

Development of the muscles associated with the mandibular and hyoid arches in the Siberian sturgeon, *Acipenser baerii* (Acipenseriformes: Acipenseridae)

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Abstract

The skeleton of the jaws and neurocranium of sturgeons (Acipenseridae) are connected only through the hyoid arch. This arrangement allows considerable protrusion and retraction of the jaws and is highly specialized among ray-finned fishes (Actinopterygii). To better understand the unique morphology and the evolution of the jaw apparatus in Acipenseridae, we investigated the development of the muscles of the mandibular and hyoid arches of the Siberian sturgeon, *Acipenser baerii*. We used a combination of antibody staining and formalin-induced fluorescence of tissues imaged with confocal microscopy and subsequent three-dimensional reconstruction. These data were analyzed to address the identity of previously controversial and newly discovered muscle portions. Our results indicate that the Anlagen of the muscles in *A. baerii* develop similarly to those of other actinopterygians, although they differ by not differentiating into distinct muscles. This is exemplified by the subpartitioning of the *m. adductor mandibulae* as well as the massive *m. protractor hyomandibulae*, for which we found a previously undescribed portion in each. The importance of paedomorphosis for the evolution of Acipenseriformes has been discussed before and our results indicate that the muscles of the mandibular and the hyoid may be another example for heterochronic evolution.

KEYWORDS

Actinopterygii, cranial muscles, paedomorphosis, three-dimensional reconstruction

1 | INTRODUCTION

Gnathostome jaws are considered a key innovation in craniate evolution (Kuratani, 2004; Mallatt, 1996), and the endoskeletal components of the jaws are considered to be evolutionary derivatives of the viscerocranium. In accordance with this hypothesis, the first visceral arch forms the mandibular arch (Goodrich, 1930), the second visceral arch forms the hyoid arch, and the five posterior visceral arches form the branchial arches. Elements of both the mandibular and the hyoid arch form the suspensorium, a functional complex supporting suction feeding in aquatic gnathostomes (e.g., Lauder, 1985). Different configurations of this basic scheme are present in extant taxa, yielding either rather stable upper jaws, by fusion of the upper jaw with the neurocranium as in chimeras, lungfishes and tetrapods (Schultze, 1986), or

highly mobile jaws, and suspensoria that allow widening of the buccal cavity and/or jaw protrusion (Bemis, Findeis, & Grande, 1997; Lauder, 1980a). Even within these basic modes many different forms have evolved and the skeletal elements and the associated muscles are highly modified (e.g., Datovo & Vari, 2013; Lauder, 1980a, 1980b; Lautenschlager, Gill, Luo, Fagan, & Rayfield, 2017).

In extant actinopterygian fishes, the upper jaw usually articulates directly with the ethmoid region of the neurocranium as well as the anterior portion of the suspensorium. The suspensorium also articulates with the ethmoid region, but is additionally linked to the otic region of the neurocranium via the hyoid arch (Lauder, 1980a). This highly mobile feeding apparatus is one of the main drivers that has led to the evolutionary success of actinopterygian fishes which accounts for nearly half of all extant craniate species (Wiens, 2015). Most of the extant species

TABLE 1 List of specimens used for histology or whole-mount clsm imaging with developmental stage and approximate total length

Stage	34	35	36	37	38	39	40	41	42	43	44	45	
Total length in mm	8	9	10	11	12	13	14	15	16	17	18	20	>
	# of specimens												
VIMS 35544			1		2	2			1	1			1
VIMS 35545			1	3	2	4	3	2	2	2	3	3	1
VIMS 35546	1	1	2	2		3	2	2	2	1	1		1
VIMS 35547	1	1	1	1		3	1	1	2	1	1		
Sections (Azan)							1	1	1	1			1
Sections (Kernechtrot)			1	1	1		1				1		1

Specimens catalogued under VIMS 35544 are stained with anti-acetylated alpha-tubulin (Sigma, T6793) and anti-desmin (Monosan, PS031). Specimens catalogued under VIMS 35545 are stained with 12/101 (Developmental Studies Hybridoma Bank). Specimens catalogued under VIMS 35546 are stained with collagen II (Developmental Studies Hybridoma Bank) and anti-desmin (Monosan, PS031). Specimens catalogued under VIMS 35547 are translucent and fluorescent due to formaldehyde fixation.

belong to Teleostei (Nelson, Grande, & Wilson, 2016) and fewer than 50 extant species are found across four orders (Polypteriformes, Acipenseriformes, Lepisosteiformes, Amiiformes) that are referred to as the basal actinopterygians (Gardiner, Schaeffer, & Masserie, 2005). Various hypotheses on the relationships among these orders have been discussed (reviewed by Sallan, 2014), although it is generally agreed that the Polypteriformes (Cladistia) are the sister group of all other extant actinopterygians (Betancur-R et al., 2013; Patterson, 1982). The group formed by Teleostei and their sister group, the Holostei (which comprise Lepisosteiformes and Amiiformes, and their fossil relatives; Grande, 2010) is known as Neopterygii. The Acipenseriformes (Chondrostei), the sturgeons and their relatives, are placed between Cladistia and Neopterygii, and together with the latter form the Actinopteri.

Acipenseriformes comprise 27 extant species in two families, Polyodontidae and Acipenseridae (Bemis et al., 1997). Their lifestyle ranges from piscivorous (*Huso* and *Psephurus*) (Chenhan & Yongjun, 1988; Vecsei, Sucui, & Peterson, 2002) and planktotrophic (*Polyodon*) (Rosen & Hales, 1981) to benthic suction feeders (*Acipenser*, *Pseudoscaphirhynchus*, *Scaphirhynchus*) (Bemis et al., 1997; Carroll & Wainwright, 2003). All Acipenseriformes, however, share a uniquely derived mode of jaw suspension that, with the exception of *Polyodon* (Grande & Bemis, 1991), allows extensive jaw protrusion (Bemis et al., 1997; Miller, 2005). The morphology of Acipenseriformes has been studied intensely since the late 19th and early 20th century (Parker, 1881; Pehrson, 1944; van Wijhe, 1882). To date, special emphasis has been put on their skeletal structures (Dillman & Hilton, 2015; Findeis, 1993, 1997; Hilton, Grande, & Bemis, 2011), especially the large dermal scutes of sturgeons (Leprévost, Azaïs, Trichet, & Sire, 2016), the development of the pectoral girdle (Dillman & Hilton, 2015), and the development of the head skeleton (e.g., de Beer, 1925; Jollie, 1980; Sewertzoff, 1928; Warth, Hilton, Naumann, Olsson, & Konstantinidis, 2017). Soft tissues have been studied to a lesser extent (Edgeworth, 1929; Sewertzoff, 1928; Stengel, 1962), in part because the study of soft tissue generally has been limited by methodological difficulties (Hilton, Schnell, & Konstantinidis, 2015; Konstantinidis et al., 2015).

In acipenseriforms, the mandibular arch skeleton is not connected to the neurocranium and only suspended via the hyoid arch (Gregory,

1904). This specialized hyostylic linkage of the palatoquadrate with the neurocranium is unique among osteichthyans but evolved convergently in some elasmobranchs (Wilga, 2005). In both taxa, this configuration allows an extreme protrusion of the upper jaw and plays an eminent role in suction feeding (Carroll & Wainwright, 2003). Subsequently, the musculoskeletal system of the mandibular and hyoid arch is highly derived in acipenseriforms (Arratia & Schultze, 1991; Véran, 1988; Warth et al., 2017). Despite their highly derived jaw suspension, the muscles associated with the mandibular and hyoid arches are considered to be rather simplified in acipenseriforms (Edgeworth, 1935) resulting in highly different feeding mechanics (Bemis, 1987; Bemis et al., 1997; Carroll & Wainwright, 2003). Sewertzoff (1928) and Edgeworth (1929) studied the early anlagen of the mandibular and hyoid arches and their differentiation to interpret their homology across taxa. Based on new methods and techniques, several recent studies (e.g., Datovo & Vari, 2013; Konstantinidis & Harris, 2011; Konstantinidis et al., 2015; Noda, Miyake, & Okabe, 2017) show alternative homology assessments of muscle subdivision in various groups of actinopterygian fishes. Herein, we studied the development of the muscles of the mandibular and hyoid arches of the Siberian sturgeon, *Acipenser baerii* Brandt 1869, using antibody staining, microcomputed tomography, and confocal microscopy to test different hypotheses of homology of the sturgeon jaw musculature based on ontogenetic information.

