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Patterns of diversification and phylogenetic structure in the dorsolateral head musculature of Neotropical electric eels (Ostariophysi: Gymnotiformes), with a myological synonymy

Correspondence:
Luiz Antônio Wanderley Peixoto
luizwp@yahoo.com.br

Luiz Antônio Wanderley Peixoto[1,2] and Mário de Pinna[1]

The present study offers a broad comparative analysis of the dorsolateral head musculature in the Gymnotiformes, with detailed descriptions and illustrations of the dorsolateral head muscles of 83 species representing combined all valid genera. Results permit a detailed assessment of primary homologies and taxonomically-relevant variation across the order. This provides the basis for a myological synonymy, which organizes 33 previously proposed names for 15 recognized muscles. Morphological variation derived from dorsolateral head musculature was coded into 56 characters. When analyzed in isolation, that set of characters results in Gymnotidae as the sister group of remaining gymnotiforms, and all other currently recognized families as monophyletic groups. In a second analysis, myological characters were concatenated with other previously proposed characters into a phenotypic matrix. Results of that analysis reveal new myological synapomorphies for nearly all taxonomic categories within Gymnotiformes. A Partitioned Bremer Support (PBS) was used to asses the significance of comparative myology in elucidating phylogenetic relationships. PBS values show strongly non-uniform distributions on the tree, with positive scores skewed towards more inclusive taxa, and negative PBS values concentrated on less inclusive clades. Our results provide background for future studies on biomechanical constraints evolved in the early stages of gymnotiform evolution.

Keywords: Anatomy, Electric fishes, Myology, Phylogeny, Partitioned Bremer Support.

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[1] Seção de Peixes, Museu de Zoologia da Universidade de São Paulo, Av. Nazaré, 481, Ipiranga, 04263-000 São Paulo, SP, Brazil. (LAWP) luizwp@yahoo.com.br (corresponding author), (MP) pinna@ib.usp.br.

[2] Núcleo de Ecologia Aquática e Pesca da Amazônia–NEAP, Universidade Federal do Pará, Av. Perimetral, 2651, Terra Firme, 66077-830 Belém, PA, Brazil.

O presente estudo fornece uma ampla análise comparativa da musculatura dorsolateral da cabeça dos Gymnotiformes, com descrições detalhadas e ilustrações dos músculos dorsolaterais da cabeça de 83 espécies representando quase todos os gêneros válidos. Resultados permitem uma avaliação das homologias primárias e da variação taxonomicamente relevante na ordem. Isto fornece a base para uma sinonímia da nomenclatura miológica que organiza 33 nomes previamente propostos para os 15 músculos reconhecidos. As variações morfológicas da musculatura dorsolateral da cabeça foram codificadas em 56 caracteres. Este conjunto de dados foi inicialmente analisado isoladamente, resultando em Gymnotidae como grupo-irmão dos demais Gymnotiformes; e todas as famílias como grupos monofiléticos. Numa segunda análise, os caracteres musculares foram concatenados com uma matriz fenotípica previamente proposta compondo uma ampla matriz morfológica combinada. Os resultados desta análise revelaram novas sinapomorfias miológicas para todas as categorias taxonômicas em Gymnotiformes. O Suporte de Bremer Particionado (SBP) foi implementado para acessar a influência da miologia em elucidar os relacionamentos filogenéticos. Os valores de SBP exibem uma distribuição não uniforme na árvore, com indicadores positivos para agrupamentos mais inclusivos e valores negativos de SBP em clados menos inclusivos. Nossos resultados fornecem subsídios para investigações futuras sobre as restrições biomecânicas envolvidas nos estágios inicias da evolução dos Gymnotiformes.

Palavras-chave: Anatomia, Peixes elétricos, Miologia, Filogenia, Suporte de Bremer particionado.

INTRODUCTION

Popularly known as “tuvíras”, “sarapós”, “knifefishes” or “neotropical electric eels”, the fishes of the order Gymnotiformes have a broad distribution in neotropical freshwater environments, occurring from southern Mexico to northern Argentina (Ferraris *et al*., 2017), with particularly rich diversity in the Amazonas-Orinoco-Guiana system (Albert, Crampton, 2005a; Dagosta, de Pinna, 2019). Those fishes are important components mostly in the nocturnal ichthyofauna (Albert, 2001), but also represent relevant diurnal elements, and occupy a wide range of habitats, from small streams to large rivers, including waterfalls, flooded forests and caves (Alves-Gomes *et al*., 1995; Albert, Crampton, 2005b). Gymnotiformes comprises about 260 valid species allocated in 34 genera (Ferraris *et al*., 2017) and five families: Apteronotidae, Gymnotidae, Hypopomidae, Rhamphichthyidae and Sternopygidae (Albert, 2001).

The order is easily distinguished from other Neotropical fish lineages by their extremely elongated, cylindrical or laterally compressed body, with the anal fin extending for much of the ventral margin and by the absence of dorsal, adipose and pelvic fins. The caudal fin is present only in Apteronotidae and in *Electrophorus* Gill, 1864 (Gymnotidae) (Mago-Leccia, 1994; de Santana *et al*., 2013; Tagliacollo *et al*., 2016). Such body pattern is related to the most conspicuous biological characteristics of gymnotiforms: electroreception and electrogenesis (Moller, 1995; Crampton, Albert, 2006). These fishes move by rippling of the anal-fin rays, allowing for body stability during swimming and thus uniformity of the electric field generated around the fish. The electric field is used in fish orientation and communication, or in prey detection (Albert, Campos-da-Paz, 1998; Albert, 2001). Discharges from the electrical organs can be of the "pulse type", characterized by short-duration sequential discharges generated at rates from 1 to 120Hz, with a long pause period or "electrical silence" (Gymnotidae, Hypopomidae and Rhamphichthyidae); or "wave type", at rates from 20 to 2200Hz, without intervals (Sternopygidae and Apteronotidae) (Albert, Crampton, 2005b).

Anatomical studies on Gymnotiformes follow the historical trend in other groups of Teleostei and focused on relatively detailed descriptions of osteological complexes (*e.g.*, Chardon, de la Hoz, 1974, 1977; Mago-Leccia, 1978; Hilton *et al*., 2007; Carvalho, Albert, 2011). These are complemented by surveys of neuroanatomic structures (*e.g.*, Albert *et al*., 1998; Crampton *et al*., 2013), and components associated with electrogenesis and electroreception (*e.g.*, Carr *et al*., 1982; Lannoo *et al*., 1989; Vischer *et al*., 1989; Hopkins, 1999; Crampton, 1998, 2019). Other studies have focused on structures recently discovered in Gymnotiformes, such as the caudal skeleton in *Electrophorus* (de Santana *et al*., 2013) and the pseudotympanum in several subgroups of the order (Dutra *et al*., 2015). Finally, secondary sexual dimorphism in Gymnotiformes has been discussed in a phylogenetic paradigm (Cox Fernandes *et al*., 2002; Rapp Py-Daniel, Cox Fernandes, 2005; Hilton, Cox Fernandes, 2006; Albert, Crampton, 2009; Evans *et al*., 2017, 2019a,b; Keeffe *et al*., 2019). In general, studies of comparative anatomy in Gymnotiformes have been restricted to traditional sources of information (*e.g.*, osteology and external anatomy), with complexes from soft anatomy being largely neglected. As a result, several biologically interesting and potentially relevant complexes remain almost entirely uncharted in the group.

Despite being one of the main anatomical complexes of vertebrates, the skeletal musculature of fishes is seldom studied (Datovo, Bockmann, 2010). In Gymnotiformes, our current knowledge is limited to observations of the dorsolateral head muscles of a few species, or brief descriptions of specific myological components. Chardon, de La Hoz (1973) were pioneers in myological studies of gymnotiforms, with descriptions and illustrations of the dorsolateral head muscles of *Sternopygus macrurus* (Bloch & Schneider, 1801) (Sternopygidae), and comparisons with some other Ostariophysi species. Subsequently, Howes (1983) presented data on ligament components of some gymnotiform species, along with brief descriptions of the insertion of subsections of the *adductor mandibulae* in *Sternopygus*, *Eigenmannia* Jordan & Evermann, 1896 (Sternopygidae) and *Rhamphichthys* Müller & Troschel, 1846 (Rhamphichthyidae). The first contribution focusing specifically on the striated musculature in Gymnotiformes was de La Hoz, Chardon (1984), who offered a detailed description of *S. macrurus*, including descriptions and illustrations of osteology, myology and ligaments.

Although such studies comprise crucial background information on the musculature of Gymnotiformes, Aguilera (1986) was the first contribution to tackle myology in gymnotiforms in a relatively broad comparative context. The author presented detailed descriptions of the dorsolateral muscles of thirteen species of the order, including representatives of all families, with emphasis on Apteronotidae. Later, Aguilera, Machado-Allison (1993) described and illustrated details of the gill arch muscles of

Gymnotiformes, also offering a discussion on their phylogenetic implications.

Subsequent to these contributions, the study of gymnotiform myology underwent a long hiatus, dotted by specific descriptive contributions (*e.g.*, Diogo, Chardon, 2000) and comparative surveys of a broad scope (Datovo, Vari, 2014). The later paper offered detailed descriptions of the *adductor mandibulae* of *Gymnotus carapo* Linnaeus, 1758 (Gymnotidae) and *Brachyhypopomus pinnicaudatus* (Hopkins, Comfort, Bastian & Bass, 1990) (Hypopomidae), along with a synonymic list for this complex in Gymnotiformes.

Studies on the phylogenetic relationships in Gymnotiformes have expectedly emphasized osteology and external-anatomical characters. Myological characters were either under-represented (*e.g.*, Albert, Campos-da-Paz, 1998; Albert, 2001; Tagliacollo *et al*., 2016) or entirely absent (*e.g.*, Triques, 1993, 2005; Alves-Gomes *et al*., 1995; Bernt *et al*., 2018, 2019, 2020; Alda *et al*., 2019). In a compehensive study on the phylogenetic relationships in Gymnotiformes, Albert, Campos-da-Paz (1998) was the first to use myology as potential source of phylogenetic signal, and listed four such characters in a data matrix with 250 characters (the same characters were later analyzed in Albert, 2001). Further, Albert *et al.* (2005) listed two characters from the *adductor mandibulae* from a total of 113 in a study focusing on the phylogenetic relationships in *Gymnotus*. Similarly, de Santana, Vari (2010), in a matrix with 88 characters, utilized a single myological character. Recently, Tagliacollo *et al.* (2016) proposed the first phylogenetic hypothesis grounded in a total-evidence model in Gymnotiformes, with a morphological database with 223 characters, only four of which were from myology. As a result, characters from myology currently represent less than 0.2% of the entire universe of morphological characters so far explored in cladistic studies of Gymnotiformes.

The present paper aims to fill out a large gap in the anatomical knowledge of this important group of freshwater fishes and to assist in the understanding of their diversity and evolution. We offer a detailed description of the dorsolateral musculature of the head in representatives of all major subgroups of the Gymnotiformes. This information forms the basis for primary homology assessments and a new standard of the myological nomenclature in the order, which is synthesized as a synonymic list. The variation detected is evaluated in a phylogenetic context by isolated and concatenated analyses combining our data with those from previous studies. Our results, set within a context of an integrated phenotypic matrix, reveal several new synapomorphies for major groups of Gymnotiformes, and provides additional data for resolving phylogenetic relationships within the order.

Finally, Partitioned Bremer Support (PBS), a technique for describing the distribution of character support and conflict among different datasets in a concatenated analysis, was used to assess the influence of myological characters in elucidating evolutionary relationships, allowing an evaluation of the contribution of dorsolateral head muscles in global analyses of the Gymnotiformes.

MATERIAL AND METHODS

Taxonomic and terminological nomenclature. Taxonomic nomenclature follows Albert (2001), with the modifications of Tagliacollo *et al.* (2016), except for "Sinusoidea", which is not based on an available generic name and therefore invalid (Ferraris *et al*., 2017; Betancur-R *et al*., 2017). Sternopygoidea is used as the correct name for that taxon. For the same reason, "Navajini" (sensu Albert, 2001) is also invalid and not used in this work. The taxonomic status of all analyzed taxa follows Ferraris *et al.* (2017) and Fricke *et al.* (2020). In phylogenetic context, the terms "basal" and "apical" refer to the phylogenetic position of a taxon in relation to the root in a tree topology.

Anatomical nomenclature. Myological nomenclature follows Winterbottom (1974a), except for the *adductor mandibulae* and associated structures, which follows Datovo, Vari (2013, 2014). Conservatively, in this study the name *adductor hyomandibulae* is used for the myological component located posterior to the *adductor arcus palatini* and anterior to the *adductor operculi* in gymnotiforms (Huysentruyt *et al*., 2009; but see Datovo, Rizzato, 2018). Osteological terminology follows Albert, Fink (1996), Albert (2001), Hilton *et al.* (2007) and Peixoto *et al.* (2015), with elements not covered therein following Weitzman (1962). Lateral-line nomenclature follows Pastana *et al.* (2020). The terms "origin" and "insertion" are used to the stationary connection site of the muscle (more stable) and the connection point that moves from muscle contraction (relatively more mobile), respectively (Winterbottom, 1974a).

In some gymnotiforms, two or more sections of the *adductor mandibulae* may be partly or entirely undifferentiated from each other, with extensive continuity among their fibers, resulting in composite sections. In such cases, sections are named according to their conformity to the homology of the *adductor mandibulae* subcomponents (*e.g*., *Adductor mandibulae, pars ricto-malaris* and *stego-malaris*), according to Datovo, Vari (2013). Although it is possible to infer correspondence between sets of fibers of undifferentiated bundles and separate sections in taxa with complete differentiation, we maintain a composite nomenclature because in many cases it is possible to observe a subtle differentiation in regions of origin and insertion.

The anteroventral portion of the lateral line nerve is called "*recurrent ramus of anteroventral part of anterior lateral line nerve*" (R-Avn) according to Carr *et al.* (1982) and Vischer *et al.* (1989). That branch originates from the electro-sensorial lobe of the lateral line and innervates electro-receptors of the trunk, being arranged differently in relation to the opercular muscles in Gymnotiformes. Recently, this nerve has been named as a "lateral line nerve" (Dutra *et al*., 2015), a nomenclature not adopted here because it does not adequately reflect the positional homology of the ramus. Terminology for other cranial nerves follows Freihofer (1978).

Synonymy. The synonymic list of names of the dorsolateral head musculature aims to include all names previously employed for that complex in Gymnotiformes. Species mentioned in previous studies were either directly examined or, if not available, represented by a close relative. In a few cases, some of the components described or illustrated in previous contributions could not be definitely identified and in those instances, they are indicated as "?", followed by comments in brackets.

Anatomical descriptions. In order to avoid excessive redundancy in anatomical descriptions, we adopt a method of hierarchical descriptions that minimizes the need for repetition. Via this style, descriptions of more inclusive groups precede those of less inclusive groups, so that general traits for each taxonomic category are described only once. For example, descriptions under the heading "Gymnotiformes" include characteristics common to all members in the order. Within "Gymnotidae", in turn, only those traits common to all members of the family yet different from the general previously-provided gymnotiform pattern are described. Finally, within *Gymnotus*, only the states exclusive to that genus are included. In all cases, there are allowances for relevant exceptions and intra-taxon variation. Due to the great morphological variability of the *adductor mandibulae* and *levator arcus palatini* among the genera of each family, these muscles are presented separately in detailed descriptions. The *dilatator operculi* and *levator operculi* are presented separately only in Gymnotidae, due to the compositional variation of muscles in the family. Descriptions of the dorsolateral head musculature follow an anteroposterior and lateromedial arrangement of the muscles in their natural position in the head .

Illustrations. Photographs were made with a Zeiss Discovery V20 stereomicroscope coupled with the Axiocam 506 color digital camera, using a self-assembling procedure, with multifocal images combined with Combine ZP program (Hadley, 2009) and later edited in Adobe Photoshop CS4 and Adobe Illustrator CS5. Anatomical abbreviations are presented in Tab. 1.

Phylogenetic inference. Two analyses were performed. "Analysis 1" includes solely the dorsolateral head musculature characters. Its main objective is to infer cladistic congruence among myological characters when analyzed in isolation and to draw comparisons with previous studies. "Analysis 2" is the myological matrix concatenated into an integrated phenotypic matrix. It aims to infer new synapomorphies and the influence of the dorsolateral head musculature within a large phenotypic dataset. Results of each analysis are synthesized in the "Discussion: ANALYSIS 1 – Dorsolateral head musculature and phylogenetic inference in Gymnotiformes: comparisons with previous studies" and "Discussion: ANALYSIS 2 – Influence of myological characters on the relationships of Gymnotiformes relationships", respectively.

ANALYSIS 1 - Dorsolateral head musculature and phylogenetic methodology. Characters from dorsolateral head musculature were compiled in a matrix of 87 terminal taxa and 56 characters from dorsolateral head musculature (Tab. **S1**) built in Notepad ++ 7.5.1 (Ho, 2019). The matrix was treated with parsimony analysis with the TNT program ("Tree Analysis using New Technology" – Goloboff, Catalano, 2016). The tree was rooted at *Chanos chanos* (Fabricius, 1775) (Gonorynchiformes), widely recognized as the sister group to remaining Ostariophysi included in the analysis (*e.g*., Fink, Fink 1981, 1996; Saitoh *et al*., 2003; Ortí, Meyer, 1996, 1997; Lavoué *et al*., 2011; Nakatani *et al*., 2011; Chen *et al*., 2013). With the exception of character 13 (see section on that character), multi-state characters were treated as unordered.

Most parsimonious trees (MPT's) were found by traditional heuristic search analysis with 1000 replications of RAS + TBR ("tree-bisection reconnection"), saving 90 trees by replication and hitting the best score at least 50 times. This strategy best suits our data set, and is recommended for the location of all the global optima in medium-sized datasets (Giribet, 2007; Goloboff *et al*., 2008). Ambiguous character-state distributions were optimized by ACCTRAN (Accelerated Transformation

TABLE 1 | Anatomical nomenclature and abbreviations.

Abbreviations			
	Musculature		**Bones**
		A	Anguloarticular
AA	*Adductor arcus*	**An**	Antorbital
AM	*Adductor mandibulae*	**Ape**	Ascendant process of the endopterygoid
DO	*Dilatator operculi*	**Au**	Autopalatine
LAP	*Levator arcus palatini*	**Cb**	Coronomeckelian bone
LO	*Levator operculi*	**D**	Dentary
SM	*Segmentum mandibularis*	**Dpo**	Dorsal process of the opercle
		E	Endopterygoid
	Ligaments and tendons	**Fr**	Frontal
		H	Hyomandibula
Ecl	Ectomaxillary ligament	**Ib**	Intermuscular bone
El	Endomaxillary ligament	**Io1+2**	Infraorbital 1+2
Ela	Endomaxillar ligament accessory	**Le**	Lateral ethmoid
Mr	Mandibular raphe	**M**	Maxilla
Mt	Mandibular tendon	**Me**	Metapterygoid
Pal	Preangular ligament	**Ms**	Mesethmoid
Pol	Post-retroarticular ligament	**O**	Opercle
Prl	Pre-retroarticular ligament	**Or**	Orbitosphenoid
T	Meckelian tendon	**P**	Preopercle
Tl	Transverse ligament	**Pa**	Parietal
		PEio1+2	Posterodorsal expansion of the infraorbital 1+2
	General	**Pm**	Premaxilla
		Pt	Pterosphenoid
BM	Buccopalatal membrane	**Q**	Quadrate
CTul	Connective tissue of the upper lip	**R**	Retroarticular
LFs	*Levator operculi* fascia	**S**	Sympletic
MC	Meckel's cartilage	**Sc**	Postotic canal segment of supracleithrum
R-Avn	Recurrent ramus of anteroventral part of anterior lateral line nerve	**So**	Subopercle
RMT	*Ramus mandibularis trigeminus*	**Sp**	Sphenotic

Optimization) optimization (de Pinna, 1991). A strict consensus tree was computed in TNT (ne*) and only synapomorphies common to all trees are presented and discussed. Consistency (CI) and retention (RI) indices were used as measures-of-fit between characters and trees (Farris, 1969, 1989) and were calculated with a TNT script "wstats.run". CI and RI are presented as ranges for characters with different performances among recovered MPT's. RI for characters that have a state in a single terminal and another state in all other terminals are mathematically indeterminate and indicated as "AUT".

Relative Bremer support (Goloboff, Farris, 2001) was calculated using 10 additional calculation runs. The relative measure corrects the distortion of the absolute value of support (Bremer support; Bremer, 1994), since it is expressed as a proportion of evidence in favor and against a given clade (Goloboff, Farris, 2001). In addition, Bootstrap (Felsenstein, 1985) and Jackknife values were calculated and expressed in GC ("group present / contradicted"; Goloboff *et al*., 2003). Zero-length branches were collapsed ("rule 3").

ANALYSIS 2 - Myological data concatenated with an integrated phenotypic matrix, and the influence of myological characters in phylogenies using PBS. Characters from dorsolateral head musculature mentioned above were concatenated with the morphological character matrix originally presented in Tagliacollo *et al.* (2016) and subsequently modified by Peixoto *et al.* (2019) (Tab. **S2**). Searches were made on TNT under equal weights using new technologies (20 iterations of fuse, drift, ratchet and sectorial search), reaching the best score 50 times (hit = 50), and with all the fundamental trees submitted to additional TBR analyses. Following Tagliacollo *et al.* (2016), the tree was rooted at *Carassius auratus* (Linnaeus, 1758). The influence of characters from dorsolateral head musculature in concatenated analyses was estimated by Partitioned Bremer support (PBS; Baker, DeSalle, 1997; Lambkin *et al*., 2002; Lambkin, 2004), using the "pbsup.run" script available for TNT (Peña *et al*., 2006).

Material examined. Material examined is listed below. Museum acronyms follow Sabaj (2020). Size of specimens is expressed in Standard Length (SL, measured from the tip of the snout to the insertion of the median rays of the caudal fin), Total Length (TL, measured from the tip of the snout to the posterior margin of the longest caudal-fin ray or caudal filament) or Length at End of the Anal Fin (LEA, measured from the tip of the snout until the insertion of the last ray of the caudal fin). Length ranges refer to specimens examined, not necessarily to all specimens in lot. Museum specimens were stained according to Datovo, Bockmann (2010). All specimens listed were prepared as myological dissections, except those indicated by an asterisk. Cleared and stained specimens are indicated by "c&s" and dry skeletons by "skl".

Clupeiformes: *Denticeps clupeoides*: **Benin**: MZUSP 84776, 2, 31.7–40.1 mm SL. **Gonorynchiformes:** *Chanos chanos*: **Australia:** USNM 173572, 1, 167.3 mm SL. **Cypriniformes:** *Carassius auratus**: **Germany**: MZUSP 91472, 3, 74.1–129.4 mm SL. *Labeo chrysophekadion*: **Thailand:** USNM 271352, 1, 81.2 mm SL. **Characiformes:** *Brycon falcatus*: **Brazil:** MZUSP 18089, 1, 102.83 mm SL. *Cyphocharax festivus**: **Brazil**: MZUSP 103174, 5, 38.2–50.1 mm SL. *Cyphocharax leucostictus*: **Brazil**: MZUSP 21156, 1 c&s, not measured. *Erythrinus erythrinus**: **Brazil**: MZUSP 34352, 13, 66.1–134.6 mm SL; MZUSP 34350, 2, c&s, 67.1–72.1 mm SL. *Serrasalmus rhombeus**: **Brazil**: MZUSP 94907, 9, 84.8–89.7 mm SL; MZUSP 95862, skl, not measured; MZUSP 94082, skl, not measured. *Dianema longibarbis**: **Peru**: MZUSP 26413, 6, 51.5–84.9 mm SL. **Siluriformes:** *Dianema* sp.: **Brazil:** MZUSP 30862, 2, c&s, not measured. *Diplomystes mesembrinus*: **Argentina:** MZUSP 62595, 2, 81.2–105.8 mm SL. *Pterygoplichthys* sp.*: **Brazil**: MZUSP, 92363, 2, not measured; MZUSP 117325, skl, not measured. *Pseudostegophilus nemurus**: **Brazil**: MZUSP 57717, 5, 62.6–78.5 mm SL. **Gymnotiformes: Apteronotidae:** *Adontosternarchus balaenops*: **Brazil**: MZUSP 83219, 2, 165.2–175.3 mm LEA. *Adontosternarchus clarkae*: **Brazil**: MZUSP 30072, 1, 79.3 mm LEA. *Adontosternarchus sachsi*: **Brazil**: MPEG 2435, 1, 116.5 mm LEA. *Apteronotus* *albifrons*: **Brazil**: MZUSP 89044, 1, 75.8 mm LEA; MZUSP 22251, 1, 150.1 mm LEA. *Apteronotus bonapartii*: **Brazil**: MPEG 3038, 2, 204.6–217.5 mm LEA. *Apteronotus camposdapazi*: **Brazil**: MZUSP 114249, 1, 120. 7 mm TL [regenerated]. *Apteronotus rostrarus*: **Colombia**: USNM 317229, 1, 142.3 mm LEA. *Compsaraia compsa*: **Brazil**: MZUSP 56206, 1, 95.4–123.4 mm LEA. *Orthosternarchus tamandua*: **Brazil**: MZUSP 55955, 1, 286.3 mm LEA; MZUSP 56541*, 112.1 mm LEA. *Parapteronotus hasemani*: **Brazil**: MPEG 1161, 1, 191.5 mm LEA. *Platyurosternarchus macrostomus*: **Brazil**: MZUSP 105584, 194.2 mm LEA; MZUSP 57686, 1, 189.5 mm LEA. *Pariosternarchus amazonensis*: **Brazil**: MZUSP 58258, 109.4 mm LEA; MZUSP 57061*, 129.1 mm LEA. *Porotergus gimbeli*: **Brazil**: MZUSP 83300, 1, 148.8 mm LEA. MZUSP 57426, 2, 127.7–154.3 mm LEA. *Tenebrosternarchus preto*: **Brazil**: MPEG 22758, 2, 248.2–268.5 mm LEA. *Sternarchogiton porcinum*: **Brazil**: MZUSP 56319, 1, 202.2 mm LEA. *Sternarchella duccis*: **Brazil**: MZUSP 57370, 1, 146.9 mm LEA. *Sternarchella raptor*: **Brazil**: USNM 374014, 1, 71.9 mm LEA. *Sternarchella schotti*: **Brazil**: MZUSP 58187, 1, 141. 9 mm LEA. *Sternarchella schotti*: **Brazil**: MPEG 3481, 2, 154.05–155.3 mm TL [regenerated]; MPEG 7989, 1, 185.6 mm LEA. *Sternarchorhynchus goeldii*: **Brazil**: MPEG 1193, 1, 148.3 mm LEA. *Sternarchorhynchus oxyrhynchus*: **Brazil**: MZUSP 55851, 1, 227.0 mm LEA. *Sternarchorhamphus mulleri*: **Brazil**: MPEG 3712, 2, 335.1–335.4* mm LEA; USNM 373030, 1, 222.2 mm LEA. **Gymnotidae:** *Electrophorus* cf. *electricus*: **Brazil**: MZUSP 103699, 1, 530.12 mm LEA; MZUSP 85509, 1, 488.2 mm LEA. *Gymnotus coatesi*: **Brazil**: MPEG 27120, 1, 115.7 mm LEA. *Gymnotus coropinae*: **Brazil**: MPEG 21510, 1, 112.5 mm LEA; MZUSP 80142, 1, 137.0 mm LEA. *Gymnotus* gr. *carapo*: **Brazil**: MPEG 3012, 1, 232.2 mm LEA; MZUSP 90618, 1, 177.8 mm LEA. *Gymnotus maculosus*: **Guatemala**: USNM 114539, 1, 189.4 mm LEA. *Gymnotus* gr. *pantherinus*: **Brazil**: MZUSP 113616, 1, 151.3 mm LEA. *Gymnotus cylindricus*: **Guatemala**: USNM 134701, 1, 178.5 mm LEA. **Hypopomidae:** *Brachyhypopomus* sp.: **Brazil**: MPEG 12067, 1, 70.5 mm LEA. *Brachyhypopomus bombilla*: **Brazil**: MZUSP 59441, 1, 66.2 mm LEA. *Brachyhypopomus beebei*: **Brazil**: MZUSP 103275, 1, 74.6 mm LEA. *Brachyhypopomus brevirostris*: **Brazil**: MPEG 2397, 2, 65.9–71.2 mm LEA; MPEG 7295, 2, 50.0–61.3 mm LEA. MZUSP 30047, 1, 144.2 mm LEA. *Brachyhypopomus draco*: **Brazil**: UFRS 8887, 1, 140.4 mm LEA. *Brachyhypopomus gaudeiro*: **Brazil**: MZUSP 25165, 1, 79.1 mm LEA. *Brachyhypopomus hendersoni*: **Brazil**: MZUSP 113218, 1, 77.8 mm LEA; MZUSP 30050, 1, 67.5 mm LEA. *Brachyhypopomus janeiroensis*: **Brazil**: MZUSP 22702, 1, 80.9 mm LEA. *Brachyhypopomus pinnicaudatus*: **Brazil**: MZUSP 23216, 1, 87.8 mm LEA. *Brachyhypopomus regani*: **Brazil**: MZUSP 110609, 1, 107. 3 mm LEA. *Brachyhypopomus sullivani*: **Brazil**: MZUSP 105803, 1, 72.7 mm LEA. *Hypopomus artedi*: **Suriname**: USNM 408442, 1, 202. 7 mm LEA. *Microsternarchus* aff. *bilineatus*: **Brazil**: MPEG 12757, 1, 69.5 mm LEA; MZUSP 102314, 1, 71.19 mm LEA. *Microsternarchus* cf. *bilineatus*: **Venezuela**: MBUCV-V 7298, 1, 59.2 mm LEA. *Hypopygus lepturus*: **Brazil**: MPEG 10169, 1, 61.0 mm LEA. MZUSP 102317, 1, 45.8 mm LEA. **Peru:** MZUSP 91426, 3, 55.4 mm LEA. *Steatogenys duidae*: **Brazil**: MPEG 14670, 1, not measured. *Steatogenys elegans*: **Brazil**: MZUSP 83331, 1, 120.5 mm LEA. **Rhamphichthyidae:** *Gymnorhamphichthys rosemariae*: **Brazil**: MZUSP 56317, 1, 116.3 mm LEA. *Gymnorhamphichthys rondoni*: **Brazil**: MPEG 14681, 1, 107.1 mm LEA. MZUSP 85130, 1, 159.8 mm LEA. *Rhamphichthys drepanium*: **Brazil**: MZUSP 36144, 1, 282.3 mm TL [regenerated]. *Rhamphichthys hahni*: **Brazil**: MZUSP 24736, 1, 479.5 mm TL [regenerated]. MZUSP 52514*, 280 mm LEA. *Rhamphichthys* *lineatus**: **Brazil**: MZUSP 44823, 1, 417.2 LEA. *Rhamphichthys marmoratus*: **Brazil**: MPEG 8833, 1, 65.8 mm HL [head only]; MZUSP 44574*, 1, 258 mm LEA; MZUSP 36016*, 1, 290 mm LEA. *Rhamphichthys rostratus**: **Brazil**: MZUSP 32233, 1, 643.6 mm LEA. **Sternopygidae:** *Archolaemus* cf. *blax*: **Brazil**: MZUSP 89304, 1, 101.5 mm LEA. *Archolaemus ferreirai*: **Brazil**: INPA-ICT 6496, 1, 128.5 mm LEA. *Archolaemus janeae*: **Brazil**: MZUSP 97383, 1, 171.0 mm LEA. *Archolaemus luciae*: **Brazil**: MPEG 23607, 1, 220.5 mm LEA. *Archolaemus orientalis*: **Brazil**: MPEG 21509, 1, paratype, 110 mm LEA. *Archolaemus santosi*: **Brazil**: LIRP 13010, 1, 171.5 mm LEA. *Distocyclus conirostris*: **Brazil**: MZUSP 23316, 1, 242.2 mm LEA; MPEG 20022, 1, 152.3 mm LEA; MCP 26287, 1, 133.0 mm LEA. *Eigenmannia oradens*: **Venezuela**: ANSP 190768, 1, paratype, 101.4 mm LEA. *Eigenmannia antonioi*: **Brazil**: MPEG 29487, 1, 80.0 mm LEA. *Eigenmannia besouro*: **Brazil**: MZUSP 98748, 1, paratype, 89.2 mm LEA. *Eigenmannia desantanai*: **Brazil**: MZUSP 38169, 1, 133.5 mm LEA. *Eigenmannia guairaca*: **Brazil**: LBP 9911, 1, 107.4 mm TL [regenerated]. *Eigenmannia humboldtii*: **Colombia**: FMNH 56812, 1, 186.2 mm LEA. *Eigenmannia limbata*: **Brazil**: MZUSP 75569, 1, 160.0 mm LEA. *Eigenmannia macrops*: **Guyana**: USNM 405266, 1, 103.2 mm LEA. *Eigenmannia* cf. *macrops*: **Brazil**: MZUSP 102072, 1, 269.4 mm LEA. *Eigenmannia matintaperera*: **Brazil**: MZUSP 29979, 113.0 mm LEA. *Eigenmannia meeki*: **Panamá**: MZUSP 119018, 1, paratype, 160.2 mm LEA. *Eigenmannia microstoma*: **Brazil**: MCP 45216, 1, 80.0 mm LEA. *Eigenmannia muirapinima*: **Brazil**: MZUSP 97577, 1, 117.0 mm LEA. *Eigenmannia nigra*: **Brazil**: MPEG 2430, 1, 154.1 mm LEA. MPEG 27121, 2, 170.6–180.1 mm LEA. *Eigenmannia pavulagem*: **Brazil**: MPEG 7308, 1, 90.9 mm LEA. *Eigenmannia sayona*: **Venezuela**: MPEG 33926, 1, paratype, 103.7 mm LEA. *Eigenmannia trilineata*: **Argentina**: MZUSP 111146, 305.0 mm LEA. *Eigenmannia vicentespelaea*: **Brazil**: MZUSP 83467, 1, 115.9 mm LEA. *Eigenmannia virescens*: **Argentina**: MZUSP 6319, 1, 155.4 mm LEA. *Eigenmannia waiwai*: **Brazil**: MZUSP 15882, 99.1 mm LEA. *Japigny kirschbaum*: **Guyana**: FMNH 50185, 1, 137.2 mm LEA. *Rhabdolichops caviceps*: **Brazil**: INPA 20157, 1, 103.9 mm LEA. *Rhabdolichops eastwardi*: **Brazil**: MZUSP 81178, 1, 188.3 mm LEA; MPEG 8148, 1, 113.7 mm LEA. *Rhabdolichops electrogrammus*: **Brazil**: INPA 28863, 1, 80.6 mm LEA. *Rhabdolichops lundbergi*: **Brazil**: INPA 11406, 1, 110.2 mm LEA. *Rhabdolichops nigrimans*: **Brazil**: INPA 28862, 1, 98.1 mm LEA. *Rhabdolichops troscheli*: **Brazil**: MZUSP 57704, 2, 122.2–140.2 mm LEA. *Rhabdolichops zareti*: **Venezuela**: CAS 57444, 1, 88.9 mm LEA. *Sternopygus astrabes*: **Brazil**: MZUSP 88795, 1, 151. 0 mm LEA. *Sternopygus macrurus*: **Brazil**: MZUSP 32215, 1, 212.6 mm LEA. MPEG 22756, 2, 240.4–245.8 mm LEA. *Sternopygus xingu*: **Brazil**: MPEG 8657, 1, 230. 5 mm LEA.

RESULTS

The dorsolateral musculature of the head of Gymnotiformes: general features

Buccopalatal membrane. The buccopalatal membrane comprises the lateral limits of the anterodorsal portion of the oral cavity, which is ventrally delimited by the mandible, anteriorly by the maxilla and posteromedially by the anterodorsal margin of the suspensorium. The degree of differentiation of the membrane in Teleostei is extremely variable, ranging from prominent to weakly differentiated from surrounding connective tissues (Datovo, Vari, 2013, 2014). In Gymnotiformes, the membrane is usually poorly differentiated, except in representatives of Gymnotidae (Figs. 1–3), where it is thick and well differentiated. Normally, few fibers of the *malaris* and *rictalis* have a weak association with the buccopalatal membrane. However, such connections are feeble and not recognized as additional insertion points for those sub-sections.

In Gymnotidae, it is not possible to identify any ligaments associated with the buccopalatal membrane. However, in other gymnotiform subgroups the endomaxillary and ectomaxillary ligaments are often well differentiated. The endomaxillary ligament is present in representatives of some families (Hypopomidae: Fig. 4; Rhamphichthyidae: Fig. 5; Peixoto, Ohara, 2019: fig. 12; Sternopygidae: Peixoto, Ohara, 2019: fig. 11; and Apteronotidae: Aguilera, 1986). In those groups, the ligament receives the anterior fibers of the *malaris* and inserts directly on the jaw or on the connective tissue between the anterior margin of the premaxilla and the upper lip (in representatives of Apteronotidae;

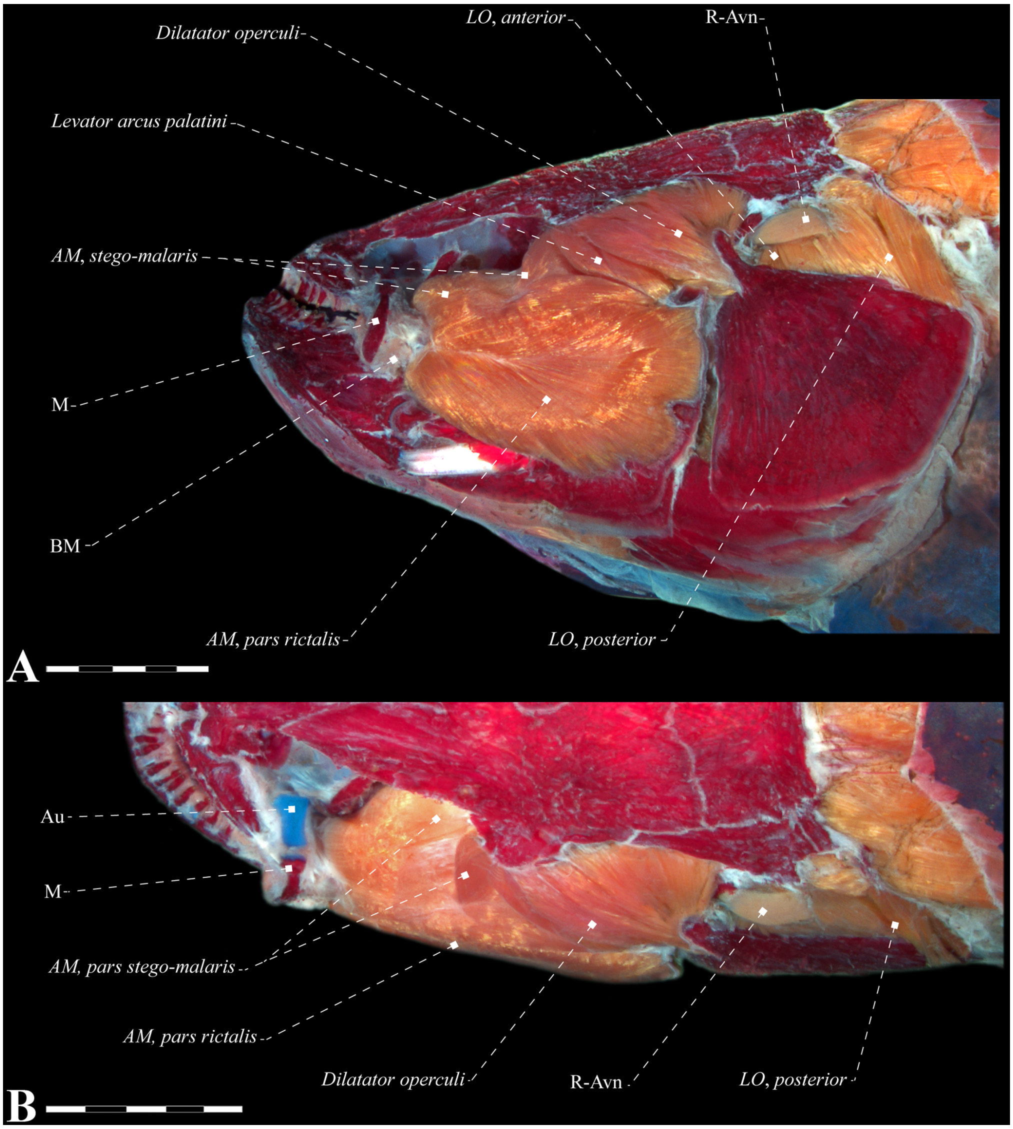


FIGURE 1 | Dorsolateral head muscles of *Gymnotus cylindricus* (Gymnotidae), USNM 134701, 178.5 mm LEA. **A.** Lateral view; **B.** dorsal view. Anatomical abbreviations in Tab. 1. Scale bars = 4 mm.

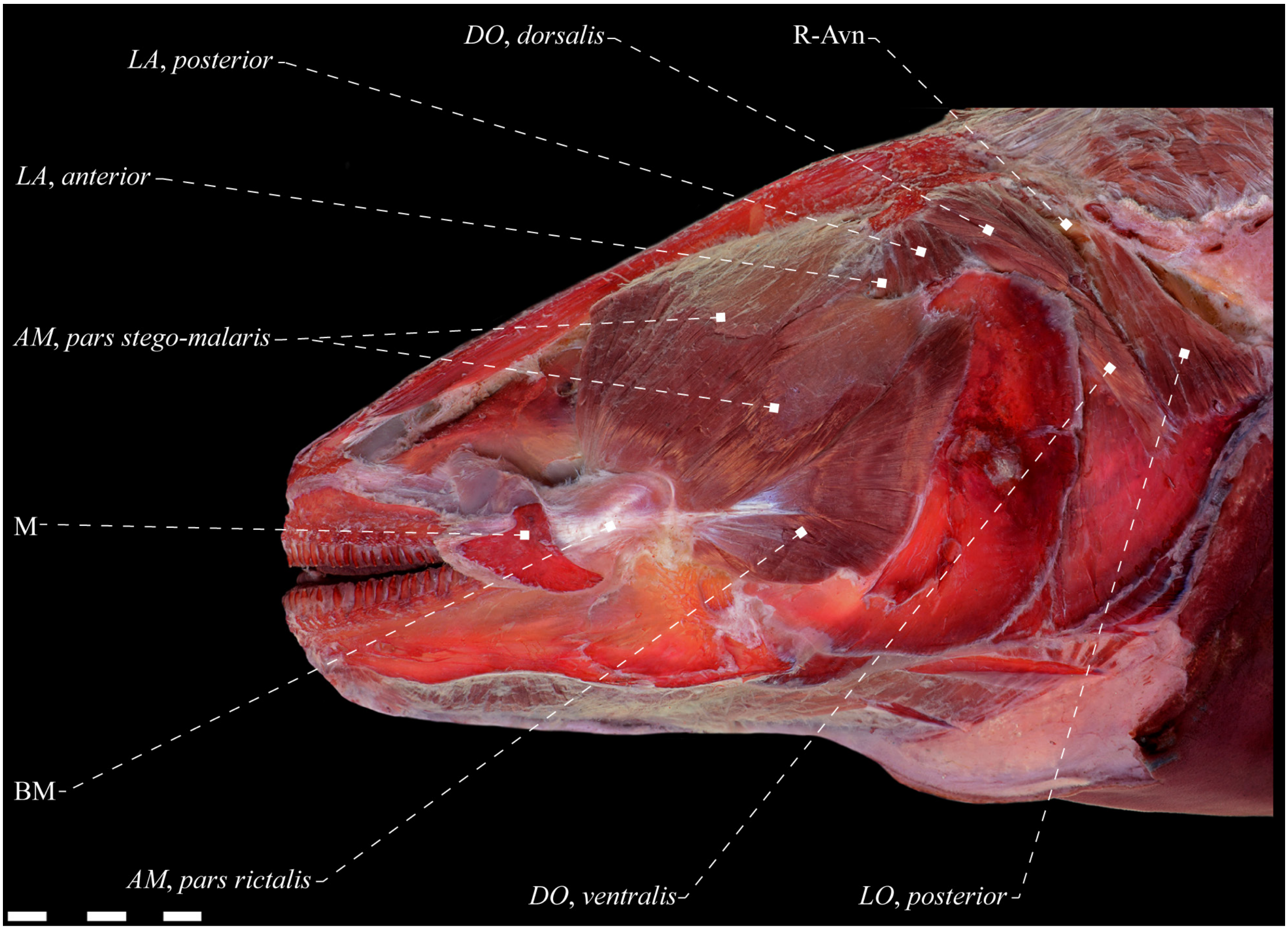


FIGURE 2 | Lateral view of dorsolateral musculature of *Electrophorus* cf. *electricus* (Gymnotidae), MZUSP 85509, 488.2 mm TL. Anatomical abbreviations in Tab. 1. Scale bar = 10 mm

Figs. 6, 7). In Apteronotidae alone, there is a well-differentiated ectomaxillary ligament, which receives the anteroventral fibers of the *malaris* and inserts onto the maxilla (Fig. 7).

