



Museu de Zoologia
Universidade de São Paulo

Vinícius Corrêa Espíndola

**Phylogenetic relationship of the
Anguilliformes (Teleostei: Elopomorpha)
with an emphasis in cephalic morphology**

**Relações filogenéticas em Anguilliformes (Teleostei:
Elopomorpha) com ênfase na morfologia cefálica**

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Advisor: Mario César Cardoso de Pinna, PhD.

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ABSTRACT

Anguilliformes are a group of Teleostei fish with more than 1,000 species and 20 families. They were commonly known as eels, congers, and morays. The lack of consensus about the relationship hypotheses of a group in the last 40 years has mostly resulted from a lack of comprehensive studies bringing all families. Our study exposed the proposal for an integrated study of osteology and cephalic muscle and gill arches as a promising new source of characters to understand the intrarelationships of families which compound the order. With 108 terminal taxa, including representants of the 20 Anguilliformes families, the present study realized the most extensive morphological analysis ever made with the group, totalizing 248 phenotypic characters. The results generated a topology which the Anguilliformes order had strong support with 28 synapomorphies, indicating *Protanguilla* basal position been a sister group of remaining members of the order. One clade compound by long snout eels presented for the first time on the present study, which “Saccopharyngoidei” shared nine characteristics with Nemichthyidae. Synphobranchidae grouped with “Chlopsidae” (not recovered as a monophyletic group), Myrocongridae and Muraenidae, a new arrangement with support of two synapomorphies non-ambiguous. The present work also clarified the homology problem, such as palatine absent in Anguilliformes, opercle sutured to hyomandibular, interopercle associated to *levator operculi*, *adductor mandibulae segmentum facialis* and *adductor hyomandibulae* (= elevator muscles) identified in Saccopharyngoidei. Moreover, we observed the presence of some structure, still present in the remaining representants, not only found in *Protanguilla*, as pre-maxillae in *Derichthys* and gill rakers in Heterocongrinae. The results pointed out that muscles characters were an essential source in clarifying Anguilliformes relationships.

RESUMO

Os Anguilliformes são um grupo de peixes teleósteos, com cerca de 1000 espécies e 20 famílias, popularmente conhecidos como enguias, congros e moreias. A ausência de consenso sobre as hipóteses de relações no grupo, durante os últimos 40 anos, decorreu em grande medida da falta de estudos abrangentes que reunissem todas as famílias. Nossa pesquisa expõe a proposta de um estudo integrado de osteologia e musculatura cefálica e dos arcos branquiais, como uma nova e promissora fonte de caracteres para entender as relações entre as famílias que compõem a ordem. Com 108 táxons terminais, incluindo representantes de todas as vinte famílias de Anguilliformes, o presente estudo realizou a maior análise morfológica já feita com o grupo, totalizando 248 caracteres fenotípicos. Os resultados geraram uma topologia na qual a ordem Anguilliformes tem um grande suporte de 28 sinapormorfias, indicando a posição basal de *Protanguilla* sendo grupo irmão dos demais membros da ordem. Um clado composto por enguias de focinho longo foi apresentado pela primeira vez no atual estudo, na qual os “Saccopharyngoidei” tiveram nove características compartilhadas com Nemichthyidae. Os Synaphobranchidae foram agrupados com “Chlopsidae” (não recuperado como grupo monofilético), Myrocongridae e Muraenidae, um arranjo inédito para a ordem com suporte de duas sinapomorfias não ambíguas. O presente estudo ainda esclareceu problemas de homologia, como a ausência de palatino em Anguilliformes, opérculo suturado a hiomandíbula, interopérculo associado ao *levator operculi*, *adductor mandibulae segmentum facialis* e *adductor hyomandibulae* identificados em Saccopharyngoidei. Além disso, observamos a presença de algumas estruturas, ainda presentes nos demais representantes, não somente em *Protanguilla*, como: pré-maxilla presente em *Derichthys* e rastros branquiais em Heterocongrinae. O resultado aponta que os caracteres musculares foram uma fonte importante nos esclarecimentos sobre as relações de parentesco de Anguilliformes.

LISTA DE FIGURAS

Figure 1 – Morphological variation in six families of Anguilliformes: A, Serrivomeridae (photo from fishbiosystem); B, Nemichthyidae (photo from Wikipedia); C, Cyematidae (photo from Andrew Wilkinson); D, Synaphobranchidae (photo from Fishes of Australia); E, Muraenidae (photo from gooddive.com); F, Saccopharyngidae (photo from digitalfishlibrary.org).....233

Figure 2 – Illustrations of leptocephalus larvae of meso- and bathypelagic eels families: A, *Cyema*; B, "Leptocephalus holti"; C, Monognathidae (metamorphic stage); D, Unidentified saccopharyngiform; E, *Saccopharynx*; F, *Eurypharynx*; G, *Serrivomer beani*; H, *Nemichthys curvirostris*; I, *Avocettina infans*; J, *Derichthys serpentinus*; K, *Nessorhamphus ingolfianus*. Illustrations A, C, D, and F to K are modified from Böhlke (1989), B is modified from Smith & Miller (1996), and E is modified from Castle (1984).....234

Figure 3 – Hypotheses of the relationships of Anguilliformes inferred from morphological characters according to (A) Morphological phylogeny of Patterson and Rosen (1977), (B) morphological phylogeny of Robins (1989), and (C) combined morphological and molecular phylogeny (12S, 16S, 28S) of Forey *et al.* (1996); (figure modified from Santini *et al.* 2014).....235

Figure 4 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Belouze (2002); most parsimonious analysis based on osteology and morphology data, including six Cretaceous fossil and Osteoglossomorpha.....235

Figure 5 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters, according to Johnson *et al.* (2012). Time tree of Anguilliformes and outgroup estimated from molecular-clock analysis. The analysis comprises molecular and morphological.....237

Figure 6 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to from Obermiller & Pfeifer (2003) most parsimonious (MP) tree for the combined 12S and 16S rRNA data set (Branch and Bound algorithm).....239

Figure 7 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Filleul & Lavoué (2002), using on molecular data from rRNA 18S, 16S and 12S a.....240

Figure 8 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Tang & Fielitz (2012) based on likelihood score. Muraenidae highlighted by the authors.....241

Figure 9 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Santini *et al.* (2013). Maximum likelihood phylogeny of Anguilliformes.....242

Figure 10 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters, according to Chen *et al.* (2014). The analysis performed was a maximum-likelihood tree of the combined dataset (3 nuclear and 3 mitochondrial genes, 4,601 bp in length).....243

Figure 11 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Poulsen <i>et al.</i> (2018). Mitogenomic phylogenetic tree of 79 taxa of the Elopomorpha based on 13 protein-coding genes in the mitochondrial genome (ML and Bayesian analyses, 11,700 base pairs)	244
Figure 12 – Neurocranium of (A) <i>Cyema atrum</i> USNM 208058 and (B) <i>Echidna nebulosa</i> BMNH uncat in dorsal view.....	246
Figure 13 – Neurocranium of (A) <i>Serrivomer beami</i> , USNM 271046, and (B) <i>Protanguilla palau</i> , USNM 396016, in dorsal view. Scale bar: 1 mm.....	247
Figure 14 – Neurocranium of (A) <i>Echidna nebulosa</i> , BMNH uncat., and (B) <i>Protanguilla palau</i> , USNM 396016, in lateral view. Scale bar: 1 mm.....	248
Figure 15 – Neurocranium of (a) <i>Protanguilla palau</i> , USNM 396016, and (b) <i>Simenchelys parasiticus</i> , USNM 326917, midportion lateral view. Caudal Skeleton of (c) <i>P. palau</i> , USNM 396016, (d) <i>Anguilla rostrata</i> , USNM 106563, in lateral view. PU2, preural centrum 2; H, hypurals (Photo was taken from Johnson <i>et.</i> , 2012: Figure 4).....	249
Figure 16 – Jaw of <i>Anguilla rostrata</i> , USNM 106563, in ventral view. (Photo was taken by Ai Nonaka).....	250

Figure 17 – Suspensorium of <i>Synaphobranchus</i> sp., USNM uncat, in lateral view. (Photo taken by Ai Nonaka).....	251
Figure 18 – Suspensorium of <i>Serrivomer beami</i> , USNM 271046, in lateral view.....	251
Figure 19 – Neurocranium of <i>Elops saurus</i> , USNM 271046, in lateral view (Photo modified from Ridewood, 1904: Fig. 8c).....	252
Figure 20 – Suspensorium of <i>Elops saurus</i> in lateral view. (Photo modified from Ridewood, 1904: Fig. 10c).....	252
Figure 21 – Neurocranium of <i>Derichthys serpentinus</i> , USNM 315025, in dorsal view.....	253
Figure 22 – Suspensorium of <i>Simenchelys parasitica</i> , USNM 326917, in lateral view.....	253
Figure 23 – Upper jaw of (A) <i>Bathydroconger vicinus</i> , USNM 179070 and (B) <i>Coloconger meadi</i> , USNM 193572, in ventral view, showing the connection between ectopterygoid and ethmovomer.....	254
Figure 24 – Cephalic and anterior portion of <i>Anguilla rostrata</i> , USNM 106563, in lateral view (Photo taken by Ai Nonaka).....	255
Figure 25 – Jaw of <i>Protanguilla palau</i> , USNM 396016, in lateral view (Photo taken by Ai Nonaka).....	255

Figure 26 – Suspensorium of <i>Protanguilla palau</i> USNM 396016, in lateral view.	256
Figure 27 – Hyoid arch with the musculature of <i>Albula vulpes</i> , USNM 218871, in dorsal view.....	257
Figure 28 – Hyoid arch of (A) <i>Cyema atrum</i> , ANSP 143871, (Leptocephalus), and (B) <i>Anarchias similis</i> , USNM 320964, in dorsal view.....	257
Figure 29 – Branchial arches of <i>Simenchelys parasitica</i> , USNM 326917, in dorsal view. Scale bar: 2 mm.....	258
Figure 30 – Branchial arches (ventral elements) of <i>Protanguilla palau</i> , USNM 396016, in dorsal view (Photo taken by Ai Nonaka).....	259
Figure 31 – Branchial arches (dorsal elements) of <i>Protanguilla palau</i> , USNM 396016, in dorsal view (Photo taken by Ai Nonaka).....	259
Figure 32 – Neurocranium of <i>Aldrovandia affinis</i> (Kanehira <i>et al.</i> 2012: figure 2) in dorsal (above), lateral (middle) and ventral (below) views. AP, anterior process; AVP, anteroventral process; BO, basioccipital; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; ET, ethmoid; F, frontal; LAP, lateral process; LP, lower process; PA, parietal; PAS, parasphenoid; PDP, posterodorsal process; PR, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; UP, upper process; V, vomer; VP, ventral process. Scale bar: 5 mm.....	260

Figure 33 – Radiographic image of <i>Gorgasia thamani</i> , Paratype, NSMT-P 68327, showing the number of vertebrae. Scale bar: 10 mm.....	261
Figure 34 – Radiographic image of <i>Ophichthus obtusus</i> , Holotype, NSMT-P 106574, showing the number of vertebrae. Scale bar: 10 mm.....	262
Figure 35 – Radiographic image of <i>Protanguilla palau</i> , USNM 396016, showing the number of vertebrae. Scale bar: 10 mm.....	262
Figure 36 – Neurocranium of † <i>Anguillavus quadripinnis</i> in lateral view (Belouze, 2003: Fig. 3).....	263
Figure 37 – Pelvic girdle of † <i>Anguillavus quadripinnis</i> in lateral view (Belouze, 2003: Fig. 14).....	263
Figure 38 – Suspensorium of † <i>Anguillavus quadripinnis</i> in lateral view (Belouze, 2002: Fig. 10).....	264
Figure 39 – Branchial arches of <i>Gorgasia punctata</i> , CAS 20752, in lateral view.....	264
Figure 40 – Lower jaw and <i>adductor mandibulae</i> complex of (A) <i>Polyacanthonothus rissoanus</i> , VIMS 4552, (B) <i>Albula vulpes</i> , MNRJ 37303, (C) <i>Aldrovandia phalacra</i> , VIMS 8390, and (D) <i>Elops saurus</i> , MNRJ 40531, in medial view.....	265

Figure 41 – Lower jaw and <i>adductor mandibulae</i> of (A) <i>Coloconger meadi</i> , UF 211407, (B) <i>Protanguilla palau</i> , USNM 396016, and (C) <i>Derichthys serpentinus</i> , USNM 444953, in medial view. <i>AM pars epistegalis</i> and <i>AM pars substegalis</i> highlighted.....	266
Figure 42 – Anterior part of the body of <i>Heteroconger camelopardalis</i> , MZUSP 57611, left side view.....	267
Figure 43 – Anterior part of the body of <i>Gymnomuraena zebra</i> , SIO 62-8, left side view....	268
Figure 44 – Anterior part of the body of <i>Albula vulpes</i> , MNRJ 37303, right side view.....	269
Figure 45 – Anterior part of the body of <i>Cyema atrum</i> , SIO 66-546, right side view.....	270
Figure 46 – Neurocranium of <i>Acromycter perturbator</i> , MNRJ 27115, in dorsal view.....	271
Figure 47 – Anterior part of the body of <i>Cyema atrum</i> , ANSP uncat, in lateral view.....	272
Figure 48 – Hyomandibular and muscles associated with <i>Eurypharynx pelecanoiodes</i> , SIO 73-43, in lateral view.....	273
Figure 49 – Branchial arches of <i>Kaupichthys</i> sp., USNM 444952, in ventral view.....	274

Figure 50 – Branchial arches of <i>Nemichthys scolopaceus</i> , USNM 358874, in ventral view.....	275
Figure 51 – Lower jaw and associated muscles of <i>Cyema atrum</i> , SIO 66-546, lateral view.....	276
Figure 52 – Anterior part of the body of <i>Neocyema</i> sp., MCZ 165900, in lateral view.....	277
Figure 53 – Anterior part of the body <i>Coloconger meadi</i> , UF 211407, in lateral view.....	278
Figure 54 – Anterior part of the body <i>Nemichthys scolopaceus</i> , ANSP 158461, in lateral view.....	279
Figure 55 – Anterior part of the body of <i>Pythonichthys asodes</i> , UF 228629, in lateral view.....	280
Figure 56 – Anterior part of the body of <i>Simenchelys parasitica</i> , SIO 05-11, in lateral view.....	281
Figure 57 – Anterior part of the body of <i>Pythonichthys asodes</i> , UF 228629, in lateral view.....	282
Figure 58 – Branchial arches of <i>Coloconger meadi</i> , USNM 443687, in dorsal view.....	283

Figure 59 – Branchial arch of <i>Serrivomer</i> sp. USNM 443689, in dorsal view.....	284
Figure 60 – Branchial arches of (A) <i>Albula vulpes</i> , USNM 218871, and (B) <i>Netastoma malanurum</i> , USNM 405025, in ventral view.....	285
Figure 61 – Branchial arches of (A) <i>Cyema atrum</i> , SIO66-546, and (B) <i>Stemodidium hypomelas</i> , ANSP 152332, in ventral view.....	286
Figure 62 – Scales of <i>Protanguilla palau</i> , USNM 396016.....	287
Figure 63 – Scales of <i>Anguilla anguilla</i> (Pankhurst, 1982: Figure 6b).....	287
Figure 64 – Strict consensus tree resultant from Implicit Weighting implied against homoplasy under K=7. Highlighted clades: Elopiformes (yellow), Albuliformes (green), Notacanthiformes (blue), Anguilliformes (red).....	288
Figure 65 – Strict consensus tree resultant from Implicit Weighting implied against homoplasy under K=7 (TNT graphics).....	289
Figure 66 – Interrelationships of the Anguilliformes, strict consensus tree resultant from Implicit Weighting implied against homoplasy under K=7.....	291

CONTENTS

1. INTRODUCTION.....	21
1.1 History.....	23
1.1.1 – Morphological and Anatomical Analyses.....	23
1.1.2 – Molecular Analyses.....	28
2. SCIENTIFIC JUSTIFICATION.....	30
3. OBJETIVES.....	31
4. MATERIALS AND METHODS.....	32
4.1 – General Anatomy.....	32
4.2 – Illustrations.....	32
4.3 – Phylogenetic Analysis.....	33
4.4 – Muscle dissection.....	34
4.5 – Material Examined.....	36
4.6 – List of Used Abbreviations for Anatomical Structures.....	42
5. RESULTS.....	44
5.1 – Osteological Characters.....	44
5.1.1 – Neurocranium.....	44
5.1.2 – Sensory canals.....	56
5.1.3 – Suspensorium.....	59
5.1.4 – Opecular Series.....	76
5.1.5 – Ventral elements of the hyoid arch.....	83
5.1.6 – Branchial arches.....	93
5.1.7 – Pectoral Girdle and paired fins.....	106
5.1.8 – Dorsal, anal and caudal fins elements.....	118
5.1.9 – Vertebrates and spines bones.....	130

5.2 – Musculature.....	141
5.2.1 – Cephalic Muscles.....	141
5.2.2 – Opercular Muscles.....	154
5.2.3 – Hyoid Muscles.....	158
5.2.4 – Branchial Muscles – Dorsal.....	160
5.2.5 – Branchial Muscles – Ventral.....	174
5.3 – General Characters.....	182
6. DISCUSSION.....	193
7. CONCLUSION.....	214
8. LITERATURE CITED.....	216
9. FIGURES.....	233
10. APPENDIX - QUALITATIVE CHARACTERS.....	293

1. INTRODUCTION

Elopomorpha is composed of Elopiformes (tarpons), Albuliformes (bony fishes), Notacanthiformes (spiny eels) and Anguilliformes (eels, morays, congers, and gulper eels), the group occurs from tropical regions to polar seas, with most species marine or estuarine. The Anguilliformes comprises 1,009 species and 20 families in 156 genera (Fricke *et al.*, 2019), being the most heterogeneous subgroup of Elopomorpha, comprising about 90% of its species (Figures 1 and 2). Anguilliformes occur in a broad array of habitats, including brackish water, reef environments, fossorial benthic, pelagic, and abyssal (Helfman *et al.*, 2009). Wiley & Johnson (2010) compiled six synapomorphies corroborating the Anguilliformes as a monophyletic group.

Feeding habits of anguilliform are as diverse as their anatomy. Although typically carnivorous, they include an enormous variety of resources, including zooplankton (*e.g.*, *Heteroconger*, *Gorgasia*), crustacea and mollusks (*e.g.*, *Echidna*, *Eurypharynx*), fish and cephalopods (*e.g.*, *Gymnothorax*, *Muraena*), or generalist or necrophages (*e.g.*, *Anguilla*, *Simenchelys*) (Helfman *et al.*, 2009; Nelson *et al.*, 2016). Their feeding mechanism was the subject of investigation, for example, some species of *Echidna* have the pharyngeal jaw system (a specialization of the fourth arch) into a shell-crushing mechanism (Mehta & Wainwright, 2008). Other species can project their pharyngeal jaw as a functional second set of jaws to help food displacement to the esophagus (Mehta & Wainwright, 2007; Mehta & Wainwright, 2008; Johnson, 2019).

The bizarre anatomy of gulper eels (Saccopharyngoidei) has attracted attention. Both *Eurypharynx* and *Saccopharynx* can swallow prey with their tremendously swollen jaws, which can be over eight times the length of the skull (Nielsen *et al.*, 1989). The Saccopharyngoidei specializations are so extreme that Tchernavin (1947) expressed doubts about the taxa therein being bony fishes. Helfman *et al.* (2009) noted that Saccopharyngoidei lacks a multitude of

bones and bony complexes, such as opercular bones, symplectic, branchiostegals, maxillae, pre-maxillae, vomer, parasphenoid, scales, pelvic and pectoral girdles. The Monognathidae have additional unique specializations such as rostral fang and poisonous glands Bertelsen & Nielsen (1987).

The discovery of *Protanguilla palau*, prompted the anatomical diagnosis of an additional ten synapomorphies (two were previously maintained) for the Anguilliformes (Johnson *et al.*, 2012; Springer & Johnson, 2015):

1. body scales absent or embedded and arranged in a basket-weave fashion
2. Ethmoid fused with vomer
3. Pterotic extends anteriorly above prootic to contact pterosphenoid
4. Dermopalatine and autopalatine absent
5. Pectoral girdle displaced posteriorly
6. First pharyngobranchial absent and pharyngobranchials without uncinata processes
7. Gill arches free from braincase and displaced posteriorly
8. Opercular series characterized by a distinctive pattern
9. Uppermost branchiostegals curving dorsally behind
10. Posterior ceratohyal almost equal to or longer than anterior ceratohyal
11. Branchiostegals more numerous on the posterior than on the anterior ceratohyals
12. Posteriormost one to four branchiostegals with spatulate expansions distally
13. Dorsal part of suture between anterior and posterior ceratohyals deflected posteriorly
14. Interhyal absent
15. Angular, articular and retroarticular fused into a single bone
16. entopterygoid absent;
17. Post-temporal absent
18. Two pairs of upper pharyngeal tooth plates present and autogenous (not fused to pharyngobranchials)

19. epurals absent;
20. one or no hypohyals;
21. dorsal and anal fins confluent;
22. less than eight rays in each caudal-fin lobe;
23. pyloric caecum absent;
24. nasal opening considerable separated, the posterior slightly anterior to the orbit;
25. branchial membrane united over isthmus, restricted opening;
26. Hypobranchial 3 cartilaginous or absent; accessory element 4 absent (lost independently in *Albula* and *Lipogenys*).

1.1 – History

1.1.1 – Morphological and Anatomical Analyses

One of the first studies about anguilliform osteology and morphology is Cope (1871, 1884), who named them Apoda subdivided into two groups: Enchelycephali (Anguillidae) and Colocephali (other eels, including Eurypharyngidae). Gill (1889a, b, 1890a, b, c, e) made a great series of publication on the anatomy and relationships of Muraenidae, Anguillidae, Muraenesocidae, Synphobranchidae, and Notacanthiformes. Gill & Ryder (1883, 1884) published two paper on saccopharyngoids, focused mostly on general anatomy and relationships with Lyomeri.

Regan (1909) proposed two new groups, the Halosauridae, and Notacanthidae + *Lipogenys* (=Heteromi). In the same publication, anguilloids (Apodes) were diagnosed by the lack of premaxillae, and anguimorph body, a fixed quadrat, the maxilla articulating with a fixed

ethmo-vomer, and the pectoral girdle free from the neurocranium. Regan (1909) mentioned the presence of pre-maxillae in *Derichthys* and was “skeptical” about its inclusion in Anguilliformes, despite their similarities. Regan (1909) also proposed that Saccopharyngoidei (=Lyomeri), in lacking parietals, and having transverse processes ankylosed with vertebral centra and restricted gill-openings based on hyomandibular position, and broad skull, are derived from Apodes. Regan (1912) reviewed his character and proposed an identification key to the 16 families of Apoda. The author also positioned Saccopharyngoidei in Lyomeri, divided Anguilliformes (=Apoda) into two suborders: Anguilloidei and Nemichthyoidei.

Bertin (1932a, b, 1934, 1936, 1938) published a series of works on adults and larvae of Anguilliformes, mostly saccopharyngoids and described a new family, Monognathidae. The author drew an interesting parallel between the jaw mechanism in *Saccopharynx* and snakes. Saccopharyngoids (=Lyomeri) was the object of a study by Tchernavin (1947), with a focus on bones, muscles, branchial arches, and viscera, with ensuing implications for phylogenetic relationships.

Berg (1940) changed Apoda to Anguilliformes, and Saccopharyngiformes to Lyomeri. The same author divided Anguilliformes into two suborders: Anguilloidei (ventral fin absent) and Nemichthyoidei (supraoccipital absent, supracleithrum absent, and scapula and coracoid unossified).

Trewavas (1933) did substantial research on different families of eels and proposed a new classification of fresh eels. Greenwood *et al.* (1966) proposed four anguilliform groups: Anguilloidei, Saccopharyngoidei, Elopiformes (Elopoidei and Albuilloidei) and Notacanthiformes, and first used the name Elopomorpha. Later, Patterson & Rosen (1977) included Saccopharyngoidei in Anguilliformes, corroborating Elopomorpha as a monophyletic group and discussing the relationship among the orders (Figure 3a). Lauder & Liem (1983) proposed Anguilliformes based on the following features: (1) leptocephalus larvae; (2) angular and retroangular fused on lower jaw; and (3) rostral and prenasal ossicles. The Elopomorpha

was divided in Albuloidei, with Albulidae + (Notacanthidae + Halosauridae) and Anguilloidei (Anguillidae + Saccopharyngoidei).

The extensive book publication about larvae generated three relevant studies about Elopomorpha and Anguilliformes were performed by (1984), Smith (1984) and Leiby (1984), which the first one raised some osteological characters. Castle (1984) pointed out the characters for Anguilliformes relationships leptocephalus nevertheless without an algorithm or cladogram, many of them overlapping characteristics. In another chapter, Smith (1984) raised larvae characters of Elopiformes, Noatacanthiformes, and Anguilliformes. Such a study was the first phylogenetic analysis using parsimony algorithm, with outstanding results. In this proposed, Serrivomeridae and Nemichthyidae formed a monophyletic group, another group formed by Muraenidae, Myrocongridae and Chlopsidae (=Xenocongridae), and additional clade with anguillids, moringuids, and heterenchelyids. Smith (1984) indicated that Colocongridae and Muraenosocidae share congrid characters, a similar hypothesis with Nettastomatids. Essential thorough research performed by Leiby (1984) was an extensive larvae examination, establishing a comprehensive anatomical feature among Ophichthidae species and increasing knowledge on leptocephalus structures development fusion, absence, or loss, such as pre-maxillae and ectopterygoid. Furthermore, that research provides a cladogram based on the light of the results of the leptocephalus of the 51 genera of ophichthids and corroborating the two subfamilies (Ophichthinae and Myrophinae) proposed by McCosker (1977).

Böhlke *et al.* (1989) provided taxonomic and osteological s of adults (part 1) and larvae (part 2) of Anguilliformes and Saccopharyngiformes. All families of Anguilliformes and Saccopharyngiformes were included, with identification keys, species diagnosis, and geographical distributions (Bertelsen *et al.*, 1989; McCosker *et al.*, 1989a, b; Robins & Robins, 1989a, b; Smith, 1989a, b, c, d, e, f, g, h; Smith *et al.*, 1989; Tighe, 1989). Robins (1989) raised 42 osteology and external morphological items, cited the Anguilliformes relationship with outgroup Elopomorpha, based on six synapomorphies, notwithstanding his survey not included Saccopharyngiformes within eels, nevertheless only four are synapomorphies (listed below).

However, it was not performance characters exhaustive searches, matrix analysis, or characters polarization. That contribution divided Anguilliformes into three suborders: Congroidei, with frontal bones, fused; Muraenoidei, with frontal bones, separated, branchial elements reduced, lateral line absent and scales absent; and Anguilloidei, with frontal separated. Saccopharyngiformes also was divided into two suborders: Cymatoidei, with lateral pores absent, relatively small and compressed body; and Saccopharyngoidei, with quadrate extremely long and pharynx extensible (Figure 3b).

Forey *et al.* (1996) listed morphological and molecular characters of Elopomorpha placing Saccopharyngoidei within Anguilliformes (Figure 3c). Forey *et al.* (1996) raised six synapomorphies for Anguilliformes:

1. extrascapular canal absent;
2. symplectic fused to quadrate;
3. branchial arches displaced posteriorly and free from neurocranium;
4. gill rakers absent;
5. pelvic girdles and fins absent;
6. body scales absent or embedded and arranged in basket-weave fashion.

In an unpublished thesis, Belouze (2002) compiled characters from many previous studies, including osteology, nerves, and circulatory system, in a total of 123 characters. The phylogenetic hypothesis included 30 Recent and 20 fossil anguilliforms, plus outgroup taxa (Figure 4). Shortly after that, Belouze *et al.* (2003) offered an extensive anatomical of †*Anguillavus quadripinnis* Hay, 1903, †*A. mazoni* and †*Luenchelys minimus*.

The first study on the cephalic musculoskeletal system in Anguilliformes was Eagderi (2010), an unpublished Ph.D. thesis. It included 67 specimens in seven different families: Anguillidae, Nettastomatidae, Heterenchelyidae, Congridae, Moringuidae, Ophichthidae and Eurypharyngidae.

Branchial arches in anguilliforms were studied by Nelson (1966, 1967), who suggested the recognition of three different lineages: Anguilloid, Synaphobranchoidei, and Congroidei. Nelson (1966) also recognized two subfamilies in Muraenidae: Muraninae (basibranchials and hypobranchials absent) and Uropterygiinae (basibranchials absent and only hypobranchials 1 and 2 present). Nelson (1967) described the muscles of five families in Anguilliformes (Congridae, Anguillidae, Moringuidae, Xenocongridae, and Muraenidae), reporting the presence of the retractor dorsal and ventral muscles in Congridae and a second insertion of the vertebrae associated with pharyngeal jaws in Muraninae.

Springer & Johnson (2004) published a comprehensive, detailed comparative anatomy of the dorsal branchial arches in various groups of bony fishes (Teleostei), including one species each of Congridae, Anguillidae, and Synaphobranchidae. The authors clarify various homology and nomenclatural problems.

Another unique and poorly explored clade is the pugnose eel *Simenchelys parasitica* Gill 1879 (family Synaphobranchidae, subfamily Simenchelyinae). That deep-water species has a unique behavior among Anguilliformes and is a parasite and scavenger. Eadgeri *et al.* (2016) offered detailed musculoskeletal anatomy and tissue analysis comparing *Ilyophis brunneus* Gilbert 1891 (Ilyophinae) and *Synaphobranchus brevidorsalis* Günther 1887 (Synaphobranchinae).

Mehta & Wainwright (2007a, b, 2008), based on species of Muraenidae, described the functional role of branchial arches as a second jaw (=pharyngeal jaw or raptorial jaw). The upper and lower tooth plates, pharyngobranchial, ceratobranchial and epibranchial of the fourth arch; the muscles associated as *levator internus* 4, *levator externus* 4, *obliquus dorsalis* 4, *rectus communis*, *dorsal retractor*, *sternohyoideus*, and *adductor dorsalis* 5, are so that the entire structure is capable of projecting until the middle of the orbit. Mehta & Wainwright (2008) reported on the ecomorphology of ten species of Muraenidae, piscivorous, or shell-crushers. Carnivorous species exhibits long jaws, small heads, long curved tooth, processing food with the pharyngeal jaws. Shell-crushing morays have short jaws, short, round teeth, and handle prey

with the oral jaws. Johnson (2019) provided an extensive revision of Muraenidae branchial muscles, reviewing terminology and anatomical nomenclature of Mehta & Wainright (2007a, b, 2008)

New anguilliform synapomorphies were proposed by Johnson *et al.* (2012), along with the of *Protanguilla palau*, known only from reef caves in Palau, Pacific Ocean. The new taxon is the sister group to the rest of the order, with three plesiomorphies found only in Cretaceous Anguilliformes: gill rakers (not seen in living Anguilliformes). The authors propose that *Protanguilla* diverged from the remaining anguilliforms in the Triassic-Jurassic, about 220 million years ago (Figure 5). Additional synapomorphies for Anguilliformes from branchial arches muscles suggested by Springer & Johnson (2015).

Da Silva & Johnson (2018) recently explored the pectoral-fin skeleton. The authors described the pectoral girdles of *Anguilla* and *Nemychthys*, correcting previous misinterpretations.

Despite the plethora of work on Recent Anguilliformes, merely two authors focused on morphological characters (Böhlke *et al.*, 1989; Belouze, 2002).

1.1.2 – Molecular Analyses

The molecular results proposed by Obermiller & Pfeiffer (2003) did not recover Elopomorpha as a monophyletic group (Figure 6), also Saccopharyngoidei in their order. The hypotheses of the relationships of Anguilliformes inferred from morphological characters according to Filleul & Lavoué (2002) pointed out Muraenidae as basal clade and Saccophayngiformes within Anguilliformes (Figure 7).

Tang & Fielitz (2012) proposed Saccopharyngoidei (*sensu* Forey *et al.*, 1996) as a sister group to Anguilloidei (Moringuidae, Serrivomeridae, Nemichthyidae, Saccopharyngoidei, and Anguillidae), Congridae as a paraphyletic group and *Protanguilla* as a sister group of Synphobranchidae (Figure 8).

After decades of pitched contention over the interrelationships of Anguilliformes, Chen *et al.* (2014) and Santini *et al.* (2013) tested some maximum likelihood analyses using nuclear and mitochondrial gene sequences to evaluate the phylogenetic relationship in Elopomorpha (Figures 9 and 10). In the two papers, Chen *et al.* (2014) and Santini *et al.* (2013) gathered *Protanguilla*, and Synphobranchidae in the same clade, and this clade as the sister group of the rest of all Anguilliformes, likewise Congridae and Muraenosocidae non-monophyly. In the light of what was written by Chen *et al.* (2014) and Santini *et al.* (2013) grouping saccopharyngoids and anguillids together. It may perhaps be observed that the position of "*Thalassenchelys*" in Chen *et al.* (2014) as the sister group of *Coloconger*, however, in Santini *et al.* (2013) the big mouth larvae are related to *Derichthys*. All researches mentioned herein recovered the Muraenosocidae and Ophichthidae together.

Many investigations have strived to determine the position of the most bizarre group of the deep-water fish, the Saccopharyngoidei, composed of Cyematidae, Monognathidae, Eurypharyngidae, and Saccopharyngidae. Their remarkable modifications include exceptional bone reductions, fusions, or losses (Tchernavin, 1947a, b; Nilsen *et al.*, 1989). The leptocephalus stage of saccopharyngoids is still undescribed. Poulsen *et al.* (2018), based on mitogenomic sequence data, performed molecular and morphological analysis over "*Leptocephalus holti*," the *incertis sedis* larvae, however, the authors pointed out these specimens as larval stage of one-jaw eels of the Monognathidae. Poulsen *et al.* (2018) also generated a cladogram in which Neocyematidae is more closely related to Eurypharyngidae and Saccopharyngidae. In that study, *Protanguilla* is not a basal group among Anguilliformes, but rather sister group of Synphobranchidae.

Lü *et al.* (2019) sequenced the complete mitochondrial genome of *Ophichthus breviceudatus* Wu & Jin 1981 and proposed a hypothesis of phylogenetic relationships of Anguilliformes including 45 species in 16 families, but not included *Protanguilla palau* in their analysis, also chose Saccopharngoidei as an outgroup. The results pointed out that a group composed by Synaphobranchidae + (Heretenchelyidae + (Myrocongridae + Muraenidae), another monophyletic clade gathering Nemychthidae + (Serrvomeridae + Anguillidae) this one as a sister group of all Anguilliformes (Figure 11).

Worthy of mentioning in all molecular analysis presented here, the Congridae not recovered as monophyletic, and the Muraenosocidae and Ophichthidae hypothesized as sister groups.

2. SCIENTIFIC JUSTIFICATION

Knowledge on musculature and branchial arches in general remains neglected not only in Anguilliformes but also in Teleostei generally (Nelson, 1966, 1967; McCosker, 1977; Castle, 1984; Smith, 1984; Bölhke, 1989; Forey *et al.*, 1996; Belouze, 2002). Among synapomorphies listed by Wiley & Johnson (2010) for Teleostei and various subgroups therein, only 6% were from myology. By contrast, the same data source includes 74% of characters from osteology.

Several authors pointed out the potential of muscles as sources of phylogenetically-informative characters, such as Nematogenyidae and Trichomycteridae (Datovo & Bockmann, 2010), Characiformes (Datovo & Castro, 2012), Stromateiformes (Pastana, 2019); Notacathiformes (Greenwood, 1977); Teleostei (Nelson, 1967a; Winterbottom, 1974; Greenwood & Lauder, 1981; Datovo & Vari, 2013), Actinopterygii (Springer & Johnson, 2004; Datovo & Rizatto, 2018) and Anguilliformes (Nelson, 1967a; Eadgeri, 2010; Springer & Johnson, 2015; Johnson, 2019).

Up to the present, there has been no attempt to combine data from osteology and cephalic musculature in Anguilliformes.

3. OBJECTIVES

- 1) Survey variation in osteological, cephalic and branchial-arch musculature complexes, illustrating structures, clarifying questions of homology and nomenclature, including representatives of all families, subfamilies, and most of the genera in Anguilliformes;
- 2) Critically examine and evaluate previous characters proposed as relevant for resolving phylogenetic relationships in Anguilliformes;
- 3) Propose new characters to be combined with previous ones into a new hypothesis of phylogenetic relationships in Anguilliformes.

4. MATERIALS AND METHODS

4.1 – General Anatomy

Skeletal muscles of the cephalic and branchial arch complexes organized into four main sets: mandibular muscles (*adductor mandibulae* [internal, external and mandibular section] and *intermandibularis*), opercular (*dilatator operculi*, *levator operculi* and *adductor operculi*), suspensorium (*levator arcus palatini* and *adductor hyomandibulae*), hyoid (*protractor hyoidei* [*intermandibularis* and *interhyoideus*], *hyohyoideus inferioris*, *hyohyoidei abductores* and *hyohyoidei adductores*) and branchial arches (*levatores externi*, *levatores interni*, *levator posterior*, *obliqui dorsales*, *obliqui ventrales*, *obliquus posterior*, *obliquus superior*, *adductores*, *transversi dorsales*, *transversi ventrales*, *rectus communis* and *sphincter oesophagi*). Extrinsic and intrinsic musculature of the eyes not included in this survey.

Preparation of material for osteological and musculature observations followed Datovo & Bockmann (2010) and Taylor & Van Dyke (1985).

Osteological nomenclature follows Weitzman (1962), Böhlke *et al.* (1989), and Grande & Beamis (1998) and musculature terminology is according to Winterbotton (1974), Datovo & Vari (2013), Nelson (1966, 1967), Springer & Johnson (2004, 2015), Datovo & Rizzato (2018), and Johnson (2019).

4.2 – Illustrations

Photographs taken with a stereomicroscope Zeiss Discovery.V20 and SteREO Discovery V12 attached to digital camera Axiocam 506 color, implementing focus stacking with Combine ZP program (Hadley, 2009). X-rays used in the case of taxa rare in collections.

4.3 – Phylogenetic Analysis

Analysis of phylogenetic relationships followed cladistic methodology, initially described by Hennig (1950; 1966) and subsequently and improved by various authors (*e.g.*, Wiley, 1981; Schuh & Brower, 2009; Wiley & Lieberman, 2011). Maximum parsimony (Farris, 1983) was used to infer the tree best supported by the data, implemented with the program T.N.T. Version 1.5 (Goloboff *et al.*, 2008).

The matrix built on Microsoft Excel and Notepad ++ (trademark - SourceForge.net), text editor and source code editor programs. Character states were polarized by rooting point (Nixon & Carpenter, 1993) in *Elops saurus* Linnaeus 1766. The root based on previous analyses (Forey *et al.*, 1996; Wiley & Johnson, 2010; Betancur *et al.*, 2013, 2017; Near *et al.*, 2013) in *Elops saurus*, considered the sister groups of all other Elopomorpha in both molecular and morphology-based analyses. Multistate characters were treated as ordered or "minimally connected" (Slowinski, 1993), according to a sequence of similarity among states (Wilkinson, 1992; de Pinna, 1991). The non-additive option adopted only when ordering states was not possible.

So-called "new technology search" (Goloboff *et al.*, 2008) applied for searching the most parsimonious trees (M.P.T.s) with the following parameters: "20" value to Tree-drift cycle replicates (Goloboff, 1999), "10" Ratchet total interactions (Nixon, 1999), with perturbation phases adjusted to eight, and Tree-fusing rounds to "10" (Goloboff, 1999). All these specifications used herein to reach 50 hits of the best score, and with the Random Seed set to zero, the remaining search parameters conserved on their defaults. Implied Weighting (I.W.) (Goloboff *et al.*, 2008), was implemented with 'unordered' settings (K=7) proposed by Goloboff

(2013) as Extended implied weighting. Searches using character weighting against homoplasy were also performed (Implied Weighting: Goloboff *et al.*, 2008).

In ambiguous optimization (where there is more than one equally parsimonious transition sequence) the choice was for the alternative where reversals are preferred to the convergences, called ACCTRAN ("accelerated transformation optimization", Swofford & Maddison, 1987), as proposed by de Pinna (1991). The consistency index (CI; Farris, 1969) and retention index (RI; Farris, 1989) were calculated with help "wstats.run" script (designed by Peterson L. Lopes). Both indices were used as the fit measurement between the characters and cladograms (Farris, 1969, 1989). All index between characters and trees, as well as optimization of the transformations on the final cladograms, were analyzed on TNT 1.5 (Goloboff *et al.*, 2008). Support for clades was estimated by Bremer support (Bremer, 1994), sampling suboptimal trees with up to 11 extra steps. Characters were viewed with WinClada (Nixon, 2002) and edited with Adobe Illustrator CC 2019 and Adobe Photoshop CC.

4.4 – Muscle dissection

This section aims to describe the anatomical dissection of the facial, hyoid, and branchial arches muscles for Elopomorpha. We understand that the excellent dissection involves minimal cutting of the complex and surgical instruments with high precision. The dissection here applied to maintain the musculature intact, without cutting essential information whenever possible. Nelson (1966), Datovo & Vari (2013, 2014) and Datovo & Rizato (2018) described just brief steps about the muscles anatomizing of the branchial arches and facial complex. However, Springer & Johnson (2015) described an extensive methodology on how the gill arches removed from the fishes, but we concluded that dissection would be destructive for opercular complex or *adductor hyomandibulae*. Another different methodology taken here

was to stain the specimens before the dissection, whereas Springer & Johnson (2004) proceeded the scalp first and then the staining. We present our method exposing the facial, opercular, hyoid, and branchial muscles, and the dissection followed steps:

1. Fish lay, and the skin was cut just behind the pectoral fin making a circle around the body;
2. The skin was removed from the pectoral girdle toward the head;
3. Nasal organs and eyes were removed and preserved for future studies;
4. ligaments, vessels, and connective tissues were removed with delicate forceps not to peel the musculature away;
5. Remove *adductor mandibulae* along with the lower jaw from one side of the head by cutting insertions on top of the neurocranium and hyomandibular and opercular ligaments;
6. *Adductor mandibulae* were removed preserving the endomaxillary ligaments and buccopalatal membrane;
7. The right side of the lower jaw was removed with *adductor mandibulae*, preserving the *dilatator operculi*, *levator arcus palatini*, *adductor hyomandibulae*, and *levator operculi* fibers;
8. Fish lay dorsal, the ventral side exposed;
9. ligaments lower jaw by interhyal or ceratohyal posterior removed;
10. *Protractor hyiodei*, *hyohyoidei inferioris*, *hyohyoidei abductors*, *hyohyoidei adductors*, hyoid arch, branchial arch, and the pectoral girdle removed together by removing the connective tissue from the roof of the mouth to find the insertion of the levator on the ventral portion of the neurocranium;
11. Transversal cut on *sphincter esophagi* and *hypaxialis* just posterior to pectoral girdle muscles and bones;
12. *Dorsal retractor* insertion cut;

13. Ligaments, nerves, and blood vessels and aorta attaching the branchial arches were cut free;
14. Branchial arches released from the hyoid arch and pectoral girdle attachments cutting ventral connections with *pharyngoclavicularis*, basibranchial 1 ligaments, *rectus communis* and/or *rectus ventrali* 1;
15. The fascia connecting the *sternohyoideus* to branchial arches also dissected;
16. All the *levators* (*externus* and *internus*) carefully kept;
17. Following the previous steps, the *pharyngocleithrales* and pectoral girdles were released from the anterior complex, and preserved;
18. In some case, the branchial arches were cut between ceratobranchial and epibranchial series to allow better dorsal and ventral views.
19. The last step was to strip off gill filaments with the micro forceps.

4.5 – Material Examined

Institutional abbreviations follow Sabaj (2016). Specimen length is expressed as total length (TL).

Musculature stained prepared specimens list

Elopiformes:

Elopidae: *Elops saurus*, MNRJ 40531, 273 mm TL, 1 of 8, Rio de Janeiro, Brazil;

Megalopidae: *Megalops atlanticus*, MNRJ 41435, 223 mm TL, 1 of 9, Ceará, Brazil; *Megalops cuyprioides*, USNM 173578, 85mm TL, 1 of 10, Groote Eylandt, Australia.

Albuliformes:

Albulidae: *Pterothrissus gissu*, NSMT 74776, 265 mm TL, 2 of 5 Honshu, Japan; *Pterothrissus gissu*, NSMT 91485, 205 mm TL, 1 of 5 Honshu, Japan; *Albula vulpes*, MNRJ 37303, 126 mm TL, 1 of 18, Rio de Janeiro, Brazil; *Albula vulpes*, USNM 218871, 87 mm TL, Coco Island, Mauritius.

Notacanthiformes:

Halosauridae: *Halosaurus pectoralis*, USNM 317567, 506 mm TL, 1 of 7, Walters Shoal, Indian Ocean; *Halosauropsis machochir*, VIMS 3110, 552 mm TL; *Aldrovandia phalacra*, VIMS 8390, 361 mm TL; *Halosaurus guentheri*, USNM 214336, 220-430 mm TL, 2 of 4, Gulf of Mexico, USA. **Nothacanthidae:** *Notacanthus sexspinis*, NSMT 66835, 587 mm TL, 1 of 3, New Zealand; *Polyacanthonothus rissoanus*, VIMS 4552, 418 mm TL; *Lipogenys gillii*, MCZ 38072, damaged, 1, USA; *Lipogenys gillii*, MCZ 37613, 350 mm TL, 1, Canada.

Anguilliformes:

Synphobranchidae: *Synphobranchus* sp., MNRJ 26716, 430 mm TL, 2 of 21, Espirito Santo, Brazil; *Synphobranchus kaupii*, USNM 444949, 195 mm TL, 1, Virginia, USA; *Synphobranchus* sp., USNM 316662, 1 of 10, South Carolina, USA; *Simenchelys parasitica*, USNM 31727, 309 mm TL, 1, Off Martha's Vineyard; *Dysomma anguillare*, ANSP 158368, 365 mm TL, 1, Philippine Islands; *Dysommia rugosa* MZUSP 86463, 288 mm TL, 1 of 12, São Paulo, Brazil; *Media abyssalis*, MUSP 84460, 467 mm TL, 1, *Diastobranchus capensis*, MNRJ 26783, 780 mm TL, 1 of 3, Bahia, Brazil; *Simenchelys parasitica*, SIO 05-11, 123 mm TL, 1 of 78, Darwin Seamount, Pacific Ocean; *Ilyophis nigeli*, NSMT 49061, 314 mm TL, 2 of

20, Honshu, Japan; *Symenchelys parasitica*, MNRJ 40772, 144 mm TL, 1 of 11, Rio de Janeiro, Brazil. **Heterenchelyidae:** *Pythonichthys asodes*, UF 228629, 253 mm TL, 1 of 3, Panama; **Myrocongridae:** *Myroconger* sp., DBUFC 81, 431 mm TL, 1, Ceará, Brazil; **Muraenidae:** *Anarchias seychellensis*, MCZ 162323, 65 mm TL, 1, Kiribati; *Muraena lentiginosa*, CAS 214486, 88 mm TL, 1 of 9, Jalisco, Mexico; *Strophidon sathete*, USNM 217007, 620 mm TL, 1, Papua New Guinea; *Rhinomuraena quaesita*, USNM 338049, 730 mm TL, 1, Tongas Islands; *Uropterygius concolor*, CAS 218255, 105 mm TL, 1 of 11, Fiji; *Anarchias allardicei*, CAS 201807, 98 mm TL, 1 of 29, Micronesia; *Enchelycore nigricans*, ZUEC 10962, 266 mm; *Monopenchelys acuta*, USNM 31284, 150 mm TL, 1 of 8, Dominica; *Gymnothorax vicinus*, MZUSP 11900, 241 mm TL, 1 of 15, Bahia, Brazil; *Echidna catenate*, MZUSP 46483, 545 mm TL, 1 of 2, Pernambuco, Brazil; *Gymnomuraena zebra*, SIO 62-8, 149 mm TL, 1 of 7, Mexico; **Nemichthyidae:** *Nemichthys scolopaceus*, ANSP 158461, 513 mm TL, 1 of 7, Ecuador; *Avocettina infans*, UF 215159, 361 mm TL, 2, Liberia; *Nemichthys scolopaceus*, USNM 358874, 700 mm TL, 1 of 5, Atlantic Ocean; **Colocongridae:** *Coloconger meadi*, USNM 443687, 333 mm TL, 1, Suriname; *Coloconger meadi*, UF 211407, 249 mm TL, 2, Nicaragua; **Derichthyidae:** *Derichthys serpentinus*, USNM 444953, 112 mm TL, 1, Bermuda; *Derichthys serpentinus*, SIO 73-132-26, 104 mm TL, 1, Oahu: off Waianae; *Nessorhamphus danae*, SIO 73-166, 105 mm TL, 1 of 3, Pacific Ocean; **Nettastomatidae:** *Nettastoma melanurum*, USNM 405025, 505 mm TL, 1, Cape Verde; *Nettastoma melanurum*, MNRJ 26821, 512 mm TL, 2 of 5, Bahia, Brazil, *Facciolella equatorialis*, SIO 91-72, 296 mm TL, 1 of 33, off Point Loma; *Venefica procera*, MNRJ 26806, 1091 mm TL, 4 of 22, Bahia, Brazil; *Hopplunnis tenuis*, USNM 444956, 320 mm TL, 1, Suriname **Moringuidae:** *Neoconger vermiformis*, USNM 444957, 95 mm TL, 1 of 2, Canal Zone, Panama; *Moringua raitaborua*, USNM 406625, 225 mm TL, 1 of 9, Negros Occidental, Phillipines; *Moringua edwardsi*, MZUSP 11810, 263 mm TL, 1 of 20, Bahia, Brazil; **Muraenesocidae:** *Oxyconger leptognathus*, NMMB-P022865, 270 mm TL, 1 of 6, Kaohsiung, Taiwan; *Gavialiceps taeniolar*, ANSP 113805, 725 mm TL, 1 of 4, Indian ocean; *Muraenesox cinereus*, CAS 51089, 235 mm TL; *Muraenesox cinereus*, USNM

431418, Damaged, 1, Ba Ria Vung Tau, Vietnam; **Serrivomeridae:** *Serrivomer beanii*, USNM 444955, 321 mm TL, 1, Bermudas; *Serrivomer* sp., USNM 443689, 610 mm TL, 1, North Pacific Ocean; *Serrivomer schmidtii*, MNRJ 26850, 576 mm TL, 2 of 7, Bahia, Brazil; *Stemonidium hypomelas*, ANSP 152332, 300 mm TL, 1 of 2, Hawaii, USA; **Anguillidae:** *Anguilla japonica*, NSMT uncat, 317 mm TL, 2, Honshu, Japan; *Anguilla rostrata*, MCP 28163, 190mm TL, 1 of 7, Maryland, USA; *Anguilla rostrata*, USNM 444959, 133 mm TL, 1, Roatan, Honduras; *Anguilla rostrata*, USNM 190998, Damaged, 1 of 5, North Carolina, USA; *Anguilla marmorata*, USNM 191271, 178mm TL, 1 of 4, Hualien County, Taiwan; **Chlopsidae:** *Kaupichthuys* sp., USNM 444952, 97 mm TL, 1 of 2, Rotuma, Fiji; *Chilorhinus suenisoni*, MZUSP 18431, 116 mm TL, 1 of 18, Bahia, Brazil; *Kaupichthys hyoporoides*, ANSP 190028, 176 mm TL, Great Bahama Bank, Bahamas; **Cyematidae:** *Cyema atrum*, SIO 66-546, 96 mm TL, 1 of 2, SW of Cortez Bank, USA; *NeoCyema* sp., MCZ 165900, 103 mm TL, 1, USA; *Cyema atrum*, MCZ 47843, 109 mm TL, 1, South Pacific; *Cyema atrum*, MCZ 60597, 35 mm TL, 1, North Atlantic; **Eurypharyngidae:** *Eurypharynx pelecanoides*, SIO 73-43, 350 mm TL, California; *Eurypharynx pelecanoides*, MCZ 80529, 155 mm TL, 1, North Atlantic; *Eurypharynx pelecanoides*, MCZ 109261, 92 mm TL, 1, North Atlantic; *Eurypharynx pelecanoides*, MCZ 101364, 44 - 165 mm TL, 5, North Atlantic; *Eurypharynx pelecanoides*, MCZ 85269, 165 mm TL, 1, North Atlantic; **Congridae:** *Macrocephenchelys brevirostris*, USNM 443688, 370 mm TL, 1, Taiwan; *Xenomystax congroides*, USNM 444950, 325 mm TL, 1 of 2, Lesser Antille, Virgin Islands, *Macrocephenchelys brachialis*, NMMB-P025654, 236 mm TL, 1 of 5, Pingtung, Taiwan; *Rhynchoconger gracilior*, FSBC 31507, 361 mm TL, 1 of 5, Florida, USA; *Conger cinereus*, USNM 115969, 345 mm TL, 1 of 19, Tutuila, American Samoa; *Gorgasia punctate*, CAS 20752, 289 mm TL, 1 of 93, Nayarit, Mexico; *Heteroconger Camelopardalis*, MZUSP 57611, 304 mm TL, 1 of 3, Pernambuco, Brazil; *Heteroconger klausewitzi*, USNM 316033, 215 mm TL, 1 of 6, Galapagos Islands, Ecuador; *Acromycter perturbator*, MNRJ 27115, 260 mm TL, 2 of 16, Rio de Janeiro, Brazil; *Conger orbignianus*, MZUSP 11950, 510 mm TL, 1 of 4, Rio Grande do Sul, Brazil; *Bathycongrus dubius*, MZUSP

12290, 222 mm TL, Brazil; *Ariosoma* sp., MZUSP 12060, 305 mm TL, 1 of 14, São Paulo, Brazil; *Congriscus megastoma*, NSMT 57574, 259 mm TL, 3 of 14, Shikoku Tosa Bay, Japan; *Gnathophis nystromi ginanago*, NSMT 65815, 330 mm TL, 2 of 5, East China Sea, *Bathydroconger vicinus*, MNRJ 26813, 745 mm TL, 2 of 4, Bahia, Brazil; **Ophichthidae**: *Ophichthus gomesii*, MNRJ 32607, 368 mm TL, 2 of 3, Rio de Janeiro, Brazil; *Myrichthys ocellatus*, MZUSP 12027, 464 mm TL, 1 of 10, Bahia, Brazil; *Stictorhinus potamius*, MNRJ 30419, 275 mm TL, 3 of 65, rio Tocantis, Brazil; *Bascanichthys* sp., MZUSP 12008, 365 mm TL, 1 of 3, Bahia, Brazil; *Letharchus velifer* MZUSP 12020, 197 mm TL, 1 of 40, Bahia, Brazil; *Pseudomyrophis frio*, MZUSP 12309-373, 214 mm TL, Brazil; *Ahlia egmontis*, MZUSP 11997, 142 mm TL, 1 of 14, Bahia, Brazil; *Myrophis punctatus*, MZUSP 60779, 204 mm TL, 1 of 10, Bahia, Brazil; *Yirrkala misolensis*, NMMB-P027671, 361 mm TL, 2, Taiwan; *Neenchelys mccoskeri*, NMMB-P027671, 310 mm TL, 1 of 3, Donggang, Pingtung, Taiwan; *Echelus uropterus*, NSMT 63505, 350 mm TL, 2 of 3, East China Sea; *Schismorhynchus labialis*, USNM 444954, 142 mm TL, 1 of 2, Tonga Islands, Tonga; *Callechelys catostoma*, USNM 444951, 540 mm TL, 1, Eniwetok Atoll, Marshall Islands; **Protanguillidae**: *Protanguilla palau*, USNM 396051, 1, 141 mm TL, Palau; **Monognathidae**: *Monognathus jerpersenii*, MCZ 164702, 124 mm, 1, USA. *Monognathus rosenblatti*, SIO 86- 42, 113 mm TL, 1 of 4, No Central Gyre.

