Biological aspects of an interesting fossil fish:
Paramblypterus duvernoyi (Amblypteridae, Actinopterygii)

Kathrin Dietze[1]

With 10 figures

Abstract

Based on three-dimensional models of the skull and body of *Paramblypterus duvernoyi*, function of the feeding apparatus and potential of locomotion are interpreted. Compared to most other lower actinopterygians, certain modified features regarding the suspensory apparatus, snout bones, gape, dermohyal and suborbital region, and palatoquadrate-maxillary chamber, are present in *P. duvernoi*. These features suggest an increased versatility of the skull and/or enlargement of underlying muscles, thus improving the ability of food uptake. The weak, pin-like teeth present in *P. duvernoyi* suggest a main diet of small or soft-bodied planktonic or benthic invertebrate organisms. Axial locomotion of *P. duvernoyi* appears to lie within the range of moderate swimming speeds. *P. duvernoyi* probably had a flat belly indicating that this species lived close to the bottom.

Key words: Lower Permian, Southwest Germany, basal actinopterygians, functional morphology, feeding, locomotion.

Zusammenfassung

Anhand drei-dimensionaler Modelle des Schädels und Körpers von *Paramblypterus duvernoyi* werden Funktionsweise des Ernährungsapparates und Möglichkeiten der Fortbewegung interpretiert. Im Vergleich mit anderen basalen Actinopterygiern erscheint die Schädelrekonstruktion von *P. duvernoyi* hinsichtlich des Suspensoriums, der Schnauzenknochen, der Mundöffnung, des Dermohyal- und Suborbitalbereiches, sowie der Palatoquadratum-Maxillare-Kammer abgeleitet. Dies deutet auf eine erhöhte Beweglichkeit in diesen Bereichen und/oder eine Vergrößerung der darunter liegenden Muskeln hin, was vorteilhaft für die Nahrungsaufnahme ist. Die schmalen, stiftförmigen Zähne von *P. duvernoyi* deuten auf eine Ernährung von kleineren oder weichkörperigen benthischen und planktischen Invertebraten hin. Vermutlich zeichnete sich die axiale Fortbewegungsweise von *Paramblypterus* durch mäßige mittlere Schwimmgeschwindigkeit aus. Der Bauch von *P. duvernoyi* war wahrscheinlich abgeflacht, was darauf hinweist, dass diese Art bodenbezogen gelebt hat.

Schlüsselwörter: Unter-Perm (Rotliegend), Südwestdeutschland, basale Actinopterygier, Funktionsmorphologie, Ernährung, Lokomotion.

Introduction

Basal actinopterygians, often referred to as "paleoniscids", are abundant in both marine and lacustrine deposits worldwide (e.g., Aldinger 1937, Blot 1966, Boy 1976, Gardiner 1963, 1967, Lowney 1980a, Kazantseva-Selezneva 1981, Long 1988, Esin 1997, Daeschler 2000). Scales of these fishes appear as early as the Silurian (e.g., Gross 1968), and skeletal remains are known since the Devonian (e.g., Gardiner 1984). They are found well into the Triassic (e.g., Hutchinson 1975), even though they are less abundant than in Paleozoic times. Still, their biology is understood only poorly. Few studies have dealt with the function of their feeding apparatus (Schaeffer & Rosen 1961, Lauder 1980a, Gottfried 1992, Veran 1988, 1996), and even less is known about their potential of locomotion (Di Canzio 1985).

The present study attempts to clarify the likely diet and food uptake, and the likely locomotor capabilities of the Lower Permian *Paramblypterus duvernoyi*. *P. duvernoyi* is a member of the family Amblypteridae and, together with the other members of this family *P. gelberti*, *P. decorus*, and *Amblypterus latus*, has been described recently (Dietze 1998, 1999, 2000). Their morphology and intra-specific variation has been examined in detail and were the basis for three-dimensional models of the skull and the body. One

objective of the restoration in three dimensions was to gain a certain understanding of the biology of *Paramblypterus duvernoyi* and its relatives. Studies of *Paramblypterus* and *Amblypterus* are connected with research on paleoecosystems of lakes from the Lower Permian of Central Europe (e.g., Boy 1994, in press, Clausing & Boy 2000, Boy et al., Rotliegend-Paläoökologie, Unpublished report to the Deutsche Forschungsgemeinschaft [DFG]). Objectives are the reconstruction of environmental conditions, paleocommunities, and food chains. To gain insight in the interactions of species, it is important to investigate their likely diet and locomotor abilities (e.g., capacity to evade predators). Information obtained from morphology and models serves to evaluate the locomotory capabilities of *Paramblypterus duvernoyi* during feeding and locomotion.

In functional morphology, function can be inferred from certain morphological structures. However, there is not always a direct correlate (Lauder 1980a, 1995). If extinct animals are involved function cannot be directly observed or experimentally tested, and interpretations need to be established carefully (Webb 1982). Moreover, structural elements often perform a multiplicity of functions and therefore should not be evaluated separately (Liem & Wake 1985). One way to avoid misleading lines of evidence when dealing with fossils, is to find closely related, and ideally similar constructed Recent species of which empirical data is available to test the validity of interpretations of certain structures. An analysis of the functional anatomy of Recent lower actinopterygians can provide data for morphological interpretations of fossil lower actinopterygians. Such observations may corroborate inference of function from structures present in fossil fishes. However, only few basal actinopterygians, the morphological traits of which may be used to interpret those in *Paramblypterus* Sauvage, 1888, exist today. Of these, *Polypterus* (e.g., Bartsch 1997), *Acipenser* (e.g., Marinelli & Strenger 1973), and *Lepisosteus* (e.g., Gemballa 1995) have been dealt with mostly. Even though Recent species are somewhat different from *Paramblypterus*, the information obtained from their structures and soft tissues not preserved in *Paramblypterus* can be employed to explain certain traits of the feeding apparatus and potential of locomotion, especially since information on functions in basal fossil actinopterygian is scarce (Schaeffer & Rosen 1961, Lund 1967, Lauder 1980a, 1989, Di Canzio 1985, Veran 1996).

Material and methods

All specimens of *Paramblypterus duvernoyi* (Agassiz 1833) examined here are from lacustrine deposits from the Lower Permian of southwest Germany (e.g., Boy 1976, 1994, Dietze 1999, 2000). For a complete list of catalogue numbers see Dietze (2000).

Specimens of *Paramblypterus duvernoyi* are preserved as compressions flattened during fossilization. Surface structure, such as sculpturing of the skull roofing bones and scales, is present on many specimens. A Wild M8 microscope equipped with a camera lucida was used to draw the specimens. Drawings of the best preserved specimens were used for three-dimensional restoration. These drawings were transferred onto thin paper which was melted on thin plates of bees' wax. These paper and wax "bones" of the skull and palate were then cut out and assembled in a three-dimensional model. Reconstruction of the postcranial part was undertaken in similar fashion and, including the restored fins, fit onto the reconstructed skull and photographed. To obtain the likely life form of *P. duvernoyi*, line drawings of the photographs were made, enlarged, redrawn with wax pencils and ink and reduced to their original size.

Trunk length (TL) was measured from the posterior margin of the supracleithrum to the center of the caudal fin (as indicated by the shaded scale in Fig. 7A). Scale rows were counted along the lateral line between supracleithrum and the inclination of the scales anterior to the caudal fin. Where possible, fin rays were counted at the base of the fins. Drawings of the tails were digitized in AUTOCAD 14 and areas were calculated. Aspect ratio was calculated by dividing the span (see below Fig. 7A) squared by the area of the caudal fin. Hypo- and heterocercal angles of the tail were measured at the "chondrostean hinge" indicated by the shaded scale in Fig. 7. Three dimensional profiles of the body as illustrated in Fig. 7B were obtained from the wax model of *P. duvernoyi*.

Terminology

Terminology follows Arratia & Schultze (1991) and Arratia & Cloutier (1996). Other terminologies set off by quotation marks, except for the "nasal", refer to earlier works (e.g., Blot 1966, Heyler 1969) and employ the common terminology for paramblypterid fishes. Different terminologies are currently being used for dermal cranial bones (e.g., Arratia & Cloutier 1996, based on homologization; Poplin & Lund 1997, traditional nomenclature). For bone terminology adopted herein differing from common usage, e.g. "nasal 1–3", dermosphenotic 1–2, jugal 1–2, see Dietze (2000).

Institutional abbreviations

The material examined belongs to the institutions listed below: CAS, California Academy of Science; GPIM, Geologisch-Paläontologisches Institut Mainz; KMMA, Koninklijk Museum voor Midden-Afrika, Tervuren; MB, Museum für Naturkunde der Humboldt-Universität, Berlin; PMNB, Pfalzmuseum für Naturkunde, Bad Dürkheim. See Dietze (2000) for a complete list of specimens.

Constructional morphology

Feeding apparatus

Suction feeding is the basic method of acquiring food in living actinopterygians (Lauder 1980a) and is probably the ancestral method of food acquisition in all groups of aquatic gnathostomes.

The inertial suction strategy of prey capture requires the creation of a center of low pressure within the buccal cavity by rapid mouth opening and expansion of the buccal floor (Lauder 1985a). The pressure differential between the buccal and opercular cavities and the surrounding water results in a flow of water into the mouth. If the velocity of the flow is sufficiently great the prey will be sucked into the mouth. According to Lauder (1980a), two phases can be distinguished during suction feeding in lower actinopterygians: an expansive and a compressive phase. The expansive phase is defined as the time from start of mouth opening to maximum gape, the compressive phase from peak gape until complete closure of the jaws (Lauder 1980a). A preparatory phase precedes these in teleosts (Lauder 1985b), but is not performed in lower actinopterygians. For teleosts, movements of the suspensorium and jaws have been predicted by four-bar models concerning the anterior jaw linkage (Westneat 1990), the opercular linkage (Anker 1974), or the hyoid linkage (Muller 1987). In Polypterus, Lepisosteus, and Amia movements might be predicted by using the mandibulo-hyoid coupling (Lauder 1980a, 1982).