2 | MATERIALS AND METHODS

All specimens used in this study originated from artificial spawning of broodstock of *Acipenser baerii* Brandt 1869 at the "Fischzucht Rhönfor-elle" (Gersfeld, Hessen, Germany) between November 2013 and November 2016. Eggs and larvae were raised and treated as listed in Warth et al. (2017). Specimens were staged according to the descriptions of *Acipenser gueldenstaedtii* by Ginsburg and Dettlaff (1991) and Schmalhausen (1991). Approximate total length (TL) of formalin-fixed specimens is indicated for each stage in Table 1 and an overview of the developmental stages is given in Figure 1. Antibody staining was conducted according to standard antibody protocols using primary

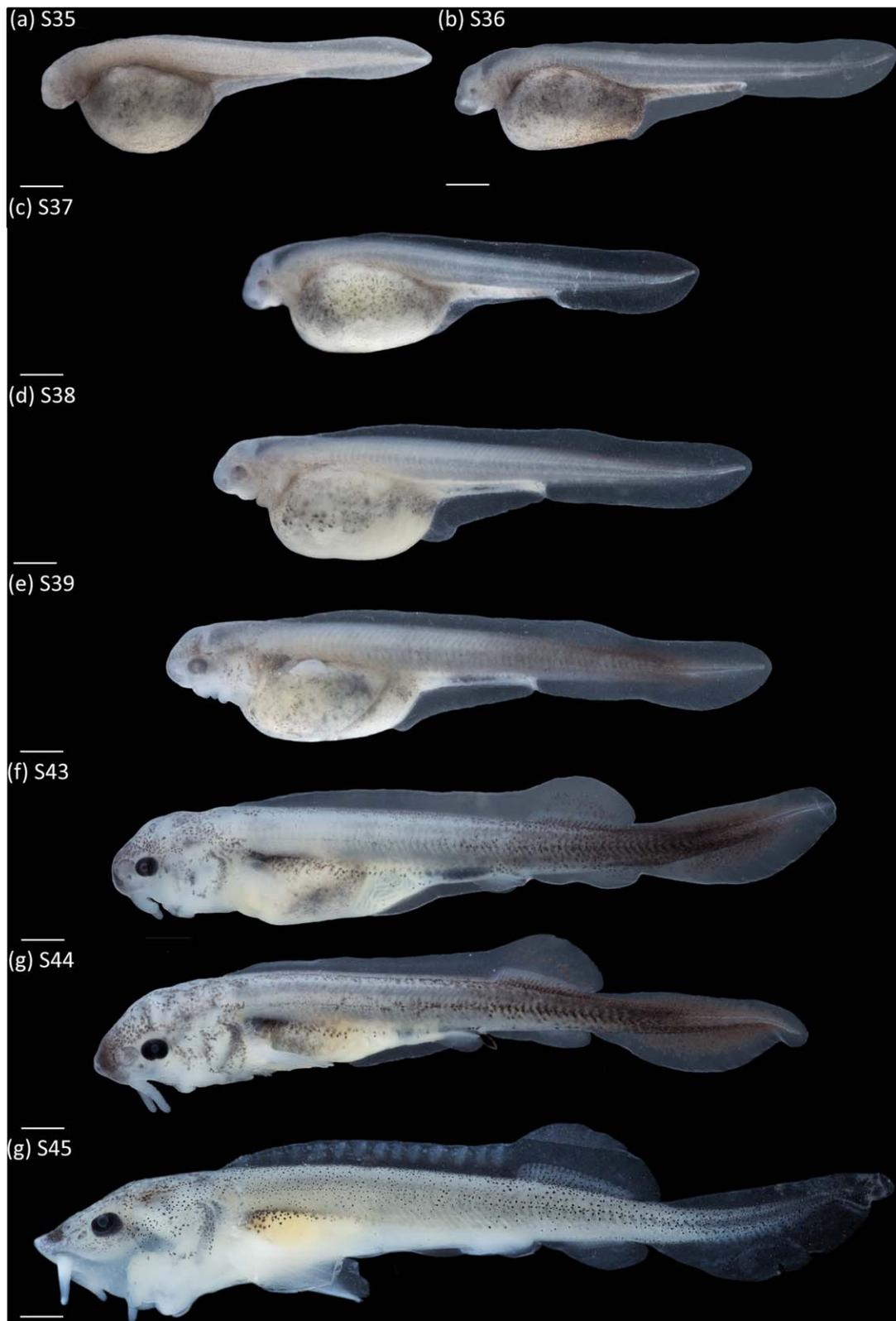


FIGURE 1 *Acipenser baerii*, developmental stages in lateral view showing transformation from pre-hatchling to feeding larva. Staging follows Ginsburg and Dettlaff (1991) and Schmalhausen (1991). Scale is 1 mm

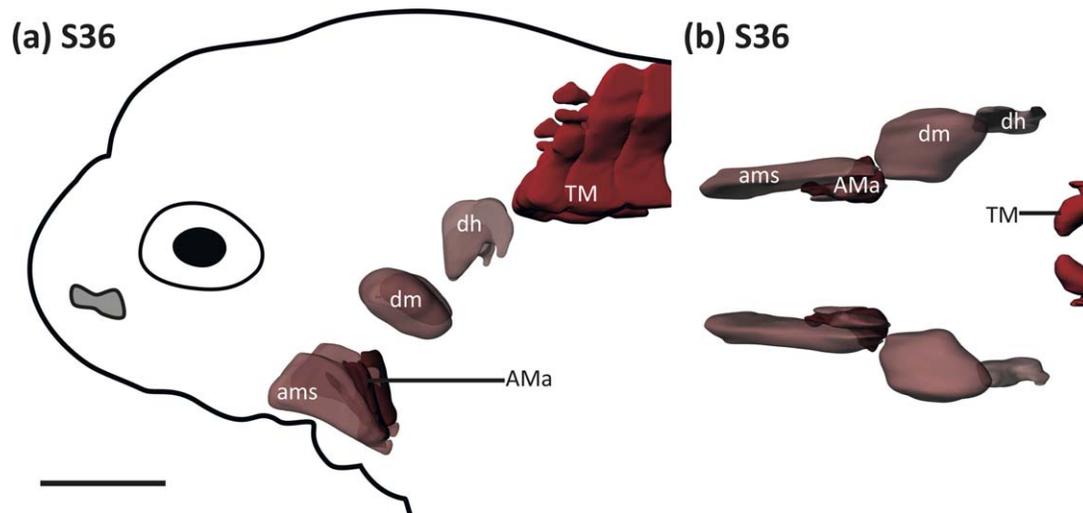


FIGURE 2 *Acipenser baerii*, mandibular and hyoid arch muscle anlagen, at Stage 36 (VIMS 35546). Anlagen of the dorsal mandibular and hyoid constrictors are undifferentiated as first muscle fibers differentiate in the anlage of the *m. adductor mandibulae*. Trunk muscles are well developed. Reconstructions based on clsm dataset. Muscles in red, mandibular arch muscles in darker tone than hyoid muscles undifferentiated anlagen are transparent. (a), Stage 36, lateral view, scale is 0.5 mm. (b), Stage 36, ventral view. Abbreviations: ams, anlage of symphyseal portion of *m. adductor mandibulae*; AMa, articular portion of *m. adductor mandibulae*; dh, anlage of dorsal hyoid constrictor; dm, anlage of dorsal mandibular constrictor; TM, trunk musculature

antibodies of 12/101 (Developmental Studies Hybridoma Bank), anti-acetylated alpha-tubulin (Sigma, T6793), anti-desmin (Monosan, PS031), and anti-collagen II (Developmental Studies Hybridoma Bank) and fluorescent secondary antibodies (Alexa 488 & Alexa 568, Invitrogen, Carlsbad, California). Imaging of fluorescent samples was conducted with a Zeiss LSM 510 confocal laser-scanning microscope (clsm).

