

Myological Variability in a Decoupled Skeletal System: Batoid Cranial Anatomy

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ABSTRACT Chondrichthyans (sharks, batoids, and chimaeras) have simple feeding mechanisms owing to their relatively few cranial skeletal elements. However, the indirect association of the jaws to the cranium (euhyostylic jaw suspension) has resulted in myriad cranial muscle rearrangements of both the hyoid and mandibular elements. We examined the cranial musculature of an abbreviated phylogenetic representation of batoid fishes, including skates, guitarfishes and with a particular focus on stingrays. We identified homologous muscle groups across these taxa and describe changes in gross morphology across developmental and functional muscle groups, with the goal of exploring how decoupling of the jaws from the skull has effected muscular arrangement. In particular, we focus on the cranial anatomy of durophagous and nondurophagous batoids, as the former display marked differences in morphology compared to the latter. Durophagous stingrays are characterized by hypertrophied jaw adductors, reliance on pennate versus fusiform muscle fiber architecture, tendinous rather than aponeurotic muscle insertions, and an overall reduction in mandibular kinesis. Nondurophagous stingrays have muscles that rely on aponeurotic insertions onto the skeletal structure, and display musculoskeletal specialization for jaw protrusion and independent lower jaw kinesis, relative to durophagous stingrays. We find that among extant chondrichthyans, considerable variation exists in the hyoid and mandibular muscles, slightly less so in hypaxial muscles, whereas branchial muscles are overwhelmingly conserved. As chondrichthyans occupy a position sister to all other living gnathostomes, our understanding of the structure and function of early vertebrate feeding systems rests heavily on understanding chondrichthyan cranial anatomy. Our findings highlight the incredible variation in muscular complexity across chondrichthyans in general and batoids in particular. *J. Morphol.* 000:000–000, 2014. © 2014 Wiley Periodicals, Inc.

KEY WORDS: Myliobatidae; batoid; gnathostome; durophagy; jaw suspension

INTRODUCTION

The batoid fishes (stingrays, electric rays, skates, and guitarfishes) possess arguably one of the most functionally autonomous feeding mechanism within vertebrates. Whereas most vertebrate species show a strong association between the

upper jaws and braincase, in batoids the only skeletal links to the upper [palatoquadrate (PQ)] and lower [Meckel's cartilage (MK)] jaws are the paired hyomandibular cartilages, rod-like connecting struts between the corners of the jaws and the otic region of the chondrocranium (Maisey, 1980; Wilga, 2002; Dean et al., 2007a; Motta and Huber, 2012). Unlike sharks, this jaw suspension of batoids (known as euhyostyly) is solely hyoid based, without the added assistance of ligaments or skeletal processes to anchor the upper jaw to the chondrocranium to limit or guide jaw movement (Fig. 1; Maisey, 1980; Wilga, 2002). The result is a feeding mechanism with a relatively simple skeletal structure that can exhibit great freedom of movement (Wilga and Motta, 1998; Dean and Motta, 2004a).

Despite the relatively few elements in the feeding mechanism, the ranges of ecological niches used by batoids are comparatively diverse (Dean et al., 2007a). Batoids exhibit a rich array of feeding modes ranging from benthic generalists to specialists on shelled prey, and from predators on large, highly mobile midwater prey to pelagic planktivores (Bigelow and Schroeder, 1953; Notarbartolo-di-Sciara, 1987; Dean et al., 2005, 2007a; Collins et al., 2007). Although the functional significance of the observed interspecific variations in hyomandibular morphology on diet is

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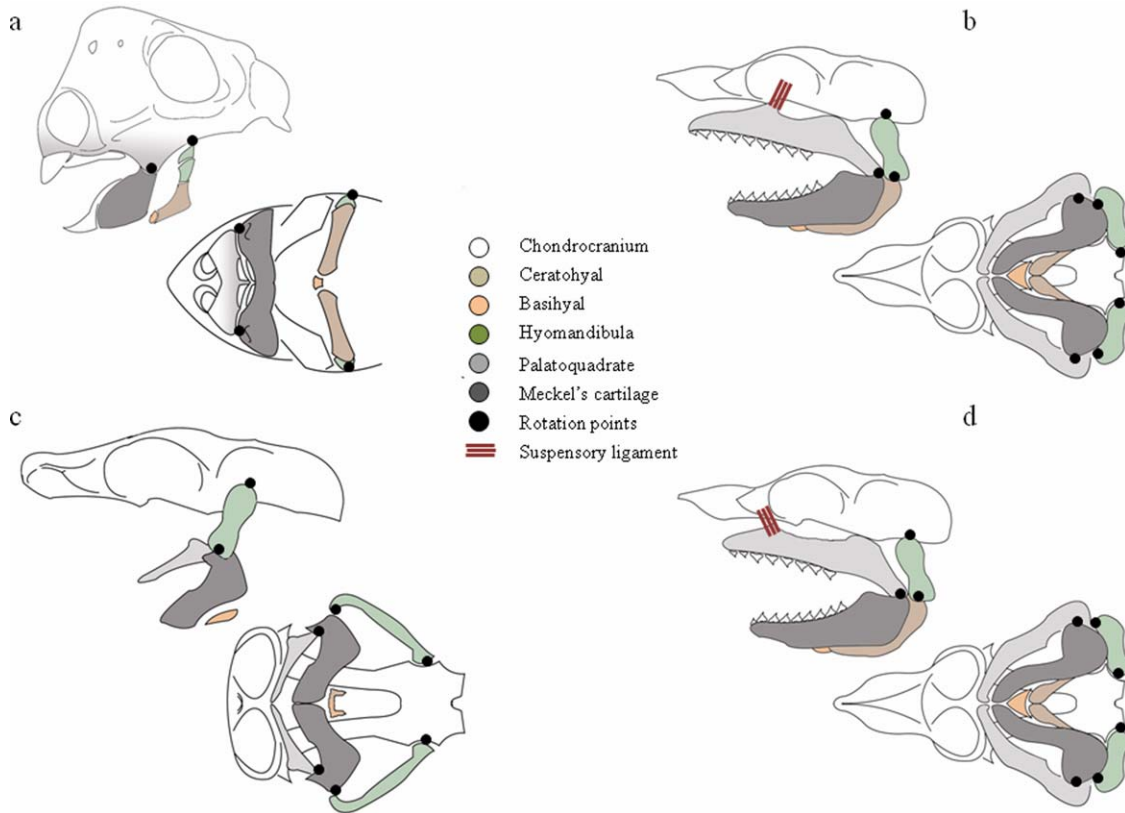


Fig. 1. Methods of jaw suspension in chondrichthyan fishes. (a) Holostylic—*Hydrolagus*, (b) Orbitostylic—*Squalus*, (c) Euhyostylic—*Urobatis*, (d) Hyostylic with ethmoid attachments—*Carcharhinus*.

unclear, jaw is thought to be highly reflective of diet (Summers, 2000; Dean et al., 2007a). The jaws of narcinid (Narcinidae) electric rays, for example, have flexible symphyses and a gape constrained laterally by labial cartilages, permitting rapid jaw protrusion for suction feeding specialization on vermiform prey (worms and eels; Dean and Motta, 2004a,b). Both torpedinid (Torpedinidae) electric rays and butterfly rays (Gymnuridae) have flexible, gracile jaws with large gapes, allowing engulfment of food items much larger than the resting mouth opening (Dean et al., 2007a). Specializations for crushing or cracking durable prey (durophagy) have evolved several times, in some guitarfishes (e.g., *Rhina* and *Zapteryx*), some basal stingrays (e.g., *Pastinachus*) and all members of the families Myliobatidae and Rhinopteridae. The advent of a durophagous feeding mode in these disparate taxa is thought to be evolutionarily independent, although durophagy in Myliobatidae and Rhinopteridae is thought to have arisen once through a common ancestor and then lost in the planktivorous Mobulidae (Notarbartolo-di-Sciara, 1987; Summers, 2000; Dean et al., 2007a). Morphological adaptations for durophagy typically involve modifications of teeth (e.g., reduction of

tooth number, flattening of teeth into pavement-like dentition) and reinforcement of the jaws via symphyseal fusion, cortical thickening and the addition of trabecular struts to buttress the interior of the jaw and prevent collapse during the crushing of molluscan prey (Summers, 2000; Dean et al., 2007a). We expect that myliobatid durophagous stingrays also share musculoskeletal traits in common with other durophagous elasmobranchs; namely, hypertrophied muscles, rigid/reinforced skeletons, and muscle fiber architecture favoring increased force generation (Kolmann and Huber, 2009).

The range of batoid diets and comparative simplicity of the skeletal system provide a fascinating palette for studies of evolutionary ecomorphology. In particular, the multiple evolutionary instances of specialized diets from hypothesized generalist ancestors (Dean et al., 2007a) and the presence of drastically different ecologies and morphologies in sister clades (e.g., narcinid vs. torpedinid electric rays, durophagous myliobatid vs. filter-feeding mobulid rays) may suggest that 1) the evolution of dietary and morphological specializations cannot simply be predicted by phylogeny and 2) the functional elements within the feeding system have

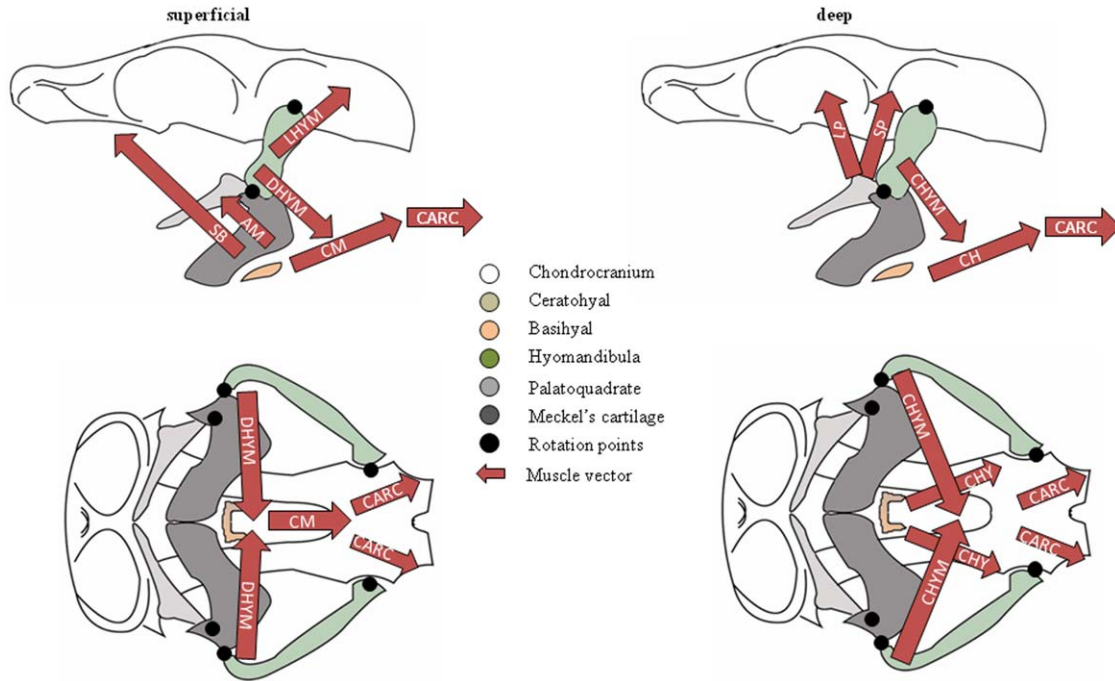


Fig. 2. Hypothetical generalized muscle vectors in batoids.

been decoupled and can therefore evolve independently. The “decoupling hypothesis” has been suggested for both teleosts (Schaefer and Lauder, 1996; Hulsey et al., 2006; Lujan and Armbruster, 2012) and elasmobranchs (Wilga and Motta, 1998; Dean et al., 2007a; Motta and Huber, 2012) and posits that as interacting skeletal elements (e.g., portions of the jaw and hyoid arches) are not constrained to evolve together, reconfiguration of the feeding mechanism can lead to a wide assemblage of drastically different functions and ecologies. That the jaws enjoy great freedom in their connection to the chondrocranium and likely rely heavily on hyomandibular movement (e.g., Dean and Motta, 2004a, b) suggests that jaw and hyoid musculature (Fig. 2) plays a vital role in suspending, stabilizing, and actuating the feeding mechanism. Understanding variation in muscular character states among species will allow insight into how dietary and kinematic diversity have evolved and are achieved with a cranial skeleton with few moving skeletal elements.

