *incertae sedis* within the galaxioid + osmeroid + argentinoide clade (Williams, 1987). However, Johnson & Patterson (1995, 1996, also G. David Johnson, personal communication) recently redefined many of Begle's (1991) characters and present new and convincing evidence that salangids belong in the Osmeridae, and are the sister group of *Mallotus*.

Another controversy is whether or not *Lepidogalaxias* is a galaxioid. Nelson (1972) noted that the cephalic pitlines in *Lepidogalaxias* resemble those of the esocoid *Dallia*. I agree, but *Dallia* has a more extensive pattern of cephalic canals than does *Lepidogalaxias*. Preopercular, infraorbital, supraorbital, and temporal canals are present in *Dallia*, but only a preopercular canal is found in *Lepidogalaxias*. The pattern of the pitlines is also different upon closer examination (e.g., compare Nelson's figures of *Dallia* with fig. 16 in Frankenberg, 1969).

Rosen (1974) placed *Lepidogalaxias* in the Esocoidei. I question this hypothesis, as did Fink & Weitzman (1982) who state (p. 80) that "Of the eleven characters Rosen (1974) used to place *Lepidogalaxias* in the Esocae [= Esocoidei], only four appear to be appropriate for inference of relationship between those groups: lack of a mesocoracoid, lack of pyloric caeca, a single rudimentary neural arch and spine over PU1, and a single uroneural." Since I am unsure why they singled out these characters the following is a list of Rosen's synapomorphies (1974: 311): (1) "Dorsal fin posterior in position, over anal fin" (shared with Galaxiidae, Retropinnidae, Salangidae and many Argentinoidei). (2) "no adipose dorsal fin" (shared with Galaxiidae, some Salangidae, and many Argentinoidei). (3) "maxillary edentulous" (shared with galaxiids, aplochitonids, prototroctids, most retropinnids, and many other salmoniforms; see McDowall, 1976, 1979; Nelson, 1994). (4) "with or without a supramaxilla" (Rosen listed both states and the derived state is ambiguous). (5) "endopterygoid [= mesopterygoid] edentulous" (shared with Salmonidae, Salangidae, Alepocephalidae, Argentinoidea, and some members of the galaxiid genus *Neochanna*). (6) "no mesocoracoid" (shared with Galaxiidae, Aplochitonidae, Retropinnidae, Prototroctidae, Salangidae, and many Argentinoidei; see Markle, 1976; Nelson, 1994; Roberts, 1984). (7) "no pyloric caeca" (shared with salangids, retropinnids, prototroctids, some galaxiids, and some aplochitonids; see McDowall, 1971; McDowall & Frankenberg, 1981). (8) "a single large, oval, strongly dentigerous tooth plate supported by the fourth infrapharyngobranchial and fourth epibranchial" (shared with Salmonidae, Stomiiformes, and many higher teleosts; see Rosen, 1973, 1974; Weitzman, 1974). A similar, but smaller, narrower toothplate with smaller teeth is found in many salmoniforms, including salangids, most osmerids (including *Plecoglossus*), retropinnids, and prototroctids. In galaxiids and aplochitonids there are usually several smaller tooth-plates in the area usually occupied by a

single large tooth-plate (see also Rosen, 1974). (9) “fourth epibranchial always somewhat reduced and without a distinct posterodorsal process for the external branchial levator muscle.” I discussed this character above. The term “somewhat reduced” is unclear if one examines Rosen’s figures of this structure. Although there is no distinct posterodorsal process in *Lepidogalaxias* and esocoids (excluding *Umbra*) this can be said of other salmoniforms he illustrates (some salmonids and retropinnids). The fourth epibranchial in *Lepidogalaxias* is also only broadly similar to that in the esocoids and more closely resembles the one in galaxioids. (10) “never more than a single rudimentary neural arch and spine over PU1.” One rudimentary neural arch is found in some osmerids (Rosen, 1974, fig. 28B), many salmonids (Rosen’s figures 25A, B, and C), some galaxiids and aplochitonids (Rosen’s figures 18 and 19), some Argentinoidea (Greenwood & Rosen, 1971; Markle, 1976), and possibly some salangids (Rosen, 1974, fig. 26B). Rudimentary neural arches in galaxiids and aplochitonids are different from those in *Lepidogalaxias* and esocoids because they are larger and usually fused ventrally with a compound centrum (but in Rosen’s fig. 19B of *Lovettia* the two rudimentary neural arches are autogenous). A rudimentary neural arch is also apparently fused ventrally to the underlying centrum in some specimens of *Lepidogalaxias* (Rosen, 1974, fig. 24C), which in this respect resembles galaxioids. (11) “a single, long, straplike uroneural.” Some galaxiids and aplochitonids have one uroneural similar in shape to that in some umbrids (Rosen’s figures 18D, 19C, 21, and 23). Rosen (p. 293) also noted that some specimens of *Lepidogalaxias* had “anterodorsal acuminate processes” on the uroneural that resemble those in esocoids. However, other salmoniforms, including galaxioids, have similarly shaped processes (figures in Rosen, 1974).