Palatoquadrate and associated elements

A complete palatoquadrate could not be observed in any specimen of Paramblypterus. Ossifications of the dermo-metapterygoid and quadrate are preserved in P. gelberti and P. duvernoyi (Fig. 1). These are the first to ossify in Polypterus, and it appears that the palatoquadrate of Paramblypterus also arose from three ossification centers (pars quadrata, pars metapterygoidea, and ?pars autopalatina) either without a bony autopalatine, as is the case in almost all lower actinopterygians (Arratia & Schultze 1991), or with an autopalatine that ossified only late in ontogeny. In contrast to Lepisosteus (Arratia & Schultze 1991), the dermo-metapterygoid does not have a dorsal process to articulate with the braincase, but is similar to the corresponding element in Polypterus (Figs 1A, H, 2C, E). The dermo-metapterygoid (Fig. 1A, D—H) sutures to the ectopterygoid laterally and slopes dorsomedially towards the posterior end of the parasphenoid. Anteriomedially, it sutures to the entopterygoid, and contacts the quadrate posteroventrally. Its ventral face is covered with small rounded granular teeth, except for a smooth margin posteriorly and dorsally. The mandibular articulation

condyle of the quadrate is oriented at almost right angles with the jaw margin (Fig. 1A, F, G) and corresponds to a similar shaped facet on the lower jaw. The anterodorsal portion of the quadrate contacts the posterior margin of the dermo-metapterygoid (Fig. 1G). The dermopalatines are in series with the ectopterygoid (Fig. 1A) as in Polypterus (Fig. 2C). The entopterygoid is similar in shape tot he ectopterygoid and lies anterior to the dermo-metapterygoid. The dorsal margin of both dermo-metapterygoid and entopterygoid abut on the lateral margin of the parasphenoid (Fig. 1A). Vomer(s) are present in Polypterus (Fig. 2C), but could not be observed in specimens of Paramblypterus examined here.

The presence of a dermo-metapterygoid as a separate element in Polypterus and other basal actinopterygians has been subject of ongoing debate (e.g., Lehn 1918, Allis 1922, Jarvik, 1980, Gardiner 1984, Arratia & Schultze 1991, Grande & Bemis 1998, Clemen et al. 1999, Wacker et al. in press). Arratia & Schultze (1991) and Grande & Bemis (1998) considered the corresponding element a metapterygoid associated or fused with tooth plate(s) during ontogeny, whereas the other authors described a plate-like dermo-metapterygoid, which is not fused to the palatoquadrate and consequently, a metapterygoid is missing. The latter appears to apply for Paramblypterus. Thus, what has been considered a metapterygoid earlier for Paramblypterus (Dietze 2000) is likely to represent a dermo-metapterygoid only.

Parasphenoid

The parasphenoid is the most prominent element of the ventral part of the braincase in Paramblypterus (Figs 1A, 3A—G). The corpus parasphenoidis lies along the midline of the skull and does not contact the premaxilla, but leaves a gap anteriorly which most likely was occupied by "vomeral platelets". Laterally, about midway along the length of the corpus parasphenoidis, abuts the entopterygoid. Posterior to the entopterygoid lies the dermo-metapterygoid which barely contacts the parasphenoid. The parasphenoid has well developed ascending processes which point laterodorsally. However, no features of the neurocranium could be observed and their articulation remains unknown. The corpus parasphenoidis is somewhat bilaterally asymmetrical and slightly variable in outline (Fig. 3C—G), which could be the result of preservation. In dorsal view (Fig. 3A), a depression probably sur-
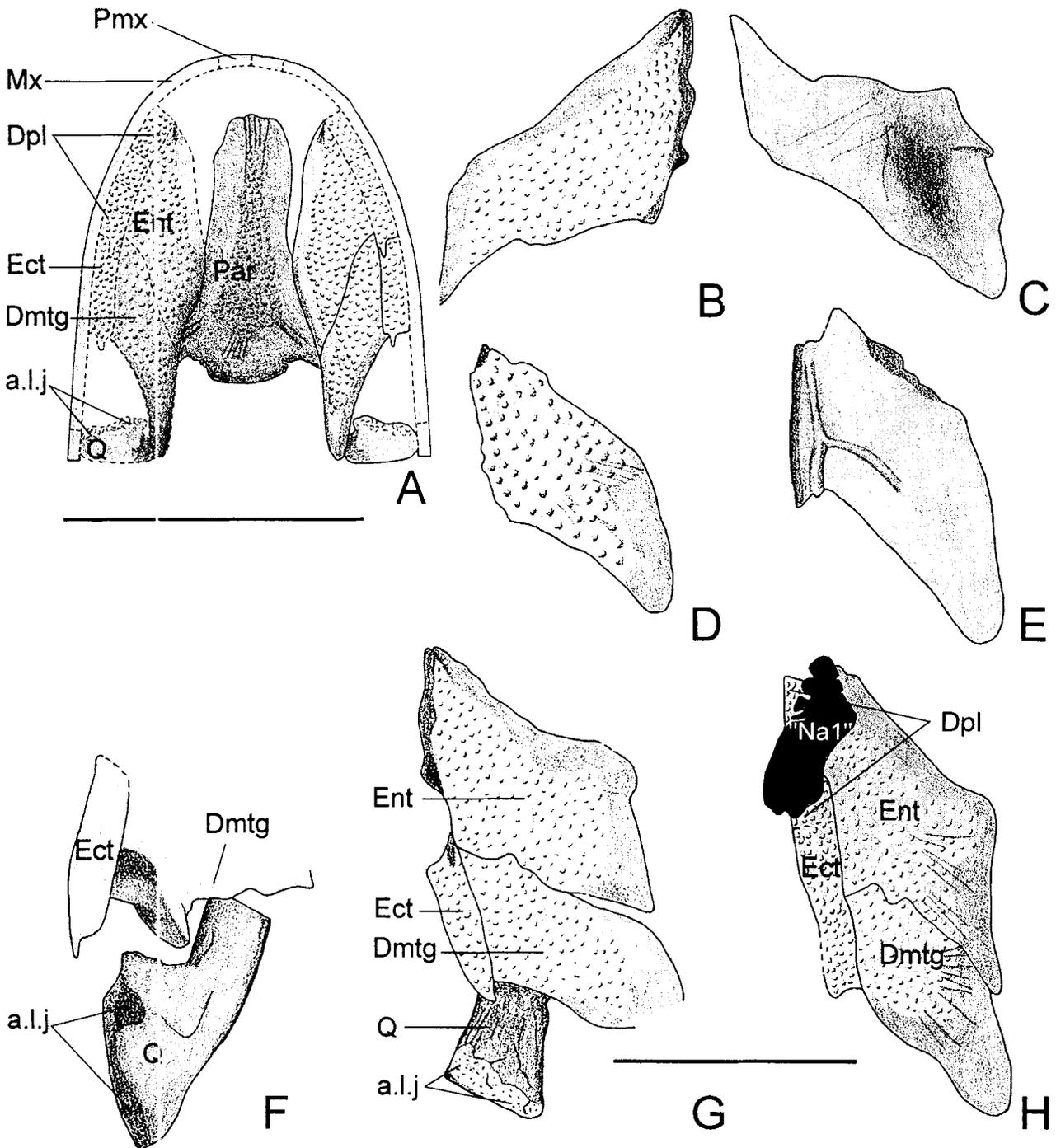
Fig. 1. **A**. Restoration of the palate of *Paramblypterus duvernoyi* and *P. gelberti*, ventral view (GPIM-M2248 & GPIM-M2315). **B**. Left entopterygoid in ventral view; GPIM-M4972. **C**. Left entopterygoid in dorsal view; GPIM-M4972. **D**. Right dermo-metapterygoid in ventral view; GPIM-M4907/3. **E**. Right dermo-metapterygoid in dorsal view; GPIM-M2267. **F**. Right dermo-metapterygoid, ectopterygoid, and quadrate in dorsal view; GPIM-M5811. **G**. Right entopterygoid, dermo-metapterygoid, ectopterygoid, and quadrate in ventral view; GPIM-M5263. **H**. Right entopterygoid, dermopalatines, dermo-metapterygoid, and ectopterygoid in ventral view; "nasal 1" (black shading) covering part of the dermopalatines; GPIM-M2291. **B−D**, **F**. *P. duvernoyi*. **E**, **G−H**. *P. gelberti*. Scale bar = 10 mm. **a.l.j**. condyle for articulation with lower jaw; **Dmtg**, dermo-metapterygoid; **Dpl**, dermopalatines; **Ect**, ectopterygoid; **Ent**, entopterygoid; **m.h.l**, mandibulo-hyoid ligament; **Mx**, maxilla; **"Na 1"**, "Nasal 1"; **Par**, parasphenoid; **Pmx**, premaxilla; **Q**, quadrate.