In Sternopygidae, there is a well-differentiated ligament located transversally in the posterior portion of the mandible and associated with the ventro-medial margin of infra-orbital 1 + 2 and posteriorly to the anguloarticular (Dutra *et al*., 2021: fig. 40). This ligament is tentatively identified as a transverse ligament (Datovo, Vari, 2013), which displays a pronounced degree of differentiation, unique to that family. Further, the vast majority of Apteronotidae, the buccopalatal membrane has two additional ligaments and their degree of differentiation is unique in the order. They are similar to the postangular and preangular ligaments (which are present in most Gymnotiformes), but contrary to the latter ligaments, they originate on the retroarticular. Such ligaments are referred to herein as pre-retroarticular and post-retroarticular ligaments (Fig. 7). The pre-retroarticular ligament differentiates anteriorly in the buccopalatal membrane towards the maxilla, and the post-retroarticular converges anteriorly on the same membrane, towards the sites of insertion of *ricto-stegalis*. Datovo, Vari (2014) illustrate and describe

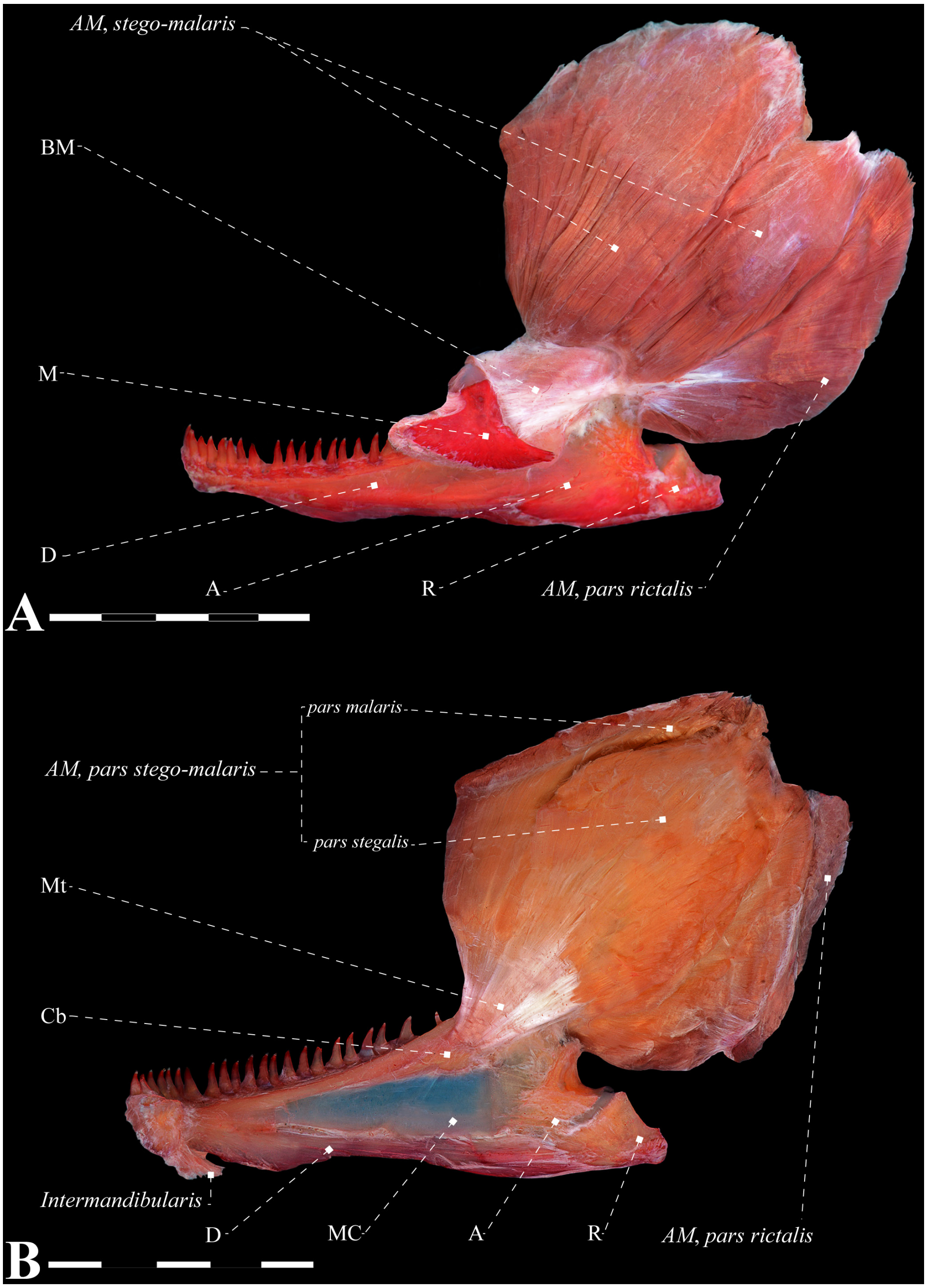


FIGURE 3 | *Adductor mandibulae* of *Electrophorus* cf. *electricus* (Gymnotidae), MZUSP 85509, 488.2 mm LEA. **A.** Lateral view; **B.** Mesial view. Anatomical abbreviations in Tab. 1. Scale bar = 10 mm.

a preangular ligament in *B. pinnicaudatus*, however, in the majority of species analyzed this ligament is not differentiated and it was therefore not included in descriptions.

Adductor mandibulae. The *adductor mandibulae* of Gymnotiformes has varying configurations and its components display different degrees of differentiation, usually consisting of the *adductor mandibulae*, *segmentum facialis* and the *adductor mandibulae*,

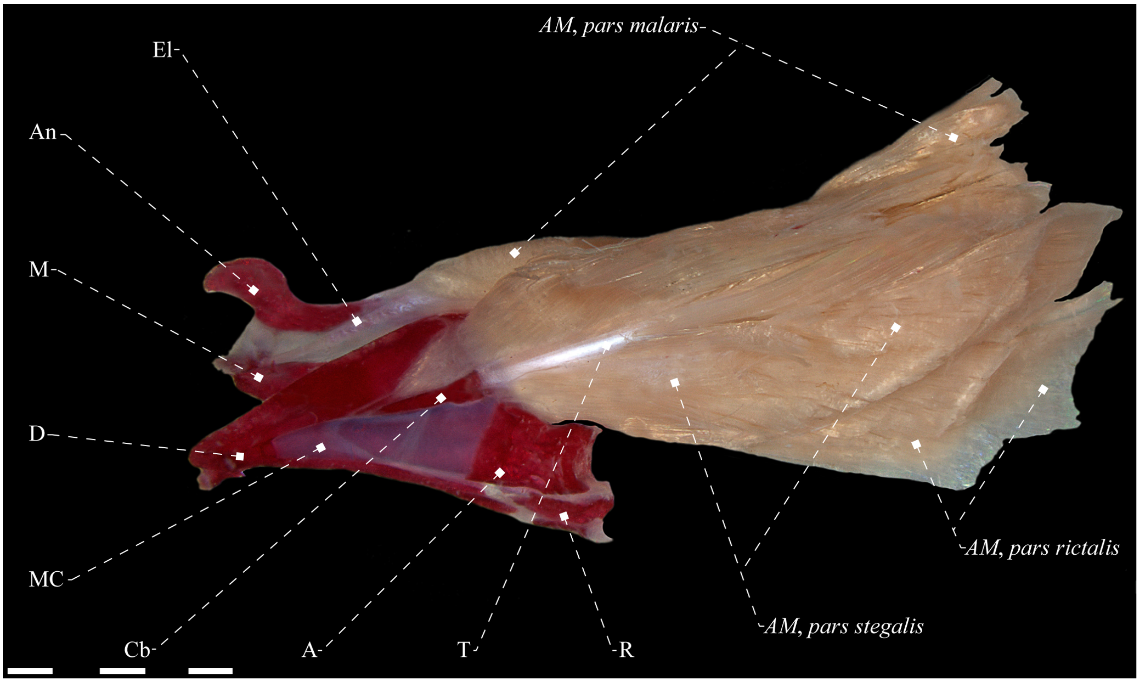


FIGURE 4 | Mesial view of *adductor mandibulae* of *Hypopomus artedi* (Hypopomidae), USNM 408442, 202. 7 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 4 mm.

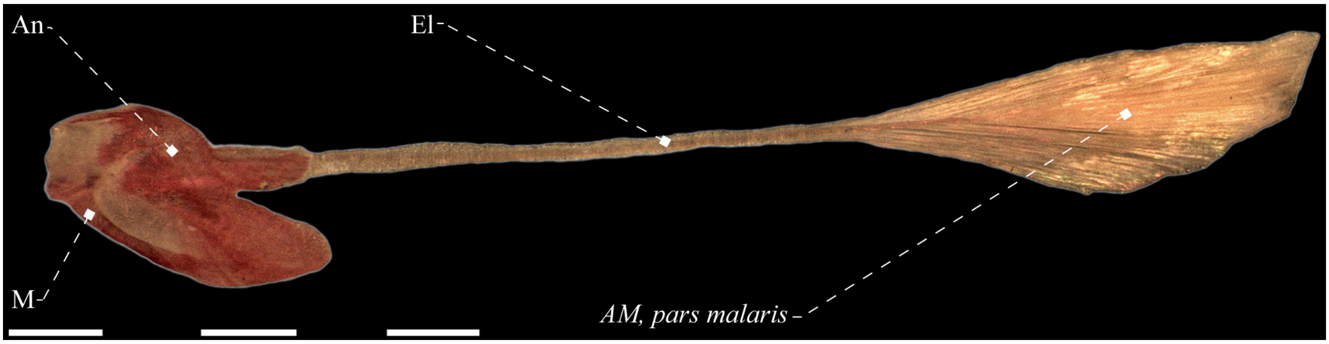


FIGURE 5 | Lateral view of *adductor mandibulae*, *pars malaris* of *Gymnorhamphichthys rosemariae* (Rhamphichthyidae), MZUSP 56317. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

segmentum mandibularis (Tab. 2). Such segments are connected by an intersegmental aponeurosis, with a mandibular tendon dorsally and a meckelian tendon ventrally. These tendons are confluent along their length but still discernible because the former is located dorsally, roundish in cross section and slightly differentiated from the anterior portion of the *segmentum facialis* and the posterior portion of the *segmentum mandibularis*. In turn, the meckelian tendon is positioned ventrally, conspicuously flattened and inserted in the coronomeckelian bone. When present, the *segmentum mandibularis* has no subsections. It arises from the mandibular tendon, enters the mandible mesially and is located dorsally to Meckel's cartilage (Figs. 4, 5). The *segmentum mandibularis* is absent in Gymnotidae (Fig. 3), Rhamphichthyidae (Fig. 8), most of the species of *Archolaemus*

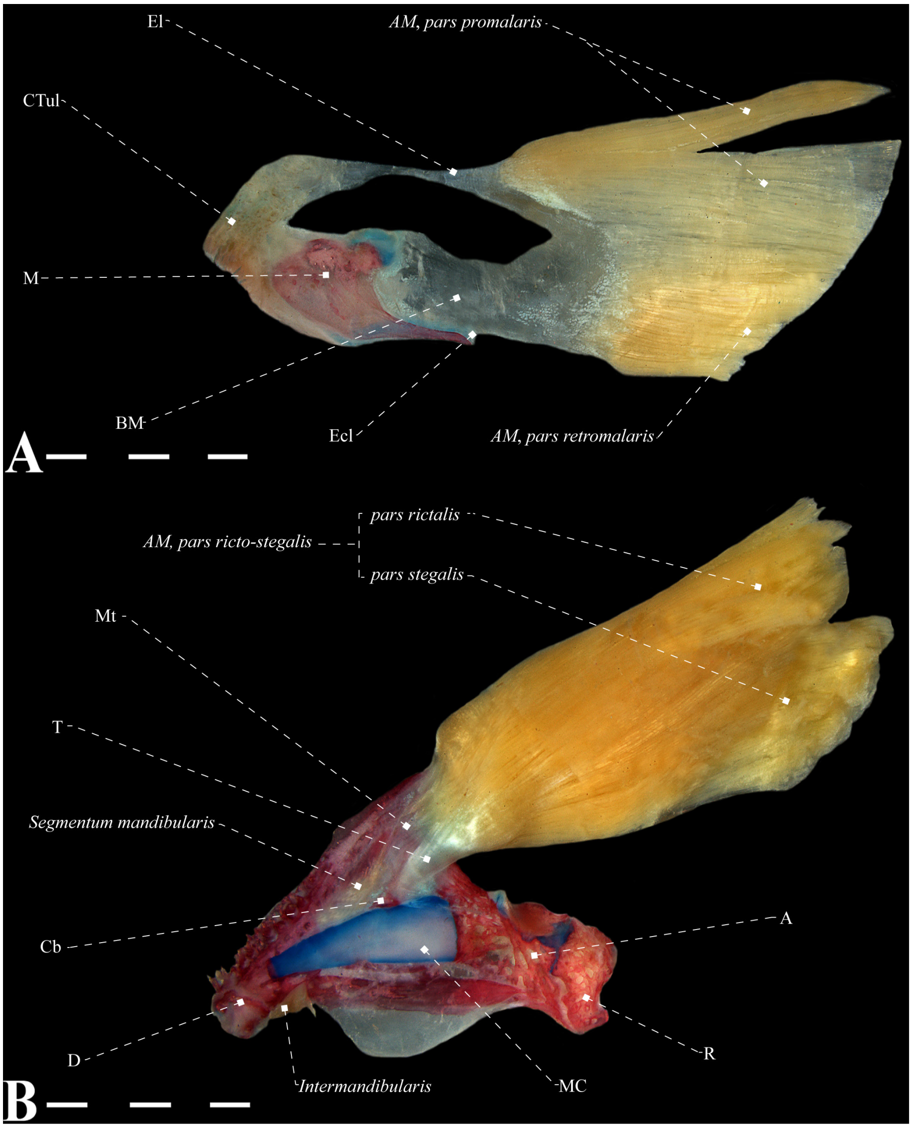


FIGURE 6 | *Adductor mandibulae* of *Tenebrosternarchus preto* (Apteronotidae), MPEG 22758, 268.5 mm LEA. **A.** Lateral view; **B.** Mesial view. Median portion of the buccopalatal membrane removed. Anatomical abbreviations in Tab. 1. Scale bars = 5 mm.

(Fig. 9) and in some representatives of Apteronotidae.

The *segmentum facialis* is positioned mostly on the lateral surface of the suspensorium and is composed of three identifiable subsections in all Gymnotiformes: *pars malaris*, *pars rictalis* and *pars stegalis*. The degree of differentiation between these components is variable and ranges from a single unit, not divided into sub-sections, to a completely sectioned segment. The generalized condition in the order consists of the complete differentiation of the three sections, however, composite sub-sections can occur, as a *stego-malaris* (in Gymnotidae) or a *ricto-stegalis* (in Rhamphichthyidae and several Apteronotidae).

The *malaris* is commonly located immediately ventral to the orbit, usually arranged dorsolaterally to the dorsal portion of the *rictalis* and latero-ventrally to the mid-ventral

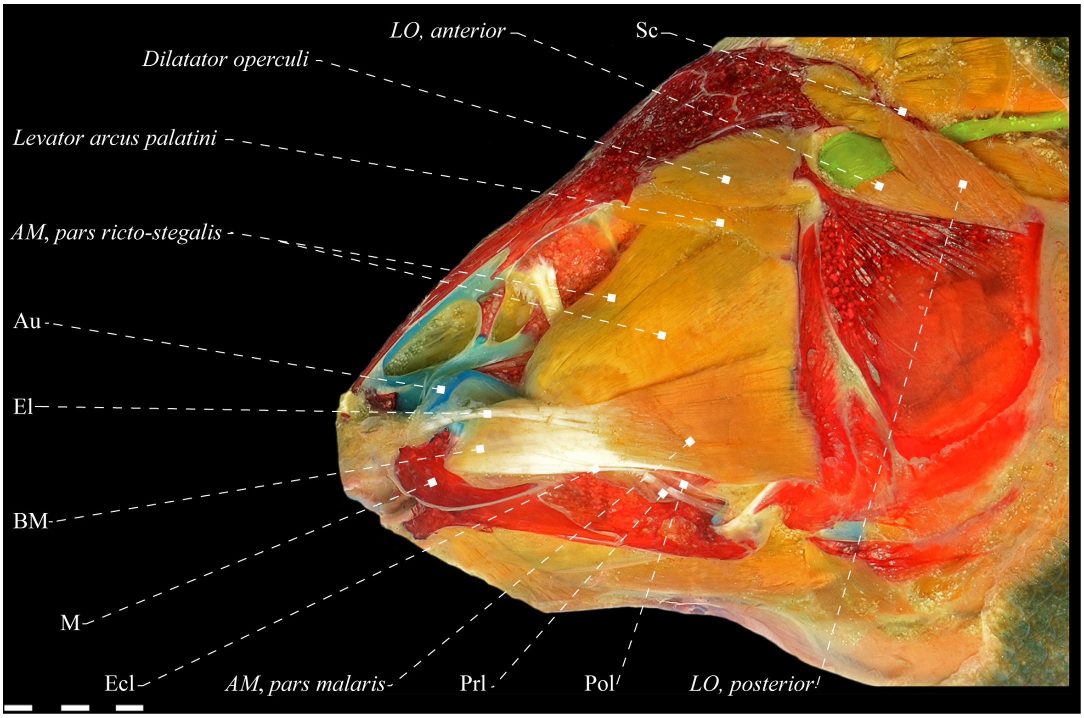


FIGURE 7 | Lateral view of dorsolateral musculature of *Apteronotus albifrons* (Apteronotidae), MZUSP 22251, 150.1 mm LEA. Green indicates the path of recurrent ramus of anteroventral part of anterior lateral line nerve. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

portion of the *stegalis* (except for some apteronotids; see comments in "Posteroventral *malaris* in Apteronotidae"; Fig. 8). This section, or its corresponding fibers, arises mostly from the bony elements of the suspensorium, and may also include some components of the neurocranium (*e.g.*, frontal, sphenotic, or parasphenoid). The insertion points are extremely variable across the order, and may involve the mandibular tendon or even in the connective tissue between the anterior margin of the premaxilla and the upper lip. The generalized pattern for gymnotiforms includes an insertion in the maxilla, and usually also involves elements of the infraorbital series (*e.g.*, antorbital in Rhamphichthyidae and Hypopomidae, and infra-orbital 1 + 2 in Sternopygidae, Figs. 4, 10A and 11), the mandible (in Gymnotidae and *Adontosternarchus*) or even the mesethmoid (in *Sternarchella*). Commonly, the *malaris* consists of a single uncut section, albeit differentiated into a dorsal and a ventral sub-section (see comments in "The *malaris* sectioned in *promalaris* and *retromalaris*").

The *rictalis* is located mid-ventrally in relation to the other sub-sections of the *adductor mandibulae*, arising strictly from the suspensorium, even in cases where it is not differentiated from the *stegalis*. The insertion sites commonly include the coronoid process, with some fibers attaching also on the posterolateral margin of the anguloarticular or on the intersegmental aponeurosis. The *stegalis* makes up the mesial-most sub-section of the *segmentum facialis*, arising from elements of the suspensorium, but normally also components of the neurocranium. Anteriorly, the *stegalis* differentiates into an intersegmental aponeurosis, dorsally entering the mandibular tendon (origin of the *segmentum mandibularis*) and ventrally the meckelian tendon, inserting into the

TABLE 2 | Segments, sections and subsections of the *adductor mandibulae* of Gymnotiformes.

		segmentum mandibularis	*segmentum facialis*	*malaris*	*promalaris and retromalaris*	*rictalis*	*stegalis*	*stego-malaris*	*ricto-stegalis*
Gymnotidae	*Electrophorus*	-	-	-	-	x	-	x	-
	Gymnotus	-	-	-	-	x	-	x	-
Rhamphichthyidae	*Gymnorhamphichthys*	-	-	x	-	-	-	-	x
	Rhamphichthys	-	-	x	-	-	-	-	x
	Steatogenys	x	-	x	-	x	x	-	-
	Hypopygus	x	-	x	-	x	x	-	-
Hypopomidae	*Brachyhypopomus*	x	-	x	-	x	x	-	-
	Hypopomus	x	-	x	-	x	x	-	-
	Microsternarchus	x	-	x	-	x	x	-	-
Sternopygidae	*Archolaemus luciae*	x	-	x	-	x	x	-	-
	Archolaemus spp.	-	-	x	-	x	x	-	-
	Distocyclus	x	-	x	-	x	x	-	-
	Eigenmannia	x	-	x	-	x	x	-	-
	Japigny	x	-	x	-	x	x	-	-
	Rhabdolichops	x	-	x	-	x	x	-	-
	Sternopygus	x	-	x	-	x	x	-	-
Apteronotidae	*Apteronotus* gr. *albifrons*	x	-	x	-	-	-	-	x
	"*A.*" gr. *bonapartii*	x	-	-	x	-	-	-	x
	A. gr. *leptothynchus*	x	-	x	-	-	-	-	x
	Adontosternarchus	x	-	x	-	x	x	-	-
	Compsaraia	x	-	x	-	-	-	-	x
	Orthosternarchus	-	-	x	-	-	-	-	x
	Parapteronotus	x	-	x	-	-	-	-	x
	Pariosternarchus	x	-	x	-	-	-	-	x
	Platyurosternarchus	-	x	-	-	-	-	-	x
	Porotergus	x	-	-	x	-	-	-	x
	Sternarchella	x	-	x	-	-	-	-	x
	Tenebrosternarchus	x	-	-	x	-	-	-	x
	Sternarchogiton	x	-	-	x	-	-	-	x
	Sternarchorhamphus	-	-	x	-	-	-	-	x
	Sternarchorhynchus	-	-	x	-	-	-	-	x

coronomeckelian bone. The path of the *ramus mandibularis trigeminus* nerve is variable across the order (Tab. 3). This nerve is invariably mesial to the *malaris* and lateral to the *stegalis* and may be mesial or lateral to the *rictalis*, occasionally penetrating it. In some cases, the *ramus mandibularis trigeminus* may be located medially to the *adductor mandibulae*.

An interesting aspect of some Gymnotiformes is the presence of intermuscular bones in the *adductor mandibulae*. In the generalized condition of the order, the *segmentum*

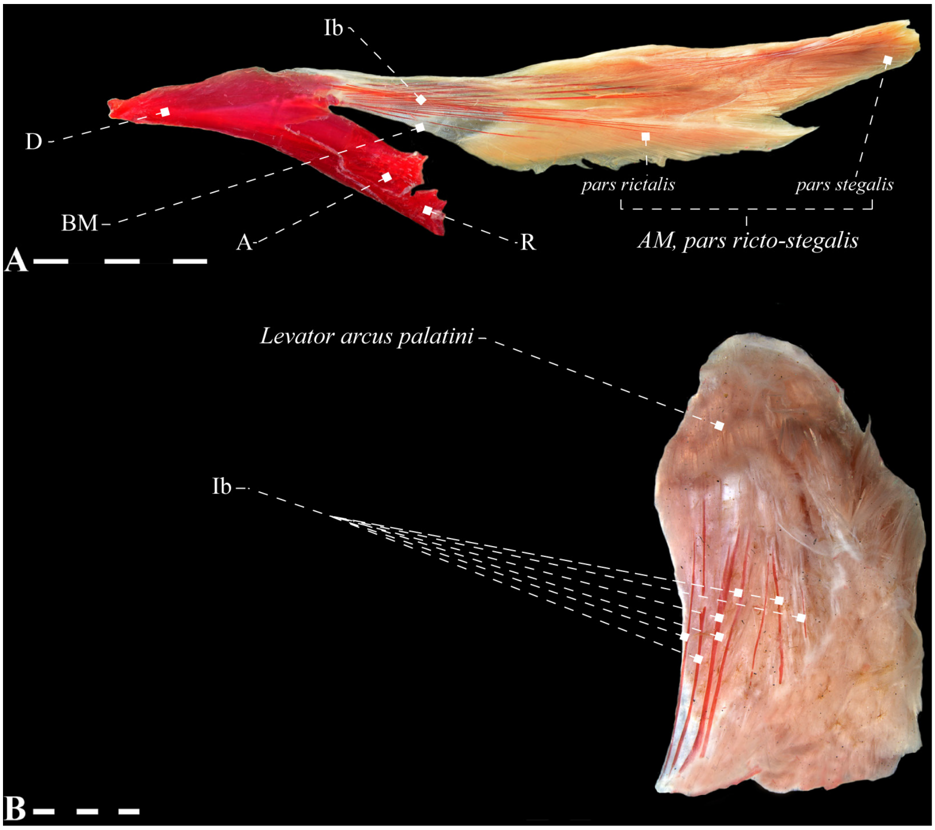


FIGURE 8 | *Rhamphichthys hahni* (Rhamphichthyidae), MZUSP 24736, 479.5 mm TL. **A.** Lateral view of *adductor mandibulae*, *pars ricto-stegalis*; **B.** Mesial view of *levator arcus palatini*. Anatomical abbreviations in Tab. 1. Scale bars = 10 mm; 2 mm.

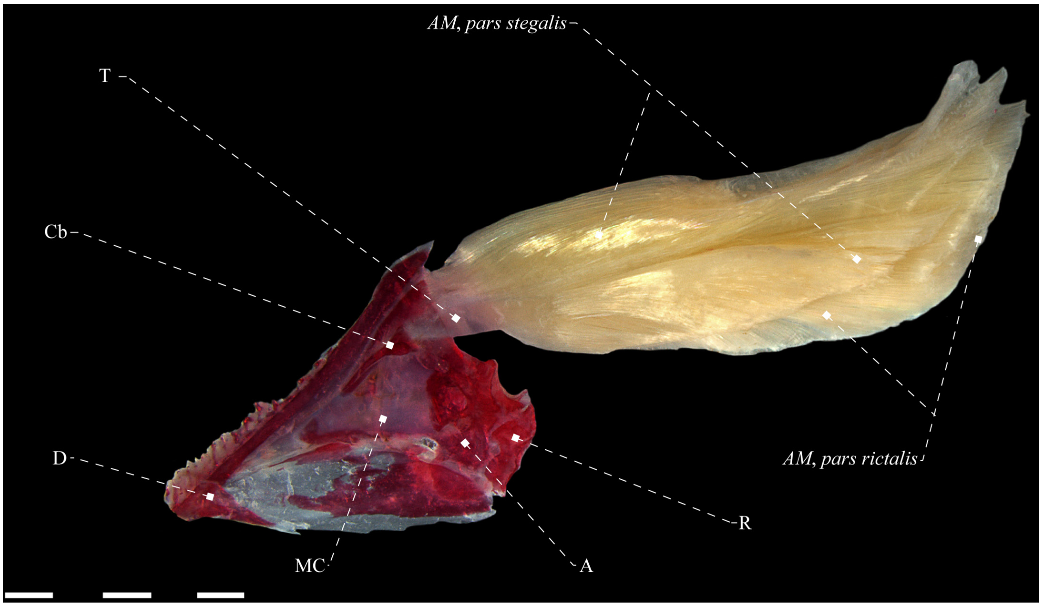


FIGURE 9 | Mesial view of *adductor mandibulae* of *Archolaemus janeae* (Sternopygidae), MZUSP 97383, 171.0 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 4 mm.

facialis composition is characterized by the absence of intermuscular bones, being essentially fibrous. However, in *Gymnotus* gr. *carapo*, *Rhamphichthys*, *Iracema* and *Orthosternarchus*, the subsections present ossifications of some tendons, resulting in bone filaments associated with the fibers or ligaments of this segment, named as intermuscular bones (Fig. 8A) (LAWP, pers. obs.; Aguilera, 1986; Albert, Campos-da-Paz, 1998; Albert, 2001; Hilton *et al*., 2007; Carvalho, Albert, 2011; Datovo, Vari, 2014).

Intermuscular bones are present in the *adductor mandibulae* of species of *Orthosternarchus* and *Rhamphichthys*, and Hilton *et al.* (2007) hypothesized that the pronounced elongation of the snout is related to the origin of those structures. Gymnotiform taxa with intermuscular bones indeed have long snouts, namely species of *Rhamphichthys* (snout length 46–64% HL; Carvalho, 2013), *Iracema* (53.8–55.4%; Carvalho, Albert, 2011) and *Orthosternarchus* (52–60% HL; LAWP, pers. obs.) when compared to the other members of the order. However, other species with similarly elongated snouts (*e.g*., 34.5–68.6% HL in *Gymnorhamphichthys* spp., Carvalho, 2013; 44–71.2% in *Sternarchorhynchus* spp., de Santana, Vari, 2010; 46.4–63.7% in *Apteronotus acidops*, Triques, 2011), do not have any ossifications of the tendons of the *adductor mandibulae* sections. Additionally, such bones also occur in *Gymnotus* gr. *carapo*, a short-snout species (approx. 32–39.4% HL). Therefore, the occurrence of intermuscular bones in the *adductor mandibulae* apparently does not have direct correlation with the length of the snout. Later, Datovo, Vari (2014) hypothesized that ossification of internal tendons of the *adductor mandibulae* as a potential origin of such intermuscular bones. The commonly mesial disposition and composition of intermuscular bones, with anterior and posterior tendon portions gradually ossified towards the middle portion, agree with that hypothesis. However, the relationship between these elements and other morphofunctional traits still needs further investigation.

Levator arcus palatini. The *levator arcus palatini* lies posterior to the orbit, with a variable general shape ranging from roughly parallelogram, trapezoidal or inverted triangle. In Gymnotiformes, the muscle is usually in a single mass of muscle, though partial sectioning occurs in *Electrophorus* where two sections are recognizable (Fig. 10). The *levator arcus palatini* originates on the mesial part of the ventral surface of the sphenotic, commonly including also the frontal and, occasionally, the pterosphenoid. The insertion is invariably on the hyomandibula and occasionally also on the preopercle. Only the posterodorsal portion of the *levator arcus palatini* is positioned mesially to the *dilatator operculi*. However, in some representatives of Apteronotidae, in *Gymnotus*, and in *Steatogenys*, it has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the medial portion of the *levator arcus palatini*. The orientation of the anterior-most fibers is also variable, ranging from oblique to the longitudinal axis of the head (at approximately 45° angle; Fig. 1), to orthogonal relative to that axis (Figs. 2, 10).

The *levator arcus palatini* has a variable insertion on the hyomandibula, with four subsets of fibers commonly recognized (anterolateral, posterolateral, anteromesial and posteromesial) according to their disposition relative to the *malaris* or *rictalis* (in representatives of Apteronotidae). The most common pattern comprises a completely lateralized arrangement of the *levator arcus palatini* in relation to the *segmentum facialis*. The *levator arcus palatini* tends to section the *malaris* of the other sections, as well as the *rictalis* of *stegalis* in their respective points of origin, even when the latter are not

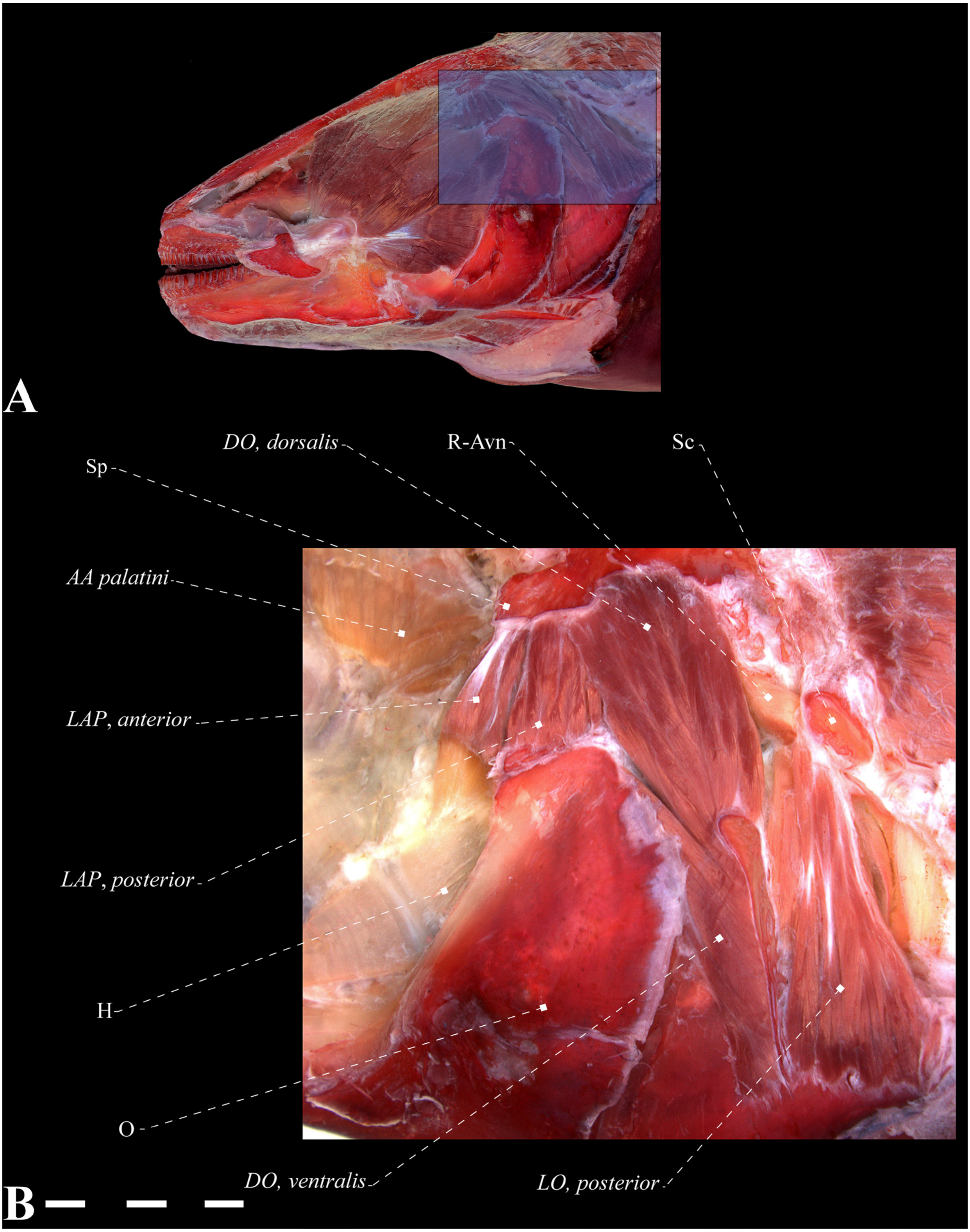


FIGURE 10 | *Electrophorus* cf. *electricus* (Gymnotidae), MZUSP 85509, 488.2 mm LEA. **A.** Lateral view of dorsolateral head muscles; **B.** Posterior portion of dorsolateral head muscles. *Adductor mandibulae* dissected in B. *LO, anterior* not visible in lateral view. Anatomical abbreviations in Tab. 1. Scale bar = 10 mm.

TABLE 3 | Path of the *ramus mandibularis trigeminus* nerve across Gymnotiformes.

		Ramus mandibularis trigeminus				
		malaris	*rictalis*	*stegalis*	*stego-malaris*	*ricto-stegalis*
Gymnotidae	*Electrophorus*	-	mesial	-	lateral or mesial	-
	Gymnotus	-	mesial or trespasses	-	mesial	-
Rhamphichthyidae	*Gymnorhamphichthys*	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Rhamphichthys	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Steatogenys	mesial	mesial	mesial	-	-
	Hypopygus	mesial	mesial	mesial	-	-
Hypopomidae	*Brachyhypopomus*	mesial	mesial	lateral	-	-
	Hypopomus	mesial	lateral	lateral	-	-
	Microsternarchus	mesial	mesial	mesial	-	-
Sternopygidae	*Archolaemus*	mesial	mesial	lateral	-	-
	Distocyclus	mesial	mesial	lateral	-	-
	Eigenmannia	mesial	mesial	lateral	-	-
	Japigny	mesial	mesial	lateral	-	-
	Rhabdolichops	mesial	lateral	lateral	-	-
	Sternopygus	mesial	mesial	lateral	-	-
Apteronotidae	*Adontosternarchus*	mesial	lateral	lateral	-	-
	Apteronotus	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Compsaraia	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Orthosternarchus	mesial	-	-	-	mesial
	Parapteronotus	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Pariosternarchus	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Platyurosternarchus	mesial	-	-	-	lateral
	Porotergus	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Sternarchella	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Tenebrosternarchus	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Sternarchogiton	mesial	-	-	-	trespasses (lateral to *stegalis* and mesial to *rictalis*)
	Sternarchorhamphus	mesial	-	-	-	mesial
	Sternarchorhynchus	mesial	-	-	-	mesial

conspicuously differentiated. The generalized pattern consists of a strictly fibrous composition of *levator arcus palatini*, however, some more mesial tendons ossify in *Sternopygus xingu* Albert & Fink, 1996 and *Rhamphichthys* (Fig. 8B).

Dilatator operculi. The *dilatator operculi* is located posterior to the *levator arcus palatini*, and is usually organized in a single block of mass, without sub-sections, except in *Electrophorus* where it is divided into dorsal and ventral component (Fig. 10). Origin is usually on the sphenotic and hyomandibula, sometimes also including the frontal and the pterotic, rarely the preopercle, orbito-sphenoid, and pteroesophoid. Insertion is invariably on the dorsal process of the opercle. The generalized pattern of the *dilatator operculi* in Gymnotiformes comprises a muscle strictly fibrous. Hilton *et al.* (2007) report and illustrate the presence of intermuscular bones in the *dilatator* (and *levator*) *operculi* of *Orthosternarchus*. However, such structures are present only in the *adductor mandibulae* and, being absent in the *dilatator* and *levator operculi* of specimens of that taxon analyzed herein.

Levator operculi. The *levator operculi* is a laminar and superficial muscle, located immediately posterior to the *dilatator operculi* and laterally to the *adductor operculi*. The generalized condition in Teleostei consists of an undivided block without sub-sections, originating from the posterodorsal elements of the posterior portion of the neurocranium and inserting on the opercle (Winterbottom, 1974a). The morphology of the *levator operculi* in Gymnotiformes departs quite markedly from the generalized teleost pattern. As previously reported (de la Hoz, Chardon, 1984; Aguilera, 1986), the *levator operculi* in Gymnotiformes has two sections, here referred to as *levator operculi anterior* and *levator operculi posterior* (Figs. 1, 2, 7). Despite the recognition of such subdivisions, their delimitation and identification are still unclear and needs re-examination.

The *levator operculi anterior* can be differentiated from the *levator operculi posterior* by the following attributes: (1) origin in the pterotic (*vs*. postotic canal segment corresponding to the supracleithrum); (2) mesial to R-Avn nerve (*vs*. lateral); (3) insertion mainly on the crest of dorsal portion of the opercle (*vs*. insertion mainly in the posterolateral face of the opercle). Thus, the recognition of these sections is possible on the basis of their points of origin, insertion and, mainly, by the layout of the R-Avn. The *levator operculi anterior* originates from the lateral surface of the mid-ventral portion of the pterotic, rarely including the hyomandibula (as in Eigenmanniinae and *Steatogenys*) or the exoccipital (as in *Electrophorus*). The insertion of that subsection is invariably on a ridge in the posterodorsal portion of the opercle, with its fibers extend beyond the dorsal margin of the bone. In addition, the nerve R-Avn is positioned laterally in relation to it in the vast majority of gymnotiform species, except in members of Eigenmanniinae (Sternopygidae), *Rhamphichthys* (Rhamphichthyidae), *Platyurosternarchus* and some species of *Sternarchella* (Apteronotidae). Contrastingly, the *levator operculi posterior* originates mainly from the postotic canal segment corresponding to the supracleithrum, including also the posterior margin of the pterotic in *Gymnotus* (Gymnotidae), *Sternopygus*, *R. lundbergi*, *R. nigrimans* (Sternopygidae), *Adontosternarchus*, *Platyurosternarchus*, and *Sternarchella* (Apteronotidae). Its insertion site is the lateral side of the posterior portion of the opercle, with its fibers ventrally-deflected when compared to those of the *levator operculi anterior*. Occasionally, the posterior section inserts on the posterior portion of the dorsal crest of the opercle (*e.g*., *Sternarchella duccius* and *S. raptor*). Finally, the nerve R-Avn is arranged mesially to the *levator operculi posterior* in all species of Gymnotiformes.

Hypopygus (Hypopomidae) is the only genus that does not present the *levator operculi posterior*, being restricted to the presence of the anterior section (Fig. 11). In that genus, the *levator operculi* originates exclusively from the pterotic, is positioned mesially to the R-Avn and inserts only on the dorsal crest of the opercle. It is therefore clearly homologous to the *levator operculi anterior* in other Gymnotiformes. The subdivision of the *levator operculi* in gymnotiforms has convergent occurrences in *Microgadus* (Gadidae;

Gadiformes) and *Stephanolepis* (Monacanthidae; Tetraodontiformes) as described by Winterbottom (1974a,b).

Adductor arcus palatini. The *adductor arcus palatini* is the mesial-most dorsolateral head muscle, located dorsally to the suspensorium and ventrally to the neurocranium. This muscle has a laminar, tapered aspect, originating mainly from the parasphenoid, but sometimes also including the prootic (several groups) and the orbitosphenoid (*Japigny* only). The insertion occurs mostly on the lateral side of the suspensorium, invariably involving the endopterygoid, metapterygoid and hyomandibula, with participation of the symplectic in some Hypopomidae. Some posterodorsal fibers of the *adductor arcus palatini* are connected with the anterodorsal fibers of the *adductor hyomandibulae*, however, differentiation between these two muscles is always present and thus they are considered entirely separated from each other (Fig. 12).

The generalized pattern of Gymnotiformes consists of an *adductor arcus palatini* totally covered by the *adductor mandibulae*, and its visualization requires removal of the former. In some representatives of Sternopygidae and Apteronotidae, only the posterior portion is overlapped by the *segmentum facialis* (Peixoto, Ohara, 2019: fig. 8; Dutra *et al*., 2021: fig. 40). Exceptions occur in the majority of *Archolaemus* species, where those muscles never overlap each other (Dutra *et al*., 2021: fig. 15).

Adductor hyomandibulae. The *adductor hyomandibulae*, along with the *adductor arcus palatini*, is derived from the *constrictor hyoideus dorsalis* (Winterbottom, 1974a; Miyake *et al*., 1992; Datovo, Rizzato, 2018). This muscle differentiates from the posterior portion of the *adductor arcus palatini* or from fibers of the *adductor operculi*, and its ontogenetic origin is variable across the Teleostei (Winterbottom, 1974a; Diogo, Vandewalle, 2003).

In Gymnotiformes, the *adductor hyomandibulae* has a laminar aspect, noticeable in mesial view of the suspensorium. The muscle arises mainly from the lateral side of the prootic, sometimes also the pterotic and, more rarely, the parasphenoid and sphenotic. The insertion is invariably on the mesial surface of the posterodorsal portion of the hyomandibula. Some anterior fibers are partially continuous with the *adductor arcus palatini* and the *adductor operculi*, but the respective muscles are completely differentiated from each other. Little variation was detected in this muscle across the Gymnotiformes.

Adductor operculi. *Adductor operculi* is a laminar-looking muscle, completely mesially arranged to the *levator operculi*, resulting in a total overlap by this muscle. The points of common origins include the exoccipital, pterotic and the pro-optic, punctually being able to include the basioccipital and the epoccipital. The insertion occurs invariably on the mesial side of the opercle (Fig. 12). Some anterodorsal fibers are associated with the mid-posterior portion of *adductor hyomandibulae*. The R-Avn nerve is invariably disposed laterally to the *adductor operculi*. Little variation was detected in this muscle along the order.

General aspects of the dorsolateral head muscles of the Gymnotidae.

Adductor mandibulae. The *stego-malaris* is positioned dorsolaterally to the *rictalis*,

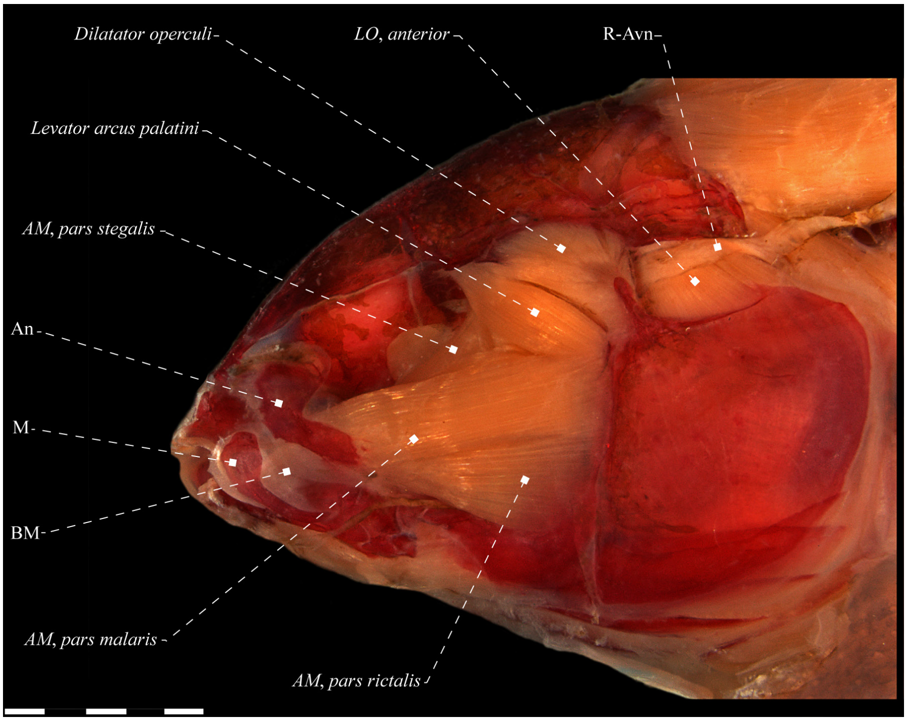


FIGURE 11 | Lateral view of dorsolateral musculature of *Hypopygus lepturus* (Hypopomidae), MZUSP 91426, 55.4 mm LEA. Some fibers of the *LO*, *anterior* accidentally removed during dissections. Anatomical abbreviations in Tab. 1. Scale bar = 2 mm.

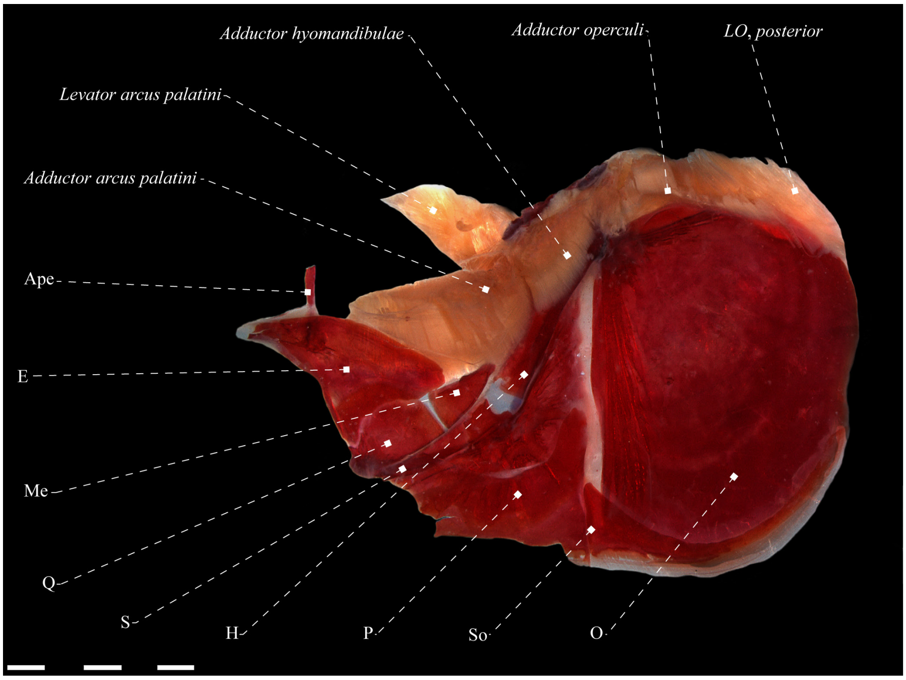


FIGURE 12 | Mesial view of suspensorium of *Brachyhypopomus janeiroensis* (Hypopomidae), MZUSP 22702, 80.9 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 4 mm.

and it originates from elements of the suspensorium and neurocranium (Figs. 1, 2). Towards their insertion, those two sub-sections become gradually differentiated, with the dorsal fibers, presumably corresponding to the *malaris*, converging in a thick mandibular tendon, which inserts on the mesial surface of the coronoid process; in *Electrophorus* such fibers converge also on the lateral side of the same spot, forming an additional insertion point. The dorsomesial fibers, corresponding to the *stegalis*, converge in a thick meckelian tendon inserted on the dorsal margin of the corono-meckelian bone. Invariably, the *stego-malaris* has some lateral fibers converging directly on the buccopalatal membrane.