Recent reevaluation of batoids as sistergroup to sharks (Douady et al., 2003; Aschliman et al., 2012) necessitates equal “weight” is given to both batoid and selachian character states in phylogenetic reconstructions of stem elasmobranch cranial anatomy. Although musculoskeletal form and function have been investigated in a variety of nonbatoid chondrichthyans (e.g., Wilga and Motta, 2000; Huber et al., 2005, 2008; Kolmann and Huber,

2009; Mara et al., 2009), the arrangement of the cranial musculature in batoids has received scant attention from a functional standpoint (but see Wilga and Motta, 1998; Summers, 2000; Dean and Motta, 2004a; Sasko et al., 2006; Mulvany and Motta, 2013). Even fewer studies have sought to reconcile study of batoid musculature with other vertebrates (but see Miyake et al., 1992). Phylogenies incorporating jaw suspension as a critical character (Maisey, 1980) have recently been supported by subsequent molecular studies (Douady et al., 2003; Aschliman et al., 2012); suggesting feeding morphology is inherently tied to the diversification of stem chondrichthyans lineages. Despite the considerable evolutionary time elapsed as the divergence of these stem lineages, jaw suspension modes remain relatively lineage specific (Maisey, 1980). That muscle morphology follows a skeletal template would lead us to hypothesize that fixation of jaw suspension modes deep within the phylogenetic history of chondrichthyans is mirrored by restriction of hyoid muscle variability to these ancient nodes as well. As a counterpoint, given the array of dietary niches occupied by modern elasmobranchs (Dean et al., 2007a), we would expect most modern ecomorphological variation to occur in mandibular musculature.

Here, we describe the feeding musculature across stingrays in contrast to other batoids (skates and guitarfishes, Fig. 3). We then identify homologous muscles across elasmobranchs

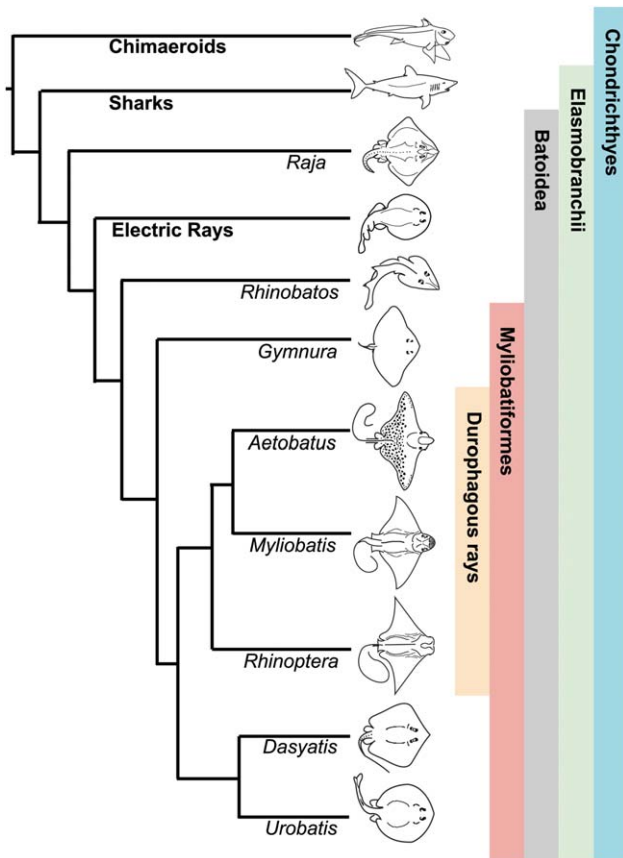


Fig. 3. Phylogenetic relationships of surveyed taxa. Modified from Aschliman et al. (2012). Branch lengths not to scale. Species used in this study in italics.

(sharks + rays) and then chondrichthyans [ratfishes + (sharks + rays), Aschliman et al., 2012] as a whole. Special attention is given to durophagous stingrays, as they exhibit quite divergent muscular anatomy from other batoids. We then use morphological observations to infer the possible functional implications of observed muscular arrangements. When possible, we follow the terminology of Miyake et al. (1992), which, building on the legacy of Edgeworth's (1935) research into homology of cranial musculature across vertebrates, incorporated an embryological and evolutionary perspective. This methodology allows further comparison to other vertebrate taxa and builds a common etymological framework. Our phylogenetic schema follows that of Aschliman et al. (2012), the most comprehensive systematic study of batoids to date, incorporating molecular, morphological, and fossil data in understanding the evolutionary history of the Batoidea (Fig. 3).

METHODOLOGY

Specimen Collection

Specimens of nondurophagous taxa, *Raja eglanteria* ($n = 2$), *Rhinobatos lentiginosus* ($n = 1$),

Gymnura micrura ($n = 3$), *Dasyatis sabina* ($n = 3$), *Urobatis jamaicensis* ($n = 2$) and durophagous taxa, *Rhinoptera bonasus* ($n = 5$), *Aetobatus narinari* ($n = 2$), and *Myliobatis freminvillei* ($n = 5$), were collected primarily via fisheries-independent surveys in collaboration with several agencies; Florida Fish and Wildlife Conservation Commission (Charlotte Harbor and Eastpoint, FLA), National Marine Fisheries Service GulfSPAN surveys, and through the Virginia Institute of Marine Science (Gloucester Point, VA). Specimens were typically frozen. Animals considered for this study showed no signs of undue stress or unusual characteristics of the cranial region. For simplicity, only the genus will be referenced, as only one species representing each genus was used throughout the study. Animals were euthanized by severing of the vertebral column near the chondrocranium, overdosing of MS-222, or by placing the animal on ice in accordance with Animal Care and Use Committee guidelines at Florida State University (Protocol 1209). Reference designations for specimens used to inform illustrations are as follows: Rajidae: *Raja eglanteria*, FSU/REGA—002, DW = 37.5 cm (male); Rhinobatidae: *Rhinobatos lentiginosus*, FSU/RLEN—001, DW = 16.5 cm, total length = 56 cm (female); Gymnuridae: *Gymnura micrura*, FSU/GMIC—002, DW = 58.5 cm (female); Rhinopteridae: *Rhinoptera bonasus*, FSU/RBON—043, DW = 78.2 cm (female); Myliobatidae: *Aetobatus narinari*, FSU/ANAR—001, DW = 99 cm (female); Myliobatidae: *Myliobatis freminvillei*, FSU/MFRE—002, DW = 72 cm (male); Dasyatidae: *Dasyatis sabina*, FSU/DSAB—002, DW = 28.5 cm (female); and Urolophidae: *Urobatis jamaicensis*, FSU/UJAM—001, DW = 21 cm (female). Additional specimen information available upon request.

Terminology

Anatomical data were organized according to embryonic muscle units, as designated by Edgeworth (1935), Miyake et al. (1992), Lovejoy (1996), and Mallat (1997); data from previous works were synthesized (with some reinterpretation as needed) to provide context and broader perspective for our data (see Tables 1 and 2). Muscles were identified with consideration of both attachment (origin and insertion) as well as general position. *Raja eglanteria*, *Rhinobatos lentiginosus*, *Gymnura micrura*, *Dasyatis sabina*, and *Urobatis jamaicensis* are referred to below as “nondurophagous” taxa, whereas *Rhinoptera bonasus*, *Aetobatus narinari*, and *Myliobatis freminvillei* are “durophagous.” Also, the term “stingray” includes all species examined except *Raja eglanteria* and *Rhinobatos lentiginosus* (see supplementary Information for details about batoid cranial muscle terminology).

TABLE 1. Cranial musculature in eight species of batoids

Abbreviation	Division	Found in	Generalized attachment		General function
			Origin	Insertion	
AMMe	Adductor mandibulae medialis	<i>Re, Gm, An, Mf, Rb, Ds, Uj</i>	Palatoquadrate	Meckel's cartilage	Jaw closure
AML_a	Adductor mandibulae lateralis	<i>all</i>	Palatoquadrate	Meckel's cartilage	Jaw closure
AMMa	Adductor mandibulae major	<i>all</i>	Palatoquadrate	Meckel's cartilage	Jaw closure
AMD	Adductor mandibulae deep	<i>An, Mf, Rb</i>	Palatoquadrate	Meckel's cartilage	Jaw closure
AML_i	Adductor mandibulae lingualis	<i>Gm, Rb</i>	Palatoquadrate	Meckel's cartilage	Jaw closure
SP	Spiracularis	<i>all</i>	Postorbital— chondrocranium	Spiracular cartilage, palatoquadrate	Ventilation
LP	Levator palatoquadrati	<i>all</i>	Preorbital— chondrocranium	Palatoquadrate	Jaw retraction
SB	Suborbitalis	<i>all</i>	Palatoquadrate	Meckel's cartilage	Protrudes jaws
PCM	Precranial muscle	<i>Gm, An, Mf</i>	Chondrocranium	Pectoral propterygium	Unknown
ETM	Ethmoideo-parethmoidalis	<i>Gm, An, Mf, Rb, Ds, Uj</i>	Chondrocranium	Pectoral propterygium	Unknown
CHV	Constrictor hyoideus ventralis	<i>all</i>	Medial region— 1st gill arch	Ventral 1st gill arch	Ventilation
CHD	Constrictor hyoideus dorsalis	<i>all</i>	Medial region— 1st gill arch	Dorsal 1st gill arch	Ventilation
LHYM	Levator hyomandibularis	<i>all</i>	Dorsal chondrocranium	Hyomandibular cartilage	Retracts hyoid cartilages
DHYM	Depressor hyomandibularis	<i>all</i>	Depressor rostri	Hyomandibular cartilage	Depresses hyoid arch
DM	Depressor mandibularis	<i>Ds, Uj</i>	Depressor rostri	Meckel's cartilage	Depresses lower jaw
DR	Depressor rostri	<i>all</i>	Antimere—ventral midline	Pectoral propterygium	Lowers snout
LR	Levator rostri	<i>Re, Rl</i>	Dorsal chondrocranium	Pectoral propterygium	Raises snout
CM	Coracomandibularis	<i>all</i>	Coracoarcualis	Meckel's cartilage	Abducts jaws
CH	Coracohyoideus	<i>all</i>	Coracoarcualis	Basihyal, hypohyal cartilages	Expands oropharynx
CARC	Coracoarcualis	<i>all</i>	Pectoral girdle	Coracomandibularis	Abducts jaws (w/ CM)
CHYM	Coracohyomandibularis	<i>all</i>	Antimere—ventral midline	Hyomandibular cartilages	Depresses hyoid arch

Abbreviations: Re, Raja eglanteria; Rl, Rhinobatos lentiginosus; Gm, Gymnura micrura; An, Aetobatus narinari; Mf, Myliobatis freminvillei; Rb, Rhinoptera bonasus; Ds, Dasyatis sabina; Uj, Urobatis jamaicensis.

RESULTS

Skeletal Overview

The range of variation in chondrichthyan cranial skeletal morphology is broad and covered in great detail in other works (e.g., see Didier, 1995; Lovejoy, 1996; Nishida, 1990, and particularly Claeson, 2011 for more thorough treatment). Here, we provide a generalized summary of the batoid cranial skeleton to illustrate the structural framework on

which the muscles attach; a visual comparison of chondrichthyan cranial skeletons is provided in Figure 1, with generalized muscles mapped on to the batoid model in Figure 2, and with a more detailed generalized batoid skeleton illustrated in Figure 4.