For microcomputed tomography (μ CT), specimens were treated with iodine to enhance contrast in soft tissues according to (Gignac et al., 2016). Tomography was conducted using a phoenix nanotom (general electric, Boston, MA). Raw clsm and μ CT-datasets were cropped and adjusted with Fiji (Schindelin et al., 2012), before reconstruction in Amira 5.4 (Visage Imaging, Berlin, Germany). Datasets were exported from Amira and further processed either in MAYA (Autodesk, San Rafael, CA) for smoothing and simplification of surface renderings or VGStudio Max (Volume Graphics, Germany) for processing of volume renderings.

Histological sections were conducted from formalin-fixed and paraffin-embedded specimens at 7 μ m section thickness and further stained according to the Kernechtrot-Kombinationsfärbung technique (Anken & Kappel, 1992) and Azan-Heidenhain (Romeis, 1989).

For dissection of adult sturgeons, carcasses were collected at the hatchery and stored frozen. Prior to dissection specimens were thawed for 24 hr and either fixed with 10% Histofix (Roth, Karlsruhe, Germany) for 24 hr or dissected immediately. Pictures were taken with a Nikon D7000 and an attached AF Micro Nikkor 60 mm 2.8 lens.

2.1 | Specimens examined

Material used for clsm analysis is listed in Table 1. Additionally, cleared and stained material as listed in Warth et al. (2017) was consulted regarding skeletal anatomy and we dissected a specimen of *Acipenser*

gueldenstaedtii (female, 1,280 mm TL) and *Acipenser baerii* (male, 1,200 mm TL); specimens were not retained.

3 | RESULTS

3.1 | Stage 36 (Figure 2)

At this stage, hatching occurs in most embryos. The head and trunk are situated on top of a large rounded yolk sac and a continuous larval fin fold surrounds the trunk. The s-shaped heart tube is situated at the anterior border of the yolk sac and anteroventral to the head. The heartbeat is apparent. The primary mouth opening has not yet broken through and the gill clefts are absent. The trunk muscles are well developed and the animals can swim short distances on external stimulation.

The first skeletal elements appear as small aggregations of chondrocytes of the *trabecula cranii* and the otic capsule (see figure 4a in Warth et al., 2017). No obvious chondrocytes are present in the viscerocranium. The anlage of the *m. adductor mandibulae* is present posteroventral to the eye. This anlage is kidney-shaped in ventral view and cuneiform in lateral view. Within the anlage, the first muscle fibers are differentiated in the articular portion (Figure 2a). Dorsoposteriorly, the undifferentiated anlagen of the dorsal constrictors of the mandibular and the hyoid arch are present. The former is much larger than the latter (Figure 2b).

3.2 | Stage 37 (Figure 3a–c)

At this stage, the hatchlings are more elongate and the yolk sac is more ovoid than in the previous stage. Anlagen of the four barbels are present anterior to the mouth opening which has now broken through. On the dorsolateral part of the yolk sac, the small anlage of the pectoral fin is present.

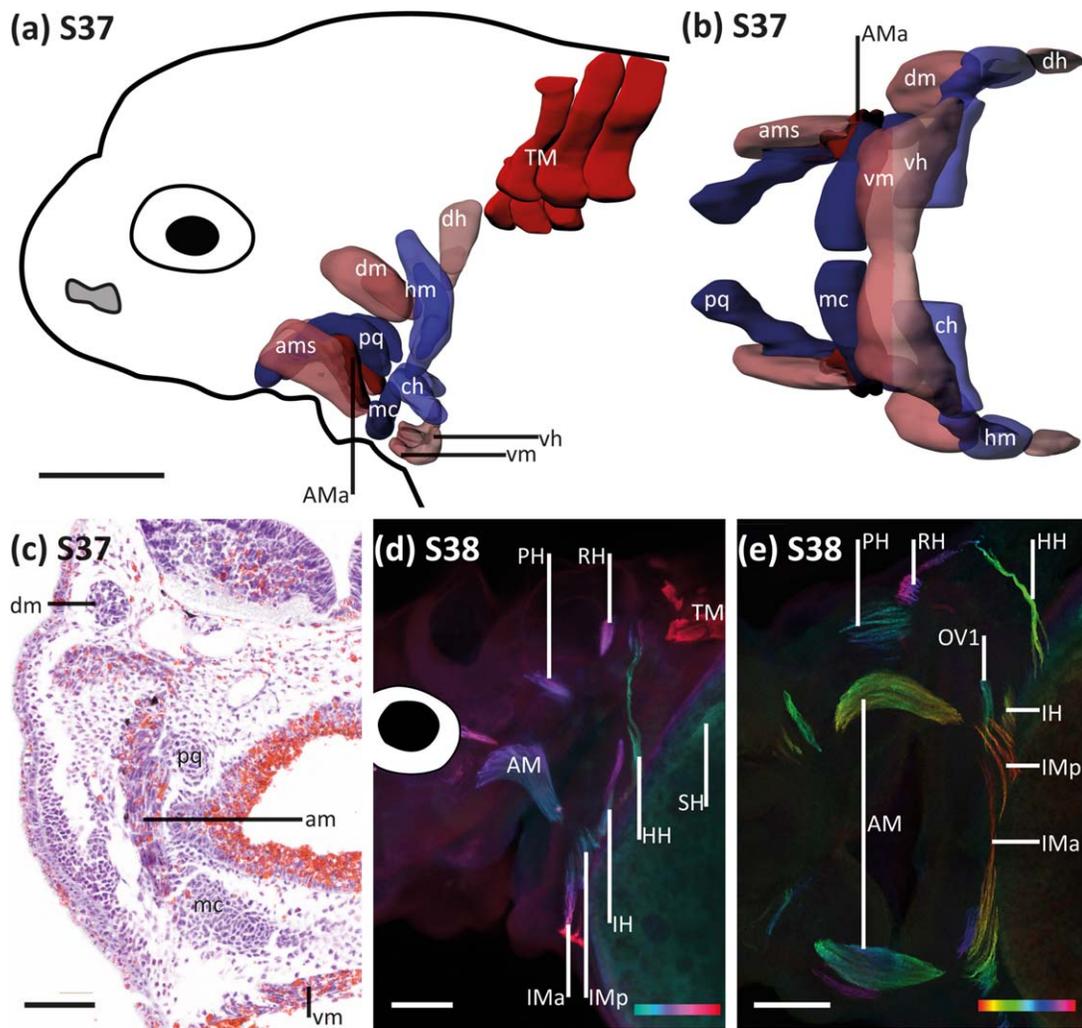


FIGURE 3 *Acipenser baerii*, mandibular and hyoid arch anlagen, at Stage 37 (VIMS 35546) and at Stage 38 (VIMS 35545). First anlagen of skeletal elements and ventral mandibular and hyoid constrictors appear at Stage 37 and muscle fibers are formed at Stage 38. Reconstruction based on clsm dataset. Muscles in red, mandibular arch muscles in darker tone than hyoid muscles. Undifferentiated anlagen are transparent. (a) Stage 37, reconstruction, lateral view, scale is 0.5 mm. (b) Stage 37, reconstruction, ventral view. (c) Stage 37, histological section (uncatalogued) at the level of the mandibular arch, scale is 0.1 mm. (d) Stage 38, specimen stained with 12/101 antibody, color coded projection of a lateral view, showing depth in different colors as indicated by scale in lower right corner, scale is 0.2 mm. (e) Stage 38, specimen stained with 12/101 antibody, color coded projection of ventral view, showing depth in different colors as indicated by scale in lower right corner, scale is 0.2 mm. Abbreviations: AM, *m. adductor mandibulae*; am, anlage of *m. adductor mandibulae*; AMa, articular portion of *m. adductor mandibulae*; ams, anlage of symphyisial portion of *m. adductor mandibulae*; ch, anlage of anterior ceratohyal cartilage; dh, anlage of dorsal hyoid constrictor; dm, anlage of dorsal mandibular constrictor; HH, *m. hyohyoideus*; hm, anlage of hyomandibula; IH, *m. interhyoideus*; IMa, *m. intermandibularis anterior*; IMp, *m. intermandibularis posterior*; mc, anlage of Meckel's cartilage; OV1, *m. obliquus ventralis 1*; PH, *m. protractor hyomandibulae*; pq, anlage of palatoquadrate cartilage; RH, *m. retractor hyomandibulae*; SH, *m. sternohyoideus*; SO, subopercle; TM, trunk musculature; vh, anlage of ventral hyoid constrictor; vm, anlage of ventral mandibular constrictor