The *rictalis* originates in bony elements of the middle-ventral portion of the suspensorium and is inserted mainly on the coronoid process, but with some lateral fibers also associated with the buccopalatal membrane. At its origin, the posterolateral fibers of the *rictalis* extend beyond the anterior margin of the preopercular fossa, reaching the posterior margin of the bone or its medial portion. Usually in Gymnotidae, ossification of tendons in the facial segment are absent, but in *Gymnotus* gr. *carapo* the lateral-most tendons of that segment have intermuscular bones. The trajectory of the *ramus mandibularis trigeminus* nerve is variable in the family. It may be disposed mesially in relation to the *rictalis* and lateral to the *stego-malaris*, trespassing the *rictalis* and lateral to the *stego-malaris* or mesial relative to all sections of *adductor mandibulae*.

Levator arcus palatini. Invariably in Gymnotidae, the *levator arcus palatini* is a roughly triangular in *Gymnotus* (Fig. 1) or trapezoidal in *Electrophorus* (Fig. 2). In *Electrophorus*, the origin of *the levator arcus palatini* is narrower than its insertion, while in *Gymnotus* the origin is twice as wide as its insertion. The anterior-most fibers of this muscle are straight relative to the axis of the head in *Electrophorus* or anteroposteriorly oblique in *Gymnotus*.

Electrophorus has the *levator arcus palatini* divided in two sections (*levator arcus palatini anterior* and *levator arcus palatini posterior*; Fig. 13), a unique condition in Gymnotiformes. The origin of the *levator arcus palatini* include the sphenotic, occasionally also the lateroventral portion of the frontal. Its insertion is mainly on the dorsal portion of the hyomandibula and, when divided, also on the preopercle. At the insertion point, the fibers of this muscle partially separate the *stegalis* from the *malaris* in their respective points of origin, arranged in different ways in relation to the *adductor mandibulae*. The *levator arcus palatini* has a variable disposition relative to the *dilatator operculi*, being mesial to it, with the anterior margin of the *dilator operculi* surpassing the medial portion of the *levator arcus palatini* in *Gymnotus* (Fig. 1), or with only the posterodorsal fibers being mesial to the *dilatator operculi* in *Electrophorus*. The *levator arcus palatini* lacks tendon ossifications in Gymnotidae (Fig. 2).

Dilatator operculi. The *dilatator operculi* has a roughly rectangular or conical shape. Like the latter, the *dilatator operculi* in *Electrophorus* is uniquely divided in two sections, here named *dilatator operculi ventralis* and *dilatator operculi dorsalis* (Fig. 11). The *dilatator operculi ventralis* differentiates as a consequence of a ventral displacement of the opercle in relation to the preopercle. The *dilatator operculi dorsalis* is probably homologous to the *dilatator operculi* of *Gymnotus* and other Gymnotiformes. The points of origin of this muscle include elements of the posterolateral portion of the neurocranium,

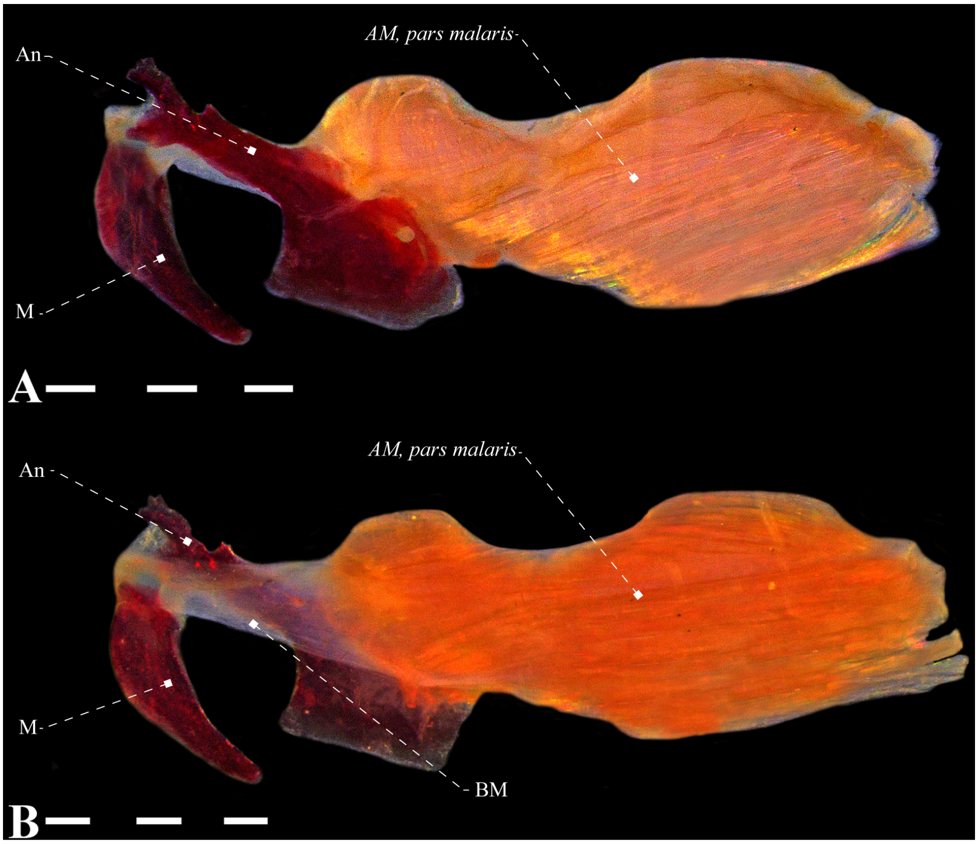


FIGURE 13 | *Adductor mandibulae, pars malaris* of *Brachyhypopomus janeiroensis* (Hypopomidae), MZUSP 22702, 80.9 mm LEA. **A.** Lateral view; **B.** Mesial view. Buccopalatal membrane dissected ventrally. Anatomical abbreviations in Tab. 1. Scale bars = 1 mm.

hyomandibula and, when divided, also the preopercle. Its insertion, contrastingly, is always on the dorsal process of the opercle.

Levator operculi. The origin of the *levator operculi anterior* is on the pterotic and may include also the exoccipital in *Electrophorus*. The *levator operculi posterior* arises primarily from the postotic canal segment corresponding to the supracleithrum, with some anterodorsal fibers sometimes originating also in the pterotic in *Gymnotus*. The R-Avn nerve is invariably lateral to the *levator operculi anterior* and mesial to the *levator operculi posterior*. The insertion of the muscle is invariably on the opercle.

The position of the *levator operculi anterior* in *Electrophorus* deserves note. In the vast majority of species in Gymnotiformes, both *levatores* are clearly visible in lateral view (Figs. 1, 7). In *Electrophorus*, contrastingly, the anterior section is displaced mesially and as a consequence it is almost invisible in lateral view (Fig. 2), requiring dislocation of the posterior section for full view.

Adductor arcus palatini. This muscle invariably originates in the parasphenoid and prootic. Anteriorly, it inserts on the lateral face of the endopterygoid and metapterygoid; as the muscle progresses posteriorly, its insertion shifts from the lateral to the medial face of the suspensorium, finally inserting on the medial surface of the hyomandibula. Examination of the *adductor arcus palatini* requires dissection and partial removal of the *adductor mandibulae*, which completely overlaps it.

Adductor hyomandibulae. This muscle arises from the ventral region of the prootic, sphenotic and pterotic, inserting on the posteromedial margin of the hyomandibula. Little or no variation in this muscle was found throughout the Gymnotidae.

Adductor operculi. The origin of the *adductor operculi* is on the exoccipital, and may also include the other post-ventral elements of the neurocranium, such as the basioccipital in *Electrophorus*; or the pterotic and epioccipital in *Gymnotus*. Anteriorly, the insertion is on the dorsal margin of a dorso-mesial crest of the opercle, and posteriorly it inserts on the mesial surface of the same bone.

Detailed description of the dorsolateral musculature of the head in the genera of Gymnotidae.

Electrophorus Gill, 1864

Adductor mandibulae. The *stego-malaris* originates in the hyomandibula, metapterygoid, endopterygoid, quadrate, parasphenoid, frontal and sphenotic. Its component subsections are increasingly differentiated towards its insertion, where dorsolateral fibers, presumably corresponding to the *malaris*, converge towards the coronoid process and dorsomesial fibers converge on a thick mandibular tendon inserted on the mesial surface of the coronoid process. The middle fibers, presumably correspond to the *stegalis*, diverge in a thick meckelian tendon inserted on the dorsal margin of the coronomeckelian bone (Fig. 3). Dorsomesial fibers corresponding to the *stegalis* are disposed laterally relative to the posterolateral region of the basal portion of the endopterygoid, not completely overlapping it but totally covering laterally the *adductor arcus palatini* (Fig. 2).

The *rictalis* originates in the preopercle, quadrate and hyomandibula, with lateral fibers surpassing the anterior margin of the preopercular fossa, but not reaching the posterior margin of the bone, being restricted to its medial portion. The *rictalis* inserts mainly on the coronoid process, but with a few lateral fibers on the buccopalatal membrane. The dorsal portion of the *rictalis* is disposed mesially to the *stego-malaris*, with anterior fibers close to its insertion fully differentiated from the latter. The *ramus mandibularis trigeminus* nerve is arranged mesially to the *rictalis* and laterally to the *stego-malaris* (n = 1) or mesially to all sections of the *adductor mandibulae* (n = 1).

Levator arcus palatini. The *levator arcus palatini anterior* originates in the anteroventral margin of the sphenotic and is inserted on the hyomandibula. The *levator arcus palatini posterior* originates in the posteroventral margin of the sphenotic and inserts onto the hyomandibula and preopercle. In the region of origin, the two sections are partially continuous and sectioned by the *truncus hyomandibularis* nerve, which is lateral to the anterior section and mesial to the posterior one (Fig. 10). At the insertion, fiber bundles of the *levator arcus palatini anterior* are mesial to the *malaris* and those of the *levator arcus* *palatini posterior* are lateral to the *malaris* and posterolaterally to the *rictalis*. The origin of the *levator arcus palatine* is narrower than its insertion and only its posterodorsal fibers are mesial to the *dilatator operculi*.

Dilatator operculi. The *dilatator operculi ventralis* has a roughly rectangular shape, originating in the posterior margin of the preopercle and inserting on the anterodorsal portion of the dorsal process of the opercle. The *dilatator operculi dorsalis* is approximately conical and originates in the ventral margin of the pterotic, sphenotic and dorsal portion of the hyomandibula. The fibers of dorsal and ventral sections are partially continuous near their insertion on the anterodorsal and dorsal part of the dorsal process of the opercle (Fig. 10).

Levator operculi. The origin of the *levator operculi anterior* occurs in the posteroventral margin of the pterotic and exoccipital, while its insertion is into a ridge on the dorsal margin of the opercle, posterior to the anterodorsal process of that bone. The origin of the *levator operculi posterior* is in the postotic canal segment corresponding to the supracleithrum and it inserts along a crest at the posterolateral margin of the opercle, with fibers surpassing the dorsal margin of that bone (Fig. 2).

Gymnotus Linnaeus, 1758

Adductor mandibulae. The *stego-malaris* originates in the hyomandibula, metapterygoid, quadrate, parasphenoid, frontal and sphenotic. The subsections become gradually differentiated towards their insertion, where the dorsolateral fibers, corresponding to the presumed *malaris*, converge on a thick mandibular tendon inserted into the mesial face of the coronoid process. The middle fibers, presumably corresponding to the *stegalis*, diverge in the meckelian tendon and are inserted on the dorsal margin of the coronomeckelian bone. Some lateral fibers near the insertion site of the *stego-malaris* are inserted on the buccopalatal membrane, which in turn is associated with the posterior margin of the maxilla.

Stego-malaris is composed mainly of fibers. However, in *Gymnotus* gr. *carapo* the more lateral fibers of this sub-section, corresponding to the presumed *malaris*, have tendinous ossifications forming intermuscular bones. The mesial fibers, corresponding to the presumed *stegalis*, are laterally positioned in relation to the posterolateral region of the basal portion of the endopterygoid, not completely overlapping it, and are lateral relative to the *adductor arcus palatini*, totally overlapping it.

The *rictalis* originates in the preopercle, quadrate and hyomandibula, with lateral fibers surpassing the anterior margin of the preopercular fossa and reaching the posterior margin of that bone. This subsection is inserted mainly on the coronoid process, but with some more lateral fibers associated with the buccopalatal membrane. The *rictalis* is normally composed of fibers only, except in *Gymnotus* gr. *carapo*, in which some tendons ossify and form intermuscular bones. The *ramus mandibularis trigeminus* nerve is mesial to all sub-sections of the *adductor mandibulae* (in one specimen of *G. coropinae*, the nerve trespasses the *rictalis*).

Levator arcus palatini. The *levator arcus palatini* has the shape of an inverted triangle; with its origin twice as wide as its insertion. This muscle originates in the ventral margin of the frontal and sphenotic and is inserted on the hyomandibula. The *levator arcus palatini* is a non-sectioned muscle, except at the insertion, where four sub-sets of fibers are identifiable. Each of them has distinct modes at its insertion point in relation to the *malaris*: the anterolateral fibers, posterolateral and posteromesial is disposed laterally in relation to the *malaris* and dorsally to the *rictalis*; and the anteromesial fibers are arranged mesially in relation to the *malaris*. This muscle is partially mesial to *the dilatator operculi*, which exceeds the medial portion of the *levator arcus palatini* (Fig. 1).

Dilatator operculi. The *dilatator operculi* is roughly conical. It originates in the posterior margin of the sphenotic, pterotic, frontal and dorsal portion of the hyomandibula, and inserts on the dorsal and anterodorsal portion of the dorsal process of the opercle. In *Gymnotus cylindricus* its insertion includes the dorsoposterior portion of the dorsal process of the opercle. The *dilatator operculi* is lateral to the *levator arcus palatini*, overlapping approximately 2/3 of its mid-posterior portion.

Levator operculi. The *levator operculi anterior* originates in the ventral margin of the pterotic and is inserted in a ridge on the dorsal margin of the opercle, posterior to its anterodorsal process. The *levator operculi posterior* originates in the postotic canal segment corresponding to the supracleithrum and posteroventral margin of the pterotic, inserting along a ridge on the posterolateral margin of the opercle, with fibers extending beyond the dorsal margin of the bone.

General aspects of the dorsolateral head muscles of the Hypopomidae.

Adductor mandibulae. The *adductor mandibulae* in Hypopomidae consists of the *segmentum facialis*, which is connected to the *segmentum mandibularis* through an intersegmental aponeurosis well-differentiated in two components. The dorsal component differentiates into a mandibular tendon, which serves as the origin of the *segmentum mandibularis*, and the ventral component differentiates into the meckelian tendon, continuous with the *stegalis* for insertion into the coronomeckelian bone (Fig. 4). The *segmentum facialis* is composed of three subsections in all species analyzed: the *adductor mandibulae*, *pars malaris*; *pars stegalis* and *pars rictalis*.

The *malaris* is positioned latero-dorsally to the dorsal portion of the *rictalis* and the latero-ventrally to the *stegalis*. This sub-section originates in the mid-dorsal portion of the hyomandibula and preopercle, except in species of *Brachyhypopomus*, where its origin is on the hyomandibula only. Its insertion is invariably on the antorbital, where the mesial fibers differentiate into a diminutive endomaxillary ligament inserted on the posteromedial margin of the maxilla (Fig. 4). In some specimens of *Brachyhypopomus*, the endomaxillary ligament is only visible after complete removal of the buccopalatal membrane (Fig. 13).

Except for a few species of *Brachyhypopomus*, the *malaris* has a concavity on its dorsal margin for the allocation of the eyeball (Figs. 13, 14). This concavity is apparently present only in the representatives of Hypopomidae but its phylogenetic significance is difficult to assess due to the existence of intermediate conditions in various taxa. The *rictalis* originates in bony elements of the mid-ventral portion of the suspensorium and is inserted mainly on the coronoid process, with some fibers on the posterior dorsal margin of the anguloarticular in some species of *Brachyhypopomus* and *Microsternarchus*. In the region of origin, the posterolateral fibers may either extend beyond the anterior margin of the preopercular fossa, reaching the posterior margin of the bone (Fig. 11), or be restricted to the medial portion of the bone. Commonly, the origin of the *stegalis* includes only bony elements of the suspensorium, with its fibers converging on an intersegmental aponeurosis ventrally differentiated into the meckelian tendon and inserting on the coronomeckelian bone; and dorsally differentiated into the mandibular tendon, itself the origin of the *segmentum mandibularis* (Fig. 4). The *adductor mandibulae, segmentum facialis* is strictly fibrous, without ossifications.

The *segmentum mandibularis* is a single section arising from the mandibular tendon and entering the mesial surface of the lower jaw, commonly involving the dentary and anguloarticular or only the latter in *Microsternarchus*. Invariably, this segment is restricted to the dorsal portion of Meckel´s cartilage and may either be directly associated with the dorsal margin of the cartilage or restricted to the dorsal portion of the coronomeckelian bone. This segment normally does not exceed 50% of the dorsal margin of the Meckel´s cartilage, but in *B. sullivani* it extends for ca. 80% of the cartilage. The course of the *ramus mandibularis trigeminus* nerve is variable across the family and may be either mesial to all subsections of the *segmentum facialis*, or lateral to the *stegalis* and mesial to the *rictalis* and *malaris*, or finally lateral to the *rictalis* and *stegalis* and mesial to the *malaris*.

Levator arcus palatini. The *levator arcus palatini* has roughly the shape of a parallelogram. The relative sizes of origin and insertion are variable, with the origin normally ca. one and a half times the size of the insertion, but equal in some species of *Brachyhypopomus* (Fig. 14). The most anterior fibers of this muscle are anteroposteriorly oblique relative to the axis of the head in all analyzed taxa (Figs. 11, 14–16). The origin of the *levator arcus palatini* is on the frontal and sphenotic and its insertion is on the hyomandibula. At the insertion point, anterolateral and posterolateral fibers are lateral to the *malaris*; while anteromesial and posteromesial fibers are mesial to the latter. In *Microsternarchus*, only the posteromesial fibers are mesial to the *malaris*. In most analyzed species, the posterodorsal fibers of the *levator arcus palatini* are parallel to the *dilatator operculi*, with no overlap between the two muscles (Fig. 11–14, 16). Some species have only the posterodorsal portion of the *levator arcus palatini* mesial to the *dilator operculi*.

Dilatator operculi. The *dilatator operculi* is commonly conical. Its origin includes the sphenotic, pterotic, frontal and hyomandibula. The origin of the anteroventral fibers of the *dilatator operculi* is anteroventrally displaced to the preopercle in *Microsternarchus* (Fig. 15) and in some species of *Brachyhypopomus* (Fig. 14). This muscle inserts invariably on the dorsal process of the opercle.

Levator operculi. The *levator operculi* is a superficial muscle located immediately posterior to the *dilatator operculi* and sectioned into anterior and posterior sections (Figs. 14–16). The origin of the *levator operculi anterior* is normally on the pterotic. The *levator operculi posterior* originates in the postotic canal segment corresponding to the supracleithrum, with both sections inserting onto the opercle.

Adductor arcus palatini. This muscle originates in the parasphenoid and prootic, except in *Hypopomus* and *Microsternarchus*, with the origin being restricted to the parasphenoid. Anteriorly, it inserts on the lateral face of the endopterygoid and metapterygoid; as the muscle progresses posteriorly, its insertion shifts from the lateral to the medial face of the suspensorium, finally inserting on the medial surface of the hyomandibula. The insertion includes the sympletic in *Microsternarchus* and *B. beebei*. Examination of the *adductor arcus palatini* requires dissection and removal of the *adductor mandibulae*, which completely overlaps it.

Adductor hyomandibulae. This muscle arises from the ventral region of the prootic, including the pterotic in *Microsternarchus*, or the posterior portion of the parasphenoid in *Brachyhypopomus* and *Hypopomus*. The insertion occurs the posteromedial margin of the hyomandibula.

Adductor operculi. The origin of the *adductor operculi* is on the pterotic, exoccipital, and prootic. The insertion occurs solely in the mesial surface of the opercle in the most species of *Brachyhypopomus*. The generalized pattern includes an insertion on the dorsal margin of a dorso-mesial crest of the opercle, and posteriorly it inserts on the mesial surface of the same bone.

Detailed description of the dorsolateral musculature of the head in the genera of Hypopomidae.

Brachyhypopomus Mago-leccia, 1994

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula and inserts on the posteromedial portion of the antorbital bone by a fibrous attachment. Its mesialmost fibers converge onto a small endomaxillary ligament, less than one-third the length of the *malaris* which, in turn, inserts on the posteromedial portion of the maxilla (Fig. 13). Except for *B. sullivani* and *B. regani*, the *malaris* has a concavity on its dorsal margin for accommodating the eyeball.

The *rictalis* originates in the preopercle, quadrate and hyomandibula, or only in the preopercle and hyomandibula in *B. pinnicaudatus*, *B. hendersoni* and *B. regani*. The lateralmost fibers of *rictalis* surpass the anterior margin of the preopercular fossa and reach the mid-portion of the preopercle in most species of *Brachypopomus* analyzed herein. It reaches the posterior margin of that bone in *B. bombilla*, *B. pinnicaudatus*, and *B. hendersoni*. That section inserts mainly on the coronoid process, but with some lateral fibers on the anguloarticular in *B. bombilla*, *B. sullivani*, and *B. gaudeiro*. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, parasphenoid, sympletic and metapterygoid. Anteriorly, the *stegalis* differentiates into an intersegmental aponeurosis, dorsally entering the mandibular tendon and ventrally the meckelian tendon, inserting onto the coronomeckelian bone. The *stegalis* is located laterally in relation to the basal region of the endopterygoid, overlapping it completely; except in *B. pinnicaudatus*, in which the *stegalis* overlaps only the posterior portion of the basal region of the bone. Normally, the *stegalis* is positioned laterally to the *adductor arcus palatini*, overlapping it completely, except in *B. pinnicaudatus*, *B. brevirostris*, *B. hendersoni*, and *B. regani*, where

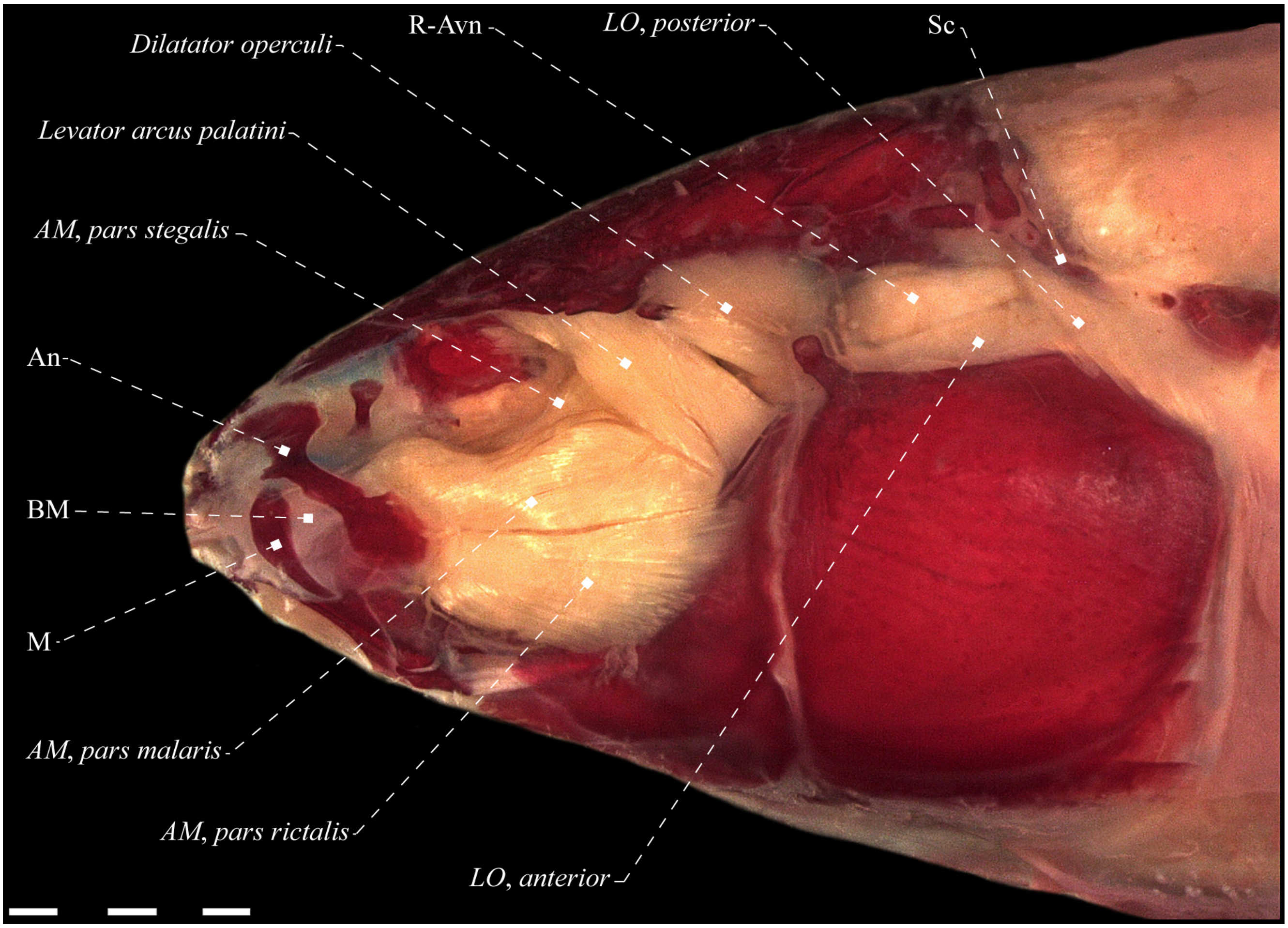


FIGURE 14 | Lateral view of dorsolateral musculature of *Brachyhypopomus janeiroensis* (Hypopomidae), MZUSP 22702, 80.9 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 3 mm.

the *stegalis* overlaps only the mid-posterior portion of the *adductor arcus palatini*.

Commonly, the *segmentum mandibularis* is located dorsally to Meckel's cartilage and contacts it, except in *B. sullivani*, *B. beebei*, *B. gaudeiro*, and *B. draco*, where the *segmentum mandibularis* is restricted to the dorsal margin of the coronomeckelian bone, and does not contact the dorsal margin of Meckel's cartilage. The path of the *ramus mandibularis trigeminus* nerve is invariably mesial to the *malaris* and *rictalis*, and lateral to the *stegalis*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion; or equal in *B. draco* and *B. hendersoni*. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its anteromesial and posteromesial bundles are medial to the *malaris*. In most examined species, the *levator arcus palatini* is parallel to the *dilatator operculi*, with no overlap. In *B. regani* only, the posterodorsal fibers of *the levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini*.

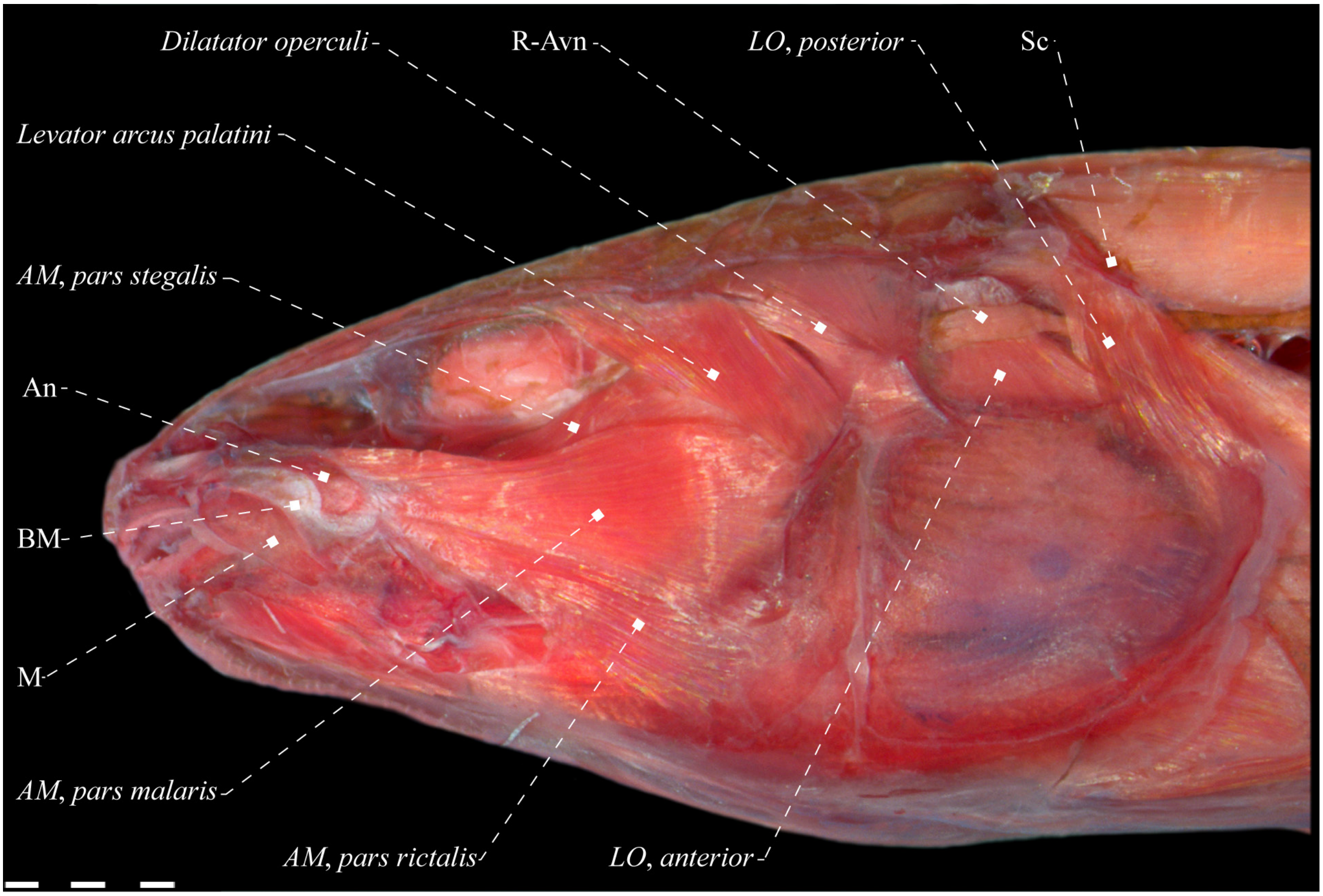


FIGURE 15 | Lateral view of dorsolateral musculature of *Microsternarchus* cf. *bilineatus* (Hypopomidae), MBUCV-V 7298, 59.2 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 1 mm.

Hypopomus Gill, 1864

Adductor mandibulae. The *malaris* originates from the mid-dorsal portion of the hyomandibula and preopercle. Its insertion occurs on the posteromedial portion of the antorbital bone by a fibrous attachment, with its mesialmost fibers converging onto a small endomaxillary ligament, less than one-third the length of the *malaris* which, in turn, inserts on the posteromedial portion of the maxilla (Fig. 4). The *rictalis* originates in the preopercle, sympletic, quadrate, and hyomandibula. The lateralmost fibers of *rictalis* surpass the anterior margin of the preopercular fossa and reach the mid-portion of the preopercle; with the posterodorsal fibers almost reaching the posterior margin of that bone. That subsection inserts on the coronoid process.

The *stegalis* arises from the sphenotic, pterosphenoid, metapterygoid and anterior margin of the hyomandibula. Towards its insertion, the fibers of *stegalis* differentiates into an intersegmental aponeurosis, dorsally entering the mandibular tendon and ventrally the meckelian tendon which, in turn, inserts onto the coronomeckelian bone (Fig. 4). The *stegalis* is located laterally in relation to the basal region of the endopterygoid and *adductor arcus palatini*, overlapping those structures completely.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage and does not contact directly the dorsal margin of Meckel's cartilage. The path of the *ramus mandibularis trigeminus* nerve is lateral to the *rictalis* and *stegalis*, and mesial to the *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape (Fig. 16), originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is wider than its insertion, approximately one and a half of its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its anteromesial and posteromesial bundles are medial to the *malaris*. Only the dorsalmost fibers of the posterior portion of the *levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini*.

Microsternarchus Fernández-Yépez, 1968

Adductor mandibulae. The *malaris* originates from the mid-dorsal portion of the hyomandibula and preopercle. Its insertion occurs on the posteromedial portion of the antorbital bone by a fibrous attachment. Its mesialmost fibers converge onto a small endomaxillary ligament, less than one-third the length of the *malaris* which, in turn, inserts on the posteromedial portion of the maxilla.

The *rictalis* originates in the preopercle, quadrate and hyomandibula. The lateralmost fibers of *rictalis* surpass the anterior margin of the preopercular fossa and reach the mid-portion of the preopercle. That subsection inserts mainly on the coronoid process, but with some lateral fibers on the anguloarticular and buccopalatal membrane. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, parasphenoid, sympletic and metapterygoid. Anteriorly, the *stegalis* differentiates into an intersegmental aponeurosis, dorsally entering the mandibular tendon and ventrally the meckelian tendon, inserting onto the coronomeckelian bone. The *stegalis* is located laterally in relation to the basal region of the endopterygoid and *adductor arcus palatini*, overlapping those structures completely.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage and contacts it by slightly more than a half of the cartilage's extension. The path of the *ramus mandibularis trigeminus* nerve is mesial to all sections of the *adductor mandibulae*, *segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is wider than its insertion, approximately one and a half of its insertion (Fig. 19). At the insertion, the anterolateral, posterolateral and anteromesial fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its posteromesial bundles are medial to the *malaris*. The posterodorsal fibers of the *levator arcus palatini* are parallel to the *dilatator operculi*, with no overlap between the two muscles. The *truncus hyomandibularis* nerve run through the lateral and mesial bundle of fibers of the *levator arcus palatini*.

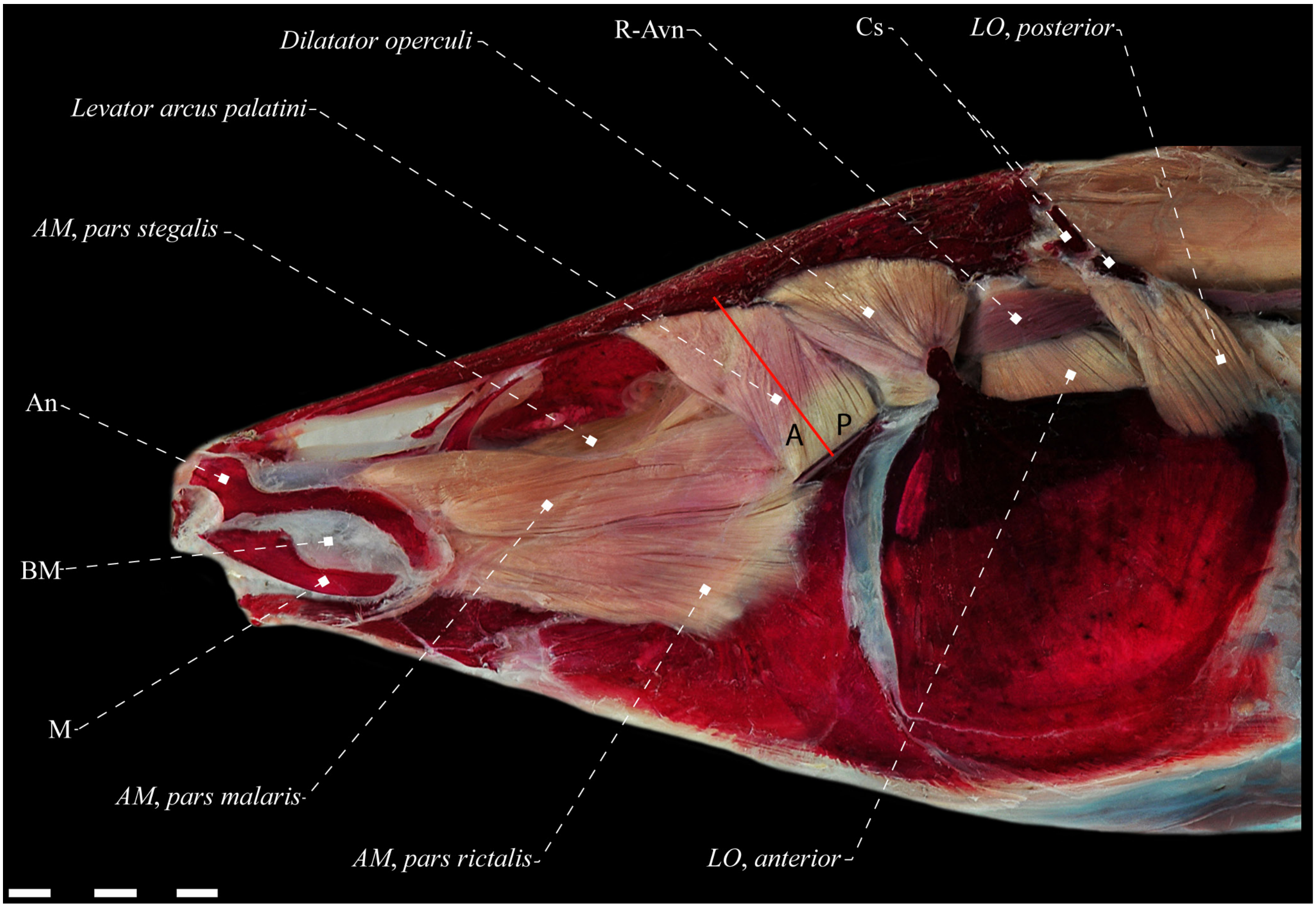


FIGURE 16 | Lateral view of dorsolateral musculature of *Hypopomus artedi* (Hypopomidae), USNM 408442, 202. 7 mm LEA. A= anterolateral fibers of the *levator arcus palatini*; P= posterolateral fibers of the *levator arcus palatini*. Remaining anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

General aspects of the dorsolateral head muscles of the Rhamphichthyidae

Adductor mandibulae. In *Rhamphichthys* and *Gymnorhamphichthys*, the *adductor mandibulae* is restricted to the *segmentum facialis*, which is composed of the *pars ricto-stegalis* and *malaris* (Figs. 5, 8; Peixoto, Ohara, 2019: fig. 12). In *Steatogenys* and *Hypopygus*, the *adductor mandibulae* consists of the *segmentum facialis* (composed of the *pars malaris*, *pars rictalis*, and *pars stegalis*), which is in turn connected to the *segmentum mandibularis* through an intersegmental aponeurosis well-differentiated in two components (mandibular tendon and meckelian tendon).

The *malaris* is positioned dorsolaterally to the dorsal portion of the *rictalis* and lateroventrally to the *stegalis*. It originates in the mid-dorsal portion of the hyomandibula and preopercle, except in species of *Rhamphichthys*, where its origin is on the hyomandibula only. The *malaris* inserts on the antorbital and maxilla, but with variations of detail within Rhamphichthyidae. In *Hypopygus* and *Steatogenys*, the *malaris* inserts on the posteromedial portion of the antorbital bone by a fibrous attachment, and its mesialmost fibers converge onto a small endomaxillary ligament, less than one-third the length of the *malaris* which, in turn, inserts on the posteromedial portion of the maxilla. In *Rhamphichthys* and *Gymnorhamphichthys*, the *malaris* converges anteriorly into an elongated endomaxillary ligament to an insertion on the posteromedial portion of the antorbital and maxilla (Fig. 5). In *Rhamphichthys*, the ventral fibers of *malaris* differentiate into an additional ligament, herein named "endomaxillary accessory ligament". Some internal portions of the endomaxillary accessory ligament ossify into intermuscular bones, and this ligament inserts solely onto the posteromedial face of the antorbital. In the generalized condition of the family, the *malaris* lacks intermuscular bones, being essentially fibrous. However, in *Rhamphichthys* and *Iracema* (Carvalho, Albert, 2011), this section has some ossified tendons, resulting in intermuscular bones (Fig. 8; Peixoto, Ohara, 2019: fig. 12).

In *Rhamphichthys* and *Gymnorhamphichthys*, the *ricto-stegalis* is mesial to the *malaris*, and originates from bones of the suspensorium and neurocranium. The *rictalis* and *stegalis* become gradually differentiated from each other towards their insertion, where fibers of the *rictalis* insert onto the coronoid process, with some fibers on the posterior margin of the anguloarticular; and the *stegalis* converges onto the meckelian tendon which, in turn, inserts on the coronomeckelian bone. Typically, a few fibers of the *ricto-stegalis* have a weak association with the buccopalatal membrane. Intermuscular bones are present in the *ricto-stegalis* in *Rhamphichthys* and *Iracema*. The *ramus mandibularis trigeminus* nerve runs through the *ricto-stegalis*, located mesial to the presumptive *rictalis* and *malaris*; and laterally to the presumptive *stegalis*.

In *Hypopygus* and *Steatogenys*, the *rictalis* and *stegalis* are completely differentiated. The *rictalis* originates from the suspensorium and inserts mainly onto the coronoid process, while the *stegalis* arises from the suspensorium and neurocranium, converging onto a poorly differentiated intersegmental aponeurosis. Towards its insertion, some lateral fibers of the *stegalis* and *rictalis* are associated with the buccopalatal membrane, which is poorly differentiated from the surrounding connective tissues. In both genera, the *segmentum mandibularis* is present, arising from the mandibular tendon, entering the mandible mesially and inserting on the anguloarticular. The dentary is an additional insertion site in *Hypopygus*.

Levator arcus palatini. The *levator arcus palatini* is trapezium-shaped in *Rhamphichthys* and *Gymnorhamphichthys* (Figs. 17, 18), or parallelogram-shaped in *Hypopygus* (Fig. 11) and *Steatogenys*. The relative sizes of origin and insertion are variable, with the origin and insertion equal in *Rhamphichthys*, with the origin ca. one and a half times the size of the insertion in *Steatogenys* or with the width of origin half that of its insertion in *Gymnorhamphichthys* and *Hypopygus*. The orientation of the anteriormost fibers is orthogonal relative to the longitudinal axis of the head in *Rhamphichthys* and *Gymnorhamphichthys* and oblique to the longitudinal axis of the head (at approximately 45° angle) in *Hypopygus* and *Steatogenys*.

The origin of the *levator arcus palatini* is on the frontal and sphenotic and its insertion occurs on the hyomandibula, including the preopercle as an insertion site only in *Gymnorhamphichthys*. At the insertion point, all fibers are located laterally to the *malaris* in *Gymnorhamphichthys* and *Rhamphichthys*. In *Hypopygus*, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its anteromesial and posteromesial bundles are medial to the *malaris*. In *Steatogenys*, only the posteromesial fibers of the *levator arcus palatini* lie medially to the *malaris*. The common pattern for Rhamphichthyidae is the posterodorsal fibers of the *levator arcus palatini* with only the posterodorsal portion of the *levator arcus palatini* mesial to the *dilator operculi*; solely in *Steatogenys*, the *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the medial portion of that muscle.

In the generalized condition of the family, the *levator arcus palatini* lacks intermuscular bones, and is entirely fibrous. However, in *Rhamphichthys* and *Iracema* (Carvalho, Albert, 2011), this muscle has some ossified tendons, resulting in intermuscular bones at its anteriormost portion (Fig. 8B).

Dilatator operculi. The *dilatator operculi* is a conical muscle. This muscle arises from the sphenotic, pterotic and dorsal portions of the hyomandibula, plus the frontal in *Rhamphichthys*, *Steatogenys*, and *Gymnorhamphichthys*. The insertion is invariably on the dorsal process of the opercle. The *dilatator operculi* shows little variation across the Rhamphichthyidae and its only noteworthy informative condition is its insertion on the ventral portion of the dorsal process of the opercle in species of *Rhamphichthys*.

Levator operculi. Rhamphichthyidae generally have a *levator operculi anterior* and a *levator operculi posterior*. However, only the former is present in *Hypopygus* (Fig. 11). The *levator operculi anterior* originates from the ventral margin of the pterotic in most members of the family, but from the hyomandibula in *Steatogenys*. It inserts on a ridge on the dorsal margin of the opercle, posterior to its anterodorsal process. The *levator operculi posterior* originates in the supracleithral canal, and inserts along a ridge on the posterolateral margin of the opercle, with fibers extending beyond the dorsal margin of the bone. The R-Avn is located laterally to the *levator operculi anterior* and mesially to the *levator operculi posterior* in *Gymnorhamphichthys* (Fig. 17) and *Steatogenys*, while in *Rhamphichthys* it is fully mesial to both sections (Fig. 18).

Adductor arcus palatini. This muscle invariably originates on the parasphenoid, extending also onto the prootic in *Hypopygus* and *Steatogenys*. Anteriorly, it inserts on the lateral face of the endopterygoid and metapterygoid; as the muscle progresses posteriorly, its insertion shifts from the lateral to the medial face of the suspensorium, finally inserting on the medial surface of the hyomandibula. Examination of the *adductor arcus palatini* requires dissection and partial removal of the *adductor mandibulae*, which completely overlaps it.

Adductor hyomandibulae. This muscle arises from the ventral region of the prootic, including also the parasphenoid in *Rhamphichthys* and *Gymnorhamphichthys*. This muscle inserts in the posteromedial margin of the hyomandibula. Little or no variation in this muscle was found throughout the Rhamphichthyidae.

Adductor operculi. The origin of the *adductor operculi* is on the pterotic, exoccipital and prootics. Anteriorly, it inserts on the dorsal margin of a dorso-mesial crest of the opercle, and posteriorly on the mesial surface of the same bone.

Detailed description of the dorsolateral musculature of the head in the genera of Rhamphichthyidae.

Gymnorhamphichthys Ellis, 1912

Adductor mandibulae. The *malaris* is fully differentiated from the *ricto-stegalis* and is positioned dorsolaterally to the dorsal portion of the presumptive *rictalis* and the lateroventrally to the *stegalis* (Fig. 5; Peixoto, Ohara, 2019: fig. 12). The *malaris* has a pectinated form, originating from the mid-portion of the hyomandibula and preopercle; and converges anteriorly onto an elongated endomaxillary ligament, equivalent to twice the width of the fibrous portion of the *malaris*, and inserts on the posteromedial portion of the antorbital and maxilla (Fig. 5), with some fibers on the buccopalatal membrane.