Batoid fishes are typically flatter than sharks and, therefore, the basic layout of the cranial skeleton can be largely understood in a two-

TABLE 2. Generalized chondrichthyan cranial muscle function

Abbreviation	Muscle unit	General function	Number of muscle divisions		
			Ratfishes	Sharks	Batoids
AM	Adductor mandibulae	Jaw closure	3	2–5	3–6
CD	Constrictor dorsalis	Jaw suspension	1	1–2	2
CH	Constrictor hyoideus	Hyoid suspension	2	3	5–6
GH	Geniohyoideus	Abducts jaws	1	1	1
RC	Rectus cervicus	Abducts jaws	1	2	3

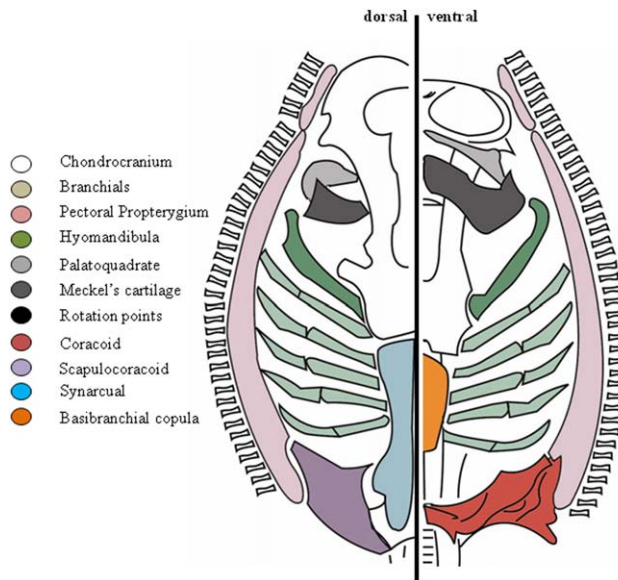


Fig. 4. Generalized anterior batoid skeletal structure.

dimensional, ventral view. There are typically 10 skeletal elements (counting paired cartilages as two independent elements—Figs. 1 and 4). The chondrocranium can exhibit complex, convoluted edges, but is essentially a rectangular braincase, with bulbous anterior nasal capsules and in some cases (e.g., skates, guitarfishes) a long rostral cartilage at the anterior end of the animal. The neurocranial fontanelle is a slight depression along the dorsal medial axis of the chondrocranium, within which a very thin cartilaginous sheath covers access to the brain cavity. The long, slender hyomandibular cartilages articulate with the lateral otic regions near the caudal end of the braincase, extending anterolaterally toward the propterygia (see below) and articulating via stout ligaments with the extreme lateral edges of the jaw complex. The spiracle, a small orifice on the dorsal body surface, opening via a short passageway into the pharynx, is located in the triangular space between the anterior edge of the hyomandibulae, the caudal edges of the jaws and the lateral edge of the cranium. The shaft of the hyomandibula and a thin, bowed spiracular cartilage form the posterior and anterior margins of the spiracle, respectively. The spiracle represents the reduced gill-slit opening between the mandibular and hyoid arches.

Although the batoids exhibit a range of dietary specializations, in all cases, the upper jaw (PQ) and lower jaw (MK) can be considered to simply span the space between the two distal hyomandibular tips, with all nondurophagous taxa (except *Mobula* and *Manta*) having unfused jaw symphyses. The teeth, whether cuspidate and arranged on pads (as in nondurophagous stingrays) or flat and pavement like (as in pelagic/durophagous sting-

rays), overlie the jaw symphyses. The wing process, a ventral projection of the MK, is found only in durophagous stingrays (Summers, 2000).

The caudal end of the braincase articulates with the synarcual, a long tube-like element believed to be derived from fused elements of the first several vertebrae (Claeson, 2011) and joins the vertebral column caudally. This region is flanked by the “branchial basket,” composed of a series of rostro-caudal jointed skeletal arches—composed of the single pseudohyoid and multiple branchial arches—extending like medially oriented crescents from the posterior braincase and synarcual to meet on the ventral pharyngeal floor in a single fused basibranchial copula. In this way, the branchial basket superficially resembles a ribcage surrounding the pharynx, with the gill pouches and gill slits between each consecutive arch. In nonpelagic stingrays, the basibranchial copula also articulates anteriorly via hypohyal cartilages with the sole additional portion of the hyoid arch, the basihyal cartilage; this ventral hyoid element is absent in pelagic stingrays.

In addition to forming the roof of the branchial basket, the synarcual articulates caudally with the medial portion of the pectoral girdle (including the scapulocoracoid and coracoid cartilage) in nontorpediniform batoids. This portion of the pectoral girdle spans lateromedially, perpendicular to the synarcual and the animal’s long axis. The pectoral propterygia, long scythe-shaped cartilages, arch anteriorly from their articulation with the lateral pectoral girdle to meet with the antorbital cartilages or rostral cartilages, effectively “framing” the cranial elements rostral of the coracoid bar. In durophagous stingrays, the dorsal surfaces of the propterygia are fused to the ventral chondrocranium. Fin radials, small skeletal elements supporting the pectoral fins, extend laterally from the propterygia (Mulvany and Motta, 2013). For our purposes, the propterygia are considered to form the lateral boundaries of the “head” of the batoids in this study, including the chondrocranium–synarcual complex as well as the associated jaw, hyoid, and branchial arches.

Hypaxial Series

This muscle series develops embryonically from the genio-hyoideus and rectus cervicus muscle groups (Tables 1 and 2, Miyake et al., 1992). Three of these muscles, the coracoarcualis (CARC or rectus cervicus, Nishida, 1990), coracomandibularis (CM or genio-coracoideus, Nishida, 1990), and coracohyoideus (CH), are present in all chondrichthyans, with the coracohyoideus (CHYM) being unique to batoids (Miyake et al., 1992; Anderson, 2008). Although muscle configurations differ considerably across vertebrate groups in terms of their attachment, the hypaxial muscles

generally originate on some aspect of the pectoral girdle (or another hypaxial muscle, which then inserts on the girdle) and insert anteriorly on the lower jaw or hyoid apparatus (Edgeworth, 1935; Miyake et al., 1992; Anderson, 2008). The hypaxial muscles are associated ancestrally in gnathostomes with jaw-opening (lower jaw abduction) and pull the feeding apparatus posteriorly and ventrally (Mallat, 1997; Anderson, 2008).

CARC and CM. In all taxa, the CARC (Figs. 6–8, all taxa) are paired, triangular muscles which typically originate on the antero-ventral surface of the coracoid bar, superficial to the ventral surface of the pericardium and insert on the CM. Paired, anterior CM antimeres, aligned in series with the posterior CARC muscles (Figs. 6 and 7 and 9 and 10) together abduct the lower jaw (Huber et al., 2011). In batoids overall, the arrangement, attachment, and presumably the function of the CM and CARC are generally conserved (*Raja*, Figs. 6 and 7a and 9 and 10a; *Rhinobatos*, Figs. 6 and 7b and 9 and 10b; *Gymnura*, Figs. 6 and 7c and 9 and 10c; *Dasyatis*, Figs. 6 and 7g and 9 and 10g; and *Urobatis*, Figs. 6 and 7h and 9 and 10h). The CARC muscle is reduced in *Myliobatis* (Figs. 6–8e). Our specimens of *Aetobatus* had been severed anterior to the origin of the CARC, precluding full examination of this muscle. Gonzalez-Isais (2003) described the condition of the CARC as being generally similar in *Aetobatus* to the condition we have described in *Myliobatis* and *Rhinoptera* (Figs. 6–8f).

CH. The CH in most taxa typically originates on the antero-medial face of the first gill arch and the CARC and inserts on the underside of the pharyngeal region and ventral aspects of the basihyal and hypohyal cartilages (Figs. 7 and 8). The CH is an embryonic derivative of the rectus cervicis (Miyake et al., 1992) and depresses the hypohyal and basihyal cartilages, which in turn expand the pharyngeal cavity (Huber et al., 2011). The CH is noticeably small and more strap like in *Rhinobatos* (Fig. 8b) than in stingrays, articulating less with the first gill arch and more with the fascia forming the junction of the CHYM and CARC. In *Gymnura* (Fig. 7c), *Dasyatis* (Fig. 7g), and *Urobatis* (Fig. 7h) the CH is also found dorsal to the CM, flanking it on both sides and originating on the combined basihyal/hypohyal cartilages. The CH is reported to be absent in pelagic myliobatiforms (Miyake et al., 1992). However, other authors (Nishida, 1990; Lovejoy, 1996) consider the “Y” muscle of Miyake et al. (1992) to be homologous to the CH. This muscle (CH in our diagrams) is found in *Rhinoptera* (Fig. 8f), *Aetobatus* (Figs. 7 and 8d), and *Myliobatis* (Figs. 7 and 8e), on the ventral aspect of the extrabranchial cartilages (in a manner consistent with the CH in other taxa—Miyake et al., 1992), stretching transversely across the first gill

arches and meeting medio-ventrally with the CHYM.

CHYM. The CHYM is a paired ventral muscle unique to batoids (Miyake et al., 1992), usually superficial to the lateral portions of the ventral pharyngeal region. In stingrays, the CHYM are columnar at their origins on the pericardium, CARC, and coracoid, extending along the ventral pharyngeal cavity and inserting on the hyomandibular cartilages. The function of the CHYM presumably involves depression and abduction of the hyomandibular cartilages (and to some extent, the lower jaw and pharyngeal region as well) ventrally and medially (Dean and Motta, 2004a). The CHYM is similar to the depressor hyomandibularis (DHYM) in depressing the hyoid cartilages ventrally, but differs in its origin being placed more posteriorly, therefore, likely retracts the hyomandibulae posteriorly as well as ventrally. In *Raja* (Fig. 8a) and *Rhinobatos* (Fig. 8b) the CHYM originates directly on the hyomandibular cartilages, without a tendon. In stingrays the CHYM inserts on the base of the tissue of the pharynx and the basihyal cartilages, inserting on the distal aspect of the ventral hyomandibular cartilages via long tendons (Figs. 7 and 8c). In *Rhinoptera* (Fig. 8f), *Aetobatus* (Fig. 8d), *Myliobatis* (Fig. 8e), *Dasyatis* (Figs. 7 and 8g), and *Urobatis* (Figs. 7 and 8h), the CHYM extend laterally over much of the ventral pharynx region, going so far *Aetobatus*, *Rhinoptera* (Fig. 8) and *Myliobatis*, to as line the dorsal surface of the MK. The arrangement of the CHYM in *Aetobatus* is slightly different, with the muscle consisting of two divisions which both insert aponeurotically on the jaw joint ligament and the entire dorsal surface of the MK, respectively.

Hyoid Series

Mallat (1997) postulates that the embryonic or early evolutionary function of the branchial constrictor muscles was primarily expiration. With the evolution of jaws in gnathostomes, the muscles of the first two gill arches (mandibular and hyoid, respectively) changed their function correspondingly. Three muscles stemming from the hyoid musculature are found in all elasmobranchs (Fig. 5), the levator hyomandibularis (LHYM), constrictor hyoideus ventralis (CHV) and constrictor hyoideus dorsalis (CHD—this muscle, however, is absent, perhaps secondarily, in holocephalans—Miyake et al., 1992). The depressor rostri (DR), DHYM, and levator rostri (LR) are unique to batoids with the latter found in skates, guitarfishes, and torpediniforms and presumably lost in myliobatiform stingrays (Miyake et al., 1992; Dean and Motta, 2004a). The depressor mandibularis (DM) is only found in dasyatoid rays (*Dasyatis*, *Urobatis*). The LHYM elevates the hyomandibular cartilages in all taxa (Mallat, 1997), specifically, in

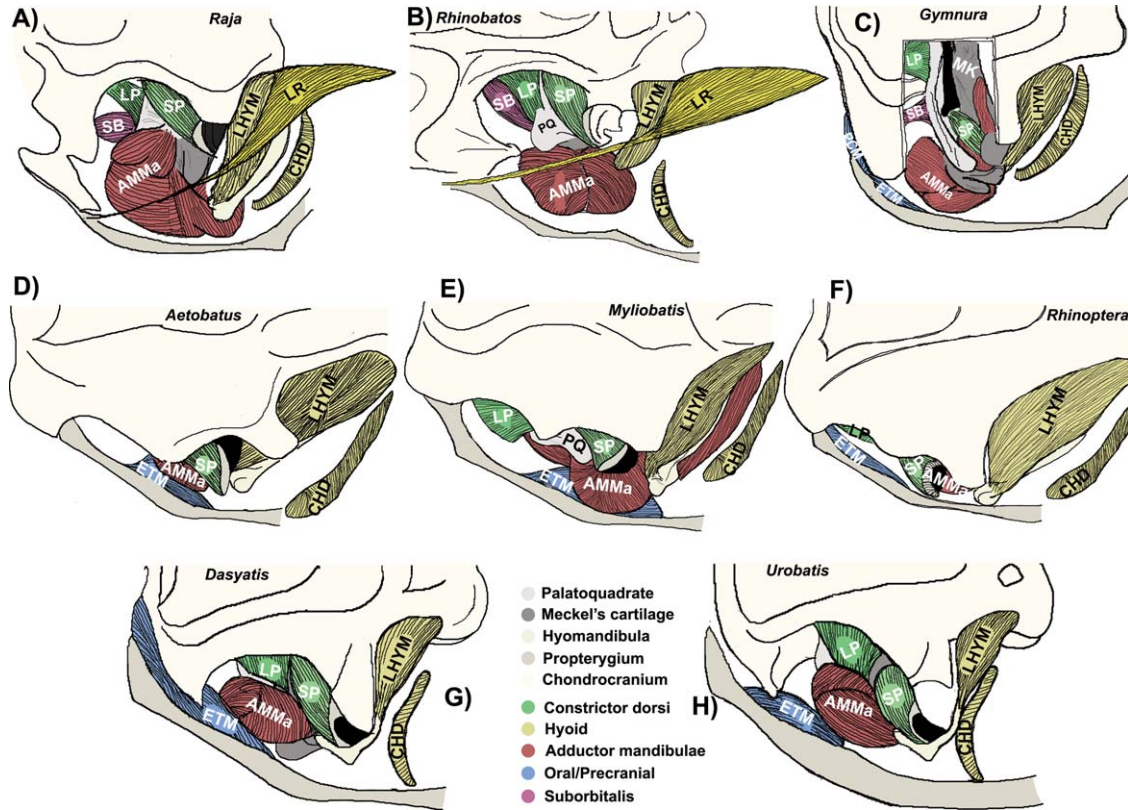


Fig. 5. Dorsal superficial cephalic musculature of six species of batoid fishes. All crania with anterior facing left. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracohyoideus mandibularis; CM, Coracomandibularis; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideo-pretremoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrate; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor hyoideus (hyoid plate); muscles in yellow are derived from the hypaxial plate (genio-hyoideus and rectus cervicis); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