Fink (1984) hypothesised that *Lepidogalaxias* may be the sister group of the Neoteleostei because they share a retractor dorsalis muscle and an occipital condyle composed of both basioccipital and exoccipital. Both are neoteleostean synapomorphies according to Fink & Weitzman (1982). Fink (1984) said that *Lepidogalaxias* was not a neoteleost because it lacked both a rostral cartilage or its homologue and teeth with a unique attachment mode. He also claimed that salmonids are a possible sister group of neoteleosts since they share a similar occipital condyle and salmonids have a homologue of the rostral cartilage. Salmonids are not neoteleosts, according to Fink, because they lack teeth with a unique attachment mode and a retractor dorsalis. Because of this uncertainty Fink placed Salmonidae, *Lepidogalaxias*, and Neoteleostei in an unresolved trichotomy.

The retractor dorsalis is a bilaterally paired muscle extending from the anterior vertebrae to the dorsal gill arch elements. It represents a specialisation of the feeding mechanism that allows more independent movement of the dorsal gill-arch elements and their toothplates (Nelson, 1967a,b; Rosen, 1973), and occurs

in the osteoglossomorph *Pantodon*, some muraenid eels (Elopomorpha), some ostariophysans (siluriforms and some cyprinids), neoteleosts, and in non-teleosts such as *Amia* and *Lepisosteus* (Nelson, 1967a; Rosen, 1973, 1985; Winterbottom, 1974; Johnson, 1992). Its presence in *Lepidogalaxias* may be related to an ability to bend the neck at a sharp angle during feeding. Facilitating this skill are wide spaces between the exoccipital, first vertebra, and second vertebra, and slightly narrower spaces between the other cervical vertebrae. Also possibly related to this ability is an occipital condyle composed of both basioccipital and exoccipital. This feature is shared with the osteoglossomorph *Hiodon*, salmonines, and neoteleosts (see also Rosen, 1985; Johnson, 1992). In these taxa a distinct tripartite occipital joint exists involving both exoccipital and basioccipital. The contact of the exoccipital with the centrum of the first vertebra is via a cartilage-covered condyle or surface on each exoccipital that contacts a separate facet (usually) on the dorsolateral corners of the anterior end of the centrum. The rest of the anterior end of the centrum contacts the basioccipital. The occipital joint in *Lepidogalaxias*, however, is different, and probably not homologous. The basioccipital forms almost the entire joint surface, with two wing-like extensions of each exoccipital overlapping each dorsolateral corner of the anterior end of the first centrum. The contact area of the exoccipital with the vertebra is smaller than in most teleosts with such a joint and is more lateral. The exoccipital also lacks a distinct cartilage-covered condyle or facet where it contacts the first vertebra, which also lacks a facet at the contact point. The exoccipital “wings” resemble the posterolateral extensions of the exoccipitals that approach the first vertebra in some galaxiids (e.g., *Galaxias brevipinnis*).

Also supporting my hypothesis that the retractor dorsalis of *Lepidogalaxias* is not homologous with the retractor dorsalis of neoteleosts is Johnson’s (1992) new synapomorphy uniting the Neoteleostei: insertion of the third internal levator muscle on the fifth upper pharyngeal toothplate. In all non-neoteleosts with a “retractor dorsalis” that Johnson examined, including *Lepidogalaxias*, the third internal levator inserts on the fourth pharyngobranchial cartilage. Johnson interprets the shift in insertion of the third internal levator in neoteleosts as related to the advent of the neoteleostean retractor dorsalis. He hypothesises that this new arrangement (p. 11) “provides for a forward pull on the fifth [upper pharyngeal] toothplate acting antagonistically to the backward pull of the retractor dorsalis on that element.” He concludes that (p. 12) the “Lack of the associated neoteleost modification is at least consistent with an independent origin of the ‘retractor dorsalis’ of *Lepidogalaxias*, although it does not specifically refute the *Lepidogalaxias*—neoteleost hypothesis.”