The *ricto-stegalis* is mesial to the *malaris*, and originates from the parasphenoid, pterosphenoid, metapterygoid, preopercle, quadrate, sympletic and hyomandibula, with its fibers restricted to the anterior margin of the preopercle. Towards its insertion, the *rictalis* and *stegalis* become gradually differentiated from each other, with the fibers of the *rictalis* inserting onto the coronoid process, and the *stegalis* converging onto the meckelian tendon which, in turn, inserts on the coronomeckelian bone. Near the insertion, a few fibers of the *ricto-stegalis* have a weak association with the buccopalatal membrane and posterior margin of the anguloarticular. The bundles of fibers corresponding to the presumptive *stegalis* are located laterally relative to the basal region of the endopterygoid and *adductor arcus palatini*, overlapping those elements completely. The *ramus mandibularis trigeminus* nerve runs through the *ricto-stegalis*, located mesial to the presumptive *rictalis* and *malaris*; and laterally to the presumptive *stegalis*.

Levator arcus palatini. The *levator arcus palatini* has a trapezoidal shape, originating from the ventral margin of the frontal and sphenotics and inserting mainly in the hyomandibula, with posterolateral fibers inserting on the preopercle. The relative size of its origin is half that of its insertion, with all fibers located laterally to the *malaris* at insertion. Only the dorsalmost fibers of the posterior portion of the *levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini* (Fig. 17).

Hypopygus Hoedeman, 1962

Adductor mandibulae. The *malaris* originates from the mid-dorsal portion of the hyomandibula and preopercle. Its insertion occurs on the posteromedial portion of the antorbital bone, by fibrous attachment, with its mesialmost fibers converging onto a small endomaxillary ligament less than one-third the length of the *malaris*. The latter inserts on the posteromedial portion of the maxilla.

The *rictalis* originates in the preopercle, quadrate and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* surpass the anterior margin of the preopercular fossa and reach the mid-portion of the preopercle while posterodorsal fibers just fall short of the posterior portion of the same bone (Fig. 11); and with its insertion occurring solely on the coronoid process. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, parasphenoid, sympletic and metapterygoid. Anteriorly, the *stegalis* differentiates into a poorly differentiated intersegmental aponeurosis, dorsally entering the mandibular tendon and ventrally the meckelian tendon, inserting onto the coronomeckelian bone. Towards the insertion, some lateral fibers are associated with the buccopalatal membrane, which is poorly differentiated from surrounding connective tissues. The *stegalis* is located laterally in relation to the proximal region of the endopterygoid and the *adductor arcus palatini*, overlaps those structures completely.

The *segmentum mandibularis* is located dorsally to coronomeckelian bone, with minimum (n = 3) or no (n = 1) contact with Meckel's cartilage, extending for *ca*. 20% of the dorsal portion of that cartilage. The *ramus mandibularis trigeminus* nerve is mesial to all sections of the *adductor mandibulae, segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* has a roughly conical shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is approximately half as wide as its insertion (Fig. 11). At insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its anteromesial and posteromesial bundles are medial to the *malaris*. Only the dorsalmost fibers of the posterior portion of the *levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini*.

Rhamphichthys Müller & Troschel, 1846

Adductor mandibulae. The *malaris* is fully differentiated from *ricto-stegalis* and is positioned dorsolaterally to the dorsal portion of the presumably *rictalis* and the lateroventrally to the *stegalis*. This muscle arises from the mid-portion of the hyomandibula. The dorsalmost fibers differentiate into an elongated endomaxillary ligament, equal in length to the fibrous portion of the *malaris*, which inserts on the posteromedial portion of the antorbital and the maxilla (Fig. 5), with some lateral fibers associated with the buccopalatal membrane. The ventral fibers of the *malaris* converge onto the accessory endomaxillary ligament, which inserts solely on the posteromedial face of the antorbital. There are many ossified tendons in the fibrous portion of the *malaris*, resulting in several intermuscular bones that are coopted towards its insertion site (Peixoto, Ohara, 2019: fig. 12).

The *ricto-stegalis* is mesial to the *malaris*, and originates from parasphenoid, pterosphenoid, metapterygoid, preopercle, quadrate, sympletic and hyomandibula, with its fibers restricted to the anterior margin of the preopercle. In the region near the origin of the *ricto-stegalis*, both subsections are easily distinguished by the direction of their fibers, with those corresponding to the presumptive *stegalis* being posteriorly-elongated and displaced dorsomedially; and those of the presumptive *rictalis* are shorter and located more laterally. At its median portion, the two sections are indistinguishable, becoming slightly differentiated towards the insertion, where fibers of the *rictalis* insert onto the coronoid process via an elongated ligament, and those of the *stegalis* converge into the meckelian tendon which, in turn, inserts onto the coronomeckelian bone. The bundles of fibers corresponding to the presumptive *stegalis* are located laterally relative to the basal region of the endopterygoid and of the *adductor arcus palatini*, completely

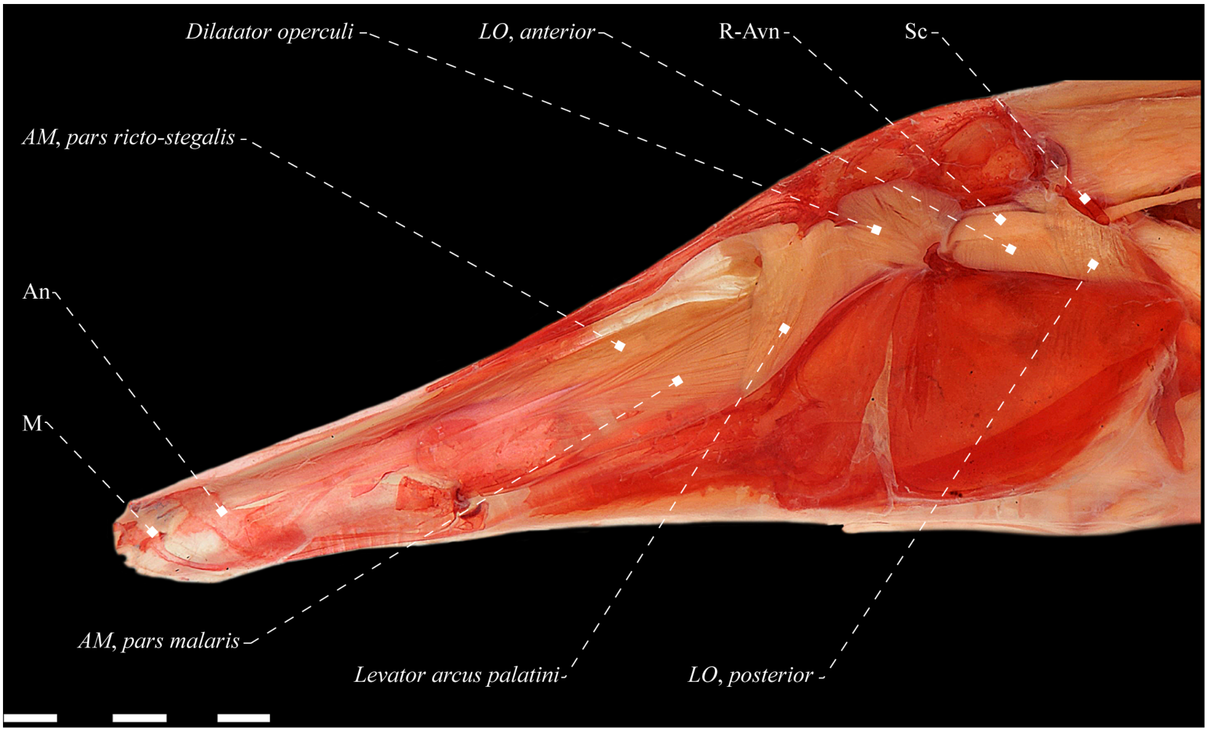


FIGURE 17 | Lateral view of dorsolateral musculature of *Gymnorhamphichthys rosemariae* (Rhamphichthyidae), MZUSP 56317, 116.3 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

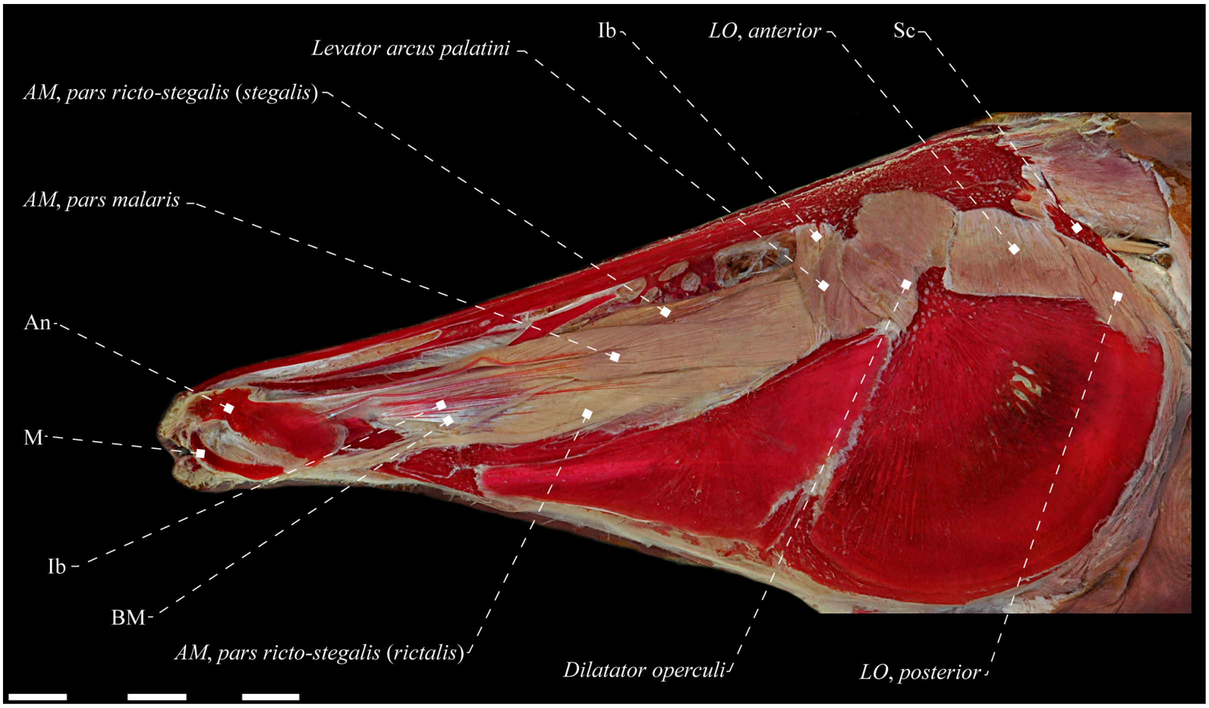


FIGURE 18 | Lateral view of dorsolateral musculature of *Rhamphichthys hahni* (Rhamphichthyidae), MZUSP 24736, 479.5 mm TL. Anatomical abbreviations in Tab. 1. Scale bar = 20 mm.

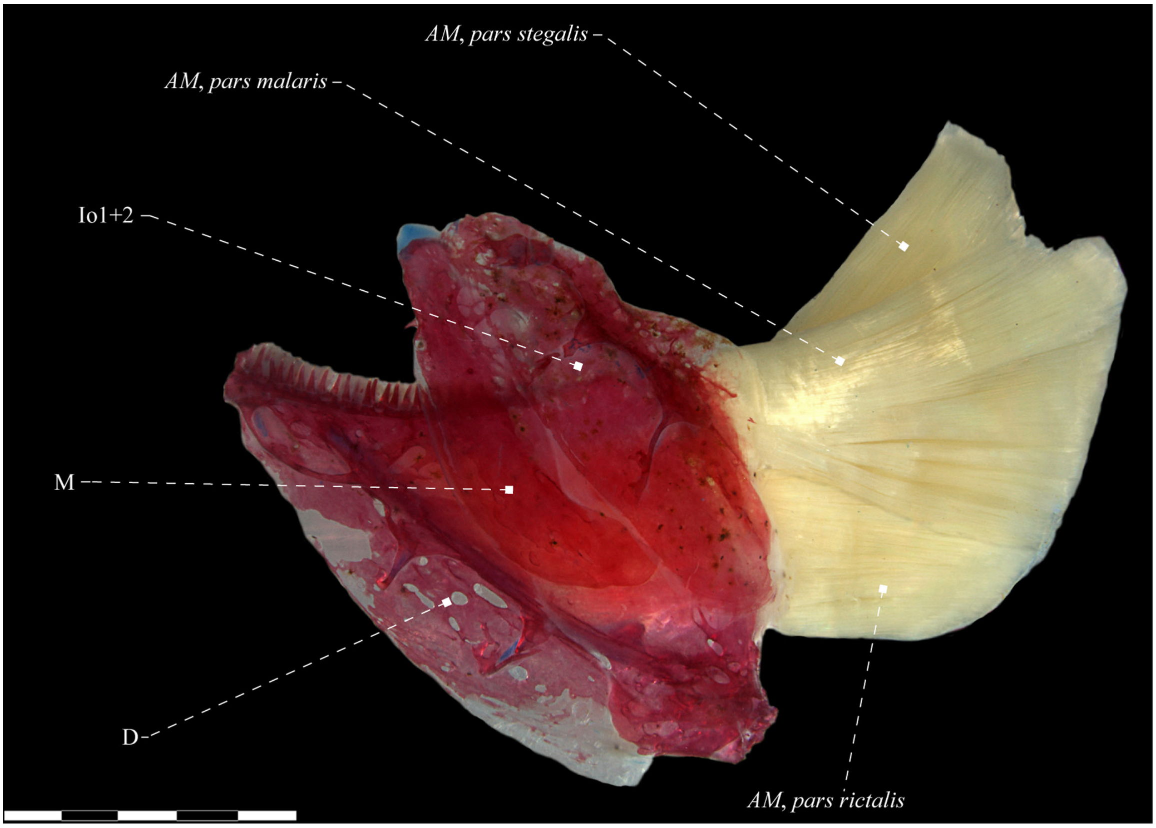


FIGURE 19 | Lateral view of *adductor mandibulae*, *pars malaris* of *Rhabdolichops eastwardi* (Sternopygidae), MZUSP 81178, 188.3 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

overlapping those structures (Fig. 18). The *ramus mandibularis trigeminus* nerve runs through the *ricto-stegalis*, located mesial to the presumptive *rictalis* and *malaris*; and laterally to the presumptive *stegalis*.

Levator arcus palatini. The *levator arcus palatini* has a trapezoidal shape, originating from the ventral margin of the frontal and sphenotics, inserting mainly on the hyomandibula, with posterolateral fibers inserting onto the preopercle. The size of its origin is half that of its insertion, with all fibers located laterally to the *malaris* at insertion. Only the dorsalmost fibers of the posterior portion of the *levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini*. The composition of the *levator arcus palatini* is mainly fibrous, with some ossified tendons forming intermuscular bones at its anteriormost portion (Fig. 8B).

Steatogenys Boulenger, 1898

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula and preopercle. Its insertion occurs on the posteromedial portion of the antorbital bone by a fibrous attachment. Its mesialmost fibers converge onto a small endomaxillary ligament, less than one-third the length of the *malaris* which, in turn, inserts on the posteromedial portion of the maxilla.

The *rictalis* originates in the preopercle, sympletic, quadrate and hyomandibula. The lateralmost fibers of the *rictalis* surpass the anterior margin of the preopercular fossa and reach the posterior portion of the same bone. That section inserts mainly on the coronoid process, but with some lateral fibers on the anguloarticular and buccopalatal membrane. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, parasphenoid, and metapterygoid. Anteriorly, the *stegalis* differentiates into a poorly-differentiated intersegmental aponeurosis, dorsally entering the mandibular tendon and ventrally the meckelian tendon which, in turn, inserts onto the coronomeckelian bone. The *stegalis* is located laterally in relation to the basal region of the endopterygoid and *adductor arcus palatini*, overlapping those structures completely.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about a half of the dorsal portion of the cartilage, but not associating with it. The *ramus mandibularis trigeminus* nerve is mesial to all sections of the *adductor mandibulae, segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* is roughly parallelogram shaped, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is approximately 50% wider than its insertion. At the insertion, the anterolateral, posterolateral and anteromesial fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its posteromesial bundles are medial to it. The *levator arcus palatini* is positioned mesially to the *dilatator operculi*, where the anterior margin of the latter exceeds the median portion of the former.

General aspects of the dorsolateral head muscles of the Sternopygidae.

Adductor mandibulae. In the generalized pattern found in Sternopygidae, the *adductor mandibulae* consists of the *segmentum facialis*, which is connected to the *segmentum mandibularis* through an intersegmental aponeurosis well-differentiated in two components. The dorsal component differentiates into a mandibular tendon, which serves as the origin of the *segmentum mandibularis*, and the ventral component differentiates into the meckelian tendon, continuous with the *stegalis* for insertion into the coronomeckelian bone (Dutra *et al*., 2021: fig. 41A). In the most *Archolaemus* species, the *segmentum mandibularis* is absent (Fig. 9). The *segmentum facialis* is composed of three subsections in all species analyzed: the *adductor mandibulae*, *pars malaris*; *pars stegalis* and *pars rictalis* (Peixoto, Ohara, 2019: fig. 11). These sections have some convergent fibers along their lengths, but the respective sections can be differentiated by their distinct origin and insertion points.

The *malaris* is positioned dorsolaterally to the dorsal portion of the *rictalis* and the lateroventrally to the *stegalis*. This section originates in the mid-dorsal portion of the hyomandibula, including the preopercle as a site of origin in *Eigenmannia* and *Archolaemus*. Its insertion is invariably on the posterodorsal expansion of the infraorbital 1+2, where the mesial fibers differentiate into a diminutive endomaxillary ligament inserted on the posteromedial margin of the maxilla (Peixoto, Ohara, 2019: fig. 11). In the generalized condition found in Sternopygidae, the *malaris* overlaps partially the *stegalis* at its origin and insertions sites (Peixoto, Ohara, 2019: fig. 8; Dutra *et al*., 2021: fig. 40), however, the *stegalis* lies completely medial to the *malaris* in the most

Archolaemus species (Fig. 9; Dutra *et al*., 2021: fig. 15).

The *rictalis* originates in bony elements of the mid-ventral portion of the suspensorium and is inserted mainly on the coronoid process, with some fibers on the posterior dorsal margin of the anguloarticular in some species of *Rhabdolichops*. In the region of origin, the posterolateral fibers never extend beyond the anterior margin of the preopercular fossa, being restricted to the anterior margin of this bone. At the region near to its insertion, some lateralmost fibers are associated with the buccopalatal membrane, with fibers inserted to the transverse ligament which, in turn, receives some lateroventral fibers of the *malaris*. The transverse ligament is well differentiated and attached in the mid-ventral portion of the infraorbital 1+2 and posterodorsal margin of the anguloarticular (Peixoto, Ohara, 2019: fig. 8; Dutra *et al*., 2021: fig. 40).

Commonly, the origin of the *stegalis* includes only bony elements of the suspensorium, however, its origin can include neurocranium bones in *Sternopygus* and *Japigny*. Invariably, the anteriormost fibers of *stegalis* converges into an intersegmental aponeurosis ventrally differentiated into the meckelian tendon and inserting on the coronomeckelian bone; and dorsally differentiated into the mandibular tendon, itself the origin of the *segmentum mandibularis*.

When present, the *segmentum mandibularis* is well developed, and restricted to a single section arising from the mandibular tendon and entering the mesial surface of the lower jaw, commonly involving the dentary and anguloarticular. Invariably, this segment is restricted to the dorsal portion of Meckel´s cartilage and may either be directly associated with the dorsal margin of the cartilage. This segment normally exceeds 40% of the dorsal margin of the Meckel´s cartilage in *Archolaemus luciae* or by almost the entire length in *Rhabdolichops* (Fig. 19). The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has roughly the shape of a parallelogram or inverted triangle. The relative sizes of origin and insertion are variable, with the origin normally a half size its insertion, but origin and insertion equal in some species. The orientation of the anteriormost fibers is orthogonal relative to the longitudinal axis of the head in the most sternopygids (Fig. 7; Dutra *et al*., 2021: fig. 15), however, the most anterior fibers of this muscle are anteroposteriorly oblique (at approximately 45° angle) in *Japigny*, *R. eastwardi*, and *Sternopygus* (Fig. 20; Peixoto, Ohara, 2019: fig. 13B). The *levator arcus palatini* originates on the hyomandibula, commonly including also the frontal in some *Eigenmannia* species and *Japigny*, or the pterosphenoid in *Archolaemus*, *Sternopygus*, and some *Eigenmannia* and *Rhabdolichops* species. Its insertion is on the hyomandibula, with some posterodorsal fibers attached to the preopercle in *Eigenmannia* and *Rhabdolichops*.

In the common pattern found in Sternopygidae, at the insertion point, the anterolateral, anteromesial and posterolateral fibers are lateral to the *malaris*; while the posteromesial fibers are mesial to the latter. However, there is significant variation in the dispositions of these subsets, which lies completely lateral to the *malaris* in *Sternopygus* and *Japigny*. In the most analyzed species, the posterodorsal fibers of the *levator arcus palatini* are parallel to the *dilatator operculi*, with no overlap between the two muscles. Some species have only the posterodorsal portion of the *levator arcus palatini* mesial to the *dilator operculi*. The generalized pattern consists of a strictly fibrous composition of *levator arcus palatini*, however, some more mesial tendons ossify in *S. xingu*, resulting in the occurrence of intermuscular bones.

Dilatator operculi. The *dilatator operculi* arises from the sphenotic, pterotic and hyomandibula, sometimes including also the frontal in *Eigenmannia limbata* and *Sternopygus*. Insertion is invariably on the dorsal process of the opercle. In some *Archolaemus* species (*A. ferreirai* and *A. santosi*), the *dilatator operculi* has a tapered anteromesial extension, which passes through the sphenotic spine and originates in the anteromesial face of this bone.

Levator operculi. The *levator operculi anterior* originates from the lateral surface of the mid-ventral portion of the pterotic and hyomandibula, but can be restricted to the pterotic in *Sternopygus*, *R. lundbergi* and *R. nigrimans*. The *levator operculi posterior* originates mainly from the postotic canal segment corresponding to the supracleithrum, including also the posterior margin of the pterotic only in *Sternopygus*, *R. lundbergi* and *R. nigrimans*. This muscle inserts on the posterodorsal portion of the opercle. In the generalized condition, the nerve R-Avn is positioned medially in relation to the entire *levator operculi* (Fig. 20; Peixoto, Ohara, 2019: fig. 13A; Dutra *et al*., 2021: fig. 15). In a juvenile specimen of *E. microstoma*, and mature specimens of *R. lundbergi*, *R. nigrimans*, and *Sternopygus*, the R-Avn lies laterally to the *levator operculi anterior* and medially to the *levator operculi posterior* (Peixoto, Ohara, 2019: fig. 13B).

Adductor arcus palatini. The *adductor arcus palatini* arises mainly from the parasphenoid and prootic, sometimes also including the orbitosphenoid in *Japigny* (Dutra *et al*., 2021: fig. 42). At its anterior portion, the insertion occurs mostly on the lateral side of the endopterygoid, metapterygoid and hyomandibula. In *A. luciae*, the insertion of the *adductor arcus palatini* includes the posterior margin of the ascendant process of the endopterygoid, a similar condition found in *Japigny*, however, without insertion on its dorsalmost portion near the attachment with the neurocranium in the latter. In the remaining sternopygids, the insertion is restricted to the basal portion of the ascendant process of the endopterygoid. Only the posterior portion of the *adductor arcus palatini* is overlapped by the *adductor mandibulae*, *segmentum facialis* in the most species; and can be totally covered by this muscle in *Sternopygus*. In the majority of *Archolaemus* species, the *segmentum facialis* does not overlap the *adductor mandibulae* (Dutra *et al*., 2021: fig. 15).

Adductor hyomandibulae. This muscle arises from the ventral region of the prootic and pterotic, inserting on the posteromedial margin of the hyomandibula. Little or no variation in this muscle was found throughout the Sternopygidae.

Adductor operculi. The origin of the *adductor operculi* is on the exoccipital, pterotic, and prootic. In *Archolaemus*, the origin does not occur in the prootic. Anteriorly, the insertion is on the dorsal margin of a dorso-mesial crest of the opercle, and posteriorly it inserts on the mesial surface of the same bone.

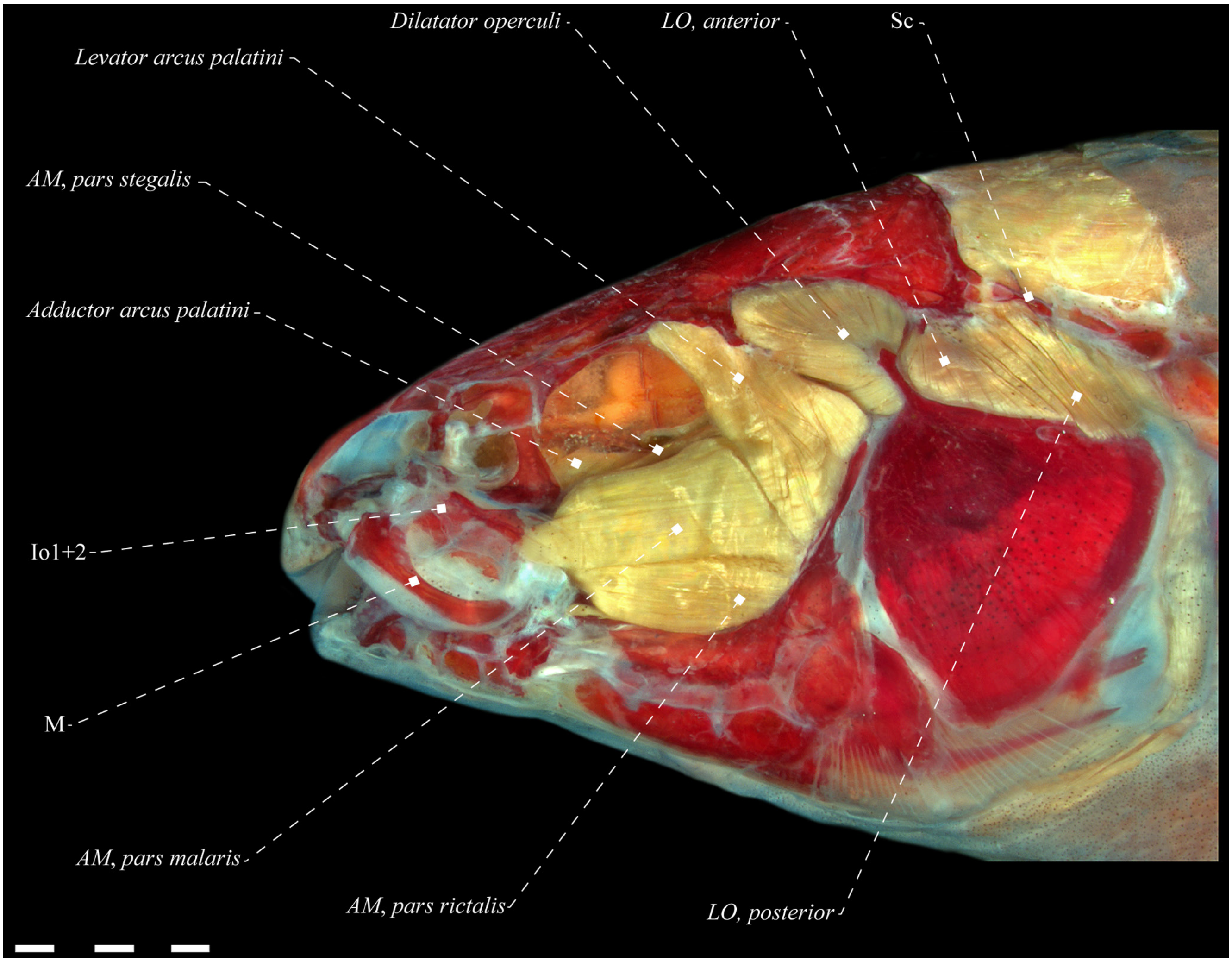


FIGURE 20 | Lateral view of dorsolateral musculature of *Japigny kirshbaum* (Sternopygidae), FMNH 50185, 137.2 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 4 mm.

Detailed description of the dorsolateral musculature of the head in the genera of Sternopygidae.

Archolaemus Korringa, 1970

Adductor mandibulae. The *malaris* is positioned dorsolaterally to the dorsal portion of the *rictalis* and completely lateral to the *stegalis* (Dutra *et al*., 2021: fig. 15), except for *Archolaemus orientalis* in which the *malaris* overlaps partially the *stegalis*.

The *rictalis* originates in the preopercle, sympletic, quadrate and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely on the coronoid process, with some lateralmost fibers associated with the buccopalatal membrane and transverse ligament. The *stegalis* arises from the hyomandibula, pterosphenoid, metapterygoid, and quadrate; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone. Usually, the *stegalis* overlaps only the ventral portion of the *adductor arcus palatini*, except in *A. orientalis*, where the *stegalis* is positioned laterally only to the mid-posterior portion of the *adductor arcus palatini*, overlapping it partially.

The *segmentum mandibularis* occurs only in *A. luciae* and arises from the mandibular tendon, enters the mandible mesially and inserts on the anguloarticular and dentary. The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 40% of the dorsal portion of this cartilage. The *segmentum mandibularis* is absent in the remaining species (Fig. 9). The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a triangular shape, originating from the ventral margin of the pterosphenoid and sphenotic, inserting in the hyomandibula. The relative size of origin is equal to a half of its insertion. At the insertion point, the anterolateral, anteromesial and posterolateral fibers are lateral to the *malaris*; while and posteromesial fibers are mesial to the latter. The posterodorsal fibers of the *levator arcus palatini* are parallel to the *dilatator operculi*, with no overlap between the two muscles.

Distocyclus Mago-Leccia, 1978

Adductor mandibulae. The *rictalis* originates in the preopercle, sympletic, quadrate and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely on the coronoid process, with some lateralmost fibers associated with the buccopalatal membrane and transverse ligament. The *stegalis* arises from the hyomandibula, metapterygoid, and quadrate; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone, with some anterodorsal fibers converging to the mandibular tendon.

The *segmentum mandibularis* arises from the mandibular tendon, enters the mandible mesially and inserts on the anguloarticular and dentary. The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 40% of the dorsal portion of this cartilage. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a triangular shape, originating from the sphenotic and inserting in the hyomandibula (Fig. 21). The relative size of origin is equal to a half of its insertion. At the insertion point, the anterolateral, anteromesial and posterolateral fibers are lateral to the *malaris*; while and posteromesial fibers are mesial to the latter. The posterodorsal fibers of the *levator arcus palatini* are parallel to the *dilatator operculi*, with no overlap between the two muscles.

Eigenmannia Jordan & Evermann, 1896

Adductor mandibulae. The *rictalis* originates in the preopercle, sympletic, quadrate and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely

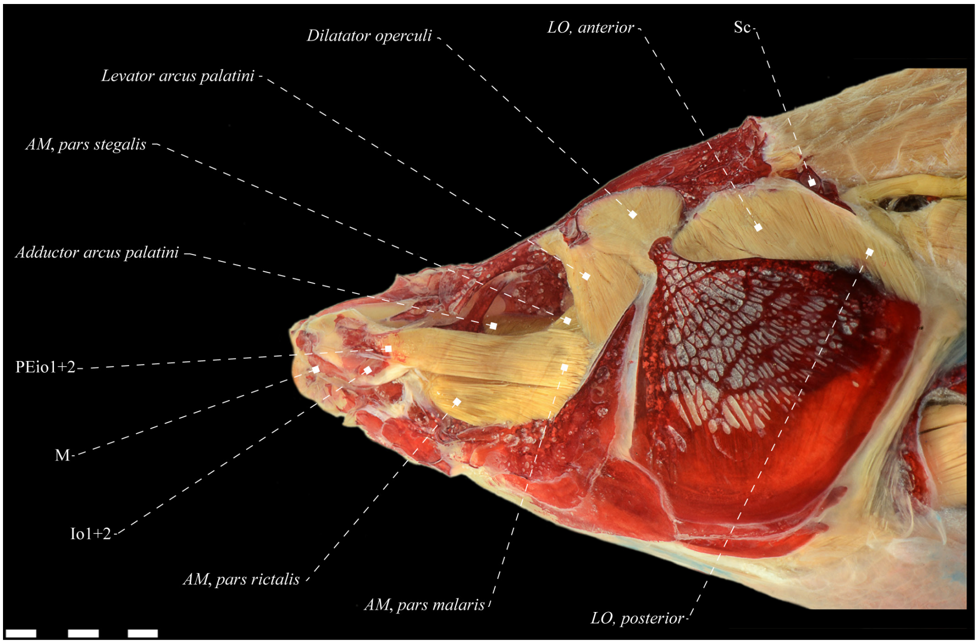


FIGURE 21 | Lateral view of dorsolateral musculature of *Distocyclus conirostris* (Sternopygidae), MZUSP 23316, 242.2 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 4 mm.

on the coronoid process, with some lateralmost fibers associated with the buccopalatal membrane and posterior margin of the anguloarticular. The *stegalis* arises from the hyomandibula, metapterygoid, and quadrate; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone, with some anterodorsal fibers converging to the mandibular tendon (Dutra *et al*., 2021: fig. 41A). In *E. humboldtii*, *E. meeki*, *E. macrops*, *E. sayona*, *E. trilineata*, *E. besouro*, *E. matintaperera*, *E. waiwai*, *E. nigra*, and *E. oradens*, the *stegalis* overlaps only the posterior portion of the basal region of the endopterygoid not overlapping it completely; in *E. microstoma*, *E. pavulagem*, *E. antonioi*, *E. virescens*, *E. guairaca*, *E. desantanai*, *E. muirapinima*, *E. limbata*, and *E. vicentespelaea*, the *stegalis* is located laterally in relation to the basal region of the endopterygoid, overlapping it completely.

The *segmentum mandibularis* arises from the mandibular tendon, enters the mandible mesially and inserts on the anguloarticular and dentary; except for *E. humboldtii*, with the insertion restricted to the anguloarticular. The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 50–60% of the dorsal portion of this cartilage. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly triangular shape. Within Eigenmannia, the generalized condition is the origin of the *levator arcus palatini* arising from the sphenotic, but including the pterosphenoid in *E. muirapinima* and *E. vicestespelaea*, or the frontal in *E. humboldtii*, *E. pavulagem*, *E. nigra, E. oradens* and *E. limbata*. The insertion occurs on the hyomandibula, and includes the preopercle in *E. muirapinima* and *E. vicentespelaea*. The relative size of origin is equal to a half of its insertion. At the insertion point, the anterolateral, anteromesial and posterolateral fibers are lateral to the *malaris*; while and posteromesial fibers are mesial to the latter. Among the analyzed species, the anteromesial fibers lies mesially to the *malaris* only in *E. limbata*. The posterodorsal fibers of the *levator arcus palatini* are mesial to the *dilatator operculi*, but without reaching the median portion of the *levator arcus palatini* in *E. humboldtii*, *E. limbata* and *E. vicentespeleae*. In *E. pavulagem*, *E. antonioi*, *E. besouro* and *E. guairaca*, the posterodorsal fibers of the *levator arcus palatini* is lateral to the *dilatator operculi*. In the remaining species, the *levator arcus palatini* is parallel to the *dilatator operculi*, with no overlap.

Japigny Meunier, Jégu & Keith, 2011

Adductor mandibulae. The *rictalis* originates in the preopercle, sympletic, and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely on the coronoid process, with some lateralmost fibers associated with the buccopalatal membrane. The *stegalis* arises from the hyomandibula, pterosphenoid, parasphenoid, metapterygoid, and sympletic; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone, with some anterodorsal fibers converging to the mandibular tendon. The *stegalis* overlaps only the posterior portion of the basal region of the endopterygoid not overlapping it completely.

The *segmentum mandibularis* arises from the mandibular tendon, enters the mandible mesially and inserts on the anguloarticular. The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 60% of the dorsal portion of this cartilage. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly narrower than its insertion (Fig. 20). At the insertion of the *levator arcus palatini*, all fibers are located laterally to the *malaris*; and with only the posterodorsal fibers being mesial to the *dilatator operculi*, where the anterior margin of the *dilator operculi* does not exceeds the medial portion of the *levator arcus palatini*.

Rhabdolichops Eigenmann & Allen, 1942

Adductor mandibulae. The *rictalis* originates in the quadrate, sympletic, preopercle, and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely on the coronoid process and anguloarticular, with some lateralmost fibers associated with the buccopalatal membrane. The *stegalis* arises from the hyomandibula, metapterygoid, and quadrate; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone, with some anterodorsal fibers converging to the mandibular tendon. The *stegalis* is located laterally in relation to the basal region of the endopterygoid, overlapping it completely; except in *R. zareti*, *R. lundbergi*, and *R. nigrimans*, in which the *stegalis* overlaps only the posterior portion of the basal region of the bone.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about its entire length of the dorsal portion of this cartilage (Dutra *et al*., 2021: fig. 41B); or extending about 70% of the dorsal portion of this cartilage in *R. lundbergi* and *R. nigrimans*. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and *rictalis*, and mesial to the *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape. Within *Rhabdolichops*, the generalized condition is the origin of the *levator arcus palatini* arising from the sphenotic in *R. lundbergi* and *R. nigrimans*, including the pterosphenoid in the remaining species, or the frontal solely in *R. troscheli*. The insertion occurs on the hyomandibula, and includes the preopercle in *R. zareti*. The origin of the *levator arcus palatini* is equal to a half of its insertion in *R. zareti, R. lundbergi,* and *R. nigrimans*; or equal to its insertion in the remaining species. At the insertion point, the anterolateral, anteromesial and posterolateral fibers are lateral to the *malaris*; while and posteromesial fibers are mesial to the latter, except for the *R. zareti*, with all fibers lateral to the *malaris*.

Sternopygus Müller & Troschel, 1849

Adductor mandibulae. The *rictalis* originates in the quadrate, sympletic, and hyomandibula. The lateralmost fibers of the ventral portion of the *rictalis* is restricted to the anterior margin of the preopercular fossa. That section inserts solely on the coronoid process, with some lateralmost fibers associated with the buccopalatal membrane. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, metapterygoid, and quadrate; and converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone, with some anterodorsal fibers converging to the mandibular tendon. The *stegalis* is located laterally in relation to the basal region of the endopterygoid, overlapping it completely; except in *S. xingu*, in which the *stegalis* overlaps only the posterior portion of the basal region of the bone. Normally, the *stegalis* overlaps only the ventral portion of the *adductor arcus palatini*, except in *S. xingu*, where the *stegalis* is positioned laterally only to the mid-posterior portion of the *adductor arcus palatini*, overlapping it partially.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 80% of the dorsal portion of this cartilage. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid, and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion (Peixoto, Ohara, 2019: fig. 13B). At the insertion of the *levator arcus palatini*, all fibers are located laterally to the *malaris* (except for one specimen of *S. macrurus*, with the posteromedial fibers mesial to the *malaris*); and with only the posterodorsal fibers being mesial to the *dilatator operculi*, where the anterior margin of the *dilator operculi* does not exceeds the medial portion of the *levator arcus palatini*. The generalized pattern consists of a strictly fibrous composition of *levator arcus palatini*, however, some more mesial tendons ossify in *S. xingu*, resulting in the occurrence of intermuscular bones.

General aspects of the dorsolateral head muscles of the Apteronotidae.

Adductor mandibulae. The *adductor mandibulae* of Apteronotidae presents the most variable configuration when compared to the other representatives of Gymnotiformes. The morphological pattern varies from components of the *segmentum facialis* undifferentiated from each other and thereby forming a largely continuous muscle mass with a partial differentiation at its insertion sites in *Platyurosternarchus* (Fig. 22) to a fully differentiation of the three primary sections of this segment (*malaris*, *rictalis*, and *stegalis*) in *Adontosternarchus*. However, the common pattern for Apteronotidae subgroups is the *segmentum mandibularis* composed of a clearly differentiated *malaris* and the remaining sections undifferentiated, equivalent to the *ricto-stegalis*.

The position of the *malaris* is variable among apteronotids, and can be located dorsolaterally (Fig. 23) or lateroventrally (Fig. 8) in relation to the dorsal portion of the *rictalis* and midventral portion of the *stegalis* (or *ricto-stegalis*, when undifferentiated). The *malaris* originates solely from suspensorium bones and usually inserts on the maxilla by means of elongated ligaments, and can include additional sites of insertions, as the connective tissues between the premaxilla and upper lip (Fig. 6), the mesethmoid and premaxilla (Fig. 24); or the posterior margin of the anguloarticular. This section is composed of a single mass of fibers in the most Apteronotidae genera. However, the *malaris* can be differentiated into *promalaris* and *retromalaris* in "*A*" gr. *bonapartii*, *Sternarchogiton*, and *Porotergus* (Figs. 6, 25) (see "Additional comments on *adductor mandibulae*, *pars malaris* of Apteronotidae").

The *rictalis*, or its corresponding fibers, arises mostly from the bony elements of the suspensorium. The insertion sites commonly include the coronoid process, with some fibers attaching also on the posterolateral margin of the anguloarticular in some species of *Adontosternarchus*, *Apteronotus*, *Parapteronotus*, and *Sternarchorhamphus*. The intersegmental aponeurosis corresponding to the mandibular tendon is coopted as an additional insertion site for *rictalis* solely in *Adontosternarchus*. In the taxa with *rictalis* arising from the preopercle, the posterolateral fibers never extend beyond the anterior margin of the preopercular fossa, being restricted to the anterior margin of this bone.

The *stegalis* arises from elements of the suspensorium, but normally also from components of the neurocranium, as the sphenotics, pterosphenoid, and parasphenoid. Anteriorly, the *stegalis* converges into an intersegmental aponeurosis with several degrees of differentiation, where its anterodorsal portion diverges into the mandibular tendon, which serves as the origin for the *segmentum mandibularis* (when present); and an anteroventral meckelian tendon, in turn, inserts on the coronomeckelian bone. The coronomeckelian bone is absent in *Sternarchorhynchus*, and the *stegalis* attaches via meckelian tendon to the mesial face of the posterior margin of the dentary. In the generalized condition, the *adductor mandibulae* composition is characterized by the absence of intermuscular bones, being essentially fibrous. However, the intermuscular bones occur solely in *Orthosternarchus*.

When present, the *segmentum mandibularis* has no subsections. It arises from the mandibular tendon, enters the mandible mesially to an insertion into the anguloarticular

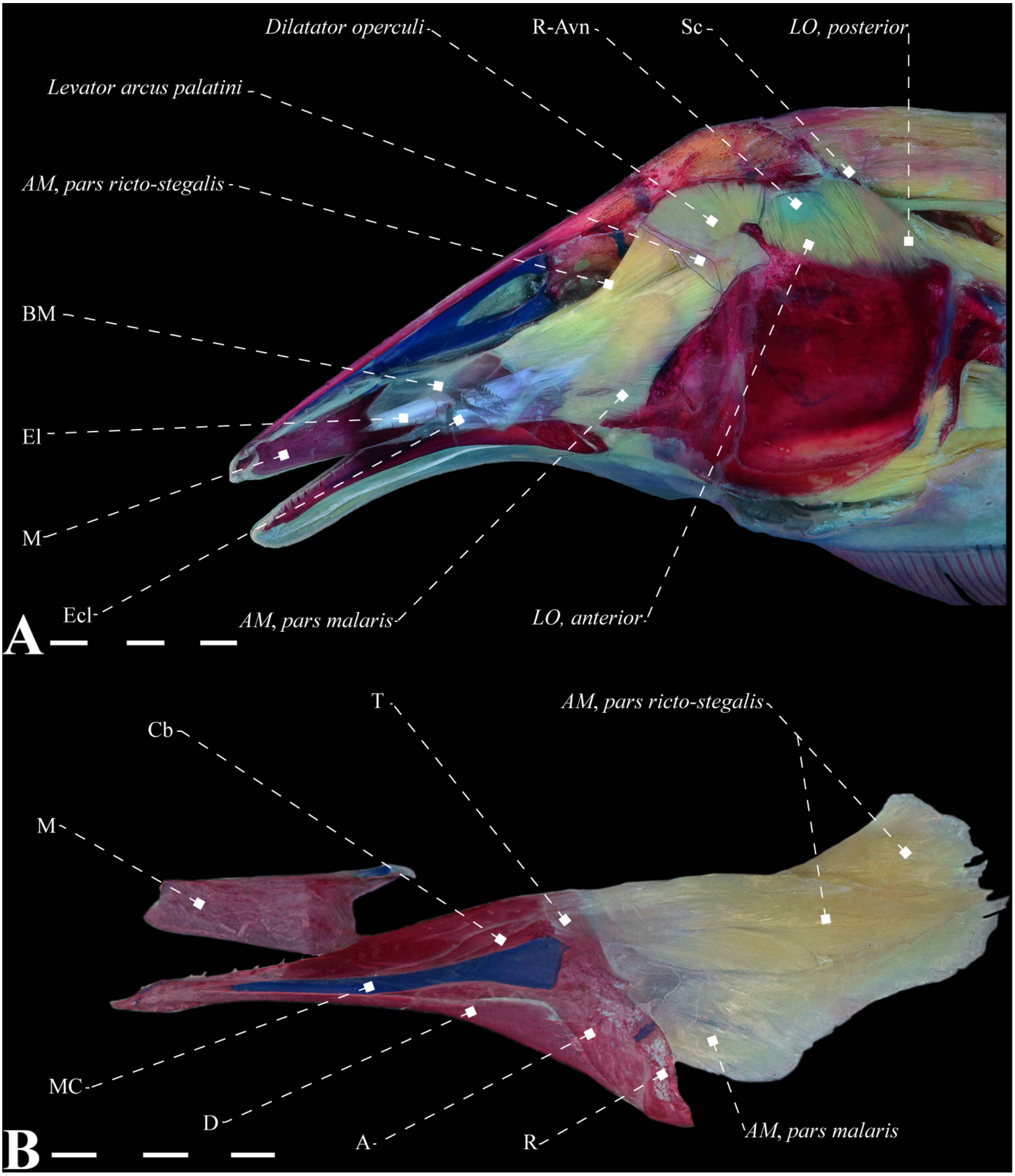


FIGURE 22 | *Platyurosternarchus macrostomus* (Apteronotidae), MZUSP 57686, 189.5 mm LEA. **A.** Lateral view of dorsolateral musculature; **B.** Mesial view of the *adductor mandibulae*. Anatomical abbreviations in Tab. 1. Scale bars = 10 mm; 5 mm.