rounding the opening of the bucco-hypophysial canal and two grooves, which correspond to the course of the parabasal canal, can be observed. The ventral surface bears a tooth patch of granular teeth which covers the middle portion of the parasphenoid (Fig. 3B). The tooth patch covers about one third of the bone anteriorly, and widens posteriorly towards the ascending processes where it covers more than half of the surface of the parasphenoid.
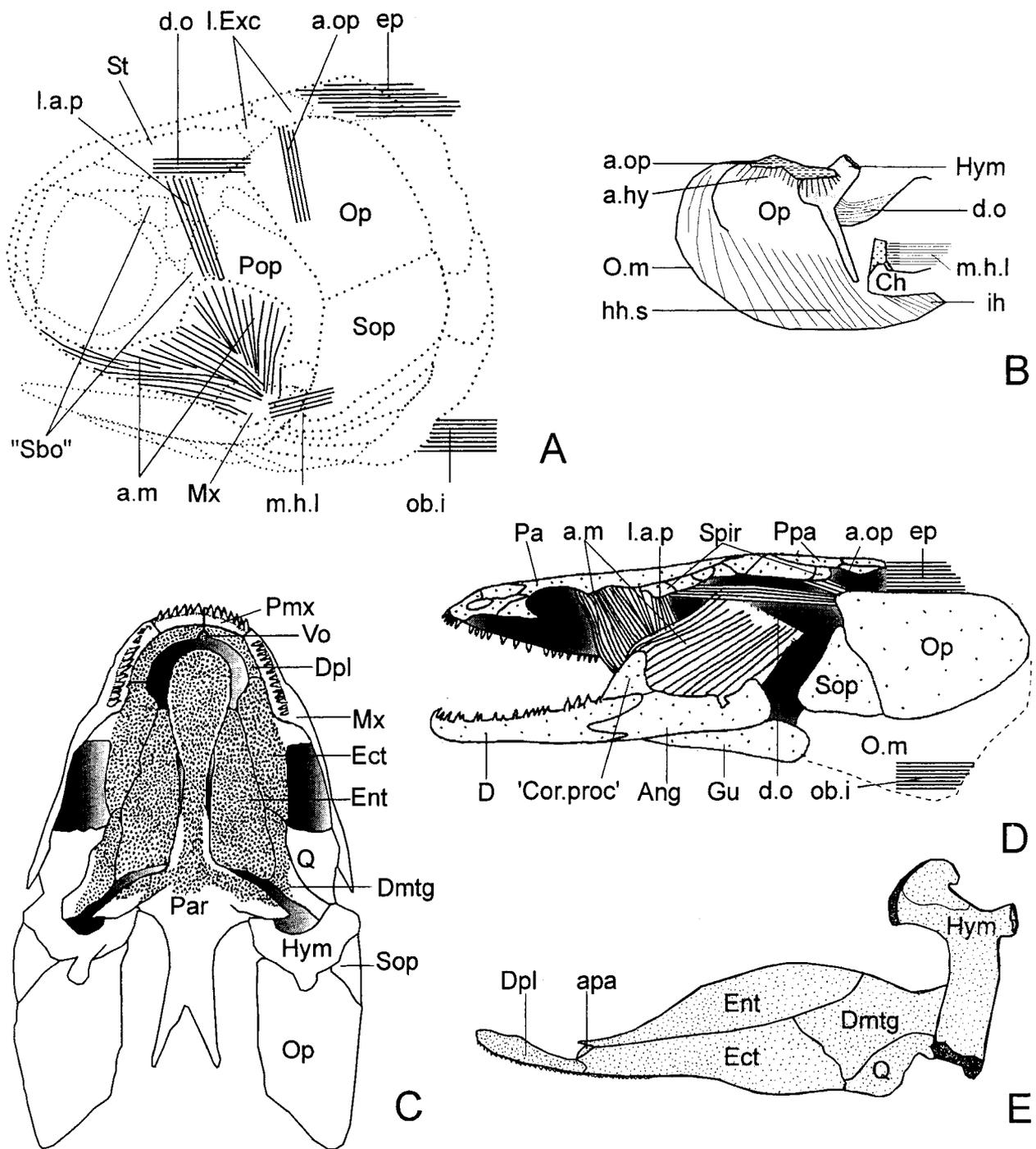
Fig. 2. **A.** *Paramblypterus duvernoyi*, tentative reconstruction of musculature. **B.** *Polypterus bichir*, muscles involved in the feeding mechanism, medial view (modified from Lauder 1980a, Starck 1979). **C.** *P. bichir*, palate in ventral view (modified from Starck 1979, Clemen *et al.* 1998; palatal granular teeth based on specimens KMMA- RG8823P166 and CAS 68161). **D.** *P. bichir*, muscles involved in the feeding mechanism, lateral view (modified from Lauder 1980a, Starck 1979). **E.** *Polypterus bichir*, palatoquadrate and associated elements in medial view, anterior facing left (modified from Allis 1922, Clemen *et al.* 1998). **a.hy**, musculus adductor hyomandibulae; **a.m**, musculus adductor mandibulae; **Ang**, angular; **a.op**, musculus adductor operculi; **apa**, autopalatine; **Ch**, ceratohyal; **Cor.proc**, 'coronoid' process; **D**, dentary; **Dmtg**, dermo-metapterygoid; **d.o**, musculus dilatator operculi; **Dpl**, dermopalatine; **Ect**, ectopterygoid; **Ent**, entopterygoid; **ep**, epaxial musculature; **Gu**, gular; **hh.s**, musculus hyohyoideus superioris; **Hym**, hyomandibula; **ih**, musculus interhyoideus; **l.a.p**, musculus levator arcus palatini; **l.Exc**, lateral extrascapular; **Mx**, maxilla; **ob.i**, musculus obliquus inferioris; **O.m**, operculo-gular membrane; **Op**, opercle; **Pa**, parietal bone; **Par**, parasphenoid; **Pmx**, premaxilla; **Pop**, preopercle; **Ppa**, postparietal; **"Sbo"**, "suborbital"; **Sop**, subopercle; **Spir**, spiracular plates; **St**, supratemporal; **Q**, quadrate; **Vo**, vomer.

Dentition

In most specimens, teeth were preserved poorly or not present at all indicating that they were fairly fragile structures. Dentary, maxilla, and premaxilla bear teeth (Figs 4A, B, 5A–C). The teeth are closely set slender, pointed structures bearing an acrodin cap (Ørvig 1978), which is
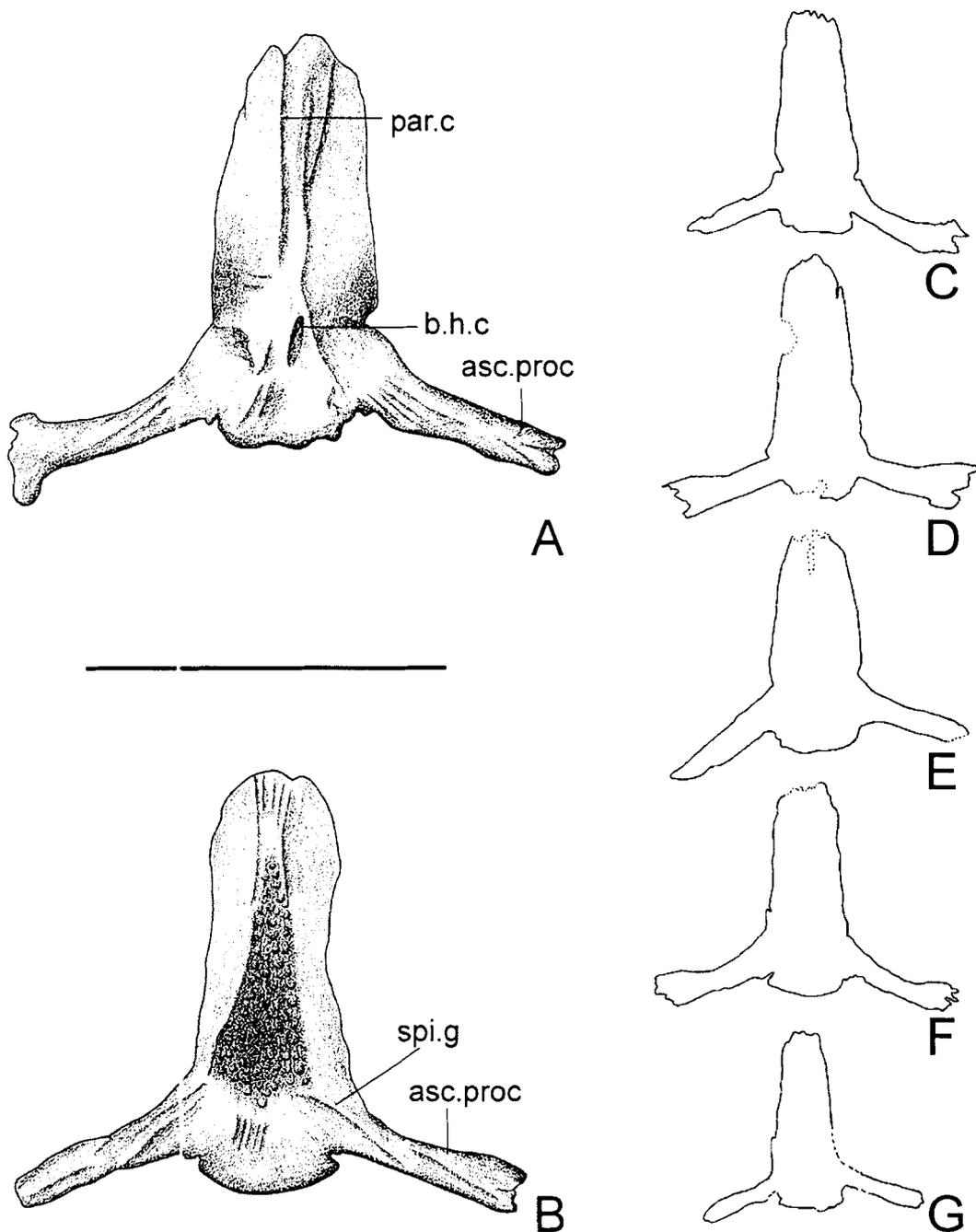
Fig. 3. Parasphenoid of *Paramblypterus*. **A**. Dorsal view of *P. gelberti*; GPIM-M2267. **B**. Ventral view of *P. gelberti*; GPIM-M2248. **C–G**. *P. d uvernoyi*. **C**. PMNB-WÖR66. **D**. GPIM-M4973. **E**. GPIM-M4972. **F**. GPIM-M5813. **G**. GPIM-M4907. Scale bar = 10 mm. **asc.proc**. ascending process; **b.h.c**. depression probably surrounding bucco-hypophysial canal; **par.c**. parabasal canal; **spi.g**. spiracular groove.

usually not preserved. Supposedly. the shafts of the teeth were composed of a thin layer of dentine surrounding a wide pulp cavity which caved in during fossilization. thus causing a secondary dorsoventral groove along the midline of the teeth (Fig. 5A) Only the anteriormost premaxillary teeth are inclined backwards (Fig. 5B). whereas the following teeth in dentary and maxilla are sitting straight. Coronoid and prearticular bear knobby teeth (Fig. 5C). Granular teeth are present on all palatal bones.