Cleared and Stained specimens list

Elopiformes:

Elopidae: *Elops saurus*, USNM 128290, 68 mm TL, 1 of 5, USA; **Megalopidae**: *Megalops cyprinoides*, USNM 173578, 155- 211mm TL, 2 of 10, USA; *Megalops cyprinoides*, USNM 164259, 75 mm TL, 1 of 13, Papua New Guinea;

Albuliformes:

Albulidae: *Albula vulpes*, USNM 183538, 56 mm TL, 1 of 256, Anguilla; *Albula vulpes*, USNM 315407, 200 mm TL, 1 of 2, British Indian Ocean Territory; *Pterothrissus* sp., BMNH 104952, 104, 1, Japan;

Notacanthiformes:

Halosauridae: *Halosaurus* sp., USNM Uncat., 1, 185 mm;

Anguilliformes:

Muraenosocidae: *Cynoponticus savanna*, ANSP 114155, 555 mm TL, 1, Colombia; *Muraenesox cinereus*, ANSP 113870, already dissected, 1, Atlantic Ocean; *Sauromuraenesox vorax*, ANSP 133595, already dissected, 1, India; **Colocongridae:** *Coloconger raniceps*, ANSP 115508, 340 mm TL, 1, North Atlantic; *Coloconger meadi*, USNM 193572, 340 mm TL, 1 of 7, Caribbean Sea; **Derichthyidae:** *Nessorhamphus danae*, USNM 288825, 123 mm TL, 1, North Pacific Ocean.; *Nessorhamphus ingolfisnus*, MCZ 41283, 153 - 175 mm TL, 3, North Atlantic Ocean; *Derichthys serpentinus*, USNM 315025, 170 mm TL, 1 of 2, Bermuda; **Chlopsidae:** *Chilorhinus suensonii*, UMML 8957, 78 mm TL, 1, USA; *Chlopsis dentatus*, UMML 23484, 101 mm TL, 1, USA; *Chlopsis bicolor*, UMML 17377, 97 mm TL, 1, USA; *Kaupichthys diodontus*, USNM 259084, 97 mm TL, 1 of 26, Fiji; **Heterenchelyidae:** *Pythonichthys asodes*, SIO 73-319, 255 mm TL, 1 of 4, Panama; *Pythonichthys asodes*, UF 228629, 201 mm TL, Pacific Ocean, Panama; **Serrivomeridae:** *Serrivomer beanii*, MCZ 62101, 163 mm TL, 1, North Atlantic Ocean; *Stemonidium hypomelas*, USNM 444960, 85 mm TL, 1, Kiribati; **Moringuidae:** *Moringua edwardsi*, ANSP 115525; 205-320 mm TL, 15,

Bahamas; *Moringua edwardsi*, USNM, 334815, 190-340 mm TL, 3 of 93, Tonga; **Anguillidae**: *Anguilla rostrata*, USNM 190998, already dissected, 1 of 5, North Carolina, USA; *Anguilla rostrata*, USNM 273101, 203 mm TL, 1, Massachusetts, USA; **Cyematidae**: *Cyema atrum*, USNM 208058, already dissected, 1, South Pacific Ocean; *Cyema atrum*, USNM 324873, 54 mm TL, 1, *Leptocephalus holti* species 3, Summit of Hancock Seamount; *Cyema atrum*, MCZ 47843, 109 mm TL, 1, North Atlantic Ocean; *Cyema atrum*, MCZ 60597, 35 mm TL, 1, Azores, Portugal; **Nettastomidae**: *Hoplunnis diomediana*, USNM 163496, 380-390, 2 of 79, Florida, USA; *Saurenhelys* sp., ANSP 156860, 295 mm TL, 1, Unknown; *Facciolella* sp., ANSP 84189, 1, Alabama, USA; *Nettastomatidae* sp., UMML 20867, 1, unknown; **Synaphobranchidae**: *Synaphobranchus brevidorsalis*, USNM 273427, already dissected, 1, Indian Ocean, Africa; *Synaphobranchus* sp., USNM 313604, 57 mm TL, *Leptocephalus*, 1, Bermuda; *Simenchelys parasitica*, VIMS 115 mm TL, 1, USA; *Dysomina rugosa*, ANSP 110408, 290 mm TL, 1, Florida, USA; **Congridae**: *Gavialiceps taeniolar*, USNM 305920, 500 mm TL, 1 of 3, Arabian Sea - Gulf of Aden, Somalia; *Bathyroconger vicinus*, USNM 179070, 455 mm TL, 1 of 12, Somalia; *Heteroconger polyzona*, USNM 316028, 250 mm TL, 1 of 5, Phillippines; *Rhychoconger flavus*, USNM 157963, 360 mm TL, 1 of 4, Gulf of Mexico; *Ariosoma selenops*, USNM 187627, 233 mm TL, 1 of 13, Cuba; *Gorgasia* sp., ANSP 147311, 340 mm TL, 1, Marshall Islands; *Chiloconger dentatus* USNM 316123, Damaged, Costa Rica; *Paraconger caudilimbatus*, USNM 218909, 390 mm TL, 1, Colombia; *Macrophenchelys brevirostris*, USNM 401090, 409 mm TL, 1 of 33, Taiwan; *Conger coner*, USNM 339139, 41 mm TL, *Leptocephalus*, 1, Mediterranean Sea; **Nemichthyidae**: *Nemichthys scolopaceus*, USNM 186312, Damaged, 2 of 35, Virginia, USA; *Nemichthys scolopaceus*, ANSP 115526, 470 mm TL, 1, Caribbean Sea, off Colombia; *Nemichthys scolopaceus*, USNM 186297, 520 mm TL, 1 of 2, Virginia, USA; *Labichthys yanoi*, USNM 207090, 430 mm, 1 of 2, North West Atlantic; **Ophichthidae**: *Apterichtus caecus*, USNM 181873, 265 mm TL, 1 of 3, South Carolina, USA; *Ophichthus melanoporus*, ANSP 128379, 520 mm TL, 1; *Aplatophis chauliodus*, FSBC 16846, 55 mm TL, *Leptocephalus*, 1, USA; *Nettenchelys inion/exoria*,

USNM 314781, 79 mm TL, 1, Bermuda; *Myrophys vafer*, USNM 167920, damaged, 1 of 70, Gulf of California, Mexico; **Muraenidae**: *Echidna polyzona*, BMNH 1974.5.25.430, 110 mm TL, 1, Unknown; *Gymnothorax minor*, USNM 192551, 225 mm TL, 1 of 3, Taiwan; *Gymnothorax pindae*, USNM 404560, 225 mm TL, 1, Red Sea, Egypt; *Enchelynassa canina*, USNM 141595, 188 mm TL, 2 of 8, Marshall Islands; *Enchelycore nigricans*, USNM 320535, 230 mm TL, 1 of 3, Trinidad and Tobago; *Anarchias similis*, USNM 320964, 125 mm TL, 1 of 9, Trinidad and Tobago; *Uropterygius micropterus*, USNM 123995, 180 mm TL, 1 of 5, Guam; *Anarchias seychellensis*, MCZ 162323, 65 mm TL, 1, Kiribati; **Eurypharyngidae**: *Eurypharynx pelecانoides*, USNM 410478, 190-300 mm TL, 1 of 2, Massachusetts, USA; **Protanguillidae**: *Protanguilla palau*, USNM 396010, already dissected, 1, Palau; *Protanguilla palau*, USNM 396051, 156 mm TL, 1, Palau.

4.5 – List of Used Abbreviations for Anatomical Structures

AD – *adductor dorsalis*

AHyo – *adductor hyomandibulae*

AM – *adductor mandibulae*

Bb – basibranchial

Cb – ceratobranchial

DO – *dilatator operculi*

Ep – epibranchial

Hb – hypobranchial

LAP – *levator arcus palatini*

LAPp - *levator arcus palatini pars primordialis*

LE – *levator externi*

LI – *levator interni*

LO – *levator operculi*

LPT – lower pharyngeal tooth plate

MPb2-Eb1 – *musculus pharyngobranchialis 2-epibranchialis 1*

MUP4-Eb4 – *musculus laminalis pharyngobranchialis dentalis 4-epibranchialis 4*

ObV – *obliquus ventralis*

OD – *obliquus dorsalis*

OP – *obliquus posterior*

Pb – pharyngobranchial

Pcl – *pharyngoclavicularis*

R – *rectus ventralis*

RecCom – *rectus communis*

RecD – *rectus dorsalis*

T – *transversus dorsalis*

TV – *transversus ventralis*

UPT – upper pharyngeal tooth plate

5.1 – Osteological Characters

Characters were contextualized concerning data by Nelson (1966, 1967), Forey *et al.* (1996), Belouze (2002), Eadgeri (2010), Johnson *et al.* (2012) and Springer and Johnson (2004, 2015). The corresponding images to characters are numbered to from 12 to 38 (osteological features), from 39 to 61 (musculature complex) and from 62 to 63 (scales).

5.1.1 – Neurocranium

1. **Supraoccipital. (Character 7 from Forey *et al.*, 1996; Character 1 from Belouze, 2002); (CI: 0.142857; RI: 0.666667)**

[0] present

[1] absent

The supraoccipital is lost in some anguilliform taxa (*e.g.*, Serrivomeridae; Saccopharyngoidei; Nemichthyds: *Nemichthys*, *Avocettina*; Nettastomatids: *Nettenchelys*, *Nettastoma*, *Venefica*, and *Hoplunnis macrura*; and congrid: *Ariosoma*, *Bathymyrus*, *Parabathymyrus*, *Congriscus*, and *Pseudophichthus*) (Figures 12 and 13), however it is present in all fossils forms examined by Belouze (2002, 2003).

- 2. Parietal. (Character 33 from Robins, 1989; Character 3 from Belouze, 2002); (CI: 0.500000; RI: 0.000000)**

[0] present

[1] absent

The loss of parietal is a synapomorphy for Saccopharyngidae (except *Cyema*), an apomorphic condition among Elopomorpha fishes.

- 3. Dorsal crest elevating the cranial roof (the supraoccipital at least). (Character 4 from Belouze, 2002); (CI: 0.500000; RI: 0.933333)**

[0] present

[1] absent

The dorsal crest is present in Myrocongridae, Muraenidae, and *Hoplunnis* (Nettastomatidae) (Figure 14). We included the anguilliform fossil taxa cited by Belouze (2002, 2003) and Belouze *et al.* (2003), as †*Anguillavus*. The importance of the dorsal crest on the

neurocranium is to help the attachment of the *adductor mandibulae* and probably relieve the pressure of the bite once this muscle is more robust when compared to the other elopomorphs (Gosline, 1951, 1971).

4. Post-temporal pit. (Character 5 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The presence of the post-temporal pit was only observed in Elopiformes, and Albuliformes, whereas the epaxial musculature attaches a pit posterior vertical semicircular canal of the epiotics. Since the post-temporal bones are lost in the derive groups of elopomorph, this condition is plesiomorphic among the clade.

It is absent in Notacanthiformes, extant and fossil species of Anguilliformes (Belouze, 2002, 2003; Belouze *et al.*, 2003) where the posterior part of the neurocranium forms a bony wall where the muscles are attached.

- 5. Intercalar. (Character 9 from Forey *et al.*, 1996; Character 6 from Belouze, 2002; Character from Wiley & Johnson, 2010); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

According to Arratia (1997), the loss of the intercalary bone is probably associated with the loss of the post-temporal bone, which the latter is present only in the outgroups, except Nothacanthiformes (Figures 14, 19 and 32). Many authors proposed the loss of the connection between pectoral girdle and neurocranium in eels and Notacanthiformes (McDowell, 1973; Robins, 1989; Forey *et al.*, 1996; Wiley & Johnson 2010).

- 6. Sphenotic dorsal shape. (Character 8 from Belouze, 2002). (CI: 0.142857; RI: 0.863636)**

[0] horn leading anteriorly

[1] wing pointing laterally

The horn shape projection of the sphenotic (Figure 13 and 14) is found only in Anguillidae, Moringuidae, Derichthyidae, Congridae, Nettastomatidae, Nemichthyidae, and

Serrivomeridae, state [1]. Whereas in the Elopiformes, Albuliformes, Notacanthiformes, and the rest of Anguilliformes, the sphenotic dorsal wing is pointing laterally, state [0]. Belouze (2002, 2003) and Belouze *et al.* (2003) described similar horn shape projection of the sphenotic in †*Urenchelys germanus* and †*Anguillavus*.

- 7. Frontals suture. (Character from Robins, 1989; Character 5 from Forey *et al.*, 1996; Character 9 from Belouze, 2002); (CI: 0.250000; RI: 0.918919)**

[0] separated

[1] Fused

Reagan (1912), Smith (1984) and Robins (1989) indicated the frontal sutured or not, as an essential characteristic to divided Anguilliformes had been widely accepted in the literature, and this arrangement is still used. Nevertheless, we understand that this classification is far more complicated. The frontals are fused in *Cyema* and *Monognathus*; partially fused in *Neocyema*; separated in *Saccopharynx* and *Eurypharynx*, and separated in the new family, Protanguillidae (Figures 13 and 14).

It is worth mentioning that possible frontal fusion in fossil †*Anguillavus quadripinnis* and †*Urenchelys* was reported by Belouze (2002, 2003) and Belouze *et al.* (2003).

We concluded that the frontal condition of fusion has different states in many groups of Anguilliformes united bones occur in two different groups, Congroidei and Monognathidae.

- 8. Subepiotic fossa. (Character 1 from Forey *et al.*, 1996; Character 9 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)**

[0] absent

[1] present

The presence of subepiotic fossa is a synapomorphy of Albuliformes.

- 9. Anterior tip of the pterotic. (Character 2 from Forey *et al.*, 1996; Character 10 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.500000; RI: 0.818182)**

[0] not reaching the sphenotic origin

[1] reaching the sphenotic origin

[2] overlapping the level of the pterosphenotic

The anterior tip of the pterotic overlapping the sphenotic and the pterosphenotic origins were proposed by Forey *et al.* (1996) as a synapomorphy for Anguilliformes. However, the pterotic tip does not reach the anterior margin of pterosphenoid, but it overlaps the sphenotics origins in *Protanguilla* and *Coloconger*, coded as [1] (Johnson *et al.*, 2012) (Figure 15).

In the rest of the eel the advanced tip of the pterotic reaches the origin of sphenotic and pterosphenotic [2]. In all outgroups, the pterotic anterior border does not advance neither the sphenotic origin nor the pterosphenotic origin, coded here as [0].

- 10. Orbitosphenoid. (Character 17 from Robins, 1989; Character 3 from Forey *et al.*, 1996; Character 12 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

The orbitosphenoid is present in Elopiformes, Albuliformes (well developed, forming an inter-orbital wall in *Albula*) and Notacanthiformes (the bone follows along the frontals, and it does not form a wall). Absent in all extant Anguilliformes [1] (Figures 14, 15, 19, and 32).

Belouze (2002, 2003) and Belouze *et al.* (2003) identified the orbitosphenoid as a derived state [1] in †*Anguillavus*, *Urenchelys*, †*Eoenchelys*, and *Enchelurus*.

11. Basisphenoid. (Character 4 from Forey *et al.* (1996); Character 13 from Belouze, 2002); (CI: 0.500000; RI: 0.909091)

[0] present

[1] absent

As the previous studies observed (McDowell, 1973; Greenwood, 1977; Belouze, 2002) and corroborated here, the basisphenoid is absent in Notacanthiformes (Figures 15 and 32).

This bone also is absent in saccopharyngoids, but it is present in all fossils added here (Belouze, 2002, 2003; Belouze *et al.*, 2003).

12. Basisphenoid position. (Character 13 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.500000; 0.750000)

[0] contacting the prootic

[1] remaining separated from the prootic

The state [0] present in Elopiformes, Albuliformes, and *Coloconger*. In all the other Anguilliformes, the position of the basisphenoid is separated from prootic (Figures 15 and 32).

The character is marked as inapplicable [-] for Notacanthiformes and Saccopharyngoidei.

- 13. Posterior extremity of parasphenoid. (Character 14 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)**

[0] bifid tip

[1] a single tip

Another unique condition of Notacanthiformes is that the posterior tip of the basisphenoid ends in a spear format [1] (Figure 32), whereas in all the other elopomorphs tip ends in a bifid structure [0].

14. Rostral region measurement. (Character 15 from Belouze, 2002); (CI: 0.285714; RI: 0.821429)

[0] less one time the eyes length

[1] 1-3 times eyes length

[2] over 4 times longer

The shortest snout [0] observed in Elopiformes, Albuliformes, and in the eels allocated in the Heterocongrinae, Colocongridae, and *Simenchelys*. While the state [1] occurs in Notacanthiformes (except Aldrovandia), muraenids, myrocongrids, chlopsids, congrids, derichthyids, muraenosocids, ophichthids, synaphobranchids, eurypharyngids, monognathids, saccopharyngids, heterenchelyids, moringuids, anguillids, and *Protanguilla* (Figures 12, 24 and 45).

In this study, we coded all the Cyematidae, Nemichthyidae, Nettastomatidae, few congrids, and Serrivomeridae in the state [2].

15. Vomerian plate in adults. (Character 16 from Belouze, 2002); (CI: 0.500000; RI: 0.500000)

[0] present

[1] absent

The state [1] is a synapomorphy(?) of monognathids and saccopharyngids.

The vomer was detected in all fossil forms reported by Belouze (2002, 2003) and Belouze *et al.* (2003).

- 16. Vomer. (Character 16 from Belouze, 2002; Character from Johnson *et al.*, 2012);
(CI: 1.000000; RI: 1.000000)**

[0] separated**[1] ethmoid fused with vomer**

The condition [1] is observed in *Notacanthus*, and Anguilliformes (Figure 16). The plesiomorphic condition in Elopiformes and Albuliformes presented the state [0] in all specimens (Figure 32). All the fossils with fused vomer plate were analyzed by Belouze (2002), Belouze *et al.* (2003) and Johnson *et al.* (2012).

We coded inapplicable [-] for all specimen cited in the previous character.

17. Ethmoidal lateral process. (Character 17 from Belouze, 2002); (CI: 0.333333; RI: 0.875000)

[0] ossified

[1] cartilaginous

The lateral process of the ethmoid of bathymyrines (atavism among eels) reported as ossified along with the outgroup, coded here as [0]. Also, pointed out by Belouze (2002, 2003) and Belouze *et al.* (2003) lateral ethmoids are present as autogenous ossicles in fossil forms. In the rest of eels, there are different shapes of the lateral process in cartilaginous structure.

18. Parietals. (CI: 0.333333; RI: 0.000000)

[0] smaller than frontals

[1] larger than frontals

The condition [1] was only recognized in *Protangilla* and *Cyema*. In all other elopomorphs examined, the frontals were larger than parietals (Figure 13).

19. Posterior portion of the pterotic. (CI: 0.500000; RI: 0.900000)

[0] limited by exoccipital on lateral view of the neurocranium

[1] pterotics are reaching the posterior part of neurocranium

The absence of the intercalar among eels benefits the posterior expansion of the pterotic to the end of the skull “pushing” the exoccipital to the ventral part. However, the posterior end of the pterotic is limited by the exoccipital in contact with epiotics only in *Protanguilla*, among Anguilliformes. The the same condition followed by the outgroup, as the intercalar associated with the elements of the pectoral girdle. This characteristic could evidence that the presence of the post-temporal elements remains in *Protanguilla* (da Silva, pers. comm.) (Figures 14 and 19).

However, in the remaining Anguilliformes, the posterior portion of the pterotic reaches the lateral limit of the neurocranium, separating exoccipital and opiotics, Belouze (2002, 2003) and Belouze *et al.* (2003) illustrations demonstrate that the state [1] is present in †*Anguillavus* and †*Urenchelys*, the rest of the forms were coded as [?].

20. Basisphenoid. (Character from Johnson *et al.*, 2011); (CI: 0.333333; RI: 0.600000)

[0] articulates dorsally with the pterosphenoid

[1] articulates dorsally with the frontal

This character was described by Johnson *et al.* (2012), and corroborated here, uniquely among eels in *Protanguilla* and *Coloconger*, which basisphenoid articulates dorsally with the pterosphenoid coded as [0], the same condition in Elopiformes and Albuilliformes. In the rest of the Anguilliformes, including forms, the basisphenoid articulates dorsally with the frontal, coded here as a state [1] (Figures 15 and 19).

The basisphenoid lost in Notacanthiformes, coded here as inapplicable [-].

5.1.2 – Sensory canals

21. Anastomosis between the supraorbital canal and the ethmoid commissure occurring outside the ethmoid. (=dermethmoid, Forey, 1973; Forey *et al.*, 1996); (Character 19 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The supraorbital canal is pierced into the ethmoid (=dermethmoid, Forey 1973; Forey *et al.* 1996), via a lateral foramen in the Albuliformes, Notacanthiformes, and some species of *Elops*, coded [1]. However, the anastomosis was not observed in Anguilliformes [1]. More ontogenetic studies should evaluate this character.

22. Foramen entrance of the mandibular sensory canal. (Character 11 from Forey *et al.*, 1996; Character 24 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] on the medial side of the mandibulae

[1] on the lateral or posterior side

This condition is a synapomorphy for Elopiformes [1], the rest of the Elopomorph including the fossils (Belouze, 2002; Belouze *et al.*, 2003) and the extant eels, coded as a state [0].

23. Protection of the mandibular. (Character 25 from Belouze, 2002); (CI: 0.500000; RI: 0.967742)

[0] present

[1] absent

Absent in derived families such as Mureanidae, Chlopsidae, Myrocongridae, Nemichthyidae, Serrivomeridae, Cyematidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae lose this bone protection. Among elopomorphs, except eels, otic canal exits the pterotics and continues to the frontal portion of the neurocranium, thought canal. The rest of Anguilliformes reproduces this pattern with a canal or a gutter relatively long.

Here it is coded [?] in fossils since Belouze (2002), and Belouze *et al.* (2003) indicated that fossilization might have damaged the sensory system.

24. Protection of the mandibular sensory canal. (Character 10 from Forey *et al.*, 1996; Character 25 from Belouze, 2002); (CI: 0.333333; RI: 0.933333)

[0] robust within a bone tube of the mandible

[1] weak within a gutter mostly open

The bone protection of the mandibular sensory canal is weak, almost delicate, in taxa such as Colocongridae, Congridae, Muraenosocidae, Ophichthidae, Nettastomatidae, Albuliformes, and Halosauridae, coded as a state [1]. While, coded as [0], notacanthids, synphobranchids, heterenchelyids, derichthyids, moringuids, muraenosocids, chlopsids, and ophichthids. Coded as inapplicable in absent groups cited in the previous character, and [?] in *Protanguilla*.

25. Supratemporal. (Character 26 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)
[0] providing complete protection (lateral and medial) of supratemporal commissure
[1] incomplete protection (lateral)

The supratemporal is absent in living forms of eels (Robins, 1989; Johnson *et al.*, 2012); nevertheless, the structure was reported for †*Anguillavus* and †*Urenchelys* by Belouze (2002) and coded for this Character as a state [1]. The rest of Elopomorph has massive supratemporals; the best example is in elopids. The *Halosaurus* has well-ossified lateral supratemporals, and a medial supratemporal fused to the supraoccipital, McDowell (1973) named it as “dermosupraoccipital.” Notacanthids present a pattern of non-protective or vestigial protection over the supratemporal. Inapplicable for the living Anguilliformes.

5.1.3 – Suspensorium

26. Quadrate/Hyomandibula joint. (Character 34 from Robins, 1989; Character 27 from Belouze, 2002); (CI: 0.200000; RI: 0.846154)

[0] vertical or slightly inclined forward

[1] strongly inclined forward

[2] inclined backward to the rear edge of the skull

The hyomandibular orientation toward the rear (a line traced from the articulation of the quadrate and hyomandibula), was considered as “basal” characteristic of Anguilliformes (Robins, 1989 – continuous character). In groups which this orientation is forward, like in Congridae, Colocongridae, and extreme examples like in Nettastomatidae, and Serrivomeridae, the previous author considers more derived forms (Figure 18). However, the Saccopharyngoid have the hyomadibular inclined backward to the rear edge of the skull, [2] (Figure 48).

Recently, with the proposal of the new family Protanguillidae (Johnson *et al.* 2012), the present study was able to observe that the *Protanguilla*, as well as the outgroup, (slightly inclined) also have the suspensorium inclined forward.

The Muraenidae Myrocongridae and Chlopsidae follow the vertical or slightly inclined forward [0] (Figure 14).

Belouze (2002, 2003) and Belouze *et al.* (2003) were able to analyze the fossil of †*Anguillavus*, †*Urenchelys germanus*, and †*Eoenchelys*. All the specimens follow the pattern inclined forward. Arratia (1997) defined the state [1] as a synapomorphy of the elopomorphs; nevertheless, it was based only in two specimens of *Elops*.

27. Articulation of the hyomandibular to the neurocranium. (Character 34 from Robins, 1989; Character 28 from Belouze, 2002); (CI: 0.666667; RI: 0.944444)

[0] via a single condyle vis-à-vis a long sphenopterotic facet

[1] via two condyles

[2] via a short anterior condyle losing the second

In many Anguilliformes, the condition of the sphenotic lateral projection covers the anterior condyle and the pterotic hidden the posterior, where the hyomandibular articulates with neurocranium gives more mobility to the suspensorium, coded as [1]. However, Serrivomeridae, *Protanguilla*, Saccopharyngoidei, and †*Enchelion* were coded as a state [2] with only the anterior articulation. The rest of eel fossil taxa share the same pattern of the most

recent forms of eels as a state [1], cited by Belouze (2002). Only one articular facet detected in Notacanthiformes (McDowell, 1973); nevertheless, in *Notacanthus*, *Polyacanthonotus*, and *Lipogenys* the neurocranial facet appears much shorter, restricted to its anterior part and mainly supported by sphenotics (=autosphenotics, McDowell, 1973).

28. Opercular process. (Character 29 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The absence of the posterior process of hyomandibular was observed in Saccopharyngoidei; we will discuss below the opercular series in these taxa (Figure 45). However, a process was recognized in †*Anguillavus* and †*Urenchelys* among forms (Belouze, 2002, 2003; Belouze *et al.*, 2003).

29. Development of posterior process of hyomandibular. (Character 29 from Belouze, 2002); (CI: 0.500000; RI: 0.952381)

[0] near the posterodorsal angle

[1] near the postero-ventral angle of the hyomandibular

The posterior process of hyomandibular is a small protuberance which ends in small cartilage on the distal end (Grande & Beamis, 1998). All fossils investigated here included the posterior process of hyomandibular near the posterodorsal angle as detected by Belouze (2002; 2003) and Belouze *et al.* (2003). The condition varies in Anguilliformes families such as Anguillidae, Derychthyidae, Colocongridae, Protanguillidae, Nemichthyidae, Serrivomeridae, Muraensocidae, Ophichthidae, Nettastomatidae, and Congridae state [0].

30. Postero-dorsal angle of the Hyomandibular. (Character 30 from Belouze, 2002); (CI: 0.400000; RI: 0.896552)

[0] acute angle

[1] slightly equal to a right angle

[2] obtuse

The posterodorsal angle of the Hyomandibula and the posterior border leading to the opercular process are generally perpendicular to each other. Belouze (2002) Belouze *et al.* (2003) described it as a “primitive” condition along elopomorph coded as a state [0] and in myrcongrids, anguillids, moringuids, ophichthids, congrids, colocongrids, nemichtyids, serrivomerids, nettastomatids, derichthyids, *Simenchelys*, and muraenosocids. The slightly equal to a right angle was observed muraenids and chlopsids. The angle is obtuse in all saccopharyngoids, coded here as a state [2].

Inapplicable for fossils forms.

31. Symplectic. (Character 16 from Robins, 1989; Character 17 from Forey *et al.*, 1996; character 33 from Belouze, 2002); (CI: 0.333333; RI: 0.818182)

[0] autogenic

[1] fused to quadrate

Since Johnson *et al.* (2012) described *Protanguilla palau* with a symplectic, this feature has changed the understanding of all living eel forms. Since the bone is only known in the basal Elopormorpha, the new taxa brought a new concept of symplectic fusion to the quadrate

(Figures 20 and 26). Nevertheless, in this study, we will keep the fusion of the symplectic and quadrate for all the eel families except for Protanguillidae (Johnson *et al.*, 2012).

The same connotation was used for fossil forms, although Belouze (2002) and Belouze *et al.* (2003) stated that symplectic is fused “still autogenic nevertheless very intimately housed in a posteromedial gutter of the square.”, coded as present in †*Enchelion*, and fused for all other fossils.

32. Hyomandibular/quadrate joint. (Character 34 from Belouze, 2002); (CI: 0.142857; RI: 0.760000)

[0] unsutured

[1] interdigital suture

Hyomandibular/quadrate joint unsutured is the primitive state of basal teleostean fishes (Arratia, 1997); nevertheless, in synphobranchids (except *Simenchelys*), heterenchelyids, congrid (except heterocongrins and *Ariosoma*), nemichthyids, saccopharyngoidei, nettastomatids, ophichthids, muraenosocids, colcongrids, derichthyids, moringuids, myrocongrids, chlopsids and muraenids, these structures are sutured. Hyomandibula/quadrate joint unsutured is presented among the rest of elopomorph and Anguillidae, Protanguillidae,

Simenchelyinae, Serrivomeridae, *Ariosoma*, and Heterocongriane. We coded inapplicable [-] for fossil forms.

33. Hyomandibular/quadrato joint in adults. (Character 34 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] highly mobile synchondrosis

[1] not very mobile

The spiny eels (Notacanthiformes) are incredibly flexible comparing to other Elopomorphs. The metapterygoid reduction for this group could explain the high mobility of the jaw. Although the joint of Elopiformes and Albuliformes are not sutured, their mobility is not high. Coded as a state [1]. Within eels, Anguillidae, Protanguillidae, Simenchelyinae, Serrivomeridae, *Ariosoma*, and Heterocongriane, the hyomandibular/quadrato joint is unsutured; nevertheless, not very mobile. We coded inapplicable [-] for fossil forms, and the families cited as an interdigital suture.

34. Palatine. (Character 35 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The character initially proposed by Tighe (1989) and supported by Belouze (2002) was not observed here for Serrivomeridae, in which palatine is sutured with the ethmo-vomer lateral projections (Figure 18). We noticed in this study a lateral projection of the ethmo-vomer anterior to the orbit connected by ligaments with the anterior tip of the ectopterygoid (=palatopterygoid, Böhlke, 1989) in Colocongridae, Congridae, and Nettastomatidae (Figure 23). Although these ligaments are transcendent even after the cleared and staining procedure, we understand that these connections between the ectopterygoid and lateral projection are fused in Serrivomeridae and connected by ligaments in the other three families. Belouze (2002, 2003) and Belouze *et al.* (2003) also cited these features as "palatine processes"; nevertheless, the palatine was not observed in †*Anguillavus*, †*Eoenchelys* and, it is uncertainty in †*Urenchelys*. The palatine is present in Outgroup (Figure 20).

Another structure noticed by Belouze (2002, 2003) and Belouze *et al.* (2003) to "dermopalatine(?)" refers still unknown. We understand it is the same condition we described above; the palatine and autopalatine are lost in Anguilliformes. Dorsal process of ectopterygoid connecting the medial surface of the adjacent infraorbital present only in Albuliformes is

another remarkable feature and possible variation of the connection with the ectopterygoid in Elopomorpha (Forey, 1973).

35. Dermopalatine. (Character 35 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Dermopalatine is absent in all Anguilliformes (Figures 17 and 18), including extant and fossil forms reported by Belouze (2002, 2003) and Belouze *et al.* (2003). Present in basal elopomorphs (Figure 20).

36. Connection between ectopterygoid and lateral process of the ethmo-vomer. (CI: 0.500000; RI: 0.965517)

[0] absent

[1] present

As described above in Character 34, Colocongridae, Congridae, Serrivomeridae, and Nettastomatidae (Figures 18 and 23) presented the connection between ectopterygoid and lateral process of the ethmo-vomer.

Inapplicable [-] for Saccopharyngoidei.

37. Connection between ectopterygoid and lateral process of the ethmo-vomer. (CI: 1.000000; RI: 1.000000)

[0] separated by ligaments

[1] sutured

Nettastomatids, Colocongrids, and Congrids have the connections by ligaments which were not stained red nor blue, retaining hyaline as illustrated in the annex (Figure 23). Serrivomerids specimens misunderstood the connections as a palatine structure (Tighe, 1989), and, nevertheless, there is no evidence of the bone even in the *leptocephalus* stage of the current family, as we discussed in Character 36. We observed in serrivomerids the connection between ectopterygoid and lateral process of the ethmo-vomer sutured (Figure 18), is a different state from colocongrids, congrids, and nettastomatids. Inapplicable for the rest of the elopomorphs.

- 38. Metapterygoid in adults. (Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

As it was observed by Johnson *et al.* (2012), Belouze (2002, 2003) and Belouze *et al.* (2003), metapterygoid is present only in Outgroup, *Protanguilla*, †*Anguillavus*, and †*Urenchelys* (Figures 17 and 26).

Also present in †*Anguillavus* and †*Urenchelys* (Figure 36) reported by Belouze (2002; 2003) and Belouze *et al.* (2003).

- 39. Autogenic premaxillae. (Character 29 from Robins, 1989; Character 20 from Forey *et al.*, 1996; Character 39 from Belouze, 2002; Johnson *et al.*, 2012); (CI: 0.333333; RI: 0.846154)**

[0] present

[1] absent

Many authors discussed the fusion and loss of the premaxillae in Anguilliformes (Norman, 1926; De Beer, 1937; Robins & Robins, 1971; Leiby, 1979; Böhlke, 1989 – different authors; Eagderi & Dominique, 2010). The first author to notice the presence of premaxillae in specimens of *Derichthys* was Reagan (1912), and he cited that it was the unique condition among the eels since he never found evidence of fusion. Trewavas (1993) and Robins & Robins (1989b) also indicated the presence of this bone in the same taxa, although the Robins & Robins (1989) considered the pre-maxillae fused to the ethmo-vomer among Anguilliformes. Nevertheless, the presence of the small premaxillae bone lateral to the ethmo-vomer tip anterior to maxillae in *Protanguilla*,

Johnson *et al.* (2012) described the structure as unique among Anguilliformes, including the specimens, disregarding the past evidence of the previous studies cited here (Figure 25). For our understanding, the pre-maxillae fusion is wrongly interpreted, since de Beer (1926) and Leiby (1979, 1984) cited the presence of the premaxillae in leptocephalus of Anguillidae and Ophichthidae; nevertheless, in both studies, the bone seems to have been lost during the formation of the specimens.

Extensive research on the development of the *Ariosoma balearicum* (Congridae) was conducted by Hulet (1978) who observed that the premaxillae are two separate bones associated with tiny teeth, no lateralis pits or canals associated; nevertheless, not part of the rostral

cartilage. In another ontogenetic study, Castle (1984) indicated in “Dysommataidae” (synphobranchids) the pair of premaxillary teeth are lost post-metamorphic specimens. There is no evidence on the premaxillae fused with the ethmo-vomer based on larval development, or sutures on the tip of those specimens examined. We corroborate with Reagan (1912), Trewavas (1933) and Robins & Robins (1989b) in this study, since we found in *Derychthys* (Figure 21) the presence of the premaxillae in front of the ethmo-vomer. Moreover, the same bone was not observed in *Nessoramphus*, in the same family.

We concluded that the premaxilla is present in leptocephalus and it could be lost or not during the post-metamorphic stage. Belouze (2002; 2003) and Belouze *et al.* (2003) also reported the presence of premaxillae in †*Anguillavus*, †*Urenchelys germanus*, and †*Luenchelys minimus* (these last taxa were not examined here).

40. Premaxillae. (CI: 0.500000; RI: 0.500000)

[0] separated by ethmo-vomer

[1] in front of the ethmoid

The premaxillae fused only in *Derichthys* (Figure 21). It is worth to mention that the structure is anterior to the ethmo-vomer, different from *Protanguilla* in which it is lateral (an

autapomorphy for the family – Figure 25). This observed pattern in all *leptocephalus* was previously described by Norman (1926), Hulet (1978) and Leiby (1979, 1984).

The presence of premaxillae lateral to ethmo-vomer in †*Anguillavus*, †*Urenchelys germanus* was also reported by Belouze (2002) and Belouze *et al.* (2002)

41. Supramaxilla. (Character 28 from Robins, 1989; Character 44 from Belouze (2002); (CI: 0.500000; RI:0.833333)

[0] present

[1] absent

The presence of the supramaxilla is observed in Elopiformes, Albuliformes, and Haulosauridae (Figure 20). The supramaxilla is absent in all extant and eel fossils and Notacanthidae (Belouze, 2002; Kanehira *et al.* 2012)

42. Supramaxilla. (Character 44 from Belouze, 2002); (CI:1.000000; RI: 1.000000)

[0] two

[1] one

Elopiformes has one or two supramaxilla (Figure 20), whereas in Albuliformes and Haulosauridae has only one supramaxilla. Inapplicable [-] state for Anguilliformes and Notacanthidae.

43. Anterior tip of the Maxillar. (Character 41 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] without well-individualized process

[1] with a well-developed process

The anterior tip of the maxilla, without a well-individualized process, it is a synapomorphy that group Anguilliformes and Notacanthiformes (Figure 22). The plesiomorphic state [0] is a straight anterior tip for Albuliformes and Elopiformes, without well-individualized process.

44. Anterior tip of the Maxillary well-individualized process with subterminal.

(Character 41 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] double process

[1] single process

The synphobranchids bear two maxillary processes which articulate with the rostrum (Robins & Robins, 1989), forming a pedicel that fits perfectly on the ethmo-vomer (Figure 22). The rest of the Anguilliformes possess a single (Figure 24), including the forms (Belouze, 2002).

45. Maxilla. (Character 43 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] exceeding the level of the coronoid process

[1] not reaching

This feature is a synapomorphy for Elopiformes, and the rest of the elopomorph; the maxillary does not reach the coronoid process.

46. Posterior extremity of the maxilla. (Character 43 from Belouze, 2002); (CI: 0.250000; RI: 0.812500)

[0] massive

[1] tapered

The character [0] observed in the Outgroup + *Protanguilla* + Heterocongrinae + *Simenchelys* + †*Urenchelys germanus* (Figures 22 and 25), the maxillary bone is almost the same width, or sometimes the posterior part is slightly wider than the anterior portion.

The other state [1] comprises the maxillary delicate with the posterior portion slender and notably less extensive than the anterior part (Figure 17), in the remaining Anguilliformes.

Inapplicable for Monognathidae which maxilla is lost.

47. Lower jaw. (CI: 0.666667; RI: 0.966667)

[0] shorter than neurocranium length

[1] equal or slightly larger

[2] more than 1.5 times larger

The lower jaw (dentary + angulo-articulo-retroarticular) has the same length as the neurocranium in Muraenidae (Figure 14), Myrocongridae, Chlopsidae, and Synaphobranchidae (except *Simenchelys*). In saccopharyngoids, the lower jaw is exceptionally long, something more than ten times larger than the head (Figure 45). Robins & Robins (1989) considered the prognathous mandibular as the pleomorphic state; nevertheless, the condition is variable in different groups of eels, and we did not find any evidence of it.

48. Articular and angulo-retroarticular. (Character 30 from Robins, 1989; Character 45 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] autogenous

[1] fusion of all components

The bones of the lower jaw are unfused in many teleostean fishes as reported by Hilton & Lavoué (2018). Such elements like articular, angular, and retroarticular are autogenous in *Arapaima* and *Heterotis*, or anguloarticular and retroarticular are autogenous in *Osteoglossum* (Hilton & Lavoué, 2018). The outgroup presents a distinct morphology with the articular free and fused [0] to anguloretroarticular in Elopiformes, Albuliformes, and Notacanthiformes (Figure 20).

49. Coronoid process of the dentary. (Character 48 from Belouze, 2002); (CI: 0.166667; RI: 0.814815)

[0] poorly developed

[1] well developed

The coronoid process is poorly developed [0] in ophichthids, nemichthyid, derichthyids, heterocongrins, nettastomatids, serrivomerids, *Macrocephenchelys*, saccopharyngoids, and †*Urenchelys*.

50. Coronoid process of the dentary. (Character 48 from Belouze, 2002); (CI: 0.250000; RI: 0.947368)

[0] posterior area of the dentary

[1] displaced anteriorly

Coronoid process is displaced anteriorly in chlopsids, myrocongrids, and muraenids.

Displaced posteriorly in anguillids, heterenchelyids, congrid, colococongrid, nemichthyid, derichthyids, moringuids, nettastomatids, muraenosocids, serrivomerids, saccopharyngoids, ophichthid, synaphobranchids, *Protanguilla*, and Outgroup possesses.

51. Endopterygoid. (Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Elopiformes, Albuliformes and Notacanthiformes also have a dermal endopterygoid (Figure 20). Nevertheless, this element is absent in all extant eels, which have a single bone, the ectopterygoid (=palatopterygoid, Böhlke, 1989). This study corroborates Johnson *et al.* (2012) who propose the endopterygoid was lost in the extant eels (Figure 17).

**52. Maxillae. (Character from Tchernavin, 1947; Character E from Robins (1989))
(CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Although Robins (1989) mentioned that it is absent in all saccopharyngoids, we agree with Trewavas (1933) and Tchernavin (1947a, b) in which the considerably derivate maxillae are present in cyematids, eurypharyngids, and saccopharyngids, with the only exception of monognathid specimens.

**53. Dentary and angulo-articulo-retroarticular. (Character from Tchernavin, 1947);
(CI: 0.500000; RI: 0.500000)**

[0] separated

[1] fused

The condition in which the dentary and angulo-articulo-retroarticular are fused in one single structure was reported by Tchernavin (1947) and Bertelsen *et al.* (1989) in eurypharyngids and some species of monognathids.

5.1.4 – Opercular Series

54. Opercle. (CI: 1.000000; RI: 1.000000)

[0] free

[1] fused to hyomandibular

The condition of the opercle fused to the hyomandibula is only present in saccopharyngoidei (Figure 45), which is better discussed in character 190.

55. Opercular bones shape opercle. (Character 50 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] Square-shaped

[1] rostrocaudally elongated [1]

We also followed McAllister (1968), which the state [1] is defined by rostrocaudally elongated opercle whose overall body and articulate through the opercular process with hyomandibular are separated by a collar and ventrally bordered, posteriorly or even dorsally,

by the curved posterior branch of the subopercle. Johnson *et al.* (2012) described an eel “pattern” as the opercle rostrocaudally elongated with a bottle-neck articular condyle and broadly bordered ventrally by subopercle (Figures, 17, 18, 22 and 24).

In fossil taxa, Belouze (2002, 2003) and Belouze *et al.* (2003) described an oval-shaped opercular body and a curved edge, funnel-shaped anterior a moderate subopercular coil in †*Anguillavus*, †*Urenchelys*, and †*Eoenchelys*); nevertheless, coded as a state [1]. The outgroup was coded as a squared bone pattern [0] (Figure 20) and inapplicable [-] for saccopharyngoids.

56. Preopercle. (Character 15 from Robins, 1989; Character D from Robins (1989); Character 50 from Belouze (2002)) (CI: 1.000000 RI: 1.000000)

[0] present

[1] absent

The absence of preopercle is a synapomorphy of Cyematidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae (Figure 45).

57. Preopercle. (Character 50 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] well-developed

[1] reduced

The preopercle is reduced to a preopercular canal in Nemichthyidae without a laminar expansion, then coded here as a state [1] (Figure 54).

**58. Subopercle. (Character 15 from Robins, 1989; Character D from Robins, 1989);
(CI: 0.500000; RI: 0.888889)**

[0] present

[1] absent

The absence of preopercle is a synapomorphy for saccopharyngoids, *Nemichthys*, and *Dysomma* (Figures 45 and 54).

**59. Interopercle. (Character 15 from Robins, 1989; Character D from Robins 1989);
Character 52 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

The only taxa lacking interopercle is *Nemichthys* (Figure 54), although Robbins (1989) proposed that in saccopharyngoids this bone is absent, we discuss that bone is associated with *Levator operculi* in Character 190 (Figure 48).

60. Interopercle. (Character 52 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] well-developed

[1] tubular or need-like

Eadgeri (2010) reported a long and slender bone connecting a posterior portion of the angulo-articulo-retroarticular to a “depressor muscle,” musculature that inserted on the posterior portion of the neurocranium. We understand that this structure is an interopercle (=sesamoid bone, Eadgeri, 2010) and it is reduced to a needle-like shaped in saccopharyngoid, which is associated with the posterior part of the jaw (Figure 48). In Eurypharyngidae, Eadgeri

(2010) identifies it as a sesamoid bone; nevertheless, we will discuss this in Character 190 which the *Levator operculi pars mandibulo-primordialis* fibers is associated with the bone in all saccopharyngoids and even *Labbichthys* and *Nemichthys* (Figure 54). The interopercle is laminar, but the size varies in different eels and elopomorphs families.

61. Posteroventral part of subopercle along the ventral edge of the opercle.

(Character 54 from Belouze, 2002); (CI: 0.500000; RI: 0.964286)

[0] nevertheless restricted underneath

[1] curved behind (sickle-shaped)

Forey (1973) reported that the development of the anterodorsal portion of the subopercle in Albuliformes is expanded ventrally compared to Elopiformes, and it is similar to few fossil eels that reaches the level of the articular condyle of the opercle (Belouze, 2002, 2002; Belouze *et al.*, 2003), coded as a state [0].

In *Protanguilla* and Muraenidae, it is restricted to the ventral part of the opercle not following the Anguilliformes “pattern.”

Whereas in remaining Anguilliformes, a sickle-shaped subopercle (Figures 17 and 22).

Inapplicable for saccopharyngoids, *Nemichthys*, and *Dysomma*

5.1.5 – Ventral elements of the hyoid arch

- 62. Gular plate. (Character 14 from Robins, 1989; Character 23 from Forey *et al.*, 1996; Character 49 from Arratia, 1997; Character 56 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

This structure is only observed in Elopiformes and Albuliformes. Absent in the remaining elopomorphs, including forms reported by Belouze (2002, 2003) and Belouze *et al.* (2003).

- 63. Branchial arches. (Character from Robins, 1989; Character 22 from Forey *et al.*, 1996; Wiley & Johnson, 2010; Character from Johnson *et al.*, 2012; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)**

[0] beneath and articulating with the neurocranium

[1], displaced posteriorly free from neurocranium

This condition of the branchial arches beneath and articulating with the neurocranium was only detected in remaining elopomorphs without eels (Figure 24).

64. Tooth plates covering the surface of the basihyal and/or the basibranchials.

(Character 57 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Another condition in elopomorphs, except eels, is the presence of many tooth plates covering the branchial arch flooring coded here as a state [0]. The tooth plate covering hyoid and branchial elements was not detected in Anguilliformes, including the forms (Belouze, 2002, 2003; Belouze *et al.*, 2003).

65. Interhyal in adults. (Character 57 from Belouze, 2002; Character from Johnson

***et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

McAllister (1968) observed only in leptocephalus among eels, the presence of the interhyal articulating the connection between posterior ceratohyal and the ventro-posterior surface of the hyomandibula, that structure is lost in Anguilliformes. Hulet (1978) noted small cartilage that he identified as “epihyal” (=posterior ceratohyal), but none evidence of interhyal. We propose that the interhyal is lost in eels (Figure 22).

Along the remaining Elopomorpha, the interhyal is present as a plesiomorphic state (Figure 27).

This character is challenging to identify in fossils (Belouze, 2002; 2003; Belouze *et al.*, 2003) and coded here as [?].

66. Hypohyal. (Character 59 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.333333; RI: 0.900000)

[0] present

[1] absent

The hypohyal is lost in *Nemyctys* (although present in *Avocettina* and *Labichthys*), saccopharyngoids, and Muraenidae.

For all the fossils, the presence of hypohyal was reported (Belouze, 2002; Belouze *et al.*, 2003).

67. Hypohyals. (Character 59 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.333333; RI: 0.857143)

[0] two

[1] one

Johnson *et al.* (2012) cited two distinct hypohyals on the anterior end of anterior ceratohyal. That feature was considered as a “primitive” state along elopomorph, whereas Elopiformes, Albuliformes, Notacanthiformes, †*Urenchelys*, and *Simenchelys* are the only groups with a pair of hypohyals (Figures 22 and 27). Worth of mentioning that *Simenchelys parasitica* was the only taxa with two separated hypohyals (not considering *Protanguilla*).

A single bone was detected in *Coloconger*, Serrivomeridae, Chlopsidae, Synapobranchidae (except *Ilyophis*), *Myroconger*, Ophichthidae, Muraenesocidae,

Nemichthyidae (except *Nemychthys*), anguillids, moringuids, heterenchelyids, and congrid.

All other recent Anguilliformes examined have no separate hypohyal.

Absent in Saccopharyngoidei and muraenids (Figure 28).

Belouze (2002), Belouze *et al.* (2003), Johnson *et al.* (2012) cited the presence of two separated hypohyals in †*Urenchelys*; nevertheless, only one in †*Anguillavus*, †*Eoenchelys*, and †*Enchelurus*.

68. Basihyal in adults. (Character 59 from Belouze, 2002); (CI: 0.333333; RI: 0.900000)

[0] present

[1] absent

The absence of the basihyal (=glossohyal, Böhlke, 1989) was reported in a few groups such as saccopharyngoids, *Avocettina* and *Nemichthys*, and Muraenidae (except for *Anarchias* with a thin bone) (Figure 28).

69. Urohyal in adults. (Character 60 from Belouze (2002); (CI: 0.333333; RI: 0.894737)

[0] present

[1] absent

Urohyal was observed in *Cyema* only in the larval stage as well as the remaining hyoid arch. Nevertheless, the structure is lost, the only two lasting bones are the ceratohyal (the anterior and posterior fused in a single structure). Absent in derived forms such as *Nemichthys*, saccopharyngoids, and Muraenidae (Figure 28).

Present in all fossils analyzed by Belouze (2002, 2003) and Belouze *et al.* (2003).

70. Urohyal. (Character 60 from Belouze, 2002); (CI: 0.500000; RI: 0.875000)

[0] well-developed posterior process

[1] with the small posterior process

Urohyal reduced to a little square-shaped structure restricted to the hyoid arch center, detected in myrocongrids, chlopsids, and anguillids coded here as a state [1].

The state [0] is applicable for remaining taxa, including fossils.

71. Ceratohyal. (Character 62 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] divided into anterior and posterior

[1] single bone indistinguishable

In all representants of the deep-sea eel groups (saccopharyngoids), the hyoid arch is indistinguishable as reported in the previous characters. However, in the leptocephalus stage of *Cyema*, it is possible to distinguish the elements (Figure 28a).

72. Anterior ceratohyal. (=ceratohyal, Böhlke, 1989); (Character 19 from Robins, 1989; Character 61 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] longer than posterior ceratohyal (=epihyal, Böhlke, 1989)

[1] equal to or shorter than posterior ceratohyal

Posterior ceratohyal almost equal or longer than anterior ceratohyal is a synapomorphy of Anguillifomes (Figures 22 and 28), including all forms (Belouze, 2002, 2002; Belouze *et al.*, 2003). Inapplicable for Saccopharyngoid.

73. Anterior ceratohyal. (=ceratohyal, Böhlke, 1989); (Character 19 from Robins, 1989; Character 61 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] without a posterior projection over posterior ceratohyal (=epihyal, Böhlke, 1989)

[1] with posterior projection overlapping posterior ceratohyal

The posterior projection of the anterior ceratohyal is unique among eel families, including forms (Belouze, 2002), except for the *Derichthys* and some ophichthids. The outgroup does not have projection overlapping posterior ceratohyal. Inapplicable for Saccopharyngoid

74. Branchiostegals rays. (Character C from Robins, 1989; Character 62 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Branchiostegals rays are absent in Saccopharyngoid (Figure 45), unique case in Elopomorpha.

75. Posterioormost branchiostegal. (Character from Johnson *et al.*, 2012); (CI: 0.400000; RI: 0.900000)

[0] rod-like distally

[1] spoon-like

[2] flat expansions distally

The presence of one to four branchiostegal with spatulate or flat expansions distally is a synapomorphy of all Anguilliformes, including forms (Belouze, 2002, 2003; Belouze *et al.*, 2003). Spatula expansions [1] of the branchiostegals are present in anguillids, synphobranchids, heterenchelyids, moringuids, and *Protoanguilla* (Figures 24, 26 and 56). For

the rest of eels, the expansion is not well developed [2], ending flat nevertheless not rounded rays. Inapplicable for Saccopharyngoid

76. Branchiostegals rays. (Character 62 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] attached in more significant numbers to the anterior ceratohyal or equally on the anterior ceratohyal and posterior ceratohyal

[1] more concentrated on the posterior ceratohyal

McAllister (1968) cited this synapomorphy for extant Anguilliformes, confirmed by Johnson *et al.* (2012), and corroborated in this study (Figure 22). The same pattern occurs in the fossils cited by Belouze (2002, 2003).