The anlage of the *m. adductor mandibulae* is more pronounced than in the previous stage. Its dorsal part is broad and overlies the anlage of the palatoquadrate cartilage, forming a symphyisial portion that is yet undifferentiated. Ventrally, it tapers to Meckel's cartilage (Figure 3a). The anlagen of the palatoquadrate cartilage and Meckel's cartilage develop laterally to medially, and at this stage they are separated from their antimeres (Figure 3b). Collagen II labeling is restricted to the very lateral part of the mouth opening. Ventral to this, the common muscle anlage of the ventral constrictors of the mandibular and hyoid arches is present but muscle fibers are not yet differentiated.

3.3 | Stage 38 (Figure 3d,e)

The anlagen of the barbels extended, forming small outgrowths anterior to the mouth opening. Gill anlagen are present on the posterior margin of the opercular flap giving it a serrated appearance. The pectoral fin has grown to a membranous paddle-like structure.

The symphyisial portion of the *m. adductor mandibulae* has started to differentiate (Figure 3d), and fibers grow medially on the dorsal surface of the anlage of the palatoquadrate cartilage. Ventral to this, the first muscle fibers are present in the ventral constrictors of the mandibular arch. The

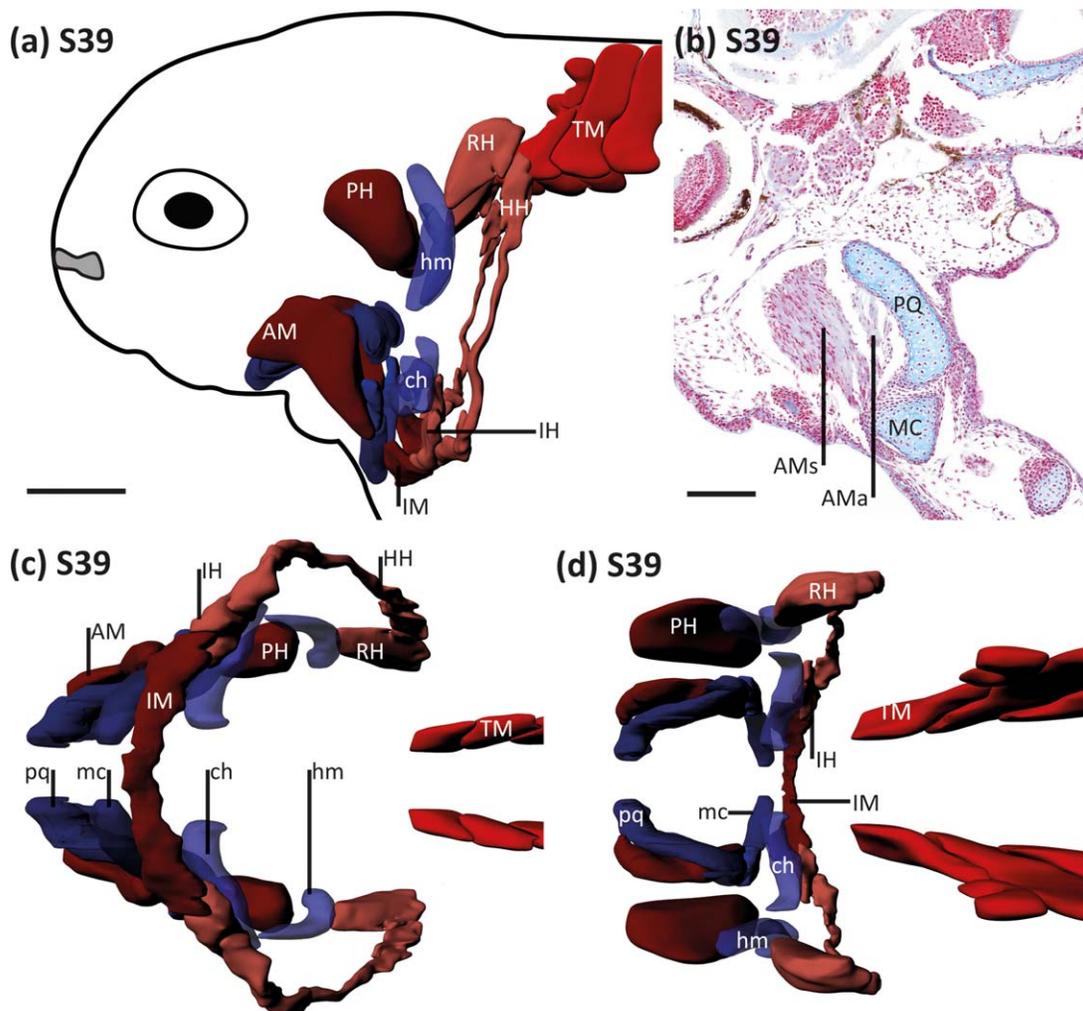


FIGURE 4 *Acipenser baerii*, mandibular and hyoid arch muscles and skeleton, at Stage 39 (VIMS 35546). Differentiation of all muscle anlagen proceeds; two *m. adductor mandibulae* portions are present and a thin *m. hyohyoideus* spans the opercular flap. (a) Stage 39, reconstruction, lateral view, scale is 0.5 mm. (b) Stage 39, parasagittal section (uncatalogued), scale is 0.15 mm. (c) Stage 39, reconstruction, ventral view. (d) Stage 39, reconstruction, dorsal view. Abbreviations: AM, *m. adductor mandibulae*; AMa, articular portion of *m. adductor mandibulae*; AMs, symphyseal portion of *m. adductor mandibulae*; ch, anlage of ceratohyal; HH, *m. hyohyoideus*; hm, anlage of hyomandibula; IH, *m. interhyoideus*; IM, *m. intermandibularis*; mc, anlage of Meckel's cartilage; MC, Meckel's cartilage; PH, *m. protractor hyomandibulae*; pq, anlage of palatoquadrate; PQ, palatoquadrate cartilage; RH, *m. retractor hyomandibulae*; TM, trunk musculature

m. intermandibularis is separated into anterior and posterior portions (Figure 3e). The anterior portion is continuous between the left and right sides of the lower jaw. The posterior portion, however, is separated by a gap in the midline and connected to the *m. interhyoideus*. Posteriorly, the *m. hyohyoideus* is present in the opercular flap (Figure 3d,e). It is neither connected to the *mm. intermandibularis* and *interhyoideus* ventrally nor to the *m. retractor hyomandibulae* dorsally. Differentiation of the *mm. protractor hyomandibulae* and *retractor hyomandibulae* has started and the thin and faint muscles are situated anterior to the myomeres of the trunk.

3.4 | Stage 39 (Figure 4)

The larvae swim actively at this stage and positive phototaxis can be observed. Gill filaments extend from the opercular cleft. The yolk sac is still large and within the larval fin fold, median fins have begun to form.