those species in which it has been studied experimentally, lifting the hyomandibular cartilages during the recovery phase of jaw protrusion toward the chondrocranium in taxa (Wilga and Motta, 1998). The CHV and CHD compress the first gill pouches (Huber et al., 2011). The DR and LR are antagonists and depress and elevate the snout, respectively. The DR also presumably serves to compress the cephalic and branchial region during the preparatory phase of prey capture (Wilga and Motta, 1998). The DHYM adduct the hyomandibular cartilages ventrally during feeding, are associated with subsequent jaw protrusion, and antagonize LHYM (Wilga and Motta, 1998). The DM aids in retracting the lower jaw cartilages during feeding (Miyake et al., 1992).

LHYM. The LHYM originates on the lateral aspect of the dorsal surface of the chondrocranium, just posterior to (although sometimes overlapping) the postorbital cartilages (Fig. 5, all taxa)

and inserting on the dorsal and posterolateral surfaces of the hyomandibular cartilage. This muscle abuts the CHD through shared connective tissue. The condition and presumed function of the LHYM appears broadly conserved across the taxa surveyed in this study. In *Aetobatus*, the LHYM muscles are covered by an overlying layer of tissue and are sunken within fossae formed by the posterior-lateral portion of the otic region and bounded laterally by the first gill arch (Fig. 5e).

LR. The LR originates on the dorsal surface of the cervicothoracic synarcual, lateral to the epaxial muscles, and superficial to the LHYM. The LR inserts on the dorsal surface of the pectoral propterygium. The LR is lacking in all myliobatiform rays surveyed, but is present in *Raja* (Fig. 5a) and *Rhinobatos* (Fig. 5b). The LR inserts on the dorsal surface of the pectoral propterygium, a configuration reminiscent of the DR insertion on the ventral surface of the propterygium. The presumed loss of

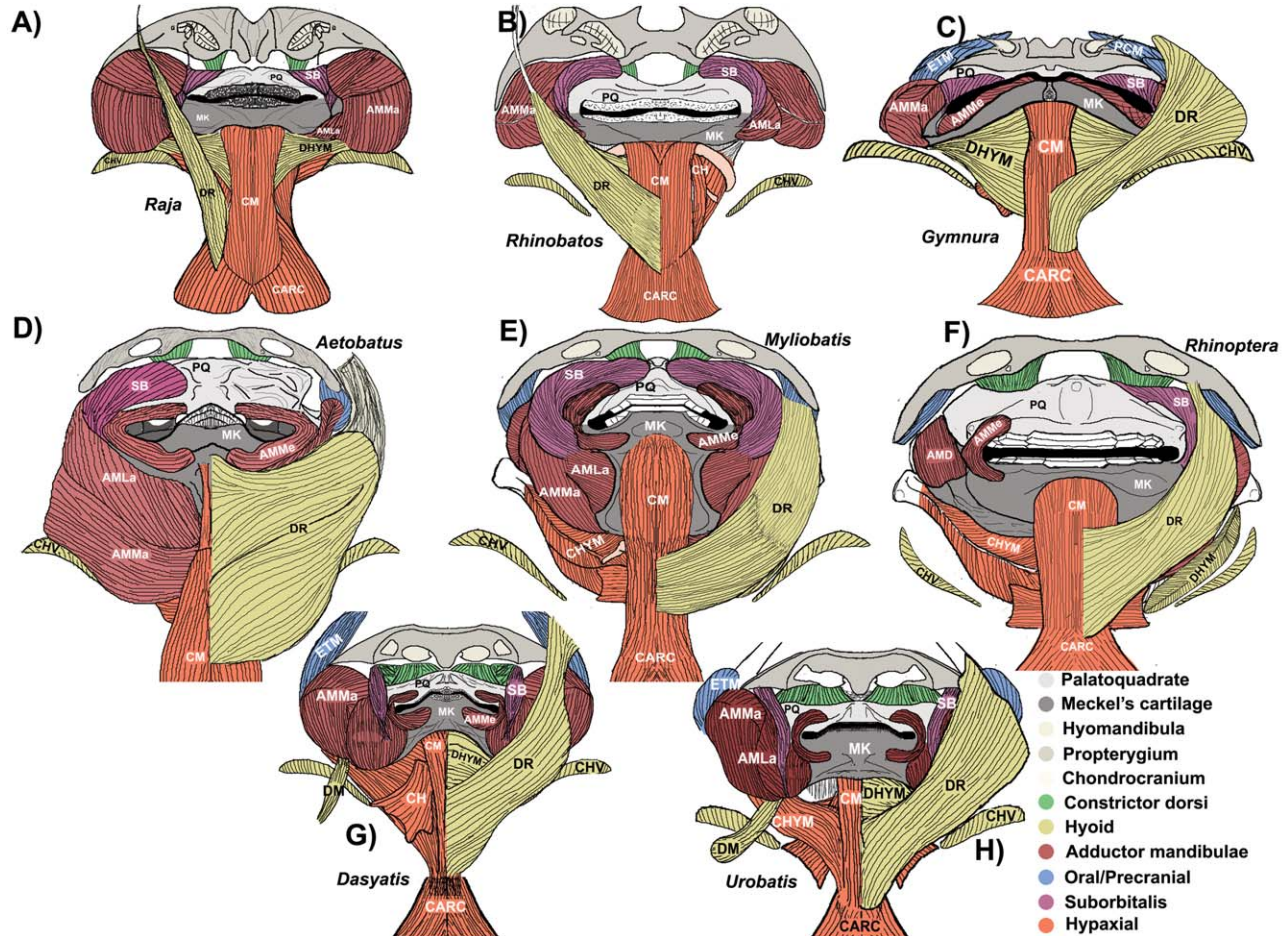


Fig. 6. Ventral superficial cephalic musculature of six species of batoid fishes; anterior is to the top. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracomandibularis; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideoparethmoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrati; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor dorsalis (mandibular plate); muscles in yellow are derived from the constrictor hyoideus (hyoid plate); muscles in orange are derived from the hypaxial plate (genio-hyoideus and rectus cervicis); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

the LR in stingrays may be correlated with the reduction of the rostral cartilages and snout rigidity in these taxa in general (as opposed to skates and guitarfish).

CHV/CHD. The CHV originates on the mid-ventral hypobranchial septa (Fig. 6), whereas the CHD originates on the dorsal aspect of the first gill arch. In all species surveyed the CHD inserts along the fascia it shares with its ventral component (Fig. 5). In this manner, the CHV and CHD cover the most anterior transverse surface of the first gill arches, forming a muscular wall separating the lateral hyoid and branchial regions.

DR. The DR generally originates on a mid-ventral raphe, superficial to the hypaxial musculature

and inserts on the rostrum, either directly or through a broad tendinous sheath of connective tissue. In some species, the DR covers nearly the entire ventral area between the anterior branchial basket and the lower jaw. The DR in *Raja* (Figs. 6 and 7a) and *Rhinobatos* (Fig. 6b), are conspicuously narrow, originating on the fascia ventral to the CARC and inserting via a long, thin tendon to the pectoral propterygium. In *Gymnura*, the DR are bilateral muscles which originate on fascia associated with the anterior portion of the CARC muscles and insert on the superficial fascia covering the ventral surface of the anterior portion of the pectoral propterygium (Fig. 6c). In *Dasyatis* (Fig. 6g) and *Urobatis* (Fig. 6h) the DR are thin

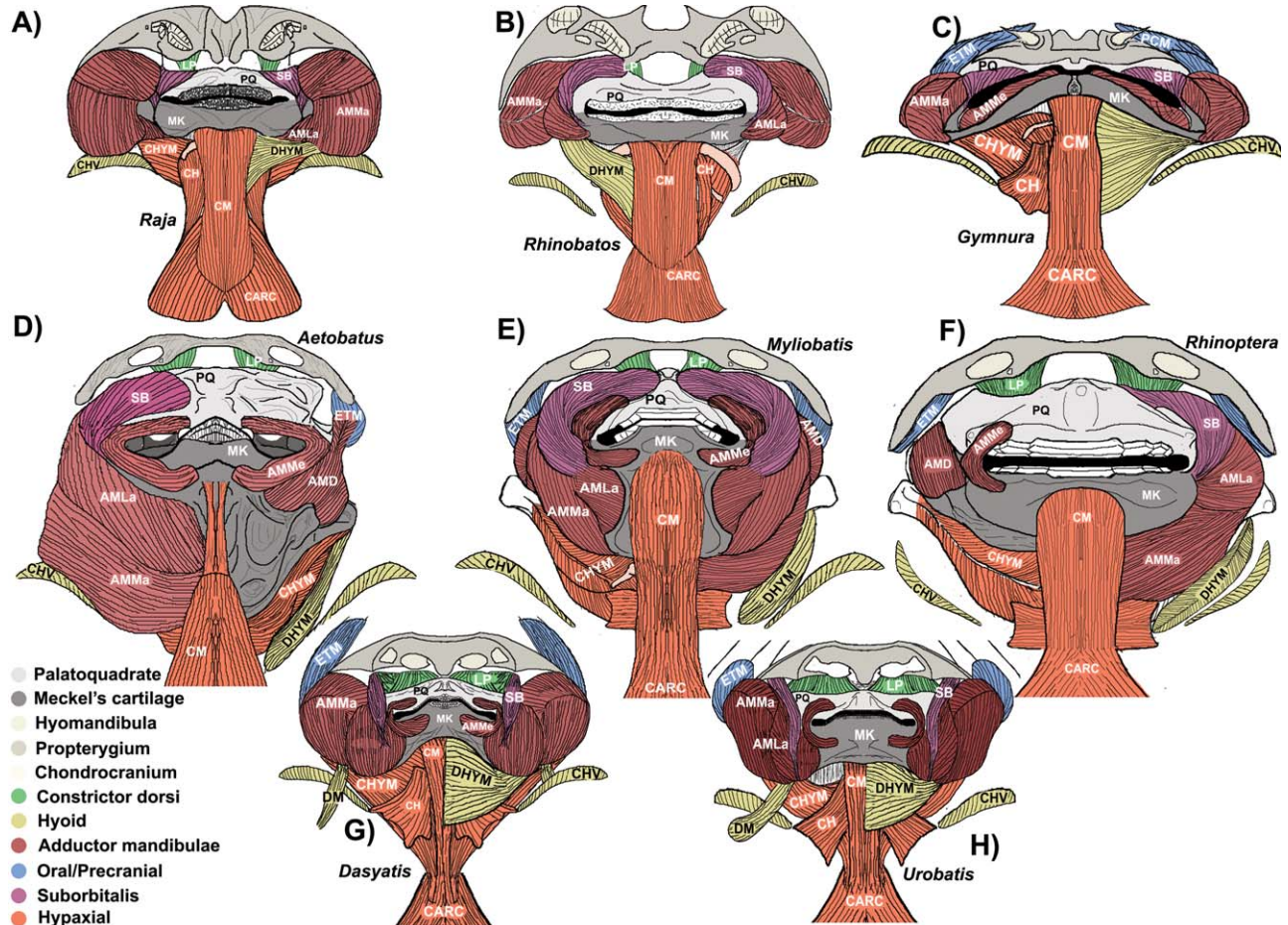


Fig. 7. Ventral middeep cephalic musculature of six species of batoid fishes; anterior is to the top. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracohyomandibularis; CM, Coracomandibularis; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideopterygoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrati; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor hyoideus (hyoid plate); muscles in orange are derived from the hypaxial plate (genio-hyoideus and rectus cervicus); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

and insert on the propterygium via connective tissue. The DR insert on the rostral region of the cranium or the rostral snout/cephalic lobe muscles in durophagous taxa and presumably serves to compress the cephalic and branchial regions during foraging (Sasko et al., 2006; Mulvany and Motta, 2013).