The branchiostegals rays are equally in the remaining elopomorphs. Inapplicable for Saccopharyngoid

77. Number of branchiostegals rays. (Character 63 from Belouze, 2002); (CI: 0.285714; RI: 0.901961)

[0] more than 20

[1] between 10 and 20

[2] less than 10

Elopiformes and ophichthids have the highest number of branchiostegals ray among elopomorphs. The state [1] was observed in Albuliformes, Notacanthiformes, synaphobranchids (except *Simenchelys*), *Protanguilla*, anguillids, nemychthids, muraenosocids, myrocongrids, heterenchelyids, and chlopsids. Moreover, less than ten branchiostegals (state [2]) were reported in muraenids, serrivomerids, derichthyids, nettastomatids, and congrids — state [0] for all Outgroup.

Inapplicable for Saccopharyngoid.

78. Branchiostegals. (Character from McCosker, 1977); (CI: 1.000000; RI: 1.000000)

[0] rays not overlapping each other of the different sides

[1] from one side protruding the other side

The branchiostegals rays from one side overlapping the other is a synapomorphy of ophichthids (Figure 34).

79. Branchiostegals overlapping. (Character from McCosker, 1977); (CI: 1.000000; RI: 1.000000)

[0] originating from anterior ceratohyal and posterior ceratohyal

[1] free from anterior ceratohyal

In Myrophinae all the overlapping branchiostegals originate from anterior and posterior ceratohyal. Meanwhile, in Ophichthinae, the first branchiostegals rays are free from anterior ceratohyal.

Inapplicable for other elopomorphs.

5.1.6 – Branchial arches

80. Gill arches. (Character 19 from Robins, 1989; Character 61 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] underneath braincase

[1] free from braincase and displaced posteriorly

The most cited character of Regan (1909, 1912), Trewavas (1933), Robins (1989), Forey *et al.* (1996) and more recently Johnson *et al.* (2012), where the gill arches displaced posteriorly is a synapomorphy among extant eels and fossils (Figure 24). In the Outgroup, underneath neurocranium (Figure 44).

81. Gill rakers. (=branchiospines, Belouze, 2002); (Character 26 from Robins, 1989; Character 24 from Forey *et al.*, 1996; Character 65 from Belouze, 2002; Character from Wiley & Johnson, 2010; Character from Johnson *et al.*, 2012; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.916667)

[0] present

[1] absent

The loss of gill rakers was used to separate the Anguilliformes from the rest of the elopomorphs (Regan, 1912; Greenwood *et al.*, 1966; Robins, 1989; Forey *et al.*, 1996; Arratia, 1997; Belouze, 2002). Nevertheless, Johnson *et al.* (2012) indicated the presence of small gill rakers in *Protanguilla* among Anguilliformes (Figure 30), including the fossils forms (Belouze, 2002, 2003; Belouze *et al.* 2003), coded as [0].

However, we detected the presence of unossified gill rakers in Heterocongrinae (*Heteroconger* and *Gorgasia*) on all branchial arches, and these features seem to be compound by small uncalcified structures (Figure 39).

- 82. Gill rakers. (=branchiospines, Belouze, 2002); (Character 26 from Robins, 1989; Character 24 from Forey *et al.*, 1996; Character 65 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] calcified

[1] not calcified

We have commented above that all the outgroup + *Protanguilla* is bearing ossified gill rakers (Figure 30). The heterocongrins bears unossified gill rakers on all branchial arches and compound by uncalcified structures (Figure 39). Inapplicable for the remaining eels.

- 83. Basibranchial 1. (Character from Nelson, 1966; Character 66 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 0.333333; RI: 0.920000)**

[0] present

[1] absent

In saccopharyngoids, all the basibranchial elements are lost, although we detected the presence of basibranchial on *Cyema* in the leptocephalus stage, we coded here as a state [1]. Also, all these bones are absent [1] in Muraenidae, Chlopsidae, and Myrocongridae (Figure 49).

In other families, some derived forms like *Dysommima* among synphobranchids, and *Schultzidia* in Ophichthids, lost all the basibranchial 1-4 elements. Present in the remaining eels (Figure 29).

- 84. Basibranchial 1 in adults. (Character from Nelson, 1966; Character 66 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)**

[0] ossified

[1], cartilaginous

The cartilaginous basibranchial 1 was only found in *Labbichthys* and *Avocettina*.

- 85. Basibranchial 1. (CI: 1.000000; RI: 1.000000)**

[0] free

[1] fused to the basihyal (=glossohyal, Böhlke, 1989)

A synapomorphy for Nettastomatidae, whereas basibranchial 1 is fused to the basihyal (=glossohyal, Böhlke, 1989 – Figure 60A). In all other groups, the Basibranchial 1 is free from basihyal

86. Basibranchial 2 in adults. (Character from Nelson, 1966; Character 67 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 0.166667; RI: 0.838710)

[0] present

[1] absent

As it was described in character 98, *Nemichthys*, and *Avocettina* (nemichthyids – both lost basibranchial 2-4), *Venefica*, *Nettenchelys* (not examined here), and *Nettastoma* (nettastomatids), miss the basibranchial 2. *Dysomma* and *Moringua* lost the basibranchial 2-4.

87. Basibranchial 2 in adults. (Character from Nelson, 1966; Character 67 from Belouze, 2002; Character from Springer & Johnson, 2015); CI: 0.200000; RI: 0.840000)

[0] ossified

[1] cartilaginous

Cartilaginous in *Neoconger* (moringuids), serrivomerids, *Facciolella* (nettastomatids) and ophichthids.

88. Basibranchial 3 in adults. (Character from Nelson, 1966; Character 68 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 0.200000; RI: 0.894737)

[0] present

[1] absent

As it was described in character 86 and 89, Basibranchial 3 is also absent in serrivomerids and anguillids.

- 89. Basibranchial 3 in adults. (Character from Nelson, 1966; Character 68 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.850000)**

[0] ossified

[1] cartilaginous

Basibranchial 3 is cartilaginous in ophichthids, *Neoconger*, nettastomatids, and heterenchelyids.

- 90. Basibranchial 4 in adults. (Character from Nelson, 1966; Character 69 from Belouze, 2002; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.903226)**

[0] present

[1] absent

Basibranchial 4 ossified is a rare condition among teleostean (Springer & Johnson, 2015). In all elopomorphs, the Basibranchial 4 is cartilaginous or absent in taxa cited above in characters 86 and 89.

- 91. Hypobranchial 1. (Character from Nelson, 1966; Character 69 from Belouze, 2002); (CI: 0.500000; RI: 0.928571)**

[0] present

[1] absent

The absence of the hypobranchial 1 is independently lost in murenins and saccopharyngoids, except *Cyema*.

- 92. Hypobranchial 2 in adults. (Character from Nelson, 1966; Character 69 from Belouze, 2002); (CI: 0.500000; RI: 0.928571)**

[0] present

[1] absent

The absence of hypobranchial 2 is lost in murenines and saccopharyngoids, except *Cyema*.

- 93. Hypobranchial 3 in adults. (Character from Nelson, 1966; Character 69 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.500000; RI: 0.956522)**

[0] present

[1] absent

The absence of hypobranchial 3 was detected in chlopsids, myrocongrids, muraenids, and saccopharyngoids, except *Cyema*. In all the remaining elopomorphs, the hypobranchial 3 is present, cartilaginous or ossified.

- 94. Hypobranchial 3. (Character from Nelson, 1966; Character 69 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.500000; RI: 0.928571)**

[0] rod-shaped ossified

[1] cartilaginous in adults

The hypobranchial 3 is cartilaginous in all eels, except the groups cited above. The rest of the elopomorph with hypobranchial 3 ossified.

- 95. Pharyngobranchial 1 in adults. (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 70 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.333333; RI: 0.833333)**

[0] present

[1] absent

First pharyngobranchial absence in all extant eels (Figure 29), however present in *Ariosoma* and chlopsids, except *Chilorhinus*, and not found in the fossils forms (Belouze, 2002, 2003; Johnson *et al.* 2012). Hulet (1978) stated that in leptocephalus, the first two arches are of the pharyngobranchial are cartilaginous, and (as we cited in pre-maxillae), this structure is in adult eels.

- 96. Uncinate process in epibranchial 1. (Character 25 from Forey *et al.*, 1996; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Absent in all current Anguilliformes (Figures 29 and 31), and absent in all fossils forms nevertheless coded as [?].

- 97. Uncinate process in epibranchial 2. (Character 25 from Forey *et al.*, 1996; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Absent in all current Anguilliformes (Figures 29 and 31), and absent in all fossil forms nevertheless coded as [?].

- 98. Uncinate process in epibranchial 3 (Character 25 from Forey *et al.*, 1996; Character from Wiley & Johnson, 2010; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Absent in all current Anguilliformes (Figures 29 and 31), and absent in all fossil forms nevertheless coded as [?].

- 99. Pharyngobranchial 2 in adults. (Character from Nelson, 1966; Character 71 from Belouze, 2002); CI: 0.333333; RI: 0.900000)**

[0] present

[1] absent

Pharyngobranchial 2 is absent in Muraenidae, Mycongridae, saccopharyngoids, coded as [1].

100. Ceratobranchial of the first 3 arches. (Character from Nelson, 1966; Character 72 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] ossified

[1] cartilaginous

Ceratobranchial of the first 3 arches are significantly reduced and cartilaginous in muraenins, Saccopharyngoidei, and the fossil †*Enchelion* (Belouze, 2002; Belouze *et al.*, 2003).

101. Ceratobranchial 5. (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 73 from Belouze, 2002); (CI: 0.250000; RI: 0.842105)

[0] present as an autogenous element

[1] absent

Bertelsen *et al.* (1989) cited the presence of the ceratobranchial 5 in Eurypharyngidae; nevertheless, it is absent in monognatids, saccopharyngids, and Cyematids (Smith *et al.*, 1989 – Figure 61a). Also, the absence of this structure was reported in muraenids, myrocongroids, and many species of ophichthids. Belouze (2002) and Belouze *et al.* (2003) confirmed the presence of the ceratobranchial 5 in †*Enchelion*.

102. Upper pharyngeal toothed epibranchial plates (UTP). (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 75 from Belouze, 2002); (CI: 0.500000; RI: 0.500000)

[0] present

[1] absent

Absent in *Cyema*, saccopharyngids, and eurypharyngids. Not observed in the form (Belouze, 2002). In Notacanthiformes, absent in *Polyacanthonotus* and *Notacanthus* (McDowel, 1973; Kanehira *et al.*, 2012).

103. Upper toothed epibranchial plates. (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 75 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.285714; RI: 0.852941)

[0] organized in multiple elements

[1] two superior pharyngeal plates

[2] single part

The UTP is fused in a single element in muraenids, myrocongrids, heterocongrins, cyematids, congrids *Ariosoma* and *Acromycter*. In all other Anguilliformes, the UTP is divided into two elements, including synphobranchids (Figure 29), *Protanguilla*, anguillids, and congrids. The state [0], for all Outgroup.

- 104. Lower toothed ceratobranchial plates (LPT). (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 75 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Lower toothed ceratobranchial plates are absent in *Notacanthus* and *Polyacanthonotus*, and synapomorphy for Notacanthidae.

105. Lower toothed ceratobranchial plates. (Character from Nelson, 1966; Character 24 from Robins, 1989; Character 75 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] organized in multiple items

[1] arranged as two pharyngeal plates inferior

[2] just one

The multiple series of LPT was first noted by Nelson (1966) who indicated that all Anguilliformes have a single tooth plate associated to ceratobranchial 5, except *Synaphobranchus* which has a series of four plates on each side. This character is relevant for his publication, considering as a primitive character observed in lower teleosts (*Elops*, *Albula*, *Hiodon*, and *Osteoglossum*; Arratia, 1997). After Nelson's analysis, Robins (1971) described the gill arches of *Synaphobranchus affinis*, *S. kaupii*, *S. oregoni*, and *Ilyophis brunneus*, and suggested the number of LPT varies in specimens even among those having one plate (Robbins, 1971; Figure 10). Belouze (2002) also reported the presence of additional small tooth plates in †*Urenchelys germanus*.

106. Basibranchial 3-Basibranchial 4-Hipobranchial 3 complex. (Character from Johnson *et al.*, 2012; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.900000)

[0] pointing forward meeting BB4

[1] entirely separated to BB4

According to Johnson *et al.* (2012), “the Hb3s have narrowed extensions that extend well forward along each side of the well-developed Bb3, which articulates tightly with a well-developed Basibranchial 4 and often has a posterior “tail” that extends below it” (Figure 30).

The outgroup presents this pattern along with *Protanguilla* (the only eel with these characteristics) and *Lypogenis* (Johnson *et al.* 2012; Kanehira *et al.*, 2012). In the remaining Anguilliformes, the Basibranchial 3 is reduced and does not reach the Basibranchial 4; its form varies a lot.

Coded inapplicable in muraenids, chlopsids, serrivomerids, anguillids, myrocongrids, saccopharyngoids, *Nemichthys* where lacking Bb 3 and/or Bb 4. This character was not examined in forms (Belouze, 2002, 2003; Belouze *et al.*, 2003; Johnson *et al.*, 2012), coded here as [?].

107. Position of the epibranchial about occiput. (Character from Johnson *et al.*, 2012);

(CI: 0.500000; RI: 0.933333)

[0] anterior

[1] posterior

All extant eels have the first two epibranchials underneath the occiput, except in *Simenchelys* and *Protoanguilla*, which have the bones located anteriorly.

5.1.8 – Pectoral Girdle and paired fins

108. Pectoral girdle. (Character 11 from Robins, 1989; Character 31 from Forey *et al.*,

1996; Character from Wiley & Johnson, 2010; Character from Johnson *et al.*,

2012); (CI: 1.000000; RI: 1.000000)

[0] attached to the skull

[1] free from the neurocranium

In all eels, including the fossils, the pectoral girdle is free and notably displaced posteriorly from neurocranium (Figure 24). Forey *et al.* (1996) also reported this synapomorphy

for Notacanthiformes + Anguilliformes. In Elopiformes and Albuliformes (the same pattern in basal teleost), the pectoral girdle is attached to the neurocranium.

109. Post-temporal. (Character 12 from Robins, 1989; Character 31 from Forey *et al.*, 1996; Character 76 from Belouze, 2002); (CI: 0.500000; RI: 0.888889)

[0] present

[1] absent

The post-temporal is absent in Anguilliformes; however, further studies should proceed (da Silva, personal communication), and the discussed in Intercalar and Pterotic posterior expansion Character's.

Belouze (2002, 2003) and Belouze *et al.* (2003) observed posttemporal in †*Anguillavus*, †*Enchelion*, and †*Urenchelys germanus* fossil specimens, except in †*Eoenchelys*.

The outgroup shows a very well-defined post-temporal with large bridge postcranium, except in *Notacanthus* and *Lipogenys*.

110. Post-temporal with two previous processes. (Character 24 from Robins, 1989; Character 76 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

**[0] ventral and dorsal, ensuring the connection of the pectoral belt to the neurocranium
[1] with a single anterodorsal process which loses contact with the neurocranium [1],
[2] reduced to their neurodermal component still ossified**

The state [0] is the plesiomorphic condition for Elopiformes and Albuliformes. The synapomorphy for Notacanthiformes is coded here as [1]. For this character, it is essential to emphasize the presence of posttemporal in fossil eels, occurring a post-temporal with a single anterodorsal process which loses contact with the neurocranium, except the †*Enchelion* whereas posttemporal reduced to their neurodermal component still ossified. Inapplicable for the living eels.

111. Supracleithrum. (Character 24 from Robins, 1989; Character 77 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The supracleithrum is absent in all saccopharyngoidei, serrivomerids, nettastomatids (except *Hoplunnis* and *Nettenchelys*), and nemichthyids. However, it is present in all forms following Belouze (2002, 2003) and Belouze *et al.* (2003)

112. Supracleithrum. (Character 24 from Robins, 1989; Character 77 from Belouze, 2002); (CI: 0.333333; RI: 0.948718)

[0] robust

[1] filiform

The well-ossified supracleithrum is present in Elopiforms, Albuliformes, Notacanthiformes, anguillids, moringuids, heterenchelyids, and congrid, and the form †*Anguillavus*, †*Eoenchelys*, and †*Urenchelys* (Belouze, 2002). Filiform in all remaining eel families.

113. Cleithrum. (Character 24 from Robins, 1989; Character 78 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The rare condition of absence of the cleithrum is unique among saccopharyngoids, except in *Cyema*.

**114. Cleithrum. (Character 24 from Robins, 1989; Character 78 from Belouze, 2002);
(CI: 0.333333; RI: 0.882353)**

[0] with a ventral branch at least developed in a robust blade

[1] reduced to a filiform rod

The state for this character coded as [0] in Outgroup examined with a ventral branch well-developed. The robust form is restrained in angullids, heretenchelyids, and fossil †*Anguillavus*, †*Eoenchelys*, and †*Urenchelys germanus* (Belouze, 2002, 2003; Belouze *et al.*, 2003).

The remaining Anguilliformes possesses a filiform rod-shape cleithrum.

115. Scapula. (Character 79 from Belouze, 2002); (CI: 0.142857; RI: 0.828571)**[0] present****[1] absent**

Absent in muraenids, chlopsids, saccopharyngoids, heterocongrins, heterenchenlyids, serrivomerids, nettastomatids (except *Hoplunnis*), and †*Enchelion* (Belouze, 2002; Belouze *et al.*, 2003)

116. Coracoid. (Character 79 from Belouze, 2002); (CI: 0.125000; RI: 0.805556)**[0] present****[1] absent**

Absent in muraenids, chlopsids, saccopharyngoids, heterocongrins, heterenchenlyids, serrivomerids, nettastomatids (except *Hoplunnis*), and †*Enchelion* (Belouze, 2002; Belouze *et al.*, 2003). All remaining examined taxa with the coracoid present.

117. Actinost bones of the pectoral girdle. (Character 79 from Belouze, 2002); (CI: 0.111111; RI: 0.764706)

[0] present

[1] absent

The loss of Actinost bone characterize muraenids, chlopsids, saccopharyngoids (except *Cyema*), heretenchenlyids, , serrivomerids, nettastomatids (except *Hoplunnis*), and †*Enchelion* (Belouze, 2002; Belouze *et al.*, 2003).

The state [0] is present in anguillids, moringuids, muraenosocids, ophichtids, myrocongrids, congrids, *Protanguilla*, colococongrids, derithyids, nemychthids and the outgroup.

118. Pectoral fins. (Character 80 from Belouze, 2002); (CI: 0.166667; RI: 0.807692)

[0] present

[1] absent

The absence of pectoral fins is frequent among eels such as the herentechelyids, chlopsids, muraenids, heterocongrins, *Nettastoma*, *Facciolela*, *Neocyema* (Figure 52). In

monognathids, it seems to be lost. Present in Outgroup, remaining eels (Figure 24) and fossils (Belouze, 2002; Belouze *et al.*, 2003)

119. Position of the pectoral fins. (Character from Mc Dowell, 1973; Character 80 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] low (in the ventral half of the body)

[1] high on the flanks (in the dorsal half)

McDowell (1973) reports a loss connection with the neurocranium. The pectoral fins are displaced to ventral position compared to basal elopomorphs. The state [0] of this character is a synapomorphy of Notacanthiformes + Anguilliformes within the clade Elopomorpha. Unknown state [?] in fossils (Belouze, 2002, 2003; Belouze *et al.*, 2003).

120. Pectoral spine (pectoral splint). (Character from Mc Dowell, 1973; Character 81 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] absent

[1] present

The condition is cited by McDowell (1973), whereas pectoral spine is absent in all elopomorphs, except in extant eels.

121. Postcleithrum. (Character 32 from Forey *et al.*, 1996; Character 82 from Belouze, 2002; Character from Wiley & Johnson, 2010); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Another synapomorphy shared by Notacanthiformes along with extant and fossils of Anguilliformes (including *Protanguilla*) is the absence of postcleithrum (Belouze, 2002).

122. Mesocoracoid. (Character from McDowell, 1973; Character 13 from Robins, 1989; Character 32 from Forey *et al.*, 1996; Character 84 from Belouze, 2002; Character from Wiley & Johnson, 2010); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Forey *et al.* (1996) and Wiley & Johnson (2010) indicate this synapomorphy uniting Notacanthiformes and Anguilliformes. According to McDowell (1973), the absence can be associated with the elevation of the pectoral fin.

123. Pelvic fin. (Character from Robins, 1989; Character 32 from Forey *et al.*, 1996; Character 85 from Belouze, 2002; Character from Wiley & Johnson, 2010); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The only occurrence of pelvic fin among eels observed by Belouze, (2002, 2003) Belouze *et al.* (2003) in †*Anguillavus mazoni* and †*Abisaadia hakeleensis* (Not examined here).

124. Pelvic girdle. (Character from Robins, 1989; Character 32 from Forey *et al.*, 1996; Character 85 from Belouze, 2002; Character from Wiley & Johnson, 2010); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The basipterygium and radials pelvic are absent in eels. The pelvic girdle is absent in extant Anguilliformes, however in fossils (Belouze, 2002, 2003; Belouze *et al.*, 2003), present in †*Anguillavus quadripinnis* (Figure 37).

125. Pelvic swim membranes. (Character from McDowell, 1973; Character 34 from Forey *et al.*, 1996); (CI: 1.000000; RI: 1.000000)

[0] separated

[1] joined on the mid-ventral line

The junction of the pelvic membranes is reduced in the notacanthids as mentioned in McDowell (1973), and it was suggested as a synapomorphy for this group in Forey *et al.* (1996).

5.1.9 – Dorsal, anal and caudal-fin elements

126. Coefficient of concentration of dorsal and anal pterygiophores between the vertebrae. (Character 86 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] one

[1] 2 or more

Condition independently acquired in notacanthids and eels coded here as a state [1], mostly 3 rays coefficient. One pterygiophore coefficient [0] was found in Albuliformes, halosaurids, and Elopiformes.

127. Lepidotrichia of the unpaired fins. (Character 87 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Absent in some ophichthids *Myriophis*, *Ahlia* and *Neenchelys*. McCosker (1977) describes the absence of ossified fin supports even if a membrane is for some derived groups of ophichthids (not included in the analysis).

128. Lepidotrichia of the unpaired fins. (Character 87 from Belouze, 2002); (CI: 0.333333; RI: 0.833333)

[0] segmented

[1] not segmented

The lepidotrichia is ossified and paired, although it can be unsegmented or unbranched in Saccopharyngoidei, heterocongrins, nemychids, myrocongrids, and notacanthids, as coded here as a state [1].

Belouze (2002, 2003) and Belouze *et al.* (2003) cited that the rays of the taxa are segmented, nevertheless the absence of segmentation first rays were detected for †*Urenchelys germanus*.

129. Distinct caudal fin. (Character 37 from Forey *et al.*, 1996); (CI: 0.500000; RI: 0.909091)

[0] absent

[1] present

A distinct caudal fin was proposed by Forey *et al.* (1996:188) for Elopomorph and described as a “clear gap between the fin rays of dorsal and/or anal fins supported by radials and the caudal fin rays supported by hypurals.”

The absent distinct caudal fin observed in Saccopharyngoids (Bertelsen *et al.*, 1989) and notacanthids (McDowel, 1973; Forey *et al.*, 1996) and corroborated in this study.

130. Uroneural. (Character 104 from Arratia, 1997; Character 93 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Uroneural is absent in all saccopharyngoid.

131. Uroneural number. (Character 37 from Forey *et al.*, 1996; Character 104 from Arratia, 1997; Character 93 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] three

[1] two

[2] one

Elopiformes possess three uroneurals, whereas two uroneurals in Albuliformes and Notacanthiformes (Forey, 1973; McDowell, 1973; Kanehira *et al.*, 2012). In Anguilliformes, †*Anguillavus*, and †*Urenchelys*, there is just one uroneural.

Some reports indicate that †*Eoenchelys* may have retained a second small uroneural, which is still debatable (Belouze, 2002). Nevertheless, this character is coded herein as [?].

132. Anterior displacement of the uroneural. (Character 103 from Arratia, 1997; Character 94 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] reaching the preural centrum 2

[1] not reaching the level of the preural centrum 2

The analysis performed by Arratia (1997) considered as primitive the condition in which the uroneural is contacting preural vertebra 3. Also, the conclusion reached by Belouze (2002, 2003) and Belouze *et al.* (2003) mentioned that all fossil taxa studied were already derived from this basal pattern.

Anguilliformes and Albuliformes present a modification in which there is a shortening of the uroneural series (Forey, 1973).

133. Epurals. (Character 45 from Forey *et al.*, 1996; Character 95 from Belouze, 2002); Johnson *et al.* (2012); (CI: 0.500000; RI: 0.750000)

[0] present

[1] absent

There is no evidence that the epural is fused to another element; therefore, like Johnson *et al.* (2012), we assumed that the bone is lost.

Epurals are absent in living and fossils forms of Anguilliformes, except in †*Enchelion* and †*Anguillavus* for which Belouze (2002) and Belouze *et al.* (2003) reported one epural.

Epurals are lost in Notacanthiformes (Fujita, 1990; Forey *et al.*, 1996).

134. Number of epurals. (Character 95 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] two or more

[1] one

The presence of two epurals were observed in Elopiformes, and a single epural in Albuliformes. A single epural is also present in fossils reported by Belouze (2002) and Belouze *et al.* (2003a, b).

135. Preural centrum 1 (PU1), ural 1 (U1) and ural 2 (U2). (Character 48 from Forey *et al.*, 1996; Character 115 from Arratia, 1997; Character 96 from Belouze, 2002); (CI: 0.500000; RI: 0.750000)

[0] separated

[1] autogenous PU1 and U1 + U2 fused

[2] PU1 + U1 + U2 fused together

We followed the Fujita (1990) interpretation of the caudal skeleton of the living eels, which assumes a fusion of the PU1+U1+U2 vertebrae in these taxa, including *Protanguilla*. Forey (1973) and Forey *et al.* (1996) mentioned the absence of bone fusion between the preural centra 1 and ural centrum 1 in Elopiformes and Albuliformes.

However, in †*Anguillavus* presents the intermediate pattern where PU1 is free, but U1+U2 are fused, simultaneously †*Eoenchelys* the same basal elopomorph.

We coded a state [2] for *Notacanthus* and *Aldrovandia*, and this is a synapomorphy gathering Anguilliformes and Notacanthiformes. However, more specimens of spiny eels should be investigated to properly elucidate the evolution of this character (McDowell, 1973; Greenwood, 1977; Fujita, 1990; Forey *et al.*, 1996; Shelyagin, 2010; Kanehira *et al.*, 2012).

Worthy of mentioning, Patterson & Rosen (1977) reported the cartilage plate attached to the neural arch of ural centrum 1 however, further studies should proceed in the caudal skeleton of eels.

136. Parhypural. (Character 39 from Forey *et al.*, 1996; Character 83 from Arratia, 1997; Character 97 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] autogenous

[1] fused to centrum preural centrum 1 (PU1)

The first state recognized by Forey *et al.* (1996), and Arratia (1997) is of an autogenous parhypural, which is observed in Elopiformes and Albuliformes. Meanwhile, Anguilliformes and Notacanthiformes showed a fused condition.

The fossil taxa have a parhypural merged to the preural 1 centrum reported by Belouze (2002, 2003) and Belouze *et al.* (2003).

137. Neural spine PU2. (Character 86 from Arratia, 1997; Character 97 from Belouze, 2002); (CI: 0.250000; RI: 0.906250)

[0] present

[1] absent

The Elongated neural spine associated with PU2 is absent in ophichthids, congrid, muraenids, and chlopsids.

138. PU2 neurospine development. (Character 86 from Arratia, 1997; Character 97 from Belouze, 2002); (CI: 0.500000; RI: 0.857143)

[0] same length as PU3

[1] shorter than PU3

The state [0] observed in *Protanguilla* is shared by Elopiformes and Albuliformes patterns, which are described by Arratia (1997) as the primitive condition among Teleostei.

139. Hypurals I and II. (Character from Forey *et al.*, 1996; Character 86 from Arratia, 1997; Character 99 from Belouze, 2002; Character from Wiley & Johnson, 2010; Johnson *et al.*, 2012); (CI: 0.500000; RI: 0.833333)

[0] not fused

[1] fused proximally

Hypurals I and II fused in a single plate are present in recent Anguilliformes (Figure 15) and Notacanthiformes.

Hypurals I and II are free from each other in †*Anguillavus*, and †*Urenchelys*, and Albuliformes and Elopiformes (Belouze, 2002, 2003; Belouze *et al.*, 2003).

140. Dorsal hypurals (H3-4). (Character 100 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] unfused

[1] fused

As reported by Johnson *et al.* (2012), *Protanguilla* exhibits unmerged (=unfused) dorsal hypural, corresponding to H3-4 (Figure 15). This condition was only present in the analyzed Outgroup and fossils eels (Belouze, 2002, 2003; Belouze *et al.*, 2003).

141. Hypural I+II. (Character 101 from Belouze, 2002; Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] not fused to centrum ural 1

[1] fused to centrum ural 1

The state [1] is recognized in all fossil taxa studied by Belouze (2002, 2003) and Belouze *et al.* (2003) and in living Anguilliformes (Figure 15). However, this condition is unknown for †*Enchelion* and coded herein as [?].

142. Upper hypurals. (Character 102 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] free from the ural centrum

[1] fused

Upper hypurals free from the ural centra are present in protanguillids, Elopiformes, Albuliformes, and in †*Anguillavus*, and †*Urenchelys*. Fused among eels (Figure 15).

143. Neural arches of the preural 1 and ural 1. (Character 103 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Neural arches associated with the preural 1 and ural 1 are recognized in living Elopiformes, and Albuliformes, but absent in the Notacanthiformes and all Anguilliformes

(McDowell. 1973; Forey *et al.*, 1996; Belouze, 2002; 2003; Belouze *et al.*, 2003; Shelyagin, 2010; Kanehira *et al.* 2012).

144. Neural arches of the preural 1 and ural 1 complex. (Character 90 and 91 from Arratia (1997); Character 103 from Belouze (2002); (CI: 1.000000; RI: 1.000000)

[0] unfused

[1] fused

The synapomorphy proposed by Patterson & Rosen (1977) and Arratia (1997) as "elapomorph neural arch," assumes a compound neural arch formed in a mass of cartilage plate over preural centrum 1 and ural centrum 1.

However, as mentioned above, this structure is absent in the Notacanthiformes and Anguilliformes. (Forey *et al.*, 1996).

Also, as mentioned by Arratia (1997) and Belouze (2002), this character is difficult to see in fossils because it requires ontogenetic monitoring of the structure, and thus coded as [?] for all fossil taxa included in the analysis.

145. Fringing fulcra are preceding the dorsal main ray. (Character 120 from Arratia, 1997; Character 105 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] absent

[1] present

Synapomorphy for Elopiformes. No fulcra were observed in fossil taxa, extant eels or other elopomorphs.

146. Urodermal. (Character 119 from Arratia, 1997; Character 106 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The presence of a small tendinous ossification contiguous to the base of central caudal-fin rays was described as “Urodermal” by Arratia (1997), found in Elopiformes (*Elops* and †*Anaethalion*), *Albula*, *Pterothrissus* and †*Lebonichthys*, and listed as a synapomorphy for the Elopomorphs.

However, this structure seems to be absent in recent and fossils eels and Notacanthiformes (Belouze, 2002; Belouze *et al.*, 2003; McDowel, 1973; Shelyagin, 2010; Kanehira *et al.* 2012).

5.1.10 – Vertebrae and spinal bones

147. Number of vertebrae. (Character 7 from Robins, 1989; Character 108 from Belouze, 2002; Character from Johnson *et al.*, 2012); (CI: 0.428571; RI: 0.923077)

[0] less than 90

[1] Between 90 and 120

[2] Between 125 and 160

[3] more than 170

Arratia (1997) used the number of 70 vertebrae to group *Elops*, *Megalops cyprinoides* and *Albula* (the number also matches the Elopiformes *Megalops atlanticus* and *Pterothrissus*, thus representing a putative synapomorphy for Outgroup. Kanehira *et al.* (2012) reported a similar number of vertebrae for most Notacanthiformes, except *Notacathus* that exhibited more than 200 vertebrae.

Until Johnson *et al.* (2012) described *Protanguilla* with 79–87 vertebrae (Figure 35), extant eels could be grouped by exhibiting more than 98-100. The exceptions *Cyema* (with 70

vertebrae) and *Monognathus* (with 82 vertebrae), which together with *Protanguilla* exhibit the lowest vertebral counts among anguilliforms and are coded herein as a state [0]. A slight increase in this number (coded as character-state [1]) includes anguillids, moringuids, and herentenchelyids, subsequently (state [2]) chlopsids, myrocongrids, muraenids, and synaphobranchids; the remaining anguilliforms all exhibit more than 170 vertebrae and coded as a state [3] (Figures 33 and 34). Relevant enough, Nettastomatidae is the family exhibiting the highest vertebral counts, ranging vertebrates between 200- 320 elements.

The Vertebrate diplospondylous centrum (present in Chondrichthyes; Compagno, 1990), but found in †*Enchelion* (Belouze, 2002) among the taxa analyzed. Monospondylous vertebrae are the prevailing condition within Elopomorpha.

148. Anterior neural arches. (Character 110 from Belouze, 2002); (CI: 0.500000; RI: 0.500000)

[0] detached from centra

[1] fused to centra

The anterior neural arches are detached from the centrum in all recent and fossils eels, notacanthiforms and *Albula*.

Elopiformes and *Pterothrissus* exhibit fused centra and coded as character-state [1].

149. Neural spines on the vertebral axis. (Character 112 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The absence of neural spines associated with the vertebral centrum is a synapomorphy for ophichthids.

150. Neural spines. (Character 112 from Belouze, 2002); (CI: 0.250000; RI: 0.875000)

[0] beginning in a central position on the neural arch

[1] in a posterior position

A neural spine associated with the posterior portion of the neural arch is a feature found in the outgroup, heterocongrins, nemychthids, nettastomatids, serrivomerids, and forms (Belouze, 2002. 2003; Belouze *et al.*, 2003).

151. Caudal transverse processes (CTP). (Character 113 from Belouze, 2002); (CI: 0.333333; RI: 0.875000)

[0] absent

[1] present

The presence of caudal transverse processes characterizes some heterocongrins, heterenchelyids, muraenids, *Nettastoma*, and *Ophichthus*. No processes have been recognized in fossil forms (Belouze, 2002; Belouze *et al.*, 2003).

152. Epipleural bones. (Character 114 from Belouze, 2002); (CI: 0.333333; RI: 0.833333)

[0] present

[1] absent

Epipleural bones are absent in nemichthyids, serrivomerids, saccopharyngoids, and *Facciolella*.

153. Epipleural bones. (Patterson & Johnson, 1995; Character 114 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] forked

[1] never forked

It is forked in most outgroup taxa, except notacanthids, anguillids, moringuids, heterenchelyids, muraenosocids, and *Protanguilla*. Among Anguilliformes, it is forked in remaining families), as well as the Outgroup.

154. Origin of the epipleural-bone series. (Patterson & Johnson, 1995; Character 115 from Belouze, 2002); (CI: 0.333333; RI: 0.666667)

[0] displaced anteriorly in the abdominal region

[1] limited to the level of the transition between the abdominal and caudal region

Patterson & Johnson (1995: 21) briefly commented that epipleurals present as an “extensive series, covering at least one-third of the abdominal region and most of the caudal region,” should be the pattern for basal teleostean (state [0]).

Character-state [0] comprises Elopiformes, Albuliformes, heretenchelyids, derichthyids, and *Ophichthus* (Figure 34).

Meanwhile, in notacanthiforms and remaining of the eels, including fossils, the epipleurals origin posterior on the body state [1].

155. Epineural bones. (Character 117 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Among Anguilliformes, epineural bones are absent in nemichthyids and saccopharyngoids. These elements are present in all remaining elopomorphs (Figures 34 and 35).

156. Epineural bones. (Character 117 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present along most of the vertebral axis

[1] restricted to the anterior portion of the abdominal region

Epineurals restricted to the anterior portion of the abdominal region is a synapomorphy of serrivomerids.

157. Epineural bones. (Character 117 from Belouze, 2002); (CI: 0.500000; RI: 0.933333)

[0] forked

[1] never forked

It is forked in most outgroup taxa, except notacanthids, anguillids, moringuids, heterenchelyids, muraenosocids, and *Protanguilla*. Among Anguilliformes, it is forked in remaining families.

The feature forked in Anguilliformes fossils (Belouze, 2002, 2003; Belouze *et al.*, 2003).

158. Anterior epineural bones. (Character 118 from Belouze, 2002); (CI: 0.166667; RI: 0.687500)

[0] fused to neural arches

[1] separated from neural arches

Anterior epineurals are fused to the neural arches in Elopiformes, anguillids, moringuids, *Conger*, muraenosocids, and serrivomerids, and all eels reported by Belouze (2002) and Belouze *et al.* (2003).

159. Ribs. (Character 119 from Belouze, 2002); (CI: 0.200000; RI: 0.924528)

[0] present

[1] absent

Ribs are lost in several anguilliform groups such as nettastomatids, nemichthyids, chlopsids, myrocongrids, mureanids, serrivomerids, saccopharyngoids, protanguillids (Figure 35), *Coloconger*, derichthyids, notacanthids in forms, and †*Eoenchelys* (Belouze, 2002; Belouze *et al.*, 2003). Present in the remaining groups (Figure 34).

160. Ribs. (Character 119 from Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present on most of the abdominal region

[1] restricted to the anterior part of the abdominal region

Ribs are present on most of the abdominal region [0] in Elopiformes, Albuliformes, halosaurids, anguillids, muraenosocids, moringuids, congrids, heterenchelyids, and all remaining fossils.

The character-state [1] is a synapomorphy for myrophins.

Inapplicable for nettastomatids, nemichthyids, chlopsids, myrocongrids, mureanids, serrivomerids, saccopharyngoids, protanguillids, *Coloconger*, derichthyids, notacanthids, whereas the ribs are absent.

161. Myorhabdoi. (Character from Patterson & Johnson, 1995); (CI: 0.333333; RI: 0.333333)

[0] absent

[1] present

Chapman (1949) was the first to describe these set of intermuscular bones are independent of any other bony structure occurring in dorsal and ventral of the myocomma, with delicate bar backward oriented.

Among eels, myorhabdoi are present only in *Ariosoma* and ophichthids. This structure is not found in fossil forms (Belouze, 2002, 2003; Belouze *et al.*, 2003).

162. Supraneurals. (Character 120 from Belouze, 2002); (CI: 0.250000; RI: 0.940000)

[0] present

[1] absent

Supraneurals are absent in recent and eels, although it is present in Elopiformes, Albuliformes, and few Notacanthiformes as reported by McDowell (1973), Greenwood (1977) and Kanehira *et al.*, (2012).

163. Accessory neural arches. (Character from Patterson & Johnson, 1995); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The structure named by Patterson & Johnson (1995) as accessory neural arches (ANA) comprehends neural arches not attached to the first vertebra. Patterson & Johnson (1995:17) concluded: “given the mosaic pattern of presence and absence of ANA [accessory neural arch] in lower teleostean groups, there are two possible interpretations: either it is synapomorphous at some level and has lost repeatedly, or it has arisen repeatedly and is nonhomologous from group to group”.

Many authors concluded that the ANA have been acquired several times (Fink & Fink, 1981; Britz & Hoffmann, 2006) among the different lineages of fishes exhibiting such structure. ANA is present in *Elops*, although absent in *Megalops*, Albuliformes, Notacanthiformes, and

extant eels. Belouze (2002) and Belouze *et al.* (2003) pointed out that in fossil forms, the back-skull is often damaged, thus making any interpretation regarding the presence of this structure problematic.

164. Additional intermuscular bones on the occipital complex. (Character from Patterson & Johnson, 1995; Character 121 from Belouze, 2002); (CI: 0.250000; RI: 0.785714)

[0] present

[1] absent

Epineurals are present at the occipital condyle in Elopiformes, *Albula*, angullids, synaphobranchids (except *Simenchelys*), heterenchelyids, colococongrids, muraenosocidae, nemichthyids, myrocongrids, derichthyids, bathymyrins, nettastomatids, *Chilorhinus*, and serrvomerids.

They are absent in Notacanthiformes, muraenids, the remaining chlopsids, moringuids, *Simenchelys*, and forms studied by Belouze (2002).

5.2 – Musculature

5.2.1 – Cephalic Muscles

Note: Based only on recent specimens only, since fossils forms lose the evidence of muscles on the mineralization process. All characters in this section are inapplicable for forms and thus coded as [-].

165. *Adductor mandibulae (AM) segmentum mandibularis.* (Character from Datovo & Vari, 2014); (CI: 0.500000; RI: 0.833333)

[0] present

[1] absent

In this study, we adopt the revised nomenclature for the Adductor Muscle Complex in Teleostean Fishes proposed by Datovo & Vari (2013). The *AM segmentum mandibularis* is defined as the muscle that inserts on the medial surface of the lower jaw and separated from the *AM segmentus facialis* by tendons (mostly mandibular raphes).

In the material examined, only Elopiformes, Albuliformes and halosaurids exhibit an *AM segmentum mandibularis* (Figure 40c-d). In all living eels (Figure 41) and notacanthids the *segmentum mandibularis* is absent (Figure 40a).

166. Adductor mandibulae segmentum mandibularis. (Character from Datovo & Vari, 2014); (CI: 1.000000; RI: 1.000000)

[0] undivided

[1] divided into *pars mentalis* and *pars coronalis*

According to the reviewed nomenclature by Datovo & Vari (2013), *Elops* and *Megalops* do not have a divided *AM segmentum mandibularis*. The muscle is present as in a single, undefined muscle mass with untraceable *pars mentalis* and *pars coronalis* subdivisions (Figure 40d).

They are coded as inapplicable [-] for notacanthids and recent Anguilliformes.

167. Endomaxillary ligament. (Character from Datovo & Vari, 2014); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The endomaxillary tendon attaches to the anteromedial region of the maxilla (Datovo & Vari, 2003) via tendon associated with the *AM segmentum facialis* (mostly from fibers of the *AM pars malaris*).

Present in all representatives of Elopiformes, Albuliformes, and Notacanthiformes. The endomaxillary tendon is lost in Anguilliformes, although the pre-maxilla is present in some groups of eels, such as in *Protanguilla* and *Derichthys*.

**168. *Adductor mandibulae segmentum facialis*. (Character from Datovo & Vari, 2014);
(CI: 0.333333; RI: 0.857143)**

[0] undivided

[1] divided

As commented above, the *adductor mandibulae* are located on the cheek and mostly associated with the lateral surface of the suspensorium bones. The origins of this muscle are variable among the examined taxa and explored in the following Characters.

In *Elops* and *Eurrypharynx* (Figures 40d and 48), the *adductor mandibulae* are superficially undivided in *pars rictalis*, *malaris* or *rictostegalis* (Figure 40). This condition differs from *Megalops*, in which *pars ricto-malaris* and *stegalis* well individualized. Moreover, an unsegmented *segmentum facialis* is reported herein for autapomorphy of *Elops*, which are coded as character-state [0].

169. *Adductor mandibulae*. (Character from Datovo & Vari, 2014); (CI: 0.333333; RI: 0.857143)

[0] *pars ricto-stegalis*

[1] *adductor mandibulae pars stegalis* divided from *AM pars rictalis*

The muscle *AM pars stegalis* herein analyzed shares fibers with *pars rictalis*, thus referred to as *AM pars ricto-stegalis*. Datovo & Vari (2013) reported a compound *ricto-stegalis* in Notacanthiformes, Albuliformes, and serrivomerids (Figure 40a-c). Meanwhile, an *AM pars stegalis* separated from the *pars rictalis* is well evident in the remaining Anguilliformes, including *Protanguilla* (Figure 41).

170. *Adductor mandibulae segmentum facialis*. (Character from Datovo & Vari, 2014);

(CI: 1.000000; RI: 1.000000)

[0] hyomandibular origin

[1] hyomandibular, pterotic, frontal and parietal origin

In Elopiformes, Albuliformes, Notacanthiformes, and Saccopharygoidei the *AM segmentum facialis* originate solely from the hyomandibular, partially covering the *levator arcus palatini* and *dilatator operculi* muscles.

Among Anguilliformes, the *AM segmentum facialis* is more robust, and origins from the hyomandibular, pterotic, frontal and parietal bones (Figures 52 and 55). In these taxa, the *segmentum facialis* completely covers other facial muscles, so that it must be removed to allow observation of other facial-muscle complexes.

171. *Adductor mandibulae pars malaris* origin. (Character from Greenwood, 1977);

Character from Datovo & Vari, 2014); (CI: 1.000000; RI: 1.000000)

[0] lateral to the *dilatator operculi*

[1] medial to the *dilatator operculi*

Dorsal fibers of the *AM pars malaris* fibers attach medially to the *dilatator operculi* is a synapomorphy grouping all Notacanthiformes [1]. This condition has been briefly commented by Greenwood (1977) as being restricted to elopomorphs.

It is worth to mention that a similar configuration [0] is present in Albuliformes and Anguilliformes.

Inapplicable for Elopiformes, the *adductor mandibulae* do not reach the *dilatator operculi*.

172. *Adductor mandibulae segmentum facialis* origin. (CI: 0.333333; RI: 0.800000)

[0] reaching the frontal, pterotic, and parietals

[0] covering the top of the neurocranium

As discussed above, the *AM segmentum facialis* of eels is robust and originates on the frontal, pterotic, and parietal bones. However, in many groups, these muscles expand medially to cover the top of the neurocranium (Figure 43). In these cases, the expansion is so coded that the contralateral *AM segmentum facialis* muscle bundles meet each other on the top of the skull.

As cited in Eadgeri (2010), some eel groups have less robust and limited *AM malaris*. These are herein coded as character-state [0] (e.g., *Protanguilla*, *Acromycter*, *Coloconger*, eurypharyngids, and heterocongrins – Figure 46).

173. *Adductor mandibulae pars stegalis*. (Character from Datovo & Vari, 2014); (CI: 0.500000; RI: 0.000000)

[0] single section

[1] divided into two sections

In the recent studies published by Datovo & Vari (2014), *Anguilla* was described as exhibiting two section of the *AM pars stegalis* – an anterodorsal *epistegalis*; originating on the ventral suture of the frontal, inserting over Meckelian tendon; and a posteroventral *substegalis*; originating on the hyomandibular (depending on the group expanding underneath *dilatator operculi* or limited to ventral portion of the bone).

We report herein the presence of two sections of *AM pars stegalis* for eel (Figure 51) but *Protanguilla* and *Coloconger*, exhibits an undivided *pars stegalis* (Figure 41a, b).

We coded serrivomerids and Outgroup as inapplicable [-] for this character since the *adductor mandibulae pars stegalis* is undivided from *AM pars rictalis*.

174. *Adductor mandibulae pars malaris*. (CI: 1.000000; RI: 1.000000)

[0] not overlapping epaxial muscles

[1] overlapping epaxial muscles [1].

A posterior expansion of the *adductor mandibulae pars malaris* that overlaps the epaxial musculature was observed in muraenids, myrcongrids, some chlopsids, and *Ophichthus* (Figure 43).

175. *Adductor mandibulae pars rictalis*. (CI: 1.000000; RI: 1.000000)

[0] not overlapping opercle muscles

[1] overlapping opercle muscles.

A posterior expansion of the *adductor mandibulae pars rictalis* that overlaps the epaxial musculature the opercular muscles was observed in muraenids, and myrcongrids (state [1]) (Figure 43).

176. *Adductor mandibulae pars malaris*. CI: 0.500000; RI: 0.833333)

[0] not divided

[1] divided into *AM pars promalaris* and *AM pars retromalaris*

An *adductor mandibulae pars malaris* entirely divided into two sections (*pro-* and *retromalaris*) was present in congrid (except heterocongrins), anguillids, albulids, moringuids, and *Simenchelys* (Figure 44).

In families such as heterenchelyids, *Protanguilla*, derichthyids, myrocongrids, muraenids, chlopsids, *Acromycter*, serrivomerids, *Cyema* and nemichthyids, a single, undivided section of the *AM pars malaris* was observed.

177. *Adductor mandibulae pars epistegalis*. (CI: 0.500000; RI: 0.947368)

[0] medial to *adductor mandibulae pars malaris*

[1] partially anterior to the *adductor mandibulae pars malaris*.

The *AM Pars epistegalis* origin is anterior to the *AM Pars malaris* and well developed in heterenchelyids, muraneids, few chlopsids, moringuids, and myrcongrids (Figure 55).

We coded inapplicable [-] for *Coloconger*, *Protanguilla*, serrivomerids, and Outgroup.

178. *Adductor mandibulae segmentum facialis*. (CI: 1.000000; RI: 1.000000)

[0] covering the sphenotic

[1] not converging sphenotics

The muscle *AM segmentum facialis* pierced sphenotics is pierced by the sphenotic with a robust lateral projection, a synapomorphy for the Serrivomeridae.

179. *Levator arcus palatini*. (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Eadgeri (2010) suggest a complex of the *AM segmentum facialis* limited dorsal by *levator arcus palatini* in eurypharyngids. However, we understand that LAP is lost in all Saccopharyngoidei (Figure 45).

180. *Levator arcus palatini pars primordialis*. (CI: 1.000000; RI: 1.000000)

[0] just behind the orbit

[1] displaced posteriorly from orbit

The muscle *levator arcus palatini pars primordialis* is located posterior to the orbit, between the skull and the palatal arch (Winterbottom, 1973).

Different from the Outgroup taxa, whereas there is no space between *levator arcus palatini primordialis* and orbit; Figure 44), in Anguilliformes there is a gap between the muscle and eye, filled by the *AM* (Figures 42 and 43).

181. *Levator arcus palatini primordialis*. (CI: 0.500000; RI: 0.944444)

[0] not underneath *Dilatator operculi*

[1] underneath *Dilatator operculi*

In synphobranchids, *Protanguilla* and outgroup, the *Levator arcus palatini pars primordialis* (LAPP) is limited posteriorly by the *dilatator operculi* and never underneath, such as the rest of the eels.

In the remaining eels, the LAPP extends underneath the *dilatator operculi*, in some species reaching the pterotic posterior limit (Figure 43).

182. *Levator arcus palatini pars temporalis*. (Character from Datovo & Rizzato, 2018);

(CI: 0.200000; RI: 0.428571)

[0] present

[1] absent

The occurrence of a *levator arcus palatini pars temporalis* varies a lot in elopomorph. However, it was possible to detect in Elopiformes, Albuliformes, *Simenchelys* (=posterior subsection of *levator arcus palatini* muscle, Eadgeri, 2010), heterenchelyids, *Venefica*, and *Nettastoma* (Figures 56 and 57).

**183. *Levator arcus palatini pars pharyngealis*. (Character from Datovo & Vari (2018);
(CI: 1.000000; RI: 1.000000)**

[0] present

[1] absent

Among elopomorphs, only two groups bear a *Levator arcus palatini Pars pharyngealis*:
Elopiformes and Albuliformes.

184. *Adductor hyomandibulae*. (CI: 1.000000; RI: 1.000000)

[0] displaced anteriorly to the *levator arcus palatini*

[1] displaced anteriorly to the *levator arcus palatini*

The *adductor hyomandibulae* origins mostly over parasphenoid and prootic, and inserts on hyomandibular, metapterygoid (outgroup) or ectopterygoid (Anguilliformes) (Figure 53).

Among gulper eels, the *adductor hyomandibulae* has an essential feature that helps to close and to open the mouth in large jaws, which has been mentioned as the “elevator muscles”

(*sensu* Trewavas, 1933; Bertelsen *et al.*, 1989). Eadgeri (2010) named the “elevator muscles” as *adductor hyomandibulae* (= *adductor arcus palatini*) for the *Eurypharynx* anatomy, a conclusion corroborated herein (Figure 48).

The long fibers of the *adductor hyomandibulae* run along with hyomandibular reaching the quadrate in Cyematidae, Monognathidae, Eurypharyngidae and Saccopharyngidae.

Although Greenwood (1997) pointed out this muscle is absent in Notacanthiformes, it was possible to detect its presence in all specimen examined. It is thus coded herein as a present for the spiny eels.

185. *Adductor hyomandibulae* about the orbit. (CI: 0.500000; RI: 0.972973)

[0] reaching the end of the orbit

[1] until the middle of the orbit

[2] near the beginning of the orbit

In heterocongrins, the *adductor hyomandibulae* is displaced anteriorly [2] (Figure 42). In other eels, it reaches the vertical through the middle of the orbit [1], a characteristic present in many congrid and cologrids, serrivomerids, *Iliophis*, and nettastomatids (Figure 53). It was unable to check the state in *Protanguilla*, and thus coded as [?].

5.2.2 – Opercular Muscles

186. *Dilatator operculi*. (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The *dilatator operculi* is present in all elopomorph examined, except monognathids, saccopharyngids, and eurypharyngids (absence also detect in larval forms).

187. *Dilatator operculi*. (CI: 0.250000; RI: 0.888889)

[0] triangular-shaped

[1] stripe-shaped

A stripe-shaped *dilatator operculi* is present in synphobranchids, herentenchelyids, chlopsids (except *Chilorhinus*), myrocongrids, *Protanguilla*, and muraenids (Figures 43 and 55).

Inapplicable for saccopharyngoid whereas *dilatator operculi* is lost.

188. *Adductor operculi*. (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The *adductor operculi* muscle stretches between the dorsomedial face of the opercle and the lateral surface of prootic. This muscle is widely spread among elopomorphs and lost in saccopharyngoids.

189. *Levator operculi*. (CI: 1.000000; RI: 1.000000)

[0] inserting on the medial face of the opercle

[1] inserting on the lateral face of the opercle

Winterbottom (1973) described as the “standard pattern” of the *levator operculi* an insertion on the dorsal or dorsomedial face of this bone. This condition is interpreted as the

putative primitive condition among elopomorphs since it is present in Elopiformes, Albuliformes, and Notacanthiformes (Figure 44).

However, all Anguilliformes examined herein exhibited a *levator operculi* that was lateral concerning the opercle. In many cases, this muscle was observed covering the opercular bone completely (Figures 42, 42, 53 and 54).

190. *Levator operculi pars mandibularis*. (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

As discussed above, the anguilliform *levator operculi* medial insertion is different from Outgroup medial site. Many authors have discussed if the muscle previously named as “depressor muscle” in saccopharyngoids was a unique feature of this taxon. In *Eurypharynx*, for example, this muscle origin on the ventromedial face of the pterotic and inserts on the anterior edge of the jaw (Eadgeri, 2010) in a thin, tube-like, sesamoid bone. In monognathids, the same “depressor muscle” was described and illustrated by Bertelsen *et al.* (1989). In monognathids, it had an origin similar to that of *Eurypharynx* but inserted in the angulo-articulo-retroarticular instead.