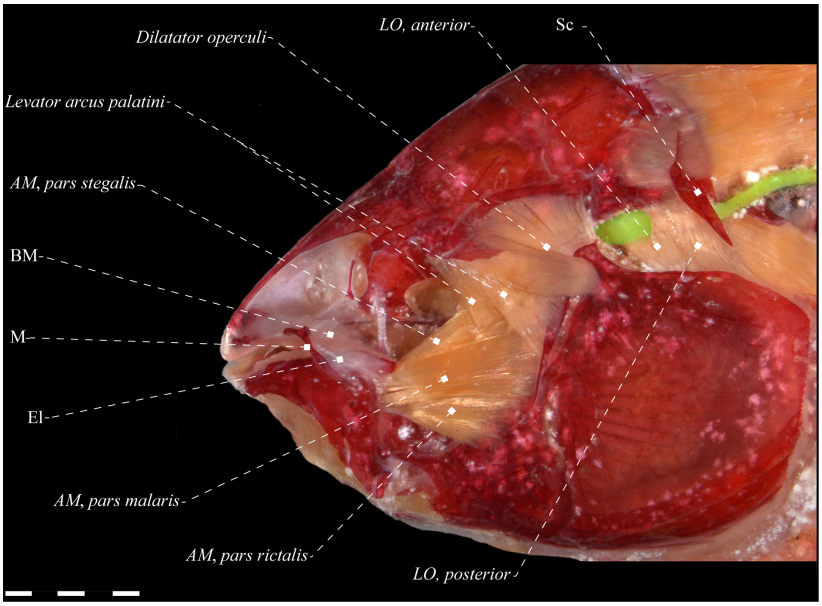


FIGURE 23 | Lateral view of dorsolateral musculature of *Adontosternarchus clarkae* (Apteronotidae), MZUSP 30072, 79.3 mm LEA. Green indicates the path of the recurrent ramus of anteroventral part of anterior lateral line nerve. Anatomical abbreviations in Tab. 1. Scale bar = 2 mm.

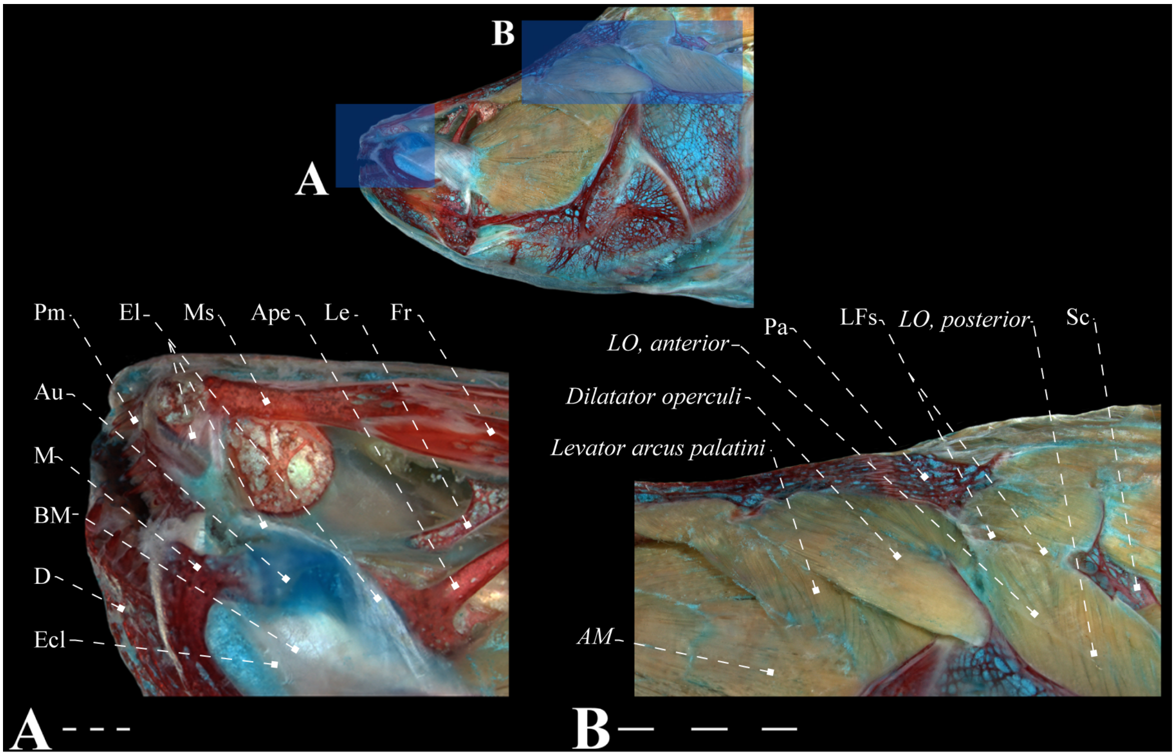


FIGURE 24 | *Sternarchella terminalis* (Apteronotidae), MPEG 3481, 155.3 mm TL [regenerated]. **A.** Detail of lateral view of anterior portion of dorsolateral head muscles; **B.** Detail of lateral view of posterior portion of dorsolateral head muscles. Anatomical abbreviations in Tab. 1. Scale bars = 5 mm.

and dentary. Invariably, the *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 20–60% of the dorsal portion of this cartilage. The *segmentum mandibularis* is absent in *Platyurosternarchus*, *Orthosternarchus*, *Sternarchorhynchus* and *Sternarchorhamphus*. In the vast majority of Apteronotidae, the buccopalatal membrane has two ligaments well differentiated, the pre-retroarticular and post-retroarticular ligaments (Figs. 7, 25). Such ligaments are not clearly differentiated in *Adontosternarchus*, *Sternarchella*, *Platyurosternarchus*, *Sternarchorhynchus*, *Orthosternarchus*, and *Sternarchorhamphus*, thus, were considered absent in those groups.

The path of the *ramus mandibularis trigeminus* nerve is variable across the family. This nerve is invariably mesial to the *malaris* and lateral to the *stegalis* and may be mesial or lateral to the *rictalis* (or to *ricto-stegalis* when not differentiated). In some taxa, the *ramus mandibularis trigeminus* may be located medially to the *adductor mandibulae*, *segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* has roughly the shape of a parallelogram or triangle. The relative sizes of origin and insertion are variable, with the origin typically equal to its insertion in the most species. The orientation of the anteriormost fibers is anteroposteriorly oblique (at approximately 45° angle) to the longitudinal axis of the head (Figs. 7, 24, 25), except for *Platyurosternarchus*, *Sternarchorhynchus*, *Orthosternarchus*, and *Sternarchorhamphus*, which presents the anteriormost fibers orthogonal to this axis (Figs. 26, 27). The common sites of origin of the *levator arcus palatini* are the frontal and sphenotics, commonly including also the pterosphenoid in some taxa. Its insertion is invariably on the hyomandibula.

In the generalized pattern found in Apteronotidae, at the insertion point, the anterolateral and posterolateral fibers of the *levator arcus palatini* are lateral to the *segmentum facialis*; while the anteromesial and posteromesial fibers are mesial to the latter. However, there is significant variation in the disposition of these subsets, ranging from a pattern with only the posterolateral fibers located laterally to the *segmentum facialis* to a completely lateral position of the *levator arcus palatini* in relation to this segment. In the generalized condition found in Apteronotidae, the posterodorsal portion of the *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle in the most apteronotid species. Some species have only the posterodorsal portion of the *levator arcus palatini* mesial to the *dilatator operculi* (*e.g.*, *Compsaraia*, *Orthosternarchus* and *Sternarchogiton*). In *Sternarchorhynchus* species, an extreme condition occurs with the anterior margin of the *dilatator operculi* reaching the anterodorsal margin of the *levator arcus palatini* (Fig. 27). The generalized pattern consists of a strictly fibrous composition of *levator arcus palatini*.

Dilatator operculi. The *dilatator operculi* is located posterior to the *levator arcus palatini*, and is organized in a single conical block of mass. Origin is usually on the sphenotic, frontal and hyomandibula, sometimes including also the pterotic, except in *Adontosternarchus*, *Sternarchogiton*, *Porotergus* and *Compsaraia*. The preopercle is included as a site of origin only in *Platyurosternarchus*. In *Sternarchorhynchus*, the *dilatator operculi* is medially displaced and includes the orbitosphenoid and pterosphenoid as its origin sites. Insertion is invariably on the dorsal process of the opercle.

Levator operculi. The *levator operculi anterior* originates from the lateral surface of the mid-ventral portion of the pterotic, and can be restricted to a fascia located at the pterotic canal in *Platyurosternarchus* (Fig. 30) and *Sternarchella* (Fig. 24). The *levator operculi posterior* originates mainly from the postotic canal segment corresponding to the supracleithrum, including also the posterior margin of the pterotic or a fascia between this point and pterotics (Fig. 24B). This muscle inserts on the posterodorsal portion of the opercle. The R-Avn is located laterally to the *levator operculi anterior* and mesially to the *levator operculi posterior*; or mesially to both sections in *Sternarchella* (Fig. 28) and *Platyurosternarchus*.

Adductor arcus palatini. The *adductor arcus palatini* arises mainly from the parasphenoid, sometimes also including the prootic in *Apteronotus*, *Adontosternarchus*, *Platyurosternarchus*, *Sternarchogiton*, *Compsaraia*, *Sternarchorhynchus*, and *Parapteronotus*. Anteriorly, it inserts on the lateral face of the endopterygoid and metapterygoid; as the muscle progresses posteriorly, its insertion shifts from the lateral to the medial face of the suspensorium, finally inserting on the medial surface of the hyomandibula. The generalized pattern of the family consists of an *adductor arcus palatini* totally covered by the *segmentum facialis*, and its visualization requires removal of the latter. Only the posterior portion of the *adductor arcus palatini* is overlain by the *segmentum facialis* in *Adontosternarchus*, *Orthosternarchus* and *Sternarchorhamphus*.

Adductor hyomandibulae. This muscle arises from the ventral region of the prootic, including the parasphenoid solely in *Adontosternarchus*, and inserting on the posteromedial margin of the hyomandibula. Little or no variation in this muscle was found throughout the Apteronotidae.

Adductor operculi. The origin of the *adductor operculi* is on the exoccipital, pterotic, and prootic. Anteriorly, the insertion is on the mesial face of a dorso-mesial crest of the opercle, and posteriorly it inserts on the mesial surface of the same bone.

Additional comments on adductor *mandibulae, pars malaris* in Apteronotidae

The anatomical complexity of the head in Apteronotidae results in more variation in the morphology of the *adductor mandibulae* than in any other gymnotiform family and the homology and nomenclature of the name "*adductor mandibulae, pars malaris*" in Apteronotidae needs discussion.

Generally, in Teleostei, the *malaris* is positioned dorsolaterally relative to other subsections of the *adductor mandibulae* and immediately ventral to the eyeball, originating on the dorsal portion (dorsal arm) of the preopercle and on the dorsoposterior region of the hyomandibula (Winterbottom, 1974a; Datovo, Vari, 2013, 2014). Such configuration is also present in the vast majority of Gymnotiformes. However, in several apteronotid subgroups (*Apteronotus*, *Sternarchella*, *Platyurosternarchus*, *Sternarchorhynchus*, *Parapteronotus* and *Sternarchorhamphus*), the section herein identified as the *malaris* is ventrally displaced relative to the eyeball, resulting in a ventrolateral position relative to the *rictalis* and *stegalis* (Figs. 22, 26–29). Such hypothesis is based on various lines of evidence.

The *malaris* (or the corresponding set of fibers when not differentiated from the *stegalis* – *e.g*., in Gymnotidae), is invariably the most lateral subsection of the *adductor mandibulae*. Likewise, the subsection identified here as the *malaris* in Apteronotidae is also the most lateral one. This applies even in those cases where the muscle is subdivided into *promalaris* and *retromalaris* ("*Apteronotus*" gr. *bonapartii*, *Sternarchogiton* and *Porotergus*). Additionally, the generalized pattern for the order, as for other teleosts (Winterbottom, 1974a; Datovo, Vari, 2013, 2014), has the *malaris* originating on the preopercle and hyomandibula, the same origins as the ventrolateral subsection (sometimes including also the quadrate as in *Sternarchella*). Also, the insertion of the *malaris* is directly or indirectly on the maxilla in all species of Gymnotiformes (except Gymnotidae), similarly to the ventrolateral *malaris* in Apteronotidae. The *malaris* is associated with the buccopalatal membrane in all gymnotiform except Gymnotidae, where its anterior fibers diverge onto an endomaxillary ligament, itself inserting onto the maxilla. The same situation is again present in the ventrolateral subsection of the *adductor mandibulae* in most apteronotids further corroborating its identity with the *malaris*.

The path of the *ramus mandibularis trigeminus* has been recognized as an unreliable landmark for determining homologies among sections of the *adductor mandibulae* (Dietz, 1914; Edgeworth, 1935; Winterbottom, 1974a; Datovo, Vari, 2014). The path of that nerve is extremely variable across different taxa, sometimes even on different sides of the same specimen (LAWP, pers. obs.; Geerinckx *et al*., 2009). Despite such caveats, its trajectory can be conserved in certain groups (Tab. 1; Datovo, Vari, 2013) and in combination with other attributes (*e.g*., place of origin, form and position), the *ramus mandibularis trigeminus* can sometimes be useful in determining homologies of subsections of the *adductor mandibulae*. In all gymnotiform taxa with a well-differentiated *malaris*, the *ramus mandibularis trigeminus* is always positioned mesially to the *malaris*, independently of the latter´s position. This provides additional evidence for the equivalence between the ventrolateral subsection of apteronotids with the dorsolateral subsection of other Gymnotiformes.

In sum, various lines of evidence related to topology, sites of origin and insertion, association with buccopalatal membrane and position of the *ramus mandibularis trigeminus* nerve corroborate the ventrolateral subsection of the *adductor mandibulae* in some apteronotids as homologous with the dorsolateral subsection of the *adductor mandibulae* in other gymnotiforms and remaining teleosts, *i.e*., the *adductor mandibulae, pars malaris*.

The hypothesis above implies that the ventrolateral position of the *malaris* in some taxa is the result of a ventral displacement of its origin. An alternative explanation is that the anomalous position of the *adductor mandibulae* in apteronotids is the result of a migration in the insertion of both the *malaris* and *rictalis*. In this case, the insertion of the *malaris* shifts from the maxilla to the coronoid process, with a simultaneous shift of the insertion of the *rictalis* from the coronoid process to the buccopalatal membrane and the maxilla. Concomitantly, this scenario requires a midlateral migration of the *rictalis* and a parasagittal displacement of the *malaris*. The latter hypothesis requires a far more complex set of modifications than its alternative, none of which required by data available, and is therefore rejected. Interestingly, a similar set of conclusions can be apprehended indirectly from the illustrations and descriptions in Aguilera (1986), although without explicit discussion.

Detailed description of the dorsolateral musculature of the head in the genera of Apteronotidae.

Adontosternarchus Ellis, 1912

Adductor mandibulae. The *malaris* is composed of a single mass of fibers, originating from the mid-dorsal portion of the hyomandibula, with its anterodorsal fibers differentiate into an elongated endomaxillary ligament, equal to the fibrous portion of the *malaris*, inserting on the posteromedial margin of the maxilla; and the its anteroventral fibers inserted to the posterior margin of the anguloarticular and dentary. The *malaris* is positioned dorsolaterally to the dorsal portion of the *rictalis* and lateroventrally to the *stegalis* (Fig. 23).

The *rictalis* originates in the metapterygoid, preopercle and hyomandibula, with its lateralmost fibers restricted to the anterior margin of the preopercular fossa. The mesialmost fibers of the *rictalis* converge into the intersegmental aponeurosis, with its lateralmost fibers inserting into the lateral margin of the anguloarticular. The *stegalis* arises from the hyomandibula, sphenotic, pterosphenoid, parasphenoid, and metapterygoid. Towards its anterior portion, the *stegalis* converges into the meckelian tendon which, in turn, inserts on the coronomeckelian bone; and with anterodorsal fibers converging to the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 60% of the dorsal portion of this cartilage. The course of the *ramus mandibularis trigeminus* nerve is lateral to the *rictalis* and *stegalis*; and mesial to the *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid, and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is narrower than its insertion, approximately a half of its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris*, while its anteromesial and posteromesial bundles are medial to the *malaris*. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

Apteronotus gr. *albifrons* (Linnaeus, 1766)

Adductor mandibulae. The *malaris* is composed of a single mass of fibers, originating from the mid-dorsal portion of the hyomandibula and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to the fibrous portion of the *malaris*, to a insertion at the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla (Fig. 8). The *malaris* is positioned lateroventrally to the *ricto-stegalis*.

The *ricto-stegalis* originates in the pterosphenoid, parasphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process and to the posterodorsal margin of the anguloarticular; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 20% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its anteromesial and posteromesial bundles are medial to the *rictalis*. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

"***Apteronotus***" **gr.** ***bonapartii*** (Castelnau, 1855)

Adductor mandibulae. The *malaris* is sectioned into a dorsal subsection *promalaris* and a ventral subsection *retromalaris*, which are well-differentiated, except for some set of fibers associated with the *ricto-stegalis*. The *promalaris* is positioned dorsolaterally to the dorsal portion of the *ricto-stegalis*, and arises from the mid-dorsal portion of the hyomandibula. This subsection converges to the buccopalatal membrane, with its anterodorsal fibers differentiate into a moderate endomaxillary ligament, equal to 2/3 of its fibrous portion, to an insertion at the connective tissue between the anterior margin of the premaxilla and upper lip. The *retromalaris* is positioned lateroventrally to the *ricto-stegalis*, arising from the anteroventral portion of the preopercle and hyomandibula, with its fibers converging into an elongated ectomaxillary ligament, equal to one and a half of its fibrous portion, that inserts at the posterolateral face of the maxilla (Fig. 25).

The *ricto-stegalis* originates in the pterosphenoid, parasphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

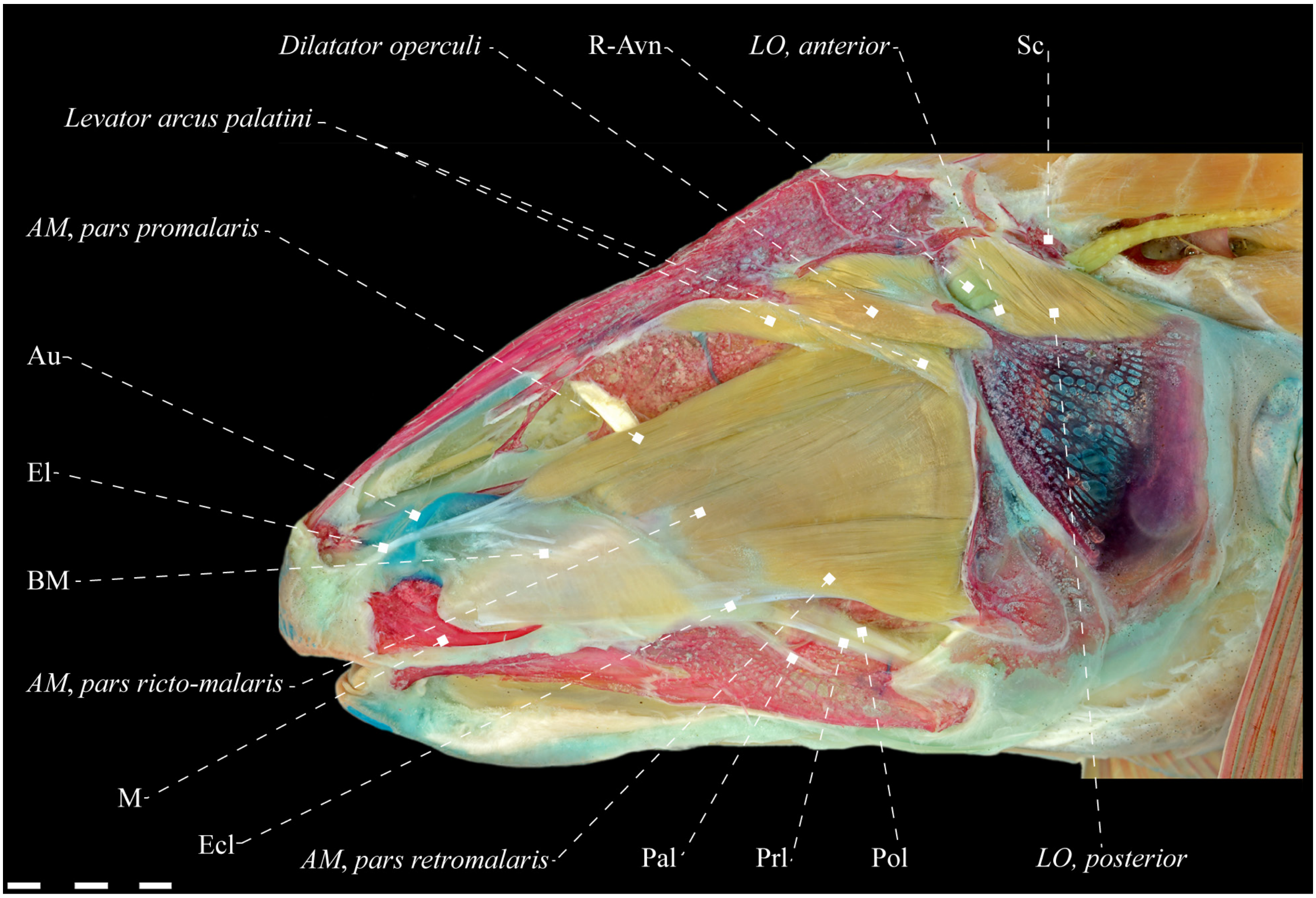


FIGURE 25 | Lateral view of dorsolateral musculature of *Apteronotus bonapartii* (Apteronotidae), MPEG 3038, 217.5 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 30% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *promalaris* and *ricto-stegalis*, while its anteromesial and posteromesial bundles are medial to the *promalaris* and *ricto-stegalis* (specifically to the presumed *rictalis*). The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

***Apteronotus* gr. *leptorhynchus* (Ellis, 1912)**

Adductor mandibulae. The *malaris* is composed of a single mass of fibers, originating from the mid-dorsal portion of the hyomandibula and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an elongated endomaxilar ligament, twice to the fibrous portion of the *malaris*, to a insertion at the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla. The *malaris* is positioned lateroventrally to the *ricto-stegalis*.

The *ricto-stegalis* originates in the preopercle, quadrate, pterosphenoid, hyomandibula, and sphenotic. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon (Fig. 30).

The *segmentum mandibularis* extends posteriorly for a significant distance, with the major portion of the segment localized beyond the posterior limit of the lower jaw, and arising along the anterior part of the intersegmental aponeurosis and from the mandibular raphe that is shared with the anterior portion of the *segmentum facialis*. The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 60% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its anteromesial and posteromesial bundles are medial to the *rictalis*. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

Compsaraia Albert, 2001

Adductor mandibulae. The *malaris* is composed of a wide single mass of fibers, with a more concentrated bundle of fibers at its dorsalmost portion than its midventral portion, and located laterally to the *ricto-stegalis*, overlapping it almost completely. The *malaris* arises from hyomandibula and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to 2/3 to the fibrous portion of the *malaris*, to an insertion at the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla (Fig. 31).

The *ricto-stegalis* originates in the pterosphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 30% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to half of its insertion. At the insertion, the posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris* and to the presumed *rictalis*, while its anteromesial, anterolateral, and posteromesial bundles are medial to those sections. The anteriormost fibers of the *levator arcus palatini* presents an aponeurotic aspect; and its posterodorsal fibers lies mesially to the *dilatator operculi*, but without reaching the median portion of this muscle.

Orthosternarchus Ellis, 1912

Adductor mandibulae. The *malaris* is composed of a single mass of fibers, originating from the mid-dorsal portion of the hyomandibula, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to three times of the fibrous portion of the *malaris*, to a insertion at the posteromesial margin of the premaxilla; and the anteroventral fibers converges into an ectomaxillary ligament poorly differentiated that inserts at the posterolateral face of the maxilla.

The *ricto-stegalis* originates in the quadrate, pterosphenoid, parasphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the *ricto-stegalis* is a single mass of fibers, and partially differentiated towards their insertion sites. The fibers corresponding to the presumed *rictalis* inserts mainly into the coronoid process throught a ligament equal to the fibrous portion of the *ricto-stegalis*; and the presumed *stegalis* converges into the meckelian tendon to an insertion to the coronomeckelian bone.

The pattern consists of a fibrous composition of *adductor mandibulae, segmentum facialis*, however, some more mesial tendons ossify, resulting in the occurrence of intermuscular bones. The *ramus mandibularis trigeminus* nerve lies mesial to the *segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* has a trapezoidal shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* corresponds to the 2/3 of its insertion. At the insertion of the *levator arcus palatini*, all fibers are located laterally to the *malaris*; and with only the posterodorsal fibers being mesial to the *dilatator operculi*, where the anterior margin of the *dilator operculi* does not exceeds the medial portion of the *levator arcus palatini*.

Parapteronotus Albert, 2001

Adductor mandibulae. The *malaris* is composed of a single mass of fibers, originating from the mid-dorsal portion of the hyomandibula and preopercle, converging anteriorly to a well differentiated buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to the fibrous portion of the *malaris*, to a insertion at the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla. The *malaris* is positioned lateroventrally to the *ricto-stegalis*.

The *ricto-stegalis* originates in the hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process and to the posterodorsal margin of the anguloarticular; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 50% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion. At the insertion, posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its anterolateral, anteromesial and posteromesial bundles are medial to the *rictalis*. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

Pariosternarchus Albert & Crampton, 2006

Adductor mandibulae. The *malaris* arises from hyomandibula and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to 2/3 to the fibrous portion of the *malaris*, to an insertion at the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla.

The *ricto-stegalis* originates in the parasphenoid, hyomandibula, sphenotic, quadrate, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 60% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *malaris* and dorsolaterally to the presumed *rictalis*; while its anteromesial and posteromesial bundles are medial to the *malaris* and to the presumed *rictalis*. The anteriormost fibers of the *levator arcus palatini* presents an aponeurotic aspect. This muscle has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds its median portion.

Platyurosternarchus Mago-Leccia, 1994

Adductor mandibulae. The *adductor mandibulae, segmentum facialis* lacks any subdivisions, however, at its origin, the segment is partially sectioned posterodorsally by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The *segmentum facialis* originates from the hyomandibula, quadrate, simpletic, pterosphenoid, parasphenoid, sphenotic, metapterygoid, and preopercle. The lateralmost fibers converge anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to the fibrous portion of this portion of the *segmentum facialis*, to a insertion at the connective tissue between the anterior margin of the premaxilla and upper lip, and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla; and, based on positional correspondence, this muscle portion presumably corresponds to the *malaris*.

The *rictalis* and *stegalis* differentiates towards their insertion sites, with the lateroventral fibers homologous, at least in part, with the *rictalis*, inserting into the coronoid process; and the medialmost set of fibers of the *segmentum facialis*, presumably homologous with the *stegalis*, converging to the meckelian tendon that, in turn, inserts on the coronomeckelian (Fig. 22). The *ramus mandibularis trigeminus* nerve trespasses the presumed *rictalis* and *stegalis*, and lies lateral to both sections and mesial to the *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is slightly wider than its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumed *rictalis* and dorsolaterally to *malaris*; while its anteromesial and posteromesial bundles are medial to the presumed *rictalis*. This muscle has a mesial arrangement where the anterior margin of the *dilatator operculi* reaching the anterodorsal margin of the *levator arcus palatini*.

Porotergus Ellis, 1912

Adductor mandibulae. The *malaris* is partially differentiated into a dorsal subsection *promalaris* and a ventral subsection *retromalaris*, which are well-differentiated from the remaining *segmentum facialis*, except for some set of fibers associated with the *ricto-stegalis*. The *promalaris* is positioned dorsolaterally to the dorsal portion of the *ricto-stegalis*, and arises from the mid-dorsal portion of the hyomandibula. This subsection converges to the buccopalatal membrane, with its anterodorsal fibers differentiate into an endomaxillary ligament equal to its fibrous portion; and inserting to the connective tissue between the anterior margin of the premaxilla and upper lip. The *retromalaris* is positioned lateroventrally to the *ricto-stegalis*, arising from the anteroventral portion of the preopercle and hyomandibula, with its fibers converging into an elongated ectomaxillary ligament, equal to one and a half of its fibrous portion, that inserts at the posterolateral face of the maxilla.

The *ricto-stegalis* originates in the hyomandibula, quadrate, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 30% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and subsections of *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid, and sphenotic; and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion. At the insertion, the posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *promalaris* and *ricto-stegalis*, while its anterolateral, anteromesial and posteromesial bundles are medial to the *promalaris* and *ricto-stegalis* (specifically to the presumed *rictalis*). The anteriormost fibers of the *levator arcus palatini* presents an aponeurotic aspect. This muscle has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds its median portion.

Sternarchogiton Eigenmann, 1905 and ***Tenebrosternarchus*** Bernt, Fronk, Evans & Albert, 2020

Adductor mandibulae. The *promalaris* and *retromalaris* subsections are continuous with each other at their origin and differentiated towards their insertion sites (Figs. 6–32). The posterodorsal portion of the *promalaris* is sectioned by the posterolateral fibers of the *levator arcus palatini*, being medial to the posterolateral fibers of that muscle; and with the remaining fibers located laterally to the *levator arcus palatini*.

The *promalaris* is positioned dorsolaterally to the dorsal portion of the *ricto-stegalis*, and arises from the mid-dorsal portion of the hyomandibula. This subsection converges to the buccopalatal membrane, with its anterodorsal fibers differentiate into an endomaxillary ligament equal to its fibrous portion; and inserting to the connective tissue between the anterior margin of the premaxilla and upper lip. The *retromalaris* is positioned lateroventrally to the *ricto-stegalis*, arising from the anteroventral portion of the preopercle and hyomandibula, with its fibers converging to the buccopalatal membrane and its ventralmost portion converging into an elongated ectomaxillary ligament, equal to one and a half of its fibrous portion, that inserts at the posterolateral face of the maxilla.

The *ricto-stegalis* originates in the parasphenoid, pterosphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 30% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and subsections of *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid, and sphenotic; and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion. At the insertion, the posterolateral fiber bundles of the *levator arcus palatini* are lateral to the *promalaris* and *ricto-stegalis*, while its anterolateral, anteromesial and posteromesial bundles are medial to the *promalaris* and *ricto-stegalis* (specifically to the presumed *rictalis*). The anteriormost fibers of the *levator arcus palatini* presents an aponeurotic aspect. Only the posterodorsal fibers of *the levator arcus palatini* located mesially to the *dilatator operculi*, where the anterior margin of the *dilator operculi* does not exceeds the median portion of the *levator arcus palatini*.

Sternarchella Eigenmann, 1905

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula, quadrate, and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to the fibrous portion of the *malaris*, to an insertion at the mesethmoid, premaxilla and the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla (Figs. 24, 28).

The *ricto-stegalis* originates in the pterosphenoid, parasphenoid, sympletic, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process and to the posterodorsal margin of the anguloarticular; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 20% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal, pterosphenoid, and sphenotic; inserting onto the hyomandibula. The origin of the *levator arcus palatini* is wider than its insertion, equal to one and a half of its insertion (Fig. 28). At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its anteromesial and posteromesial bundles are medial to the *rictalis*. The anteromesial fibers are inserted into the hyomandibula through an aponeurotic attachment, with the remaining subsets of fibers being essentially fibrous. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

S. duccis and ***S. raptor*** [“***S. duccis clade***” *sensu* Evans *et al.*, 2017]

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula, quadrate, and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to the fibrous portion of the *malaris*, to a insertion at the mesethmoid, premaxilla and the connective tissue between the anterior margin of the premaxilla and upper lip; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the maxilla. Some medialmost fibers attaches to the posterior margin of the anguloarticular. The *malaris* is positioned lateroventrally to the *ricto-stegalis* (Fig. 29).

The *ricto-stegalis* originates in the pterosphenoid, parasphenoid, sympletic, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers corresponding to the *rictalis* inserts mainly into the coronoid process; and the presumed *stegalis* converges into an intersegmental aponeurosis weakly differentiated, where its ventral portion differentiates into the meckelian tendon to an insertion to the coronomeckelian bone, and the anterodorsal fibers converges into the mandibular tendon.

The *segmentum mandibularis* is located dorsally to Meckel's cartilage, extending about 60% of the dorsal portion of this cartilage. The *ramus mandibularis trigeminus* nerve trespasses the *ricto-stegalis*, and lies lateral to the presumptive *stegalis* and mesial to the *rictalis* and *malaris*.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic; inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion. At the insertion, the anterolateral, anteromesial and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its posteromesial bundles are medial to the *rictalis*. The anterolateral fibers are inserted into the hyomandibula through an aponeurotic attachment, with the remaining subsets with a fibrous aspect. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the median portion of this muscle.

Sternarchorhamphus Eigenmann, 1905

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula, preopercle, and simpletic; converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into an endomaxilar ligament, equal to a half of the fibrous portion of the *malaris*, to an insertion at the posteromesial margin of the premaxilla; and the anteroventral fibers converges to the same membrane which, in turn, attaches to the dorsal and posterior margins of the maxilla (Fig. 26).

The *ricto-stegalis* originates in the hyomandibula, quadrate, metapterygoid, sphenotic, parasphenoid, pterosphenoid, and sympletic. At its origin, the *ricto-stegalis* is a single mass of fibers, and partially differentiated towards their insertion sites. The fibers corresponding to the presumed *rictalis* inserts mainly into the posterior margin of the anguloarticular; and the presumed *stegalis* converges into the meckelian tendon to an insertion to the coronomeckelian bone. The *ramus mandibularis trigeminus* nerve lies mesial to the *segmentum facialis*.

Levator arcus palatini. The *levator arcus palatini* has a trapezoidal shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* corresponds to its insertion. At the insertion of the *levator arcus palatini*, all fibers are located laterally to the *malaris*; and with only the posterodorsal fibers being mesial to the *dilatator operculi*, where the anterior margin of the *dilator operculi* exceeds the median portion of the *levator arcus palatini*.

Sternarchorhynchus Castelnau, 1855

Adductor mandibulae. The *malaris* arises from the mid-dorsal portion of the hyomandibula and preopercle, converging anteriorly to the buccopalatal membrane, where the anterodorsal portion differentiates into a poorly differentiated endomaxilar ligament, equal to three time of the fibrous portion of the *malaris*, to an insertion at the posterodorsal face of the maxilla; and the anteroventral fibers converges into an ectomaxillary ligament that inserts at the posterolateral face of the same bone (Fig. 27). The *malaris* is positioned lateroventrally to the *ricto-stegalis*.

The *ricto-stegalis* originates in the quadrate, sympletic, endopterygoid, pterosphenoid, parasphenoid, hyomandibula, sphenotic, and metapterygoid. At its origin, the lateralmost portion of the *ricto-stegalis*, presumably corresponding to the *rictalis*, is separated dorsally from the fibers of the presumed *stegalis* by the *levator arcus palatini*, becoming continuous at their mid-portion and partially differentiated towards their insertion sites. The fibers presumably corresponding to the *rictalis* inserts mainly into the coronoid process throught a ligament equal to the fibrous portion of this section; and the presumed *stegalis* converges into the meckelian tendon which, in turn, inserts on the posterodorsal margin of the dentary. The *segmentum mandibularis* is absent (Fig. 27B). The *ramus mandibularis trigeminus* nerve lies mesial to the *segmentum facialis*.

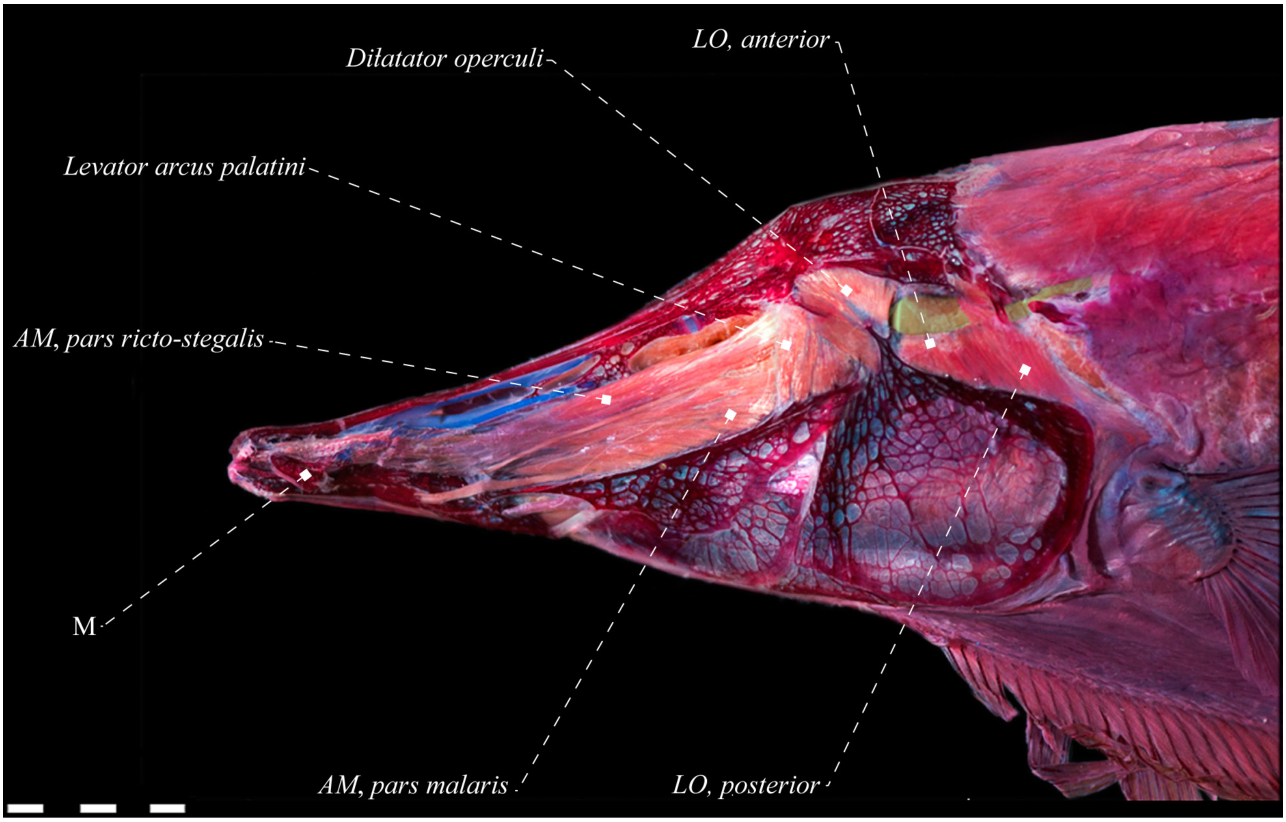


FIGURE 26 | Lateral view of dorsolateral musculature of *Sternarchorhamphus mulleri* (Apteronotidae), USNM 373030, 222.2 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 10 mm.

Levator arcus palatini. The *levator arcus palatini* has a roughly parallelogram shape, originating from the ventral margin of the frontal and sphenotic and inserting onto the hyomandibula. The origin of the *levator arcus palatini* is equal to its insertion. At the insertion, the anterolateral and posterolateral fiber bundles of the *levator arcus palatini* are lateral to the presumptive *rictalis*, while its anteromesial and posteromesial bundles are medial to the *rictalis*. The *levator arcus palatini* has a mesial arrangement where the anterior margin of the *dilator operculi* exceeds the anterodorsal margin of this muscle.

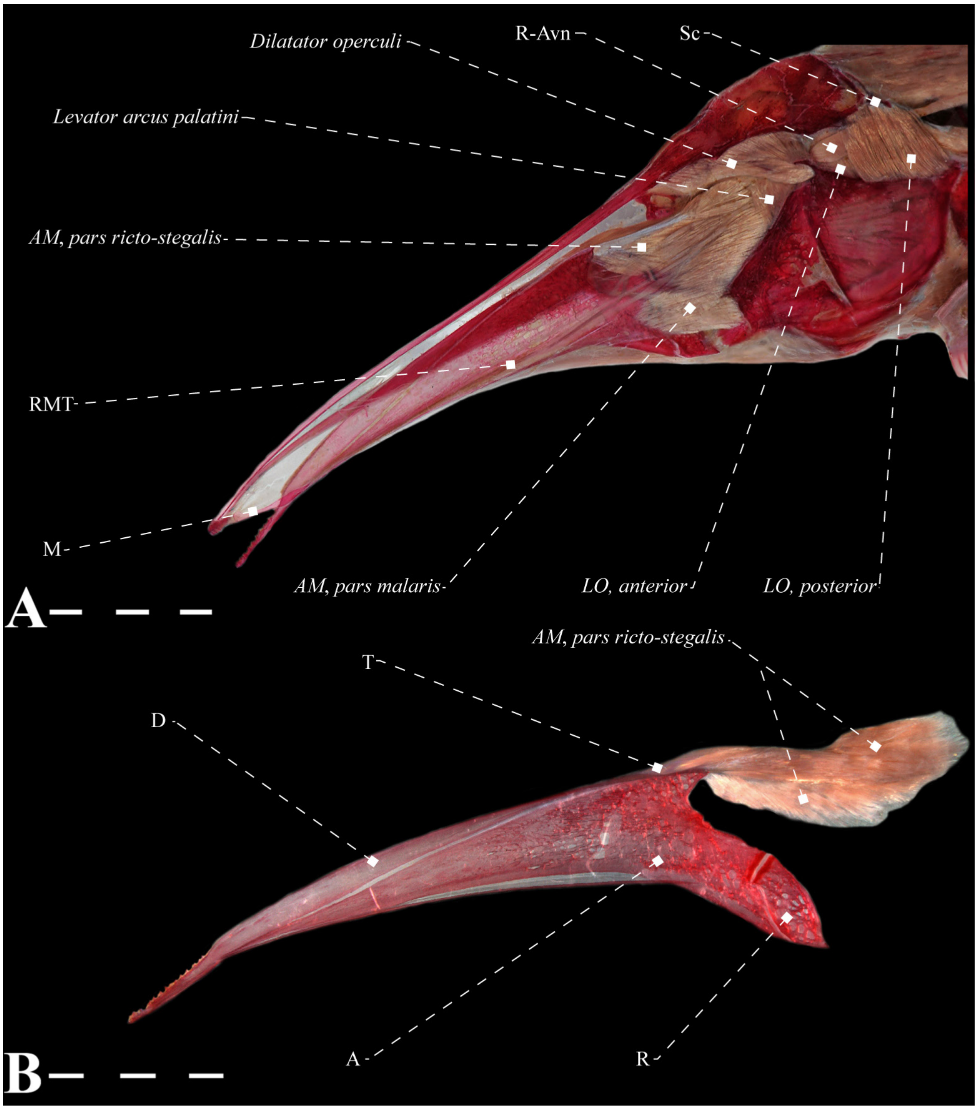


FIGURE 27 | *Sternarchorhynchus goeldii* (Apteronotidae), MPEG 1193, 1, 148.3 mm LEA. **A.** Lateral view of dorsolateral musculature; **B.** Mesial view of the *adductor mandibulae*. Anatomical abbreviations in Tab. 1. Scale bars = 5 mm.