Contrary to Blot (1966), the teeth of *Paramblypterus decorus* are similar to those of *P. gelberti* and *P. duvernoyi*. Specimen MNHN-PA (Blot 1966: pl. IXB) shows what has often been referred to as tubular dentine (Blot & Heyler 1963. Blot 1966, Heyler 1969, Poplin & Heyler 1993). In my interpretation of this specimen, the so-called tubular dentine are impressions of dentary and maxillary teeth, and the rough surface is not part of the maxilla, but is caused by the teeth of both sides having been pressed against
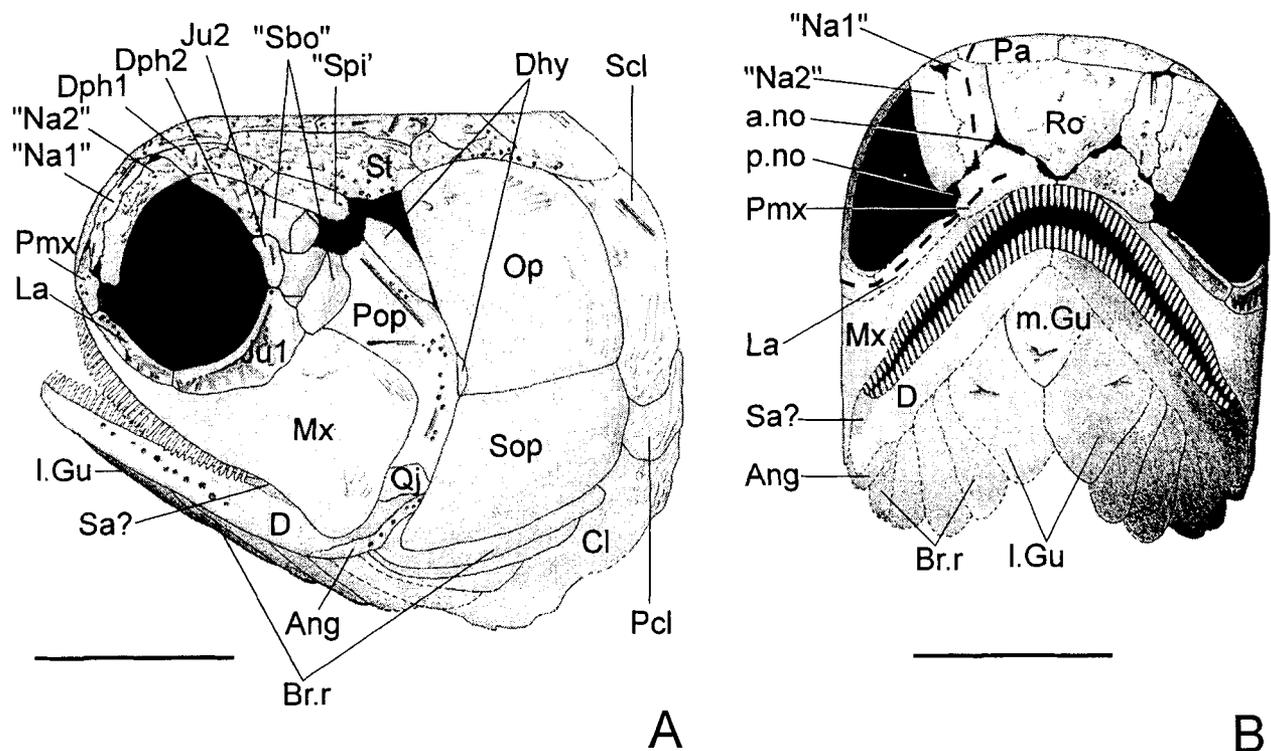
Fig. 4. *Paramblypterus duvernoyi*, restoration of the skull (GPIM-M5819 and GPIM-M4939). **A**. Lateral view. **B**. Anterior view. Scale bar = 10 mm. **Ang**, angular; **a.no**, anterior nostril; **Br.r**, branchiostegal rays; **Cl**, cleithrum; **D**, dentary; **Dhy**, dermohyal; **Dph 1–2**, dermosphenotic 1–2; **Hym**, hyomandibula; **Ju 1–2**, jugal 1–2; **La**, lacrimal; **l.Gu**, lateral gular; **m.Gu**, median gular; **Mx**, maxilla; **"Na 1–2"**, "Nasal 1–2", secondarily split up "nasal" (see Dietze 2000); **Op**, opercle; **Pa**, parietal bone; **Pcl**, postcleithrum; **Pmx**, premaxilla; **p.no**, posterior nostril; **Pop**, preopercle; **Q**, quadrate; **Qj**, quadratojugal; **Ro**, rostral bone; **Sa**, surangular; **"Sbo"**, "suborbital"; **Scl**, supracleithrum; **Sop**, subopercle; **sorb.s.c**, supraorbital sensory canal; **"Spi"**, "spiracular" bone; **St**, supratemporal.

each other. Casts of this region show rows of closely set teeth dislocated from the maxilla, but no loose bony material in which the teeth were embedded. The same feature can be observed in specimens of *Amblypterus latus* (e.g., MB. f.3809c) that are preserved in nodules.

Granular teeth are present on palatal bones in *Paramblypterus duvernoyi*. Small, pointed teeth are present on the palate of *Polypterus* and are used for holding and manipulating prey (Clemen et al. 1998). *Lepisosteus* and *Amia* also have tiny teeth on the oral surface of the palate. In contrast, the oral denticulate pavement is usually much reduced in favor of a complex of mobile tooth plates on branchial arches in more advanced actinopterygians (e.g., cyprinids, percomorphs).

Jaw articulation, suspensorium, and associated elements

The lower jaw consists of a fairly narrow dentary and an angular which sutures at its posterior margin (Figs 4A, B, 5C). Three small coronoid bones and a prearticular are present. A 'coronoid' process in the lower jaw has been de-

scribed for Carboniferous (Gottfried 1992), Triassic (Veran 1996), and extant lower actinopterygians, such as *Polypterus* (Fig. 2D) (e.g., Allis 1922), *Lepisosteus* (e.g., Nelson 1973), and *Amia* (e.g., Grande & Bemis 1998), but it is absent in *Paramblypterus*. The 'coronoid' process is composed of the surangular in the Carboniferous and Triassic taxa, of the prearticular in *Polypterus*, and of the dentary and surangular in *Lepisosteus* and *Amia* (Nelson 1973).

The maxilla of *Paramblypterus* is elongated and narrow anteriorly, and greatly expanded posteriorly, thus covering most of the cheek region (Fig. 4A, B). As can be seen in ventral view, the maxilla is attached to the premaxilla anteriorly, to the dermopalatines medially, and to the ectopterygoid medioposteriorly (Fig. 1A). No processes on the premaxillae could be observed by which they could have been fixed to the ethmoid region. The ventral portion of the preopercle sutures to the maxilla anteriorly and contacts the subopercle posteriorly (Fig. 4A). Its anterodorsal portion sutures with the "suborbital" series anteriorly, and dermohyal(s) and opercle posteriorly (Fig. 4A). Ventrally, the preopercle articulates with the quadratojugal (Fig. 4A). Thus, the cheek
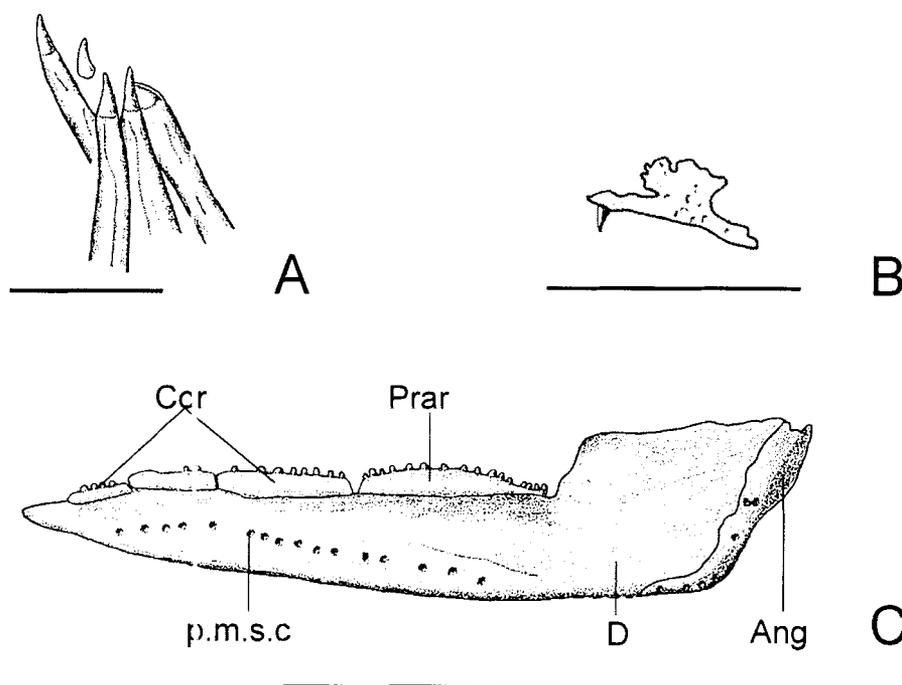
Fig. 5. **A**. Teeth of *Paramblypterus duvernoyi* (GPIM-M5819). **B**. Left premaxilla of *P. duvernoyi* in lateral view (GPIM-M5816). **C**. Left lower jaw of *P. gelberti* in lateral view (GPIM-M2291). **A**. Scale bar = 1 mm. **B**, **C**. Scale bar = 10 mm. **Ang**, angular; **Cor**, coronoid bone; **D**, dentary; **p.m.s.c**, preoperculomandibular sensory canal; **Prar**, prearticular.

bones of *Paramblypterus* form a fairly tight arrangement. The preopercle is oriented less oblique than in o her fossil lower actinopterygians such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993).