Dissections carried out in specimens of *Avocettina* and *Nemichthys*, revealed that both species show the *levator operculi* with a lower section, fibers running ventral to angulo-articulo-retroarticular (Figure 54). This lower section was able to clarify this new arrangement of fibers *levator operculi* was very similar to the “depressor muscle” of the gulper eels. Also, this lower connection observed for *Cyema* without the pterotic insertion with the fibers sitting over the posterior expansion of the hyomandibular, whereas we understand that is the opercle sutured (Figure 45).

We believe that the “depressor muscle” is homologous to and represents an additional section of *levator operculi* muscle complex (Figure 48). We thus offer the term *pars mandibularis* to refer to the subdivision of the *levator operculi* that originates from opercle and inserts to the angulo-articulo-retroarticular. Our decision comes in agreement to the recent musculature revision and nomenclature proposed by Datovo & Vari (2013) and Datovo & Rizzato (2018), which recognized many subunits and subdivisions for the *adductor mandibulae* and hyopalatal muscle complexes.

191. *Levator operculi pars primordialis*. (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

The absence of a *levator operculi pars primordialis* is a synapomorphy for *Cyema* (Figures 45 and 47), in which only the *levator operculi pars mandibularis* was observed.

192. *Levator operculi*. (CI: 1.000000; RI: 1.000000)

[0] attaches to opercle

[1] not attached to opercle

The state [1] is observed only in monognathids, and saccopharyngids whereas the *levator operculi* fibers insert in pterotic directly to the posterior portion of the angulo-articulo-retroarticular, without attaching to opercle. In the rest of the elopomorph, fibers sit on opercle.

193. *Levator operculi*. (CI: 1.000000; RI: 1.000000)

[0] originating from the pterotic

[1] originating from the pterotic and epaxial muscles

A condition in which the *levator operculi* originated both from the pterotic and the epaxial muscles is a synapomorphy for Serrivomeridae.

5.2.3 – Hyoid Muscles

194. *Intermandibularis*. (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The *intermandibularis* is located on the ventral surface of the head, displaced transversely in the tip of the lower jaw, connecting both dentary bones (Winterbottom, 1973).

This muscle is probably a section of the *protractor hyoidei*, although further investigation is needed to attest this hypothesis. The *Intermandibularis* is present only found among outgroup taxa (Figure 27), occurring in some specimens of *Notacanthus*, *Polyacantlionotus*, and *Halosauropsis* in Notacanthiformes.

The *intermandibularis* is absent in all Anguilliformes examined (state [1]), except in *Protanguilla* whereas the specimens were already dissected (coded as [?]).

195. *Protractor hyoidei*. (CI: 1.000000; RI: 1.000000)**[0] present****[1] absent**

The loss of a *protractor hyoidei* was detected in Cyematids, saccopharyngids monognathids, eurypharyngids.

196. *Protractor hyoidei*. (CI: 1.000000; RI: 1.000000)**[0] covering the basihyal****[1] exposing the basihyal**

An exposed ventral view of basihyal on which is *protractor hyoidei* do not cover the bone, a synapomorphy grouping Anguilliformes and Notacanthiformes. In Elopiformes and Albuliformes, the muscle is robust, covering the anteriormost structures of the hyoid arch (Figure 27).

5.2.4 – Branchial Muscles - Dorsal

197. *Retractor dorsalis*. (Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The *retractor dorsalis* is a paired dorsal branchial muscle that links the posterior-most pharyngobranchial element(s) to the vertebral column (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004, 2015; Johnson, 2019).

In this study, we agree with Nelson's (1967) interpretations that argued that this muscle appeared independently in many teleostean lineages. Absent in Elopiformes, Albuliformes, Notacanthiformes, and saccopharyngoids.

198. *Retractor dorsalis*. (Character from Nelson, 1967); (CI: 1.000000; RI: 1.000000)

[0] attached to the esophageal wall

[1] attached to the vertebral column

Neslon (1966) and Johnson (2019) reported that the *Rectrator dorsalis* extended anteriorly from the esophageal wall and attached to the posteriormost portion of the upper pharyngeal Tooth plate. However, in muraenids a portion of the dorsal retractor attaches to the vertebral column. In *Rhinomuraena* this represents a large bundle of the *retractor dorsalis* fibers.

This Character is coded as [?] in myrocongrids and in saccopharyngoids, except *Cyema*.

199. Interbranchiales (Gill filament muscle). (Character from 88 Belouze, 2002); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Interbranchiales are small muscles associated primarily with the gill filaments, which are found in all elopomorph. The few taxa reported loss *interbranchiales* are saccopharyngoids. Nevertheless, Tchernavin (1947b) reported the occurrence for the saccopharyngoid. Unfortunately, the specimens of *Saccopharynx*, *Neocyema*, *Monognathus*, and *Myroconger* are rare, and it was not possible to dissect the branchial arches (coded as a state [?]).

200. *Levator externus* (LE). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.666667; RI: 0.944444)

[0] four levatores

[1] three levatores

[2], two levators

The *levator externus* in elopomorph has the same origin as the rest of teleost, which is on the occipito/otic region of the neurocranium (Figure 48). It inserts on the dorsal surface of the epibranchial bones (Springer & Johnson, 2015). In Chlopsidae and Muraenidae, there are three relatively thin *levatores externi*. The subgenus *Neomuraena*, (not examined herein) appears to exhibit the primitive condition of exhibiting four *levatores externi* (Johnson, 2019).

Mehta and Wainwright (2007a, b) wrongly reported the presence of a LE4 in Muraenidae. In *Cyema*, a *levator externus* 1 is lost.

Unfortunately, the specimens of *Saccopharynx*, *Neocyema*, *Monognathus*, and *Myroconger* are rare, and it was not possible to dissect the branchial arches (coded as a state [?]).

201. *Levator internus* (LI). (Character from Nelson, 1967); Character from Springer & Johnson, 2015). (CI: 1.000000; RI: 1.000000)

[0] with three *levatores*

[1] two *levatores*

[2] one *levator*

The muscles have the same origin as cited in Character above and insert on the corresponding one or more pharyngobranchials (in Anguilliformes the pharyngobranchial 1 is lost). This muscle is sometimes inserted into upper tooth plates (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004; Springer & Johnson, 2015).

The condition of three *levatores* is a synapomorphy of Teleostei (Springer & Johnson, 2004). However, all Anguilliformes exhibit only two *levatores interni* is a synapomorphy for the group (Figures 58 and 59).

The loss of the one *levator interni* in *Notacanthus*, and *Polyacanthonotus*, we understand as independently lost (Johnson *et al.*, 2012).

In *Cyema*, a *levator internus* 1 is lost, a condition interpreted to be shared with the rest of saccopharyngoids. In *Megalops cyprinoides* LI1 is the only muscle present. Mehta & Wainwright (2007a, b) wrongly reported the presence of an LI4 in Muraenidae

This Character is coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

**202. *Musculus pharyngobranchialis 2- epibranchialis*. (Character from Nelson, 1967);
Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)**

[0] absent

[1] present

Among elopomorphs, a small dorsal branchial muscle is present in eels, connecting pharyngobranchial 2 to epibranchial 1 or 2 (Figures 58 and 59). Absent in *Cyema*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

**203. *Musculus pharyngobranchialis 2*. (Character from Springer & Johnson, 2015);
(CI: 1.000000; RI: 1.000000)**

[0] associated with epibranchial 1

[1] associated with epibranchial 2

Springer & Johnson (2015) cited *musculus pharyngobranchialis 2-epibranchialis 1* as a synapomorphy for Anguilliformes. This muscle connects the second pharyngobranchial to epibranchial 1 or 2.

A pharyngobranchial 2 – epibranchial 1 connection is restricted to the genus *Synaphobranchus*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

204. *Musculus laminalis pharyngobranchialis dentalis 4-epibranchialis 4*. (Character from Springer & Johnson, 2015); CI: 0.333333; RI: 0.000000)

[0] present

[1] absent

This muscle present in *Conger* and *Coloconger* (Figure 58), and possibly represents an anterior extension of the dorsal retractor (Springer & Johnson, 2015).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

205. *Transversus dorsalis* (TD) anterior attachment. (Character from Nelson, 1967; Character from Springer & Johnson, 2015). (CI: 0.250000; RI: 0.880000)

[0] epibranchial 4

[0] not attached epibranchial 4

The muscle *transversus dorsalis* (= *transversus anterior*, Nelson 1966) represents a subdivision of the *sphincter oesophagi* (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004; Springer & Johnson, 2015).

A *transversus dorsalis* attached to epibranchial 4 is present in congrid (except in heterocongrins), anguillids, muraenosocids, colocongrids, elopiforms, and *Notacanthus* (Figures 58 and 59).

This Character was coded as a state [?] in myrocongrids and saccopharyngoids, except *Cyema*.

206. *Transversus dorsalis* (TD) anterior attachment (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.875000)

[0] on upper toothplates 3

[1] not attached on toothplates

The *transversus dorsalis* is attached to upper pharyngeal tooth plate 3 in synphobranchids. This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

207. *Tranversus dorsalis* (TD) attachment. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.125000; RI: 0.681818)

[0] upper toothplates 4

[1] not attached to upper toothplates 4

The *tranversus dorsalis* is attached to epibranchial 4 in eels, except congrids (not including heterocongrins), colococongrids, Notacanthiformes, Elopiformes, and *Simenchelys*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

208. *Obliquus dorsalis* 3 (OD3). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.166667; RI: 0.722222)

[0] present

[1] absent

The muscle *obliquus dorsalis 3* (= *obliquus superior*, Nelson, 1967), is synapomorphic for Teleostei (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004, 2015; Johnson, 2019). Fibers of dorsal obliquus muscles usually attach to the epibranchials and infrapharyngobranchials of the same or adjacent branchial arches (Winterbottom, 1973). In the case of *obliquus dorsalis 3*, fibers link epibranchial 3 to infrapharyngobranchial 3.

This muscle is of a rare occurrence and present only in basal elopomorphs, *Synphobranchus*, anguillids, and serrivomerids (Figure 59).

Recently, Springer & Johnson (2015) reported the absence of *obliquus dorsalis 3* for serrivomerids. However, our observations indicate the presence of this muscle in *Serrivomer beanii* and *Stemonidium hypomelas* (Figure 60b). Nelson (1967) described the OD3 and OD4 both as a single muscle OD3 (= *obliquus superior*, Nelson, 1967).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

209. *Obliquus dorsalis 3*. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] not sharing fibers with *obliquus dorsalis* 4

[1] sharing fibers with *obliquus dorsalis* 4

The condition of an undivided OD3-OD4, or these muscles sharing fibers, is a synapomorphy of *Synaphobranchus*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

210. *Obliquus dorsalis* 4 (OD4). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.903226)

[0] present

[1] absent

The OD4 (= *obliquus posterior*, Nelson, 1967) is common among eels but absent in Muraenidae, *Cyema*, and eurypharyngids. Mehta and Wainwright (2007a, b) wrongly reported the presence of an OD4 (=OBL.DIV, Mehta and Wainwright, 2007a, b) in muraenids.

Johnson (2019) pointed out that this muscle represents an anterior expansion of the *sphincter oesophagi/ retractor dorsalis* complex.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

211. *Rectus dorsalis* 1 (RecD1). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.923077)

[0] present

[1] absent

Springer & Johnson (2015) describes the first *rectus dorsalis* as originating from an epibranchial and inserting to the adjacent epibranchial. The numbering of *recti dorsales* is based on the corresponding epibranchial (= *obliquii inferiores*, Nelson, 1967).

The muscle is present in *Protanguilla*, anguillids, moringuids, chlopsids, colococongrids, nettastomatids, derichthids, heterenchelyids, serrivomerids and muraenins (Figures 58 and 59). It is also present in serrivomerids, although Springer & Johnson (2015) reported it as absent for the taxon. A *rectus dorsalis* 1 is absent among basal elopomorphs.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

212. *Rectus dorsalis* 2 (RecD2). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

A RecD2 is absent in *Cyematidae* and *Simenchelys*. Although Springer & Johnson (2015) listed it is absent in serrivomerids, we were able to observe *Rectus dorsalis* 2 in this taxon (Figure 59).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

213. *Rectus dorsalis* 3 (RecD3). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

A *Rectus dorsalis* 3 is absent in *Simenchelys*, and *Cyema* and eurypharyngids.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

214. *Rectus dorsalis* 4 (RecD4). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Among all elopomorphs, a *Rectus dorsalis* 4 was reported only in *Protanguilla* and *Cyema*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

215. *Adductor dorsalis* 1 (AD1). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.400000)

[0] present

[1] absent

The dorsal gill-arch muscle described as *adductor dorsalis* (=adductor, Nelson, 1967; Winterbottom, 1973; =pharyngeal tooth plate adductor muscle, Eadgeri *et al.*, 2016) has its

fibers stretched between the anterior surfaces of the epibranchial and the ceratobranchial (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004; 2015, Johnson, 2019).

However, a different configuration is observed on AD1, which originates from the posterodorsal surface of Cb1 and inserts along the ventral surface of Eb1. This condition is restricted to *Notacanthus*, anguillids, and *Simenchelys*.

Worthy of mentioning, AD4 is currently in all elopomorphs examined.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

216. Adductor dorsalis 2 (AD2). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.250000; RI: 0.400000)

[0] present

[1] absent

Together with *Adductor dorsalis* 3, this is one of the rarest *Adductor dorsalis* muscles among elopomorphs, present only in anguillids, *Notacanthus* and *Simenchelys*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

217. *Adductor dorsalis* 3 (AD3). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

The rarest *Adductor dorsalis* muscles among elopomorphs, present only in *Notacanthus* and *Simenchelys*.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

218. *Adductor dorsalis* 5 (AD5). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.333333; RI: 0.857143)

[0] present

[1] absent

An *Adductor dorsalis* 5 is widespread among eels. Nevertheless, it is absent in muraenids and *Cyema*.

Mehta and Wainwright (2007a, b) wrongly reported the presence of an AD5 in Muraenidae, describing it attached to the fourth branchial arch. The correct terminology for a muscle attaching to the fourth branchial arch is AD4.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

5.2.5 – Branchial Muscles – Ventral

219. *Pharyngoclavicularis*. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.833333)

[0] divided into *externus* and *internus* sections

[1] not divided into *externus* and *internus* sections

The *pharyngoclavicularis* (= *coracobranchialis*, Nelson, 1967) of elopomorphs originates from the cleithrum and insert on Cb5, or related to tooth plate (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004; 2015). In elopomorphs, except in notacanthids and Anguilliformes, this muscle is subdivided into an *externus* and *internus* sections (Figures 60 and 61).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

220. *Transversus ventralis* 4. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Transversus ventralis 4 is the transverse ventral gill-arch muscle connecting the Ceratobranchials 4 from each side (= *transversi ventralis anterior*, Nelson, 1967). This muscle is absent in Nemichthyidae and Cyematidae (Figures 50 and 61).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

221. *Transversus ventralis* 5. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Transversus ventralis 5 is the transverse ventral gill-arch muscle connecting the Ceratobranchials 5 from each side and often continuous posteriorly with *sphincter oesophagi* (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004, 2015; Johnson, 2019).

The absence of *transversus ventralis 5* is characteristic for Uropterygiinae.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

222. *Obliquus ventralis 1*. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

The *obliquus ventralis* series link a ceratobranchial of a given gill arch to its associated hypobranchial (Figure 60). The *obliquus ventralis 1* is present in all outgroup, and all eels except *Simenchelys* and *Cyema* (Figure 61a). This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

223. *Obliquus ventralis 2*. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.000000)

[0] present

[1] absent

An *obliquus ventralis* 2 present is present in all outgroup, and all eels except *Simenchelys* and *Cyema* (Figure 61a).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

224. *Obliquus ventralis* 3. (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.333333; RI: 0.777778)

[0] present

[1] absent

An *obliquus ventralis* 3 is present in Elopiformes, Albuliformes and Notacanthiformes and in many Anguilliformes families. However, it is absent in *Protanguilla*, synphobranchids, *Cyema* (Figure 61a).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

225. *Rectus ventralis* 1 (R1). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.333333; RI: 0.937500)

[0] present

[1] absent

The *rectus ventralis* muscle series (=rectus, Nelson, 1967) connects a ceratobranchial of one branchial arch to the hypobranchial of the previous arch (Nelson, 1967; Winterbottom, 1973; Springer & Johnson, 2004; 2015). Within elopomorphs, Springer & Johnson (2015) considered the presence of *recti ventrales* as synapomorphic for eels (Figure 60). However, according to Nelson (1967b), the genus *Elops* exhibits an R4, condition corroborated herein.

We conclude that the *rectus ventralis* 4 and *Rectus communis* are fused in all elopomorph. Nevertheless, the attachment sites are variable, and these will be further discussed in Character 228.

Among eels, we observed a *rectus ventralis* 1 in all groups exhibiting a “*Subpharyngealis*.” We understand that the fibers between R’s-REcCom share the same site, which occurs in synphobranchids, chlopsids, muraenids, and moringuids.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

226. *Rectus ventralis* 2 (R2). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] absent

[1] present

Rectus ventralis 2 is absent in outgroup and present in all Anguilliformes examined, except *Cyema* (Figure 61a).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

227. *Rectus ventralis* 3 (R3). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Rectus ventralis 3 is absent in outgroup and present in all Anguilliformes examined, except *Cyema* (Figure 61a).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

228. *Rectus communis* (RecCom). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 1.000000; RI: 1.000000)

[0] attached to Ceratobranchial 5

[1] attached to Ceratobranchial 4

Here, we present our homology hypothesis for the *Rectus communis* in Elopomorpha and basal teleost. The first author to describe this muscle was Allis (1897), referring to this muscle as *obliquus ventralis 2*, which would connect the articular process of the third hypobranchial to ceratobranchial 5.

Later, Nelson (1967a) pointed out that the RecCom developed more than once during the evolution of the teleost since it was present in all elopomorphs except *Elops*. He observed in elopiforms R4 fibers grouping into an aponeurotic fascia and joining its antimeres anterior to Cb5. These fibers were absent in *Albula* (Figure 60a), which had lost the connection between the RecCom and Cb5. Consequently, this muscle was named R4Com (Springer & Johnson, 2004; 2015).

Posteriorly, Springer & Johnson (2015) mentioned that the RecCom could be a derivation among eels and suggesting a new name for the muscle in the group: a *rectus ventralis 4 communis*. The muscle would be defined as fibers related to Cb4 (together with R4) extending anteriorly to a gill-arch element, anterior to Hb3, *e.g.*, Hb2, Hb1, urohyal. They justified the following: “loss of a tendinous connection with Cb5, consequent muscular attachment to Cb4,

and increased its anterior attachment to a skeletal element anterior to Hb3” (Springer & Johnson, 2015: 599).

However, our conclusions contrast from Springer & Johnson (2004, 2015). We believe that the absence of a connection between RecCom with Cb5 should not generate a new nomenclature. We think that a shift affecting the muscles connections would be the most parsimonious assumption. Therefore, according to our interpretation, the different fiber-attached sites should be coded in the same character with different states based on the muscles connections.

The state [0] is unique for Elopiformes, remaining Elopomorpha posterior attach to ceratobranchial 4.

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

229. *Rectus communis* (RecCom) anterior attachment. (Character from Nelson, 1967;

Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.949153)

[0] hypobranchial 3

[1] attached to hypobranchial 2

[2] attached to hypobranchial 1

[3] to hyoid arch

The only reported eel coded as a state [0] was *Protanguilla*, which together with the rest of elopomorph exhibit the RecCom's (= *rectus ventralis 4 communis*, Springer & Johnson, 2015 – Figure 60a) anterior attachment site at the hypobranchial 3. The state [1] was present in anguillids, colocongrids, congrids, and derichthyids.

The RecCom reaches anteriorly Hypobranchial 1 in ophichthids (except *Callechelys*), nemichthyids, *Neoconger*, nettastomatids, and serrivomerids (Figures 50, 60a and 61). An anterior attachment at the hyoid arch is present in chlopsids, muraenids, *Moringua*, heterenchelyids, and synaphobranchids in the state [3] (Figure 49).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

230. *Rectus communis* (RecCom). (Character from Nelson, 1967; Character from Springer & Johnson, 2015); (CI: 0.500000; RI: 0.964286)

[0] fibers occurring on the ventral surface of the ventral branchial arches

[1] both ventral and dorsal to the ventral branchial arches

The *Rectus communis* connects the Cb4 to Hyoid arch through a dense and robust set fibers that spreads along the branchial bones flooring and ventral surface of the ventral branchial

arches (=subpharyngealis, Nelson, 1967; Eadgeri, 2010; Springer & Johnson, 2004, 2015; Eadgeri *et al.*, 2016; Johnson, 2019), also cited in Character 228.

We report the presence of an additional dorsal set of *rectus communis* fibers (character-state [1]) occurring in synphobranchids, muraenids, chlopsids, and moringuids (Figure 49).

This Character was coded as [?] in myrocongrids and saccopharyngoids, except *Cyema*.

5.3 – General Characters

231. Scales. (Character 6 from Robins, 1989; Character 122 from Belouze, 2002; Character from Wiley & Johnson, 2010; Character from Johnson *et al.*, 2012); (CI: 0.200000; RI: 0.818182)

[0] present

[1] absent

Several authors have reported the absence of scales among living Anguilliformes (Reagan, 1912; Trewavas, 1933; Greenwood *et al.*, 1966; Smith, 1984; Robins, 1989; Forey *et al.*, 1996). Scales are also absent in fossils forms †*Eoenchelys* (Belouze, 2002; Belouze *et al.* 2003; Belouze, 2003). However, after the description of *Protanguilla* by Johnson *et al.* (2012),

the distribution of scales was reinterpreted among eels and basal elopomorphs. Scales were considered primitively present in these taxa and secondarily lost in different groups independently.

Among Anguilliformes, scales are present in *Protanguilla* (Figure 62), anguillids (Figure 63), synphobranchids (except *Diastobranchnus*), and in fossils †*Anguillavus* and †*Urenchelys germanus* (Belouze, 2002; Belouze *et al.* 2003; Belouze, 2003).

232. Scales of the body. (Character 6 from Robins, 1989; Character 122 from Belouze, 2002; Character from Johnson *et al.*, 2012; (CI: 1.000000; RI: 1.000000)

[0] present in an overlapping pattern

[1] present in a non-overlapping pattern or arranged in ‘basket-weave fashion’

The scales on the body of the outgroup exhibit an imbricate pattern where one scale overlaps the other. Nevertheless, in all Anguilliformes examined scales are arranged in a ‘basket-weave fashion’ (eel-like pattern; Figures 62 and 63; Robins, 1989; Johnson *et al.*, 2012).

An eel scale pattern is present in *Protanguilla*, anguillids, synphobranchids (except *Diastobranchnus*), in the fossil †*Anguillavus*, and †*Enchelurus* (Belouze, 2002)

233. Lace-like lateral-line scales. (Character from Johnson *et al.*, 2012); (CI: 0.250000; RI: 0.928571)

[0] absent

[1] present

A lace-like lateral line scale was found in *Protoanguilla*, ophichthids, congrid, and nettastomatids. Taxa lacking body scales were mentioned above in character. Nevertheless, due to its unclear description for fossils, these taxa are coded herein as [?].

This Character is inapplicable state [-] in fossils forms.

234. Leptocephali larva. (Character 39 from Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] forked caudal fin

[1] rounded caudal fin

Among Elopomorpha, the *leptocephali* larva vary in having a distinct round (Anguilliformes) or forked caudal fin (Elopiiformes, Albuliformes, and Notacanthiformes). The

leptocephalus larvae of the recently described taxon *Protanguilla* is still unknown, thus coded herein as [?].

This Character is inapplicable state [-] in fossils forms.

235. Larvae Myomers. (Character 41 from Robins, 1989); (CI: 0.500000; RI: 0.909091)

[0] V-shaped

[1] W-shaped

The W-shaped larval myomere pattern is present in all Anguilliformes, Albuliformes, and Elopiformes. Saccopharyngoids and Notacanthiformes exhibit a V-shaped larval myomere.

This Character is inapplicable state [-] in fossils forms.

236. Spermatozoa flagellum. (Character from Jamieson, 1991; Character 55 from Forey *et al.*, 1996); (CI: 1.000000; RI: 1.000000)

[0] containing 2 central axonemes and 9 peripheral axonemes

[1] 0 central axons, 9 peripheral and proximal centrioles divided into two groups of 4 or 5 triplets

The condition of having 0 central axons, 9 peripheral and proximal centrioles divided into two groups of 4 or 5 triplets is a synapomorphy for living eels.

This Character is inapplicable state [-] in fossils forms.

237. Pyloric caeca. (Character 8 from Robins, 1989; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Pyloric caeca absent in all recent Anguilliformes (Smith, pers. Comm.), although more studies should be performed.

This Character is inapplicable state [-] in fossils forms.

238. Branchial membranes. (Character 4 from Robins, 1989; Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] not united to the isthmus, broad gills

[1] united across the isthmus, gill-openings restricted

Gill membranes united across the isthmus is a synapomorphy for living Anguilliformes.

This Character is inapplicable state [-] in fossils forms.

239. Oviducts in adults. (Character 35 from Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

Absence of oviducts is a synapomorphy for living the clade comprised by Anguilliformes and Notacanthiformes. However, Hulet (1978) reported the presence of oviducts in the larval stages of these fishes.

This Character is inapplicable state [-] in fossils forms.

240. Genital pore. (Character 35 from Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] single pore

[1] double pore

Two genital pores are uniquely present in Muraenidae. All the remaining elopomorph are characterized by having a single genital pore. This character has also been proposed by Regan (1909, 1912).

This Character is inapplicable state [-] in forms.

241. Pseudobranch in adults. (Character 4 from Robins, 1989; Character from Johnson *et al.*, 2012); (CI: 0.500000; RI: 0.875000)

[0] present

[1] absent

Hulet (1978) examined larval stages of ophichthids and reported the loss of pseudobranch (=mandibular hemibranchia) during metamorphosis. In *Protanguilla*, Johnson *et*

al. (2012) did not confirm the presence of this structure, although they reported a corrugated ovoid structure inside the opercular cavity in the usual position of a pseudobranch that could be shrunk. The Pseudobranch is also lost in *Megalops*. This Character is inapplicable state [-] in forms.

242. Attachment of gas bladder to vertebrae. (Character 36 from Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] absent

[1] present

Gas bladder attached to vertebrae groups Notacanthiformes and Anguilliformes (Tchernavin, 1947 a,b; Greenwood, 1977; Robins, 1989). In Elopiformes and Albuliformes the gas bladder is detached from the vertebrae.

243. Branchial efferent arteries. (Character I from Robins (1989); (CI: 1.000000; RI: 1.000000)

[0] separated

[1] united by commissural vessels

Branchial efferent arteries are united by commissural vessels above and below the gill slits in all saccopharyngoids. This Character is inapplicable state [-] in fossils forms.

244. Luminogenic organ at the caudal end of the fish. (Character L from Robins, 1989);

(CI: 1.000000; RI: 1.000000)

[0] absent

[1] present

A luminogenic organ characterizes Saccopharyngidae and Eurypharyngidae within Saccopharyngoidei. The lateral line pores are possible illuminated as well (Tchernavin, 1947a, b; Bertelsen *et al.*, 1989). This Character is inapplicable state [-] in forms.

245. Lateral line. (Character from Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] present

[1] absent

The lateral line is absent in muraenids, myrocongrids, and chlopsids. The organ is present in all other groups. This Character is inapplicable state [-] in fossils forms.

246. Dorsal Fins. (Character from Robins, 1989; Character from Johnson *et al.*, 2012);

(CI: 1.000000; RI: 1.000000)

[0] not confluent with anal fins

[1] dorsal and anal fins confluent

The dorsal and anal fins are confluent in all Recent eels. This contrasts to the outgroup taxa, which have well defined and well separated dorsal and anal fins. This Character is inapplicable state [-] in fossils forms.

247. Caudal fin lobe. (Character from Johnson *et al.*, 2012); (CI: 1.000000; RI: 1.000000)

[0] with more than 8 rays in each caudal fin lobe

[1] 7 or fewer rays in each caudal fin lobe

Living eels can be separated from the other Elopomorpha by exhibiting seven or fewer rays in each lobe of the caudal fin. This Character is inapplicable state [-] in fossils forms.

248. Gill Slits. (Character from Robin & Robins, 1989); (CI: 1.000000; RI: 1.000000)

[0] Collar-like

[1] lateral to the body

[2] ventral surface

The state [2] is a synapomorphy for synphobranchs. A collar like is an autapomorphy for *Protanguilla*.

6 – DISCUSSION

The phylogeny of the Anguilliformes

The present analysis is the largest yet done on the basis of phenotypic characters for the Anguilliformes, both in number of taxa and characters, with 248 characters coded for 108 terminal taxa, including all 26 families of the Elopomorpha.

We offer a brief discussion on some of these groups and list the characters that were corroborated. Analysis under implied weight (K=7) resulted in 15 most-parsimonious trees; the strict consensus is shown in Figures 64, 65 and 66.

Herein we discuss each clade resulting from the analysis, with numbering coordinated with Figures 64, 65 and 66.

We will discuss each clade herein presented in the further items below and divided to better understanding the interrelationships:

The intrarelationships of Anguilliformes:

Clade A = Order Anguilliformes:

Synphobranchus sp., *Synphobranchus kaupii*, *Dysomma anguillare*, *Dysommia rugosa*, *Media abyssalis*, *Diastobranchus capensis*, *Symenchelys parasitica*, *Ilyophis nigeli*, *Pythonichthys asodes*, *Myroconger sp.*, *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa*

canina, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Nemichthys scolopaceus*, *Avocettina infans*, *Coloconger meadi*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys sp.*, *Nettastoma melanurum*, *Facciolella equatorialis*, *Hoplunnis tenuis*, *Venefica procera*, *Moringua raitaborua*, *Neoconger vermiformis*, *Moringua edwardsi*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidti*, *Serrivomer sp.*, *Serrivomer beanii*, *Stemonidium hypomelas*, *Anguilla japonica*, *Anguilla marmorata*, *Anguilla rostrata*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoprroides*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma sp.*, *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyuroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys sp.*, *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neenchelys mcoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Protanguilla palau*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanaoides*, *Saccopharynx ampullaceus*.

Cretaceous fossils: †*Anguillavus quadripinnis*, †*Urenchelys germanus*, †*Eoenchelys*, †*Enchelion*.

Synapomorphies: Char.#18:(0>1); Char.#21:(0>1); Char.#34:(0>1); Char.#35:(0>1);
Char.#39:(0>1); Char.#48:(0>1); Char.#55:(0>1); Char.#63:(1>0); Char.#71:(0>1);
Char.#74:(0>1); Char.#75:(0>1); Char.#80:(0>1); Char.#81:(0>1); Char.#95:(0>1);

Char.#103:(0>1); Char.#105:(0>1); Char.#107:(1>2); Char.#120:(0>1); Char.#124:(0>1);
Char.#131:(0>1); Char.#138:(0>1); Char.#147:(0>1); Char.#162:(0>1); Char.#230:(0>1).

Without Cretaceous fossils – Synapomorphies: Char.#16:(0>2) Char.#27:(0>1);
Char.#51:(0>1); Char.#94:(0>1); Char.#103:(0>1); Char.#136:(0>1); Char.#139:(0>1);
Char.#158:(0>1); Char#170 (0>1).; Char#189 (0>1)..

Support: relative Bremer = 95%

Remarks: Several characteristics previously proposed as synapomorphies for Anguilliformes were tested here (Nelson, 1966, 1967; Robins, 1989; Forey *et al.*, 1996; Johnson *et al.*, 2012; Springer & Johnson, 2015). The first one verified here was the fusion vomer plate and ethmoid bone (Char. 16). A similar synapomorphy of fusion happens with the angulo-articulo-retroarticular, (Char. 48) fused in a single piece in eels (in more extreme conditions the angulo-articulo-retroarticular is also fused with the dentary in eurypharyngids and monognathids – Char. 53). The articulation with neurocranium was also observed as a unique condition of Anguilliformes (Char. 27), except Saccopharyngoidei, where there is a single condyle, a condition originated homologous in Notacanthiformes.

Recently, Johnson *et al.* (2012) described the first living eel with a metapterygoid, the homology of which clarified the loss of endopterygoid (Char. 51) as another feature for eels as the rostro-caudally orientation of the opercular series (Char. 55). The fusion of hypurals I and II and the ural centrum (Char. 138 and 142), observed by Johnson *et al.* (2012), was also corroborated.

Another anatomical feature corroborated here and by many authors (Regan, 1909, 1912; Trewavas, 1933; Robbins, 1989; Forey *et al.*, 1996; Johnson *et al.*, 2012) is Char. 63 and 80 (Hyoid and branchial arches displaced posteriorly relative to the neurocranium). As was also observed repeatedly by other authors (Robins, 1989; Forey *et al.*, 1996; Johnson *et al.*, 2012)

Pharyngobranchial 1 is absent in living eels (Chr. 95), and Basibranchial 3 is entirely cartilaginous (Char. 88 and 89). The pelvic fins and girdles are lost in living eels as well (Char. 123 and 124), the elongation of anterior end of ceratohyal is equally the same length of the posterior ceratohyal (Char. 72 and 73), the uppermost branchiostegals curved behind the opercle, more concentrated over posterior ceratohyal and spatula-shaped (Char. 75).

Robins (1989) and Forey *et al.* (1996) reported the absence of Gill rakers (=branchiospines, Belouze, 2002) in Anguilliformes. However, this synapomorphy was refuted in Johnson *et al.* (2012). Herein, gill rakers (unossified) are reported for the first time in Heterocongrinae. Regarding the loss of pre-maxillae (Char. 39), we concur with Hulet (1978) and Johnson *et al.* (2012) who consider it lost in adults of Anguilliformes, during the metamorphosis of leptocephalus to adults. There is no evidence of the fusion into the premaxilla-ethmovomerine complex. Herein, we identified independent paired pre-maxillae in *Derichthys*, anteriorly to the ethmo-vomer (previously reported by Trewavas, 1933), in a position different from that of Cretaceous forms and *Protanguilla*. The losses of orbitospheniod (Char. 11) reported by Robins (1989) is confirmed here. The scale traits observed by Robins (1989) as synapomorphy for eels (non-overlapping pattern or arranged in 'basket-weave fashion') was corroborated here (Char. 232).

As new synapomorphies for Anguilliformes, we report the pterotic extending anteriorly above the prootic to contact the pterosphenoid (Char. 18), and the loss of palatine and auto-palatine (Char. 34 and 35). Tighe (1989) reported the palatine for Serrivomeridae. However, that structure is a connection between the ectopterygoid (=palatopterygoid, Tighe, 1989) and a lateral projection of the ethmo-vomer, also present in Congridae and Nettastomidae (Char. 36 and 37). The lack of tooth covering on the ventral surface of gill arches (Char. 79) is also a confirmed previously cited synapomorphy for eels (Nelson, 1966, 1967; Robins, 1989; Forey *et al.*, 1996). The articulation of the hyomandibular to the neurocranium via two condyles (Char. 40) is also present in all eels, except Saccopharyngoidei, where there is a single condyle, a condition originated independently in Notacanthiformes.

All characters proposed by Johnson *et al* , (20012) and Springer & Johnson (2015 were corroborated here , thus we added two new synapomorphies (Char. 170) *adductor mandibulae segmentum facialis* origin on hyomandibular, pterotics, frontals and parietal covering *dilatator operculi* and *levator arcus palatini* entirely. And *levator operculi* inserting on lateral surface of the opercle (Char. 189).

Clade B = New - Anguiloidei (Anguilloidea + Synphobranchoidea + Ophichthoidea + Congroidea):

Synphobranthus sp., *Synphobranthus kaupii*, *Dysomma anguillare*, *Dysommia rugosa*, *Media abyssalis*, *Diastobranthus capensis*, *Symenchelys parasitica*, *Ilyophis nigeli*, *Pythonichthys asodes*, *Coloconger meadi*, *Myroconger sp.*, *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa canina*, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Nemichthys scolopaceus*, *Avocettina infans*, *Labichthys carinatus*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys sp.*, *Nettastoma melanurum*, *Facciolella equatorialis*, *Hopplunnis tenuis*, *Moringua raitaborua*, *Neoconger vermiformis*, *Moringua edwardsi*, *Venefica procera*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidtii*, *Serrivomer sp.*, *Serrivomer beanii*, *Stemonidium hypomelas*, *Anguilla japonica*, *Anguilla marmorata*, *Anguilla rostrata*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoproroides*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger*

cinereus, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma* sp., *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyuroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys* sp., *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neechelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanoides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#38:(0>1); Char.#140:(0>1); Char.#173:(0>1); Char.#181:(0>1); Char.#230:(0>1).

Support: relative Bremer = 68%

Remarks: The Anguilloidea arrangement was recovered as a monophyletic group and sister group of all remaining eels (Synaphobranchoidea and Congroidea), one branching above *Protanguilla*. The Anguilloidea clade was only observed by Smith (1984) and Robbins (1989) based on two characteristics (*see* History), none of these characteristics proved to be valid synapomorphies.

In this block, we present the support for the hypothesis as *Protanguilla* as the sister group to all eels. The loss of Metapterygoid among remaining Anguilliformes (Char. 38) dorsal hypurals (H3-4) fused (Char. 140). Moreover, three new muscles characters were implied as synapomorphies for the rest of the eels, *levator arcus palatini primordialis* overlapping underneath the *dilatator operculi* (Char. 181) (reversed in Synaphobranchoidea and vestigial Saccopharyngoidei); *adductor mandibulae segmentum facialis* origin covering the top of the neurocranium (Char. 173); *rectus communis* anterior attachment to hypobranchial to hyoid arch or hypobranchial 1-2 (Char. 230).

According to Bayesian inference, the molecular analysis of Johnson *et al.* (2012), and compatible with our analysis (Figures 64 and 68), the basal position of *Protanguilla* (Figure 7) whereas shared a lot of characteristics with Outgroup and with five autapomorphy, the new family is clearly a basal taxa contradicting all molecular phylogeny discussed in the introduction (Figures 8, 9, 10 and 11).

Clade C = Superfamily Anguilloidea:

Pythonichthys asodes, *Moringua raitaborua*, *Neoconger vermiformis*, *Moringua edwardsi*, *Anguilla japonica*, *Anguilla marmorata*, *Anguilla rostrata*.

Synapomorphies: Char.#88:(0>1); Char.#159:(0>1)

Support: relative Bremer = 20%

Remarks: The Anguilloidea is composed by Heterenchelyidae + (Anguillidae + Moringuidae), this topology is unique since the previous morphological analysis (Smith, 1984; Robbins, 1989 – Figure 3b) reported as a trichotomy. All the molecular analysis gathers Anguillidae + Moringuidae with Nemichthyidae, Serrivomerida, and Saccopharyngoidei, and Heterenchelyidae is related to Myrocongridae + Muraenidae.

Two synapomorphies were raised here, following: basibranchial 3 cartilaginous (Char. 89), absent in Anguillidae and *Moringua*; ribs present (Char. 159).

Clade D = Synaphobranchoidea + Congroidea + Ophichthoidea

Synaphobranchus sp., *Synaphobranchus kaupii*, *Dysomma anguillare*, *Dysommia rugosa*, *Media abyssalis*, *Diastobranchus capensis*, *Symenchelys parasitica*, *Ilyophis nigeli* *Coloconger meadi*, *Myroconger* sp., *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa canina*, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Nemichthys scolopaceus*, *Avocettina infans*, *Labichthys carinatus*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys* sp., *Nettastoma melanurum*, *Facciolella equatorialis*, *Hoplunnis tenuis*, *Venefica procera*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidtii*, *Serrivomer* sp., *Serrivomer beanii*, *Stemonidium hypomelas*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoproroides*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma* sp., *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys* sp., *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neeenchelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanooides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#32:(1>0); Char.#112:(0>1); Char.#114:(0>1); Char.#153:(0>1); Char.#157:(0>1).

Support: relative Bremer = 58%

Remarks: For the first time, our analysis grouped Synaphobranchidae, Chlopsidae, Myrocongridae, Muraenidae, Muraenosocidae, Ophichthidae, Derichthyidae, Congridae, Colococongridae, Nesttastomatidae, Nemichthyidae, Serrivomeridae, Cyematidae, Eurypharyngidae, Saccopharyngidae and Monognathidae.

Curiously, the arrangement incompatible with all previous phylogenetic analyses and the synapomorphies supported were: Hyomandibular/quadrato joint unsutured (Char. 32), supracleithrum, when present, delicate in filiform-shape (Char. 112 and 114); epipleurals and epineurals never forked (Char. 153 and 157).

Clade E = New - Superfamily Synaphobranchoidea:

Synaphobranchus sp., *Synaphobranchus kaupii*, *Dysomma anguillare*, *Dysommia rugosa*, *Media abyssalis*, *Diastobranchus capensis*, *Symenchelys parasitica*, *Ilyophis nigeli*, *Myroconger sp.*, *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa canina*, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoprroides*.

Synapomorphies: Char.#47:(0>1); Char.#226:(1>0); Char.#231:(0>1).

Support: relative Bremer = 56%

Remarks: The clade proposed here is a new hypothesis for eels, supported by three new synapomorphies. This new clade includes the Muraenoidei *sensu* Robbin (1989), Muraenidae, Myrocongridae and Chlopsidae plus the Synaphobranchidae. Cutthroat eels were never recovered as the sister group of Chlopsidae + Myrocongridae + Muraenidae in molecular and morphological analyses. Moreover, Chlopsidae is usually positioned as a basal group in a clade with Congridae, Colocongridae, Muraenosocidae, Ophichthidae, and Derichthyidae (Figures 7-11).

The new superfamily was only possible based on muscles characters, and this branch was well supported by lower jaw as the same length as neurocranium (Char. 47); *rectus ventralis* 1 present (Char. 226); *rectus communis* fiber occurring both ventral and dorsal to the ventral branchial arches (Char. 231).

Clade F = Muraenidae + Myrocongridae + “Chlopsidae”:

Myroconger sp., *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa canina*, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoprорoides*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*.

Synapomorphies: Char.#43:(0>1); Char.#62:(0>1); Char.#65:(0>1); Char.#85:(0>1); Char.#98:(0>1); Char.#101:(0>1); Char.#105:(0>1); Char.#108:(0>1); Char.#193:(0>1); Char.#194:(0>1); Char.#221:(0>1); Char.#251:(0>1).

Support: relative Bremer = 80%

Remarks: The topology offered herein, was previously proposed by Smith (1984), Robins (1989), and Belouze (2002), gathering eels with frontal bones separated, branchial elements reduced and scales absent. None of these characteristics proved to be valid synapomorphies, and the only feature corroborated was lateral line absent. However, the “Muranoidei” differs from ours, which here the Chlopsidae was not recovered as monophyletic.

Of those 12 synapomorphies, only one was previously proposed by Robins (1989), and ten are new, including four based on the musculature.

Clade G = New – Congroidea + Ophichthoidea

Nemichthys scolopaceus, *Avocettina infans*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys sp.*, *Nettastoma melanurum*, *Facciolella equatorialis*, *Hopplunnis tenuis*, *Venefica procera*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidti*, *Serrivomer sp.*, *Serrivomer beanii*, *Stemonidium hypomelas*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma sp.*,

Congriscus megastoma, *Gnathophis nystromi ginanago*, *Bathyroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys sp.*, *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neenchelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanooides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#186:(0>1);

Support: relative Bremer = 20%

Remarks: This is a new clade gathering families Congridae, Nettastomatidae, Muraenosocidae, Serrivomeridae, Nemychthyidae, Cyematidae, Derichthyidae, Ophichthidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae.

A single synapomorphy supports this group- *adductor hyomandibulae* reaching until the middle of the orbit or, more extreme case, near the beginning of the orbital (Heterocongrinae) although reversed in Cyematidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae (Char. 186).

Clade H = Superfamily Ophichthoidea:

Oxyconger leptognathus, *Muraenesox cinereus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys sp.*, *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala*

misolensis, *Neenchelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*.

Synapomorphy: Char.#158:(1>0).

Support: relative Bremer = 20%

Remarks: The clade displays the lowest relative Bremer value in our analysis and is supported by one ambiguous synapomorphy: Anterior epineural bones fused to neural arches (Char. 158).

The topology presented for this branch, in general, is compatible with the molecular analysis presented in the Introduction (Figures 7-11), and according to Robins (1989) grouped in Congoidei along with other families, without interrelations between all of them.

Clade I = New - Superfamily Congroidea:

Nemichthys scolopaceus, *Avocettina infans*, *Coloconger meadi*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys sp.*, *Nettastoma melanurum*, *Facciolella equatorialis*, *Hopplunnis tenuis*, *Venefica procera*, *Moringua raitaborua*, *Neoconger vermiformis*, *Moringua edwardsi*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidti*, *Serrivomer sp.*, *Serrivomer beanii*, *Stemonidium hypomelas*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma sp.*,

Congriscus megastoma, *Gnathophis nystromi ginanago*, *Bathyroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys sp.*, *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neenchelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Protanguilla palau*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanooides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#26:(0>1); Char.#77:(1>2).

Support: relative Bremer = 100%

Remarks: Our Bremer support value strongly corroborates the monophyly of the Congroidea, whereas the most basal family here is Derichthyidae, the group with pre-maxillae present and sutured between them, previously reported by Regan (1912), Trewavas (1933) and Robins & Robins (1989).

The synapomorphies supporting this clade: quadrate/hyomandibula joint strongly inclined forward (Char. 26), reversed in Cyematidae, Monognathidae, Eurypharyngidae, and Saccopharyngidae; a small number of branchiostegal (Char. 77).

Clade J = New (Colocongridae + Congridae + Nettastomatidae + Serrivomeridae + Nemichthyidae + Cyematidae + Monognathidae + Eurypharyngidae + Saccopharyngidae):

Nemichthys scolopaceus, *Avocettina infans*, *Labichthys carinatus*, *Hoplunnis diomediana*, *Saurenychelys sp.*, *Nettastoma melanurum*, *Facciolella equatorialis*, *Hoplunnis tenuis*,

Venefica procera, *Serrivomer schmidti*, *Serrivomer sp.*, *Serrivomer beanii*, *Stemonidium hypomelas*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma sp.*, *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyuroconger vicinus*, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanoides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#24:(0>1); Char.#36:(0>1).

Support: relative Bremer = 56%

Remarks: Some of the most distinct characters backing the Congroidea which the unique arrangement gather all the Saccopharyngoidei families, we erected this new clade. From a morphological perspective, members of these particularly noticeable are the protection of the mandibular sensory canal weak and exposed (Char. 24).

The connection between ectopterygoid and small lateral projections of the ethmo-vomer misunderstood with the presence of palatine in Serrivomeridae. In this study, we clarified this connection employing comparisons involving all relevant families (Char. 36), reserved in Nemichthyidae, Cyematidae, Monognathidae, Eurypharyngidae, and Saccopharyngidae.

Clade K = New - “Nettastomatidae” + Serrivomeridae + Nemichthyidae + Cyematidae + Monognathidae + Eurypharyngidae + Saccopharyngidae:

Nemichthys scolopaceus, *Avocettina infans*, *Labichthys carinatus*, *Hoplunnis diomediana*, *Saurenychelys* sp., *Nettastoma melanurum*, *Facciolella equatorialis*, *Hopplunnis tenuis*, *Venefica procera*, *Serrivomer schmidti*, *Serrivomer* sp., *Serrivomer beanii*, *Stemonidium hypomelas*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanooides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#0:(0>1); Char.#14:(1>2); Char.#111:(0>1); Char.#115:(0>1); Char.#116:(0>1).

Support: relative Bremer = 27%

Remarks: The most crucial difference from recent molecular phylogenies is the group gathers all the long-snout eels. From a morphological perspective, members of these particularly noticeable arean ethmo-vomer length (Char. 14) reversed in *Hoplunnis*, supracleithrum lost (Char. 111) reversed in *Hoplunnis* and *Nettenchelys*; supraoccipital, coracoid and scapula lost (Char. 1, 115 and 116), reversed in *Hoplunnis*

The Nettastomatidae was not recovered as a monophyletic group with *Facciolella* as the sister group of Serrivomeridae, Nemichthyidae, Monognathidae, Eurypharyngidae, and Saccopharyngidae, the same arrangement as Belouze (2002).

Clade L = New - Serrivomeridae + Nemichthyidae + Cyematidae + Monognathidae + Eurypharyngidae + Saccopharyngidae:

Nemichthys scolopaceus, *Avocettina infans*, *Labichthys carinatus*, *Serrivomer schmidti*, *Serrivomer* sp., *Serrivomer beanii*, *Stemonidium hypomelas*, *Monognathus jerpersenii*,

Neocyema erythrosoma, *Cyema atrum*, *Eurypharynx pelecanoioides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#88:(0>1); Char.#152:(0>1); Char.#164:(0>1).

Support: relative Bremer = 27%

Remarks: From a morphological perspective, members of Serrivomeridae and Nemichthyidae were proposed as closely related by Regan (1912), Trewavas (1933), Smith (1984); Tighe (1989), Belouze (2002) and Springer & Johnson (2015). Molecular studies show another arrangement, involving the Anguillidae and Moringuidae, our results disagree with those molecular results.

Clade M = New - Nemichthyidae + “Saccopharyngoidei”:

Nemichthys scolopaceus, *Avocettina infans*, *Labichthys carinatus*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanoioides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#58:(0>1); Char.#66:(0>1); Char.#68:(0>1), Char.#86:(0>1); Char.#90:(0>1); Char.#128:(0>1); Char.#191:(0>1); Char.#212:(0>1); Char.#221:(0>1).

Support: relative Bremer = 80%

Remarks: The morphological data derived from a previous study (Smith, 1984; Belouze, 2002) place this clade, which comprises families Nemichthyidae, Cyematidae, Monognathidae, Saccopharyngidae, and Eurypharyngidae. Few previous studies found a relationship between Nemichthyidae to saccopharyngoids, Belouze (2002) and Santini *et al.* (2013). The node specifying a sister-group relationship between Nemichthyidae and “Saccopharyngoidei” well supported with numerous synapomorphies. The analysis clarified homologies problems with opercles bones nameless muscles (“depressor” and “elevator muscles) in Monognathidae, Eurypharyngidae, and Saccopharyngidae

Two new myological synapomorphies help clarify some problems of homology. The interopercle and opercle considered as lost among saccopharyngoidei. Comparisons with Nemichthyidae show a different pattern of muscle insertion on the posterior part of the jaw and opercle.

The fibers sharing sites with the *pevator operculi* identifiable as the ventral sector of that muscle, here named *levator operculi pars mandibularis* (Char. 191). The fibers sharing sites with the *levator operculi* identifiable as the ventral sector of that muscle, here named *levator operculi pars mandibularis* (Char. 191). The loss of the *tranversus ventralis* 4 (Char. 221). In *Cyema*, only the lower section is presently associated with a bony structure posterior to the hyomandibular. This landmark shows that the opercle is fused to suspensorium, rather than lost. The rest of saccopharyngoidei *levator operculi pars mandibularis* and *levator operculi pars primordialis* associated with a long and slender bone which is the interopercle. We proposed the nomenclature for “elevator muscle” as *adductor hyopalatine* and “depressor muscles” as *levator operculi pars mandibulo-primordialis*.

Clade N = “Saccopharyngoidei”

Monognathus jerpsereni, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanoioides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#11:(0>1); Char.#27:(0>1); Char.#28:(0>1), Char.#30:(1>2); Char.#47:(0>1); Char.#54:(0>1); Char.#56:(0>1); Char.#71:(0>1); Char.#74:(0>1); Char.#82:(0>1); Char.#98:(0>1); Char.#101:(0>1); Char.#129:(0>1); Char.#130:(0>1); Char.#189:(0>1); Char.#195:(0>1); Char.#236:(0>1); Char.#244:(0>1).

Support: relative Bremer = 90%

Remarks: Some of the most distinct characters supporting the clade from past works, as Cope (1871, 1884) was the first to place Eurypharyngidae with Muraenidae in a clade called Colocephali, supported by reductions and displacements of the hyoid and branchial arches. However, subsequent researches disagreed with that hypothesis. Regan (1909, 1912) placed the group its own order Lyomeri, a view shared by Trewavas (1933; though placing *Cyema* in Anguilliformes). Tchernavin (1947a, b) reported reductions of the neurocranium, suspensorium and branchial arches in saccopharyngoids, going as far as questioning their placement among bony fishes. Greenwood *et al.* (1966), Forey *et al.* (1996), and Belouze (2002) positioned Saccopharyngoidei within eels.

All molecular studies to date have placed saccopharyngoidei within Anguilliformes (Obermiller & Pfeiffer, 2003; Johnson *et al.* 2012; Tang & Fielitz, 2013; Chen *et al.*, 2013; Santini *et al.*, 2014; Poulsen *et al.* 2018). In general, both morphology and molecules recover all extant Saccopharyngoidea group as monophyletic except Inoue *et al.* (2010) who proposed them as a sister group of all eels.

Clade O = New - Superfamily Congroidea:

Coloconger meadi, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzi*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma sp.*, *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyuroconger vicinus*.

Synapomorphies: Char.#205:(1>0); Char.#206:(1>2).

Support: relative Bremer = 50%

Remarks: The *Coloconger* + Congridae group is a typical result in morphological analyses, (Smith, 1989; Robins, 1989), although Belouze (2002) hypothesizes Colocongridae as the sister group to Muraenosocidae. In all molecular studies, Congridae is paraphyletic (Tang & Fielitz, 2012; Chen *et al.*, 2013; Santini *et al.*, 2013; Poulsen *et al.*, 2018). Our analysis shows the family as monophyletic. Two synapomorphies support Congridae: *transversus dorsalis* attached to epibranchial 4 and *musculus laminalis pharyngobranchialis dentalis 4-epibranchialis 4* present.