The symphyseal portion of the *m. adductor mandibulae* is now further differentiated and enlarged anteromedially (Figure 4a). It follows the middle portion of the s-shaped palatoquadrate cartilage and its tapered ventral end is slightly recurved and encompasses Meckel's cartilage before inserting to its anterolateral aspect (Figure 4b). The *m. intermandibularis* originates from the lateral part of Meckel's cartilage from where its course is directed medially. The skeletal hyoid arch elements are faint anlagen and no collagen II signal is apparent yet. The *m. hyohyoideus* spans in a dorsoventral direction in the opercular flap, with wider ventral and dorsal ends (Figure 4a). Its ventral end is in close proximity to the *m. interhyoideus* (Figure 4c,d). Close to its dorsal end, a large *m. retractor hyomandibulae* originates from the otic capsule, which at this stage is delineated by a thin but intensely collagen II-labeled area along its ventral surface. From that point, the *m. retractor hyomandibulae* tapers anteroventrally toward the undifferentiated anlage of the hyomandibula. Its dorsoposterior part is extended and connected

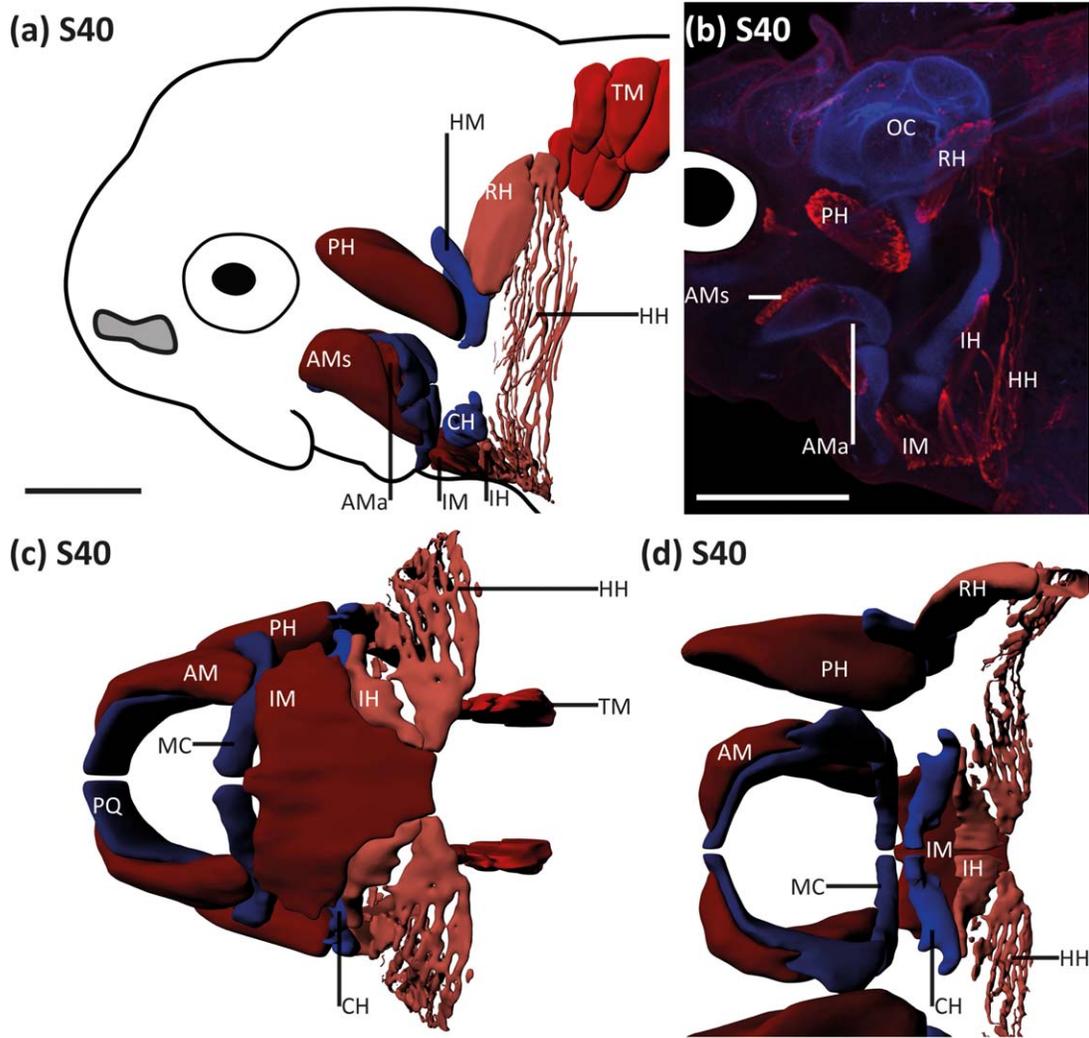


FIGURE 5 *Acipenser baerii*, mandibular and hyoid arch muscles and skeleton, at Stage 40 (VIMS 35546). The *m. intermandibularis* is expanded and several fibers of the *m. hyohyoideus* are present while the dorsal constrictor muscles are more massive than previously. (a) Stage 40, reconstruction, lateral view, scale is 0.5 mm. (b) Stage 40, maximum intensity projection of collagen II/desmin stained specimen, lateral view, scale is 0.5 mm. (c) Stage 40, reconstruction, ventral view. (d) Stage 40, reconstruction, dorsal view. Abbreviations: AMa, articular portion of *m. adductor mandibulae*; AMs, symphyseal portion of *m. adductor mandibulae*; CH, anterior ceratohyal cartilage; HH, *m. hyohyoideus*; HM, hyomandibular cartilage; IH, *m. interhyoideus*; IM, *m. intermandibularis*; MC, Meckel's cartilage; OC, otic capsule; PH, *m. protractor hyomandibulae*; PQ, palatoquadrate cartilage; RH, *m. retractor hyomandibulae*; TM, trunk musculature

to the *m. hyohyoideus*. The *m. protractor hyomandibulae* has increased in size as muscle fiber differentiation in the anlage proceeds.

3.5 | Stage 40 (Figure 5)

The pelvic fins are present as small skin folds lateral to the median larval fin-fold. A large nasal opening is present on each side of the head, and teeth are formed on the dentary. Respiratory movements of the jaws can be observed.

The dorsomedial edge of the symphyseal portion of the *m. adductor mandibulae* is further extended medially and covers the dorsal part of the well-developed palatoquadrate cartilage. Ventrally, the symphyseal portion of the *m. adductor mandibulae* inserts on the anterodorsal aspect of Meckel's cartilage (Figure 5a,b). In the posterior part, close to the jaw articulation, the articular portion of the *m. adductor mandibulae*

connects the posteroventral part of the palatoquadrate cartilage to the dorsal margin of Meckel's cartilage (Figure 5a). The *m. intermandibularis* spreads posteriorly as a thin sheet of lateromedially directed muscle fibers and covers the main part of the *m. interhyoideus* (Figure 5c). In the posteromedial part, the *m. intermandibularis* and the *m. interhyoideus* have merged together but toward its origin from the posterolateral process of the anterior ceratohyal cartilage, the *m. interhyoideus* is well separated. Posteriorly, the *m. hyohyoideus* attaches to the *m. interhyoideus* (Figure 5d) and extends dorsally in the opercular flap as separated muscle fibers. Not all fibers of the *m. hyohyoideus* cross the entire distance to the otic capsule. Instead, they end freely in the connective tissue where new fibers emerge (Figure 5b). At the dorsal origin, it is joined with the *m. retractor hyomandibulae* that now inserts on the posterior aspect of the hyomandibula. The hyomandibula at this stage is an elongate slightly curved cartilage. It articulates with a facet of the otic

