



The quadrate-metapterygoid fenestra of otophysan fishes, its development and homology

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Abstract

We compare the ontogeny of the hyopalatine arch in representatives of the Otophysi to shed light on the homology of the so-called quadrate-metapterygoid fenestra, QMF. Described initially as a character of characiforms (tetras and allies), presence of a QMF has also been reported for cobitid loaches and a handful of cyprinids among cypriniforms, as well as for a few clupeoids. In characiforms the QMF is either already present as an opening in the palatoquadrate cartilage in the earliest developmental stages we studied, or it forms later in the cartilage by resorption of chondrocytes. Some characiforms may lack a QMF during all stages of development. In cobitids the so-called QMF develops after the bones have ossified and forms mainly by resorption of bone tissue of quadrate and metapterygoid. Previous reports of a QMF in cyprinids are erroneous and the opening in this area forms by spatial separation of the quadrate and metapterygoid from the symplectic and not by the formation of a fenestra in the palatoquadrate cartilage. We suggest referring to this type as a quadrate-metapterygoid gap, QMG. Presence of a QMF in the palatoquadrate cartilage is a putative synapomorphy of characiforms. Development of a QMF by bone resorption in the ossified palatoquadrate is a putative synapomorphy of Cobitidae. A QMG is variously present and developed to different degrees in opsariichthyine and danionine cyprinids. A QMF is also present in several clupeoids and deserves further study.

Keywords

Characiformes, Cobitidae, Cypriniformes, hyopalatine arch, ontogeny, Ostariophysi, Otophysi

Introduction

The hyopalatine arch comprises the hyomandibular, symplectic, quadrate, metapterygoid, ecto- and endopterygoid, and palatine (dermo- and or autopalatine), and has been modified in many different, sometimes bizarre, ways during the evolution of Teleostei. Modifications include extreme changes in size and shape or

loss of bones that have sometimes made it difficult to assess homology of the components. One prominent evolutionary change in the structure of the hyopalatine arch is the formation of a conspicuous opening between two bones, the so-called quadrate-metapterygoid fenestra (QMF from here on). The presence of this unusu-

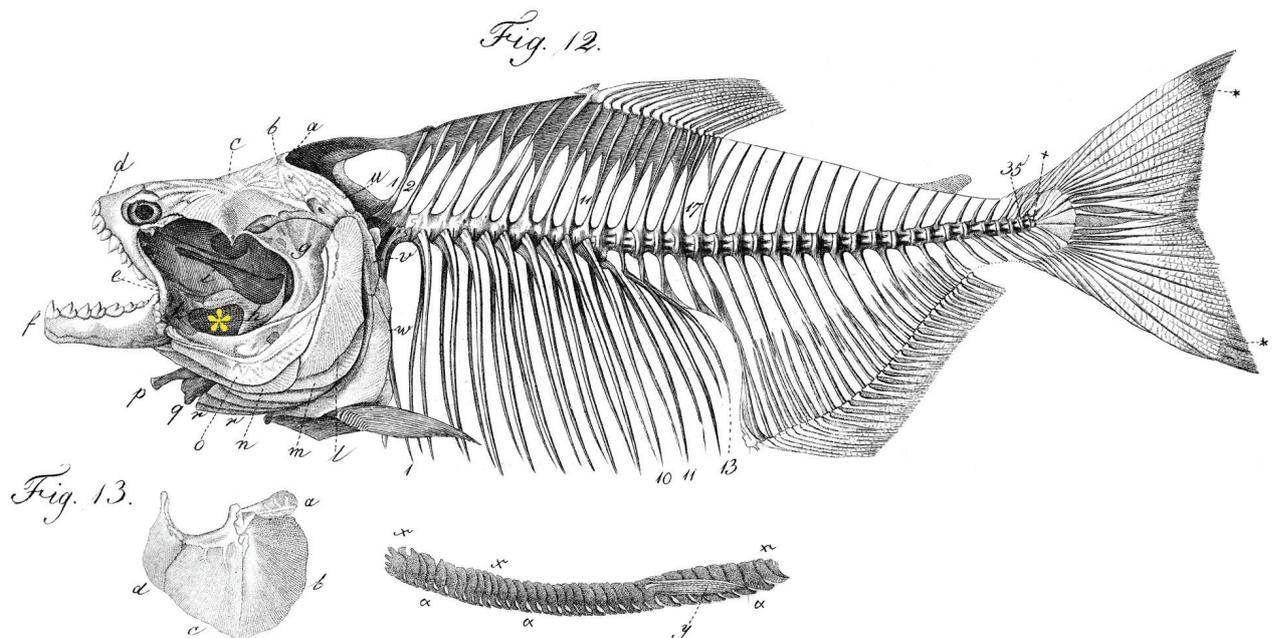


Figure 1. The earliest illustration of the quadrate-metapterygoid fenestra (marked with yellow asterisk) in the hyopalatine arch of the South American characiform *Serrasalmus rhombeus*. Illustration from Rosenthal (1816).

al opening was first illustrated (Fig. 1) in *Serrasalmus rhombeus* (Linnaeus) by Rosenthal (1816), and described by Sagemehl (1885) for representatives of the South American characiform families Lebiasinidae, Characidae and Erythrinidae, and the African Alestidae, Hepsetidae, and Citharinidae, and illustrated in detail for *Erythrinus*, *Hydrocynus* and *Citharinus*. Presence of a QMF has since been confirmed for a large number of African, as well as New World characiforms (e.g., Weitzman 1962, 1964; Daget 1962, 1963; Roberts 1966, 1969, 1974; Winterbottom 1980; Brewster 1986; Vari 1989, 1995; Zanata and Vari 2005; Mattox and Toledo-Piza 2012).

A QMF has also been reported in a number of cypriniforms (Regan 1911; Chranilov 1927; Greenwood et al. 1966; Howes 1976, 1978, 1979; Sawada 1982; Arratia 1992; Ashiwa and Hosoya 1998; Conway 2011; Miyata et al. 2011), and several clupeoids (Ridewood 1905; Gosline 1973; Schultze and Arratia 1991). Interpretation of the phylogenetic significance of the QMF, however, differs depending on the authors and ranges from being a putative synapomorphy of Otophysi (Fink and Fink 1981) to being independently derived in the different taxa in which this fenestra is present (Gosline 1973; Arratia 1992; Conway 2011).

Few data have been published on how the fenestra develops in the different groups, and so far only ontogenetic information from hepsetid and characid characiforms (Bertmar 1959; Vandewalle et al. 2005; Walter 2013; Mattox et al. 2014; Marinho 2022) and opsariichthyine cypriniforms (Arratia 1992) has been available.

Access to several developmental series of key taxa (different Ostariophysi and outgroups) has enabled us to revisit the issue of QMF homology and describe its development in each taxon in detail.

Materials and methods

Specimen preparation and examination

Specimens studied and illustrated here were cleared and double stained (c&s) following Taylor and Van Dyke (1985). Specimens were dissected with fine-tipped scissors and tungsten needles. Dissected hyopalatine arches were then photographed under a Zeiss Discovery V20 at different depths of focus. Deep-focus images were then produced in Helicon Focus 7 or Zeiss Zen software. Images were cleaned of dust specks in Adobe Photoshop 2021 and species ontogeny figures were assembled in Adobe Illustrator 2021. Lengths are given as notochord length (NL) or standard length (SL). The illustrated material is deposited in the following collections: Biodiversity Research and Teaching Collections, Texas A&M University, College Station (TCWC); Senckenberg Naturhistorische Sammlungen Dresden (MTD).

Material examined

The following c&s specimens were examined during the course of this study:

Elopidae: *Elops saurus* Linnaeus, MTD-F 40156), 33.8 mm SL; TCWC 16790.01, 2, 78.9–112.0 mm SL; TCWC 16807.17, 20, 17.2–31.5 mm SL. — **Denticipitidae:** *Denticeps clupeoides* Clausen, MTD-F 40157, 4, 18.7–30.0 mm SL; TCWC 20322.02, 2, 33.0–34.0 mm SL; TCWC 18339.18, 1, 28.0 mm SL. — **Clupeidae:** *Alosa sapidissima* (Wilson), TCWC 5264.01, 3, 62.4–63.7 mm SL; *Brevoortia patronus* Goode, TCWC 19718.02, 9,

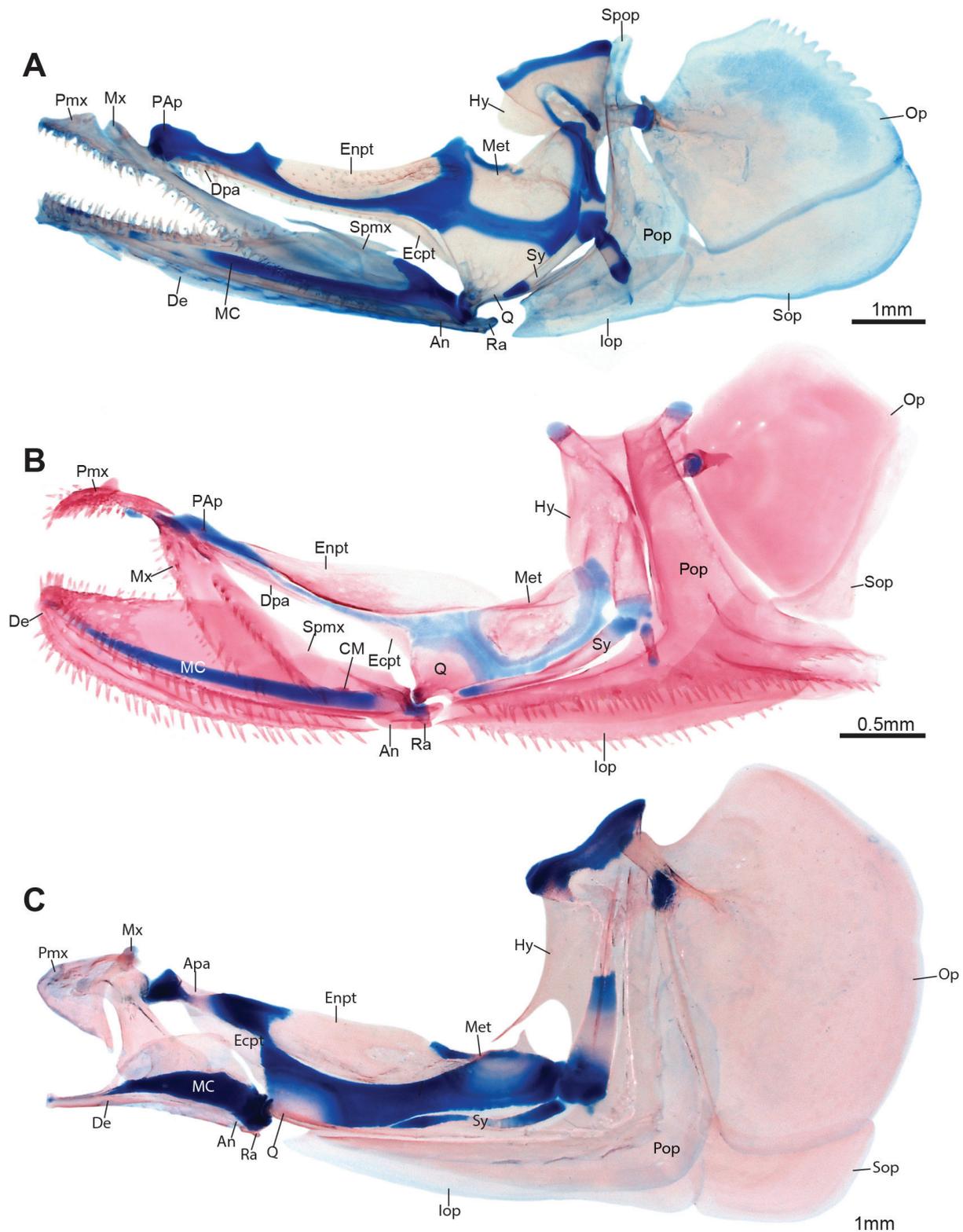


Figure 2. Cleared and double stained hyopalatine arch, jaws, and opercular series of selected teleosts lacking a quadrate-metapterygoid fenestra. **A** *Elops saurus*, MTD-F 40156, 33.6 mm SL. **B** *Denticeps clupeioides*, MTD-F 40157, 18.7 mm SL. **C** *Chanos chanos*, MTD-F 40158, 26.5 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Dpa, dermopalatine; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, pars autopalatina; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Spmx, supramaxilla; Spop, suprapreopercle; Sy, symplectic.