The intrarelations of Elopomorpha:

Clade P = Order Anguilliformes + Notacanthiformes:

Halosaurus pectoralis, *Halosauropsis machochir*, *Aldrovandia phalacra*, *Lypogenys gillii*, *Notacanthus sexspinis*, *Polyacanthonothus rissoanus* *Synaphobranchus* sp., *Synaphobranchus kaupii*, *Dysomma anguillare*, *Dysommia rugosa*, *Media abyssalis*, *Diastobranchus capensis*, *Symenchelys parasitica*, *Ilyophis nigeli*, *Pythonichthys asodes*, *Myroconger* sp., *Gymnothorax minor*, *Anarchias smilis*, *Enchelynassa canina*, *Uropterygius micropterus*, *Muraena lentiginosa*, *Uropterygius concolor*, *Anarchias allardicei*, *Enchelycore nigricans*, *Gymnothorax vicinus*, *Anarchias seychellensis*, *Strophidon sathete*, *Rhinomuraena quaesita*, *Monopenchelys acuta*, *Echidna catenata*, *Gymnomuraena zebra*, *Nemichthys scolopaceus*, *Avocettina infans*, *Coloconger meadi*, *Derichthys serpentinus*, *Nessorhamphus danae*, *Hoplunnis diomediana*, *Saurenychelys* sp., *Nettastoma melanurum*, *Facciolella equatorialis*, *Hopplunnis tenuis*, *Venefica procera*, *Moringua raitaborua*, *Neoconger vermiformis*, *Moringua edwardsi*, *Oxyconger leptognathus*, *Muraenesox cinereus*, *Serrivomer schmidti*, *Serrivomer* sp., *Serrivomer beanii*, *Stemonidium hypomelas*, *Anguilla japônica*, *Anguilla marmorata*, *Anguilla rostrata*, *Chilorhinus suensonii*, *Chlopsis dentatus*, *Chlopsis bicolor*, *Kaupichthys diodontus*, *Kaupichthys hyoprroides*, *Macrocephenchelys brachialis*, *Macrocephenchelys brevirostris*, *Rhynchoconger gracilior*, *Chiloconger dentatus*, *Ariosoma selenops*, *Gorgasia punctate*, *Heteroconger camelopardalis*, *Acromycter perturbator*, *Xenomystax congroides*, *Conger cinereus*, *Gavialiceps taeniola*, *Heteroconger klausewitzii*, *Conger orbignianus*, *Bathycongrus dubius*, *Ariosoma* sp., *Congriscus megastoma*, *Gnathophis nystromi ginanago*, *Bathyuroconger vicinus*, *Apterichtus caecus*, *Aplatophis chauliodus*, *Ophichthus gomesii*, *Myrichthys ocellatus*, *Stictorhinus potamius*, *Bascanichthys* sp., *Letharchus velifer*, *Pseudomyrophis frio*, *Ahlia egmontis*, *Myrophis punctatus*, *Yirrkala misolensis*, *Neeenchelys mccoskeri*, *Echelus uropterus*, *Schismorhynchus labialis*, *Callechelys catostoma*, *Protanguilla*

palau, *Monognathus rosenblatti*, *Monognathus jerpersenii*, *Neocyema erythrosoma*, *Cyema atrum*, *Eurypharynx pelecanooides*, *Saccopharynx ampullaceus*.

Synapomorphies: Char.#4:(0>1); Char.#42:(0>1); Char.#61:(0>1), Char.#104:(0>1); Char.#107:(0>1); Char.#119:(0>1); Char.#120:(1>0); Char.#121:(0>1); Char.#125:(0>1); Char.#133:(1>2); Char.#135:(0>1); Char.#136:(0>1); Char.#141:(0>1); Char.#143:(0>1); Char.#146:(0>1); Char.#164:(0>1); Char.#184:(0>1); Char.#240:(0>1); Char.#243:(0>1).

Support: relative Bremer = 88%

Remarks: The relation between of Anguilliformes and Notacanthiformes has long been debated by several authors, however, the first work to gather these two orders in Elopomorpha as sister groups were Greenwood *et al.* (1966). Their proposal based on larvae Bauplan, oviducts absent, many-rayed anal fin, abdominally situated, eight- to 10-rayed pelvic fins, and "spectacles" (a bright patch of head skin) over the eyes.

Wiley & Johnson (2010) gathered 17 synapomorphies uniting Notacanthiformes and Anguilliformes, and it is compatible with this study. Our analysis strongly supports the Notacanthiformes + Anguilliformes relationship, which is sustained by 18 synapomorphies, one new feature of the facial muscles complex (Char.184) whereas *levator arcus palatini pars pharyngealis* absent. All those synapomorphies were corroborated here, except pelvic fin webs joined in the midline which is ambiguous because eels lack that fin and spiny eels have it and hypural 2 not fused to ural centrum (fused at least in Notacanthidae)

Recent analyses based on molecular data mostly support Greenwood *et al.* (1966) topology hypothesis. In general, both morphology and molecules recover all extant subfamilies as monophyletic apart from Robins (1989), Filleul & Lavoué (2002) and Obermiller & Pfeifer (2003).

As pointed out Wiley & Johnson (2010: 132) for this group “These may be grouped into characters that represent losses within the context of elopiform evolution (and frequently loss of states that are apomorphic at varying levels of teleost, actinopterygian, Osteichthyes or even gnathostome phylogeny) and those that are apparent gains (acquisition of novelties)”. The proper elucidation of the limits of this clade is that they are also losing, fusing, or changed completely format of the “pattern” Teleostei.

7.CONCLUSION

Since Johnson *et al.* (2012) described the new family Protanguillidae performing a shred of morphological and molecular evidence supporting the basal position of *Protanguilla palau* presenting unique synapomorphies for Anguilliformes and a new relationship between eels. However, the Johnson *et al.* (2012) new taxa position was never recovered by molecular analyses. Our comparative anatomy resulted in *Protanguilla* as basal clade among Anguilliformes, including unique synapomorphies osteological and muscles sources cited in the discussion shared only by the Outgroup (pteroic not extending posteriorly and the possible presence of posttemporal elements – da Silva, pers. Comm)

Another impressive result was the close relation between Nemichthyidae and “Saccopharyngoidei, clade gathered herein by phenotypic characters. The muscle character states as putative synapomorphies were able to solve report for the first time the problem of homology of the opercle elements and muscles associated. The same situation was observed in Serrivomeridae, whereas the condition shared by Nettastomatidae, Colocongridae, and Congridae comparative anatomy helped us understand the palatine bone was wrongly reported for the eels.

We also clarified nomenclature problems for branchial arches muscles such as *rectus communis* 4 (R4Com= Springer &Johnson, 2004, 2015), and *subpharyngealis* (Nelson, 1967;

Springer & Johnson, 2004, 2015), whereas the comparative study showed all denomination is a different configuration of *rectus communis*.

A noteworthy homoplasy was observed in Anguilliformes anatomical complex, whereas losing elements tendencies in eels as cited by Springer & Johnson (2015). However, we raised two new synapomorphies based on *adductor mandibulae* origin on frontals, pterotics, and parietal covering all the facial muscles and *levator operculi* inserting on lateral dorsal of the opercle.

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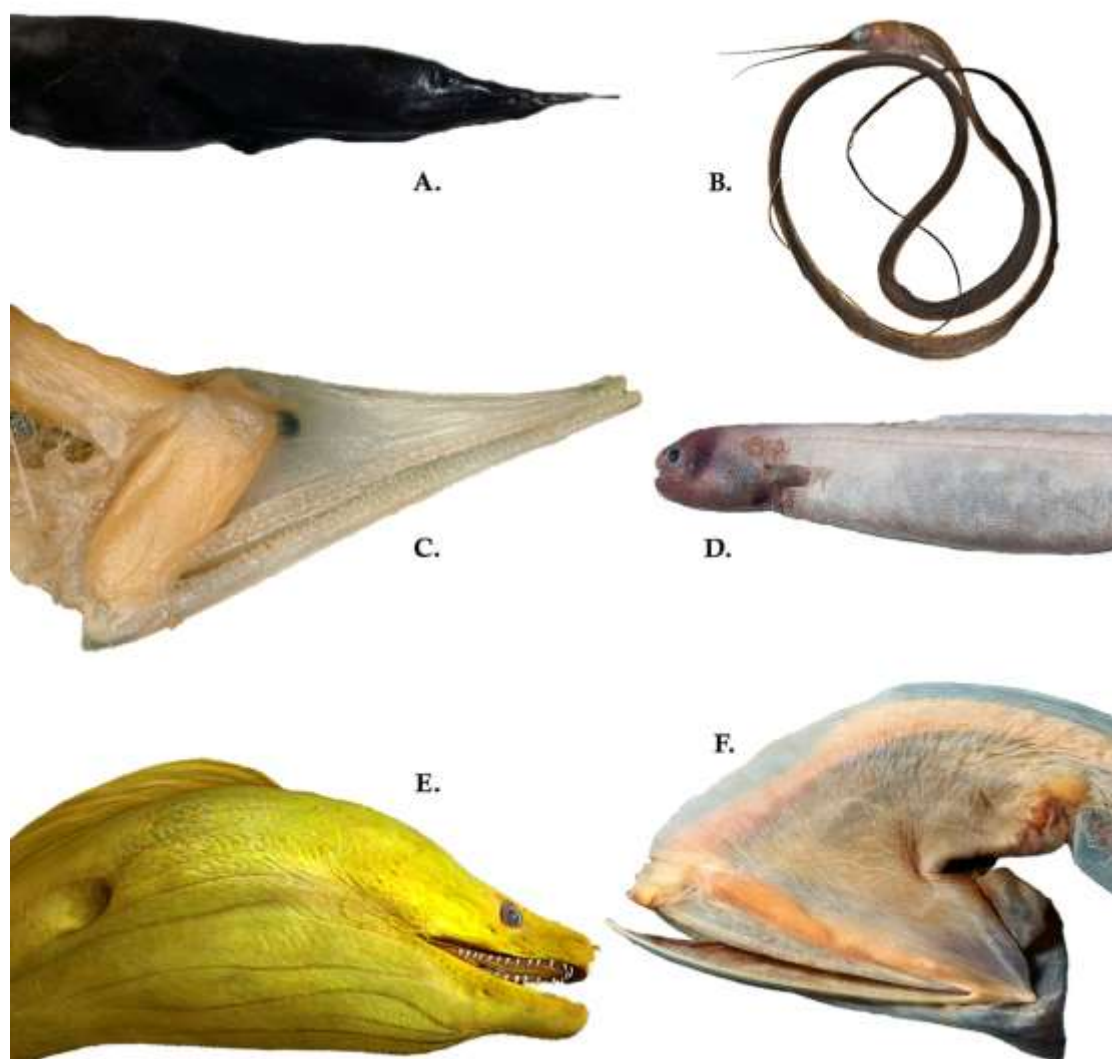


Figure 1 – Morphological variation in six families of Anguilliformes: A, Serrivomeridae (photo from fishbiosystem); B, Nemichthyidae (photo from Wikipedia); C, Cyematidae (photo from Andrew Wilkinson); D, Synaphobranchidae (photo from Fishes of Australia); E, Muraenidae (photo from gooddive.com); F, Saccopharyngidae (photo from digitalfishlibrary.org).

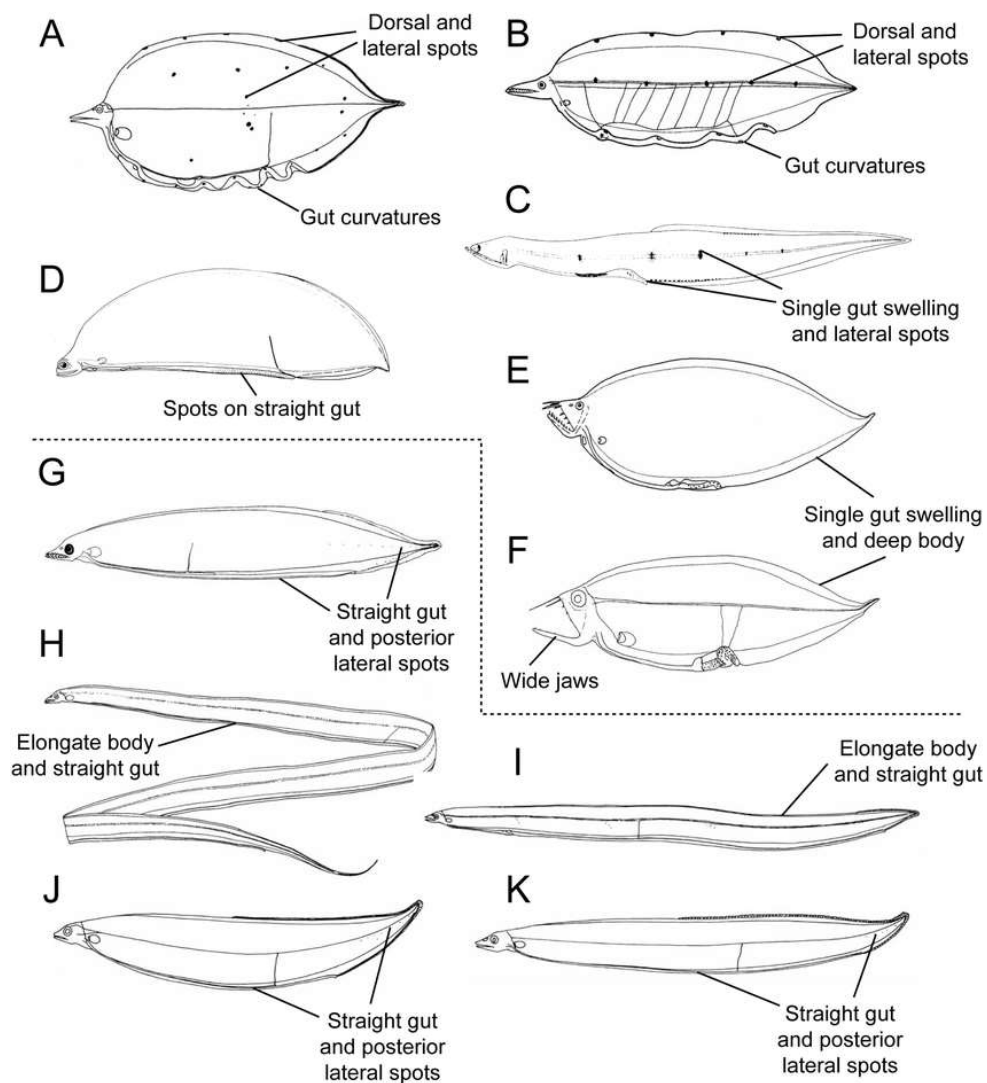


Figure 2 – Illustrations of leptocephalus larvae of meso- and bathypelagic eels families: A, *Cyema*; B, "*Leptocephalus holti*"; C, Monognathidae (metamorphic stage); D, Unidentified saccopharyngiform; E, *Saccopharynx*; F, *Eurypharynx*; G, *Serrivomer beani*; H, *Nemichthys curvirostris*; I, *Avocettina infans*; J, *Derichthys serpentinus*; K, *Nessorhamphus ingolfianus*.

Illustrations A, C, D, and F to K are modified from Böhlke (1989), B is modified from Smith & Miller (1996), and E is modified from Castle (1984).

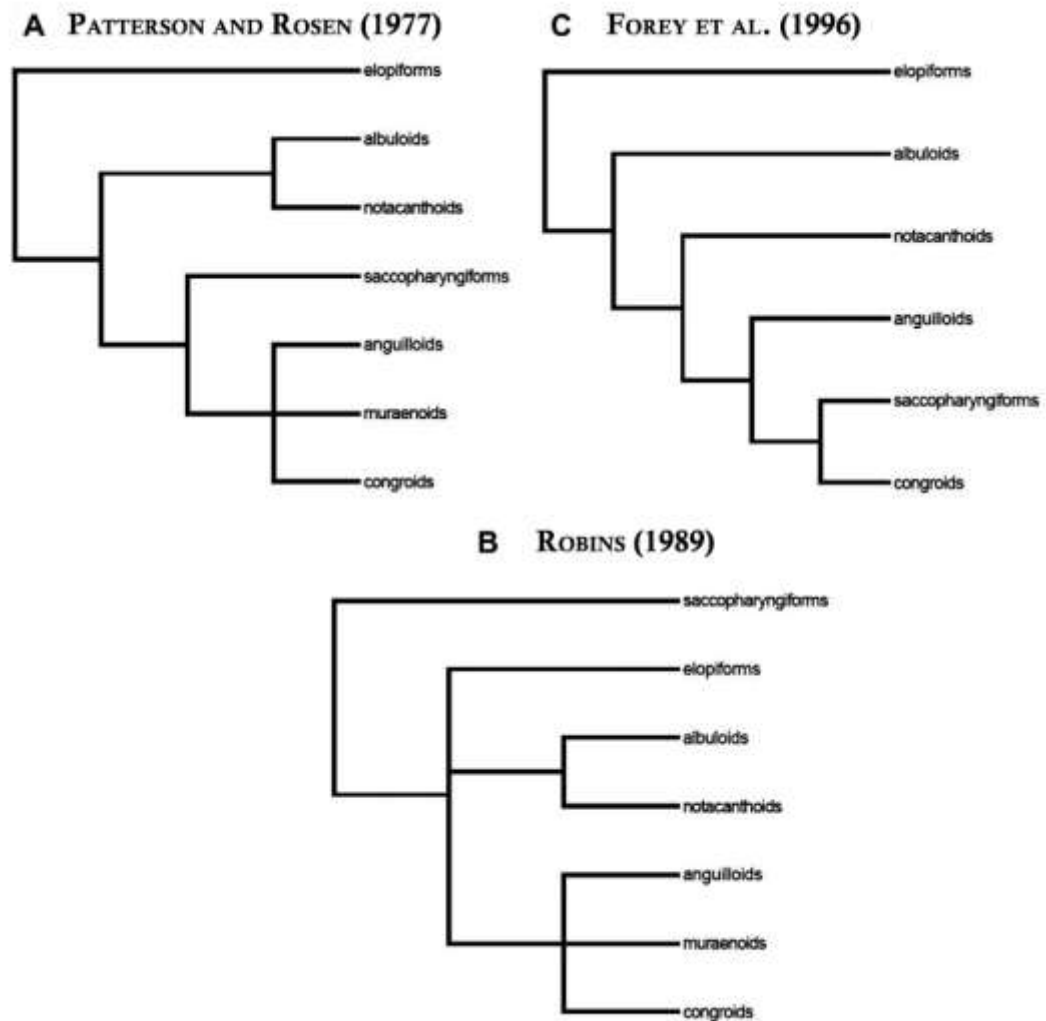


Figure 3 – Hypotheses of the relationships of Anguilliformes inferred from morphological characters according to (A) Morphological phylogeny of Patterson and Rosen (1977), (B) morphological phylogeny of Robins (1989), and (C) combined morphological and molecular phylogeny (12S, 16S, 28S) of Forey *et al.* (1996); (figure modified from Santini *et al.* 2014).

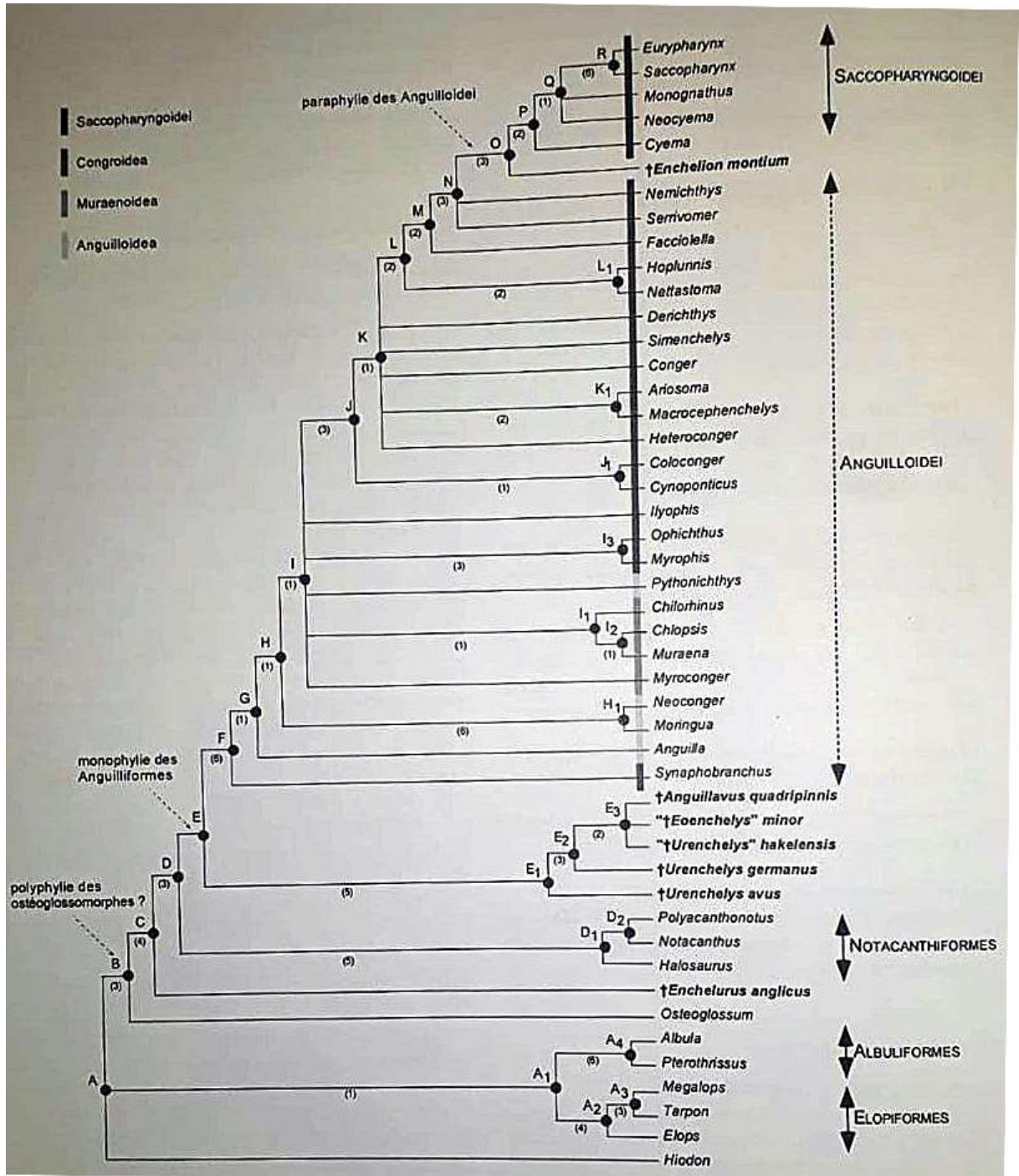


Figure 4 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Belouze (2002); most parsimonious analysis based on osteology and morphology data, including six Cretaceous fossil and Osteoglossomorpha.

Figure 5 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Johnson *et al.* (2012). Time tree of Anguilliformes and outgroup estimated from relaxed molecular-clock analysis. The analysis comprises molecular and morphological data.

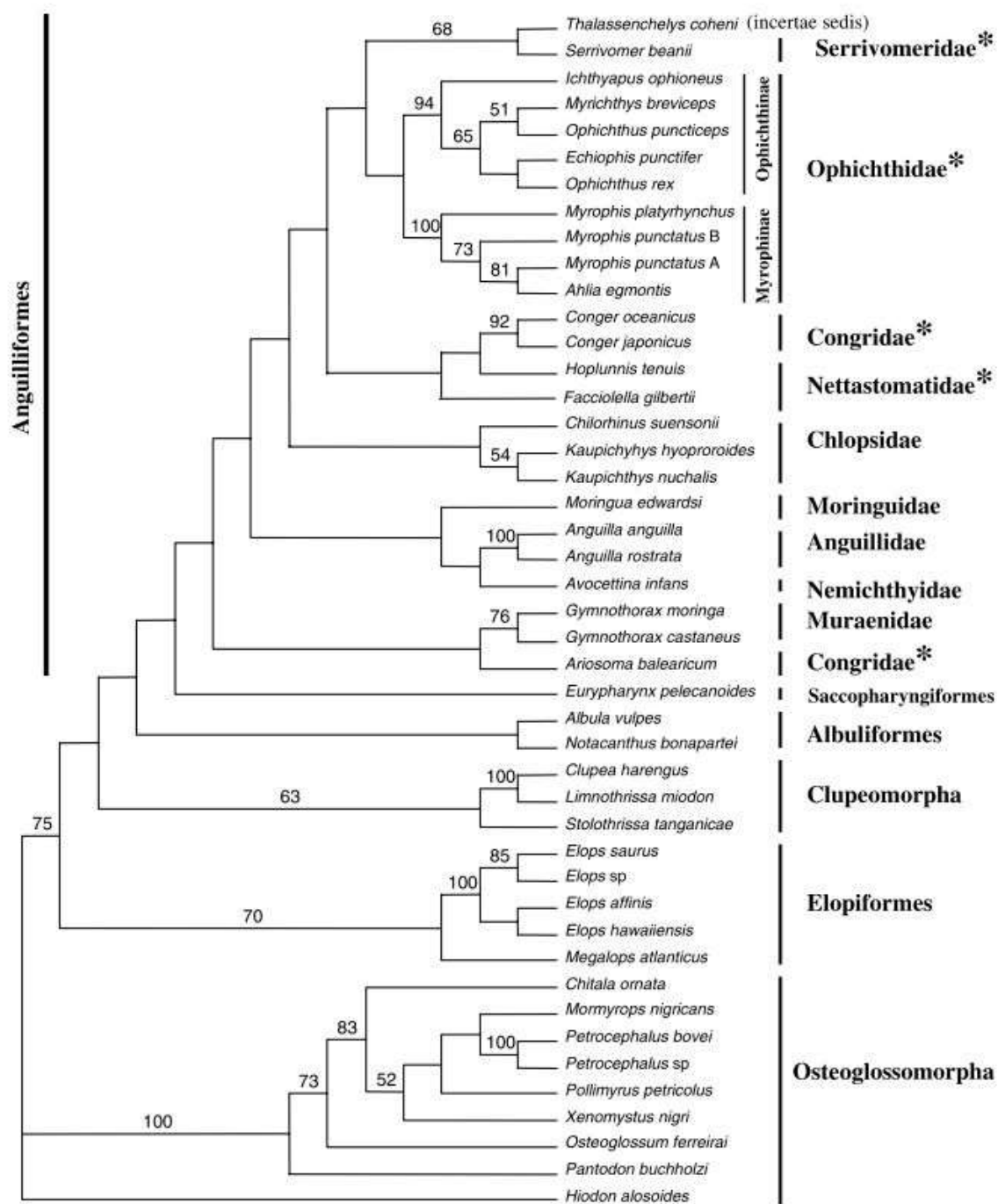


Figure 6 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to from Obermiller & Pfeifer (2003) most parsimonious (MP) tree for the combined 12S and 16S rRNA data set (Branch and Bound algorithm).

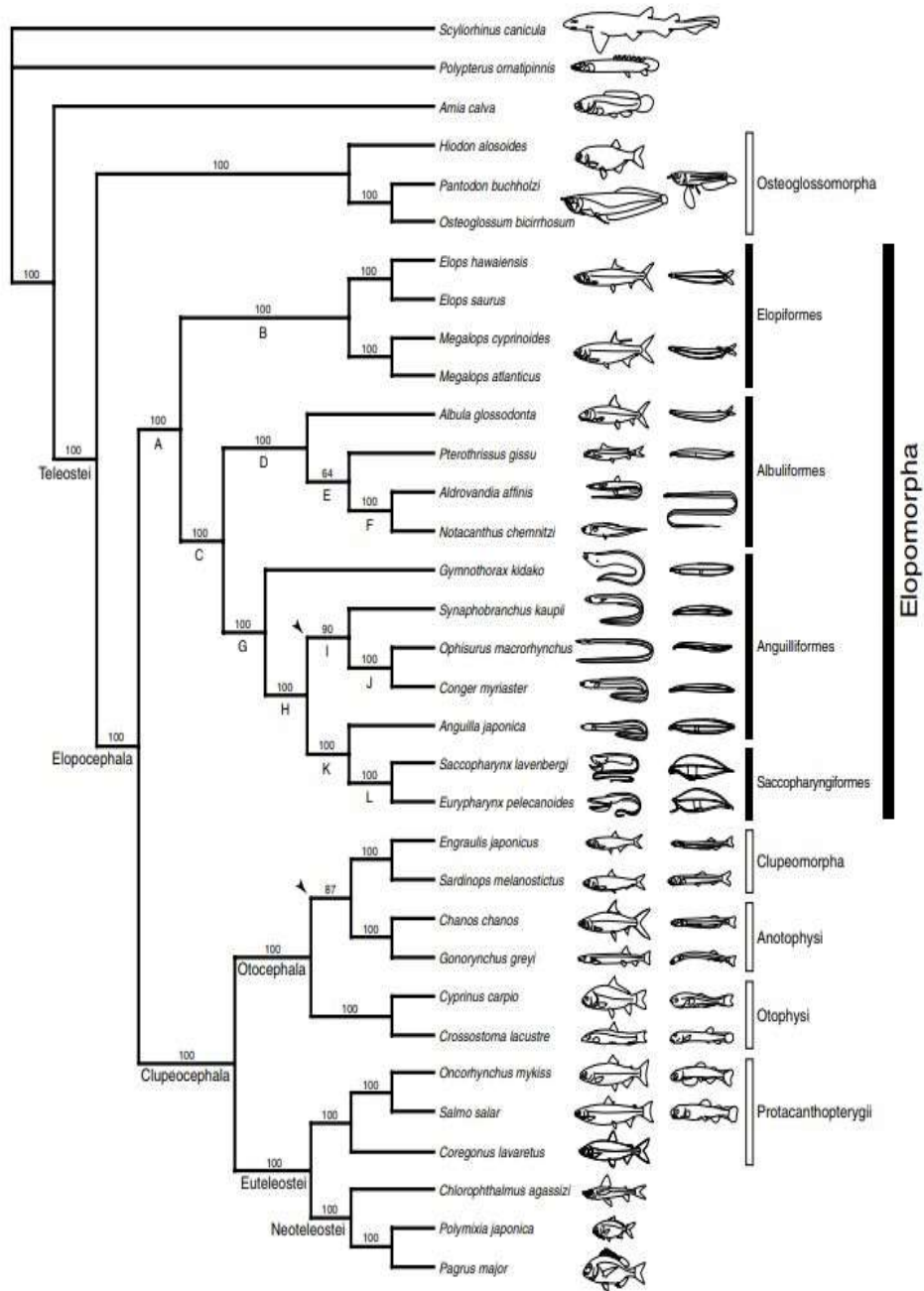


Figure 7 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Filleul & Lavoué (2002), using on molecular data from rRNA 18S, 16S and 12S.

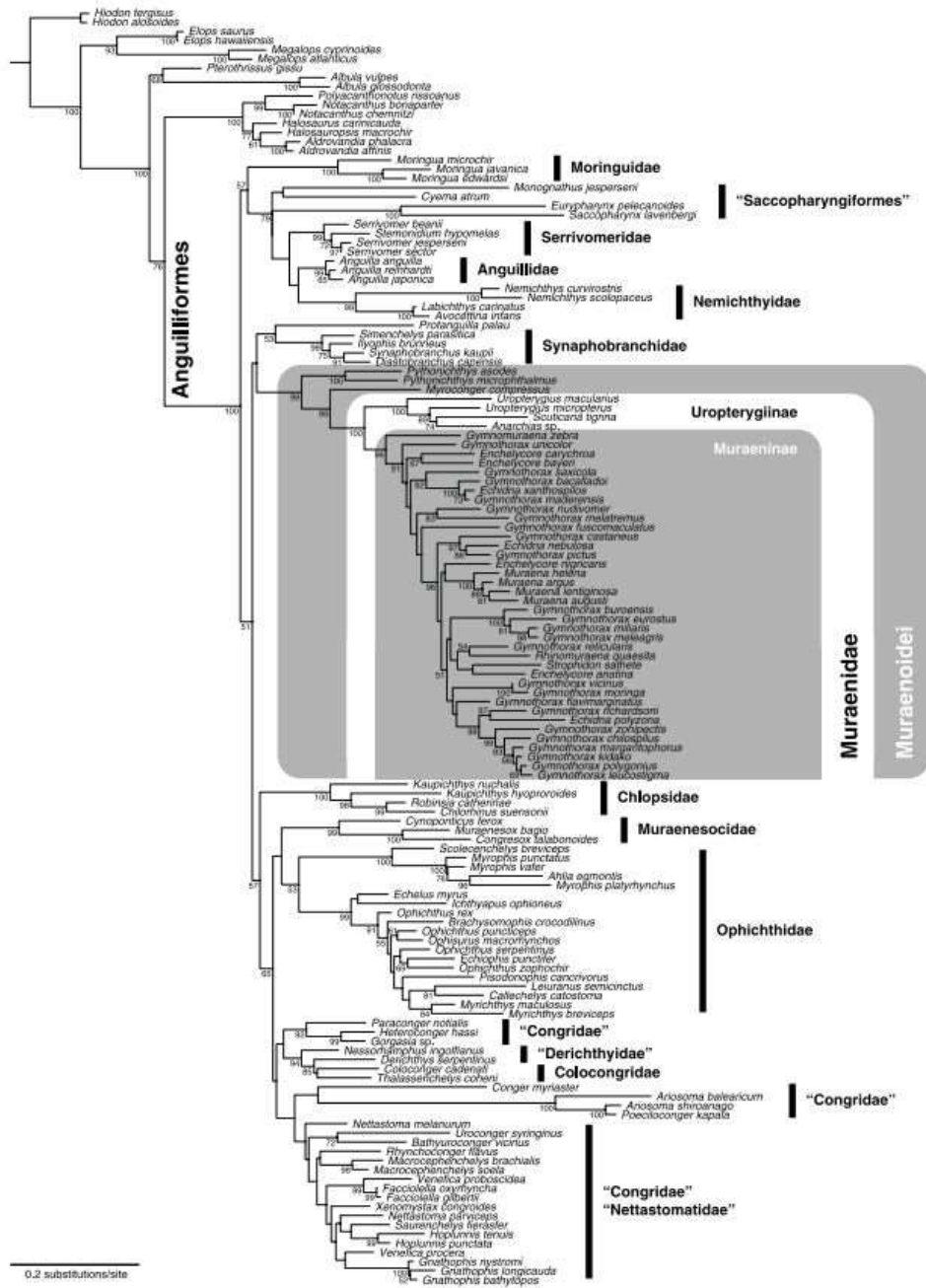


Figure 8 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Tang & Fielitz (2012) based on the best log likelihood score. Muraenidae highlighted by the authors.

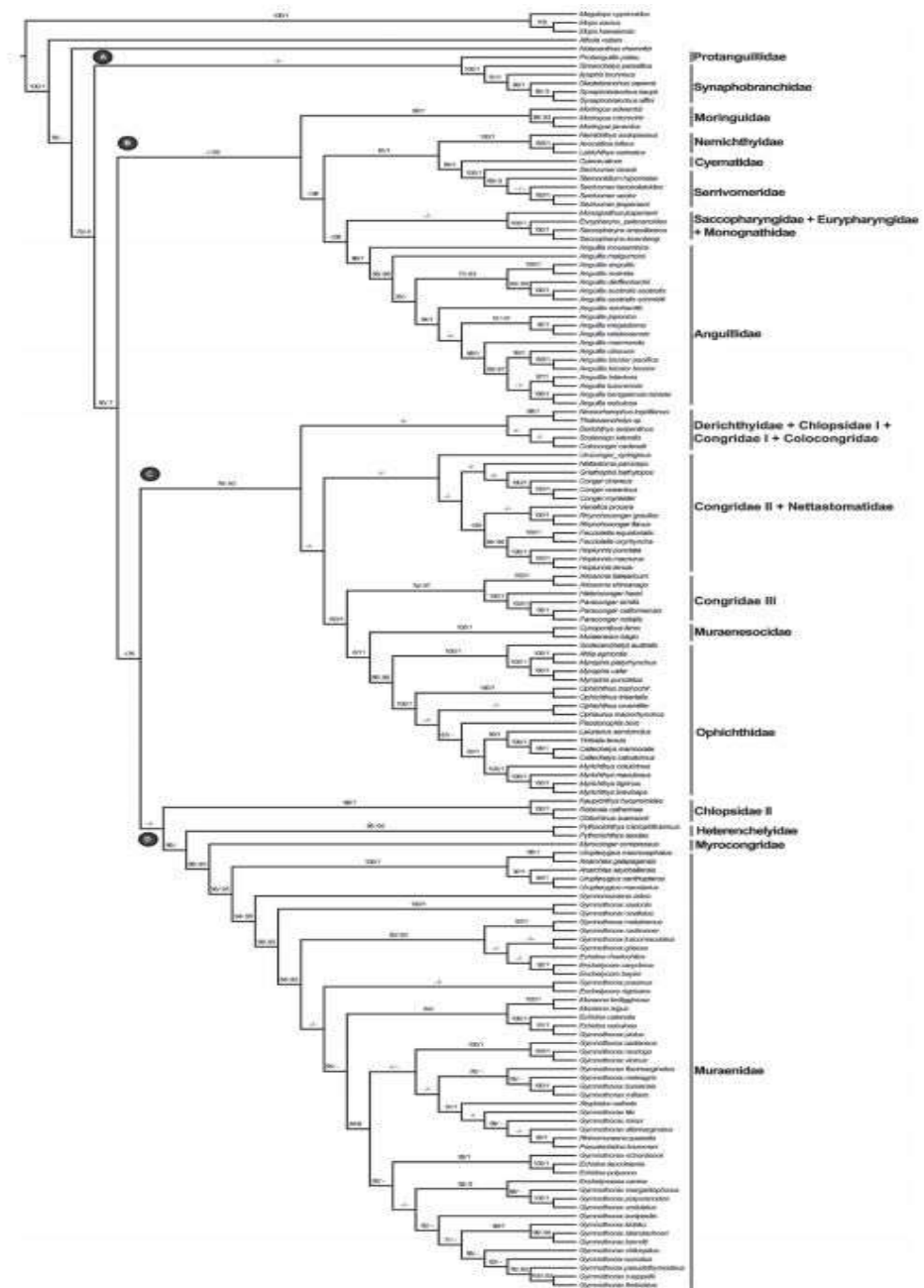


Figure 9 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Santini *et al.* (2013). Maximum likelihood phylogeny of Anguilliformes.

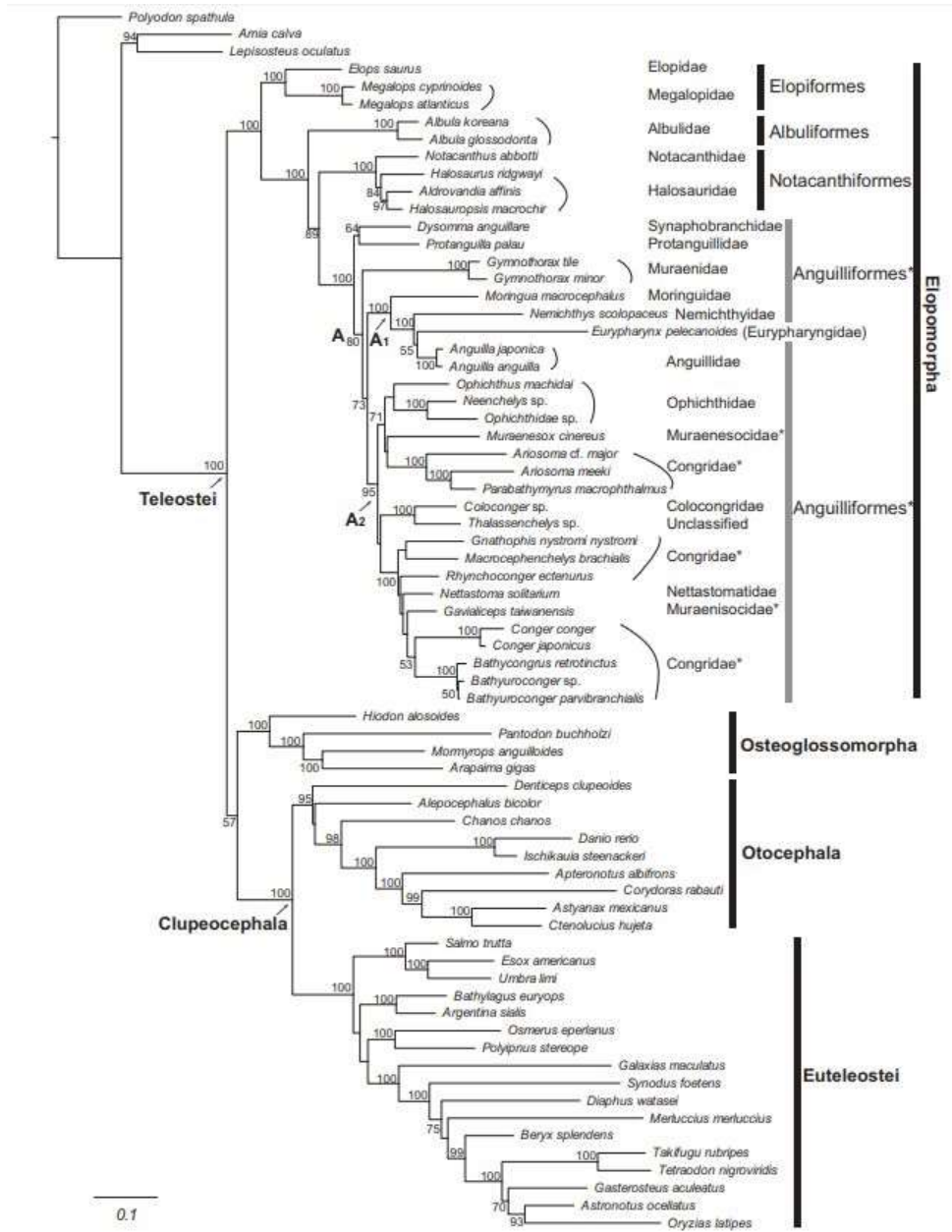


Figure 10 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Chen *et al.* (2014). The analysis performed was maximum-likelihood tree of the combined dataset (3 nuclear and 3 mitochondrial genes, 4,601 bp in length).

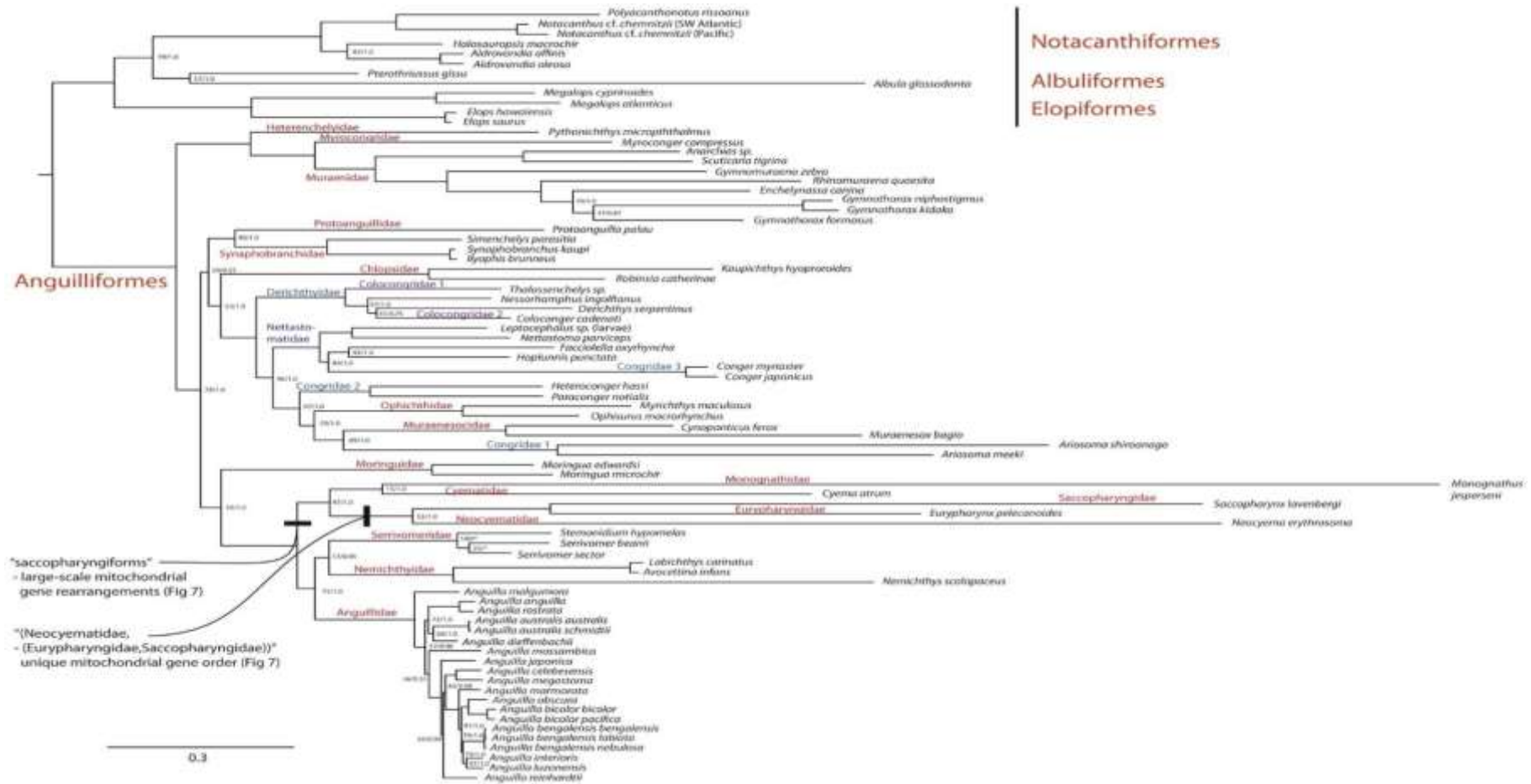


Figure 11 – Hypothesis of the relationships of Anguilliformes inferred from morphological characters according to Poulsen *et al.* (2018). Mitogenomic phylogenetic tree of 79 taxa of the Elopomorpha based on 13 protein-coding genes in the mitochondrial genome (ML and Bayesian analyses, 11,700 base pairs).

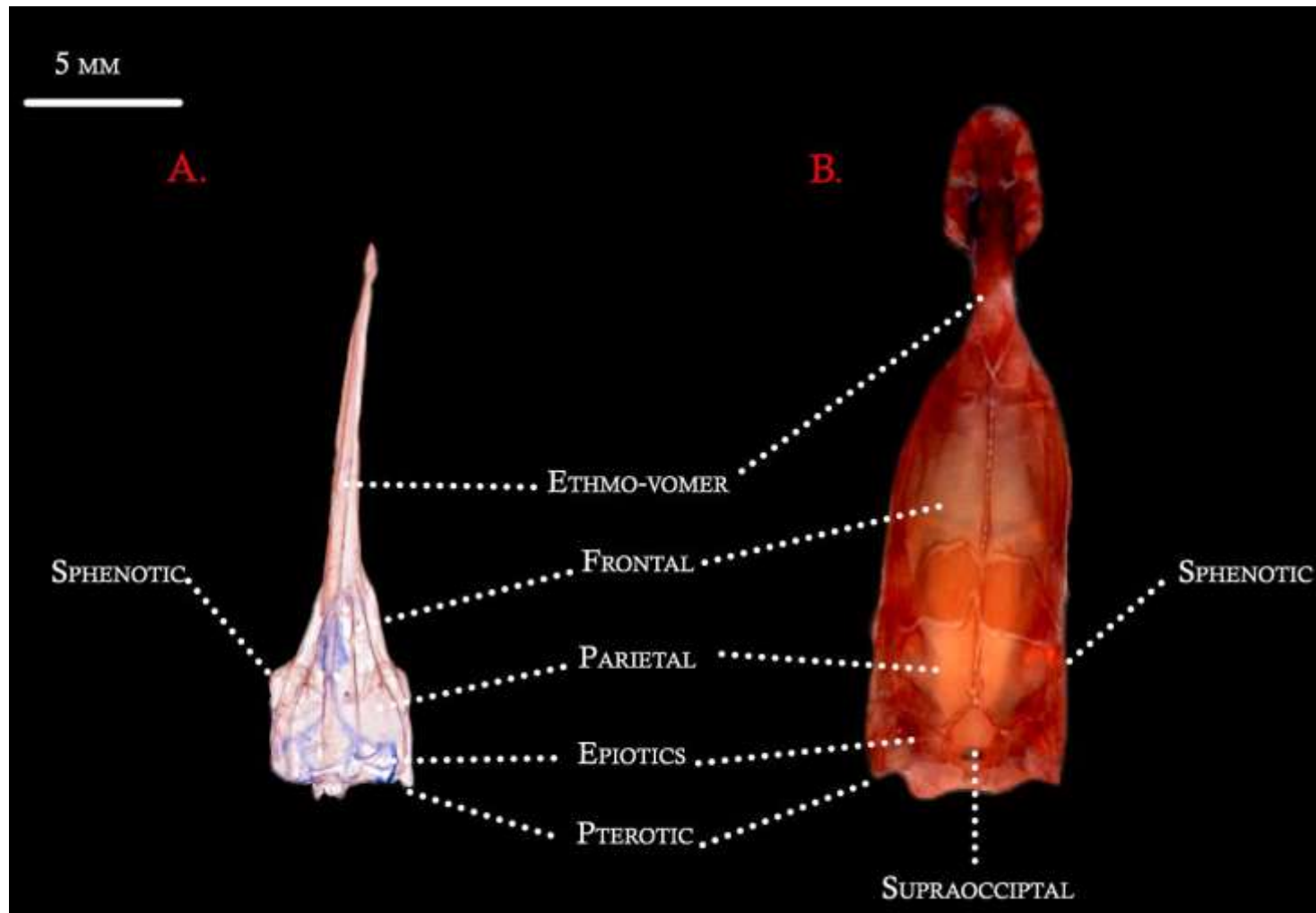


Figure 12 – Neurocranium of (A) *Cyema atrum* USNM 208058 and (B) *Echidna nebulosa* BMNH uncat in dorsal view.

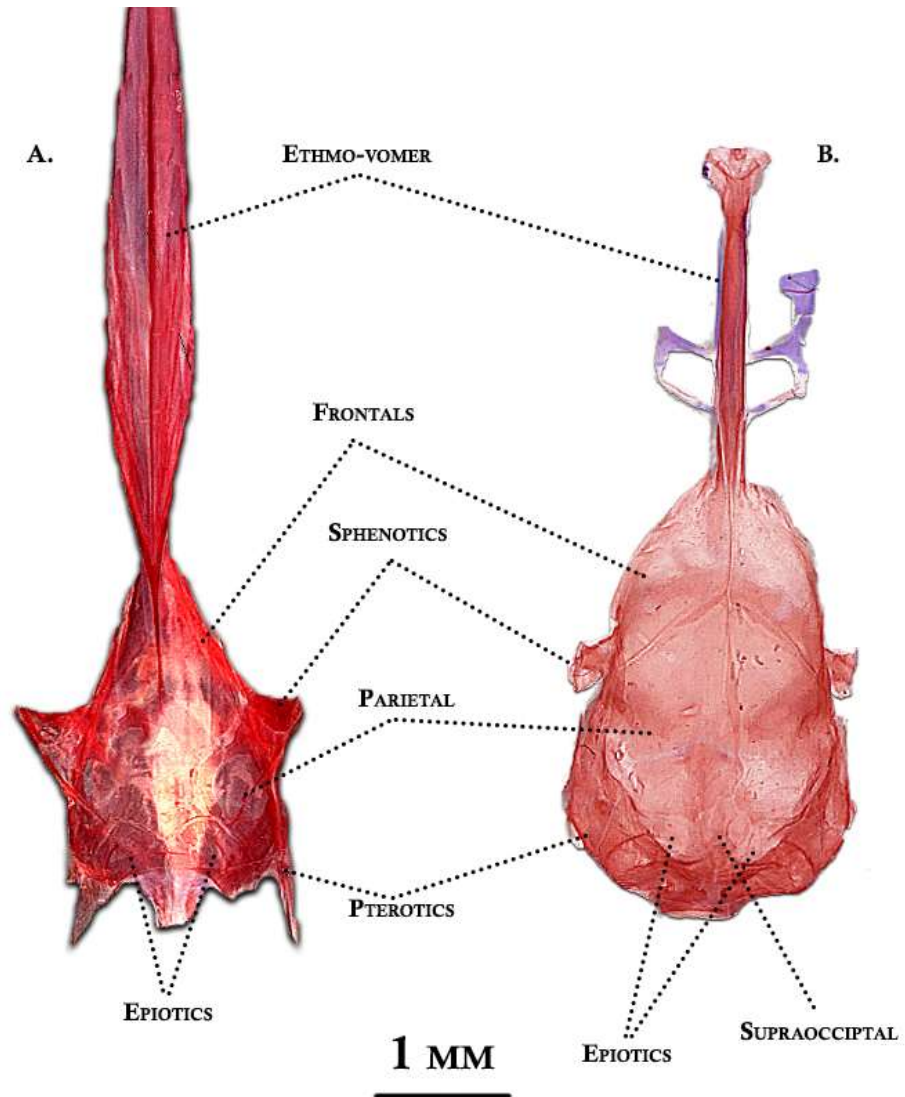


Figure 13 – Neurocranium of (A) *Serrivomer beami*, USNM 271046, and (B) *Protanguilla palau*, USNM 396016, in dorsal view. Scale bar: 1 mm.

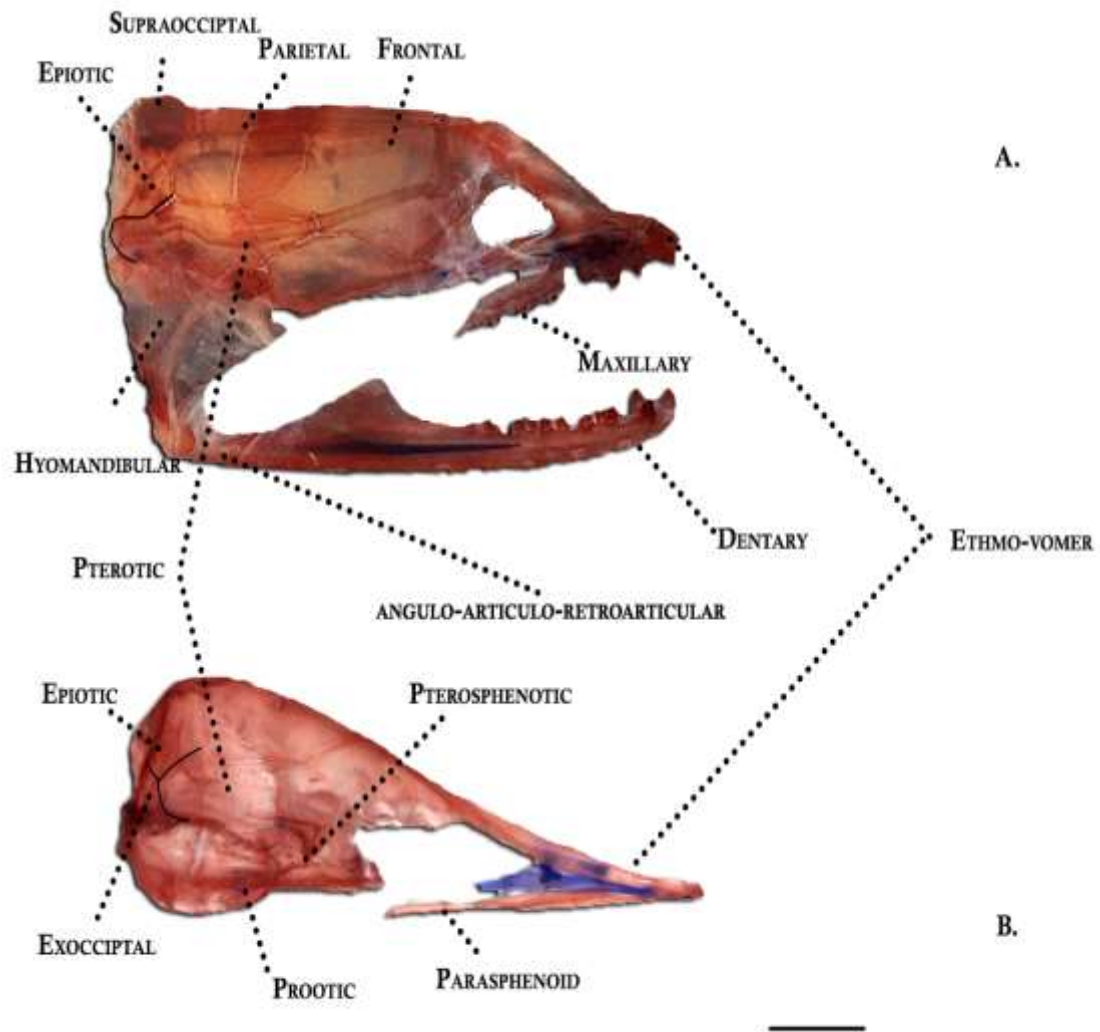


Figure 14 – Neurocranium of (A) *Echidna nebulosa*, BMNH uncat., and (B) *Protanguilla palau*, USNM 396016, in lateral view. Scale bar: 1 mm.