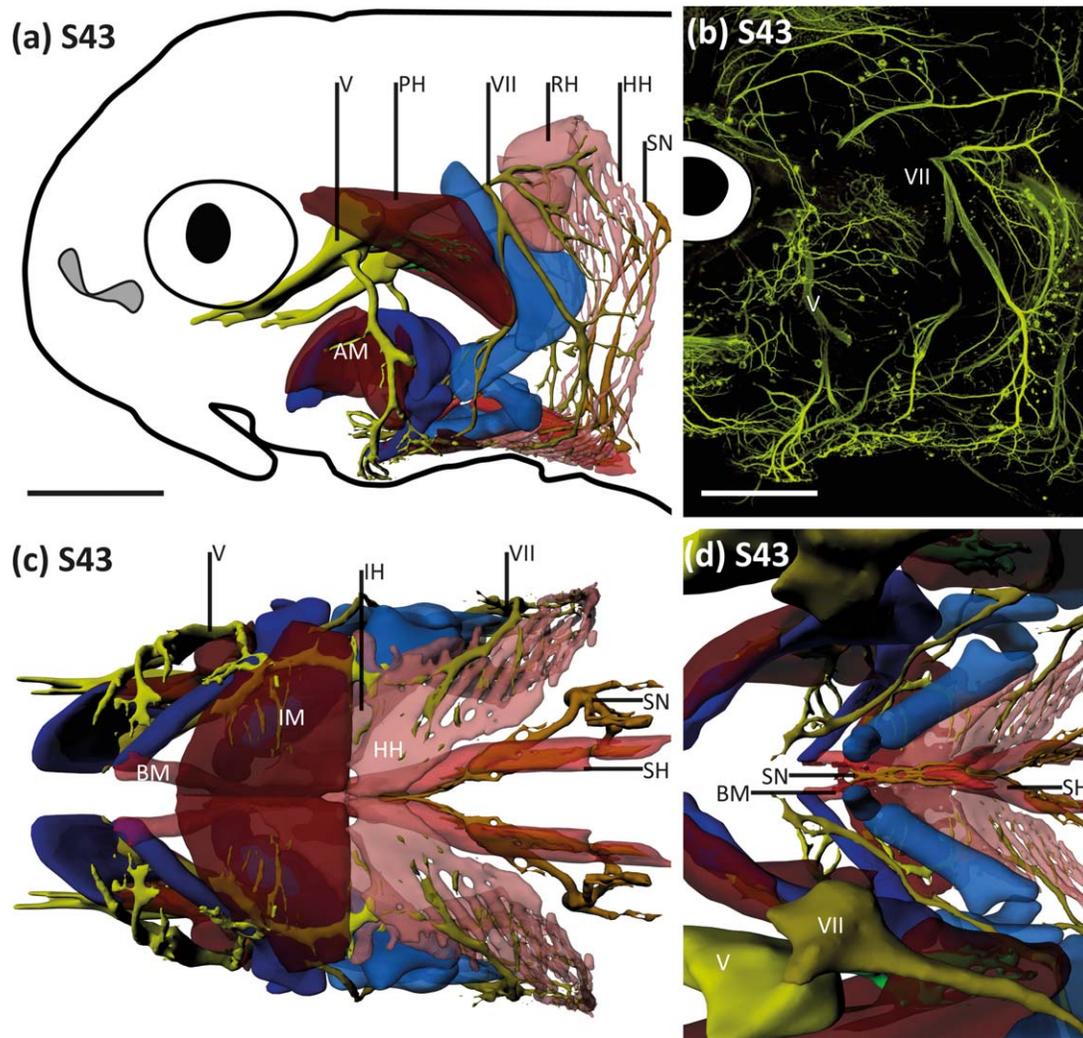


FIGURE 6 *Acipenser baerii*, mandibular and hyoid arch muscles and skeleton, at Stage 43 (VIMS 35544). Innervation of the cranial and hypobranchial muscles by the trigeminal, facial and the hypoglossal nerve respectively. (a) Stage 43, lateral view, scale is 0.5 mm. reconstruction, lateral view, scale is 0.5 mm. (b) Stage 43, maximum intensity projection of tubulin stained specimen, lateral view, scale is 0.5 mm. (c) Stage 43, reconstruction, ventral view. (d) Stage 43, reconstruction, dorsal view. Abbreviations: AM, *m. adductor mandibulae*; BM, *m. branchiomandibularis*; IH, *m. interhyoideus*; HH, *m. hyohyoideus*; IM, *m. intermandibularis*; PH, *m. protractor hyomandibulae*; RH, *m. retractor hyomandibulae*; SH, *m. sternohyoideus*; SN, hypoglossal nerve; V, trigeminal nerve; VII, facial nerve

capsule dorsally but does not contact a skeletal element ventrally as the interhyal has not formed yet. The *m. protractor hyomandibulae* inserts on the anterior surface of the hyomandibula and stretches anterodorsally.

3.6 | Stage 41 (not illustrated)

The nasal opening is divided by outgrowths of its dorsal and ventral margin into an anterior and a posterior opening; these outgrowths are not yet fused at this stage. Formation of the rostrum and head elongation has started. The barbels grow to small rods.

In comparison to the previous stage the symphyseal portion of the *m. adductor mandibulae* and the underlying palatoquadrate cartilage have grown medially and now almost meet their antimeres in the midline. The insertion of the symphyseal portion on Meckel's cartilage is further extended medially. The *mm. intermandibularis posterior*,

interhyoideus and *hyohyoideus* join in a common raphe in the ventral midline, although they are clearly distinct muscles, particularly toward their respective sites of origin. Underneath this sheet of muscles, which covers the viscerocranium ventrally, the *m. branchiomandibularis* stretches in an anteroposterior direction and inserts on the posterior surface of Meckel's cartilage. Posteriorly, it is not attached to a skeletal element but reaches as far back as to the pericardium. The hyomandibula is now connected to the mandibular arch via the interhyal.

3.7 | Stage 43 (Figure 6)

The nares are separated into anterior and posterior openings by fusion of dorsal and ventral outgrowths of skin. The ventral fin has enlarged and is clearly visible lateral to the larval fin fold. The yolk sac has shrunk considerably but the anterior trunk region is still swollen ventrally.

The symphyseal portion of the *m. adductor mandibulae* inserts with two distinct sites on Meckel's cartilage. The superficial fibers insert on