DHYM. The DHYM originates on a shared, midline raphe attached to the dorsal surface of the CM and extends laterally to insert on the posterolateral aspect of the hyomandibular cartilages. The antimeres of the DHYM in skates (*Raja*, Fig. 7a) do not share a common medial origin, instead originating lateral and slightly dorsal to either side of the CM. In guitarfish (*Rhinobatos*, Fig. 7b),

the DHYM divisions originate on the ventral midline, attaching to the dorsal side of the CM. In *Gymnura* (Fig. 7c), the two triangular-shaped antimeres of the DHYM share a common raphe at the ventral body midline, ventral to the CM and dorsal to the DR and inserting on the hyomandibular cartilage via tendons. In *Dasyatis* (Figs. 6 and 7g) and *Urobatis* (Figs. 6h), the DHYM inserts directly (without a tendon) on the hyomandibular cartilages. In *Rhinoptera* (Fig. 8f), *Aetobatus* (Fig. 8d), and *Myliobatis* (Figs. 7 and 8e), the DHYM originates on the medial, postero-dorsal side of the DR and inserts on the postero-lateral surface of the hyomandibular cartilages via a long tendon. The DHYM in *Myliobatis* and *Aetobatus* is narrower

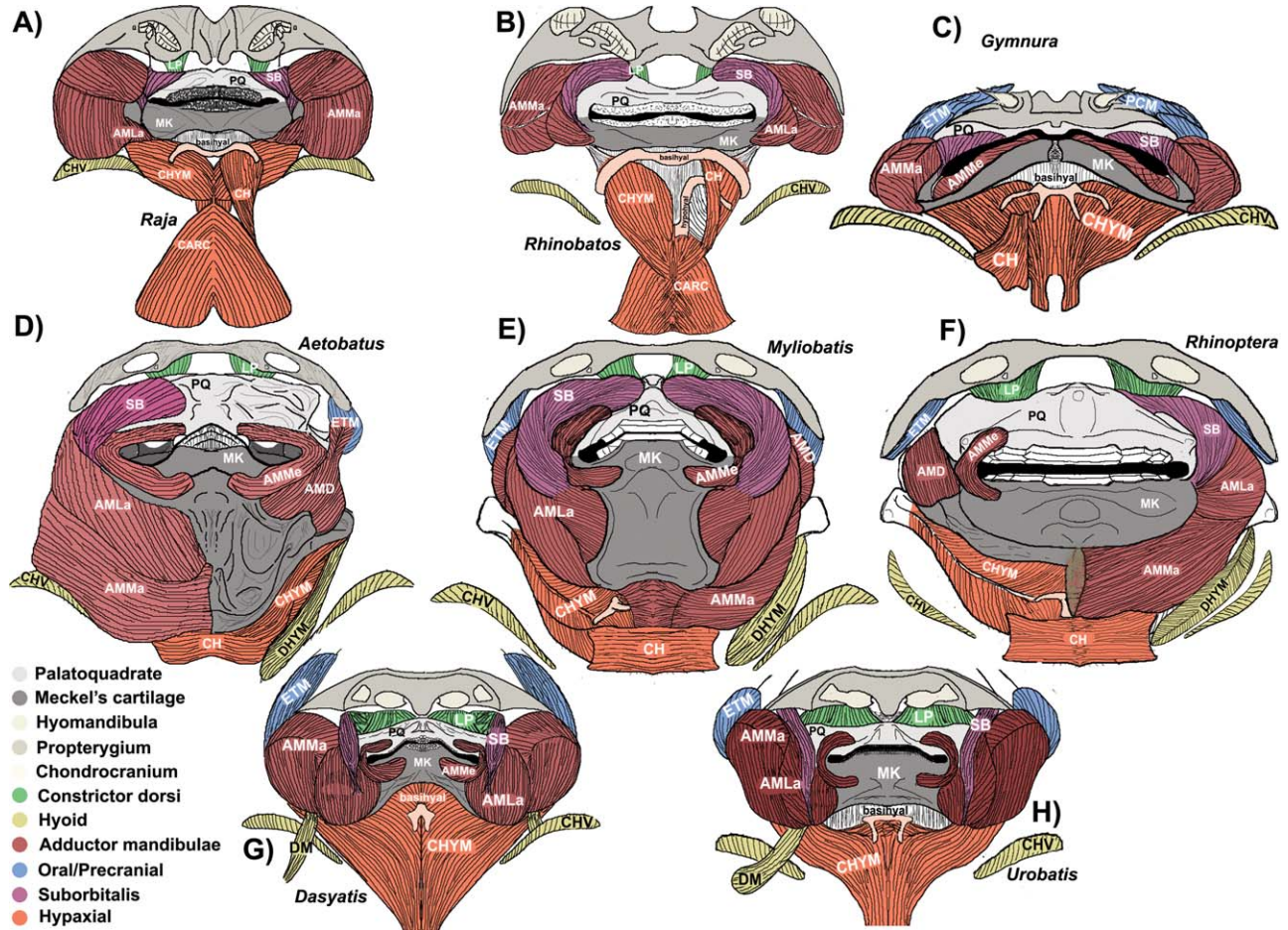


Fig. 8. Ventral deep cephalic musculature of six species of batoid fishes; anterior is to the top. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, and (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracohyoideus ventralis; CM, Coracomandibularis; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideo-parethmoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrati; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor dorsalis (mandibular plate); muscles in yellow are derived from the constrictor hyoideus (hyoid plate); muscles in orange are derived from the hypaxial plate (genio-hyoideus and rectus cervicis); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

than in the nondurophagous species and pennate fibered in *Rhinoptera* (Fig. 8). The DHYM in *Aetobatus* is considerably reduced compared to *Rhinoptera* and *Myliobatis*. In *Rhinoptera*, a division of the DHYM runs along the postero-lateral surface of the hyomandibular cartilage, overlying the CHYM.

DM. In those taxa where the DM was present, the muscle originates on the anterior edge of the DHYM (just dorsal to the DR, in most cases) and inserts directly on the most postero-lateral process of the MK, just posterior to the hyomandibular articulation with the jaws. The DM is associated with the DHYM and may not represent a distinct muscle, and its presence is variable in batoids (Miyake et al., 1992). The DM was found conclu-

sively in *Dasyatis* (Figs. 9 and 10g) and *Urobatis* (Figs. 9 and 10h), but was not located in *Raja*, *Rhinobatos* or *Gymnura* (where it is expected—Miyake et al., 1992). The DM is lacking altogether in myliobatids and rhinopterids (Miyake et al., 1992).

Oral/Precranial Series

These muscles are the vestige (along with the labial cartilages and lip folds) of the pregnathostome "oral" mouth (Mallat, 1996, 1997), the jaws of modern gnathostomes representing a pharyngeal or branchial-derived mouth. The specific relationship between the ethmoideo-parethmoidalis (ETM), precranial muscles (PCM), and suborbitalis [SB = levator labii superioris, Edgeworth (1935)

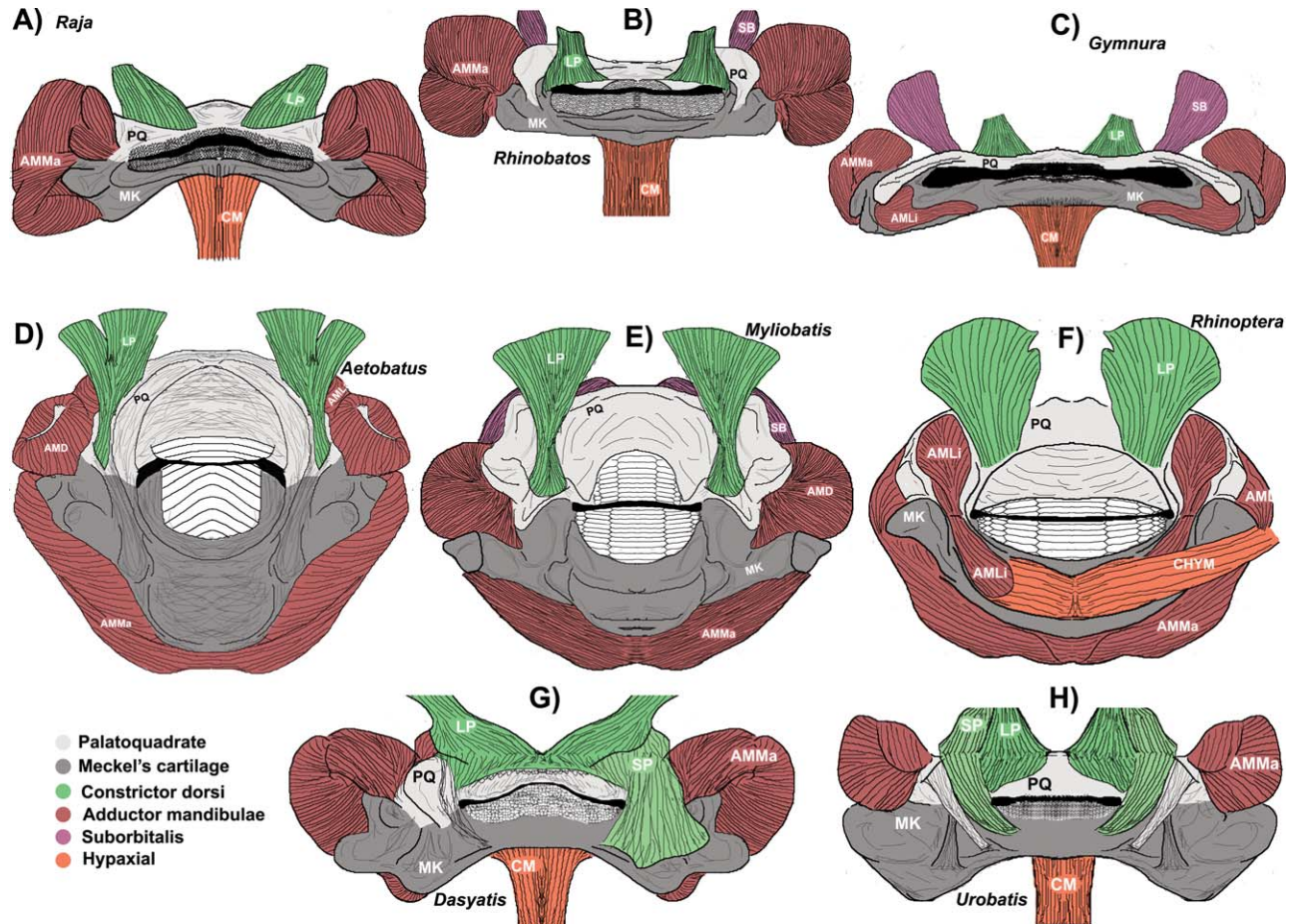


Fig. 9. Dorsal jaw adducting musculature of six species of batoid fishes; anterior is to the top. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, and (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracohyoideus; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideo-parethmoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrati; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor dorsalis (mandibular plate); muscles in yellow are derived from the constrictor hyoideus (hyoid plate); muscles in orange are derived from the hypaxial plate (genio-hyoideus and rectus cervicis); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

or = preorbitalis, Mallat (1996, 1997)] is unknown and more generally, the embryonic origin of the two former muscles is entirely uncertain (we suggest here, based on placement and orientation that they may be precranial). The oral/PCM, including the SB, precranial, and ETM, likely deal with retraction and possibly controlled realignment of the jaw-adductor muscle complex back toward the cranium during jaw protrusion (Mallat, 1997), or more generally with maintaining anterior contact between the cranium and jaws. Both the ETM and PCM are miniscule in *Raja* and *Rhinobatos*, but seem to articulate the jaw adductors (and the jaws themselves) to the pectoral propterygium. It is possible that the PCM and ETM muscles may simply be different divisions of the same muscle, however, it is possible in most spe-

cies to differentiate these two divisions based on fiber direction.