Since the orientation of the underlying suspensory apparatus is reflected by the position of the preopercle (Lauder 1982), the suspensorium of *Paramblypterus* would have been oriented more vertically as well. A complete hyomandibula could not be observed in any of the specimens examined. Par of it is preserved in specimen GPIM-5819 (Dietze 1999: fig. 2A) where its dorsal portion appears to be more upright than in *Pteronisculus* (Patterson 1982). The orientation of the hyomandibula of specimen GPIM-5819 accounts for a more posterior articulation with the neurocranium. thus suggesting an improved mobility of the suspensory apparatus as was proposed for other fishes by Schaeffer & Rosen (1961). Features of the articulation with the opercle could not be observed on either hyomandibula or medial face of the opercle. The operculogular series is composed of opercle. subopercle, about eight branchiostegal rays. paired lateral gulars and a single median gular (Fig. 4A. B). No endoskeletal elements of the ventral hyoid arch are preserved in the specimens examined.

Feeding — Reconstruction and comparison

Teeth (Fig. 5A) of *Paramblypterus* are weak and not inclined backwards for the most part. which

would be needed to prevent evasive prey from escaping. ruling out predation on large animals. Thus. I assume that its diet consisted of small planktonic or benthic organisms which were taken in by suction feeding or grazing. Movements of the feeding apparatus during suction feeding are mediated by musculoskeletal couplings (Lauder 1982). i.e. ligaments and muscles, and their associated bones. Unfortunately, none of these can be accounted for in *Paramblypterus*.

In lower actinopterygians, such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993), lateral expansion of the buccal cavity was limited by numerous immobile elements on the skull, the premaxilla and maxilla being firmly sutured to the other dermal skull bones, a not very mobile opercular series and branchiostegal rays, and the oblique angle of the suspensory apparatus resulting in a distinctly postorbital jaw articulation (Lauder 1982). In advanced actinopterygians. force and velocity of mouth opening and closing can be predicted using the distances of joints to insertion sites of muscles and ligaments in relation to the distance of the joints to the tip of the snout (Westneat 1994). In basal actinopterygians. such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993), the insertion site of the adductor musculature is very close to the joints. Thus. force of the bite was directly related to mass and disposition of the adductor mandibulae muscle (Schaeffer & Rosen 1961, Lauder 1982). The adductor mandibulae muscle of lower actinopterygians consists of a posterolateral, a medial. and a suborbital component (Lauder

1980b), the latter being absent in *Polypterus* (Fig. 2D). In contrast to species where the maxilla is freed from the palatoquadrate, e.g., *Amia calva* (Fig. 6B) and teleosts, the closed skull of basal actinopterygians, such as *Pteronisculus* (Schaeffer & Rosen 1961) or *Moythomasia* (Gardiner 1984), caused spatial constraints and did not allow for improvement of performance by expansion of muscles. The adductor mandibulae muscle was confined to the space between palatoquadrate medially and maxilla laterally (Lauder 1982) as can be seen in the skull of *Pteronisculus stensioei* (Fig. 6A) (Schaeffer & Rosen 1961). In *Paramblypterus*, teeth were present along the complete margin of the maxilla indicating that all of the bone was exposed during mouth opening. Therefore, a complex labial fold system, as in *Polypterus* (Bartsch 1997), for creating a more effective suction funnel was probably not present in *Paramblypterus*. Teeth on the palate could have been used for manipulating prey or grinding as in *Polypterus*.

In comparison to the basic pattern of lower actinopterygians, such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993), with a closed skull and oblique suspensorium, certain features (Fig. 2A) of *Paramblypterus* indicate a somewhat derived situation. According to the orientation of the hyomandibula (Dietze 1999: fig. 2A) and preopercle (Fig. 4A), the suspensory apparatus was less oblique than in other basal actinopterygians suggesting a greater lateral mobility. A short maxilla reduces load of the upper jaws. Furthermore, muscle insertion close to the joint accounts for a more rapid closing of the jaws (Westneat 1994) in *Paramblypterus*. Fragmenta-

tion of the suborbital region accounts for an expansion of the underlying levator arcus palatini muscle (Gardiner 1967) which mediates lateral movement of the suspensory apparatus. Fragmentation of the dermohyal region indicates an expansion of the dilatator operculi and / or adductor mandibulae. In *Paramblypterus*, the dorsal cheek region is not covered with dermal bones which might have contributed to additional mobility of the cheek and suspensory apparatus. Since the size of the muscles depend on the palatoquadrate-maxillary chamber which in turn is reflected by the size of the maxillary plate (Schaeffer & Rosen 1961), the size of the maxillary plate suggests an expansion of the adductor mandibulae muscles in *Paramblypterus*. In contrast to other lower actinopterygians, such as *Mimia* or *Moythomasia* (Gardiner 1984), the bones of the snout region of *Paramblypterus* are arranged loosely (Fig. 4B) which allows a certain mobility of that region and could be related to increased lateral versatility of the posterior cheek region. The mouth opening of *Paramblypterus* is more terminal, thus shortening the gape which would improve suction during mouth opening (Liem 1993).

Two key features, i.e. neurocranial elevation and mandibular depression, were suggested to represent the basal method of mouth opening in actinopterygians (Lauder 1980a). Assuming that this general mechanisms occurred during feeding of *Paramblypterus*, a basal actinopterygian with a closed skull, mandibular depression would have been effected by retraction of the hyoid apparatus mediated by contraction of the obliquus inferioris and sternohyoideus muscle *via* a mandi-
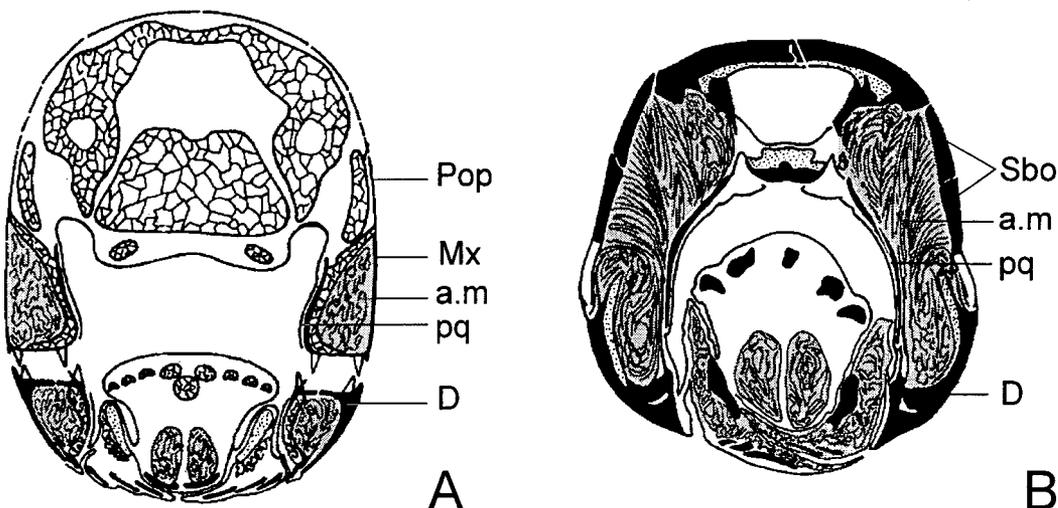

Fig. 6. Cross section through head. **A.** *Pteronisculus stensioei.* **B.** *Amia calva.* Adductor musculature shaded (modified after Schaeffer & Rosen 1961). **a.m**, musculus adductor mandibulae; **D**, dentary; **Pop**, preopercle; **pq**, palatoquadrate; **Sbo**, suborbitals.

bulohyoid ligament at the onset of the expansive phase (Lauder 1980a, 1982). Contraction of the anterior epaxial musculature would have elevated the anterior vertebrae and the head (Tchernavin 1947). Movement of the opercle and subopercle would have been accomplished by the dilatator and adductor operculi muscle, allowing limited control over opercular movements during feeding (Lauder 1980a). Activity of the levator arcus palatini muscle would have mediated lateral movement of the suspensory apparatus (Lauder 1980a). According to the somewhat derived condition in *Paramblypterus* due to a possible expanded mandibular musculature and less oblique orientation, mobility of the suspensory apparatus should have been improved. Adduction of the opercle would have occurred at the start of the buccal expansion and the final phase following closure of the jaws at the end of the compressive phase (Lauder 1980a). Opercular abduction which is mediated by the dilatator operculi muscle would have occurred at the onset of the compressive phase. Control over opercular movement, which is controlled by the adductor and dilatator operculi muscles, might have been improved given a possible expansion of these muscles. Occlusion of the jaws should have been more effective if the adductor mandibulae was enlarged. Suction could have been improved based on a more rapid jaw closing and the mouth opening being oriented more arteriorly, thus shortening the gape. The mouth of lower actinopterygians, such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993), opens in a grin, which allows water to enter at the sides of the mouth, thus reducing sucking speed (Alexander 1970). However, a more vertical articulation of the hyomandibula with the neurocranium allows for anterior movements of the suspensorium (Schaeffer & Rosen 1961). In *Paramblypterus*, this mechanism might have served to fill in the corners of the open mouth, which in turn improves suction.