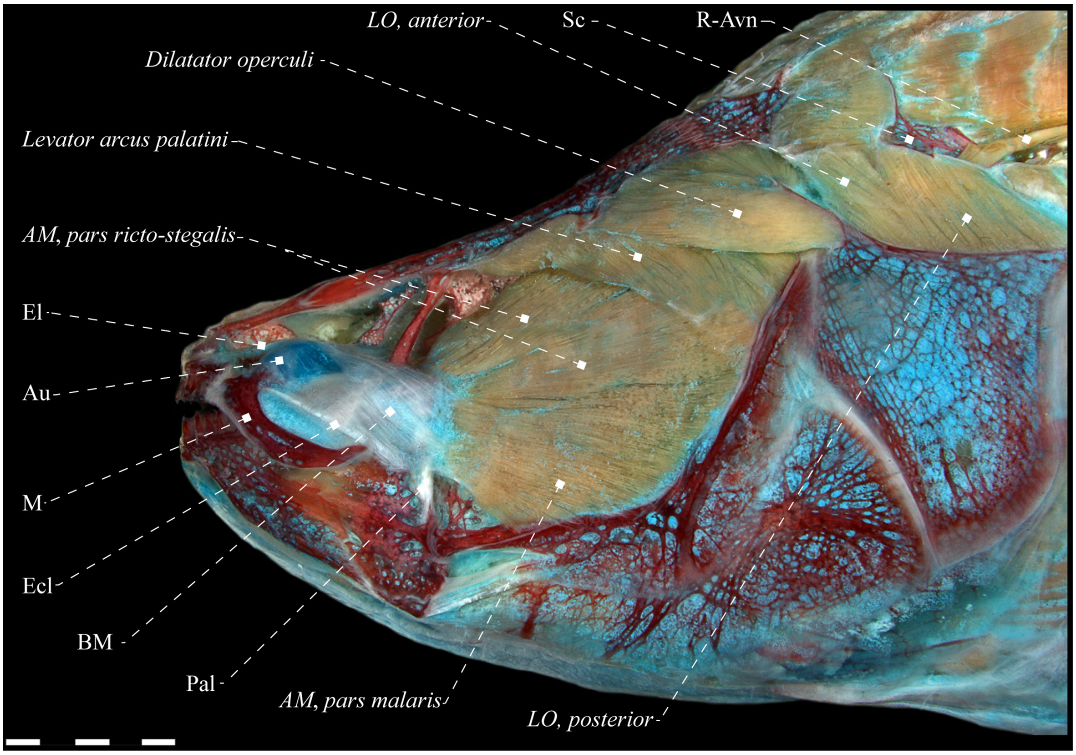


FIGURE 28 | Lateral view of dorsolateral musculature of *Sternarchella terminalis* (Apteronotidae), MPEG 3481, 155.3 mm TL [regenerated]. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

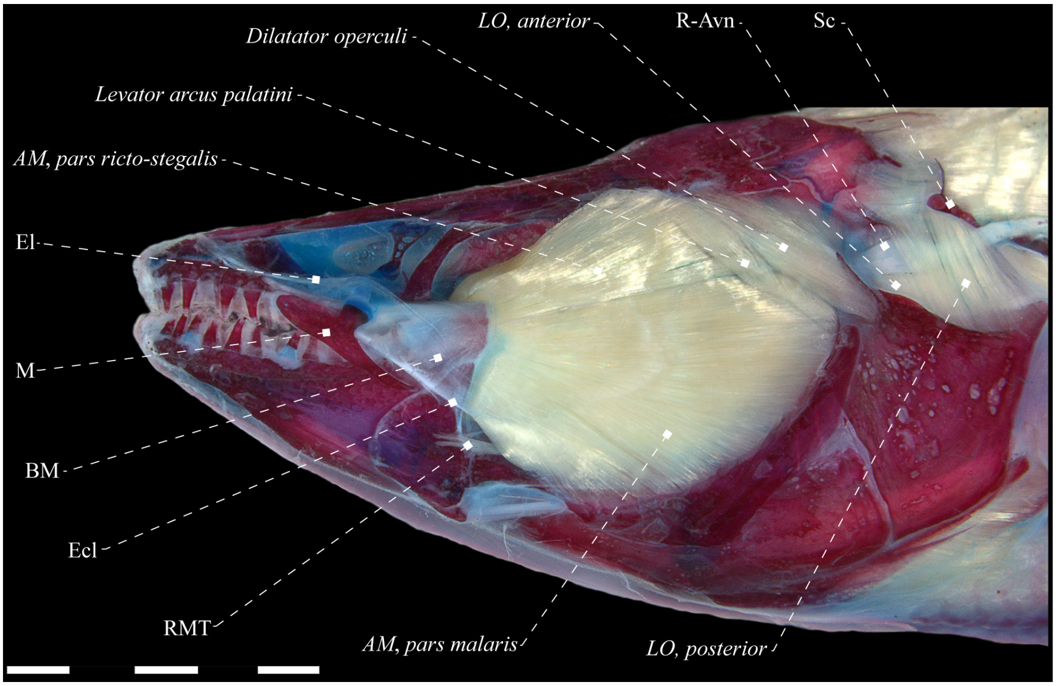


FIGURE 29 | Lateral view of dorsolateral musculature of *Sternarchella raptor* (Apteronotidae), USNM 374014, 71.9 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

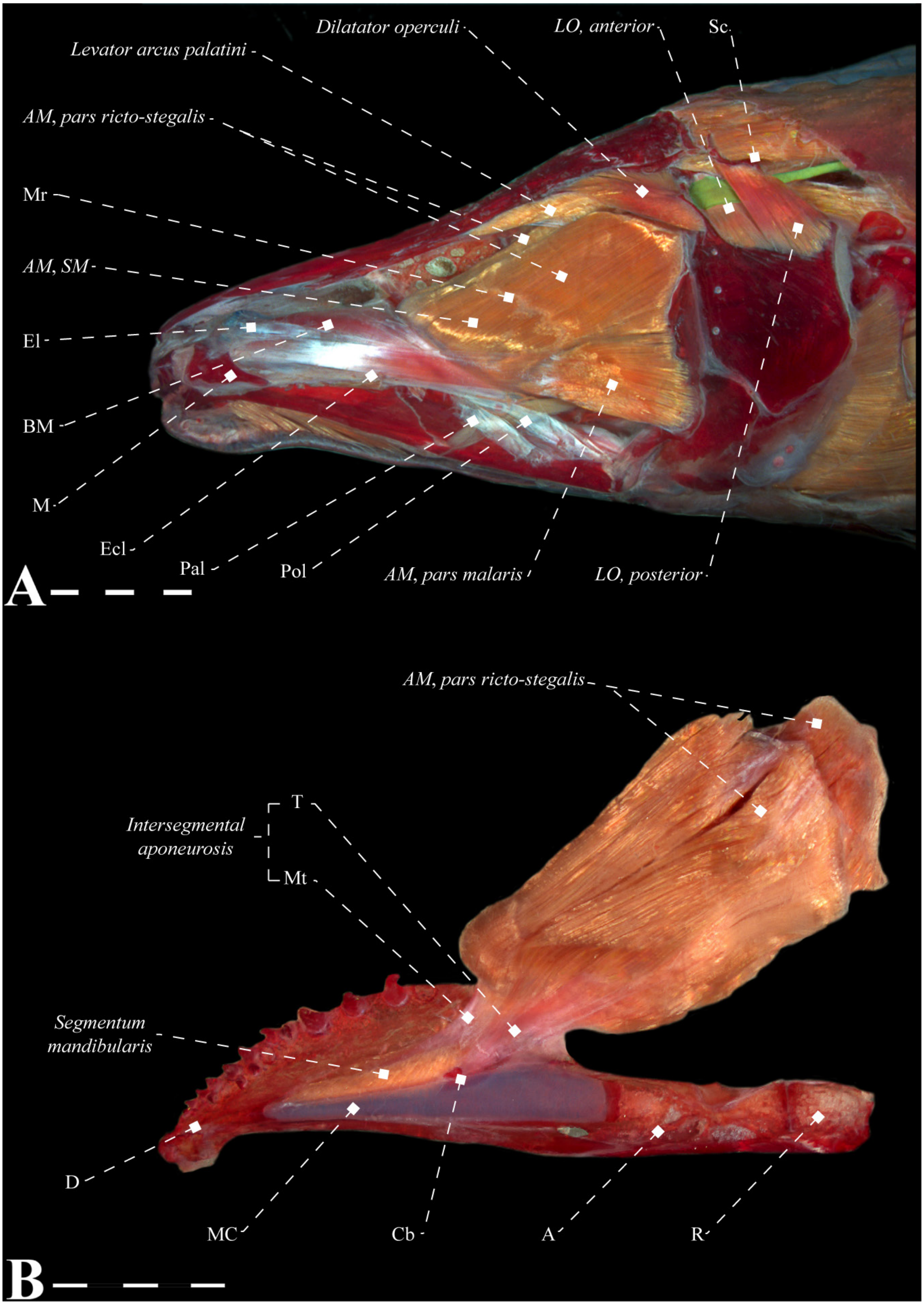


FIGURE 30 | *Apteronotus rostratus* (Apteronotidae), USNM 317229, 142.3 mm LEA. **A.** Lateral view of dorsolateral musculature; **B.** Mesial view of the *adductor mandibulae*. Green indicates the path of the recurrent ramus of anteroventral part of anterior lateral line nerve. Anatomical abbreviations in Tab. 1. Scale bars = 5 mm; 4 mm.

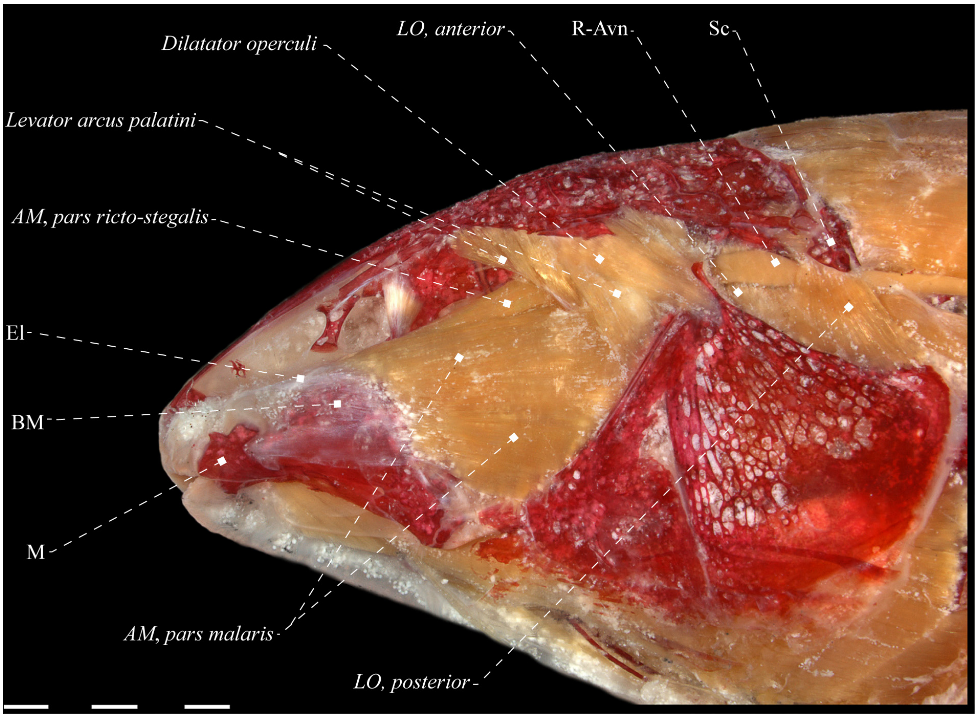


FIGURE 31 | Lateral view of dorsolateral musculature of *Compsaraia compsa* (Apteronotidae), MZUSP 56206, 123.4 mm LEA. Anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

Synonymy of the dorsolateral musculature of the head of Gymnotiformes.

The list below includes all muscle elements treated in this work and synthetizes conclusions about homology and valid names, organizing information in previous publications. The 15 different muscles recognized in this study have received 33 names in the literature. The main criterion for nomenclatural identity of each myological component is phylogenetic homology, in some cases with topological qualifiers, such as the *levator operculi anterior* and *levator operculi posterior*. The names employed with priority are highlighted in bold face and are properly referenced. Senior names are followed by their respective junior synonyms and after that their authors organized chronologically, with respective examined taxa on which their observations were based. Muscles which are newly named herein are indicated as "[n. nom.]".

A large portion of available names refers to the *adductor mandibulae*, which comprises 20 previous names for its nine configurations herein identified. Remaining names are available for six muscles of the suspensorium, three each for the *levator operculi posterior* and the *dilatator operculi*, two each for the *levator arcus palatini* and *levator operculi posterior*. Other muscles have received a single name.

Adductor mandibulae, segmentum facialis Datovo, Vari, 2013.
    Adducteur de la mandibulae.
        Chardon, de La Hoz (1973): *Sternopygus*.
    Adductores mandibulares.

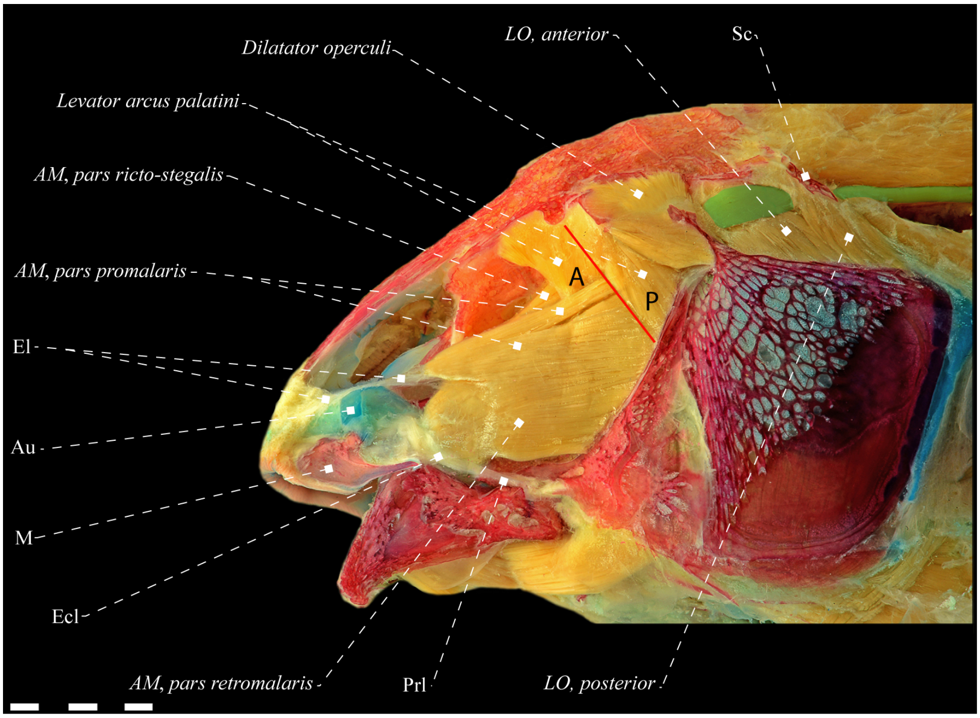


FIGURE 32 | Lateral view of dorsolateral musculature of *Tenebrosternarchus preto* (Apteronotidae), MPEG 22758, 268.5 mm LEA. A= anterolateral fibers of the *levator arcus palatini*; P= posterolateral fibers of the *levator arcus palatini*. Remaining anatomical abbreviations in Tab. 1. Scale bar = 5 mm.

de La Hoz, Chardon (1984): *Sternopygus*.

Adductor mandibula.

Albert, Campos-da-Paz (1998): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, "*Apteronotus*" *anas* (= *Parapteronotus hasemani*), "*Apteronotus*" *hasemani* (= *Parapteronotus hasemani*), *Brachyhypopomus*, *Distocyclus*, *Eigenmannia*, †*Ellisella kirschbaumi* (= †*Humboldtichthys kirschbaumi*), *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Microsternarchus fimbriipinnus* (= *Racenisia fimbriipinna*), *Oedemognathus exodon* (= *Sternarchogiton nattereri*), *Orthosternarchus*, *Platyurosternarchus*, "*Porotergus*" *compsus* (= *Compsaraia compsa*), *Porotergus*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Albert (2001): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia*, *Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Platyurosternarchus*, *Porotergus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Tagliacollo *et al.* (2016): *Adontosternarchus*, *Akawaio*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia*, *Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Japigny*, *Magosternarchus* (= *Sternarchella*), *Megadontognathus*, *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Pariosternarchus*, *Platyurosternarchus*, *Porotergus*, *Procerusternarchus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*.

Adductor mandibulae, pars malaris Datovo, Vari, 2013**.**

A_1.

Fink, Fink (1981): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Gymnotus*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchorhamphus macrostomus* (= *Platyurosternarchus macrostomus*?), *Sternopygus*. Aguilera (1986): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Gymnorhamphichthys*, *Rhamphichthys*, *Rhabdolichops*, *Steatogenys*, *Sternarchella*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*.

A1a or m.ad.m.I (a).

de La Hoz, Chardon (1984): *Sternopygus*.

m.ad.m.I or 1er faisceaux des muscles adducteurs de la mandibulae.

Chardon, de La Hoz (1973): *Sternopygus*.

Outer segment of the adductor muscle or outer segment of the adductor.

Howes (1983): *Eigenmannia*, *Gymnotus*, *Rhamphichthys*, *Sternopygus*.

Ventrolateral branch of m. Adductor mandibulae (ostariophysan A1).

Albert (2001): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Platyurosternarchus*, *Porotergus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Tagliacollo *et al.* (2016): *Adontosternarchus*, *Akawaio*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Japigny*, *Magosternarchus* (= *Sternarchella*), *Megadontognathus*, *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Pariosternarchus*, *Platyurosternarchus*, *Porotergus*, *Procerusternarchus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*.

Adductor mandibulae, pars promalaris Datovo, Vari, 2013.

$A_1\alpha$.

Aguilera (1986): *Apteronotus bonaparti* (= *Apteronotus bonapartii*).

Adductor mandibulae, pars retromalaris Datovo, Vari, 2013.

A1β.

Aguilera (1986): *Apteronotus bonaparti* (= *Apteronotus bonapartii*).

Adductor mandibulae, pars rictalis Datovo, Vari, 2013.

A_2.

Aguilera (1986): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Rhabdolichops*, *Steatogenys*, *Sternarchella*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*. Albert (2001): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Platyurosternarchus*, *Porotergus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Tagliacollo *et al.* (2016): *Adontosternarchus*, *Akawaio*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Japigny*, *Magosternarchus* (= *Sternarchella*), *Megadontognathus*, *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Pariosternarchus*, *Platyurosternarchus*, *Porotergus*, *Procerusternarchus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*.

A1b or m.ad.m.I (b).

de La Hoz, Chardon (1984): *Sternopygus*.

m.ad.m.II or 2^e faisceaux des muscles adducteurs de la mandibulae.

Chardon, de La Hoz (1973): *Sternopygus*.

Adductor mandibulae, pars ricto-stegalis Datovo, Vari, 2013.

A_{2-3}.

Aguilera (1986): *Gymnorhamphichthys*, *Rhamphichthys*, *Sternarchorhamphus*, *Sternarchorhynchus*.

Adductor mandibulae, pars stegalis Datovo, Vari, 2013.

A_3.

Aguilera (1986): *Adontosternarchus*, *Eigenmannia*, *Rhabdolichops*, *Steatogenys*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*.

M. ad. m. II and m. ad. m. III [?- muscle identify with two subsections]

de La Hoz, Chardon (1984): *Sternopygus*.

m.ad.m.III or 3^e faisceaux des muscles adducteurs de la mandibulae.

C\hardon, de La Hoz (1973): *Sternopygus*.

Adductor mandibulae, pars stego-malaris **and** ***pars rictalis*** Datovo, Vari, 2013.

Complejo adductor mandibulae [?- muscle identify with two subsections].

Aguilera (1986): *Electrophorus and Gymnotus*.

Adductor mandibulae, segmentum mandibularis Datovo, Vari, 2013.

Aw.

de La Hoz, Chardon (1984): *Sternopygus*.

Levator arcus palatini *sensu* Winterbottom (1974a).

m.le.hm or muscle élévateur de l'arc palatin et de l'hyomandibulaire.

Chardon, de La Hoz (1973): *Sternopygus*.

Levator hyomandibulae [?- unidentified muscle].

de La Hoz, Chardon (1984): *Sternopygus*.

Dilatator operculi *sensu* Winterbottom (1974a).

Dilator operculi.

Carvalho, Albert (2011): *Gymnorhamphichthys*, *Iracema* e *Rhamphichthys*.

Dilator operculi or *dilator opérculi*.

Aguilera (1986): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Rhamphichthys*, *Rhabdolichops*, *Steatogenys*, *Sternarchella*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*.

m.dil.op or muscle dilatateur de l'opercule.

Chardon, de La Hoz (1973): *Sternopygus*.

Levator operculi *sensu* Winterbottom (1974a).

Levator opercularis.

Freihofer (1963): *Gymnotus*, *Sternopygus*.

Levator operculi anterior Aguilera (1986).

Levator operculi anterior or *Levator opérculi anterior*.

Aguilera (1986): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Rhamphichthys*, *Rhabdolichops*, *Steatogenys*, *Sternarchella*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*.

m.le.op.a or muscle élévateur antérieur de l'opercule.

Chardon, de La Hoz (1973): *Sternopygus*.

Levator operculi posterior Aguilera (1986).

Levator operculi posterior or *levator opérculi posterior.*

Aguilera (1986): *Adontosternarchus*, *Apteronotus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Rhamphichthys*, *Rhabdolichops*, *Steatogenys*, *Sternarchella*, *Sternarchorhamphus*, *Sternarchorhynchus*, *Sternopygus*.

Levator posterior.

Albert, Campos-da-Paz (1998): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, "*Apteronotus*" *anas* (= *Parapteronotus hasemani*), "*Apteronotus*" *hasemani* (= *Parapteronotus hasemani*), *Brachyhypopomus*, *Distocyclus*, *Eigenmannia*, †*Ellisella kirschbaumi* (= †*Humboldtichthys kirschbaumi*), *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Microsternarchus fimbriipinnus* (= *Racenisia fimbriipinna*), *Oedemognathus exodon* (= *Sternarchogiton nattereri*), *Orthosternarchus*, *Platyurosternarchus*, "*Porotergus*" *compsus* (= *Compsaraia compsa*), *Porotergus*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Albert (2001): *Adontosternarchus*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, †*Ellisella kirschbaumi* (= †*Humboldtichthys kirschbaumi*), *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Magosternarchus* (= *Sternarchella*), *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Platyurosternarchus*, *Porotergus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*. Tagliacollo *et al.* (2016): *Adontosternarchus*, *Akawaio*, *Archolaemus*, *Apteronotus*, *Brachyhypopomus*, *Compsaraia, Distocyclus*, *Eigenmannia*, *Electrophorus*, *Gymnotus*, *Gymnorhamphichthys*, *Hypopygus*, *Hypopomus*, *Iracema*, *Japigny*, *Magosternarchus* (= *Sternarchella*), *Megadontognathus*, *Microsternarchus*, *Orthosternarchus*, *Parapteronotus*, *Pariosternarchus*, *Platyurosternarchus*, *Porotergus*, *Procerusternarchus*, *Racenisia*, *Rhamphichthys*, *Rhabdolichops*, *Sternarchorhamphus*, *Sternarchella*, *Steatogenys*, *Sternopygus*, *Sternarchorhynchus*, *Sternarchogiton*.

m.le.op.p or muscle élévateur postérieur de l'opercule.

Chardon, de La Hoz (1973): *Sternopygus*.

Adductor arcus palatini *sensu* Winterbottom (1974a).

Adductor hyomandibulae anterior [?- name supposedly designated to the posterior portion of the *adductor arcus palatini*].

de La Hoz, Chardon (1984): *Sternopygus*.

Adductor hyomandibulae *sensu* Winterbottom (1974a).

Adductor hyomandibulae posterior.

de La Hoz, Chardon (1984): *Sternopygus*.

Phylogenetic inference

The comparative analysis of the dorsolateral head muscles of Gymnotiformes yielded 56 morphological characters listed below, which were organized into a data matrix (Tab. **S1**). This matrix was analyzed according to the methods described in the Material and Methods section above (Analysis 1). Subsequently, the myological matrix was concatenated with phenotypic characters from Tagliacollo *et al.* (2016) with the modifications of Peixoto *et al.* (2019) (Analysis 2). Results are discussed and further analyzed by means of a partitioned Bremer support as to their significance for the phylogeny of Gymnotiformes and for elucidating the impact of myology on phylogenetic hypotheses. Descriptions of phylogenetically-informative variation identified in the present study are organized by morphological complex. Each character is presented with a short title followed by recognized states, original source when not the present paper, respective CI and RI and any needed explanation.

Characters of the dorsolateral musculature of the head of Gymnotiformes: Description and Analysis 1. A parsimony analysis containing only characters from dorsolateral head miology for 87 terminals (4 outgroups and 83 Gymnotiformes) and 56 characters (Tab. **S1**), resulted in 40 equally parsimonious trees with 192 steps (CI: 0.37, RI: 0.87). A strict consensus tree (Fig. 33) is the basis for referring to clades mentioned below. Support indices and mapping of synapomorphies are presented in Fig. 34.

1) Degree of separation between *malaris* and *stegalis*: (0) completely differentiated; (1) partially continuous, forming *stego-malaris* [CI: 0.33–0.66; RI: 0.66].

The generalized condition in Ostariophysi consists of a completely differentiated *malaris* and *stegalis*, although cases of non-differentiation have been recorded (Datovo, Vari, 2013).

The apomorphic condition (State 1) is present in basal Siluriformes and Gymnotiformes and interpreted as a synapomorphy for Siluriphysi (sensu Fink, Fink, 1981; Siluriformes + Gymnotiformes), with a reversal in the ST clade and subsequent reacquisition in *Platyurosternarchus*.

2) Degree of separation between *rictalis* and *stegalis*: (0) completely differentiated; (1) partially continuous, forming *ricto-stegalis* [CI: 0.50; RI: 0.95].

The generalized pattern for Gymnotiformes and all outgroup representatives, consists of a total differentiation of the *rictalis* and the *stegalis*.

According to our analysis, the differentiation between *rictalis* and *stegalis* is plesiomorphic among gymnotiforms, whereas a continuous *ricto-stegalis* is an apomorphy for Ramphichthyidae and some Apteronotidae, convergent in Clades R and PC (Fig. 33).

3) Origin of *malaris* on suspensorium: (0) on hyomandibula, preopercle and other elements of suspensorium; (1) origin on hyomandibula only [CI: 1; RI: 0.71].

The origin of the *malaris* in all representatives of outgroups and in some gymnotiforms includes the hyomandibula and preopercle, in addition to other elements of the suspensorium. In some cases, the *malaris* may originate on the hyomandibula only.

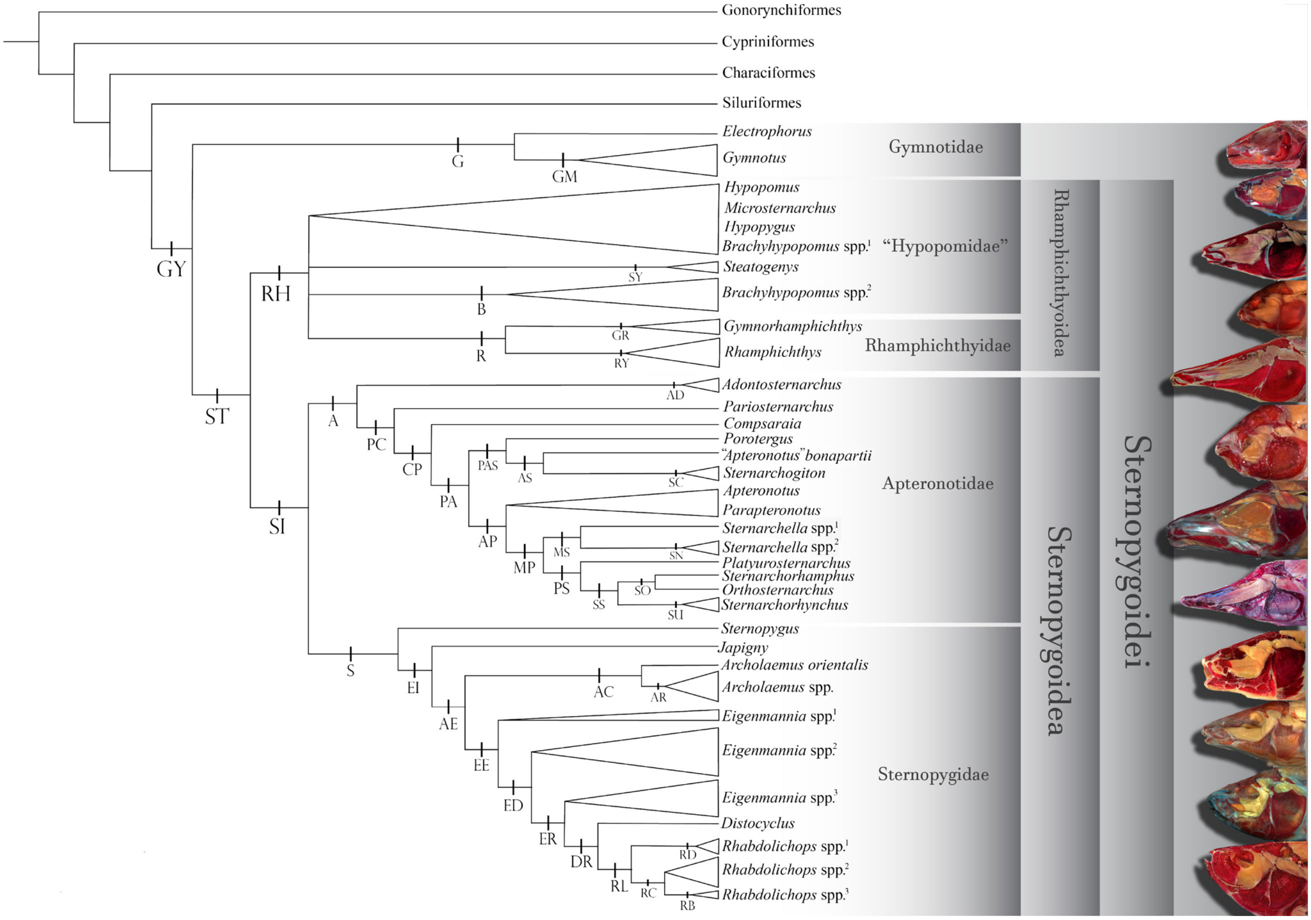
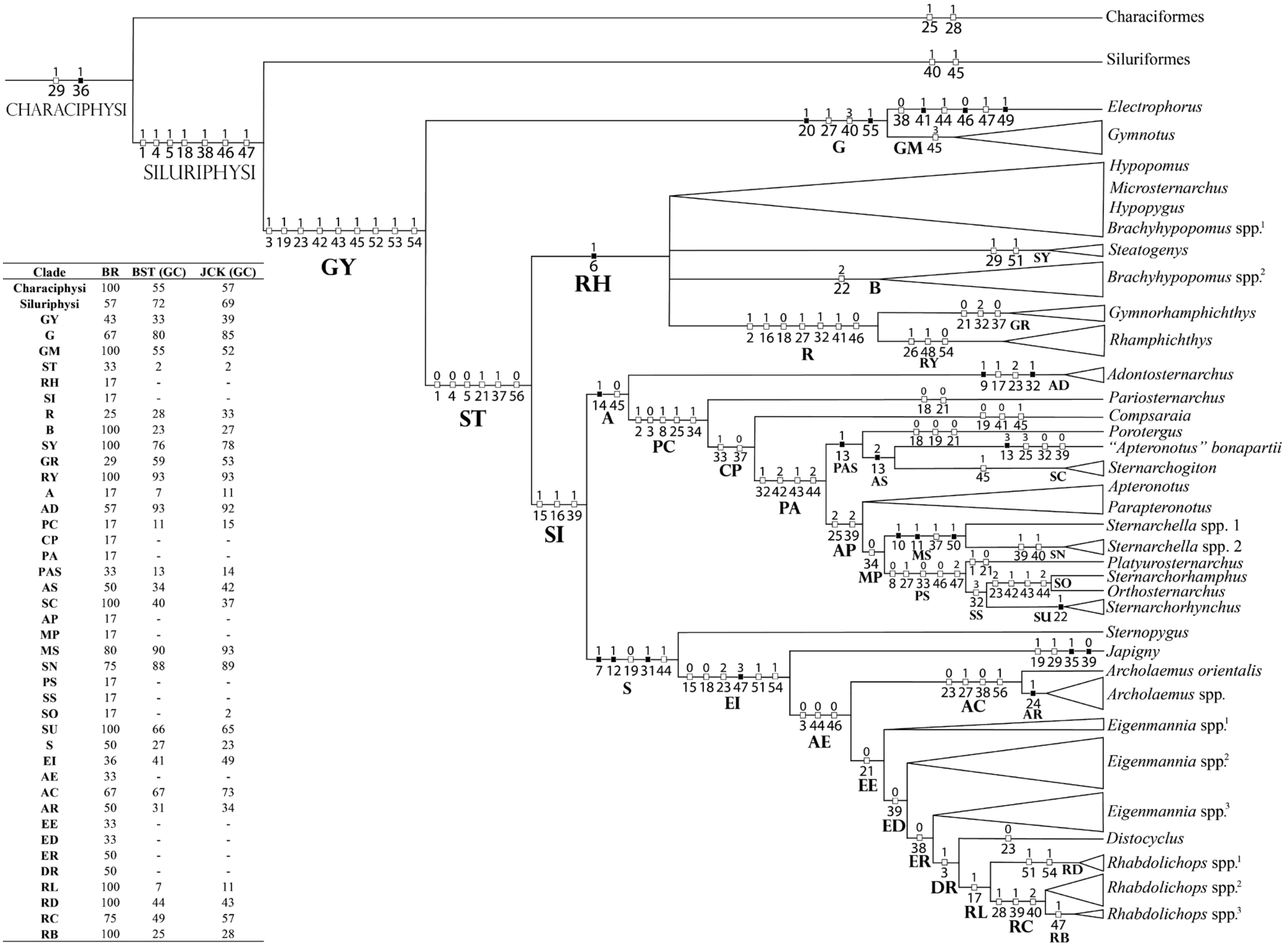


FIGURE 33 | Strict consensus of MPT's resulting from parsimony analysis of character matrix in **S1** [Score: 192; RI: 0.87; CI: 0.37]. Abbreviations below each branch are those used in text for respective clades. Taxon legends: *Brachyhypopomus* spp.¹ (*B. beebei*, *B. bombilla*, *B. draco*, *B. gaudeiro*, *B. janeiroensis*, and *B. sullivani*); *Brachyhypopomus* spp.² (*B. brevirostris*, *B. hendersoni*, *B. pinnicaudatus* and *B. regani*); *Sternarchella* spp.¹ (*S. duccis* and *S. raptor*); *Sternarchella* spp.² (*S. schotti* and *S. terminalis*); *Eigenmannia* spp.¹ (*E. muirapinima* and *E. vicentespelaea*); *Eigenmannia* spp.² (*E. humboldtii*, *E. limbata*, *E. nigra*, *E. pavulagem*, and *E.* sp. "ventuari"); *Eigenmannia* spp.³ (*E. antonioi*, *E. besouro*, *E. desantanai*, *E. guairaca*, *E. matintaperera*, *E. macrops*, *E. meeki*, *E. microstoma*, *E. sayona*, *E. trilineata*, *E. virescens*, and *E. waiwai*); *Rhabdolichops* spp.¹ (*R. nigrimans* and *R. lundbergi*); *Rhabdolichops* spp.² (*R. caviceps*, *R. electrogrammus*, and *R. zareti*); *Rhabdolichops* spp.³ (*R. eastwardi* and *R. troscheli*).



Clade	BR	BST (GC)	JCK (GC)
Characiphysi	100	55	57
Siluriphysi	57	72	69
GY	43	33	39
G	67	80	85
GM	100	55	52
ST	33	2	2
RH	17	-	-
SI	17	-	-
R	25	28	33
B	100	23	27
SY	100	76	78
GR	29	59	53
RY	100	93	93
A	17	7	11
AD	57	93	92
PC	17	11	15
CP	17	-	-
PA	17	-	-
PAS	33	13	14
AS	50	34	42
SC	100	40	37
AP	17	-	-
MP	17	-	-
MS	80	90	93
SN	75	88	89
PS	17	-	-
SS	17	-	-
SO	17	-	2
SU	100	66	65
S	50	27	23
EI	36	41	49
AE	33	-	-
AC	67	67	73
AR	50	31	34
EE	33	-	-
ED	33	-	-
ER	50	-	-
DR	50	-	-
RL	100	7	11
RD	100	44	43
RC	75	49	57
RB	100	25	28

FIGURE 34 | Same tree as in Fig. 33, with numbered dorsolateral head musculature characters (below branches) and respective character states (above branches). Black squares indicate homoplasy-free characters and white squares indicate homoplastic characters. Table on left indicates support values for each node: BR (Relative Bremer support), BST (Bootstrap), and JCK (Jackknife). Taxon legends as in Fig. 33.

The condition described in State 1 is a synapomorphy for the Gymnotiformes (clade GY), with reversals in the clade PC (and subsequent redevelopment in *Orthosternarchus*) and in the clade AE (and redevelopment in the clade DR).

4) Origin of *malaris* on skull: (0) not including sphenotic; (1) including sphenotic (modified from Datovo, Vari, 2014: ch. 8) [CI: 0.50–0.80; RI: 0.80].

The generalized condition in Teleostei is to have the origin of the *malaris* limited to the elements of the suspensorium, not including the sphenotic (Winterbottom, 1974a; Diogo *et al*., 2008; Datovo, Vari, 2014). Contrastingly, in the vast majority of Siluriformes (including basal lineages such as Diplomystidae and Cetopsidae), and basal members of Gymnotiformes, the origin of the *malaris* extends dorsally and includes the sphenotic. Datovo, Vari (2014: 60) proposed the "origin of the *malaris* extending dorsally and connecting with the neurocranium" as synapomorphic for the Siluriphysi. Herein, the sphenotic is identified as the exact reference point of attachment of the *malaris* on the neurocranium.

The *malaris* with origin in the sphenotic is a synapomorphy for the Siluriphysi, with a reversal in the clade ST.

5) Insertion of the *malaris* on the mandibular tendon: (0) absent; (1) present [CI: 0.50–0.80; RI: 0.80].

Insertion sites of the *malaris* are variable (Winterbottom, 1974a; Datovo, Vari, 2013). In Ostariophysi, it ranges from an inter-segmental aponeurosis (subocular tendon *sensu* Datovo, Vari, 2014) in *Chanos* (LAWP, pers. obs.; Datovo, Vari, 2014), to a layer of connective tissue between the upper lip and the premaxilla in some Apteronotidae. In basal Siluriformes and Gymnotiformes, the fibers of the *malaris* converge onto a thick mandibular tendon inserted on the mesial surface of the coronoid region (Fig. 3).

In Gymnotidae there is no evident differentiation between the *malaris* and the *stegalis*, which are thus jointly referred to as the *stego-malaris*. The topological inference about the insertion site referable to the *malaris* follows the same reasoning explained in Character 3 above. Some publications (*e.g.,* Diogo, Chardon, 2000; Diogo, 2004) reported insertion sites for the *malaris* different from those observed here in outgroups. The codification of states included in the data matrix utilized here corresponds to the states directly observed in the material examined.

The insertion of the *malaris* on the mandibular tendon is herein listed as a synapomorphy for Siluriphysi, with a reversal in the clade ST.

6) Insertion of *malaris* on antorbital: (0) absent; (1) present [CI: 1; RI: 1].

With exception of Gymnotidae, the *malaris* of Gymnotiformes converges onto an endomaxillary ligament, itself inserted on different sites in various taxa across order.

In representatives of the Rhamphichthyoidea (Rhamphichthyidae + "Hypopomidae"; clade RH) that muscle – by means of its endomaxillary ligament – inserts on the mesial surface of the antorbital and maxilla (Figs. 4, 5, 8, 13), a synapomorphy for that clade.

7) Insertion of the *malaris* on infraorbital 1+2: (0) absent; (1) present (modified from Albert, Campos-da-Paz, 1998: ch. 46; Albert, 2001: ch. 45; Albert *et al*., 2005: ch. 82; Tagliacollo *et al*., 2016: ch. 57; Dutra *et al*., 2021: ch. 115) [CI: 1; RI: 1].

As described on characters 5 and 6, there is ample variation in the insertion of the *malaris* among gymnotiforms. Uniquely in Sternopygidae, that muscle inserts on the compound infraorbital 1+2 (Peixoto, Ohara, 2019: fig. 11), with mesial fibers differentiated into a minute endomaxillary ligament inserted on the posteromesial surface of the maxilla. For historical overview of this character see Dutra *et al*., 2021.

The condition described above is unique among Ostariophysi, and is an exclusive synapomorphy for the Sternopygidae (clade S).

8) Insertion of *malaris* through an endomaxillary ligament on connective tissue between premaxilla and upper lip: (0) absent; (1) present [CI: 0.50; RI: 0.92].

The most conspicuous variation relative to the insertion of the *malaris* among gymnotiforms is seen in some Apteronotidae. In those species, the dorsal fibers of the *malaris* diverge onto a long endomaxillary ligament while ventral fibers attach to a medium-sized ectomaxillary ligament. As a result, this muscle has two insertions (Figs. 6, 7, 28–30, 31, 32).

The insertion of the *malaris* through a long endomaxillary on the connective tissue between the anterior margin of the premaxilla and the upper lip is an unusual condition and it is recovered as a synapomorphy for the clade PC with a reversal in the clade PS.

9) Insertion of ventrolateral fibers of *malaris* on posterior margin of dentary and anguloarticular: (0) absent; (1) present (Aguilera, 1986) [CI: 1; RI: 1].

In Gymnotiformes in general, the anterior fibers of the *malaris* are differentiated into ligaments with variable insertion sites across the order. Species of *Adontosternarchus* have an additional macroscopically fibrous insertion directly on the posterodorsal margin of the dentary.

The condition described in the State 1 is synapomorphic for *Adontosternarchus* (clade AD).

10) Insertion of mesial fibers of *malaris* on posterior margin of anguloarticular: (0) absent; (1) present [CI: 1; RI: 1].

Plesiomorphically in Gymnotiformes, all fibers of the *malaris* converge to respective insertions sites, be they single or multiple (*e.g.,* clade PC). In species of *Sternarchella*, only the mesialmost fibers of the *malaris* diverge in the parasagittal region and insert on the posterior margin of the anguloarticular.

The condition of the State 1 is an exclusive synapomorphy for *Sternarchella* (clade MS).

11) Insertion of *malaris* on mesethmoid and premaxilla: (0) absent; (1) present [CI: 1; RI: 1].

As explained in Character 8 above, some Apteronotidae (clade PC) have the *malaris* inserting on the connective tissue between the anterior margin of the premaxilla and the upper lip by means of the endomaxillary ligament.

Species of *Sternarchella* have an additional attachment site for the ligament at the dorsal region of the mesethmoid and posterodorsal surface of the premaxilla (Fig. 24), a synapomorphy for the genus (clade MS).

12) Attachement type of *malaris*: (0) mostly tendinous; (1) fibrous [CI: 1; RI: 1].

In the vast majority of Gymnotiformes and outgroups, the insertion of the *malaris* is mostly or exclusively by aponeurotic or ligamentous connections. In Sternopygidae, contrastingly, the insertion is mostly through muscle fibers (Peixoto, Ohara, 2019: fig. 11), with only a few medial fibers differentiated in an endomaxillary ligament.

The fibrous attachement of *malaris* is synapomorphic for the Sternopygidae (clade S).

13) Composition of *malaris*: (0) *malaris* undivided, as a single muscle bundle; (1) *malaris* partly divided into *promalaris* and *retromalaris* towards insertion; (2) median and dorsoposterior regions of *promalaris* completely differentiated from its ventromedial region and from *retromalaris*; (3) *promalaris* and *retromalaris* entirely separated, from origin to insertion (ordered multistate) [CI: 1; RI: 1].

The general pattern in Gymnotiformes, as well as in outgroup taxa, is to have a consolidated *malaris*, not divided in subsections. A different situation occurs in *Porotergus*, *Sternarchogiton* and "*Apteronotus*" gr. *bonapartii*, where the *malaris* has some degree of subdivision, ranging from partial sectioning to fully differentiated subsections (Figs. 6, 25, 32). Hypothetically, the division into *promalaris* and *retromalaris* results from a gradual and apparently sequential set of modifications. That sequence ranges from a broad *malaris* positioned laterally to remaining sections of the *adductor mandibulae*, to a total differentiation into *promalaris* and *retromalaris*.

Species of *Porotergus* exemplify the initial extreme of the series, with a wide *malaris* having a dorsal portion incipiently differentiated from the ventral one, each corresponding to *promalaris* and *retromalaris*, continuous at the origin and middle portion but gradually diverging towards the buccopalatal membrane. The situation is more conspicuous in *Sternarchogiton*, where the *malaris* is partly divided into *promalaris* and *retromalaris*. The posterodorsal region of the *promalaris* is completely differentiated from the remaining fibers of that section, and are oriented medially relative to the fibers of the *levator arcus palatini*. The subdivision of the *malaris* is complete in "*Apteronotus*" gr. *bonapartii*, where the muscle is entirely separated into dorsal (*promalaris*) and ventral (*retromalaris*) subsections.

Clearly, there is a clinal sequence starting from a broad *malaris* located almost totally laterally to the *ricto-stegalis* and with dorsal-ventral differentiation mostly indicated by differential fiber densities. A subsequent condition has the dorsal portion of the *promalaris* differentiated from the rest of the muscle. Finally, there is complete separation of the *malaris* into *promalaris* and *retromalaris*. Such sequence of similarity supports a natural ordering of States 0, 1, 2 and 3.

In the hypothesis presented here, State 1 is a synapomorphy exclusive to clade PAS, with subsequent transition to State 2 in the clade AS and to State 3 in "*Apteronotus*" gr. *bonapartii*.

14) *Malaris* and buccopalatal membrane: (0) *malaris* not entirely continous to the lateral membrane to buccopalatal membrane; (1) *malaris* entirely continous to the lateral layer of buccopalatal membrane [CI: 1; RI: 1].

Plesiomorphically in Gymnotiformes, the *malaris* is continuous to ligaments of the buccopalatal membrane, which in turn serve as insertion elements on various sites (Datovo, Vari, 2013). In Apteronotidae, all lateral fibers of the *malaris* are directly associated with the external layer of the buccopalatal membrane (Figs. 8, 25).

The latter state is obtained as a synapomorphy for Apteronotidae (clade A).

15) Origin of *rictalis* in relation to the preopercle: (0) including preopercle; (1) not including preopercle [CI: 0.33–0.95; RI: 0.90].

In the general condition found in Gymnotiformes, the origin of the *rictalis* includes the preopercle, among other elements of the suspensorium. In the vast majority of apteronotids and some sternopygids, the muscle is mesially and dorsoposteriorly displaced. As a result, the origin of the *rictalis* no longer includes the preopercle.

The State 1 is synapomorphic for Sternopygoidea (clade SI; Apteronotidae + Sternopygidae; "Sinusoidea" of Albert, 2001), with reversals in *Apteronotus* gr. *leptorhynchus* and in clade EI.

16) Origin of ventrolateral fibers of *rictalis* in relation to the preopercle: (0) extending posteriorly beyond middle portion of preopercle; (1) restricted to anterior portion of preopercle, not extending beyond preopercular fossa [CI: 0.50; RI: 0.95].

In the primitive ostariophysan and in some Gymnotiformes, the *rictalis* has a posteriorly-displaced origin where its lateral fibers originate from the lateral surface of the preopercle and extend beyond the preopercular fossa (Figs. 1, 11). Sternopygoidea and Rhamphichthyidae are different in that regard and the origin of their *rictalis* is restricted to the anteromesial margin of the preopercle (Figs. 17, 18; Peixoto, Ohara, 2019: fig. 8; Dutra *et al*., 2021: figs. 15, 40).

State 1 is convergent in Rhamphichthyidae (clade R) and Sternopygoidea (clade SI). This character was coded as inapplicable in *Sternopygus* and all members of clade PC (except *Apteronotus* gr. *leptorhynchus*), because they lack an association between the *rictalis* and the preopercle.

17) Insertion of lateral fibers of the *rictalis* on the posterior margin of the anguloarticular: (0) absent; (1) present [CI: 0.83; RI: 0.52].

Primitively in Gymnotiformes, the *rictalis* inserts on the coronoid process, which is formed by the posterodorsal portion of the dentary and the dorsal margin of the anguloarticular. In some Gymnotiformes, that insertion is broader and also includes a considerable portion of the posterior margin of the anguloarticular.

State 1 is convergent in *Adontosternarchus* (clade AD), *Sternarchorhamphus*, and in *Rhabdolichops* (Clade RL).

18) Origin of the *stegalis* in relation to the sphenotic: (0) absent; (1) present (Peixoto, Ohara, 2019; Dutra *et al*., 2021: ch. 117) [CI: 0.16; RI: 0.87].

Primitively in Teleostei, the origin of the *stegalis* is restricted the suspensorium, not including elements of the neurocranium (*e.g*., Winterbottom, 1974a; Datovo, Vari, 2013, 2014). In basal Siluriformes and in the vast majority of Gymnotiformes, the origin of the *stegalis* is extended dorsoposteriorly and also includes the sphenotic.

The origin of the *stegalis* in the sphenotic is interpreted herein as a synapomorphy for Siluriphysi, with reversals in *Apteronotus* gr. *leptorhynchus*, *Porotergus*, *Pariosternarchus*, and in clades EI and R.

19) Origin of the *stegalis* in relation to the parasphenoid: (0) absent; (1) present [CI: 0.12–0.85; RI: 0.82–0.85].

As explained in the preceding character, the origin of the *stegalis* in teleosts is restricted to the suspensorium. In Gymnotiformes, the vast majority of species has a mesial displacement of the dorsoposterior part of the stegalis, so that its origin comprises also the posteromedial part of the parasphenoid.

The condition described in the State 1 is a synapomorhy for Gymnotiformes (clade GY), with reversals at Sternopygidae (clade S; and subsequent reacquisitions in *Japigny*) *Hypopomus*, *Compsaraia*, *Porotergus*, *Parapteronotus*, *Apteronotus* gr. *leptorhynchus*.

20) Origin of the *stegalis* in relation to the frontal: (0) absent; (1) present [CI: 1; RI: 1].