16.4–51.0 mm SL. — **Chanidae:** *Chanos chanos* (Fabricius), MTD-F 40158, 26.5 mm SL — **Cyprinidae:** *Candidia barbata* (Regan), MTD-F 40159, 4, 8.0–79.3 mm

SL. *Opsariichthys uncirostris* (Temminck & Schlegel), MTD-F 40160, 1, 70.4 mm SL. — **Cobitidae:** *Cobitis dalmatina* Karaman, MTD-F 40161, 5, 8.6–22.5 mm SL.

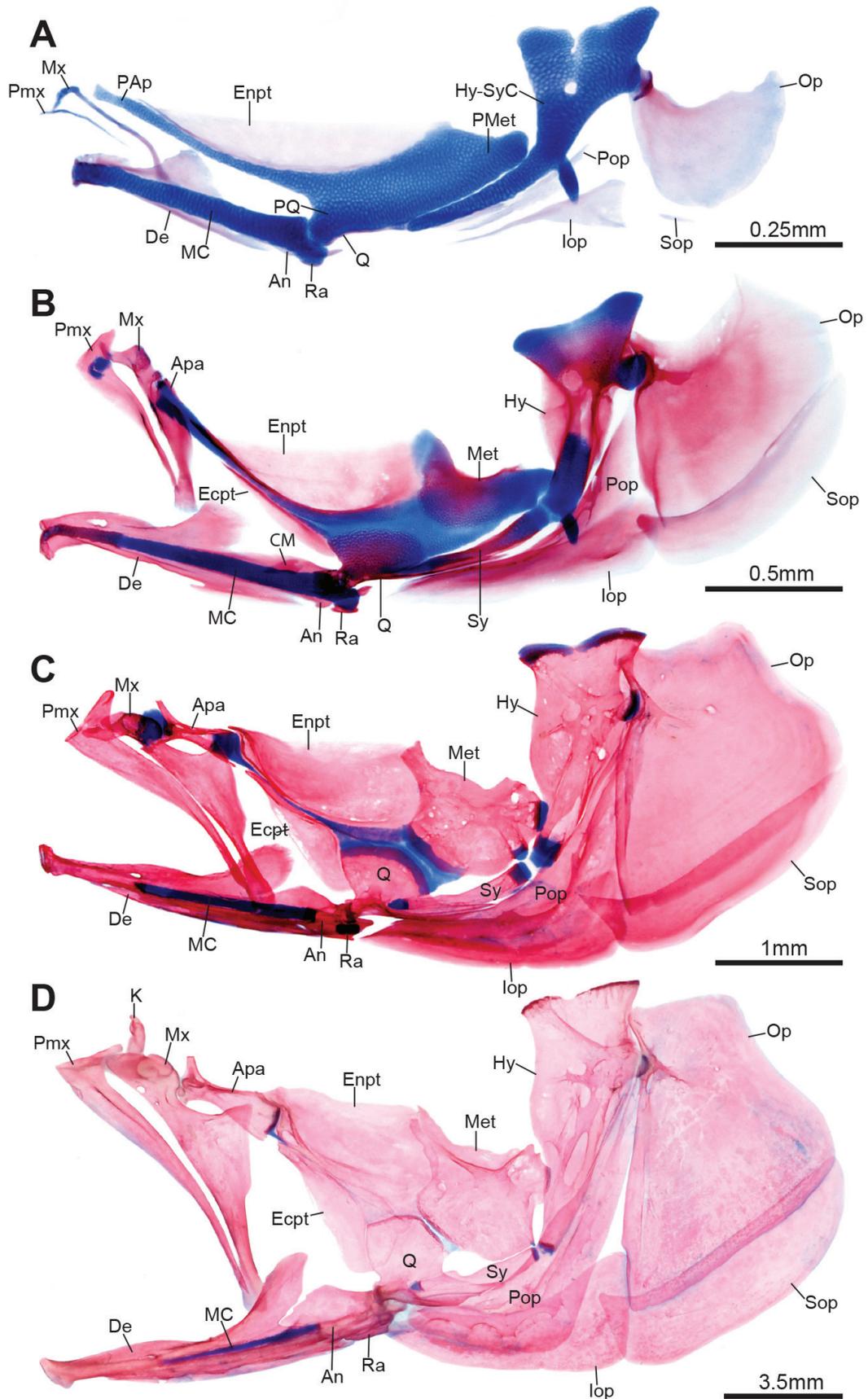


Figure 3. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Candidia barbata* (MTD-F 40159, cleared and double stained). **A** 8.0 mm SL. **B** 12.3 mm SL. **C** 24.7 mm SL. **D** 79.3 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Hy-SyC, hyo-symplectic cartilage; K, kinethmoid; lop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoides*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

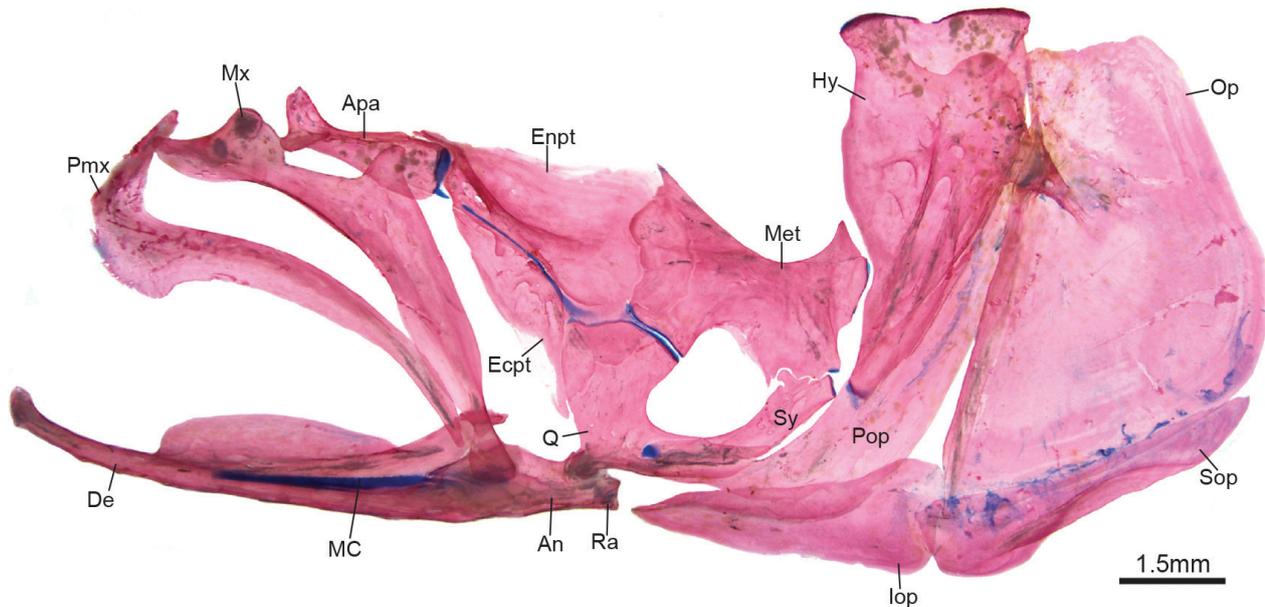


Figure 4. Hyopalatine arch, jaws, and opercular series of *Opsariichthys uncirostris* (MTD-F 40160, 70.4 mm SL, cleared and double stained). Abbreviations: An, angulo-articular; Apa, autopalatine; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

— **Ctenoluciidae:** *Ctenolucius hujeta* (Valenciennes), MTD-F 40162, 5, 4.3 mm NL – 38.3 mm SL. — **Lebiasinidae:** *Lebiasina bimaculata* Valenciennes, MTD-F 40163, 4, 6.0 mm NL – 20.6 mm SL; *Pyrrhulina spilota* Weitzman, MTD-F 40164, 4, 5.1 mm NL – 33.8 mm SL; — **Alestidae:** *Alestopetersius smykalai* Poll, MTD-F 40165, 4, 6.0 mm NL – 52.1 mm SL; *Rhabdalestes septentrionalis* (Boulenger), MTD-F 40166, 1, 43.0 mm SL. — **Callichthyidae:** *Megalechis thoracata* (Valenciennes), MTD-F 40167, 4, 5.3–22.0 mm SL. — **Siluridae:** *Silurus glanis* Linnaeus, MTD-F 40168, 3, 11.2–29.6 mm SL. — **Apterontidae:** *Apterontus leptorhynchus* (Ellis), MTD-F 40169, 4, 8.6 mm NL – 66 mm SL.

Results

The hyopalatine arch in *Elops*, *Chanos* and *Denticeps* as phylogenetically primitive representatives of teleosts, ostariophysans and clupeomorphs

We begin our comparison with juvenile stages of key taxa that illustrate the primitive condition for our groups of interest. In the 33.8 mm SL specimen of the elopomorph *Elops* (Fig. 2A) the palatoquadrate cartilage is still quite extensive and spans from *pars autopalatina* to *pars metapterygoidea* and separates the quadrate from the metapterygoid. The 18.7 mm SL clupeomorph *Denticeps* (Fig. 2B) and the 26.5 mm SL gonorynchiform *Chanos* (Fig. 2C) show a similar condition of quadrate and metapterygoid association as that in *Elops*. As in *Elops*, large parts of the palatoquadrate cartilages in these two

taxa are still present, with the quadrate and metapterygoid still widely separated by cartilage in the three taxa. No opening exists in the cartilage between the quadrate and metapterygoid. In subsequent development, not shown here, both ossifications of the quadrate and metapterygoid eventually replace the cartilage between the two bones, which then abut each other in a straight suture (e.g., Ride-wood 1904 for *Elops* and *Chanos*, and Greenwood 1968 for *Denticeps*).