As a final point I will briefly discuss pedomorphosis in galaxioids. Reductive evolution is common in teleosts, and galaxioids are no exception. If you define a reductive character as one that involves obvious truncation of development (Begle, 1991), only four (19%) of my 21

characters are clearly reductive (2, 4, 13, and 19). Paedomorphosis in the galaxioids, at least regarding the suspensorium and its muscles, is not as common as one might predict after reading earlier studies. For example, 20 (54%) of the 37 characters that supported Begle's (1991) hypothesis of galaxioid relationships were reductive. His characters were osteological with two exceptions (24, 51). Other galaxioid studies also relied on osteological characters (e.g., McDowall, 1969), hence the conclusion that galaxioids exhibit extensive paedomorphosis. This is true if one considers only osteology. However, an important finding of my study is that galaxioids exhibit little paedomorphosis regarding the muscles of the suspensorium. This is also true of osmerids and salangids (see also Williams, 1987). The only galaxioid reductive muscle character is loss of the supramaxillary ligament, a feature correlated with loss of the supramaxillae. These findings illustrate the value of examining new anatomical systems when studying problematic taxa. Paedomorphosis in one organ system is not necessarily correlated with paedomorphosis in another, and not all functional units of the skeleton appear to exhibit this phenomenon to the same degree. This is not surprising since characters within the same species evolve at different rates.

Conclusions

This study provides significant new osteological and myological information, some of which constitutes important new evidence bearing on galaxioid intrarelationships and the phylogenetic position of *Lepidogalaxias*. My phylogeny, based strictly on the bones and muscles of the suspensorium, suggests that the galaxioids are monophyletic and include *Lepidogalaxias*. *Lepidogalaxias* is the sister group of Galaxiidae + Aplochitonidae based particularly on synapomorphies of the adductor mandibulae. The following galaxioid pattern, based on the suspensorium and its muscles, is proposed: ([Retropinnidae + Prototroctidae] + [*Lepidogalaxias* + (Galaxiidae + Aplochitonidae)]).

Placement of the southern salmoniforms in one group has significance for historical biogeography since the number of events, dispersal or vicariance, which must be assumed to account for their distribution is fewer if *Lepidogalaxias* is a galaxioid rather than an esocoid. Their distribution across the southernmost end of the Southern Hemisphere could be explained either by very ancient vicariant events (Rosen, 1974) or by some form of transoceanic dispersal (McDowall, 1984; Berra *et al.*, 1995). In support of the latter hypothesis is the observation that marine stages are found in numerous galaxioids (McDowall, 1984), including the disjunct species *Galaxias maculatus* from eastern and western Australia, New Zealand, South America and associated oceanic islands. Berra *et al.* (1995) provide convincing new genetic evidence that distribution of *G. maculatus* is best interpreted as due to dispersal through the sea.

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Appendix 1. Input data matrix of taxa, characters, and character states analysed using PAUP version 3.1.1. (Swofford, 1993). Character numbers correspond to those in the text.

Taxa	Characters																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Retropinnidae	1	1	1	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	0	0	0
Prototroctidae	1	1	1	1	1	1	1	2	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Lepidogalaxias</i>	1	1	1	1	1	1	2	1	0	0	0	0	1	1	1	1	1	1	0	0	0
Galaxiidae	1	1	1	1	1	1	3	1	2	0	0	0	2	1	1	1	1	1	1	1	1
Aplochitonidae	1	1	1	1	1	1	3	1	2	0	0	0	2	1	1	1	1	1	1	1	1

Appendix 2. The following is a list of specimens examined and their method of preparation: cs = cleared and stained for cartilage and bone, csb = cleared and stained for bone only, ds = dry skeleton, r = radiographed, md = muscle dissection, • = extinct taxon, f = fossil. Number of galaxioid specimens examined are indicated. For detailed information, including catalogue numbers, refer to Williams, 1987. Supraspecific taxa are listed roughly phylogenetically while species are listed alphabetically