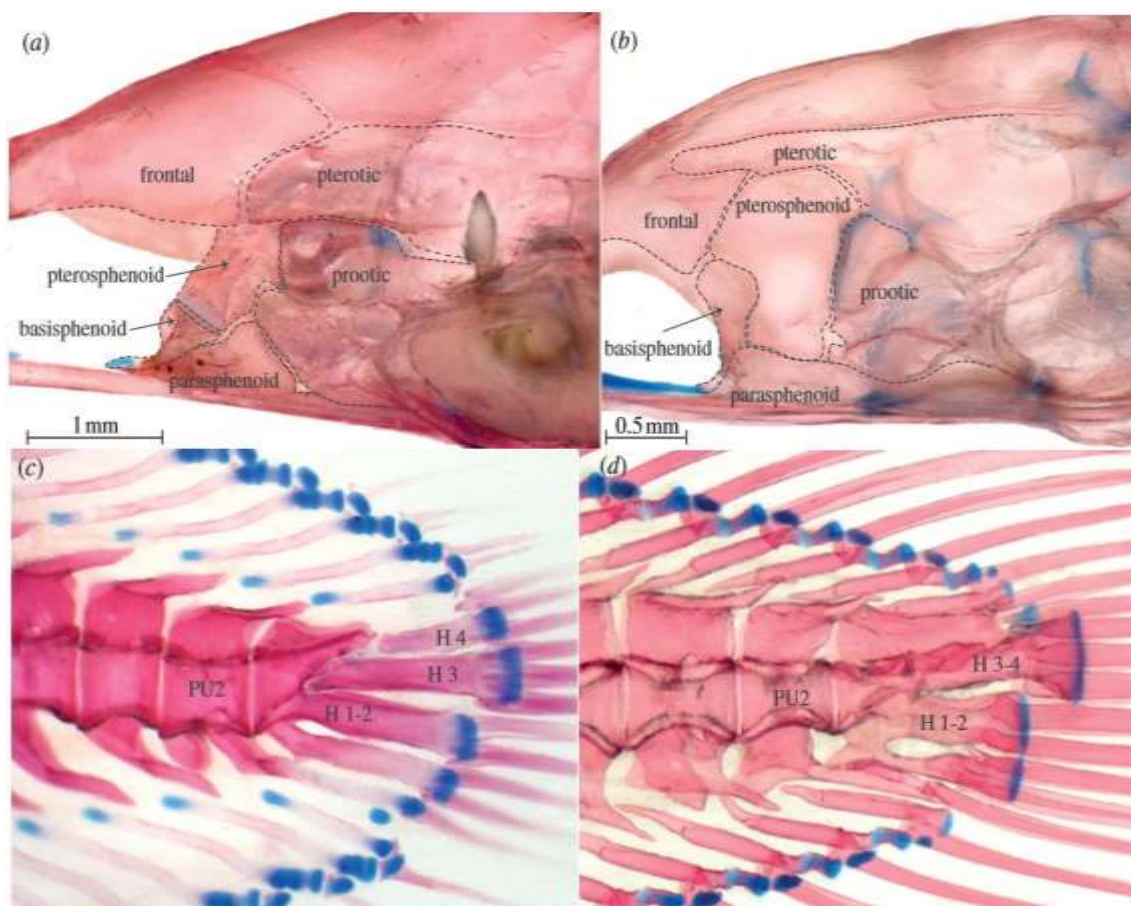


Figure 15 – Neurocranium of (a) *Protanguilla palau*, USNM 396016, and (b) *Simenchelys parasiticus*, USNM 326917, midportion lateral view. Caudal Skeleton of (c) *P. palau*, USNM 396016, (d) *Anguilla rostrata*, USNM 106563, in lateral view. PU2, preural centrum 2; H, hypurals (Photo taken from Johnson *et al.*, 2012: Figure 4).

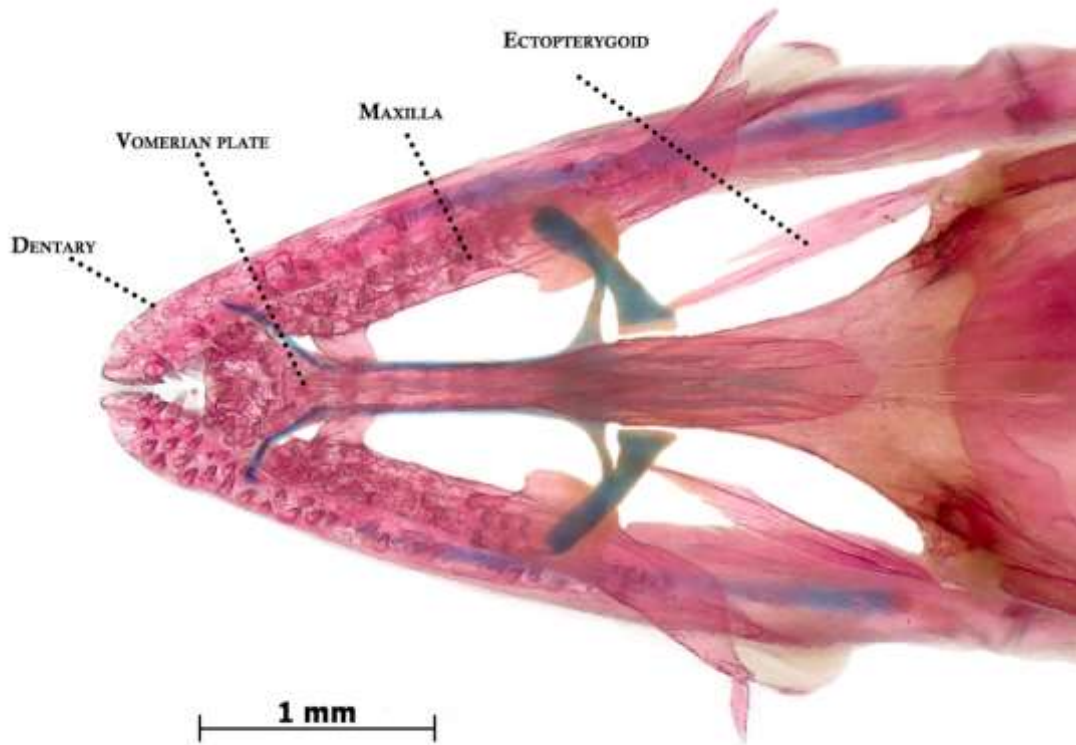


Figure 16 – Jaw of *Anguilla rostrata*, USNM 106563, in ventral view. (Photo taken by Ai Nonaka).

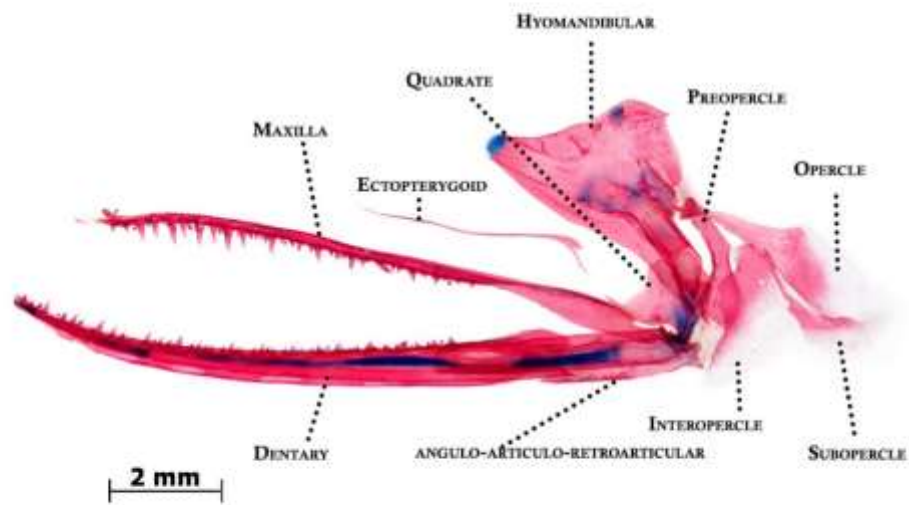


Figure 17 – Suspensorium of *Synphobranchus* sp., USNM uncat, in lateral view. (Photo taken by Ai Nonaka).

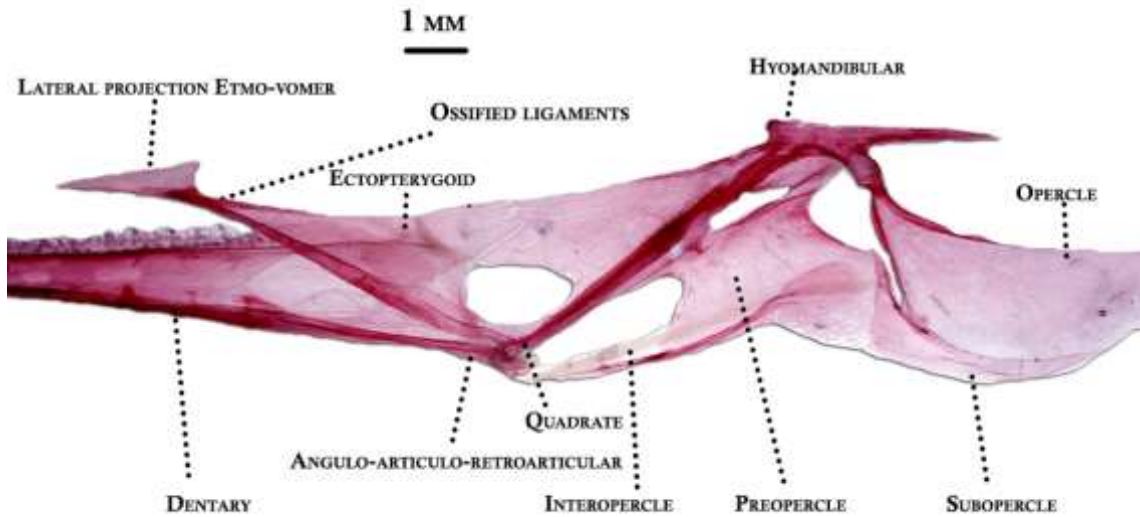


Figure 18 – Suspensorium of *Serrivomer beami*, USNM 271046, in lateral view.

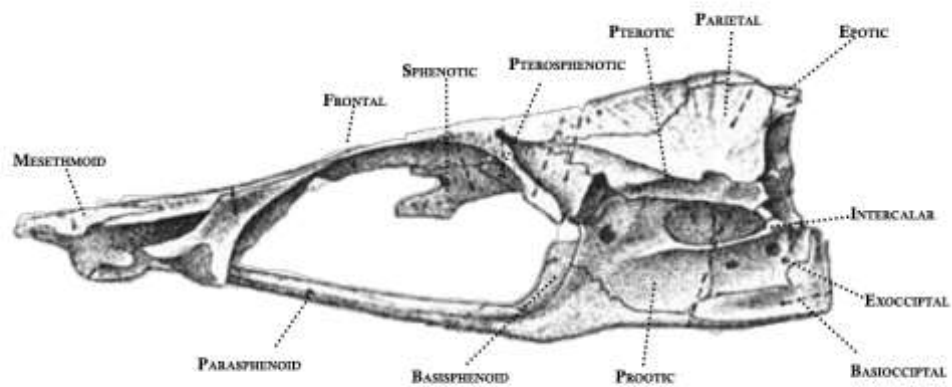


Figure 19 – Neurocranium of *Elops saurus*, USNM 271046, in lateral view (Photo modified from Ridewood, 1904: Fig. 8c).

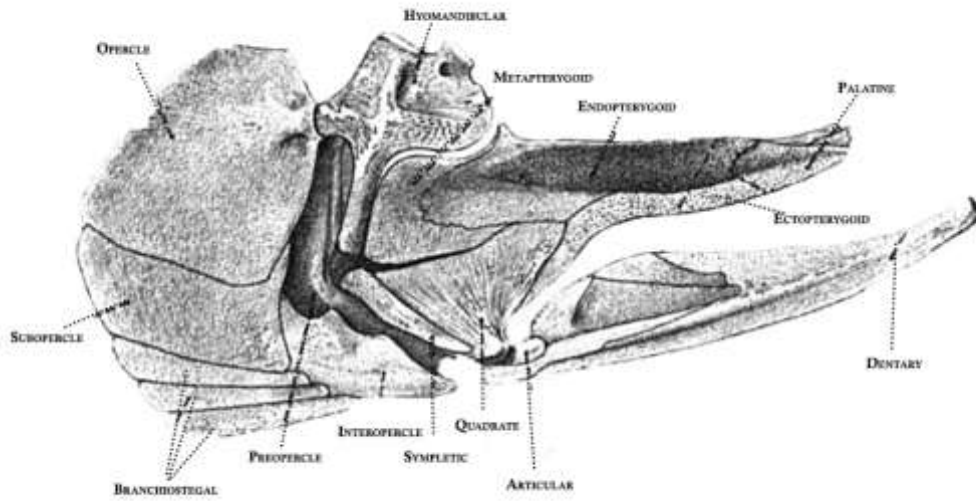


Figure 20 – Suspensorium of *Elops saurus*, in lateral view. (Photo modified from Ridewood, 1904: Fig. 10c).

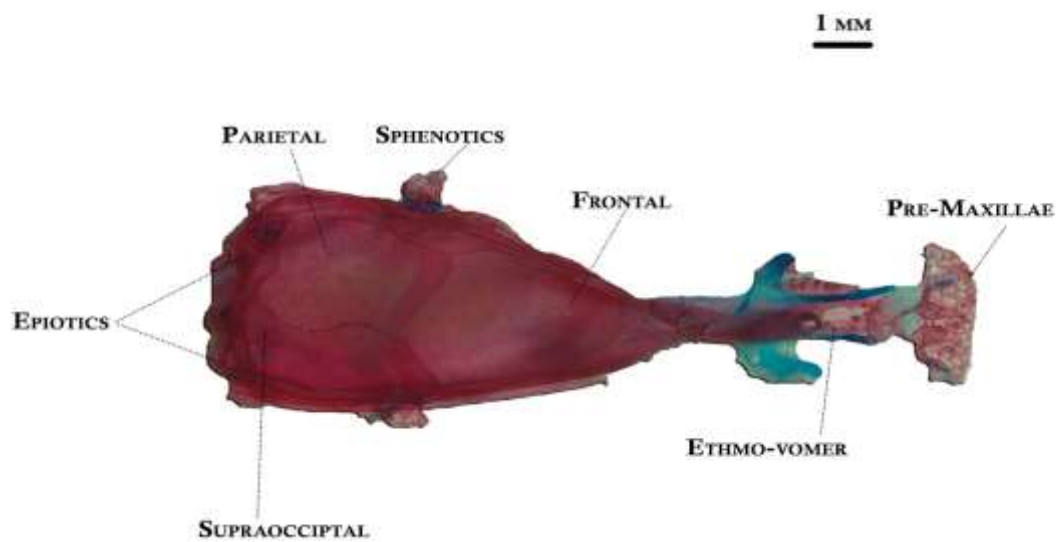


Figure 21 – Neurocranium of *Derichthys serpentinus*, USNM 315025, in dorsal view.

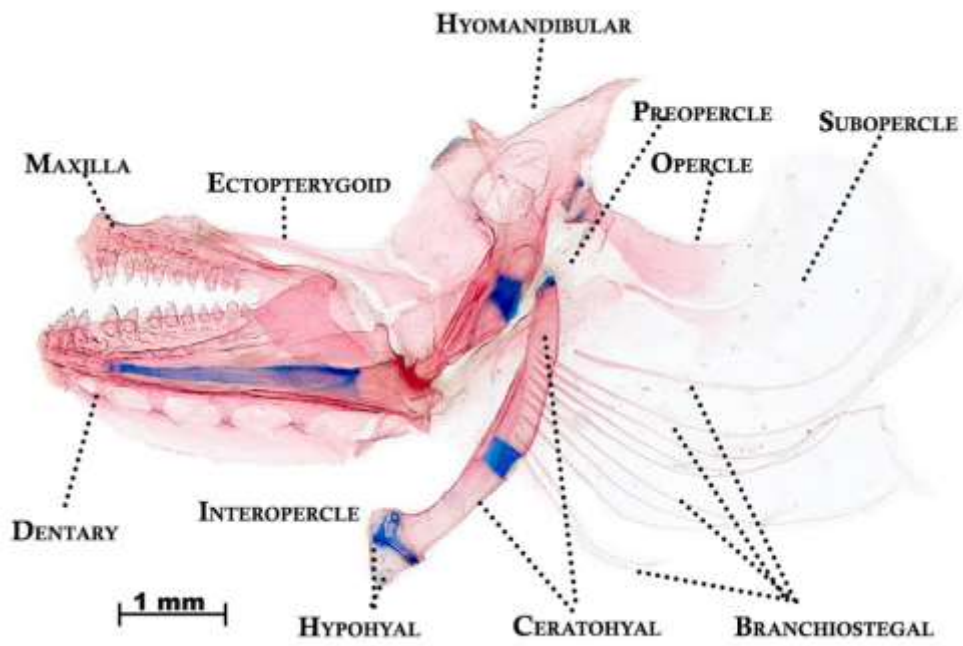


Figure 22 – Suspensorium of *Simenchelys parasitica*, USNM 326917, in lateral view.

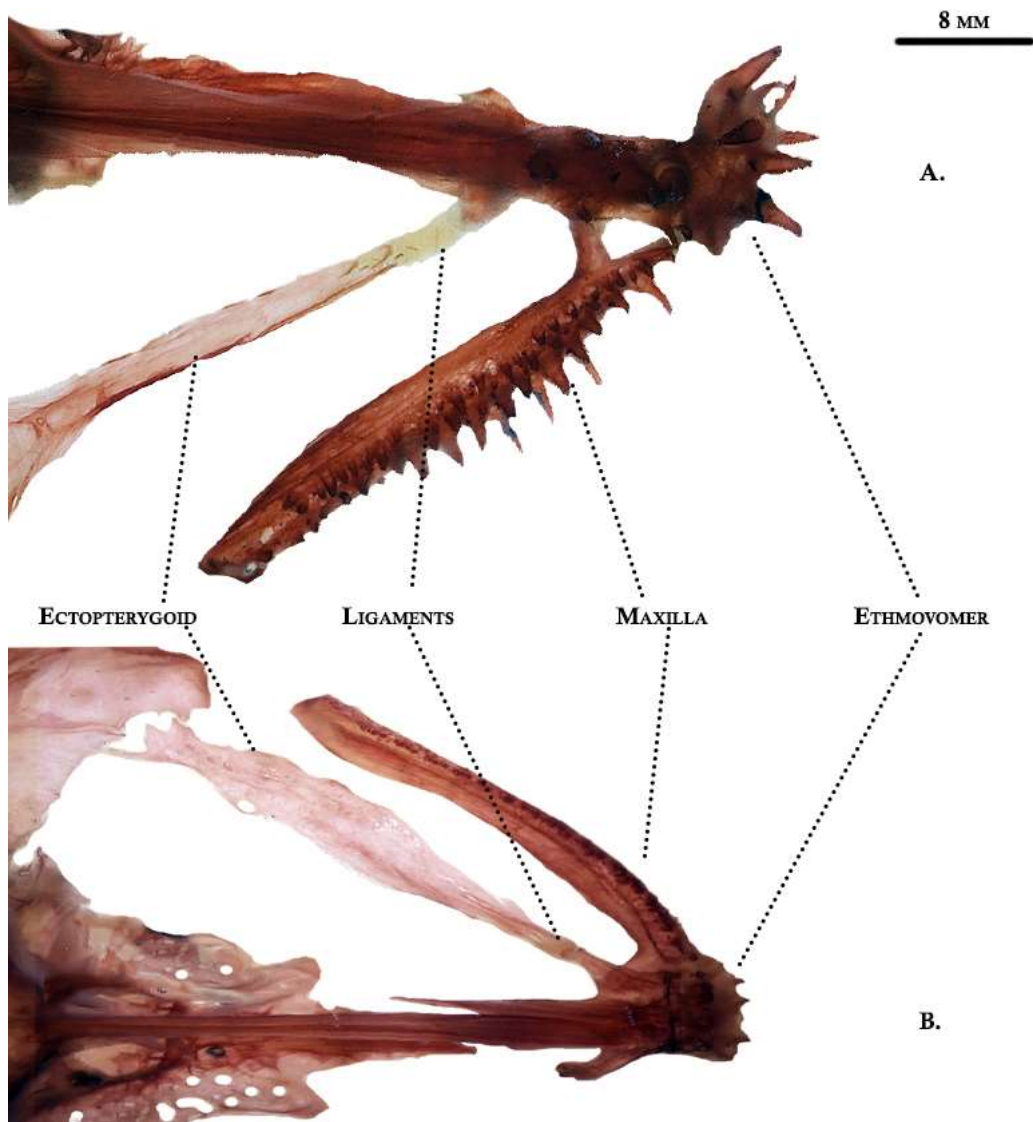


Figure 23 – Upper jaw of (A) *Bathyuroconger vicinus*, USNM 179070 and (B) *Colococonger meadi*, USNM 193572, in ventral view, showing connection between ectopterygoid and ethmovomer.

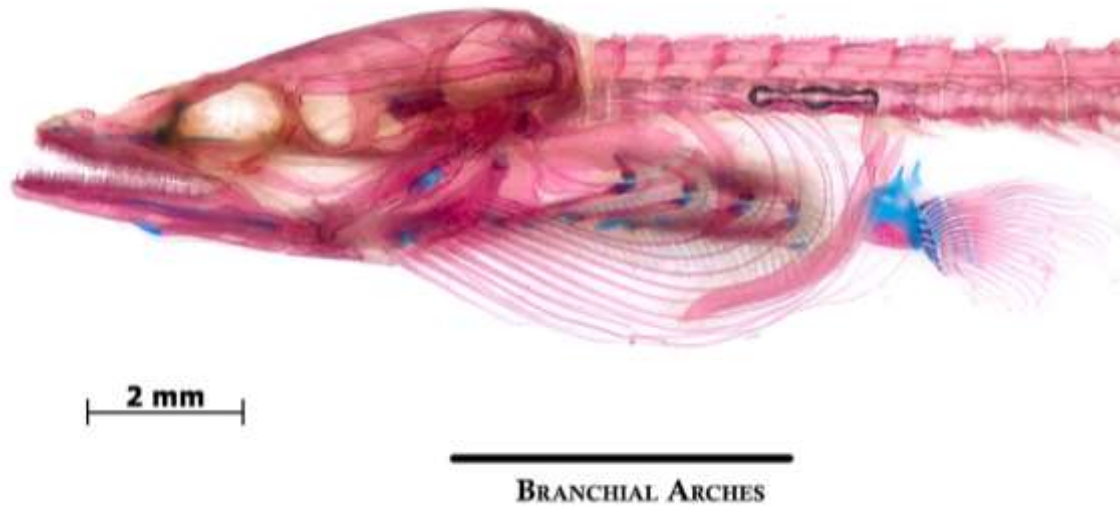


Figure 24 – Cephalic and anterior portion of *Anguilla rostrata*, USNM 106563, in lateral view (Photo taken by Ai Nonaka).

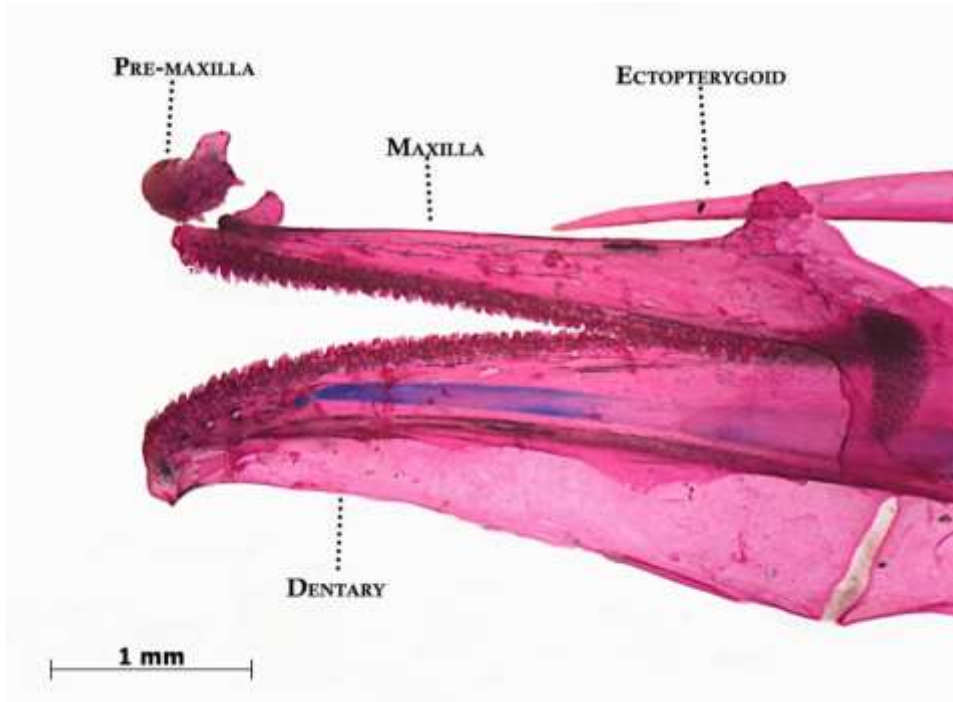


Figure 25 – Jaw of *Protanguilla palau*, USNM 396016, in lateral view (Photo taken by Ai Nonaka).

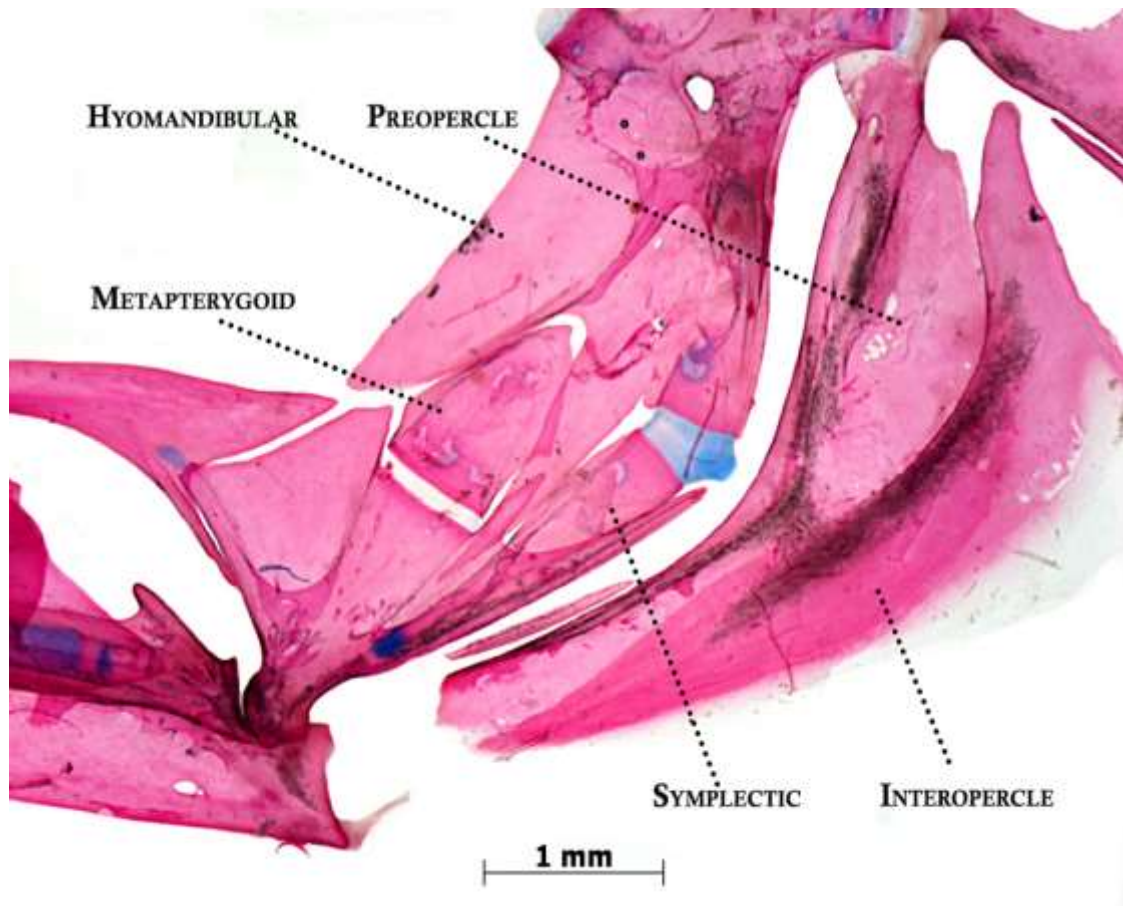


Figure 26 – Suspensorium of *Protanguilla palau* USNM 396016, in lateral view.

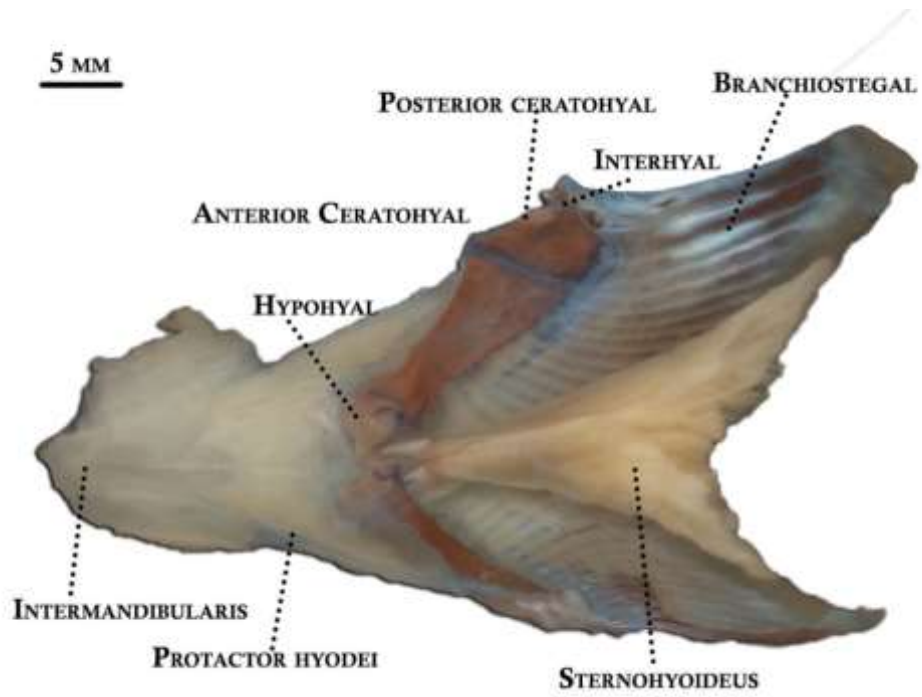


Figure 27 – Hyoid arch with musculature of *Albula vulpes*, USNM 218871, in dorsal view.

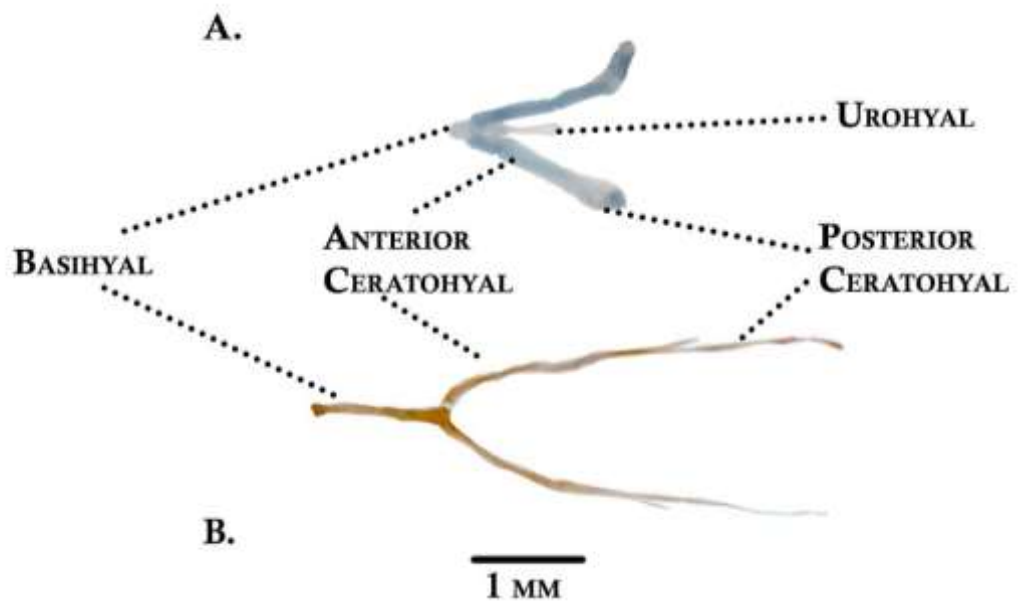


Figure 28 – Hyoid arch of (A) *Cyema atrum*, ANSP 143871, (Leptocephalus), and (B) *Anarchias similis*, USNM 320964, in dorsal view.

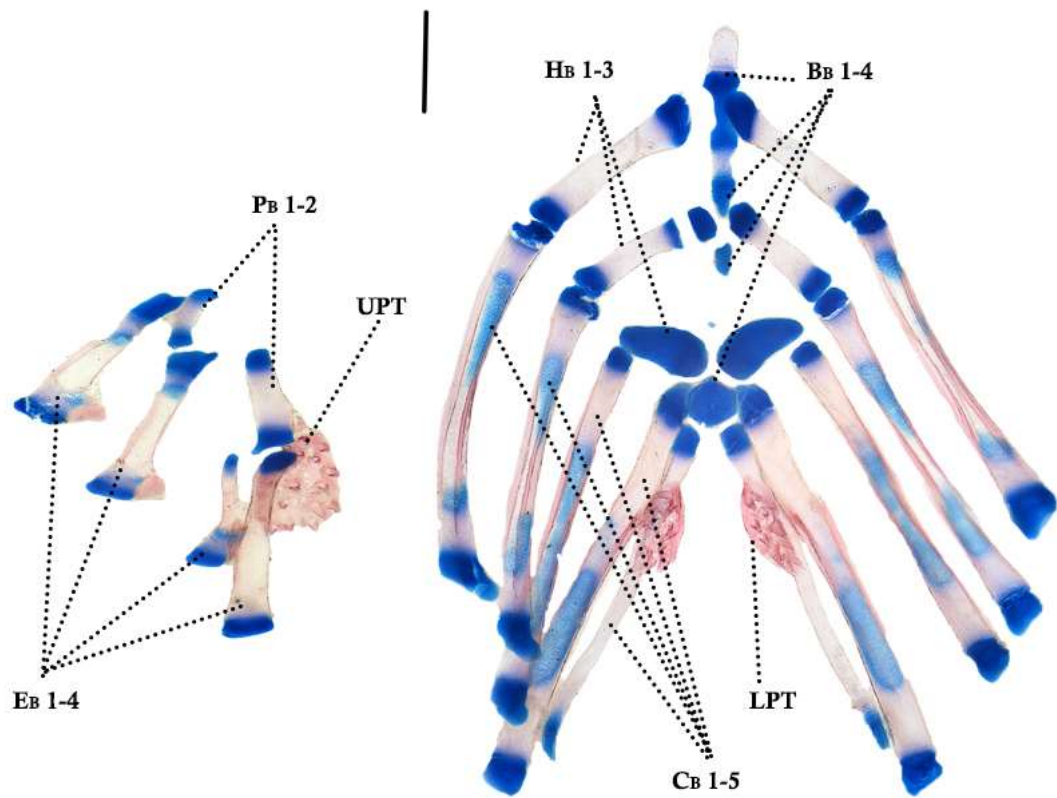


Figure 29 – Branchial arches of *Simenchelys parasitica*, USNM 326917, in dorsal view.

Scale bar: 2.0 mm.

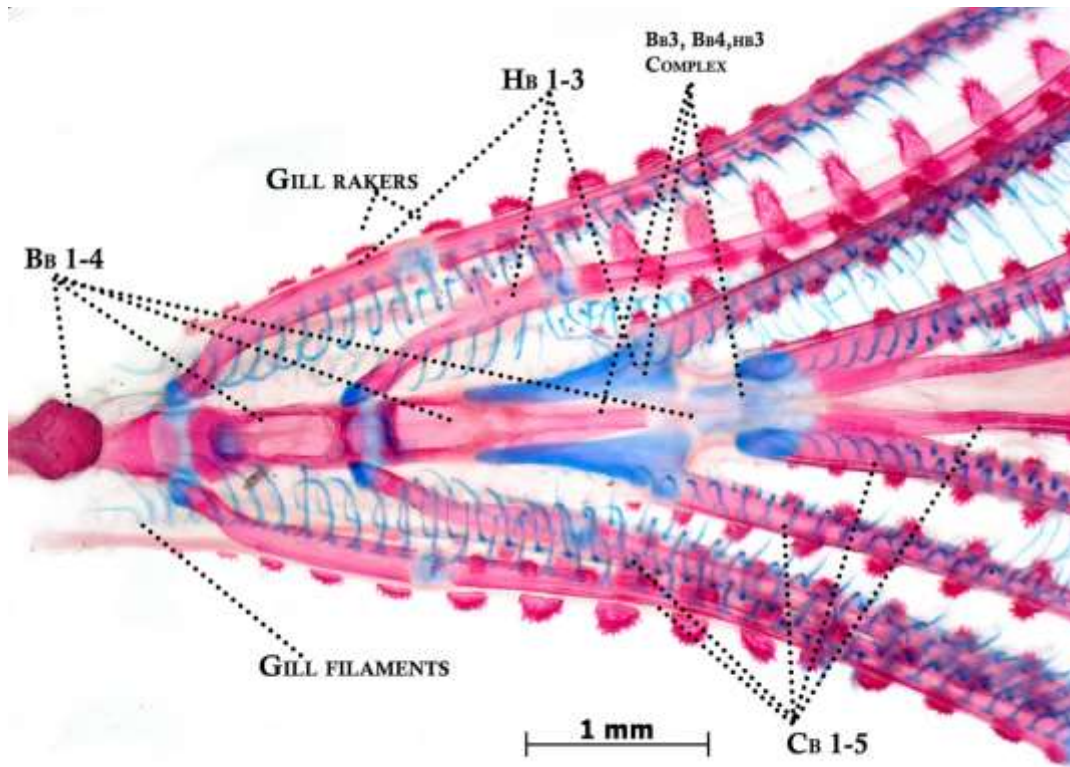


Figure 30 – Branchial arches (ventral elements) of *Protanguilla palau*, USNM 396016, in dorsal view (Photo taken by Ai Nonaka).

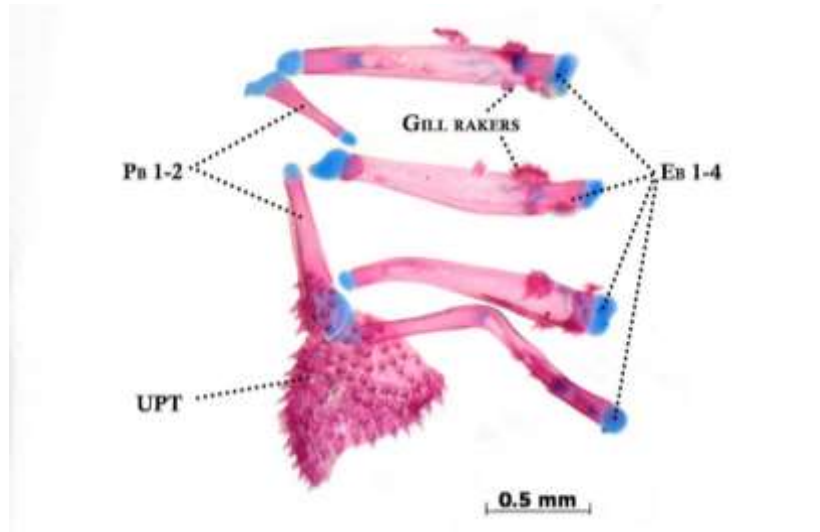


Figure 31 – Branchial arches (dorsal elements) of *Protanguilla palau*, USNM 396016, in dorsal view (Photo taken by Ai Nonaka).

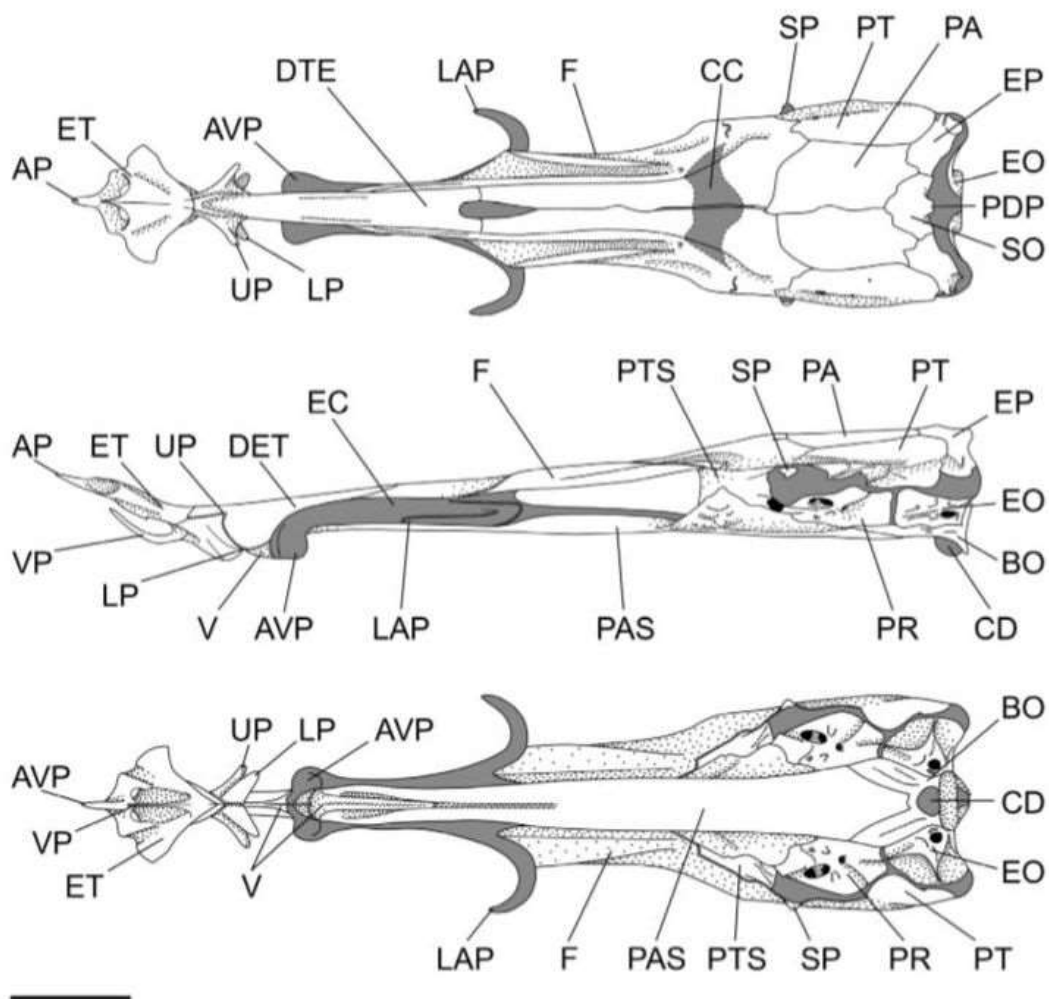


Figure 32 – Neurocranium of *Aldrovandia affinis* (modified from Kanehira *et al.* 2012: figure 2) in dorsal (above), lateral (middle) and ventral (below) views. AP, anterior process; AVP, anteroventral process; BO, basioccipital; CC, cartilage C; CD, cartilage D; DET, dermethmoid; EC, ethmoid cartilage; EO, exoccipital; EP, epiotic; ET, ethmoid; F, frontal; LAP, lateral process; LP, lower process; PA, parietal; PAS, parasphenoid; PDP,

posterodorsal process; PR, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital;
SP, sphenotic; UP, upper process; V, vomer; VP, ventral process. Scale bar: 5 mm.

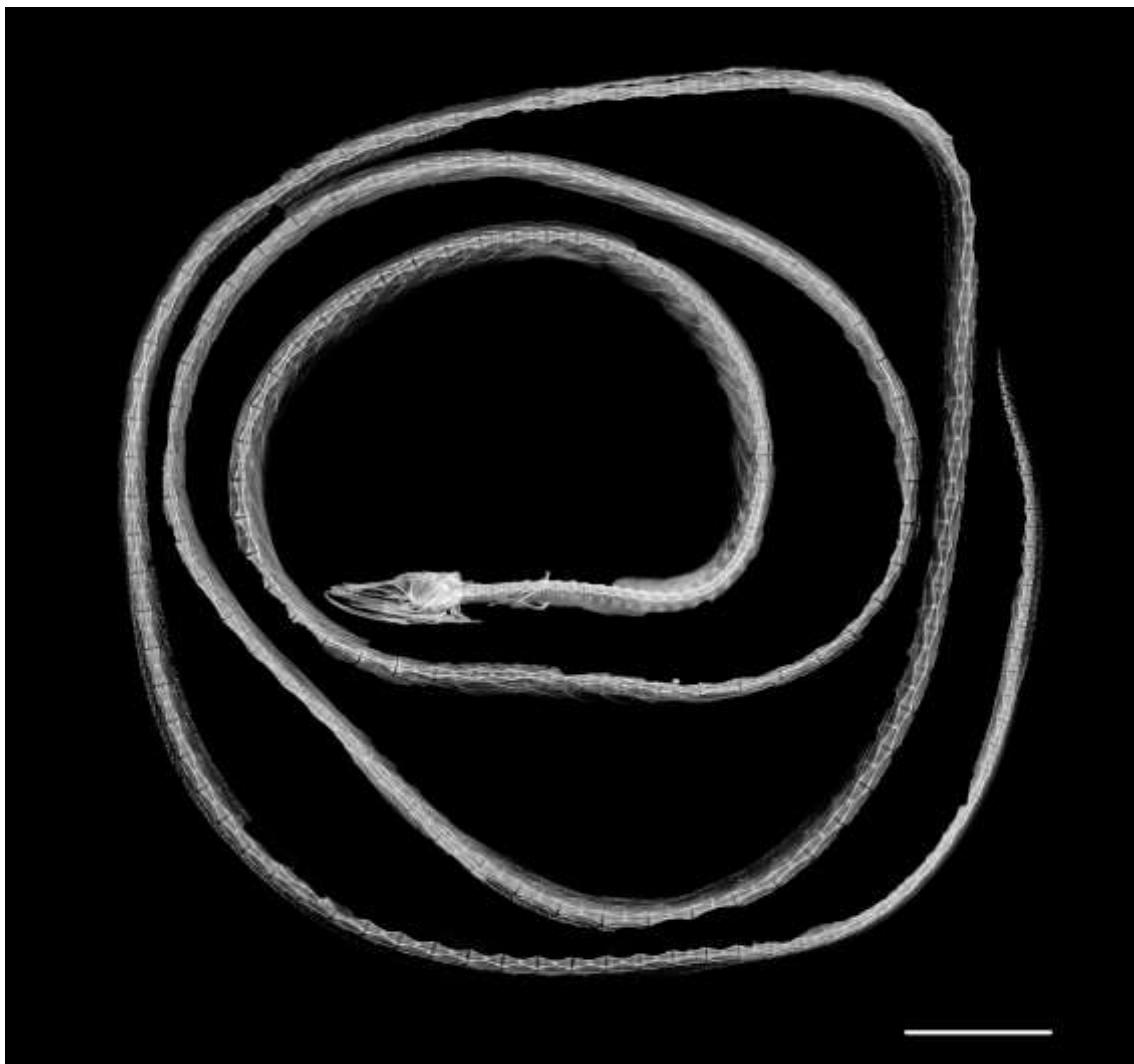


Figure 33 – Radiographic image of *Gorgasia thamani*, Paratype, NSMT-P 68327, showing the number of vertebrae. Scale bar: 10 mm.

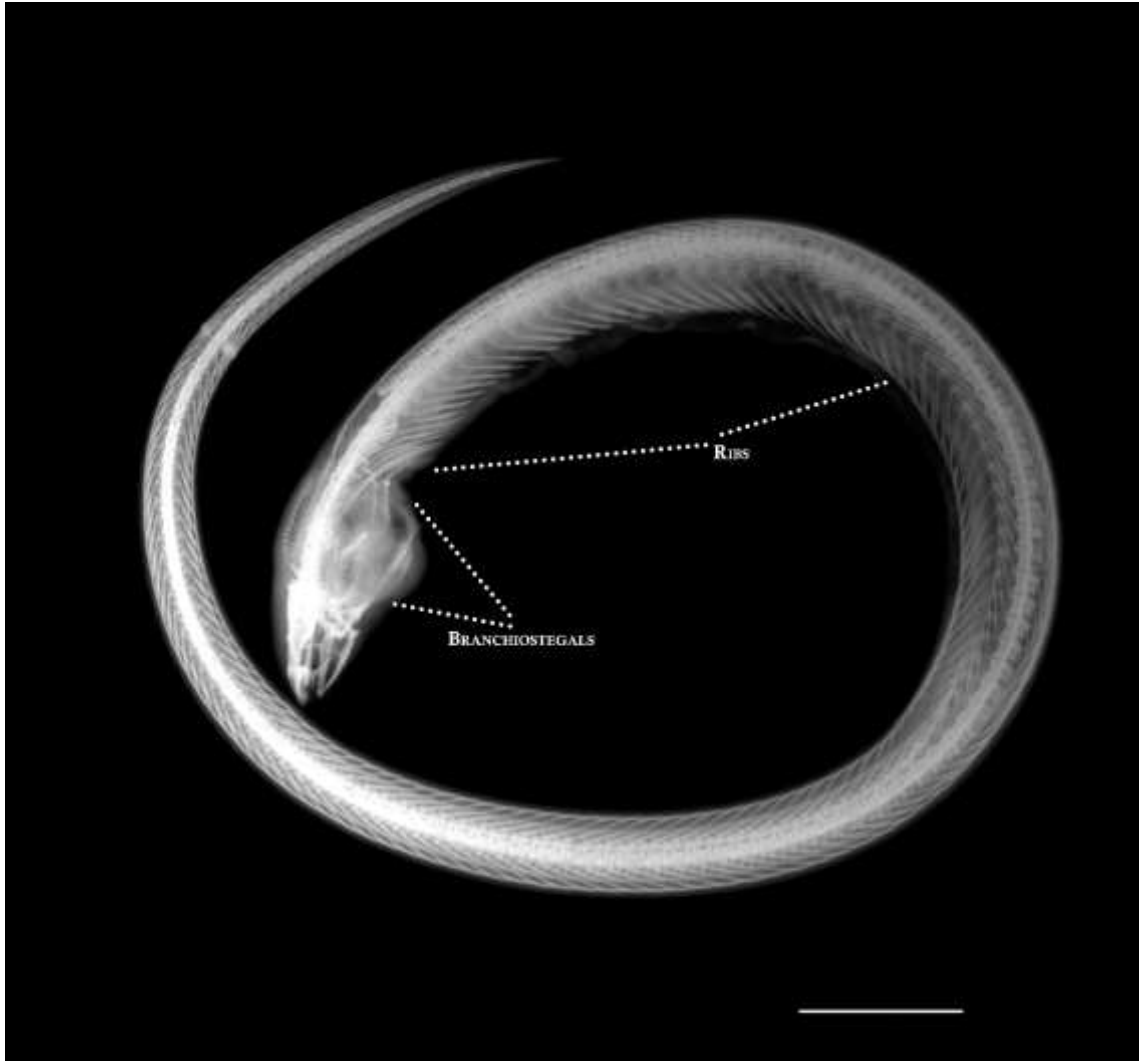


Figure 34 – Radiographic image of *Ophichthus obtusus*, Holotype, NSMT-P 106574, showing the number of vertebrae. Scale bar: 10 mm.



Figure 35 – Radiographic image of *Protanguilla palau*, USNM 396016, showing the number of vertebrae. Scale bar: 10 mm.