Essentially, this is the mechanism described for *Polypterus* (Fig. 2B, D) and *Lepisosteus* (Lauder 1980a), where only a single musculoskeletal coupling exists for mandibular depression, i.e. by the sternohyoideus muscle *via* the mandibulohyoid ligament. In contrast to *Amia*, an interopercular bone, which is the key element for transmitting the pull of the levator operculi muscle to the mandible, is absent in basal actinopterygians, such as *Polypterus*, *Lepisosteus* (Lauder 1980a, 1982), or *Paramblypterus*. The maxilla of *Paramblypterus* was not freed from the palatoqua-

drate and cheek as in *Amia* (Grande & Bemis 1998) and therefore could not be moved independently. The adductor mandibulae muscle was still confined to the palatoquadrate-maxillary chamber as in *Pteronisculus* (Fig. 6A). Advanced teleosts and *Amia* can generate negative pressures of 400 to 600 cm H_2O (Liem 1978) and 120 cm H_2O (Osse 1976) within their buccal cavities, respectively. In contrast, negative pressures of fossil lower actinopterygians were probably small, about 50 cm H_2O (Lauder 1980a), and water flow through the mouth cavity during feeding may have been primarily controlled by body velocity in *Paramblypterus*.

Locomotion

Water is a dense, viscous medium that places severe constraints on the function and design of effective propulsive mechanisms (Lindsey 1978, Reif 1982, Webb 1982, Lauder 1989, Videler 1993). For the propulsion in water, weight support is not a dominant factor (Webb 1994). Locomotion is affected by buoyancy, drag or friction, stabilizing factors, and the power needed to generate the desired movement most efficiently in dealing with these (Webb & Blake 1985). Features such as shape and size of body and fins, positioning and flexibility of the fins, squamation, and the degree of ossification of the vertebral column all interact to influence performance (Böss 1982, Webb 1982, Webb & Blake 1985, Di Canzio 1985, Weihs 1989).

Axial mechanisms, i.e. body and / or caudal fin, are associated with large muscle mass, thus being able to convert more than 90% of muscle energy into thrust energy (Webb & Blake 1985). In contrast, the other median and paired fins are associated with little muscle mass and can be used for slow swimming (Webb & Blake 1985). Performance of a heterocercal caudal fin depends on its aspect ratio, i.e. length of the span divided by the length of the chord (Di Canzio 1985) or span of the fin squared divided by its area (Lighthill 1969, Videler 1993), and the size of the ventral lobe of the caudal fin (Thomson & Simanek 1977). Median fins serve primarily to reduce rolling action of the body during turns (Di Canzio 1985), whereas paired fins, mostly the pectoral fin, function in attitude control, turning control, and braking (Keast & Webb 1966, Di Canzio 1985).

Body scaling, which has often been regarded as protection from predators, serves as a coun-
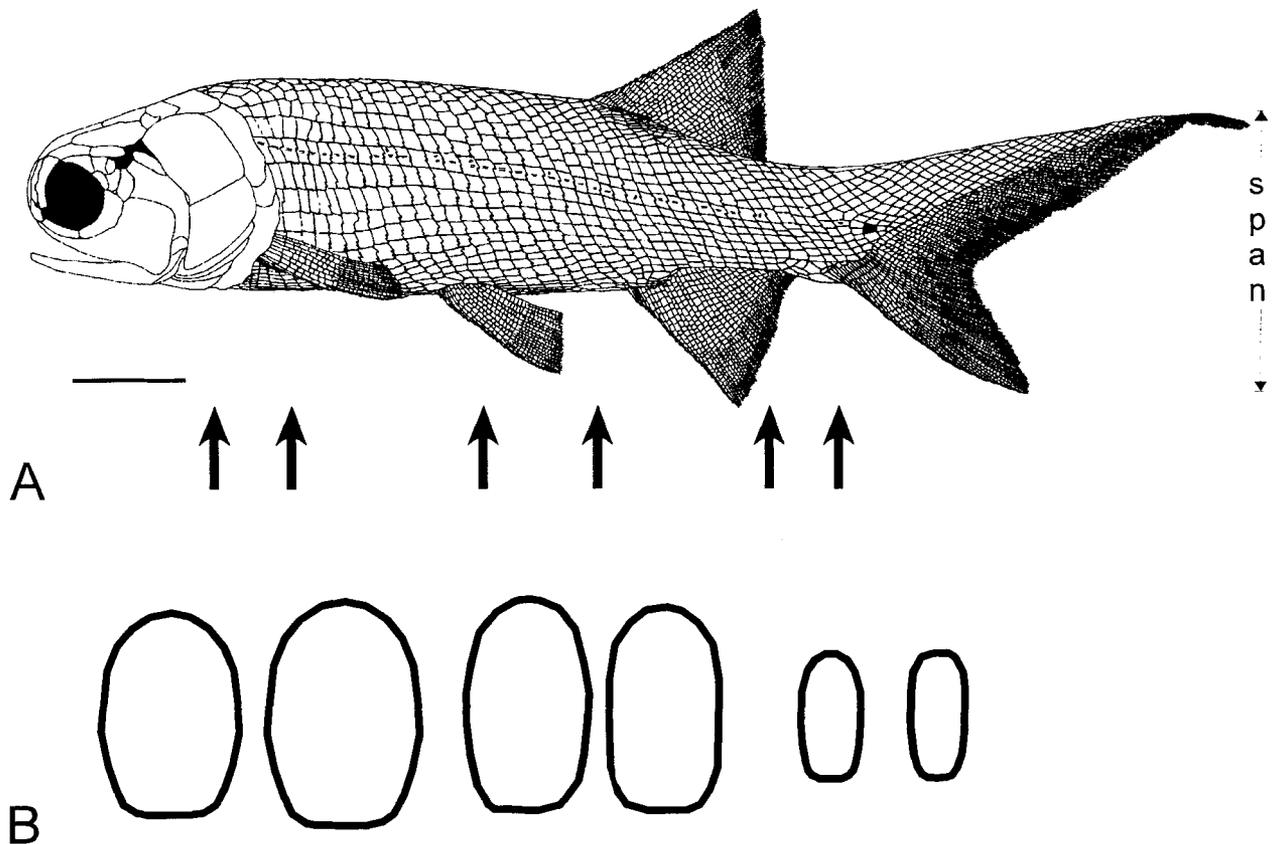
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Fig. 7. **A.** Restoration of *Paramblypterus duvernoyi* (GPIM-M5819 and GPIM-M5816). Teeth omitted, arrows indicate position of transverse sections below. Scale bar = 10 mm. **B.** Transverse sections of the three-dimensional model of *P. duvernoyi.*

teracting element during swimming (Starck 1979). Scales arranged at an angle of about 45 to the longitudinal axis of the fish allows shearing between rows and prevents torsion of the body during locomotion (Pearson 1982). The size of the scales (Aleev 1969) and their thickness affect lateral movement (Böss 1982). Peg and socket articulation affects flexibility of the skin (Pearson 1982), thus reducing the effectivity of propulsion (Webb & Blake 1985), but also serves to maintain architectural integrity of the scale rows by preventing adjacent scales to slip during compression (Pearson 1981). Moreover, they increase the dead weight and density of the fish which in turn increase inertia (Webb 1982, 1996) if features to increase buoyancy, such as fat or lungs, are absent. The vertebral column is important in stabilizing muscle operation and resisting deformation and deflections caused by locomotion, which is related to the degree of ossification of the vertebrae (Böss 1982).

Body form, squamation, and ossification of the vertebrae

Trunk length of specimens of *Paramblypterus duvernoyi* examined here ranges from 19–220 mm.

Its body is laterally compressed and according to profiles of the three-dimensional model, lateral compression of the body increases posteriorly (Fig. 7B). Vertical and horizontal fineness ratios (Blake 1983) are about 55 and 81, respectively. The reconstruction of the whole fish shows a fairly slender body with only a little hump posterior to the head. L_H, i.e. the distance of the nose to maximum depth of the body (Webb 1988), divided by the length of the three dimensional model is 0.23.

Paramblypterus bears a cover of ganoid scales (Fig. 7A) with peg and socket articulation (Fig. 8B). The peg represents about 10% of the overall height of the lateral scales. Along the
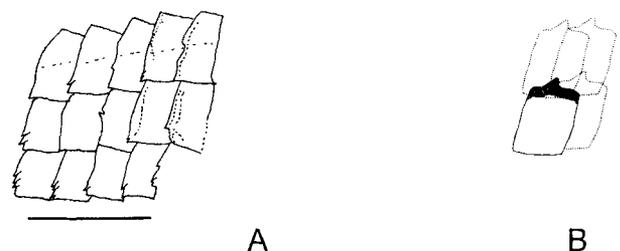

A   B

Fig. 8. *Paramblypterus duvernoyi,* detail of squamation. Anterior facing right. **A.** Ornamentation. **B.** Peg and socket articulation, shaded area indicates articulation surface. Scale bar = 5 mm.

lateral line, 42 ± 2 scale rows between supracleithrum and the inclination of the scales anterior to the caudal fin are present. Below the lateral line, the dorsoventral height of the scales on the body decreases progressively in *P. duvernoyi*. According to Breder (1926), this feature indicates a flat bely. Unlike other lower actinopterygians, such as *Mimia* (Gardiner 1984) or *Elonichthys* (Schindler 1993), scales of *P. duvernoyi* bear only very scarce ornamention (Fig. 8A). Moreover, not all the scales on the body are serrated, and the area on the body bearing ornamented scales appears to decrease during ontogeny (Dietze 1998). As mentioned earlier, specimens of *P. duvernoyi* were flattened during fossilization. Features of the axial skeleton could not be observed in any of the disarticulated specimens of either *P. duvernoyi* or *P. gelberti*. Thus, it is likely for these elements not to have been ossified or only weakly.

In general, data on the axial skeleton of lower actinopterygians, such as *Elonichthys* (Schindler 1993), is hard to come by, because their body is covered with ganoin scales. In species where these elements can be observed, they consist of dorsal and ventral arches, vary in the fusion of elements and the degree of ossification, and for the most part do not form true centra (e.g., Aldinger 1937, Lowney 1980a, Kazantseva-Selezneva 1981, Gardiner 1984).