Development of the hyopalatine arch in *Candidia barbata*

We illustrate four stages: 8.0 mm SL, 12.3 mm SL, 24.7 mm SL, and 79.3 mm SL. Here and in following accounts of the ontogeny, we restrict our description to the parts of the hyopalatine arch that are important for formation of the QMF. In our earliest stage (Fig. 3A), the hyosymplectic and palatoquadrate cartilages are well developed and arranged so that there is only a narrow gap between the *pars metapterygoidea* and the symplectic process. Ossification of metapterygoid and symplectic has not started, but the quadrate is present and carries a long posteroventral process (*sensu* Arratia and Schultze 1991) of membrane bone. At 12.3 mm (Fig. 3B), autopalatine, metapterygoid and symplectic are present as perichondral ossifications that cover the respective cartilages. The symplectic has moved away from the palatoquadrate so that a slightly wider gap has been established. At 24.7 mm (Fig. 3C), larger areas of the palatoquadrate and hyosymplectic cartilages ossify, so that in the adult of 79.3 mm (Fig. 3D) only narrow strips of cartilage remain between the bones. The main development in the context of formation of the opening previously referred to as a QMF

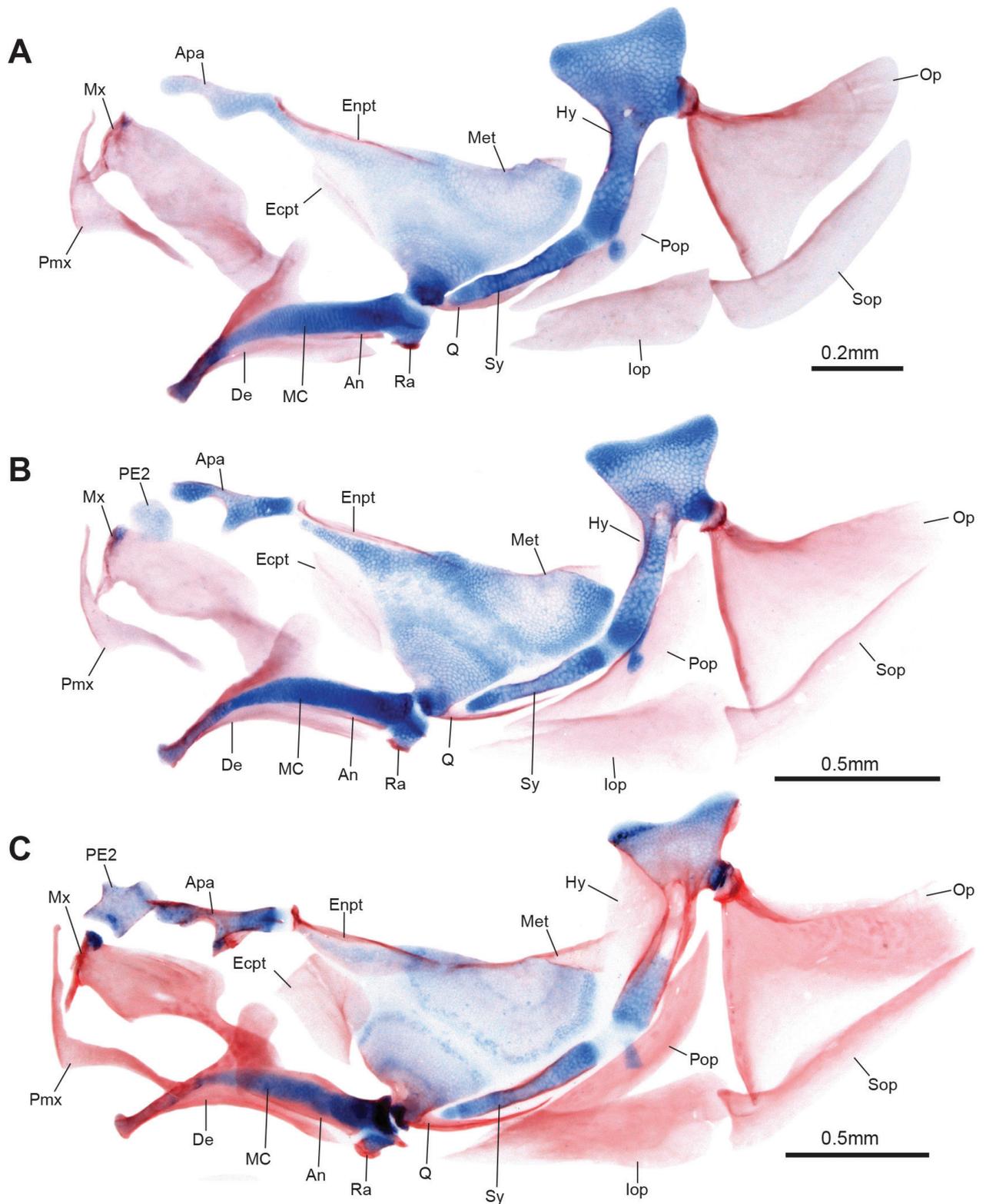


Figure 5 – part 1. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Cobitis dalmatina* (MTD-F 40161, cleared and double stained). **A** 8.6 mm SL. **B** 11.0 mm SL. **C** 13.0 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PE2, second pre-ethmoid; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

is the further spatial separation between the symplectic and the quadrate/metapterygoid. The fenestra in *Candidia* is thus not a true QMF but only a gap that forms between the symplectic and the quadrate and metapterygoid of

the palatoquadrate. This quadrate-metapterygoid gap, or QMG, is especially prominent in *Opsariichthys*, a taxon from where it was initially reported in cyprinids (Fig. 4).

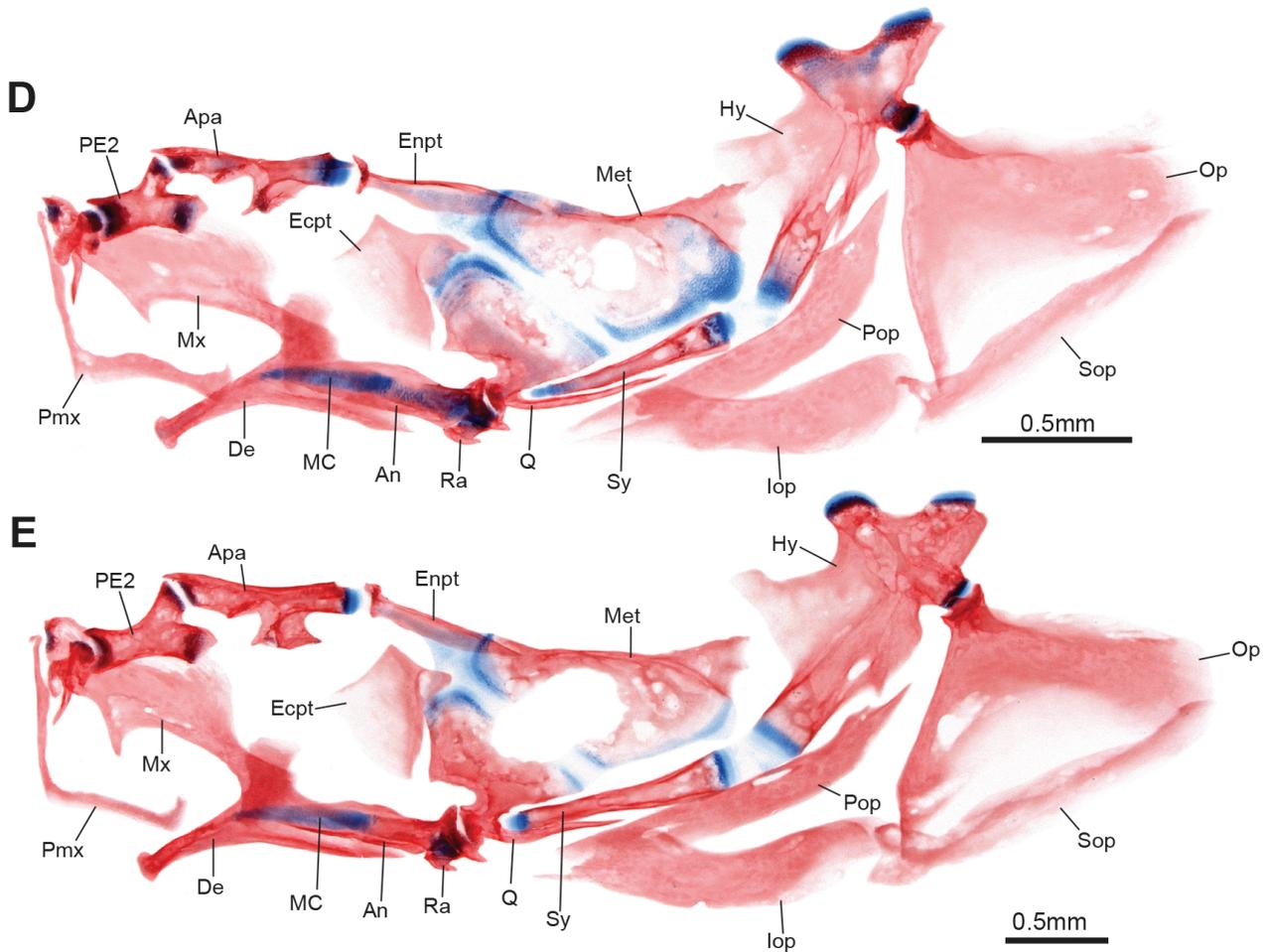


Figure 5 – part 2. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Cobitis dalmatina* (MTD-F 40161, cleared and double stained). **D** 20.3 mm SL. **E** 22.5 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PE2, second pre-ethmoid; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

Development of the hyopalatine arch in *Cobitis dalmatina*

We illustrate five developmental stages: 8.6 mm SL, 11.0 mm SL, 13.0 mm SL, 20.3 mm SL, and 22.5 mm SL (Fig. 5). In our smallest specimen of 8.6 mm SL (Fig. 5A), the hyopalatine arch still has large areas of cartilage and the autopalatine, quadrate and metapterygoid are only weakly ossified as perichondral lamellae. The cartilage between quadrate and metapterygoid is still continuous. At 11.0 mm (Fig. 5B) the strip of cartilage between metapterygoid and quadrate is still present but less prominently stained. The metapterygoid has acquired a small process of membrane bone at its posterodorsal corner. At 13.0 mm SL (Fig. 5C) quadrate and metapterygoid cover larger areas of the cartilage with the posterodorsal membrane bone process of the metapterygoid now reaching an anterior membrane process of the hyomandibular. At 20.3 mm SL (Fig. 5D), the most significant change is the beginning of the formation of the opening between metapterygoid and quadrate. The cartilage between the two bones has been resorbed in the middle of their contact zone and does not stain with Alcian blue in the more

peripheral areas of this zone. The bone matrix in the metapterygoid and quadrate that is adjacent to this middle zone shows signs of resorption, which has led to the formation of irregular openings, larger in the metapterygoid. In our largest stage of 22.5 mm SL (Fig. 5E), the opening between metapterygoid and quadrate is fully developed and represented by a circular gap in the middle of these two bones from which both cartilage and bone are fully resorbed.

Development of the hyopalatine arch in *Ctenolucius hujeta*

We illustrate 5 stages, 4.3 mm NL, 7.5 mm SL, 9.6 mm SL, 15.9 mm SL, 38.3 mm SL (Fig. 6). The QMF is already developed in the palatoquadrate cartilage of the smallest stage we studied (Fig. 6A). It is an oval fenestra in the cartilage between the well-chondrified thick *pars quadrata* and the thinner, more delicate *pars metapterygoidea*. At 7.5 mm SL (Fig. 6B), the quadrate has ossified around the anteroventral corner of the fenestra and the metapterygoid has started to form at its posterodorsal