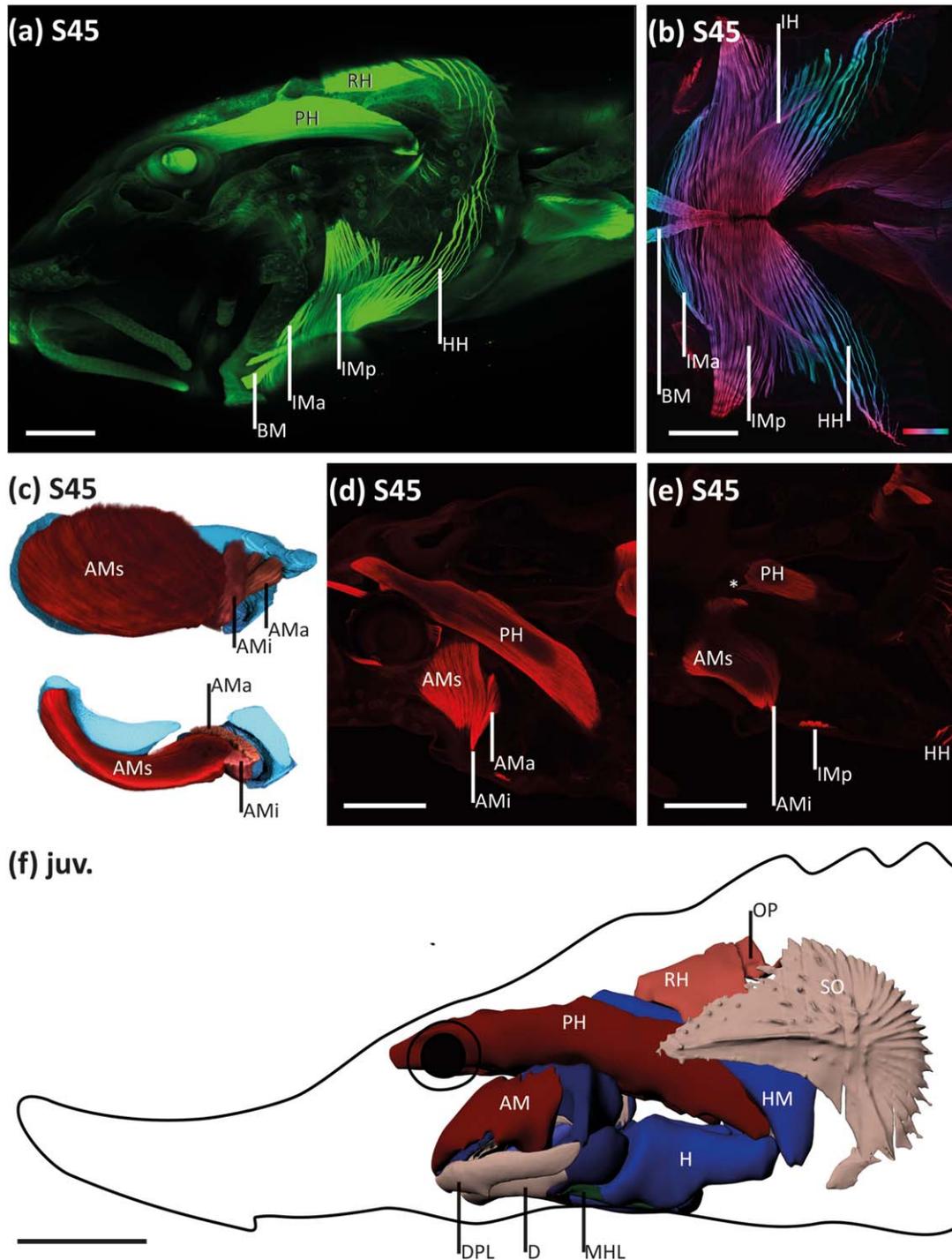


FIGURE 7 *Acipenser baerii*, mandibular and hyoid arch muscles and skeleton, at Stage 45 (VIMS 35545) and juvenile stage. Visualization of the separate ventral constrictors and the subpartitions of the *m. adductor mandibulae* and the *m. protractor hyomandibulae*. (a) Stage 45, maximum intensity projection, 12/101 antibody stained specimen, lateral view, scale is 0.5 mm. (b) Stage 45, color coded projection of 12/101 stained specimen, showing depth in different colors as indicated by scale in lower right corner, ventral view, scale is 0.5 mm. (c) Stage 45, reconstructions of *m. adductor mandibulae*, dorsolateral view. (d) Stage 45, optical section of specimen stained with 12/101 antibody, scale is 0.5 mm. (e) Stage 45, optical section of same specimen as shown in e but in a deeper layer, scale is 0.5 mm. (f) reconstruction of juvenile stage, lateral view, ventral constrictors omitted, scale is 5 mm. Abbreviations: AM, *m. adductor mandibulae*; AMa, articular portion of *m. adductor mandibulae*; AMi, intermediate portion of *m. adductor mandibulae*; AMs, symphyseal portion of *m. adductor mandibulae*; BM, *m. branchiomandibularis*; D, dentary; DPL, dermopalatine; H, interhyal cartilage; HH, *m. hyohyoideus*; HM, hyomandibular cartilage; IH, *m. interhyoideus*; IMa, *m. intermandibularis anterior*; IMp, *m. intermandibularis posterior*; MHL, mandibulohyoid ligament; OP, *m. adductor operculi*; PH, *m. protractor hyomandibulae*; RH, *m. retractor hyomandibulae*; SO, subopercle; *muscle fibers of *m. protractor hyomandibulae*

the anterodorsal aspect and the deeper fibers insert further posteromedially. The *m. intermandibularis posterior* and the *m. interhyoideus* both receive their innervation from the trigeminal as well as the facial nerves (Figure 6b–d). The origin of the *m. protractor hyomandibulae* has extended both anteriorly and posteriorly on the otic capsule and is interrupted by the trigeminal nerve and its ganglion (Figure 6a). The muscle is thereby given a bipartite appearance that is further enhanced by the difference in the direction of muscle fibers between different portions. The fibers of the superficial portion originate posterodorsal to the eye along the anterolateral part of the otic capsule, and attach to the entire anterior aspect of the shaft of the hyomandibula. The fibers of the deep portion originate posteroventrally on the otic capsule and attach to the distal part of the hyomandibula.

The *m. branchiomandibularis* is now in contact with the ventral tip of the third hypobranchial. The *m. sternohyoideus* migrates anteriorly from its origin in the trunk and clearly shows segmentation, reflecting its origin from three myomeres. It does not reach as far anterior as the hyoid arch, but rather ends freely at the height of where the conus arteriosus separates into the branchial arteries. The invading *mm. branchiomandibularis* and *sternohyoideus* retain their spinal innervation (Figure 6d).

3.8 | Stage 45 (Figure 7a–e)

The larvae at this stage start to feed actively. Scutes are present in the dorsal-fin fold and the large parts of the head are covered by thin dermal ossifications. The yolk sac of the embryo is largely consumed and larvae are long and slender, resembling juveniles in their outer appearance. The larval fin fold is mostly reduced and distinct median and paired fins are present.

The symphyseal portion of the *m. adductor mandibulae* is divided into an intermediate and a deep partition (Figure 7c–e). The intermediate portion is superficial and inserts on the anterodorsal aspect of the lateral part of Meckel's cartilage, while the deeper and main part of the symphyseal portion inserts further medially on Meckel's cartilage. The *m. intermandibularis* is clearly divided into an anterior, medially confluent portion that originates from Meckel's cartilage, and a posterior portion that is divided by a raphe in the midline and extends laterally and anterodorsally over the hyoid arch without directly attaching to a skeletal element (Figure 7a,b). Posteriorly, the *m. intermandibularis* overlaps with the *m. interhyoideus* and is confluent with the *m. hyohyoideus* (Figure 7a,b). The *m. protractor hyomandibulae* is more elongated at this stage compared to previous stages, reaching farther anteriorly and deeper into the optic chamber, where its anterior portion originates from the skull roof. This is also the adult condition. In one specimen additional muscle fibers (* in Figure 7e) are present that project toward the palatoquadrate cartilage.

3.9 | Juvenile to adult stages (Figure 7f)

The dermal skeleton of the head and trunk area is well developed and certain ossifications of the endoskeleton occur (e.g., on the ceratohyal and the hyomandibular cartilages). Teeth are absent in the mandibular arch elements, although individual teeth are present posteriorly on hypobranchial 1 and on the anterior part of the basibranchial in juveniles.

In juveniles, the *m. adductor mandibulae* inserts directly on Meckel's cartilage after passing through a fenestra in the dentary, and retains its bipartite to tripartite appearance to the adult stage without clearly separating into distinct muscles. The *m. intermandibularis anterior* is reduced in the adult. The muscle fibers project medially from their origin on Meckel's cartilage but their appearance differs from the larval stages, as they no longer span the midline. The prominent *m. branchiomandibularis* and its attachment on Meckel's cartilage are therefore directly visible. The *m. intermandibularis posterior* becomes a thick muscle in the adult that inserts by a tendon to the lateral ethmoid region of the skull. The *m. interhyoideus* is a slender but distinct muscle. The *m. hyohyoideus* extends from the common raphe with the aforementioned muscles in the midline to the branchiostegals; no fibers are present posterior to the subopercle in the opercular flap. The *m. protractor hyomandibulae* is massive and originates from the braincase medial to the eye. It inserts along the posteroventral three quarters of the anteroventral surface of the hyomandibula (Figure 7f). Its counterpart, the *m. retractor hyomandibulae*, forms a thick sheet from its origin at the dorsolateral surface of the otic capsule to its insertion on the hyomandibula, thereby covering most of the dorsoposterior surface of the hyomandibula and the cartilaginous hyomandibular blade. Directly posteriorly, the *m. opercularis* connects the otic capsule with the subopercle. It is closely associated with the *m. retractor hyomandibulae* and not well separated at the origin.