ETM. The ETM muscles in *Gymnura* originate on the antero-lateral regions of the chondrocranium, just ventral to the eye (see Appendix for more information). They insert on the disto-lateral pectoral propterygium cartilage, which encircles the cranial region in these stingrays, running along the medio-lateral surface, intimately associating with the PCM (Fig. 8). In *Myliobatis*, the PCM and ETM muscles are difficult to reveal, as they are found on the medial surface of the pectoral propterygium (Gonzalez-Isais, 2003). The ETM in this species originates on the medio-lateral surface of the posterior PCM and inserts onto the jaw adductor musculature, in particular the adductor mandibulae deep's (AMD) point of origin on the

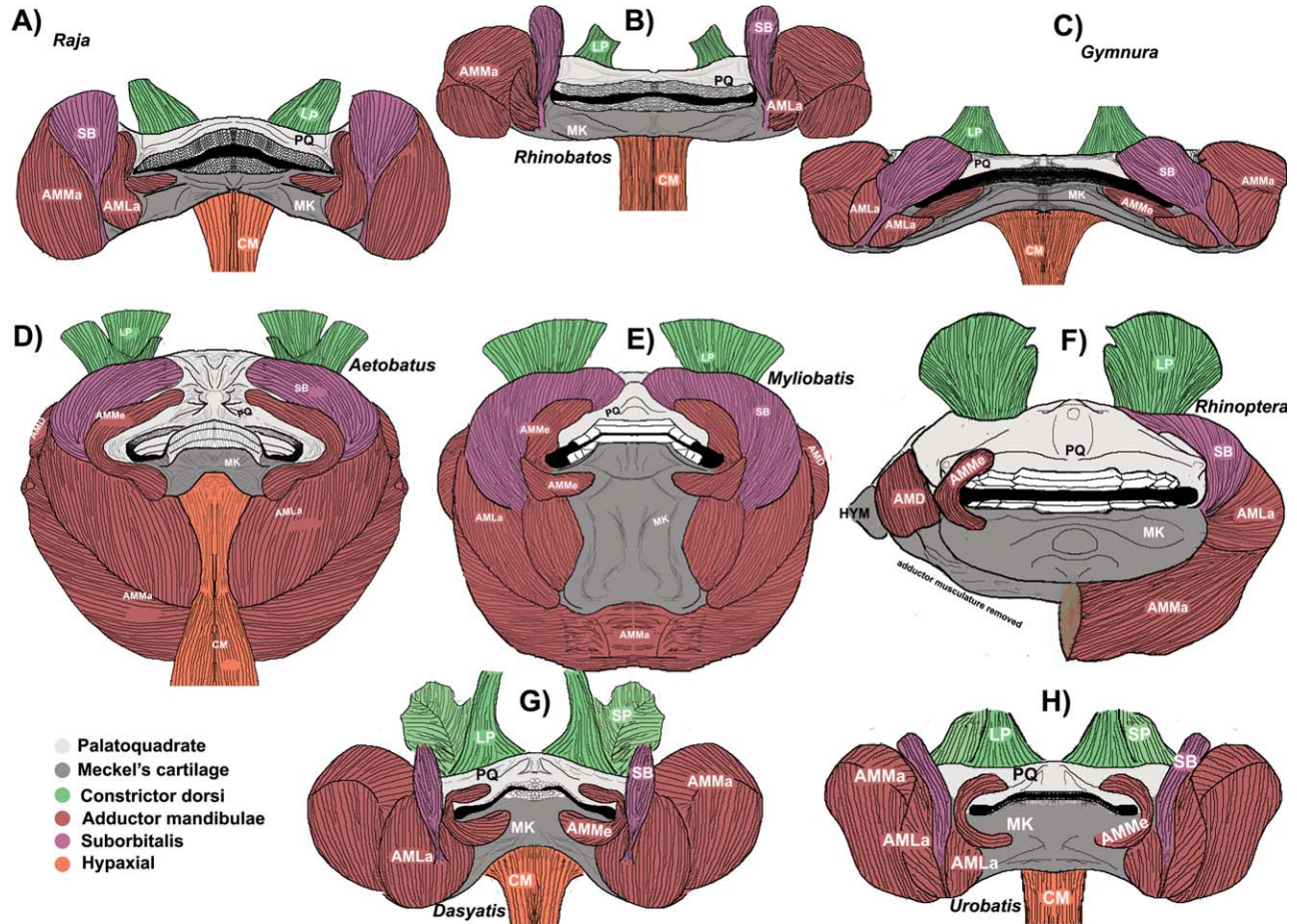


Fig. 10. Ventral jaw adducting musculature of six species of batoid fishes; anterior is to the top. (a) *Raja eglanteria*, (b) *Rhinobatos lentiginosus*, (c) *Gymnura micrura*, (d) *Aetobatus narinari*, (e) *Myliobatis freminvillei*, (f) *Rhinoptera bonasus*, (g) *Dasyatis sabina*, and (h) *Urobatis jamaicensis*; AMD, Adductor mandibulae deep; AMMa, Adductor mandibulae major; AMMe, Adductor mandibulae medialis; AMLa, Adductor mandibulae lateralis; AMLi, Adductor mandibulae lingualis; CARC, Coracoarcualis; CH, Coracohyoideus; CHD, Constrictor hyoideus dorsalis; CHV, Constrictor hyoideus ventralis; CHYM, Coracohyoideus; CM, Coracomandibularis; DHYM, Depressor hyomandibularis; DM, Depressor mandibularis; DR, Depressor rostri; ETM, Ethmoideo-parethmoidalis; LHYM, Levator hyomandibularis; LP, Levator palatoquadrate; LR, Levator rostri; PQ, Palatoquadrate; PCM, Precranial muscles; MK, Meckel's cartilage; SB, Suborbitalis; SP, Spiracularis. Muscles in red are derived from the adductor mandibulae (mandibular plate); muscles in green are derived from the constrictor dorsi (mandibular plate); muscles in yellow are derived from the constrictor hyoideus (hyoid plate); muscles in orange are derived from the hypaxial plate (genio-hyoideus and rectus cervicis); the SB is shaded purple to highlight its unique position (oral/premandibular plate), other oral/premandibular muscles are shaded in blue.

PQ (Fig. 8e). The PCM muscles in *Aetobatus* are either reduced or entirely absent, the ETM are thin (Fig. 8d). The ETM in *Rhinoptera* are found medial and dorsal to the origin of the cephalic lobe musculature, ventral to the inferior eye muscles. The ETM in *Rhinoptera* originates on the ventral side of the rostral cartilage, anterior and slightly dorsal to the cartilage surrounding the nares (Fig. 8f). The ETM inserts on the pectoral propterygium just ventral to the posterior-most region of the spiracular opening (Figs. 4 and 6–8). In *Dasyatis* (Figs. 7 and 8g) and *Urobatis* (Figs. 7 and 8h), only the ETM is readily distinguishable, associating closely with the jaw adductor musculature and the anterior pectoral propterygium. In both *Dasyatis* and *Urobatis* the ETM originates on the lateral surface of the anterior neurocranial region and

inserts directly on the jaw adductor musculature and the pectoral propterygium.

PCM. The left and right PCM divisions in *Gymnura* (Figs. 7 and 8c) originate on the rostral midline at the anterior surface of the chondrocranium (anterior to the fontanelle) and proceed laterally, hugging the postero-medial surface of the anterior pectoral propterygium, eventually inserting on the lateral corner of the chondrocranium, ventral to the preorbital processes (Nishida, 1990; Gonzalez-Isais, 2003). The PCM in *Myliobatis* underlie the inferior muscles of the eye (and partly the eye itself), inserting on the posterior-ventral surface of the rostral cartilages. For *Aetobatus*, see ETM section above. The PCM in *Rhinoptera* are either reduced or indistinguishable from the ETM muscles. Further inquiry into the function,

relationship, and embryological derivation of the PCM and ETM are needed, particularly considering their variable presence and morphology among species and nonintuitive function.

SB. The SB originates on the ventral side of the chondrocranium and inserts on the MK via a narrow tendon, likely functioning in *Raja* (Fig. 9a), *Rhinobatos* (Figs. 9 and 10b), *Gymnura* (Figs. 8c, 9, and 10c), *Dasyatis* (Fig. 10g), and *Urobatis* (Fig. 10h) as a means of lifting the jaws toward the chondrocranium. In *Rhinoptera* (Fig. 10f), *Aetobatus* (Fig. 10d), and *Myliobatis* (Figs. 9 and 10e), the SB has become disassociated from the chondrocranium and likely functions instead in jaw adduction. The SB in these durophagous taxa is a relatively large, parallel-fibered, delta-shaped muscle originating on the latero-ventral surface of the PQ, inserting via a tendon [shared with the adductor mandibulae lateralis (AMLa) complex] on the anterior-most lateral portion of the wing process on the MK. Consistent insertion of this muscle via a tendon on the lower jaw is common across all taxa as well as its innervation by the mandibular nerve V₃ (Mallat, 1996, 1997).

Mandibular Series

The muscles of the mandibular series are derived from either the embryonic constrictor dorsalis or adductor mandibulae. These muscles evolved from gill constrictors on pregathostome anterior gill arches (but see Supporting Information). In elasmobranchs, the constrictor dorsalis gives rise to two muscles: the levator palatoquadrate (LP) and the spiracularis (SP). In batoids, the embryonic adductor mandibulae gives rise to a large number of muscle divisions, namely the adductor mandibulae medialis (AMMe), AMLa, AMD, adductor mandibulae lingualis (AMLi) and the adductor mandibulae major (AMMa). The intermandibularis of sharks is not present in Batoidea. Muscles of the constrictor dorsalis (LP and SP) originate on the ventral surface of the chondrocranium and insert on the PQ (to some extent). Specifically, the SP originates posterior to the LP and inserts along the rostral portion of the spiracular cartilage as well as portions of the anterior and dorsal PQ. The muscles of the AM complex all originate on the ventral PQ cartilage and insert on the ventral MK (but see AMLi). The LP and SP aid in retraction of the PQ toward the chondrocranium. The SP specifically rotates the spiracular cartilage to expose the spiracular opening. The adductor mandibulae muscles predominantly adduct the upper and lower jaws.

LP. The LP is always closely aligned with the SP and distinguishing where one muscle begins and the other ends is sometimes difficult. In all species surveyed the LP originates on the ventral face of the chondrocranium, on the medial surface

of the otic region, posterior and perpendicular (transverse) to the origin of the SB in species where the SB still maintains contact with the cranium (see above), but still anterior to the origin of the SP. In all taxa surveyed, the LP inserts on the soft tissue surrounding the lingual interior of the jaws, dorsal to the PQ as well as directly attaching to the PQ itself (Figs. 9 and 10). The LP is noticeably smaller reduced in *Myliobatis* than in *Rhinoptera*. In *Rhinoptera* and *Aetobatus* the LP consists of three muscle heads, two of which originate medially within the otic region (one slightly anterior to the other) and the third originating far posterior to the other two and lining the dorsal tissue of the pharyngeal chamber (Figs. 9 and 10 d–f). In *Aetobatus* and *Myliobatis* the LP inserts directly on the dorsal anterior edge of the PQ with a tendon and aponeurotically to the surrounding oral tissue (Fig. 9e).

SP. The SP is generally a small, strap-like muscle that originates on the lateral aspect of chondrocranium, runs adjacent (medio-posteriorly) to the LP, inserts along the dorsal surface of the spiracular cartilage and wraps around the cartilage until it covers both the posterior and anterior faces. In all batoids except the durophagous taxa (Fig. 5), the SP predominantly covers the anterior face of the spiracular cartilage as well as the dorsal aspect. However, in both *Dasyatis* and *Urobatis*, an additional “ventral extension” of the SP (Miyake et al., 1992) extends across the entire surface of the spiracular cartilage to insert on the dorsal face of the upper and lower jaws (Figs. 9g,h and 10g,h). The SP in *Rhinoptera* originates on the lateral aspect of the chondrocranium, ventral to the postorbital process (Fig. 5). It then inserts via two muscle heads, on the antero-dorsal region of the hyomandibular cartilage and anteriorly on the PQ. One of these two muscle heads in *Rhinoptera* may be homologous to Miyake’s (1992) “ventral extension” of the SP.