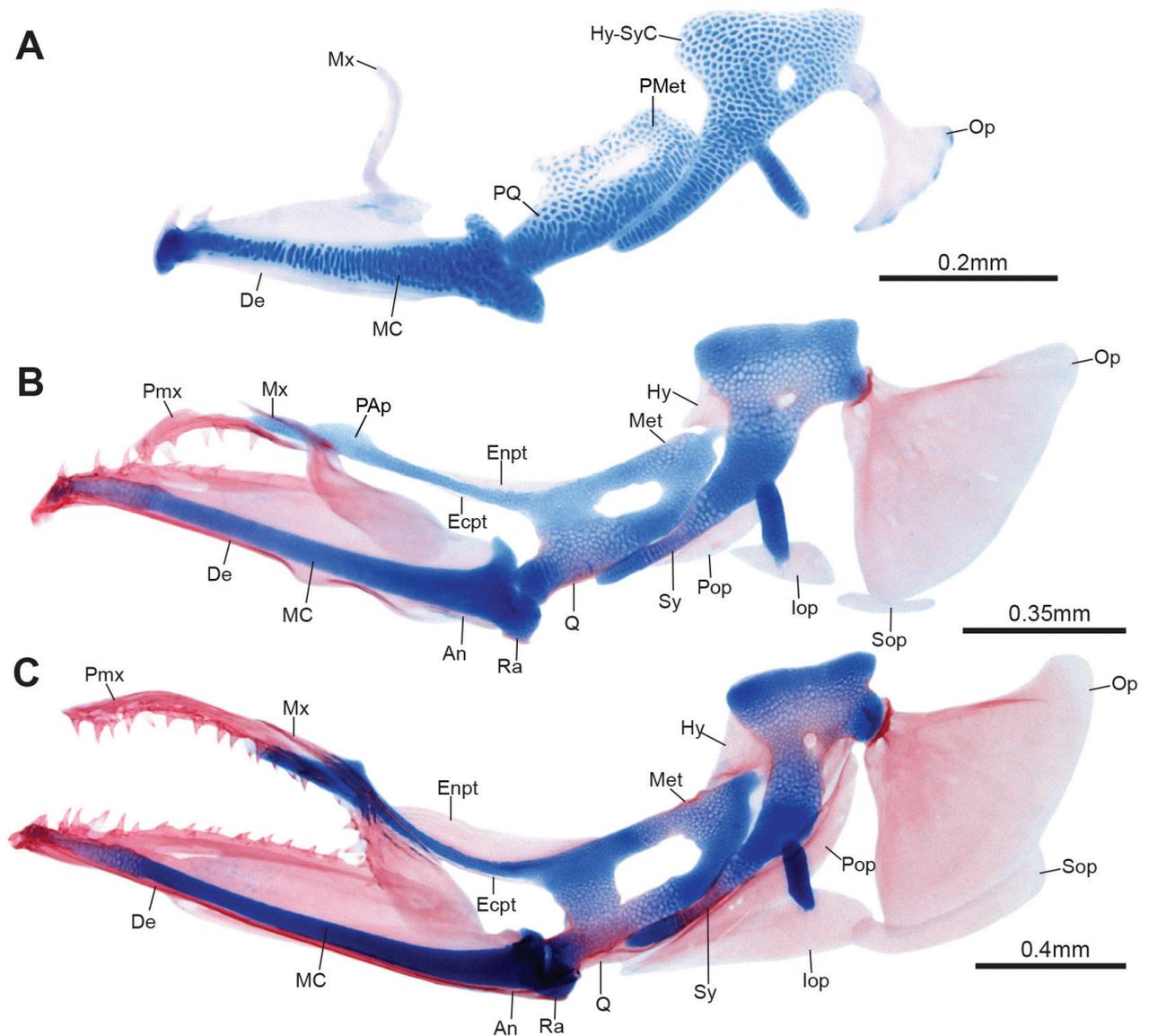


Figure 6 – part 1. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Ctenolucius hujeta* (MTD-F 40162, cleared and double stained). **A** 4.3 mm NL. **B** 7.5 mm SL. **C** 9.6 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; HY-SC, hyo-symplectic cartilage; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoidea*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

corner. During further development, the relative size of the fenestra increases, and as the cartilage ossifies further it acquires a round, rather than an oval shape. At 9.6 mm SL (Fig. 6C), metapterygoid and quadrate cover larger areas of the cartilage perichondrally, contributing to the anteroventral and posterodorsal corners of the slightly more elongate QMF. At 15.9 mm SL (Fig. 6D), both bones have started to replace the cartilage of the dorsal and ventral arms around the QMF. The quadrate has developed a triangular flange of membrane bone that fills in the anteroventral corner of the QMF. At 38.3 mm SL (Fig. 6E), a similar flange of membrane bone is present on the metapterygoid filling in the posterodorsal corner of the QMF. Both metapterygoid and quadrate are now more extensive and leave only small areas of cartilage between them. The quadrate forms the bony ventral arm, and the metapterygoid, the bony dorsal arm around the QMF.

Thus the QMF is mostly surrounded by bone, except at its anterodorsal and posteroventral corners, closely resembling the adult condition illustrated by Roberts (1969).

Development of the hyopalatine arch in *Lebiasina bimaculata*

We illustrate 4 stages: 6 mm NL, 10.0 mm SL, 14.7 mm SL, 20.6 mm SL (Fig. 7). In the smallest stage at 6 mm NL (Fig. 7A), the palatoquadrate cartilage is still complete from *pars quadrata* and *pars metapterygoidea* to *pars autopalatina*. At 10 mm SL (Fig. 7B), an oval elongate QMF has formed in the cartilage and the quadrate and metapterygoid have begun to ossify as perichondral lamellae of bone, the latter covering the dorsal arm of the cartilage surrounding the QMF. At 14.7 mm SL (Fig. 7C),

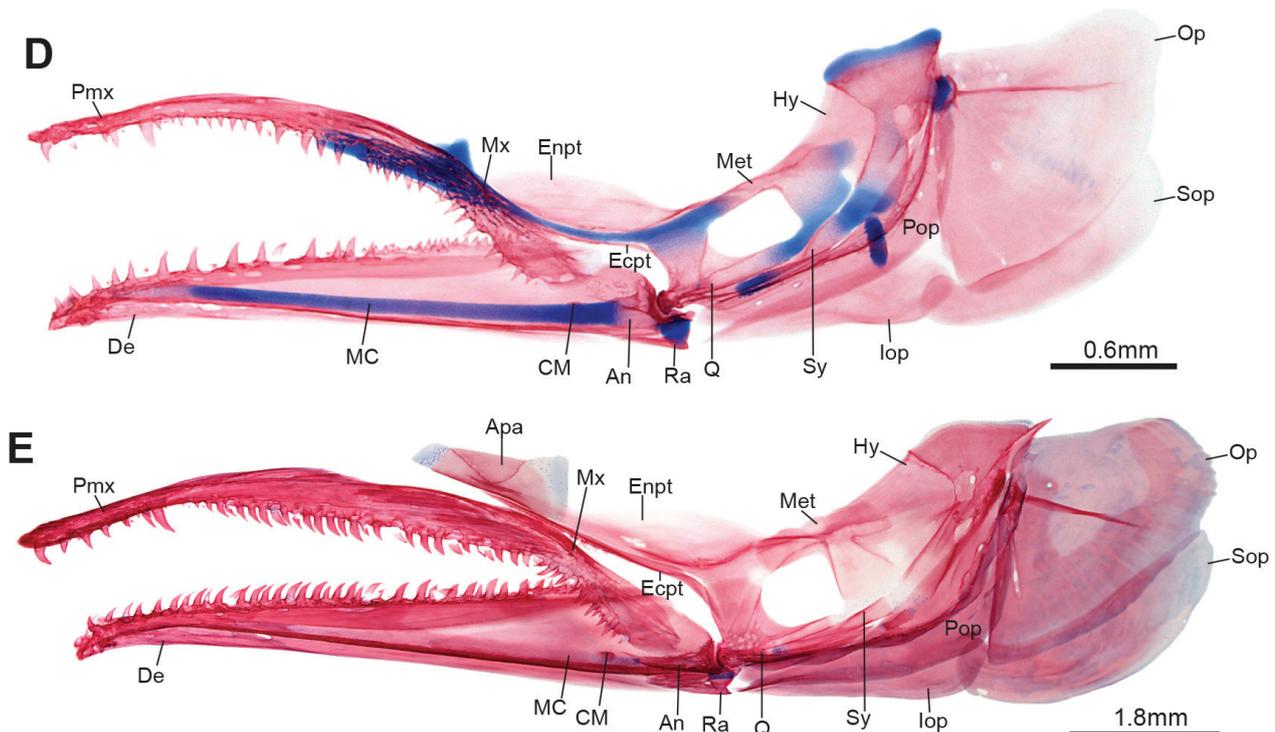


Figure 6 – part 2. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Ctenolucius hujeta* (MTD-F 40162, cleared and double stained). **D** 15.9 mm SL. **E** 38.3 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

both bones are well ossified. The quadrate does not extend along the ventral arm of the cartilage that makes up the ventral margin of the QMF and stops at its base. The metapterygoid, which surrounds almost the entire length of the dorsal arm of the cartilage has formed a ventral flange of membrane bone. This flange covers the dorsal half of the fenestra reducing the opening to a narrow gap between it and the remnants of the palatoquadrate cartilage above the anterior tip of the symplectic. At 20.6 mm SL (Fig. 7D), the metapterygoid membrane bone flange has now covered the QMF almost completely resulting in an even narrower gap between quadrate, metapterygoid and symplectic.

Development of the hyopalatine arch in *Pyrhulina spilota*

We illustrate four stages: 5.1 mm NL, 8.8 mm SL, 14.1 mm SL, 33.8 mm SL (Fig. 8). In our smallest stage (Fig. 8A), there is no sign of a QMF. The palatoquadrate cartilage resembles that of the smallest stage of *Lebiasina* in that it is a complete, continuous cartilage from *pars autopalatina* anteriorly to *pars metapterygoidea* posteriorly. At 8.8 mm SL (Fig. 8B), quadrate and metapterygoid have started to ossify perichondrally at the articular head of the jaw articulation and around the posterior process of *pars metapterygoidea*, respectively, still leaving the posteriormost tip of it cartilaginous and unossified. At 14.1 mm SL (Fig. 8C), the quadrate covers a larger area of *pars quadrata* and the metapterygoid, also larger, has

formed a ventral flange of membrane bone that extends into the narrow space between the metapterygoid and the symplectic. In the largest stage examined (Fig. 8D), the quadrate and metapterygoid have grown considerably and now leave only a narrow strip of cartilage between each other. The metapterygoid has acquired a dorsally directed flange of membrane bone and its ventral flange now closely approaches a similar dorsal flange from the symplectic, separated from it by only a very narrow gap. Unlike in *Lebiasina*, a QMF never forms in the development of *Pyrhulina* based on our material.

Development of the hyopalatine arch in *Alestopetersius smykalai*

We illustrate five stages: 6.0 mm NL, 9.0 mm SL, 12.3 mm SL, 15.6 mm SL (Fig. 9) and 52.1 mm SL (Fig. 10). In our smallest specimen of this African characiform (Fig. 9A), there is a narrow elongate QMF in the otherwise complete palatoquadrate cartilage. At 9 mm SL (Fig. 9B), the area between *pars quadrata* and *pars metapterygoidea* has lengthened so that the QMF is now even more elongate. The quadrate has now formed, too. At 12.3 mm SL (Fig. 9C), the quadrate is well-developed. The metapterygoid is also present as a perichondral ossification around the cartilage of the dorsal arm of the QMF, almost extending to the posterodorsal corner of the fenestra. The ventral arm of cartilage that forms the ventral border of the QMF shows some signs of resorption at the posteroventral cor-