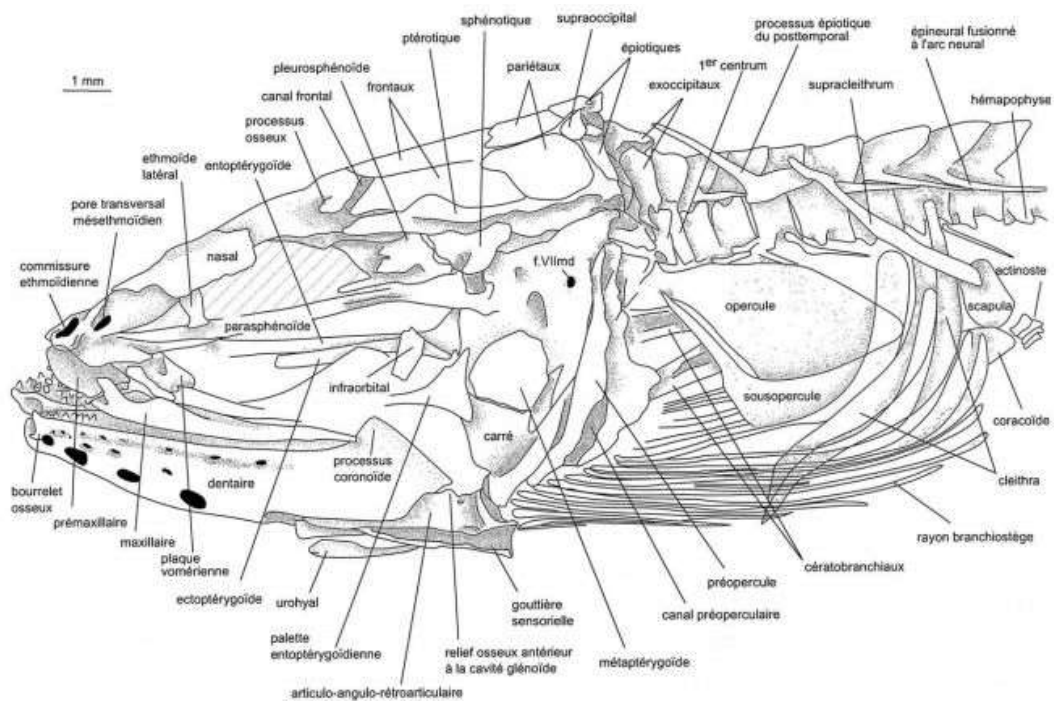


Figure 36 – Neurocranium of †*Anguillavus quadripinnis* in lateral view (Belouze, 2003: Fig 3).

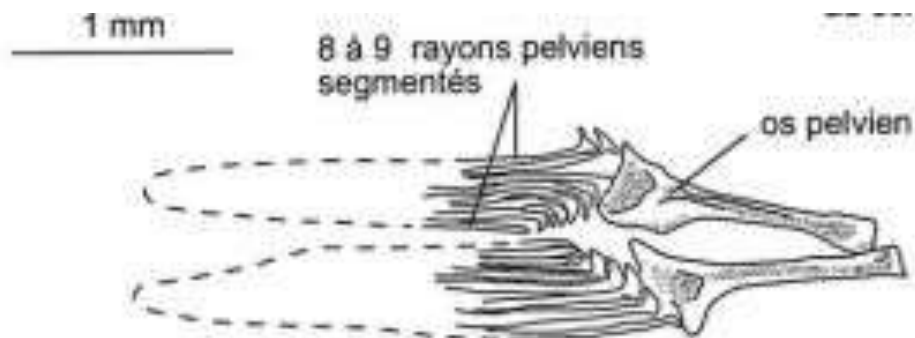


Figure 37 – Pelvic girdle of †*Anguillavus quadripinnis* in lateral view (Belouze, 2003: Fig. 14).

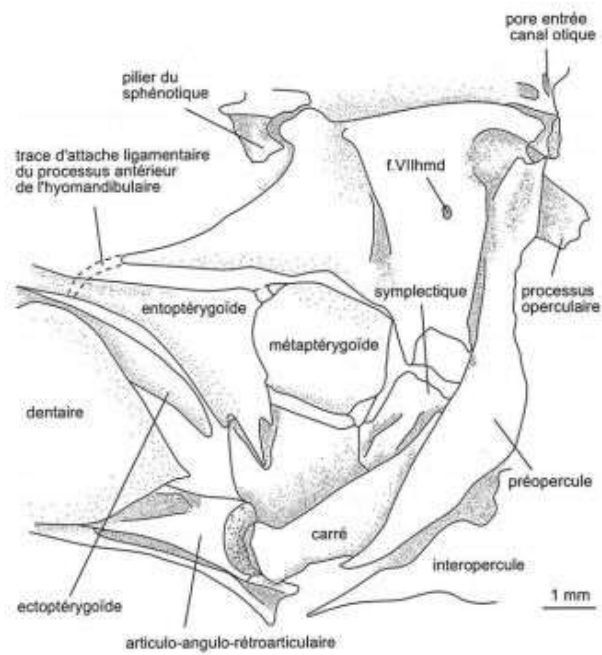


Figure 38 – Suspensorium of †*Anguillavus quadripinnis* in lateral view (Belouze, 2002: Fig. 10).

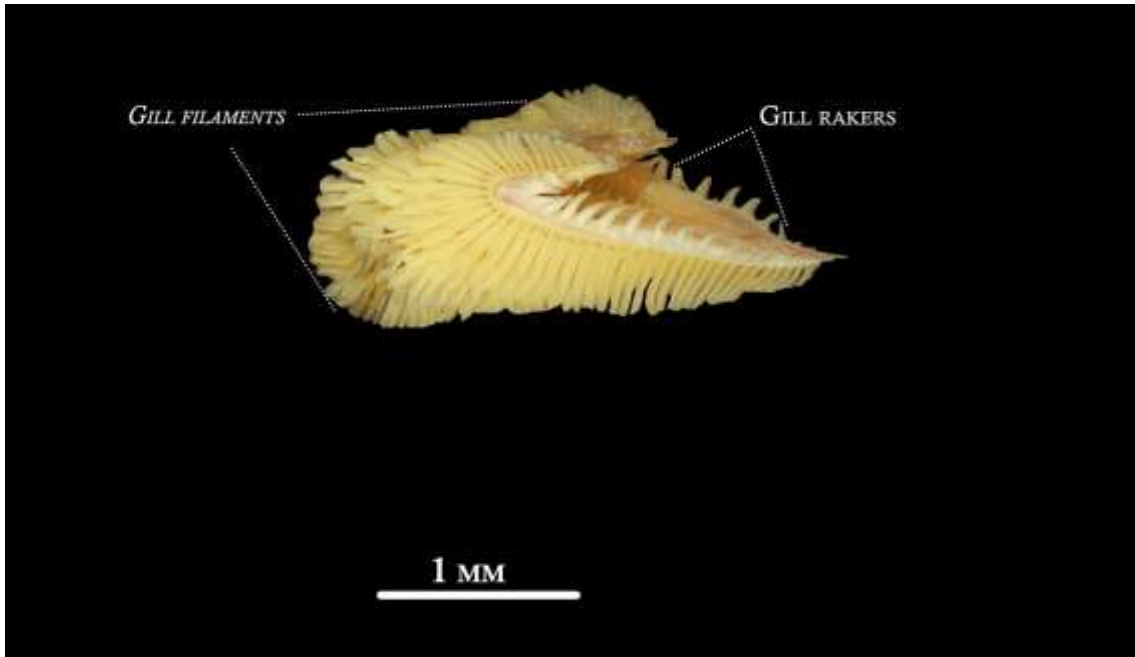


Figure 39 – Branchial arches of *Gorgasia punctata*, CAS 20752, in lateral view.

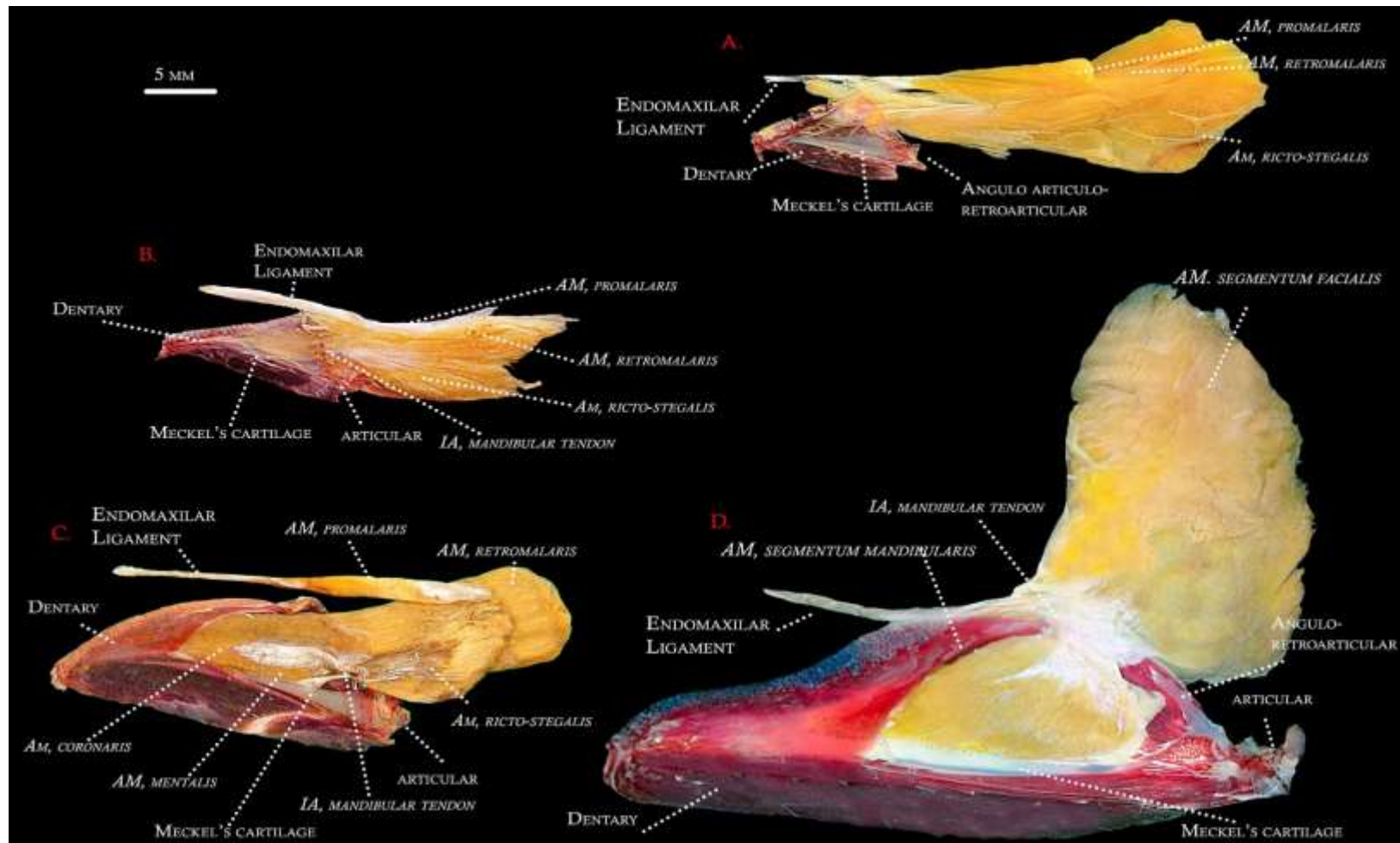


Figure 40 – Lower jaw and *adductor mandibulae* complex of (A) *Polyacanthonothus rissoanus*, VIMS 4552, (B) *Albula vulpes*, MNRJ 37303, (C) *Aldrovandia phalacra*, VIMS 8390, and (D) *Elops saurus*, MNRJ 40531, in medial view.

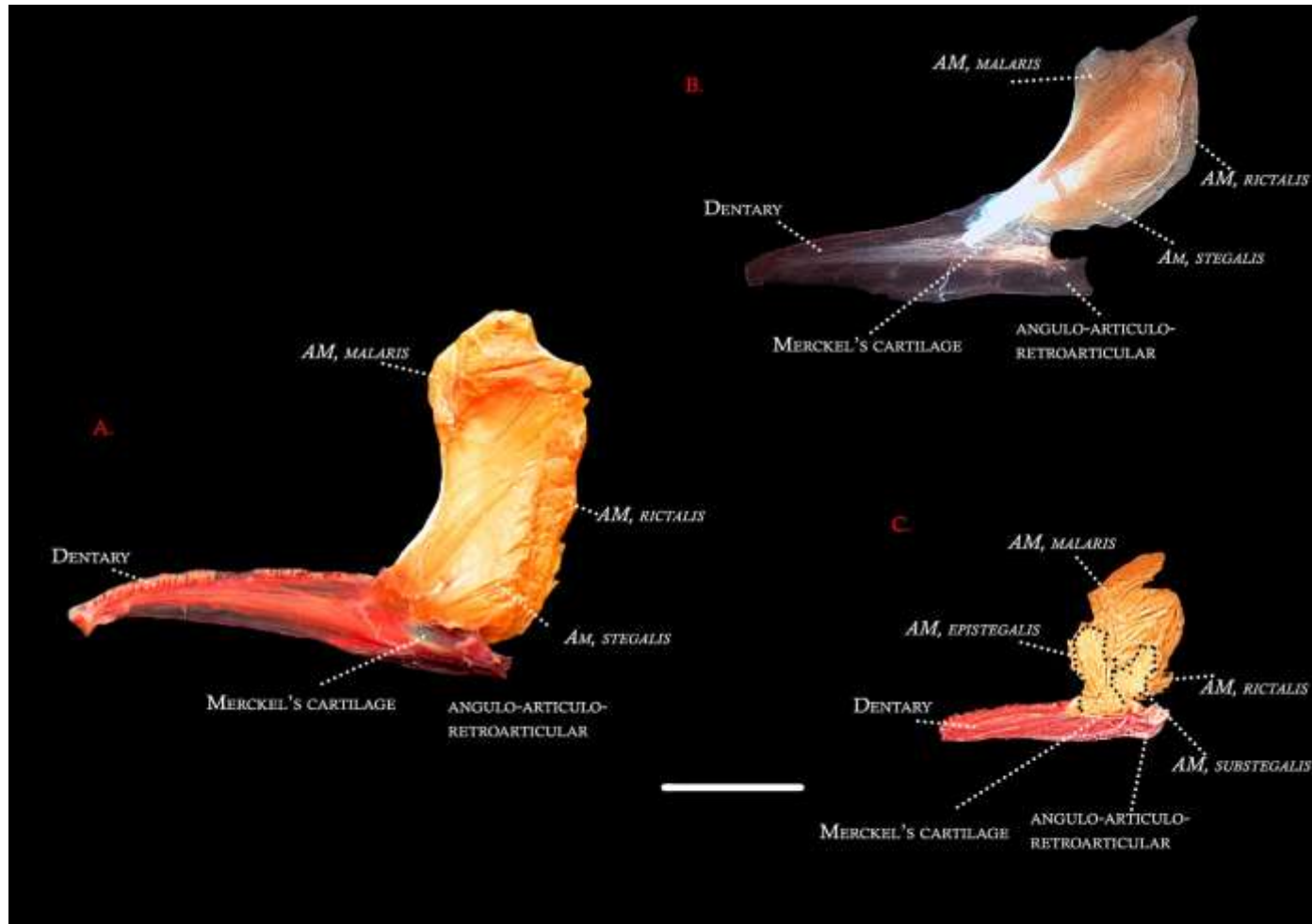


Figure 41 – Lower jaw and *adductor mandibulae* of (A) *Coloconger meadi*, UF 211407, (B) *Protanguilla palau*, USNM 396016, and (C) *Derichthys serpentinus*, USNM 444953, in medial view. *AM pars epistegalis* and *AM pars substegalis* highlighted.

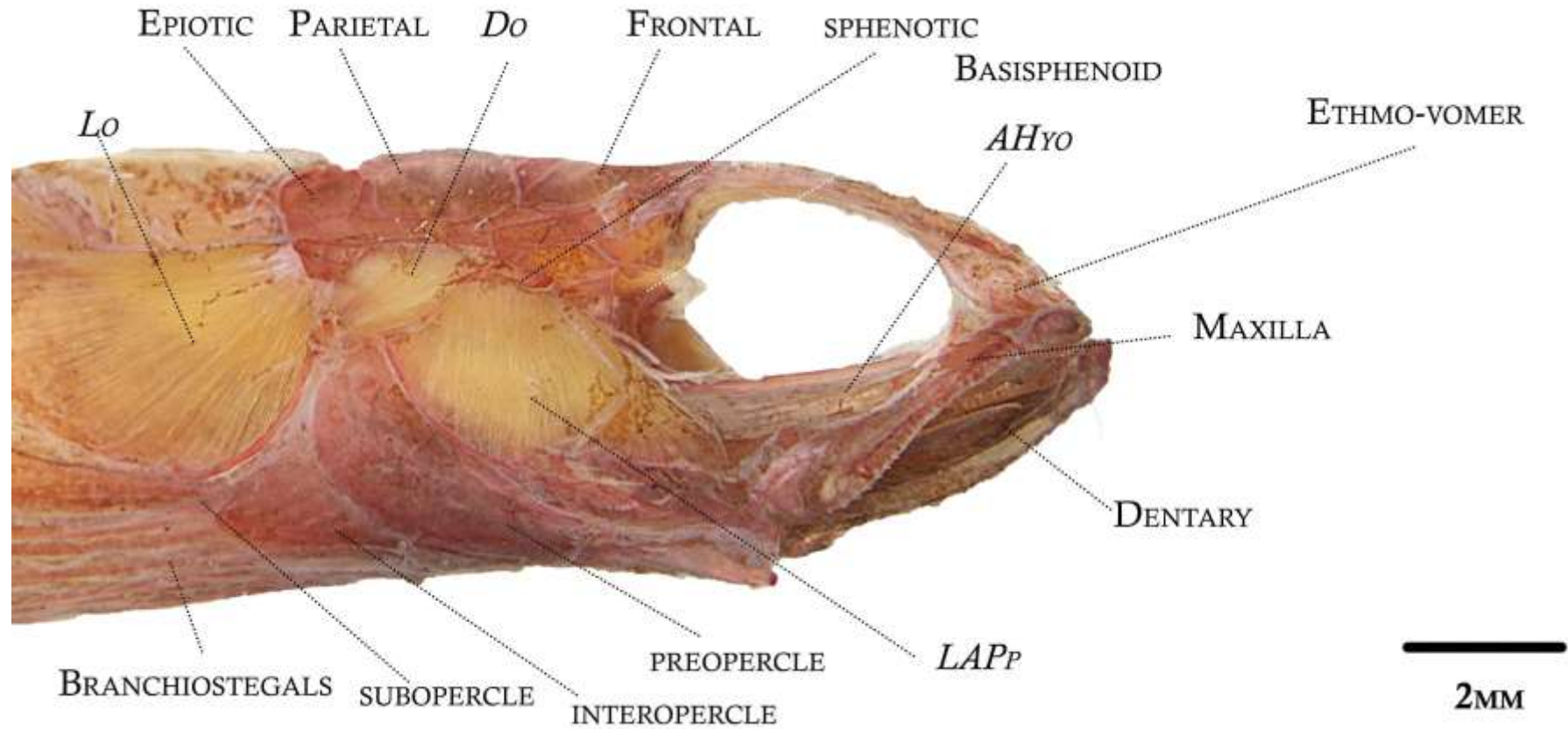


Figure 42 – Anterior part of the body of *Heteroconger camelopardalis*, MZUSP 57611, left side view.

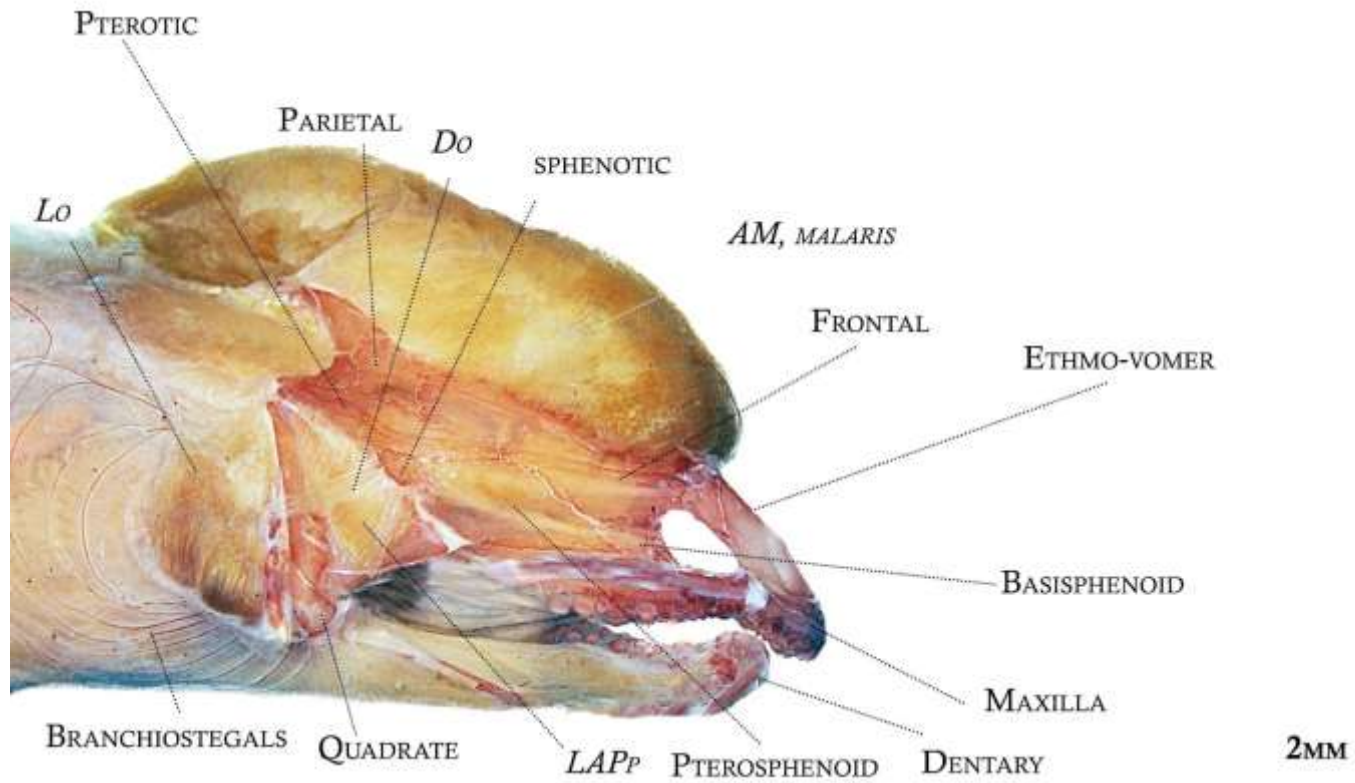


Figure 43 – Anterior part of the body of *Gymnomuraena zebra*, SIO 62-8, left side view.

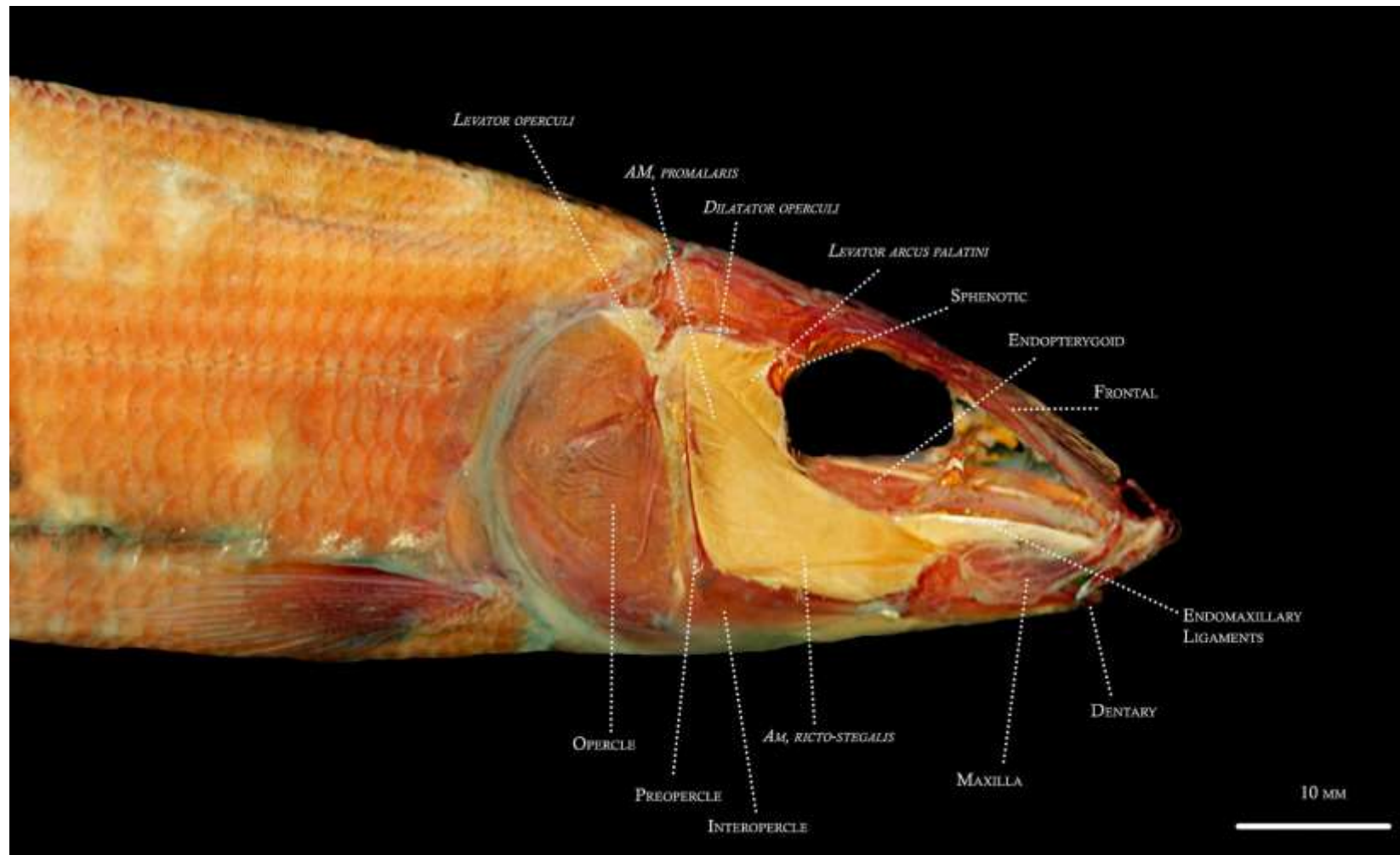


Figure 44 – Anterior part of the body of *Albula vulpes*, MNRJ 37303, right side view.

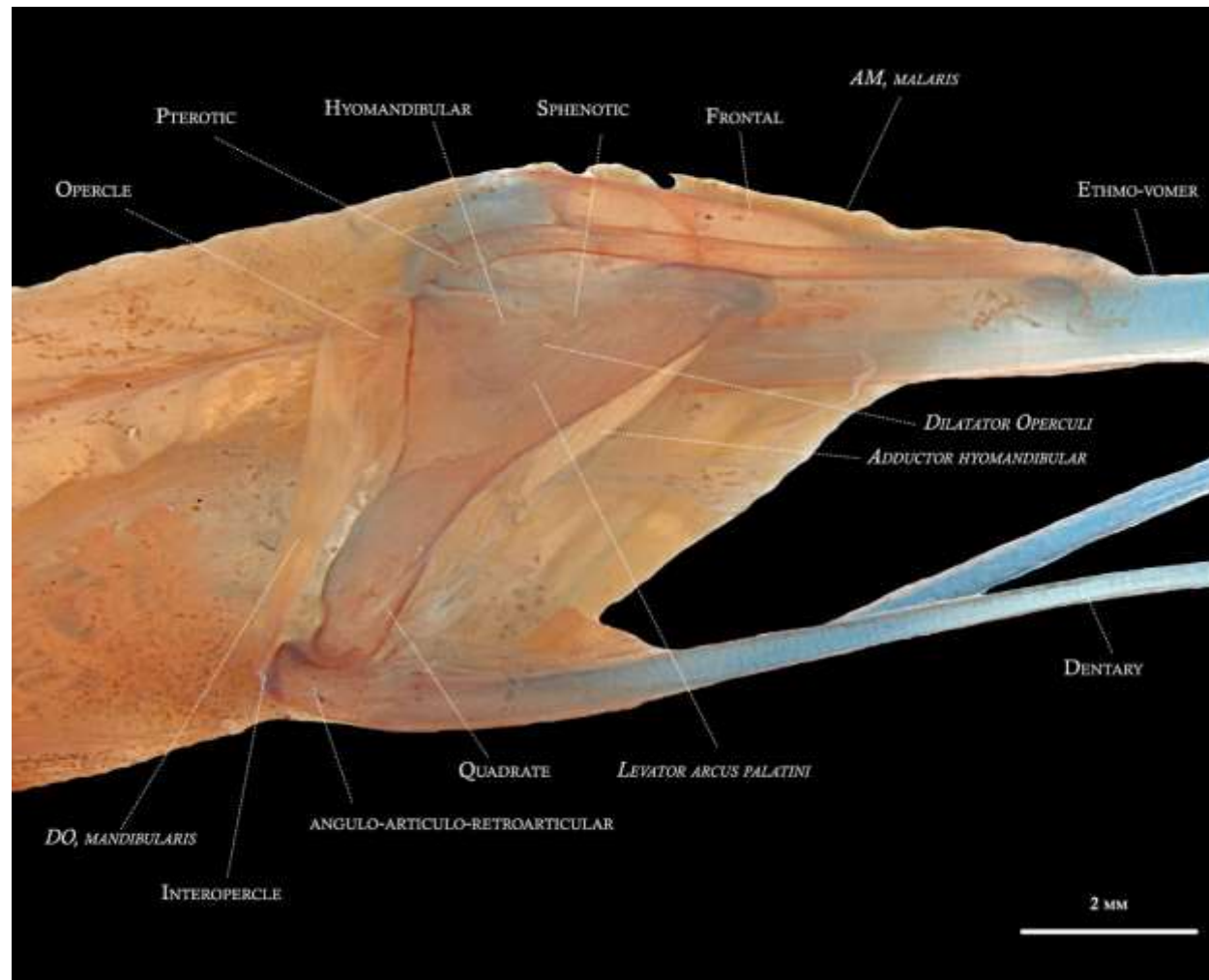


Figure 45 – Anterior part of the body of *Cyema atrum*, SIO 66-546, right side view.

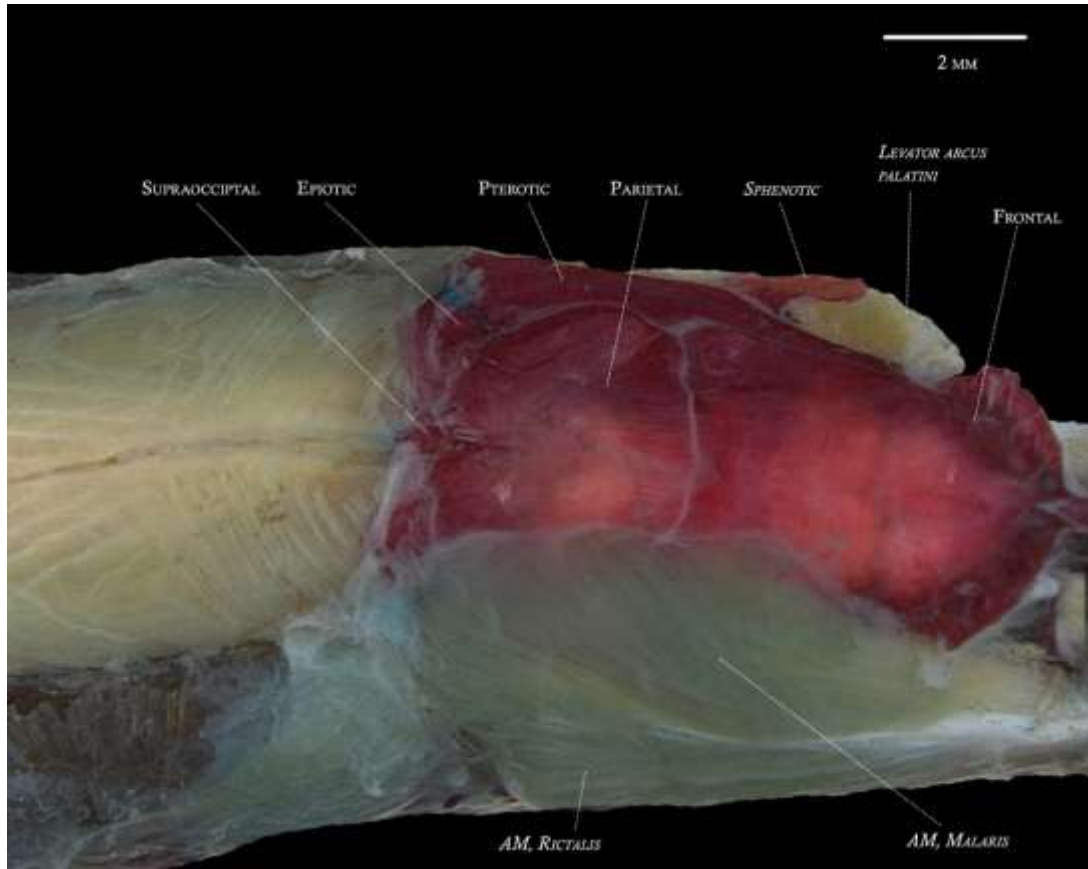


Figure 46 – Neurocranium of *Acromycter perturbation*, MNRJ 27115, in dorsal view.

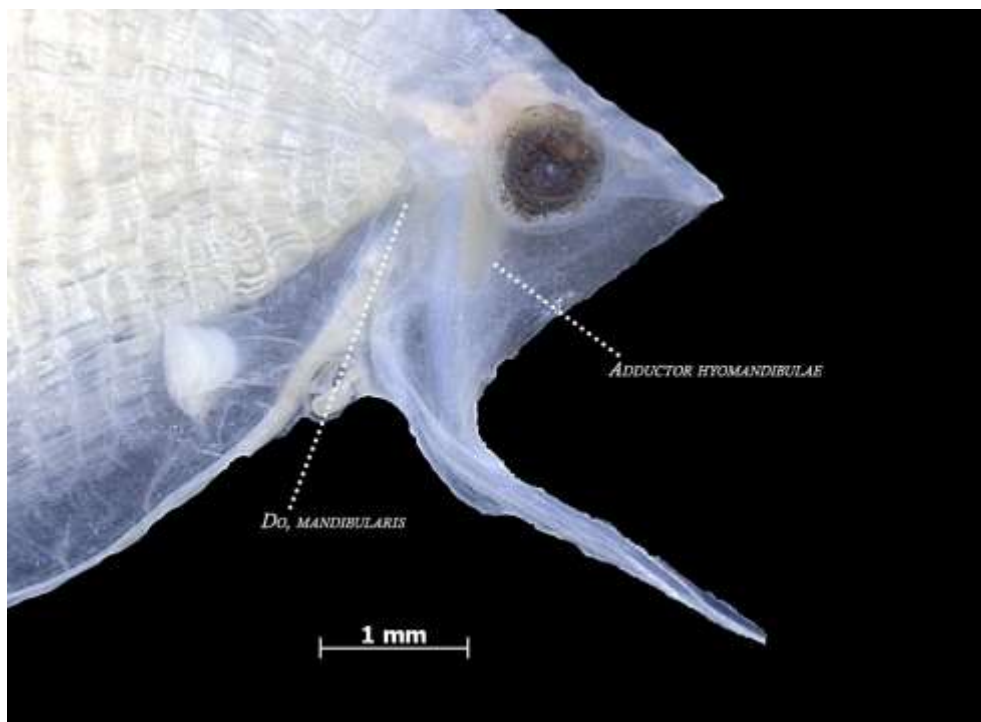


Figure 47 – Anterior part of the body of *Cyema atrum*, ANSP uncat, in lateral view.

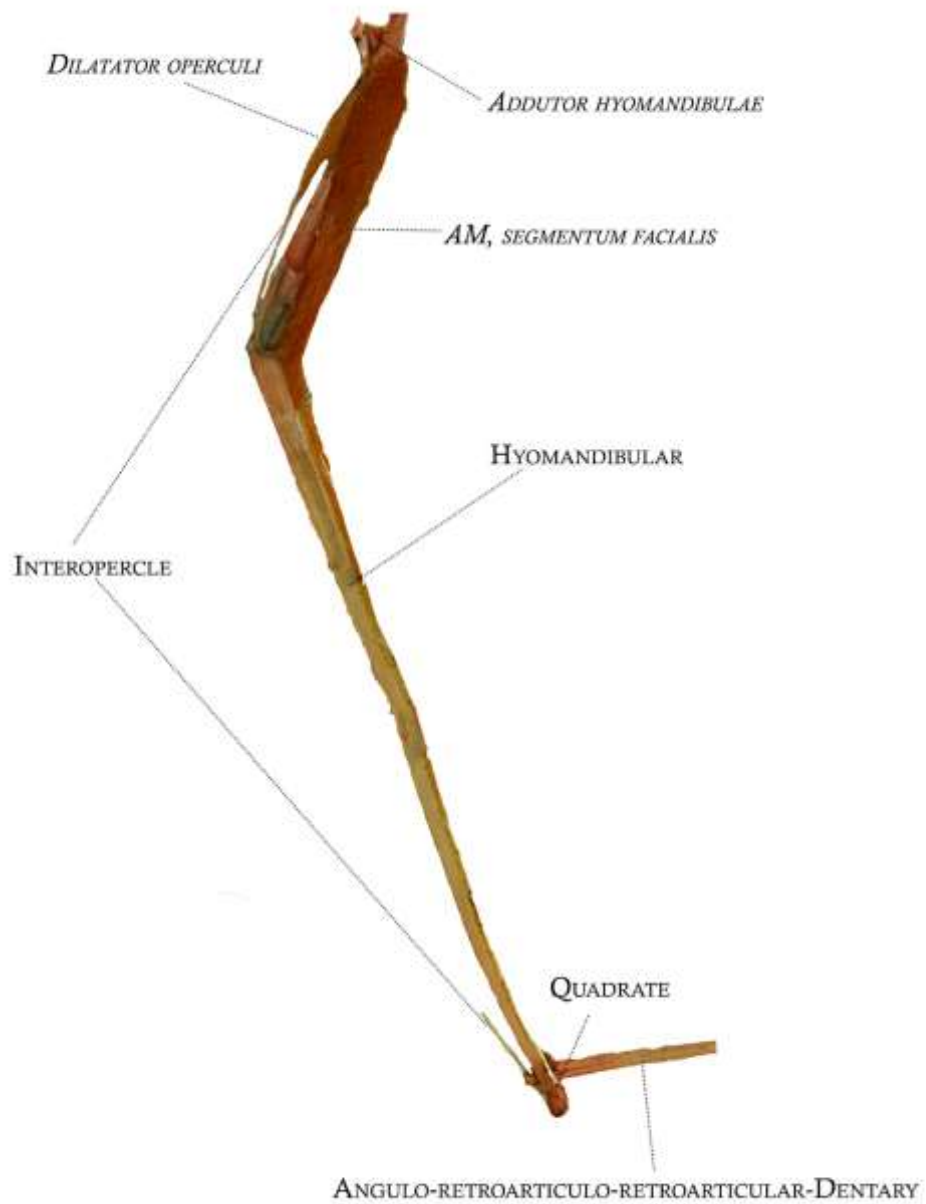


Figure 48 – Hyomandibular and muscles associated of *Eurypharynx pelecanooides*, SIO 73-43, in lateral view.

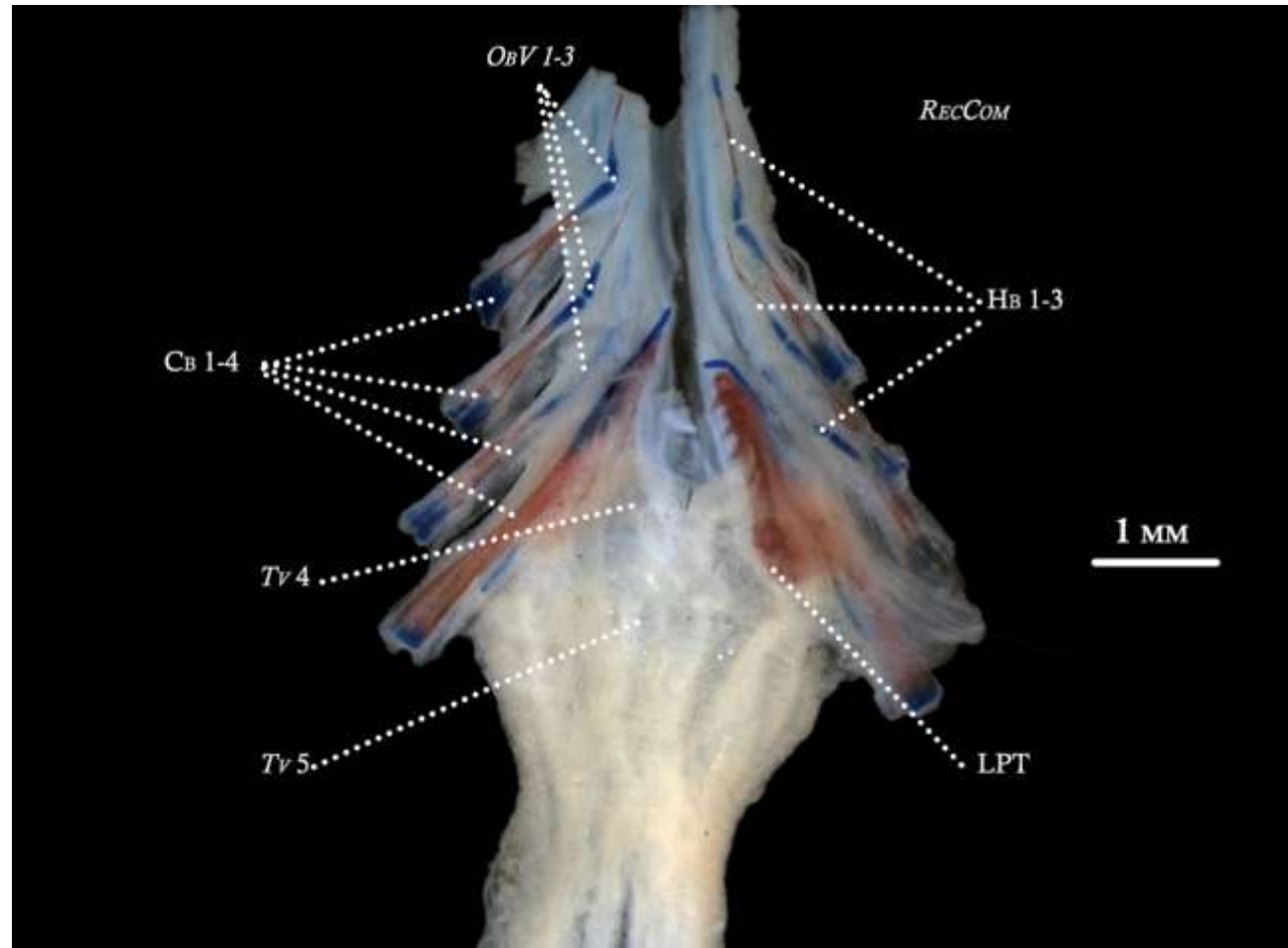


Figure 49 – Branchial arches of *Kaupichthys* sp., USNM 444952, in ventral view.

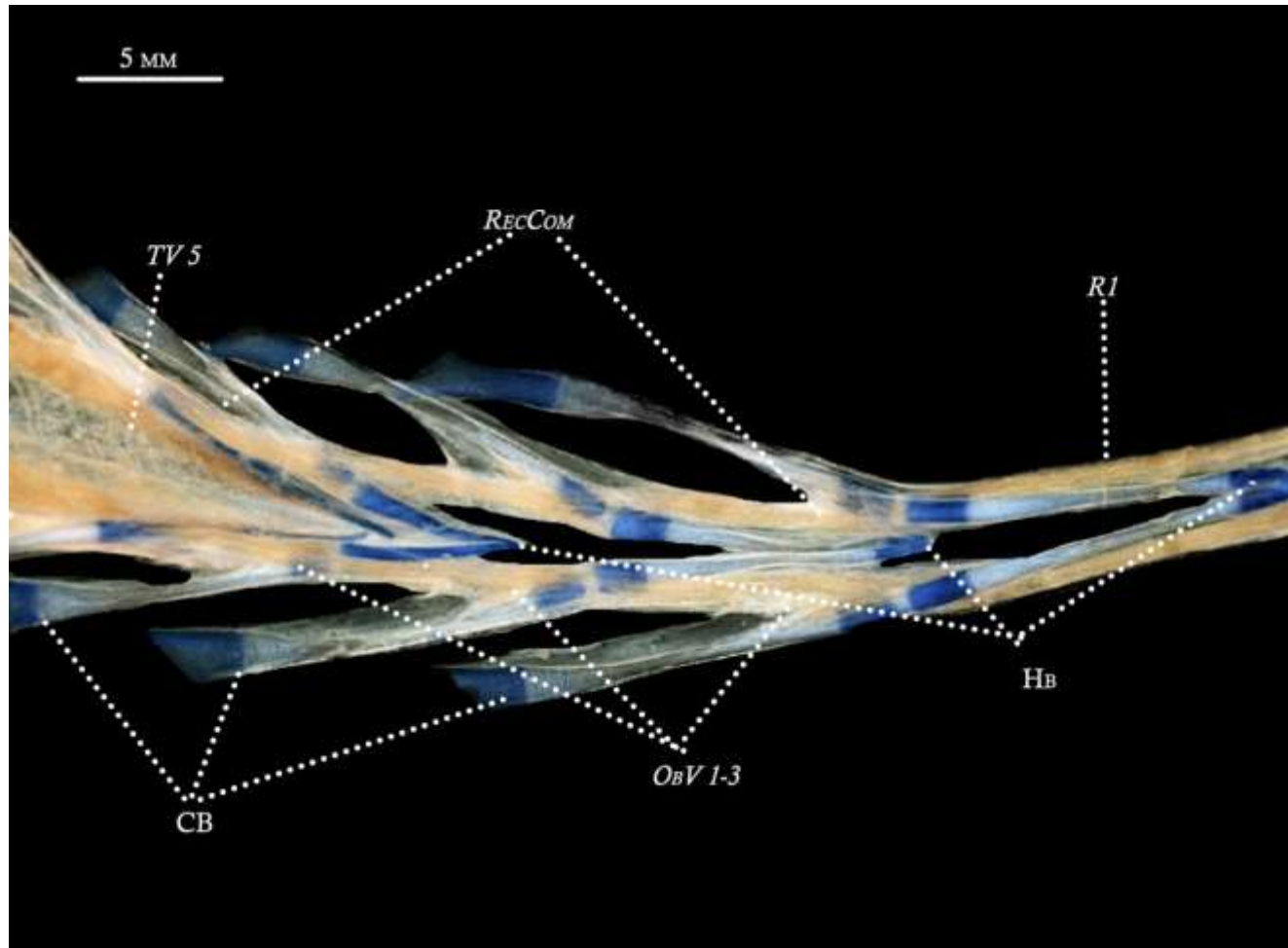


Figure 50 Branchial arches of *Nemichthys scolopaceus*, USNM 358874, in ventral view.

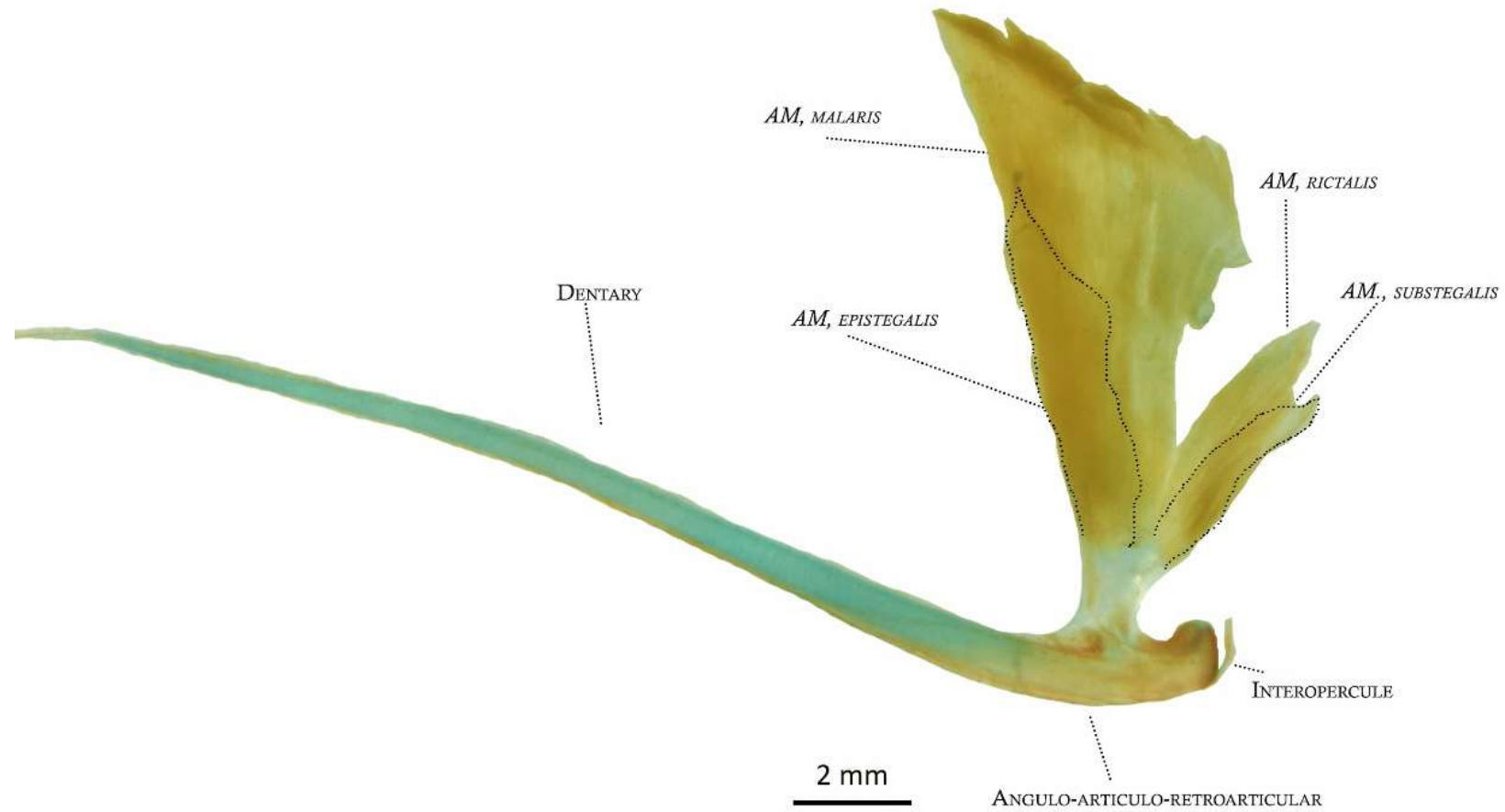


Figure 51 – Lower jaw and associated muscles of *Cyema atrum*, SIO 66-546, in lateral view.

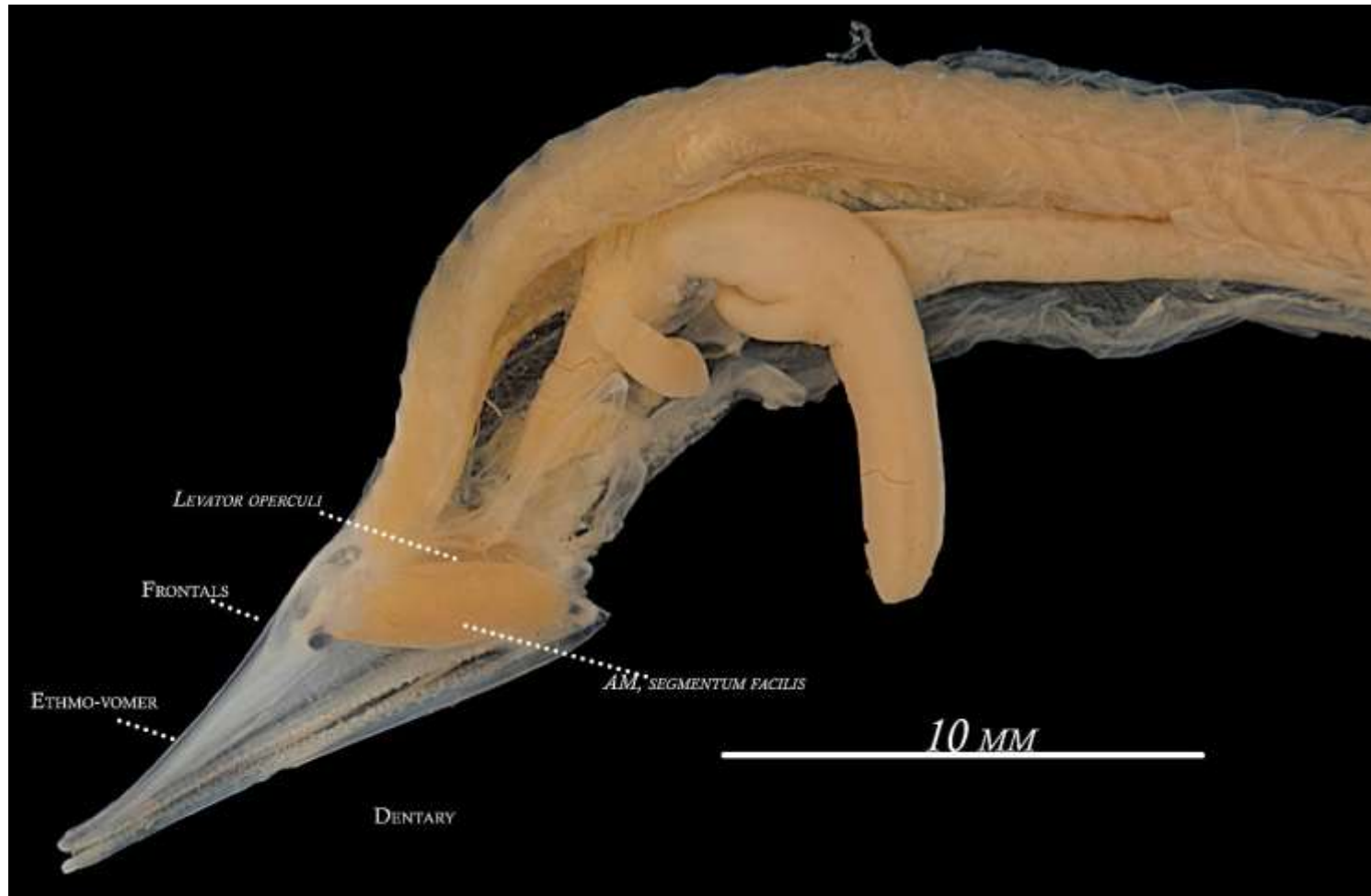


Figure 52 – Anterior part of the body of *Neocyema* sp., MCZ 165900, in lateral view.