As yet, ossified centra in lower actinopterygians have been described for the Late Carboniferous species *Microhaplolepis* (syn. *Haplolepis*) *ovoidea* (Baum & Lund 1974, Lowney 1980b), the Middle Permian to Triassic species *Pygopterus nielseni* (Aldinger 1937), the Early to Middle Triassic species *Australosomus kochi* (Stensiö 1932, Nielsen 1949), the Middle to Late Triassic species *Peltopleurus splendens* (Laerm 1979a), and the Late Triassic genus *Turseodus* (Schaeffer 1967a).

In these species, centra are either confined to the region posterior to the head (*Microhaplolepis*) or to the caudal region (*Pygopterus* and *Peltopleurus*), whereas *Turseodus* and *Australosomus* have centra throughout the body (Laerm 1979a). Centra of lower actinopterygians, which have not been assigned to a certain species, have also been found in Late Paleozoic deposits of North America (Schultze & Chorn 1986). Even though features of the vertebral column of *Paramblypterus* are not known, it is likely to have had a persistent notochord as in other lower actinopterygians, such as *Palaeoniscum* or *Birgeria*, probably similar to that of *Acipenser* (Remane 1936, Schaeffer 1967b) (Fig. 9A).

Contrary to Pearson (1982), a relationship of scale rows to the number of vertebrae, and thus myomeres, appears to be 1:1 in almost all fossil as well as living lower actinopterygians (e.g., Jessen 1968, Bartsch 1988, Gemballa 1995, Grande & Bemis 1998). This pattern has also been described in *Semionotus* (Olsen & McCune 1991). Outgroup comparison with the osteolepiform *Eusthenopteron* (Jarvik 1996) further corroborates an earlier appearance of this relationship than suggested by Pearson (1982). *Cheirolepis*, which has different scales than the remainder of the basal actinopterygians, has a higher number of scales per vertebra (Pearson 1982, Arratia & Cloutier 1996). According to Gardiner (1984: 366, 386). *Mimia toombsi* has about 25 vertebrae and 75 scale rows. However, according to Gardiner's figure 123, the overall number of vertebrae appears to have been higher than that. If the general pattern of 1:1 was present in *Paramblypterus* its vertebral column would have been composed of about 42 posteriorly in length decreasing vertebrae, indicating the number of myomeres present.

Fins

Paramblypterus has a heterocercal tail with a terminal flap on its dorsal lobe (Figs 7A, 10A). For the three dimensional model, the hetero- and hypocercal angles of the lobes are 28 and 34, respectively. The aspect ratio, i.e. span squared divided by the area of the fin (Lighthill 1969, Videler 1993), is about 2.4 (Fig. 10A), which is similar to that of other basal actinopterygians (Fig. 10B–H). The dorsal margin of the caudal fin is covered by four or five basal scutes followed by a series of elongated scutes which become progressively smaller caudally. The dorsal and anal fin are broad based, of triangular shape, and positioned in the posterior part of the body (Fig. 7A). The pectoral and pelvic fins are small, rectangular in outline, and broad based. The pectoral fin is inserted rather dorsally. The pelvic fin is inserted more ventrally, located about midway along the body. Nothing is known of the endoskeletal elements in *Paramblypterus*. However, Watson (1925) described the hinder part of the pectoral girdle of *Amblypterus*, the sister taxon of *Paramblypterus*, as being very similar to, but less massive than that of *Acipenser*. Apart from the lepidotrichia, the only detail of the pectoral fin is a drop shaped marginal fin ray (Fig. 9E, F). According to Jessen (1972), this element is composed of fused lepidotrichia. In *Para-*
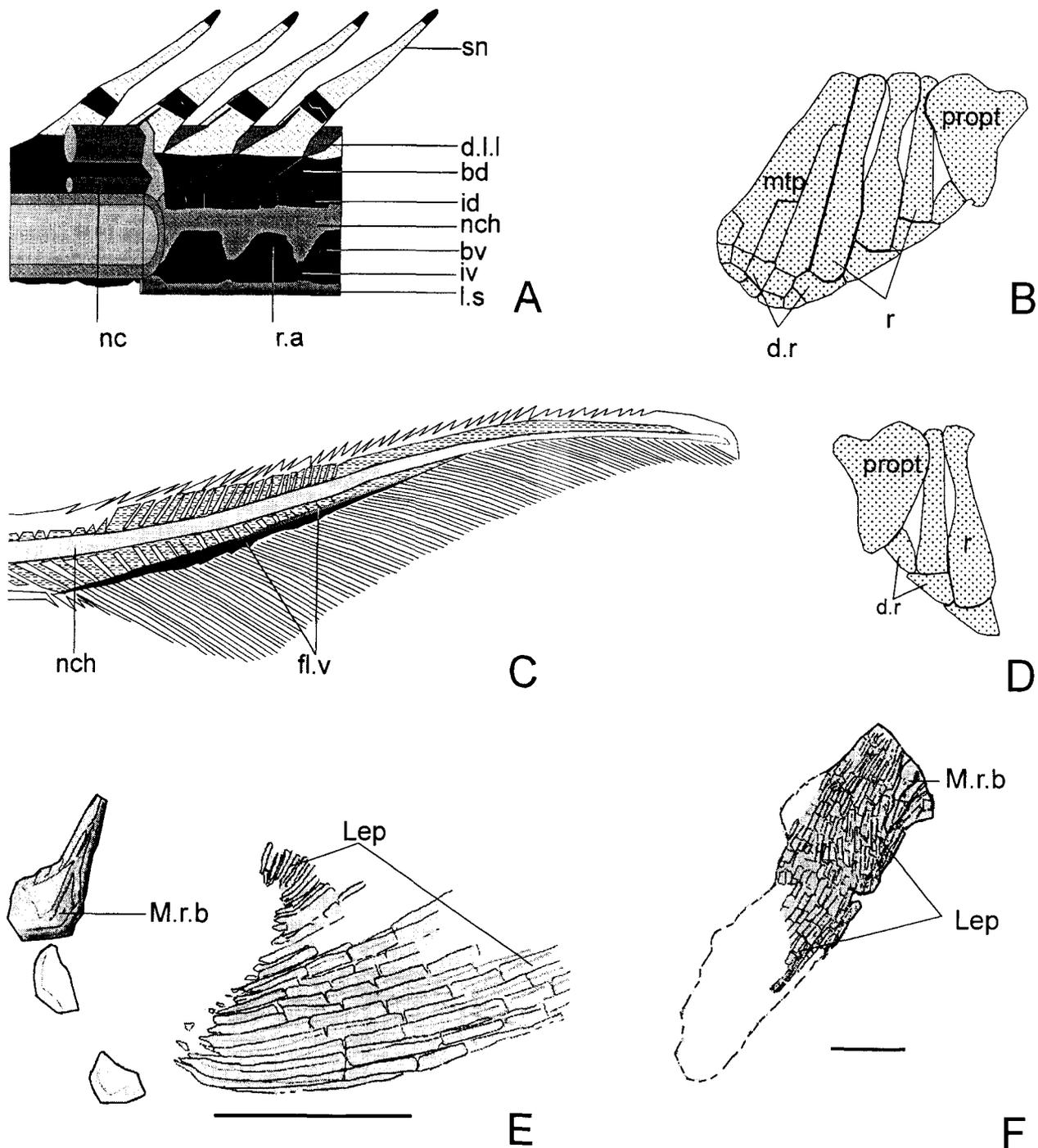
Fig. 9. **A.** *Acipenser sturio*, vertebral column, anterior facing left, cartilage black, bone hatched (modified after Goodrich 1930, Marinelli & Strenger 1973). **B.** *A. sturio*, endoskeleton of the pectoral fin, dorsal view (after Jessen 1972). **C.** *A. sturio*, detail of the caudal fin (modified after Bartsch 1988, Lauder 1989). **D.** *A. sturio*, endoskeleton of the pectoral fin, medial view (after Jessen 1972). **E, F.** *Paramblypterus duvernoyi*, detail of the pectoral fin (PMNB-WÖR27 and GPIM-M2894). Scale bar = 5 mm. **bd**, basidorsal; **bv**, basiventral; **d.l.l**, dorsal longitudinal ligament; **d.r**, distal radial; **id**, interdorsal; **fl.v**, musculus flexor ventralis; **iv**, interventral; **Lep**, lepidotrichia; **l.s**, subvertebral ligament; **M.r.b**, base of marginal fin ray; **mtp**, metapterygium; **nc**, neural chord; **nch**, notochord; **propt**, propterygium; **r.a**, rib attachment; **sn**, supraneural; **r**, radial.

mblypterus, all of the fins are composed of closely packed fin rays and bear fringing fulcra on their leading edges.