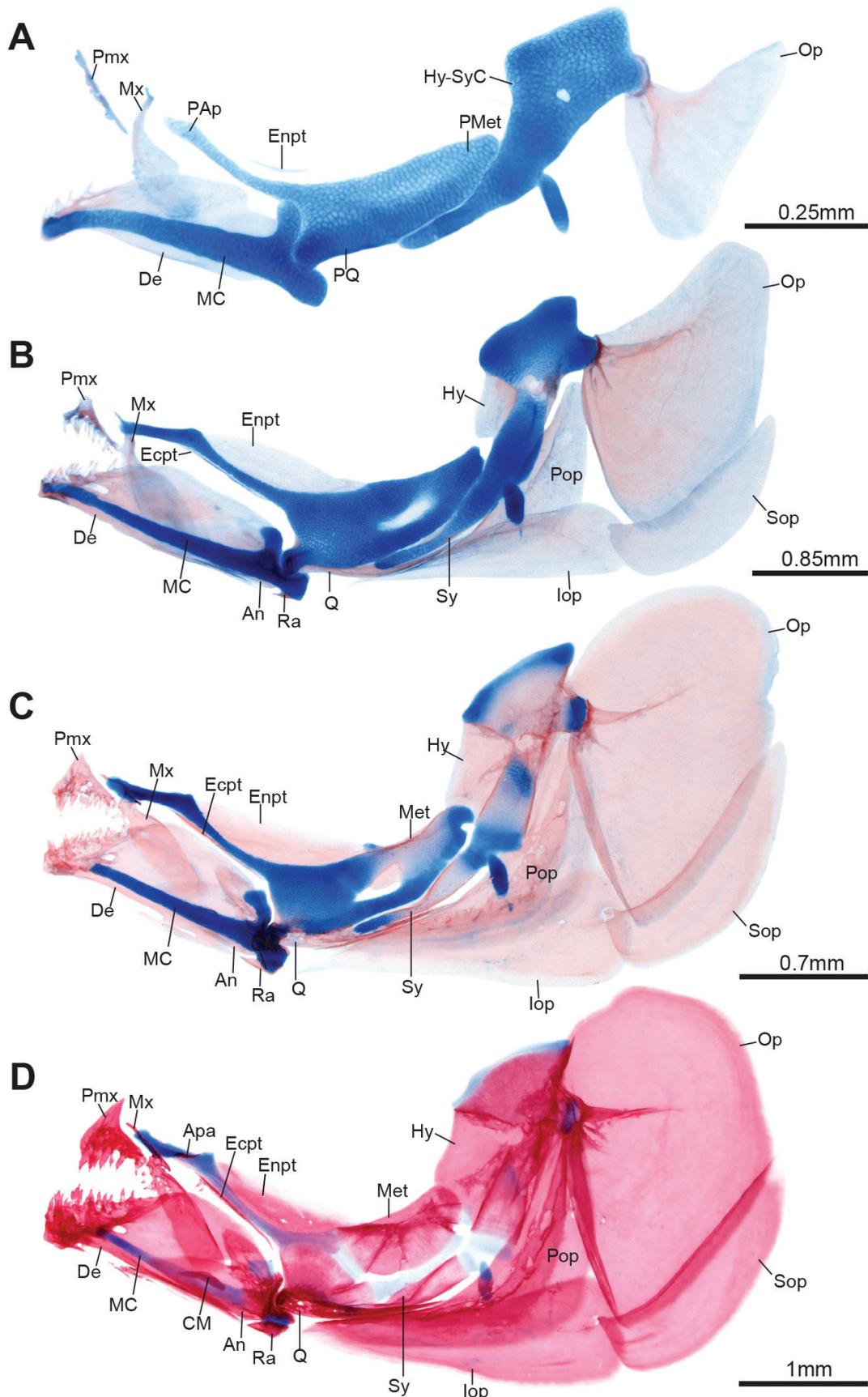


Figure 7. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Lebiasina bimaculata* (MTD-F 40163, cleared and double stained). **A** 6.0 mm NL. **B** 10.0 mm SL. **C** 14.7 mm SL. **D** 20.6 mm. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Hy-SyC, hyo-symplectic cartilage; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoida*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic

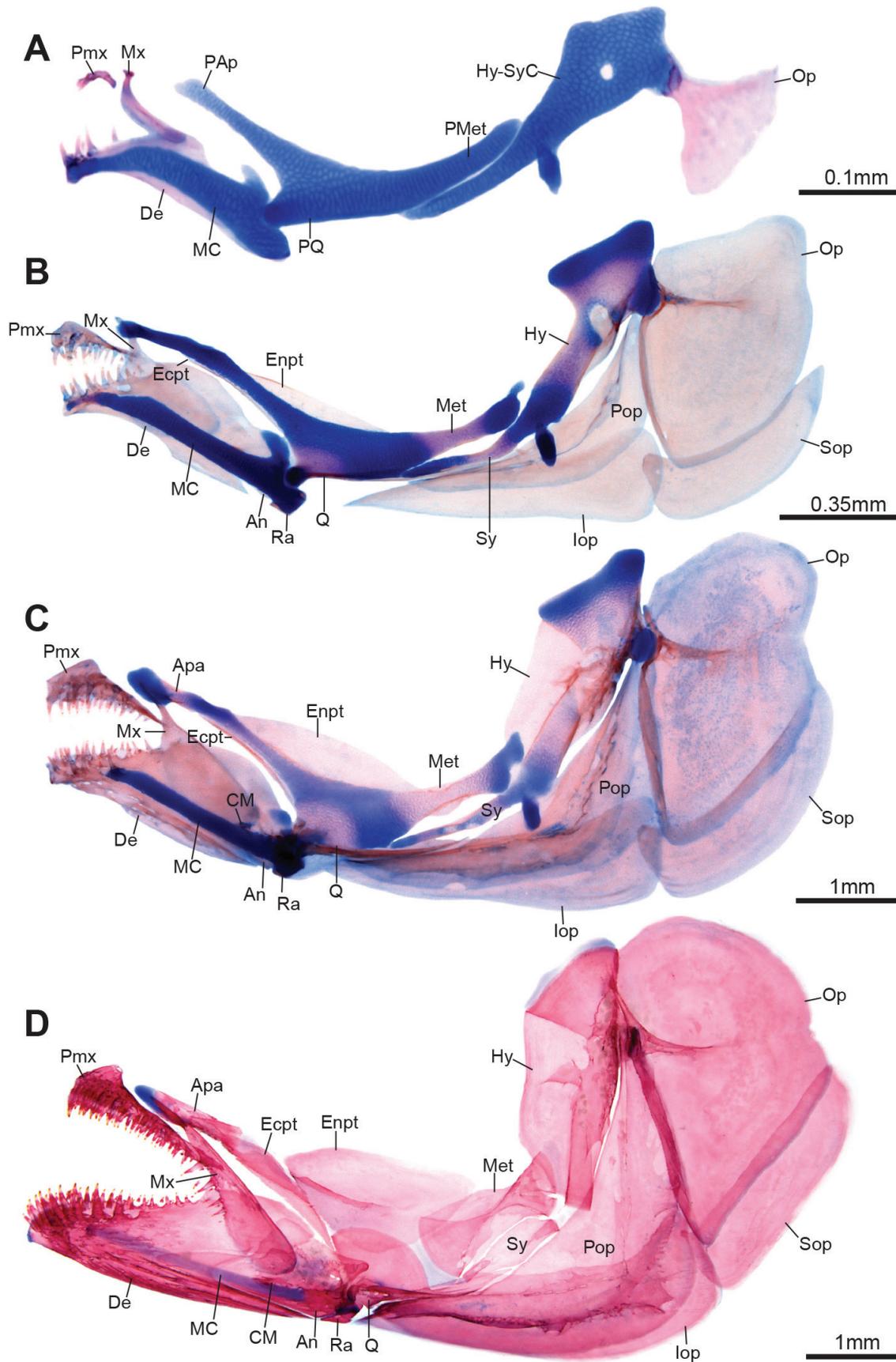


Figure 8. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Pyrrhulina spilota* (MTD-F 40164, cleared and double stained). **A** 5.1 mm NL. **B** 8.8 mm SL. **C** 14.1 mm SL. **D** 33.8 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Hy-SyC, hyo-symplectic cartilage; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoidea*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic

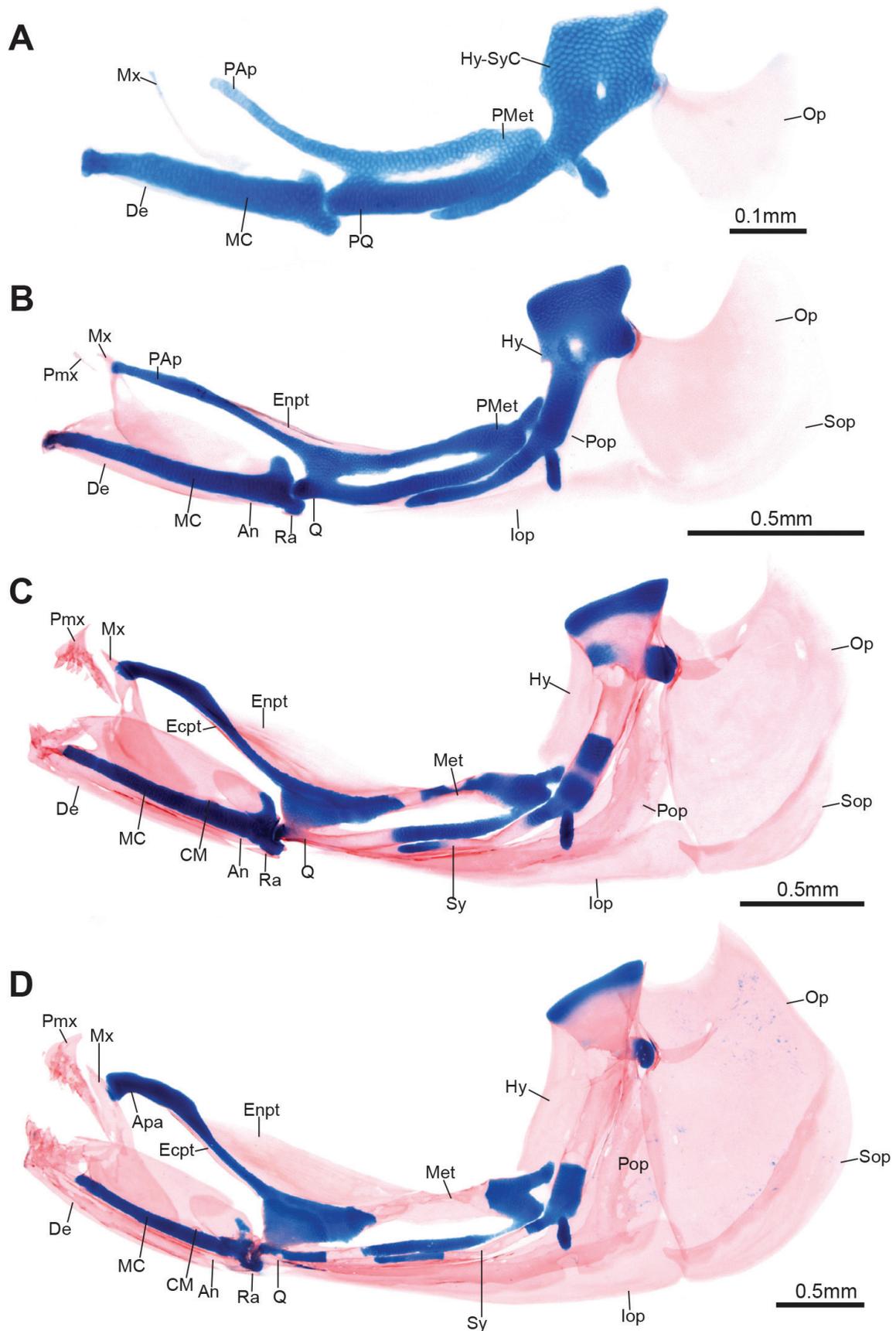


Figure 9. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Alestopetersius smykalai* (MTD-F 40165, cleared and double stained). **A** 6.0 mm NL. **B** 9.0 mm SL. **C** 12.3 mm SL. **D** 15.6 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; CM, coronomeckelian; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Hy-SyC, hyo-symplectic cartilage; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoides*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