AMMe. The AMMe is absent in *Rhinobatos* and is only present along the lower jaw in *Raja* (Fig. 10a) and *Gymnura* (Fig. 10c), originating on the upper jaw at the corner of the mouth via connective tissue. In *Rhinoptera* (Fig. 10f), *Aetobatus* (Fig. 10d), *Dasyatis* (Fig. 10e), and *Urobatis* (Fig. 10h) the AMMe makes a complete circuit around the corner of the mouth. In *Aetobatus* specifically, the AMMe is parallel fibered, elongate, and wraps around the mouth opening, originating just anterior to the upper tooth row and inserting on the MK just posterior to the most procumbent (oldest) tooth row (Fig. 10d). This muscle is typically associated with the labial cartilages. In *Myliobatis* (Fig. 10e), this muscle does not continue its entire circuit around the corners of the mouth and is instead divided into two divisions (anterior and posterior) connected by a weak fibrous connection. In addition, the labial cartilages in *Myliobatis* are

conspicuously reduced, compared to the condition seen in *Rhinoptera* and *Aetobatus* (Fig. 10d–f).

AMLa. The AMLa complex is typically treated as two divisions, (named AML1 and AML2, Gonzalez-Isais, 2003; Nishida, 1990; Wilga and Motta, 1998) which we refer to as the AMLa proper (AML1) and AMMa (AML2). We observe that the AMLa shares a common tendinous insertion with the SB on the MK, while the AMMa insertion is restricted to the lateral corners of the lower jaw or the base of the wing process (in durophagous myliobatiforms). In *Raja* (Fig. 10a), *Rhinobatos* (Fig. 10b) and *Gymnura* (Fig. 10c) the AMLa is smaller (compared to other taxa surveyed), originating on the anterior edge of the PQ and inserting on the ventral face of the MK. In *Aetobatus* (Figs. 9 and 10d) and *Myliobatis* (Figs. 9 and 10e), differentiation between the AMLa, AMMa, and SB can be difficult due to the manner in which all these muscles seem to attach in parallel (see AMMa description below), although the differing fiber direction of these muscles are clearly identifiable. The AMLa and SB insert via a shared tendon on the MK, with the SB insertion slightly anterior to that of the AM lateralis. The AMLa in *Aetobatus* and *Myliobatis* also inserts aponeurotically along the ventral face of the MK (Fig. 9d,e). The AMLa in *Rhinoptera* (Figs. 9 and 10f) is closely associated with both the SB and AMMa, separated from the former by the trigeminal nerve and the latter via the AMMa tendinous connection to the upper jaw (which the AMLa overlays). The AMLa in *Rhinoptera* originates just anterior to the PQ's jaw joint attachment site and the posterior portion of the SB and then inserts on the MK via a tendon it shares with the SB. In *Dasyatis* (Figs. 9 and 10g) and *Urobatis* (Figs. 9 and 10h), the AMLa is a pennate muscle which originates on the dorsal side of the PQ (on the antero-lateral processes) and then inserts on the lateral, anterior-most process on the ventral side of the MK. It is worth noting that the AMLa, SB, and AMMa are joined by several layers of connective tissue.

AMMa. The AMMa is by far the largest jaw adductor in all species surveyed. The angle at which each muscle division's myofibers attach to these fascia is reminiscent of a pennate-fibered muscle or several muscles working in parallel. More research is needed to investigate if these three divisions act as a concerted muscular unit. In *Raja* (Figs. 9 and 10a), *Rhinobatos* (Figs. 9 and 10b), *Gymnura* (Figs. 9 and 10c), *Dasyatis* (Figs. 9 and 10g), and *Urobatis* (Figs. 9 and 10h), the AMMa is a pennate-fibered muscle which covers the entire jaw joint region. In nondurophagous stingrays, the AMMa originates on the anterior lateral curvature of the PQ and inserts via tendon on the ventral posterior region of the MK. In *Rhinoptera*, *Aetobatus*, and *Myliobatis* the AMMa is

massive, generally larger than all other jaw adductors combined; it is a pennate-fibered muscle which originates on the PQ via stout tendons on both sides of the mouth and wraps around and up under the "chin" of the animal's lower jaw in a large "U" shape (Figs. 8–10d–f). In *Rhinoptera* (Figs. 9 and 10f) the AMMa fits intimately within the "shelf" created by the wing process of the MK (Figs. 8f and 10f). In *Aetobatus* (Figs. 8d, 9, and 10d) and to a lesser extent *Myliobatis* (Figs. 8e, 9, and 10e), and *Rhinoptera* (Figs. 9 and 10f), a portion of AMMa also originates aponeurotically on the dorsal lateral surface of the PQ far anteriorly of the tendinous insertion. The AMMa tendons wrap around the lateral labial region of the MK via a stout fibrocartilaginous pad which has been posited to redirect AMMa contractile force to an antero-posterior direction more in line with occlusion (see Summers, 2000; Summers et al., 2003). In *Aetobatus* and *Myliobatis* (Figs. 9 and 10e,f), the AMMa insertion on the posteroventral surface of the MK is similar to *Rhinoptera*, although the muscle actually covers the comparatively reduced wing process in the former two taxa (Fig. 10e,f).

AMD. The AMD, a parallel-fibered muscle, lies medial and slightly dorsal to the tendinous region of the AMMa, originating partly in a fossa just ventral to the jaw joint and separated from the AMMa via myosepta. The AMD is presumably absent or far reduced in *Raja*, *Rhinobatos*, *Gymnura*, *Dasyatis*, and *Urobatis*. In *Rhinoptera* the AMD originates and inserts entirely within the fossa created by the gap between the jaws antero-posteriorly and the jaw joint dorsally (Figs. 8f and 10f). The AMD inserts on the MK within the lower jaw's region of the same fossa, also just ventral to the jaw joint. In *Aetobatus* (Figs. 8d, 9, and 10d) and *Myliobatis* (Figs. 8e, 9, and 10e), the AMD originates far anteriorly on the PQ on a narrow skeletal projection, wrapping around the entire (dorsal, lateral, and ventral) surface of this projection (Fig. 8e). This muscle may be an interior division of the AMMa complex in *Rhinoptera*, but is strongly independent in *Myliobatis* and *Aetobatus*. In both *Myliobatis* and *Aetobatus*, the AMD extends far posterior and laterally from the other adductor divisions and is considerably greater in size than in *Rhinoptera*. The AMD in *Myliobatis* is particularly large and articulates via connective tissue to the PCM of the propterygium (Figs. 9 and 10e).

AMLi. The AMLi, is present in *Gymnura* and *Rhinoptera*, is found medially, on the dorsal (lingual) surface of the jaws and jaw adductor bundle (facing the chondrocranium) and extends across both the upper and lower jaws, adjacent (medial) to the jaw joint. The AMLi is a dumbbell-shaped, parallel-fibered muscle apparently split into two divisions closely associated with the ligaments holding the dorsal surfaces of the upper and lower

jaws together in articulation. This muscle is reduced or absent in *Raja*, *Rhinobatos*, *Aetobatus*, *Myliobatis*, *Dasyatis* and *Urobatis*. The AMLi originates on the rostral-most, dorsal point of the PQ and inserts upon the posterior-most lateral region of the MK and is partly covered by the CHYM in *Rhinoptera* (Fig. 10f). In *Gymnura* (Fig. 9c), the AMLi is smaller and wraps around the dorsal (lingual) surface of the lower jaws along the corners of the mouth, medial to the jaw joint. The arrangement and orientation of the AMLi in *Rhinoptera* may suggest this muscle division is a dorsal extension of the AMD, perhaps given the more dorsoventrally compressed jaws in *Rhinoptera* compared to sister myliobatids.

DISCUSSION

The relationship between muscle morphological diversity, jaw suspension, and ecological niche is largely unknown in batoids. We expected that due to biomechanical constraints on skeletal materials and performance, durophagous stingrays will broadly resemble (in terms of jaw muscle hypertrophy, molariform teeth, etc.) other durophagous taxa, like horn sharks (Huber et al., 2005; Kolmann and Huber, 2009). Given patterns of morphological evolution in chondrichthyans, namely that jaw suspension modes are fixed at deep phylogenetic nodes and, independent lineages each occupy an array of trophic niches, we expected that muscle variation would follow patterns of skeletal evolution. That is, mandibular musculature will be remarkably disparate both within and between lineages, while hyoid musculature will show disparity only between lineages (Table 2).

Durophagy in Myliobatiform Stingrays

Our data show several consistent differences between durophagous stingrays and other batoid species apparent in the arrangement of the feeding musculature, particularly in the larger size and number of jaw adductors, a reduction in the size of nonjaw adducting muscles, and a potential increase in jaw joint stabilization across durophagous rays. The most obvious similarity between durophagous rays and other durophagous elasmobranchs (Huber et al., 2005; Kolmann and Huber, 2009) is that the jaw adductor musculature in these taxa are noticeably hypertrophied compared to species which do not consume hard-shelled prey. Pennate-fibered muscles are more prevalent in durophagous taxa (Huber et al., 2008), which increase force generation over fusiform musculature, while conserving volume (Cochran, 1982).

Although not restricted to durophagous rays, but particularly interesting within batoids is the manner in which some muscles insert over the maximum available surface area of the jaw skeleton. In *Dasyatis* and *Urobatis* (as well as the elec-

tric ray, *Narcine*, see Dean and Motta, 2004 a,b), the primary jaw adductor muscle originates on the dorsal surface of the jaw structure, usually covering the jaw joint, to wrap anteriorly over and then sharply posterior to insert on the lower jaw. In *Aetobatus* and *Myliobatis* this is exemplified by the condition of the AMD, which extends far anteriorly to wrap around an anterior projection of the PQ (Figs. 8–10d,e). Another functional interpretation of this arrangement may simply be to displace muscle action as far from the fulcrum (jaw joint in this case) as possible, increasing the speed at which the jaws can close (Fig. 2). In *Myliobatis* and *Rhinoptera* we also see an expansion of the wing process of the MK (lower jaw) associated with the increase in size of the AMMa (Figs. 8–10e,f). However, no other taxa exhibit the “chin-strap” morphology of the primary jaw adductor (AMMa) as seen in durophagous stingrays. In durophagous sharks, jaw adductor muscle mass is usually increased by expanding the cross-sectional area of the quadratomandibularis (homologous to adductor mandibulae) muscles (Summers et al., 2004; Kolmann and Huber, 2009; Habegger et al., 2012). In contrast, the batoid bauplan may constrain the available area for muscle hypertrophy; lateral expansion of the jaw adductors may be inhibited in batoids owing to the anteriorly directed expansion of the pectoral fins and by necessity, the encircling pectoral propterygium (Figs. 4 and 6–10). The deepening of the cranial region in durophagous stingrays when compared to their epibenthic relatives presumably “makes room” for larger jaw adductors, which may also constrain the size of other cranial muscles not involved in jaw adduction (see below).

Greater emphasis of the AMMa for jaw adduction is exemplified in durophagous rays, where a muscle–tendon complex is thought to orient the AMMa muscle force in a plane perpendicular to the dental occlusal surface (see Summers, 2000; Summers et al., 2003; Kolmann, 2012). Also, appropriation of the SB (SB) from an upper jaw retracting muscle to a jaw adductor in durophagous taxa could potentially be associated with maximizing the overall muscle force available for forceful biting (Figs. 2 and 8–10d–f). Expansion of the muscle coverage overlying the jaw joint in *Rhinoptera* is also notable, mostly in the AMLa and AMMa (Figs. 8–10d–f). The AMLi and the AMD are found only in durophagous taxa. Both muscles flank (dorsally and ventrally) the jaw joint region (Fig. 2). This may aid in increasing joint stability by resisting tensile loading of the jaw joint, as might occur during biting in a class 2 lever system as proposed by Summers’ (2000) “nutcracker” model of rhinopterid jaw mechanics. These muscles may also keep the jaws aligned during feeding as the jaw joints are conspicuously slack, exhibiting a high range of motion when the

surrounding jaw musculature is removed (Summers, 2000, Figs. 9f and 10f).