The origin of the *stegalis* is dorsally expanded in Gymnotidae, where it includes not only the suspensorium but also the frontal.

State 1 represents an exclusive synapomorphy for Gymnotidae (clade GY).

21) Origin of the *stegalis* in relation to the pterosphenoid: (0) absent; (1) present (Dutra *et al*., 2021: ch. 118) [CI: 0.14; RI: 0.85].

Plesiomorphically in Teleostei (Winterbottom, 1974a; Datovo, Vari, 2013, 2014), the origin of the *stegalis* is limited to the suspensorium, not including neurocranial components. In most Gymnotiformes, however, the origin of the muscle is displaced posteromesially to also include the ventroposterior margin of the pterosphenoid.

The State 1 is a synapomorphy for clade ST, with reversals in *Gymnorhamphichthys* (clade GR), *Platyurosternarchus*, *Porotergus*, *Parapteronotus*, *Pariosternarchus*, and clade EE.

22) Insertion of *stegalis* on posteromesial margin of dentary: (0) absent; (1) present [CI: 1; RI: 1].

Generally, in teleosts, the *stegalis* differentiates into a meckelian tendon, connected to the dorsoposterior margin of the coronomeckelian bone (Diogo, Chardon, 2000; Wu, Shen, 2004; Datovo, Vari, 2013; 2014). The same configuration happens in Gymnotiformes (LAWP, pers. obs.; Aguilera, 1986; Datovo, Vari, 2014). In fact, the coronomeckelian bone is considered an ossification of the meckelian tendon (= "sesamoid articular" in Ridewood, 1904; Starks, 1916; Haines, 1973), and thus it is invariably associated with the insertion of the *stegalis*.

The *stegalis* inserting on the posteromesial surface of the dorsoposterior process of the dentary are exclusive for the *Sternarchorhynchus* (Fig. 27).

23) Relative position of the *stegalis* in relation to the *adductor arcus palatini*: (0) *stegalis* not overlapping the *adductor arcus palatini*; (1) *stegalis* completely overlapping the *adductor arcus palatini*; (2) *stegalis* partially overlapping the *adductor arcus palatini* (Dutra *et al*., 2021: ch. 119) [CI: 0.28; RI: 0.88].

In outgroup taxa, the *stegalis* is always ventral to the insertion of the *adductor arcus palatini*, and thus never overlaps it. In most Gymnotiformes, the *stegalis* is lateral to the *adductor arcus palatini* and overlaps it completely (Figs. 1, 2). In some species of the order, only the posteromedial and posterior portions of the *adductor arcus palatini* are positioned mesially to the *stegalis* (Peixoto, Ohara, 2019: fig. 13A). This character is based on a relational landmark (position of a muscle relative to another) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

According to our analysis, State 1 is a synapomorphy for Gymnotiformes (clade GY), with convergent instances to State 2 in *Adontosternarchus* and clades B, SO and EI (with subsequent transformations to State 0 in clade AR and in *Distocyclus*).

24) Relative position of *malaris* and *stegalis*: (0) *malaris* partly overlapping the *stegalis*; (1) *malaris* completely overlapping the *stegalis* (Dutra *et al*., 2021: ch. 116) [CI: 1; RI: 1].

In Gymnotiformes, the *malaris* is usually located laterally and partially overlaps the ventromedial portion of the *stegalis*. In species of *Archolaemus* (except *A. orientalis*), the *stegalis* is dorsoventrally compacted and completely mesial to the *malaris*, thus not visible in lateral view (Dutra *et al*., 2021: fig. 15).

State 1 is synapomorphic for clade AR.

25) Position of the *malaris* in relation to the *rictalis*: (0) *malaris* positioned dorsolaterally to dorsal portion of *rictalis*; (1) *malaris* lateral to dorsal portion of *rictalis*, overlapping it almost entirely; (2) *malaris* ventral relative to dorsal portion of *rictalis*; (3) dorsal portion of *malaris* (*promalaris*) dorsolateral to dorsal portion of *rictalis*, with its ventral region (*retromalaris*) ventrolateral to dorsal portion of *rictalis* [CI: 0.60; RI: 0.87].

The most common configuration among gymnotiforms is of a *malaris* dorsolaterally to the dorsal portion of the *rictalis* and ventrolateral to the ventromedial portion of the *stegalis*, occupying the region immediately ventral to the eyeball (State 0). The majority of species of Apteronotidae, however, diverge from that configuration. For a discussion on the homology of the *malaris* in Apteronotidae, especially in species of the clade AP, cf. section "Additional comments on the *adductor mandibulae, pars malaris* in Apteronotidae". This character is based on a relational landmark (position of a muscle relative to another) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

State 1 is hypothesized as a synapomorphy for the clade PC (convergent in *Brycon* among outgroups), with subsequent transition to State 2 in clade AP (with reversal to state 0 in *Orthosternarchus*) and to 3 in "*Apteronotus*" *bonapartii*.

26) Intermuscular bones in *adductor mandibulae*, *segmentum facialis*: (0) absent; (1) present (Albert, Campos-da-Paz, 1998: ch. 45; Albert, 2001: ch. 44; Albert *et al*., 2005: ch. 83; Hilton *et al*., 2007; Tagliacollo *et al*., 2016: ch. 56) [CI: 0.33; RI: 0.50].

The most common condition of the *adductor mandibulae, segmentum facialis* in gymnotiforms and other ostariophysans is to lack any internal ossifications. In a few taxa, like *Gymnotus* gr. *carapo*, *Rhamphichthys* and *Orthosternarchus*, the *segmentum facialis* exhibits bony filaments resulting from tendinous or ligamentous ossifications (Peixoto, Ohara, 2019: fig. 12). Additional discussion on such ossifications is presented section "General aspects of the dorsolateral head musculature in Gymnotiformes", subsection "*Adductor mandibulae*".

The presence of such ossifications is convergently developed in *Gymnotus* gr. *carapo*, *Rhamphichthys* and *Orthosternarchus*.

27) *Segmentum mandibularis*: (0) present; (1) absent (Dutra *et al*., 2021: ch. 120) [CI: 0.16; RI: 0.75].

The *adductor mandibulae* segment inserted medially on the mandible is called *segmentum mandibularis* (Datovo, Vari, 2013) and it originates from the mandibular tendon. The *segmentum mandibularis* is present in the vast majority of Ostariophysi, as well as in Gymnotiformes. However, this segment is absent in *Labeo* (Cypriniformes), Gymnotidae (clade G), Rhamphichthyidae (clade R), clade SS and *Archolaemus* (clade AC, with reversal in *A. luciae*).

All cases describe above represent convergent losses.

28) Length of *segmentum mandibularis* in relation to Meckel´s cartilage: (0) *segmentum mandibularis* contacting up to 2/3 of the dorsal margin of Meckel´s cartilage; (1) *segmentum mandibularis* contacting the entire dorsal margin of Meckel´s cartilage

(Dutra *et al*., 2021: ch. 121) [CI: 0.33; RI: 0.66].

When present in Gymnotiformes, the *segmentum mandibularis* usually contacts up to two-thirds of the dorsal margin of Mecke´s cartilage. Contrastingly, the *segmentum mandibularis* in *Parapteronotus* and *Rhabdolichops* (Dutra *et al*., 2021: fig. 41B) contacts practically the entire dorsal margin of Meckel´s cartilage.

This character is inapplicable in *Labeo* (Cypriniformes), Gymnotidae (clade G), Rhamphichthyidae (clade R), remaining *Archolaemus* and speies on Clade SS, because the *segmentum mandibularis* is absent in those taxa.

In Analysis 1, State 1 is convergent in *Brycon*, clade RC and *Parapteronotus*.

29) Insertion of *segmentum mandibularis*: (0) restricted to dentary; (1) including anguloarticular and dentary; (2) restricted to anguloarticular (Dutra *et al*., 2021: ch. 122) [CI: 0.33; RI: 0.20].

In primitive members of Ostariophysi, the *segmentum mandibularis* inserts on the dentary only (State 0). In other taxa of the ingroup, the insertion can be on the dentary and anguloarticular (State 1) or restricted to the anguloarticular (State 2).

The *segmentum mandibularis* is absent in *Labeo* (Cypriniformes), Gymnotidae (clade G), Rhamphichthyidae (clade R), *Archolaemus* (except *A. luciae*) and species in clade SS. This character is therefore coded as inapplicable in those taxa.

State 1 is hypothesized as a synapomorphy for Characiphysi, with convergent transitions to state 2 in *Microsternarchus*, *Steatogenys* (clade SY), *Japigny* and *E. humboldtii*, and a reversal to State 0 in *A. luciae*.

30) Posterior extension of *segmentum mandibularis* beyond posterior margin of mandible: (0) absent; (1) present [CI: AUT; RI: AUT].

In the primitive condition in Gymnotiformes and basal representatives of other Ostariophysi, the *segmentum mandibularis* is limited to the mesial face of the dentary and is not visible in lateral view. In *Apteronotus* gr. *leptorhynchus*, the *segmentum mandibularis* originates from a mandibular raphe on the anteromedial portion of the *adductor mandibulae, segmentum facialis*, emerging posteriorly relative to the posterior margin of the anguloarticular and visible laterally (Fig. 30).

The *segmentum mandibularis* is absent in *Labeo* (Cypriniformes), Gymnotidae (clade G), Rhamphichthyidae (clade R), *Archolaemus* (except *A. luciae*) and species in clade SS. This character is therefore coded as inapplicable in those taxa.

The condition described in the State 1 is synapomorphic for *Apteronotus* gr. *leptorhynchus*.

31) Transverse ligament: (0) undifferentiated; (1) well differentiated [CI: 1; RI: 1].

Tendinous or ligamentous structures associated to the buccopalatal membrane usually result from mechanical stress associated with forces during opening and closing of the mouth. Collagen strips concentrate in regions of greater tension, differentiating into ligaments associated with the buccopalatal membrane (Osse, 1969; Gosline, 1986; Datovo, Castro, 2012). One of those ligaments is called transverse ligament (Datovo, Vari, 2013) and it arises from the inter-segmental aponeurosis and runs along the posterior margin of the retrojugal lamina. The transverse ligament is not differentiated in the majority of Gymnotiformes, except in species of Sternopygidae, where it is modified into a conspicuous ligament transversely oriented relative to the anterior margin of the *segmentum facialis* (Fig. 7).

State 1 is a synapomorphy for Sternopygidae (clade S).

32) Endomaxilar ligament, lenght relative to fibrous portion of *malaris*: (0) shorter than 2/3; (1) equal; (2) twice; (3) triple. [CI: 0.37; RI: 0.73].

Several ligaments are associated with the buccopalatal membrane. Among those, the endomaxilar ligament is present in the vast majority of Gymnotiformes, always associated with the lateral subsection of the *adductor mandibulae*, *pars malaris*.

The endomaxillary ligament is variable in size, with the most common situation in gymnotiforms being a minute condition, shorter than 2/3 the length of the fibrous portion of the *malaris*. That ligament, however, can be variably elongated in different taxa, reaching up to three times the length of the fibrous portion of the *malaris*. This character is based on a relational landmark (length of a ligament *vs*. that of fibrous portion of a muscle) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

There is no endomaxilary ligament in *Chanos* and Gymnotidae (clado G), which are thus coded as inapplicable.

In the Analysis 1, State 1 (Peixoto, Ohara, 2019: fig. 12) is convergent in Rhamphichthyidae (clade R), with a modification to State 2 (Fig. 5) in *Gymnorhamphichthys* (clado GR), *Adontosternarchus* and clade PA. In the latter, there is a reversal to State 0 in "*Apteronotus*" *bonapartii*, a transition to State 2 in *Apteronontus* gr. *leptorhynchus* to State 3 in clade SS (reversed to State 0 in *Sternarchorhamphus*).

33) Endomaxillary ligament position in relation to the autopalatine: (0) ventrolateral; (1) dorsolateral [CI: 0.33; RI: 0.81].

The endomaxillary ligament in Gymnotiformes is usually located ventrolaterally to the autopalatine. Unusually, in some Apteronotidae the ligament is dorsomedially displaced to a dorsolateral position relative to the autopalatine (Figs. 7, 32).

The State 1 is a synapomorphy for clade CP, with independent reversals in clade PS and *Parapteronotus*.

34) Post-retroarticular and pre-retroarticular ligaments: (0) undifferentiated; (1) differentiated [CI: 0.50; RI: 0.88].

Buccopalatal ligaments in gymnotiforms are usually poorly differentiated, except for those involved in the connection with the *adductor mandibulae* or with bony elements (*e.g.,* endomaxillary and ectomaxillary ligaments). In some Apteronotidae, two ligaments are differentiated from the posterior portion of the buccopalatal membrane, originating from the retroarticular and diverging anteriorly to the dorsoposterior portion of the membrane. They are here called post-retroarticular and pre-retroarticular ligaments (Figs. 7, 25), and not considered homologous to the preangular and postangular ligaments of Datovo, Vari (2013) because all ligaments are present in some taxa, thus failing the conjunction test of homology (Patterson, 1982; de Pinna, 1991).

The presence of such ligaments is synapomorphic for the clade PC, with a reversal in clade MP.

35) Origin of *adductor arcus palatini*: (0) not including orbitosphenoid; (1) including orbitosphenoid (Dutra *et al*., 2021: ch. 123) [CI: AUT; RI: AUT].

The *adductor arcus palatini* in Gymnotiformes usually originates on the ventrolateral surface of the parasphenoid and anteroventral part of the prootic (LAWP, pers. obs.; Aguilera, 1986). The origin of that muscle is anterodorsally displaced in *Japigny*, resulting in the incorporation of the ventrolateral surface of the orbitosphenoid (Dutra *et al*., 2021: fig. 42).

This condition is an autapomorphy for *Japigny*.

36) Origin of *adductor arcus palatini* in relation to the parasphenoid: (0) restricted to posterior half of orbit; (1) extending along entire orbit [CI: 1; RI: 1].

The origin of the *adductor arcus palatini* is normally in the parasphenoid and prootic but can also involve other bones (Winterbottom, 1974a). Its trajectory is also variable among teleosts. In Ostariophysi, the generalized pattern is an *adductor arcus palatini* originating on the posterior half of the parasphenoid and extending along the posterior half of the orbit. Contrastingly, in the majority of taxa examined for this study, both ingroup and outgroup, the origin of the *adductor arcus palatini* is on the anterior half of the parasphenoid and the muscle extends along the orbit.

In the present analysis, the orign of this muscle along the entire orbial region is synapomorphic for Characiphysi (Characiformes + Siluriphysi; *sensu* Fink, Fink, 1981; 1996).

37) Insertion of *adductor arcus palatini* on endopterygoid: (0) limited to dorsolateral portion of the bone, not extending beyond the horizontal line through the midline of this bone; (1) on dorsolateral and median portion of bone, reaching the horizontal line through the midline of this bone (modified from Diogo *et al*., 2008: Character 140) [CI: 0.25; RI: 0.87].

Diogo *et al.* (2008) proposed the insertion of a significant part of the *adductor arcus palatini* on the lateral surface of the suspensorium as a synapomorphy for the Gymnotiformes (character 140; state 1). Herein, we provide a more detailed description of this condition and describe the insertion to be specifically at the endopterygoid, a configuration shared among all gymnotiforms. Despite that general pattern, there is still phylogenetically informative variation in this complex.

Primitively in Ostariophysi, the insertion of the *adductor arcus palatini* is restricted to the dorsal portion of the lateral surface of the endopterygoid. However, in most Gymnotiformes, the insertion of the *adductor arcus palatini* is ventrally displaced, surpassing the horizontal line through the middle portion of the endopterygoid of the lateral surface (Dutra *et al*., 2021: fig. 42).

The latter condition is a synapomorphy for clade ST, with reversals in *Gymnorhamphichthys* (clade GR) and in clade CP (with subsequent reacquisition in clade MS).

38) Origin of *levator arcus palatini* in relation to the frontal: (0) absent; (1) present (Dutra *et al*., 2021: ch. 125) [CI: 0.20; RI: 0.85].

Generally, in Ostariophysi, the *levator arcus palatini* originates on the sphenotic (LAWP, pers. obs.; Winterbottom, 1974a). In basal members of the Siluriformes and in the great majority of Gymnotiformes, the muscle has an anterior displacement so that its origin includes the frontal.

The State 1 is a synapomorphy for Siluriphysi, with reversals in *Electrophorus*, *Archolaemus* (clade AC), and in clade ER (with reacquisition in *R. troscheli*).

39) Origin of *levator arcus palatini* in the pterosphenoid: (0) absent; (1) present (Dutra *et al*., 2021: ch. 126) [CI: 0.14; RI: 0.75].

As with the preceding character, basal representatives of Ostariophysi have the origin of the *levator arcus palatini* is mostly restricted to the sphenotic, sometimes also involving elements of the posterior part of the neurocranium (LAWP, pers. obs.; Winterbottom, 1974a). Within Gymnotiformes, some species of Apteronotidae and Sternopygidae have the *levator arcus palatini* in a more mesial position, resulting in a connection with the pterosphenoid.

The latter condition is apomorphic for SI, with independent reversals in "*Apteronotus*" *bonapartii*, clade AP (reacquired in clade SN), *Japigny*, and clade ED (reacquired in *Rhabdolichops*, clade RL).

40) Relative width of origin and insertion of *levator arcus palatini*: (0) origin narrower than insertion; (1) origin wider than insertion, up to 150% width of insertion; (2) width of origin equal to that of insertion; (3) width of origin twice that of insertion (Dutra *et al*., 2021: ch. 129) [CI: 0.21; RI: 0.75].

The *levator arcus palatini* in ostariophysians a roughly triangular shape, with its origin narrower than its insertion. In Gymnotiformes, the relation between the width of the origin and that of the insertion is variable, ranging from an origin narrower than the insertion to cases in which the origin is twice as wide as the insertion. This character is based on a relational landmark (origin *vs.* insertion) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

In the hypothesis here advanced, State 1 is convergent in *Diplomystes* (Siluriformes) and clade SN. State 2 is synapomorphic for clade RC and State 3 for *Gymnotus* (clade GM).

41) Structure of *levator arcus palatini*: (0) as a single muscle; (1) subdivided into two sections [CI: AUT; RI: AUT].

In nearly all examined taxa, the *levator arcus palatini* is a single muscle, without subdivisions. Uniquely in *Electrophorus*, this muscle is differentiated in two well-defined sections, herein named *levator arcus palatini anterior* and *levator arcus palatini posterior* (Figs. 2, 10). The two sections have a single origin on the ventral margin of the sphenotic, but their insertions differ with the anterior section converging entirely on the hyomandibula and the posterior one inserting mostly on the preopercle, with a few fibers on the hyomandibula.

Aguilera (1986) described the *levator arcus palatini* as a single muscle in gymnotiforms, including *Electrophorus* (Aguilera, 1986: fig. 10). Our own observations on the dual structure of the muscle is based on two sides of two specimens of *E. electricus*.

The division of the *levator arcus palatini* into *anterior* and *posterior* sections is retrieved as a synapomorphy for *Electrophorus*.

42) Insertion of the anterolateral fibers of *levator arcus palatini* at relative to *adductor mandibulae, pars malaris*: (0) mesial; (1) lateral; (2) dorsal (modified from Diogo *et al*., 2008: ch. 130; Datovo, Vari, 2014: ch. 9; Dutra *et al*., 2021: ch. 123) [CI: 0.50; RI: 0.88].

At its insertion, the *levator arcus palatini* is completely mesial in relation to the *adductor mandibulae* (Diogo *et al*., 2008; Datovo, Vari, 2014). In the Gymnotiformes, the *levator arcus palatini* has a different configuration, and is generally lateral to the *malaris* (LAWP, pers. obs.; Chardon, de La Hoz, 1973; Aguilera, 1986), a condition listed as synapomorphic for the order (Diogo *et al*., 2008; ch. 130; Datovo, Vari, 2014; ch. 9).

However, fibers of the *levator arcus palatini* at its insertion are variable in relation to the *malaris* of Gymnotiformes. This requires the recognition of four subsets of fibers (Figs. 16–32; anterolateral, posterolateral, anteromesial and posteromesial). Those different muscle regions are anatomically distinct and were therefore treated as independent characters herein. This character is based on a relational landmark (position of two separate muscles) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

Under this new interpretation, the lateral position of the anterolateral fibers of the *levator arcus palatini* relative to the *malaris* (State 1) is a synapomorphy for Gymnotiformes, with reversal in *Compsaria* and further transition to State 2 in Clade PA, (within the latter with reversal to State 1 in Clade SO).

43) Insertion of the posterolateral fibers of *levator arcus palatini* in relation to the *adductor mandibulae, pars malaris*: (0) mesial; (1) lateral; (2) dorsal [CI: 0.66; RI: 0.94].

In outgroup representatives, the *levator arcus palatini* is entirely mesial to the *malaris*. In Gymnotiformes, the posterolateral fibers of the *levator arcus palatini* are positioned completely laterally (Fig. 16) or dorsal (Fig. 30) to the *malaris*. This character is treated as unordered for the same reason as the previous one.

The condition described as State 1 is a synapomorphy for Gymnotiformes (clade Gy), with transition to State 2 in clade PA (therein with reversal to State 1 in clade SO).

44) Insertion of the anteromesial fibers of *levator arcus palatini* in relation to the *adductor mandibulae, pars malaris*: (0) mesial; (1) lateral; (2) dorsal [CI: 0.28–0.76; RI: 0.82–0.85].

As mentioned under characters 42 and 43, the generalized pattern found in teleosts consists of the *levator arcus palatini* being positioned mesially to the *malaris*. In Gymnotiformes, the anteromesial fibers of the *levator arcus palatini* are positioned laterally or dorsal to the *malaris*. This character is treated as unordered for the same reason as the previous one.

The lateral position of anteromesial fibers of the *levator arcus palatini* at insertion, relative to the *malaris* (State 1), is abundantly convergent, occurring in *Electrophorus*, Rhamphichthyidae (clade R) and Sternopygidae (clade S, with a reversal in clade AE). The dorsolateral position of the same fibers (State 2), on the other hand, is synapomorphic for clade PA, with subsequent transition to State 1 in clade SO.

45) Position of *dilatator operculi* in relation to the *levator arcus palatini*: (0) *dilatator operculi* covering anterior half of the *levator arcus palatini*; (1) *dilatator operculi* covering less than anterior half of the *levator arcus palatini*; (2) *dilatator operculi* mesial to *levator arcus palatini* [CI: 0.25–0.76; RI: 0.76].

In basal members of Ostariophysi, including some Gymnotiformes, the *dilatator operculi* is located laterally to the *levator arcus palatini*, with the anterior margin of the former covering half or more of the latter. In a majority of Gymnotiformes, the *dilatator operculi* overlaps only the posterior margin of the *levator arcus palatini* (Figs. 11, 15–18, 20; Peixoto, Ohara, 2019: fig. 8, 13; Dutra *et al*., 2021: fig. 40). This character is treated as unordered for the same reason as the previous one.

The latter condition (State 1) is synapomorphic for the order, with reversals in *Gymnotus* (clade GM) and Apteronotidae (clade A, with independent transitions back to State 1 in *Compsaraia*, *Orthosternarchus* and *Sternarchogiton*). State 2 is exclusive to *Diplomystes* among examined taxa.

46) Orientation of anterior margin of *levator arcus palatini*: (0) anterolateral fibers of *levator arcus palatini* approximately straight relative to the horizontal arm of preopercle, forming an angle of *ca*. 90° relative to the longitudinal axis of head; (1) anterolateral fibers of *levator arcus palatini* oriented obliquely relative to the horizontal arm of preopercle, forming a 45° angle relative to longitudinal axis of head (modified from Dutra *et al*., 2021: ch. 128) [CI: 0.16; RI: 0.87].

Primitively in ostariophysans, the *levator arcus palatini* has its anterolateral fibers of *levator arcus palatini* approximately straight relative to the horizontal arm of preopercle, forming an angle of *ca*. 90° relative to the longitudinal axis of head. On a different configuration, in basal representatives of Siluriformes and in the majority of Gymnotiformes, that muscle is oblique relative to the horizontal arm of the preopercle, forming with it an angle of approximately 45° (Figs. 1, 7, 15, 16, 28, 30).

State 1 is a synapomorphy for Siluriphysi, with reversals in *Electrophorus*, Rhamphichthyidae (clade R), clades PS and AE (here with a return to State 1 in *R. eastwardi*).

47) Relative position of *levator arcus palatini*: (0) *levator arcus palatini* overlapping posterior margin of pterosphenoid only; (1) *levator arcus palatini* overlapping pterosphenoid almost entirely, except for its anterior region; (2) *levator arcus palatini* overlapping half of pterosphenoid; (3) *levator arcus palatini* overlapping posterior third of pterosphenoid [CI: 0.50; RI: 0.92].

Primitively in teleosts, the *levator arcus palatini* is located posteriorly to the pterosphenoid, not covering it and leaving the bone visible in lateral view. In most Siluriformes and Gymnotiformes, the muscle has a more anterior origin, with a horizontally expanded anterodorsal portion. As a result, the *levator arcus palatini* is lateral to the pterosphenoid, covering it and making it invisible in lateral view. In some taxa the degree to which the *levator arcus palatini* covers the pterosphenoid is variable, for example it covers the posterior half of the bone in *Hypopygus*, and the posterior third in some Sternopygidae. This character is based on a relational landmark (relative size or shape of a muscle relative to that of a bone) and as such cannot be ordered by simple similarity because a single primary variable cannot be determined. It is thus treated as unordered.

State 1 is a synapomorphy for Siluriphysi, com reversal to State 0 in *Electrophorus*, transition to State 2 in *Hypopygus* and to State 3 in clade EI (with transformation to State 1 in clade RB).

48) Intermuscular bones in the anterior portion of *levator arcus palatini*: (0) absent; (1) present [CI: 0.50; RI: 0.66].

Ostariophysi in general lack ossifications in the *levator arcus palatini*. In species of *Rhamphichthys* and *S. xingu*, however, the *levator arcus palatini* has some ossified tendons, forming intermuscular bones (Peixoto, Ohara, 2019: fig. 12).

The presence of such ossifications is a synapomorphy for *Rhamphichthys* (clade RY), with a convergent occurrence in *S. xingu*.

49) *Dilatator operculi*: (0) single; (1) subdivided [CI: AUT; RI: AUT].

The *dilatator operculi* is a single muscle bundle in nearly all gymnotiforms, with no subdivisions (LAWP, pers. obs.; Aguilera, 1986).

Uniquely in *Electrophorus*, the muscle is subdivided in two sections, here named *dilatator operculi ventralis* and *dilatator operculi dorsalis* (Fig. 10), an autapomorphy for the genus.

50) Origin of *dilatator operculi* on sphenotic: (0) origin of dorsal fibers on sphenotic and pterotic not overlapping the bones entirely and not reaching suture with parietal; (1) origin of dorsal fibers on sphenotic and pterotic overlapping the bones completely and extending to suture with parietal [CI: 1; RI: 1].

Normally in gymnotiforms, the *dilatator operculi* originates on the ventromedial portion of the sphenotic and pterotic, some distance from the suture with the parietal, so that all those bones are visible in lateral view. Contrastingly, o *dilatator operculi* in *Sternarchella* is more robust, with its origin dorsally displaced relative towards the suture of the pterotic and sphenotic with the parietal.

State 1 is synapomorphic for clade MS.

51) Origin of *levator operculi anterior*: (0) not including hyomandibula; (1) including hyomandibula (Dutra *et al*., 2021: ch. 131) [CI: 0.25; RI: 0.91].

The anterior fibers of the *levator operculi*, called *levator operculi anterior* in Gymnotiformes (see Section "The dorsolateral musculature of the head of Gymnotiformes: General features- *levator operculi*"), origin on the pterotic (LAWP, pers. obs.; Chardon, de La Hoz, 1973; Aguilera, 1986).

In some members of the order, the origin of the *levator operculi* is anteriorly expanded to include also the hyomandibula, a convergent condition in *Labeo* (Cypriniformes), *Steatogenys* (clade SY) and clade EI (with reversal in clade RD).

52) *Levator operculi posterior*: (0) absent; (1) present (Albert, Campos-da-Paz, 1998: Character 47; Albert, 2001: ch. 46 [?]; Diogo *et al*., 2008: Character 151) [CI: 0.50; RI: 0.75].

Albert (2001) proposed the absence of the muscle "*levator posterior*" as a synapomorphy for Gymnotiformes (their character 46). There are no descriptions or illustrations associated the character in that publication, but we presume the reference is to the same muscle here called "*levator operculi posterior*". Similarly, Diogo *et al.* (2008) suggested that the division of the *levator operculi* (their character 151) as a synapomorphy for Sternopygidae + Gymnotidae (clade 51 of Diogo *et al*., 2008), reporting the absence of such subdivision in Hypopomidae. Such observations and proposals are in stark contrast to those made herein, which indicate that the posterior section of the *levator operculi* is present in the vast majority of Gymnotiformes (except in *Hypopygus*).

The *levator operculi posterior*, apparently results from a secondary differentiation of the posterior fibers of the *levator operculi*, on the basis of its posterior and more superficial relative position. Such division of the *levator operculi* in a posterior section (State 1) is a synapomorphy for Gymnotiformes (with a reversal in *Hypopygus*).

53) Insertion of *levator operculi*: (0) on the mesial surface of dorsal region of opercle; (1) on a dorsal crest on the lateral surface of opercle [CI: 1; RI: 1].

Generally in Ostariophysi, the *levator operculi* inserts on the mesial surface (sometimes on a crest) of the opercle (LAWP, pers. obs.; Takahasi, 1925; Diogo *et al*., 2008). Contrastingly, the *levator operculi* in gymnotiforms inserts on a crest on the lateral surface of the opercle, surpassing the dorsal margin of the opercle.

State 1 is a synapomorphy for the Gymnotiformes.

54) Position of nerve R-Avn in relation to *levator operculi anterior*: (0) mesial; (1) lateral (Dutra *et al*., 2021: ch. 130) [CI: 0.16; RI: 0.87].

The nerve ramus R-Avn originates on the electrosensory lobe of the lateral line and innervates electroreceptors of the trunk (Carr *et al*., 1982; Vischer *et al*., 1989). Generally in teleosts, it is positioned medially relative to the *levator operculi*. However, the widespread condition in Gymnotiformes is to have the nerve positioned laterally relative to the *levator operculi anterior* and mesially to the *levator operculi posterior* (State 1) (Fig. 1).

This character is polymorphic in *Eigenmannia microstoma*, because one juvenile specimen (80.0 mm LEA) of the species has the right-side nerve disposed laterally to the muscle, differing from the usual condition found in all specimens with the both sides presenting the condition described in the State 0.

The condition in State 1 is listed as a synapomorphy for the order, with independent reversals in *Rhamphichthys* (clade RY), clade SN, *Platyurosternarchus* and clade EI (in the later with reacquisition of State 1 in Clade RD).

55) Origin of *adductor hyomandibulae*: (0) not including the sphenotic; (1) including the sphenotic [CI: 1; RI: 1].

In Gymnotiformes, the *adductor hyomandibulae* is a laminar muscle visible only in a mesial view of the suspensorium. It originates from the lateral surface of the prootic and sometimes the pterotic and parasphenoid (LAWP, pers. obs.; de La Hoz, Chardon, 1984). In Gymnotidae, the muscle has a posteromesially displaced origin, also including the sphenotic.

State 1 is synapomorphic for Gymnotidae.

56) Origin of *adductor operculi*: (0) including prootic; (1) not including prootic [CI: 0.33–0.81; RI: 0.81].

The pterotic, prootic and exoccipital are usual points of origin of the *adductor operculi* in some Gymnotiformes and outgroup representatives (LAWP, pers. obs.; Aguilera, 1986; Diogo *et al*., 2008). In basal members of Siluriformes and subgroups of Gymnotiformes, the origin of the *adductor operculi* is posteromesially displaced and does not include the prootic as part of its.

State 1 is a synapomorphy for Siluriphysi, with a reversal in clade ST (reacquired in *Archolaemus*, clade AC).

DISCUSSION

ANALYSIS 1 – Dorsolateral head musculature as phylogenetic characters in Gymnotiformes: comparisons with previous studies

Analyses of characters from the dorsolateral head musculature strongly support the monophyly of Gymnotiformes (Fig. 33). This further corroborates a long list of studies based on morphology (Fink, Fink, 1981; Triques, 1993; Gayet *et al*., 1994; Albert, Campos-da-Paz, 1998; Albert *et al*., 1998; Albert, Crampton, 2005a; Albert, Fink, 2007; Peixoto *et al*., 2019), on molecular data combined with electrophysiological and phenotypic characters (Alves-Gomes *et al*., 1995), on molecular data combined with morphological data (Tagliacollo *et al*., 2016), and on molecular data (Elbassiouny *et al*., 2016; Alda *et al*., 2019). Beyond that, the hypothesis presented here differs in some important points relative to previous proposals.

In our hypothesis of relationship based solely on myological data, a monophyletic Gymnotidae is sister group to all other Gymnotiformes, which is in agreement with various other previous proposals, both morphological and/or molecular (Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Albert, Crampton, 2005a; Albert, Fink, 2007; Tagliacollo *et al*., 2016). Some other studies based on phenotypic data have proposed Apteronotidae occupying a basal position in gymnotiforms, mostly due to a putatively plesiomorphic presence of a caudal fin and skeleton (Triques, 1993; Elbassiouny *et al*., 2016; with the latter study based on an extremely limited taxonomic representation of only eight taxa). However, Santana *et al.* (2013) demonstrated the presence of a well-developed caudal skeleton also in the gymnotid *Electrophorus*, thus rendering the distribution of this character ambiguous in the order. The evolution of the caudal skeleton in the group remains uncertain.

The clade named Sternopygoidei by Mago-Leccia (1978; clade E of Albert, 2001), composed of all families of Gymnotiformes except Gymnotidae (*i.e*., including Rhamphichthyidae, Hypopomidae, Apteronotidae and Sternopygidae), is corroborated here, as in various other studies (Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Albert, Crampton, 2005a; Albert, Fink, 2007; Tagliacollo *et al*., 2016). However, the monophyly of Sternopygoidei was not corroborated in some other hypotheses (*see* Triques, 1993; Alves-Gomes *et al*., 1995; Elbassiouny *et al*., 2016; Alda *et al*., 2019). A monophyletic Rhamphichthyoidea is recovered by myological data, and has also previously been found in other morphological (Triques, 1993, 2007; Gayet *et al*., 1994; Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Albert, Fink, 2007; Tagliacollo *et al*., 2016) molecular (Alves-Gomes *et al*., 1995; Maldonado-Ocampo *et al*., 2014; Tagliacollo *et al*., 2016) and total evidence (Tagliacollo *et al*., 2016) studies. However, composition and relationships between and among constituent families remain controversial, as discussed below.

Analyses based on morphology (Triques, 1993; Albert *et al*., 1998; Albert, 2001; Albert, Fink, 2007), molecular (Alves-Gomes, 1998; Maldonado-Ocampo *et al*., 2014) and total evidence (Tagliacollo *et al*., 2016; Crampton *et al*., 2016) supported a clade composed of *Hypopygus* and *Steatogenys*. The two genera, traditionally allocated in Hypopomidae (sensu Mago-Leccia, 1994; Albert, Campos-da-Paz, 1998; Albert, 2001), have recently been proposed as more closely related to Rhamphichthyidae (Maldonado-Ocampo *et al*., 2014; Tagliacollo *et al*., 2016; Crampton *et al*., 2016). As a result, the family is nowadays composed of *Rhamphichthys*, *Iracema*, *Gymnorhamphichthys* and the clade called "Steatogenae" (*Steatogenys* + *Hypopygus*; *sensu* Tagliacollo *et al*., 2016). Alternatively, *Hypopomus*, *Microsternarchus*, *Brachyhypopomus*, *Procerusternarchus* and *Racenisia* are part of Hypopomidae (Maldonado-Ocampo *et al*., 2014; Tagliacollo *et al*., 2016).

Myological data did not recover any of the aforementioned clades, resulting in a polytomy involving *Hypopomus*, *Hypopygus*, *Microsternarchus*, *Brachyhypopomus*, *Steatogenys* and the genera of Rhamphichthyidae (*sensu* Mago-Leccia, 1994; Albert, Campos-da-Paz, 1998; Albert, 2001; Albert, Fink, 2007). Such result may be due to the lack of specimens of *Iracema*, *Procerusternarchus* and *Racenisia* for study. Despite discrepancies in the internal relationships of Rhamphichthyoidea, its position as sister group of Sternopygoidea (Sternopygidae + Apteronotidae; Albert's 2001 "Sinusoidea") is repeatedly corroborated in other studies (Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Triques, 2005; Albert, Fink, 2007; Tagliacollo *et al*., 2016), including the present one.

Some molecular analyses have indicated a non-monophyletic Sternopygidae. Such results prompted suggestions to restrict the family to the genus *Sternopygus* and to allocate the remaining Sternopygidae in a separate Eigenmanniidae (Alves-Gomes *et al*., 1995, 1998). However, the monophyly of Sternopygidae has been well corroborated in various other studies, both previous and subsequent, and on both morphological and molecular data (Mago-Leccia, 1978, 1994; Mago-Leccia, Zaret, 1978; Fink, Fink, 1981; Triques, 1993; Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Albert, Fink, 2007; Tagliacollo *et al*., 2016; Alda *et al*., 2019).

Myological data decisively support the monophyly of Sternopygidae and of its two subfamilies, Sternopyginae and Eigenmanniinae (*sensu* Albert, 2001; clade EI). The latter point disagrees with Triques (1993), where *Rhabdolichops* was sister group to all other Sternopygidae and *Sternopygus* was in a polytomy with *Eigenmannia* and a clade formed by *Archolaemus* plus *Distocyclus* (thus resulting in a paraphyletic Eigenmanniinae). Five characters from dorsolateral head musculature support the monophyly of Eigenmanniinae, corroborating previous proposals based on molecular data and total evidence (Albert, 2001; Alves-Gomes *et al*., 1995; Tagliacollo *et al*., 2016). Our data also strongly support *Sternopygus* as sister group to all the rest of the family. Beyond that, relationships among general of Eigenmanniinae remain uncertain.

Conflicting ideas about the most basal taxon in Eigenmanniinae have been recurrent, regardless of the kind of data employed. Some analyses place *Rhabdolichops* in that position (Mago-Leccia, 1978; Triques, 1993; Alves-Gomes *et al*., 1995, 1998; Tagliacollo *et al*., 2016; Alda *et al*., 2019), others allocate instead *Archolaemus* as sister group to all other Eigenmanniinae (Fink, Fink, 1981; Lundberg, Mago-Leccia, 1986; Albert, Fink, 1996; Albert, Campos-da-Paz, 1998; Albert, 2001). Myological data presented herein support *Japigny* as sister group to remaining eigenmanniins, corroborating Vari *et al*. (2012) and Dutra *et al*. (2021).

Leaving aside *Japigny*, a clade formed by *Archolaemus*, *Eigenmannia*, *Distocyclus* and *Rhabdolichops* is supported by Analysis 1 (clade AE), in agreement with a number of previous morphological studies (Fink, Fink, 1981; Lundberg, Mago-Leccia, 1986; Albert, Fink, 1996; Albert, Campos-da-Paz, 1998; Albert, 2001; Dutra *et al*., 2021). Our results also corroborate the monophyly of *Archolaemus*, with *A. orientalis* as the sister group to the rest of the genus (in agreement with Vari *et al*., 2012) but no resolution beyond that (clade AR). *Archolaemus* is sister group to clade EE, composed of *Eigenmannia*, *Distocyclus* and *Rhabdolichops*, again a grouping previously supported by independent evidence both morphological (Fink, Fink, 1981; Lundberg, Mago-Leccia, 1986; Albert, Fink, 1996; Albert, 2001) and molecular (Alves-Gomes *et al*., 1995). Species of *Eigenmannia* do not form a monophyletic group, a possibility already suggested in other studies (Mago-Leccia, 1978, 1994; Triques, 1993; Alves-Gomes *et al*., 1995; Alves-Gomes, 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Tagliacollo *et al*., 2016). However, the monophyly of Eigenmannia was recently recovered in Dutra *et al*. (2021).

The clade composed of *Distocyclus* and *Rhabdolichops* (clade DR) corroborates Lundberg, Mago-Leccia (1986), and not other proposals where the former genus is sister to either *Archolaemus* (Triques, 1993; Tagliacollo *et al*., 2016), or to *Eigenmannia* (Alves-Gomes *et al*., 1995; Alves-Gomes, 1998; Alda *et al*., 2019), or to *Eigenmannia* plus *Rhabdolichops* (Albert, Campos-da-Paz, 1998; Albert, 2001). Other suggestions have positioned *Distocyclus* in a polytomy with *Eigenmannia* and *Archolaemus* (Mago-Leccia, 1978) or in a polytomy with *Rhabdolichops* and *Eigenmannia* (Fink, Fink, 1981; Lundberg, Mago-Leccia, 1986; Albert, Fink, 1996). Our support of the monophyly of *Rhabdolichops* agrees with Lundberg, Mago-Leccia (1986) and Correa *et al*. (2006), and our result showing the clade *R. nigrimans* + *R. lundbergi* (clade RD) as sister group to remaining species of *Rhabdolichops* is in line with Correa *et al*. (2006).

Myology data analyzed separately support the monophyly of Apteronotidae (clade A). Despite considerable effort in untangling the phylogenetic relationships of the family, there is still little consensus on the subject (Triques, 1993, 2005; Alves-Gomes *et al*., 1995; Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Ivanyisky III, Albert, 2014; Tagliacollo *et al*., 2016; Evans *et al*., 2017; Peixoto *et al*., 2019; Bernt *et al*., 2019, 2020). Our results show *Adontosternarchus* as monophyletic (clade AD), in agreement with numerous previous contributions (*e.g*., Lundberg, Cox Fernandes, 2007; Albert, 2001; Triques, 2005; de Santana, Vari, 2012; Bernt *et al*., 2020). However, our placement of the genus as sister group to all other Apteronotidae is new. As sister group to all other Apteronotidae, previous proposals have placed either the clade formed by *Platyurosternarchus*, *Sternarchorhynchus*, *Sternarchorhamphus* and *Orthosternarchus* (Sternarchorhynchinae *sensu* Albert, 2001; Albert *et al*., 1998, Albert, Campos-da-Paz, 1998; Peixoto *et al*., 2019) or alternatively the group composed of *Sternarchorhamphus* + *Orthosternarchus* (*i.e*., Sternarchorhamphinae *sensu* Tagliacollo *et al*., 2016; Triques, 2005; Bernt *et al*., 2019).

Analysis 1 places *Pariosternarchus* as the sister to all other genera of Apteronotidae except *Adontosternarchus* (clade PC). Such placement for *Pariosternarchus* also has no precedent in the literature. Previous studies have placed the genus as close to *Sternarchella* (Sternarchellini *sensu* Ivanyisky III, Albert, 2014; Tagliacollo *et al*., 2016; Evans *et al*., 2017; Peixoto *et al*., 2019) or to a clade composed of *Compsaraia* + *Melanosternarchus* (Bernt *et al*., 2019, 2020). Again, at odds with previous proposals, our analysis places *Compsaraia* as sister to clade PA. Formerly, the genus was considered as sister group either to a clade composed of *Porotergus*, *Adontosternarchus* and *Sternarchogiton* (Albert, 2001), or of *Apteronotus anas* (= *Parapteronotus hasemani*; Albert, Campos-da-Paz, 1998), or of "*Apteronotus*" gr. *bonapartii* + *Porotergus* (Tagliacollo *et al*., 2016), or still of *Melanosternarchus* (Bernt *et al*., 2019, 2020).

The clade here denominated PA is split in two subgroups, PAS and AP. Clade PAS includes *Porotergus* + *Sternarchogiton* + "*Apteronotus*" gr. *bonapartii*, and is supported by a unique subdivision of the *adductor mandibulae, pars malaris* into *retromalaris* and *promalaris* (see Character 13 above). The close proximity among the genera in clade PAS was partly retrieved by Tagliacollo *et al.* (2016), except for their inclusion of *Compsaraia* therein. Within clade AP, the most relevant result is the non-monophyly of *Apteronotus sensu stricto*, a finding that disagrees with previous studies (Albert, 2001; Triques, 2005; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019; Bernt *et al.,* 2019, 2020).

Clade MP is composed of species of *Sternarchella* (clade MS) and clade PS, and is equivalent to Sternarchorhynchinae (*sensu* Albert, 2001). Clade MS includes species traditionally allocated in *Sternarchella* (*S. schotti* and *S. orthos*) and species previously in *Magosternarchus* (*M. raptor* and *M. duccis*; the genus was recently considered as a junior synonym of *Sternarchella* by Ferraris *et al*., 2017 and Evans *et al*., 2017). Clade MS is one of the few groups unanimously supported in all previous hypotheses of relationships among Apteronotidae (*e.g*., Albert, Campos-da-Paz, 1998; Albert, 2001; Triques, 2005; Tagliacollo *et al*., 2016; Ivanyisky III, Albert, 2014; Evans *et al*., 2017; Peixoto *et al*., 2019; Bernt *et al*., 2019, 2020) and is also supported here.

Our results on the monophyly of Sternarchorhynchinae (clade PS) corroborates the ideas of Albert, Campos-da-Paz (1998) and Albert (1998, 2001), who placed *Platyurosternarchus*, *Sternarchorhynchus*, *Sternarchorhamphus*, *Orthosternarchus* as a clade, with the two former genera forming a group which is sister to the two latter ones. Despite the agreement about the entire clade, our hypothesis of intrarelationships differs somewhat, placing *Platyurosternarchus* as sister group to the remaining three genera (clade SO). Of course, differences exist also about the position of Sternarchorhynchinae within Apteronotidae, with cited authors placing it in a basal position in the family, while our myological data place it more deeply internested therein. Clade SO has also been routinely supported in previous studies (Alves-Gomes *et al*., 1995; Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Triques, 2005; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019; Bernt *et al*., 2019, 2020).

All things considered, there is substantial agreement between the phylogenetic signal inferred from myological characters studied herein and other hypotheses based on other natural partitions, as external anatomy, DNA sequences, electrophysiology, neuroanatomy and osteology. Some of the most relevant parallels are: (1) Gymnotidae as sister group to remaining Gymnotiformes, (2) monophyly of Rhamphichthyoidea,

(3) monophyly of Sternopygoidea, (4) monophyly of Sternopygidae, including Eigenmanniinae, and (5) monophyly of Apteronotidae and of its subclades.

Such congruence with other data sources obviously suggests confidence that reiterated components reflect actual features of the phylogenetic history of Gymnotiformes. Still, despite the effort invested here in detecting all phylogenetically-informative variation in dorsolateral head musculature, it is unavoidable that any single data source is but a tiny sample of the rich phenotypic variation observed in gymnotiforms. The next Section explores this topic by quantifying the influence of myological characters against a broader sample of morphological characters (Tagliacollo *et al*., 2016; Peixoto *et al*., 2019).