SALMONIFORMES

Esocidae

- Esox lucius* (cs, ds, md)
- E. masquinongy* (cs, md)
- *E. tiemani* (f)

Umbridae

- Dallia pectoralis* (cs, md)
- Novumbra hubbsi* (cs, md)
- *N. oregonensis* (f)
- Umbra krameri* (cs, md)
- U. limi* (cs, md)
- U. pygmaea* (csb, md)

Salmonidae

- Brachymystax coregonoides* (r)
- B. lenok* (md)
- Coregonus artedii* (cs, md)
- C. clupeaformis* (cs, md)
- *Eosalmo driftwoodensis* (f)
- Oncorhynchus gairdneri* (cs)
- O. kisutch* (cs)
- O. nerka* (cs, md)
- Prosopium cylindraceum* (md)
- P. williamsoni* (cs, md)
- Salmo trutta* (cs, ds, md)
- Salvelinus alpinus* (ds)
- S. fontinalis* (cs, md)
- S. namaycush* (cs)
- Stenodus leucichthys* (cs, ds, md)
- Thymallus arcticus* (cs, md)

Osmeridae

- Allosmerus elongatus* (cs, md)
- Hypomesus olidus* (cs)
- H. pretiosus* (cs, md)
- Mallotus villosus* (cs, f, md)
- Osmerus mordax* (cs, md)
- Plecoglossus altivelis* (cs, md)
- Spirinchus starksi* (cs, md)
- S. thaleichthys* (cs, md)
- Thaleichthys pacificus* (cs, md)

Salangidae

- Salangichthys ishikawae* (cs, md)
- S. microdon* (cs, md)
- Salanx cuvieri* (md)
- S. prognathus* (cs, md)

Retropinnidae

- Retropinna retropinna* (2 cs, 3 md)

Prototroctidae

- Prototroctes maraena* (2 cs, 2 md)

Lepidogalaxiidae

- Lepidogalaxias salamandroides* (1 cs, 2 r, 2 md)

Galaxiidae

- Brachygalaxias bullocki* (1 cs, 1 md)
- Galaxias brevipinnis* (1 cs, 1 md)
- G. fasciatus* (2 md)
- G. maculatus* (2 cs, 3 md)
- G. paucispondylus* (1 cs, 1 md)
- Neochanna apoda* (1 cs, 1 md)

Aplochitonidae

- Aplochiton taeniatus* (1 cs, 1 md)
- Lovettia sealii* (2 cs, 6 md)

Argentinidae

- Argentina silus* (cs, md)

Bathylagidae

- Bathylagus pacificus* (cs, md)

Opisthoproctidae

- Dolichopteryx longipes* (cs, md)
- Macropinna microstoma* (cs, md)
- Opisthoproctus soleatus* (csb, md)

Platyroctidae

- Holtbyrnia latifrons* (cs, md)
- Mirrorictus taningi* (cs, r, md)
- Pellisulus facilis* (cs, md)
- Platyroctes apus* (cs, r, md)
- Sagamichthys abei* (cs, md)
- Searsia koefoedi* (cs, r, md)
- Searsioides multispinus* (cs, md)

Alepocephalidae

- Alepocephalus bairdii* (cs)
- A. tenebrosus* (cs, md)

Appendix 2. Continued.