Differences between durophagous and nondurophagous taxa are also evident outside the mandibular musculature. Given the changed role of the SB in durophagous rays from jaw suspension to jaw adduction, it is perhaps no surprise then that the LP in durophagous stingrays are relatively immense (Figs. 8–10d–f). Together, the SP and the LP may have rendered the jaw elevating role of the SB (Fig. 2) redundant, allowing the SB to shift to a purely adductive function, another example of interplay between jaw adductor and other cranial muscles. The DHYM in *Aetobatus*, *Myliobatis*, and *Rhinoptera* (Figs. 6–8d–f) are comparably smaller than what is seen in nondurophagous rays (Figs. 6–8a–c,g,h), and in *Rhinoptera* (compared to *Myliobatis* and *Aetobatus*) the DHYM has shifted to a pennate-fiber morphology (Figs. 6–8d–f), which suggests a reduction in muscle volume without a decrease in performance (Cochran, 1982; Huber et al., 2008). In contrast, the size and position of the DHYM in nondurophagous stingrays (Figs. 6–8a–c,g,h) suggests that in addition to depressing the hyomandibular cartilages, the DHYM may also adduct those cartilages and perhaps even the jaws (Fig. 2). In this position, the DHYM is capable of constricting the floor of the pharynx, depressing the hyomandibular cartilages, and possibly aiding in jaw protrusion via medial compression of the right and left halves of the jaws about their flexible symphyses (as seen in narcinid electric rays—Dean and Motta, 2004a; Dean et al., 2008). As the jaw symphyses are fused in durophagous rays (Figs. 8–10d–f), the DHYM may have lost some of its functional repertoire, and correspondingly, durophagous taxa are the only stingrays in which the DHYM does not attach to the lower jaw as well as the hyomandibulae. Taken together, this suggests that the high degree of hyoid-driven jaw protrusion seen in nondurophagous stingrays is impossible for durophagous rays, although rapid, cyclical jaw movements are still a major function of feeding/excavation of prey (Sasko et al., 2006; Collins et al., 2007). Durophagous stingrays in particular offer a fascinating evolutionary system in which to test biomechanical hypotheses regarding musculoskeletal function and ecomorphology, and for investigating ontogenetic trends in feeding performance.

In batoids we observed a number of muscles that attach to the jaws via direct tendinous insertions as well as aponeurotic (tendinous) sheets. Aponeurotic muscle attachments (as opposed to tendinous point insertions) are prevalent in chondrichthyans, perhaps related to the relatively pliable nature of the skeletal cartilage relative to bony skeletons (Summers and Koob, 2002; Summers et al., 2003). In taxa with aponeurotic insertions, the muscle attachment is integrated broadly into

the fibrous outer perichondrium that wraps the skeleton, thereby distributing strain on the skeleton over a larger area. In durophagous taxa, however, a more robust jaw skeleton (stiffened by cortical thickening and trabecular internal reinforcement; Summers, 2000) coupled with fusion of certain skeletal elements (i.e., jaw symphyses) makes aponeurotic insertions unnecessary. These direct tendinous insertions are more amenable to efficient force transfer (Dean et al., 2007b) across a rigid (jaw) structure and reduce the area needed for muscles to attach. Analysis of correlations among muscle activity, skeletal strains during natural feeding behaviors, and muscle attachment morphologies in these animals will help to elucidate basic form-function relationships in elasmobranch skeletal anatomy, which remain woefully understudied.

Conservation and Variation in Chondrichthyan Feeding Musculature

In general, differences in the cranial anatomy of chondrichthyan fishes are primarily observed in the muscles stemming from the hyoid and mandibular embryonic muscle plates (Miyake et al., 1992, Table 2). The evolutionary malleability of these two embryonic plates has played a large role in driving ecological diversity at different points in the diversification of cartilaginous fishes. Broad comparisons across the major groups of chondrichthyans—sharks, batoids and holocephalans—illustrates that muscle variability within these taxa is explained by both developmental identity and functionality (Miyake et al., 1992). Phylogenetic differences in the arrangement of muscles stemming from the branchial muscle plate are not as apparent as in the mandibular and hyoid plates (Table 2); therefore we restrict our brief discussion to the latter two muscle groups and the hypaxials (see Miyake et al., 1992 for additional information).

The hyoid muscle plate in chondrichthyan fishes is overwhelmingly disparate between batoids and sharks, with even more overt differences between batoids and holocephalans (Table 2, Miyake et al., 1992; Anderson, 2008). This is presumably associated with the increasing decoupling between the jaws and chondrocranium (mediated by the hyomandibular cartilages, Fig. 1), and specific to batoids, the ventral orientation of the mouth. Holocephalans are characterized by fusion of the upper jaw to the cranium (holostyly—Fig. 1a). Sharks exhibit various configurations of pre and postorbital, as well as hyostylic (Fig. 1b,d) connections between the jaws, hyomandibulae, and the cranium. Finally, batoids exclusively are characterized by “euhyostylic” suspension (or an “unsuspended” PQ—Maisey, 1980; Fig. 1c). Most of the differences in the overall arrangement of the

hyoid muscle plate seem to be restricted to crown clades. Between squaloid and galeoid sharks, for example, hyoid muscle arrangement (Wilga, 2005; Soares and de Carvalho, 2013) is conserved, despite these two clades having evolved independently from each other (~200 mya) for nearly as long as sharks have been separated from batoids (Aschliman et al., 2012). Two of the muscles arising from the hyoid plate in batoids (LHYM and DHYM, Figs. 5 and 6) are involved with jaw suspension and another two (DR and LR, Figs. 5 and 6) deal with manipulation of the rostral region in some batoids (skates and guitarfish, Table 1). Sharks do not have flexible snouts, but do exhibit highly kinetic jaws, whereas holocephalans have neither flexible snouts nor kinetic jaws (Maisey, 1980), making the absence of three of the four above muscles in nonbatoids unsurprising. This may suggest that further decoupling of the hyoid has allowed muscle divisions to acquire novel functionality beyond hyoid movement, as is the case for the depressor and LR, which position the snout in batoids.

Our data support the hypothesis that jaw suspension musculature, classified here as muscles which adduct the hyomandibular cartilages toward the cranium, are conserved across elasmobranchs (Table 2). During ventilation and feeding the DHYM and CHYM are oriented to depress and draw the hyomandibulae medially to expand the pharynx (Fig. 2). LHYM works as an antagonist to the DHYM and CHYM, drawing the hyomandibular cartilages dorsally, thus returning the hyomandibulae to a resting position (Fig. 2). In sharks, which lack the CHYM (Miyake et al., 1992; Anderson et al., 2008), depression of the hyomandibular cartilages are modulated solely by the CH. Movement of the hyoid then is always actuated by both a hyoid and hypaxial muscle component, with more divisions used in batoids (two hypaxial and two hyoid muscles, Fig. 2) than sharks (one hypaxial and one hyoid muscle, Table 2). The rectus cervicus (first embryonic hypaxial precursor) gives rise to the CH, and CARC muscles in sharks, in addition to the CHYM in batoids (Table 2). The genio-hyoideus (another embryonic hypaxial precursor) gives rise to the CM in all taxa. The rectus cervicus is undifferentiated in ratfishes (Didier, 1995, Table 2). Given the increasingly hyostylic nature of the jaws in batoids when compared to ratfish, and to a lesser extent, sharks, the CHYM may have evolved to maintain control and stability in this comparatively “free” jaw suspension.

In terms of “total” jaw suspension, involving both suspension of the hyoid AND the jaws, mandibular plate muscles are also implicated (Tables 1 and 2). The SP, with its association in some taxa with the hyomandibular cartilages (durophagous rays) and the upper jaw (*Dasyatis* and *Urobatis*), assist in jaw suspension in addition to regulating

the spiracular aperture. In all batoids, the LP is involved with retracting the jaw after the expansive phase of feeding (Wilga and Motta, 1998). The LP and SP (and the SB in some taxa) are always present as separate divisions in batoids, aiding in elevation of the PQ (Miyake et al., 1992). These muscles are variably expressed in sharks, depending on the presence or absence of the spiracle in these clades (Huber et al., 2011; Soares and de Carvalho, 2013); however, only the LP is found in ratfishes (Didier, 1995; Huber et al., 2011, Table 2).

Further variation in mandibular muscles is obvious between lineages and within clades. The levator series of muscles in ratfish (levator mandibulae, levator cartilaginis, and levator anguli and labialis muscles) stem from the mandibular muscle plate and presumably aid in movement of the labial cartilages (Didier, 1995; Huber et al., 2011). The specific relationship of these muscles to those in batoids and sharks is poorly known, besides general developmental homology (mandibular plate, Miyake et al., 1992, Table 2). In holocephalans, the jaw adductors consist of only two divisions, the AM anterior and posterior (Huber et al., 2008, 2011, Table 2). The quadratomandibularis in sharks is generally divided into four or five major divisions, each with slight differences in muscle fiber direction and architecture (Motta and Wilga, 1995, 1999; Wilga and Motta, 1998; Huber and Motta, 2004; Soares and de Carvalho, 2013, Table 2). The adductor mandibulae complex in batoids is divided in a similar manner into multiple divisions (AMMe, AMLa, AMMa, AMD, and AMLi). However, these muscles in batoids may serve a greater variety of functions related to feeding. The AMMe presumably functions in conjunction with the labial cartilages during suction feeding to manipulate the corners of the mouth (Dean and Motta, 2004 a,b). We suggest the AMD and AMLi in *Rhinoptera* and *Myliobatis* may help to stabilize the jaw joint during forceful biting, especially when unilateral adductor activity places the contralateral jaw joint in tension (Summers, 2000). Lastly, the AMLa and AMMa serve as the primary jaw adductors (Kolmann, 2012). In both elasmobranch clades, the SB (or preorbitalis, Mallat, 1997) is involved in lower jaw adduction and upper jaw protrusion (Wilga and Motta, 1998; Huber et al., 2011).

CONCLUSIONS

Our evolutionary understanding of jawed vertebrates is predicated within the context of neontological cranial anatomy. In particular, understanding current anatomical, functional and ecological diversity in organisms like chondrichthyans gives us perspective on ancient radiations and their legacy. The considerable degree of

variation in muscle position, muscle size and prevalence of novel muscle divisions is remarkable given the relatively low species diversity of batoid fishes and other elasmobranchs when compared to teleosts. We believe that the euhyostylic jaw suspension plays a considerable role in explaining trophic diversity in batoid fishes, analogous to how skeletal decoupling has been proposed to have facilitated functional, morphological, and ecological diversification in some teleosts (Schaefer and Lauder, 1996; Hulsey et al., 2006; Lujan and Armbruster, 2012). The comparatively “free” jaw suspension of batoids seems to have provided opportunities for some muscles (e.g., hyoid and mandibular muscles) to contribute to new behaviors while other muscles (e.g., branchial muscles) remain relatively unchanged. Our data suggest then, among derived stingrays at least, decreasing skeletal support for the feeding apparatus and an increase in muscular control and stability. This tendency in batoids is illustrated by muscles originating and then inserting on other muscles, the prevalence of novel or subdivided muscles, as well as the frequency with which direct tendon attachment to the skeleton are supplemented by aponeurotic sheets. The numerous adductor subdivisions in the jaws of durophagous stingrays, some of which overlie a conspicuously slack jaw joint ligament, are particularly suggestive of reliance on muscular, rather than skeletal support and control.

Repurposing of certain muscles for novel roles as we have described in batoids is probably not atypical for vertebrates, however, we document these novelties and their potential functional ramifications in a clade that has not received much attention from evolutionary or ecological studies. We conclude by stating several functional-evolutionary hypotheses, which need further testing:

1. Less direct skeletal articulation in jaw suspension promotes greater functional diversity, either caused by or related to a release of constraints from developmental associations. Following this, we would expect the mandibular and hyoid muscles to exhibit greater functional and behavioral variability than hypaxial and in particular, branchial musculature.
2. Less direct skeletal articulation in jaw suspension facilitates greater muscular morphological complexity (in terms of muscle division multiplicity, novelty, method of attachment, pennation).
3. The more compliant skeleton in cartilaginous fish necessitates direct muscle insertions supplemented by aponeuroses, which perhaps mitigates point-loading strains.

These hypotheses require experimental validation at the level of genotype expression, biomechanical and physiological traits, as well as

behavioral kinematics. Updated studies of embryological development through tissue density-specific staining methods is recommended to confirm muscle developmental homology across chondrichthyans and other fishes considering both phylogeny and ontogeny. To explore the functional diversity of cranial muscles, kinematic evaluation of feeding and respiration behaviors need to be examined. Electromyography methods documenting muscle activity during kinematic events in chondrichthyan fishes (as has been performed to a much broader degree in sharks; see Wilga et al., 2012) are needed to confirm whether muscle behavioral variability follows morphological and physiological variability. Taken together, these avenues of research would build off of previous and current anatomical study, providing an integrated direction for investigating form-function relationships in this understudied, yet trophically diverse group of fishes.

AUTHOR CONTRIBUTIONS

M.A.K., R.D.G., and D.R.H. procured specimens and funding. M.A.K., M.N.D. and D.R.H. performed dissections and exploratory muscle descriptions. M.A.K., D.R.H., R.D.G. and M.N.D. wrote the bulk of the article. The authors declare no conflict of interest in the publication of this submission.

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