ANALYSIS 2 - Influence of myological characters on the relationships of Gymnotiformes

A parsimony analysis of the entire set of dorsolateral head myology data, concatenated with phenotypic characters from Tagliacollo *et al.* (2016; subsequently modified by Peixoto *et al*., 2019), resulted in 99,999 MPT's (score: 795; CI: 0.37; RI: 0.92), which served as a basis for a strict consensus tree and for mapping synapomorphies from the dorsolateral head musculature (Fig. 35; general synapomorphies listed in Tab. **S3**).

Results from the analysis 2 are reasonably consistent with most previous hypotheses of gymnotiform relationships. Seven new myological synapomorphies are listed for Gymnotiformes (Chs. 19, 23, 42, 43, 52, 53, 54), including a condition unique among Ostariophysi, the presence of the secondary section of the *levator operculi*, herein named *levator operculi posterior* (Ch. 52; reversed in *Hypopygus*). A similar division in the *levator operculi* is only seen homoplastically in unrelated percomorphs, such as tetraodontiforms, stromateiforms and pleuronectiforms (Pastana *et al*., 2021).

The Gymnotidae is corroborated as monophyletic (in line with all previous hypotheses, *e.g*., Alves-Gomes *et al*., 1998; Albert *et al*., 1995; Albert, 2001; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019; Alda *et al*., 2019) and sister group to Sternopygoidea. The absence of the *adductor mandibulae*, *segmentum mandibularis* is a new synapomorphic condition for the family (Ch. 27). Within Gymnotidae, *Electrophorus* alone has both the *levator arcus palatini* and *dilatator operculi* each divided in two sections, conditions recovered as unique synapomorphies for that genus (Chs. 41 and 49, respectively). The monophyly of Sternopygoidei, although often corroborated in different studies (Albert *et al*., 1998; Albert, 2001; Albert, Crampton, 2005a; Albert, Fink, 2007; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019), is not without controversy, mainly because of the position of Apteronotidae (Triques, 1993; Alves-Gomes *et al*., 1995; Gayet *et al*., 1994; Elbassiouny *et al*., 2016; Alda *et al*., 2019). In this study, a monophyletic Sternopygoidei is corroborated, with two new myological synapomorphies (Chs. 21 and 37).

Rhamphichthyoidea and Sternopygoidea are both monophyletic, a hypothesis previously supported by both morphological and/or molecular data (Albert, Campos-da-Paz, 1998; Albert, 2001; Triques, 2005, 2007; Albert, Fink, 2007; Carvalho, 2013; Maldonado-Ocampo *et al*., 2014; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019; Alda *et al*., 2019).

The taxonomic composition of Rhamphichthyidae corroborates traditional classifications of the family (including *Rhamphichthys*, *Iracema* and *Gymnorhamphichthys*; Albert, Campos-da-Paz, 1998; Albert, 2001), thus contradicting results based on molecular data, which also allocated *Steatogenys* and *Hypopygus* (Steatogeninae) in that family (Maldonado-Ocampo *et al*., 2013; Tagliacollo *et al*., 2016). The monophyly of "Rhamphichthyidae", excluding Steatogeninae, is supported by four synapomorphies from the dorsolateral head musculature (Chs. 2, 18, 27, 46). *Gymnorhamphichthys* is the sister group of *Iracema* + *Rhamphichthys* (Rhamphichthyini), in agreement with recent hypotheses based on morphological analysis and total evidence (Carvalho, Albert, 2011; Tagliacollo *et al*., 2016), but contrary to previous morphological studies which supported *Iracema* as more closely related to *Gymnorhamphichthys* (Albert, Campos-da-Paz, 1998; Albert, 2001). The position of the clade composed of *Steatogenys* + *Hypopygus* (Steatogeninae) is still a source of generalized controversy between hypotheses based on phenotypic (Albert, Campos-da-Paz, 1998; Albert, 2001), molecular (*e.g.*, Maldonado-Ocampo *et al*., 2014) and total evidence (Carvalho, 2013; Tagliacollo *et al*., 2016) analyses. In the present study, a monophyletic Steatogeninae is unresolved at a polytomy at the base of Rhamphichthyoidea. No myological characters exist for the

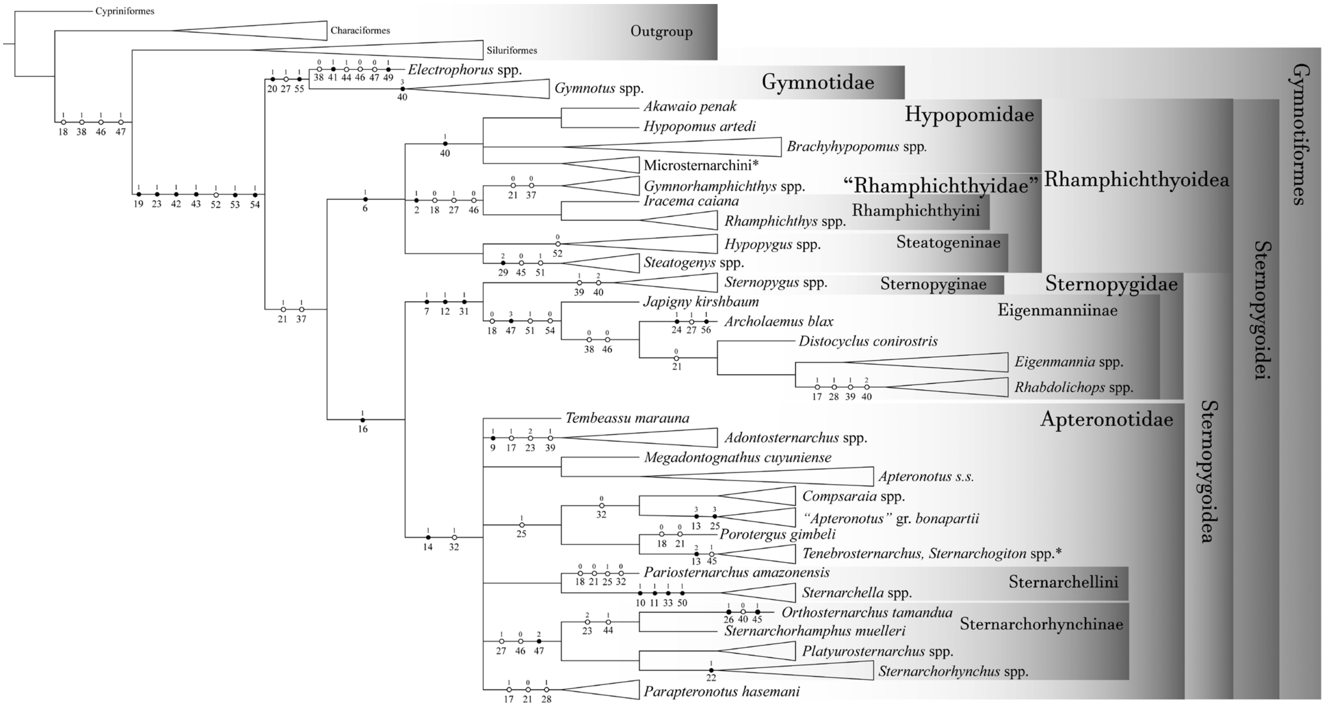


FIGURE 35 | Strict consensus of MPT's resulting from parsimony analysis of character matrix in Peixoto *et al.* (2019), concatenated with dorsolateral head musculature characters of this study [Score: 795; RI: 0.92; CI: 0.37], with numbered dorsolateral head musculature characters (below branches) and respective characters states (above branches). Black circles indicate homoplasy-free characters and white circles indicate homoplastic characters. Taxon legends: *Gymnotus* spp.[1] (*G. panamensis*, *G. maculosus*, and *G. cylindricus*); *Gymnotus* spp.[2] (*G. varzea*, *G. pantanal*, *G. obscurus*, *G. chaviro*); *Gymnotus* spp.[3] (*G. ucamara*, *G. sylvius*, *G.* sp, *G. omamorum*, *G. mamiraua*, *G. bahianus*); *Gymnotus* spp.[4] (*G. choco* and *G. ardilai*); *Gymnotus* spp.[5] (*G. carapo* and *G. arapaima*); *Gymnotus* spp.[6] (*G. tigre* and *G. hehni*); *Gymnotus* spp.[7] (*G. stenoleucus*, *G. pedanopterus*, *G. pantherinus*, *G. jonasi*, *G. javari*, *G. coropinae*, *G. coatesi*, *G.* cf. *anguilaris*, and *G. cataniapo*); *Brachyhypopomus* spp.[1] (*B.* sp., *B. accidentalis*, and *B. diazi*); *Brachyhypopomus* spp.[2] (*B. pinnicaudatus*; *B.* sp. 2); *Brachyhypopomus* spp.[3] (*B. bullocki* and *B. brevirostris*); *Rhabdolichops* spp. (*R. jegui* and *R.* cf. *stewarti*); *Adontosternarchus* spp. (*A. nebulosus*, *A. devenanzii*, *A. clarkae*, *A. balaenops*); *Apteronorus* spp.[1] (*A. caudimaculosus* and *A. albifrons*); *Apteronorus* spp.[2] (*A. magdalenensis* and *A. cuchillo*); *Apteronorus* spp.[3] (*A. leptorhynchus* and *A. eschemeyeri*); *Sternarchorhynchus* spp. (*S. starski*, *S. hagedornae*, *S. galibi*, *S.* sp.).

entire subfamily, although synapomorphies from musculature were newly found for each of its constituent genera.

As mentioned above, the *levator operculi* divided in two sections is an exclusive condition in Gymnotiformes, with a reversal in *Hypopygus*. According to hypotheses of primary homology in the discussion of Ch. 52 above, the portion of the *levator operculi* present in *Hypopygus* is homologous to the *levator operculi anterior* of other gymnotiforms. The single *levator operculi* in *Hypopygus* shares all characteristics of the *levator operculi anterior* in other gymnotiforms (*e.g*., sites of origin and insertion, and position relative to the R-Avn nerve- cf. Section "General aspects of the dorsolateral head musculature in Gymnotiformes- *levator operculi*", above), with no remaining myological component or subsection corresponding to the *levator operculi posterior*. Thus, a loss of *levator operculi posterior* is postulated in the genus.

Losses of entire myological components or sections in fishes are unusual. When a muscle, bundle or section is apparently absent, what most often happens is that it is simply not differentiated as a separate element, but its corresponding fibers are still present, undifferentiated from those of another adjacent muscle (*e.g*., Edgeworth, 1929; Datovo, Vari, 2013, 2014). However rare, losses of entire myological components do happen in some instances, as is the case of the *adductor mandibulae*, *segmentum mandibularis* in several teleosts (*e.g*., Gymnotiformes- Gymnotidae; Siluriformes- Aspredinidae, Callichthyidae, Loricariidae; Anguiliformes- *Anguilla*, *Ariosoma*; Osteoglossiformes- Arapaimidae; LAWP, pers. obs.; Diogo, 2004; Diogo *et al*., 2012; Datovo, Castro, 2012; Datovo, Vari, 2013, 2014).

Interestingly, de Santana, Crampton (2011) listed a series of reductive characters for *Hypopygus*, including partial or total loss of cranial bones, reduction of anal-fin rays, loss of scales, and simplification of laterosensory canal system (reductions reaching their extreme conditions in *Hypopygus minissimus* de Santana & Crampton, 2011, the smallest know gymnotiform, with *ca*. 42 mm TL). Those authors recognized *Hypopygus* as the only miniature taxon within Gymnotiformes. The absence of the *levator operculi posterior* may be part of that general trend of reduction, with simplification of a myological component. If corroborated by ontogenetic studies, this may be the first case of miniaturization-related reductive modification in myology among Ostariophysi.

Monophyly of Hypopomidae is corroborated in our results, a result also in line with several previous cladistic studies. The origin of the *levator arcus palatini* being wider than its insertion (Ch. 40) is a new synapomorphy for the family. Our proposed relationships among hypopomid genera, however, disagree with previous hypotheses. Monophyly of Microsternarchini (*sensu* Cox Fernandes *et al*., 2014) is supported, but its position in a polytomy at the base of Hypopomidae and the unresolved relationships among its genera do not support results of other studies, where it was sister group to *Hypopomus* (Cox Fernandes *et al*., 2014; Tagliacollo *et al*., 2016). The monophyly of Brachyhypopominae (*Hypopomus* + *Brachyhypopomus*; *sensu* Albert, 2001), usually corroborated in studies of both phenotypic (*e.g*., Albert, 2001) and total evidence (Carvalho, 2013) data, was instead refuted herein, with *Hypopomus* surprisingly supported as sister-group of *Akawaio*.

Crampton *et al.* (2016) proposed three potential synapomorphic characters for *Brachyhypopomus*, however, they also underscored the need of additional analyses to account for ontogenetic variation in the genus. Herein, species of *Brachyhypopomus* form a monophyletic group, but with all its synapomorphies from morphological complexes other than myology (Tagliacollo *et al*., 2016: chars. 122 and 171). *Brachyhypopomus*, however, is a highly diverse taxon and examination of additional species is necessary.

Sternopygoidea is monophyletic and sister group to Rhamphichthyoidea, a hypothesis congruent with the vast majority of previous studies (Albert, 2001; Triques, 2005; Albert, Fink, 2007; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019) and further supported by the attachment of the fibers of the *rictalis* restricted to the anterior portion of preopercle, not extending beyond the preopercular fossa (Ch. 16).

Within Sternopygoidea, Sternopygidae is supported by three homoplasy-free synapomorphies in dorsolateral head musculature (Chs. 7, 12, 31), including an insertion of the *malaris* on infraorbitals 1+2 (Ch. 7) which is otherwise unknown within Ostariophysi. Within Sternopygidae, Eigenmanniinae is monophyletic, with *Japigny* as the sister group to the other genera in the subfamily. Tagliacollo *et al.* (2016) was the first study to insert *Japigny* into a published phylogenetic analysis, and concluded that the sole species in the genus was actually a member of *Eigenmannia*. That hypothesis is not corroborated in our results, which instead support the previous proposals regarding the basalmost position of *Japigny* within Eigenmaniinae (Vari *et al*., 2012; Dutra, 2015; Dutra *et al*., 2021). *Archolaemus* is sister group to a clade composed of *Distocyclus* and *Eigenmannia* + *Rhabdolichops*, a hypothesis identical to those previously proposed on the basis of phenotypic data (Fink, Fink, 1981; Lundberg, Mago-Leccia, 1986; Albert, Fink, 1996; Albert, Campos-da-Paz, 1998).

Eigenmannia is proposed as monophyletic, with a synapomorphic origin of the *malaris* not exclusively on the hyomandibula (Ch. 3). *Eigenmannia* was usually considered as paraphyletic in previous phylogenetic studies (Alves-Gomes *et al*., 1998; Albert *et al*., 1995; Albert, 2001; Tagliacollo *et al*., 2016; Peixoto *et al*., 2019; Dutra *et al*., 2021). However, ultraconserved elements and morphological studies support the monophyly of the genus (Alda *et al*., 2019). Of course, *Eigenmannia* is the most diverse genus in its family (Peixoto *et al*., 2015, 2020; Peixoto, Ohara, 2019) and examination of musculature of additional species is critical for a solid assessment of its monophyly.

Two new myological synapomorphies support apteronotid monophyly (Chs. 14, 32), a hypothesis widely supported in the literature (Albert *et al*., 1994, 1995; Alves-Gomes *et al*., 1998; Tagliacollo *et al*., 2016; Bernt *et al*., 2018, 2019, 2020; Peixoto *et al*., 2019). Relationships within Apteronotidae are similar to those presented in Peixoto *et al.* (2019), with multiple apteronotid subclades unresolved in a polytomy (a situation similar to that proposed in Triques, 2005). Overall, however, there is rampant disagreement with previous studies (Triques, 1993, 2005; Alves-Gomes *et al*., 1995; Albert *et al*., 1998; Albert, Campos-da-Paz, 1998; Albert, 2001; Ivanyisky III, Albert, 2014; Tagliacollo *et al*., 2016; Evans *et al*., 2017; Bernt *et al*., 2018, 2019, 2020; Peixoto *et al*., 2019). For example, Sternarchorhamphinae (*Sternarchorhamphus* + *Orthosternarchus*; *sensu* Albert, 2001), has support from three new myological synapomorphies (Chs. 27, 46, 47), one of them homoplasy-free (Ch. 47). The same holds for ((*Porotergus* + *Sternarchogiton*, *Tenebrosternarchus*) + (*Compsaraia* + "*Apteronotus*" gr. *bonapartii*)), a proposal first advanced in Peixoto *et al.* (2019) which received additional support from one new myological synapomorphy (Ch. 25).

Tenebrosternarchus was proposed by Bernt *et al.* (2020), to allocate *Sternarchogiton preto* de Santana & Crampton, 2007. According to the molecular analysis performed in Bernt *et al.* (2020), *S. preto* was the sister-group of all remaining "Navajini" genera (*sensu* Bernt *et al*., 2019; Navajini is an invalid name- see Ferraris *et al*., 2007), including *Sternarchogiton*, a situation which would require the proposal of a new genus. Our results contradict those of Bernt *et al.* (2020), and support *T. preto* at a position internested with *Sternarchogiton* species, with two myological synapomorphies recovered for that clade (Chs. 13, 45).

Character sets from different data sources (*e.g.*, bones, muscles, nuclear and mitochondrial genes) are commonly concatenated in cladistic analyses. This is based on the long-held premise that the most reliable hypothesis of phylogenetic relationship is the one that covers all available data (Cracraft, Mindell, 1989). While this premise is broadly unchallenged, understanding the relationship between evidence and hypotheses requires an understanding of the degree to which different data sources contribute to the support of each branch within a global analysis (Baker, DeSalle, 1997). Among the procedures to investigate that issue, PBS is one of the most consistent, permitting an estimate of the congruence or incongruence of a specific dataset, quantifying and

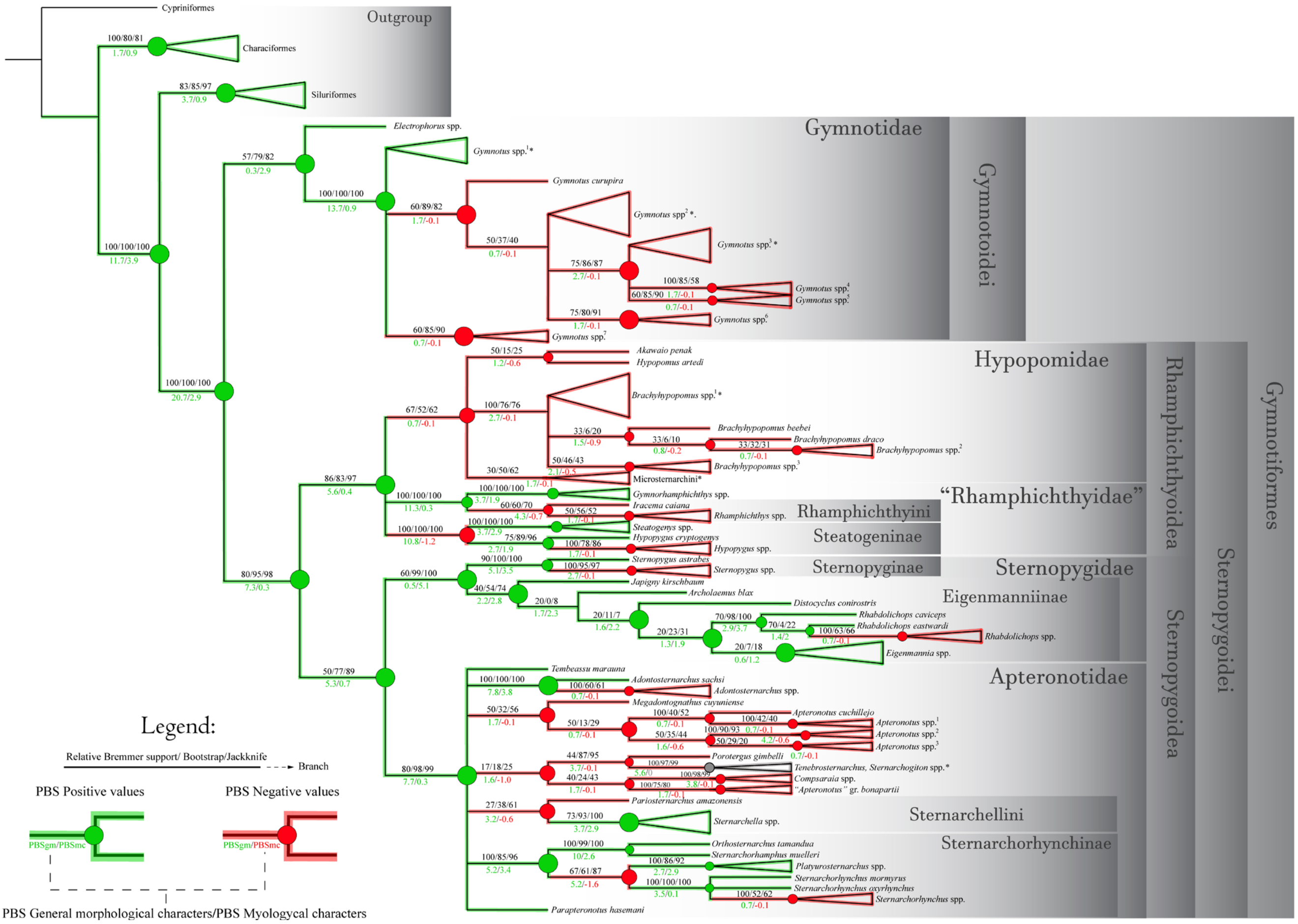


FIGURE 36 | Strict consensus of MPT's resulting from parsimony analysis of character matrix in Peixoto *et al.* (2019), concatenated with dorsolateral head musculature characters of this study [Score: 795; RI: 0.92; CI: 0.37]. PBS values for general morphological characters and myological characters are indicated below each branch. Circle size is arbitrary; gray indicate neutral values of PBS for myologycal characters. Taxon legends as in Fig. 35.

mapping it on a topology (Baker, DeSalle, 1997; Koepfli, Wayne, 2003). Negative PBS values (PBS–) for a node indicate that data partitions support relationships not corroborated in the global analyses, while positive PBS values (PBS+) mean complete congruence with that topology (Lambkin, 2004; Peña *et al*., 2006).

The application of PBS on two partitions focal to this study (general morphological characters *vs*. myological characters) allows an assessment of the influence of dorsolateral head musculature characters within the phylogeny of Gymnotiformes. In the global analysis, the myological data set conflicts in 34 of the 64 nodes of the strict consensus tree (*i.e*., PBS–), while providing favorable evidence in 29 other nodes (PBS+) and neutral value for a single clade (PBS= 0) (Fig. 36). PBS analysis further reveals that the contribution of myological characters is not uniformly distributed on the tree, instead concentrating on specific portions of the topology.

Support from myological characters is disproportionately concentrated in basal portions of the tree, with positive values to almost all more inclusive groups, such as orders (*e.g*., Characiformes, Siluriphysi, Siluriformes and Gymnotiformes), suborders (Gymnotoidei and Sternopygoidei) and superfamilies (*e.g*., Rhamphichthyoidea and Sternopygoidea). Nearly all gymnotiform families also received PBS+ from musculature, the only exception being Hypopomidae (PBS: –0.1). Among subfamilies, 63.3% received PBS+, with Steatogeninae being the only one in which myological and general characters conflict. Musculature and general data partitions also disagree regarding the resolution of the Microsternarchini, the only tribe with more than two genera included in the analysis. This is revealed by PBS = –0.1 for the myological partition. Contrastingly, among less inclusive clades, relationships at generic level received PBS+ in 52%, and PBS- in 44% of all nodes. A neutral value (PBS = 0) was found exclusively for the polytomy comprising *Tenebrosternarchus* and *Sternarchogiton*, indicating non-existing support from musculature characters. Curiously, general morphology and myological data partitions strongly disagree on interspecific relationships, with musculature characters yielding negative values of PBS for all such minor clades.

Myological characters are thus more effective in reconstructing deeper nodes of the combined tree in the equally weighted parsimony analysis, roughly corresponding to levels of order, suborder, superfamily, family, and subfamily, but with negative or no correlation in the ranks of tribe, intergeneric and interspecific levels (Fig. 37). The reasons for such skewed distribution of support from myology remain a matter of speculation at this time, but it offers interesting lines for future research. It may be related to underlying biomechanical constraints evolved in the early stages of gymnotiform evolution, but with more recent variants subject to less stringent parameters and thus undergoing more labile rates of state change. It also remains to be investigated whether such effects hold for other groups of fishes or if it is instead a phenomenon restricted to gymnotiforms.

Evidence presented here suggests the relevance of musculature as a source of reliable phylogenetic signal, a view foreshadowed by Borden (1999). That author found little intraspecific variability in the muscles of *Naso* species (Acanthuridae; Perciformes) when compared to other anatomical complexes (*e.g*., osteology) and, in combination with data from other studies, concluded that myological characters are reliable indicators of relationships at deep levels of phylogeny. Therefore, in spite of the difficulties related to the acquisition of material, myological preparation and dissection (Datovo, Bockmann,

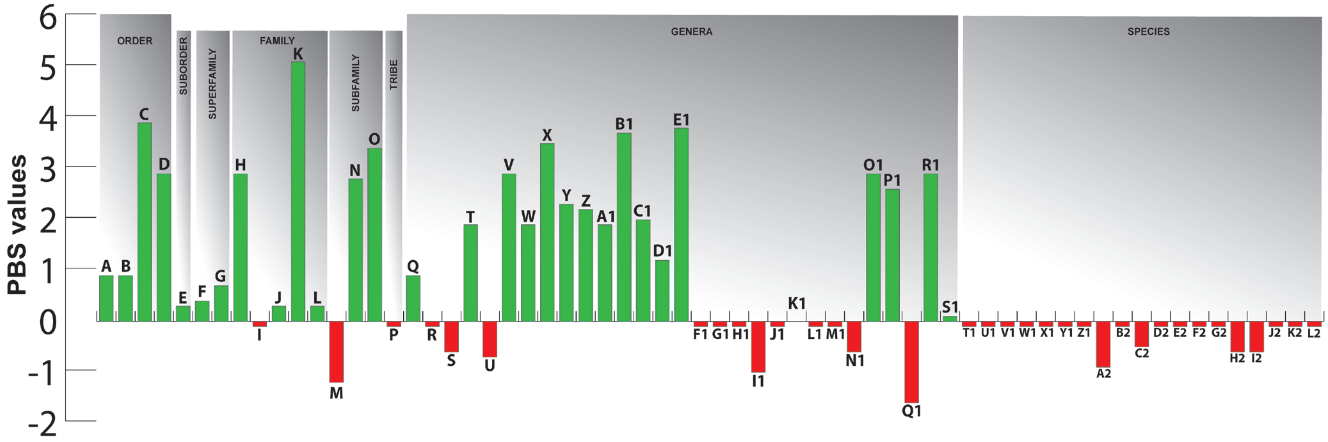


FIGURE 37 | Patterns of PBS value distribution of myologycal characters per taxonomic level in the phylogeny based on phenotypic data (Figs. 35, 36). Green bars indicate positive PBS values and red bars indicate negative PBS values. Bar for tribes include only non-monogeneric tribes. Taxon legends: A) Characiformes; B) Siluriformes; C) Siluriphysi; D) Gymnotiformes; E) Sternopygoidei; F) Rhamphichthyoidea; G) Sternopygoidea; H) Gymnotidae; I) Hypopomidae; J) Rhamphichthyidae; K) Sternopygidae; L) Apteronotidae; M) Steatogeninae; N) Eigenmanniinae; O) Sternarchorhynchinae; P) Microsternarchini; Q) *Gymnotus*; R) *Brachyhypopomus*; S) *Akawaio* + *Hypopomus*; T) *Gymnorhamphichthys*; U) *Iracema* + *Rhamphichthys*; V) *Steatogenys*; W) *Hypopygus*; X) *Sternopygus*; Y) *Archolaemus* + remaining Eigenmanniinae genera (except *Japigny*) Z) *Distocyclus* + remaining Eigenmanniinae genera (except *Archolaemus* and *Japigny*); A1) *Eigenmannia* + *Rhabdolichops*; B1) *Rhabdolichops*; C1) *R. eastwardi* + *Rhabdolichops* spp.; D1) *Eigenmannia* spp.; E1) *Adontosternarchus*; F1) *Megadontognathus* + *Apteronotus*; G1) *Apteronotus*; H1) *A. cuchillejo* + *A.* spp.^{1}; I1) ((*Porotergus* + *Tenebrosternarchus*, *Sternarchogiton*) + (*Compsaraia* + *"A." bonapartii*)); J1) (*Porotergus* + *Tenebrosternarchus*, *Sternarchogiton*); K1) (*Tenebrosternarchus*, *Sternarchogiton*); L1) (*Compsaraia* + *"A." bonapartii*); M1) *Compsaraia*; N1) *Pariosternarchus* + *Sternarchella*; O1) *Sternarchella*; P1) *Orthosternarchus* + *Sternarchorhamphus*; Q1) *Platyurosternarchus* + *Sternarchorhynchus*; R1) *Platyurosternarchus*; S1) *Sternarchorhynchus*; T1) *G. curupira* + *Gymnotus* subgroups; U1) *Gymnotus* spp.^{2,3,4,5}; V1) *Gymnotus* spp.^{3}; W1) *Gymnotus* spp.^{4}; X1) *Gymnotus* spp.^{5}; Y1) *Gymnotus* spp.^{6}; Z1) *Gymnotus* spp.^{7}; A2) *B. beebei* + *Brachyhypopomus* subgroups; B2) *B. draco* + *Brachyhypopomus* spp.^{2}; C2) *Brachyhypopomus* spp.^{3}; D2) *Hypopygus* spp.; E2) *Rhabdolichops* spp.; F2) *Adontosternarchus* spp.; G2) *Apteronotus* spp.^{1}; H2) *Apteronotus* spp.^{2} + *Apteronotus* spp.^{3}; I2) *Apteronotus* spp.^{2}; J2) *Apteronotus* spp.^{3}; K2) *"A." bonapartii*; L2) *Sternarchorhynchus* spp.

2010), the information thus gained is worth the effort, especially in deeper components of the relationships in fishes.

Some studies (Diogo, 2004; Diogo *et al*., 2012) attempted to empirically investigate the influence and relevance of myological characters in cladistic analyses by comparing the mean consistency and retention indices of myological and osteological characters, concluding that the former have, on average, higher values than those of the latter. Such results show that some data sets are more homoplastic than others (consistency index) and express the degree to which global character change is informative in the favored phylogeny (retention index). Those metrics, however, do not allow an estimate of the contribution of each data source at different taxonomic levels across the phylogeny. In this paper, we have shown that PBS reveals the location and degree of contribution of each data set to the topology resulting from concatenated analyses (Baker, DeSalle, 1997; Lambkin *et al*., 2002) and is a valid tool to detect the influence (or congruence) of characters from different sources at different levels of the phylogeny.

ANALYSIS 2– Summary of myological synapomorphies

In this section we list all myological synapomorphies currently known for the clades found in this study. They are listed per clade, following the numbering in preceding character description sections and with information on their specific cases of homoplastic changes when pertinent.

Clade Siluriformes + Gymnotiformes

– Origin of *stegalis* including sphenotic (Ch. 18, State 1; reversed in Eigenmanniinae, *Porotergus*, *Pariosternarchus* and Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– Origin of *levator arcus palatini* including frontal (Ch. 38, State 1; reversed to State 0 in *Electrophorus* and Clade *Archolaemus* + *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– Anterolateral fibers of *levator arcus palatini* oriented obliquely relative to the horizontal arm of preopercle, forming a 45° angle relative to longitudinal axis of head (Ch. 46, State 1; reversed in *Electrophorus*, Eigenmanniinae, Sternarchorhynchinae and Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– *Levator arcus palatini* overlapping pterosphenoid almost entirely, except for its anterior region (Ch. 47, State 1; reversed in *Electrophorus*).

Gymnotiformes

– Origin of *stegalis* including parasphenoid (Ch. 19, State 1).

– *Stegalis* positioned lateral to entire *adductor arcus palatini*, totally overlapping it (Ch. 23, State 1).

– Orientation of anterolateral fibers of *levator arcus palatini* at insertion lateral relative to *adductor mandibulae, pars malaris*: (Ch. 42, State 1).

– Posterolateral fibers of *levator arcus palatini* at insertion lateral relative to *adductor mandibulae, pars malaris* (Ch. 43, State 1).

– *Levator operculi posterior* present (Ch. 52, State 1; reversed to State 0 in *Hypopygus*).

– Insertion of *levator operculi* on a dorsal crest on lateral surface of opercle (Ch. 53, State 1).

– R-Avn nerve lateral relative to *levator operculi anterior* or its anterior fibers (Ch. 54, State 1; reversed to State 0 in Eigenmanniinae).

Gymnotidae

– Origin of *stegalis* including frontal (Ch. 20, State 1).

– *Segmentum mandibularis* absent (Ch. 27, State 1; convergent in *Archolaemus*, Sternarchorhynchinae and in Clade *Iracema* + *Gymnorhamphichthys* + *Rhamphichthys*).

– Origin of *adductor hyomandibulae* including sphenotic (Ch. 55, State 1).

Gymnotus

– Origin of *levator arcus palatini* twice that of insertion (Ch. 40, State 3).

Electrophorus

– Origin of *levator arcus palatini* not including frontal (Ch. 38, state 0; reversal of State 1 in Clade Gymnotiformes + Siluriformes; also reversed in Clade *Archolaemus* + *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– *Levator arcus palatini* subdivided in two sections (Ch. 41, State 1).

– Anteromesial fibers of *levator arcus palatini* at insertion lateral to *adductor mandibulae, pars malaris* (Ch. 44, State 1; convergent in Clade *Orthosternarchus* + *Sternarchorhamphus*).

– Anterolateral fibers of *levator arcus palatini* approximately straight relative to the horizontal arm of preopercle, forming angle of ca. 90° relative to the longitudinal axis of head (Ch. 46, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; reversed also in Eigenmanniinae, Sternarchorhynchinae and Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– *Levator arcus palatini* overlapping pterosphenoid only at posterior margin (Ch. 47, State 0, reversal of State 1 in Clade Siluriformes + Gymnotiformes).

– *Dilatator operculi* divided into two sections (Ch. 49, State 1).

Sternopygoidei

– Origin of *stegalis* including pterosphenoid (Ch. 21, State 1; reversed to State 0 in *Gymnorhamphichthys*, *Porotergus*, *Pariosternarchus*, *Parapteronotus* and Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– Insertion of *adductor arcus palatini* on dorsolateral and median portion of endopterygoid, reaching middle of bone (Ch. 37, State 1; reversed to State 0 in *Gymnorhamphichthys*).

Rhamphichthyoidea

– *Malaris* inserting on antorbital (Ch. 6, State 1).

Hypopomidae

– Origin of *levator arcus palatini* wider than its insertion, up to 150% width insertion (Ch. 40, State 1; modified into State 2 in *Sternopygus* and in *Rhabdolichops*).

Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*

– *Rictalis* and *stegalis* partially continuous, forming *ricto-stegalis* (Ch. 2, State 1)

– Origin of *stegalis* not including sphenotic (Ch. 18, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in Eigenmanniinae, *Porotergus* and *Pariosternarchus*).

– *Segmentum mandibularis* absent (Ch. 27, State 1; convergent in *Archolaemus* and Sternarchorhynchinae).

– Anterolateral fibers of *levator arcus palatini* oriented approximately straight relative to the horizontal arm of preopercle, forming an angle of ca. 90° relative to the longitudinal axis of head (Ch. 46, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in *Electrophorus*, Eigenmanniinae and Sternarchorhynchinae).

Gymnorhamphichthys

– Origin of *stegalis* not including pterosphenoid (Ch. 21, State 0; reversal of State 1 in Sternopygoidei; also reversed in *Porotergus*, *Pariosternarchus*, *Parapteronotus* and Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– Insertion of *adductor arcus palatini* limited to dorsolateral portion of endopterygoid, not extending beyond middle of bone (Ch. 37, State 0; reversal of State 1 in Sternopygoidei).

Steatogeninae

No myological synapomorphies found.

Hypopygus

– *Levator operculi posterior* absent (Ch. 52, State 0; reversal of State 1, in Clade Siluriformes + Gymnotiformes).

Steatogenys

– Insertion of *segmentum mandibularis* restricted to anguloarticular (Ch. 29, State 2).

– *Dilatator operculi* lateral to *levator arcus palatini*, covering anterior half of latter (Ch. 45, State 0).

– Origin of *levator operculi* including hyomandibula (Ch. 51, State 1; convergent in Eigenmanniinae).

Sternopygoidea

– Attachment of ventrolateral fibers of *rictalis* restricted to anterior portion of preopercle, not extending beyond preopercular fossa (Ch. 16, State 1).

Sternopygidae

– *Malaris* inserting on infraorbital 1+2 (Ch. 7, State 1).

– Connection of *malaris* fibrous (Ch. 12, State 1).

– Transverse ligament well differentiated (Ch. 31, State 1).

Sternopyginae

– Origin of *levator arcus palatini* including pterosphenoid (Ch. 39, State 1; convergent in *Rhabdolichops* and *Adontosternarchus*).

– Origin and insertion of *levator arcus palatini* equally wide (Ch. 40, State 2; convergent in *Rhabdolichops*).

Eigenmanniinae

– Origin of *stegalis* not including sphenotic (Ch. 18, State 0; reversal of State 1, in Clade Siluriformes + Gymnotiformes; also reversed in Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*, Eigenmanniinae, *Porotergus* and *Pariosternarchus*).

– *Levator arcus palatini* overlapping posterior third of pterosphenoid (Ch. 47, State 3)

– Origin of *levator operculi* including hyomandibula (Ch. 51, State 1; convergent in *Steatogenys*).

– R-Avn nerve entirely mesial to *levator operculi* (Ch. 54, State 0; reversal of State 1 in Gymnotiformes).

Clade *Archolaemus* + *Distocyclus* + *Eigenmannia* + *Rhabdolichops*

– Origin of *levator arcus palatini* not including frontal (Ch. 38, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in *Electrophorus*).

– Anterolateral fibers of *levator arcus palatini* oriented approximately straight relative to the horizontal arm of preopercle, forming ca. 90° angle relative to longitudinal axis of head (Ch. 46, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in *Electrophorus*, “Rhamphichthyidae” and Sternarchorhynchinae).

Archolaemus blax

– *Malaris* totally overlapping *stegalis* (Ch. 24, State 1).

– *Segmentum mandibularis* absent (Ch. 27, State 1; convergent in Sternarchorhynchinae).

– Origin of *adductor operculi* not including prootic (Ch. 56, State 1).

Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*

– Origin of *stegalis* not including pterosphenoid (Ch. 21, State 0; reversal of State 1 in Sternopygoidei; also reversed in *Gymnorhamphichthys*, *Pariosternarchus*, *Porotergus* and *Parapteronotus*).

Eigenmannia

No myological synapomorphies found.

Rhabdolichops

– Lateral fibers of *rictalis* inserting on posterior margin of anguloarticular (Ch. 17, State 1; convergent in *Adontosternarchus* and *Parapteronotus*).

– *Segmentum mandibularis* contacting entire dorsal margin of Meckel´s cartilage (Ch. 28, State 1; convergent in *Parapteronotus*).

– Origin of *levator arcus palatini* including pterosphenoid (Ch. 39, State 1; convergent in *Sternopygus* and *Adontosternarchus*).

– Origin and insertion of *levator arcus palatini* equally wide (Ch. 40, State 2; convergent in Sternopyginae).

Apteronotidae

– *Malaris* entirely differentiated into a lateral layer of buccopalatal membrane (Ch. 14, State 1).

– Length of endomaxilar ligament equal to that of fibrous portion of *malaris* (Ch. 32, state 1; reversed to State 0 in Clade *Compsaraia* + "*Apteronotus*" gr. *bonapartii* and *Pariosternarchus*).

Adontosternarchus

– Insertion of ventrolateral fibers of *malaris* inserting on posterior margin of dentary and anguloarticular (Ch. 9, State 1).

– Lateral fibers of *rictalis* inserting on posterior margin of anguloarticular (Ch. 17, State 1; convergent in *Rhabdolichops* and *Parapteronotus*).

– *Stegalis* positioned laterally to middle and posterior portion of *adductor arcus palatini* (Ch. 23, State 2; convergent in Clade *Orthosternarchus tamandua* + *Sternarchorhamphus muelleri*).

– Origin of *levator arcus palatini* including pterosphenoid (Ch. 39, State 1; convergent in *Rhabdolichops* and *Sternopyginae*).

Clade *Apteronotus* + *Compsaraia* + "*Apteronotus*" gr. *bonapartii* + *Porotergus gimbeli* + *Tenebrosternarchus* + *Sternarchogiton*

– *Malaris* positioned laterally to dorsal portion of *rictalis* and to ventromedial portion of *stegalis*, overlapping both almost entirely (Ch. 25, State 1; convergent in *Pariosternarchus*).

Clade *Compsaraia* + "*Apteronotus*" gr. *bonapartii*

– Length of endomaxillary ligament shorter than 2/3 length of fibrous portion of *malaris* (Ch. 32, State 0; reversal from State 1 in Apteronotidae; also reversed in *Pariosternarchus*).

“*Apteronotus*” gr. *bonapartii*

– *Malaris* entirely differentiated into *promalaris* and *retromalaris*, from origin to insertion (Ch. 13, State 3).

– Dorsal portion of *malaris* (*promalaris*) positioned dorsolaterally to dorsal portion of *rictalis* and *stegalis*, with its ventral region (*retromalaris*) ventrolateral to dorsal portion of *rictalis* and *stegalis* (Ch. 25, State 3).

Porotergus gimbeli

– Origin of *stegalis* not including sphenotic (Ch. 18, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in Eigenmanniinae, *Pariosternarchus* and in Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– Origin of *stegalis* not including pterosphenoid (Ch. 21, State 0; reversal of State 1 in Sternopygoidei; also reversed in *Gymnorhamphichthys*, *Pariosternarchus*, *Parapteronotus* and Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

Clade *Tenebrosternarchus* + *Sternarchogiton*

– *Malaris* with median and dorsoposterior regions of *promalaris* differentiated from its ventromedial region and from *retromalaris* (Ch. 13, State 2).

– *Dilatator operculi* positioned laterally to *levator arcus palatini*, covering less than anterior half of latter (Ch. 45, State 1; convergent in *Orthosternarchus*).

Sternarchellini

No myological synapomorphies found.

Pariosternarchus amazonensis

– Origin of *stegalis* not including sphenotic (Ch. 18, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; also reversed in Eigenmanniinae, *Porotergus* and in Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– Origin of *stegalis* not including pterosphenoid (Ch. 21, State 0; reversal of State 1 in Sternopygoidei; also reversed in *Porotergus*, *Gymnorhamphichthys*, *Parapteronotus* and Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– *Malaris* positioned laterally to dorsal portion of *rictalis* and to ventromedial portion of *stegalis*, overlapping both almost entirely (Ch. 25, State 1; convergent in Clade *Apteronotus* + *Compsaraia* + “*Apteronotus*” gr. *bonapartii* + *Porotergus gimbeli* + *Tenebrosternarchus* + *Sternarchogiton*).

– Length of endomaxillary ligament shorter than 2/3 length of fibrous portion of *malaris* (Ch. 32, State 0; reversal from State 1 in Apteronotidae; also reversed in Clade *Compsaraia* + “*Apteronotus*” gr. *bonapartii*).

Sternarchella

– Mesial fibers of *malaris* inserting on posterior margin of anguloarticular (Ch. 10, State 1).

– *Malaris* inserting on mesethmoid and premaxilla (Ch. 11, State 1).

– Endomaxillary ligament dorsolateral to autopalatine (Ch. 33, State 1).

– Origin of dorsal fibers of *dilatator operculi* on sphenotic and pterotic overlapping the bones completely and extending to suture with parietal (Ch. 50, State 1).

Sternarchorhynchinae

– *Segmentum mandibularis* absent (Ch. 27, State 1; convergent in Gymnotidae, *Archolaemus*, and Clade *Iracema* + *Gymnorhamphichthys* + *Rhamphichthys*).

– Anterolateral fibers of *levator arcus palatini* approximately straight relative to the horizontal arm of preopercle, forming angle of ca. 90° relative to the longitudinal axis of head (Ch. 46, State 0; reversal of State 1 in Clade Siluriformes + Gymnotiformes; reversed also in *Electrophorus*, Eigenmanniinae and Clade *Gymnorhamphichthys* + *Iracema* + *Rhamphichthys*).

– *Levator arcus palatini* overlapping half of pterosphenoid (Ch. 47, State 2).

Clade *Orthosternarchus tamandua* + *Sternarchorhamphus muelleri*

– *Stegalis* positioned laterally to middle and posterior portion of *adductor arcus palatini* (Ch. 23, State 2; convergent in *Adontosternarchus*).

– Anteromesial fibers of *levator arcus palatini* at insertion lateral to *adductor mandibulae, pars malaris* (Ch. 44, State 1; convergent in *Electrophorus*).

Orthosternarchus tamandua

– Intermuscular bones present in *adductor mandibulae, segmentum facialis* (Ch. 26, State 1).

– *Dilatator operculi* positioned laterally to *levator arcus palatini*, covering less than anterior half of latter (Ch. 45, State 1; convergent in Clade *Tenebrosternarchus* + *Sternarchogiton*).

Sternarchorhynchus

– *Stegalis* inserting on posteromesial margin of dentary (Ch. 33, State 1).

Parapteronotus hasemani

– Lateral fibers of *rictalis* inserting on posterior margin of anguloarticular (Ch. 17, State 1; convergent in *Adontosternarchus* and *Rhabdolichops*).

– Origin of *stegalis* not including pterosphenoid (Ch. 21, State 0; reversal of State 1 in Sternopygoidei; also reversed in *Porotergus*, *Gymnorhamphichthys*, *Pariosternarchus* and Clade *Distocyclus* + *Eigenmannia* + *Rhabdolichops*).

– *Segmentum mandibularis* contacting entire dorsal margin of Meckel´s cartilage (Ch. 28, State 1; convergent in *Rhabdolichops*).

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AUTHORS' CONTRIBUTION

Luiz Antônio Wanderley Peixoto: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

Mário de Pinna: Conceptualization, Data curation, Methodology, Project administration, Resources, Supervision, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENTS

This study was carried out under approval of the Animal Care and Use Committee (ACUC) of the Instituto de Biociências, Universidade de São Paulo (Project #226/2015; CIAEP #01.0165.2014). The research employed only ethanol-preserved specimens deposited in museums and did not involve animal experimentation or fossil examination.

COMPETING INTERESTS

The authors declare no competing interests.

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