4 | DISCUSSION

4.1 | Mandibular arch muscles

Previous studies found that the mandibular arch muscles of sturgeons are restricted to the *m. adductor mandibulae* (with either one or two portions), the *m. intermandibularis*, and the *m. protractor hyomandibulae* (e.g., Edgeworth, 1935; Luther, 1913). This is a relatively simple condition compared to most actinopterygians, and has been correlated with lack of insertion sites (e.g., for the *m. dilatator operculi* and the opercular bone) as well as related to the specialized jaw suspension. Our results, however, show previously unreported subdivision and specialization within these muscles.

The development and form of the *m. adductor mandibulae* in acipenseriforms has been variably described in past studies. For example, Carroll and Wainwright (2003), Edgeworth (1935), and Kurz (1924) described the muscle as a single portion in sturgeons, while Danforth (1913) and Adams (1918) reported two portions in *Polyodon spathula*. Luther (1913) in contrast, who studied *A. gueldenstaedtii*, *A. ruthenus* and *Scaphirhynchus platorhynchus* as well as *Polyodon*, discussed a "symphyseal" and an "articular" portion present in all taxa, although less obvious in species of *Acipenser*. We consistently found these two portions in all specimens of *A. baerii* from Stage 39 to the adult. Tracing fiber direction in high resolution datasets further made it possible to resolve a third portion in feeding larvae (Stage 45) resembling the reconstructed plesiomorphic state for actinopterygians in number (Lauder, 1982). It is unclear whether the portions of *A. baerii* are homologous to those of other extant actinopterygians, where the *m. adductor mandibulae* is typically much more diversified (Datovo & Vari, 2013,

2014; Hernandez, Patterson, & Devoto, 2005; Jarvik, 1980; Konstantinidis & Harris, 2011; Konstantinidis et al., 2015; Noda et al., 2017). Luther (1913) suggested the symphyseal portion of the *m. adductor mandibulae* in acipenseriforms to be homologous to the preorbital portion of *Lepisosteus* and *Amia*. This is consistent with our results for *Acipenser baerii* (which can probably be extended to other acipenserids) and the comparison with the sequence in *Lepisosteus osseus* where the *m. preorbitalis* develops after the *m. adductor mandibulae* (Konstantinidis et al., 2015). Data for *Polyodon* and *Psephurus* would be valuable to further investigate this, although it is intriguing that sub partitioning takes place early in ontogeny but no true separation is established.

The ventral constrictor muscles of acipenserids are unusual in comparison to other actinopterygians and up to six portions have been described (Meinel, 1962). We found two ventral constrictors belonging to the mandibular arch but the anterior portion of the *m. intermandibularis* is largely reduced in adults while the posterior portion is hypertrophied and anterolaterally extended. This portion reaches around the jaws and dorsally to attach to the neurocranium (Edgeworth, 1935; Gegenbaur, 1898; Vetter, 1878). Adams (1918) and Vetter (1878) speculated that it might be a *m. adductor mandibulae* portion, but our ontogenetic series indicates that it is the *m. intermandibularis posterior*. As the *m. intermandibularis* consists of two clearly distinct portions in *Acipenser baerii*, the assumption of only one portion to be present in acipenseriforms (Diogo, 2008; Diogo, Hinitis, & Hughes, 2008) needs to be reevaluated (see also Edgeworth, 1911). The aforementioned studies refer to *Psephurus gladius*, a species of the Polyodontidae on the verge of extinction, with very rare material present in museums. We were, therefore, unable to examine this taxon and we are not aware of any original peer-reviewed data confirming their statement.

The derivative of the *constrictor mandibularis dorsalis* in acipenseriforms only inserts on the hyomandibula and hence has been termed the *m. protractor hyomandibulae* (Edgeworth, 1935) as opposed to *mm. levator arcus palatini* (and *dilatator operculi*) as is the case in other actinopterygians. The differing terminology established by Edgeworth (1935) for these homologous muscles is confusing as the *constrictor mandibularis dorsalis* and its derivatives in acipenseriforms differ only slightly from the state found in other actinopterygians: in *Polypterus*, all derivatives are connected to each other and they at least partly insert on the hyomandibula (Allis, 1922); even the term *m. protractor hyomandibulae* was applied for this taxon (Allis, 1922; Pollard, 1892). A similar condition is found for *Lepisosteus osseus* (Edgeworth, 1935; Konstantinidis et al., 2015), *Amia calva* (Luther, 1913), and some teleosts (Edgeworth, 1935; Winterbottom, 1973). Also, the multiple origins on the neurocranium and subsequent partition of the *m. protractor hyomandibulae* in *A. baerii* show that the condition in sturgeons is not as simple as previously reported. The absence of a *m. dilatator operculi* can be explained by the loss of the opercular bone.

4.2 | Hyoid arch muscles

The muscles of the hyoid arch comprise the dorsal hyoid constrictor muscles (*m. retractor hyomandibulae* and *m. opercularis*) and the ventral hyoid constrictor muscles (*m. interhyoideus* and *m. hyohyoideus*). The

elements of the dorsal portion have been reported to either be joined (Adams, 1918; Luther, 1913) or separated (Kurz, 1924) in different species of acipenserids, whereas *Polyodon* appears to lack a *m. opercularis* (Danforth, 1913). Our ontogenetic series shows that the anlage of the dorsal hyoid constrictor muscle differentiates into the *m. retractor hyomandibulae* anteriorly and that the *m. opercularis* forms later in relation to the *m. hyohyoideus*. At later stages these two muscles together originate from the lateral surface of the otic capsule; they can be distinguished but no clear separation is present.

Recently Noda et al. (2017) concluded that the *m. hyohyoideus* in *Polypterus senegalus*, another basal actinopterygian, is derived from the dorsal hyoid constrictor anlage and therefore not homologous to that of other actinopterygians. However, in a recent paper (Konstantinidis et al., 2015) it was shown, that in *Lepisosteus osseus*, the *m. hyohyoideus* covers the entire opercular membrane in larvae around 10 mm NL. At this stage, the muscle is confluent with the muscles derived from the ventral and the dorsal hyoid constrictor anlagen. The dorsal portion later differentiates into the *m. adductor opercularis* and the *m. adductor hyomandibularis*, while the ventral portion remains without a specific attachment in the opercular flap. The same pattern is shown by our ontogenetic series of *Acipenser*. We observed first muscle differentiation in the opercular flap (Figure 3d) with no clear origin from the dorsal and ventral anlagen, which is very similar to the pattern showed by Noda et al. (2017) for *Polypterus*. Later in ontogeny, the *m. hyohyoideus* is confluent and appears derived from both anlagen, before the upper portion in even more advanced stages attaches to the subopercle to form the *m. opercularis*. The condition of the hyoid arch constrictors in *Polypterus* is certainly obscured by the presence of an external gill on the hyoid arch, which makes interpretation of the data difficult. However, we see no evidence against the homology of the *m. hyohyoideus* among actinopterygians. Further research is needed to clarify the fate of the *m. hyohyoideus*, including a clear definition of the muscle and its sub portions in actinopterygians.

4.3 | Conclusions

As previously reported for acipenseriforms, the muscles associated with the mandibular and hyoid arches of *A. baerii* have a low number of distinct muscles compared to other actinopterygians (compare e.g., Konstantinidis et al., 2015). We did, however, find a subpartitioning of the muscles (e.g., the *m. adductor mandibulae* and the *m. protractor hyomandibulae*), with different sites of origin and insertion resulting in variable fiber direction within the muscles. The muscles therefore appear to be specialized with respect to the unique jaw configuration, but without clear separation into individual muscles. Our comparison of muscle development in *A. baerii* and other basal actinopterygians suggests that the ontogeny of the musculature in *A. baerii* is truncated, so that the muscles do not separate. Paedomorphosis, which is frequently considered to be a dominant phenomenon within acipenseriform evolution, might play a large role in establishing this condition. Functional data related to feeding mechanics of acipenserids are scarce (Bemis et al., 1997; Carroll & Wainwright, 2003; Miller, 2005), and questions such as the role of the hypertrophied posterior portion of the *m.*

intermandibularis with its ligamentous connection to the hyomandibula, and the mechanism of opercular abduction in the absence of the *m. dilatator operculi* remain to be critically tested.

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