- Bajacalifornia burraigei* (cs, md)
Bathylaco nigricans (cs, r, md)
Bathylaco sp. (r, md)
Bathytroctes microlepis (cs, md)
Binghamichthys (= *Talismania*) *aphos* (cs, md)
Conocara mcdonaldi (cs, md)
Leptoderma macrops (cs, md)
Narctes stomias (cs, md)
Photostylus pycnopterus (cs, md)
Rouleina maderensis (cs, md)
R. nudus (md)
Talismania antillarum (cs, md)
T. bifurcata (md)
Xenodermichthys copei (cs, r, md)
- OTHER TELEOSTEI**
- Pholidophoriformes •
- *Pholidophorus* sp. (f)
- Osteoglossiformes
- *Eohiodon rosei* (f)
 - Hiodon alosoides* (cs, md)
 - Osteoglossum bicirrhosum* (cs, md)
 - Pantodon buchholzi* (md)
 - *Phareodus testis* (f)
 - Xenomystus nigri* (cs, md)
- Elopiformes
- Elops affinis* (md)
 - E. hawaiiensis* (cs)
 - Megalops cyprinoides* (cs, md)
- Ellimmichthyiformes •
- *Diplomystus* (f)
- Clupeiformes
- Chirocentrus dorab* (csb, md)
 - Alosa pseudoharengus* (cs)
 - A. sapidissima* (csb, md)
 - Anodontostoma chacunda* (md)
 - Clupea harengus* (cs, md)
 - Dorosoma petenense* (cs)
 - Dussumieria hasselti* (csb, md)
 - Etrumeus teres* (csb)
 - Harengula thrissina* (csb)
 - Hyperlophus sprattellides* (csb)
 - Ilisha furthii* (csb, md)
 - Jenkinsia stolicifera* (csb)
 - *Knightia eocaena* (f)
 - *Knightia* sp. (f)
 - Nematalosa erebi* (csb)
 - Odontognathus compressus* (csb)
 - O. panamensis* (csb)
 - Amentum devisi* (md)
 - Anchoa mundeoloides* (md)
 - A. panamensis* (csb)
 - Cetengraulis mysticetus* (csb)
 - Engraulis* sp. (csb)
 - Thryssa* (= *Thrissocles*) *hamiltoni* (csb, md)
- Gonorrhynchiformes
- Chanos chanos* (cs, md)
 - *Notogoneus osculus* (f)
- Cypriniformes
- Catostomus commersoni* (md)
 - Couesius plumbeus* (cs)
 - Notropis blennioides* (md)
- Characiformes
- Astyanax fasciatus* (md)
- Stomiiformes
- Argyropelecus pacificus* (cs, md)
 - Chauliodus macouni* (md)
 - Diplophos taenia* (cs, md)
 - Tactostoma macropus* (cs, md)
 - Vinciguerria nimbaria* (cs, md)
- Aulopiformes
- Aulopus filamentosus* (md)
 - Chlorophthalmus agassizi* (cs)
 - *Nematonotus* sp. (f)
 - Saurida tumbil* (csb)
 - Synodus foetens* (md)
 - S. saurus* (md)
 - S. synodus* (cs)
- Myctophiformes
- Myctophum* sp. (cs, md)
 - Protomyctophum thompsoni* (cs, md)
 - Stenobranchius leucopsarus* (md)
 - Symbolophorus* sp. (cs, md)
- Percopsiformes
- Chologaster agassizi* (md)
 - Percopsis omiscomaycus* (cs, md)
 - *Tricophanes foliarum* (f)
 - unidentified percopsid fossils (f)
- Gadiformes
- Lota lota* (ds, md)
 - Microgadus proximus* (md)
- Batrachoidiformes
- Porichthys notatus* (csb)
- Cyprinodontiformes
- Fundulus diaphanus* (cs)
 - Xiphophorus maculatus* (cs)
- Atheriniformes
- Hypoatherina* (= *Allanetta*) *harringtonensis* (md)
 - Menidia menidia* (cs)
- Stephanoberyciformes
- Melamphaes lugubris* (md)
- Beryciformes
- Plectrypops retrospinis* (cs, md)
 - Sargocentron* (= *Adioryx*) *coruscus* (md)
- Gasterosteiformes
- Gasterosteus aculeatus* (csb)
 - Pungitius platygaster* (csb)
- Scorpaeniformes
- Apistops caloundra* (md)
 - Chitonotus pugetensis* (csb)
 - Cottus cognatus* (csb)
 - Liparis fucensis* (md)
 - Malacocottus kincaidi* (csb)
 - Sebastes ruberrimus* (ds)
- Perciformes
- Caprodon schlegeli* (md)
 - Centropristis striata* (md)
 - Chanda* (= *Ambassis*) sp. (md)
 - Epinephelus sexfasciatus* (md)
 - Etheostoma blennioides* (md)
 - *Mioplosus* sp. (f)
 - Morone americana* (csb)
 - Perca flavescens* (csb, md)
 - *Priscacara* sp. (f)
 - *P. liops* (f)
 - Stizostedion vitreum* (ds)