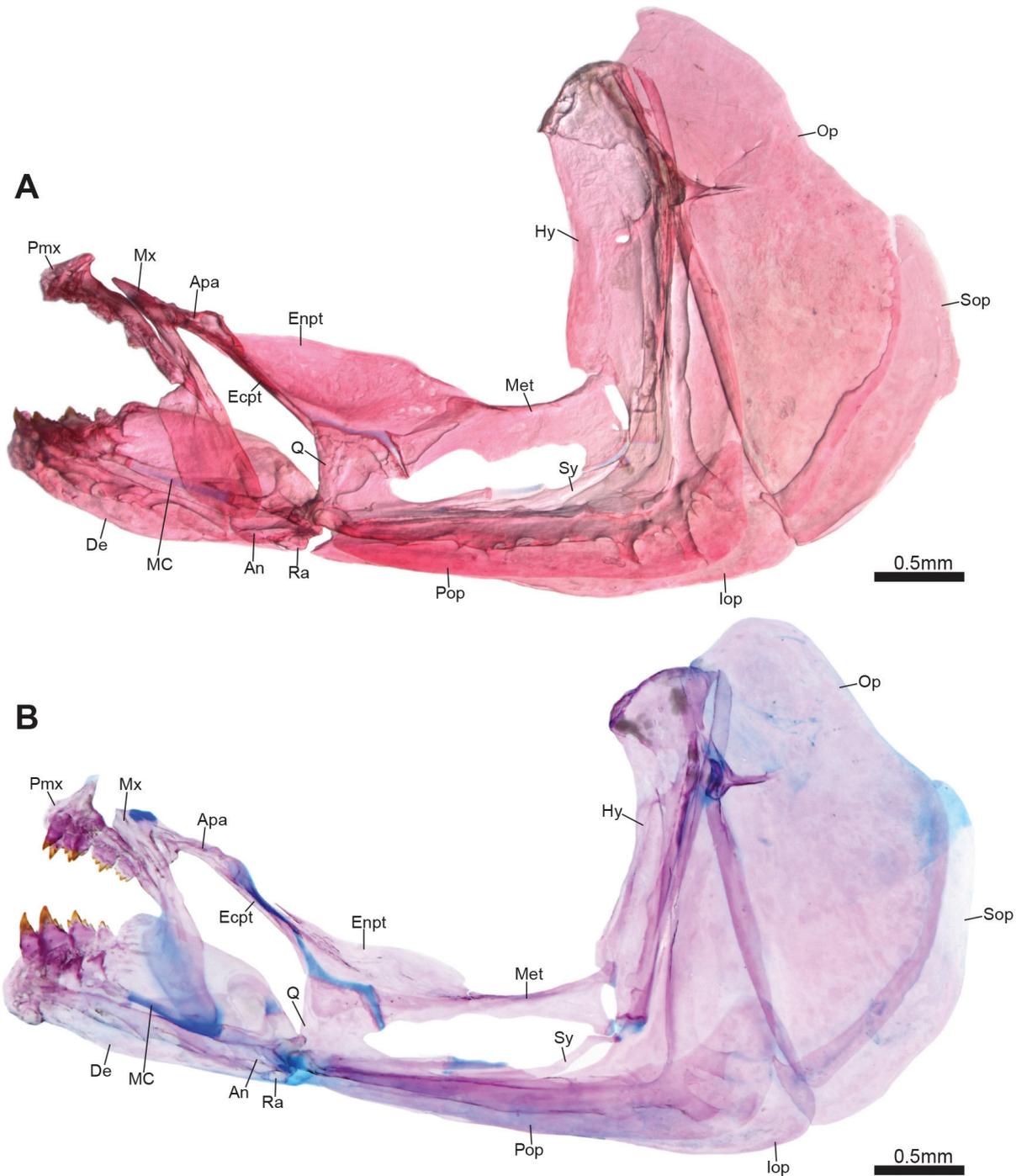


Figure 10. Adult hyopalatine arch, jaws, and opercular series of two Alestidae (cleared and double stained). **A** *Alestopetersius smykalai* (MTD-F 40165), 52.1 mm SL. **B** *Rhabdalestes septentrionalis* (MTD-F 40166), 43.0 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, preopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

ner of the QMF where it meets the dorsal arm. Finally, at 15.6 mm SL (Fig. 9D), further resorption of cartilage has almost disconnected the ventral and dorsal arms of the QMF. The metapterygoid has also formed a narrow ventral extension of membrane bone which has narrowed the rather elongate QMF to a narrow gap between it and the cartilage of the ventral arm. In the 52.1 mm SL adult (Fig. 10A), the QMF is well developed and elongate and its posterior and dorsal border is formed by the metapter-

ygoid. The quadrate contributes the anterior border of the QMF and the anterior half of its ventral border. A cartilage remnant of the *pars quadrata* forms another quarter of its ventral border with the posteriormost quarter of the QMF border provided by the symplectic. This results in a wide spatial separation of the quadrate and metapterygoid along the ventral margin of the QMF. The adult 43 mm SL *Rhabdalestes septentrionalis*, another species of alestid, shows a similar condition (Fig. 10B).

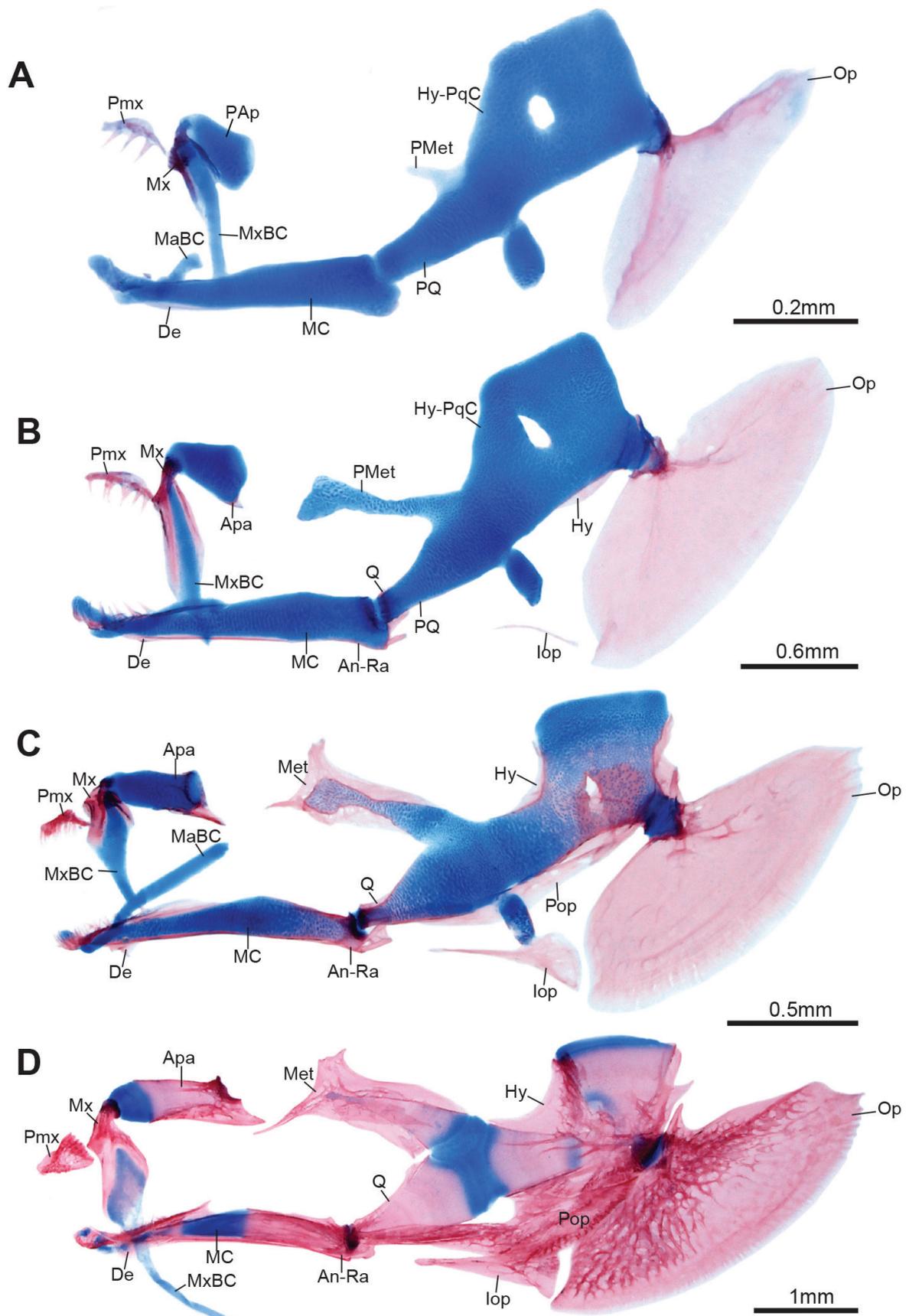


Figure 11. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Megalechis thoracata* (MTD-F 40168, cleared and double stained). **A** 5.3 mm SL. **B** 6.5 mm SL. **C** 9.5 mm SL. **D**. 22.0 mm SL; distal tip of maxillary barbel cartilage not shown. Abbreviations: An-Ra, angulo-articular-retroarticular; Apa, autopalatine; De, dentary; Hy, hyomandibular; HyQC, hyomandibulo-pala-toquadrate cartilage; Iop, interopercle; MaBC, cartilage of Mandibular barbel; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; MxBC, cartilage of maxillary barbel; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoidea*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate.

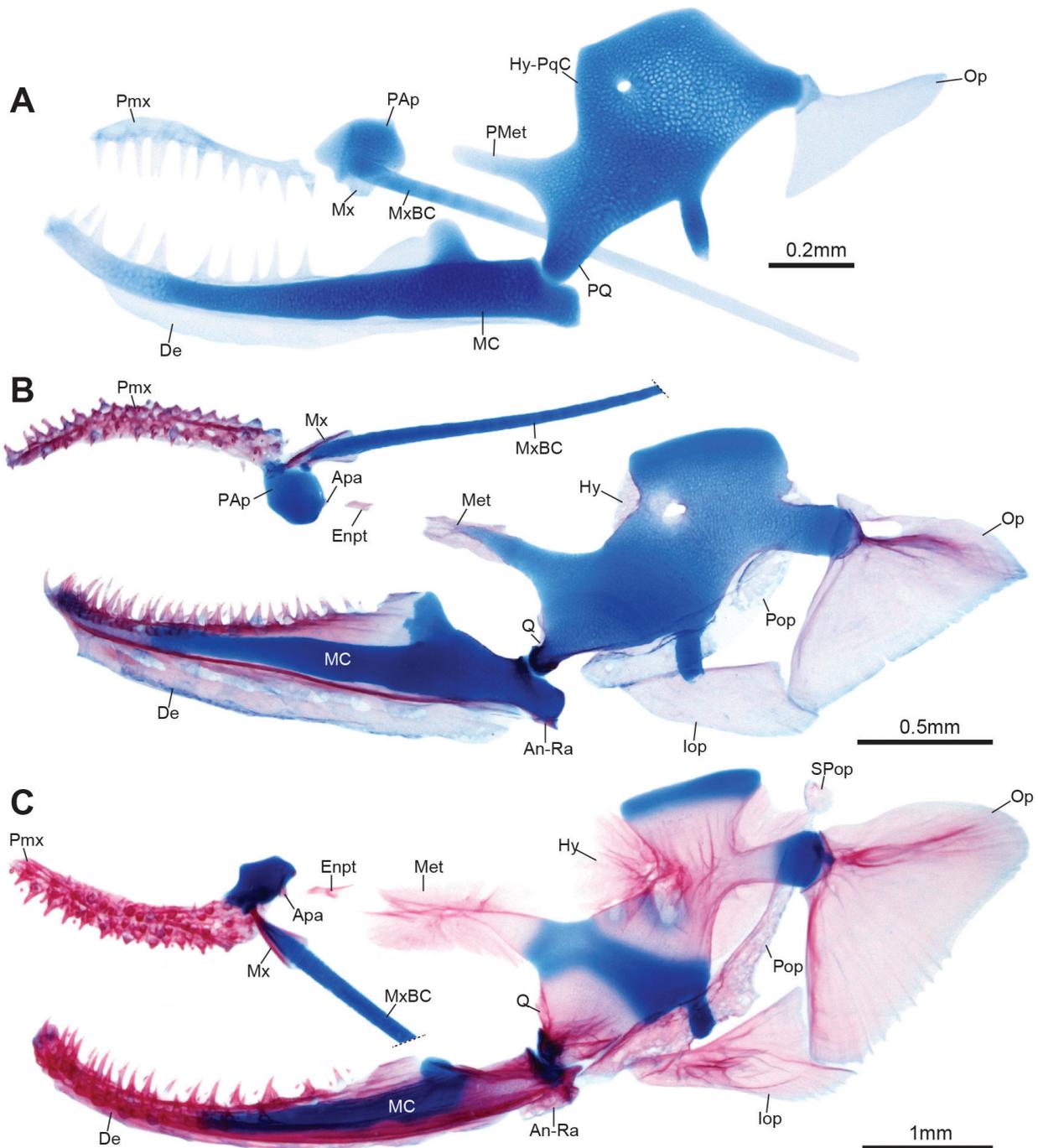


Figure 12. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Silurus glanis* (MTD-F 40168, cleared and double stained). **A** 11.2 mm SL. **B** 18.1 mm SL. **C** 29.6 mm SL. Distal tip of maxillary barbel cartilage not shown in b and c. Abbreviations: An-Ra, angulo-articulo-retroarticular; Apa, autopalatine; De, dentary; Enpt, endopterygoid; Hy, hyomandibular; Hy-PqC, hyomandibulo-palatoquadrate cartilage; Iop, interopercle; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; MxBC, cartilage of maxillary barbel; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoidea*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; SPop, suprapreopercle.