Contrary to Lauder (1989), the heterocercal tail of *Acipenser* (Fig. 9C) does not lack intrinsic caudal muscles, but has a two-partite flexor ventralis muscle (Bartsch 1988). *Polypterus* has a simple flexor ventralis muscle (Bartsch 1988). In addition to a complex flexor ventralis muscle, a hypochordal longitudinalis muscle with lateralis superficialis muscles inserting on the head of the fins has been described in *Lepisosteus* (Schmalhausen 1912, Bartsch 1988), however see Gemballa (1995). The caudal musculature of *Amia* is
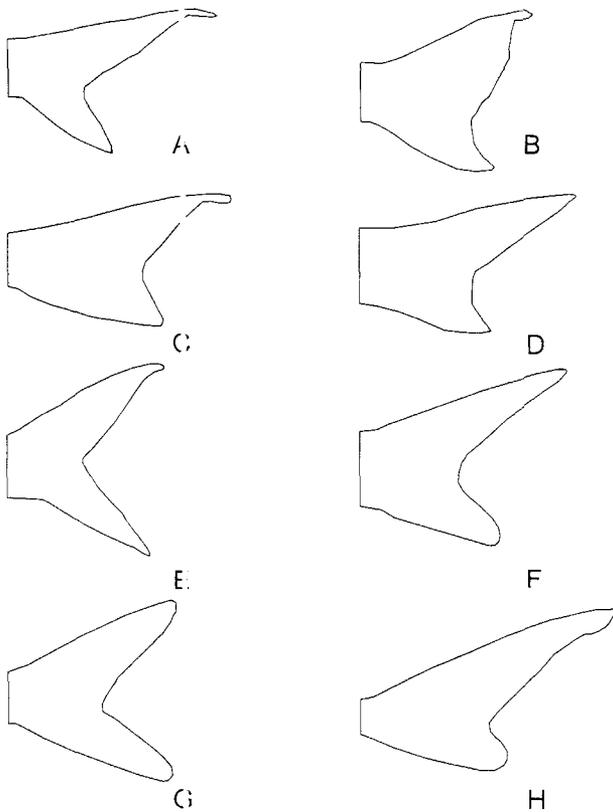
Fig. 10. Caudal fin shape and aspect ratios (AR) of several basal actinopterygians. **A.** *Paramblypterus duvernoyi*. AR ca. 2.4. **B.** *Cheirolepis canadensis* (after Arratia & Cloutier 1996). AR ca. 2.1 **C.** *Cheirolepis trailli* (after Bartsch 1988). AR ca. 1.4. **D.** *Moythomasia nitida* (after Jessen 1968). AR ca. 1.6. **E.** *Howqualepis rostridens* (after Long 1988). AR ca. 3.6. **F.** *Limnomis delaneyi* (after Daeschler 2000). AR ca. 2.3. **G.** *Birgeria greonlandica* (after Bartsch 1988). AR ca. 2.5. **H.** *Acipenser ruthenus* (after Bartsch 1988). AR ca. 1.8.

differentiated further in having a large flexor ventralis muscle and antagonistic interradialis and supracarir alis muscles to collapse or expand the fin (Bartsch 1988, Lauder 1989).

In *Acipense*·, enlarged marginal rays embrace the paired lepidotrichia of the pectoral fin (Jessen 1972). Towards the base of the fin, the lepidotrichia diverge and form a gap where the propterygium, the radials, and metapterygium lie (Fig. 9B, D). One portion of the pectoralis muscle inserts on the ventral lepidotrichia, and the other portion on the dorsal lepidotrichia (Jessen 1972). Thus, adduction and abduction of the fin is mediated by contraction of the muscles attached to the dorsal and ventral portion, respectively (Jessen 1972). The anterior portion of the pectoralis muscle inserts ventrally and dorsally on the marginal ray, which is formed by fusion of several anteriormost lepidotrichia (Jessen 1972). These muscles are antagonistic to each other and mediate ventral and dorsal movement of the marginal ray (Jessen 1972).

Pectoral fins of *Lepisosteus* and *Amia* are similar to those of *Acipenser*, but the lepidotrichia are thickened proximally (Jessen 1972). These thickened ends represent insertion sites for the pectoralis musculature allowing for a greater variation of pectoral movement (Jessen 1972).

In the Late Triassic species *Birgeria groenlandica*, the parhypural bears a process, which resembles the hypurapophysis of certain teleost fishes, where the process is the insertion site of the hypochordal longitudinalis and the flexor ventralis muscles (Nielsen 1949, Bartsch 1988, Lauder 1989). Features of the endoskeleton suggesting differentiation of musculature of the paired and median fins have not been described for Devonian to Lower Triassic lower actinopterygians. It appears likely that differentiated features were absent in the skeleton of the fins of *Paramblypterus* and that the paired fins, as in *Acipenser*, lacked the thickened ends on the lepidotrichia, which are the insertion sites for the pectoralis musculature. Thus, the construction of the fins probably allowed only restricted movement of the lepidotrichia without being able to expand and collapse fin area, and closely packed fin rays reduced the active mobility of the individual rays in all fins.

Locomotor capability

The body of *Paramblypterus duvernoyi* is compressed laterally (Fig. 7A, B) which reduces yaw. Its vertical fineness ratio is similar to that of cruising fishes, but higher than that of species designed for acceleration (Blake 1983, Webb 1988). A hump about 60% posterior to the snout and rapid reduction of cross section afterward minimizes drag (Weihs & Webb 1983), which is not the case in *P. duvernoyi*. Presumably, about 42 vertebrae were present along its body axis, which is not suitable for an anguilliform mode of propulsion.

Scale rows of *Paramblypterus duvernoyi* are arranged at an angle of about 45 degrees to the horizontal axis which allows shearing between rows and reduces torsion of the body during locomotion (Pearson 1982). Frequently, the squamation pattern in ganoid fishes has been considered to restrict the performance of lateral movement (e.g., Böss 1982, Lund 1967). However, this is not true for either *Polypterus* or *Lepisosteus* (Gemballa 1995). Whereas scales are more or less immovable against one another dorsoventrally (Sewertzoff 1926), shearing ranges from 42% to 96% and 73% to 88% between

scale rows on the concave side in *Polypterus* and *Lepisosteus*, respectively (Bartsch & Gemballa 1992, Gemballa 1995). Moreover, scales of *Polypterus* have been supposed to be involved in energy storage for respiration (Brainerd 1994) and represent a well-designed means for propulsion (Sewertzoff 1926, Pearson 1981).

For transient swimming at low to moderate speeds, drag becomes the dominant resistance component with body area as restraining feature (Webb & Blake 1985). Ganoine scales, which cover all of the body in *Paramblypterus*, increase dead weight which in turn increases inertia, i.e. if mechanisms to increase buoyancy are absent. Fulcra on the leading edges of the fins reduce resistance. An incompletely ossified vertebral column has been supposed to result in slow speeds caused by low amplitude of axial movement (Böss 1982). However, this does not seem true for Recent Dipnoi, *Latimeria*, or *Acipenser*, all of which have a persisting notochord (Laerm 1979a, b).

The paired fins of *Paramblypterus* are broad based, fairly large, and muscle insertion on the lepidotrichia probably allowed for upward and downward movements only. According to Keast & Webb (1966), this limits the performance of turning, attitude control, and braking. Moreover, fins that cannot be collapsed increase drag (Alexander 1970). The median fins appear to be posterior to and not over the center of mass in *Paramblypterus*, the latter of which would be needed for precise maneuvers (Webb & Blake 1985). However, the median fins are positioned close to the caudal fin which adds to the area of the caudal fin, thus improving acceleration for spurts. Caudal fin ray stiffness and position were probably not greatly alterable during locomotion except as direct consequence of myotomal contraction (Lauder 1989), but stiff caudal fins have been shown to increase thrust (Katz & Weihs 1978).

The position of the anal and dorsal fins in the posterior part of the body, and the large hypaxial lobe on the caudal fin result in high frictional resistance in the posterior part of the body in *Paramblypterus*. This is disadvantageous for covering longer distances effectively, but improves the performance of turns and sudden spurts (Webb & Blake 1985). A terminal flap has been considered to improve the performance of the caudal fin by preventing it from stalling (Di Canzio 1985). A reduced heterocercal angle results in slower speeds, but is related to a powerful turning moment (Lighthill 1970, Thom-

son & Simanek 1977). Caudal fins suitable for cruising and sprinting, so-called lunate tails, have aspects ratios of about 13 (Videler 1993). An aspect ratio of 2.4 in *P. duvernoyi* compares to those fishes that are specialized for acceleration (Webb 1988). Posterior lateral compression improves hydromechanical efficiency and creates a large momentum as well (Lighthill 1970). Necking anterior to the caudal fin reduces recoil (Lighthill 1969). Contrary to Pearson (1982), the caudal scale inversion does not weaken the caudal peduncle, but more likely served to prevent torsion (Bartsch 1988).

Locomotor capability of *Paramblypterus duvernoyi* during swimming could have been one of moderate speeds, combined with sprints and turns as means for escape, but without the ability of precise maneuvers. This agrees with its assumed feeding habit. Since *Paramblypterus* has small and weak teeth, it could not prey on large animals. Therefore, a diet of small planktonic or benthic invertebrate organisms is likely. In fishes with few mobile elements on their skull, water flow is primarily controlled by velocity (Lauder 1982). Therefore, a fairly steady mode of locomotion would have been required for breathing and feeding in *Paramblypterus*. A flat belly is also present in *Acipenser* and *Amia*, but it is absent in forms that live in open waters, such as salmon or trout. Apparently, a cambered body reduces drag in close proximity to the ground and represents and adaptation to bottom-dwelling (Morelli 1960, 1983). A tentative reconstruction of the habitat of *Paramblypterus* would be the littoral or bottom zone of a lake or river. Intermittent excursions into deeper waters are suggested by specimens found occasionally in sediments corresponding to the profundal facies of the lakes.

Conclusions

Based on a three-dimensional model of *Paramblypterus* and comparisons to other extant lower actinopterygians, such as *Polypterus*, *Lepisosteus*, *Acipenser*, or *Amia* and fossil lower actinopterygians, such as *Pteronisculus*, *Elonichthys*, or *Microhaplolepis*, function of the feeding apparatus and patterns of locomotion of *Paramblypterus* are interpreted. Certain modified features, such as a less inclined suspensory apparatus, loosely arranged snout bones, the mouth opening being oriented further anteriorly, fragmentation of the dermohyal and "suborbital" re-

gion, and an enlarged palatoquadrate-maxillary chamber. are present in *Paramblypterus*. This may have improved suction feeding by allowing for expansion of underlying muscles and/or increasing the mobility of the skull. The locomotor capability of *Paramblypterus* appears to have been one of moderate steady swimming speeds. combined with sprints and turns as means for escape. but with a limited ability of precise maneuvers.

The weak teeth present in *Paramblypterus* suggest a diet of small or soft-bodied planktonic or benthic organisms. Water flow during feeding might have been controlled mostly by body velocity which requires a steady mode of locomotion. In contrast to pelagic species. *Paramblypterus* probably had a flat belly which suggests that it was a bottom dwelling species.

Acknowledgements

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