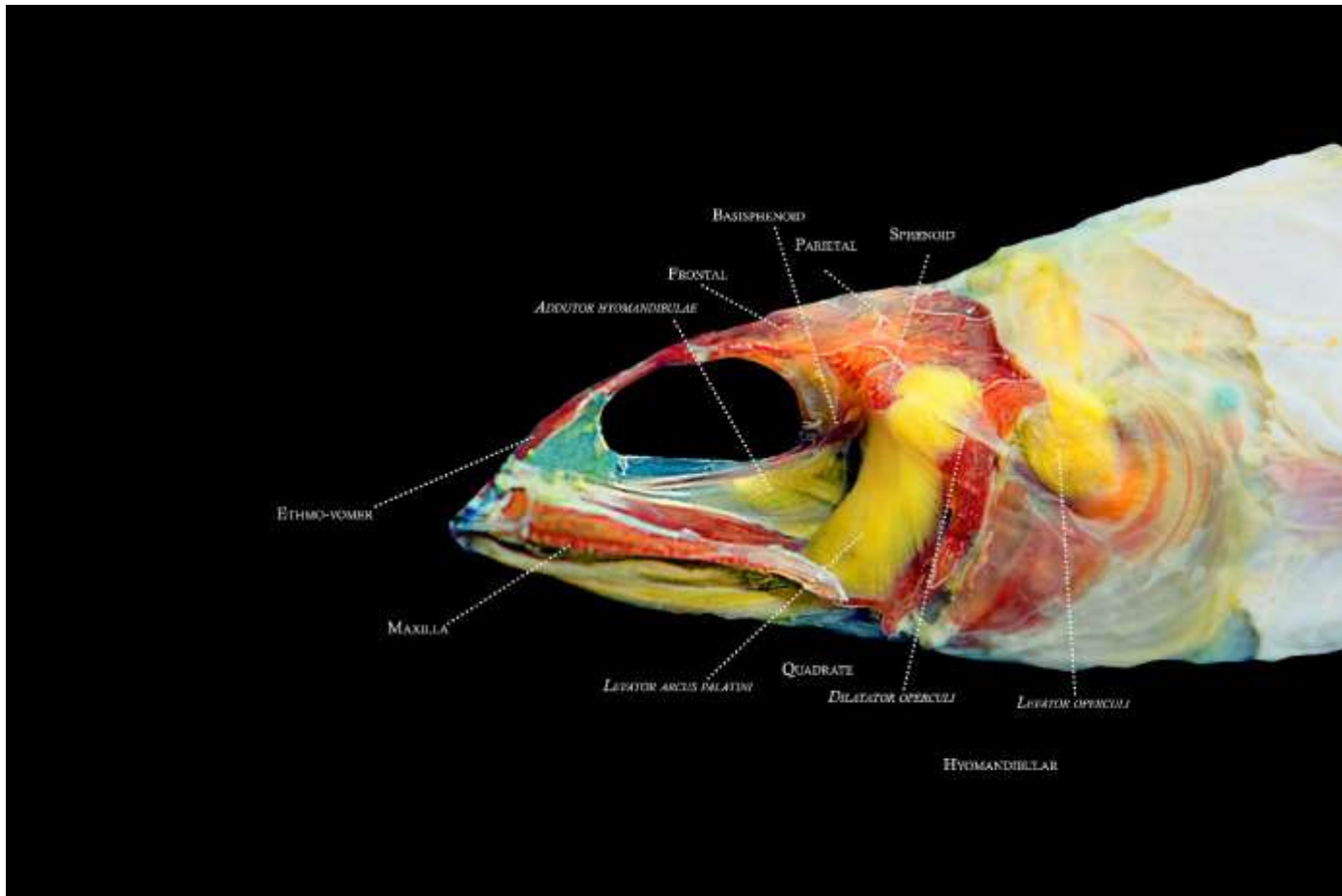


Figure 53 – Anterior part of the body *Coloconger meadi*, UF 211407, in lateral view.

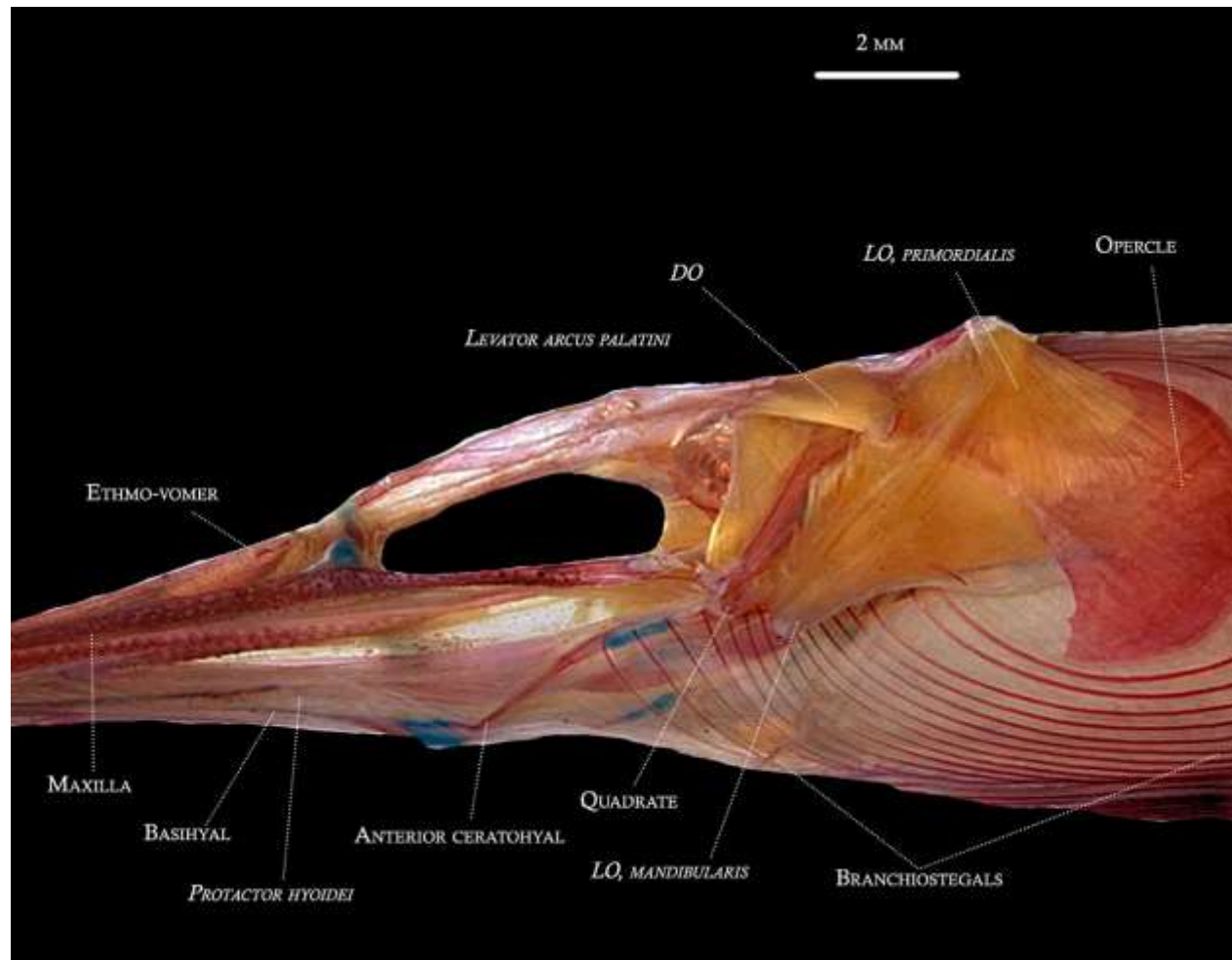


Figure 54 – Anterior part of the body *Nemichthys scolopaceus*, ANSP 158461, in lateral view.

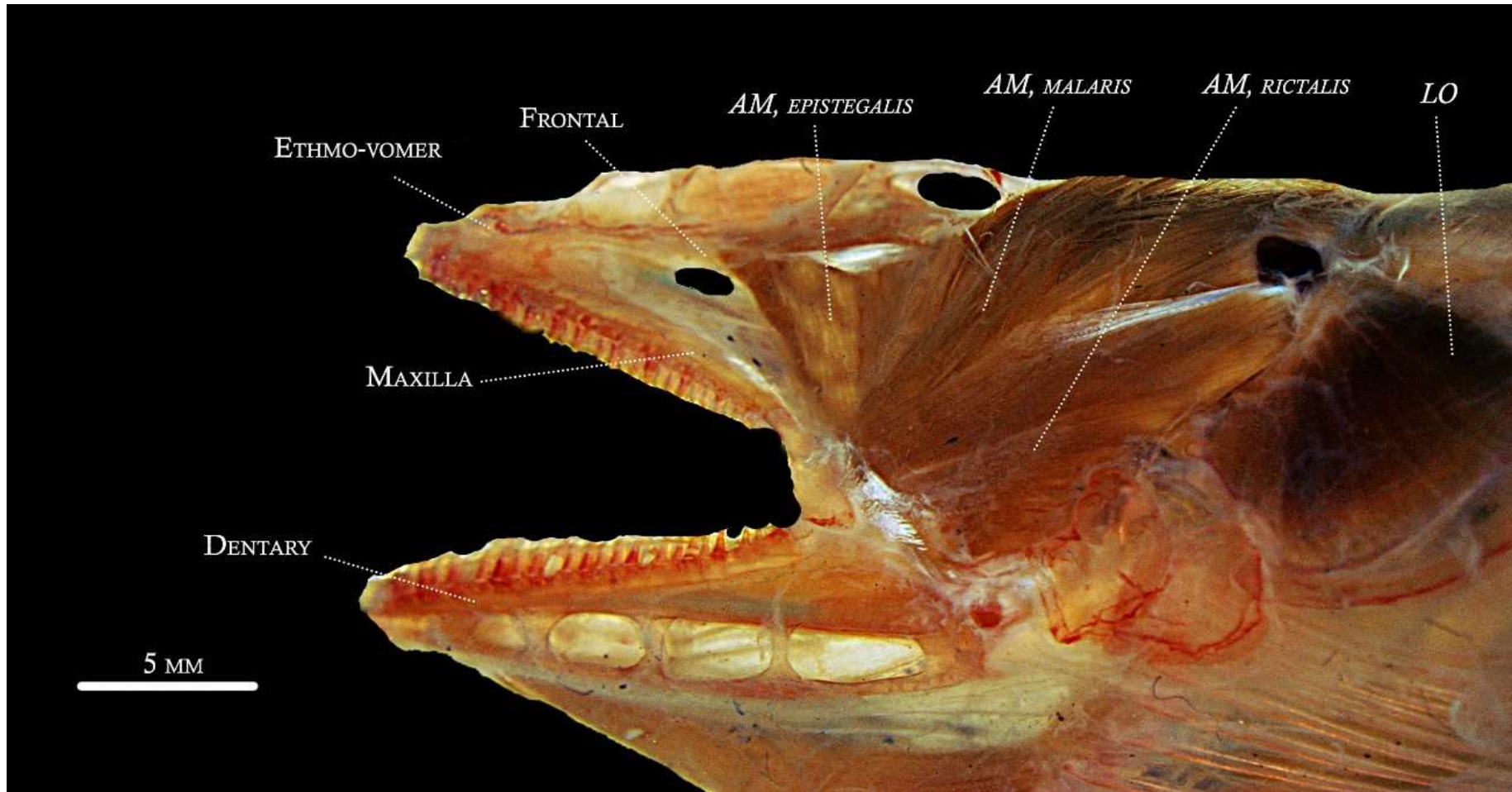


Figure 55 – Anterior part of the body of *Pythonichthys asodes*, UF 228629, in lateral view.

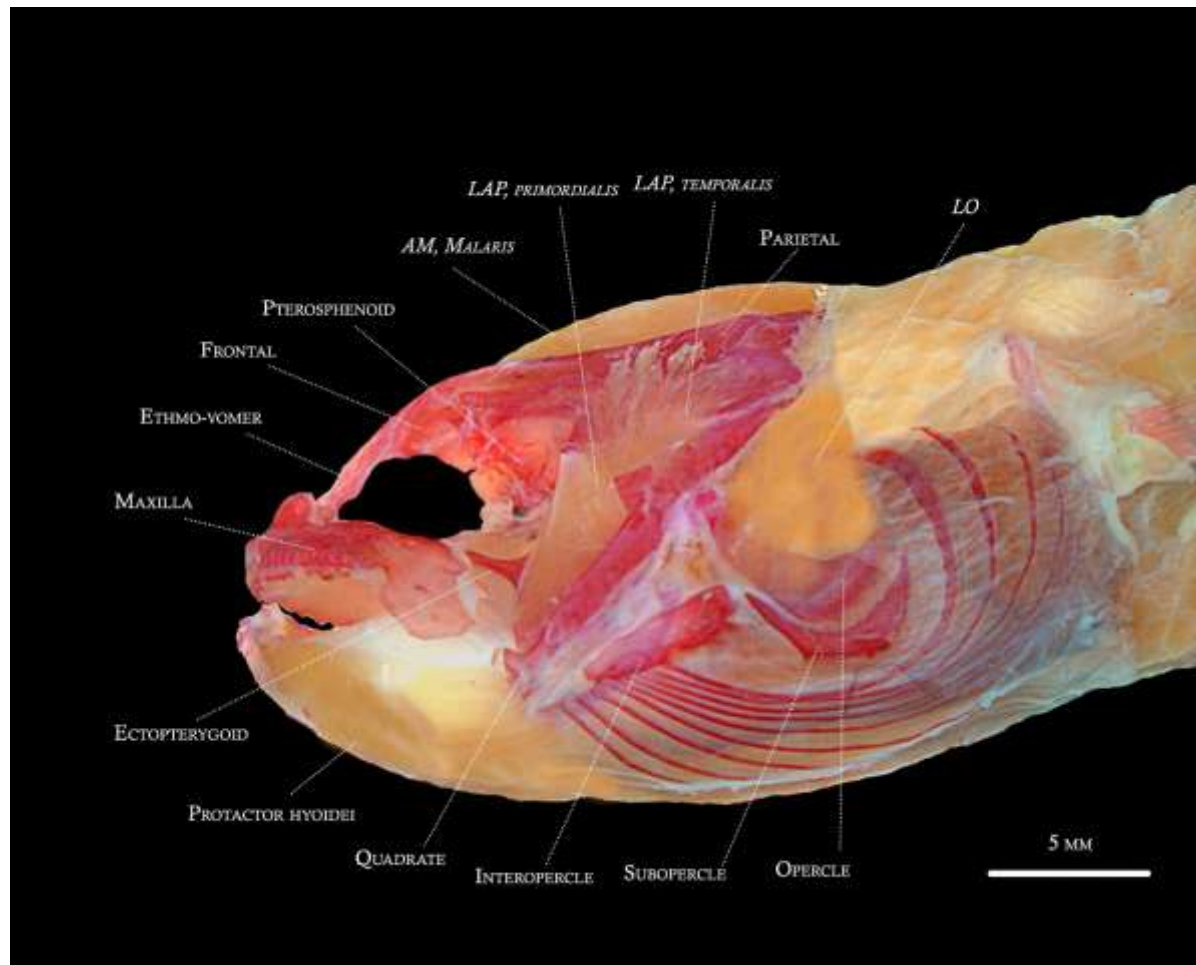


Figure 56 – Anterior part of the body of *Simenchelys parasitica*, SIO 05-11, in lateral view.

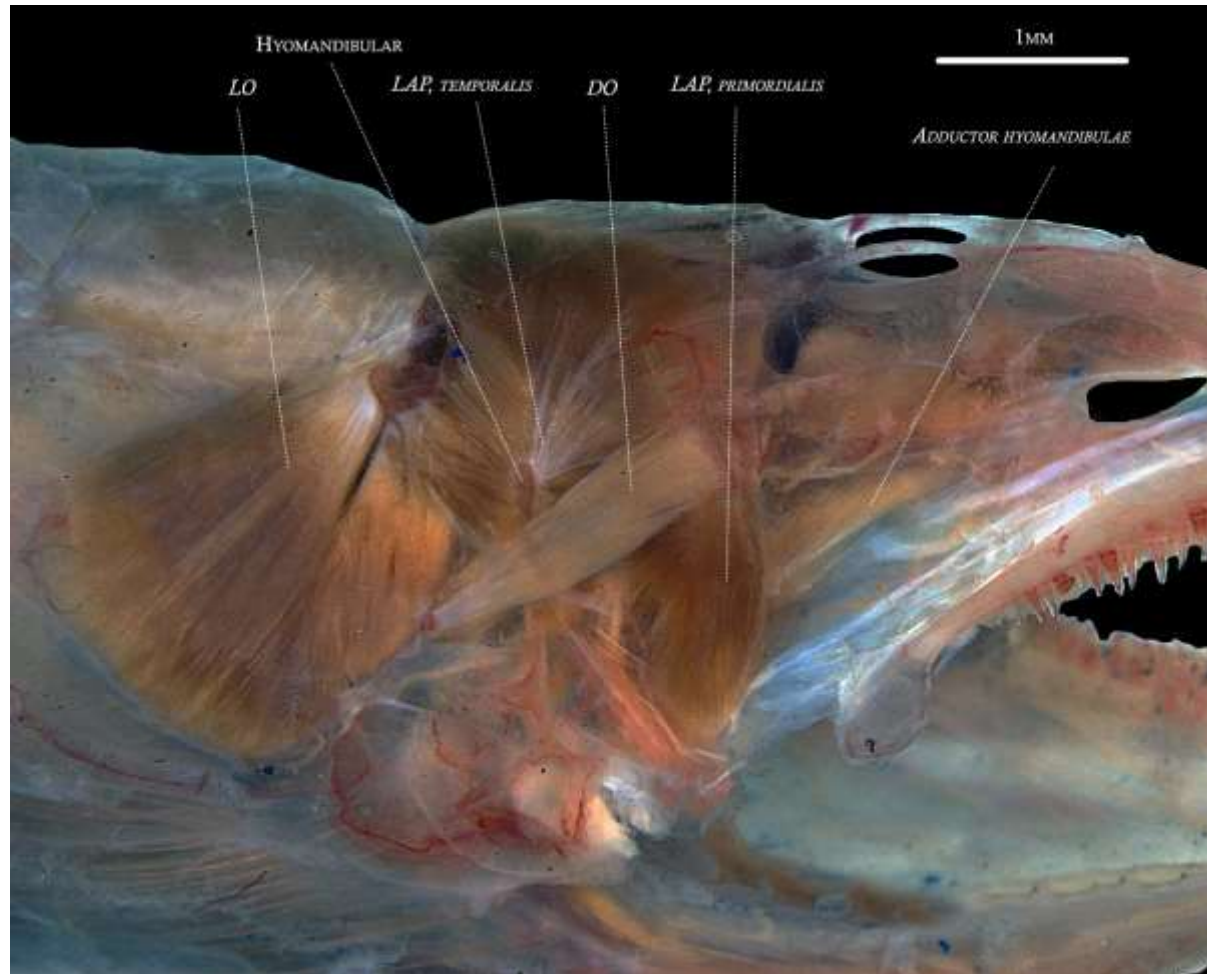


Figure 57 – Anterior part of the body of *Pythonichthys asodes*, UF 228629, in lateral view.

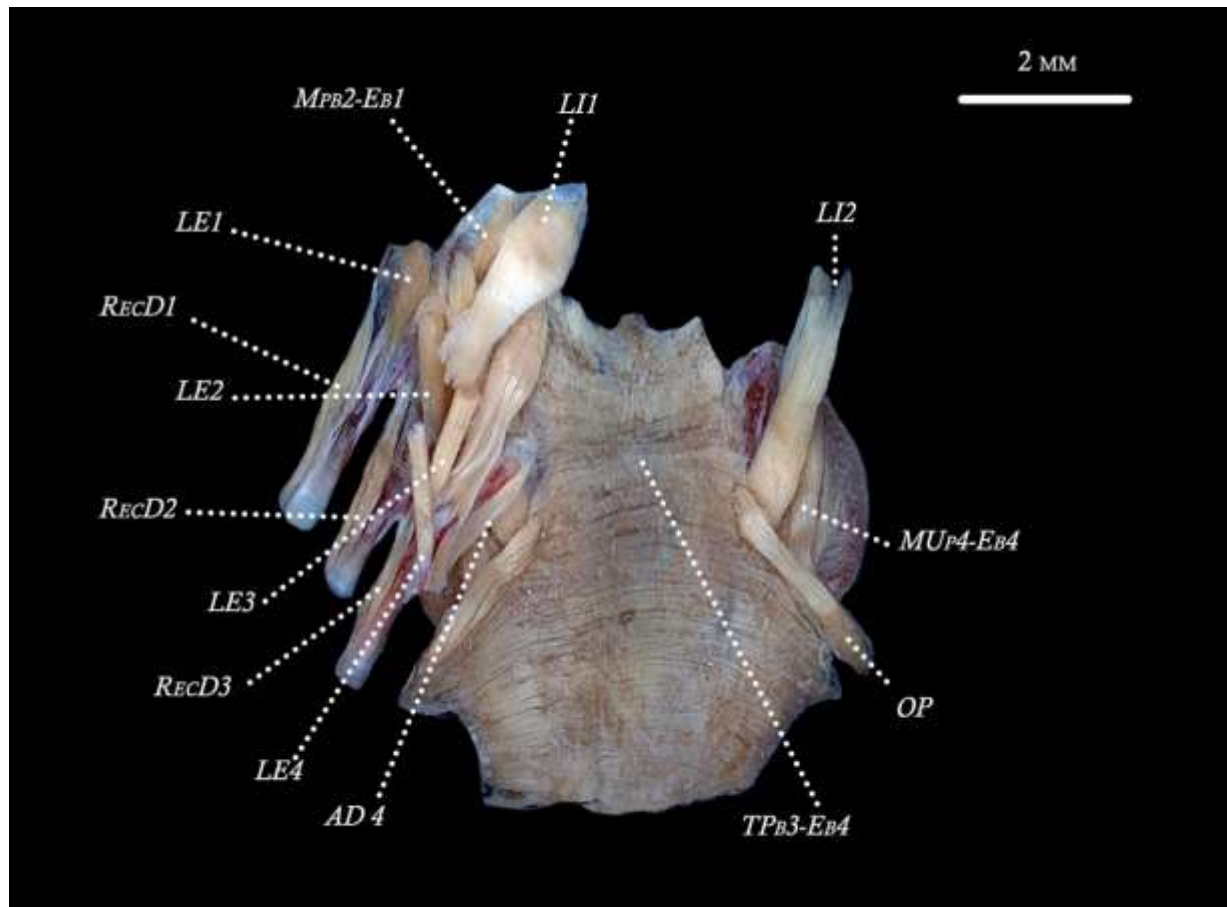


Figure 58 – Branchial arches of *Coloconger meadi*, USNM 443687, in dorsal view.

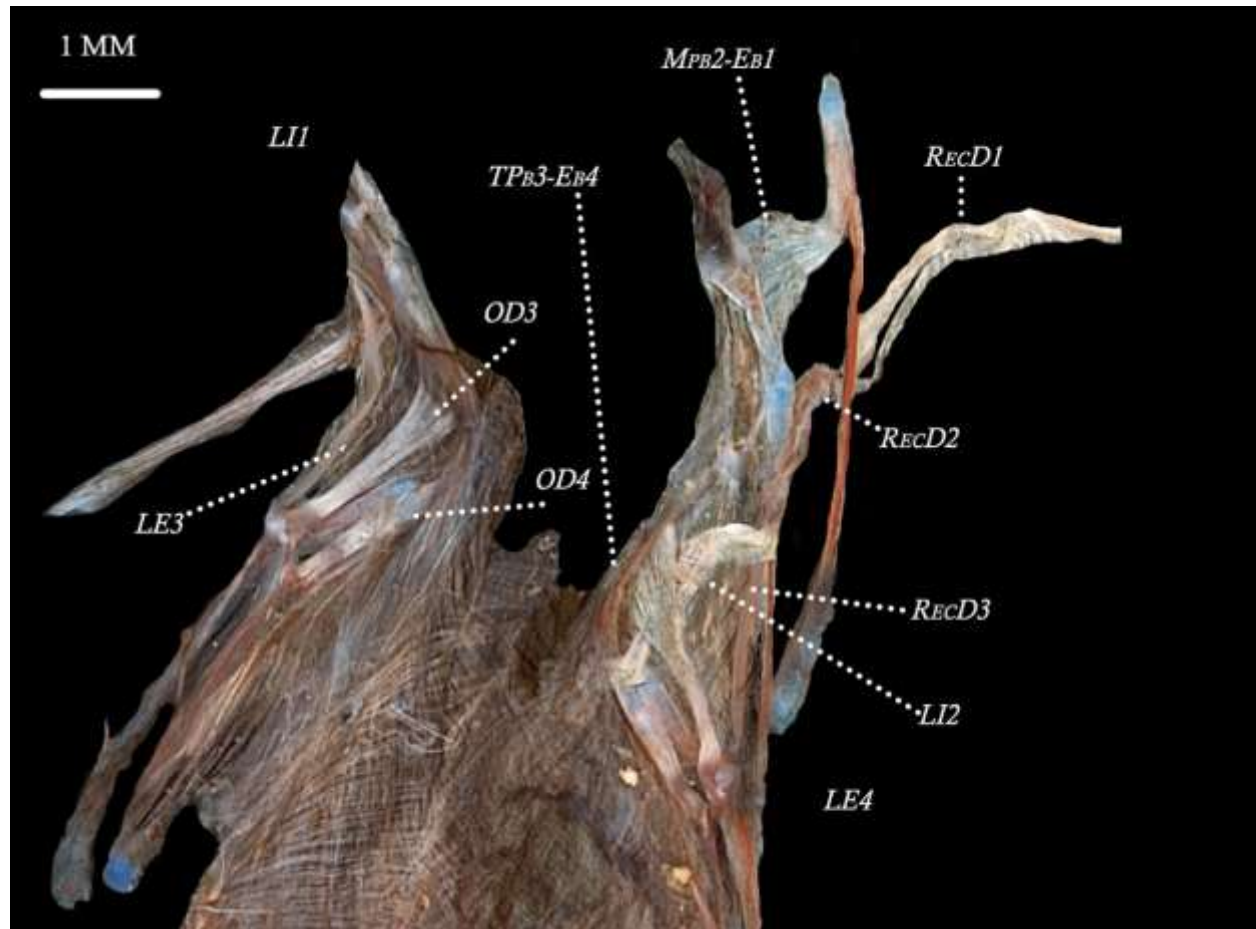


Figure 59 – Branchial arch of *Serrivomer* sp., USNM 443689, in dorsal view.

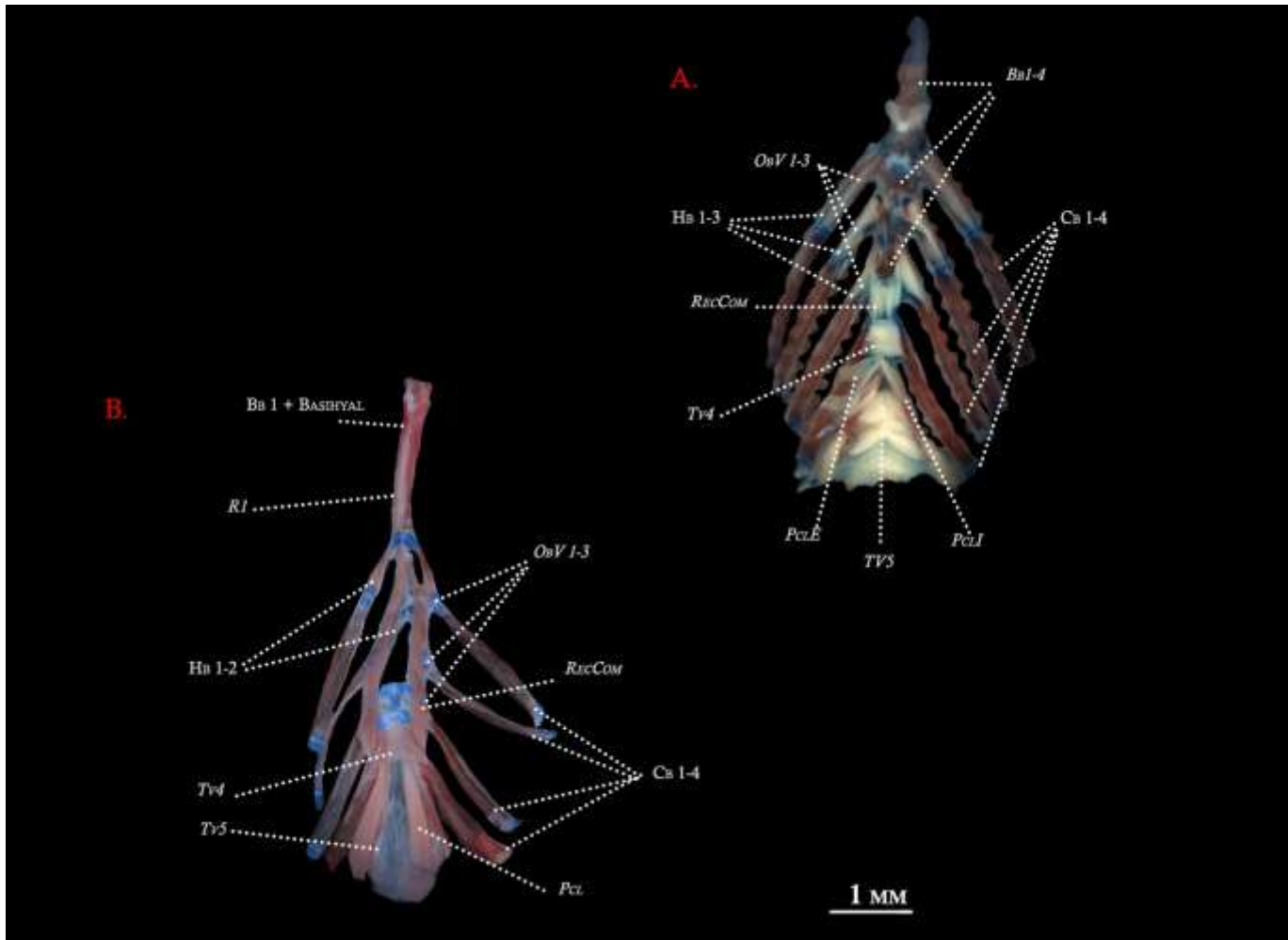


Figure 60 – Branchial arches of (A) *Albula vulpes*, USNM 218871, and (B) *Netastoma malanurum*, USNM 405025, in ventral view.

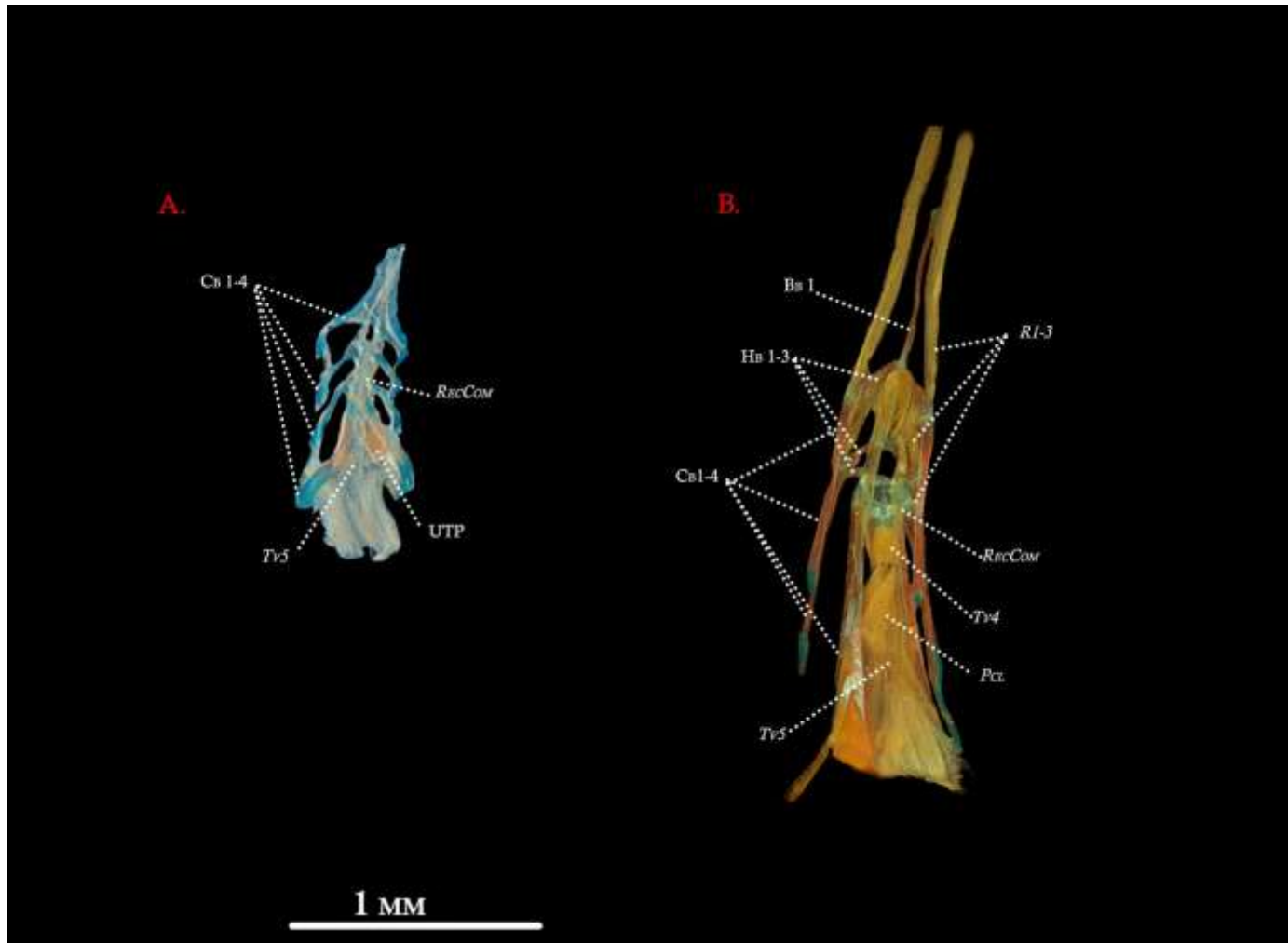


Figure 61 – Branchial arches of (A) *Cyema atrum*, SIO66-546, and (B) *Stenodinium hypomelas*, ANSP 152332, in ventral view.



Figure 62 – Scales of *Protanguilla palau*, USNM 396016.

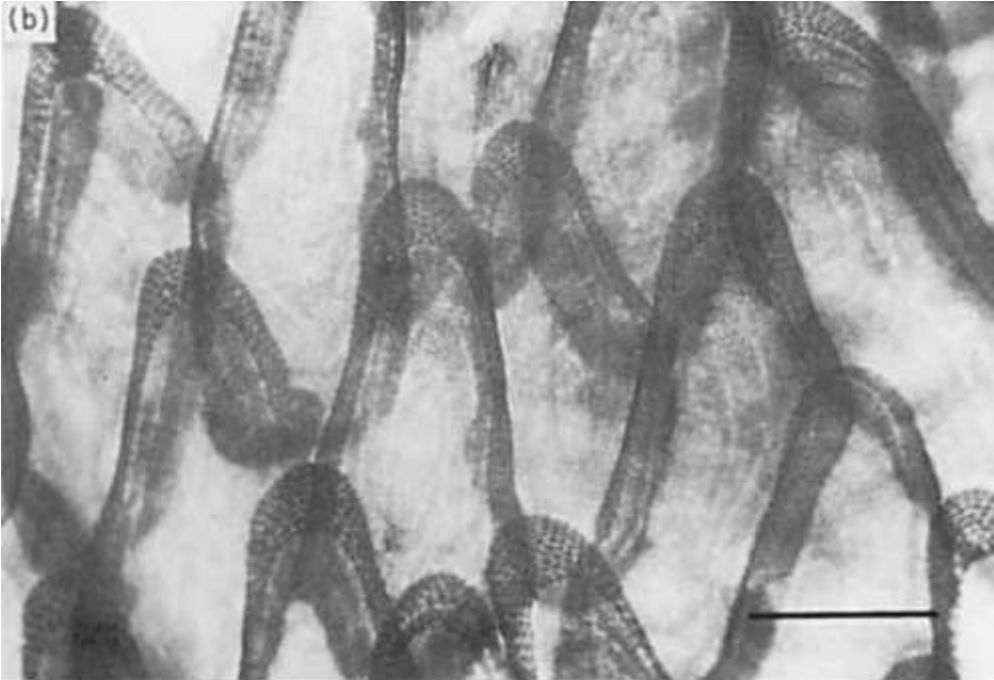


Figure 63 – Scales of *Anguilla anguilla* (Pankhurst, 1982: Figure 6b).

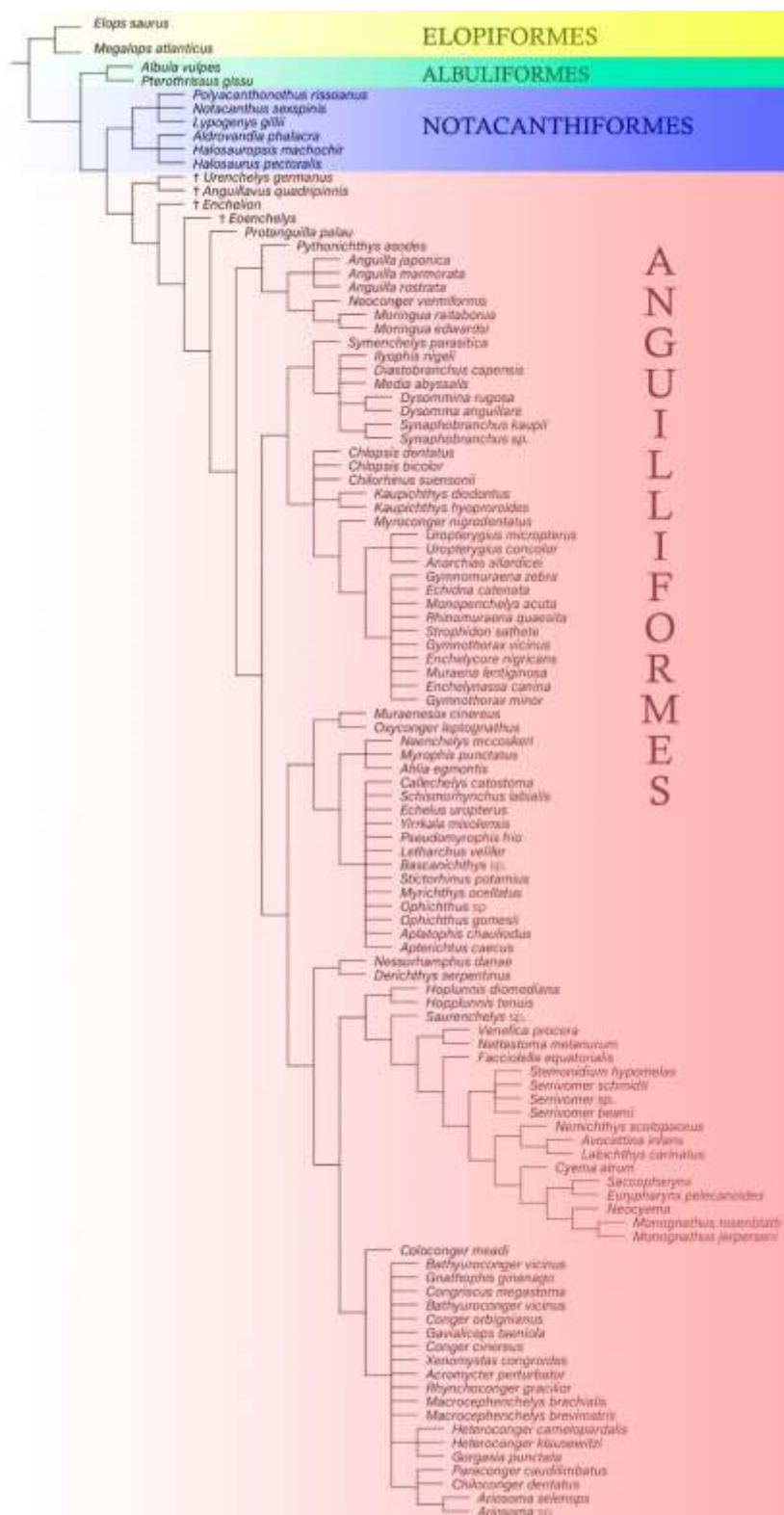


Figure 64 – Strict consensus tree resultant from Implicit Weighting implied against homoplasy under K=7. Highlighted clades: Elopiformes (yellow), Albuliformes (green), Notacanthiformes (blue), Anguilliformes (red).

Relative bremer supports (from 9914 trees, cut 0)



Figure 65 – Strict consensus tree resultant from Implicit Weighting implied against homoplasy under $K=7$ (TNT graphics).

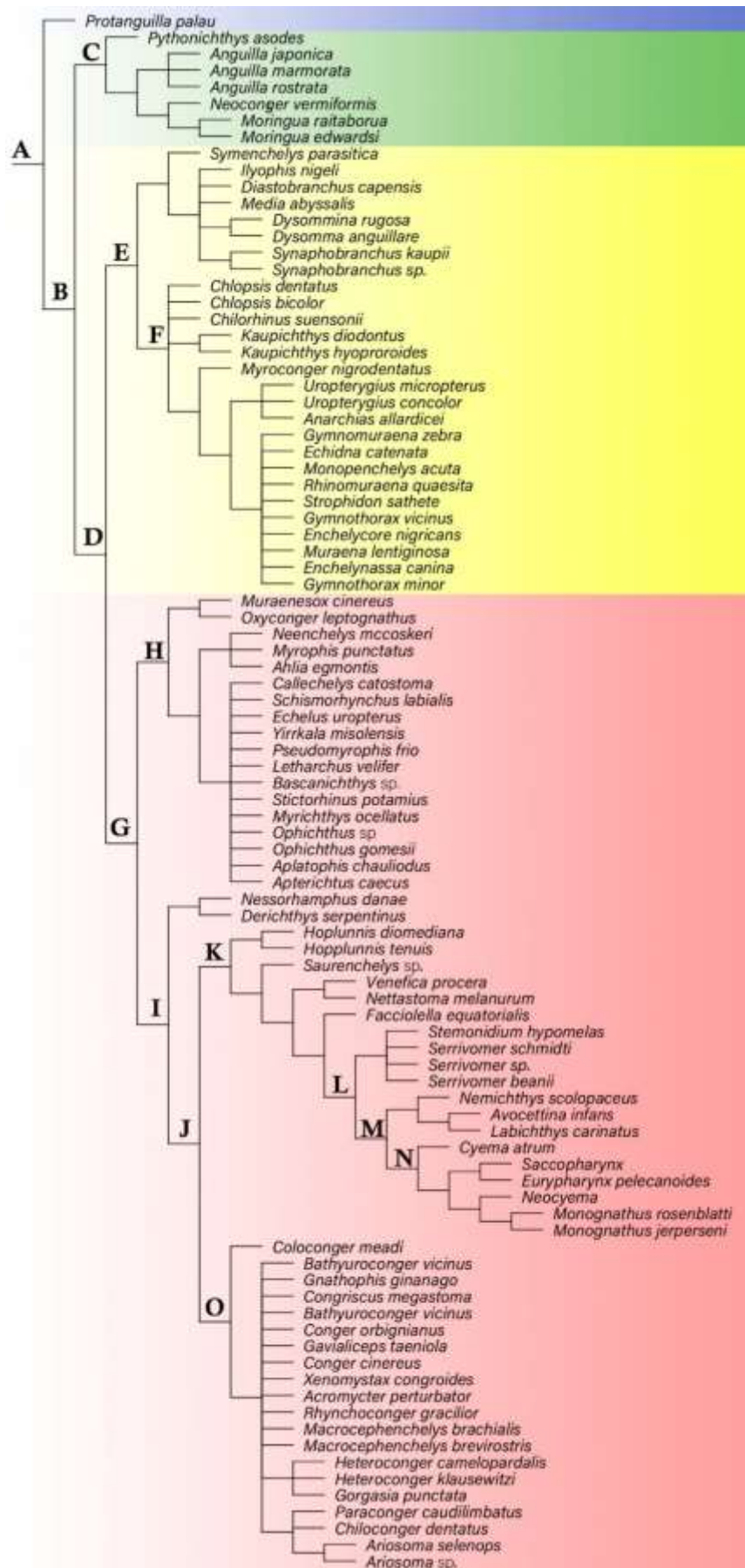


Figure 66 – Interrelationships of the Anguilliformes, strict consensus tree resultant from Implicit Weighting implied against homoplasy under $K=7$. Highlighted taxa represent: Protanguillidae (blue), Anguilloidea (green), Synaphobranchoidea (yellow), Ophichthoidea + Congroidea (red).

10. APPENDIX - QUALITATIVE CHARACTERS

Outgroup

Albula vulpes 010000001000001000000000000010100000000000?001
 010110000100000000000000000000000000000010?000000000000
 000110100000
 000011000000000000010000000100000??000?0000000?00010
 00?00000000000??1101?1000000000000000000100000000000
 00000000000

Aldrovandia phalacra 010011000001?10100000?00001102000000000
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 000010010000000

Elops saurus 0100000000000000000000000000100010000000000?001
 0001000001000000000000000000000000000000?000000000000
 000
 000000001000000000000000000000000000?????0000000?00000
 00?00000000000??01100100000000000000000000?00000000000
 00000000000

Halosauropsis machochir 010011000001?10100000?00001102000000000
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Lypogenys gillii 010011000001?10000000?0000010200000000?00
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 010010000000

Megalops atlanticus 01000000000000000000000000000100010000000000
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Notacanthus sexspinis 010011000001?10000000?00000102000000000
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Polyacanthonothus rissoanus 010011000001?10000000?0000010200000
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 0?0001000?000000000000??1110?10000000010000000010000
 001000010010000000

Pterothrissus gissu 0100000010000010000000000001010000000000?
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 000110100
 00000001100100000000010000000100000??000?0000000?00
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 0000000000000000

Anguilliformes

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 210111111?113001001100110011111?1111000000000111111
 0001100?01011100011000001?0100000001000000111101?11
 0110110110001101

Ahlia egmontis 010011010210100101101111000?0100011?110?11
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 100?01011100011001101?0100000001000000111201?110110
 110110001101

Anarchias smilis 01011100021010010110111101??0101111?110?11
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 11111?112001101100111?11111?11110101101001111100101
 100?01011110111001101?1000000011010001111311?010110
 111110011101

Anguilla japonica 010011110210100101101111000?11000101110?1
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 0000111100000102?111?00000000111111?10000100211?210
 111111?111001001100100011101?1111010001000111110000
 1100?0101110001100000010000011001000000111100101011
 0110110001101

Anguilla marmorata 010011110210100101101111000?11000101110
 ?11?1?111101011000100000111110100101001110?11?00001
 1?0000111100000102?111?00000000111111?10000100211?2
 10111111?111001001100100011101?11110100010001111100
 001100?01011100011000000100000110010000001111001010
 110110110001101

Anguilla rostrata 010011110210100101101111000?11000101110?1
 1?1?111101011000100000111110100101001110?11?000011?

0000111100000102?111?00000000111111?10000100211?210
 111111?111001001100100011101?1111010001000111110000
 1100?0101110001100000010000011001000000111100101011
 0110110001101

Aplatophis chauliodus 010011010210100101101111000?0100011?11
 0?11?1?111101111000100000111110100001002101011?0000
 10100001111000001021111?01010000111111?10??1100211?
 21111111?113011001100110111111?1111010000000111111
 0001100?01011100011001101?0100000001000000111201?11
 0110110110001101

Apterichtus caecus 010011010210100101101111000?0100011?110?
 11?1?111101111000100000111110100001002101011?000010
 100001111000001021111?01010000111111?10001100211?21
 1111111?113011001100110111111?111101000000011111100
 01100?01011100011001101?0100000001000000111201?1101
 10110110001101

Ariosoma selenops 1?0011110210100101001111001?110001011110
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 000001011000002021111?00010000111111?10001100211?21
 0111111?113001001100110001101?111101000000011111100
 01100?01011100011000001?0100000001000000111101?1101
 10110110001101

Ariosoma sp. 1?0011110210100101101111001?11000101111011?
 1?111101011000100000111110100001002120?11?00000000
 001011000002021111?00010000111111?10001100211?21011
 1111?113001001100110011101?111101000000011111100011
 00?01011100011000001?0100000001000000111101?1101101
 10110001101

Avocettina infans 1?001111021010020110111101??0100011?110?
 1?1?11110111100010111??11110110001002110?11?0101?1?
 10001111000001021111?1?010000111111?10111100211?210
 111111?11300001?11??1?11101?1111010000000111110000
 1110001011100011001101?0100000001100001111201?01011
 1110110001101

Bascanichthys sp. 0 1 0 0 1 1 0 1 0 2 1 0 1 0 0 1 0 1 1 0 1 1 1 1 0 0 0 ? 0 1 0 0 0 1 1 ? 1 1 0 ? 1
 1 ? 1 ? 1 1 1 1 0 1 1 1 1 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 0 1 0 0 2 1 0 1 0 1 1 ? 0 0 0 0 1 0 1
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 1 1 0 0 ? 0 1 0 1 1 1 0 0 0 1 1 0 0 1 1 0 1 ? 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 2 0 1 ? 1 1 0 1 1
 0 1 1 0 1 1 0 0 0 1 1 0 1

Bathycongrus dubius 0 1 0 0 1 1 1 1 0 2 1 0 1 0 0 1 0 1 1 0 1 1 1 1 0 0 1 ? 1 1 0 0 0 1 1 ? 1 1 1
 0 1 1 ? 1 ? 1 1 1 1 0 1 0 1 1 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 0 1 0 0 2 1 2 0 ? 1 1 ? 0 0 0 0 0
 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 0 2 1 1 1 1 ? 0 0 0 1 0 0 0 0 1 1 1 1 1 1 ? 1 0 0 0 1 1 0 0 2 1 1 ? 2
 1 0 1 1 1 1 1 1 ? 1 1 3 0 0 1 0 0 1 1 0 0 1 1 0 0 1 1 1 1 1 ? 1 1 1 1 0 1 0 0 0 0 0 0 0 1 1 1 1 1 1 0
 0 0 1 1 0 0 ? 0 1 0 1 1 1 0 0 0 1 1 0 0 0 0 0 1 ? 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 1 0 1 ? 1 1 0
 1 1 0 1 1 0 1 1 0 0 0 1 1 0 1

Bathyurocongrus vicinus 0 1 0 0 1 1 1 1 0 2 1 0 1 0 0 1 0 1 1 0 1 1 1 1 0 0 1 ? 1 1 0 0 0 1 1 ? 1 1
 1 0 1 1 ? 1 ? 1 1 1 1 0 1 0 1 1 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 0 1 0 0 2 1 2 0 ? 1 1 ? 0 0 0 0
 0 0 0 0 0 0 0 1 1 1 1 0 0 0 0 0 1 0 2 1 1 1 1 ? 0 0 0 1 0 0 0 0 1 1 1 1 1 1 ? 1 0 0 0 1 1 0 0 2 1 1 ?
 2 1 0 1 1 1 1 1 1 ? 1 1 3 0 0 1 0 0 1 1 0 0 1 1 0 0 1 1 1 1 1 ? 1 1 1 1 0 1 0 0 0 0 0 0 0 1 1 1 1 1 1
 0 0 0 1 1 0 0 ? 0 1 0 1 1 1 0 0 0 1 1 0 0 0 0 0 1 ? 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 1 1 1 1 0 1 ? 1 1
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Callechelys catostoma 0 1 0 0 1 1 0 1 0 2 1 0 1 0 0 1 0 1 1 0 1 1 1 1 0 0 0 ? 0 1 0 0 0 1 1 ? 1 1
 0 ? 1 1 ? 1 ? 1 1 1 1 0 1 0 1 1 1 0 0 0 1 0 0 0 0 0 1 1 1 1 1 0 1 0 0 0 0 1 0 0 2 1 0 1 0 1 1 ? 0 0 0 0
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 0 1 1 0 1 1 0 1 1 0 0 0 1 1 0 1

Chilocongrus dentatus 0 1 0 0 1 1 1 1 0 2 1 0 1 0 0 1 0 1 0 0 1 1 1 1 0 0 1 ? 1 1 0 0 0 1 1 ? 1 1 1
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Chilorhinus suenonii 0 1 0 0 1 1 0 0 0 2 1 0 1 0 0 1 0 1 1 0 1 1 1 1 0 1 ? ? 0 1 0 1 1 1 0 1 1 1 0
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Conger orbignianus 010011110210100101101111001?1100011?1110
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Cyema atrum 1?0011100211?0020111111101??221?211?11??11?1
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Hoplunnis diomediana 010111010210100001101111001?1100011?11
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Hoplunnis tenuis 010111010210100001101111001?1100011?11101
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Kaupichthys diodontus 01001100021010010110111101??1101111?11
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Labichthys carinatus 0?001111021010020110111101??0100011?110
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Letharchus velifer 010011010210100101101111000?0100011?110?1
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Macrocephenchelys brachialis 010011110210100101101111001?110001
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Media abyssalis 010011010210100101101111000?2100111?110?11
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Monognathus jerpsereni 1?0011110211?0011?10111101??221?211?11
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Monopenchelys acuta 01011100021010010110111101??0101111?110
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Moringua edwardsi 010011110210100101101111000?0101011?110?
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Myroconger nigrodentatus 01011100021010010110111101??0101011?
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Nessorhamphus danae 000011110210100101101111000?1100011?11
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Nettastoma melanurum 1?0011010210100201101111001?1100011?11
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Oxyconger leptognathus 010011010210100101001111000?0101011?1
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Rhinomuraena quaesita 01011100021010010110111101??0101111?11
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Saccopharynx 1?1011100211?0011?10111101??221?211?11??11?
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Serrivomer beanii 1?001111021010020110111101??1100010111111
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Serrivomer schmidti 1?001111021010020110111101??1100010111111
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Stemonidium hypomelas 1?001111021010020110111101??110001011
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Strophidon sathete 01011100021010010110111101??0101111?110?
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Symenchelys parasitica 010011010210100001101111000?2100010111
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Synaphobranchus kaupii 010011010210100101101111000?2100111?1
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Uropterygius micropterus 01011100021010010110111101??0101111?1
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Venefica procera 1?0011010210100201101111001?1100011?11101
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Xenomystax congroides 010011110210100201101111001?1100011?11
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Yirrkala misolensis 010011010210100101101111000?0100011?110?
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Cretaceous Fossils

†*Anguillavus quadripinnis* 0100111002101001010011100??000001??
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