Development of the hyopalatine arch in *Megalechis thoracata*

We illustrate four stages: 5.3 mm SL, 6.5 mm SL, 9.5 mm SL, 22.0 mm SL (Fig. 11). In the earliest stage (Fig. 11A) the hyomandibulo-palatoquadrate cartilage, as is typical in siluriforms, consist of the autogenous *pars autopalatina* and the confluent *pars hyomandibularis* and *pars quadrata* from which *pars metapterygoidea* projects as a

short and tiny anterodorsally projecting cartilage process. At 6.5 mm SL (Fig. 11B) *pars metapterygoidea* has enlarged, grown anteriorly towards *pars autopalatina* and developed a wide anterior tip. The quadrate has started to ossify around the articulation with the lower jaw. At 9.5 mm SL (Fig. 11C), the quadrate covers most of the cartilage of *pars quadrata* perichondrally. The metapterygoid has perichondrally ossified around the *pars metapterygoidea* and has developed dorsal, ventral and anterior

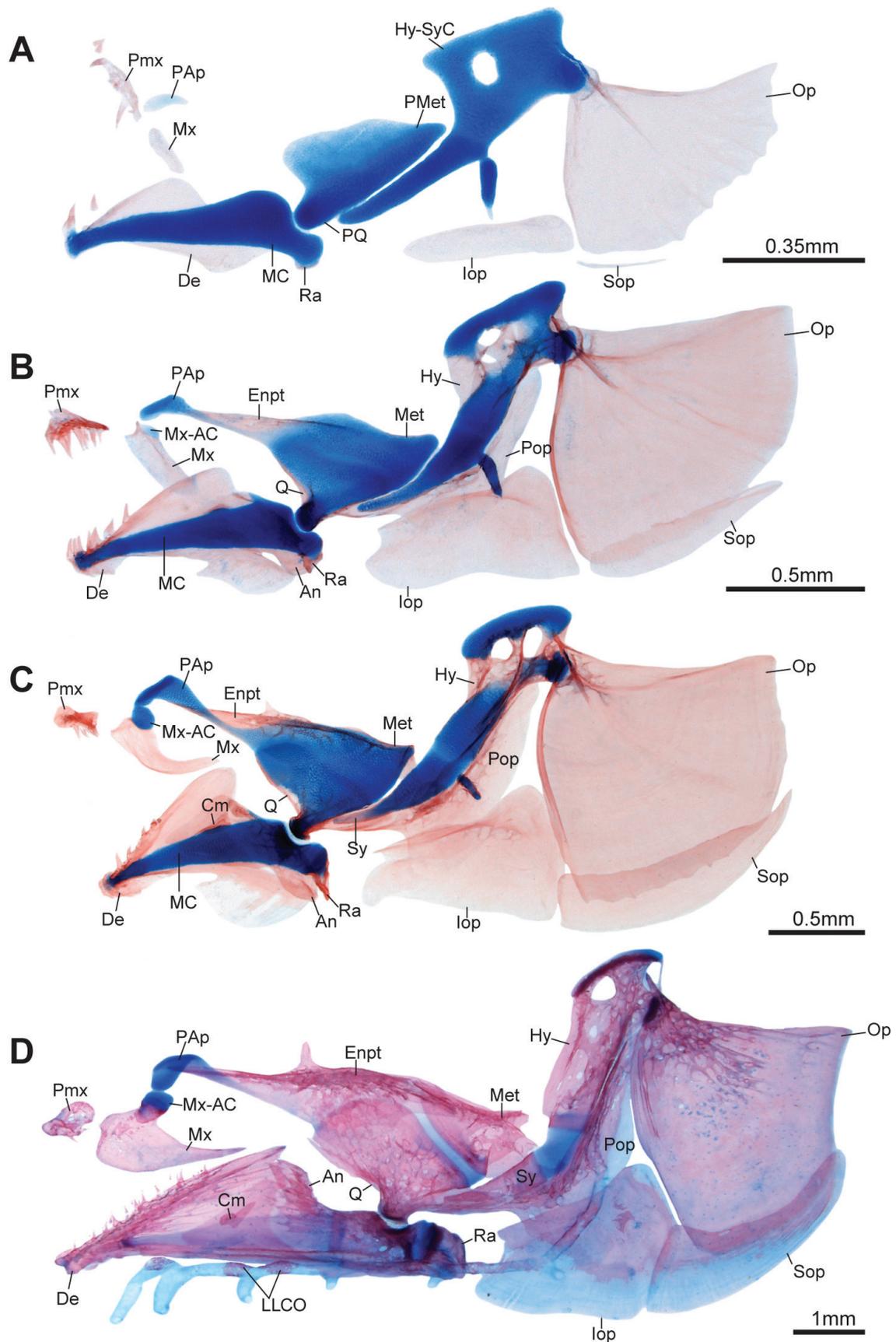


Figure 13. Ontogeny of the hyopalatine arch, jaws, and opercular series of *Apteronotus leptorhynchus* (MTD-F 40169, cleared and double stained). **A** 8.6 mm NL. **B** 12.1 mm SL. **C** 20.4 mm. **D** 66.0 mm SL. Abbreviations: An, angulo-articular; Cm, coronomeckelian; De, dentary; Enpt, endopterygoid; Hy, hyomandibular; Hy-SyC, hyo-symplectic cartilage; lop, interopercle; LLCO, lateral line canal ossification; MC, Meckel's cartilage; Met, metapterygoid; Mx, maxilla; Mx-AC, articular cartilage of maxilla; Op, opercle; PAp, *pars autopalatina*; PMet, *pars metapterygoidea*; Pmx, premaxilla; Pop, preopercle; PQ, *pars quadrata*; Q, quadrate; Ra, retroarticular; Sop, subopercle; Sy, symplectic.

flanges of membrane bone with a dorsally directed pointed process and a sharply tapering, needle like anterior process. At 22.0 mm SL (Fig. 11D), most of the hyomandibulo-palatoquadrate cartilage has been replaced by the autopalatine, metapterygoid, quadrate and hyomandibular, leaving only narrow zones of cartilage between the last three bones. A QMF does not form in development.

Development of the hypopalatine arch in *Silurus glanis*

We illustrate three stages: 11.2 mm SL, 18.1 mm SL, 29.6 mm SL (Fig. 12). Our smallest stage (Fig. 12A) resembles that of *Megalechis*, but the hyomandibulo-palatoquadrate cartilage is wider. At 18.1 mm SL (Fig. 12B), the quadrate, metapterygoid and the hyomandibular have ossified in the respective parts of the cartilage. As in *Megalechis*, the metapterygoid forms around the anteriorly-directed *pars metapterygoidea* and develops membrane bone flanges dorsally, ventrally and anteriorly. At 29.6 mm SL (Fig. 12C), the metapterygoid, quadrate and hyomandibular have enlarged and cover larger parts of the cartilage restricting it to a smaller area between the three bones. A QMF is not developed.

Development of the hypopalatine arch in *Apteronotus leptorhynchus*

We illustrate four stages: 8.6 mm NL, 12.1 mm SL, 20.4 mm SL, 66.0 mm SL (Fig. 13). In our smallest stage (Fig. 13A), *pars autopalatina* is spatially separated from *pars quadrata* plus *metapterygoidea* by a large gap, resembling the condition in the siluriforms described above. This gap remains and is bridged only by the developing endopterygoid. In our 12.1 mm SL stage (Fig. 13B), quadrate and metapterygoid are developed as perichondral lamellae around the cartilage of *pars quadrata* plus *metapterygoidea*. *Pars autopalatina* remains cartilaginous. At 20.4 mm SL (Fig. 13C), ossification of quadrate and metapterygoid has proceeded and in some areas replaced the cartilage via endochondral ossification. A small articular cartilage has developed between *pars autopalatina* and the maxilla. At 66 mm SL, our largest stage (Fig. 13D), quadrate and metapterygoid have replaced most of the cartilage of *pars quadrata* plus *metapterygoidea* and only a narrow cartilage strip separates these two bones. A QMF is not developed at any stage during the development of *Apteronotus*.

Discussion

The QMF has received considerable attention in the past and different researchers have commented on its distribution among bony fishes and its phylogenetic significance. Early morphologists, like Sagemehl (1885) and

Regan (1911), were only concerned with the distribution of this character, and reported the presence of the QMF in characiform and some cypriniform taxa. Greenwood et al. (1966: 385) concluded that the presence of the QMF “is common in characoids...and from this it may be assumed that its presence is primitive for cyprinids and, indeed, all cyprinoids” and thus consequently homologous between these two groups. Gosline (1973: 769) argued against homology of the QMF in characoids and that in cyprinoids and noted that a similar fenestra also occurred in clupeoids, citing Ridewood (1905). In Gosline’s (1973) opinion, evolutionary development of the fenestra has a functional reason and “provides increased space for the contracted adductor mandibulae,” and he (Gosline 1975: 9) later added that this also facilitated “vertical movement of the hyoid bar internally.” Howes (1978: 47) considered the fenestra in cyprinoids to be a “plesiomorph” feature and reported it in *Macrochirichthys*, *Salmostoma* and *Securicula* (as *Pseudoxygaster*). He offered a different interpretation of the functional role of the QMF, suggesting it may relieve “stresses by directing forces generated in the lower jaw around the perimeter of the pterygoid bones and into the cranium” or act “as a type of hinge which enables the pterygoid bones to undergo lateral rotatory movements.” Howes (1979) subsequently reported the presence of the fenestra also in *Cabdio* (as *Aspidoparia*) and *Luciosoma*.

Sawada (1982) concluded that the QMF is a derived feature among Cobitoidei and criticized previous functional explanations by Gosline (1973, 1975) and Howes (1978) as unsatisfactory.

Fink and Fink (1981) used the presence of a QMF as a putative synapomorphy for the teleost taxon Otophysi. In contrast, Arratia’s (1992) analyses resolved this character either as synapomorphy of cypriniforms plus characiforms or as independently derived in both groups, a result of her optimization method DELTRAN. She also pointed out that the quadrate-metapterygoid fenestra in *Opsariichthys* forms after the two bones have ossified, by changes in the shape of their ventral margins and their spatial removal from the symplectic, with which the metapterygoid is sutured in early stages.

In the update and revision of their influential 1981 paper, Fink and Fink (1996) discussed the presence of a quadrate-metapterygoid fenestra as an otophysan synapomorphy, and pointed out that their earlier mention of this structure in some homalopterids, citing Ramaswami (1952b) in support, was in error, but that Ramaswami (1952a) illustrated such a fenestra in *Homaloptera amphisquamata* in *Homaloptera amphisquamata* (Weber & de Beaufort).

In a morphology-based phylogenetic study of cypriniform fishes, Conway (2011) coded the QMF (his character 43) as present in all members of Cobitidae and in the characiform outgroup *Distichodus antonii* Schilthuis. Though *Zacco* (*Z. cf. platypus* (Temminck & Schlegel)) was included as a member of the ingroup by Conway (2011), he did not consider its quadrate-metapterygoid opening to be homologous with that of cobitids and characiforms. He therefore coded the QMF as absent for

Zacco in his data matrix. Conway's analysis (2011) recovered the QMF as a derived character of the Cobitidae, and one acquired independently of the characiform QMF, thus supporting Sawada's (1982) view.

Our results show that the so-called quadrate-metapterygoid fenestra in cypriniforms and characiforms is a structure with greatly differing development and adult anatomy.

Among cypriniforms, a quadrate-metapterygoid fenestra has been previously reported from the opsariichthyine cyprinids *Opsariichthys* and *Zacco* (Regan 1911; Greenwood et al. 1966; Arratia 1992), the danionine cyprinids *Salmostoma*, *Macrochirichthys*, *Securicula*, *Cabdio* (as *Aspidoparia*), and *Luciosoma* (Gosline 1975; Howes 1978, 1979) and the cobitids *Acantopsis*, *Cobitis*, *Iksookimia*, *Lepdiocephalichthys*, *Niwaella*, *Pangio* (as *Acanthopthalmus*), and *Sabanejewia* (Chranirov 1927; Ramaswami 1953; Sawada 1982; Conway 2011). Of these cypriniform taxa, ontogenetic information on the hyopalatine arch is only available for the cyprinid *Opsariichthys* from Arratia (1992). She noted that what she called QMF in this taxon develops from an early developmental condition in which metapterygoid and symplectic are initially (at 26.5 mm SL) sutured to each other with no space between them and the quadrate. The fenestra forms in subsequent development by spatial changes in the relative position of the three bones, starting at 30 mm SL and leading to the formation of a large gap between them by 120 mm SL (see Fig. 4).

Our results of the development of the closely related opsariichthyine cyprinid *Candidia* confirm Arratia's (1992) description. The so called QMF in *Candidia* forms by a separation of the quadrate and metapterygoid from the symplectic, which results in the formation of a more or less circular gap between the two former bones and the latter (Fig. 3D). As the so called QMF in opsariichthyine cyprinids does not form as a true fenestra (an opening within a skeletal structure) we propose to refer to this type of opening as the quadrate-metapterygoid gap or QMG. The QMG can be distinguished from the QMF in that the former is not limited ventrally by the quadrate and metapterygoid. Judging from the published images and our reinvestigation of the cypriniform material mentioned by Howes (1979) and utilizing this difference, we hypothesize that the opening between quadrate and metapterygoid in those cyprinids (*Salmostoma*, *Macrochirichthys*, *Securicula*, *Cabdio*, *Luciosoma*) represents a QMG and not a QMF. The opening in *Homaloptera amphisquamata* in Fig. 5c in Ramaswami (1952a) which was interpreted by Fink and Fink (1996) as a QMF, is almost certainly also a QMG as it is identical in terms of its relationship to the quadrate, metapterygoid and symplectic as the QMG of *Candidia* and *Opsariichthys*.

Our ontogenetic study of the cobitid *Cobitis dalmanina* demonstrates that the quadrate and metapterygoid develop initially in a typical fashion from a continuous and entire palatoquadrate cartilage (Fig. 5A–C). From ca. 20 mm SL the area in the middle between the two bones begins a process of bone absorption (Fig. 5d), resulting in a large fenestra surrounded by the quadrate and metapter-

ygoid. Thus, the opening in *Cobitis* is a QMF, though it develops in a way dramatically different from the QMF in characiforms.

Since Sagemehl's (1885) seminal monograph on characiform osteology, the presence of a QMF in members of this group is well known (Regan 1911; Weitzman 1962). A number of papers on characiforms have been published (Fink and Fink 1996; Vandewalle et al. 2005; Walter 2013; Mattox et al. 2014; Carvalho and Vari 2015; Marinho 2022) that include information on the development of the hyopalatine arch. The most comprehensive is Mattox et al. (2014), who showed that a QMF is already present between *pars quadrata* and *pars metapterygoida* in the unossified palatoquadrate cartilage at very early developmental stages in the basal South American characid (now bryconid) *Salminus brasiliensis*. Two of the characiforms we studied herein, the African alestid *Alestopetersius* and the South American ctenoluciid *Ctenolucius*, are very similar in terms of their development of the hyopalatine arch and QMF. Already early stages show a QMF in the palatoquadrate cartilage, with the fenestra persisting beyond the start of the ossification process into the adult. *Alestopetersius* differs, however, from *Ctenolucius* in that the quadrate fails to develop along the ventral arm of the cartilage bordering the QMF, so that this fenestra is not entirely surrounded by the quadrate and metapterygoid, but also by the symplectic in its posteroventral corner (Fig. 10). This condition in adult *Alestopetersius*, superficially resembles the QMG in *Candidia* and *Opsariichthys*, but develops, of course, completely differently.

We also studied the hyopalatine arch development of two other characiforms *Lebiasina* and *Pyrrhulina*, belonging to the South American family Lebiasinidae, which have been cited as lacking a QMF by Weitzman (1964), a character that has been considered a synapomorphy of this family by Vari (1995:24). We found an interesting and intriguing developmental pattern relating to the QMF in lebiasinids that seems to be exclusive to this clade. In early developmental stages of *Lebiasina*, a QMF is absent from the palatoquadrate cartilage unlike in most other characiforms, in which it is present from even the earliest stages (see Fig. 6 *Ctenolucius*, Fig. 9 *Alestopetersius*, Vandewalle et al. 2005; Walter 2013; Mattox et al. 2014). Instead, a fenestra develops in the palatoquadrate cartilage at a later stage by resorption of cartilage before ossification of quadrate and metapterygoid starts. Later in ontogeny, when the bones start to form, a thin membrane bone flange develops from the metapterygoid to cover the fenestra, fully closing it in the adult. Thus, the QMF in *Lebiasina* is transient in ontogeny. In *Pyrrhulina*, the condition seems more extreme because the QMF never develops in the palatoquadrate cartilage and the quadrate and metapterygoid develop in the solid, non-fenestrated cartilage as in non-characiforms otophysans. The condition in *Lebiasina* seems to be an intermediate character state between the regular characiform condition of a normal fenestra developing in the cartilage and that of the more derived lebiasinid condition, in which the QMF never develops.

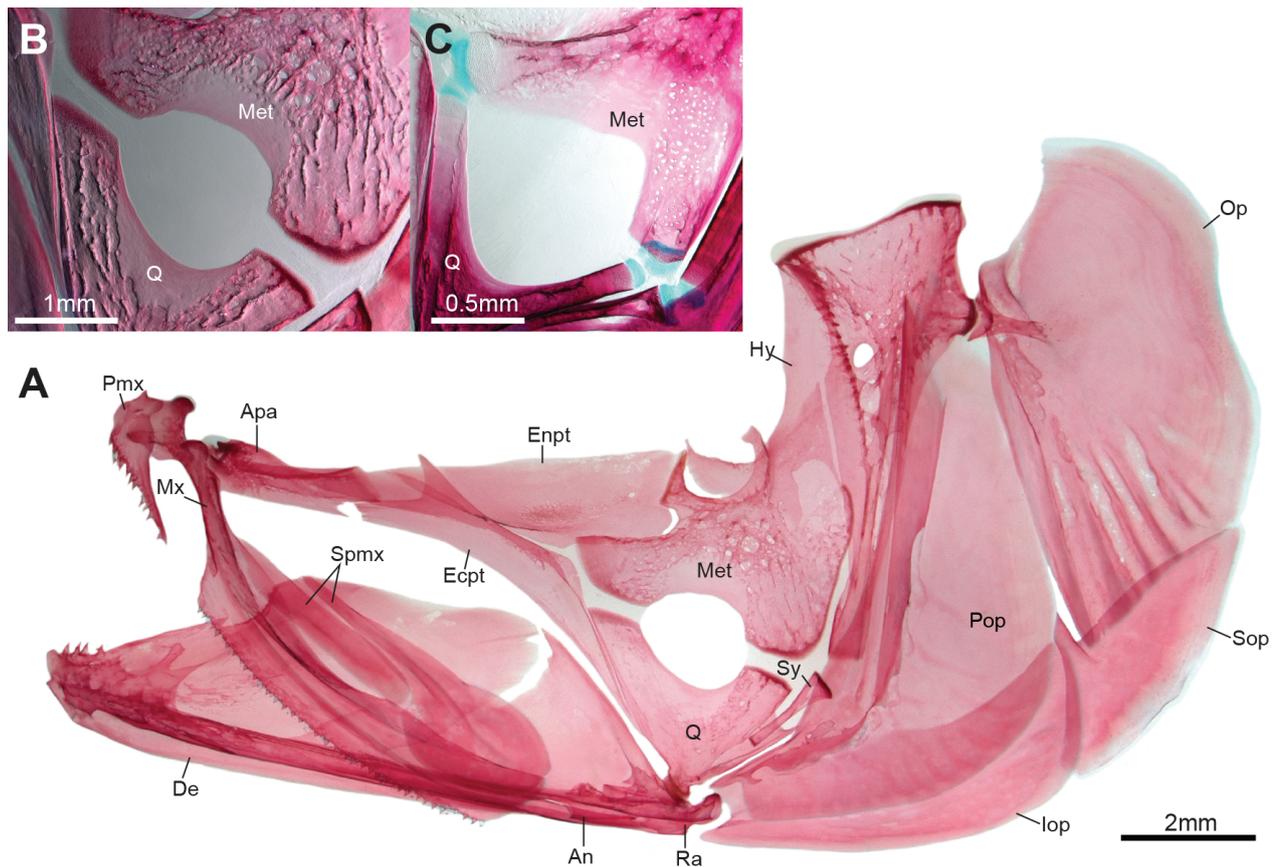


Figure 14. Metapterygoid-quadrate fenestra (QMF) in cleared and double stained Clupeidae. **A** Hyopalatine arch, jaws and opercular series of *Alosa sapidissima*, TCWC 5264.01, 63.7 mm SL. **B** Close up of QMF, same specimen as in **A**. **C** QMF of *Brevoortia patronus*, TCWC 19718.02, 51.0 mm SL. Abbreviations: An, angulo-articular; Apa, autopalatine; De, dentary; Ecpt, ectopterygoid; Enpt, endopterygoid; Hy, hyomandibular; Iop, interopercle; Met, metapterygoid; Mx, maxilla; Op, opercle; Pmx, premaxilla; Pop, proopercle; Q, quadrate; Ra, retroarticular; Sop, subopercle; Spmx, supramaxilla; Sy, symplectic.

Although widespread in the Characiformes, the QMF has been reported as absent in adults not only in some members of the family Lebiasinidae (see above, and Weitzman 1964; Vari 1995), but also in some Chilodontidae and Curimatidae (e.g., *Curimatopsis*, Vari 1989), and Anostomidae, such as *Leporinus* (Roberts 1969), *Anostomus* and *Gnathodolus* (Winterbottom 1980). The development of the hyopalatine arch in most of these taxa is currently unknown. Further study may be able to clarify whether absence of a QMF in the adult is the result of closure of the fenestra during development, as in *Lebiasina*, or true absence of the QMF from all developmental stages, as in *Pyrrhulina*.

Notwithstanding the absence of a QMF in some derived characiforms, the fact that it is present in the African distichodontids, citharinids, alestids, hepsetids and in members of most South American characiform families, indicates that it is a homologous structure in Characiformes and at the same time a convincing synapomorphy of this order of otophysan Ostariophysi. Based on the significant differences in development of the QMF in characiforms and in cobitid cypriniforms we conclude that the QMFs of the two taxa are not homologous. This is further supported by the phylogenetic position of the two groups, with cobitids deeply embedded within not only Cypriniformes but also Cobitoidei, and we concur

with Sawada (1982) who suggested that the cobitid QMF is a character restricted to this group of Ostariophysi.

Among clupeiforms, a QMF has been illustrated by Ridewood (1905) in *Alosa*, and subsequently reported also in *Brevoortia* (Gosline 1975) and *Jenkinsia* (Arratia and Schultze 1991). Its presence has been confirmed by us in *Alosa* and *Brevoortia* (Fig. 14). Unfortunately nothing seems to be known about the development of this structure in these clupeoids, but absence of a QMF in *Denticeps* and most other clupeomorphs and all anotoophysan Ostariophysi suggests that the QMF in these taxa is not homologous to the QMF in characiforms or cobitids. Further study of this structure in clupeoids is warranted.

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